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Skull Sizes and Proportions in Western Palearctic Wood Mice (*Sylvaemus*, Muridae, Rodentia) from Eastern Europe: 2. Intraspecific Variability

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Abstract—Intraspecific variability of craniometric characters (absolute measurements and indices) has been studied in the pygmy wood mouse *Sylvaemus uralensis* and the yellow-necked mouse *S. flavicollis* from a number of localities of Eastern Europe. A total of 478 skulls of *Sylvaemus* specimens were measured and analyzed. Cluster analysis of skull measurements showed that both *S. uralensis* and *S. flavicollis* could be split into two groups, the northern and the southern ones, which completely correspond to the genetically described intraspecific structure of *S. flavicollis*, but only partly in regards to *S. uralensis*. The northern and southern groups of both species are distinguished for the first time using discriminant analysis. Indices (relative skull measurements) related to the character of feeding are discussed. The intraspecific craniometric variability of *S. flavicollis* is suggested to be related to distinctions in the diet and the ways of getting food, whereas for *S. uralensis* no relation between the values of the indices of the dental apparatus and feeding features in different parts of its distribution range has been revealed.

Keywords: Sylvaemus, craniometry, absolute measurements, indices, intraspecific variability, feeding adaptations, evolution

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INTRODUCTION

Over the past few decades, the intraspecific structure of species of the genus *Sylvaemus* has been studied mainly with the involvement of genetic approaches, such as biochemical, chromosomal, and molecular-genetic (Mezhzherin and Zykov, 1991; Vorontsov et al., 1992; Orlov et al., 1996; Bogdanov, 2001, 2004; Filippucci et al., 2002; Kartavtseva, 2002; Bogdanov and Rozanov, 2005; Michaux et al., 2005; Chelomina, 2005; Illarionova et al., 2005; Balakirev et al., 2007; Gashchak et al., 2008; Rubtsov et al., 2011; Bogdanov et al., 2009, 2012; etc.) and only occasionally other research methods were used (Reutter et al., 1999; Orlov and Okulova, 2001; Gorodilova and Vasil'eva, 2014). A number of genetically discrete intraspecific forms were detected in the wood mouse (*S. sylvaticus* Linnaeus 1758) (Michaux et al., 1996, 1998, 2005; Gashchak et al., 2008). In the pygmy wood mouse (*S. uralensis* Pallas 1811) Asian and European races were described, and within the latter, the Eastern European and Southern European chromosomal forms (Bogdanov, 2001, 2004; Bogdanov and Rozanov, 2005). After separation of the Caucasus wood mouse (*S. ponticus* Sviridenko 1936) and the alpine wood mouse (*S. alpicola* Heinrich 1952) from the former polytypic species *S. flavicollis* Melchior 1834 s. lato (Mezhzherin, 1991; Vogel et al., 1991), in the yellow-necked mouse two genetically discrete forms were found: the northern and the southern ones, differing from each other by several mitochondrial genes, and, first of all, by the gene fragment of the first subunit of cytochrome oxidase *COI* (Bogdanov et al., 2012, 2013, 2014). The significantly more fractional structure of *S. flavicollis* can be traced in analysis of the frequency of occurrence of chest spot (Orlov and Okulova, 2001). A narrow-range species *S. ponticus* inhabiting the Caucasus and Transcaucasia also has a

† Deceased.

karyological differentiation separating the eastern and western populations (Kartavtseva, 2002). These data require further investigation.

Previously, while studying the hantaviruses near the city of Sochi (Klempa et al., 2008), among the Caucasus wood mice, individuals with a sharply different mitochondrial control region (*D-loop*) were found. These animals were divided into a separate group Syria. In the studies provided by these authors, the Syria group constituted about 1/7 of the total number of all Caucasus wood mice studied. In order to detect this form, A.S. Bogdanov determined the complete *D-loop* sequence in 20 Caucasus wood mice from different locations in the Northwestern Caucasus, but he failed to identify any forms that differ from the typical *S. ponticus*.

The degree of coincidence of genetic variability with morphological and morphometric variations and with environmental features has not yet been studied.

The aim of this report is to investigate intraspecific craniometric variability in *S. uralensis* and *S. flavicollis* using the methods of multidimensional statistics and to compare craniometric characteristics of different populations within each of the two species.

MATERIALS AND METHODS

Our own collection and museum materials (collections of the Zoological Museums of Moscow State University and the Zoological Institute of the Russian Academy of Sciences) of representatives of the genus *Sylvaemus* used in this work are shown in detail in Table 1 and Fig. 1.

The measurements and indices of 253 skulls of yellow-necked mice from nine localities were used in this work. The localities include the Republic of Belarus (Belovezhskaya Pushcha, $n = 58$), Sweden ($n = 12$), Lviv oblast of Ukraine (Roztochya Biosphere Reserve, $n = 23$); Moscow and Ryazan ($n = 9$), Tver ($n = 23$), Leningrad ($n = 40$), and Voronezh (Tellerman Forestry, $n = 34$) oblasts; and the republics of Bashkiria ($n = 35$) and Mordovia ($n = 19$) of Russia.

Craniometric studies of *S. uralensis* include 225 individuals from seven localities: the Dniprovsko Orilskyi Nature Reserve of Ukraine ($n = 55$) and six sites in the Russian Federation: Northwest Caucasus, the region of the municipal district of the city of Sochi ($n = 23$); the Republic of Dagestan ($n = 53$); and Ivanovo ($n = 19$), Moscow ($n = 21$), Yaroslavl ($n = 18$), and Ryazan ($n = 36$) oblasts. The measurements of 478 specimens of *Sylvaemus* are used in this work. The problems of genetic identification of the samples of *S. uralensis* and *S. flavicollis* are discussed in the first part of the article (Report 1).

The natural conditions of most of the sampling sites were described earlier: for the Northwest Caucasus (Okulova et al., 2005), Dagestan (Lavrenchenko and Likhnova, 1995), the Dniprovsko Orilskyi Nature Reserve (Okulova and Antonets, 2002), and the Ivanovo oblast, where the samplings were made in the subzone of coniferous-deciduous forests (Okulova and Khelevina, 1989).

Measurement of the skulls in millimeters was performed using an MBS microscope and an ocular micrometer at magnifications of ×04, ×7.5, and ×25. 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; and (21) Bi, the width of the incisor in the lateral direction at the end of the tooth. For specimens from Dagestan, 17 cranial signs were measured (all except Hmax, Li, Bi, and D2).

Based on these measurements, 24 indices were calculated, including the indices (Zyg/Cbl, Lmd/Cbl, D1/Cbl, Lm^{1-3}/Cbl, and Bcra/Cbl) that characterize the granivorous or folivorous specialization of the studied populations of *Sylvaemus* species in different parts of their ranges.

Statistical data processing was carried out on a computer using Statistica software in modules: descriptive statistics (arithmetic average M, its error m, and data standard deviation σ), cluster analysis (one linkage method and calculation of Euclidean distances), and discriminant analysis. Construction of clusters was carried out according to average values for all features. The reliability of the coefficients of the equations in the discriminant analysis was estimated using the Fisher criteria F, $W\lambda$, χ^2, and 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 intraspecific groups. As a result of the calculations, the animal was attributed to the species for which the maximum value of the discriminant function was obtained.

RESULTS AND DISCUSSION

Yellow-Necked Mouse

Considering the values of craniometric parameters in different parts of the range of *S. flavicollis* (Tables 1, 2),

Table 1. Absolute values (mm) of the dimensions of the skull and its parts in the yellow-necked mice (*S. flavicollis*) in different parts of the range ($M \pm m$)

Measurement	Roztochya Biosphere Reserve $n = 23$	Moscow oblast $n = 10$	Belovezhskaya Pushcha National Park $n = 58$	Tver oblast $n = 23$	Republic of Bashkiria $n = 35$	Leningrad oblast $n = 39$	Republic of Mordovia $n = 19$	Sweden $n = 12$	Voronezh oblast $n = 34$
Cbl	27.15 ± 1.93	25.84 ± 0.75	26.65 ± 0.25	27.14 ± 0.26	27.77 ± 0.41	25.52 ± 0.42	28.43 ± 0.23	27.49 ± 0.24	29.64 ± 0.24
Zyg	15.29 ± 0.44	11.32 ± 0.31	11.53 ± 0.12	11.49 ± 0.16	12.04 ± 0.15	11.35 ± 0.17	11.99 ± 0.13	11.93 ± 0.09	16.14 ± 0.23
Hmax	7.07 ± 0.12	N.d.	N.d.	N.d.	N.d.	N.d.	N.d.	N.d.	7.70 ± 0.13
Lmd	15.32 ± 0.24	11.77 ± 0.51	12.63 ± 0.010	12.96 ± 0.15	13.18 ± 0.19	12.05 ± 0.19	13.35 ± 0.12	12.97 ± 0.33	16.14 ± 0.23
Iob	4.44 ± 0.09	3.67 ± 0.08	3.74 ± 0.02	3.72 ± 0.04	3.64 ± 0.03	3.57 ± 0.04	3.53 ± 0.05	3.50 ± 0.08	4.85 ± 0.06
Lna	9.61 ± 0.27	8.03 ± 0.31	8.60 ± 0.02	8.64 ± 0.19	8.86 ± 0.18	7.46 ± 0.13	9.46 ± 0.15	8.26 ± 0.23	11.23 ± 0.26
Bna	3.20 ± 0.08	2.69 ± 0.15	2.68 ± 0.03	2.75 ± 0.04	2.84 ± 0.04	2.44 ± 0.05	2.86 ± 0.04	2.70 ± 0.08	3.68 ± 0.08
Lbull	6.12 ± 0.18	5.68 ± 0.18	5.98 ± 0.04	5.97 ± 0.08	5.97 ± 0.07	4.25 ± 0.05	5.97 ± 0.06	4.41 ± 0.11	6.46 ± 0.11
Lfi	5.31 ± 0.08	4.67 ± 0.14	4.88 ± 0.05	4.88 ± 0.06	5.13 ± 0.07	4.42 ± 0.06	5.02 ± 0.07	4.73 ± 0.10	6.32 ± 0.10
Bfi	1.99 ± 0.04	1.752 ± 0.07	1.69 ± 0.02	1.73 ± 0.03	1.87 ± 0.03	1.66 ± 0.03	1.80 ± 0.03	1.67 ± 0.04	2.36 ± 0.05
Lm^{1-3}	4.33 ± 0.05	3.47 ± 0.14	3.69 ± 0.03	3.79 ± 0.03	3.96 ± 0.04	3.43 ± 0.04	3.94 ± 0.05	3.43 ± 0.09	5.15 ± 0.06
Lm_{1-3}	4.64 ± 0.06	N.d.	N.d.	N.d.	N.d.	N.d.	N.d.	N.d.	4.83 ± 0.11
Lm^1	1.98 ± 0.03	1.68 ± 0.11	1.82 ± 0.01	1.88 ± 0.06	1.92 ± 0.02	1.68 ± 0.03	1.86 ± 0.02	1.54 ± 0.06	2.31 ± 0.03
Bm^1	1.39 ± 0.02	1.12 ± 0.05	1.16 ± 0.01	1.16 ± 0.02	1.20 ± 0.02	1.28 ± 0.23	1.18 ± 0.02	1.06 ± 0.03	0.81 ± 0.03
D1	7.34 ± 0.20	6.01 ± 0.23	6.20 ± 0.07	6.60 ± 0.12	6.65 ± 0.13	5.76 ± 0.11	6.79 ± 0.10	6.09 ± 0.27	8.35 ± 0.18
D2	4.02 ± 0.09	N.d.	N.d.	N.d.	N.d.	N.d.	N.d.	N.d.	4.24 ± 0.12
M^{1-1}	3.15 ± 0.05	2.61 ± 0.06	2.53 ± 0.03	2.59 ± 0.04	2.73 ± 0.03	2.34 ± 0.05	2.67 ± 0.04	2.54 ± 0.06	3.38 ± 0.06
Bcra	12.78 ± 0.31	10.04 ± 0.22	10.20 ± 0.05	10.48 ± 0.16	10.38 ± 0.08	9.89 ± 0.09	10.47 ± 0.08	10.09 ± 0.12	13.89 ± 0.22
Hcra	5.30 ± 0.26	7.30 ± 0.16	7.62 ± 0.13	7.75 ± 0.07	7.63 ± 0.06	7.45 ± 0.08	7.72 ± 0.08	7.67 ± 0.07	6.24 ± 0.08
Li	2.14 ± 0.08	2.09 ± 0.19	2.07 ± 0.04	2.02 ± 0.07	2.41 ± 0.07	2.06 ± 0.06	2.57 ± 0.07	2.19 ± 0.14	N.d.
Bi	0.68 ± 0.02	0.63 ± 0.04	0.67 ± 0.01	0.63 ± 0.02	0.68 ± 0.02	0.59 ± 0.01	0.64 ± 0.02	0.60 ± 0.03	0.86 ± 0.05

N.d., no data; *n*, sample size.

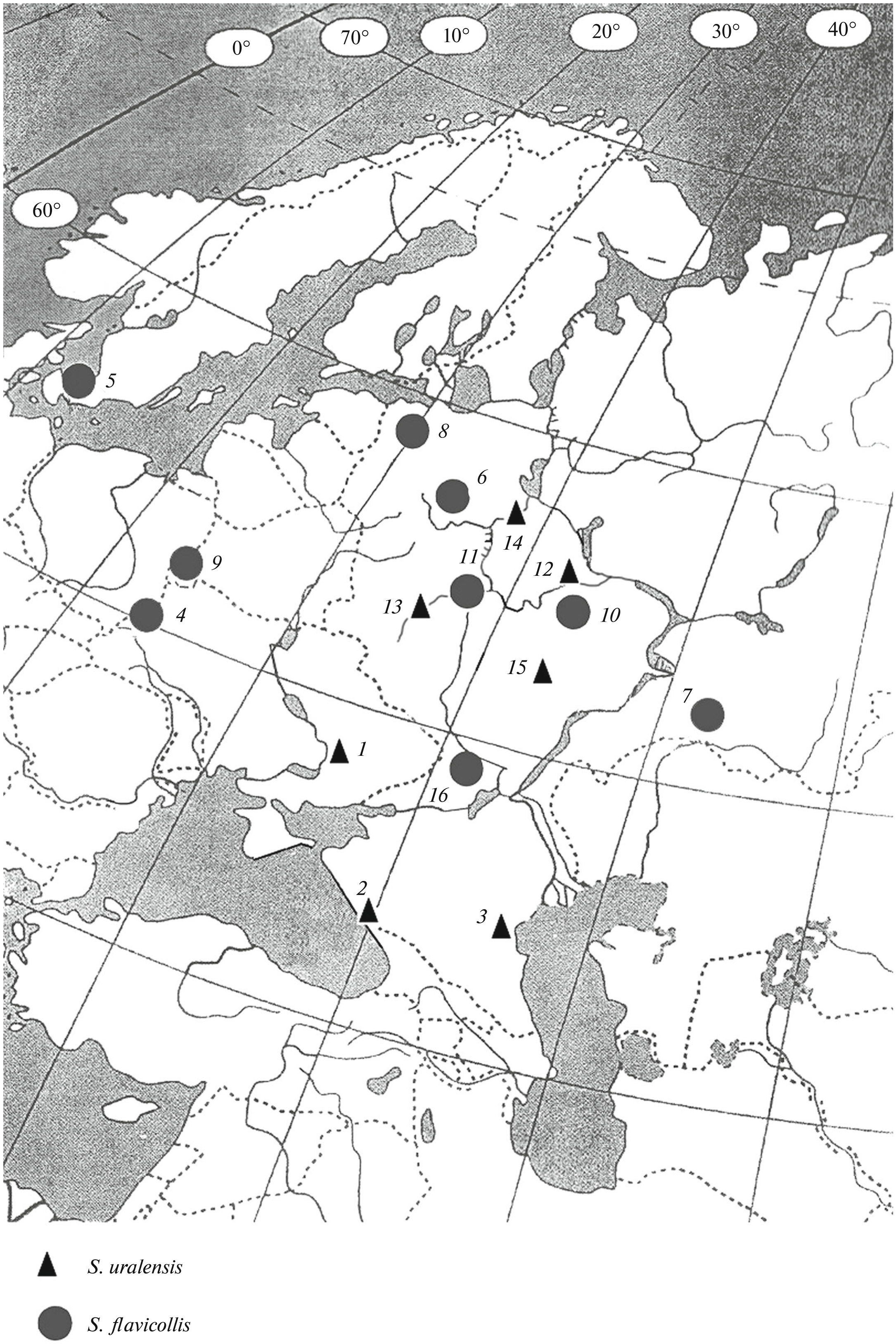

Fig. 1. Sampling localities for the craniometric studies of *S. uralensis* and *S. flavicollis*: *1*, Dniprovsko Orilskyi Nature Reserve, Ukraine; *2*, Northwest Caucasus, region of the municipal district of the city of Sochi; *3*, Republic of Dagestan; *4*, Roztochya Biosphere Reserve, Lviv oblast, Ukraine; *5*, Sweden; *6*, Tver oblast; *7*, Bashkirskii Nature Reserve; *8*, Leningrad oblast; *9*, Belovezhskaya Pushcha National Park, Belarus; *10*, Republic of Mordovia; *11*, Moscow and Ryazan oblasts; *12*, Ivanovo oblast; *13*, Moscow oblast; *14*, Yaroslavl oblast; *15*, Ryazan oblast; *16*, Voronezh oblast.

we found that the largest skulls are typical for the yellow-necked mice in Voronezh oblast (Table 1). They are also quite large in the Republic of Mordovia, little bit smaller in Roztochya Biosphere Reserve, Tver oblast, the Republic of Bashkiria, and Sweden, and even smaller in Moscow oblast and Belovezhskaya Pushcha. The smallest parameters were characteristic for the yellow-necked mice in Leningrad oblast. The relations of the areas of the range with all the sizes according to our data are presented in Fig. 2. It is seen clearly that the areas of the southern part of the range, Roztochya Biosphere Reserve (Lviv oblast, Ukraine) and Tellerman oak forest (Voronezh oblast), are closest to each other according to the craniometric characteristics of the populations. Among others, the most similar according to the craniometric indicators are populations from Bashkiria, Mordovia, Tver oblast, and Belarus (Belovezhskaya Pushcha). Populations from Moscow and Leningrad oblasts are close to them, and Swedish yellow-necked mice differ more strongly from the others in this cluster.

The search for ecological and morphological parallels between the distribution and craniometric features of the populations of this species led to the conclusion that, among the areas studied, the Roztochya Biosphere Reserve is represented by deciduous forests with high productivity not only of oak seeds, but also of nut-bearing trees, hornbeam, and beech. Tellerman oakwood in Voronezh oblast is a territory with domination and rich harvests of oak in favorable areas. In other localities studied, the yellow-necked mouse lives in areas of broad-leaved and coniferous-broad-leaved forests depleted in seed food. In these, more northern areas of the range, the basis of the seed feeding of the animal consists of much less abundant oak seeds (acorns) and hazel seeds, which are much less abundant than oak.

Thus, in the southern parts of the range of the species, the adaptation of mice to nutrition should largely consist in the ability to peel hard shells and to grind the seeds of woody nut-bearing plants. Morphologically, this can be expressed in strengthening the bones and the muscles of the skull in those parts that are associated with feeding, as well as in adapting the bone system to peeling nuts and acorns (incisors) and then grinding the seed mass (molars). The morphometric indices developed by Lebedkina (1949), Vorontsov (1967), and later supplemented by us (Okulova, 2000) allow us to conclude that, for the most successful cracking of solid feed shells, the following features are important: (1) the parameters of the cracking levers, the lower and upper jaws, especially the length of the lower jaw; (2) the strength of the muscles that compress the jaws, which morphologically can be expressed in the width of various parts of the skull as sites for attaching large bundles of muscles and in the size of the "gate" for the location of the contracting muscles (archus zygomaticus); (3) enhanced structure of the cracking device—incisors—both in dimensional

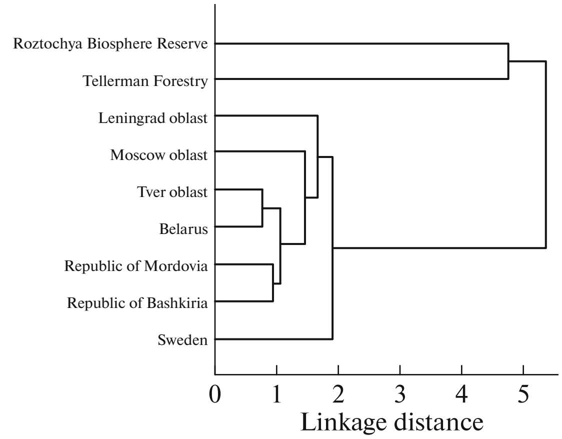

Fig. 2. Cluster analysis of craniometric parameters of the yellow-necked mice from nine regions.

parameters (length, width, and thickness) and in strength, which depends on the metric parameters and on the architecture of the teeth, as well on the strength of the substance that composes them. The grinding mechanisms of the extracted kernels of nuts and acorns consist in the destruction of them by molars.

Comparison of the Zyg/Cbl index in different parts of the range of the yellow-necked mouse shows that the values of this index are highest in two southern areas of the range (0.51 in Roztochya Biosphere Reserve and 0.57 in Voronezh oblast), while in the more northern areas this index is reduced: 0.45 and less. Comparison of different *Sylvaemus* species shows that this index is maximal in *S. witherbyi* and *S. ponticus*: 0.51–0.58 (Okulova et al., Rep. 1). Among the indices represented in Table 2 (except for the last two), three characters associated with the proportions of the teeth (Lm^1/Bfi, Lfi/Lm^1, and Bfi/Cbl) do not indicate an increased granivorous mode of the two southern populations, but rather indicate an increased folivorous one, while the other five characters associated with the proportions of the skull correspond to our ideas about the value of these indices.

In Roztochya Biosphere Reserve, in comparison with other parts of the range, the maximum number of indices with the highest levels (15) is observed (Table 2). It is important that mainly the highest are signs of width (zygomatic, occipital parts, rostrum, interorbital, and interdental spaces, M^1). In this part of the range, the lower jaw, auditory bulla, upper dentition, upper diastema, and nasal bone are extended in the yellow-necked mice. The skull height Hcra/Cbl is minimal.

In Voronezh oblast, the length of the skull is the highest; many proportions (11 features) are maximum or close to the maximum, as in Roztochya Biosphere Reserve. They include seven signs of the cranial width (Iob, Bcra, Bm^1, M^{1-1}, Bfi/Cbl, Bna/Lna, and Bfi/Lfi) and three signs of the cranial length (Lm^{1-3}/Cbl,

Table 2. Proportions (indices) of measurements of the skull and its parts in the yellow-necked mice (*S. flavicollis*) in different parts of the range ($M \pm m$)

Index	Roztochya Biosphere Reserve $n = 23$	Moscow oblast $n = 10$	Belovezhskaya Pushcha National Park $n = 58$	Tver oblast $n = 23$	Republic of Bashkiria $n = 35$	Leningrad oblast $n = 39$	Republic of Mordovia $n = 19$	Sweden $n = 12$	Voronezh oblast $n = 34$
Zyg/Cbl	0.568 ± 0.039	0.439 ± 0.006	0.433 ± 0.003	0.423 ± 0.005	0.435 ± 0.004	0.448 ± 0.006	0.422 ± 0.003	0.443 ± 0.009	0.513 ± 0.006
Iob/Zyg	0.294 ± 0.004	0.326 ± 0.008	0.327 ± 0.004	0.325 ± 0.004	0.304 ± 0.004	0.317 ± 0.004	0.296 ± 0.005	0.283 ± 0.015	0.321 ± 0.005
Bfi/Cbl	0.172 ± 0.016	0.135 ± 0.005	0.139 ± 0.002	0.140 ± 0.001	0.144 ± 0.003	0.135 ± 0.002	0.138 ± 0.002	0.125 ± 0.002	0.174 ± 0.003
Hmax/Cbl	0.291 ± 0.009	N.d.	N.d.	N.d.	N.d.	N.d.	N.d.	N.d.	0.260 ± 0.015
Lmd/Cbl	0.607 ± 0.043	0.454 ± 0.008	0.475 ± 0.003	0.477 ± 0.004	0.475 ± 0.003	0.476 ± 0.008	0.470 ± 0.003	0.472 ± 0.008	0.541 ± 0.008
Iob/Cbl	0.168 ± 0.014	0.143 ± 0.003	0.141 ± 0.001	0.137 ± 0.002	0.132 ± 0.002	0.141 ± 0.002	0.124 ± 0.002	0.128 ± 0.004	0.164 ± 0.002
Lna/Cbl	0.379 ± 0.041	0.311 ± 0.008	0.322 ± 0.002	0.317 ± 0.005	0.316 ± 0.003	0.292 ± 0.004	0.332 ± 0.003	0.301 ± 0.006	0.378 ± 0.004
Bna/Cbl	0.227 ± 0.010	0.220 ± 0.004	0.225 ± 0.002	0.220 ± 0.003	0.215 ± 0.003	0.168 ± 0.003	0.210 ± 0.002	0.157 ± 0.003	0.219 ± 0.004
Lbull/Cbl	0.212 ± 0.014	0.181 ± 0.005	0.183 ± 0.001	0.180 ± 0.002	0.185 ± 0.001	0.173 ± 0.002	0.176 ± 0.002	0.173 ± 0.003	0.214 ± 0.003
Lfi/Cbl	0.057 ± 0.006	0.043 ± 0.002	0.044 ± 0.001	0.043 ± 0.001	0.044 ± 0.001	0.051 ± 0.009	0.041 ± 0.001	0.039 ± 0.001	0.055 ± 0.008
Lm^{1-3}/Cbl	0.309 ± 0.022	0.233 ± 0.005	0.232 ± 0.001	0.243 ± 0.003	0.239 ± 0.002	0.226 ± 0.004	0.238 ± 0.002	0.221 ± 0.005	0.282 ± 0.034
Lm^{1-3}/Bfi	1.708 ± 0.047	1.747 ± 0.076	1.68 ± 0.021	1.743 ± 0.028	1.682 ± 0.034	1.687 ± 0.035	1.727 ± 0.028	1.779 ± 0.056	1.625 ± 0.003
Lm_{1-3}/Bfi	0.731 ± 0.011	0.760 ± 0.030	0.69 ± 0.008	0.683 ± 0.010	0.691 ± 0.009	0.688 ± 0.017	0.683 ± 0.008	0.775 ± 0.018	0.660 ± 0.013
Lm^1/Bfi	0.463 ± 0.005	0.484 ± 0.029	0.493 ± 0.005	0.497 ± 0.016	0.484 ± 0.007	0.489 ± 0.008	0.474 ± 0.007	0.451 ± 0.019	0.451 ± 0.008
Lfi/Lm^1	0.703 ± 0.12	0.686 ± 0.045	0.641 ± 0.007	0.623 ± 0.015	0.628 ± 0.011	0.763 ± 0.012	0.634 ± 0.009	0.709 ± 0.005	0.710 ± 0.109
Bm^1/Cbl	0.172 ± 0.012	N.d.	N.d.	N.d.	N.d.	N.d.	N.d.	N.d.	0.164 ± 0.004
Bcra/Cbl	0.090 ± 0.016	0.079 ± 0.005	0.078 ± 0.001	0.074 ± 0.003	0.086 ± 0.002	0.080 ± 0.002	0.090 ± 0.002	0.079 ± 0.004	N.d.
Hcra/Bcra	0.325 ± 0.013	0.314 ± 0.023	0.327 ± 0.007	0.321 ± 0.015	0.286 ± 0.008	0.295 ± 0.011	0.250 ± 0.002	0.282 ± 0.019	N.d.
Li/Cbl	0.296 ± 0.005	0.284 ± 0.006	0.287 ± 0.005	0.286 ± 0.003	0.295 ± 0.003	0.294 ± 0.005	0.271 ± 0.002	0.281 ± 0.009	0.211 ± 0.003
Bi/Lmd	0.263 ± 0.005	N.d.	N.d.	N.d.	N.d.	N.d.	N.d.	N.d.	0.265 ± 0.047
Bfi/Lmd	0.283 ± 0.004	0.298 ± 0.013	0.293 ± 0.003	0.293 ± 0.003	0.303 ± 0.005	0.286 ± 0.005	0.294 ± 0.003	0.264 ± 0.005	0.321 ± 0.005
Lfi/Bfi	0.374 ± 0.014	0.323 ± 0.013	0.315 ± 0.004	0.306 ± 0.005	0.303 ± 0.004	0.373 ± 0.0642	0.300 ± 0.005	0.311 ± 0.006	0.316 ± 0.001
M^{1-1}/Cbl	0.475 ± 0.027	0.390 ± 0.008	0.384 ± 0.003	0.386 ± 0.006	0.376 ± 0.005	0.390 ± 0.005	0.368 ± 0.002	0.368 ± 0.006	0.471 ± 0.048
D2/Lna	0.335 ± 0.009	0.335 ± 0.012	0.313 ± 0.003	0.321 ± 0.007	0.324 ± 0.006	0.326 ± 0.004	0.304 ± 0.004	0.328 ± 0.009	0.333 ± 0.010
D1/Lbull	0.378 ± 0.009	0.377 ± 0.017	0.347 ± 0.004	0.356 ± 0.006	0.365 ± 0.006	0.377 ± 0.005	0.361 ± 0.005	0.352 ± 0.007	0.374 ± 0.007
Lm_{1-3}/Cbl	0.128 ± 0.008	0.101 ± 0.002	0.095 ± 0.001	0.095 ± 0.001	0.099 ± 0.001	0.093 ± 0.002	0.094 ± 0.001	0.093 ± 0.002	0.115 ± 0.002
D1/Cbl	0.081 ± 0.000	0.068 ± 0.001	0.063 ± 0.007	0.064 ± 0.001	0.068 ± 0.001	0.065 ± 0.001	0.063 ± 0.001	0.061 ± 0.001	0.080 ± 0.001

N.d., no data; *n*, sample size.

D1/Cbl, and Lm^{1-3}/Lmd). In Roztochya Biosphere Reserve, only one sign is minimal, but in Voronezh oblast there are three of them: D1/Lm^{1-3}, Lm^1/Lm^{1-3}, and M^{1-1}/Lm^{1-3}. Thus, in Roztochya Biosphere Reserve the skull of the yellow-necked mouse is the widest and strongest, and in Voronezh oblast, it is larger, but less strong, especially in relation to the length of the upper dentition.

The most different from the other populations is the population from Sweden. It is characterized, with medium skull sizes, by the greatest number of small proportions: the minimum levels of proportions were found in ten cases (Iob/Zyg, Lm^{1-3}/Cbl, Lbull/Cbl, Bm^1/Cbl, D1/Cbl, Lm^1/Lm^{1-3}, Lm^{1-3}/Lmd, Bfi/Cbl, M^{1-1}/Cbl, and Bcra/Cbl), and three more are close to minimum (Iob/Cbl, Lna/Cbl, and Lfi/Cbl). Furthermore, the proportions of D1 and M^{1-1} with respect to Lm^{1-3} are the highest; the relative width of the incisor foramen (Bfi/Lfi) is close to the maximum. The other proportions are close to the average levels. Thus, the Swedish population is characterized by the narrowest (or close to the narrowest) interorbital and interdental spaces, M^1, by the shortest (in relation to the skull length) auditory bullas, diastema, incisor foramens, upper dentition, width of the skull in the area of the auditory bullas, etc. With medium sizes of the skull and zygomatic width relative to the length of the skull, the length and width of the muzzle, a number of elements of the facial part of the skull and the dental apparatus (diastema, upper dentition, and length and width M^1), and the length of the auditory bullas are minimal.

For the other part of the range, the animals from Bashkiria are closest to the average indicators. Here, only two features are close to the minimum (according to the indices Bm^1/Lm^1 and Bm^1/Lm^{1-3}, the width M^1 is narrowed relative to its length and the length of the upper dentition), and the two features are close to the maximum values: the height of the skull (Hcra/Cbl) and proportions of the upper dentition and the length of the lower jaw (Lm^{1-3}/Lmd).

Very close in the size and proportions to the skulls of the yellow-necked mice from Bashkiria are those of Mordovia, but here many parts of the skull are narrowed. In contrast to Bashkiria, the zygomatic width and width of the skull in the area of the auditory bullas in Mordovian yellow-necked mice are, as in Sweden, minimal; width of the teeth (Bi/Li, Bm^1/Lm^{1-3}, and Bm^1/Cbl) and the widths of the nasal bones and of the incisor foramens are close to the minimum. The length of the lower jaw and interdental space relative to the condilobasal length of the skull is also minimal. But, as in Roztochya Biosphere Reserve, the relative length of the upper incisor (Li/Cbl) is maximal.

The skulls of yellow-necked mice from Tver oblast and Belarus (Belovezhskaya Pushcha) are craniometrically close. The sizes and proportions of the skulls of *S. flavicollis* from Tver oblast are closer to the averages. Here, four indicators are close to the minimum or minimal: the width of the interorbital space in relation to Cbl and Lm^{1-3} and the dental indices Bm^1/Lm^{1-3} and Li/Cbl. In Belarus (Belovezhskaya Pushcha), three indicators are close to minimum or minimal (two indicators of the width of the nasal bones and incisor foramens, Bna/Lna and Bfi/Lfi as well Li/Cbl), and three are maximal (the interorbital space Iob/Zyg) or close to the maximum (Lbull/Cbl and Lm^1/Lm^{1-3}).

In Moscow and Ryazan oblasts, with a large proportion of the mean values and relatively small skull size, the mandibular length is minimal, while the interorbital interval Iob/Zyg, two indicators of the width of the nasal bones and incisor foramen (Bna/Lna and Bfi/Lfi), and the length of the diastema relative to the length of the upper dentition D1/Lm^{1-3} are of maximum values or close to the maximum.

In Leningrad oblast, the size of the skull is minimal, as well as six indicators are minimal or close to the minimum (all in relation to Cbl): the length of the upper dentition, diastema, auditory bullas, interdental space, and parameters of the length of the nasal bones and incisor foramens. Five indicators are maximal or close to maximum: Lm^1/Lm^{1-3}, the width of the 1st upper molar (Bm^1/Lm^1 and Bm^1/Lm^{1-3}), the height of the skull (Hcra/Cbl), and the width of the incisor foramen (Bfi/Lfi).

In general, in the southern part of the range studied, the skulls of the yellow-necked mice are wider and larger. To the northwest, the skull is smaller. The skull, the width of the nasal bones, and the incisor foramen of the representatives of this species become narrower and shorter from Lviv oblast to Belarus and further to Leningrad oblast and Sweden. The length of the upper dentition there also decreases; the teeth become shorter and narrower. Compared with the south, there is an increase in indices related to the folivorous mode of animals in Belarus and Leningrad oblast: Lm^1/Lm^{1-3} increases, the length of the auditory bullas increases in Belarus, and the muzzle decreases (according to Lna, Bna, Lfi, and Bfi). In Leningrad oblast, Bm^1 rises to the maximum (increase of folivory). In Tver oblast in comparison to Leningrad oblast, M^1 is shortened (a sign of folivory, as the proportion of M^1 in the length of the upper dentition decreases, while the last molar is reduced only slightly).

In Moscow oblast the skulls of *S. flavicollis* are smaller than in the southern locations (for example, in Voronezh oblast), in the northern (in Tver oblast), or in the western ones (Belarus); they are only smaller in Leningrad oblast. In Moscow oblast the parameters of the interorbital space, two indicators of the width of the nasal bones and incisor foramens, and the ratio D1/Lm^{1-3} are higher. To the east and northeast from

Table 3. Discriminant analysis of cranial measurements of the yellow-necked mice (*S. flavicollis*) of two intraspecific groups

Measurement, index	Northern genetic form	Southern genetic form
Bcra	19.414	31.657
Iob	49.927	68.417
Cbl	–0.962	–4.111
Zyg	1.630	5.691
Lmd	–	–
Lbull	–5.158	–9.942
Lfi	–	–
Bm^1	–	–
Li	0.909	5.514
Hcra	7.153	–0.290
Lm^{1-3}	26.322	44.067
Const.	–250.319	–454.327
Eigenvalue	8.560	
F-criterion	187.25	
P (*F* criterion)	<0.0000	
Criterion Wλ	0.105	
Criterion χ^2	401.847	
df (χ^2)	8	
R_{can}	0.946	

Moscow oblast (Mordovia and Bashkortostan), the length of the lower jaw increases, the interorbital space decreases, and the width of the nasal bones and incisor foramens narrows, as do Bm^1 and $D1/Lm^{1-3}$ (in general, according to the indices, the granivorous mode increases in this direction). The height of the skull varies irregularly. It is maximum in Bashkiria and minimal in Mordovia.

Thus, to the northwest and north, the skull of *S. flavicollis* decreases and some signs of granivory are gradually lost (according to the indices), but this occurs in different directions and only slightly. The only thing that is common is the narrowing and shortening width of the nasal bones and the incisor foramens. To the east and northeast, the size of the skull and some granivory indices increase, but all these indicators are smaller than in the southern part of the range.

Two southern localities of the range studied belong to the southern genetic form of the species (Bogdanov et al., 2013, 2014). In the southern part of Moscow oblast, the same authors found populations with mitotypes of the northern and southern forms, and the northern form lives to the north. In general, according to our data, it turns out that the northern form is characterized by smaller sizes of the skull and a shorter and narrowed muzzle and is a little bit less adapted to feeding on seeds of trees. Discriminant analysis carried out on material from two forms of the yellow-necked mouse (data from Moscow oblast were not included in these calculations, since the border between the northern and southern forms lies here) showed that their representatives differ clearly and reliably, and 100% separation requires eight measurements of different parts of the skull (Table 3).

Pygmy Wood Mouse

The sizes and proportions of the skulls of the pygmy wood mice (*S. uralensis*) from the examined regions (near the city of Sochi, Dagestan, Dniprovsko Orilskyi Natural Reserve, and the non-black earth region of Russia, i.e. Yaroslavl, Ryazan, Ivanovo, and Moscow oblasts) are presented in Tables 4 and 5. The minimal absolute dimensions of the skull (less than 22 mm) were found in mice from the vicinity of the municipal district of the city of Sochi and Dagestan. The average sizes of the condilobasal length of the skull were found in specimens from the non-black earth region of Russia (23–23.5 mm), and the maximum ones, in southeastern Ukraine, in the Dniprovsko Orilskyi Natural Reserve. Compared with the northern populations, three southern populations (Dniprovsko Orilskyi Natural Reserve, the vicinity of Sochi, and Dagestan) showed a distinct increase in eight skull indices: width M^1 relative to the length of the upper dentition (0.33–0.37 vs. 0.31–0.34), the indices of the archus zygomaticus length (0.52–0.56 versus 0.44), the length of the upper dentition (0.15–0.16 vs. 0.12–0.13), the mandible length (0.55–0.62 vs. 0.47–0.48), M^1 width (0.05–0.06 vs. 0.4), the length of the upper diastema (0.28–0.31 vs. 0.24–0.26), the maximum width (0.46–0.49 vs. 0.40–0.41), and the height (0.37–0.41 vs. 0.29–0.30) of the skull in relation to its condilobasal length.

Thus, in comparison to the non-black earth region of the European part of Russia, in the southern part of the range, the pygmy wood mouse has a higher and wider skull, with relatively larger upper diastema, lower jaw, longer upper dentition, and a wider M^1, although the total size of the skull can vary from the largest to the minimum sizes. Differences in feeding preferences identified by us in different parts of the species range do not show a relationship with the values of the dental apparatus indices.

Comparison of the dimensions of different skull parts of the pygmy wood mice by cluster analysis (Fig. 3) according to our data (7 sites, 16 signs) showed that according to the craniometric data there is a clear division of the populations of the studied part of the species range into two groups: the northern (non-black earth region) and southern (Dniprovsko Orilskyi Nature Reserve, Dagestan, vicinity of Sochi) ones, which partly corresponds to the division into previously identified Eastern European and Southern

Table 4. Absolute values (mm) of the dimensions of the skull and its parts in the pygmy wood mice (*S. uralensis*) in different parts of the range ($M \pm m$)

Measurement	Krasnodar krai $n = 23$	Dniprovsko Orilskyi Nature Reserve $n = 56$	Republic of Dagestan $n = 53$	Ryazan oblast $n = 36$	Moscow oblast $n = 21$	Ivanovo oblast $n = 19$	Yaroslavl oblast $n = 18$
Cbl	21.82 ± 0.37	24.60 ± 0.34	22.40 ± 0.13	23.15 ± 0.15	23.47 ± 0.32	23.45 ± 0.24	23.28 ± 0.24
Zyg	11.32 ± 0.18	13.06 ± 0.17	12.43 ± 0.07	10.17 ± 0.07	10.36 ± 0.14	10.23 ± 0.13	10.11 ± 0.09
Hmax	5.57 ± 0.10	6.16 ± 0.06	7.87 ± 0.04	N.d.	N.d.	7.01 ± 0.09	6.65 ± 0.09
Lmd	12.9 ± 0.16	13.53 ± 0.14	13.94 ± 0.08	10.95 ± 0.08	10.97 ± 0.13	11.13 ± 0.13	10.97 ± 0.12
Iob	1.93 ± 0.03	4.17 ± 0.04	4.17 ± 0.02	3.45 ± 0.03	3.45 ± 0.04	3.53 ± 0.03	3.34 ± 0.06
Lna	7.84 ± 0.13	8.42 ± 0.06	8.98 ± 0.05	6.98 ± 0.11	7.21 ± 0.14	7.28 ± 0.21	7.18 ± 0.06
Bna	2.84 ± 0.08	3.01 ± 0.05	2.83 ± 0.02	2.22 ± 0.03	2.38 ± 0.05	2.39 ± 0.05	2.28 ± 0.04
Lbull	4.53 ± 0.05	5.19 ± 0.18	4.55 ± 0.02	5.04 ± 0.04	5.16 ± 0.04	5.48 ± 0.13	5.46 ± 0.11
Lfi	4.18 ± 0.07	5.07 ± 0.06	4.94 ± 0.04	4.04 ± 0.04	4.32 ± 0.05	4.88 ± 0.09	4.99 ± 0.07
Bfi	1.52 ± 0.03	1.52 ± 0.04	1.62 ± 0.06	1.43 ± 0.02	1.39 ± 0.03	1.51 ± 0.03	1.78 ± 0.03
Lm^{1-3}	3.30 ± 0.09	3.70 ± 0.03	3.58 ± 0.02	3.02 ± 0.02	3.09 ± 0.03	2.87 ± 0.03	2.98 ± 0.04
Lm_{1-3}	3.67 ± 0.04	3.72 ± 0.05	N.d.	N.d.	N.d.	N.d.	N.d.
Lm^1	1.73 ± 0.02	1.83 ± 0.02	1.75 ± 0.01	1.44 ± 0.02	1.48 ± 0.02	1.45 ± 0.02	1.39 ± 0.02
Bm^1	1.22 ± 0.02	1.22 ± 0.01	1.28 ± 0.05	0.95 ± 0.01	1.97 ± 0.01	0.97 ± 0.02	0.96 ± 0.01
D1	6.71 ± 0.14	6.74 ± 0.07	6.82 ± 0.04	5.523 ± 0.073	5.739 ± 0.082	5.708 ± 0.091	6.104 ± 0.108
D2	3.83 ± 0.06	3.73 ± 0.05	N.d.	N.d.	N.d.	N.d.	N.d.
M^{1-1}	2.93 ± 0.03	2.82 ± 0.02	2.83 ± 0.02	2.43 ± 0.03	2.56 ± 0.04	2.49 ± 0.03	2.45 ± 0.06
Bcra	10.53 ± 0.13	11.41 ± 0.17	10.82 ± 0.05	9.34 ± 0.07	9.38 ± 0.09	9.54 ± 0.08	9.29 ± 0.11
Hcra	8.93 ± 0.15	8.74 ± 0.14	N.d.	6.92 ± 0.05	6.90 ± 0.06	6.99 ± 0.06	6.82 ± 0.07
Li	4.28 ± 0.16	3.51 ± 0.06	N.d.	1.82 ± 0.05	1.88 ± 0.07	1.99 ± 0.05	1.85 ± 0.04
Bi	0.76 ± 0.02	0.63 ± 0.01	N.d.	0.53 ± 0.01	0.51 ± 0.02	0.54 ± 0.06	0.60 ± 0.02

N.d., no data; *n*, sample size.

Table 5. Proportions (indices) of measurements of the skull and its parts in the pygmy wood mice (*S. uralensis*) in different parts of the range ($M \pm m$)

Index	Krasnodar krai $n = 23$	Dniprovsko Orilskyi Nature Reserve $n = 56$	Republic of Dagestan $n = 53$	Ryazan oblast $n = 36$	Moscow oblast $n = 21$	Ivanovo oblast $n = 19$	Yaroslavl oblast $n = 18$
Zyg/Cbl	0.519 ± 0.007	0.519 ± 0.007	0.555 ± 0.002	0.440 ± 0.003	0.442 ± 0.004	0.438 ± 0.008	0.435 ± 0.005
Iob/Zyg	0.173 ± 0.003	0.319 ± 0.006	0.336 ± 0.002	0.340 ± 0.003	0.333 ± 0.005	0.346 ± 0.006	0.331 ± 0.006
Bfi/Cbl	0.147 ± 0.005	0.153 ± 0.003	0.160 ± 0.001	0.131 ± 0.001	0.132 ± 0.002	0.123 ± 0.002	0.128 ± 0.002
Hmax/Cbl	0.252 ± 0.006	0.25 ± 0.004	0.352 ± 0.002	N.d.	N.d.	0.298 ± 0.005	0.286 ± 0.004
Lmd/Cbl	0.593 ± 0.012	0.546 ± 0.007	0.623 ± 0.003	0.473 ± 0.004	0.468 ± 0.005	0.475 ± 0.003	0.471 ± 0.004
Iob/Cbl	0.089 ± 0.002	0.171 ± 0.002	0.186 ± 0.001	0.149 ± 0.002	0.148 ± 0.002	0.151 ± 0.002	0.144 ± 0.003
Lna/Cbl	0.358 ± 0.007	0.241 ± 0.004	0.401 ± 0.001	0.302 ± 0.004	0.306 ± 0.004	0.311 ± 0.008	0.308 ± 0.002
Bna/Cbl	0.209 ± 0.004	0.376 ± 0.009	0.203 ± 0.001	0.218 ± 0.002	0.220 ± 0.003	0.235 ± 0.007	0.234 ± 0.005
Lbull/Cbl	0.194 ± 0.003	0.203 ± 0.003	0.221 ± 0.001	0.174 ± 0.002	0.185 ± 0.002	0.209 ± 0.004	0.215 ± 0.003
Lfi/Cbl	0.056 ± 0.001	0.049 ± 0.001	0.057 ± 0.002	0.041 ± 0.001	0.042 ± 0.001	0.041 ± 0.001	0.041 ± 0.001
Lm^{1-3}/Cbl	0.302 ± 0.007	0.278 ± 0.004	0.305 ± 0.001	0.239 ± 0.003	0.245 ± 0.005	0.243 ± 0.005	0.262 ± 0.003
Lm^{1-3}/Bfi	2.184 ± 0.063	1.832 ± 0.026	1.908 ± 0.015	1.829 ± 0.027	1.857 ± 0.042	1.989 ± 0.041	2.048 ± 0.042
Lm_{1-3}/Bfi	0.910 ± 0.033	0.766 ± 0.009	0.79 ± 0.006	0.808 ± 0.011	0.83 ± 0.015	0.904 ± 0.016	0.821 ± 0.020
Lm^1/Bfi	0.543 ± 0.010	0.497 ± 0.007	0.49 ± 0.002	0.477 ± 0.004	0.480 ± 0.004	0.505 ± 0.010	0.466 ± 0.009
Lfi/Lm^1	0.709 ± 0.14	0.668 ± 0.008	0.732 ± 0.030	0.664 ± 0.008	0.659 ± 0.010	0.669 ± 0.012	0.695 ± 0.012
Bm^1/Cbl	0.170 ± 0.003	0.154 ± 0.003	N.d.	N.d.	N.d.	N.d.	N.d.
Bcra/Cbl	0.196 ± 0.007	0.145 ± 0.002	N.d.	0.078 ± 0.002	0.080 ± 0.002	0.085 ± 0.002	0.079 ± 0.002
Hcra/Bcra	0.179 ± 0.006	0.183 ± 0.004	N.d.	0.296 ± 0.009	0.277 ± 0.09	0.281 ± 0.017	0.318 ± 0.011
Li/Cbl	0.411 ± 0.009	0.367 ± 0.009	N.d.	0.299 ± 0.002	0.295 ± 0.010	0.299 ± 0.005	0.293 ± 0.004
Bi/Lmd	0.300 ± 0.004	0.278 ± 0.004	N.d.	N.d.	N.d.	N.d.	N.d.
Bfi/Lmd	0.248 ± 0.011	0.275 ± 0.004	0.257 ± 0.001	0.276 ± 0.003	0.282 ± 0.003	0.259 ± 0.005	0.272 ± 0.004
Lfi/Bfi	0.374 ± 0.014	0.329 ± 0.003	0.359 ± 0.016	0.316 ± 0.004	0.316 ± 0.004	0.336 ± 0.006	0.323 ± 0.005
M^{1-1}/Cbl	0.485 ± 0.010	0.462 ± 0.007	0.484 ± 0.002	0.404 ± 0.003	0.400 ± 0.005	0.408 ± 0.004	1.85 ± 0.04
D2/Lna	0.362 ± 0.005	0.356 ± 0.004	0.315 ± 0.002	0.320 ± 0.007	0.331 ± 0.006	0.335 ± 0.016	0.399 ± 0.004
D1/Lbull	0.217 ± 0.003	0.301 ± 0.006	0.328 ± 0.011	0.354 ± 0.006	0.323 ± 0.007	0.310 ± 0.008	0.276 ± 0.007
Lm_{1-3}/Cbl	0.135 ± 0.003	0.116 ± 0.002	0.126 ± 0.001	0.105 ± 0.001	0.109 ± 0.002	0.106 ± 0.001	0.105 ± 0.003
D1/Cbl	0.035 ± 0.001	0.061 ± 0.002	0.072 ± 0.002	0.062 ± 0.001	0.060 ± 0.001	0.064 ± 0.001	0.059 ± 0.001

N.d., no data; *n*, sample size.

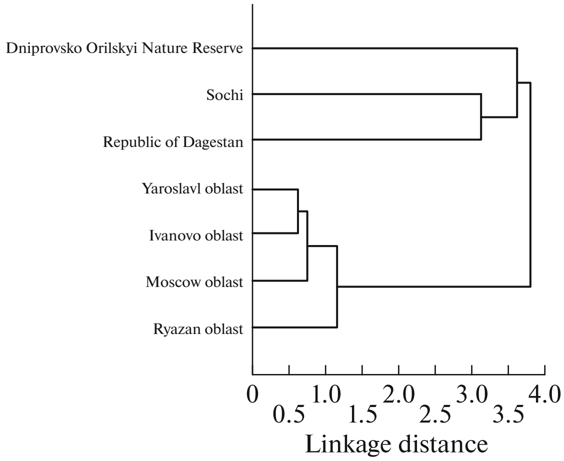

Fig. 3. Cluster analysis of craniometric parameters of the pygmy wood mice from seven regions.

European chromosomal forms of the European race (Bogdanov, 2001, 2004; Bogdanov and Rozanov, 2005; Karamysheva et al., 2010; Stakheev et al., 2011).

We also conducted a discriminant analysis of the craniometric data for intraspecific groups (northern and southern) of the pygmy wood mouse (Table 6).

Table 6. Discriminant analysis of cranial measurements of the pygmy wood mice (*S. uralensis*) of two intraspecific groups

Measurement, index	Northern group	Southern group
Bcra	–	–
Iob	–	–
Cbl	7.86	14.044
Zyg	–5.46	3.686
Lmd	24.08	14.271
Lbull	51.47	14.326
Lfi	–12.99	5.828
Bm^1	389.00	287.468
Li	3.63	–29.76
Hcra	51.11	39.13
Lm^{1-3}	138.19	108.763
Const.	–1173.19	–719.741
Eigenvalue	32.005	
F-criterion	507.50	
P (*F* criterion)	<0.0000	
Criterion Wλ	0.303	
Criterion χ^2	396.87	
df (χ^2)	7	
R_{can}	0.985	

Discriminant analysis of the dimensions of the skulls of the pygmy wood mice made it possible to establish that the northern and southern groups are 100% and with a high degree of confidence divided according to eight indicators of the skull dimensions. As in the case with the yellow-necked mouse, the results are located on the same canonical axis, $R_{can} = 0.946$ with $F = 187.25$ ($p < 0.0000$). The eigenvalue is 8.56, the criterion $W\lambda = 0.105$, and $\chi^2 = 401.847$ (df = 8, $p < 0.00$).

CONCLUSIONS

The analysis of intraspecific craniometric variability among representatives of the genus *Sylvaemus* revealed the following trends in the variability of metric signs of the skull, based mainly on the formation of adaptations to a particular food type during evolution.

S. flavicollis in the southern part of its range (Lviv and Voronezh oblasts) is characterized by a wider and larger skull, the dimensions of which decrease to the north; to the northwest of Belarus (toward Leningrad oblast and Sweden), the skull becomes even smaller. According to the indices characterizing the type of feeding, in the southern part of the range of this species there are more signs related to granivory; in the north, to folivory. The similar features in this direction are the narrowing and shortening of the muzzle. However, to the east and northeast of Moscow oblast (Bashkortostan and Mordovia), the size of the skull and signs of granivory in the yellow-necked mouse increase again, but all these indices are less than in the southern part of the range of this species.

Specimens of *S. uralensis* in the southern part of the range compared to the non-black earth region of the European part of Russia are characterized by higher and wider skulls, with relatively larger upper diastema and a lower jaw, longer upper dentition, and wider M^1, although the overall dimensions of the skull may vary from the largest to the smallest. Differences in food preferences, identified by us in various parts of the species' range, do not show a relationship to the values of the indices of the dental apparatus.

The craniometric differences between the northern and southern intraspecific groups of each of these two species confirm the findings of genetic studies.

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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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