

## DISTRIBUTION AND VARIATION OF WOOD MICE OF THE *SYLVAEMUS MICROPS* & *URALENSIS* GROUP IN EASTERN EUROPE: FRAGMENTATION AND CLINES

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**Distribution and variation of wood mice of the *Sylvaemus microps* & *uralensis* group in Eastern Europe: fragmentation and clines.** — I. Zagorodniuk. — The species names *Sylvaemus microps* and *Sylvaemus uralensis* mark the two key stages in recognition of the taxonomic heterogeneity of *Sylvaemus sylvaticus* (s. str.), to which they have long been included. The first was described in 1952 from Central Europe, while the second 140 years earlier (1818) from the Southern Urals. Both taxa have a complicated taxonomic history and are now considered conspecific. However, some gaps exist between them, in particular geographic ones. These taxa are considered here as two groups of populations: a western (*microps*) and an eastern (*uralensis*). The taxonomic history of wood mice of the group *Apodemus microps*—*Sylvaemus uralensis* and the history of increase in knowledge on their distribution are considered. An analysis of geographic variability of key diagnostic characters of the species was carried out, which revealed a quite well expressed morphological homogeneity. Within the Western Palaearctic populations, there is a clear clinal variation from relatively large southern and eastern to small northern and western forms. Geographic range analysis shows the presence of several relatively isolated range fragments, including a clear gap between the western forms of the *microps* group (Central Europe, the Balkans, and the Western Carpathians region) and the eastern forms of the *uralensis* group (from the Dnipro region and the Baltics to the Urals, including the Caucasus and Asia Minor). Proposals to recognise the specific level of differentiation between the northern and southern forms seem to be far too hypothetical, as well as the idea to assign the Caucasian form (*ciscaucasicus*) to the Central European *microps* and the Crimean form (*baessleri*) to the Upper Volga *mosquensis*. In general, the available data indicate differences between the western and eastern forms of *Sylvaemus uralensis*. Detailed information on marginal records of the two groups of populations is given, including the easternmost (essentially north-eastern) findings of the *microps* group and the westernmost findings of the *uralensis* group. There is a significant geographic gap between these two forms covering the entire area of Volyn, Podillia, Western and Central Polissia, but narrowing to the south, towards the Black Sea. Connection between the two range fragments may exist in the south, but the available and verified data essentially show a gap across the interfluvium between the Dnister and Tylihul rivers.

**Key words:** rodents, *Sylvaemus*, distribution limits, geographic variation, biogeography, Europe.

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*In memory of Oleksandr Mikhaïlenko (1955–1998), the inspired and tireless explorer of the fauna of Bessarabia and adjacent regions*

### Introduction

In the past half-century, especially after 1990, views on the taxonomy and distribution of rodents of the genus *Apodemus* (s. l.) have changed significantly. Wood mice, i.e. species of the subgenus (or genus) *Sylvaemus*, have been considered in the fauna of Europe for a long time as a pair of morphologically similar species *A. flavicollis* and *A. sylvaticus* (Corbet 1978). The first serious taxonomic event was the description of a new wood mouse species — *A. microps* — from Central Europe (Kratochvil & Rosicky 1952, Kratochvil & Zeida 1962), to which this work is devoted to.

After thirty years, a series of new descriptions appeared, including *A. falzfeini* (Mezhzherin & Zagorodniuk 1989), *A. hermonensis* (Fillipucci *et al.* 1989), *A. alpicola* (Storch & Lutt 1991), *A. ponticus* (Mezhzherin 1991), and *A. hyrcanicus* (Vorontsov *et al.* 1992). It was mainly facilitated by the wide use of protein electrophoresis techniques (Gemmeke 1980; Mezhzherin 1987; Britton-

Davidian *et al.* 1991). However, the achievements of taxonomists led to a crisis among practitioners: the nomenclature, diagnostics, and geographic range of all forms of the genus needed a revision, particularly in the scope of Ukraine's fauna (Mezhzherin 1993). This issue also fully concerned regions of Eastern Europe and the Caucasus, where, as it turned out, *A. sylvaticus* is absent in many areas but other species occur instead (Zagorodniuk & Milyutin 1992; Vorontsov *et al.* 1992). These new species were considered as hybrids of *A. sylvaticus* x *flavicollis* (Zagorodniuk *et al.* 1997), according to the then accepted concept that these species widely hybridise in the nature (Larina 1958).

Further research revealed a highly limited distribution of *Sylvaemus sylvaticus* (s. str.) to the east: the geographic range of the species extends not far from the eastern borders of Lithuania, Belarus, and Ukraine (Zagorodniuk 1993, 2005b). This species is replaced by *S. falzfeini* = *witherbyi* to the south and south-east (Zagorodniuk *et al.* 1995). East of the abovementioned range limits, only *Sylvaemus* ex gr. *microps-uralensis* occur, particularly in the Baltics (Zagorodniuk & Milyutin 1992; Zagorodniuk & Mezhzherin 1992), in the European part of Russia to the Urals and Altay (Mezhzherin & Zagorodniuk 1989; Mezhzherin & Mikhailenko 1992), in the Caucasus (Vorontsov *et al.* 1992), and in the Northern Black Sea Region and Crimea (Zagorodniuk & Fedorchenko 1993).

Nevertheless, wood mice species form wide zones of sympatry in Eastern Europe (Zagorodniuk 1996; Zagorodniuk 2005b; and others), which complicates their discrimination and external characters are often insufficient for confident conclusions. Under such circumstances, museum collections are of high value in research into variation and distribution patterns of wood mice allowing to revise the specimens collected earlier and to analyse fauna changes through time. Due to studies using collection specimens it was revealed earlier that 'hybrids' of the European wood mouse and the yellow-necked wood mouse in reality are not hybrids but other species, including the southern *Sylvaemus* ex gr. *falzfeini* (Zagorodniuk *et al.* 1997).

The aim of the present paper is to clarify distribution patterns of wood mice of the group *Apodemus microps-Sylvaemus uralensis* in Eastern Europe with an analysis of clinal variation of diagnostic characters of different forms of this species complex.

## Materials and Methods

**Collections.** Over 10 large museum collections have been analysed, including those deposited in zoological museums of universities of Tartu, Moscow, Kharkiv, and Lviv. Valuable are academic collections — part of which are genetically marked — stored at the ecological departments of the Institute of Zoology, National Academy of Sciences of Ukraine (partly collected and marked by the author together with S. Mezhzherin), Institute of Evolutionary Biology, Czech Academy of Sciences (collections of J. Kratochvíl, J. Zima, and M. Macholán), and the Laboratory of Cytogenetics of the Institute of Developmental Biology, Russian Academy of Sciences (collections of M. Vorontsov's research group, including G. Boeskorov). Collection data are given with acronyms of museums (NMNH — National Museum of Natural History, NAS of Ukraine, ZMLU — Zoological Museum of Lviv University, ZMTU — Zoological Museum of Tartu University, ZMMU — Zoological Museum of Moscow University) and types of museum specimens (ss — study-skin, ss+sk — study-skin and skull, fs — fluid-preserved specimen).

**Re-identifications.** Special attention was given to re-identifications of wood mouse specimens collected in the territory of Ukraine and neighbouring countries, in accordance with the earlier clarified general scheme of distribution of *Sylvaemus* ex gr. *microps-uralensis* in the zone of their sympatry with *Sylvaemus sylvaticus* (s. str.) (after Mezhzherin & Zagorodniuk 1989; Zagorodniuk 1996, 2005b). Type specimens and samples of topotypes were of particular interest allowing to re-identify most of the specimens (Zagorodniuk 1996, and others).

Re-identifications were based on diagnostic keys and systems of morphometric characters, which had been developed by the author earlier (Zagorodniuk 1996; Zagorodniuk & Fedorchenko 1992; Zagorodniuk 2003), considering the fact that all diagnostically relevant characters of wood

mice are affected by significant age-related (Zagorodniuk & Kavun 2000) and geographic variation (Zagorodniuk 2005a). When ignoring these variation patterns, species discrimination using morphologic characters often becomes impossible. Adult specimens with fully preserved skulls are of key importance, while the most important diagnostic characters are as follows:

- coat colouration — general tone, clear difference between the colouration of the back and belly, white colouration expanding onto the fur of thighs, development of the chest spot between the forelimbs;
- body measurements — the standard L, Ca, Pl, Au (body length, tail length, hindfoot length, and auricle length); controlling the measurements, especially of hindfoot length (Pl), on dry study-skins is important since erroneous data are often indicated on labels;
- cranial measurements — species discriminate the most by four key characters (CbL, condylobasal length; HCb, height of cranium with bullae; M13, upper molars coronal length; LFI, length of incisive foramens); in many cases, the form of the fronto-temporal suture, posterior end of palatine bones, and incisive foramens are also important diagnostic characters.

In order to collect materials on the geographic variation of species, data were also analysed from publications, which appeared in large number after the description of high species richness of wood mice (Table 1).

**Key terms** used in subheadings in this article:

- *Disjunct range* — a term used to describe the distribution range of species with complex contours, which cannot be described by polygons or simple outlines. Disjunct distribution is especially common at the borders of species ranges, in zones of dispersal of species, and in zones of range contraction with subsequent range fragmentation. Disjunct distribution also characterises species that disperse to adjacent biomes beyond their natural habitats. Examples are the dispersal of lowland species into the mountains along mountain valleys or floodplain species into the steppe along rivers; thus, describing the geographic range of such species in simple contours is incorrect.

- *Clinal variation* (cline, from the Greek κλίνειν, meaning ‘to lean’). The term ‘cline’ was proposed in 1938 by J. S. Huxley to describe the gradients in variation of the same character through the entire geographic range, and it can describe both genetic features (e.g. allele frequencies) and size-related characters (e.g. body dimensions). It is one of the nine characters (along with clade, grade, morph, mentifact, etc.) introduced by Huxley for the description of the structure and heterogeneity of biotic communities in space and time, from population to ethnos. Ecogeographical rules are the most well-known manifestations of clinal variation. In many cases, clines indicate the directions of former dispersals of species, when the most primitive and generally initial states of characters are preserved in the most ancient parts of the species range<sup>1</sup>.

### Discoveries of *Apodemus microps*

The taxonomic and biogeographic history of ‘*Apodemus microps*’ started when it was described based on materials from vicinities of Košice in Slovakia (Kratochvil & Rosicky 1952). However, until its re-description, which presented a sufficient number of characters and an analysis of their variation (Kratochvil & Zeida 1962), the species has basically remained unknown and unrecognised, although the presence of both small and large forms of wood mice in Transcarpathia (Zakarpattia Oblast in Ukraine) was already noted by Turianin (1959).

Later, the species was suddenly reported from many localities in different regions, including Ukraine (Polushina & Vozniuk 1980), Poland (Huminski 1964), Moldova (Muntianu & Savin 1986), the Caucasus (Vorontsov *et al.* 1989, 1992), Belarus, Estonia, Pskov Oblast in Russia (Zago-

<sup>1</sup> Despite the general trend of increasing dimensions to the north (Rodríguez *et al.* 2006), body dimensions of wood mice decrease northwards, which contradicts Bergman’s rule. Therefore, other factors must dominate here (e.g. small-sized fruits of food plants, slow growing rates, inbreeding, burrowing lifestyle).

rodniuk & Mezhzherin 1992; Zagorodniuk & Milyutin 1992), and the entire European part of Russia (Zagorodniuk & Mezhzherin 1992), including Belgorod and Voronezh Oblasts (Zagorodniuk 1993). The species was also identified among materials from the Altay (Mezhzherin & Mikhailenko 1991). Eventually, samples of wood mice from the Urals, wherefrom the form *Mus sylvaticus uralensis* Pallas was described a hundred years earlier, were also assigned to *A. microps* (Zagorodniuk & Fedorchenko 1993; Kolcheva 2006).

The latter resulted in the fixation the name *Sylvaemus uralensis* for the species, which has become widely accepted (Wilson & Reeder 2005). Meanwhile, '*Apodemus microps*' has changed not only its name, but also its status from being a species with an occurrence limited to regions of Central Europe to one of the most widely distributed rodent species of Eurasia. Respectively, views on the geographic range of its 'mother species' *S. sylvaticus* have also changed substantially.

### On the taxonomic heterogeneity of the group *microps+uralensis*

The increased attention to the 'new' wood mice species prompted researchers to develop different diagnostic systems, including those based on generic criteria, which allowed to amass data on the taxonomic heterogeneity of this group. The same was indicated by morphological data.

According to such diagnostic characters as upper molars length, samples from the north (the Baltics and Valdai), just as small typical *microps*, had lower values of this measurement (3.4–3.7 mm) compared to samples from the Donbas, the Caucasus, and the Urals (Table 1). In general, the samples are notably similar and the existing differences have a clearly expressed clinal variation. This variation can be interpreted as an indication of routes of post-glacial dispersal of the (super)species, and the revealed configuration of contour lines (Fig. 1) fully reflects the post-glacial configuration of the geographic range of many pairs of close species, which was described by the author earlier (Zagorodniuk 2005b).

The first important result of molecular studies was the hypothesis on the presence within *S. uralensis* a number of 'small' species (Orlov *et al.* 1996), among which the cited authors distinguish three (respectively, *S. uralensis* is considered as superspecies):

- 1) *Apodemus (S.) mosquensis* (Ognev, 1913) — Novgorod, Voronezh, and Crimea [the Crimean form *baessleri* Dahl (Dahl 1929) is far too remote from *mosquensis*];
- 2) *A. (S.) ciscaucasicus* (Ognev, 1924), syn.: *A. microps* Kratochvil & Rosicky, 1952 — the Carpathians, the Balkans, and the Caucasus;
- 3) *A. (S.) uralensis* (Pallas, 1811) — given as a name of superspecies with the comment: 'wood mice from the Ural, interfluvium Volga-Ural and N Kazakhstan [...] may represent a different species (Orlov *et al.* 1996: 198).

Another division was proposed based on cytochrome *b* analysis (Chelomina *et al.* 2007), according to which there are two races within the single species *S. uralensis* — a European and an Asian. The European race includes specimens from Turkey, Kabardino-Balkaria, Orenburg, and Omsk, but not one from regions north of Kursk, Ryazan, and Tambov. That is, the actual European populations of the species (from the Baltics, Poland, Bessarabia, Pannonia, and the Balkans), which represent a group of small-sized forms, have not been studied.

### Diagnosis of *Sylvaemus uralensis*

The form *uralensis* is given by P. Pallas at the end of the description of *Mus sylvaticus* in a rather short form: '*Uralensis varietas minor, supra magis murini coloris, neque adeo eleganti et distincta albedine; pondere sesquiquatuor drachmarum; longitudine 3".2 1/2"*, *cauda 2".8"*. *Taurica varietas contra multo major et elegantissimi velleris.*' (Pallas 1811: 168).

That is, '*the variant uralensis is small, with more mouse-like colours, not as elegant, and differs by its whiteness; weights 4.5 drachmae; its length is 3" and 2 1/2", its tail is 2" and 8" long. The variant taurica is much bigger with a more elegant coat.*' Since 1" = 25.4 mm, and 1 drachma is 3.73 g, the given parameters are L = 83 and Ca = 71 mm, W = 16.8 g. This corresponds to body dimensions of modern *S. uralensis* (see Table 1).

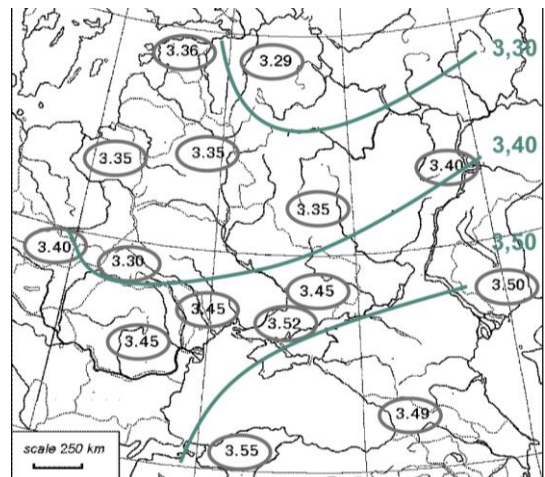
Table 1. Diagnostic measurements of *Sylvaemus uralensis* from different parts of the species range (mean value and standard deviation)Таблиця 1. Діагностичні проміри *Sylvaemus uralensis* з різних частин ареалу виду (середнє значення та стандартне відхилення)

Sample	Body measurements, mm				Cranial measurements, mm				Ref*
	L	Ca	Pl	Au	CBL	HCb	M13	LFI	
<i>north and west</i>									
W Poland	79.3±6.0	71.6±6.4	18.4±0.8	12.7±0.5	20.8±0.8	—	3.34±0.11	4.31±0.22	3
S Poland	83.9±4.2	78.5±5.3	19.0±0.0	13.1±0.4	20.9±0.6	—	3.45±0.14	—	4
Slovakia	83.8±7.0	75.8±6.2	18.6±0.8	13.1±0.8	21.3±0.8	8.40±0.36	3.40±0.18	—	13
Estonia	87.4±2.5	87.1±6.1	21.2±0.3	14.3±0.7	21.8±0.8	8.73±0.24	3.36±0.09	4.65±0.12	8
Valdai	84.7±7.9	81.4±6.5	20.2±1.0	—	21.7±0.6	8.54±0.24	3.29±0.14	4.58±0.28	9
Bulgaria	79.3	73.8	19.0	13.5	20.6	8.00	3.25	—	17
Romania	84.5	78.5	18.5	12.9	21.5	—	3.45	—	12
Austria	86.4±4.2	74.7±4.2	18.3±0.5	13.2±0.9	21.3±0.6	—	3.35±0.09	4.23±0.23	18
Carpath1	82.2±5.1	77.5±7.9	18.6±0.4	12.2±0.4	21.4±1.0	8.81±0.28	3.28±0.10	4.46±0.25	6
Carpath2	84.4±5.0	78.3±5.2	18.6±0.4	12.7±0.8	21.1±0.6	8.46±0.21	3.31±0.11	4.45±0.29	7
Moldova1	81.9±5.9	73.6±6.1	18.4±0.7	12.7±0.8	22.5±0.4	8.01±0.18	3.18±0.09	4.16±0.17	10
Moldova2	88.0±4.5	81.6±8.8	18.6±0.8	12.8±0.5	21.9±0.7	8.26±0.22	3.47±0.16	4.57±0.27	11
<i>south and east</i>									
S Ukraine	85.6±5.2	81.7±6.9	19.8±0.8	13.5±0.8	22.9±0.7	8.40±0.19	3.52±0.10	4.56±0.24	15
Donetsk	82.4±5.8	74.7±6.8	20.4±0.5	14.3±1.1	21.3±0.6	8.46±0.23	3.45±0.08	4.37±0.20	5
Volga	90.0	87.1	20.1	—	21.3	8.40	3.40	4.50	14
Ural	83.2±5.4	81.7± 7.5	19.7±0.6	14.3±1.8	22.6±0.9	8.59±0.25	3.50±0.07	4.93±0.24	1
Altay	84.2±0.9	76.6±0.9	18.8±0.2	13.2±0.1	21.7±0.1	8.03±0.05	3.51±0.02	4.69±0.06	11
Caucasus	81.0±5.5	82.1±6.5	20.7±0.7	14.9±0.8	22.9±0.5	8.40±0.25	3.49±0.09	4.49±0.25	2
Turkey	94.3±4.0	91.7±2.9	19.8±0.8	14.7±0.8	23.0±0.6	8.63±0.06	3.50±0.10	4.57±0.06	16

\* References: 1 — Zagorodniuk & Fedorchenko 1993 (n = 17, Ilmen Nature Reserve, Miass, Chelyabinsk Oblast, Russia); 2 — Vorontsov *et al.* 1992 (Transcaucasia, n = 28–34 for cranial measurements, n = 60–77 for body measurements); 3 — Glazaczow 1984 (n = 60–72, W Poland); 4 — Haitlinger 1972 (n = 29 for body measurements, n = 19 for cranial measurements; Pieniny, SW Poland); 5 — Zagorodniuk 1993 (n = 32, Artemivsk, Donbas, Ukraine); 6 — Kyseliuk 1993 (n = 10; Chronohora, the Carpathians, Ukraine); 7 — Zagorodniuk & Peskov 1993 (n = 13, the Carpathian region); 8 — data based on materials from A. Milyutin (n = 8, SW Estonia and Izborsk, Pskov Oblast, Russia); 9 — data based on materials from A. Istomin (n = 20, Nelidovo, Tver Oblast, Russia); 10 — Muntianu & Savin 1981 (n ~ 40, Criuleni District, Moldova); 11 — Mezhzherin & Mikhailenko 1991 (n = 30, Moldova, n = 30, Cherga, the Altay Republic, Russia); 12 — Simionescu 1974 (n = 28–34; Romania); 13 — Kratochvil & Zejda 1962 (n = 51–70, mainly Slovakia); 14 — Egorov 1983 (n = 50, Volga Region, Russia; body measurements from Popov 1960); 15 — Mezhzherin & Zagorodniuk 1989 (S Ukraine, left bank Ukraine, n = 23); 16 — data based on materials from G. Storch (n = 3; Ulu Dağlar, W Turkey); 17 — Markov 1968 (n = 4 Maslovo, Bulgaria); 18 — Steiner 1968 (n = 29; Stockerau, Austria).

Fig. 1. Distribution of values of the upper molars length (M13) in geographic samples of *Sylvaemus uralensis* (according to Table 1). The growth of values from south to north is obvious, which may reflect the ways of expansion of the species, in particular in the post-glacial era, when most species expanded their range to the north.

Рис. 1. Розподіл значень довжини верхнього ряду кутніх зубів (M13) у географічних вибірках *Sylvaemus uralensis* (за даними з табл. 1). Очевидний ріст значень з півдня на північ, що може відображати шляхи розселення виду, зокрема й в постгляціальну епоху, коли більшість видів розширили свої ареали на північ.



According to body and cranial measurements, it is one of the smallest species of *Sylvaemus*: its body length does not exceed 95–100 mm, its tail is slightly shorter than its body, hindfoot length is to 22 mm (usually 19–21), and auricle length is to 15 mm (usually 12–14). The fur on the back is reddish-grey; the belly is white with no chest spot. The white colouration from below exceeds onto the thighs. The skull is small, CbL = 19–24 mm, M13 = 3.3–3.6 mm. The incisive foramina are short and narrow, 4.2–4.6 x 1.3–1.7 mm in average, clearly not reaching the front edge of M1 crowns. The fronto-temporal suture is cline-like (about 110–120°), without rounding; the posterior palatal notch is narrow and rounded (Fig. 2). The specifics of skull morphology of *S. uralensis* are shown in Fig. 2 in comparison with *A. agrarius* (left), *S. sylvaticus*, and *S. witherbyi* (right).

The re-identification of materials from Podillia and adjacent regions of Ukraine presented in publications (especially in publications on owl pellets) as '*S. uralensis*' showed a number of incorrect identifications: skull fragments of *Apodemus agrarius*, *Micromys minutus*, and *Sylvaemus sylvaticus* are often diagnosed as *S. uralensis*. With the assistance of M. Drebet and I. Zahorodnyi, the author has revised the osteological materials based on which the species was mentioned earlier (e.g. Zaytseva & Drebet 2007; Shtyk & Zahorodnyi 2015), but recently it was not indicated for the same locations (e.g. Drebet 2011). In samples from more eastern regions (Azov Region and Crimea), this species is the most often confused with *S. witherbyi* and *Mus musculus*.



Fig. 2. Cranial features of *Sylvaemus uralensis* in comparison with morphologically similar species with which the former is often confused (left to right): *Apodemus agrarius*, *S. uralensis*, *S. sylvaticus* and *S. witherbyi*. The upper row shows skulls in dorsal view, while the bottom row shows them in ventral view.

Рис. 2. Краніальні особливості *Sylvaemus uralensis* в порівнянні з морфологічно подібними видами, з якими його плутають (зліва направо): *Apodemus agrarius*, *S. uralensis*, *S. sylvaticus* та *S. witherbyi*. Верхній ряд — вид черепів згори, нижній — знизу.



### The disjunct range of *Sylvaemus uralensis* in Europe

The distribution of wood mouse species in Eastern Europe is uneven and it has not been described yet in detail. Especially in regions where boundaries of species ranges are located, except for the Czech Republic (Andera 2011), Poland (Cichocki *et al.* 2011), and Lithuania (Juškaitis *et al.* 2001). The general outlines of species range of *S. uralensis* are given in the IUCN database (Kryštufek *et al.* 2008; Juškaitis *et al.* 2016).

Detailed range boundaries are given here only for Eastern Europe, within Ukraine, Belarus, and adjacent regions of Russia and the Baltic countries (in particular, Estonia, Latvia, and Lithuania).

The species range is described here for its two main segments: western (range segments A1–A3) and eastern (range segments B1–B3) (Fig. 3), which corresponds to the respective taxonomic groups, i.e. the western to *Sylvaemus uralensis microps* and the eastern to *S. uralensis* (s. str.). There is a clear disjunction between these segments; marginal records are listed below.



Fig. 3. The disjunct range of *Sylvaemus uralensis*, in Europe with three range fragments: Pannonian-Danubian (green), Carpathian (red), and East European (blue). The Crimean isolate (form *baessleri*) was described earlier (Evstafiev 2015). Grey signs mark the eastern boundary of the geographic range of *S. sylvaticus* (after Zagorodniuk 1993, additions after Stakheev *et al.* 2011). Record localities of *S. uralensis* are given only based on materials personally verified by the author.

Рис. 3. Мереживо ареалу *Sylvaemus uralensis* у Європі. Виявляються чотири основні сегменти: паннонсько-дунайський (зелений полігон), прикарпатський (червоний полігон) та східний (блакитні позначки); кримський ізолят (форма *baessleri*) детально описано раніше (Евстаф'єв 2015). Сірі значки показують східну межу ареалу *S. sylvaticus* (за: Загороднюк 1993, з доповненнями за: Стахеев *et al.* 2011). Точки знахідок *Sylvaemus uralensis* — тільки за перевіреними особисто автором матеріалами.

**The western group of record localities (*Sylvaemus uralensis microps*)**

Three segments are described below: Transcarpathia, Prykarpattia and Podillia, and Bessarabia.

**Segment A1** (Transcarpathia). The first records of the species were reported in 1980 from Mukachevo Raion (Polushina & Vozniuk 1980), and later also from lowland regions of Transcarpathia (Emelyanov *et al.* 1987; Korchinsky 1988). A highland population of the species was found in the Chornohora (Kyseliuk 1993). In the neighbouring Hungary and Slovakia, it is also a lowland species (Cserkész 2005; Čanády *et al.* 2014). A review of records of the pygmy wood mouse in Transcarpathia was presented by Barkaszi (2018, 2020).

- a1.1. Pistrialovo, Mukachevo Raion, July 1975, meadow near vineyard, several specimens (Polushina & Vozniuk 1980);
- a1.1'. Lalove, Mukachevo Raion, ZMLU, n = 5 (ss), September–October 1985, leg. N. Polushina (Zatushevskyy *et al.* 2010; =? former record);
- a1.2. Berehovo, October 1976, blackthorn and rose shrubbery, several specimens (Polushina & Vozniuk 1980); *ibidem*, October 1985, n = 2 (Emelyanov *et al.* 1987);
- a1.3. Vynohradiv, bank of the Tisza; NMNH, n = 1 (ss+sk), 9 May 1948, leg. I. Sokur; ZMLU, n = 1 (ss), 13 July 1979, leg. O. Protsyk (Zatushevskyy *et al.* 2010).
- a1.4. Trosnyk, Vynohradiv Raion; NMNH, n = 3 (ss+sk), 10 May 1948, leg. I. Sokur.
- a1.5. Vynohradiv, July 1979, vineyard, several specimens (Polushina & Vozniuk 1980);
- a1.6. Sobatyn, Irshava Raion; ZMLU, n = 2 (ss), 12–13 July 1985, leg. N. Polushina (Zatushevskyy *et al.* 2010);
- a1.7. Bushtyno, Tiachiv Raion, October 1985, n = 1 (Emelyanov *et al.* 1987).

**Segment A2** (Prykarpattia and Podillia). Detailed data are available only for Poland (Cichocki *et al.* 2011). In Ukraine, data are scarce, there are no museum specimens, although there are reports from Opillia (map in Shevchyk 1998) and from owl pellets collected in Khmelnytskyi (Zaytseva & Drebet 2007) and Ternopil oblasts (Shtyk & Zahorodnyi 2015). All these data are not confirmed by museum specimens. Obviously, the distribution of wood mice in Podillia needs to be studied based on full-fledged collections. Currently, no reliable records of the species are known from Vinnytsia, Ternopil, and Lviv oblasts, which could be undoubtedly identified as *S. uralensis*: all of the revised specimens were confined to either *S. sylvaticus* or *S. tauricus* (or even to other species).

- a2.1a. Reniv, Ternopil Raion, Ternopil Oblast; n = ?, trappings, genetic labelling (Shevchyk 1998);
- a2.1b. Mshanets, Ternopil Raion (*ibidem*);
- a2.2a. Bila, Ternopil Raion (*ibidem*);
- a2.2b. Velyka Berzovysia, Ternopil Raion (*ibidem*);
- a2.2c. Petrykiv, Ternopil Raion (*ibidem*);
- a2.3. Podillia, Ternopil Raion (*ibidem*);
- a2.4. Koropets, Chortkiv Raion (*ibidem*);
- a2.5a. Nyrkiv, Chortkiv Raion (*ibidem*);
- a2.5b. Ustechko, Chortkiv Raion (*ibidem*);
- a2.6. Medobory Nature Reserve, Hrymailiv, Ternopil Oblast; n = 2 ('0.2%' of 952 specimens), pellets of *Asio otus* (Shtyk & Zahorodnyi 2015) [1 cf. *uralensis* + 1 *agrarius*!];
- a2.7. Kamianets-Podilskyi, 'n = 10' (Zaytseva & Drebet 2007); revision showed only 1 specimen of *S. cf. uralensis* (M13 = 3.4, LFI = 4.9 mm), but the bone fragment is insufficient;
- a2.8. Ivankivtsi (near Sataniv), Horodok Raion, Khmelnytskyi Oblast, NMNH, n = 1 (ss+sk), 1950, leg. I. Sokur;
- a2.9. Tynna, Dunavtsi Raion, pellets of *Asio otus*, n = 3 (Zaytseva & Drebet 2007) — in the collections of Podilski Tovtry National Nature Park, three specimens were found labelled as '*S. uralensis*' (received from M. Drebet), but only one of them (No. 57) belongs to *S. cf. uralensis* (M13 = 3.6, LFI = 4.8 x 1.6 mm, + 2 mandibles with m13 = 3.4–3.5 mm).

**Erroneous or dubious records:** records of the species from the Kamianets Dniester Region (Zaytseva & Drebet 2007) should be revised: • Kamianets-Podilskyi, pellets of *Asio otus*, 'n = 10' — specimens from the collection of Podilski Tovtry National Nature Park, of the 10 specimens one corresponds to characters of *uralensis* [record 'a2.8'], but another specimen (No. 97) is undoubtedly *S. sylvaticus*; • Tynna, Dunavtsi Raion, pellets of *Asio otus*, 'n = 3' — specimens from the collection of Podilski Tovtry National Nature Park, all three labelled as '*S. uralensis*,' but only one (No. 57) is *S. cf. uralensis* (see above), one (No. 23) is without bones of *Sylvaemus*, and another one (No. 49) is *Micromys*.

**Segment A3** (Bessarabia) — record localities within Ukraine and Moldova. The first and still important analysis was carried out by A. Mikhailenko, who reported data on 87 specimens trapped in 1985 to 1988 in the Cahul District of Moldova (Mikhailenko 1990).



Further studies expanded the geography of records. At the same time, a significant part of records, including published ones (Shevchenko & Zolotukhina 2002), turned out to be incorrect. This range segment is obviously isolated from the adjacent other segments (Fig. 2). In particular, in Odesa Oblast, according to data provided by colleagues from the Odesa Anti-Plague Institute, the pygmy wood mouse does not occur in Savran, Kodyma, Balta, Okny, and Ananyiv Raions (D. Sokolovskiy, personal reports). Reliable and relatively reliable (by external characters) identifications belong to the eastern segment *B2* (see further).

- a3.1. Hristovaia, Camenca District, Moldova; NMNH, n = 11 (fs), July–August 1905, 20 June 1913, leg. O. Brauner (Shevchenko & Zolotukhina 2002);
- a3.2. Vionova, Orhei District, Moldova; NMNH, n = 3 (fs), 1934, leg. O. Brauner;
- a3.3. Chişinău, Moldova, pellets of *Asio otus*, n = 25, 2011–2013 (Nisteanu *et al.* 2020);
- a3.4. Zloţi, Cimişlia District, Moldova, NMNH, n = 15 (fs), 9–20 June 1913, leg. M. Goronovich ('O. Brauner' after Shevchenko & Zolotukhina 2002);
- a3.5. Cimişlia, Moldova; NMNH, n = 2 (ss+sk), May 1985, leg. I. Zagorodniuk (Shevchenko & Zolotukhina 2002; author's data);
- a3.6. Tarutyn polygon, 2007–2010, n = 13 (Rusev *et al.* 2012);
- a3.7. Sarata Raion, between Sarata and Petropavlivka, blackthorn shrubbery, several specimens trapped, ca. 2016 (D. Sokolovskiy, personal report);
- a3.8. Aliyaga River, 2 km east of Delen, Artsyz Raion, Odesa Oblast, 1991, n = 1 (Fedorchenko & Zagorodniuk 1994);
- a3.9. Kytai Lake, 2 km east of Pryozerne, 1983, n = 1 (*ibidem*);
- a3.10. Katlabukh, 4 km south of Bahate, 1983, n = 2 (*ibidem*).

**Erroneous or dubious records:** • 'Balta, Odesa Oblast': NMNH, n = 2 (fs), 26–27 June 1947, leg. I. Sokur (Shevchenko & Zolotukhina 2002) = Velyka Bakta, Berehovo Raion, Zakarpattia Oblast (I. Sokur had worked at that time in Velyka Bakta and in 1952 published a book on mammals of Zakarpattia); • Lisky, Kiliya Raion, Odesa Oblast, NMNH, n = 3 (fs), 31 July 1960, leg. O. Gizenko<sup>2</sup> (Shevchenko & Zolotukhina 2002); the specimens were not found in the collection; • 'Kostiantynivka, Sarata Raion, Odesa Oblast': NMNH, n = 5 (fs), 1910–1920, leg. O. Brauner = actually, it should be 'Kostiantynodariivka' (E. Ulyura, personal report), i.e. Mayory of Odesa Raion<sup>3</sup>; specimens were not found.

### ***The eastern group of record localities (Sylvaemus uralensis s. str.)***

*Sylvaemus uralensis* (s. str.) is the eastern (Asian) race with clear gaps in its geographic range from the Baltics to the Valdai, Volga Region, and further to the Urals and Altay. Geneticists denote this race as 'European' including populations also from the Urals, the Caucasus, and Turkey (Chelomina *et al.* 2007). The segments of this group concern not as much the geographic range as range boundaries, or rather belts of extreme record localities, which allow range boundaries to be estimated in a particular segment.

**Segment B1** (the Baltics, north-west segment). The geography of record localities is described in detail for Lithuania (Juškaitis *et al.* 2001, 2016), as well as for Estonia and adjacent regions of Russia and Belarus (Zagorodniuk & Milyutin 1992), and thus there are not fully repeated here (Fig. 2). Records of the species in Belarus, also accepted in the recent review of mammals of this country (Savitsky *et al.* 2005) are based on Zagorodniuk & Milyutin 1992. The finding of the species in Gomel (Savarin 2011) is the only description that presents detailed morphologic data confirming the correct species diagnosis of the specimen.

- b1.1. Vastseliina, Võru County, Estonia, n = 1, leg. A. Milyutin, ZMTU (Zagorodniuk & Milyutin 1992);
- b1.2. Izborsk, Pskov Oblast, Russia, n = 5, leg. A. Milyutin, ZMTU (*ibidem*);
- b1.3. Polotsk, Belarus, a series of specimens, ZMMU (*ibidem*);
- b1.4. Osino, Sebezh Raion, Pskov Oblast, Russia (materials of T. Aksenova and E. Mikhaylova) (Zagorodniuk & Mezhzherin 1992);
- b1.5. Drissa [Vierchnie-

<sup>2</sup> It is dubious since Gizenko worked on the Dnipro, not on the Danube. Also, there is a park called 'Lisky' in Mykolaiv, near the Dnipro.

<sup>3</sup> It is known from Brauner's biography that from 1969 he had been living in Odesa and in the hamlet 'Kostiantynodariivka 3 versts away from Odesa' (Curriculum 2007). According to the website 'Kraeved' (<https://bit.ly/3qCzfCh>), it is 'Konstantyno-Darevka ... Mangeym Uyezd (Limberov, Mayorskiy).' After the deportation of the Germans in the autumn of 1945, Mangeym was re-named to Kamyanka, which is now part of Odesa Raion (halfway between Odesa and Tiraspol).

dvinsk], Vitebsk Oblast, Belarus, ZMMU (Zagorodniuk & Milyutin 1992); ● b1.6. Berezinski Biosphere Reserve, Belarus (Kashtalyan & Springer 2012); ● b1.7. Haradok Raion, Vitebsk Oblast, Belarus (website ‘Vertebrates of Belarus’); ● b1.8. Yelnya, Smolensk Oblast, Russia, ZMMU (Zagorodniuk & Milyutin 1992); ● b1.9. Gomel, bank of the Sozh River, Belarus, June–November 1990, n = 2 (Savarin 2011).

**Segment B2** (southern segment). The western boundary of distribution of *S. uralensis* (s. str.) within Ukraine. All specimens mentioned from the collection of NMNH are given according to the collection catalogue of the family Muridae (Shevchenko & Zolotukhina 2002). Records from Snihurivka, Domanivka, and Veselynove are one of the most northern finds of the species in the Northern Black Sea Region, according to the data of the Ukrainian Anti-Plague Institute, UAPI (D. Sokolovskyi, personal report). It could generally be expected that this segment is a continuation of the Bessarabian range segment (*Segment A3*, see above), but *de facto* the species is absent (has not been found or identified) within the Dniester–Tyliluh interfluvium. Noteworthy, that the Tyliluh is also considered as a boundary between geographic ranges of two mole rat species — eastern for *Nannospalax leucodon* and western for *Spalax zemni* (Zagorodniuk *et al.* 2017).

● b2.1. Boryspil, Kyiv Oblast<sup>4</sup>, NMNH, n = 1 (sk), 22 August 1992, leg. I. Zagorodniuk; ● b2.2. Svichivka, Lubny Raion, Poltava Oblast, NMNH, n = 1 (sk), 1988, leg. S. Shevchenko; ● b2.3. Kropyvnytskyi (‘Kirovohrad’), NMNH, n = 1 (fs), January 1907, leg. O. Brauner; ● b2.4. Ratsynska Dacha, Voznesensk Raion, Mykolaiv Oblast, NMNH, n = 1 (ss+sk), 24 July 1951, leg. I. Sokur; ● b2.5. Volodymyrivka, Bratske Raion, Mykolaiv Oblast, NMNH, n = 4 (ss+sk), 10 and 14 November 1949, 19 July 1954, 23 September 1957, leg. V. Abelentsev; ● b2.6. Snihurivka, Mykolaiv Oblast, NMNH, n = 1 (ss), 6 July 1952, leg. V. Abelentsev; ● b2.7–2.9. Domanivka, Veselynove, Mykolaivka, Mykolaiv Oblast, trapping of the UAPI (D. Sokolovskyi, personal report); ● b2.10. Berezivka, Odesa Oblast, station of the UAPI (D. Sokolovskyi, personal report); ● b2.11. Tyliluh National Nature Park, trappings (Merzlikin 2012).

**Segment B3** (southern segment, Taurida and Northern Azov Region). It is one of the most confusing range segments. The species definitely occurs in the Kinburn Peninsula (V. Kyrychenko and it is considered the most common rodent species in the area of the Black Sea Reserve (Z. Selynina, personal report) and Zaporizhia Oblast with an increasing abundance to the south (Ye. Chebotok, personal report)<sup>5</sup>. On the other hand, *S. uralensis* has not been reported from the Askanian steppe (Polischuk 2009, personal report), wherefrom *S. falzfeini* (= *S. witherbyi*) was described (Mezhzherin & Zagorodniuk 1989). There is a similar situation in the lowland part of Crimea: *S. uralensis* is distributed here only in the mountains and along river valleys that flow towards the Azov Sea (Evstafiev 2015; see Fig. 3). Despite the similarity by metric characters, these species differ by colouration: *S. uralensis* has no chest spot and the white colouration of the belly extends onto the sides of thighs (Fig. 4). Of course, this species differs from *S. witherbyi* by several cranial characters (Zagorodniuk *et al.* 1997; see: Fig. 2).

● b3.1. Kinburn, Mykolaiv Oblast, numerous specimens, including osteological materials (V. Kyrychenko, personal report); ● b3.2. Hola Prystan, Kherson Oblast, 17 November 1936, n = 1 (ss+sk), leg. V. Velykaniv (Shevchenko & Zolotukhina 2002); ● b3.3. Fedorivske forestry, Donetsk Oblast, abundant species (Melnychenko & Pylypenko 2006); ● b3.4. Kamiani Mohyly Reserve, Nazarivka, Nikolske Raion, Donetsk Oblast, n = 7, only *S. uralensis* (Zagorodniuk 2007) [earlier *S. sylvaticus* was reported from here and no *S. uralensis* (Kondratenko *et al.* 2006)]; ● b3.5. Khomutovsky Steppe, Samsonove, Boikivske Raion, Donetsk Oblast, from pellets of *Asio otus*, n = 26 (along with 48 specimens of *S. witherbyi* and 17 specimens of *S. sylvaticus*) (Zaika 2009).

<sup>4</sup> In the catalogue of NMNH, there are records of 2 specimens of *S. uralensis* from Poliske, Kyiv Oblast (‘Khabne’), ss+sk, 14–15 August 1925, leg. I. Pidoplichko. One specimen has been found, but only the study-skin without skull. According to measurement on the label (L 87; Ca 72; PI 22.8; Au 16.6), the specimen is closer to *S. sylvaticus*, but revised measurements (PI 19.1; Au 11.9) correspond to *S. uralensis*. This specimen is not considered here in the description of the species’ geographic range.

<sup>5</sup> Both of the latter reports should have been supported by osteological characters. The author has seen only *S. falzfeini* in samples from the Black Sea Biosphere Reserve.

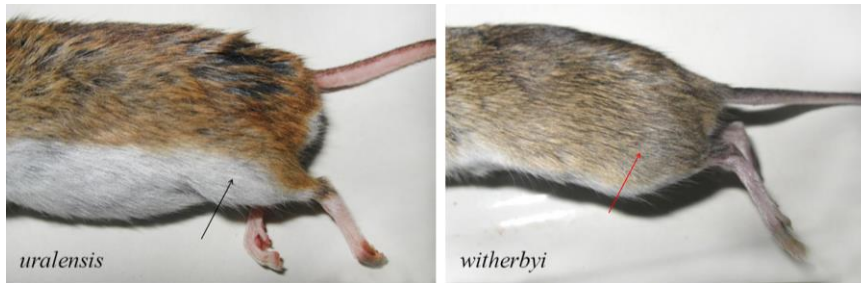


Fig. 4. Details of coat coloration of *S. uralensis* and *S. witherbyi* from the region of Taurida steppes (samples from the Crimea). Courtesy of I. Evstafiev and M. Tovpynets.

Рис. 4. Особливості забарвлення хутра мишаків уральського і степового з регіону таврійських степів (зразки з Криму). Фото І. Євстаф'єва та М. Товпинця, з дозволу його авторів.

## Discussion

### *Uneven spatial distribution*

The data show that the geographic range of *Sylvaemus uralensis* in Eastern Europe, i.e. at the western border of the species' distribution, is highly fragmented and cannot be described using convex polygons. It is due to a number of reasons, of which two the author considers as key factors:

- 1) Heterogeneity of natural zones and the presence of five biomes (semi-desert, steppe, forest steppe, temperate forest, and taiga) and three mountain systems (the Carpathians, the Crimean Mountains, and the Caucasus), where the distribution of the species has its own specifics. For example, the species is absent in the Carpathians, Roztocze, Podillia, Polissia, and the Ukrainian Steppe, but it is common in the forest steppe east of the Dnipro, in the Crimean Mountains, in Ciscaucasia, and further to the east;
- 2) Complex biogeographic history of the species (actually, superspecies), in particular former range fragmentations in the post-glacial zone of Eastern Europe, where the Dnipro Rift area was the main axis (after Zagorodniuk 2005b). However, it cannot be excluded that differentiation took place beyond this area with the formation of a Balkan-Pannonian centre through the Bosphorus, and not due to range fragmentation.

Such picture is in contrast with the former attempts to classify and consider allospecies the different geographic races of *S. uralensis* (s. l.). Differences between the western and eastern groups (*S. u. microps* versus *S. u. mosquensis*, *bessleri*, *uralensis* s. str., *ciscaucasicus*, etc.) seem to be more significant than differences among species of the eastern group (of course, Asian forms such as *cherga* are not discussed here). Different versions of discrimination of allospecies within the eastern group are considered above (with references to Orlov *et al.* 1996; Chelomina *et al.* 2007).

The current distribution of the species in the Northern Black Sea Region indicates the absence of a clear hiatus in the distribution of eastern and western forms. However, distribution patterns of other rodent species allow seeing certain similarities. In particular, the geographic range of the group 'microps' generally corresponds to the distribution of species of the Balkan-Pannonian steppe core, such as the European ground squirrel (*Spermophilus citellus*), 'western' mole rats (*Spalax leucodon*, *S. graecus*), and several other forms.

Data on the distribution of specimens of *S. uralensis* and *S. sylvaticus* (s. str.), represented in the collection of NMNH, by different regions is generalised in Table 2. All specimens have been revised during the catalogisation of the collections of NMNH (Shevchenko & Zolotukhina 2002). Specimens of *S. uralensis* clearly dominate in numbers (511 specimens against 315 specimens of *S. sylvaticus*), although by geography (number of oblasts and raions) *S. uralensis* is less represented compared to the European wood mouse (49 versus 80 record localities).

Collections confirm the restricted distribution and low relative abundance of *S. uralensis* in Polissia and Podillia and the formation of a disjunction between the ranges of the eastern *S. uralensis* (s. str.) and western *S. u. microps*.

Table 2. Distribution of records of *S. uralensis* and *S. sylvaticus* (s. str.) by oblasts of Ukraine and in Moldova (data from the collection catalogue of NMNH NAS of Ukraine)

Таблиця 2. Розподіл знахідок *S. uralensis* та *S. sylvaticus* (s. str.) за областями України та в Молдові (дані з каталогу колекції ННІМ НАН України)\*

Oblasts west of the Dnipro	<i>uralensis</i>	<i>sylvaticus</i>	Oblasts east of the Dnipro	<i>uralensis</i>	<i>sylvaticus</i>
Rivne Oblast	0/0	4/2	Chernihiv Oblast	0/0	17/7
Zhytomyr Oblast	0/0	20/2	Sumy Oblast	1/1	1/1
Khmelnyskyi Oblast	0/0	8/4	Poltava Oblast	73/4	15/4
Ivano-Frankivsk Oblast	0/0	6/3	Kharkiv Oblast	74/12	32/4
Vinnysia Oblast	0/0	2/2	Lunahsk Oblast	111/4	5/2
Kirovohrad Oblast	2/2	1/1	Donetsk Oblast	131/4	14/2
Kyiv Oblast	3/2	49/5	Dnipropetrovsk Oblast	0/0	36/3
Cherkasy Oblast	0/0	2/2	Zaporizhia Oblast	4/2	9/3
Mykolaiv Oblast	6/3	35/5	Crimea**	44/5	0/0
Odesa Oblast	30/7	25/6	Moldova	28/3	14/4
Zakarpattia Oblast	4/1	20/5	Total	511/49	315/80

\* There are no specimens of this group from Volyn, Ternopil, and Chernivtsi oblasts; in the sample from Kherson Oblast, the group of small wood mice is represented by 54 specimens of *S. witherbyi* collected in three raions (+ 6 dubious *S. sylvaticus*); \*\* The Crimean sample also contains 8 specimens of *S. witherbyi* from one raion.

### *Interactions with geographic ranges of adjacent species*

The distribution of *Sylvaemus uralensis* (s. l.) in respect to the two other ‘small’ *Sylvaemus* species is, in general, marginally sympatric, i.e. only range edges overlap. In fact, probably this is what determines the significant gap in the species range of *S. uralensis* (s. l.) in the Volyn-Podillia region extending southeast to the Black Sea.

The eastern boundaries of distribution of *S. sylvaticus* have a general configuration that is similar to the abovementioned gap, although they are located more eastward, which can be considered a secondary phenomenon as a result of the species’ dispersal to the east. In the north, including the Baltics, the two species are strictly allopatric, whereas in the Valdai there is a narrow zone of sympatry. However, their geographic ranges fully overlap in south-east Belarus and in Ukraine east of the Dnipro River. In southern regions of Ukraine east of the Dnipro, including Taurida and the Northern Azov Region, the geographic ranges of these species have a more complex configuration due to the presence of a third wood mouse species — *S. witherbyi* (also known as *S. falzfeini* and *S. arianus*). This third species is strictly parapatric with *S. sylvaticus* and partly with *S. uralensis*. In the Askanian and Crimean steppes, *S. witherbyi* is the only representative of the genus.

On the contrary, *S. uralensis* is common in the Crimean Mountains and partly in the foothills (particularly along river valleys that belong to the drainage basin of the Azov Sea). In the mountains, it co-occurs with *S. tauricus* and both species in Crimea are strictly associated with forested habitats. This feature of Crimean *S. uralensis* notably distinguishes them from continental forms, especially from the group ‘*microps.*’ Distribution patterns of wood mice in the Northern Black Sea and Northern Azov regions (including the area of the Black Sea Biosphere Reserve) should be a subject of separate detailed studies.

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