Malacologica Bohemoslovaca (2022), 21: 30–48
ISSN 1336-6939

Comparative analysis of phenotypic variability of introduced land snail *Cepaea nemoralis* (Gastropoda: Helicidae) in two large Eastern European cities

Nina Gural-Sverlova[1] & Oksana Kruglova[2]

[1]*State Museum of Natural History, National Academy of Sciences of Ukraine, Teatralna 18, UA-79008 Lviv, Ukraine, e-mail: sverlova@pip-mollusca.org (corresponding author), https://orcid.org/0000-0002-3892-5338*
[2]*Belarusian State University, Nezavisimosti Avenue 4, BY-220030 Minsk, Republic of Belarus, e-mail: kruglovaoksana@mail.ru, https://orcid.org/0000-0003-0049-412X*

Gural-Sverlova N. & Kruglova O., 2022: Comparative analysis of phenotypic variability of introduced land snail *Cepaea nemoralis* (Gastropoda: Helicidae) in two large Eastern European cities. – Malacologica Bohemoslovaca, 21: 30–48. https://doi.org/10.5817/MaB2022-21-30
Publication date: 14. 7. 2022.

Variation in the shell colour and banding polymorphism of *Cepaea nemoralis* was recorded in 20 sites in Minsk, Belarus (a total of 3965 adults collected in 2014–2021). This variation was compared with that in 16 sites from Lviv, Western Ukraine (total 3235 adults collected in 2019–2021). Unlike in Lviv, a remarkable spatial differentiation of the phenotypic composition was found in Minsk. The samples collected in the north-eastern part of Minsk were characterized by a greater degree of phenotypic diversity and by higher frequencies of unbanded and brown shells. Samples from the southern and eastern parts of the city were generally lighter and characterised by high frequencies of shells with a single central band (mid-banded). Differences between the two parts of Minsk were greater than those between Minsk and Lviv. This may be related to the history of colonization of Minsk by *C. nemoralis*. The Lviv samples were, on average, darker, they contained less frequently mid-banded shells and more frequently unbanded shells, especially pink unbanded ones. The F_{st} values characterizing the level of phenotypic variability and calculated for Minsk and Lviv are quite high and comparable with those for other urban areas recently colonized by *C. nemoralis*.

Key words: *Cepaea nemoralis*, brown-lipped snail, polymorphism, Belarus, Western Ukraine

Introduction

The land snail *Cepaea nemoralis* (Linnaeus, 1758) is the subject of many studies on its exuberant shell colour and banding polymorphism (Cameron & Cook 2012, Cook 2017, Jones et al. 1977, Lamotte 1951, Ożgo et al. 2019, Schilder & Schilder 1957), both in the natural range of this species and outside it. In particular, some papers have been published on the variability of shell colouration of this species in certain areas of Central and Northern Europe, where this species was introduced at different times – from the 19th century to last decades (Cameron et al. 2009, 2014, Cameron & von Proschwitz 2020, Honěk 1995, Ożgo 2005, Pokryszko et al. 2012).
Since the end of the 20th and the beginning of the 21st century, a rapid spread of *C. nemoralis* in the settlements of Eastern Europe has also been recorded, caused by anthropochory and often associated with the activities of garden centres (Egorov 2018, Gural-Sverlova et al. 2021a). This led to the appearance of a number of publications on the polymorphism of *C. nemoralis* in Western Ukraine, Belarus, and the European part of Russia (Gural-Sverlova et al. 2020, 2021b, Gural-Sverlova & Egorov 2021, Kolesnik & Kruglova 2016, Kruglova 2018, Ostrovsky & Prokofieva 2017, etc.), for a more complete list see Gural-Sverlova et al. (2021a).
Although the first attempt to introduce *C. nemoralis* into Western Ukraine (to Lviv) was made in 1892 (Łomnicki 1899), in the 1990s this species with a low abundance and reduced phenotypic composition (Sverlova 2002) was found only in one of the city parks, and subsequently almost completely died out there. In 2019–2021, relatively young (not older than 10–20 years) populations of this species were found in different parts of the city, associated with repeated introductions of *C. nemoralis* to Lviv and characterized by a greater phenotypic diversity (Gural-Sverlova et al. 2020, 2021a, 2021b). In recent years, there have also been more and more reports of reliable findings of *C. nemoralis* in other settlements of Ukraine (Balashov & Markova 2021, Gural-Sverlova et al. 2020, 2021b, iNaturalist 2022, UkrBIN 2022).
In Belarus, *C. nemoralis* was first recorded for Brest at the turn of the 20th and 21st centuries (Ivankova & Zemoglyadchuk 2001), and is now known from all six administrative regions of the country (Gural-Sverlova et al. 2021a). Unfortunately, the time of the first discovery of *C. nemoralis* in Minsk is not documented in the literature. However, starting from 2014, the study of the

shell colour and banding polymorphism of this species began here (Kolesnik & Kruglova 2016, Kruglova 2018, Kruglova & Guminskaya 2019, Kruglova et al. 2018). The data collected during this period call for a generalizing analysis.

The recently published paper on the variability of the phenotypic composition of *C. nemoralis* within the city of Lviv (Gural-Sverlova et al. 2021b) provides also a unique opportunity to compare the patterns of this variability in two large Eastern European cities remote from each other, in which intensive colonization by this species has apparently begun approximately in the same time period (see above). We also wanted to evaluate the spatial variation of the shell colour and banding polymorphism in Minsk itself.

Material

Samples of *C. nemoralis* were collected at 20 sites in Minsk in 2014–2021. Locations of the studied sites shown in Fig. 1, and their details are given in Appendix. In total, the shell colouration in 3965 adult specimens was analyzed (Tab. 1).

For comparison, similar data for 16 sites in Lviv, Western Ukraine, obtained in 2019–2021 were used. Detailed descriptions of 14 sites designated in this article as L1–L3 and L5–L15 as well as their schematic location are given in a previous publication (Gural-Sverlova et al. 2021b). The site L4, from which only seven adults of *C. nemoralis* were collected in 2020, and which underwent a strong transformation in 2021, was excluded. Descriptions of two additional sites studied in 2021 (L16 and L17) are given in Appendix. In total, the shell colouration in 3235 adults of *C. nemoralis* was analyzed (Tab. 2).

Part of the collected samples from Minsk are stored at the Department of Zoology of the Faculty of Biology of the Belarusian State University, and part of the samples from Lviv are stored in the malacological collection of the State Museum of Natural History in Lviv. In other cases, the snails were released back to their collection sites.

Methods

Phenotypes were recorded following Clarke (1960). Bands were designated by Arabic numerals from 1 to 5, counting them from the apex to the base of the shell. The absence of band(s) was indicated as "0" in place of the corresponding numeral(s), the fusion of adjacent bands by round brackets, weak bands by square brackets. The bands were considered to be fused if they were fully or partially merged for no less than a quarter of a whorl before the aperture. The ground colour of the shell was designated as "Y" (yellow, this group also included less common white shells), "P" (pink) or "B" (brown).

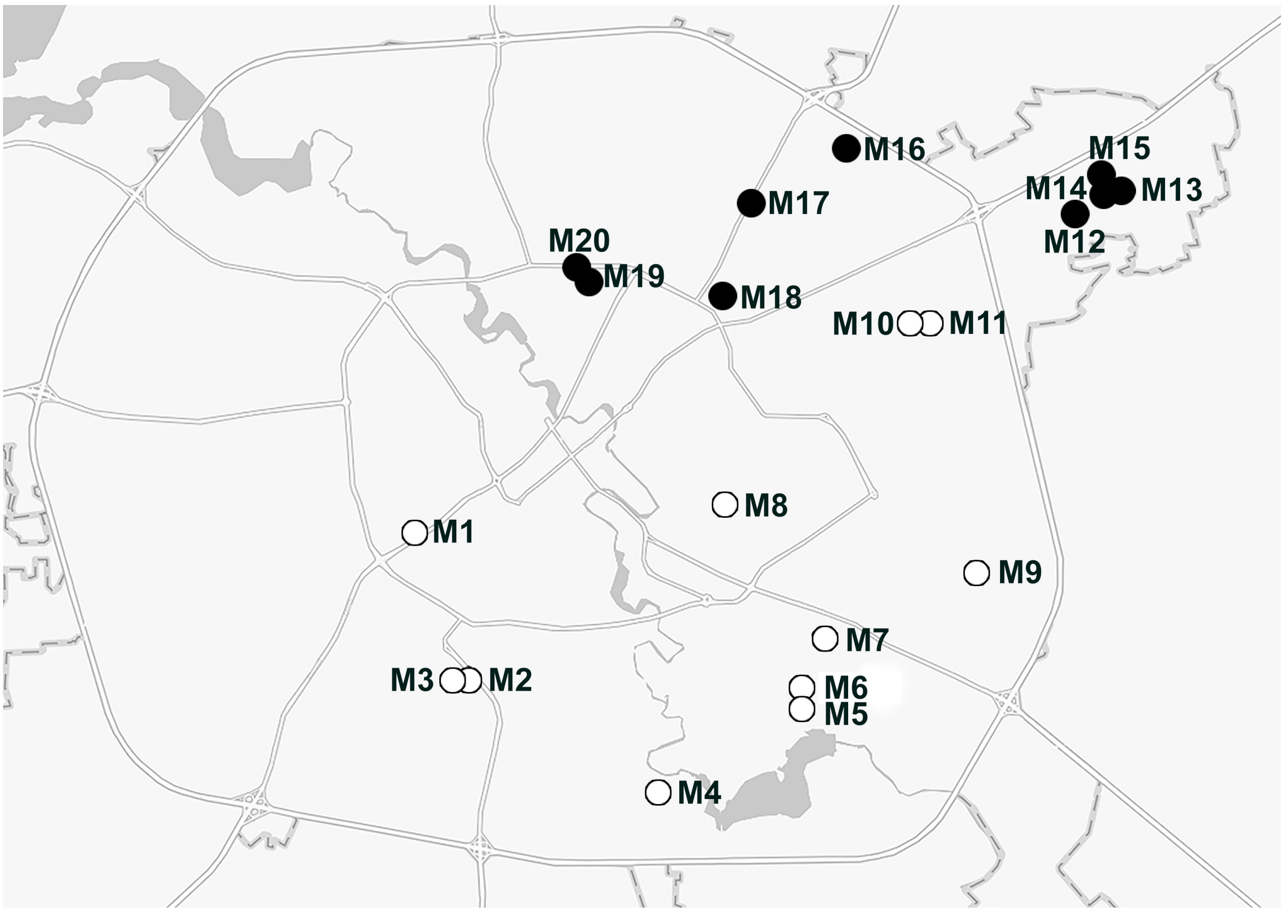

Fig. 1. Location of the studied sites in Minsk. The white circles show the sites designated as a group Minsk-1, the black circles show the sites designated as Minsk-2.

In the subsequent analysis of the phenotypic composition, individual phenotypes distinguished by the shell banding were combined into four groups: unbanded, mid-banded, three-banded, and five-banded (Tab. 1–2). Weak, blurred bands, indicated in Tabs 1 and 2 with square brackets, were not taken into account, since they can appear on shells as modifications. Since in *C. nemoralis* the absence/presence of bands on the shell and its ground colour are linked (MURRAY 1975), when comparing the phenotypic composition at the studied sites, these groups were considered in combination with the shell ground colour, similar to the previous publication (GURAL-SVERLOVA et al. 2021b).

For the dendrogram and multidimensional scaling, the phenotypic similarity of *C. nemoralis* from the studied sites in Minsk was calculated:

$$r=\sqrt{p_1 q_1}+\sqrt{p_2 q_2}+\ldots+\sqrt{p_m q_m} \;;$$

where *m* is the total number of phenotype groups (see above) recorded at the two compared sites; $p_1, p_2 \ldots p_m$ are the frequencies of phenotype groups at one site; $q_1, q_2 \ldots q_m$ – frequencies of the same groups at another site.

To assess the phenotypic diversity in the compared areas, in addition to the number of phenotype groups (*m*) in the analyzed samples, two indices proposed by ZHIVOTOVSKY (1982) were used: the index of intrapopulation diversity (μ) and the rate of rare morphs (*h*):

$$\mu=\left(\sqrt{p_1}+\sqrt{p_2}+\ldots+\sqrt{p_m}\right)^2 \;;$$

$$h=1-\frac{\mu}{m} \;;$$

the symbols are similar to the previous formula.

According to ZHIVOTOVSKY (1982), the index μ evaluates the degree of phenotypic diversity. Its values vary from 1 in monomorphic populations (samples) to m in the case of equal frequencies of all phenotypes (in our case, groups of phenotypes). The index *h* evaluates the structure of diversity. Its values decrease to zero in monomorphic populations and in the case of equal frequencies of all phenotypes (phenotype groups) and increase with an increase in the heterogeneity of their quantitative ratio.

To assess the spatial variability of the phenotypic composition of *C. nemoralis*, we used the inbreeding coefficient F_{st} calculated from the frequencies of the phenotypic manifestation of some inherited traits (CAMERON et al. 2009) or from the frequencies of the corresponding alleles (GURAL-SVERLOVA et al. 2021b). Allele frequencies were calculated conditionally, using the Hardy-Weinberg formula for an ideal panmictic population.

Generalized data from the monograph by SCHILDER & SCHILDER (1957, table 13) were used to assess the typicality or specificity of the ratio of frequencies of different phenotypes with fused bands, as well as the frequencies of fusion of different band pairs in introduced Eastern European populations of *C. nemoralis*. These data came from various countries, but mainly from Germany, which is part of the natural range of *C. nemoralis*. Therefore, they can be used as a control when studying introduced populations of this species (SVERLOVA 2004).

All data about the phenotypic composition of *C. nemoralis* in Minsk were collected under the guidance of the second author. The first author took part in their statistical processing and interpretation.

Results

During the primary (visual) analysis of the phenotypic composition of *C. nemoralis* from Minsk, it was found that the frequencies of unbanded (Fig. 2A) and yellow unbanded (Fig. 2B) shells differ greatly in two groups of sites located in the southern and eastern (hereinafter referred to as Minsk-1, see Fig. 1) and northeastern (Minsk-2) parts of the city. These patterns did not have the character of clinal variability (Fig. 2). Although the northernmost sites of the first group (M10 and M11) are located quite close to the sites of the second group, they are separated from them by one of two major highways – Independence Avenue or the Minsk Ring Road.

Subsequent statistical analysis showed that the aforementioned groups of sites differ significantly in frequencies of almost all phenotype groups (Tab. 3). The only exceptions were three-banded shells with yellow and pink ground colour, which were relatively rare or absent at most of the studied sites, regardless of their spatial location. In general, the differences revealed between different parts of Minsk were more significant than those between the Minsk and Lviv samples of *C. nemoralis* (Tab. 3).

The sites M1–M11 (Minsk-1) were characterized by low frequencies of unbanded shells (Tab. 3), up to their complete absence in five samples (Tab. 4). The mean frequency of unbanded shells for this group of sites was almost 22 times lower than that for sites M12–M20 (Minsk-2). Moreover, the fluctuations of frequencies of unbanded and yellow unbanded shells did not even overlap in the two groups of sites, resulting in null values of the Mann-Whitney test. And the minimum frequency of yellow unbanded shells for Minsk-2 was four times higher than their maximum frequency for Minsk-1.

The decrease in the frequency of unbanded shells in the southern and eastern parts of Minsk was accompanied by a more frequent occurrence of shells with one central band (both among all specimens and among snails with banded shells). A large proportion of such phenotypes led to a statistically significant increase in the total frequency of the lightest variants of shell colouration in *C. nemoralis* (Tab. 3), which include yellow unbanded, yellow mid-banded, pink unbanded, and pink mid-banded.

For this area, a lower level of phenotypic diversity was also noted, which is especially noticeable when comparing the values of μ (Tab. 3). Higher values of the rate of rare morphs (h) indicate a greater heterogeneity in the quantitative ratio of phenotype groups, which increases the risk of accidental disappearance of some hereditary traits (Tab. 4).

Differences in the phenotypic composition of the samples collected in different parts of Minsk are also confirmed by the dendrogram of phenotypic similarity (Fig. 3), based on a comparison of the frequencies of 10 groups of phenotypes recorded in the city (Tab. 1). Only two sites (M15 and M17) showed greater similarity with sites from the

Fig. 2. Frequencies of yellow (A) and yellow unbanded (B) shells in Minsk.

other group. This is due to the frequent occurrence at these sites of both yellow unbanded (which is typical for Minsk-2) and yellow mid-banded shells (which is typical for Minsk-1). At both sites, the proportion of the latter was 41–47%, which is 2.5–2.9 times higher than their mean frequency in the northeast of Minsk (Tab. 3). The samples from the area designated as Minsk-1 were divided into two groups, one of which was characterized by a clearly pronounced predominance of yellow mid-banded shells (usually more than half of the sample), while the other group was characterized by an equally distinct predominance of pink mid-banded shells.

Multidimensional scaling (Fig. 4) also showed that all sites of the first group and most of the sites of the second group diverge well in the first dimension, while the above-mentioned sites M15 and M17 occupy an intermediate position. At the same time, both groups demonstrate a significant scatter along the second dimension, which is associated with a large variation in the ratio of yellow and pink shells.

Statistically significant differences between the studied Minsk and Lviv samples of *C. nemoralis* were revealed for shells with one central band (both yellow and pink), pink unbanded and pink five-banded, as well as for the total frequency of the four lightest variants of shell colouration, see above (Tab. 3). In particular, the mean frequency of the phenotype P00000 in Lviv was more than seven times higher than that in Minsk. There were no significant differences in the average level of phenotypic diversity, although the quantitative ratio of phenotype groups was more heterogeneous in Minsk, as indicated by higher values of *h*.

The calculated values of the inbreeding coefficient F_{st} are given in Tab. 5, and their comparison with some other European cities is shown in Tab. 6. For all the considered inherited traits, they were higher when used in the calculations the frequencies of their phenotypic manifestation, rather than the alleles of the corresponding genes. The smallest contribution to the phenotypic and genetic variability of *C. nemoralis* in all compared areas is made by

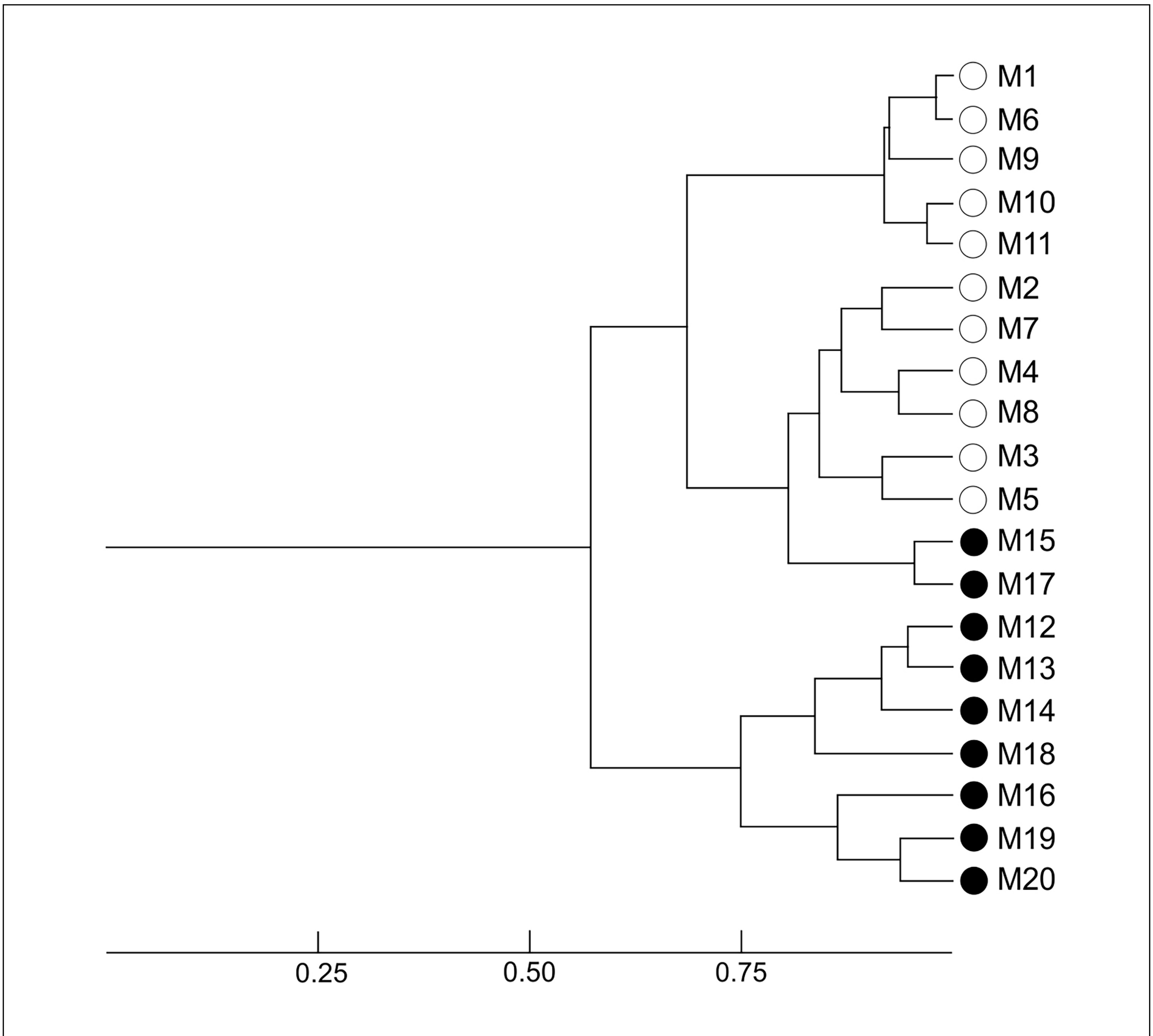

Fig. 3. The similarity of the phenotypic composition of *C. nemoralis* at the studied sites in Minsk. The designations of the sites are similar to Figure 1.

the brown colour of the shell (a rare trait) and the complete absence of bands on it (a common trait in Lviv and a less common trait in Minsk). And the greatest contribution to the mentioned variability is made by such a trait as the absence of two upper bands in banded shells (Tab. 5).

The samples from Minsk-2 were more stable in the ratio of yellow and pink shells and in the occurrence of three-banded shells among the multi-banded ones compared to Minsk-1, as evidenced by lower F_{st} values for the corresponding traits (Tab. 5). At the same time, they were more variable in the frequencies of unbanded and mid-banded shells. The samples from Minsk and Lviv showed, in general, a similar level of variability (Tab. 5), although the former were more stable in the occurrence of brown and three-banded shells, i.e., two relatively rare traits (Tab. 3).

If we compare the occurrence of different variants of band fusion in five-banded shells, in Minsk phenotypes with fusion of the 2nd and 3rd bands are less common and those with fusion of the 3rd and 4th bands are more common. This pattern is observed when compared with both the generalized data from the entire range of *C. nemoralis* and with other settlements of Eastern Europe (Tab. 7). The record of a rare phenotype 12(345) at some sites of Minsk, which has not yet been found in Western Ukraine and in the Moscow Region of Russia as well as is very rare in the natural range of *C. nemoralis*, is especially indicative. In Minsk, this variant of band fusion was noted in 22% of five-banded shells with fused bands (Tab. 7).

Discussion

The pattern of the spatial variability of the phenotypic composition of *C. nemoralis* in Minsk is very different from that previously described for another large Eastern European city, Lviv (Gural-Sverlova et al. 2021b). In Lviv, changes in the phenotypic composition did not depend on the spatial location of the studied sites. Therefore, the sites less distant from each other often showed less phenotypic similarity than more distant ones (Gural-Sverlova et al. 2021b, Fig. 2). This was in good agreement with the isolation of urban areas inhabited by *C. nemoralis*, the possible influence of stochastic population genetic factors, primarily the founder effect and genetic drift at the initial stages of colony formation, as well as with the possible different origin of these colonies.

It is known that garden centres importing seedlings of garden and ornamental plants from abroad play an important role in the present spreading of *C. nemoralis* in the settlements of Eastern Europe (Gural-Sverlova et al. 2021a). Currently, snails of this species have been found near different garden centres located in Lviv itself (Gural-Sverlova et al. 2021b) and in its immediate vicinities. Individuals of the related species *C. hortensis* with the variants

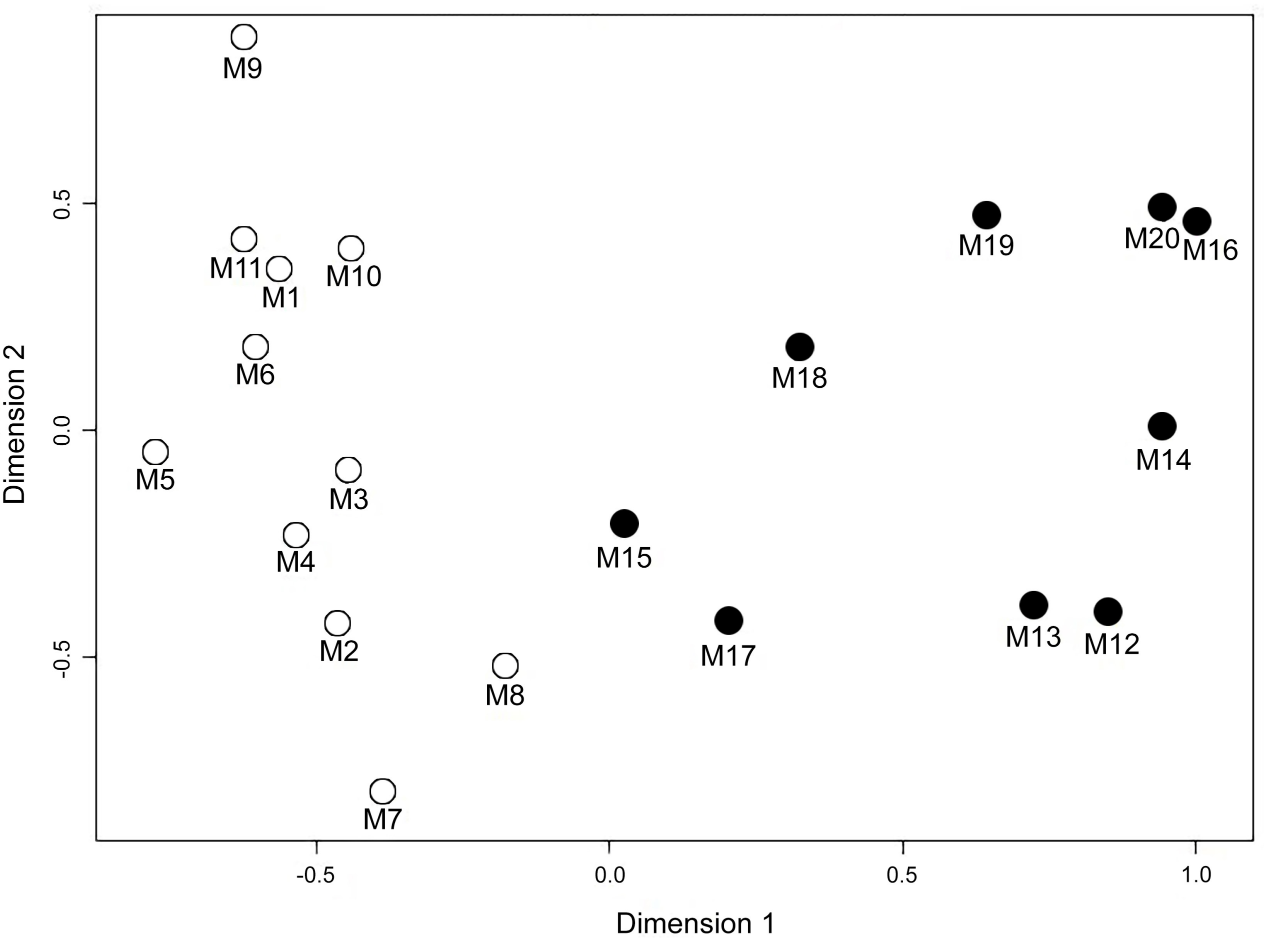

Fig. 4. The results of multidimensional scaling based on the phenotypic similarity of *C. nemoralis* in Minsk.

of shell colouration that was previously absent in Lviv and in general in Western Ukraine (Gural-Sverlova & Gural 2021a) are often found together with them, which indicates relatively recent joint introduction of both species (Gural-Sverlova et al. 2020, 2021b, Gural--Sverlova & Gural 2021a). It is significant that the snails with pink shells, which had only a dark lip (a rare hereditary trait in *C. hortensis*), were recorded near one of the largest garden centres (Club of Plants) and at several sites in Lviv. And near another large garden centre (Galsad) and at two sites in Lviv and its immediate vicinity (village of Solonka), individuals of *C. hortensis* with pink shells and a light lip were found. This can be considered a clear confirmation that the colonization of Lviv by both species has a different origin.

In contrast to Lviv, a distinct spatial differentiation of the phenotypic composition of *C. nemoralis* was found in Minsk. The samples located in the north-east of the city (Minsk-2) were characterized not only by the higher occurrence of brown and unbanded shells (two traits that are relatively rare in Minsk), but also by a higher level of phenotypic diversity. In addition, the shell colouration in them was, on average, darker than in the samples from the southern and eastern parts of the city (Tab. 3). Apparently, this could be only partially related to the nature of the habitats inhabited by snails. Only four out of nine sites were located in park or forest park biotopes; in other cases, snails were collected near buildings, among ornamental or fruit plantations. In Minsk-1 snails were often collected among similar ornamental and fruit plantations, but in household plots of private houses or near them, less often at mostly open sites along streets, wastelands. Differences in the degree of phenotypic diversity are also not related to the size of the samples, the mean size of which was 196.6 for Minsk-1 and 200.2 for Minsk-2.

Such a spatial differentiation can also hardly be the result of a different origin of snails. In particular, the phenotype 12(345) mentioned in the Results and rare for *C. nemoralis* was found at separate sites both in the northeast (M13–M15) and in the southwest (M1) of the city (Tab. 1). The ratio of different phenotypes among shells with fused bands is rarely taken into account when analyzing the phenotypic composition of *Cepaea*. However, our long-term studies of *C. hortensis* in Western Ukraine have shown that it can be quite informative and even indicate the beginnings of genetic differentiation in urban populations. Even greater temporal stability, along with possible spatial variability, is demonstrated by the ratio of the frequencies of fusion of different band pairs among shells with fused bands (Gural-Sverlova & Gural 2018, Fig. 2). Compared to other data in Tab. 7, phenotypes with the fusion of the 2nd and 3rd bands were relatively less common in both parts of Minsk. And only here the fusion frequency of the 3rd and 4th bands was almost the same (Minsk-1) or noticeably exceeded (Minsk-2) that for the 2nd and 3rd bands. It is quite possible that this also indicates the common origin of snails in different parts of Minsk.

In different parts of Minsk, despite the different occurrence of unbanded shells, their proportion among yellow shells exceeds, on average, that among pink ones (Fig. 5). In such distant areas of Eastern Europe as Lviv in Western Ukraine and the Moscow Region of Russia, a clearly pronounced opposite trend is observed (Fig. 5), often leading to a high frequency of pink unbanded shells in the samples, and sometimes to a complete absence of pink banded and yellow unbanded shells at some sites (Gural-Sverlova & Egorov 2021, Gural-Sverlova & Gural 2021b, Gural-Sverlova et al. 2020). Perhaps this can also indirectly confirm the common origin of individuals living at all or at least at most of the studied sites in Minsk.

In Poland, a shift in linkage disequilibrium has been found between shell colour and the presence or absence of bands in *C. nemoralis* from pink unbanded/yellow banded in the north to yellow unbanded/pink banded in the south, the latter being characterized as unusual. It has been suggested that this is due to the different origins of the Polish populations of this species (Ożgo et al. 2019).

If we accept the assumption of the common origin of *C. nemoralis* in Minsk, the greater phenotypic diversity at sites located in the northeast of the city can be either associated with a large number of founding individuals (including not only adults and juveniles, but also their eggs on the roots of seedlings), or because this area was colonized first, and then served as a source for the accidental spreading of snails by humans to other parts of the city. A similar pattern was already observed in Bohorodcha-

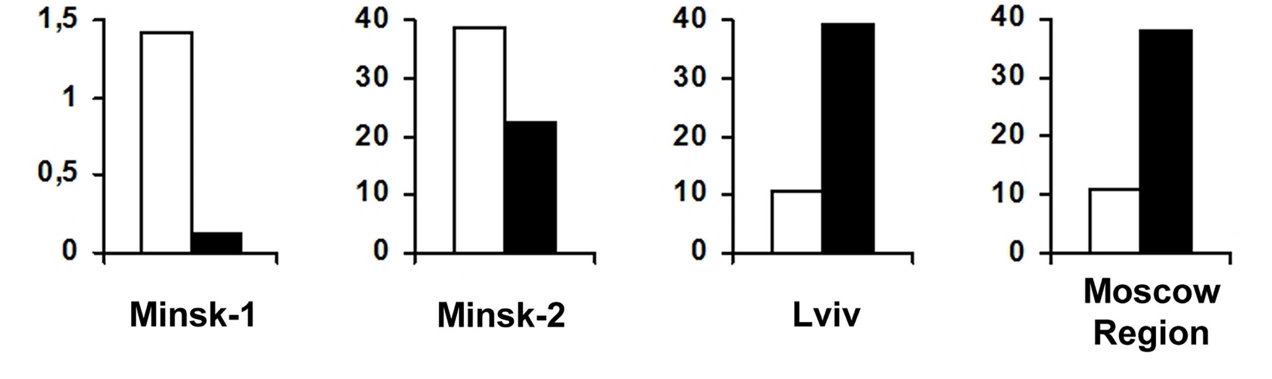

Fig. 5. Mean percentages of unbanded shells among yellow (white columns) and pink (black columns) in samples. The graph for the Moscow Region was made according to published data (Gural-Sverlova & Gural 2021b, Tab. 1).

ny (Western Ukraine) and Nakhabino (Moscow Region of Russia), where despite the rather similar character of urban biotopes inhabited by snails, on one side of the street there were sites with greater phenotypic richness of *C. nemoralis*. And on the other side of the street, not only some phenotype groups "dropped out", but also one of the light variants of shell colouration (pink unbanded) more or less clearly predominated (Gural-Sverlova & Egorov 2021, Gural-Sverlova et al. 2020).

We have previously already referred to an interesting experiment carried out in the Czech Republic (Honěk & Martínková 2003). A few years after the colonization of sites by snails with different phenotypes from the same sample, they generally increased in the proportion of yellow mid-banded shells, the lightest phenotype present in the initial sample (Gural-Sverlova & Gural 2021b).

Recently, a number of publications have appeared trying to relate the level of phenotypic variability in introduced and/or urban populations of *Cepaea* with the time of their colonization of the corresponding areas (Cameron et al. 2009, 2014, Cameron & von Proschwitz 2020, Gheoca et al. 2019). It has been suggested that a high level of variability, assessed by the inbreeding coefficient F_{st}, is characteristic of recently populated areas, regardless of whether they are within the natural ranges of species or outside them (Cameron et al. 2009). However, in addition to the time of colonization of certain areas, F_{st} values can be influenced by other factors (Cameron & von Proschwitz 2020, Gural-Sverlova & Egorov 2021), in particular, whether these areas were colonized by individuals of one or different origin.

The F_{st} values calculated for Minsk and Lviv (Tab. 5) are quite high and comparable with those for other urban areas recently colonized by *C. nemoralis* (Tab. 6). However, they are noticeably lower for unbanded shells in different parts of Minsk, especially for Minsk-1, and do not exceed F_{st} for Wroclaw, Poland (Cameron et al. 2009), colonized by this species more than a century ago.

Conclusions

Similar to Lviv, in Minsk there is quite a high level of spatial variability of phenotypic composition in *C. nemoralis*, which, in general, is considered characteristic of relatively recently colonized areas. However, these cities differ in the pattern of the spatial variability of the phenotypic composition of the model species. While in Lviv the frequencies of some inherited traits as well as the frequencies of phenotype groups vary regardless of the spatial location of the studied sites, in Minsk there is a clearly pronounced phenotypic differentiation between two groups of samples collected in the southern and eastern (Minsk-1) and north-eastern (Minsk-2) parts of the city. It is possible that this is related to the history of the colonization of Minsk by *C. nemoralis*.

The described patterns of phenotypic variability of *C. nemoralis* in the urbanized habitats of Minsk can be used in the future to monitor possible temporal changes in the phenotypic composition of this species (at studied sites, in groups of sites or for the city as a whole), which can be associated, in particular, with adaptation of snails to the climatic conditions of Belarus.

Acknowledgments

We sincerely thank all the persons listed in Appendix for their help in collecting samples of *C. nemoralis* from Minsk, as well as the staff of the State Museum of Natural History in Lviv: Roman Gural for technical assistance in preparing the manuscript, Anatoly Mamchur for information on the history of landscaping at the site L16. Special thanks go to Robert A. D. Cameron (University of Sheffield and Natural History Museum in London) for valuable comments that helped improve the manuscript.

References

Balashov I. & Markova A., 2021: The first records of an invasive land snail *Cepaea nemoralis* (Stylommatophora: Helicidae) in Central and Southern Ukraine. – Ruthenica, Russian Malacological Journal, 31(3): 121–125. https://doi.org/10.35885/ruthenica.2021.31(3).2

Cameron R. A. D. & Cook L. M., 2012: Habitat and the shell polymorphism of *Cepaea nemoralis* (L.): interrogating the Evolution Megalab database. – Journal of Molluscan Studies, 78: 179–184. https://doi.org/10.1093/mollus/eyr052

Cameron R. A. D., Cox R. J., von Proschwitz T. & Horsák M., 2014: *Cepaea nemoralis* (L.) in Göteborg, S. W. Sweden: variation in a recent urban invader. – Folia Malacologica, 22(3): 169–182. https://doi.org/10.12657/folmal.022.016

Cameron R. A. D., Pokryszko B. M. & Horsák M., 2009: Contrasting patterns of variation in urban populations of *Cepaea* (Gastropoda: Pulmonata): a tale of two cities. – Biological Journal of the Linnean Society, 97: 27–39. https://doi.org/10.1111/j.1095-8312.2008.01187.x

Cameron R. A. D. & von Proschwitz T., 2020: *Cepaea nemoralis* (L.) on Öland, Sweden; recent invasion and unexpected variation. – Folia Malacologica, 28(4): 303–310. https://doi.org/10.12657/folmal.028.026

Clarke B. C., 1960: Divergent effects of natural selection on two closely-related polymorphic snails. – Heredity, 14(3–4): 423–443. https://doi.org/10.1038/hdy.1960.39

Cook L. M., 2017: Reflections on molluscan shell polymorphisms. – Biological Journal of the Linnean Society, 121: 717–730. https://doi.org/10.1093/biolinnean/blx033

Egorov R., 2018: On the distribution of introduced species of the genus *Cepaea* Held, 1838 (Gastropoda: Pulmonata: Helicidae) in European Russia. – Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft, 25: 79–102.

Gheoca V., Benedek A. M., Cameron R. A. D. & Stroia R. C., 2019: A century after introduction: variability in *Cepaea hortensis* (Müller, 1774) in Sibiu, central Romania. – Journal of Molluscan Studies, 85(2): 197–203. https://doi.org/10.1093/mollus/eyy064

Gural-Sverlova N. V. & Egorov R. V., 2021: Shell colour and banding polymorphism in *Cepaea nemoralis* (Gastropoda, Pulmonata, Helicidae) from the Moscow region. – Ruthenica, Russian Malacological Journal, 31(1): 27–38. https://doi.org/10.35885/ruthenica.2021.31(1).4

Gural-Sverlova N., Egorov R., Kruglova O., Kovalevich N. & Gural R., 2021a: Introduced land snail *Cepaea nemoralis* (Gastropoda: Helicidae) in Eastern Europe: spreading history and the shell colouration variability. – Malacologica Bohemoslovaca, 20: 75–91. https://doi.org/10.5817/MaB2021-20-75

Gural-Sverlova N. V. & Gural R. I., 2018: Многолетняя динамика фенетической структуры в колониях интродуцированного вида *Cepaea hortensis* (Gastropoda, Pulmonata, Helicidae) [Long-term dynamic of phenetic structure in colonies of the introduced species, *Cepaea hortensis* (Gastropoda, Pulmonata, Helicidae)]. – Zoologicheskij Zhurnal, 97(7): 751–761. (in Russian). https://doi.org/10.1134/S0044513418070097

Gural-Sverlova N. V. & Gural R. I., 2021a: Shell banding and colour polymorphism of introduced snail *Cepaea hortensis* (Gastropoda, Pulmonata, Helicidae) from some parts of Eastern Europe. – Ruthenica, Russian Malacological Journal, 31(2): 59–76. https://doi.org/10.35885/ruthenica.2021.31(2).2

Gural-Sverlova N. V. & Gural R. I., 2021b: Polymorphism of the introduced snail *Cepaea nemoralis* (Gastropoda, Helicidae) from two distant parts of Eastern Europe: accidental similarity or regularity? – Zoodiversity, 55(5): 369–380. https://doi.org/10.15407/zoo2021.05.369

Gural-Sverlova N. V., Gural R. I. & Savchuk S. P., 2020: Новые находки *Cepaea nemoralis* (Gastropoda, Pulmonata, Helicidae) и фенетическая структура колоний этого вида на западе Украины [New records of *Cepaea nemoralis* (Gastropoda, Pulmonata, Helicidae) and phenotypic composition of its colonies in Western Ukraine]. – Ruthenica, Russian Malacological Journal, 30(2): 75–86. (in Russian) https://doi.org/10.35885/ruthenica.2021.30(2).1

Gural-Sverlova N. V., Gural R. I. & Rodych T. V., 2021b: Shell banding and color polymorphism of the introduced snail *Cepaea nemoralis* (Gastropoda, Helicidae) in Lviv, Western Ukraine. – Zoodiversity, 55(1): 51–62. https://doi.org/10.15407/zoo2021.01.051

Honěk A., 1995: Distribution and shell colour and banding polymorphism of the *Cepaea* species in Bohemia. – Acta Societatis Zoologicae Bohemicae, 59: 63–77.

Honěk A. & Martínková Z., 2003: Persistence and shell band morph frequencies in urban populations of *Cepaea*. – In: BCPC Symposium Proceedings, 80. Slugs & Snails: Agricultural, Veterinary & Environmental Perspectives: pp. 165–170.

iNaturalist, 2022: iNaturalist: A Community for Naturalist. – Online at http://www.inaturalist.org accessed at June 8, 2022.

Ivankova A. F. & Zemoglyadchuk K. V., 2001: Наземные моллюски в урбанизированных и природных ландшафтах Брестского района [Land molluscs in urbanized and natural landscapes of the Brest district]. – In: Влияние антропогенных факторов на состояние и динамику экосистем Полесья [Influence of anthropogenic factors on the state and dynamics of ecosystems in Polesie], Brest State University, Brest: pp.123–125. (in Russian)

Jones J. S., Leith B. H. & Rawlings P., 1977: Polymorphism in *Cepaea* – a problem with too many solutions? – Annual Review of Ecology and Systematics, 8: 109–143. https://doi.org/10.1146/annurev.es.08.110177.000545

Kolesnik V. G. & Kruglova O. Yu., 2016: Фенотипическая изменчивость в популяциях *Cepaea nemoralis* Linnaeus, 1758 (Gastropoda, Pulmonata, Helicidae) из г. Минска и Минского района [Phenotypic variability in the populations of *Cepaea nemoralis* Linnaeus, 1758 (Gastropoda, Pulmonata, Helicidae) from Minsk city and Minsk region]. – In: Актуальные проблемы экологии [Actual problems of ecology], Grodno State University, Grodno: pp. 102–103. (in Russian)

Kruglova O. Yu., 2018: Сравнительный анализ фенофондов городских колоний *Cepaea nemoralis* Linnaeus, 1758 (Gastropoda, Pulmonata) [Comparative analysis of the phene pools of urban colonies of *Cepaea nemoralis* Linnaeus, 1758 (Gastropoda, Pulmonata)]. – In: Биологические ресурсы: изучение, использование, охрана [Biological resources: study, use, protection], Vologda State University, Vologda: pp. 291–296. (in Russian)

Kruglova O. Yu. & Guminskaya A. S., 2019: Оценка фенотипического разнообразия популяций *Cepaea nemoralis* Linnaeus, 1758 (Gastropoda, Pulmonata), населяющих парки г. Минска и Бреста [Assessment of the phenotypic diversity of populations of *Cepaea nemoralis* Linnaeus, 1758 (Gastropoda, Pulmonata) inhabiting parks in Minsk and Brest]. – In: Зоологические чтения [Zoological readings], YurSaPrint, Grodno: pp. 148–151. (in Russian)

Kruglova O. Yu., Guminskaya A. S. & Kolesnik V. G., 2018: Полиморфизм интродуцированного вида брюхоногих моллюсков *Cepaea nemoralis* Linnaeus, 1758 в условиях г. Минска [Polymorphism of introduced species of gastropods *Cepaea nemoralis* Linnaeus, 1758 in Minsk]. – In: Современные проблемы адаптации [Modern problems of adaptation], Belgorod State University, Belgorod: pp. 141–143. (in Russian)

Lamotte M., 1951: Recherches sur la structure génétique des populations naturelles de *Cepaea nemoralis* (L.). – Bulletin biologique de la France et de la Belgique: Supplément, 35: 1–239. (in French)

Łomnicki M., 1899: *Helix nemoralis* L. – Kosmos, 23: 382.

Murray J., 1975: The genetics of the Mollusca. – In: Handbook of genetics, 3, King R. C. (ed.) Plenum Press, New York, pp. 3–31. ISBN 030637613X

Ostrovsky A. M. & Prokofieva K. V., 2017: Фенотипическая структура интродуцированных популяций *Cepaea nemoralis* (Linnaeus, 1758) (Gastropoda, Pulmonata, Helicidae) в условиях городской среды [The phenotypic structure of introduced populations of *Cepaea nemoralis* (Linnaeus, 1758) (Gastropoda, Pulmonata, Helicidae) in urban environments]. – In: Актуальные вопросы современной малакологии [Actual issues of modern malacology], Publishing House Belgorod, Belgorod: pp. 85–89. (in Russian)

Ożgo M., 2005: *Cepaea nemoralis* (L.) in southeastern Poland: association of morph frequencies with habitat. – Journal of Molluscan Studies, 71: 93–103. https://doi.org/10.1093/mollus/eyi012

Ożgo M., Cameron R. A. D., Horsák M., Pokryszko B., Chudaś M., Cichy A., Kaczmarek S., Kobak J., Marzec M., Mierzwa-Szymkowiak D., Parzonko D., Pyka G., Rosin Z., Skawina A., Soroka M., Sulikowska-Drozd A., Surowiec T., Szymanek T., Templin J., Urbańska M., Zając K., Zielska J., Żbikowska E. & Żołądek J., 2019: *Cepaea nemoralis* (Gastropoda: Pulmonata) in Poland: patterns of variation in a range-expanding species. – Biological Journal of the Linnean Society, 20: 1–11. https://doi.org/10.1093/biolinnean/blz029

Pokryszko B. M., Cameron R. A. D. & Horsák M., 2012: Variation in the shell colour and banding polymorphism of *Cepaea nemoralis* (L.) in rural areas around Wrocław. – Folia Malacologica, 20(2): 87–98. https://doi.org/10.2478/v10125-012-0012-4

Schilder F. A. & Schilder M., 1957: Die Bänderschnecken. Eine Studie zur Evolution der Tiere. Schluß: Die Bänderschnecken Europas [*Cepaea*. A study of the animal evolution. Conclusion: Europe's *Cepaea*]. – Gustav Fischer Verlag, Jena, 93–206 pp. (in German)

Sverlova N., 2002: Einschleppung und Polymorphismus der *Cepaea*-Arten am Beispiel von Lwow in der Westukraine (Gastropoda: Pulmonata: Helicidae) [Introduction and polymorphism of *Cepaea* species by the example of Lvov in Western Ukraine (Gastropoda: Pulmonata: Helicidae)]. – Malakologische Abhandlungen Museum für Tierkunde Dresden, 20(2): 267–274. (in German)

Sverlova N., 2004: Zur Auswertung der Diversität und Struktur des Polymorphismus bei den Bänderschnecken *Cepaea hortensis* (Müller 1774) und *C. nemoralis* (Linné 1758) am Beispiel isolierter Populationen [On the evaluation of the diversity and structure of shell polymorphism in *Cepaea hortensis* (Müller

1774) and *C. nemoralis* (Linné 1758) as demonstrated by insular populations]. – Mitteilungen aus dem Zoologischen Museum in Berlin, Zoologische Reihe, 80(2): 159–179. (in German) https://doi.org/10.1002/mmnz.20040800203

UkrBIN, 2022: UkrBIN: Ukrainian Biodiversity Information Network [public project & web application]. – Online at http://www.ukrbin.com accessed at June 8, 2022.

Zhivotovsky L. A., 1982: Показатели популяционной изменчивости по полиморфным признакам [Indicators of population variability by polymorphic traits]. – In: Фенетика популяций [Phenetics of populations], Nauka, Moscow: pp. 38–44. (in Russian)

Table 1. The phenotypic composition of *C. nemoralis* at the studied sites in Minsk, Belarus.

Phenotypes	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16	M17	M18	M19	M20	Total
Yellow unbanded																					
Y00000	–	2	1	–	–	–	–	1	–	6	1	8	49	181	80	28	31	6	12	18	424
Yellow mid-banded																					
Y00300	287	60	51	43	35	13	28	34	10	64	38	5	29	35	154	2	68	6	6	2	970
Y003[4]0	–	–	–	1	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	4
Y00340	–	–	–	–	–	–	–	1	–	–	–	–	4	–	–	–	–	–	–	–	5
Y00(34)0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	2
Y02300	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	11
Y0(23)00	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1
Y0030[5]	–	–	–	–	–	–	–	–	–	1	2	–	–	–	–	–	–	–	–	–	3
Y00305	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1
Y003[4][5]	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1
Yellow three-banded																					
Y00345	3	–	–	–	–	–	–	–	–	4	4	–	–	6	4	2	2	–	6	7	38
Y003(45)	–	–	1	–	–	–	–	–	–	–	–	–	–	3	2	–	1	–	3	1	11
Y[1][2]345	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1

Table 1. Continued.

Phenotypes	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16	M17	M18	M19	M20	Total
Yellow five-banded																					
Y12345	17	1	1	12	1	–	4	14	–	8	–	1	–	12	9	1	21	4	3	5	114
Y12045	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	2
Y120(45)	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1
Y023(45)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1
Y[1]2345	–	–	–	–	–	2	1	–	–	–	–	1	–	–	–	–	5	–	–	–	9
Y(12)345	6	–	–	–	–	–	–	–	–	–	–	–	–	6	1	1	–	1	–	–	15
Y(123)45	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
Y1(23)45	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	5	–	–	–	7
Y123(45)	5	–	–	–	–	–	1	9	–	–	–	–	10	12	17	–	5	–	2	–	61
Y12(345)	10	–	–	–	–	–	–	–	–	–	–	–	80	23	1	–	–	–	–	–	114
Y1(23)(45)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–	2	1	11
Y(12)3(45)	15	–	–	3	–	–	–	8	–	–	–	11	6	104	6	–	6	–	1	–	160
Y(12)(345)	–	–	–	–	–	–	–	–	–	–	–	–	11	2	–	–	2	–	–	–	15
Y(123)(45)	7	–	–	–	–	1	–	1	–	–	–	3	–	27	3	–	–	–	–	–	42
Y(12345)	–	–	–	–	–	–	–	–	–	–	–	1	–	13	–	–	–	–	–	–	14
Pink unbanded																					
P00000	2	–	–	–	–	–	–	–	–	2	–	–	8	46	9	20	1	1	12	9	110
Pink mid-banded																					
P00300	820	2	14	15	16	20	–	4	78	146	61	–	2	36	39	7	6	12	11	7	1296
P003[4]0	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	2
P00340	1	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	4
P00305	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	4
P02300	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	7
P0(23)00	–	–	–	–	–	1	–	–	–	–	4	–	–	–	–	–	–	–	–	–	5
P003[4][5]	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1
P[1]0300	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	2
P[1]03[4]0	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1
P[1][2]30[5]	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1

Table 1. Continued.

Phenotypes	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16	M17	M18	M19	M20	Total
Pink three-banded																					
P00345	1	–	–	–	–	–	–	–	1	22	3	–	–	1	1	1	–	–	11	9	50
P003(45)	–	–	–	–	–	–	–	–	–	–	3	–	–	3	–	–	1	–	13	5	25
P00(345)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1
Pink five-banded																					
P12345	16	1	1	–	–	–	–	–	2	3	1	–	–	8	–	4	–	3	5	5	49
P02345	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
P023(45)	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	1	–	–	–	1
P123[4]5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1
P(12)345	7	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	9
P(123)45	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	3
P1(23)45	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1
P123(45)	6	–	–	1	–	–	–	–	–	–	–	–	2	15	–	1	–	1	5	3	34
P[1]23(45)	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1
P12(345)	8	–	–	–	–	–	–	–	–	–	–	–	3	16	–	–	–	–	–	–	27
P1(23)(45)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1
P(12)3(45)	24	–	–	–	–	1	–	–	–	–	–	4	–	56	1	1	–	1	–	–	88
P(12)(345)	1	–	–	–	–	–	–	–	–	–	–	–	3	2	–	–	–	–	–	–	6
P(123)(45)	5	–	–	–	–	–	–	–	–	–	–	1	–	10	–	–	–	–	4	–	20
P(12345)	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	–	6
Brown unbanded																					
B00000	3	–	7	–	–	–	–	–	–	–	–	6	12	113	1	4	1	12	–	7	166
Brown mid-banded																					
B00300	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Total	1264	66	76	75	53	38	34	73	93	267	124	43	219	739	331	73	167	50	99	81	3965

Table 2. The phenotypic composition of *C. nemoralis* at the studied sites in Lviv, Ukraine.

Phenotypes	L1	L2	L3	L5	L6	L7	L8	L9	L10	L11	L12	L13	L14	L15	L16	L17	Total
Yellow unbanded																	
Y00000	4	–	1	–	–	28	–	14	–	–	13	5	–	23	–	–	88
Yellow mid-banded																	
Y00300	280	4	27	16	47	–	1	5	4	–	7	117	63	9	4	–	584
Y0[2]300	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1
Y0030[5]	2	–	–	–	1	–	–	–	–	–	–	2	–	–	–	–	5
Y003[4]0	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Yellow three-banded																	
Y00345	39	–	–	–	–	19	2	–	2	–	2	12	3	–	–	1	80
Y003(45)	24	–	–	–	–	1	5	1	10	–	2	11	2	–	–	–	56
Y00(345)	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1
Y00045	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Y[1][2]345	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Yellow five-banded																	
Y12345	–	10	6	2	10	21	7	2	9	3	4	106	–	13	3	–	196
Y10345	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	2
Y(12)345	–	–	–	–	–	1	1	–	–	–	–	14	–	–	1	1	18
Y1(23)45	–	–	–	1	1	–	1	–	–	–	–	3	–	1	–	–	7
Y123(45)	–	2	8	–	2	–	1	4	3	4	–	38	–	3	8	–	73
Y(123)45	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	3
Y(12)3(45)	–	4	2	–	11	1	1	8	8	1	1	87	–	1	7	2	134
Y1(23)(45)	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	2
Y(123)(45)	–	2	–	–	3	–	1	1	2	1	1	35	–	–	15	–	61
Y(12)(345)	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1
Y(12345)	–	1	–	–	1	–	–	1	2	–	–	3	–	–	7	–	15
Pink unbanded																	
P00000	590	294	37	–	–	1	19	2	33	48	6	73	–	1	15	17	1136

Table 2. Continued.

Phenotypes	L1	L2	L3	L5	L6	L7	L8	L9	L10	L11	L12	L13	L14	L15	L16	L17	Total
Pink mid-banded																	
P00300	186	19	5	14	8	–	1	2	5	–	9	63	18	–	6	–	336
P0030[5]	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1
P003[4]0	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1
P(12)300	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1
Pink three-banded																	
P00345	18	–	–	–	–	3	3	–	–	–	6	12	7	–	–	4	53
P003(45)	18	–	–	–	–	–	1	1	7	–	1	14	1	–	–	4	47
P00(34)5	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1
P[1]0345	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2
P[1][2]3(45)	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Pink five-banded																	
P12345	–	8	1	1	1	2	3	–	2	2	5	30	–	1	3	3	62
P12045	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	2
P10345	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1
P(12)345	–	–	1	–	1	1	–	–	–	–	–	5	–	–	1	–	9
P1(23)45	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1
P123(45)	–	29	–	1	1	2	–	–	1	2	–	19	–	–	3	8	66
P(12)3(45)	–	11	5	–	1	2	2	–	7	3	1	37	–	1	6	10	86
P1(23)(45)	–	1	–	–	–	–	–	–	–	–	–	1	–	–	1	–	3
P(123)(45)	–	3	–	–	2	–	2	–	2	–	–	32	–	–	6	1	48
P1(2345)	–	–	–	–	–	–	–	–	1	–	–	1	–	–	1	–	3
P(12345)	–	–	–	–	–	–	–	–	1	–	–	1	–	–	4	–	6
Brown unbanded																	
B00000	–	–	–	–	–	–	–	21	3	–	–	–	13	–	–	–	37
Total	1167	388	95	35	90	82	51	62	103	65	60	732	107	53	92	53	3235

Table 3. Differences in the frequencies of inherited colouration traits, phenotype groups and indices of phenotypic diversity. The frequencies of brown unbanded shells are not indicated, as they almost always coincided with those of brown shells. *The difference is significant at p = 0.05. **The same at p = 0.01.

Phenotype groups / Traits /Indices	Minsk, Belarus		Lviv, Western Ukraine		Mann- -Whitney test	Minsk-1 (M1 – M11)		Minsk-2 (M12 – M20)		Mann- -Whitney test
	Min – Max	Mean	Min – Max	Mean		Min – Max	Mean	Min – Max	Mean	
Phenotype groups distinguished by the combination of shell ground colour and banding										
Yellow unbaded	0 – 38.4	10.1	0 – 43.4	7.7	126	0 – 3.0	0.8	12.0 – 38.4	21.4	0**
Yellow mid-banded	2.5 – 90.9	34.4	0 – 58.9	17.1	91*	10.7 – 90.9	49.2	2.5 – 47.1	16.2	13**
Yellow three-banded	0 – 9.9	1.7	0 – 24.4	4.7	134.5	0 – 4.0	0.6	0 – 9.9	2.9	34.5
Yellow five-banded	0 – 48.9	14.5	0 – 45.6	19.6	122.5	0 – 45.2	9.4	2.7 – 48.9	20.8	22*
Pink unbanded	0 – 27.4	3.3	0 – 75.8	24.0	81.5**	0 – 0.7	0.1	0 – 27.4	7.3	11.5**
Pink mid-banded	0 – 86.0	23.7	0 – 40.0	8.3	104*	0 – 86.0	36.0	0 – 28.0	8.7	21.5*
Pink three-banded	0 – 25.2	3.0	0 – 17.0	4.0	144.5	0 – 4.8	1.3	0 – 25.2	5.0	39.5
Pink five-banded	0 – 16.2	5.0	0 – 43.4	11.5	103.5*	0 – 5.5	1.5	0.3 – 16.2	9.3	17**
Inherited traits (shell ground colour)										
Yellow	10.7 – 100	60.7	5.9 – 94.3	49.1	125	10.7 – 100	60.1	34.0 – 94.0	61.4	48
Pink	0 – 89.2	35.1	5.7 – 94.1	47.9	118	0 – 89.2	38.9	5.4 – 64.6	30.4	42
Brown	0 – 24.0	4.2	0 – 33.9	3.1	126.5	0 – 9.2	1.0	0 – 24.0	8.2	17.5**
Inherited traits (absence of all or part of the bands)										
Unbanded	0 – 71.2	17.6	0 – 75.8	34.8	94*	0 – 10.5	1.7	19.8 – 71.2	36.9	0**
Mid-banded among banded	17.8 – 98.1	65.2	0 – 86.2	34.7	76.5**	54.2 – 98.1	87.0	17.8 – 80.9	38.6	4**
Three-banded among multi-banded (i.e. with 3-5 bands)	0 – 91.7	19.9	0 – 100	25.5	153.5	0 – 91.7	21.0	0 – 58.6	18.6	48
Yellow and pink unbanded, yellow and pink mid-banded together										
Light coloured	32.6 – 97.0	71.5	27.2 – 90.3	57.2	89*	54.8 – 97.0	86.1	32.6 – 85.8	53.6	5**
Indices of phenotypic diversity										
Number of phenotype groups (m)	2 – 9	6.4	3 – 8	5.8	133	2 – 8	5.1	5 – 9	8.0	10.5**
Index of intrapopulation diversity (μ)	1.76 – 8.43	4.57	2.50 – 7.79	4.72	141	1.76 – 4.78	3.14	4.76 – 8.43	6.32	1**
Rate of rare morphs (h)	0.04 – 0.54	0.28	0.03 – 0.37	0.19	93*	0.12 – 0.54	0.35	0.04 – 0.42	0.20	21*

Table 4. The number of samples monomorphic in any trait. *The samples monomorphic in two traits. **The only sample monomorphic in three traits, including the shell ground colour (yellow only).

Inherited phenotypic traits	Number of samples monomorphic by		Site numbers
	its presence	its absence	
Minsk-1 (a total of 11 sites)			
Unbanded	–	5	M4–M7, M9
Mid-banded	–	–	–
Three-banded	–	6	M2, M4–M8
Any of the above	–	7	M2, M4*, M5*, M6*, M7**, M8, M9
Minsk-2 (a total of 9 sites)			
Unbanded	–	–	–
Mid-banded	–	–	–
Three-banded	–	3	M12, M13, M18
Lviv (a total of 16 sites, not including L4 – see Material and methods)			
Unbanded	–	2	L5, L6
Mid-banded	–	3	L7, L11, L17
Three-banded	2	7	L1–L3, L5, L6, L11, L14–L16
Any of them	2	9	L1–L3, L5*, L6*, L7, L11*, L14–L17

Table 5. Values of the inbreeding coefficient F_{st} in Minsk and Lviv.

Inherited phenotypic traits	F_{st} calculated from the frequencies of							
	phenotypes				alleles			
	Minsk-1	Minsk-2	Minsk	Lviv	Minsk-1	Minsk-2	Minsk	Lviv
Ground colour								
Brown	0.068	0.079	0.106	0.243	0.035	0.041	0.056	0.133
Pink	0.375	0.189	0.302	0.315	0.239	0.112	0.193	0.228
Yellow	0.360	0.205	0.291	0.263	0.230	0.114	0.181	0.199
Number of bands								
Unbanded	0.052	0.090	0.280	0.225	0.027	0.061	0.166	0.136
Mid-banded	0.127	0.206	0.387	0.390	0.102	0.140	0.286	0.264
Three-banded	0.585	0.337	0.480	0.558	0.423	0.196	0.335	0.635

Table 6. Values of F_{st} in some European cities.

City, country, literature source	Comments	Inbreeding coefficient F_{st}		
		Yellow	Banded/ unbanded	Mid-banded
Wrocław, Poland (Cameron et al. 2009)	Outside the natural range, introduced over a century ago	0.089	0.092	0.123
Rzeszów, Poland, calculated based on data in Ożgo (2005), given according to Gural-Sverlova & Egorov (2021)	Outside the natural range, introduced at the end of the 19th century	0.163	0.193	0.153
Sheffield, England (Cameron et al. 2009)	Within the natural range, but actively colonizing the city only in the last decades	0.207	0.350	0.284
Göteborg, Sweden (Cameron et al. 2014)	Outside the natural range, introduced no later than the middle of the 19th century, increased spread in the last decades	0.212	0.302	0.277
Lviv, Ukraine (this paper)	Outside the natural range, first attempt at introduction at the end of the 19th century, but active colonization of the city in recent decades	0.263	0.225	0.390
Minsk, Belarus (this paper)	Outside the natural range, probably introduced no earlier than the late 20th or early 21st century	0.291	0.280	0.387

Table 7. Percentages of phenotypes among shells with 5 normally developed bands and band fusions in species range and in introduced Eastern European populations of *C. nemoralis*. References: *(Schider & Schilder 1957), **(Gural-Sverlova et al. 2020), ***(Gural-Sverlova & Egorov 2021).

Phenotypes	Species range* N = 33345	Minsk, Belarus N = 637	Minsk-1 N = 125	Minsk-2 N = 512	Lviv, Western Ukraine N = 540	Bohorodchany, Western Ukraine** N = 236	Moscow Region, Russia*** N = 339
Common phenotypes							
(12)3(45)	32.8	38.9	40.8	38.5	40.7	11.4	28.0
(123)(45)	27.6	9.7	11.2	9.4	20.6	33.5	16.8
123(45)	14.7	14.9	17.6	14.3	25.7	23.3	30.4
-12345	13.5	3.1	–	3.9	3.9	10.2	7.1
(12)345	5.6	3.8	10.4	2.1	5.0	0.4	7.4
Less common but regularly occurring phenotypes							
1(23)45	2.0	1.3	0.8	1.4	1.7	8.0	2.9
(123)45	1.5	0.9	4.0	0.2	0.6	0.8	0.6
1(23)(45)	1.4	1.9	–	2.3	0.9	12.3	5.6
Rare phenotypes							
(12)(345)	0.4	3.3	0.8	3.9	0.2	–	0.9
1(2345)	0.2	–	–	–	0.7	–	0.3
12(345)	0.1	22.1	14.4	24.0	–	–	–
Others	0.1	–	–	–	–	–	–
All phenotypes with fusion of a band pair							
Bands 1 and 2	81.5	59.8	67.2	58.0	70.9	56.4	60.8
Bands 2 and 3	46.2	16.9	16.0	17.2	28.3	64.8	33.3
Bands 3 and 4	14.3	28.6	15.2	31.8	4.8	10.2	8.3
Bands 4 and 5	90.8	94.0	84.8	96.3	92.8	90.7	89.1

Appendix

Descriptions of all studied sites in Minsk (M1–M20) and two additional sites in Lviv (L16 and L17).

For details on other sites in Lviv, see in Gural-Sverlova et al. (2021b).

M1 – 1st Zemlemernaya Street, No. 14, 53°53'18.4"N 27°31'01.0"E, length about 10 m, repeated sampling on 8. 7. 2014 (coll. Kolesnik), 27. 6. 2015 (coll. Kruglova, Kolesnik), 9. 9. 2017 and 10. 8. 2018 (coll. Guminskaya). Thickets of high ruderal herbaceous vegetation, partly shaded by fruit trees (plums, cherries), along the fence of a household plot.

M2 – near the intersection of Brestskaya Street and Lieutenant Kizhevatov Street, between 53°51'53.9"N 27°31'47.7"E and 53°51'43.6"N 27°32'02.3"E, width 30–40 m, length about 400 m, 2. 9. 2018, coll. Guminskaya. On one side, the mostly open site is limited from the roadway by shrubs and single trees; on the other side, there are apartment buildings and private houses.

M3 – near the intersection of Chernigovskaya Street and Lieutenant Kizhevatov Street, 53°51'49.6"N 27°31'48.1"E, length about 3 m, 15. 7. 2019, coll. Volk. A few cherry and cherry plum trees on the lawn along the roadway.

M4 – Loshitskiy Lane, No. 14, 53°50'43.4"N 27°34'52.9"E, length 3–4 m, 11. 5. 2021, coll. Silina. Fence of a private house with thickets of *Parthenocissus*, one sea buckthorn tree.

M5 – Pavel Fedotov Street, No. 20, 53°51'41.7"N 27°37'28.3"E, 23–29. 8. 2021, coll. Paltarak. Household plot of 300 m^2 near a private house with flower beds and garden plantings (raspberries, apple trees).

M6 – 1st Yunosheskiy Lane, No. 3, 53°51'50.3"N 27°37'27.7"E, length about 5 m, 18. 5. 2021, coll. Vachinskaya. Honeysuckle bushes, cherries and maples near a private house.

M7 – Dmitriy Zhilunovich Street, No. 22, 53°52'14.9"N 27°37'39.9"E, length about 3 m, 17. 5. 2021, coll. Vachinskaya. Bushes of *Caragana* and lilac.

M8 – Evgeniy Klumov Street, No. 20, 53°53'33.3"N 27°36'07.0"E, length about 20 m, 29. 6. 2017, coll. Titkova. Lawn with grassy vegetation.

M9 – 2nd Yeniseyskiy Lane No. 96, 53°52'53.7"N 27°40'15.4"E, 17. 5. 2021, coll. Sokolovskaya. Household plot of 200 m^2 near a private house with berry bushes (raspberries, currants, gooseberries).

M10 – Stepyanka microdistrict, Dacha Street, No. 3, 53°55'22.8"N 27°39'28.8"E, sampling from June to November 2020, coll. Nikiforov. Household plot of 500 m^2 near a private house with garden plantings.

M11 – Stepyanka microdistrict, 100–150 m from the site M10, 53°55'22.8"N 27°39'39.7"E, May 2021, coll. Nikiforov. A wasteland with ruderal vegetation is a former dump where garbage was brought.

M12 – forest park area near the intersection of Starinovskaya Street and Vyacheslav Nikiforov Street, 53°56'29.9"N 27°41'58.0"E, length about 20 m, 20–26. 5. 2019, coll. Balashko. Shaded site with a predominance of spruces, maples, rowans.

M13 – forest park area near the Street of Heroes of the 120th division, 53°56'39.7"N 27°42'58.1"E, length about 60 m, repeated sampling on 9. 9. 2017 and 10. 8. 2018, coll. Guminskaya. Shaded site with a predominance of spruces and maples, fragments of herbaceous vegetation in places.

M14 – a forest park area near Sadovaya Street, No. 5, about 200–250 m from the site M13, between 53°56'41.0"N 27°42'44.6"E and 53°56'41.4"N 27°42'45.7"E, length about 80 m, repeated sampling on 20. 7. 2015 (coll. Kruglova), 1. 10. 2016 and 3. 7. 2017 (coll. Kruglova, Kruglov). A very shaded area dominated by spruces and maples, in some places along the walking paths there is grassy vegetation with a predominance of nettles.

M15 – Pochtovaya Street, No. 2, about 150 m from the site M14, 53°56'45.2"N 27°42'41.2"E, length about 20 m, repeated sampling on 12. 7. 2014, 20. 7. 2015 (coll. Kruglova), 8. 8. 2017 (coll. Kruglova, Kruglov). Front garden near an apartment building with some cherry and cherry plum trees, ornamental flowers and herbaceous vegetation.

M16 – Dmitriy Karbyishev Street, No. 11, 53°57'08.6"N 27°38'05.4"E, length 3 m, 30. 6. 2020, coll. Volk. Wild rose bushes in the yard of an apartment building.

M17 – Sevastopolskiy Park, 53°56'33.9"N 27°36'39.4"E, repeated sampling on 27. 7. 2018 (coll. Guminskaya) and 15. 7. 2019 (coll. Volk). The first sample was collected on a plot with herbaceous vegetation, partially shaded by trees (spruces, maples, lindens). The second sample was collected on a plot 10–15 m long, 15 m from the first one, with herbaceous vegetation dominated by nettles and with bushes of *Physocarpus*.

M18 – Mihail Kalinin Street, No. 17, 53°55'39.5"N 27°36'11.9"E, length about 2 m, coll. Volk. Decorative plantings (bushes of *Physocarpus*) near secondary school No. 73.

M19 – Kahovskaya Street, No. 45, 53°55'47.0"N 27°33'46.6"E, length about 10 m, 5. 7. 2020, coll. Volk, Grinevich. A flower bed with ornamental flowers in the yard of an apartment building.

M20 – Gaya Gay Street, No. 14, 53°55'48.0"N 27°33'44.6"E, length about 10 m, 5. 7. 2020, coll. Volk, Grinevich. A flower bed in the yard of an apartment building with lilac and hydrangea bushes.

L16 – a church near the market “Pivdennyi”, 49°48'49.5"N 23°58'32.6"E, length up to 30 m, several samples from April to June 2021, coll. Gural-Sverlova. Ornamental trees and shrubs around the church, which were gradually planted since 2004. Thus, the age of the studied colony did not exceed 17 years.

L17 – Kost Levytskyi Street, Nos. 110 and 112, 49°49'51.4"N 24°02'50.1"E, length about 30 m, multiple sampling in July 2021, coll. Gural-Sverlova. Several small groups of junipers along the fence of one mansion and a row of arborvitae along the fence of another.