FOLIA MALACOLOGICA
Folia Malacol. forthcoming paper
ISSN 1506-7629 (print) • ISSN 2300-7125 (on-line)
The Association of Polish Malacologists
Faculty of Biology, Adam Mickiewicz University
Bogucki Wydawnictwo Naukowe
Poznań, 2026
https://doi.org/10.12657/folmal.034.010

CEPAEA NEMORALIS (GASTROPODA: HELICIDAE) IN UKRAINE, A PHENOTYPIC DIVERSITY IN NEWLY COLONISED AREAS

Nina Gural-Sverlova[1], Taras Rodych[2], Roman Gural[1]

[1] Department of Biosystematics and Evolution, State Museum of Natural History, Theatralna St 18, 79008, Lviv, Ukraine (e-mail: sverlova@pip-mollusca.org); NGS https://orcid.org/0000-0002-3892-5338; RG https://orcid.org/0000-0002-1546-1956
[2] Faculty of Fine Arts and Restoration, Lviv National Academy of Arts, Ukraine; https://orcid.org/0009-0008-8093-6381

Abstract: This paper analyses the results of our own research from 2019 to 2025, as well as other available data on the shell colouration in *C. nemoralis* from different parts of Ukraine. Qualitative data from more than 70 localities (usually settlements, less often their environs) in 17 administrative regions were summarised. Quantitative data (7 regions, 28 localities, almost a hundred collection sites, and more than 13 thousand specimens) represent mainly the western part of the country, especially the city of Lviv and its immediate surroundings. It has been shown that western Ukrainian populations of *C. nemoralis* have, in general, a large phenotypic diversity and a very variable phenotypic composition. The latter can be considered characteristic of recently established populations outside the natural range. A comparison with similar data for other parts of Eastern Europe was made.

Keywords: *Cepaea*; land snail; introduced species; polymorphism; Ukraine

INTRODUCTION

Cepaea nemoralis (Linnaeus, 1758) is one of the best known species of European land molluscs. It is also a classic subject for population genetic studies due to a number of heritable traits of the shell colouration (Murray 1975). Numerous publications, including monographs (Lamotte 1951, Schilder & Schilder 1953a, 1957), reviews and discussion papers (Jones et al. 1977, Clarke et al. 1978, Cameron 1997, Cook 1998, Sverlova 2004, Ożgo 2008, etc.), were devoted to its shell colour and banding polymorphism. Not long ago, *C. nemoralis* and another species of the same genus, *Cepaea hortensis* (O. F. Müller, 1774), were the focus of European citizen science thanks to the large project Evolution MegaLab (Silvertown et al. 2011, Cameron & Cook 2012, Cameron 2013).

The current range of *C. nemoralis* has expanded significantly due to human activity, both intentional (deliberate introductions of attractive snails) and more often accidental (usually together with seedlings of garden and ornamental plants). Already in the second half of the 19th century, this species was introduced to North America (Howe 1898, Alexander 1952), south-eastern Poland (Bąkowski 1880, Łomnicki 1899), and the Czech Republic (Peltanová et al. 2012). Almost immediately after the first discovery of *C. nemoralis* in the south-east of present Poland (Bąkowski 1880), an attempt was made to introduce it from there to Lviv (Łomnicki 1899), which was then also part of Poland, but is now the largest city in western Ukraine. However, this attempt was not successful (Gural-Sverlova et al. 2020). In the first half of the 20th century, *C. nemoralis* was mentioned only once for Lviv, when Urbański (1933) found several immature specimens in the Lychakiv cemetery. By the end of the 20th century, only one of the Lviv parks was inhabited by a declining population of *C. nemoralis* of unknown origin, with low abundance and limited phenotypic composition (Sverlova 2002a).

In other administrative regions of Ukraine, *C. nemoralis* was not reliably known until the beginning of the 21st century (Gural-Sverlova et al. 2024a: table 5). Some earlier mentions were most likely based on erroneous identifications of *Caucasotachea vindobonensis* (C. Pfeiffer, 1828), widespread in Ukraine (Sverlova 2006). In recent years, the number of known records of *C. nemoralis* in different parts of Ukraine has been rapidly increasing, both published (Gural-Sverlova et al. 2020, Balashov & Markova 2021, Gural-Sverlova & Lyzhechka 2021, Gural-Sverlova & Gural 2023, Martynov & Nikulina 2023) and those made by amateur naturalists especially via iNaturalist (2025) and UkrBIN (2025).

Similar trends have been observed in other parts of Eastern Europe (Gural-Sverlova et al. 2021a), which may be related to the activities of garden centres importing seedlings from other European countries (Gural-Sverlova & Gural 2025a), global warming and milder microclimates in urbanised areas. In particular, *C. nemoralis* is now already quite widespread in Minsk (Gural-Sverlova & Kruglova 2022), Moscow and the Moscow region (Egorov 2018, Gural-Sverlova & Egorov 2021, iNaturalist 2025). East of the Moscow region, *C. nemoralis* is found sporadically, according to published data, to Nizhny Novgorod (Mukhanov & Lisitsyn 2018), and according to observations in the database iNaturalist (2025), much further – to the Urals (Ufa) and even Central Asia (suburb of Almaty in Kazakhstan).

Far beyond its natural range, Eastern European populations of *C. nemoralis* are forced to adapt to a more continental climate, which is only partially mitigated by global climate change (in particular, warmer winters) and microclimatic features of settlements. This may affect their phenotypic composition (Gural-Sverlova & Gural 2021a). The combination of climatic selection and random population genetic processes (primarily the founder effect and genetic drift at the initial stages of the formation of new populations) can lead to a unique suite and/or ratio of inherited colouration traits, as was recently shown for western Ukrainian populations of the related species *C. hortensis* (Gural-Sverlova & Gural 2025b). This makes the phenotypic composition of Eastern European *Cepaea* populations particularly attractive for research. Given the youth of most populations of *C. nemoralis* in Eastern Europe, a detailed description of their polymorphism could provide an important basis for monitoring possible subsequent changes.

In Ukraine, the shell colour and banding polymorphism in *C. nemoralis* has so far been quantitatively studied almost exclusively in the west of the country (Gural-Sverlova et al. 2020, Gural-Sverlova & Lyzhechka 2021, Gural-Sverlova & Gural 2023, 2025a), mainly in Lviv and its immediate surroundings (Gural-Sverlova et al. 2021b, Gural-Sverlova & Kruglova 2022, Gural-Sverlova et al. 2024a). In recent years, however, we have accumulated quite a lot of data that has not yet been published. In eastern Ukraine, the phenotypic composition of one population of *C. nemoralis* from Donetsk has been described so far (Martynov & Nikulina 2023). Balashov & Markova (2021) list some phenotypes recorded in the central (Kyiv and surrounding areas) and southern (Odesa) parts of the country. In addition, a fairly large number of *C. nemoralis* photographs from different administrative regions of Ukraine have already been accumulated in citizen science databases (iNaturalist 2025, UkrBIN 2025).

In this paper we have aggregated the available quantitative and qualitative data on the shell polymorphism of *C. nemoralis* in Ukraine, and, as far as possible, attempted to assess the level of phenotypic diversity in recently formed populations of this species. In the future, this may become a good basis for monitoring possible changes in the phenotypic composition of *C. nemoralis* populations in urbanised areas of Ukraine.

MATERIAL AND METHODS

We analysed available data on the shell colouration in populations of *C. nemoralis*, found in different parts of Ukraine at the beginning of the 21st century:

1. own collecting and observations in the west of Ukraine, primarily in Lviv and its immediate surroundings, made from 2019 to 2025 and partially used in previous publications (Gural-Sverlova et al. 2020, 2021b, 2024a, Gural-Sverlova & Gural 2021a, 2023, 2025a, Gural-Sverlova & Lyzhechka 2021, Gural-Sverlova & Kruglova 2022);
2. some samples from other collectors, donated to the malacological collection of the State Museum of Natural History in Lviv;
3. published data from other researchers (Balashov & Markova 2021, Martynov & Nikulina 2023);
4. observations in two citizen science databases currently popular in Ukraine (iNaturalist 2025, UkrBIN 2025), as well as some posts on

the social network Facebook and personal correspondence with the authors, if this information was confirmed by photographs that allow for the reliable identification of the species (*C. nemoralis*) and the shell colouration (ground colour, banding pattern).

In total, we aggregated and analysed qualitative data for more than 70 localities (usually settlements, less often their environs) from 17 administrative regions of Ukraine (Appendix 1). Quantitative data, primarily for the western part of the country, are presented in Appendix 2: seven regions, 28 localities, almost a hundred collection sites, more than 13 thousand specimens. Figure 1 shows the locations of all localities mentioned in Appendices 1 and 2.

Samples were usually collected at sites without significant anthropogenic barriers that would impede the movement of snails (Sverlova 2002b). Their size often did not exceed the diameter of the panmictic unit, which for *C. nemoralis* is estimated at 50–60 (Jones et al. 1977) or 100 m (Schnetter 1950). When searching for populations of *C. nemoralis*, we paid particular attention to sites with relatively young ornamental plantings, especially the currently popular thujas, junipers, and other conifers, as well as areas adjacent to garden centres, either operating or recently closed. Two typical habitats of *C. nemoralis* in Lviv are shown in Gural-Sverlova et al. (2021a: fig. 2).

In most cases, phenotypes were counted only for adult live snails or their empty shells with well-preserved colouration. The surface of empty shells was sometimes moistened with water, which made it possible to better distinguish their ground colour. If the related species *C. hortensis* was completely absent at the collection sites, and the abundance of *C. nemoralis* was low (Boiarka in the Kyiv region, Rava-Ruska in the Lviv region) or the population had an interesting colouration trait (spotted and split bands in Chortkiv, Ternopil region, see in Gural-Sverlova et al. 2021a: fig. 5), samples could additionally include immature specimens with a shell diameter of at least 1 cm. Since the bands on *Cepaea* shells do not appear immediately and not all at the same time, using younger specimens may lead to an incorrect determination of the banding type. Immature individuals of the two *Cepaea* species also cannot always be reliably distinguished. This is especially true of yellow unbanded shells common in *C. hortensis*.

The shell ground colour was classified as yellow (Y), pink (P), or brown (B). The group of yellow shells traditionally also included those with a white ground colour (Fig. 2, top), occurring in both *Cepaea* species (Gural-Sverlova & Gural 2022a). Unlike western Ukrainian populations of *C. hortensis* (Gural-Sverlova & Gural 2025b), white shells in *C. nemoralis* are found much less frequently here and are present in far from all populations (Gural-Sverlova et al. 2021b: 55). Therefore, we did not consider it appropriate to distinguish them as a separate group.

In the group of pink shells, the ground colour varied from orange (Fig. 3, left) or pale greyish-pink to intense pink. We considered orange to be a combination of pink and yellow (maybe as a result of incomplete dominance of pink in heterozygotes?). Moreover, neither *C. nemoralis* nor *C. hortensis* ever produce orange shells in areas where pink ones are absent.

The third group included unbanded shells with a brown ground colour of varying intensity (Fig. 4), but most often dark, sometimes with a lilac or cherry tint (Fig. 5). Brown banded shells were absent.

For possible reasons for the large variation in shell colour within the groups described above, see Chowdhury et al. (2024).

According to the banding pattern, the shells were divided into four groups: unbanded, mid-banded, three-banded, and five-banded. In the group of unbanded shells, dark spiral bands were usually completely absent; only traces of them could occasionally be seen, more often near the aperture itself.

Shells with one distinct central (third) band were classified as mid-banded. Occasionally, the dark band

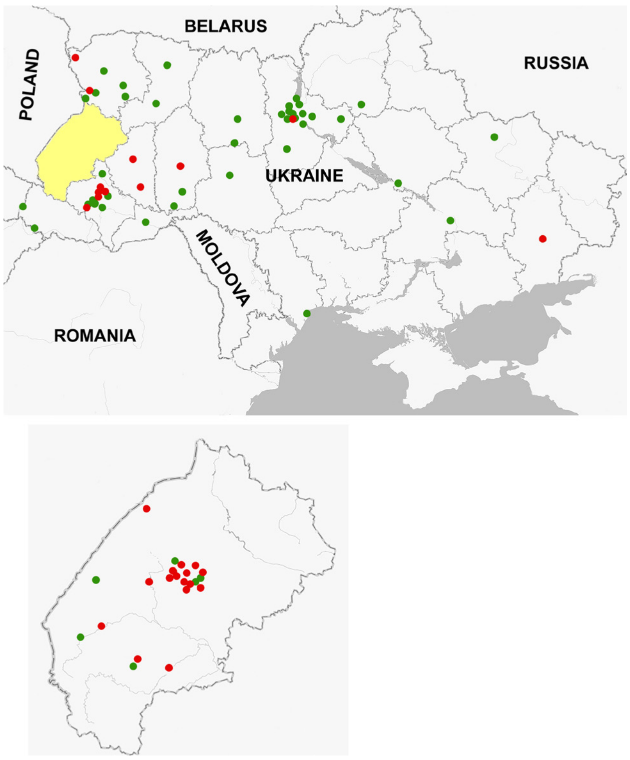

Fig. 1. Localities of *C. nemoralis* in Ukraine (top) and its Lviv region (bottom), mentioned in Appendices 1 and 2 (qualitative and quantitative data on the phenotypic composition, in red) or only in Appendix 1 (qualitative data, in green)

was absent (a modification), but a lighter zone was visible on the shell periphery (Fig. 6), which is not the case for true (heritably) unbanded specimens. Such specimens, in particular, can be sometimes observed where there are no true unbanded shells, but mid-banded ones are often found (Gural-Sverlova

Figs 2–10. Specimens of *C. nemoralis* from Lviv designated as yellow (2), pink (3), brown (4, 5), mid-banded (6–8), and three-banded (9, 10). For more details, see Material and Methods

et al. 2021b). Also included in this group were shells with one, or less often two, weak (blurred, rudimentary) bands below (Fig. 7) or above the shell periphery (Fig. 8).

In the three-banded group, the two upper bands are usually completely absent, occasionally appearing as traces or blurred. The three lower bands are distinct and may fuse together (Fig. 10), sometimes one of them is missing, weak, or appears on the shell somewhat late (Fig. 9).

Five-banded shells usually have five distinct spiral bands, discrete or fused. Sometimes one of the bands is missing (commonly the second or third from the top).

The combination of ground colour and banding gives nine variants of the shell colouration recorded in Ukraine. Below are their symbols in alphabetical and numerical order:

– B-0 – brown unbanded;
– P-0 – pink unbanded;
– P-1 – pink mid-banded;
– P-3 – pink three-banded;
– P-5 – pink five-banded;
– Y-0 – yellow unbanded;
– Y-1 – yellow mid-banded;
– Y-3 – yellow three-banded;
– Y-5 – yellow five-banded.

RESULTS

Today, both the greatest colouration diversity (Table 1) and the largest number of *C. nemoralis* observations (Fig. 1) have been recorded in western and central Ukraine. This primarily concerns Lviv and Kyiv with their immediate surroundings. All nine variants of the shell colouration, including the rare brown shells without bands, were also found in Ternopil (regional centre in western Ukraine) and near a large garden centre in Horodok, Lviv region. From the Khmelnytskyi region, adjacent to Ternopil one, some observations of *C. nemoralis* with a yellow five-banded shell are currently known, in particular from the botanical garden of Khmelnytskyi National University. Although in Khmelnytskyi itself, another phenotype (pink unbanded) was also found twice. Data for other parts of Ukraine (the east and especially the south) is so far very scarce.

In different settlements of Ukraine (Table 1), the most frequently observed specimens of *C. nemoralis* were those with yellow five-banded, pink unbanded, and yellow mid-banded shells, and somewhat less frequently those with pink five- and mid-band-

Table 1. Phenotypes of *C. nemoralis* recorded in different regions of Ukraine (numbers indicate the number of settlements, for more details see Appendix 1)

Administrative regions	Phenotypes								
	Y-0	Y-1	Y-3	Y-5	P-0	P-1	P-3	P-5	B-0
Western Ukraine									
Chernivtsi	–	–	–	–	–	1	1	–	–
Ivano-Frankivsk	1	4	2	4	7	6	1	4	–
Khmelnytskyi	–	–	–	3	1	–	–	–	–
Lviv	11	17	13	17	14	12	11	14	5
Rivne	–	1	2	1	1	1	–	1	–
Ternopil	2	2	2	2	2	2	2	2	1
Transcarpathian	–	–	–	–	–	–	–	2	–
Volyn	3	3	–	4	3	3	–	2	–
Central Ukraine									
Dnipropetrovsk	–	1	–	1	–	–	1	–	–
Poltava	–	–	–	–	–	1	–	–	–
Kyiv	2	5	4	5	9	3	2	5	2
Vinnytsia	–	–	1	–	–	–	–	–	–
Zhytomyr	–	–	–	1	–	–	–	–	–
Eastern Ukraine									
Donetsk	–	1	–	1	–	1	–	1	–
Kharkiv	–	1	–	1	1	1	–	1	–
Southern Ukraine									
Odesa	–	1	1	–	–	–	–	–	–
Number of regions	5	10	7	11	8	10	6	9	3
Number of localities	19	36	25	40	38	31	18	32	8

Table 2. Qualitative composition of phenotypes in *C. nemoralis* samples from western Ukraine (for the quantitative composition of samples, see Appendix 2)

Parameters	Sample size (number of specimens)		
	less than 20	from 20 to 50	more than 50
Number of samples	48	37	32
Number of phenotypes per sample			
Min–Max	1–8	2–8	2–9
Mean	3.3	4.4	6.1
Percentage of samples monomorphic for the following traits (combination of traits)			
Ground colour	20.8	8.1	–
Presence / absence of bands	37.5	29.7	3.1
Banding type	22.9	2.7	–
Ground colour and presence / absence of bands	14.6	2.7	–
Ground colour and banding type	12.5	–	–
Percentage of samples polymorphic for both traits			
Ground colour and banding type	68.7	89.2	100
Ground colour and presence / absence of bands	56.2	64.9	96.9
Percentage of samples missing the following phenotypes (phenotype groups)			
Unbanded	33.3	29.7	3.1
Unbanded with yellow colour	70.8	67.6	50.0
Unbanded with pink colour	43.8	35.1	12.5
Mid-banded	54.2	21.6	18.8
Three-banded	68.8	73.0	34.4
Five-banded	12.5	5.4	9.4
Yellow	8.3	5.4	–
Pink	16.7	2.7	–
Brown	95.8	91.9	78.1

Table 3. Variability of the phenotypic composition in *C. nemoralis* populations from western Ukraine and some other areas of Eastern Europe (for western Ukraine, only samples of 20 or more specimens were taken into account; if there were several such samples from one location, see Appendix 2, the average frequencies of phenotypes in them were used)

Phenotypes (phenotype groups)	Western Ukraine (this paper)		Moscow Region, Russia (Gural-Sverlova & Gural 2021a)		Minsk, Belarus (Gural-Sverlova & Kruglova 2022)	
	Mean	Min–Max	Mean	Min–Max	Mean	Min–Max
Phenotypes (B-0 is not mentioned because its frequencies almost always coincide with those of brown shells), %						
Y-0	6.1	0–43.4	2.4	0–21.6	10.1	0–38.4
Y-1	12.8	0–62.4	5.7	0–21.0	34.4	2.5–90.9
Y-3	4.2	0–61.4	2.5	0–17.4	1.7	0–9.9
Y-5	20.9	0–66.7	12.8	0–40.7	14.5	0–48.9
P-0	25.3	0–77.3	19.1	0–56.0	3.3	0–27.4
P-1	10.4	0–52.4	21.8	0–71.3	23.7	0–86.0
P-3	2.8	0–34.4	3.7	0–20.5	3.0	0–25.2
P-5	14.7	0–58.3	17.2	0–37.9	5.0	0–16.2
Phenotype groups, %						
Yellow	44.0	0–100	23.4	0–48.4	60.7	10.7–100
Pink	53.2	0–100	61.8	39.5–100	35.1	0–89.2
Brown	2.7	0–48.7	14.8	0–58.6	4.2	0–24.0
Unbaded	34.1	0–82.7	36.2	0–74.5	17.6	0–71.2
Mid-banded among banded	33.3	0–100	37.9	2.8–87.3	65.2	17.8–98.1
Three-banded among multi-banded	16.7	0–100	16.5	0–69.2	19.9	0–91.7
Light coloured (Y-0, Y-1, P-0, P-1)	54.6	0–100	49.0	17.8–89.4	71.5	32.6–97.0

ed shells. Other colouration variations, especially brown shells, can be considered rare or sporadically occurring. This, in general, coincided with the results of the qualitative (Table 2) and quantitative (Table 3) analysis of the phenotypic composition in western Ukrainian samples of *C. nemoralis*. The only exception was the rather frequent (more than 50%) absence of shells with one central band in small samples of this species (Table 2). On average, in the quantitatively analysed samples from western Ukraine, about 25% of specimens had a pink unbanded shell, and about 21% had a yellow shell with five bands (Table 3).

Samples from western Ukraine were usually polymorphic both in the shell colour and banding (Table 2). Even among small samples, this was true for more than half of them. As expected, the average number of phenotypes found increased with sample size, while the proportion of samples that are monomorphic for one or two traits decreased. In samples containing at least 20 specimens, monomorphism was most often manifested only in the presence/absence of bands due to the absence of unbanded shells. However, even in such cases, variability in ground colour and banding type (mid-banded, three-banded or five-banded) among banded shells almost always persisted.

The ratio of phenotypes in samples was very variable (Table 3). Any of the phenotypes, even the rarest one, could locally be the prevailing colouration variant. But most often it was a pink unbanded shell, especially where the proportion of the predominant phenotype was 50% or more (Table 4). On the other hand, any of the common phenotypes could be completely absent in some areas. Thus, of the 60 sites used for the quantitative analysis of the phenotypic composition in western Ukrainian populations of *C. nemoralis* (Table 3), the above-mentioned P-0 phenotype was prevailing at 22 sites and absent at eight.

Table 4. Percentage of sites where one of the phenotypes was prevailing (the total number of sites and the minimum size of the samples used in the calculations are similar to Table 3)

Phenotypes	Proportion of the prevailing phenotype	
	50% or more (26 sites)	less than 50% (34 sites)
Y-0	–	8.8
Y-1	11.5	5.9
Y-3	3.8	2.9
Y-5	15.4	23.5
P-0	50.0	26.5
P-1	3.8	14.7
P-3	–	5.9
P-5	15.4	5.9
B-0	–	5.9

On average, banded shells occurred at higher frequency than unbanded ones, multi-banded shells than mid-banded ones, and five-banded shells than three-banded ones (Table 3). However, the average number of light phenotypes, which we consider to include not only unbanded but also mid-banded shells with yellow and pink ground colours slightly exceeded that of darker ones (multi-banded and brown shells) (Table 3). Pink unbanded shells were present in more samples than yellow unbanded ones (Table 2).

DISCUSSION

The first reports of *C. nemoralis* findings in many settlements of Ukraine appeared quite recently, often in the last few years (Gural-Sverlova et al. 2024a, iNaturalist 2025, UkrBIN 2025). However, it is already safe to assume that we are witnessing the beginning of a rather rapid transformation of this species into a common component of urban fauna, at least in the western and central parts of the country. Somewhat earlier, a similar process was observed for another western invader, *Arion vulgaris* Moquin-Tandon, 1855 (Balashov et al. 2018), which is still the most widespread in western and central Ukraine (Gural-Sverlova et al. 2024b: fig. 19). Numerous garden centres, which often import seedlings of garden and ornamental plants from abroad, could have played a decisive role in both the initial penetration of both species into different parts of Ukraine and in their subsequent dispersal (Gural-Sverlova & Gural 2025a). Already a century ago, Boettger (1926) noted that both *C. nemoralis* and *C. hortensis* are easily spread along with garden plants, which even then made it problematic to determine the exact boundaries of their natural ranges.

Nowadays, seedlings are usually sold in containers with soil or a special potting mix. The overgrown roots together with the soil form a dense lump, which is transferred undamaged from the container to the planting site. This way, the root system of the seedling remains intact, and the seedling takes root better. On the other hand, this creates very favourable conditions for the unintentional dispersal of a number of land mollusc species. These could be eggs laid in the ground, juveniles and even adults using containers as shelters. It is no coincidence that recently formed populations of both *C. nemoralis* and the related species *C. hortensis* (secondary introductions of the latter) in western Ukraine are usually found at sites with young ornamental plantings, especially conifers, or near them (Gural-Sverlova et al. 2021a, Gural-Sverlova & Gural 2025b). These can be both public places and areas with private houses. We previously observed a similar pattern in the initial stages of the colonisation of Lviv by *A. vulgaris* (Gural-Sverlova et al. 2024b). However, due to its high locomotor activity, this species soon spread over almost all suitable urban habitats, becoming ubiquitous.

Cepaea species can be brought to garden centres repeatedly from different foreign sources, further increasing the phenotypic diversity of the populations formed there. Large batches of "infected" seedlings may also be delivered there at once. It is not without reason, that the greatest number of inherited variants of the shell colouration in both *C. nemoralis* and *C. hortensis* was discovered by us near two of the largest garden centres in the Lviv region: Plants Club in Pidbirtsi and Elit Flora in Horodok (Gural-Sverlova & Gural 2022a, 2025a). Thus, large populations of *Cepaea* can arise in garden centres and adjacent areas, facilitating not only their further dispersal along with the products sold, but also the maintenance of a sufficiently high level of phenotypic diversity in recently colonised regions.

When landscaping public and private areas, the phenotypic diversity of newly formed *Cepaea* populations, in addition to random factors (founder effect), obviously depends on the number of planted seedlings and the degree of their "infection" with *Cepaea*. It is not surprising that at those sites of Lviv and its immediate environs where we recorded a recent co-introduction of two *Cepaea* species, the phenotypic diversity of *C. nemoralis* was usually higher (Gural-Sverlova et al. 2024a). This may be due to the larger number of founder individuals. Where only *C. nemoralis* was introduced relatively recently, we often noted the absence of phenotypes less common in the study area: brown, three-banded, yellow unbanded shells, see Results. Moreover, a clearly pronounced predominance of one variant of the shell colouration was also more often observed there. Most commonly it was a pink unbanded or yellow mid-banded shell.

Secondary introductions of *C. hortensis*, coinciding in time with the beginning of the rapid dispersal of *C. nemoralis* over urbanised areas, have already led to the appearance in western Ukraine of many inherited colouration traits that were absent in the descendants of the primary introduction (second half of the 20th century). Among them there are both the colouration forms common for *C. hortensis* (yellow banded and pink shells), and rarer ones (brown shells) as well as traits that are sporadically found even in the natural range of this species (dark shell lip, banded shell with the absence of the second and fourth bands) (Gural-Sverlova & Gural 2023, 2025b). In another part of Eastern Europe, far distant from western Ukraine (Moscow region of Russia), where the first known populations of *C. hortensis* were discovered just over 10 years ago (Egorov 2015), shells with a dark lip were also recorded in one of them almost immediately (Egorov 2018: fig. 5F; Gural-Sverlova & Gural 2021b: fig. 5A). In the Moscow region, a dark lip was present only in some pink unbanded shells; other phenotypes (yellow unbanded, yellow banded, pink banded) had a light lip typical of *C. hortensis*, sometimes with only a slight pinkness in the columellar area (Gural-Sverlova & Gural 2021b). In western Ukraine, where the dark lip in *C. hortensis* has so far been recorded only from Lviv and the Lviv region, it is usually found in all pink shells in the population (both banded and unbanded), and somewhat less frequently also in all brown or some yellow shells (Gural-Sverlova & Gural 2025b). Thus, although *C. hortensis* has only recently appeared in many areas of Eastern Europe, two cases of independent importation of carriers of a rare allele causing atypical lip colouration have already been discovered there.

Unlike *C. hortensis*, both in Ukraine, with its best-studied western part, and in other areas of Eastern Europe, almost no colouration traits have been recorded in *C. nemoralis* that could be considered rare or sporadically occurring in the natural range. Even brown banded shells are almost completely absent here (Gural-Sverlova et al. 2021a: table 1). The only exception is an interesting population of *C. nemoralis* in the Ternopil region of Ukraine (Chortkiv), where many banded shells had the uneven pigmentation of bands, making them appear spotty, almost intermittent (*interrupta* form), sometimes longitudinally split (Gural-Sverlova & Lyzhechka 2021, Gural-Sverlova et al. 2021a: fig. 5). Such band colouration is inherited in a linked manner with the shell ground colour (Murray 1975). According to Schilder & Schilder (1957: map 77), there are two centres in Europe where this trait is most common and where it could have arisen independently: in the north (Denmark, northern Germany, see also Schlesch 1952, Schilder & Schilder 1953b) and the south (northern Italy and southern France up to the Pyrenees). In the first case, spotted bands are more often present in pink shells than in yellow ones. In the second case, rather the opposite trend is observed (Schilder & Schilder 1957: 165). In a large sample from Chortkiv that we examined in 2020 (Gural-Sverlova & Lyzhechka 2021), unevenly coloured (spotted) bands were present in about 18% of yellow and about 41% of pink banded shells.

In Ukrainian populations, as in other Eastern European populations of *C. nemoralis*, there is usually no variability in the lip colouration. However, at one site in Lviv we found three adult specimens with lighter coloured bands and lip: from a light pink lip combined with brownish-pink bands to hyalozonate bands, a pale shell and a white lip with a barely noticeable pinkish tint (Gural-Sverlova et al. 2021a: fig. 6). In another Lviv population, one juvenile with hyalozonate bands was discovered (Gural-Sverlova et al. 2021b). Although such colouration forms are heritable in *C. nemoralis* (Murray 1975), it is possible that these single individuals were modifications. For comparison: in some populations of *C. hortensis* with signs of secondary introductions observed in the Lviv region (Gural-Sverlova & Gural 2025b), hyalozonate (completely colourless and transparent) or more often just weaker pigmented bands can be present in a fairly large number of banded specimens. According to Schilder & Schilder (1957), a white

Table 5. Values of the inbreeding coefficient (Fst) in some European areas, according to literature data and our research (the frequencies of mid-banded shells were calculated from the number of banded ones)

Locality, country, literature source	Comments	Inbreeding coefficient Fst		
		Yellow	Unbanded	Mid-banded
Within the natural range				
Central England (Cameron & von Proschwitz 2020)	Well established populations	0.116	0.096	0.137
City of Sheffield, England (Cameron et al. 2009)	Within the natural range, but actively colonising the city only in the last decades	0.207	0.350	0.284
Outside of the natural range, Northern Europe				
City of Göteborg, Sweden (Cameron et al. 2014)	Introduced no later than the middle of the 19th century, increased spread in the last decades	0.212	0.302	0.277
Town of Skara, Sweden (Cameron & von Proschwitz 2025)	Introduced no earlier than the 21st century	0.152	0.179	0.109
Island of Gotland, Sweden (Cameron & von Proschwitz 2019)	First recorded in the second half of the 19th century, but remained uncommon and restricted through the first half of the 20th century	0.037	0.271	0.249
Island of Öland, Sweden (Cameron & von Proschwitz 2020)	Reliably recorded only in the 21st century	0.107	0.071	0.254
East of the natural range, Central Europe				
City of Wrocław, south-western Poland (Cameron et al. 2009)	Introduced over a century ago	0.089	0.092	0.123
Rural areas around city of Wrocław, south-western Poland (Pokryszko et al. 2012)	Probably recently established populations	0.137	0.249	0.314
Town of Kudowa Zdrój, south-western Poland (Cameron & von Proschwitz 2025)	Probably introduced no earlier than the late 20th - early 21st century	0.049	0.110	0.072
City of Rzeszów, south-eastern Poland, calculated based on data in Ożgo (2005), given according to Gural-Sverlova & Egorov (2021)	Introduced at the end of the 19th century	0.163	0.193	0.153
Subcarpathian Voivodeship, south-eastern Poland (similar to the previous)	5 settlements, including Rzeszów (see above)	0.194	0.218	0.186
All Poland (Ożgo et al. 2019)	Introduced to different parts of the country, possibly with the exception of its north (along the Baltic Sea)	0.219	0.250	0.284
East of the natural range, Eastern Europe				
City of Lviv, Ukraine (Gural-Sverlova & Kruglova 2022)	First attempt at introduction at the end of the 19th century, but active colonisation of the city in recent decades	0.263	0.225	0.390
Western Ukraine (this paper)	Four administrative regions, but mainly Lviv and its surroundings	0.238	0.314	0.396
City of Minsk, Belarus (Gural-Sverlova & Kruglova 2022)	Introduced probably no earlier than the late 20th or early 21st century	0.291	0.280	0.387
Moscow region, Russia (Gural-Sverlova & Egorov 2021)	First introduced in the early 1980s; Moscow and 7 other settlements	0.187	0.243	0.265

lip in combination with a well-expressed ground colour and dark bands, which cannot be considered a manifestation of albinism, is found in *C. nemoralis* only in limited areas, but within them it can be common. Such shells are not yet known from Eastern Europe.

A characteristic feature of the western Ukrainian populations of *C. hortensis* is the very high frequency of unbanded specimens, which we tend to interpret as a possible consequence of climatic selection in a more continental climate (Gural-Sverlova & Gural 2025b). In our samples of *C. nemoralis* from the same area, on average only about a third of individuals had unbanded shells (Table 3). Even if we additionally take into account shells with one central band, the total number of light phenotypes (Y-0, Y-1, P-0, and P-1) in *C. nemoralis* samples from western Ukraine is, on average, approximately 1.5 times lower than that of unbanded shells in *C. hortensis*. In other areas of Eastern Europe compared in Table 3, it exceeded 70% only in Minsk (Belarus), mainly due to the mid-banded shells frequently found there, and despite the low proportion of unbanded ones.

We cannot yet say what causes the differences in the proportion of light phenotypes in the two *Cepaea* species in western Ukraine. All the populations of *C. nemoralis* that we studied are still very young, while the descendants of the primary introduction of *C. hortensis* to western Ukraine had already widely spread in Lviv and the Lviv region before the beginning of the 21st century. It is possible that the influence of climatic selection may become more pronounced in western Ukrainian populations of *C. nemoralis* over time. Only long-term monitoring at model sites can confirm or refute this. It is also possible that *C. nemoralis* populations are more polymorphic, so that even strong climatic selection does not lead (or does not lead as quickly) to such a pronounced prevailing of any one phenotype or trait in them. Although even now, at sites where one phenotype clearly predominates (50% or more, see Table 4), it is more often light (usually pink unbanded, less often yellow with a central band), and not dark (yellow or pink with five bands). Based on the monograph by Schilder & Schilder (1957: table 13), who summarised the data on the phenotypic composition of two *Cepaea* species from different parts of their ranges, unbanded shells are found in *C. nemoralis*, in general, noticeably less frequently than in *C. hortensis*.

In the three best-studied areas of Eastern Europe (western Ukraine and especially Lviv with its immediate surroundings, the Moscow region in Russia, and Minsk in Belarus), presented in Table 3, not only the average level of phenotypic diversity (Gural-Sverlova & Kruglova 2022: table 3), but also the average ratio of different inherited traits (different variants of the shell ground colour and banding) and the phenotypes formed by their combination are quite similar. We had previously found statistically significant differences for only a few of them. Compared to western Ukraine, in the Moscow region yellow shells were significantly less common, and pink shells with one central band were significantly more common (Gural-Sverlova & Gural 2021a: table 2). In Minsk, the main differences from Lviv were related to the rare occurrence of pink unbanded shells and a high proportion of mid-banded ones (Gural-Sverlova & Kruglova 2022: table 3). In all cases, the variability of the phenotypic composition of populations within each studied area was very higher than the differences between areas.

Recently, the possible relationship between the level of phenotypic variability in introduced and/or urban populations of both *Cepaea* species and the time when they colonised certain areas has been analysed (Cameron et al. 2009, 2014, Cameron & von Proschwitz 2020, Gheoca et al. 2019, etc.). It has been suggested that a high level of variability, assessed by the inbreeding coefficient Fst, is characteristic of recently populated areas, both within the natural range and outside it (Cameron et al. 2009). However, low Fst values even in recently colonised areas may also be caused by common origin and/or strong climatic selection outside natural ranges (Cameron & von Proschwitz 2020, Gural-Sverlova & Gural 2022b). Populations of *C. nemoralis* from different regions of Eastern Europe show high Fst values (Table 5), which is quite expected given their youth and the high probability of heterogeneous origin (from different European countries through different garden centres or other routes).

ACKNOWLEDGEMENTS

We are grateful to all persons who helped us obtain material and information from different regions of Ukraine: Sofiia Savchuk (Head of the Botany and Zoology section of Junior Academy of Sciences of the Ivano-Frankivsk City Council), Orest Lyzhechka (Chortkiv, Ternopil region), Volodymyr Rizun (State Museum of Natural History, Lviv), Andrii Churilov (National University of Life and Environmental Sciences of Ukraine, Kyiv), Serhii Pisaryev (Karazin Kharkiv National University), Gennadii Romanov (Khmelnitskyi), Liubov Bezugla (Ternopil). We also thank all observers who posted their photographs of *C. nemoralis* in two citizen science databases (iNaturalist, UkrBIN) or on the social network Facebook.

REFERENCES

Alexander R. C. 1952. Introduced species of land snails in New Jersey. The Nautilus 65: 132–135.

Balashov I., Khomenko A., Kovalov V., Harbar O. 2018. Fast recent expansion of the Spanish slug (Gastropoda, Stylommatophora, Arionidae) across Ukraine. Vestnik Zoologii 52: 451–456.

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

Bąkowski J. 1880. Mięczaki zebrane w r. 1879 w okolicy Rzeszowa. Sprawozdanie Komisyi Fizyjograficznej 14: 254–257.

Boettger C. R. 1926. Die Verbreitung der Landschneckengattung *Cepaea* Held in Deutschland. Archiv für Molluskenkunde 58: 11–24.

Cameron R. A. D. 1997. *Cepaea* research 1900-1950; to many problems for a solution? Archives of Natural History 25: 401–412. https://doi.org/10.3366/anh.1998.25.3.401

Cameron R. A. D. 2013. The poor relation? Polymorphism in *Cepaea hortensis* (O. F. Müller) and the Evolution Megalab. Journal of Molluscan Studies 79: 112–117. https://doi.org/10.1093/mollus/eyt001

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., Proschwitz T. von, Horsák M. 2014. *Cepaea nemoralis* (L.) in Göteborg, S.W. Sweden: variation in a recent urban invader. Folia Malacologica 22: 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., Proschwitz T. von 2019. *Cepaea nemoralis* (L.) on Gotland, Sweden: spread and variation. Folia Malacologica 27: 307–313. https://doi.org/10.12657/folmal.027.027

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

Cameron R. A. D., Proschwitz T. von 2025. Variation in metapopulations of the polymorphic land snail *Cepaea nemoralis* (L.) in two small towns beyond its natural range. Folia Malacologica 33: 258–264. https://doi.org/10.12657/folmal.033.025

Chowdhury M., Johansen M., Davison A. 2024. Continuous variation in the shell colour of the snail *Cepaea nemoralis* is associated with the colour locus of the supergene. Journal of Evolutionary Biology 37: 1091–1100. https://doi.org/10.1093/jeb/voae093

Clarke B. C., Arthur W., Horsley D. T., Parkin D. T. 1978. Genetic variation and natural selection in pulmonate molluscs. In: Fretter V., Peake J. P. (eds). Pulmonates. Vol. 2A. Systematics, evolution and ecology. Academic Press, New York, pp. 219–270.

Cook L. M. 1998. A two-stage model for *Cepaea* polymorphism. Philosophical Transactions of the Royal Society of London Series B 353: 1577–1593. https://doi.org/10.1098/rstb.1998.0311

Egorov R. 2015. The first record of introduced snail *Cepaea hortensis* (Müller, 1774) (Stylommatophora: Helicidae) in the central part of European Russia. Ruthenica 25: 93–97.

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: 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 31: 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. 2021a. Polymorphism of the introduced snail *Cepaea nemoralis* (Gastropoda, Helicidae) from two distant parts of Eastern Europe: accidental similarity or regularity? Zoodiversity 55: 369–380. https://doi.org/10.15407/zoo2021.05.369

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

Gural-Sverlova N., Gural R. 2022a. Shell colouration and different introductions of the land snail *Cepaea hortensis* (Gastropoda: Helicidae) into Western Ukraine. Folia Malacologica: 30: 221–233. https://doi.org/10.12657/folmal.030.025

Gural-Sverlova N. V., Gural R. I. 2022b. Variability of the phenotypic composition of *Cepaea hortensis* (Gastropoda, Helicidae) in Western Ukraine: in space and time. Zoodiversity 56: 243–256. https://doi.org/10.15407/zoo2022.03.243

Gural-Sverlova N. V., Gural R. I. 2023. Two introduced *Cepaea* species (Gastropoda, Helicidae) in Ternopil, Western Ukraine, and specifics of their phenotypic composition. Zoodiversity 57: 507–520. https://doi.org/10.15407/zoo2023.06.507

Gural-Sverlova N. V., Gural R. I. 2025a. Garden centres and the alien land mollusk spread in the Lviv Region, Ukraine. Zoodiversity 59: 505–518. https://doi.org/10.15407/zoo2025.06.505

Gural-Sverlova N., Gural R. 2025b. Different introductions and the spread of *Cepaea hortensis* (Gastropoda, Helicidae) across Ukraine: new data and an impetus for further research. Folia Malacologica 33: 235–257. https://doi.org/10.12657/folmal.033.026

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: 51–62. https://doi.org/10.15407/zoo2021.01.051

Gural-Sverlova N. V., Gural R. I., Savchuk S. P. 2020. New records of *Cepaea nemoralis* (Gastropoda, Pulmonata, Helicidae) and phenotypic composition of its colonies in Western Ukraine. Ruthenica 30: 75–86. [in Russian] https://doi.org/10.35885/ruthenica.2021.30(2).1

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

Gural-Sverlova N. V., Lyzhechka O. F. 2021. First record of the grove snail *Cepaea nemoralis* (Gastropoda, Helicidae) in Ternopil region and specificity of the phenotypic composition of the found colony. Proceedings of the State Natural History Museum 37: 173–180. [in Ukrainian] https://doi.org/10.36885/nzdpm.2021.37.173-180

Gural-Sverlova N. V., Rodych T. V., Gural R. I. 2024a. Comparison of the spreading history of two introduced *Cepaea* species (Gastropoda, Helicidae) in Ukraine with remarks on their phenotypic variability. Zoodiversity 58: 39–58. https://doi.org/10.15407/zoo2024.01.039

Gural-Sverlova N., Zinenko O., Gural R., Shparyk V. 2024b. First record of *Arion ater* s. l. (Gastropoda, Arionidae) in Ukraine. Folia Malacologica 32: 247–258. https://doi.org/10.12657/folmal.032.021

iNaturalist 2025. iNaturalist: A Community for Naturalist. Available online at https://www.inaturalist.org (accessed 31 December 2025).

Howe J. L. 1898. Variation in the shell of Helix nemoralis in the Lexington, Va., colony. The American Naturalist 32 (384): 913–920.

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

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

Łomnicki M. 1899. Helix nemoralis L. Kosmos 23: 382.

Martynov V. V., Nikulina T. V. 2023. The first finding of *Cepaea nemoralis* (Linnaeus, 1758) (Mollusca: Gastropoda: Helicidae) in Donbass and the phenetic structure of the identified colony. Russian Journal of Biological Invasions 14: 361–367. https://doi.org/10.1134/S2075111723030128

Mukhanov A. V., Lisitsyn P. A. 2018. New data on distribution of two alien species of the land snail of the family Helicidae in European Russia. Russian Journal of Biological Invasions 9: 57–62.

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

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. 2008. Current problems in the research of *Cepaea* polymorphism. Folia Malacologica 16: 55–60. https://doi.org/10.12657/folmal.016.009

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 M., 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-expanded species. Biological Journal of the Linnean Society 127: 1–11. https://doi.org/10.1093/biolinnean/blz029

Peltanová A., Dvořák L., Juřičková L. 2012. The spread of non-native *Cepaea nemoralis* and *Monacha cartusiana* (Gastropoda: Pulmonata) in the Czech Republic with comments on other land snail immigrants. Biologia 67: 384–389.

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: 87–98. https://doi.org/10.2478/v10125-012-0012-4

Schilder F. A., Schilder M. 1953a. Die Bänderschnecken. Eine Studie zur Evolution der Tiere. Gustav Fischer Verlag, Jena.

Schilder F. A., Schilder M. 1953b. Nochmals über *Cepaea nemoralis interrupta* Moquin-Tandon. Archiv für Molluskenkunde 82: 71–75.

Schilder F. A., Schilder M. 1957. Die Bänderschnecken. Eine Studie zur Evolution der Tiere. Schluß: Die Bänderschnecken Europas. Gustav Fischer Verlag, Jena.

Schlesch H. 1952. Die Verbreitung von *Cepaea nemoralis interrupta* und andere Binnenmollusken im südwestlichen Ostseegebiet in Beziehung zur Kontinentalzeit. Archiv für Molluskenkunde 81: 127–131.

Schnetter M. 1950. Veränderungen der genetischen Konstitution in natürlichen Populationen der polymorphen Bänderschnecken. Verhandlungen der Deutschen Zoologischen Gesellschaft 13: 192–206.

SILVERTOWN J., COOK L., CAMERON R., DODD M., MCCONWAY K., WORTHINGTON J., SKELTON P., ANTON C., BOSSDORF O., BAUR B., SCHILTHUIZEN M., FONTAINE B., SATTMANN H., BERTORELLE G., CORREIA M., OLIVEIRA C., POKRYSZKO B., OŻGO M., STALAŽS A., GILL E., RAMMUL Ü., SÓLYMOS P., FÉHER Z., JUAN X. 2011. Citizen science reveals unexpected continental-scale evolutionary change in a model organism. PLoS ONE 6: e18927. https://doi.org/10.1371/journal.pone.0018927

SVERLOVA N. 2002a. Einschleppung und Polymorphismus der *Cepaea*-Arten am Beispiel von Lwow in der Westukraine (Gastropoda: Pulmonata: Helicidae). Malakologische Abhandlungen des Staatlichen Museums für Tierkunde Dresden 20: 267–274.

SVERLOVA N. V. 2002b. The influence of anthropogenic barriers on phenotypical structure of populations of *Cepaea hortensis* (Gastropoda, Pulmonata) under urban conditions. Vestnik zoologii 36: 61–64. [in Russian]

SVERLOVA N. 2004. Landschnecken-Farbpolymorphismus aus physikalischen Gründen (Gastropoda: Pulmonata: Stylommatophora). Malakologische Abhandlungen des Staatlichen Museums für Tierkunde Dresden 22: 131–145.

SVERLOVA N. V. 2006. On the distribution of some species of land molluscs on the territory of Ukraine. Ruthenica 16: 119–139. [in Russian]

UKRBIN 2025. UkrBIN: Ukrainian Biodiversity Information Network [public project & web application]. Available online at https://www.ukrbin.com (accessed 31 December 2025)

URBAŃSKI J. 1933. Mięczaki z okolic Rawy Ruskiej i z kilku innych miejscowości na Roztoczu Lwowsko-Tomaszowskiem. Sprawozdanie Komisyi Fizyjograficznej Polskiej Akademji Umiejętności 67: 43–98.

Received: January 31st, 2026
Revised: March 15th, 2026
Accepted: March 16th, 2026
Published on-line: April 20th, 2026

APPENDIX 1

The shell colouration of *C. nemoralis* recorded in different localities of Ukraine: ap2 – for quantitative data see Appendix 2, FB – Facebook, iN – iNaturalist, LD – literature data, PM – personal messages from other observers, supported by photographs, PO – personal observations of the authors, SOC – samples of other collectors, UB – UkrBIN. The asterisks indicate the settlements, the samples from which are stored in the malacological collection of the State Museum of Natural History in Lviv, Ukraine. For other designations, see Material and Methods

Settlements	Years	Phenotypes									Information sources
		Y-0	Y-1	Y-3	Y-5	P-0	P-1	P-3	P-5	B-0	
Chernihiv region											
Pryluky	2023	–	–	–	–	–	?	?	–	–	iN
Chernivtsi region											
Chernivtsi	2018–2025	–	–	–	–	–	+	+	–	–	FB, iN
Dnipropetrovsk region											
Novooleksandrivka	2021	–	+	–	+	–	–	+	–	–	UB
Donetsk region											
Donetsk	2022	–	+	–	+	–	+	–	+	–	LD, ap2
Ivano-Frankivsk region											
*Ivano-Frankivsk	2019–2025	–	+	–	–	+	+	–	–	–	PO, iN, ap2
*Burshtyn	2025	–	–	–	–	–	+	–	–	–	PO
*Bohorodchany	2019	–	+	–	+	+	+	–	+	–	PO, ap2
Dzvyniach	2025	–	–	–	–	–	–	–	+	–	UB
*Huta	2024	–	–	–	–	+	–	–	–	–	PO
Khomiakivka	2025	–	–	–	–	–	–	+	–	–	iN
Nadvirna	2022–2023	–	–	+	–	+	–	–	–	–	iN
near Solotvyn	2023	–	–	–	–	–	+	–	–	–	iN
*Stara Huta	2024	+	+	–	+	+	+	–	+	–	PO, iN, ap2
*Uhryniv	2018–2019	–	–	+	+	+	+	–	+	–	PO, iN, UB, ap2
*Zahvizdia	2025	–	+	–	+	+	–	–	–	–	PO, ap2
Kharkiv region											
Kharkiv	2019–2025	–	+	–	+	+	+	–	+	–	iN, FB
Khmelnytskyi region											
*Khmelnytskyi and surroundings	2020–2025	–	–	–	+	+	–	–	–	–	iN, PM, SOC, UB, ap2
Dunaivtsi district	2023	–	–	–	+	–	–	–	–	–	iN
Kytaihorod	2007 or 2008	–	–	–	+	–	–	–	–	–	SOC

Settlements	Years	Phenotypes									Information sources
		Y-0	Y-1	Y-3	Y-5	P-0	P-1	P-3	P-5	B-0	
Kyiv region											
Kyiv	2019–2025	+	+	+	+	+	+	+	+	+	iN, FB
*Boiarka	2025	–	+	–	–	+	+	–	+	–	iN, SOC, ap2
near Boryspil (airport)	2024	–	–	–	–	+	–	–	+	–	iN
Bucha	2023	–	–	–	–	+	–	–	–	–	iN
Chabany	2024	–	–	–	+	+	?	?	–	–	iN
Irpin	2023–2025	–	+	–	–	+	–	–	–	?	iN
near Liutezh	2025	–	–	+	–	–	–	–	–	–	iN
Romankiv	2022	–	–	–	+	–	–	–	–	–	iN
Severynivka	2020	–	–	+	–	–	–	–	–	–	iN
Shkarivka	2021	–	+	–	–	–	–	–	–	–	iN, UB
Sofiivska Borshchahivka	2020–2025	+	+	+	+	+	+	+	+	+	iN, LD
near Supii Lake	2021	–	?	?	–	–	–	–	–	–	iN
Vyshhorod and surroundings	2019–2020	–	–	–	+	+	–	–	+	–	iN, LD, UB
Zabíria	2018	–	–	–	–	+	–	–	–	–	iN
Lviv region											
*Lviv	2019–2025	+	+	+	+	+	+	+	+	+	PO, iN, ap2
*Birky	2024	–	–	+	+	–	–	–	–	–	PO
*Briukhovychi	2024	+	+	+	+	+	+	+	+	+	PO, ap2
near *Davydiv	2021–2024	–	+	+	+	+	+	–	+	–	PO, ap2
*Horishnii	2025	–	+	–	?	+	–	–	–	+	PO
*Horodok	2023	+	+	+	+	+	+	+	+	+	PO, ap2
*Konopnytsia	2023	–	+	+	+	–	+	+	+	–	PO, ap2
*Malekhiv	2022–2025	–	–	+	+	+	–	–	+	–	PO, ap2
*Mostyska	2025	–	+	–	+	+	+	–	–	–	PO
*Pidbirtsi	2021–2024	+	+	+	+	+	+	+	+	+	PO, ap2
*Rava-Ruska	2024	+	+	–	+	–	+	–	–	–	PO, ap2
Rudno and surroundings	2022–2025	+	+	+	+	+	+	+	+	–	PO, ap2
*Sambir	2025	+	+	+	+	–	–	+	–	–	PO, ap2
*Sokilnyky	2023–2025	+	+	–	+	+	–	+	+	–	PO, ap2
*Solonka	2021–2023	–	+	–	+	+	+	+	+	–	PO, ap2
near Staryi Sambir	2023	+	–	–	–	–	–	–	–	–	UB
*Stebnyk	2023–2024	+	–	+	–	+	+	–	+	–	PO, ap2
*Stryi	2025	–	+	–	+	–	+	+	+	–	PO, ap2
*Truskavets	2025	–	+	+	–	–	–	+	+	–	SOC, iN
Vynnyky	2024	–	–	–	–	+	–	–	–	–	iN
*Zubra	2019–2020	+	+	–	+	+	–	–	+	–	PO, ap2
Zymna Voda	2023	–	+	+	+	–	–	–	–	–	PO, ap2
Odesa region											
Odesa	2020–2021	–	+	+	–	–	–	–	–	–	iN, LD
Poltava											
Kremenchuk	2020	–	–	–	–	–	+	–	–	–	FB
Rivne region											
Rivne	2022–2025	–	+	+	+	+	+	–	+	–	iN
Sarny	2018	–	–	+	–	–	–	–	–	–	UB
Ternopil region											
*Ternopil	2022–2023	+	+	+	+	+	+	+	+	+	PO, FB, ap2
*Chortkiv	2017–2021	+	+	+	+	+	+	+	+	–	SOC, PM, UB, ap2
Transcarpathian region											
Uzhhorod	2023–2024	–	–	–	?	–	–	–	+	–	iN
Berehove	2025	–	–	–	–	–	–	–	+	–	iN

Settlements	Years	Phenotypes									Information sources
		Y-0	Y-1	Y-3	Y-5	P-0	P-1	P-3	P-5	B-0	
Volyn region											
*Lutsk	2025	–	+	–	+	–	–	–	–	–	PO, iN
Khobultova	2025	+	–	–	–	–	–	–	–	–	iN
Kovel	2020–2023	+	–	–	+	–	+	–	–	–	iN
Novovolynsk and surroundings	2021–2023	–	?	?	–	+	?	?	–	–	FB, iN
Rozhyshche	2022	–	–	–	+	–	–	–	–	–	FB
*Svitiaz	2021	+	+	–	+	+	+	–	+	–	SOC, ap2
*Volodymyr and surroundings	2022–2025	?	+	–	?	+	+	–	+	–	PO, iN, ap2
Vinnytsia region											
Vinnytsia	2024	–	–	+	–	–	–	–	–	–	iN
Zhytomyr region											
Zhytomyr	2018	–	–	–	+	–	–	–	–	–	UB
Berdychiv	2023	–	–	–	–	–	–	?	?	–	iN

APPENDIX 2

Composition of *C. nemoralis* samples from Ukraine. Pluses indicate the phenotypes that were observed only in immature individuals. Samples marked with one asterisk were collected by the first and third authors; those marked with two asterisks were collected by the second author. For other designations, see Material and Methods

Settlements	Coordinates	Years	Phenotypes									Total
			Y-0	Y-1	Y-3	Y-5	P-0	P-1	P-3	P-5	B-0	
Donetsk region (Martynov & Nikulina 2023)												
Donetsk	48°00'44.4"N, 37°48'06.7"E	2022	–	44	–	24	–	229	–	69	–	366
Ivano-Frankivsk region												
Ivano-Frankivsk	48°56'49.6"N, 24°41'48.2"E	2019*	–	+	–	–	9	3	–	–	–	12
Bohorodchany	48°48'42.3"N, 24°32'31.7"E	2019*	–	–	–	29	66	–	–	–	–	95
	48°48'46.9"N, 24°32'34.3"E	2019*	–	3	–	58	97	5	–	196	–	359
Stara Huta	48°37'27.2"N, 24°12'49.8"E	2024*	4	2	–	5	18	1	–	2	–	32
Uhryniv	48°57'26.8"N, 24°41'25.8"E	2019*	–	–	1	1	2	+	–	3	–	7
Zahvizdia	48°56'08.9"N, 24°41'01.5"E	2025*	–	2	–	1	3	–	–	–	–	6
Khmelnytskyi region												
Khmelnytskyi	49°24'28.4"N, 26°57'43.3"E	2022	–	–	–	5	–	–	–	–	–	5
Kyiv region												
Boiarka	50°18'24.0"N, 30°18'28.5"E	2025	–	3	–	–	3	2	–	1	–	9
Lviv region												
Lviv	49°49'34.9"N, 23°54'34.7"E	2022**	30	3	–	14	122	14	–	20	–	203
	Ibidem	2022*	2	1	–	1	3	+	–	+	–	7
	49°49'16.0"N, 23°55'03.5"E	2020**	4	282	66	–	590	186	39	–	–	1167
	Ibidem	2020*	–	34	11	–	99	31	8	–	–	183
	Ibidem	2025**	5	1324	373	2	2777	804	208	1	–	5494
	49°49'31.0"N, 23°56'09.2"E	2021*	–	8	–	11	1	–	–	–	–	20
	49°49'31.4"N, 23°57'27.9"E	2020*	–	+	–	4	–	1	1	1	–	7
	49°49'33.0"N, 23°57'43.1"E	2020–2021*	–	16	–	3	–	14	–	2	–	35
	49°49'47.0"N, 23°58'06.3"E	2025**	–	4	3	1	–	11	8	3	–	30
	49°49'53.1"N, 23°58'33.0"E	2020*	–	48	–	28	–	8	–	6	–	90
	49°49'51.8"N, 23°58'44.4"E	2022**	–	–	35	35	24	–	3	5	–	102
	Ibidem	2022–2023*	–	+	18	14	12	–	+	2	–	46
	49°48'59.6"N, 23°57'19.6"E	2020*	–	4	–	19	294	19	–	52	–	388
	49°49'09.7"N, 23°57'35.0"E	2020**	1	28	–	17	37	5	–	7	–	95
	Ibidem	2021*	–	2	–	2	3	–	–	–	–	7
	49°49'07.1"N, 23°57'36.8"E	2021**	–	8	–	6	11	13	–	2	–	40

Settlements	Coordinates	Years	Phenotypes									Total
			Y-0	Y-1	Y-3	Y-5	P-0	P-1	P-3	P-5	B-0	
Lviv	49°48'49.5"N, 23°58'32.6"E	2021*	–	4	–	42	15	6	–	25	–	92
	49°48'41.1"N, 23°58'24.6"E	2022**	–	–	–	4	11	–	–	6	–	21
	Ibidem	2024**	–	–	–	3	3	–	–	5	–	11
	49°48'37.0"N, 23°58'23.6"E	2022**	–	9	–	5	20	14	–	5	–	53
	Ibidem	2022*	–	8	–	5	18	5	–	5	–	41
	49°48'41.5"N, 23°58'29.1"E	2024**	–	–	–	5	–	–	–	11	–	16
	49°48'46.1"N, 23°58'31.3"E	2023**	–	–	–	15	–	–	–	21	–	36
	49°48'48.2"N, 23°58'36.1"E	2022–2024**	–	–	–	3	–	–	–	12	–	15
	49°48'37.2"N, 23°58'44.5"E	2022**	–	29	–	5	–	13	–	1	–	48
	Ibidem	2022*	2	27	–	4	1	7	–	1	–	42
	49°48'32.1"N, 24°00'57.5"E	2022**	–	2	1	3	7	–	–	–	–	13
	49°48'10.0"N, 24°00'06.5"E	2022–2023**	2	–	–	5	4	–	–	1	+	12
	Ibidem	2023–2025*	5	–	–	1	–	–	–	1	–	7
	49°48'11.4"N, 24°00'29.8"E	2022**	–	–	–	5	17	–	–	–	–	22
	Ibidem	2023*	–	–	–	2	11	–	–	–	–	13
	Ibidem	2024**	–	–	–	3	5	–	–	–	–	8
	49°48'10.9"N, 24°00'38.6"E	2022**	2	–	–	23	4	2	–	19	–	50
	Ibidem	2023–2025*	–	+	–	10	–	–	–	9	–	19
	Ibidem	2024**	–	–	–	2	–	–	–	2	–	4
	49°47'58.7"N, 24°02'05.9"E	2020*	–	63	5	–	–	18	8	–	13	107
	Ibidem	2023*	–	24	2	1	–	15	2	1	6	51
	49°47'50.3"N, 24°03'00.7"E	2022*	–	3	–	9	–	4	–	4	–	20
	49°48'46.1"N, 23°59'59.3"E	2024–2025**	–	10	1	11	–	9	–	1	–	32
	49°49'00.4"N, 23°59'49.3"E	2023–2024**	–	22	8	4	41	–	–	–	11	86
	49°49'00.9"N, 23°59'50.7"E	2023–2025**	–	13	–	1	6	–	–	–	19	39
	49°48'58.5"N, 24°00'03.1"E	2025**	–	3	–	–	–	–	–	–	–	3
	49°49'05.8"N, 23°59'46.4"E	2023–2024**	–	2	–	5	17	8	–	4	–	36
	49°49'05.4"N, 23°59'46.7"E	2023–2024**	–	–	–	–	16	2	–	3	–	21
	49°49'08.4"N, 23°59'40.3"E	2023–2025**	–	4	–	1	–	12	–	1	–	18
	49°49'20.1"N, 24°00'01.1"E	2020–2021*	28	–	20	23	1	–	3	7	–	82
	49°49'27.6"N, 24°00'23.9"E	2020*	–	1	7	12	19	1	4	7	–	51
	49°49'37.4"N, 24°00'17.4"E	2023*	–	–	–	10	–	–	–	–	–	10
	49°49'39.6"N, 24°00'10.8"E	2023*	–	–	13	2	–	–	2	2	–	19
	49°49'43.2"N, 24°00'14.8"E	2022–2023*	–	1	–	17	–	–	–	23	–	41
	49°49'38.5"N, 23°59'51.9"E	2024–2025**	–	–	–	–	10	2	1	1	–	14
	49°49'59.8"N, 24°00'26.1"E	2022–2023*	5	17	–	4	1	4	–	3	8	42
	49°49'47.8"N, 24°01'32.8"E	2020–2021*	14	5	1	16	2	2	1	–	21	62
	49°50'06.3"N, 24°01'34.3"E	2019–2020*	–	4	13	24	33	5	7	14	3	103
	49°50'05.8"N, 24°01'57.6"E	2022*	–	–	–	1	1	–	–	1	–	3
	49°49'39.4"N, 24°01'06.9"E	2023*	–	–	–	8	–	–	–	–	–	8
	49°49'35.9"N, 24°01'31.4"E	2023*	–	–	1	2	6	–	–	1	–	10
	49°49'17.3"N, 24°01'12.8"E	2023**	–	6	–	4	3	8	1	3	–	25
	49°49'07.2"N, 24°01'32.8"E	2023–2025**	–	1	–	22	10	–	–	–	–	33
	49°48'47.2"N, 24°01'21.1"E	2019–2020*	5	120	23	291	73	66	27	127	–	732
	Ibidem	2020**	2	8	4	14	3	5	3	5	–	44
	Ibidem	2024*	–	11	–	19	10	13	3	21	–	77
	49°48'59.4"N, 24°02'22.3"E	2023*	2	1	2	–	–	+	1	+	–	6
	49°48'59.7"N, 24°02'03.5"E	2023–2024**	–	11	–	10	–	14	1	6	–	42
	Ibidem	2023*	–	6	–	1	–	8	–	4	–	19
	49°49'27.5"N, 24°02'49.5"E	2019–2020*	13	7	4	6	6	9	7	8	–	60
	Ibidem	2019**	2	1	–	–	1	1	3	1	–	9

Settlements	Coordinates	Years	Phenotypes									Total
			Y-0	Y-1	Y-3	Y-5	P-0	P-1	P-3	P-5	B-0	
Lviv	Ibidem	2023**	2	1	1	1	2	5	3	3	–	18
	49°49'51.4"N, 24°02'50.2"E	2021*	–	–	1	3	17	–	9	23	–	53
	49°49'51.3"N, 24°02'17.9"E	2023*	–	1	–	2	–	11	–	7	–	21
	49°50'08.8"N, 24°02'30.0"E	2021–2023*	–	–	5	–	6	–	1	–	–	12
	49°50'10.8"N, 24°02'48.0"E	2023*	1	10	–	52	–	5	–	33	–	101
	49°50'22.5"N, 24°02'10.4"E	2022*	–	4	–	4	–	6	–	10	–	24
	49°50'34.9"N, 24°01'38.7"E	2023*	4	–	–	+	11	–	–	2	–	17
	49°50'29.6"N, 24°01'20.9"E	2020*	–	–	–	10	48	–	–	7	–	65
	49°50'25.5"N, 24°01'13.5"E	2024*	4	–	–	7	–	–	–	–	–	11
	49°50'24.6"N, 24°01'09.9"E	2024*	2	–	–	–	10	–	–	4	–	16
	49°50'23.8"N, 24°01'09.8"E	2023–2024*	–	–	–	5	18	–	–	3	–	26
	Ibidem	2024**	–	–	–	–	17	–	–	–	–	17
	49°50'59.9"N, 24°00'17.8"E	2023*	4	–	–	3	10	–	–	9	–	26
	49°52'03.1"N, 24°00'58.9"E	2022*	–	+	–	+	1	+	–	+	2	3
Briukhovychi	49°53'44.1"N, 23°57'15.5"E	2024*	1	5	–	21	–	–	–	1	7	35
	49°53'55.9"N, 23°57'36.8"E	2024*	1	5	3	2	1	6	1	–	+	19
near Davydiv	49°45'59.8"N, 24°06'34.8"E	2021–2024*	–	2	1	6	14	3	–	3	–	29
Horodok	49°47'25.6"N, 23°42'54.1"E	2023*	20	14	3	27	23	12	+	12	19	130
Konopnytsia	49°48'35.0"N, 23°51'25.8"E	2023*	–	+	2	2	–	1	1	4	–	10
Malekhiv	49°53'00.6"N, 24°04'32.2"E	2022–2025*	–	–	+	1	2	–	–	5	–	8
Pidbirtsi	49°50'30.1"N, 24°09'04.9"E	2021*	5	2	1	5	8	3	2	–	–	26
	Ibidem	2024*	14	19	14	24	13	7	2	15	1	109
Rava-Ruska	50°14'23.9"N, 23°37'08.5"E	2024*	2	3	–	2	–	4	–	–	–	11
Rudno and surroundings	49°50'13.2"N, 23°52'59.2"E	2023–2024**	10	1	–	13	12	3	–	6	–	45
	49°50'06.9"N, 23°52'59.0"E	2023**	–	–	–	1	4	3	–	2	–	10
	49°50'06.7"N, 23°52'57.3"E	2023–2024**	6	–	–	–	11	–	–	5	–	22
	49°50'17.4"N, 23°53'42.6"E	2023–2025**	–	–	–	13	–	–	–	–	–	13
	49°50'18.5"N, 23°53'39.3"E	2025**	–	–	1	3	–	–	–	–	–	4
	49°50'46.5"N, 23°53'15.2"E	2024–2025**	1	–	–	11	5	2	–	20	–	39
	49°50'58.0"N, 23°53'14.0"E	2023–2025**	1	6	11	15	14	11	17	15	–	90
Sambir	49°31'22.1"N, 23°13'18.5"E	2025*	16	–	27	–	–	–	1	–	–	44
Sokilnyky	49°47'05.8"N, 23°59'48.3"E	2025*	23	–	–	3	44	–	4	7	–	81
Solonka	49°44'57.2"N, 23°59'40.4"E	2021–2023*	–	1	–	1	1	2	2	3	–	10
Stebnyk	49°18'34.2"N, 23°30'28.9"E	2023–2024*	3	–	+	–	2	1	–	+	–	6
Stryi	49°15'17.1"N, 23°51'04.6"E	2025*	–	1	–	2	–	2	1	2	–	8
Zubra	49°46'42.7"N, 24°03'05.0"E	2019–2020*	23	9	–	18	1	–	–	2	–	53
Zymna Voda	49°49'49.9"N, 23°54'12.5"E	2023**	–	18	6	19	–	–	–	–	–	43
Ternopil region												
Ternopil	49°33'23.4"N, 25°38'55.9"E	2023*	79	14	2	1	85	104	22	15	–	322
	49°33'02.3"N, 25°37'47.6"E	2023*	–	1	–	11	–	–	–	–	2	14
	49°33'09.8"N, 25°35'25.5"E	2025*	13	–	–	1	1	–	–	–	–	15
Chortkiv	49°01'32.1"N, 25°47'34.9"E	2020	3	6	34	28	2	5	77	69	–	224
Volyn region												
Svitiaz	51°29'22.4"N, 23°52'21.2"E	2021	2	1	–	1	4	+	–	7	–	15
Volodymyr	50°51'19.0"N, 24°19'21.9"E	2025*	–	–	–	–	21	9	–	–	–	30