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COMPARISON OF THE SPREADING HISTORY OF TWO INTRODUCED *CEPAEA* SPECIES (GASTROPODA, HELICIDAE) IN UKRAINE WITH REMARKS ON THEIR PHENOTYPIC VARIABILITY

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Comparison of the Spreading History of Two Introduced *Cepaea* Species (Gastropoda, Helicidae) in Ukraine with Remarks on Their Phenotypic Variability. Gural-Sverlova, N. V., Rodych, T. V., Gural, R. I. — Trends of the current dispersal of *Cepaea nemoralis* and *C. hortensis* in Ukraine are analysed, which are closely related to the activities of several garden centres, which export a part of the sold seedlings of ornamental and garden plants from other European countries. Using Lviv and its environs as an example, we compared the qualitative and quantitative phenotypic composition of *C. nemoralis* at sites where both *Cepaea* species or only *C. nemoralis* were recently introduced. On average, the former were characterised by a greater phenotypic diversity of *C. nemoralis*, which may be due to a greater number of founding individuals of such colonies. At the sites of the second group, hereditary traits (brown ground colour, shell with three lower bands) or phenotypes (yellow unbanded), which are less common in the study area, were more often absent. Also, a clearly pronounced predominance of any one variant of the shell colouration was more often noted there, most often pink unbanded or yellow mid-banded.
Key words: land mollusks, *Cepaea nemoralis*, *Cepaea hortensis*, polymorphism, Ukraine.

Introduction

Cepaea nemoralis (Linnaeus, 1758) and *C. hortensis* (O. F. Müller, 1774) are among the best known species of European terrestrial mollusks. Many publications have been devoted to the colour and banding polymorphism of their shells, including a number of generalizations and discussions (Cameron, 1997; Clarke et al., 1978; Cook, 1998; Jones et al., 1977; Schilder & Schilder, 1957; Sverlova, 2004). The first species is of Western European origin, the second one is of Central European origin (Boettger, 1926; Taylor, 1914), and their natural ranges partially overlap and covering large areas of Western, Central, and Northern Europe.

For Ukraine, both *Cepaea* species are alien. Although the first attempt to introduce *C. nemoralis* to the west of the country (to Lviv) was made already at the end of the 19th century (Łomnicki, 1899), most of the reliable records of this species in Ukraine were made only in recent years (Balashov & Markova, 2021; Gural-Sverlova & Gural, 2021 a; Gural-Sverlova et al., 2020, 2021 b). The rapid spreading of *C. nemoralis* in settlements is now observed also in other Eastern European countries, which can be associated both with global climate change and with the activities of numerous garden centres that import seedlings of ornamental and garden plants (Gural-Sverlova et al., 2021 a).

C. hortensis was introduced into Western Ukraine no later than the 1970s (Gural-Sverlova & Gural, 2021 b). When our observations began in the late 1990s, it was a typical representative of Lviv's terrestrial mollusk fauna (Sverlova, 2002 b). Recently, however, thanks to the activities of the same garden centres, the shell colouration variants that are not typical for the descendants of the primary introduction began to appear here (Gural-Sverlov & Gural, 2022 a, b). Often these phenotypes are found together with relatively young colonies of *C. nemoralis*, which may indicate a possible joint introduction of the two species with ornamental plants from garden centres (Gural-Sverlova & Gural, 2021 b).

In this paper, using Lviv and its immediate environs as an example, we aim to assess the frequency of co-introductions of *C. nemoralis* and *C. hortensis*, and to compare the phenotypic diversity of *C. nemoralis* from sites where such introductions were or were not recorded. We also want to compare current trends in the spread of both *Cepaea* species in Ukraine, particularly in the western part of the country.

Material and Methods

The phenotypic composition of *C. nemoralis* samples was analyzed at 36 sites in Lviv and its immediate environs (Malekhiv, Pidbirtsi, Solonka, Zubra), where at least 10 adults or juveniles with a shell diameter of at least 1 cm were collected in 2019–2022. Since dark spiral bands in *Cepaea* do not appear immediately and simultaneously on the shells of juveniles (Andreassen 1978; Lang, 1904; Sverlova, 2002 a, 2004), the use of smaller snails can lead to incorrect identification of phenotype groups. The coordinates of the studied sites are given in table 1.

If the studied colonies were found close to each other and could have a common origin, such sites were designated by the same number with different lowercase letters. For example, this applies to different ornamental plantings in the Pivdennyi market (sites 10 a, 10 b and 10 c), separated by rather large anthropogenic barriers that prevent the free movement of snails.

For quantitative analysis, only 28 sites were used, where at least 20 adult live snails or their empty shells were collected. If two independent collections by different authors were carried out on the same site (sites 2, 10 c, 11), the average frequencies of phenotype groups were used for calculations.

As in previous publications (Gural-Sverlova & Gural, 2021 a; Gural-Sverlova & Kruglova, 2022; Gural-Sverlova et al., 2021 b), the collected phenotypes of *C. nemoralis* were divided into 9 groups according to the combination of the shell ground colour and banding:

Y-0 — yellow unbanded;
Y-1 — yellow mid-banded (with one central band);
Y-3 — yellow three-banded (with three lower bands);
Y-5 — yellow five-banded;
P-0, P-1, P-3, P-5 — similar for pink shells;
B-0 — brown unbanded.

About the nature of inheritance of these traits, see Murray (1975). The group of yellow shells traditionally included not only those with different yellow intensity, but also shells with a white ground colour (Gural-Sverlova & Gural, 2022 b: fig. 12), which are less common in *C. nemoralis*. In *C. hortensis*, white and yellow shells were considered separately, which is of particular importance for studying the spreading history of this species in Ukraine (Gural-Sverlova & Gural, 2021 b, 2022 a, b). Orange shells in both species were assigned to the pink group.

At all the studied sites, the presence or absence of such specimens of *C. hortensis* was additionally noted, which had the shell colouration variants, absent in the descendants of the primary introduction of the spe-

Table 1. Phenotypic composition of *C. nemoralis* samples from Lviv and its immediate environs

Settle-ments	Coordinates	Total**	Y-0	Y-1	Y-3	Y-5	P-0	P-1	P-3	P-5	B-0	Comments
Lviv-1*	49°49'34.9"N 23°54'34.7" E	203	30	3	–	14	122	14	–	20	–	–
Lviv-2*	49°49'16.0"N 23°55'03.5" E	1167	4	282	66	–	590	186	39	–	–	–
Lviv-2	Re-sampling	183	–	34	11	–	99	31	8	–	–	–
Lviv-3	49°49'31.0"N 23°56'09.2" E	20	–	7	1	11	1	–	–	–	–	–
Lviv-4	49°49'31.4"N 23°57'27.9" E	7	–	+	–	4	–	1	1	1	–	–
Lviv-5	49°49'33.0"N 23°57'43.1" E	35	–	16	–	3	–	14	–	2	–	–
Lviv-6	49°49'53.1"N 23°58'33.0" E	90	–	48	–	28	–	8	–	6	–	–
Lviv-7*	49°49'51.8"N 23°58'44.4" E	102	–	+	35	35	24	–	3	5	–	–
Lviv-8	49°48'59.6"N 23°57'19.6" E	388	–	4	–	19	294	19	–	52	–	–
Lviv-9a*	49°49'09.7"N 23°57'35.0" E	95	1	28	–	17	37	5	–	7	–	–
Lviv-9b*	49°49'06.6"N 23°57'36.2" E	41	–	9	–	6	11	13	–	2	–	–
Lviv-10a	49°48'49.5"N 23°58'32.6" E	92	–	4	–	42	15	6	–	25	–	–
Lviv-10b*	49°48'41.1"N 23°58'24.6" E	21	–	–	–	4	11	–	–	6	–	–
Lviv-10c*	49°48'37.0"N 23°58'23.6" E	53	–	9	–	5	20	14	–	5	–	Ch
Lviv-10c	Re-sampling	41	–	8	–	5	18	5	–	5	–	Ch
Lviv-11*	49°48'37.2"N 23°58'44.5" E	53	–	29	–	5	–	14	–	5	–	–
Lviv-11	Re-sampling	42	2	27	–	4	1	7	–	1	–	–
Lviv-12*	49°48'10.0"N 24°00'06.5" E	10	2	–	–	3	4	–	–	1	–	Ch-DL
Lviv-13*	49°48'11.4"N 24°00'29.8" E	22	–	–	–	5	17	–	–	–	–	–
Lviv-14*	49°48'10.9"N 24°00'38.6" E	50	2	–	–	23	4	2	–	19	–	–
Lviv-15*	49°48'32.1"N 24°00'57.5" E	13	–	2	1	3	7	–	–	–	–	–
Lviv-16	49°48'47.2"N 24°01'21.1" E	732	5	120	23	291	73	66	27	127	–	Ch, GC
Lviv-17	49°47'58.7"N 24°02'05.9" E	107	–	63	5	++	–	18	8	++	13	GC
Lviv-18	49°47'50.3"N 24°03'00.7" E	20	–	3	–	9	–	4	–	4	–	–
Lviv-19	49°49'27.6"N 24°00'23.9" E	51	–	1	7	12	19	1	4	7	–	–
Lviv-20	49°49'20.1"N 24°00'01.1" E	82	28	–	20	23	1	–	3	7	–	Ch-DL
Lviv-21	49°49'59.2"N 24°00'25.2" E	5	–	5	–	+	–	–	–	+	–	–
Lviv-22	49°49'47.8"N 24°01'32.8" E	62	14	5	1	16	2	2	1	–	21	Ch
Lviv-23	49°50'06.3"N 24°01'34.3" E	103	–	4	13	24	33	5	7	14	3	Ch-DL
Lviv-24	49°50'29.6"N 24°01'20.9" E	65	–	–	–	10	48	–	–	7	–	–
Lviv-25	49°49'27.5"N 24°02'49.5" E	60	13	7	4	6	6	9	7	8	–	–
Lviv-26	49°49'51.4"N 24°02'50.2" E	53	–	–	1	3	17	–	9	23	–	–
Lviv-27	49°50'08.8"N 24°02'30.0" E	8	–	–	3	–	4	–	1	–	–	Ch-DL
Lviv-28	49°50'22.5"N 24°02'10.4" E	24	–	4	–	4	–	6	–	10	–	–
Lviv-29	49°52'03.1"N 24°00'58.9" E	3	–	+	–	+	1	+	–	+	2	–
Malekhiv	49°53'00.6"N 24°04'32.2" E	4	–	–	+	1	1	–	–	2	–	GC
Pidbirtsi	49°50'30.1"N 24°09'04.9" E	26	5	2	1	5	8	3	2	–	–	Ch-DL, GC
Solonka	49°44'57.2"N 23°59'40.4" E	6	–	–	–	–	–	2	2	2	–	Ch
Zubra	49°46'42.7"N 24°03'05.0"E	53	23	9	–	18	1	–	–	2	–	Ch-DL

*Collected by T. Rodych; **number of adults; + — coloration variants recorded only in juveniles; ++ — recorded in adults during repeated examinations of the same site; Ch — presence of *C. hortensis* specimens with a shell coloration not typical for the descendants of the primary introduction; Ch-DL — similar, but there are also shells with a dark lip; GC — collected near garden centres, active (Lviv-17, Malekhiv, Pidbirtsi) or recently closed (Lviv-16). See Material and Methods for other designations. Only sites where at least 10 adult and juvenile individuals of *C. nemoralis* or their empty shells were found are listed in the table.

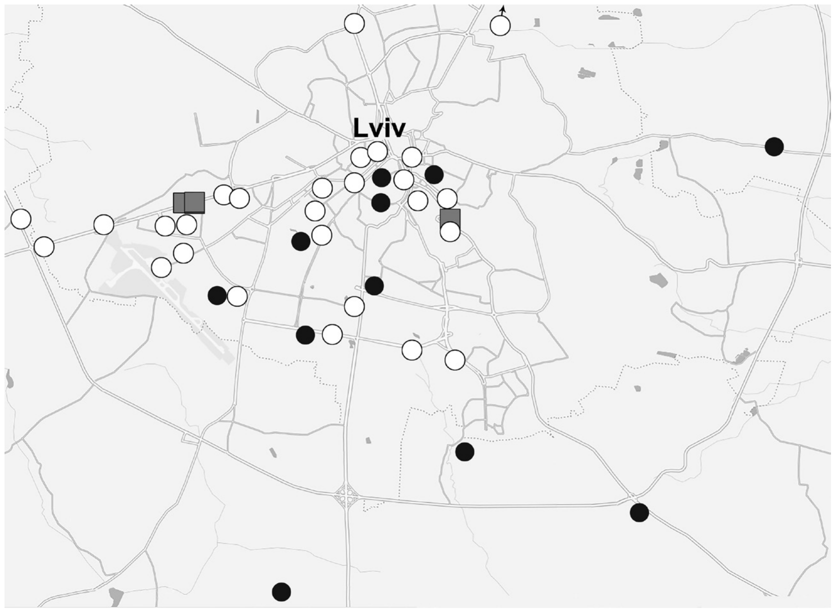

Fig. 1. Locations of sites in Lviv and its immediate environs where colonies or single specimens of *C. nemoralis* (white circles), *C. hortensis* phenotypes, absent in the descendants of the primary introduction of this species to Western Ukraine (gray squares), both together (black circles) were found in 2019–2022.

cies to Western Ukraine (see Introduction): yellow banded, pink or brown, dark lip (Gural-Sverlova & Gural, 2022 a, b: figs 2–5). As another trait indirectly indicating the presence of a relatively recent joint introduction of *C. hortensis* and *C. nemoralis* to the studied sites, a well-pronounced variability in the body colouration of *C. hortensis* was considered. In the descendants of the primary introduction of this species to Western Ukraine, the body is always light, without a distinct gray or reddish pigmentation, and the shell colouration is limited to three main variants: white unbanded, white banded, yellow unbanded (Gural-Sverlova & Gural, 2021 b: fig. 3A, 2022 b: fig 1).

For a qualitative comparison of the phenotypic composition of *C. nemoralis* at the studied sites and the corresponding dendrogram, the Jaccard similarity index was used. For quantitative comparison, the index of phenotypic similarity of samples 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 recorded at the two compared sites; p_1, $p_2 \ldots p_m$ are the frequencies of phenotype groups at one site; q_1, $q_2 \ldots q_m$ are the frequencies of the same groups at another site.

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

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

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

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.

The maps of known records of *C. nemoralis* and *C. hortensis* in Ukraine were compiled based on our own long-term research, stock materials of the State Museum of Natural History of the National Academy of Sciences of Ukraine in Lviv, some published data (Balashov & Markova, 2021; Rybka, 2017) as well as on observations of other persons, mainly placed in two citizen science databases (iNaturalist, 2023; UkrBIN, 2023). For a partial review of relevant data for *C. nemoralis*, see Gural-Sverlova et al. (2021 a: table 1).

Results

In 2019–2022 in Lviv and its immediate environs (fig. 1), we found 14 sites with the shell colouration variants of *C. hortensis* that are not typical for descendants of the primary introduction of this species to Western Ukraine (see Material and Methods). The locations of 12 of them, as well as the phenotypic composition of the samples collected there, are in previous publications (Gural-Sverlova & Gural, 2022 a: table 3; 2022 b: table 2). The remaining two sites discovered in 2022 are characterised below.

1) The territory of the Pivdennyi market, several flower beds with ornamental shrubs near the sculpture of a Cossack, site 10 c in table 1. Two snails (one adult, one juvenile) had banded shells with a light yellow apex. The phenotype Y-0 prevailed. Of the 50 adult live snails collected in September, 94 % had yellow shells without dark spiral bands. The sample also included single white banded, white unbanded, and yellow banded (see above) specimens. In other areas of the market landscaped with ornamental plants (sites 10 a,

Table 2. Variability in phenotypic composition and phenotypic diversity in two groups of *C. nemoralis* samples

Phenotype groups or indices	Joint introduction of two *Cepaea* species					
	not recorded			recorded		
	Min	Max	M ± E_M	Min	Max	M ± E_M
Combination of shell ground colour and banding, in percent						
*Y-0	0	21.7	2.1 ± 1.21	0	43.4	17.1 ± 6.12
Y-1	0	59.5	18.0 ± 4.59	0	18.2	10.2 ± 2.38
Y-3	0	34.3	3.4 ± 1.72	0	24.4	6.5 ± 3.25
Y-5	0	55.0	20.6 ± 3.56	10.8	39.8	25.8 ± 2.75
P-0	0	77.3	28.1 ± 6.04	1.2	40.8	17.1 ± 5.21
P-1	0	40.0	10.7 ± 2.54	0	19.3	6.8 ± 1.81
P-3	0	17.0	2.4 ± 1.03	0	7.7	3.3 ± 1.04
P-5	0	43.4	14.1 ± 3.02	0	17.3	7.7 ± 2.50
Shell ground colour, in percent						
Yellow	5.9	95.0	44.1 ± 5.35	29.1	94.3	59.7 ± 7.58
Pink	5.0	94.1	55.3 ± 5.49	5.7	70.9	35.1 ± 8.17
Brown	0	12.1	0.6 ± 0.58	0	33.9	5.2 ± 4.72
Number of bands, in percent						
Unbanded	0	75.8	30.8 ± 6.02	10.7	59.7	39.5 ± 5.81
Mid-banded	0	85.7	28.7 ± 6.34	0	37.6	17.0 ± 3.33
Three-banded	0	37.3	5.8 ± 2.23	0	28.0	9.9 ± 3.70
Five-banded	0	84.0	34.7 ± 5.03	19.2	57.1	33.6±4.52
Indices of phenotypic diversity						
*m	3	8	4.9 ± 0.30	5	8	6.7 ± 0.45
*μ	1.84	7.79	4.02 ± 0.26	3.94	6.36	5.59 ± 0.39
h	0.03	0.37	0.17 ± 0.02	0.06	0.24	0.16 ± 0.02

Note. E_M — error of the arithmetic mean; h — rate of rare morphs; M — arithmetic mean; m — number of phenotype groups; μ — index of intrapopulation diversity. The frequencies of brown unbanded shells (B-0) are not indicated, as they coincided with those of brown shells. An asterisk indicates significant differences in the two groups of samples.

Table 3. Sites where *C. nemoralis* shells with the absence of all or part of the bands were not found

Absent traits	Site numbers
Joint introduction with *C. hortensis* is not recorded (in total 26 sites)	
Unbanded	Lviv-4, 5*, 6*, 17, 18*, 21*, 28* (=26.9 %)
Mid-banded	Lviv-10b*, 13*, 24*, 26, Malekhiv (=19.2 %)
Three-banded	Lviv-1, 5*, 6*, 8, 9a, 9b, 10a, 10b*, 11, 13*, 14, 18*, 21*, 24*, 28*, 29 (=61.5 %)
Joint introduction with *C. hortensis* is recorded (in total 10 sites)	
Unbanded	Solonka (=10.0 %)
Mid-banded	Lviv-12*, 20, 27 (=30.0 %)
Three-banded	Lviv-10c, 12*, Zubra (=30.0 %)

Note. An asterisk indicates sites where the absence of two of the listed traits was recorded.

10 b, etc.), only *C. nemoralis* and/or phenotypes of *C. hortensis* typical for Lviv and Western Ukraine were recorded.

Near the building of the business centre Optima Plaza (Naukova Street, No. 7 d), site 12 in table 1. Flowerbed with ornamental shrubs, planted in 2015. There was no special sampling of *C. hortensis*, however, several specimens of the species with yellow banded and pink unbanded shells were found there in July-August. The latter had a dark lip.

At 11 sites with *C. hortensis* phenotypes unusual for Western Ukraine, colonies of *C. nemoralis* were also found. Information about 10 of them is in table 1. Another case of joint discovery of two *Cepaea* species was recorded near the garden centre Galsad between Lviv and Davydiv (49°45'57.1" N 24°06'29.6" E), where we collected only a few specimens of *C. nemoralis*.

Only at three sites in Lviv we found the shell colouration variants of *C. hortensis*, not typical for the descendants of the primary introduction, but there was no *C. nemoralis* (fig. 1):

1) near the garden centre on Horodotska Street, closed in 2022, 49°49'50.1" N 23°57'57.1" E, yellow banded and pink unbanded shells with a light lip (Gural-Sverlova & Gural, 2022 b: table 2);

2) ornamental shrubs near the mansion on the opposite side of the road, 49°49'47.2" N 23°57'50.5" E, one yellow banded shell of *C. hortensis*;

3) decorative plantings along the streets of General Hrytsai (49°49'39.0" N 24°02'47.8" E) and Mariia Slobodivna (49°49'39.3" N 24°02'51.9" E), yellow banded and pink shells with light lip (Gural-Sverlova & Gural, 2022 a: table 3; 2022 b: table 2).

A dark (from pinkish to reddish-brown) lip in pink, occasionally in yellow shells of *C. hortensis* was found near the garden centre Club of Plants in Pidbirtsi, at one site in Zubra, and at four sites in Lviv (table 1). In all cases, colonies of *C. nemoralis* were also recorded there.

From 2019 to 2022, we found *C. nemoralis* and/or *C. hortensis* with regionally rare variants of the shell colouration near 6 garden centres located in Lviv (3 cases) and the surrounding area. In Lviv (site 16), Pidbirtsi (Club of Plants), and near Davydiv (Galsad), both were recorded. Only *C. nemoralis* was found at site 17 in Lviv and in Malekhiv, while *C. hortensis* was represented exclusively by phenotypes common in Western Ukraine and, in particular, in the areas surrounding garden centres. And only in one case, described above, unusually coloured specimens of *C. hortensis*, without *C. nemoralis*, were found near the fence of the garden centre.

In *C. nemoralis*, the frequencies of the analysed phenotype groups and traits (different ground colour or shell banding) varied greatly both at sites where only this species was recently introduced, and at sites where a joint introduction of two *Cepaea* species was recorded (table 2). A significant difference was found only for yellow unbanded shells, which are more common in the second group of samples (table 2, fig. 2). Phenotypic diversity, on average, was also greater in the second group, as evidenced by higher values of m and μ (table 2).

Let us compare not the quantitative, but only the qualitative phenotypic composition of *C. nemoralis*. In addition to the aforementioned yellow unbanded shells, the first group of samples also more often lacked three-banded (regardless of the ground color) and brown shells (fig. 3). These are phenotypes that are less common in the study area as a whole (table 2, fig. 2).

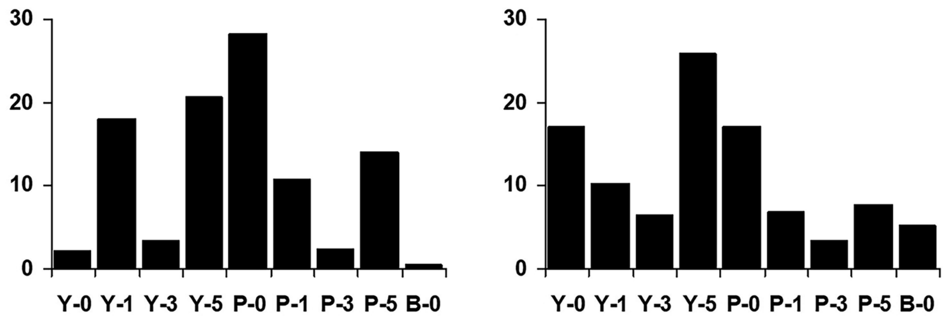

Fig. 2. Average frequencies of the phenotype groups in *C. nemoralis* at the studied sites. On the left, for sites where the joint introduction of *C. nemoralis* and *C. hortensis* was not recorded; on the right, where it was recorded (see Material and Methods). Calculated for samples containing at least 20 adults.

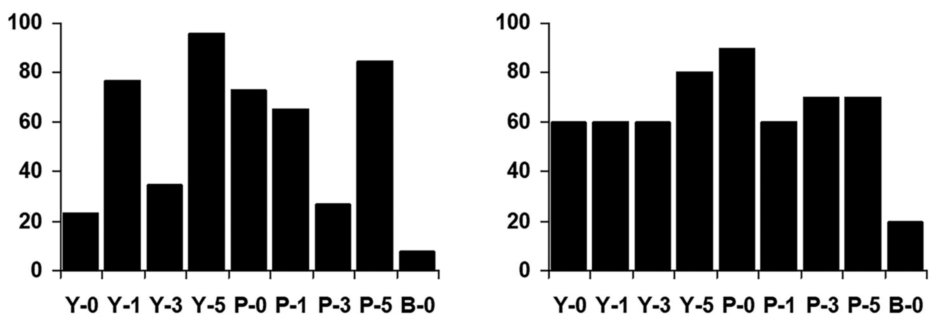

Fig. 3. Percentages of sites where different phenotype groups of *C. nemoralis* were found. Left and right graphs are similar to figure 2. Calculated for all samples in table 1.

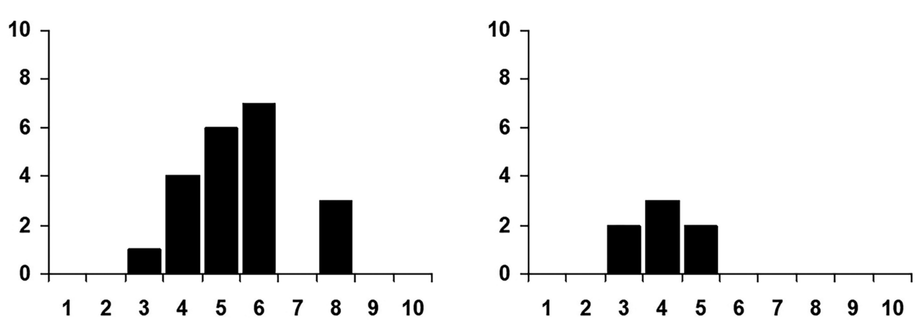

Fig. 4. The number of sites with different frequencies of the predominant phenotype group. The numerals on the abscissa indicate the frequency intervals: 1 — up to 10 %, 2 — from 11 to 20 %, etc. Left and right graphs are similar to figure 2. Calculated for samples containing at least 20 adults.

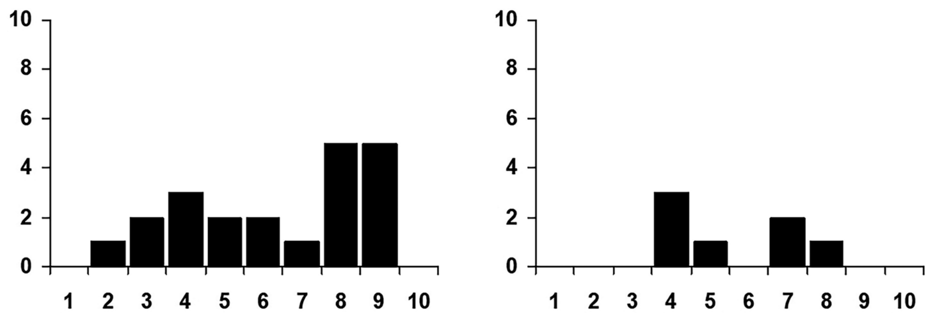

Fig. 5. The number of sites with different total frequencies of four light phenotypes (Y-0, Y-1, P-0, P-1). Similar to figure 4.

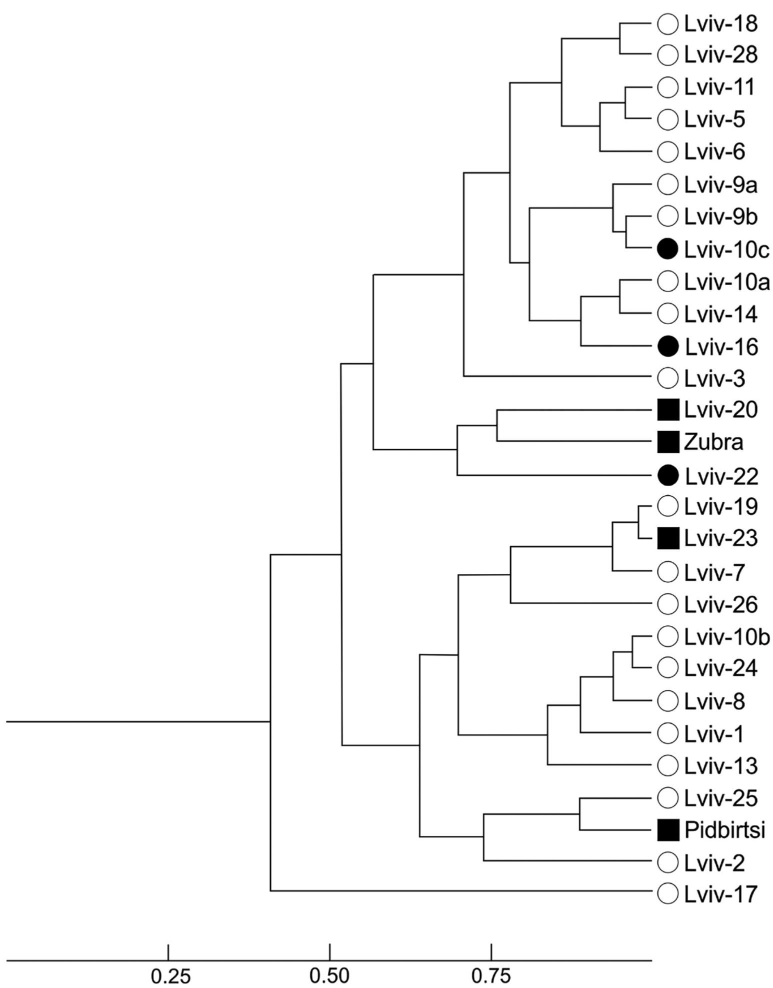

Fig. 6. Similarity of the quantitative composition of *C. nemoralis* samples from Lviv and surroundings, containing at least 20 adults: white circles — no *C. hortensis* was found or only its phenotypes were present, common for Western Ukraine; black circles — a recent joint introduction of two *Cepaea* species has been recorded; black squares — the same, but there were also *C. hortensis* shells with a dark lip.

If the ground colour is not taken into account, the shells lacking not only the top two bands, but also all five bands were absent much more often in the first group of samples (table 3). Also, there were more frequent cases when several hereditary traits, associated with the complete or partial absence of dark spiral bands on the shell, were absent in one sample: unbanded and three-banded, mid-banded and three-banded.

At sites where no joint introduction of two *Cepaea* species was recorded, a clearly pronounced predominance of any one variant of the shell colouration in *C. nemoralis* was more often observed (fig. 4). In almost half of the samples from this group used for quantitative analysis (see Material and Methods), the frequencies of such shells exceeded 50 %. Most often, these were pink unbanded shells, half as often yellow mid-banded ones, in one case yellow five-banded ones. Correspondingly, the number of sites with an increased total proportion of the four lightest phenotypes (yellow unbanded and mid-banded, pink

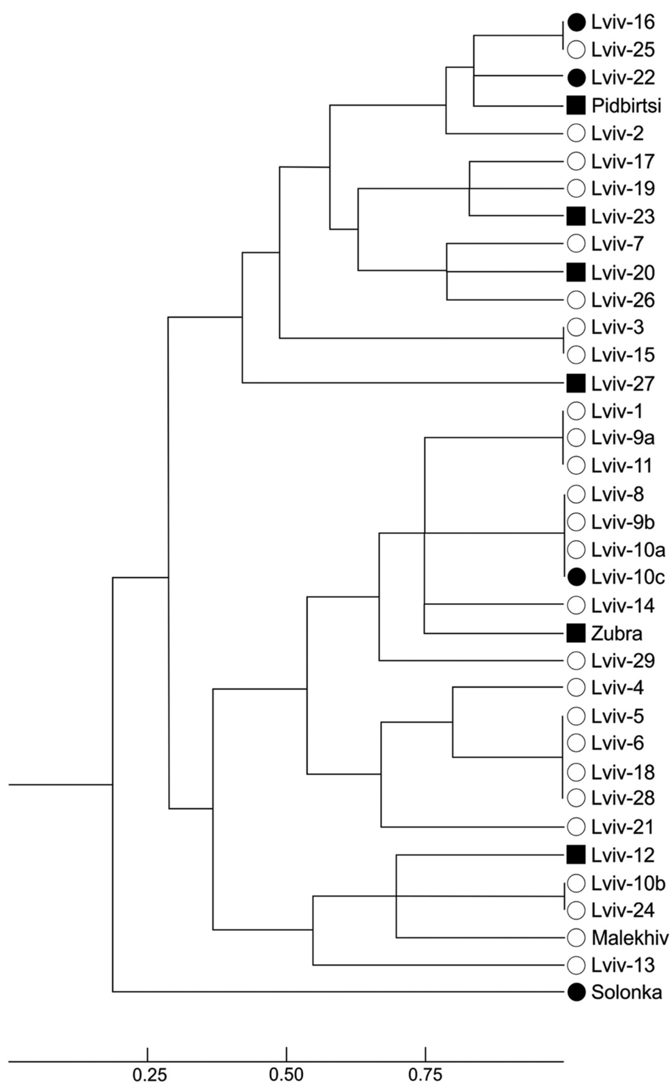

Fig. 7. Qualitative similarity of the phenotypic composition of *C. nemoralis* (Jaccard coefficient), calculated for all sites in table 1. Designations are similar to figure 6.

unbanded and mid-banded) also increased (fig. 5). Their total frequencies exceeded 70 % in almost half of the samples from the first group.

In general, the variability of both quantitative (fig. 6) and qualitative (fig. 7) composition of *C. nemoralis* samples is weakly depended on the spatial location of the studied sites. Closely spaced sites with consecutive numbers were often less similar than more distant pairs of sites. The same can be said about the presence or absence of *C. hortensis* pheno-

Fig. 8. Records of *C. nemoralis* (A) and *C. hortensis* (B) in Ukraine as of the end of 2022. Different findings in and near one settlement are shown by one dot.

types, not typical for Western Ukraine, at the studied sites, as well as about the presence among them of a trait that is rare for this species — a dark-coloured lip.

With single exceptions, the studied sites were divided into two groups on both similarity dendrograms (figs 6–7). Each of these groups included sites where only *C. nemoralis* colonies or also the colouration variants of *C. hortensis* shells, absent in the descendants of the primary introduction, were recorded.

If we compare the quantitative composition of the samples, in the first group (the upper part of the dendrogram in figure 6), the total number of mid-banded and five-banded shells almost always exceeded the number of unbanded and three-banded ones, up to their complete absence at sites 5, 6, 18, and 28. The opposite trend was observed in the second group. In the samples of the first group, on average, pink unbanded shells were 4.5 times less common and yellow mid-banded shells were 5.5 times more common. A separate cluster in the first group was formed by 3 sites, where the joint introduction of *C. nemoralis* and *C. hortensis* was registered, and at the same time yellow unbanded shells of *C. nemoralis* were often found.

When comparing the qualitative composition of the phenotypes recorded at the studied sites (fig. 7), the first group always contained three-banded shells. The shells with yellow, pink, or brown ground colour combined with a complete absence of bands were found there somewhat more frequently. In this group, cases of joint introduction of two *Cepaea* species were noted relatively more commonly. In the second group, three-banded shells were almost always absent, and pink five-banded ones were recorded somewhat more often.

Currently, both species of *Cepaea* are recorded in different parts of Ukraine, however, the largest number of reliable findings is known from the west of the country, especially from the Lviv Region (fig. 8). The latter pattern is especially noticeable for *C. hortensis* (fig. 8, B). In Central Ukraine, *C. nemoralis* has been increasingly found in recent years in

Table 4. Settlements in or near which the variants of *C. hortensis* coloration, not typical for the descendants of the primary introduction of this species to Western Ukraine, were recorded

Region	Settlement	Shell coloration					Dark body
		Y-5	P-0	P-5	B-0	DL	
Lviv	Lviv	+	+	+	–	+	+
	near Davydiv	+	+	–	–	–	+
	Solonka	+	–	+	–	–	+
	Obroshine (single specimen)	+	–	–	–	–	–
	Pidbirtsi	+	+	+	+	+	+
	Zhovkva	+	–	–	–	–	+
	Zubra	+	+	+	–	+	+
Transcarpathian	Uzhhorod	–	+	–	–	–	+
	near Podobovets* (need confirmation)	–	–	+	–	–	–
Kharkiv	Kharkiv*	+	+	–	–	–	–
Zhytomyr	Zhytomyr*	+	–	–	–	–	+

Note. An asterisk indicates localities that are given only according to information from databases (iNaturalist, 2023; UkrBIN, 2023). See Material and methods for other designations.

and near Kyiv. So far, there have been no reports of *Cepaea* findings in the Crimea. And the most southern records of both species in Ukraine are those in Odesa.

Despite the frequent occurrence of *C. hortensis* in the urbanised and suburbanised areas of the Lviv Region, most often we are talking about the descendants of the primary introduction of this species into Western Ukraine, with a very limited phenotypic composition, see Material and Methods. Only in recent years, in the west and in other parts of Ukraine, other variants of shell colouration, associated with later and independent introductions, began to be found. So far, they have been reported from a very limited number of settlements (table 4). In such cases, yellow banded shells were most often recorded, and pink shells were somewhat less common.

Discussion

The history of the spreading of both *Cepaea* species in Ukraine is closely connected with ornamental plantations. Thanks to planned landscaping with ornamental shrubs, which were planted in large numbers as hedges along streets, near railway stations, administrative buildings, educational institutions, hospitals, etc., *C. hortensis* spread widely in Lviv and reached many other settlements in the Lviv Region already in the second half of the 20th century (Gural-Sverlova & Gural, 2021 b, 2022 b).

The only reliable record of *C. hortensis* outside the Lviv Region, dating from before the end of the 20th century, was made in Shatsk, Volyn Region. According to O. Korniushin, he discovered *C. hortensis* in the arboretum of the forest technical school in the early 1990s (Sverlova & Kirpan, 2002). In 2002 we found several immature snails of this species with yellow unbanded shells on ornamental shrubs in the arboretum. In 2000, *C. hortensis* was also found near Shatsk, at the biostation of the Ivan Franko National University of Lviv (Sverlova & Kirpan, 2002), where this species may have been introduced with seedlings of ornamental shrubs from Lviv.

From the beginning of the 20th century to the present, some records of *C. hortensis* were also made in all other administrative regions traditionally attributed to Western Ukraine (table 5): Ivano-Frankivsk (known since 2002, own data), Khmelnytskyi (since 2016, observations by G. Romanov), Transcarpathian (since 2015, own data), Chernivtsi (2018, according to iNaturalist, 2023), Rivne (since 2020, the same source), Ternopil (2022, observations by L. Bezugla).

However, it is only since 2015 that the phenotypes of *C. hortensis*, which are absent in the descendants of the primary introduction of this species, have been found in several localities of Western Ukraine (Gural-Sverlova & Gural, 2022 a: table 3; 2022 b: figs 2–5, table 3). Since 2018, some reports of *C. hortensis* findings from other parts of Ukraine, confirmed by photographs of live snails or empty shells, have also started to appear in the analysed databases (iNaturalist, 2023; UkrBIN, 2023).

Both last trends (the appearance of other shell colouration variants and a significant expansion of the range of *C. hortensis* in Ukraine to the east and south) actually coincided in time with the beginning of an increasingly frequent registration in different parts of the country of a related species, *C. nemoralis* (Balashov & Markova, 2021; Gural-Sverlova & Gural, 2021 a; Gural-Sverlova et al., 2020, 2021 a, b; iNaturalist, 2023, UkrBIN, 2023). Unlike *C. hortensis*, most of the reports about *C. nemoralis* in Ukraine made before the end of the 20th century were most likely based on the incorrect identification of shells of the autochthonous species *Caucasotachea vindobonensis* (C. Pfeiffer, 1828) (Gural-Sverlova et

Table 5. Chronology and localities of discovery of two introduced *Cepaea* species in Ukraine

Administrative region	Settlement or its environs	First recorded, year	Information sources: published	Information sources: databases (observation number, year, coordinates), others
		Cepaea nemoralis		
Dnipropetrovsk	Novooleksandrivka	2021		UkrBIN: No. 205383–205384 – 2021, 48°21'08.4"N 35°01'02.2"E; No. 215600–215602 – 2021, 48°21'08.2"N 35°01'03.0"E
Ivano-Frankivsk	Bohorodchany**	2019	Gural-Sverlova et al., 2020: fig. 1E	
	Ivano-Frankivsk**	2019	Gural-Sverlova et al., 2020: fig. 1F	
	Nadvirna	2022		iNaturalist: No. 121619272 – 2022, 48°38'08.5"N 24°34'13.9"E
	Uhryniv**	2018	Gural-Sverlova et al., 2020	UkrBIN: No. 92619 – 2018, 48°57'26.5"N 24°41'25.9"E
Kharkiv	Kharkiv	2019		iNaturalist: No. 47021513 – 2019, 50°01'54.8"N 36°14'12.4"E
Khmelnytskyi	Khmelnytskyi** and surroundings	2020		iNaturalist: No. 55127888 – 2020, 49°29'04.6"N 26°54'28.4"E; No. 123269764 – 2022, 49°24'27.8"N 26°57'44.4"E; UkrBIN: No. 153275 – 2020, 49°24'00.4"N 26°55'10.5"E
	Kytaihorod*	2007 or 2008	Balashov et al., 2013: fig. 2	
Kyiv	Kyiv	2019	Balashov & Markova, 2021	iNaturalist: No. 30809918 – 2019, 50°25'25.8"N 30°33'40.0"E ; No. 55963924 – 2020, 50°22'20.4"N 30°27'11.5"E; No. 83429804 – 2021, 50°27'29.3"N 30°31'18.2"E; No. 99612624 – 2021, 50°24'57.6"N 30°33'22.1"E, etc.
	Severynivka	2020		iNaturalist: No. 50455338 – 2020, 50°23'50.8"N 29°58'51.9"E
	Shkarivka	2021		iNaturalist: No. 95665093 – 2021, 49°45'13.5"N 30°09'23.1"E; No. 95665165 – 2021, 49°45'13.0"N 30°09'25.3"E; UkrBIN: No. 219963 – 2021, 49°45'17.93"N 30°09'29.84"E
	Sofiivska Borshchahivka	2020	Balashov & Markova, 2021: fig. 1	iNaturalist: No. 47605276 – 2020, 50°24'12.1"N 30°23'32.3"E ; No. 57015096 – 2020, 50°24'40.7"N 30°22'43.7"E; No. 74124076 – 2021, 50°24'35.7"N 30°23'02.0"E, etc.
	Supii Lake	2021		iNaturalist: No. 105492727 – 2021, 50°19'17.3"N 31°43'32.4"E
	Vyshhorod	2019	Balashov & Markova, 2021	iNaturalist: No. 34819309 – 2019, 50°34'47.8"N 30°28'56.8"E; UkrBIN: No. 167046 – 2020, 50°34'54.9"N 30°27'41.1"E
Lviv	near Davydiv**	2021		Collected by authors – 2021, 49°45'57.1"N 24°06'29.4"E
	Lviv**	1994	Sverlova, 2002a; Gural-Sverlova et al., 2020, 2021b, etc.	iNaturalist: No. 115854499–115855500 – 2022, 49°50'22.4"N 24°02'10.4"E
	Malekhiv**	2022	In this publication	
	Pidbirtsi**	2021	In this publication	
	Solonka**	2021	In this publication	
	Zubra**	2019	Gural-Sverlova et al., 2020: fig. 1D	

Odesa	Odesa	2020	Balashov & Markova, 2021	iNaturalist: No. 88704210 – 2021, 46°25'13.8"N 30°45'05.2"E
Poltava	Kremenchuk	2020		Information from T. Matviienko – 2020, coordinates unknown
Rivne	Rivne	2022		iNaturalist: No. 114748566 – 2022, 50°35'00.3"N 26°15'06.3"E; No. 117468345 – 2022, 50°35'00.1"N 26°15'05.3"E
	Sarny	2018		UkrBIN: No. 90550–90551 – 2018, 51°20'06.2"N 26°35'43.4"E
Ternopil	Chortkiv**	2017	Gural-Sverlova et al., 2021a: fig. 5; Gural-Sverlova & Lyzhechka, 2021	UkrBIN: No. 140315 – 2017, 49°01'32.5"N 25°47'34.4"E; No. 145252–145254 – 2020, 49°01'34.3"N 25°47'31.4"E; No. 149617–149621 – 2020, 49°01'34.2"N 25°47'31.4"E
Volyn	Kovel	2020		iNaturalist: No. 49206754 – 2020, 51°12'28.5"N 24°42'27.2"E (inaccurate); No.119479440 – 2020, 51°12'26.5"N 24°41'48.2"E
	Novovolynsk	2021		iNaturalist: No. 85468683 – 2021, 50°44'14.0"N 24°09'57.2"E
	Rozhyshche	2022		Information from O. Petruk – 2022, coordinates unknown
	Svitiaz**	2021		Museum** collection (coll. V. Rizun) – 2021, 51°29'22.4"N 23°52'21.2"E
	Volodymyr	2022		iNaturalist: No. 108256045 – 2022, 50°50'37.7"N 24°18'47.7"E; No. 126603740 – 2022, 50°50'59.1"N 24°17'56.2"E
Zhytomyr	Romaniv district	2022		iNaturalist: No. 117996294 – 2022, 50°08'58.3"N 27°44'22.4"E
	Zhytomyr	2018		UkrBIN: No. 70309 – 2018, coordinates unknown
			Cepaea hortensis	
Chernivtsi	Chernivtsi	2018		iNaturalist: No. 10771444 – 2018, 48°16'27.9"N 25°56'51.9"E
Ivano-Frankivsk	Bohorodchany**	2019		Collected by authors – 2019, 48°48'46.8"N 24°32'34.2"E
	Ivano-Frankivsk**	2002	Sverlova & Kirpan, 2002; Gural-Sverlova & Gural, 2021b	
	Tysmenytsia district	2021		iNaturalist: No. 87449950 – 2021, 48°54'45.0"N 24°36'26.2"E
	Uhryniv*	2019		Observed by authors – 2019, 48°57'10.5"N 24°42'01.9"E
Kharkiv	Kharkiv	2021		iNaturalist: No. 141984138, 141984257, 141984341 (different phenotypes from one site) – 2022, 50°01'42.1"N 36°15'33.0"E; UkrBIN: No. 196202 – 2021, 50°01'03.2"N 36°13'55.4"E
	Vysokyi	2021		iNaturalist: No. 79411262 – 2021, 49°53'46.5"N 36°09'07.8"E
Khmelnytskyi	Khmelnytskyi	2016	Gural-Sverlova & Gural, 2021b	
Kyiv	Kyiv	2022		iNaturalist: No. 106616457 – 2022, 50°23'53.5"N 30°38'34.5"E; No. 135644543 – 2022, 50°25'39.3"N 30°29'38.6"E
Luhansk	Luhansk	2018		UkrBIN: No. 65484–65485 and 65560–65561 – 2018, 48°34'18.7"N 39°18'55.1"E
Lviv	Bendiuha		Rybka 2017	
	Bibrka*	late 1990s		Observed by authors and other persons in different years – 49°38'20.2"N 24°17'39.4"E

Birky**	2019	Gural-Sverlova & Gural, 2021b	
Boryslav**	2019	Gural-Sverlova & Gural, 2021b	
Briukhovychi**	2017	Gural-Sverlova & Gural, 2021b	
Brody	2020		iNaturalist: No. 146426600 – 2020, 50°04'45.5"N 25°08'58.4"E
Chervonohrad**	2007	Rybka, 2017; Gural-Sverlova & Gural, 2021b	
near Davydiv**	2021	Gural-Sverlova & Gural, 2022a, 2022b	
Drohobych**	2009		Collected by authors – 2009, coordinates unknown
Dubliany**	2017	Gural-Sverlova & Gural, 2021b: fig.5B	
Hirnyk		Rybka, 2017	
Horodok**	2017	Gural-Sverlova & Gural, 2021b	
Ivano-Frankove**	2006	Gural-Sverlova & Gural, 2021b	
near Konopnytsia**	2005		Collected by authors – 2005, coordinates unknown
Lapaivka*	2021		iNaturalist: No. 96489723 – 2021, 49°48'49.0"N 23°53'47.9"E
Lviv**	late 1970s	Sverlova, 2001, 2002b: fig. 1 (distribution map); Gural-Sverlova & Gural, 2021b, 2022a, 2022b, etc	A number of observations in iNaturalist and UkrBIN that do not expand the published data
Malekhiv**	2019	Gural-Sverlova & Gural, 2021b	
Mykolaiv** and surroundings**	2003	Gural-Sverlova & Gural, 2021b	
Navariia	2021		iNaturalist: No. 75868175 – 2021, 49°45'06.3"N 23°55'34.5"E
Obroshyne**	2016	Gural-Sverlova & Gural, 2021b	
Pidbirtsi**	2021	Gural-Sverlova & Gural, 2022a, 2022b: figs 3–5	
Pustomyty** and surroundings**	2000	Sverlova & Kirpan, 2002; Gural-Sverlova & Gural, 2021b; 2022a	
Radekhiv		Rybka, 2017	
near Rakovets	2021		iNaturalist: No. 99770252 – 2021, 49°39'16.1"N 24°00'35.0"E
Skhidnytsia	2018		iNaturalist: No. 19758598 – 2018, 49°12'50.1"N 23°22'38.8"E (inaccurate); UkrBIN: No. 82440–82443 and 82646–82646 – 2018, 49°14'01.8"N 23°20'34.4"E; No. 83705 – 2018, 49°13'59.3"N 23°20'41.2"E
Slavske	2020		iNaturalist: No. 56499258 – 2020, 48°51'57.1"N 23°30'37.9"E (inaccurate); No. 92587106 – 2021, 48°50'43.5"N 23°26'51.1"E
Solonka**	2019	Gural-Sverlova & Gural, 2021b, 2022a, 2022b	

	Stryi*	2019		Observed by authors – 2019, coordinates unknown
	Truskavets*	2019		iNaturalist: No. 121360343 – 2019, 49°16'28.3"N 23°30'05.6"E (inaccurate)
	Velyki Hlibovychi**	2017		Collected by authors – 2017, coordinates unknown
	Velyki Mosty		Rybka, 2017	
	Voroniaky	2022		iNaturalist: No. 121257217 – 2022, 49°46'51.0"N 24°53'15.3"E (inaccurate)
	Vynnyky**	2019	Gural-Sverlova & Gural, 2021b	
	Zapytiv*	2005		Observed by authors – 2005, coordinates unknown
	Zhovkva**	2018	Gural-Sverlova & Gural, 2021b: figs 3, 5; 2022a	
	Zolochiv	2016		iNaturalist: No. 141366963 – 2021, 49°47'51.6"N 24°54'05.2"E; UkrBIN: No. 53439–53443 – 2016, 49°48'24.2"N 24°54'56.3"E; No. 203630 – 2021, 49°47'51.6"N 24°54'05.2"E
	Zubra**	2019	Gural-Sverlova & Gural, 2021b, 2022b	
Odesa	Odesa	2022		iNaturalist: No. 41444956 – 2022, 46°23'51.8"N 30°44'18.3"E
Rivne	Zdolbuniv	2020		iNaturalist: No. 53721427 – 2020, 50°31'32.5"N 26°14'30.5"E; No. 131566482 – 2022, 50°31'32.5"N 26°14'32.5"E; No. 131932804 – 2022, 50°31'45.6"N 26°13'35.6"E, etc.
Sumy	Hlukhiv district	2022		iNaturalist: No. 119149823 – 2022, 51°46'43.3"N 33°54'09.7"E (inaccurate)
Ternopil	Ternopil	2022		Information from L. Bezugla – 2022, 49°33'17.1"N 25°38'53.2"E
Transcarpathian	Mukachevo**	2018	Gural-Sverlova & Gural, 2021b	iNaturalist: No. 89446698 – 2021, 48°26'43.5"N 22°43'21.2"E
	near Podobovets	2021		UkrBIN: No. 178049 – 2021, 48°39'55.1"N 23°16'32.1"E; No. 217518 – 2021, 48°39'53.5"N 23°15'46.3"E
	Uzhhorod**	2015	Gural-Sverlova & Gural, 2021b: fig. 3E; 2022a	
Volyn	Shatsk*	early 1990s	Baidashnikov, 1992; Sverlova & Kirpan, 2002	Information from O. Korniushin – early 1990s, 51°29'23.9"N 23°55'24.8"E
	Shatsk district, Pisochne Lake**	2000	Sverlova & Kirpan, 2002; Gural-Sverlova & Gural, 2021b	
Zhytomyr	Zhytomyr	2018		iNaturalist: No. 112490287 – 2022, 50°15'53.3"N 28°39'24.7"E; No. 117325758 – 2022, 50°15'50.1"N 28°39'19.9"E; No. 137625021 – 2022, 50°15'44.5"N 28°41'34.8"E; UkrBIN: No. 69460 – 2018, coordinates unknown, etc.

Notes. The table systematizes data from the end of the 20th century to 2022 used for distribution maps (fig. 8). * — the presence of the species was confirmed by the authors of the article; ** — also available in the malacological collection of the State Museum of Natural History, Lviv. The authors cannot confirm the accuracy of coordinates from databases.

al., 2021 a). The latter is widely distributed in Ukraine, and was previously also assigned to the genus *Cepaea*.

In particular, by the end of the 20th century, only one small colony of *C. nemoralis* was known in Lviv (Sverlova, 2002 a), which subsequently became almost completely extinct (Gural-Sverlova & Savchuk, 2019). Previously, we assumed that the process of fairly rapid colonization of Lviv by *C. nemoralis* began at the turn of the 20th and 21st centuries or a little later, at the very beginning of the 21st century (Gural-Sverlova et al., 2021 a). This coincides with the end of a sharp economic decline in Ukraine in the 1990s and the beginning of an active and almost uncontrolled import of garden and ornamental plants from other European countries. At about the same time, the warming of the climate as a result of global changes is becoming increasingly noticeable. Significantly, the rapid spread of *C. nemoralis* through urban areas has recently been observed also in Belarus and the European part of Russia (Gural-Sverlova et al., 2021 a; iNaturalist, 2023). A clear link between the spread of *C. nemoralis* and horticulture was already mentioned by Boettger (1926).

Most of the new (from 2019 to 2022) records of *C. nemoralis* in Lviv were made on or near sites where ornamental plants, especially the now fashionable conifers, were planted relatively recently. Several typical cases are shown in Gural-Sverlova et al. (2021 a: fig. 2). According to our observations, junipers and other low-growing conifers are the main contributors, creating favourable conditions for snails even on constantly mowed lawns.

The crucial role of garden centres in the current distribution of *Cepaea* is confirmed by the frequent presence near them of both *C. nemoralis* and phenotypes of *C. hortensis,* which until recently were not found in Western Ukraine. Of particular interest among the latter is the dark lip (Gural-Sverlova & Gural, 2022 b: figs 3–4), a hereditary trait that is locally present even in the natural range of *C. hortensis* (Ożgo, 2010; Schilder & Schilder, 1957). We found that carriers of this trait in Lviv and the surrounding area spread from the Club of Plants (Gural-Sverlova & Gural, 2022 a, b), one of the largest local garden centres.

If for *C. hortensis* we were able to identify several convenient phenotypic markers associated with different times and sources of its introduction into Ukraine (Gural-Sverlova & Gural, 2022 a, b), this is impossible for *C. nemoralis*. Moreover, the general patterns of phenotypic variability in *C. nemoralis* are quite similar even in neighbouring Eastern European countries (Gural-Sverlova et al., 2021 a; Gural-Sverlova & Gural, 2021 a; Gural-Sverlova & Kruglova, 2022). The only exception so far can be considered shells with unevenly pigmented (spotted) bands found in one settlement of the Ternopil Region (Gural-Sverlova et al., 2021 a: fig. 5; Gural-Sverlova & Lyzhechka, 2021).

In Lviv and its environs, colonies of *C. nemoralis* are now found much more often than the shell colouration variants of *C. hortensis*, which are unusual for Western Ukraine (fig. 1). This may indirectly indicate that unintentional transfers of individuals of the first species from garden centres to landscaped sites of the study area occur also more often. Another explanation could be the poorer survival of *C. hortensis* at newly colonised sites. However, this hypothesis contradicts the successful introduction of this species into Western Ukraine already in the second half of the 20th century, see above.

It is significant that at the sites where both *Cepaea* species were relatively recently introduced, the samples of *C. nemoralis* show greater phenotypic diversity. They also less often lack phenotypes (yellow unbanded) or traits (brown shells, ones with three lower bands), which are less common in Western Ukraine (Gural-Sverlova et al., 2021 b; Gural-Sverlova & Gural, 2021 a) as well as in other parts of Eastern Europe and in the present range of *C. nemoralis* as a whole (Gural-Sverlova et al., 2021 a; Gural-Sverlova & Gural, 2021 a). The absence of rarer forms in newly formed colonies may be due to a smaller number of founding individuals, to which we include not only adult and juvenile snails, but also eggs, which may be in the ground on the roots of seedlings. It is very likely that a greater number of planted seedlings “infected” with *Cepaea* increases the likelihood of the formation of both a mixed colony of two species, and a *C. nemoralis* colony with a large variety of shell colouration.

The initial limitation of genetic and phenotypic diversity may also cause a more pronounced predominance of any one group of phenotypes in *C. nemoralis* at sites, where the joint introduction of two *Cepaea* species was not recorded (fig. 4). However, the fact that this occurs most often with light phenotypes, and that the total frequency of the four lightest variants of shell colouration also often increases (fig. 5), may also indicate possible selective nature of the observed patterns. The possible selective advantages of lighter phenotypes in introduced populations of *Cepaea*, which are often forced to adapt to life in a more continental climate, were discussed by us in a previous publication (Gural-Sverlova & Gural, 2021 a). Honěk & Martinkova (2003) showed that the experimental formation of *C. nemoralis* colonies with an initially limited phenotypic composition can lead to a noticeable increase in the proportion of one of the light phenotypes. We analyzed the results of this experiment in more detail earlier (Gural-Sverlova & Gural, 2021 a).

Conclusions

Considering the increasing number of records of *C. nemoralis* in Ukraine and the general trends in its current spreading in Eastern Europe, we can draw the following conclusions. Already in the near future, this species may become a common component of the land mollusk fauna of urbanised areas, primarily in Western Ukraine and Kyiv Region. Although *C. hortensis* can spread in the same way, and often from the same garden centres, the process of its dispersal in different parts of Ukraine can be slower. Only in the Lviv Region, where *C. hortensis* had spread widely already by the end of the 20th century, this species can remain more common than *C. nemoralis* for a long time.

Studies in Lviv and its immediate environs have shown that the joint introduction of *C. nemoralis* and *C. hortensis* during landscaping is usually accompanied by the formation of colonies of the first species with greater phenotypic diversity. This may be due to the larger number of founding individuals. At sites where only *C. nemoralis* was relatively recently introduced, the absence of some phenotypes and hereditary traits, which are less common in the study area, was more often observed. Also, a clearly pronounced predominance of any one variant of the shell colouration was more often noted there, most often pink unbanded or yellow mid-banded.

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