FOLIA MALACOLOGICA
Folia Malacol. 30(4): 221–233
ISSN 1506-7629 (print) • ISSN 2300-7125 (on-line)
The Association of Polish Malacologists
Faculty of Biology, Adam Mickiewicz University
Bogucki Wydawnictwo Naukowe
Poznań, December 2022
https://doi.org/10.12657/folmal.030.025

SHELL COLOURATION AND DIFFERENT INTRODUCTIONS OF THE LAND SNAIL *CEPAEA HORTENSIS* (GASTROPODA: HELICIDAE) INTO WESTERN UKRAINE

NINA GURAL-SVERLOVA, ROMAN GURAL

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

ABSTRACT: The primary introduction of *C. hortensis* into Western Ukraine, most likely in the second half of the 20th century, led to the formation of many populations characterised not only by a reduced phenotypic composition, but also by a peculiar phenotypic marker (absence of banded shells with a non-white ground colour). White banded shells, common in Western Ukraine, are also found in different parts of the present species range, but less frequently than yellow banded ones. When studying the shell colour and banding polymorphism in *C. hortensis*, white shells are often combined into one group with yellow ones. Therefore, the findings of these two phenotypes as well as white unbanded shells in Europe were mapped based on the analysis of more than 7 thousand photographs from citizen science database iNaturalist. The results of later introductions of *C. hortensis* to Western Ukraine, which may occur through different garden centres, are easily distinguished by the presence of yellow banded and/or pink shells. And the presence of a dark lip in all pink shells can be a phenotypic marker of snails, whose ancestors were introduced to the west of Ukraine through the garden centre "Club of Plants" near Lviv. Only near this garden centre were also found three brown-shelled snails not known for other introduced Eastern European populations of *C. hortensis*.

KEY WORDS: terrestrial molluscs; introduced species; *Cepaea*; polymorphism; phenotypic markers; Ukraine

INTRODUCTION

Cepaea hortensis (Müller, 1774) is a species of the Central European origin (TAYLOR 1914, BOETTGER 1926), the natural range of which also includes apparently many countries of the Northern and Western Europe (GURAL-SVERLOVA & GURAL 2021a). This species was also introduced at different times to other European countries (EGOROV 2015, GHEOCA et al. 2019, GURAL-SVERLOVA & GURAL 2021a) as well as to North America (COCKERELL 1890, JOHNSON 1906).

C. hortensis was introduced into Western Ukraine most likely in the second half of the 20th century, but no later than the 1970s (GURAL-SVERLOVA & GURAL 2021a). The rapid spreading of *C. hortensis* in the largest city of Western Ukraine (Lviv), as well as in other settlements of the Lviv region, was facilitated by planned landscaping with ornamental shrubs, often planted as hedges along the streets, near railway stations, hospitals, sanatoriums, etc. Previously, we have suggested that the snails could first get into the nursery where the planting material was grown (SVERLOVA 2002). Plant nurseries are often sources for the distribution of non-native species of land molluscs (BERGEY et al. 2014).

In addition to the still traceable connection with certain landscaping, the populations formed by the descendants of this primary introduction of *C. hortensis* into Western Ukraine are characterised by a reduced phenotypic composition. This is manifested in the absence of not only pink or brown shells, but

also yellow banded ones, common in other parts of the species range. They also lack variability in body colouration, and all snails have a light body without greyish or reddish pigmentation (Gural-Sverlova & Gural 2021a).

In general, in such populations there are no more than three variants of shell colouration (Fig. 1): yellow unbanded (predominant), white banded (common, but not so abundant), white unbanded (less common, absent more often than other forms). And the most characteristic feature that makes it easy to identify these populations is the presence of dark spiral bands only in shells with a white ground colour.

The presence of white shells in *C. hortensis* has been known for a long time (Taylor 1914). However, when studying the shell colour and banding polymorphism of this species, they are usually combined into one group with yellow ones (Clarke 1960: 424). Therefore, most of the available literature data (Carter 1968, Mazon et al. 1990, Cameron 1992, Honěk 1995, Cameron & Pokryszko 2008, etc.), and even generalising publications (Schilder

Figs 1–5. Shell colouration of *C. hortensis* in Lviv (1–3) and near the garden centre "Club of Plants" in its vicinity (4–5): 1 – three colouration variants (white unbanded, white banded, yellow unbanded), present in the descendants of the primary introduction; 2 – banded shells with white and yellow ground colours, collected near a recently closed garden centre in Lviv; 3–4 – shells with dark lip; 5 – one pink (left) and three brown shells collected at one site

& SCHILDER 1957, CAMERON 2013) do not give an idea of how widespread the white ground colour is in different parts of the present range of *C. hortensis*. It is also not known how often banded shells with white and yellow ground colour are found there. But the citizen science database iNATURALIST (2022) has already accumulated thousands of photographs with observation coordinates, which makes it possible to preliminarily analyse this issue. This is important for understanding the specificity of the pattern observed in Western Ukraine.

Since 2015, shell colouration variants of *C. hortensis*, absent in the descendants of the primary introduction (Figs 2–5), have been recorded in a few, still very spatially limited sites of Western Ukraine (GURAL-SVERLOVA & GURAL 2021a, 2022). We explain their appearance by relatively recent repeated introductions of this species to the west of the country, closely related to the activities of garden centres. It is significant that the joint introduction of two related species, *C. hortensis* and *Cepaea nemoralis* (Linnaeus, 1758), is observed in many cases (GURAL-SVERLOVA et al. 2020, 2021, GURAL-SVERLOVA & GURAL 2021a: table 5).

In contrast to the primary introduction of *C. hortensis* to Western Ukraine, the snails brought here recently are of different origins. For example, this is clearly demonstrated by the presence of pink shells with only a light lip (a trait typical of this species) or only a dark one (a rare trait) at some sites in Lviv and its environs (GURAL-SVERLOVA & GURAL 2022). Such multiple introductions contribute to a gradual increase in the genetic and phenotypic diversity of the studied species in some urbanised areas of Western Ukraine.

Based on the above, the main purpose of this publication was to analyse some of the hereditary shell colouration traits found to date in Western Ukraine, and to assess their potential value for documenting the introduction history and further dispersal of *C. hortensis* in this area.

MATERIAL AND METHODS

To evaluate how widespread shells with a white ground colour are in the present range of *C. hortensis* and, first of all, in its European part (Figs 6–7), more than 7 thousand photographs identified as *C. hortensis* and placed with observation coordinates in the database iNATURALIST (2022) were analysed. These observations cover the period from 2011 to June 1, 2022. Among the examined photographs, only those were taken into account, where fully formed shells of adults were clearly visible, which made it possible to check the correctness of the identifications. Next, images were selected that showed white shells (with or without dark spiral bands) common in Western Ukraine and, for comparison, yellow banded shells, which are regionally rare in Western Ukraine.

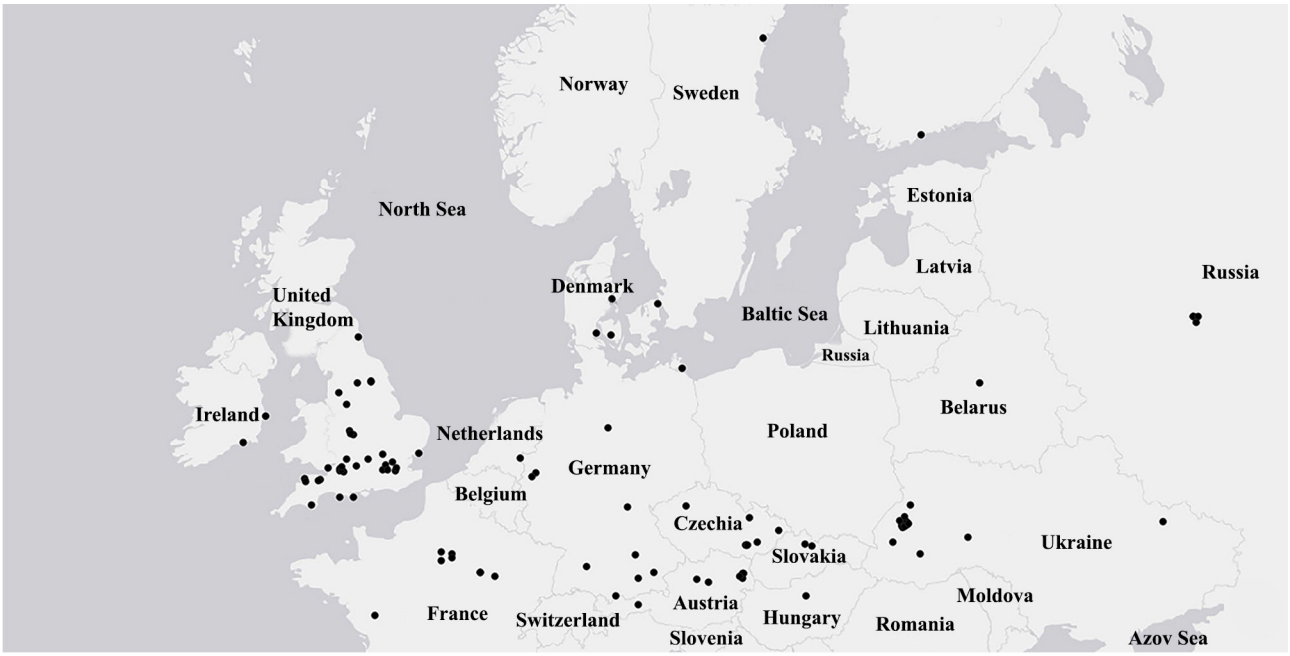
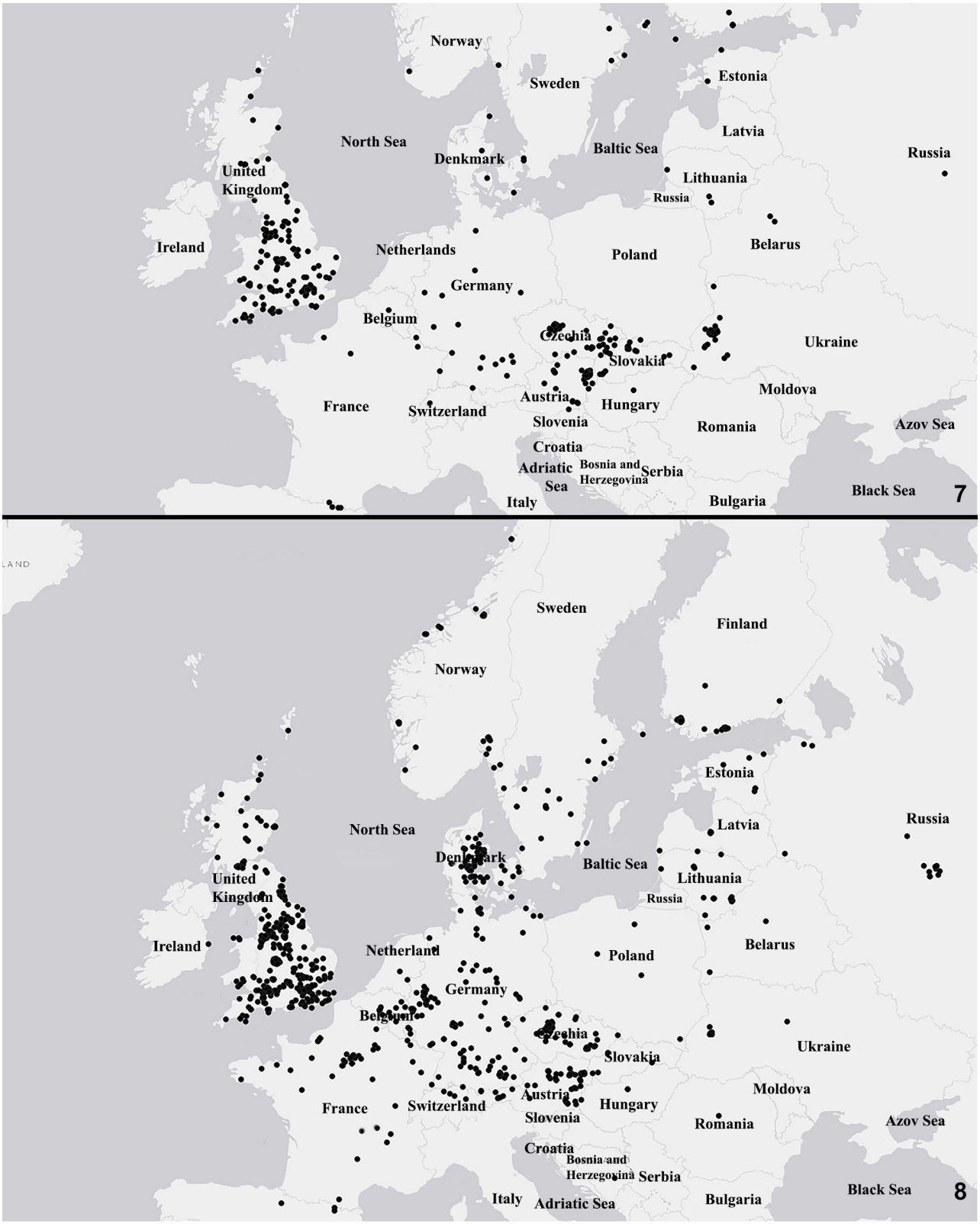
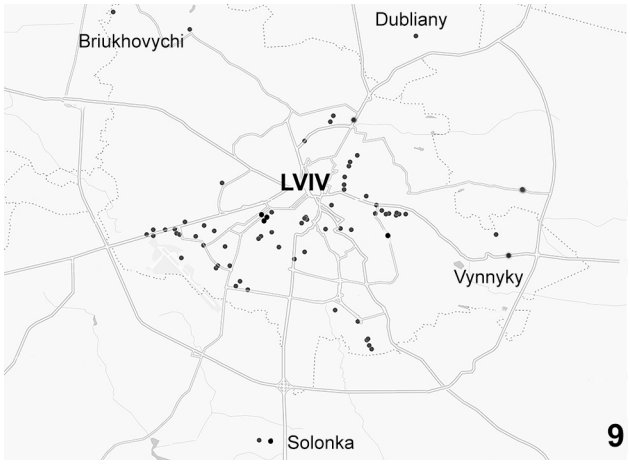


Fig. 6. Records of *C. hortensis* with white unbanded shells in Europe according to two databases and our own data (see Material and Methods)



Figs 7–8. Records of *C. hortensis* with white (7) and yellow (8) banded shells in Europe according to two databases and our own data (see Material and Methods)

Images of low quality or with lighting that makes it impossible to reliably determine the ground colour were not taken into account. Since the ground colour of banded shells is best seen near the apex (Gural-Sverlova & Gural 2021a), we did not take into account also photographs in which it was impossible to see this part of the shell clearly. If one snail or an empty shell was photographed in different posi-



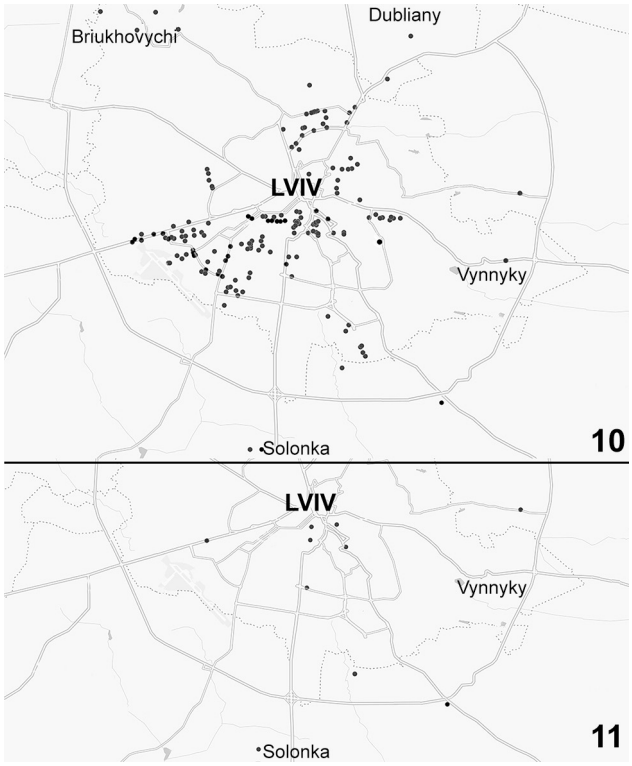


Fig. 9–11. Records of *C. hortensis* with white unbanded shells (9), white (10) and yellow (11) banded shells in Lviv and its immediate environs in 2015–2021

tions, additional attention was paid to the colour of the monochromatic part of the shell under the lower band (Fig. 2).

When mapping the records of white unbanded, white banded and yellow banded shells of *C. hortensis* in Europe (Figs 6–8), we also used our own data on the phenotypic composition of this species in Western Ukraine and in the Moscow region of Russia (Gural-Sverlova & Gural 2021a, 2022) as well as a few observations from another database focused primarily on the biodiversity of Ukraine (UkrBIN 2022).

Both of the databases mentioned above are citizen science databases curated by professional biologists and scientific organisations. iNaturalist is a joint initiative by the California Academy of Sciences and the National Geographic Society. Currently, it brings together more than a million scientists and naturalists from around the world. UkrBIN (Ukrainian Biodiversity Information Network) is a web project and application documenting biodiversity, launched in cooperation with the Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine (Kyiv). Initially, it was focused exclusively on the biodiversity of Ukraine, but in recent years there have also been some observations from other countries.

For a similar mapping of Lviv (Figs 9–11), we used data on the presence of different variants of shell colouration in 184 sites surveyed in 2015–2021

Table 1. Composition of the samples and correlation of white ground colour and band presence. Legend: A-0 – white unbanded, A-b – white banded, D – coefficient of linkage disequilibrium, N – sample size, r – correlation coefficient, Y-0 – yellow unbanded. An asterisk denotes values that are significant at p = 0.01

Site no.	Coordinates	N	Percentages				D	r
			A-0	A-b	Y-0	Others		
Lviv Region of Ukraine, Lviv								
1	49°52'14.5"N, 24°03'20.6"E	111	2.7	37.8	59.5	–	0.22	0.94*
2	49°51'52.8"N, 24°01'08.1"E	274	6.6	9.5	83.9	–	0.08	0.74*
3	49°51'29.8"N, 24°01'25.5"E	2010	4.0	19.0	77.1	–	0.15	0.89*
4	49°51'45.3"N, 24°01'46.4"E	607	3.8	6.3	90.0	–	0.06	0.77*
5	49°51'51.9"N, 24°02'09.9"E	295	1.7	3.4	94.9	–	0.03	0.81*
6	49°51'55.7"N, 24°02'35.4"E	434	0.5	11.5	88.0	–	0.10	0.98*
7	49°51'02.4"N, 24°03'26.0"E	101	1.0	14.9	84.2	–	0.12	0.96*
8	49°50'55.4"N, 24°01'59.4"E	102	2.0	9.8	88.2	–	0.09	0.90*
9	49°52'21.5"N, 24°03'32.4"E	118	0.8	27.1	72.0	–	0.20	0.98*
10	49°52'17.0"N, 24°02'17.2"E	124	7.3	17.7	75.0	–	0.13	0.80*
11	49°52'16.4"N, 24°02'13.8"E	566	12.2	14.1	73.7	–	0.10	0.68*

Table 1 continued

Site no.	Coordinates	N	Percentages				D	r
			A-0	A-b	Y-0	Others		
12	49°52'15.9"N, 24°02'10.9"E	760	5.0	16.4	78.6	–	0.13	0.85*
13	49°52'15.4"N, 24°02'07.7"E	1209	6.3	16.5	77.3	–	0.13	0.82*
14	49°52'15.0"N, 24°02'04.2"E	141	2.8	17.0	80.1	–	0.14	0.91*
15	49°49'39.7"N, 24°02'14.5"E	102	2.9	20.6	76.5	–	0.16	0.92*
16	49°49'40.5"N, 24°02'08.8"E	162	2.5	26.5	71.0	–	0.19	0.94*
17	49°49'53.6"N, 24°00'55.2"E	170	3.5	29.4	67.1	–	0.20	0.92*
18	49°49'07.4"N, 24°01'19.3"E	210	14.3	21.4	64.3	–	0.14	0.70*
19	49°49'38.3"N, 24°01'29.9"E	274	12.4	10.9	76.6	–	0.08	0.64*
20	49°49'56.6"N, 24°02'38.5"E	341	18.2	5.0	76.8	–	0.04	0.42*
21	49°50'07.2"N, 24°02'14.9"E	103	36.9	8.7	54.4	–	0.05	0.34*
22	49°49'58.1"N, 24°04'00.8"E	107	–	1.9	98.1	–	0.02	1.00*
23	49°49'53.9"N, 24°01'31.9"E	102	9.8	17.6	72.5	–	0.13	0.75*
24	49°50'05.5"N, 24°01'41.6"E	102	15.7	12.7	71.6	–	0.09	0.61*
25	49°50'06.2"N, 24°01'34.6"E	159	8.8	10.7	41.5	39.0	0.02	0.11
26	49°49'38.7"N, 24°02'48.8"E	107	–	9.3	65.4	25.2	0.08	0.65*
27	49°48'42.2"N, 24°01'24.9"E	375	20.3	4.0	75.2	0.5	0.03	0.33*
28	49°49'28.6"N, 23°56'21.8"E	102	–	3.9	96.1	–	0.04	1.00*
29	49°49'08.9"N, 23°57'34.3"E	113	0.9	59.3	39.8	–	0.24	0.98*
30	49°49'30.7"N, 23°56'08.8"E	105	–	23.8	76.2	–	0.18	1.00*
31	49°47'30.6"N, 24°03'13.8"E	123	4.9	4.1	91.1	–	0.04	0.66*
32	49°48'48.0"N, 23°58'23.6"E	182	3.3	15.9	80.8	–	0.13	0.89*
33	49°51'01.6"N, 23°58'33.9"E	114	5.3	12.3	82.5	–	0.10	0.81*
34	49°49'18.7"N, 24°00'02.2"E	109	15.6	31.2	53.2	–	0.17	0.72*
35	49°48'36.8"N, 23°59'31.1"E	108	26.9	5.6	67.6	–	0.04	0.35*
36	49°48'17.2"N, 23°59'36.8"E	104	–	15.4	84.6	–	0.13	1.00*
37	49°48'23.3"N, 23°59'32.0"E	113	1.8	23.9	74.3	–	0.18	0.95*
Lviv Region of Ukraine, Briukhovychi								
38	49°54'03.0"N, 23°57'36.6"E	97	15.5	12.4	72.2	–	0.09	0.60*
Lviv Region of Ukraine, Dubliany								
39	49°53'59.0"N, 24°05'22.4"E	531	0.6	14.7	84.7	–	0.12	0.98*
Lviv Region of Ukraine, Horodok								
40	49°47'12.5"N, 23°38'31.1"E	650	–	68.9	31.1	–	0.21	1.00*
41	49°46'40.2"N, 23°38'19.2"E	130	–	28.5	71.5	–	0.20	1.00*
Lviv Region of Ukraine, Obroshyne								
42	49°47'13.8"N, 23°52'24.6"E	380	0.3	53.2	46.6	–	0.25	0.99*
Lviv Region of Ukraine, Pidbirtsi								
43	49°50'30.5"N, 24°09'04.8"E	110	3.6	2.7	70.0	23.6	0.01	0.13
Lviv Region of Ukraine, Pustomyty								
44	49°43'00.3"N, 23°54'04.7"E	217	6.0	37.3	56.7	–	0.21	0.88*
Lviv Region of Ukraine, Solonka								
45	49°44'56.8"N, 24°00'24.2"E	107	2.8	1.9	95.3	–	0.02	0.62*
Lviv Region of Ukraine, Velyky Liubin								
46	49°43'24.6"N, 23°42'49.8"E	126	–	15.9	84.1	–	0.13	1.00*
Lviv Region of Ukraine, Zhovkva								
47	50°03'13.4"N, 23°59'11.4"E	108	–	5.6	94.4	–	0.05	1.00*
48	50°03'12.5"N, 23°58'48.3"E	344	11.3	21.8	66.9	–	0.15	0.75*
Lviv Region of Ukraine, Zubra								
49	49°46'42.7"N, 24°03'06.6"E	118	1.7	5.1	93.2	–	0.05	0.86*
Ivano-Frankivsk Region of Ukraine, Ivano-Frankivsk								
50	48°55'30.7"N, 24°43'39.6"E	86	18.6	8.1	73.3	–	0.06	0.49*
51	48°56'51.3"N, 24°41'47.8"E	92	1.1	8.7	90.2	–	0.08	0.94*
Moscow Region of Russia, Vidnoe								
52	55°33'26.4"N, 37°43'18.6"E	153	9.2	5.9	49.0	35.9	0.02	0.15

(Gural-Sverlova & Gural 2022: table 2). In addition to the city itself, the maps show also findings made in nearby smaller settlements (Birky, Briukhovychi, Dubliany, Malekhiv, Solonka, Vynnyky, Zubra) and near two large garden centres: Club of Plants (Pidbirtsi) and Galsad (near Davydiv).

The correlation of the white ground colour of the shell and the presence of bands in *C. hortensis* from Western Ukraine was analysed using quantitative data collected in 2015–2021 (Gural-Sverlova & Gural 2022) at 37 sites in Lviv, 12 sites in other settlements of the Lviv region and 2 sites in Ivano-Frankivsk (Table 1). The length of the studied sites usually ranged from 20–30 to 50–60 m, which does not exceed the diameter of the panmictic unit in *Cepaea*, estimated from 50–60 m (Jones et al. 1977) to 100 m (Schnetter 1950). The samples consisted only of adult live snails, in some cases also of well-preserved empty shells of adults, suitable for reliable determination of the ground colour. For more details on places and methods of collection, see previous publications (Gural-Sverlova & Gural 2021a, 2022). For comparison, one sample of *C. hortensis* from the Moscow region of Russia (Vidnoe) was used, where unbanded and banded shells with a white ground colour were also found (Gural-Sverlova & Gural 2021a). Some of these samples are stored in the malacological collection of the State Museum of Natural History in Lviv.

As in previous publications (Gural-Sverlova & Gural 2021a, 2022), the shells of adult *C. hortensis* were considered dark-lipped if their aperture edges were pink or reddish-brown along the entire length (Figs 3–4). This did not take into account the slight pinkishness near the columella (Gural-Sverlova & Gural 2021a: fig. 5B), which is sometimes observed in single specimens of this species even in those populations where there are no snails with a true dark lip (Schilder & Schilder 1957: 163, Gural-Sverlova & Gural 2021a).

RESULTS

About a hundred images were selected from the database iNaturalist (2022) showing the shells of adult *C. hortensis*, the colouration of which could be reliably identified as white unbanded. Similarly, more than 300 images were selected for white banded shells and over 900 for yellow banded ones. Our analysis showed that the white shell ground colour is widespread in the present range of *C. hortensis*. It is found in different parts of Europe (Figs 6–7) as well as in North America (Canada, USA) and is more common in banded than in unbanded shells.

In Europe, most records of white banded shells were concentrated in England and in southern part of Central Europe (Czech Republic, Slovakia, Austria) (Fig. 7), although this may be partly correlated with the total number of *C. hortensis* observations in different countries. However, the ratio of observations of white banded and yellow banded shells in different European countries also varied considerably. In most cases, yellow banded shells were recorded more often than white banded ones. On the maps (Figs 7–8), this is especially noticeable for such countries as, for example, Denmark, Belgium, Germany, France, and England. At the same time, in Slovakia, as well as in neighboring Western Ukraine, the opposite trend was observed.

As in other European countries (Figs 6–7), white banded shells were more common than white unbanded ones in Lviv and its immediate environs (Figs 9–10). In contrast, yellow banded shells have so far been found only in a few sites (Fig. 11), and in four cases they were recorded near large garden centres – two operating in the vicinity of Lviv and two in the city itself, closed in 2018 and 2022.

In most of the analysed samples of *C. hortensis* from Western Ukraine (Table 1), a strong correlation between white ground colour and band presence was observed indicating the linked inheritance of these two traits. In more than two-thirds of cases, the correlation coefficient (r) exceeded 70%.

Shells of *C. hortensis* with a pink ground colour were found at 9 sites in Lviv and its environs (Table 2). In five cases, all pink shells, regardless of the presence or absence of bands, had a dark coloured lip (Figs 3–4). Sometimes this trait was also observed in single yellow unbanded shells (Fig. 4). In the other four sites, pink shells had only a white lip typical for *C. hortensis* (Table 2).

The greatest phenotypic diversity of *C. hortensis*, both in Lviv with its environs (Table 2) and in Western Ukraine in general, was recorded near the garden centre Club of Plants in Pidbirtsi. Brown shells, the colour of which varied from light brown to yellowish brown (Fig. 5) were found only here. They differed from the pink shells collected at the same site (Fig. 5, left) not only in the ground colour, but also in the white lip and somewhat larger size.

Data on the time of the first discovery and known records of some inherited traits that are not typical for most Western Ukrainian populations of *C. hortensis* are summarised in Table 3. For comparison: *C. hortensis* is currently known from many settlements of the Lviv region, and there are also some findings of this species from the Ivano-Frankivsk, Transcarpathian, Volyn, Khmelnytsky, Rivne, and Chernivtsi regions in Western Ukraine.

Table 2. Phenotypic composition of *C. hortensis* from those sites in Lviv and its environs where pink shells were recorded. Legend: A-0 – white unbanded, A-b – white banded, B-0 – brown unbanded, DL – dark lip, N – sample size, P-0 – pink unbanded, P-b – pink banded, SO – single observations, no quantitative sampling, WL – light (white) lip, Y-0 – yellow unbanded, Y-b – yellow banded. An asterisk indicates samples made along the fences of garden centres

Localities and coordinates	Years	N	Lip	A-0	A-b	Y-0	Y-b	P-0	P-b	B-0
There are pink shells with a dark lip										
Lviv, Kalicha Hora St. 49°50'06.2"N, 24°01'34.6"E	2019–2022	204	WL	17	23	92	37	–	–	–
			DL	–	–	–	–	11	24	–
Lviv, Tershakovtsi St. 49°50'09.1"N, 24°02'29.8"E	2021–2022	23	WL	–	–	5	12	–	–	–
			DL	–	–	1	–	3	2	–
Lviv, General Chuprynka St. 49°49'19.9"N, 23°59'59.0"E	2020	SO	WL	–	–	+	–	–	–	–
			DL	–	–	–	–	1	–	–
Zubra, unnamed street 49°46'41.5"N, 24°03'08.9"E	2022	8	WL	1	–	3	1	–	–	–
			DL	–	–	–	–	1	2	–
*Pidbirtsi, Club of Plants 49°50'30.5"N, 24°09'04.8"E	2021	110	WL	4	3	76	18	–	–	3
			DL	–	–	1	–	1	4	–
There are pink shells with a light lip										
Lviv, General Hrytsai St. 49°49'38.7"N, 24°02'48.8"E	2020–2022	121	WL	–	11	78	9	19	4	–
			DL	–	–	–	–	–	–	–
*Lviv, Horodotska St. 49°49'50.1"N, 23°57'57.0"E	2022	16	WL	2	–	8	1	5	–	–
			DL	–	–	–	–	–	–	–
Solonka, Ivan Sirko St. 49°44'57.5"N, 23°59'40.5"E	2021	SO	WL	–	–	+	1	–	1	–
			DL	–	–	–	–	–	–	–
*Near Davydiv, Galsad 49°45'57.3"N, 24°06'29.2"E	2021	14	WL	–	2	5	6	1	–	–
			DL	–	–	–	–	–	–	–

Table 3. Inherited traits that began to be recorded in Western Ukrainian populations of *C. hortensis* only in recent years. Asterisks indicate findings near garden centres

Trait or phenotype	Time of first record	Lviv region	Transcarpathian region
Yellow banded shell	2018	Lviv, Davydiv*, Pidbirtsi*, Solonka, Zhovkva, Zubra	–
Pink shell	2015	Lviv, Davydiv*, Pidbirtsi*, Solonka, Zubra	Uzhgorod
Brown shell	2021	Pidbirtsi*	–
Dark lip	2019	Lviv, Pidbirtsi*, Zubra	–

DISCUSSION

The presence of white shells in *C. hortensis* has long been known. So, Taylor (1914: 343–345) mentioned in his monograph several "variations" of this species described already in the 19th century, having a white, whitish or "dirty cream" shell and registered in England, Scotland, Ireland, Germany, France, Norway, and USA. Later, Rost (1952: table 1) mentioned the coexistence of snails of this species with white and yellow shells in some areas of Norway.

But since the middle of the 20th century, there has been an increase in interest in quantitative studies of the shell colour and banding polymorphism in *Cepaea*. In general the entire variety of shell ground colours in *C. hortensis* and *C. nemoralis* has been reduced to three (yellow, pink, and brown) (Clarke 1960) or even two (yellow and pink) (Schilder & Schilder 1953, 1957), although it is known that there are heritable variations in the intensity and shade of colour (Murray 1975). With this approach, white and yellow shells are combined into one group. According to Clarke (1960: 424), "in *C. hortensis*… the commonest colours are white, yellow, pink and brown… The first two colours… are often difficult to separate, and appear to have every sort of intermediate between them. I have included them both in the "yellow" class".

However, our long-term study of the shell colour and banding polymorphism in introduced populations of *C. hortensis* in Western Ukraine, which began in the late 1990s (Sverlova 2001) and continues to this day (Gural-Sverlova & Gural 2018, 2021a, 2022), allowed us to formulate as follows:

1. Shells with a white ground colour do not have even traces of yellow pigment (Figs 1–2), which makes it possible to differentiate them reliably from light yellow shells, both unbanded (Gural-Sverlova & Gural 2018) and banded (Gural-Sverlova & Gural 2021a). There are no transi-

tional forms between white and light yellow shells. Only the periostracum darkened from external influences can make it somewhat difficult to determine. Because of this, white shells may look grayish or even light beige (Gural-Sverlova & Gural 2021a).

2. In most cases, it is possible to reliably distinguish a white ground colour from yellow one even in partially faded empty shells. It is enough to moisten their surface (for unbanded) or the top (for banded) with water (Gural-Sverlova & Gural 2021a). In general, the differentiation of white and yellow shells is no more difficult and no less reliable than that of yellow and pink ones. Judging by the studied shells from the Moscow region of Russia (Gural-Sverlova & Gural 2021a), where *C. hortensis* was introduced independently of Western Ukraine, and photographic materials (iNaturalist 2022, UkrBIN 2022) from other countries, this may be true for the entire present range of *C. hortensis*, including its native part. But it may need further study.
3. In Lviv, the proportion of white shells among unbanded ones demonstrates significant temporal stability at different sites of the city. At the same time, it varies noticeably between sites (Gural-Sverlova & Gural 2018: table 1). This may be considered an indirect confirmation of the hereditary nature of the white ground colour in *C. hortensis*.
4. Despite the fact that almost all Western Ukrainian populations formed by the descendants of the primary introduction of *C. hortensis* to Western Ukraine (Gural-Sverlova & Gural 2021a) contain white banded and yellow unbanded shells (Table 1), this does not lead to the appearance of even a small number of yellow banded shells. This is especially clearly confirmed by Lviv populations, some of which have been observed by us for more than 20 years (Gural-Sverlova & Gural 2018, 2022). The appearance of yellow banded shells (Fig. 2) at a few sites of Lviv and Lviv region, recorded in recent years (Gural-Sverlova & Gural 2021a, 2022), cannot be the result of recombinations, because it is usually accompanied by the presence of other inherited traits that were previously completely absent in Western Ukraine. These are pink shells and/or variability in body colouration, less often a dark lip (Gural-Sverlova & Gural 2021a: table 5).
5. Similarly, in sites where white unbanded shells are completely absent, snails with this phenotype can obviously appear only as a result of migration or repeated introduction. So, in Horodok, Lviv region, where almost 300 unbanded specimens (live snails or empty shells) were collected from 2017 to 2021, none of which had a white ground colour (Table 1). This is in good agreement with the data of Gonzalez et al. (2019), who experimentally showed the absence of recombination between colour/banding loci in *C. nemoralis*. At the same time, the overestimated values of the recombination rate given by previous researchers could be associated with incomplete penetrance and epistasis in individuals obtained by crossing, whose phenotypes could only seem to be recombinant.
6. The appearance of yellow banded shells (Fig. 2) in *C. hortensis*, as well as other hereditary traits that are absent in the descendants of the primary introduction (Figs 3–5), at some sites of Western Ukraine is possible only as a result of repeated independent introductions of this species. Recently, such introductions are increasingly taking place through garden centres (Gural-Sverlova & Gural 2021a, 2022), often together with *C. nemoralis* (Gural-Sverlova et al. 2020, 2021, Gural-Sverlova & Gural 2021a: table 5).

When studying the related species *C. nemoralis* in Lviv, we also found white shells without traces of yellow, pink, or brown pigment (Gural-Sverlova et al. 2021), which were easily distinguished from yellow and were similar to the white shells of *C. hortensis* (Fig. 12). However, in *C. nemoralis*, this colouration was much less common than in *C. hortensis*. On the contrary, it is known that darker variants of the shell ground colour (pink and, especially, brown) are more typical for *C. nemoralis* than for *C. hortensis*.

Goodhart (1962) reported specimens of *C. nemoralis* with "milky" shells rare in the Hundred Foot Bank (east bank of New Bedford River, England). However, his description "the colour is almost completely suppressed to give a milky-white shell sometimes with a purplish tinge" and the image suggest that in this case it could be a very pale variation of the pink colour sometimes found in *C. nemoralis*.

It is known that the loci for shell ground colour and the presence/absence of bands in *Cepaea* are linked (Murray 1975, Gonzalez et al. 2019), which often leads to a different ratio of banded and unbanded shells among specimens from the same population or from the same area, but with different ground colours. This is most often expressed as an increase in the proportion of banded shells among snails with a lighter ground colour (for example, yellow versus pink) and, consequently, in an increase in the proportion of unbanded shells with a darker ground colour (Schilder & Schilder 1957: 162, Cameron 2013: 114, Gural-Sverlova & Gural 2021b: fig. 1). The opposite trend is also found, for example, in *C. nemoralis* in southern Poland (Ożgo et al. 2019: 6) or in Minsk, Belarus (Gural-Sverlova & Kruglova 2022: fig. 5). A similar pattern is observed in Western Ukrainian populations of *C. hor-*

Fig. 12. Yellow (top) and white (bottom) shells of *C. nemoralis* from Lviv

tensis, where the band presence is inherited linked to a lighter (white) ground colour, and yellow shells predominate among unbanded ones (Table 1).

Unfortunately, in the summarising publication of MURRAY (1975) there are no data on the nature of inheritance of the white ground colour in *Cepaea*. However, in both species, a yellow ground colour is known to be recessive to darker colouration variants (pink or brown), and a light yellow colour is recessive to dark yellow (MURRAY 1975: tables 2–3). Therefore, we have previously suggested that the white colour of the shell in *C. hortensis* is recessive in relation to the yellow one (GURAL-SVERLOVA & GURAL 2018, 2021a). However, even regardless of the nature of inheritance of the white ground colour in *C. hortensis*, a separate consideration of phenotypes with yellow and white ground colours is of decisive importance for studying the spreading history of this species in Western Ukraine.

The white shell ground colour is widespread in different parts of the species range of *C. hortensis*, as shown by our analysis (Figs 6–7). Therefore, almost any European area inhabited by this species could theoretically serve as a source of primary introduction to Western Ukraine. We have not been able to find any part of Europe or a single country with a complete absence of banded shells with a non-white ground colour, which until recently was observed in Western Ukraine. Therefore, it is logical to assume that such pattern is an anomaly that appeared at the initial stage of the introduction of *C. hortensis* into Western Ukraine, before this species, together with seedlings of ornamental shrubs, was unintentionally resettled in the urbanised biotopes of Lviv (SVERLOVA 2002) and other settlements (GURAL-SVERLOVA & GURAL 2021a).

Because the initial introduction of *C. hortensis* to Western Ukraine took place before the collapse of the Soviet Union, it is more likely that the snails could have been introduced from one of the former Soviet block countries (GURAL-SVERLOVA & GURAL 2021a). Probably of particular interest in this regard may be the territory of the former Czechoslovakia, where white banded shells are also common (Fig. 7), and especially Slovakia. Judging by the number of points plotted on the maps (Figs 7–8), it is likely that white banded shells can be found there even more often than yellow banded ones (see Results). Another favourable factor is the territorial proximity of Slovakia and the western part of Ukraine. However, verification of this hypothesis is impossible without a comparative phenotypic and genetic analysis of Czech, Slovak, and Western Ukrainian populations of *C. hortensis*.

The colouration traits that have appeared in Western Ukraine only recently (Table 3) can be divided into two groups according to how common they are in the natural range of *C. hortensis* and how

informative they are for research of the spreading history of this species in the study area. Yellow banded and pink shells (if the pink colour is not accompanied by a dark lip – Table 2) can be brought to the west of Ukraine simultaneously from different European countries and through different garden centres. Therefore, their discovery in some sites of Western Ukraine indicates only that a recent introduction took place here, but does not provide any information about its possible origin.

More interesting are the records of brown shells and, especially, shells with a dark lip, which are much rarer even in the natural range of *C. hortensis*. We found out that both of them were brought to Western Ukraine through one garden centre, Club of Plants. This garden centre was opened near Lviv (Pidbirtsi) in 2008. The official website indicates that imported plant varieties are brought from Germany, the Netherlands, Italy, and Poland. In two of these countries (Germany and Poland), the records of *C. hortensis* with a dark lip are known (Schilder & Schilder 1957, Ożgo 2010).

In general, the dark lip in *C. hortensis* occurs in different parts of Europe, but locally (Schilder & Schilder 1957: map 66). In Western Europe, this trait is recorded from France and northeast Spain (Catalonia), in Northern Europe – from England, Denmark and Norway, in Central Europe – from Germany, northern Austria (Upper Austria), western Czech Republic (Bohemia) (Schilder & Schilder 1957: table 20), and also for north-western Poland (Ożgo 2010). In Eastern Europe, until 2019, when dark-lipped *C. hortensis* was first discovered in Western Ukraine (Gural-Sverlova & Gural 2021a), only one introduced population with dark-lipped specimens of this species was known in Moscow, Russia (Egorov 2018, Gural-Sverlova & Gural 2021a). However, in contrast to Ukraine, only some snails with pink unbanded shells had a dark lip in Moscow. All pink banded and yellow shells were light-lipped there, at most with a slight pinkishness near the columella.

In the related species *C. nemoralis*, lip colour is inherited linked to the shell ground colour and the presence/absence of bands (Murray 1975). This apparently also occurs in *C. hortensis*. In *C. hortensis*, a dark lip is much more common in shells with a darker, pink and/or brown ground colour (Schilder & Schilder 1957, Ożgo 2010). It can also be associated only with unbanded shells of this colour or appear on both unbanded and banded shells (Schilder & Schilder 1957: 163). Interestingly, both of these variants have already been found in some introduced populations of *C. hortensis* in Eastern Europe: the first in central European Russia, the second in Western Ukraine.

The brown ground colour is also found in different parts of the present European range of *C. hortensis*, but is much rarer than pink and especially yellow. It is also more common in the western part of this range (Cameron 2013: table 4), i.e. in areas more remote from Ukraine. This is apparently why brown-shelled snails have previously not been reported from introduced Eastern European populations of *C. hortensis* (Gural-Sverlova & Gural 2021a). We consider it quite probable that brown shells with a light lip and pink ones with a dark lip, registered near the garden centre in Pidbirtsi (Fig. 5), could have been brought there with imported plants independently of each other and at different times. It is indicative that the last variant of shell colouration in *C. hortensis* was also recorded at four sites in and near Lviv (Table 2), and brown shells have so far been found only near the garden centre itself (Table 3). In all sites of Germany and Poland studied by Ożgo (2010), where the dark lip, pink and brown shells in *C. hortensis* were found simultaneously, the dark lip was present in all or part of the shells of both colours.

Differences in morph frequencies observed in *Cepaea* populations may be the result of an interaction of selective (climatic and visual selection) and non-selective factors (Jones et al. 1977). However, the absence of common and, conversely, the presence of rare hereditary traits or their combinations in areas where *C. nemoralis* or *C. hortensis* were introduced can be more logically explained by the founder effect. A classic example was the frequent occurrence of *C. nemoralis* with split bands in Lexington, USA, where this species was accidentally introduced from Italy or the British Isles at the end of the 19th century (Howe 1898).

Thus, two convenient phenotypic markers are already known in the west of Ukraine, which make it possible to distinguish the descendants of two different introductions of *C. hortensis* into the study area: the complete absence of banded shells with a non-white ground colour (primary introduction in the 20th century) and the presence of a dark lip in all pink specimens (one of the later introductions, associated with the garden centre Club of Plants). Brown shells found near the same garden centre have not yet been recorded in other areas of Western Ukraine. Since the mentioned garden centre has an online store selling decorative and garden plants throughout the country, snails with a dark lip or brown shell in the future may be found not only in other administrative regions of Western Ukraine, but also in other parts of Ukraine. But only in the western part of the country, and especially in the Lviv region, there is a unique opportunity to observe the process of "mixing" in one area of the descendants of different introductions of *C. hortensis*, even without their genetic study.

ACKNOWLEDGEMENTS

We sincerely thank S. P. SAVCHUK, Head of the Botany and Zoology section of Junior Academy of Sciences of the Ivano-Frankivsk City Council, for help in collecting of *C. hortensis* in Ivano-Frankivsk in 2018.

REFERENCES

BERGEY E. A., FIGUEROA L. L., MATHER C. M., MARTIN R. J., RAY E. J., KURIEN J. T., WESTROP D. R., SURIYAWONG P. 2014. Trading in snails: plant nurseries as transport hubs for non-native species. Biological Invasions 16: 1441–1451.

CAMERON R. A. D. 1992. Change and stability in *Cepaea* populations over 25 years: a case of climatic selection. Proceedings of the Royal Society of London B, Biological Sciences 248: 181–187. https://doi.org/10.1098/rspb.1992.0060

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., POKRYSZKO B. 2008. Variation in *Cepaea* populations over 42 years: climate fluctuations destroy a topographical relationship of morph-frequencies. Biological Journal of the Linnean Society 95: 53–61. https://doi.org/10.1111/j.1095-8312.2008.01042.x

CARTER M. A. 1968. Studies on *Cepaea* II. Area effects and visual selection in *Cepaea nemoralis* (L.) and *Cepaea hortensis*. Philosophical Transactions of the Royal Society of London B, Biological Sciences 253: 397–446. https://doi.org/10.1098/rstb.1968.0006

COCKERELL T. D. A. 1890. *Helix hortensis* in America. The Nautilus 3: 139–140.

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

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

EGOROV R. 2015. The first record of introduced snail *Cepaea hortensis* (Müller, 1774) (Stylommatophora: Helicidae) in the central part of European Russia. Ruthenica, Russian Malacological Journal 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

GONZALEZ D. R., ARAMENDIA A. C., DAVISON A. 2019. Recombination within the *Cepaea nemoralis* supergene is confounded by incomplete penetrance and epistasis. Heredity 123: 153–161. https://doi.org/10.1038/s41437-019-0190-6

GOODHART C. B. 1962. Variation in a colony of the snail *Cepaea nemoralis* (L.). Journal of Animal Ecology 31: 207–237.

GURAL-SVERLOVA N. V., GURAL R. I. 2018. Long-term dynamic of phenetic structure in colonies of the introduced species, *Cepaea hortensis* (Gastropoda, Pulmonata, Helicidae). Zoologicheskij Zhurnal 97: 751–761. https://doi.org/10.1134/S0044513418070097

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

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

GURAL-SVERLOVA N. V., GURAL R. I. 2022. 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., SAVCHUK S. P. 2020. New records of *Cepaea nemoralis* (Gastropoda, Pulmonata, Helicidae) and phenotypic composition of its colonies in Western Ukraine. Ruthenica, Russian Malacological Journal 30: 75–86. https://doi.org/10.35885/ruthenica.2021.30(2).1

GURAL-SVERLOVA N. V., GURAL R. I., RODYCH T. V. 2021. 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., 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

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

HOWE J. L. 1898. Variation in the shell of *Helix nemoralis* in the Lexington, Va., colony. The American Naturalist 32: 913–920.

iNATURALIST 2022. iNaturalist: A community for naturalist. Available online at https://www.inaturalist.org (accessed on 1 June 2022).

JOHNSON C. W. 1906. On the distribution of *Helix hortensis* Mueller, in North America. The Nautilus 20: 73–80.

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.

MAZON L. I., VICARIO A., MARTINEZ DE PANCORBO M. A., LOSTAO C. M. 1990. Polymorphism in *Cepaea hortensis* in marginal populations in Spain. Genetica 81: 109–115.

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. 2010. Populations of *Cepaea hortensis* (O. F. Müller, 1774), polymorphic for the colour of shell lip in north-western Poland and north-central Gernany. Folia Malacologica 18: 93–97. https://doi.org/10.2478/v10125-010-0011-2

OŻGO M., CAMERON R. A. D., HORSÁK M., POKRYSZKO B. M., 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., ZAJĄC K., ZIELSKA J., ŻBIKOWSKA E., ŻOŁĄDEK J. 2019. *Cepaea nemoralis* (Gastropoda: Pulmonata) in Poland: patterns of variation in a range-expanding species. Biological Journal of the Linnean Society 20: 1–11. https://doi.org/10.1093/biolinnean/blz029

ROST H. 1952. Studies on *Cepaea hortensis* (Müll.) in Northern Norway. Astarte 2: 1–10.

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

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

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

SVERLOVA N. V. 2001. Polymorphism of the introduced species *Cepaea hortensis* (Gastropoda, Pulmonata, Helicidae) in Lvov. 1. General regularities of polymorphism. Zoologicheskij Zhurnal 80: 520–524.

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

TAYLOR J. W. 1914. Monograph of the land & freshwater Mollusca of British Isles. Zonitidae, Endodontidae. Helicidae. Taylor Brothers, Leeds.

UKRBIN 2022. UkrBIN: Ukrainian Biodiversity Information Network [public project & web application]. Available online at https://www.ukrbin.com (accessed on 1 June 2022).

Received: July 27th, 2022
Revised: September 19th/29th, 2022
Accepted: October 10th, 2022
Published online: November 8th, 2022