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Shell banding and colour polymorphism of introduced snail *Cepaea hortensis* (Gastropoda, Pulmonata, Helicidae) from some parts of Eastern Europe

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ABSTRACT. The phenotypic composition of *C. hortensis* colonies was studied in Western Ukraine (more than 30 thousand adults from 23 settlements and 5 administrative regions) and the Moscow region of Russia (more than 500 adults and juveniles from two colonies in Moscow and Vidnoe). Most Western Ukrainian colonies were characterized by the absence of pink shells, the high frequencies of unbanded shells (70% or more), as well as the white ground colour in all banded shells. It is supposed that the latter feature makes it possible to reliably identify the colonies formed by the descendants of the primary introduction of *C. hortensis* into Western Ukraine, which occurred in the 20th century, from later and independent repeated introductions of this species. Unlike Western Ukraine, snails with yellow banded and pink shells were found in both colonies from the Moscow region. Pink banded shells were registered only in Moscow as well as in two colonies from Lviv. In two of the three colonies mentioned, part of the pink unbanded (Moscow) or all pink shells (Lviv) had a dark lip.

Полиморфизм окраски раковины интродуцированной улитки *Cepaea hortensis* (Gastropoda, Pulmonata, Helicidae) из отдельных регионов Восточной Европы

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РЕЗЮМЕ. Исследован фенетический состав колоний *C. hortensis* на западе Украины (более 30 тыс. взрослых особей из 23 населенных пунктов и 5 административных областей) и в Московской области России (более 500 взрослых и неполовозрелых особей из двух колоний в Москве и Видном). Для большинства западноукраинских колоний было характерно отсутствие розовых раковин, высокие частоты бесполосых раковин (70% и более), а также белый фоновый цвет у всех полосатых раковин. Предполагается, что последний признак позволяет надежно идентифицировать колонии, образованные потомками первичной интродукции *C. hortensis* на запад Украины, произошедшей еще в XX в., от более поздних и независимых повторных интродукций этого вида. В отличие от запада Украины, в обоих колониях из Московской области встречались улитки с желтыми полосатыми и розовыми раковинами. Розовые полосатые раковины были отмечены только в Москве и в двух колониях изо Львова. В двух из трех упомянутых колоний часть розовых бесполосых (Москва) или все розовые раковины (Львов) имели темную губу.

Introduction

Cepaea hortensis (Müller, 1774) is a species of the Central European origin [Boettger, 1926; Taylor, 1914], the natural range of which also includes apparently many countries of the Northern and Western Europe [Kerney *et al.*, 1983, map 364]. It can reach the Iberian Mountains in Spain in the southwest [Mazon *et al*., 1990], as well as Sweden, Finland and Norway in the north. The eastern and northeastern boundaries of the natural range of *C. hortensis* can pass through western Slovakia [Kerney *et al*., 1983], western and northern Poland [Wiktor, 2004] and the eastern Baltic states, in the northeast reaching the Leningrad region of Russia, where some marginal populations of this species are known [Alexandrov, Sergievsky, 1980].

C. hortensis was first successfully introduced to the west of Ukraine no later than the second half of the 20th century, most likely together with seedlings of ornamental shrubs [Sverlova, 2002a]. In the largest city in Western Ukraine, Lviv, this species appeared no later than the 1970s. At the end of the 1970s, according to the observations of the first author there were already some colonies of this species.

Earlier malacological studies conducted in the city and its environs at the end of the 19th century [Bąkowski, 1882, 1884] as well as numerous conchological materials collected on this territory in the second half of the 19th century and at the beginning of the 20th century and deposited in the malacological collection of the State Museum of Natural History in Lviv [Gural-Sverlova, Gural, 2020], indicate the absence of *C. hortensis* in Lviv until the beginning

of the 20th century inclusive. Unfortunately, later the land molluscs of the city were not investigated until the end of the 20th century when *C. hortensis* had already become a typical representative of the urban fauna [Sverlova, 2002a; Sverlova *et al*., 2006].

A study carried out in 1998 and covering most of Lviv revealed a clear connection between *C. hortensis* and ornamental shrubs (snowberry, privet, spirea, etc.), often planted in the form of hedges, less often in separate small groups along the streets and in parks. This relationship was especially noticeable in the new microdistricts of Lviv, where planned planting of ornamental shrubs was carried out relatively recently and the snails have not yet had time to populate other habitats suitable for them [Sverlova, 2002a]. The noted regularity suggested that at the initial stage of introduction into Western Ukraine, *C. hortensis* could enter the nursery that supplied seedlings for landscaping the city.

Later, we revealed the same patterns not only for Lviv but also for other settlements of the Lviv region, where similar hedges from ornamental shrubs were often planted near railway stations, hospitals, sanatoriums, educational and administrative buildings, in parks and just along large streets. In the Ivano-Frankivsk region, where *C. hortensis* is still known from only a few settlements (Ivano-Frankivsk and its immediate vicinity, Bogorodchany) [Gural-Sverlova, Gural, 2020], in some cases, snails were also found in places with similar landscaping.

Other finds made in household plots and summer cottages in both regions may result from secondary transfers of snails by humans, most often along with plants, as well as during children's games [Sverlova, 2002a]. Together with plant waste, snails also often end up on wastelands, roadsides, forest belts planted alongside them, etc. At the biogeostationary of the Ivan Franko National University of Lviv in the north of the Volyn region, *C. hortensis* was also brought along with seedlings of ornamental shrubs from Lviv.

Today, numerous finds of this species are known in the Lviv region, there are single records in other administrative regions of Western Ukraine [Gural-Sverlova *et al*., 2020, fig. 3B]. *C. hortensis* has not yet been found in other parts of Ukraine, except for the only find in 2018 in the city of Lugansk in the east of the country [UkrBIN, 2020].

Unlike Western Ukraine, only two colonies of *C. hortensis* are currently found and examined in the Moscow region of Russia, the first of which was recorded in 2012 in Vidnoe, the second in 2015 in Moscow [Egorov, 2015, 2018]. However, their shell colour and banding polymorphism has been described only in general terms, without a complete phenotypic composition of the samples.

The mass occurrence of *C. hortensis* in Lviv made it possible already at the turn of the 20th and 21st centuries to study shell colour and banding polymorphism in urban colonies of this species on large quantitative material, describe its main peculiarities [Sverlova, 2001a], and the variability of the phenotypic composition within the city [Sverlova, 2001b, 2005], compare the results with data from other parts of the species range [Sverlova, 2001a, 2002b, 2004], and subsequently analyze the long-term dynamics of the morph frequencies in model colonies [Gural-Sverlova, Gural, 2018].

However, there has recently been an urgent need to summarize the quantitative data accumulated from 1999 to 2020, and not only in Lviv but also in other surveyed localities of *C. hortensis* in Western Ukraine. Also, only very recently we found one specific feature of banded shells in almost all known colonies of *C. hortensis* in Western Ukraine, which will be described for the first time in detail and illustrated in this article. This feature most probably not only indicates the kinship of most Western Ukrainian colonies but also makes it possible to distinguish the descendants of the initial introduction of *C. hortensis* into this region (most likely in the second half of the 20th century) from relatively recent, independent transfers [Gural-Sverlova *et al*., 2020]. We would also like to compare the features of the phenotypic structure of *C. hortensis* from different parts of Eastern Europe with similar data described for the main part of the species range.

Material and methods

Shell colour and banding polymorphism was studied in the colonies of *C. hortensis* from 5 administrative regions in Western Ukraine: Lviv (mainly), Volyn, Ivano-Frankivsk, Transcarpathian and Khmelnitsky. Live adult snails, less often their empty shells, were collected from April 1999 to June 2020 at 23 settlements. The shell ground colour and banding pattern were determined for more than 30 thousand specimens of *C. hortensis*.

Detailed information about the sites and time of collection is given in Supplementary material. There is also information about one additional site in Lviv (designated as L0), which was not used for quantitative analysis of the phenotypic composition, but where several snails with shell or body colouration not typical for Western Ukraine were found. The locations of the collecting sites in Lviv are shown in Fig. 1, in other settlements of Western Ukraine in Fig. 2.

We also studied samples from two colonies of *C. hortensis* in the Moscow region (Moscow and Vidnoe), collected from 2014 to 2019 by R.V. Egorov. The total number of adults was 412, juveniles with a shell diameter of at least 1 cm – 122. The habitats of *C. hortensis* in the Moscow region are described in more detail in the publications of Egorov [2015, 2018] and shorter in Supplementary material.

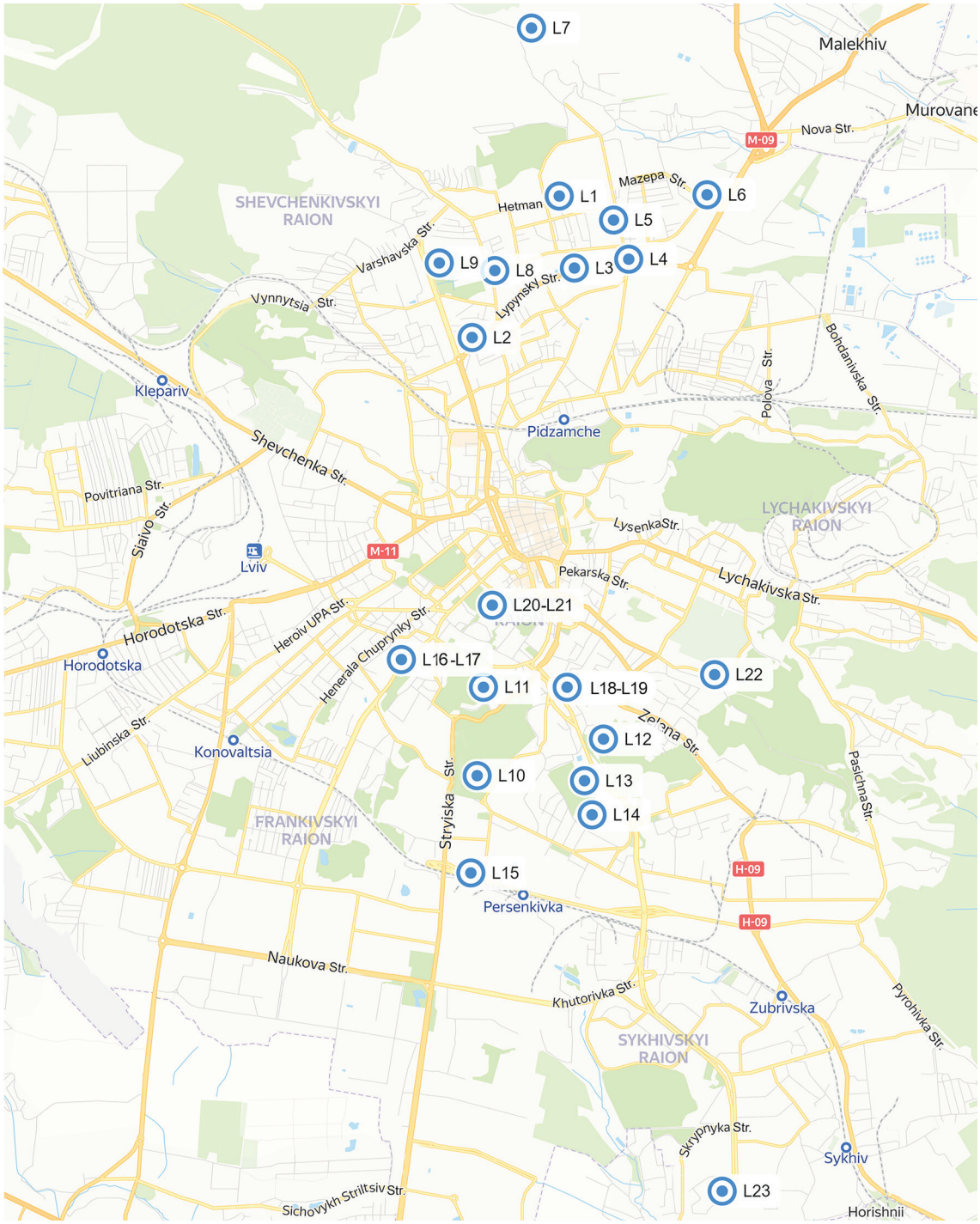

FIG. 1. The locations of the collecting sites in Lviv. Codes and descriptions of sites see Supplementary material.

РИС. 1. Расположение мест сбора во Львове. Коды и описания участков см. в Supplementary material.

In a number of cases, samples collected in different years, as well as at neighboring sites, were combined. In particular, this made it possible to noticeably reduce the number of analyzed samples from Lviv. At 7 sites (L1-L3, L7, L9-L11), the aggregates of samples collected in different time periods were separately considered: from 1999 to 2004 (indicated by the letter "a") and from 2015 to 2018 ("b"). The long-term dynamics of the phenotypic composition of *C. hortensis* at these sites was described in detail in a previous publication [Gural-Sverlova, Gural, 2018].

For the convenience of further analysis, all the investigated sites were divided into 4 groups according to the territorial principle and indicated by the corresponding letter codes: L – the administrative territory of Lviv city; LR – other settlements in Lviv region; WU – other administrative regions in Western Ukraine; MR – Moscow Region of Russia. When

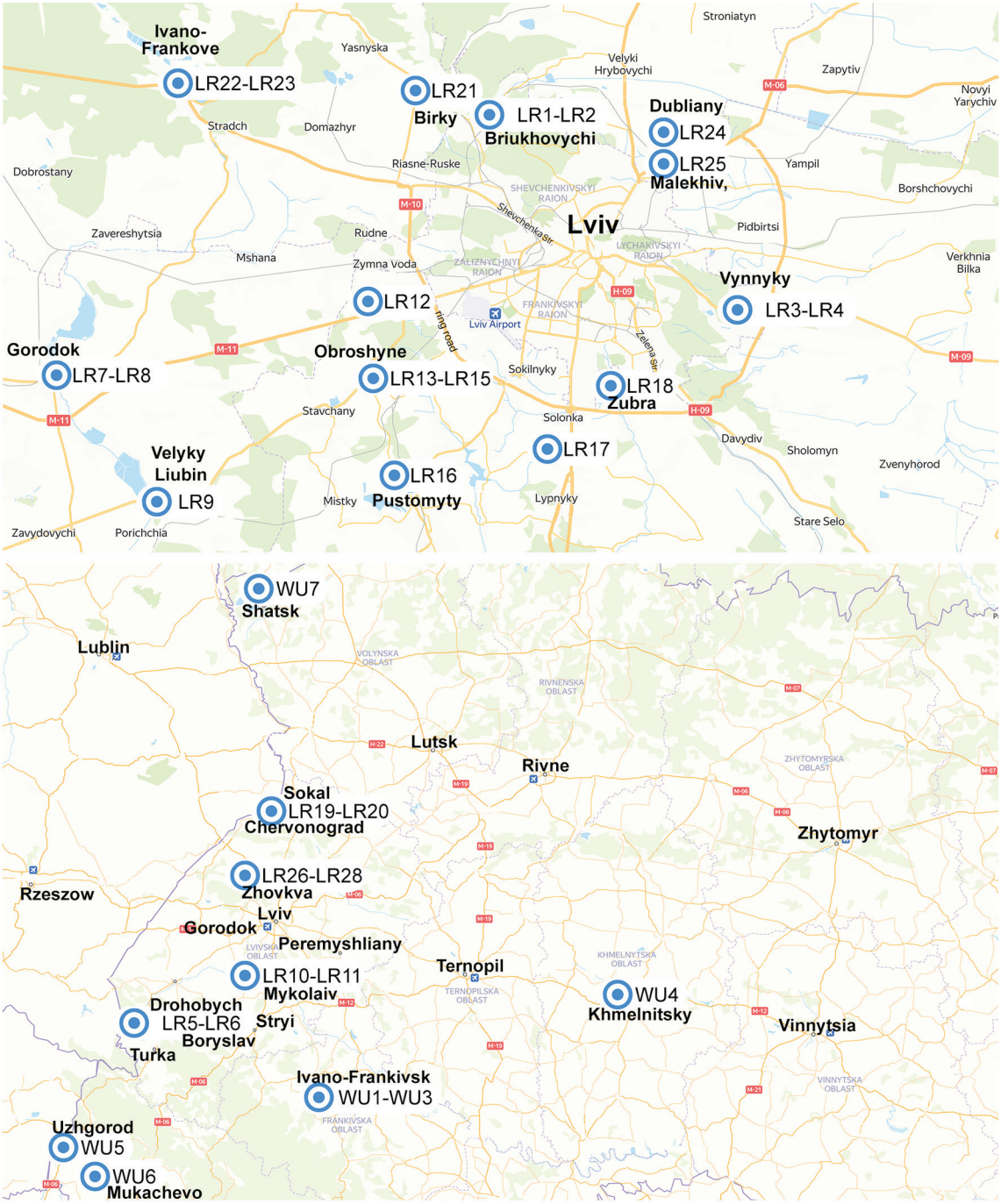

FIG. 2. The locations of the collecting sites in Western Ukraine except Lviv. Codes and descriptions of sites see Supplementary material.

РИС. 2. Расположение мест сбора на западе Украины вне Львова. Коды и описания участков см. в Supplementary material.

analyzing the quantitative distribution of phenotypes among banded shells, due to the small number of banded shells in many samples, the second and third groups were considered together.

A possible relation of the phenotypic composition of the West Ukrainian colonies of *C. hortensis* with vegetation was considered using the example of the most well-studied Lviv park – Stryisky Park (L10). To do this, all samples were divided into three groups collected in the following habitats: 1) open sites overgrown with nettles, horse sorrel, and other tall herbage; 2) ornamental shrubs planted in separate groups or in the form of hedges; 3) forest-like sites, in most cases with sparse tree and shrub vegetation. Each group included samples collected in different parts of the park. The minimum sample size was 89 specimens.

Phenotypes were scored based on the ground

colour of the shells and banding pattern of their body whorl according to the standard method [Clarke, 1960]. Spiral dark bands were designated by Arabic numerals from 1 to 5, counting them from the apex to the base of the shell. The absence of band(s) was indicated as "0" in place of the corresponding numeral(s). The fusion of adjacent bands was indicated with parentheses. The bands were considered to be fused if they were fully or partially merged for no less than a quarter of a whorl before the aperture.

In addition to the three shell ground colours (yellow, pink, or brown), which are usually considered in such studies, we additionally distinguished a group of shells with a white ground colour. This was due to the fact that white shells are often found in Western Ukraine, both in unbanded [Gural-Sverlova, Gural, 2018] and especially in banded snails [Gural-Sverlova *et al*., 2020]. When determining the ground colour of banded shells, particular attention was paid to the shell apex (usually more intensely coloured in non-white shells) and to the unicolour zone around the umbilicus. In order to more reliable determine the colour of empty shells or shabby shells of living individuals, their surface was moistened with water. The ground colour of the shells was scored as A – white, Y – yellow, P – pink (brown shells were completely absent in the studied samples).

When determining frequencies of different phenotypes among banded shells, only adult snails or their empty shells were taken into account. Additional samples of juveniles from the Moscow region were used only for a more accurate calculation of the frequencies of individuals with different ground colours, as well as with unbanded and banded shells.

When phenotypes not typical for Western Ukraine were found (yellow banded, pink shells, etc.), we additionally examined the territories adjacent to the site in order to more accurately assess how limited these forms are in space. The presence of colonies of another introduced species, *Cepaea nemoralis* (Linnaeus, 1758), was also noted, which only relatively recently began to spread intensively across Lviv along with ornamental plants [Gural-Sverlova *et al*., 2020].

In addition to the shell colouration, the presence of some individuals with a distinct gray body pigmentation, also very rare in Western Ukraine, were noted. This body colouration was considered as "dark", in contrast to the usual "light" colouration, in which the snail's body usually appears light beige, almost white. When dark-coloured individuals move, a narrow light longitudinal band on the body can be seen from above. In light-coloured snails, this band does not differ from the colouration of adjacent parts of the body.

The materials used in this study were partially deposited in the malacological collection of the State Museum of Natural History of the National Academy of Sciences of Ukraine in Lviv [Gural-Sverlova, Gural, 2020]. This is primarily related to samples collected in Western Ukraine outside Lviv city and to all samples from the Moscow region of Russia. Most of the snails collected in Lviv, after scoring the phenotypes, were released to the same site (in 1999-2004) or to another site in the city (49°50.51'N, 24°03.65'E) that was not included in the study (in 2015-2018). In the latter case, the possibility of repeated scoring of some individuals during the repeated collection of snails for several consecutive years was excluded. In earlier samples, this possibility existed, but it decreased significantly for two reasons. Firstly, about half of adult individuals in colonies can be replaced annually by young snails that have reached maturity [Schnetter, 1950]. Secondly, only a part of adults are picked up for the samples.

To compare the frequencies of one trait in two large samples (more than 100 individuals), the Student's test was used; for low frequencies (less than 20%), the significance of the differences was additionally checked using the arcsine transformation [Shebanin *et al.*, 2008]. When comparing the frequencies of one or more traits in a larger number of samples, the Chi-square test was used.

The article uses the term "colony" to denote the aggregation of individuals of the same species (in this case, *C. hortensis*), found by us in a certain limited territory, but, in contrast to some definitions of the term "population", not necessarily isolated, completely or at least partially, from other similar aggregations. We also prefer not to use the term "population" for recently formed isolated colonies with a small number of individuals, since it is not known whether they will be able to become established populations in the future, capable of maintaining their numbers for a long time, which is also considered one of the population criteria.

Results

In almost all studied Western Ukrainian colonies of *C. hortensis*, two shell ground colours were recorded: yellow (expressed with different intensities, from pale to intense yellow) and white (on empty or shabby shells it may look grayish, and sometimes even light beige due to a darkened periostracum, but always without a yellow tint). The yellow ground colour was recorded almost exclusively in unbanded shells, white in almost all banded and about 7% of all unbanded shells collected in Western Ukraine (Table 1).

Snails with yellow banded shells (Fig. 3 B-D) have so far been found only in few colonies from Lviv (first recorded in 2019) and one from Zhovkva (in 2018). The collecting place for such specimens was limited to tree and shrub plantings near one (L0, LR26) or few (L20, L23) buildings or several tens

of meters of a fence near the former garden centre (L15). On the adjacent sites, only banded snails with a white ground colour were observed, for example, on the site L21 (Table 1) which was no more than 100 m away from L20.

In addition to the sample described in Table 1, which had a very low frequency of banded shells, several additional collections of exclusively banded snails were carried out at the site L15. In total, 41 adult snails with banded shells were collected on a plot more than 100 m long, among which there were only three yellow specimens found in the central part of the site, near the grapes planted at the fence. Among the immature banded snails at the same site, not a single yellow one was found.

In 2020, one specimen of *C. hortensis* with yellow banded shell was first found in Obroshine, at the edge of the site LR13. It is possible that its appearance in Obroshine was associated with ornamental shrubs planted on the adjoining household plot several years ago.

In the Moscow region, white shells (banded and unbanded) were found only in Vidnoe, yellow – in both colonies (Table 1). Unlike Western Ukraine, banded shells here most often had a yellow ground colour, less often white (in Vidnoe) or pink (in Moscow).

In Western Ukraine, snails with pink shells were first recorded by us in one small colony in Uzhgorod in 2015 (Fig. 3E). The specificity of this colony (WU5) also lies in the fact that so far neither white nor banded shells have been found there. In Lviv, so far, only two colonies with unbanded and banded pink shells have been registered at the above-mentioned sites L20 and L23, together with yellow banded shells (Fig. 3C). No snails with pink shells have yet been found in other settlements in Western Ukraine. On the contrary, pink shells occur in both known colonies of *C. hortensis* in the Moscow Region: only among the unbanded in Vidnoe, both among the unbanded and banded in Moscow (Table 1).

About half of the snails collected in Vidnoe and about 73% of the snails from Western Ukraine had yellow unbanded shells. In many colonies, the frequency of this phenotype was even higher (Table 1). Only in a few cases, shells of a different colouration predominated in Western Ukraine, for example, pink unbanded in Uzhgorod (WU5). On the contrary, in Moscow, almost half of the collected snails had yellow banded shells (Table 1).

The following phenotypic composition of *C. hortensis* colonies can be considered typical of Western Ukraine: yellow unbanded (predominant), white unbanded and white banded shells (Fig. 3A). In some cases, white unbanded shells were not found (Table 1) due to their complete absence or, possibly, a very low frequency of occurrence. Despite the relatively low frequencies of banded shells at most of the studied sites, colonies monomorphic by the absence of bands are rare.

With rare exceptions, in the colonies of *C. hortensis* in Western Ukraine, there is a pronounced predominance of snails with unbanded shells (Table 1). A high frequency of such shells was observed at sites with different vegetation (with a predominance of trees, ornamental shrubs and hedges of them or herbage, see below) and with varying degrees of shading of the sites by trees and apartment buildings. In the Moscow region, a similar trend was noted only in the mostly open biotope in Vidnoe. In the park of the Timiryazev Agricultural Academy in Moscow, about two-thirds of the collected snails had banded shells with different ground colour.

In the large park of Lviv (L10), the ratio of the main variants of shell colouration (yellow unbanded, white unbanded, banded) varied greatly in all types of habitats (Table 2). A similar pattern was observed for the relative frequencies of white unbanded shells calculated from the number of unbanded shells in the samples, and shells with fused bands calculated from the number of banded shells (Fig. 4). On average, the lowest frequencies of unbanded and yellow unbanded shells were observed in forest-like sites, although here, too, they exceeded 60% (Table 2). Snails with white unbanded shells were more common in shrubs and hedges.

About three fourth of the banded shells collected in the studied East European colonies of *C. hortensis* were represented by phenotype 12345 (Table 3). Among the shells with fused bands, the phenotype (12)345 prevailed. In the park biotopes of Lviv, phenotypes (12)345 and 1(23)45 were almost equally common. Shells with the absence of one band were much rarer than with different band fusions. They were mainly represented by the phenotype 12045. The phenotypes with the fusion of the lower (4th and 5th) bands were, on average, 3-4 (Western Ukraine) or 7 (Moscow region) times more rare than those with upper bands fused (Table 4).

In Moscow, snails with pink unbanded shells showed a pronounced variability of lip colour – from the white lip characteristic of *C. hortensis* or a small pinkish spot near the columella to the dark lip resembling that of the related species *C. nemoralis* (Fig. 5A). In snails of other phenotypes in the same colony, the lip was always light, with a maximum with a small pinkish spot. Similar pinkness on the parietal wall of the aperture and/or on the lip part near the columella was occasionally also observed in Lviv and other Western Ukrainian colonies of *C. hortensis* (Fig. 5B). At the site L20 in Lviv, all pink shells (both unbanded and banded) had a dark lip (Fig. 5C, D). Most often, it was only slightly lighter than that of *C. nemoralis*, less often light pink (Fig. 5C) but along its entire length. In another Lviv colony

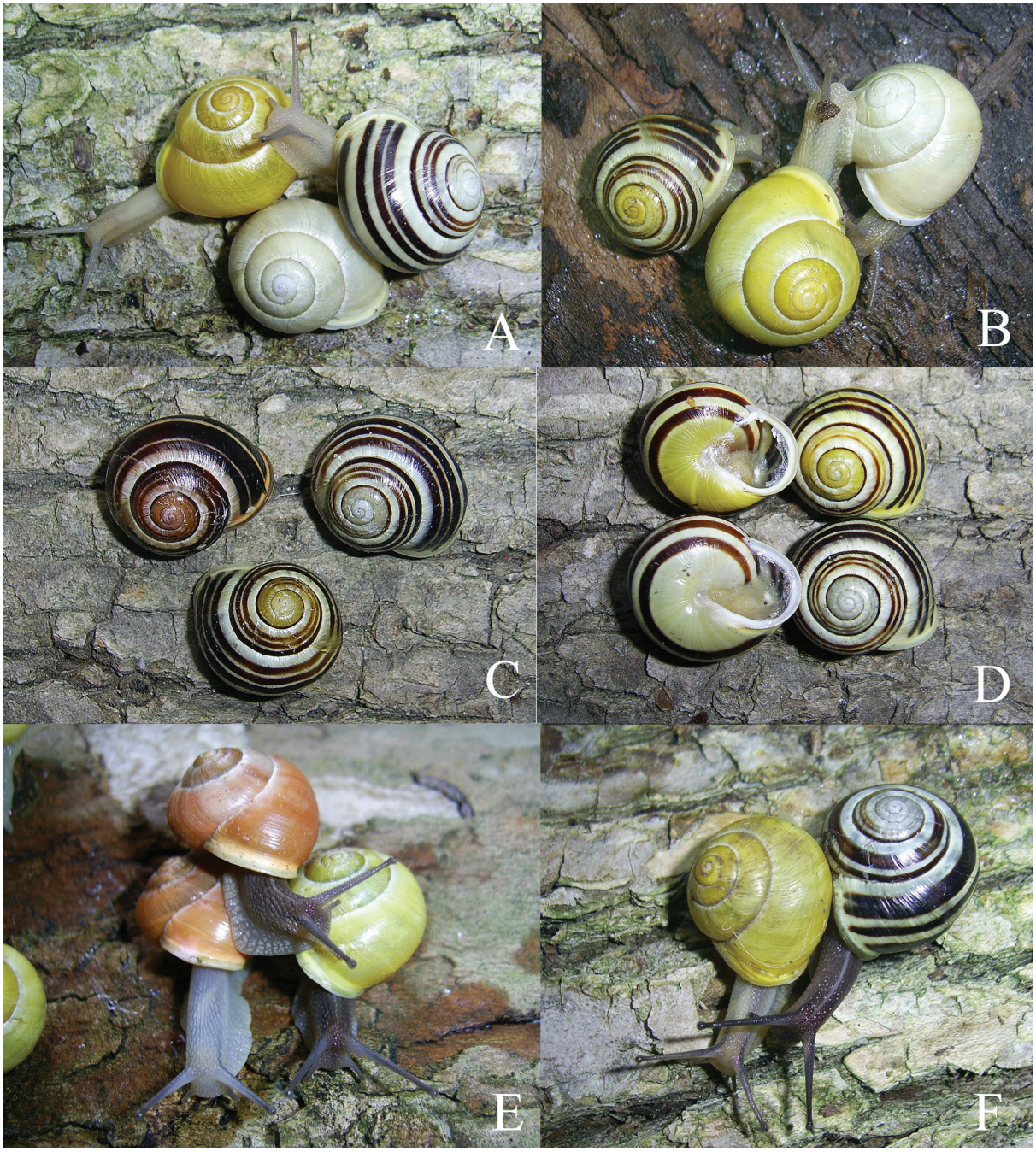

FIG. 3. Variability in shell and body colouration of *C. hortensis* in Western Ukraine. **A.** Lviv (L11), a typical set of phenotypes (Y00000, A00000, A12345) and a light-coloured body. **B**. Lviv (L20), with a regionally rare phenotype Y12345. **C**. The same site, banded shells with three ground colours (pink, white, yellow). **D**. Lviv (L15), banded shells with yellow (top) and white (bottom) ground colour. **E**. Uzhgorod (WU5), with a regionally rare phenotype P00000 and well expressed body colour variability. **F.** Zhovkva (LR26). Codes of sites see Supplementary material.

РИС. 3. Изменчивость окраски раковины и тела у *C. hortensis* на западе Украины. **A**. Львов (L11), типичный набор фенотипов (Y00000, A00000, A12345) и светлая окраска тела. **B.** Львов (L20), присутствует редкий для региона фенотип Y12345. **C.** Тот же участок, полосатые раковины с тремя фоновыми цветами (розовый, белый, желтый). **D**. Львов (L15), полосатые раковины с желтым (вверху) и белым (внизу) фоновым цветом. **E.** Ужгород (WU5), присутствует редкий для региона фенотип P00000 и хорошо выраженная изменчивость окраски тела. **F.** Жовква (LR26). Коды участков см. в Supplementary material.

of *C. hortensis* with pink shells (L23), they all had a white lip.

In one small colony in Zhovkva (LR26), part of the banded shells had not only a yellow ground colour, very rare in Western Ukraine (see above), but also thin, weakly pigmented bands (Fig. 5E, F). Such bands had 13 of 20 adult and juvenile (with a shell diameter of at least 1 cm) banded snails and their empty shells collected at this site. Another adult snail with the same shell colouration was found several

Table 1. The phenotypic composition of the studied samples of *Cepaea hortensis*.

Табл. 1. Фенетическая структура исследованных выборок *Cepaea hortensis.*

Codes	Total	Frequencies, %						
		White		Yellow		Pink		Total unbanded
		unbanded	banded	unbanded	banded	unbanded	banded	
Western Ukraine – Lviv city								
L1a	1565	7.6	17.0	**75.4**	–	–	–	**83.0**
L1b	2808	7.0	16.1	**76.9**	–	–	–	**83.9**
L2a	1843	4.4	20.5	**75.1**	–	–	–	**79.5**
L2b	2010	4.0	19.1	**77.1**	–	–	–	**81.0**
L3a	2307	2.1	15.5	**82.4**	–	–	–	**84.5**
L3b	1336	2.2	7.3	**90.4**	–	–	–	**92.6**
L4	742	–	**81.1**	18.9	–	–	–	18.9
L5	999	0.1	37.4	**62.5**	–	–	–	**62.6**
L6	111	2.7	37.8	**59.5**	–	–	–	**62.2**
L7a	179	3.9	36.3	**59.8**	–	–	–	**63.7**
L7b	102	2.9	3.9	**93.1**	–	–	–	**96.0**
L8	366	4.1	11.2	**84.7**	–	–	–	**88.8**
L9a	408	6.6	7.4	**86.0**	–	–	–	**92.6**
L9b	274	6.6	9.5	**83.9**	–	–	–	**90.5**
L10a	8163	7.2	22.8	**70.0**	–	–	–	**77.2**
L10b	328	10.7	23.8	**65.5**	–	–	–	**76.2**
L11a	1502	6.5	12.1	**81.5**	–	–	–	**87.9**
L11b	274	12.4	10.9	**76.6**	–	–	–	**89.0**
L12	123	22.0	7.3	**70.7**	–	–	–	**92.7**
L13	69	4.3	17.4	**78.3**	–	–	–	**82.6**
L14	327	2.1	12.5	**85.3**	–	–	–	**87.5**
L15	375	20.3	4.0	**75.2**	0.5	–	–	**95.5**
L16	170	3.5	29.4	**67.1**	–	–	–	**70.6**
L17	27	11.1	22.2	**66.7**	–	–	–	**77.8**
L18	162	2.5	26.5	**71.0**	–	–	–	**73.5**
L19	102	2.9	20.6	**76.5**	–	–	–	**79.4**
L20	159	8.8	10.7	41.5	18.9	5.7	14.5	**56.0**
L21	64	14.1	15.6	**70.3**	–	–	–	**84.4**
L22	90	–	45.6	**54.4**	–	–	–	**54.4**
L23	107	–	9.3	**65.4**	6.5	14.9	3.7	**80.4**
L24	39	–	7.7	**92.3**	–	–	–	**92.3**
Total	27131	5.7	20.4	**73.6**	0.1	0.1	0.1	**79.3**
Western Ukraine – Lviv region								
LR1	97	15.5	12.4	**72.2**	–	–	–	**87.6**
LR2	78	–	16.7	**83.3**	–	–	–	**83.3**
LR3	54	5.6	13.0	**81.5**	–	–	–	**87.0**
LR4	42	38.1	–	**61.9**	–	–	–	**100**
LR5	63	1.6	28.6	**69.8**	–	–	–	**71.4**
LR6	16	–	12.5	**87.5**	–	–	–	**87.5**
*LR7	538	–	**72.1**	27.9	–	–	–	27.9

Codes	Total	Frequencies, %						
		White		Yellow		Pink		Total unbanded
		unbanded	banded	unbanded	banded	unbanded	banded	
LR8	130	–	28.5	**71.5**	–	–	–	**71.5**
LR9	126	–	15.9	**84.1**	–	–	–	**84.1**
*LR10	172	–	–	**100**	–	–	–	**100**
LR11	35	–	2.9	**97.1**	–	–	–	**97.1**
LR12	10	–	–	**100**	–	–	–	**100**
*LR13	380	0.3	**53.2**	46.6	–	–	–	46.8
LR14	78	6.4	19.2	**74.4**	–	–	–	**80.8**
LR15	32	3.1	28.1	**68.8**	–	–	–	**71.9**
LR16	389	7.7	14.4	**77.9**	–	–	–	**85.6**
LR17	13	7.7	+	**92.3**	–	–	–	**100**
LR18	118	1.7	5.1	**93.2**	–	–	–	**94.9**
LR19	62	–	–	**100**	–	–	–	**100**
LR20	98	1.0	10.2	**88.8**	–	–	–	**89.8**
LR21	19	5.3	15.8	**78.9**	–	–	–	**84.2**
LR22	36	11.1	2.8	**86.1**	–	–	–	**97.2**
LR23	35	17.1	11.4	**71.4**	–	–	–	**88.6**
LR24	531	0.6	14.7	**84.7**	–	–	–	**85.3**
LR25	13	–	7.7	**92.3**	–	–	–	**92.3**
*LR26	21	+	4.8	**52.4**	42.9	–	–	**52.4**
LR27	108	–	5.6	**94.4**	–	–	–	**94.4**
*LR28	344	11.3	21.8	**66.9**	–	–	–	**78.2**
Total	3638	3.5	26.5	**69.7**	0.2	–	–	**73.2**
Western Ukraine – other regions								
WU1	86	18.6	8.1	**73.3**	–	–	–	**91.9**
WU2	92	1.1	8.7	**90.2**	–	–	–	**91.3**
WU3	16	**100**	–	–	–	–	–	**100**
WU4	13	38.5	–	**61.5**	–	–	–	**100**
*WU5	24	–	–	45.8	–	**54.1**	–	**100**
WU6	12	–	**100**	–	–	–	–	–
*WU7	24	–	25.0	**75.0**	–	–	–	**75.0**
Total	267	14.2	12.3	**68.5**	–	4.9	–	**87.6**
Russia – Moscow region								
MR1	259	–	–	12.0	49.8	22.0	16.2	34.0
**MR1	351	–	–	10.8	47.0	20.5	21.7	31.3
MR2	153	9.2	5.9	49.0	17.6	18.3	–	**76.5**
**MR2	184	9.3	7.1	48.1	16.4	19.1	–	**76.5**
Total	412	3.4	2.2	25.7	37.9	20.6	10.2	49.7
**Total	535	3.2	2.4	23.5	41.7	20.0	9.1	46.7

Notes: an asterisk denotes samples that included empty shells; two asterisks – samples with adults and juveniles; pluses – colouration variats that were observed only in juveniles; in bold and underlined, frequencies in excess of 50%.

Table 2. The phenotypic composition at sites with different vegetation (Stryisky Park, Lviv).

Табл. 2. Фенетическая структура выборок на участках с разной растительностью (Стрыйский парк, Львов).

Statistical parameters	Frequencies, %			
	White banded (= total banded)	White unbanded	Yellow unbanded	Total unbanded
		Herbage (7 samples)		
Min – Max	0.7 – 39.6	0 – 7.0	53.4 – 99.3	60.4 – 99.3
Mean	15.1	3.9	81.0	84.9
Standart error	117.2	2.5	143.2	117.2
		Shrubs / Hedges (17 samples)		
Min – Max	3.1 – 29.2	0.5 – 24.5	56.2 – 95.0	70.8 – 96.9
Mean	15.1	9.6	75.3	84.9
Standart error	17.0	13.9	37.5	17.0
		Forest-like (7 samples)		
Min – Max	23.2 – 39.2	0 – 10.6	59.7 – 67.4	60.8 – 68.8
Mean	31.3	4.1	64.6	68.7
Standart error	11.1	7.7	7.6	11.1
		Differences of mean values for three groups of habitats		
Chi-square test	10.74**	3.79	7.14*	10.74**
The same for three variants of shell colouration (banded, white and yellow unbanded)			13.98**	

Notes: asterisks indicate significant differences for $\alpha < 0.05$ (*) or $\alpha < 0.01$ (**).

hundred meters away from LR26, in a habitat that was soon completely destroyed by construction. In other colonies of Zhovkva, quantitative data on which are given in Table 1 (LR27, LR28), as well as during route inspections of the city, such shells were not found.

In addition to the above-described and mainly inherited traits, in the studied Western Ukrainian colonies of *C. hortensis* some rare shell colouration variants were recorded that were found only in single individuals and are probably modifications. These include shells with an unclear third (Fig. 6A), fourth (Fig. 6B) or first band, which we considered in the calculations (Table 1) as the phenotype Y00000. Rare modifications are also cases of an abrupt change in the phenotype of the forming shell after wintering (Fig. 6D, E). A little more often in Western Ukraine occurs additional (split) bands (Fig. 6F, G), described in more detail in one of the previous publications [Sverlova, 2003]. One such shell was also found in the Moscow region (Fig. 6H). Sometimes there are traces of hyalozonate bands on the unbanded shells from Western Ukraine, most often the 3rd band. Only in single cases are all five transparent bands more or less clearly visible on the shells (Fig. 6C).

Most studied Western Ukrainian colonies of *C. hortensis* were characterized not only by the absence of yellow banded shells (see above), but also by the presence of snails with only a light-coloured body (Fig. 3A). On the contrary, body colour variability was well expressed in Uzhgorod (Fig. 3E), at few sites in Lviv (Table 5) as well as in the Moscow region. Single individuals with a dark-coloured (dark gray) body were found in Zhovkva (Fig. 3F) and Zubra. Almost always, such snails were found at sites where rare for Western Ukraine variants of shell colouration were also recorded (Table 5), often together with *C. nemoralis*.

Discussion

The assumption about the common origin of most of the known Western Ukrainian colonies of *C. hortensis* (see Introduction) is with a high probability confirmed by the peculiarities of their phenotypic composition. The most indicative in this respect is not the absence of pink shells, which are more rare than yellow also in the natural range of the species [Cameron, 2013, table 2; Schilder, Schilder, 1957, map 65], as well as not the very high frequencies of unbanded shells, which theoretically can be the result of climate selection [Gural-Sverlova, Gural, 2018]. A specific feature of most Western Ukrainian colonies of *C. hortensis* is the linked inheritance of the presence of bands on the shell and the absence of yellow pigment in it, as a result of which the banded

Table 3. Composition of the phenotypes among banded shells (regardless of their ground color).

Табл. 3. Распределение фенотипов среди полосатых раковин (независимо от их фонового цвета).

Phenotypes	Western Ukraine							Russia		Total	In percent
	Lviv		Gorodok	Dubliany	Obroshyne	Zhovkva	Other localities	Moscow	Vidnoe		
	Parks	Other habitats									
12345	1665	2422	403	63	153	70	159	98	28	5061	74.20
With band fusion											
(12)345	167	584	10	8	53	9	12	44	2	889	13.03
1(23)45	156	84	1	1	–	1	3	7	4	257	3.77
(123)45	45	113	–	1	–	1	1	10	1	172	2.52
(12)3(45)	46	84	–	1	6	6	4	6	–	153	2.24
123(45)	43	27	–	4	7	1	6	2	–	90	1.32
(123)(45)	25	39	–	–	1	1	–	–	1	67	0.98
(12345)	24	7	–	–	1	–	1	1	–	34	0.50
1(23)(45)	16	3	–	–	–	–	–	1	–	20	0.29
1(234)5	15	2	–	–	1	–	–	–	–	18	0.26
1(2345)	13	–	–	–	–	–	–	–	–	13	0.19
(1234)5	3	1	–	–	–	–	–	–	–	4	0.06
12(34)5	–	2	–	–	–	–	–	–	–	2	0.03
12(345)	–	–	–	–	–	1	–	–	–	1	0.01
One band absent											
12045	7	9	9	–	2	1	–	1	–	29	0.42
10345	–	2	2	–	1	–	1	–	–	6	0.09
02345	–	–	–	–	–	–	–	1	–	1	0.01
Combination of band absence and fusion											
(12)0(45)	–	2	–	–	–	–	–	–	–	2	0.03
(12)045	–	1	–	–	–	–	–	–	–	1	0.01
103(45)	–	–	–	–	1	–	–	–	–	1	0.01
Total	2225	3382	425	78	226	91	187	171	36	6821	

shells with a yellow ground colour are completely absent in such colonies.

It is significant that the yellow banded shells apparently are often found in introduced colonies of *C. hortensis* from other parts of Eastern Europe. In the Moscow region, they were present in both investigated colonies, with white banded shells (Vidnoe) or without them (Moscow). Moreover, shells with a yellow ground colour in both cases prevailed among banded shells (Table 1). From the photographs kindly provided to us by O.Yu.Kruglova (Belarusian State University), we can conclude that snails with unbanded and banded shells of both colours occur in Minsk. Unfortunately, so far we have not been able to obtain similar information on the ground colour of the banded shells of *C. hortensis* in Brest [Sverlova *et al*., 2006], located near the Belarusian-Ukrainian border.

The few local findings in Western Ukraine of *C. hortensis* specimens with yellow banded and/or pink shells are most probably caused by relatively recent repeated introductions of this species to Ukraine independent of its introduction and subsequent unintentional spreading in Lviv region (mainly) and neighbouring regions in the 20th century. An additional, although perhaps less reliable feature indicating such independent and later introductions may be frequent presence in the same colonies of snails with a dark-coloured body (Table 5), which are absent in most Western Ukrainian colonies of *C. hortensis*. As shown by the experiments [Cain *et al*., 1968; Wolda, 1969], in the related species *C.*

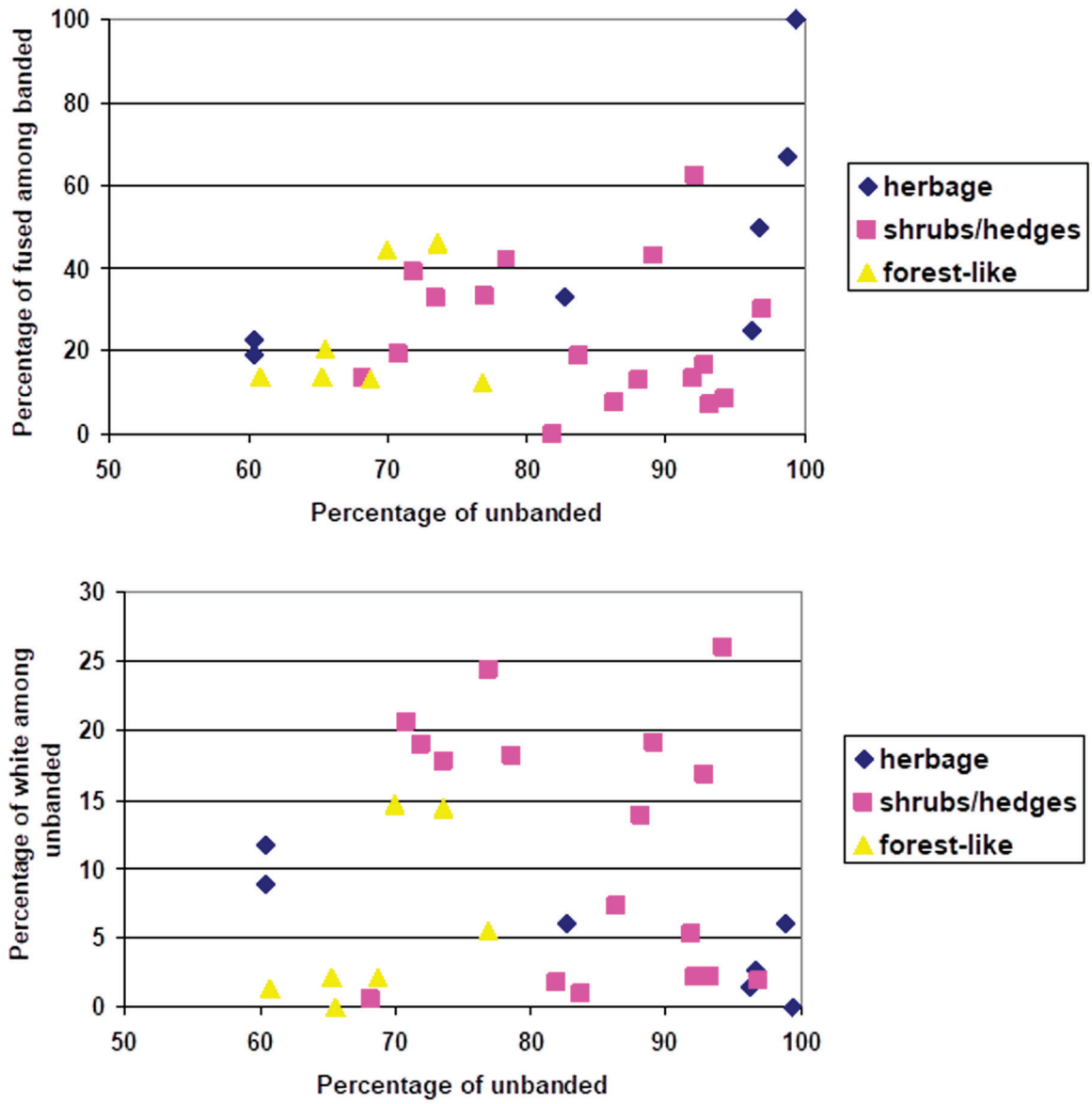

FIG. 4. Percentage of shells with different colouration in the samples collected at sites with different vegetation, Stryisky Park, Lviv.

РИС. 4. Доля раковин с разной окраской в выборках, собранных на участках с разной растительностью, Стрыйский парк, Львов.

nemoralis, the pale (yellowish) body colour is recessive in relation to dark (gray).

Significantly, the colonies where the unusually coloured individuals of *C. hortensis* are found in some cases live together with the relatively young [Gural-Sverlova *et al*., 2020] colonies of another introduced species, *C. nemoralis* (Table 5), which suggests their relatively recent joint introduction along with ornamental plants.

Unfortunately, in publications devoted to shell colour and banding polymorphism in *C. hortensis*, shells with a white ground colour are usually not distinguished as a separate group, and, obviously, they are considered together with yellow shells. Therefore, we are not able to compare our results with quantitative data from different parts of the natural range of this species. However, in the Western Ukrainian colonies there are no transitional forms between light yellow and white unbanded shells, which makes it possible to reliably identify them in samples [Gural-Sverlova, Gural, 2018], in most cases even on empty shells or on shells with a very shabby surface. This is also true for banded shells, in which the ground colour is usually clearly visible at the apex and near the umbilicus (Fig. 3D).

Also, we do not have information about the heritability of white shell colour in *Cepaea*. However, it is known that the pink ground colour in *C. nemoralis* and *C. hortensis* is dominant in relation to yellow, and brown is dominant in relation to pink and yellow [Murray, 1975]. Therefore, we can assume that the presence of a white shell is a recessive trait. The hereditary na-

Table 4. Percentages of different fusions among five-banded shells.

Табл. 4. Частоты различных слияний среди 5-полосых раковин, %.

Fusion types	Species range [Schilder, Schilder, 1957]	Western Ukraine		Russia
		Lviv	Other localities	Moscow Region
Phenotypes with fused bands				
(12)345	10.8	13.4**	9.3	22.4**
(123)(45)	2.7	1.1**	0.2**	0.5[A]
(12345)	2.3	0.6**	0.2**	0.5[A]
(12)3(45)	2.3	2.3	1.7	2.9
123(45)	2.2	1.3**	1.8	1.0
1(23)45	2.1	4.3**	0.6**	5.4**
(123)45	2.0	2.8**	0.3**	5.4**
Other	0.8	1.0	0.2*	0.5
In total	25.1	26.8*	14.3**	38.5**
Pairs of fused bands				
Bands 1 and 2	20.3	20.4	11.7**	31.7**
Bands 2 and 3	9.8	9.8	1.4**	12.2
Bands 3 and 4	2.8	1.2**	0.4**	0.5*
Bands 4 and 5	9.9	5.9**	4.0**	5.4*
Relative to the 3rd band				
Above the 3rd band	22.9	25.5**	12.4**	37.6**
Below the 3rd band	10.3	6.3**	4.1**	5.4*
Number of 5-banded shells	67285	5586	990	205

Notes: in the calculations, shells with the absence of one or more bands were not taken into account. Statistically significant differences from the data from the monograph [Schilder, Schilder, 1957] are indicated as: * $\alpha < 0.05$; ** $\alpha < 0.001$ (Student's t test); [A] significant when using arcsine transformation.

ture of this trait in *C. hortensis* is indirectly confirmed by the long-term relative stability of the frequencies of white unbanded shells at the studied sites in Lviv with rather large variability of these frequencies between the sites [Gural-Sverlova, Gural, 2018].

Among the banded phenotypes that are relatively common in at least some parts of the natural range of *C. hortensis* [Schilder, Schilder, 1957], 00300 and 10305 were absent in the introduced colonies of this species studied by us. Over the entire period of research in Western Ukraine, a single shell with a fuzzy third band was found (Fig. 6A), most likely a modification from 00000. Within the natural range of *C. hortensis*, the average frequency of phenotype 00300 decreases to the north and east, up to its complete absence [Schilder, Schilder, 1957, map 61], which is also confirmed by later studies [Cameron, 2013, table 7]. In the eastern part of the natural range, the phenotype 10305 also disappears [Schilder. Schilder, 1957, map 62]. If the absence of both mentioned phenotypes in the studied colonies is not a random result of the founder effect, it may indirectly indicate that the snails were introduced, most likely, from a relatively close part of the natural range of *C. hortensis*. Since the primary introduction of *C. hortensis* into Western Ukraine apparently occurred in the second half of the 20th century, the transfer of molluscs from some country of the former socialist camp is also the most probable in this case.

In general, the absence of some bands on banded shells is rarely found in the studied East European introduced colonies of *C. hortensis* (Table 3). Moreover, they are most often represented by the phenotype 12045, the inheritance of which in *Cepaea* was questioned by many researchers [Diver, 1939; Lang, 1906; Wolda, 1969]. Since the 3rd band appears first on the shells of juvenile snails [Andreassen, 1978], it is possible that its phenotypic manifestation may depend more strongly on the adverse influence of the environment.

Both the presence and even predominance of the phenotypes Y00300 and P00300 were described for two introduced colonies of *C. hortensis* in Minsk, Belarus [Kruglova, Kolesnik, 2017], the data about which are shown in Table 6. However, a year earlier, the same authors published data on the phenotypic composition of introduced colonies of *C. nemoralis* [Kolesnik, Kruglova, 2016], living at the same sites and having not only the same set but also similar frequencies of the predominant phenotypes (Table 6).

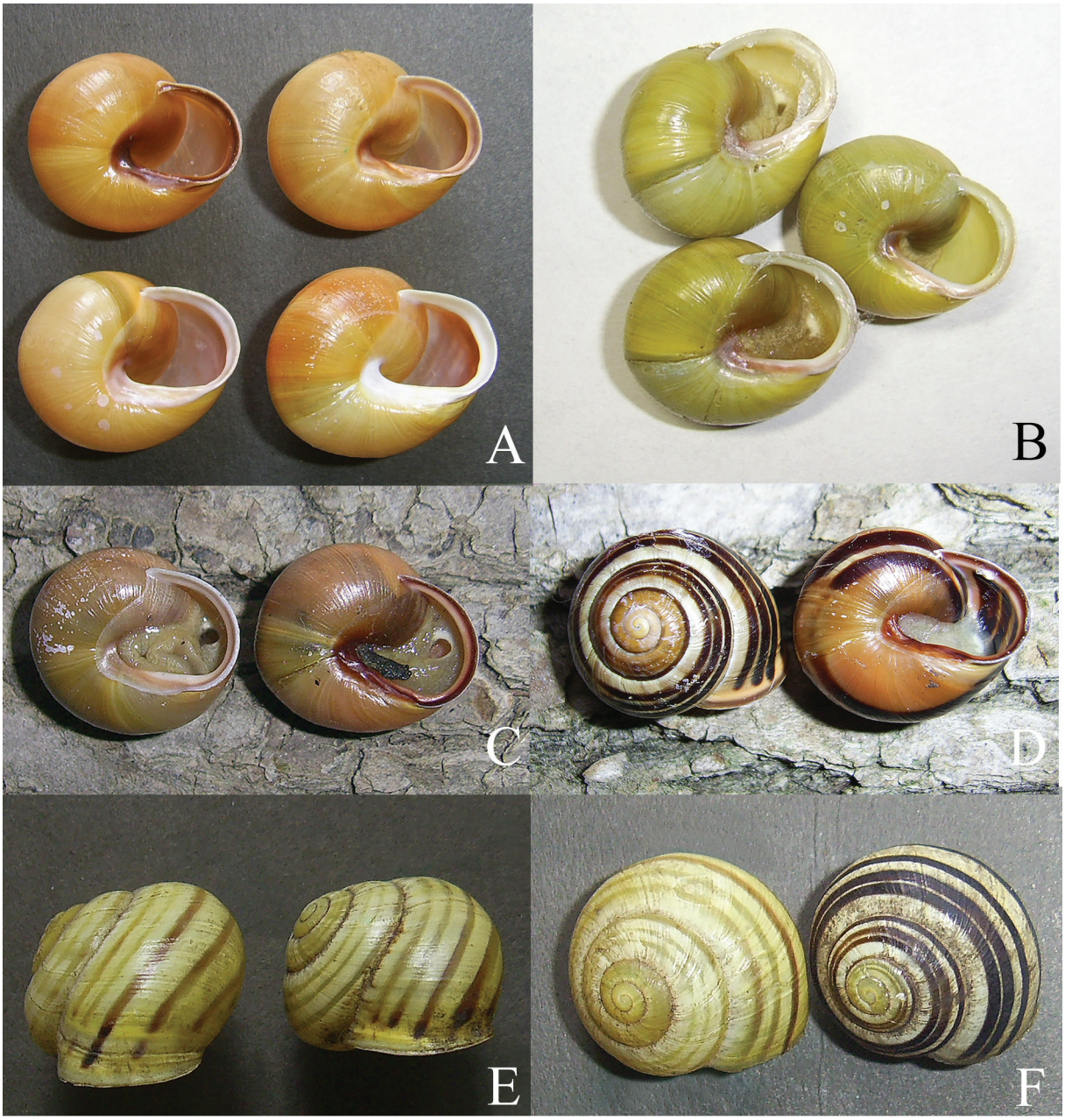

FIG. 5. Not typical colouration of the shell lip and bands in some specimens of *C. hortensis* in the studied samples. **A.** Moscow (MR1), lip colouration variability in the phenotype P00000. **B**. Dubliany (LR24), a pinkish tint on the parietal wall of the aperture and on the lip near the columella. **C**. Lviv (L20). Dark lip in pink unbanded shells. **D**. The same in pink banded shells. **E.** Zhovkva (LR26), weakly pigmented bands. **F**. The same site, weakly and normally pigmented bands. Codes of sites see Supplementary material.

РИС. 5. Нетипичная окраска губы и полос на раковине у некоторых особей *C. hortensis* в исследованных выборках. **A**. Москва (MR1), изменчивость окраски губы у фенотипа P00000. **B.** Дубляны (LR24), розоватый оттенок на париетальной стенке устья и на участке губы возле столбика. **C**. Львов (L20). Темная губа у розовых бесполосых раковин. **D**. То же для розовых полосатых раковин. **E.** Жовква (LR26), слабо пигментированные полосы. **F**. Тот же участок, слабо и нормально пигментированные полосы. Коды участков см. в Supplementary material.

Since snails were not determined by malacologists, it is possible that instead of *C. hortensis*, the authors dealt with immature *C. nemoralis* or with a mixture of both species. The latest version is supported by a sharp increase in the frequencies of the phenotypes Y00000 and Y12345 common for *C. hortensis*, recorded near the metro station “Grushevka” in 2017. The other two colonies of *C. hortensis* from Minsk and its environs (Table 6), were represented only by the most common for *C. hortensis* phenotypes: Y00000, Y12345 and Y(12)345 . However, separation of the shell ground colour into yellow and white, in this case was not carried out (O.Yu.Kruglova, personal communication).

Table 5. Occurrence of rare variants of shell and body colouration in the studied Western Ukrainian colonies of *Cepaea hortensis*.

Табл. 5. Встречаемость редких вариантов окраски раковины и тела в исследованных западноукраинских колониях *Cepaea hortensis*.

Locality, code	Shell		Shell lipe	Body	Presence of *Cepaea nemoralis*
	yellow banded	pink	dark	dark (gray)	
Lviv, L0	+	–	–	+	+
Lviv, L15	+	–	–	–	+
Lviv, L20	+	+	+	+	+
Lviv, L23	+	+	–	+	–
Zubra, LR18	–	–	–	+	+
Zhovkva, LR26	+	–	–	+	–
Uzhgorod, WU5	–	+	–	+	–

A specific feature that allows one to significantly reduce the number of territories that could become a potential source of introduction of *C. hortensis* into Moscow as well as to the site L20 in Lviv is the presence of a dark lip in some pink unbanded shells in the first case (Fig. 5A) and in all pink shells in the second case (Fig. 5C, D). The spatial distribution of this locally occurring trait in Europe is detailed in the monograph [Schilder, Schilder, 1957, p. 163, 185, 187, map 66]. Not taking into account the weak pinkness, which is sometimes observed on the parietal wall of the aperture and on the lip fragment near the columella, as in the natural area of *C. hortensis* [Schilder, Schilder, 1957, p. 163], and in introduced Western Ukrainian colonies of this species (Fig. 5B), German researchers identified three types of expression of this trait, confined to different regions. In the first case, as in Moscow, a dark lip is found only in the phenotype P00000. In the second case, as in Lviv, it is found only in pink (banded and unbanded) shells, in the third it can also appear on yellow shells. According to their geographical distribution [Schilder, Schilder, 1957, map 66], the first type was called Thuringian, the second Danish-Norwegian, and the third French-English. But it should be borne in mind that the mentioned researchers called pink (or rather, red) both pink and brown shells in *Cepaea*.

According to later, but more geographically limited data [Ożgo, 2010], in different regions of Europe, a dark lip can locally occur in shells of different colours. So, in north-western Poland, it was noted in shells of brown (mainly) and pink (in a single sample) colour. Judging by the photograph in the article, the lip, pinkish over its entire length, was found there in both unbanded and banded shells (similar to the "Danish-Norwegian type" by Schider, Schider [1957]). In Germany, between Midlich and Halberstadt, a dark lip was found predominantly in pink and brown shells (without specifying of their banding phenotypes), and occasionally also in yellow shells. In Wiltshire, UK, there was a linked inheritance of the dark lip and pink shell, which was only occasionally disturbed by the presence of a dark lip in the yellow shells [Ożgo, 2010]. Unfortunately, in this case, it is also not known whether the pink shells with the dark lip were banded or unbanded. Earlier it was suggested that the colony of *C. hortensis* in the park of the Timiryazev Agricultural Academy could be formed by snails accidentally introduced from East Germany already in the second half of the 20th century [Egorov, 2018].

Compared with the data from different parts of the species range (but mainly from Germany), generalized in the monograph [Schilder, Schilder, 1957], phenotypes with fusions of the lower bands were less common in the colonies studied by us (Table 4). The frequencies of the fusion of the 1st and 2nd, 2nd and 3rd bands were the same in Lviv, decreased in other habitats in Western Ukraine, increased in the Moscow region.

Earlier, we found that the ratio of the frequencies of the most common phenotypes with fused bands and, especially, that of the frequencies of the fusion of different pairs of bands, demonstrates temporal stability in Lviv colonies of *C. hortensis* and, at the same time, may vary between colonies [Gural-Sverlova, Gural, 2018; Sverlova *et al*., 2006]. The latter was considered as the possible beginnings of the genetic and phenotypic differentiation within the city [Gural-Sverlova, Gural, 2018].

Well-marked differences can also be observed between different areas (Table 4) and between different settlements in the same region (Table 3). For instance, in Gorodok, where at one of the studied sites a high frequency of banded shells was noted, which is not typical for Western Ukraine (LR7, see Table 1), almost all of these shells were represented

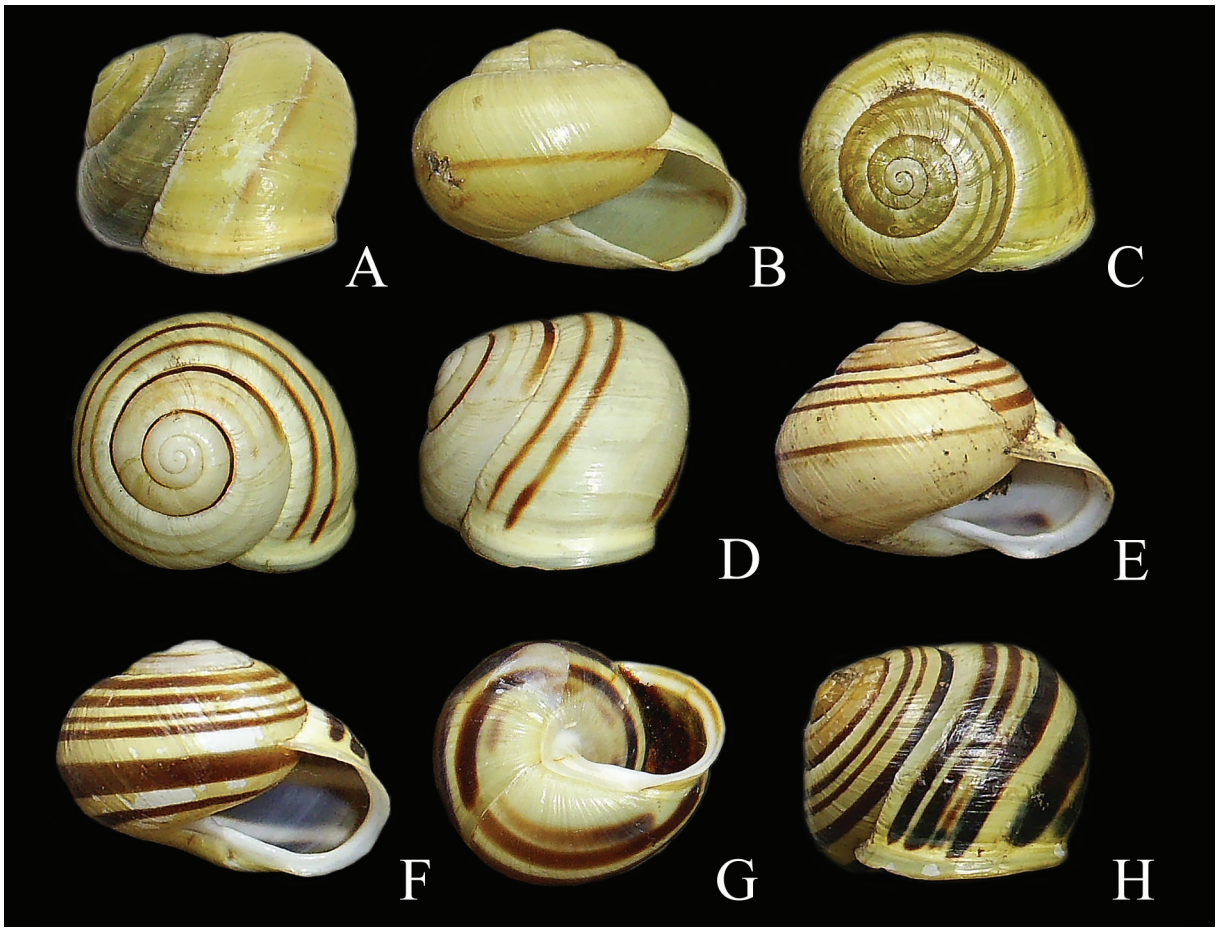

FIG. 6. Rare colouration variants, which are obviously modifications. **A**. Lviv (L14), a fuzzy third band on a genetically unbanded shell. **B**. Lviv (L10), the same for the fourth band. **C**. Lviv (L1), hyalozonate bands. **D, E.** Lviv (L1 and L3), abrupt change in the phenotype of the forming shell after wintering. **F, G**. Lviv (L10), additional (split) band. **H**. Vidnoe (MR2), similar to F. Codes of sites see Supplementary material.

РИС. 6. Редкие варианты окраски, очевидно, являющиеся мофицикациями. **A**. Львов (L14), нечеткая третья полоса на генетически бесполосой раковине. **B.** Львов (L10), то же самое для четвертой полосы. **C**. Львов (L1), гиалозонатные полосы. **D, E.** Львов (L1 и L3). Резкое изменение фенотипа строящейся раковины после зимовки. **F, G.** Львов (L10), дополнительная (расщепленная) полоса. **H**. Видное (MR2), аналогично F. Коды участков см. в Supplementary material..

by phenotype 12354, and rare shells with fused bands were represented almost exclusively by phenotype (12)345 (Table 3). In Obroshyne, the phenotypes with the fusion of the 2nd and 3rd bands were very rare. And the phenotype 1(23)45, quite common in Lviv and, especially, in city parks (Table 3), has not yet been registered there.

The average frequency of unbanded shells in the Western Ukrainian colonies of *C. hortensis* exceeds that in any part of the natural range of this species [Cameron, 2013, table 6]. This is especially noticeable when compared with the average values indicated for a similar diapason of geographical latitude (most of the studied sites in Western Ukraine are located between 48 and 50°N): 68% in the west, 41% in the centre and 40% in the east.

Earlier it was suggested that such a high proportion of unbanded shells in Western Ukraine, usually observed even in the habitats most shaded by trees (Table 2; Fig. 4) and/or multi-storey buildings, may be the result of the influence of a more continental climate in this region [Sverlova *et al*., 2006]. This can be confirmed by a statistically significant decrease in the frequencies of banded shells at several sites in Lviv, found by comparing data from 1999-2004 and 2015-2017 [Gural-Sverlova, Gural, 2018]. Simultaneously, an increase in the average daily temperature, daily temperature fluctuations, the number of days with a maximum temperature of +30°C or more, and also a decrease in the amount of precipitation in the summer were observed in the city due to global warming [Gural-Sverlova, Gural, 2018, Table 3], with the result that the climate has become even more continental.

In the immediate future, similar studies of the long-term dynamics of the phenotypic composition

Table 6. The phenotypic composition of the introduced colonies of *Cepaea* in the Minsk region, Belarus.

Табл. 6. Фенетическая структура интродуцированных колоний *Cepaea* в Минской области, Беларусь.

Years	Sample size	Frequencies, %								
		Yellow*				Pink				Total unbanded
		Y0	Y1	Y3	Y5	P0	P1	P3	P5	
Minsk, Uruchye microdistrict, near a military town										
**C. hortensis* [Kruglova, Kolesnik, 2017]										
2015	100	20.0	44.0	2.0	15.0	4.0	13.0	2.0	–	24.0
The same site, *C. nemoralis* [Kolesnik, Kruglova, 2016]										
?	?	28.2	46.7	?	?	?	?	?	?	?
Minsk, near the metro station “Grushevka”										
**C. hortensis* [Kruglova, Kolesnik, 2017]										
2014	151	–	43.0	–	6.6	–	50.3	–	–	–
2015	91	3.3	33.0	1.1	6.6	1.1	52.7	–	2.2	4.4
2017	78	42.2	7.7	–	35.8	–	10.2	–	3.8	42.2
The same site, *C. nemoralis* [Kolesnik, Kruglova, 2016]										
?	?	?	21.9	?	?	?	64.5	?	?	?
Minsk region, agricultural town of Priluki										
C. hortensis [Kruglova, Kolesnik, 2017]										
2015	193	50.8	–	–	49.2	–	–	–	–	50.8
Minsk, Alibegov street										
C. hortensis (personal communication of O.Yu.Kruglova)										
2019	108	95.4	–	–	4.6	–	–	–	–	95.4

Notes: * may also include the shells with a white ground colour; ** the data may concern immature *C. nemoralis* or a mixture of both species; P0 – P00000; P1 – P00300; P3 – P00345 and other pink three-banded; P5 – P12345 and other pink five-banded; Y1-Y5 – similarly for yellow shells; ? – cannot be calculated from published data.

would be desirable to carry out also in the Moscow region, even more distant from the natural range of *C. hortensis*, as well as with an even more continental climate. No less interesting is the fact that about 40% of snails in Moscow and almost 20% in Vidnoe have pink shells (Table 1), a feature that is extremely rare in Western Ukraine. Further study will help to determine whether the frequencies of this trait will remain relatively stable or decrease in favor of a lighter ground colour (yellow).

In Western Ukraine, special attention will be paid to sites where the frequencies of banded shells were recorded, which are atypically high for this region, as well as to colonies that could have formed here as a result of relatively recent repeat introductions of *C. hortensis* from other countries and independent of the primary introduction of this species that occurred in the 20th century. First of all, the presence of yellow banded shells absent in the descendants of the primary introduction can be used for the detection of these colonies.

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References

Alexandrov D.A., Sergievsky S.O. 1980. Genetic structure of peripheral populations of land mollusc *Cepaea hortensis* (Müll.*). Doklady Akademii nauk SSSR*, 225(1): 206–208.

Andreassen E.M. 1978. Polymorphisme hos hagesnegl, *Cepaea hortensis*. *Fauna Norge*, 31: 105–114.

Bąkowski J. 1882. Mięczaki z okolicy Lwowa, Gródka i Szczerca. *Sprawozdanie Komisyi Fizyjograficznéj*, 16(2): 56–63.

Bąkowski J. 1884. Mięczaki galicyjskie. *Kosmos*, 9: 190–197, 275–283, 376–391, 477–490, 604–611, 680–697, 761–789.

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

Cain A.J., Sheppard P.M., King J.M.B. 1968. Studies on *Cepaea*. The genetics of some morphs and varieties of *Cepaea nemoralis*. *Philosophical Transactions of the Royal Society of London. Series B,* 253: 383–396.

Cameron R.A.D. 2013. The poor relation? Polymorphism in *Cepaea hortensis* (O.F.Müller) and the Evolution Megalab. *Journal of Molluscan Studies*, 79(2): 112–117.

Clarke B.C. 1960. Divergent effects of natural selection on two closely-related polymorphic snails. *Heredity*, 14(3-4): 423–443.

Diver C. 1939. Aspects of the study of variation in snails. *Journal of Conchology*, 21: 91–141.

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(3): 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.

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(7): 751–761 [In Russian].

Gural-Sverlova N.V., Gural R.I. 2020. *Catalog of the collection of land molluscs of the State Museum of Natural History of the NAS of Ukraine*. State Museum of Natural History, Lviv. 227 p. [In Ukrainian].

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(2): 75–86 [In Russian].

Kerney M.P., Cameron R.A.D., Jungbluth J.H. 1983. *Die Landschnecken Nord- und Mitteleuropas*. Parey, Hamburg-Berlin, 384 p.

Kolesnik V.G., Kruglova O.Yu. 2016. Phenotypic variability in the populations of *Cepaea nemoralis* Linnaeus, 1758 (Gastropoda, Pulmonata, Helicidae) from Minsk city and Minsk region. In.: *Actual problems of ecology*. Grodno State University, Grodno: 102–103 [In Russian].

Kruglova O.Yu., Kolesnik V.G. 2017. Phenetic structure of populations of *Cepaea hortensis* (O.F.Müller, 1774) (Gastropoda, Pulmonata) in the conditions of Minsk City and Minsk region. In: *Actual issues of modern malacology*. Publishing House Belgorod, Belgorod: 66–70 [In Russian].

Lang A. 1906. Über die Mendelschen Gesetze, Art- und Varietätenbildung, Mutation und Variation, insbesondere bei unsern Hain- und Garetnschnecken. *Verhandlungen der Schweizerischen Naturforschenden Gesellschaft in Luzern:* 209–254.

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*, 3. Plenum Press, New York: 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(2): 93–97.

Schilder F. A., Schilder M. 1957. *Die Bänderschnecken. Eine Studie zur Evolution der Tiere. Schluß: Die Bänderschnecken Europas*. Gustav Fischer Verlag, Jena: 93–206.

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

Shebanin V.S., Melnyk S.I., Kramarenko S.S., Ganganov V.M. 2008. *Analysis of populations structure*. Mykolaiv State Agrarian University, Mykolaiv. 240 p. [in Ukrainian].

Sverlova N.V. 2001a. Polymorphism of the introduced species *Cepaea hortensis* (Gastropoda, Pulmonata, Helicidae) in Lvov. 1. General regularities of polymorphism. *Zoologicheskij Zhurnal*, 80(5): 520–524 [In Russian].

Sverlova N.V. 2001b. Polymorphism of the introduced species *Cepaea hortensis* (Gastropoda, Pulmonata, Helicidae) in Lvov. 2. Variability of polymorphic structure within the city. *Zoologicheskij Zhurnal*, 80(6): 643–649 [In Russian].

Sverlova N.V. 2002a. The influence of anthropogenic barriers on phenotypical structure of populations of *Cepaea hortensis* (Gastropoda, Pulmonata) under urban conditions. *Vestnik zoologii*, 36(5): 61–64 [In Russian].

Sverlova N. 2002b. Einschleppung und Polymorphismus der *Cepaea*-Arten am Beispiel von Lwow in der Westukraine (Gastropoda: Pulmonata: Helicidae). *Malakologische Abhandlungen aus dem Staatlichen Museum für Tierkunde Dresden*, 20: 267–274.

Sverlova N. 2003. Zum Vorkommen der zusätzlichen Bänder in den natürlichen und eingeschleppten Populationen von Bänderschnecken *Cepaea* (Gastropoda: Pulmonata: Helicidae). *Malakologische Abhandlungen aus dem Staatlichen Museum für Tierkunde Dresden*, 21: 137–144.

Sverlova N. 2004. Zur Auswertung der Diversitaet und Struktur des Polymorphismus bei den Bänderschnecken *Cepaea hortensis* (Müller, 1774) und *C. nemoralis* (Linne, 1758) am Beispiel isolierter Populationen. *Mitteilungen aus dem Museum für Naturkunde in Berlin. Zoologische Reihe*, 80(2): 159–180.

Sverlova N.V. 2005. Variability of the polymorph structure of the urban colonies of the introduced species *Cepaea hortensis* (Gastropoda, Pulmonata). *Vestnik zoologii*, 39(4): 29–34 [In Russian].

Sverlova N.V., Khlus L.N., Kramarenko S.S. et al. 2006. *Fauna, ecology and intraspecific variability of land molluscs under urban conditions*. State Museum of Natural History, Lviv, 226 p. [in Russian].

Taylor J.W. 1914. *Monograph of the land & freshwater Mollusca of British Isles. Zonitidae, Endodontidae. Helicidae*. Taylor brothers publishers, Leeds, 522 p.

UkrBIN. 2020. UkrBIN: Ukrainian Biodiversity Information Network [public project & web application]. Available online at http://www.ukrbin.com. [Accessed on April 13, 2020.]

Wolda H. 1969. Genetics of polymorphism in the land snail *Cepaea nemoralis*. *Genetica*, 40: 475–502.

Wiktor A. 2004. *Ślimaki lądowe Polski*. Mantis, Olsztyn. 302 p.

Supplementary material

The description of the collecting sites in Western Ukraine and in the Moscow region