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Specific Features of Phenetic Structure of the Terrestrial Snail *Cepaea vindobonensis* (Pulmonata; Helicidae) in Urbanized and Natural Populations

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Abstract—The phenetic structure of natural and urbanized populations of the terrestrial snail *Cepaea vindobonensis* has been studied with respect to polymorphism in the shell-band color and pattern. It is noted that *C. vindobonensis* snails populating different artificial habitats in the city of Nikolaev and its suburbs are characterized by a higher level of both intra- and interpopulation diversity with respect to the type of this polymorphism. In addition, urban populations show a very wide range of variation in the frequencies of particular morphs or their groups. Conversely, natural populations are characterized by a more uniform frequency structure with respect to polymorphism of the shell banding pattern.

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The terrestrial snail *Cepaea vindobonensis* (Férussac, 1821) is a widespread species in the malacofauna of the northwestern Black Sea region (Sverlova et al., 2000). It inhabits all natural and artificial forest stands, open woodland, and anthropogenic biotopes in the city of Nikolaev and other cities and villages of Nikolaev oblast (Kramarenko and Sverlova, 2001). In addition, the presence of this species in urban malacocenoses has been recorded in many populated areas of Ukrainian Polesye (Baidashnikov, 1992) and western Ukraine (Kirpan et al., 2002). Beyond Ukraine, *C. vindobonensis* is distributed in southeastern Europe and the Northern Caucasus (Shileiko, 1978).

Unlike two other species of the genus, *C. nemoralis* and *C. hortensis*, which are favorite objects of research in comparative polymorphology (Khokhutkin, 1997; Clarke et al., 1978), *C. vindobonensis* has not been studied adequately. There are only a few papers dealing with various aspects of its population ecology (Sacchi, 1984; Staikou, 1998, 1999). Specific features of *C. vindobonensis* polymorphism with respect to the shell banding pattern (the presence or absence of helical colored bands, their fusion, and the shape of individual bands on the shell) are considered in the papers by Schilder (1923) and Rotarides (1926). The formation of this polymorphism in *C. vindobonensis* from Yugoslavian populations is analyzed in a series of publications (Jones, 1974, 1975; Jones and Parkin, 1977). A recent study concerns populations of this species in the Czech Republic (Honek, 2003).

Although this species is widespread in Ukraine and is obviously synanthropic, the problems of ecology and polymorphology of *C. vindobonensis* from Ukrainian populations have received little attention. Relevant papers are limited to our studies on reproduction of this species (Kramarenko and Popova, 1997) and the formation of intrapopulation color polymorphism in its populations from the Northwestern Black Sea region (Kramarenko, 2003a, 2003b) and the study by Sverlova and Kirpan (2004) on the phenetic structure of *C. vindobonensis* populations in western Ukraine.

Colonization of anthropogenic biotopes by terrestrial snails leads to the emergence of specific features in their intra- and interpopulation polymorphism in the banding pattern. It may be expected that, upon the formation of anthropochorous populations (due to accidental introduction of snails from natural populations to city parks, gardens, hedges, etc.), their genetic structure would depend primarily on random genetic processes such as the founder effect and genetic drift (Sverlova, 2001a). In this case, the level of polymorphism would decrease due to homozygotization of the allele pool in combination with elimination of rare morphs not typical of natural populations (Sverlova, 2001a,

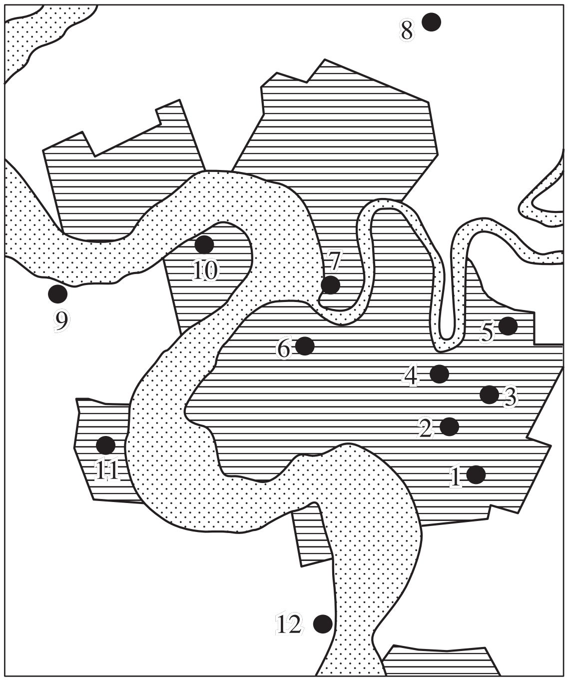

Fig. 1. Scheme of sampling of *Cepaea vindobonensis* snails in the city of Nikolaev (densely built areas are shaded). Numbers of populations correspond to those in Table 1.

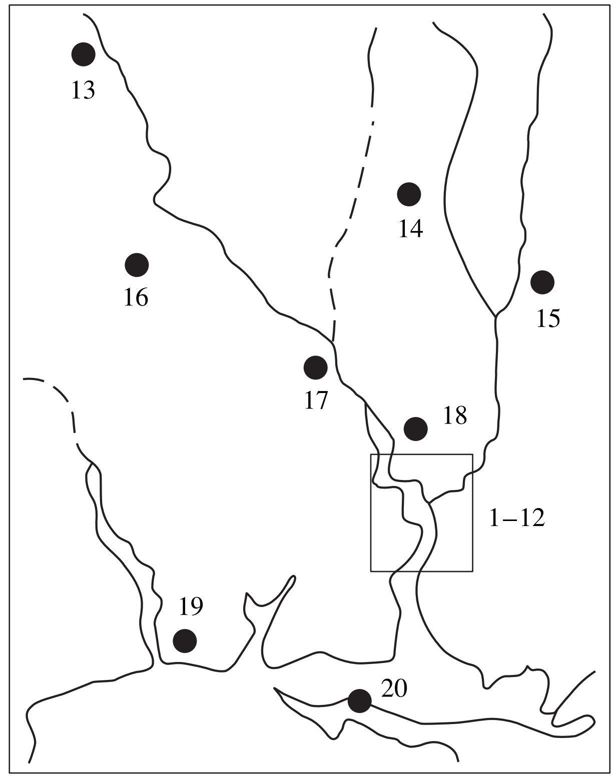

Fig. 2. Scheme of sampling of *Cepaea vindobonensis* snails in Nikolaev oblast (the quadrangle delimits the area shown in Fig. 1). Numbers of populations correspond to those in Table 2.

2001b). Therefore, the level of intrapopulation diversity in synanthropic populations would be lower, whereas interpopulation differences would increase.

The main purpose of this study was to perform a comparative analysis of specific features of banding polymorphism in *C. vindobonensis* populations living within the Nikolaev city limits and in natural biotopes.

MATERIAL AND METHODS

Living snails and their shells were collected between 1995 and 2003 from 12 local populations living within the city limits of Nikolaev and in its suburbs (Fig. 1). Only mature specimens with a well-developed lip of the shell opening were included in the analysis. Collections were made in 150- to 200-m^2 plots, which therefore were smaller than the size of the panmictic unit for representatives of the genus *Cepaea* (Lamotte, 1951). Seven out of 12 populations inhabited city parks or shrub hedges, and five populations inhabited suburban semianthropogenic habitats (mainly windbreak forest strips). As the city of Nikolaev is at the confluence of two large rivers (the Southern Bug and Ingul), groups of *C. vindobonensis* populations were separated from each other by wide water barriers (Fig. 1). To obtain a more complete picture of polymorphism in urbanized habitats, the data on eight natural populations from different regions of Nikolaev oblast were also included in the analysis (Fig. 2).

Specific features of *C. vindobonensis* polymorphism with respect to shell and band color and the banding pattern were analyzed under laboratory conditions. In the first case, all shells were separated into two groups: one group comprised the shells of greenish sandy color with light bands (the form pallescens), and the other group comprised the shells of light (almost white) background color with clear dark brown or black bands.

In the case of the banding pattern, phenotypes were designated according to the standard system (Cain and Sheppard, 1950). The bands were designated by numbers from 1 to 5, counting from the seam between the ultimate and penultimate whorls toward the umbilicus. When a band was missing, its number in the phene formula was replaced by zero; the numbers of fused bands were placed in parentheses. Thus, the formula for the most widespread phene with all five bands was 12345, the formula for the phene with the second band missing was 10345, and that for the phene with fused second and third bands was 1(23)45. Moreover, all specimens with the phene 12345 were divided into three groups with respect to the relative width of the first three bands: the phene [1] = [2] = [3] was characterized by equal width of all these bands; in the phene [1] = [2] < [3], the third band was noticeably wider than the first two bands; and in the phene [1] > [2] < [3], the second band was narrower than the first and third bands. This type of morphs differing in the width of the first three bands was previously described for *C. vindobonensis* living in Hungary (Rotarides, 1926).

The frequencies of individual phenes were calculated for snails from each population and group of populations (from urban, suburban, or natural habitats). The results were treated by means of the Fisher arcsine transform to level off the effect of sample size. Parameters characterizing the structure of population diversity—the average number of morphs and the proportion of rare morphs (Zhivotovsky, 1991)—were calculated for both individual populations and groups of populations from the aforementioned habitats.

The levels of intrapopulation diversity and the arcsine-transformed frequencies of individual phenes or their groups depending on the type of habitat were compared using methods of nonparametric statistics (Kruskal–Wallis rank ANOVA).

In addition, ordination of 20 investigated samples in the space of the first two dimensions was performed by the method of multidimensional nonparametric scaling. The initial matrix of distances contained the parameters of percent disagreement between each pair of samples with respect to the presence or absence of certain phenes:

$$P_D = \frac{b+c}{a+b+c},$$

where a is the number of phenes recorded in both the first and second samples simultaneously, b is the number recorded in the first sample but absent from the second sample, and c is the number of phenes recorded in the second sample but absent from the first sample.

Interpretation of dimensions (along axis 1, 2) was based on the significance level of the Spearman coefficient of rank correlation between the coordinates of samples along each axis and the data of the initial matrix of phene absence or presence. The phenes with correlation coefficients having a significance level of $p < 0.01$ were considered to make the largest contribution to interpretation of the corresponding factor.

Discriminant analysis was performed to reveal the phenes whose frequencies in the three groups of populations differed to the greatest extent. The matrix used for this purpose contained the following parameters of each population studied: the proportion of snails of the morph pallescens relative to the total number of snails in the sample; the proportion of snails with phene 12345 relative to the number of snails with dark bands on the shell; the proportion of snails with phene [1] = [2] = [3] relative to the total number of snails with phene 12345; the proportion of snails with phene [1] = [2] < [3] relative to the total number of snails with phene 12345; the proportion of snails with phene [1] > [2] < [3] relative to the total number of snails with phene 12345; the proportion of snails with missing bands (phenes 12045 and 10345) relative to the total number of snails with dark bands on the shell; and the proportion of snails with fused bands relative to the total number of snails with dark bands on the shell. These parameters were also arcsine transformed.

Statistical data processing was performed by standard methods (*Komp'yuternaya biometrika*, 1990) using the STATISTICA v. 5.5 applied program package.

RESULTS AND DISCUSSION

Altogether, 3604 shells of *C. vindobonensis* snails from 20 populations were studied (Tables 1, 2). In the course of laboratory treatment of the material, it was found that virtually all populations contained two *C. vindobonensis* morphs differing in the main background color of the shell and the color of bands: some shells had a greenish sandy background with light, almost indistinguishable bands (morph pallescens), whereas other shells had a whitish background with dark brown or black bands. Only one population (from the village of Novo-Petrovskoe) was monomorphic, containing no snails of the pallescens morph.

Among shells with distinct bands, we revealed ten different phenes with respect to relative band width and the absence or fusion of some bands (variations of phene 12345 in the relative width of the first to third bands were recorded as separate phenes). The absolute frequencies of these phenes are shown in Tables 1 and 2. Using these data, we calculated the values of intrapopulation diversity for each population (Table 3).

All ten phenes were discovered in *C. vindobonensis* populations from urban habitats, but individual populations significantly differed in the level of polymorphism. In the population from the Nikolaev zoo, for example, only four phenes were detected, compared to all ten phenes recorded in the population from the lawn near the regional observatory (Table 1). In addition, urban populations strongly differed in the parameters of intrapopulation diversity, with the average number of morphs ranging from 3.17 to 6.58 and the proportion of rare morphs ranging from 0.07 to 0.47 (Table 3).

In *C. vindobonensis* populations from suburban biotopes, the number of phenes varied from five to seven. This decrease in the level of diversity was explained primarily by the disappearance of phene 12045 and the absence (or sporadic occurrence) of phenes with fused bands: (123)45, 123(45), and (123)(45) (Table 1). Due to the impoverishment of the phenetic structure, the parameters of their intrapopulation diversity were more uniform: the average number of morphs varied from 3.25 to 4.61, and the proportion of rare morphs varied from 0.14 to 0.42 (Table 3).

The lowest phenetic diversity was characteristic of *C. vindobonensis* from natural biotopes, in which only

Table 1. Absolute frequencies of different morphs in urbanized populations of *Cepaea vindobonensis* snails

No.	Population	Morph											Sample size, ind.
		pallescens	12345			10345	12045	(12)345	1(23)45	(123)45	123(45)	(123)(45)	
			[1] = [2] = [3]	[1] = [2] < [3]	[1] > [2] < [3]								
		Urban populations											
1	YuTZ Park	82	21	55	79	6	1	–	–	–	1	–	245
2	Yuzhnaya ul.	24	22	113	57	9	–	4	17	3	–	–	249
3	Vodopoi Park	26	11	200	194	6	2	–	–	–	1	–	440
4	Zoo	47	12	29	51	16	–	–	–	–	–	–	155
5	Dubki Park	38	11	97	37	1	–	7	–	–	2	1	194
6	Observatory	79	52	97	49	6	1	15	14	6	1	2	322
7	Park Pobedy	92	27	60	28	16	–	–	8	–	1	–	232
	Total	388	156	651	495	60	4	26	39	9	6	3	1837
		Suburban populations											
8	Ternovskaya gully	13	8	170	140	51	–	–	1	–	–	–	383
9	Rodniki Hotel	2	6	88	65	2	–	–	3	–	–	1	167
10	Varvarovka	47	5	23	16	2	–	1	3	–	–	–	97
11	Verkhnyaya Korenikha	18	8	28	30	16	–	2	–	–	–	–	102
12	Radsad	47	13	14	59	1	–	6	6	5	–	–	151
	Total	127	40	323	310	72	–	9	13	5	–	1	900

two phenes were recorded: 12345 (with variations) and 10345. Shells with fused bands occurred as rare exceptions: only five out of 867 shells had phene (12)345 with the first and second bands fused (Table 2). Accordingly, the parameters of the intrapopulation diversity in the natural populations of *C. vindobonensis* were also minimal: the average number of morphs varied from 2.91 to 3.56 and the proportion of rare morphs varied from 0.03 to 0.25 (Table 3).

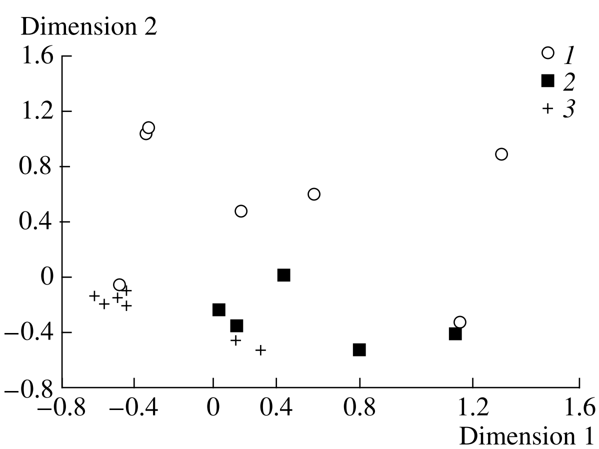

Fig. 3. Distribution of 20 samples of *Cepaea vindobonensis* snails from the city of Nikolaev and Nikolaev oblast in the space of the first two dimensions: (*1*) urban, (*2*) suburban, and (*3*) natural populations.

The type of habitat (urban, suburban, or natural) has a significant effect on the level of intrapopulation polymorphism in the banding pattern (Kruskal–Wallis rank ANOVA): for the average number of phenes, $H = 6.15$; $df_1 = 2$; $df_2 = 20$; $p < 0.05$; for the proportion of rare morphs, $H = 6.10$, $df_1 = 2$, $df_2 = 20$, $p < 0.05$. The average number of morphs gradually decreases upon transition from urbanized to natural biotopes. With respect to the proportion of rare morphs, urban and suburban populations are similar and superior to populations from suburban biotopes (Table 3).

Thus, synanthropic populations of *C. vindobonensis* are characterized by a considerable increase in phenotypic diversity due primarily to the appearance of phenes with different fusions of individual bands, which rarely occur in snails from suburban biotopes and are absent in natural populations (Tables 1, 2). A high level of interpopulation differences in the phenetic structure is characteristic of urban *C. vindobonensis* populations: some of them are highly polymorphic,

Table 2. Absolute frequencies of different morphs in natural populations of *Cepaea vindobonensis* from Nikolaev oblast

No.	Population	Morph											Sample size, ind.
		pallescens	12345			10345	12045	(12)345	1(23)45	(123)45	123(45)	(123)(45)	
			[1] = [2] = [3]	[1] = [2] < [3]	[1] > [2] < [3]								
13	Kuripchino	6	9	9	21	4	–	1	–	–	–	–	50
14	Elanetskaya Steppe Reserve	16	4	63	79	16	–	–	–	–	–	–	178
15	Bashtanka	44	1	6	28	10	–	–	–	–	–	–	89
16	Porech'e	58	–	13	30	26	–	–	–	–	–	–	127
17	Novo-Petrovskoe	–	21	11	28	1	–	–	–	–	–	–	61
18	Sebino	132	1	4	28	8	–	–	–	–	–	–	173
19	Koblevo	22	4	20	13	–	–	–	4	–	–	–	63
20	Vasil'evka	45	10	17	46	8	–	–	–	–	–	–	126
	Total	323	50	143	273	73	–	1	4	–	–	–	867

whereas others contain only certain phenes (as is the case with *C. vindobonensis* from the natural habitats).

The results of multidimensional scaling show that all natural populations of *C. vindobonensis* form a compact nucleus, whereas synanthropic populations are characterized by considerable scattering with respect to both the first and second dimensions (Fig. 3). Most synanthropic populations are separated from others along the second dimension, which may be interpreted as the presence of phenes 12045 and 123(45). The first dimension, in turn, may be interpreted as the presence of phenes with various fusions of the first to third bands: (12)345, 1(23)45, and (123)45.

In addition to qualitative differences, there are differences in the frequency of some phenes or their groups between urban and natural populations of *C. vindobonensis*. This concerns mainly the frequency of phenes with fused bands ($H = 6.55$; $df_1 = 2$; $df_2 = 20$; $p < 0.05$) and the frequency of phene [1] > [2] < [3] ($H = 6.26$, $df_1 = 2$, $df_2 = 20$; $p < 0.05$). The latter gradually increases upon transition from urban to natural populations (Tables 1, 2).

The results of discriminant analysis show that natural populations of *C. vindobonensis* are separated from urban and suburban populations, which, in turn, form a single pool (Fig. 4). However, two synanthropic populations are located close to natural populations along the first canonical axis. This axis may be interpreted as the frequency ratio of phenes [1] = [2] < [3] (factor load along the first canonical axis is +0.754) and [1] > [2] < [3] (factor load along the first canonical axis is –0.638) in the population. Therefore, natural populations differ from (semi)synanthropic primarily in the high frequencies of phene [1] > [2] < [3] and, conversely, the low frequencies of phene [1] = [2] < [3].

However, comparing the polymorphism of natural and synanthropic populations of *C. vindobonensis*, it may be concluded that the frequencies of phenes and their groups in urban populations manifest wide scattering, whereas the frequency structure of morphotypes in natural populations is more uniform.

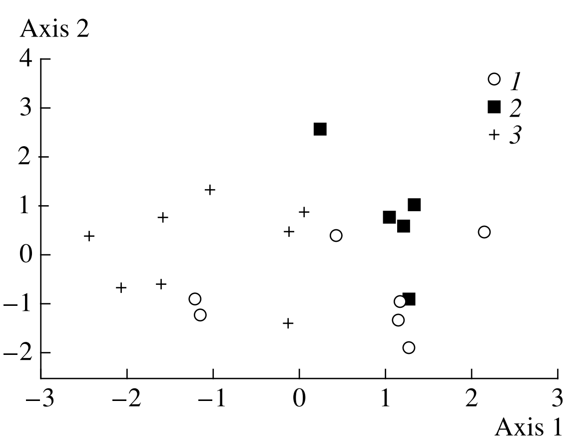

Fig. 4. Distribution of 20 samples of *Cepaea vindobonensis* snails from the city of Nikolaev and Nikolaev oblast in the space of the first two canonical axes: (*1*) urban, (*2*) suburban, and (*3*) natural populations.

Table 3. Parameters of intrapopulation diversity with respect to shell banding pattern in different *Cepaea vindobonensis* populations from the city of Nikolaev and Nikolaev oblast

No.	Population	Number of morphs (m)	Average number of morphs ($\mu \pm SE\mu$)	Proportion of rare morphs ($h_\mu \pm SEh_\mu$)
	Urban populations			
1	YuTZ Park	6	3.94 ± 0.22	0.34 ± 0.04
2	Yuzhnaya ul.	7	5.06 ± 0.21	0.28 ± 0.03
3	Vodopoi Park	6	3.17 ± 0.15	0.47 ± 0.02
4	Zoo	4	3.70 ± 0.10	0.07 ± 0.03
5	Dubki Park	7	4.11 ± 0.28	0.41 ± 0.04
6	Observatory	10	6.58 ± 0.30	0.34 ± 0.03
7	Park Pobedy	6	4.85 ± 0.20	0.19 ± 0.03
	Total	10	5.41 ± 0.13	0.46 ± 0.01
	Suburban populations			
8	Ternovskaya gully	5	3.47 ± 0.12	0.31 ± 0.12
9	Rodniki Hotel	6	3.50 ± 0.23	0.42 ± 0.04
10	Varvarovka	6	4.61 ± 0.36	0.23 ± 0.06
11	Verkhnyaya Korenikha	5	4.30 ± 0.19	0.14 ± 0.04
12	Radsad	7	3.25 ± 0.27	0.35 ± 0.05
	Total	8	4.69 ± 0.14	0.41 ± 0.02
	Natural populations			
13	Kuripchino	5	4.19 ± 0.28	0.16 ± 0.02
14	Elanetskaya Steppe Reserve	4	3.22 ± 0.12	0.20 ± 0.03
15	Bashtanka	4	3.15 ± 0.24	0.21 ± 0.06
16	Porechye	3	2.91 ± 0.06	0.03 ± 0.02
17	Novo-Petrovskoe	4	3.30 ± 0.19	0.17 ± 0.05
18	Sebino	4	3.02 ± 0.27	0.25 ± 0.07
19	Koblevo	4	3.56 ± 0.20	0.11 ± 0.05
20	Vasil'evka	4	3.52 ± 0.14	0.12 ± 0.04
	Total	5	3.95 ± 0.09	0.21 ± 0.02

Thus, urbanized populations of *C. vindobonensis*, compared to natural populations, are characterized by higher intra- and interpopulation diversity with respect to polymorphism in the banding pattern. This may be explained by the emergence of rare morphs resulting from random genetic processes (the founder effect and genetic drift).

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