Phenetic Population Structure of the Land Snail *Helix albescens* (Gastropoda, Pulmonata, Helicidae) in the Crimea

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Abstract—The polymorphism of shell banding pattern has been studied in Crimean populations of the land snail *H. albescens*. The results show that snails from different regions of the Crimea are characterized by specific types of shell polymorphism, the differences between them concerning mainly the number of observed shell morphs rather than their occurrence frequency. In particular, the proportion of snails with darkly colored shells increases in relatively cool habitats. However, among the microevolutionary processes determining the type and degree of polymorphism in *H. albescens* populations, a major role is also played by stochastic genetic phenomena, because the species exists in semi-isolated colonies with low effective abundance and high risk of local extinction.

In Ukraine, the genus *Helix* L., 1758 is represented by four species: *H. albescens* Rossmässler, 1839, *H. lucorum* L., 1758, *H. lutescens* Rossmässler, 1839, and *H. pomatia* L., 1758. Only the first two species live in the Crimea, with *H. albescens* being more widespread and abundant. This species has a circumpontic range; it is little known from Europe and occurs in Ukraine only in the Black Sea Region, Sea of Azov Region, and Crimea (Shileiko, 1978), locally reaching relatively high abundance.

The shell banding pattern polymorphism in this species is similar to that in species of the genus *Cepaea*. The first attempts to analyze the phenetic variation of the shell banding pattern in *H. albescens* were made by Popov and his students (Popov and Kramarenko, 1997; Kramarenko, 2002), and this research was subsequently developed in Leonov's (2005) dissertation. However, additional material obtained in the past few years provided a basis for analyzing the formation of the phenetic structure of Crimean *H. albescens* populations in more detail.

The main purpose of this study was to analyze manifestations of the shell banding pattern polymorphism in *H. albescens* from populations living in different physiographic regions of the Crimea and to elucidate possible mechanisms of its formation.

MATERIAL AND METHODS

Samples were taken from 28 local *H. albescens* populations that represented all physiographic regions of the Crimea, collecting adult snails or their shells within 150- to 200-m^2 plots. Five out of the 28 populations (nos. 1–5) were from parks or hedges in the city of Simferopol; ten (nos. 6–15), from different biotopes of the southern Crimean coast; nine (nos. 16–24), from the steppe Crimea; and four (nos. 25–28), from different biotopes of the Kerch Peninsula (Fig. 1).

All this material is stored in the malacological collection of the Department of Zoology, Taurida National University (Simferopol).

The banding pattern polymorphism of *H. albescens* shells was analyzed in the laboratory, designating different morphs according to the conventional system (Cain and Sheppard, 1950). The frequency of each morph was calculated for snails from each population and group of populations (from the city, southern coast, steppe, and Kerch Peninsula). These values were subsequently transformed using Fisher's arcsine transformation to level off the influence of sample size.

The degree of diversity in individual samples or their groups was estimated by calculating the number of recorded morphs differing in shell banding pattern (*m*). In addition, parameters of population diversity were calculated: the average number of morphs (μ) and the proportion of rare morphs (h_μ) according to Zhivotovsky's (1991) formulas, the Shannon index (H_{Sh}), and the Simpson (*D*). The calculated parameters of the diversity of particular populations were compared between areas of the Crimea using the procedure of bootstrap (permutation) resampling with 10000 iterations (Shitikov et al., 2008) in the EcoSim v. 7.72 program (Gotelli and Entsminger, 2001).
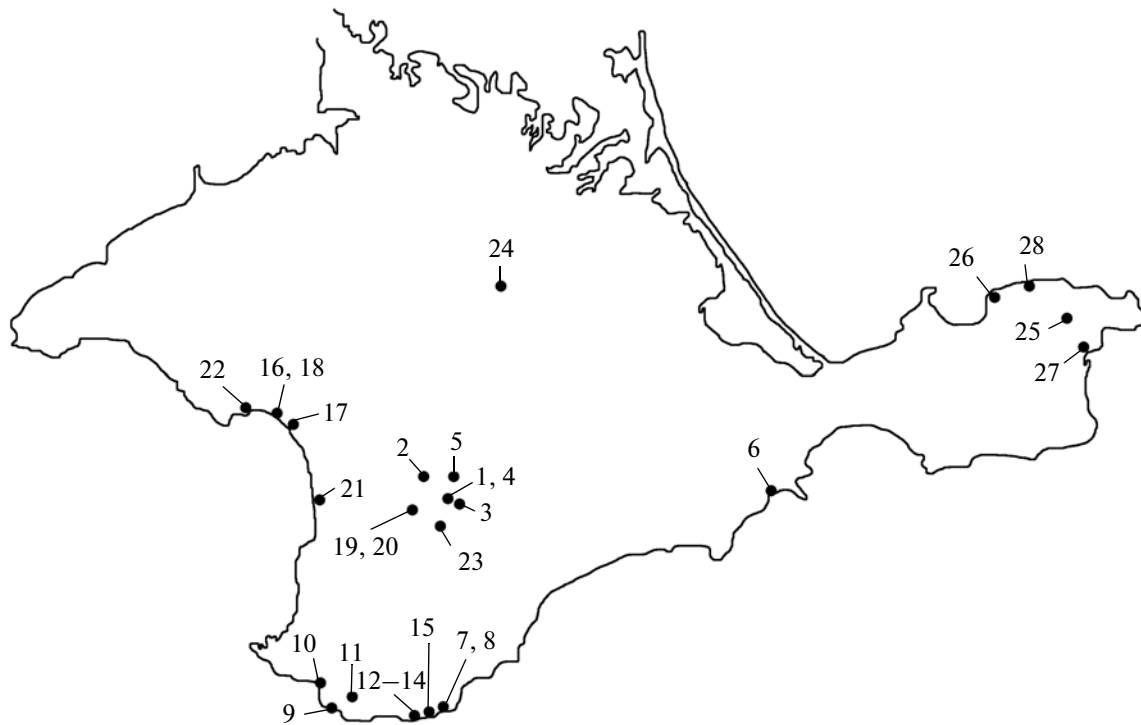
Fig. 1. Schematic map of the Crimea and Locations of *H. albescens* populations used in the study (the populations are numbered as in Table 1).

The degree of phenetic differentiation between populations and their regional groups was estimated using the algorithm of two-way hierarchical ANOVA for qualitative characters (Kramarenko, 2006). The significance of these estimates (P_{RT}, P_{PR}, and P_{PT}) was calculated using a permutation test with 999 iterations (Shitikov et al., 2008) in the GenAIEx v. 6.0 program (Peakall and Smouse, 2006).

A more detailed analysis of the partition of variation in the phenetic structure of different populations and population groups was performed with the PARTITION v. 2.0 program (Veech and Crist, 2007), which allows the assessment of diversity on the basis of different measures, namely, the number of morphs and the Simpson and Shannon indices. This program divides the total variation into components and, using the randomization approach, tests the probability of obtaining random estimates; therefore, it can be used for calculating the significance of the results (Veech et al., 2002).

Discriminant analysis was performed for revealing the morphs whose frequencies differ most strongly among the four population groups.

Canonical correlations were analyzed using the long-term average values of the following climatic parameters for each population: the number of frostless days per year, temperatures of the coldest (January) and warmest (July) months, annual precipitation, total precipitation at temperatures above 10°C, and the precipitation−evaporation ratio. All basic data

were taken from the reference book by Podgorodetskii (1988).

The last two analyses were performed by conventional methods (*Komp'yuternaya biometrika*, 1990) using the STATISTICA v. 5.5 application program package.

RESULTS AND DISCUSSION

Laboratory processing of the material resulted in identification of 14 morphs differing in shell banding pattern. Their frequency distribution in different samples is characterized in Table 1. The greatest number of these morphs ($m = 13$) was recorded in different biotopes of Simferopol; 11 morphs were found on the southern Crimean coast; 10 morphs, in the steppe Crimea; and only 9 morphs in the Kerch Peninsula (Table 2). A considerable increase in the level of phenetic diversity in urbanized populations, compared to natural populations, was already noted in our previous study on *Cepaea vindobonensis*, another land snail species inhabiting southern Ukraine (Kramarenko et al., 2007).

A distinctive feature of the Simferopol populations of *H. albescens* is the complete absence of morphs 12 305 and 12 005, and, on the other hand, a high frequency of morphs 12 045 and 10 045. A relatively high frequency of morph 00000 as well as of morphs 10 345 and 10 305 is characteristic of populations from the southern coast. A strongly depleted composition of

Table 1. Numbers of different shell banding morphs in *H. albescens* snails from different Crimean populations

No.	Population	Morph														Sample size, ind.
		12345	1(23)45	10345	12045	12305	10045	12005	10005	10305	02045	00005	00000	1(23)(45)	123(45)	
		Simferopol														
1	Simferopol-1	43	19	1	13	1	4	–	–	–	–	–	–	–	1	82
2	Simferopol-2	14	1	–	21	–	6	–	8	–	1	3	1	–	–	55
3	Simferopol-3	104	31	–	40	–	1	1	2	–	–	–	–	–	–	179
4	Simferopol-4	72	18	6	5	–	14	–	4	4	–	–	–	–	–	123
5	Simferopol-6	37	14	8	4	1	11	–	10	–	–	–	–	–	–	85
	Total	**270**	**83**	**15**	**83**	**2**	**36**	**1**	**24**	**4**	**1**	**3**	**1**	**–**	**1**	**524**
		Southern Crimean coast														
6	Koktebel	16	7	1	5	–	–	1	13	2	–	–	11	–	–	56
7	Simeiz-1	34	8	8	2	2	3	5	5	5	–	–	3	–	–	75
8	Simeiz-2	33	67	4	–	–	–	1	3	8	–	–	–	–	–	116
9	Cape Aiya	93	8	3	1	–	–	–	–	8	–	–	–	–	–	113
10	Balaklava	53	1	12	4	1	1	6	2	–	–	–	–	–	–	80
11	Laspi Pass	59	3	14	–	2	–	–	–	12	–	–	–	–	–	90
12	Ponizovka-1	40	–	9	5	–	–	4	1	3	–	–	–	–	–	62
13	Ponizovka-2	49	–	13	–	8	–	–	5	8	2	–	–	–	–	85
14	Cape Uzun	41	12	1	–	–	1	–	1	–	–	–	–	–	–	56
15	Mt. Koshka	30	20	4	1	2	–	5	4	2	–	–	3	–	–	71
	Total	**448**	**126**	**69**	**18**	**15**	**5**	**22**	**34**	**48**	**2**	**–**	**17**	**–**	**–**	**804**
		Steppe Crimea (without Kerch Peninsula)														
16	Pribrezhnoe-1 Station	53	1	3	5	2	3	8	4	–	–	–	–	–	–	79
17	Pribrezhnoe-2 Station	96	8	31	13	1	18	2	42	19	–	–	–	–	–	230
18	Pribrezhnoe-3 Station	60	8	–	8	–	7	2	3	5	–	–	–	–	–	93
19	Klyuchi-1	25	16	3	1	–	–	–	–	3	–	–	–	–	–	48
20	Klyuchi-2	80	123	6	3	7	–	1	3	2	–	–	–	–	–	225
21	Nikolaevka	78	16	1	11	–	2	8	2	–	–	–	–	–	–	118
22	Yevpatoria	83	30	5	13	7	1	–	–	–	–	–	–	–	–	139
23	Fontany	38	132	5	8	9	–	–	1	–	–	–	–	–	–	193
24	Krasnogvardeiskoe	126	35	4	17	–	5	2	23	8	–	–	–	4	–	224
	Total	**639**	**369**	**58**	**79**	**26**	**36**	**23**	**78**	**37**	**–**	**–**	**–**	**4**	**–**	**1349**
		Kerch Peninsula														
25	Bagerovo	75	93	3	2	1	–	–	1	1	–	–	–	1	–	177
26	Zolotoe	57	90	–	–	–	–	–	–	–	–	–	–	–	–	147
27	Kerch	5	51	1	–	–	–	–	–	–	–	–	–	–	–	57
28	Mt. Skala	36	108	2	3	5	–	–	–	–	–	–	–	2	1	157
	Total	**173**	**342**	**6**	**5**	**6**	**–**	**–**	**1**	**1**	**–**	**–**	**–**	**3**	**1**	**538**

Table 2. Parameters of intrapopulation diversity of shell banding morphs in *H. albescens* snails from different Crimean populations

No.	Population	Number of morphs	Shannon index (H_{Sh})	Simpson index (D)	Average number of morphs ($\mu \pm SE\mu$)	Proportion of rare phenes ($h_\mu \pm SEh_\mu$)
			Simferopol			
1	Simferopol-1	7	1.366 ± 0.327	0.357 ± 0.151	4.65 ± 0.37	0.336 ± 0.052
2	Simferopol-2	8	1.721 ± 0.214	0.248 ± 0.074	6.11 ± 0.46	0.236 ± 0.057
3	Simferopol-3	6	1.103 ± 0.374	0.418 ± 0.186	3.63 ± 0.22	0.394 ± 0.037
4	Simferopol-4	7	1.347 ± 0.093	0.383 ± 0.085	5.14 ± 0.28	0.265 ± 0.040
5	Simferopol-5	7	1.620 ± 0.155	0.258 ± 0.050	5.76 ± 0.29	0.177 ± 0.041
	Total	**13**	**1.518 ± 0.290**	**0.323 ± 0.116**	**6.55 ± 0.28**	**0.496 ± 0.022**
			Southern Crimean Coast			
6	Koktebel	8	1.833 ± 0.172	0.200 ± 0.048	6.60 ± 0.41	0.176 ± 0.051
7	Simeiz-1	10	1.874 ± 0.116	0.246 ± 0.032	8.00 ± 0.46	0.200 ± 0.046
8	Simeiz-2	6	1.141 ± 0.248	0.421 ± 0.161	3.98 ± 0.26	0.336 ± 0.044
9	Cape Aiya	5	0.706 ± 0.293	0.688 ± 0.375	2.88 ± 0.23	0.424 ± 0.046
10	Balaklava	8	1.267 ± 0.245	0.471 ± 0.191	4.81 ± 0.44	0.399 ± 0.055
11	Laspi Pass	5	1.051 ± 0.096	0.473 ± 0.141	3.61 ± 0.24	0.277 ± 0.047
12	Ponizovka-1	6	1.204 ± 0.158	0.451 ± 0.131	4.28 ± 0.34	0.286 ± 0.057
13	Ponizovka-2	6	1.319 ± 0.101	0.377 ± 0.071	4.66 ± 0.27	0.223 ± 0.045
14	Cape Uzun	5	0.914 ± 1.095	0.583 ± 0.695	2.96 ± 0.33	0.409 ± 0.066
15	Mt. Koshka	9	1.697 ± 0.104	0.273 ± 0.062	6.66 ± 0.47	0.260 ± 0.052
	Total	**11**	**1.517 ± 0.042**	**0.350 ± 0.092**	**6.82 ± 0.19**	**0.380 ± 0.017**
			Steppe Crimea (without Kerch Peninsula)			
16	Pribrezhnoe-1 Station	8	1.282 ± 0.132	0.471 ± 0.148	5.18 ± 0.43	0.353 ± 0.054
17	Pribrezhnoe-2 Station	9	1.713 ± 0.192	0.242 ± 0.057	6.71 ± 0.26	0.254 ± 0.029
18	Pribrezhnoe-3 Station	7	1.269 ± 0.116	0.441 ± 0.108	4.94 ± 0.33	0.294 ± 0.047
19	Klyuchi-1	5	1.195 ± 0.196	0.391 ± 0.131	3.78 ± 0.31	0.245 ± 0.062
20	Klyuchi-2	8	1.110 ± 0.306	0.427 ± 0.199	4.27 ± 0.27	0.466 ± 0.033
21	Nikolaevka	7	1.171 ± 0.224	0.469 ± 0.169	4.41 ± 0.31	0.370 ± 0.044
22	Yevpatoria	6	1.186 ± 0.219	0.416 ± 0.135	4.17 ± 0.23	0.305 ± 0.039
23	Fontany	6	0.993 ± 0.257	0.511 ± 0.209	3.70 ± 0.21	0.384 ± 0.035
24	Krasnogvardeiskoe	9	1.443 ± 0.073	0.360 ± 0.093	5.96 ± 0.28	0.338 ± 0.032
	Total	**10**	**1.533 ± 0.029**	**0.310 ± 0.088**	**6.49 ± 0.13**	**0.351 ± 0.013**
			Kerch Peninsula			
25	Bagerovo	8	1.021 ± 0.423	0.456 ± 0.264	3.66 ± 0.30	0.543 ± 0.037
26	Zolotoe	2	0.668 ± 0.018	0.525 ± 0.643	1.97 ± 0.02	0.013 ± 0.009
27	Kerch	3	0.437 ± 0.455	0.809 ± 0.527	1.89 ± 0.19	0.370 ± 0.064
28	Mt. Skala	7	0.965 ± 0.310	0.528 ± 0.253	3.73 ± 0.28	0.468 ± 0.040
	Total	**9**	**0.884 ± 0.462**	**0.508 ± 0.293**	**3.52 ± 0.19**	**0.609 ± 0.021**

Table 3. Results of two-way ANOVA for phenetic variation in Crimean populations of *H. albescens* snails

Source of variation	Sum of squared deviations, *SS*	Number of degrees of freedom, *df*	Mean square, *MS*	Expected mean square, *E*(*MS*)
Between regions	60.783	3	20.261	0.020
Between populations within a region	110.699	24	4.612	0.039
Intrapopulation	925.735	3187	0.290	0.290
Total	1097.216	3214	25.164	0.349

morphs was found in Kerch samples: 95.8% of snails were of morph 12345 or 1(23)45, with the latter being prevalent and three to four times as frequent as in other regions of the Crimea (Table 1).

Quantitative analysis of phenetic diversity provides data not only on the number of different morphs but also on their frequency distribution. The levels of phenetic diversity (expressed in the average number of morphs and the proportion of rare morphs, according to Zhivotovsky) in individual populations and their groups and respective Shannon and Simpson indices are shown in Table 2. At the population level, the lowest diversity was recorded in samples from Kerch ($\mu = 1.89$) and Zolotoe ($\mu = 1.97$), both on the Kerch Peninsula; and the highest diversity ($\mu = 8.00$), in the sample from Simeiz (the southern Crimean coast). In population groups, phenetic diversity reached the highest average level in samples from the southern Crimean coast ($\mu = 6.82 \pm 0.19$), was slightly lower in populations from Simferopol and the steppe Crimea (6.55 ± 0.28 and 6.49 ± 0.13, respectively), and dropped almost by half in samples from the Kerch Peninsula ($\mu = 3.52 \pm 0.19$). Estimations of phenetic diversity based on the Shannon and Simpson indices generally comply with the above pattern. Moreover, the permutation test confirmed that the four regional population groups of *H. albescens* differ significantly in parameters of phenetic diversity ($p_{\text{perm}} < 0.05$ in all cases). The only exception is the proportion of rare morphs, which proved to be approximately equal in populations from different areas of the Crimea (Table 2).

Table 3 shows the results of two-way hierarchical ANOVA for the level of phenetic differentiation between the regional population groups and between populations of *H. albescens* within each region. In general, interpopulation differentiation with respect to the frequencies of different morphs is relatively high, reaching almost 17% ($P_{PT} = 0.1673$; $p = 0.01$). On the other hand, the regional groups are more similar to each other ($P_{RT} = 0.0563$; $p = 0.01$) than individual populations within the region ($P_{PR} = 0.1177$; $p = 0.01$).

Data on the total phenetic variation expressed by different metrics (the number of recorded morphs and the Simpson and Shannon indices for the 28 populations of *H. albescens*) was partitioned into separate components. The possibility of using these metrics in tasks of diversity partitioning into hierarchical components was shown by Lande (1996). The results are shown in Fig. 2. It can be seen that variation between populations accounts for more than 50% of the total variation in the number of morphs (Fig. 2), with contributions of intra- and interregional variation to this component being almost equal (26.43% and 24.29%, respectively). In cases of Simpson and Shannon indices, the interpopulation component of variation is smaller (14.56% and 22.87%, respectively); almost one third of it is accounted for by interregional variation, and two-thirds, by variation between populations within the regions. With any of the three metrics, however, estimates of both inter- and intraregional components of variation in phenetic diversity are highly significant ($p < 0.05$ in all cases).

Despite variance in qualitative and quantitative parameters of phenetic structure, individual populations display certain specific features depending on their geographic location.

The results of discrimination analysis show that the accuracy of attributing *H. albescens* populations to a particular group on the basis of phene frequencies is 96.4%; i.e., an error can be made in one out of 28 cases (thus, one of the nine populations from the steppe Crimea was erroneously included in the group from the southern Crimean coast). The greatest contributions to discrimination of populations along the canonical axes are made by the frequencies of morphs 12045 and 10045 (canonical axis 1) and 1(23)45 (canonical axis 2).

Thus, the distribution of *H. albescens* populations in the plane of the first two canonical axes is as shown in Fig. 3. Variation in their phenetic structure shows two major trends: the first is that the population frequency of morphs 12045 and 10045 increases in the direction from the southern Crimean coast to the city of Simferopol, and the second indicates a similar increase in the frequency of morph 1(23)45 in the direction from the southern coast to the Kerch Peninsula.

On the other hand, Leonov (2005) noted that there is a connection between climatic conditions in habitats of *H. albescens* populations and the type of their phenetic structure. To study the form of such connections in more detail, we used canonical correlation analysis with two sets of initial data: (1) a matrix of transformed morph frequencies in the populations studied and (2) a matrix of data on climatic conditions
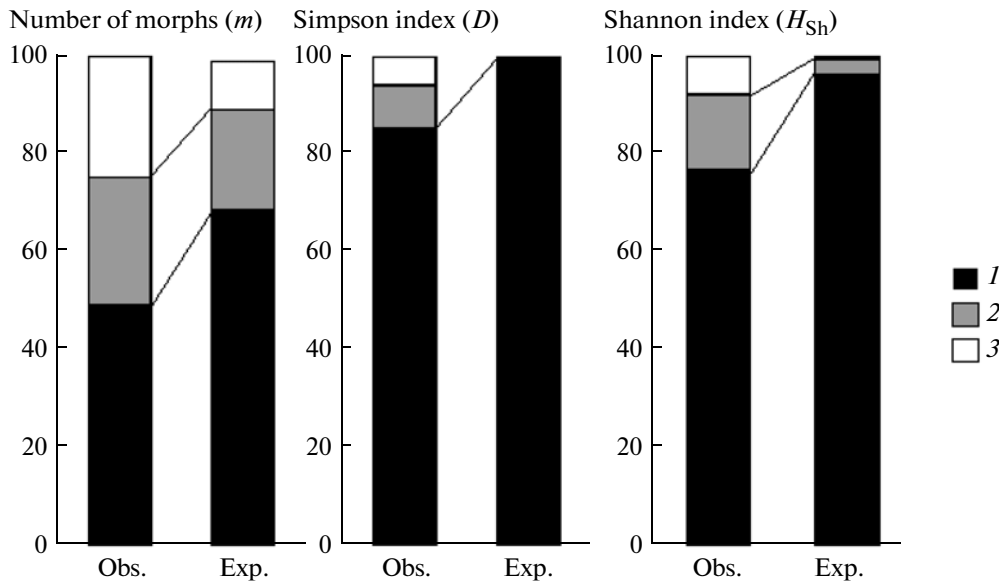
Fig. 2. Partitioning of the phenetic diversity of *H. albescens* populations (estimated from the number of morphs and the Simpson and Shannon indices) into individual components (%): (*1*) intrapopulation diversity, (*2*) interpopulation diversity within regions, and (*3*) diversity between regions. Actual values (Obs.) and values calculated from 1000 iterations (Exp.) are shown.
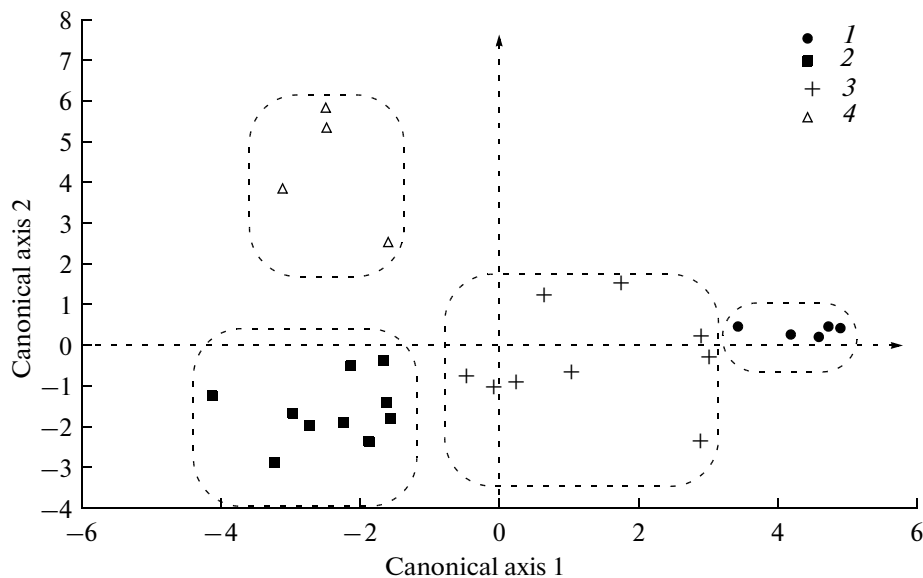

Fig. 3. Position of the centroids of Crimean *H. albescens* populations in the plane of the first two canonical axes of factor discriminant analysis: (*1*) Simferopol, (*2*) southern Crimean coast, (*3*) steppe Crimea, and (*4*) Kerch Peninsula.

in their habitats. The first two canonical axes were most important in this case. Table 4 shows the loadings of phenetic characters and climatic parameters on these axes. It can be seen that the greatest loadings on the first canonical axis are those of the frequencies of morphs 12345, 10345, 10305 (positive) and of morph 1(23)45 (negative). Thus, this set includes the shell banding pattern morphs that are most widespread in *H. albescens*. Among climatic parameters, the greatest loading on the first canonical axis was that of two cli-

mate-forming parameters: the long-term average temperature of July and annual precipitation.

The greatest loading on the second canonical axis was that of morphs 12045 and 10045, and, among climatic parameters, of those characterizing the mildness of winter (the number of frostless days per year and long-term average temperature of January). The mildness of winter was already noted as one of the most important climatic factors that have an effect on the variation pattern of metric shell parameters among

Table 4. Results of analysis of canonical correlations between phenetic variation in Crimean *H. albescens* populations and climatic parameters

Canonical axis 1 ($\tau = 0.858$; $p < 0.001$)			
Morph		Climatic parameters	
"12345"	+0.506	Temperature of July	+0.571
"1(23)45"	−0.631	Annual precipitation	+0.504
"10345"	+0.584		
"10305"	+0.636		
Canonical axi 2 ($\tau = 0.875$; $p < 0.001$)			
Morph		Climatic parameters	
"12045"	−0.691	Number of frost-free days	+0.504
"10045"	−0.779	Temperature of January	+0.446

different Crimean populations of another mollusk species, *Brephulopsis cylindrica* (Kramarenko, 1997).

In addition, significant correlations with the long-term average temperature of July were revealed for the population frequencies of shells with fused bands and of shells without bands, the former correlation being negative ($r = -0.390$, $p = 0.040$; $n = 28$), and the latter positive ($r = 0.403$, $p = 0.033$; $n = 28$). These results show that the proportion of dark-colored shells tends to increase in relatively cool habitats, while the proportion of lightly colored shells is higher in warmer habitats, as was observed earlier in mollusks of the genus *Cepaea* (Jones et al., 1977).

However, considerable variance in phenetic structure among *H. albescens* populations living under similar climatic conditions may be evidence that random factors, such as the founder effect or the bottleneck effect, also play a considerable role played in the formation of shell banding polymorphism. This is confirmed by the extremely low estimates of the effective population size calculated for this species: $N_e = 17-39$ (Kramarenko, 2009).

Thus, specific types of shell banding pattern polymorphism have been found in populations of the *H. albescens* snail from different areas of the Crimea, with the differences between them concerning mainly the number of shell morphs rather than their occurrence frequency. Trends in the distribution of morphs in the Crimea, especially the connection between their occurrence frequencies and climatic parameters, may be evidence that this form of polymorphism is of adaptive significance. However, among the microevolutionary processes determining the type and degree of polymorphism in *H. albescens* populations, a considerable role is also played by stochastic genetic phenomena, because the species exists in semi-isolated colonies with low effective abundance and high risk of local extinction, i.e., under conditions corresponding to the metapopulation model.

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