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PATTERNS OF SPATIO-TEMPORAL VARIATION IN LAND SNAILS: A MULTI-SCALE APPROACH

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ABSTRACT: Mechanisms which govern patterns of intra-specific vatiation in land snails were traced within areas of different size, using *Brephulopsis cylindrica* (Menke), *Chondrula tridens* (O. F. Müller), *Xeropicta derbentina* (Krynicki), *X. krynickii* (Krynicki), *Cepaea vindobonensis* (Férussac) and *Helix albescens* Rossmässler as examples. Morphometric shell variation, colour and banding pattern polymorphism as well as genetic polymorphism (allozymes and RAPD markers) were studied. The results and literature data were analysed in an attempt to link patterns to processes, with the following conclusions. Formation of patterns of intra-specific variation (initial processes of microevolution) takes different course at three different spatial scales. At micro-geographical scale the dominant role is played by eco-demographic characteristics of the species in the context of fluctuating environmental factors. At meso-geographical scale a special part is played by stochastic population-genetic processes. At macro-geographical scale more or less distinct clinal patterns are associated with basic macroclimatic indices, while the stochastic processes tend to lose importance. The basic factors of microevolutionary process which act at different spatial scales result from processes which progress over different lengths of time: micro-geographical variation patterns reflect processes which are in progress at the moment; meso-geographical variation is to a larger extent determined by processes which occurred in historic past; macro-geographical variation reflects processes which coincided with formation of the respective landscapes or climate zones.

KEY WORDS: intra-specific vatiation, *Brephulopsis cylindrica, Chondrula tridens*, *Xeropicta*, *Cepaea vindobonensis*, *Helix albescens*, spatial scale, microevolution, multi-scale approach, morphometric variation, colour polymorphism, genetic polymorphism

INTRODUCTION

The relatively easy collecting and field observations, as well as laboratory experiments, have made land snail variation a popular object of studies. Land snails display a very easily observable intra- and inter-population variation of both qualitative and quantitative characters of their shells and soft parts, and small mobility; their mostly bi-parental reproduction is combined with hermaphroditic reproductive system. In their case it is relatively easy to collect large samples, since even after death the shells remain, and to keep and breed them in laboratory (CLARKE et al. 1978, CAIN 1983, THOMAZ et al. 1996).

Variation patterns depend not only on genetic factors (mutations, gene flow, drift and natural selection), but also on the climatic, faunal and geobotanical history of the habitats. It is however difficult to discern between the results of microevolutionary processes which are in progress at the moment and those which have occurred in the recent past. One of the most reliable ways of solving the problem is comparison of spatial patterns of variation of different kinds (anatomical-morphological, biochemical, molecular etc.), which are to different extent susceptible to various genetic and demographic processes (MOUSSEAU et al. 2000, SCHOVILLE et al. 2012).

The concept of distribution pattern, either of taxa or of genotypes, is necessarily associated with the concept of scale. Moreover, it is also necessary to define the scale in order to achieve an adequate estimate of variation (LEVIN 1992, CONOVER et al.

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2006, Cushman & Landguth 2010, Schoville et al. 2012). Due to the fact that evolutionary forces act at different (and species-specific) scales, a multi-scale approach to the analysis of the populations' genetic and phenotypic structure is necessary.

Two scales are most often considered during sampling and subsequent analysis of the resulting data: micro-geographical (fine-scale, small-scale; Selander & Kaufman 1975, Colgan 1981, Baur 1988, Tatarenkov & Johannesson 1994, Fletcher 1995) and macro-geographical (large-scale; Groue 1980, De Wolf et al. 1988, 1998, Däumer et al. 2012). However, no sharp dividing line between the two has yet been proposed, which leads to various authors using completely different scales, even when dealing with the same group of animals.

In the analysed literature (around 150 papers), dealing with numerous kinds of intra-specific variation in land snails (morphometric variation, colour and banding pattern polymorphism or genetic polymoprhism), I found different scales adopted by different authors in their sampling procedures. There is a considerable prevalence of research on variation of shell size and form at macro-geographical scale on the one hand, and a deficit of studies dealing with formation of intra-population variation patterns at micro- and meso-geographical scales on the other.

Moreover, the proportion of studies which use two or more scales of spatial organisation of sampling and data analysis at the same time is very small. Likewise, the percentage of papers using hierarchical (nested) method of data collecting and processing to estimate the components of variation at various levels of the scales applied is very small. Overall, not more than 10% of the published papers apply both multi-scale approach to sampling and hierarchical procedures to estimate the components of variation, which are defined by different scales of investigation. Exceptions are publications dealing with analysis of genetic variation at intra- and inter-population levels, which obviously results from the wide application of the "hierarchical AMOVA" method (Excoffier et al. 1992) with the use of corresponding software. There is also a deficit of studies which at the same time consider expressions of various kinds of intra-specific variation (genetic and morphometric, or genetic and variation in shell colour and banding pattern) in land snails at intra- and inter-population levels.

On the other hand, processes which take place at various spatial scales should be considered through different lengths of time, hence the resulting patterns of intra-specific variation should be regarded as spatio-temporal. At present analyses of chronological variation of shell size and form in land snails include periods of time ranging from one year (Cook & O'Donald 1971, Kramarenko 2006) to a few tens of years (Pettitt 1977, Cook & Pettitt 1979, Cain & Cook 1989).

Analyses of chronological patterns of variation in land snail populations with regard to shell banding polymorphism also testify to the existence of various scales; the patterns differ significantly depending on the scale. Over short periods (10–15 years) formation of random patterns is observed, and changes in morph frequencies are unpredictable (Wolda 1969, Cowie 1992, Ożgo & Bogucki 2011). In long-term analyses (40–60 years) significant decrease or increase in the frequencies of some morphs occurs (Cameron & Pokryszko 2008, Silvertown et al. 2011, Ożgo & Schilthuizen 2012, Cameron et al. 2013). Thus chronological patterns of variation of terrestrial snails also display a scale-dependent variation.

The main objective of my study was analysis of mechanisms of formation of spatio-temporal patterns of intra-specific (intra- and inter-population) morphometric and genetic variation of land snails at various spatial and temporal scales.

MATERIAL AND METHODS

MORPHOMETRIC ANALYSIS

Morphometric analysis used four species which are widespread in Ukraine and adjacent countries – *Chondrula tridens* (O. F. Müller, 1774), *Brephulopsis cylindrica* (Menke, 1828), *Cepaea vindobonensis* (Férussac, 1821) and *Helix albescens* Rossmässler, 1839. Two shell parameters were measured for each of them: for *B. cylindrica* and *Ch. tridens* shell height (HS) and greatest shell width (WS), and two indices of shell proportion were calculated: FS1 = HS/WS and FS2 = lnHS/lnWS. In the case of the two helicids shell diameter (DS) and shell height (HS) were used, as well as proportion index (FS = HS/DS). All the measurements were taken with slide calliper (accuracy 0.05 mm) according to the commonly adopted method (Sverlova et al. 2006).

The main object of the study was morphometric shell variation within and between populations of the selected snail species. The analysis was based on the estimation of variance components of the dependent variable (morphometric character), which were obtained using the general linear model (GLM) (Scheffé 1999). Besides the estimate of variance components of the dependent variable (in order to compare variation of different characters), the estimates of variance components were transformed into relative values (M_{ST}), which expressed the proportional effect of the inde-

pendent variable on the variation of the dependent variable (fixed effects model; KRAMARENKO 2009a). Jackknifing was used for confidence interval of these values (EFRON 1988). The presence and character of the structured morphometric variation of the studied species were estimated using Moran's coefficient of spatial autocorrelation (I_M) for different distances.

My own materials and literature data (mean population values for the basic shell measurements) were used in the analysis of macro-geographical variation of shell characters. The analysis included 70 populations of *B. cylindrica* and 64 populations of *H. albescens* from Crimea and southern Ukraine, 82 populations of *C. vindobonensis* from Ukraine and the Russian Federation, 40 populations of *Ch. tridens* from Ukraine and Moldova. The location of sampling sites is shown in Fig. 1.

Geographical coordinates were determined for each site (GPS format). Besides, four hydro-climatic indices were used – mean monthly temperature of January (T1), mean monthly temperature of July (T7), duration of period with temperatures exceeding 10°C (D10) and annual total precipitation (ATP). All the data were obtained from the Geographic Encyclopedia of Ukraine (MARYNYCH 1989–1993).

Methods of parametric and non-parametric statistics as well as geostatistics were used in the analysis. Calculations were done with SAM v. 4.0 (RANGEL et al. 2010), PAST v. 2.14 (HUMMER et al. 2001) and ROOKCASE (SAWADA 1999) software.

ANALYSIS OF SHELL COLOUR AND BANDING PATTERN VARIATION

The analysis of shell colour and banding pattern included four species which are widespread in Ukraine and adjacent countries – *Xeropicta derbentina* (Krynicki, 1836), *X. krynickii* (Krynicki, 1833), *H. albescens* and *C. vindobonensis*.

Three banding variants were observed in *X. derbentina* and *X. krynickii*: a) unbanded; b) pale, with poorly pigmented bands; c) dark, with well-pigmented bands. The basic characters were: presence (B)/absence of bands (UB) and presence (P)/absence of pigment in bands (UP). Absolute numbers of specimens with each type of banding were scored for each population, and the relative frequencies of UB and UP types were calculated.

Two types of polymorphism were considered for *C. vindobonensis* and *H. albescens*. The first one (*C. vindobonensis*) involved shell colour and presence of pigment in bands. Two morphs were distinguished – common (yellowish shell with brown or black bands; black-banded morph) and FB (greenish shell with

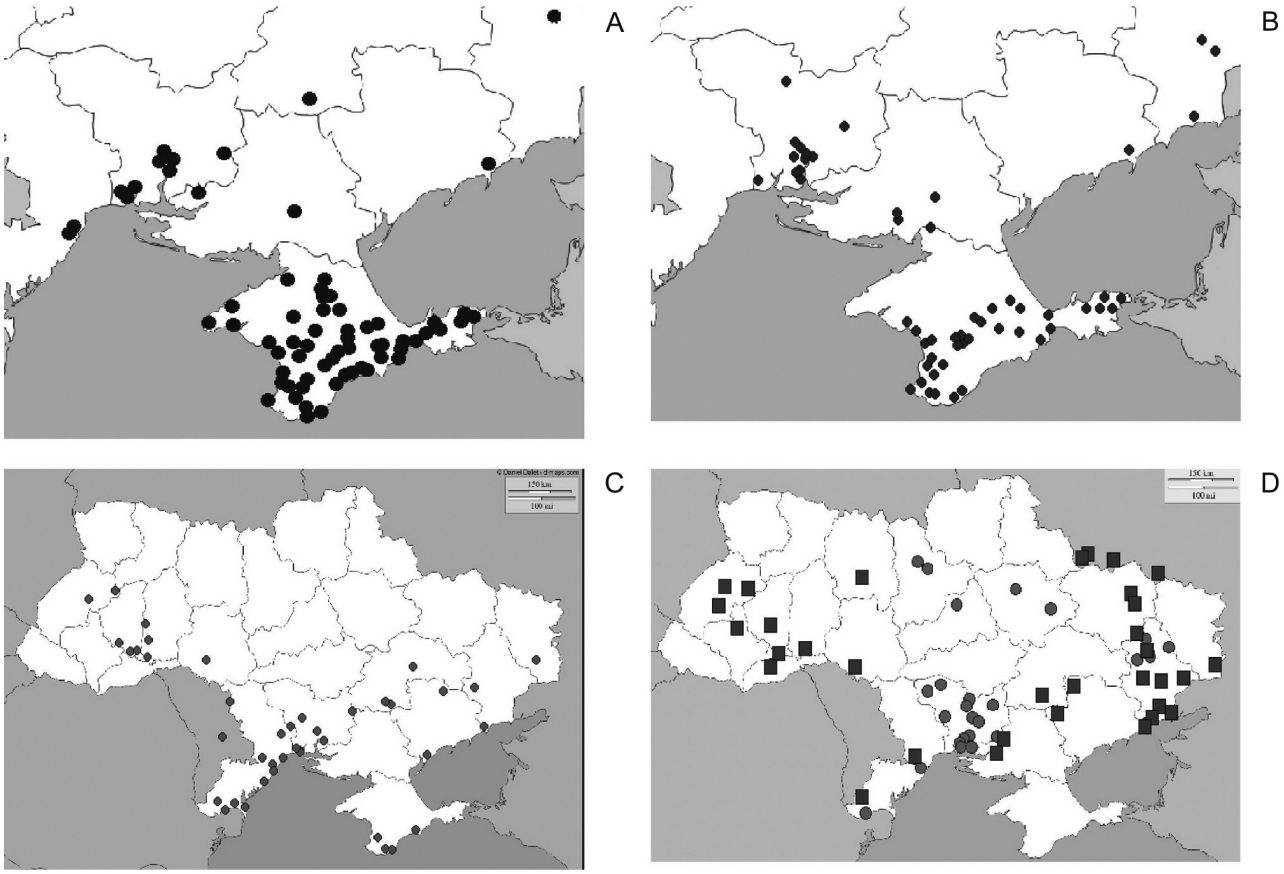

Fig. 1. Location of sampling sites of snails for analysis of macro-geographical variation: A – *B. cylindrica*; B – *H. albescens*; C – *Ch. tridens*; D – *C. vindobonensis* (circles – own data; squares – literature data)

non-pigmented bands; faint-banded morph). The second, the banding polymorphism (*C. vindobonensis* and *H. albescens*), was assessed according to the commonly accepted system (CAIN & SHEPPARD 1950). The bands were assigned numbers from 1 to 5, counting from the suture between the penultimate and body whorls toward the umbilicus. When a band (or bands) was absent it was assigned 0 in the banding formula. When two bands were fused, their numbers in the formula were listed in brackets. Morph frequencies were calculated for each population. These values were transformed using Fisher's arc-sin transformation to eliminate the effect of sample size.

The studies at micro-geographical scale focussed on the intra-population phenetic variation, whose point and interval estimates were based on methods described by SHITIKOV et al. (2008). In short, the procedure in its concept is close to the ANOVA algorithm, while the index of phenetic differentiation (P_{ST}) is the proportion of variation (between sites or populations) in the sum variation (between sites or populations, respectively) with respect to the frequencies of phenetic characters.

The variation within samples (or their groups) was estimated through simple counting of the number of observed shell banding morphs (m). Besides, indices of population diversity – mean number of morphs (μ) and proportion of rare morphs (h_{μ}), were calculated using ZHIVOTOVSKY's (1991) formulas, as well as Shannon's (H_{SH}) and Simpson's (D) indices.

Re-sampling procedure (permutation method) based on 10,000 permutations (SHITIKOV et al. 2008) with software EcoSim v.7.72 (GOTELLI & ENTSMINGER 2001) was used to compare diversity indices of the populations of *H. albescens* between the regions.

Indices of intra-population diversity (mean number of morphs and proportion of rare morphs) and morph frequencies (arcsine transformed), or frequencies of groups of morphs, were compared using non-parametric statistics (Kruskal-Wallis ANOVA).

Phenetic differentiation among populations at macro-geographical scale and also among groups of populations, based on the regional principle, was estimated using algorithm of two-way nested ANOVA for qualitative characters (KRAMARENKO 2006). The level of significance of population estimates (P_{RT}, P_{PR}, P_{PT}) was calculated with permutation test (SHITIKOV et al. 2008) using software GenAlEx v.6.0 (PEAKALL & SMOUSE 2006), based on 999 permutations.

A more detailed analysis of the distribution of variation of phenetic structure of populations (or their groups) was done with software PARTITION v. 2.0 (VEECH & CRIST 2007), which makes it possible to use different means of diversity assessment, namely number of morphs, Simpson's and Shannon's indices. This software divides the sum variation into its components and also, using randomisation approach, estimates the likelihood of random obtaining of the respective values, and thus can be used for assessment of the level of statistical significance of the results (VEECH et al. 2002).

ANALYSIS OF GENETIC POLYMORPHISM

Analysis of genetic polymorphism included *B. cylindrica* from nine populations from Crimea and southern Ukraine (Table 1). Two genetic systems were studied – allozyme variation (300 specimens from 12 samples) and variation of RAPD markers (130 specimens from 8 samples).

The allozyme analysis was carried out in the laboratory of molecular genetics and toxicology of the Belgorod State National Research University (Belgorod, Russian Federation), using methods described by SNEGIN (2011a) and SNEGIN & SYCHOV (2011). Four allozyme systems with six loci were used as genetic markers: non-specific esterases Est3 (monomer, four alleles) and Est4 (monomer, two alleles), superoxidismutase Sod2 (monomer, three alleles), malate dehydrogenases Mdh1 (dimer, two al-

Table 1. Numbers of specimens of *B. cylindrica* used in analysis of genetic polymorphism

No	Population	Region, locality	Number of specimens	
			allozymes	RAPD markers
1	Dubky-1	Mykolaiv region, Mykolaiv, Park Dubky	25	15
2	Dubky-2	Mykolaiv region, Mykolaiv, Park Dubky	25	–
3	Neftebaza-1	Mykolaiv region, Mykolaiv, Kosmonavtov Street	25	15
4	Neftebaza-2	Mykolaiv region, Mykolaiv, Kosmonavtov Street	25	–
5	Park Pobedy-1	Mykolaiv region, Mykolaiv, Park Pobedy	25	15
6	Park Pobedy-2	Mykolaiv region, Mykolaiv, Park Pobedy	25	–
7	Kosmos	Mykolaiv region, Mykolaiv, cinema Kosmos	25	15
8	Morekhodnaya	Mykolaiv region, Mykolaiv, Morekhodnaya Street	25	15
9	Mira	Mykolaiv region, Mykolaiv, Mira Street	25	15
10	Ochakov	Mykolaiv region, Ochakov	25	20
11	Vilino	Crimea, Vilino	25	20
12	Sevastopol	Crimea, Sevastopol	25	–

leles) and Mdh2 (dimer, three alleles). The following population genetics indices were calculated for each sample based on the genotype frequencies: observed (Ho) and expected (He) heterozygosity, fixation index (Fis) and effective number of alleles (Ae).

Inter-population differences were estimated with two methods. The first (assignment test) estimates the correctness of assignment of each specimen to its own or another sample based on the empirical distribution of frequencies of multi-locus genotypes (PAETKAU et al. 2004). The second (AMOVA – analysis of molecular variance) gives the estimates of genetic differentiation (F_{ST} or Φ_{ST}) based on the separation of matrices of genetic distances between specimens into separate components analogously to Fischer's ANOVA (EXCOFFIER et al. 1992). The level of significance of population estimates was assessed with re-sampling procedure (999 permutations). Gene flow for allozymic loci was estimated with WRIGHT's (1969) formula:

$$Nm = \frac{1}{4} \cdot \left(\frac{1}{F_{ST}} - 1 \right)$$

For genetic markers with dominant inheritance, the formula was slightly different (MCDERMOTT & MCDONALD 1993):

$$Nm = \frac{1}{2} \cdot \left(\frac{1}{F_{ST}} - 1 \right)$$

Spatial ordination of samples was done using principal coordinate analysis (PCoA) based on matrices of Nei's genetic distances. The degree of compatibility between matrices of genetic distances and geographical distances between the samples was estimated with the Mantel test with 999 permutations.

The analysis of polymorphism of RAPD markers was carried out in the laboratory of molecular genetics of the O. V. Kvasnitsky Pig-breeding Institute (National Academy of Agrarian Sciences of Ukraine). DNA was extracted using phenol-chloroform method and a standard commercial kit for nucleic acid extraction from biological samples produced by the Institute of Epidemiology (AmpliSens®, Moscow, Russian Federation). The RAPD-PCR used primers OPA-01 (5'CAGGCCCTTC3') and OPA-04 (5'AATCGGGCTG-3') (Operon Technologies, USA). PCR amplification used commercial kit «Tapotili» (GENETIKA, Scientific Centre of Russian Federation, Research Institute for Genetics and Selection of Industrial Microorganisms, Moscow, Russian Federation) in 25 µl reaction mixture which contained 2.5 µl of buffer, 100 pm of primer (1 µl per reaction), 1.25 unit of polymerase (0.1 µl) and 10–12 ng of genomic DNA per reaction. Amplification using RAPD primers included 45 cycles according to the scheme: initial DNA denaturation: 95°C – 1 min, annealing: 36°C – 2 min, synthesis: 72°C – 2 min, denaturation: 94°C – 1 min, final extension in the final, 45th, cycle: 72°C – 7 min. Amplification products were separated in 2% agarose gel and stained with ethidium bromide. Visualisation of DNA fingerprints was done on a UV-transilluminator; the DNA fingerprints were photographed with digital camera Canon. The resulting matrix with binary data was processed with standard methods of analysis for data from dominant molecular markers. All calculations were done with software GenAIEx v. 6.0 (PEAKALL & SMOUSE 2006) and PopGene v. 1.31 (YEH et al. 1999).

Abbreviations used in Tables and Figures: DS – shell diameter, FS – shell form, HS – shell height, WS – shell width, CI – confidence interval. Abbreviations used for different colour morphs: UB – unbanded *X. krynickii* and *X. derbentina*, UP – unpigmented bands of *X. krynickii* and *X. derbentina*, FB – faint-banded *C. vindobonensis*.

VARIATION IN SHELL SIZE AND FORM

MICRO-GEOGRAPHICAL SCALE

Spatial variation

The results of analysis of processes of intra-population structuring in terrestrial snails (example: morphometric shell variation in *B. cylindrica*) in the absence of visible isolating barriers are presented below. Three local populations from the town of Mykolaiv (southern Ukraine) served as mode units. In each of those populations, each year in 2004–2006, 10 samples were taken along transects with 7 m intervals (KRAMARENKO 2009a).

Figures 2–4 present the mean values of morphometric characters of *B. cylindrica* from 10 sites in different populations during the three-year study. Notwithstanding the diverse character of the variation in the studied populations, several intra-population patterns can be distinguished. Pattern A consists in a random (chaotic) distribution of shell measurements, or indices, within individual sites along a spatial continuum. An example is the spatial arrangement of between-site variation of shell height in different populations. The pattern is characterised by the unpredictability of the behaviour of shell height in the next neighbouring locality: the shell may be higher or lower without obvious reasons and spatial

limits. Pattern B is characterised by the presence of a more or less pronounced clinal variation in shell measurements or indices. Such a pattern, for example, is characteristic of the between-site variation of shell width in the Dubky population (2004–2006), variation of FS1 in Dubky (2005), or shell width in the population Park Pobedy (2005). Pattern C shows the presence of a sharp boundary ("step") in shell measurements or proportions within the studied area. It is observed in the intra-population variation in FS1 in the Dubky population (2005–2006), as well as FS1 and FS2 in the population Park Pobedy (2004–2006). Combinations of these three patterns are also encountered. For example, for shell height in Park Pobedy (2004) in sites 1–6 there is a random component of intra-population variation while in sites 7–10 there is a distinct cline with a tendency to height decrease (Fig. 4). Besides, within a population two boundaries between groups of sites can be present, as for example for FS2 in the Neftebaza population in 2006 (Fig. 3).

Table 2 presents estimates of morphological differentiation (M_{ST}) for the morphometric characters in the populations of *B. cylindrica*. Overall, for shell height only once in nine cases (three populations and three-year investigation) was a significant intra-population variation observed – in 2004 in the population Neftebaza (15.29%) (Table 2). It resulted from considerable differences in shell size between samples from sites 1–4 and 5–10 in this population in the same year (Fig. 3). For the remaining shell measurements and indices, the intra-population variation was more pronounced (Table 2). For shell width the level of intra-population variation (considering only significant differences) ranged from 12.76% (Dubky population, 2004) to 29.75% (Neftebaza population, 2004). On average, the between-site component of variation was 16.00%, and discounting those sites which did not differ significantly, it ranged from zero to 18.90%.

Besides, the analysis of spatial structure of shell morphometric variation within the studied popula-

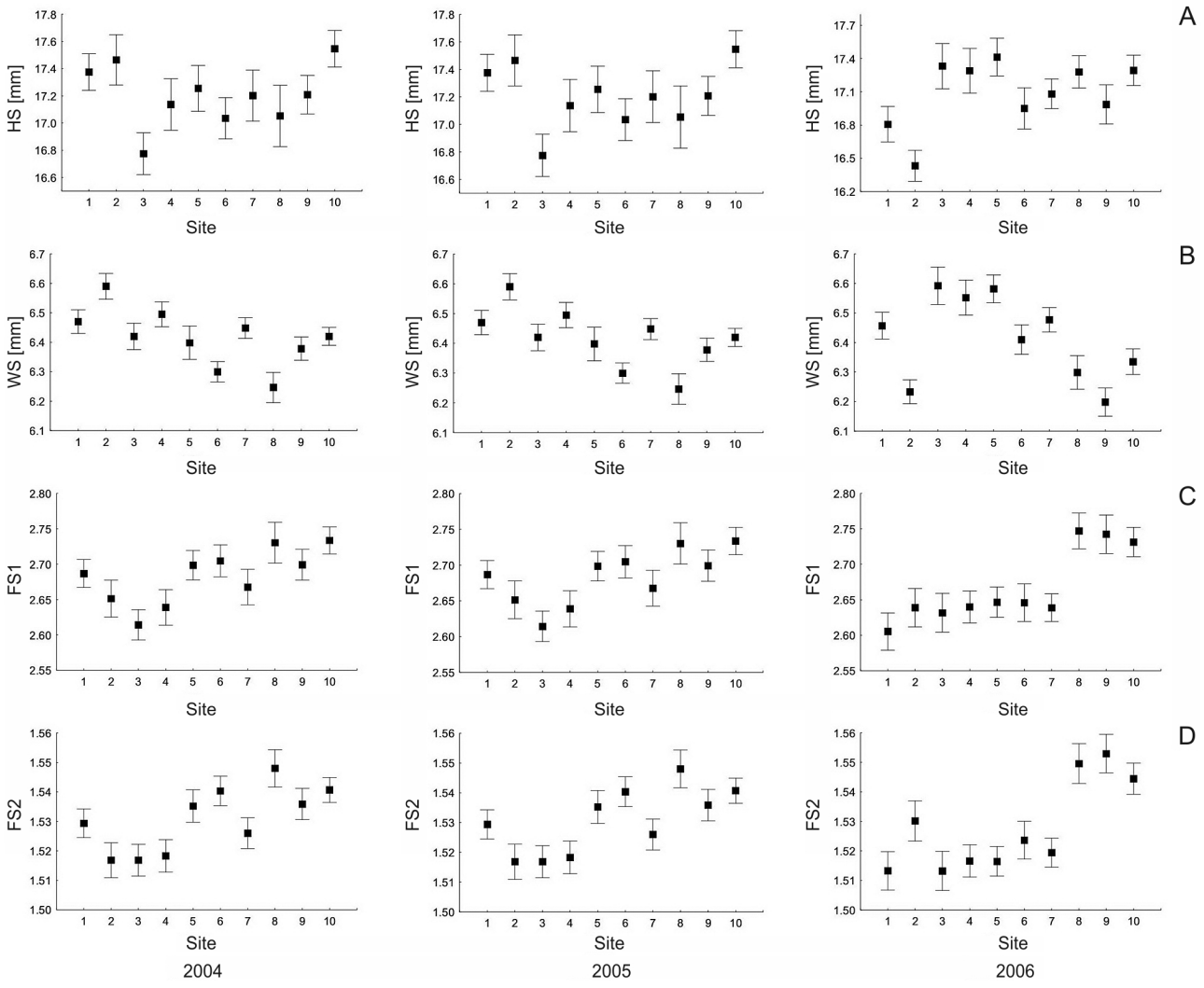

Fig. 2. Variation ($\overline{X} \pm SE$) of morphometric shell characters of *B. cylindrica* from population Dubky in 2004–2006: A – shell height; B – shell width; C – shell form 1; D – shell form 2

Table 2. Variance components of intra-population variation in shell characters (M_{ST}) in *B. cylindrica*. Values significantly higher than 0 indicated in bold

Year	Population	Shell character			
		HS	WS	FS1	FS2
2004	Dubky	0.0239±0.0294	**0.1276**±0.0625	0.0580±0.0328	**0.1007**±0.0327
	Park Pobedy	0.0108±0.0197	**0.1366**±0.0639	0.0302±0.0230	0.0703±0.0411
	Neftebaza	**0.1529**±0.0526	**0.2975**±0.0659	0	0.0436±0.0306
2005	Dubky	0.0956±0.0495	**0.1690**±0.0471	**0.0848**±0.0262	**0.1110**±0.0533
	Park Pobedy	0	**0.2027**±0.0663	**0.0929**±0.0347	**0.1591**±0.0471
	Neftebaza	0.0131±0.0272	0.0740±0.0519	0	0.0151±0.0192
2006	Dubky	0.0706±0.0557	**0.1954**±0.0542	**0.1071**±0.0409	**0.1578**±0.0499
	Park Pobedy	0.0012±0.0141	**0.1939**±0.0789	0.0857±0.0526	**0.1560**±0.0768
	Neftebaza	0	0.0435±0.0291	**0.0675**±0.0216	**0.0803**±0.0262
$\overline{X}$ ± SE		**0.0416**±0.0173	**0.1605**±0.0232	**0.0586**±0.0122	**0.0991**±0.0170
95% CI		[0.0146; 0.0832]	[0.1183; 0.2069]	[0.0332; 0.0796]	[0.0640; 0.1298]

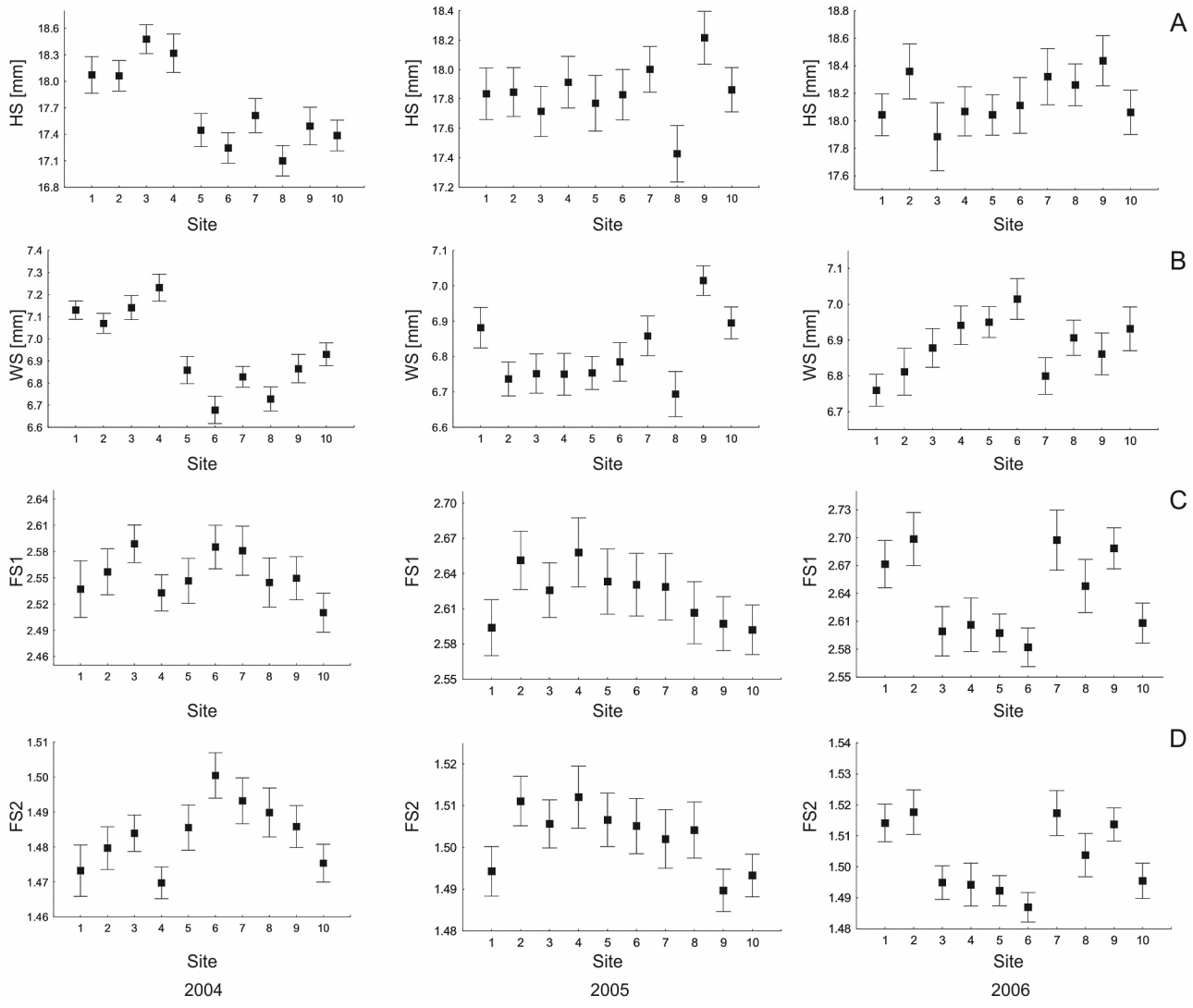

Fig. 3. Variation ($\overline{X}$ ± SE) of morphometric shell characters of *B. cylindrica* from population Neftebaza in 2004–2006: A – shell height; B – shell width; C – shell form 1; D – shell form 2

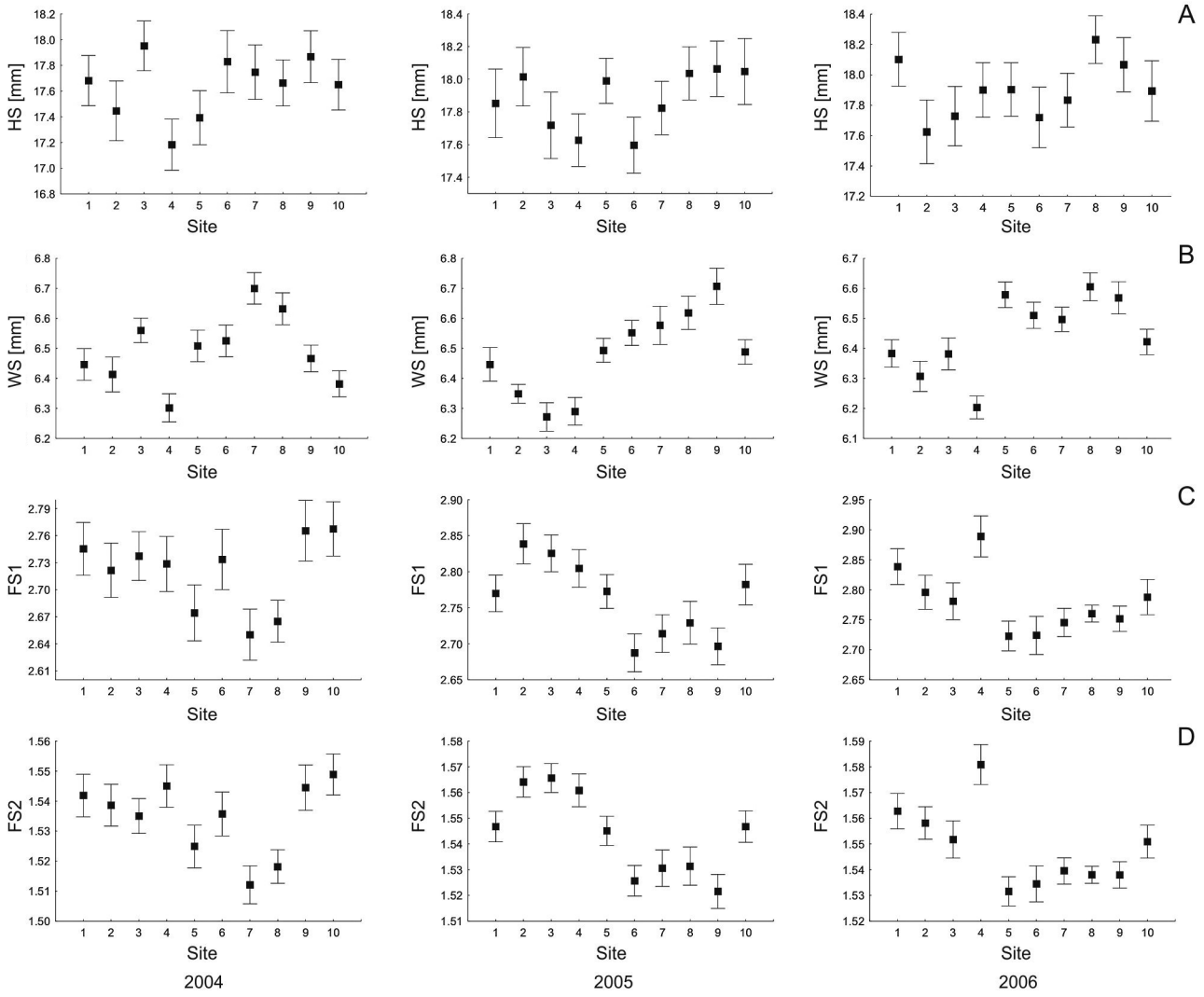

Fig. 4. Variation ($\overline{X}$ ± SE) of morphometric shell characters of *B. cylindrica* from population Park Pobedy in 2004–2006: A – shell height; B – shell width; C – shell form 1; D – shell form 2

tions shows that the clinal variation (pattern B) is the most frequent. The same is indicated by the form of correlograms for different spatial scales (Fig. 5). Out of the 36 significant estimates of Moran's autocorrelation coefficient, 13 were positive and 23 were negative. However, the distribution of positive and negative values of Moran's coefficient for different distances (7, 14, 21, 28 and 35 m) was distinctly disproportionate. Out of the 13 positive estimates, 10 were obtained for distances of 7 m, two for 14 m and one for 28 m. Among the 23 negative estimates, one was obtained for the distance of 7 m, one for 14 m, four for 21 m, six for 28 m and 11 for 35 m (Fig. 5). Thus, the positive spatial autocorrelation for morphometric shell variation of *B. cylindrica* obtains for closely located sites (distances 7–14 m), and, conversely, distinctly pronounced negative spatial autocorrelation – for remote sites (distances 28–35 m). Such a regularity of distribution of the values of coefficients of spatial autocorrelation testifies to clinal morphometric variation.

In order to assess to which extent the above regularities can be extrapolated to populations of other land snail species, and to estimate the role of isolating barriers (in the case of snails, e.g. roads), I studied the spatial pattern of intra-population variation of morphometric shell characters in another species from southern Ukraine – *C. vindobonensis* from the population in Park Dubky (Mykolaiv 2007). The park is composed of more or less uniform planted stands of oak, with few clumps of shrubs. The area where the samples were taken was a rectangle of ca. 800 × 400 m. The material was collected from 14 sites (Fig. 6) which were divided by buildings and asphalted roads into three parts, marked as A, B and C. This made it possible to estimate the indices of spatial variation for all the population (M_{ST}), between the three parts (M_{RT}), and within each part (M_{SR}).

Table 3 shows the estimates of morphometric variation for the population of *C vindobonensis*. Significant intra-population variation was observed

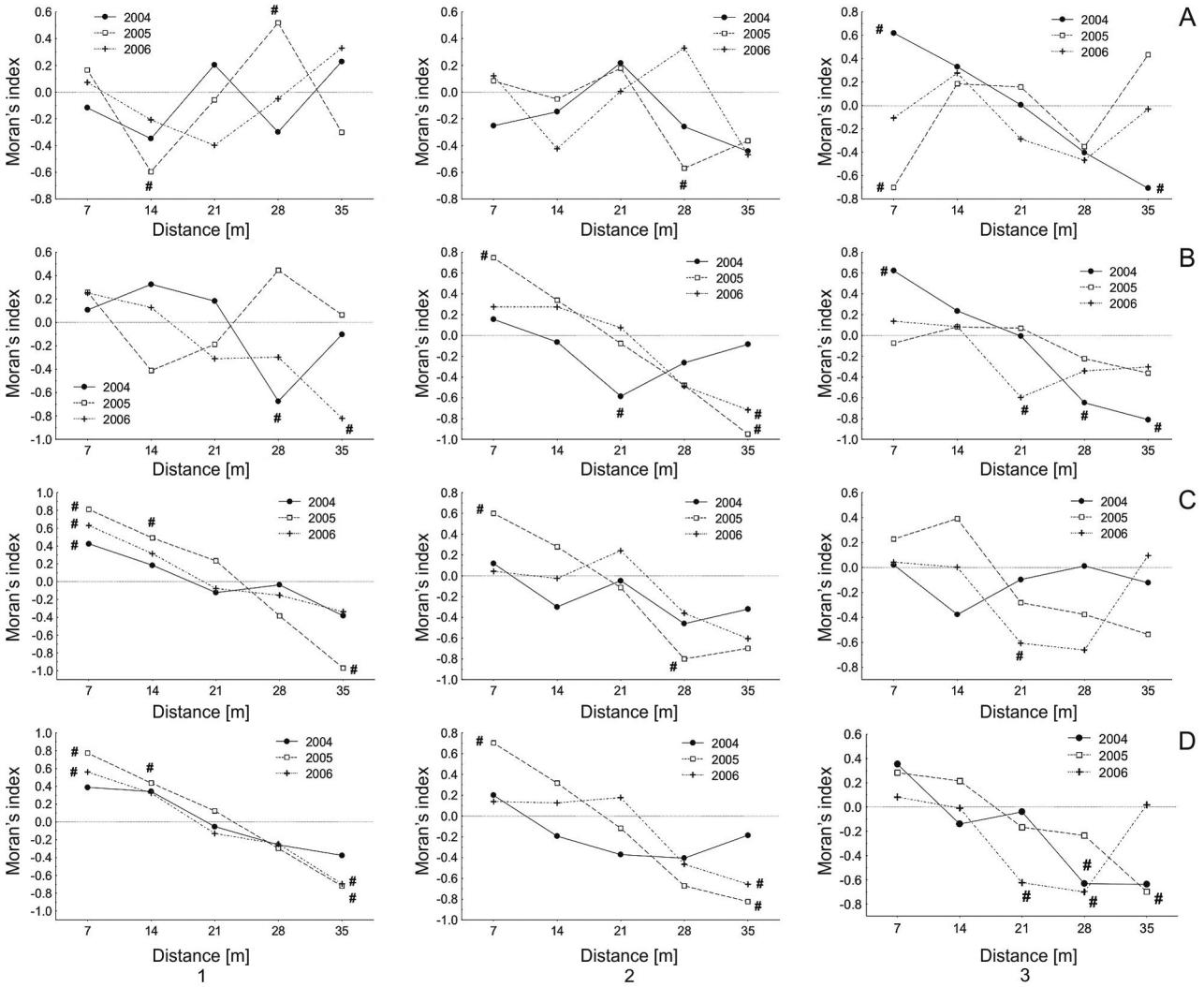

Fig. 5. Moran's index for morphometric shell characters of *B. cylindrica* from three populations (1 – Dubky, 2 – Park Pobedy, 3 – Neftebaza) in Mykolaiv during three years: A – shell height; B – shell width, C – shell form 1; D – shell form 2 (significant values of Moran's index indicated as #)

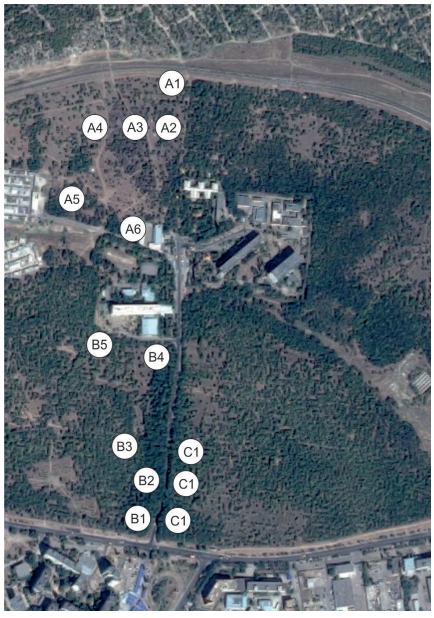

Fig. 6. Location of sampling sites of *C. vindobonensis* from population Dubky (Mykolaiv 2007)

Table 3. Variance components of intra-population variation in shell characters of *C. vindobonensis*. Values significantly higher than 0 indicated in bold

Shell character	Variance components		
	M_{RT}	M_{SR}	M_{ST}
DS	0.0177 ±0.0268	0	0.0119 ±0.0131
HS	0	**0.1091** ±0.0557	**0.1133** ±0.0350
FS	0	0	0

only for shell height. There were also significant differences between the sites and within the three parts of the sampling area, and within the studied area as a whole. *C. vindobonensis* from particular sites did not differ from each other in their shell diameter or form (Fig. 7A1, C1).

The spatial pattern of variation of each of the studied shell parameters was different. Shell diameter showed a very high positive autocorrelation at a very small spatial scale and the value of Moran's index decreased with increasing distance between the sites (even to reach negative values). This indicates a more or less pronounced cline in the spatial variation of shell major diameter in the studied population (Fig. 7A2). The pattern of shell form variation was the opposite: closely situated sites differed considerably in their shell form whereas more remote sites were similar (Fig. 7C2). The variation in shell height was completely random, as shown in the correlogram (Fig. 7B2).

Chronological variation

Variation through time was studied in detail for nine populations of *B. cylindrica*, sampled in 2006 and 2012 (Table 4). The basic object of the studies was the intra-population chronological morphometric variation, and the degree of compatibility of variation among individual sites during the study period.

Chronological changes in shell measurements and form in *B. cylindrica* in each of the sites were specific and their magnitude and direction were not compatible (Fig. 8). For all the studied morphometric characters there were significant estimates of Fisher's F for the factors "population" and "year of study" (crossed two-way ANOVA; in all cases $p < 0.05$; Fig. 8).

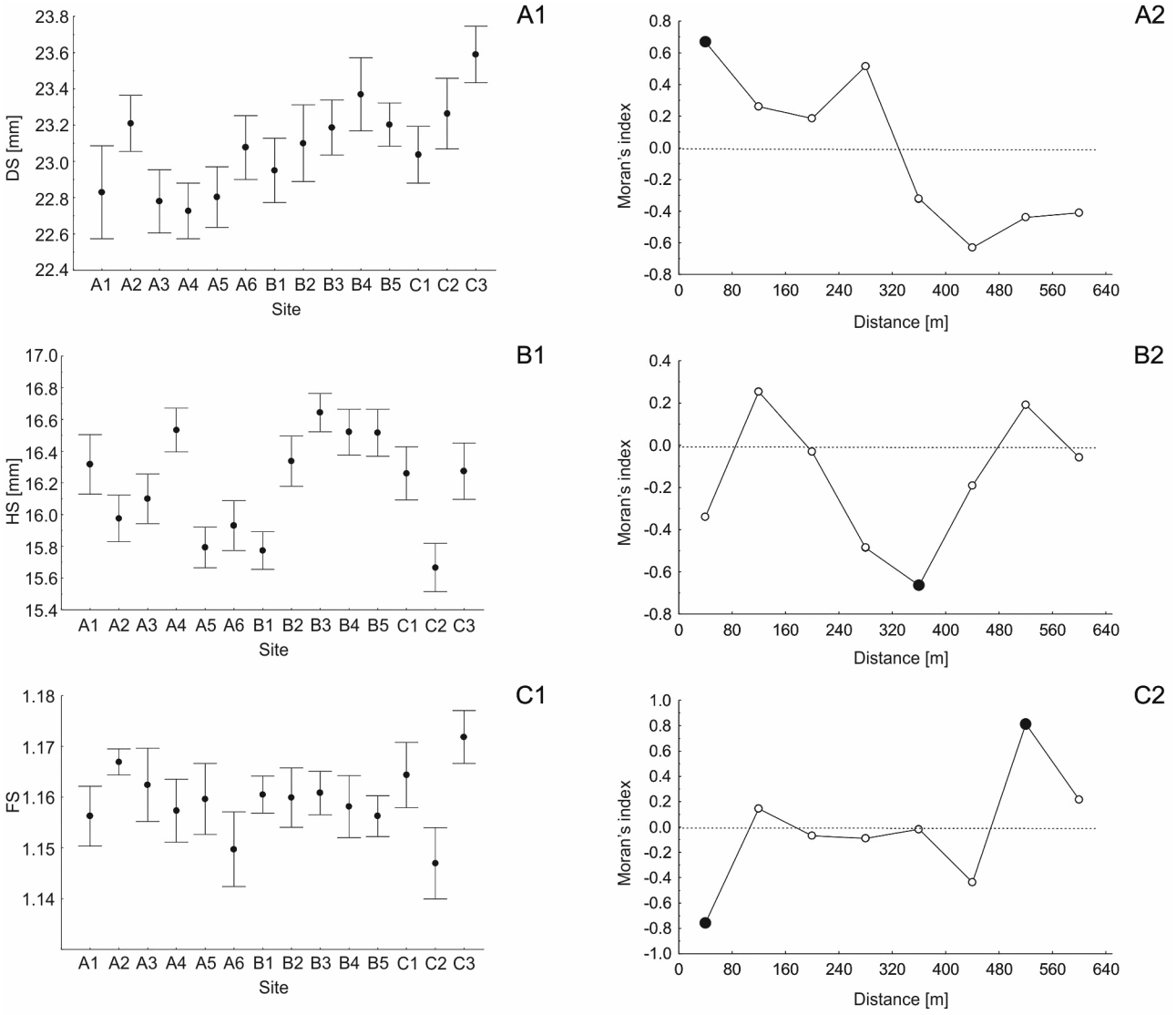

Fig. 7. Variation ($\overline{X} \pm SE$) (1) and Moran's index (2) for spatial variation of morphometric shell characters in *C. vindobonensis* from population Dubky: A – shell diameter; B – shell height; C – shell form (significant values of Moran's index indicated as solid circles)

However, the asymmetry of chronological changes of morphometric characters within particular sites within the study period was more visible when it was considered for two measurements: shell height and width (Fig. 9). A whole range of patterns of chronological changes was observed: from significant changes in height and width to virtually complete stability of the two parameters (Fig. 9).

In order to check if the results depended on the selection of sampling period, I extended the observation period (2004, 2006, 2008 and 2012), though this required limiting of the number of populations to three. Even with increased frequency of observations, only the "population" factor had a significant effect (Table 5). Intra-population chronological changes were differently pronounced in different populations, and again the factors with significant effect were "population" and "year of study" (Fig. 10).

MESO-GEOGRAPHICAL SCALE

Interdependences between the intra- and inter-population components of morphometric variation were analysed based on three populations of

Table 4. Number of specimens of *B. cylindrica*, analysed in 13 local populations in Mykolaivskya in 2004–2012

No.	Population	Study year					Total
		2004	2005	2006	2008	2012	
1	Park Dubky	30	30	30	30	30	150
2	Park Pobedy	30	30	30	30	30	150
3	Neftebaza	30	30	30	30	30	150
4	Morekhondaya Street	30	–	–	30	30	90
5	Karpenko Street	30	–	30	–	30	90
6	Mykolaivskaya Street	30	30	30	–	30	120
7	Mykolaiv Zoo	30	–	–	–	–	30
8	Beach Varvarovka	30	–	–	–	–	30
9	City hospital #3	–	30	30	–	30	90
10	1st Slobodskaya Street	–	30	30	–	30	90
11	Beach Strelka	–	30	30	–	30	90
12	1st Liniya Street	–	–	30	–	30	60
13	Park Kommunarov	–	–	30	–	30	60
	Total	240	210	300	120	330	1200

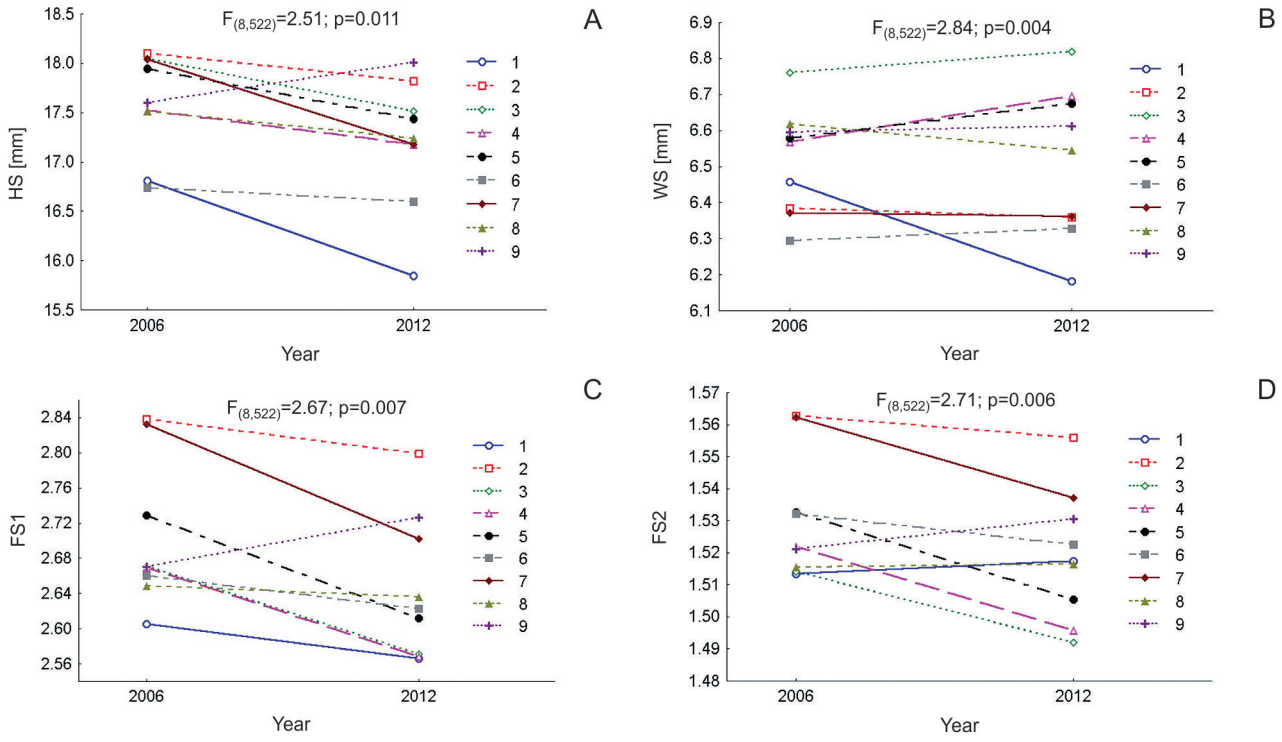

Fig. 8. Direction and magnitude of changes of shell morphometric characters and indices of form in nine populations of *B. cylindrica* in 2006 and 2012: A – shell height; B – shell width; C – shell form 1; D – shell form 2

B. cylindrica in 2004–2006 (see: Variation in shell size and form: Micro-geographical scale: Spatial variation). The full model used in the analysis included three factors: "year of study" – A (three grades), "population" – B (three grades) and "site" – C (ten grades). Since in many years sampling from each population was conducted in many sites, the factor "site" turned out to be hierarchically subordinate to the first two factors (year of study and population).

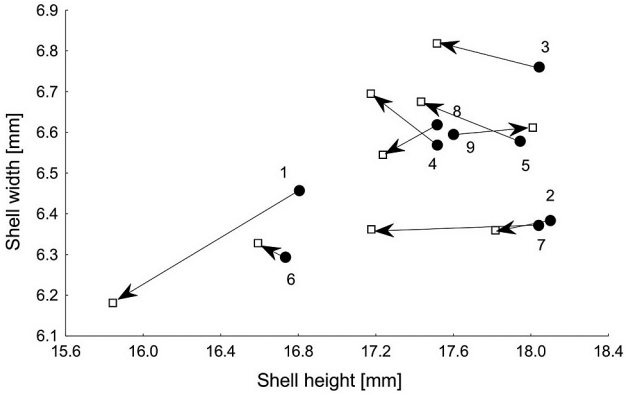

Fig. 9. Direction and magnitude of changes of shell morphometric characters and indices of form in nine populations of *B. cylindrica* in 2006 and 2012

Table 6 shows the estimates of variation components for the three factors. The morphometric variation of *B. cylindrica* was to a large extent determined by the inter-population component of variance. Due to the linear character of the model it was possible not only to estimate individual components of variance of the dependent variable, but also to sum the individual components. The proportion of intra-population variation in the sum of inter- and intra-population variation for many shell characters was roughly the same and ranged from 16.75% (for shell width) to 21.20% (for FS1); the intra-population component of variation was ca. 1/5 of the total inter- and intra-population variation.

Shell measurements of 13 local populations from Mykolaiv from 2004–2006 were used for a more detailed analysis of inter-population morphometric var-

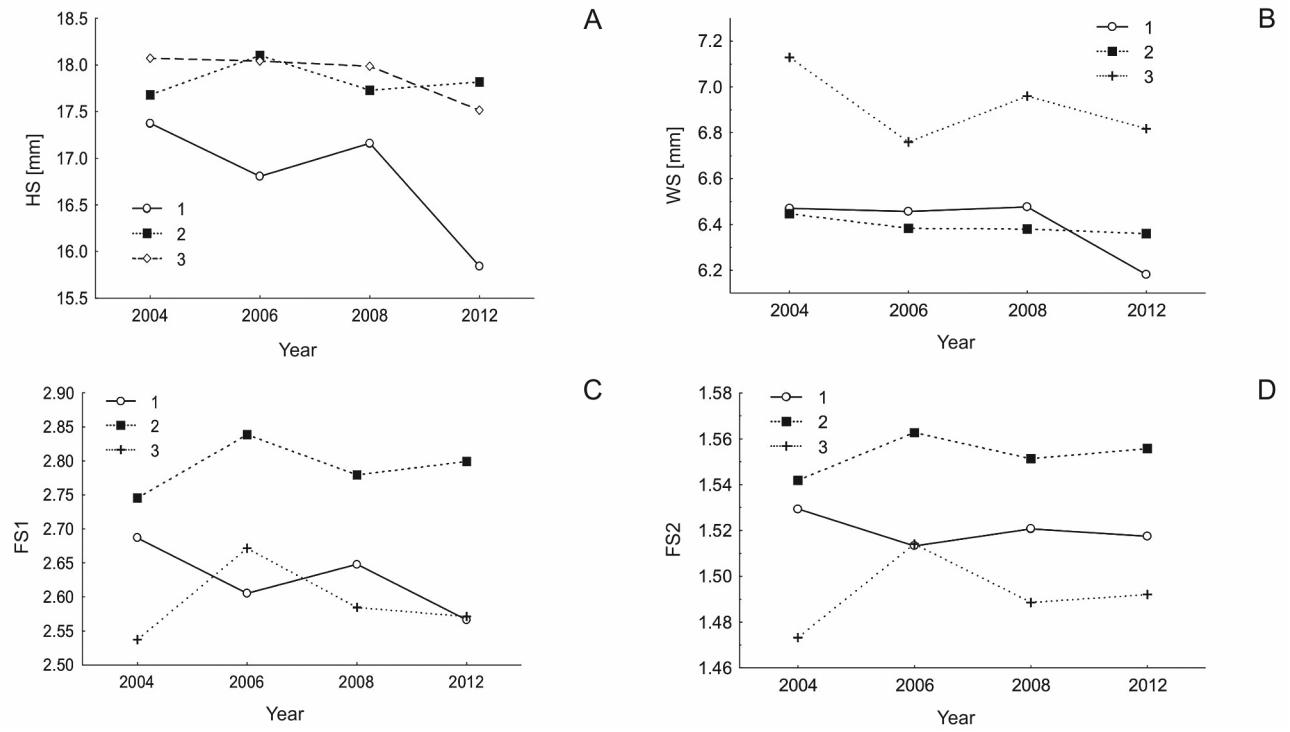

Fig. 10. Direction and magnitude of changes of shell morphometric characters and indices of form in three populations of *B. cylindrica* in 2004–2012: A – shell height; B – shell width; C – shell form 1; D – shell form 2. For population numbers see Table 4

Table 5. Significance level (p) of chronological changes in shell size and form of *B. cylindrica* from three populations in 2004, 2006, 2008 and 2012. Significant values indicated in bold

Source of variation	HS		WS		FS1		FS2	
	F	p	F	p	F	p	F	p
Population (A)	9.302	0.015	**29.882**	0.001	**13.478**	0.006	**20.757**	0.002
Year (B)	2.037	0.210	2.873	0.126	0.752	0.560	0.822	0.528
Interaction effect (A×B)	**3.605**	0.002	**4.365**	0.000	**3.563**	0.002	**3.547**	0.002

Table 6. Variance components of intra-population variation in shell characters of *B. cylindrica* from three local populations. Values significantly exceeding 0 indicated in bold

Shell character	Variance components		
	Year (M_A)	Population (M_B)	Locality ($M_{C(AB)}$)
HS	0.0052±0.0422	**0.1643**±0.0911	**0.0539**±0.0177
WS	0.0122±0.0534	**0.4345**±0.1148	**0.0874**±0.0216
FS1	0.0194±0.0386	**0.1989**±0.0744	**0.0535**±0.0173
FS2	0.0202±0.0575	**0.3186**±0.1065	**0.0772**±0.0198

Table 7. Variance components of intra-population variation in shell characters of *B. cylindrica* from 13 local populations. Values significantly exceeding 0 indicated in bold

Shell character	Variance components		
	Year (M_A)	Population (M_B)	Locality ($M_{C(AB)}$)
HS	0.0087±0.0374	**0.3028**±0.1582	0.0161±0.0289
WS	0.0238±0.0618	**0.3323**±0.0813	0.0534±0.0510
FS1	0.1080±0.0773	**0.2349**±0.0721	0.0212±0.0344
FS2	0.1164±0.0878	**0.2538**±0.0832	0.0290±0.0406

iation (Fig. 11). The distribution of samples in time and space is shown in Table 4. Figure 12 presents variation in two shell measurements and two indices of *B. cylindrica* from these 13 populations. There was a considerable scatter of the mean values among the studied populations. One of the local populations showed a much smaller shell size than the remaining 12; it was a population from a lawn in Morekhodnaya Street. The shells from this population were on average by 2–3 mm lower (which at the mean shell height of ca. 15 mm is 13–20%). No such difference was observed for shell width (Fig. 12).

The observed pattern may result from the effect of stochastic population-genetic processes which gain special significance in small isolated populations in anthropogenic habitats. Only the "population" factor was significant in the estimates of variance components (Table 7), while considering only three populations, also the "site" factor had a significant effect (Table 6). This is explained by the small number of analysed sites (25 sites in 13 populations), while the analysis of three populations used 90 sites (10 in each population in each year of studies).

Fig. 11. Location of sampling sites of *B. cylindrica* in Mykolaiv. For population numbers see Table 4

Another characteristic feature of the results was that the estimates of variance components for shell form indices considering 13 populations were by an order of magnitude higher than the corresponding values when only three populations were included in the analysis (for FS1: 0.1080 and 0.0194; for FS2: 0.1164 and 0.0202, respectively), while for shell measurements such estimates were rather similar (for shell height: 0.0087 and 0.0052; for shell width: 0.0238 and 0.0122, respectively) (Tables 6 and 7).

Considering the estimates of variance components which reflect inter-population differences, it is noteworthy that for shell height increasing the number of examined populations from three to 13 led to an increase in the effect of the factor (from 0.1643 to 0.3028), while for shell width it led to a slight decrease in the corresponding values (from 0.4345 to 0.3323). For the two indices of shell form the values were similar for three and for 13 populations.

The relationship between the estimate of the effect of "population" factor and the number of analysed populations was also analysed. In order to exclude the effect of the order in which populations were included, the order was decided by random numbers generator. A total of 25 random selections was analysed, containing populations 1 to 13 in random order. In each of these relative variance components were estimated for two, three, four etc. to 12 populations included in the analysis. Arithmetic mean and standard deviation (M_{ST} ± SD) of inter-population variation were calculated based on the results. Figure 13 shows estimates of the inter-population variation, depending on the number of populations included in the analysis for various morphometric characters. M_{ST} increased with in-

creasing number of analysed populations, but only to a certain level (6–8 populations). Further increase in the number of populations did not change the M_{ST} value, and only decreased the level of its uncertainty (Fig. 13).

As opposed to the intra-population variation which had a more or less pronounced spatial pattern (most often in the form of clines or sharp "steps" between demes, with similar values of morphometric characters), the inter-population variation at

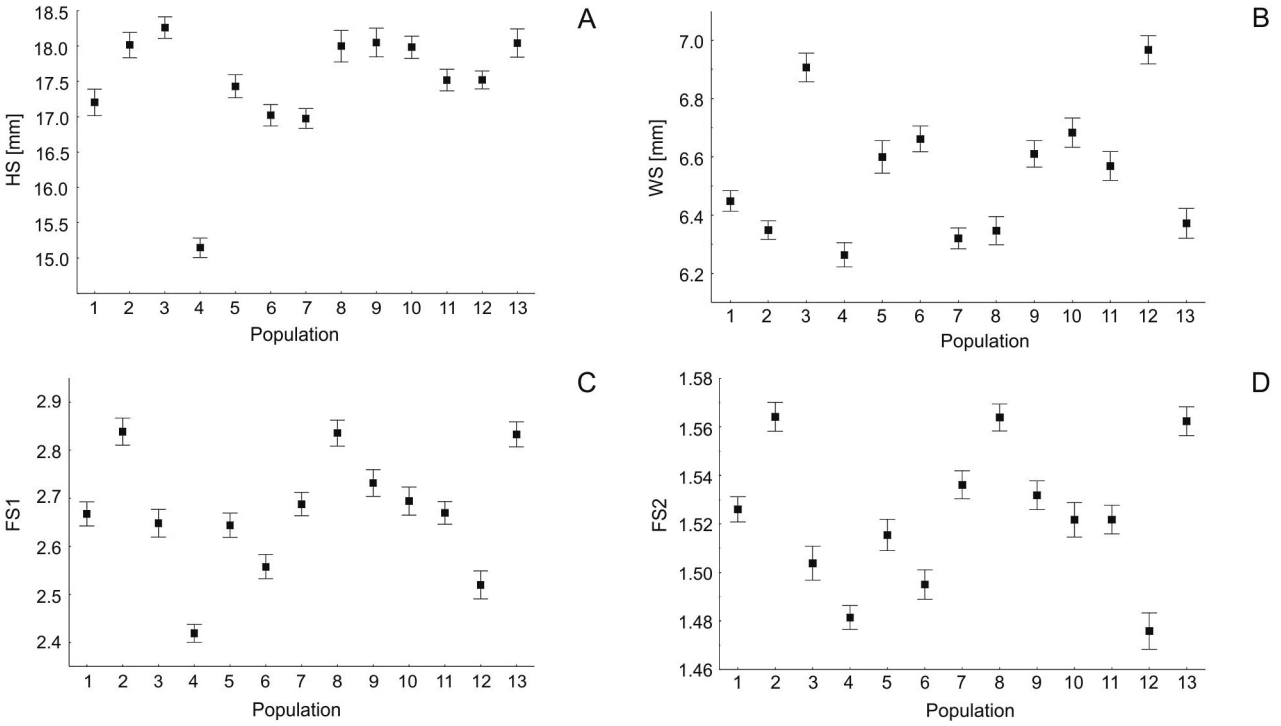

Fig. 12. Variation ($\overline{X}$ ± SE) of morphometric shell characters in the studied populations of *B. cylindrica* from Mykolaiv: A – shell height; B – shell width; C – shell form 1; D – shell form 2. For population numbers see Table 4

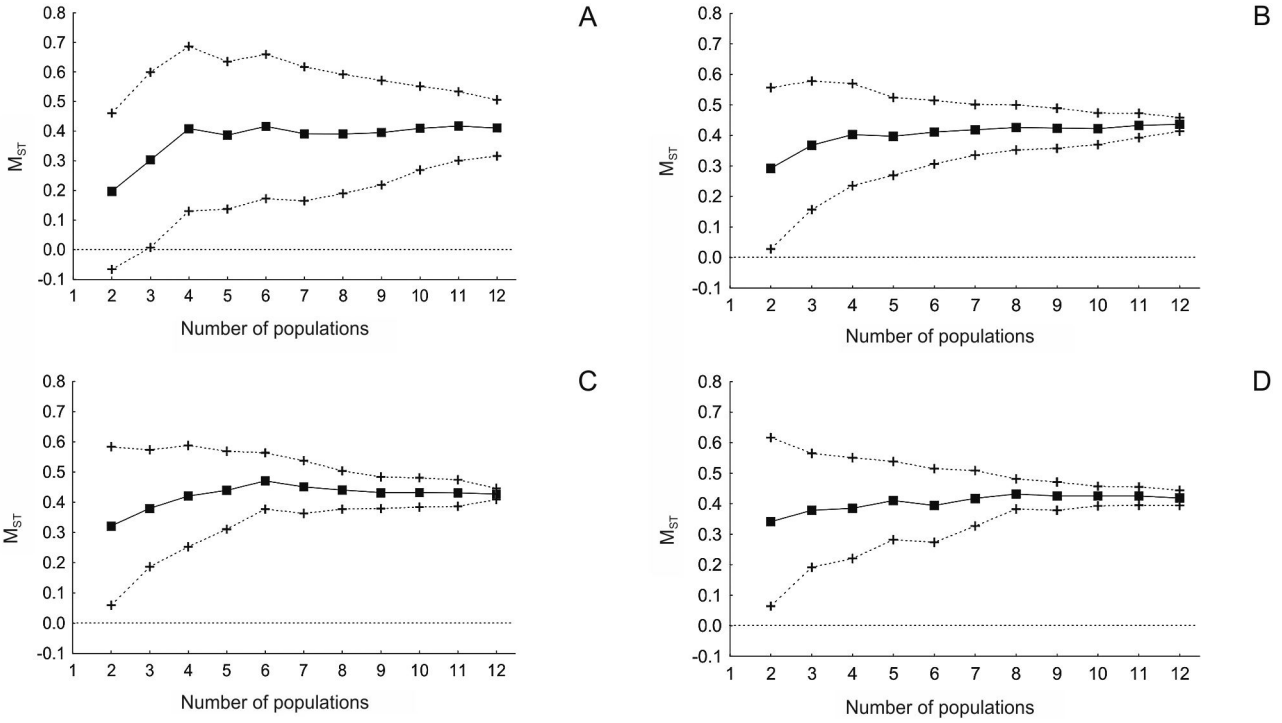

Fig. 13. Indices of inter-population shell variation (M_{ST}) depending on the number of populations of *B. cylindrica* from Mykolaiv: A – shell height; B – shell width; C – shell form 1; D – shell form 2 ($\overline{X}$ ± SD)

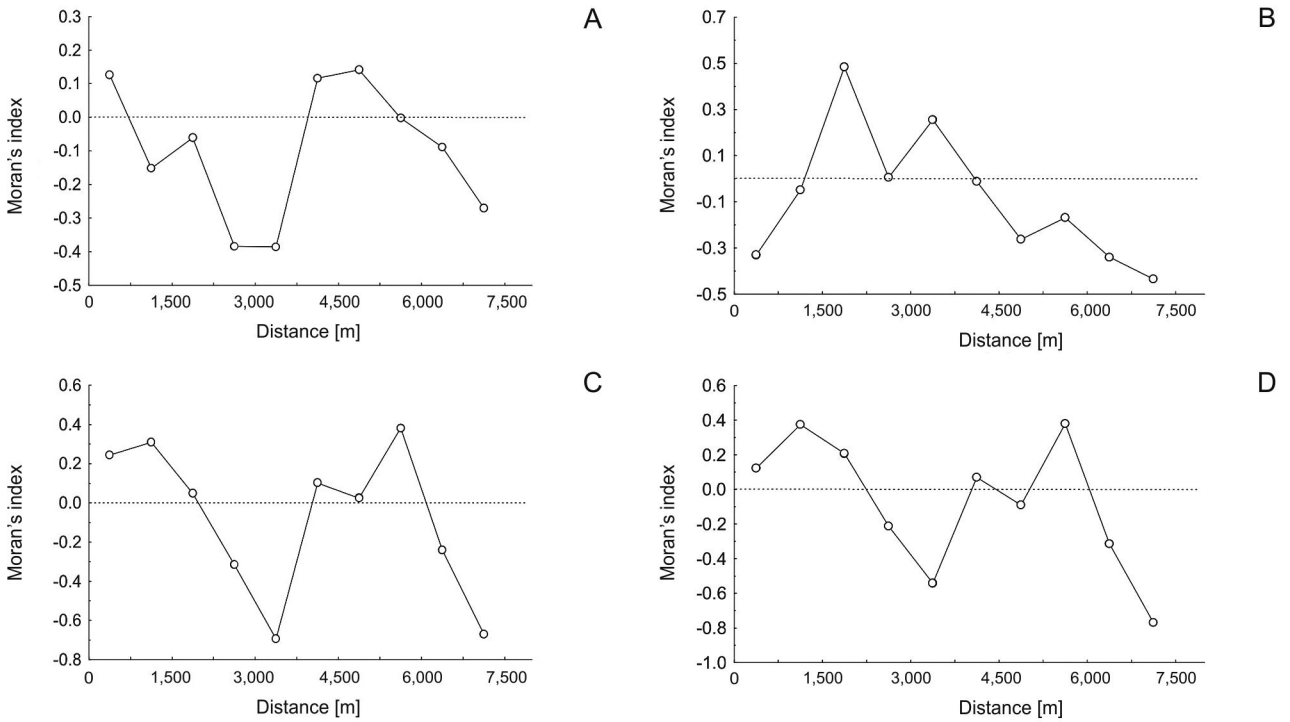

Fig. 14. Moran's index for inter-population shell variation in *B. cylindrica* from Mykolaiv: A – shell height; B – shell width; C – shell form 1; D – shell form 2

meso-geographical scale showed a random pattern (Fig. 14). Neighbouring populations of *B. cylindrica* can differ distinctly in their shell measurements and proportions (e.g. populations from lawns on Karpenko Street and Morekhodnaya Street), whereas geographically remote populations may be similar in their morphometric characters (Fig. 12). The situation can be explained by the fact that the shaping of morphometric variation in land snails from anthropogenic habitats is random, determined by colonisation processes (single or repeated) in favourable habitats (lawns, gardens, cemeteries, wasteland etc.). Besides, existence in the form of small and practically isolated populations leads to unpredictable responses to the same factors (Fig. 9).

MACRO-GEOGRAPHICAL SCALE

Geographical variation of *Brephulopsis cylindrica*

B. cylindrica lives in a variety of habitats of all climatic-vegetation zones of the Crimean Peninsula (Shileyko 1984, Kramarenko 1995), and also occurs in natural and urban habitats of southern parts of Ukraine: districts of Odessa, Mykolaiv, Kherson, Zaporozhe, Dnepropetrovsk and Donetsk (Kramarenko & Sverlova 2001, Vitchalkovskaya 2008, Gural-Sverlova & Gural 2012). There are also single records from Lvov and Kiev (Sverlova 1998, Vitchalkovskaya & Kramarenko 2008) which are probably introductions; such materials were not included in the analysis. In all, the distribution area extends from 44° to 48°N and from 30° to 38°E, roughly 400 km from north to south and from west to east. As a consequence of the varied relief of Crimea (from coastal plains to the Crimean Mountains), within its range *B. cylindrica* encounters a wide spectrum of different habitats, each inhabited by snails of different morphometric characters.

Graphs in Figs 15 and 16 present variation of basic shell measurements and indices of *B. cylindrica*, depending on the geographical location. There is a close relationship between the shell measurements and indices on the one hand and the latitude of the locality on the other. The shell measurements tend to decrease eastward (Fig. 15). The tendency is especially pronounced in the case of shell height, and of both indices of shell form. However, within the area there is a local reversal of the dependence between temperature and latitude of localities – the coldest localities are situated in the southernmost part of the range (Crimean Mountains).

On the other hand, there is no relationship between the morphometric characters and the longitude of the localities (Fig. 16). There is a very wide range of mean values of morphometric characters along the east-west transect. Continental (non-Crimean) populations (solid circles in Figs 15 and 16) mostly show morphometric characters similar to those of the populations from the steppe parts of the Crimean Peninsula, though they are located on average 2° more

to the north. These populations may have a more recent origin as a result of anthropochoric dispersal (VITCHALKOVSKAYA 2008). An argument in favour of their anthropogenic origin is the fact that including them in the analysis most often leads to weakening of the latitudinal correlation which is more pronounced in the eastern part of the range (Crimean Peninsula). Overall, the geographical variation of the species shows a more or less pronounced cline with its base in the south coast and montane populations of Crimea.

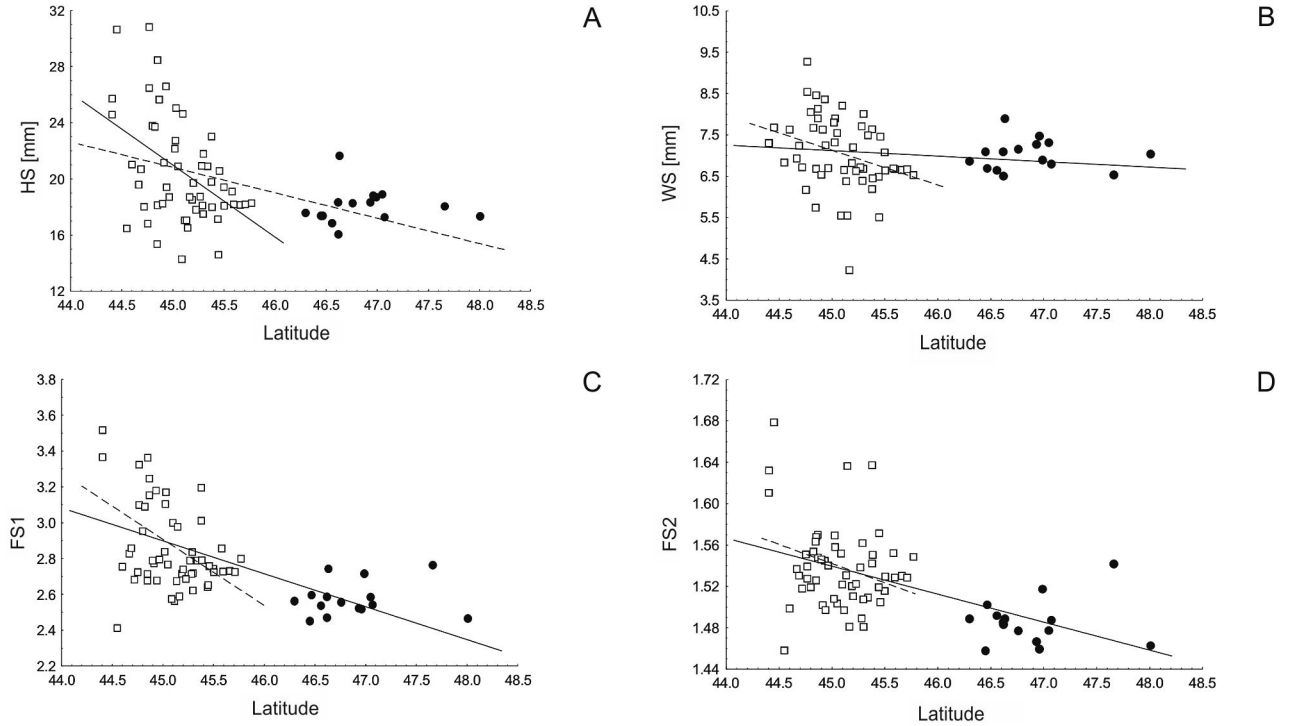

Fig. 15. Dependence between latitude and shell measurements and proportions in *B. cylindrica*: A – shell height; B – shell width; C – shell form 1; D – shell form 2

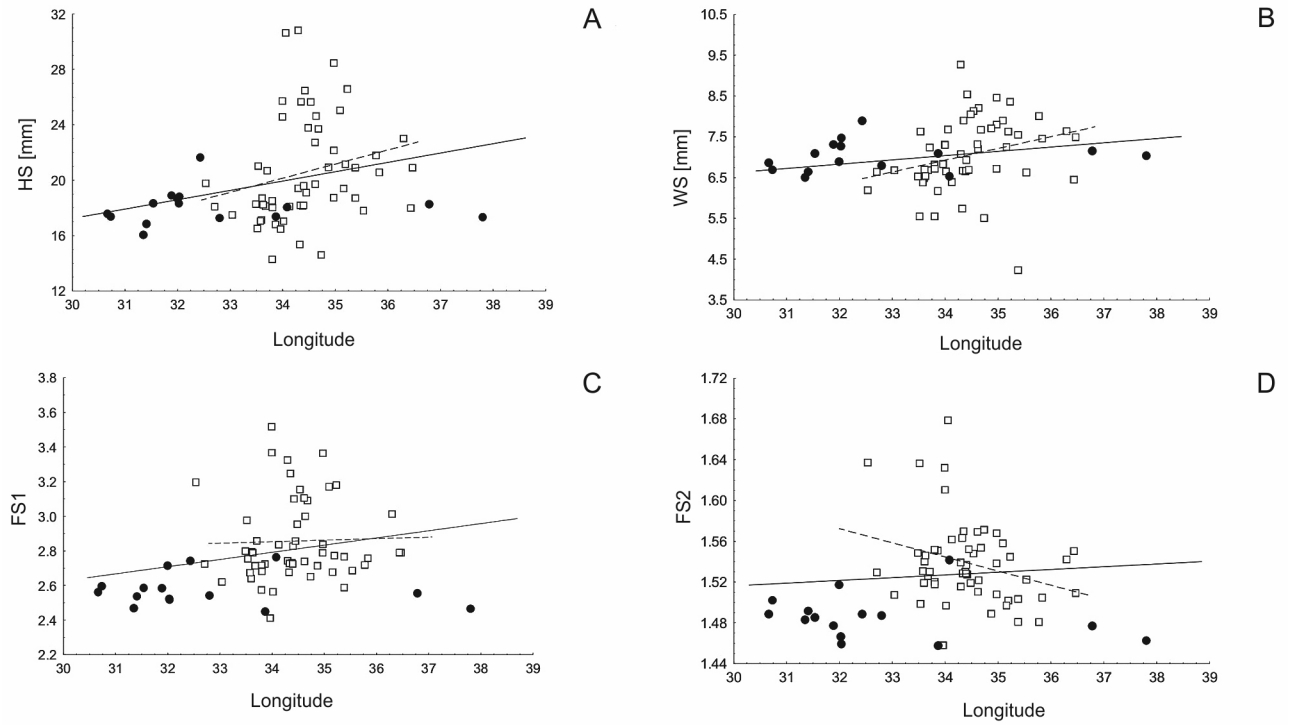

Fig. 16. Dependence between longitude and shell measurements and proportions in *B. cylindrica*: A – shell height; B – shell width; C – shell form 1; D – shell form 2

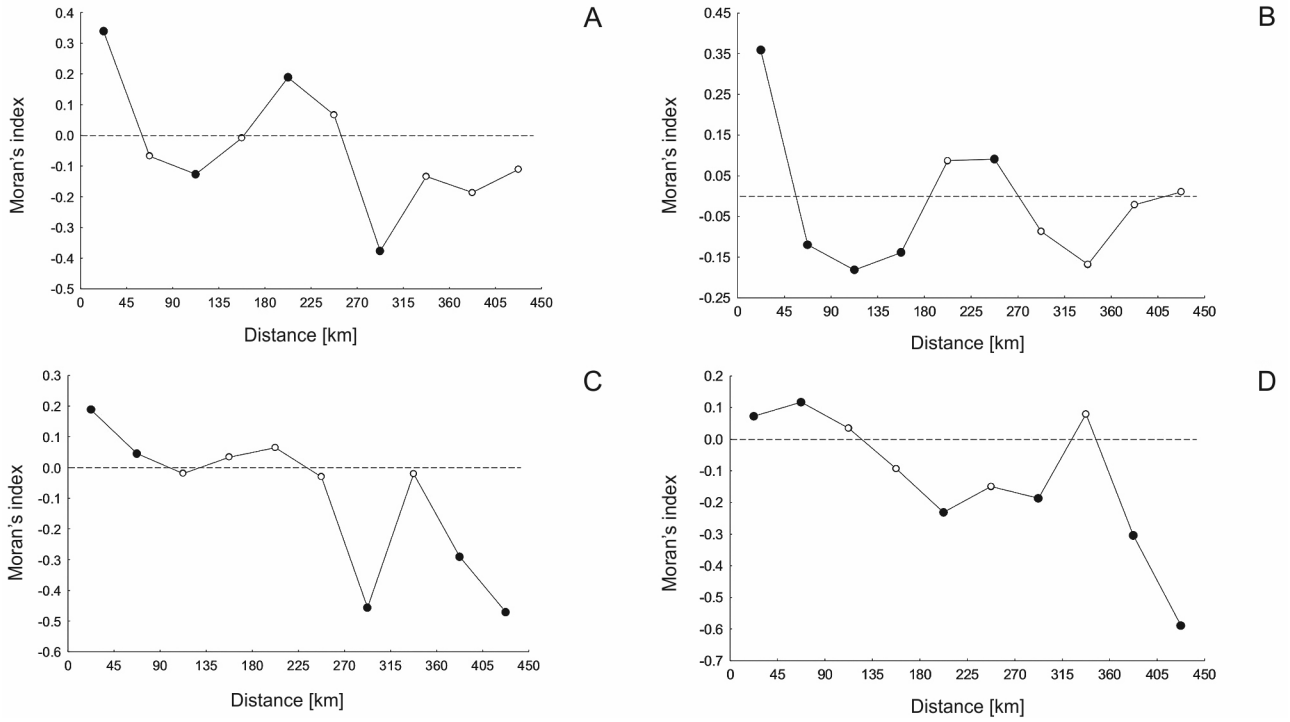

Fig. 17. Moran's index for morphometric shell characters of *B. cylindrica* depending on geographical distance between localities: A – shell height; B – shell width; C – shell form 1; D – shell form 2 (significant values of Moran's index indicated as solid circles)

The degree of spatial autocorrelation of the variation of morphometric characters of *B. cylindrica* was estimated using Moran's index. Highly significant values of the index were obtained for the shortest distances (0–45 km) for shell height and width (Fig. 17). Increasing the distance to 90–135 km led to insignificant or negative values of the index. As a result, the shells from geographically close populations (distance 40–50 km) had similar morphometric characters while the shells from populations 100–150 km apart differed distinctly. The pattern may be explained on the one hand by active dispersal of the snails over relatively short distances, or by hydrochory (KRAMARENKO 2009b), on the other by the wide range of habitats in the montane and submontane regions of Crimea. This is also confirmed by the fact that, irrespective of the latitudinal gradient in morphometric characters, there is a considerable scatter of values within groups of localities with similar latitudinal position (Fig. 15A, B). For the two indices of shell form there are significant positive values of Moran's index for the smallest distances, and significant negative values for the largest distances, which indicates a distinctly pronounced cline in the geographical variation of *B. cylindrica* within its distribution area (Fig. 17C, D).

Relationships between the mean values of morphometric characters of *B. cylindrica* from various populations and the hydro-climatic parameters of the localities were analysed using geostatistical methods (CRESSIE 1993). The geographical coordinates of the localities were included in the analysis of correlation coefficient (Table 8). There was a significant correlation between the hydro-climatic parameters of the localities and the morphometric shell characters. Overall the shell measurements tended to decrease in warmer and drier habitats. The integral assessment of this relationship was obtained with analysis of canonical correlations, which on the one hand used four shell characters, on the other – four hydro-climatic parameters. There was a strict and highly significant correlation between the shell variation and the hydro-climatic parameters of the localities (for the first canonical axis: $R^2 = 0.549$; $\chi^2 = 69.69$; df = 16; $p < 0.001$). The first canonical axis for the hydro-climatic parameters had high loads for T7 (+0.692), D10 (+0.695) and ATP

Table 8. Coefficients of Spearman's rank correlation (R_S) between morphometric shell characters of *B. cylindrica* from various populations and hydro-climatic parameters of localities. Significant values ($p < 0.05$) of correlation coefficient indicated in bold

Shell character	Hydro-climatic parameter			
	T1	T7	D10	ATP
HS	0.187	**–0.445**	**–0.477**	**0.546**
WS	0.030	–0.322	–0.320	**0.401**
FS1	0.303	**–0.407**	**–0.486**	**0.508**
FS2	**0.338**	–0.227	**–0.310**	**0.285**

For hydro-climatic parameters see: Material and methods.

Table 9. Results of Trend Surface Analysis (TSA) of morphometric shell characters of *B. cylindrica* depending on geographical coordinates and hydro-climatic parameters of localities. Significant values of determination coefficient (R^2) indicated in bold

Shell character	Geographical coordinates	Hydro-climatic parameters	Geographical coordinates + hydro-climatic parameters
HS	**0.192**; $p < 0.001$	**0.429**; $p < 0.001$	**0.445**; $p < 0.001$
WS	0.073; $p = 0.079$	**0.164**; $p = 0.008$	**0.214**; $p = 0.003$
FS1	**0.290**; $p < 0.001$	**0.507**; $p < 0.001$	**0.504**; $p < 0.001$
FS2	**0.264**; $p < 0.001$	**0.293**; $p < 0.001$	**0.315**; $p < 0.001$

For hydro-climatic parameters see: Material and methods.

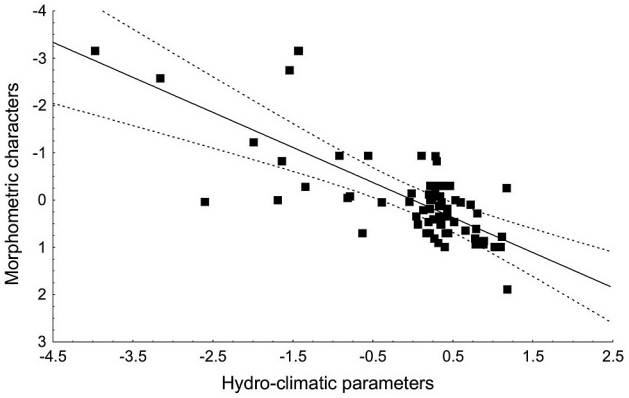

Fig. 18. Distribution of centroids of samples of *B. cylindrica* in the space of the first canonical axis for hydro-climatic parameters and shell characters

(–0.800), while the first canonical axis for the morphometric characters had the highest loads for shell height (–0.897) and FS1 (–0.960). Increasing aridity led to a decrease in shell size (Fig. 18). There was a correlation with the second canonical axis (R^2 = 0.212; χ^2 = 18.55; df = 9; p = 0.029): for the hydro-climatic parameters it had its maximum for T1 (+0.813), and for the morphometric characters for FS2 (+0.442). Thus a part of morphometric variation (mainly pertaining to shell form) was closely correlated with cold temperatures (Kramarenko 1997).

Since the geographical morphometric variation of *B. cylindrica* was affected by the geographical coordinates of the localities and by the hydro-climatic parameters, I estimated the relative contribution of the two factors with Trend Surface Analysis (TSA). It turned out that different factors had a different effect on different morphometric characters (Table 9). Irrespective of some relationship of shell height and FS1 with the geographical coordinates, the major role in forming the pattern of geographical variation was played by the hydro-climatic parameters. In the case of shell width only the hydro-climatic parameters played a role in the shaping of the geographical variation pattern while in the case of FS2 both factors played an equal role and appeared to be congruent.

Geographical variation of *Helix albescens*

The species has a circum-Pontic distribution and is little known in Europe; in Ukraine it is found only on the Black Sea coast, on the Azov Sea coast and in Crimea (Shileyko 1978, Kramarenko & Leonov 2011), and locally may reach high abundance. Overall, the distribution area extends from 44° to 48°N and from 30° to 38°E, that is ca. 400 km from north to south and from west to east. However, in contrast to *B. cylindrica, H. albescens* practically never occurs at high altitudes in the Crimean Mountains, but only at the foothills. Besides, the species is a pronounced mesophile of forest and scrub habitats (including anthropogenic landscapes).

Graphs in Fig. 19 show variation of basic morphometric characters of *H. albescens* depending on the geographical coordinates of its localities. Neither shell height nor shell diameter show any obvious latitudinal or longitudinal clines. In contrast, the pattern of shell form variation has a rather distinct geographical component – the shell becomes increasingly globular northward (Fig. 19C1). While no statistically significant differences in shell measurements were found between the groups of samples from Crimea and from southern Ukraine (Mann-Whitney test: in both cases $p > 0.05$), such differences in shell form were highly significant (Mann-Whitney test: Z = 3.015; p = 0.003). On the other hand, along the west-east gradient the shells tended to become increasingly flattened (Fig. 19C2). The tendency was more pronounced in south-Ukrainian populations than in the Crimean ones. Some of the Crimean populations had extremely tall shells. Omitting them from the analysis led to a more pronounced relationship of shell form with the geographical coordinates, in terms of both latitude and longitude (stippled line in Fig. 19C1, C2).

Neither shell height nor shell diameter showed any more or less pronounced spatial pattern of variation; the values of Moran's index for numerous distances were very small and close to zero (Fig. 20). For shell form, as could be expected, there was a rather distinct spatial pattern (Fig. 20C). Statistically significant values of Moran's index were obtained for the smallest distances (20–25 km) which indicates a

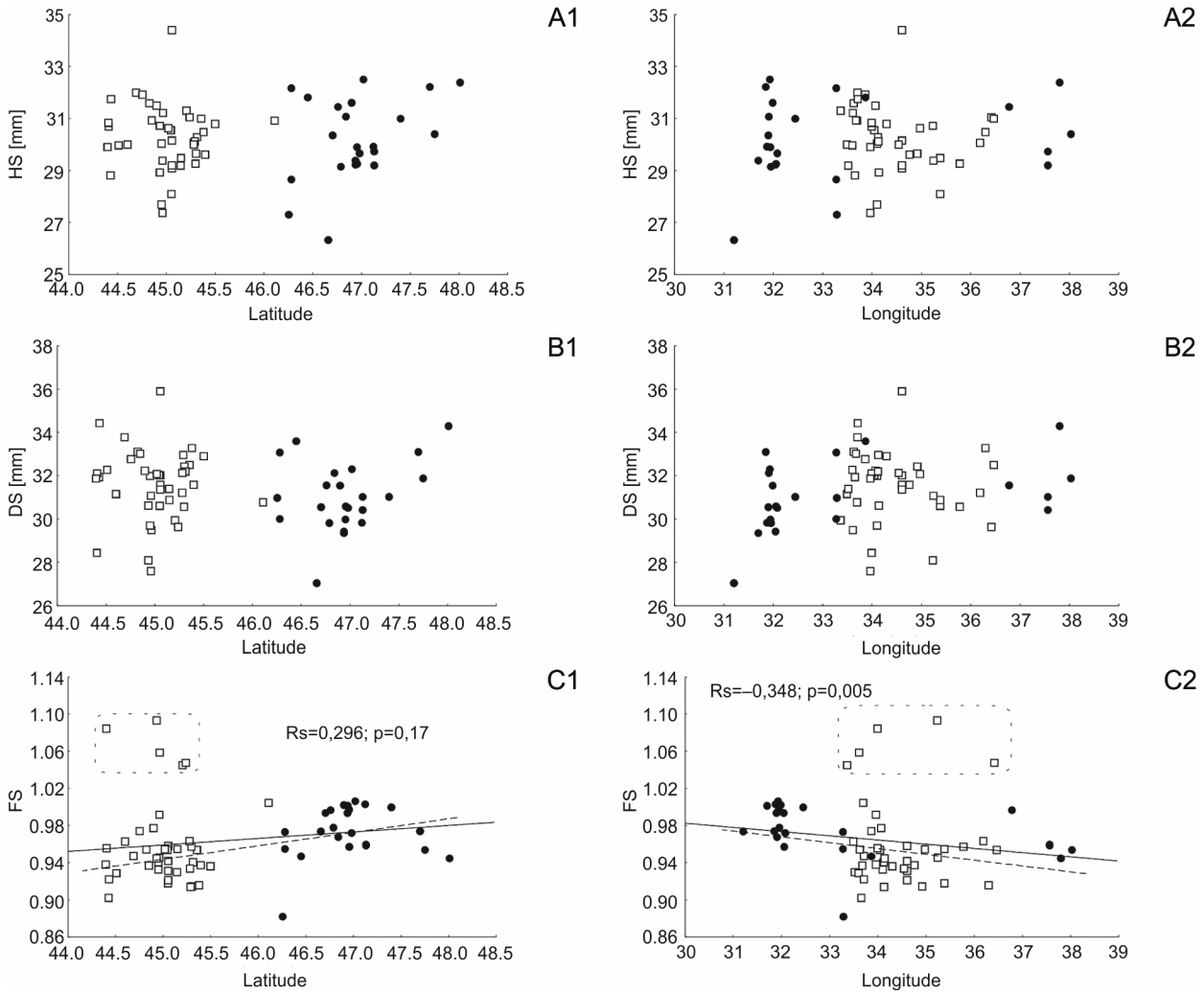

Fig. 19. Dependence between latitude (1) and longitude (2) and morphometric shell characters of *H. albescens*: A – shell height; B – shell major diameter; C – shell form (solid circles – localities in southern Ukraine)

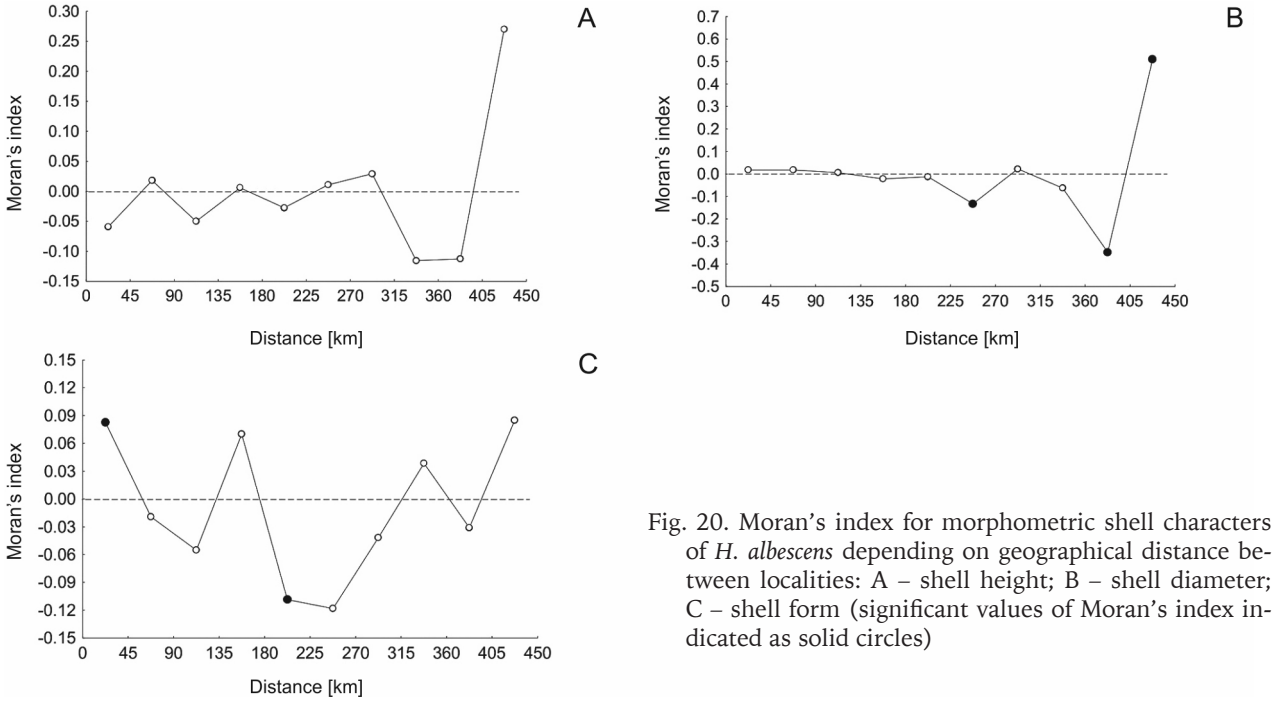

Fig. 20. Moran's index for morphometric shell characters of *H. albescens* depending on geographical distance between localities: A – shell height; B – shell diameter; C – shell form (significant values of Moran's index indicated as solid circles)

positive autocorrelation: closely situated populations were more similar among themselves in their shell form than were remote populations.

The positive autocorrelation of shell form for small distances in *H. albescens,* as in the case of *B. cylindrica*, may be associated with anthropochory and hydrochory (KRAMARENKO 2009b). On the other hand, forming such a pattern may depend on the possible association between shell measurements and proportions on the one hand and the habitat conditions in the localities on the other. The conjecture is supported by the significant correlation between shell form of *H. albescens* in the various studied populations, and the mean monthly temperature of January (Table 10). The most tumid shells of *H. albescens* are found in the populations from the easternmost parts of the distribution area in Ukraine (Donetsk district), where the January temperatures are the lowest.

Table 10. Coefficients of Spearman's rank correlation (R_S) between hydro-climatic parameters of localities and shell characters of *H. albescens* from various populations. Significant values of correlation coefficient indicated in bold

Shell character	Hydro-climatic parameters			
	T1	T7	D10	ATP
HS	–0.028	–0.112	0.077	0.087
DS	0.110	**–0.319**	0.052	0.118
FS	**–0.294**	0.219	–0.071	–0.041

For hydro-climatic parameters see: Material and methods.

Geographical variation of *Cepaea vindobonensis*

In Ukraine the species is widespread, and its range extends for ca. 600 km from north to south (45°–51°N) and ca. 1,000 km from west to east (24°–40°E). Besides my own data, I included in the analysis the results of other authors (KHLUS 2003, 2004, 2011, SVERLOVA & KYRPAN 2004, SVERLOVA 2007, GURAL-SVERLOVA & MARTYNOV 2007, SNEGIN 2011b). In all,

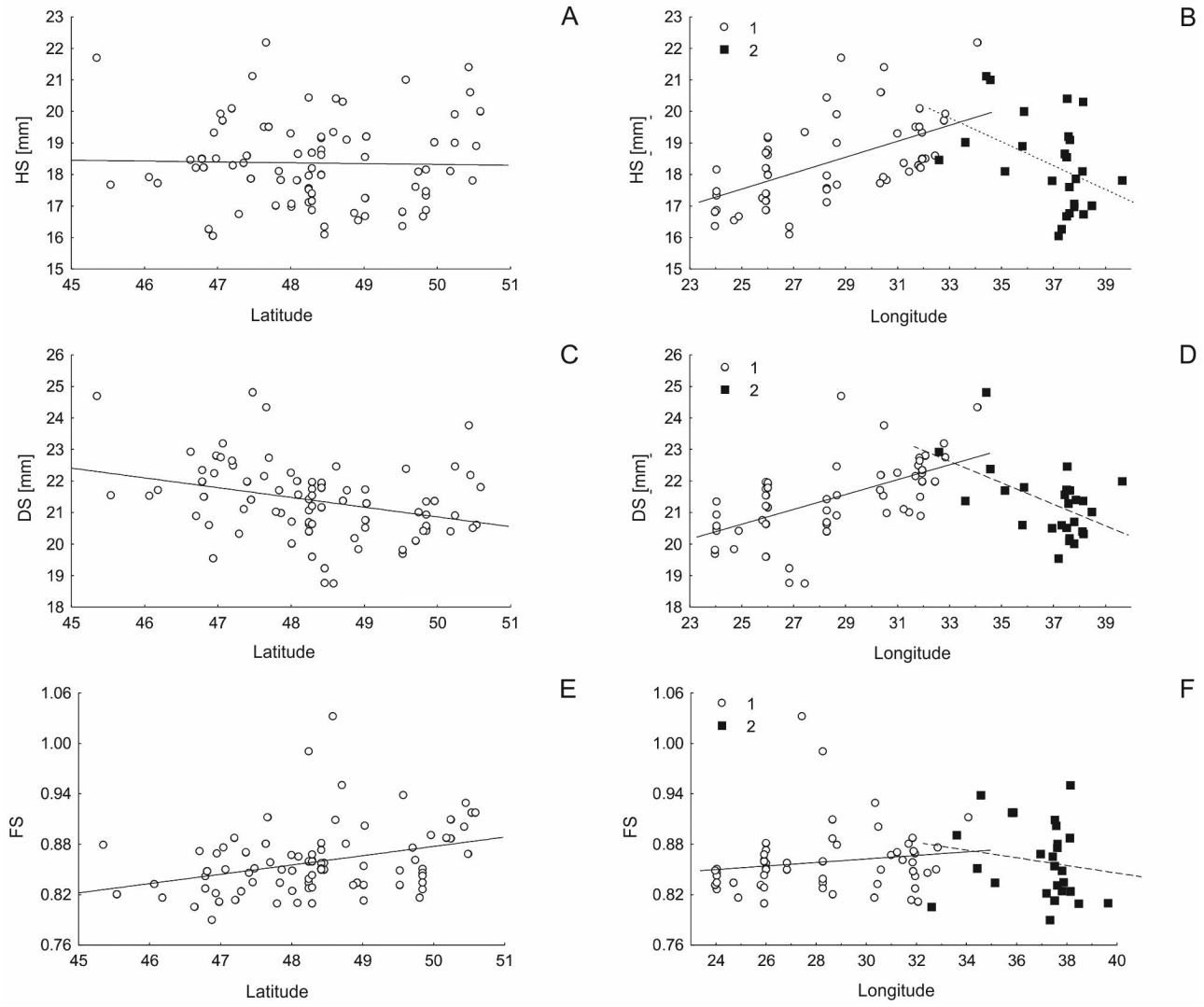

Fig. 21. Variation in shell height (A, B), shell diameter (C, D) and shell form (E, F) of *C. vindobonensis* depending on geographical location: 1 – right-bank Ukraine; 2 – left-bank Ukraine

data from 82 populations were analysed, from various regions of Ukraine and from the Belgorod district of the Russian Federation.

Graphs in Fig. 21 show variation of morphometric shell characters in *C. vindobonensis* depending on the geographical position of the localities. Latitudinally, the mean shell height varies randomly, while the shell diameter, and especially the shell form, show a distinct trend (Figs 21C, E). Along the south-north gradient the major shell diameter tends to decrease (R_S = –0.352; p = 0.0011), and the degree of shell globularity, conversely, increases (R_S = 0.372; p = 0.0006). The longitudinal pattern of the geographical variation of morphometric characters is more complicated. For the two measurements (and shell proportion indices based on them) the dependence on longitude has a Λ-shaped form. The boundary between the zone where the values increase along the west-east gradient and the zone where they start to decrease runs roughly at 34°E and corresponds to the Dnieper River (Fig. 21B, D). In right-bank Ukraine the shell measurements increase from west to east (for shell height: R_S = 0.604; n = 56; p < 0.001; for shell diameter: R_S = 0.657; n = 56; p < 0.001), while in left-bank Ukraine the tendency is reversed, and the measurements decrease from west to east (for shell height: R_S = –0.340; n = 26; 0.05 < p < 0.1; for shell diameter: R_S = –0.332; n = 26; 0.05 < p < 0.1).

The latitudinal and longitudinal correlations combine to form a complicated pattern of geographical variation. The pattern is only poorly approximated when using exclusively linear trends with respect to latitude and longitude. Using curvilinear relationships of the second and also third order considerably increases the adequacy of the model of dependence between the shell measurements and the locality coordinates (Table 11). Overall, 43–45% of the inter-population variation of morphometric parameters depends on the geographical location.

The morphometric variation of populations of *C. vindobonensis* in Ukraine displays a distinct spatial

Table 11. Results of Trend Surface Analysis (TSA) of morphometric variation of *C. vindobonensis* depending on geographical coordinates of localities. Significant values of determination coefficient (R^2) indicated in bold

Shell character	Model		
	Linear trend	Square trend	Cuboid trend
HS	0.041; p = 0.336	**0.296**; p < 0.001	**0.429**; p < 0.001
DS	**0.126**; p = 0.005	**0.271**; p < 0.001	**0.456**; p < 0.001
FS	**0.128**; p = 0.004	**0.311**; p < 0.001	**0.330**; p < 0.001

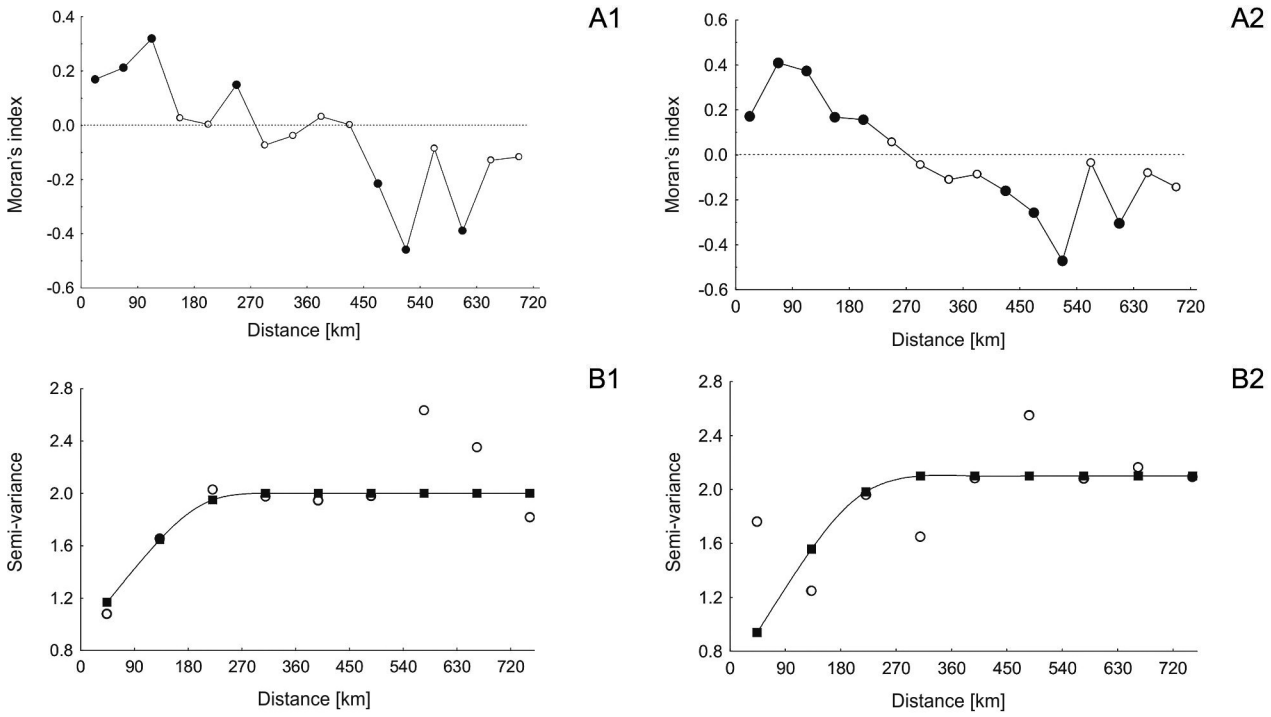

Fig. 22. Correlograms (A) and variograms (B) of geographical variation of shell characters of *C. vindobonensis*: 1 – shell height; 2 – shell diameter

Table 12. Coefficients of Spearman's rank correlation (R_S) between hydro-climatic parameters of localities and shell characters of *C. vindobonensis* from various populations. Significant values of correlation coefficient indicated in bold

Shell character	Hydro-climatic parameters			
	T1	T7	D10	ATP
HS	–0.028	0.185	0.165	**–0.258**
DS	**0.210**	**0.367**	**0.456**	**–0.431**
FS	**–0.287**	–0.137	**–0.231**	0.097

For hydro-climatic parameters see: Material and methods.

autocorrelation, as indicated by the graphs in Fig. 22. It is characteristic that the mean range within which the shell measurements are relatively constant is about 270–300 km. The spatial autocorrelation can be partly explained by the gradient of hydro-climatic parameters in the area, since larger shells are found in warm and dry places, while in cooler and damper places the shells are smaller (Table 12). It is characteristic that inclusion of hydro-climatic parameters in the TSA model, as supplementary to geographical coordinates, increases adequacy only in the case of linear geographical trend, whereas there is no increase in quality of curvilinear models.

Geographical variation of *Chondrula tridens*

In Ukraine the species displays a considerable inter-population variation (KRAMARENKO & SVERLOVA 2003, 2006). The distribution range of *Ch. tridens* includes virtually the whole of Ukraine and extends for ca. 550 km from north to south (44°–50°N) and 950 km from west to east (24°–40°E).

Graphs in Fig. 23 show variation of morphometric characters of *Ch. tridens* depending on the geographical location. Along the latitudinal gradient the mean shell height and shell form show a statistically significant decrease tendency from south to north (for shell height: $R_S = –0.523$; $p = 0.001$; for shell

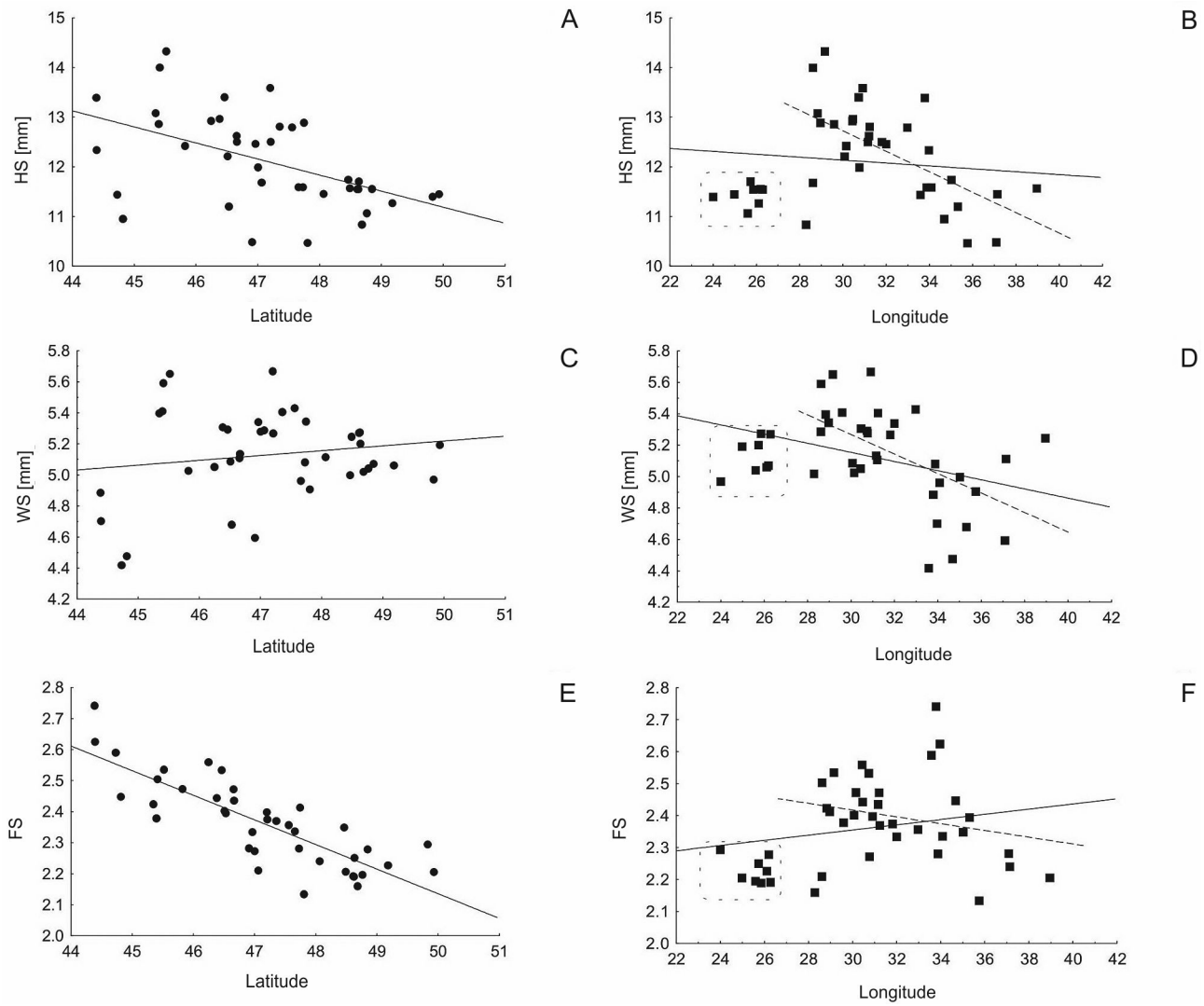

Fig. 23. Variation in shell height (A, B), shell width (C, D) and shell form (E, F) of *Ch. tridens* depending on geographical location (regression line excluding western-Ukrainian samples indicated as dotted line)

form: R_S = –0.846; p < 0.001) (Fig. 23A, E), while shell width varies randomly (Fig. 23C). Along the longitudinal gradient shell height and width tend to decrease from west to east. When the westernmost populations are excluded, the tendency very nearly reaches statistically significant level (for shell height: R_S = –0.328; n = 35; p = 0.054; for shell width: R_S = –0.454; n = 35; p = 0.006) (Fig. 23B, D). No statistically significant pattern of inter-population variation is observed for shell form (Fig. 23F). Besides, the degree of development of apertural barriers in *Ch. tridens* also shows a considerable geographical variation (Table 13). The degree of development of angular tooth and suprapalatal tooth decreases in the populations from northern regions of Ukraine and the degree of development of suprapalatal tooth is higher in the eastern Ukrainian populations. In the parts of Ukraine with more arid conditions *Ch. tridens* have larger shells and better developed apertural barriers, while in damper places they have smaller shells with weaker apertural barriers (Table 14).

Overall, the pattern of geographical variation of morphometric characters of *Ch. tridens* shows a very high spatial autocorrelation with respect to both shell measurements and degree of development of apertural barriers (Fig. 24). The area within which the values of morphometric characters remain similar is ca. 300–350 km in diameter. The results of Trend Surface Analysis (TSA) show that linear trends, for both latitude and longitude, adequately describe most of the inter-population variation (Table 15). The model considering both geographical coordinates and hydro-geological parameters describes the pattern of inter-population variation in shell height and width more adequately than the model which considers geographical location and hydro-geological

Table 13. Coefficients of Spearman's rank correlation (R_S) between geographical coordinates of localities and degree of development of apertural barriers in *Ch. tridens*. Significant values (p < 0.05) of correlation coefficient indicated in bold

Apertural barrier	Geographical coordinates	
	latitude	longitude
Angular tooth	**–0.460**	0.266
Suprapalatal tooth	**–0.489**	**0.591**
Columellar tooth	–0.124	0.046

Table 14. Coefficients of Spearman's rank correlation (R_S) between hydro-climatic parameters of localities and shell characters of *Ch. tridens* from various populations. Significant values of correlation coefficient (p < 0.05) indicated in bold

Shell character	Hydro-climatic parameters			
	T1	T7	D10	ATP
HS	**0.523**	0.264	**0.517**	**–0.340**
WS	0.040	–0.149	**0.364**	–0.164
FS	**0.812**	**0.549**	**0.536**	**–0.511**
Apertural barriers	**0.459**	**0.514**	0.280	**–0.385**

For hydro-climatic parameters see: Material and methods.

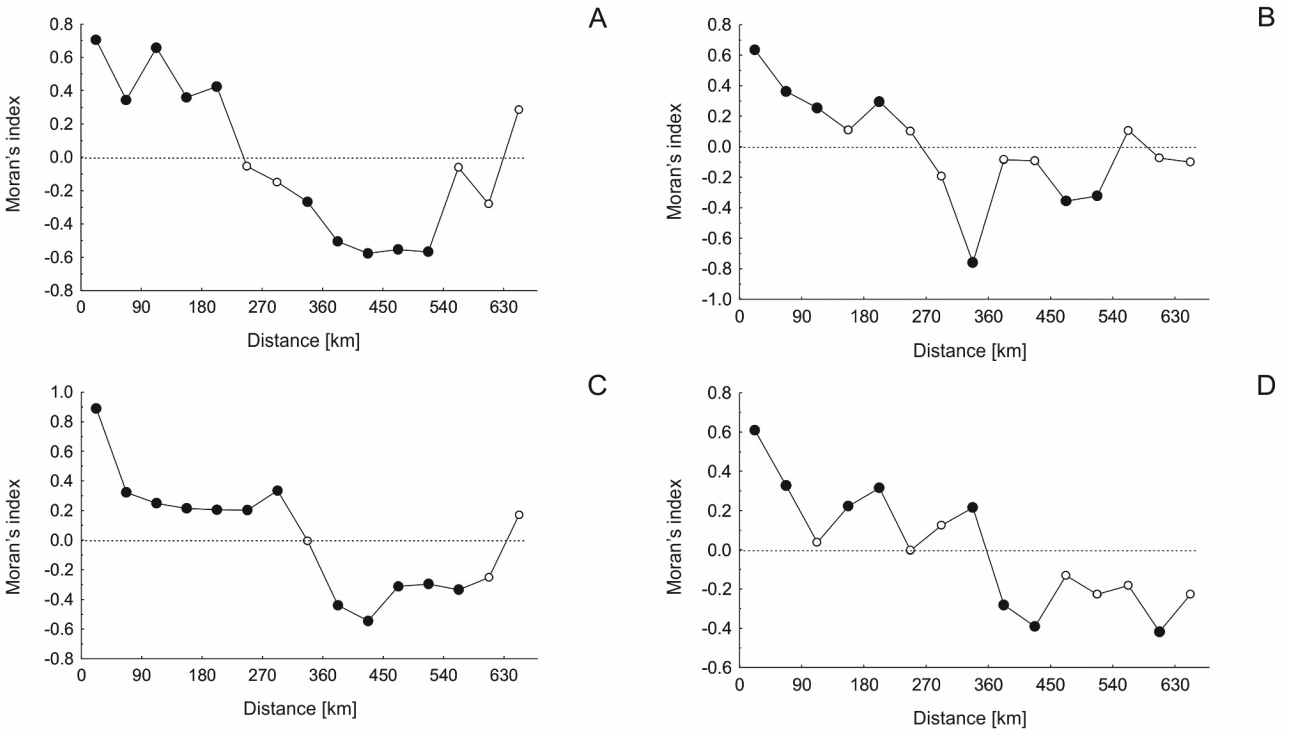

Fig. 24. Correlograms of geographical variation of morphometric shell characters of *Ch. tridens*: A – shell height; B – shell width; C – shell form; D – index of development of apertural barriers (significant values of Moran's index indicated as solid circles)

Table 15. Results of Trend Surface Analysis (TSA) of morphometric variation of *Ch. tridens* depending on geographical coordinates and hydro-climatic parameters of localities. Significant values of determination coefficient (R^2) indicated in bold

Shell character	Geographical coordinates	Hydro-climatic parameters	Geographical coordinates + hydro-climatic parameters
HS	**0.348;** $p < 0.001$	**0.237**; $p = 0.020$	**0.490**; $p < 0.001$
WS	0.123; $p = 0.089$	**0.251**; $p = 0.015$	**0.541**; $p < 0.001$
FS	**0.690;** $p < 0.001$	**0.673**; $p < 0.001$	**0.689**; $p < 0.001$

For hydro-climatic parameters see: Material and methods.

parameters separately (Table 15). This suggests that processes of adaptation of the snails to the macroclimate in which they live are superimposed on the effects of geographical isolation of the populations in terms of distance.

POLYMORPHISM OF SHELL COLOUR AND BANDING PATTERN

MICRO-GEOGRAPHICAL SCALE

Spatial variation

Intra-population spatial variation was investigated in snails of the genus *Xeropicta*. Snails were collected along transects, with samples taken every 7 m (Table 16).

Figures 25 and 26 show frequencies of shell banding patterns in *Xeropicta*. There was some intra-population variation, but in most cases no significant differences among samples taken from the same populations were observed (Table 17). The only exception was the population of *X. derbentina* from Neftebaza for which the estimate of among-sample differentiation regarding the UB morph significantly exceeded zero.

Microhabitat features may have significant impact on spatial patterns of shell polymorphism in terrestrial snails even within small areas (BENGTSON et al. 1976, BANTOCK & RATSEY 1980, JOHNSON 1980). Characteristically, in places where the two species of *Xeropicta* co-occurred, polymorphic structure of *X. derbentina* and *X. krynickii* formed independently of each other. Frequencies of UB and UP morphs were not correlated between the samples of *X. derbentina* and *X. krynickii* collected from the same plots in the Namyv population in 2005 (Fig. 27). This indicates that shell polymorphism in these species was determined by random rather than by microbiotic factors (see below). On the fine spatial scale formation of intra-population patterns of shell banding variation does not occur. The appearance of "spots" with morph frequencies differing from the population's average is usually accidental.

For a more detailed analysis, 27 samples within a population of *X. derbentina* located on a vacant lot in Vilino (Crimea, Bakhchisaray district) were collected in 2008. Sampling was carried out in a regular grid, with 5 m distance between the centres of sampling plots. In total 5,950 shells were collected and analysed. As in the case of transect sampling, frequencies of unbanded (UB) individuals and individuals

Table 16. Number of samples and individuals of *Xeropicta* used in analysis of intra-population variation of shell banding

Species	Population/year	Number of sampling sites	Number of collected snails
X. derbentina	Mykolaiv, Namyv, 2005	10	589
X. derbentina	Mykolaiv, Neftebaza, 2005	10	616
X. derbentina	Mykolaiv, Kosmos, 2005	8	602
X. krynickii	Mykolaiv, Namyv, 2005	10	1022
X. krynickii	Vilino, 2007	14	535

Table 17. Intra-population (among-sample) differentiation of banding morphs (P_{ST}) for different populations of *Xeropicta*. Significant values of P_{ST} ($p < 0.05$) indicated in bold

Species	Population/year	UB	UP
X. derbentina	Mykolaiv, Namyv, 2005	0.0318±0.0178	0.0175±0.0176
X. derbentina	Mykolaiv, Neftebaza, 2005	**0.0705**±0.0322	0.0442±0.0240
X. derbentina	Mykolaiv, Kosmos, 2005	0	0.0192±0.0177
X. krynickii	Nikolaeyv, Namyv, 2005	0.0181±0.0118	0.0109±0.0097
X. krynickii	Vilino, 2007	0	0

with non-pigmented bands (UP) were calculated. Figure 28 shows spatial variation of polymorphism in the examined population. There was significant intra-population heterogeneity for both UB and UP, although the estimates of variation in absolute values differed almost by a factor of five (for UB: P_{ST} = 0.0126 ± 0.0043; for UP: P_{ST} = 0.0609 ± 0.0258). There were also differences in the spatial structure of intra-population variation (Fig. 29). For morph UP there was a pronounced spatial structure, with a high positive spatial autocorrelation for small distances. Adequacy of the model of spherical functions for empirical estimates of semi-variance is 81.5%, and the ratio $C/(C+C_0)$, an estimate of increasing variation caused by the presence of spatial heterogeneity with-

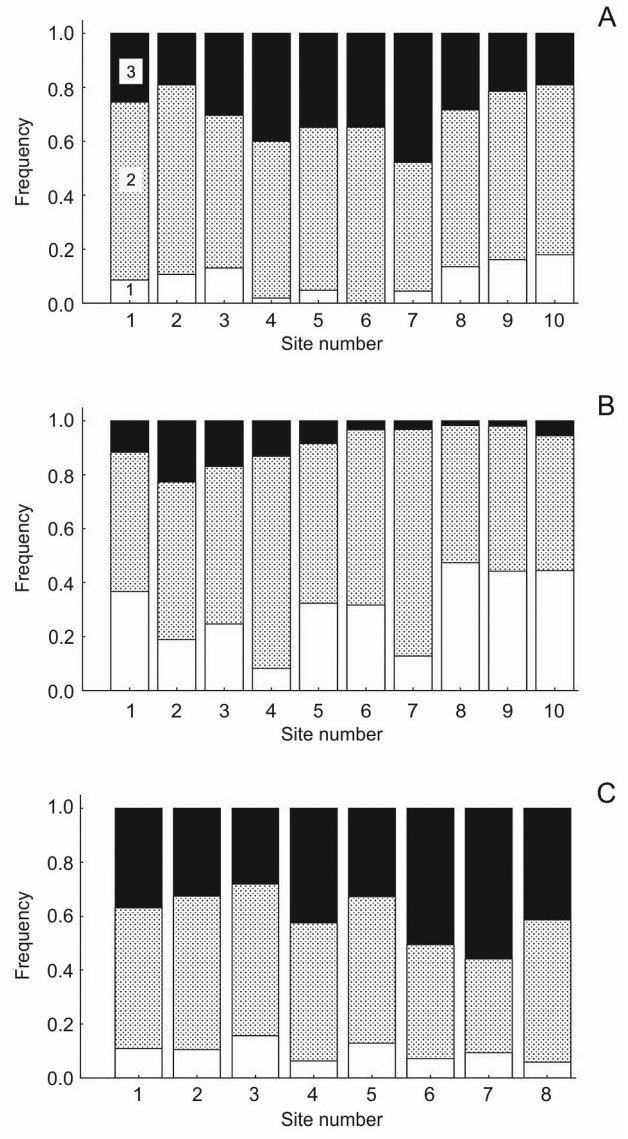

Fig. 25. Frequency distribution of different banding patterns in *X. derbentina* (1 – no bands, 2 – light bands, 3 – dark bands) from different populations: A – Mykolaiv, population Namyv; B – Mykolaiv, population Neftebaza; C – Mykolaiv, population Kosmos

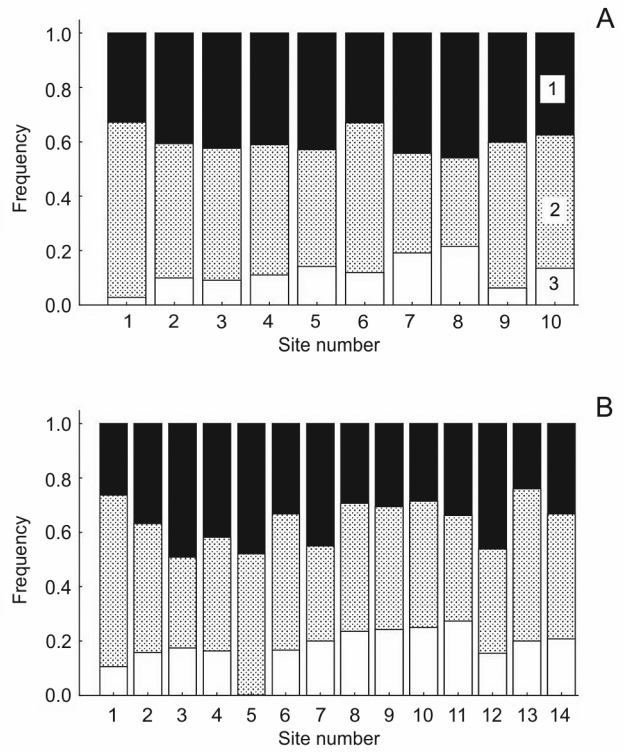

Fig. 26. Frequency distribution of different banding patterns in *X. krynickii* (1 – no bands, 2 – light bands, 3 – dark bands) from different populations: A – Mykolaiv, population Namyv; B – population Vilino

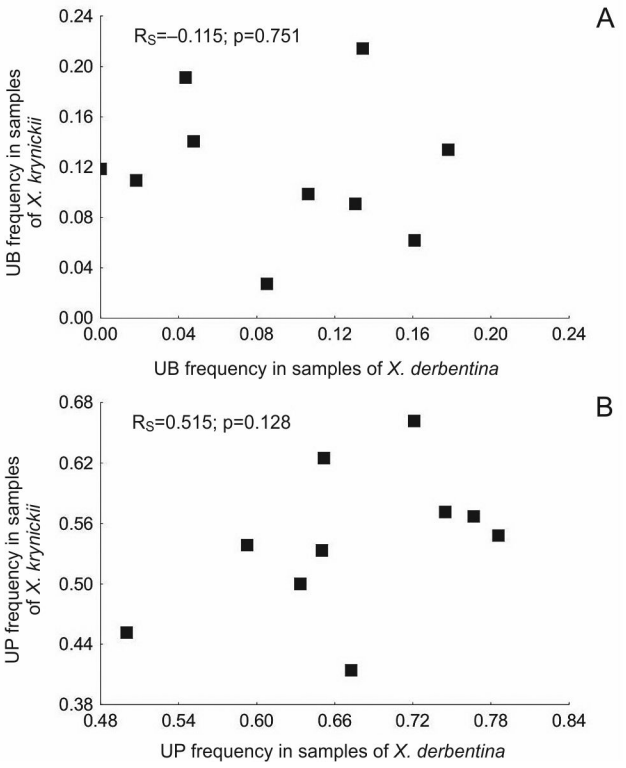

Fig. 27. Frequencies of morphs UB (A) and UP (B) in samples of *X. derbentina* and *X. krynickii* collected within the same sample plots, Mykolaiv, population Namyv

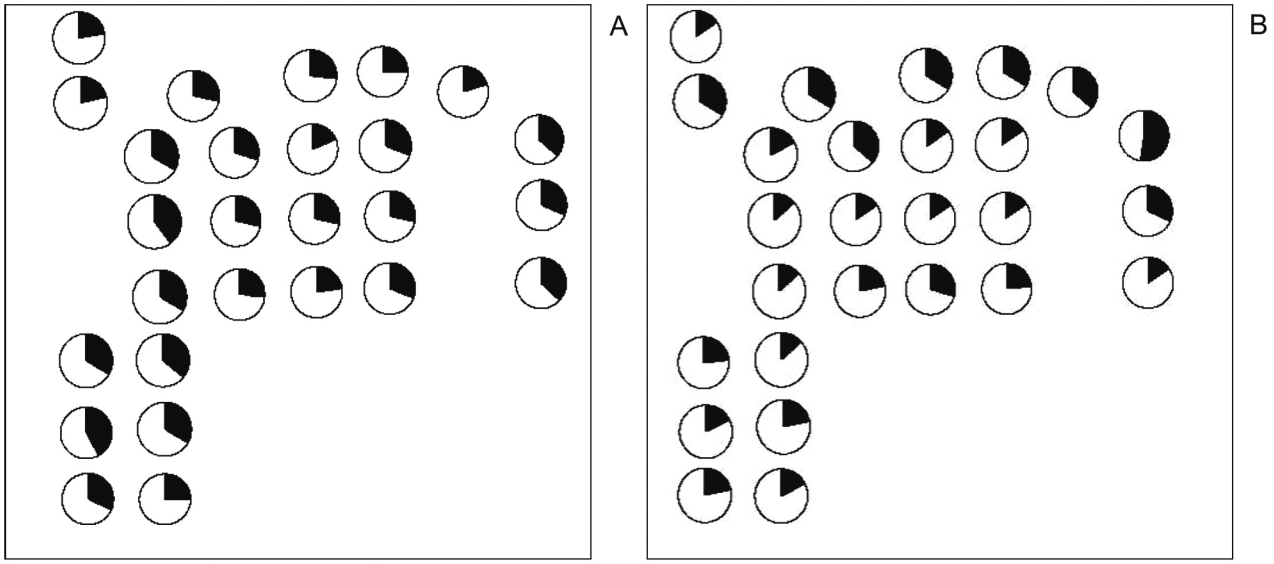

Fig. 28. Spatial variation within Vilino population of *X. derbentina*: A – morph UB, B – morph UP

in individual sampling sites, is 0.523 (Fig. 29A1, A2). For morph UB the pattern of spatial variation was completely random (Fig. 29B1, B2).

The effect of the number of sampling sites included in the analysis on the estimate of the degree of spatial structuring of the population in relation to shell banding was evaluated according to the algorithm previously described for morphometric characters (see: Variation in shell size and form: Microgeographical scale: Spatial variation). As expected, with increasing number of sampling sites, the performance of the assessment of morph differentiation increased, while the degree of their uncertainty decreased (Fig. 30).

As noted above, mixed populations of land snails are often found in Crimea and southern Ukraine, especially in various anthropogenic habitats. Most often they are represented by two species of *Xeropicta* (*X. derbentina* and *X. krynickii*). Comparative analysis of polymorphism of these two species co-occurring in the same habitats was carried out in order to determine the role of various mechanisms in the for-

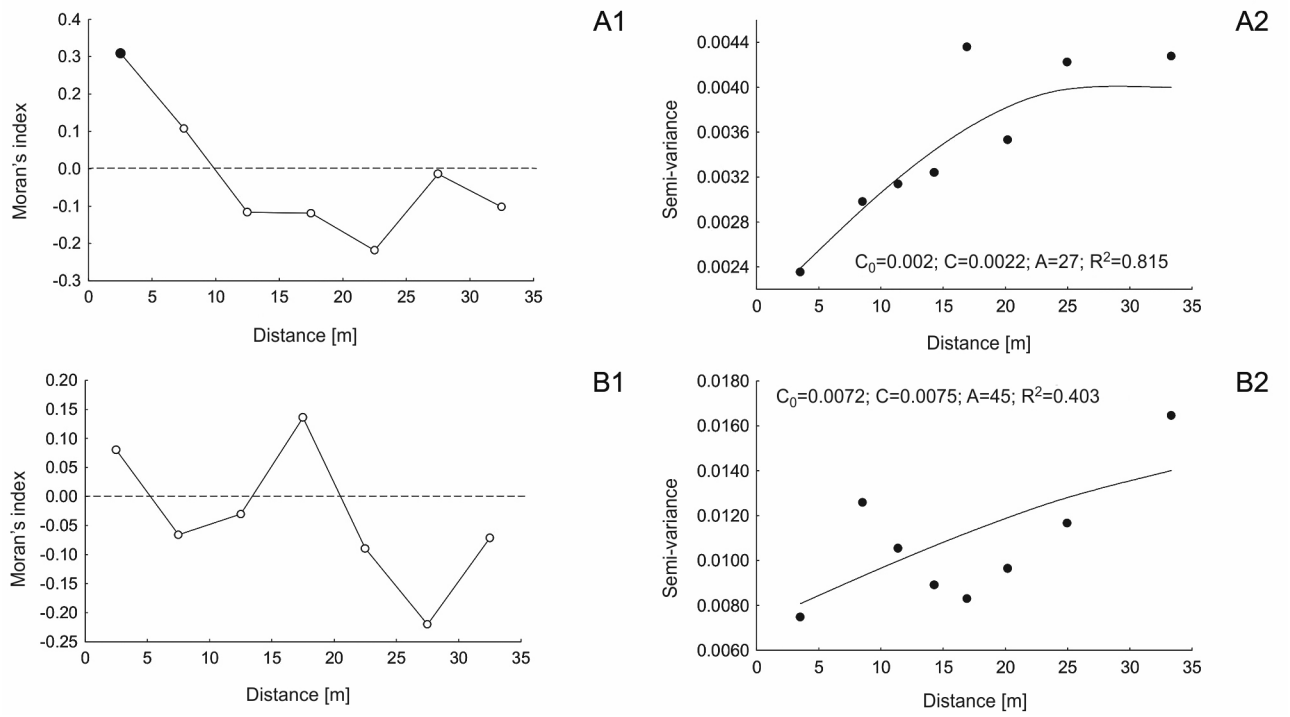

Fig. 29. Correlograms (1) and semi-variograms (2) of spatial variation of morphs UB (A) and UP (B) of *X. derbentina* in Vilino population (solid circles denote significant values of Moran's index)

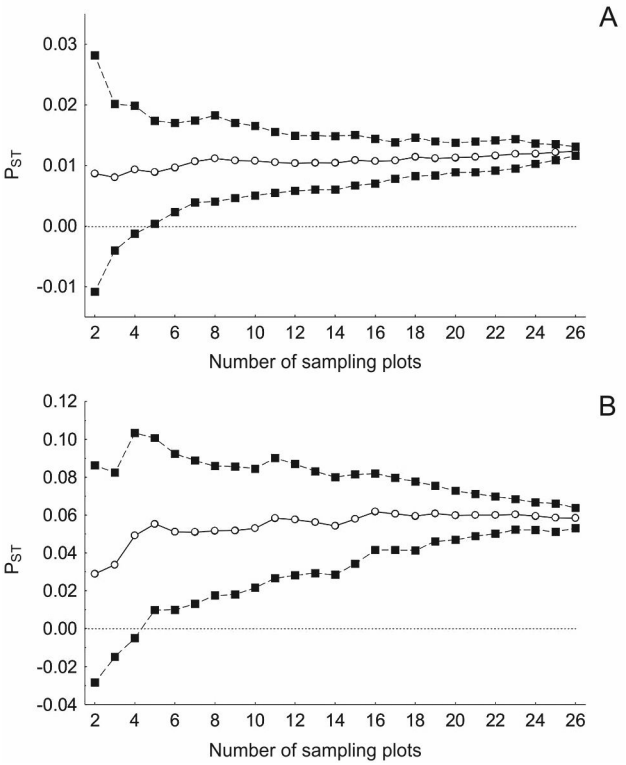

Fig. 30. Effect of number of sampling sites on P_{ST} values for morphs UB (A) and UP (B) of *X. derbentina* in Vilino population ($\overline{X} \pm SD$)

mation of micro-spatial structure of polymorphic populations of land snails, in particular: a) the role of isolating barriers, b) the role of microhabitat factors, c) the role of species-specific features of life cycle, and d) the role of stochastic population genetic processes.

The material was collected from eight sampling sites located in a vacant lot in Vilino (Crimea, Bakhchisaray district) in 2005 (Fig. 31). In total 4,053 snails were collected and examined (1,600 individuals of *X. derbentina* and 2,453 of *X. krynickii*). In this case, distances among the sampling sites were larger than in the previous cases (the effect of isolation by distance), and sites F and G were isolated from the rest by residential buildings and a road.

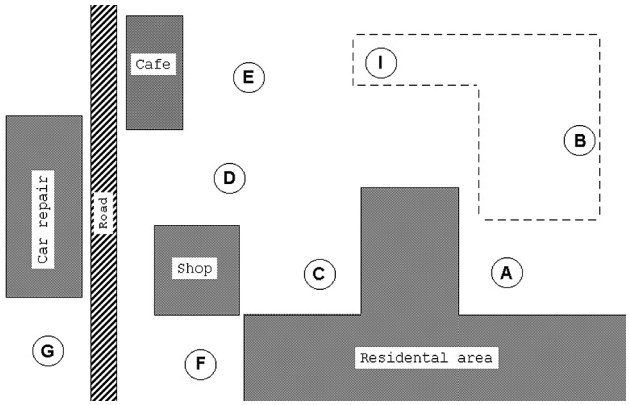

Fig. 31. Location of sampling sites of *X. derbentina* and *X. krynickii* in Vilino population in 2005 (dotted line marks the border of the area in which polymorphism of *X. derbentina* was investigated in 2008)

Figure 32 shows frequencies of UB and UP morphs in co-occurring *X. derbentina* and *X. krynickii*. There was some spatial variation in morph frequencies in both species; in most localities UB and UP frequencies were higher in *X. derbentina* than in *X. krynickii*. There was practically no variation among individual sites. However, as expected, morph frequencies in sites F and G were significantly different from those in the other localities. This was especially evident in *X. derbentina* (Fig. 32). However, significant estimates of variation were obtained only for *X. krynickii* (for UB: $P_{ST} = 0.0406 \pm 0.0184$; for UP: $P_{ST} = 0.0244 \pm 0.0090$). While the corresponding values for *X. derbentina* were generally higher (for UB: $P_{ST} = 0.0577 \pm 0.0521$; for UP: $P_{ST} = 0.0423 \pm 0.0333$), the presence of an outlier sample (from G site) significantly increased the estimate of statistical error and reduced the significance of the results.

The results of two-way variance analysis (2 species × 8 sites) confirm the large inter-specific variation in morph frequencies (Tables 18 and 19). Additionally, the patterns of spatial variation are different for those two species, as shown by significant F values in the analysis of simultaneous effects of the factors "species" × "site". This discrepancy is

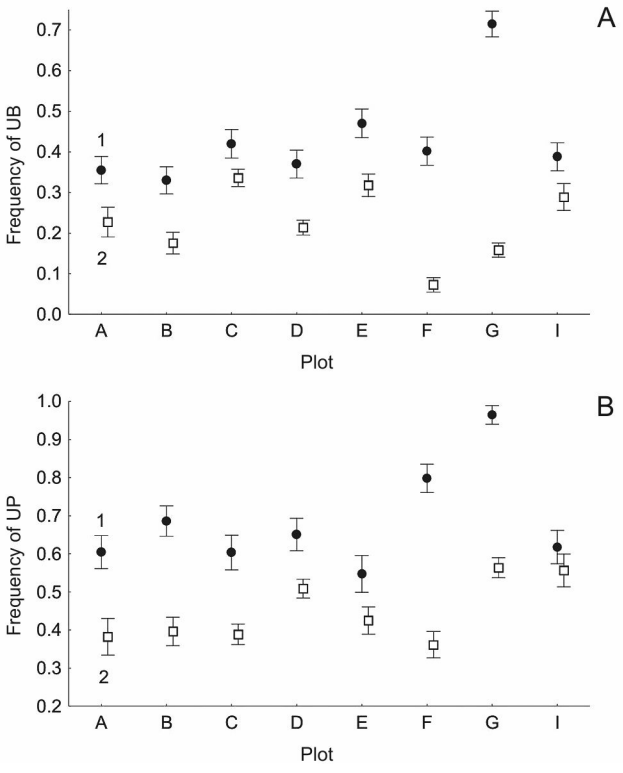

Fig. 32. Frequencies ($\overline{X} \pm SD$) of morphs UB (A) and UP (B) in samples of *X. derbentina* (1) and *X. krynickii* (2) collected at the same sites

Table 18. Results of two-way analysis of variance of effect of species and sampling site on frequencies of morph UB in *X. derbentina* and *X. krynickii* in Vilino. Significant values of P_{ST} ($p < 0.05$) indicated in bold

Source of variation	SS	df	MS	F	p	E(MS)	P_{ST}
Species (A)	38.303	1	38.303	9.973	0.016	0.0172	**0.0755**
Site (B)	10.547	7	1.507	0.392	0.880	0.0000	0.0000
A×B	26.885	7	3.841	19.563	0.000	0.0146	**0.0639**
Residual	792.555	4037	0.196			0.1963	0.8605
Total	868.290	4052					

Table 19. Results of two-way analysis of variance of effect of species and sampling site on frequencies of morph UP in *X. derbentina* and *X. krynickii* in Vilino. Significant values of P_{ST} ($p < 0.05$) indicated in bold

Source of variation	SS	df	MS	F	p	E(MS)	P_{ST}
Species (A)	25.775	1	25.775	14.503	0.007	0.0176	**0.0674**
Site (B)	8.702	7	1.243	0.700	0.675	0.0000	0.0000
A×B	12.440	7	1.777	7.602	0.000	0.0090	**0.0347**
Residual	649.183	2777	0.234			0.2338	0.8979
Total	696.100	2792					

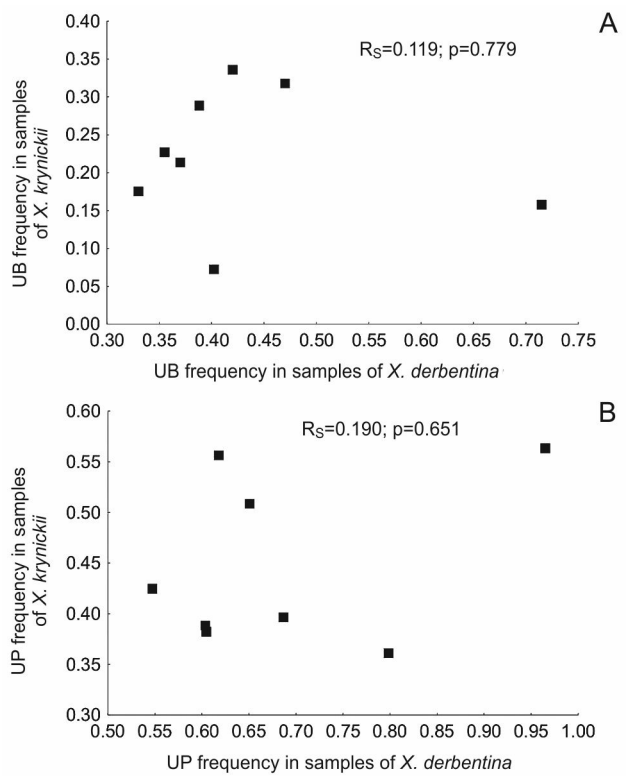

Fig. 33. Frequencies of morphs UB (A) and UP (B) in samples of *X. derbentina* and *X. krynickii* collected at the same sites in Vilino population (2005)

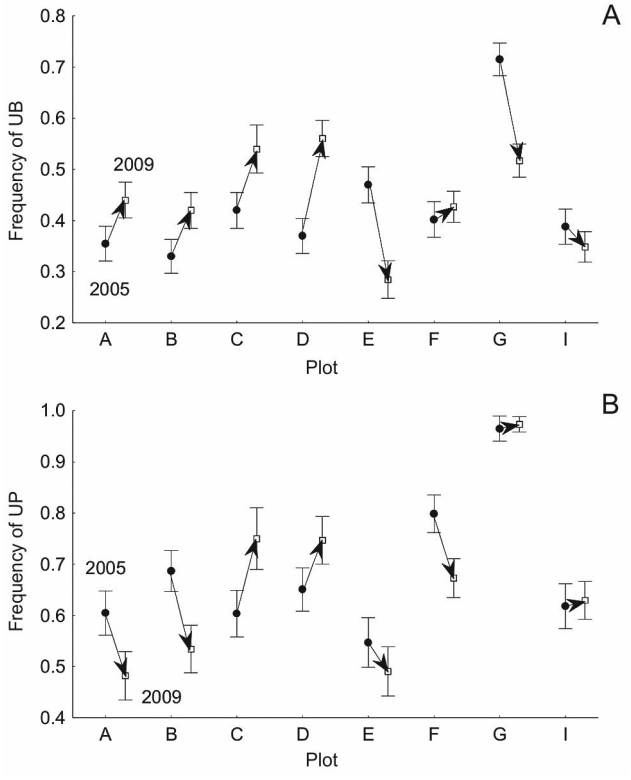

Fig. 34. Absolute values and direction of changes in frequencies of morphs UB (A) and UP (B) of *X. derbentina* in 2005–2009 at different sites in Vilino population

also reflected in the fact that there is no correlation between UB and UP frequencies in the samples of *X. derbentina* and *X. krynickii* collected from the same sampling plots (Fig. 33).

Thus, on micro-geographical scale, the structuring of shell colour polymorphism in the studied land snail populations is non-existent, or has a significant random component. Besides, patterns obtained for different co-occurring morphs or species have specific character and do not coincide spatially.

Chronological variation

Material for the analysis of chronological variation was collected in the same eight sites in the vacant lot in Vilino (Crimea, Bakhchisaray district) (Fig. 31). Samples of *X. derbentina* were collected four

years later, in 2009, from the same eight localities. Together 1,624 snails were collected and examined.

Figure 34 shows absolute magnitude and directions of changes in frequencies of UB and UP morphs of *X. derbentina* in 2005–2009. There were significant differences among the collection sites regarding both values and sign of those changes. The frequency of UB increased slightly in four sites, decreased in two, and in another two it showed no significant changes. The frequency of UP decreased in three sites, increased in two, and in three it did not change. Characteristically, there was almost no association among the sites regarding the magnitude and direction of changes. For example, in sites A–D, the frequencies of UB increased in 2009 compared to 2005. The frequencies of UP increased only in sites C and D, whereas in sites A and B, on the contrary, they decreased.

The independence and multi-directional character of changes in morph frequencies at different sites is clearly visible in the scatter diagram (Fig. 35). More or less matching patterns of chronological change could be observed for sites A, B and F. However, while for sites A and B it was possible to explain this similarity by their spatial proximity, site F was spatially distant and isolated by residential buildings. Perpendicular to them was the change in sites C and D, which were also close to each other. Changes in sites E and G went in the opposite direction, while no changes were observed in site I (Fig. 35).

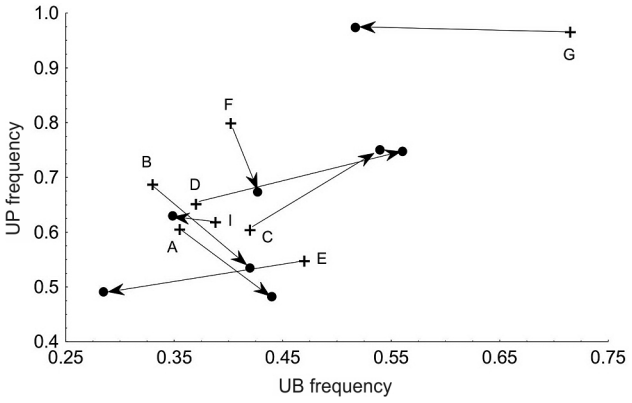

Fig. 35. Absolute values and direction of changes in frequencies of morphs UB and UP of *X. derbentina* at different sites in Vilino population. Arrows directed from 2005 to 2009

The results of two-way variance analysis of (2 years × 8 sites) also confirm that significant changes in morph frequencies occurred over the observation period (Tables 20 and 21). The spatial structure of shell banding polymorphism in *X. derbentina* changed over four generations differently in different parts of the studied population. This suggests that micro-habitat factors played an important role in shaping of this variation.

MESO-GEOGRAPHICAL SCALE

Samples of *C. vindobonensis* were collected according to a hierarchical approach to compare the patterns of variation at meso-geographical scale. The basic material for the analysis consisted of 12 samples from anthropogenic habitats and suburban areas of Mykolaiv (maximum distance between samples ca. 16,000 m). In addition, 14 more samples were collected within one of them (park Dubky). Here, the maximum distance between the sampling sites was about 900 m (Fig. 36). In total 4,082 snails (and empty shells) were collected and examined. The proportion of individuals with faintly-coloured bands (FB – faint-banded morph) was estimated for each sample.

There was a considerable variation in the frequency of FB morphs. In the samples from the Dubky population the frequency ranged from 0.013 to 0.791, while in the populations from Mykolaiv and its environs it

Table 20. Results of two-way analysis of variance of influence of year and sampling site on frequencies of morph UB in *X. derbentina* in Vilino. Significant values of P_{ST} ($p < 0.05$) indicated in bold

Source of variation	SS	df	MS	F	p	E(MS)	P_{ST}
Year (A)	0.049	1	0.05	0.025	0.8782	0.000	0.0000
Site (B)	18.716	7	2.67	1.380	0.3406	0.002	0.0074
A×B	13.558	7	1.94	8.174	0.0000	0.008	**0.0342**
Residual	760.129	3208	0.24			0.237	0.9584
Total	792.451	3223					

Table 21. Results of two-way analysis of variance of influence of year and sampling site on frequencies of morph UP in *X. derbentina* in Vilino. Significant values of P_{ST} ($p < 0.05$) indicated in bold

Source of variation	SS	df	MS	F	p	E(MS)	P_{ST}
Year (A)	0.102	1	0.10	0.152	0.7081	0.000	0.0000
Site (B)	26.028	7	3.72	5.521	0.0191	0.013	**0.0591**
A×B	4.715	7	0.67	3.210	0.0022	0.004	**0.0180**
Residual	378.698	1805	0.21			0.210	0.9229
Total	409.543	1820					

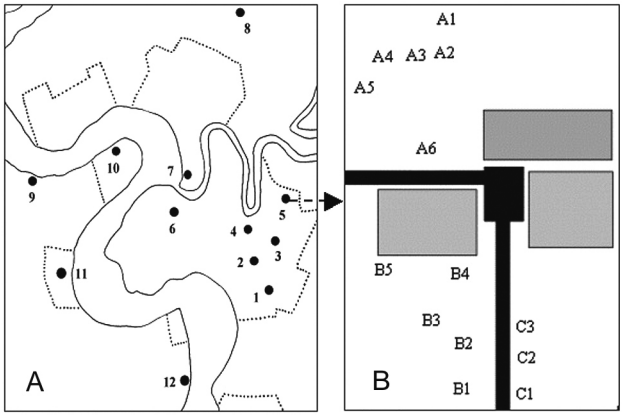

Fig. 36. Location of sampling sites of *C. vindobonensis*: A – Mykolaiv and its environs, B – Park Dubky

ranged from 0.012 to 0.485 (Fig. 37). However, any non-randomness in the spatial pattern of variation was observed only in Dubky. Two roads (Fig. 36B) dividing the area occupied by *C. vindobonensis* into three parts apparently played an isolating role, as can be inferred from the fact that the FB frequencies were significantly different among those areas, whereas within them they were relatively constant (Fig. 37B). Nevertheless, regardless of the size of the studied area, there was significant differentiation among populations or sites within a single population (for Dubky: P_{ST} = 0.291 ± 0.085; for Mykolaiv and suburbs: P_{ST} = 0.133 ± 0.039). The number of samples included in the analysis had practically no effect on the estimate of the level of differentiation, but it significantly reduced the level of uncertainty (Fig. 38).

The less pronounced variation in the FB frequencies among the samples from Dubky, compared to the larger area of Mykolaiv and its suburbs, apparently reflects a "coarse" pattern of spatial variation of this trait. The samples collected in the park Dubky form three sets within which the FB frequencies are similar; this apparently reflects the migration barrier posed by the roads (Fig. 37B). On the other hand, the 12 samples from Mykolaiv and its suburbs represent independently existing isolated populations in which the FB frequency can vary randomly (Fig. 37A). As a result, at meso-geographical scale, the pattern of spatial variation in the FB frequencies is random (Fig. 39A), whereas a more or less pronounced spatial autocorrelation is observed in the population from Dubky (Fig. 39B).

Considering all the possible variants of colour and banding pattern, 10 different morphs were detected in urban populations of *C. vindobonensis* (KRAMARENKO et al. 2007). Variation among the populations was significant. For example, while in a population in Mykolaiv Zoo (population #4) only four morphs were detected, all 10 morphs were found in a population on the lawn of the Regional Observatory (population #6). Urban populations differed significantly in their intra-population var-

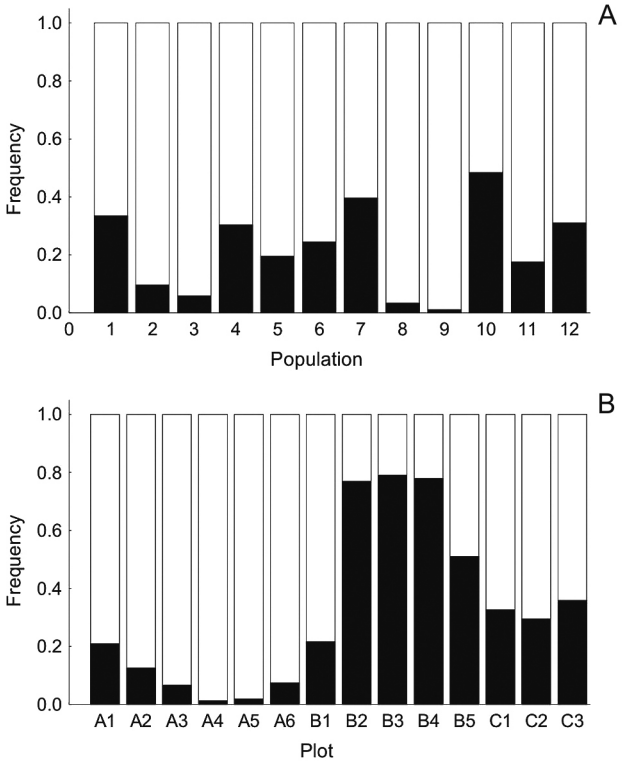

Fig. 37. Frequency of morph FB (in black) in *C. vindobonensis*: A – Mykolaiv and its environs; B – Park Dubky

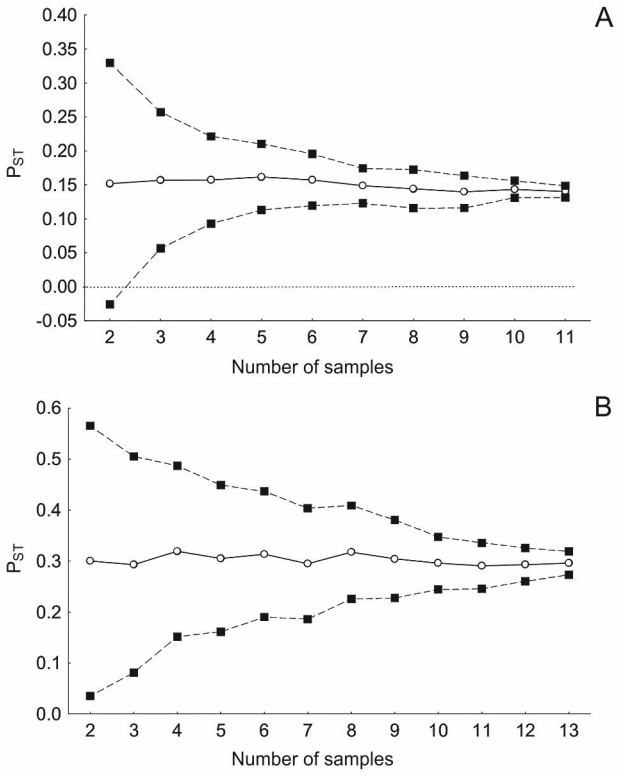

Fig. 38. Effect of number of samples on P_{ST} value for morph *FB* in *C. vindobonensis*: A – Mykolaiv and its environs, B – Park Dubky ($\overline{X}$ ± SD)

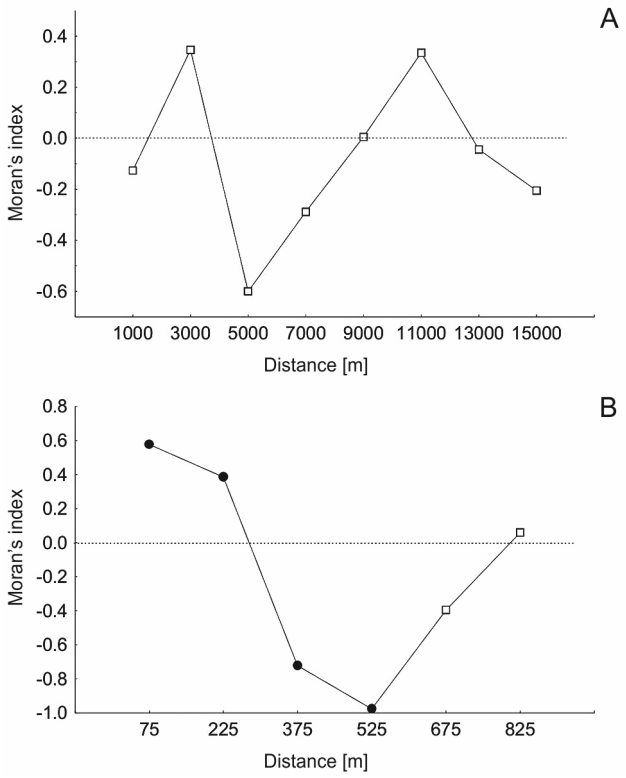

Fig. 39. Correlogram of spatial variation in frequencies of morph FB in *C. vindobonensis*: A – Mykolaiv and its environs; B – Park Dubky (solid circles denote significant values of Moran's index)

iation estimates: the mean number of morphs (ZHIVOTOVSKY 1991) ranged from 3.17 to 6.58 (Fig. 40). Besides, there was a gradual decrease in its values from urban to natural habitats. The proportion of rare morphs was similar in urban and suburban populations, and it was significantly higher than in populations from natural habitats (KRAMARENKO et al. 2007). The populations from anthropogenic habitats in Mykolaiv and its environs showed higher levels of both intra- and inter-population variation in their banding patterns. This can be explained by

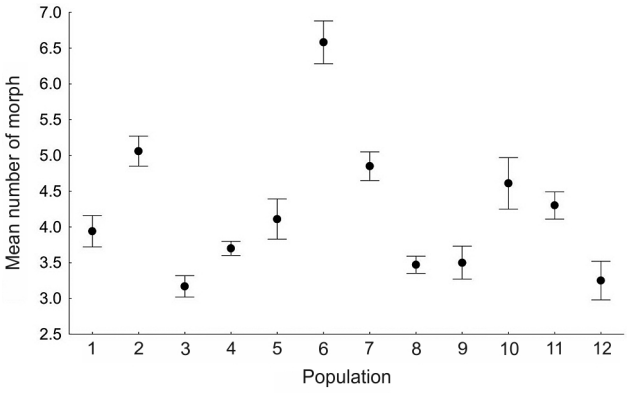

Fig. 40. Variation in the number of morphs (μ ± SE) in populations of *C. vindobonensis* from Mykolaiv and its environs

random loss of rare morphs (founder effect and genetic drift) in small populations from artificial sites. Besides, a wide variation in frequencies of individual morphs or groups of morphs was observed among urban populations. Natural populations, in contrast, were characterised by a more uniform structure of banding polymorphism (KRAMARENKO et al. 2007).

MACRO-GEOGRAPHICAL SCALE

Geographical variation in *Helix albescens*

Material for this analysis was collected in 28 populations of *H. albescens*, located in various physiographic regions of Crimea (Fig. 41).

In total 14 banding morphs were distinguished (KRAMARENKO & LEONOV 2011). The largest number of morphs was observed in various habitats of Simferopol (13), on the southern coast of Crimea (11), in steppe Crimea (10), and on the Kerch Peninsula (9) (Table 22). A higher diversity of urban populations compared to natural ones was also recorded for *C. vindobonensis* in southern Ukraine (see: Polymorphism of shell colour and banding pattern: Meso-geographical scale). A characteristic feature of the Simferopol populations of *H. albescens* was the absence of morphs 12305 and 12005 and high frequencies of morphs 12045 and 10045. The south coast populations were characterised by relatively high frequencies of morphs 00000, 10345, and 10305. The samples from Kerch were very uniform: 95.8% of individuals were 12345 or 1(23)45, with the dominance of 1(23)45 whose frequency was 3–4 times higher than in the other regions of Crimea (Table 22). The smallest diversity was recorded in the samples from the Kerch Peninsula (μ = 1.89–1.97), and the greatest (μ = 8.00) in a sample from Simeiz. The greatest diversity was observed in the populations from the Crimean southern coast (μ = 6.82 ± 0.19) (Table 23). The urban populations in Simferopol and the populations in steppe Crimea showed approximately the same level of polymorphic diversity (μ = 6.55 ± 0.28 and 6.49 ± 0.13, respectively), whereas in the samples from the Kerch Peninsula it was almost twice smaller (μ = 3.52 ± 0.19). The values of Shannon and Simpson indices reflect this regularity. Polymorphic variation in the four regional groups of populations was significantly different (in all cases: $p_{perm} < 0.05$). The only exception was the proportion of rare morphs, which was approximately the same in populations from different regions of Crimea (Table 23).

Table 24 presents the results of two-way hierarchical ANOVA assessing the level of polymorphic variation among different regions and different populations within the regions. Overall, the inter-population variation in morph frequencies was rather

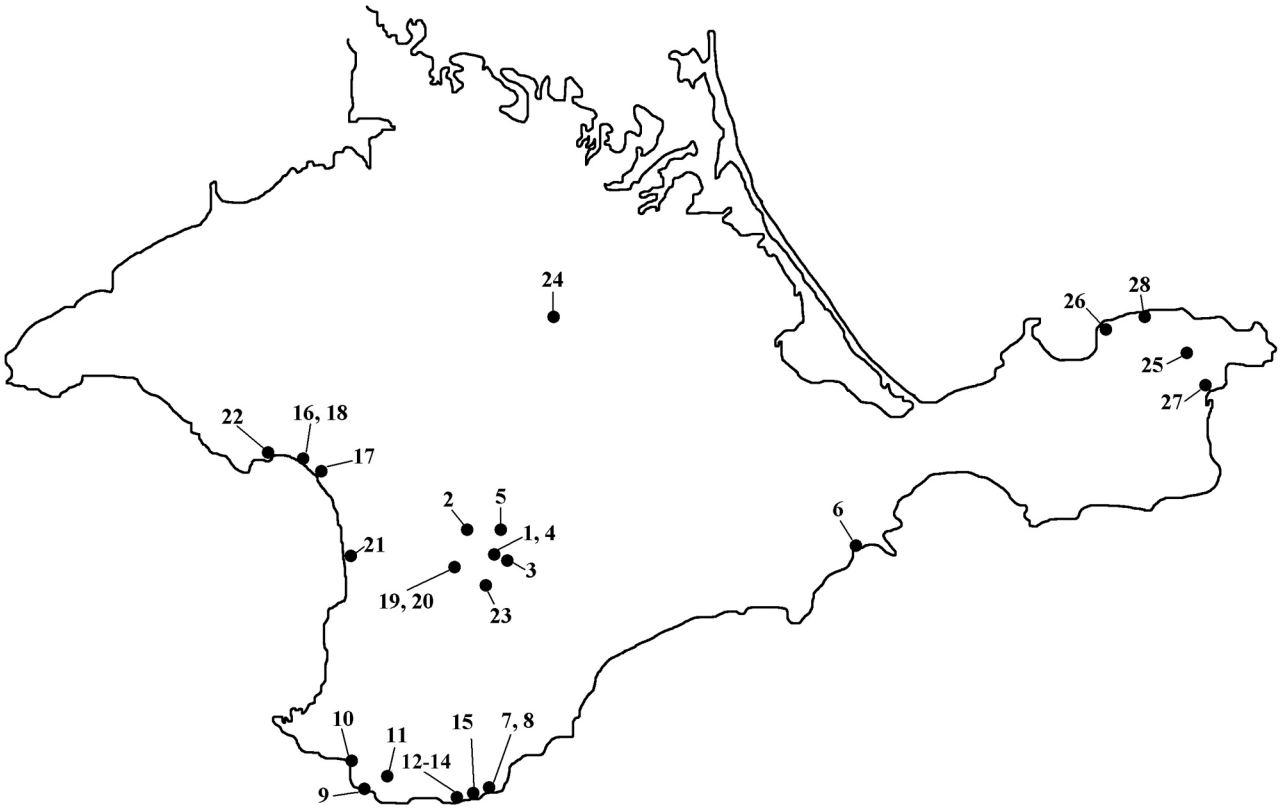

Fig. 41. Location of sampled populations of *H. albescens* in Crimea. For population numbers see Table 22

high and amounted to almost 17% (P_{PT} = 0.1673; p = 0.01). On the other hand, some regions of Crimea were more similar to each other (P_{RT} = 0.0563; p = 0.01) than were populations within those regions (P_{PR} = 0.1177; p = 0.01).

Figure 42 shows the distribution of polymorphic variation expressed by various metrics (number of detected morphs, Simpson and Shannon indices) in the 28 populations of *H. albescens*, divided into separate components according to LANDE (1996). Variation among populations accounted for more than 50% of the total variation in the number of morphs. The remaining 50% was almost equally divided into intra- and inter-regional variation (26.43% and 24.29%, respectively). For the Simpson and Shannon indices, the inter-population component was smaller (14.56% and 22.87%, respectively); almost a third accounted for the inter-regional variation and two-thirds for the variation among populations within the regions. However, for all three metrics the estimates of inter- and intra-regional variation were significant (in all cases: p < 0.05).

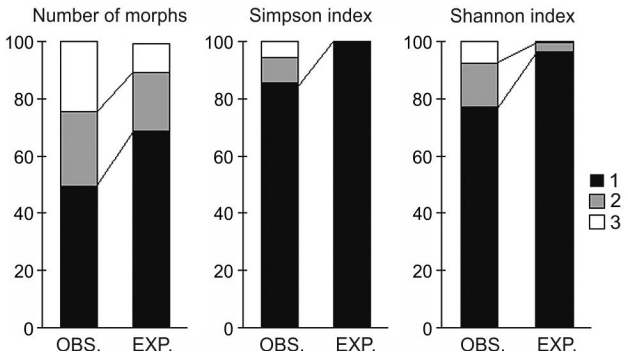

Fig. 42. Distribution (%) of polymorphic variation (expressed as number of morphs, and Simpson and Shannon indices) in *H. albescens* among separate components: 1 – intra-population variation, 2 – variation among populations within regions, 3 – variation among regions. Obs. – actual values; Exp. – after 1,000 permutations

Regardless of the variation in qualitative and quantitative structure of polymorphism, some populations displayed features which were specific to their geographical location. The results of discriminant analysis indicate that the accuracy of classification of populations to appropriate groups based on morph frequencies is 96.4% (i.e. erroneous decision can be made in one out of 28 cases; of the nine populations from the steppe Crimea, one was mistakenly attributed to the group from the southern coast of Crimea). The frequencies of morphs 12045 and 10045 contributed most to the discrimination of populations (first canonical axis), followed by the frequencies of morph 1(23)45 (second canonical axis).

There were two main trends in the variation of polymorphic structure of *H. albescens*: an increase in frequencies of 12045 and 10045 from the southern

Table 22. Composition of samples of *H. albescens* from Crimea

No.	Population	Morph														
		12345	1(23)45	10345	12045	12305	10045	12005	10005	10305	02045	00005	00000	1(23)(45)	123(45)	Total
							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-5	37	14	8	4	1	11	–	10	–	–	–	–	–	–	85
	Total	270	83	15	83	2	36	1	24	4	1	3	1	–	1	524
							southern coast of Crimea									
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	Koshka Mnt.	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-2 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	Mykolaivka	78	16	1	11	–	2	8	2	–	–	–	–	–	–	118
22	Evpatoria	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	–	1,349
							Kerch Peninsula									
25	Bagerovo	75	93	3	2	1	–	–	1	1	–	–	–	1	–	177
26	Zolotoye	57	90	–	–	–	–	–	–	–	–	–	–	–	–	147
27	Kerch	5	51	1	–	–	–	–	–	–	–	–	–	–	–	57
28	Skala Mnt.	36	108	2	3	5	–	–	–	–	–	–	–	2	1	157
	Total	173	342	6	5	6	–	–	1	1	–	–	–	3	1	538

coast to Simferopol, and an increasing frequency of morph 1(23)45 from the southern coast to the Kerch Peninsula (Fig. 43). Besides, there was a significant correlation between the hydro-meteorological parameters and the frequencies of some morphs. The proportion of shells with fused bands was negatively correlated with the long-term mean July temperature (R_S = –0.390; n = 28; p = 0.040), while the proportion of shells with missing bands was positively associated with the long-term mean July temperature (R_S = 0.403; n = 28; p = 0.033). These results indicate that there is a tendency for dark-coloured shells to occur in higher proportions in cooler places and for light-coloured shells in warmer places. This is consistent with the earlier results obtained for snails of the genus *Cepaea* (JONES et al. 1977).

Table 23. Intra-population diversity in banding polymorphism of *H. albescens* from populations of Crimea

No.	Population	Number of morphs	Shannon index (H_{SH})	Simpson index	Mean number of morphs ($\mu \pm SE$)	Proportion of rare morphs ($h \pm SE$)
			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 coast of Crimea			
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	Koshka Mnt.	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-2 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	Mykolaivka	7	1.171±0.224	0.469±0.169	4.41±0.31	0.370±0.044
22	Evpatoria	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	Zolotoye	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	Skala Mnt.	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 24. Hierarchical two-way analysis of variance of frequencies of shell banding morphs in *H. albescens* in Crimea

Source of variation	SS	df	MS	E(MS)
Among regions	60.783	3	20.261	0.020
Among populations within regions	110.699	24	4.612	0.039
Within populations	925.735	3187	0.290	0.290
Total	1097.216	3214	25.164	0.349

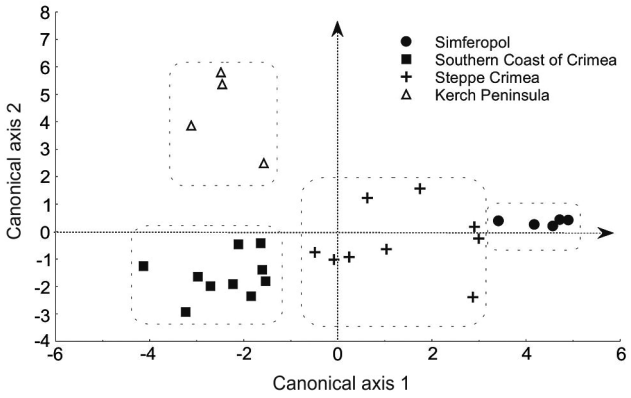

Fig. 43. Distribution of centroids of populations of *H. albescens* in Crimea in the space of the first two canonical axes of the discriminant analysis

Using the data presented above and the data published by SVERLOVA et al. (2006), I analysed the pattern of macro-geographical variation in the frequency of morph 12345 within 40 Crimean populations *H. albescens* (Fig. 44). The frequencies of this morph varied widely: from 0.025 (Belogorsk) to 0.982 (Balaklava), with a distinct cline from the south and west coasts of Crimea to the Kerch Peninsula (KRAMARENKO 2009c). Characteristically, populations from anthropogenic habitats in Simferopol showed a high level of inter-population variation, which corresponds with the results obtained for *C. vindobonensis* (see above). The existence of a macro-geographical cline in the distribution of morph 12345 is confirmed in the correlogram (Fig. 45).

The significant positive estimates of Moran's index for small distances (20–80 km) and the significant negative estimates for large distances (150–250 km) indicate a positive spatial autocorrelation, in which frequencies of morph 12345 are similar in neighbouring populations and differ significantly in distant populations. At macro-geographical scale, as in the case of morphometric characters (see: Variation in shell size and form: Macro-geographical scale), the distribution of shell polymorphism in *H. albescens* suggests the effect of climatic gradients resulting in formation of distinct clines.

Geographical variation of *Cepaea vindobonensis*

In this analysis I used original and published data (GURAL-SVERLOVA & MARTYNOV 2007) on a total of 7,647 snails (and empty shells) from 37 populations (Fig. 46).

The frequencies of FB morph varied considerably, from 0.000 to 0.807 (Sebino, Novaya Odessa district, Mykolaiv area). The morph was absent in the majority of east Ukrainian populations (Fig. 46). In general, there was a highly significant inter-population differentiation in the frequencies of morph FB (P_{PT} =

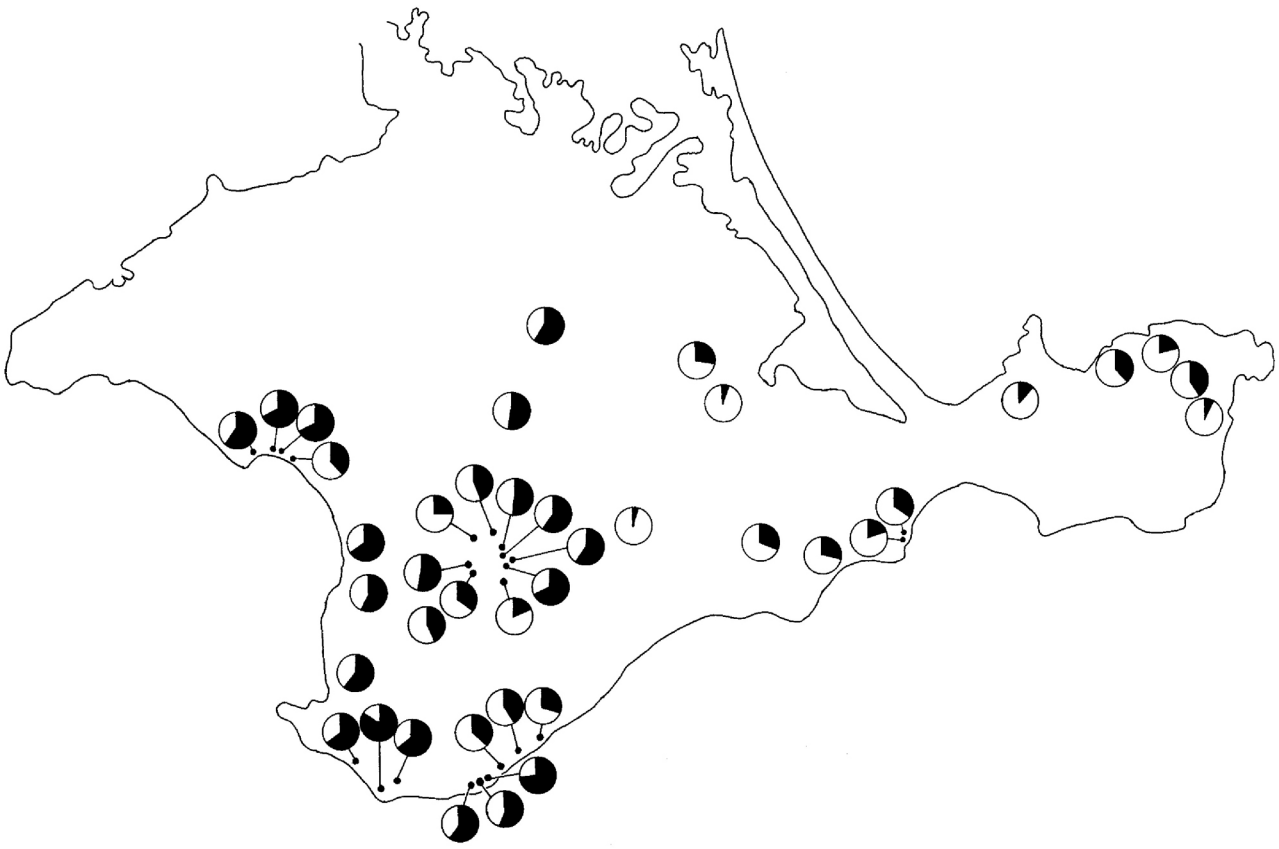

Fig. 44. Geographical variation in frequency of morph 12345 in populations of *H. albescens* in Crimea

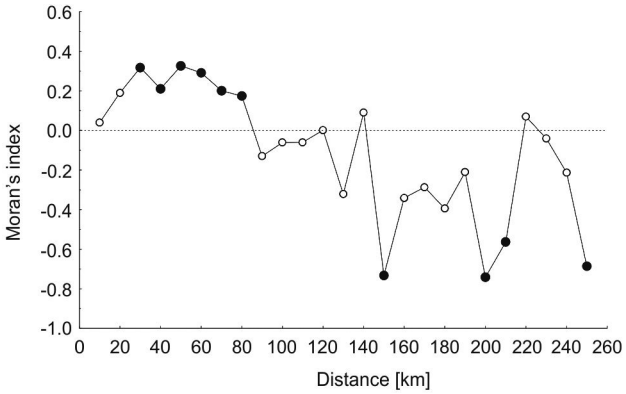

Fig. 45. Correlogram of frequencies of morph 12345 in populations of *H. albescens* in Crimea (solid circles indicate significant values of Moran's index)

0.3617; $p < 0.01$) (Table 25), with significant differences both among the whole regions (southern, eastern and central Ukraine) ($P_{RT} = 0.0915$; $p < 0.05$), and among the populations within those regions ($P_{PR} = 0.2974$; $p < 0.01$).

Distribution patterns of the FB frequencies show a significant geographical component (Fig. 47), with a significant decreasing trend from west to east. The latitudinal trend is less pronounced, mostly because of the very high frequency of morph FB in one central-Ukrainian population (Kanev, Cherkassy district). When it is deleted, the association between the latitude and the frequency of morph FB becomes significant ($R_S = –0.356$; $n = 36$; $p = 0.033$) (dotted line in Fig. 47). Apparently, this pattern results from the influence of macro-climatic conditions, as indicated by the significant correlation between the frequencies of morph FB and the hydro-climatic parameters: in warmer and more arid areas the frequencies of faint-banded *C. vindobonensis* tend to increase. However, no such correlation was found for the other morphs (Table 26).

GENETIC POLYMORPHISM

MICRO-GEOGRAPHICAL SCALE

In this analysis I used data on *B. cylindrica* collected from three populations (Dubky, Neftebaza and

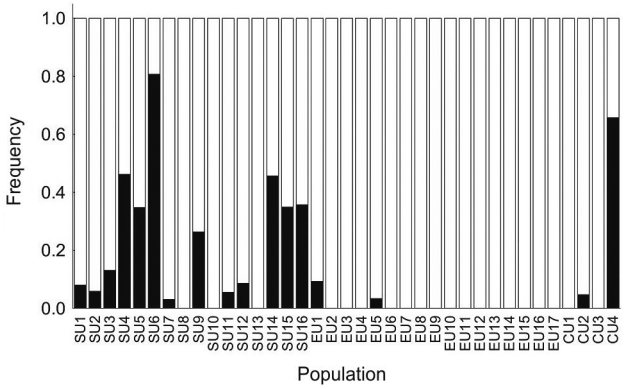

Fig. 46. Frequencies of morph FB in populations of *C. vindobonensis*. SU – south Ukrainian; EU – east Ukrainian; CU – central Ukrainian

Table 25. Hierarchical two-way analysis of variance of frequencies of morph FB in *C. vindobonensis*

Source of variation	SS	df	MS	E(MS)
Among regions	53.485	2	26.742	0.0092
Among populations within regions	182.632	34	5.372	0.0273
Within populations	490.448	7610	0.064	0.0644
Total	726.565	7646		

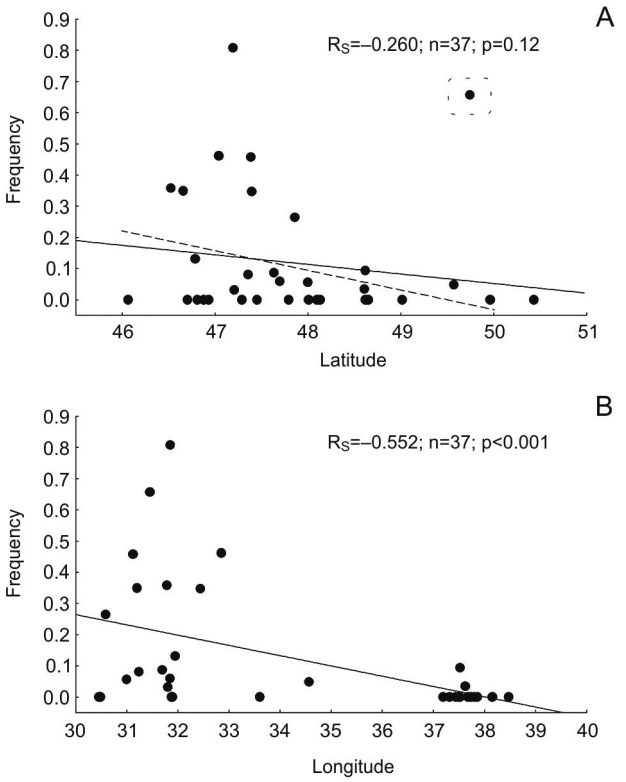

Fig. 47. Variation in frequency of morph FB in populations of *C. vindobonensis* in relation to latitude (A) and longitude (B)

Table 26. Coefficients of Spearman's rank correlation (R_S) between frequencies of main morphs in populations of *C. vindobonensis* and hydro-climatic parameters of places of their occurrence. Significant values of correlation coefficient ($p < 0.05$) indicated in bold

Morph	Hydro-climatic parameters			
	T1	T7	D10	ATP
FB	**0.497**	0.074	**0.419**	**–0.362**
12345	0.019	–0.005	–0.093	–0.008
10345	–0.029	–0.049	0.049	0.048
1(23)45	–0.198	0.015	–0.182	0.205

For hydro-climatic parameters see: Material and methods.

Park Pobedy) in anthropogenic habitats in Mykolaiv (Fig. 48). In each population I collected two samples of 25 mature individuals; the distance between sampling sites was 50 m.

Table 27 presents data on genetic variation of six allozymic loci in the studied populations of *B. cylindrica*. These loci were monomorphic in nine out of 36 cases (twice locus Est4, three times locus Sod4, and four times locus Sod2). The distribution of genotypes deviated from equilibrium in only four cases, and this was due to the deficiency of heterozygotes in the samples (Table 27). In general, there was no excess or deficiency of homozygotes among the examined individuals (Fig. 49). The mean heterozygosity for all six loci was smaller in the samples from Dubky (0.192 and 0.056) than in those from Neftebaza (0.232 and 0.270) and Park Pobedy (0.220 and 0.279).

The snails were genetically diverse, both within and among the populations. This was indicated by the low values of assignment indices of individuals in relation to the samples of origin in the assignment-test (Table 28). On average, only 43% of individuals were correlated with the population of their origin. In this respect Dubky-2 was genetically unique: 21 out of 25 examined individuals were correctly assigned to their own population.

The genetic structure differed significantly among the samples (and their respective populations) (Table 29); there were highly significant differences both between the samples within populations (F_{SP} = 0.033; p = 0.001), and among the populations (F_{PT} = 0.088; p = 0.001). As expected, differences between the samples from different populations were most significant (F_{ST} = 0.119; p = 0.001). However, in only one case (population Dubky) samples collected from the same continuous population differed significantly from each other in their genetic structure (Table 30). In general, differences between the samples in almost all cases were highly significant, and the estimates of gene flow between them varied from 0.555 to 9.220 individuals per generation.

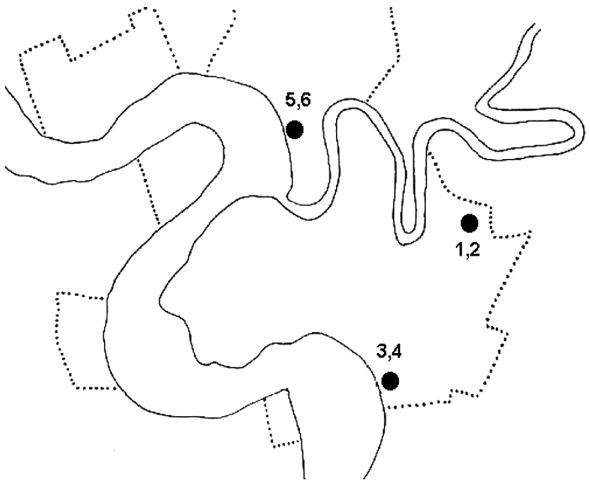

Fig. 48. Location of sampling sites of *B. cylindrica* in Mykolaiv: 1, 2 – Dubky 3, 4 – Neftebaza; 5, 6 – Park Pobedy

Figure 50 shows the distribution of samples of *B. cylindrica* based on matrices of estimates of genetic differentiation. Similar results were obtained on the basis of different estimates – all samples were differentiated into three separate groups. The first group consisted of two samples from the population Park Pobedy, the second included only the sample

Table 27. Data on allozymic diversity in populations of *B. cylindrica*. Mono – monomorphic locus. Loci with significant deviation from Hardy-Weinberg equilibrium indicated in bold

Locus	Ae	Ho	He	Fis
Dubky-1				
Est3	2.399	0.560	0.583	0.040
Est4	1.041	0.040	0.039	–0.020
Mdh1	1.083	0.080	0.077	–0.042
Mdh2	1.836	0.360	0.455	0.209
Sod2	1.000	0.000	0.000	mono
Sod4	1.000	0.000	0.000	mono
Dubky-2				
Est3	1.041	0.040	0.039	–0.020
Est4	1.000	0.000	0.000	mono
Mdh1	1.041	0.040	0.039	–0.020
Mdh2	1.220	0.200	0.180	–0.111
Sod2	1.000	0.000	0.000	mono
Sod4	1.083	0.080	0.077	–0.042
Neftebaza-1				
Est3	2.197	0.560	0.545	–0.028
Est4	1.041	0.040	0.039	–0.020
Mdh1	1.173	0.160	0.147	–0.087
Mdh2	1.523	0.200	0.343	**0.417**
Sod2	1.083	0.000	0.077	**1.000**
Sod4	1.317	0.280	0.241	–0.163
Neftebaza-2				
Est3	1.997	0.520	0.499	–0.042
Est4	1.000	0.000	0.000	mono
Mdh1	1.368	0.320	0.269	–0.190
Mdh2	1.874	0.400	0.466	0.142
Sod2	1.448	0.120	0.310	**0.612**
Sod4	1.083	0.080	0.077	–0.042
Park Pobedy-1				
Est3	3.444	0.640	0.710	**0.098**
Est4	1.317	0.200	0.241	0.169
Mdh1	1.419	0.360	0.295	–0.220
Mdh2	1.083	0.080	0.077	–0.042
Sod2	1.000	0.000	0.000	mono
Sod4	1.000	0.000	0.000	mono
Park Pobedy-2				
Est3	3.444	0.720	0.710	–0.015
Est4	1.574	0.240	0.365	0.342
Mdh1	1.625	0.280	0.385	0.272
Mdh2	1.274	0.160	0.215	0.257
Sod2	1.000	0.000	0.000	mono
Sod4	1.000	0.000	0.000	mono

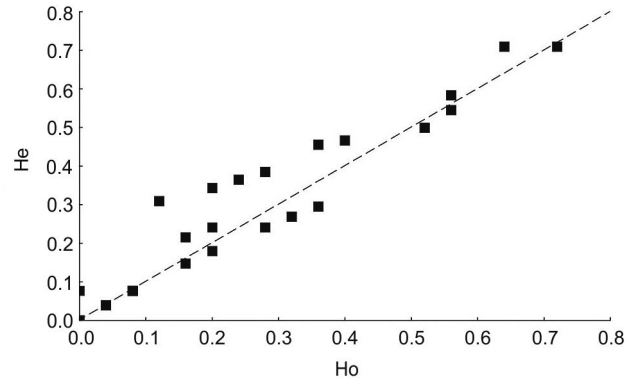

Fig. 49. Relationship between observed (Ho) and expected (He) heterozygosity at six allozyme loci in samples of *B. cylindrica*

Table 28. Results of assignment-test for allozymes among samples of *B. cylindrica*

Population/ sample	Number of individuals	
	correctly assigned	incorrectly assigned
Dubky-1	5/20%	20/80%
Dubky-2	21/84%	4/16%
Neftebaza-1	12/48%	13/52%
Neftebaza-2	6/24%	19/76%
Park Pobedy-1	12/48%	13/52%
Park Pobedy-2	9/36%	16/64%
Mean	65/43%	85/57%

Dubky-1, and the third comprised both samples from the population Neftebaza and the sample Dubky-2. Thus, while there were distinct genotypic differences among individuals from different populations, within the population Dubky there was a considerable intra-population differentiation between the sampling sites, which were spatially separated from each other by a relatively short distance. However, in the other two populations no such differentiation was observed (KRAMARENKO & SNEGIN 2015).

MESO-GEOGRAPHICAL SCALE

In the analysis at meso-geographical scale I used six populations of *B. cylindrica* – the three described above, and another three (Fig. 51). In addition to the allozyme variation, RAPD marker polymorphism

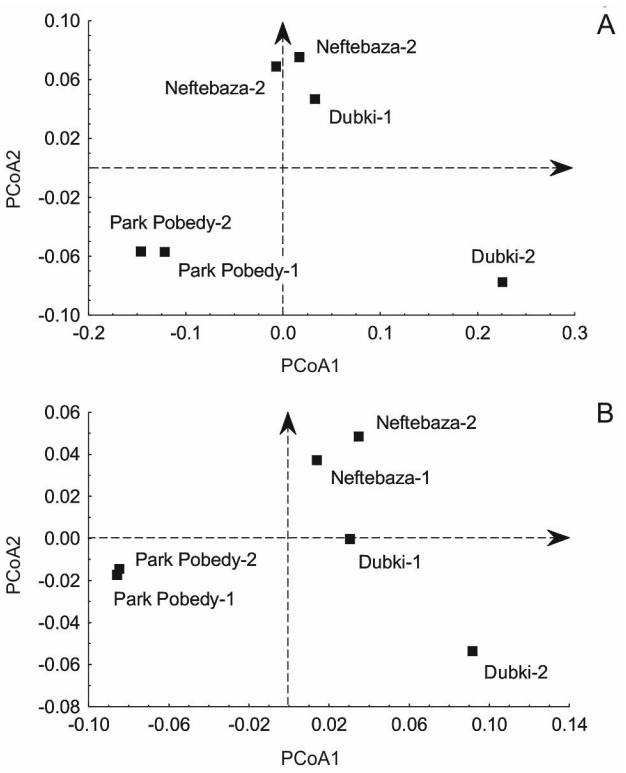

Fig. 50. Distribution of centroids of samples of *B. cylindrica* in the space of the first two principal coordinates based on matrices of pairwise genetic differentiation F_{ST} (A) and matrices of Nei's genetic distances (B)

Table 29. AMOVA results for tests of differentiation among populations of *B. cylindrica* on micro-geographical scale based on allozyme loci. Significant levels of F_{ST} ($p < 0.05$) are based on 999 permutations and indicated in bold

Source of variation	SS	df	MS	E(MS)	F-statistics
Among populations	16.223	2	8.112	0.064	F_{PT} = **0.088**; p = 0.001
Among samples within populations	5.220	3	1.740	0.022	F_{SP} = **0.033**; p = 0.001
Within samples	187.480	294	0.638	0.638	F_{ST} = **0.119**; p = 0.001
Total	208.923	299	10.489	0.723	

Table 30. Pairwise F_{ST} (below diagonal) and Nm (above diagonal) among 6 samples of *B. cylindrica* based on allozyme loci. Significant levels of F_{ST} ($p < 0.05$) after Bonferroni correction are based on 999 permutations and indicated in bold

Population/sample	Dubky-1	Dubky-2	Neftebaza-1	Neftebaza-2	Park Pobedy-1	Park Pobedy-2
Dubky-1	X	1.655	8.727	9.220	2.165	2.486
Dubky-2	**0.131**	X	1.203	1.386	0.555	0.671
Neftebaza-1	**0.028**	**0.172**	X	26.581	2.822	3.295
Neftebaza-2	0.025	**0.153**	0.009	X	2.133	2.788
Park Pobedy-1	**0.104**	**0.311**	**0.081**	**0.105**	X	126.554
Park Pobedy-2	**0.091**	**0.271**	**0.071**	0.082	0.002	X

was analysed in order to compare the patterns obtained for different types of molecular genetic markers.

The mean heterozygosity for six allozyme loci in the populations of *B. cylindrica* varied widely – from 0.143 (population Morekhodnaya) to 0.300 (population Mira). The range of mean heterozygosity for 46 loci of RAPD markers was considerably narrower: from 0.363 (population Neftebaza) to 0.407 (population Morekhodnaya).

The analysis of molecular variation among the populations of *B. cylindrica* showed a highly significant genetic differentiation in both allozyme and RAPD marker loci (Tables 31 and 32). However, the level of genetic differentiation obtained using allozymes was almost 3.5 times higher than the estimate obtained using RAPD markers.

Different results were obtained for allozymes and RAPD marker loci in pair-wise estimates of genetic differentiation between the studied populations (Tables 33 and 34). The analysis of allozyme loci indicates significant differences in the genetic structure among the populations in Mykolaiv, whereas the analysis of RAPD markers indicates genetic uniqueness of individuals from the populations Dubky and Neftebaza, and genetic similarity of the remaining populations (Table 34). In general, the patterns of inter-population variation of genetic structure of the examined populations obtained using allozymes and RAPD markers differ from each other (Fig. 52). The Mantel correlation coefficient between the matrices of genetic differentiation obtained for different types of markers is $R_M = -0.301$ ($p = 0.197$).

Not all the allozyme loci contributed equally to the genetic differentiation of the populations (Table 35). The mean score of the G_{ST} index for six loci was similar to that obtained using molecular analysis of variation (0.198 and 0.213, respectively), although for different loci this estimate ranged from 0.047 (locus Est4) to 0.294 (locus Est3).

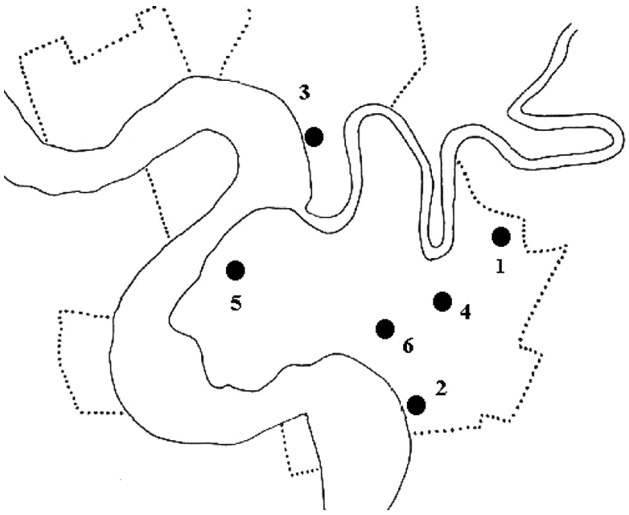

Fig. 51. Location of sampling sites of *B. cylindrica* in Mykolaiv: 1 – Dubky; 2 – Neftebaza; 3 – Park Pobedy; 4 – Kosmos; 5 – Morekhodnaya; 6 – Mira

The mean gene flow between the populations ranged from 0.602 to 5.067 individuals/generation for different allozyme loci. This means that with respect to some loci (Est3 and Sod2) the populations of *B. cylindrica* represented a single genetic entity, while for others (Mdh1 and Est4) they were genetically isolated from each other.

As expected, the distribution of populations in the space of the first two axes based on the matrix of pairwise Nei's distances showed significant differences for the two types of genetic markers (Fig. 53). The analysis of allozymes indicated a significant variation of centroids of the populations of *B. cylindrica* along both the first and the second principal coordinates (Fig. 53A), whereas the analysis of RAPD markers showed genetically distinct populations Dubky and Neftebaza, while the other populations formed a single pool (Fig. 53B).

Examination of the IBD (isolation by distance) models showed that for allozymes and RAPD markers the null hypothesis remained valid – there was no in-

Table 31. AMOVA results for tests of differentiation among populations of *B. cylindrica* on meso-geographical scale based on allozyme loci. Significant levels of F_{ST} ($p < 0.05$) are based on 999 permutations and indicated in bold

Source of variation	SS	df	MS	E(MS)	F-statistics
Among populations	47.40	5	9.480	0.177	F_{ST} = **0.213**; p = 0.001
Within populations	191.50	294	0.651	0.651	
Total	238.90	299	10.131	0.828	

Table 32. AMOVA results for tests of differentiation among sampled populations of *B. cylindrica* on meso-geographical scale based on RAPD-marker loci. Significant levels of Φ_{ST} ($p < 0.05$) are based on 999 permutations and indicated in bold

Source of variation	SS	df	MS	E(MS)	Φ-statistics
Among populations	104.200	5	20.840	0.700	Φ_{ST} = **0.063**; p = 0.001
Within populations	868.267	84	10.337	10.337	
Overall variability	972.467	89	31.177	11.037	

Table 33. Pairwise F_{ST} (below diagonal) and Nm (above diagonal) among six populations of *B. cylindrica* on meso-geographical scale based on allozyme loci. Significant levels of F_{ST} ($p < 0.05$) after Bonferroni correction are based on 999 permutations and indicated in bold

Population	Dubky	Neftebaza	Park Pobedy	Kosmos	Morekhodnaya	Mira
Dubky	×	8.727	2.165	0.832	1.766	1.285
Neftebaza	0.028	×	2.822	0.705	1.049	1.127
Park Pobedy	**0.104**	**0.081**	×	0.441	0.465	1.307
Kosmos	**0.231**	**0.262**	**0.362**	×	1.019	0.612
Morekhodnaya	**0.124**	**0.193**	**0.350**	**0.197**	×	0.532
Mira	**0.163**	**0.182**	**0.161**	**0.290**	**0.320**	×

Table 34. Pairwise Φ_{ST} (below diagonal) and Nm (above diagonal) among six populations of *B. cylindrica* on meso--geographical scale based on RAPD-marker loci. Significant levels of Φ_{ST} ($p < 0.05$) after Bonferroni correction are based on 999 permutations and indicated in bold

Population	Dubky	Neftebaza	Park Pobedy	Kosmos	Morekhodnaya	Mira
Dubky	×	4.845	8.003	5.119	7.071	4.956
Neftebaza	**0.094**	×	5.118	4.447	9.100	7.104
Park Pobedy	0.059	**0.089**	×	6.852	14.915	23.818
Kosmos	**0.089**	**0.101**	0.068	×	23.550	8.366
Morekhodnaya	**0.066**	0.052	0.032	0.021	×	11.076
Mira	0.092	0.066	0.021	0.056	0.043	×

crease in the level of genetic differentiation between the populations with increasing geographical distance between them (Fig. 54). Moreover, for the allozymes the genetic similarity between the populations even increased between the most distant populations. Thus, formation of inter-population genetic variation at meso-geographical scale is rather unpredictable, as it depends on a number of random factors associated primarily with the founder effect resulting from anthropochory, which plays an important role in dispersal of this species from its native habitats (mountains and steppes of Crimea) into natural and man-made

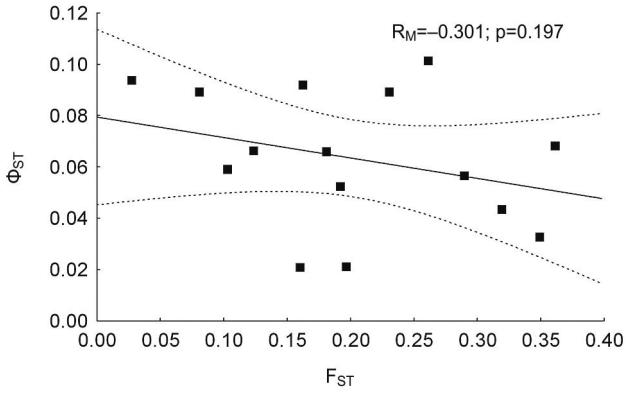

Fig. 52. Correlation of genetic variation among populations of *B. cylindrica* estimated with allozymes (F_{ST}) and RAPD-marker loci (Φ_{ST})

Table 35. Estimates of G-statistics and gene flow (Nm) for allozymes in populations of *B. cylindrica*

Locus	Gis	Git	Gst	Nm
Est3	0.0102	0.3008	**0.294**	0.602
Est4	0.1900	0.2281	0.047	5.067
Mdh1	–0.1335	–0.0638	0.062	3.817
Mdh2	0.1572	0.2467	0.106	2.104
Sod2	0.6212	0.7221	**0.266**	0.688
Sod4	–0.1628	–0.0239	0.120	1.843
Mean	0.1540	0.3219	0.198	1.010

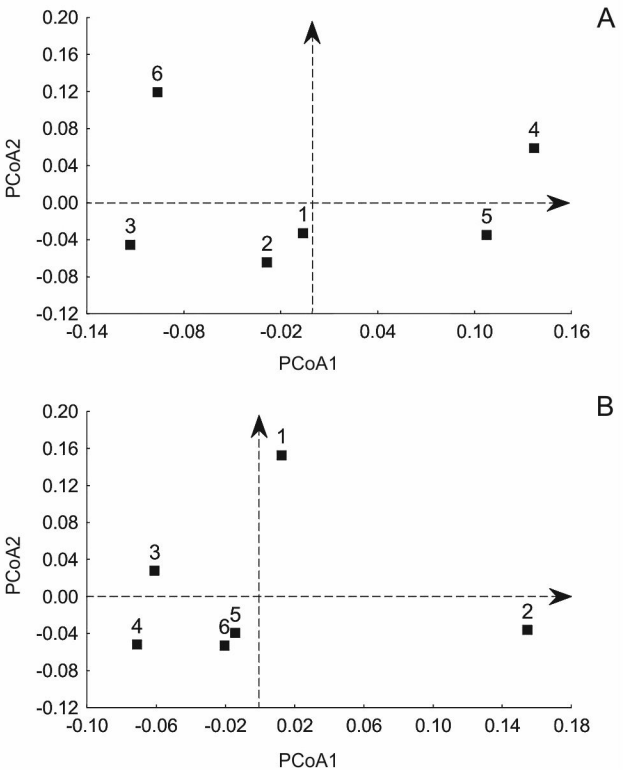

Fig. 53. Distribution of centroids of six populations of *B. cylindrica* in the space of the first two principal coordinates based on matrices of pairwise Nei's genetic distances for allozymes (A) and RAPD-marker loci (B): 1 – Dubky; 2 – Neftebaza; 3 – Park Pobedy; 4 – Kosmos; 5 – Morekhodnaya; 6 – Mira

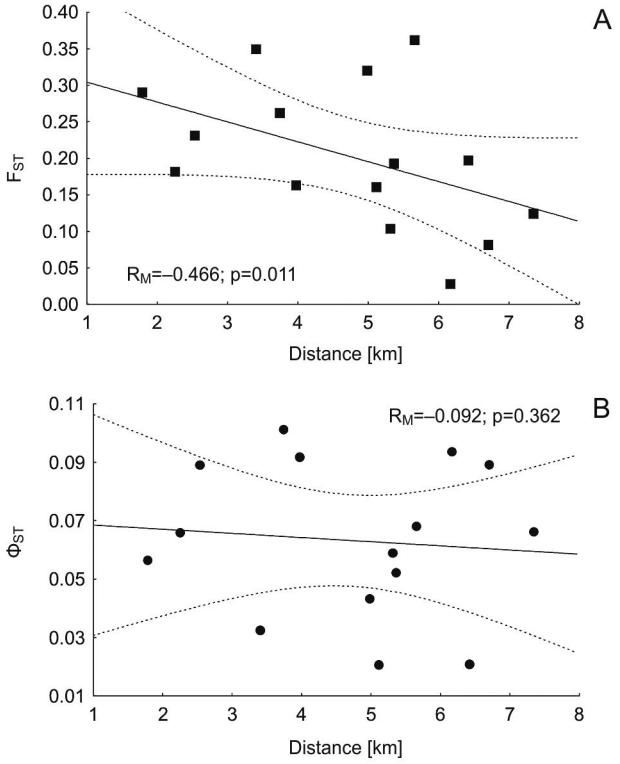

Fig. 54. Correlation between genetic differentiation among populations of *B. cylindrica* estimated with allozymes (A) and RAPD-marker loci (B) and geographical distance between them

(mostly) habitats (SVERLOVA 1998, VITCHALKOVSKAYA & KRAMARENKO 2008, KRAMARENKO 2009d, 2014). This is also confirmed by the fact that the patterns of genetic differentiation between the populations resulting from the analyses of different types of genetic markers are not congruent.

MACRO-GEOGRAPHICAL SCALE

Material for macro-geographical scale analysis was collected from six populations located in Crimea and in the north-western Black Sea region (Fig. 55). The level of genetic variation was assessed among populations, and among three regions (Mykolaiv, Ochakov and Crimea).

Hierarchical analysis of molecular variation of six allozyme loci showed highly significant differences both among populations from the same region (F_{PR} = 0.107; p = 0.001) and among the whole regions (F_{RT} = 0.027; p = 0.001) (Table 36). On the other hand, the level of genetic differentiation among the six studied populations was the highest (F_{PT} = 0.130; p = 0.001).

Similar results were obtained in the hierarchical analysis of RAPD markers (Table 37). Moreover, the use of genetic markers of DNA polymorphism disproves the hypothesis of genetic uniqueness of the studied regions (Crimea and north-western Black Sea) (F_{RT} = 0.010; p = 0.167). All variation among populations within a region (Φ_{PR} = 0.085; p = 0.001) can be interpreted as inter-population variation, irrespective of the geographical location of the populations (Φ_{PT} = 0.094; p = 0.001). Thus, variation in the genetic polymorphism on the regional level is determined not as much by differences among regions as by very high level of genetic diversity among populations within regions (see Genetic polymorphism: Meso-geographical scale).

Analysis of pairwise estimates of genetic differentiation among the populations (Table 38) shows that, in general, the most geographically distant populations were also genetically most dissimilar. The highest scores of F_{ST} were those between the pop-

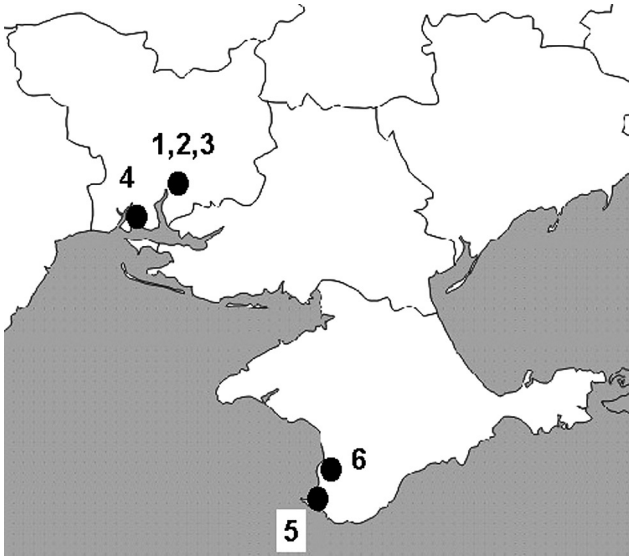

Fig. 55. Location of sampling sites of *B. cylindrica* in Crimea and north-western Black Sea: 1 – Mykolaiv, Dubky; 2 – Mykolaiv, Neftebaza; 3 – Mykolaiv, Park Pobedy; 4 – Ochakov; 5 – Sevastopol; 6 – Vilino

Table 36. Hierarchical AMOVA results for tests of geographical differentiation among populations of *B. cylindrica* based on allozyme loci. Significance levels of F_{ST} ($p < 0.05$) are based on 999 permutations and indicated in bold

Source of variation	SS	df	MS	E(MS)	F-statistics
Among regions	12.810	2	6.405	0.017	F_{RT} = **0.027**; p = 0.001
Among populations within regions	18.523	3	6.174	0.067	F_{PR} = **0.107**; p = 0.001
Within populations	250.740	444	0.565	0.565	F_{PT} = **0.130**; p = 0.001
Total	282.073	449	13.144	0.649	

Table 37. Hierarchical AMOVA results for tests of geographical differentiation among sampled populations of *B. cylindrica* based on RAPD-marker loci Significance levels of Φ_{ST} ($p < 0.05$) are based on 999 permutations and indicated in bold

Source of variation	SS	df	MS	E(MS)	Φ-statistics
Among regions	60.354	2	30.177	0.110	Φ_{RT} = 0.010; p = 0.167
Among populations within regions	47.600	2	23.800	0.924	Φ_{PR} = **0.085**; p = 0.001
Within populations	795.317	80	9.941	9.941	Φ_{PT} = **0.094**; p = 0.001
Total	903.271	84	63.918	10.975	

Table 38. Pairwise F_{ST} (below diagonal) and Nm (above diagonal) among six populations of *B. cylindrica* on macro-geographical scale based on allozyme loci. Significance levels of F_{ST} ($p < 0.05$) after Bonferroni correction are based on 999 permutations and indicated in bold

Population	Mykolaiv-1	Nikolaeyv-2	Mykolaiv-3	Ochakov	Sevastopol	Vilino
Mykolaiv-1	×	3.866	1.256	0.594	2.753	–
Mykolaiv-2	**0.061**	×	2.793	2.533	4.109	3.063
Mykolaiv-3	**0.166**	**0.082**	×	1.743	3.242	1.194
Ochakov	**0.296**	**0.090**	**0.125**	×	0.987	0.478
Sevastopol	**0.083**	**0.057**	**0.072**	**0.202**	×	2.165
Vilino	0.000	**0.075**	**0.173**	**0.344**	**0.104**	×

Table 39. Pairwise Φ_{ST} (below diagonal) and Nm (above diagonal) among five populations of *B. cylindrica* on macro-geographical scale based on RAPD-marker loci. Significance levels of Φ_{ST} ($p < 0.05$) after Bonferroni correction are based on 999 permutations and indicated in bold

Population	Mykolaiv-1	Nikolaeyv-2	Mykolaiv-3	Ochakov	Vilino
Mykolaiv-1	×	4.845	8.003	2.701	7.127
Mykolaiv-2	**0.094**	×	5.118	3.285	8.830
Mykolaiv-3	0.059	0.089	×	5.462	8.236
Ochakov	**0.156**	**0.132**	**0.084**	×	4.051
Vilino	**0.066**	0.054	**0.057**	**0.110**	×

ulations Ochakov and Sevastopol (F_{ST} = 0.202), between Ochakov and Mykolaiv-1 (F_{ST} = 0.296) and between Ochakov and Vilino (F_{ST} = 0.344). On the other hand, the populations Mykolaiv-1 and Vilino were genetically almost identical.

RAPD markers gave an even clearer picture of the inter-regional differences in the levels of genetic polymorphism (Table 39). The majority of significant differences between populations located in different regions (north-western Black Sea and Crimea) and the highest estimates of Φ_{ST} were observed between the populations Ochakov and Mykolaiv (Φ_{ST} = 0.132–0.156) and between Ochakov and Vilino (Φ_{ST} = 0.110).

The distribution of the populations of *B. cylindrica* in the space of the first two principal coordinates based on the matrix of pair-wise Nei's distances for allozymes and RAPD markers also shows the importance of geographical distance in determining the genetic distance among populations in different regions (Fig. 56). However, the role of random events such as anthropochoric movement of snails resulting in the formation of new populations in suitable habitats is also evident.

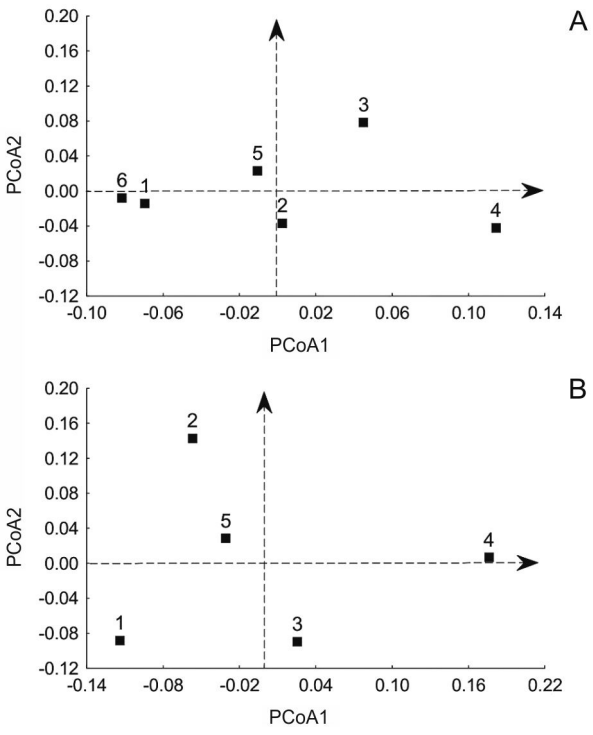

Fig. 56. Distribution of centroids of populations of *B. cylindrica* from different regions in the space of the first two principal coordinates based on matrix of pairwise Nei's genetic distance estimated for allozymes (A) and RAPD-marker loci (B). For names of populations see caption to Fig. 55

FORMATION OF INTRA-SPECIFIC VARIATION PATTERNS AT VARIOUS SPATIAL SCALES

The peculiarities of formation of intra-specific variation patterns in terrestrial snails offer an opportunity to observe cardinal changes in the basic mechanisms when passing from one level of spatial scale to the next. At the same time, different effects of the scale are observed for different aspects of variation (morphometric variation, colour and banding pattern polymorphism, genetic polymorphism). The levels of spatial scale can be called: micro-geographical (for areas of extension of the order of 10^2–10^3 m), meso-geographical (10^5 m) and macro-geographical (10^6 m).

MICRO-GEOGRAPHICAL SCALE

Local continuous populations exist at this level; in some cases they may be fragmented (e.g. subdivided by roads). Nevertheless, also at this level hierarchical intra-population patterns are formed, and the variation is phenotypically and genetically structured.

Though till today the simplest sampling system prevails, in which only one sample (though sometimes with numerous specimens) is taken from each population, terrestrial snails are known to display a very wide intra-population variation (see: Variation in shell size and form: Micro-geographical scale; Polymorphism of shell colour and banding pattern: Micro-geographical scale; Genetic polymorphism: Micro-geographical scale). In continuous populations of *B. cylindrica* I found genuine differences in shell size and form between sites which were only 35–70 m apart. Moreover, patterns of such intra-population variation very often showed a high degree of spatial autocorrelation.

Clinal variation of morphometric characters at a very small spatial scale (distances 200–1,000 m) was noticed already earlier for *Cepaea hortensis* (Bengtson et al. 1979) and *Rhagada convicta* (Stankowski 2011). Such variation in areas from a few dozen to a few hundred metres long is also frequent among other mollusc taxa. Clinal patterns were observed, for example, for the marine *Littorina striata* (De Wolf et al. 1997) and the freshwater *Mexipyrgus churinceanus* (Hershler & Minckley 1986).

Clinal variation can be expected within areas with weak or interrupted gene flow (Endler 1977). Consequently, formation of the observed clinal patterns of morphometric shell variation may be associated with active dispersal of the snails. Distances covered by snails are sometimes considerable, for example, within a month *Theba pisana* covered at most 55 m (Baker 1988), in half a year an individual of *Xeropicta derbentina* covered a maximum of 42 m (Aubry et al. 2006), and *Cepaea nemoralis* – 46 m (Schnetter 1951). The common belief that snails are extremely slow does not correspond to reality, especially in view of the recent study in which *C. nemoralis* covered a distance of 1,000–1,500 m from the place of their release within slightly more than 40 years (Örstan et al. 2011). Cameron (2001) showed that within around 60 years individuals of this species covered 500 m from the place of release.

On the other hand, disturbance of the clinal pattern of morphometric variation at micro-geographical scale is associated with the distribution of individuals and/or their groups in the population (see Kramarenko et al. 2014 for rewiev). In this case interrupted gene flow between subpopulations, especially those spatially remote, may lead to a pattern of morphological area effect, analogous to the one described earlier for the shell colour and banding pattern (Cain & Currey 1963a, b), and also for the allozyme polymorphism (Ochman et al. 1983).

The micro-geographical pattern of morphometric variation, in the absence of microhabitat differences between sites within a continuous population, does not necessarily reflect genetic differences between groups of snails which differ in their shell size and form. It may be a simple manifestation of phenotypic plasticity of morphometric characters, with polygenic inheritance and relatively high degree of heritability. Overall, in a number of studies on terrestrial snails the heritability coefficient (h^2) of morphometric shell characters ranged from 0.16 to 0.81 (Table 40).

The relatively great role of phenotypic plasticity in formation of intra-population variation patterns is supported by the results of analysis of inter-population chronological variation (see: Variation in shell size and form: Micro-geographical scale). The reaction of morphometric variation of each of the studied populations of *B. cylindrica* to environmental changes in 2004, 2006, 2008 and 2012 was unpredictable, and the shell size and form in two consecutive years could either decrease or increase with equal significance (Fig. 8).

On the other hand, numerous authors point to a great plasticity of morphometric shell characters in terrestrial snails; the plasticity is manifest, first of all, as strict correlation of shell size with population density (Tattersfield 1981, Dan & Bailey 1982, Burla & Stahel 1983, Burla 1984, Perry & Arthur 1991, Anderson et al. 2007). The correlation is most often explained by the effect of intra-specific competition, though the character of such interaction is only rarely possible to specify. The results

Table 40. Estimates of heritability coefficient (h^2) of shell morphometric characters in land snails

Species	Shell character	h^2	Reference
Arianta arbustorum	diameter	0.17	Cook 1965
Arianta arbustorum	diameter	0.35–0.66	Burla 1984
Arianta arbustorum	height	0.54	Cook 1965
Arianta arbustorum	aperture width	0.63	Cook 1965
Arianta arbustorum	number of whorls	0.53	Cook 1965
Cepaea nemoralis	diameter	0.60	Cook 1967
Cepaea nemoralis	growth rate	0.49	Oosterhoff 1977
Partula suturalis	height	0.81±0.42	Murray & Clarke 1968
Partula suturalis	diameter	0.53±0.13	Murray & Clarke 1968
Partula taeniata	height	0.36±0.17	Murray & Clarke 1968
Partula taeniata	diameter	0.40±0.14	Murray & Clarke 1968
Cornu aspersum	diameter	0.16±0.06	Panella 1982
Cornu aspersum	diameter	0.49	de Matos 1989
Cornu aspersum	diameter	0.40	Madec 1989
Cornu aspersum	diameter	0.36±0.16	Dupont-Nevit et al. 1997a, b

of experiments with *Cepaea* suggest the presence of growth-inhibiting pheromones in snail mucus trails (Cameron & Carter 1979, Baur 1990, 1991, Baur & Baur 1990, 1992).

Moreover, many studies in both natural (Yom-Tov 1972, Butler 1976, Williamson et al. 1976, Tattersfield 1981) and laboratory populations of helicids (Herzberg 1965, Oosterhoff 1977, Cameron & Carter 1979, Dan & Bailey 1982, Reichardt et al. 1985, Kramarenko & Popov 1999) showed that high population density in land snails led to decrease in activity, growth rate, definitive shell size and fecundity.

The results presented here show that a great proportion of intra-population variation depends on environmental factors and thus has a non-genetic character. Diver (1939) was the first to show that the major part of the apparently genetic-based variation in molluscs was actually a manifestation of non-genetic phenotypic plasticity, and was expressed in response to imperceptible changes in environmental factors (see also Cain 1983, Baur & Raboud 1988). Disappearance of phenotypic differences is observed in terrestrial snails kept in constant conditions; this indicates their environment-controlled, non-genetic character (Baur 1988).

In an array of land snails fecundity was observed to depend on individual size (Baur 1984, 1988, Baur & Raboud 1988, Madec et al. 2000, Vitchalkovskaya & Kramarenko 2006): larger snails have a higher reproductive potential compared to smaller ones. However, the dependence between size and reproductive parameters varies widely among populations.

Besides the size-specific fecundity, size was experimentally shown to have a directional effect on batch size, hatching success and juvenile mortality (Wolda 1970, Yom-Tov 1972, Oosterhoff 1977, Reichardt et al. 1985, Lazaridou-Dimitriadou et al. 1998, Ligaszewski et al. 2007). It is possible that the density of land snail populations may be regulated through growth rate, adult size and fecundity. It was also found that the degree of dispersion in snails often increased considerably in populations of higher density. In *C. nemoralis* dispersion was negatively correlated with density (Cain & Currey 1968, Greenwood 1974, Oosterhoff 1977).

Consequently, formation of micro-geographical patterns of intra-population variation in terrestrial snails is determined by both eco-demographic factors which constitute a complex system of cause-and-effect relations (because of the rather high level of heritability of conchological characters), which act according to the mechanism: population density → shell size → fecundity → population density, against the background of fluctuating environmental factors.

However, the patterns are unstable through time for a variety of reasons, both anthropogenic (e.g. frequent fires or other effects of human activities which disturb snail populations), and natural (land snails are very susceptible to drought, especially during periods with extremely high temperatures and low precipitation), due to which individual parts of continuous populations disappear and are then re-created by surviving individuals.

The intra-population system can be described by the meta-population model (Hanski & Gilpin 1997), when the processes of local extinction and re-colonisation by individuals from the neighbouring areas form specific spatio-temporal patterns of morphometric shell variation.

MESO-GEOGRAPHICAL SCALE

The scale is characterised by the presence of many populations which are spatially separated, but dispersal of adults and/or eggs between them, even

though infrequent, still takes place. Increasing the scale from one locality to a more complicated landscape is accompanied by some increase in heterogeneity of environmental conditions within the studied area. Consequently, the potential role of local selection, as the factor which determines the pattern of inter-population variation, increases, though overall the macroclimate parameters remain relatively uniform (WARD 2006).

The main processes which determine meso-geographical patterns of inter-population variation are very varied forms of passive dispersal of snails (transport by wind, water, animals or man, in all its forms) from more continuous donor populations. Besides, the distance of dispersal does not depend on the snail size or the possibility of active migration.

Two mechanisms can be distinguished which determine genetic and, correspondingly, phenetic structure of populations as a consequence of accidental colonisation. In the case of a single colonisation, following dispersal, the new population is based on the colonisers, while in the case of multiple colonisation the recipient population is based on emigrants from numerous donor populations. Selection of one of these mechanisms is based on testing models of isolation by distance. In the first case the degree of genetic differentiation will increase with the distance between the studied populations, in the second no such dependence will be observed (WARD 2006).

Testing models of isolation by distance (IBD) for my data showed that for both allozymes and RAPD markers null hypothesis remained in force – the degree of genetic inter-population differentiation did not increase with increasing geographical distance between the populations (Fig. 54). Thus formation of inter-population genetic variation at meso-geographical scale depended on an array of random factors, associated first of all with founder effect resulting from anthropochory which played an important role in dispersal of the species from native to anthropogenic (most often) habitats. This is also supported by the fact that the patterns of genetic differentiation between the studied populations, obtained using different genetic markers, were not congruent (Fig. 52).

On the other hand, considering formation of meso-geographical inter-population variation patterns of morphometric characters, besides random passive dispersal of snails (single or repeated, see KRAMARENKO 2014 for rewiev) it is also necessary to consider the role of eco-demographic characteristics which ensure high probability of "anchoring" of even few individuals in the new area (high fecundity, self-fertilisation, fast growth and maturation, etc.). It can be expected that in this case small, semelparous r-species with numerous physiological adaptations (most of all desiccation-resistance) and thus resistant to adverse conditions should have priority (KRAMARENKO 2013).

The fastest colonisers among land snails are hygromiids *Theba pisana* and *Cernuella virgata* (POMEROY & LAWS 1967, ODENDAAL et al. 2008, DÄUMER et al. 2012), and in Ukraine a hygromiid *Xeropicta derbentina* and an enid *Brephulopsis cylindrica* (SVERLOVA et al. 2006, SON 2009). However, a high rate of colonisation was also observed for a large achatinid *Achatina fulica* (CIVEYREL & SIMBERLOFF 1996), a slug *Arion lusitanicus* (KOZŁOWSKI & KORNOBIS 1994, HORSÁK & DVOŘÁK 2003, HERA 2005, GURAL-SVERLOVA & GURAL 2011a, b) and helicids *Helix lucorum* and *H. albescens* (BALASHOV & VASILYUK 2007, KHLUS & TKACHUK 2012, BALASHOV et al. 2013).

As mentioned above (see: Variation in shell size and form: Meso-geographical scale), even snail populations living very close to each other may considerably differ in both size and proportions of their shells at meso-geographical scale. At the same time remote populations may be morphometrically similar. This can be explained by the mostly random character of formation of morphometric variation among land snail populations in anthropogenic habitats; the variation is determined solely by colonisation (single or repeated) of adequate habitats (lawns, hedges, cemeteries, ruins etc.). Besides, existence in the form of practically isolated populations, composed of few individuals, leads to unpredictable responses of each of such populations to the same vectors of natural selection in urban environment.

At meso-geographical scale the leading role in formation of morphometric variation patterns is played by random passive dispersal and demographic factors; effective population size (Ne) can be regarded as their integral indicator.

MACRO-GEOGRAPHICAL SCALE

Considerations at this level include considerable parts of continents. As opposed to the meso-geographical scale, in this case populations are distributed along a wide gradient of environmental factors and, accordingly, selection which leads to formation of local adaptations is the most significant factor determining the patterns of genetic and phenotypic inter-population variation (WARD 2006).

At this level centrifugal forces whose sources are macroclimatic factors (hydro-climatic parameters, closely associated with latitude, longitude, and altitude of localities), which govern the expression of clinal patterns, begin to predominate over the centripetal forces which affect individual populations – different vectors of microhabitat selection. Besides, random factors described above may obscure the expression of clinality because of local increase or de-

crease in size or morph frequency of shells in relation to the general macro-geographical trend.

The most important factors governing formation of inter-population morphometric variation in land snails at macro-geographical scale are macroclimatic parameters, often closely correlated with altitude, latitude and longitude of habitats (see GOODFRIEND 1986 for rewiev). The regularities presented here are also characteristic of other species of land snails from various parts of the world (Appendix 1).

Besides, models including both geographical coordinates and hydro-climatic parameters of habitats describe the patterns of inter-population variation in shell size more adequately than the models which consider geographical coordinates and hydro-climatic parameters separately (Table 15). This shows that processes which determine local adaptations of snails to macroclimatic conditions are superimposed on the effects of isolation by distance between individual populations. It can be supposed that clinal variation has an adaptive character.

For the reasons discussed above introduced populations should depart from the general macro-geographical trend. This conjecture was confirmed for *B. cylindrica*: its south Ukrainian urban populations (Fig. 15: black circles in the graph) do not conform to the regularities which were observed for the Crimean populations from natural habitats.

Macroclimatic parameters have an effect on the shell colour and banding pattern. Populations of *H. albescens* and *C. vindobonensis* from cooler habitats showed a tendency to increase the proportion of dark-coloured shells, and in warmer habitats the percentage of light-coloured shells was higher (see: Polymorphism of shell colour and banding pattern: Macro-geographical scale), which is compatible with the observations on *Cepaea* from western and eastern European populations (JONES et al. 1977). Three basic mechanisms of pattern formation operate for this type of variation in land snails: microhabitat selection, visual selection by predators (birds) and climatic selection. Besides, the so called area effect was described: random distribution of morph frequency in an apparently uniform habitat (CAIN & CURREY 1963a).

Appendix 2 presents correlations of colour and banding pattern polymorphism in various land snail species with a variety of environmental factors. In open habitats (grassland or hedges) or on south-facing slopes snails are exposed to insolation, and light-coloured individuals (yellow in *Cepaea*) without pigmented bands have selective advantage, whereas in shaded habitats (forests) or on north-facing slopes the majority is formed by snails with dark-coloured shells (brown in *Cepaea*) and with pigmented bands which may fuse (CURREY et al. 1964, ARNOLD 1970, BANTOCK 1974, 1980, BENGTSON et al. 1976, HARVEY 1976, JOHNSON 1980, 1981, BURKE 1989, ARTER 1990, OŻGO 2005, OŻGO & KOMOROWSKA 2009).

The regularity pertains to individual studies and to the whole species ranges of the snails of the genus *Cepaea* (CAMERON & COOK 2012, OŻGO 2012). However, as observed by CAMERON & COOK (2012), who analysed data for 870 pairs of open and shaded habitats in various parts of Europe, the microhabitat selection was true in only 67% of the cases. Besides, the significance of the dependence decreased with increasing scale (i.e. distance between the pairs of studied areas) (CAMERON & COOK 2012).

The soil colour is no less important, since visually-hunting predators (birds) act as an important selection force, due to which darker-coloured morphs (and/or those with more numerous pigmented bands) have selective advantage on darker substratum and, conversely, snails with lighter-coloured shells (and/or without pigmented bands) have such advantage on light background (CARTER 1968, PARKIN 1971, 1973, JONES et al. 1974, LEWIS 1977, SHELTON 1984). It can be expected that at some point up the scale these mechanisms should cease to operate, and the variation patterns should correspond to the area effect.

An important role in the pattern formation is played by passive dispersal (possibly repeated) of snails, with their subsequent spread to adjacent areas (KRAMARENKO 2014). As a result the similarity of phenetic structure is high only for those populations which are a few kilometres apart (POKRYSZKO et al. 2012).

On the other hand, the pattern is characteristic of urban habitats with highly unstable conditions, resulting from active human interference (CAMERON et al. 2009). Overall, stability of conditions is a very important factor in formation of relations between the population's phenetic structure and the habitat's characteristics (CAMERON & COOK 2012).

In this light an important part is played by chronological patterns of land snail variation in terms of shell colour and banding pattern (Appendix 3). Overall, with increasing length of observation period, the likelihood of observing significant changes in morph frequencies in the population increases (logistic regression: $\chi^2 = 5.92$; df = 1; p = 0,015; Fig. 57). However, in some long-term studies (more than 30 years) no genuine changes were observed because the observations included the period in the first half of the 20th c., when anthropogenic changes in the habitats were minimal (CLARKE et al. 1968). Studies from the end of the 20th – beginning of the 21st c. show that in land snail populations there is a general tendency of increase in the frequency of morphs with light ground colour and/or without pigmented bands, which is associated with the global warming (OŻGO & SCHILTHUIZEN 2012).

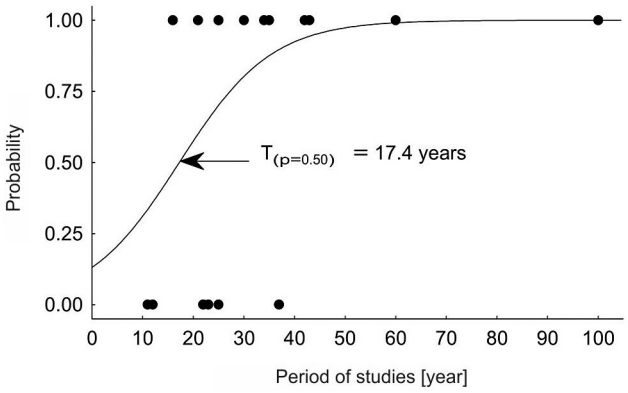

Fig. 57. Logistic regression of dependence between length of time and significance of changes in land snail populations

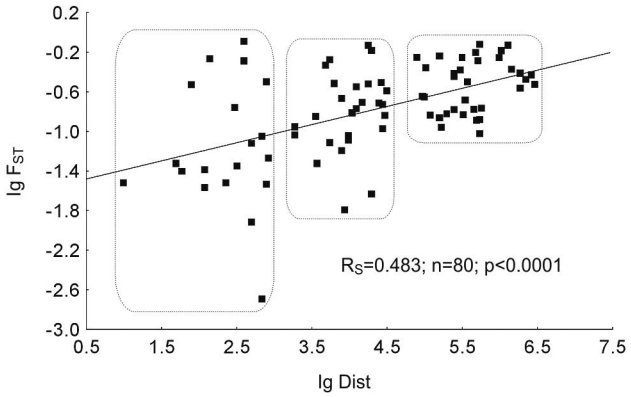

Fig. 58. Dependence between size of study area and level of genetic differentiation (F_{ST}) in land snail populations

This rule (increase in the frequency of light unbanded shells with increasing temperature) reflects also the basic macro-geographical pattern for land snails (JONES 1973, 1974, HELLER & VOLOKITA 1981, MAZON et al. 1987, 1990). It can be illustrated for various macroclimatic indices, such as latitude and longitude, and the climate type as a whole (JONES 1973, VICARIO et al. 1988, SILVERTOWN et al. 2011, OŻGO 2012).

Another picture was obtained in the analysis of genetic polymorphism. In order to trace the effect of spatial scale on the formation of spatial-genetic structure I analysed publications on land snails which presented estimates of genetic differentiation between populations from study areas of corresponding size (Appendix 4). The genetic markers were divided in two groups: allozymes (the number of loci used was also considered) and markers reflecting DNA polymorphism (mitochondrial DNA, microsatellites, RAPD-markers etc.). Overall, the maximum extension of the studied area varied from 10 m to 2,950 km, i.e. from 10^1 to 2.95×10^6 m, and the corresponding estimates of genetic differentiation ranged from 0.002 to 0.807 (Appendix 4).

Because of the pronounced left-handed asymmetry of the distribution of both geographical distances and estimates of F_{ST} (or its analogues), they were $\log_{10}$-transformed prior to the analysis, which resulted in normal distribution (Kolmogorov-Smirnov criterion, in both cases $p > 0.05$). I found that with increasing size of the studied area there was a significant tendency to increase in genetic differentiation between land snail populations ($R_S = 0.483$; $n = 80$; $p < 0.001$) (Fig. 58).

It should be noted that the range of F_{ST} values is much wider for small distances than for medium or long ones. This indicates that high F_{ST} is likely to be obtained in studies on populations a few tens or a few hundred metres apart. The estimate of genetic differentiation of two neighbouring demes of *Trochoidea geyeri*, 18 m apart, turned out to be comparable with such estimate for the whole studied area (0.592 and 0.535, respectively) (PFENNINGER et al. 1996). In the case of *B. cylindrica* the genetic differentiation between two samples only 50 m apart ranged from 0.002–0.009 to 0.131 (see: Genetic polymorphism: Meso-geographical scale). On the other hand, small F_{ST} estimates are likely for populations separated by a distance of a few hundred or even one or two thousand of kilometres. Remote populations always differ significantly in their genetic structure but this is not always determined simply by the distance. It is characteristic that within the territories from each of the three spatio-genetic scales (micro-, meso- and macro-geographical scale) no significant association between the level of genetic differentiation and the size of the study area was found in any case.

The model of isolation by distance (IBD; WRIGHT 1943) was proposed for continuous populations; it predicts that the level of genetic differentiation will be higher for samples separated by a greater distance, while demes which are spatially close to each other will be more genetically similar. I analysed 28 cases of presence/absence of IBD for numerous land snail species depending on the size of the study area. In those studies the distances between the populations (or demes) varied very widely, from 140 to 1,900,000 m. Thirteen cases corresponded to the model of isolation by distance, in the other 15 cases the pattern was absent. The results of applying models of logistic regression to the data showed that there was no significant relation between the area size and the correspondence with the IBD model ($\chi^2 = 1.888$; $df = 1$; $p = 0.169$). The proportion of correct predictions of the presence/absence of isolation by distance based on the area size using the IBD model was only slightly greater than 60%. Moreover, the numbers of cases of the presence/absence of IBD did not differ significantly between the three scales ($\chi^2 = 3.04$; $df = 2$; $p = 0.218$).

False isolation by distance may arise in some cases. Firstly, it is observed when a few sufficiently remote populations are added to a set of populations

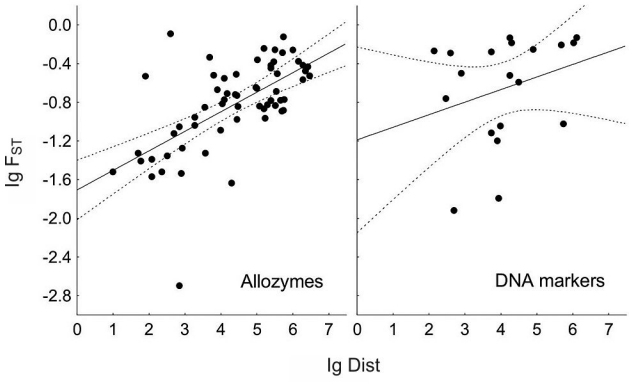

Fig. 59. Dependence between size of study area and level of genetic differentiation (F_{ST}) in land snail populations for different kinds of genetic markers

from a relatively small area (SHIMIZU & USHIMA 2000, JORDAENS et al. 2001, DAVISON & CHIBA 2006, KAUTENBURGER 2006, SINCLAR 2010). Secondly, the situation may arise because of disproportionate number of samples taken in different parts of the study area. HAASE et al. (2003), who studied the pattern of genetic structure of *Arianta arbustorum* from 45 populations located in various countries of Central Europe, observed the presence of IBD. However their analysis included a large number of samples from central Austria. When that number was reduced in order to achieve proportional representation for all the regions, the IBD disappeared.

On the other hand, in some cases the absence of significant IBD may be false. When there is a strong isolating barrier, for example river, populations on the same bank will be more similar to each other though separated by a greater distance, while populations from different banks will be geographically closer but genetically more differentiated (ANDERSON & MCCRACKEN 1986). Besides, the IBD model assumes a relatively uniform decrease in the degree of similarity between samples with increasing distance between them, which is disturbed by the complexity of habitats. In this case geostatistical methods, for example, autocorrelation coefficient (JONES et al. 1980, ARTER 1990, LAZARIDOU-DIMITRIADOU et al. 1994, PFENNINGER 2002), seem to be more adequate for the analysis of patterns of spatial genetic structure.

I also observed the effect of qualitative and quantitative characteristics of genetic markers on the formation of patterns of spatio-genetic structure in land snails. It turned out that DNA markers more weakly reflected the increase tendency of genetic differentiation with increasing size of the study area, compared to allozymes (Fig. 59). Thus, complex studies with simultaneous use of genetic markers of different kinds may provide a more adequate and comprehensive picture of the factors maintaining the genetic structuring of a species.

Moreover, also the number of examined loci (when using allozymes) has an effect on the level of genetic inter-population differentiation, however this relation is noticeable only on meso- and macro-geographical scale (R_S = 0.406; n = 51; p = 0.003). Apparently, a greater number of examined loci more adequately reflects random genetic processes, which take place in the population (genetic drift, bottleneck effect, founder effect), and which are the basic factors in formation and maintaining of spatio-genetic structure of inter-population variation on greater spatial scale, as mentioned above.

Among the demographic characteristics the mating system is important for terrestrial gastropods, since an array of species (like among freshwater pulmonates) are capable of self-fertilisation. Three species known to be capable of self-fertilisation: *Deroceras laeve* (FOLTZ et al. 1982), *Zonitoides nitidus* (JORDAENS et al. 1998) and *Rumina decolata* (SELANDER & HUDSON 1976), show fairly high F_{ST} estimates, which are practically independent of the size of the study area.

CONCLUSIONS

Intra-specific variation should be considered as a function of differentiation between populations, or between intra-population entities, depending on the distance (geographical, chronological, ecological etc.) between them. Using the same approach to estimate variation of various kinds (morphometric variation, colour and banding polymorphism, genetic polymorphism) makes it possible to compare the variation patterns and the underlying eco-genetic processes. Formation of intra-specific variation patterns (initial processes of microevolution) in terrestrial snails take different course on three different spatial scales: micro-, meso- and macro-geographical.

At micro-geographical scale the dominant role is played by eco-demographic characteristics of the species; they form a complex system of cause-and-effect relations (population density → individual size → fecundity → population density), against the background of fluctuating environmental factors.

At meso-geographical scale a special part is played by stochastic population-genetic processes which acquire a special importance in small, isolated populations of anthropogenic or semi-anthropogenic habitats, founded as a result of a single (or multiple) colonisation event(s).

At macro-geographical scale more or less distinct clinal patterns are formed; they are associated with basic macroclimatic indices (latitude, longitude, altitude). With increasing spatial scale the stochastically formed variation patterns tend to lose importance.

The lack of complete congruence in formation of patterns of intra-specific variation of different kinds on different scales is explained by different reactions of different kinds of variation to changes in environmental factors, since some of them (morphometric variation, polymorphism of colour and banding pattern) are selection-dependent, while others (molecular-genetic polymorphism) are selection-neutral.

The basic factors of microevolutionary process which act at different spatial scales are results of processes which progress at different chronological scales. Thus micro-geographical variation patterns reflect the processes which are in progress at the moment. Variation at meso-geographical scale is to a larger extent determined by processes which took place in historic past (most of all anthropogenic, with the associated gene flow and founder effect). Finally, macro-geographical variation reflects processes which coincided with formation of the respective landscapes or climate zones.

Thus studies on variation at the various spatial scales reflect microevolutionary processes from their very start to their outcome. However, regardless of the set of basic microevolutionary factors being constant (gene flow, genetic drift, isolation, various means of dispersal, hybridisation, etc.), at different spatial scales those factors have worked for different lengths of time. Accordingly, a multi-scale approach makes it possible to consider and interpret the results of microevolution with corresponding corrections for the scale.

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Appendix 1

Effect of environmental factors on shell size

Species	Region	Effect	Reference
		Altitude	
Oreohelix cooperi	USA	Shell size decreases with increasing altitude	Anderson et al. 2007
Arianta arbustorum	Switzerland	Shell size decreases with increasing altitude	Burla & Stahel 1983, Gittenberger 1991
Euhadra herklotsi	Japan	Shell size decreases with increasing altitude	Nishi & Sota 2007
Boettgeria lowei	Madeira	Shell size decreases with increasing altitude	Cameron et al. 1996
Vestia turgida	Carpathians (Poland)	Shell size decreases with increasing altitude	Sulikowska-Drozd 2001
Mandarina polita	Japan	Shell size decreases with increasing altitude	Chiba & Davison 2007
Brephulopsis bidens	Crimea	Shell size decreases with increasing altitude	Kramarenko 1995
Plagiodontes patagonicus	Argentina	Shell size increases with altitude	Cazzaniga et al. 2005
Neohelix major	USA	Shell size increases with altitude	Emberton 1995
Albinaria idaea	Crete	Shell size increases with altitude	Engelhard & Slik 1994
Brephulopsis cylindrica	Crimea	Shell size increases with altitude	Own data, Kramarenko 1997
Albinaria idaea	Crete	Shell size increases with altitude, but from 1,250 m upward decreases	Welter-Schultes 2000
Euhadra herklotsi	Japan	Shell size increases with altitude	Nishi & Sota 2007
Mesodon normalis	USA	No effect	Emberton 1995
Marmorana serpentine	Sicily	No effect	Fiorentino et al. 2008a, b
Helix lucorum	Georgia	No effect	Mumladze 2013
		Latitude	
Vestia elata	Poland, Romania	Shell size decreases northward	Abraszewska-Kowalczyk & Sulikowska 1998
Neohelix major	USA	Shell size decreases northward	Emberton 1995
Gastrocopta procera	USA	Shell size decreases northward	Nekola & Coles 2001
Cochlicopa morseana	USA	Shell size decreases northward	Nekola et al. 2012
Brephulopsis cylindrica	Ukraine	Shell size decreases northward	Own data
Cepaea vindobonensis	Ukraine	Shell size decreases northward	Own data
Chondrula tridens	Ukraine	Shell size decreases northward	Own data
Helicodonta obvoluta	Western and central Europe	Shell size increases northward	Maltz 2007
Cochlicopa lubrica	USA	Shell size increases northward	Nekola et al. 2012
Cochlicopa lubricella	USA	Shell size increases northward	Nekola et al. 2012
Carychium exiguum	USA	Shell size increases northward	Nekola & Barthel 2002
Carychium exile	USA	Shell size increases northward	Nekola & Barthel 2002
Mesodon normalis	USA	No effect	Emberton 1995
Gastrocopta rogersensis	USA	No effect	Nekola & Coles 2001
Helix albescens	Ukraine	No effect	Own data

Species	Region	Effect	Reference
		Longitude	
Carychium exile	USA	Shell size decreases eastward	Nekola & Barthel 2002
Euhadra herklotsi	Japan	Shell size decreases eastward	Nishi & Sota 2007
Chondrula tridens	Ukraine	Shell size decreases eastward (beyond 28°E)	Own data
Carychium exiguum	USA	No effect	Nekola & Barthel 2002
Brephulopsis cylindrica	USA	No effect	Own data
Helix albescens	Ukraine	No effect	Own data
		Temperature	
Oreohelix cooperi	USA	Shell size increases with temperature	Anderson et al. 2007
Cepaea hortensis	Iceland	Shell size increases with temperature	Bengtson et al. 1979
Cepaea nemoralis	Europe	Shell size increases with temperature	Rensch 1932
Cepaea hortensis	Europe	Shell size increases with temperature	Rensch 1932
Cepaea vindobonensis	Ukraine	Shell size increases with temperature	Own data
Chondrula tridens	Ukraine	Shell size increases with temperature	Own data
Cornu aspersum	Greece	Shell size decreases with increasing temperature	Lazaridou-Dimitriadou et al. 1994
Euhadra herklotsi	Japan	Shell size decreases with increasing temperature	Nishi & Sota 2007
Brephulopsis cylindrica	Crimea	Shell size decreases with increasing temperature	Own data
Helix albescens	Ukraine	Shell size decreases with increasing temperature	Own data
Marmorana sp.	Sicily	No effect	Fiorentino et al. 2008a, b
Helix lucorum	Georgia	No effect	Mumladze 2013
		Precipitation/Humidity	
Euhadra herklotsi	Japan	Shell size increases with precipitation sum	Nishi & Sota 2007
Chondrula tridens	Europe	Shell size increases with precipitation sum	Rensch 1932
Levantina spiriplana	Israel	Shell size increases with precipitation sum	Heller 1979
Mandarina polita	Japan	Shell size increases with precipitation sum	Chiba & Davison 2007
Cepaea vindobonensis	Ukraine	Shell size decreases with increasing precipitation sum	Own data
Chondrula tridens	Ukraine	Shell size decreases with increasing precipitation sum	Own data
Marmorana serpentine	Sicily	No effect	Fiorentino et al. 2008a, b
Helix lucorum	Georgia	No effect	Mumladze 2013
		Calcium content in soil	
Limicolaria martensiana	East Africa	Shell size increases with calcium content	Owen 1965
Cepaea hortensis	Iceland	No effect	Bengtson et al. 1979
		Soil pH	
Discus rotundatus	Germany	Shell size decreases with increasing soil pH	Kappes et al. 2009
		Population density	
Oreohelix cooperi	USA	Shell size decreases with increasing population density	Anderson et al. 2007
Arianta arbustorum	Switzerland	Shell size decreases with increasing population density	Burla 1984
Cepaea nemoralis	UK	Shell size decreases with increasing population density	Perry & Arthur 1991
Cepaea hortensis	UK	Shell size decreases with increasing population density	Perry & Arthur 1991
Helicella itala	UK	Shell size decreases with increasing population density	Tattersfield 1981
Candidula intersecta	UK	Shell size decreases with increasing population density	Tattersfield 1981
Cochlicella acuta	UK	Shell size decreases with increasing population density	Tattersfield 1981
Discus rotundatus	Germany	Protoconch size decreases with increasing population density	Kappes et al. 2009
Helix lucorum	Georgia	No effect	Mumladze 2013

Species	Region	Effect	Reference
		Habitat character	
Placostylus hongii	New Zealand	Shells from forests are larger than those from scrub	Brook & McArdle 1999
Heterostoma paupercula	Madeira	Shells from sandy habitats are larger than those from rocky habitats	Cameron et al. 1996
Neohelix major	USA	Shells from cool, shaded habitats are larger than those from warm, open habitats	Emberton 1995
Mesodon normalis	USA	Shells from warm, open habitats are larger than those from cool, shaded habitats	Emberton 1995
Helix lucorum	Georgia	Shells from natural habitats are larger than those from anthropogenic habitats	Mumladze 2013
Ainohelix editha	Japan	Shells in rocky habitats are more flat and have keel	Teshima et al. 2003
Rhagada spp.	Rosemary Island (Western Australia)	Shells in rocky habitats are more flat and have keel	Stankowski 2011
		Habitat age	
Discus rotundatus	Germany	Shell size variation is wider in younger habitats	Kappes et al. 2009
Albinaria idea	Crete	Shell size variation is wider in older habitats	Welter-Schultes 2000

Appendix 2

Effect of environmental factors on shell colour and banding pattern

Species	Region	Effect	Reference
		Habitat open/shaded	
Cepaea hortensis	Iceland	In open habitats frequency of unbanded shells decreases	Arnason & Grant 1976
Cepaea hortensis	Iceland	In open habitats frequency of unbanded and yellow shells increases	Bengtson et al. 1976
Theba pisana	Australia	In open habitats frequency of effectively unbanded shells increases	Johnson 1980, 1981
Cepaea nemoralis	UK	In open habitats frequency of light-coloured shells increases	Burke 1989
Cepaea nemoralis	Poland	In open habitats frequency of light-coloured shells increases	Ożgo & Bogucki 2011
Cepaea nemoralis	Poland	In open habitats frequency of yellow shells increases	Ożgo 2005
Arianta arbustorum	UK	In open habitats frequency of light-coloured shells increases	Parkin 1971
Cepaea vindobonensis	Poland	In open habitats frequency of morph pallescens and unbanded shells increases	Ożgo & Komorowska 2009
Cepaea nemoralis	Poland	In open habitats frequency of yellow, unbanded and mid-banded shells increases	Ramos 1985
Cepaea nemoralis	Europe	In open habitats frequency of light-coloured morphs increases	Ożgo 2012
Cepaea nemoralis	Europe	In open habitats frequency of unbanded and yellow shells increases	Cameron & Cook 2012
Cepaea hortensis	Iceland	In shaded habitats frequency of unbanded shells and shells with fused bands increases	Bengtson et al. 1976
Cepaea nemoralis	UK	In shaded habitats frequency of unbanded shells increases	Cameron & Cook 2012
Cepaea nemoralis	Poland	In shaded habitats frequency of brown and unbanded shells increases	Cameron et al. 2011
Cepaea nemoralis	UK	In shaded habitats frequency of yellow shells decreases and frequency of effectively unbanded shells increases	Currey et al. 1964
Cepaea nemoralis	France	In shaded habitats frequency of yellow shells decreases	Arnold 1970
Cepaea nemoralis	UK	In shaded habitats frequency of pink and five-banded shells increases	Harvey 1976
Theba pisana	Australia	In shaded habitats frequency of dark-coloured shells increases	Hazel & Johnson 1990
		Light/dark soil	
Hygromia striolata	UK	On dark soils frequency of dark-coloured shells increases	Jones et al. 1974
Trichia hispida	UK	On dark soils frequency of dark-coloured shells increases	Shelton 1984
Arianta arbustorum	UK	On dark soils frequency of dark-coloured shells increases	Parkin 1973
Cochlicella acuta	Western and central-western Europe	On dark soils frequency of dark-coloured shells increases	Lewis 1977
Helicella (Cernuella) virgata	Western and central-western Europe	On dark soils frequency of dark-coloured shells increases	Lewis 1977
		North/south-facing slope	
Cepaea nemoralis	UK	On north-facing slopes frequency of brown and unbanded shells is higher	Bantock 1974
Cepaea nemoralis	UK	On north-facing slopes frequency of brown shells is higher	Bantock 1980
Arianta arbustorum	Switzerland	On north-facing slopes frequency of dark-coloured shells is higher	Arter 1990
Cepaea nemoralis	Ireland	On north-facing slopes frequency of dark-coloured shells is higher	Burke 1989

Species	Region	Effect	Reference
		Latitude	
Cepaea nemoralis	Europe	Frequency of yellow shells increases southward	Jones 1973
Cepaea nemoralis	Europe	Frequency of yellow shells increases southward	Silvertown et al. 2011
Cepaea nemoralis	UK, France	Frequency of shells with pigmented bands increases southward	Harvey 1971
Cochlicella acuta	Western and central-western Europe	Frequency of shells with pigmented bands increases northward	Lewis 1977
		Longitude	
Cepaea nemoralis	UK	Frequency of yellow, pink and mid-banded shells increases eastward	Bantock & Price 1975
Cepaea nemoralis	Europe	Frequency of pink and mid-banded shells increases eastward	Ożgo 2012
		Climate type	
Cepaea nemoralis	UK	In temperate climate frequency of five-banded shells increases	Bantock & Price 1975
Cepaea nemoralis	France, Spain	In continental climate frequency of pink shells and shells with pigmented bands increases	Harvey 1971
Cepaea nemoralis	Spain	In continental climate frequency of pink shells and shells with pigmented bands increases	Vicario et al. 1988
		Temperature	
Cepaea nemoralis	Yugoslavia	In cooler habitats frequency of pink shells increases	Jones 1973
Cepaea vindobonensis	Yugoslavia	In warmer habitats frequency of morph pallescens increases	Jones 1974
Helix albescens	Crimea	In cooler habitats frequency of dark-coloured shells increases	Own data
Cepaea nemoralis	Pyrenees	In warmer habitats frequency of yellow shells increases	Mazon et al. 1987
Cepaea hortensis	Pyrenees	In warmer habitats frequency of pink shells increases	Mazon et al. 1990
Xeropicta vestalis	Israel	In warmer habitats frequency of light-coloured shells increases	Heller & Volokita 1981
Theba pisana	Medi-terranean	In warmer habitats body colour is lighter	Cowie 1984
		Relative humidity	
Arianta arbustorum	UK	In more humid habitats frequency of light-coloured shells increases	Parkin 1972
		Altitude	
Cepaea nemoralis	Ireland	At high altitudes frequency of yellow and mid-banded shells increases	Cameron 1969
Cepaea nemoralis	Pyrenees	At high altitudes frequency of yellow shells decreases	Mazon et al. 1987
Cepaea nemoralis	Pyrenees	At high altitudes frequency of yellow and unbanded shells increases	Cameron et al. 1973
Cepaea nemoralis	Pyrenees	At high altitudes frequency of pink shells and shells with pigmented bands increases	Mazon et al. 1987
Cepaea nemoralis	Pyrenees	At highest and lowest altitudes frequency of yellow and unbanded shells increases	Arnold 1968
Cepaea nemoralis	Pyrenees	At highest and lowest altitudes frequency of unbanded shells increases	Jones & Irving 1975
Cepaea hortensis	Pyrenees	At high altitudes frequency of pink shells decreases	Mazon et al. 1990
Cepaea hortensis	UK	At high altitudes frequency of brown and unbanded shells decreases and frequency of shells with fused bands increases	Bantock & Noble 1973

Appendix 3

Chronological changes in frequency of colour and banding morphs

Species	Region	Period [years]	Character of change	Reference
Cepaea nemoralis	Poland (cities)	11	No change	Ożgo & Bogucki 2011
Cepaea nemoralis	The Netherlands	12	No change	Wolda 1969
Theba pisana	UK	13	No change	Cowie 1992
Cepaea nemoralis	UK	16	Decrease in frequency of unbanded shells	Arthur et al. 1993
Helix albescens	Crimea	16	Changes in morph frequencies	Kramarenko & Kramarenko 2009
Cepaea hortensis	UK	21	Decrease in frequency of shells with pigmented bands	Wall et al. 1980
Theba pisana	Australia	22	No change	Johnson 2011
Cepaea nemoralis	UK	23	No change	Cain et al. 1990
Cepaea hortensis	UK	25	Decrease in frequency of shells with pigmented bands	Cameron 1992
Cepaea nemoralis	UK	25	Decrease in frequency of brown shells	Cowie & Jones 1998
Cepaea nemoralis	UK	25	No change	Cowie & Jones 1998
Cepaea hortensis	UK	25	Increase in frequency of unbanded shells	Cowie & Jones 1998
Cepaea hortensis	UK	25	Decrease in frequency of shells with fused bands	Cowie & Jones 1998
Cepaea nemoralis	UK	30+	Changes in morph frequencies	Cameron et al. 1998
Cepaea nemoralis	UK	34	Increase in frequency of mid-banded shells	Clarke & Murray 1962
Theba pisana	Australia	34	Increase in frequency of effectively unbanded shells	Johnson 2011
Cepaea nemoralis	UK	35	Increase in frequency of mid-banded shells	Cook & Pettitt 1998
Cepaea nemoralis	UK	35	Decrease in frequency of yellow shells	Cook & Pettitt 1998
Cepaea nemoralis	UK	37	No change	Clarke et al. 1968
Cepaea hortensis	UK	42	Decrease in frequency of yellow shells	Cameron & Pokryszko 2008
Cepaea hortensis	UK	42	Increase in frequency of unbanded shells	Cameron & Pokryszko 2008
Cepaea nemoralis	The Netherlands	43	Increase in frequency of yellow shells	Ożgo & Schilthuizen 2012
Cepaea nemoralis	UK	43	Increase in frequency of yellow shells	Cameron et al. 2013
Cepaea nemoralis	UK	43	Decrease in frequency of shells with pigmented bands	Cameron et al. 2013
Cepaea nemoralis	UK	50	Decrease in frequency of brown shells	Murray & Clarke 1978
Cepaea nemoralis	UK	50	Increase in frequency of mid-banded shells	Murray & Clarke 1978
Cepaea nemoralis	UK	60+	Increase in frequency of mid-banded shells	Cameron 2001
Cepaea nemoralis	Europe	100	Increase in frequency of yellow shells	Silvertown et al. 2011
Cepaea nemoralis	Europe	100	Increase in frequency of unbanded shells	Silvertown et al. 2011
Cepaea nemoralis	Europe	100	Increase in frequency of mid-banded shells	Silvertown et al. 2011

Appendix 4

Dependence between genetic differentiation and size of study area

Species	Type	NPop	NLoci	Maximum extension of study area [m]	F_{ST} (or its analogues)	Reference
Albinaria corrugata	allozyme	4	7	10	0.030	Schilthuizen & Lombaerts 1994
Brephulopsis cylindrica	allozyme	2	6	50	0.047	Own data
Albinaria corrugata	allozyme	5	7	60	0.039	Schilthuizen & Lombaerts 1994
Rumina decollata	allozyme	24	13	80	0.294	Selander & Hudson 1976
Cornu aspersum	allozyme	20	5	120	0.027	Selander & Kaufman 1975
Cornu aspersum	allozyme	23	5	120	0.041	Selander & Kaufman 1975
Trochoidea geyeri	RAPD	9	–	140	0.535	Pfenninger et al. 1996
Albinaria corrugata	allozyme	5	7	230	0.030	Schilthuizen & Lombaerts 1994
Albinaria caerulea	mtDNA	8	–	300	0.172	Giokas et al. 2010
Cornu aspersum	allozyme	15	7	325	0.044	Arnaud et al. 1999b
Chondrina avenacea	RAPD	8	–	400	0.510	Armbruster et al. 2007
Pomatias elegans	allozyme	3	1	400	0.807	Pfenninger 2002
C.nemoralis	MS	11	5	500	0.012	Schweiger et al. 2004
Pomatias elegans	allozyme	8	1	500	0.075	Pfenninger 2002
Pomatias elegans	allozyme	8	1	700	0.002	Pfenninger 2002
Pomatias elegans	allozyme	16	1	700	0.088	Pfenninger 2002
Cepaea vindobonensis	RAPD	7	–	800	0.314	Kramarenko 2009d
Pomatias elegans	allozyme	16	1	800	0.029	Pfenninger 2002
Cornu aspersum	allozyme	21	5	850	0.053	Arnaud et al. 2001
Mandarina anijima	allozyme	16	6	1,900	0.091	Chiba 1998
Mandarina mandarina	allozyme	12	5	1,900	0.110	Chiba 1998
Theba pisana	allozyme	4	4	3,600	0.140	Johnson 1988
Cornu aspersum	allozyme	14	3	3,750	0.047	Arnaud et al. 1999a
Albinaria corrugata	allozyme	5	7	4,900	0.461	Schilthuizen & Lombaerts 1994
Cepaea nemoralis	microsatellite	11	5	5,500	0.076	Schweiger et al. 2004
Euchemotrema hubrichti	mtDNA	7	–	5,500	0.524	Anderson 2007
Theba pisana	allozyme	4	4	6,350	0.301	Johnson 1988
Brephulopsis cylindrica	RAPD	6	–	8,000	0.063	Own data
Brephulopsis cylindrica	allozyme	6	6	8,000	0.213	Own data
Ventridens ligera	microsatellite	14	5	8,800	0.016	Sinclar 2010
Cornu aspersum	allozyme	32	4	9,900	0.081	Arnaud 2003
Cornu aspersum	microsatellite	32	5	9,900	0.090	Arnaud 2003
Leptaxis azorica	allozyme	9	12	11,000	0.152	van Riel et al. 2003
Partula taeniata	allozyme	22	17	12,500	0.279	Johnson et al. 1988
Partula suturalis	allozyme	23	16	12,500	0.168	Johnson et al. 1988
Deroceras laeve	allozyme	8	4	15,000	0.194	Foltz et al. 1982
Arianta arbustorum	mtDNA	46	–	18,000	0.298	Haase & Misof 2009
Chondrina avenacea	RAPD	8	–	18,000	0.730	Armbruster et al. 2007
Achatinella mustelina	mtDNA	21	–	20,000	0.650	Holland & Hadfield 2007
Rhagada sp.	allozyme	19	3	20,000	0.023	Johnson et al. 2006
Cepaea nemoralis	allozyme	47	6	25,000	0.190	Johnson 1976
Leptaxis azorica	allozyme	10	12	27,000	0.307	van Riel et al. 2003
Cepaea nemoralis	allozyme	20	5	28,000	0.185	Jones et al. 1980
Cepaea nemoralis	allozyme	79	7	28,000	0.105	Jones et al. 1980
Cerion spp.	allozyme	34	8	30,000	0.143	Gould & Woodruff 1986
Trochulus caelatus	microsatellite	9	8	32,000	0.254	Ursenbacher et al. 2010
Succinea caduca	mtDNA	12	–	80,000	0.556	Holland & Cowie 2007

Species	Type	NPop	NLoci	Maximum extension of study area [m]	F_{ST} (or its analogues)	Reference
Fruticicola fruticum	allozyme	16	7	95,000	0.224	Falniowski et al. 2004
Cepaea nemoralis	allozyme	74	6	100,000	0.220	Caugant et al. 1982
Heterostoma paupercula	allozyme	34	3	105,000	0.435	Cook & Lace 1993
Amphidromus atricallosus	allozyme	4	11	120,000	0.144	Prasankok et al. 2007
Fruticicola fruticum	allozyme	18	4	160,000	0.135	Snegin 2011a
Solatopupa similis	allozyme	5	10	160,000	0.568	Boato 1988
Cyclophorus fulguratus	allozyme	8	13	170,000	0.108	Prasankok et al. 2009
Cepaea nemoralis	allozyme	31	16	200,000	0.149	Mazon et al. 1988
Helicopsis striata	allozyme	19	4	250,000	0.356	Snegin & Sychev 2011
Chondrula tridens	allozyme	19	9	250,000	0.164	Snegin 2012
Cyclophorus fulguratus	allozyme	4	13	250,000	0.380	Prasankok et al. 2009
Sphincterochila boissieri	allozyme	12	29	300,000	0.414	Nevo et al. 1983
Amphidromus atricallosus	allozyme	8	11	320,000	0.551	Prasankok et al. 2007
Arianta arbustorum	allozyme	14	15	330,000	0.146	Haase & Bisenberger 2003
Cryptozona siamensis	allozyme	6	13	350,000	0.204	Prasankok & Panha 2011
Cryptozona siamensis	allozyme	9	13	375,000	0.312	Prasankok & Panha 2011
Helix pomatia	allozyme	9	5	460,000	0.165	Järvinen et al. 1976
Succinea caduca	mtDNA	24		484,000	0.618	Holland & Cowie 2007
Cornu aspersum	allozyme	24	12	500,000	0.128	Lazaridou-Dimatriadou et al. 1994
Solatopupa similis	allozyme	9	14	520,000	0.512	Boato 1988
Brephulopsis cylindrica	allozyme	6	6	550,000	0.130	Own data
Brephulopsis cylindrica	RAPD	5		550,000	0.094	Own data
Plutonia atlantica	allozyme	8	13	550,000	0.750	Medeiros et al. 2000
Cryptozona siamensis	allozyme	10	13	580,000	0.169	Prasankok & Panha 2011
Isognomostoma isognomostoma	allozyme	13	11	1,000,000	0.550	van Riel et al. 2001
Candidula unifasciata	mtDNA	40	–	1,060,000	0.648	Pfenninger & Magnin 2001
Arianta arbustorum	mtDNA	45	–	1,300,000	0.733	Haase et al. 2003
Cepaea nemoralis	allozyme	25	9	1,440,000	0.419	Guiller & Madec 1993
Cornu aspersum	allozyme	32	14	1,900,000	0.382	Guiller et al. 1994
Cornu aspersum	allozyme	32	13	1,900,000	0.270	Guiller et al. 1996
Pomatias elegans	allozyme	11	11	2,250,000	0.332	Jordaens et al. 2001
Zonitoides nitidus	allozyme	17	15	2,650,000	0.368	Jordaens et al. 1998
Cornu aspersum	allozyme	75	14	2,950,000	0.295	Guiller et al. 1994