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Phenotypic Variability of the Pearly Heath, *Coenonympha arcania* L. (Lepidoptera, Satyridae) in Natural and Anthropogenically Transformed Habitats in the Middle and South Urals

E. Yu. Zakharova

Institute for Plant and Animal Ecology, Ural Branch of Russian Academy of Sciences, Yekaterinburg, Russia

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Abstract—Analysis of variation of the wing length and eyespots in *Coenonympha arcania* (Linnaeus, 1761) (Lepidoptera, Satyridae) in the Middle and South Urals showed greater differences between populations from the forest and steppe zones than between populations from natural habitats and those subjected to chemical and radionuclide pollution. Based on small values of the fluctuating asymmetry (FA) index in all the habitats examined, it may be concluded that *C. arcania* finds favorable environment in both natural and anthropogenically transformed habitats in the Middle and South Urals.

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The pearly heath *Coenonympha arcania* (Linnaeus, 1761) is a European species which is absent in the Far North and extends as far eastwards as the Urals. The nominotypical subspecies occupies most of the range, including the territories of the Middle and South Urals. Adults in various regions fly in one generation from early June to late July, whereas the flight of the second generation was observed in August in the South Urals (Gorbunov et al., 1992; Korshunov and Gorbunov, 1995; *Antti Roine Lepibase*, 2001; Korshunov, 2002). According to the literature, its food plants are various grasses (family Poaceae: *Agrostis* L., *Brachypodium* P. Beauv., *Bromus* Scop., *Cynosurus* L., *Danthonia* DC., *Festuca* L., *Holcus* L., *Melica* L., *Poa* L.) and sedges (family Cyperaceae: *Carex* L.) (Gorbunov and Kosterin, 2007, etc.).

The species is not uniformly distributed over Europe. For example, it can be considered quite common in the central and southern regions of Sweden (Windig et al., 2000), whereas it is rare in Finland (*Antti Roine Lepibase*, 2001). In Denmark, relic populations of *C. arcania* were recorded in 1990; occasional individuals were observed in 1996, and the species has not been recorded since that time. According to the Danish entomologists, the butterfly may have disappeared due to disturbance of its habitats by the newly created bicycle paths (http://www.bugbase.dk/arcania.htm).

Coenonympha arcania inhabits forest margins, glades, and clearings, whereas in the steppe regions it occurs in river floodlands, on roadsides, in oakeries and other deciduous and mixed forest areas. Adults usually occur in open forest areas and under the forest canopy (Korshunov, 2002; Lvovsky and Morgun, 2007). We collected *C. arcania* in various habitats of the Middle and South Urals. In the natural communities of the southern taiga subzone, which includes the area of the Ural State University (UrSU) biological station, as well as the "buffer" and "background" territories of the Middle Ural Copper Smelter (MUCS), the adults fly on the periphery of birch, pine, and mixed forests, and also on the forest glades and the sides of country roads. The most preferred habitats in the Middle Urals are various types of grass and forb-grass meadows. In the steppe and forest-steppe zones the adults fly on the slopes of hills, keeping close to steppe groves and thickets of willows and other shrubs. According to the published data and our own observations, *C. arcania* occupies a wide range of habitats. The abundance of the species in a particular part of the range is affected by two factors: (1) the presence of large (with a radius of at least 100 m) open meadow areas with food plants (grasses and sedges) and (2) the presence of shrubs in these areas, on which the butterflies rest and bask. The habitat is not used by the species if at least one of the above factors is absent (Binzenhöfer et al., 2005; Hein et al., 2007).

We have studied the variability of some morphological characters (the wing length and the size and frequency of occurrence of eyespots in the wing pattern) of *C. arcania* in the Middle and South Urals. The adults were sampled during several years, both in natural habitats and in those subject to anthropogenic transformation (affected by chemical and radioactive pollution).

MATERIALS AND METHODS

The work was based on collections of *Coenonympha arcania* made in several habitats in the territories of Sverdlovsk, Chelyabinsk, Orenburg Provinces and the Republic of Bashkortostan. All the samples together comprised 1315 specimens. The size of each sample is given in Table 1, and the collection sites (*1–8*) are shown in the map (Fig. 1).

(1) The territory of the biological station of Ural State University (the environs of Dvurechensk, Sysert District of Sverdlovsk Province) lies in the interfluve of the rivers Iset and Sysert, which belongs to the pine-birch pre-forest-steppe area of the Trans-Ural hill-piedmont and plain province of the West Siberian forestry region (*Forest Conditions…*, 1973). The zonal complexes belong to the southern taiga subzone of the taiga zone. The vegetation of the territory in question is quite diverse, including nearly all the principal types of natural plant communities of the Middle Urals (forest, meadow, riparian, petrophilous, aquatic, and periaquatic), and also different variants of synanthropic habitats: pascual, ruderal, and segetal. The prevalent plant community in the area of the biological station is the pine forest. The meadow communities, mostly of anthropogenic origin, are used as hayfields and less frequently as pastures. Considerable areas are used for agriculture, mostly as arable lands occupied by grain and forage crops. Ruderal vegetation is characteristic of fallow lands, land fills, and the periphery of traffic and service lines (Mukhin et al., 2003).

The butterflies were captured from 2001 to 2007. In the environs of the biological station *C. arcania* can be considered a common species.

The three territories described below ("impact," "buffer," and "background") are positioned at different distances from MUCS near Revda, Sverdlovsk Province. The specificity of the toxic effect of pollution emitted by the copper smelting plant consists in combined action of heavy metals and sulfurous anhydride (Vorobeichik et al., 1994). According to the physiographic regionalization, this territory belongs to the southern taiga subzone and to the low mountain province of the Middle Urals (Prokaev, 1976). Complex ecological studies of technogenic transformation of different components of biogeocenoses in the territory adjacent to MUCS have been carried out for more than 20 years at the Institute for Plant and Animal Ecology, Ural Branch of Russian Academy of Sciences. An area lying to the west of the smelter, i.e., on the predominantly windward side, was traditionally selected for the study.

(2) The "impact" territory lies 1–2 km west of MUCS. The formation of the meadows in the impact zone was undoubtedly the result of technogenic pollution. The smelter was originally surrounded by sorrel-forb spruce-fir forests which gradually dried out and were destroyed by fires. The forest vegetation did not restore spontaneously in the burned-out areas; instead, there appeared a moss wasteland with the prevalence of the explerent moss species *Pohlia nutans* L. and some horsetail assemblages. Then the moss cover was replaced by grasses: the browntop *Agrostis tenuis* Sibth. with admixture of the tufted hair grass *Deschampsia caespitosa* (L.) Beauv. The grass cover is complete, very low, and turns yellow early in autumn; the root mat is dense. This very simple meadow community has been present in the area for a long time already with no apparent changes. The area is not mown, whereas the dense root mat prevents not only herbaceous but also arboreal plants from sprouting (Khantemirova, 2004, 2006).

(3) The "buffer" territory lies in the environs of Khomutovka, Pervouralsk District of Sverdlovsk Province, 4–5 km west of MUCS. The meadow communities are affected there by two combined anthropogenic factors: mowing and pollution. The phytomass and species diversity are much greater in this territory than in the impact zone but these parameters are quite non-uniform due to the different age of the buffer meadows (Khantemirova, 2006).

(4) The "background" territory lies in the environs of Il'movka, Pervouralsk District of Sverdlovsk Province, 15–16 km west of MUCS. The plant diversity in the meadows of this territory comprises from 63 to 69 species, and the herbaceous communities are multi-layered. Forbs constitute the prevalent group in the vegetation (70–80%) while grasses comprise 20%; the fractions of sedges and legumes are small, which is generally typical of meadows developing in the originally forested areas (Khantemirova, 2004, 2006).

Table 1. Wing length variation (mm) in samples of *Coenonympha arcania* L. from the Middle and South Urals

Collection site	Sex	Year	*n*	Min	Max	*M* ± *m*	Min	Max	*M* ± *m*
				fore wing			hind wing		
Sverdlovsk Province, UrSU biol. station	males	2001	30	17.1	20.2	18.4 ± 0.8	14.3	16.7	15.3 ± 0.6
	females		12	17.0	20.0	18.4 ± 0.9	14.0	16.8	15.6 ± 0.9
	males	2002	19	17.7	19.3	18.4 ± 0.5	13.9	15.5	14.6 ± 0.5
	females		20	17.1	21.0	19.5 ± 1.0	14.5	17.2	15.9 ± 0.8
	males	2003	23	18.9	21.8	20.4 ± 0.8	14.9	17.7	16.3 ± 0.7
	females		21	19.2	22.6	21.1 ± 0.9	15.7	18.4	17.2 ± 0.8
	males	2004	31	16.3	19.3	18.1 ± 0.7	13.0	15.4	14.4 ± 0.5
	females		34	16.8	20.0	18.7 ± 0.7	13.6	16.4	15.3 ± 0.7
	males	2005	17	16.9	19.3	17.9 ± 0.6	14.1	15.6	14.8 ± 0.4
	females		9	17.4	19.3	18.3 ± 0.6	14.8	16.5	15.7 ± 0.6
	males	2006	8	16.6	18.8	17.9 ± 0.6	13.8	15.0	14.4 ± 0.4
	females		17	17.1	19.5	18.7 ± 0.6	13.8	16.2	15.2 ± 0.6
	males	2007	12	17.1	19.2	18.0 ± 0.6	13.6	15.2	14.4 ± 0.5
	females		10	16.9	19.5	18.6 ± 0.8	13.6	16.0	15.1 ± 0.8
	males	total	140	16.3	21.8	18.6 ± 0.7	13.0	17.7	15.1 ± 0.6
	females		123	16.8	22.6	18.9 ± 0.8	13.6	18.3	15.5 ± 0.7
Sverdlovsk Province, MUCS “impact”	males	2002	54	15.6	19.5	17.8 ± 0.7	12.4	15.4	14.3 ± 0.6
	females		41	16.3	20.7	18.5 ± 0.8	13.3	16.7	15.1 ± 0.6
	males	2003	80	17.9	20.8	19.6 ± 0.7	14.2	16.9	15.6 ± 0.6
	females		34	18.0	21.4	20.1 ± 0.7	14.2	17.4	16.4 ± 0.7
	males	2006	27	16.1	19.3	17.8 ± 0.9	12.9	15.5	14.3 ± 0.7
	females		22	17.0	20.4	18.6 ± 1.0	14.1	17.1	15.2 ± 0.9
	males	total	161	15.6	20.8	18.4 ± 0.8	12.4	16.9	14.7 ± 0.6
	females		97	16.3	21.4	19.1 ± 0.8	13.3	17.4	15.6 ± 0.7
Sverdlovsk Province, MUCS “buffer”	males	2002	38	16.4	19.1	17.7 ± 0.7	13.0	15.3	14.1 ± 0.6
	females		20	17.2	21.2	18.7 ± 0.9	14.1	17.5	15.4 ± 0.8
	males	2003	39	17.0	21.6	19.5 ± 1.0	13.3	17.3	15.4 ± 0.9
	females		13	18.0	21.8	20.4 ± 1.0	14.8	17.6	16.5 ± 0.9
	males	2006	42	15.4	19.1	17.5 ± 0.8	11.8	15.7	14.0 ± 0.8
	females		18	17.1	19.2	18.2 ± 0.6	13.8	15.5	14.8 ± 0.5
	males	total	119	15.4	21.6	18.2 ± 0.8	11.8	17.3	14.5 ± 0.8
	females		51	17.1	21.8	19.1 ± 0.8	13.8	17.6	15.6 ± 0.7
Sverdlovsk Province, MUCS “background”	males	2002	33	16.8	19.2	17.8 ± 0.6	13.2	15.0	14.3 ± 0.5
	females		9	17.8	19.3	18.6 ± 0.5	13.9	15.9	15.3 ± 0.6
	males	2003	12	17.1	20.2	19.2 ± 0.8	13.2	16.1	15.2 ± 0.8
	females		3	18.9	21.1	20.2 ± 1.2	15.8	17.2	16.6 ± 0.8
	males	2006	30	16.7	19.6	18.4 ± 0.7	13.4	15.6	14.7 ± 0.5
	females		16	17.7	20.2	18.8 ± 0.8	14.2	16.6	15.3 ± 0.7
	males	total	75	16.7	20.2	18.5 ± 0.7	13.2	16.1	14.7 ± 0.6
	females		28	17.7	21.1	19.2 ± 0.8	13.9	17.2	15.7 ± 0.7

Table 1 (Contd.).

Collection site	Sex	Year	*n*	Min	Max	$M \pm m$	Min	Max	$M \pm m$
				fore wing			hind wing		
Chelyabinsk Province,	males	2007	71	16.8	19.9	18.4 ± 0.6	13.3	16.2	14.6 ± 0.5
Lake Berdyanish	females		35	17.7	20.0	18.9 ± 0.6	14.5	16.3	15.4 ± 0.4
Chelyabinsk Province,	males	1998	38	16.1	20.6	18.6 ± 0.9	13.5	17.1	15.5 ± 0.8
Ilmen State Reserve	females		41	17.5	21.2	19.2 ± 0.8	14.8	18.1	16.4 ± 0.8
	males	1999	17	16.9	19.3	18.1 ± 0.7	13.0	15.5	14.3 ± 0.7
	females		2	18.1	18.2	18.1 ± 0.1	14.3	14.8	14.6 ± 0.3
	males	2000	7	17.6	19.3	18.6 ± 0.6	13.9	15.9	14.7 ± 0.8
	females		8	18.1	19.8	18.9 ± 0.7	14.6	16.8	15.8 ± 0.8
	males	2001	5	19.0	20.0	19.4 ± 0.4	14.5	15.9	15.2 ± 0.5
	females		8	17.4	21.1	19.2 ± 1.3	13.8	17.0	15.5 ± 1.2
	males	total	67	16.1	20.6	18.7 ± 0.7	13.0	17.1	14.9 ± 0.7
	females		59	17.4	21.2	18.9 ± 0.7	13.8	18.1	15.6 ± 0.8
Bashkortostan,	males	2008	104	16.8	20.2	18.4 ± 0.6	13.2	16.3	14.8 ± 0.5
Nurali Range	females		15	17.0	20.1	18.5 ± 0.8	13.7	16.1	15.1 ± 0.7
Orenburg Prov.,	males	2005	46	16.5	19.3	18.2 ± 0.6	13.4	16.4	15.0 ± 0.7
Kuvandyk	females		28	17.0	19.6	18.7 ± 0.7	14.4	17.3	16.0 ± 0.7
	males	2007	89	16.9	20.9	18.7 ± 0.7	13.6	17.0	15.0 ± 0.6
	females		7	17.7	20.0	18.9 ± 0.9	14.3	16.4	15.5 ± 0.8
	males	total	135	16.5	20.9	18.5 ± 0.7	13.4	17.0	15.0 ± 0.7
	females		35	17.0	20.0	18.8 ± 0.8	14.3	17.3	15.8 ± 0.8

In the three above territories ("impact," "buffer," and "background") the butterflies were captured simultaneously, during June–July of 2002, 2003, and 2006.

(5) The territory on the bank of Lake Berdyanish is located in Kasli District of Chelyabinsk Province and is included in the head part of the East Ural Radioactive Trace (EURT). According to the geobotanical subdivision of Chelyabinsk Province (Kolesnikov, 1961), this territory lies in the northern forest-steppe subzone of the Trans-Ural region and the West Siberian Plain. There had been a village on the bank of the lake, which was abandoned after the Kyshtym nuclear disaster (1957); therefore the territory in question is a secondary upland forb-grass meadow with multilayered herbaceous vegetation (from 20 cm to 1.5 m tall) and a 100% projective cover. The community is dominated by the bearded wheat grass *Elytrigia canina* (L.) Drob. and the smooth brome *Bromopsis inermis* (Leyss.) Holub. There are also vast areas of the common nettle *Urtica dioica* L. and the ruderal hemp *Cannabis ruderalis* Janisch. A birch forest adjoins the meadow on the opposite side from the lake bank (Pozolotina et al., 2005).

Adults of *Coenonympha arcania* were captured in July 2007 along country roads, in forb-grass meadows, and on the periphery of a light birch forest with admixture of pine trees and birch and willow coppice. The density of contamination with ^{90}Sr was 18.5 MBq/m^2, or 500 Ci/km^2 (Grigorkina et al., 2006).

(6) The territory of Ilmen State Reserve lies in Chelyabinsk Province, on the east slope of the South Ural mountain region. According to Kolesnikov (1961), the territory of the reserve belongs to the subzone of pre-forest-steppe pine-birch forests of the eastern low mountains and foothills of the South Urals; it is limited on the west by taiga forests on the watershed ranges, and on the east, by forest-steppes of the East Ural peneplain. The density of contamination with ^{90}Sr does not differ from the background values for the Ural region (Grigorkina et al., 2006). The butterflies were captured in the central part of the reserve, near Lake Bol'shoe Miassovo, from 1998 to 2001.

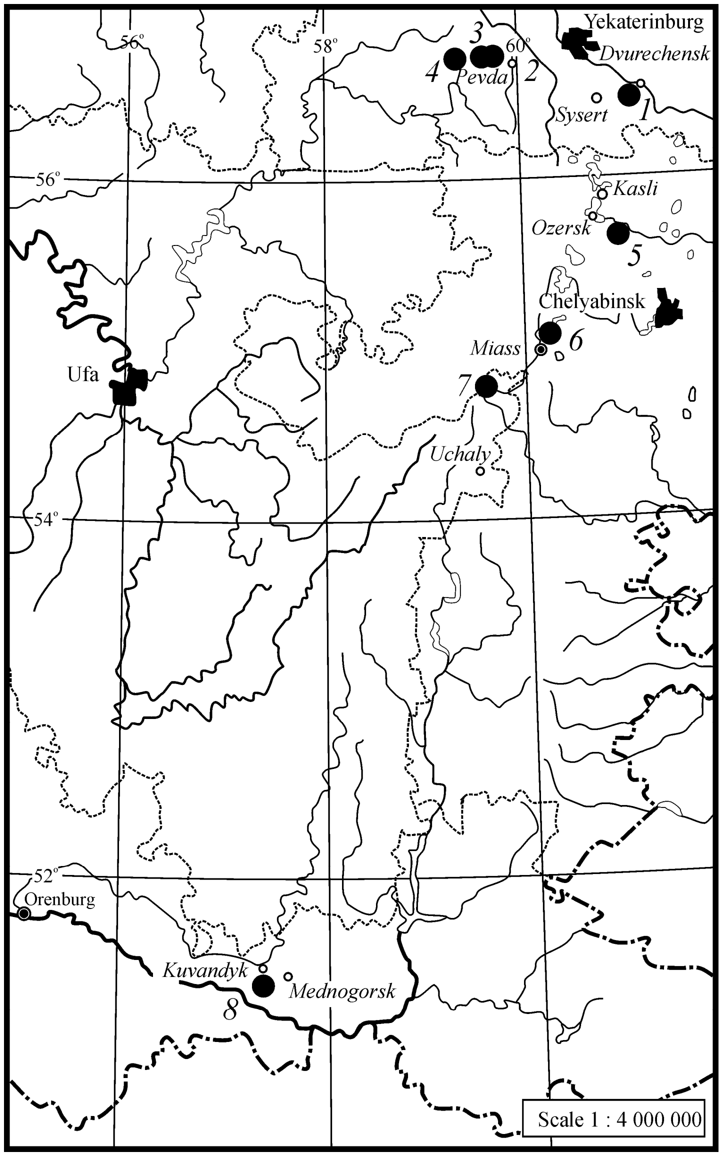

Fig. 1. Schematic map of the study region. Numbers mark the material collection sites: Sverdlovsk Province: *1*, Sysert District, Dvurechensk, biological station of Ural State University; *2*, Revda, 1–2 km W of Middle Ural Copper Smelter, "impact"; *3*, Pervouralsk District, Khomutovka, 4–5 km W of MUCS, "buffer"; *4*, Pervouralsk District, Il'movka, 15–16 km W of MUCS, "background"; Chelyabinsk Province: *5*, Kasli District, the head part of the East Ural Radioactive Trace, bank of Lake Berdyanish; *6*, Ilmen State Reserve; Bashkortostan: *7*, Uchaly District, Yal'chigulovo, the Nurali Range; Orenburg Province: *8*, Kuvandyk District, Kuvandyk.

(7) The territory of the Nurali Range (Uchaly District, Republic of Bashkortostan) belongs to the subzone of pine-birch forests of the east slope of the Urals and is located in Kundravino-Uchaly pine-birch forest region (Kolesnikov, 1961). The sample of *C. arcania* was obtained in June 2008 near Yal'chigulovo. The butterflies were captured in grass-forb and steppe-like meadows subjected to moderate pasture load and mowing, and also in the periphery of birch groves on the slopes of the Nurali Range.

(8) The territory in the environs of Kuvandyk, Orenburg Province, lies on the boundary of forb-feathergrass and thyme-feathergrass steppes of the forb-sod-grass steppe subzone. Most of the region is occupied by ridgy hills and low mountains, and also hilly plains dissected by the valleys of the Ural, Sakmara, and their tributaries. According to the plant geographic subdivision, the territory in question belongs to Zalair-Sakmar low-mountain steppe province (*Geographic Atlas…*, 1999). In the environs of Kuvandyk material was collected in June–July of 2005 and 2007.

Processing of the material included measurement of the length of the fore (LF) and hind wing (LH) and the diameter of eyespots in the wing pattern (measured on the underside, along the middle line of the wing cell containing the spot). The measurements were carried out using a MBS-10 dissecting microscope with an eyepiece micrometer, at 8 × 0.6 magnification. The fore wing length was measured from the base of vein *Sc* to the wing apex, and the hind wing length, from the base of vein *Rs* to the end of vein Cu_1. All the measurements were repeated on the left and the right sides of each specimen. According to Schwanwitsch (1935), the hypothetical form *Protocoenonympha*, i.e., a realization of the prototypic nymphaloid wing pattern in the genus *Coenonympha* Hübner, may have up to 6 eyespots on the fore wing and up to 7 spots on the hind wing. According to our data, the maximum number of eyespots on the fore wing of *C. arcania* is 5; the spots are located in cells R_5-M_1, M_1-M_2, M_2-M_3, M_3-Cu_1, and Cu_1-Cu_2 and can be designated as *P1*, *P2*, *P3*, *P4*, and *P5*, respectively. The hind wing can have no more than 6 spots located in cells *Rs*-M_1, M_1-M_2, M_2-M_3, M_3-Cu_1, Cu_1-Cu_2, and Cu_2-*2A*; they were designated as *G1*, *G2*, *G3*, *G4*, *G5*, and *G6*.

Variability of the metric characters (the wing length and the eyespot size) was studied using discriminant analysis within Statistica 5.5 software package. Geographic variation of non-metric characters (phenes) was analyzed by calculating the phenetic distances (Hartman, 1980) within FEN 3.0 software package developed by Prof. A.G. Vasil'ev at the Institute for Plant and Animal Ecology. The phenetic distances were visualized by cluster analysis and building of the sample similarity dendrogram using the unweighted pair group method with arithmetic mean (UPGMA) (Vasil'ev et al., 2000).

For the meristic characters, i.e., those reflecting the number of certain structures (in our case, the eyespots), we used the simplest measure of development stability, namely the mean frequency of asymmetry cases per character (*FA*):

$$FA = (\Sigma X_i)/n,$$

where X is the number of asymmetric characters in each specimen related to the number of characters used, and n is the number of specimens in the sample (Zakharov et al., 2001).

RESULTS

Analysis of Variation of the Metric Characters of the Wings

According to the literature, the fore wing length of *Coenonympha arcania* in different parts of its distribution varies within the following ranges: 15–21 mm in Eastern Europe (Lvovsky and Morgun, 2007), 16–20 mm in the Caucasus (Nekrutenko, 1990), 16–19 mm in the Asian part of the range (Korshunov and Gorbunov, 1995; Korshunov, 2002), and 17–20 mm in the same region, according to a different source (Gorbunov and Kosterin, 2007). In our material from the Middle and South Urals, the fore wing length of the males varies from 15.4 to 21.8 mm, that of females, from 16.3 to 22.6 mm. The measurements of different samples of *C. arcania* in different years are shown in Table 1.

As in most other species of the genus *Coenonympha*, females of *C. arcania* are larger than males (Davenport, 1941; Nekrutenko, 1990; Wiklund and Forsberg, 1991; Wiklund et al., 1991; Zakharova, 2002, etc.). As can be seen from Table 1, the wings of females are on average 0.5–1.0 mm longer than those of males. Moreover, females have on average more eyespots than males do, and these eyespots are larger (Table 2); this is also typical of other congeners, for example *C. hero* (Linnaeus, 1761) (Zakharova et al., 2006), *C. oedippus* (Fabricius, 1787) (Zakharova and Ivanov, 2009, in print), and *C. pamphilus* (Linnaeus, 1758) (Zakharova, 2008).

Due to the presence of sex dimorphism in the above morphological characters, further analysis of chronographic and geographic variation was carried out separately for each sex. The results of discriminant analysis of the complex of metric characters (*LF*, *P2*, *LH*, *G1*, *G2*, *G3*, *G4*, *G5*, *and G6*) of males of *C. arcania* are shown in Fig. 2. The size of some eyespots in the fore wing (*P1*, *P3*, *P4*, *and P5*) was not included in the analysis because these eyespots were rarely (in no more than 5% of cases) found in the wing pattern of males (Table 2). The first canonical discriminant function (DF1) accounted for 42.4% of inter-group variance, and the second (DF2), for 19.4%. The generalized Mahalanobis distances (D^2) for samples of males, considering the year of sampling, are shown in Table 3. The discriminant analysis showed that differences between generations from the same locality could be comparable with geographic differences or even surpass them. For example, the value of D^2 between the samples from the Ural State University biological station for 2003 and 2005 was 21.4 ($p < 0.05$), whereas the difference between the sample from this locality (2007) and the sample from Lake Berdyanish, positioned 130 km away, was found to be statistically non-significant ($D^2 = 1.8$, see Table 3).

Table 2. The mean diameters of eyespots (mm; above) and frequencies of their occurrence (%; below) in the wing pattern of *Coenonympha arcania* L.

Collection site	Sex	Fore wing eyespots					Hind wing eyespots					
		P1	*P2*	*P3*	*P4*	*P5*	*G1*	*G2*	*G3*	*G4*	*G5*	*G6*
Sverdlovsk Province,	males	0.3	1.4	0.3	0.2	0.0	2.1	0.9	1.2	1.9	1.8	0.7
UrSU biol. station		0.6	99.1	4.9	0.8	0.0	100	95.3	100	100	100	77.8
	females	0.7	1.7	0.6	0.5	0.3	2.2	1.1	1.4	2.0	1.9	0.6
		0.4	100	25.6	8.1	1.7	100	96.9	100	100	100	67.5
Sverdlovsk Province,	males	0.2	1.4	0.2	0.0	0.0	2.3	1.0	1.3	1.8	1.9	0.6
MUCS		0.3	98.6	2.5	0.0	0.0	100	91.5	99.4	100	100	67.5
“impact”	females	0.0	1.8	0.7	0.4	0.0	2.3	1.2	1.5	2.1	2.1	0.7
		0.0	100	17.3	6.0	0.0	100	99.5	100	100	100	74.0
Sverdlovsk Province,	males	0.0	1.4	0.5	0.1	0.0	2.3	1.0	1.3	1.8	1.8	0.6
MUCS		0.0	97.9	5.6	0.4	0.0	100	94.1	100	100	100	66.9
“buffer”	females	0.0	1.9	0.7	0.4	1.3	2.4	1.2	1.5	2.1	2.0	0.7
		0.0	100	20.9	9.6	2.6	100	98.3	100	100	100	76.4
Sverdlovsk Province,	males	0.0	1.5	0.2	0.0	0.0	2.3	1.0	1.3	1.8	1.9	0.6
MUCS		0.0	97.4	1.1	0.0	0.0	100	83.2	98.9	100	99.0	69.8
“background”	females	0.0	1.8	0.6	0.7	0.4	2.3	1.1	1.4	2.0	2.0	0.8
		0.0	100	28.7	21.1	9.3	100	85.2	100	100	100	54.3
Chelyabinsk Province,	males	0.4	1.2	0.2	0.1	0.0	2.2	0.8	1.1	1.8	1.8	0.5
Lake		1.4	94.2	4.3	0.7	0.0	100	90.9	100	100	97.7	59.1
Berdyanish	females	0.0	1.5	0.4	0.2	0.4	2.2	1.0	1.3	2.0	1.9	0.5
		0.0	100	19.2	5.7	4.2	100	100	100	100	100	68.6
Chelyabinsk Province,	males	0.3	1.3	0.4	0.5	0.5	2.2	1.1	1.3	1.9	1.9	0.7
Ilmen State Reserve		2.8	99.3	16.2	7.7	4.9	100	98.6	100	100	100	82.0
	females	0.0	1.7	0.5	0.3	0.2	2.3	1.1	1.5	2.1	2.0	0.7
		0.0	100	30.0	21.4	1.4	100	100	100	100	100	73.9
Bashkortostan,	males	0.1	1.4	0.4	0.3	0.3	2.2	1.0	1.4	1.9	1.9	0.7
Nurali Range		1.0	98.1	16.3	7.7	3.8	100	96.1	100	100	100	88.8
	females	0.0	1.7	0.8	0.4	0.2	2.4	1.2	1.5	1.9	1.9	0.6
		0.0	100	56.7	26.7	3.3	100	100	100	100	100	85.7
Orenburg Prov.,	males	0.2	1.3	0.5	0.2	0.0	2.2	1.1	1.4	2.0	2.1	0.8
Kuvandyk		1.1	96.9	14.0	4.3	0.3	100	96.9	100	100	99.4	91.2
	females	0.7	1.6	0.9	0.5	0.4	2.3	1.2	1.5	2.2	2.1	0.8
		7.1	100	34.8	17.0	5.4	100	100	100	100	100	93.3

Similar results were obtained by analysis of variation of the same complex of metric characters in the females. In our opinion, the overlap of intra- and inter-population differences can be explained by small (in some cases) and unequal samples. Moreover, *C. arcania* in the Middle and South Urals appears to be quite uniform with respect to such metric characters as the wing length and the eyespot diameters.

To obtain the general pattern of geographic variation of the species within the given part of its range, we united the data for different years from each habitat. The results of discriminant analysis of the complex of metric characters based on all the samples of males and females are shown in Table 4 and Fig. 3. The first canonical discriminant function, accounting for about 55.3% of inter-group variance, revealed sex-related

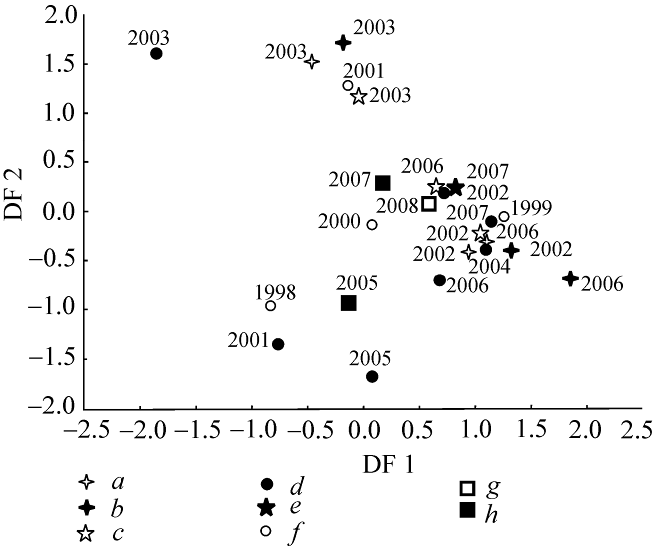

Fig. 2. Results of discriminant analysis of the wing length and the eyespot size in males of *Coenonympha arcania* L.: centroids of samples relative to the first two canonical discriminant functions (DF). Letters *a–h* designate the localities *1–8* (see Fig. 1).

differences; the second function, accounting for 20.7% of variance, revealed geographic differences. The polygons of males and females did not overlap (Fig. 3); all the Mahalanobis distance values between the samples of males and females were significant (Table 4).

The samples of both sexes of *C. arcania* from steppe habitats (the Nurali Range and the environs of Kuvandyk) and the Ilmen Reserve, and also males from the bank of Lake Berdyanish were significantly different from all the other samples, whereas the Mahalanobis distances between samples of the same sex were not always significant (Table 4). The butterflies inhabiting Sverdlovsk Province and the north areas of Chelyabinsk Province appear to be quite uniform with respect to the complex of metric characters used (the wing length and the diameter of eyespots in the wing pattern). The butterflies living in the direct proximity of the chemical pollution source (the "impact" territory near MUCS) did not form a group phenotypically distinct from those living 5–6 or 15 km from the smelter, and even from those living near the UrSU biological station, 65 km from the smelter. The females of *C. arcania* captured within the radioactive pollution zone of EURT (bank of Lake Berdyanish) could not be differentiated from those sampled near the UrSU biological station or the "impact" and "background" territories of MUCS (Table 4). At the same time, the butterflies living in forest communities of the Middle Urals differed from those living in forest-steppe and steppe habitats of the South Urals, in the wing length and the eyespot size.

Analysis of Variation of the Eyespots as Non-metric Characters

Some eyespots in the wing pattern of *C. arcania*, as well as of other species of this family, have a discrete probability of appearance and can be considered as phenes (Zakharova, 2002). As can be seen from Table 2, all the eyespots in the fore wing of males represented discrete characters and might be absent. About 1% (up to 5% in some samples) of males had no eyespots on their fore wings. In females, spot *P2* was found in 100% of specimens. The hind wing eyespots (*G1*, *G3*, *G4*, *G5*) were always present in females, whereas spots *G3* and *G5* were absent in 1–2% of males in some samples. Spots *G2* and *G6* behaved as true phenes in both sexes. In order to estimate the degree of phenogenetic differentiation of the natural populations, we calculated the phenetic distances between the samples (Table 5) and built the dendrogram (Fig. 4).

The phenetically closest and the most distant samples were revealed by cluster analysis. The dendrogram (Fig. 4) contains two large clusters, one formed by the samples of males, and the other, of females. Thus, besides the sex dimorphism in size, the males and females of this species show significant differences in the frequency of occurrence of eyespots in the wing pattern, this frequency being greater in females. The phenetic distances between samples of different sexes were nearly always large and statistically significant (Table 5).

Each of the above clusters can be further subdivided into two clusters. One cluster unites the samples of males from territories of Sverdlovsk Province (the UrSU biological station and the "impact," "buffer," and "background" territories of MUCS), and also from Ilmen Reserve; the phenetic distances between them are small and mostly non-significant (Table 5). The other cluster is formed by samples from quite distant forest-steppe and steppe habitats: Bashkortostan, Chelyabinsk and Orenburg Provinces. The clusterization pattern of the samples of females is similar to that of males. The only difference is that the first cluster includes only the samples from Sverdlovsk Province, whereas the sample of females from Ilmen Reserve is phenetically similar to that from Lake Berdyanish area.

Table 3. Generalized Mahalanobis distances (D^2) between samples of *Coenonympha arcania* L. males by the complex of metric characters for several years

No.	UrSU biological station							Ilmen Reserve				MUCS "impact"			MUCS "buffer"			MUCS "background"			Lake Ber-dyanish	Nurali Range	Kuvandyk	
	2001	2002	2003	2004	2005	2006	2007	1998	1999	2000	2001	2002	2003	2006	2002	2003	2006	2002	2003	2006	2007	2008	2005	2007
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	0.0	**8.1**	**20.1**	**10.2**	**4.7**	9.1	**10.2**	**6.9**	15.7	29.3	**16.9**	**6.7**	**14.2**	**7.5**	**8.1**	**15.3**	**11.7**	**7.3**	**12.5**	**9.1**	**12.2**	**10.0**	**4.3**	**11.7**
2		0.0	**12.9**	**3.4**	**7.5**	3.3	3.8	**9.7**	**3.7**	16.7	6.2	**3.0**	**6.9**	**4.0**	**2.8**	**6.0**	**5.3**	2.4	4.3	2.5	**3.4**	**3.2**	**7.1**	**6.1**
3			0.0	**15.0**	**21.4**	13.9	**16.2**	**14.6**	13.9	29.6	6.4	**19.9**	**5.4**	**19.5**	**20.3**	**6.0**	**25.2**	**20.1**	**7.9**	**11.8**	**11.4**	**11.5**	**19.4**	**10.8**
4				0.0	**6.2**	2.7	2.0	**8.7**	**3.5**	17.7	6.6	**5.8**	**8.1**	2.6	**3.8**	**8.0**	**3.5**	**5.3**	**7.2**	2.4	**2.4**	1.5	**5.6**	**3.8**
5					0.0	6.4	**5.1**	**5.1**	8.7	26.8	**14.7**	**7.4**	**15.8**	**5.8**	**5.7**	**16.7**	**7.5**	**7.3**	**13.5**	**7.3**	**7.8**	**6.3**	**3.6**	**8.2**
6						0.0	2.4	10.4	**4.9**	18.7	6.4	5.6	8.6	3.5	4.8	8.7	4.1	6.8	6.5	2.6	3.3	3.0	5.8	5.2
7							0.0	**8.0**	**2.9**	16.6	7.1	**4.1**	**8.0**	1.7	2.2	**7.8**	2.5	**4.1**	**6.6**	1.6	1.8	1.6	**4.6**	**3.6**
8								0.0	9.3	27.6	**12.6**	**9.6**	**11.1**	**7.5**	**8.2**	**12.7**	**11.4**	**9.8**	**11.7**	**7.0**	**7.8**	**5.6**	**4.4**	**6.2**
9									0.0	16.8	6.6	**5.9**	**8.8**	**5.4**	**4.0**	**7.8**	**4.7**	**6.0**	**8.0**	2.5	2.2	**2.7**	**10.0**	**5.3**
10										0.0	16.4	14.7	23.5	17.3	17.5	22.4	19.4	17.7	25.1	16.6	16.1	18.7	21.5	18.6
11											0.0	**11.4**	4.5	9.2	10.6	4.6	**13.1**	**11.4**	6.9	5.1	4.0	4.6	10.6	4.1
12												0.0	**11.0**	**2.9**	1.4	**10.1**	**3.9**	1.2	**8.6**	**3.3**	**5.8**	**5.8**	**6.1**	**9.2**
13													0.0	**9.6**	**10.4**	0.4	**13.6**	**10.4**	3.0	**4.4**	**4.9**	**4.6**	**11.3**	**4.6**
14														0.0	1.5	**9.8**	1.5	**3.0**	**8.0**	2.3	**3.4**	**2.4**	**2.9**	**4.5**
15															0.0	**9.8**	**2.1**	0.8	**7.8**	**2.7**	**3.6**	**3.6**	**5.4**	**7.0**
16																0.0	**12.9**	**9.3**	3.0	**4.0**	**4.8**	**4.9**	**12.6**	**5.6**
17																	0.0	**4.5**	**11.5**	**3.1**	**4.6**	**4.0**	**6.2**	**7.3**
18																		0.0	**7.5**	**3.9**	**5.5**	**5.4**	**6.6**	**9.0**
19																			0.0	**5.1**	**5.6**	**5.0**	**11.7**	**7.6**
20																				0.0	1.4	1.0	**5.0**	**2.8**
21																					0.0	**0.9**	**6.3**	**1.8**
22																						0.0	**4.3**	**1.3**
23																							0.0	**4.4**
24																								0.0

Note: The differences that are significant by the F-test at $p < 0.05$ are shown in bold.

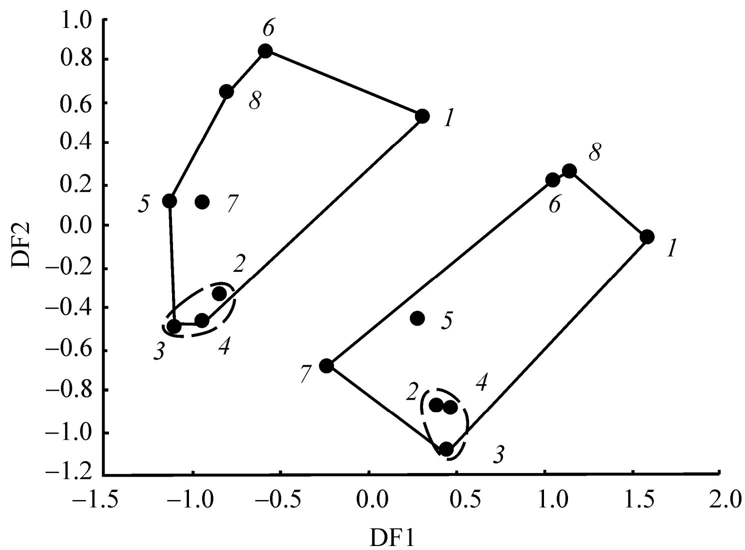

Fig. 3. Results of discriminant analysis of geographic variation of the wing length and the eyespot size in *Coenonympha arcania* L.: centroids of samples relative to the first two canonical discriminant functions (DF); *1–8* are the sampling localities (see Fig. 1).

Analysis of Fluctuating Asymmetry of Eyespots in the Wing Pattern

Fluctuating asymmetry (FA) is often used now in evolutionary and eco-genetic studies as a measure of development stability. The method of assessing the state of environment based on FA criteria proposed by Zakharov (1987, 1993) has been broadly accepted (Vasil'ev and Vasil'eva, 2000; Zakharov et al., 2001, etc.). Analysis of the size parameters in some *Coenonympha* species, including *C. arcania*, revealed both

Table 4. Generalized Mahalanobis distances (D^2) between samples of *Coenonympha arcania* L. males and females by the complex of metric characters

No.	UrSU biol. station		Ilmen Reserve		MUCS "impact"		MUCS "buffer"		MUCS "background"		Lake Berdyanish		Nurali Range		Kuvandyk	
	males	females	males	females	males	females	males	females	males	females	males	females	males	females	males	females
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	0.00	**3.43**	**2.20**	**10.48**	**1.49**	**3.69**	**1.78**	**4.40**	**1.40**	**3.15**	**2.31**	**2.39**	**1.54**	**6.41**	**2.38**	**8.42**
2		0.00	**4.91**	**4.46**	**4.64**	**0.96**	**5.31**	1.08	**4.94**	1.12	**6.71**	1.08	**5.52**	**3.51**	**6.32**	**4.09**
3			0.00	**7.55**	**3.32**	**5.56**	**3.52**	**6.60**	**3.48**	**5.46**	**2.96**	**4.12**	**1.91**	**6.08**	**2.25**	**7.87**
4				0.00	**12.67**	**5.82**	**13.52**	**5.63**	**13.24**	**6.62**	**14.03**	**6.44**	**11.75**	**6.88**	**10.89**	**1.93**
5					0.00	**3.96**	**0.49**	**4.65**	0.44	**3.95**	**1.96**	**3.18**	**1.61**	**5.10**	**2.69**	**11.85**
6						0.00	**4.23**	0.48	**4.24**	1.30	**5.56**	1.12	**4.75**	**3.12**	**5.59**	**5.14**
7							0.00	**4.85**	0.27	**4.14**	**1.44**	**3.68**	**1.25**	**4.93**	**2.99**	**12.61**
8								0.00	**4.62**	1.08	**6.76**	**1.93**	**5.83**	3.11	**7.40**	**5.48**
9									0.00	**3.66**	**2.11**	**3.41**	**1.80**	**5.39**	**3.63**	**12.16**
10										0.00	**6.76**	1.42	**5.12**	**3.99**	**7.07**	**5.27**
11											0.00	**5.24**	**0.92**	**5.99**	**1.99**	**13.46**
12												0.00	**3.85**	**4.07**	**3.94**	**4.67**
13													0.00	**5.49**	**1.14**	**10.69**
14														0.00	**6.66**	**7.78**
15															0.00	**9.23**
16																0.00

Note: The differences that are significant by the F-test at $p < 0.05$ are shown in bold.

fluctuating and directed asymmetry (in males) with respect to the complex of metric characters, namely the wing length and the eyespot diameters (Windig et al., 2000; Zakharova and Chibiryak, 2002).

We calculated the mean frequency of asymmetry per character (*FA*) for all the samples of *C. arcania* (Fig. 5). This value was found to vary from 0.018 (females from the environs of Kuvandyk) to 0.090 (females from the EURT zone, the bank of Lake Berdyanish). Pairwise comparison of the *FA* values using the χ^2 test showed the differences between all the variants to be statistically non-significant. Despite the absence of significant differences in this parameter, the *FA* value clearly tended to increase in the butterflies living within the radioactive pollution zone of EURT. It is interesting that butterflies captured in chemically polluted territories (the "impact" and "buffer" zones of MUCS) revealed the values of *FA* similar to those from the control territories not subject to anthropogenic disturbance, such as the Ilmen Reserve and the Nurali Range.

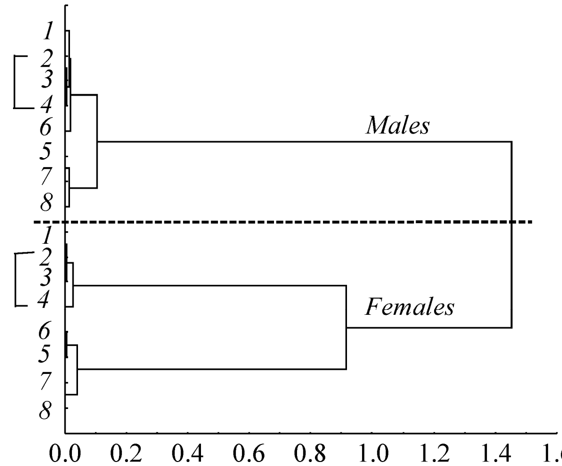

Fig. 4. Similarity dendrogram of samples of *Coenonympha arcania* L. based on non-metric characters of the wing pattern.

DISCUSSION

Analysis of intraspecific variation of *C. arcania* in the Middle and South Urals with respect to the complex of metric characters (the length of the fore and

Table 5. Phenetic distances between samples of *Coenonympha arcania* L.

No.	UrSU biol. station		Ilmen Reserve		MUCS "impact"		MUCS "buffer"		MUCS "background"		Lake Berdyanish		Nurali Range		Kuvandyk	
	males	females	males	females	males	females	males	females	males	females	males	females	males	females	males	females
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	–	**0.034**	0.006	0.004	**0.028**	**0.064**	**0.066**	**0.057**	**1.243**	**2.026**	**1.176**	**1.138**	**1.163**	**1.997**	**1.963**	**2.056**
2	0.006	–	**0.019**	**0.013**	0.013	**0.104**	**0.113**	**0.111**	**0.963**	**1.612**	**0.927**	**0.883**	**0.871**	**1.589**	**1.600**	**1.677**
3	0.004	0.006	–	-0.001	-0.001	**0.120**	**0.120**	**0.110**	**1.198**	**1.887**	**1.125**	**1.093**	**1.120**	**1.883**	**1.898**	**1.964**
4	0.004	0.006	0.004	–	0.008	**0.092**	**0.096**	**0.088**	**1.120**	**1.890**	**1.054**	**1.022**	**1.041**	**1.873**	**1.868**	**1.962**
5	0.006	0.008	0.005	0.006	–	**0.159**	**0.153**	**0.146**	**1.135**	**1.710**	**1.069**	**1.032**	**1.047**	**1.714**	**1.761**	**1.811**
6	0.006	0.008	0.005	0.006	0.007	–	0.001	0.023	**1.131**	**2.071**	**1.121**	**1.043**	**1.023**	**1.995**	**1.856**	**1.993**
7	0.005	0.007	0.004	0.005	0.006	0.006	–	0.005	**1.073**	**1.911**	**1.062**	**0.984**	**0.971**	**1.835**	**1.697**	**1.826**
8	0.004	0.006	0.004	0.004	0.006	0.006	0.005	–	**1.029**	**1.924**	**0.990**	**0.937**	**0.959**	**1.850**	**1.723**	**1.851**
9	0.004	0.006	0.004	0.005	0.006	0.006	0.005	0.004	–	**0.909**	**0.018**	-0.005	0.004	**0.874**	**0.846**	**0.921**
10	0.007	0.009	0.006	0.007	0.008	0.008	0.007	0.007	0.007	–	**1.085**	**0.956**	**0.774**	0.004	**0.083**	**0.042**
11	0.005	0.007	0.004	0.005	0.006	0.007	0.005	0.005	0.005	0.007	–	0.000	**0.066**	**1.062**	1.075	**1.133**
12	0.007	0.010	0.007	0.008	0.009	0.009	0.008	0.007	0.008	0.010	0.008	–	0.009	**0.923**	**0.915**	**0.973**
13	0.001	0.014	0.011	0.012	0.013	0.013	0.012	0.012	0.012	0.014	0.012	0.015	–	**0.720**	**0.689**	**0.777**
14	0.010	0.012	0.009	0.010	0.011	0.011	0.010	0.010	0.010	0.012	0.010	0.013	0.017	–	0.017	0.026
15	0.020	0.022	0.019	0.020	0.021	0.021	0.020	0.020	0.020	0.022	0.021	0.023	0.027	0.025	–	0.002
16	0.010	0.012	0.009	0.010	0.011	0.011	0.010	0.010	0.010	0.012	0.011	0.013	0.017	0.015	0.025	–

Notes: The phenetic distances (MMD) are shown in the upper right part of the matrix, the mean standard deviations (MSD), in the lower left part. The differences that are significant by the χ^2 test at $p < 0.05$ are shown in bold.

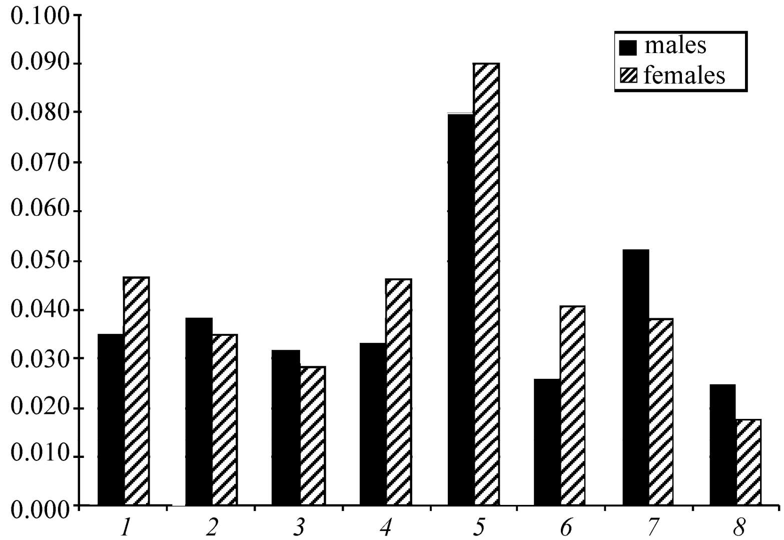

Fig. 5. The mean frequency of asymmetry per character (*FA*) in samples of *Coenonympha arcania* L.

hind wings and the diameters of eyespots in the wing pattern) has revealed sex-related, chronographic, and geographic differences between the samples. Sex dimorphism in size manifests itself in females being larger than males and having larger eyespots. The chronographic differences are comparable with geographic ones in some cases. However, summarized data for all the samples from each geographic locality show that the butterflies living in the southern taiga subzone of the Middle Urals (all the samples from Sverdlovsk Province) are largely similar. *Coenonympha arcania* inhabiting the forest-steppe and steppe zones (samples from Bashkortostan and Orenburg Province) show some phenotypic specificity and are significantly different from the forest-dwelling populations of *C. arcania*. The same result was obtained during comparison of the samples by the complex of non-metric wing characters (the presence or absence of eyespots in the wing pattern). The females of *C. arcania* have a significantly greater number of eyespots and a higher frequency of occurrence of these spots. The butterflies from different landscape zones (forest and steppe) within the studied part of their range differ significantly in both phenetic and metric characters.

Besides the natural communities not subjected to economic activity or affected by moderate pasture load and mowing (the UrSU biological station area, the "background" territory of MUCS, the Ilmen Reserve, the Nurali Range, and the environs of Kuvandyk), we also collected butterflies in anthropogenically disturbed habitats, namely in zones of chemical and radioactive pollution. Calculation of the frequency of asymmetry per character (*FA*) for all the samples of *C. arcania* produced small values which did not differ significantly by the χ^2 test. If we consider this parameter to be a measure of development stability, as some authors suggest (Zakharov et al., 2001), it may be assumed that the living conditions of *C. arcania* are favorable in all the habitats examined. This result may be related to the specific traits of metal and radionuclide accumulation in insects and their food plants.

Within the "impact" territory of MUCS, *C. arcania* fly in grass meadows, keeping close to willow shrubs and scraggy birch coppice. According to Khantemirova (2006), the biomass and species diversity of forbs decrease in polluted meadows whereas the fraction of grasses increases. These grasses (the browntop *Agrostis tenuis* and the tufted hair-grass *Deschampsia caespitosa*) are the food plants of the larvae of *C. arcania*. The browntop *Agrostis tenuis* is a pseudometallophyte that accumulates heavy metals (Zn, Cd, Pb, and Cu) in small concentrations, mostly in the rootage. The tolerance of this grass species to chemical pollution with heavy metals has been described in detail (Bradshaw, 1952; Chadwick and Salt, 1969; Dahmani-Muller et al., 2000, etc.).

Besides the MUCS zone polluted with heavy metals and sulfurous anhydride, we also captured *C. arcania* in the head part of the East Ural Radioactive Trace formed as the result of a contamination incident at the Mayak nuclear fuel reprocessing plant in 1957, known as the Kyshtym disaster. The principal radionuclides in the EURT are strontium-90 and cesium-137, whose migration in the trophic chains has been studied in different biogeocenoses of the affected region (Pokarzhevskii and Usachev, 1993; Martyushov et al., 1999, etc.).

Strontium-90, being an osteotropic element, is most strongly concentrated in the skeletons of vertebrates. Since most insects do not have calcium-rich skeletons, they accumulate this radionuclide less actively. In the tissues of phytophagous insects strontium-90 is not concentrated at all, its contents comprising only 20% of that observed in plants. Cesium-137 is present in the biogeocenoses in smaller quantities than strontium-90. Among insects, the maximum concentrations of this radionuclide were recorded in ants, whereas the rest of the species examined had low contents of cesium-137.

Long-term data have shown that, given the same density of soil contamination, the radionuclide content in plants is determined by the soil properties, the depth of the root system, and the amount of analogous elements required by the plant. The latter depends on the biochemical specificity of the plant and its taxonomic position, the tendency for radionuclide accumulation varying between families. Plants of the madder, orpine, figwort, and legume families tend to accumulate high levels of radionuclides, whereas grasses, sedges, and umbellates accumulate less radionuclides (Martyushov et al., 1999). Considering the published data, we may conclude that radionuclides do not accumulate in the trophic chain comprising the food plants (grasses and sedges) and the larvae of *C. arcania*. This may be the reason why the *FA* values in the polluted areas do not significantly differ from those in the control territories not subject to anthropogenic disturbance.

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