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Phenogenetic Analysis of Pygmy Wood Mouse (*Apodemus uralensis* Pall.) Populations in the Zone of the Eastern Ural Radioactive Trace (EURT)

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Abstract—Monitoring of *A. uralensis* populations in Kamenskii raion, Sverdlovsk oblast, in 1992–2002 and in Kaslinskii raion, Chelyabinsk oblast, in 2000–2001 revealed an increase in the proportion and diversity of minor morphogenetic aberrations and abnormalities in the structure of the cranium along the axis of the Eastern Ural Radioactive Trace (EURT). The samples from the southern and northern parts of the EURT (contaminated with ^{90}Sr to 500 and 4 Ci/km^2, respectively) were characterized by directed deviations from the control with respect to the frequencies of phenes of nonmetric cranial traits and an increase in the level of their fluctuating asymmetry in young females, which is indicative of epigenetic rearrangements in populations living in a radioactive environment.

Key words: pygmy wood mouse, EURT, nonmetric traits, aberrations, phenes, fluctuating asymmetry.

The analysis of minor and major morphological aberrations of the skeleton is often used for studying the effects of various environmental factors, including radioactive contamination of territory, on animal ontogeny in populations (Grüneberg, 1964; Il'enko, 1974; Yablokov, 1987; Parsons, 1992; Vasil'ev *et al.*, 1996). In a broad sense, phenes—stable states of threshold nonmetric cranial traits (Vasil'ev, 1996)—may be regarded as morphogenetic aberrations. Therefore, the methods based on the evaluation of incidence of various morphogenetic disturbances and phene frequencies, as well as of ontogenetic stability by the level of fluctuating asymmetry of bilateral structures, may be used for assessing the ecological state of populations (Zakharov and Clarke, 1993). As the frequencies of phenes of nonmetric skeletal traits are determined by epigenetic threshold limits (Berry and Searle, 1963), their ratio reflects specific features of the epigenetic system in different populations (Vasil'ev, 1996).

The Eastern Ural Radioactive Trace (EURT) was formed in Chelyabinsk oblast, Southern Urals, as a result of an accident at the Mayak Radiochemical Plant in 1957, when up to 2 × 10^6 Ci of radionuclides were emitted into the environment. The head, southern part of the EURT extends as a narrow band over Chelyabinsk oblast northeast of Kyshtym. In the sites located close to the epicenter of the accident, the density of radioactive contamination with ^{90}Sr reaches 500–700 Ci/km^2 and even more (*Ekologicheskie posledstviya...*, 1993). In the northern part of the EURT, in the Kamenskii raion of Sverdlovsk oblast, the level of radioactive contamination of the territory is generally low. However, in the most contaminated area along the EURT axis, the densities of contamination with ^{137}Cs and ^{90}Sr are 1.7–3.2 and 7–40 times greater, respectively, than those beyond its boundaries (Yushkov *et al.*, 1993).

In 1992 and 1993, we studied the populations of northern red-backed voles (*Clethrionomys rutilius* Pall., 1779) from the Kamenskii raion of Sverdlovsk oblast, which inhabited the EURT areas contaminated to different degrees for almost 100 generations. That study revealed an increased morphological diversity and consistent difference with respect to nonmetric cranial traits between the populations inhabiting the impacted area near Lake Tygish (the EURT zone), and those inhabiting the control area beyond the EURT boundary. Similar to the northern red-backed vole, the pygmy wood mouse (*Apodemus uralensis* Pallas, 1811) inhabiting the same territory is regarded as a radionuclide carrier (Il'enko and Krapivko, 1993). However, it differs from the former in some ecological characteristics, including food specialization, mobility, and physiological characteristics, which has an effect on the level and dynamics of radionuclide accumulation (Il'enko, 1974; Martyushov *et al.*, 1999).

Hence, the purpose of this study was to perform similar comparative analysis of *A. uralensis* populations in the EURT areas with different levels of radio-

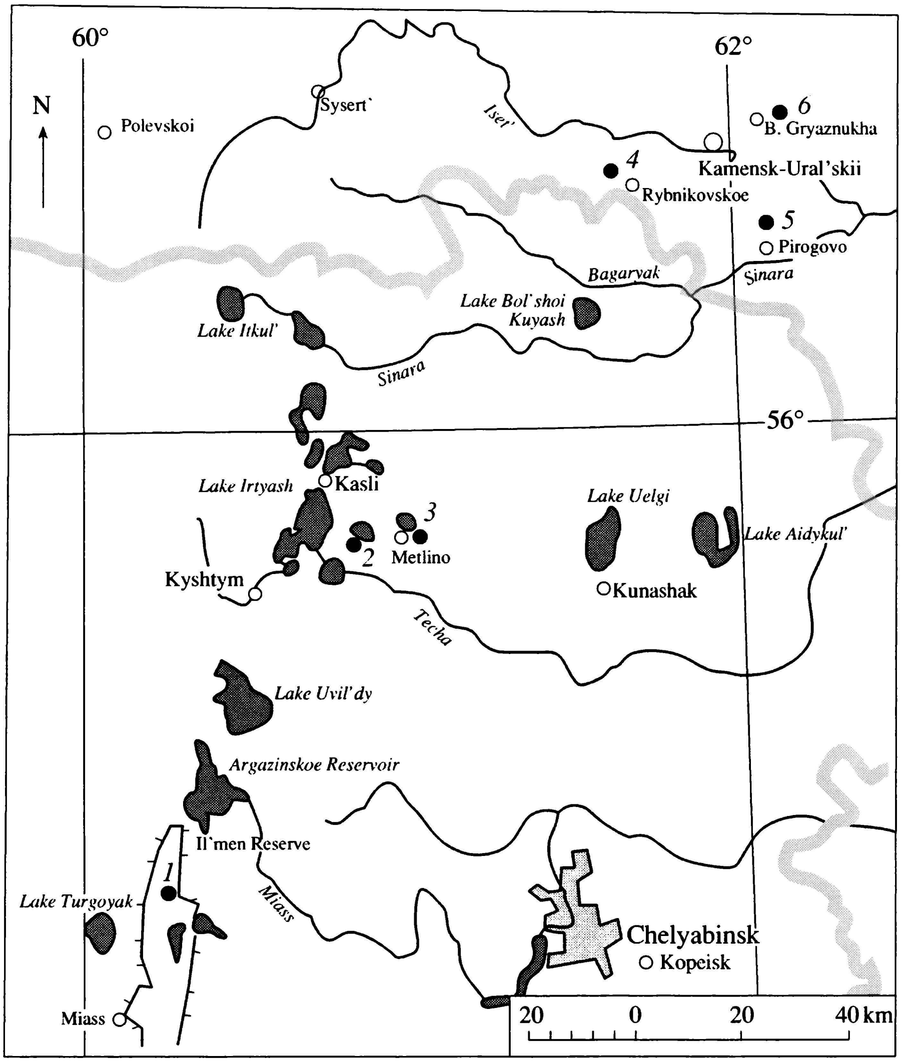

Fig. 1. Map of the areas studied in Chelyabinsk (*1*–*3*) and Sverdlovsk (*4*–*6*) oblasts: (*1*) Il'men State Reserve (ISR); (*2*) Eastern Ural Reserve, impacted site (EURT-1); (*3*) Metelino, control site (Control-1); (*4*) Rybnikovskoe, impacted site (EURT-2); (*5*) Pirogovo, control site (Control-3); and (*6*) Bol'shaya Gryaznukha, control site (Control-2).

active contamination in order to estimate the probable remote morphogenetic consequences of chronic irradiation manifested in characteristic aberrations and abnormalities in the structure of the cranium. It was also important to determine whether the morphogenetic effects of radioactive environmental contamination on *A. uralensis*, compared to *C. rutilus*, were characterized by species-related ecological specificity. Although the latter species was studied only in the northern part of the EURT, we also analyzed the data on *A. uralensis* populations from its southern part, which was most heavily contaminated with radionuclides.

MATERIAL AND METHODS

The study was performed in the Eastern Urals State Reserve (Kaslinskii raion, Chelyabinsk oblast) in 2000–2001 and in Kamenskii raion of Sverdlovsk oblast in 2000–2002. In addition, we analyzed the samples of *A. uralensis* collected at the same sites of Sverdlovsk oblast region in 1992–1993 and in the Il'men State Reserve (ISR) in 2000. The sites where the animals were captured are shown on the map (Fig. 1). In the head part of the EURT, we studied the site near Lake Berdenish with a contamination density of up to 500 Ci/km^2 (EURT-1). The control site with a contamination density of 0.1 Ci/km^2 (Control-1) was located 10 km away near Lake Kozhakul', 2 km northeast of the village of Metlino. Both sites were used earlier for long-term radioecological studies of small mammals in the EURT area (Il'enko and Krapivko, 1993; Krapivko, 2002). The sample from the ISR, where the level of radioactive contamination did not differ from the background level characteristic of the Ural region (0.04 Ci/km^2) (Aarkrog *et al.*, 1998), served as a remote control.

In Sverdlovsk oblast, we studied three sites. The first, impacted site, with the initial contamination level of approximately 4 Ci/km^2 (EURT-2), was located within the EURT boundaries 3–4 km northwest of the village of Rybnikovskoe, near Lake Tygish. Two control sites with the initial contamination level of approximately 0.1 Ci/km^2 were beyond the EURT boundaries, near the villages of Bol'shaya Gryaznukha (Control-2) and Pirogovo (Control-3). These sites were located at almost the same distances from each other and from the impacted site (25–30 km). The plots for capturing rodents were established in herbaceous birch–aspen forests growing under similar site conditions. In total, we studied 373 *A. uralensis* craniums. The relative age of the animals was determined using a set of parameters, with the degree of molar tooth wear being the main criterion. The group of juvenile animals was excluded from further analysis.

The search for and detection of the cranial aberrations were performed under an MBS-10 microscope at a 2 × 8-fold magnification. Originally, we detected more than 80 medial and bilateral aberrations (including singular and very rare aberrations). Then, we analyzed the frequencies of 55 nonmetric traits that occurred more or less regularly. The majority of traits and their states (phenes) were homologous to those described earlier by us and other researchers for other rodent species (Berry and Searle, 1963; Hartman, 1980; Vasil'ev *et al.*, 1996). As international Latin nomenclature for nonmetric threshold cranial traits is absent, we used their working names (Fig. 2) and codes based on aberrations of their Latin names (Table 1). Probable correlation of some traits with animal sex or age could result in biased estimations, and their correlation with each other could provide redundant information. Hence, we revealed such traits by calculating Spearman's rank correlation coefficients and excluded them from analysis. With the same purpose, the relationship between phene expression and animal size (body length) was estimated. The remaining 34 nonmetric traits are listed in Table 1, and their location is shown in Fig. 2.

The phenes of bilateral traits were recorded on the left and right sides of the cranium, and the their frequencies for each trait were calculated taking into account the total number of the sides analyzed (Hartman, 1980). Multiple comparisons of the samples with respect to individual traits were performed using the *G*-test (Sokal and Rohlf, 1981). Smith's mean measures of divergence (*MMD*), or phenetic distances between the samples, and their standard deviations (*MSD*) were calculated using Hartman's equation, with the differences regarded as statistically significant at *MMD* > 2MSD ($p < 0.05$) (Hartman, 1980). Cluster analysis was performed by the UPGMA method. To estimate the level of intrapopulation phenetic diversity, we used the index μ (the average number of variations of a trait in the sample) proposed by Zhivotovsky (1991). The population index of fluctuating asymmetry FA_{nm} was calculated as the average proportion of asymmetrically manifested traits per individual (Zakharov, 1987; Vasil'ev *et al.*, 1996). The significance of differences between the samples with respect to this index was estimated using the nonparametric Kruskal–Wallis test (an analogue of one-way ANOVA). The data were processed statistically using the PHEN 3.0 (developed by A.G. Vasil'ev) and Statistica 5.5 software packages.

RESULTS

Of more than 80 aberrations in the structure of the *A. uralensis* cranium, 27 rarely occurring aberrations could be classified as major anomalies. We discovered several variants of bone reduction in the region of foramen ovale, deletions of large fragments of the frontal and parietal bones (including the region of coronal suture), the squamosal growing together with the frontal or parietal bones, anomalous structure of the orbit, a fissure in the palate, malformations (outgrowths) of the mandible, fragmentation of the third molar, etc. The variants of these anomalies were much more numerous in the EURT-1, EURT-2, and Control-3 samples than in the Control-1 sample, and no such cases were detected in the ISR and Control-2 samples. As the boundary between major and minor aberrations is arbitrary, some of the 55 regularly occurring aberrations analyzed below (FPO', *IF1, IF2, PTF*, etc.) may be also regarded as major anomalies.

Preliminary analysis of all material showed that the expression of six phenes (FPM, FMDS, etc.) was formally sex-dependent. Because the samples did not differ in the sex ratio ($p = 0.064$) and Spearman's rank correlation coefficients varied from –0.12 to 0.08, we did not exclude these traits from further analysis. Significant correlations with animal age and body size were revealed for 15 out of 55 traits, and the traits with Spearman's coefficients greater than 0.20 were excluded from analysis. Some traits (12.7%) correlated with each other and were excluded to avoid redundancy of information. Eventually, we selected 34 out of 55 traits. We did not find any statistically significant differences in the frequency of their occurrence on the left and right body sides ($p = 0.598$), i.e., any manifestations of directed asymmetry.

First, it was important to estimate the possible displacement of phenetic estimates in two consecutive years differing in climatic and phenological characteristics. For this purpose, we compared phene frequencies in the samples taken in 1992 and 1993 from the control (Control-2) and impacted (EURT-2) populations, as well as between the samples taken in 2000 and 2001 from the impacted population (EURT-1). The phenetic distances (*MMD*) between the samples of different years from the impacted and control populations were negligible and statistically nonsignificant (the maximal *MMD* between the EURT-2 samples taken in different years was 0.011 ± 0.016). Thus, the chrono-

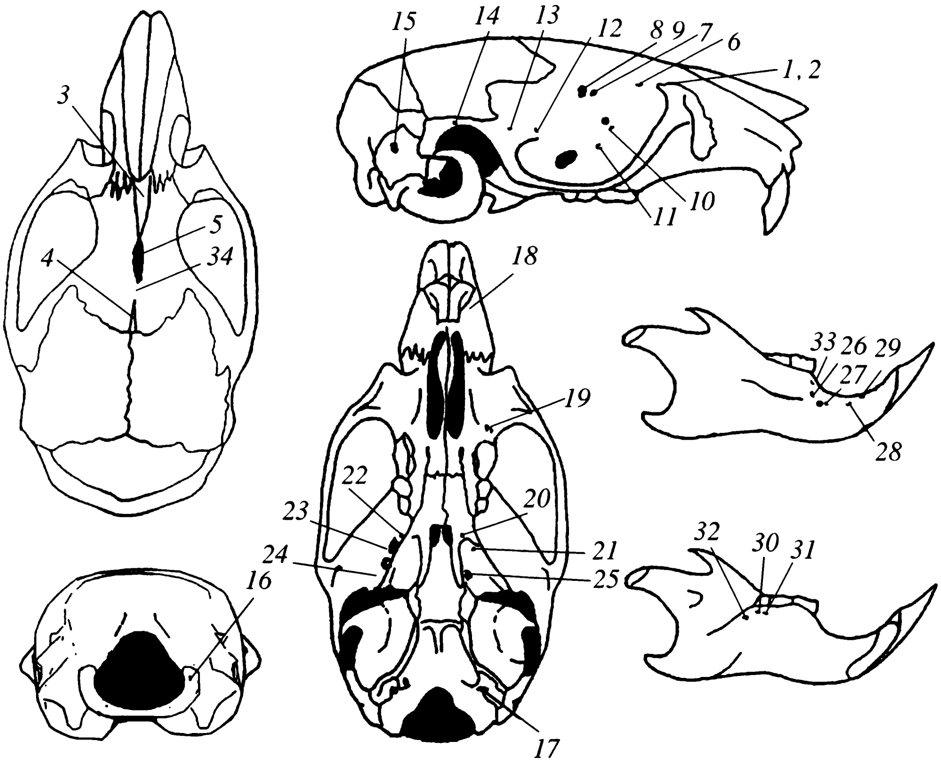

Fig. 2. Phenes of nonmetric cranial traits of *Apodemus uralensis*: (*1*) doubled preorbital foramen, (*2*) absence of preorbital foramen, (*3*) interfrontal bone in the anterior half of the frontal suture; (*4*) interfrontal bone in the posterior half of the frontal suture, (*5*) spindle-form dilatation in the anterior half of the frontal suture, (*6*) anterior frontal foramen, (*7*) additional frontal foramen anterior to the main foramen; (*8*) additional frontal foramen posterior to the main foramen, (*9*) doubled frontal foramen, (*10*) doubled ethmoid foramen, (*11*) inferior orbital foramen, (*12*) anterior foramen in the squamosal, (*13*) central foramen in the squamosal, (*14*) temporal meatus, (*15*) fenestra in the mastoid, (*16*) condylar foramen, (*17*) doubled hypoglossal foramen, (*18*) anterior premaxillary foramen, (*19*) doubled intermediate maxillary foramen, (*20*) foramen in the base of pterygoid process, (*21*) foramen in the pterygoid fossa, (*22*) additional round foramen, (*23*) foramen in the septum between the round and oval foramina, (*24*) additional foramen located laterally to the oval foramen, (*25*) doubled alar foramen, (*26*) additional mental foramen above the main foramen, (*27*) additional mental foramen in front of the main foramen, (*28*) mandibular foramen I, (*29*) mandibular foramen II, (*30*) foramen at the lingual side of M_2 alveole, (*31*) doubled foramen at the lingual side of M_2 alveole, (*32*) foramen at the lingual side of M_3 alveole, (*33*) foramen in the dorsal surface of mandible in its incisive part, and (*34*) accretion of frontal bones (over least two-thirds of the frontal suture). Asterisks indicate medial traits.

graphic displacement of phene frequencies proved to be slight and random. This allowed us to pool the samples of the same name taken in different years and to perform further calculations with the pooled data (Table 1).

The comparison of initial phene frequencies in the pairs of samples taken in the south (Control-1 vs. EURT-1) and north (Control-2 vs. EURT-2) of the study area showed that differences in many traits between the control and impacted samples in the northern and southern pairs were characterized by similar tendencies (Table 1). This was especially true in the case of five traits: FUF, FDS, FPM, IF2, and FFDP. As this parallelism manifested itself in a series of traits (29.4%), it cannot be regarded as random. The above traits characterize specific features of cranial osteogenesis (bone accretion, intercalary bone formation, and deletions of bone fragments) and reflect the increased frequency of certain foramina for blood vessels and nerves in the maxilla and mandible.

To test the hypothesis concerning a possible increase in the level of morphogenetic aberrations in the populations inhabiting the areas affected by the EURT, we calculated the mean aberration frequencies (*MAF*), i.e., the average proportions of the phenes of all traits per cranial side. This approach is reasonable, because the correlation between these traits was statistically nonsignificant or negligible (the traits correlating with each other were excluded from analysis).

We revealed no statistically significant correlation between *MAF* and animal sex, age, or body size. To simplify data processing and make the pattern of differences more distinct, all samples were ranked with respect to the level of radioactive contamination of the environment. As a result, we distinguished three groups: (1) control (background level), (2) EURT-2 (low level), and (3) EURT-1 (high level). The comparison of these groups showed that the mean aberration frequency significantly increased along the ascending

Table 1. Frequencies of the phenes of nonmetric traits (%) in the impacted and control populations of *Apodemus uralensis*

Trait	EURT-1	Control-1	ISR	EURT-2	Control-2	Control-3	Multiple *G*-test
	$N = 192$	$N = 52$	$N = 42$	$N = 154$	$N = 60$	$N = 230$	
1. FPO	15.05	17.65	11.90	16.99	8.62	9.91	
2. FPO'	0.00	0.00	0.00	0.00	0.00	4.04	***
3. *IF1*	0.00	0.00	0.00	0.00	0.00	4.76	*
4. *IF2*	1.09	0.00	0.00	1.37	0.00	4.76	
5. *PTF*	8.70	12.50	19.05	12.33	21.43	5.71	
6. FFA	9.63	16.00	11.90	18.54	15.79	16.59	
7. FFDA	18.13	13.73	21.43	28.67	21.43	23.15	
8. FFDP	18.23	13.73	28.57	18.67	16.07	19.44	
9. FFDU	3.31	0.00	0.00	1.32	0.00	2.31	
10. FE	21.62	26.00	35.71	31.33	25.00	31.48	
11. FIO	68.82	76.00	83.33	82.55	67.24	76.71	*
12. FTA	20.21	23.08	16.67	22.92	12.73	25.46	
13. FTM	21.39	23.53	19.44	18.62	7.27	13.89	
14. MT	41.85	37.25	25.00	22.79	34.62	35.41	**
15. FFL	79.14	88.24	57.14	74.10	76.79	75.48	*
16. FCS	80.00	86.00	72.73	79.41	67.80	70.68	
17. FH	37.22	48.00	58.82	41.98	35.59	36.84	
18. FPM	56.83	9.80	35.71	30.52	15.79	34.93	***
19. FMX2	32.62	42.31	42.86	33.33	26.32	37.56	
20. FPT	15.51	13.46	4.76	25.00	25.00	14.41	**
21. FPTI	46.52	42.00	54.76	68.06	46.43	42.79	***
22. FRD	85.03	87.50	90.00	55.41	38.18	42.23	***
23. FLT1	96.83	97.92	95.24	92.52	96.43	86.89	**
24. FODP	27.87	26.09	29.27	32.21	28.30	15.76	**
25. FAL	4.28	12.00	2.38	8.28	0.00	4.48	*
26. FMTS	53.40	30.00	21.95	29.22	29.31	32.17	***
27. FMTA	8.38	8.00	4.88	0.65	1.72	9.13	***
28. FMDA	25.13	32.00	56.10	24.84	15.52	16.52	***
29. FMDS	40.31	34.00	39.02	37.91	31.03	28.70	
30. FAL	93.65	98.04	100.00	96.08	98.18	89.04	*
31. FAL2	39.79	35.29	42.50	31.37	22.81	17.54	***
32. FALP	24.74	25.49	25.00	23.53	21.43	27.19	
33. FDS	45.55	33.33	51.22	50.98	36.84	42.17	
34. *FUF*	80.43	58.33	66.67	73.97	57.14	54.29	**

Note: N is the number of cranial sides analyzed. Asterisks indicate that differences are statistically significant at * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$. Names of medial traits are italicized.

gradient of radioactive contamination (from 34.36 ± 0.34 to 37.42 ± 0.42 and to 39.49 ± 0.39; $H = 85.1$, $p < 0.0001$), with the variance of this parameter significantly decreasing (45.47, 29.26, and 27.36, respectively; $p < 0.0001$). Thus, *MAF* in the impacted sample proved to be significantly greater than in the control.

At the next stage, we assessed the level of intrapopulation phenetic diversity using Zhivotovsky's μ index characterizing the mean number of phenes per trait in the six populations compared (Fig. 3). The phenetic diversity in the impacted populations was significantly greater than in the control (including ISR). However,

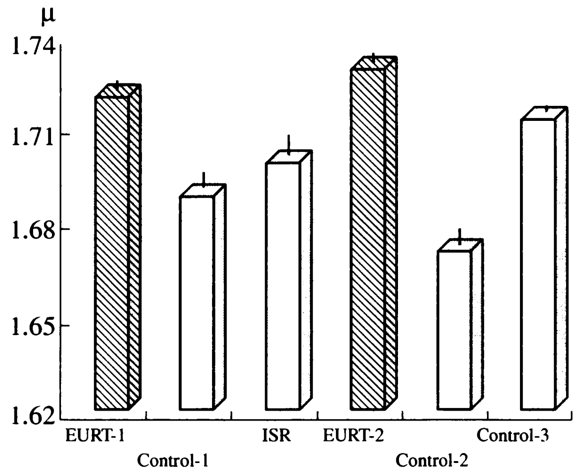

Fig. 3. Levels of "phenetic diversity" (μ) in the impacted and control populations of *Apodemus uralensis* within and beyond the EURT zone.

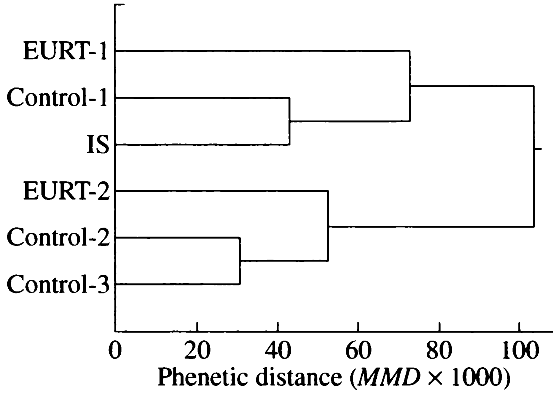

Fig. 4. Cluster analysis (UPGMA) of *Apodemus uralensis* samples based on the matrix of phenetic distances (*MMD*).

this parameter was slightly increased in the Control-3 sample taken near the UAZ sludge storage, which could be due to a high level of fluorides in the environment. It is known that fluorine has osteotropic properties, and its intake at early ontogenetic stages may affect morphogenesis of the cranium.

Multiple comparisons with the use of *G*-test revealed statistically significant differences in phene frequencies between the six samples with respect to 18 out of 34 traits (Table 1).These traits were used to calculate *MMDs* between the samples in order to estimate possible phenogenetic divergence of impacted populations from the control. The data summarized in Table 2 show that the greatest *MMDs* were recorded between the geographically remote northern and southern samples. The pairs of control samples slightly differed from one another both in the north ($MMD = 0.031 \pm 0.009$) and in the south ($MMD = 0.043 \pm 0.017$). Cluster analysis of the *MMD* matrix showed that, both in the south and north, the impacted groups generally differ from the control more significantly than the control groups from one another (Fig. 4).

As we found a weak yet significant relationship between the mean index of fluctuating asymmetry FA_{nm} and animal age ($r_s = -0.12$, $p < 0.019$), its values were compared in the more abundant group of young of the year. We determined FA_{nm} values for males and females separately in two pooled samples composed of all control and all impacted groups. The comparison showed that FA_{nm} for females from the impacted samples was significantly higher than that for the control females ($H = 9.15$; $df_{1-2} = 2, 132$; $p < 0.0103$), but no such difference was found for males.

DISCUSSION

The analysis of *A. uralensis* populations in the areas of Sverdlovsk and Chelyabinsk oblasts affected by the EURT revealed an increase in the phenetic diversity and average frequency of cranial aberrations in the animals inhabiting the impacted sites. As shown earlier, the phenetic distances between the groups in continuous parts of the range are usually proportional to the geographic distances between them (Vasil'ev, 1996). However, the assessment of the ratio between the phenetic and geographic distances between the groups compared shows that the phenetic segregation of impacted groups is not proportional to the geographic distance between them (Figs. 1, 4). This tendency is especially distinct in the southern part of EURT: *MMD* for the EURT-1 and Control-1 samples taken at a dis-

Table 2. Smith's mean measures of divergence (*MMD*) between the impacted and control *Apodemus uralensis* populations, with mean standard deviations (*MSD*) shown in the lower triangle (all *MMD* values are statistically significant)

Population	EURT-1	Control-1	ISR	EURT-2	Control-2	Control-3
EURT-1		0.0732	0.0724	0.0864	0.1272	0.1223
Control-1	0.0097		0.0430	0.0701	0.0708	0.1005
ISR	0.0111	0.0167		0.0723	0.1364	0.1445
EURT-2	0.0047	0.0103	0.0116		0.0339	0.0712
Control-2	0.0088	0.0145	0.0158	0.0094		0.0306
Control-3	0.0038	0.0045	0.0108	0.0044	0.0086	

tance of 10 km from one another is even greater than *MMD* for the Control-1 and ISR samples taken at a distance of more than 80 km. Interestingly, there is a positive cophenetic correlation between the matrices of geographic distances and the corresponding phenetic distances ($r = 0.65$; $p < 0.009$), which significantly increased when the impacted groups are excluded from comparison ($r = 0.89$; $p < 0.019$). A similar effect was observed for the northern red-backed vole in the northern part of EURT (Vasil'ev *et al.*, 1996). Therefore, the EURT influence may be a factor increasing the extent of differentiation of rodent populations. The phenetic specificity of impacted groups in both species, which does not fit the predicted scheme of phenetic relationships, may be regarded as evidence for a directed change in the epigenetic system of impacted populations.

Fluctuating asymmetry—independent and unequal expression of bilateral traits on different body sides—is regarded as a generalized epigenetic measure of developmental stress (Parsons, 1992) that makes it possible to assess the stability of development in a group of individuals and is used in population biomonitoring (Palmer and Strobeck, 1986; Zakharov, 1987). In this connection, the increased FA_{nm} index of young females in both *A. uralensis* groups from the EURT area is noteworthy. In the impacted populations, this index is relatively high in young females ($FA_{nm} = 26.02 \pm 0.80$) and decreases in older females ($FA_{nm} = 20.86 \pm 1.75$); in the control females, it is generally lower and does not change with age ($FA_{nm} = 23.22 \pm 0.77$ and 23.39 ± 1.32, respectively). Thus, we observe a significant interaction between the factors "chronic irradiation intensity" and "age" with respect to FA_{nm} ($F = 4.92$; $p = 0.028$). Note that the Bartlett test for the homogeneity of variances have not revealed any significant differences ($p = 0.992$). A decrease in FA_{nm} with age in the impacted sites may be due to more active elimination of "asymmetric" animals in the EURT zone. As succession in the functioning of the epigenetic system is provided mainly by females, increasing developmental instability in young females from the EURT area is a symptom of epigenetic transformations in the impacted populations.

A rapid process related to the development of radioresistance in the same *A. uralensis* populations was reported earlier by Il'enko and Krapivko (1993). Experiments on crossing the mice from the control (Control-1) and impacted (EURT-1) populations under laboratory conditions with subsequent assessment of their radioresistance showed that the offspring of females from the EURT-1 group were more radioresistant than their parents (Krapivko, 2002). The level of radioresistance in the offspring after reciprocal crossing was similar to that in the animals from the impacted site. These phenogenetic data suggest that radioresistance is also related to the rearrangement of the epigenetic system in the impacted groups.

Thus, the morphogenetic responses of *A. uralensis* populations to long-term "low-intensity irradiation" [the term proposed by Krapivko (2002)] in the EURT-1 site and chronic irradiation at low loses in the EURT-2 site are similar in many parameters. It is unlikely that this similarity is due to the direct effect of radiation, because the level of contamination with radionuclides in the EURT-2 site has markedly decreased. If we regard this phenomenon as a probable delayed consequence of chronic irradiation, we should accept that the populations of *Apodemus uralensis* inhabiting the zone of EURT, irrespective of contamination density over the period since the accident (up to 135 generations), have been undergoing parallel directed rearrangements of the epigenetic system. The pattern of epigenetic thresholds determining the probability of expression of certain nonmetric traits (phenes), which possibly play an adaptive role, has changed during this period. As phene frequencies in the impacted and control populations remain fairy stable in different years, the situation is apparently close to stabilization. All these adaptive and inadaptive rearrangements in impacted populations are accompanied by an increase in their radioresistance (Il'enko and Krapivko, 1993, 1998).

The results of analysis of impacted *A. uralensis* populations are consistent with the earlier data for the northern red-backed vole (Vasil'ev *et al.*, 1996). It can be assumed that, in both these rodent species, the effects described above are determined by two simultaneous processes: (1) the chronic influence of radioactive contamination on ontogeny and the accumulation of small epigenetic aberrations, which account for the increased number of phenotypic anomalies in the EURT area, and (2) selection for radioresistance among reproductive animals, which is accompanied by adaptive rearrangements of the epigenetic system in the impacted populations.

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REFERENCES

Aarkrog, A., Dahlgaard, H., Nielsen, S.P., *et al.*, Radionuclides in the Impact Zones of two Nuclear Accidents: Kyshtym (1957) and Lake Karachai (1967), in *Problemy radioekologii i pogranichnykh distsiplin* (Problems in Radioecology and Related Disciplines), Zarechnyi, 1998, pp. 5–49.

Berry, R.J. and Searle, A.G., Epigenetic Polymorphism of the Rodent Skeleton, *Proc. Zool. Soc. London*, 1963, vol. 140, pp. 557–615.

Ekologicheskie posledstviya radioaktivnogo zagryazneniya na Yuzhnom Urale (Ecological Consequences of Radioactive Contamination in the Southern Urals), Moscow: Nauka, 1993.

Grüneberg, H., Genetical Research in an Area of High Natural Radioactivity in South India, *Nature* (London), 1964, vol. 204, no. 4955, pp. 222–224.

Hartman, S.E., Geographic Variation Analysis of *Dipodomys ordii* Using Nonmetric Cranial Traits, *J. Mammal.*, 1980, vol. 61, pp. 436–448.

Il'enko, A.I., *Kontsentrirovanie zhivotnymi radioizotopov i ikh vliyanie na populyatsiyu* (Concentration of Radioisotopes by Animals and Their Effect on the Population), Moscow: Nauka, 1974.

Il'enko, A.I. and Krapivko, T.P., Ecological Consequences of Radioactive Contamination for the Populations of Small Mammals as Strontium Carriers, in *Ekologicheskie posledstviya radioaktivnogo zagryazneniya na Yuzhnom Urale* (Ecological Consequences of Radioactive Contamination in the Southern Urals), Moscow: Nauka, 1993, pp. 171–180.

Il'enko, A.I. and Krapivko, T.P., Results of Radioecological Monitoring of a Bank Vole Population after the Chernobyl Accident, *Zool. Zh.*, 1998, vol. 77, no. 1, pp. 108–116.

Krapivko, T.P., The Ecology of Natural Rodent Populations in the Zone of the Eastern Ural Radioactive Trace, *Regional'naya nauchno-prakticheskaya konferentsiya VURS-45* (Regional Scientific and Practical Conference EURT-45), Ozersk: Redaktsionno-Izdatel'skii Tsentr VRB, 2002, pp. 137–166.

Martyushov, V.Z., Krivolutskii, D.A., Smirnov, E.G., and Tarasov, O.V., Ecological Consequences of Long-Term Radioactive Contamination in the Southern Urals, in *Bioindikatsiya radioaktivnykh zagryaznenii* (Bioindication of Radioactive Contamination), Moscow: Nauka, 1999, pp. 49–71.

Palmer, A.R. and Strobeck, C., Fluctuating Asymmetry: Measurement, Analysis, Patterns, *Annu. Rev. Ecol. Syst.*, 1986, vol. 17, pp. 391–421.

Parsons, P.A., Fluctuating Asymmetry: A Biological Monitor of Environmental and Genomic Stress, *Heredity*, 1992, vol. 68, pp. 361–364.

Sokal, R.R. and Rohlf, F.J., *Biometry: The Principles and Practice of Statistics in Biological Research*, New York: Freeman, 1981, 2nd ed.

Vasil'ev, A.G., Phenetic Analysis of Biodiversity at the Population Level, *Abstract of Doctoral (Biol.) Dissertation*, Yekaterinburg: Inst. Plant Anim. Ecol., Ural Division, Russian Acad, Sci., 1996.

Vasil'ev, A.G., Vasil'eva, I.A., and Bol'shakov, V.N., Phenetic Monitoring of the Northern Redbacked Vole (*Clethrionomys rutilus* Pall.) Populations in the Zone of the Eastern Ural Radioactive Trace, *Ekologiya*, 1996, vol. 27, no. 2, pp. 117–124.

Yablokov, A.V., *Populyatsionnaya biologiya* (Population Biology), Moscow: Vysshaya Shkola, 1987.

Yushkov, P.I., Trapeznikov, A.V., Molchanova, I.V., *et al.*, Radioecological Investigations in the Shore Zone of Lake Catchment Area on the Eastern Ural Radioactive Trace Territory in Sverdlovsk Oblast, in *Realizatsiya Gosudarstvennoi programmy Rossiiskoi Federatsii po radiatsionnoi reabilitatsii Ural'skogo regiona* (Implementation of the Russian Federation State Program for Radiation Rehabilitation of the Ural Region), Ekaterinburg, 1993, pp. 9–10.

Zakharov, V.M., *Asimmetriya zhivotnykh: populyatsionno-fenogeneticheskii podkhod* (Asymmetry in Animals: A Population-Phenogenetic Approach), Moscow: Nauka, 1987.

Zakharov, V.M. and Clarke, G.M., *Biotest. Integral'naya otsenka zdorov'ya ekosistem i otdel'nykh vidov* (Biotest: An Integral Assessment of the State of Ecosystems and Individual Species), Moscow: Biotest, 1993.

Zhivotovsky, L.A., *Populyatsionnaya biometriya* (Population Biometrics), Moscow: Nauka, 1991.