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Chorological and Geochemical Factors of Morphogenesis, Using Deviant Forms of *Rana arvalis* Nilsson, 1842 as an Example

V. L. Vershinin[a, b, *] and S. D. Vershinina[a]

[a] *Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Science, Yekaterinburg, 620144 Russia*

[b] *Ural Federal University, Department of Biodiversity and Bioecology, Yekaterinburg, 620002 Russia*

**e-mail: vol_de_mar@list.ru*

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Abstract—The frequencies of five abnormal variants of juveniles in populations of the moor frog *Rana arvalis* in urbanization gradient are analyzed based on 39-year-long monitoring. The data on the limits of occurrences of this deviations in natural conditions are obtained. An increase in the frequency of features under study with the growth of concentration of certain ions, general mineralization, and pH is recorded. Notwithstanding fragmentation of environment and insulation of continuous geographical range, parallelism of the trends in morphological changes in particular isolates is shown. At the same time, the distribution of relatively rare anomalies can be limited by the presence of natural physical barriers.

Keywords: Amphibia, morphological anomalies, morphogenesis, geochemical factors

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INTRODUCTION

Morphological anomalies of amphibians, their frequency, spectrum, and distribution in populations of various species of the world becomes more and more discussed question in connection with global reduction of their number and decreasing biodiversity. Attempts at organization of local, regional, and global monitoring for the establishment of the reasons for their mass manifestation, revelation of patterns of their fluctuations, explanation of this phenomenon, and prediction of potential *hot points* are performed. However, this is precluded by the complex character of distribution and temporal dynamics of this phenomenon, which is connected with the incidental character of their appearance and also disproportionally high contribution of local factors (Reeves et al., 2013).

In the history of the biosphere, examples of a sharp increase in phenotypic manifestation of latent variability, which is associated with transition of a particular group to the noncoherent phase of evolution, are well known (Krassilov, 1986). As Shishkin (2015, 2017) emphasized, both extinction and appearance of a new taxon are accompanied by a burst of variability (terminal instability and archaic initial diversity). As the concentration of some elements in environment is high and fluctuations of geochemical factors are significant, the rates of evolutionary transformations increase due to genotypic distinctions in tolerance of individuals in populations (Kovalsky, 1963). The ideas concerning possible influence of the geochemical parameters of environment on evolutionary processes and morphogenesis appeared even at the beginning of the 20th century. Labbé (1924) believed that the main invertebrate groups could be formed because of influence on the egg of changes in salinity and pH of waters. Modern data provide evidence that an increase in concentration of ions (growth of mineralization) results not only in an increase in the death rate, but also influences the physical mechanics of ontogeny (von Dassow and Dawidson, 2011), which can change the definitive shape. It is shown that the change in ionic composition causes stress and increases the level of corticosterone in tadpoles (Chambers, 2009), promoting manifestation in phenotype of variants deviating from the wild type. The change in the hormonal background under the influence of artificial selection also results in manifestation in phenotype of new features which come out of the range of the usual spectrum of morphological variability (Belyaev, 1974; 1979).

The mosaicism of geochemical parameters of environment can appear a background of speciation within a very small site continuous geographical range. In particular, alkalization of soils in Lord Howe Island because of volcanic activity resulted in divergence in the time of flowering and, in due course, isolation of two species of palm trees, *Howea forsteriana* and *H. belmoreana,* following the pattern of sympatric speciation (Savolainen et al., 2006). In conditions of anthropogenic pollution, the change in pH of soils can cause divergence in the flowering time of the grass *Anthoxanthum odoratum* and reproductive isolation of neighboring populations (Snaydon and Davies, 1976). Using modern ecosystem crises (drying of the Aral Sea) as an example, adaptive radiation in the mollusk *Cerastoderma isthmicum* was described. The effect of critical salinity promoted the growth of the proportion of developmental anomalies and explosive expansion to phenotypic variability, which is greater than the limits of the species reaction norm and reflects fundamental reorganization of the gene pool of populations (Andreev and Andreeva, 2003).

The Ural Region is characterized by complex natural landscape and geochemical conditions, that is, consists of many biogeochemical provinces. In addition, natural geochemistry is complicated by industrial pollution combined with urbanization. Amphibians are anamniotes, whose ontogeny develops in open environment of small water bodies, having a complex life cycle and high penetrability of skin, significantly depend on the external environmental factors, which provide prerequisites for the appearance of deviant morphological forms. The acceleration of embryogeny in conditions of thermal pollution (Vershinin, 2011) and, on the contrary, retardation of larval development under the effect of pollutants (Slepyan and Grefner, 1989) disturb normal course of ontogeny, promoting heterochronies. The presence of endocrine disrupters in the environment (Hayes et al., 2006; Skelly et al., 2010) can result in changes in the hormonal background, which is known to influence definitive morphology of the skeleton (Merkulov, 2011). In general, in tadpoles of the moor frogs, seven variants of deviations composing 26.8% of the total number of anomalies are formed as heterochronies (Vershinin, 2017). Dependence of many morphological characters of amphibians on the level of pollution of the environment has been established. In particular, high positive reliable correlation between the proportion of tadpoles of *Lissotriton vulgaris* and the closed median suture of the skull and the level of mineralization of surface waters in their habitats (Perekhrest and Trofimov, 2016) and also between the frequency and spectrum of skeletal anomalies of tadpoles of *R. temporaria* and mineralization of spawning water bodies (Neustroeva, 2012). Natural, nonfragmented populations of *R. temporaria* occupying natural biogeochemical provinces are sometimes characterized by a high frequency of anomalies in the peripheral skeleton, but a narrow spectrum of such deviations compared to the urbanized territories (Vershinin, 2009).

Thus, the study of deviant morphology of amphibians in conditions of geochemical specificity of fragmentary urbanized territory is undoubtedly of interest.

MATERIAL AND METHODS

The purpose of the present paper is the study of the appearance and distribution of some anomalies in the urbanized territory of a large megacity (Yekaterinburg), depending on the geochemical gradient.

Comparative analysis in the urbanized territory was performed based of the previously developed typification of urbanized territories (Vershinin, 1980, 2002). The zonal assignment of a particular habitat is determined primarily by the extent of the total anthropogenic transformation rather than its topographical position (Vershinin, 1997). Zone I is the central part of the city with multi-storey buildings, massive asphalt cover, water bodies with strong industrial pollution, small rivers and creeks enclosed in pipes. In this zone, amphibians are absent. Zone II is areas of multi-storey buildings with developed territories, waste grounds, sites with exposed soils, small water bodies with high impurity. Zone III is low building, mostly areas occupied by houses of the private sector, with gardens and kitchen gardens, waste grounds, and parks. Biotopes of this zone often adjoin forest parks. Zone IV is forest park zone of the city. Habitats of this zone are basically under influence of recreational loading. The control is the forestland 23 km from Yekaterinburg.

Landscape typification is confirmed by annual hydrochemical analyses of spawning water bodies. Hydrochemical analyses were performed in the Institute of Water Industry and Protection of Water Resources, Laboratory of Physical and Chemical Analyses of Ural State Mining University.

City and country populations of the moor frog (the most eurytopic amphibian species in natural and anthropogenic landscapes of the region under study) were investigated (Vershinin, 2007). The total number of tadpoles of *R. arvalis* is 17257 specimens.

The analysis of morphological anomalies was performed according to the modern methodology (Vershinin, 2015); classification and terminology follows Henle et al. (2017). For natural populations, the territorial distribution and frequency of five variants of anomalies (of 23 established) with stable (discrete) manifestation and unique for moor frog populations in the working territory were analyzed. Two anomalies are most frequent (Vershinin, 2017) and most widespread (Fig. 1) in the urbanized territory; these are depigmentation of the iris and dissipation of melanin. Depigmentation of the iris of *R. arvalis* is controlled by a recessive mutation (Rostand and Darre, 1970; Rostand, 1953; Dubois, 1968), the expressivity and penetrance of which depend on conditions (Vershinin, 2004). The dissipation of melanin is connected with the disturbance of reactivity of skin melanophores at a high level of pollution (Voronova et al., 1983). In addition, we estimated the frequency of microphthalmia, an anomaly connected with dysfunction of the integrin gene, which results in a gradual decrease in the level of all integrins in the crystalline lens and, hence, deviation from the norm (Simirskii et al., 2013). We also analyzed the frequency and distribution of two sublethal anomalies, which are manifested as the metamorphosis is accomplished, i.e., mandibular hypoplasia (reduced lower jaw) and arthrogryposis of

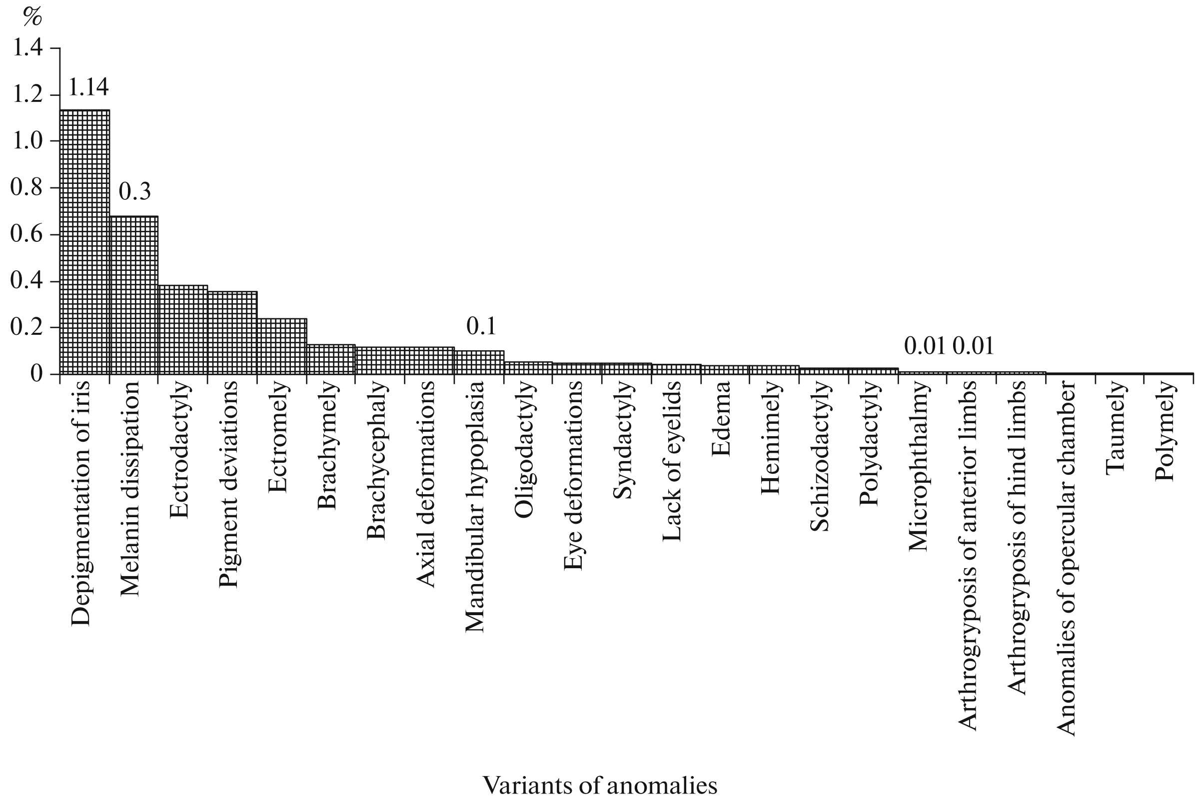

Fig. 1. Frequency of particular anomalies: Sum data on tadpoles of *R. arvalis* during all years of the study, % of total number of animals.

anterior limbs (syndrome of fixed anterior limbs after Kovalenko (2000)). The data obtained are compared with ecological geochemical gradients and chorological specificity of urbanized territories (Yekaterinburg).

RESULTS AND DISCUSSION

Long-term monitoring of conditions of surface waters in habitats in the city agglomeration of Yekaterinburg has shown a stable geochemical gradient (Vershinin, 2011), i.e., an increase in pH, the growth of general mineralization (Tables 1, Fig. 2) and concentration of sulfates, chlorides, and some other ions (Vershinin et al., 2015).

Significant changes in geochemistry of environment due to the accumulating character of city ecosystems and also fragmentation of habitats resulting in the formation of small isolated populations have a considerable effect on the limits of the population phenotypic norm, accompanying spectrum of extreme variants of variation, and frequency of anomalies. The presence of positive linear dependence (R = 0.988, F = 79.1; p = 0.01) between general mineralization of spawning water bodies and total frequency of morphological anomalies in tadpoles of the moor frog (Fig. 3).

The terrestrial area of habitats decreases with the growth of urbanization, while isolation and fragmentation of environment become more pronounced (Vershinin, 2002). The physical (spatial and territo-

Table 1. Change in the concentration of mineral substances in the urbanized territory from (sum from 1980 to 2016)

Parameter	Multistorey building zone	Low building zone	Forest park zone	Country area
pH	7.4 ± 0.09 (n = 86)	7.2 ± 0.1 (n = 74)	7.0 ± 0.07 (n = 123)	6.6 ± 0.1 (n = 63)
Mineralization, mg/dm^3	532.4 ± 25.5 (n = 51)	257.6 ± 23.7 (n = 59)	186.5 ± 18.2 (n = 100)	133.3 ± 25.3 (n = 52)
Sulfates, mg/dm^3	98.5 ± 8.2 (n = 82)	62.3 ± 8.5 (n = 75)	35.8 ± 6.8 (n = 121)	19.0 ± 9.7 (n = 59)
Chlorides, mg/dm^3	43.3 ± 2.9 (n = 68)	28.1 ± 2.9 (n = 69)	16.9 ± 2.3 (n = 109)	17.3 ± 3.2 (n = 58)

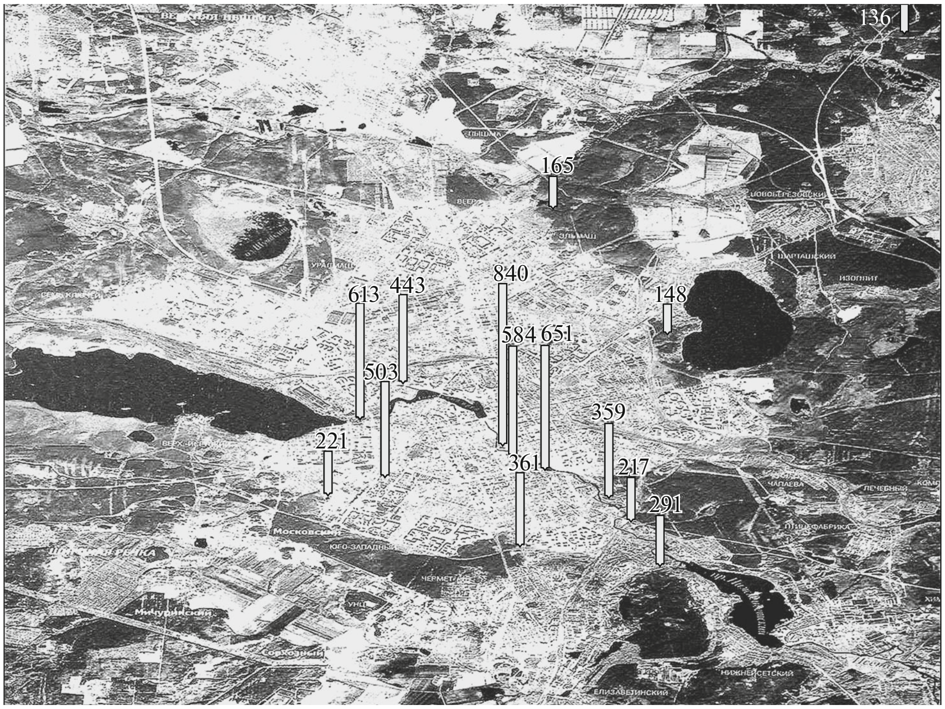

Fig. 2. Gradient of mineralization of surface waters in habitats of the urbanized territory and beyond its limits. Note: white figures designate the data on country population.

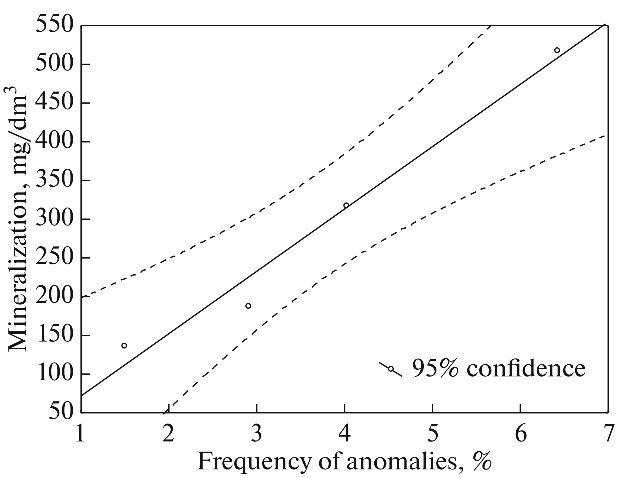

Fig. 3. Correlation of the total frequency of exterior anomalies of tadpoles of *R. arvalis* with mineralization of spawning water bodies (1980–2016).

rial) isolating barriers are also an important factor of the formation of specificity of the genetic composition and new general phenotypic pattern of populations in conditions of increasing inbreeding. Isolates are often characterized by the growth of homozygosity and, as a result of inbreeding, manifestation in the phenotype of rare and deviating variants with constitutive weakness (after Gershenzon, 1941, 1985). In particular, in populations of the city agglomeration, the frequency of depigmentation of the iris, a marker of the extent of homozygosity of populations, increasers from 0.19% in country population to 2.9% in populations of the residential parts of the city (Fig. 4).

The frequency of melanin dissipation in the skin cover grows in the gradient of urbanized environments from 0.06% in the forest population to 7.6% in some populations of multi-storey buildings (Fig. 5). Chronographic variation of deviations caused by the specificity of particular seasons is also observed (Table 2). As indicated above, the total frequency of morphological anomalies in populations of the urbanized territory is connected with the level of pollution in habitats.

Notwithstanding cessation of the gene flow between individual isolates, the trend of variation of deviant forms with reference to the main variants of

Table 2. Limits of the frequency of an anomaly in new generation during 1980–2016 (%, of total number of individuals)

Character	Lim, %
Depigmentation of iris	0.5–14.3
Melanin dissipation	1.1–44.4
Mandibular hypoplasia	0.3–7.1
Microphthalmia	0.025–0.28
Arthrogryposis of anterior limbs	1.6–3.1

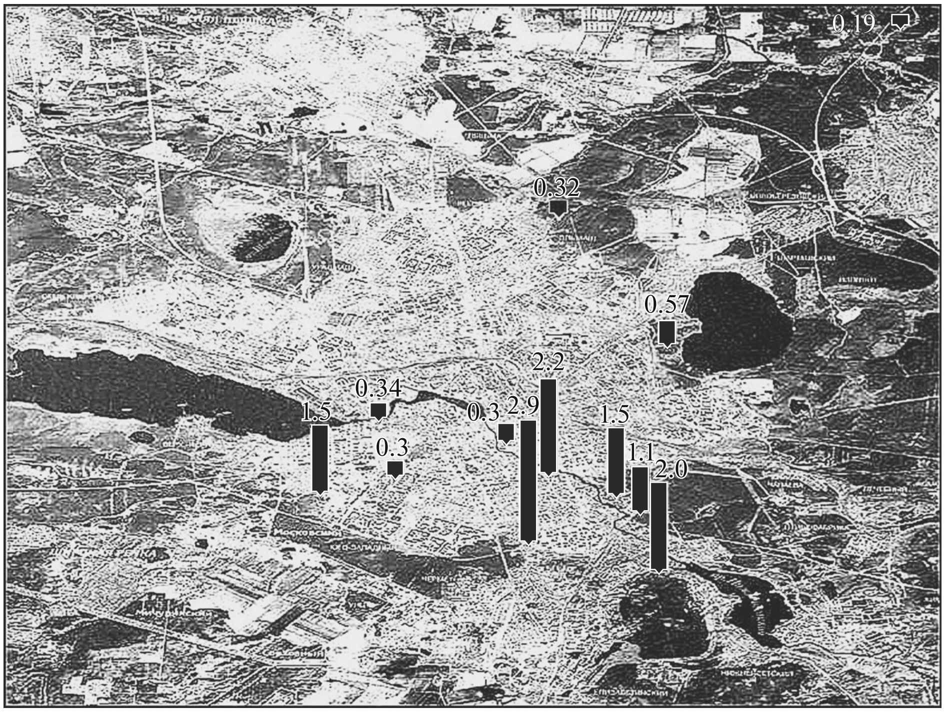

Fig. 4. Distribution and the total frequency of depigmentation of the iris in tadpole populations of *R. arvalis* (% of the total number of animals) in Yekaterinburg. Note: white figures designate the data on country population.

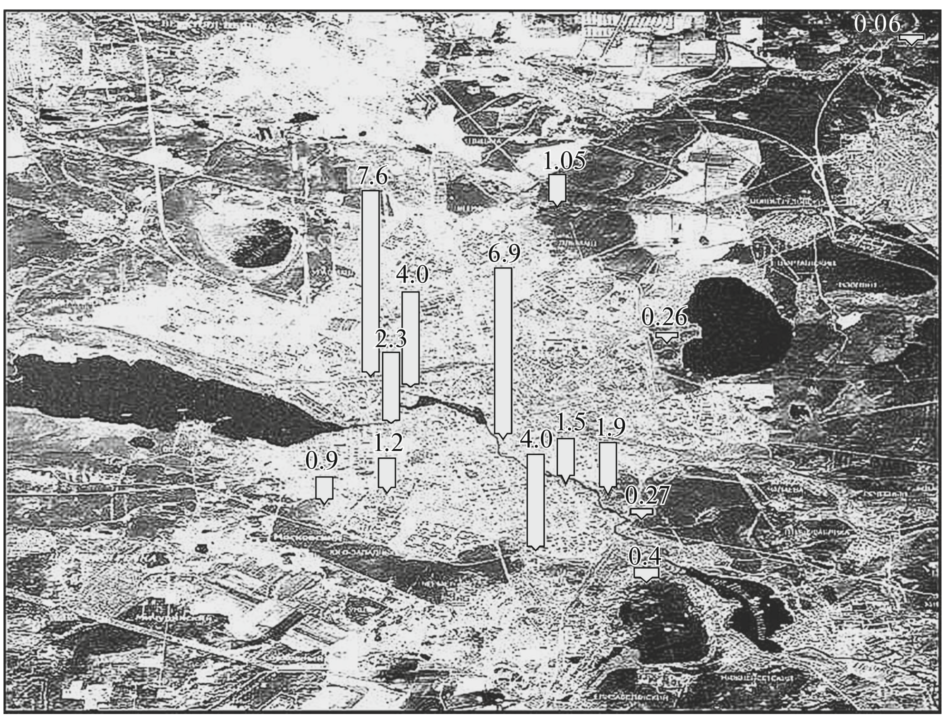

Fig. 5. Distribution and total frequency of melanin dissipation in tadpole populations of *R. arvalis* (% of the total number of animals) in Yekaterinburg. Note: white figures designate the data on country population.

Fig. 6. Distribution and total frequency mandibular hypoplasia in tadpole populations of *R. arvalis* (% of the total number of animals) in Yekaterinburg. Note: white figures designate the data on country population.

the spectrum of anomalies remains similar (Figs. 4, 5). At the same time, although the frequencies of morphological deviations are connected with local geochemical features of habitats, the set of variants beyond the norm is more likely species-specific (Vershinin, 2017) rather than depends on the composition of pollutants.

Based on an example of adaptive radiation and speciation in *Cerastoderma,* as a critical salinity is reached, parallelism and vectorization of morphological variations in populations of the isolated Small and Large Aral Sea are recorded (Andreev and Andreeva, 2003). Local populations inhabiting urbanized territories are specific modeling units isolated from each other, in which similar trends in morphological transformations of phenotypes are also observed in the absence of gene exchange, which is evidenced by the growth of homozygosity in city populations (Vershinin, 2004; Makeeva et al., 2006).

The presence of certain (vector) canalization of evolutionary pathways as a result of the past history of a species was indicated by Berg (1922). He associated the universality of parallelisms, convergences, and parallel variations with the ordered character of ontogeny. "Frequent despite outer conditions, the development follows certain trends because of internal constitutional causes connected with the chemical composition of protoplasm" (Berg, 1977).

At the same time, the picture of spatial distribution of rare hereditary deviations, such as mandibular hypoplasia, microphthalmia, and arthrogryposis (Figs. 6–8), are evidence that their distribution in populations is restricted by the presence of physical territorial barriers.

CONCLUSIONS

Geochemical background and insularization of the continuous geographical range into a number of isolates change considerably the population norm of phenotypes and accompanying spectrum of extreme phenotypic variants.

An increase in the range of population variability in certain city populations shows a similar picture and is characterized by limitation and certain vectorization.

The effect of the presence of isolating barriers on the distribution of anomalies is shown in the case of a number of rare unique deviations.

The specificity of the spectrum and frequency of deviant forms can be used as an indicator of the level of ontogenetic stability, reduction of genetic diversity, decrease in viability of populations, and potential threat of their existence.

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Fig. 7. Distribution and total frequency of microphthalmia in tadpole populations of *R. arvalis* (% of the total number of animals) in Yekaterinburg. Note: white figures designate the data on country population.

Fig. 8. Distribution and total frequency of arthrogryposis of anterior limbs in tadpole populations of *R. arvalis* (% of the total number of animals). Note: white figures designate the data on country population.

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