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ECOLOGY

Amphibian Anomalies as a Source of Information on the Adaptive and Evolutionary Potential

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Abstract—Long-term data on the morphological anomalies of four anuran species (family Ranidae) and two tailed amphibian species (families Hynobiidae and Salamandridae), inhabiting forest and urbanized areas in the eastern slope of the Middle Urals, have been studied. The morphological deviations of amphibians were investigated in terms of the module principle, which predetermines the similarity of evolutionary transformations in different taxa and limit the number of possible directions of diversification in morphogenesis. The definitive spectra and frequencies of morphological anomalies in juvenile and adult individuals are compared in the urbanization gradient. Original methodological and methodical approaches to using the potential and implemented spectra of deviation are proposed for assessing the role of the ecological component in their formation. The possibility of using deviant forms of variability for assessing the evolutionary and adaptive potentials of the species is discussed.

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INTRODUCTION

The definitive aspect of an individual is formed in the course of ontogenesis as a result of the integration of the genotype carrier into specific environmental conditions. The variability is formed on the basis of the complex interaction of the replicable genotype with the expression of regulators of morphogenesis, in which the environmental conditions play a mediator role (Inge-Vechtomov, 2010). The structural phenotypic traits (e.g., a five-toed limb) and color phenotypic traits (the pattern typical for the species) are formed during ontogenesis on the basis of intragenomic interactions of regulator gene systems (Kondo and Mura, 2010; Sheth et al., 2012) according to the principle of Turing's reaction-diffusion model (Turing, 1952). Under specific environmental conditions, the level of expression of morphogenesis integrating genes determines the definitive aspect of the individual.

The studies limited by the morphological "norm" (within modal classes of the normal distribution curve) are mainly associated with study of the intraspecific diversity, which is determined by the homeostation of species populations under the conditions of a heterogeneous environment within the species range (Vavilov, 1967). Interpopulation differences consist in the phenotypically expressed genetic polymorphism of natural populations, which is the basis for the genetic flexibility of a species (Gershenzon, 1974, 1985) and is not so much associated with the incompleteness of evolutionary processes (Vavilov, 1967) as with the specificity of population integration into certain environmental conditions. Therefore, the study of variability within the modal part of the distribution makes it possible to assess the adaptive specificity of populations, while the marginal, most deviant variants (according to Ch. Darwin) provide information on the potential of evolutionary innovations (Vershinin, 2009a). The patterns of the formation of morphoses and evolutionary transformations have a "common logic," since they have the same material basis that orients them in a certain way. Evolution acts by changing the old material (Jacob, 1977), since its potential is determined by the biochemical features of a species (variants with no hereditary basis for the formation will not emerge (Timofeev-Resovskii et al., 1973)).

Every species is characterized by the presence of a specific spectrum and specific frequencies of morphological anomalies, i.e., "the function of a certain type of morphogenesis" as long as this species exists (Kovalenko, 2003). According to the homologous series law, closely related taxa have the simultaneous manifestation of many traits, which is most clearly observed at the genus level (Rozanov, 1973). At the same time, structural variants representing a stable feature for some taxa may be present as rare modifications in other related forms (Shishkin, 2015). It is known that deviant or abnormal forms of some species may occur in closely related species of the same taxon as a norm (Alberch, 1981; Oster et al., 1988).

The objective of this study was to analyze the spectra and occurrence of deviant morphological forms in six amphibian species (*Salamandrella keyserlingii*, *Lissotriton vulgaris*, *Rana temporaria*, *R. arvalis*, *R. amurensis*, and *Pelophylax ridibundus*) that inhabit forest and urbanized areas on the eastern slope of the Middle Urals for assessing their adaptive and evolutionary potential.

MATERIALS AND METHODS

The material was sampled in 26 amphibian habitats in the urban agglomeration of Yekaterinburg and at a distance of 23 km from it from 1977 to 2013. A typification scheme of urban landscapes was developed to perform a comparative analysis (Vershinin, 1980, 2002). Four zones were delimited in the large industrial city, and amphibian habitats were ranked by these zones. The zonal ranking of a certain habitat is mainly determined by the degree of the total anthropogenic transformation of a site under consideration rather than by its topographical position (Vershinin, 1997).

Zone I: the central part of the city with multistory buildings, massive asphalt coverings, water bodies with severe industrial pollution, and small rivers and streams drained by pipes. There are no amphibians in this zone. Zone II: areas with multistory buildings, including territories being developed, waste grounds, sites with open soil, and small ponds with high levels of pollution. Zone III: low-rise building areas generally occupied by private sector houses with gardens and kitchen gardens, as well as by waste grounds and parks. The biotopes of this zone often adjoin forest parks. Zone IV: the forest park belt of the city. The habitats of this zone are generally under the influence of recreational pressure. A forest area that is located 23 km to the north of Yekaterinburg was chosen as the control (Rezhevskoi Path); this area is inhabited by the Siberian salamander, smooth newt, common toad, and moor frog. The brown frog was sampled from a suburban population in Sysertskii raion, Sverdlovsk oblast (near the village of Klyuchi). The Siberian wood frog was caught in Makushinskii raion in Kurgan oblast.

The landscape typification was confirmed by hydrochemical analyses of spawning ponds that were carried out from 1980 to 2013. Samples were taken during the spawning season and during metamorphosis. The analyses were performed at the Institute of Water Management and Conservation (1980–1981 and 1987–1989), the Ural Research Institute of Aquatic Bioresources and Aquaculture (2003–2008), and the laboratory of Physicochemical Analyses, Ural State Mining University (in 2009 to 2013). We used long-term (1977 to 2013) data on the qualitative features of the deviant morphology of six amphibian species (*S. keyserlingii*, *L. vulgaris*, *R. temporaria*, *R. arvalis*, *R. amurensis*, and *P. ridibundus*; total of 28027 specimens) in the natural and anthropogenic landscapes of the Urals. Morphological deviations were analyzed according to the developed classification of abnormal amphibian forms and methods of their analysis (Dubois, 1979; Tyler, 1989; Vershinin, 2015).

The detailed study of the morphology of the skeleton of juvenile anuran amphibians used the soft tissue clearing method proposed by Dawson (1926). The degree of overlap of spectra of anomalies was calculated with the modified Morisita index (Hurlbert, 1978):

$$C_{\mathrm{m}} = 2\Sigma x_i y_i / \Sigma x_i^2 + \Sigma y_i^2,$$

where x_i and y_i are the parts of the *i*th variant of anomalies in the sampled spectra *x* and *y*.

RESULTS AND DISCUSSION

The potential spectra of external morphological deviations recorded in the Middle Urals were established for the species studied. On the whole, we recorded 12 anomalies for the Siberian salamander, 13 anomalies for the smooth newt, 17 anomalies for the lake frog, 22 anomalies for the moor frog, 17 anomalies for the brown frog, and six anomalies for the Siberian wood frog (Table 1).

An important feature of the morphological deviation spectra is the presence of deviant variants, which is normal for other species (Table 2). In total, 11 such variants were revealed: eight variants for the moor frog, four variants for the brown frog, two variants for the Siberian salamander, and one variant for the lake frog.

The limits of the morphogenetic potential of each species are defined by its genetic specificity and represent the reaction norm on which the potential spectrum of variability depends, while the implemented spectrum of variability is determined by the ecological component of the ontogenesis process that guides this spectrum and forms a definitive spectrum. Analysis of the spectra of the anomaly for populations inhabiting the background and contaminated areas in terms of qualitative and quantitative parameters (combinations of the spectrum of deviant forms and their frequencies) showed that this approach is the most informative and adequately reflects the gradient of anthropogenic transformation of the environment (Vershinin, 2005; Neustroeva and Vershinin, 2011; Neustroeva, 2012).

The stability of processes of amphibian morphogenesis and the correlation between the potential, implemented, and background spectra of anomalies definitely characterize the environment in which the population exists. Consequently, they also characterize the conditions under which the expression of *Hox*-genes (morphogenesis regulators and coordinators (Ferrier and Holland, 2001)) shapes the morphological aspect of the population, including the spectrum of anomalies. Each species has deviation variants that are

Table 1. Spectrum of possible external anomalies in populations of the study species inhabiting the Middle Urals

Anomalies	*S. k*	*L. v*	*R. t*	*R. a*	*P. r*	*R. am*
Brachycephaly	–	–	–	+	–	–
Mandibular hypoplasia	–	–	–	+	–	–
Iris depigmentation	–	–	+	+	+	–
Microphthalmia	+	–	+	+	–	+
Other eye anomalies	–	–	+	+	+	–
Axial skeleton deformities	+	+	+	+	+	–
Opercular chamber deformities	–	–	–	+	+	–
Edema	+	+	+	+	+	–
Melanin dissipation	–	–	+	+	+	–
Pigment aberrations	+	+	+	+	+	+
Fixed limb syndrome	–	–	–	+	+	–
Hemimelia	–	–	+	+	+	+
Brachymelia	+	+	+	+	+	–
Ectromelia	+	+	+	+	+	+
Taumelia	+	+	+	+	–	–
Polymelia	+	–	+	+	+	–
Ectrodactyly	+	+	+	+	+	+
Syndactyly	+	+	+	+	–	+
Oligodactyly	+	+	–	+	+	–
Schizodactyly	+	+	+	+	+	–
Polydactyly	+	+	+	+	+	–
Defects of internal organs	–	–	+	+	+	–
Neoplasms	–	+	–	–	–	–

+, presence of anomaly, –, absence of anomaly. *S. k*, *Salamandrella keyserlingii*; *L. v*, *Lissotriton vulgaris*; *R. t*, *Rana temporaria*; *R. a*, *Rana arvalis*; *P. r*, *Pelophylax ridibundus*; and *R. am*, *Rana amurensis*.

Table 2. Revealed deviations that are normal for other species

Trait	Species norm	Anomaly
Urostyle containing vertebrae	*Triadobatrachus massinoti*	*Rana arvalis*
Rudimentary tail	*Leiopelma* sp., *Ascafus* sp.	Same
Absence of eyelids	*Xenopus* sp.	*R. temporaria, R. arvalis*
Oligodactyly	*Psyllophryne hermogenesi*	Same
Brachycephaly	*Breviceps mossambicus*	"
Brachymelia	*B. adspersus*	*Pelophylax ridibundus*, *R. arvalis*
Ectro-, oligo-, and syndactyly	*Bolitoglossa dofleini*	*Salamandrella keyserlingii*
Absence of hindlimbs	*Siren lacertina*	*R. arvalis*
Polydactyly	*Ichthyostega* sp.	*S. keyserlingii*
"	*Acanthostega* sp.	*R. arvalis*

characteristic only of anthropogenically transformed areas.

In tailed amphibians, the capability for regeneration is maintained throughout their life and regulated by the same key regulatory proteins that control the development of embryo limbs (Wnt/beta-catenin and BMP); both processes are controlled by the same gene-regulatory cascades (Kawakami et al., 2006). *S. keyserlingii*, a representative of the basic taxon of terrestrial tetrapods (family Hynobiidae), had a significant increase in the total occurrence of syn-, ectro-, and oligodactyly among adult animals from the popu-

Table 3. Occurrence of external morphological anomalies in adult tailed amphibians (%)

Anomalies	*Salamandrella keyserlingii*			*Lissotriton vulgaris*			
	III (22)	IV (500)	K (68)	II (179)	III (103)	IV (99)	K (19)
Eye defects	0	0.61	0	0	0	1.01	0
Axial skeleton deformities	4.55	1.21	4.41	0	3.88	0	5.26
Edemas	0	0	0	0	0	0	0
Pigment deviations	0	1.21	1.47	0	0.97	1.01	0
Brachymelia	0	0.2	0	0.56	0	0	0
Ectromelia	0	0.2	0	0	0	2.02	0
Taumelia	0	0.2	0	0.56	0	1.01	0
Polymelia	0	0.4	0	0	0	0	0
Ectrodactyly	0	3.03	1.47	1.12	2.91	6.06	0
Syndactyly	4.55	1.01	1.47	0.56	0	0	0
Schizodactyly	0	0.2	2.94	1.68	3.88	1.01	0
Oligodactyly	18.18	2.22	1.47	1.68	0	0	0
Polydactyly	4.55	0.4	1.47	1.12	3.88	1.01	0
Neoplasms	0	0	0	1.68	0.97	0	0

(II) Multistory buildings; (III) low-rise buildings; (IV) forest park; K, suburban population at a distance of 23 km from the Rezhevskoi Path; the number of animals is given in brackets; for Tables 3–7.

lations in low-rise building areas and the forest park zone ($p < 0.01$ and <0.001 at $\chi^2 = 51.05$ and 336.24, respectively) compared to their occurrence in the suburban population (Table 3). A trend towards the polymerization of distal limb elements (a growth in the share of poly- and schizodactyly) was recorded for representatives of the family Salamandridae *L. vulgaris* in the populations of urbanized areas among adult individuals, which is possibly due to abnormal regeneration under polluted conditions. The functional disintegration of the morphogenesis of carpal and metacarpal regions of the limbs in representatives of two tailed amphibian taxa is species-specific and bidirectional (oligomerization and reduction in the first case and polymerization in the second) during their regeneration under urbanization and environmental pollution conditions (Vershinin, 2014).

In juvenile and adult individuals of moor frog populations, the variants and frequencies of external morphological deviations vary, depending on the degree of urbanization (Table 4). For instance, the frequency of external anomalies in juvenile *R. arvalis* significantly increases with growth in urbanization and is significantly ($R = 0.98$, $F = 44.3$, $p = 0.02$) correlated with the mineralization of spawning ponds. The total share of unusual color variants increases in the urbanization gradient: the pigment deviations are 73.8% of the total number of anomalies in the zone with multistory buildings and 43.1% in the suburban population ($p < 0.001$, $\chi^2 = 153.6$).

One of the unusual color variants (iris depigmentation) results from recessive mutation. The frequency of this anomaly is significantly ($p < 0.001$, $\chi^2 = 20.7$–39.2) higher in urban moor frog populations (Table 4). This is a good marker of population homozygosity. As was previously established, the phenotypical manifestation of a trait is determined by the presence or absence of spring frosts (Vershinin, 2006). A number of anomalies were recorded only in juvenile individuals in the populations of the area with multistory buildings: brachycephaly (0.16%), the absence of eyelids (0.16%), opercular chamber defects (0.02%), and oligodactyly (0.12%), except for arthrogryphosis (fixed limb syndrome), which occurs in juvenile and adult individuals in zone II with frequencies of 0.01 and 0.38%, respectively. Sublethal anomalies, such as mandibular hypoplasia, or opercular chamber anomalies never occur in adult animals (Table 4).

Undoubtedly, the data on the total occurrence of deviations in the population are not enough to separate the influence of pollution from the features of natural geochemistry. For instance, it is known that the natural geochemical anomaly of the chrome content contributes to a high occurrence (~20%) of anomalies in the brown frog population with a narrow spectrum of morphological limb deviations, which consist of three variants (ectro-, syn-, and schizodactyly) (Vershinin, 2009b). An adequate understanding of morphological variability requires one to consider the combination of the spectrum of deviant forms and their frequencies. It is particularly remarkable that the spectra have their own unique parameters, which vary, depending on the degree of urbanization and animal age group. The dynamics of these two parameters in

Table 4. Occurrence of external morphological anomalies in juvenile and adult *Rana arvalis* (%)

Anomalies	Juvenile individuals				Adult individuals			
	II (4314)	III (1684)	IV (6747)	K (3791)	II (266)	III (104)	IV (315)	K (192)
Mandibular hypoplasia	0.05	0.06	0.1	0.16	0	0	0	0
Iris depigmentation	1.76	1.48	1.17	0.32	0.75	0.97	0.63	1.04
Microphthalmia	0	0	0	0.03	0	0	0	0.52
Eye defects	0.09	0	0.01	0.03	0	0	0.32	0.52
Axial deformities	0.19	0.36	0.12	0.11	0.38	0	0.95	0
Edemas	0.02	0.24	0.01	0	0	0	0.63	0
Melanin dissipation	1.72	0.48	0.28	0.03	4.14	2.91	0.32	0.52
Pigment aberrations	0.95	0.24	0.12	0.13	1.88	2.91	1.59	1.04
Hemimelia	0.02	0.12	0.01	0.05	0	0.97	0.32	0
Brachymelia	0.25	0.18	0.09	0.05	0.38	0	0	0
Ectromelia	0.21	0.24	0.21	0.03	1.13	0	0.32	0.52
Ectrodactyly	0.32	0.30	0.5	0.13	2.63	2.91	2.22	2.6
Syndactyly	0.02	0.12	0.03	0.03	0.75	0	0.95	0
Schizodactyly	0.02	0	0	0	0	0	0.32	0.52
Polydactyly	0.02	0.06	0.03	0	0	0	0.32	0

the urbanized environment gradient reflects the ecological risk effect.

The definitive spectra of the deviant forms of the skeletal structures of representatives of the same family (Ranidae) include both general and specific variants (Table 5). Of the 23 variants revealed by us, 18 variants were recorded for *R. arvalis*, 16 variants were recorded for *R. temporaria*, and 12 variants were recorded for *P. ridibundus*. In the moor frog, 50% of these deviations are presented by variants associated with the axial skeleton (nine variants); these variants cover 37.5% (six of 16 variants) in the brown frog and 58.3% (seven of 12 variants) in the lake frog. The axial skeletal anomalies mainly contribute to the skeletal deviations of these species. The occurrence of axial skeleton deviations is 41.5% of the total number of anomalies in *R. arvalis*; it is almost two times lower in *P. ridibundus* (21.4) and four times lower in *R. temporaria* (9%). The total percentage of juvenile individuals with skeletal anomalies is 28.09% in *R. arvalis*, 27.89% in *P. ridibundus*, and 14.18% in *R. temporaria*. The differences were significant in all three cases ($\chi^2 = 4.5$–19.39, $p < 0.05$–0.001). In total, the occurrence of anomalies was 44.6 for juvenile moor frogs, 40.1 for juvenile lake frogs, and 21.8% for brown frogs. The differences were also significant in all cases ($\chi^2 = 4$–39.9, $p < 0.05$–0.001).

The estimate of the degree of overlap of the spectra of skeletal anomalies for juvenile individuals of each of the studied species on the basis of the Morisita index showed that *R. arvalis* and *P. ridibundus* had the most similar spectra ($C_m = 0.97$), *P. ridibundus* and *R. temporaria* had similar spectra ($C_m = 0.69$), and the spectra of *R. arvalis* and *R. temporaria* had the lowest degree of overlapping ($C_m = 0.67$). The high peculiarity of the deviation spectrum, which includes a small portion of axial skeleton variants, and the comparatively high share (%) of peripheral skeleton anomalies made the brown frog most distant from the two other species with respect to the total spectrum of skeletal deviations and the frequency of their occurrence.

The implementation of the morphogenetic potential is determined by the ecological conditions of a certain habitat, as well as by the plasticity, tolerance, and features of the reproductive strategy of the species, which influence the definitive morphological aspect of the new generation. The change in the spectrum and frequency of skeletal deviations in the urbanized environment gradient is most completely presented for the moor frog (Table 6).

In *R. arvalis*, the occurrence of animals with deviant skeletal forms is two times higher in urbanized areas than in the suburban population (Table 7). The frequency of anomalies also increases significantly. The number of variants of deviation is higher in urbanized areas; the maximum diversity is recorded in the forest park zone and the zone with low-rise buildings (Table 7). The asymmetry of the transverse processes of vertebra and ectrodactyly occurs only in the urbanized area (Table 6).

The proportions of combined anomalies are similar in all zones (Table 7) and only slightly increased in the zone with multistory buildings. At the same time, the average number of anomalies per individual is steadily

Table 5. Occurrence of skeletal deviations in juvenile *Rana arvalis*, *R. temporaria*, and *Pelophylax ridibundus* (%)

Deviation	*R. arvalis* (509)	*R. temporaria* (275)	*P. ridibundus* (294)
Brachycephaly	0.2	1.09	0
Mandibular hypoplasia	0	0.73	0
Vertebral rupture	18.27	7.27	17.35
Asymmetry of			
vertebra	15.32	5.82	14.29
transverse processes of vertebra	1.2	0.36	3.4
foot length	0.2	0	0
finger bone thickness	0.39	0.36	0
thigh proportions	0	0.36	0
limb bone diameter	0	0.36	0
Vertebral fragmentation	0.79	0	0.34
Disturbance of the pelvis attachment to the vertebral column	0.2	0	0.34
Vertebral fusion	0.39	0	0.34
Deviations in the urostyle structure	4.91	1.09	0.34
Incomplete vertebral ossification	0.2	0	0
Ectromelia	0.39	0.36	0.68
Brachymelia	0	0.36	0
Phalange falling	0.2	0	0
Ectrodactyly	0.79	0.73	1.02
Schizodactyly	0.2	0	1.02
Oligodactyly	0.2	0.73	0.68
Toe phalange thickening	0.2	0.36	0.34
Phalange curvature	0	0.36	0
Limb bone deformation	0.59	1.45	0

higher in urbanized areas. The frequency of anomalies and individuals with skeletal deviations reaches maximum values in the forest park zone and smoothly and insignificantly decreases towards the zone with low-rise buildings (Table 7). For the urbanized areas, the maximum share of anomalies of the axial skeleton in the moor frog is recorded in the forest park zone (49.2%), which is due to the influence of trematode cysts in combination with the pollution and eutrophication of water bodies. The total contribution of trematode invasion to the formation of deviant skeletal forms is 57.14% in the forest park zone, while in the suburban population, it is 18.9% ($\chi^2 = 7.15$, $p < 0.01$) (Vershinin and Neustroeva, 2011).

With respect to the spectra and frequency of occurrence of skeletal anomalies, the samples from zones with different degrees of urbanization were similar to each other and distant from the suburban population. The overlap of spectra of skeletal deviations in juvenile individuals from different zones indicates a significant similarity of all populations inhabiting the urbanized areas with respect to this parameter (C_m = 96.1–98.06%) and their difference from the suburban population (C_m = 62.3–68.4%).

The change in the spectrum of skeletal anomalies in juvenile moor frogs begins with destabilization (its broadening and the growth in the frequency of occurrence of deviations and abnormal individuals) in zones IV and III, followed by its stabilization in zone II, which forms the new norm (Shishkin, 1988) characteristic of the urbanized environment (Andrzejewski et al., 1978). Presumably, the synergism of factors and the emergence of adaptive changes (Vershinin and Kamkina, 2001) in moor frog populations in zones II and III is one of the causes of the nonlinearity of changes in the frequencies of occurrence of skeletal anomalies and abnormal animals in the urbanization gradient (Table 7).

Table 6. Occurrence of skeletal deviations in juvenile *Rana arvalis* in the urbanization gradient (%)

Deviations	Zone			
	II (116)	III (110)	IV (130)	K (118)
Brachycephaly	0	0.91	0	0
Mandibular hypoplasia	0	0	0	0
Vertebral rupture	21.55	17.27	20	8.47
Asymmetry of				
vertebra	14.66	17.27	17.69	5.08
transversal processes of vertebra	1.77	1.82	0.77	0
foot length	0	0.91	0	0
finger thickness	0	0	0	1.69
Vertebral fragmentation	0	0	3.08	0
Vertebral fusion	0	0.91	0.77	0
Deviations in the urostyle structure	0.86	4.55	6.15	7.63
Incomplete vertebral ossification	0	0	0.77	0
Ectromelia	0	0.91	0	0.85
Ectrodactyly	1.72	0.91	0	0
Schizodactyly	0	0	0.77	0
Oligodactyly	0	0	0.77	0
Toe phalange thickness	0	0	0	0.85
Limb bone deformation	0	1.82	0.77	0

Table 7. Change in the occurrence of skeletal anomalies and abnormal juvenile individuals of *Rana arvalis*, depending on the degree of urbanization

Zone	Frequency of anomalies, % (significance of differences from K)	Frequency of abnormal individuals, % (significance of differences from K)	Number of variants of anomalies	Share of combined anomalies, %	Average number of anomalies per individual
II	40.5 ($\chi^2 = 4.9$, $p < 0.05$)	25 ($\chi^2 = 6.8$, $p < 0.05$)	5	38.3	0.41
III	47.3 ($\chi^2 = 9.1$, $p < 0.01$)	31.5 ($\chi^2 = 10.9$, $p < 0.01$)	10	32.7	0.47
IV	50.8 ($\chi^2 = 12$, $p < 0.001$)	32.5 ($\chi^2 = 17.4$, $p < 0.001$)	11	30.3	0.51
K	24.6	13.6	6	34.5	0.25

The lower the plasticity, tolerance, and, accordingly, survival rate of each new generation of individuals during the ontogenesis period, the greater the differences between the potential and implemented spectra. It is the level of elimination of a portion of each generation that is used for determining the diversity and occurrence of deviant skeletal forms of metamorphosing juvenile individuals.

The morphological variations that lie in the modal part of trait distribution reflect the adaptive resource of the population within the existing reaction norm. In contrast, the spectrum of the morphological variants from the marginal area of the normal distribution, which are classified as "phenodeviants" (Altukhov, 2003), makes it possible to evaluate the evolution reserve of the morphogenetic potency of a population or a species.

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