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Cenogeneses: Ecology and Evolution (Using the Example of Amphibian Larvae)

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Abstract—Known anomalies of amphibian larvae are analyzed based on literature data and our own materials. The variability in the spectrum and frequency of anomalies of moor frog larvae are considered in an urbanization gradient. It is shown that the occurrence of deviant forms of larvae is significantly higher in high-rise areas, and their greatest diversity is recorded in the residential part of the city. A decrease in the equifinality of ontogeny contributes to an increase in the diversity and occurrence of cenogenetic and other larval anomalies. An increase in the proportion of morphological anomalies during destabilization of habitats reduces the fitness of larvae and poses a serious threat to the reproduction and continued existence of such populations. The issue of deviant forms of larval adaptations of amphibians is discussed as a possible source of information about potential evolutionary innovations of morphogenesis. The larvae of dominant amphibian species can be used as indicators of environmental health.

Keywords: cenogeneses, deviant forms, morphoses, urbanization, amphibians, morphogenesis

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INTRODUCTION

According to Aristotle, the "*essence of a thing is its form.*" Everything consists of matter, has a form, is in motion, and tends towards some goal (Aristotle, 1991). Movement is the process of transformation of potential into actual, as a result of the activity of the form during its contact with matter. In our opinion, definitive morphology is the optimal range of structural and functional solutions to the needs of the organism under certain environmental conditions. In the matter–movement–form–goal ratio, the form serves as the specific goal on which the living matter existing only in motion is currently oriented.

The term *cenogenesis* was introduced by Haeckel (see Russel, 1916). He considered cenogeneses as intermediate stages with their own adaptive evolution, which distorts the ontogenetic record of transformations of the adult stage: (a) any disturbances of palingeneses and (b) adaptations at early stages, i.e., any transformations that are not related to the evolution of the adult stage and the improvement of its mode of implementation. Therefore, within Haeckel's assumptions, these are deviations that complicate the study of phylogenesis through analysis of ontogenesis.

Provisional adaptations, or, in other words, larval adaptations, as well as the whole of ontogeny, are strictly determined and confined to certain stages of development; deviations in their structure should negatively affect the viability of carriers of such deviations. There is an adaptive modification variability of larval adaptations; a striking example of this is the appearance of a predatory form in the larvae of American spade-footed toads during conditions of drying up of water bodies (Ledon-Rettig and Pfennig, 2011). Less known, but quite common variants are variants of paratypic variability of larvae associated with the presence/absence of predators in a spawning water body (Calsbeek and Kuchta, 2011), density-dependent effects (Merilä et al., 2004), and the influence of flow velocity. In turn, nonadaptive evasive variants (deviant forms) make it possible to assess the formative potential of test taxa (Vershinin et al., 2016, 2018). Chemical-genetic screening of morphoses in larvae can be a valuable tool to identify early morphogenesis pathways leading to ecologically and evolutionarily significant morphological variations (Bloom et al., 2013). The paralogous cenogenetic structure that performed a certain function at the larval stage can be changed to perform a new function. Evolution acts by changing the old material (Jacob, 1977). Thus, the gills of mayfly larvae, which are a provisional adaptation, are formed based on the expression of the same genes that control the formation of a morphological structure such as wings (Averof and Cohen, 1997). Cenogeneses can influence the features of definitive structures. Thus, a number of differences in the course of morphogenesis and the structure and functioning of the

Table 1. Hydrochemistry of spawning water bodies (2019–2023)

Zone	Cl^-	SO_4^-	Na^+	K^+	pH	Mineralization, mg/L
High-rise area ($n = 8$)	20.8 ± 15.1	72.0 ± 32.9	18.2 ± 6.7	20.3 ± 2.5	6.8 ± 0.2	518.8 ± 103.7
Low-rise area ($n = 2\ 5$)	57.9 ± 8.5	96.1 ± 18.6	29.9 ± 3.8	9.0 ± 1.4	6.7 ± 0.13	520.0 ± 58.7
Forest park area ($n = 2\ 2$)	12.8 ± 9.1	34.3 ± 19.9	3.1 ± 4.1	6.2 ± 1.5	6.3 ± 0.14	129.2 ± 62.6
Suburban area ($n = 15$)	14.2 ± 11.0	37.7 ± 24.0	3.7 ± 4.9	8.4 ± 1.9	6.2 ± 0.17	142.9 ± 75.8
Significance of differences	$F(3, 66) = 5.6$, $p = 0.002$	$F(3, 66) = 2.1$, $p = 0.1$	$F(3, 66) = 9.75$, $p = 0.00002$	$F(3, 66) = 6.4$, $p = 0.0002$	$F(3, 65) = 7.6$, $p = 0.0002$	$F(3, 66) = 10.0$, $p = 0.00002$

limbs in Urodela are secondary and have a cenogenetic nature (Blanco and Alberch, 1992; Vorobyeva et al., 1997; Vorobyeva and Hinchliffe, 2001; Vorobyeva and Hinchliffe, 1996).

The purpose of this study is to analyze the spectra and frequencies of larval anomalies in amphibian populations in urbanized areas as a potential for variability in morphogenesis preceding the definitive morphology.

MATERIAL AND METHODS

The objective of this research is to study the variants and spectra of deviant forms of larval adaptations of three species of tailless amphibians from the family Ranidae and a representative of Caudata (*Lissotriton vulgaris*), which inhabit urbanized areas, as well as to assess the degree of equifinality of ontogeny in the gradient of anthropogenic transformation of the environment based on a model species. The material was collected from 1980 to 2023 from amphibian populations inhabiting urbanized areas of the city of Yekaterinburg and adjacent forest areas on the eastern slope of the Middle Urals. Variants of morphological anomalies were analyzed in the larvae of smooth newt *Lissotriton vulgaris* (134 specimens) at stages 37–54 (Liozner, 1975) and tadpoles of tailless amphibians (marsh frog *Pelophylax ridibundus* (246 specimens), grass frog *Rana temporaria* (231 specimens), and moor frog *R. arvalis* (1176 specimens)) at stages 40 to 51 (Dabagyan and Sleptsova, 1975).

Deviation variants were analyzed in accordance with the modern terminology (Henle et al., 2017) and author's methodological approaches (Vershinin, 2015). For the larvae of moor frog, the most dominant species from the urban landscapes of the city of Yekaterinburg, we analyzed the change in the spectrum and frequency of larval anomalies in the gradient of the urbanized environment. Urbanized areas are typified (Vershinin, 1980) according to the pattern of their use by humans and the level of pollution ((I) city center with multistory buildings, where there are no open soils and spawning water bodies and the level of pollution is high; there are no amphibians in this zone); (II) high-rise area, where there are small areas with open soils and small water bodies with a high level of pollution; (III) low-rise area, areas with open soils, and many small water bodies and rivers; the biotopes of this area are often adjacent to forest parks). (IV) city forest parks influenced by recreational load; K, suburban forest areas (23 km from Yekaterinburg) outside urbanized areas. The urban gradient corresponding to this typification is confirmed by annual hydrochemical analyses of surface waters (Table 1) that were carried out at the laboratory of physical and chemical analysis of the Ural State Mining University, as well as at the laboratory of engineering and environmental testing of AquaSolum LLC. The data were statistically processed using the Statistica for Windows 8.0 software package.

RESULTS

Analysis of the spectra of morphological anomalies of amphibian larvae based on literature data and our own data revealed 26 variants of anomalies (Table 2).

The above data suggest that the proportion of deviations in provisional adaptations is 61.5% (of the total number of larval anomalies); 46.2% of them do not influence the definitive morphology of carriers, 38.5% do not influence the survival of deviant individuals, and not less than 15.4% of larval deviations cause mortality during metamorphosis.

The presence of anomalies in provisional adaptations, as well as the possibility of their complete or partial preservation in individuals with completed development and preservation of the possible functional role are reflected in Table 3.

Table 3 shows that the complete or partial functionality of larval adaptations can be maintained through neoteny or progenesis (*Ambystoma mexicanum*, *Amphiuma tridactylum*, *Necturus punctatus*, *Proteus anguinus*, and *Siren lacertina*), as well as in paedo-

Table 2. Anomalies of amphibian larvae

No.	Variant of anomaly	Source
1	Bicephaly	McFadden et al., 2011
2	Anencephaly	Kuranova and Saveliev, 1997, 1999
3	Microphthalmia	Xenbase url http://www.xenbase.org/gene/show-gene.do?method=display&geneId=484552&
4	Anophthalmia (symmetrical and asymmetrical = cyclopia)	Raff and Coffman, 1986; Xenbase url http://www.xen-base.org/
5	Anomalies of the oral apparatus (horny jaws and lips and labial teeth in tailless amphibians)	Vershinin, 2007; Drake et al., 2007; Trubetskaya, 2006
6	Atypical formation of the gill apparatus (hyobranchial arches) and opercular chamber (in tailless amphibians)	Vershinin, 2009; Lajmanovich et al., 2003; Kollros, 1961; Ruiz et al., 2010
7	Chondrocranium deformations	Lajmanovich et al., 2003
8	Rhomboid body	Krishnamurthy and Smith, 2010
9	Shortened body	Snawder and Chambers, 1990
10	Tail bifurcation	Vershinin et al., 2023
11	Curvature of the notochord (scoliosis, lordosis, kyphosis, and "hard" tail)	Cooke, 1981; Krishnamurthy and Smith, 2010
12	Shortened tail	Vershinin et al., 2023
13	Twisting of the tail tip	Wijesinghe et al., 2011
14	Curvature of the tail tip	Vershinin et al., 2023
15	Rounded tail tip	Vershinin et al., 2023
16	Edema of the tail base	Wijesinghe et al., 2011
17	Formation of bubbles on the fin	David and Kartheek, 2015
18	Abnormal initiation of limb girdles (up to their complete absence)	Vershinin, unpublished
19	Lateral asynchrony	Vershinin et al., 2023
20	Depigmented or weakly pigmented skin cover	Brigitte, 1997
21	Unusual color variants	Vershinin and Vershinina, unpublished
22	Skin neoplasms (melanomas, etc.)	Henle et al., 2017
23	Abdominal edema	Flindt, 1985; Vershinin, 1989, Vershinin, 2002
24	Hernia (protrusion of organs beyond the body wall)	Vershinin and Berzin, 2018
25	Neoteny	Vershinin, 2002
26	Gigantism	Borkin et al., 1981; Mil'to, 2011; Borkin et al., 1984

morphic forms with incomplete metamorphosis, such as *Notophthalmus viridescens* (Reilly, 1987) or the extinct Oligocene *Brachyciormus noachicus* (Roček, 1996). A change in the function of provisional organs with loss of full-fledged larval stages as a result of the reduction of the long life cycle was recorded in Jamaican robber frogs without a tadpole (*Eleutherodactylus coqui* and *E. nubicola*) *(*Lynn, 1936; Laslo et al., 2019), as well as in *A. truei* and *L. archeyi*, which retain the muscles enabling rotational movements of the tail up to the definitive shape (Stephenson, 1961).

Analysis of the change in the frequency and spectrum of larval anomalies of moor frog in the urbanization and pollution gradient (Table 4) showed that their occurrence increased in urbanized areas. The appearance of a significant proportion of variants deviating from the wild type in the phenotype reflects the blurring of the previous norm, reaching significant differences (Table 5) in the high-rise area.

Above the diagonal are χ^2 values; below the diagonal are p values; (II) high-rise area, (III) low-rise area, (IV) forest park area, K, suburban area.

Table 3. Larval adaptations, their deviations, manifestation, and function in adults

No.	Larval adaptation	Deviation at the larval stage	Presence in adults	New function
1	Keratin "beak" and labial tooth lines	*R. temporaria* and *R. arvalis*	None	None
2	Absence of eyelids	None	*R. temporaria* and *R. arvalis*	None
3	Opercular chamber	*P. temporaria*, *P. ridibundus*, and *R. arvalis*	*P. ridibundus* and *R. arvalis*	None
4	Gill arches	None	*L. vulgaris,*	None
5	Gill arches	None	*Ambystoma mexicanum*, *Amphiuma tridactylum*, *Necturus punctatus*, *Proteus anguinus*, *Siren lacertina*, *Notophthalmus viridescens*, and *Brachyciormus noachicus*	None
6	Pronephros	*L. vulgaris*, *P. ridibundus*, and *R. arvalis* (edema)	None	None
7	Spiral elongated intestine	none	*P. ridibundus*	None
8	Skin pigmentation	*R. arvalis* (weak pigmentation and albinism)	*R. arvalis* (albinism)	*Proteus anguinus*: depigmentation as a result of the cave mode of life
9	Caudal fin	*P. ridibundus*, *R. temporaria*, and *R. arvalis*	None	*Eleutherodactylus coqui* and *E. nubicola* (gas metabolism organ)
10	Notochord	*P. ridibundus* and *R. arvalis*	*R. arvalis*	None
11	Caudal muscles for tail rotation	*Leiopelma archeyi* change of the function for the opening of the egg capsule	*Ascaphus truei* and *Leiopelma archeyi*	*Ascaphus truei* (in combination with the cloaca outgrowth, they are used as a copulative organ

The spectrum of deviations is most diverse (55.6% wider) in the residential part of the city (high-rise and low-rise areas) than in the suburban population (Fig. 1). The significant dependence of amphibians on a set of environmental factors, as well as the complex life cycle including necrobiotic metamorphosis in tailless amphibians, make the morphogenesis of amphibians dependent on a large number of factors, the interaction of which (Baier et al., 2016) determines both the definitive morphology and morphology of the larval stages and leads to the amplification of ontogenetic deviations and an increase in their frequency and variability in the case of anthropogenic environmental transformation, which may significantly affect the success of the new generation.

The study of the relationship between the equifinality of ontogeny based on the example of provisional adaptations of tadpoles of Himalayan toads showed an increase in the frequency of anomalies with increase in water mineralization (Vershinin et al., 2023). It was

Table 4. Occurrence of larval abnormalities in *R. arvalis* in the urbanization gradient (% of the total number of animals)

Zone	N total	n anomalies	Frequency of anomalies
High-rise area	31	15	48.4
Low-rise area	137	16	11.03
Forest park area	162	29	17.5
Suburban area	136	15	10.1

Table 5. Significance of differences in anomaly frequencies between different urbanization zones

	II	III	IV	K
II		24.56	12.67	24.2
III	$p = 0.00001$		2.1	0.0
IV	$p = 0.0004$	$p = 0.148$		2.91
K	$p = 0.00001$	$p = 0.95$	$p = 0.09$	

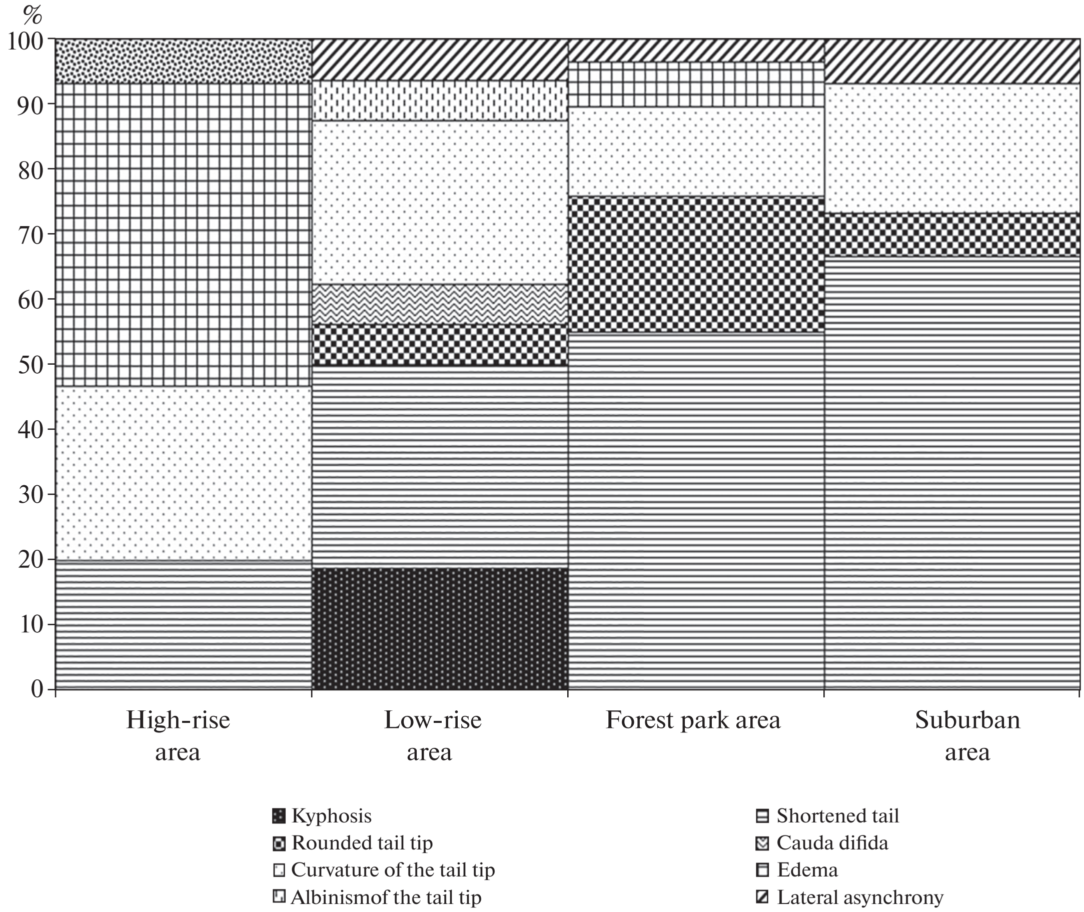

Fig. 1. Spectrum of variants of anomalies of tadpoles (*R. arvalis*) in the urbanization gradient (2020–2023). (II) high-rise area, (III) low-rise area, (IV) forest park area; K, suburban area.

found that the occurrence of larvae with morphological deviations, as well as their total frequency and spectrum diversity, significantly increased under conditions combining the residential complex and agrocenoses. Therefore, tadpoles of widespread amphibian species can be used as indicators of surface water quality and, accordingly, environmental health.

The study of larval anomalies is also of general theoretical interest, since a number of deviations of cenogeneses may be covered by the field of morphological changes that fall within the spectrum of potential morphofunctional innovations. There are morphoses that "precede a feature" (Berg, 1922) when "...ontogeny can both repeat and precede its phylogeny; phylogeny can both repeat and precede alien phylogeny," since "...morphogenesis regularly takes place in both these cases." As noted by Isidore Saint-Hilaire, "anomalies should not be considered a disorder; they involve another order subject to the same patterns" (Saint-Hilaire, 1832). The regular pattern of morphogenesis is determined by the modular organization of regulation of structural transformations during the evolutionary process (Dassow von and Munro, 1999; Gilbert and Bolker, 2001).

Amphibians as the first terrestrial vertebrates with a complex life cycle are significantly exposed to the danger of disruption of the equifinality of ontogeny as a result of deviations that appear in larval adaptations during destabilization of the habitat environment where they develop.

Based on the example of *R. arvalis* populations from an urban agglomeration, it was found that the occurrence of deviant forms of the larvae was significantly higher in the high-rise area (p = 0.0004–0.00001; χ^2 = 12.67–24.56, with Yates correction) and their diversity was much higher in the residential part of the city (zones II and III).

Changes in the synergistic vector of morphogenesis and the associated decrease in the equifinality of ontogeny contribute to the growth of diversity and frequency of occurrence of cenogenetic and other larval anomalies. A number of deviant variants can be considered as potential directions of evolutionary innovations.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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