Morphological Differentiation of Nominative and Dagestan Forms of the Complex Lacerta caucasia (Sauria, Lacertidae) in the Contact Zone: Sympatric Populations from Dagestan and Southeastern Chechnya

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Abstract—The morphological differentiation of two closely related forms of rock lizards, Lacerta (c.) caucasia and L. (c.) dagestania, was examined using 382 individuals belonging to five sympatric populations from the eastern part of the Northern Caucasus. The color pattern (qualitative parameters), diversity of seven morphometric parameters of the phalldosis, and five ratios between measurements were analyzed by multivariate and univariate statistics. In all of the populations studied, L. c. dagestania differed from L. c. caucasia by higher mean values of morphometric features of the phalldosis: a relatively long, wide, and flattened head; and by relatively long hindlegs. The extent of phenetic differentiation between these forms varied from distinct species level (with a hiatus in the number of clinate gradate) in the southeast of Chechnya to only slight intergradation in the parameters examined in southwestern Dagestan. These differences in the level of morphological divergence were concordantly expressed in sets of morphometric and plastic parameters, although the discriminant potential of the latter was lower. Taking into account the data on the geographical interrelations between caucasia and dagestania, a hypothesis was put forward, according to which different stages of evolutionary divergence occurred in different regions of the contact zone.

INTRODUCTION

The caucasian lizard (Lacerta caucasia sensu lato) is a background reptile species inhabiting many mountain landscapes of the Great Caucasus and belonging to the group of Caucasian rock lizards of the subgenus Archaeolacerta (Darevsky, 1967; Arnold, 1989). Darevsky (1984) distinguished three forms of this taxon: (1) alpina, inhabiting high mountains of the western part of the Great Caucasus; (2) caucasia, the nominative form, found on both slopes of the Main Caucasus Ridge from its northeast extremities (in the east) to the Elbrus (in the west); and (3) dagestania, inhabiting the eastern part of the northern macroslope from the Dar’yal Gorge in Northern Ossetia to Daghestan and southeastern part of Azerbaijan (Fig. 1). Until recently, these three forms were regarded as subspecies (Darevsky, 1964), and Darevsky (1967) indicated intergradation between caucasia and dagestania in the southern part of Dagestan. However, special studies on the intraspecific diversity of L. caucasia (sensu lato) revealed that, at certain points of the eastern part of the Northern Caucasus, nominative and Dagestan forms were sympatric but did not show intergradation (Roytberg and Levton, 1992; Roytberg, 1994); the extent of phenetic divergence differed in different populations of the contact zone.

In this study, the morphological differentiation of caucasia and dagestania is analyzed on the basis of material from five sympatric points located in the southeastern parts of Chechnya and Dagestan. The analysis of genetic differentiation among the forms alpina, caucasia, and dagestania by the method of protein electrophoresis (Fu et al., 1995) revealed obvious differences in several loci; in particular, caucasia and dagestania differed in two loci. The researchers proposed ranking these taxa as species, Lacerta alpina, L. caucasia, and L. dagestania (Fu et al., 1995; Murphy et al., 1996). At the same time, these studies were based on a small number of lizards (two L. alpina and 11 L. caucasia from the same population were examined), and the conclusion concerning the specific independence of three forms needs additional confirmation. Therefore, in this study, I designate caucasia and dagestania by a neutral term "form" (Mayr, 1971).

MATERIALS AND METHODS

The size and structure of the samples studied and information on the points of lizard capture are listed in Table 1. The geographic location of these points is shown in Fig. 1.
In each lizard, I analyzed qualitative parameters of the color pattern, seven labial features (measurements), and a great number of scale (pholidosis) parameters. In this study, I consider the following.

Numerical parameters of the pholidosis included (1) the number of preanal scales, Prean; (2) the number of ventral pores, Porr; (3) the number of transverse rows of abdominal scales, Ventr; (4) the number of scales around the middle of the body, Sq; (5) the number of cili- late granules between the supratemporal and supraciliary scales, Gran; (6) the number of scales between the first supratemporal and auxiliary openings, Trap; and (7) the number of supraciliary scales, St. The parameters Ventr and Sq were estimated by the previously described original criteria (Roytberg, 1994a, 1994b).

Measurements included (1) the length of the body and head, L; (2) length of the righthindleg, Leg; (3) length of the pelves (the upper part of the hind), PL; (4) length with the level of contact between supraciliary scales 2–3, PW; (5) head height, HD (according to Perez-Mellado and Gasta, 1988); and (6) head height from the lower edge of the infraorbital scale to the upper edge of the supraciliary scales, HDI.

I measured L and Leg with a ruler to an accuracy of 1 and 0.5 mm, respectively; PL and HD by sliding calipers, to 0.1 mm; PW1 and HDI by ocular micrometer (graduated in 0.1 mm) of a stereomicroscope MBS-9 at a magnification of 1 x 9. When measuring PW1, I positioned the lizard's head strictly horizontally; and HDI was measured using a strictly vertical position of the

<table>
<thead>
<tr>
<th>Point</th>
<th>Physiographic position, elevation above sea level</th>
<th>Date of capture</th>
<th>Sample size, caucasica/ daghestanica</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Xhorachoi</td>
<td>Southern slope of the Andinskii Ridge (southeastern Chechnya), 1000 m</td>
<td>Aug. 3–9, 1991, E.S. Roytberg and K.Ye. Lotiev</td>
<td>22/13</td>
</tr>
<tr>
<td>(3) Bethla</td>
<td>Southeastern slope of the Bogoskii Ridge (western Daghestan), 1000 m</td>
<td>July 26 and 31, 1990, E.S. Roytberg</td>
<td>2/16</td>
</tr>
<tr>
<td>(4) Geral'</td>
<td>Northern slope of the Main Caucasian Ridge (southern Daghestan), 2000 m</td>
<td>July 20 and 27, 1964, E.S. Roytberg and E.V. Il'in</td>
<td>25/25</td>
</tr>
<tr>
<td>(5) Rutul</td>
<td>Northern slope of the Kabarti Ridge near Mount Deavghi (southern Daghestan), 1800 m</td>
<td>Aug. 19 and 20, 1963, I.S. Durevsky</td>
<td>8/21</td>
</tr>
</tbody>
</table>
head, so that head scales of the right side were invisible from above and from below. When measuring Leg, I extended the hindleg perpendicular to the body and along the working edge of a measuring ruler, pressing the body to the tip of the ruler.

Ptn and Gran were estimated on both sides of the body, and data processing concerned the sum of right and left values; the other bilateral parameters were estimated on the left (Tmp2, St, and HDI) or right (Leg) side only.

The sample from each sympatric population was initially divided into two groups (similar to caucasic and or to doghestanica in coloration, primarily in the pattern of the dorsal body side).

Preliminary estimation of the agreement between a division of the samples into caucasic and doghestanica based on coloration and division based on the complex of numerical photodiosis parameters, was performed by the method of principal components. In general, the results of this analysis were in good agreement with the division based on coloration. In single instances of evident disagreement between two variants of division (in the space of the first two principal components, several lizards were located far from the boundary of their group in the main body of the "for-eign" group), a repeated analysis of coloration and a number of other external morphological features revealed errors in initial identification. Thus, division into groups was corrected.

Subsequently, I estimated the extent and pattern of differences among ten groups (caucasic and doghestanica from five localities) using the discriminant (canonical) analysis of two sets of quantitative parameters (photodiosis and measurement); and these ten were taken as a priori groups.

The quantitative parameters used in this study ranged substantially (five to ten, and a greater number of particular values occurred), were usually characterized by normal distribution, and were almost independent of age variation. When analyzing the labile parameters, I excluded the lizards with 1. < 43 mm from consideration and used the ratios Leg/L, P/L, PW1/PL, HD/PL, and HDI/PL, instead of initial measurements, to reduce the effect of variation in size.

2These corrections should not be regarded as "the adjustment" of the visual division into groups to the results of the multivariate analysis, as they were based on important evidence provided by qualitative features excluded from the initial analysis.
Table 2. Characteristics of the pattern on the dorsal body side in two forms of the Lacerta caucasia complex in the sympatric zone

<table>
<thead>
<tr>
<th>Components of pattern</th>
<th>caucasia</th>
<th>daghestanica</th>
</tr>
</thead>
<tbody>
<tr>
<td>Occipital stripe</td>
<td>Relatively narrow, usually with straight edges, and dark spots located in two parallel lines</td>
<td>Relatively wide, frequently with serrated edges, dark spots located disorderly</td>
</tr>
<tr>
<td>Parietal stripes</td>
<td>Anterior ends weakly narrowed and extend to posterior edge of pupils</td>
<td>Anterior ends strongly narrowed and do not extend to posterior edge of pupils</td>
</tr>
<tr>
<td>Boundary between parietal and temporal stripes</td>
<td>Usually straight</td>
<td>Usually serrated</td>
</tr>
<tr>
<td>Light lateral stripe (line)</td>
<td>Usually occurs</td>
<td>Almost always absent</td>
</tr>
<tr>
<td>General appearance of pattern</td>
<td>Usually distinct</td>
<td>Frequently diffused</td>
</tr>
</tbody>
</table>

RESULTS

Coloration

The pattern of the dorsal body side of L. caucasia consists of the following elements, named according to the head scales from which they stretch caudally: dark occipital (ridge) stripe, light parietal stripes, dark temporal (lateral) stripes, and light narrow lines located along the lateral boundary of the temporal stripes (Fig. 2). This pattern shows a substantial intrapopulation and interpopulation variation in both forms. The occipital stripe strongly varies in relative width and in the extent of development (pigmentation intensity); in some cases, it is represented by spots forming two parallel lines or located disorderly. Frequently, it is barely distinguishable, if at all, against the light background of the parietal stripes. The boundaries between the occipital and parietal stripes and between the parietal and temporal stripes vary in shape from regularly straight to strongly serrated (scalloped). The light lateral stripe varies in contrast; in some cases, it is discontinuous or completely absent.

Table 2 shows the summarized data on the differences between caucasia and daghestanica in dorsal pattern, revealed in the samples from five sympatric populations. The points vary in the extent to which the two forms differ in each parameter examined; these differences are most stable in parameters 2 and 4.

Numerical Parameters of the Photodosis

Figure 3 shows the outlines and centroids of male samples of caucasia and daghestanica from five sympatric populations in the space of the first and second canonical variables of the discriminant analysis based on seven numerical parameters of the photodosis. To gain a better understanding, the position of individual lizards is shown in a series of figures, each including samples of caucasia and daghestanica from one point only (Figs. 5a–5e).

These scatterplots show that, in point 1 (Khechaoi), the phenetic divergence between the nominative and Degustanti forms is extremely well pronounced; the distance between respective lizard groups is comparable to the extent of each group. At point 2 (Khvash), caucasia and daghestanica diverge to a lesser extent but rather distinctly; whereas at point 4 (Gem6), the differences are small, so that the lizard groups overlap each other. In points 3 (Bechta) and 5 (Ruttii), the extent of phenetic divergence between caucasia and daghestanica is close to that at point 2, but because of the small number of lizards of nominative form, this estimate is rather approximate.

In females, discriminant analysis (Figs. 4, 6a–6e) revealed a similar pattern; the caucasia and daghestanica forms sharply diverge at point 1; the differences are smaller at points 2, 3, and 5; and the lowest divergence is observed at point 4.

Figures 3 and 4 show that, in all samples (sympatric populations), the caucasia and daghestanica forms are distinguished by the first canonical variable (CV1), describing 63-67% of differences among the ten groups studied (Table 3); at points 2 and 5, variable CV 1 also contributes substantially to the differences between the two forms (16-17%).

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In either sex, CV I is characterized by positive standard coefficients for all parameters (except for Pran). This reflects the pattern of morphological differences between the two forms; thus, caucasica is characterized by greater means of Pran and lower means of all other numerical parameters examined (Royston, 1994). CV II is characterized by high positive coefficients for Prm and S1 and negative coefficients for Gran and Temp2 in either sex (Table 3). The pattern (direction) of differences between caucasica and daghestanica in the pholidosis parameters is the same in all of the sympatric populations examined; however, the contributions of individual parameters to the phenetic divergence of two forms substantially differ at different points. This is distinctly expressed by the coefficients of difference (Mayr, 1971) between caucasica and daghestanica, calculated on the basis of the seven parameters used in the discriminant analysis (Table 4, CD). Thus, at point 1, the differences in the number of ciliate granules (Gran) are substantially greater even though those is the number of supratemporal scales (St), whereas at point 5, the opposite ratio is observed.

The means of CD for seven parameters provide a generalized measurement of the phenetic distances between two sympatric forms and show a pattern similar to that revealed by the discriminant analysis, the greatest and lowest divergence being observed at points 1 and 4, respectively.

Note that positive and negative values of these coefficients (and orientation of the discriminant axes in the scatterplots) are conditions. An important point is the same or opposite signs of coefficients compared.

Morphometric Indices

Figure 7 shows the outlines and centroids for male samples of caucasica and daghestanica forms from five sympatric populations in the space of the first and second canonical variables of the discriminant analysis based on five ratios between measurements. As for the discriminant analysis based on the pholidosis parameters, the positions of particular lizards are shown in a set of figures (Figs. 9a–9c). The results of the discriminant analysis for the same morphometric indices in females are shown in Figs. 8 and 10.

These scatterplots show that, in either sex (but especially in males), a well-pronounced division into cau-
Fig. 6. Scatterplots for females of (c) caspica and (d) daghestanica from five sympatric points (1–5, see Fig. 1 and Table 1) in the space of the first and second canonical variables of the discriminant analysis based on seven pholidosis parameters.

caspica and daghestanica occurs at point 1 (Figs. 9a and 10a), whereas at point 4, such a division is weakly expressed (Figs. 9d and 10d). At the other three points, this division is of an intermediate type, characterized by a weak overlap in all cases involving more than five lizards of each sympatric form. The absence of an overlap between the caspica and daghestanica forra in males from point 3 (Fig. 9c) and females from point 5 (Fig. 10e) is attributable to the fact that, in each case, the nominate form is represented by two lizards only.

In either sex, 3 and caspica are distinguished mainly by the first canonical variable (CV I), describing 65–70% of differences among the ten groups (Figs. 7 and 8, Table 5). Different samples (populations) of the same form are also distinguished by the values of CV I. This is most pronounced in daghestanica, so that the outlines and centroids of samples 3 and 5 are strongly shifted to the region of values characteristic of the caspica samples (Figs. 7 and 8). It is noteworthy that CV I reflects the interpopulation differences to a greater extent than CV II.

Table 5 shows that, in either sex, CV I is characterized by negative standard coefficients for the index Leg/L and positive coefficients for HD/PL and HDU/PL (the coefficient of the latter index is low in males but high in females); a high positive coefficient of this variable is observed for PNI/PL in males and for PL/L in females. Thus, the most stable characteris-
ties of the first discriminant function is the contrast between relative height of the head and relative length of the hindlegs. A comparison of the two sympatric forms in particular parameters revealed that, in general, *dugong* differs from *canusica* by a greater head flattening and longer legs.

In either sex, CV II is characterized by high negative coefficients for the indices PL/L and HD1/PL and high positive coefficients for three other indices (Table 5). As this variable does not show regular intergroup differences, its interpretation is of no particular value.

The coefficients of difference (CD) between *canusica* and *dughestana* based on five morphometric indices are shown in Table 6. A comparison of the data from Tables 4 and 6 shows that the mean and maximal differences in the ratios between measurements are substantially lower than those in numerical parameters of the pholidosis. Thus, 20% of the highest values of CD for the pholidosis parameters (seven of 35) range within 1.5-3.0, whereas 20% of the highest values of CD for morphometric indices (five of 25) range within 1-1.7. The mean CD for five morphometric indices shows a distinct maximum (1.19) at point 1, minimum (0.27) at point 4, and intermediate values (0.56-0.66) at points 2, 3, and 5.

### DISCUSSION

When comparing the results of the discriminant analysis based on two sets of parameters, one can conclude that, in general, phenetic divergence of *canusica* and *dughestana* is substantially greater in the numerical parameters of the pholidosis than in morphometric indices. However, both sets of parameters reveal a similar pattern of variation in the extent of divergence of two sympatric forms in different points, namely, the highest, lowest, and intermediate extent of divergence are observed in points 1, 4, and others, respectively.

The analysis of the color pattern of the dorsal body side is in agreement with these results: the preliminary division of lizards into *canusica* and *dughestana* was easy to perform at point 1 and difficult to perform at point 4 (unfortunately, I failed to describe color variation quantitatively).

At point 1 (Khoracoi), the morphological differences between the two forms are at the level of true species; they are discretely divergent (separated from each other by a hiatus in both the complex of numerical pholidosis parameters and the complex of morphometric indices). A distinct hiatus is also observed in an individual feature, the number of ciliate granules, which ranged from 0 to 11 (n = 44) in *canusica* and from 15 to 33 (n = 28) in *dughestana* (Royberg, 1994). It is reasonable to propose that the gene interchange is completely absent in this region of the sympatric area (in the southeastern part of Chechaya).

At point 2, and probably at points 3 and 5 (western and southwestern parts of Dagestan), the phenetic divergence of *canusica* and *dughestana* is expressed to a lesser extent and shows differentiation without an overlap but without a pronounced hiatus in the complex of the pholidosis parameters and a weak overlap in the complex of morphometric indices. Thus, in Khoracoi, the reproductive isolation of two forms is probably more complete than in the high mountains of Dagestan. The study on allozyme polymorphism (Fu et al., 1995) provided certain evidence for limited hybridization at point 2 (Khrvars).
Table 5. Standardized discriminant coefficients for five ratios between measurements used in the discriminant analysis of the samples, including causcanica and diaphastenica from five sympatric points (ten classification groups)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Males (CV I)</th>
<th>Males (CV II)</th>
<th>Females (CV I)</th>
<th>Females (CV II)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LegL</td>
<td>-0.29</td>
<td>0.52</td>
<td>-0.23</td>
<td>0.27</td>
</tr>
<tr>
<td>PL/L</td>
<td>-0.08</td>
<td>-0.76</td>
<td>0.44</td>
<td>-0.99</td>
</tr>
<tr>
<td>PW/PW</td>
<td>0.62</td>
<td>0.36</td>
<td>0.08</td>
<td>0.46</td>
</tr>
<tr>
<td>HD/PD</td>
<td>0.48</td>
<td>0.36</td>
<td>0.37</td>
<td>0.30</td>
</tr>
<tr>
<td>HDU/PD</td>
<td>0.21</td>
<td>-0.90</td>
<td>0.91</td>
<td>-0.52</td>
</tr>
<tr>
<td>Relative proportion (% of canonical functions)</td>
<td>70.4</td>
<td>13.4</td>
<td>65.7</td>
<td>23.2</td>
</tr>
</tbody>
</table>

Table 6. Coefficients of difference (CD, after May, 1971) between the forms causcanica and diaphastenica from five sympatric points for five ratios between measurements

<table>
<thead>
<tr>
<th>Index</th>
<th>(1) Khorachir</th>
<th>(2) Khor. Bvazh</th>
<th>(3) Bezhta</th>
<th>(4) Gerel'</th>
<th>(5) Rutal</th>
</tr>
</thead>
<tbody>
<tr>
<td>LegL</td>
<td>0.71</td>
<td>0.45</td>
<td>0.06</td>
<td>0.12</td>
<td>0.67</td>
</tr>
<tr>
<td>PL/L</td>
<td>0.64</td>
<td>0.40</td>
<td>0.28</td>
<td>0.20</td>
<td>0.49</td>
</tr>
<tr>
<td>PW/PW</td>
<td>-1.48</td>
<td>-0.54</td>
<td>-1.04</td>
<td>-0.23</td>
<td>-1.32</td>
</tr>
<tr>
<td>HD/PD</td>
<td>-1.72</td>
<td>-1.00</td>
<td>-0.57</td>
<td>-0.29</td>
<td>-1.32</td>
</tr>
<tr>
<td>HDU/PD</td>
<td>-1.40</td>
<td>-0.72</td>
<td>-0.84</td>
<td>-0.51</td>
<td>-0.40</td>
</tr>
<tr>
<td>Mean CD for five indices</td>
<td>1.19</td>
<td>0.62</td>
<td>0.56</td>
<td>0.27</td>
<td>0.66</td>
</tr>
</tbody>
</table>

Sample size: causcanica=29, diaphastenica=30.

Note: See the note to Table 4.

Darevsky (1967) believed that a large-scale hybridization between causcanica and diaphastenica could occur in the contact zone. It is noteworthy that this hypothesis was primarily based on the visual examination of a sample from point 5, which is examined in this study as well (Table 1). Among the 52 lizards of this series, Darevsky identified 16 as more or less pure diaphastenica, 11 as causcanica, and the others (about 5%) as "possessing hybrid parameters, which makes their identification impossible" (Darevsky, 1967, p. 189). When performing preliminary visual classification of lizards from this series, I also faced substantially greater problems than in the case of the samples from points 2 and 3.

However, the discriminant analysis based on seven pholidosis parameters shows that causcanica and diaphastenica are distinctly differentiated in the male sample from this point (Fig. 5e). A similar situation is also observed in females, but one lizard identified by color as diaphastenica and characterized by the body proportions typical of diaphastenica joins the group causcanica in the space of the first and second discriminant functions.

These results do not corroborate the hypothesis of mass hybridization between causcanica and diaphastenica in the southern part of Dastgan, but agree with the assumption that a limited hybridization occurs. Hybridization is even more probable if the vicinity of Gerel' (presumably where the difference between the sympatric forms in the parameters examined are only slightly expressed, so that a small overlap for the complex of the pholidosis parameters and a strong overlap for the complex of the morphometric indices are observed.

If the differences between the sympatric populations or pholidosis divergence of the forms causcanica and diaphastenica reflect different degrees of reproductive isolation, one can propose that an incomplete speciation occurs and consider these forms to be species in statu nascendi. However, conclusive evidence for their hybridization has not yet been obtained. It is possible that, not only in Khorachir, but also in Dastgan as well, they are completely isolated from each other in both reproduction and pholidotic parameters, and diagnostic features have not been revealed. This problem could be solved with the use of data on protein electrophore- sis and experiments on production of the mentioned forms, examined, in particular, those from the sites of the contact zone, where the divergence in external morpholog- ical features is only slightly expressed.

In any case, the fact that differences in morphologi- cal divergence of two sympatric forms from different points is concordantly expressed in several systems of parameters (pholidosis, measurements, and coloration) shows that, in different sites of the contact zone, different stages of evolutionary divergence occur. The description and analysis of such situations are of profound importance for understanding the ways and patterns of phyletic diversity formation (Mina, 1986).

Let us consider briefly the ecological and geographical interrelations of examined lizards' forms. Within the entire range, Darevsky (1967) and Muskeshvili (1970) characterized the biotopes inhabited by diaphas- tenica as dry and moderately dry and those inhabited by causcanica as moderately moist. In the sympatric points examined, diaphastenica predominantly occurs in open stony biotopes, whereas causcanica prefers the sites covered by thick herbaceous vegetation. However, this spatial differentiation is not strict, and lizards of different forms are frequently neighbors.

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At points 2, 3, and probably 5, daghestanica predominates; at point 4, the two forms are similar in number and distribution over the territory; and at point 1, caulacasa distinctly prevails. It is noteworthy that, at point 1, daghestanica is found on rock outcrops at the boundary of the hornbeam forest extending for several hundred meters only, whereas in the surrounding area, only caulacasa occurs. This caulacasa population is a geographic isolate located inside the range of daghestanica (Fig. 1); it sharply (at the level of a subspecies) differs from all known caulacasa populations (and more so, from daghestanica) by a small number of ciliate granules (Darevsky, 1967; Darevskij, 1984; Roytberg, 1994). The latter feature of this caulacasa population and the complex structure of geographic interrelations between the two forms in this sympatric site (isolate in an isolate) are evidently secondary; this, along with a high level of phenetic differentiation, corresponds to an advanced stage of evolutionary divergence.

On the contrary, in the gorge of the Dzhurmat River (southwestern Dagestan, northern slope of the Main Caucasian Ridge), where phenetic differentiation of caulacasa and daghestanica is weakly expressed, the geographic interrelations are rather simple: 20-30 km below point 4 (in the vicinity of the village of Tyaratu and Tsiumuluk), only daghestanica occurs, and 10-15 km above point 4, it is almost completely...
replaced by caucasia. Thus, it appears probable that, in the gorge of the Dzhurmat River, the early stage of species isolation of the lizards forms examined occurs.

As the recent range of caucasia extends along both slopes of the Main Caucasian Ridge (Fig. 1), each inhabited by sympatric populations of caucasia and daghestanica (Darevsky, 1967), one can propose that the initial stages of evolutionary isolation of the two forms developed on the Main Caucasian Ridge, from which one or both of them migrated along its flanks (Andisikii, Bogoskii, and other large ridges), deep into the Great Caucasus. If this is the case, one should expect an increase in the level of divergence of the two forms, which would depend on the distance from the Main Caucasian Ridge, which is actually observed in the sympatric populations examined.

The above reasoning agrees with the hypothesis by Darevsky (1967, p. 196) that the high-mountain form caucasia deviated from daghestanica during the post-glacial term in the course of migration of the latter from xerophilic refuges of inland Dagestan to the mountains along with receding glacier. At the same time, these evolutionary reconstructions are preliminary and can be corrected as a result of future studies on the structure of phenetic diversity in the Lacerta caucasia complex within the entire range of this taxon.

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ROTYBERG

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