

Morphological Differentiation of Nominative and Dagestan Forms of the Complex *Lacerta caucasica* (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.) caucasica* and *L. (c.) daghestanica*, 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 pholidosis, and five ratios between measurements were analyzed by multivariate and univariate statistics. In all of the populations studied, *L. c. daghestanica* differed from *L. c. caucasica* by higher mean values of morphometric feature of the pholidosis; a relatively long, wide, and flattened head; and by relatively long hindlegs. The extent of phenetic differentiation between these forms varied from distinctly species level (with a hiatus in the number of ciliate granules) 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 *caucasica* and *daghestanica*, 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 caucasica* 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). Darevskij (1984) distinguished three forms of this taxon: (1) *alpina*, inhabiting high mountains of the western part of the Great Caucasus; (2) *caucasica*, 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) *daghestanica*, inhabiting the eastern part of the northern macroslope from the Dar'yal Gorge in Northern Ossetia to Dagestan and southeastern part of Azerbaijan (Fig. 1). Until recently, these three forms were regarded as subspecies (Darevskij, 1984), and Darevsky (1967) indicated intergradation between *caucasica* and *daghestanica* in the southern part of Dagestan. However, special studies on the intraspecific diversity of *L. caucasica* (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 Lotiev, 1992; Roytberg, 1994); the

extent of phenetic divergence differed in different populations of the contact zone.

In this study, the morphological differentiation of *caucasica* and *daghestanica* 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*, *caucasica*, and *daghestanica* by the method of protein electrophoresis (Fu *et al.*, 1995) revealed obvious differences in several loci; in particular, *caucasica* and *daghestanica* differed in two loci. The researchers proposed ranking these taxa as species, *Lacerta alpina*, *L. caucasica*, and *L. daghestanica* (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. caucasica* 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 *caucasica* and *daghestanica* 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.

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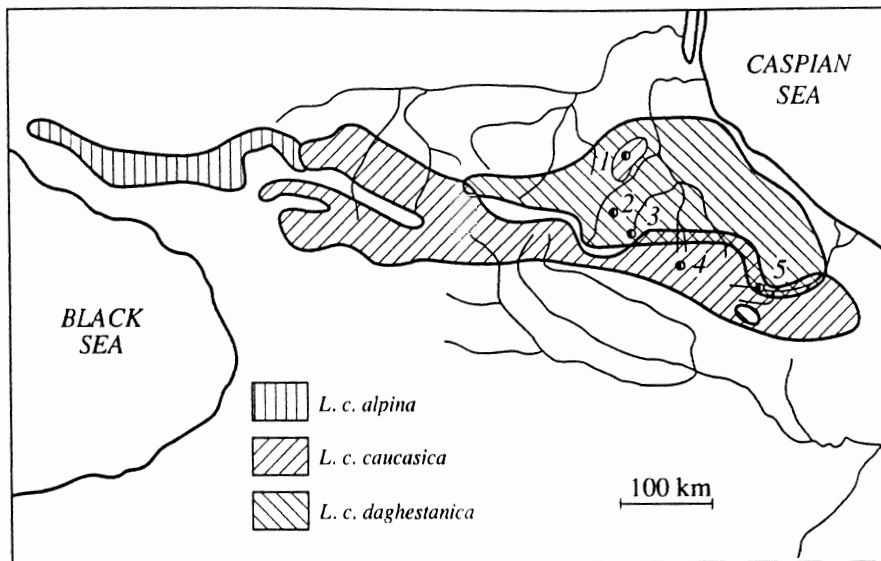


Fig. 1. Geographic distribution of forms of the *Lacerta caucasica* complex (after Darevsky, 1967). Numerals designate examined sympatric populations of *caucasica* and *daghestanica*, and the numbers of the points correspond to those in Table 1.

In each lizard, I analyzed qualitative parameters of the color pattern, seven labile 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, **Pran**; (2) the number of femoral pores, **Pfm**; (3) the number of transverse rows of abdominal scales, **Ventr**; (4) the number of scales round the middle of the body, **Sq**; (5) the number of ciliate granules between the supraorbital and supraciliate scales, **Gran**; (6) the number of scales between the first supratemporal and auditory openings, **Tmp2**; and (7) the number of supratemporal 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 right hindleg, **Leg**; (3) length of the pileus (the upper part of the head), **PL**; (4) pileus width at the level of contact between supraorbital scales 2–3, **PW1**; (5) head height, **HD** (according to Perez-Mellado and Gosa, 1988); and (6) head height from the lower edge of the infraorbital scale to the upper edge of the supraciliate scales, **HD1**.

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 **HD1** by ocular micrometer (graduated in 0.1 mm) of a stereomicroscope MBS-9 at a magnification of 1×8 . When measuring **PW1**, I positioned the lizard's head strictly horizontally; and **HD1** was measured using a strictly vertical position of the

Table 1. Size and structure of samples, date of capture, and physiographic characteristics of five sympatric points of the forms *caucasica* and *daghestanica* in the eastern part of the Northern Caucasus

Point	Physiographic position, elevation above sea level	Date of capture	Sample size, <i>caucasica</i> / <i>daghestanica</i>	
			males	females
(1) Khorachoi	Southern slope of the Andiiskii Ridge (southeastern Chechnya), 1000 m	Aug. 3–9, 1991, E.S. Roytberg and K.Yu. Lotiev	22/13	22/15
(2) Khvarshi	Northwestern slope of the Bogoskii Ridge (western Dagestan), 1800–2200 m	June 17–23, 1991, E.S. Roytberg	15/30	20/29
(3) Bezhta	Southeastern slope of the Bogoskii Ridge (western Dagestan), 1700 m	July 26 and 31, 1990, E.S. Roytberg	2/16	7/17
(4) Gerel'	Northern slope of the Main Caucasian Ridge (southwestern Dagestan), 2000 m	July 20 and 27, 1994, E.S. Roytberg and E.V. Il'ina	25/23	35/29
(5) Rutul	Northern slope of the Kabyaktepe Ridge near Mount Deavgai (southern Dagestan), 1800 m	Aug. 19 and 20, 1963, I.S. Darevsky	8/21	2/21

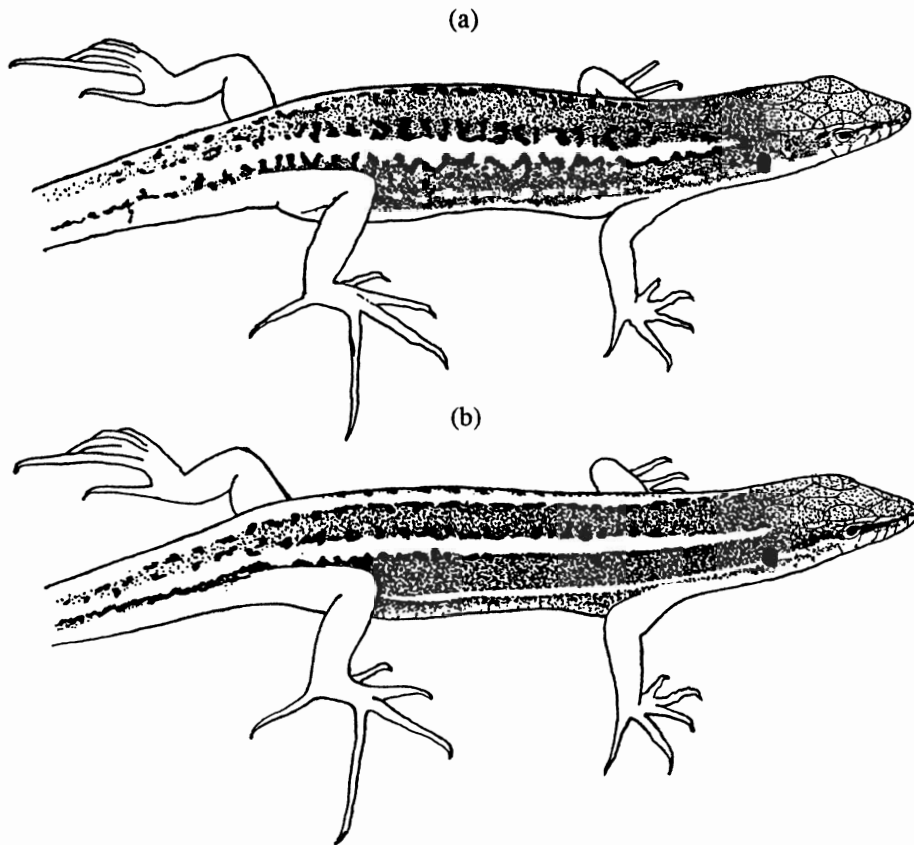


Fig. 2. The pattern of the dorsal body side in (a) Dagestan and (b) nominative forms of the *Lacerta caucasica* complex.

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.

Pfm 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 **HD1**) or right (**Leg**) side only.

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

Preliminary estimation of the agreement between a division of the samples into *caucasica* and *daghestanica* based on coloration and division based on the complex of numerical pholidosis 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.²

Subsequently, I estimated the extent and pattern of differences among ten groups (*caucasica* and *daghestanica* from five localities) using the discriminant (canonical) analysis of two sets of quantitative parameters (pholidosis 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 $L < 43$ mm from consideration and used the ratios **Leg/L**, **PL/L**, **PW1/PL**, **HD/PL**, and **HD1/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 caucasica* complex in the sympatric zone

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

RESULTS

Coloration

The pattern of the dorsal body side of *L. caucasica* 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 hardly 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 *caucasica* 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 Pholidosis

Figure 3 shows the outlines and centroids of male samples of *caucasica* 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 pholidosis. To gain a better understanding, the position of individual lizards is shown in a series of figures, each including samples of *caucasica* and *daghestanica* from one point only (Figs. 5a–5e).

These scatterplots show that, in point 1 (Khorachoi), the phenetic divergence between the nominative and Dagestani forms is extremely well pronounced; the distance between respective lizard groups is comparable to the extent of each group. At point 2 (Khvarshi), *caucasica* and *gaghestanica* diverge to a lesser extent but rather distinctly; whereas at point 4 (Gerel'), the differences are small, so that the lizard groups overlap each other. In points 3 (Bezhta) and 5 (Rutul), the extent of phenetic divergence between *caucasica* 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 *caucasica* 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 *caucasica* and *daghestanica* forms are distinguished by the first canonical variable (CV I), describing 63–67% of differences among the ten groups studied (Table 3); at points 3 and 5, variable CV II also contributes substantially to the differences between the two forms (16–17%).

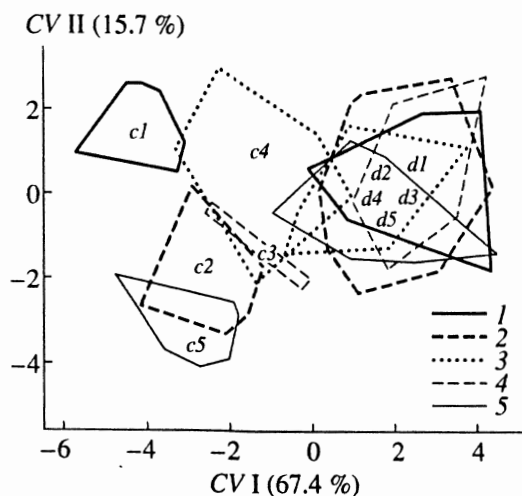


Fig. 3. The outlines and centroids of male samples of (c) *caucasica* and (d) *daghestanica* from five sympatric points (1–5, see Fig. 1 and Table 1) in the space of the first and second canonical variables of the discriminant analysis based on seven pholidosis parameters.

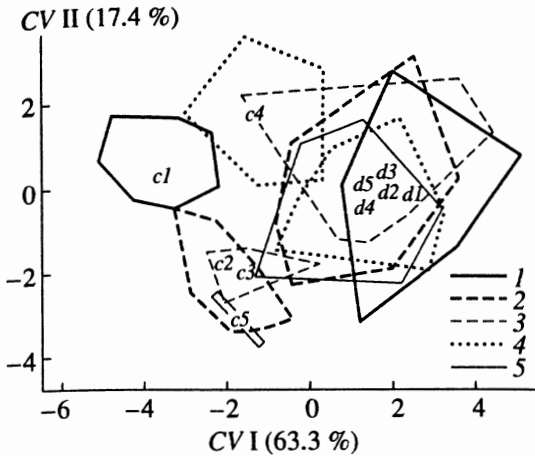


Fig. 4. The outlines and centroids of female samples of (c) *caucasica* and (d) *daghestanica* from five sympatric points (1–5, see Fig. 1 and Table 1) in the space of the first and second canonical variables of the discriminant analysis based on seven pholidosis parameters.

In either sex, CVI is characterized by positive standard coefficients for all parameters (except for **Pran**);³ 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 (Roytberg, 1994). CV II is characterized by high positive coefficients for **Pfm** and **St** and negative coefficients for **Gran** and **Tmp2** 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 than those in 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.

³Note that positive and negative values of these coefficients (and orientation of the discriminant axes in the scatterplots) are conditional. An important point is the same or opposite sign of coefficients compared.

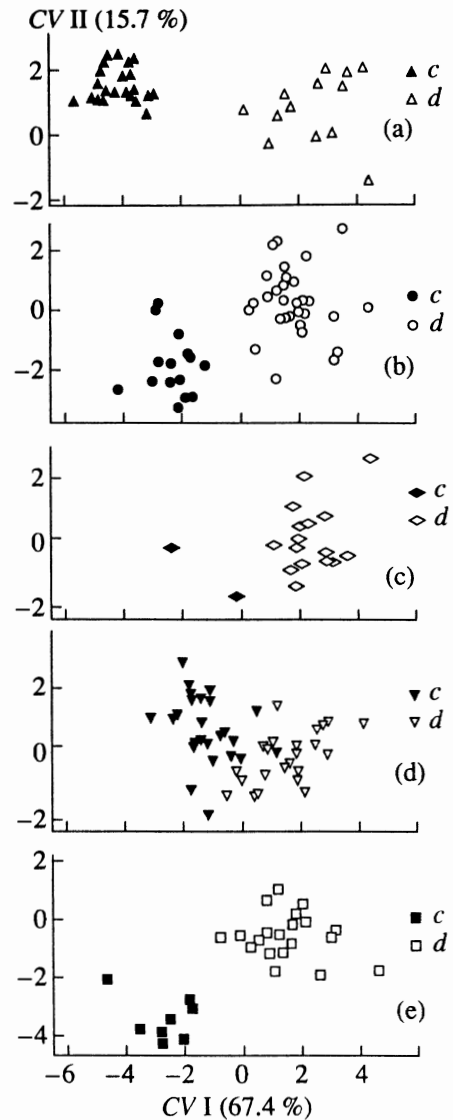


Fig. 5. Scatterplots for males of (c) *caucasica* and (d) *daghestanica* from five sympatric points (1–5, see Fig. 1 and Table 1) in the space of the first and second canonical variables of the discriminant analysis based on seven pholidosis parameters.

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–9e). 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-*

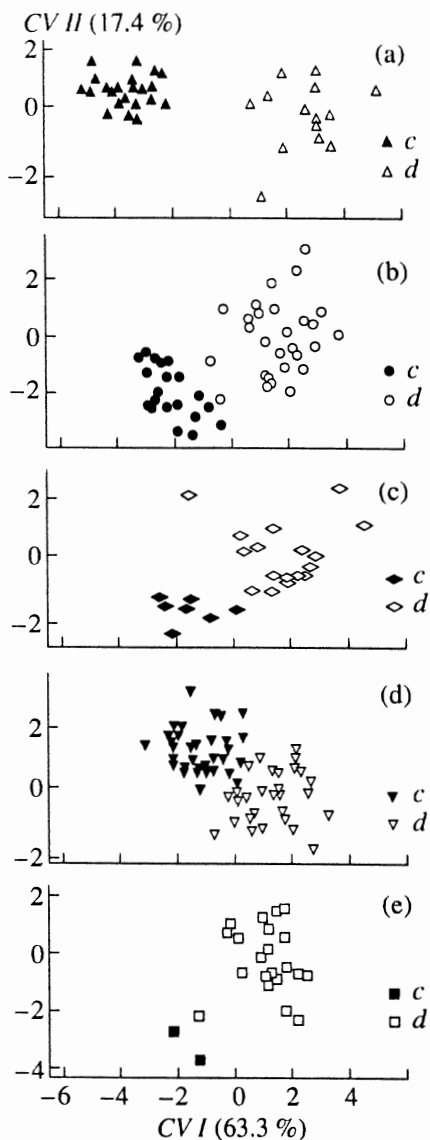


Fig. 6. Scatterplots for females of (*c*) *caucasica* and (*d*) *daghestanica* from five sympatric points (1–5, see Fig. 1 and Table 1) in the space of the first and second canonical variables of the discriminant analysis based on seven pholidosis parameters.

caucasica 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 *caucasica* and *daghestanica* forms in males from point 3 (Fig. 9c) and females from point 5 (Fig. 10e) is attributable to the fact that, in each case, the nominative form is represented by two lizards only.

In either sex, 5 and *caucasica* 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

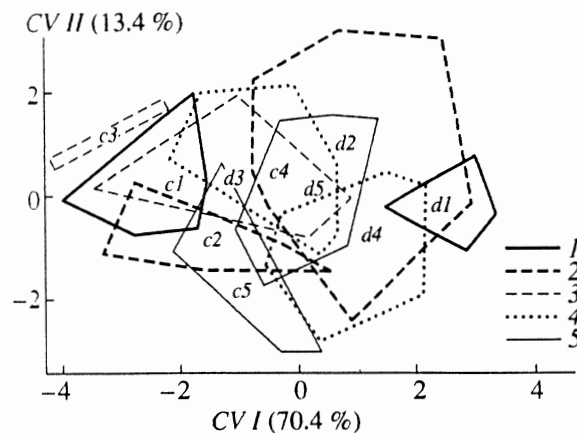


Fig. 7. The outlines and centroids of male samples of (*c*) *caucasica* and (*d*) *daghestanica* from five sympatric points (1–5, see Fig. 1 and Table 1) in the space of the first and second canonical variables of the discriminant analysis based on five morphometric indices (ratios between measurements).

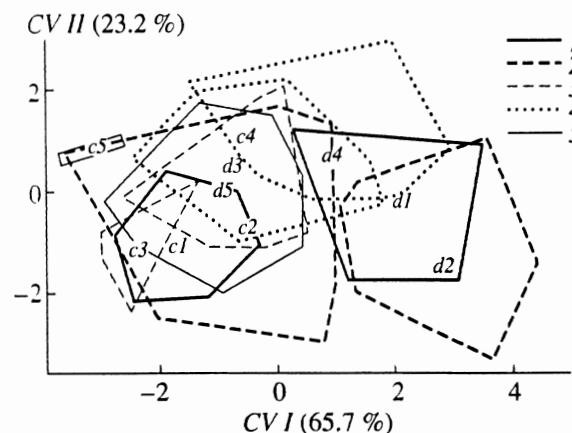


Fig. 8. The outlines and centroids of female samples of (*c*) *caucasica* and (*d*) *daghestanica* from five sympatric points (1–5, see Fig. 1 and Table 1) in the space of the first and second canonical variables of the discriminant analysis based on five morphometric indices.

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 *caucasica* 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 **HD1/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 **PW1/PL** in males and for **PL/L** in females. Thus, the most stable characteris-

tics 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, *daghestanica* differs from *caucasica* 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 *caucasica* and *daghestanica* 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 1.0–1.7. 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 *caucasica* and *daghestanica* 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 *caucasica* and *daghestanica* 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 (Khorachoi), 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 that 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 *caucasica* and from 18 to 33 ($n = 28$) in *daghestanica* (Roytberg, 1994). It is reasonable to propose that the gene interchange is completely absent in this region of the sympatric area (in the south-eastern part of Chechnya).

At point 2, and probably at points 3 and 5 (western and southwestern parts of Dagestan), the phenetic

Table 3. Standardized discriminant coefficients for seven pholidosis parameters used in the discriminant analysis of the samples, including *caucasica* and *daghestanica* from five sympatric points (ten classification groups)

Parameter	Males		Females	
	<i>CV I</i>	<i>CV II</i>	<i>CV I</i>	<i>CV II</i>
Pran	-0.26	0.19	-0.27	0.10
Pfm	0.24	0.59	0.34	0.62
Ventr	0.15	0.08	0.08	-0.04
Sq	0.47	0.22	0.39	0.10
Gran	0.57	-0.50	0.57	-0.20
Tmp2	0.37	-0.18	0.19	-0.71
St	-0.06	0.52	0.22	0.59
Relative percentage of canonical functions	67.35	15.70	63.33	17.48

Table 4. Coefficients of difference (*CD*, after Mayr, 1971) between the forms *caucasica* and *daghestanica* from five sympatric points for seven numerical parameters of the pholidosis

Parameter	Point				
	(1) Khorachoi	(2) Khvarshi	(3) Bezhta	(4) Gerel'	(5) Rutul
Pran	-0.95	-0.45	-0.36	-0.28	-0.21
Pfm	1.66	1.55	1.32	0.08	2.17
Ventr	0.76	0.43	0.30	0.10	0.30
Sq	1.27	1.42	1.50	0.96	1.35
Gran	3.05	0.86	0.59	0.81	0.56
Tmp2	1.60	0.64	0.32	1.54	0.98
St	0.26	1.10	0.78	0.12	2.95
Mean <i>CD</i> for seven parameters	1.36	0.92	0.73	0.56	1.22
Sample size, <i>caucasica/daghestanica</i>	44/28	35/59	9/33	60/52	10/42

Note: *CD* values are averaged for males and females; (-) in *caucasica*, the mean of this parameter is greater than in *daghestanica* (in all other cases, the means are greater in *daghestanica*).

divergence of *caucasica* and *daghestanica* 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 Khorachoi, 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 (Khvarshi).

Table 5. Standardized discriminant coefficients for five ratios between measurements used in the discriminant analysis of the samples, including *caucasica* and *daghestanica* from five sympatric points (ten classification groups)

Parameter	Males		Females	
	CV I	CV II	CV I	CV II
Leg/L	-0.29	0.52	-0.23	0.27
PL/L	-0.08	-0.76	0.44	-0.99
PW/PL	0.62	0.36	0.08	0.46
HD/PL	0.48	0.36	0.37	0.30
HD1/PL	0.21	-0.90	0.91	-0.52
Relative proportion (%) of canonical functions	70.4	13.4	65.7	23.2

Table 6. Coefficients of difference (CD, after Mayr, 1971) between the forms *caucasica* and *daghestanica* from five sympatric points for five ratios between measurements

Index	Point				
	(1) Khorachoi	(2) Kharvarshi	(3) Bezhta	(4) Gerel'	(5) Rutul
Leg/L	0.71	0.45	0.06	0.12	0.67
PL/L	0.64	0.40	0.28	0.20	0.49
PW/PL	-1.48	-0.54	-1.04	-0.23	0.44
HD/PL	-1.72	-1.00	-0.57	-0.29	-1.32
HD1/PL	-1.40	-0.72	-0.84	-0.51	-0.40
Mean CD for five indices	1.19	0.62	0.56	0.27	0.66
Sample size, <i>caucasica</i> / <i>daghestanica</i>	28/13	23/44	7/22	51/47	9/37

Note: See the note to Table 4.

Darevsky (1967) believed that a large-scale hybridization between *caucasica* and *daghestanica* 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 *daghestanica*, 11 as *caucasica*, and the others (about 50%) 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 *caucasica* and *daghestanica*

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 *daghestanica* and characterized by the body proportions typical of *daghestanica* adjoins the group *caucasica* ($n = 2$) in the space of the first and second discriminant functions.

These results do not corroborate the hypothesis of mass hybridization between *caucasica* and *daghestanica* in the southern part of Dagestan, but agree with the assumption that a limited hybridization occurs. Hybridization is even more probable in the vicinity of Gerel' (point 4), where the differences between the sympatric forms in the parameters examined are only slightly expressed, so that a limited 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 in phenetic divergence of the forms *caucasica* and *daghestanica* 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 Khorachoi, but in Dagestan as well, they are completely isolated from each other in both reproduction and phenetic parameters, and diagnostic features have not been revealed.⁴ This problem could be solved with the use of data on protein electrophoresis and experiments on hybridization of the forms examined, in particular, those from the sites of the contact zone, where the divergence in external morphological features is only slightly expressed.

In any case, the fact that differences in morphological 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 phenetic diversity formation (Mina, 1986).

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

⁴Thus, at point 4, the sympatric forms were easily distinguished from each other by abdomen color; it was whitish in *daghestanica* and bright yellow in *caucasica*; however, the use of this parameter is limited by the fact that these differences disappear after fixation and are completely absent in young lizards.

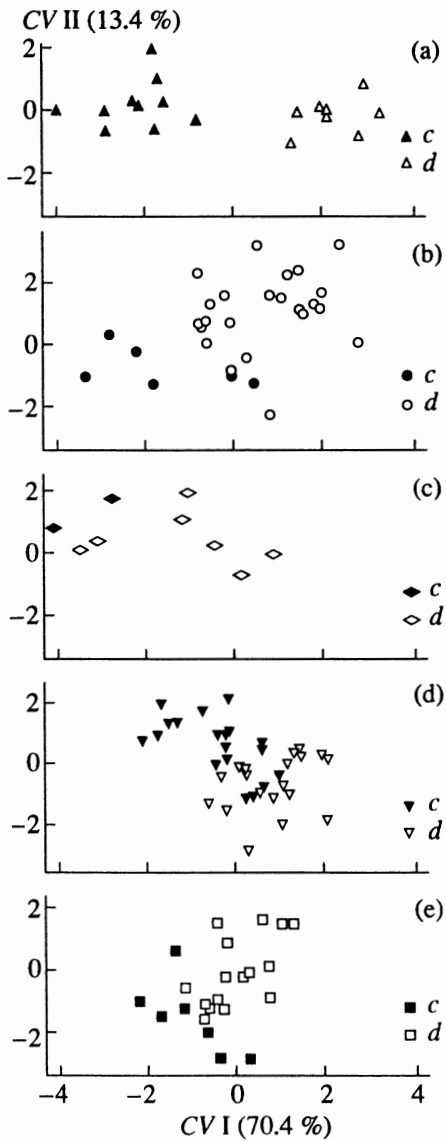


Fig. 9. Scatterplots for males of (c) *caucasica* and (d) *daghestanica* from five sympatric points (1–5, see Fig. 1 and Table 1) in the space of the first and second canonical variables of the discriminant analysis based on five morphometric indices.

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, *caucasica* 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 *caucasica* occurs. This *caucasica* 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 *caucasica* populations (and more so, from *daghestanica*) by a small number of ciliate granules (Darevsky, 1967; Darevskij, 1984; Roytberg, 1994). The latter feature of this *caucasica* popu-

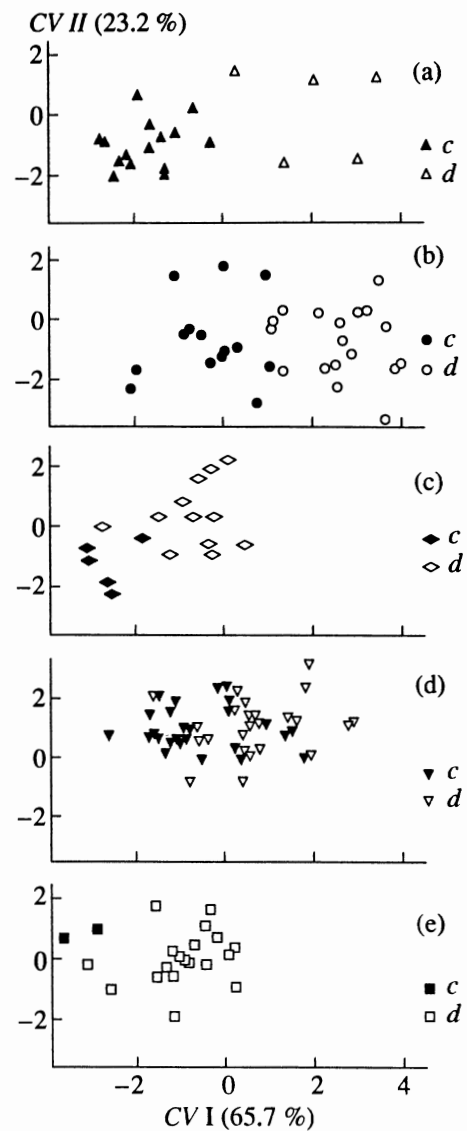


Fig. 10. Scatterplots for females of (c) *caucasica* and (d) *daghestanica* from five sympatric points (1–5, see Fig. 1 and Table 1) in the space of the first and second canonical variables of the discriminant analysis based on five morphometric indices.

lation 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 Dzhurmut River (southwestern Dagestan, northern slope of the Main Caucasian Ridge), where phenetic differentiation of *caucasica* and *daghestanica* is weakly expressed, the geographic interrelations are rather simple: 20–30 km below point 4 (in the vicinity of the village of Tlyarata and Tsumilukh), only *daghestanica* occurs, and 10–15 km above point 4, it is almost completely

replaced by *caucasica*. Thus, it appears probable that, in the gorge of the Dzhurmut River, the early stage of species isolation of the lizard forms examined occurs.

As the recent range of *caucasica* extends along both slopes of the Main Caucasian Ridge (Fig. 1), each inhabited by sympatric populations of *caucasica* 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 offspurs (Andiiskii, 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 *caucasica* deviated from *daghestanica* during the post-glacial term in the course of migrations 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 caucasica* complex within the entire range of this taxon.

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