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A COMPARATIVE STUDY OF INTRA- AND INTER-POPULATION VARIATION IN TWO SYMPATRIC LIZARDS, *Lacerta agilis boemica* AND *L. strigata* IN DAGHESTAN

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Using methods of statistical analysis, the extent of morphological inter- and intra-population variation in two sympatric lizard species (*Lacerta agilis boemica* and *L. strigata*) from the North Caucasus (Daghestan) was compared. 1042 specimens from 7 localities of lowland and foothill Dadhestan were scored for 8 pholidotic features and 22 characters of head scutellation. The occurrence of evident differences in the extent of the interpopulation variation was revealed: the latter is higher in *L. agilis* as compared with *L. strigata* from the same localities. Two factors are proposed to be responsible for this difference: a) gene flow among populations which seems to be more intense in *L. strigata* and b) developmental homeostasis which seems to be higher in *L. strigata* if compared with *L. agilis*.

Key words: lacertids, pholidosis, head scutellation, variability

The sand lizard, *Lacerta agilis*, and the Caspian green lizard, *L. strigata*, are closely related species belonging to the *Lacerta agilis* group (Arnold 1989). *L. agilis* is a widespread species whose range extends from southern England and the Pyrenees on the west to the Baikal lake on the east (Bischoff 1988), whereas *L. strigata* inhabits eastern Caucasus and adjacent parts of Turkey and Iran (Darevskii 1984). The two species, particularly *L. agilis*, have been used in a considerable number of microevolutionary studies (Yablokov et al. 1980; Zakharov 1987; Melkumyan 1987; Roytberg 1989, and many others) concerning different aspects of phenetic variation. In the eastern Caucasus *L. agilis* and *L. strigata* are broadly sympatric and often coexist in the same habitats (Roytberg 1982, and references therein), providing an opportunity to study comparative patterns of phenetic variation in two species in a coincident range of environmental conditions. Daghestan (east part of the North Caucasus) seems particularly promising for such studies due to its complicated relief and, therefore, considerable landscape/climatic heterogeneity within a small area. Moreover, *L. agilis* is represented here by a very peculiar subspecies, *L. a. boemica* whose coloration, scalation and body proportion features make it the most similar to other related species (*L. strigata*, *L. viridis*, etc.) and the most distinct phenetically, compared to the other subspecies of *L. agilis* (Darevsky et al. 1976; Roytberg 1987).

This report is aimed to compare quantitatively the extents of inter-population (microgeographic) variation in *L. agilis* and *L. strigata* within the area of their sympatry in Daghestan for age- and size-independent scalation characters. Some parameters of individual variability of scalation are also considered.

MATERIALS AND METHODS

Sampling

This report is based on examining 1042 specimens of *L. agilis* and *L. strigata* from seven localities in

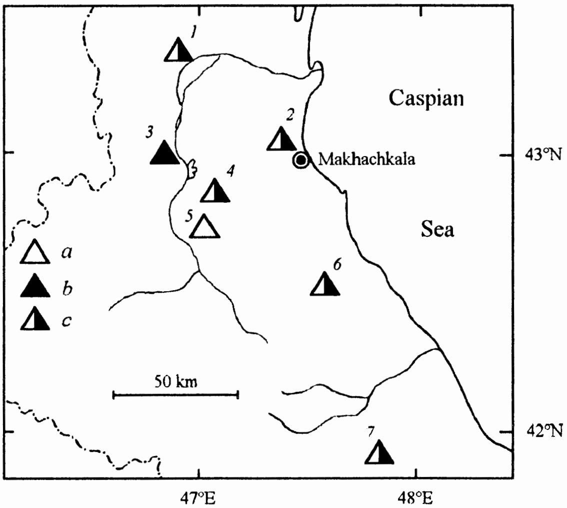

Fig. 1. Geographic relationships of localities from which samples of *Lacerta agilis boemica* and *L. strigata* were taken. *a*) A pure population of *L. a. boemica*; *b*) a pure population of *L. strigata*; *c*) sympatric populations of the two species.

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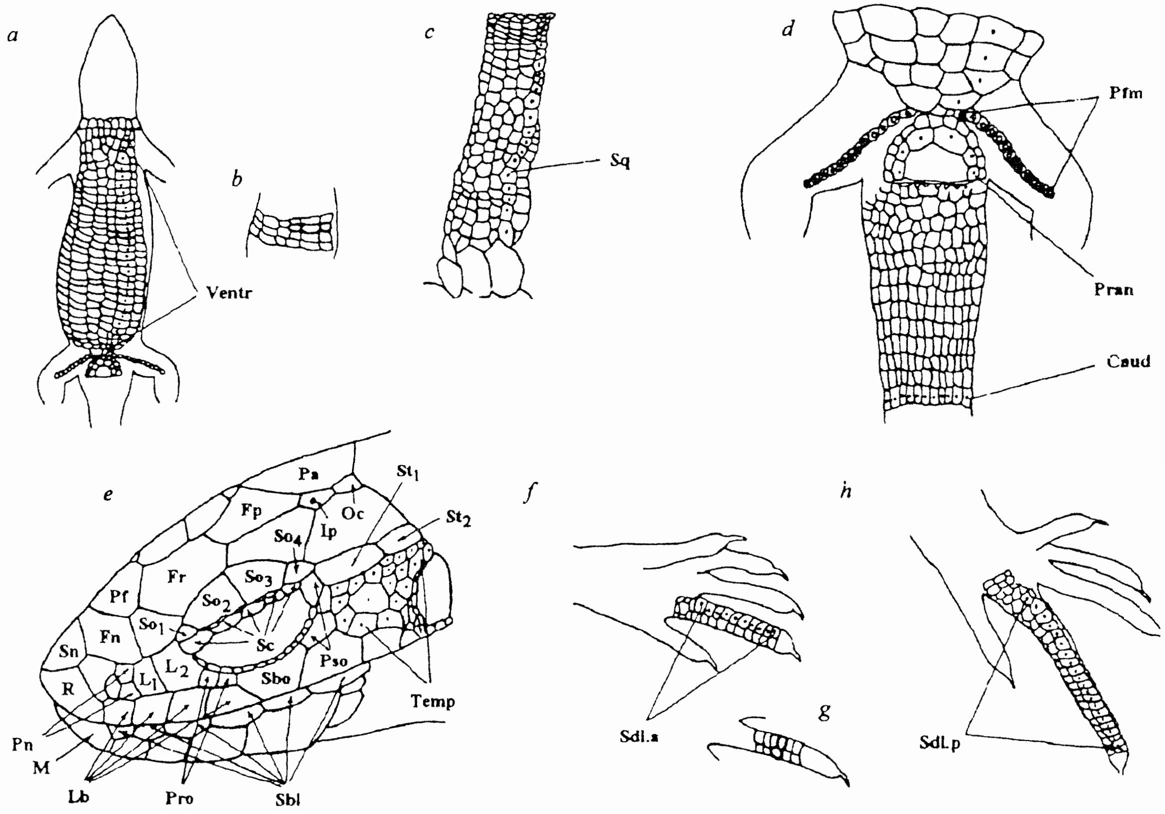

Fig. 2. Scalation of *Lacerta agilis boemica.* Dots indicate scalation elements which are to be counted as meristic characters. All characters are described in the text. Head shields: **Fn**) frontonasal, **Fp**) frontoparietal, **Fr**) frontal, **Ip**) interparietal, **L**) loreals, **Lb**) upper labials anteriorly the subocular, **M**) mental, **Oc**) occipital, **Pf**) prefrontal, **Pn**) postnasals, **Pro**) preocular, **Pso**) postoculars, **R**) rostral, **Sbl**) lower labials (sublabials), **Sbo**) subocular, **Sc**) superciliaries, **Sn**) supranasal, **So**) supraoculars, **St**) supratemporals. Shield names and their designations generally follow Salvador (1985), with some modifications and additions.

lowland and foothill Daghestan (Fig. 1, Table 1). In localities *1, 2, 6,* and *7* the two species occurred syntopically, both having a high density, and sampled from the same collection sites. In locality *4* the sampling site of *L. agilis* was some 2 km from that of *L. strigata,* because no plots with a high density of both species had been revealed. The populations (samples) from these five localities were considered as sympatrical. In addition, samples from a pure *L. agilis* population (locality *5*) and a pure *L. strigata* population (locality *3*) were used for some analyses, taking into account their geographical proximity to locality *4* as well as their relatively high altitudes.

On each sampling site all specimens were captured within an area of a few hectars or a few dozen hectars, and appear to belong to a single local population. All sampling occurred from 1979 to 1986, each local sample consisting of subsamples collected for at least two different years.

Characters

All specimens were scored for two sets of scalation characters. The first of them includes typical meristic characters with generally normal distribution. These are:

1. **An** — number of scales surrounding anteriorly the large anal shield (Fig. 2 *d*);
2. **Pfm** — number of femoral pores (Fig. 2 *d*);
3. **Ventr** — number of ventral scales in the left central longitudinal row from the fold to and including the first scale contacting femoral pores Fig. 2 *a, d*);
4. **Sq** — number of dorsal scales around midbody at the position of the ($n/2$)-th ventral transverse row, counting from the rear (n is the ventral scales number, if n was odd, the ($n/2 - 0.5$)-th ventral row was used) (Fig. 2 *c*);

5. **Caud** — number of scales around the tail in the 13th coil counting from the vent (Fig. 2 *d*);
6. **Sdl.a** — number of subdigital lamellae beneath the fourth toe of fore leg (Fig. 2 *f*);
7. **Sdl.p** — number of subdigital lamellae beneath the fourth toe of hind leg (Fig. 2 *h*);
8. **Temp** — number of temporals (after Peters (1962), but including the tympanicum) (Fig. 2 *e*).

These meristics were selected to provide a representative sample of the phenotype as reflected by pholidotic characters. They include most of meristic characters used by previous authors in studies of intraspecific taxonomy within *Lacerta* (Darevsky 1967; Orlova 1975; Peters 1964; Schmidtler 1975, 1986; Brown and Pérez-Mellado 1993; etc.).

The second character set, describing details of head scutellation pattern (Fig. 2 *e*), includes meristic characters with a small number of states (usually 2 or 3), one of which being often sharply predominant, and non-metric characters. These are:

9. **Pn + L** — number of postnasals and loreals;
10. **Pro** — number of preoculars;
11. **Lb** — number of upper labials (including additional shields) lying anteriorly the subocular;
12. **Sbl** — number of lower labials;
13. **Sc** — number of superciliaries;
14. **Tmp1** — minimal number of temporal shields between the first supratemporal and the ear opening;
15. **Tmp2** — minimal number of temporal shields between the second supratemporal and the ear opening;
16. **Fn-ad** — polymeric states (i.e., having more elements than in the typical pattern) of the frontonasal: 0 — absent, 1 — present;
17. **Pf-ad-Pf** — additional shield between the prefrontals: 0 — absent, 1 — present;
18. **Fp-ad-Fp** — additional shield(s) between the frontoparietals: 0 — absent, 1 — present;
19. **So_4-ad** — polymeric states of the fourth supraocular: 0 — absent, 1 — present;
20. **St_1-ad-St_2** — additional shield(s) between the first and second supratemporals: 0 — absent, 1 — present;
21. **Sbo-ad-Pso** — additional shield between the suboculars and the postoculars: 0 — absent, 1 — present;
22. **PnL//P** — pattern of the contact between the shields of the naso-loreal area and the shields of the pileus: 0 — the typical pattern (Fig. 2 *e*), 1 — upper postnasal contacts prefrontal, 3 — other patterns.

See Roytberg (1987, 1991) for fuller explanations and pictures of the variants of head scutellation in the species studied. Characters of this sort — called below multistate characters — have not been widely used in taxonomic studies, but they were successfully employed in microevolutionary research on *L. agilis* (Yablokov et al. 1980) to reveal the chorologic/phenetic structure of a population and of the whole species.

Characters 8, 14 — 17, 20 — 22 were recorded from the left side; other bilateral characters (2, 6, 7, 10 — 13) were taken from both sides, and total bilateral numbers were used.

In addition, two most frequent irregular deviations from the typical scalation pattern were recorded in each specimen: incomplete transverse rows in ventralia (Fig. 2 *b*) and in subdigital lamellae (Fig. 2 *g*).

Statistical Analysis

Coefficients of variation were calculated for each meristic character within the sex-locality samples to determine the amount of individual variation, and the frequency procedure was used for irregular deviations.

Also, for 22 characters a matrix of product-moment correlation coefficients (*r*) was calculated for each homogeneous (sex-locality-year) sample. Then for each species, the matrix of pooled within-locality correlation coefficients was obtained, using the procedure described by Thorpe (1979). In these pooled matrices, most of the correlation coefficients were less than 0.3, a few reached 0.3 to 0.4, and only the correlations between serially homologous meristics (**Sdl.a** and **Sdl.p**) lied within a range of 0.4 — 0.5. So a derived character (**Sdl**), which is the sum of **Sdl.a** and **Sdl.p**, was used in multivariate procedures.

Two multivariate techniques were employed to compare the patterns of microgeographic variation in the two species. Principal component analysis was used to

TABLE 1. Localities and sizes of samples of *Lacerta agilis boemica* and *L. strigata* used in this study. Numbers of localities as for Fig. 1.

Sample No.	Locality	Number of specimens			
		L. a. boemica		*L. strigata*	
		Males	Females	Males	Females
1.	Kostek	41	44	37	28
2.	Makhachkala	25	29	34	31
3.	Dubki	absent		34	39
4.	Buynaksk	61	68	39	34
5.	Termenlik	23	32	absent	
6.	Sergokala	79	72	63	79
7.	Khuchni	35	36	35	43
	In total	264	281	243	254

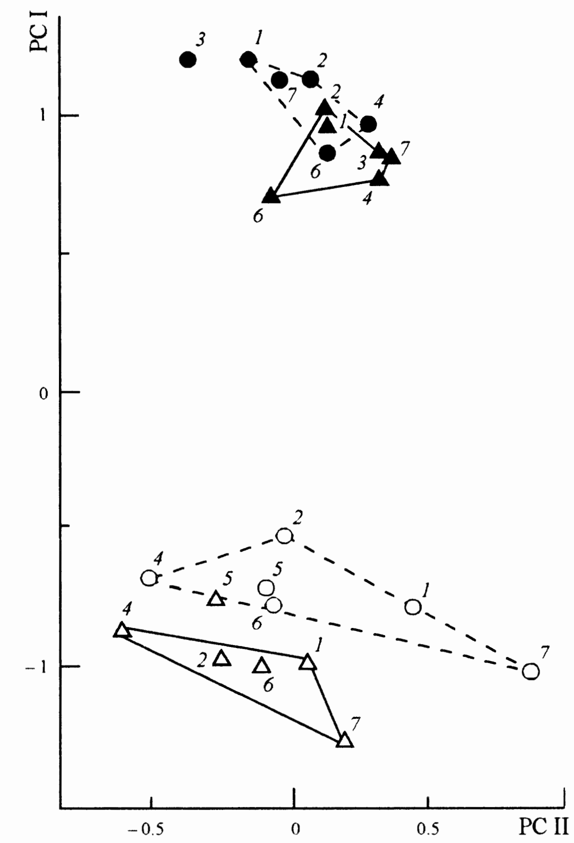

Fig. 3. Projections of population means for males and females on the first two principal components (PC I = 37%, PC II = 19%) of variation in 7 meristic characters for 1042 specimens of *Lacerta agilis boemica* and *L. strigata* from Daghestan. Open symbols indicate local populations of *L. agilis*, solid symbols indicate local populations of *L. strigata* (triangles for male samples, and circles for female samples). For sympatric populations of each species, the centroids of male samples are enclosed by a solid line, and those of female samples are enclosed by a dashed line. Numbers of localities as in Fig. 1.

ordinate various specimens and samples in a reduced morphological space. The components were extracted from a matrix of product-moment correlation coefficients between standardized character values of the 1042 specimens. To estimate more precisely the extent of generalized phenetic differences between the local populations, Euclidean distances (D^2) for each pair of locality samples within the species were calculated. Each multivariate procedure was performed on both character sets. Male and female locality samples were treated as separate OTUs to prevent possible effects of sex differences, detected in some characters, as well as to provide a replicate analysis.

TABLE 2. Coefficients of variation (in %) of 8 meristic scale characters in *Lacerta agilis boemica* and *L. strigata* from Daghestan. Each coefficient is the mean, value for 5 sympatric populations. Characters are described in the text.

Character	*L. a. boemica*		L. strigata	
	Males	Females	Males	Females
	$N = 218$	$N = 249$	$N = 209$	$N = 215$
1. **An**	15.75	13.81	10.58	8.75
2. **Pfm**	7.24	6.32	5.24	6.18
3. **Ventr**	3.60	3.33	3.34	3.18
4. **Sq**	4.71	4.65	4.52	4.64
5. **Caud**	4.66	5.04	4.52	4.50
6. **Sdl.a**	8.09	9.18	6.58	7.06
7. **Sdl.p**	4.50	4.22	4.56	4.48
8. **Temp**	21.18	19.78	19.38	18.84

TABLE 3. Frequencies (in %) of irregular deviations from the typical pattern of ventral and subdigital scalation in *Lacerta agilis boemica* and *L. strigata* from Daghestan. For each species, mean values for 5 sympatric populations are given.

Species	Sex	Location of irregular deviations	
		ventrals	subdigital lamellae
L. agilis	Males	46.4 ($N = 218$)	50.0 ($N = 203$)
	Females	48.8 ($N = 249$)	40.7 ($N = 236$)
L. strigata	Males	31.4 ($N = 209$)	25.1 ($N = 187$)
	Females	35.2 ($N = 215$)	28.6 ($N = 189$)

RESULTS

Individual Variation

Table 2 displays the coefficients of variation (CV) of eight meristics in *L. agilis* and *L. strigata*, averaged for five sympatric populations in each species. For 7 of 8 characters ($p < 0.05$ for the sign test) the CVs in *L. agilis* were higher than in *L. strigata*. Being expressed in both sexes, this tendency indicates a difference in the overall level of individual variability which is higher in *L. agilis* than in sympatric *L. strigata*.

Table 3 shows frequencies of two different deviations, disturbing the regular scalation pattern in the ventrals and subdigital lamellae. These data indicate that for both kinds of deviations, in both sexes, *L. agilis* consistently has higher frequencies than sympatric *L. strigata*.

TABLE 4. Factor loadings and percents of trace associated with the first four principal components of variation in 7 meristic characters for 1042 specimens of *Lacerta agilis boemica* and *L. strigata* from Daghestan. Characters are described in the text.

Character		PC I	PC II	PC III	PC IV
1.	**An**	0.776	0.104	0.049	–0.123
2.	**Pfm**	0.667	0.413	–0.382	0.124
3.	**Ventr**	0.249	0.203	0.803	0.476
4.	**Sq**	–0.729	0.447	–0.149	–0.081
5.	**Caud**	–0.545	0.476	–0.292	0.497
6.	**Sdl**	0.794	0.301	–0.278	0.086
7.	**Temp**	–0.080	0.764	0.364	–0.472
Accumulated percent of trace		36.8	18.9	15.9	10.6

Interlocality Variation

Principal component analyses. Ordination of centroids of the male and female locality samples of *L. agilis* and *L. strigata* in the space of the first four principal components of variation in the 7 meristic characters is shown in Fig. 2 and Fig. 3. The associated factor loadings and percents of trace are shown in Table 4. PC I, accounting for 36.8% of the total variation, mainly reflects the differences between species. Inter-locality variation along this axis is rather small, so that sample centroids of *L. agilis* are markedly different from those of *L. strigata* (Fig. 3). In both species, there are also some sex differences along PC I. PC I is strongly associated with **Sdl**, **An**, and **Pfm** (positively) as well as with **Sq** and **Caud** (negatively). As for **Ventr** and **Temp**, their loadings on PC I are very small (Table 4).

PC II (18.9%) reflects inter-population variation within each species. The extent of this variation in *L. agilis* is larger than in *L. strigata*, especially for females (Fig. 3). *L. agilis* also shows weak sex differences along this axis. PC II is positively correlated with all 7 meristics and therefore can be interpreted as a factor ordinating specimens and samples on the basis of increasing scale numbers, i.e., a factor of overall polymerization. **Temp** has the heaviest loading on PC II which is much larger than those of the other characters (Table 4).

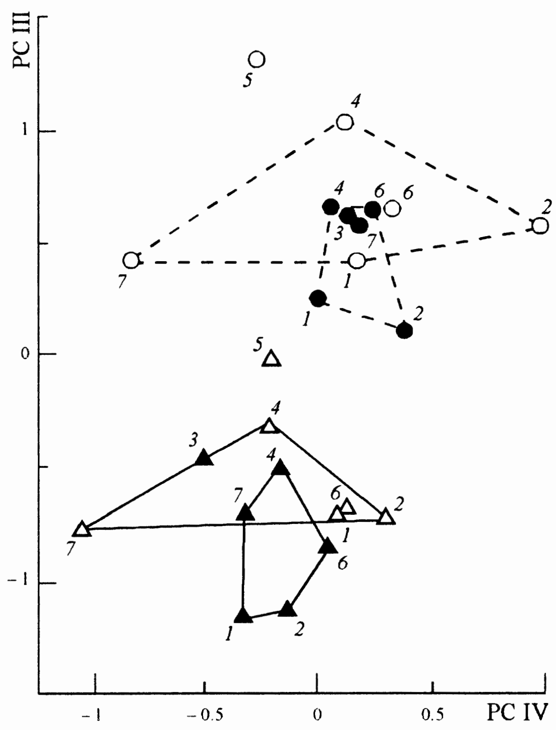

Fig. 4. Projections of population means for males and females on the third and fourth principal components (PC I = 16%, PC II = 11%) of variation in 7 meristic characters for 1042 specimens of *Lacerta agilis boemica* and *L. strigata* from Daghestan. All designations as in Fig. 3.

TABLE 5. Factor loadings and percents of trace associated with the first two principal components of variation in 14 multistate characters for 1042 specimens of *Lacerta agilis boemica* and *L. strigata* from Daghestan. Characters are described in the text.

Character		PC I	PC II	Character		PC I	PC II
9.	**Pn + L**	0.776	0.104	16.	**Fn-ad**	0.089	0.257
10.	**Pro**	–0.719	0.231	17.	**Pf-ad-Pf**	0.512	0.257
11.	**Lb**	0.058	0.402	18.	**Fp-ad-Fp**	–0.301	0.203
12.	**Sbl**	0.363	0.283	19.	**So$_4$-ad**	0.404	0.166
13.	**Sc**	–0.299	0.460	20.	**St$_1$-ad-St$_2$**	–0.285	0.467
14.	**Tmp1**	0.029	0.643	21.	**Sbo-ad-Pso**	0.561	0.030
15.	**Tmp2**	0.236	0.581	22.	**PnL//Pil**	–0.407	0.113
				Percent of trace		13.8	12.2

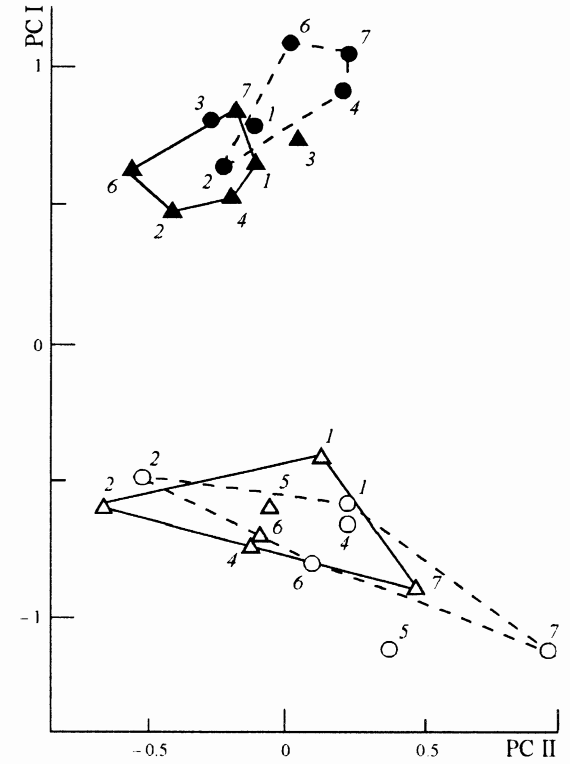

Fig. 5. Projections of population means for males and females on the first two principal components (PC I = 14%, PC II = 12%) of variation in 14 multistate characters for 1042 specimens of *Lacerta agilis boemica* and *L. strigata* from Daghestan. All designations as in Fig. 3.

PC III (15.9%) reflects primarily the sex differences in both species. There is also some inter-population variation along PC III. In *L. strigata* the centroids of the lowland samples (*1*, *2*) are separated from those of the foothill samples (*3*, *4*, *6*, *7*) in both sexes (Fig. 4). Somewhat similar separation appears to take place in *L. agilis* too, but in this species it goes partly along PC IV (10.6%), and in both sexes the centroids of foothill sample 13 are placed near those of the lowland samples. The extent of population differentiation in the two species does not differ markedly along PC III, being substantially higher in *L. agilis* along PC IV (Fig. 4). PC III is very strongly positively associated with **Ventr**, other characters having minor loadings. PC IV has its highest correlations with **Ventr** and **Caud** (positive), and with **Temp** (negative) (Table 4).

Results of the principal component analysis for 14 multistate characters are shown in Fig. 5 and Table 5. As in the case of meristic characters, PC I sharply separates sample centroids of *L. agilis* from those of *L. strigata*, and PC II displays substantial interlocality differences in *L. agilis*, which are clearly larger than in *L. strigata*. These results are, however, not so informative as those for meristic characters because PC I and PC II explain only 13.8% and 12.2% of the total variation, respectively.

Analyses of Euclidean distances. Matrices of Euclidean distances between centroids of locality samples (males and females separately) within *L. agilis* and *L. strigata* on 7 meristic characters are given in Table 6. The corresponding matrices of Euclidean distances based on 14 multistate characters are presented in Table 7. Pairwise comparisons of inter-population phenetic distances in *L. agilis* and *L. strigata* from the same pairs of localities (only sympatric populations were considered) show the following results.

For meristic characters, interlocality phenetic (Euclidean) distances in *L. agilis* are greater than in *L. strigata* for 8 of 10 pairwise comparisons in males and females. Thus, in total, *L. agilis* exhibits larger interlocality differences in 16 of 20 comparisons ($p < 0.01$ for the sign test). For females this tendency is also significant ($p < 0.01$) for the Wilkoxon pairwise test.

Analogous comparisons of Euclidean distances based on the multistate characters show the same tendency: inter-population distances of *L. agilis* exceed those of *L. strigata* in 7 of 10 comparisons in males, and in 8 of 10 comparisons in females (in total, 15 of 20 cases giving $p < 0.01$ for the sign test). In each sex this tendency is significant ($p < 0.05$) for the Wilkoxon pairwise test.

To summarize, the results of both multivariate analyses for both character sets corroborate the conclusion that *L. agilis* exhibits greater population differentiation than *L. strigata* taken from the same localities.

DISCUSSION

Higher variation coefficients of nearly all the meristics studied found in *L. agilis*, compared with sympatric *L. strigata* together with higher frequencies of two different deviations, disturbing the regular scalation pattern, in the former species are in good concordance with Zakharov's (1987) inference that the two taxa differ in the level of developmental homeostasis. This inference was based on comparing the levels of fluctuating asymmetry in bilateral scalation characters which were in general higher in *L. agilis* than in *L. strigata* (Zakharov 1987) (the material used in that study was from localities *2* and *6*).

The principal conclusion of this study is that *L. agilis* and *L. strigata* in an area of their sympatry in the eastern North Caucasus differ clearly in the extents

TABLE 6. Matrices of generalized Euclidean distances (D^2) between centroids of locality samples within *Lacerta agilis boemica* (*a*) and within *L. strigata* (*b*) from Daghestan, based on the 8 meristic scalation characters. Elements above the principal diagonal are distances between male samples; those below the principal diagonal are distances between female samples. Numbers of localities as in Fig. 1 and Table 1.

(*a*) Localities (samples)	1	2	4	5	6	7
1	—	6.60	9.08	10.84	2.86	9.60
2	7.20	—	11.95	15.43	7.32	14.21
4	13.21	13.21	—	6.42	7.01	12.20
5	12.15	13.80	5.38	—	9.80	13.42
6	7.08	8.29	6.60	7.12	—	10.12
7	10.83	16.51	16.59	13.33	12.33	—

(*b*) Localities (samples)	1	2	3	5	6	7
1	—	2.89	8.16	8.12	7.28	6.19
2	3.73	—	8.36	9.81	8.34	6.21
3	5.89	6.07	—	6.25	6.08	4.50
5	5.56	7.54	7.10	—	6.71	6.48
6	8.76	8.89	5.59	8.38	—	6.50
7	6.04	6.38	5.48	4.26	6.34	—

TABLE 7. Matrices of generalized Euclidean distances (D^2) between centroids of locality samples within *Lacerta agilis boemica* (*a*) and within *L. strigata* (*b*) from Daghestan, based on the 14 multistate scalation characters. All designations as in Table 5.

(*a*) Localities (samples)	1	2	4	5	6	7
1	—	6.74	5.67	6.36	4.39	8.11
2	6.68	—	6.40	6.80	5.08	10.10
4	4.66	6.72	—	4.66	4.12	7.43
5	9.33	12.23	8.62	—	5.89	8.52
6	4.69	5.69	3.43	9.44	—	7.08
7	9.67	12.03	8.03	10.63	7.99	—

(*b*) Localities (samples)	1	2	3	5	6	7
1	—	5.09	6.67	4.53	5.96	4.32
2	4.21	—	4.27	4.55	3.20	4.30
3	6.05	6.08	—	5.04	4.90	5.48
5	4.08	4.87	6.87	—	5.60	5.64
6	3.32	4.24	4.47	3.56	—	4.17
7	4.66	5.33	4.86	5.99	3.69	—

of inter-population (microgeographic) variation, which is higher in *L. agilis* as compared with *L. strigata* from the same localities. Two factors potentially responsible for this difference have been proposed (Roytberg 1989). 1. Gene flow among the populations may have been more intense in *L. strigata* as it is more widely distributed and in general more abundant in the study area (especially in its lowland portion) than *L. agilis*. The role of gene flow as a factor impeding population differentiation has been repeatedly discussed in literature. Mayr (1970) and Dobzhansky (1970) regarded its role as very substantial. This theoretical viewpoint was subsequently challenged (Ehrlich and Raven 1969; Endler 1977) and supported again (Jackson and Pounds, 1979; Grant 1985). Anyhow, in a number of elaborate studies on different tetrapod species (Metter and Pauken 1969; Rees 1970; Vasiliev 1984), including lizards (Pounds and Jackson 1981) effect of gene flow on phenetic differentiation of populations has been demonstrated rather clearly. 2. Developmental homeostasis, also known to impede phenetic differentiation (Mayr 1970; Schmalhausen 1969) should be higher in *L. strigata*, compared with *L. agilis*, as deduced from the analysis of their individual variability (see above).

To my knowledge, there are very few papers on Squamata aimed to compare extents of morphological variation in two (or more) related species. A combination of relatively high levels of intrapopulational and microgeographic variation for most of scalation and mensural characters appears to characterize a lacertid, *Podarcis hispanica* as compared with *P. muralis*, studied in several areas of Spain (Gosá et al. 1986; Martinez Rica and Laplaza 1988). Although the latter study dealt with non-sympatric populations of the two species, the situation seems quite similar to that in *L. agilis* and *L. strigata*, arguing indirectly in favor of the intrinsic (developmental) factor to be responsible for the difference in the extent of population differentiation. Zweifel (1965) reported on sharp differences in the degree of individual variability for a few scalation characters between two sympatric tepid lizards, *Cnemidophorus tigris* and *C. tesselatus*, a lower variation of the latter species was attributed to a reduced level of genic recombinations due to its parthenogenesis. Thorpe (1985), using multivariate analyses of 47 scalation and body proportion characters, compared the extents of microgeographic (inter-island) variation in lacertids, *Gallotia galloti* and *G. atlantica* inhabiting two different island groups of the Canary Islands. A relatively low level of this variation found in the latter species he explained by a more recent origin (insulation) of respective islands, i.e., by historical factors. Extents of individual variability were not considered in that study.

Recurring to the analysis of the situation with *L. agilis* and *L. strigata*, it should be noted that the two species differ clearly in the extent to which subspecies are recognized. While *L. strigata* has no trinomials, *L. agilis* has nine subspecies, of which four (*L. a. exigua*, *L. a. brevicaudata*, *L. a. iorensis*, *L. a. boemica*) are within the area of sympatry with *L. strigata*. The Caucasus is regarded as the center of origin and dispersal of *L. agilis*, its subspecific differentiation being attributed to the isolation of various population stocks during the glacial period and their microevolutionary adaptations to different climates (Darevsky et al. 1976; Yablokov et al 1980; Bischoff 1988). If so, lack of such a strong differentiation in *L. strigata* should imply that its evolutionary origin or, at least its dispersal occured more recently than in *L. agilis*. However, the fact that a lower extent of phenetic differentiation of *L. strigata* is manifested at both micro- and macro-geographical levels appears to argue that not only historical but also "developmental" factors may be involved. Additional comparative data from other portions of the area of the sympatry are necessary for adequate solution of this interesting problem.

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