PHENETIC RELATIONSHIPS BETWEEN
Lacerta caucasica, L. daghestanica AND *L. praticola*
(REPTILIA, LACERTIDAE): A MULTIVARIATE
TREND IN EXTERNAL MORPHOLOGY

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Roitberg, E. S.: **Phenetic relationships between** *Lacerta caucasica, L. daghestanica* **and** *L. praticola* **(Reptilia, Lacertidae): a multivariate trend in external morphology. Nat. Croat., Vol. 8, No. 3., 189–200, 1999, Zagreb.**

Based on 270 specimens from 7 populations of *Lacerta alpina, L. caucasica, L. daghestanica* and *L. praticola*, morphological relationships between the four species were studied for 7 meristic characters and 5 morphometric characters, using canonical variate analysis. In both scalation and morphometry, the contours and centroids of the studied populations form a trend: *L. praticola – L. caucasica – L. daghestanica*, which represents the main direction of phenetic differentiation between the studied taxa (60–80% of the total among-group variation). Possible factors, determining this trend, as well as the problem of evolutionary polarity in the morphological series of the three species are discussed.

Keywords: Squamata: Lacertidae: *Lacerta caucasica, Lacerta daghestanica, Lacerta praticola*, morphological variation

Roitberg, E. S.: **Fenetički odnosi između** *Lacerta caucasica, L. daghestanica* **i** *L. praticola* **(Reptilia, Lacertidae): multivarijantni trend u vanjskoj morfologiji. Nat. Croat., Vol. 8, No. 3., 189–200, 1999, Zagreb.**

Na temelju 270 primjeraka iz 7 populacija *Lacerta alpina, L. caucasica, L. daghestanica* i *L. praticola* proučavani su morfološki odnosi između četiri vrste, i to s obzirom na 7 merističkih vrijednosti i 5 morfometrijskih vrijednosti, koristeći kanonsku varijantnu analizu. I usporedba i morfometrija pokazale su da obrisi i centroidi proučavanih populacija čine trend: *L. praticola – L. caucasica – L. daghestanica*, koji predstavlja glavni pravac fenetičke diferencijacije među proučavanim svojtama (60–80 % sveukupne varijacije unutar grupe). Raspravlja se o mogućim činiteljima koji određuju taj trend, kao i problem evolucijskog polariteta u morfološkim serijama te tri vrste.

Keywords: Squamata: Lacertidae: *Lacerta caucasica, Lacerta daghestanica, Lacerta praticola*, morfološke varijacije

INTRODUCTION

Lacerta caucasica sensu lato (=*L. caucasica* complex) belongs to the group of Caucasian rock lizards called the *Lacerta saxicola* group (DAREVSKY, 1967; ARNOLD, 1989). It is distributed over the Great Caucasus and includes three taxa: *alpina*, the nominate *caucasica* and *daghestanica* (DAREVSKIJ, 1984; see also Fig. 1 in ROITBERG, 1994). Previously the three forms have been regarded as subspecies, with their possible specific status being only hypothesized (DAREVSKIJ, 1984; BÖHME, 1984). Later on, special morphological investigations demonstrated that *caucasica* and *daghestanica* can occur in sympatry without apparent intergradation (ROYTBERG & LOTIEV, 1992; ROITBERG, 1994), and recently, specific status for all three taxa has been confirmed by electrophoretic studies (FU *et al.*, 1995).

A preliminary phylogenetic analysis of electrophoretic data on 12 bisexual species of Caucasian rock lizards (MURPHY *et al.*, 1996) also demonstrated that a ground-dwelling lizard, *Lacerta praticola*, is not only related to the clade of rock lizards – as was stated earlier (ARNOLD, 1989; MAYER & LUTZ, 1989), but occupies a position within this clade as a sister group of the *Lacerta caucasica* complex. A close relatedness of *L. praticola* to the *L. caucasica* complex was also shown by a DNA taxoprint analysis (GRECHKO *et al.*, 1998; but see FU et al., 1997). These findings stimulate additional interest in the striking morphological similarity between *L. caucasica* (*s.str.*) and *L. praticola* (ROYTBERG & LOTIEV, 1992).

In this paper, morphological relationships among *L. praticola* and the three taxa of the *L. caucasica* complex are studied using multivariate statistical procedures.

MATERIAL AND METHODS

270 specimens from 7 populations of four taxa were used in this study (Tab. 1). This material was examined for 7 meristic characters and 6 morphometric characters, most of which are traditionally used in studies on morphological differentiation in *Lacerta* (DAREVSKY, 1967; PEREZ-MELLADO *et al.*, 1993; ARRIBAS, 1993a, b, etc.).

The meristic characters were the number of praeanalia (=circumanalia) (**Pran**), femoralia (**Pfm**), ventralia (**Ventr**), dorsalia around midbody (**Sq**), superciliary granulae (**Gran**), temporalia between the 1st supratemporal scale and the ear opening (**Tmp2**) and supratemporalia (**St**). Body dimensions were snout-vent length (**SVL**), hind leg length (**HLL**), pileus length (**PL**), pileus width (**PW**), head height (**HH**), and partial head height (**HH2**). See ROITBERG (1994, 1999) for details of recording the above mentioned characters.

The main statistical method was a canonical variate analysis (CVA), that is a linear discriminant function analysis used as an exploratory ordination (rather than

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[1] Although it was shown that this and some other groups within *Lacerta* s. l. deserve a generic status (MAYER & BISCHOFF, 1996 and references therein), I use here for the studied species the traditional generic name *Lacerta* as the new nomenclature is not yet finally established (MAYER & BENYR, 1994). Recently HARRIS *et al.* (1998) erected the nominal subgenus *Caucasilacerta* to accomodate the *L. saxicola* group.

Tab. 1. Samples of four *Lacerta* species used in this study

Species	Subspecies	Sample code	Locality	Sample size	Males Females
L. alpina		a1	Achishkho Mount, Krasnodar region (NW North Caucasus)	6	8
L. caucasica	*vedenica**	c1	Khorachoi, SE Chechen Republic (SE North Caucasus)	22	22
	caucasica	c2	Khvarshi, W Daghestan (SE North Caucasus)	15	20
L. daghestanica		d1	the same locality as for c1	13	15
		d2	the same locality as for c2	30	29
L. praticola	*pontica*	p1	Novorossiisk, Krasnodar region (NW North Caucasus)	15	3
	praticola	p2	Grosny, Chechen Republic (SE North Caucasus)	40	32

* description of this taxon see in DAREVSKY & ROITBERG (in press).

classification) procedure (JAMES & MACCULLOCH, 1990). The seven samples of the studied four species formed 7 a priori groups. A separate analysis was conducted for each set of characters (scalation and morphometry) and for each sex.

CVAs of the morphometric characters were performed using 5 ratios of the six body dimensions (Tab. 3). Such ratios help in removing a large proportion of variation exclusively due to size and have been applied in a number of studies with similar research design (CUNDALL & ROSSMAN, 1984; DWYER & KAISER, 1997). To further diminish size-dependent variation, young specimens with **SVL** < 43 mm were not included in these CVA analyses.

Taking into account that the use of ratios has been controversial in biometric studies (e.g., ATCHLEY & ANDERSON, 1978 and other papers in that issue of *Syst. Zool.*; MOSIMANN & JAMES, 1979), I also examined the body shape differences between the studied populations by one-way analysis of covariance (ANCOVA), in which log-transformed (base e) dimensions were used. The adjusted means of **HLL** and **PL** (with **SVL** as the covariate); **PW**, **HH** and **HH2** (with **PL** as the covariate) were then subjected to a principal component analysis (PCA) based on the variance-covariance matrix.

RESULTS

Fig. 1 presents the results of CVA of male samples for scalation characters. As can be seen from the plot, phenetic relationships between *L. daghestanica*, *L. caucasica* and *L. praticola* form a trend, so that in the morphospace of scalation the characters that distinguish *L. caucasica* from *L. daghestanica* are further developed in the
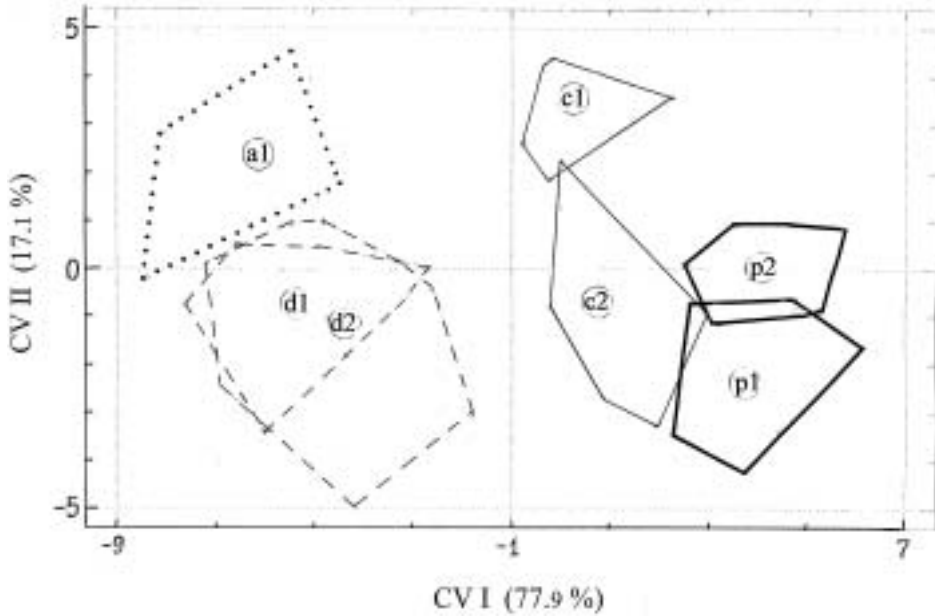
Fig. 1. Polygon boundaries and sample centroids of seven *Lacerta* populations
in a canonical variate analysis for 7 meristic characters. Males.
a1 – *L. alpina*; c1, c2 – *L. caucasica*; d1, d2 – *L. daghestanica*; p1, p2 – *L. praticola.*

same direction in *L. praticola*. This trend occurs along the 1-st canonical variate
which includes nearly 80% of the total among-group variation (Fig. 1). This axis re-
flects an increase in the number of **Pran** and a pronounced decrease of all other
meristic counts – **Sq**, **Pfm**, **Tmp2**, etc (Tab. 2). We can therefore designate this ca-
nonical axis as a factor of overall level of pholidotic fragmentation. Indeed, *L. cauca-*

Tab. 2. Standardized coefficients of the first two canonical variates of canonical variate
analyses for 7 scalation characters. Samples of *Lacerta alpina* (1), *L. caucasica* (2), *L. daghes-
tanica* (2) and *L. praticola* (2) form 7 a priori groups.

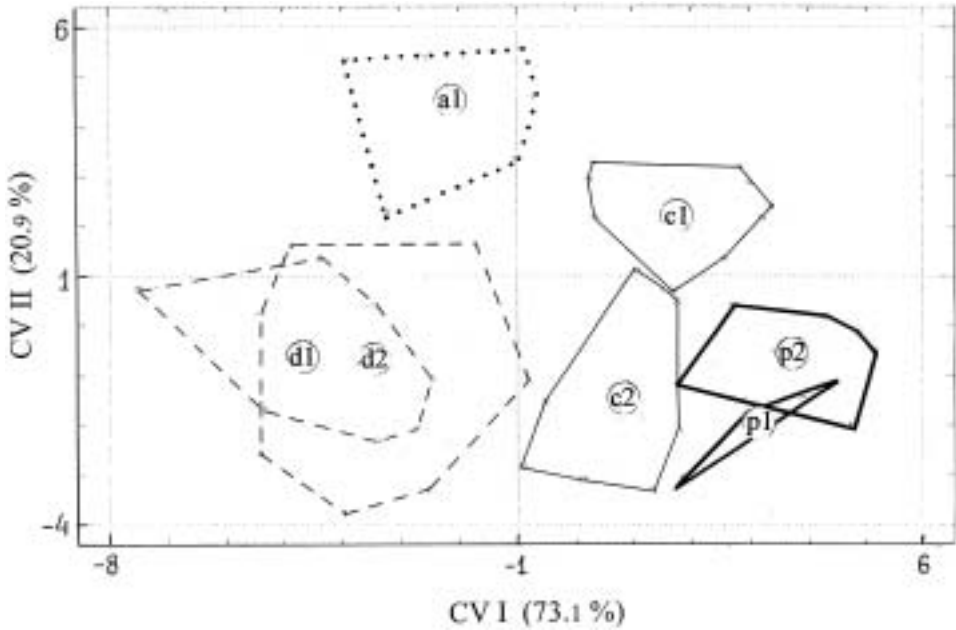| Variables	Males		Females	
(characters)	CV 1	CV 2	CV 1	CV 2
Pran	–0.08	–0.27	–0.32	–0.08
Pfm	0.56	–0.35	0.41	–0.43
Ventr	–0.01	0.10	0.05	0.24
Sq	0.53	–0.14	0.45	–0.41
Gran	0.15	0.92	0.42	0.77
Tmp2	0.36	–0.10	0.18	0.15
St	0.19	–0.15	0.32	–0.09
% variance summarized	77.90	17.05	73.07	20.87

Fig. 2. Polygon boundaries and sample centroids of seven *Lacerta* populations
in a canonical variate analysis for 7 meristic characters. Females.
a1 – *L. alpina*; c1, c2 – *L. caucasica*; d1, d2 – *L. daghestanica*; p1, p2 – *L. praticola.*

sica, and *L. praticola* even more so, has lower scale numbers in different meristic
rows, than *L. daghestanica*. The only exception is the number of **Pran**.

The 2nd canonical axis tends to separate the sample of *L. alpina* from the samples
of *L. daghestanica* (the two taxa exhibit a strong overlap along the 1st axis), and to dif-
ferentiate between conspecific populations within *L. caucasica* and within *L. praticola*
(Fig. 1). In both species, two populations represent different subspecies (Tab. 1).

Tab. 3. Standardized coefficients of the first two canonical variates of canonical variate
analyses for 5 ratios of body dimensions. Samples of *Lacerta alpina* (1), *L. caucasica* (2), *L.
daghestanica* (2) and *L. praticola* (2) form 7 a priori groups.

Variables	Males		Females	
(characters)	CV 1	CV 2	CV 1	CV 2
HLL / SVL	–0.44	–0.28	0.77	0.50
PL / SVL	0.84	0.90	–0.28	0.56
PW / PL	0.03	–0.01	–0.46	0.20
HH / PL	1.03	0.20	–0.20	0.04
HH2 / PL	0.27	–0.61	–0.34	0.58
% variance summarized	76.3	13.3	59.2	23.1

The corresponding CVA for females (Fig. 2, Tab. 2) also exhibits the considered trend: *daghestanica – caucasica – praticola*.

The CVAs for 5 ratios show that the morphometric relationships between the studied taxa exhibit the same trend: *daghestanica – caucasica – praticola*, as was found in scalation, but with a weaker separation between species (Fig. 3 and 4). PCA for the adjusted means of the corresponding (log-transformed) dimensions has con-
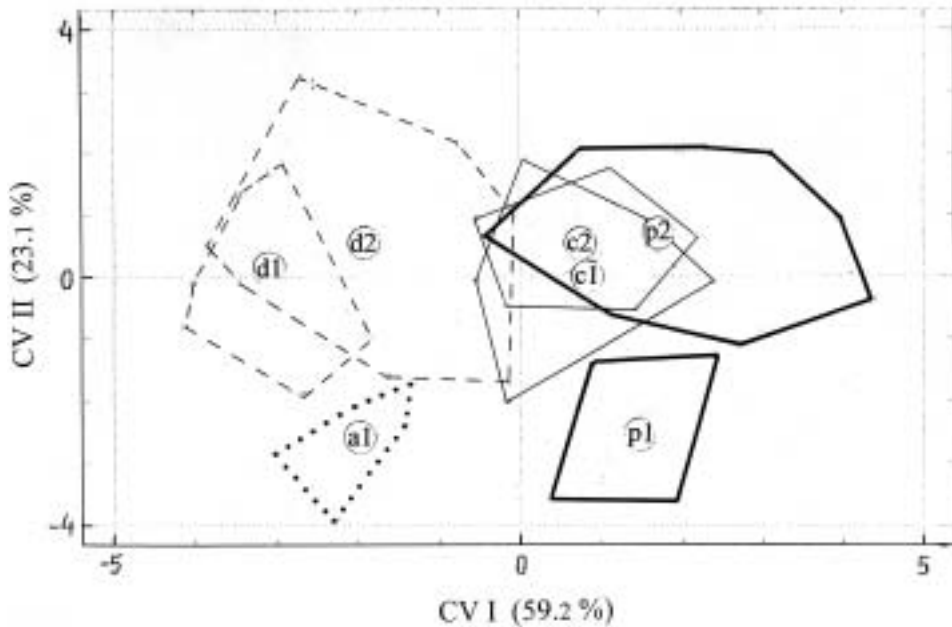

Fig. 3. Polygon boundaries and sample centroids of seven *Lacerta* populations in a canonical variate analysis for 5 ratios of body dimensions. Males.
a1 – *L. alpina*; c1, c2 – *L. caucasica*; d1, d2 – *L. daghestanica*; p1, p2 – *L. praticola*.

firmed this trend, at least for males (Fig. 5, a). In females, PCA also showed a similar pattern of relationships among the four species, but without any differences between *caucasica* and *praticola* (Fig. 5, b).

One more interesting result can be extracted from both analyses of the morphometric data. In males, the sample *L. alpina* shows a strong overlap with the samples of *L. daghestanica* (but not with *L. caucasica* and *L. praticola*) along the 1st axes, being separated from them only along the 2nd axes. A similar position was occupied by *L. alpina* in the morphospace of scalation (Fig. 1).

In males the 1st canonical axis of ratios and the 1st principal component of the adjusted means of dimensions can be described as a contrast between relative leg length and head height (Tab. 3 and 4). This reflects a difference between the »rock-

Tab. 4. Factor loading and percent of trace associated with first two principal components extracted from variance-covariance matrices between size-adjusted sample means of 5 body dimensions in seven samples of *Lacerta alpina*, *L. caucasica*, *L. daghestanica* and *L. praticola*.

Variables (characters)	Males		Females	
	PC 1	PC 2	PC 1	PC 2
HLL (adjusted for **SVL**)	−0.56	0.63	−0.10	0.71
PL (adjusted for **SVL**)	−0.25	0.42	0.03	0.57
PW (adjusted for **PL**)	0.26	0.33	0.29	0.38
HH (adjusted for **PL**)	0.55	0.20	0.69	−0.12
HH2 (adjusted for **PL**)	0.50	0.52	0.66	0.09
percent of trace	77.0	18.2	50.3	38.2

lizard habitus« of *daghestanica* (long legs and flattened head) and »*vivipara*-like habitus« of *caucasica* and *praticola* (relatively short legs and robust head).

In females, only head height contributes substantially to the differences along the first axes of CVA and PCA (Tab. 3 and 4).
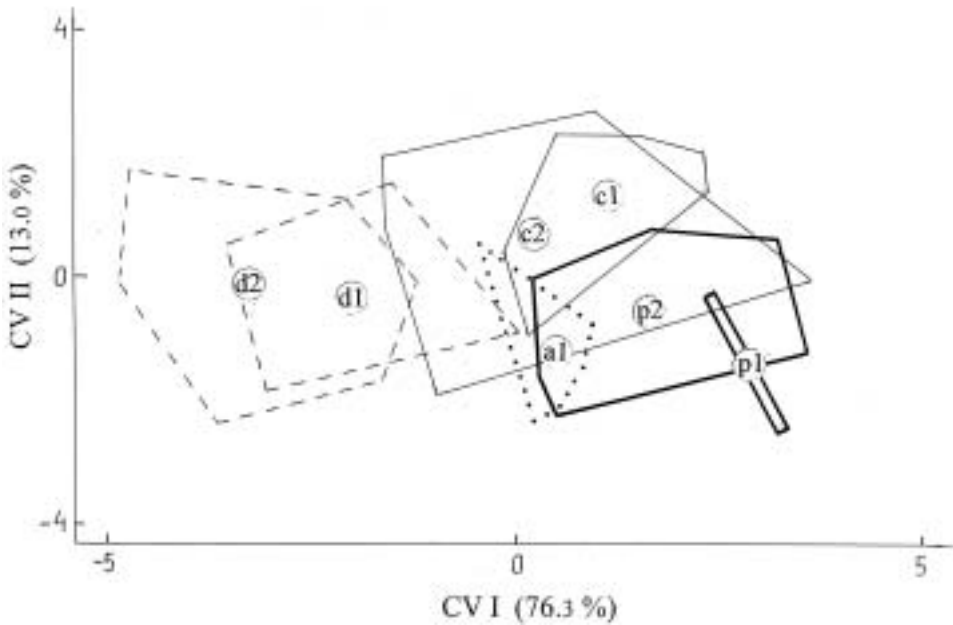

Fig. 4. Polygon boundaries and sample centroids of seven *Lacerta* populations in a canonical variate analysis for 5 ratios of body dimension. Females.
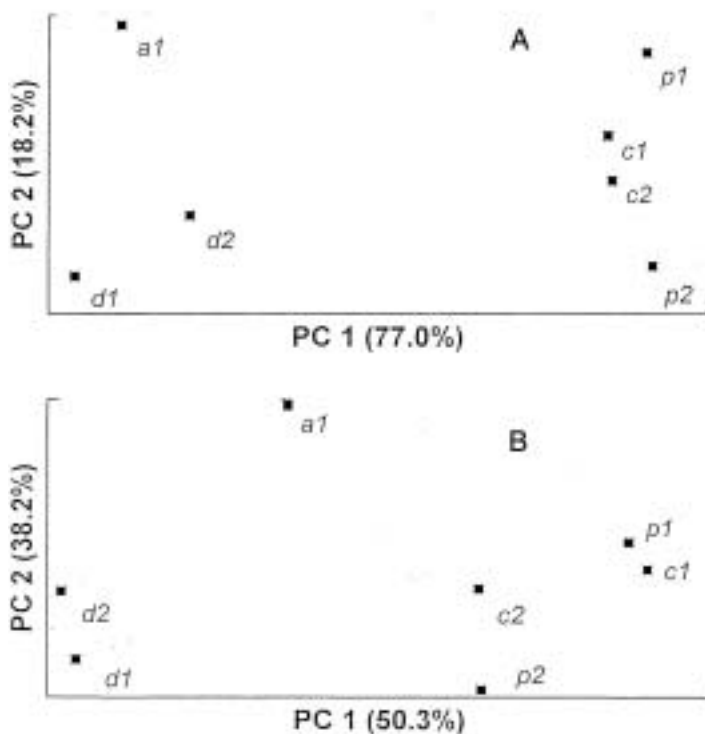a1 – *L. alpina*; c1, c2 – *L. caucasica*; d1, d2 – *L. daghestanica*; p1, p2 – *L. praticola*.

Fig. 5. Plot of scores of the first two principal components extracted from variance-covariance matrices between size-adjusted sample means of 5 body dimensions in seven samples of *Lacerta alpina* (a1), *L. caucasica* (c1, c2), *L. daghestanica* (d1, d2) and *L. praticola* (p1, p2). A- males, B- females.

A qualitative examination of interspecific differences in colouration also demonstrates good correspondence with the considered trend: the rather diffused dorsal pattern of *daghestanica* can be contrasted to the clear, regular pattern of *caucasica* (ROITBERG, 1999) and *praticola*.

DISCUSSION

Thus in the series of related *Lacerta* species, *daghestanica – caucasica – praticola*, the external morphology exhibits a pronounced trend involving many traits of scalation, body proportions and colour pattern. The morphometric component of the considered trend can be easily attributed to ecology: *L. daghestanica* is a rock species, *L. caucasica* is a partly rocky, partly ground-dwelling form, and *L. praticola* is a ground-dwelling lizard. A habitus with short legs and deep (not flattened) head – the so-called »*vivipara*-like habitus« – was repeatedly described for species and populations of archaeolacertas which exhibit a shift to ground-dwelling habits

(DAREVSKY, 1967; PEREZ-MELLADO, 1982; ARRIBAS, 1993a. But see VAN DAMME *et al.*, 1997).

It is more difficult to ascribe a directly adaptive significance to the meristic component of the considered trend expressed in differences between *daghestanica*, *caucasica* and *praticola* in the overall level of pholidotic fragmentation. Hypotheses proposed to relate the number of body scales – which is inversely proportional to scale size – to the heat exchange and cutaneous evaporation capacities (e.g., SOULE & KERFOOT, 1972) seem questionable, because patterns of geographic correlations of meristic scale characters with climatic parameters can be quite different even in related species (HORTON, 1972; ROITBERG, 1989; BROWN *et al.*, 1993).

Following HORTON (1972) we can, however, suppose that such geographic (and sometimes interspecific) changes in scale numbers, being nearly neutral in themselves, can manifest a pleiotropic effect involved in physiological adaptation.

According to ARNOLD (1973), fine, smooth dorsal scales can be an adaptation to rock-dwelling life, allowing animals to move easily in narrow crevices, while relatively large, convex dorsal scales help to protect the body when moving through dense vegetation. A corresponding tendency of association between external morphology and habitat preferences among *Lacerta* species was also mentioned (*op. cit.*, p. 320–323). Even so, the question remains of why so many pholidotic structures (dorsal scales, superciliary granules, femoral scales, etc.) change in the considered series in the same direction – towards low counts, if from *daghestanica* to *praticola.*

I suggest that this pattern of interspecific differences is at least partly determined by developmental constraints (sensu ALBERCH, 1980; MAYNARD SMITH *et al.*, 1985), that is by intrinsic factors of scalation morphogenesis. If so, we should find a similar pattern of differences between individuals within populations. My intensive study of correlations between meristic characters in a large number of homogenous samples of *Lacerta agilis*, *L. strigata* and *L. daghestanica* (ROITBERG, 1989, 1992 and unpubl.) showed, that although these correlations are quite low ($r < 0.3$–0.4), they exhibit a regularity: nearly all statistically significant correlations are positive, and this pattern of overall positive co-variation is rather consistent in different taxa. Interestingly, this co-variation, involving such traits as **Sq**, **Pfm**, **Gran**, **Tmp,** consistently does not involve **Pran**, which is in good agreement with the pattern of interspecific differences between *daghestanica*, *caucasica* and *praticola*.

So in this case the multivariate direction of interspecific differences coincides with the main direction of individual variability. One can expect evolutionary changes along such »developmentally encouraged« morphological pathways to occur easier and more frequently than evolutionary changes that have to overcome developmental correlations.

My analysis of numerous data on pholidotic variation in *Lacerta* provided some evidence to conform this prediction. For instance, *Lacerta bonnali* differs from the other Iberian archaeolacertas by a higher number of praeanalia and lower numbers of many other meristics (ARRIBAS, 1993b; PEREZ-MELLADO et al., 1993) – that is in the same way as *caucasica* and *praticola* differ from *daghestanica*.

To summarize the evidence and considerations given above, both extrinsic (ecological) and intrinsic (developmental) factors appear to determine the considered

multivariate trend in external morphology, but a further investigation, involving various populations of each species, is needed for more definite conclusions.

A few words on the problem of evolutionary polarity in the series *daghestanica – caucasica – praticola.* According to DAREVSKY (1967), *L. caucasica* has diverged from a *daghestanica*-like ancestor in the course of postglacial expansion of the latter form from submontane refuges to high mountains. Also, the ground-dwelling niche of *L. praticola* (like that of *L. derjugini*) was supposed to have derived from the typical rocky habitat preferred by most other Caucasian archaeolacertas (MACCULLOCH *et al.*, 1997).

To determine the ancestral forms in the group of the Caucasian rock lizards, DAREVSKY (1967) accepted the rule of oligomerization, that is, the rule of evolutionary reduction of meristic counts (DOGIEL, 1954; BROWN, 1965). So he considered species with high values of meristic characters as primitive. Indeed, such evolutionary reduction of scale numbers was repeatedly noted for many genera of squamate reptiles (BALLINGER & TINKLE, 1972; GREER, 1974; CHERLIN, 1983, etc.). However, some cases of the opposite trend are also known – e.g., in viperid snakes (MARX *et al.*, 1988). Moreover, as was stated above, quantitative changes in the general level of pholidotic segmentation are pre-determined developmentally and can be frequent and reversible in the course of morphological evolution.

There is one more difficult point in considering *L. praticola* as a relatively young species. While the geographic distribution of *L. alpina, L. caucasica* and *L. daghestanica* is restricted to the Caucasus, the range of *L. praticola* is much more extensive and includes two disjunct portions: the Caucasus and the Balkan Peninsula.

So, as usual with the Lacertidae, the phylogenetic reconstruction is difficult and we need to examine additional character systems – both in morphology and molecular genetics – reliably to solve the problem of evolutionary polarity in the series *daghestanica – caucasica – praticola.* In any case, the pronounced multivariate trend, found in the pattern of phenetic differences between these three species seems to be of general interest and contributes to our knowledge of the structure of morphological diversity in the genus *Lacerta*. MINA (1986), having profoundly analysed regularities of phenetic diversity in fishes, specified such trends as multiple analogies of phenetic divisions and stressed their importance for the understanding of factors and pathways of morphological evolution.

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