# Allozyme variation in three closely related species of Caucasian rock lizards (*Lacerta*)

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**Abstract.** Genetic diversity at 37 allozyme loci was surveyed from *Lacerta valentini* (4 populations), *L. portschinskii* and *L. rudis* (1 population each). The number of polymorphic loci ranged from 1 (*L. valentini*) to 11 (*L. rudis*). Mean heterozygosity (direct count) ranged from 0.003 (*L. valentini*) to 0.071 (*L. rudis*). Nei's (1978) genetic distance ranged from 0-0.03 among populations of *L. valentini*, 0.127-0.163 between *L. valentini* and *L. rudis* and 0.366-0.487 between *L. portschinskii* and the two other taxa. Indices of genetic variability for species having disjunct distributions were lower than in species with contiguous distributions, similar to the case of insular populations, which have lower values than do mainland populations.

## Introduction

The subgenus *Archaeolacerta* of the genus *Lacerta* is extremely diverse, with some 17 species, both bisexual and parthenogenetic, in the Caucasus Mountains region. The geomorphological and vegetative diversity of the region provide many microhabitats for lizards. One consequence of this habitat diversity is the disjunct distributions of some species (Darevsky, 1967; Darevsky et al., 1985).

Gorman et al. (1975) found that indices of genetic variability (heterozygosity and percentage of loci exhibiting polymorphism) were lower in island populations of lacertids (*Podarcis*) than in mainland populations. Two of the species occurring in the Caucasian region, *L. valentini* and *L. portschinskii*, have disjunct distributions; the range of a third species, *L. rudis*, is contiguous (Darevsky et al., 1985). The primary aim of the study is to compare genetic variability in disjunct and contiguous populations. We hypothesize that geographically restricted disjunct populations will resemble insular populations in exhibiting relatively lower levels of genetic variability than exhibited by more widespread contiguous populations.

The three species, *L. valentini*, *L. portschinskii* and *L. rudis*, were chosen because they are closely related, forming a three-taxon monophyletic clade within the subgenus *Archaeolacerta* (unpublished data). These three species have been the subject of recent morphological study (Darevsky and Eiselt, 1980; Eiselt and Darevsky, 1991; Eiselt et al., 1992).

*Lacerta valentini* and *L. portschinskii* are also two of the parent species of a complex of parthenogenetic species (Darevsky and Danielyan, 1968; Uzzell and Darevsky, 1975; Darevsky et al., 1985). Moritz et al. (1992) have shown that the level of genetic diversity in parthenogenetic species and their parent species can be used to make inferences about the origins of the parthenogens. Therefore, the second aim of this study is to examine allozyme variation in *Lacerta valentini* and *L. portschinskii*, as well as in the closely related *L. rudis*.

## Methods and materials

Specimens were collected in the Lesser Caucasus during the summers of 1993 and 1994. *Lacerta valentini* were collected from four locations in Armenia: a rocky hillside above Sevan (N=33), the slopes of Adis mountain in the Gegam range (N=26), Gukasyan (N=16) and Kutchak, on the eastern slopes of Aragats Mountain (N=20). *Lacerta valentini* is restricted to higher elevations within its range (Darevsky, 1967). *Lacerta portschinskii* (N=39) were collected at Gosh, Armenia, in a disjunct southern portion of the species' range. Specimens of *L. portschinskii* from the principal portion of its range were not available. *Lacerta rudis* (N=26) were collected at Achaldaba, Georgia, in the central part of the species' range. The distributions of the species and collecting locations are shown in fig. 1. Specimens are deposited in the herpetological collection of the Royal Ontario Museum (ROM). Appendix 1 lists collecting locations and museum catalogue numbers of collected specimens.

Specimens were euthanised by an overdose of sodium pentobarbitol and dissected immediately. Liver, heart and skeletal muscle were removed and frozen in liquid nitrogen. Some specimens were frozen whole and dissected later.

Enzymes were separated by horizontal starch gel electrophoresis on 11% gels. Homogenates of a combination of heart, liver and muscle tissues were used. All procedures, protocols and allelic nomenclature followed Murphy et al. (1990). Names, Enzyme Commission Numbers and buffer systems used for the loci are listed in table 1. The analysis utilized 28 enzyme systems encoding 37 presumptive loci. Wherever possible, loci were resolved on two buffer systems to maximize expression of all variants.

Allozyme data were analysed using BIOSYS-1 release 1.7 (Swofford and Selander, 1989). The three species were treated separately for analysis of population genetics and together for genetic distance analysis. All loci were evaluated for genetic polymorphism (heterozygosity, number of alleles per locus, percentage of loci that are polymorphic), conformity to Hardy-Weinberg expectations using Levene's (1949) correction for small sample sizes and for genetic structuring using Wright's (1978) F statistics. Genetic

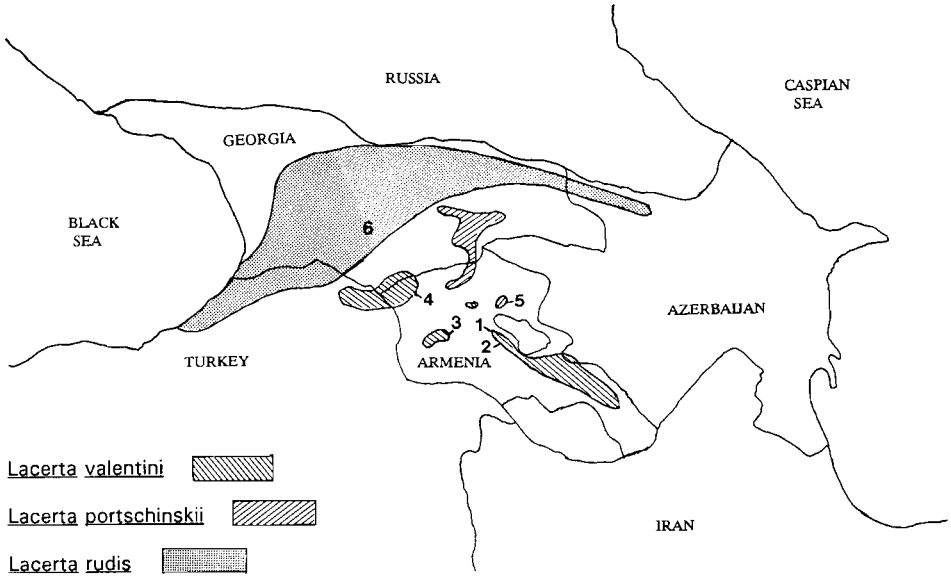


**Figure 1.** Map of the Caucasus region showing the distributions of the species and collecting locations. 1 = Sevan; 2 = Adis Mountain; 3 = Gukasyan; 4 = Kutchak; 5 = Gosh; 6 = Achaldaba.

divergence among populations and species was examined using genetic distance coefficients (Nei, 1978; Rogers, 1972). These were phenetically summarised by clustering using the Distance Wagner procedure (Farris, 1972) of BIOSYS-1.

## Results

*Lacerta valentini*

All four populations were monomorphic for 30 of the 37 loci: sAat-A, mAat-A, Acp-B, Ada-A, Cbp-1, Ck-A, Ck-C, Est-D, Gcdh-A, Gda-A, βGlus-A, βGlur-A, Gpi-A, Gpi-B, Gtdh-A, βGa-1, βGa-2, sldh-A, mldh-A, Ldh-A, Ldh-B, sMdh-A, mMdh-A, sMdhp-A, Mpi-A, Pep-A, Pep-B, Pk-A and Tpi-A. At some other loci (mAcoh-A, Cat-A, G6pdh-A, Pgm-A, Pnp-A) the variability resulted from a single appearance by rare alleles.

The Adis population exhibited variation at four loci (mAcoh-A, Cat-A, G6pdh-A, sSod-A) which were monomorphic in the other populations. Variation occurred at Pgm-A in the Sevan population only, and at Pnp-A in the Gukasyan population only. In all populations, sAcoh-A was the most variable locus.

Locus polymorphism is summarised in table 2. None of the variable loci failed to conform to Hardy-Weinberg expectations. The contingency chi-square analysis reveals four loci that show significant heterogeneity ($P < 0.05$) in allele frequencies (table 3). The

**Table 1.** Names and Enzyme Commission numbers of enzyme systems analysed and buffer systems used in analysis of 37 loci. Names and numbers follow those used by Murphy et al. (1990).

| Enzyme Name and Number | Buffer[a] |
|---|---|
| N-Acetyl-β-glucosaminidase (βGA) (EC 3.2.1.30) | 2, 6 |
| Acid Phosphatase (ACP-B) (EC 3.1.3.2) | 1 |
| Aconitase Hydratase (ACOH) (EC 4.2.1.3) | 3, 4 |
| Adenosine Deaminase (ADA) (EC 3.5.4.4) | 6 |
| Aspartate Aminotransferase (AAT) (EC 2.6.1.1) | 1, 2 |
| Calcium-Binding Proteins (CBP) (Nonspecific) | 2, 6 |
| Catalase (CAT) (EC 1.11.1.6) | 3 |
| Creatine Kinase (CK) (EC 2.7.3.2) | 4, 5 |
| "Esterase-D" (Est-D) (EC 3.1.1.-) | 6, 7 |
| Glucose Dehydrogenase (GCDH) (EC 1.1.1.118) | 4, 5 |
| Glucose-6-phosphate Dehydrogenase (G6PDH) (EC 1.1.1.49) | 1 |
| Glucose-6-phosphate Isomerase (GPI) (EC 5.3.1.9) | 4, 7 |
| β-Glucosidase (βGLUS) (EC 3.2.1.21) | 6 |
| β-Glucuronidase (βGLUR) (EC 3.2.1.31) | 6 |
| Glutamate Dehydrogenase (GTDH) (EC 1.4.1.2) | 6 |
| Guanine Deaminase (GDA) (EC 3.5.4.3) | 1, 6 |
| Isocitrate Dehydrogenase (IDH) (EC 1.1.1.42) | 1, 2 |
| L-Lactate Dehydrogenase (LDH) (EC 1.1.1.27) | 4, 6 |
| Malate Dehydrogenase (MDH) (EC 1.1.1.37) | 1 |
| Malate Dehydrogenase (NADP+) (MDHP) (EC 1.1.1.40) | 4, 6 |
| Mannose-6-phosphate Isomerase (MPI) (EC 5.3.1.8) | 2 |
| Peptidase-A (glycyl-leucine) (Pep-A) (Ec 3.4,-.-) | 2, 3 |
| Peptidase-B (leucyl-glycyl-glycine) (Pep-B) (EC 3.4.-.-) | 2, 3 |
| Phosphoglucomutase (PGM) (EC 5.4.2.2) | 1, 2 |
| Purine-nucleoside Phosphorylase (PNP) (EC 2.4.2.1) | 1, 2 |
| Pyruvate Kinase (PK) (EC 2.7.1.40) | 3, 4 |
| Superoxide Dismutase (SOD) (EC 1.15.1.1) | 5, 7 |
| Triose-phosphate Isomerase (TPI) (EC 5.3.1.1) | 5 |

[a] 1 = Amine-citrate Morpholine, pH 6.1; 2 = Amine-citrate Morpholine, pH 7.5; 3 = Tris-citrate, pH 7.0; 4 = Tris-citrate, pH 8.0; 5 = Tris-citrate/borate, pH 8.7; 6 = Tris-HCl, pH 8.2; 7 = Tris-borate EDTA, pH 8.6.

F statistics (table 6) showed a slight intrapopulational heterozygote deficiency (positive $F_{is}$) and a greater interpopulational deficiency ($F_{it}$). The high $F_{st}$ value suggests that the four populations do not form a panmictic group.

Genetic distances among the populations are shown in table 7. The greatest distances were between the Sevan population and the other populations, whereas the smallest distance values were between the Kutchak and Gukasyan populations.

*Lacerta portschinskii*

All individuals were monomorphic at all but four loci; mldh-A, Pep-A, Pep-B and Pgm-A. Polymorphism at these loci is summarised in table 2. Allele frequencies in all four loci conformed to Hardy-Weinberg expectations. Two loci showed significant frequency

**Table 2.** Genotype frequencies for polymorphic loci in *Lacerta valentini*, *L. portschinskii* and *L. rudis*.

| Locus | *valentini* Sevan | *valentini* Adis | *valentini* Kutchak | *valentini* Gukasyan | *portschinskii* Gosh | *rudis* Achaldaba |
|---|---|---|---|---|---|---|
| sAat-A | aa(33) | aa(26) | aa(20) | aa(16) | bb(39) | bb(26) |
| sAcoh-A | aa(17)<br>ab(5)<br>bb(1)<br>ac(7)<br>cc(2)<br>bc(1) | aa(8)<br>ab(2)<br>ac(7)<br>cc(2)<br>bc(2) | aa(18)<br>ab(1)<br>ac(1) | aa(14)<br>ac(2) | dd(39) | aa(6)<br>ab(5)<br>bb(1)<br>ac(8)<br>cc(4)<br>bc(2) |
| mAcoh-A | aa(33) | aa(25)<br>ab(1) | aa(20) | aa(16) | aa(39) | aa(26) |
| Acp-B | aa(33) | aa(26) | aa(20) | aa(16) | bb(39) | cc(26) |
| Cat-A | aa(33) | aa(25)<br>ab(1) | aa(20) | aa(16) | cc(39) | aa(26) |
| Ck-C | aa(33) | aa(26) | aa(20) | aa(16) | dd(39) | aa(19)<br>ab(2)<br>bb(1)<br>ac(1)<br>cc(2) |
| Est-D | aa(33) | aa(24) | aa(20) | aa(16) | aa(39) | aa(23)<br>ab(3) |
| Gcdh-A | aa(33) | aa(26) | aa(20) | aa(16) | aa(39) | aa(25)<br>bb(1) |
| Gpi-A | aa(33) | aa(26) | aa(20) | aa(16) | aa(39) | aa(17)<br>ab(8)<br>bb(1) |
| G6pdh-A | aa(33) | aa(25)<br>ab(1) | aa(20) | aa(16) | aa(39) | aa(26) |
| sIdh-A | aa(33) | aa(26) | aa(20) | aa(16) | aa(39) | aa(15)<br>ab(11) |
| sMdh-A | aa(33) | aa(26) | aa(20) | aa(16) | aa(39) | aa(24)<br>ab(2) |
| sMdhp-A | aa(33) | aa(26) | aa(20) | aa(16) | aa(39) | aa(16)<br>ab(4)<br>ac(1)<br>bd(2) |
| Pep-A | aa(33) | aa(26) | aa(20) | aa(16) | bb(33)<br>bc(6) | dd(12)<br>dc(11)<br>ee(3) |
| Pep-B | aa(33) | aa(26) | aa(20) | aa(16) | aa(31)<br>ab(7)<br>bb(1) | aa(26) |
| Pgm-A | aa(32)<br>ab(1) | aa(26) | aa(20) | aa(16) | aa(37)<br>ab(2) | aa(24)<br>ab(1)<br>bb(1) |
| Pnp-A | aa(33) | aa(26) | aa(20) | aa(15)<br>ab(1) | aa(39) | aa(23)<br>ab(3) |
| sSod-A | aa(33) | aa(20)<br>ab(6) | aa(20) | aa(16) | aa(39) | aa(26) |
| PLP[a] | 2.78 | 5.56 | 2.78 | 5.56 | 5.56 | 25.00 |
| MNA (±SE)[b] | 1.08(0.06) | 1.17(0.07) | 1.06(0.06) | 1.06(0.04) | 1.11(0.07) | 1.42(0.11) |
| MHD (±SE)[c] | 0.012(.011) | 0.024(.016) | 0.003(.003) | 0.004(.004) | 0.011(.007) | 0.071(.025) |

[a]PLP = percentage of loci polymorphic (0.95 criterion)
[b]MNA = mean number of alleles per locus
[c]MHD = mean heterozygosity by direct count

**Table 3.** Contingency chi-square analysis at all variable loci resolved from *Lacerta valentini*.

| Locus | No. of alleles | Chi-square | D.F. | P |
|---|---|---|---|---|
| sAcoh-A | 3 | 21.712 | 6 | .00137 |
| mAcoh-A | 2 | 185.704 | 3 | .00000 |
| Cat-A | 2 | 2.668 | 3 | .44571 |
| G6pdh-A | 2 | 2.668 | 3 | .44571 |
| Pgm-A | 2 | 1.889 | 3 | .59582 |
| Pnp-A | 2 | 9.980 | 3 | .01874 |
| sSod-A | 2 | 16.442 | 3 | .00092 |
| Totals | | 241.063 | 24 | .00000 |

**Table 4.** Contingency chi-square analysis at all variable loci resolved from *Lacerta portschinskii*.

| Locus | No. of alleles | Chi-square | D.F. | P |
|---|---|---|---|---|
| Pep-A | 3 | 78.000 | 2 | .00000 |
| Pep-B | 3 | 78.000 | 2 | .00000 |
| Pgm-A | 2 | 1.554 | 1 | .21258 |
| Totals | | 157.554 | 5 | .00000 |

**Table 5.** Contingency chi-square analysis at all variable loci resolved from *Lacerta rudis*.

| Locus | No. of alleles | Chi-square | D.F. | P |
|---|---|---|---|---|
| sAcon-A | 3 | 67.778 | 2 | .00000 |
| Ck-C | 3 | 9.137 | 2 | .01038 |
| Est-D | 2 | 3.689 | 1 | .05477 |
| Gcdh-A | 2 | 1.806 | 1 | .17898 |
| Gpi-A | 2 | 9.851 | 1 | .00170 |
| sldh-A | 2 | 10.961 | 1 | .00093 |
| sMdh-A | 2 | 2.044 | 1 | .15276 |
| sMdhp-A | 4 | 9.976 | 3 | .01877 |
| Pep-A | 3 | 98.000 | 2 | .00000 |
| Pgm-A | 2 | 2.849 | 1 | .09143 |
| Pnp-A | 3 | 98.000 | 2 | .00000 |
| Totals | | 314.091 | 17 | .00000 |

**Table 6.** Summary of F statistics for *Lacerta valentini*, *L. portschinskii* and *L. rudis* obtained through BIOSYS-1 (Swofford and Selander, 1989).

| Species | $F_{is}$ | $F_{it}$ | $F_{st}$ |
|---|---|---|---|
| *L. valentini* | 0.095 | 0.540 | 0.492 |
| *L. portschinskii* | 0.113 | – | – |
| *L. rudis* | 0.114 | – | – |

**Table 7.** Genetic distance coefficients. Above diagonal: Nei (1978) genetic distance; below diagonal: Rogers (1972) genetic distance.

| Population | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| 1 *L. valentini* Sevan | **** | .028 | .030 | .029 | .163 | .487 |
| 2 *L. valentini* Adis | .035 | **** | .003 | .002 | .127 | .431 |
| 3 *L. valentini* Kutchak | .034 | .014 | **** | .000 | .138 | .447 |
| 4 *L. valentini* Gukasyan | .035 | .015 | .003 | **** | .135 | .445 |
| 5 *L. rudis* Achaldaba | .177 | .151 | .155 | .154 | **** | .366 |
| 6 *L. portschinskii* Gosh | .389 | .357 | .364 | .363 | .328 | **** |

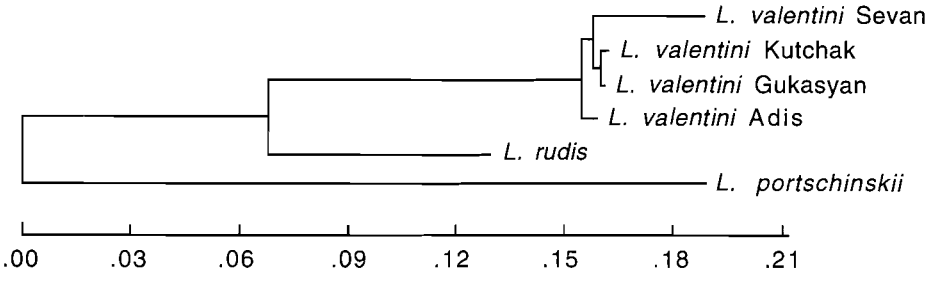


**Figure 2.** Wagner tree from Rogers distance matrix (table 7). The tree was produced by rooting at midpoint of longest path (after optimization). Farris' (1972) "f" = 0.005. Cophenetic correlation = 1.000. Total length of tree = 0.458.

heterogeneity ($P < 0.05$; table 4). The $F_{is}$ value shows a slight deficiency of heterozygotes in the population (table 6).

*Lacerta rudis*

This species exhibited the greatest amount of variation of the three species examined. Of the 37 loci, 11 (sAcoh-A, Ck-C, Est-D, Gcdh-A, Gpi-A, sldh-A, sMdh-A, sMdhp-A, Pep-A, Pgm-A, Pnp-A) were polymorphic (table 2). Allele frequencies at four of the variable loci (Ck-C, sldh-A, sMdhp-A, Pgm-A) do not conform to Hardy-Weinberg expectations. Chi-square contingency tests found that seven loci exhibited significant heterogeneity in allele frequency ($P < 0.05$; table 5). The value of $F_{is}$ demonstrates a slight heterozygote deficiency (table 6).

Genetic distance coefficients (Nei, 1978; Rogers, 1972) among the species and populations are shown in table 7. The Distance Wagner phenogram based on Rogers' (1972) distance is shown in fig. 2. *Lacerta rudis* is placed adjacent to *L. valentini*; this reflects the results of our unpublished phylogenetic analysis. Indeed, these two taxa were separated by fixed allelic differences at only 3 (sAat-A, Acp-B, Pep-A) of 37 loci examined. Fixed differences between *L. portschinskii* and the two other taxa occurred at 5 (sAcoh-A, Acp-B, Cat-A, Ck-C, Pep-A) of 37 loci.

## Discussion

Differences in genetic variation among the populations of *L. valentini* are considerable, with the Adis population exhibiting the greatest variation. Genetic distance analysis, however, placed the Sevan population as the most divergent (table 7). The coefficients of this variation, especially mean heterozygosity, in the Sevan population of *L. valentini* are closer in numerical value to those of *L. portschinskii* than they are to those of the Adis population; the Kutchak and Gukasyan populations exhibit still lower heterozygosity. The greatest degree of variability (all 3 coefficients) was found in *L. rudis*.

Genetic variation in *L. caucasica* and *L. daghestanica* (MHD = .015-.055, MNA = 1.21-1.32, PLP = 2.94-20.59; Fu et al., in press) was greater than that in both *L. valentini* and *L. portschinskii*, although less than that found in *L. rudis*. Examination of several Armenian populations of *L. raddei* and *L. nairensis* revealed that values of genetic polymorphism were generally higher (MHD = .009-.027, MNA = 1.08-1.33, PLP = 2.56-12.82; unpublished data) than those found in *L. valentini* and *L. portschinskii* but lower than those found in *L. rudis*. *Lacerta caucasica*, *L. daghestanica*, *L. raddei* and *L. nairensis* all have contiguous distributions (Darevsky, 1967). Busack (1987) found very high genetic variation in *L. lepida* and *L. pater*.

Genetic distance coefficients among populations of *L. valentini* were within the range of distances found among island populations of the lacertids *Podarcis melisellensis* and *P. sicula* (Gorman et al., 1975). Genetic distance coefficients among the populations of *L. valentini* were approximately equal to those found among populations of *L. daghestanica* (Nei's Distance = 0-.029; Fu et al., in press), even though the latter species has a contiguous distribution. Low values of variability, however, produce relatively lower distance values.

Heterozygosity ranged from 0.003 in *L. valentini* (Kutchak population) to 0.071 in *L. rudis*. The value for *L. rudis* is within the range of heterozygosity found in mainland populations of *Podarcis sicula* from the Adriatic coast, whereas heterozygosity values in *L. portschinskii* and *L. valentini* are even lower than that found in island populations of *P. sicula* (Gorman et al., 1975). Only the most variable population of *L. valentini*, from Adis, approaches the heterozygosity values of insular *P. sicula*. Heterozygosity in 3 bisexual species of *Cnemidophorus* averaged about 0.05 (Dessauer and Cole, 1984). A summary by Gorman et al. (1977) reported mean heterozygosity values of 0.01 in fossorial lizard species, 0.05 in "sit and wait" species and 0.09 in mainland populations of Lacertidae. In this study only the species with a contiguous distribution (*L. rudis*) exhibited heterozygosity similar to mainland lacertid populations, whereas the disjunct populations of *L. portschinskii* and *L. valentini* resembled island populations.

Dessauer and Cole (1984) reported a range of 1.10-1.21 alleles per locus in bisexual *Cnemidophorus*. These values are close to those obtained for *Lacerta valentini* and *L. portschinskii* but lower than that found in *L. rudis* (table 2). Gorman et al. (1977) reported a much higher value (1.88-2.08) in *Cnemidophorus tigris*.

The incidence of polymorphism (percentage of loci polymorphic) in *L. portschinskii* and *L. valentini* is much less than the 25% exhibited by *L. rudis*, which, in turn, is lower still

than the 34% found in *Cnemidophorus tigris* by Gorman et al. (1977). The preceding values were calculated using the 0.95 criterion. Dessauer and Cole (1984) and Gorman et al. (1975) did not use this criterion, but included all variable loci. Removal of the 0.95 criterion from our data revealed the following percentages of polymorphic loci: 5.56% in *L. valentini* from Sevan and Gukasyan, 2.78% in *L. valentini* from Kutchak, 13.89% in *L. valentini* from Adis, 11.11% in *L. portschinskii* and 30.56% in *L. rudis*. Values from mainland populations of *Podarcis sicula* reported by Gorman et al. (1975) ranged from 27-45%, whereas values from 3 species of *Cnemidophorus* were 10-21% (Dessauer and Cole, 1984). Island populations of *Podarcis melisellensis* and *P. sicula* ranged from 0-32% (Gorman et al., 1975). Again, *Lacerta* from disjunct Caucasian populations exhibited values similar to those in insular populations whereas the contiguous *L. rudis* more closely resembled mainland lacertid populations.

Our comparisons show that estimates of genetic variability (heterozygosity and percentage of loci polymorphic) are lower in the two species from disjunct distributions (*L. valentini* and *L. portschinskii*) than in the species from a contiguous range (*L. rudis*). Other species of *Lacerta* which have contiguous ranges also exhibit higher levels of variability than do *L. valentini* and *L. portschinskii*. The lowest variability is found in *L. valentini*; this species' occurrence at high elevations only, resulting in "islands" within its range, may be the reason for this.

Genetic variability in species having disjunct distributions is lower than variability in species from contiguous distributions. This situation resembles that found in island populations of lacertids, where variability is lower than in mainland populations (Gorman et al., 1975).

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## References

Busack, S.D. (1987): Morphological and biochemical differentiation in Spanish and Moroccan populations of the lizard, *Lacerta lepida*. J. Herpetol. **21**: 277-284.

Darevsky, I.S. (1967): Rock Lizards of the Caucasus: systematics, ecology and phylogenesis of the polymorphic groups of Caucasian rock lizards of the subgenus *Archaeolacerta*. Nauka, Leningrad (English translation).

Darevsky, I.S., Danielyan, F.D. (1968): Diploid and triploid progeny arising from natural mating of parthenogenetic *Lacerta armeniaca* and *L. unisexualis* with bisexual *L. saxicola valentini*. J. Herpetol. **2**: 65-69.

Darevsky, I.S., Eiselt, J. (1980): Neue Felseneidechsen (Reptilia, Lacertilia) aus dem Kaukasus und aus der Türkei. Amphibia-Reptilia **1**: 29-40.

Darevsky, I.S., Kupriyanova, L.A., Uzzell, T. (1985): Parthenogenesis in reptiles. In: Biology of the Reptilia **15**, Development B, p. 411-526. Gans, C., Billett, F., Eds., New York, Wiley.

Dessauer, H.C., Cole, C.J. (1984): Influence of gene dosage on electrophoretic phenotypes of proteins from lizards of the genus *Cnemidophorus*. Comp. Biochem. Physiol. **77B**: 181-189.

Eiselt, J., Darevsky, I.S. (1991): *Lacerta rudis chechenica* ssp. nov. aus dem Kaukasus (Reptilia, Lacertilia). Ann. Naturhist. Mus. Wien **92**: 15-29.

Eiselt, J., Darevsky, I.S., Schmidtler, J. (1992): Untersuchungen an Felseneidechsen (*Lacerta saxicola* komplex) in der östlichen Türkei. 1. *Lacerta valentini* Boettger. Ann. Naturhist. Mus. Wien **93**: 1-18.

Farris, J.S. (1972): Estimating phylogenetic trees from distance matrices. Am. Nat. **106**: 645-668.

Fu, J., Darevsky, I.S., MacCulloch, R.D., Kupriyanova, L.A., Roytberg, E.S., Sokolova, T.M., Murphy, R.W. (in press): Genetic and Morphological Differentiation among Caucasian Rock Lizards of the *Lacerta caucasica* complex. Russian J. Herpetol.

Gorman, G.C., Kim, Y.J., Taylor, C.E. (1977): Genetic variation in irradiated and control populations of *Cnemidophorus tigris* (Sauria, Teiidae) from Mercury, Nevada, with a discussion of genetic variability in lizards. Theor. Appl. Genet. **49**: 9-14.

Gorman, G.C., Soulé, M., Yang, S.Y., Nevo, E. (1975): Evolutionary genetics of insular Adriatic lizards. Evolution **29**: 52-71.

Levene, H. (1949): On a matching problem arising in genetics. Ann. Math. Stat. **20**: 91-94.

Moritz, C., Uzzell, T., Spolsky, C., Hotz, H., Darevsky, I.S., Kupriyanova, L., Danielyan, F. (1992): The maternal ancestry and approximate age of parthenogenetic species of Caucasian rock lizards (*Lacerta*: Lacertidae). Genetica **87**: 53-62.

Murphy, R.W., Sites, J.W., Buth, D.G., Haufler, C.H. (1990): Proteins I: Isozyme electrophoresis. In: Molecular Systematics, p. 45-126. Hillis, D.M., Moritz, C., Eds., New York: Sinauer.

Nei, M. (1978): Estimation of average genetic heterozygosity and genetic distance from a small number of individuals. Genetics **89**: 583-590.

Rogers, J.S. (1972): Measures of genetic similarity and genetic distance. Studies in Genetics VII. Univ. Texas. Pub. **7213**: 145-153.

Swofford, D.I., Selander, R.B. (1989): BIOSYS-1: A computer program for the analysis of allelic variation in population genetics and biochemical systematics, Release 1.7. Illinois Nat. Hist. Survey.

Uzzell, T., Darevsky, I.S. (1975): Biochemical evidence for the hybrid origin of the parthenogenetic species of the *Lacerta saxicola* complex (Sauria: Lacertidae), with a discussion of some ecological and evolutionary implications. Copeia **1975**: 204-222.

Wright, S. (1978): Evolution and genetics of populations, vol. 4. Variability within and among natural populations. Chicago: Univ. Chicago Press.

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## Appendix I

Specimens Examined

*Lacerta portschinskii*: ROM 23926-23940, 24854-24878, Armenia, Gosh, 40°44′51″ N, 045°01′26″ E.

*Lacerta rudis*: ROM 24304-24332, ROM 24401-24404, Georgia, Achaldaba, 41°54′24″ N, 043°30′05″ E.

*Lacerta valentini*: ROM 23862-23887, Armenia, Gegam Range, Adis Mountain, 40°23′ N, 044°42′ E; ROM 23861, 23888-23925, Armenia, Sevan, 40°30′58″ N, 044°56′16″ E; ROM 24958-24977, Armenia, Kutchak, 40°18′ N, 043°40′ E; ROM 24729-24746, Armenia, Gukasyan, 41°01′ N, 043°50′ E.