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# Allozyme variation patterns and multiple hybridization origins: clonal variation among four sibling parthenogenetic Caucasian rock lizards

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**Abstract**

Allozyme electrophoresis of four sibling parthenogenetic Caucasian rock lizards *Darevskia unisexualis, D. uzzelli, D. sapphirina,* and *D. bendimahiensis* found seven clones and five variable loci. The data supported the hypothesis that *D. raddei* and *D. valentini* are the parental species of all four parthenogens. Variation patterns in *Darevskia* were summarized. Species that originated from a single $F_1$ typically consisted of one widespread clone with a few rare clones. Species with multiple origins displayed variation only slightly higher than species with a single origin. This is contrary to other genera of parthenogenetic lizards, in which cases massive clonal variations were observed.

## Introduction

Unisexuality in vertebrates has received wide attention since it was first discovered early this century. In squamate reptiles, unisexuality originates from interspecific hybridization between bisexual species and represents true parthenogenesis (Darevsky, Kupriyanova & Uzzell, 1985; Dawley, 1989). Recognition of variation among clones within parthenogenetic species has provided insight into both the age and the mode of origin of particular parthenogenetic events, and has important implications for species definition (Frost & Wright, 1988). Genetic variation among clones of several genera of lizards has been investigated (e.g., *Cnemidophorus*, *Heteronotia* and *Darevskia*); variation found in some taxa was much higher than expected (see review in Moritz et al., 1989b). Parthenogenetic species which originated from multiple hybridization, as hypothesized in *Heteronotia* and *Cnemidophorus*, tend to have considerable clonal diversity. Moritz et al. (1989a) reported substantial allozyme variation, 18 variable loci and a minimum of 52 genotypes among populations of *H. binoei*. Parker and Selander (1976) detected six variable loci and 12 clones of *C. tesselatus*. In contrast, parthenogenetic species with a single hybrid origin typically consist of one widespread clone with a few rare clones, each of which is usually represented by only a few individuals. The majority of parthenogenetic reptiles are considered to be of single hybrid origin. Parker, Walker and Paulissen (1989) summarized the observed allozyme variation patterns and proposed a hierarchical model to predict whether the origin was from single or multiple hybridization.

The maternal parentage of parthenogenetic Caucasian rock lizards (genus *Darevskia*, formerly *Lacerta*; Arribas, 1997) has been well established from morphological and mitochondrial DNA data (Darevsky, 1992; Moritz et al., 1992; Fu, Murphy & Darevsky, 1999, 2000). Among these, four partheno-

genetic forms – *D. unisexualis, D. uzzelli, D. sapphirina*, and *D. bendimahiensis* share the same maternal parent *D. raddei*, and possibly share *D. valentini* as the paternal parent as well (Darevsky & Danielyan, 1977; Schmidtler, Eiselt & Darevsky, 1994). By evaluating the phylogenetic relationships of the mtDNA haplotypes among populations of *D. raddei* and its parthenogenetic daughter species, Fu, Murphy and Darevsky (2000) concluded that the four sibling forms are a clear case of multiple hybridization origins. The hybridization between *D. raddei* and *D. valentini* has occurred at least two times, and the *D. raddei* involved in the hybridization were from different populations, which has not been reported in other parthenogenetic vertebrates (='unrelated females', Moritz et al., 1989b).

What constitutes an unisexual species is a controversial issue (see review by Dawley, 1989). In order to avoid confusion in this paper, we use 'species' to refer to unisexual populations that share the same paternal and maternal species. Therefore, *D. unisexualis, D. uzzelli, D. sapphirina*, and *D. bendimahiensis* are considered one unisexual species but different forms. For convenience, we continue to use the four Latin names, but they do not bear any formal nomenclatural meaning.

In this study, we examined allozyme variation among three sibling parthenogens of Caucasian rock lizards, *D. uzzelli, D. sapphirina*, and *D. bendimahiensis*, which has not been previously reported, and gathered additional data for the fourth sibling parthenogen, *D. unisexualis*. Subsequently, we compared these results with those of other parthenogenetic *Darevskia* as well as *Cnemidophorus* and *Heteronotia*. Furthermore, the correlation between general allozyme variation patterns and different modes of origin is discussed and Parker, Walker and Paulissen's (1989) model is tested.

## Materials and methods

One population of each parthenogen, *D. bendimahiensis* ($n = 25$, Muradiye, 39°00′N, 043°44′E), *D. sapphirina* ($n = 27$, Patnos, 39°14′N, 042°52′E), *D. unisexualis* ($n = 1$, Horason, 39°50′N, 042°20′E), and *D. uzzelli* ($n = 26$, Horason, 39°50′N, 042°20′E) was sampled from eastern Turkey. Political instability in the area limited the scope of our field work. Three populations of *D. unisexualis* from Armenia, previously examined by Fu et al. (1998), were also included in this study. Following accepted animal welfare protocols, specimens were euthanized with an overdose of sodium pentobarbitol. Liver, heart and tail muscles were removed and frozen in liquid nitrogen and subsequently stored at −80°C for molecular examination.

Enzymes were separated by horizontal gel electrophoresis on 11% starch gels. Electrophoretic procedures and protocols and enzyme system nomenclature follow Murphy et al. (1996b). Whenever possible, gene products were resolved on two buffer systems to maximize the detection of variation. Buffer systems used are as in Fu et al. (1995), MacCulloch et al. (1995a), and Bobyn et al. (1996). All loci were analyzed for genetic polymorphism (mean heterozygosity, mean number of alleles per locus, percentage of loci exhibiting polymorphism) using BIOSYS-1 (Swofford & Selander, 1989). Alleles resolved in the parthenogenetic forms were compared to those found in sexually reproducing species of *Darevskia* (Murphy et al., 1996a) to determine parentage.

## Results

Thirty presumed loci were resolved and scored. All individuals in all populations exhibited homozygosity at the following 16 loci: mAat-A, Ada-A, Ck-A, Est-D, Gda-A, ßGlur-A, ßGlus-A, Gtdh-A, ßGa-A, mIdh-A, sIdh-A, Ldh-A, mMdh-A, sMdh-A, Pgm-A, Tpi-A. Nine loci, sAat-A, Acp-B, Ck-C, Gcdh-A, Gpi-A, sMe-A, Pep-A, Pnp-A, sSod-A, were heterozygous for all individuals. All alleles that appeared in the parthenogens were present in their hypothetical parental species, *D. raddei* and *D. valentini* (Murphy et al., 1996a).

Variation occurred at five loci, sAcoh-A, mAcoh-A, Cat-A, Ldh-B, and Pep-B, and resulted in seven clones among the four sibling parthenogens. The genotypic data for the five variable loci are presented in Table 1. There were no fixed allelic differences among the four parthenogenetic forms. Fu et al. (1998) found three clones of *D. unisexualis*, with one widespread and two rare clones. The single individual of *D. unisexualis* from the Horason population appeared to be a new clone that differs from the other clones at two loci: sAcoh-A and Pep-B. It was homozygous at these two loci while all other *D. unisexualis* were heterozygous. Two clones of *D. uzzelli* were detected; at Ldh-B, all individuals but two were heterozygous. Two clones of *D. bendimahiensis* were found; at Pep-B, all but two individuals were heterozygous. In *D. sapphirina*

*Table 1.* Genotypes of the four parthenogenetic species and their parental bisexual species

| Loci | *valentini*[1] | *unis*(An)[2] | *unis*(Ku)[2] | *unis*(No)[2] | *unis*(Ho) | *uzze*(Ho) | *bend*(Mu) | *sapp*(Pa) | *raddei*[3] |
|---|---|---|---|---|---|---|---|---|---|
| sAcoh-A | b+ | ab(27) | ab(7) | ab(23) | **bb(1)** | ab(26) | ab(25) | ab(27) | a+ |
| mAcoh-A | b | aa(27) | aa(7) | aa(23) | aa(1) | **ab**(26) | aa(25) | aa(27) | a+ |
| Cat-A | b+ | ab(27) | ab(5)<br>**aa(1)**<br>**bb(1)** | ab(23) | ab(1) | ab(26) | ab(25) | ab(27) | a+ |
| Ldh-B | b | ab(27) | ab(7) | ab(23) | ab(1) | ab(24)<br>**aa(2)** | ab(25) | ab(27) | a |
| Pep-Ba | a | ab(27) | ab(7) | ab(23) | **bb(1)** | ab(26) | ab(23)<br>**aa(2)** | ab(27) | b+ |
| H | | 0.417 | 0.409 | 0.417 | 0.367 | 0.471 | 0.431 | 0.433 | |
| P | | 41.67 | 41.67 | 41.67 | 36.67 | 46.67 | 43.33 | 43.33 | |
| A | | 1.42 | 1.42 | 1.42 | 1.37 | 1.47 | 1.43 | 1.43 | |

[1]Data adapted from MacCulloch et al. (1995a).
[2] Data adapted from Fu et al. (1998).
[3] Data adapted from Bobyn et al. (1996).
Species abbreviations: *unis*(An) = *D. unisexualis* (Ankavan); *unis*(Ku) = *D. unisexualis* (Kutchak); *unis*(No) = *D. unisexualis* (Nozaduz); *unis*(Ho) = *D. unisexualis* (Horason); *uzze*(Ho) = *D. uzzelli* Horason; *bend*(Mu) = *D. bendimahiensis* Muradiye; *sapp*(Pa) = *D. sapphirina* (Patnos).
'+' indicated there are more alleles than shown at the locus.
Numbers in parentheses are numbers of individuals.
For the complete allele arrays, see MacCulloch et al. (1995a) and Bobyn et al. (1996).
H = mean heterozygosity; P = percentage of loci polymorphic (0.95 criterion); A = mean number of alleles per locus.

*Table 2.* Comparison of allozyme variability of the seven unisexual Caucasian rock lizards

| | H | P | A | Ln | Pn | Sn | Cn |
|---|---|---|---|---|---|---|---|
| *D. armeniaca*[1] | 0.437–0.457 | 45.71 | 1.46 | 3 | 8 | 117 | 4 |
| *D. dahli*[2] | 0.392–0.400 | 40.00 | 1.40–1.43 | 2 | 6 | 161 | 5 |
| *D. rostombekowi*[3] | 0.424 | 42.42 | 1.42 | 0 | 4 | 65 | 1 |
| *D. unisexualis* and siblings | 0.367–0.471 | 36.67–46.67 | 1.37–1.47 | 5 | 7 | 136 | 7 |
| *D. bendimahiensis* | 0.431 | 43.33 | 1.43 | 1 | 1 | 25 | 2 |
| *D. sapphirina* | 0.433 | 43.33 | 1.43 | 0 | 1 | 27 | 1 |
| *D. unisexualis*[4] | 0.367–0.417 | 36.67–41.67 | 1.37–1.42 | 3 | 4 | 58 | 4 |
| *D. uzzelli* | 0.471 | 46.67 | 1.47 | 1 | 1 | 26 | 2 |

[1]Date adapted from MacCulloch et al. (1995b) and Fu et al. (2000).
[2]Data adapted from Murphy et al. (1997).
[3]Data adapted from MacCulloch et al. (1997).
[4]Data adapted from Fu et al. (1998) and this study.
H = mean heterozygosity; P = percentage of loci polymorphic (0.95 criterion); A = mean number of alleles per locus; Ln = number of variable loci; Pn = number of populations; Sn = number of specimens; Cn = number of clones.

no variation was detected. All were identical to the widespread clone *of D. bendimahiensis*.

For each of the populations examined, estimates of mean heterozygosity, mean number of alleles per locus and percentage of loci exhibiting polymorphism (95% criterion) are presented in Table 1. Comparisons with other parthenogenetic *Darevskia* species are listed in Table 2.

## Discussion

### *Confirmation of paternal parentage*

Without exception, all alleles in the four parthenogens are present either in *D. raddei* or *D. valentini*. This corroborates earlier morphological findings that these are the parental species of *D. uzzelli*, *D. sapphirina*

and *D. bendimahiensis* (Darevsky & Danielyan, 1977; Schmidtler, Eiselt & Darevsky, 1994).

*Clonal variation in the four sibling parthenogens*

As in other parthenogenetic *Darevskia*, the four parthenogens have loci fixed either in homozygous or heterozygous states and exhibit high levels of heterozygosity (Table 2). These data are similar to those from *Cnemidophorus*. For example, Dessauer and Cole (1984) reported mean heterozygosities of 0.41–0.59 and mean number of alleles per locus of 1.45–1.69 in six species of diploid parthenogenetic *Cnemidophorus*. Murphy et al. (1997) suggested that these measures may reflect the divergence between the two parental species rather than variability within the parthenogens themselves; the fewer alleles the two parental species share, the higher the heterozygosities of the parthenogens.

In all cases but one, variation appeared to be changes from heterozygosity to homozygosity, rather than the presence of unique alleles. Furthermore, these changes occurred in only one or two individuals. At mAcoh-A, all individuals of *D. uzzelli* displayed heterozygous status (ab), while all of the other three parthenogens were homozygous (aa). Considering the genotypes of the two parental species, *D. valentini* (ab) and *D. raddei* (aa), the difference between *D. uzzelli* (ab) and the other parthenogens (aa) could be the result of a different combination of alleles from the parental species.

The above mentioned variations sorted the four sibling parthenogens into seven clones; one widespread common clone which occurs in five of the seven populations, and six rare clones. The rare clones typically comprise a very small portion of the populations, except in *D. uzzelli* from Horason, in which case the entire population is made up of two rare clones. We could not determine the scope of the rare clone of *D. unisexualis* from Horason because only one specimen was examined. Therefore, whether it consists of a few specimens or the majority of the population needs to be further investigated. With one exception, the rare clones differ from the common clone at only one locus. Only *D. unisexualis* from Horason exhibited differences at two loci.

*Patterns in species from single/multiple hybridization origins*

Parker and Selander (1976) suggested three potential sources of variation in parthenogenetic species: mutation, recombination and multiple hybridization. Recombination at heterozygous loci may result in the loss of heterozygosity. Mutation may result in a new allele, or the loss of function of existing alleles (Muller, 1964; Asher, 1970; Lokki, 1976; cited in Moritz et al., 1989a).

Unisexual species with a single hybridization origin typically contain little variation. Based on observations of *Cnemidophorus*, Parker, Walker and Paulissen (1989) summarized several common patterns of allozyme variation for such species. The parthenogen usually consists of a widespread common clone with a few rare clones. And, the rare clones usually comprise only a small portion of the populations and differ from the common clone by one allele.

The observed patterns in parthenogenetic *Darevskia* generally followed Parker, Walker and Paulissen's (1989) model. Among these species, *D. rostombekowi* and *D. dahli* are clearly of single origin. They have one and five clones, respectively, and fit the model (MacCulloch et al., 1997; Murphy et al., 1997). However, exceptions do exist. *Darevskia armeniaca* has one 'rare' clone composed of numerous individuals that constitute the majority of two populations. This raises the question of whether this clone has a unique origin (Fu et al., 2000). An apparent 'mutant' clone of *D. armeniaca* from Ankavan, Armenia, possesses at least two variable loci (Fu et al., 2000).

Multiple hybridization may result in different combinations of alleles that are segregating within populations of the bisexual ancestors (Moritz et al., 1989a). Parker, Walker and Paulissen (1989) further elaborated this model. In particular, clones with multiple origins should differ from one another at several gene loci and should show random association of genotypes, assuming loose linkage between variable loci in the parental species. Furthermore, Moritz et al. (1989b, 1992) hypothesized that the number of individuals involved in hybridization and the size of the area of origin would also affect the degree of divergence among the parthenogens. Moritz et al. (1989b) also proposed two scenarios for multiple origins: multiple hybridization involving closely related females and multiple hybridization involving distantly related females.

Multiple hybrid origins in *Darevskia* are the most complicated among parthenogenetic reptiles, and the original hybridization involved distantly related females. MtDNA data showed that the four sibling parthenogens, *D. unisexualis, D. uzzelli, D. sapphirina* and *D. bendimahiensis*, formed two maternal lin-

eages, *D. unisexualis* with *D. uzzelli* and *D. sapphirina* with *D. bendimahiensis*. Furthermore, each lineage is closely associated with different maternal populations (Fu, Murphy & Darevsky, 2000). In contrast to other parthenogenetic reptiles, these two maternal lineages are distantly related, exhibiting 3.64–3.74% divergence in their cytochrome *b* sequences (Fu, Murphy & Darevsky, 2000), much higher than that within the maternal parents of *Cnemidophorus tesselatus* and *Heteronotia binoei* (0.0–0.74%; Moritz et al., 1989b).

Allozyme variation among the four sibling parthenogens *D. unisexualis, D. uzzelli, D. bendimahiensis*, and *D. sapphirina* partially resembles the patterns suggested by Moritz et al. (1989b) and Parker, Walker and Paulissen (1989). Together, the four sibling parthenogens displayed greater clonal variation (seven clones and five variable loci) than any one of the other three parthenogenetic Caucasian rock lizards (Table 2). At the mAcoh-A locus, *D. uzzelli* follows the pattern of Moritz et al. (1989b) in exhibiting an allele combination different from its siblings; both alleles are present within extant populations of the parental species. As only a single locus is variable, we can not test Parker, Walker and Paulissen's (1989) allele random association model. However, deviations from the model are apparent.

The majority of the variation did not appear to be the result of random allele combination, or at least could be explained by mutation or recombination. Although *D. unisexualis* and *D. bendimahiensis* (and *D. sapphirina*) originated from different hybridization events, no different allele combinations were observed among them. Furthermore, the clonal variation within the four sibling parthenogens is much lower than in other parthenogenetic lizards with multiple origins. For instance, within *Cnemidophorus tesselatus*, examination of 21 loci revealed six variable loci and 12 clones (Parker & Selander, 1976), and in *Darevskia*, examination of 30 loci only found five variable loci and seven clones. The difference is more pronounced when considering that the multiple hybridization in *Darevskia* involved distantly related females (Fu, Murphy & Darevsky, 2000), while in *Cnemidophorus tesselatus* and *Heteronotia binoei* only closely related females were involved (Moritz et al., 1989b). Although massive clonal variations and random allele combinations suggest multiple hybridization origin, according to Parker, Walker and Paulissen's (1989) model, low variations and lack of random allele combinations do not necessarily imply single origin, as in the case of *Darevskia*. In detecting modes of origin, patterns of variation are informative, but the phylogeny of the variable forms is equally important, if not more so.

Given their origin from multiple hybridization events, why is clonal diversity so low among the four sibling parthenogens? What does the uniformity imply? Low variation within parental species may be partially responsible. Bobyn et al. (1996) examined 36 allozyme loci among 10 *D. raddei* populations and reported low mean heterozygosity (0.002–0.024) and percentage of loci polymorphic (0.00–16.67%). MacCulloch et al. (1995a) found mean heterozygosity of 0.003–0.024 and 2.78%–5.56% of loci polymorphic in *D. valentini* from evaluation of 37 loci in four populations. These values are much lower than bisexual parental *Cnemidophorus*. For example, Dessauer and Cole (1984) reported a mean heterozygosity of 0.05, with 30% of loci polymorphic in *C. tigris*, a parental species of the parthenogenetic *C. tesselatus*.

An alternative explanation is that certain genotypes of bisexual lizards are more likely to hybridize, or that certain genotypes of $F_1$ hybrids have greater ability to establish a unisexual lineage than do others. There have been many studies at the species level, but few at the genotype level. Clearly, only a small fraction of the possible combinations of genotypes has been realized in *Cnemidophorus* and *Darevskia*.

## Conclusion

For parthenogenetic species of single hybrid origin, the usual pattern of allozyme variation is that of one widespread common clone with a few rare clones. The rare clones consist of a few individuals each and typically differ from the common clone at one locus. For species with multiple hybridization origins, the allozyme variation pattern is highly variable. At one extreme, the species may display massive genotypic variation with different allelic combinations, as in *Heteronotia binoei*. At the other extreme, the species may show little variation, as in *Darevskia*. A better way to infer modes of origin is to consider both the patterns of variation and the phylogeny of the variable forms, and to use multiple techniques, including allozyme electrophoresis, mtDNA sequencing and morphology.

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