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How many *Archaeolacerta* inhabit the Corso-Sardinian Plate? Allozyme variation and differentiation in *Archaeolacerta bedriagae* (Camerano, 1885)

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Abstract. *Archaeolacerta bedriagae* is a rock lizard endemic to Corsica and Sardinia. Four subspecies have been recozied to date on the basis of morphological traits. Previous allozyme investigations revealed high genetic differentiation among populations of the species. Based on these results some authors hypothesized that more than one species of *Archaeolacerta* may occur on Corsica and Sardinia. In this paper we investigated allozyme variation at 19 gene loci in 5 populations belonging to all subspecies of *A. bedriagae* in order to study genetic differentiation among populations from Corsica and Sardinia, and to compare our results with those obtained in previous studies carried out on allozyme variation and taxonomy of the species. Low levels of genetic differentiation (average Nei's $D = 0.026$) and heterogeneity (mean $F_{ST} = 0.147$) were found comparing the *A. bedriagae* populations, and there was no evidence of interruption or restriction of gene flow. This is in agreement with the available molecular and morphometric data, while it is not in accordance with allozyme data reported in the previous studies. Our data do not support the hypothesis of an unrecognized criptic species of *Archaeolacerta* in Corsica and Sardinia, and indicate that the definitive assessment of the taxonomic status of the *A. bedriagae* populations requires further investigation.

Keywords: Corsica, gene flow, genetic differentiation, Lacertidae, population heterogeneity, Sardinia.

Introduction

The Bedriaga's rock lizard, *Archaeolacerta bedriagae* (Camerano, 1885), belongs to a monotypic genus of the tribe Lacertini Oppel, 1811 (Squamata: Lacertidae: Lacertinae; Arnold, Arribas and Carranza, 2007). This lizard is endemic to two large Mediterranean islands, Sardinia and Corsica, and their satellite islands and islets: La Maddalena Archipelago and Isola Rossa (Sardinia), and Folaca islet (Corsica). *Archaeolacerta bedriagae* is a strictly rock-dwelling lizard confined to large rocky outcrops (Bombi and Vignoli, 2004; Bombi et al., 2009); it occurs from the sea level up to the highest mountain peaks (1800 m a.s.l. in Gennargentu Massif, Sardinia, and 2710 m a.s.l. in Mount Cinto, Corsica). Based on weak morphological traits four subspecies have been described to date. The nominate subspecies (*A. b. bedriagae*) occurs on Corsica. The other subspecies inhabit different geographic areas of Sardinia: *A. b. sardoa* (Peracca, 1903): Gennargentu Massif (central Sardinia); *A. b. paessleri* (Mertens, 1927): Mount Limbara (northern Sardinia); *A. b. ferrerae* (Stemmler, 1962): coastal Gallura (northern Sardinia). Based on morphometric investigations, Guillaume (1987) suggested that the populations from the Settefratelli Mountains (southern Sardinia) should be ascribed to a new subspecies, but this latter was never described. The individuals from Sardinia are morphologically well differentiated from those from Corsica, being more delicately built and with a finer dark reticulation enclosing in very small spots the greenish-brownish background; individuals from Corsica have a reduced dark marking and reticulation that do not completely hide the ground colour (Arnold and Burton, 1978).

Allozyme variation of *A. bedriagae* was investigated by Guillaume and Lanza (1982) in a comparative study including four species be-

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longing to the genus *Podarcis*. Although the main goal of this study was to point out the inter-specific genetic relationships among *Podarcis* species and to investigate on the generic status of *Archaeolacerta*, interesting data about genetic differentiation among *A. bedriagae* populations were also provided. In this paper very high values of Nei's (1972) standard genetic distance were found among three populations of *A. bedriagae* (one from Corsica and two from Sardinia), ranging from 0.172 to 0.309. However, it must be noted that the values of genetic distance indicated by Guillaume and Lanza (1982) were completely wrong because of a miscalculation (see Guillaume, 1987). Subsequently, Guillaume (1987) provided corrected values of Nei's (1972) standard genetic distance among the three populations of *A. bedriagae*, with *D* ranging from 0.133 to 0.186. These values, although being much lower than those estimated by Guillaume and Lanza (1982), are in fact very high, falling into the range obtained from comparisons between well recognized biological species of the genera *Lacerta* and *Podarcis* (see, e.g., Mayer and Tiedmann, 1982; Capula, 1994a, 1994b). In spite of these controversial results, Guillaume (1987) proposed to synonymise two subspecies of *A. bedriagae* (*A. b. paessleri* and *A. b. ferrerae*), and Lanza (1983), Lanza, Cesaraccio and Malenotti (1984), and Amori et al. (1993) questioned the systematic validity of the Sardinian subspecies (*A. b. paessleri*, *A. b. ferrerae*, *A. b. sardoa*). On the other hand, based on the genetic data reported by Guillaume and Lanza (1982), Arribas (1999) hypothesized the occurrence of unrecognized species of the genus *Archaeolacerta* in the Corso-Sardinian area. In addition, in a paper devoted to the systematics of the tribe Lacertini, Arnold, Arribas and Carranza (2007) found considerable mitochondrial DNA variation among three individuals of *A. bedriagae* from Corsica, and hypothesized the occurrence of more than one species as well. To date mitochondrial and nuclear DNA sequences from Corsican and Sardinian individuals of *A. bedriagae* have never been compared in any study dealing with molecular phylogeny of Lacertidae (Fu, 1998, 2000; Harris, Arnold and Thomas, 1998; Mayer and Arribas, 2003; Carranza, Arnold and Amat, 2004; Arnold, Arribas and Carranza, 2007; Mayer and Pavličev, 2007). Thus, so far the hypothesis of an unrecognized cryptic *Archaeolacerta* species in Corsica and Sardinia suggested by Arribas (1999) has never been tested.

Aim of this paper is to investigate allozyme variation in *A. bedriagae* populations belonging to all recognized or putative subspecies in order (i) to study genetic differentiation among populations from Corsica and Sardinia, and (ii) to compare our results with those obtained in previous studies carried out on allozyme variation and taxonomy of the species. It must be stressed that, although in previous studies high values of genetic distance were found among populations of *A. bedriagae*, a predictive rule about the degree of genetic divergence required for the recognition of separate species is not possible (Ferguson, 2002). A much more compelling evidence for the statement about the species status of taxa can be provided by incorporating population genetic data to investigate differentiation in fixed genetic characteristic and the occurrence of gene flow between taxa (Ferguson, 2002). Allozyme electrophoresis can provide very useful data on both genetic variability and genetic differentiation among populations, occurrence of gene flow between populations, and occurrence of natural hybridization between species (see, e.g., Ayala, 1976). Moreover, allozyme electrophoresis has proved to be a useful tool to study the taxonomy of several lacertid species, and to investigate on the occurrence of cryptic species (Capula, 1994a, 1994b; Bobyn et al., 1996; Mayer and Arribas, 1996; MacCulloch et al., 2000; Sá-Sousa et al., 2000; Pinho et al., 2002, 2007).

Materials and methods

Samples of *A. bedriagae* used in this study were obtained between April 2003 and September 2006 from five local-

ities: one from Corsica (Roccapina), and four from Sardinia (Punta Falcone, Mount Limbara, Gennargentu Massif, Settefratelli Mountains). A total of 59 individuals were analysed. Sampling details are shown in fig. 1 and reported in table 1. All subspecies recognized to date were included in the analysis. In addition, we included a sample from southern Sardinia (Settefratelli Mts), for which the recognition of the subspecific status was suggested by Guillaume (1987). For inter-specific comparison, one sample (11 individuals) of *Iberolacerta cyreni* (Müller and Hellmich, 1937) from Central Spain (Sierra de Guadarrama, see table 1) was also analysed. Since the phylogenetic position of *A. bedriagae* within the Palaearctic lizard radiation is not yet clear (Arnold et al., 2007; Mayer and Pavličev, 2007), we selected *I. cyreni* for the inter-specific comparison because it belongs to the same tribe of *A. bedriagae* (i.e., Lacertini Oppel, 1811 *sensu* Arnold et al., 2007).

Figure 1. Sampling locations (geometric symbols) and distribution (light shaded area) of *Archaeolacerta bedriagae*. The range of the species is based on data points from Delaugerre and Cheylan (1992) and Bombi and Vignoli (2004). Symbols refer to different subspecies (■ = *A. b. bedriagae*, Roccapina, Corsica; ▲ = *A. b. ferrerae*, Punta Falcone, Sardinia; ◆ = *A. b. paessleri*, Mount Limbara, Sardinia; ● = *A. b. sardoa*, Gennargentu Massif, Sardinia; * = *A. b.* subsp. inquirenda, Settefratelli Mountains).

To avoid killing animals or injurious biopsy, a portion of approximately 2 cm of the tail tip was removed from each lizard, and stored at −70°C until electrophoretic analysis. All lizards were released after this procedure. Standard horizontal starch gel electrophoresis was performed on muscle tissue homogenates using buffer systems and procedures described by Capula (1994a, 1994b). Gene products for the following 19 presumptive gene loci were analysed: *αGpd* (Glycerol-3-phosphate dehydrogenase, E.C. 1.1.1.8), *Ldh-1*, *Ldh-2* (Lactate dehydrogenase, E.C. 1.1.1.27), *Mdh-1*, *Mdh-2* (Malate dehydrogenase, E.C. 1.1.1.37), *Me-1*, *Me-2* (Malic enzyme, E.C. 1.1.1.40), *Idh-2* (Isocitrate dehydrogenase, E.C. 1.1.1.42), *6Pgd* (6-phosphogluconate dehydrogenase, E.C. 1.1.1.44), *Sod-1* (Superoxide dismutase, E.C. 1.15.1.1), *Ck* (Creatine kinase, E.C. 2.7.3.2), *Ak* (Adenylate kinase, E.C. 2.7.4.3), *Est-1* (Esterase, E.C. 3.1.1.1), *Mpi* (Mannose-6-phosphate isomerase, E.C. 5.3.1.8), *Gpi* (Glucose-6-phosphate isomerise, E.C. 5.3.1.9), *Pgm-1*, *Pgm-2* (Phosphoglucomutase, E.C. 5.4.2.2), *Gp-1*, *Gp-2* (general proteins).

Genotype and allele frequencies were determined by direct count from allozyme phenotypes. Statistical significance of multiple tests was assessed adopting the Bonferroni's correction (Rice, 1989). The significance of association between genotypes was tested with genotype randomizations in each sample (17 100 permutations) and overall samples (3420 permutations) between all pairs of loci with FSTAT 2.9 (Goudet, 2001). In the overall tests the P-values of samples were weighted on the basis of polymorphism level. Hardy-Weinberg equilibrium was tested for each locus in each sample with allele randomizations within samples (1900 permutations per test) with FSTAT. The genetic divergence among the studied populations was evaluated using Nei's (1972) standard genetic distance (D) with BIOSYS-2 (Swofford and Selander, 1999). We used Nei's (1972) standard genetic distance (D) in order to maximize the comparability of our results with those obtained by Guillaume and Lanza (1982). The distribution of genetic variation within and among populations was assessed calculating Wright's (1965) F-statistics according to the method of Weir and Cockerham (1984) implemented in FSTAT. In addition, a test for population differentiation was performed (10 000 permutations) and the pairwise F_{ST} were also calculated. An indirect estimation of gene flow among populations was extrapolated from the genetic variance among populations, under the assumptions of the island model, following the Wright's (1978) formula $F_{ST} = 1/(4Nm + 1)$,

Table 1. Geographical location and sample size of the analysed populations. * = *terra typica*.

Sample		Locality	Altitude (m a.s.l.)	Coordinate	Sample size
A	*A. b. bedriagae*	Roccapina (Sartène), Corsica*	83	8°56′E/41°29′N	16
B	*A. b. ferrerae*	Punta Falcone* (S. Teresa di Gallura), Sardinia	3	9°14′E/41°15′N	5
C	*A. b. paessleri*	Mount Limbara* (Tempo Pausania), Sardinia	1306	9°10′E/40°51′N	11
D	*A. b. sardoa*	Gennargentu Massif* (Fonni), Sardinia	1783	9°19′E/39°59′N	12
E	*A. b.* subsp. inquirenda	Settefratelli Mountains (Burcei), Sardinia	483	9°24′E/39°17′N	15
OUT	*Iberolacerta cyreni*	Puerto de Navacerrada (Sierra de Guaderrama), Spain	2140	3°59′W/40°47′N	11

where N is the effective population size and m is the migration rate between populations. Principal Component Analysis (PCA) on gene frequencies was computed using the software PCAGEN 1.2 (Goudet, 1999), and the statistical significance of the axes were evaluated over 15 000 permutations.

Results

Allele frequencies for the populations studied are given in table 2. Eleven loci were found to be monomorphic, i.e., fixed for the same allele, in all populations (*αGpd*, *Ldh-2*, *Mdh-1*, *Mdh-2*, *Idh-2*, *Sod-1*, *Ak*, *Pgm-1*, *Pgm-2*, *Gp-1*, *Gp-2*). Three out of eight polymorphic loci were weakly polymorphic (*Ldh-1*, *Me-2*, *Mpi*). A total of 29 alleles were identified, with the number of allelic variants per locus ranging from 1 to 3. No fixed alternative allele was found. Lizards from Corsica were characterized by two unique alleles, i.e., Mpi^{102} and $6Pgd^{95}$. Four private alleles were found in the Sardinian populations: $Est\text{-}1^{102}$ in all populations, $Me\text{-}2^{95}$ in the populations from Punta Falcone and Mount Limbara, $6Pgd^{105}$ and $Ldh\text{-}1^{95}$ in the populations from the Settefratelli Mts. There was not evidence of genetic linkage disequilibrium between any pair of loci in any samples and in overall samples ($P > 0.05$ nominal value in every comparisons). Genotypic frequencies were consistent with Hardy-Weinberg expectations, after adjustment of significance levels for multiple comparison tests. The values of Nei's (1972) standard genetic distance and F_{ST} for each pairwise comparison are shown in table 3. Low levels of genetic differentiation were found in *A. bedriagae*, Nei's D ranging from 0.013 to 0.042, with an average genetic distance of 0.026 (SD = 0.010). A similar average value of Nei's D was found between Corsican and Sardinian populations ($D = 0.025$; SD = 0.009). Low Nei's genetic distance values were found comparing the four recognized subspecies (average $D = 0.023$; SD = 0.007). The sample from the Settefratelli Mountains (southern Sardinia) was relatively differentiated from the other ones (average $D = 0.031$; SD = 0.013), as evidenced also in the PCA plot (fig. 2). As to the genetic differentiation between *A. bedriagae* and *I. cyreni*, the average value of Nei's D was 0.688 (SD = 0.024). The mean F_{ST} value (0.147) indicates that differentiation among populations contributes for less than 15% to the genetic variation observed in *A. bedriagae*. The population differentiation test was significant after 10 000 permutations ($P < 0.05$). Indirect estimates of gene flow ($Nm = 0.70$) suggest that there is no evidence of interruption or restriction of gene flow within *A. bedriagae*. As to the PCA (see fig. 2), the first axis explains 53% of the total genetic variance, and the second 35%. The variance associated with the second axis is significant ($P < 0.05$). The sample from Settefratelli Mountains (sample E) is well differentiated from the other populations (samples A-D) along the first principal axis. The arrangement of populations is not geographically coherent (fig. 2).

Discussion

The results of our analyses indicate low levels of genetic differentiation among *A. bedria-*

Table 2. Allele frequencies at 14 polymorphic loci in populations of *Archaeolacerta bedriagae* (A-E) and *I. cyreni* (OUT). Alleles were coded in order of increasing anodal mobility. Reference letter of samples corresponds to those in fig. 1 and table 1.

Locus	Allele	Sample					
		A	B	C	D	E	OUT
Ldh-1	95	0.00	0.00	0.00	0.00	0.04	0.00
	100	1.00	1.00	1.00	1.00	0.96	1.00
Mdh-1	90	0.00	0.00	0.00	0.00	0.00	1.00
	100	1.00	1.00	1.00	1.00	1.00	0.00
Mdh-2	80	0.00	0.00	0.00	0.00	0.00	1.00
	100	1.00	1.00	1.00	1.00	1.00	0.00
Me-1	100	0.40	0.67	0.80	0.38	0.75	0.00
	104	0.60	0.33	0.20	0.63	0.25	0.00
	105	0.00	0.00	0.00	0.00	0.00	0.40
	111	0.00	0.00	0.00	0.00	0.00	0.60
Me-2	95	0.00	0.13	0.06	0.00	0.00	0.00
	100	1.00	0.88	0.94	1.00	1.00	0.00
	105	0.00	0.00	0.00	0.00	0.00	0.40
	110	0.00	0.00	0.00	0.00	0.00	0.60
Idh-2	100	1.00	1.00	1.00	1.00	1.00	1.00
	105	0.00	0.00	0.00	0.00	0.00	0.00
6Pgd	93	0.00	0.00	0.00	0.00	0.00	1.00
	95	0.06	0.00	0.00	0.00	0.00	0.00
	100	0.94	1.00	1.00	1.00	0.93	0.00
	105	0.00	0.00	0.00	0.00	0.07	0.00
Ck	95	0.10	0.50	0.30	0.14	0.40	0.00
	100	0.90	0.50	0.70	0.86	0.60	0.00
	105	0.00	0.00	0.00	0.00	0.00	1.00
Pgm-1	100	1.00	1.00	1.00	1.00	1.00	0.00
	105	0.00	0.00	0.00	0.00	0.00	0.57
	107	0.00	0.00	0.00	0.00	0.00	0.43
Pgm-2	90	0.00	0.00	0.00	0.00	0.00	0.00
	100	1.00	1.00	1.00	1.00	1.00	1.00
Ck	95	0.10	0.50	0.30	0.14	0.40	0.00
	100	0.90	0.50	0.70	0.86	0.60	0.00
	105	0.00	0.00	0.00	0.00	0.00	1.00
Mpi	88	0.00	0.00	0.00	0.00	0.00	1.00
	100	0.94	1.00	1.00	1.00	1.00	0.00
	102	0.06	0.00	0.00	0.00	0.00	0.00
Gpi	100	0.59	1.00	0.73	1.00	0.30	1.00
	105	0.41	0.00	0.27	0.00	0.70	0.00
Est-1	100	0.79	0.38	0.39	0.75	0.64	0.00
	102	0.00	0.63	0.56	0.25	0.36	0.00
	105	0.21	0.00	0.06	0.00	0.00	0.00
	115	0.00	0.00	0.00	0.00	0.00	0.58
	118	0.00	0.00	0.00	0.00	0.00	0.42

gae populations, clearly suggesting that full genetic continuity exists among them. The majority of alleles detected within *A. bedriagae*

Table 3. Nei's (1972) standard genetic distance (below diagonal) among populations of *Archaeolacerta bedriagae* (A-E) and *Iberolacerta cyreni* (OUT), and pairwise estimates of F_{ST} (above diagonal) for the samples of *A. bedriagae* (A-E); see table 1 and fig. 1 for geographic origin and codes of populations.

	A	B	C	D	E
A	–	0.225	0.153	0.057	0.126
B	0.033	–	0.057	0.187	0.220
C	0.028	0.017	–	0.090	0.055
D	0.013	0.022	0.023	–	0.254
E	0.024	0.041	0.015	0.042	–
OUT	0.692	0.684	0.675	0.664	0.726

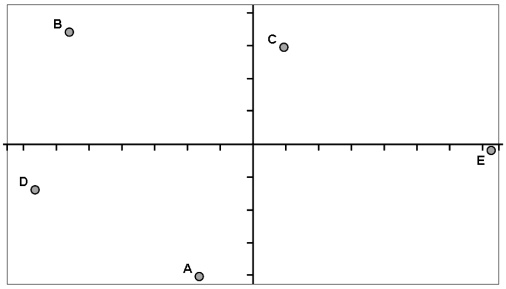

Figure 2. Principal Component Analysis on allozyme frequencies in five samples of *Archaeolacerta bedriagae*. The first axis (abscisse) of the PCA explains 53% of the total genetic variance, and the second axis (ordinate) about 33%. Reference letter of samples corresponds to those in fig. 1 and table 1.

(80%) are shared among populations, and the private alleles occur with frequency lower than 15%. There is no evidence of linkage disequilibrium between any pair of loci, and the observed genotypic frequencies are consistent with H-W expectations, thus excluding the potential occurrence of intergradation phenomena. The level of genetic divergence found among *A. bedriagae* populations is far from that observed comparing well recognized biological species of lacertid lizards (Mayer and Tiedemann, 1982; Capula, 1994b; see also the value obtained for the inter-specific comparison between *A. bedriagae* and *I. cyreni*, this paper), falling into the range obtained from comparisons among populations of the same species (see, e.g., Capula, 1994, 2004; Capula and Ceccarelli, 2003). Moreover, the population heterogeneity analyses carried out by the estimation of Wright's *F*-statistic

show that genetic differentiation among populations is lower than that found in other Mediterranean lizard species (Capula, 1994a, 2004; Capula and Ceccarelli, 2003: F_{ST} ranging from 0.153 to 0.610). The indirect estimate of gene flow ($Nm = 0.70$), although far to be accurate (Withlock and McCauley, 1999), indicates that there is no evidence of interruption or restriction of gene flow within *A. bedriagae*. It must be noted that in the lacertid lizard *Podarcis tiliguerta* (Gmelin, 1789), which is endemic to Corsica and Sardinian as well, and likely represents a species complex (Harris et al., 2005), Capula (1996) found a very small level of gene flow ($Nm = 0.29$). The absence of genetic discontinuity between Corsican and Sardinian populations of *A. bedriagae* is also evident in the ordering pattern of populations in the main factorial planes of the PCA. Although the southern Sardinian sample is rather separated, the genetic differentiation is roughly of the same level among the populations. The repeated land connection between Corsica and Sardinia up to at least about 12 000 years ago (Lambeck et al., 2004) could account for the lack of substantial genetic divergence between Corsican and Sardinian populations of *A. bedriagae*.

The results obtained in the present study are not in accordance neither with those reported by Guillaume and Lanza (1982), nor with those reported by Guillaume (1987), and the genetic divergence among the recognized subspecies resulted to be much lower than that previously estimated. Moreover, we found high intrapopulation variability within *A. bedriagae*. Several reasons might account for these discrepancies, including differential sampling across tissues and loci, and differences concerning the electrophoretic conditions. For instance, when comparing the papers by Guillaume and Lanza (1982) and Guillaume (1987), the higher number of loci, populations, and individuals analysed in our study may account for the higher number of alleles detected.

The results of this investigation are in agreement with the available DNA sequences data and with the preliminary morphometric investigations carried out by Salvi et al. (2008). When analysing the available DNA sequences, the comparison between Corsican and Sardinian specimens is possible between few specimens for ribosomal 12S and 16S genes fragments about 400 base pairs long (sequences: AF080325, AF080327 from Harris, Arnold and Thomas, 1998; AY256654, AY256655 from Carranza, Arnold and Amat, 2004; AF440599, AF440614 from Mayer and Arribas, 2003; AF206592 from Fu, 2000). In all the comparisons among Corsican and Sardinian samples it was always found a nucleotide divergence lower than 1.5%, i.e., an amount of nucleotide divergence lower than that found between well recognized lizard species. As to morphometric data, the pattern of variation observed in *A. bedriagae* does not reflect any geographical pattern of discontinuity across the range (Salvi et al., 2008).

Finally, the results of our analyses do not support the current intra-specific taxonomy of *A. bedriagae*. The currently recognized Sardinian subspecies are likely to be synonymised. On the other hand, the taxonomic status of the populations from southern Sardinia (Guillaume, 1987; this study) is worthy of consideration and should be furtherly investigated. A definitive assessment of the taxonomic status of the *A. bedriagae* subspecies will probably require further genetic and morphological investigations, as well as the analysis of a larger number of samples from Corsica and Sardinia.

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