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Genetic variability in mainland and insular populations of *Podarcis muralis* (Reptilia: Lacertidae)

Massimo Capula[1] & Claudia Corti[2]
[1]Museo Civico di Zoologia, Via U. Aldrovandi, 18, I-00197 Roma, Italy;
E-Mail: massimo.capula@comune.roma.it
[2]Museo di Storia Naturale dell'Università di Firenze, Sezione di Zoologia "La Specola", Via Romana, 17, I-50125 Firenze, Italy, E-Mail: claudia.corti@unifi.it

Abstract. Allozyme electrophoresis was used to study the distribution of genetic variation within and among mainland and insular populations of the lacertid lizard *Podarcis muralis* from western, southern and eastern Europe. Genetic variability in the species is low and genetic subdivision is high. The highest values of percent polymorphism and heterozygosity were found in the samples from two Tyrrhenian islands (Elba Island, La Scola Islet). The occurrence of higher levels of genetic variability in insular populations is probably because these populations inhabit marginal environments characterized by temporal-ecological instability. In these environments high heterozygosity levels can be preserved after colonization events, unless founder populations are so small that bottleneck effects occur. The genetic heterogeneity analysis demonstrates a certain amount of genetic differentiation among local populations of *P. muralis*, with a relatively high level of genetic subdivision. Allozyme data show that genetic variation in *P. muralis* is distributed into two major population groups: the first includes the closely related samples from Spain and SW France, the second the genetically recognizable samples from Germany, Italy, and Greece. The average genetic distance between the two groups is relatively high (Nei's $D = 0.059$), with D ranging from 0.043 to 0.100.

Key words. *Podarcis muralis*, Lacertidae, allozyme electrophoresis, population heterogeneity, Tyrrhenian islands, Europe.

INTRODUCTION

There have been numerous surveys of the genetic structure of insular populations of vertebrates, especially reptiles (e.g. Soulé & Yang 1974; Gorman et al. 1975; Patton et al. 1975). From these studies it became evident that many demographic, historical, and geographic factors influence the pattern of genetic variation in the insular populations (e.g. Soulé et al. 1973; Soulé 1976).

The Mediterranean lacertid lizards of the genus *Podarcis* seem to be particularly useful for this type of investigation because they are widespread on several Mediterranean islands and are normally characterized by high inter- and intra-population morphological and genetic variability (e.g. Harris & Arnold 1999; Arnold & Ovenden 2002; Corti & Lo Cascio 2002; Salvi et al. 2009). Although the evolutionary significance of the pattern of variation observed in these lacertid lizards has been unstudied for most taxa, in some cases at least it was pointed out that species which are characterized by a high degree of phenotypic plasticity in the pattern of the upper parts may have levels of genetic variability higher than those found in the morphologically low variable species (see e.g. Selander 1976; Capula 1994a, 1996, 1997; Losos et al. 1997; Capula & Ceccarelli 2003; Caputo et al. 2008).

In this paper, based primarily on allozyme data, the distribution of genetic variation within and among mainland and insular populations of the lacertid lizard *Podarcis muralis* from western, southern and eastern parts of its European range was estimated. *Podarcis muralis* was chosen as it is a morphologically and ecologically variable species occurring in a wide variety of habitats over its distribution range, which extends from the northern border of the Iberian Peninsula to north-western Turkey, and throughout central and southern Europe (Arnold & Ovenden 2002; Corti & Lo Cascio 2002). In the northern part of its range this lizard is typically a thermophilous and lowland species, with a reduced variability in the pattern of the upper parts, while in the southern part it is more often a mountain species, occurs especially in wet and shady habitats, and is characterized here by high phenotypic variability (see Capula et al. 1993, 2009; Corti et al.

Table 1. Geographic and collecting data for the *Podarcis muralis* samples used in this study.

Population	Locality	Sample size
A	Guadarrama (Spain)	5
B	Anso (Spain)	5
C	Ordesa (Spain)	3
D	Deba (Spain)	4
E	Albaran (Spain)	3
F	Bidache (SW France)	5
G	Le Chiroulet (SW France)	5
H	St. Gaudens (SW France)	5
I	Bonn (Germany)	5
J	Cavalese (Italy)	20
K	Cesena (Italy)	20
L	Resceto (Italy)	2
M	Chiusdino (Italy)	6
N	Populonia (Italy)	4
O	Uccellina Mountains (Italy)	3
P	Ostia (Italy)	10
Q	Elba Island, Tuscan Archipelago (Italy)	10
R	Scoglietto di Portoferraio Islet, Tuscan Archipelago (Italy)	2
S	Gorgona Island, Tuscan Archipelago (Italy)	4
T	Pianosa Island, Tuscan Archipelago (Italy)	2
U	La Scola Islet, Tuscan Archipelago (Italy)	2
V	Palmaiola Island, Tuscan Archipelago (Italy)	3
Z	Viotia (Greece)	6

in press). Allozyme variation in some Italian, Spanish and Austrian populations of *P. muralis* was studied by Capula (1997), who provided evidence of high level of genetic variability in insular populations. Genetic variation and differentiation in the Italian populations of the species were recently investigated also by Caputo et al. (2008) and Giovannotti et al. (2010), based on the sequencing of a portion of a mitochondrial gene.

MATERIAL AND METHODS

Sampling. Samples of *P. muralis* used in this study were obtained from 17 mainland localities of western, southern and eastern Europe (Spain, SW France, Germany, Italy, Greece) and six islands of the Tuscan Archipelago in the Tyrrhenian Sea (Elba, Scoglietto di Portoferraio, Gorgona, Pianosa, La Scola, Palmaiola). The precise geographic origin of each sample and the number of individuals analysed per population are indicated in Table 1.

Electrophoresis. The electrophoretic analysis was undertaken for 134 specimens from all 23 localities. Standard horizontal starch gel electrophoresis was performed on tail muscle tissue, parts of which were crushed in 0.1 mL of distilled water. Gene products for the following 21 presumptive enzyme loci were analysed: glycerol-3-phosphate dehydrogenase (E.C. 1.1.1.8, ∝*Gpd*), lactate dehydrogenase (E.C. 1.1.1.27, *Ldh-1*, *Ldh-2*), malate dehydrogenase (E.C. 1.1.1.37, *Mdh-1, Mdh-2*), malic enzyme (E.C. 1.1.1.40, *Me-1, Me-2*), isocitrate dehydrogenase (E.C. 1.1.1.42, *Idh-1, Idh-2*), 6-phosphogluconate dehydrogenase (E.C. 1.1.1.44, *6Pgd*), glyceraldehyde-3-phosphate dehydrogenase (E.C. 1.2.1.12, *Gapd*), superoxide dismutase (E.C. 1.15.1.1, *Sod-1*), glutamate-oxaloacetate transaminase (E.C. 2.6.1.1, *Got-1, Got-2*), creatine kinase (E.C. 2.7.3.2, *Ck*), adenosine deaminase (E.C. 3.5.4.4, *Ada*), carbonic anhydrase (E.C. 4.2.1.1, *Ca*), mannose-6-phosphate isomerase (E.C. 5.3.1.8, *Mpi*), glucose-6-phosphate isomerase (E.C. 5.3.1.9, *Gpi*), phosphoglucomutase (E.C. 5.4.2.2, *Pgm-1, Pgm-2*) (enzymes codes are accord-

Table 2. Chi-square values resulting from contingency χ^2 analysis of the polymorphic loci among populations of *Podarcis muralis*. d.f. = degree of freedom; NS = nonsignificant.

Locus	No. of alleles	χ^2	d.f.	P
Ldh-1	2	172.417	22	<0.001
Ldh-2	2	33.841	22	<0.05
Me-1	4	462.317	66	<0.001
Me-2	2	32.622	22	NS
6Pgd	4	222.142	66	<0.001
Gapd	2	42.987	22	<0.004
Got-1	2	63.179	22	<0.001
Pgm-2	2	80.490	22	<0.001
Ca	2	75.142	22	<0.001
Gp-1	2	24.986	22	NS
Gp-2	2	38.449	22	NS
Gp-3	3	331.439	44	<0.001
Total		**1580.010**	**374**	**<0.001**

ing to Richardson et al., 1986). In addition, three unidentified non-enzymatic proteins were studied: *Gp-1, Gp-2, Gp-3*. The buffer systems used, electrophoretic procedures, staining techniques, and loci and allele designations were those described by Capula (1990, 1994b).

Analysis. Genotypic and allelic frequencies were determined by direct counts from allozyme phenotypes, and the resulting data were analysed by various statistical methods to describe the genetic structure of the *P. muralis* populations. Genotypic proportions expected on the basis of Hardy-Weinberg equilibrium were calculated by Levene's formula (Levene 1949) for small samples. The statistical significance of departures from Hardy-Weinberg equilibrium was estimated using a test for calculating exact significance probabilities, analogous to Fisher's exact test (Elston & Forthofer 1977). To determine whether the heterogeneity in the genotypic distribution reflects differences in allele frequencies, the variation in genic proportions among populations was subjected to a contingency χ^2

Table 3. Genetic variability parameters in *Podarcis muralis* populations. *A*, mean number of alleles per locus; *P*, mean proportion of polymorphic loci; H_o, observed mean heterozygosity; H_e, expected mean heterozygosity; SE, standard error.

Population	*A*	*P*	H_o	SE	H_e	SE
Guadarrama	1,0	0.0	0.000	0.000	0.000	0.000
Anso	1.0	0.0	0.000	0.000	0.000	0.000
Ordesa	1.0	4.2	0.026	0.026	0.022	0.022
Deba	1.0	4.2	0.010	0.010	0.010	0.010
Albaran	1.0	0.0	0.000	0.000	0.000	0.000
Bidache	1.1	8.3	0.038	0.027	0.038	0.027
Le Chiroulet	1.0	4.2	0.008	0.008	0.008	0.008
St. Gaudens	1.1	4.2	0.031	0.031	0.029	0.029
Bonn	1.0	4.2	0.015	0.015	0.015	0.015
Cavalese	1.0	0.0	0.000	0.000	0.000	0.000
Cesena	1.1	12.5	0.038	0.023	0.040	0.024
Resceto	1.1	8.3	0.038	0.027	0.042	0.029
Chiusdino	1.2	16.7	0.064	0.032	0.066	0.033
Populonia	1.1	8.3	0.038	0.027	0.036	0.025
Uccellina Mountains	1.2	12.5	0.038	0.028	0.067	0.039
Ostia	1.1	12.5	0.031	0.018	0.030	0.017
Elba Island	1.1	12.5	0.077	0.046	0.055	0.031
S.to Portoferraio Islet	1.1	12.5	0.019	0.019	0.077	0.043
Gorgona Island	1.1	8.3	0.029	0.021	0.028	0.020
Pianosa Island	1.1	8.3	0.038	0.027	0.042	0.029
La Scola Islet	1.2	16.7	0.077	0.046	0.097	0.046
Palmaiola Island	1.1	8.3	0.032	0.023	0.024	0.017
Viotia	1.0	0.0	0.000	0.000	0.000	0.000

Table 4. Values of Nei's (1978) unbiased genetic distance among populations of *Podarcis muralis*. For geographical origin of populations (A–Z) see Table 1.

	POPULATION																						
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	Z
A	–																						
B	0.000	–																					
C	0.003	0.003	–																				
D	0.000	0.000	0.003	–																			
E	0.000	0.000	0.003	0.000	–																		
F	0.010	0.010	0.000	0.008	0.010	–																	
G	0.000	0.000	0.003	0.000	0.000	0.009	–																
H	0.006	0.006	0.000	0.007	0.006	0.000	0.007	–															
I	0.070	0.070	0.074	0.071	0.070	0.083	0.071	0.079	–														
J	0.043	0.043	0.046	0.043	0.043	0.054	0.043	0.050	0.026	–													
K	0.055	0.055	0.059	0.056	0.055	0.068	0.056	0.063	0.039	0.011	–												
L	0.043	0.043	0.043	0.044	0.043	0.050	0.044	0.046	0.027	0.000	0.001	–											
M	0.046	0.046	0.049	0.046	0.046	0.058	0.046	0.054	0.013	0.009	0.014	0.006	–										
N	0.046	0.046	0.050	0.047	0.046	0.059	0.047	0.054	0.013	0.003	0.004	0.000	0.001	–									
O	0.053	0.053	0.057	0.053	0.053	0.065	0.053	0.061	0.006	0.008	0.004	0.001	0.000	0.000	–								
P	0.045	0.045	0.049	0.045	0.045	0.057	0.045	0.053	0.022	0.002	0.005	0.000	0.005	0.000	0.001	–							
Q	0.059	0.059	0.063	0.059	0.059	0.072	0.059	0.067	0.042	0.014	0.010	0.010	0.021	0.013	0.009	0.012	–						
R	0.082	0.082	0.087	0.083	0.082	0.096	0.082	0.091	0.029	0.036	0.047	0.037	0.017	0.029	0.017	0.034	0.042	–					
S	0.045	0.045	0.048	0.045	0.045	0.057	0.045	0.052	0.011	0.001	0.013	0.002	0.003	0.000	0.001	0.001	0.016	0.027	–				
T	0.043	0.043	0.047	0.044	0.043	0.056	0.044	0.051	0.027	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000	0.032	0.002	–			
U	0.082	0.082	0.087	0.083	0.082	0.097	0.083	0.092	0.047	0.036	0.041	0.038	0.029	0.035	0.024	0.037	0.031	0.000	0.033	0.026	–		
V	0.045	0.045	0.049	0.046	0.045	0.057	0.045	0.053	0.023	0.002	0.012	0.002	0.003	0.003	0.002	0.003	0.010	0.020	0.002	0.000	0.020	–	
Z	0.087	0.087	0.091	0.087	0.087	0.100	0.087	0.095	0.035	0.043	0.055	0.043	0.031	0.035	0.030	0.041	0.059	0.014	0.034	0.043	0.059	0.038	–

analysis (Workman & Niswander 1970). The genetic variability of populations was estimated using the following parameters: mean number of alleles per locus (A); percentage of polymorphic loci, at the 99% level (P); observed mean heterozygosity (H_o); expected mean heterozygosity in Hardy-Weinberg equilibrium (H_e) (unbiased estimate; Nei 1978). The genetic relationships among the studied populations were evaluated using Nei's unbiased genetic distance (D, Nei 1978). All genetic variability and genetic distance measures were calculated using the computer program BIOSYS-2 (Swofford & Selander 1999). An estimation of phenetic relationships among populations was obtained by generating a phenogram of all samples by means of the unweighted pair-group method with arithmetic averaging (UPGMA) based on the matrix of Nei's unbiased genetic distances (Sneath & Sokal 1973).

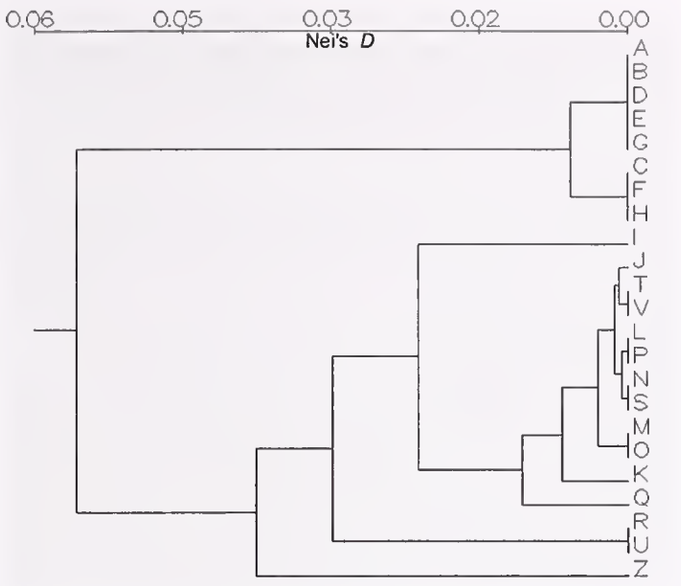

Fig. 1. Phenogram generated by UPGMA cluster analysis based on Nei's (1978) unbiased genetic distances among *Podarcis muralis* populations. For geographic origin of populations (A–Z) see Table 1.

RESULTS

Of the 24 electrophoretic loci analysed, ten (46%) were monomorphic and fixed for the same allele in all samples (*Mdh-1, Mdh-2, Idh-2, Gapd, Sod-l, Got-2, Mpi, Gpi, Pgm-1, Ada*). Fourteen loci (54%) were found to be polymorphic (∝*Gpd, Ldh-l, Ldh-2, Me-l, Me-2, Idh-l, 6Pgd, Got-l, Ck, Pgm-2, Ca, Gp-1, Gp-2, Gp-3*). The *Me-1* and *Pgm-2* loci only were highly polymorphic, while the other 12 loci were weakly polymorphic. Four samples out of the 23 analysed were characterized by a unique allele (sensu Slatkin 1987): St. Gaudens ($6Pgd^{110}$), Ostia ($Gp\text{-}1^{105}$), Gorgona Island ($Me\text{-}2^{105}$), Elba Island ($Got\text{-}1^{104}$). The results of the contingency χ^2 analysis are given in Table 2. The analysis reveals that 9 out of 12 variable loci exhibit statistically significant heterogeneity in the allele frequencies. This result shows that there are significant differences among the gene pools of the studied samples, indicating local genetic differentiation and a relatively high degree of substructuring among populations. Significant deviations from Hardy-Weinberg equilibrium in the direction of heterozygote deficiences were found in the following populations and loci: Bonn (*Me-l*, P<0.005), Chiusdino (*Gp-3*, P<0.05).

Genetic variability parameters (A, P, H_o, H_e) are reported in Table 3. The overall number of alleles per locus (A) was 1.07, ranging from 1.0 to 1.2. The proportion of polymorphic loci (P) ranged from 0 (Guadarrama, Anso, Albaran, Cavalese, Viotia) to 16.7% (Chiusdino, La Scola Islet), averaging 7.25%. The observed heterozygosity (H_o) showed a similar trend, ranging from 0 (Guadarrama, Anso, Albaran, Cavalese, Viotia) to 0.077 (Elba Islands, La Scola Islet), and averaging 0.028. The samples from Spain, Germany and Greece are characterized by very low levels of genetic variability (Spain: average P = 1.68%, average H_o = 0.007; Germany: P = 3.8%, H_o = 0.015; Greece: P = 0%, H_o = 0) when compared with the ones from France (average P = 5.57%, average H_o = 0.023) and mainland Italy (average P=10.11%, average H_o = 0.036). However, it must be noted that Germany and Greece were represented in the analysis only by a sample respectively. Percent polymorphism and observed heterozygosity detected in island populations from the Tuscan Archipelago (Tyrrhenian Sea) were higher than those found in mainland samples (islands: average P = 9.52%; average H_o= 0.045; mainland: average P = 5.89%; average H_o= 0.022); however the differences in polymorphism and heterozygosity values between mainland and insular samples were not statistically significant (P, P = 0.141; H_o, P = 0.029, t-test). The samples from La Scola and Elba islands show the highest heterozygosity (H_o = 0.077), and the sample from La Scola Islet exhibits the greatest genetic variation, with A = 1.2, P = 16.7%, and H_o = 0.077.

The values of genetic distance for each pairwise comparison are given in Table 4. Nei's genetic distance (D) ranges from 0 to 0.100, averaging 0.036. Based on the analysis of genetic distance data, two main population groups can be recognized: the first includes the samples from Spain and SW France, which are genetically very close (average D = 0.003; D ranging from 0 to 0.010), the second includes all other samples (Germany, Italy, Greece) (average D = 0.017; D ranging from 0 to 0.059; see Table 4). The ave-rage genetic distance between the two groups is relatively high (D = 0.059; D ranging from 0.043 to 0.100). The comparison between the populations from western Europe (Spain, SW France) and Greece (Viotia) gives the highest genetic distances (D ranging from 0.087

to 0.100; see Table 4). Genetic differentiation was rather low among insular populations from the Tuscan Archipelago (average $D = 0.017$; D ranging from 0 to 0.042), and relatively low between insular and mainland populations (average $D = 0.040$).

The genetic relationships among the samples studied are presented in Figure 1. The UPGMA clustering procedure revealed two main clusters in the phenogram constructed on the basis of the matrix of Nei's unbiased genetic distances. The first cluster includes the closely related samples from Spain and SW France. Within the second cluster the existence of four subclusters should be noted. The first subcluster includes the sample from Bonn (Germany), which is linked to the subcluster containing the closely grouped samples from Italy and four Tyrrhenian islands (Elba, Palmaiola, Pianosa, Gorgona), the third includes the samples from other two Tyrrhenian islands, i.e. Scoglietto di Portoferraio and La Scola, the fourth contains the sample from Viotia (Greece).

DISCUSSION

The results of the allozyme analyses indicate that genetic variability is relatively low in *P. muralis*. The Common wall lizard shows values of polymorphism and heterozygosity higher than those estimated by Capula (2004) for *P. raffonei* ($P = 4.8\%$; $H_o = 0.011$), similar to those observed by Capula & Ceccarelli (2003) for Italian populations of *P. sicula* ($P = 10\%$; $H_o = 0.029$), and lower than (i) those detected in the phylogenetically related *P. wagleriana* from Sicily ($P = 15\%$; $H_o = 0.037$; Capula, 1994b) and *P. tiliguerta* from Sardinia and Corsica ($P = 22\%$; $H_o = 0.066$; Capula, 1996), (ii) the average ones calculated by Capula (1990) for nine species of the genus *Podarcis* ($P = 13\%$; $H_o = 0.053$), and (iii) the average ones calculated by Nevo (1978) for 17 species of reptiles ($P = 22\%$; $H_o = 0.047$). The highest values of heterozygosity were found in the samples from Elba Island and La Scola Islet (Tuscan Archipleago, Tyrrhenian Sea), whereas the lowest ones were observed in some samples from Spain (Guadarrama, Anso, Albaran), Italy (Cavalese) and Greece (Viotia). Based on the theory (see e.g. Nei et al. 1975, Gorman et al. 1975, 1978) we expected to find low levels of genetic variability in the insular samples of *P. muralis*. Our results were in some way not congruent with these expectations, as some samples from the Tuscan Archipelago (e.g. Elba, La Scola) were characterized by levels of percent polymorphism and heterozygosity higher than those found in most of the populations from mainland Italy, Spain, SW France, Germany and Greece. This result in agreement with the allozyme data provided by Capula (1997) indicating that the insular *P. muralis* populations from Elba Island, Isolotto di Porto Ercole Islet and Argentarola Islet (Tyrrhenian islands) are characterized by levels of percent polymorphism and heterozygosity higher than those found in the populations from the Italian Peninsula, and much higher than those observed in the continental populations from the Italian Alps, Spain and Austria (Capula 1997). Within the lacertid lizards, levels of genetic variation are known to be large only in mainland populations of a few species (e.g. Adriatic populations of *P. sicula*: average $H_o = 0.09$ (Gorman et al. 1975); *Acanthodactylus* spp.: average $H_o = 0.18$, average $P = 50\%$; Blanc & Cariou 1980), while populations living on relict islands and on tiny fringing islands (i.e. very small islands that are separated by a short linear distance from the mother island or continent) are usually characterized by very low values of per cent polymorphism and heterozygosity (Gorman et al. 1975). However, the investigated Tyrrhenian islands can be considered as relict islands, as their lizard populations are genetically differentiated from the mainland ones. Moreover, one of the islands considered here (Elba) is a large island (223 km^2), while the other (La Scola) is a tiny island (0.016 km^2), and both are separated by a relatively short geographic distance from mainland (peninsular Italy).

Among reptiles, high levels of genetic variation found in populations of some species (e.g. *Podarcis sicula*, *Chemidophorus tigris*) are ascribed to high vagility and consequent low levels of inbreeding (Gorman et al. 1977). This does not seem to be true in the genetically highly variable species of *Acanthodactylus*, as these are territorial lizards (Blanc & Cariou 1980). *Podarcis muralis* is a territorial lizard as well (Steward 1965), but in this case only some populations – almost exclusively island populations (Elba and La Scola: this paper; Elba, Isolotto di Porto Ercole, Argentarola: Capula 1997) – exhibit high genetic variability. As suggested by Capula (1997), this is probably because the insular populations inhabit marginal environments characterized by temporal and ecological instability. According to Lewontin (1974), in such environments no particular genotype is favoured for long periods and natural populations usually show levels of genetic variability higher than those found in more stable environments. On the basis of these considerations, finding greater genetic variability in insular populations of *P. muralis* could indicate that high heterozygosity levels can be preserved after colonization events in marginal populations of vertebrates, unless founder populations are so small that bottleneck effects occur.

The genetic heterogeneity analysis demonstrates a certain amount of genetic differentiation among local populations of *P. muralis*, with a relatively high level of genetic subdivision. Allozyme data show that, at the scale of the study, genetic variation in *P. muralis* is distributed into two major population groups: the first includes the closely relat-

ed samples from Spain and SW France, the second the genetically recognizable samples from Germany, Italy, and Greece. Genetic distance values found between the two groups are relatively high (Nei's *D* ranging from 0.043 to 0.100), although falling below those normally encountered comparing populations of well recognized biological species of the genus *Podarcis* (see e.g. Mayer 1981; Thorpe 1983; Capula 1994a, b, c, 1996). The high genetic affinity between the French and Spanish samples is congruent with their geographic origin, as French samples are from Pyrenean localities (F–H) close to the Spanish ones (A–E). On the other hand, the large geographic distances separating the French localities from the German one (Bonn) could explain the relatively high genetic differentiation observed between the samples from these countries, which cluster separately in the UPGMA phenogram (see Fig. 1).

The data presented here are in agreement with the results of the allozyme investigations carried out by Capula (1997) on some *P. muralis* populations from Italy, Spain and Austria, and are congruent with the results of the molecular investigations (analysis of mitochondrial DNA sequences) carried out by Caputo et al. (2008) and Giovannotti et al. (2010) on several Italian samples, which indicate a certain amount of molecular divergence among *P. muralis* populations, and a pronounced geographical structure of the Italian populations.

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