Biochemical Systematics and Ecology, Vol. 21, No. 3, pp. 373–380, 1993.
Printed in Great Britain.

0305-1978/93 $6.00+0.00

Natural Hybridization in *Podarcis sicula* and *P. wagleriana* (Reptilia: Lacertidae)

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Key Word Index—*Podarcis sicula*; *P. wagleriana*; Lacertidae; Reptilia; hybridization; allozyme electrophoresis; Sicily; Aegadian Islands; Aeolian Islands.

Abstract—An allozyme survey revealed instances of natural hybridization between *Podarcis sicula* and *P. wagleriana* from the Aegadian and Aeolian islands (Sicily). Pure specimens of both species together with F_1 hybrids were found on Vulcano (Aeolian Islands) and Marettimo (Aegadian Islands). Limited evidence of backcrossing was detected on Marettimo. The two hybrid zones were interpreted as secondary overlap zones, being due to the relatively recent extension of the range of *P. sicula* into the peripheral range of *P. wagleriana*. On both islands, hybrids were found only in areas of habitat disturbance. At Lipari (Aeolian Islands) some specimens morphologically recognized as *P. sicula* had an *Idh*-1 allele typical of *P. wagleriana*, although the latter species is not known from the island. This may result from past hybridization and introgression, followed by the extinction of *P. wagleriana* on the island. Natural hybridization between *P. sicula* and *P. wagleriana* was not evidenced on the island of Favignana and in Sicily.

Introduction

Allopatric speciation seems to have been the rule in lacertid lizards (Arnold, 1973, 1989; Guillaume, 1987; Capula *et al.*, 1989), and isolating mechanisms may involve both ecological and behavioral characteristics (Verbeek, 1972). Some evidence of hybridization has been reported within *Lacerta* and *Podarcis*, but in all these cases hybridization was assumed from morphologically intermediate animals or from individuals arising from captive breeding of parent species (Mertens, 1950, 1956, 1964, 1968; Arnold, 1973; Mayer and Tiedemann, 1985).

Little is known about genetic differentiation and successful natural hybridization in lacertid lizards. The best documented cases are those involving speciation by hybridization pointed out in the so-called *Lacerta saxicola* Complex. The electrophoretic examination of bisexual and unisexual species of this Caucasian polymorphic group indicates that the parthenogenetic forms arose as a result of hybridization of distinct biological species (Uzzell and Darevsky, 1973a, 1973b, 1975).

Within the genus *Podarcis* the only known case for which natural hybridization has been documented by allozyme data is that of the *P. melisellensis* population from the Adriatic island of Pod Mrčaru (Yugoslavia) (Gorman *et al.*, 1975). The electrophoretic analysis shows that the Pod Mrčaru population has three presumed alleles that are unique among *P. melisellensis* populations. Two of these alleles (*Est*-4^b and *Gp*-1^a) are electrophoretically identical with alleles found in *P. sicula*, which is not sympatric with *P. melisellensis* on Pod Mrčaru. The evidence is circumstantial, and it is difficult to explain the absence of *P. sicula* on this island, but hybridization and introgression are strongly implicated (Gorman *et al.*, 1975).

In this paper we report the first genetic instance of natural hybridization between *P. sicula* and *P. wagleriana*. This phenomenon was detected studying allozyme variation in a number of populations of *P. sicula* and *P. wagleriana* from Sicily, Aegadian Islands and Aeolian Islands. *Podarcis sicula* occurs as autochthonous species in peninsular Italy, Sicily, Sardinia, along the Adriatic coast of Yugoslavia, and in a number of Tyrrhenian and Adriatic islands (Henle and Klaver, 1986). *Podarcis wagleriana* inhabits

(*Received* 21 *April* 1992)

Sicily (with the exception of the NE part) and some minor Sicilian islands (Aegadian, Stagnone, Aeolian) (Böhme, 1986; Capula *et al.*, 1987; Capula, 1990). In Sicily and on Favignana, Levanzo, and Marettimo (Aegadian Islands), as well as on Isola Grande (Stagnone Islands), and Vulcano (Aeolian Islands) the pattern of distribution is completely interdigitating and both species are broadly sympatric (Capula, 1990). At the morphological level, identification of *P. wagleriana* and *P. sicula* in the localities where they coexist may be difficult. In fact, these two lacertid lizards are quite similar in most anatomical features, differing slightly only in colour pattern (Arnold and Burton, 1978). On the other hand, the detection of electrophoretically diagnostic loci between the two species allows a correct identification of all individuals, either in allopatry or in overlapping areas (Capula *et al.*, 1990).

Materials and Methods

Samples were obtained from 10 localities of Sicily, Aegadian Islands, and Aeolian Islands (Table 1, Fig. 1). In 8 out of these localities *P. sicula* and *P. wagleriana* were sympatric. In order to identify morphologically doubtful specimens and to detect natural hybrids between *P. sicula* and *P. wagleriana* we first suspected at Vulcano, the electrophoretic analysis was undertaken for 302 specimens from all 10 localities.

Collected specimens were anesthesized with ethyl ether and then dissected. Homogenates were stored below −70°C. Standard horizontal starch gel electrophoresis was performed on leg muscle tissue, which was crushed in distilled water. Homogenates from single individuals were absorbed into 5×5 mm pieces of chromatography paper (Whatman 3 MM) and inserted in 10% Connaught starch gel trays. Electrophoresis was carried out at 7–9 V/cm for 4–6 h at 5°C. After the run, gels were sliced in two parts and each slice was stained for a specific enzyme. Gene products for the following presumptive enzyme loci were analysed: glycerol-3-phosphate dehydrogenase (E.C. 1.1.1.8, αGpd), 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, 6*Pgd*), glyceraldehyde-3-phosphate dehydrogenase (E.C. 1.2.1.12, *Gapd*), superoxide dismutase (E.C. 1.15.1.1, *Sod*), purine nucleoside phosphorylase (E.C. 2.4.2.1, *Np*), glutamate-oxaloacetate transaminase (E.C. 2.6.1.1, *Got*-1, *Got*-2), creatine kinase (E.C. 2.7.3.2, *Ck*), adenylate kinase (E.C. 2.7.4.3, *Ak*), phosphoglucomutase (E.C. 2.7.5.1, *Pgm*-1, *Pgm*-2), adenosine deaminase (E.C. 3.5.4.4, *Ada*), carbonic anhydrase (E.C. 4.2.1.1, *Ca*), mannose phosphate isomerase (E.C. 5.3.1.8, *Mpi*), glucose phosphate isomerase (E.C. 5.3.1.9, *Gpi*). In addition, three unidentified non-enzymatic proteins ('general proteins', *Gp*-1, *Gp*-2, *Gp*-4) were studied. Only four loci showed different frequencies between reference populations (diagnostic loci): *Gapd* (continuous Tris/citrate buffer, pH 8.0), *Got*-1

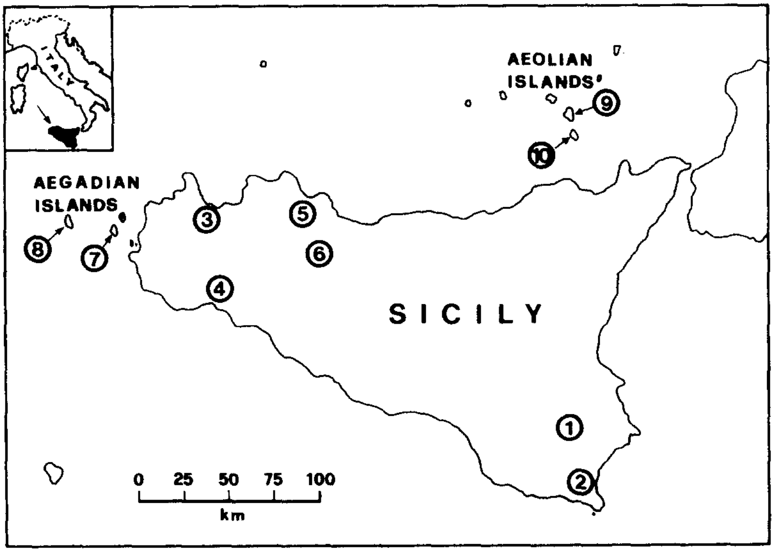

FIG. 1. MAP OF SICILY, AEGADIAN ISLANDS, AND AEOLIAN ISLANDS SHOWING LOCALITIES FROM WHICH LIVING MATERIAL WAS EXAMINED BIOCHEMICALLY. 1, Palazzolo Acreide; 2, Portopalo; 3, Castellammare del Golfo; 4, Selinunte; 5, Palermo; 6, Ficuzza; 7, Favignana; 8, Marettimo; 9, Lipari; 10, Vulcano. Insert shows location of the study area.

(Phosphate/citrate buffer, pH 6.3), and two unidentified non-enzymatic proteins (*Gp*-1, *Gp*-2) (discontinuous Tris/citrate–Poulik buffer, pH 8.7). These loci were found to be diagnostic also between allopatric populations of *P. sicula* (from continental Italy) and *P. wagleriana* (from Sicily) (Capula, 1990). At these loci no common allele was shared between *P. sicula* and *P. wagleriana*, and hybrids were characterized by heterozygous patterns (see Fig. 2). Electrophoretic procedures (staining techniques, loci and allele designations) were those described by Nascetti *et al.* (1988) and Capula (1990).

The BIOSYS-1 program of Swofford and Selander (1981) was used to quantify differentiation between samples. The amount of genetic divergence between populations was evaluated using Nei's (1978) unbiased genetic distance (*D*).

Results

The electrophoretic analysis of the populations from Sicily revealed genetically pure *P. sicula* and *P. wagleriana* in areas of sympatry (localities 1–5) as well as in allopatry (locality 6) (Table 1), the samples studied always showing fixed differences at the four diagnostic loci. *Podarcis sicula* was homozygous for the following alleles: *Gapd*^{100}, *Got*-1^{100}, *Gp*-1^{100}, *Gp*-2^{100}. *Podarcis wagleriana* was homozygous for *Gapd*^{94}, *Got*-1^{105}, *Gp*-1^{105}, and *Gp*-2^{95}. The samples of *P. sicula* and *P. wagleriana* from localities 1–6 (Sicily) were genetically quite distinct, with Nei's average $D = 0.416$ based on the analysis of 26 loci (five monomorphic, 21 polymorphic).

Table 1 shows the frequencies of parental types, presumptive F$_1$ hybrids, and backcross progeny (an F$_1$ individual was expected to have the following genotypes: *Gapd*$^{94/100}$, Got-1$^{100/105}$, Gp-1$^{100/105}$, Gp-2$^{95/100}$). The data from the other loci were compatible with the interpretations in Table 1.

Natural hybridization was detected only on Marettimo and Vulcano, and possibly on Lipari. At Marettimo, genetically pure *P. sicula* and *P. wagleriana*, together with two F$_1$ hybrids were found, and the rate of hybridization was relatively low (frequency of hybrids = 0.078). Moreover, two backcrossed individuals were found, thus indicating limited introgression between the two species on this island. These two specimens were probably backcrosses to *P. sicula*, as they were characterized by a *P. sicula*-like morphological pattern (Fig. 3), and showed the same electrophoretic alleles of *P. sicula* at three out of four diagnostic loci (*Gapd*^{100}, *Gp*-1^{100}, *Gp*-2^{100}). At *Got*-1 however, these

TABLE 1. COLLECTING LOCALITIES FOR *PODARCIS SICULA* AND *P. WAGLERIANA* AND NUMBERS OF PARENTAL TYPES (in parentheses) AND HYBRIDS IDENTIFIED ELECTROPHORETICALLY FROM EACH SITE

Locality	Taxon		Number of hybrids
1. Palazzolo Acreide (Sicily)	*P. s. sicula*	(15)	0
	P. w. wagleriana	(4)	
2. Portopalo (Sicily)	*P. s. sicula*	(4)	0
	P. w. wagleriana	(5)	
3. Castellammare del Golfo (Sicily)	*P. s. sicula*	(4)	0
	P. w. wagleriana	(10)	
4. Selinunte (Sicily)	*P. s. sicula*	(21)	0
	P. w. wagleriana	(11)	
5. Palermo (Sicily)	*P. s. sicula*	(8)	0
	P. w. wagleriana	(10)	
6. Ficuzza (Sicily)	*P. w. wagleriana*	(8)	0
7. Favignana (Aegadian Islands)	*P. s. sicula*	(11)	0
	P. w. wagleriana	(18)	
8. Marettimo (Aegadian Islands)	*P. s. sicula*	(15)	4*
	P. w. marettimensis	(32)	
9. Lipari (Aeolian Islands)	*P. s. sicula*	(16)	5†
10. Vulcano (Aeolian Islands)	*P. s. sicula*	(72)	15‡
	P. w. antoninoi	(14)	

*Two F$_1$ hybrids and two progeny from backcrossing to *P. sicula*.
†All presumed hybrids of undetermined status (see text).
‡All F$_1$ hybrids.

specimens were homozygous for the allele diagnostic of *P. wagleriana* (*Got*-1^{105}). This electromorph has not been detected in *P. sicula* (Capula *et al.*, 1987, 1990; Capula, 1990). The Nei's *D* value observed between *P. sicula* and *P. wagleriana* from Marettimo was low ($D = 0.384$) relative to that found between Sicilian populations of the two species. Marettimo is characterized by an area of 12.06 km^2, and it is the least altered island of the Aegadian Archipelago. *Podarcis wagleriana* is widespread on this island, while *P. sicula* is very localized, occurring only in the vicinity of the Marettimo village. *Podarcis wagleriana* seems to have colonized actively Marettimo (Capula, 1990), while *P. sicula* was probably introduced by man at the end of the last century (Taddei, 1949). *Pocarcis sicula* and *P. wagleriana* coexist only in the degraded fields and secondary maquis areas near the tiny village of Marettimo; the two species meet and hybridize only in a very narrow zone (no more than a few hundred metres in width).

At Vulcano, an island located about 230 km from Marettimo, we detected genetically pure *P. sicula* and *P. wagleriana* together with 15 F_1 hybrids. The rate of hybridization was higher than that observed at Marettimo (frequency of hybrids = 0.148). Hybrid specimens had atrophied gonads and appeared morphologically intermediate between the parent species (Fig. 4). It is perhaps more than coincidence that the Nei's *D* value observed between *P. sicula* and *P. wagleriana* from Vulcano was much lower ($D = 0.307$) than that found between the Sicilian populations of these species. This and the high frequency of hybrids suggest the occurrence of past introgression. Vulcano, with an area of 21.2 square kilometers, is one of the most anthropized Aeolian Islands, having suffered intense habitat alteration due to fire, deforestation, and human touristic activities during the last 20 years (Racheli, 1976). *Podarcis sicula* is widespread and abundant on Vulcano. The species was probably introduced to the island by man in historical times (Capula *et al.*, 1987, 1990), and it seems to have replaced most of the original populations of *P. wagleriana*. As a consequence, *P. wagleriana* has become very rare, and is presently confined to two sites, one in the southern part of the island and the other in the northern part. *Podarcis sicula* and *P. wagleriana* meet and hybridize in these sites, and the overlap zones are wider (about 2 km in width) than that found at Marettimo.

At Lipari, five out of 21 analysed specimens, all of which were morphologically identified as *P. sicula*, were homozygous for an allele (*Idh*-1^{106}) previously known only in *P. wagleriana*. These five specimens were homozygous for the alleles of *P. sicula* at the four diagnostic loci. At present, *P. wagleriana* seems absent from Lipari (Mertens, 1952, 1955; Lanza, 1973; Böhme, 1986; Capula, 1990). The occurrence of *Idh*-1^{106}, however, indicates (i) that *P. wagleriana* has gone extinct on the island, possibly due to competition with the more opportunistic *P. sicula* (Capula *et al.*, 1987; Capula, 1992), and (ii) that when the two species were sympatric on the island, they met and hybridized.

Discussion

Evidence of natural hybridization between *P. sicula* and *P. wagleriana* was not observed in Sicily, where these species appeared to be genetically well differentiated. This testifies to the existence of effective isolating mechanisms, which are probably the result of relatively ancient contact between the two species in the island.

On the other hand, some F_1 hybrids and backcrossed individuals were found on Marettimo, and a high rate of hybridization was detected on Vulcano, where the hybrid zone was wider than that found on Marettimo. Evidence of possible past hybridization and introgression between *P. sicula* and *P. wagleriana* was documented on Lipari, where the local *P. sicula* population seems to have incorporated in its genome some genetic character of a now extinct population of *P. wagleriana*.

These data indicate that free interbreeding between the two species is unlikely, but

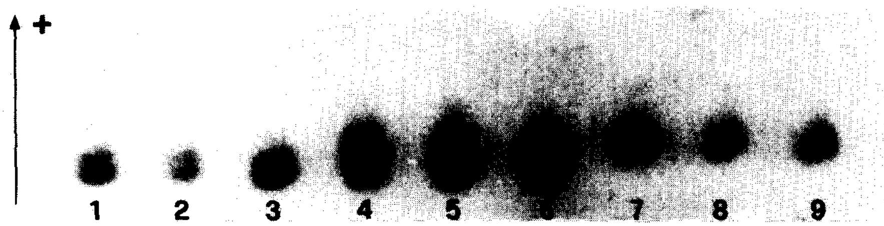

FIG. 2. GLUTAMATE-OXALOACETATE TRANSAMINASE-1 (*Got*-1) PHENOTYPES FOR *PODARCIS SICULA*, F_1 HYBRID *P. SICULA* × *P. WAGLERIANA*, AND *P. WAGLERIANA*. 1–3, *P. sicula* (slow allelic product); 4–6, F_1 hybrids *P. sicula* × *P. wagleriana* (triple banded pattern indicating heterozygous genotype for this dimeric enzyme); 7–9, *P. wagleriana* (fast allelic product).

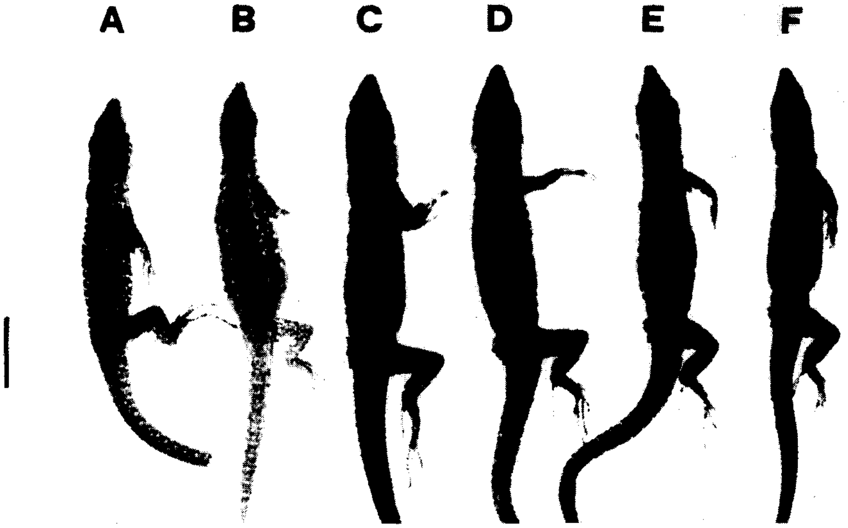

FIG. 3. MORPHOLOGICAL PATTERN OF *PODARCIS SICULA* (A, B), F_1 HYBRID *P. SICULA* × *P. WAGLERIANA* (C), BACKCROSS TO *P. SICULA* (D), *P. WAGLERIANA* (E, F) FROM THE ISLAND OF MARETTIMO. Scale bar = 2 cm.

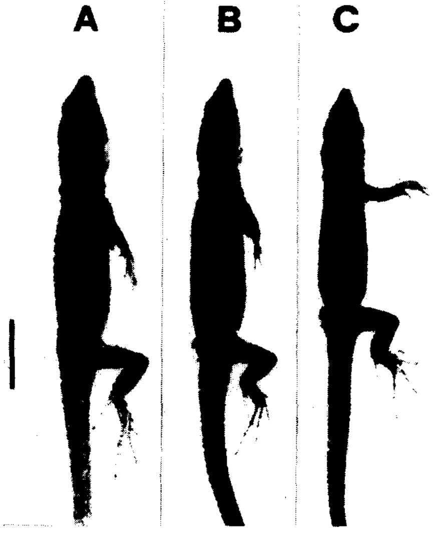

FIG. 4. MORPHOLOGICAL PATTERN OF *PODARCIS SICULA* (A), F_1 HYBRID *P. SICULA* × *P. WAGLERIANA* (B), *P. WAGLERIANA* (C) FROM THE ISLAND OF VULCANO. Scale bar = 2 cm.

that limited hybridization and backcrossing has occurred on some small islands around Sicily (Aegadian and Aeolian), where *P. sicula* and *P. wagleriana* have recently come into contact.

Since evidence of the predominance of allopatric differentiation in *Podarcis* lizards is strong (Gorman *et al.*, 1975; Arnold, 1989; Capula *et al.*, 1989; Capula, 1990), we consider that natural hybridization between *P. sicula* and *P. wagleriana* is the result of a recent overlap in the above mentioned islands of genetically well differentiated species, in which pre-mating isolating mechanisms may have not operated owing to the very particular selective pressures acting in the microinsular ecosystems or to some environmental perturbation. As is usually the case in biogeographic studies, we lack evidence as to the past history of contact zones between *P. sicula* and *P. wagleriana*. However, we can tentatively interpret the two hybrid zones found on Marettimo and Vulcano as secondary overlap zones (see Mayr, 1949; Barton, 1979; Barton and Hewitt, 1985; White, 1985; Hewitt, 1988) as they are probably due to the relatively recent extension of the range of *P. sicula*—that would have spread through passive transport—into the peripheral range of *P. wagleriana*.

It is well known that cases of natural hybridization are often associated with habitat alteration (Woodruff, 1973; Sbordoni *et al.*, 1982). In the case of Aegadian and Aeolian populations of *P. sicula* and *P. wagleriana*, habitat disturbance related to human activity appears to have clearly influenced either the present distribution of the lizards (e.g., the accidental introduction of *P. sicula* by man on Marettimo and Vulcano), or the extent of sympatry. Habitat alteration of insular ecosystems could have also weakened premating isolation of the two lacertid lizards. This hypothesis requires further investigation, but on Marettimo and Vulcano the two species do coexist in areas of local habitat disturbance only. It is perhaps more than coincidence that on these islands natural hybridization appears restricted to such environmental circumstances.

Acknowledgements—The author wishes to extend his gratitude to L. Bullini and G. Nascetti, who provided facilities, financial support, and assistance during the electrophoretic analysis and made helpful comments on the earlier drafts of the manuscript. The author is gratefully indebted also to Maurizio Sarà and Gabriele Sorci for direct help in the field and logistical advice during collecting lizards in western Sicily, to Ingrid Schatz, who assisted diligently through two field seasons in Sicily and Aegadian Islands, and to the anonymous reviewer for suggesting improvements in the manuscript.

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