

SIZE AND SHAPE IN MEDITERRANEAN INSULAR LIZARDS: PATTERNS OF VARIATION IN *PODARCIS RAFFONEI*, *P. SICULA* AND *P. WAGLERIANA* (REPTILIA: SQUAMATA: LACERTIDAE)

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ABSTRACT Landmark based geometric morphometrics was applied to the analysis of the cephalic scales of three phylogenetically related lacertid lizards (*Podarcis raffonei*, *P. sicula*, *P. wagleriana*) from some islands of the central Mediterranean area in order to assess the pattern of geographic variation and the phenetic relationships among and within the three species. Twenty nine homologous landmarks were recorded on the half configuration of the cephalic scales. To compare geometric and biometric patterns of variation and to evaluate any static allometry, seven biometric measurements were also recorded on the whole body. The three species significantly differ from each other in both shape and size of the skull. The shape of the Supraocular and the Parietal scales appears to be highly diagnostic and species-specific. The analysis of intraspecific variation in shape of the cephalic scales indicates that *P. sicula* is the less variable species within the studied geographic area, whereas *Podarcis raffonei* is the most variable species both in size and shape. *Podarcis raffonei* is characterized by a divergent allometric pattern, likely related to the small population size and highly fragmented geographic range of the species.

KEY WORDS Geometric morphometrics, biometry, geographic variation, *Podarcis*, Lacertidae, Sicily

INTRODUCTION

The genus *Podarcis* Wagler, 1830 comprises 20 currently recognized species. Most of the species occur in southern Europe, where they are the predominant reptile group in terms of biomass (Harris & Arnold, 1999). Many studies have been devoted to investigate genetic and molecular variation in several species of this genus (e.g. Capula, 1994a, 2004; Oliverio et al., 1998; Harris & Arnold, 1999; Capula & Ceccarelli, 2003; Poulakakis et al., 2003; Arnold et al., 2007; Caputo et al., 2008), while only a few data are available about the pattern of morphometric variation of some species (e.g. Bruner & Costantini, 2007; Kaliontzopoulou et al., 2007). The insular Mediterranean *Podarcis* lizards seem to be particularly useful for the analysis of morphological variation - which can highlight microevolutionary processes of divergence and adaptation (cf. Heywood, 2000) - because they are normally characterized by high inter- and intra-population morphological variability (e.g. Arnold & Ovenden, 2002; Corti & Lo Cascio, 2002).

In this paper we investigate the morphometric relationships among three phylogenetically related lacertid lizards of the genus *Podarcis* occurring on some islands of the central Mediterranean area, i.e. *P. raffonei* (Mertens, 1952), *P. sicula* (Rafinesque, 1810) and *P. wagleriana* Gistel, 1868. *Podarcis raffonei* is endemic to the Aeolian Islands, where it is sympatric with *P. sicula* on Vulcano Island (Capula, 1994a, 2004; Corti & Lo Cascio, 2002). *Podarcis raffonei* has recently received attention because it is threatened with extinction (Capula et al., 2002; Capula, 2004, 2006a; Capula & Lo Cascio, 2006). *Podarcis sicula* occurs in peninsular Italy, in Sicily, along the Adriatic coast of Dalmatia and in a

number of Tyrrhenian and Adriatic islands (Henle & Klaver, 1986; Corti & Lo Cascio, 2002). *Podarcis sicula* appears to be an efficient colonizer, as it has been successfully introduced and acclimatized to several extralimital areas (cf. Capula, 1994b; Corti & Lo Cascio, 2002 for an updated list of localities). *Podarcis wagleriana* is endemic to Sicily and some small satellite islands (Egadi Islands and Stagnone Islands) (Arnold & Ovenden, 2002; Corti & Lo Cascio, 2002; Capula, 2006b), and is broadly sympatric with *P. sicula*. The three species are anatomically and ecologically similar (cf. Lanza, 1968; Sorci, 1990; Capula, 1992; Arnold & Ovenden, 2002; Corti & Lo Cascio, 2002; Capula & Ceccarelli, 2006). Their colour patterns are also similar, but *P. raffonei* typically has dark markings on the throat, while *P. sicula* has a throat which is normally white and unspotted (Arnold & Ovenden, 2002; Corti & Lo Cascio, 2002). *Podarcis wagleriana* has a throat which is generally salmon red and, in some cases at least (e.g. Marettimo Island populations), it may have dark markings. Therefore, morphological identification of the species may be difficult, especially in the areas where they coexist (e.g. Sicily and Egadi Islands, where *P. sicula* and *P. wagleriana* occur sympatrically, and Vulcano Island, where *P. sicula* and *P. raffonei* are known to coexist). In spite of this, no comparative morphometric investigation has been carried out on the above mentioned species to date.

To assess the pattern of geographic variation and the relationships among and within the three species, geometric morphometrics of the cephalic scales was compared with traditional biometry. Geometric morphometrics has several advantages over traditional

methods, as (i) it provides independent description of size and shape variation, (ii) it can be used with multivariate statistics to test for statistical differences in shape (Bookstein 1991; Bookstein 1996; Marcus et al., 1996), (iii) it makes it possible to relate shape variation to other sets of independent variables, i.e. size, latitudinal gradients, etc., and (iv) it can be used to describe differences in shape among objects in terms of deformation grids (Adams et al., 2004). This is possible because the geometry of shape is preserved throughout the analysis.

MATERIALS AND METHODS

All the samples analysed were from three central Mediterranean insular areas, namely Sicily, Egadi Islands and Aeolian Islands. For comparative analysis (biometric analyses only), two samples of *Podarcis sicula* from the southern Italian Peninsula (Calabria) were also used (Fig. 1). Details regarding geographic origin and number of specimens analyzed are reported in tab. 1. All the lizards studied were obtained from the collections of the Museo Civico di Zoologia di Roma (Italy). The same lizards analysed here were previously used for allozyme studies (Capula, 1994a, 1994b, 2004, 2006a).

To avoid any problem in species recognition, the identification of the individuals studied was based both on (1) throat colouration pattern (*P. raffonei*: dark markings on the throat; *P. sicula*: white and unspotted throat; *P. wagleriana*: salmon red throat, in some cases at least with small dark markings; cf. Arnold & Ovenden, 2002), and (2) recognition of alternative alleles at the Ada electrophoretic locus (*P. raffonei*: Ada¹⁰³; *P. sicula*: Ada¹⁰⁰; *P. wagleriana*: Ada¹¹⁰), according to previous allozyme analyses of the same individuals by Capula (1994a).

In this paper landmark based morphometrics has been applied to analyse the cephalic scales of the three *Podarcis* lizards described above. Lacertid lizards have well-shaped cephalic scales which are easily distinguishable and the geometric properties of which make them suitable markers for taxonomic, biogeographical and phylogenetic studies (cf. Arnold, 1989; Bruner et al., 2005; Bruner & Costantini, 2007; Kaliontzopoulou et al., 2007). Twenty nine homologous landmarks were recorded on the half configuration of the cephalic scales of 109 adult males of the three species (*P. raffonei*, N = 13; *P. sicula*, N = 47; *P. wagleriana*, N = 49; see tab. 1; for nomenclature of the analysed scales see fig. 2). Females were not analysed in order to avoid problems in the analyses due to sex-related morphological differences. The low number of *P. raffonei* individuals used for the analysis is because the species is at present critically endangered (IUCN, 2007) and extremely rare (Capula et al., 2002; Capula, 2006a); we decided to

analyse the specimens stored in the museum collections only and to not collect other individuals in the field in order to avoid depletion of the few, very small and protected remaining populations of *P. raffonei*. Only lizards with a snout-vent length (SVL) ≥ 5 cm, i.e. sexually mature lizards, were considered for the analysis. Digital images of the dorsal part of the skulls were recorded by placing the head of the lizard under a binocular microscope connected to a digital camera and a PC (Leica QuantiLite Image Acquisition System[®]), taking care of distortions and scale as described by Bruner et al. (2005). A file with list and address of images was created through tpsUtil (Rohlf, 2006) to allow the consecutive recording of landmarks on predefined groups of specimens. Cartesian x and y coordinates of landmarks were recorded on digital images using the tpsDig program (Rohlf, 2006). The centroid of each configuration was translated to the origin, and configurations scaled to a common, unit centroid size (Bookstein, 1986). Centroid sizes were extracted through tpsRelw (Rohlf, 2006) and stored in a separate file for successive analyses. The configurations were optimally rotated to minimize the squared differences between corresponding landmarks (Gower, 1975; Rohlf & Slice, 1990) by using the Generalized Procrustes Analysis (GPA, Rohlf & Slice, 1990) in the tpsRelw (Rohlf, 2006) and Morphue (Slice, 1994-1999) programs. Landmark vectors of all configurations were first plotted and visualised to detect wildly incorrect or mislabelled points rapidly. Size variation among and within species was examined through ANOVA and MANOVA of centroid sizes. Shape differences were evaluated through the analysis of the residuals from superimposition (partial warp scores). Ordination of specimens was obtained through Relative Warp Analysis run on the partial warp scores (weight matrix), using the tpsRelw program, by setting the parameter α to 0, as recommended for exploratory analyses (Rohlf, 1996). The same program was used to produce the thin plate spline transformation grids associated with variation along the relative warp axes. Relative warp scores with eigenvalues greater than zero were used as data input for a canonical variate analysis. The tpsRegr program (Rohlf, 2006) was used to correlate shape coordinates with variation along the first canonical axes, and to produce transformation grids of shape changes associated with the patterns observed in the canonical space.

Seven biometric measurements were also recorded on 135 adult males (*P. raffonei*, N = 13; *P. sicula*, N = 76; *P. wagleriana*, N = 46; see tab. 1) using a precision caliper (± 0.1 mm), following the standards provided by Guillaume (1987), in order to compare geometric and biometric patterns of variation and to evaluate any static

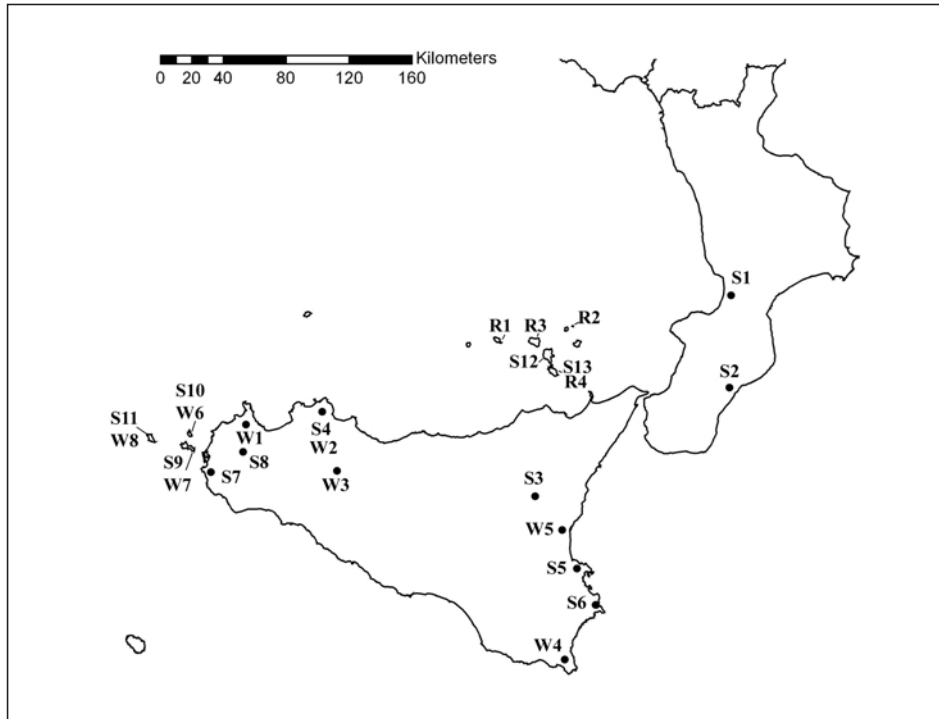


Fig. 1 Map of Sicily and Southern Italy showing sampling localities (for sample codes see table 1).

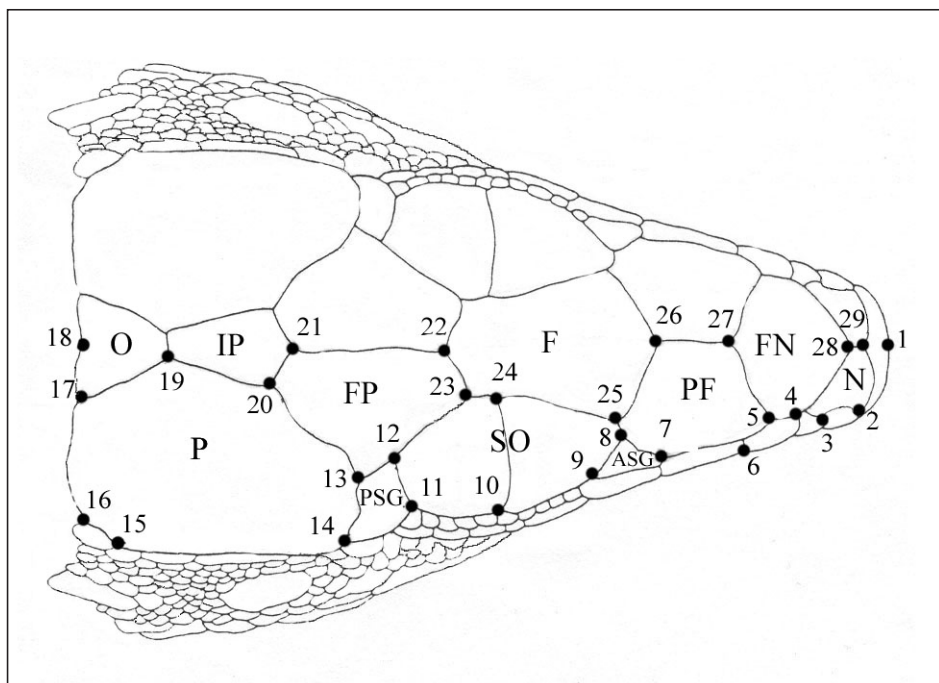


Fig. 2 Localization of landmarks recorded on the cephalic scales of *Podarcis* lizards. ASG = anterior supraciliar granule; F = frontal; FN = frontonasal; FP = frontoparietal; IP = interparietal; N = nasal; O = occipital; P = parietal; PF = prefrontal; PSG = posterior supraciliar granule; SO = sopraocular.

Species	Locality	Nb	Ngm	Code
<i>Podarcis sicula</i>	Trecchina (S Italy)	10	0	S1
<i>Podarcis sicula</i>	Catanzaro (S Italy)	6	0	S2
<i>Podarcis sicula</i>	Linguaglossa (Sicily)	7	7	S3
<i>Podarcis sicula</i>	Monte Pellegrino (Sicily)	11	11	S4
<i>Podarcis sicula</i>	Targia (Sicily)	3	3	S5
<i>Podarcis sicula</i>	Sortino (Sicily)	7	7	S6
<i>Podarcis sicula</i>	Marsala (Sicily)	6	5	S7
<i>Podarcis sicula</i>	Erice (Sicily)	4	5	S8
<i>Podarcis sicula</i>	Favignana Island (Egadi Islands)	5	5	S9
<i>Podarcis sicula</i>	Levanzo Island (Egadi Islands)	4	0	S10
<i>Podarcis sicula</i>	Marettimo Island (Egadi Islands)	5	0	S11
<i>Podarcis sicula</i>	Lipari Island (Aeolian Islands)	4	4	S12
<i>Podarcis sicula</i>	Vulcano Island (Aeolian Islands)	4	0	S13
Total		76	47	
<i>Podarcis wagleriana</i>	Zingaro (Sicily)	3	3	W1
<i>Podarcis wagleriana</i>	Monte Pellegrino (Sicily)	8	8	W2
<i>Podarcis wagleriana</i>	Ficuzza (Sicily)	6	6	W3
<i>Podarcis wagleriana</i>	Porto Palo (Sicily)	1	1	W4
<i>Podarcis wagleriana</i>	Simeto (Sicily)	1	2	W5
<i>Podarcis wagleriana</i>	Levanzo Island (Egadi Islands)	3	3	W6
<i>Podarcis wagleriana</i>	Favignana Island (Egadi Islands)	4	4	W7
<i>Podarcis wagleriana</i>	Marettimo Island (Egadi Islands)	20	22	W8
Total		46	49	
<i>Podarcis raffonei</i>	La Canna Islet (Aeolian Islands)	1	1	R1
<i>Podarcis raffonei</i>	Strombolicchio Islet (Aeolian Islands)	5	5	R2
<i>Podarcis raffonei</i>	Scoglio Faraglione Islet (Aeolian Islands)	3	3	R3
<i>Podarcis raffonei</i>	Vulcano Island (Aeolian Islands)	4	4	R4
Total		13	13	

Tab. 1 Geographic and collecting data for *Podarcis sicula*, *P. wagleriana* and *P. raffonei* samples used in the present study. Nb = number of individuals utilized for biometrical analysis; Ngm = number of specimens utilized for geometric morphometrics of the dermal skull. For geographic origin of the studied material see figure 1.

Characters	<i>P. sicula</i> (N = 76)		<i>P. wagleriana</i> (N = 46)		<i>P. raffonei</i> (N = 13)	
	X	SE	X	SE	X	SE
SVL	66.13	0.860	61.81	0.897	71.71	2.003
HL	16.96	0.231	14.92	0.207	16.83	0.310
HH	0.69	0.013	0.58	0.012	0.68	0.024
AL	25.54	0.311	22.03	0.305	25.03	0.729
PL	42.80	0.581	39.82	0.569	43.47	1.013
FL	21.62	0.269	21.11	0.827	21.20	0.402
TL	143.26	2.183	128.25	4.040	149.25	6.238

Tab. 2 Mean (X) and Standard Error (SE) of seven biometric characters in *P. sicula*, *P. wagleriana*, and *P. raffonei*. AL = hind leg length, FL = hind foot length, HH = head height, HL = head length, PL = forefoot length, SVL = snout-vent length; TL = tail length.

allometry (sensu Klingenberg, 1996). The following biometric measurements were registered: SVL = snout-vent length; HL = head length, HH = head height, AL = hind leg length, PL = forefoot length, FL = hind foot length, TL = tail length (original tails only). Ranges of variation and covariation of biometric characters were explored through ANOVA and MANOVA. Static allometry was investigated through regression analysis and Partial Least Square analysis using tpsPLS (Rohlf, 2006) comparing centroid size, shape variables, and biometric characters.

All analyses were performed at the Laboratorio di Morfometria Geometrica of the Museo Civico di Zoologia di Roma.

RESULTS

Interspecific variation

To depict the morphometric relationships among *Podarcis raffonei*, *P. sicula*, and *P. wagleriana*, the partial warp scores and the uniform components of all samples were used as input data for relative warps and canonical variate analysis. The results are shown in fig. 3. Ordination of individuals along the first and second relative warps (accounting for 28.43 % of cumulative variance) shows a clear separation of *P. sicula* from *P. wagleriana*, while *P. raffonei* is characterized by a wide range of variation and overlap with the other two species. On the other hand, multivariate discrimination between the three taxa is highly significant (Wilk's lambda = 0.1813; $F = 81.59$; $P < 0.0001$), and the species are clearly distinct along both the first and the second canonical variate axes (Fig. 4). Transformation grids related to extremes of variation along the first canonical axis (accounting for 96 % of total variance) indicate that major differences regard the shape of the Parietal, the Supraocular, the Posterior supraciliar granule, and the Anterior supraciliar granule scales (respectively P, SO, PSG, ASG in fig. 2). The skull of *Podarcis sicula*, lying at one extreme of variation, is characterized by a narrower rostral and nasal region with respect to the central portion, while *P. wagleriana* shows the opposite pattern, i.e. the rostral and nasal regions are wider than the central part. In this context, the skull of *P. raffonei* is intermediate between *P. sicula* and *P. wagleriana*. The shape of the Supraocular and Parietal scales appears to be useful for the taxonomic analysis. More specifically, Supraocular scales are much larger and wider in *Podarcis sicula* than in *P. wagleriana*, while in *P. raffonei* the shape of these scales is intermediate between *P. sicula* and *P. wagleriana*. This is clearly recognizable in the pictures shown in fig. 5. The observed modifications in the shape of the Supraocular scale are

related to the modifications of the shape of the Parietal scale, which appears to be diagnostic too between *P. sicula* and *P. wagleriana*.

MANOVA of centroid size for the three species indicates a significant size difference ($F = 5.45$; $P = 0.0053$). The skull of *Podarcis sicula* (mean $CS_{Ps} = 5886$) is larger than that of *P. wagleriana* (mean $CS_{Pw} = 5528$), and smaller than that of *P. raffonei* (mean $CS_{Pr} = 6094$).

In tab. 2 the means and standard errors of the seven biometric characters analysed are reported. *Podarcis wagleriana* shows the smallest body length (Mean SVL = 61.81 ± 0.90), while *P. raffonei* is the largest species (Mean SVL = 71.71 ± 2.00). The snout-vent length of *Podarcis sicula* is intermediate between those of *P. raffonei* and *P. wagleriana* (Mean SVL = 66.57 ± 0.88). No relationship was found between the shape and the centroid size of the skull, as indicated by the regression coefficient of the PLS analysis ($r = 0.44087$; percentage of correlation = 12 %; percent of squared singular value = 93 %). Differences in the size of the skull (HL) are not related to differences in snout-vent length (SVL) ($r = 0.066$; $P = 0.23$, fig. 6), suggesting a different allometric static pattern among the three species (sensu Klingenberg, 1996). *Podarcis wagleriana* is characterized both by a small head and body length, while *P. sicula* has a head larger than *P. wagleriana* and a body length which is intermediate between *P. wagleriana* and *P. raffonei*. *Podarcis raffonei* shows the largest body length, but its head size is intermediate between *P. sicula* and *P. wagleriana*. The allometric patterns within the three species were investigated through the analysis of variation of snout-vent length (SVL) vs head length (HL). As it is evident from fig. 7, *P. raffonei* shows the most diverging pattern, differing in both intercept and slope coefficients (intercept = 6.18; slope = 0.14; $r = 0.91$; $F = 126.53$, $P < 0.0001$), while *P. wagleriana* and *P. sicula* show similar patterns (intercept = 1.30 and -0.23, respectively; slope = 0.22 and 0.26, respectively).

Intraspecific variation

The analysis of relative warp scores for each sample provided further information concerning the extent and distribution of morphometric variation among populations of each species. Box plots of the first (RW1) and the second (RW2) relative warps scores (accounting for 15.99 % and 12.43 % of total variance respectively) for individual populations are shown in fig. 8. *Podarcis sicula* is characterized by reduced morphometric variation of the skull, and no morphometric gap is evident between the samples from the small islands (Favignana Island, Lipari Island) and those from Sicily. The situation is different in *P. wagleriana*, where the

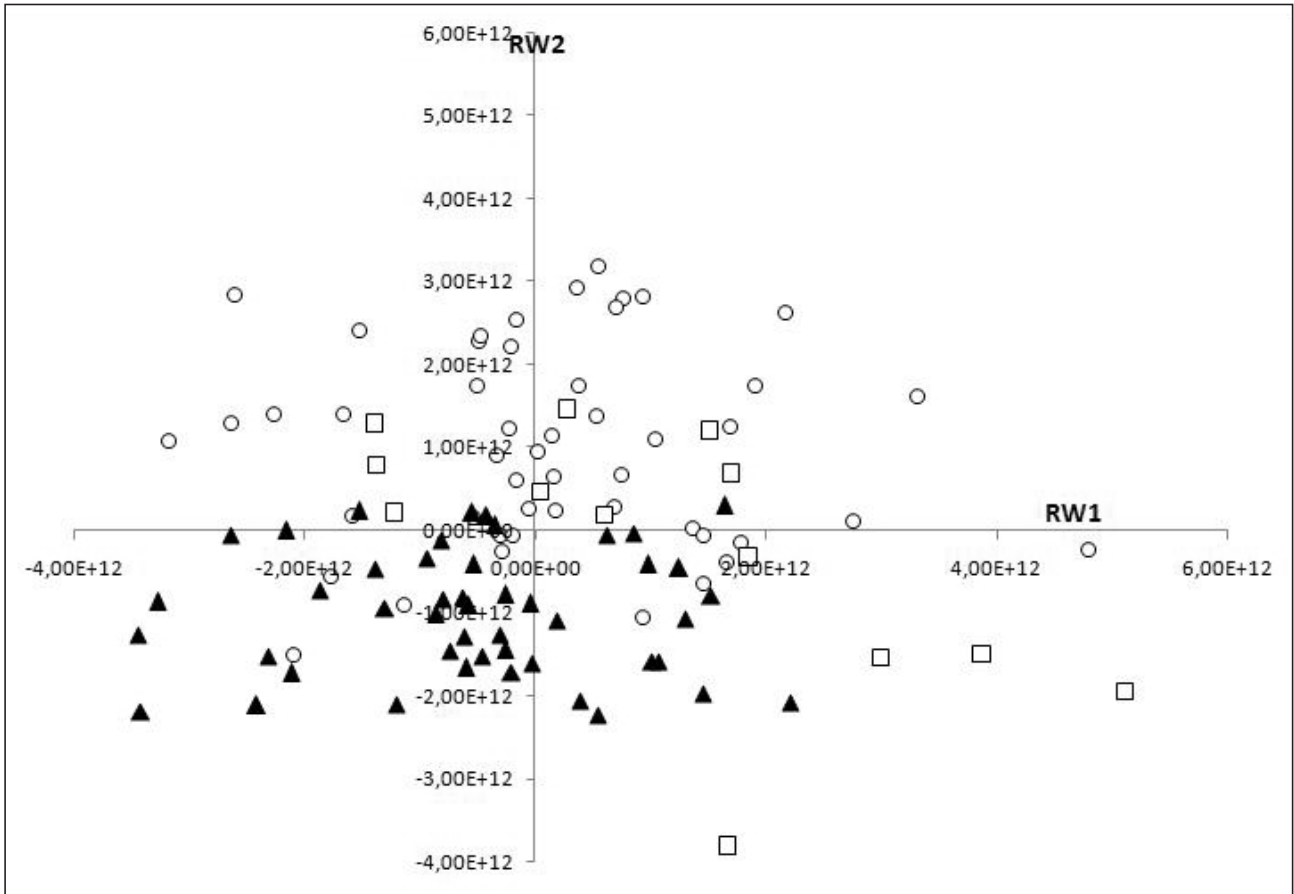


Fig. 3 Results from ordination analysis of partial warp scores for the samples. The scatterplot shows the distribution of the first two Relative Warp scores (RW1, RW2). Triangles = *P. sicula*; circles = *P. wagneriana*; squares = *P. raffonei*.

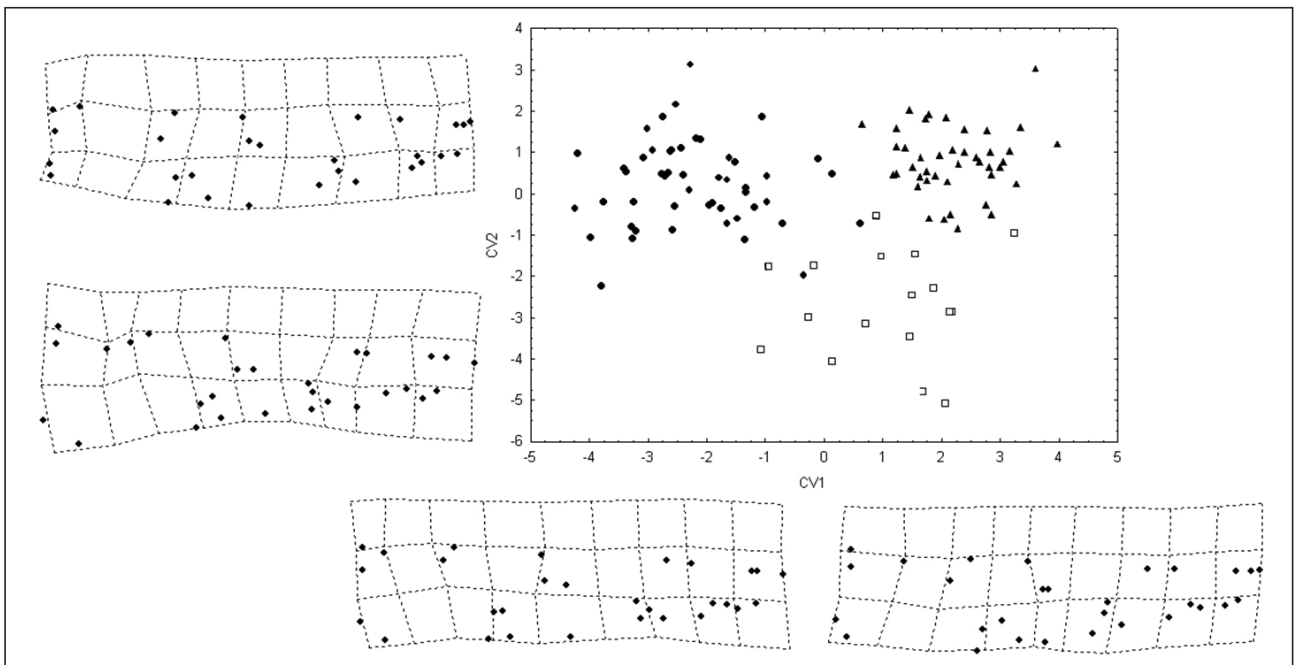


Fig. 4 Results from the canonical variate analysis run on the samples. Deformation grids were produced from regression of partial warps on CV1 and CV2 scores, using the tpsRegr program (Rohlf, 2006); grids have been magnified three times. Symbols as in fig. 3.

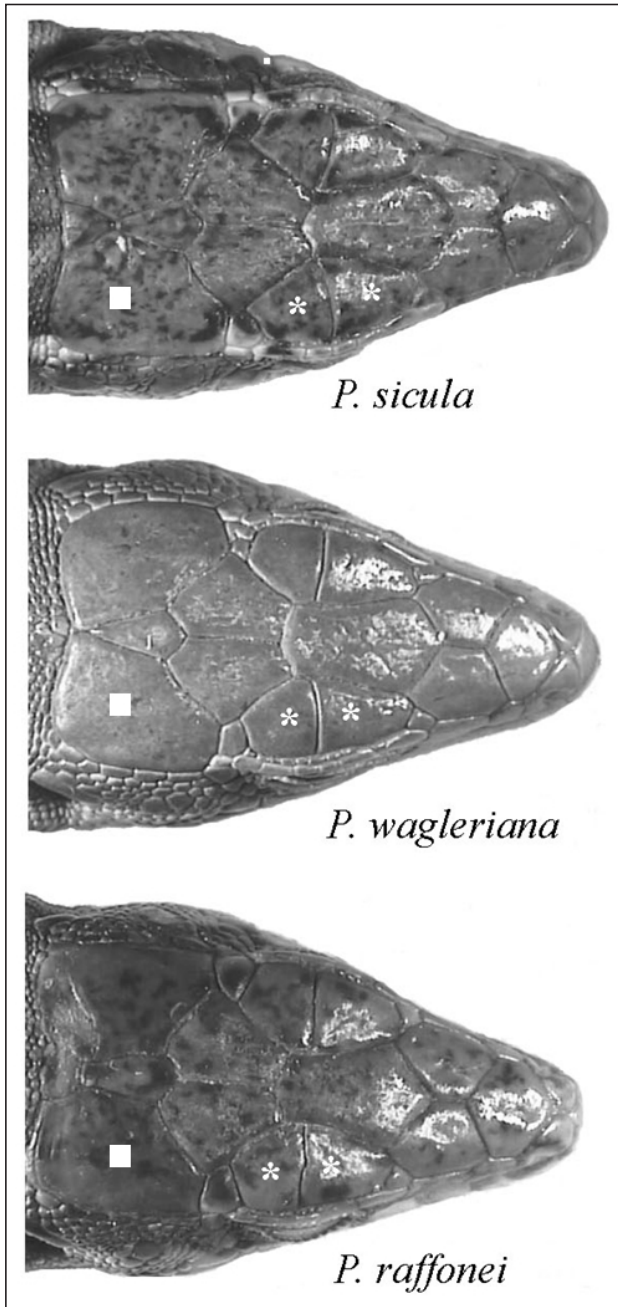


Fig. 5 Digitalized images of the cephalic scales of *P. sicula*, *P. wagleriana*, and *P. raffonei*. Parietal (white square) and Supraocular (white asterisks) scales were found to be diagnostic for the three species. The skulls are equal in size to allow comparison of shapes.

analysed samples show high morphometric variation (cf. fig. 8). In particular, the sample from Zingaro (Sicily, W1) shows a very reduced morphometric variability and is morphologically differentiated from all other populations. On the other hand, the sample from the small island of Marettimo (W8) is characterized by a number of outliers and extremes of variation which

would indicate the occurrence of highly divergent individuals in the population. As it is evident from fig. 8, *Podarcis raffonei* is the most variable species. In particular, the sample from Scoglio Faraglione (R3) shows the highest variability and is morphologically differentiated from the samples of Strombolicchio (R2) and Vulcano (R4).

DISCUSSION

Landmark based morphometrics applied to the analysis of the cephalic scales of *Podarcis raffonei*, *P. sicula*, and *P. wagleriana* was found to be a powerful tool in the detection of the pattern of geographic variation and the phenetic relationships among and within species. The three species significantly differ from each other in both shape and size of the skull. *Podarcis sicula* is characterized by narrow and long rostral and nasal regions. On the contrary, in *Podarcis wagleriana* the rostral and nasal regions are wider and shorter than in *P. sicula*. In *Podarcis raffonei* the shape of the skull is intermediate between *P. sicula* and *P. wagleriana*. The shape of the Parietal and Supraocular scales appears to be highly diagnostic and species-specific, thus representing a useful tool for recognition of the species (cf. fig. 5): they are much larger and wider in *Podarcis sicula* than in *P. wagleriana*, while in *P. raffonei* the shape of these scales is intermediate between *P. sicula* and *P. wagleriana*.

Size is another important component of interspecific variation. The three species are characterized by different allometric static patterns, as revealed by the relationship between size of the skull and body length. *Podarcis wagleriana* is characterized both by a smaller head and body length, while *P. sicula* has a larger head and body length which is intermediate between *P. wagleriana* and *P. raffonei*. *Podarcis raffonei* shows the largest body length, but its head size is intermediate between *P. sicula* and *P. wagleriana*.

According to the results of landmark based morphometrics and biometric analysis, *P. sicula* and *P. wagleriana* appear to be relatively differentiated from each other, while *P. raffonei* seems to be phenetically intermediate between *P. sicula* and *P. wagleriana*. It must be noted that phenetic analyses are partially congruent with allozyme and molecular investigations (Capula, 1994a; Harris & Arnold, 1999; Vasconcelos et al., 2006), which indicate that *Podarcis sicula* is genetically differentiated from both *P. wagleriana* and *P. raffonei*, and that *Podarcis raffonei* is genetically closely related to *P. wagleriana*.

The analysis of the intraspecific variation in shape of the cephalic scales indicates that *P. sicula* is the less variable species. This pattern is evident both in the

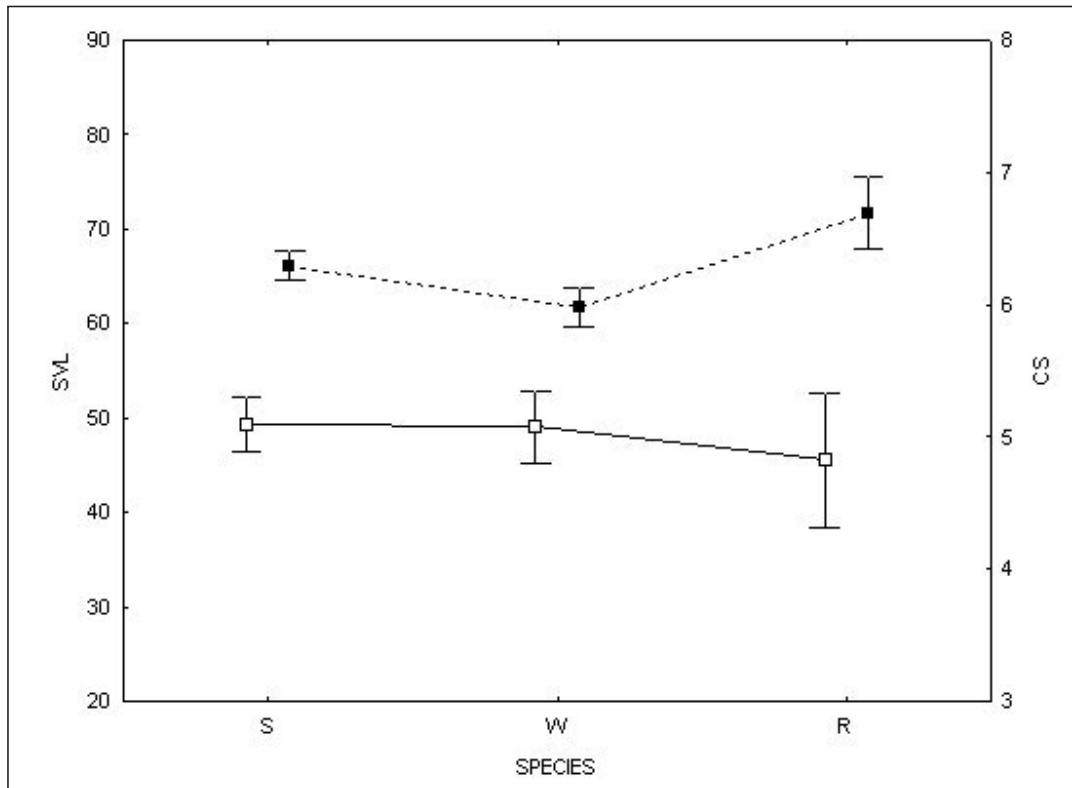


Fig. 6 Whiskers plot for mean and confidence intervals (± 0.95) of centroid size (CS; solid line) and snout-vent length (SVL; dashed line) for *P. sicula* (S), *P. wagleriana* (W), and *P. raffonei* (R).

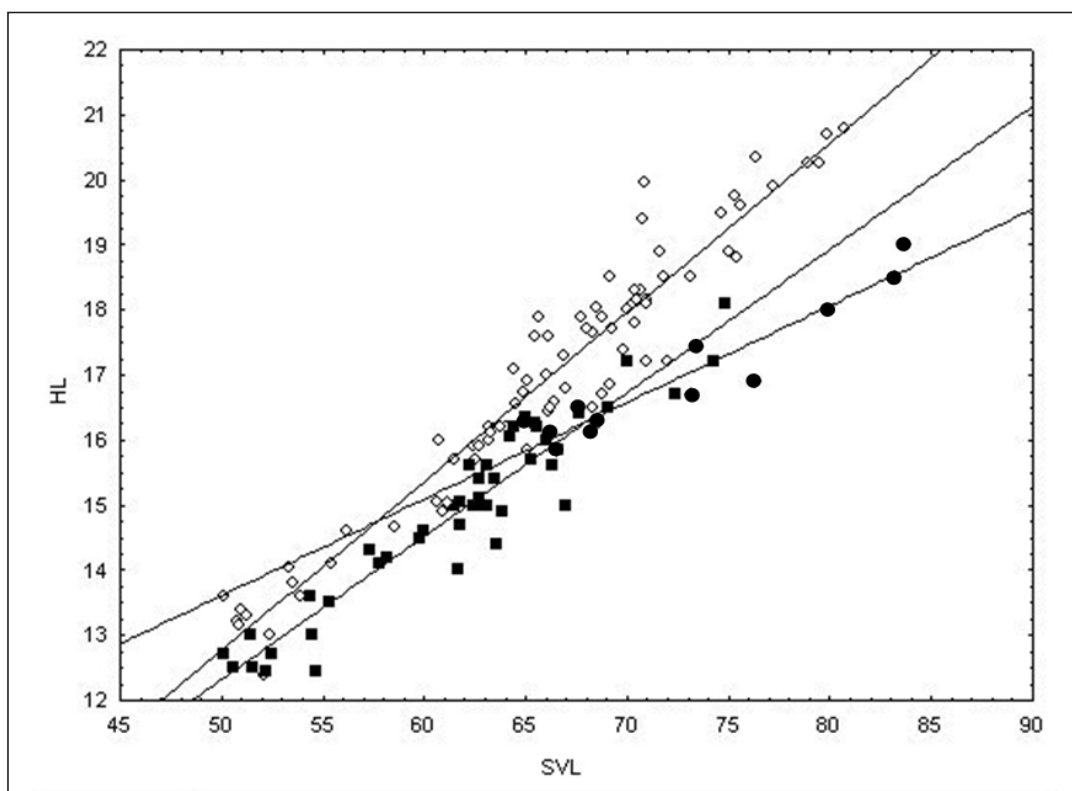


Fig. 7 Variation of head length (HL) and snout-vent length (SVL) in *Podarcis sicula* (empty rhombi), *P. wagleriana* (filled squares), and *P. raffonei* (filled circles).

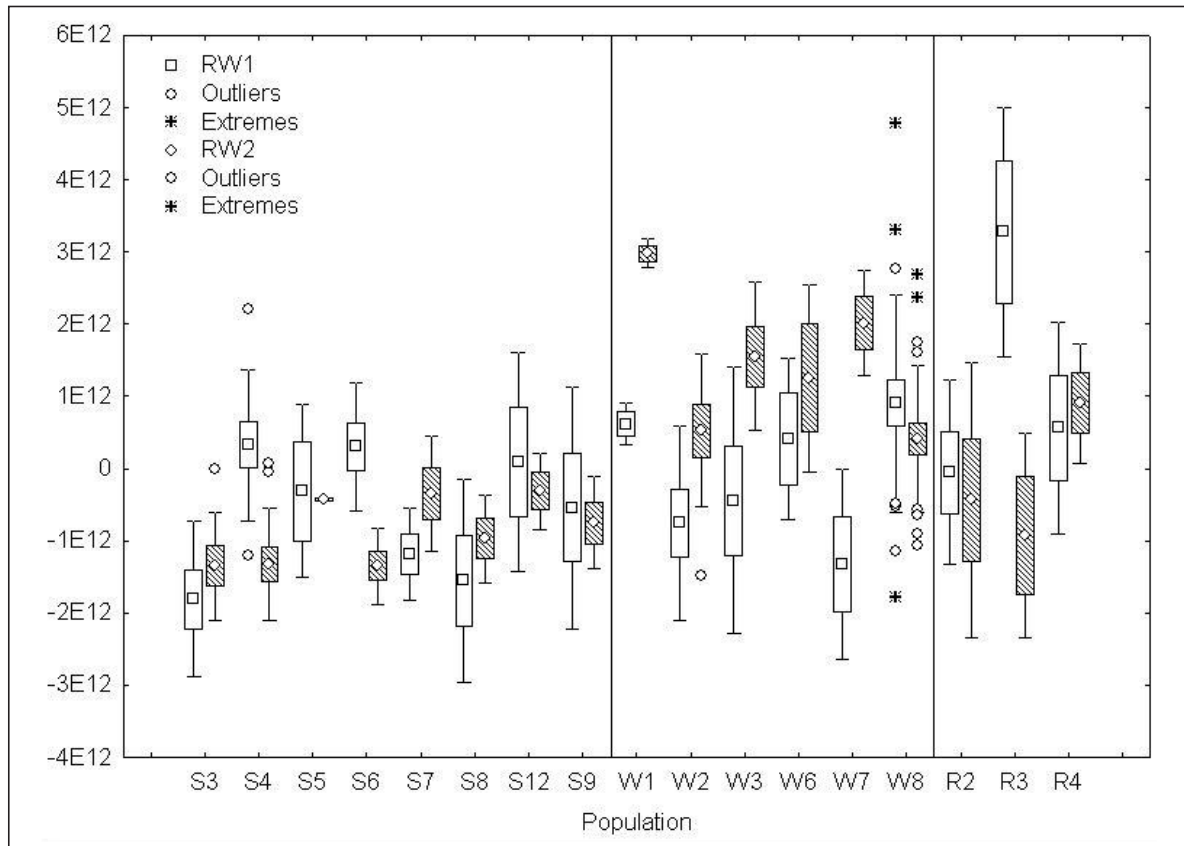


Fig. 8 Box plots of Relative Warps 1 and 2 (RW1, RW2) in populations of *Podarcis sicula* (S3, S4, S5, S6, S7, S8, S9, S12), *P. wagleriana* (W1, W2, W3, W6, W7, W8), and *P. raffonei* (R2, R3, R4). For population codes see table 1. Samples with $N < 3$ were excluded from the analysis.

samples from large (Sicily) and small islands (e.g. Favignana, Lipari). The fact that *P. sicula* is characterized by a reduced size and shape variability in this part of its range is worthy of note, and it must be stressed that the same samples of *P. sicula* used in this study were characterized by low levels of genetic variability, probably because of genetic drift phenomena (Capula, 1994a, 1994b; Oliverio et al., 1998; Capula & Ceccarelli, 2003). Morphometric variation in *Podarcis wagleriana* is higher than in *P. sicula*, and *Podarcis raffonei* is the most variable species, both in size and shape. This species is also characterized by an allometric pattern which is different from that of the other two species. In particular, the sample from Scoglio Faraglione (R3) shows the highest variability and is morphologically differentiated from the Strombolicchio (R2) and Vulcano (R4) samples. Intraspecific morphological variation of *Podarcis* lizards from Sicily and the circumsicilian islands seems to be related to the pattern of geographic population fragmentation and population size. In this respect, *P. sicula* appears to be the less morphologically variable and at the same time the most widespread species, with large or very large

populations occurring all over the study area (e.g. Capula, 1992; Corti & Lo Cascio, 2002). On the other hand, *P. raffonei*, which displays a high degree of phenotypic plasticity when compared to *P. sicula* and *P. wagleriana*, has a very reduced geographic range (Capula et al., 2002; Capula & Lo Cascio, 2006). On this regard, it is to be noted that *Podarcis raffonei* has a genetic structure more subdivided than *P. sicula* and *P. wagleriana* (cf. Capula, 2004, 2006a), but is characterized by very reduced levels of genetic variation (Capula, 2006b). This species is geographically highly fragmented, with small or very small populations occurring almost exclusively on small or very small islands (Capula, 2004, 2006a; Capula et al., 2002).

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