Multivariate and Geometric Morphometrics in the Analysis of Sexual Dimorphism Variation in *Podarcis* Lizards

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ABSTRACT *Podarcis bocagei* and *P. carbonelli* are two closely related lacertid species, very similar morphologically and ecologically. We investigated sexual dimorphism patterns presented by both species in allopatry and in sympatry. Sexual size and shape dimorphism patterns were analyzed using both multivariate and geometric morphometric techniques. Multivariate morphometrics revealed a marked sexual dimorphism in both species—males being larger with more robust habitus and females presenting a longer trunk. General patterns of sexual size dimorphism are not modified in sympatry, although there is evidence for some morphological change in male head size. The application of geometric morphometrics offered a more detailed image of head shape and revealed that males present a more developed tympanic area than do females, while females have a more rounded head. Differences in the degree of sexual shape dimorphism were detected in sympatry, but no consistent patterns were observed. From the results of the study, and based on previous knowledge on the populations studied, we conclude that the morphological differences observed are probably not caused by exploitative competition between the species, but rather appear attributable to the modification of the relative influence of sexual and natural selection on both sexes. *J. Morphol.* 268:152–165, 2007   © 2007 Wiley-Liss, Inc.

KEY WORDS: sexual dimorphism; Podarcis; Lacertidae; geometric morphometrics; sympatry; Portugal

Sexual dimorphism (SD) is a common trait in animals, most species being dimorphic rather than monomorphic (Schoener, 1977; Mouton and van Wyk, 1993; Andersson, 1994). Different evolutionary mechanisms have been proposed for the development of sexual dimorphism in various animal taxa. However, most of them can be summarized by three major forces differentially acting on males and females of a population: sexual, fecundity, and natural selection. In those species where males engage in fights and copulation is forced, sexual selection may act via male–male combats or/and female choice and thus favor bigger male body size, whereas fecundity selection may favor bigger female body size (Olsson et al., 2002; Cox et al., 2003). Moreover, natural selection acting on both sexes might pose constraints to the evolution of certain characters, for example via habitat use. In any case, it is clear that different selective pressures acting on members of the two sexes can produce sexual differences (Slatkin, 1984).

Most species of Lacertidae present a male-biased SD. In many lacertid lizards, as in other lizard families, males present larger body size and head dimensions (Cooper and Vitt, 1989; Anderson and Vitt, 1990; Mouton and van Wyk, 1993; Andersson, 1994; Braña, 1996; Herrel et al., 1996, 1999, 2001a,b; Kratochvil et al., 2003; Molina-Borja, 2003; Uller and Olsson, 2003), while females have a longer trunk (Andersson, 1994; Braña, 1996; Butler and Losos, 2002; Olsson et al., 2002; Schwarzkopf, 2005). Moreover, both head dimensions and trunk length have been shown to present a positive allometric relationship with total size in males and females, respectively, offering indirect support of sex-specific selection for these traits (Carothers, 1984; Braña, 1996; Hews, 1996; Olsson et al., 2002; Kratochvil et al., 2003). Abdomen length has been shown to be positively correlated to clutch size in various lacertid species (Braña, 1996; Olsson et al., 2002), while head dimensions are directly related to the jaw musculature and affect jaw force, a structure implicated not only in competitive behavior and copulation, but also in feeding, antipredatory behavior, and refuge use (Herrel et al., 1996, 1999, 2001a,b).

Apart from sexual differences in total body size, the variation of relative size and shape of different

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body parts is of special interest in SD studies, because it could reveal differential selection acting on body parts of each sex (Butler and Losos, 2002). In lizard studies, total size is usually represented by snout-vent length (SVL) (Hews, 1996; Butler and Losos, 2002; Kratochvil et al., 2003), and shape variation is analyzed via statistical size correction of the rest of the body-parts. However, in recent years the development of geometric morphometrics has allowed the direct study of shape variation (Bookstein, 1984; Rohlf, 1990; Rohlf and Slice, 1990; Corti, 1993; Adams and Rohlf, 2000; Adams et al., 2004). Although the application of geometric morphometrics in SD studies still needs to be explored, some authors report interesting SD patterns revealed by the application of such techniques in various animal taxa (Hood, 2000; Rosas and Bastir, 2002; Loy et al., 2004; Rufino et al., 2004; Valenzuela et al., 2004; Bruner et al., 2005). Until the present, geometric methods have not been extensively applied to study the external morphology of lizards, and very few authors have applied such methods in reptiles (Monteiro et al., 1997; Claude et al., 2003; Marugán-Lobón and Buscalioni, 2003; Manier, 2004; Bruner et al., 2005; Stayton, 2005; Vidal et al., 2005). In the case of lacertid lizards, geometric morphometrics could be of great use, since SD patterns in this group involve sexual variation in head dimensions and shape. The lizard head, covered by relatively large scales, is ideal for geometric morphometrics, since it facilitates the definition of landmarks that could be both evolutionarily and functionally informative.

Podarcis bocagei and *P. carbonelli* are two closely related species that were thought to be conspecific until recently, *P. carbonelli* being considered a subspecies of *P. bocagei* (Pérez-Mellado, 1981a,b, 1997a). However, morphological and molecular studies corroborate the specific status of *P. carbonelli* (Sá-Sousa et al., 2000; Sá-Sousa, 2001a; Sá-Sousa and Harris, 2002) and confirm that the two species are separated by a considerable genetic distance and are not sister taxa (Harris and Sá-Sousa, 2001, 2002; Pinho et al., 2004, 2006). The two species are found in sympatry in a restricted contact zone in the south of the estuary of the river Douro in Portugal, where they maintain their genetic (Pinho et al., 2006) and morphological (Kaliontzopoulou, 2004) identities.

This contact zone is of special interest, because it is the only known area of strict syntopy between the two species (Carretero et al., 2002). *Podarcis bocagei* and *P. carbonelli* are very similar both morphologically (Harris and Sá-Sousa, 2001; Sá-Sousa et al., 2000; Sá-Sousa and Harris, 2002; Kaliontzopoulou, 2004; Kaliontzopoulou et al., 2005) and ecologically, both having ground-dwelling habits—a characteristic that differentiates them from the rest of the Iberian *Podarcis* which are mainly saxicolous (Pérez-Mellado, 1997b; Sá-Sousa, 2001a,b; Carre-

tero et al., 2002). Therefore, the coexistence of both could stimulate differential evolutionary processes and result in the variation of SD patterns (Slatkin, 1980). According to the character displacement theory, SD is expected to decrease in sympatry, if competition by exploitation takes place, in order to lower intersexual competition under the pressure of interspecific competition (Schoener, 1977; Ebenman, 1986). Moreover, interactions between two closely related species could affect both sexes in different ways. Natural selection on both sexes due to the presence of congeneric competitors, sexual selection on males, and fecundity selection on females are mechanisms that acting simultaneously could modify SD patterns in the two species in sympatry.

We investigated sexual size and shape dimorphism patterns presented by both species in allopatry and then compared them to those when in sympatry, in order to identify possible variation related to the species' coexistence. To obtain a full image of morphological patterns, we examined size and relative size variation, scaling of certain dimorphic characters, and shape variation through the application of geometric morphometrics.

MATERIALS AND METHODS
Specimens Studied

Animals were captured in NW Portugal between April 2001 and August 2002, killed by cold torpor, and were preserved in 96% ethanol until their examination. Specimens used for this study were initially collected for analyzing the diet and reproductive biology of the populations in question (Carretero et al., unpublished data), studies that required sacrificing the animals. However, both species are very abundant in the study areas and inspections of the populations in the three years following field work did not reveal any demographic decrease.

Sex and state of sexual maturity were verified after dissection (Carretero et al., 2006) and only adults were included in the study, since we were interested in adult SD patterns. Three study sites separated by a maximum distance of 40 km, exposed to very similar climatic conditions (Direcção Geral do Ambiente, 1995) and with similar habitats corresponding to coastal Atlantic dunes (Barreto-Caldas et al., 1999) were selected, in order to minimize the effect of the environment on the lizards' morphology (Fig. 1). A total of 55 adult males and 48 adult females of *Podarcis bocagei* were collected from Mindelo-Vila Chã (UTM 29T NF27). Simultaneously, 53 adult males and 46 adult females of *P. carbonelli* were collected from Torreira, in the sand bar of São Jacinto situated in the north part of the Aveiro coastal lagoon system (UTM 29T NF21). Finally, the only known site where the two species are found in strict syntopy (sharing both the same geographic area and habitat, Carretero et al., 2002) was studied. This site is found in Espinho-Granja, 15 km south to the estuary of Douro in Porto (UTM 29T NF24, NF34). This has been considered to be a very recent contact zone between the two species (Sá-Sousa, 2001b). From this site, we collected a total of 42 adult males and 24 adult females of *P. bocagei* and 52 adult males and 44 adult females of *P. carbonelli*.

Multivariate Morphometrics

To quantify sexual size dimorphism (SSD) in the populations studied, we measured 10 biometric characters (Fig. 2): snout-
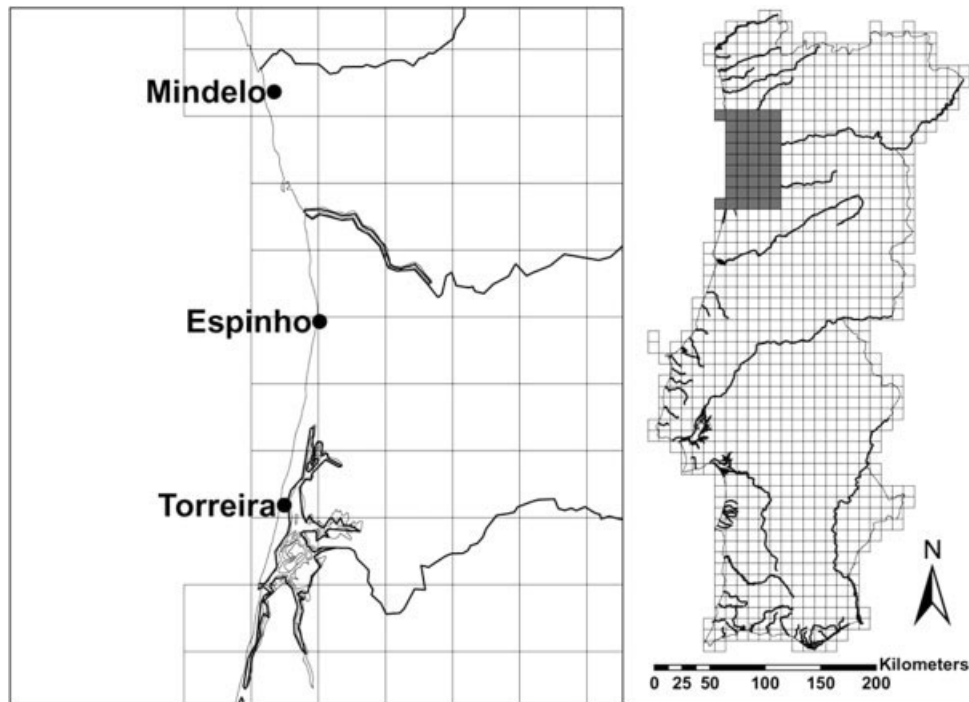
Fig. 1. Location of the study areas on the map of Portugal (right).

vent length (SVL), trunk length (TRL), head length from the tip of the snout to the posterior border of the collar (HL), pileus length (PL), distance from the middle of the eye to the tip of the snout (ESD), head width (HW), head height (HH), mouth opening (MO) defined as the distance between the tip of the snout and the posterior border of the last supralabial scale, front and hind foot length (FFL and HFL respectively). All measurements were taken to the closest 0.01 mm, using an electronic calliper
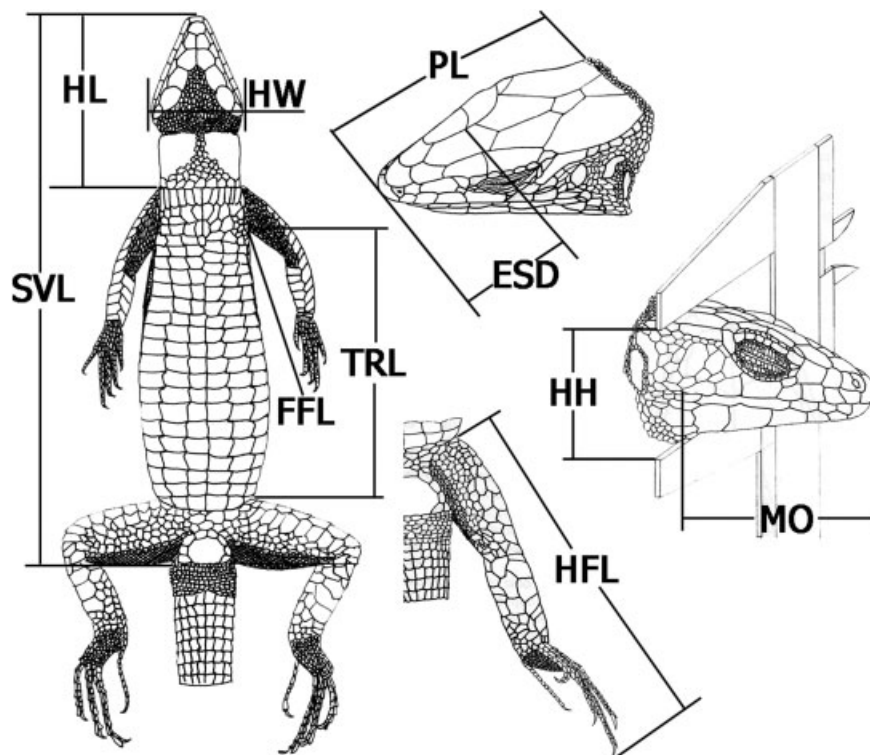

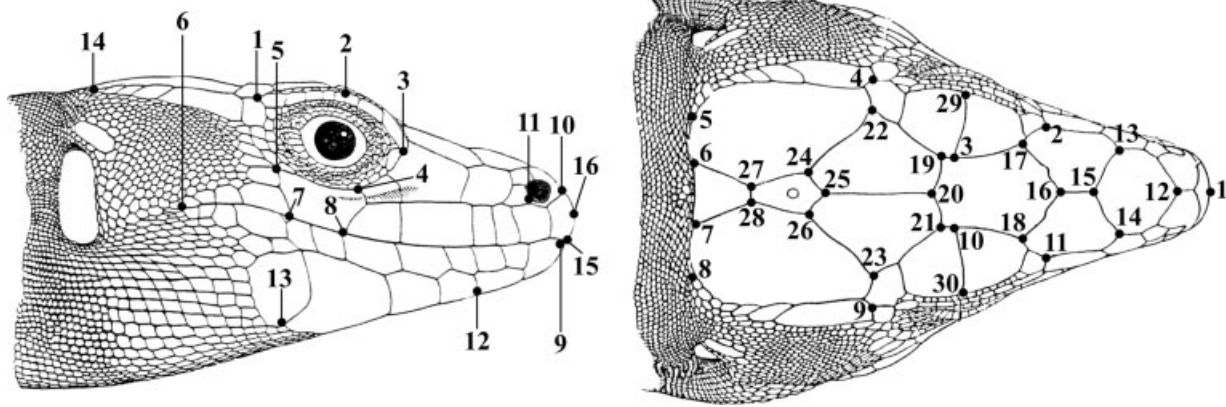Fig. 2. Linear measurements that were recorded.

Fig. 3. Landmarks recorded on the dorsal and lateral view of the lizards' head. Descriptions of landmarks in Table 1.

and by following the suggestions of Pérez-Mellado and Gosá (1988) on the biometry of the Lacertidae, unless mentioned otherwise. One-way ANOVAs were applied to each species separately to examine variation between the sexes and the two (allopatric and sympatric) populations in SVL, which is the usual total body size measure in lizard studies. Next, one-way and multivariate ANCOVAs were run to investigate variation in the rest of the characters, using SVL as a covariate. Because multiple comparisons were evaluated simultaneously, we implemented the Positive False Discovery Rate (pFDR) procedure to evaluate the significance of statistical tests (Storey, 2002). For this purpose, we used the q-value package for R (Dabney and Storey, 2004) to estimate q-values corresponding to each of the P-values calculated. The q-value for a particular character is the expected proportion of false positives incurred when calling that feature significant (Storey and Tibshirani, 2003), we therefore evaluated q-values at significance level $a < 0.05$ to determine the significance of each test. Discriminant (DA) and canonical variate analyses (CVA) were also conducted, in order to detect the characters that most differentiate sexes and populations. We used Squared Mahalanobis Distances (D^2) between both sexes (derived from separate DAs for each population) as a multivariate measure of SSD. Three D^2 were calculated for each population, taking into account (i) all the biometric variables studied, (ii) only head dimensions and (iii) only limb lengths, in order to examine possible variation in SD of different body parts.

The scaling of head characters with SVL was examined (after log-transformation of variables), treating the two sexes separately. To do this, reduced major axis (RMA) regression was applied, using the software developed by Bohonak (2002), as ordinary least-squares regression would provide biased values for the allometry equations due to the presence of measurement error in both the independent and the dependent variables (McArdle, 1988; Sokal and Rohlf, 1995). Deviation from isometry was tested using the formulae given in Clarke (1980). Homogeneity of slopes of the allometric equations between sexes was evaluated by inspection of the 95% confidence intervals and slopes were considered to differ significantly when lack of overlap was observed.

Geometric Morphometrics

We took high-resolution photos of all specimens using a digital camera (Canon PowerShot G3, resolution 4.0 MP) and both the dorsal and lateral view of each lizard's head was captured. For the lateral view, we always recorded the right side of the lizard's head. We placed graph paper underneath the head in order to re-

cord scale. All images were downloaded to a PC and a file in tps format was created for each of the groups studied using tpsUtil (Rohlf, 2004). In continuation, we recorded 30 and 16 landmarks on the dorsal and lateral view, respectively, using tpsDig2 (Rohlf, 2005a) (Fig. 3, Table 1). Specimens with malformations or abnormalities in general, in which any of the landmarks could not be defined properly, were excluded from the study (see results and tables for sample sizes). Because the dorsal side of the head is structurally symmetrical and because we were not at present interested in studying asymmetry, we averaged both sides to avoid effects of lateral asymmetry in the analysis (Corti and Rohlf, 2001). To do this, landmark No. 1 of the dorsal side was set at the origin with landmarks 12, 15, 16, 20, and 25 lying along the x-axis, and then the rest of the corresponding landmarks were averaged across the midline. Subsequent analyses of the dorsal view were conducted on these half configurations. However, deformation grids are presented for the total dorsal configuration of landmarks, in order to make easier the visualization of shape change.

Using the tpsSmall software (Rolhf, 2003a), we confirmed that shape variation between the specimens was sufficiently small and therefore the distribution of points in the shape space can be represented satisfactorily by their distribution in the tangent space. We then applied a Generalized Procrustes Analysis (GPA, Rolhf and Slice, 1990; Rolhf, 1999) using tpsRelw (Rolhf, 2005b), in order to standardize the size and to translate and rotate the configurations of landmark coordinates. The effect of species, sex, and sympatry on shape was evaluated running MANOVAs on the partial warps matrix. We extracted relative warp scores with $a = 0$, using the tpsRelw software (Rohlf, 2005b). Using relative warps, we computed canonical scores for males and females of each population in order to visualize sexual shape dimorphism (SShD). Deformation grids were produced by regression of shape variables against canonical scores using tpsRegr (Rohlf, 2003b) to view shape changes related to the patterns observed in the canonical space. We used Squared Mahalanobis Distances between both sexes (based on separate discriminant analyses for each population) for the dorsal and lateral side of the head as a measure of SShD.

RESULTS
Sexual Size Dimorphism

The ANOVAs and ANCOVAs conducted showed that a marked SSD exists in all the populations studied—the effect of sex being statistically signifi-

TABLE 1. Description of landmarks used for capturing head shape

Landmark N°	Description
Dorsal view	
1	Point of maximum curvature on the tip of the snout
2, 11	Joint of the 1st supraocular and the prefrontal
3, 10	Joint between the two middle supraoculars and the frontal
4, 9	Posterior border of the last supraocular
5, 8	Joint of the last supratemporal and the parietal
6, 7	Posterior borders of the occipital
12	Anterior border of the frontonasal
13, 14	Middle-posterior borders of the frontonasal
15	Posterior border of the frontonasal
16	Anterior border of the frontal
17, 18	Middle-anterior borders of the frontal
19, 21	Middle-posterior borders of the frontal
20	Posterior border of the frontal
22, 23	Lateral border of the frontoparietal
24, 26	Middle-anterior border of the interparietal
25	Anterior border of the interparietal
27, 28	Posterior borders of the interparietal
29, 30	Joint of the two middle supraoculars and the supraciliary granules
Lateral view	
1	Posterior border of the last supraocular
2	Joint between the 3rd and 4th supraocular
3	Anterior border of the 1st supraocular
4	Anterior upper border of the subocular
5	Posterior upper border of the subocular
6	End of the mouth opening. Posterior border of the last supralabial
7	Posterior lower border of the subocular
8	Anterior lower border of the subocular
9, 15	Extreme of the lower and upper jaw respectively
10	Posterior border of the rostral
11	Joint of the rostril, the postnasal and the supralabial that borders it
12	Posterior border of the 2nd chin shield
13	Anterior border of the last chin shield
14	Joint of the last supratemporal and the parietal
16	Point of maximum curvature on the tip of the snout

In the dorsal view, when two landmarks are described together, the first always refers to the left and the second to the right side of the head.

cant in all cases (Table 2). Males present higher SVL values than do females in all the populations, but snout-vent length dimorphism does not vary between sympatric and allopatric populations. A male-biased SSD exists in both species for all the characters studied, except for trunk length, for which females always present a higher mean relative to SVL. The effect of sympatry is only significant in some cases. A significant interaction of sex and sympatry was detected for head length in both species and hind foot length in *P. bocagei*. It is interesting to note that the Bonferroni post hoc comparisons for head length revealed that males of both species present a relatively longer head in

sympatry, while males of *P. bocagei* also present shorter hind limbs in sympatry. Moreover, males of *Podarcis bocagei* present a wider head in sympatry, while those of *P. carbonelli* have higher heads in sympatry. The discriminant analyses conducted for each species separately showed that the characters involved in the discrimination of sexes and populations are those related to head size, as well as snout-vent length and hind foot length (Table 3). A perfect (100% correct) discrimination between the sexes is possible on the basis of biometric characters; however, the percentages of correct classification between allopatric and sympatric populations are low (Table 4).

Head Character Scaling

Snout-vent length and head dimensions seem to be the most important variables in the discriminant analyses; therefore, we examined the scaling of head characters in males and females of the populations studied (Table 5). Head height presents a positive allometric relationship with snout-vent length (slope >1) in males of both species, both in allopatry and in sympatry. The rest of the characters are always isometric, except for head length and pileus length in females of *Podarcis bocagei* in sympatry. No significant differences in RMA slopes were found between males and females of the populations studied.

Sexual Shape Dimorphism

Multivariate ANOVAs run on the shape variables of the dorsal and lateral view of the head confirmed that the effect of sex and sympatry, as well as the interaction between them, are significant for both species ($P < 0.05$ in most cases). The only exception is observed in the dorsal view of *Podarcis carbonelli*, where the interaction of sex and sympatry is not significant ($P = 0.19$). Discriminant analyses conducted on the relative warp scores of the dorsal and lateral projections of both sexes of the allopatric and sympatric populations of each species provide a highly correct classification of individuals, both of sexes and of allopatric and sympatric populations. Percentages of correct classification are slightly higher for the dorsal view (88.57% in *P. bocagei* and 84.30% in *P. carbonelli* vs. 71.25% in *P. bocagei* and 80.77% in *P. carbonelli* for the lateral view, Table 6). Discriminant and canonical variates' analyses were also run separately for the different populations and histograms of canonical scores can be seen in Figure 4. In all the groups examined, SShD on the lateral view primarily involves the tympanic area, which is more developed in males than in females (Fig. 5). SShD of the dorsal view of the head is more difficult to describe; however, the heads of females are more rounded than those of

TABLE 2. *Descriptive statistics of the biometric variables for males and females of the populations studied and ANOVA (for SVL) or ANCOVA (rest of the characters) comparisons for the factors of sex and symp. with q-values from Positive False Discovery Rate (pFDR) procedure*

character	Males allopatry	Females allopatry	Males sympatry	Females sympatry	AN(C)OVA (sex, symp, sex*symp)		
					F	P-value	q-level
Podarcis bocagei							
SVL	57.00 ± 4.22[a]	53.11 ± 4.07	57.60 ± 4.11	52.84 ± 4.19	41.64	1.17E-09	1.001E-08
	47.93–64.90[b]	44.81–64.02	46.98–64.20	45.89–59.71	0.06	0.809	0.239
	55[c]	48	42	24	0.43	0.515	0.184
TRL	25.28 ± 2.88	28.15 ± 2.70	25.09 ± 2.89	28.46 ± 2.68	171.43	0.001	0.001
	20.65–31.95	20.47–33.72	19.99–32.83	20.65–30.62	0.09	0.762	0.239
	55	48	42	24	1.41	0.238	0.097
HL	19.66 ± 1.40	17.48 ± 0.93	19.95 ± 1.44	17.41 ± 1.26	578.72	0.001	0.001
	17.01–22.74	14.60–18.89	16.66–22.92	14.79–19.07	1.71	0.193	0.083
	55	48	42	24	4.28	0.040	0.026
PL	13.25 ± 0.99	11.58 ± 0.64	13.36 ± 0.95	11.66 ± 0.83	669.07	0.001	0.001
	11.42–15.13	9.75–12.28	11.45–15.04	9.86–12.63	2.66	0.105	0.056
	55	48	42	24	0.06	0.801	0.239
ESD	7.06 ± 0.50	6.32 ± 0.37	7.10 ± 0.51	6.29 ± 0.47	383.46	0.001	0.001
	5.95–8.15	5.36–6.75	6.10–8.17	5.28–6.87	0.02	0.875	0.250
	55	48	42	24	0.68	0.410	0.160
HW	8.86 ± 0.71	7.54 ± 0.42	8.44 ± 1.01	7.37 ± 0.58	170.08	0.001	0.001
	7.55–10.47	6.34–8.06	5.21–10.14	6.11–7.85	13.16	3.82E-04	0.003
	55	48	42	24	2.34	0.128	0.060
HH	6.52 ± 0.84	5.48 ± 0.45	6.68 ± 0.71	5.43 ± 0.39	185.03	0.001	0.001
	4.87–9.46	4.34–6.25	5.34–8.19	4.15–5.73	0.46	0.497	0.184
	55	48	42	24	2.09	0.150	0.067
MO	11.83 ± 1.00	10.26 ± 0.74	11.77 ± 0.96	10.27 ± 0.94	268.05	0.001	0.001
	9.27–13.93	8.46–11.45	9.50–13.64	8.29–11.97	0.09	0.761	0.238
	55	48	42	24	0.22	0.642	0.219
FFL	18.36 ± 1.33	16.21 ± 0.77	17.95 ± 1.07	16.18 ± 0.94	215.87	0.001	0.001
	15.36–21.65	13.02–17.14	15.98–20.24	14.10–17.36	3.45	0.065	0.037
	55	48	42	24	2.53	0.113	0.056
HFL	29.70 ± 2.17	25.51 ± 1.46	28.86 ± 1.85	25.56 ± 1.40	256.54	0.001	0.001
	25.66–34.60	21.10–27.63	24.34–33.49	22.25–27.14	3.58	0.060	0.036
	53	45	42	24	4.43	0.037	0.026
Podarcis carbonelli							
SVL	49.69 ± 4.71	48.44 ± 3.78	50.48 ± 0.67	48.15 ± 3.61	8.34	4.32E-03	7.15 E-03
	40.20–58.92	42.73–57.28	38.97–60.55	40.34–57.72	0.17	0.684	0.496
	53	46	52	44	0.75	0.386	0.335
TRL	22.69 ± 2.65	25.20 ± 2.62	22.40 ± 0.15	25.26 ± 2.70	278.60	0.001	0.002
	17.20–28.39	18.47–31.01	15.98–27.51	19.98–30.19	0.53	0.469	0.372
	53	46	52	44	1.22	0.271	0.274
HL	17.41 ± 0.07	15.62 ± 1.03	17.72 ± 0.07	15.62 ± 0.94	655.46	0.001	0.002
	14.84–20.67	13.77–18.42	13.66–22.37	13.27–18.58	4.87	0.029	0.040
	53	46	52	44	4.33	0.039	0.048
PL	11.73 ± 0.05	10.40 ± 0.67	11.86 ± 0.05	10.44 ± 0.64	812.42	0.001	0.002
	9.84–13.91	8.93–11.99	9.52–14.76	8.68–11.91	3.40	0.067	0.081
	53	46	52	44	0.76	0.385	0.335
ESD	6.31 ± 0.03	5.67 ± 0.36	6.31 ± 0.03	5.67 ± 0.37	358.66	0.001	0.002
	5.12–7.31	4.97–6.49	4.9–7.66	4.62–6.53	0.00	0.957	0.590
	53	46	52	44	0.00	0.972	0.590
HW	7.76 ± 0.05	6.67 ± 0.43	7.70 ± 0.05	6.69 ± 0.62	431.79	0.001	0.002
	6.43–9.02	5.77–7.72	5.98–9.68	5.75–9.75	0.30	0.585	0.444
	53	46	52	44	0.02	0.883	0.575
HH	5.66 ± 0.05	4.88 ± 0.51	5.85 ± 0.05	4.98 ± 0.42	242.80	0.001	0.002
	3.87–7.36	3.78–5.87	4.22–7.81	3.47–5.82	7.72	6.01E-03	9.12 E-03
	53	46	52	44	0.63	0.428	0.354
MO	10.20 ± 0.06	9.03 ± 0.71	10.33 ± 0.06	9.05 ± 0.78	370.95	0.001	0.002
	7.87–12.50	7.39–10.59	7.88–13.14	7.19–11.38	1.47	0.226	0.242
	53	46	52	44	0.85	0.358	0.334
FFL	16.14 ± 0.20	14.30 ± 0.88	16.31 ± 0.10	14.42 ± 0.94	307.37	0.001	0.002
	13.02–18.85	12.31–16.43	12.53–19.05	12.11–16.47	1.87	0.173	0.196
	53	46	52	44	0.08	0.777	0.524
HFL	26.16 ± 0.14	22.79 ± 1.13	26.66 ± 0.15	23.17 ± 1.43	499.67	0.001	0.002
	21.95–30.50	20.16–26.09	21.86–32.04	19.27–26.47	8.58	3.82E-03	6.95 E-03
	53	45	51	44	0.14	0.708	0.496

d.f. = 1 for all comparisons. a: Mean ± SD (in mm), b: Range, c: Sample size.

TABLE 3. *Summary of the discriminant analysis conducted on biometric variables between males and females of allopatric and sympatric populations of* Podarcis bocagei *and* P. carbonelli

	Wilks' Lambda	Partial Lambda	F-remove[a]	*P*-level	Toler.	1-Toler. (R-Sqr.)
Podarcis bocagei						
SVL	0.098	0.818	10.953	1.54E-06	0.061	0.939
TRL	0.082	0.975	1.253	0.293	0.181	0.819
HL	0.088	0.907	5.066	0.002	0.094	0.906
PL	0.089	0.898	5.622	0.001	0.058	0.942
ESD	0.082	0.973	1.360	0.257	0.107	0.893
HW	0.097	0.822	10.664	2.18E-06	0.442	0.558
HH	0.082	0.977	1.138	0.336	0.444	0.556
MO	0.081	0.981	0.954	0.416	0.188	0.812
FFL	0.082	0.980	0.983	0.402	0.256	0.744
HFL	0.085	0.940	3.142	0.027	0.282	0.718
Podarcis carbonelli						
SVL	0.154	0.788	16.139	2.47E-09	0.036	0.964
TRL	0.122	0.994	0.387	0.763	0.126	0.874
HL	0.128	0.949	3.253	0.023	0.076	0.924
PL	0.139	0.878	8.351	3.14E-05	0.029	0.971
ESD	0.129	0.941	3.744	0.012	0.075	0.925
HW	0.126	0.964	2.241	0.085	0.175	0.825
HH	0.123	0.986	0.824	0.482	0.178	0.822
MO	0.123	0.992	0.505	0.680	0.105	0.895
FFL	0.122	1.000	0.016	0.997	0.189	0.811
HFL	0.130	0.933	4.322	0.006	0.168	0.832

[a]F-remove (3.148) for *Podarcis bocagei;* F-remove (3.180) for *Podarcis carbonelli.*

males, whose posterior border of the pileus is broader (Fig. 6).

Because the interaction of sex and sympatry was significant in most cases, we conducted a discriminant and canonical analysis on the relative warp scores for all the groups studied, in order to visualize overall shape changes. The means of each group's first and second canonical root for the dorsal and lateral view are presented in Figure 7. Concerning the dorsal view of the head, *Podarcis carbonelli* change little from allopatry to sympatry, whereas a marked shape change is observed in *P. bocagei*, especially in females. As for the lateral view of the head, *P. carbonelli* and males of *P. bocagei* present some, however small, differentiation

TABLE 4. *Classification matrices of the discriminant analyses based on biometric variables between males and females of allopatric and sympatric populations for* Podarcis bocagei *and* P. carbonelli

	% correct	FA (*P* = 0.28)	FS (*P* = 0.14)	MS (*P* = 0.25)	MA (*P* = 0.33)
Podarcis bocagei					
FA	95.56	43	2	0	0
FS	26.09	17	6	0	0
MS	70.00	0	0	28	12
MA	88.68	0	0	6	47
Total	*77.02*	*60*	*8*	*34*	*59*
Podarcis carbonelli					
FA	50.00	22	21	0	1
FS	60.00	18	27	0	0
MS	56.86	0	0	29	22
MA	69.81	0	0	16	37
Total	*59.59*	*40*	*48*	*45*	*60*

FA, females in allopatry; FS, females in sympatry; MA, males in allopatry; MS, males in sympatry.

from sympatry to allopatry, but shape change is more marked in females of *P. bocagei*.

Degree of Sexual Dimorphism

Results on the degree of SD quantified by different methods gave variable results. Although it is impossible to compare different methods, from the D^2 (Table 7) we deduce that overall SSD, based on linear body measurements, decreases in sympatry for both species. However, when analyzing SSD for the head and the limbs separately, patterns become more complicated. On the basis of linear measurements, the degree of head SD is not affected by sympatry in *Podarcis bocagei* and is just marginally higher in sympatry for *P. carbonelli*, contrasting the findings for male head length. The results from geometric morphometric methods are also confusing, showing different patterns for the dorsal and lateral configuration of landmarks and between the two species. SShD seems to decrease in sympatry for *P. bocagei* and increase for *P. carbonelli* when examining the dorsal side of the head. The opposite pattern is observed for the lateral side of the head. *P. bocagei* showing higher and *P. carbonelli* lower SShD in sympatry.

DISCUSSION

Trying to isolate the effect of species coexistence on morphology is a complicated task, mainly due to the many factors that could be acting on it simultaneously. When examining SD patterns, we have to keep in mind that sexual and/or natural selection

TABLE 5. *Intercept and slope obtained by Reduced Major Axis regression of head characters against SVL*

	Character	N	Intercept	CI Intercept	95%	Slope	CI Slope	95%	R²
Podarcis bocagei									
FA	HL	48	−0.022	−0.199	0.155	**0.724**	0.621	0.826	0.772
	PL	48	−0.243	−0.389	−0.098	**0.748**	0.663	0.832	0.855
	ESD	48	−0.595	−0.780	−0.409	0.799	0.692	0.907	0.795
	HW	48	−0.468	−0.657	−0.279	0.770	0.660	0.880	0.770
	HH	48	−1.211	−1.574	−0.847	1.118	0.907	1.328	0.597
	MO	48	−0.684	0.992	−0.376	0.972	0.793	1.151	0.616
FS	HL	24	−0.398	−0.720	−0.075	0.940	0.753	1.128	0.797
	PL	24	−0.546	−0.875	−0.216	0.925	0.734	1.116	0.781
	ESD	23	−1.005	−1.375	−0.636	1.035	0.821	1.249	0.792
	HW	24	−0.953	−1.364	−0.543	1.045	0.807	1.284	0.734
	HH	23	−0.744	−1.065	−0.423	0.845	0.659	1.031	0.764
	MO	23	−0.866	−1.237	−0.494	1.076	0.860	1.292	0.805
MA	HL	56	−0.358	−0.507	−0.209	0.946	0.861	1.031	0.892
	PL	56	−0.598	−0.739	−0.457	0.985	0.905	1.065	0.911
	ESD	56	−0.771	−0.912	−0.630	0.928	0.847	1.008	0.899
	HW	56	−0.893	−1.070	−0.716	1.053	0.953	1.154	0.877
	HH	54	−1.784	−2.117	−1.451	**1.484**	1.294	1.674	0.789
	MO	55	−0.810	−1.051	−0.568	1.078	0.940	1.216	0.785
MS	HL	42	−0.413	−0.613	−0.212	0.980	0.866	1.094	0.868
	PL	42	−0.579	−0.805	−0.354	0.976	0.848	1.104	0.831
	ESD	42	−0.888	−1.167	−0.609	0.995	0.837	1.153	0.752
	HW	40	−0.829	−1.144	−0.513	1.010	0.830	1.189	0.709
	HH	42	−1.691	−2.141	−1.241	**1.437**	1.182	1.693	0.690
	MO	42	−0.878	−1.239	−0.517	1.115	0.910	1.320	0.668
Podarcis carbonelli									
FA	HL	45	−0.245	−0.444	−0.046	0.849	0.731	0.968	0.797
	PL	45	−0.412	−0.583	−0.241	0.844	0.742	0.945	0.848
	ESD	45	−0.628	−0.868	−0.388	0.816	0.673	0.959	0.678
	HW	45	−0.614	−0.882	−0.347	0.849	0.691	1.008	0.632
	HH	45	−1.707	−2.104	−1.309	1.414	1.179	1.650	0.707
	MO	45	−0.776	−1.070	−0.482	1.023	0.849	1.198	0.694
FS	HL	44	−0.183	−0.360	−0.006	0.813	0.707	0.918	0.828
	PL	43	−0.397	−0.570	−0.224	0.835	0.732	0.938	0.847
	ESD	44	−0.796	−1.083	−0.509	0.916	0.745	1.086	0.644
	HW	43	−0.612	−0.918	−0.306	0.846	0.664	1.029	0.535
	HH	42	−0.940	−1.295	−0.585	0.965	0.754	1.175	0.533
	MO	43	−1.028	−1.345	−0.712	1.172	0.984	1.360	0.742
MA	HL	52	−0.342	−0.477	−0.207	0.935	0.855	1.014	0.910
	PL	52	−0.589	−0.701	−0.476	0.979	0.913	1.046	0.943
	ESD	53	−0.962	−1.146	−0.779	1.041	0.932	1.149	0.862
	HW	52	−0.807	−1.001	−0.612	0.999	0.884	1.114	0.836
	HH	51	−1.801	−2.100	−1.503	**1.508**	1.332	1.684	0.836
	MO	53	−0.810	−1.009	−0.611	1.074	0.956	1.191	0.849
MS	HL	51	−0.581	−0.722	−0.440	1.080	0.997	1.162	0.929
	PL	51	−0.703	−0.838	−0.568	1.049	0.969	1.128	0.931
	ESD	51	−1.002	−1.179	−0.826	1.064	0.960	1.167	.0.885
	HW	51	−0.853	−1.022	−0.684	1.027	0.927	1.126	0.887
	HH	51	−1.961	−2.312	−1.610	**1.608**	1.402	1.814	0.801
	MO	50	−0.965	−1.162	−0.768	1.168	1.052	1.284	0.884

Slopes that significantly deviated from isometry (1) are marked in bold letter. FA, females in allopatry; FS, females in sympatry; MA, males in allopatry; MS, males in sympatry.

could be acting on both sexes, resulting in the morphological patterns observed. On the other hand, genetic correlations between the sexes (Lande, 1980), as well as phylogenetic inertia, could be factors affecting the observed morphologies.

Podarcis bocagei and *P. carbonelli* offer a good model for studying the possible effects of species coexistence on SD patterns and the factors acting on males and females. The sites studied present very similar habitat structures and environmental conditions. Preliminary analyses on the lizards' feeding ecology show that the diets of the two species are more similar in sympatry than in allopatry, suggesting that no or little

competition for food takes place (unpublished data). Consequently, habitat variation and trophic competition probably can be excluded as factors affecting the species morphology, and morphological modifications most probably appear as a result of other types of intra- and interspecific interactions.

Size Dimorphism and Ecological Considerations

Although both species are sexually dimorphic following the patterns observed in most lacertid liz-

TABLE 6. Classification matrices of the discriminant analyses based on shape variables of the dorsal and lateral view of the head between males and females of allopatric and sympatric populations for the two species studied

	% correct	FA	FS	MS	MA
Podarcis bocagei					
Dorsal					
FA	90.48	38	2	2	0
FS	86.96	1	20	1	1
MS	87.80	1	2	36	2
MA	88.24	0	1	3	30
Total	*88.57*	*40*	*25*	*42*	*33*
		$P = 0.3$	$P = 0.16$	$P = 0.29$	$P = 0.25$
Lateral					
FA	68.89	31	5	7	2
FS	73.91	5	17	0	1
MS	65.38	10	0	34	8
MA	80.00	1	1	6	32
Total	*71.25*	*47*	*23*	*47*	*43*
		$P = 0.28$	$P = 0.14$	$P = 0.33$	$P = 0.25$
Podarcis carbonelli					
Dorsal					
FA	85.00	34	3	3	0
FS	82.50	4	33	0	3
MS	80.85	4	1	38	4
MA	88.89	0	2	3	40
Total	*84.30*	*42*	*39*	*44*	*47*
		$P = 0.23$	$P = 0.23$	$P = 0.27$	$P = 0.27$
Lateral					
FA	78.95	30	4	2	2
FS	75.61	6	31	2	2
MS	86.54	1	2	45	4
MA	80.39	2	4	4	41
Total	*80.77*	*39*	*41*	*53*	*49*
		$P = 0.21$	$P = 0.22$	$P = 0.29$	$P = 0.28$

FA, females in allopatry; FS, females in sympatry; MA, males in allopatry; MS, males in sympatry.

ards, SSD patterns are not modified in sympatry. Males are generally larger than females, with more robust heads and longer extremities, but size differences between the sexes remain constant when the two species are syntopic. This, combined with the minute differences in diet between sympatric and allopatric populations, excludes the hypothesis of character displacement and, hence, exploitative competition as a cause for the shifts observed in SD patterns in both species (Schoener, 1967, 1977; Watkins, 1996). Furthermore, if morphological differences in sympatry were due to niche competition (Schoener, 1977), we would expect modifications of head dimensions in both sexes, whereas our results only revealed such changes in males. As no evidence on habitat segregation between males and females was recorded in the population studied (Carretero and Kaliontzopoulou, personal observation), this hypothesis can also be excluded as a reason for the different patterns observed in both sexes.

Therefore, explanations for the variation of SD patterns should be sought in sexual and/or natural selection acting differentially on males and females of the sympatric and allopatric populations, thus modifying intersexual differences in morphology.

Evidence for Sexual and Natural Selection

Separate examination of morphological characters revealed some patterns that could be explained on the basis of selective mechanisms. Head relative size seems to be an important trait for males and there is evidence that it is modified when both species are syntopic. SD in relative head length was more marked in sympatry than in allopatry because of the fact that males of both species have longer heads than their allopatric conspecifics. Moreover, head height was found to be positively allometric in males of all the populations studied. Additionally, geometric morphometric analyses revealed that males present an over-development of the tympanic area compared with females.

Head size is known to be a sexually selected trait in lacertids and in lizards in general—males usually presenting bigger heads than females (Braña, 1996; Olsson et al., 2002). The head is involved in mating in the Lacertidae both directly, males grabbing females in order to immobilize them and copulate with them (Verbeek, 1972; Heulin 1988; Hews,
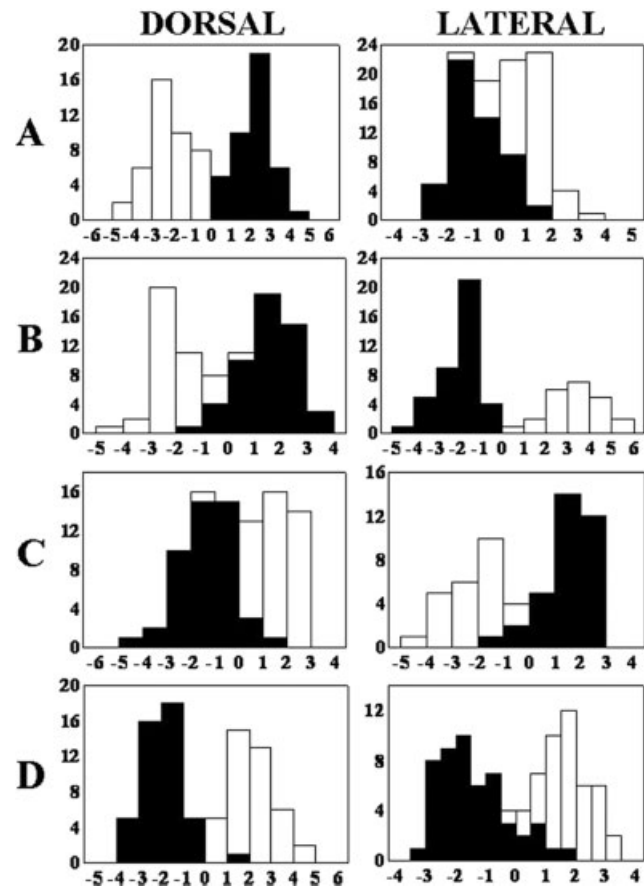

Fig. 4. Canonical scores of shape variables of males (black bars) and females (white bars) of the different groups. **A**: *Podarcis bocagei* in allopatry. **B**: *Podarcis bocagei* in sympatry. **C**: *Podarcis carbonelli* in allopatry. **D**: *Podarcis carbonelli* in sympatry.
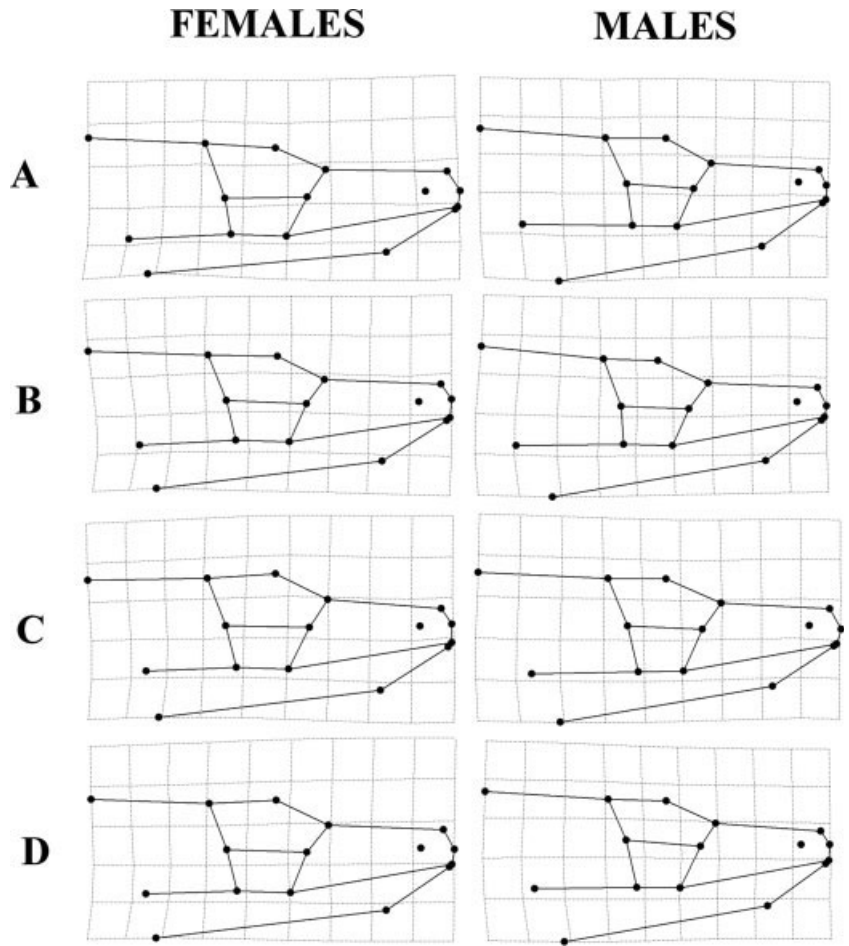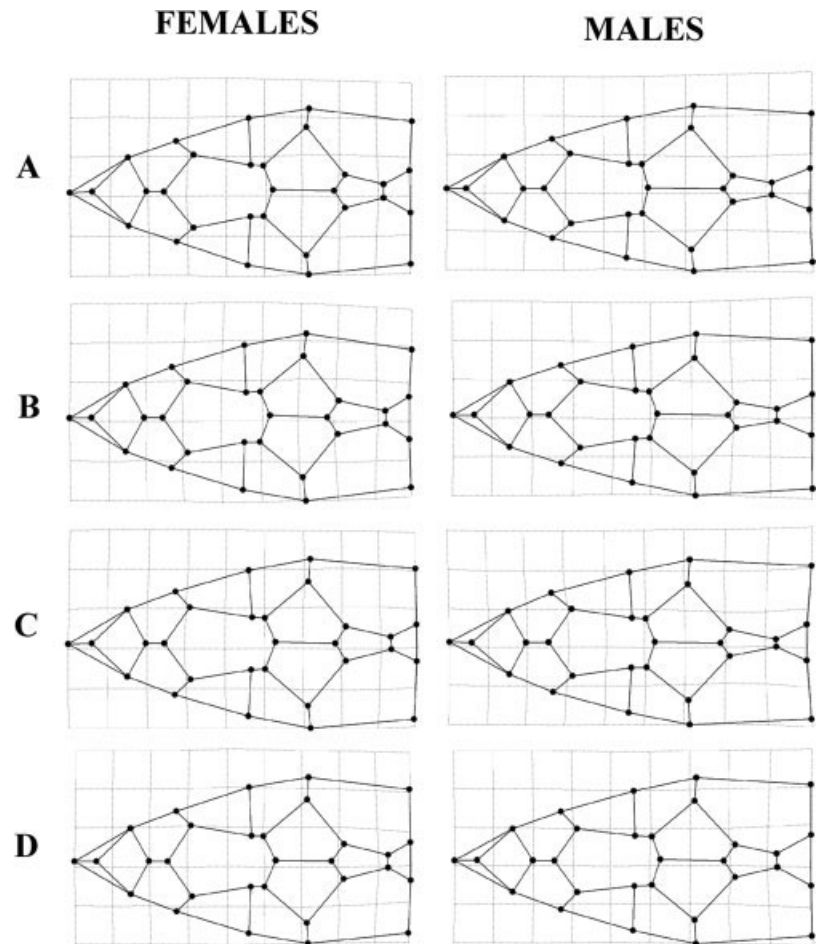
Fig. 5. Deformation grids between males and females of the four groups studied for the lateral view of the head. **A**: *Podarcis bocagei* in allopatry. **B**: *Podarcis bocagei* in sympatry. **C**: *Podarcis carbonelli* in allopatry. **D**: *Podarcis carbonelli* in sympatry.

Fig. 6. Deformation grids between males and females of the four groups studied for the dorsal view of the head. **A**: *Podarcis bocagei* in allopatry. **B**: *Podarcis bocagei* in sympatry. **C**: *Podarcis carbonelli* in allopatry. **D**: *Podarcis carbonelli* in sympatry.
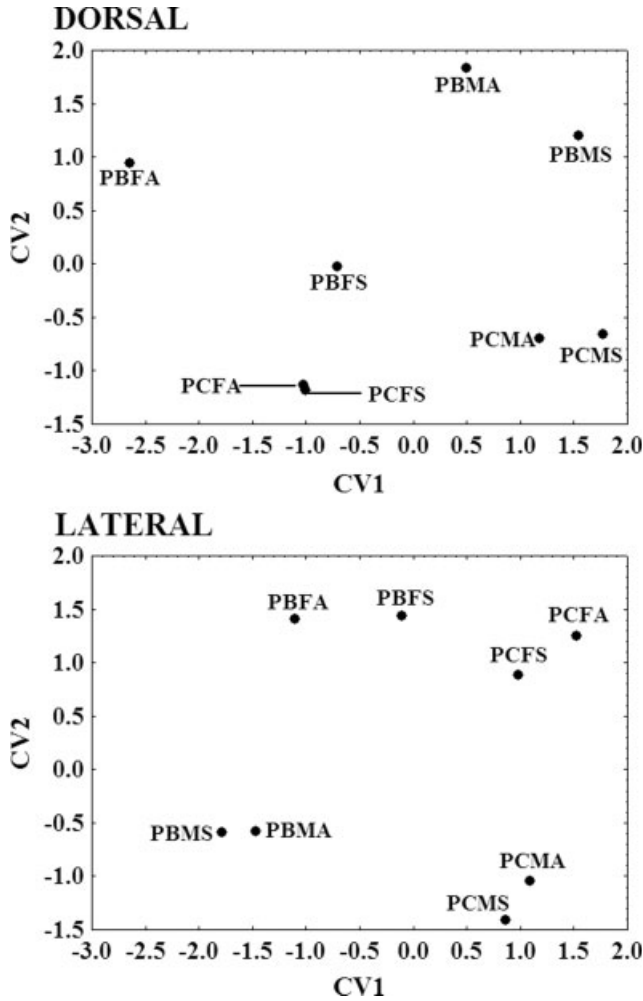
DORSAL

LATERAL

Fig. 7. Means of each group's scores on the first and second canonical root of the canonical variate analysis conducted on relative warps for the dorsal and lateral view. The two first roots resume information on shape patterns of each group and differences between groups can be evaluated. PBFA: *Podarcis bocagei* females, allopatry; PBFS: *Podarcis bocagei* females, sympatry, PBMA: *Podarcis bocagei* males, allopatry; PBMS: *Podarcis bocagei* males, sympatry, PCFA: *Podarcis carbonelli* females, allopatry; PCFS: *Podarcis carbonelli* females. sympatry; PCMA: *Podarcis carbonelli* males, allopatry; PCMS: *Podarcis carbonelli* males, sympatry.

1990; Gvozdik and Van Damme, 2003), and indirectly when fights between males for territory defense take place (Verbeek, 1972; Stamps, 1983; Heulin 1988; Gvozdik and Van Damme, 2003, Perry et al., 2004). Moreover, it has been stated by various authors that characters that present positive allometry with body size in one of the two sexes, probably represent sexually selected traits (Green, 1992; Petrie, 1992; Bondurianksy and Day, 2003). Given that head dimensions, and especially head height, have been shown to be directly related to the volume and power of the jaw muscle (Herrel et al., 1996, 1999, 2001a,b), the positive allometry of HH in these two *Podarcis* species suggests sexual selection. This hy-

pothesis is corroborated by the sexual differences present in the shape of the lateral view of the head involving the tympanic area, but the relation between lateral head shape and jaw musculature should be further explored in the future. Moreover, correlation of head shape data with male reproductive traits could offer more details on the possible effect of head shape on male reproductive success.

Apart from intraspecific pressures, males seem to be subjected to selection driven by interspecific interactions when both species are sympatric. The increase of males' head size in sympatry could be explained if interspecific male–male combats take place or if access to females is restrained because of the presence of a closely related species. Although no behavioral studies are available for the populations in question, a bigger head is known to be advantageous in fights between male lizards (Fitch, 1981; Anderson and Vitt, 1990; Mouton and van Wyk, 1993; Perry et al., 2004) and the pattern observed could be the result of the presence of both conspecific and interspecific rivals when both species coexist. The absence of such morphological modifications in females does not contradict such a hypothesis, because there is no evidence for combats between female lizards, at least in these species (Carretero and Kaliontzopoulou, personal observation). Behavioral field studies on the species in question, analyzing intra- and interspecific interactions in sympatry could shed light into the precise mechanisms involved.

Considering females, although no significant modifications of body parts were observed in sympatry, there is evidence for fecundity selection shaping body proportions. Longer trunks in females than in males of both species could be an evidence of natural selection related to the fecundity advantage attained with a longer trunk, by facilitating more space for the allocation of eggs and enhancing clutch size. However, such a hypothesis needs to be tested by correlating morphological and reproductive traits in these species.

Multivariate vs. Geometric Morphometrics

The simultaneous application of multivariate and geometric morphometrics for the study of SD pat-

TABLE 7. *Squared Mahalanobis Distances between males and females of each population, estimated by the different methods applied and for different body parts in the case of linear biometry*

	P. bocagei		P. carbonelli	
	allopatry	sympatry	allopatry	sympatry
Multivariate, whole body	44.82	31.62	31.86	25.43
Multivariate, head	9.71	9.51	3.80	4.60
Geometric, dorsal	18.77	13.46	8.26	16.41
Geometric, lateral	4.50	26.81	12.39	9.50

terns in these two *Podarcis* species offers the chance for a first approach to the application of geometric morphometrics to the study of head shape in lacertid lizards. To begin with, geometric morphometrics seems to be a powerful tool for the detection of small-scale morphological differences because it allows a quite good discrimination of very closely related populations, much better than that achieved by multivariate methods. Moreover, we have to note that this high discriminative power of GM vs. multivariate methods would probably be still more marked if we used only head dimensions for multivariate analyses. Although the shape differences detected are difficult to describe, they coincide with the available knowledge on head characteristics of the Lacertidae. The sexual differences detected in the tympanic area coincide with differences in head dimensions and are in accordance with previous studies on the structural and functional differences between male and female lacertids. Similarly, the representation of sexual differences on the dorsal configuration of landmarks by deformation grids coincides with the empirical notion of specialists that males have a more "robust" habitus, while females a more "rounded" head, and with the single previous study available on head shape dimorphism in the Lacertidae (Bruner et al., 2005).

The lack of concordance in the results on the grade of SD between multivariate and geometric methods does not constitute an incongruence. Because size and shape are, in principle, different traits and do not necessarily follow the same patterns, they could be driven by different evolutionary forces. The simultaneous application of multivariate and geometric morphometrics helps us to analyze different morphological aspects and determine the evolutionary processes involved. However, the application of geometric morphometrics for the study of head shape in lacertid lizards still needs to be explored, for example, to determine what part of the information captured by landmark methods constitutes a phylogenetic signal. Although the results of this study reveal a great discriminatory capability of geometric morphometrics for closely related populations, it would be interesting to investigate what happens when higher taxonomic units are compared. Moreover, considering the hypotheses formulated during this study, the combination of geometric morphometric techniques and data available on the populations' ecology and reproductive characteristics may shed light into the evolutionary mechanisms implicated. From a purely morphological point of view, examination of the ontogenetic trajectories and allometric patterns of head shape could help in further understanding the forces implicated in the evolution of SD in this trait (Stamps, 1993; Watkins, 1996; Fairbairn, 1997).

The results of our study give evidence for a considerable morphological modification of the species studied in a relatively short (on the evolutionary time-scale) period of time, resulting in a change in SD patterns. The evolution of sexual differences in morphology could be viewed as a case of mosaic evolution, with the mechanisms of sexual, natural, and fecundity selection acting differentially on both sexes and on different body parts. In sympatry, the effect of intersexual competition is combined with that of interspecific interactions, thus modifying SD patterns.

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