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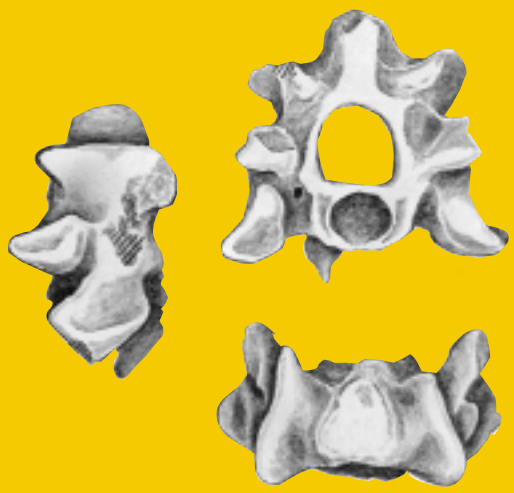

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Differences in the pholidotic patterns of *Podarcis bocagei* and *P. carbonelli* and their implications for species determination

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Abstract: *Podarcis bocagei* and *Podarcis carbonelli* are two closely related species, endemic to the western Iberian Peninsula, whose biometric differences have already been established. However, their pholidosis has not been investigated in detail. We studied various pholidotic characters, often used for taxonomic purposes in the Lacertidae, in order to analyse scalation patterns in the two species and detect characters that could be useful for their diagnosis. The results show that both species present significant differences in various pholidotic characters, although patterns differ between the sexes. The combination of continuous and meristic characters allowed a good discrimination between *P. bocagei* and *P. carbonelli*, especially when sexes were separated *a priori*. However, the close phylogenetic relationship between the two species, along with their high intraspecific morphological variability, complicate the use of pholidotic characters as diagnostic tools in the field.
Key words: pholidosis, *Podarcis bocagei*, *P. carbonelli*, Portugal, species recognition, taxonomy.

Resumen: Diferencias en los patrones folidóticos de *Podarcis bocagei* y *P. carbonelli* e implicaciones para la distinción de ambas especies. – *Podarcis bocagei* y *Podarcis carbonelli* son dos especies cercanas de lacértidos endémicos del oeste de la Península Ibérica, cuyas diferencias biométricas ya han sido demostradas. Sin embargo, su folidosis nunca se ha estudiado detalladamente. Hemos estudiado diversos caracteres folidóticos, habitualmente utilizados en la taxonomía de lacértidos, con el objetivo de analizar los patrones que caracterizan ambas especies y detectar aquellos que podrían emplearse para su distinción. Los resultados demuestran que ambas especies presentan diferencias significativas en varios caracteres, aunque los patrones observados varían entre los sexos. La combinación de caracteres cuantitativos y cualitativos permitió una aceptable discriminación entre *P. bocagei* y *P. carbonelli*, especialmente cuando los sexos se separaron *a priori*. Sin embargo, las estrechas relaciones filogenéticas entre ambas especies y su elevada variabilidad morfológica intraespecífica dificultan la selección de caracteres que podrían servir como herramientas de diagnosis en el campo.
Palabras clave: distinción de especies, folidosis, *Podarcis bocagei*, *P. carbonelli*, Portugal, taxonomía.

INTRODUCTION

Pholidosis has always been an intriguing feature for herpetologists interested in lizard morphology. Many authors have sought adaptive explanations of their variation patterns. For example, the number of subdigital lamellae has been shown to be related to habitat use (GLOSSIP & LOSOS, 1997), femoral pores may be implicated in territory acquisition, reproductive signalling (COLE, 1966; BLASCO, 1975; ALBERTS, 1993; CARRETERO & LLORENTE, 1993) and both intra- and interspecific recognition (GÓMEZ *et*

al., 1993; COOPER, 2004; LÓPEZ & MARTÍN, 2004; BARBOSA *et al.*, 2005), the number of ventral scales in females could be constrained by the necessity to devote space for the allocation of eggs (CARRETERO & LLORENTE, 1993), and dorsal scale number could be related to climatic conditions (SOULÉ & KERFOOT, 1972; LANZA *et al.*, 1993). More recently, the scope of research on scalation has widened to include examination of scale microornamentation (ALIBARDI, 1999; ARNOLD, 2002) and analyses of fluctuating asymmetry (CARRETERO *et al.*, 2003; CRNOBRNJA-ISAILOVIC *et al.*, 2005; ZHDANOVA & ZAKHAROV, in press).

Apart from their potential adaptive value, scalation characters may bear information on the species evolutionary history and have frequently been used in lizard taxonomy (PÉREZ-MELLADO & GOSÁ, 1988). Therefore, many taxonomic keys are based on or at least include information on pholidosis (BÖHME, 1986; SALVADOR, 1997; BARBADILLO *et al.*, 1999; FERRAND DE ALMEIDA *et al.*, 2001; ARNOLD & OVENDEN, 2002). Features used for this purpose include scale counts, presence or absence of certain scales, patterns of contact between them, and scale shape and texture. Within the Lacertidae, pholidotic characters have been used for species identification as well as for reconstruction of phylogenetic relationships (ARNOLD, 1989; HARRIS *et al.*, 1998). Many pholidotic characters exhibit important interspecific variation within this family, including femoral pore count (CARRETERO *et al.*, 2003), masseteric scale size (GUILLAUME, 1976; PÉREZ-MELLADO & GALINDO, 1986), and number of supraciliary scales and granules (PÉREZ-MELLADO & GOSÁ, 1988).

Podarcis bocagei (Seoane 1884) and *Podarcis carbonelli*, Pérez-Mellado 1981 are two lacertid species endemic to the western Iberian Peninsula. Until recently, *P. carbonelli* was considered a subspecies of *P. bocagei* (PÉREZ-MELLADO, 1981a, b, 1997a). However, morphological and molecular studies support the specific status of *P. carbonelli* (SÁ-SOUSA *et al.*, 2000; SÁ-SOUSA, 2001b; SÁ-SOUSA & HARRIS, 2002) and confirm that they are not even sister taxa (HARRIS & SÁ-SOUSA, 2001, 2002). Differences in biometry and colouration between the two species have already been demonstrated (SÁ-SOUSA *et al.*, 2000; HARRIS & SÁ-SOUSA, 2001; SÁ-SOUSA, 2001b; SÁ-SOUSA & HARRIS, 2002; KALIONTZOPOULOU, 2004). Moreover, studies on their reproduction (CARRETERO *et al.*, 2006), behaviour (BARBOSA *et al.*, 2005), and ecological preferences (SÁ-SOUSA, 2001a) suggest that they probably differ in other aspects of their biology as well. However, differences in the pholidotic patterns of these two species have never been extensively studied.

The goal of this study is to describe pholidotic patterns in *Podarcis bocagei* and *Podarcis carbonelli* and investigate their differences. We present a detailed study of pholidotic characters previously used in the taxonomy of the Lacertidae and we attempt to identify those that could be useful for species diagnosis. To minimise extrinsic inter-population variability, we chose two study sites with similar environmental conditions but sufficiently separated to prevent hybridisation and gene flow between populations.

MATERIALS & METHODS

Animals and study sites

All specimens were collected by hand in NW Portugal between April 2001 and August 2002, sacrificed by freezing and preserved in ethanol 96% until their examination. The individuals used were initially captured for conducting studies of their reproductive biology (CARRETERO *et al.*, 2006) and diet

(MARQUES *et al.*, 2005) requiring that the animals be sacrificed. However, in the three years following the present study, the populations were inspected and no demographic reduction was observed, lizards still being very abundant in the study areas.

Sex and sexual maturity was determined following dissection by inspecting the presence of enlarged follicles or oviductal eggs in females, and the size and appearance of testes and epididymes as well as the presence of spermatozoa in males (CARRETERO *et al.*, 2006; M.A. Carretero, D. Barbosa, P. Sá-Sousa & D.J. Harris, unpublished data). In order to minimise measurement errors and to discard possible age effects on pholidosis, only adult animals were included in the study. We selected two study sites separated 40 km, exposed to very similar weather conditions (DIRECÇÃO GERAL DO AMBIENTE, 1995) and with similar habitats of coastal Atlantic dunes (BARRETO-CALDAS *et al.*, 1999). A total of 56 adult males and 48 adult females of *P. bocagei* were collected from Mindelo-Vila Chã (UTM 29T NF27). Simultaneously, 53 adult males and 45 adult females of *P. carbonelli* were collected from Torreira, in the sand bar of São Jacinto located in the northern part of the Aveiro coastal lagoon system (UTM 29T NF21). Previous genetic analyses using nuclear markers demonstrated the absence of gene flow and hybridisation between both populations (PINHO *et al.*, 2003, 2004).

Characters studied

To investigate the pholidotic patterns of *P. bocagei* and *P. carbonelli* we examined a total of 25 characters, previously used in various taxonomic studies with lacertids. Ten were meristic scalation characters, 10 were categorical, and five were continuous. Meristic scalation characters studied included the number of femoral pores (FPN), subdigital lamellae (SLN), collar scales (CSN), gular scales (GSN), transversal rows of ventral scales (VSN), dorsal scales around mid-body (DSN), supraciliary scales (SCSN), supraciliary granules (SCGN), supratemporal scales (StSN) and supralabial scales (SLSN). Bilateral meristic scalation characters were recorded in both sides of the body and their mean was used for the analyses in order to avoid pseudoreplication. The following variables were recorded: TYMP: tympanic scale entire (1) or divided (2); MASS_EXIST: masseteric scale absent (0) or present (1); MASS_DIVID: masseteric scale entire (1) or divided (2) (only if masseteric scale was present); M/ST: masseteric scale in contact (1) or not (0) with supratemporals; R/FN: rostral scale in contact (1) or not (0) with frontonasal; 3rdR/FN: presence (1) or absence (0) of a third scale between rostral and frontonasal; FN/F: frontonasal scale in contact (1) or not (0) with frontal; 3rdFN/F: presence (1) or absence (0) of a third scale between frontonasal and frontal; O/IP: occipital scale in contact (1) or not (0) with interparietal; 3rdO/IP: presence (1) or absence (0) of a third scale between occipital and interparietal.

Finally, we recorded the maximum and minimum diameter of the tympanic scale (TSD1 and TSD2, respectively) and of the tympanic opening (TD1 and TD2 respectively), as well as the maximum diameter of the masseteric scale (MSD). All categorical characters, as well as scale diameters and tympanic openings, were always recorded from the right side of the lizards' body. We also recorded snout-vent length (SVL) in order to correct for size when necessary. All linear measurements were recorded to the closest 0.01 mm using electronic callipers.

Statistical procedures

We first examined the presence of sexual

dimorphism for all the characters studied. Since differences between the sexes were significant for most variables (see Results), interspecific differences were examined separately for males and females.

All meristic scalation character variables deviated from normality in at least one of the groups studied (Anderson-Darling normality test: $p < 0.05$). Therefore, Mann-Whitney U tests were used to investigate the existence of sexual and interspecific differences in these characters. Scale and tympanic opening diameters were found to be normally distributed (Anderson-Darling normality test: $p > 0.1$ for all variables) and homogeneity of variances between different groups was significant (Levene's test: $p > 0.1$ for all variables). Moreover, inspection of the dataset revealed no outliers. Thus, parametric statistics were applied to these measurements. To investigate the presence of sexual and interspecific differences we conducted ANCOVAs using SVL as a covariate. We also conducted ANCOVAs on maximum tympanic scale diameter using masseteric scale diameter as a covariate in order to investigate sexual and interspecific variation in relative size between the two characters. Frequencies of the different character states were examined for categorical character variables. Because frequencies were usually below five, Fisher's exact test was applied to investigate the existence of differences in these variables. Finally, in order to identify those characters that could be useful for species discrimination, we conducted a backward stepwise discriminant (DA) and canonical variate analysis (CVA).

RESULTS

Intraspecific comparison: sexual dimorphism

Sexual dimorphism varied depending on the pholidotic character examined. Descriptive statistics and the results of statistical comparisons between the sexes are shown for *Podarcis bocagei*, in Table 1A-C, and for *Podarcis carbonelli*, in Table 2A-C. With the exception of the number of ventral scales (VSN), which was higher in females of both species, males always showed higher values than females when significant differences were present.

Interspecific comparison: meristic characters

The two species exhibited significant differences in several meristic scalation characters, although patterns were different between the sexes (Table 3). Both male and female *Podarcis carbonelli* presented more femoral pores (FPN) and subdigital lamellae (SLN) and less collar (CSN) and supraciliary scales (SCSN) than male and female *P. bocagei*. Males of *P. bocagei* presented less gular scales (GSN), and females more ventral (VSN) and supralabial scales (SLSN) than *P. carbonelli* of the corresponding sex.

Interspecific comparison: categorical variables

The same variables exhibited significant interspecific differences in males and in females (Table 4). All such variables were related to the masseteric scale. The percentage of individuals lacking the masseteric scale was higher in *P. carbonelli* than in *P. bocagei*, irrespective of sex. Among the individuals that had a masseteric scale, the masseteric contacted the supratemporal scales in a higher percentage in *P. carbonelli* (Fisher's exact test: $p < 0.05$, see Tables 1A-C and 2A-C for group frequencies).

Interspecific comparison: diameters of scales and tympanic opening

Interspecific differences were also significant for most of the variables related to the diameter of scales and to the tympanic

opening (Table 5). The ANCOVAs conducted revealed differences between the two species for the maximum diameter of the tympanic opening, which was relatively higher in *P. bocagei* than in *P. carbonelli* for both sexes. The examination of the relationship between

TABLE 1 A-C. Descriptive statistics and comparisons for males and females of *Podarcis bocagei*. Numbers indicate median ± quartile range for not normally distributed variables and mean ± SE for normally distributed variables, range and sample size. Note that p-values presented are not corrected for multiple tests effect since such correction does not modify the significance of the results. See Materials & Methods for abbreviations of variables.

TABLA 1 A-C. Estadísticos descriptivos y comparaciones para machos y hembras de *Podarcis bocagei*. Los números indican la mediana ± rango intercuartílico para las variables no normales y media ± EE para las variables normales, el rango y el tamaño de muestra. Los p-valores presentados no han sido corregidos para el efecto de comparaciones múltiples puesto que dicha corrección no modificaría la significación de los resultados. Las abreviaturas de las variables se hallan en la sección de Material y Métodos.

TABLA 1A

Variable	Males	Females	Mann-Whitney U	p-value
FPN	17.0 ± 2.0 14.0-20.0 56	16.5 ± 1.5 13.5-19.0 48	2.122	3.4×10^{-3}
SLN	24.0 ± 2.0 20.5-29.5 54	23.0 ± 2.0 20.0-27.0 45	2.221	2.6×10^{-3}
CSN	11.0 ± 1.0 7.0-14.0 56	10.0 ± 2.0 7.0-13.0 48	1.575	0.115
GSN	27.0 ± 3.0 23.0-33.0 56	27.0 ± 3.0 22.0-31.0 48	0.551	0.582
VSN	27.0 ± 2.0 23.0-29.0 56	30.0 ± 2.0 27.0-35.0 48	–8.213	2.17×10^{-16}
DSN	59.0 ± 4.5 52.0-65.0 56	56.5 ± 4.5 51.0-64.0 48	3.889	10^{-5}
SCSN	6.0 ± 1.0 5.0-7.0 56	6.0 ± 0.5 4.5-7.0 48	–2.093	3.6×10^{-2}
SGSN	10.5 ± 3.5 4.5-16.0 56	10.0 ± 2.75 3.0-15.0 48	0.730	0.465
StSN	5.0 ± 1.5 2.5-9.5 56	5.0 ± 1.5 2.5-7.0 48	0.173	0.863
SLSN	7.0 ± 1.0 5.5-7.5 56	7.0 ± 1.0 5.0-8.0 48	–1.007	0.314

TABLA 1B

Variable	Males	Females	ANCOVA F	p-value
TSD1	1.87 ± 0.04 1.3-2.7 56	1.56 ± 0.03 1.1-2.0 48	15.441	1.56×10^{-4}
TSD2	0.70 ± 0.04 0.5-2.6 56	0.55 ± 0.03 0.4-2.0 48	2.633	0.108
TD1	2.44 ± 0.02 2.1-2.9 55	2.05 ± 0.03 1.7-2.5 48	90.774	1.11×10^{-15}
TD2	1.06 ± 0.02 0.7-1.5 55	1.04 ± 0.02 0.7-1.4 48	0.527	0.469
MSD	1.51 ± 0.05 0.7-2.2 54	1.14 ± 0.04 0.5-1.8 48	15.377	1.62×10^{-4}

TABLA 1C

Variable	Males			Females			Fisher exact test
	State	%	N	State	%	N	
TYMP	1 2	96.36 3.64	55	1 2	89.58 10.42	48	0.247
MASS_EXIST	0 1	3.57 96.43	56	0 1	0 100	48	0.498
MASS_DIVID	1 2	77.78 22.22	54	1 2	81.25 18.75	48	0.807
M/ST	0 1	92.86 7.14	56	0 1	95.83 4.17	48	0.684
R/FN	0 1	100 0	56	0 1	89.58 10.42	48	0.374
3rdR/FN	0 1	96.43 3.57	56	0 1	100 0	48	0.374
FN/F	0 1	92.86 7.14	56	0 1	100 0	48	0.730
3rdFN/F	0 1	92.86 7.14	56	0 1	89.58 10.42	48	0.122
O/IP	0 1	9.26 90.74	54	0 1	16.67 83.33	48	0.498
3rdO/IP	0 1	90.74 9.26	54	0 1	83.33 16.67	48	0.019

TABLE 2 A-C. Descriptive statistics and comparisons for males and females of *Podarcis carbonelli*. Numbers indicate median ± quartile range for not normally distributed variables and mean ± SE for normally distributed variables, range and sample size. Note that p-values presented are not corrected for multiple tests effect since such correction does not modify the significance of the results. See Materials & Methods for abbreviations of variables.

TABLA 2 A-C. Estadísticos descriptivos y comparaciones para los dos sexos de *Podarcis carbonelli*. Los números indican la mediana ± rango intercuartílico para las variables no normales y media ± EE para las variables normales, el rango y el tamaño de muestra. Los p-valores presentados no han sido corregidos para el efecto de comparaciones múltiples puesto que dicha corrección no modificaría la significación de los resultados. Las abreviaturas de las variables se hallan en la sección de Material y Métodos.

TABLA 2A

Variable	Males	Females	Mann-Whitney U	p-value
FPN	19.0 ± 1.5 16.0-21.5 53	17.5 ± 2.0 15.0-19.0 45	5.040	4.7×10^{-7}
SLN	25.5 ± 2.0 21.0-30.5 52	25.0 ± 1.0 22.5-28.5 45	3.078	2.08×10^{-3}
CSN	10.0 ± 2.0 8.0-12.0 53	10.0 ± 1.0 8.0-11.0 45	1.764	7.77×10^{-2}
GSN	28.0 ± 2.0 25.0-32.0 53	26.0 ± 2.0 23.0-31.0 45	3.579	3.45×10^{-4}
VSN	26.0 ± 2.0 22.0-28.0 53	29.0 ± 2.0 27.0-32.0 45	–8.149	3.7×10^{-16}
DSN	59.0 ± 4.0 49.0-65.0 53	56.0 ± 3.0 49.0-62.0 45	4.363	1.28×10^{-7}
SCSN	5.0 ± 1.0 4.0-6.5 53	5.0 ± 0.5 4.0-6.5 45	0.578	0.564
SGSN	10.0 ± 2.0 4.5-13.5 53	10.0 ± 2.0 5.5-14.0 45	1.921	0.055
StSN	5.5 ± 1.5 2.5-7.5 53	5.0 ± 1.5 2.5-7.5 45	0.588	0.556
SLSN	7.0 ± 1.0 6.0-8.0 53	6.0 ± 1.0 5.0-7.0 45	1.679	0.0932

TABLA 2B

Variable	Males	Females	ANCOVA F	p-value
TSD1	1.67 ± 0.03 1.2-2.1 53	1.53 ± 0.02 1.3-1.9 44	19.061	3.25×10^{-5}
TSD2	0.67 ± 0.01 0.5-0.9 53	0.53 ± 0.01 0.4-0.7 44	63.767	3.43×10^{-12}
TD1	2.03 ± 0.03 1.6-2.5 53	1.81 ± 0.02 1.6-2.1 45	46.88	7.40×10^{-10}
TD2	1.06 ± 0.02 0.8-1.4 53	1.01 ± 0.02 0.7-1.3 45	3.062	0.083
MSD	1.29 ± 0.04 0.4-2.0 50	1.06 ± 0.04 0.7-1.7 43	16.338	1.11×10^{-4}

TABLA 2C

Variable	Males			Females			Fisher exact test
	State	%	N	State	%	N	
TYMP	1 2	98.11 1.89	53	1 2	95.56 4.44	45	0.592
MASS_EXIST	0 1	7.55 92.45	53	0 1	6.67 93.33	45	1.000
MASS_DIVID	1 2	93.88 6.12	49	1 2	97.62 2.38	42	0.621
M/ST	0 1	73.58 26.42	53	0 1	75.56 24.44	45	1.000
R/FN	0 1	92.45 7.55	53	0 1	97.78 2.22	45	0.371
3rdR/FN	0 1	100 0	53	0 1	100 0	45	
FN/F	0 1	100 0	53	0 1	97.78 2.22	45	0.459
3rdFN/F	0 1	100 0	53	0 1	100 0	45	
O/IP	0 1	7.84 92.16	51	0 1	6.67 93.33	45	1.000
3rdO/IP	0 1	94.12 5.88	51	0 1	93.33 6.67	45	1.000

TABLE 3. Mann-Whitney U test statistics for comparisons between the two species in males and females. Note that p-values presented are not corrected for multiple tests effect since such correction does not modify the significance of the results. See Materials & Methods for abbreviations of variables. Sample sizes as in Table 1.
TABLA 3. Estadísticos de los tests U de Mann-Whitney para las comparaciones entre las dos especies en machos y hembras. Los p-valores presentados no han sido corregidos para el efecto de comparaciones múltiples puesto que dicha corrección no modificaría la significación de los resultados. Abreviaturas de las variables en la sección de Material y Métodos. Tamaños de muestra igual que en la Tabla 1.

	Males		Females	
Variable	Z	p-value	Z	p-value
FPN	–6.278	3.44 x 10–10	–4.101	4.11×10^{-5}
SLN	–4.370	1.24 x 10–5	–4.249	2.15×10^{-5}
CSN	2.228	2.59 x 10–2	2.064	3.90×10^{-2}
GSN	–2.464	1.37 x 10–2	0.365	0.715
VSN	1.167	0.243	2.768	5.65×10^{-3}
DSN	0.821	0.411	1.445	0.148
SCSN	2.510	1.21 x 10–2	4.616	3.90×10^{-6}
SCGN	0.067	0.947	0.838	0.402
StSN	–1.413	0.158	–0.849	0.396
SLSN	0.273	0.785	2.633	8.46×10^{-3}

TABLE 4. Fisher's exact probabilities for comparisons of categorical variables between the two species in males and females. Missing values are due to absolute group uniformity. See Materials & Methods for abbreviations of variables. Sample sizes as in Table 1.

TABLA 4. Probabilidades exactas de Fisher de las comparaciones para las variables categóricas entre las dos especies para machos y hembras. La ausencia de algunos valores se debe a la uniformidad absoluta de algunos grupos. Las abreviaturas de las variables se hallan en la sección de Material y Métodos. Tamaños muestrales como en la Tabla 1.

	Males	Females
Variable	p-value	p-value
TYMP	1.0000	0.4365
MASS_EXIST	0.0257	0.0175
MASS_DIVID	0.4294	0.1094
M/ST	0.0091	0.0063
R/FN	0.0526	0.2048
3rdR/FN	0.4958	–
FN/N	0.1187	0.4839
3rdFN/N	0.1187	0.0565
O/IP	1.0000	0.2005
3rdO/IP	0.7166	0.2005

TD1 and MSD also revealed significant differences, both sexes of *P. bocagei* presenting higher values for the ratio TD1/MSD than *P. carbonelli*.

Discriminant and canonical variate analysis

The discriminant analysis conducted using continuous variables to discriminate between males and females of the two species resulted in a relatively high level of classification (see Table 6 and Fig. 1). The variables that contributed most to group discrimination were the maximum diameter of the tympanic opening relative to the diameter of the masseteric scale, the number of femoral pores (FPN), and the number of ventral scales (VSN). To improve the classification level of the discriminant analysis, we examined both sexes separately trying to discriminate only between the species. As a result, we obtained a higher classification level (close to 90% for all groups) (see Table 7A, B).

TABLE 5. Statistics of ANCOVA comparisons of diameter related variables between the two species for males and females. SVL was used as a covariate for all comparisons, except for the last one (TD1/MSD) that refers to the comparison of TD1 using MSD as a covariate. Note that p-values presented are not corrected for multiple tests effect since such correction does not modify the significance of the results. See Materials & Methods for abbreviations of variables. Sample sizes as in Table 1.

TABLA 5. Estadísticos de las comparaciones ANCOVA de las variables que están relacionadas a diámetros entre las dos especies para machos y hembras. La covariable usada fue SVL en todas las comparaciones, menos en la última (TD1/MSD) que se refiere a la comparación de TD1 usando MSD como covariable. Los p-valores presentados no han sido corregidos para el efecto de comparaciones múltiples puesto que dicha corrección no modificaría la significación de los resultados. Las abreviaturas de las variables se hallan en la sección de Material y Métodos. Tamaños muestrales igual que en la Tabla 1.

	Males		Females	
Variable	ANCOVA F	p-value	ANCOVA F	p-value
TSD1	0.105	0.747	2.822	0.097
TSD2	2.674	0.105	0.516	0.474
TD1	34.729	6.43×10^{-8}	24.695	3.18×10^{-6}
TD2	0.139	0.710	1.965	0.165
MSD	0.200	0.656	0.230	0.633
TD1/MSD	94.218	4.44×10^{-16}	53.622	1.10×10^{-10}

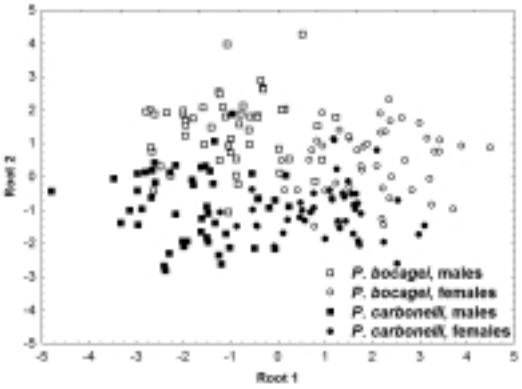

FIGURE 1. Canonical variate analysis plot for males and females of the two species.

FIGURA 1. Representación del análisis canónico para machos y hembras de las dos especies.

DISCUSSION

Sexual dimorphism

The analysis of the pholidotic patterns of *Podarcis bocagei* and *Podarcis carbonelli* revealed that both species show marked sexual dimorphism in some characters. Males of both species have more femoral pores and subdigital lamellae and a bigger tympanic opening and masseteric scale than females, while females have more ventral scales than males. Sexual dimorphism in the shape and size of femoral pores is a common trait in lizards (COLE, 1966; BLASCO, 1975) and while no detailed studies exist, others have also reported sexual variation in the number of femoral pores, males always exhibiting a higher number of pores than females (BÖHME, 1986; CARRETERO, 1993; CARRETERO & LLORENTE, 1993; SALVADOR, 1997; CARRETERO *et al*., 2003). Femoral pores are known to play an important role in chemically-based communication (GÓMEZ *et al.*, 1993). Femoral pore secretions could be involved in conspecific and sex recognition (COOPER & VITT, 1986; GÓMEZ *et al.*, 1993), territory marking (ARAGÓN *et al.,* 2001a, b; LÓPEZ & MARTÍN, 2004) and mate quality advertisement (MARTÍN & LÓPEZ, 2000). The relationship between sexual dimorphism in femoral pore number and behavioral traits has never been investigated; however femoral gland secretions seem crucial for certain

TABLE 6. Statistics of the discriminant analysis conducted on the continuous variables for males and females of the two species. PBM: *P. bocagei* males, PBF: *P. bocagei* females, PCM: *P. carbonelli* males, PCF: *P. carbonelli* females. See Materials & Methods for abbreviations of variables.

TABLA 6. Estadísticos del análisis discriminante realizado con las variables continuas para machos y hembras de las dos especies. PBM: *P. bocagei* machos, PBF: *P. bocagei* hembras, PCM: *P. carbonelli* machos, PCF: *P. carbonelli* hembras. Abreviaturas de las variables en la sección de Material y Métodos.

Variable	Wilks' Lambda	Partial Lambda	F-remove (3.179)	p-level	Tolerance	1 – Toler. (R-Sqr.)
FPN	0.213	0.668	29.661	1.29×10^{-15}	0.963	0.037
VSN	0.355	0.401	89.309	0	0.965	0.035
RES TD1/MSD	0.239	0.596	40.434	5.32×10^{-20}	0.997	0.003

	Percent correct	PBM p = 0.265	PBF p = 0.243	PCM p = 0.260	PCF p = 0.232
PBM	77.36	41	3	7	2
PBF	79.17	1	38	0	9
PCM	82.00	4	0	41	5
PCF	74.42	0	5	6	32
Total	78.35	46	46	54	48

TABLE 7. Classification matrix and functions of the discriminant analysis between the two species, considering separately the two sexes. PB: *P. bocagei*, PC: *P. carbonelli*. See Materials & Methods for abbreviations of variables.

TABLA 7. Matriz y funciones de clasificación del análisis discriminante entre las dos especies, considerando los sexos por separado. PB: *P. bocagei*, PC: *P. carbonelli*. Abreviaturas de las variables en la sección de Material y Métodos.

TABLA 7A

	Males			Females		
	Percent correct	PB p = 0.51	PC p = 0.49	Percent correct	PB p = 0.52	PC p = 0.48
PB	86.79	46	7	84.44	38	7
PC	90.00	5	45	90.70	4	39
Total	88.35	51	52	87.50	42	46

TABLA 7B

	PB		PC	
	Males	Females	Males	Females
FPN	10.791		12.021	
SLN		10.859		11.584
SCSN		16.116		14.308
RESIDUAL TD1/MSD	1.651	–10.471	–6.919	–17.614
Constant	–92.611	–174.626	–113.917	–182.807

behavioral traits and are thus expected to be influenced by natural selection. Therefore, the higher number of femoral pores in males could be an indication of the adaptive value of this character. On the other hand, the variation observed in ventral scale number could be related to the fact that females have longer trunks than females (KALIONTZOPOULOU, 2004) and are constrained by the need of space for the allocation of eggs (CARRETERO & LLORENTE, 1993; BRAÑA, 1996).

Interspecific comparison

The comparison of pholidotic characteristics between *Podarcis bocagei* and *Podarcis carbonelli* agrees with previous results based on biometric characters (HARRIS & SÁ-SOUSA, 2001; SÁ-SOUSA, 2001b, SÁ-SOUSA & HARRIS, 2002) and confirms the existence of a morphological distinction between them. Our results show that *P. bocagei* and *P. carbonelli* differ in some of the scalation characters normally used for taxonomic purposes in the Lacertidae. Both sexes have more femoral pores and subdigital lamellae and less collar and supraciliary scales in *P. carbonelli* than in *P. bocagei*. Moreover, the masseteric scale is often absent in *P. carbonelli* but very rarely so in *P. bocagei*. Furthermore, among individuals having a masseteric scale, it is much more often in contact with the supratemporal scales in *P. bocagei* than in *P. carbonelli*. Finally, *P. carbonelli* presents a smaller tympanic opening than *P. bocagei*. Although no comparative data on the pholidosis of *P. carbonelli* are available, our results on scalation characteristics of *P. bocagei* are within the ranges reported by other authors for this species (GALÁN, 1986; PÉREZ-MELLADO, 1997a).

Implications for species identification

Based on the results of our study we can confirm that scalation patterns are unique to each of the two species studied, in accordance with what has been previously demonstrated for their genetic identities and their biometric and colouration characteristics (SÁ-SOUSA *et al.*, 2000; HARRIS & SÁ-SOUSA, 2001; SÁ-SOUSA & HARRIS, 2002; PINHO *et al.*, 2006). Not only did both species differ significantly in many pholidotic characters, but we were also able to construct discriminant functions that result in a high level of correct classification. However, the strength of discriminant functions a) depends on previous sex identification of individuals, and b) involves many different characters. Although sex identification of adults in the field might not pose such a serious problem, at least for experienced herpetologists, the need to quantify many scalation characters makes their usefulness as diagnostic tools in the field doubtful.

In part, this is probably due to the high intraspecific variability that characterises the genus *Podarcis*. The large overlap in most of the pholidotic variables studied seems typical of most Iberian *Podarcis* species. For example, femoral pore number varies from 10 to 24 in *P. hispanica* (*sensu lato*), 12-22 in *P. muralis*, 16-27 in *P. lilfordi*, 12-30 in *P. pityusensis* and 17-21 in *P. sicula* (PÉREZ-MELLADO, 1997b), compared to 13.5-20 in *P. bocagei* and 15-21.5 in *P. carbonelli* (this study).

From the above it becomes evident that considering the degree of distinctiveness of pholidotic patterns between the two species, scalation characters are probably not the most adequate for species diagnosis. Biometric characters could be more suitable for such a task, since they offer a higher discriminatory power (SÁ-SOUSA & HARRIS, 2002; KALIONTZOPOULOU, 2004). Still, biometric characters could differ among populations, mainly due to demographic factors.

Therefore, it seems that colouration patterns are the most powerful diagnostic tool for the discrimination of *P. bocagei* and *P. carbonelli* in the field. This is evident in the diagnosis offered for *P. carbonelli* in the study that elevated it to species rank (SÁ-SOUSA *et al.*, 2000; SÁ-SOUSA & HARRIS, 2002) and becomes obvious when seeing the two species in the wild, especially for males.

Even acknowledging that scalation characters would be poor tools for diagnosing *P. bodagei* and *P. carbonelli* in the field, one cannot deny their taxonomic value, since a combination of scalation characters allows a good discrimination between both species. Although *Podarcis* species usually show high morphological variability and the two species studied here shared a common, not direct ancestor in Western Iberia, they show more divergence in their pholidotic patterns than their respective sister taxa, namely *P. hispanica* type 1 and *P. hispanica* type 2 (PINHO *et al.*, 2006). As concluded by SÁ-SOUSA *et al.* (2002) for the latter two forms, "they [scalation results] do not have a taxonomic value such as in the case of the Iberian rock-lizards *Archaeolacerta*" (p. 63). This further complicates the explanation of scalation pattern variation within the group, because varying or even contradictory degrees of divergence are being evidenced. Of course, pholidosis does not need to strictly follow phylogeny and environmental and/or ecological factors could also play an important role in shaping it. Understanding of variation in scalation and other morphological patterns within the group of Western Iberian *Podarcis* could improve a) by incorporating other populations of *P. bocagei* and *P. carbonelli* from other, less conflictive areas (further apart from the species' distribution borders), and b) by integrating data on the phylogenetic history and the pholidotic, biometric and colouration patterns observed.

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