

Podarcis carbonelli Pérez-Mellado, 1981 is a distinct species

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Abstract. *Podarcis carbonelli* is considered a full species on the basis of its morphological and genetic divergence from *P. bocagei* and *P. hispanica*. *Podarcis carbonelli* differs from *P. bocagei* in all twelve biometric variables compared and also in chromatic patterns. *Podarcis carbonelli* diverges from *P. bocagei* by more than 13% between cytochrome *b* sequences (mitochondrial DNA), a value typically reported between congeneric reptile species. Biogeographical criteria also support this hypothesis, as both lizard forms have different distribution ranges with a limited parapatric zone of contact without morphological intermediates.

Introduction

Pérez-Mellado (1981) described *Podarcis bocagei carbonelli* from the western part of the ‘Sistema Central’ mountain range, where sub-Atlantic climate prevails, and where it occurs in sympatry with the Iberian wall lizard *P. hispanica*. The nominal *P. bocagei bocagei* (Seoane, 1884) was thought to range from NW Iberia (e.g. W Asturias, Cantabria, Galicia, north of Portugal) to the Portuguese region of Extremadura, north of Lisbon (Galán, 1986; Pérez-Mellado, 1986, 1997, 1998). Another subspecies, *P. b. berlengensis* Vicente, 1985 was described from the Berlengas islands off the western coast of Portugal (Vicente, 1985). *Podarcis b. carbonelli* was later reported in the dunes of Coto Doñana, south of Andalusia, more than 400 km south of the Sistema Central range (Magraner, 1986), but this was often refuted (Pérez-Mellado, 1997, 1998; Barbadillo et al., 1999). Magraner (1986) suggested *P. b. carbonelli* should also be looked for in southern Portugal. Following this, extensive prospecting in Portugal has uncovered *P. b. carbonelli* in additional mountains to the Sistema Central and along the Atlantic lowlands (Sá-Sousa, 1995, 1999, 2000; fig. 1). The southern range of *P. b. bocagei* was re-established to near the river Douro, northern Portugal

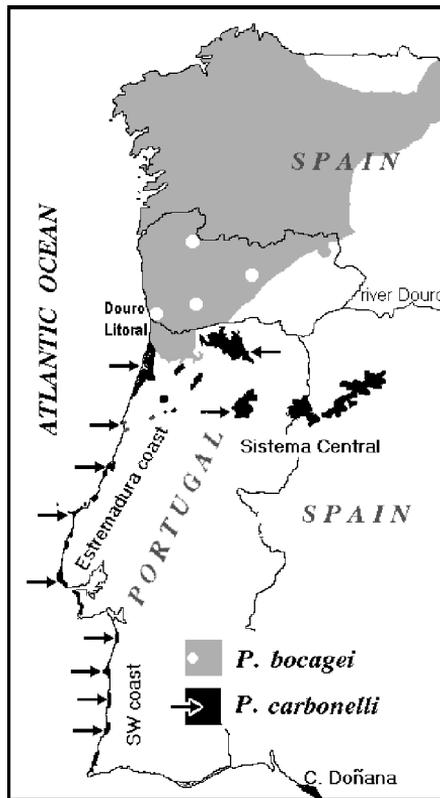


Figure 1. Distribution ranges of *P. bocagei* and of *P. carbonelli* in W Iberia. Sampled localities are indicated.

(Sá-Sousa, 1998, 2001; fig. 1). Thus, instead of distinct allopatry, *P. b. bocagei* and *P. b. carbonelli* show a narrow parapatric zone of contact along the provinces of Douro Litoral and Beira Litoral, in Portugal (Sá-Sousa, 2000, 2001). Within this contact zone individuals with an intermediate appearance between both forms have not been found, which suggests that *P. b. bocagei* and *P. b. carbonelli* do not interbreed in the wild. In such a case, the populations are usually treated as different species (Mayr and Ashlock, 1991). Thus, in this study we revise the status of *P. b. carbonelli*, taking into account its morphology, and recent analyses derived from mitochondrial DNA sequences (Harris and Sá-Sousa, 2001, 2002) and allozyme variation (Sá-Sousa et al., 2000).

Material and methods

Samples of the two lizard forms (*bocagei* and *carbonelli*) were collected in Portugal from localities across their known distribution ranges (fig. 1, appendix 1). Twelve biometric variables were measured (fig. 2): SVL (snout-vent length); HL (head length); HW (head width); OW (inter-orbital width); FW (inter-frontal width);

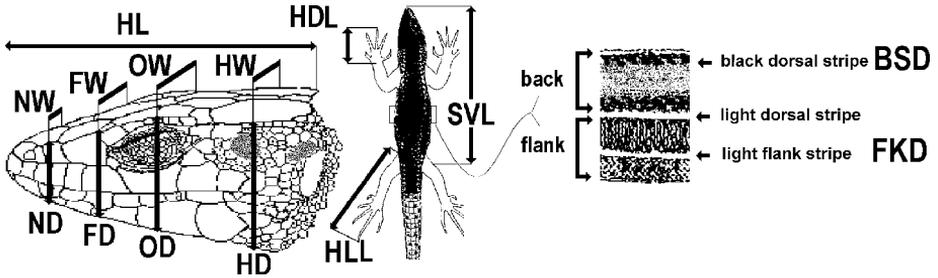


Figure 2. Scheme illustrating the linear measurements of biometry and some body parts that reveal the chromatic patterns.

NW (inter-nasal width); HD (head depth); OD (orbital depth); FD (frontal depth); ND (nasal depth); HDL (hand length); and HLL (hind limb length). Nine variables of chromatic patterns were recorded (see for details fig. 2; Galán, 1986; Pérez-Mellado and Gosá, 1988): mid-back/dorsal pattern (MBD), type of black dorsal stripes (BSD) and pattern of the flanks (FKD); black pigmentation of the cephalic plates (CEP), pairs of longitudinal rows of ventral scales pigmented with black spots (VTP), presence of blue/green spots on the outer ventral scales (BGS), mid-back/dorsal coloration (MBC), colour of the flanks (FKC) and ventral coloration (VTC).

Each sex was analysed separately, due to sexual dimorphism found in both forms, *bocagei* and *carbonelli* (Pérez-Mellado, 1997, 1998). A total of 158 females and 308 males were included in all statistical analyses. A principal component analyse (PCA) on the product-moment correlated matrices of biometric data was used with varimax rotation in order to discriminate better the two lizard forms. UPGMA clustering was used on the biometric matrix (mean squared Mahalanobis distances of centroids) to detect group congruence among the main samples (appendix 1, $n = 12$), within and between both lizard forms (De Luca and Grbac, 1995; Sokal and Rohlf, 1995). MANOVA (lizard form as fixed factor; all biometric characters as dependent variables) and one-way ANOVA's (Scheffé test, $P < 0.05$) were performed to test the statistical significance of biometric differences in means between both forms and sexes. (Legendre and Legendre, 1998). A standard discriminant analysis (DA) was also applied on the biometric matrix to determine the correct classification between both lizard forms (Legendre and Legendre, 1998). DA functions were derived using all specimens. Chi-squared tests (χ^2 , $P < 0.05$) were used to compare each chromatic pattern variable between both forms and sexes. All statistical analyses were performed with the software *Statistica 5.5*.

Results

Morphological data. Descriptive statistics for biometric variables are shown in appendix 2. The form *carbonelli* is clearly shorter than *bocagei*, in both sexes. UPGMA clustering shows the biometric separation between *bocagei* and *carbonelli* (fig. 3). MANOVA revealed significant variation between the two lizard forms: males Wilks' $\lambda = 0.18955$, approx. $F_{12,295} = 105.1124$, $P < 0.001$; females Wilks' $\lambda = 0.27342$, approx. $F_{12,143} = 31.66634$, $P < 0.001$. One-way ANOVAs demonstrate significant variation for all biometric variables studied (Scheffé tests, $P < 0.001$). These results show that *bocagei* is larger than *carbonelli* and males are larger than respective females. The ordination of males and females in the space of the first two principal components of variation (PC1, PC2), deduced from the twelve biometric variables, is shown in fig. 3. PC1 (males 53.7%; females 54.0%) is positively and strongly (>0.70) associated with all cephalic measures (table 1),

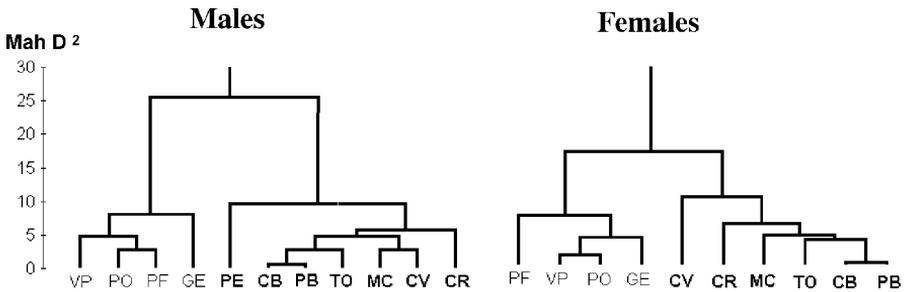


Figure 3. UPGMA trees based on the squared Mahalanobis distances found among samples of *P. bocagei* and of *P. carbonelli* (bold labels).

Table 1. Factor loadings for the principal components axes (PCA) rooted to show maximal variance.

Variable	Males		Females	
	PC1	PC2	PC1	PC2
SVL	0.666	0.709	0.702	0.633
HL	0.710	0.671	0.779	0.541
HW	0.751	0.598	0.795	0.505
OW	0.732	0.553	0.772	0.490
FW	0.772	0.538	0.646	0.639
NW	0.735	0.484	0.740	0.507
HD	0.864	0.357	0.881	0.311
OD	0.897	0.372	0.906	0.290
FD	0.861	0.401	0.848	0.338
FD	0.814	0.449	0.784	0.460
HDL	0.339	0.895	0.258	0.896
HLL	0.439	0.858	0.439	0.808
Expl.var. %	53.7	35.9	54.0	31.8
Cum var. %	53.7	89.6	54.0	85.8

particularly those that express the head depth (HD, OD, FD). PC2 (males 35.9%; females 31.8%) is predominantly determined (>0.80) by limb lengths (HDL, HLL), secondarily by body size (SVL). The discriminant functions (DA) classify correctly 97% of cases between males (*bocagei* = 97% and *carbonelli* = 98%) and 92% between females (*bocagei* = 90% and *carbonelli* = 94%), using all biometric variables. The variables that contributed to discrimination between both forms were HDL, HLL and FW (for both sexes), plus SVL, HW, OD and FD (for males).

Chromatic patterns are also different. More males of *bocagei* were found with striped dorsal patterns (e.g. MBD, FKD) than males of *carbonelli* (table 2). Males of *bocagei* usually have thick black reticulations, whereas the *carbonelli* ones have thin diffused reticulations or speckled patterns. Males of both species have bright green dorsal colorations during the mating period (e.g. MBC, FKC). Only the males of *carbonelli* typically show blue spots on the outer ventral scales (BGS). The bellies of *bocagei* are coloured (VTC),

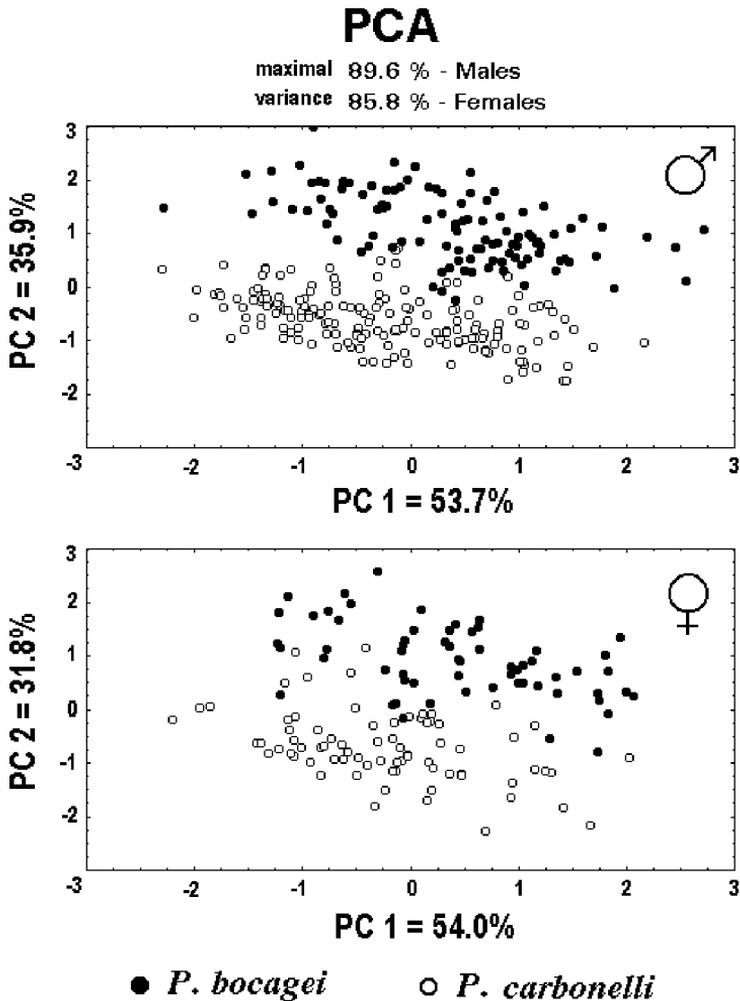


Figure 4. Scatterplot of *P. bocagei* and *P. carbonelli* on the principal components axes of biometry.

while *carbonelli* have whitish bellies. Females have significantly less reticulated flanks (FKD), less pigmentation on the body (e.g. CPP, VTP, BGS) and less green patterns (MBC, FKC), than respective males (table 2).

Discussion

Morphological data. Unlike the data from Pérez-Mellado and Galindo (1986), the males of *carbonelli* of the present sample were significantly larger than respective females. Both *bocagei* and *carbonelli* lizards show a pronounced sexual dimorphism (Pérez-Mellado,

Table 2. Comparisons of chromatic patterns (Chi-squared tests) between *P. bocagei* and *P. carbonelli*. n.s., not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Variable	Two-state	<i>P. bocagei</i>			<i>P. carbonelli</i>			between species	
		<i>n</i>		χ^2	<i>n</i>		χ^2	χ^2	
		Males	Females		Males	Females		Males	Females
		83	51	between sexes	106	57	between sexes		
MBD	±striped	48	27	n.s.	18	9	n.s.	***	***
	speckled/reticulated	35	24		88	48			
BSD	±striped	58	35	n.s.	61	38	n.s.	n.s.	n.s.
	not striped	25	16		45	19			
FKD	reticulated	55	14	***	87	22	***	*	n.s.
	not reticulated	28	37		19	35			
CEP	>50%	20	1	**	26	1	***	n.s.	n.s.
	<50%	63	50		80	56			
VTP	(2)-3 paired rows	63	12	***	53	11	***	***	n.s.
	(0)-1 paired rows	20	39		53	46			
BGS	yes	0	0	–	105	16	***	***	***
	no	83	51		1	41			
MBC	greenish-green	79	21	***	56	1	***	***	***
	not green/browish	4	30		50	56			
FKC	greenish-green	2	0	n.s.	90	3	***	***	n.s.
	not green/browish	81	51		16	54			
VTC	yellow/orange	71	37	n.s.	12	22	***	***	***
	withish/pale tones	12	14		94	35			

1997, 1998). UPGMA clustering showed a clear separation of the samples between the two forms (fig. 2). PC1 reflects the general head shape, whereas PC2 reflects size variation in the limbs and body: both males and females show a clear separation between *bocagei* and *carbonelli* (fig. 3). Diagnostically, *carbonelli* has a “compact” small body with the head and body quite robust but proportionally shorter than in *bocagei* and other Iberian *Podarcis*. Male *P. carbonelli* have bright green flanks, whereas *P. bocagei* always have brown or orange-brown flanks contrasting with its green dorsal coloration. Some of these contrasting characters were previously pointed out by Pérez-Mellado (1981, 1986) and Galán (1986).

Molecular data. In addition to the morphological data presented here, recent analyses based on mitochondrial DNA sequence data also support the separation of *carbonelli*. Harris and Sá-Sousa (2001), using partial cytochrome *b* and Cytochrome oxidase I (COI) sequence data, showed that *bocagei* and *carbonelli* were genetically distinct lineages. Variation between them was 9-9.96% between the COI sequences and 13.5-15.5% between the cytochrome *b* sequences. This divergence can be compared to a mean genetic distance for the cytochrome *b* gene of 13.6% between congeneric reptile species (Harris, 2002). In another comparison, no sequences of cytochrome *b* from the same species of reptile for which data were available on GenBank had an uncorrected divergence greater than 8.5% (Hendry et al., 2000). Variation in the 12S rRNA gene between the two forms was

similarly well above that normally found within a species (Harris and Sá-Sousa, 2002). Variation within *bocagei* and *carbonelli*, however, was very low — less than 1% sequence divergence in any of the genes examined. Evidence from allozyme variation likewise shows a high degree of genetic differentiation between the two forms (Sá-Sousa et al., 2000).

Conclusions. Both lizard forms *bocagei* and *carbonelli* are morphologically and genetically distinct. Both forms maintain their morphological uniformity throughout their ranges in Portugal. For instance, individuals of *carbonelli* from Monte Clérigo (Algarve) are not distinguishable from those in Serra da Estrela (Portuguese ‘Sistema Central’). Populations of *bocagei* from the north of Portugal do not differ from those of Galicia (Galán, 1986; Sá-Sousa, 1998). Although the two forms co-occur only along a narrow parapatric zone of contact, predictive models show that both species potentially could colonize the ranges of each other (Sá-Sousa, 2001). In the contact zone (e.g. Praia da Aguda, Gaia, and Silvade, Espinho) both *bocagei* and *carbonelli* maintain their morphological distinctness, and extensive prospecting has not uncovered any morphological intermediates (Carretero et al., 2002). All this constitutes evidence that the two forms deserve species status (Mayr and Ashlock, 1991). Therefore we recommend recognising *P. carbonelli* as a full species, which includes the insular subspecies *berlengensis* (Sá-Sousa et al., 2000; Harris and Sá-Sousa, 2001).

Biogeographically, both *P. bocagei* and *P. carbonelli* avoid areas with Mediterranean conditions. However, *P. carbonelli* may have strong climatic constraints on the availability of suitable habitats, particularly throughout its southern range, where it is scarcely distributed (Sá-Sousa, 2000, 2001). A parallelism exists between the southern range of Schreiber’s green lizard *Lacerta schreiberi* Bedriaga 1878 and the known range of *P. carbonelli* (see Riva de la Viña, 1987; Brito et al., 1998; Sá-Sousa, 2001). As a consequence one could predict the presence of *P. carbonelli* in other eastern mountain ranges with Atlantic influence, such as the Sierra São Mamede, Mts. Guadalupe, Mts. Toledo, and Sierra Morena. Further prospecting would be useful to confirm this.

Diagnosis. According to Pérez-Mellado (1981) *P. carbonelli* is a small lizard with SVL <63.5 mm, less robust than *P. bocagei*. Head (pileous) is relatively short. The mid-back coloration is often uniform brown, sometimes with a series of small black points in the vertebral zone. The light dorsal stripes are bright green with irregular edges in case of the males while having regular ones in the females. The mid-back coloration during the mating season shows shifts in relative frequencies from the western part towards the eastern part of the distribution range of *P. carbonelli*: the bright green or brown-greenish tones in the mid-back of males are more frequent in Portugal, whereas the the brown tones with green dorsal stripes predominate in the Spanish western ‘Sistema Central’. However, the *concolor* pattern (= single uniform brown without black pigmentation) is found in low frequency in males/females from all populations studied.

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Appendix 1. Sampling localities for *P. bocagei* and *P. carbonelli* in Portugal.

Id	Locality	Province	Males	Females
<i>P. bocagei</i>			<i>n</i>	<i>n</i>
GE	Serra do Gerês	Minho	29	26
PF	Penafiel	Douro Litoral	26	12
PO	Porto	Douro Litoral	30	13
VP	Vila Pouca de Aguiar	Trás-os-Montes	24	12
Total			109	63
<i>P. carbonelli</i>			<i>n</i>	<i>n</i>
AV	Aveiro	Beira Litoral	3	2
TO	Torreira	Beira Litoral	33	22
BU	Buarcos	Beira Litoral	1	
PB	Serra Cascalheira	Beira Alta	24	12
CB	Serra da Estrela	Beira Alta	24	12
AM	Água de Madeiros	Extremadura	12	3
BA	Baleal	Extremadura	9	
CR	Cabo Raso	Extremadura	27	13
CV	Praia do Carvalhal	Alentejo	24	12
CS	Cabo de Sines	Alentejo	5	4
VM	Vila Nova de Milfontes	Alentejo	3	1
MC	Monte Clérigo	Algarve	34	12
Total			199	93

Appendix 2. Descriptive statistics of biometry in *P. bocagei* and *P. carbonelli*.

Variable	<i>P. bocagei</i>						<i>P. carbonelli</i>					
	Males (<i>n</i> = 109)			Females (<i>n</i> = 63)			Males (<i>n</i> = 199)			Females (<i>n</i> = 93)		
	\bar{x}	<i>s</i>	cv	\bar{x}	<i>s</i>	cv	\bar{x}	<i>s</i>	cv	\bar{x}	<i>s</i>	cv
SVL	60.09	3.12	5.19	56.48	3.68	6.52	50.70	3.24	6.39	49.44	3.12	6.31
HL	14.22	0.90	6.33	11.56	0.71	6.14	12.10	0.80	6.61	10.27	0.56	5.45
HW	6.98	0.51	7.31	5.68	0.40	7.04	5.88	0.44	7.48	5.00	0.32	6.40
OW	5.79	0.42	7.25	4.95	0.32	6.46	5.04	0.35	6.94	4.43	0.24	5.42
FW	4.56	0.36	7.89	3.87	0.22	5.68	3.88	0.31	7.99	3.40	0.21	6.18
NW	3.47	0.29	8.36	2.92	0.19	6.51	2.93	0.32	10.92	2.58	0.22	8.53
HD	6.38	0.48	7.52	5.20	0.33	6.35	5.71	0.47	8.23	4.70	0.31	6.59
OD	5.86	0.44	7.51	4.77	0.33	6.92	5.25	0.42	8.00	4.33	0.31	7.16
FD	4.93	0.42	8.52	4.02	0.30	7.46	4.33	0.40	9.24	3.58	0.35	9.78
ND	3.72	0.31	8.33	3.08	0.23	7.47	3.15	0.33	10.48	2.65	0.24	9.06
HDL	8.44	0.58	6.87	7.01	0.50	7.13	6.82	0.48	7.04	5.90	0.52	8.81
HLL	30.40	1.64	5.39	24.54	1.22	4.97	25.14	1.66	6.60	21.22	1.30	6.13

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