Morphological variability of *Podarcis hispanica* (Sauria: Lacertidae) in Portugal

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Abstract. A total of 35 morphological characters (biometry, scalation, chromatic pattern) were studied through multivariate analyses on 10 populations sampled across the range of the Iberian wall lizard (*Podarcis hispanica*) in Portugal. Biometry clearly splits the samples into two different types. Differences in scalation between the two types were not clear, but multiple correspondence analyses showed that different chromatic patterns fit each of the types: one presented dark dorsal patterns (e.g. reticulated, eyeled, striped) and whitish-pearly belly, while the other showed green or yellow-brown patterns and yellow-orange belly. These two morphotypes constitute different molecular lineages and have different ranges of distribution.

Introduction

The Iberian Wall Lizard, *Podarcis hispanica* Steindachner, 1870 is a polymorphic species found in SW France, Iberian Peninsula (except in the northernmost border area) and NW Africa (Salvador, 1974, 1986; Pérez-Mellado and Galindo, 1986; Guillaume, 1987, 1997; Pérez-Mellado, 1997, 1998). Its type locality is Mount Agudo, near Murcia (SE Spain), restricted by Mertens and Müller (1928). Several subspecies and forms have been recognised (Boulenger, 1905, 1920; Guillaume, 1987; Géniez, 2001). The nominal subspecies was restricted to SE Spain, while the greenish *P. h. vaucheri* Boulenger, 1905 was both reported in NW Africa and SW Iberia (Boulenger, 1905, 1920; Klemmer, 1959; Salvador, 1974, 1986; Guillaume, 1987). *Podarcis h. liolepis* Boulenger, 1905 was recorded in NE Spain. The insular lizard that inhabits Mt. Urgull and the island of Santa Clara (off San Sebastian, The Basque Country, Spain) was renamed as *P. h. sebastiani* (Bea et al., 1986). The brownish *P. h. cebennensis* Guillaume & Géniez in Fretey, 1986 was reported in SW France and North of Catalonia, Spain (Fretey, 1986; Guillaume, 1987, 1997). The insular lizard *P. h. atrata* from Columbretes (off Castellón, SE Spain) was

recently raised to specific rank (Castilla et al., 1998). Pérez-Mellado (1981) separated the greenish Bocage wall lizard *P. bocagei* Seoane, 1884, a species endemic to NW Iberia, from the sympatric *P. hispanica.* Guillaume (1987) suggested this NW Iberian *P. hispanica* to be its '*lusitanica*' form. Finally, Pérez-Mellado and Galindo (1986) grouped all Iberian forms under the nominal subspecies, including *P. h. atrata,* but leaving *P. h. vaucheri* as a subspecies exclusive to NW Africa. This taxonomic status remained unchanged in the literature (e.g. Pérez-Mellado, 1997, 1998; Barbadillo et al., 1999).

Here we analyse some morphological data (biometry, scalation and chromatic patterns) obtained from Portuguese samples of *P. hispanica,* to test for morphological differences among groups of local populations.

Material and methods

Sampling. A total of 360 adults of *P. hispanica* longer (snout-vent lengths) than 46 mm were captured (using a running knot). Each local sample contained 24 males and 12 females. Differences in sexual ratio probably reflect differences in capture efficiency (Galán, 1986; Pérez-Mellado and Galindo, 1986). *Podarcis hispanica* was sampled from 10 sites all over its Portuguese distribution range: (SG) Serra do Gerês, (SA) Serra do Alvão, (SL) Serra da Lapa, (SC) Serra do Caramulo, (SE) Serra da Estrela, (BU) Buarcos, (ET) Estoril, (SI) Sines, (EV) Évora and (PT) Portalegre (fig. 1).

Morphology. The first author (PSS) made all linear measurements (to avoid variability among observers) with callipers to the nearest 0.05 mm, following Pérez-Mellado and Gosá (1988). Thirteen biometric variables were measured (fig. 2): SVL (snout-vent length); HL (head length); SD (lateral distance of the head-side); HW (head width); OW (inter-orbital) width; FW (inter-frontal width); NW (inter-nasal width); HD (head depth); OD (orbital depth); FD (frontal depth); ND (nasal depth); HDL (hand length); and HLL (hind limb length). Scalation was assessed through 11 variables, using a fixed 5× magnifying glass. There were seven unilateral linear counts: DOR (dorsal scales around mid-body); GUL (gular scales along the throat midline); COL (large scales in the collar); VTR (inner ventral scales counted longitudinally); TAI (caudal scales around the fifth whorl of the tail); L4F (lamellar scales beneath the fourth finger); and L4T (lamellar scales beneath the fourth toe). There were four bilateral counts (the sum of scales in both sides): TPL (supratemporal scales); GRA (supraciliary granules); CIL (supraciliary scales); and FPO (femoral pores). A total of 11 characters of chromatic patterns were recorded (fig. 2): dorsal patterns (four variables) found on the BDS (black dorsal stripes), LDS (light dorsal stripes), MBZ (mid-back zone) and FKZ (flank zone); BGS (blue or green spots on the outer ventral scales); black pigmentations (two variables) that occur on CEP (cephalic plates) and VTP (ventral scales), as well as body colorations (four variables) that dye the LDSC (light dorsal stripes), MDC (mid-back), FKC (flank) and VTC (belly).

Statistical analyses. Each sex was analysed separately, due to *P. hispanica* sexual dimorphism (Pérez-Mellado, 1997, 1998). Biometric variables were log-transformed; a Multivariate Analysis of Covariance (MANCOVA) was performed to evaluate the biometric distinctiveness of the samples, using SVL as covariate (see Pérez-Mellado et al., 1993; Sokal and Rohlf, 1995; Dytham, 1999). Samples were compared (45 paired-combinations) using Scheffé's test (Sokal and Rohlf, 1995; Dytham, 1999). Squared Mahalanobis distances (MD^2) were calculated to the sample centroids (Mascort et al., 1999). MD^2 takes into account correlations among the biometric variables, and is independent of their relative scales (Legendre and Legendre, 1998). UPGMA and the 'complete'-linkage methods were used on the MD^2 values to detect phenetic relationships (De Luca and Grbac, 1995). Stinebrickner consensus trees between both UPGMA and 'complete'-linkage trees were obtained in order to increase the validity of cluster analysis (Rohlf, 1993). Finally, a canonical variate analysis (CVA) was used to elucidate the pattern of biometric variation among samples (see Taylor and Buschman, 1993; Mascort et al., 1999). The nonparametric Kruskal-Wallis ANOVA (Analysis of Variance on Ranks) was used to analyse scalation data that showed a significant deviation from normality (Kolmogorov-Smirnov test) and from

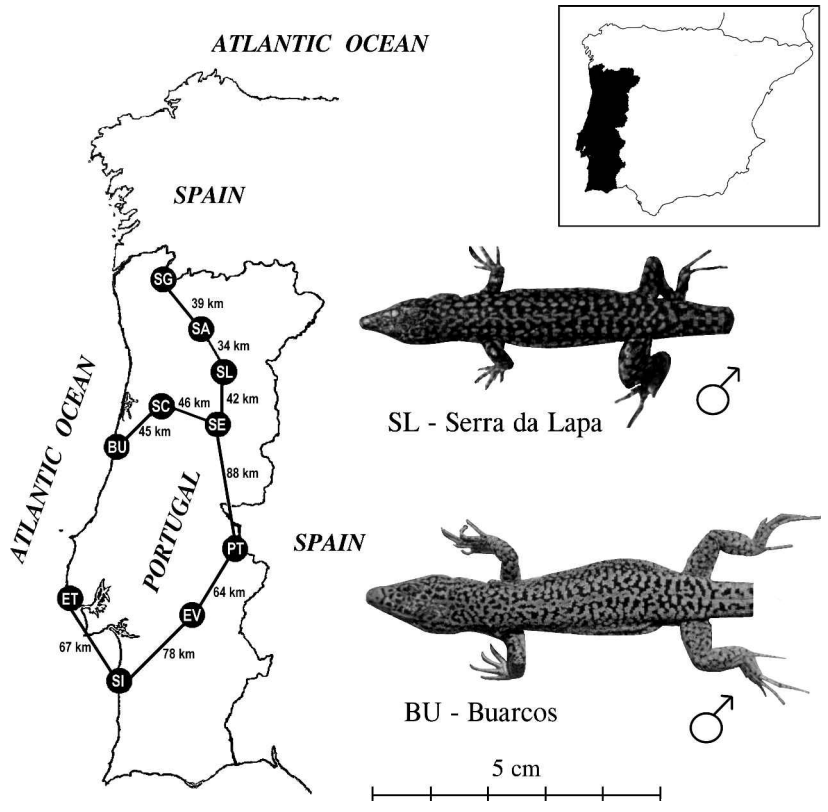

Figure 1. Sampling sites where *P. hispanica* was collected in Portugal. Minimal geographic distances between sites are given (straight lines). Abbreviations are shown as in text. Photos of two males measured.

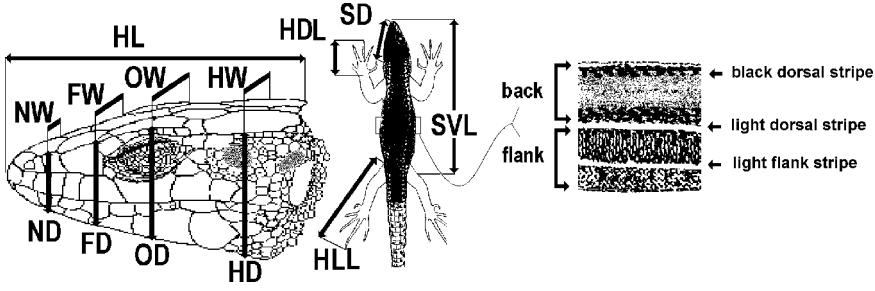

Figure 2. Scheme illustrating the linear measurements of biometry and some body parts that reveal the chromatic patterns.

homogeneity of variance (Levene test), in spite of variables being previously squared-root transformed (Siegel and Castellan, 1988; Dytham, 1999). The nonparametric Student-Newman-Keuls' like test (nSNK) was used to test for pairwise significant differences among samples (Siegel and Castellan, 1988). A Multiple Correspondence

Analysis (MCoA) was used to reduce the original set of 11 nominal chromatic variables to a 3D space. In this way, objects within the same category were plotted close to each other, whereas objects in different categories were plotted far apart (Legendre and Legendre, 1998). This MCoA used an iterative procedure (Meulman and Heiser, 1999).

Results

Males. Descriptive statistics of the biometric variables are given in Appendix 1. Significant multivariate differences were found for biometry (MANCOVA, Wilks' Lambda = 0.0834, $P < 0.001$). The head variables HL, OD, SD, HD and FD showed differences across the paired-comparisons of samples (23 to 33 pairs), while HDL did not (5 pairs) (Scheffé tests, $F = 4.30$ to 38.21, $P < 0.001$). Few variables (2 to 6) were found different between the samples SA-SG and SC-SL, between these and EV-PT-SI, or between the latter and SE-BU-ET. On the contrary, several variables (10-13) discriminated all other pair-wise combinations of samples. The consensus tree based on the MD^2 distances groups two major types (table 1, fig. 3): type 1 includes the 'Serra' samples (SA-SC-SL-SG), while type 2 comprises the lowland populations (BU-ET-EV-PT-SI), to which the sample of Serra da Estrela (SE) is linked. The first three canonical variates (CV1-3) accounted for about 80% of the total variance (60, 12 and 8%, respectively). The first canonical variate discriminated the two types (tables 2 and 3, fig. 4): the positive part of the CV1 separated the mountain type 1 and it was characterised by the greatest value for SVL (1.228); its negative part refers to the lowland type 2, showing the lowest values for HL (−0.588), OD (−0.579), HLL (−0.556) and HD (−0.482). The second canonical variate has higher loadings of ND (0.592) and OW (0.362), but lower loading of SVL (−1.089) and HLL (−0.310). The sample SE scored between type 1 and type 2 (table 3, fig. 4).

Descriptive statistics for the scalation are given in Appendix 2. Scalation showed higher intra-sample variation than did biometry (see CV values). Significant univariate comparisons (Kruskal-Wallis ANOVA's, H's = 34.93 to 110.30, $P < 0.001$) were found

Table 1. Biometric matrices (MD^2 distances) between the sample centroids. Males are above diagonal, females below. • distance is not significant, $P > 0.05$.

	SA	SC	SE	SG	SL	BU	ET	EV	PT	SI
SA		4.49	14.53	7.81	5.21	21.34	21.82	14.45	10.81	21.41
SC	5.15		5.17	6.91	3.17	10.69	11.74	6.64	5.98	13.18
SE	8.70	13.22		14.32	9.18	6.61	7.74	4.27	5.11	9.99
SG	9.79	20.57	20.74		8.88	24.14	25.52	19.08	13.52	25.47
SL	•3.42	8.20	10.20	11.33		10.06	10.94	5.83	4.44	10.45
BU	32.49	36.56	16.58	44.92	35.78		6.19	4.10	4.96	5.83
ET	25.11	33.50	9.88	39.12	25.54	7.84		4.51	6.14	4.23
EV	15.06	21.72	5.35	22.84	17.52	11.85	8.52		3.90	4.08
PT	15.27	27.99	8.36	16.80	16.49	18.70	8.04	6.66		5.18
SI	13.18	20.83	7.62	19.53	13.06	13.90	6.17	•3.58	•3.02	

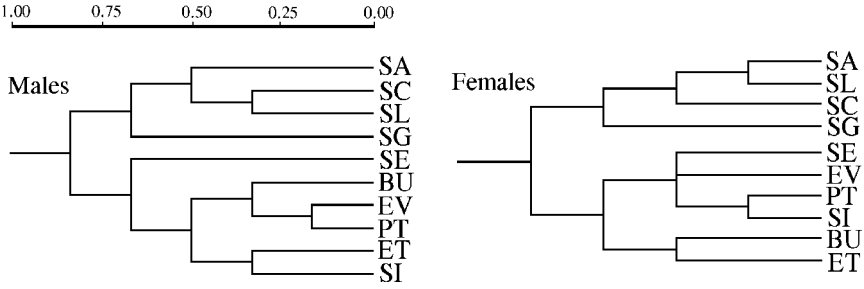

Figure 3. Stinebrickner consensus trees based on the MD^2 distances found among samples.

Table 2. Means of the biometric canonical variates for each sample.

Loc.	Males			Females		
	CV1	CV2	CV3	CV1	CV2	CV3
SA	2.341	0.964	−0.734	−1.997	0.448	−0.087
SC	1.122	−0.279	−0.562	−2.297	2.119	0.202
SE	−0.353	−1.512	−0.441	0.226	0.612	−0.552
SG	2.749	−0.753	1.191	−2.554	−1.995	1.193
SL	0.833	0.845	−0.050	−2.052	0.249	−0.745
BU	−1.641	−0.425	−0.352	3.082	0.992	1.547
ET	−1.821	0.131	0.301	2.626	0.113	−0.862
EV	−1.023	0.064	−0.455	1.168	−0.188	0.187
PT	−0.371	0.182	0.333	0.882	−1.694	−0.514
SI	−1.836	0.783	0.769	0.915	−0.657	−0.369

for several variables of scalation (e.g. DOR, GRA, L4T, TAI), comprising 24 to 39 pairs of samples. Otherwise, VTR and CIL did not vary among samples. The scalation variables did not show any clear pattern of geographic variation for the samples.

The chromatic data are summarised in Appendix 3. For male samples, the chromatic variation pattern is consistent with the biometric pattern in splitting the samples into two types, leaving the sample SE in between (fig. 5). In the first correspondence variate (MCo1), coloration variables such as MBC (0.754), FKC (0.748) and VTC (0.614) account for most of the variation. Type 1 has positive mean scores, while type 2 has negative ones (tables 4 and 5). MCo2 emphasises the differences among samples mainly based on the dorsal patterns: BDS (0.494), LDS (0.515) and MBZ (0.606).

Females. On average, females had lower biometric measures than males (Appendix 1; MANCOVA, Wilks' Lambda = 0.0357, $P < 0.001$). As in the case of males, the head variables HL, OD, SD, HD and FD were significantly different in 17 out of 26 pairs of samples (Scheffé tests: $F = 3.66$ to 14.51, $P < 0.001$). Differences within types were considerably lower (1-2 variables) than between types (7-13 variables). The sample SE did not differ from type 2 and diverge from type 1 in 4 to 8 significant variables. The MD^2 consensus tree splits the samples into types 1 and 2 (table 2, fig. 3). The first three

Table 3. Standardised coefficients for the canonical variates of biometry.

Variable	Males			Females		
	CV1	CV2	CV3	CV1	CV2	CV3
SVL	1.228	−1.089	−0.710	−0.189	0.485	−0.064
HL	−0.588	−0.143	0.357	0.334	−0.440	0.637
SD	−0.088	−0.092	0.480	−0.305	−0.947	−0.953
HW	0.085	0.151	0.092	0.156	0.090	0.823
OW	0.051	0.362	0.390	−0.314	0.032	−0.667
FW	−0.108	0.130	−0.838	0.223	−0.380	−0.119
NW	0.000	−0.217	−0.122	−0.016	1.082	0.057
HD	−0.482	−0.187	−0.332	0.107	0.267	0.140
OD	−0.579	0.249	0.167	0.425	−0.030	−0.694
FD	0.042	0.013	−0.345	−0.183	−0.428	0.498
ND	0.049	0.592	−0.104	0.504	0.468	−0.187
HDL	0.049	−0.126	−0.059	−0.398	0.037	−0.347
HLL	−0.556	−0.310	0.799	0.744	−0.130	0.370
Eigenvalues	2.680	0.566	0.375	4.301	1.466	0.644
Variance explained cum. %	59.55	72.13	80.46	58.07	77.86	86.55

Table 4. Mean sample scores for the first three correspondence variates.

Loc.	Males			Females		
	MCo1	MCo2	MCo3	MCo1	MCo2	MCo3
SA	0.645	0.416	1.830	0.645	0.416	1.830
SC	0.192	−0.381	−0.696	0.192	−0.381	−0.696
SE	0.451	−0.405	0.185	0.451	−0.405	0.185
SG	1.014	−0.127	−0.715	1.014	−0.127	−0.715
SL	0.918	0.033	0.326	0.918	0.033	0.326
BU	−0.864	0.216	−0.279	−0.864	0.216	−0.279
ET	−0.989	−0.498	−0.376	−0.989	−0.498	−0.376
EV	−0.923	−0.309	0.376	−0.923	−0.309	0.376
PT	−0.575	1.589	−0.436	−0.575	1.589	−0.436
SI	−1.018	−0.849	−0.217	−1.018	−0.849	−0.217

canonical variates (CV1-3) account for about 87% of the total variance (58, 20 and 9%, respectively). The first canonical variate discriminates the female samples by respectively shifting to negative (type 1) and positive (type 2) loadings (tables 2 and 3, fig. 4). The second canonical variate has higher loadings of NW (1.082), SVL (0.485) and ND (0.468), while it has lower loadings of SD (−0.947), HL (−0.440) and FD (−0.428).

In general, the females had lower number of scales than males, except for the higher number of ventral scales (Appendix 2). Unlike the males, the scalation hardly differs in the paired comparisons of female samples, the number of femoral pores (FPO) was the most variable character (21 pairs of samples).

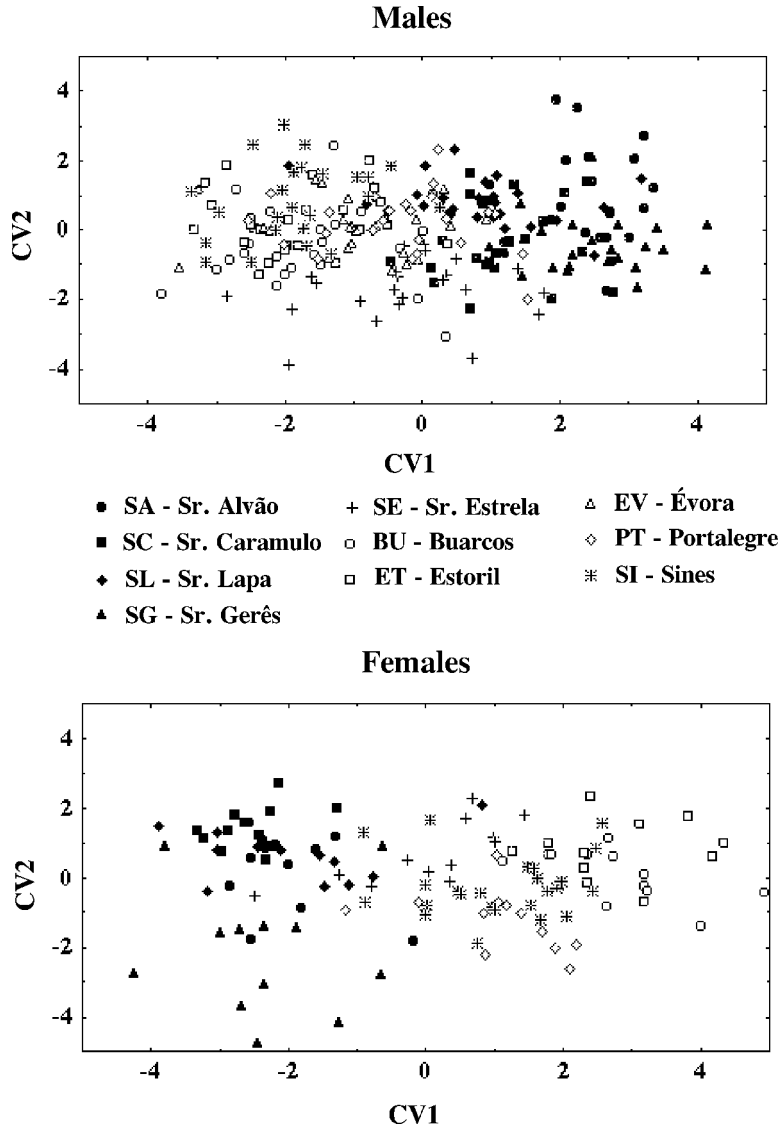

Figure 4. Scatterplots from the first two canonical variates of biometry.

The chromatic patterns also split the female samples into two types (1 and 2), but the sample SE had intermediate scores between both types (fig. 5). The mean scores are positive for the type 1, while they are negative for the type 2 (table 4). MCo1 combines higher contributions from (table 5): dorsal patterns such as MBZ (0.713) and FKZ (0.511); cephalic black pigmentation (0.577); and body colorations such as MBC (0.540), FKC (0.503) and VTC (0.524).

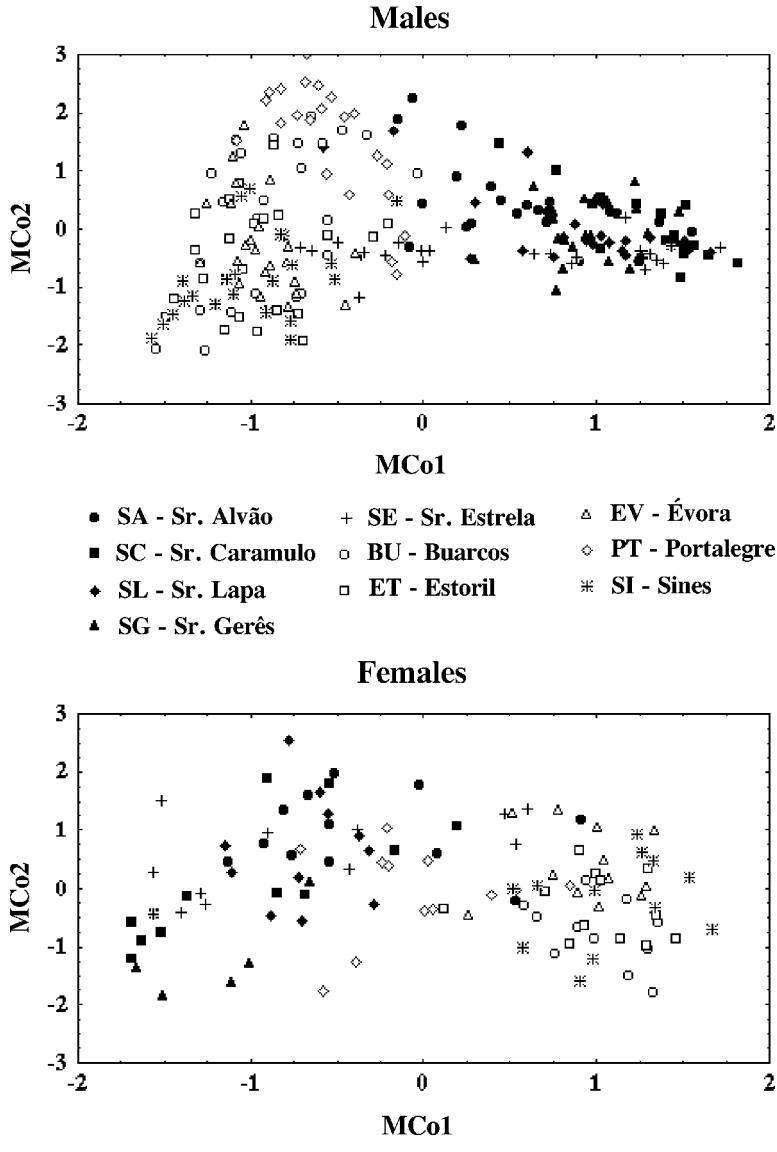

Figure 5. Scatterplots from the first two correspondence components of the chromatic patterns.

Discussion

The head profile of *P. hispanica* was often assessed with only three variables HL, HW and HD (Galán, 1986; Gosá et al., 1986; Pérez-Mellado and Galindo, 1986; Salvador, 1986; Martínez-Rica and Laplaza, 1989). Here we added more head variables (e.g. OW, FW, NW, OD, FD, ND) that discriminate two types of *P. hispanica* in Portugal. Type 1

Table 5. Squared component loadings of the chromatic data computed for the first three correspondence variates. Eigenvalues accounted for the total variance explained by each dimension. Note that all these values have a possible maximum of 1.00.

Variable	Males			Females		
	MCo1	MCo2	MCo3	MCo1	MCo2	MCo3
			Dorsal pattern			
BDS	0.479	0.494	0.312	0.302	0.501	0.198
LDS	0.361	0.515	0.177	0.053	0.362	0.338
MBZ	0.516	0.606	0.119	0.713	0.372	0.336
FKZ	0.555	0.056	0.035	0.511	0.352	0.253
			Pigmentation			
BGS	0.496	0.160	0.029	0.271	0.116	0.059
CEP	0.430	0.133	0.135	0.577	0.013	0.007
VTP	0.165	0.009	0.112	0.037	0.072	0.087
			Coloration			
LDSC	0.332	0.048	0.061	0.045	0.114	0.207
MBC	0.754	0.125	0.535	0.540	0.129	0.455
FKC	0.748	0.093	0.532	0.503	0.298	0.066
VTC	0.614	0.126	0.035	0.524	0.332	0.042
Eigenvalues	0.495	0.215	0.189	0.370	0.242	0.186

has a flattened head (and body), and it is often found in rupicolous habitats in NW Iberia where often some sympatric ground-dwelling lizards such as *P. bocagei*, *P. carbonelli* or *P. muralis* occur (Galán, 1986; Gosá et al., 1986; Pérez-Mellado, 1997, 1998; Barbadillo et al., 1999; Sá-Sousa, 2000, 2001). Type 2 has a head (and body) more robust, being more ubiquitous in its use of Mediterranean habitats in SW Iberia, where it often is the only *Podarcis* species (Guillaume, 1997; Sá-Sousa, 2000).

Differences in scalation among samples of *P. hispanica* were not clear, merely local/ecological variation was found (see Thorpe et al., 1991). Only the number of dorsal scales and of the supraciliary granules of the males supported the separation into two types. All these scalation results contrast, for example, with the clinal pattern found in *P. sicula* (Lanza et al., 1993) and they do not have a taxonomic value such as in the case of the Iberian rock-lizards *Archaeolacerta* (Arribas, 1993, 1996; Brown and Pérez-Mellado, 1993; Pérez-Mellado et al., 1993). Why females of *P. hispanica* tend to be non-divergent in scalation is difficult to assess on the basis of the current data.

The different chromatic patterns fit each of the types: type 1 presented dark dorsal patterns (e.g. reticulated, eyeled, striped) and whitish-pearly belly, while type 2 showed green or yellow-brown patterns and yellow-orange belly. The chromatic patterns are often explained by the processes of sexual selection, social structure, specific recognition, ecological background crypsis, etc. (Bauwens et al., 1987; Cirer and Martínez-Rica, 1990; Cooper and Greenberg, 1992; Galán, 1995). Why the dorsal patterns of the type 1 seem to match the background pattern of the granitic outcrops where it usually lives, while the green patterns of the type 2 are probably adaptative in a Mediterranean environment, is

a question that remains untested. But, if the dorsal coloration can influence crypsis with substrate and/or vegetation cover, the lizard populations that have different use of habitat may progressively diverge (Brown and Thorpe, 1991; López-Jurado and Mateo, 1992; Davenport and Dellinger, 1995).

The two morphotypes of *P. hispanica* found in Portugal have parapatric distributions, which are largely explained by environmental factors, showing a narrow zone of contact (Sá-Sousa, 2000). The morphotype 1 is found in northern Portugal, where either highlands or Atlantic environmental conditions prevail. This lizard was also reported in Galicia and in the mountain range of 'Sistema Central', agreeing to the form '*lusitanica*' described by Guillaume (1987) and Géniez (2001). The morphotype 2 occurs in central and southern Portugal and Spain, where Mediterranean conditions are typical (Sá-Sousa, 2000; Géniez, 2001).

In addition, these two morphotypes represent highly divergent lineages showing 10-15% pairwise sequence divergence within the cytochrome b gene (Harris and Sá-Sousa, 2001a). Indeed, the Iberian *P. hispanica* is a paraphyletic species complex, although the four identified morphotypes detected so far are monophyletic (Harris and Sá-Sousa, 2001b).

However, the sample SE (from Vale Rossim, Serra da Estrela, 1400 m alt.) is either intermediate between both morphotypes or it has the type 2 pattern, particularly in the males. We do not know if that pattern is widespread in the whole Serra da Estrela, though some robust specimens were recorded in the Sistema Central (Pérez-Mellado and Galindo, 1986; Pérez-Mellado, 1998). If both morphotypes of *P. hispanica* meet in a zone of contact in Portugal (see Sá-Sousa, 2000), the sample SE might constitute an example of intergradation (e.g. biometry like type 2 joined with the chromatic patterns like type 1). Only further genetic data will be able to clarify this case. A similar situation was found in Rijeka (Croatia) between two subspecies of *P. muralis* (De Luca and Grbac, 1995).

In conclusion, we argue in face of the present data that: 1) *P. hispanica* needs taxonomic revision; 2) two types of *P. hispanica* were found in Portugal and morphologically differ from each other; 3) these morphotypes comprise divergent molecular lineages and have parapatric distributions and thus 4) two distinct (sub)species (see Mayr and Ashlock, 1991) may occur in Portugal and elsewhere in western Iberia.

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Appendix 1. Descriptive statistics (mean, standard deviation and coefficient of variation) for the biometric variables. Abbreviations are shown as in text.

Loc.	SA			SC			SE			SG			SL			BU			ET			EV			PT			SI		
Var.	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV
Males																														
SVL	54.08	4.18	7.73	57.21	2.99	5.23	61.21	3.13	5.12	55.67	2.75	4.93	54.63	1.71	3.14	58.25	2.63	4.51	57.67	2.65	4.59	56.58	2.47	4.36	56.88	2.54	4.47	55.50	2.59	4.66
SD	6.45	0.39	6.03	6.78	0.42	6.26	7.26	0.47	6.47	6.64	0.30	4.56	6.70	0.29	4.31	7.29	0.37	5.10	7.32	0.40	5.44	6.88	0.37	5.35	7.10	0.36	5.05	6.98	0.38	5.45
HL	12.33	0.85	6.89	13.09	0.70	5.33	14.06	0.76	5.44	12.57	0.59	4.70	12.78	0.50	3.94	13.94	0.61	4.41	13.98	0.65	4.65	13.33	0.62	4.64	13.55	0.58	4.30	13.37	0.64	4.76
HW	5.94	0.41	6.86	6.24	0.42	6.68	6.74	0.45	6.66	5.99	0.33	5.59	6.14	0.34	5.52	6.78	0.40	5.90	6.52	0.30	4.58	6.43	0.29	4.47	6.51	0.31	4.77	6.58	0.35	5.39
OW	5.10	0.33	6.43	5.25	0.31	5.92	5.55	0.36	6.41	5.03	0.25	4.93	5.12	0.23	4.40	5.36	0.25	4.71	5.58	0.23	4.13	5.33	0.31	5.90	5.46	0.23	4.22	5.48	0.28	5.18
FW	4.09	0.26	6.34	4.23	0.25	5.93	4.47	0.23	5.09	3.93	0.17	4.33	4.05	0.18	4.40	4.44	0.24	5.39	4.39	0.21	4.89	4.29	0.19	4.51	4.32	0.20	4.64	4.25	0.21	4.91
NW	2.96	0.19	6.44	3.20	0.20	6.31	3.34	0.20	6.14	2.94	0.17	5.85	3.05	0.11	3.66	3.32	0.20	6.12	3.28	0.21	6.29	3.20	0.18	5.70	3.20	0.19	6.00	3.18	0.24	7.50
HD	5.24	0.29	5.57	5.60	0.34	6.01	6.04	0.38	6.27	5.06	0.21	4.07	5.51	0.29	5.31	6.17	0.37	6.08	6.18	0.30	4.81	6.08	0.34	5.57	5.70	0.31	5.48	6.06	0.43	7.10
OD	4.73	0.32	6.77	4.98	0.23	4.72	5.44	0.37	6.83	4.56	0.24	5.22	4.98	0.21	4.25	5.55	0.35	6.30	5.49	0.32	5.91	5.34	0.31	5.78	5.25	0.26	4.95	5.44	0.25	4.62
FD	3.92	0.31	7.92	4.18	0.26	6.15	4.53	0.33	7.35	3.79	0.17	4.55	4.22	0.21	4.87	4.65	0.33	7.02	4.54	0.30	6.65	4.52	0.25	5.62	4.41	0.28	6.45	4.43	0.25	5.53
ND	2.98	0.23	7.86	3.20	0.20	6.33	3.39	0.27	8.04	2.88	0.18	6.17	3.19	0.18	5.51	3.36	0.21	6.16	3.47	0.25	7.29	3.31	0.23	6.80	3.26	0.30	9.06	3.32	0.20	5.97
HDL	26.49	1.52	5.73	28.57	1.48	5.19	30.75	1.50	4.88	28.30	1.39	4.90	27.74	1.48	5.32	30.09	1.43	4.74	30.11	1.11	3.69	29.59	1.47	4.96	29.38	1.32	4.49	29.99	1.35	4.49
HLL	7.66	0.48	6.30	7.82	0.63	7.99	8.63	0.59	6.78	7.92	0.44	5.60	7.81	0.49	6.22	7.99	0.64	7.97	8.26	0.46	5.62	8.40	0.49	5.89	8.18	0.61	7.40	8.22	0.67	8.20
Females																														
SVL	52.33	2.81	5.36	54.08	2.02	3.74	57.83	2.89	4.99	51.01	3.53	6.92	53.00	2.30	4.33	57.42	2.15	3.75	58.33	2.64	4.53	55.50	2.15	3.88	55.92	1.78	3.19	55.33	3.63	6.55
SD	5.48	0.14	2.58	5.40	0.14	2.62	5.84	0.39	6.66	5.55	0.42	7.64	5.65	0.35	6.26	5.83	0.22	3.76	6.27	0.30	4.78	5.89	0.32	5.40	6.20	0.24	3.78	6.14	0.21	3.46
HL	10.62	0.43	4.02	10.56	0.40	3.74	11.38	0.48	4.26	10.71	0.69	6.42	10.48	0.53	5.06	11.96	0.45	3.77	12.19	0.44	3.64	11.50	0.31	2.65	11.93	0.41	3.42	11.71	0.71	6.09
HW	5.12	0.24	4.72	5.12	0.33	6.40	5.43	0.29	5.42	5.24	0.40	7.70	5.15	0.21	4.04	5.82	0.22	3.74	5.80	0.25	4.30	5.49	0.22	3.92	5.75	0.17	2.95	5.66	0.29	5.15
OW	4.50	0.24	5.28	4.45	0.39	8.68	4.77	0.27	5.57	4.42	0.29	6.55	4.53	0.16	3.63	4.81	0.17	3.46	5.08	0.30	5.82	4.67	0.20	4.37	5.00	0.14	2.85	4.88	0.32	6.60
FW	3.56	0.23	6.45	3.49	0.18	5.08	3.83	0.28	7.35	3.39	0.29	8.68	3.45	0.14	4.05	3.96	0.21	5.22	4.04	0.16	4.01	3.70	0.17	4.66	3.90	0.33	8.54	3.75	0.33	8.68
NW	2.61	0.11	4.33	2.73	0.18	6.75	2.80	0.19	6.72	2.40	0.29	11.92	2.58	0.14	5.39	2.96	0.14	4.89	3.02	0.17	5.75	2.78	0.12	4.42	2.81	0.10	3.48	2.87	0.21	7.37
HD	4.46	0.33	7.37	4.44	0.16	3.62	4.84	0.27	5.52	4.24	0.40	9.41	4.47	0.23	5.19	5.25	0.27	5.09	5.28	0.30	5.77	5.10	0.29	5.64	4.97	0.24	4.78	5.07	0.27	5.26
OD	4.00	0.26	6.53	3.95	0.18	4.47	4.40	0.28	6.46	3.84	0.30	7.88	4.03	0.17	4.31	4.74	0.27	5.78	4.81	0.19	3.96	4.57	0.16	3.60	4.55	0.25	5.46	4.58	0.20	4.40
FD	3.26	0.21	6.57	3.19	0.31	9.61	3.63	0.24	6.69	3.28	0.31	9.57	3.28	0.20	6.21	3.88	0.24	6.30	3.90	0.26	6.59	3.81	0.14	3.58	3.79	0.16	4.18	3.78	0.19	5.05
ND	2.50	0.16	6.55	2.50	0.19	7.68	2.80	0.17	6.15	2.35	0.22	9.17	2.56	0.18	7.07	2.95	0.12	3.99	3.10	0.31	10.04	2.79	0.16	5.81	2.77	0.07	2.60	2.79	0.15	5.31
HDL	15.03	0.76	5.08	15.03	0.60	4.00	16.81	0.82	4.89	15.30	0.47	3.07	14.97	0.74	4.93	16.46	0.88	5.34	17.46	0.62	3.57	16.98	0.62	3.64	17.07	0.67	3.91	16.72	1.18	7.03
HLL	22.82	1.45	6.33	22.65	0.82	3.61	24.98	1.01	4.06	23.02	0.35	1.54	22.71	1.33	5.84	26.60	1.33	5.00	26.41	1.01	3.81	25.88	1.05	4.08	25.80	0.98	3.79	25.39	1.37	5.41

Appendix 2. Descriptive statistics (mean, standard deviation, coefficient of variation) for the meristic variables. Abbreviations are shown as in text.

Loc.	SA			SC			SE			SG			SL			BU			ET			EV			PT			SI		
Var.	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV	$\bar{x}$	*s*	CV
Males																														
DOR	56.63	4.34	7.67	60.46	3.93	6.51	60.21	3.35	5.56	55.50	3.41	6.15	60.33	2.84	4.70	62.58	2.65	4.24	63.00	3.81	6.05	62.17	3.46	5.57	65.00	2.84	4.38	66.75	3.69	5.52
GUL	27.42	1.93	7.05	29.17	2.16	7.41	28.13	2.58	9.16	28.00	1.84	6.58	28.46	1.64	5.77	29.04	1.73	5.96	27.58	2.10	7.63	27.92	2.57	9.20	29.50	2.17	7.35	28.13	2.51	8.92
COL	9.88	1.42	14.42	10.58	1.35	12.74	10.46	0.93	8.91	9.33	0.82	8.75	10.50	1.02	9.73	11.42	1.25	10.93	10.33	1.13	10.93	10.46	1.10	10.54	10.08	1.10	10.91	10.96	1.33	12.18
VTR	27.08	1.10	4.06	27.29	1.12	4.11	27.21	1.22	4.47	27.00	1.06	3.94	26.46	1.32	4.98	26.38	0.92	3.50	27.25	0.85	3.11	27.17	1.79	6.57	27.21	0.93	3.42	26.75	0.79	2.97
TAI	32.92	1.77	5.37	34.29	2.39	6.96	33.17	1.79	5.38	31.08	1.89	6.07	34.71	2.54	7.33	31.58	1.91	6.04	33.00	2.25	6.81	33.21	3.46	10.43	32.25	2.13	6.61	30.79	2.57	8.35
TPL	12.50	2.41	19.31	12.29	1.85	15.07	11.17	2.26	20.23	10.25	2.13	20.80	12.58	2.08	16.56	12.50	1.84	14.73	12.92	2.32	17.96	12.13	1.94	16.01	14.29	3.29	23.02	13.38	1.97	14.76
GRA	18.29	2.71	14.82	18.29	2.58	14.10	17.88	2.51	14.03	19.75	3.69	18.66	19.08	3.54	18.54	26.63	6.49	24.39	23.38	4.62	19.78	21.13	5.89	27.89	19.96	3.51	17.57	21.54	7.47	34.66
CIL	9.75	1.29	13.27	9.83	0.96	9.79	8.63	1.56	18.03	9.83	1.27	12.96	9.75	1.22	12.56	9.58	1.14	11.88	10.21	1.50	14.72	9.42	1.28	13.62	9.58	0.93	9.69	9.75	1.29	13.27
L4F	16.17	1.61	9.93	16.71	0.86	5.14	17.58	1.89	10.73	16.67	1.17	7.00	16.54	1.18	7.13	15.33	1.20	7.85	16.21	1.25	7.71	16.46	1.61	9.81	16.83	1.01	5.98	14.96	1.57	10.52
L4T	23.75	2.29	9.64	24.08	1.53	6.35	25.13	1.70	6.77	23.96	1.85	7.73	24.75	1.78	7.17	23.46	1.22	5.18	24.50	1.82	7.42	25.42	1.41	5.55	25.83	2.01	7.80	23.67	2.58	10.91
FPO	34.17	2.82	8.26	34.75	2.23	6.42	34.25	2.44	7.11	33.63	2.46	7.33	36.38	3.35	9.20	34.54	1.82	5.26	33.71	3.30	9.80	36.63	2.70	7.37	37.33	3.12	8.35	36.21	2.89	7.98
Females																														
DOR	54.42	2.02	3.71	59.50	3.73	6.27	60.83	2.37	3.89	55.20	2.23	4.04	56.75	3.62	6.38	60.67	3.65	6.02	61.58	2.91	4.72	59.83	4.28	7.16	62.00	4.84	7.81	61.00	3.52	5.76
GUL	26.75	1.71	6.40	29.00	1.86	6.41	28.42	2.02	7.11	27.60	2.11	7.66	26.92	2.11	7.83	28.67	2.46	8.59	27.42	2.02	7.37	27.17	2.41	8.86	28.33	1.92	6.79	28.08	2.64	9.42
COL	9.58	1.08	11.31	10.50	0.90	8.61	10.67	1.23	11.54	10.40	0.54	5.19	10.92	1.31	12.01	11.42	1.31	11.49	9.67	1.07	11.10	10.75	0.87	8.06	10.58	1.08	10.24	10.25	0.97	9.42
VTR	31.00	1.28	4.13	31.75	1.29	4.06	30.33	1.30	4.29	31.00	0.60	1.95	30.75	1.54	5.02	29.33	1.44	4.89	30.25	3.44	11.38	30.25	0.97	3.19	30.08	1.24	4.12	30.67	1.23	4.01
TAI	28.33	2.87	10.13	28.50	2.11	7.41	30.42	1.93	6.34	27.20	1.31	4.81	28.42	1.78	6.27	28.17	1.85	6.57	28.75	1.76	6.14	28.42	1.88	6.62	29.25	2.70	9.23	28.25	2.60	9.20
TPL	12.17	1.75	14.38	13.42	2.15	16.04	12.17	2.04	16.75	12.40	0.91	7.38	11.92	2.19	18.41	12.83	1.80	14.03	11.67	2.31	19.79	14.00	2.30	16.40	14.00	2.86	20.43	13.67	2.02	14.74
GRA	16.33	2.67	16.37	19.58	3.20	16.36	19.92	2.78	13.95	19.60	1.63	8.31	19.58	2.15	10.99	28.58	6.05	21.17	21.92	7.15	32.64	22.50	3.87	17.21	21.33	3.14	14.73	18.17	4.82	26.54
CIL	9.42	1.38	14.64	9.42	0.79	8.42	9.33	1.30	13.96	9.60	0.91	9.53	10.08	0.67	6.63	9.17	0.94	10.23	9.92	1.24	12.51	9.17	2.17	23.64	9.17	1.19	13.02	10.17	0.58	5.68
L4F	15.17	2.72	17.97	15.92	0.90	5.66	16.92	1.51	8.90	15.40	0.33	2.14	15.92	1.08	6.81	16.25	1.66	10.20	14.50	1.51	10.40	16.42	1.44	8.79	16.83	1.85	10.99	14.33	1.83	12.74
L4T	23.17	2.59	11.17	23.75	1.54	6.50	24.92	2.27	9.13	23.40	0.54	2.30	23.50	1.73	7.37	24.50	1.62	6.63	22.17	1.80	8.12	24.83	2.12	8.56	24.92	1.98	7.93	21.83	2.59	11.85
FPO	32.33	2.74	8.48	34.08	3.12	9.15	33.33	2.31	6.93	31.20	1.16	3.72	32.50	2.54	7.82	33.92	3.58	10.55	31.83	3.13	9.83	36.25	2.80	7.72	35.25	2.30	6.53	31.75	2.53	7.96

Appendix 3. Observations of the categorical chromatic variables studied on the populations. Abbreviations are shown as in text.

			Males										Females									
	Loc.		SA	SC	SE	SG	SL	BU	ET	EV	PT	SI	SA	SC	SE	SG	SL	BU	ET	EV	PT	SI
	Variables											*Dorsal pattern*										
	c1	speckled	0	0	0	0	1	5	9	1	0	9	0	0	0	0	0	1	4	5	1	6
BDS	c2	reticulated	2	2	0	4	2	15	8	8	15	5	2	0	0	2	0	1	2	2	4	2
	c3	spotted-eyeled	11	21	18	20	18	2	5	7	5	8	1	8	6	10	4	9	6	0	3	3
	c4	striped	11	1	6	0	3	2	2	8	4	2	9	4	6	0	8	1	0	5	4	1
	c1	speckled	1	0	0	0	0	7	4	0	2	7	0	0	0	0	1	3	0	0	1	0
LDS	c2	reticulated	4	3	0	1	3	10	7	2	16	0	1	1	0	0	4	0	0	0	0	0
	c3	spotted-eyeled	12	20	15	23	19	4	6	6	5	9	5	6	5	12	1	8	11	6	6	11
	c4	striped	7	1	9	0	2	3	7	16	1	8	6	5	7	0	6	1	1	6	5	1
	c1	speckled	2	0	14	8	3	10	19	17	0	19	4	1	6	0	2	11	11	11	3	11
MBZ	c2	reticulated	4	6	0	8	5	14	3	7	20	2	1	1	0	2	0	1	1	0	5	1
	c3	spotted-eyeled	8	13	6	7	9	0	2	0	4	3	0	5	0	10	0	0	0	0	2	0
	c4	striped	10	5	4	1	7	0	0	0	0	0	7	5	6	0	10	0	0	1	2	0
	c1	speckled	1	0	0	0	0	4	1	1	2	4	3	0	3	0	1	7	5	2	1	4
FKZ	c2	reticulated	10	3	14	0	4	18	16	18	20	17	6	4	1	0	2	5	6	6	8	6
	c3	spotted-eyeled	13	19	10	24	20	2	7	5	2	3	3	7	7	12	6	0	1	3	3	2
	c4	edge striped	0	2	0	0	0	0	0	0	0	0	0	1	1	0	3	0	0	1	0	0
												Pigmentation										
	c1	small spots	20	21	14	17	19	6	1	0	0	0	12	11	12	9	12	11	7	4	9	4
BGS	c2	few blue spots	2	0	1	0	1	0	6	1	8	2	0	1	0	3	0	0	0	0	1	1
	c3	many blue spots	2	3	9	7	4	18	17	23	16	22	0	0	0	0	0	1	5	8	2	7
	c1	<40%	2	0	1	7	2	9	21	17	2	21	4	3	3	2	5	11	11	10	4	12
CEP	c2	40-50%	18	4	10	14	15	11	3	7	15	3	6	7	8	10	6	1	1	2	8	0
	c3	>50%	4	20	13	3	7	4	0	0	7	0	2	2	1	0	1	0	0	0	0	0
	c1	outer v.s.	9	12	14	10	21	17	22	18	21	20	10	12	11	12	12	8	10	9	10	11
VTP	c2	midle v.s.	0	10	7	13	3	6	1	6	3	3	0	0	1	0	0	3	1	2	1	1
	c3	all v.s.	15	2	3	1	0	1	1	0	0	1	2	0	0	0	0	1	1	1	1	0
												Coloration										
	c1	background	15	22	9	23	15	11	9	0	9	2	3	0	1	5	0	0	1	1	1	1
LDS	c2	pearly-yellow	7	1	4	1	7	3	15	13	15	17	7	9	11	7	12	6	10	11	10	10
	c3	green	2	1	11	0	2	10	0	11	0	5	2	3	0	0	0	6	1	0	1	1
	c1	yellow brown	6	0	2	1	2	4	5	1	12	1	6	2	2	10	6	2	5	4	7	3
	c2	hazel-brown	6	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	1	0	2
MBC	c3	brown-dark	1	21	11	21	12	0	0	0	0	0	0	5	5	0	2	0	0	0	0	0
	c4	light green	4	0	10	0	1	20	19	22	11	23	0	0	1	0	2	10	6	7	2	7
	c5	dark green	7	3	1	2	7	0	0	1	1	0	6	4	4	2	2	0	1	0	3	0
	c1	yellow brown	2	0	8	0	0	19	16	18	22	21	6	2	1	3	3	12	7	6	12	6
	c2	hazel-brown	12	0	1	0	3	3	0	4	1	1	2	1	3	0	4	0	4	6	0	4
FKC	c3	brown-dark	4	24	14	24	17	0	1	0	0	2	1	7	8	9	4	0	0	0	0	1
	c4	light green	2	0	1	0	0	2	7	2	1	0	0	0	0	0	1	0	1	0	0	1
	c5	dark green	4	0	0	0	4	0	0	0	0	0	3	2	0	0	0	0	0	0	0	0
	c1	orange-yellow	5	5	10	0	10	0	0	1	7	0	2	6	3	10	6	0	0	0	7	0
VTC	c2	light yellow	18	17	11	15	12	0	0	0	3	0	8	4	5	2	4	0	0	3	2	2
	c3	pale tones	1	2	0	9	1	2	0	7	11	5	2	2	4	0	2	1	3	3	0	3
	c4	white-pearly	0	0	3	0	1	22	24	16	3	19	0	0	0	0	0	11	9	6	3	7