

Population differentiation in scalation of the Iberian rock lizard (*Lacerta monticola*)

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(With 2 figures in the text)

The rock lizard *Lacerta monticola* is a climatic relict confined to three mountain ranges and one coastal region of the Iberian peninsula. Scalation was studied in specimens from localities encompassing all major parts of its range. Population differentiation was analysed using analyses of variance, z-transformations of within-locality character-correlations, canonical variate analyses, principal components analysis, and matrix association tests. Substantial differentiation was found between Pyrenees specimens and those from other localities, supporting a recent study which indicated that the Pyrenees populations could represent a different species. Considerable geographic variation is also found among populations from the remaining parts of its range, the pattern of which is not compatible with existing racial categories designated for this species.

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Introduction

The lacertid lizard *Lacerta monticola* Boulenger (1905), also referred to as *Archaeolacerta monticola* (Guillaume & Lanza, 1982), is indigenous to the Iberian peninsula, where it is confined to four geographical areas; the Pyrenean mountains in the north, the 'Sistema Central' mountain range in the centre, the Cantabrian mountains and coastal areas of the north-western tip of Spain (Galicia) (Lantz, 1927; Mertens, 1929; Müller & Hellmich, 1937; Galán-Regalado, 1982). The species is montane in the Pyrenees and the Sistema Central, being recorded only above 1968 m in the former and above 1550 m in the latter (reviewed by Salvador, 1984). It is also found at high altitudes (up to 1700 m) in the Cantabrian mountains, although it extends down to an altitude of 400 m on the humid north-facing slopes of this range (Elvira & Vigal, 1982). In contrast with its montane affinities in the aforementioned areas, it is found at sea level (although up to 400–500 m) in the humid, temperate region of Galicia, north-west Spain (Galán-Regalado, 1982).

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There is no present-day contact between populations from these four regions because the three mountain ranges are non-contiguous and the only populations recorded from coastal Galicia are well separated from those in the Cantabrian mountains (Elvira & Vigal, 1982). Further population isolation is found within the above regions. In the Sistema Central, for example, the fact that large areas appear to be below the altitudinal limit of the species in the range, and that it is absent from several apparently suitable localities such as the Sierra de Ayllón (V. Pérez-Mellado, pers. obs.), results in a very patchy distribution.

Given the degree of isolation and the biotopic differences experienced by the different populations, one would predict considerable geographic variation within this species. This appears to be the case, with four subspecies being currently recognized on the basis of external morphology; *L. m. monticola* Boulenger (1905) from the western extreme of the 'Sistema Central' in Portugal (Serra da Estrela), *L. m. cyreni* Müller & Hellmich (1937) from the centre (Sierras de Gredos and Francia) and east (Sierra de Guadarrama) of the 'Sistema Central', *L. m. cantabrica* Mertens (1929) from coastal Galicia and the Cantabrian mountains, and finally *L. m. bonnali* Lantz (1927) from the Pyrenees.

Despite these taxonomic designations, there has been no attempt to make rigorous quantitative comparisons of morphological divergence among populations of this species. Furthermore, the current status of *L. m. bonnali* is in doubt because, as well as being superficially quite different from the other subspecies in terms of morphology, recent electrophoretic data (Nascetti *et al.*, unpubl. data) indicates far greater biochemical differentiation than that normally expected within a species.

The aim of this study was to make a multivariate among-population comparison of the scalation to enable a quantitative evaluation of the differentiation among Iberian lizard populations currently recognized as *L. monticola*.

Materials and methods

(i) *Specimens and characters*

A total of 327 specimens belonging to the Departamento de Zoología, Universidad de Salamanca, were studied from 7 localities within the Iberian peninsula (Fig. 1). Three of the localities (1, 3, 4) can be considered as single sites, as specimens were from within very localized areas. However, specimens from proximate sites had to be pooled in order to give workable sample sizes for the remaining 4 compound localities. This was done after checking that they constituted homogeneous units, thus minimizing any possible confusion of within- and between-locality components of variation (Thorpe, 1976) (the pooling protocol was also supported by an *a posteriori* examination of individual Mahalanobis D^2). The localities were (Fig. 1):

1. Circo de Gredos, Sierra de Gredos (Sistema Central), Avila Province, central Spain (97 males, 84 females).
2. The Sierras de Francia and Candelario (Sistema Central), Salamanca Province, central Spain (6 males, 8 females).
3. Navacerrada, Sierra de Guadarrama (Sistema Central), Madrid/Segovia, central Spain (16 males, 8 females).
4. Penhas da Saude, Serra da Estrela (Sistema Central), Guarda Province, northern Portugal (30 males, 11 females).
5. Coastal Galicia (12 localities), north-western Spain (16 males, 16 females).
6. Sanabria, Zamora Province, and Piornedo, Lugo Province (Cantabrian mountains), north-western Spain (10 males, 6 females).
7. Cotatuero, Goriz and Lac Bleu de Bigorre (central Pyrenees), France/Spain border (14 males, 7 females).

The following 7 multistate scalation characters were recorded from each specimen; number of gular scales,

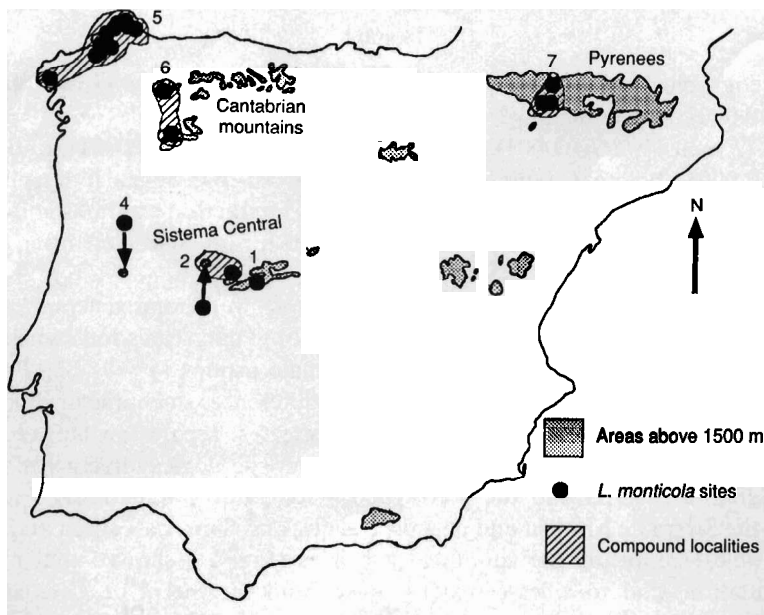


FIG. 1. The Iberian peninsula sites from which *L. monticola* were studied. Sites which were pooled for the analyses are indicated as compound localities. Localities are: (1) Circo de Gredos, Sierra de Gredos (Sistema Central); (2) Sierras de Francia and Candelario (Sistema Central); (3) Navacerrada, Sierra de Guadarrama (Sistema Central); (4) Penhas da Saude, Serra da Estrela (Sistema Central); (5) Coastal Galicia; (6) Sanabria, Zamora Province, and Piornedo, Lugo Province (Cantabrian mountains); (7) Cotatuero, Goriz and Lac Bleu de Bigorre (central Pyrenees).

number of dorsal scales, number of ventral scales, number of collar scales, number of femoral pores, number of lamellae on the fourth rear toe, degree of contact between rostral and frontonasal scale (tri-state). Animals were sexed by examination of the gonads.

(ii) Statistical analyses

Two-way analyses of variance were used to test for sexual dimorphism and among-locality variation in each character. Given that the Pyrenean population could represent a different species, the ANOVAs were also repeated using only localities 1–6.

Among-locality variation of within-group character correlations were tested for via z-transformations (Hotelling, 1953) of product-moment correlation coefficients computed between character pairs (males and females separate).

Canonical variate analyses (CVA) were computed on the 7 male and female groups, using all characters that showed significant among-locality variation. In order to test whether the CVAs had been significantly perturbed by potential within-group problems of heteroscedasticity and non-normal multivariate distributions, principal components analyses (PCA) were also run on the group means of the 6 characters.

Congruence between patterns of male and female geographic differentiation was tested for by computation of a measure of association (G) between male and female distance matrices (Mahalanobis D^2), with the probability of significance determined by randomization methods (Mantel, 1967; Manly, 1986; Brown & Thorpe, 1991; Thorpe, 1991).

Results

Significant geographic variation (ANOVA) among the seven localities was found in gular scales ($F=10.18$, $P<0.0001$), dorsal scales ($F=22.22$, $P<0.0001$), ventral scales ($F=29.37$, $P<0.0001$), femoral pores ($F=20.42$, $P<0.0001$), toe lamellae ($F=11.10$, $P<0.0001$), and rostral scales ($F=21.38$, $P<0.0001$), but not in collar scales ($F=1.43$, $P=0.204$). Sexual dimorphism was found only in ventral scales ($F=47.91$, $P<0.0001$). Sex-locality interaction was not significant for any of the characters. Geographic variation was still significant for all characters after removal of the Pyrenean locality ($P<0.0005$ in all cases).

Within-locality character correlations (product-moment) were homogeneous among the seven localities for males and females, with the exception of gular scales/toe lamellae, for which correlation coefficients differed significantly among male groups ($\chi^2=18.88$, $P<0.005$). Thus there was little detectable evidence of among-locality differences in character linkage.

Locality pair-wise comparisons for males showed greatest separation between the Pyrenees populations and the other six groups (Table I). Notable morphological divergence was also found between the Serra da Estrela and the Sierra de Guadarrama populations. The most similar localities were the Sierra de Francia and coastal Galicia, and Serra da Estrela and the Cordillera Cantabrica (Table I). Plotting the canonical variables (Fig. 2a) showed that males from the Pyrenean population, and to a lesser extent those from the Sierra de Guadarrama, can be discriminated from the other five groups by the first two canonical variables (representing 71.7% of the among-group variation). A PCA computed on group means gave the same pattern of differentiation. Variables contributing most to the first canonical vector (48.0% of among-locality variation) were the dorsal scale, femoral pore and rostral scale characters (Table II).

For females, populations from the Pyrenees locality were most divergent (Mahalanobis D^2), with greatest morphological differentiation being found between the Pyrenees and Cantabrian mountain localities. Substantial differentiation was also found between the Guadarrama and the Cantabrian, Serra da Estrela and Sierra de Gredos populations (Table I). The Pyrenees and Guadarrama population were discriminated from the remaining localities by the first canonical variable (57.8%), and from each other by the third canonical variable (16.4%) (Fig. 2b). Ventral

TABLE I
Mahalanobis D^2 between localities for male and female groups

Group	Locality					
	1	2	3	4	5	6
2 (♂♂)	5.70					
2 (♀♀)	8.13					
3 (♂♂)	8.73	10.98				
3 (♀♀)	19.07	10.59				
4 (♂♂)	8.39	7.97	18.26			
4 (♀♀)	3.61	5.68	21.55			
5 (♂♂)	4.58	2.77	10.96	10.40		
5 (♀♀)	4.69	4.71	7.67	6.85		
6 (♂♂)	3.27	4.79	12.90	1.48	6.43	
6 (♀♀)	10.89	10.82	36.36	4.21	11.27	
7 (♂♂)	26.93	28.72	21.26	31.41	31.30	24.64
7 (♀♀)	21.17	22.14	15.08	20.88	13.62	39.85

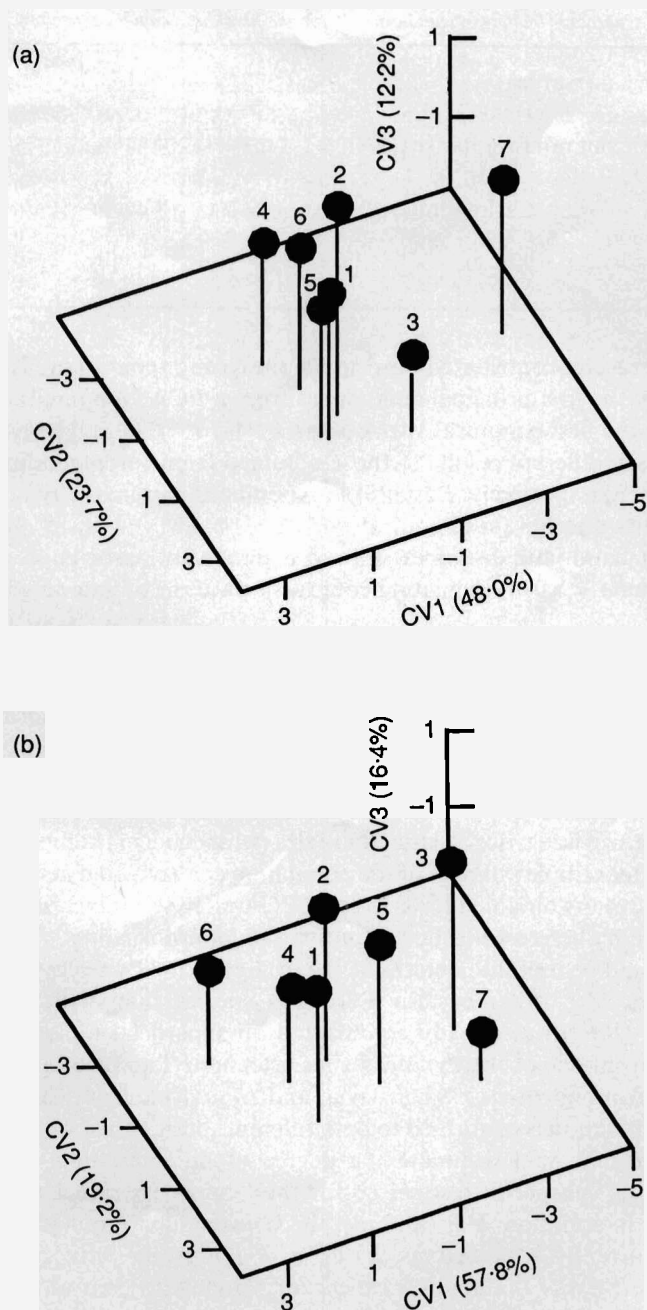


FIG. 2. Canonical variate (CV) plots for (a) male and (b) female groups (see Table II for character loadings on the canonical vectors).

TABLE II
 Character loadings (standardized) for the first three canonical vectors

Character	CV1		CV2		CV3	
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
Gular	0.06	0.14	0.34	0.19	-0.07	0.02
Dorsal	0.37	0.63	-0.17	-0.10	0.07	-0.05
Ventral	1.26	0.34	0.55	-0.32	-0.19	0.78
Femoral	0.34	0.68	-0.34	0.66	0.74	-0.06
Lamellae	-0.25	0.04	-0.69	-0.14	0.16	-0.55
Rostral	1.09	0.82	-3.39	-3.39	-1.09	-0.67

and rostral scale characters contributed most to among-group separation (Table II). The pattern of variation given by the first principal component from a PCA computed on group means was highly correlated to the first canonical variable ($r=0.944$, $P<0.005$). However, the second and third components gave different results to those obtained from corresponding canonical vectors ($r=0.305$ and $r=0.313$, respectively, $P>0.05$) so generalized patterns of geographic variation are not identical for the two techniques.

Male and female taxonomic distances showed a significant association ($G=1.932$; P (2000 matrix randomizations) <0.014) indicating congruent patterns of among-group differentiation.

Discussion

Male specimens from the Pyrenees locality are well differentiated from those from other parts of the Iberian peninsula, supporting preliminary biochemical evidence that the Pyrenees population could represent a different species (Nascetti *et al.*, unpubl. data). Why the pattern should be less obvious, although statistically congruent, in females is not clear. However, it is worth bearing in mind that the sample size was twice as large for males (14 specimens) compared to females, which may have given a better sample estimate of the population centroid, and also that small differences were found between results obtained for CVA and PCA analyses, indicating that the former was potentially perturbed by heteroscedasticity/multivariate non-normality.

Future studies would be useful to determine the origins of the Pyrenees population, i.e. does it have closer affinities with other eastern European species than with Iberian *L. monticola* populations? Lanza (1963) has already commented on superficial morphological resemblance between specimens from one of the Pyrenean sites used here (Lac Bleu) and two other montane species, *L. horvathi* from north-west Yugoslavia, and *L. saxicola* from Crimea.

If the Pyrenees population is confirmed to be a different species, then it could be contended that the current analyses may underestimate the degree of differentiation among the remaining localities. Even so, the subspecies recognized for these areas are rather poor predictors of the pattern of variation in scalation. For example, the Guadarrama population is clearly the most divergent, but is currently classified as *L. m. cyreni* together with other Sistema Central populations from the 'Sierras' of Gredos, Francia and Candelario (Salvador, 1984). Grouping the populations in this manner therefore gives a spurious representation of the pattern of morphological differentiation in scalation.

Why the Guadarrama population should be so divergent is difficult to assess on the basis of the current data. The species currently survives only in the coolest, most humid parts of the Iberian

peninsula. Hence, a feasible scenario explaining the geographic variation would be one of population vicariance owing to Holocene range contraction as the Iberian climate started to become warmer and much drier around 7000 BC (Font-Tullot, 1986). If this was the primary cause of the variation, extent of divergence should be related to time of separation, which probably approximates to current relative geographic isolation. This does not fit the described pattern of greatest differentiation within the Sistema Central. A climate-based ecogenetic scenario also appears to be inappropriate; such a model would predict greatest morphological divergence between populations from the ecologically very different coastal and montane localities, which is clearly not the case. In sum, the divergence of the Sierra de Guadarrama population does not appear to be readily interpretable, possibly because it may have arisen from events in the population's history not easily reconstructed on the basis of its current biogeography. Whether or not the current finding that it shows greater affinities with the Pyrenees population than do other populations (in terms of scalation), as well as being the geographically closest, proves to be important will depend on future phylogenetic studies on the origins of these populations.

Finally, it may be useful to compare the degree of geographic variation among these insular continental populations with that found in true island species. Despite the likelihood that population vicariance in *L. monticola* has occurred relatively recently, the extent of differentiation in scalation is commensurate with that found among Madeiran island populations of the related species *L. dugesii*, where time of divergence and degree of isolation must be much greater (Cook, 1979). Indeed, for ventral scales the among-population variation is much lower in the insular species, with means ranging from 25.8 to 26.1 among islands, compared with 21.75 (Sierra de Guadarrama) to 25.1 (Cordillera Cantabrica) in *L. monticola* (with comparable within-population variation) suggesting more rapid microevolution in the latter.

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