

Patterns and causes of morphological population differentiation in the Tenerife skink, *Chalcides viridanus*

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Recent studies indicate that differential selection between mesic and xeric habitats is the most plausible explanation of within-island geographic variation in the Gran Canarian skink, *Chalcides sexlineatus*. The island of Tenerife shows mesic/xeric heterogeneity similar to that on Gran Canaria, so we tested the prediction of parallel geographic patterns of morphological population differentiation in the Tenerife skink, *Chalcides viridanus*. Geographic variation was found to be complex; patterns of differentiation in body dimensions and scalation show evidence of both mosaic and latitudinal facets. Using randomization and regression methods, significant relationships were found between a hypothesized xeric/mesic model of population differentiation and geographic variation in female body dimensions, as well as with substantial proportions of the geographic variation in male and female scalation and, to a lesser extent, body dimensions. Matrix comparisons based on the entire morphological distance matrices show that the patterns of variation are not concordant with an alternative hypothesis of historical secondary contact, or with an isolation-by-distance model. It is argued that a substantial component of the geographic variation in body dimensions and scalation of *C. viridanus* is due to differential selection along an aridity gradient.

ADDITIONAL KEY WORDS:—Body dimensions – *Chalcides* – cline – ecogenesis – geographic variation – Mantel tests – microevolution – scalation.

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INTRODUCTION

Studies of among-population differentiation within small oceanic islands have shown that considerable geographic variation in morphology can occur in continuously distributed lizard species over very short geographic distances (Cook, 1979; Thorpe & Brown, 1989a,b, 1991; Brown & Thorpe, 1991a,b; Malhotra & Thorpe, 1991a; Thorpe, 1991; Thorpe & Báez, 1992). In some of these cases, morphological divergence among populations within an island appears to be equal to or greater than that in species distributed across entire continents. While the novelty of these findings makes them interesting in themselves, the fact that the number of feasible causes is often reduced in island situations also provides the evolutionary biologist with a valuable opportunity to test putative causes of population differentiation.

Observations of clinal variation in traits which correspond to environmental gradients may lead researchers to invoke *in situ* natural selection as the cause. However, the probability of congruence between the observed pattern and at least one ecological variable is quite high (Endler, 1986). Moreover, historically-caused geographic variation due to secondary contact can produce clines which are structurally indistinguishable from those of ecogenetic origin (Endler, 1977; but see Thorpe *et al.*, 1991). Stronger evidence for *in situ* selection as a cause of geographic variation is therefore provided when closely related allopatric species show parallel trait variation along similar environmental gradients (Endler, 1982, 1986). Under these circumstances, it may be possible to assume that the species have not undergone parallel vicariance/secondary contact events, as could occur in sympatric species. The probability of independent population vicariance/secondary contact events having given rise to patterns of geographic variation that are both coincidentally correlated with similar environmental variables will also generally be low. Hence, putative phylogenetic explanations can largely be rejected.

Two species of scincid lizard (Lacertilia: Scincidae) are found in the Canary Islands (Spain); *Chalcides sexlineatus*, endemic to the island of Gran Canaria, and *C. viridanus* from the Western Canary Islands of Tenerife, La Gomera and El Hierro. *Chalcides sexlineatus* and *C. viridanus* are morphologically very similar and appear to be sister species (Pasteur, 1981).

Two of the most heterogeneous islands in the archipelago are Gran Canaria and Tenerife (Fernandopulle, 1976; Garcia *et al.*, 1990; Huetz de Lemps, 1969). Gran Canaria has a surface area of only 1532 km² but reaches a height of 1949 m. This topography and the prevailing north/north-east trade winds combine to produce marked climatic differences within the island. The south-facing slopes of the island exhibit xeric conditions, which contrasts sharply with the mesic biotope found on the north-facing slopes. *Chalcides sexlineatus* shows pronounced within-island geographic variation in colour pattern, scalation and body dimensions which corresponds closely to the ecological variation and led Brown & Thorpe (1991a,b) to infer differential selection between habitats as the cause. Geographic variation in the electrophoretic mobility of enzymes (Mayr & Tiedemann, 1991) (spatially congruent with the morphological variation) suggests that this is not simply a result of superficial environment-phenotype interaction.

Tenerife lies just to the west of Gran Canaria. It is slightly larger (2032 km²), higher (3718 m), and shows parallel north/south contrasts in aridity.

Within-island population differentiation in scalation and body dimensions is known to occur in the Tenerife skink, *C. viridanus*, (Báez & Thorpe, 1991; Pasteur *et al.*, 1988), although the actual spatial patterns of this variation have not yet been described. Patterns of geographic variation in colour pattern, particularly tail colour, have been shown to parallel those in *C. sexlineatus* (Brown *et al.*, 1991).

Here, we extend the latter-mentioned work by analysing two new character systems, body dimensions and scalation, in *C. viridanus*. Thus, we further explore the hypothesis that if ecogenesis (as opposed to phylogenesis) is the cause of the morphological variation in *C. sexlineatus*, then parallel trait-environment covariation should be found in *C. viridanus*.

MATERIALS AND METHODS

Specimens and localities

Preserved *C. viridanus* (on loan from the Zoology Department, University of La Laguna) from 18 localities within Tenerife were studied (Fig. 1). All specimens had been collected over a ten month period. Lizards were sexed by examination

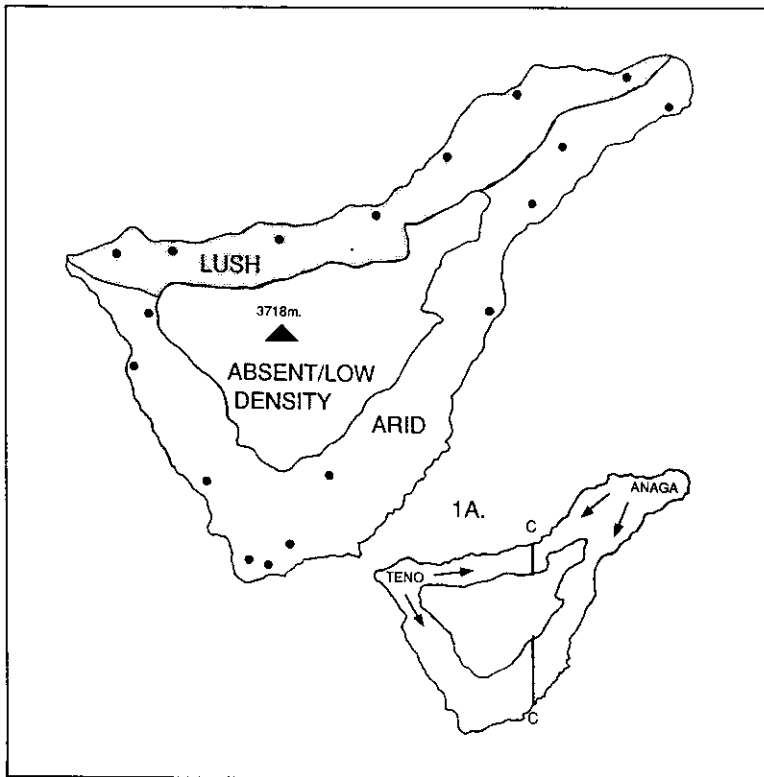


Figure 1. *C. viridanus* sample localities on the island of Tenerife (filled circles). The 1100 m contour delineates the central high altitude area where the species is absent/present only at very low population densities. The north(shaded)/south change in biotope aridity within the island (xeric/mesic selection hypothesis) is also shown. Inset(1A), the historical secondary contact hypothesis modelling the putative remecting of Teno and Anaga populations in the centre of the island (C).

of the gonads. Mean locality sample sizes were 11.7 ± 4.16 for males (210 specimens) and 15.1 ± 7.24 for females (271 specimens). All localities were from low altitude parts of Tenerife, with none above 950 m. During fieldwork we saw no specimens above 1100 m, approximately coinciding with the lower limit of the ring of pine forest encircling the volcano. Thus, for current purposes, *C. viridanus* will be considered as absent or present at only very low population density above 1100 m.

Characters

Nine linear body dimensions and six scalation characters were recorded on each specimen. The body dimensions (measured to 0.01 mm) were: (1) snout-vent length (SVL); (2) head length between the tip of the snout and the ears (HL); (3) body length between limb insertions (BL); (4) head depth at the position of the ears (HD); (5) rear limb length between its insertion on the body and the tip of the toe (RLL); (6) thorax width at the fore-limbs (TW), (7) head width (HW) between the eyes; (8) head to shoulder distance (HSD); (9) length of the fourth toe on the rear limb (TOE).

The scalation characters were: (1) ventral scale number counting down the belly from the snout to the vent (V); (2) number of scales around the mid-trunk (SRMT); (3) number of infra-digital lamellae on the fourth toe of the rear limb (IDR); (4) number of leg scales counting from the limbs insertion with the body to the foot (LS); (5) number of infra-digital lamellae on the middle toe of the front limb (IDF); (6) number of temporal scales around the ear opening (EAR). All bilateral characters were recorded from the right hand side.

Statistical analyses

Distances between localities are large in relation to the maximum possible lifetime dispersal distances of this small terrestrial species. Statistical independence of locality samples was therefore assumed.

Males and females were separated, giving 18 + 18 groups. Analysis of variance (ANOVA) tested for among-locality and between-sex variation in SVL. Analyses of covariance (ANCOVA) tested for size (i.e. SVL) independent among-locality variation and sexual dimorphism in the remaining eight body dimensions. The presence of significant geographic variation in the characters meant that they were all used in the multivariate analyses.

Product-moment correlation between group means were used to investigate (1) congruence between male and female patterns of geographic variation, and (2) congruence between patterns of geographic variation shown by different characters (within sexes). Type-I error rates were expected to be high due to the large number of correlations, indicating the need for a simultaneous inference technique. The standard Bonferroni correction has the disadvantage that it tends to be overly conservative in cases where more than one null hypothesis could be falsely rejected. This problem is alleviated to some extent if a sequential Bonferroni adjustment is used, as it incorporates a progressive reduction in significance levels for the null hypotheses, according to the number of null hypotheses to be rejected in the group of tests being considered (Rice, 1989, and references therein). Type-I error rates were therefore controlled for each of the

three groups of tests (between-sexes, and between different characters for males and females) using the sequential Bonferroni adjustment.

A multiple group principal components analysis (MGPCA) was computed on the logarithmically-transformed body dimensions across the 36 groups. MGPCA extracts orthogonal eigenvectors from the within-group covariance matrix (Thorpe, 1988, and references therein). Hence, if a broad growth band is represented within the samples, as is the case here, the first component is a general size vector. Given that body dimension characters are unlikely to be totally independent, this method allows assessment of within-group size-independent character covariation.

Generalized among-group variation was computed by separating male and female component scores from the MGPCA and inputting them into two canonical variate analyses (CVA). This has been shown to give the same results as inputting raw body dimensions into the CVA while also allowing calculation of the contribution of each orthogonal component to the among-group variation (Thorpe *et al.*, 1982; Thorpe, 1983a,b). We also repeated these CVAs with the first MGPC (size) components omitted. This did not affect patterns of differentiation, as represented by the group centroids, so among-group discrimination was known to be based on variation in shape and not size.

For scalation, pooled within-group correlations were calculated between pairs of characters to determine degree of independence. Two way ANOVAs were then computed, testing for among-locality and between-sex variation. Congruence between patterns of geographic variation was investigated in the same way as that described for body dimensions, i.e. correlations between mean group character scores with the sequential Bonferroni technique being used to assess statistical significance.

CVAs were computed on male and female groups using all six scalation characters. One of the advantages of a CVA is that it reduces the influence of covarying characters when calculating among-group separation. Canonical variates representing substantial proportions of among-group variation in body dimensions and scalation were plotted on maps, and contouring used to aid visualization of geographic trends (Golden Software, 1990).

Testing hypothesized causes of the geographic variation

If natural selection is the cause of the observed geographic variation, one would expect covariation with some aspect(s) of the within-island ecological heterogeneity. Two ecogeographical variables covary with morphology in the Gran Canarian skink, namely altitude and mesic/xeric habitat variation (Brown *et al.*, 1991; Brown & Thorpe, 1991a,b). Although altitudinal variation could not be tested for in our samples of *C. viridanus* (all but two localities were below 550 m), a testable hypothesis could be constructed on the basis of the xeric/mesic habitat variation.

Historical causes of the geographic variation are also possible. Bischoff (1982) previously suggested that geographic variation in *G. galloti* on Tenerife was due to secondary meeting of isolated populations after the formation of the island by an eruption joining the two ancient islands of Anaga and Teno. Although this hypothesis has since been shown to be unlikely (Thorpe & Brown, 1989a), when simultaneous methods are available it is obviously advantageous to test all putative models.

An isolation-by-distance model could also be pertinent to the observed geographic variation. This predicts that the effects of gene flow cause individuals from proximate localities to show greater similarity than those from distant localities. Proximate localities are also likely to be ecologically similar, so simultaneous methods are necessary in order to separate gene flow from 'ecology' when testing hypothesized causes (see below; Manly, 1986; Thorpe & Brown, 1989a,b).

The aforementioned putative causes of the geographic variation were modelled to give three numerically testable hypotheses:

(1) *Xeric/mesic selection*. We modelled latitudinal variation in habitat aridity in Tenerife in the way described by Thorpe & Brown (1989a,b). Cloud formation on the north-facing slopes below 1500 m gives rise to a wetter climate and consequently a lush vegetation (Fernandopulle, 1976; Garcia *et al.*, 1990; Huetz de Lemps, 1969). The acuteness of this north/south transition in habitat aridity allowed division of the island into mesic (north) and xeric (south) areas (Fig. 1), giving a 0,1 dissimilarity matrix.

(2) *Historical secondary contact*. To give a simple simulation of a possible pattern of geographic variation caused by the putative meeting of Teno and Anaga populations after they had dispersed along the new landbridge (Bischoff, 1982), a longitudinal division line was placed which was equidistant to the eastern and western extremes of the island. Localities were assigned zero or one values according to whether they lay to the east or the west of this line (Fig. 1A). Unlike the previous ecogenetic hypothesis, this model predicts congruent variation in all characters (Thorpe *et al.*, 1991; Thorpe & Báez, 1992).

(3) *Isolation-by-distance*. This models the shortest geographical distances between localities, representing the effects of gene flow. Between-locality distances were measured on a map using a flexible rule to measure around the area of 'absence/very low population density' over which gene flow was assumed to approximate to zero (see Methods and Fig. 1). Geographic variation due to gene flow should produce geographically congruent changes among characters (Sokal & Wartenburg, 1983).

Mantel tests (Manly, 1986) were used to test two hypotheses simultaneously against each morphology matrix. These methods determine significance of statistics computed between matrices (Mantel, 1967). This can be achieved by comparing actual measures of matrix association with those obtained after matrix randomization (Dietz, 1983; Dow & Cheverud, 1985; Smouse *et al.*, 1986). Here, three possible hypotheses were to be tested against four distance matrices (body dimensions and scalation, males and females).

There is no reason to expect ecogenetically-caused among-locality variation to be unidimensional (Thorpe *et al.*, 1991) so testing the entire morphology matrices may not be appropriate (Thorpe & Báez, 1992). Thus the xeric/mesic habitats hypothesis was also tested against individual components of the among-locality variation, as represented by the first three canonical variates from the canonical variate analyses. We computed a measure of matrix association, G (based on the Z statistic proposed by Mantel, 1967), between each CV expressing a substantial proportion of the among-locality variation (CV1-3) and the mesic/xeric selection hypothesis (Brown & Thorpe, 1991b). Probabilities were determined by distribution-robust matrix randomization methods (see Cheverud *et al.*, 1989) and adjusted using the sequential Bonferroni technique.

TABLE 1. Product-moment correlation coefficients between group means of the nine body dimensions (size-specific except for SVL) testing for congruent geographic variation (1) between sexes (B.S.), (2) between characters for males (M), and (3) between characters for females (F)

Ch.	B.S.		HL	BL	HD	TW	HW	HSD	RLL	TOE
SVL	0.21	M	-0.06	-0.18	0.06	0.02	0.05	-0.25	0.07	0.08
		F	0.02	0.08	0.41	0.37	-0.04	-0.30	-0.22	-0.40
HL	<i>0.61**</i>	M		-0.63**	0.49*	0.16	0.39	<i>0.86***</i>	<i>0.70**</i>	0.41
		F		-0.64**	0.40	0.43	0.39	<i>0.68**</i>	<i>0.47*</i>	0.17
BL	<i>0.74***</i>	M			-0.18	0.04	-0.14	-0.62**	-0.61**	-0.18
		F			0.01	-0.24	0.00	-0.68**	-0.55*	-0.46
HD	<i>0.83***</i>	M				<i>0.74***</i>	<i>0.47*</i>	0.22	0.17	-0.24
		F				<i>0.70**</i>	<i>0.56*</i>	-0.16	-0.03	-0.47*
TW	<i>0.78***</i>	M					0.12	0.00	-0.05	-0.18
		F					0.28	-0.19	0.04	-0.28
HW	<i>0.74***</i>	M						0.24	0.22	-0.21
		F						0.18	0.36	-0.06
HSD	<i>0.63**</i>	M							<i>0.73***</i>	0.46
		F							0.51*	0.51*
RLL	<i>0.87***</i>	M								0.63*
		F								<i>0.79***</i>
TOE	<i>0.61**</i>									

Italicized values are significant after sequential Bonferroni adjustment (here, and elsewhere, calculated for 0.05 significance level). Individual probabilities denoted by asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

RESULTS

Geographic variation in body dimensions

Mean SVL was found to vary between sexes but not among localities (Sex, $F=7.05$, $P<0.001$; locality, $F=1.34$, $P>0.05$). The remaining eight body dimension characters all varied significantly among localities and showed sexual dimorphism (HL, locality $F=8.01$, sex $F=155.3$; BL, locality $F=8.47$, sex $F=39.0$; HD, locality $F=5.71$, sex $F=128.7$; RLL, locality $F=7.49$, sex $F=64.6$; TW, locality $F=9.19$, sex $F=32.2$; HW, locality $F=6.44$, sex $F=91.7$; HSD, locality $F=10.20$, sex $F=96.1$; TOE, locality $F=5.76$, sex $F=31.8$; $P<0.001$ for all).

All characters except for SVL showed generally congruent patterns of geographic variation between sexes (Table 1). Between-character congruence was found between head depth and thorax width, and between head length and head to shoulder distance in both males and females.

In the MGPCA, almost all of the within-group variation (98.33%) in body dimensions was expressed by the first (size) MGPC (Table 2). Sexual dimorphism in size was found to be significant (Table 2). Size vectors contributed very little to the total among-locality variation (males, 3.43%; females, 2.62%). All subsequent MGPCs showed highly significant geographic variation and all (except MGPC8) were sexually dimorphic. MGPC3 contributed most to the among-locality variation (males, 25.29%; females, 19.26%). This was a shape component which combined increasing neck and head length (HSD) with increasing hind limb length (RLL) and decreasing length of the trunk (BL). MGPC9 represented only 0.01% of the within-group variation but contributed 14.59% (males) and 9.61% (females) to the among-group variation.

TABLE 2. Within-group facets of variation in body dimensions, represented by the MGPCs. Sexual dimorphism (Sex *F*) and among-locality variation (Locality *F*) of each MGPC (Component) are given by *F* ratios from the ANOVAs. 'Within-group (%)' gives proportions of within-group variation expressed by each MGPCA. Proportions of male (M) and female (F) among-group variation expressed by each component are given as 'Among-group (%)'

Component	Within-group (%)	Among-group (%)		Sex <i>F</i>	Locality <i>F</i>
		Male	Female		
MGPC1	98.33	3.43	2.62	6.99**	1.34
MGPC2	0.94	5.84	16.82	11.71***	2.41**
MGPC3	0.39	25.29	19.26	112.5 ***	12.60***
MGPC4	0.13	6.55	6.46	17.12***	3.21***
MGPC5	0.09	8.01	17.57	28.59***	6.68***
MGPC6	0.05	12.48	14.09	64.46***	5.15***
MGPC7	0.03	15.10	6.89	5.45*	5.64***
MGPC8	0.02	8.91	6.66	1.58	3.62***
MGPC9	0.01	14.59	9.61	16.68***	5.70***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Among-locality variation in body dimensions is clearly multidimensional. The first two canonical variates expressed just over half of the total variation (males, 61.9%; females, 54.7%). Some evidence of latitudinal patterns of variation was seen in the first canonical variates for both males and females, expressing 43.1% and 32.1% of among-locality variation, respectively (Fig. 2A,B). Generally mosaic (i.e. geographically irregular) variation was found in the remaining vectors that expressed substantial proportions of among-locality variation.

Geographic variation in scalation

The scalation characters had generally low pooled within-group correlations indicating independence (Table 3). All six characters showed significant among-locality variation, but only ventral scale number is sexually dimorphic (V, locality $F=9.50$ $P<0.001$, sex $F=7.72$ $P<0.01$; SRMT, locality $F=7.39$ $P<0.001$, sex $F=0.17$ $P>0.05$; IDR, locality $F=7.79$ $P<0.001$, sex $F=0.00$ $P>0.05$; LS, locality $F=5.67$ $P<0.001$, sex $F=0.00$ $P>0.05$; IDF, locality

TABLE 3. Pooled within-group correlations between scalation characters for males (M) and females (F). The values are generally low indicating that the characters express independent facets of the phenotype

Ch.		SRMT	IDR	LS	IDF	EAR
V	M	0.263	0.190	0.108	0.011	0.164
	F	0.230	0.146	0.108	0.051	-0.067
SRMT	M		0.063	0.049	-0.004	0.178
	F		0.154	-0.015	-0.037	0.026
IDR	M			0.071	0.253	0.116
	F			0.084	0.309	0.032
LS	M				0.069	0.108
	F				0.141	0.170
IDF	M					-0.027
	F					0.068

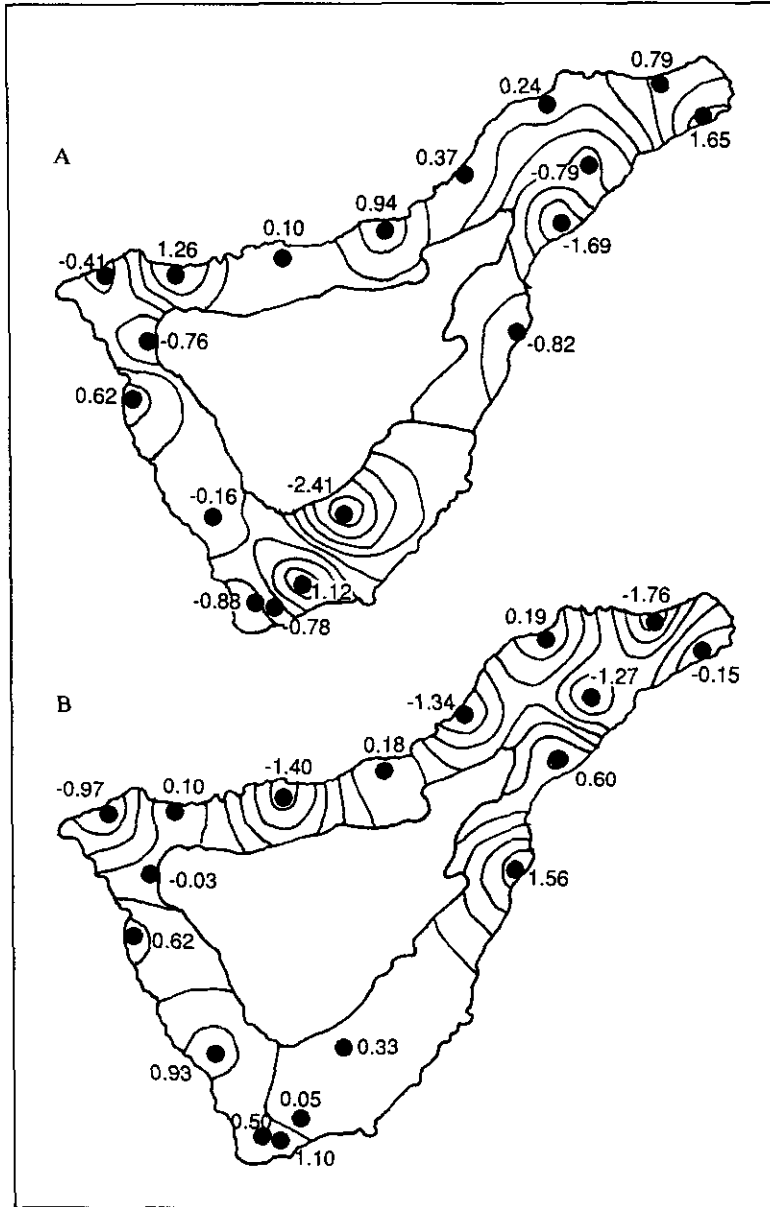


Figure 2. Contoured patterns of geographic variation in generalized body dimensions with contour line frequencies of one tenth of the maximum range between group centroids for each canonical variate. A, male CV1; 43.1% of among-locality variation loaded positively by MGPC6 (component which primarily represents increasing head length), and negatively by MGPC7 (decreasing head length/increasing head width). B, female CV1; 32.1% of variation loaded negatively by MGPC9 (increasing head depth/decreasing head width).

$F=10.13$ $P<0.001$, sex $F=0.86$ $P>0.05$; EAR, locality $F=2.86$ $P<0.001$, sex $F=0.65$ $P>0.05$). The patterns of geographic variation were generally incongruent between individual characters (Table 4).

Most of the among-locality variation was expressed by the first three canonical variates (males, 83.7%; females, 83.3%). Male CV2 (27.0% of among-locality

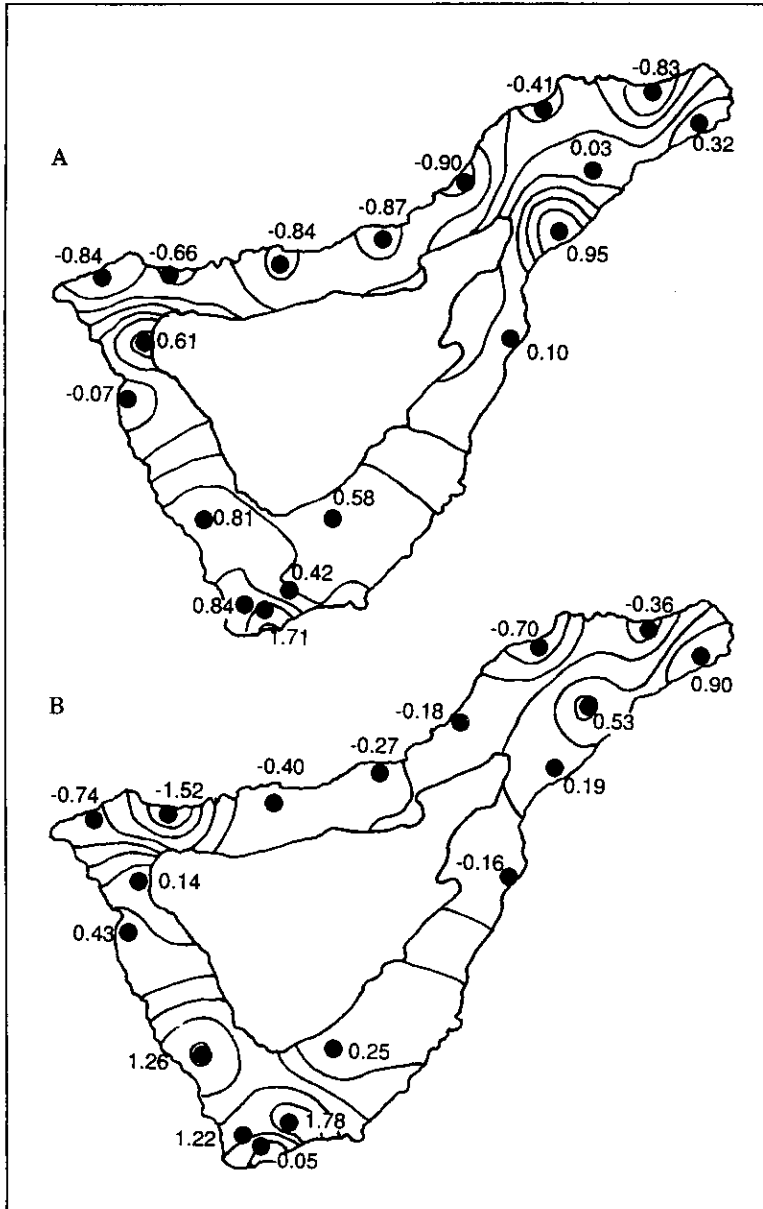


Figure 3. Contoured patterns of geographic variation in generalized scalation with contour line frequencies of one tenth of the maximum range between group centroids for each canonical variate. A, male CV2; vector representing 27.0% of among-locality variation, loaded negatively by SRMT, and positively by V and IDF. B, female CV1; 36.5% of variation, loaded heavily by IDF, and also V and SRMT (polarities as for males). C, male CV3; 17.4% of variation, loaded negatively by SRMT and positively by IDR.

variation) and female CV1 (36.5%) showed very clear patterns of geographic variation (Fig. 3A,B). In both cases, populations situated on the north-facing slopes had lower scores than those situated in other parts of the island. The rest of the variation was generally mosaic, although there was evidence of an east/west cline on the central/eastern north coast in males (Fig. 3C).

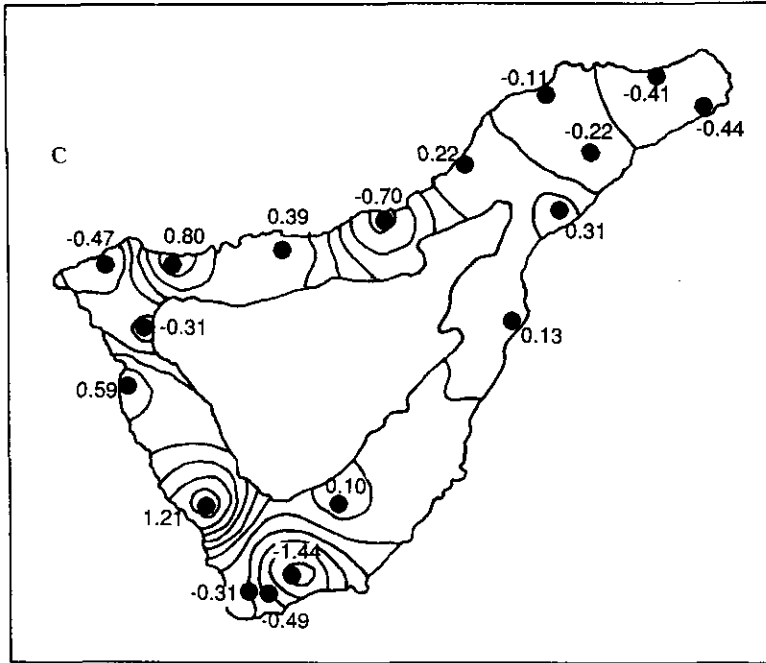


Fig. 3.

Hypotheses

See Table 5. A significant association was found between the xeric/mesic hypothesis and the variation in female body dimensions. The historical secondary contact and isolation-by-distance hypotheses were not significant for male or female body dimensions. None of the hypotheses/models were significant for scalation.

Testing individual facets of the among-locality variation (Table 6) gave

TABLE 4. Product-moment correlation coefficients between group means of the six scalation characters, for (1) males (M) and (2) females (F). Significant values indicate that patterns of geographic variation are congruent between characters. The only sexually dimorphic character, V, shows congruent between-sex variation ($r = 0.83$, $P < 0.001$).

Ch.		SRMT	IDR	LS	IDF	EAR
V	M	0.05	0.12	0.01	0.45	0.13
	F	-0.21	-0.08	-0.18	0.25	-0.04
SRMT	M		0.02	0.43	0.00	0.55*
	F		0.54*	0.39	-0.08	-0.05
IDR	M			0.65**	0.67**	0.07
	F			0.41	0.42	0.16
LS	M				0.41	0.37
	F				0.38	0.24
IDF	M					0.14
	F					0.64**

Italicized value is significant after sequential Bonferroni adjustment. Individual probabilities denoted by asterisks: * $P < 0.05$, ** $P < 0.01$.

TABLE 5. Hypothesis testing on the body dimensions and scalation matrices. Three matrices Mantel tests computed the following measures of matrix association: $g_{1,2}$ a simple regression between the morphology matrix (1) and the first hypothesized matrix (2); $g_{1,3}$ a simple regression between the morphology matrix (1) and the second hypothesized matrix (3); g_A a partial regression between the first hypothesized and the morphology matrices with the effects of the second hypothesized matrix regressed out; g_B a partial regression between the second hypothesized and the observed matrices with the effects of the first hypothesized matrix regressed out. The hypotheses were: lush/arid habitats (Lush/arid), isolation by distance (Distance), and historical secondary contact (2°Contact). The probabilities of no association were determined from the distribution of the statistics given by 500 random associations of the matrices. The sequential Bonferroni technique was used to control the type-I error rates for the twelve independent simple regressions (each represented twice), and both the groups of twelve partial regressions.

Morphology matrix	Hypotheses		Measures of Association			
	2	3	$g_{1,2}$	$g_{1,3}$	g_A	g_B
Body dimensions:						
Male	Lush/arid	Distance	0.031	0.014	0.042	-0.014
Male	2°Contact	Distance	-0.023	0.014	-0.030	0.024
Male	Lush/arid	2°Contact	0.031	-0.023	0.048	-0.056
Female	Lush/arid	Distance	<i>0.112***</i>	0.032	<i>0.109***</i>	0.007
Female	2°Contact	Distance	-0.002	0.032	0.008	0.033
Female	Lush/arid	2°Contact	<i>0.112***</i>	-0.002	<i>0.118***</i>	-0.028
Scalation:						
Male	Lush/arid	Distance	0.063*	0.072**	0.053	0.064
Male	2°Contact	Distance	0.004	0.072**	-0.026	0.047
Male	Lush/arid	2°Contact	0.063*	0.004	0.072	-0.014
Female	Lush/arid	Distance	0.042	0.021	0.032	-0.004
Female	2°Contact	Distance	-0.038	0.021	-0.012	-0.007
Female	Lush/arid	2°Contact	0.042	-0.038	0.067**	-0.083

Italicized values are significant after sequential Bonferroni adjustment (for $P < 0.05$). Individual probabilities denoted by asterisks: * $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$.

significant associations between the xeric/mesic hypothesis and CV2 for male scalation (27.0% of total), and CV1 for female scalation (36.5% of total).

DISCUSSION

Body dimensions and scalation of *C. viridanus* show evidence of north/south geographic variation within the island of Tenerife. Facets of variation in male and female scalation are concordant with the xeric/mesic variation within the island. These patterns are subtle, however, and in both cases represent less than 37% of the total among-locality variation. The remaining facets of among-locality variation appear to be largely mosaic (irregular). This demonstrates the importance of testing individual components (as opposed to generalized multivariate distances) of among-locality variation when considering putative ecogenetic causes, where characters do not necessarily vary in a spatially congruent manner (Thorpe, 1987; Thorpe *et al.*, 1991; see also Thorpe & Báez, 1992).

The two other models that were tested against the observed pattern (isolation-by-distance and historical secondary contact) both infer common micro-evolutionary mechanisms for all characters. They therefore predict congruent spatial patterns among characters (see Materials and Methods) so testing the

TABLE 6. Comparisons between the lush/arid habitats model and individual generalized facets of among-locality variation, as represented by group centroids of the first three canonical variates. The measure of association computed between the matrices, G , is based on Mantel's χ statistic (Mantel, 1967); where $G = (\chi - \text{Exp})/\text{SE}$. The actual value of G was compared with the distribution of values of the same statistic computed after 1000 random permutations of the matrices

	Canonical variate	G	P
Body dimensions:	Male CV1	0.994	0.170
	Male CV2	-0.779	0.707
	Male CV3	-0.665	0.706
	Female CV1	2.957	0.016
	Female CV2	0.158	0.334
	Female CV3	0.127	0.348
Scalation	Male CV1	-0.653	0.680
	Male CV2	8.414	< 0.001
	Male CV3	-1.050	0.821
	Female CV1	4.802	0.002
	Female CV2	0.354	0.330
	Female CV3	-0.713	0.752

Italicized values are significant after sequential Bonferroni adjustment.

generalized multivariate matrices was appropriate. This indicated that the patterns of variation do not conform to that hypothesized for the historical secondary contact scenario, and also that the isolation-by-distance model is a rather poor predictor (here) of among-locality differentiation.

Clear parallels between the described geographic variation and that in *C. sexlineatus* from Gran Canaria are found. The north/south facet to the geographic variation in *C. viridanus* corresponds to variation in the body dimensions, scalation and colour pattern of the Gran Canarian skink (Brown & Thorpe, 1991a,b). This provides strong evidence that ecogenesis is the cause of the geographic variation. The improbability of analogous vicariance events on the two islands means that phylogenetic explanations can be largely ruled out. Furthermore, the islands have quite independent geological histories which show no evidence of parallel latitudinal events likely to have separated existing populations (Abdel-Monem, Watkins & Gast, 1971; Borley, 1974; Hansen, 1987, 1988).

The polarities of the character changes are of clear importance to the ecogenetic differentiation argument, assuming that mechanisms of selection and genetic correlations are parallel between the species. Head length contributes considerably to the latitudinal component of the geographic variation in body dimensions and, as in *C. sexlineatus* in Gran Canaria, shows a tendency to be longer in the mesic northern areas (see Brown & Thorpe, 1991a, for a discussion of possible adaptive explanations of body dimension and scalation character variation in *C. sexlineatus*). The two body scale characters (i.e. ventral scales and scales around midtrunk) show strong latitudinal variation in both species. However, in *C. sexlineatus* the trend in both characters is for a greater number of

scales in the north, while in *C. viridanus* the mid-body scales show the opposite pattern. This between-species difference appears to run counter to the parallel ecogenesis explanation of population differentiation. While one could counter-argue that geographic variation in mid-body scales could be non-adaptive and the opposing trends between the two species are solely a result of differing genetic covariance structures, the close species affinities makes this appear improbable. However, at the present time we are unable to offer an alternative explanation.

Although N/S aspects of the geographic variation are parallel in the Tenerife and Gran Canarian skinks, substantial differences also exist. For example, among-locality variation in body dimensions and scalation of *C. viridanus* is complex (multidimensional), while variation in the same character systems in *C. sextineatus* is largely unidimensional (i.e. the xeric/mesic habitat correlated pattern is clearly dominant). Furthermore, character divergence is less pronounced in *C. viridanus*. For example, maximum among-population differentiation in head length (male means, size-specific) is around 8.8% in this species, compared to 17.1% in the Gran Canarian skink. Similarly, ventral scale divergence can be up to 19.2% between populations of the Gran Canarian skink compared to only 5.0% in *C. viridanus* (see Brown & Thorpe, 1991a,b).

Ecological variation appears to be broadly the same in the two islands due to their adjacent position and the fact that the within-island climatic variation is the result of a similar process. Thus, a steeper selection gradient in Gran Canaria does not appear to explain the differing magnitudes of microevolution in the two species. Even so, there are ecological differences between the two species which could affect their interaction with a selection gradient; both species tend to be found at lower population densities in the more arid southern parts of the islands, but this is much more pronounced in the Tenerife skink which appears to be solely confined to artificially irrigated areas.

The Tenerife skink shows little morphological differentiation between islands indicating that it is a relatively recent species (Báez & Thorpe, 1991). Thus, an alternative hypothesis is that the Gran Canarian skink has undergone a longer period of *in situ* divergence. However, this argument is not without problems. Malhotra and Thorpe (1991b) demonstrated significant differential survivorship within a few months for lizard ecotypes transplanted to 'foreign' environments, propagating the view that vertebrate population differentiation can arise over very short time scales (Eastel, 1985; Gingerich, 1983).

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