

GEOGRAPHIC VARIATION WITHIN AN ISLAND:
UNIVARIATE AND MULTIVARIATE CONTOURING OF
SCALATION, SIZE, AND SHAPE OF THE
LIZARD GALLOTIA GALLOTTI

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Abstract.—Microgeographic variation of the vegetarian lizard *Gallotia galloti* within the island of Tenerife is described using univariate analysis, correlation, multiple group principal component analysis, canonical analysis, transects, and contours. The size varies locally in a mosaic pattern while head shape shows a WNW-ESE cline in the south. The scalation (scale and femoral pore counts) has two facets to its geographic variation, both of which are incongruent with the primary variation in the size and shape. The scalation shows categorical variation (stepped cline) between northern and southern populations and also a strong clinal relationship with altitude. The possible causes of this variation are considered and adaptation to current ecological conditions appears to be implicated for at least the altitudinal variation, although the pertinent factors are not obvious. It is apparent that vertebrate populations distributed across small islands do not necessarily offer the advantage of a discrete homogeneous unit for evolutionary studies but can offer the opportunity for studying microgeographic variation.

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From the days of Darwin's study of the Galápagos fauna to the present, island populations have been a favored source of evolutionary and systematic studies. Among other attributes, a species on a small island appears to offer a discrete, racially homogeneous entity for interisland comparison. Consequently, with some exceptions (Woodruff and Gould, 1980), evolutionary studies of island forms have tended to emphasize interisland comparison rather than microgeographic variation within small islands. This is particularly the case with vertebrates such as lizards (Clover, 1979; Gardner, 1984; Gorman et al., 1975; Gorman and Kim, 1976; Snell et al., 1984; Soulé, 1967; Thorpe, 1986; Thorpe et al., 1985).

This study is an investigation of the patterns of microevolutionary differentiation of the lizard *Gallotia galloti* within Tenerife, an Atlantic island in the Canary archipelago, which is situated between 28° and 29°N, and between 16° and 17°W, 270 km off the coast of northwest Africa. The Canaries are composed of an arid eastern group of islands and a more humid, western group (Fernandopulle, 1976). It is to this latter group that the largest of them, Tenerife (2,058 km²)

belongs. In simple terms, Tenerife consists of two main ancient regions, Anaga in the NE and Teno in the NW (Fig. 1). These were once probably separate islands but joined ca. two million or more years ago when volcanic activity occurred from the sea bed between them, thereby forming the single island of Tenerife (Borley, 1974). The western islands are mountainous and are separated by deep sea channels. Consequently they do not appear to have been joined to one another or segmented by relative sea level changes in the recent past.

Teide, in the center of Tenerife (Fig. 1), is the highest mountain in Spain (3,718 m). It extends through the cloud layer, so that there is a ring of cloud cover and also a ring of pine forest in the middle altitudes. Broadly speaking, the altitudinal zonation gives hot, dry conditions in low altitudes (especially in the south), cool humid conditions at middle altitudes (especially in the north), and bright conditions with sharp seasonal and daily contrast in temperature at high altitudes. This cloud cover is particularly dense in some northern regions, and there can be a remarkable contrast between the cooler, humid, low-solation climate of the

north and the hot, arid, high-solation climate in the south.

The lizard under investigation is a medium-sized, vocal, herbivorous/frugivorous lacertid (up to 130 mm snout-vent length [SVL]) belonging to the endemic genus *Gallotia*. It lives over almost all of the island (often in considerable densities), with the possible exceptions of the unvegetated tip of Teide, parts of the northern cloud zone, and relict patches of dense "Laurisilva" forest. One can see from the combined collection sites of this study (Fig. 1) and Bischoff's (1982) study that there can be no very large regions without this species. Currently, every island is occupied by one, and only one widespread species (Thorpe et al., 1985) although sympatric species with very restricted ranges may be found. The species *galloti* is found in the western islands (Tenerife, Hierro, Gomera, and La Palma), while *atlantica* is found on the eastern islands. In Tenerife, *galloti* currently has no congeneric competitor.

The color pattern shows obvious differences between populations. Previous authors have noted this (Carnero and Perez Padron, 1977; Bings, 1980; Bischoff, 1982), and two conventional subspecies within the main island of Tenerife have been recognized (Bischoff, 1982), i.e., *G. g. galloti* in the south and *G. g. eisentrauti* in the north (Fig. 1). However, these authors did not attempt to analyze the variation in a range of characters quantitatively.

This paper is an attempt to analyze the geographic variation by quantitative univariate, bivariate, and multivariate methods and to illustrate this variation by geographical transects and contours. The patterns of geographic variation in the scelation, size, and shape, once described, are then considered in the light of possible causative factors such as phylogenesis and adaptation to current ecological conditions.

MATERIALS AND METHODS

Both linear body proportions and scelation characters were studied. The following body proportions (i.e., direct linear measurements—not ratios) were recorded: 1) snout-vent length, 2) head length, 3) foreleg to snout length, 4) head depth, 5) head width, 6) foreleg length, 7) rear-leg length, and 8)

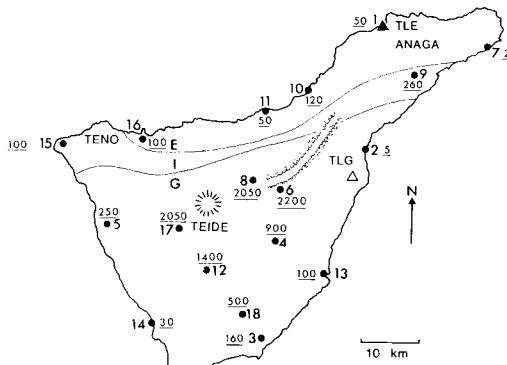


FIG. 1. Sample localities on Tenerife. Sample localities are marked as dots, and the locality number is indicated in bold type. Altitude of the locality is indicated in underlined type. The ancient areas of Teno in the northwest and Anaga in the northeast are indicated, as is the mountain Teide and the high ridge to the east. The type locality of the subspecies *galloti* (TLG) and *eisentrauti* (TLE) are given, and their distributions (*galloti*: G; intermediates: I; *eisentrauti*: E) are indicated by thin lines.

length of the fourth toe on the rear foot. The following scelation characters were recorded: the number of 1) gular scales, 2) collar scales, 3) transverse dorsal scale rows, 4) ventral scale rows from collar to vent, 5) femoral pores, 6) scales along the fourth toe of the rear foot. Bilateral measurements were taken on the right-hand side.

These features were recorded from 207 adult male and female specimens from 18 localities distributed across the island (Fig. 1). Those localities referred to as "southern" correspond to the range of Bischoff's (1982) southern subspecies and are numbered 2–6, 8, 12–14, 17, and 18. The localities were at altitudes varying from sea level to above the cloud zone 2,200 m. The 18 localities were treated as statistical groups and the sexes kept separate, except where stated.

The scelation characters were all independent, i.e., a low within-group correlation, but the body proportions measurements all increase with growth/size and are consequently within-group correlated. Independent size and shape components were obtained using multiple-group principal component analysis (MGPCA) computed across all 36 (18 + 18) groups. MGPCA has the advantage over ordinary principal component analysis in that it does not confuse the within- and between-group variation

when several groups are used but, rather, gives the pooled within-group components (Thorpe, 1983; Thorpe and Leamy, 1983, and references therein). The resultant within-group components were subject to a one-way analysis of variance, separately for each sex, to detect geographic variation. The mean score for each group, per component, was computed.

Canonical variate analysis (CVA) was run on all 36 groups to summarize the between-group variation in all body-proportion characters. All the MGPCA scores were used as input for the CVA, as it gives the same results as using all the characters but allows an assessment of the contribution of the size and various shape components. There is no reason for having (and no general tendency to have) the within-group components contributing to the between-group differentiation in proportion to the size of the associated within-group eigenvalues (Thorpe, 1983).

The geographic variation in individual scalation characters was tested by analysis of variance with the sexes both separate and pooled. Canonical variate analysis was run for all scalation characters separately for each sex to summarize the geographic variation in scalation.

Congruence between patterns of geographic variation (between sexes [for a given character, principal component, or canonical variate], between characters, between principal components, or between canonical variates) was assessed by a product-moment correlation coefficient between group means. No precise data were available for the climatic conditions at each sample locality. The correlations were computed between longitude, latitude, and altitude on the one hand and group means scores for individual characters, principal component scores, and canonical variates on the other hand. This was done as a preliminary attempt to reveal any pattern of geographic variation broadly associated with these geographic variables. Since significance is partly a function of sample size, a greater number of "significant" associations may have been revealed in these biological versus geographical correlations by using individuals in some cases rather than group means. However, the above procedure does allow

the primary patterns of association to be revealed, which is the aim of this study.

The correlations between these biological and geographical variables were computed across the total set of 18 groups. These correlations were also computed for just the 11 southern groups, so that altitudinal and latitudinal effects would not be confused. This was necessary because the localities are dispersed in such a way that the northern localities are of a lower altitude than several southern localities.

The geographic variation in character, principal components, and canonical variates was portrayed by contouring, using the Surface II algorithm (Sampson, 1978). These variables were coded on a 0–10 scale, and the contours were plotted at unit intervals. Where males and females have congruent patterns of geographic variation, the codes were added and recoded on a 0–10 scale so that only one figure was required.

RESULTS

Body Proportions

Size. — The MGPCA of body proportions revealed that the within-group component associated with the largest eigenvalue (90% of the within-group variation) was a general size component. This size component showed significant geographic variation for both sexes, but their patterns of geographic variation are not congruent ($r = 0.37$, $P > 0.05$). The geographic variation in both sexes is a mosaic of high and low values with no clear broad trend (Fig. 2A, B). Size is not significantly correlated to longitude, latitude, or altitude when group means are used (Table 1).

Head Shape. — The seventh MGPCA component expresses only a small proportion (0.26%) of the within-group variation but shows significant and congruent ($r = 0.80$, $P < 0.05$) geographic variation for both sexes. This component is clearly a head-shape component, as it contrasts high positive loadings for head width and length, with high negative loadings for head depth. It is a measure of dorso-ventral flattening of the head. Head shape is correlated with longitude (Table 1) in the south because it exhibits a WNW to ESE cline in this area (Fig. 2C), the populations in the west tend-

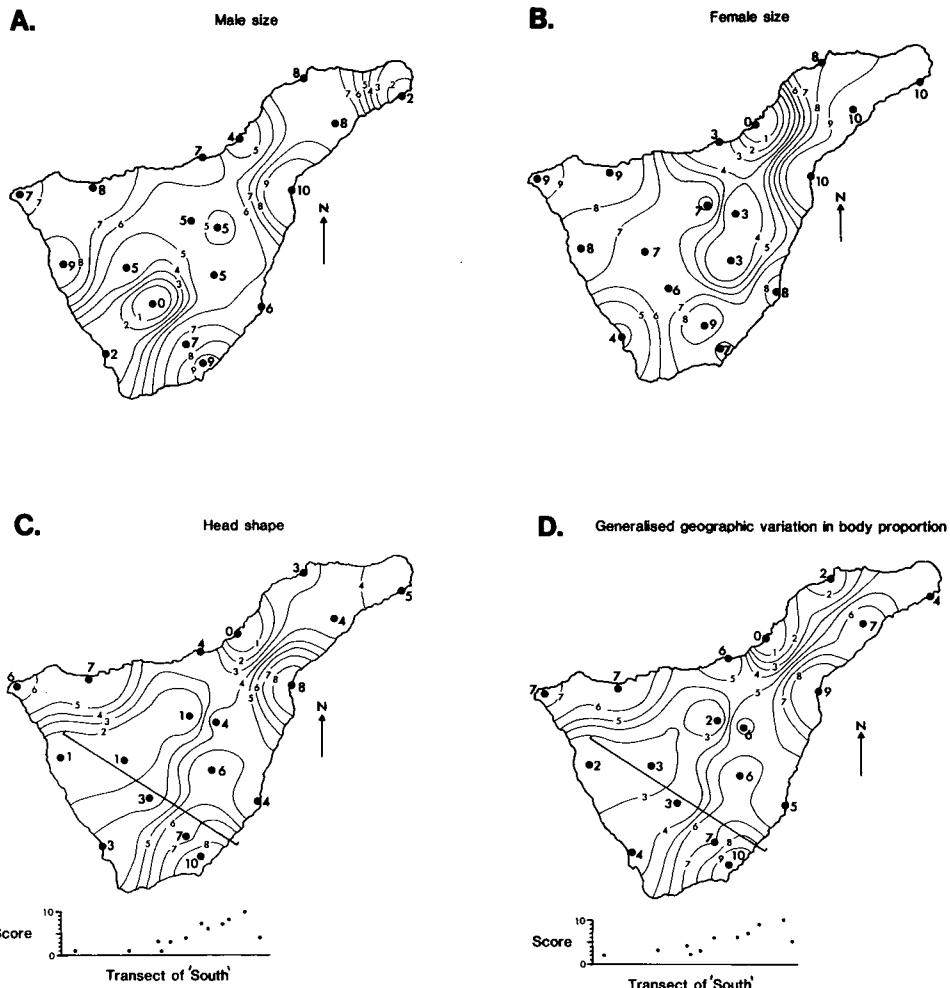


FIG. 2. Facets of the body proportions. Sample means, rounded to integers on a 0–10 scale in bold type and contour values in faint type. A (male size) and B (female size) show microgeographic variation in the “size” component from MGPCA. C (head shape MGPCA component) and D (generalized geographic variation in body proportions from CVA) show clinal variation along the indicated transect in the southern portion of the range.

ing to have shallower heads than those in the east.

Generalized Geographic Variation in Body Proportions.—Canonical variate analysis reveals both sexual and geographic variation. The first canonical variate (CVI) separates the sexes. This is to be expected, as males are larger than females and have proportionally larger heads and shorter bodies. The second canonical variate (CVII) summarizes most of the geographic variation and can be considered as representing the generalized geographic variation in body proportions. It is strongly influenced by head

shape ($r = 0.9$; Table 2) and shows a similar pattern of variation (Fig. 2D), i.e., a WNW–ESE cline in the south. The generalized geographic variation, summarized in this way, is congruent between the sexes ($r = 0.74$, $P < 0.05$) but is incongruent with the generalized geographic variation in scalation, both for males ($r = -0.01$, $P > 0.05$), and females ($r = -0.15$, $P > 0.05$).

Incongruence of Geographic Variation in Body Proportions.—The head shape and generalized patterns are congruent between sexes, but head shape and size do not have congruent patterns of geographic variation

TABLE 1. Significant correlations ($P < 0.05$) between biological characteristics (size = size component from MGPCA, head shape = head-shape component from MGPCA, generalized body proportion = geographic [II] variate from CVA on body proportions, generalized scalation = geographic variate [I] from CVA on scalation), and geographic factors. M = male, F = female.

| Character | Sex | Figure | Total set | | | Southern subset | | |
|-------------------------|-----|--------|-----------|----------|----------|-----------------|----------|----------|
| | | | Longitude | Latitude | Altitude | Longitude | Latitude | Altitude |
| Body proportions | | | | | | | | |
| Size | M | 2A | | | | | | |
| Size | F | 2B | | | | | | |
| Head shape | MF | 2C | | | | 0.65 | | |
| Generalized | MF | 2D | | | | 0.70 | | |
| Scalation | | | | | | | | |
| Dorsals | MF | 3A | 0.47 | 0.60 | -0.74 | | | -0.85 |
| Gulars | MF | 3B | | 0.51 | | | | |
| Femoral pores | M | 3C | | | -0.69 | | | -0.71 |
| Femoral pores | F | 3D | | -0.48 | | | | |
| Generalized | MF | 4 | | -0.60 | -0.77 | | | -0.89 |

with each other (Table 2); neither component, nor the generalized pattern (CVII), is congruent with the N-S subspecies (color pattern), the latitudinal or altitudinal climatic variation (based on group means), or the primary patterns of scalation. It may be possible to reveal some congruence given sufficiently large samples. The various facets of the body proportions, i.e., male size, female size, head shape, and generalized pattern all show an inverse correlation with altitude of between -0.4 and -0.5 in the south but, being based on group means ($d.f. = 9$), these values are not large enough to be significant. When the correlations are computed across all southern individuals, then a slight relationship between body proportions and altitude is apparent. Using individuals, the female body size is not significantly correlated with altitude ($r =$

-0.08, $P > 0.05$), but that of males is ($r = -0.25$, $P < 0.05$), with the higher altitude populations tending to have smaller individuals. Using individuals, there is also a significant (pooled within-sex) correlation between head shape and altitude ($r = -0.31$, $P < 0.001$) and between generalized geographic variation and altitude ($r = -0.29$, $P < 0.001$). However, in all cases, the magnitude of the correlation is low and may simply reflect an interaction between the primary pattern of geographic variation and the altitude of the sample localities.

Scalation

Dorsal Scales.—The scalation character with the strongest pattern of geographic variation (i.e., highest F value) is the number of dorsal scale rows. There is significant geographic variation for both sexes and significant congruence ($r = 0.82$, Table 3) in the pattern of geographic variation between the sexes. There are two facets to the geographic variation in dorsal scales, a latitudinal facet and an altitudinal facet (Table 1, Fig. 3A).

The number of dorsal scales is correlated with latitude ($r = -0.60$), the northern populations tending to have a greater mean number than the southern populations (Fig. 3A). There is quite a marked change over a short distance between northern populations 10 and 11 (95/98 scales) and the "southern" high-altitude populations 6 and 8 (82/87 scales), but elsewhere, insofar as

TABLE 2. Body proportions. Between-group correlations, indicating the extent of congruence in patterns of geographic variation for components and canonical variates that show significant geographic variation (critical value of $r = 0.468$ for $P = 0.05$). Character codes as for Table 1.

| Character (sex) | A | B | C | D | E |
|--------------------|------|------|------|------|------|
| A. Size (M) | — | | | | |
| B. Size (F) | 0.37 | — | | | |
| C. Head shape (M) | 0.49 | | — | | |
| D. Head shape (F) | | 0.28 | 0.80 | — | |
| E. Generalized (M) | 0.54 | | 0.92 | | — |
| F. Generalized (F) | | 0.36 | | 0.90 | 0.74 |

TABLE 3. Sculation. Between-group correlations, indicating the extent of congruence in patterns of geographic variation for characters and canonical variates that show significant geographic variation (critical value of $r = 0.468$ for $P = 0.05$). Character codes as for Table 1.

| Character (sex) | A | B | C | D | E | F | G |
|----------------------|------|------|-------|------|------|------|------|
| A. Gulars (MF) | — | | | | | | |
| B. Dorsals (M) | 0.70 | — | | | | | |
| C. Dorsals (F) | 0.58 | 0.82 | — | | | | |
| D. Ventrals (MF) | 0.16 | 0.11 | -0.03 | — | | | |
| E. Femoral pores (M) | 0.55 | 0.51 | | 0.27 | — | | |
| F. Femoral pores (F) | 0.46 | | 0.36 | 0.34 | 0.33 | — | |
| G. Generalized (M) | 0.72 | 0.95 | | 0.08 | 0.74 | | — |
| H. Generalized (F) | 0.67 | 0.85 | 0.96 | 0.10 | | 0.58 | 0.82 |

the distribution of sample localities allows, the latitudinal change appears more gradual. The largest number of dorsal scales (95–98) is found on the northern coast of the northeast peninsula (i.e., localities 1, 10, and 11), while the populations on the south-facing slopes and coast of this peninsula (localities 2, 7, and 9) have a smaller mean number of scales (92–94). Although there is variation within the northern and southern regions, the latitudinal variation is not a smooth north–south cline throughout the island but is rather a weak categorical, “stepped clinal” variation with a transition between the latitudinal categories (but see Thorpe [1985a] regarding terminology).

The number of dorsal scales is marginally correlated to longitude (Table 1), but this is a statistical artifact of the tendency for the populations to be arranged on a SW–NE axis, together with the fact that there is strong latitudinal variation on this character. When the variation within the north and within the south is considered independent of latitude, then no longitudinal variation is found (Table 1).

The number of dorsal scales also clearly varies with altitude across all populations (Table 1) and the southern subset ($r = -0.85$). Southern populations from high altitudes can have means as low as 82 scales (locality 6 at 2,200 m), while at sea level there are means of around 90 scales.

Gular Scales and Male Femoral Pores.—Two of the other sculation characters that show significant geographic variation have patterns of geographic variation that are significantly congruent to that of the dorsal scales. They are the gular scales (sexes combined) and the male femoral pores (Table

2). These characters do not have significant associations with both latitude and altitude, as do the dorsal scales, but each shows only one of the facets (Table 1). The number of gular scales shows a significant correlation with latitude ($r = 0.51$); the populations in the north generally have a mean of 43–44 scales while those in the “south” generally have a mean of 40–43 scales (Fig. 3B).

The number of femoral pores (Fig. 3C) in males is significantly correlated with altitude for all populations and the southern subset ($r = -0.71$). The high-altitude populations have fewer femoral pores (23–26) while low-altitude populations tend to have, in the south, more femoral pores (26–28). While the main feature of the variation in dorsal scales is latitude, and the main feature of the variation in male femoral pores is altitude, both may be influenced by altitudinal and latitudinal variation, even if the effects are not pronounced enough to reach the $P < 0.05$ level of significance with 18 locality means. Indeed the highest mean value for male femoral pores are found on the northern coast, and the lowest value for gular scales are found at high altitudes.

Female Femoral Pores.—The female femoral pores (Fig. 3D), while showing significant geographic variation, do not have a pattern congruent to that of males (Table 3). This feature shows significant latitudinal effects (Table 1), as the northern populations tend to have means of 26–27 pores while the southern populations usually have means of 23–26 pores. There is however, no obvious sharp transition between two distinct geographical categories for this character (Fig. 3D).

Ventral Scales.—The number of ventral

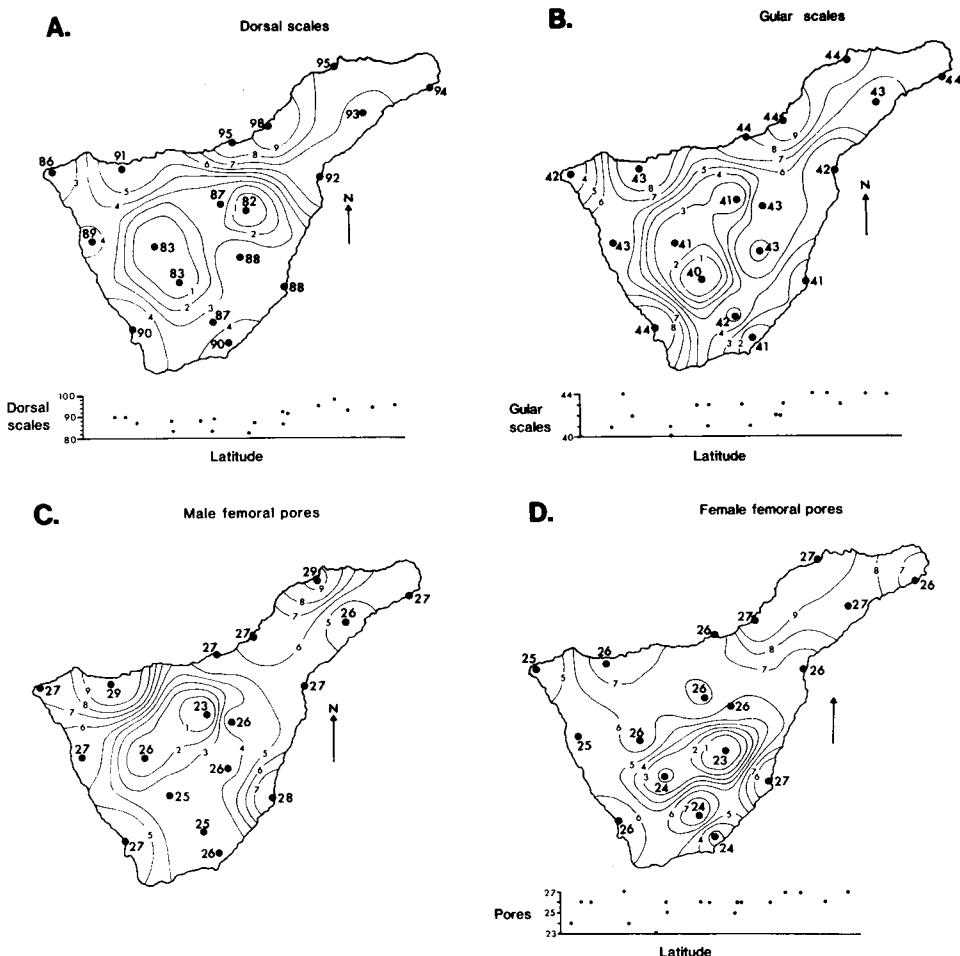


FIG. 3. Scalation. Sample means, in original counts, rounded to integer values, in bold type; contours, on 0–10 scale, in faint type. A (dorsal scales) shows both latitudinal (see transect) and altitudinal variation, B (gular scales) shows latitudinal variation, C (male femoral pores) shows altitudinal variation, and D (female femoral pores) shows latitudinal variation.

scales shows significant interlocality variation (sexes combined), but the pattern of geographic variation is not correlated with any other character or any geographic variable. The range of variation in the mean values for this character is low (29–31), and no broad trend in the pattern of geographic variation emerges, although locality 3 had noticeably fewer ventral scales along the body. This southern population also tended to have drastically fewer ventral scales across the width of the body in some specimens but this latter character was not used in this study.

Generalized Geographic Variation in

Scalation.—The generalized geographic variation, taken over the six scalation characters, is represented by the first canonical variate. The pattern of generalized geographic variation is congruent ($r = 0.82$, $P < 0.05$) between the sexes and shows both the latitudinal ($r = 0.60$) and altitudinal ($r = 0.89$) facets encountered in the individual characters, the altitudinal facet being most pronounced.

The latitudinal variation is categorical (stepped-clinal), rather than smoothly clinal (Fig. 4). The transition from northern to southern forms in the longitudinal center of the island (i.e., between localities 6 + 8 and

10 + 11) is quite sharp, as the northern forms are geographically close to the high-altitude southern forms. Although recent (unpublished) studies indicate that the distribution may be continuous in this area, the density is relatively low because of the dense cloud cover on the northern slopes. Consequently, it is possible that the differentiation between the northern and southern populations could be facilitated in this limited area by a belt of low population density. However, elsewhere, i.e., the eastern and western coasts, the transition appears more gradual.

In the west and center of the island, the position of the two categories conforms quite well to the range of the conventional subspecies (Figs. 1 and 4) described by Bischoff (1982), but in the east the transition zone is to the south of that indicated by the subspecies. Consequently, the type locality of the *galloti* subspecies (Fig. 1) appears to be in the transition zone between the categories (Fig. 4).

There is some geographic variation within the northern category, as the populations of the northwest-facing localities (1, 10, and 11) have higher scores than those of the southeast-facing localities (2, 7, and 9). However, it is the geographic variation within the southern category that is the most remarkable. The generalized geographic variation is strongly correlated with altitude in both sexes. The scores for populations from high altitudes are consistently lower (0–2) than those for populations from lower altitudes (3–5).

DISCUSSION

Patterns of Geographic Variation.—The primary patterns of geographic variation of *G. galloti* within Tenerife have been investigated using three character systems. The scalation and body proportions have been subject to quantitative analysis in this study, and the color pattern has been used, qualitatively, to erect subspecies (Bischoff, 1982). The geographic variation within this relatively small island is quite noticeable, as is the incongruence between some of the characters. The subspecies, based on color pattern, imply latitudinal categories; the scalation showed primarily latitudinal categories and altitudinal clines; and the

Generalised geographic variation in scalation

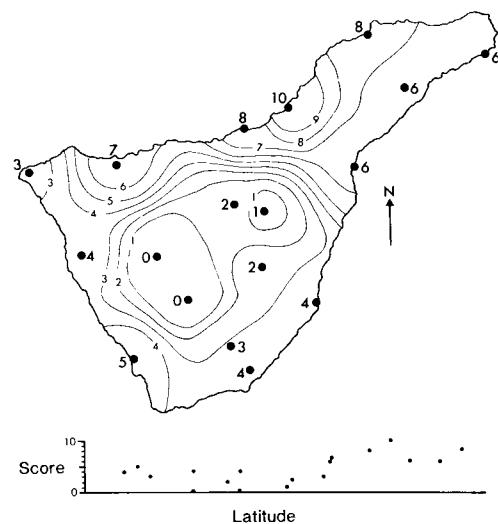


FIG. 4. Generalized geographic variation in scalation from canonical variate I, showing clear altitudinal and latitudinal variation. Sample means (rounded to integers) are in bold type, and contour values are in faint type.

body proportions showed primarily mosaic variation in size and clinal variation in head shape.

The difference in methodology does not allow a rigorous comparison between the color-pattern subspecies and the geographic variation in the other character systems, but an arbitrary comparison is still possible if one scores one of the subspecies as 1, the other subspecies as -1, and the intermediate as 0. When this is done, the correlation between the color-pattern subspecies and the generalized scalation is high ($r = 0.83$), because both patterns are latitudinal categories. However, there is disagreement in the position of these categories (i.e., population 2, population 9 and one type locality are "misplaced"), and the color-pattern subspecies give no hint of the profound altitudinal variation in scalation. Moreover, the color-pattern subspecies are completely unpredictable of the mosaic variation in size ($r = 0.04$ [males], $r = -0.04$ [females]), in spite of the fact that the subspecies are described as differing in size (Bischoff, 1982). Similarly, the color-pattern subspecies are completely unpredictable of the clinal variation in head shape ($r = 0.04$) and gener-

alized geographic variation in body proportions ($r = -0.19$).

There are problems associated with analyzing the geographic variation in size of unaged specimens with telometric growth. Even though no juveniles were used, the samples do contain specimens in a range of growth stages, so that a group mean is influenced by bias in the age structure of the sample. Tests were carried out using other parameters, e.g., maximum overall size and maximum SVL, but no broad geographic trends or congruence was found. If such a broad geographic trend in size does exist, it is too subtle to be revealed by the size of the samples in this study.

In general then, if we take, for the sake of argument, the subspecies as an accurate reflection of the geographic variation in color or pattern, there appears to be limited congruence between color pattern and the primary patterns of geographic variation in scalation and no congruence between the primary patterns of geographic variation in body proportions and those of the scalation or color pattern. Thorpe (1987) has previously pointed out that if subspecies are to be of any value they have to be predictive of the predominantly congruent patterns of variation in a wide range of character systems. Thorpe (1987) believes this is most likely to arise when phylogenesis, rather than adaptation to current ecological conditions, is the main cause of the patterns of geographic variation. This is the case in the phylogenetically caused geographic variation in the grass snake *N. natrix* (Thorpe, 1984, 1985a). In the current study, there are too few character systems (i.e., color, scalation, and body proportions) to test for widespread congruence between systems, but nevertheless it is useful to discuss the possible cause of these patterns, even though the process is difficult and often indecisive (Endler, 1983).

Possible Causes of Variation in Body Proportions.—There have been only a few studies on size adaptation of lizards to current ecological conditions. Gardner (1984) relates between-island size differences in green geckos (Gardner, 1984; Thorpe, 1986) to adaptation to defend permanent food resources, and Soulé (1966) also suggests that size in island populations of the agamid *Uta*

is associated with interspecific competition. This does not appear to be pertinent to the size variation of *G. galloti* within Tenerife.

Nevo suggested that geographic variation in size of agamids (Nevo, 1981) and frogs and toads (Nevo, 1972, 1973) in the Negev (Israel) is related to aridity, as a larger body size is better adapted for dryer conditions as a result of the lower surface area to volume ratio. In Tenerife, there is no indication that the more arid southern area (Fernandopulle, 1976) has larger lizards. Also, the interisland size differences of *galloti* within the western islands is not related to aridity, as the wettest island, La Palma (Fernandopulle, 1976), has intermediate-sized lizards. Moreover, the strong interspecific differences in size of *Gallotia* is the opposite of that predicted by Nevo's hypothesis (the dry eastern islands have the smallest lizards, and the wet western islands have the largest lizards).

Even though some of the body-proportion features are slightly correlated with altitude, the primary patterns do not seem to be associated with obvious climatic variables. Nevertheless, the variation, particularly the clear cline in head shape, is presumably maintained by current ecological conditions rather than being the by-product of a past event (e.g., vicariance), as no conceivable historical event explains the observed pattern. Similarly, size may be adapted for local conditions (e.g., food availability due to climate and agriculture) for which there is no clear geographic trend, given the number of localities sampled. The incongruence in the pattern between the sexes may result from size serving different functions in the sexes. Large size is an advantage in males for agonistic purposes but an advantage in females for egg-carrying capacity. The balance and intensity of advantage results in males being larger than females. This sexual dimorphism is best explained by natural selection on genetically based characters rather than environmental induction, because the sexes share the same environment but differ genetically (karyotypically) (E. Olmo, pers. comm.). Similarly, the pattern of between-group variation in body proportions in this and most other cases (e.g., Baker, 1980; Baker and Mooed, 1979; Johnston and Selander, 1971, 1973;

Fleischer and Johnston, 1982) has been interpreted in terms of selection even though the characters will be influenced by both genotype and environment. While one must bear in mind environmental influence, size and shape can be highly heritable (Atchley and Rutledge, 1980; Atchley et al., 1981), and the sexual dimorphism in size and shape in this case argues for a strong genetic influence.

Possible Causes of Variation in Sculation.—On the other hand, the primary patterns of geographic variation in the sculation are strongly correlated with altitude and latitude and with the concomitant climatic variation. However, in this case, it is difficult to see how the variation in sculation activity confers adaptive advantage in relation to specific environmental variables.

Seasonality, extent of diurnal rhythms, temperature, solation, and humidity all show geographic variation within Tenerife. While no systematic study of the climate is available, Fernandopulle (1976) and Huetz de Lemps (1969) give some pertinent information. Broadly speaking, there are hot dry "subtropical" conditions at low altitudes with arid or semi-desert conditions in the south, cooler humid conditions at middle altitudes with some dense fogs in the north, and bright conditions with sharp seasonal and daily contrasts in temperature at high altitudes. The lower altitudes, especially in the north, have low seasonal and diurnal rhythms in temperature while at high altitudes (over 2,000 m) there are marked rhythms, with frost and snow in winter. Consequently, the lizards can be active all year in the low altitudes but not at the high altitudes. Mean monthly temperature also varies with altitude and latitude. At altitudes of 0–250 m, this varies between 20–22°C in the north and 20–25°C in the south; at altitudes of 250–600 m, it is between 15–20°C in the north and 15–25°C in the south; and at higher altitudes, the latitudinal difference in temperature declines as does the temperature itself, until, above 2,500 m, the mean monthly temperature is around 10°C or less.

Aridity and solation are greater on the southern slopes than on the northern slopes. Fogs can occur at middle latitudes on the southern slopes. On the northern slopes

around 1,000 m, dense cloud banks occur permanently in the summer, but at higher altitudes the weather is sunnier and drier than this. It is apparent that there are profound latitudinal and altitudinal differences in climate within Tenerife.

Previous workers have suggested that adaptation to current climatic conditions has caused geographic variation in lizard sculation. When larger dorsal scales are more sculptured, they increase the surface area to volume ratio. Based on this, Soulé (1966) suggested that in hotter environments the island population of the agamid *Uta stansburiana* has fewer, larger dorsal scales to facilitate heat loss. He referred to geographic variation in other lizard species to support this, e.g., *Liolaemus* (Hellmich, 1951) and *Sceloporus magister* (Phelan and Brattstrom, 1955). Later, Soulé and Kerfoot (1972) extended this thesis by explaining geographic variation in scale size of the agamid *Sceloporus graciosus* in terms of adaptation to aridity. They argued that in regions with higher aridity there would be selection for more, smaller (hence less sculptured) scales, giving a lower surface area to volume ratio. Consequently, their hypothesis predicts many small scales in cool, dry regions and few large scales in hot, wet regions.

Horton (1972), based on his work on skinks, criticized several facets of Soulé and Kerfoot's (1972) approach, including the assumption that the surface area pertinent to desiccation increases with scale size. In *Gallotia*, at least between species, the larger dorsal scales of *G. atlantica* are heavily sculptured while the small dorsal scales of *G. galloti* are not. However, in Tenerife we are generally comparing cool, humid regions to hot, arid regions (rather than comparing cool, dry regions with hot, wet regions). Consequently, the direction of change in scale size in these Tenerife populations is not entirely predictable from Soulé's (1966) and Soulé and Kerfoot's (1972) thesis.

If one takes temperature as the pertinent factor, then the latitudinal geographic variation of dorsal scale size/number within Tenerife conforms to the above thesis, i.e., the hot southern area has populations with few large scales, while the cool northern area has

populations with many small scales. The limitation of this approach is self evident; if one takes desiccation as the pertinent factor, then the observed pattern is the opposite to what one would expect. It is not just the dorsal scales that show this trend but the scalation in general including female femoral pores. It is difficult to relate the number of female femoral pores to surface area to volume ratios or to explain their geographic variation on the basis of linkage to other scalation features, as the low within-group correlation of the scalation characters implies genetical independence.

The altitudinal component of the variation in scalation within Tenerife is extremely pronounced. In this case, the variation in dorsal scale numbers (fewer in higher latitudes) in relation to temperature runs opposite to that of the latitudinal variation. That is, it is the populations from cooler (higher-altitude) regions that have fewer scales. However, climatic factors other than temperature and humidity change with altitude; both diurnal and annual variation in temperature become more extreme in higher altitudes, and this may be pertinent.

Other facets of the scalation also show parallel altitudinal variation, i.e., male femoral pores and generalized scalation. Although the function of the male femoral pores is obscure (Cole, 1966) they are known to vary in size with seasonality. Why one should then require fewer femoral pores in a more seasonal environment is not apparent. However, the adaptive nature of the variation is perhaps supported by the fact that in males, where they are thought to be functional, they show strong altitudinal variation while in females, where they are smaller and thought to be nonfunctional, they do not show this pattern of variation. The altitudinal variation in scalation then has no obvious functional or adaptive significance. However, since no plausible explanation based on historical events or phylogenesis presents itself, this correlation between scales and altitudinal variation in climate appears most likely to be due to the scalation being adapted to current ecological conditions.

The latitudinal variation in scalation must be considered in light of possible historical events or phylogenesis. There have been

several reviews of the geology of Tenerife (Borley, 1974; Mitchell-Thome, 1976; Schmincke, 1976). The island consists of several areas of ancient rocks, especially Teno (northwest) and Anaga (northeast). Borley (1974) believes that "later volcanicity led to a merging of these initially separate regions." Volcanic activity continued, resulting in a large central volcano that collapsed to give the large, central Canadas crater through which Teide later erupted. The central eruptions that joined the ancient islands overlapped in time (Borley, 1974). Their eruption and the central Las Canadas rocks are dated at 0.6–2.0 million years ago (Schmincke, 1976; Mitchell-Thome, 1976). Tenerife has not been connected to any of the other current islands or the mainland and is separated from them by deep-water channels. Moreover, there are no very low-lying areas of Tenerife that would allow for the island to be segmented into subunits by Pleistocene sea-level changes. It is evident that Tenerife has been a single coherent island for a long period.

Bischoff (1982) has suggested that the junction of the ancient Anaga and Teno islands by the volcanic activity between them caused the once-separate populations living on these islands to meet, thereby explaining the existence of two parapatric forms on Tenerife. This, however, is untenable, because such an event would result in a longitudinal (and not the observed latitudinal) pattern of geographic variation. Moreover, as indicated above, the volcanic activity that joined Teno and Anaga was itself very old, as the Canadas formation is up to 2.0 million years old (Borley, 1974). This is an excessively great period of time against which to consider the cause of the present, relatively restricted patterns of geographic variation. Such geographic patterns can develop very quickly, i.e., in less than 100 years (Johnston and Selander, 1971, 1973; Baker, 1980; Baker and Mooed, 1979). Even the east–west patterns of speciation and incipient speciation in Europe due to Pleistocene events (Thorpe, 1979) may only be measured in tens or hundreds of thousands of years.

A second "historical" hypothesis of temporary vicariance within Tenerife due to recent sea-level changes is not plausible, as

the sea would need to have risen over 600 m. However temporary vicariance due to locally unfavorable climatic conditions may be plausible. For example, dense "permanent" cloud cover on the northern slopes may have temporarily separated northern coastal and southern populations. Although recent (unpublished) evidence indicates that the lizard populations are currently present in most north-facing areas, the drop in population density in the areas with cloud cover may not be conducive to the eradication of northern and southern differences by gene flow.

A third historical hypothesis must also be considered. It is feasible that the species *galloti* arose on one of the other western islands and then spread to the remaining western islands by dispersal. If Tenerife were colonized twice from separate islands, e.g., in the north from La Palma and in the south from Hierro, this could cause the observed latitudinal categories. However, when this type of range expansion was tested by numerical phylogenetics, as in Thorpe's study of *Natrix* (1984) the preliminary results (Thorpe, 1985b) did not support this hypothesis.

It can be seen that, while the altitudinal variation is most likely due to adaptation for current ecology, the latitudinal variation could be either "historically" or "ecologically" caused. As with the body-proportions, these scalation characters can be influenced by both environmental and genetic sources. However, unlike the body proportions, the scalation is fixed from an early stage and is not subject to later environmental conditions. Moreover, clear differences in the scalation of closely related sympatric species and the observation that functional, male femoral pores show altitudinal variation, while nonfunctional, female femoral pores do not, indicates that the patterns are not determined primarily by environmental induction.

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LITERATURE CITED

- ATCHLEY, W. R., AND J. J. RUTLEDGE. 1980. Genetic components of size and shape. I. Dynamics of components of variability and covariability during ontogeny in the laboratory rat. *Evolution* 34:1161-1173.
- ATCHLEY, W. R., J. J. RUTLEDGE, AND D. E. COWLEY. 1981. Genetic components of size and shape. II. Multivariate covariance patterns in the rat and mouse skull. *Evolution* 35:1037-1055.
- BAKER, A. J. 1980. Morphometric differentiation in New Zealand populations of the house sparrow (*Passer domesticus*). *Evolution* 34:638-653.
- BAKER, A. J., AND A. MOOD. 1979. Evolution in the introduced New Zealand populations of the common mynah, *Acridotheres tristis* (Aves: Sturnidae). *Can. J. Zool.* 57:570-584.
- BINGS, W. 1980. Herpetologische studien auf Teneriffa (Kanarische Inseln). *Salamandra* 16:203-214.
- BISCHOFF, W. 1982. Die innerartliche gliederung von *Gallotia galloti* (Dumeril & Bibron 1939) (Reptilia: Sauria: Lacertidae) auf Teneriffa, Kanarische Inseln. *Bonn. Zool. Beitr.* 33:363-382.
- BORLEY, G. D. 1974. Aspects of the volcanic history and petrology of the island of Tenerife, Canary Islands. *Proc. Geol. Assoc.* 85:259-279.
- CARNERO, A., AND F. PEREZ PADRON. 1977. Los Lagartos de las Islas Canarias. *Bol. Ina. Crida (Canarias)* 11:248-253.
- CLOVER, R. C. 1979. Phenetic relationships among populations of *Podarcis sicula* and *P. melisellensis* (Sauria: Lacertidae) from islands in the Adriatic sea. *Syst. Zool.* 28:284-298.
- COLE, C. J. 1966. Femoral glands in lizards: A review. *Herpetologica* 22:199-206.
- ENDLER, J. A. 1983. Testing causal hypotheses in the study of geographic variation, pp. 424-443. *In* J. Felsenstein (ed.), *Numerical Taxonomy: Proceedings of a NATO Advanced Study Institute*. Springer-Verlag, N.Y.
- FERNANDOPULLE, D. 1976. Climatic characteristics of the Canary Islands, pp. 185-206. *In* G. Kunkel (ed.), *Biogeography and Ecology of the Canary Islands*. Junk, The Hague, Neth.
- FLEISCHER, R. C., AND R. F. JOHNSTON. 1982. Natural selection on body size and proportions in house sparrows. *Nature* 298:747-749.
- GARDNER, A. S. 1984. The evolutionary ecology and population systematics of day geckos (*Phelsuma*) in the Seychelles. Ph.D. Diss. Univ. Aberdeen, Aberdeen, U.K.
- GORMAN, G. C., AND Y. J. KIM. 1976. *Anolis* lizards of the eastern Caribbean: A case study in evolution. II. Genetic relationships and genetic variation of the *Gimmaculatus* group. *Syst. Zool.* 25:62-77.
- GORMAN, G. C., M. SOUË, S. Y. YONG, AND E. NEVO. 1975. Evolutionary genetics of insular Adriatic lizards. *Evolution* 29:52-71.

- HELLMICH, W. C. 1951. On ecotypic and autotypic characters, a contribution to the knowledge of the genus *Liolemaus* (Iguanidae). *Evolution* 5:359-369.
- HORTON, D. R. 1972. Lizard scale, size, and adaptation. *Syst. Zool.* 21:441-443.
- HUETZ DE LEMPS, A. 1969. Le climat de Illes Canaries. Tome 54, Publ. Facul. Lett. Sci. Hum. Paris Sorbonne, Paris, France.
- JOHNSTON, R. F., AND R. K. SELANDER. 1971. Evolution in the house sparrow. II. Adaptive differentiation in North American populations. *Evolution* 25:1-28.
- . 1973. Evolution in the house sparrow. III. Variation in size and sexual dimorphism in Europe and North and South America. *Amer. Natur.* 107: 373-390.
- MITCHELL-THOME, R. C. 1976. Geology of the Middle Atlantic Islands. Gebruder Borntraeger, Berlin, W. Ger.
- NEVO, E. 1972. Climatic adaption in the green toad (*Bufo viridis*). *Isr. J. Zool.* 8:1010.
- . 1973. Adaptive variation in size of cricket frogs. *Ecology* 54:1271-1281.
- . 1981. Genetic variation and climatic selection in the lizard *Agama stellio* in Israel and Sinai. *Theoret. Appl. Genet.* 60:369-380.
- PHELAN, R. L., AND B. H. BRATTSTROM. 1955. Geographic variation in *Sceloporus magister*. *Herpetologica* 11:1-14.
- SAMPSON, R. J. 1978. Surface II graphics system. Kans. Geol. Surv. Lawrence, Kansas.
- SCHMINCKE, H. U. 1976. The geology of the Canary Islands, pp. 67-184. In G. Kunkel (ed.), Biogeography and Ecology of the Canary Islands. Junk, The Hague, Neth.
- SNELL, H. I., H. M. SNELL, AND C. R. TRACY. 1984. Variation among populations of Galápagos land iguanas (*Conolophus*): Contrasts of phylogeny and ecology. *Biol. J. Linn. Soc.* 21:185-207.
- SOULÉ, M. 1966. Trends in the insular radiation of a lizard. *Amer. Natur.* 100:47-64.
- . 1967. Phenetics of natural populations. I. Phenetic relationships of insular populations of the side-blotched lizard. *Evolution* 21:584-591.
- SOULÉ, M., AND W. C. KERFOOT. 1972. On the climatic determination of scale size in a lizard. *Syst. Zool.* 21:97-105.
- THORPE, R. S. 1979. Multivariate analysis of the population systematics of the ringed snake *Natrix natrix*. *Proc. R. Soc. Edinburgh* 78B:1-62.
- . 1983. A review of the numerical methods for recognising and analysing racial differentiation, pp. 404-423. In J. Felsenstein (ed.), Numerical Taxonomy: Proceedings of a NATO Advanced Study Institute. Springer-Verlag, Berlin, W. Ger.
- . 1984. Primary and secondary transition zones in speciation and population differentiation: A phylogenetic analysis of range expansion. *Evolution* 38: 233-243.
- . 1985a. Character number and the multivariate analysis of simple patterns of geographic variation: Categorical or "stepped clinal" variation. *Syst. Zool.* 34:127-139.
- . 1985b. Alternative hypotheses for the causation of geographic variation in the western Canary Island lizard *Gallotia galloti*. *Bonn. Zool. Beitr.* 36: 533-539.
- . 1986. Evolution and character congruence in some western Indian Ocean *Phelsuma*: Numerical analysis of biochemistry, shape, and scalation. *J. Zool. Lond.* (A) 208:429-441.
- . 1987. Geographic variation: A synthesis of cause, data, pattern and congruence in relation to subspecies, multivariate analysis and phylogenesis. *Boll. Zool. In press*.
- THORPE, R. S., AND L. LEAMY. 1983. Morphometric studies in inbred and hybrid house mice (*Mus* sp.): Multivariate analysis of size and shape. *J. Zool. Lond.* 199:421-432.
- THORPE, R. S., K. WATT, AND M. BAEZ. 1985. Some interrelationships of the Canary Island lizards of the genus *Gallotia*. *Bonn. Zool. Beitr.* 36:577-584.
- WOODRUFF, D. S., AND S. J. GOULD. 1980. Geographic variation and speciation in Cerrion—A preliminary discussion of patterns and processes. *Biol. J. Linn. Soc.* 14:389-416.

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