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Alternative hypotheses for the causation of geographic variation in the western Canary Island lizard *Gallotia galloti*

by

R.S. Thorpe

Introduction

Broadly speaking one can divide the factors causing geographic variation into two categories. One set of factors, which can be referred to as 'current ecology', include natural selection for current physical and biotic conditions and current gene flow between populations. An example of this would be the temperature related differentiation of the house sparrow which has been recently introduced to North America (Johnston & Selander 1971). The other set of factors can be referred to as 'historical' factors as 'phylogenesis' and is exemplified by the east-west differentiation of the grass snake *Natrix natrix* (Thorpe 1979, 1984a). In this species complex the eastern and western forms are thought to have differentiated in S.E. and S.W. Pleistocene refugia and met along a secondary contact zone in central Europe. Consequently, the differentiation across the zone is a consequence of the phylogenesis in the species (historical events) and not directly due to a change in current physical biotic conditions across the zone.

Previous work (Thorpe 1984a) has indicated that the shape of numerical cladograms may be useful in helping indicate the causative factors. If extent of divergence is wholly or partly related to time of divergence then the cladogram should be the shape of an ordinary tree, i.e. early branches should be longer than recent branches. If this shape occurs then the causative factor is likely to be phylogenesis as there is no reason for ecological factors to create this pattern. On the other hand if there is no such relationship between length of branches and 'time of derivation' (Thorpe 1984a) then either phylogenesis or current ecology could have caused the differentiation. In order to clarify what hypothesized causes of the geographic variation in *G. galloti* (Thorpe, 1985a) are feasible the populations were subjected to a numerical phylogenetic analysis.

The main western islands inhabited by *G. galloti* are all fairly widely separated by stretches of deep water. The sea level changes during the Pleistocene were of insufficient magnitude to join them in this period. Moreover, rises in sea level during the Pleistocene were also of insufficient magnitude to submerge any of the major islands or split them into separate islands. For example, Bischoff

(1982) suggests that it is possible that north-east Tenerife was separated from the rest by a change in relative sea level because the land joining N.E. Tenerife to the rest of the island is only 1800 ft. above sea level. There is, however, no evidence that a relative rise in sea level of this magnitude has taken place recently (i.e. Pleistocene).

Bischoff (1982) also points out that La Palma and Hierro are the youngest islands at 2 million years old (Mitchell-Thome 1976) and therefore assumes that the species arose in Tenerife and have racially differentiated due to vicariance etc. in the 15+ million since the oldest part of the Canaries were formed. However, Bischoff tends to argue for certain geological events because of the pattern of divergence within *galloti* rather than the other way around. For example, he argues that Anaga (east) and Teno (west) were joined by the eruption of Teide because of the racial differentiation of *galloti* within Tenerife. Apart from the fact that this argument seems to be the wrong way around it ignores the fact that differentiation can be due to primary differentiation in situ (Endler 1977; Thorpe 1984a) and the fact that this possible event may have caused east-west differentiation on Tenerife but not the north-south pattern that is actually observed (Bischoff 1982; Baez & Thorpe 1985).

Since there is no published evidence to indicate that the different races of *galloti* have existed for many millions of years it is reasonable, as a starting point, to consider that *galloti* underwent the major differentiation into races with most of the main western Canary Islands largely as they are today. The two million years since the formation of the youngest islands is more than ample time for geographic variation to develop. Indeed Stanley's (1979) discussion of Kurten's (1968) research on European mammals indicates that 15 genera evolved in the Pleistocene (1.8 million years). Moreover, the major pattern of east-west racial differentiation and speciation due to ice age events in Europe could have taken place in much less time i.e. in units of 10,000's of years (Thorpe 1979) and research on birds introduced to the new world by man shows that geographic variation can develop in just a hundred years (Johnston & Selander 1971; Baker & Moored 1979). Consequently, it is reasonable to start with the working hypothesis that racial differentiation in *galloti* has taken place over the last tens or hundreds of thousands of years with the main western islands largely as they are today.

Materials and Methods

A single locality sample was taken from each of the main islands; Hierro, Gomera and La Palma and two from Tenerife, i.e. south Tenerife or north east Tenerife as in Thorpe (1985a). Twenty-four adjusted body proportions (Thorpe et al. 1985) and 23 scalation characters were recorded from males and the sample means computed. As an expedient for this preliminary study the means were range coded (Thorpe 1984b) and a Wagner tree computed from the population x character matrix. All twelve sampled populations from three species studied (Thorpe et al. 1985) were used so that an out-group root for *galloti* could be found.

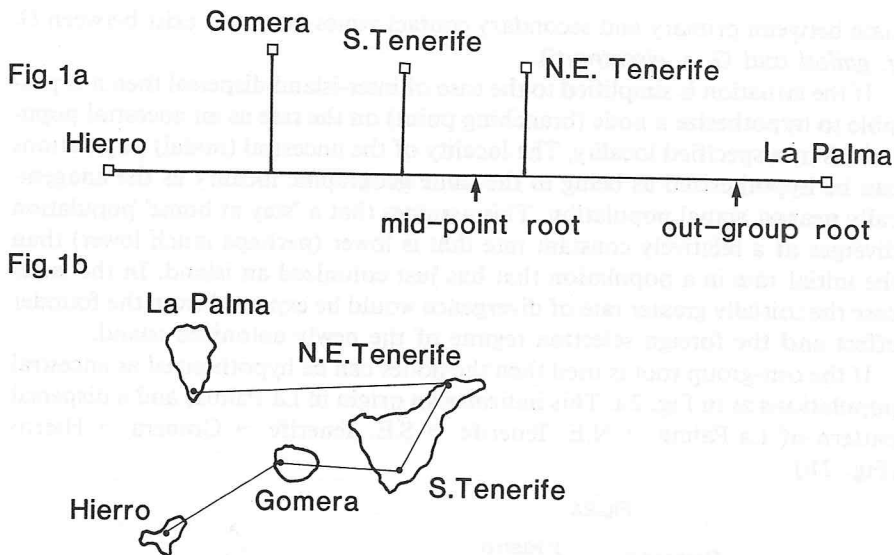


Fig. 1 a: Unrooted Wagner tree. Fig. 1 b: Line joining localities (solid circles) is the selection gradient implied by a "current selection" interpretation of the unrooted tree of Fig. 1 a.

Alternative hypotheses

(1) 'Current ecology' — Irrespective of whether the *galloti* tree is rooted by the outgroup (Fig. 1 a) or the mid-point then there is no link between extent of divergence and 'time' of divergence, i.e. the branches nearer the root are not longer. Consequently, one cannot reject the hypothesis that the pattern of geographic variation is primarily due to selection for current ecological conditions. That is, a selection gradient between the two extreme populations, i.e. Hierro and La Palma, could exist that results in the pattern of geographic variation and explains the linkage of the samples on the tree in the order Hierro — Gomera — S. Tenerife — N.E. Tenerife — La Palma. Gene flow is unlikely to be important in the pattern of inter-island affinities as the islands are all widely separated so rafting between islands could not be sufficient to be of any significant magnitude. Moreover, the sea between current main islands is far too deep for the islands to be have been joined to allow recent gene flow between islands.

(2) 'Phylogenesis' — The pattern of anagenesis in the cladogram could also reflect phylogenetic relationships. Since all the main islands occupied by *galloti* have been separated for a very substantial period of time the phylogenetic interpretation of the differentiation between islands is considered (in this first instance) to be on the basis of dispersal (presumably by rafting) rather than vicariance. The interpretation of the differentiation within Tenerife is more complicated but it can be possible for numerical phylogenetic analyses to differen-

tiate between primary and secondary contact zones (as could exist between *G. g. galloti* and *G. g. eisentrauti*).

If the situation is simplified to the case of inter-island dispersal then it is possible to hypothesize a node (branching point) on the tree as an ancestral population in a specified locality. The locality of the ancestral (nodal) populations can be hypothesized as being in the same geographic locality as the anagenically nearest actual population. This assumes that a 'stay at home' population diverges at a relatively constant rate that is lower (perhaps much lower) than the initial rate in a population that has just colonized an island. In the latter case the initially greater rate of divergence would be expected from the founder effect and the foreign selection regime of the newly colonized island.

If the out-group root is used then the nodes can be hypothesized as ancestral populations as in Fig. 2a. This indicates an origin in La Palma, and a dispersal pattern of La Palma → N.E. Tenerife → S.E. Tenerife → Gomera → Hierro (Fig. 2b).

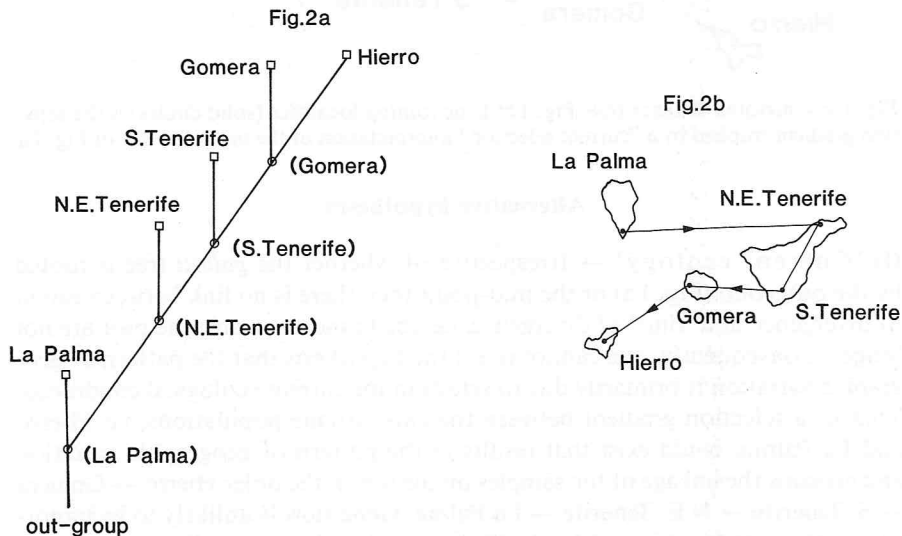


Fig. 2a: Out-group rooted tree. Taxa indicated by squares and the locality of the hypothesized ancestral populations (circles) given in brackets. Fig. 2b: Direction of dispersal hypothesized by a phylogenetic interpretation of the out-group rooted tree.

If the mid-point root is used then the nodes can be hypothesized as ancestral populations as in Fig. 3 a. This (Fig. 3 b) indicates the same pattern of interconnection between islands as when the out-group root is used (Fig. 2b). However in this case the island of origin is Tenerife (N.E. Tenerife is only marginally closer to the root than S. Tenerife) with colonization of La Palma from N.E. Tenerife and colonization of Gomera from S. Tenerife and subsequent colonization of Hierro from Gomera.

The 'dispersal' interpretation of the phylogenetic tree does not indicate an outright secondary origin of the *G. eisentrauti* (N.E. Tenerife), *G. galloti* (S. Tenerife) contact within Tenerife as it possibly could have. That is, it is possible to envisage an origin in La Palma, colonization of N.E. Tenerife from La Palma, colonization of Hierro from La Palma, Gomera from Hierro and S. Tenerife from Gomera. This would lead to a secondary contact between *G. galloti galloti* and *G. galloti eisentrauti*. However, both hypothesized pathways (Fig. 2b, 3b) are consistent with a primary origin of this zone *in situ*. It would be unwise to preclude a secondary origin from this zone within Tenerife on the basis of the preliminary analysis particularly since one can envisage a temporary vicariance of northern and southern populations within Tenerife (resulting in a secondary contact) that would be consistent with the colonization sequence of Figs. 2b and 3b.

The pattern of dispersal indicated by the out-group root (Fig. 2b) conforms to the past and current distribution of the species, *G. simonyi*. *Gallotia simonyi* has a relict distribution which may typify a late stage in the taxon cycle (Wilson 1961) where an early species has differentiated but has been out-competed by newer species and has consequently become extinct over much of its former range. In the west, *G. simonyi* has a small relict population on one cliff in Hierro and was until recently found on the small islets off Hierro and Tenerife (Baez & Bravo 1983). However, fossil evidence indicates that it previously had a wider western distribution across Hierro, Gomera and Tenerife (but not La Palma). The absence of *G. simonyi* on La Palma would allow its colonization by a population that evolved into *G. galloti* as suggested by the La Palma origin in Fig. 2a. The subsequent expansion of *G. galloti* out of La Palma into Tenerife, Gomera and lastly Hierro is consistent with the extinction of *G. simonyi* on the first two of these islands (i.e. Tenerife and Gomera) and the decline, stopping just short of extinction, on the last island to be colonized, i.e. Hierro. Man's

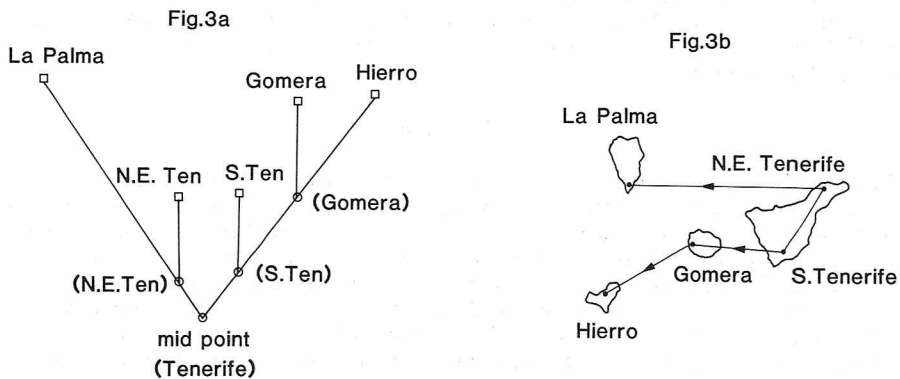


Fig. 3a: Mid-point rooted tree. Symbols as Fig. 2a. Fig. 3b: Direction of dispersal hypothesized by a phylogenetic interpretation of the mid-point rooted tree.

influence may have accelerated the decline of *simonyi* and this is discussed in Thorpe et al. (1985).

It should be noted that a decision between the alternative hypotheses requires a fuller analysis of the character changes between the populations. A wider range of characters need to be investigated including colour pattern characters. Also, the recoding and selection of characters used in the construction of a Wagner tree need to take into account the different evolutionary rates in the characters (1984b). When this is done the 'anagenic' rates, upon which the decision depends, may be more reliable. Moreover, if evidence is produced that the races of *galloti* are atypically old (2–15 million years) then the geological changes in the western Canaries will have to be taken into account.

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Zusammenfassung

Fünf Populationen von *Gallotia galloti* (N-Teneriffa, S-Teneriffa, Gomera, La Palma, Hierro) wurden in einem numerischen Kladogramm zusammengefaßt, das auf 23 Schuppenmerkmalen und 24 angepaßten Körperproportionen basiert. Die Hypothese, daß ein Selektionsgradient von La Palma über N-Teneriffa, S-Teneriffa, Gomera, Hierro verantwortlich für das Muster der geographischen Variationen sei, konnte auf der Basis der Anagenesemuster nicht widerlegt werden. Die Hypothese einer Beziehung zwischen geographischer Variation und historischen Dispersionsvorgängen (Phylogenese) ist ebenfalls brauchbar. Wenn die Verzweigungspunkte des Kladogramms als Populationen spezifischer geographischer Lokalitäten genommen werden, dann verbindet das Ausbreitungsmuster die Populationen in folgender Sequenz: La Palma — S-Tenerife — N-Tenerife — Gomera — Hierro. Der Verzweigungspunkt im innerartlichen Vergleich weist auf Teneriffa als Ausbreitungszentrum, während der Verzweigungspunkt im out-group-Vergleich auf La Palma weist.

Resumen

Cinco poblaciones, (de Tenerife norte, Tenerife sur, Gomera, La Palma, y Hierro) se unieron en un cladograma numérico basado en 23 caracteres de las escamas junto con 24 dimensiones corpóreas corregidas. La hipótesis de que una gradiente de selección de La Palma-Tenerife norte-Tenerife sur-Gomera-Hierro sea responsable del cuadro de variación geográfica no podía rechazarse en base al cuadro de anagénesis. La hipótesis de que el cuadro de variación geográfica se debe mayormente al pasado proceso de dispersión (filogénesis) es también posible. Cuando los nodos del cladograma reciben nombres de poblaciones en localidades geográficas específicas el cuadro de dispersión une las poblaciones en el orden siguiente, La Palma-Tenerife sur-Tenerife norte-Gomera-Hierro. La raíz central sugiere que el origen de la dispersión es de Tenerife mientras que la raíz "out-group" sugiere que el origen de la dispersión es de La Palma.

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R.S. Thorpe, Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen, AB92TN, Scotland.