

Some interrelationships of the Canary Island lizards of the genus *Gallotia*

by

R.S. Thorpe, K. Watt & M. Baez

Introduction

In the Canary islands there are, depending on the author, three or four extant nominal species of the endemic genus *Gallotia*, i. e. the large *simonyi* and *stehlini*, the typically 'medium' sized *galloti* and the typically 'small' *atlantica*. Their distribution and differentiation is of interest. Every island and substantial islet is occupied yet the level of sympatry between extant populations is extremely low, that is, the remaining small population of *simonyi simonyi* is sympatric with *galloti* and the population of *stehlini* on Gran Canaria may be sympatric with a small, possibly introduced, population of *atlantica* (Barquín & Martín 1982). Nevertheless the distribution of *atlantica* and *galloti* is completely mutually

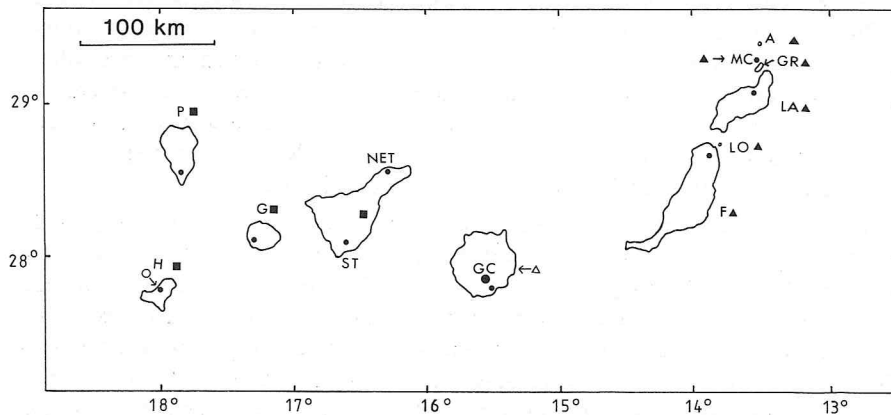


Fig. 1. Distribution of extant populations of *Gallotia* and locality samples. *G. galloti* (solid squares) is widespread in La Palma (P), North East Tenerife (NET), South Tenerife (ST), Gomera (G) and Hierro (H). *G. atlantica* is widespread (solid triangles) in Alesgranza (A), Graciosa (GR), Montana Clara (MC), Lanzarote (LA), Lobos (LO) and Fuerteventura (F) and is reported to have a small population (open triangle) on Gran Canaria (GC). The large lizard, *G. stehlini* is widespread on Gran Canaria (solid circle) and a small population of *G. simonyi* still (open circle) exists on Hierro.

exclusive and no island contains more than one species that is widely distributed across the island (Fig. 1). The fact that every island and major islet is occupied and contains one widespread species but no more than 1 widespread species may be due to interspecific competition. We think that it is unlikely that difference in maximum body size between species results in the avoidance of substantial competition as discussed in Arnold (1973). At least these body size differences exist in allopatry and are therefore not likely to be the result of direct character displacement to avoid interspecific competition.

Apart from the information about competition the distribution and differentiation of the species conform to some of the facets of Wilson's (1961) taxon cycle. *G. atlantica* is presumably a 'new species' as it has a widespread, complete, distribution (i. e. all the eastern islands) with relatively little racial differentiation (Thorpe 1985 a). *G. galloti* is at a later stage, it has a complete widespread distribution (all the western islands) but with greater racial differentiation (Thorpe 1985 a, b, c) whilst *G. simonyi* appears to be at the final stage with a relict extant distribution which is smaller than its previous distribution as indicated by the fossil record (Baez 1982; Hutterer 1985).

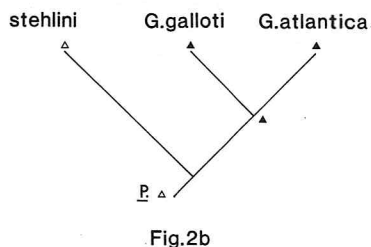
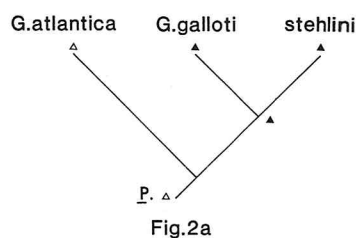
It is not clear to what extent this decline in the large lizards is due to natural evolutionary/ecological processes such as a competition with *galloti* and to what extent it is due to the influence of man. Both processes are likely to have contributed and both processes may well interact. For example, it is feasible that mans' activities, such as agriculture, benefit one species (i. e. *galloti*) at the expense of another (i. e. *simonyi*) enabling one species to outcompete the other. Any hypothesis to explain the decline of the large lizards that is based solely on mans' influence founders completely on the fact that on the island most heavily populated by man, Gran Canaria, *stehlini* is widespread and abundant, particularly so where man, his pets and his agriculture are most evident. A complete size range of *stehlini* is found in these areas including many very large, old specimens and this may render some hypotheses unlikely (Machado 1985). It is perhaps significant that *galloti* is not found on this island.

Since *galloti* and *atlantica* are not sympatric one cannot (Thorpe 1979) invoke the biological species concept as a criteria for species recognition. Moreover, some of the obvious diagnostic characters, such as the presence of a masseteric, and difference in maximum body size do not stand up to close examination. In any event, the existence of 'diagnostic' characters does not indicate specific status; subspecies may have diagnostic characters as well. Consequently, there is a *prima facie* case for considering whether the differences between *atlantica* and *galloti* are racial rather than specific.

Arnold (1973) and many subsequent authors treat *stehlini* as a subspecies of *simonyi* but fuller investigation may indicate that it warrants recognition as a separate species (there appear to be clear differences in dentition [Hutterer 1985] and head size). The status of the relationship between *G. simonyi simonyi* and *G. simonyi stehlini* is under review but not considered in this preliminary study.

Linked with this question of species recognition is how much racial variation there is within species compared to the level of differentiation between species. Also of interest is the phylogenetic relationship between the species, i. e. which two of the three nominal species under consideration are sister taxa. If we take *Psammodromus* as the outgroup (Arnold 1973), the evidence from conventional qualitative characters is contradictory. The shallow supratemporals and neck crease imply that *galloti* and *atlantica* are sister taxa whereas the small dorsal scales and usually clear masseteric imply that *galloti* and *stehlini* are sister taxa (Fig. 2).

Fig. 2. Some of the alternative cladograms for the genus *Gallotia*. *atlantica*, *galloti* and *stehlini* are linked in a cladogram which is out-group rooted by *Psammodromus* (P). Fig. 2a, *galloti* and *stehlini* appear as sister taxa defined by small dorsal scales and usually clear masseteric shield (solid triangle) whilst *atlantica* and the out-group have large dorsal scales and usually no clear masseteric shield (open triangle). Fig. 2b, *galloti* and *atlantica* appear as sister taxa defined by a clear ventral neck crease and shallow supratemporals (solid triangle) whilst *stehlini* and the out-group have no clear neck crease and have deep supratemporals (hollow triangle).



Materials and Methods

In this preliminary analysis of the interspecific relationships no account is given of the colour pattern or of qualitative differences. The numerical analyses are based on 23 quantitative scalation characters and 24 linear body proportions plus snout-vent length (SVL). The 24 linear proportions are adjusted by regression against SVL using the pooled within-group slope / (Thorpe 1976, 1983). For some analyses the SVL was used together with adjusted characters and for other appropriate analyses all 25 linear dimensions were used in unadjusted form.

Every widespread extant form from the main islands was represented by a sample taken from a single locality (Fig. 1). In Tenerife separate samples were taken from north-east and south of the island in light of the distinct differentiation (Bischoff 1982; Baez & Thorpe 1985) of *G. galloti* within this island. This gave 12 'groups' in all, six representing island populations of *atlantica*, five representing the subspecies of *galloti* and one representing *stehlini* from Gran Canaria. The giant Hierro lizard, *G. simonyi* was not represented and there was no outgroup comparison in the quantitative analyses. Sexes were kept separate throughout the study.

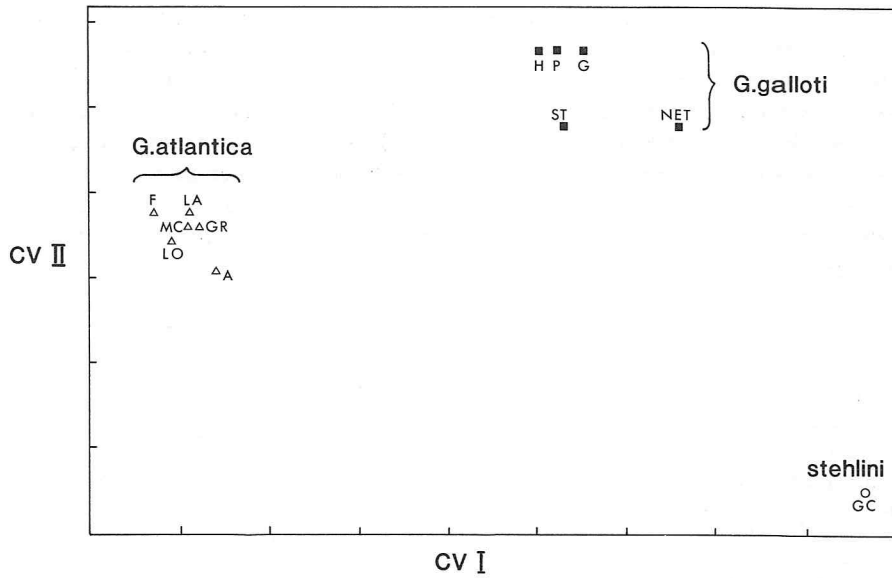


Fig. 3. Canonical analysis of female body proportions. Island locality symbols as for Fig. 1. *G. atlantica* samples are indicated by empty triangles, *G. galloti* samples by solid squares and the *stehlini* sample by an empty circle. Canonical variates (CV I and CV II) express 87 % of the variation and are marked in units of 2 within-group standard deviations.

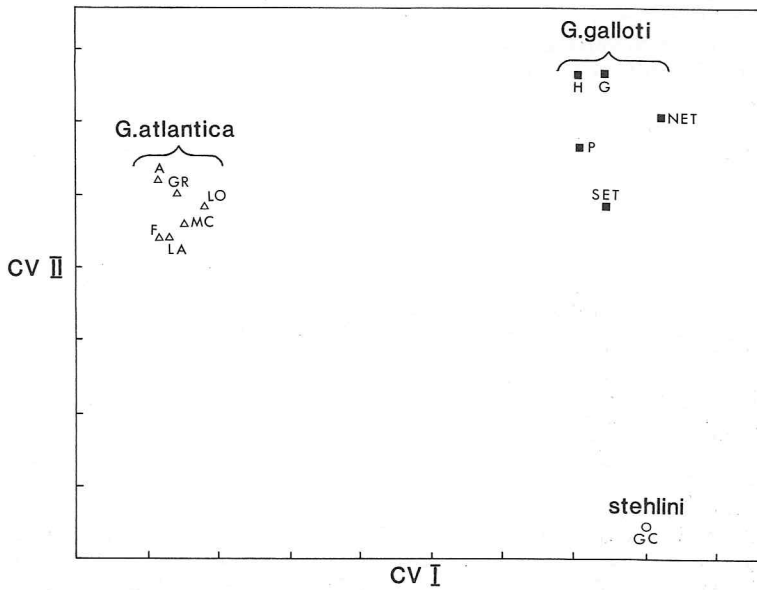


Fig. 4. Canonical analysis of female scalation. Canonical variates I and II express 88 % of the variation. Symbols as for Fig. 3.

Results

The relative similarity was measured by the Mahalanobis D^2 between the 12 groups and was summarized by canonical variate analysis. These methods take into account the within-group covariance between characters (Thorpe 1976, 1983). All canonical analyses, i. e. male body proportions, male scalation, female body proportions (Fig. 3) and female scalation (Fig. 4), show that the populations of *atlantica* form a compact cluster which is widely separated from the compact cluster of *galloti* populations. Similarly, all analyses show that *stehlini* is distinct from the other two species. These results are consistent irrespective of the statistical treatment of the body proportions, i. e. the inclusion or exclusion of snout-vent length and the use of raw or size-adjusted data. The D^2 values (Fig. 5) consistently show that the extent of divergence between species (i. e. *stehlini* and *galloti*) is greater than the divergence between allopatric races and subspecies within the species.

A preliminary numerical phylogenetic analysis was carried out by constructing a Wagner tree based on the range coded (Thorpe 1984) means of the 23 scalation plus 24 adjusted body proportions characters (Fig. 6). Mid-point rooting of this cladogram indicates that *galloti* and *stehlini* are sister taxa and *atlantica* is less closely related.

Discussion

From a phenetic standpoint the three forms considered appear to be good species. There is clearly greater divergence between species than between even the most differentiated races and this is different to the situation found in some other species complexes (Thorpe 1979, Lessios 1981).

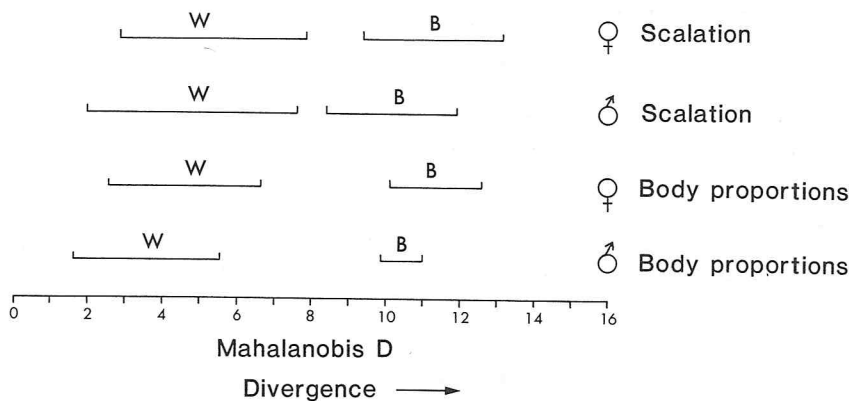


Fig. 5. Divergence within and between species of *Gallotia*. W is the range of racial divergence between island populations within *atlantica* and within *galloti* whilst B is the range of divergence between the species *galloti* and *stehlini*.

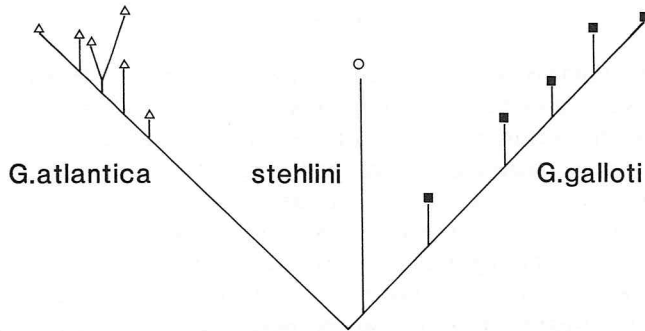


Fig. 6. Cladogram (mid-point rooted Wagner tree). Populations of *atlantica* are symbolised by empty triangles, those of *galloti* by solid squares and that of *stehlini* by an empty circle.

The numerical phylogenetic evidence that *galloti* and *stehlini* are sister taxa must be regarded as equivocal because of the unreliability of the mid point root, particularly when a coding method is used that does not take into account the different evolutionary rates of characters (Thorpe 1984). This point should be resolved when later studies use more appropriate character coding, character selection, a wider range of character types, larger samples and a full complement of species (i. e. including *simonyi*).

Acknowledgements. This research was funded by two grants from the Royal Society and the Consejo Superior de Investigaciones to R. S. Thorpe for visits to the Jardín Botánico 'Viera y Clavijo', Gran Canaria in 1983 and the Department of Zoology, University of La Laguna in 1984. R. S. Thorpe would like to thank Dr. Bramwell and Dr. Ibañez for the invitation to visit their respective institutions and for their support and would also like to thank the staff of ICONA in the Canary Islands and Madrid for processing the collection permits.

Zusammenfassung

Die Verbreitung und Inkonsistenz einiger konventioneller diagnostischer Merkmale bei zwei rezenten Formen von *Gallotia* (*galloti* und *atlantica*) sind Anlaß zu einer Untersuchung, ob es sich bei diesen um eigenständige Arten handelt. Phylogenetische und multivariate Analysen einer großen Anzahl von Merkmalen der Beschuppung und von Körperproportionen zeigen, daß die Unterschiede zwischen *galloti* und *atlantica* durchgehend größer sind als zwischen Populationen beider Formen; sie sind also „gute“ Arten. Es gibt einige, allerdings nicht eindeutige Hinweise darauf, daß es sich bei *galloti* und *stehlini* um Schwesterarten handelt, während *atlantica* mit beiden weniger nah verwandt ist.

Resumen

La distribución geográfica y la inconsecuencia de algunos caracteres diagnósticos convencionales ofrecen a primera vista razones para considerar si dos de las formas existentes de *Gallotia* (*galloti* y *atlantica*) son buenas especies. Análisis filogenéticos numéri-

cos y de variables múltiples de una gran cantidad de caracteres de las escamas y de dimensiones de cuerpo indican que estas dos formas son buenas especies fenéticas y filogenéticas. La diferencia entre especies es constantemente mayor que la máxima divergencia racial dentro de una especie para las poblaciones estudiadas. Hay unos datos filogenéticos equívocos que indican que *galloti* y *stehlini* son taxa hermanos mientras que *atlantica* tiene un parentesco menos estrecho.

Literature

- Arnold, E.N. (1973): Relationships of the Palaearctic lizards assigned to the genus *Lacerta*, *Algyroides* and *Psammodromus* (Reptilia: Lacertidae). — Bull. Br. Mus. nat. Hist. (Zool.) 25 (8): 289—366.
- Baez, M. (1982): Consideraciones sobre las características zoogeográficas de la fauna de Canarias. — Instituto de Estudios Canarios 50 Aniversario. Aula de Cultura de Exmo. Cabildo Insular de Tenerife, pp. 23—70.
- & R.S. Thorpe ((1985): Microevolution of the lizard *Gallotia galloti* within the island of Tenerife. — Bonn. zool. Beitr. 36:
- Barquín, J. & A. Martín (1982): Sobre la presencia de *Gallotia* (= *Lacerta*) *atlantica* (Peters y Doria, 1882) en Gran Canaria (Rept., Lacertidae). — Doñana, Acta Vertebr. 9: 377—380.
- Bischoff, W. (1982): Die innerartliche Gliederung von *Gallotia galloti* (Dumeril & Bibron 1939) (Reptilia: Sauria: Lacertidae) auf Teneriffa, Kanarische Inseln. — Bonn. zool. Beitr. 33 (2—4): 363—382.
- Hutterer, R. (1985): Neue Funde von Rieseneidechsen (Lacertidae) auf der Insel Gomera. — Bonn. zool. Beitr. 36: 365—394.
- Lessios, H.A. (1981): Divergence in allopatry: molecular and morphological differentiation between sea urchins separated by the Isthmus of Panama. — Evolution 35: 618—634.
- Machado, A. (1985): Hypothesis on the reasons for the decline of the large lizards in the Canary Islands. — Bonn. zool. Beitr. 36: 563—575.
- Thorpe, R.S. (1976): Biometric analysis of geographic variation and racial affinities. — Biol. Rev. 51: 407—452.
- (1979): Multivariate analysis of the population systematics of the ringed snake *N. natrix* (L.). — Proc. R. Soc. Edin. 78B: 1—62.
- (1983): A review of the numerical methods for recognising and analysing racial differentiation. — Numerical Taxonomy: Proc. of NATO ASI series G. (Ecological sciences) No. 1, ed. Felsenstein, J., Berlin, Heidelberg and New York (Springer-Verlag), pp. 404—423.
- (1984): Coding morphometric characters for constructing distance Wagner networks. — Evolution 38: 244—255.
- (1985 a): Extent of racial divergence in the eastern Canary Island lizard *Gallotia atlantica*. — Bonn. zool. Beitr. 36: 507—512.
- (1985 b): Relative similarity between subspecies of the western Canary Island lizard *Gallotia galloti*. — Bonn. zool. Beitr. 36: 529—532.
- (1985 c): Alternative hypotheses for the causation of geographic variation in the western Canary Island lizard *Gallotia galloti*. — Bonn. zool. Beitr. 36: 533—539.
- Wilson, E.O. (1961): The nature of the taxon cycle in the Melanesian ant fauna. — Am. Nat. 95: 169—193.

R.S. Thorpe, K. Watt, Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen, AB9 2TN, Scotland; M. Baez, Department of Zoology, University of La Laguna, Tenerife, Canary Islands.