

Origin, colonization, adaptive radiation, intrainsular evolution and species substitution processes in the fossil and living lizards of the Canary Islands.

L.F. LÓPEZ-JURADO¹ & J.A. MATEO²

¹*Departamento de Biología, Universidad de Las Palmas de Gran Canaria, Campus de Tafira, 35016 Las Palmas (Canary Islands, Spain).*

²*Estación Biológica de Doñana-C.S.I.C., Apartado 1056, 41080 Sevilla (Spain).*

Abstract: The Canary Island lizards constitute a monophyletic group which separated from the rest of the family shortly after the first islands of the archipelago emerged. Five living and at least one recently extinct species belong to the genus *Gallotia*. In addition, two of the living species, *Gallotia simonyi* and *Gallotia stehlini* have become extinct on Gomera and Tenerife, respectively. Juveniles of all species present tricuspid teeth. This character is preserved in the adults with changes to one degree or another in *G. galloti*, *G. caesaris*, *G. simonyi* and *G. goliath*. In *G. atlantica* there are only two cuspids and *G. stehlini* has 4 or more. It has been confirmed that in current species there is a direct relationship between the number of cuspids in the adults and the extent to which they are herbivorous. The number and arrangement of teeth on the pterigoides also presents some differences in terms of species: only one row in *G. atlantica*, *G. galloti*, *G. caesaris*, *G. stehlini*, *G. goliath* from La Gomera and the smaller *G. simonyi*. *Gallotia goliath* on other islands and the larger *G. simonyi* specimens present a lot of teeth in two rows. A model is suggested according to which the phenomenon of giantism in these lizards is related to favourable environments of recent volcanic origin, while the extinction of large species is associated with selective predation on the larger breeders by Man and by domestic animals.

Key words: Canary Islands, Lacertidae, lizard, evolution, giantism, extinction.

INTRODUCTION

The seven islands that make up the Canary Islands archipelago are situated from East to West with the nearest to the African coast, Fuerteventura, at less than 100 kms, and the furthest, La Palma, over 450 kms away (Figure 1). Distances between islands are variable, but they are relatively near to each other.

The winds on this archipelago generally come from the sea, with the northwesterly winds that make up the so-called Trade Winds predominating and blowing strongest in the summer. A southeasterly or easterly wind is also relatively frequent, bringing large quantities of fine dust from the Sahara, particularly to the South- and East-facing slopes of the islands (FERNANDO PULLÉ, 1976). The system of prevailing winds on the Canary Islands gives rise to a phenomenon crucial to an understanding of the biological processes: the formation of a cloud layer. This is caused by the wind from the sea, which, as it rises along the altitudinal gradient of the most mountainous islands, determines the differential climatic features of any one island.

As a result of this phenomenon, in the Canary Islands and in other Atlantic archipelagos, relict examples of ecosystems that were once numerous throughout the Mediterranean region have been conserved: the Laurisilva forests (See AXELROD, 1975). There were many of these

forests and their specialized transitional ecotones on the islands with more pronounced relief (all except Lanzarote and Fuerteventura) until the arrival of people approximately 2,000 years ago. On each island the disposition of these forests was determined by the direction of the trade wind, the geomorphological features and the relief in such a way that on islands like Tenerife they were arranged in long narrow strips, and, on other more or less circular islands, the upland parts were capped with continuous cover. (See Figures in LÓPEZ JURADO & MATEO, 1992).

However, in the scientific literature those islands that present the largest area of *larisilva* are usually wrongly identified as wet when, in fact, the high relative humidity is only maintained in the interior of the forest. Below the forest the environment is always dry (See, for example, LÓPEZ JURADO, 1992).

The Canary Islands are of different geological ages. Their volcanic origin caused them to take shape gradually in such a way that the most easterly islands, Lanzarote and Fuerteventura, are the oldest. The most westerly, La Palma and El Hierro, are the youngest (See ABDEL-MONEM *et al.*, 1971; ABDEL-MONEM, 1972; SCHIMINCKE, 1982; MAYER & BISCHOFF, 1991).

All the eastern islands and islets (Fuerteventura, Lanzarote, Lobos, Montaña Clara, Alegranza and Graciosa) were apparently (See the diagram suggested by MAYER & BISCHOFF, 1991) once joined and formed one

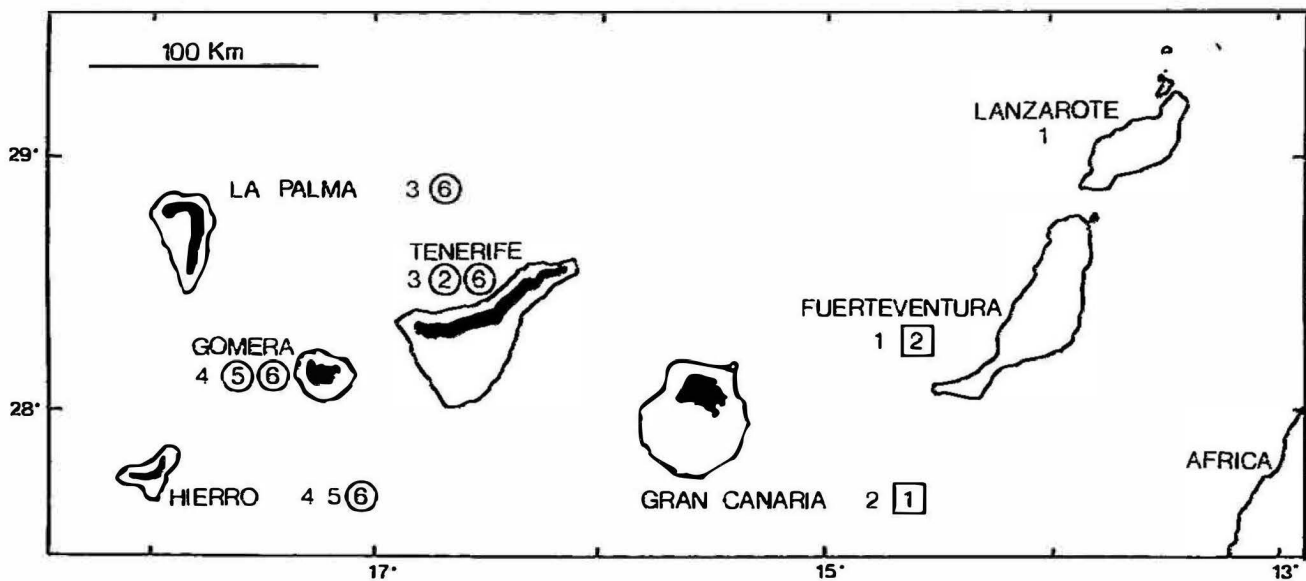


Figure 1: The Canary Island Archipelago. The areas that are potentially covered in laurisilva are shown in black. The numbers that appear with the name of each island are the species of the genus *Gallotia* that are present or have been present on each one of them. 1. *Gallotia atlantica* 2. *G. stehlini* 3. *G. galloti* 4. *G. caesaris* 5. *G. simonyi* 6. *G. goliath*. The circled numbers are the species currently extinct on an island. The numbers in a square represent recently introduced species.

large island quite close to the African coast.

Subsequently, Gran Canaria, Gomera and the Anaga peninsula (now the island of Tenerife) formed. An island later emerged in the area that is today occupied by the Teno peninsula. Anaga and Teno were subsequently joined following the eruption and formation of Teide.

El Hierro and La Palma were the last two islands to emerge. All these events began about 33 million years ago and finished about 2 million years ago (ABDEL-MONEM, *et al.* 1971; ABDEL-MONEM, 1972; SCHMINCKE, 1982; MAYER & BISCHOFF, 1991).

However, the volcanic nature of the islands means that this type of activity has never really finished. In fact, the lava flows are continually destroying and creating land on all the islands.

The fields of recent lava constitute what is known in the Canary islands as "malpaís": rocky areas clearly separated from the adjacent ecosystems. These "malpaíses" may appear in any part of the islands and the speed of their meteorization and biological colonization depends fundamentally on geographic position in relation to the prevailing winds and on altitude (See LÓPEZ JURADO & DELGADO LUZARDO, 1989).

On islands with a predominantly dry

environment and low altitude above sea level such as Lanzarote and Fuerteventura, the "malpaíses" constitute differentially wet environments. In fact, thanks to its porosity, the volcanic rock has the peculiar characteristic of trapping the humidity of the winds from the sea. At the same time, the rock cover on these lava areas efficiently prevents evaporation (LÓPEZ JURADO & DELGADO LUZARDO, 1989). In these conditions, when the weather has started to generate soil, the "malpaíses" contain the greatest density of invertebrate and land vertebrate species (reptiles and small mammals) on the whole island (LÓPEZ JURADO & DELGADO LUZARDO, 1989; LÓPEZ JURADO & MATEO, 1992). At the same time, within a limited space such as the island, the "malpaíses" represent a new "island" to colonize, and, as we will see later, during this process the Canary Island lizards experience evolutionary phenomena that are unique in the world (See LÓPEZ JURADO & MATEO, 1992).

ORIGIN OF THE CANARY ISLAND LIZARDS

In the past some authors recommended classifying the Canary Island lizards with other, very different, lizard species such as *Lacerta*

lepida, *Psammodromus algirus* or *Lacerta jayakari*, basing their argument on characteristics such as body shape, behaviour or sounds (PETERS, 1961; BÖHME, 1971; BÖHME & BISCHOFF, 1976). However, advances in knowledge have demonstrated that it is impossible to prove a close relationship between any of the living species of lacertidae and the Canary Island lizards (See LUTZ, BISCHOFF & MAYER, 1986, own data).

When it became known that the karyotype of the Canary Island lizards was clearly separate from other known lizards and that it was identical for the 3 most common Canary Island lizard species, this established the bases for the definitive separation of the genus *Gallotia* from any direct link with current lacertidae (CANO *et al.*, 1984; LÓPEZ JURADO *et al.*, 1986).

The latest immunological and molecular research carried out with these species suggests that the Canary Island lizards have been isolated from other continental lizards for between 27 and 35 million years, in other words, since the end of the Oligocene (LUTZ, BISCHOFF & MAYER, 1986; MAYER & BISCHOFF, 1991; own data), coinciding with the origin of the Canary Island archipelago (See ABDEL-MONEM *et al.*, 1971 and 1972, MITCHELL THOME, 1976, SCHMINCKE, 1982). At that time, many species of the family, especially the bigger ones and the more specialized, disappeared due to the profound change in climate (RAGE, 1986; AUGÉ, 1989), while other more generalist lizards underwent a great radiation (BUSACK & MAXSON, 1987).

All the fossil lizards found in European and North African deposits from the beginning of the Miocene were small and presented not very specialized dentition, with many almost undifferentiated teeth and generally three symmetrically spaced cusps, as occurs today in several species of the genus *Gallotia* (See COOPER, 1963, HUTTERER, 1985). *Miolacerta tenuis* from Central Europe, *Lacerta filholi* from the South of France or *Lacerta* sp. from Bni Mellal follow this description (ROCEK 1984; AUGÉ, 1989; RAGE, 1976). Consequently, although the similarity in dental features speculatively suggests that the origin of the Canary Islands lizards lies in one of the small lizard species that lived in southwest Europe or northwest Africa during this period.

Of all the species of the genus *Gallotia* described to date, four present tricuspid teeth (*G. galloti*, *G. caesaris*, *G. simonyi* and *G. goliath*). In one the adults present bicuspid teeth (*G. atlantica*) and another presents four or more

cusps (*G. stehlini*) (Figure 2). Our analysis of the Canary Island lizards will begin with a study of dental morphology in order to understand the colonization and evolution processes.

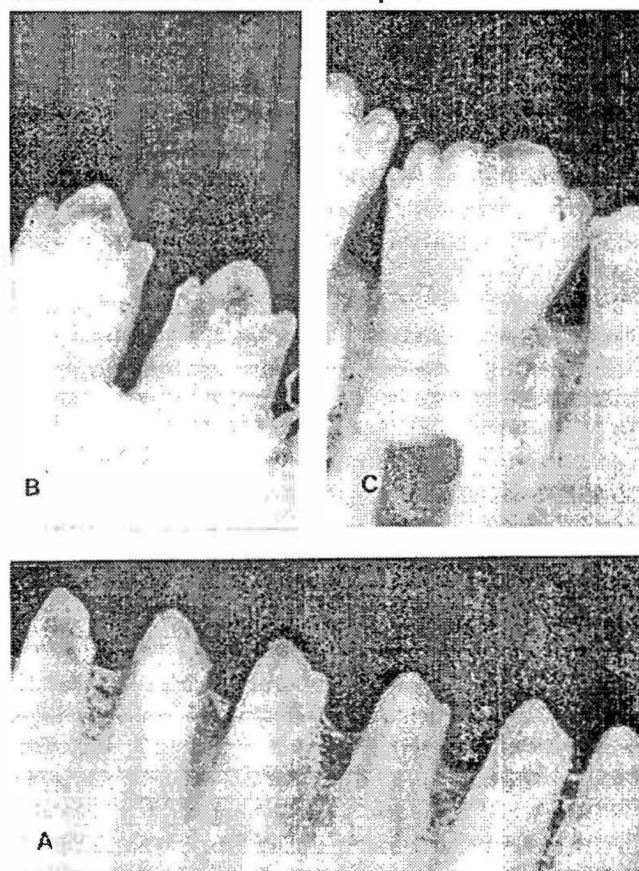


Figure 2: The dental morphology of species of the genus *Gallotia*. A. bicuspid teeth in *Gallotia atlantica* B. tricuspid teeth in *G. galloti* C. polycuspid teeth in *G. stehlini*.

CHARACTERIZATION OF EXTINCT FORMS ACCORDING TO BODY SIZE AND DENTAL MORPHOLOGY

To date all the lizards studied have had symmetrical tricuspid teeth at birth. The central cuspid is somewhat bigger than the lateral ones (COOPER, 1963, own data). As they develop they change towards bicuspid shapes typical of the teeth of almost all current lizards (*Lacerta*, *Podarcis*, *Psammodromus*, *Acanthodactylus*, *Eremias*, etc.), with some variations in the larger species such as *Lacerta lepida*, *Lacerta pater* or *Lacerta siculimelitensis* (See BÖHME & ZAMMIT MAEMPEL, 1982; ESTES & WILLIAMS, 1984) and in some *Gallotia* species at very different levels.

In the skeletons of both fossil and living Canary Island lizards we found variations that allow us to distinguish taxa on the basis of body

size, morphology of dental cuspids and the toothed region of the pterigoides.

On the basis of this, other authors described 3 possible forms of Canary Island lizards: *Gallotia goliath*, *Gallotia maxima* and *Gallotia* aff. *stehlini* (See MARTENS, 1942; BRAVO, 1953; LÓPEZ JURADO, 1985; own data). Besides this, two living species (*Gallotia simonyi* and *Gallotia stehlini*) are now considered extinct on different islands to those that they now inhabit (See HUTTERER 1985, own data). All the lizards that were already extinct had in common their large size.

However, the value of some conclusions, and even of some of the species and subspecies descriptions, may be considered rather doubtful since they were arrived at with little evidence and do not include a study of ontogenic variations or any other type of variation in the population. For example, it would be necessary to check that the occurrence of two large species such as *G. goliath* and *G. simonyi* on one island is not really a case of two different size classes of a single species. Until a more thorough study is carried out, we will assume, on the basis of data in the literature and on our own unpublished data, that *Gallotia goliath* was present on Tenerife (MERTENS, 1942, BRAVO, 1953), Gomera (HUTTERER, 1985), Hierro (IZQUIERDO *et al*, 1989) and La Palma (MERTENS, 1942, own data), and that *Gallotia simonyi* is apparently found as a fossil on Gomera (HUTTERER, 1985) and, of course, living on El Hierro.

Gallotia stehlini is one of the two living species whose distribution area has decreased. We found a fossil example of this species that nowadays lives only on Gran Canaria (we will not include the accidental introduction on Fuerteventura - See NARANJO *et al*, 1991). We found a fossil example from the Pleistocene on the Anago peninsula (Tenerife). It is a contemporary of most of the known fossils of *Gallotia goliath*, and was with *Canariomys bravoii* in the same deposit with no trace of *G. goliath*. As with the living form from Gran Canaria its teeth present 4 or more cuspids formed by divisions in the three original cuspids.

On Gran Canaria *Gallotia stehlini* became smaller at the time people arrived on the island, changing from about 35 cm SVL 2,000 years ago to 28 cm, which is what some current specimens measure (MATEO & LÓPEZ JURADO, 1992). However, the remaining bone characteristics that were analyzed had not undergone any changes since then.

The other living species is *Gallotia simonyi*.

This lizard recently disappeared from a small islet off the coast of El Hierro and today only survives on an almost inaccessible cliff on that island. Fossil and subfossil bones attributed to this species have also been found on La Gomera (HUTTERER, 1985). Their teeth are tricuspid and perfectly symmetrical with the central cuspid only a little bigger than the lateral ones.

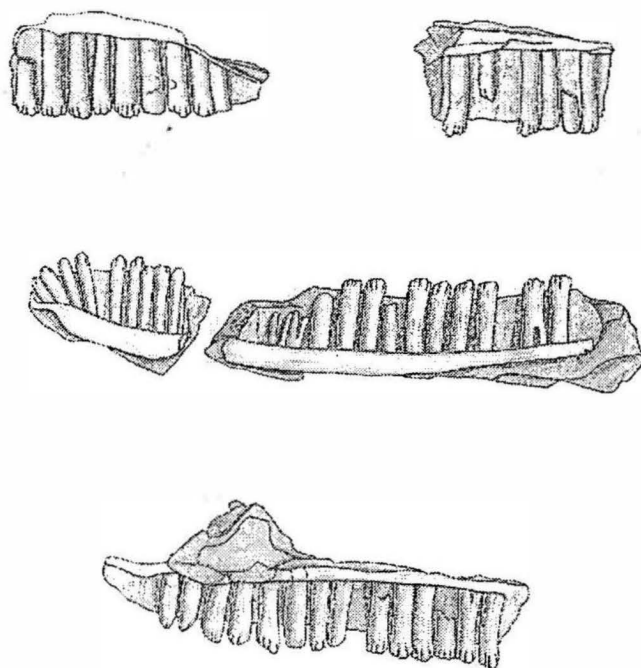


Figure 3: Fossil remains of *Gallotia* aff. *stehlini* from Taganan (North of Tenerife).

The largest Canary Island fossil lizard (*Gallotia goliath*) sometimes measures over 50 cm from head to tail and numerous remains have been found of specimens whose estimated size was between 40-45 cm head-tail (Figure 4). Their teeth always present 3 cuspids, but important differences in the robustness of the dental samples have been found. In fact, the following mandibula types are easily recognizable in the La Gomera deposits: relatively robust in the North of Tenerife and another more delicate type in the South of the same island (Figure 5). La Palma and El Hierro are different and should be considered separately.

Apart from robustness, these forms show certain differences in dental cuspids. The most robust present a very developed central cuspid to the detriment of the two lateral ones, which are sometimes vestigial. On the other hand, in the most delicate, all three cuspids are well-

developed although the central one is always the most developed. This character is much more noticeable in the fossil lizard population in the South of Tenerife. A large *simonyi* would be easy to identify among them.

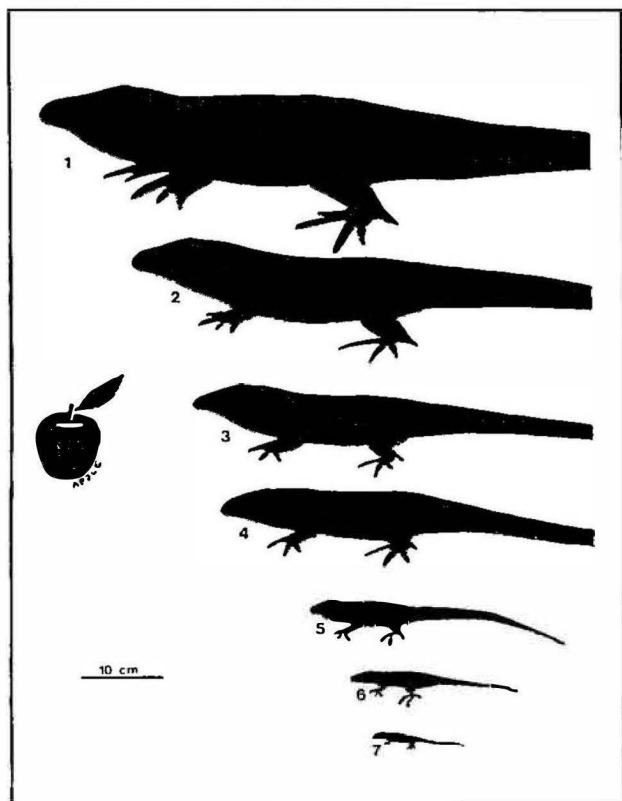


Figure 4: Relative size of the species of the genus *Gallotia*. 1. large specimen of the species *Gallotia goliath* 2. large *Gallotia stehlini* specimen prior to the arrival of people. 3. the biggest current *G. stehlini* specimen 4. maximum size of *Gallotia simonyi* at present 5. adult male *Gallotia galloti* 6. maximum size of *Gallotia caesaris* 7. maximum size of *Gallotia atlantica* from the islet of Montaña Clara.

Therefore, we found that, except for *Gallotia stehlini*, the dental morphology of the remaining forms of extinct or almost extinct Canary Island lizards are almost identical to that of the species considered as their possible ancestors. Following this criterion, the "*simonyi-goliath*" group of forms (living in the most recently formed islands) would have conserved some of the original characteristics of the colonizing species.

In the description of *Gallotia goliath*, MERTENS (1942) stated that in this species the parietal foramen was closed and that it presented about 18 teeth in each pterigoides arranged in two convergent rows. In his diagnosis of *Gallotia maxima*, BRAVO (1953) maintained that

in relation to *G. goliath* this last species was characterized by being bigger and by having up to 55 irregularly arranged pterigoides teeth and an open parietal foramen. However, the fact is that, apart from the types used in these two descriptions, until now on Tenerife only the remains of lizards with open parietal foramen have been found as in *Gallotia maxima* and with pterigoides teeth similar in number and arrangement to *Gallotia goliath*.

The interpretation of the pterigoides of the form described by Bravo may be made if we study the biggest current living specimen of all the lizards: *G. stehlini* on Gran Canaria. In most of the individuals of this species the pterigoides teeth are arranged in one row (Figure 6). However, there is a little studied phenomenon that consists of excessive and rapid growth in some males. These individuals become very big and present a large number of teeth on the pterigoides arranged around an irregularly shaped mound in exactly the same way as occurs in the holotype of *Gallotia maxima*.

All the above, and the fact that the parietal of the type of *Gallotia goliath* was broken at the level of the foramen suggests that *Gallotia maxima* and *Gallotia goliath* would, in fact, be the same species and that *maxima* should be considered as synonymous with *goliath*. This observation had already been made by GASC (1971) who added that *G. goliath* could be a giant form of *G. simonyi* judging by the similar morphology and by the large quantity of spongy tissue in the bones of the larger specimens. CASTILLA *et al* (1994) recently corroborated this hypothesis when they described the finding of mummified remains of *G. goliath*.

Gallotia goliath individuals in the North of Tenerife and El Hierro generally present two rows of pterigoides teeth, one usually being twice as long as the other although, in some cases, both are equal. In the South of Tenerife the morphology and arrangement of the pterigoides teeth is more varied as, in addition to the cases described, some smaller individuals have only one row.

On La Palma they all present two short rows of teeth on each pterigoides (Figure 6), including in the smaller individuals. On the other hand, on La Gomera almost all the pterigoides found presented a single row, including those whose estimated head-tail length exceeded 45 cm. Some specimens on the latter island had a second row made up of a few teeth as in the larger *Gallotia simonyi* specimens from the Caserio de Guinea (lizards eaten by the El Hierro aborigines).

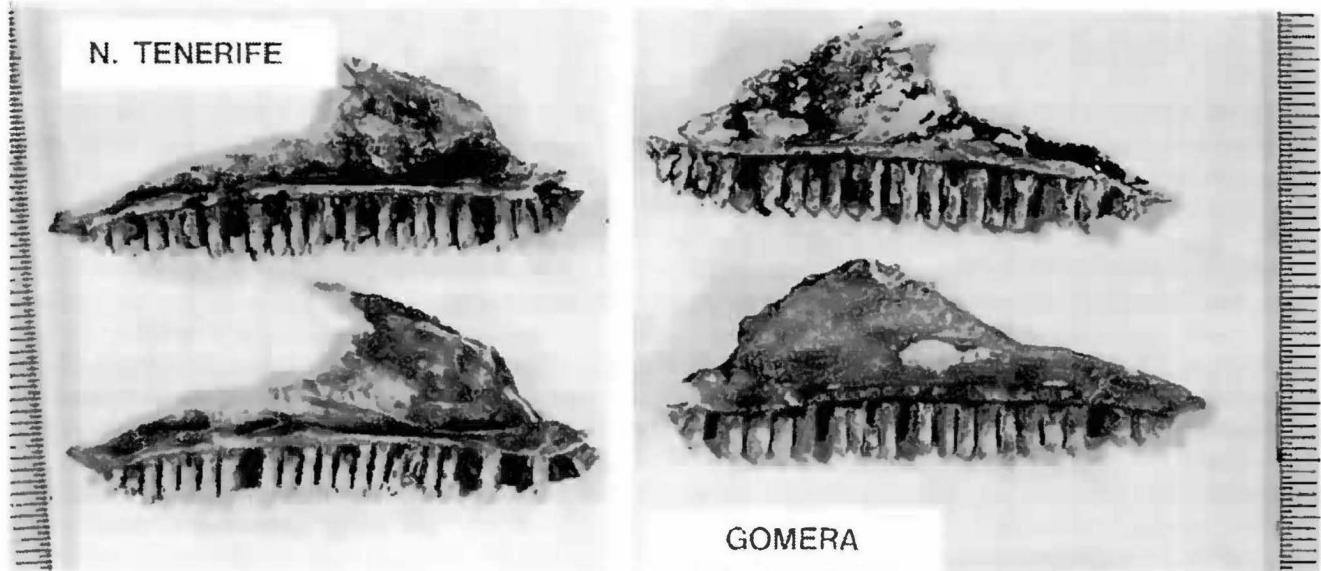


Figure 5: On the right, maxiliaries of *Gallotia goliath* from La Gomera (robust); on the left, maxiliares of the same species from deposits in the Cueva de la Arena (North of Tenerife).

THE COLONIZATION, ADAPTIVE RADIATION AND INTRAISULAR EVOLUTION PROCESSES.

Some authors have hypothesized about island colonization processes in the Canary Islands. For example, BISCHOFF & MAYER (1991), using immunological data, suggest that the large eastern island (Lanzarote and Fuerteventura and islets) must have been the first to be colonized from the continent by a pre-*Gallotia*. Subsequently and as a result of this, Gran Canaria would have been colonized by a pre-*stehlini*, the primitive island of Anaga (North of Tenerife) by a common precursor of *Gallotia galloti* and of *G. simonyi*. After this, the lizards of Anaga colonized the island of Teno (southwest of Tenerife) and with the later union of Teno and Anaga into the large island of Tenerife the conditions were right for both forms to mix, and they are now differentiated in the subspecies of North and South Tenerife (*G. g. galloti* and *G. g. eisentrauti*).

These hypotheses are merely speculations based more or less on some kind of evidence, but, even so, they do not explain the origin of *Gallotia goliath* in the strict sense or the *goliath-simonyi-galloti* relationship in the wider sense. Perhaps an approximation to what occurred at that time should consist of exposing the facts that exist today as a result of the colonization of the young volcanic ecosystems or "malpaises" on islands that are not very complex ecologically such as Lanzarote and Fuerteventura.

In the Canary Islands in the last few thousand years vulcanism has caused eruptions of

different magnitudes on almost all the islands. From an ecological point of view, the characteristics of these recently created neo-systems known as "malpaises" vary according to geographical location due to the effects of altitude and island geomorphology. The degree and speed of colonization fundamentally depend on climate, type of volcanic soil and time, in that order of importance.

The most easterly islands of the Canary Island archipelago are not very high above sea level. Fuerteventura, in particular, is 807 m and Lanzarote only 670 m above sea level. The slight elevation and proximity to the Sahara desert coast (about 100 kms away) explains why rain is very scarce, and also why the moisture-laden trade winds do not release it on these islands, unlike on the rest of the islands. As a result, on Lanzarote and Fuerteventura an arid ecosystem almost always prevails with very little diversity in both plant and animal populations. In this situation, the biomass is concentrated in the existing "malpaises" and maximum levels of biological diversity and population density are reached there (LÓPEZ JURADO & MATEO, 1992).

The *Gallotia atlantica* populations which colonize the young volcanic ecosystems (malpaises) undergo a rapid increase in body measurements and weight as well as a change in other phenotype characteristics (CASTROVIEJO *et al.*, 1985; LÓPEZ JURADO & MATEO, 1992).

Average body measurements vary from about 55 mm for males from Montaña Clara and Lobos to almost 90 mm for males from the La Corona "malpais" on Lanzarote with weights of between

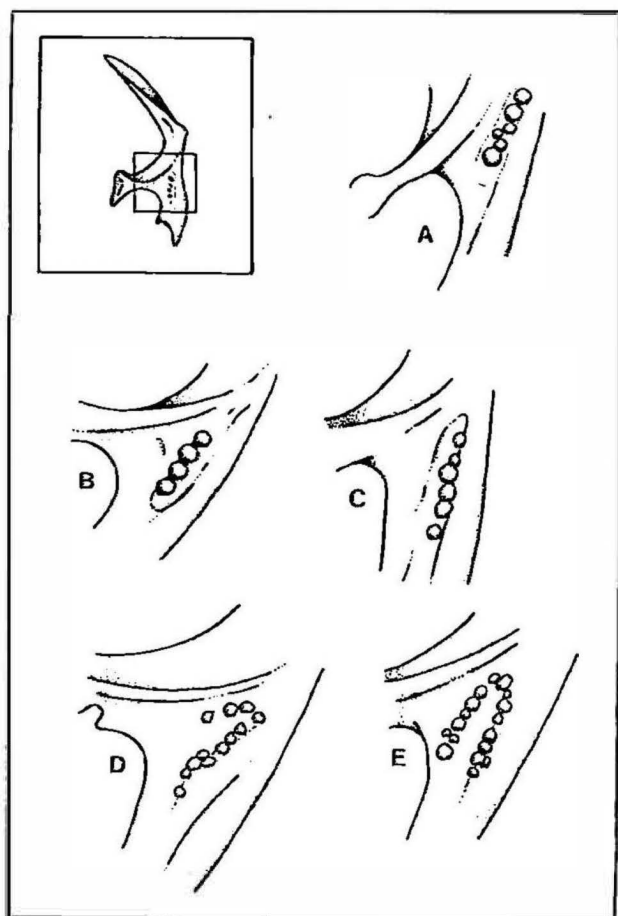


Figure 6: Arrangement of the teeth on the Pterigoides bone (inside the square). A. *Gallotia atlantica* from Fuerteventura, just one row. B. *Gallotia galloti* from Tenerife, just one row (*Gallotia caesaris* presents a similar arrangement).

7 and 35 grammes.

In addition, on Lanzarote and Fuerteventura several phenotypes associated with this species exist. The main difference between them is related to body size and the size, position and colour of the lateral spots (LÓPEZ JURADO, MATEO & GENIEZ, 1995). One of them consists of two rows of small round light green patches that generally extend from the scapular region to the inguinal. It is present both in juveniles and in males and females of all the populations on Lanzarote, Fuerteventura and the islets.

There is a second phenotype in which these green circular marks become bigger until sometimes they form a large green mark which extends along both flanks and even reaches the stomach, dorsolateral parts, limbs and lips. The third presents, in a similar way to the first, two rows of small blue spots. The fourth consists of a much more irregular series of spots (sometimes

just one in the scapular region) often joined up in a large dorso-lateral patch. The spots or patches are blue.

The most important thing is that the second and fourth phenotypes are only present in the "giant" males of the *G. atlantica* populations living in young volcanic ecosystems (to the northeast and west) of Lanzarote. It has not been observed in any recent hatchling, juvenile, subadult or female; only in some (not all) adult males of the two abovementioned populations. It is, therefore, a character linked to sex and size.

In fact, the taxa described (See CASTROVIEJO *et al*, 1985) constitute more or less the extremes of a clinal variation with a strong adaptive component for the lizard populations on Lanzarote island. The data from our own observations allows us to confirm that the maximum values for size are reached in young volcanic ecosystems and the lowest in areas that are geologically much older with few resources. Moreover, in volcanic areas, recent hatchlings are always bigger (LÓPEZ JURADO & MATEO, 1992).

Between both ecosystems, which can be considered extremes, there exist intermediate situations that are always linked to specific microclimatic conditions in such a way that nowadays in the *Gallotia atlantica* populations on Lanzarote one can see a true adaptive radiation as regards average lizard size, which is manifested throughout the old and recent volcanic ecosystems and through large expanses of sand and clay terrain dispersed over the whole island.

In this respect, the high correlation existing between *G. goliath* fossil remains and their physical location in young volcanic terrain should not be forgotten.

The clinal characteristics of the distribution of lizard populations on Lanzarote are in stark contrast to the monotony on an ecologically similar island such as Fuerteventura (CASTROVIEJO *et al*, 1985; BISCHOFF, 1985). Apparently, no great clinal variation as regards the characters described above (size, weight and phenotype) exists there despite the fact that different microclimatic situations, including young volcanic ecosystems, also exist.

What then causes the differences in patterns of morphological variation to be so pronounced in similar ecological environments? A close analysis of both islands indicates that in biological terms the only important difference consists of the absence on Lanzarote and adjacent islets of the skink *Chalcides simonyi*.

This omnivorous lizard can weigh 65 grammes and is especially numerous in the young volcanic ecosystems of Fuerteventura.

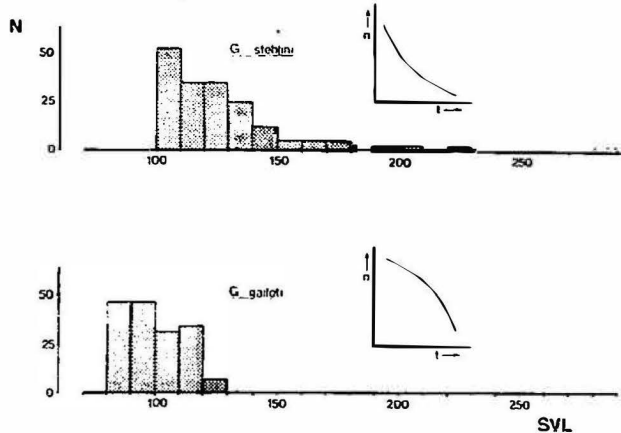


Figure 7: Size structure (frequency histograms) of the *Gallotia stehlini* adults in the Barranco del Taurito population (South of Gran Canaria) (above), and of *Gallotia galloti* adults on San Andrés (North of Tenerife).

On the eastern islands there is also a native species of insectivorous mammal (*Crociodura canariensis*) with very high population densities in the "malpaíses" where there are more arthropods available. Outside of the "malpaíses" it is only present on the islets of Montaña Clara and Lobos where the density of invertebrate prey is very low. On the former, the shrews feed on *Gallotia atlantica* and *Tarentola angustimentalis* which they paralyze beforehand with their poisonous glands (LÓPEZ JURADO & MATEO, 1995) (Figure 7). On this islet adult *G. atlantica* are by far the smallest sizes for the species (See CASTROVIEJO *et al*, 1985 & LÓPEZ JURADO & MATEO, 1992).

In this way, competition and predation appear to be important regulatory elements in lizard growth on these islands.

In short, it can be said that the adaptive radiation of the Lanzarote lizards is, without doubt, a direct result of the appearance of volcanic phenomena, and responds to subtle and different environmental stimulæ. It manifests itself due to the peculiarities of the most extreme ecosystems and fundamentally the phenomena of predation and competition at work there.

Consequently, the neo-volcanic character of the "malpaíses" and their geological recentness define the young nature of the lizard populations there, which must of necessity be descendents of the populations located on the periphery. This indicates that the selection pressures undergone by these animals underwent a very rapid process

of morphological change, increasing the intersexual differences already manifested by the original population. Therefore, it seems clear that the "malpaíses" do not actually constitute a barrier, but simply a new ecosystem to be colonized.

The problem lies in the fact that the temporary persistence of the "malpaíses" as differentiated ecosystems does not, in general, appear to be enough to complete the speciation process whose first stage of development takes place there. A generalized and well-distributed situation at the time of the volcanic events of this nature, which is not an unusual hypothesis in the context of volcanic islands like the Canaries, could, however, complete that process.

THE PROCESSES INVOLVED IN SPECIES SUBSTITUTION

Over the last 35,000 years at least on the eastern islands (Lanzarote and Fuerteventura) there has only existed one species of small lizard without any important variations in individual size or any other character having been noticed (MICHIAUX *et al*, 1991). On the other hand, over the last 2,000 years on Gran Canaria no extinctions have been recorded but the size of the biggest individuals has decreased considerably (MATEO & LÓPEZ JURADO, 1992), thus adapting to a process that appears to have been common in various island areas during the Holocene (PRIGILL, 1986).

Some of the 4,000 year old remains found in deposits in Gran Canaria correspond to individuals whose estimated head-tail length was over 35 cm. However, in deposits subsequent to the arrival of people (approximately 2,000 years ago), or between present day wild specimens it is very rare to find any over 25 cm SVL (two cases of captive lizards measuring 28 cm SVL are known - Figure 4).

However, on the rest of the western islands the situation was very different: all the large lizards became extinct, or are in a critical situation, as on El Hierro with *Gallotia simonyi* where there are less than 500 in the Wild (MACIADO, 1985). It would be meet to ask why the large specimens have disappeared or almost disappeared on the western islands while on Gran Canaria *Gallotia stehlini* can be found in almost every part of the island in densities that sometimes exceed 400 adults per hectare (unpublished data).

The answer appears to lie in the fact that in the western islands there are at least two species of lizard living at the same time, while in Gran

Canaria there was only one with very special characteristics.

Figure 7 shows the differences in adult size between a *G. stehlini* population from the South of Gran Canaria and a *Gallotia Gallotia* one from the northeast of Tenerife. This confirms that most of the *Gallotia stehlini* lizards scarcely reach 13 cm SVL as in *G. galloti*, but some are very different from the average values and sometimes reaching 22 cm STL. The latter have a more vegetarian diet (Figure 9) and make different use of space to the smaller lizards, to all effects, behaving like a different species (MATEO & LÓPEZ JURADO, 1992).

The arrival of people on Gran Canaria apparently gave rise to a reduction in size in the larger lizards due either to selective predation on the latter or through competition with the animals they brought (MATEO & LÓPEZ JURADO, 1992). Nevertheless, this has not affected the demographic viability of the populations since it left a very important part of the breeding population intact: lizards measuring 10 to 15 cm SVL.

The other large species about which we can still obtain data is *Gallotia simonyi*. The few individuals that still remain of this species behave very differently to *G. stehlini* as they only begin to breed after they have reached five when they measure over 15.5 cm SVL and the number of juveniles smaller than this is low (CASTENET & BAEZ, 1989; MACIADO 1985); although from our own data we deduce that sexual maturity is attained from three years old, at least for animals kept in optimum conditions in captivity.

All this allows us to suppose that the stability of this and other species of giant lizards from the western islands must have been based on the longevity and size of the individuals. The arrival of people on these islands, without doubt, had a very different effect from that on the Gran Canaria lizards since the differences in some breeding parameters such as age and minimum size at maturity and the presence of another smaller lizard of the same genus on these islands, which behaved like a competitor, drove them directly to extinction.

In lizards an increase in body size obviously brings with it some related advantages that have

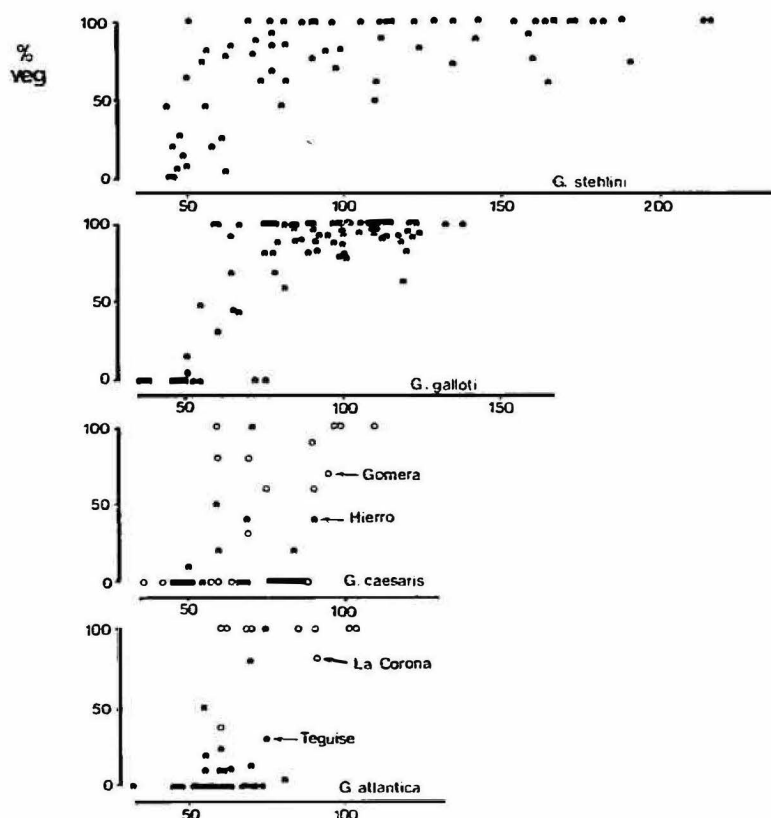


Figure 8: Percentage of vegetable matter in the total dry weight of the stomach contents of *Gallotia stehlini* specimens (several locations on Gran Canaria), *G. galloti* (San Andrés, Tenerife), *G. caesaris* (black circles: Parador of El Hierro; white circles: Playa Santiago on Gomera), and *G. atlantica* (black circles: Tegüise; white circles: La Corona "malpais").

repercussions on the demographic strategy of the population (STEARNS, 1984; SINERVO, 1990), or on the trophic physiology of the animal (POUGH, 1974), which, in this way, increases the efficiency with which it digests vegetables. However, it also involves some effects that may have a negative consequences: one of them is greater exposure of larger individuals to predation. Until the arrival of people, this effect must not have had serious consequences for the giant Canary Island lizards as there were no land predators on the islands and the birds of prey (*Milvus milvus*, *Buteo buteo* and *Falco tinnunculus*) do not appear to have been great specialists in prey that can weigh more than 4 kilograms. With the arrival of people and their domestic animals, their large size must have become a serious problem.

The three species of surviving large Canary Island lizard present diets with an important vegetarian component (See MACIADO, 1985, and Figure 8). On the other hand, both *Gallotia*

atlantica and *Gallotia caesaris* (Gomera and Hierro) where the adults are considerably smaller than those on Tenerife and La Palma, even though they are also omnivorous, prefer insects. However, within this framework there is a very interesting fact: the lizard population that lives in the La Corona "malpais" on Lanzarote, which, as we have seen, underwent a rapid growth process, reproduces the feeding characteristics described for large and medium-sized species since the individuals become vegetarian to a great degree in an environment like the "malpaises" where the conditions particularly favour it.

The giant extinct lizards like *Gallotia goliath* or the big *Gallotia stehlini* of the La Aldea deposit (See LÓPEZ JURADO, 1985; MATEO & LÓPEZ JURADO, 1992), were associated, at least at the beginning, with especially favourable environments (= differentially wet areas) such as the "malpaises" or the bottom of ravines, but they were phylogenetically very close to other populations of smaller lizards (perhaps what is today known as *Gallotia simonyi*), as occurs nowadays with *Gallotia atlantica*. According to this model, before people arrived on the western islands, there existed on all of them a varied mosaic of populations with lizards of different sizes and with equally different densities and geographical distributions.

REFERENCES

- ABDEL-MONEM, A., N.D. WATKINS, & P.W. GAST (1971): Potassium-Argon ages, volcanic stratigraphy, and geomagnetic polarity history of the Canary islands: Lanzarote, Fuerteventura, Gran Canaria, and La Gomera. *Am. J. Sci.*, 271: 490-521.
- ABDEL-MONEM, A.. (1972): Potassium argon ages, volcanic stratigraphy and geomagnetic polarity history of the Canary Islands: Tenerife, La Palma and Hierro. *Am. J. Sci.* 272: 805-825.
- AUGÉ, M. (1988): Une nouvelle espèce de Lacertidae (Sauria, Lacertilia) de L'Oligocène français: *Lacerta filholi*. Place de cette espèce dans l'histoire des Lacertidae de l'Eocène supérieur au Miocène inférieur. *N. Jb. Geol. Paläont. Mh.* 8: 464-478.
- AXELROD, D.I. (1975): Evolution and Biogeography of Madrean-Tethyan sclerophyll vegetation. *Ann. Missouri Bot. Gard.*, 62: 280-334.
- BISCHOFF, W. 1985. Bemerkungen zur innerartlichen Variabilität von *Gallotia atlantica* (Peters & Doria, 1882) (Lacertidae): *Bonn. Zool. Beitr.* 36 : 489 - 506.
- BÖHME, W. (1971): Über das Stachelepithel am Hemipenis Lacertider Eidechsen und seine systemetische Bedeutung. *Z. f. Zool. Syst. Evolut.*, 9 (3): 187-223.
- BÖHME, W. & W. BISCHOFF (1976): Das Paarungsverhalten der kanarischen Eidechsen (Sauria, Lacertidae) als systematisches Merkmal. *Salamandra* 12: 109-119.
- BÖHME, W. & ZAMMIT-MAEMPEL, G. (1982): *Lacerta siculimelitensis* sp. n. (Sauria: Lacertidae), a giant lizard from the late Pleistocene of Malta. *Amph. Rept.* 3: 257-268.
- BRAVO, T. (1953): *Lacerta maxima* n. sp. de la fauna continental extinguida en el Pleistoceno de las islas Canarias. *Estudios Geológicos del Instituto de Investigaciones Geológicas Lucas Mallada* 9: 7-34.
- BUSACK, S. & L.R. MAXSON. (1987): Molecular relationship among Iberian, Moroccan, and South African Lacertid lizards (Reptilia, Lacertidae): *Amph. Rept.* 8: 383-392.
- CANO J., M. BAEZ, L.F. LOPEZ JURADO & G. ORTEGA. 1984. Karyotype structure in the lizard *Gallotia galloti* in the Canary Islands. *J. Herpetol.* 18 : 344 - 346.
- CASTANET, J., & M. BAEZ (1991): Adaptation and evolution in *Gallotia* lizards from the Canary islands: Age, growth, maturity and longevity. *Amph. Rept.* 12: 81-102.
- CASTILLO, C., J.C. RANDO & JF. ZAMORA (1994). Discovery of mummified extinct giant lizards (*Gallotia goliath*) in Tenerife, Canary Islands. *Bonn. zool. Beitr.* 45: 113-124.
- CASTROVIEJO J., J.A. MATEO & COLLADO. (1985): Sobre la sistemática de *Gallotia atlantica* (Peters y Doria, 1882). *Doñana Acta Vertebrata*, Publicación Ocasional 1 : 1 - 85.
- COOPER, S.J. (1963): *The dental anatomy of the genus Lacerta*. MSc. Thesis : Bristol Univ., U.K. 95 pp.
- ESTES, R. & E. WILLIAMS (1984): Ontogenetic variation in the molariform teeth of lizards. *J. Vert. Pal.* 4: 96-107.
- FERNANDO PULLE, D. (1976): Climatic characteristics of the Canary islands. In Kunkel, G. (Ed), *Biogeography and Ecology in the Canary islands. Monogr. Biologicae* 30: 185-206.
- GASC, J.P. 1971. Les variations columnaires dans la région présacrée des sauriens; application a la reconstitution de *Lacerta goliath* Mertens. *Ann. Paleontol. Vert.* 57: 133-155.
- HUTTERER, R. (1985): Neue Funde von

- Rieseneidechsen (Lacertidae) auf der Insel Gomera. *Bonn. zool. Beitr.* 36: 365-394.
- IZQUIERDO, I., A.L. MEDINA & J.J. FERNANDEZ (1989): Bones of giants lacertids from a new site in El Hierro (Canary Islands). *Amph. Rept.* 10: 63-69.
- LOPEZ JURADO, L.F. (1992): Synopsis of the canarian herpetofauna. *Rev. Esp. Herp.*, 6: 107-118.
- LOPEZ JURADO, L.F., J. CANO & M. BAEZ (1986): Estudios sobre la herpetofauna canaria. I. El cariotipo de *Gallotia simonyi stehlini* y de *G. atlantica* spp. en poblaciones de la isla de Gran Canaria. *Amph. Rept.* 7: 259 - 279.
- LOPEZ JURADO, L.F. & A. DELGADO LUZARDO (1989): Importancia de los Malpais volcánicos como centros de evolución morfológica, biológica y ecológica de las biocenosis insulares. *ESF Meeting on Canarian Volcanism*, Lanzarote: 343 - 344.
- LOPEZ JURADO, L.F. & J.A. MATEO (1992): Two models of evolution in Canarian lizards based on the use of spatial resources. *Biol. J. Linn. Soc.* 46: 25 - 37.
- LOPEZ JURADO, L.F. & J.A. MATEO (1995): Evidence of venom in the Canarian shrew (*Crocidura canariensis*): immobilizing effects on the Atlantic lizard. *J. Zool. London*, in press.
- LOPEZ JURADO, L.F., J.A. MATEO & P. GENIEZ (1995): Los fenotipos y subespecies de *Gallotia atlantica*. *Boletín de la Sociedad Española de Herpetología*, en prensa.
- LUTZ, D., W. BISCHOFF & W. MAYER (1986): Chemosystematische Untersuchungen zur Stellung von *Lacerta jayakari* Boulenger, 1887 sowie der Gattungen *Gallotia* Boulenger und *Psammodromus* Fitzinger (Sauria; Lacertidae). *Z. zool. Syst. Evolut.* 24: 144-157.
- MACHADO, A. (1985): New data concerning the Hierro Giant Lizard and the Lizard of Salmor (Canary Island). *Bonn. zool. Beitr.* 36: 429-470.
- MATEO, J.A. & L.F. LOPEZ JURADO (1992): Study of dentition in lizards from Gran Canaria Island (Canary Islands) and its ecological and evolutionary significance. *Biol. J. Linn. Soc.* 46: 39-48.
- MERTENS, R. (1942): *Lacerta goliath* n. sp., eine ausgestorbene Rieseneidechse von den Kanaren. *Senck. Biol.* 25: 330 - 339.
- MICHAUX, J., R. HUTTERER & N. LOPEZ-MARTINEZ (1991): New fossil faunas from Fuerteventura, Canary Islands: Evidence for a Pleistocene age of endemic rodents and shrews. *C.R. Acad. Sci. Paris* 312: 801-806.
- MITCHELL-THOME, R.C. (1976): Geology of the Middle Atlantic islands. *Beitr. reg. Geol. Erde* 12: 1-382.
- NARANJO J.J., M. NOGALES & V. QUILIS (1991): Sobre la presencia de *Gallotia stehlini* en la isla de Fuerteventura (Canarias) y datos preliminares de su alimentación. *Rev. Esp. Herp.* 6: 45-48.
- PETERS, G. (1961): Die Perledeichse (*Lacerta lepida* Daudin) gehört zum Subgenus *Gallotia* Boulenger. *Mitt. zool. Mus. Berlin*, 37: 271-284.
- POUGH, F.H. (1973): Lizard Energetics and diet. *Ecology*, 54: 837-844.
- PREGILL, G.K. (1986): Body size of insular lizards: a pattern of holocene dwarfism. *Evolution* 40: 997-1008.
- RAGE, J.C. (1986): Extinctions chez les Squamates (Reptiles) à la fin de l'Oligocène en France. Adaptations et modifications de l'environnement. *Mém. Soc. Géol. France*, 150: 145-149.
- RAGE, J.C. (1976): Les Squamates du Miocène de Beni Mellal, Maroc. *Geol. Médit.* 3: 57-70.
- ROČEK, Z. (1984): *Lizards (Reptilia; Sauria) from the Lower Miocene locality Dolnice (Bohemia, Czechoslovakia)*. Academia Nakladatelství Československé Akademie Ved, Praha. 69 pp.
- SCHMINCKE, H.U. (1982): *Volcanic and chemical evolution of the Canary islands*. In *Geology of the Northwest African Continental margin*. Springer, Berlin: 273-306.
- SINERVO, B. (1990): The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution*, 44, 279-294.
- STEARNS, S. (1984): The effects of size and phylogeny on patterns of covariation in the life history traits of lizards and snakes. *Am. Nat.* 123: 56-72.