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Endemism, gigantism and extinction in island lizards: the genus *Gallotia* on the Canary Islands

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Abstract

In the Canary Islands five extant and two extinct giant lacertid lizards belonging to the endemic genus *Gallotia* are known. A comparative study of the living and subfossil specimens from the Western Canary Islands demonstrates that the extinct giant species *Gallotia goliath* and *Gallotia maxima* are synonymous with the living *Gallotia simonyi*. Characters formerly used in the diagnosis of the extinct species and subspecies fall within the range of intraspecific variation (ontogenetic and individual) of the living species. The only significant difference between living and subfossil populations of *G. simonyi* is size, and there is strong evidence to suggest that the reduction in size in living populations reflects shorter life expectancy, a factor that should be taken into account in the current conservation projects on this species.

Key words: subfossil lizards, Holocene, comparative anatomy, gigantism, conservation, *Gallotia*, Canary Islands

INTRODUCTION

Islands have always been attractive for the study of evolution and in particular of speciation because their ecosystems are relatively simple. In addition, they often show high levels of endemism, and organisms of very different origin may be found to have taken similar paths under similar insular conditions.

The Canary Archipelago is formed of seven main islands and a number of small ones. It is located off the north-west coast of Africa at a minimum distance of 90 km from the land. The age of the islands varies from east to west, with the oldest being Fuerteventura (22.5 My) and Lanzarote (15.5 My), followed by Gran Canaria (14–16 My), Tenerife (12–16 My), La Gomera (10 My), La Palma (2 My) and El Hierro (0.8 My) (Abdel-Monem, Watkins & Gast, 1971, 1972; Cantagrel *et al*., 1984; Ancochea, Fuster *et al*., 1990; Coello *et al*., 1992; Fuster *et al*., 1993; Ancochea, Hernan *et al*., 1994).

Today, three families of lizards live on the Canary Islands: lacertids, scincids and geckos. Lacertids are represented by the endemic genus *Gallotia* (Arnold, 1973), the taxonomy of which has received considerable attention (e.g. Boettger & Müller, 1914; Böhme & Bings, 1975; Klemer, 1976; Bischoff, 1982, 1985; Castroviejo, Mateo & Collado, 1985; Martin, 1985; Arnold, 1989; Thorpe, McGregor & Cumming, 1993*a*; López-Jurado, Mateo & Guillaume, 1997). The living species of *Gallotia* fall into two distinct size groups. A first group of small to medium-sized lizards (maximum snout–vent length, SVL, 67–136 mm) is formed by *G. atlantica*, present on the eastern islands, *G. galloti*, in Tenerife and La Palma, and by *G. caesaris*, on La Gomera and El Hierro. The second group of large lizards, 'giants' (SVL 201–232 mm), is formed by *G. stehlini*, a common species found throughout the island of Gran Canaria, and by *G. simonyi* which survives in limited numbers on a cliff on El Hierro and has recently been discovered in the Teno region of Tenerife (Anon., 1996*a–e*; Rando *et al*., 1997) (Fig. 1). During the last two decades, two species have been introduced to islands where they were not native: *G. atlantica* to Gran Canaria and *G. stehlini* to Fuerteventura (Barquín & Martín, 1982; Naranjo, Nogales & Quilis, 1991). Subspecific populations have been described for all species except for *G. stehlini*.

The phylogenetic relations between the living species are still uncertain, and virtually every combination of relationships between the species has been proposed

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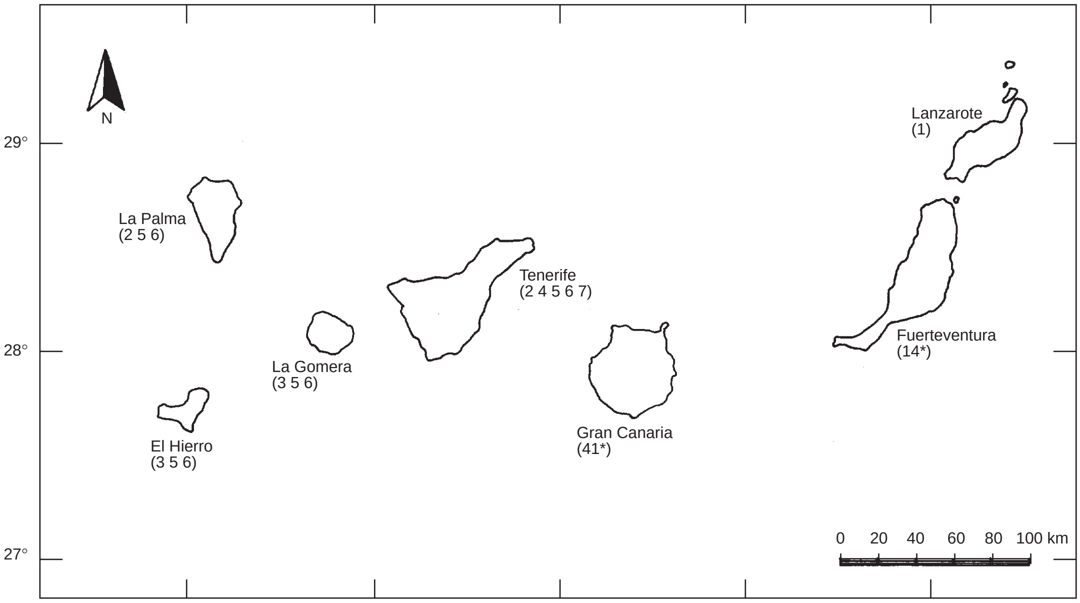


Fig. 1. The Canary Islands and the living and extinct lacertids described to date. 1, *G. atlantica*; 2, *G. galloti*; 3, *G. caesaris*; 4, *G. stehlini*; 5, *G. simonyi*; 6, *G. goliath*; 7, *G. maxima*; *, introduced.

(Thorpe, 1985*a*,*b*; Arnold, 1989; Mayer & Bischoff, 1991; Thorpe *et al.*, 1993*b*; González *et al.*, 1996; Rando *et al.*, 1997).

Although the current subfossil record of this genus goes back no more than 35,000 years, two extinct giant species have been described – *G. goliath* on Tenerife, La Palma (Mertens, 1942), La Gomera (Hutterer, 1985) and El Hierro (Izquierdo, Medina & Hernández, 1989), and *G. maxima* on Tenerife (Bravo, 1953). Subfossil material of living *G. stehlini* and *G. simonyi* has also been recorded in islands where they are now extinct, the first on Tenerife (López-Jurado & Mateo, 1995) and the second on La Gomera (Lehrs, 1909; Hutterer, 1985) and El Hierro (Izquierdo *et al.*, 1989). These large lizards were distributed on the western islands, reached even larger size than living forms, and apparently disappeared with the arrival of humans approx. 2000 years ago (Mateo & López-Jurado, 1992). According to this interpretation, five species (*G. galloti, G. stehlini, G. goliath, G. maxima* and *G. simonyi*) coexisted on Tenerife before the arrival of humans, with three on the small islands of La Gomera and El Hierro (*G. caesaris, G. simonyi* and *G. goliath*) (Fig. 1). This diversity is unexpectedly high. To complicate matters, the taxonomy of the extinct forms is also confused. Some authors have proposed that *G. maxima* is a junior synonym of *G. goliath* (Gasc, 1971; López-Jurado & Mateo, 1995), while others have suggested that both may be giant forms of the surviving *G. simonyi* (Pregill, 1986; Bischoff, 1998).

Resolution of this question requires a clear understanding of the range of inter- and intraspecific variation in the osteology of the living *Gallotia*. This information can then be used to evaluate the validity of the characters used by Mertens (1942), Bravo (1953) and Hutterer (1985) to diagnose their giant species.

MATERIAL AND METHODS

The material

The study of inter- and intraspecific variation in the osteology of living *Gallotia* spp. was made using post-natal series of both articulated and disarticulated specimens (Appendix 1). Hatchling through adults of both sexes were included for all the species except the rare *G. simonyi* where only 4 adult skulls (from La Fuga de la Gorreta, Hierro), 4 alcohol specimens (Natural History Museum, London) and 25 field specimens (Research and Breeding Centre of the El Hierro Giant Lizard and the Viceconsejería de Medio Ambiente de Canarias) were available.

Subfossil material was available from several fossil sites and from all the western islands. Material in the Department of Biology, Universidad de Las Palmas (BUPGC) and Museo de Ciencias Naturales de Tenerife (TNHM) is catalogued by fossil site. The number of fossil sites and the amount of material varies for each island, with Tenerife having most and La Gomera and La Palma, least. The subfossil material ranges from complete articulated skeletons, to isolated skulls and girdles, and then to disarticulated bones and bone fragments. The holotype and paratypes of *G. maxima* that were held in the Museo Nacional de Ciencias Naturales (MNCN) and in the Instituto de Geología de Madrid (ILM) are lost (Borja-Sanchiz, MNCN, pers. comm.), so we have had to rely on Bravo's (1953) original description.

Age data were only available for some fossil sites and ranged from Upper Pleistocene to Holocene (López-Jurado, 1985; García-Talavera, Paredes-Gil & Martín-Oval, 1989; Mateo & López-Jurado, 1992) (Appendix 1).

Method

To obtain ontogenetic series for the living species, we prepared further material (cleared/stained and dry skeletons) from existing collections using the methods described in Taylor (1967) and Zug & Crombi (1970), and also using bacterial cultures. Subfossil material was identified on the basis of comparison with the living species of *Gallotia*, and observations were made using stereomicroscopy and Scanning Electron Microscopy (especially for teeth). Statistical analysis of the data (correlations; *t*, *F*, ANCOVA and Scheffé tests) were made using the programs BMDP (Dixon, 1987), BMDP 6D (bivariate plots; Chasen, 1983) and BMDP 1V one way analysis of variance and covariance (Engelman, 1983). Maximum SVL of subfossil individuals was estimated by comparison with living *G. stehlini, G. galloti* and *G. caesaris* (Appendix 3). Skeletochronological analysis of subfossil femora used the methods described by Castanet & Báez (1991*b*); age estimates were made on the basis of annular rings within the cortex (Castanet *et al.*, 1997).

The characters

Apart from the osteological characters derived from the study of living *Gallotia*, we have re-analysed those used by Mertens (1942), Bravo (1953) and Hutterer (1985) in the diagnosis of extinct species and subspecies (involving size, tooth number, number and arrangement of pterygoid teeth, presence of a parietal foramen and skull shape). Further information was derived from previous studies on the anatomy of living and extinct species of *Gallotia* (Boulenger, 1891; Siebenrock, 1894; Gasc, 1971; García Cruz, 1978; Marrero-Rodríguez & García Cruz, 1978; López-Jurado, 1985; Arnold, 1989; Barbadillo, 1989; Izquierdo *et al.*, 1989; Castanet & Báez, 1991*a*; Mateo & López-Jurado, 1992; Castillo, Rando & Zamora, 1994; López-Jurado & Mateo, 1995; Barahona, 1996; Barahona & Barbadillo, 1998).

RESULTS

Living species

Twenty two osteological characters vary within and among the living species, some of them were described previously by other authors but others are new. Of these, 17 characters show ontogenetic variation and 11 have states that are limited to one of five species: *G. atlantica* (4), *G. caesaris* (1), *G. stehlini* (3) and *G. simonyi* (3) (Appendix 2, Fig. 2).

Of these characters, the highest degree of ontogenetic variation is shown by those related to tooth number, tooth morphology in the maxilla and dentary, and the tooth arrangement on the dentary/maxilla and the pterygoid. On the dentary and maxilla, tooth number increases with the size of the individual, and generally this is also true of the degree of heterodonty. The number of cuspules increases along the tooth row, there is a zonal distribution of the different morphological tooth types along the dental shelf, and between two and six recurved ('hooked') anterior teeth develop in the maxilla. These can be mono-, bi- or tricuspid (*G. galloti, G. atlantica, G. caesaris* and *G. simonyi*), while in *G. stehlini* some teeth bear four cuspules. However, some individuals of all species have a lower maxillary and dentary tooth number than is expected, and in some the last tooth positions are occupied by one to three small mono- or tricuspid teeth as opposed to a single large tricuspid tooth (in *G. galloti, G. caesaris* and *G. atlantica*) or several four to six cusped teeth (*G. stehlini*).

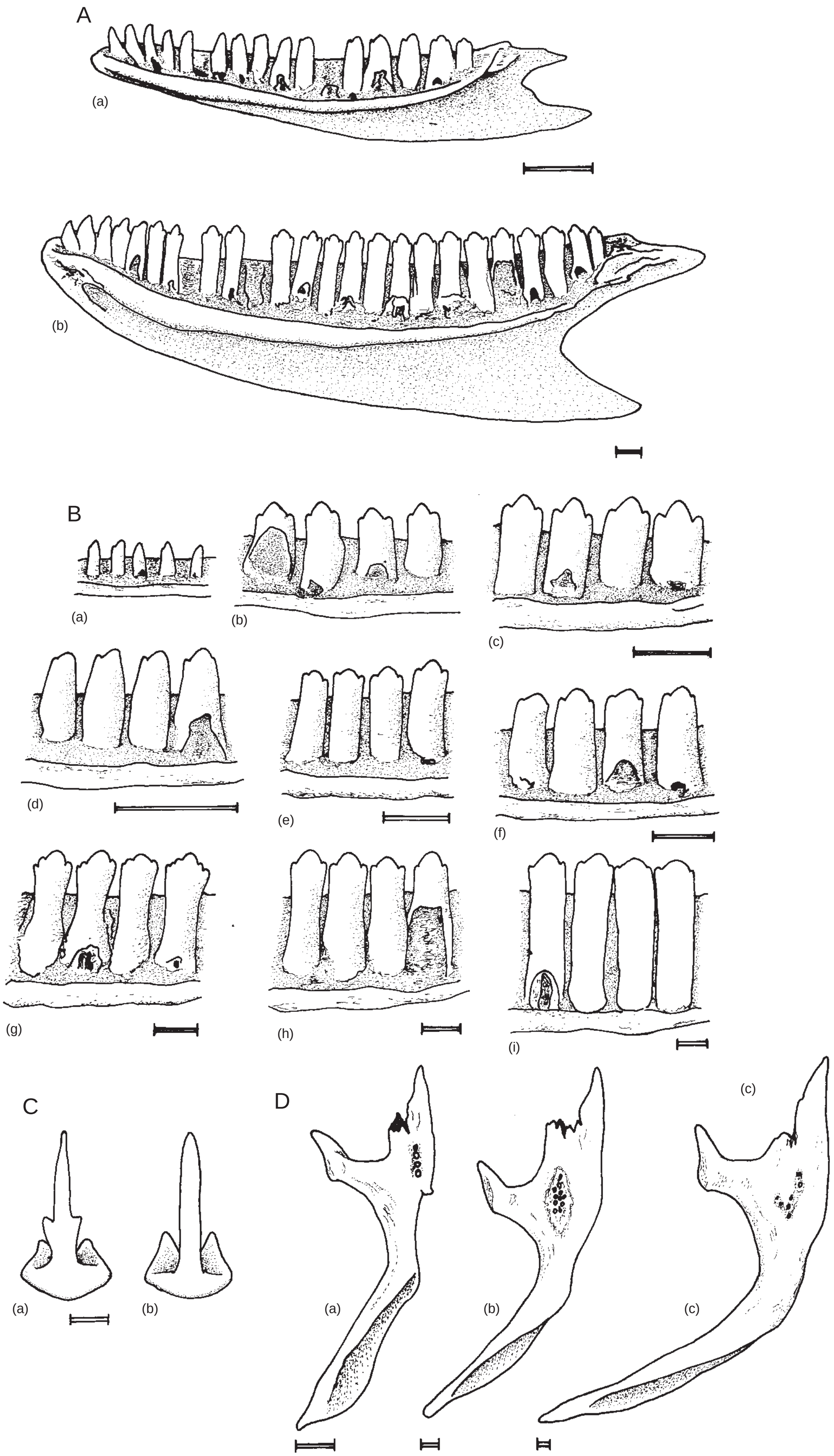
Subfossil specimens

The subfossil remains from the western islands fall into two discrete size categories 'small' and 'giant'. The number of 'small' specimens is much lower, but this is probably because of a combination of taphonomic and sampling bias. The small specimens are attributable to *G. galloti* and *G. caesaris* and they show the same level and type of intraspecific variation as the living forms (Appendix 2). These two small species occur as subfossils on all the western islands, except Gran Canaria. Comparison of the maximum SVL of the subfossil and living species shows that the average size of the subfossil *G. galloti* and *G. caesaris* does not differ significantly from that of the living species (Case & Bolger, 1991; Case, Bolger & Richman, 1992) (Appendix 3). This is not true for the 'giant' forms, for which the subfossil material is significantly larger (Appendix 3). The results of a skeletochronological analysis of subfossil material is shown in Appendix 3, Fig. 3.

To date, representatives of two extinct and two surviving giant lizard species have been described in the subfossil material from the Canary Islands. *G. stehlini*, still common today on Gran Canaria, is known from Gran Canaria (Bravo, 1953; López-Jurado, 1985; Helmdag, 1995; López-Jurado & Mateo, 1995) and Tenerife (López-Jurado & Mateo, 1995). *Gallotia simonyi*, surviving today in relict populations on El Hierro and Tenerife, is recorded in subfossil material from La Gomera (Lehrs, 1909; Hutterer, 1985), El Hierro (Böhme *et al.*, 1981) and Tenerife (Bravo, 1953). By contrast, *G. goliath* from Tenerife (Mertens, 1942; Castillo *et al.*, 1994), La Palma (Mertens, 1942), El Hierro (Izquierdo *et al.*, 1989) and La Gomera (Hutterer, 1985), and *G. maxima* from Tenerife (Bravo, 1953; Marrero Rodríguez & García Cruz, 1978; García Cruz & Marrero Rodríguez, 1979) are regarded as extinct.

Giant lizards: evaluation of the characters used in the diagnosis of extinct giant species

Until relatively recently, the living *G. stehlini* Schenkel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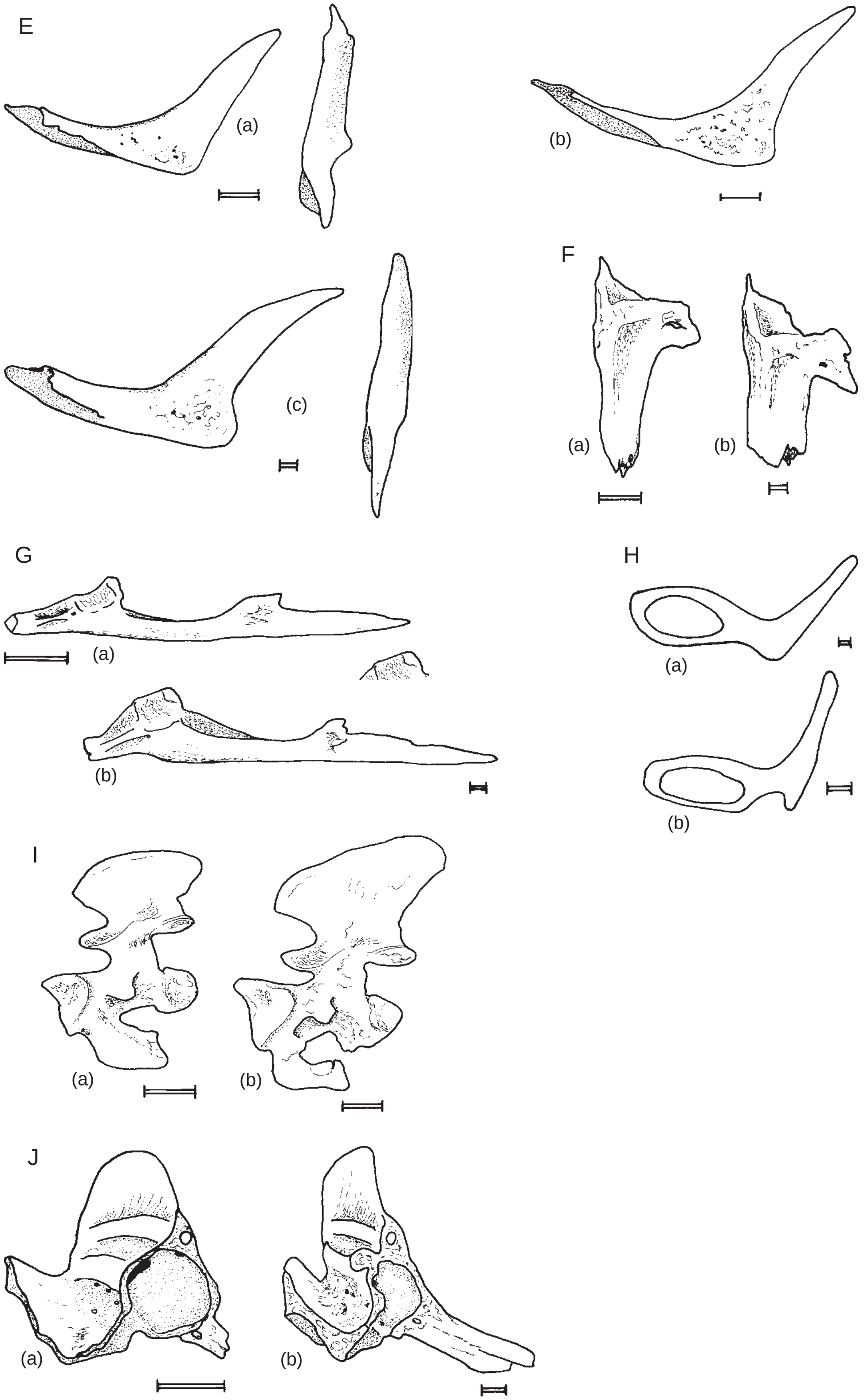

Fig. 2. A. Dentary, medial view: (a) *G. caesaris*; (b) *G. simonyi*. B. Juvenile teeth (central positions): (a) *G. atlantica*; (b) *G. caesaris*; (c) *G. stehlini*. Adult teeth (central positions): (d) *G. atlantica*; (e) *G. galloti*; (f) *G. caesaris*; (g) *G. stehlini*; (h), (i) (large individuals), *G. simonyi*. C. Posterodorsal process of the premaxilla: (a) *G. atlantica;* (b) *G. galloti*. D. Arrangement of the pterygoid teeth: (a) *G. atlantica*; (b) *G. stehlini*; (c) *G. simonyi*. E. Jugal shelf and quadratojugal process: (a) *G. atlantica*; (b) *G. caesaris*; (c) *G. simonyi*. F. Palatine: (a) *G. galloti*; (b) *G. stehlini*. G. Retroarticular process of the articular: (a) *G. galloti*; (b) *G. stehlini*. H. Clavicle: (a) *G. stehlini*; (b) *G. galloti*. I. Axis: (a) *G. atlantica*; (b) *G. galloti*. J. Prootic: (a) *G. atlantica*; (b) *G. stehlini*. Samples used in the illustrations are: *G. caesaris* (UCL.Gca1, 8); *G. simonyi* (BP.Gsi); *G. atlantica* (EBD16597, UCL.Ga20,26); *G. stehlini* (UCL.Gst2, EBD.Gst16,18); *G. galloti* (UAM.R.Ga14,20,23). Scale bars = 1 mm.

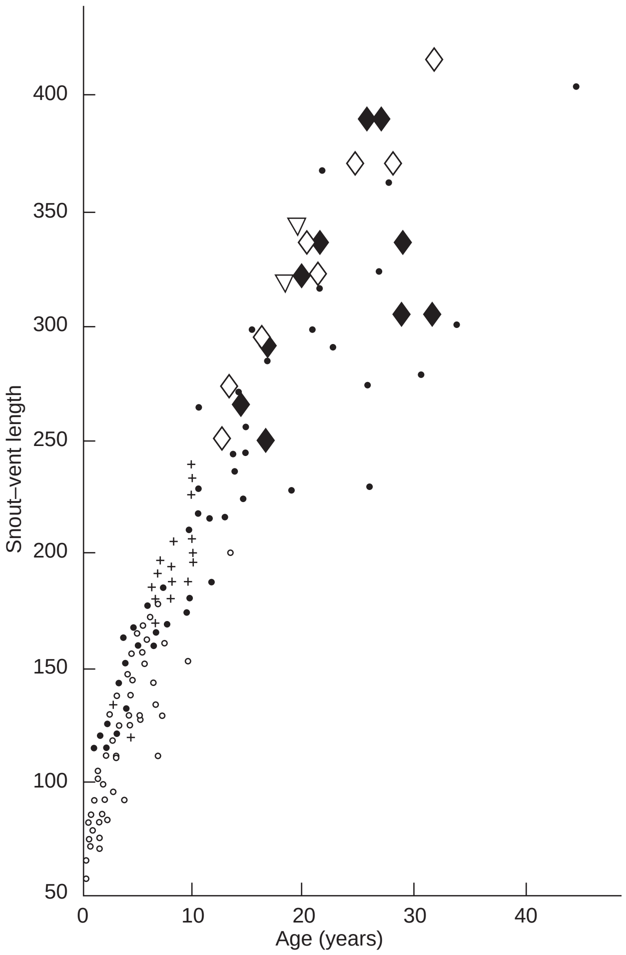

Fig. 3. Variation in snout–vent length with age in living *G. simonyi* from Risco de Tibataje (○) and from captivity (+) (Romero-Beviá *et al.*, in press) and subfossil specimens from El Hierro (●), La Gomera (◆), La Palma (▽) and Tenerife (◇).

1901 from Gran Canaria was regarded as a subspecies of *G. simonyi* Steindachner 1889 (*G. s. stehlini*, e.g. Arnold, 1973; Böhme & Bings, 1977*)*, but after joint agreement at the Symposium 'Herpetologia Canariensis, Bonn, 1985' (Böhme & Hutterer, 1985), most authors have given *G. stehlini* full specific rank (e.g. Böhme, Hutterer & Bings, 1985; López-Jurado, 1985; Salvador, 1985; Barbadillo, 1987). *Gallotia stehlini* and *G. simonyi* resemble one another in external appearance, although they may be distinguished from one another on the basis of coloration and some features of the scalation (e.g. Salvador, 1985; Barbadillo, 1987*)*. Moreover, all recent DNA analyses (e.g. González *et al.*, 1996; Rando *et al.*, 1997) have confirmed the specific distinction. In terms of osteological characters, the two species differ from one another on the basis of dental morphology, pterygoid tooth number and pattern, and features of the jugal, frontals and palatine:

(1) In juveniles of *G. simonyi*, most teeth are tricuspid (except for two to three mono- or bicuspid teeth anteriorly), and this condition is retained in the adult. Only in a few large individuals, may an additional anterior or posterior cuspule appear. In *G. stehlini*, the juvenile tricuspid teeth are replaced by multicuspid teeth, formed by subdivision of the anterior and posterior cusps. The first subdivisions occur in the anterior cuspule, which may subdivided to form two or three cuspules (a complete tooth thus having four, five or six cusps). Division of the posterior cuspule generally follows subdivision of the anterior cusp into three. Thus, a single adult mandible presents teeth with different numbers of cusps, which increase from the anterior to the posterior end of the dentary and maxilla.

(2) Numbers of pterygoid teeth are similar (0–25 in *G. stehlini*; 4–27 in *G. simonyi*), but their arrangement differs in the adult. Thus, the pterygoid teeth of *G. stehlini* typically form a patch on a raised bony prominence, while those of *G. simonyi* form a V or, more accurately, a tick-shaped pattern in which the medial row is the longer. In juveniles, however, this character must be treated with caution. In hatchlings, the pterygoids lack teeth, but these start to appear early and their number and arrangement change with age/size (Appendix 2). Medium-sized individuals of *G. stehlini* and *G. simonyi* have only a single row of pterygoid teeth, but in large individuals of *G. stehlini* more lateral teeth arise and become incorporated into this row to produce a distinct tooth patch on a bony prominence. In large individuals of *G. simonyi* from El Hierro (SVL of captive individuals = 232, 228, 227 and 225 mm), the positioning of additional teeth produces a tick mark pattern, the medial row being the longest. Rarely, some full grown adults of *G. stehlini* keep the juvenile linear arrangement of the pterygoid teeth rather than developing a tooth patch.

(3) The frontals of both species are generally paired, although there is a tendency towards co-ossification of the frontals in adults of *G. stehlini*. In subfossil specimens of *G. stehlini* from Gran Canaria, a relatively high proportion (18%) of frontals (length 19–31 mm) were partially fused.

(4) The jugal of *G. simonyi* lacks a medial process; in *G. stehlini*, a shelf-like medial process is variably present, particularly in subfossil material (13.8%).

(5) The recurved anterior (hooked) teeth of *G. simonyi* are mono-, bi- or tricuspid while in *G. stehlini* some of these teeth may present with four cuspules.

(6) The margins of the posterior process of the palatine are convergent in *G. simonyi* while in *G. stehlini* they are in parallel.

The two extinct subfossil species, *G. goliath* Mertens 1942 and *G. maxima* Bravo 1953 were diagnosed on the basis of five major characteristics: parietal morphology, tooth number, tooth morphology, and body size. However, the more detailed knowledge of intraspecific variation in *Gallotia* forces a re-evaluation of the diagnostic validity of these features.

Parietal foramen

Mertens (1942) diagnosed *G. goliath* (Tenerife, La Palma) as being characterized by a closed parietal

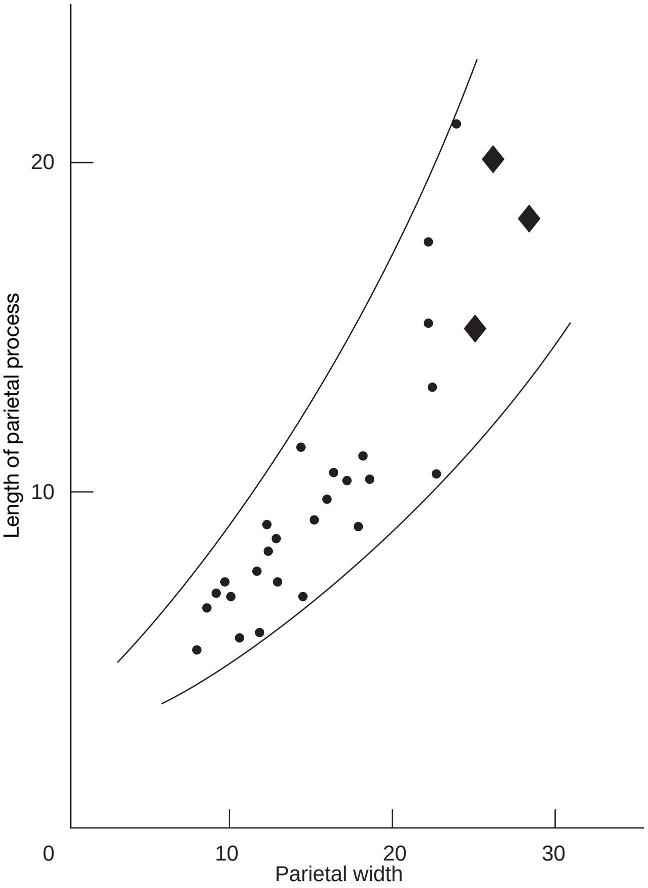

Fig. 4. Variation in length of parietal process with parietal width in specimens from La Dehesa (●, *G. simonyi*) and Juaclo de la Molera (◆, *G. goliath*) according to Izquierdo *et al.* (1989). Both curves correspond to the 95% confidence limits obtained for the covariance of both variables in *G. stehlini*.

foramen, while *G. maxima* (Tenerife) was distinguished from it in retaining an open foramen (Bravo, 1953). However, we have found that subfossil parietals from all the islands, Tenerife and La Palma included, typically have an open parietal foramen. The foramen is closed only in a few large individuals from Gran Canaria and Tenerife. Thus closure of the foramen appears to be size/age related and cannot be used to distinguish *G. maxima* from *G. goliath*, nor *G. goliath* from extant species.

Parietal shape

Hutterer (1985) used the relationship between parietal width and the length of the parietal processes as a character to differentiate between *G. simonyi* + the smaller species of *Gallotia* on the one hand, and *G. stehlini* + *G. goliath* on the other. According to Hutterer, the posterolateral process of the parietal is relatively shorter and straighter in the first group than in either *G. stehlini* or *G. goliath*. However, in extant *G. stehlini* the relationship between parietal width and the length of the parietal processes varies during ontogeny and can be adjusted to an exponential curve ($y = e^{1,284 + 0.061x}$, $R^2 = 94.5\%$). The introduction of data from large subfossil parietals from all the islands shows that there is no significant difference between populations either in the slopes ($F_{4,79} = 0.45$, $P > 0.40$), adjusted averages ($F_{4,79} = 1.32$, $P > 0.25$), or between pairs of subfossil populations (Fig. 4).

Tooth number

Mertens (1942) distinguished *G. goliath* from extant *G. simonyi* on the basis of 28 maxillary teeth (as compared with a maxillary count of 16–20, and a dentary count of 17–24 in the living *G. simonyi*, Rodríguez-Domínguez *et al.*, 1998; the values for *G. stehlini* are 13–23 and 16–27, respectively), while Bravo (1953) distinguished *G. maxima* from *G. goliath* on the basis of 33 maxillary and 36 dentary teeth.

Our studies of extant species show that tooth number increases with the size of the individual. This relationship also exists in the subfossil material examined in this study, but the precise relationship between tooth number and body size varies in each island population. In the dentary, this variation adjusts to a linear regresion (Tenerife: $R^2 = 84.3\%$, $P < 0.001$; La Palma: $R^2 = 78.6\%$, $P < 0.01$; El Hierro: $R^2 = 87.8\%$, $P < 0.001$; La Gomera: $R^2 = 76.9\%$, $P < 0.01$). The slope value shows significant differences between islands ($F_{3,84} = 18.97$, $P < 0.01$). Scheffés' test (Engelman, 1983) shows that for the same body size, the population from La Gomera has fewest teeth, followed by the population from El Hierro and La Palma. Maxillary teeth show a similar pattern. The subfossil remains from Tenerife present the highest tooth number (Appendix 3, Fig. 5) overall, but there is no trace of the bimodal distribution of this character which would be expected if Mertens' and Bravo's diagnoses are valid.

Number and arrangement of pterygoid teeth

According to Mertens (1942), *G. goliath* differs from *G. simonyi* in having 18 pterygoid teeth in V-pattern, while Bravo (1953) differentiates *G. maxima* from *G. goliath* as having > 50 pterygoid teeth raised on a bony concretion and arranged in an arc of three to four rows.

Pterygoid tooth numbers in extant *G. simonyi* range from four to 27, and they form an asymmetric V-shaped (or tick-mark) pattern in large individuals. Therefore Mertens' distinguishing character for *G. goliath* in relation to *G. simonyi* fails. Moreover, in subfossils, as in extant species, the number and arrangement of the pterygoid teeth shows ontogenetic variation. Subfossil pterygoids from El Hierro and Tenerife show a similar pattern to that of extant *G. simonyi* thus the pterygoids of individuals with an estimated SVL < 220 mm bear only a single tooth row while those with SVL > 250 mm have teeth in a tick-mark pattern, with the lateral row

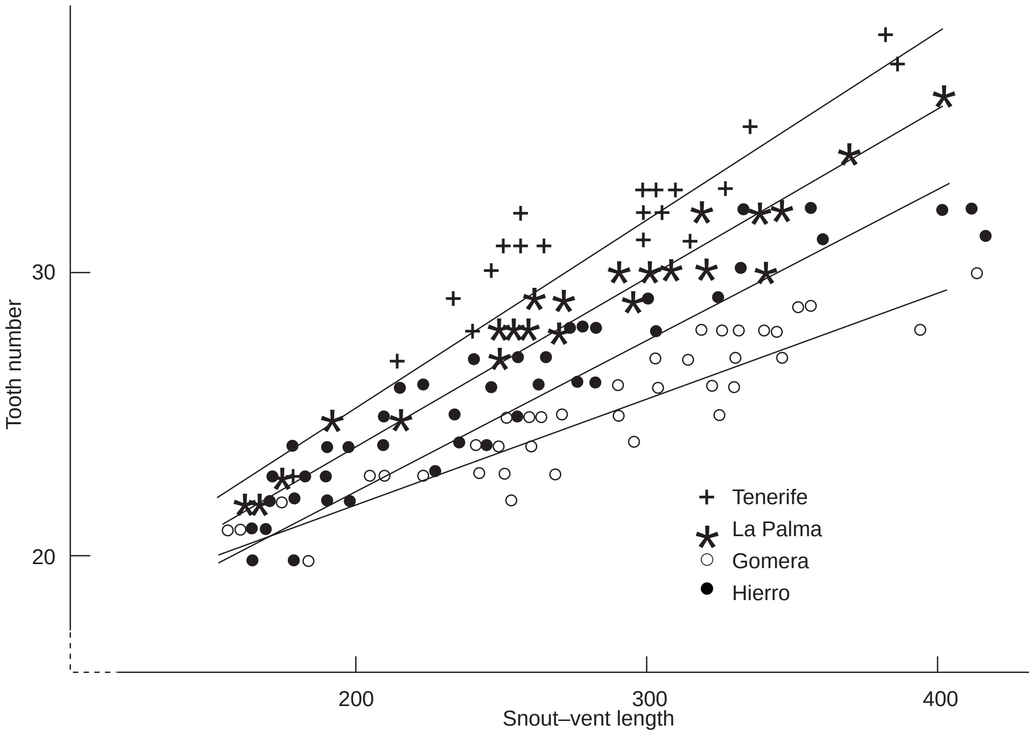

Fig. 5. Variation in tooth number with snout–vent length. (+), Tenerife: TN = 12.38 + 0.065SVL; (∗), La Palma: TN = 12.47 + 0.065SVL; (●), El Hierro: 12.08 + 0.051SVL; (○), La Gomera: TN = 14.81 + 0.036SVL.

smallest. Individuals of intermediate size can show either one or the other pattern. In La Palma subfossils, the tick-mark pattern develops earlier, with the full adult pattern in all individuals having a SVL of around 140 mm. In contrast, at La Gomera, none of the subfossil pterygoids studied have more than a single tooth row (including two individuals with SVL > 350 m). These pterygoid tooth patterns are consistent for the La Palma and La Gomera subfossil populations and permit them to be distinguished from those on other islands, although some individual variation was found in very large pterygoids from Tenerife (SVL > 250 mm), where teeth may be absent, or arranged in either a row or a patch. This may explain the condition in Bravo's material attributed to *G. maxima*. However, in general, the large subfossil pterygoid sample we studied shows no support for species level separation.

Tooth morphology

Mertens (1942) characterized *G. goliath* as having mainly bicuspid teeth, with some tricuspids, and a few with four cusps. *Gallotia maxima* is said to differ from *G. goliath* in having teeth with six cuspules in all but the most anterior positions (Bravo, 1953), thus apparently resembling *G. stehlini* more than *G. simonyi*.

In all living species of *Gallotia*, tooth morphology changes througout ontogeny, especially in *G. stehlini* and *G. atlantica* (Appendix 2). On the basis of tooth morphology, two groups of lizards can be distinguished within the giant subfossil material. Most dentaries from Gran Canaria, as well as two maxillae from Tenerife, fall into the first group. These specimens show the same tooth pattern throughout ontogeny as the living *G. stehlini*. The second group of dentaries comes from Tenerife, La Palma, El Hierro and La Gomera. In this second group, small to medium size specimens have same tooth morphology as extant *G. simonyi*, i.e. the dentary and maxillary teeth change morphology from the anterior to posterior end of the dental shelf. Thus, the first two to six tooth positions are occupied by a few mono- and/or bicuspid teeth followed by tricuspid teeth mostly with diverging margins to the crown. In large individuals of this second group, the crown margins become straighter (Fig. 2b) and some specimens have a few (one to seven) teeth with a fourth cuspule, positioned either anterior or posterior to the main one, although the former is more common (Fig. 2b).

The tooth morphology described by Mertens (1942) for *G. goliath* matches the general condition for extant *G. simonyi* and provides no basis for specific distinction. The condition described by Bravo (1953) for *G. maxima* is more problematic. In all the subfossil material studied, we have found neither dentaries nor maxillae with a dentition in which central and posterior positions are occupied by teeth with six cusps. However, there is one possible explanation. We have observed that the teeth of large individuals can become very worn, so that the integrity of the cusps is no longer clearly visible.

Worn teeth of this kind might be interpreted as having more cusps than they actually have.

Size

Although the above morphological characters fail to discriminate between living and subfossil giant species, the body size of the subfossil specimens, estimated by comparison with extant *G. stehlini* and *G. simonyi*, shows that the extinct forms were significantly larger. On the basis of their holotype specimens, Mertens (1942) and Bravo (1953) estimated a total length of 0.9–1 m for *G. goliath* (= approx. 0.48 m SVL) and of 1.2–1.25 m (= approx. 0.59 m SVL) for *G. maxima*, although Bischoff (1985) produced higher maxima of 1.25 m and 1.4 m, respectively. Our own estimates of SVL for the subfossil material we studied are given in Appendix 3, but reach a maximum of 0.5 m. This contrasts with maximum SVLs of 0.16 m (Fuerteventura) to 0.23 m (Gran Canaria) for the living *G. stehlini*, and 0.15 m (Tenerife) to 0.2 m (El Hierro) for *G. simonyi*, a striking difference. The size distribution of the subfossils differs per island. Allowing for differences in sample size (Appendix 1), specimens from Tenerife and La Gomera appear to have reached a larger size than those from La Palma, El Hierro and Gran Canaria (Appendix 3).

The skeletochronological studies carried out by Castanet & Baez (1988, 1991*b*) on extant and extinct *Gallotia* spp., and our own studies on subfossil femora, show that the distance between lines of arrested growth (LAG) are practically constant throughout the life of the lizards, so the relation between SVL and age adjusts to a linear regresion (Fig. 3) (subfossils from El Hierro: $R^2 = 81\%$, $P < 0.01$). Thus the largest femora correspond to the oldest lizards. The maximum recorded age was 45 years (a subfossil specimen from El Hierro), although the true age of old individuals may be underestimated by 1 or 2 years. This is because growth in cortical thickness can stop before the death of the animal, and because in large specimens the LAGs of the first 2 years may be completely removed (Castanet & Báez, 1991*b*). A comparative study of the subfossil data from El Hierro with those obtained by Romero-Beviá, Mateo & Pérez-Mellado (in press) for wild and captive living populations of *G. simonyi*, also from El Hierro, shows that although there are differences in the adjusted averages ($F_{3,129} = 6.48$, $P > 0.5$), there are no differences in the slopes ($F_{3,129} = 0.35$, $P < 0.01$). Scheff's test (Engelman, 1983) shows that the adjusted averages differ between the wild living specimens on the one hand, and the subfossil ($F_{2,101} = 9.37$, $P > 0.5$) and captive specimens ($F_{2,99} = 7.76$, $P > 0.5$) on the other, but not between captive and subfossil specimens ($F_{2,82} = 1.24$, $P < 0.01$). In Fig. 3, subfossil data from other islands (La Gomera, Tenerife, La Palma) has also been added, but the results fall within the distribution of *G. simonyi* (living and subfossil) from El Hierro.

DISCUSSION

The status of *G. goliath* Mertens 1942 and *G. maxima* Bravo 1953

We examined a large new sample of subfossil material from the Canary Islands and studied variation within and among living species of *Gallotia*. The results have permitted a re-evaluation of the characters used by Mertens (1942) and Bravo (1953) to diagnose the extinct species *G. goliath* and *G. maxima*. There are two clear conclusions. Firstly, the two subfossil species cannot be reliably distinguished from one another. Secondly, with the exception of their much larger size, the supposed diagnostic character traits of these species fall within the range of variation of the living *G. simonyi* and/or are shown to be directly related to size. There is no evidence of any conspecific relationship with *G. stehlini*.

Species diversity on the Canary Islands

Currently, five species of *Gallotia* can be recognized from the Canary archipelago. In the past, *G. simonyi* co-existed with each of the small species on La Gomera and La Palma. This is the only major difference between past and present patterns of distribution. The few subfossil *G. stehlini* are from a single fossil site on Tenerife and this suggests either a human introduction or an unsuccessful colonization. Thus, one giant and one small species were originally sympatric on each of the western islands, except Gran Canaria.

As noted in the introduction, the phylogenetic relationships within the genus *Gallotia* are still uncertain. While morphological characters (i.e. ventral body scales tessellated) unite *G. simonyi* and *G. stehlini* as sister taxa (Arnold, 1989), molecular data place *G. simonyi* as the sister taxon of *G. galloti* + *G. caesaris*, with either *G. atlantica* or *G. stehlini* as the most basal of the group (González *et al.*, 1996). Until these problems are resolved, it would be premature to interpret the size distribution of the lizards in the western islands as a consequence of either a divergence in body size of coexisting species (competitive character displacement) or the prevention of colonization by a species of similar size (size assortment) (e.g. as discussed for lizards of the genus *Anolis* in the Lesser Antilles; Schoener, 1970; Williams, 1972, 1983; Losos, 1990).

Extinction and reduced life expectancy for the large *Gallotia* sp.

The remaining questions concern the reason for reduction in size of both *G. stehlini* and *G. simonyi* throughout the western islands in the last few thousand years (Appendix 3), and the disappearance of *G. simonyi* from La Gomera and La Palma over the same period. What has happened on the Canary Islands is not an isolated case. Reduction in size and total or partial extinction of lizard taxa have already been demonstrated by Pregil (1986) and Case *et al.* (1992) in other archipelagos. These authors suggest that such effects result from the alteration of insular environments after the arrival of humans, and this general conclusion is supported by our study.

The data described above (Appendix 3, Fig. 3) fail to demonstrate significant differences in the growth rates of extant and extinct populations of *G. simonyi*; size differences between these populations simply reflect lifespan. Growth rates do vary between species and these are inversely related to the specific adult size of the taxon (Castanet & Báez, 1991*a*). In *Gallotia*, the smallest and most short-lived species grow faster that the largest and more long-lived species. However, the very large size spectrum of body size within the genus *Gallotia* mainly seems to be a consequence of differences of longevity and the timing of sexual maturity, allowing a more or less protracted growth period.

On Gran Canaria, the maximum recorded SVL of *G. stehlini* has changed from 0.37 to 0.23 m, while that of *G. simonyi* has been reduced to an even greater extent, for example from 0.5 to 0.15 m on Tenerife, and from 0.43 to 0.2 m on El Hierro. Extant specimens of *G. stehlini* and *G. simonyi* show the anatomical characteristics necessary for extended growth to reach large size, characteristics acquired via paedomorphosis. Examples include the failure or delay in ossification of articular condyles such as those of the quadrate and basipterygoid processes, the weak development of the retroarticular process of the articular, the non-fusion of the vertebral neurocentral sutures in the juvenile and their late fusion in the cervical vertebrae, and the late fusion of the components of the pectoral and pelvic girdles.

Studies involving *G. simonyi* on El Hierro (Romero-Beviá *et al.*, in press) and the results presented here (Appendix 3, Fig. 3) suggest that reduction in size of the giant species is principally the result of a reduction in life expectancy of wild adults, coincident with the arrival of humans on the islands. This, in turn, suggests a deterioration of the habitat resulting in fewer resources to maintain large animals, competition with imported herbivores (e.g. rats, rabbits and goats; Machado, 1985), or selection against large animals (of both *G. stehlini* and *G. simonyi*) by introduced predators (cats are thought to be particularly harmful; García-Márquez *et al.*, 1997; Rodríguez-Domínguez *et al.*, 1997). All three factors may have been involved.

Why has *G. simonyi* become extinct on some islands (La Gomera, La Palma) and is in danger of extinction on the remainder (El Hierro and Tenerife), while *G. stehlini* is still abundant on Gran Canaria? The proposed cause, the arrival of humans and their domestic animals, is the same for all islands (Machado, 1985; Izquierdo *et al.*, 1989; Castanet & Báez, 1991*a*; García-Márquez *et al.*, 1997), and thus for both large species. However, it seems that *G. simonyi* and *G. stehlini* reacted differently to humans. A combination of factors may have made *G. simonyi* more vulnerable. Time to sexual maturity differs, being 5–8 years for *G. simonyi*, compared to 3 years for *G. stehlini* and usually 2 years for *G. galloti* and *G. caesaris*, although *G. simonyi* may rarely breed early in captivity (M. A. Rodríguez-Domínguez, pers. comm.). Both large species have larger clutch sizes than their smaller congenerics (six to 13 in *G. simonyi*, up to 12 in *G. stehlini* (increasing with age/size), as opposed to one to four in the smaller taxa) (Barbadillo, 1987; Rodríguez-Domínguez *et al.*, 1998; Rodríguez-Domínguez & Molina-Borja, in press), but although young adult *G. stehlini* (like the smaller congenerics) may produce two clutches per year, only one has ever been recorded for *G. simonyi*. This combination of delayed sexual maturity and lower birth rate would make recovery from a population crash far more difficult for *G. simonyi* than for *G. stehlini*. In addition, *G. stehlini* is without congeneric competitors, while immature individuals of *G. simonyi* must compete for resources with *G. galloti* (Tenerife) and *G. caesaris* (El Hierro), and *G. stehlini* is both faster and more aggressive than *G. simonyi* (Cejudo & Márquez, 1998), and may therefore fare better against predators. Nevertheless, a full understanding of the factors affecting breeding age, longevity and survival in *G. stehlini* and *G. simonyi* in the wild require more detailed ecological, behavioural and developmental studies of the two species, and of their interactions with other components of the faunal assemblage.

CONCLUSIONS

(1) It is not valid to differentiate between *G. maxima* and *G. goliath* on the basis of size and individual variation in the nature of the parietal foramen or variation in the arrangement of the pterygoid teeth (Mertens, 1942; Bravo, 1953; Estes, 1983; Izquierdo *et al.*, 1989). In addition, we propose the synonymy of *G. simonyi* and *G. goliath* (including *G. maxima*) because:

(a) only two species (one small and one large) can be distinguished amongst the fossil remains on El Hierro and Tenerife (as is the case today),

(b) the morphological characteristics of the subfossils attributed to *G. goliath* match those of *G. simonyi* from Tenerife and La Palma, and any differences observed in the subfossil forms fall with the range of variation of the living species or are shown to be directly related to size.

(2) Both *G. stehlini* and particularly *G. simonyi* have undergone a significant reduction in maximum size which appears to be correlated with a reduction in life expectancy (and thus of growth period). This in turn may be related to the detrimental effects on the ecosystem caused by the arrival of humans and domestic animals (predation, increased competition for reduced resources).

(3) *Gallotia simonyi* and *G. stehlini* appear to have reacted differently to human interference, with *G. simonyi* showing greater vulnerability, probably as the result of a

combination of factors including its delayed sexual maturity (Castanet & Báez, 1991*b*; J. A. Mateo, pers. obs), breeding pattern, behaviour and, perhaps, competition during immaturity with congenerics.

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Appendix 1. Collections and material studied

Abbreviations for the collections are as follows: BMNH, Natural History Museum, London; BUPGC, Departamento de Biología Universidad de Las Palmas, Gran Canaria; EBD, Estación Biológica de Doñana, Sevilla; SMF, Natur-Museum und Forschungs-Institut Senckenberg; TFMC, Museo de Ciencias Naturales de Tenerife; UAMR, U. Paleontología, Universidad Autónoma de Madrid; UCL, University College London; ZFMK, Museum Alexander Koenig, Bonn.

(A) Living specimens, including hatchlings to adults of both sexes in all species except in *G. simonyi*

G. atlantica (89 examples): BMNH 1967/1438–53, 1496; UAMRGat1–13; UCLGat.ib1–11, UCLGatla20–35, UCLGatat20–51; ZFMK 4110, 4117, 34964.

G. galloti (38 examples): UAM.R.Gg1–38.

G. caesaris (20 examples): UCLGaca1–14; ZFMK4105, 4109–4112, 4114, 4187, 7854.

G. stehlini (28 examples): BP3–19; UAMRgst1–3; UCLgst1–3; ZFMK4097–4100, 4116, 7876, 7881.

G. simonyi: 4 skulls (EBD), 4 preserved examples (BMNH–91331, 92.8.31.1,1967 1736.37, 1903.9.16.5), 21 field specimens from the Research and Breeding Center of the Hierro Giant Lizard (La Frontera, Hierro) and 4 field specimens from Tenerife Enviromental Agency.

(B) Subfossil specimens

B1. Identified subfossil material.

SMF 36068–36075. Holotype and paratype of *Gallotia goliath*. ZFMK 42392–42398. Holotype and paratype of *Gallotia goliath bravoana*. ZFMK 42399–42405. Holotype and paratype of *Gallotia simonyi gomerana*. ZFMK 42406. *Gallotia galloti*. ZFMK 7878–7879. *Gallotia simonyi machadoi*. ZFMK 7880. *Gallotia galloti caesaris*. ZFMK 58250. *Gallotia goliath*. (Whole example). ZFMK 58251. *Gallotia goliath* (Part of the skull). ZFMK 58252. *Gallotia cf. stehlini*.

B2. Unidentified subfossil material belong to TFMC and BUPGC collections.

B2.1 Tenerife fossil sites

Cueva del Barranco de Santos (Holocene) (TFMC); Cueva de Chirche, Guía de Isora (Holocene) (TFMC); Cueva en Barranco de Icod (Holocene) (TFMC); Cañada las Pilas, Parque Nacional del Teide (Holocene) (TFMC); Punta de Antequera (Neotirreniense) (TFMC); Bujero del Silo (TFMC); El Sobrado (Holocene) (TFMC); Playa de las Trochas (Upper Pleistocene) (TFMC); Barranco Hondo, Cueva de la Arena (Holocene) (TFMC) (BUPGC); Galeria de los Ingleses, Cueva del Viento (TFMC); Hoya de San Felipe (Holocene) (TFMC); Cueva El Michel, Santa Ursula (TFMC); Barranco Grande (TFMC); Martiánez (Pleistocene) (BUPGC); Masca (BUPGC); San Marcos (Holocene) (BUPGC) and Benijo (BUPGC).

Numbers of elements studied from these sites include: angulars (15), articulars + surangulars (38), articulars (1), clavicles (11), coronoids (8), dentaries (81), ectopterygoids (7), fibulae (2), frontals (33), humeri (3), interclavicles (7), jugals (26), maxillae (88), nasals (5), neurocrania (15), palatines (13), parietals (52), pelvic and pectoral girdles (17), postorbitofrontals (26), prefrontals (8), premaxillae (2), prootic (1), pterygoids (79), quadrates (15), almost complete skull (1), splenials (5), supraoccipital (1), surangulars (2), vertebrae (113), ribs (many) and vomers (14).

B2.1 La Palma fossil sites

Cueva Los Murciélagos, Los Tilos (Holocene) (BUPGC), (TFMC); Roque de Mazo (Upper Pleistocene) (BUPGC) and La Puntilla (BUPGC).

Bones studied: articulars + surangulars (8), clavicles (1), coronoids (1), dentaries (25), femora (2), frontals (2), frontals + parietal + postorbitofrontal (two specimens), humeri (4), interclavicles (1), jugals (5), maxillae (13), neurocrania (1), parietals (6), pectoral girdles (3), pelvic girdles (2), postorbitofrontals (5), prefrontals (1), pterigoids (16), quadrates (2), vertebrae (11), vomers (1).

B2.3 Gran Canaria subfossil sites

El Ingenio (Pleistocene) (BUPGC) and La Aldea (Pleistocene) (BUPGC)

Bones studied: angulars (39), articulars + surangulars (21), articulars (33), clavicles (60), coronoids (4), dentaries (45), ectopterygoids (148), epipterygoids (3), frontals (170), interclavicles (53), jugals (225), maxillae (71), nasals (33), neurocrania (51), opisthotics (13), palatine (29), parietals (126), postorbitofrontals (247), prefrontals (99), prootics (38), pterygoids (65), quadrates (158), skull (1), sphenoids (24), splenials (38), squamosals (3), supraoccipitals (2), surangulars (57).

B2.4 La Gomera subfossil sites

Puntallana (TFMC) and Bujero del Silo (Holocene) (BUPGC)

Bones studied: complete mandibulae (2), dentaries (50), maxillae (36), parietals (13), postorbitofrontals (2), pterygoids (13).

B2.5 El Hierro subfossil sites

Juaclo de Las Moleras (Holocene) (TFMC) (BUPGC), El Pinar (BUPGC), Conchero de los Herreños (BUPGC), Charco Azul (BUPGC), Conchero del Parador (BUPGC) and EL Julan (BUPGC)

Bones studied: angulars (4), articulars and surangulars (6), articulars (3), skull (1), clavicles (4), coracoids (11), dentaries (89), ectopterygoids (4), frontals (9), ilia (6), interclavicles (2), ischia (3), jugals (13), maxillae (56), neurocrania (8), palatines (10), parietals (27), parietals + frontals articulated (3), pectoral girdles (8), pelvic girdles (7), postorbitofrontals (8), prefrontals (5), premaxillae (1), pterygoids (28), pubes (2), quadrates (10), splenials (4), surangulars (3), vertebrae (150), vomers (1).

Appendix 2. List of characters which vary within and between living species of *Gallotia*

(a) Arrangement of the posterior projections of the dentary. All juveniles with ventral process longer than dorsal one. Adults of *G. caesaris* and *G. atlantica* with projections almost the same size, but *G. galloti, G. simonyi* and *G. stehlini* with dorsal process longer than ventral.

(b) Crown morphology in the premaxilla. Monocuspid teeth in adult and throughout ontogeny in *G. atlantica, G. galloti* and *G. caesaris*, but with some bicuspid/ tricuspid teeth in adults of *G. stehlini* and *G. simonyi*.

(c) Adult tooth number in the premaxilla. 7 in *G. caesaris* and *G. atlantica*, up to 8 in *G. galloti* and more than 8 in *G. simonyi* and *G. stehlini*.

(d) Crown morphology in the dentary and maxilla. Teeth in juveniles of *G. atlantica* are monocuspid (a few teeth with an incipient anterior cuspule can appear in posterior positions), while in juveniles of *G. galloti, G. caesaris* and *G. stehlini*, only 2 or 3 anterior teeth are monocuspid and/or bicuspid and the remaining teeth are tricuspid. Adults of *G. atlantica* have more bicuspid teeth than monocuspid teeth, with some tricuspid teeth occasionally posteriorly. *G. galloti* and *G. simonyi* have a majority of tricuspid teeth, while *G. caesaris* has bi- or tricuspid teeth in almost the same proportions. *G. stehlini* has a majority of multicuspid teeth (4, 5 and 6 cusps) rather than mono-, bi- or tricuspid teeth.

(e) Tooth crown with margins divergent in *G. stehlini* and *G. simonyi* and in parallel in the remaining species.

(f) Margins of the posterodorsal process of the premaxilla parallel except in adult of *G. atlantica* where the process is arrow shaped.

(g) Frontals are usually paired in *Gallotia* spp., but there is a tendency towards fusion in adults of *G. galloti, G. caesaris, G. atlantica laurae* and *G. stehlini*.

(h) Anteromedial process of the pterygoid is straight in all species except in adults of *G. atlantica* where it is stepped.

(i) Pterygoid tooth number. Pterygoid teeth are absent in hatchlings but appear early in postnatal ontogeny. Numbers of pterygoids teeth vary as follows: *G. atlantica* (0–4), *G. stehlini* (0–25), *G. galloti* (0–8), *G. caesaris* (0–9) and *G. simonyi* (?–27).

(j) Arrangement of the pterygoid teeth. In juveniles of all species pterygoid teeth starts in a row, a condition retained by adults of *G. galloti, G. atlantica* and *G. caesaris*. In *G. stehlini*, further teeth erupt laterally, producing a patch pattern on a bony concretion in the adult. In *G. simonyi*, a second row erupts in a lateral position, giving a tick-shaped pattern with the medial row longer than the lateral one.

(k) Jugal shelf with a medium process in *G. galloti, G. caesaris* and *G. atlantica*. Variable in *G. stehlini* and absent in *G. simonyi*.

(l) Quadratojugal process of jugal absent in *G. atlantica* and present in the remaining species, although in adults of *G. caesaris* and *G. galloti* this process has lost its posterior embayment.

(m) Margins of the posterior process of palatine convergent except in *G. stehlini* where are in parallel.

(n) Supratrigeminal process absent in juveniles and present in adults of all species except in *G. atlantica* and *G. caesaris* where this character is variable.

(o) Retroartiucular process of the articular straight in adults of *G. galloti*, *G. caesaris* and *G. atlantica* but ventrally deflected in adults of *G. simonyi* and *G. stehlini*.

(p) Infratemporal osteoderms present in subadults and adults of all species except in *G. galloti* and *G. caesaris*.

(q) Posterolateral process of the clavicle expanded anteriorly in *G. galloti* and *G. caesaris*, absent in *G. stehlini* and variable in *G. atlantica* and *G. simonyi*.

(r) Axis with a straight neural arch in *G. atlantica* and higher at the posterior end in adults of remaining species.

(s) Depressed skull in large individuals of *G. stehlini* and *G. simonyi*, but flat in remaining species.

(t) Parietal foramen generally open in all species but closed in a few large individuals of *G. stehlini* and *G. galloti*.

(u) Cephalic condyle of the quadrate usually fully ossified in only large individuals of *Gallotia* spp., but occasionally remains unossified.

(v) Cervical ribs are generally unossified, but may be partially or fully ossified in large individuals of *G. stehlini, G. simonyi* and *G. galloti*.

Appendix 3. Statistics

3.1 Size relations between living and extinct population of *Gallotia* spp.

Type/island	*G. stehlini*	*G. galloti*	*G. caesaris*	*G. simonyi*
Lanzarote				
Fuerteventura	abst, 163[a]			
Gran Canaria	367[b], 232[a]			
Tenerife	134[b], ext	130[b], 136[a]		502[b], 150[a]
La Palma		118[b], 122 [a]		444[b], ext
El Hierro			95[b], 94[a]	434[b], 201[a]
La Gomera			98[b], 103[a]	466[b], ext

Maximum snout–vent length (SVL in mm) estimated in subfossil ([b]) and living ([a]) species of *Gallotia*. abst, absent and ext, extinct.

3.2 Correlation between dentary tooth number (Y) and SVL (X) in subfossil specimens with SVL estimated > 120 mm. Scheffé test *P* values

Tenerife				
La Palma	0.038*			
El Hierro	0.007**	0.031*		
La Gomera	< 0.0001**	< 0.0001**	< 0.0001**	
	Tenerife	La Palma	El Hierro	La Gomera