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Study of dentition in lizards from Gran Canaria Island (Canary Islands) and its ecological and evolutionary significance

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The dentition of *Gallotia stehlini* from one extant and two subfossil populations dated as 4000 and 2000 years before present was studied. Body measurements were similar in the two subfossil populations, but much greater than the largest sizes observed today in *G. stehlini*. The morphology of the dental cusps in this *G. stehlini* differs greatly from that of other Lacertidae, including other congeneric Canarian species; this has been connected with a vegetarian diet. A decrease in heterodonty with size of the animal is also seen which contrasts strongly with the models observed in the Mediterranean lacertid lizards.

KEY WORDS:—Dentition – lizards – Canary Islands – ecology – evolution.

CONTENTS

INTRODUCTION

Four species of lizard belonging to the family Lacertidae are found in the Canarian archipelago. These species are further differentiated into ten subspecies (Boettger & Muller, 1914; Bischoff, 1982, 1985; Castroviejo, Mateo & Collado,

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1985; Martín, 1985; López-Jurado, 1989) of proven monophyletic origin (López-Jurado, Cano & Báez, 1986).

On Gran Canaria Island, two species are currently found: *Gallotia stehlini*, the largest extant lacertid species, which occupies all the biotopes on the island including those of highest altitude, and a small form, *G. atlantica*, thought to have been introduced to this island (Barquín & Martin, 1982; Castroviejo *et al.*, 1985).

The dental morphology of *G. stehlini* differs from that of all other species of Canarian lizards (see Hutterer, 1985; López-Jurado, 1989) as well as European and Mediterranean ones (Cooper, 1963; Rocek, 1984).

The object of this study was to investigate the relationship between dentition and food in current populations of the species; and also to study the variation in the dentition of the species by comparing contemporary population data with data from specimens from two fossil beds of known geological age on Gran Canaria Island.

MATERIALS AND METHODS

Maxillaries from two palaeontological beds (Fig. 1) were used: Ingenio (A) provided, among others, 55 maxillar bones and La Aldea de San Nicolás de Tolentino (B) 17 maxillar bones. The material was compared with 47 present-day lizard maxillaries from a south-west Gran Canaria population (Morán, C).

Through ^{14}C dating, the age of the La Aldea bones was found to be *c.* 2000 years before present (BP) (López-Martínez & López-Jurado, 1987), and the Ingenio bones 4000 years BP (Hutterer, personal communication).

For the present-day population, sex determination and snout-vent length (SVL), pileus length (PilL) 'from the snout to the end of the parietal bones) and dental crest length (*sensu* Rocek, 1984) (DCL) were recorded. Because bones are dissociated, only the DCL was recorded on the subfossil material.

For each maxillary bone the number of teeth (NT), the number of cusps (CN) and the heterodonty (H) were recorded. Tooth number included empty sockets that would have been filled in life.

Heterodonty was calculated using two indices which are based on the coefficients of variation (Sokal & Rohlf, 1969) in the height (HH) and width (HW) of each room.

Gross diet characteristics were assessed by measuring the dry weight percentages of ingested plant matter found in the stomachs of 62 lizards from the south-west region of Gran Canaria Island in the herpetological collections of the Doñana Biological Station (CSIC, Sevilla).

For statistical analysis of the data, the programs BMDP (Dixon, 1987), BMDP 6D (bivariate plots; Chasen, 1983) and BMDP 1V one way analysis of variance and covariance; Engelman, 1983) were used.

RESULTS

Number of teeth

As in other species of lacertids, newborn *G. stehlini* have relatively few teeth. The number increases with growth (Cooper, 1963; Rocek, 1984) and as Fig. 2 shows the increase in linear.

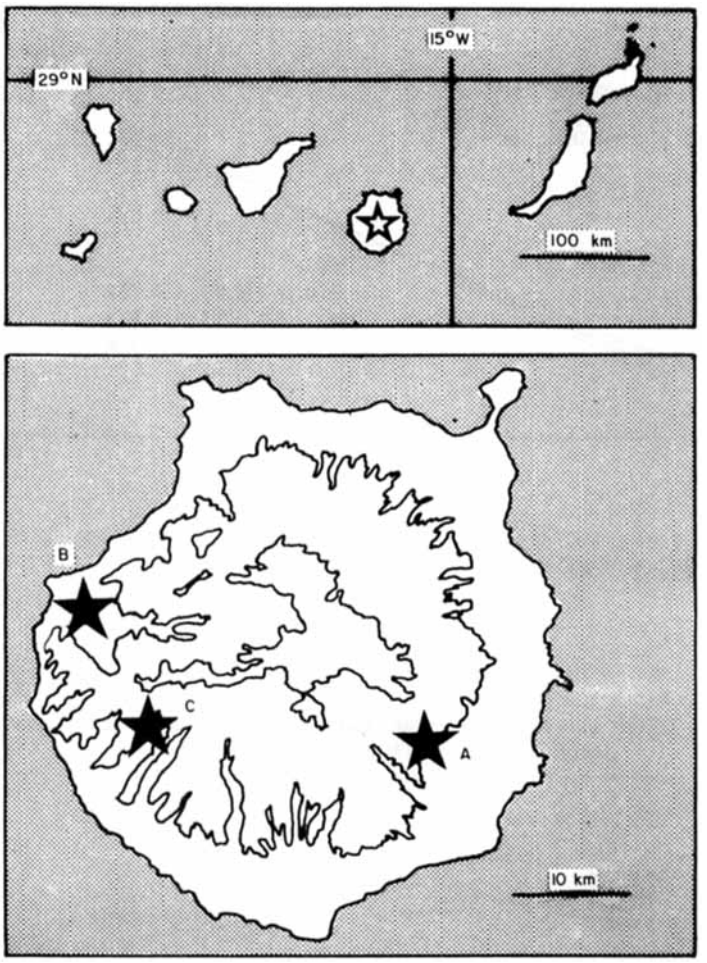

Figure 1. Geographic situation of the localities Ingenio (A), La Aldea (B) and Mogán (C) on Gran Canaria Island.

Unlike other lacertids (Arnold & Bureton, 1978), the current populations of giant lizards on Gran Canaria Island do not show significant differences between males and females in the head length (= pileus length, PilL) with respect to the snout-vent length (SVL), in measurements dependent upon the size of the head, such as the dental crest length (DCL) (Fig. 3, Table 1) or in the increase in the number of teeth with dental crest length (Table 2). Thus the comparison between present-day populations and subfossils is not hindered by the need to know the sex of the subfossil specimens.

Analysis of covariance applied to the number of teeth and the size of the maxillary bone (DCL), with the individuals being grouped separately (subfossils and extant populations), confirmed the absence of significant differences between adjusted means or between regression slopes (Fig. 2, Table 3). However, there were differences in the real means (Table 3) as shown by the greater size of the lizard subfossils, from both Ingenio and La Aldea, e.g. it was calculated, using the equation in Fig. 2, that the largest maxillary bone found

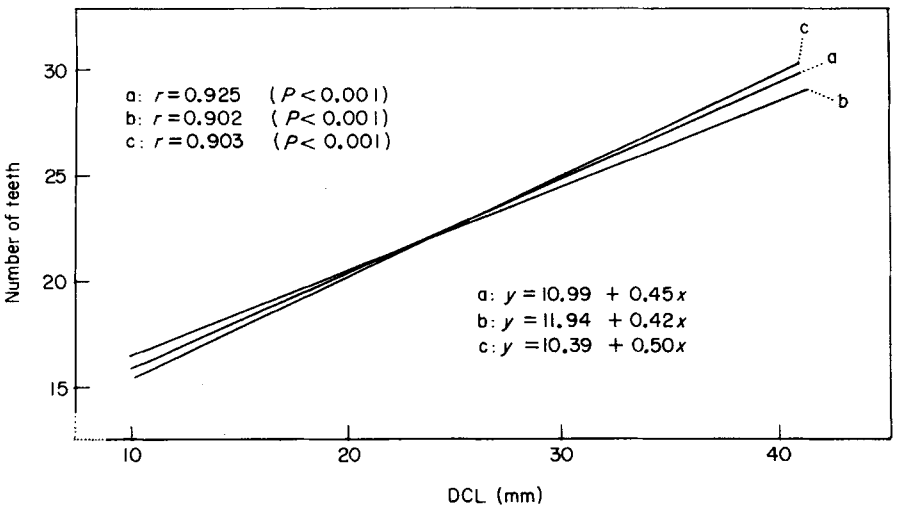

Figure 3. Variation of number of teeth with dental crest length in lizard populations of Ingenio (a), La Aldea (b) and Mogán (c).

TABLE 1. Results of the ANOVA between sexes with snout-vent length versus pileus length and with snout-vent length versus dental crest length. Data only from extant population

		d.f.	Probability
PilL-SVL			
Covariate			
Regression coefficient	0.25		
t-value	33.20		$P < 0.001$
Adjusted group means			
Males	27.91		
Females	27.21		
Equality of adjusted means			
F value	2.29	1	$P = 0.173$
Zero slopes			
F value	1102.26	1–74	$P < 0.001$
Equality of slopes			
F value	1.20	1–73	$P = 0.277$
DCL-SVL			
Covariate			
Regression coefficient	0.12		
t-value	28.25		$P < 0.001$
Adjusted group means			
Males	13.82		
Females	13.84		
Equality of adjusted means			
F value	0.01	1	$P = 0.934$
Zero slopes			
F. value	798.38	1–37	$P < 0.001$
Equality of slopes			
F value	0.32	1–36	$P = 0.573$
t-test for adjusted group means			
t-value	0.08		$P = 0.933$

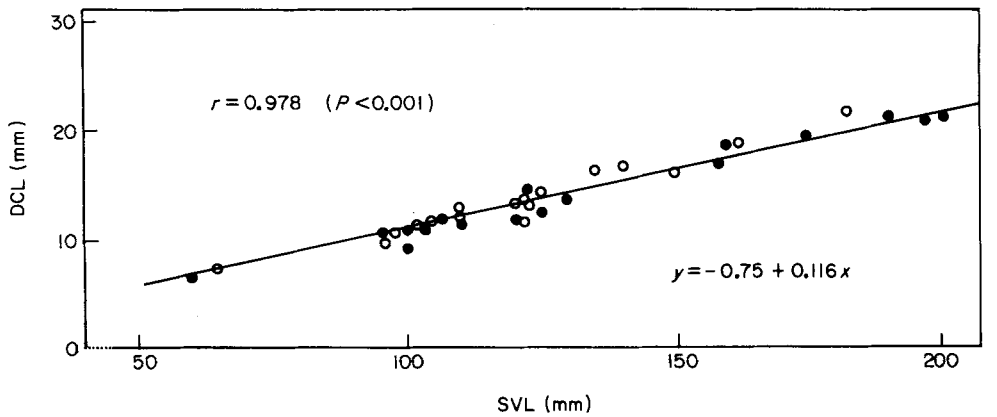

Figure 2. Correlation between dental crest length (DCL) and snout-vent length (SVL) in living *Gallotia stehlini*. ●, Males; ○, females.

(40 mm DCL–Ingenio) must have belonged to a lizard with an SVL greater than 350 mm whereas the largest live specimen we found, a male from Agaete (north-west region of Gran Canaria Island) had a SVL of 280 mm.

Heterodonty and number of cusps

In contrast to other species of Lacertidae such as *Lacerta lepida* or *L. pater*, *G. stehlini* shows a reduction in heterodonty with an increase in the DCL and, hence, in the SVL (Fig. 4). The negative slope between heterodonty and DCL is determined by the presence of wider teeth (HW) in the distal region of the maxillary bone in juveniles. This difference is much smaller in the adults. On the contrary, the height of the teeth shows no variation with respect to the SVL.

As with the number of teeth, no differences in the patterns of variation in heterodonty were observed between the subfossil and the extant populations.

TABLE 2. Results of the ANOVA between sexes with dental crest length versus number of teeth. Data only from extant population

		d.f.	Probability
Covariate			
Regression coefficient	0.49		
t-value	9.10		$P < 0.001$
Adjusted group means			
Males	18.18		
Females	17.69		
Equality of adjusted means			
F value	0.42	1	$P = 0.524$
Zero slopes			
F value	82.80	1–19	$P < 0.001$
Equality of slopes			
F value	2.01	1–18	$P = 0.321$
t-test for adjusted group means			
t value	0.65		$P = 0.524$

TABLE 3. Results of the ANOVA between populations with dental crest length versus number of teeth. Data from the three populations studied

		d.f.	Probability
Covariate			
Regression coefficient	0.25		
t value	24.42		$P < 0.001$
Adjusted group means			
Ingenio (4000 BP)	21.08		
S. Nicolás (2000 BP)	21.46		
Present day	21.25		
Equality of adjusted means			
F value	0.85	1	$P = 0.565$
Zero slopes			
F value	458.16	1–86	$P < 0.001$
Equality of slopes			
F value	0.42	1–84	$P = 0.660$
Between each group and all others			
Ingenio (4000 BP)	0.00	1–85	$P = 0.989$
S. Nicolás (2000 BP)	0.35	1–85	$P = 0.557$
Present day	0.62	1–85	$P = 0.434$

t-test for Adjusted group means

t value:			probability:		
	Ing.	S. Nic.		Ing.	S. Nic.
S. Nic.	1.07		S. Nic.	0.29	
P. Day	0.43	0.49	P. Day	0.67	0.62

TABLE 4. Results of the ANOVA between populations with dental crest length versus heterodonty. Data from the three populations studied

		d.f.	Probability
Covariate			
Regression coefficient	−3.53		
t value	−6.72		$P < 0.001$
Adjusted group means			
Ingenio (4000 BP)	182.84		
S. Nicolás (2000 BP)	190.50		
Present day	201.92		
Equality of adjusted means			
F value	1.99	2	$P = 0.143$
Zero slopes			
F value	45.14	1–85	$P < 0.001$
Equality of slopes			
F value	0.00	2–83	$P = 0.998$
Between each group and all others			
Ingenio (4000 BP)	0.62	1–84	$P = 0.979$
S. Nicolás (2000 BP)	3.26	1–84	$P = 0.953$
Present day	1.55	1–84	$P = 0.967$

t-test for adjusted group news

t value:			Probability:		
	Ing.	S. Nic.		Ing.	S. Nic.
S. Nic.	0.87		S. Nic.	0.39	
P. Day	1.98	1.07	P. Day	0.06	0.29

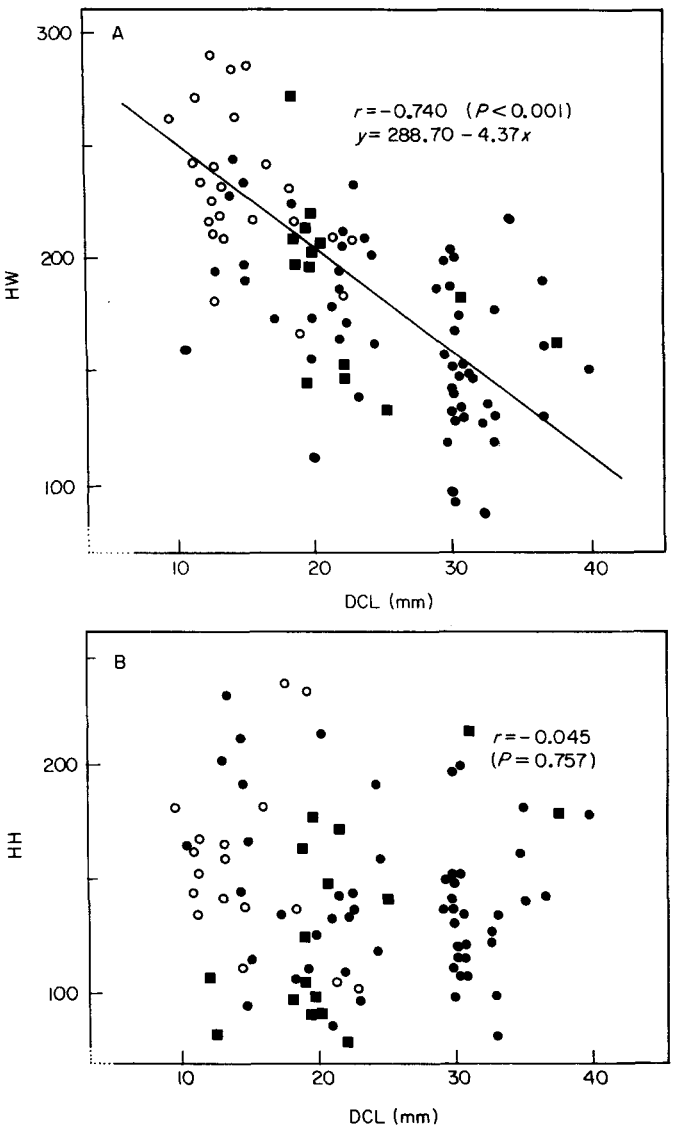

Figure 4. Variation of heterodonty with the DCL. A, Width variation; B, height variation. ●, Ingenio; ■, La Aldea; ○, Mogán.

Thus, the present-day population where the *r* value is not significant can be considered the same statistically, for example Ingenio and La Aldea (Fig. 4, Table 4).

The mean number of cusps per tooth remains constant throughout the adult life of both extant and fossil animals. In newborn and very young individuals (SVL less than 60 mm) each tooth has only three well-defined cusps, the same number as in the newborn of the rest of the species of the Lacertidae family analysed. Shortly after birth and in any case before the end of one year, some teeth begin to acquire one or two additional cuspids in the anterior or posterior

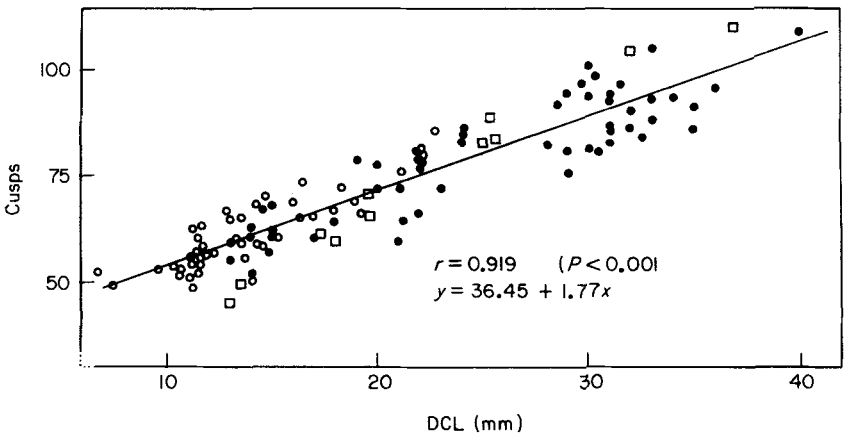

Figure 5. Variation of cuspid number with DCL. ●, Ingenio; □, La Aldea; ○, Mogán.

maxillary region, respectively. Some teeth may show up to six cusps. The total number of cusps per maxillary bone is dependent on the size of the lizard (Fig. 5).

Food

Figure 6 shows the dry weight percentages of plant matter ingested by 62 lizards of different size. The values show a gradual increase with lizard size and approach 100% in the larger animals.

The plant component in the food of *G. stehlini* consist mainly of flowers, florescences, seeds and fruits; and to a lesser extent shoots, leaves and stems. Animal prey were almost exclusively insects (mainly Diptera and also small Coleoptera and Hymenoptera).

DISCUSSION

From the results it is clear that in dental morphology and food type *G. stehlini* is unusual within the Lacertidae family. Unlike other species in the family, such as *Lacerta lepida*, *L. pater*, *Archaeolacerta bedriagae* or *Psammodromus algirus* (Cooper, 1963; own data), the giant lizards of Gran Canaria lack 'projecting' teeth in the anterior region of the maxillar bone. The canine-like teeth have been linked to the need to pierce chitinous shells of arthropods which make up the largest part of their diet (own data). However, these prey are absent from the food of *G. stehlini*. The decrease in width of the posterior maxillary and dentarium teeth as the animal grows, coincides with a decrease in the presence of insects in the diet. The presence of molariform teeth in Sauria has been interpreted as an adaptation to the ingestion of hard animal prey (Edmund, 1969; Estes & Williams, 1984; Augé, 1986).

As the giant lizards of Gran Canaria island grow, the mean number of cusps per maxillary bone increases (Fig. 5) which, together with the gradual increase in the number of teeth, causes the dentarium and maxillary bones of the adults animals to function like serrated knives. This effect has also been described in the

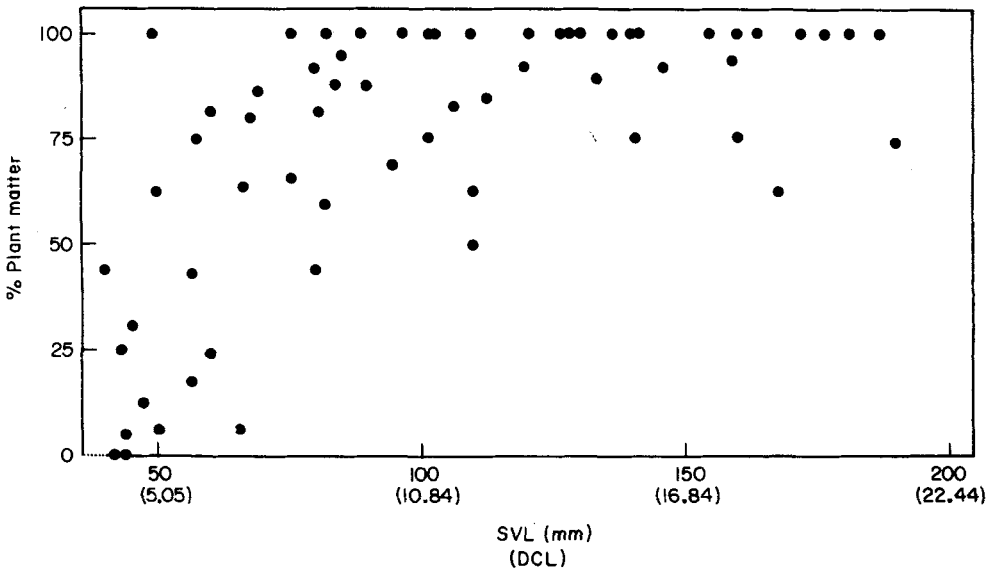

Figure 6. Dry weight percentages of plant matter ingested by 62 different-sized *Gallotia stehlini* from Gran Canaria Island.

Iguanidae family (Montanucci, 1968), where species which have a greater numbers of cusps also show a more herbivorous diet.

Regarding the changes that *G. stehlini* has undergone in the last 4000 years, it is clear that the giant lizards of Gran Canaria are smaller than the fossil lizards. From 4000 to 2000 years ago the maximum sizes between the two subfossil populations studied did not change; however, in the period from 2000 years ago to the present a decrease in the maximum size of the species occurred coinciding with the arrival of man on Gran Canaria (1890 years BP; Onrubia, 1987). Competition with mammals introduced by man (goats and, later, rabbits) must have had an effect on the maximum size and also possibly on the mean size of the species. This relationship between the arrival of man on an island and a reduction in size of certain species of reptiles has already been shown on other islands (Pregill, 1981, 1986).

The dentition traits of the giant lizards inhabiting the island before the human settlement suggest an almost totally herbivorous diet, including possibly a considerable consumption of leaves and shoots.

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