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MORPHOLOGICAL VARIATION IN THE LACERTID *GALLOTIA SIMONYI MACHADOI* AND A COMPARISON WITH THE EXTINCT *GALLOTIA SIMONYI SIMONYI* FROM EL HIERRO (CANARY ISLANDS)

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Morphological variation was investigated in 56 live adult specimens (31 male, 25 female) and ten dead near-hatching embryos of *G. simonyi machadoi* from the "Centro de Reproducción e Investigación del lagarto gigante del Hierro" (Frontera, El Hierro). Dimensions, scalation and teeth traits were measured and quantified. Males and females differed significantly (multivariate analysis of variance) in most of these traits, with values for males being greater than those for females. All traits significantly increased with SVL at a greater rate in males than in females, except for body weight, where no significant difference was found. A qualitative comparison between data from *G. s. machadoi* and those for ten *G. s. simonyi* showed that for most biometric traits, ranges overlapped for the two subspecies, but mean and maximum values were higher in *G. s. simonyi.* Hind limb length increased at a greater rate relative to SVL in *G. s. simonyi* than in *G. s. machadoi.*

INTRODUCTION

The lacertids from the Canary Islands are included within the endemic genus *Gallotia* (Arnold, 1973) and are represented by four living species and one or two that are extinct. Two of the living species are large (up to 265 mm snout-to-vent length): *G. stehlini,* Schenkel 1901 (Gran Canaria) and *G. simonyi* Steindachner, 1889 (El Hierro). The remaining two species: *G. galloti* Oudart, 1839 and *G. atlantica* Peters & Doria, 1882 are smaller (up to 145 mm. SVL).

Two extinct species were giant lizards that have been classified on the basis of biometry and teeth number: *G. goliath* Mertens 1942 and *G. maxima* Bravo 1953. Four extant and extinct subspecies of *G. simonyi* have been described. Now extinct are *G. s. simonyi,* known only from a small islet near the NW coast of El Hierro island, and *G. s. gomerana,* restricted to La Gomera island (Hutterer, 1985). A very reduced population of the subspecies *G. s. machadoi* still persists in the NW of El Hierro island (López-Jurado, 1989). A new subspecies of *G. simonyi* has been recently discovered in the NW of Tenerife (Hernández *et al.*, submitted).

The first data on morphological traits of the living *G. s. machadoi* were published by Machado (1985) and López-Jurado (1989), but due to danger of extinction of this population, few specimens were studied and morphological variation has been reported only in a few cases. The general biology, behaviour and ecology of *G. s. machadoi* is almost unknown. The remaining population lives on a small rocky platform on a very steep inland cliff near Frontera. The species is mostly herbivorous (Machado, 1985), oviparous (4-14 eggs per clutch) and the reproductive breeding time occurs between May and June-July (Rodríguez-Domínguez & Molina-Borja, in press).

Based on immunological and genetic analyses, some hypotheses have been suggested to explain the origin and later diversification of *Gallotia* forms on different islands of the archipelago (Mayer & Bischoff, 1991; Thorpe *et al.*, 1993*a,b*). Comparing the results of the latter papers with those of more recent analyses (González *et al.*, 1996), different taxonomic relationships are shown for *Gallotia* species. While *G. galloti* is divided into two lineages (*G. g. galloti* and *G. g. caesaris*) in the study by Thorpe *et al* (1993*a*), the traditional subspecies are maintained by González *et al.* (1996). Overall, no clear picture yet exists to explain the present distribution and evolution of the Canarian lizards.

The study of endemic Canarian lizards can thus be considered as important both from an evolutionary point of view and as a means to evaluate different palaeobiogeographic models.With this evolutionary approach in mind, the aims of the present work are: (1) to characterize the morphological variability of living male and female specimens of *G. s. machadoi*; and (2) to compare these parameters with those obtained from published and unpublished data of some specimens of the extinct *G. s. simonyi* and *G. goliath.* The present results present the first quantitative data on living specimens of the endangered *G. s. machadoi.*

MATERIAL AND METHODS

Fifty-six live adult specimens (31 males and 25 females) and ten embryos which died close to hatching of *G. s. machadoi* from the "Centro de Reproducción e

Investigación del lagarto gigante del Hierro" (Frontera) were studied in the present work. Data on some *G. s. simonyi* (Bischoff, unpublished) and fossil *G. goliath* (Castillo *et al.*, 1994) were also compared with those of *G. s. machadoi.*

Twenty-seven biometric traits were measured in all the specimens using the criteria expressed by Pérez-Mellado & Gosá (1988). The traits were (a) Body parameters: body weight (BW), snout-to-vent length (SVL), head length (HL), head width (HW), head depth (HD), fore limb length (FLL), hind limb length (HLL), rostral to anterior eye edge (REE), nostril to anterior eye edge (NEE); (b) Scalation traits: masseteric scale diameter (MSD), number of temporal scales (temporalia, T), supraciliary granules (SG), supraciliary scales (supraciliaria, SS), gular scales (gullaria, G), dorsal scales (dorsalia, D), ventral longitudinal scales (ventralia longitudinalis, VL), ventral transversal scales (ventralia transversalis, VT), femoral pores (FP), fourth finger scales (lamellae, L); and (c) dentary traits: number of premaxillary teeth (PT), maxillary teeth (MAX), dentary teeth (DEN) and pterygoid teeth (PTE). A digital caliper (0.01 mm precision) was used to record the biometric data and body weight was obtained by a dynamometer (1 g precision). All individuals of nine years old or less were born in captivity in the "Centro de Reproducción e Investigación del lagarto gigante del Hierro" and maintained (usually in pairs) in outdoor large terraria. The five remaining individuals, aged between 12-16 years old (extrapolated from animals of known age and SVL), were captured in their natural habitat and also maintained in outdoor terraria. The lizards had no predator pressure and were fed *ad libitum* with plant food obtained from the natural vegetation of the area and with insects and newborn mice. The diet was supplemented with vitamins and calcium.

Descriptive statistics were obtained for all traits. Measurements were not independent, so male-female trait comparison was analysed by Multivariate Analysis of Variance (MANOVA, with SVL as covariate). Least square regression analyses (LSR) were also performed to explore the relationship between individual morphological traits and SVL (as the independent variable) within each sex. For LSR, simple linear regression of log-transformed data was used. Slope values for each regression were compared with theoretical values (3.0 for body weight and 1.0 for the other traits) by means of a *t*-test. Analysis of covariance (ANCOVA) was used to compare single body dimensions among sexes taking into account SVL as the covariate (all data log-transformed).

RESULTS

MORPHOLOGICAL TRAIT VARIATIONS IN *G. S. MACHADOI*

Age and weight or size relationships. The relationships between snout-to-vent length and age, and body weight variation and age, of all posthatching lizards are presented in Fig. 1. The increase in the rate of both traits is greater in the earlier adult stages (4-8 years old), slowing down in the later ones (>8 years old).

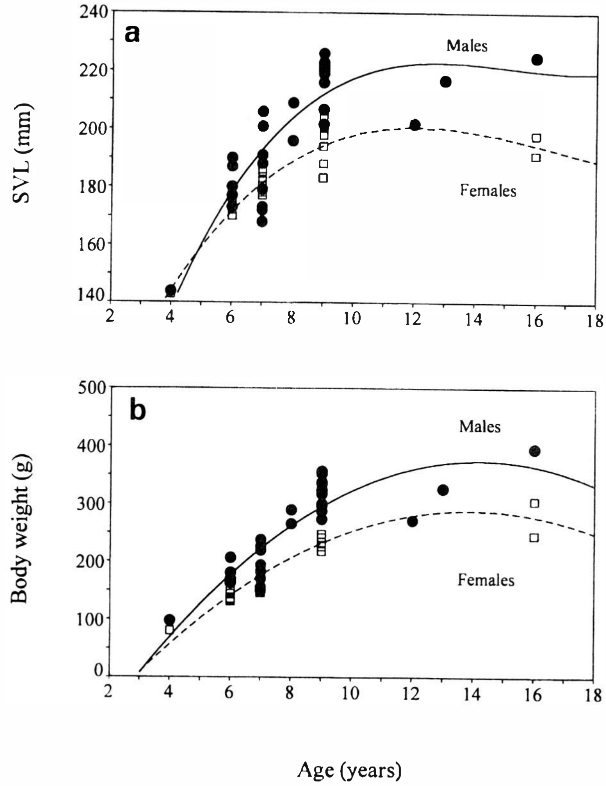

FIG. 1. Growth curves for male (closed circles) and female (open squares) *G. s. machadoi.* SVL (a) and body weight (b) regressed on age.

Body traits. Mean values, standard errors, range, sample size and coefficient of variation for different body traits of embryos (E), males (M) and females (F) are shown in Table 1a. Males and females differed significantly when considering body dimensions (BW, SVL, HL, HW, HD, FLL, HLL, REE and MSD) with SVL as the covariate (MANOVA, $F_{9,45}=17.08$, $P<0.0001$).

Scalation and teeth traits. Considering scale size and morphology, two zones are distinguished in the temporal region: (1) a central zone around the masseteric scale showing a great variability in number and size of scales; and (2) a tympanic region with small size scales and nearly constant scale number. Some females showed a very reduced scale number in the central zone of temporal region, the scale sizes being of a similar size to the masseteric one.

In the embryos, dentition in dentary and maxilar bones was heterodont. The first five to six dentary teeth are small and incisor-like. The first two had well-developed cuspids pointing to the rear of the mouth. Teeth posterior to the sixth are large, wide and tricuspid with well-developed lateral cuspids. Similar heterodonty is found in maxillar teeth. Adult dentary and maxillar bones also exhibit a similar dentition. Adult pterygoid teeth are usually situated in one row but were aligned in two rows for seven individuals.

TABLE 1. Mean, standard error, range, sample size and coefficient of variation for: (a) Body Weight (BW), Snout-to-Vent Length (SVL), Head Length (HL), Head Width (HW), Fore Limb Length (FLL), Hind Limb Length (HLL), Rostral-to-Eye Edge (REE), Nostril-to-Eye Edge (NEE); (b) Masseteric Scale Diameter (MSD), Number of: Temporals (T), Supraciliary Granules (SG), Supraciliary Scales (SS), Gular scales (G), Dorsal Scales (D), Ventral-Longitudinal scales (VL), Ventral-Transversal scales (VT), Femoral pores (F) and fourth finger Lamellae (L) of *G. s. machadoi*, *G. s. simonyi* and *G. goliath*; and (c) teeth numbers: Premaxilar (PRM), Maxillar (MAX), Dentary (DEN) and Pterygoides (PTE) in *G. s. machadoi* and *G. goliath*. * SVL values for *G. goliath* have been extrapolated from the regression function relating Head Length and SVL in *G. s. machadoi* and therefore are approximate figures.

	BW	SVL	HL	HW	HD	FLL	HLL	REE	NEE
G.s.machadoi									
(E)									
mean	-	40.81	12.27	6.07	5.45	17.25	27.0	4.67	3.45
±SE	-	0.85	0.47	0.18	0.16	0.32	0.98	0.16	0.18
range		35.4-43.7	11.4-15.9	5.0-7.0	4.4-6.20	14.5-18.8	20.4-30.4	3.5-5.3	2.5-4.1
n		9	9	10	9	10	10	10	9
CV(%)		6.3	11.6	9.5	9.3	7.0	11.5	11.1	15.6
G.s.machadoi									
(ad. male)									
mean	251.42	198.61	47.98	19.98	26.29	70.82	97.7	21.38	15.99
±SE	13.74	3.85	1.04	0.41	0.72	1.18	1.41	0.43	0.31
range	98-396	144-226	32.1-56.4	15.1-25.1	16.5-34.1	54.4-84.2	79.3-114.2	14.2-24.9	11.0-19.2
n	31	31	31	31	31	31	31	31	31
CV(%)	30.4	10.8	12.1	11.4	15.2	9.3	8.1	11.3	11.1
G.s.machadoi									
(ad. female)									
mean	186.2	182.04	40.08	17.45	22	63.18	88.3	18.23	13.55
±SE	10.44	2.5	0.59	0.29	0.52	0.55	0.75	0.29	0.18
range	81-306	143-204	31.2-45.1	14.6-20.1	15.8-27.0	55.1-67.9	76.7-96.1	14.5-21.4	11.3-15.8
n	25	25	25	25	25	25	25	25	25
CV(%)	28	6.9	7.5	8.5	11.9	4.4	4.3	8	6.7
G.s.simonyi									
(male)									
mean	-	227.6	53.93		31.36	82.16	124.57	-	
±SE	-	4.17	1.87		2.28	1.59	2.91	-	
range		223-236	50.4-56.8		27.4-35.3	79.5-85.0	120-130		
n		3	3		2	3	3		
CV(%)		3.2	6		12.6	3.4	4.1		
G.s.simonyi									
(female)									
mean	-	197.9	45.41		27.48	73.24	92.24	-	
±SE	-	20.65	4.63		4	6.69	6.3	-	
range		119-255	27.4-60.0		14.9-44.2	62.5-99.0	70.0-107.5		
n		6	6		6	5	5		
CV(%)		2.6	2.5		35.7	20.4	15.3		
G. goliath									
1		308.8*	76.84	52.51					
2		361.5*	90.62	-					

Significant differences were also found between male and female scalation: T, F and L (MANOVA, $F_{9,45}$=2.72, P=0.013), but no significant difference was obtained when considering teeth (PRM, MAX, DEN, PTE) numbers ($F_{3,52}$=1.13, P=0.34).

Isometric/allometric relationships. Male body traits increased with SVL at a greater rate than those for females as shown by ANCOVA (as an example, see Fig. 2 for HL-SVL relationship), except for HD and MSD (Fig. 3) where the contrary occured. Slopes of regressions were significantly greater than 1.0 for HL and HD in males and for HD and MSD in females (Table 2), and significantly greater than 3.0 in BW for females.

MORPHOLOGICAL TRAIT VARIATIONS IN *G. S. SIMONYI* AND COMPARISON WITH *G. S. MACHADOI*.

Mean values, standard errors, range, sample size and coefficients of variations for the different morphological traits of male (M) and female (F) *G. s. simonyi* are shown in lower cells of Tables 1a, b and c.

A qualitative comparison between *G. s. simonyi* and *G. s. machadoi* reveals that although mean and maximum values are higher (both sexes) in *G. s. simonyi*, there is an overlap in range for most biometric traits.

Overall ranges for the scalation traits are very similar except in the male temporal region where *G. s. simonyi*

TABLE 1b. Details as Table 1a.

	MSD	T	SG	SS	G	D	VL	VT	F	L
G.s.machadoi										
(E)										
mean		56.1	9.66	6.66	29.9	90.6	17.4	37.25	27.88	32.5
±SE		1.42	0.66	0.37	0.58	1.91	0.52	0.75	0.96	0.8
range		50-65	6-13	4-8	27-32	80-99	14-19	35-40	24-33	28-36
n		10	9	9	10	10	10	8	9	10
CV(%)		8.0	20.7	16.8	6.2	6.7	9.5	5.7	10.4	7.8
G.s.machadoi										
(ad. male)										
mean	5.12	63.77	8.94	6.26	31.65	89.55	18.81	35.61	27.74	32.45
±SE	0.14	1.38	0.3	0.19	0.32	0.59	0.25	0.22	0.29	0.25
range	3,7-7,2	50-81	4-12	4-8	27-36	83-95	16-23	32-39	24-32	30-35
n	31	31	31	31	31	31	31	31	31	31
CV(%)	15.8	12.1	18.9	17.0	5.7	3.7	7.6	3.5	6.0	4.3
G.s.machadoi										
(ad. female)										
mean	4.13	56.24	9.44	6.28	31.4	89.0	18.04	35.44	26.24	30.64
±SE	0.13	1.65	0.28	0.17	0.34	0.64	0.21	0.15	0.31	0.39
range	2,7-5,6	39-78	7-13	5-8	27-34	85-96	16-20	34-37	23-29	24-35
n	25	25	25	25	25	25	25	25	25	25
CV(%)	15.8	14.7	15.0	14.2	5.5	3.6	5.9	2.2	5.9	6.5
G.s.simonyi										
(male)										
mean		31.5	14.0	5.0	31.33	94.0	19.0	32.66	30.33	33.0
±SE		1.5	0	0	1.2	3.46	1	0.88	0.33	1
range		30-33	14-14	5-5	29-33	88-100	18-21	31-34	30-31	31-34
n		2	2	3	3	3	3	3	3	3
CV(%)		0.067	0	0	6.6	6.4	9.1	4.7	1.9	5.2
G.s.simonyi										
(female)										
mean		30.6	12.75	5.16	32.33	96.0	20.0	33.86	30.83	33.16
±SE		2.29	0.62	0.16	1.11	1.32	0.72	0.67	1.04	0.4
range		25-39	11-14	5-6	29-36	93-103	18-23	31-36	27-33	32-34
n		5	4	6	6	7	7	7	6	6
CV(%)		16.8	9.9	7.9	8.5	3.7	9.6	5.2	8.3	3
G. goliath										
1	11.72	25	7	6						
2	16.55	21	7	6						

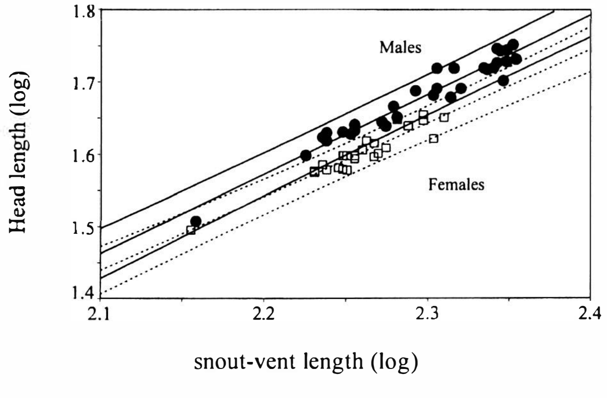

FIG. 2. Relationships of Head Length to Snout-to-Vent Length in *G. s. machadoi* males (closed circles, HL=0.14 + 1.1 SVL, R^2= 94.22%, F=473.06, P<0.0001) and females (open squares, HL = 0.199 + 1.02 SVL, R^2= 89.85%, F=203.53, P<0.0001). Lines lateral to the central regression lines (solid for males and dashed for females) correspond to 95% confidence intervals.

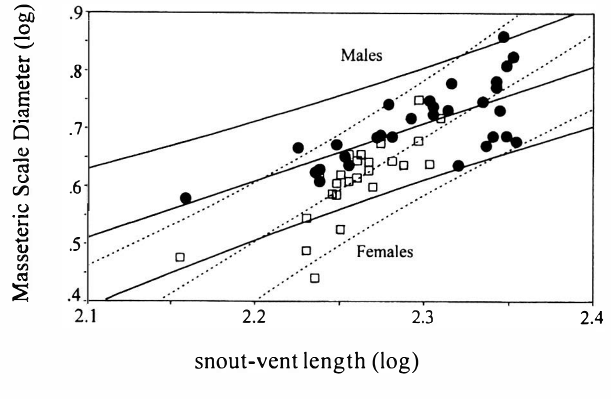

FIG. 3. Regression of Masseteric Scale Diameter on SVL for males (closed circles, MSD = 0.04 + 0.91 SVL, R^2= 52.63, F=31.11, P<0.0001) and females (open squares, MSD = 0.00072 + 1.66 SVL, R^2= 67.16, F=44.98, P<0.0001). External lines as in the previous figures.

TABLE 1c. Details as Table 1a.

	PRM	MAX	DEN	PTE
G.s.machadoi (ad. male)				
mean	6.9	18	21.45	5.12
±SE	0.12	0.2	0.27	0.96
range	6-9	16-20	18-24	3-9
n	31	31	31	31
CV(%)	10.1	6.3	7.1	29.24
G.s.machadoi (ad. female)				
mean	6.44	17.4	20.52	4.25
±SE	0.11	0.17	0.29	0.2
range	5-7	16-19	17-23	3-7
n	25	25	25	25
CV(%)	9.1	5	7.2	23.13
G.goliath				
1	9	25	31	18
2	9	25	32	/

has a lower scale number than *G. s. machadoi*. The scale range in the temporal region of females is also lower in *G. s. simonyi* but it is continuous with that of *G. s. machadoi*; this is due to the reduced number of scales in some females of the last subspecies.

Two-way ANCOVA analysis showed that the increasing rate of HLL in relation to SVL was significantly greater in *G. s. simonyi* than in *G. s. machadoi* (F= 75.36; df=1,62; P<0.001), significantly greater in males than in females (F=20.28; df=1,62; P<0.001).The effect of interaction between sex and species on HLL was only close to significant (F=3.92; df=1,62; P=0.052), probably due to the small number of data for *G. s. simonyi*.

DISCUSSION

SEXUAL DIMORPHISM IN *G. S. MACHADOI*

Sexual size dimorphism. Mean SVL was significantly higher in male *G. s. machadoi* than in females, as observed in the closely-related species *G. galloti galloti* and *G. g. eisentrauti* (Molina-Borja *et al*., 1997). Several factors can affect sexual size dimorphism when animals mature at a small size and then continue to grow to a larger asymptotic size (Stamps, 1993), as is the case with *G. s. machadoi* (Rodríguez-Domínguez, unpublished observations). For example, studies have demonstrated sex differences in the size at maturity (Lovich & Gibbons, 1990) and asymptotic size (Dunham, 1978). These factors, in turn, can be affected by several ecological characteristics of the species under study, as for example, differential survival rates of males and females, and sex differences in spatial or temporal distribution (see Stamps *et al*., 1994 for a review).

TABLE 2. Slopes of the regression lines of different body traits on SVL, and significance levels (P, t-test) of the comparisons with theoretical values (3.0 for body weight and 1.0 for the rest). ** P<0.01; *P<0.05; NS, not significant).

	Males	Females
Body weight	2.88 NS	3.68*
Head length	1.10*	1.02 NS
Head width	0.89 NS	0.92 NS
Head depth	1.30**	1.49**
Forelimb length	0.78**	0.42**
Hind limb length	0.67**	0.38**
Rostral to anterior eye edge	1.00 NS	0.92 NS
Masseteric scale diameter	0.91 NS	1.66**
Maxillar teeth	0.34**	/
Dentary teeth	0.43**	/

Since all *G. s. machadoi* specimens were raised under the same semi-captive conditions, the resulting sexual size dimorphism cannot be due to ecological factors which differentially affect males and females. It is therefore suggested to be due to intrinsic differential growth rates of males and females (size at maturity is usually lower in females than in males of other *Gallotia* species, Castanet & Báez, 1991). Future research is needed to determine if the same growth patterns occur in free-living *G. s. machadoi*.

Intersexual differences in head parameters. In *G. s. machadoi* relative male head length was significantly greater than female head length (Fig. 2). Previous studies in other Canarian lizards have shown a similar pattern in HL-SVL relationships. For example, in *G. galloti galloti* and *G. g. eisentrauti* (from Tenerife island), males had significantly longer heads than females in relation to SVL (Molina-Borja *et al*., 1997). Preliminary data show the same pattern for *G. g. palmae* and *G. g. caesaris* (Molina-Borja & Rodríguez-Domínguez, in preparation). However, this pattern of sexual dimorphism was not found in a previous study on *G. stehlini* (Mateo & López-Jurado, 1992). On the other hand, while HL increased at a greater rate in males than in females, the contrary occurred for HD.

Sexual dimorphism in head size could result from sexual selection (Hews, 1990; Anderson & Vitt, 1990) or sexual segregation in resource food utilization (Simon & Middendorf, 1976; Schoener, 1977; Shine, 1990). However, intersexual differences in adult head sizes of herbivorous lizards do not correlate with differences in consumed food sizes (Carothers, 1981; Auffenberg, 1982; Dugan & Wiewandt, 1982). Herbivorous iguanid species having high male aggression usually have a positive HL-SVL allometry (Carothers, 1984). Differential energetic demands in both sexes would presumably have much less effect on head size than on body size, if any. For that reason, head dimorphism might more clearly be a consequence of sexual selection than would body size dimorphism.

Adult *G. s. machadoi*. are omnivorous, with a greater proportion of vegetable matter than of insects in their diet (Machado, 1985), and a possible resource partitioning between the sexes cannot be ascertained at present. On the other hand, although inter-male aggression has been reported (Machado, 1985), there is no specific study of the influence of head size (or any other trait) on male intrasexual competition or mate choice. Therefore, the possible contribution of sexual selection on male head size remains to be determined in *G. s. machadoi* and other Canarian lizards. However, for *G. g. galloti* the contribution of intrasexual competition on male head size has been suggested (Molina-Borja *et al*., 1998).

Intersexual differences in limb length and pholidotic traits. Our analyses revealed significant sexual size dimorphism in anterior and posterior limb lengths in relation to SVL, those of males increasing at a greater rate than that of females (although the increase rate of limb growth is lower than that of SVL, as reflected in slopes < 1.0). The functional significance of this difference in the increased rate of limb length growth is not known, but it could reflect a need for higher running speed or endurance in males than in females as has been suggested for the adult-juvenile comparison in other species (Huey *et al*., 1984; Tsuji *et al*., 1989).

Although males had a larger masseteric scale than females ($P<0.01$), females did show a greater rate of increase of the masseteric scale diameter in relation to SVL than that of males (Fig. 3).

COMPARISON OF *G. S. MACHADOI* WITH *G. S. SIMONYI*

Overall, *G. s. simonyi* was larger than *G. s. machadoi*. Hind limbs of the first subspecies were much longer than those of the second, both in absolute and relative terms. Relatively longer HLL have been considered and shown to be positively correlated with higher maximum sprint speeds in several lizard species (Garland, 1985; Losos, 1990; Bauwens *et al*., 1995). This may apply also to the comparison between *G. s. simonyi* and *G. s. machadoi* but data on maximum sprint speed are not available for the second subspecies and cannot be gathered from the now extinct *G. s. simonyi*.

COMPARISON WITH *G. GOLIATH*

A recent study of two mummified specimens assigned to *G. goliath* from Tenerife (Castillo *et al*., 1994) described for the first time some head external characteristics (see lowest cells of Table 1) and showed their similarities to those of *G. s. simonyi*.

Although statistical comparisons between *G. s. simonyi* and *G. goliath* are not feasible (only two specimens available), the two *G. goliath* individuals measured so far showed much larger SVL and HL values than *G. s. machadoi* and *G. s. simonyi*. Furthermore, *G. goliath* has a higher number of maxilary and dentary teeth than *G. s. machadoi*, a result already reported by previous studies (Mertens, 1942; Hutterer, 1985).

With respect to scalation, *G. goliath* had a lower number of temporal scales than *G. s. machadoi*, but in one case this number is equal to the minimum found in a female *G. s. simonyi*. In contrast, SG and SS numbers are similar in both species.

In conclusion, our analyses revealed that adult males and females *G. s. machadoi* differed in growth curves and also in body traits. The latter increased with SVL at a greater rate in males than in females, except Head Depth and Masseteric Scale Diameter where the contrary ocurred. The rate of increase of body weight with SVL did not differ between males and females. Ranges of most biometric traits overlapped between *G. s. machadoi* and *G. s. simonyi*, but mean and maximum values were higher in the second subspecies. For the available data, Hind Limb Length increased at a greater rate than SVL in *G. s. simonyi* than in *G. s. machadoi*.

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