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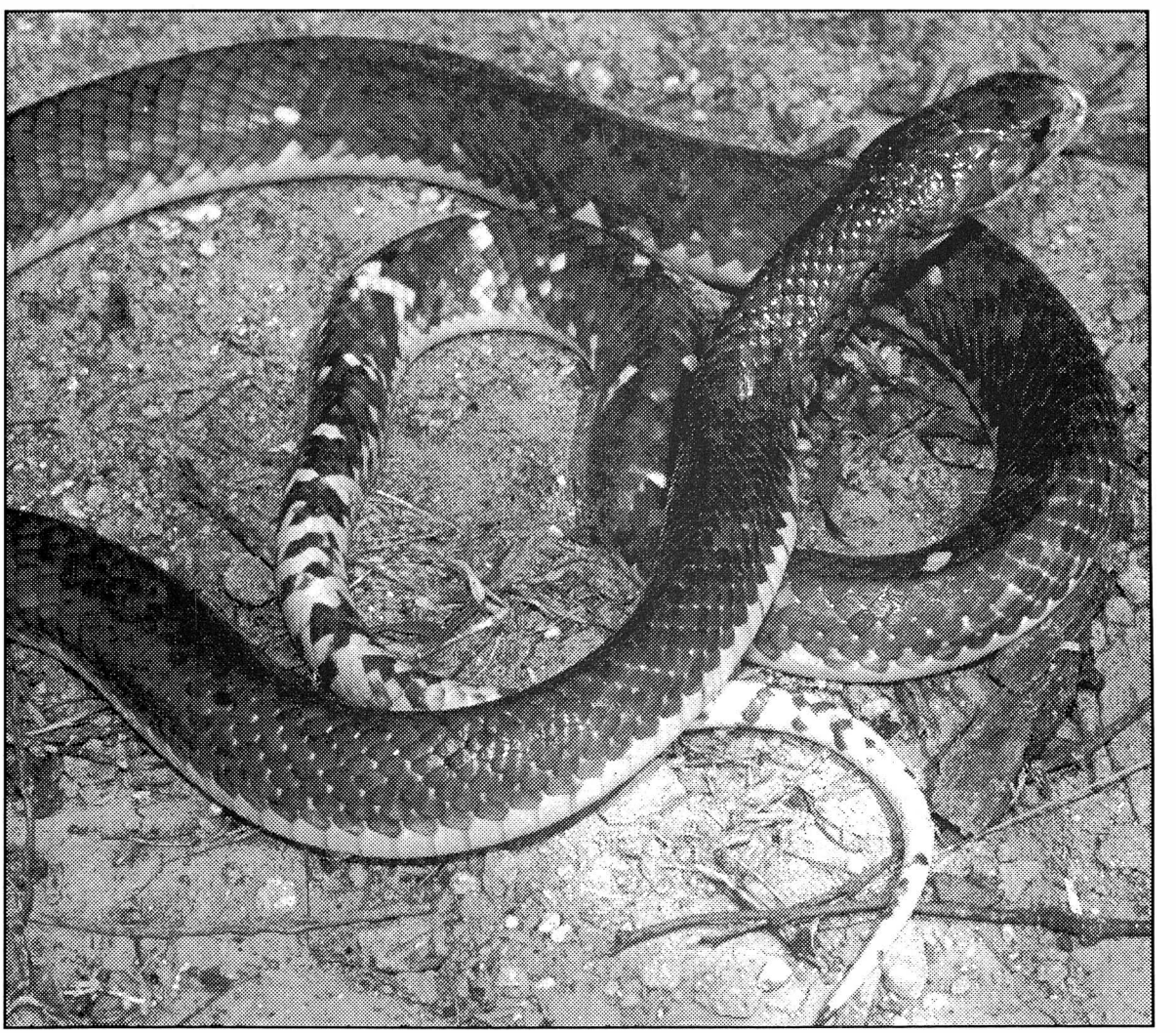

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FRONT COVER: Male indigo snake, *Drymarchon caudomaculatus* (W. Wüster)

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SPECIES DISTINCTION AND RELATIONSHIPS OF THE WESTERN IBERIAN *PODARCIS* LIZARDS (REPTILIA, LACERTIDAE) BASED ON MORPHOLOGY AND MITOCHONDRIAL DNA SEQUENCES

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Wall lizards (*Podarcis*) are the dominant reptile group across most of southern Europe. Their taxonomy is complex because most species exhibit substantial intraspecific morphological polymorphisms. We have estimated the phylogeny of the particularly diverse western Iberian forms using partial cytochrome oxidase and cytochrome *b* mitochondrial DNA sequence data and have compared this against morphological variation. Of the two currently recognized species in the area – *Podarcis hispanica* and *P. bocagei* – neither is monophyletic, and extremely high genetic diversity between newly identified forms (up to 15% cytochrome *b* divergences) indicates that both are species complexes. *Podarcis b. bocagei* is genetically distinct from *P. (b.) carbonelli* which appears to be a separate species using both mtDNA and protein electrophoretic data. The insular form previously assigned to *P. b. berlengensis*, and sometimes argued to deserve species status is not genetically distinct from *P. (b.) carbonelli* using the mtDNA sequences. *P. hispanica* can be separated into at least four highly divergent groups, two in western Iberia, one in eastern Iberia and one in North Africa.

Key words: phylogeny, cytochrome *b*, cytochrome oxidase, morphology, Iberian lizards

INTRODUCTION

On the Iberian Peninsula three species of insectivorous wall lizards have been recognized – the Iberian wall lizard, *Podarcis hispanica* Steindachner 1870; Bocage's wall lizard, *Podarcis bocagei* Seoane 1884; and *Podarcis muralis* Laurenti 1768. *Podarcis bocagei* and *P. hispanica* live in sympatry in large areas of NW Iberia (Galán, 1986; Pérez-Mellado & Galindo, 1986; Sá-Sousa, 1995*a*). Both exhibit pronounced sexual dimorphism, adult males being larger than females and having more intense colour patterns (Galán, 1986; Pérez-Mellado & Galindo, 1986).

Podarcis hispanica is a medium sized (SVL 65-70 mm), morphologically variable rock-dwelling lizard, which is found in SW France (Langedoc-Rousillon and Cévennes), the Iberian Peninsula (except the northernmost corner) and NW Africa (Galán, 1986; Guillaume, 1987, 1997). Despite taxonomic controversy about *P. hispanica* subspecies, two forms have been recognized in Portugal (Sá-Sousa 1995*a*, 2000*a*). First, there is a NW Iberian form (*P. hispanica* type 1) that resembles the "lusitanica" form of Guillaume (1987). *P. hispanica* type 1 is found in Galicia, in the 'Submeseta Norte' plateau, in the northern half of Portugal and on the 'Sistema Central' mountain range (Sá-Sousa, 2000*a*). In Portugal, *P. hispanica* type 1 seems to inhabit mainly highlands (>400 m) where either Atlantic or continental climatic conditions may prevail. It has been found in the northern part of Portugal, north of the Tagus river (Sá-Sousa, 2000*a*). *P. hispanica* type 1 has the following characteristics: flattened head and body; either reticulated or striped dark dorsal patterns; and whitish-pearly coloured belly (for details see Pérez-Mellado, 1981*a,b*; Galán, 1986; Pérez-Mellado and Galindo, 1986; Guillaume, 1987; Sá-Sousa, 1995*a*).

P. hispanica type 2 (SW Iberian form) has been found in Andalusia, in Extremadura, in the Madrid region, and in the western and southern parts of Portugal (Sá-Sousa, 2000*a*). In Portugal, *P. hispanica* type 2 seems to prefer lowlands (<400 m) with a Mediterranean climate (Sá-Sousa, 2000*a*). This form has the following characteristics: head and body moderately robust; green and/or light brown patterns, and yellow-orange belly (see Klemmer, 1957; Salvador, 1986; Guillaume, 1987; González de la Vega, 1989; Sá-Sousa, 1995*a*). Given several records of *P. hispanica vaucheri* in SW Iberia (Boulenger, 1905; Klemmer, 1957; Salvador, 1974, 1986; Busack, 1986; Guillaume, 1987) one might hypothesize that morphologically *P. hispanica* type 2 and *P. hispanica vaucheri* are the same. However, we retain the *P. hispanica* type 2 denomination until further studies confirm whether similarity in phenotype corresponds to a common genotype across the entire range. So far all allopatric greenish morphotypes of wall lizard found in the southern part of Iberia (e.g. southern Portugal, Andalusia and Levant) have been considered as *P. h. hispanica* (Pérez-Mellado, 1998). Also *P. hispanica* type 2 is often mistaken for *P. b. bocagei*, because of their green or light-brown chromatic patterns, although the species show several differences and have allopatric distributions (Sá-Sousa, 1995*a*, 1998, 2000*a*).

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Podarcis b. bocagei is a medium-sized (adult snout-vent length, SVL=65-70 mm), ground-dwelling lizard, the males of which show green dorsal patterns, while females are brown with a pair of green stripes (Galán, 2000; Pérez-Mellado, 1981*a,b*, 1986; Sá-Sousa, 1995*a*). This species is an Iberian-Atlantic endemic occurring in W Asturias, Cantabria, Galicia and north of Portugal (Galán, 1986, 1997; Sá-Sousa, 1998). On a coarse scale, the distribution of *P. b. bocagei* can be largely explained by macroenvironmental variables and type of climate (Sá-Sousa, 2000*b*).

It has been suggested that *P. b. carbonelli* Pérez-Mellado 1981 merits species distinction (Sá-Sousa, in prep.; Sá-Sousa *et al.* 2000). *P. b. carbonelli* (SVL=50-55 mm) is a small, green ground-dwelling lizard, initially thought to be restricted to the W Sistema Central range (Pérez-Mellado, 1981*a,b*, 1986). However, it has been found in other mountain systems as well as along the Atlantic lowlands, particularly in Portugal (Magraner, 1986; Sá-Sousa, 1995*b*, 1999, 2000*b*). There, the type of climate – but also the balance between the number of frost days per year and the degree of aridity – appear important to explain the distribution of *P. b. carbonelli* (Sá-Sousa, in prep.).

Morphological characters and the existence of parapatric zones of contact between different types (i.e. without interbreeding) suggested that *P. bocagei* and *P. hispanica* might in fact be species complexes (Sá-Sousa, 2000*a* and in prep.). To resolve relationships between and within these groups, and to determine whether recognized clades based on morphological characters are genetically distinct, a phylogenetic analysis was conducted using DNA sequences derived from two mitochondrial genes, cytochrome *b* and cytochrome oxidase 1. Populations across the range of the accepted subspecies of *P. bocagei* were sampled. For the cytochrome *b* data sets previously published sequences of *P. hispanica* from eastern Spain and Morocco (Castilla *et al.*, 1998; Harris & Arnold, 1999) were included in the analyses.

TABLE 1. List of lizards examined in the mtDNA phylogeny. * indicates previously published data was included in the analysis. Sequences are deposited in Genbank (accession numbers AF372051 to AF372089). Map codes are shown in Fig. 1.

Species	mtDNA Code	Locality	CO1/ Cyt *b*	Map Code
Gallotia galloti		Gran Canaria	1/-	
Lacerta dugesii dugesii		Madeira	1/*	
Lacerta perspicillata		Mallorca	-/*	
Podarcis hispanica '*liolepis*'		Castellón, Spain	-/*	
Podarcis hispanica "type 1"	*P.h.*1	Vila Real, Pt.	1/1	B
	*P.h.*2	Montesinho, Pt.	1/-	A
	*P.h.*3	Montesinho, Pt.	1/-	A
Podarcis hispanica "Moroccan"	*P.h.m1*	High Atlas, Morocco	-/1	T
	P.h.m2	High Atlas, Morocco	1/1	T
	P.h.m3	High Atlas, Morocco	1/1	T
Podarcis hispanica "type 2"	*P.h.v1*	Leiria, Pt.	1/-	C
	P.h.v2	Portalegre, Pt.	1/1	D
	P.h.v3	Beja, Pt.	1/1	E
	P.h.v4	Marvao, Pt.	1/-	F
	P.h.v5	Águeda, Pt.	1/-	G
Podarcis bocagei bocagei	*P.b.b1*	Montesinho, Pt.	1/-	A
	P.b.b2	Montesinho, Pt.	1/-	A
	P.b.b3	Vila Pouca d Aguiar, Pt.	1/-	K
	P.b.b4	Serra do Gerês, Pt.	1/-	H
	P.b.b5	Vairão, Pt.	1/-	J
	P.b.b6	Vairão, Pt.	1/1	J
	P.b.b7	Vairão, Pt.	1/1	J
	P.b.b8	Braga, Pt.	1/-	I
	P.b.b9	Viana do Castelo, Pt.	1/-	L
	P.b.b10	Viana do Castelo, Pt.	1/-	L
	P.b.b11	Viana do Castelo, Pt.	1/1	L
Podarcis carbonelli carbonelli	*P.c.c1*	Serra da Estrela, Pt.	1/1	M
	P.c.c2	Torreira, Aveiro, Pt.	1/1	N
	P.c.c3	Monte Clérigo, Pt.	1/1	Q
	P.c.c4	Peniche,Pt.	1/-	P
Podarcis carbonelli berlengensis	*P.c.b.*	Berlenga isle, off Peniche	1/-	O

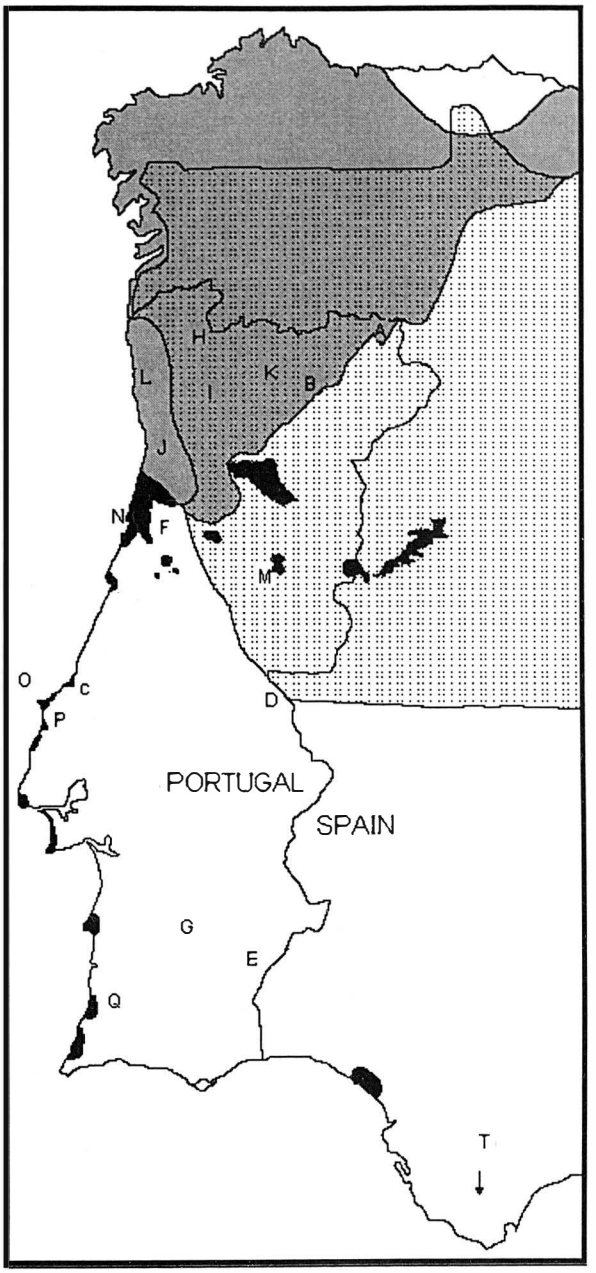

FIG. 1. Map showing the sampling localities used for the mtDNA analysis. The ranges of *P. hispanica* 1 (stippled), *P. b. bocagei* (grey) *and P. (b.) carbonelli* (black) are shown. *P. hispanica* 2 is found in the region south *of P. hispanica* 1, but the complete extent of its range is unknown.

MATERIALS AND METHODS

LABORATORY PROCEDURES

Localities of the lizards from which DNA was extracted and/or biometric characters were scored are given in Table 1. Tissue samples consisted of tail tips stored in 100% ethanol. Voucher specimens are kept at the University of Évora. Total genomic DNA was extracted from tail tissue using standard methods (Sambrook *et al.*, 1989). Polymerase Chain Reaction (PCR) primers used in both the amplification and the sequencing were cytochrome *b*1 and *b*2 (Kocher *et al.*, 1989) and CO1e and CO1f (Palumbi, 1998). These amplified regions of approximately 350 bp and 550 bp respectively. Thermocycling consisted of 30 cycles of 93°C for 30 secs, 55°C for 1 min and 72°C for 1 min, followed by a single cycle at 72°C for 5 min. Successful PCR bands were purified using a QIAEX II kit (Quiagen) and sequenced on an Applied Biosystems Model 373A DNA Sequencing System, using a PRISM Ready Reaction DyeDeoxy Terminator Cycle Sequencing kit. Centrisep spin columns (Princeton Separations Inc.) were used for excess dye extraction.

PHYLOGENETIC ANALYSES

Sequences were aligned using Clustal W (Thompson *et al.*, 1994). There were no insertions or deletions. They were then imported into PAUP* (Swofford, 2001) for phylogenetic analyses. When estimating phylogenetic relationships among sequences, one assumes a model of evolution regardless of the optimality criteria employed. Determining which model to use given one's data is a statistical problem (Goldman, 1993). We used the approach outlined by Huelsenbeck and Crandall (1997) to test alternative models of evolution, employing PAUP* and Modeltest (Posada & Crandall, 1998). A starting tree was obtained using neighbour-joining. With this tree, likelihood scores were calculated for various models of evolution and compared using a chi-square test, with degrees of freedom equal to the difference in free parameters between the models being tested. The null hypotheses tested in this way included: (1) nucleotide frequencies are equal; (2) transition rates are equal to transversion rates; (3) transition rates are equal,; (4) transversion rates are equal; (5) rate homogeneity within the data set; and (5) no significant proportion of invariable sites (Table 2). Once a model of evolution was chosen, it was used to estimate a tree using maximum likelihood. Ten replicate heuristic searches were made with random sequence addition. Confidence in resulting nodes was assessed using the bootstrap technique (Felsenstein, 1985) with 1000 replicates. Genes were analysed separately and in combination.

BIOMETRICS

Eleven biometric variables were obtained from 12 females and 24 males from each of 20 populations (exact localities available on request), using 0.05 mm callipers (see procedure in Pérez-Mellado & Gosá, 1988): (1) snout-vent length; (2) head length; (3) head width; (4) inter-orbital width; (5) frontal width; (6) inter-nasal width; (7) head depth; (8) orbital depth; (9) frontal depth; (10) nasal depth; and (11) hind limb length (Fig. 2). Sexes were analysed separately. Squared Mahalanobis distance between centroids was used since it takes into account the correlations among biometric variables and is independent of the relative scales of the various variables (Legendre & Legendre 1998). UPGMA clustering was applied to the distance matrix to assess the lizard phenetic relationships (Rohlf, 1993; Sokal & Rohlf, 1995).

TABLE 2. Tests of hypotheses relating to the model of evolution appropriate for phylogeny reconstruction (Huelsenbeck & Crandall, 1997). *P*-values were obtained with Modeltest (Posada & Crandall, 1998). For each hypothesis the data set with cytochrome oxidase (top), cytochrome *b* (middle) and then with the combined regions (below) is tested. Due to the performance of multiple tests, the significance level of rejection of the null hypothesis was adjusted via the Bonferroni correction to α=0.01.

Null hypothesis	Models compared	-lnL_0	-lnL_1	df	*P*
Equal nucleotide frequencies	H_0: JC69, H_1: F81	2035	2009	3	0.000
		1558	1509		0.000
		2843	2822		0.000
Equal ti and tv rates	H_0: F81, H_1: HKY85	2009	1907	1	0.000
		1509	1439		0.000
		2822	2684		0.000
Equal ti rates	H_0: HKY85, H_1: TrN	1907	189	1	0.000
		1439	1425		0.000
		2684	2684		0.581
Equal tv rates	H_0: TrN, H_1: TIM	1896	1896	1	0.275
		1425	1425		0.322
	H_0: HKY85, H_1: K81uf	2684	2684		0.380
Equal rates among sites	H_0: TrN, H_1: TrN+G	1896	1817	1	0.000
		1425	1357		0.000
	H_0: HKY85, H_1: HKY85+G	2684	2591		0.000
Proportion of invariable sites	H_0: TrN+G, H_1: TrN+G+i	1817	1817	1	0.999
		1357	1355		0.057
	H_0: HKY85+G, H_1: HKY85+G+i	2591	2589		0.032

RESULTS

Twenty-six individuals from 15 populations of *P. hispanica* or *P. bocagei* were sequenced for the cytochrome oxidase gene. The closely related *L. dugesii* (Harris *et al.*, 1998) was sequenced as an outgroup, and the sequence from the more distantly related *Gallotia galloti* was also included in the analyses. The most appropriate model of evolution for this data set was the Tamura Nei model (TrN) model with a discrete approximation of a gamma distribution of variable sites (base frequencies A: 0.31, C: 0.16, G: 0.24, T: 0.29, equal transversion ratios and A/G 13.8, C/T 8.3, gamma shape parameter 0.18 - Table 2). Using this model, a ten replicate heuristic search found a single most likely tree, with a log likelihood of -1811 (Fig. 3A). Twelve individuals from nine populations were also sequenced for the cytochrome *b* gene. This was combined with four previously published sequences for *P. hispanica* (Harris & Arnold, 1999), and two additional outgroups, *Lacerta dugesii* and *L. perspicillata*. For this data set the most appropriate model of evolution was again the TrN model with a discrete approximation of a gamma distribution of variable sites (base frequencies A: 0.26, C: 0.29, G: 0.13, T: 0.32, equal transversion ratios and A/G 3.5, C/T 9.7, gamma shape parameter 0.26 - Table 2). Using this model, a ten replicate heuristic search found a single most likely tree, with a log likelihood of -1348 (Fig. 3B). Since both genes are mitochondrial and therefore inherited as a single locus, a combined analysis was also carried out. *L. dugesii* was used as the outgroup, and 12 individuals of *P. hispanica* or *P. bocagei* were included. For this data set the most appropriate model of evolution was the HKY model (transition/transversion ratio of 4.99) with a discrete approximation of a gamma distribution of variable sites (Table 2). Using this model, a ten replicate heuristic search found a single most likely tree, with a likelihood of -2586 (Fig. 3C). This ML-based hypothesis of relationships was compared against two alternatives, with *P. bocagei* monophyletic, and *P. hispanica* monophyletic respectively, and other relationships unrestrained. Using the same model of evolution, ten replicate heuristic searches found short-

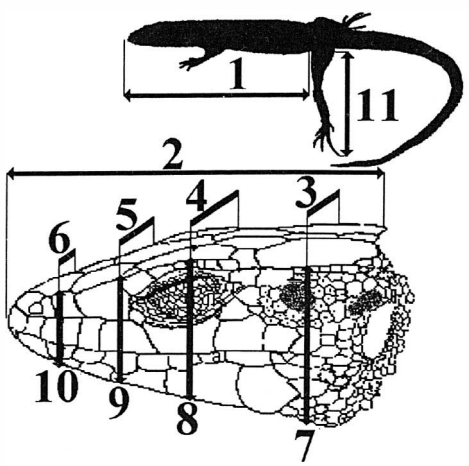

FIG 2. The 11 biometric variables used in the analysis. 24 males and 12 females from each of 19 populations were measured, including all four mainland morphotypes.

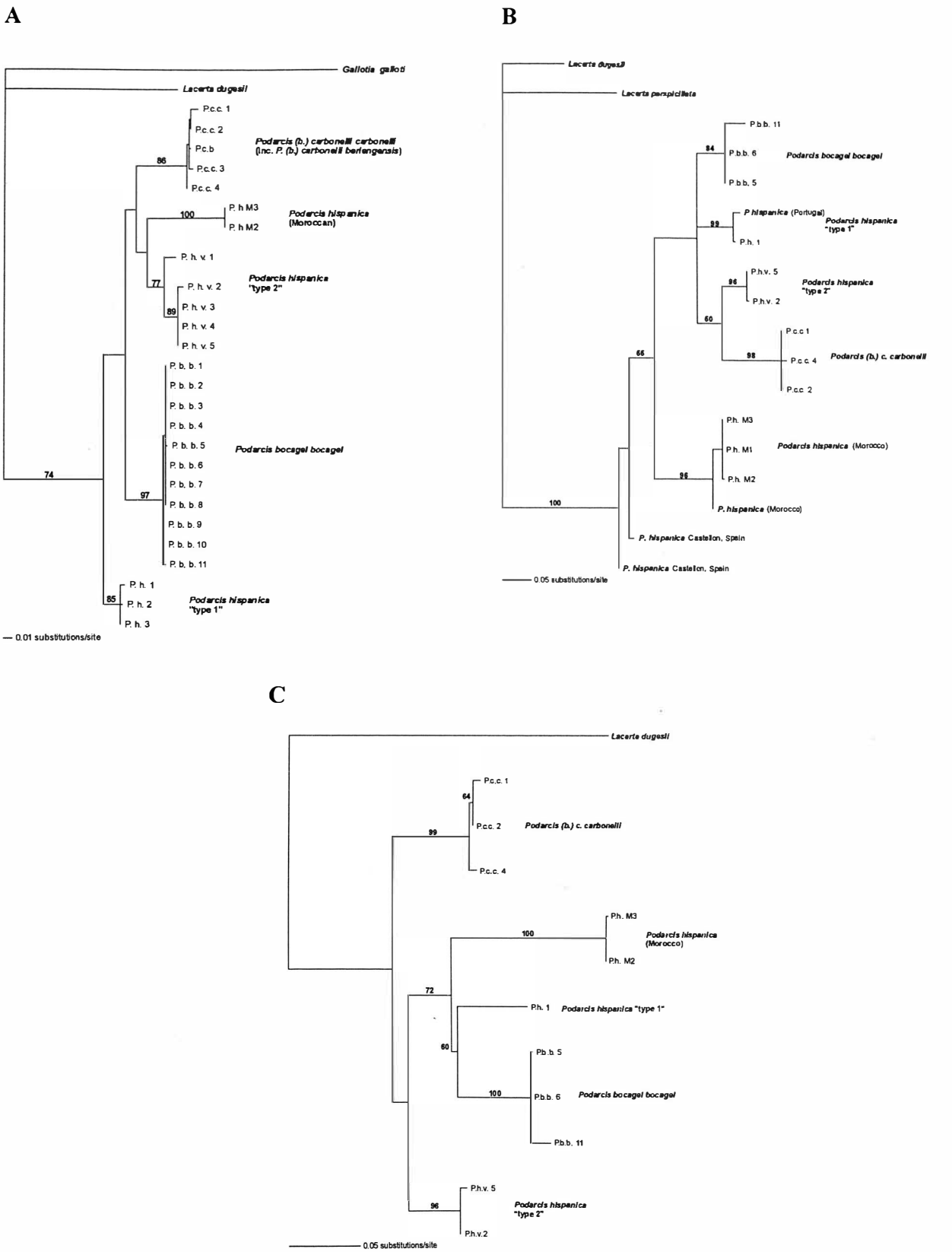

FIG. 3. A, maximum likelihood tree derived from cytochrome oxidase sequences. The tree was rooted using *Gallotia galloti* and *Lacerta dugesii* as outgroups. Numbers above nodes indicate bootstrap support (1000 replicates). B, maximum likelihood tree derived from cytochrome *b* sequences. The tree was rooted using previously published sequences of *L. perspicillata* and *L. dugesii* sequences as outgroups. Numbers above nodes indicate bootstrap support (1000 replicates). C, maximum likelihood tree derived from combined cytochrome *b* and cytochrome oxidase sequences. The tree was rooted using *L. dugesii* as an outgroup. Numbers above nodes indicate bootstrap support.

TABLE 3. Maximum-Likelihood Tests (Shimodaira & Hasegawa, 1999) of alternative tree topologies for *Podarcis* lizards. Trees compared were the maximum likelihood tree based on the combined DNA sequence data (Fig. 2C), and those based on alternative hypotheses where either *Podarcis bocagei* or *Podarcis hispanica* are monophyletic. **P* is the probability of obtaining a more extreme t-value under the null hypothesis of no difference between trees. Both these hypotheses show significantly decreased fit relative to the maximum likelihood tree.

Tree	Log likelihood	Δ Log likelihood	*P
Max. likelihood tree	-2586	-	-
Monophyletic *P. bocagei*	-2598	12	0.029
Monophyletic *P. hispanica*	-2599	13	0.021

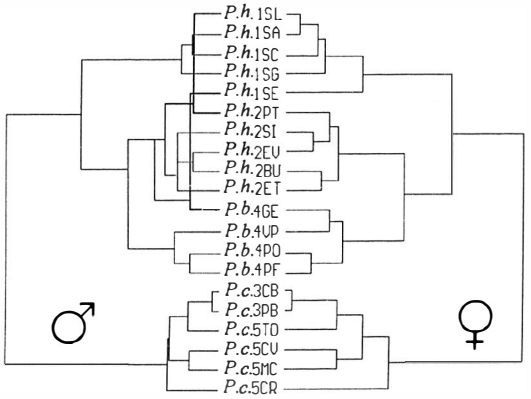

FIG. 4. UPGMA cluster analysis of the biometric variables. Included are *P. hispanica* type 1 (*P.h.* 1) and type 2 (*P.h.* 2), *P. bocagei* (*P.b.*) and *P. (b.) carbonelli* (*P.c.*). Separation of the four forms is effective in the females, but less so in the males.

est trees of –ln 2599 and –ln 2598 respectively. These were compared against the ML tree with the likelihood variance test of Shimodaira and Hasegawa (1999) using 1000 RELL bootstraps. Both were significantly less likely (Table 3).

The UPGMA trees derived from the morphological data show that each major cluster corresponds to one of the four forms of wall lizard (Fig. 4). Clear separation is found in females, while some populations of males belonging to one group cluster with other forms. *P. bocagei bocagei* clusters with *P. hispanica* type 2; both grouped in the next step with *P. hispanica* 1; and finally, *P. bocagei carbonelli* is the most dissimilar.

DISCUSSION

The reciprocal monophyly of the designated subspecies *P. b. bocagei* and *P. (b.) carbonelli*, is strongly supported by the mtDNA analysis. Specimens from across the ranges form monophyletic groups in all analyses and bootstrap support is strong, especially in the combined analysis – 99% for *P. (b.) carbonelli*, 100% for *P. b. bocagei*. The degree of genetic differentiation between *P. b. bocagei and P. (b.) carbonelli* is high: 9-9.6% between the CO1 sequences and 13.5-15.5% between the cytochrome *b* sequences. The mean cytochrome *b* genetic distance for congeneric reptile species is 13.6% (Harris, in press), and lower levels of CO1 divergence in the iguanian lizards of the genus *Tropidurus* have been used to recommend species candidates (Frost *et al.*, 1998). Further, within these two groups genetic distances are very low – 0-0.06% within *P. (b.) bocagei* and 0.004-0.09% within *P. (b.) carbonelli*. Maintenance of the present taxonomic system is further complicated by the rejection of *P. bocagei* monophyly using both morphological and molecular data. We recommend raising *P. (b.) carbonelli* to species status, following Sa Sousa *et al.* (2000) using protein electrophoretic data.

P. b. berlengensis shows no genetic differentiation from mainland *P. carbonelli* using the CO1 sequence data, and so should be referred to as *P. c. berlengensis*. This has previously been suggested based on the low genetic distance found between these groups, *D*=0.08 (Sá Sousa *et al.*, 2000). *P. c. berlengensis* does show some distinct morphological features primarily associated with an increased mean body size (Vicente, 1985). A similar case has been shown for *Gallotia simonyi simonyi* and *G. s. machadoi*, where an extinct subspecies from a small island showed no difference in mtDNA sequences from the mainland form, despite morphological differences (Carranza *et al.*, 1999). It is, however, markedly different from the example of *Podarcis atrata* from the Columbretes Islands, where inter-island cytochrome *b* divergence is high (Castilla *et al.*, 1998). Much has been made of the expected decrease in genetic diversity of organisms on small islands, and the associated increased risks of extinction. Given the large numbers of insular subspecies of *Podarcis* lizards (nearly 300; Böhme, 1986), it is important to determine which of these phenomena is more common.

Subspecies-level taxonomy within *P. hispanica* has been controversial. Some authors accept one subspecies in Iberia, *P. h. hispanica* and one in North Africa, *P. h. vaucheri* (e.g. Pérez-Mellado, 1986, 1998). Others argue that *P. h. vaucheri* is also found in the southern Iberian Peninsula, and more separate forms within the Iberian Peninsula are to be recognized, though as yet with undetermined taxonomic status (e.g. Guillaume, 1987, 1997). Electrophoretic analyses have given conflicting results – Busack (1986) found a low genetic distance (*D*=0.07) between Andalusian and Moroccan populations of *P. hispanica*, while Capula (1997) suggests they are well differentiated (*D*=0.237), and could represent sibling species.

Our analyses support the conclusions of Sá-Sousa (2000*a*) that *P. hispanica* in Portugal is composed of

two genetically distinct clades. However the southern form (either *P. hispanica* type 2 or *P. hispanica vaucheri)* is also distinct from the population sampled from Morocco. Whether there are multiple cryptic African species, as has been suggested – based on immunological data (Joger & Bischoff, 1989) cannot be assessed from the present data. It is clear, however, that *P. hispanica* taxonomy needs to be reassessed – our data indicate that *P. hispanica* is made up of multiple genetically distinct clades that do not form a monophyletic group relative to *P. bocagei* and *P. carbonelli.* Additional data from nuclear loci will be needed to confirm this finding based on mtDNA, and to determine whether introgression occurs. Only extensive sampling across the remainder of the range, especially central and eastern Spain and North Africa will allow a more appropriate assessment of the status of these clades.

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A PHYLOGENETIC ANALYSIS OF LIZARDS OF THE *LIOLAEMUS CHILIENSIS* GROUP (IGUANIA: TROPIDURIDAE)

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The lizard genus *Liolaemus* includes over 160 species of which almost half are in the *chiliensis* group. Although some researchers have attempted to define smaller species groups within this large clade, the relationships among the taxa within the group as a whole remain enigmatic. The objectives of this study were to (1) identify characters that will be useful for present and future phylogenetic studies of this group, and (2) generate preliminary phylogenetic hypotheses for taxa within this large clade of lizards. I examined more than 800 specimens of 73 taxa belonging to the *chiliensis* group from which I identified 55 phylogenetically informative morphological characters. Additional characters (6) were derived from published and unpublished data on chromosomes, life history, and ecology. Four species considered basal for the genus were taken as outgroups. A tree-building program (PAUP 4.0b2) recovered three trees of length 11.516 (Retention index: 0.59). Differences found among these topologies were restricted to the relationships of species of the *elongatus* group, in which monophyly was recovered in only one tree. Results from PAUP's analysis support the monophyly of several previously proposed species groups: *alticolor*, *altissimus*, *gravenhorstii*, *hellmichi*, *kriegi*, *leopardinus*, *monticola*, *nigromaculatus*, *nigroviridis*, *pictus* and *tenuis*. Interestingly, most of the groups indicated above are endemic to areas that have recently been described as areas of high endemism for southern South America.

Key words: phylogeny, cladistics, iguanids, South American lizards

INTRODUCTION

Liolaemus is one of the most species-rich genera of lizards. Currently, more than 160 taxa have been described and many others await description (Etheridge & Espinoza, in review). Species belonging to *Liolaemus* are distributed primarily throughout South America's southern portion, from the southern tip of the continent in Tierra del Fuego to central Perú. They are found on both the east and west sides of the Andes and are important vertebrate components of the Patagonian steppe, and the Monte, Prepuna, Puna and Andean ecosystems (Cabrera & Willink, 1980). Perhaps as a consequence of their high species diversity, the intrageneric relationships are largely unresolved.

The first comprehensive taxonomic treatments of *Liolaemus* were conducted by Ortiz (1981) and Laurent (1983, 1984, 1985). Ortiz (1981) divided the species then included in *Liolaemus* into 25 groups, (17 of which are included in the *chiliensis* group [sensu Etheridge 1995]; see Table 1), but he did not propose any hypothesis concerning the relationships among these groups. Ortiz (1981) also performed the first cladistic analysis of members of the genus (the *nigromaculatus* group). Based on morphometric analyses, and through examination of additional characters, Laurent (1983*a*) defined two main groups which he considered distinct subgenera: the "chileno group" (*Liolaemus sensu stricto*) and the "argentino group" (*Eulaemus*) distributed on the western and eastern sides of the Cordillera de los Andes, respectively. Laurent (1983*a*) also recognized the basal position of *L. archeforus*, *L. kingii*, *L. lineomaculatus*, and *L. magellanicus* – and the relationship between the latter two species – with species described under the genus *Vilcunia* (Donoso-Barros & Cei, 1971). Laurent (1983) considered valid the subgenus *Ortholaemus* (Cei, 1979). Laurent's (1983*a*) proposal was amplified in a subsequent publication (Laurent, 1985) which also included a hypothesis concerning the main *Liolaemus* species groups. Despite the lack of a cladistic analysis, Laurent's (1985) paper provided an important first step toward understanding the evolutionary history of the genus.

Other subdivisions of the genus have been proposed by Cei (1986, 1993): 28 species groups, 12 of which are subsets of the *chiliensis* group (*sensu* Etheridge, 1995; Table 1). These proposed groupings were based on combinations of characters used for identification purposes (not apomorphies). Hence they may or may not represent natural groups.

Laurent (1992) added to his previous morphometric studies (Laurent, 1983*a*) other differences between the subgenera *Liolaemus* and *Eulaemus*: the position of the nasal openings (lateral in the chileno group and laterodorsal in the argentino group), and the shape of the supralabials – longer and flattened with the fourth one turned upward in the chileno group. According to Etheridge (1995), the upturned fourth supralabial is shared with *magellanicus* and the members of the *lineomaculatus* group. Laurent (1992) also provided a

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list of the species of both subgenera, *Liolaemus* and *Eulaemus*. In this list, the chileno group included 68 taxa.

Most recently, Etheridge (1995) re-examined the taxonomy of *Liolaemus* from a cladistic perspective. He rejected or questioned the validity of the subgenera *Liolaemus*, *Eulaemus* and *Ortholaemus*, as well as the genera *Rhytidodeira* Girard 1858 (resurrected by Laurent, 1985), *Phrynosaura* Werner 1907, *Vilcunia* Donoso-Barros & Cei 1971, *Pelusaurus* Donoso-Barros 1973*b* (previously assigned to subgenus *Ortholaemus* by Laurent [1983*b*]), *Velosaura* and *Abas* Núñez & Yáñez 1984, and *Ceiolaemus* Laurent 1984, because each of these taxa exhibit the synapomorphies of *Liolaemus* and/or their monophyly was uncertain at that time. Etheridge (1995) renamed the chileno group (*Liolaemus* sensu stricto, Laurent [1983*a*]) the *chiliensis* group, which he defined as those *Liolaemus* with a lower number of precloacal pores (four or fewer) and a fused Meckel's groove. Etheridge (1995) also provided an indented taxonomy of currently valid *Liolaemus* species and subspecies. The composition of his *chiliensis* group is coincident with that of the *chileno* group of Laurent (1992), with additions for newly described species. However, Etheridge (1995) considered as valid or taxonomically uncertain *L. lativittatus* (considered a synonym of *L. alticolor* by Donoso-Barros [1966]), and *L. modestus* (considered as *Stenocercus* by Laurent [1984], and later confirmed by Ortiz [1989*a*]). Also included in his *chiliensis* group is the problematic species *L. chacoensis*. According to Etheridge (in litt.), *isabelae* should have been placed in the *chiliensis* group, and not in the *montanus* group. According to this last list (Etheridge; op.cit.), the *chiliensis* group has 74 species and subspecies. Two thirds of these taxa are distributed in Chile, whilst the remaining third are from Argentina, Bolivia and Perú.

As a first attempt to resolve the phylogenetic relationships among members of the *chiliensis* group, I assembled data on most of the known species and subspecies of this group. Data were taken from external morphology and anatomy, as well as ecological and cytogenetic data from the literature for use in this preliminary phylogenetic analysis.

MATERIAL AND METHODS

Approximately 800 specimens were examined, representing 77 species and subspecies of *Liolaemus*. The majority of the species studied (73) was from the *chiliensis* group, (Etheridge, 1995). Most of the morphological characters were taken from specimens preserved in alcohol. Some characters were examined with the aid of a hand lens (x 10) or a binocular dissecting microscope (x 10-40). Measurements were taken with electronic vernier calipers to ± 0.01 mm. Neck-fold terminology follows Frost (1992). Hemipenes were everted and studied following Bohme (1988). Tooth morphology characters were taken from Richard Etheridge's skeleton collection and from alcohol preserved specimens.

The majority of the characters used in this analysis were taken from the external morphology, including 24 characters associated with squamation; 18 body pattern; two coloration; two neck-fold morphology; one neck fat pouches; two precloacal pores; one hemipenes, three size and ratios; two tooth morphology; one osteology; one karyotype; and five physiology and ecology. Apomorphic characters of the *nitidus*, *lineomaculatus* and *chiliensis* groups identified by Etheridge (1995) were included in this analysis. Character states 58 to 61 were kindly provided by Robert Espinoza (unpubl. data), taken mainly from dissections.

Although the taxonomic status of several members of the *chiliensis* group has been controversial, I included each taxon (species and subspecies) belonging to the group (following Etheridge, 1995) as a terminal OTU. Indeed, this analysis may provide reasons for revisiting the taxonomic status of many forms. *L. kingii*, *archeforus*, *sarmientoi* and *lineomaculatus* were included as outgroups (following Etheridge, 1995). *Liolaemus kingii*, *L. archeforus* and *L. sarmientoi* were recently recognized as full species by Cei & Scolaro (1996). Twelve taxa were represented by only one or two specimens (*L. cristiani*, *L. curicensis*, *L. cyanogaster brattstroemi*, *L. monticola chillanensis*, *L. neuquensis*, *L. nigroviridis nigroroseus*, *L. pictus argentinus*, *L. pictus talcanensis*, *L. sanjuanensis*, *L. tacnae*, *L. tenuis punctatissimus*, *L. variegatus*). The following members of the *chiliensis* group were not included in this study: *Liolaemus ceii*, *L. petrophilus*, *L. lativittatus*, *L. modestus*, *L. nigroviridis minor*, *L. pictus major*. Most of the above were excluded because of lack of specimens for this study, and others because their validity was uncertain (e.g. *L. lativittatus* and *L. modestus*).

Binary characters that exhibited polymorphism were coded using the frequency bins method (Wiens, 1993, 1995), with 25 character states (a-y). These characters were numbers 1, 3, 5-8, 12-13, 16, 18, 24, 28 and 31. The gap weighting method of Thiele (1993) was applied for characters 2, 4, 9, 14, 19, 22-23, 47-48 and 50-52, which represent continuous characters with overlapping ranges – morphometrics or multistate polymorphics. The number of states were 25 (a-y) for maintaining parity with the rest of the characters. Binary characters not polymorphic were: 15, 21, 26-27, 29-30, 32-39, 41-43, 46, 49, 54-55 and 58. Multistate characters not polymorphic were: 17, 25, 40, 44-45, 53, 56-57 and 59-61. Only characters 17, 20, 53 and 59 were analysed as being unordered because no evident series of change were observable. The other characters not coded using frequency bins or the gap weighting method were weighted by 24. The analysis was performed using PAUP* Version 4.0b2 for 32-bit Microsoft Windows (Swofford, 1999), applying an

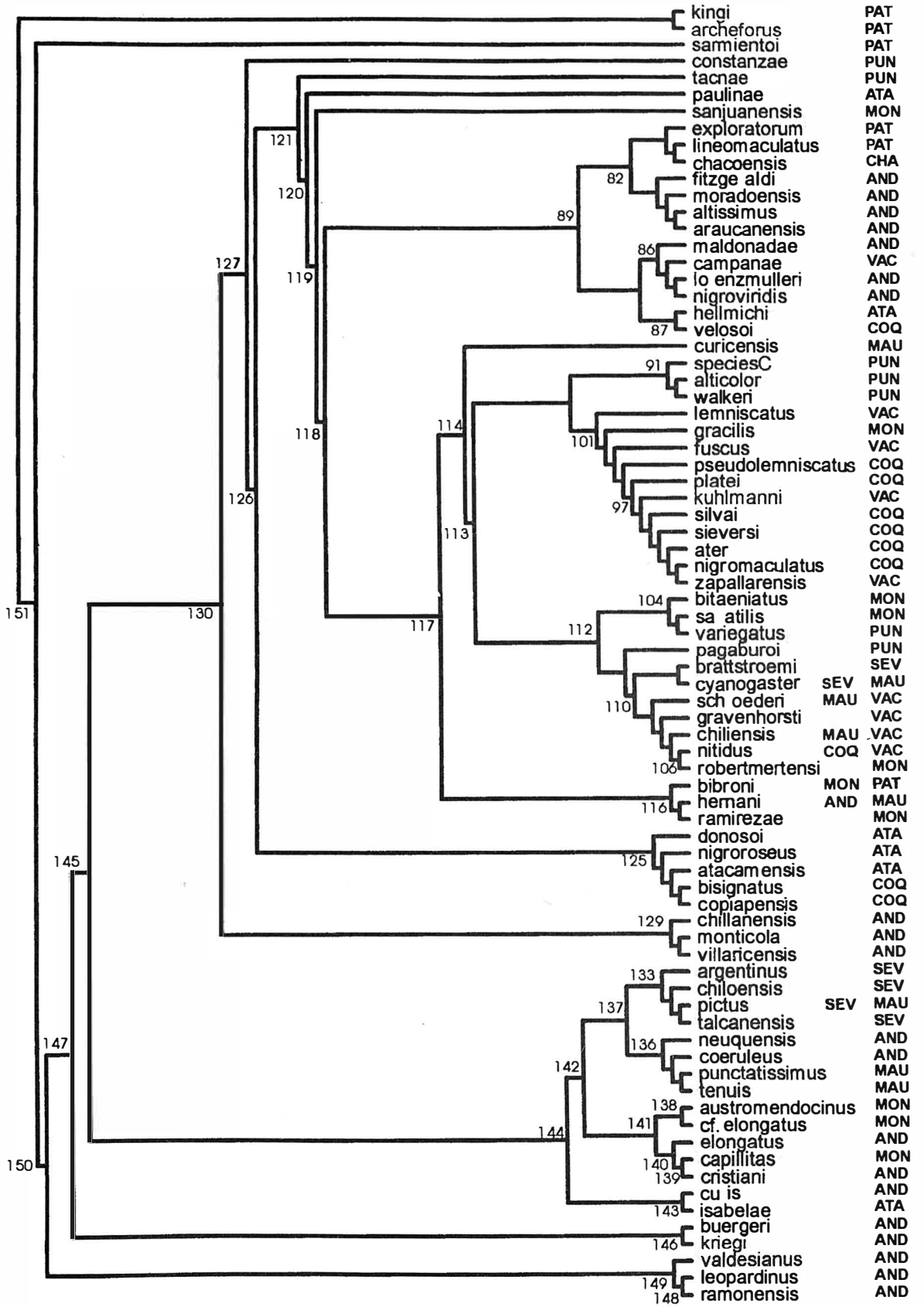

FIG. 1. Cladogram of the *chiliensis* group, the result of a parsimony analysis using PAUP* Version 4.0b2. Considering *Liolaemus kingii*, *archeforus*, *sarmientoi* and *lineomaculatus* as outgroups (note the inclusion of *lineomaculatus* within the *chiliensis* group). Congruence values: Consistency index = 0.20; Retention index = 0.59. Abbreviations for species distribution are: AND- Andina; ATA- Atacama; CHA- Chaco; COQ- Coquimbo; MAU- Maulina; MON- Monte (western Argentina); PAT- Patagonia; PUN- Puna; SEV- Selva Valdiviana; VAC- Valle Central. For more comments see the text.

heuristic search with the tree bisection-reconnection (TBR) option for branch swapping. For each analysis, 1000 random addition sequence replicates were performed, saving 40 trees at each step. *Liolaemus kingii*, *archeforus*, *sarmientoi* and *lineomaculatus* were considered outgroups following Etheridge (1995). Bootstrap analysis (Felsenstein, 1985) was used to evaluate the support for internal nodes (100 replicates). The list of characters is shown in Appendix 1.

RESULTS

After PAUP analysis, three trees were obtained with a length of 11516 and RI=0.59 (retention index, Farris, 1989). One of these trees is shown in Fig. 1. Differences among the three trees are related to the placement of the clade including *elongatus*, *cristiani* and *capillitas* (nodes 141 and 139, Figs 2A and B respectively). In Fig. 2A this clade is the sister taxon of another containing the *pictus* group (node 133), the *tenuis* group (node 136) and the pair *austromendocinus* c.f. *thermarum* (node 138). In Fig. 2B is shown other alternative relationship found, in this tree the *elongatus* clade (node 139) is sister taxon only of the group including *pictus* and *tenuis* groups (node 137). The tree shown in Fig. 1 is the one in which the entire *elongatus* group is monophyletic.

Bootstraping was performed on this data set, but found almost no support in the results. The asymmetry of this matrix – with more taxa than characters – probably makes the deletion/resampling methods for yielding consistent results problematical. The best supported nodes from 100 replicates are: *bisignatus – copiapensis* (94.9%); *punctatissimus – tenuis* (52.2%); *chillanensis – monticola – villaricensis* (*monticola* group, 47.5%); *gravenhorstii – schroederi* (46.8%); *austromendocinus* – c.f. *thermarum* (46.7%); *lineomaculatus – chacoensis* (44.3%); *nitidus* group (*lineomaculatus* plus all *chiliensis* group species, 43.0%); *capillitas – cristiani* (42.1%) and *hellmichi – velosoi* (40.7%).

The topology of the recovered phylogeny is shown in Figs 1 and 2. The general structure of the trees show the *leopardinus* group as the sister taxon of all other species of the *chiliensis* group. This is a monophyletic group including *monticola*, *chillanensis* and *villaricensis*. Subsequently, the *kriegi* group is the most external to node 145, which includes a clade (node 144, containing *pictus*, *tenuis* and *elongatus* groups) and the remaining species of the *chiliensis* group. Node 130 includes the *monticola* group as a sister taxon of the remaining species. The next sister taxon is *constanzae*, followed by the *copiapensis* group (5 spp.). Following the structure of the tree we have as subsequent sister taxa *tacnae*, *paulinae*, *sanjuanensis* and a node containing two big subclades (nodes 89 and 117). The first subclade (89), includes *altissimus*, *nigroviridis* and *hellmichi* groups, and a small group formed by *exploratorum*, *chacoensis* and *lineomaculatus*. Subclade 117 includes as most external group that formed by *bibroni*, *hernani* and *ramirezae* (node 116); subsequent sister taxa are *curicensis*, node 112 (which includes *gravenhorstii* group, the pair *cyanogaster – brattstroemi*, and the group formed by *bitaeniatus, saxatilis* and *variegatus*) and finally, the terminal pair of sister taxa: the *alticolor* group (node 91) and node 101 (containing the *nigromaculatus* group at node 97). The content of different groups recovered in this analysis are shown in Table 1.

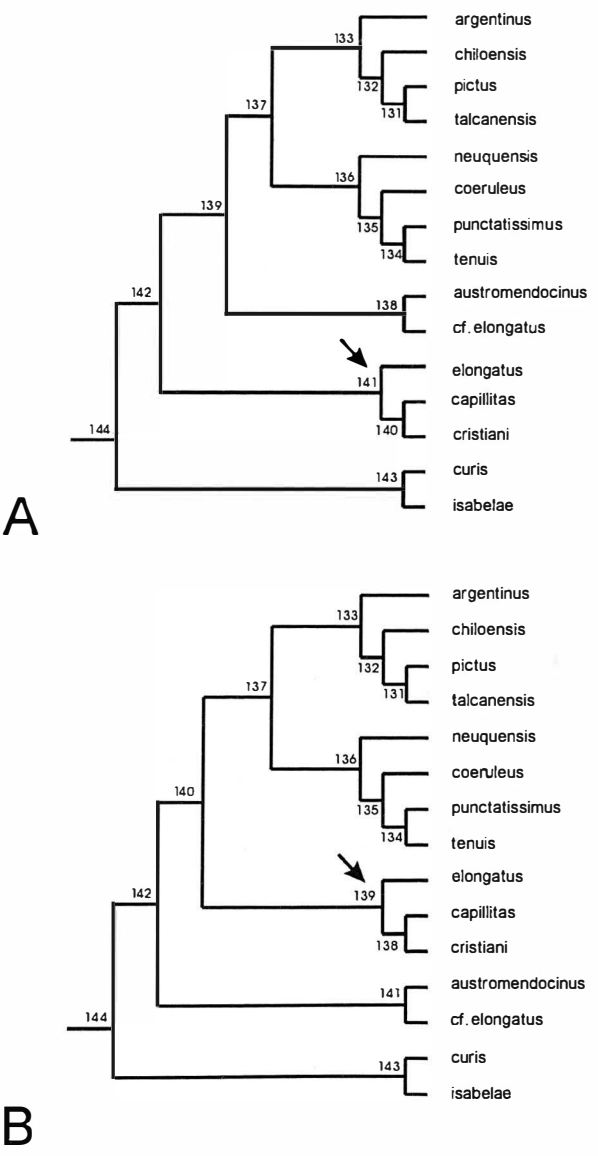

FIG. 2. Two equally parsimonious trees different to that shown in FIG.1. A, clade including *elongatus*, *capillitas* and *cristiani* (node 141) is sister taxon of the group containing both the *tenuis-pictus* groups and the species pair *austromendocinus* and cf. *thermarum*. Cladogram of the *chiliensis* group based on a parsimony analysis considering all characters equally weighted (PAUP) rooting in *Liolaemus kingii*. B, same clade (node 139), exclusively sister taxon of the pair *tenuis-pictus* groups.

TABLE 1. Comparisons of taxonomic arrangements proposed for species of the *chiliensis* group (sensu Etheridge, 1995). Groups in the third column are those recognized here, based on the results of the present analysis. Groups without equivalents in the third column did not have their monophyly supported in this analysis. Nine of the seventeen groups of Ortiz (1981) are monophyletic. *Groups proposed by Cei (1986, 1993) only included Argentine species, hence they may not contain all the species belonging to these groups. Cei (1986) proposed a *bibronii* group including *L. bibronii*, *L. sanjuanensis* and *L. exploratorum* and a *gracilis* only group for this species. Later, Cei (1993) included *L. gracilis* in the *bibronii* group. ** The monophyly of the *elongatus* group is recovered in one of the three most parsimonious trees founded.

Ortiz (1981)	Cei (1986, 1993)*	This study
1. *elongatus-kriegi* group: *austromendocinus*, *buergeri*, *ceii*, *elongatus elongatus*, *elongatus petrophilus*, *kriegi*.	*elongatus* group: *austromendocinus*, *capillitas*, *elongatus elongatus*, *elongatus petrophilus*.	***elongatus* group: *austromendocinus*, *capillitas*, *cristiani*, *elongatus*, c.f. *elongatus*.
	kriegi group: *buergeri*, *ceii*, *kriegi*.	*kriegi* group: *buergeri*, *kriegi*.
2. *alticolor-walkeri* group: *alticolor*, *walkeri*, *tacnae*.	*alticolor* group: *alticolor alticolor*, *alticolor walkeri*.	*alticolor* group: *alticolor*, *walkeri*, sp. nov.
3. *constanzae-paulinae* group: *constanzae*, *paulinae*.		
4. *leopardinus* group: *leopardinus leopardinus*, *leopardinus ramonensis*, *leopardinus valdesianus*		*leopardinus* group: *leopardinus*, *ramonensis*, *valdesianus*.
5. *altissimus-fitzgeraldi* group: *altissimus altissimus*, *altissimus araucanensis*, *altissimus moradensis*, *altissimus neuquensis*, *fitzgeraldi*.	*altissimus* group: *altissimus [altissimus]*, *fitzgeraldi*.	*altissimus group: altissimus*, *araucanensis*, *moradoensis*, *fitzgeraldi*.
6. *nigroviridis-lorenzmulleri* group: *nigroviridis nigroviridis*, *nigroviridis nigroroseus*, *lorenzmulleri*.	*nigroviridis* group: *nigroviridis*, *constanzae*.	*nigroviridis* group: *campanae*, *lorenzmulleri*, *maldonadae*, *nigroviridis*.
8. *pictus* group: *pictus argentinus*, *pictus chiloensis*, *pictus pictus*, *pictus major*, *pictus talcanensis*.	*pictu* group: *pictus pictus*, *pictus argentinus*.	*pictus* group: *argentinus*, *chiloensis*, *pictus*, *talcanensis*.
9. *tenuis* group: *tenuis tenuis*, *tenuis punctatissimus*.	*tenuis* group: *tenuis*, *coeruleus*.	*tenuis* group: *coeruleus*, *neuquensis*, *punctatissimus*, *tenuis*.
10. *gravenhorstii-schroederi* group: *gravenhorstii*, *schroederi*.	*gravenhorstii* group: *gravenhorstii*, *cyanogaster*.	*gravenhorstii* group: *chiliensis*, *gravenhorstii*, *nitidus*, *robermertensi*, *schroederi*.
11. *chiliensis-nitidus* group: *chiliensis*, *nitidus*.	*chiliensis* group: *chiliensis*, *robermertensi*.	
12. *monticola* group: *monticola monticola*, *monticola chillanensis*, *monticola villaricensis*, *curicensis*.		*monticola* group: *monticola*, *chillanensis*, *villaricensis*.
13. *fuscus-lemniscatus:* group: *fuscus*, *lemniscatus*.	*lemniscatus* group: *lemniscatus*.	
14. *hellmichi* group: *hellmichi*.		*hellmichi* group: *hellmichi*, *velosoi*.
15. *donosoi* group: *donosoi*.		see below *copiapensis* group.
16. *nigromaculatus* group: *bisignatus*, *copiapensis*, *kuhlmanni*, *nigromaculatus*, *platei*, *zapallarensis zapallarensis*, *zapallarensis ater*, *zapallarensis sieversi*, *n. sp.1*, *n. sp.2*.		*nigromaculatus* group: *ater*, *kuhlmanni*, *nigromaculatus*, *platei*, *sieversi*, *silvai*, *zapallarensis*. *copiapensis* group. *atacamensis*, *bisignatus*, *copiapensis*, *donosoi*, *nigroroseus*.
17. *modestus* group: *modestus*.		
18.	*bibronii* group: *bibronii*, *bitaeniatus*, *exploratorum*, *gracilis*, *sanjuanensis*, *saxatilis*.	

DISCUSSION

TAXONOMIC STATUS OF TERMINAL TAXA

In the *chiliensis* group, there are several taxa that have proved to be taxonomically contentious. Many of these controversies are discussed in Núñez & Jaksic (1992). These researchers proposed specific status for the three subspecies of *leopardinus* and they disagree with splitting the subspecies *nigroviridis* and *tenuis*. They also suggested conspecificity of *pictus talcanensis* and *pictus major*. Following the observations of Veloso *et al.* (1982), they also considered the possible conspecificity of *constanzae* and *donosoi*. Núñez & Jaksic (1992) included in their "*nomina dubia*" section *L. hernani* which they considered a possible synonym of *L. curicensis*.

According to the results obtained in these analysis, many taxa considered subspecies are independent lineages that should be considered full species: *moradoensis* (*altissimus moradoensis*), *campanae* (*nigroviridis campanae*), *ater* (*zapallarensis ater*), *sieversi* (*zapallarensis sieversi*), *nigroroseus* (*nigroviridis nigroroseus*), *chillanensis* (*monticola chillanensis*), *argentinus* (*pictus argentinus*), *chiloensis* (*pictus chiloensis*), *neuquensis* (*altissimus neuquensis*), *valdesianus* (*leopardinus valdesianus*).

SYSTEMATIC CONCLUSIONS

In the literature, there exist only a few proposals for grouping the species now included in the *chiliensis* group (*sensu* Etheridge, 1995). Two authors presented systematic arrangements in this sense: Ortiz (1981) and Cei (1986, 1993). In both cases the definition of groups were based on character combination instead of synapomorphies. Ortiz (1981) divided *Liolaemus* into 25 groups, 17 of them now should be included in the *chiliensis* group. Cei (1986, 1993) divided species in the *chiliensis* group into 12 more inclusive subgroups. Although the objective of this study was not to propose a new systematic rearrangement of the *chiliensis* group, it is useful to analyse the previous proposals and compare them to the cladistic approach presented here. Table 1 summarizes the systematic arrangements made by these two authors; there is a general overlap among the two arrangements. The composition of the different groups (previously recognized in the literature) that were monophyletic in PAUP analysis are included in the third column of Table 1.

The interesting finding of this study is the inclusion of *lineomaculatus* in the *chiliensis* group. The character apomorphic for the *chiliensis* group which is the enclosure of Meckel's groove is reverted in this taxon; the other character described by Etheridge (op. cit) – lower number of precloacal pores – exhibits great variation: evenmore precloacal pores are lost in *cristiani*, *thermarum*, *neuquensis* and *coeruleus* than in the *lineomaculatus* group. The results of this analysis can be taken as preliminary, and more studies are needed to confirm or reject the hypothesis of the inclusion of *lineomaculatus* in the *chiliensis* clade.

SPECIES GROUPS

Species belonging to the *Liolaemus monticola* group form a monophylethic group. There is no evidence of a relationship between these three species and *curicensis* as proposed by Ortiz (1981; see Table 1).

Navarro & Núñez (1993) describe *isabelae,* which they include in the *nigroviridis* group based on the fact that these species plus *maldonadae* share some similar karyological features. In this analysis, these species were placed in different groups. PAUP analysis showed (*maldonadae (campanae (lorenzmulleri nigroviridis*))) as the *nigroviridis* group. It is interesting to note that Ortiz (op. cit.) included *lorenzmulleri* in this group; Cei (1993) did the same with *constanzae* (which is rejected in this analysis) and Navarro & Núñez (1993) with *maldonadae*.

The *Liolaemus altissimus* group (Ortiz, 1981; Cei, 1986) is monophyletic, including *moradoensis* as a sister taxon of the pair *altissimus – araucanensis*. The form named *neuquensis* was excluded from this group, being related to the *tenuis* group. *Liolaemus fitzgeraldi* is the sister taxon of the clade formed by *moradoensis*, *altissimus* and *araucanensis*. The relationship of *fitzgeraldi* with the *altissimus* group was postulated previously by Ortiz (op. cit.) and Cei (op. cit.).

The cladogram of Ortiz (op. cit, Fig. 28) for the *nigromaculatus* group differs mainly from those obtained here in that the pair of sister taxa *copiapensis* - *bisignatus* is nested within a group that also contains *zapallarensis*, *kuhlmanni* and *silvai*. These last species, plus *sieversi*, *ater* and *nigromaculatus* form a monophyletic group and *copiapensis* and *bisignatus* form an independent lineage, as can be seen in Fig. 1. In fact, in his original description of *silvai*, Ortiz (1989)*b* notes the proximity of this taxon to *kuhlmanni* and *zapallarensis,* and provides a rigorous comparisons between them.

According to the results of this phylogenetic analysis, the *nigromaculatus* group should be considered as consisting of the following species: *nigromaculatus*, *zapallarensis*, *ater*, *sieversi*, *silvai*, *kuhlmanni* and *platei*. The other species previously considered belonging to this group are not related and form an independent clade (Fig. 1, node 125): (*donosoi* (*nigroroseus* (*atacamensis* (*copiapensis bisignatus*)))), with the exception of *velosoi* which is the sister taxon of *hellmichi* (Fig. 1, node 87).

Species belonging to the *elongatus-kriegi* group (Ortiz, 1981) do not form a monophyletic group. Only as separate groups (Cei, 1986, 1993) is the *elongatus* group monophyletic in one of three trees, and the *kriegi* group monophyletic in all trees. Videla & Cei (1996) described a new species of the *chiliensis* group called *thermarum* and they suggested that it is related to *neuquensis*, *coeruleus* and *cristiani* because all these lizards lack precloacal pores. In this analysis, characters related to precloacal pores were included (numbers 47-48), scoring the state "precloacal pores absent" for these species (with the exception of *thermarum* for

which we could not examine specimens for this study). In Fig 1 these species are included in different and independent lineages. It is, therefore, preferable not to consider this grouping as valid until we have more evidence supporting the hypothesis of monophyly.

Species belonging to Cei's *bibronii* group (Table 1) in this analysis do not form a monophyletic group and are split into three independent lineages (nodes 101, 112 and 116).

Separate groupings of the *chiliensis* group and the *gravenhorsti* group as were proposed (see Table 1) are not recovered. There is only the *chiliensis* group (*sensu* Ortiz, 1981) plus *robertmertensi*. A broader, more inclusive group is proposed here including species of both groups previously proposed in the literature, containing: *chiliensis*, *nitidus*, *robertmertensi*, *gravenhorstii and schroederi*. (Table 1).

DISTRIBUTION

The species of the *chiliensis* group are distributed over a wide latitudinal–elevational range. For example, *bisignatus* lives in low-elevational coastal areas, whereas *walkeri* lives at elevations as high as 4800 m in the Peruvian Andes (Veloso & Navarro, 1988). They occupy almost every type of habitat, from grasslands of the Puna and other high elevation regions, to low elevation habitats such as deserts and *Nothofagus* forests. They can live in deserts (Atacama), going through the central valleys of Chile to the southern *Nothofagus* forests, etc. Thus, almost every group of *Liolaemus* has representatives in these quite different areas. It is also valid to say that each region has generated sufficient conditions for the origin and development of groups of species (as we will see below).

The major clades discovered in this analysis have a high geographic homogeneity. Species belonging to the *kriegi*, *leopardinus*, *monticola* and *altissimus* groups all inhabit the Andina region. The majority of species of the *nigroviridis* group are distributed in the Andina area as well. The *pictus* group is distributed mainly in Selva Valdiviana and Maulina areas (80% of the species). The stem of the *nigromaculatus* group, comprising 71.4% of the species (5 spp.), is distributed in Coquimbo area (two other species live in the Valle Central area 28.6%). Species belonging to the *alticolor* group are all distributed in Puna. Species included in the *gravenhorstii* group are distributed mainly (80% of the species) in Valle Central and Maulina and another lives in the Monte area (*robertmertensi*).

Hellmich (1951, 1952) compared the distribution of *Liolaemus nigromaculatus* and its races, the species living in central Chile, the Andes and the austral forests with his own biogeographic regions (Atacama, Espinal, de los Bosques, Andina). He compared his observations with those for mammals and he divided the Puna and the southern Argentine-Chilean Andes into different areas. Later, Donoso-Barros (1966; lam. 1XXV) indicated six ecological areas for Chile (Desiertos, Matorral, Centrochilena, Selva, Patagonia and Cordillera). Veloso & Navarro (1988; Fig. 1), based on Di Castri (1968), described seven ecological areas of distribution for the Chilean herpetofauna, adding one area to the six described by Donoso-Barros (1966): Desertica, Tropical, Mediterránea Arida, Mediterránea, Mediterránea Húmeda, Oceánica and Andina. Veloso & Navarro (1988) divided the Cordillera of Donoso-Barros (1966) into Tropical and Andina, Selva into Mediterránea Húmeda and Oceánica, but they did not recognize Patagonia.

For assigning areas to terminal taxa in the cladograms of Fig. 1, I followed Hellmich (1952): Atacama; Roig Juñent (1994): Coquimbo, Valle Central, Maulina, Selva Valdiviana; Cabrera and Willink (1980): Chaco, Monte, Patagonia; Veloso and Navarro (1988): Andina; Morrone (1996): Puna. I prefer the divisions proposed by Roig Juñent (1994) and Morrone (1996) because they applied a cladistic methodology for determining areas of endemism.

Among the basic requirements needed today for cladistic biogeographic studies are: (1) the delimitation of areas of endemism, and (2) the phylogenetic analysis of different groups of organisms (plants or/and animals). In this manner, Roig Juñent (1994) identified 12 areas of endemism for southern South America, based on overlaying the distribution of different groups of Arthropoda and plants. In that paper, the historical relationships between these areas, and New Zealand, New Caledonia, Australia and South Africa were analysed cladistically. *Liolaemus* has representatives in every area. However those areas specially rich in species of this genus are located in the western half of southern South America, including his Coquimbo, Valle Central, Maulina, Selva Valdiviana, Monte and Bosques Orientales areas and his three subdivisions of Patagonia. The major groups identified in the *chiliensis* group seem to represent endemic areas of speciation in almost every one of the areas discovered by Roig Juñent (op. cit.). There are 11 monophyletic groups, eight of which exclusively inhabit the Puna area (one species group), Coquimbo area (one species group), Valle Central and Maulina (one species group), Selva Valdiviana (one species group) or the Andean area (four species groups). These main *Liolaemus* areas were previously drawn by Hellmich (1951; Fig1).

The species selected for rooting the analysis (*kingii*) and those most basal for the genus (*archeforus*, *lineomaculatus*) are distributed mainly in Central Patagonia. The *pictus* group (four subspecies) is found in the Selva Valdiviana. This area shows the climatic and ecological characteristics of the Zona Mediterránea húmeda and Zona Oceánica described by Veloso & Navarro (1988). *Liolaemus brattstroemi* is another endemic of that area. The *Liolaemus gravenhorstii* group (five spp.) is present in Valle Central and Maulina (Chile, between 32 and 38° of latitude) and in western Argentina (*L. robertmertensi*). Other species are distributed in Valle Central and/or Maulina (*L. fuscus*, *L. lemniscatus*, *L. hernani*, etc.). Another monophyletic

group, the *nigromaculatus* group (seven spp.) extends its distribution mainly through the Coquimbo area, an area between 32 and 27° of latitude. The Andean areas: Puna and southern Chilean Andes of moderate to high elevations, exhibit their own endemisms. The Puna region has the *alticolor* group (three spp.) and the Andes of southern Chile and Argentina have the *altissimus* group (four spp.), *kriegi* group (two spp.), *leopardinus* group (three spp.), *monticola* group (three spp) and *nigroviridis* group (three out of four spp.).

The Puna province extends across north-western Argentina, north-eastern Chile, western Bolivia and south-western Perú (Morrone, 1996). The equivalent zones of Veloso & Navarro (op. cit.) are Zona Andina and Tropical (Puna). The individual areas of distribution and the ecological regions of the species of the *chiliensis* group can be traced from Donoso-Barros (1966), Donoso-Barros (1973*a*) and Veloso & Navarro (1988), but only for Chilean species. Data on the Argentine species can be found in Cei (1986, 1993).

The results presented here represent the first cladistical approach to the analysis of the chiliensis group of *Liolaemus*. New observations and characters are been studied at this time that hopefully will bring new evidence for a better understanding of the phylogenetic relationships within this large clade of *Liolaemus*.

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APPENDIX 1

LIST OF CHARACTERS

Squamation. A total of 24 characters were scored:

1. Nasal-rostral contact (Fig. 3): (0) absent; (1) present. FREQ. BINS.
2. Width of the nasal at the mid-point of the external nares / width of the scale in contact with the rostral (Fig. 3): ranging from a mean of 18.2 to 1.6. GAP WEIGHTING METHOD.
3. Number of scales between canthal and nasal (Fig. 4): (0) two scales; (1) one scale. FREQ. BINS.
4. Dorsal head scales (rostral to occiput): ranging from a mean 16.0 to 10.5. GAP WEIGHTING METHOD.
5. Neck scales (along the longitudinal fold where present, or mid-distance between auditory meatus and shoulder): (0) granular, hemispherical; (19) laminar (flattened). FREQ. BINS.
6. Neck scales II: (0) smooth; (2) keeled. FREQ. BINS.
7. Dorsal head surface: (0) smooth; (1) rugose. FREQ. BINS.
8. Temporal surface: (0) smooth; (1) keeled. FREQ. BINS.
9. No. of temporals in a vertical count (counted at the mid-distance between subocular and auditory meatus from the oral commisure upwardly to the level of supraciliars): means ranging from 12.0 to 5.5. GAP WEIGHTING METHOD.
10. Number of scales in contact with the interparietal: (0) 8 scales; (1) 7 scales; (2) 6 scales; (3) 5 scales. MAJORITY RULE.
11. Number of enlarged supraoculars: (0) 6 scales; (1) 5 scales; (2) 4 scales; (3) 3 scales. MAJORITY RULE.
12. Posterior circumorbital scales: (0) forming a complete row of scales; (1) forming an interrupted row of scales. FREQ. BINS.
13. Contact between 4th supralabial and subocular (Fig. 5): (0) no contact; (1) contact. FREQ. BINS.
14. Number of lorilabials: means ranging from 9 to 5. GAP WEIGHTING METHOD.
15. Height of supralabials: (0) wide and short with the fourth scale not differentiated; (1) slender with the fourth usually showing its posterior tip encurved upwardly. This character is the synapomorphy of Etheridge's (1995) *nitidus* group. BINARY NOT POLYMORPHIC.
16. Auricular scale (Fig. 6): (0) not differentiated; (1) differentiated. FREQ. BINS.
17. Scales along the anterior border of the auditory meatus (Fig. 6): (0) no enlarged scales at the anterior margin of the auditory meatus. (1) one or two small laminar to granular scales differentiated slightly projecting on the anterior margin; (2) one enlarged laminar scale; (3) two to four enlarged laminar scales; (4) two to four enlarged lobulate scales. MULTISTATE NOT POLYMORPHIC. UNORDERED.

18. Separation of second chinshields (Fig. 7): (0) second chinshields always separated one from the other by one or two scales; (1) second chinshields in contact. In *copiapensis* and *bisignatus* more than 90% of individuals have these scales in contact. In other species it is less common (*silvai*, *platei*, *nigromaculatus*, *hellmichi*, *zapallarensis*, *sieversi*). All the remaining species of the *chiliensis* group exhibit the first condition. FREQ. BINS.

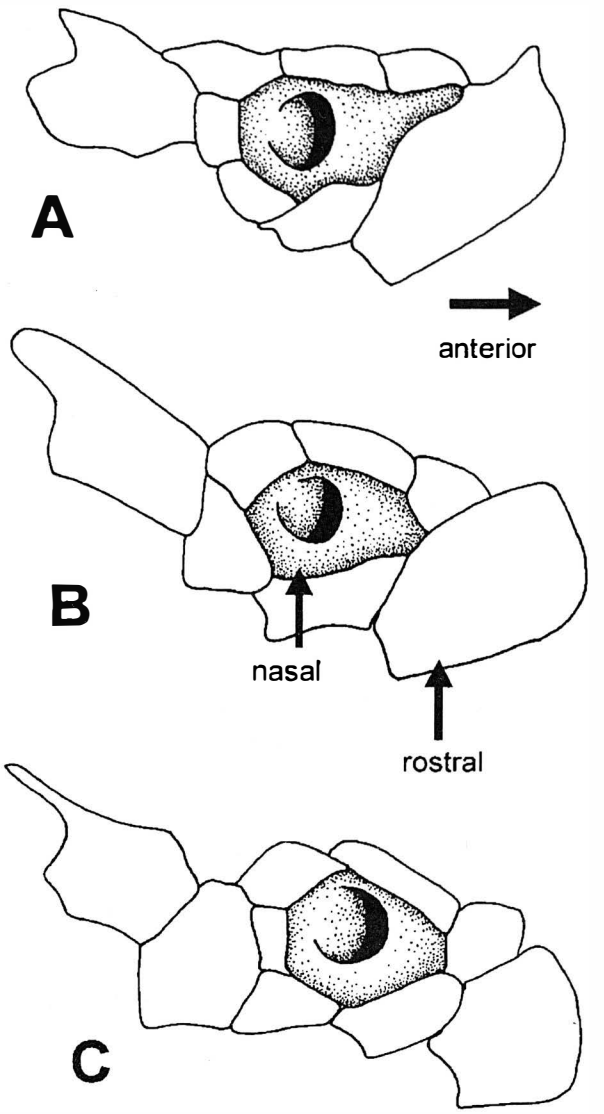

FIG. 3. A, *Liolaemus pagaburoi* (FML 2248). Character 1, state 1 (nasal-rostral contact present); character 2 (broad contact between nasal and rostral scales). B, *Liolaemus ramirezae* (FML 2940). Character 1, state 1 (nasal-rostral contact present); character 2 (slight contact between these scales). C, *Liolaemus capillitas* (FML 1229). Character 1, state 0 (nasal-rostral contact absent). Drawings made at different scales.

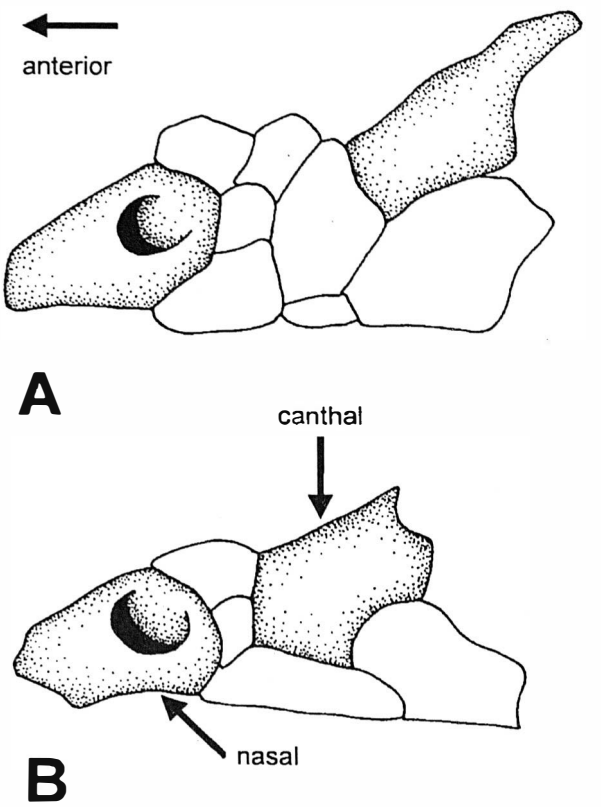

FIG. 4. A, *Liolaemus capillitas* (FML 1229). Character 3, state 0: canthal separated from nasal by two scales. B, *Liolaemus bitaeniatus* (FML 2918). Character 3, state 1: canthal separated from nasal by one scale. Drawings made at different scales.

19. Number of chinshields (Fig. 7): means ranging from 5.6 to 3.0. GAP WEIGHTING METHOD.
20. Shape of dorsal body scales: (0) with the posterior margin rounded; (1) rhomboidal; (2) lanceolate. MAJORITY RULE
21. Keels of dorsal body scales: (0) not forming a projecting spine at the median posterior margin (mucrone); (1) forming a mucrone. BINARY NOT POLYMORPHIC.
22. Number of midbody scales (mean value): from 99.5 to 32. GAP WEIGHTING METHOD.
23. Infradigital scales of fourth finger (counted over the entire finger): means ranging from 24.4 to 15.4. GAP WEIGHTING METHOD.

Body patterns. A total of 18 characters were scored:

24. Subocular distinct from the general coloration of the head: (0) subocular not distinct; (1) subocular white distinct. FREQ. BINS.
25. Ventral melanism (belly plus abdomen): (0) immaculate white. (1) spotted. (2) black. MULTISTATE NOT POLYMORPHIC.
26. Prescapular spot: (0) absent; (1) present. BINARY NOT POLYMORPHIC.

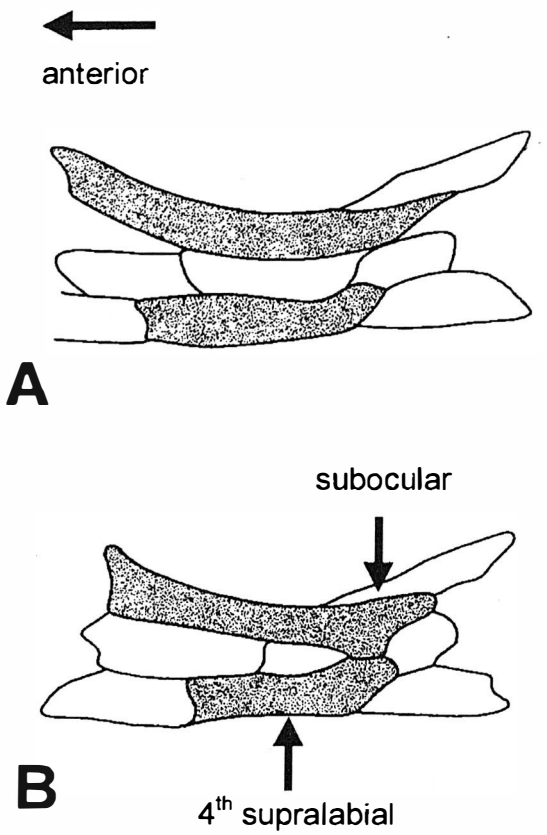

FIG. 5. A, *Liolaemus pagaburoi* (FML 2248). Character 13, state 0: fourth supralabial and subocular scales separated one from the other. B, *Liolaemus* n.sp. (FML 1761). Character 13, state 1: fourth supralabial and subocular scales in contact. Drawings made at different scales.

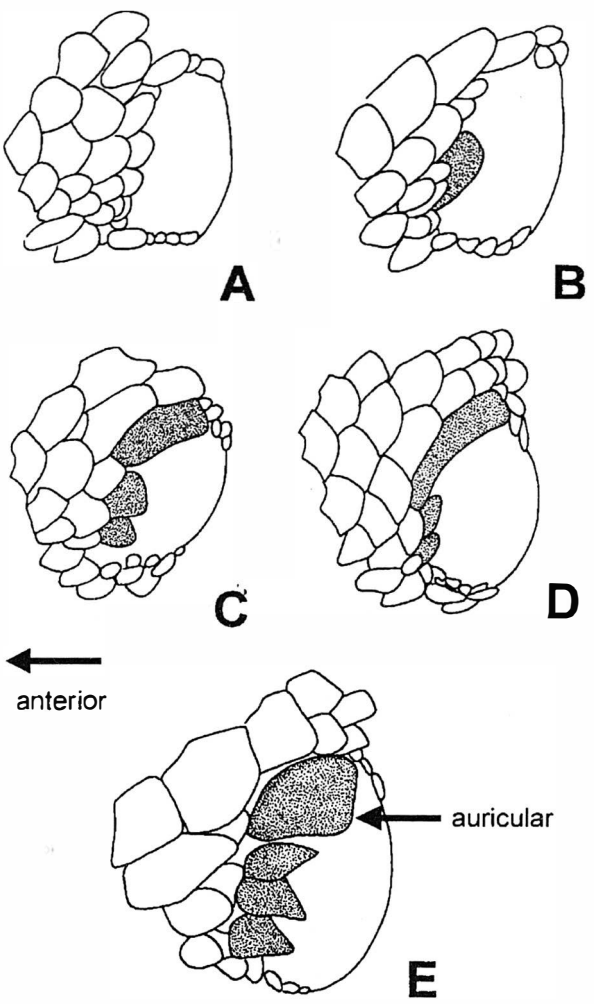

FIG. 6. A, *Liolaemus alticolor* (AMNH 16904). Character 16, state 0: auricular scale not differentiated; character 17, state 0: auditory meatus without enlarged scales on anterior bordering. B, *Liolaemus gravenhorsti* (AMNH 80054). Character 16, state 0: auricular scale not differentiated; character 17, state 3: auditory meatus with one enlarged laminar scale. C, *Liolaemus fuscus* (AMNH 131833) and D, *Liolaemus lemniscatus* (AMNH 21145). Character 16, state 1: auricular scale differentiated plus two other enlarged scales (character 17, state 2). Notice the elongated auricular scale of *lemniscatus* reaching at least half the length of the auditive meatus height. E, *Liolaemus zapallarensis* (AMNH 37574). Character 16, state 1: auricular present plus three enlarged lobed scales (character 17, state 4) which in this case, sometimes almost completely enclose the meatus. Drawings made at different scales.

27. Postcapular spot: (0) absent; (1) present. BINARY NOT POLYMORPHIC.
28. Paravertebral markings: (0) present; (1) absent. Paravertebral markings are those symmetrically positioned markings in the dorsal field of many members of the *chiliensis* group (see also Lobo and Espinoza, in review). Although these markings exhibit variation in shape and number, at this point, I only considered their presence. Paravertebral markings can be shaped subquadrate (for example *lemniscatus*, *walkeri*, etc.), slender transversal stripes (as in *altissimus*), subtriangular (*pictus* group), etc. FREQ. BINS.
29. Throat in males: (0) spotted; (1) immaculate. BINARY NOT POLYMORPHIC.
30. Throat II (females): (0) spotted; (1) immaculate. BINARY NOT POLYMORPHIC.
31. Vertebral stripe: (0) present (in some individuals fragmented); (1) absent. "Vertebrallinie" of Hellmich (1934). FREQ. BINS.
32. Dorsolateral stripes: (0) absent; (1) present; (2) present only in females. These stripes were termed "parietalband" by Hellmich (1934; Abb. 2). Donoso-Barros (1966) referred to them as "bandas supraoculares" because they initiate from this area of the head. Cei (1993) used the name "bandas dorsolaterales." Lobo & Espinoza (1999) provide a figure and detailed descriptions of dorsal patterns and their variation among species of the *alticolor* group. BINARY NOT POLYMORPHIC.
33. Dorsolateral stripes II: (0) uniformly slender exhibiting the same width all along their extension. (1) Slender over the neck and shoulders and becoming wider posteriorly. BINARY NOT POLYMORPHIC.
34. Subtriangular paravertebral markings in zigzag pattern: (0) absent; (1) present. This pattern is distinct

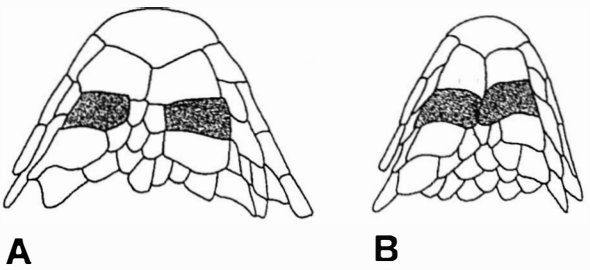

FIG. 7. A, *Liolaemus donosoi* (FML 1340). Character 18, state 0: second chinshields separated one from the other by two scales; character 19 (number of chinshields). B, *Liolaemus hellmichi* (FML 1339). Character 18, state 1: second chinshields in contact; character 19 (number of chinshields). Drawings made at different scales.

in members of the *pictus* group, having subtriangular markings at each side of the vertebral band or field (vertebral line is absent in these taxa), alternately positioned on either side. *Liolaemus fitzgeraldi* has similar pattern, but almost no vertebral band, and these markings (left and right sides) are in contact with the vertebral line; this was not considered homologous in this analysis. BINARY NOT POLYMORPHIC.

35. Paravertebral markings transversely elongated: (0) absent; (1) present. This pattern, very often, is more evident in females than males.
36. Occellations over the dorsum: (0) absent; (1) present. These markings are big and black and resemble the skin pattern of a leopard. This pattern is present in the three forms of the *leopardinus* group with varying degrees of distinctness. BINARY NOT POLYMORPHIC.
37. Irregularly fine "spotted" pattern on dorsum in males: (0) absent; (1) present. BINARY NOT POLYMORPHIC.
38. Same pattern in females: (0) absent; (1) present. BINARY NOT POLYMORPHIC.
39. Dorsal pattern formed by scattered longitudinal dark markings, like very short segments irregularly located: (0) absent; (1) present. Originally this character was drawn by Cei (1986, Fig. 50) for *exploratorum*, *bibroni*, *sanjuanensis*.

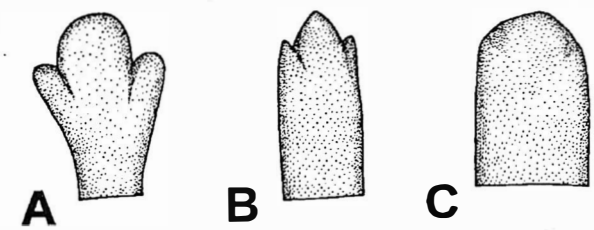

FIG. 8. A, *Liolaemus kriegi* (REE 2412). Character 53, state 0: maxillary teeth crowns expanded, tricuspid. B, *Liolaemus bibroni* (REE 2305). Character 53, state 1: maxillary teeth crowns slender, untapering, cusps reduced. C, *Liolaemus copiapensis* (REE 2560). Character 53, state 2: maxillary teeth with crowns broad and untapering, almost round, cusps slightly differentiated or absent. Drawings made at different scales.

40. Melanism on flanks: (0) absent; (1) present as a variegated pattern of large, fused spots; (2) uniformly black. State 1 is typical (with some variation) in *monticola* subspecies. State 2 is exhibited by *cristiani* and *maldonadae*. MULTISTATE NOT POLYMORPHIC.
41. Metallic or irridescent scales on the belly or flanks: (0) absent; (1) present. Distinct in *chiliensis*, and present, but less evident in *fitzgeraldi*, *gravenhorsti* and *robertmertensi*. BINARY NOT POLYMORPHIC.

Colours. Two characters were scored:

42. Pregnancy colour restricted to cloacal and adjacent areas: (0) absent; (1) present. This colour is bright red, strongly marked on the cloacal region, proximal part of ventral surfaces of thighs and posterior extreme of the abdomen. BINARY NOT POLYMORPHIC.
43. Sexual dichromatism showing a dense pattern of ligth blue to green or turquoise scales scattered on flanks and dorsum of males: (0) absent; (1) present. BINARY NOT POLYMORPHIC.

Neck-folds. Two characters were scored:

44. Lateral neck-folding (rictal, postauricular and longitudinal): (0) absent; (1) poorly developed (foldings slightly projecting over the lateral wall of the neck); (2) well developed (foldings strongly projected over the lateral wall of the neck). The folds identified in this case are equivalent to those described by Frost (1992). Rictal, postauricular and longitudinal folds appears always to exhibit the same degree of development. The antegular fold appears to change independently of the others. MULTISTATE NOT POLYMORPHIC.
45. Antegular fold: (0) present as a deep pocket; (1) not forming a pocket (evident because of differences in the size of the scales); (2) absent (no pocket and all scales between ear and shoulder identical). MULTISTATE NOT POLYMORPHIC.

Fat pouches. Only one character scored:

46. Fat pouches prominent on the sides of the neck: (0) present; (1) absent. BINARY NOT POLYMORPHIC.

Precloacals pores. Two characters were scored:

47. Number of precloacal pores in males: means ranging from 8.0 to 0.0. GAP WEIGHTING METHOD.
48. Precloacal pores in females: means ranging from 4.0 to 0.0 GAP WEIGHTING METHOD.

Hemipenis. Only one character scored:

49. Hemipenis ornamentation: (0) with calices restricted to the base of apical lobes, up to the level of the sulcus spermaticus bifurcation; (1) calices extended below that level.

Size and ratios. Three characters were scored:

50. Snout-vent length (taken from adult specimens only): means from 92.0 to 41.5 mm. GAP WEIGHTING METHOD.
51. Tail length / Snout-vent length ratio (tail length measured on apparently non-regenerated tails): ranging from means of 1.0 to 2.1. GAP WEIGHTING METHOD.
52. Subocular length / eye diameter (eye diameter taken between both angles formed by upper and lower ciliar scales): ranging from means of 1.1 to 1.7. GAP WEIGHTING METHOD.

Teeth and lower jaw. Three characters were scored:

53. Maxillary teeth crowns (Fig. 8): (0) expanded and tricuspid; (1) slender, untapering, anterior and posterior cusps reduced; (2) broad and untapering, crown almost round, cusps slightly differentiated or absent. Only mid-maxillary teeth were considered in this analysis. MULTISTATE NOT POLYMORPHIC. UNORDERED.
54. Heterodonty (cusped posterior maxillary teeth becoming uncusped anteriorly): (0) absent (all maxillary teeth have the same cusp morphology); (1) present (anterior maxillary teeth become uncusped and subconically shaped). BINARY NOT POLYMORPHIC.
55. Meckel's groove: (0) open; (1) enclosed. The second condition is the synapomorphy uniting the *chiliensis* group (Etheridge, 1995). BINARY NOT POLYMORPHIC.

Karyotype. Only one character was scored:

56. Number of macrochromosomes: (0) 12 macrochromosomes; (1) 14 macrochromosomes; (2) 15 macrochromosomes; (3) 16 macrochromosomes; (4) 18 macrochromosomes; (5) 20 macrochromosomes; (6) 22 macrochromosomes; (7) 24 macrochromosomes. *Liolaemus monticola* was scored polymorphic (14/15/16 at its type locality) data taken from Lamborot, Alvarez, Campos & Espinoza (1981). Data for karyotypes were taken from Valencia, Veloso & Sallaberry (1975); Espinoza & Formas (1976); Lamborot, Espinoza & Alvarez (1979); Navarro, Veloso, Valencia & Sallaberry (1979); Lamborot et al. (1981), Navarro, Sallaberry, Veloso & Valencia (1981); Sallaberry, Núñez & Yáñez (1982); Veloso, Sallaberry, Navarro, Iturra, Valencia, Penna & Díaz (1982); Lamborot & Alvarez-Sarret (1989); Lamborot (1991); Navarro & Núñez (1992, 1993); Navarro (1992); Iturra, Veloso, Espejo & Navarro (1994); Quatrini, Bunge & Albino (1997); Aiassa, Gorla, Avila & Martori (1998). MULTISTATE NOT POLYMORPHIC.

Biology and ecology. A total of five characters were scored:

57. Maximum number of yolked-follicles: (0) 4; (1) 5; (2) 6; (3) 7; (4) 8; (5) 9; (6) 10; (7) 11; (8) 12; (9) 13; (10) 14; (11) 15. Data were taken from Ortiz (1981), Leyton, Miranda & Bustos Obregón (1980), Leyton, Veloso & Bustos Obregón (1982) and Ramírez Pinilla (1991). No raw data available to analyzing using the Gap Weighting Method. MULTISTATE NOT POLYMORPHIC.
58. Reproductive mode: (0) viviparous; (1) oviparous. Robert Espinoza pers. obs. BINARY NOT POLYMORPHIC.
59. Life style I: (0) saxicolous; (1) terrestrial; (2) psamophilous. Robert Espinoza pers. obs. MULTISTATE NOT POLYMORPHIC. UNORDERED.
60. Life style II: (0) not arboreal; (1) terrestrial with arboreal tendencies; (2) arboreal. Those scored 1 were coded terrestrial (1) for character 52. MULTISTATE NOT POLYMORPHIC.
61. Diet: (0) insectivorous; (1) omnivorous; (2) herbivorous. Robert Espinoza pers. obs. MULTISTATE NOT POLYMORPHIC.

Data matrix and information on specimens studied is available at: http://www.unsa.edu/ar/acunsa/index02.html

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FOOD HABITS OF THE RACER (*COLUBER CONSTRICTOR MORMON*) IN THE NORTHERN PART OF ITS RANGE.

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Dietary habits of the racer, *Coluber constrictor mormon*, were studied based on stomach and faecal contents from 26 road-killed specimens and 297 live animals collected in the field during 1992–1994 in southern British Columbia, Canada. Thirty percent of the specimens examined contained gut contents. *Coluber constrictor mormon* feeds mainly on insects (91% of prey; Acrididae > Gryllidae > Tettigoniidae > Gryllacrididae) and occasionally rodents (7.5% of prey), as well as frogs and snakes (both < 1%). There were proportionally more vertebrates in the diets during the early part of the season (April – May). Diet was related to individual attributes, such as size or sex of the snake. Thus, larger individuals – primarily females – were more likely to feed on vertebrates, although insects were not absent from the diet of larger individuals. Diet composition (mammals vs. insects only) did not depend upon the method of sampling snakes. This study adds to the growing number of dietary studies on *Coluber constrictor* that continue to provide insights into the evolutionary ecology of this widespread but poorly-known species.

Keywords: *Coluber constrictor*, feeding ecology, British Columbia, Canada, diet, food habits

INTRODUCTION

A renewed interest in the feeding ecology of snakes (Arnold, 1993; Cundall & Greene, 2000) reflects a recognition of its importance as an aid to understanding other ecological and evolutionary phenomena such as habitat use, activity periods, and movement patterns within and between populations (Greene, 1983; Rodríguez-Robles, Bell & Greene, 1999). On a larger scale, patterns of food resource utilization may explain species assemblages and provide insights into the evolution of life history traits of snakes (Brown & Parker, 1982; Rodríguez-Robles, Mulcahy & Greene, 1999).

The racer (*Coluber constrictor*) is a common and polytypic species found across continental North America, from southern Canada to Guatemala. In western USA it occurs in a wide variety of habitats (e.g. grasslands, woodlands, meadows, rocky wooded hillsides and shrub-steppe desert), at elevations from sea level to 2150 m (Stebbins, 1985; Conant & Collins, 1991). Its wide distribution and morphological variation have resulted in 11 subspecific designations, some of which are the focus of taxonomic debate (Fitch, Brown & Parker, 1981; Greene, 1984; Corn & Bury, 1986; Collins, 1991). Detailed life history studies have been conducted in Utah (e.g. Brown, 1973; Brown & Parker, 1984) and Kansas (Fitch, 1963), and dietary information is available from Illinois (Klimstra, 1959), Utah (Brown, 1973; Brown & Parker, 1984), Kansas (Fitch, 1999), Georgia (Hamilton & Pollack, 1956), and South Carolina (Cooper, Burghardt & Brown, 2000). Together, these studies demonstrate some distinct dietary differences among eastern and western populations. Logically one would also predict dietary differences between northern and southern populations, possibly related to differences in length of feeding season, habitat or prey availability.

We present information on the diet of the western yellow-bellied racer, *Coluber constrictor mormon*, at the northernmost limits of its range in southern British Columbia, Canada. Our data are based on stomach and faecal samples collected from both live and road-killed specimens over three field seasons. We describe variation in the taxonomic constitution of the racer diet and relate these data to published reports from more southerly and easterly populations. We also investigate whether diet varies according to season, sex or snake size.

MATERIALS AND METHODS

This study was conducted in the extreme southern portion of the Okanagan Valley of British Columbia, Canada, from 1992 to 1994. The main study site was approximately 1.5 x 1.9 km in extent and located near the town of Osoyoos (49°02'N, 119°28'W, elevation 285m). Additional data were gathered opportunistically from road-killed snakes collected in the area surrounding the main study site. The Okanagan Valley is characterized by grassland and shrub steppe habitat with a narrow riparian zone occurring along the Okanagan river. The Okanagan Valley typically has hot, dry summers, with near desert conditions (mean annual precipitation 340 mm, mean daily min/max temperatures -5.7/-0.1°C in Jan. to 14.8/28.9°C in July; Environment Canada).

During the active season (April–Oct.) snakes were captured using eight funnel traps or by hand. In total 297 live snakes were examined for stomach or faecal

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contents by palpation. Road-killed snakes (n=26) were dissected and gut contents examined. Snakes were weighed, measured for snout-vent length (SVL) and sexed by everting the hemipenes or by probing (Gregory, 1983; Schaefer, 1934). For some animals (primarily road-kills, n=22 of 26) sex could not be confidently determined and these were subsequently left out of sex-related analyses. Similarly, some heavily damaged animals (n=19 of 26) were not measured for SVL.

Insects were identified to family where possible, following Bland & Jaques (1978). A reference collection was used to assist identifications. Quantification and identification of prey items were conservative in that insect head capsules were counted to ensure that prey items were not over-represented. If a unique prey item was identified by a body part other than a head, it was scored as a single item. Faecal samples that contained mammalian hair were assumed to be the remains of a single prey item (hair was not analysed to determine species).

Prey items are reported by frequency of occurrence (stomachs containing the item divided by the total number of stomachs containing food). The large number of near completely digested insects in the diet precluded measures of prey volume. Values given are sample means ±SD and significance was assessed at the α=0.05 level.

RESULTS

A total of 323 racers were examined for stomach or faecal material, 98 of which contained prey items (60 of stomach samples, 38 of fecal samples). Road-kill (DOR) samples made up a small portion of the records (26, of which 13 contained food). Of the 79 snakes captured in traps, 28 (35%) contained prey.

Diet consisted primarily of orthopterans, but representatives of three vertebrate classes (Amphibia, Reptilia and Mammalia) were also identified. We identified four orthopteran families: Acrididae (grasshoppers) were the dominant food item, followed by Gryllidae (crickets), Tettigoniidae (longhorned grasshoppers) and Gryllacrididae (Jerusalem crickets) (Table 1). We were unable to identify a number of miscellaneous orthopteran parts found in stomach or faecal contents. Evidence of unidentified orthopterans usually consisted of wing parts or body segments that may have been the result of unsuccessful prey capture or that may have passed through the digestive tract at different speeds from the rest of the prey (Gunzburger, 1999). The predominant type of vertebrate prey was rodents (Table 1). Two anuran amphibians (*Pseudacris regilla*) and a tail portion of a garter snake (*Thamnophis* sp.) were also identified. Plant matter occurred in 7% of guts, and was probably ingested accidentally while feeding. Multiple prey taxa were identified in 17 snakes (6 stomach records, 11 faecal records), excluding records featuring unidentified taxa (Table 2).

Prey items were categorized into 'vertebrates' and 'insects' for the purpose of testing whether there were sexual differences in prey frequency. No significant difference in frequency of these prey groups by sex was detected. There were fewer than half as many vertebrates in male guts (6 of 37; 4 rodents, 2 frogs) as in female guts (14 of 39: all rodents; χ^2=2.83, df=1, P>0.09). when the smaller vertebrates (i.e. frogs) were removed from the analysis, this dietary difference between the sexes was significant (χ^2=4.85, df=1, P<0.05). The presence of mammalian prey was restricted to larger snakes (>55.0 cm SVL), with the exception of one male snake (SVL=38.5 cm) that had one rodent in its stomach. The snake may have been attracted to the rodent in the trap in which it was captured and this may therefore represent an opportunistic feeding event. Nonetheless, a significant difference in SVL was observed between snakes with only insects in their diet (n=53, mean SVL=54.5±10.4) and those containing mammals and insects (n=18, mean

TABLE 1. Prey items identified in gut contents of *Coluber constrictor mormon*. Frequency refers to the number of times prey items were found in snakes (n=98). Figures in parentheses refer to the number of snake guts that contained particular prey items.

Prey Type	Frequency				% of total
	Males (n=37)	Females (n=39)	Undetermined	Total	number of prey
Insects					
Acrididae	29 (18)	40 (16)	26 (11)	95 (45)	35.6
Gryllidae	10 (6)	31 (9)	27 (9)	68 (24)	25.5
Tettigoniidae	2 (2)	2 (1)	1 (1)	5 (4)	1.9
Gryllacrididae	10 (6)	31 (9)	27 (9)	68 (24)	25.5
Unidentified	4 (4)	3 (3)	1 (1)	8 (8)	3.0
Vertebrates					
Rodents	3 (3)	16 (14)	1 (1)	20 (18)	7.5
Frogs	2 (2)	0 (0)	0 (0)	2 (2)	0.7
Snakes	0 (0)	0 (0)	1 (1)	1 (1)	0.3
Totals	60 (41)	123 (52)	84 (33)	267 (126)	100

TABLE 2. Gut contents of *Coluber constrictor mormon* with more than one prey taxon. Sex: male (M), female (F), unknown (U). Sample refers to stomach (s) or faecal (f). Figures in parentheses following prey taxa refer to the number of individual prey items in that sample.

Sex	SVL (cm)	Sample	Taxa
F	48.0	f	Acrididae (1), Gryllidae (1)
F	74.0	f	Acrididae (4), mammal (2)
F	61.0	f	Acrididae (1), mammal (1)
F	61.0	f	Gryllacrididae (1),Gryllidae (1), Acrididae (1)
F	71.6	f	Acrididae (1), Gryllidae (3)
F	73.0	s	mammal (1), Acrididae (2)
M	60.0	s	Acrididae (3), mammal (1)
M	45.0	s	Acrididae (2), Gryllacrididae (1)
M	45.0	f	Acrididae (1), Tettigonidae (1)
M	55.0	s	Acrididae (1), Tettigonidae (1)
U	48.5	f	Acrididae (1), Gryllidae (1)
U	49.0	s	Gyllacrididae (1), Gryllidae (1)
U	U	f	*Thamnophis* (1), Gryllidae (3), Tettigonidae (1)
U	U	f	Gryllidae (1), Acrididae (1)
U	U	f	Acrididae (1), Gryllidae (8)
U	U	f	Gryllidae (7), Acrididae (2)
U	U	s	Acrididae (2), Gryllidae (1)

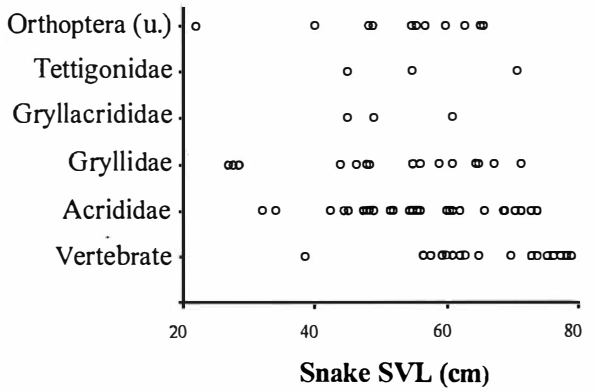

FIG. 1. Relationship between prey category (Vertebrates, Acrididae, Gryllidae, Gryllacrididae, Tettigonidae, and unidentified Orthoptera) and body size (SVL) of *Coluber constrictor mormon* (n=76).

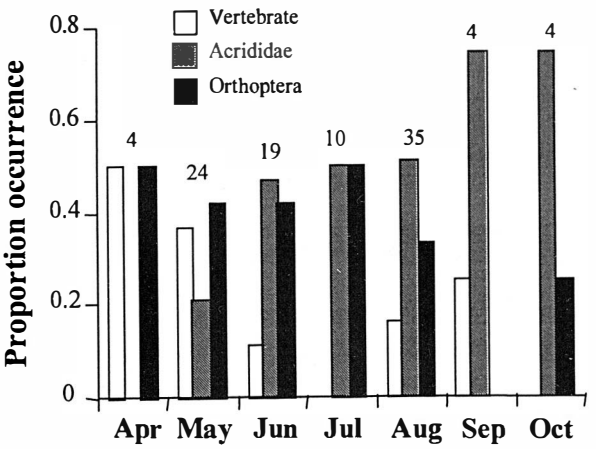

FIG. 2. Relative occurrence of prey (Vertebrate, Acrididae, other Orthoptera) by month (all years combined). Data shown as proportion occurrence. Numbers above months represent the number of snake guts that particular prey categories occurred in (n=68). Excluded are snake guts with unidentified Orthoptera.

SVL=67.3±10.9; one-tailed t=4.46, df = 30, P<0.001). Six of the 28 snakes caught in traps contained mammals, while 12 of the 70 snakes caught by hand contained mammals. Thus the incidence of mammals in the diet was not significantly related to method of capture (χ^2=0.22, df=1, P>0.5).

Two other trends are worth noting. First, it appears that larger snakes did not make a definitive switch from insect to vertebrate prey (Fig. 1, Table 2), although the largest six snakes in our study (range= 75.5–79.0 SVL, all female) contained only rodents. Second, there was a seasonal variation in diet composition, the proportion of mammals and other vertebrate prey decreasing in gut contents through the feeding season with a concomitant increase in acridids and other insect taxa (Fig. 2).

Anecdotal observations of foraging racers suggest that foraging behaviour may favour the detection and capture of specific prey species. A foraging racer was observed to place the side of its head against a grass stem and then slowly raise it up the stem while still maintaining contact with the stem. The snake raised its head approximately 25 cm before proceeding to a new stem. His behaviour was continued and eventually resulted in the detection and pursuit of a grasshopper that had been disturbed from a stem. It is well documented that *Coluber constrictor* are visual predators (e.g. Herzog & Burghardt, 1974, Cooper *et al.*, 2000), and such fixed behaviours as described here may be efficient when prey concentrations are high, as is often the case with Acrididae.

DISCUSSION

Our study supports the generalization that *Coluber constrictor mormon* rely largely on insect prey, although larger vertebrate prey are also taken (Fitch, 1963; Brown, 1973, Cooper *et al.*, 2000). Brown's

(1973) study in Utah offers the only thorough examination of the diet of *C. c. mormon*. Brown (1973) examined 411 snakes, retrieving stomach contents from 101 (24%), a slightly smaller proportion than reported here (30%). In both Brown's study and ours, acridid grasshoppers made up the bulk of the diet, being proportionately more important in Utah (76%) than in British Columbia (45%). Gryllacrididae were also more prevalent in racer diets in Utah (26% vs. 3%), whereas Gryllidae were more prominent in British Columbia (4% vs 24%). Brown (1973) found that noctuid moths occurred in 11% of stomachs, but moth prey items were not detected in our study. Most interesting is the greater proportion of mammals in the diet of British Columbia racers as compared to those in Utah (19% vs. 3%). Amphibians and reptiles were also recorded in British Columbia racer diets; these ectotherms were not observed as prey in Brown's (1973) Utah population, although snakes and birds were infrequent prey items in other studies (Brown & Parker, 1982; Cooper *et al.*, 2000). The interpretation of these differences remains equivocal as neither study measured relative prey availability. Furthermore, caution must be used when interpreting these results, as we found a definite seasonal variation in the diet of racers (Fig. 2), whereas Brown's (1973) study was restricted to September and October.

Seasonal shifts in prey type are rarely examined in the snake literature (e.g. Auffenberg, 1949; Klimstra, 1959; Fitch, 1963), although such data provide important ecological information. Seasonal changes observed in the diet of British Columbia racers may reflect changes in food availability. Adult insects are at a seasonal low in the spring as few insect species overwinter. During spring, mammals may be one of the main food resources for larger racers. As the season progresses, insect numbers increase and racers may switch to this abundant food resource. In Illinois and Kansas, *Coluber constrictor flaviventris* similarly demonstrated a dietary shift from a high proportion of mammals in the spring to a higher proportion of insects in the summer (Klimstra, 1959; Fitch, 1963). Conversely, in Texas, *Coluber constrictor stejnegerianus* have been observed to shift away from insects as the season progresses (Auffenberg, 1949).

Food habits of organisms also require consideration of sex-related differences (Shine, 1991). *Coluber constrictor* is a sexually dimorphic species, with females being the larger sex (Fitch, 1963; Brown & Parker, 1984). Our data suggest that there may be a sexual difference in diet, but this difference may simply reflect a tendency for larger snakes to eat larger prey items (Mushinsky, Hebrard & Vodopich, 1982; Shine, 1991; Arnold, 1993). Our data reveal two size-related trends: first, vertebrates appeared predominantly in the diets of larger snakes; second, the range of prey taxa increased with snake size, apart from the largest snakes (Fig. 1). The six largest snakes observed in this study contained only mammals, which suggests a difference in feeding preference when compared with smaller snakes, in which we found vertebrates, insects or both.

The racer is a diurnal, visual predator and actually prefers moving prey (Herzog & Burghardt, 1974; Cooper *et al.*, 2000). However, in one instance a rodent palpated from a racer stomach contained maggots (dipteran larvae), suggesting opportunistic ingestion of carrion, as has been shown for other colubrids (e.g. Rodriguez-Robles, Bell & Greene, 1999).

Mammals appear to be an important part of the diet of larger racers in British Columbia, but our data suggest that smaller prey species are not dropped from the diet of larger individuals. Predation on orthopteran insects may be beneficial if their relatively low individual energy content is offset by high abundance, thus making location and capture economically efficient. This would help to explain apparent seasonal shifts in *Coluber constrictor* diet composition as well as continued predation on insects by larger snakes.

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A NEW SPECIES OF INDIGO SNAKE FROM NORTH-WESTERN VENEZUELA (SERPENTES: COLUBRIDAE: *DRYMARCHON*)

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We describe a new species of snake of the genus *Drymarchon* from Falcón State, north-western Venezuela. The distinctive nature of this species, compared to the two other South American mainland taxa of *Drymarchon*, is supported by principal components analysis of scalation and colour pattern characters. The taxa *corais* and *melanurus*, hitherto considered conspecific, are found to be highly distinct, but homogeneous throughout their considerable ranges; consequently, we consider *melanurus* to be a full species, separate from *Drymarchon corais*.

Key words: *Drymarchon*, taxonomy, systematics, new species, multivariate morphometrics, South America

INTRODUCTION

The last two decades have seen a revival in interest in the alpha taxonomy of many groups of animals. This resurgent interest can be traced to several factors, including the increasing awareness of the extreme rate of extinction caused by human activities, the development of new molecular (e.g. Avise, 1994) and numerical (e.g. Thorpe, 1976, 1987) methods for the investigation of species-level systematics, and a widespread shift from process-based species concepts (in particular, the biological species concept) towards historical concepts, such as the evolutionary and phylogenetic species concepts (Wiley, 1981; Cracraft, 1989; Frost & Hillis, 1990). In general, the current trend has been towards the recognition of clearly distinct taxa as separate species rather than subspecies, without undue concern for often untestable questions of reproductive compatibility.

During this paradigm shift, it has become apparent that the use of the biological species concept – which groups similar populations together on the basis of established or assumed reproductive compatibility – is likely to result in a serious underestimate of biological diversity and a misrepresentation of phylogeny (Cracraft, 1989). A number of studies have found that groups of populations formerly regarded as subspecies of a single species in reality represent divergent and independently evolving lineages, which should be given taxonomic recognition at the species level.

In many long-recognized, widespread, polytypic species, conspecificity of the various subspecies has never been investigated, but has become fixed in the literature through a three-stage process. The three stages are an initial plethora of species described independently for various "forms" (usually in the 19th century), followed by largely evidence-free lumping into a single species, followed by inertia, whereby later workers accepted the various populations as conspecific subspecies out of habit, without fresh evidence of conspecificity. These lumped, polytypic species were described by Good (1994) as consequences of the "inertial species concept", where polytypic species are retained due to inertia and lack of study rather than positive evidence of conspecificity. The use of this "concept" has been particularly prevalent in easily identified, monotypic genera, and in well-defined, distinctive groups (e.g. Asiatic cobras – Wüster & Thorpe, 1991; *Echis "carinatus"* – see Wüster & McCarthy, 1996; bushmasters – Zamudio & Greene, 1997), where most researchers appear to have contented themselves with the casual identification of specimens as *Naja naja*, *Echis carinatus* or *Lachesis muta*, without further questioning the affinities of the individual populations involved.

Another likely example of this phenomenon is represented by the colubrid genus *Drymarchon*, a widespread group of large and conspicuously distinctive colubrid snakes from South America, Central America and south-eastern North America. The nomenclatural history of the genus corresponds to the three-stage scenario described above: six taxa were described as full species between 1827 and 1905. However, throughout most of the 20th century, *Drymarchon* has been considered monotypic (e.g. Amaral, 1929; Smith, 1941; McCranie, 1980), consisting of the single species *D. corais* (Boie, 1827). Only two authors questioned the monotypy of *Drymarchon*: (1) Roze (1959) described *Drymarchon margaritae* as a full species, but later regarded it as a subspecies of *D. corais* (Roze, 1964); this was followed by practically all later authors (e.g. Peters & Orejas-Miranda, 1970; Lancini, 1986; Lancini & Kornacker, 1989), with the exception of Roze (1966), who returned *margaritae* to full species status while simultaneously expressing doubt about this; (2) Collins (1991) raised the Florida indigo snake to the status of a full species, *Drymarchon couperi*, but without providing any

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TABLE 1. Morphological characters used for multivariate analysis of South American *Drymarchon*

1. Ventrals
2. Subcaudals
3. Anterior temporals
4. Contact upper anterior temporal - posterior temporal(s) (0 = none, 0.5 = one side, 1 = both sides)
5. Posterior temporals
6. %VS position of reduction 19 to 17 rows
7. %VS position of reduction 17 to 15 rows
8. %CS position of reduction 10 to 8 rows
9. %CS position of reduction 8 to 6 rows
10. %CS position of reduction 6 to 4 rows
11. Change of colour along dorsum (1 = darker at front, 0 = uniform, -1= darker at back)
12. Oblique black mark on side of neck (1 = present, 0 = absent)
13. Presence of individual paler scales (1 = present, 0 = absent)
14. Change of colour along ventral side (1 = darker at front, 0 = uniform, -1= darker at back)
15. Underside of tail pale or dark (1 = dark, 0 = pale)
16. Presence of individual dark subcaudals (1 = present, 0 = absent)
17. Presence of obvious dark edges on supralabials

evidence to support this action, which has not been widely followed. The monospecifity of the remainder of the genus has not been questioned, despite conspicuous qualitative differences in coloration (see illustrations in Mehrtens, 1987, for example), as well as scalation differences (Smith, 1941) between different subspecies.

On the mainland of South America, two well-differentiated subspecies of *Drymarchon corais* have been widely recognized: *Drymarchon corais corais* (Boie, 1827) is reported from east of the Andes, and *D. c. melanurus* (Duméril, Bibron & Duméril, 1854) from west of the Andes as well as northern Venezuela (Peters & Orejas-Miranda, 1970; Roze, 1966). The ranges of the two forms meet in northern Venezuela, albeit with an element of ecological separation: *D. c. corais* is reported from hot lowlands, whereas *D. c. melanurus* is reported to occur in higher, mesic areas in the west and north of the country (Roze, 1966; Lancini, 1986; Lancini & Kornacker, 1989; La Marca *et al.*, 1995). During work in Falcón State, Venezuela, the authors encountered specimens of the genus *Drymarchon* that could not be assigned to either of these two taxa. This prompted the present investigation of the population systematics of this genus in South America.

MATERIALS AND METHODS

In order to analyse the affinities of the new Venezuelan taxon in relation to the established taxa, we used multivariate analysis of characters of scalation and colour pattern. Compared to character-by-character approaches to morphological systematics, multivariate morphometrics has the advantage of comparing the generalised phenotypes of the animals concerned, resulting in a more robust assessment of patterns of morphological differentiation and the elucidation of relatively subtle patterns of geographic variation missed in conventional systematics (e.g., Wüster *et al.*, 1992). Furthermore, multivariate techniques such as principal components analysis, which do not rely on *a priori* grouping of specimens, can reveal patterns of geographic variation unconstrained by prior assumptions of taxon membership. This avoids the circularity inherent in assigning each specimen to a predetermined taxon based on some aspect of morphology or appearance, and then comparing these taxa.

For this analysis, we used preserved material from a number of natural history collections, listed in the Acknowledgements. The assessment of the distinctiveness of the new form requires an appraisal of as much of the spectrum of geographic variation of the other relevant taxa as possible. We therefore examined specimens from most parts of the range of *D. corais corais* (Venezuela to southern Brazil) and *D. c. melanurus* (Mexico to Ecuador). The specimens used are listed in Appendix 1.

Based on initial observations and literature data, 17 morphological characters were selected and recorded from all available specimens (Table 1). In order to characterize the position of dorsal scale row reductions along the body and tail, the ventral scales were numbered according to the method of Dowling (1951), and the subcaudal scales starting from the first pair in contact along the ventral midline behind the vent (not including the tail spine). In *Drymarchon*, dorsal scale row reductions involve fusions of scale rows 3 and 4, 4 and 5, or 5 and 6. On the tail, the reductions generally involve the highest pair of rows on each side of the vertebral line. The position of each scale row reduction was noted as the number of the ventral or subcaudal pair directly above which it was situated. This was then converted to % ventral scale row count (%VS) or % caudal scale count (%CS), to compensate for differences in the numbers of ventral and subcaudal scales among different individuals.

In order to visualize the pattern of variation in morphology among the three taxa included in the study, we used principal components analysis (PCA), run on the

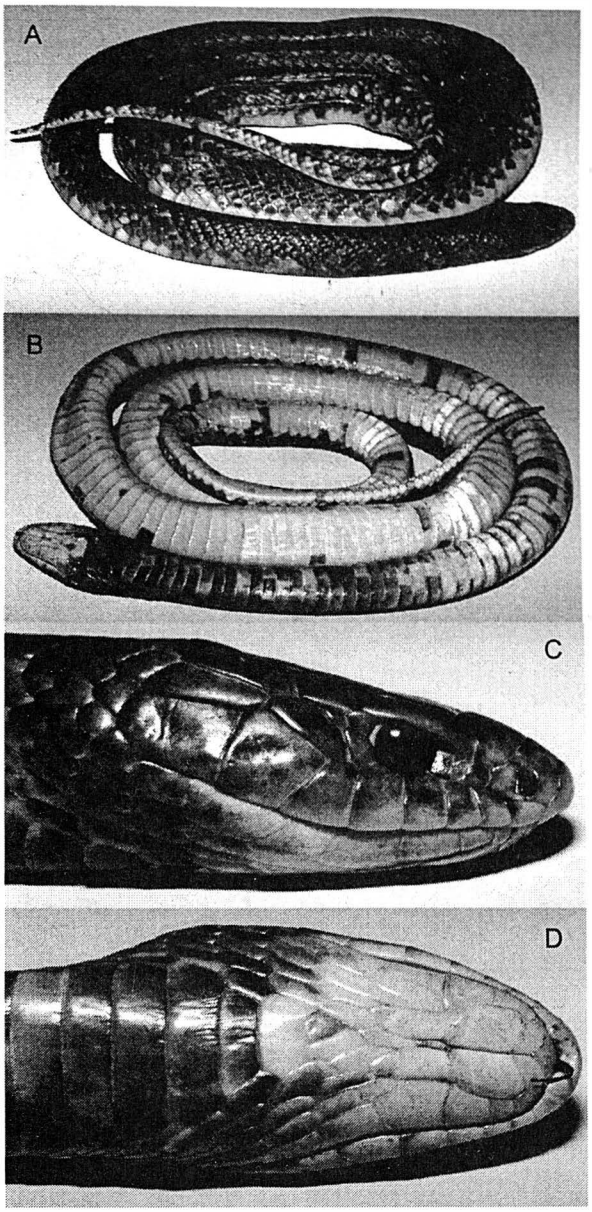

FIG. 1. A, dorsal side; B, ventral side of the holotype of *Drymarchon caudomaculatus* (EBRG 3412). Note the pale mottling, the dark throat, the isolated dark subcaudals and the lack of colour change along the body. C, lateral view; D, ventral view of the head of EBRG 3412.

data recorded from individual specimens. Before analysis, each character was converted to zero mean and unit standard deviation. Analyses were carried out both separately for the two sexes, and for specimens of the two sexes combined. Since sexual dimorphism among the characters studied did not confound the analysis, the results of the combined analysis are presented here. The ordination of individual specimens along the first two principal components was plotted out.

RESULTS

DRYMARCHON CAUDOMACULATUS SP. NOV.

Holotype. EBRG 3412, an adult female (Fig. 1). On the road to Los Tablones, 1 km from the junction with the new Coro-Churuguara road, Municipio Colina, Estado Falcón, Venezuela. Found freshly road-killed at 9.20 am on 16.7.1997. The locality is situated approximately 1 km from the village of Las Dos Bocas (11°18'N, 69°24'W), in the eastern foothills of the Sierra de San Luís, at an altitude of approximately 110 m. The vegetation consists of semi-deciduous tropical forest, with a canopy height of approximately 5-10 m, and moderate anthropogenic intervention. Collected by W. Wüster and J.L. Yrausquin.

Diagnosis. Drymarchon caudomaculatus is easily distinguishable from the other two taxa of *Drymarchon* found on the South American mainland (see Table 2).

In their colour pattern, adults of *Drymarchon caudomaculatus* differ from *D. c. corais* in lacking any obvious change of hue along the dorsal side of the body, in having the anterior part of the venter more or less covered with dark pigment, in having scattered paler scales on the posterior body, and in having isolated dark subcaudals under an otherwise pale tail. Additionally, *D. caudomaculatus* has consistently lower subcaudal scale counts than any of the *D. c. corais* examined in this study or listed by Amaral (1929) (65 or fewer, vs. 66 or more in *D. c. corais*). In most specimens of *D. c. corais*, the dorsal scale row reductions are situated in a more posterior position and the caudal scale row positions in a more anterior position than in the new species. Almost all adult specimens of *D. c. corais* show a conspicuous change in body coloration along the dorsum, being dark anteriorly and pale posteriorly. This is contrary to the key to the subspecies of *Drymarchon corais* in Peters & Orejas Miranda (1970), which erroneously states *D. c. corais* to be uniformly black above. The extent of melanization in this form is in fact very variable (pers. obs.; compare photographs in Moonen *et al.* (1979) and Murphy (1997)). Finally, *D. c. corais* also lacks dark pigmentation of the throat area, and we have not seen specimens with isolated paler scales on the body.

The colour pattern of adult *D. caudomaculatus* differs from that of adult *D. c. melanurus* in lacking any obvious change of hue along the dorsal side of the body (posterior body and tail conspicuously darker in *D.c. melanurus*), in having the anterior part of the venter more or less covered with dark pigment (anterior part pale, posterior part dark in *D. c. melanurus*), in having scattered paler scales on the posterior body and isolated dark subcaudals under an otherwise pale tail (subcaudal surface uniformly dark in *D. c. melanurus*), in lacking the distinct black, oblique bars found on the side of the neck in *D. c. melanurus*, and in lacking distinct black supralabial edges. In its scalation, *D. caudomaculatus* displays consistently lower subcaudal scale counts (65 or fewer) than any *D. c. melanurus* examined in this study or by Amaral (1929) or Smith (1941) (71 or more). However, McCranie (1980) listed subcaudal scale counts as low as 59 for *D. c. melanurus*, without indicating the origin of the specimens concerned. The caudal scale row reductions are generally in a more anterior position in *D. c. melanurus* than in *D. caudomaculatus*.

TABLE 2 Range of variation of selected scalation and colour pattern characters in the three South American species of *Drymarchon*.* General colour pattern and ventral and subcaudal scale counts, were recorded from two additional live specimens.

	D. caudomaculatus	*D. corais*	*D. melanurus*
Sample size	2-4*	29	12
Ventrals	195-200	188-216	196-214
Subcaudals	61.5-64.5	66-81	71-93
%VS position of reduction from 19 to 17 rows	6.7-9.1	3.2-8.4	5.0-8.4
%VS position of reduction from 17 to 15 rows	66.0-77	70.5-94.8	59.8-78.0
%CS position of reduction from 10 to 8 rows	7.3-7.9	2.8-8.6	2.8-5.9
%CS position of reduction 8 to 6 rows	17.9-27.0	6.3-26.5	9.9-21.5
%CS position of reduction 6 to 4 rows	56.1-56.3	31.2-64.2	35.9-50.0
Change of colour along dorsum in adults	Uniform	Darker anteriorly, paler posteriorly	Paler anteriorly, darker posteriorly
Oblique black mark on side of neck	Absent	Absent	Present
Presence of individual paler or darker scales	Present	Absent	Absent
Change of colour along ventral side	Often dark or mottled anteriorly	Uniform	Darker posteriorly
Underside of tail	Pale	Pale	Dark
Presence of individual dark or pale subcaudals	Present or absent	Absent	Absent

Drymarchon caudomaculatus is easily distinguished from the remaining taxa of *Drymarchon*, which are not found on the South American mainland. *Drymarchon couperi* is uniformly blackish-blue above as an adult, and the antepenultimate supralabial is excluded from contact with the postoculars or temporals by a contact between the two adjoining labials below the eye. *Drymarchon corais unicolor* lacks the dark throat, has a darker posterior venter, 70 or more subcaudals, and often over 200 ventrals. Adult *D. c. rubidus* are black dorsally, lack a dark throat, have a dark posterior belly, black-edged supralabials, and more subcaudals (69 or more) than *D. caudomaculatus*. Adult *D. c. orizabensis* are black dorsally, all but the anterior third of the venter is black, and they have higher subcaudal counts (71-78). Adult *D. c. erebennus* are blackish above posteriorly, spotted anteriorly, and have dark diagonal markings on the sides of the neck. Additionally, this subspecies usually has 14 dorsal scale rows anterior to the vent.

Etymology. The term *caudomaculatus* refers to the spotted aspect of the tail of adult specimens.

DESCRIPTION OF HOLOTYPE

Body scalation. 197 ventrals, 61/62 subcaudals, all paired, anal entire. Dorsal scales smooth, with double apical pits, in 17 rows at midbody. Dorsal scale reduction formula: 21 4+5(6/8) 19 2+3(15/21) 17 2+3(129)/3+4(131) 15 7+8(195) 14 +8(196/196) 16. Caudal scale reduction formula: 12 3+4(3) 11 3+4(4)/4+5(4) 9 4+5(5) 8 3+4(10/12) 6 2+3(34/35) 4 1+2(61) 3.

Head scalation. 8/8 supralabials, fourth and fifth enter orbit, seventh and eighth very large; 9/9 infralabials; 1/1 preoculars (very high); 2/2 postoculars; 2/2 anterior temporals, upper very small; lower anterior temporal contacts parietal behind upper anterior temporal, excluding latter from contact with posterior temporals. 2/2 posterior temporals, lower long and narrow. Two pairs of chin shields, posterior pair separated by small scale.

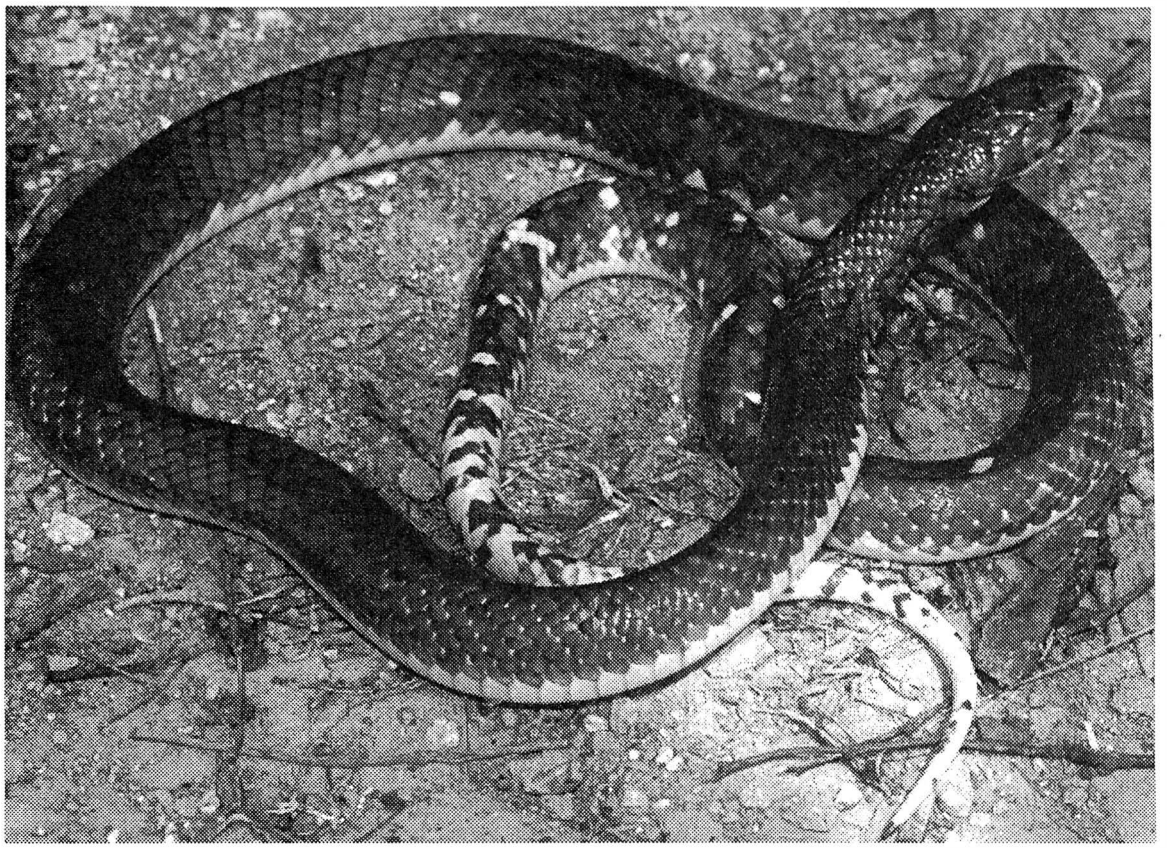

FIG. 2. Live specimen of *Drymarchon caudomaculatus*, a male with a total length of 1360 mm, from an unknown locality in Falcón State, Venezuela.

Posterior pair slightly longer but narrower than anterior pair. Rostral visible from above, broader than high. Internasals small, half the length of prefrontals. Frontal slightly broader (8.9 mm) than long (8.2 mm), straight anterior edge, narrower posteriorly, ends in obtuse angle, shorter than distance from rostral. Eye elongate, length 6.5 mm, height 4.6 mm, distance from edge of mouth 5.1 mm.

Dorsal pattern. Dorsum medium-brown throughout, without change along body. Extensive mottling with paler colours, becoming denser and more contrasting towards the posterior part of the body and the tail. Especially on the posterior body, some individual scales tend to be cream coloured, contrasting strongly with the ground colour. This is especially pronounced on the tail

Head pattern. Top of head of the same colour as dorsum, with cream marbling, especially along the parietal suture and along the sides. Rostral scale and anterior and central part of internasals cream. Chin shields, first 5 infralabials and other scales under head dirty white. Infralabials 6 and 7 white along edge of mouth, brown on lower part, infralabials 8 and 9 entirely brown. Posterior edges of supralabials slightly more densely pigmented, but no obvious dark edges.

Ventral pattern. Second preventral and first 24 ventrals largely covered in dark brown pigment, with some cream mottling; next 17 ventrals approximately half covered with dark pigment; dark and pale blotches occupy total width (anterior-posterior) of ventral. After ventral 41, venter predominantly cream, with occasional dark spots occupying the entire width of their respective ventral, of variable lateral extent. Underside of tail predominantly cream, but 15 dark, isolated half-subcaudals (half of pair) out of a total of 123 are medium to dark brown.

Dimensions. Snout-vent length 1305 mm; tail length 257 mm; head length from snout to end of quadrate: 49.9 mm; head width across supraoculars: 18.0 mm.

VARIATION

Paratype. EBRG 3413, a female. Locality: Approximately 15 km (by road) SE of Coro, on the new Coro-Churuguara road, Municipio Colina, Estado Falcón, Venezuela (approximately 11°21' N and 69°35' W). Collected at an altitude of approximately 150 m, at 1730 hr on 19.01.1993, while crossing the road. Generally similar to the holotype, with the following differences: 195 ventrals; 61 subcaudals, but the tail tip is missing, and the true subcaudal count is likely to have been about 2 or 3 scales higher. The upper anterior temporal is missing on the left, and does not contact the posterior temporal on the right, due to a contact between the lower anterior temporal and the parietal. Body scale row reduction: 23 4+5(4/4) 21 4+5(6/7) 19 3+4(12/14) 17 3+4(149/150) 15 +3(195/195)/7+8(195) 16. Tail scale row reduction formula: 10 3+4(5)/4+5(5) 8 3+4(16/18) 6 2+3(34/37) 4. Pattern: generally as in the holotype; however, this specimen displays far more scattered pale

TABLE 3. Eigenvector coefficients of the 17 characters along the first two principal components of the PCA. For details of characters, see Table 1.

	PC1	PC2
1. Ventrals	0.093	0.251
2. Subcaudals	0.215	0.115
3. Anterior temporals	-0.060	0.184
4. Contact ant.-post. temporals	0.185	0.213
5. Posterior temporals	0.097	-0.002
6. Reduction 19-17 rows	0.006	-0.319
7. Reduction 17-15 rows	-0.254	0.250
8. Reduction 10-8 rows	-0.220	-0.302
9. Reduction 8-6 rows	-0.165	-0.300
10. Reduction 6-4 rows	-0.258	-0.178
11. Dorsal colour change	-0.355	0.276
12. Oblique bars on neck	0.388	-0.194
13. Individual pale scales	-0.158	-0.428
14. Ventral colour change	-0.397	0.083
15. Underside of tail	0.388	-0.194
16. Dark subcaudals	-0.124	-0.355
17. Supralabial edges	0.259	-0.012

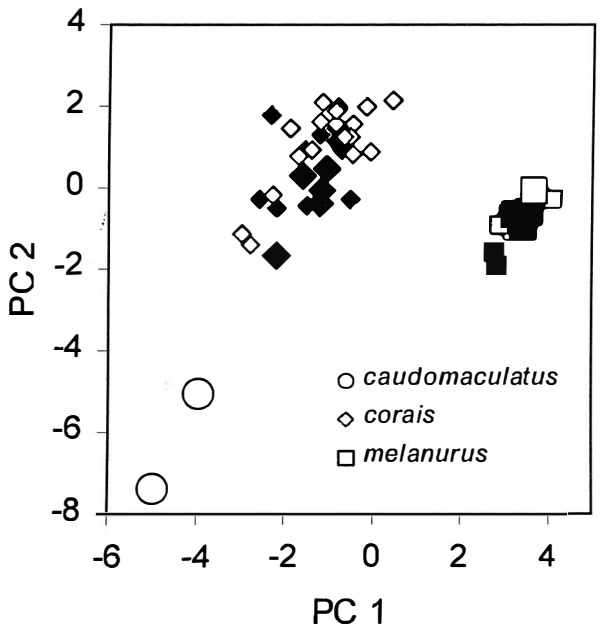

FIG. 3. Ordination of the specimens of the South American taxa of *Drymarchon* along the first two principal components of PCA 1. The distinctiveness of the three forms, and the very minor role played by sexual dimorphism, are obvious. The first and second principal components summarize 33.1% and 17.1% respectively, of the total variance of the data. Solid and hollow symbols denote male and female specimens, respectively, and enlarged symbols denote specimens from western Venezuela, where the distributions of the three taxa approach each other or overlap.

scales, and the throat and anterior part of the venter contains only isolated dark markings instead of a large mottled area.

Other preserved material: MCNC 1019, Coro, Estado Falcón, Venezuela (11°25' N, 69°41' W), coll. 1959 by Erasmo Durán; MCNC 2251, Taratara, Estado Falcón, Venezuela (11°29' N, 69°30' W) coll. April 1962 by Erasmo Durán. In addition, two live specimens from unknown localities in Falcón State were observed in a private collection. The first was a male with a snout-vent length of 1134 mm and a tail length of 226 mm, 192 ventrals and 64.5 subcaudal pairs; the upper anterior temporals were in contact with the posterior temporals on both sides; the pattern was as described previously, with extensive pale mottling on the tail (Fig. 2). The second live specimen was another male with a snout-vent length of 1452 mm and a tail length of 280 mm, 200 ventrals and 64 subcaudals; the upper anterior temporals were in contact with the posterior temporals on both sides; the pattern was as described in the other specimen, although with relatively little pale mottling on the dorsum.

Three further road-killed specimens were recorded by one of us (JLY), but not collected due to their bad condition. The localities were Tocópero, Municipio Tocópero (11°30' N, 69°16' W), Sector Barrialito, Cumarebo, Municipio Zamora (11°28' N, 69°19' W), and an additional specimen from Coro, all in Falcón State, Venezuela.

It should be noted that no juvenile specimens of this form are known. In other *Drymarchon*, the juvenile pattern can differ substantially from the adult pattern.

MULTIVARIATE MORPHOMETRICS

The PCA ordination plot (Fig. 3) clearly shows the existence of three cohesive, highly distinct clusters. These correspond to the two widely recognized South American subspecies of *D. corais* (*D. c. corais* and *D. c. melanurus*) and *D. caudomaculatus*. The first principal component primarily separates *D. c. melanurus* from the remaining specimens. Separation along this axis is primarily related to variation in the patterns of colour change along the dorsum, the presence or absence of oblique black bars on the neck, and colour change along the ventral surface (Table 3). The second principal component separates the specimens of *D. caudomaculatus* from those of *corais* and *melanurus*. Separation of specimens along the second axis is mostly related to the presence of individual pale scales, and also the number of ventrals, the position of caudal scale reductions, and the presence or absence of dark edges along the supralabials (Table 3).

It can be seen that sexual dimorphism had minimal effect on the ordination of the specimens. Furthermore, it can also be seen that specimens from western Venezuela, where the distributions of the three taxa involved approach each other or overlap, show no tendency towards intergradation.

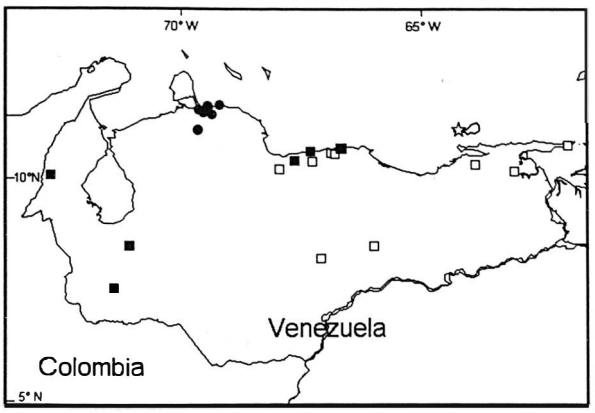

FIG. 4. Locality records of the four species of *Drymarchon* found in northern Venezuela. Records refer to specimens examined as part of this study, and locality records provided by Roze (1966). Circles represent *D. caudomaculatus*; hollow squares, *D. corais*; solid squares, *D. melanurus*; and the star, *D. margaritae*.

DISCUSSION

The results of the principal components analysis show clearly that three taxa of *Drymarchon* are found in mainland South America. Two correspond to the conventional subspecies *corais* and *melanurus*, and the third corresponds to the new taxon from Venezuela.

It is particularly notable that the two conventional subspecies, *Drymarchon corais corais* and *D. c. melanurus*, form cohesive clusters in the ordination, despite the geographically and ecologically diverse origins of the specimens involved. Furthermore, specimens from adjoining localities in northern and western Venezuela do not show any evidence of intergradation. Amaral (1929) suggested the existence of specimens intermediate between *corais* and *melanurus* in Colombia, but without providing further details; on the other hand, Pérez-Santos & Moreno (1988) indicate sympatry between the two forms in central and northern Colombia, but these records must be treated with scepticism (Cadle, 1992). It is also obvious that the new taxon is not morphologically intermediate between *D. c. corais* and *D. c. melanurus*. The hypothesis that it represents a hybrid population between the two subspecies can therefore be rejected.

The principal question is therefore the taxonomic level at which these taxa should be recognized. In recent years, there has been an increasing trend for diagnostically distinct populations to be recognized as full species, whereas the recognition of subspecies has become increasingly uncommon (Frost & Hillis, 1990). This use of the evolutionary species concept contrasts with the biological species concept, in which the potential or actual ability to interbreed is taken as a sign of conspecificity.

The three taxa of *Drymarchon* revealed here differ qualitatively, being unambiguously diagnosable in a number of features of colour pattern – and quantitatively in various scalation characters – often with little or no overlap between the three forms (see Table 2). The distributions of the three forms approach each other in northern Venezuela (Fig. 4), very closely in the case of *D. c. corais* and *D. c. melanurus*, but there are no reliably documented zones of sympatry or intergradation between them. Consequently, we have no data on whether they are reproductively compatible. However, in view of the degree of differentiation of the three forms, and the homogeneity of two of them across a broad range, we believe that all three should be considered distinct evolutionary species: *Drymarchon corais*, *D. melanurus* and *D. caudomaculatus*.

The affinities of the remaining conventional subspecies of *Drymarchon* remain unresolved for the time being. There are no obvious reasons for believing that any of these forms is conspecific with *D. corais* sensu stricto. The taxon *margaritae* displays a unique combination of pattern characters, including a dorsal colour change similar to that of *D. corais* (dark anteriorly, paler markings posteriorly), but a ventral pattern change more akin to that of *D. melanurus* (darker posteriorly, compared to uniformly pale throughout in *D. corais*). The only known specimen has 76 subcaudals, compared to a documented maximum of 64.5 in *D. caudomaculatus*. In the light of these clear, categorical differences, and pending further studies, we consider this form to be a separate species, *D. margaritae*, as originally proposed by Roze (1959).

In North America, like Collins (1991), we regard *Drymarchon couperi* as a separate species from other *Drymarchon*, on account of apparently consistent differences in labial scalation (Smith, 1941). However, further studies are required to confirm the status of this taxon.

In Central America, Smith (1941) noted the existence of hybrid zones between *melanurus* on one hand and the taxa *erebennus*, *orizabensis* and *rubidus* on the other. Additionally, juveniles and some adults of *erebennus*, *rubidus* and *unicolor* display oblique dark bars on the sides of the neck, which appear to be homologous with the marks seen in *D. melanurus* (no *orizabensis* were examined). Although the sister taxon to *Drymarchon* is unresolved, these dark marks appear to be unique to these taxa, and can therefore be regarded as a synapomorphy for these populations. This makes the classification of the taxa *erebennus* Cope, 1860, *rubidus* Smith, 1941, *unicolor* Smith, 1941 and, presumably, *orizabensis* Dugès, 1905, as subspecies of *D. melanurus* (Duméril, Bibron & Duméril, 1854), a tenable provisional arrangement. Further studies of the complex as a whole are clearly urgently required, and molecular methods may make a significant contribution towards the illumination of the evolution and systematics of this group.

NATURAL HISTORY NOTES

Little is known of the biology of the new species. It appears to be diurnal, and the two specimens in which

time of capture is known were active in the early morning or late afternoon. Most known specimens originate from within 45 km of the city of Coro, Estado Falcón, Venezuela, to the east and south-east of the city (Fig. 4), but Mijares-Urrutia & Arends (2000) cite a specimen from El Paují (10°48' N, 69°37' W). The actual distribution of the species may be greater. Until very recently (Mijares-Urrutia & Arends, 2000), the herpetofauna of Falcón State has received much less attention from collectors than most other parts of Venezuela. For instance, Roze (1966) lists a record for only one single species of snake for the entire western half of the state, and many species common even in the surroundings of Coro (pers. obs.) have no records for the state. However, it is worth noting that no *Drymarchon* was included in a collection from south-eastern Falcón State (Shreve, 1947).

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APPENDIX 1

Material examined (specimens marked with *asterisks were not included in PCAs due to missing characters):

Drymarchon caudomaculatus

VENEZUELA: Falcón: 15 km SE Coro, on Coro-Churuguara Road (EBRG 3413); Las Dos Bocas (EBRG 3412); Coro (MCNC 1019*); Taratara (MCNC 2251*).

Drymarchon corais

BOLIVIA: "Bolivia" (BM 94.5.4.3); BRAZIL: Amazonas: Boca do Tefé (MHNP 1900-460); Bahia: Cabuçu, Santo Amaro (IB 23027); Mato Grosso: Barracão Queimado (IB 22567); Nobres (IB 54995); Pará: Caripe (BM rr 1964.1521); Ilha de Marajó (BM 1923.11.9.108-110); São Paulo: Fernandópolis: Usina Hidroelétrica Agua Vermelha (IB 41744, 41918, 41929, 41937, 41950, 42173, 42216, 42030, 42229, 42232); Sergipe: Maruim (ZMUC r 60271); FRENCH GUYANA: Cayenne (MHNP 3332*, 3369); GUYANA: Demerara (BM 55.8.28.19); "Demerara River" (BM 1929.7.13.12); Dora Mission, 30 mi. North of Linden (BM 1977.308); PARAGUAY: Alto Paraguay: Primavera (BM 1956.1.16.36); SURINAME: "Suriname" (ZMUC r 60270); Paramaribo (BM 1946.4.4.15); Zanderij (BM 1946.4.4.14); TRINIDAD AND TOBAGO: "Trinidad" (BM rr 1964.1522, 1900.11.8.1); Hollis Dam Road: (BM 1964.1986); VENEZUELA: "La Morrocoy" (IB 25704); Aragua: Pie del Cerro, La Victoria (CM s 7420); Bolívar: Camarata (BM 1976.236); Carabobo: Valencia (ZMUC r 60317); Guárico: Paso del Caballo (IB 25707).

Drymarchon melanurus

BELIZE: Stann Creek (BM 91.3.4.4); COLOMBIA: Cauca: Buenaventura (NRM KVS 1964.820084887); Chocó: Condoto: Piña Lisa (BM 1914.5.21.37); COSTA RICA: Cartago (BM 71.1a.22.7); ECUADOR: Esmeraldas: Paramba (BM 1901.2.29.106); Loja: Catamayo Valley 30 km SW of Loja (BM 1935.11.3.73); Hacienda Juanes, 20 km W of Loja (BM 1935.11.3.74); GUATEMALA: Alta Verapaz: San Cristóbal Verapaz: Baleú (BM 1967.287); "Guatemala" (BM 1967.289); HONDURAS: ISLAS DE LA BAHÍA: Isla Borraca (BM 1938.10.4.90); MEXICO: "Yucatán" (BM 80.7.13.14); Tabasco: Teapa (BM 93.4.26.31); NICARAGUA: San Juan del Norte (NRM 517*); VENEZUELA: Distrito Federal: Camuri (MHNG 1363.35), Puerto La Cruz (CM s 7292); Mérida: Mérida (BM 1905.5.31.64); Santa María de Caparo (CM 86900)

SHORT NOTES

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A PRELIMINARY REPORT ON THE LATE PLEISTOCENE AMPHIBIANS AND REPTILES FROM GORHAM'S CAVE AND VANGUARD CAVE, GIBRALTAR

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The Gibraltar Caves Project is a collaborative effort between the Natural History Museum, London (NHM), Oxford Brookes University and the Gibraltar Museum. Excavations of Late Pleistocene deposits took place at several caves in the south face of the Rock between 1994 and 1999, in search of neanderthal hominid remains and associated environmental evidence. Reports on the excavations and vertebrate remains are given by Barton *et al.* (1998), Stringer *et al.* (2000) and Cooper (2000). The following report results from a preliminary study by the author on the subfossil amphibian and reptile remains recovered from bulk sample analyses. A more or less random selection of eighty-six samples was chosen: fifty-six from Gorham's Cave and thirty from Vanguard Cave. Most samples are from the 1995 season, while the remainder are from the 1996 excavations. The overall species list contains at least twenty-eight amphibian and reptile species and probably more. As there are several thousand further samples to study, it is envisaged that this natural archive of subfossil remains will provide an invaluable record of herpetofaunal diversity and faunal change in a western Mediterranean refugium during the Late Pleistocene. No previous studies have examined such an abundant and species-rich herpetofaunal assemblage from a glacial refugium.

Identifications were made with reference to modern comparative material in the author's collection (at Coventry University), collections at the Museo Nacional de Ciencias Naturales, in Madrid (MNCN), and that of J. Barbadillo at the Universidad Autónoma, Madrid (UAM). Most of the remains (up to 90%) belong to *Pelobates cultripes* (western spadefoot toad) – a species with very distinctive cranial osteology (Fig. 1). Cranial and ilial remains were most commonly used to identify the other anurans: vertebrae were most useful for salamanders, shell and limb bones for tortoises, cranial bones and vertebrae for lizards (Figs 3-4), and vertebrae for snakes. Most species were present only sporadically, except for the Moorish gecko, *Tarentola mauritanica* (Fig. 3), which was present in about half the samples. Table 1 shows the list of amphibian and reptile species recovered so far from both caves studied. The snake identifications are incomplete (* signifies presence in an unknown number of samples), but *Elaphe scalaris* seems to be the most common snake. Vertebrae of undetermined viper species #1 belong to either the Iberian adder, *Vipera seoanei,* or northern adder, *Vipera berus*. The second undetermined species is either Lataste's viper, *Vipera latastei,* or asp viper, *Vipera aspis*.

The age of most (if not all) of the remains from Gorham's Cave is Oxygen Isotope Stage (OIS) 3 (A. Currant, pers. comm.), c.25-60 000 years ago (Lowe & Walker, 1997, pp.332-334). Nearly all of the Vanguard Cave material dates to OIS 5a/b (N. Barton, pers. comm.), c.75-95 000 years ago (Lowe & Walker, 1997, pp.334-340). Further lithostratigraphic analyses are awaited to determine the full temporal range of the assemblages. All of the herpetofaunal remains are held in the Department of Palaeontology at the NHM.

This preliminary study has produced surprisingly diverse herpetofaunal assemblages, especially as the Gorham's material dates from a period when global climate was heading towards the last glacial maximum c.20 000 years ago (OIS 2). The western Mediterranean climate was humid and significantly cooler than today during OIS 3 (Rose *et al.*, 1999), with sea level 75-85 m lower than today (van Andel & Tzedakis, 1998). The assemblages contain several Iberian endemics, and nearly all species have Iberian and Mediterranean ranges today (Gasc *et al.*, 1997; Pleguezuelos, 1997). They were probably accumulated in the caves by avian predators, and possibly also by humans, with most bones lacking the digestive damage characteristic of mustelids (cf. Pinto Llona & Andrews, 1999).

Excluding the North African ranges of some species, the European ranges of most species identified are either restricted to Iberia or have clearly originated postglacially from Iberian refugia. Gibraltar would have almost been the most southerly refuge possible in Iberia, with the Gibraltar Strait forming a constant marine barrier throughout the Pleistocene (Busack, 1986). This is a true refugium, at the extreme south of a continental peninsula. Climate would have become harsher, globally, during the ensuing glacial maximum of OIS 2, and the south-western coastal zone of Iberia is likely to have been crucial to the survival of many thermophilous species.

For them to have survived until today, the thermal requirements of all the subfossil species identified must have been met throughout the Late Pleistocene in southern Iberian refugia. Amphibians and reptiles are much more dependent on suitable climatic parameters than are other vertebrate groups, especially mammals.

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TABLE 1. Preliminary list of Late Pleistocene amphibian and reptile taxa recovered (and relative occurrence in samples) from OIS 3 sediments in Gorham's Cave and OIS 5a/b sediments in Vanguard Cave, Gibraltar. Some of the snake identifications are currently incomplete, hence their presence (in at least one sample) is denoted by "*".

	No. of samples	
	Gorham's (out of 56)	Vanguard (out of 30)
Sharp-ribbed salamander, *Pleurodeles waltl*	1	1
Pygmy marbled newt, *Triturus marmoratus pygmaeus*	4	1
Undeterminate newt, *Triturus* sp.	2	
A discoglossid frog, *Discoglossus* sp.	1	
Western spadefoot toad, *Pelobates cultripes*	55	26
Mediterranean common toad, *Bufo bufo spinosus*	1	2
Natterjack toad, *Bufo calamita*	1	1
Stripeless tree frog, *Hyla meridionalis*	13	17
A ranid frog, *Rana* sp.	2	1
Hermann's tortoise, *Testudo hermanni*	2	3
An emydid cf. stripe-necked terrapin, *Mauremys leprosa*	1	
Moorish gecko, *Tarentola mauritanica*	15	19
Spiny-footed lizard cf. *Acanthodactylus erythrurus*	3	2
Large Psammodromus, *Psammodromus* cf. *algirus*	8	5
Ocellated lizard, *Lacerta lepida*		1
Iberian wall lizard, *Podarcis* cf. *hispanica*	2	
A skink, *Chalcides* sp.	7	1
Undeterminate lizard no. 1		1
Undeterminate lizard no. 2		2
Amphisbaenian cf. *Blanus cinereus*		16
Montpellier snake, *Malpolon monspessulanus*	*	*
Horseshoe whip snake, *Coluber hippocrepis*	*	*
Ladder snake, *Elaphe scalaris*	>13	>3
Grass or ringed snake, *Natrix natrix*	1	1
Viperine snake, *Natrix* cf. *maura*	1	1
Southern smooth snake, *Coronella girondica*	*	*
Undeterminate viper no. 1 *Vipera* sp.	3	
Undeterminate viper no. 2 *Vipera* sp	5	1

Even if summer temperatures were not as dramatically reduced as in other parts of Europe, the mechanisms by which the most demanding thermophiles survived have yet to be adequately explained. Perhaps species which breed today during the winter/spring may have shifted their breeding season to the spring/summer in response to thermal deterioration during the Late Pleistocene. There is probably no direct way of determining whether this occurred during the Late Pleistocene, but it can be observed in many species today. *Bufo calamita* (natterjack toad) breeds during the spring and summer across most of its range, but in Iberia it breeds during the winter and spring. The glacial refugium for *B. calamita* was in Iberia, therefore one of the modern scenarios must have been an adaptation achieved after the end of the last glaciation. Clearly, climate-induced breeding season shifts can happen. If winter hibernation could replace summer aestivation, this mechanism might help to explain some species' survival during Pleistocene glacial periods. It is less easy to explain how the most thermally demanding reptiles could survive. Perhaps only rarely were breeding seasons successful, but this was just enough for a species to hold on.

As the effects of climatic deterioration were more severe on the Iberian Plateau, many upland species are likely to have been forced to lower altitudes. It seems probable that some coastal areas of southern Portugal and southwest Spain were subject to the moderating effects of the Gulf Stream during the Late Pleistocene (Zagwijn, 1992). Displaced southwards from its current position, the Gulf Stream may have maintained mild conditions in coastal refugia (at least in some years), allowing the survival of Iberia's most thermophilous species.

Arising from this study, there are several noteworthy taxonomic issues, which can be mentioned briefly. A very large partial skeleton of common toad from Vanguard Cave (estimated snout-vent length of 180 mm; Fig. 2) must belong to the Mediterranean subspecies *Bufo bufo spinosus*. The literature does not record *B. b. spinosus* subfossils any larger than this. Z. Szyndlar (pers. comm.), who examined a small amount of snake

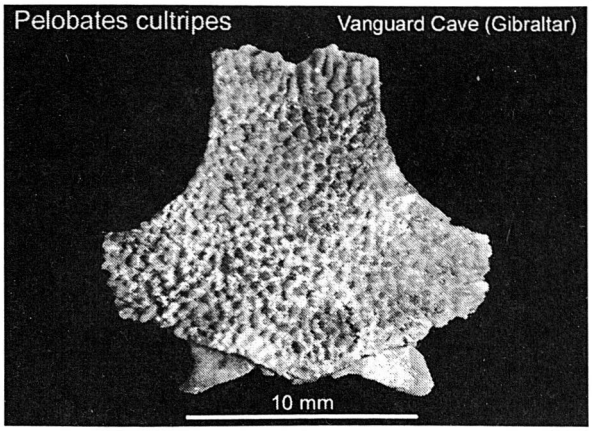

FIG. 1. Frontoparietal (dorsal view) of southern spadefoot toad *Pelobates cultripes* from Vanguard Cave, Gibraltar (sample VAN 95 105).

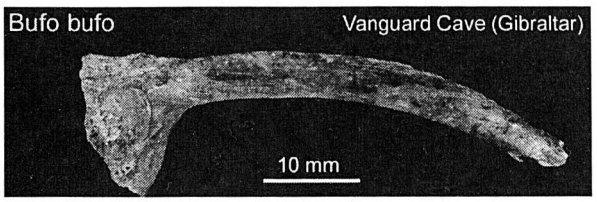

FIG. 2. Right ilium (lateral view) of Mediterranean common toad *Bufo bufo spinosus* from Vanguard Cave, Gibraltar (sample VAN 96 376).

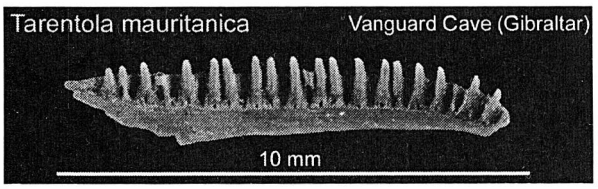

FIG. 3. Left dentary (lingual view) of Moorish gecko *Tarentola mauritanica* from Vanguard Cave, Gibraltar (sample VAN 95 172).

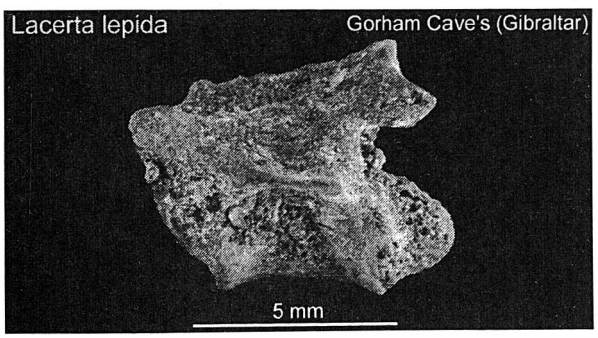

FIG. 4. Trunk vertebra (left lateral view) of ocellated lizard *Lacerta lepida* from Gorham's Cave, Gibraltar (sample GOR C 95 248).

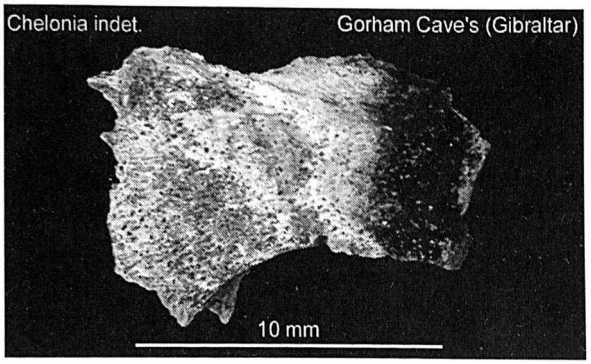

FIG. 5. Burnt fragment of chelonian shell from Gorham's Cave, Gibraltar (sample GOR C 95 408).

material, suggests that two vertebrae seen could not be matched with any Iberian species. They have some similarities with *Telescopus* – a genus not present in Iberia today but known from the Spanish uppermost Pliocene (Szyndlar, pers. comm.). The uncertain taxonomy of the viper remains would also merit further attention if more material were identified. As an Iberian endemic, *V. seoanei* is perhaps more likely during OIS 3 than *V. berus*, which is absent from Iberia today. The second viper species is most likely to be the Iberian endemic *V. latastei,* based on modern range characteristics, but the vertebrae resemble the largely non-Iberian *V. aspis* (Szyndlar, pers. comm.).

Several shell fragments of *Testudo hermanni* (Hermann's tortoise) are burnt (cf. Fig. 5), suggesting that tortoises were eaten by contemporary humans. Blackened bones of *P. cultripes* may also indicate that spadefoot toads were used as food. Little archaeozoological work has been carried out on the use of European herpetofauna as food by humans or hominids, although this would certainly have presented an easy-to-catch resource.

A large amount of fossil material (>5000 samples) from a range of Late Pleistocene ages at Gorham's and Vanguard Caves on Gibraltar, has still to be studied. Future study should fully identify these assemblages and investigate their palaeoenvironmental implications. The application of the Mutual Climatic Range method to provide quantified palaeoclimatic reconstructions is also intended.

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ADDITION OF A NEW LIVING GIANT LIZARD FROM LA GOMERA ISLAND TO THE PHYLOGENY OF THE ENDEMIC GENUS *GALLOTIA* (CANARIAN ARCHIPELAGO)

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The lacertid lizards of the endemic genus *Gallotia* (Arnold, 1973) from the Canary Islands represent one of the most important and best studied examples of island reptile radiation and evolution (Klemmer, 1976). Although there have been several attempts to reconstruct their phylogeny and evolution using molecular techniques (Thorpe, McGregor & Cumming, 1993*a*,*b*; Thorpe *et al.*, 1994), only the most recent (González *et al.*, 1996; Rando *et al.*, 1997) included all known extant species of the group and could therefore be used to understand the magnitude of this island- lizard radiation. These phylogenies suggested that the ancestor of *Gallotia* colonized the eastern islands of Lanzarote and Fuerteventura first, moving later to the islands of Gran Canaria, Tenerife, La Gomera, La Palma and El Hierro, following an eastern-western geographic transect (González *et al.*, 1996). Rando *et al.* (1997) positioned the recently discovered species *G. intermedia* from Tenerife (Hernández, Nogales & Martín, 2000) in the phylogeny of *Gallotia* (González *et al.*, 1996) and demonstrated that it was sister to the rediscovered *G. simonyi machadoi* from El Hierro (Böhme & Bings, 1975; Machado, 1985; Carranza *et al.*, 1999). In total, Rando *et al.* (1997) recognized five species of *Gallotia* at the molecular level: *G. atlantica* from the eastern islands of Lanzarote and Fuerteventura, *G. stehlini* from the central island of Gran Canaria, *G. simonyi* from the westernmost island of El Hierro, *G. intermedia* from Tenerife and *G. galloti* from Tenerife, La Palma, La Gomera and El Hierro. However, experiments – based on mating, viability of hybrid offspring and allozyme distances – on this last species suggested that the lizards present in La Gomera and El Hierro should be considered as a different species (*G. caesaris*) (López-Jurado, Mateo & Guillaume, 1997). Genetic distances between *G. simonyi machadoi* and *G. intermedia* (belonging to the '*simonyi* group', which includes all giant lizards from the western islands) were very similar to those between *G. galloti* and *G. caesaris* ('*galloti-caesaris* group'), suggesting that colonization of the western Canary Islands by each lineage was probably simultaneous.

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The casual discovery of this new lizard in Tenerife led to the possibility that other giant lizards could still survive in some remote areas of La Gomera and La Palma islands. Therefore, in June 1999, we started a systematic search mainly focused on the most coastal areas of La Gomera, and fortunately, a new giant lizard was found still living in the westernmost part (Valle Gran Rey) (Valido *et al.*, 2000).

Hutterer (1985), based on the analysis of subfossil material from La Gomera, described two new subspecies of giant lizards, *G. goliath bravoana* and *G. simonyi gomerana*. Morphological studies (Nogales *et al.* 2001) indicate that this new extant lizard belongs to the '*simonyi* group' and could correspond with the form described as *G. simonyi gomerana*, but with enough differences as to be treated as a full species (*G. gomerana*).

This finding provides an opportunity for further insight into the evolution and radiation of the genus *Gallotia* in the western Canary Islands. Therefore, in order to establish the phylogenetic position of this new lizard at the molecular level, we amplified and sequenced two enlarged segments of the previously analysed mtDNA gene fragments (500 bp of the 12S ribosomal RNA (rRNA) and 405 bp of the cytochrome *b* (cyt*b*) using the same methods and conditions as in González *et al.* (1996) and Rando *et al.* (1997). Representatives of the *Gallotia* genus at specific and subspecific levels – as well as the six specimens of the new lizard captured in La Gomera – were analysed. For this, new primers were designed: L14724 (5' TGACTTGAAGAACCACCGTTG 3') and H15149 (5' AAACTGCAGCCCCTCAGAATGATATTTGTCCTCA 3') for cyt*b* and L1064 (5' TTGACCACACGAAAGCTTAGAA 3') and H1565 (5' TTCCGGTACGCTTACCATGT 3') for 12S rRNA fragments. The new lizard sequences were deposited in the GenBank/EMBL with accession numbers AJ272395 and AJ272396 for 12S rRNA and for cyt*b*, respectively.

Out of the 405 bp analysed for the cyt*b*, 144 were variable and 108 parsimony-informative. For the 12s rRNA fragment, 122 out of 500 bp were variable and 69 parsimony-informative. Parsimony analyses were performed using PAUP, version 3.1.1 (Swofford, 1993). Confidence in the nodes was determined by 1000 bootstrap replications using Branch-and-Bound searches. Phylogenetic relationships were also determined with the neighbour-joining algorithm as implemented in MEGA version 1.01 (Kumar, Tamura & Nei, 1993) using the Kimura 2N-parameters distance (Kimura, 1980). Since both methods gave similar topologies, only the results from the parsimony analysis are reported.

Phylogenetic relationships among the different representatives of the genus *Gallotia* based on the cyt*b* and 12S rRNA sequences are shown in Figs. 1A and 1B respectively. Discrepancies at the specific level between both phylogenies commented upon in our previous arti-

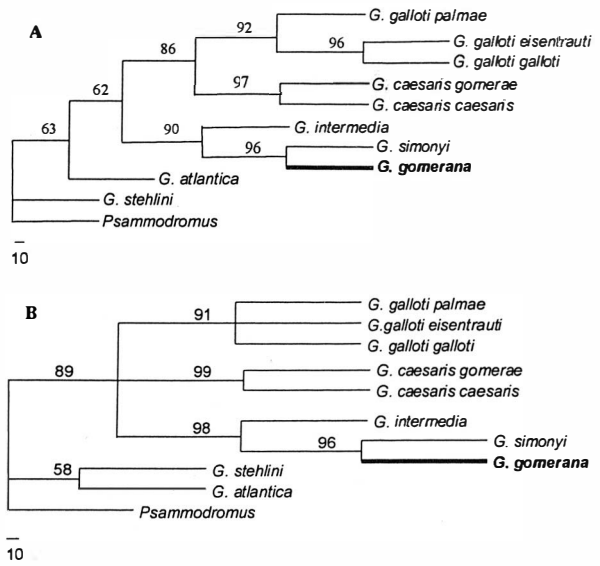

FIG. 1. Phylogenetic relationships among the Canarian endemic lizard genus *Gallotia* and one outgroup, based on cytochrome *b* (A) and 12S rRNA (B) partial sequences. Numbers on branches indicate the percentage of bootstrap support. The new branch is highlighted with bold lines. *Psammodromus* sequences for cyt*b* and 12S rRNA have been taken from GenBank (Accession numbers: AF206535 and AF206588, respectively) (Fu, 2000).

cles (González *et al.*, 1996; Rando *et al.*, 1997) persist. *G. stehlini* is basal to the rest of the *Gallotia* species from the Canary Islands on the cyt*b* tree, but it is sister to *G. atlantica* on the 12S rRNA one. In González *et al.* (1996) we propose that cyt*b*, due to its faster divergence rate, would be a good marker only at subspecific level. A similar situation has been found by Graybeal (1993) in bufonid frogs, evidencing that the cyt*b* gene has little phylogenetic signal for solving deep nodes. In spite of the relatively poor performance of the cyt*b* gene, there seems to be no controversy in the position of the new giant lizard from La Gomera (Figs. 1A and 1B). In both cases it is related to other taxa of the '*simonyi* group' and more closely to *G. simonyi* from El Hierro (1.5% and 0.2% divergence for cytb and 12S rRNA, respectively) than to *G. intermedia* from Tenerife (5.2% and 1.9%). Curiously the relationship among the giant lizards of Tenerife, La Gomera and El Hierro runs parallel to that of the '*galloti-caesaris* group', with *G. caesaris caesaris* from El Hierro closer to *G. caesaris gomerae* from La Gomera than to *G. galloti galloti* from Tenerife. This supports our hypothesis that both groups followed the same colonization pattern on the western islands: stepwise sequence from the oldest (La Gomera) to the youngest (El Hierro) (Rando *et al.*, 1997). This is in agreement with the stepping-stone model proposed for several taxa from the Canary Islands (Juan *et al.*, 2000). Nucleotide divergence, measured as the maximum number of differences between taxa within the '*simonyi* group' (20 and 9 substitutions for cyt*b* and 12S rRNA, respectively) or by the Kimura 2N-parameters distance (Kimura, 1980) (0.052±0.011 and 0.023±0.006 for cyt*b* and 12S rRNA, respectively), is always lower than that found among subspecies of the '*galloti-caesaris* group' (33 and 25 substitutions; 0.092± 0.017 and 0.053±0.011, for cyt*b* and 12S rRNA, respectively), suggesting that the '*galloti-caesaris* radiation' could predate that of *simonyi*. Nevertheless, the existence of a common ancestor of the '*simonyi* and *galloti-caesaris* groups', suggested by Rando *et al.* (1997), is supported by the fact that both conform to a monophyletic group (Fig. 1B).

It is also interesting to note that *G. intermedia* was considered morphologically as a different species from *G. simonyi* (Hernández *et al.*, 2000), but the Kimura 2N-parameters distances are only 0.023 for 12S rRNA and 0.046 for cyt*b*. In the case of the '*galloti-caesaris* group' the two lineages (Tenerife-La Palma and La Gomera-El Hierro) should also be treated as two different species as proposed by López-Jurado *et al.* (1997) on the basis of interspecific-cross incompatibilities, which is reflected in the higher genetic distances (0.048± 0.004 and 0.076±0.014 for 12S rRNA and cyt*b*, respectively).

Finally, the null variation observed for both fragments among the only six individuals of *G. gomerana* captured after four months of intensive trapping, seems to indicate that this lizard is in danger of extinction. In the last twenty-five years, living giant lizards from the '*simonyi* group' have been found in El Hierro, Tenerife and La Gomera; La Palma is currently the only western Canary Island where their presence is unknown. In this island giant fossil bones have been recorded (see Bischoff, 1998) but, after prospecting 57 suitable localities for its presence, we have not yet succeeded in finding living animals.

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BOOK REVIEWS

Hylid Frogs of Middle America. William E. Duellman (2001). 1170 pp. (2 volumes). Society for the Study of Amphibians and Reptiles, Ithaca, New York. US $125.00 (cloth).

Hylid Frogs of Middle America was originally published in 1970, as a limited edition of 1200 copies as Monograph Number 1 by the Museum of Natural History at the University of Kansas. It was the culmination of Bill Duellman's two decades of arduous fieldwork in "Middle America" – Central America plus Mexico – and was a massive work of two volumes, with 748 pages of text and 72 plates, mostly paintings by the biological illustrator David Dennis.

The original has long been out of print and copies cost a small fortune on the second-hand market. Duellman himself has worked mainly in South America since 1970, but in the late 1990's he persuaded the Society for the Study of Amphibians and Reptiles (SSAR) to publish a revised version: this magnificent, two-volume, "new and expanded" edition, published at the remarkable clothbound price of $125 (partly aided by a benefactor), is the result, and is volume 19 of the Society's Contributions to Herpetology monograph series.

Pages 1-748 and plates 1-72 are reprints of the 1970 edition, but the plates have been improved by using laser-scans from the original paintings, rather than photographic reproduction. The new material is a 410 page Supplement with 20 new plates. Helpfully, the original index has been discarded and replaced by a new index covering both old and new material. The literature-cited lists have been kept separate: the new one contains over 400 citations, evidence enough of the need for this revised edition.

David Wake supplies a thoughtful Foreword to the new edition, raising issues about the puzzlingly different distribution patterns of plethodontid salamanders and hylid frogs in middle America. Duellman begins the Supplement with an Introduction, summarizing the reasons for the new edition, particularly the large number of new taxa named since the original: 49 added to the original 115. This is partly the result of new taxonomic decisions where Duellman had been conservative, but there have also been numerous genuine discoveries, mainly from mountainous areas. This is part of the evidence that drew Hanken (1999) to note that the class Amphibia is currently the fastest expanding vertebrate group in terms of newly described species. Unfortunately – as both Wake and Duellman note – many of the new and old species may already be extinct as a result of the combined ravages of habitat loss and the suite of factors contributing to the declining amphibian populations saga.

The bulk of the text – both original and Supplement – is taken up by generic and individual species accounts, with the Supplement devoted to new information (new species, reclassifications and new information on species described in the original). Most detail is devoted to anatomical descriptions of adult morphology, with additional notes – where there is information – on tadpoles, oviposition, natural history, mating call and distribution. Illustrations include distribution maps, drawings of tadpoles, call sonagrams and David Dennis's very beautiful paintings, mainly in colour. For genera with several or many species, the account of the genus includes character matrices and phylogenetic analyses.

As expected of this author, these accounts are detailed, highly authoritative and bang up to date (remarkably, including some 2001 citations). They will be essential reading for anyone interested in middle American hylids for decades to come, but – at a combined book weight of 4.5 kg – probably not as a field guide! Where there are controversies, Duellman recounts the evidence clearly, occasionally where his own previous interpretations now seem wrong. On occasion, there are flashes of dry humour: I liked especially his invention of Starrett's Law, from a casual remark by Patricia Starrett that "the most bizarre types of tadpole develop into ordinary frogs, whereas highly distinctive species of frogs usually have very ordinary looking tadpoles".

In addition to these accounts are a set of keys to the adult frogs. In the 1970 version, these were initially to genera, then to the species within each genus. In the Supplement, he dispenses with the generic keys on the grounds that they rely too much on difficult characters. Instead, he gives a set of geographically-based keys: Costa Rica and Panama; North-west etc. Sadly, there are no keys to the tadpoles. This is because many of the tadpoles, at stages where their morphology is fully developed, remain unknown. He does, however, give tables of the known tadpole characters. This lack of data on tadpoles is a problem throughout the neotropics. As I know from my own work in Trinidad, rearing tadpoles of some species is very difficult.

The remainder of the book is devoted to general topics which synthesize what is known of the frogs of the region and their evolution, with several new topics introduced in the 2001 Supplement. Not surprisingly, one of the new topics is conservation. Duellman writes: "When I first visited Middle America in 1951, I was greatly impressed with the extent of relatively undisturbed natural landscape. Subsequent degradation and destruction of the formerly undisturbed areas has been nothing short of appalling".

Another topic given extended treatment in the Supplement is the evolutionary history of the region, particularly the contribution of plate tectonics to an understanding of the distribution of amphibians: not an easy read for the non-geologically minded, but an indication of the ambition and scope of Duellman's approach. This is followed by sections on hylid evolution, distribution and diversity, with a final comparison of two groups that co-occur with the hylids, the plethodontid salamander genus *Bolitoglossa* and the anurans referred to *Eleutherodactylus*.

A major take-home message from all this is the provisional state of our knowledge. This is in large part because of the relatively few molecular analyses so far performed on the middle American hylids. Duellman fully expects his phylogenetic conclusions to require revision once new data are available, but is clearly concerned that such data may be hard to come by, given the reality of declining amphibian populations and consequent concerns even over small-scale sampling for legitimate scientific purposes.

I particularly liked the final general topic in the Supplement, on future research. Duellman here lists a whole series of themes where our knowledge of the hylids of middle America (and all frogs, everywhere in the tropics) is deficient. In addition to unknown tadpoles and molecular data, already mentioned, he notes the ecophysiology of tropical anurans, of which "essentially nothing is known", and the factors which affect the dynamics of larval communities. It is likely that these themes will long remain unexplored in the rarer and more inaccessible species, but there are some hylids where the sort of treatment Michael Ryan gave to the *Tungara Frog* (1985) should be possible.

It is very encouraging that a book with this level of scholarship and high production standards can still be produced. Now that he has completed this task and is now emeritus, perhaps Professor Duellman, Dr Trueb and the SSAR can be persuaded to revise the frogger's bible, the *Biology of Amphibians*?

Duellman finishes his section on the future with two visions: a dream of all the future research that could be done, and a "nightmare of continuing habitat destruction and declining populations". With him, we all wish that it will be the dream that comes true.

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Amphibia: aspetti di ecologia della conservazione [Amphibia: aspects of conservation ecology]. C. Scoccianti. (2001). WWF Italia, Sezione Toscana. Guido Persichino Grafica Ed., Firenze: XIII + 430 pp., 70 figs.

After many years spent working in the field on WWF/Italia's conservation projects for amphibians, Carlo Scoccianti felt the need to share the knowledge he gained from this experience with other conservationists. This book is the result, and integrates his personal views with a thorough analysis of the literature.

The book consists of three sections. The first is an overview of the main threats to the survival of amphibian populations, such as the alteration of natural aquatic and terrestrial environments, the consequences of agricultural transformation, and the impact of fires, pollutants and invasion of alien species on various habitats important for amphibians. Later, conservation perspectives and proposals for practical action aimed at limiting the impact of the factors threatening these animals are also presented. The second part of the book contains a detailed analysis of the factors that can cause habitat fragmentation – certainly one of the main causes of amphibian decline – and the impact it has on population dynamics is also discussed. The final part of this section opens an interesting discussion about global declines, after reviewing the factors that have been so far hypothesized as its main causes, such as the increased acidity of aquatic and terrestrial habitats, global warming, and the increase of UV-B radiation and of chemical pollutants. Finally, the third part of the book is much more practical, and offers guidelines for various measures that may be taken in amphibian conservation programmes. It gives technical suggestions about possible actions when amphibian populations are under threat. For instance, guidelines for the construction of tunnels that allow amphibians to pass under roads without injury are given, as well as instructions to follow when creating new breeding ponds for the animals. Useful photographs and explanatory drawings accompany the text.

I read this book with increasing enthusiasm, knowing that it will be very helpful in many situations that I will have to face during my future activities in the field. I am also sure that I will take advantage of the 50 pages of references collated at the end of the volume.

Copies of the book can be obtained from: WWF Toscana, Via Sant'Anna 3, 50124 Florence, Italy (Email: toscana@wwf.it). Those not familiar with the Italian language can read the very comprehensive abstracts in English at the end of each chapter of parts one and two. Unfortunately, the third section of the book is not translated. The keys to all the photographs, tables and figures are also presented in English.

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THE HERPETOLOGICAL JOURNAL

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(revised July 2000)

1. The *Herpetological Journal* publishes a range of features concerned with reptile and amphibian biology. These include: *Full Papers* (no length limit); *Reviews* and *Mini-reviews* (generally solicited by a member of the editorial board); *Short Notes*; controversies, under *Forum* (details available from the Editor); and *Book Reviews*. Faunistic lists, letters and results of general surveys are not published unless they shed light on herpetological problems of wider significance. Authors should bear in mind that the *Herpetological Journal* is read by a wide range of herpetologists from different scientific disciplines. The work should therefore appeal to a general herpetological audience and have a solid grounding in natural history.

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3. Authors should consult a recent issue of the Journal regarding style. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed or produced on a good-quality printer, and double-spaced with wide margins all round. The journal is typeset direct from the author's computer diskette, so all manuscripts should be prepared using a wordprocessor (preferably on a PC-compatible microcomputer). If figures are prepared using computer graphics, they should be supplied separately and NOT embedded in the text of the wordprocessor file. Preferred formats are MS Word for Windows (text) and MS Excel, Bitmap, TIFF, or JPEG files (graphics). It is not necessary to submit a computer diskette with the initial manuscript, but this will be required in the event of the manuscript being accepted for publication.

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   Boycott, B. B. & Robins, M. W. (1961). The care of young red-eared terrapins (*Pseudemys scripta elegans*) in the laboratory. *British Journal of Herpetology* **2**, 206–210.

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