

Taxonomic revision of the Iberian 'Archaeolacertae' I.: A new interpretation of the geographical variation of '*Lacerta monticola*' BOULENGER, 1905 and '*Lacerta cyreni*' MÜLLER & HELLMICH, 1937 (Squamata: Sauria: Lacertidae)

Taxonomische Revision der iberischen 'Archaeolacertae' I.:
Eine neue Interpretation der geographischen Variabilität von '*Lacerta monticola*
BOULENGER, 1905 und '*Lacerta cyreni*' MÜLLER & HELLMICH, 1937
(Squamata: Sauria: Lacertidae)

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KURZFASSUNG

Die vorliegende morphologische Arbeit analysiert die geographische Variabilität von '*Lacerta monticola*' BOULENGER, 1905 und '*L. cyreni*' MÜLLER & HELLMICH, 1937 mit Hilfe univariater und multivariater statistischer Verfahren. Die Stichproben von '*L. monticola*' weisen eine weitgehende Überlappung der Variationsbereiche der entsprechenden Merkmalsausprägungen auf, doch läßt sich das Sample von S^a da Estrella ('*L. m. monticola*' BOULENGER, 1905) von der übrigen kantabrischen Stichprobe ('*L. m. cantabrica*' MERTENS, 1929) abtrennen. '*L. cyreni*' umfaßt mehrere allopatrische Populationen mit jeweils bedeutendem Differenzierungsgrad. Die Population von Gredos erscheint von den Guadarrama-Populationen ('*L. c. cyreni*' MÜLLER & HELLMICH, 1937) subspezifisch verschieden und die kleine bestandsgefährdete Population von Peña de Francia unterscheidet sich von den beiden erstgenannten bedeutend.

ABSTRACT

The present morphological study analyzes the geographical variation of '*Lacerta monticola*' BOULENGER, 1905 and '*L. cyreni*' MÜLLER & HELLMICH, 1937 by means of univariate and multivariate statistical analyses. '*L. monticola*' shows a low degree of morphological interpopulation differentiation (considerable overlap of the ranges of respective character states). Yet, one sample (S^a da Estrella) is separable from the rest of the Cantabric samples. The first corresponds to '*L. m. monticola*' BOULENGER, 1905, the second to '*L. m. cantabrica*' MERTENS, 1929. '*L. cyreni*' forms several allopatric populations which have reached a considerable degree of divergence. The populations of Gredos seem to be subspecifically distinct from the Guadarrama ones ('*L. c. cyreni*' MÜLLER & HELLMICH, 1937) and the small endangered Peña de Francia population is strongly different from both.

KEY WORDS

Lacertidae, 'Archaeolacerta', '*Lacerta monticola*', '*L. cyreni*', new subspecies, systematics, taxonomy, biogeography, Iberian Peninsula

INTRODUCTION

The original description of '*Lacerta monticola*' (BOULENGER, 1905) has apparently been based on two adult specimens, and a young female from S^a da Estrella, and another young animal from 'Spain'. No individual was declared type. Later, in his monograph of the Lacertidae, BOULENGER (1920/21) designated specimens from both 'Spain' and 'Estrella' as types.

CYRÈN (1928) assigned the type locality of '*L. monticola*' to S^a de Guadarrama' and described the S^a da Estrella

populations as '*L. estrellensis*' while MERTENS & MÜLLER (1928) restricted BOULENGER's type localities of '*L. monticola*' to S^a de Estrella' before describing '*L. monticola cantabrica*' (MERTENS 1929).

The latter opinion prevailed despite MERTENS' paper of 1929 where he again mentioned 'Guadarrama' as type locality of this species. Later, MÜLLER & HELLMICH (1937) described '*L. m. cyreni*' and synonymized '*L. estrellensis*' with '*L. monticola*' which both had been reported from

the same locality.

Apart from the original description (BOULENGER, 1905), papers dealing with the North Spanish populations of '*L.*' *monticola* have been usually very incomplete, being based on few specimens, small areas or mixed samples of more than one taxon.

In '*L.*' *monticola*, maximum morphological variation can be expected in North Spanish specimens of the Picos de Europa Massif through the Cantabric Mountains up to the mountains of Galicia and Sanabria, with a number of recently discovered disjunctive coastal populations at sea level (GALAN 1982; ELVIRA & VIGAL 1982). '*L.*' *monticola* also inhabits S^a da Estrella, where it is now isolated from the main area (fig. 1).

L.' *cyreni* lives in the Spanish Sistema Central and forms several disjunctive populations, from east to west: S^a de Guadarrama (type locality of the species); Gredos (with several peripheral isolates in S^a de la Paramera, La Serrota, S^a de Bejar), and a more western relict population in the summit region (uppermost 100 m) of the Peña de Francia mountain (SALVADOR 1984; BARBADILLO 1987; LIZANA & al. 1993) (fig. 1).

L.' *cyreni*, although closely related to '*L.*' *monticola* (ODIerna & al. in press; MAYER & ARRIBAS 1996) is different from the latter in pattern and coloration, karyotype and some genetic loci (see SALVADOR 1984; ARRIBAS 1993; PEREZ MELLADO &

al. 1992 - for morphology of the two taxa; ODIerna & al. 1994, 1996 in press - for karyology; and MAYER & ARRIBAS 1996 - for genetics).

L.' *cyreni* differs from '*L.*' *monticola* in having a completely heterochromatinized W sex chromosome, except for a little intercalary euchromatic band. (all euchromatic in *monticola*), and NOR (nucleolar organizer) in a different chromosome and position (subtelomeric in a pair of small to medium sized chromosomes in '*L.*' *cyreni*, and in the telomeric apex of a large pair of chromosomes in '*L.*' *monticola*) (ODIerna & al. 1994, 1995, in press). In particular, the NOR localization has proved to be of diagnostic value and relevance for phylogenetic studies in lacertids (ODIerna & al. 1987). Likewise, starch gel electrophoresis found differences between the two taxa (two different out of 6 variable alleles, in West European 'Archaeolacertae' studied - MAYER & ARRIBAS 1996).

The aim of the present paper is to review the geographical variation of '*L.*' *monticola* and '*L.*' *cyreni*, starting from the assumption that they are closely related species (allospecies, sensu MAYR & ASHLOCK 1991), and to pay special attention to the patterns of their geographical differentiation through the Iberian mountains. The uncertain systematic status of the lizards of the 'Archaeolacerta' type is indicated by placing the name *Lacerta* between quotation marks.

MATERIAL AND METHODS

Material

A total of 313 specimens (snout-vent length > 45 mm) were studied from the collections of the author (CA, University of Barcelona), PEDRO GALAN (CG, La Coruña), MANUEL MEJIDE (CM, Soria) and Estación Biológica de Doñana (EBD, Sevilla, Spain). Type specimens in CA, will be transferred to 'Centro Pirenaico de Ecología (CSIC) after finishing the studies.

[S1]..[S1.5] = sample 1..sample 1.5.

'*Lacerta*' *monticola* BOULENGER, 1905

[S1] S^a da Estrella, Portugal (A Torre, Lagoa Comprida): 9 males, 15 females.

[S2] La Coruña, coastal localities, Spain (see GALAN 1982 for a detailed list): 14 males, 17

females.

[S3] Lugo, coastal localities, Spain (S. Xulian de Cabarcos, Insúa, S. Cosme de Barreiros): 18 males, 17 females.

[S4] Lugo, mountain localities, Spain (S^a de Caurel, Incio, Saá de Incio, Sta. Cruz de Incio, Hospital de Incio, Herrería de Incio, Trascastro de Incio): 19 males, 16 females.

[S5] Sanabria - Truchillas area, Sierra de la Cabrera, Spain: 1 male.

[S6] West Cantabric Mountains, Spain (S^a de Ancares: Vilarello de Donis, Piornedo de Donis): 12 males, 3 females.

[S7] Central Cantabric Mountains, Spain (Somiedo area: Rebollada, Villar de Vildas, Lago de la Cueva, Lagos de Calabazosa, Puerto de Somiedo): 29 males, 19 females.

[S8] East Cantabric Mountains, Spain (Puerto de Vegarada, Puerto de las Señales, Puerto de Tarna): 13 males, 19 females.

[S9] Picos de Europa Massif, Spain (Vega de Enol): 5 males, 8 females.

'Lacerta' *cyreni*
MÜLLER & HELLMICH, 1937

[S1.2] S^a de la Peña de Francia, Spain: 1 male, 1 female.

[S1.3] S^a de Bejar, Spain: 1 male, 3 females.

[S1.4] S^a de Gredos, Spain (Plataforma de Gredos, Laguna Grande de Gredos, Portilla de los Machos and Puerto de Angosturas): 20 males, 36 females.

[S1.5] S^a de Guadarrama, Spain (Puerto de Navacerrada): 13 males, 21 females.

A more detailed list of specimens studied is available from the author.

For statistical analyses, samples from adjacent localities had to be pooled to achieve minimum sample size (five measurable specimens of each sex). Pooling was done only in case of similar physiographic localities; individuals to be pooled were added to the population with the nearest centroid.

Thus, all coastal specimens were put in one sample. Female '*L.*' *monticola* specimens from inland Lugo localities [S4] and West Cantabric mountains [S6] were pooled. Specimens of the Central Cantabric localities, and the three mountain passes from the East Cantabric Mountains were grouped into two samples (Central [S7] and East Cantabric Mts. [S8]). All samples are composed by specimens belonging to adjacent localities except for the coastal Coruña sample [S2] and the female sample from Ancares-Incio [S4 + S5].

Characters studied

B i o m e t r y: Snout-vent length (SVL); forelimb length (FLL); hindlimb length (HLL); pileus length (PL); pileus width (PW); parietal scale length (PaL); masseteric scale diameter (ØM); tympanic scale diameter (øT); anal scale width (AW); anal scale length (AL).

All linear measurements were made with digital callipers to the nearest 0.01 mm by the author to avoid inter observer variability.

True lengths were transformed into the non-dimensional ratios: FLL/SVL; HLL/SVL; PL/PW; ØM/PaL; øT/PaL; AW/AL. All ratios are given multiplied by 100.

P h o l i d o s i s [Counts]: Supraciliar granulae - right and left side (GrSr, GrSl); gularia (GUL); collaria (COLL);

dorsalia across mid-body (DORS); ventralia - transversal rows (VENT); femoralia - right and left side (FEMr, FEMl); lamellae underneath 4th toe (LAM); circumanal (CircA).

[Dichotomous characters]: Contact of rostral-internal and postocular-parietal shields present (+) or not present (-).

C o l o r a t i o n: Dark punctuation on ventral scales (VP) present or not present.

Only specimens from which complete character sets were available were used in numerical analyses.

Statistical procedures

Statistical analyses performed in the present study are phenetic, based on relative similarity or dissimilarity of populations with many characters considered simultaneously without a priori weighing (JARDINE & SIBSON 1971; SNEATH & SOKAL 1973).

D e s c r i p t i v e statistics comprised arithmetic mean, standard deviation, coefficient of variation, maximum, and minimum. The sum of variation coefficients was used as an estimator of the intrinsic population variability.

U n i v a r i a t e statistics: A one-way (single classification) ANOVA was generated with NCSS (HINTZE 1991). ANOVA was carried out separately for males and females (SOKAL & ROHLF 1969). Where significant differences were found, a STUDENT-NEWMAN-KEULS test was run at $p < 0.05$ (significant) and SCHEFFÉ's test at $p < 0.01$ (highly significant) for multiple comparisons among means.

M u l t i v a r i a t e analyses were done with the CANP program of the MULTICUA package (ARENAS & al. 1991). Canonical Variate Analysis (CVA) was performed to arrange the populations along orthogonal axes (Canonical Variates) with maximum discriminative power using MAHALANOBIS distances. Each population is represented by a centroid (a hypothetical middle individual) and a confidence region of 90%. CVA is an appropriate method for group representation based on metric variables, but can also be used in dichotomous and meristic data (MAXWELL 1961; CLARINGBOULD 1958; CUADRAS 1981).

Table 1: *Lacerta monticola* - eight samples of males. Statistical report of biometric and pholidosis characters. For sample numbers and character abbreviations see 'Material and Methods'. (mean - arithmetic mean, std - standard deviation, CV - coefficient of variation, min - minimum, max - maximum).

Tab. 1: *Lacerta monticola* - acht Stichproben von Männchen. Statistiken zur Variabilität biometrischer und pholidotischer Merkmale. Zifferncode und Abkürzungen siehe 'Material and Methods'. (mean - arithmetisches Mittel, std - Standardabweichung, CV - Variationskoeffizient, min - Minimum, max - Maximum).

Character Merkmal	[S1] Estrella (n=9)			[S2] La Coruña, Coast (n=14)			[S3] Lugo, Coast (n=18)			[S4] Lugo Mts. (n=19)			[S5] Enol, Pic. Europa (n=5)							
	mean	std	CV	min	max	mean	std	CV	min	max	mean	std	CV	min	max	mean	std	CV	min	max
SVL	65.41	7.36	0.11	49.5	71.1	61.13	7.62	0.12	45.81	72.03	61.05	6.53	0.1	50	71.4	62.28	7.55	0.12	45.88	72.69
GrSr	10.66	1.11	0.1	10	13	10.07	2.23	0.22	6	15	9.94	1.69	0.17	7	13	11.11	1.84	0.16	7	14
GrSI	10.44	1.23	0.11	9	12	10.35	1.94	0.18	7	15	10.33	1.87	0.18	7	13	11.16	2	0.18	8	15
GUL	24	1.58	0.06	22	26	25.5	2.56	0.1	22	29	24.94	2.81	0.11	19	30	23.84	1.92	0.08	20	27
COLL	10	1	0.1	9	11	11.14	1.29	0.11	9	13	11.44	1.75	0.15	8	14	11	0.88	0.08	9	13
DORS	52.44	3.32	0.06	46	56	55	2.8	0.05	51	59	56.05	3.36	0.06	51	62	55.73	3.57	0.06	48	62
VENT	26.88	0.33	0.01	26	27	26.42	1.15	0.04	24	28	27	0.84	0.03	26	29	26.31	0.74	0.02	25	27
FEMr	19	1.93	0.1	16	22	17.64	1.78	0.1	15	21	19.22	1.8	0.09	16	23	18.1	1.37	0.07	16	21
FEMl	19	2.44	0.12	16	24	17.78	1.25	0.07	15	20	19.33	1.81	0.09	16	23	18.31	1.56	0.08	16	21
LAM	24.55	1.42	0.05	22	26	25.64	1.69	0.06	23	28	25.16	1.38	0.05	23	28	25.94	2.17	0.08	22	30
CircA	7	1.11	0.15	6	9	7.14	0.86	0.12	6	8	6.72	0.82	0.12	6	8	6.73	1.09	0.16	5	9
FLL*100/SVL	35.94	0.25	0.07	32.39	40.4	35.89	0.01	0.03	32.75	37.88	36.68	0.02	0.05	32.8	39.56	35.82	0.01	0.04	33.58	38.85
HLL*100/SVL	50	0.02	0.04	45.86	54.33	54.36	0.09	0.16	47.38	84.54	52.11	0.02	0.04	46.99	55.74	52.23	0.02	0.05	47.91	59.06
PL*100/PW	214.72	0.1	0.05	196.77	231.57	215.14	0.07	0.03	201.76	232.11	211.37	0.06	0.03	198.5	221.42	208.27	0.07	0.03	195.02	223.28
ØM/PaL	41.53	0.07	0.18	32.07	57.14	35.52	0.09	0.25	12.27	54.03	34.47	0.11	0.32	22.98	45.97	38.13	0.06	0.16	25.85	49.1
ØT/PaL	35.72	0.06	0.17	28.12	48.78	32.36	0.05	0.17	21.29	39.78	32.84	0.05	0.15	23.4	40.9	31.73	0.05	0.17	17.88	39.5
AW / AL	54.13	0.07	0.13	42.1	69.23	60.85	0.07	0.12	44.94	68.34	55.48	0.06	0.11	43.47	73.33	51.28	0.05	0.11	39.47	60.83
Rostral-Internal contact (+/-)	(1/8)									(13/2)					(14/4)					(20/3)
Postocular-Parietal contact (+/-)	(1/8)									(5/9)					(2/16)					(3/19)
Character Merkmal	[S6] S [*] Ancares, W. Cant. Mts (n=12)			[S7] Somiedo, C. Cant. Mts (n=29)			[S8] Vegarada, E. Cant. Mts (n=13)			[S9] Enol, Pic. Europa (n=5)										
SVL	64.76	4.57	0.07	51.97	69.96	60.76	5.67	0.09	47.6	71.8	58.37	5.32	0.09	47	68.4	60.92	3.09	0.05	58.1	64.9
GrSr	10.91	2.19	0.2	7	14	9.55	1.4	0.14	7	13	9.2	1.2	0.13	6	10	9.4	1.14	0.12	8	11
GrSI	10.66	2.6	0.24	7	15	9.72	1.55	0.16	5	12	9.06	1.38	0.15	6	11	9.8	1.09	0.11	9	11
GUL	23.83	1.99	0.08	21	27	23.68	1.87	0.08	20	28	23.26	1.79	0.07	20	27	23.8	1.92	0.08	22	27
COLL	11	1.2	0.11	10	13	10.72	1.22	0.11	8	14	10.86	0.91	0.08	10	12	10.6	1.51	0.14	9	12
DORS	54.33	3.28	0.06	48	60	50.13	2.29	0.04	47	55	50.6	2.6	0.05	46	55	47.4	1.14	0.02	46	49
VENT	26	1.04	0.04	25	28	25.86	0.99	0.03	24	28	25.8	0.86	0.03	24	27	26.8	1.3	0.04	25	28
FEMr	18.08	2.23	0.12	15	21	16.96	1.14	0.06	15	19	17.2	0.86	0.05	16	18	17.7	0.7	0.04	16	18
FEMl	17.66	2.22	0.12	14	21	17.41	1.15	0.06	16	20	17.2	0.86	0.05	16	19	17.6	1.14	0.06	16	19
LAM	26.75	1.91	0.07	24	30	24.07	1.51	0.06	21	27	24.26	1.16	0.04	22	26	25.6	1.34	0.05	25	28
CircA	7.16	0.93	0.13	6	8	6.92	0.85	0.12	5	9	6	0.53	0.08	5	7	7.6	1.51	0.19	5	9
FLL*100/SVL	35.43	0.02	0.07	30.14	39.8	35.78	0.01	0.05	33.62	43.06	34.67	0.01	0.04	30.65	38.29	36.48	0.01	0.03	35.22	38.52
HLL*100/SVL	51.09	0.02	0.05	44.76	55.38	49.17	0.09	0.2	63.13	51.23	51.23	0.01	0.03	48.49	53.74	51.79	0.01	0.01	50.62	52.83
PL*100/PW	217.35	0.08	0.04	200.88	231.99	209.86	0.08	0.04	197.56	229.68	206.33	0.06	0.02	197.15	220.77	215.3	0.1	0.04	201.36	229.57
ØM/PaL	40.3	0.03	0.07	35.48	44.42	41.16	0.04	0.11	29.31	53.48	41.09	0.04	0.1	34.87	46.93	42.34	0.04	0.1	36	47.36
ØT/PaL	34.77	0.04	0.11	28.01	40.83	35.81	0.08	0.24	0	46.55	39.33	0.09	0.24	28.93	68.57	36.11	0.04	0.1	31.57	40.35
AW/AL	54.49	0.04	0.08	48	62.99	56.99	0.04	0.07	50	68.42	57.32	0.05	0.1	45.08	65.7	50.83	0.04	0.08	47.72	60.46
Rostral-Internal contact (+/-)	(8/4)									(17/12)					(15/10)					(5/0)
Postocular-Parietal contact (+/-)	(1/11)									(7/22)					(2/13)					(3/2)

Table 2: 'Lacerta monticola' - seven samples of females. Statistical report of biometric and pholidosis characters. For sample numbers and character abbreviations see 'Material and Methods'. (mean - arithmetic mean, std - standard deviation, CV - coefficient of variation, min - minimum, max - maximum).
 Tab. 2: 'Lacerta monticola' - sieben Stichproben von Weibchen. Statistiken zur Variabilität biometrischer und pholidotischer Merkmale. Zifferncode und Abkürzungen siehe 'Material and Methods'. (mean - arithmetisches Mittel, std - Standardabweichung, CV - Variationskoeffizient, min - Minimum, max - Maximum).

Character Merkmal	[S1] Estrella (n=15)			[S2] La Coruña, Coast (n=17)			[S3] Lugo, Coast (n=17)			[S4+S6] Lugo Mts+ W. Cant. Mts (n=19)										
	mean	std	CV	min	max	mean	std	CV	min	max	mean	std	CV	min	max					
SVL	62.1	8.42	0.13	46.7	73.7	61.63	5.54	0.09	51.8	70.17	65.09	3.77	0.05	60.5	71.31	58.81	8.2	0.13	46.65	70.84
GrSr	10.2	1.01	0.1	9	12	9.82	1.26	0.12	7	12	10	1.41	0.14	7	11	11.36	1.97	0.17	9	18
GrSI	9.46	1.64	0.17	7	12	9.58	1.46	0.15	7	12	10.42	1.13	0.1	9	12	11.26	1.75	0.15	9	16
GUL	22.86	2.26	0.1	20	27	25.11	2.42	0.1	22	31	23.85	3.28	0.13	19	27	23.15	2.31	0.1	19	28
COLL	9.6	0.73	0.07	9	11	10.23	1.03	0.1	8	12	10.57	0.53	0.05	10	11	10.42	0.76	0.07	9	12
DORS	51.73	3.15	0.06	47	59	52.35	2.76	0.05	47	56	56.14	1.67	0.02	54	58	52.47	3.58	0.06	45	58
VENT	30.2	1.01	0.03	29	32	29.11	0.85	0.03	27	30	30.28	0.95	0.03	29	31	29.31	1.15	0.04	27	31
FEMr	16.93	1.79	0.1	13	19	16.64	1.22	0.07	15	19	18.14	1.77	0.09	16	21	17.26	1.4	0.08	15	20
FEMl	16.53	1.35	0.08	14	19	17.23	1.14	0.06	15	19	18.14	2.11	0.11	16	22	17.26	1.55	0.09	14	20
LAM	23.66	1.17	0.04	22	26	25.11	1.26	0.05	23	27	24	1.63	0.06	22	26	25.36	1.73	0.06	22	28
CircA	7.07	0.99	0.14	6	9	7.17	1.07	0.14	5	9	7	0.81	0.11	6	8	6.73	0.93	0.13	6	9
FLL*100/SVL	32.15	0.02	0.08	26.38	36.95	32.57	0.02	0.06	29.21	36.93	30.88	0.01	0.05	28.53	32.72	32.93	0.02	0.07	29.6	38.63
HLL*100/SVL	45.51	0.03	0.07	39.14	50.19	46.62	0.02	0.04	43.61	49.8	42.65	0.01	0.02	40.02	44.52	47.03	0.03	0.06	42.16	55
PL*100/PW	210.8	0.07	0.03	197.01	224.59	206.33	0.03	0.1	200	213.38	209.37	0.06	0.02	198.58	215.38	211.08	0.09	0.04	196.81	227.53
ØM/PaL	39.43	0.07	0.17	24.39	48.78	32.11	0.7	0.2	18.43	43.83	39.53	0.02	0.06	38.04	45.45	36.81	0.08	0.22	21.55	49.34
ØT/PaL	38.12	0.16	0.43	0	56.09	35.5	0.7	0.2	17.58	42.97	34.13	0.02	0.08	28.57	37.62	38.85	0.05	0.13	26.34	48.83
AW/AL	54.48	0.05	0.1	46.15	64.51	62.45	0.6	0.1	51.87	73.99	52.5	0.08	0.17	40	63.88	82.29	1.01	0.23	49.82	50
Rostral-Internasal contact (+/-)					(1/14)					(16/0)					(5/2)					(18/1)
Postocular-Parietal contact (+/-)					(4/11)					(6/11)					(2/5)					(5/14)

Character Merkmal	[S7] Somiedo, C. Cant. Mts (n=19)			[S8] Vegarada, E. Cant. Mts. (n=19)			[S9] Enol, Pic. Europa (n=8)								
	mean	std	CV	min	max	mean	std	CV	min	max	mean	std	CV	min	max
SVL	58.74	8.19	0.14	42.9	68.5	56.48	5.79	0.1	45.88	67.1	62.5	3.89	0.06	56.7	68.5
GrSr	9.42	1.42	0.15	7	13	9.21	1.39	0.15	6	11	9.87	1.24	0.12	8	12
GrSI	9.52	1.98	0.2	6	15	8.94	1.39	0.15	6	11	10.12	0.99	0.1	9	12
GUL	23.31	2.26	0.09	19	25	22.73	2.05	0.09	19	27	23.5	2.07	0.08	21	27
COLL	10.42	1.26	0.12	9	14	10.42	0.96	0.09	8	12	11.37	1.06	0.09	10	13
DORS	48.42	2.31	0.04	45	53	48.68	3.19	0.06	43	54	49.37	1.5	0.03	47	52
VENT	29.05	1.07	0.03	26	31	29.47	1.12	0.03	28	31	29.37	1.18	0.04	28	31
FEMr	16.11	1.36	0.08	14	19	16.05	1.12	0.07	14	19	15.75	1.16	0.07	14	18
FEMl	16.26	2.13	0.13	12	23	16.42	1.5	0.09	14	20	17.25	3.28	0.19	14	25
LAM	24.11	1.6	0.06	21	27	23.47	1.38	0.06	21	26	24.87	1.12	0.04	23	26
CircA	7.52	1.07	0.14	6	9	6.47	1.07	0.16	4	8	7.87	0.83	0.1	7	9
FLL*100/SVL	32.08	0.02	0.06	28.64	36.65	32.4	0.01	0.05	29.5	35.75	32.56	0.02	0.06	30.05	35.36
HLL*100/SVL	42.79	0.1	0.24	0	48.95	45.18	0.01	0.04	43.2	49.91	45.02	0.02	0.05	41.08	48.05
PL*100/PW	197.64	0.13	0.07	150	217.46	200.32	0.05	0.02	189.58	207.11	203	0.05	0.02	194.36	207.81
ØM/PaL	41.99	0.07	0.17	30.61	56.81	38.45	0.06	0.17	21.09	48.71	38.34	0.06	0.15	27.65	48.88
ØT/PaL	41.32	0.05	0.11	29.41	47.82	38.1	0.05	0.13	28	46.8	38.01	0.05	0.13	27.65	43.47
AW/AL	58.51	0.06	0.11	45.09	72.72	59.45	0.07	0.12	48.39	74.3	55	0.05	0.1	45.45	63.41
Rostral-Internasal contact (+/-)					(10/9)					(14/5)					(7/1)
Postocular-Parietal contact (+/-)					(4/15)					(15/4)					(7/1)

Cluster analysis: Phenetic distances between population centroids are represented numerically by squared MAHALANOBIS distances (D^2). Their values were used for calculation of the phenograms. The closer two populations appear in the

branching sequence, the closer are their population centroids in the hyperespace (the smaller is D^2). For cluster aggregation in the phenogram representation, UPGMA was used (ROHLF 1962; SNEATH & SOKAL 1973).

RESULTS

Descriptive and univariate statistics

'*L. monticola*, males (table 3)

For descriptive statistics see table 1. Concerning the biometric variables, there is almost no difference between samples, except for anal plate shape between La Coruña [S2] and Lugo Mts. [S4] ($p < 0.01$), and relative pileus width between West Cantabric Mts. [S6] and East Cantabric Mts. [S8] ($p < 0.05$).

There are some differences in pholidosis among populations, but usually scattered and without clear pattern of variation. Significant differences are more frequently found between the geographically distant samples, due to the more extreme values of their character states. As to the number of dorsalia, the sample of Picos de Europa [S9] differs significantly from all other samples, and highly significant from all Galicia and West Cantabric ones [S5 - S9]. Interestingly, the S^a da Estrella sample [S1] shows only five significant differences to all others, while these other samples differ from each other by 4 to 14 significant and/or highly significant differences revealing more differentiation than the sample of the nominate subspecies of the type locality.

'*L. monticola*, females (table 4)

For descriptive statistics see table 2. There are differences between samples in

the number of dorsalia, with maximum values in Galicia [S1-S4] decreasing along the Cantabric Mts. range towards the east [S5-S9]. Some character states (numbers of ventralia, femoralia, lamellae underneath 4th toe, shape of pileus) show numerical differences between the geographically most distant samples, but without clear pattern of variation.

'*L. cyreni* (males and females)

Descriptive statistics and t-test results are shown in tables 5 and 6 for males and females respectively.

As only two sufficiently large samples were available (S^a de Gredos [S1.4] and S^a de Guadarrama [S1.5]), only these two are compared, leaving the allocation of the the samples of Bejar and Peña de Francia to the multivariate representation.

Both males and females of S^a de Guadarrama and S^a de Gredos show highly significant differences in the numbers of ventralia (Gredos > Guadarrama) and circumanalia (Guadarrama > Gredos), females also in dorsalia and gularia (Gredos > Guadarrama). Females are significantly different in the number of left side supraciliar granulae, relative hindlimb length and relative masseteric size, whereas males differ highly significant in this last character.

Multivariate statistics

'*L. monticola*, males (fig. 2 - top, tables 7 and 8)

The first two canonical axes account for 59.5 % of the samples' total variance.

The main characters that load on the first axis are number of dorsalia (negative), and VP (dark punctuation on ventral scales)

(positive). Less important are the loadings for number of collaria and rostral-internalsal contact (negative), masseteric diameter and number of circumanalia (positive).

There is a discrete separation of the S^a de Estrella [S1] and Picos de Europa [S9] samples (both in the positive part of the first axis) from the main group of

Galicia and Cantabric populations (in the negative part of the axis). The considerable overlap in these latter indicates little differentiation between samples.

The second axis has important loadings for the numbers of dorsalia and femoralia (negative) and for rostral-internasal contact (positive). One can see a gradual change from Estrella [S1] to Picos de Europa [S9] which are the geographically most distant populations (fig. 1). Centroid coordinates and confidence radius are indicated in table 8.

L. monticola, females
(fig. 2 - bottom, tables 7 and 8)

The first two canonical axes account for 63.3 % of the samples' total variance. The principal positive loadings on the first axis come from postocular-parietal contact and VP, the negative from number of dorsalia and righth femoralia, and - less important - shape of pileus. The first axis shows a considerable overlap of samples.

The positive loadings of the second axis are high for rostral-internasal contact and - less important - for number of lamellae underneath 4th toe and collaria. Negative loadings are caused by VP and masseteric diameter. The second axis shows a slight separation of the Estrella sample [S1] in the negative part from the main group of Cantabric samples. Centroid coordinates and confidence radius are given in table 8.

L. cyreni, males
(fig. 3 - top, tables 8 and 9)

For better understanding the systematic relationship of the 'Archaeolacertae' along the Iberian Sistema Central, Estrella populations of '*L. monticola* [S1] have been included in the analyses of '*L. cyreni*. The Peña de Francia [S1.2] and Bejar [S1.3] specimens are represented by their centroids only.

The first two canonical axes allow for total discrimination of all samples (100 % of the samples' total variance is ex-

plained). The main loadings for this first axis come from number of ventralia and VP (positive) and rostral-internasal contact (negative). This axis separates Estrella [S1] specimens ('*L. monticola*) in the positive part (associated with high values for number of ventralia and VP) from '*L. cyreni* populations [S1.2 - S1.5] (usually with rostral-internasal contact, low values for number of ventralia and VP) in the negative part.

The second axis discriminates the samples of Gredos [S1.4] and Guadarrama [S1.5] without overlap. The main discriminant characters are number of ventralia (positive) and circumanalia (negative).

The single Peña de Francia specimen [S1.2] appears separated from the rest, somewhat displaced towards '*L. monticola* [S1], which is due to the lack of rostral-internasal contact in the specimen. According to its geographic position, the Bejar specimen [S1.3] appears very close to the Gredos [S1.4] sample.

L. cyreni, females
(fig. 3 - bottom, tables 8 and 9)

The first two canonical axes represent 81 % of the samples' total variance. The first axis receives a high loading from rostral-internasal contact (positive), less important from number of ventralia (negative) and a negative loading from VP. This axis separates '*L. monticola* of Estrella [S1] from all samples of '*L. cyreni*.

The second axis discriminates the samples of Guadarrama [S1.5] and Gredos [S1.4] without overlap of the 90% confidence regions. The characters which contribute most are number of dorsalia and gularia (both highly positive). The Bejar specimens' [S1.3] centroid appears close to the Guadarrama sample [S1.5] which is in conflict with the result of the analysis of males. The Peña de Francia specimen [S1.2] appears intermediate and without overlap between the two main '*L. cyreni* samples.

Cluster analysis (fig. 4, table 10)

Cluster analyses of male as well as female '*L. monticola* (fig. 4) show that populations differ considerably although

there is a marked overlap in character states. The morphologically most different populations are the geographically most

Table 5: 'Lacerta' cyreni, males. Statistics (biometry, pholidosis) and t-test comparison of [S1.5] and [S1.4]. For abbreviations see table 1 legend and 'Material and Methods'.
 Tab 5: 'Lacerta' cyreni, Männchen. Statistiken (Biometrie, Pholidose) und t-Test Vergleich von [S1.5] und [S1.4]. Abkürzungen s. Legende Tab. 1 und 'Material and Methods'.

Character / Merkmal	[S1.5] Guadarrama (n=13)				[S1.4] Gredos (n=20)				T	p	** - p < 0.01	
	mean	std	CV	min	max	mean	std	CV				min
SVL	61.07	9.18	0.15	45.1	70.80	66.22	7.10	0.10	49.90	72.88	1.81	0.07
GrSr	10.30	2.05	0.19	6	13	10.90	3.05	0.28	6	13	0.61	0.54
GrSI	10.23	1.58	0.15	8	13	10.55	2.32	0.22	7	16	0.43	0.66
GUL	24.23	1.73	0.07	21	27	25.35	2.10	0.08	23	31	1.59	0.12
COLL	10.61	0.87	0.08	9	12	10.85	1.30	0.12	7	13	0.56	0.57
DORS	49.92	2.36	0.04	45	53	51.30	3.55	0.06	46	57	1.22	0.22
VENT	24.61	1.12	0.04	23	26	26.10	1.20	0.04	24	29	3.54	0.0013
FEMr	19.15	1.28	0.06	17	21	18.30	1.65	0.09	15	22	1.57	0.12
FEMI	18.84	1.40	0.07	16	21	18.15	1.59	0.08	16	22	1.28	0.21
LAM	25.38	1.38	0.05	22	27	25.35	1.84	0.07	21	28	0.05	0.95
CircA	8.46	1.19	0.14	7	12	6.47	0.84	0.13	5	8	5.52	0
FLL*100/SVL	36.88	0.02	0.04	34.5	39.91	35.58	0.03	0.08	29.22	42.37	1.41	0.16
HLL*100/SVL	50.92	0.02	0.03	47.11	54.83	50.55	0.02	0.04	43.39	55.02	0.49	0.62
PL*100/PW	215.72	0.11	0.05	194.69	231.34	212.09	0.22	0.10	120.16	226.31	0.54	0.59
ØM/PaL	36.17	0.03	0.11	30.90	43.75	42.66	0.05	0.13	32.30	53.84	3.59	0.0011
ØT/PaL	36.01	0.06	0.19	21.81	48.83	36.37	0.05	0.16	27.40	49.18	0.16	0.87
AW/AL	55.89	0.06	0.11	45.83	66.66	58.04	0.09	0.15	40.81	81.48	0.74	0.46
Rostral-Internasal contact (+/-)					(14/0)					(20/1)		
Postocular-Parietal contact (+/-)					(2/12)					(20/18)		

Table 6: 'Lacerta' cyreni, females. Statistics (biometry, pholidosis) and t-test comparison of [S1.5] and [S1.4]. For abbreviations see table 1 legend and 'Material and Methods'.
 Tab 6: 'Lacerta' cyreni, Weibchen. Statistiken (Biometrie, Pholidose) und t-Test Vergleich von [S1.5] und [S1.4]. Abkürzungen s. Legende Tab. 1 und 'Material and Methods'.

Character / Merkmal	[S1.5] Guadarrama (n=21)				[S1.4] Gredos (n=36)				T	p	* - p < 0.05 ** - p < 0.01	
	mean	std	CV	min	max	mean	std	CV				min
SVL	66.3	8.7	0.13	49.4	79.2	65.07	5.69	0.08	49.4	73.6	0.64	0.52
GrSr	10	1.18	0.11	8	12	10.86	2.08	0.19	5	17	1.73	0.08
GrSI	9.85	1.82	0.18	6	13	11.13	2.08	0.18	5	16	2.33	0.02
GUL	23.85	2.05	0.08	19	27	25.72	2.58	0.1	22	33	2.82	0.0066
COLL	10.61	1.35	0.12	8	14	10.5	1.05	0.1	9	13	0.36	0.71
DORS	48.28	3.4	0.07	43	54	52.25	2.97	0.05	47	59	4.6	0
VENT	27.66	1.01	0.03	25	29	29	1.23	0.04	26	31	4.16	0.0001
FEMr	18.23	1.94	0.1	14	21	17.97	1.78	0.09	15	22	0.52	0.6
FEMI	17.85	1.98	0.11	15	22	17.94	1.41	0.07	15	20	0.19	0.84
LAM	24.19	1.72	0.07	21	27	24.61	1.87	0.07	20	29	0.84	0.4
CircA	8.55	0.68	0.08	8	10	7.17	1.07	0.14	5	9	5.12	0
FLL*100/SVL	33.09	0.01	0.05	29.74	36.45	33.76	0.02	0.08	29.87	39.68	1	31
HLL*100/SVL	45.22	0.03	0.06	40.1	50.9	47.39	0.03	0.06	37.82	52.75	2.49	0.015
PL*100/PW	209.57	0.06	0.03	194.22	220.68	212.68	0.15	0.07	132.4	232.75	0.87	0.38
ØM/PaL	34.97	0.09	0.28	0	50	40.1	0.06	0.17	25.53	50	2.3	0.02
ØT/PaL	35.43	0.03	0.09	30.55	41.77	32.69	0.09	0.29	0	46.93	1.25	0.21
AL/AW	56.26	0.05	0.09	46.03	66.66	57.74	0.06	0.1	37.25	68.29	0.89	0.37
Rostral-Internasal contact (+/-)					(18/3)					(35/2)		
Postocular-Parietal contact (+/-)					(7/14)					(11/26)		

distant ones (S^a Estrella and Picos de Europa). In the latter population, however, this distant position might have been overestimated because of small sample size. MAHALANOBIS distances between samples of identical taxa from the same locality increased progressively when sample size was reduced, feigning considerable morphological distances between identical taxa. The same effect could have led to the sample's response to ANOVA and CVA.

Only two '*L. cyreni*' populations (Gredos and Guadarrama) of the Spanish Sistema Central are sufficiently represented in this analysis. For comparative purposes, MAHALANOBIS distances are given for all four samples studied and against '*L. monticola*'

from S^a de Estrella (table 10).

The great differences between allopatric samples of the Sistema Central are due to a categorical discrepancy in the character states of VP (ventral punctuation) and rostral-internasal contact that show divergent values in '*L. cyreni*' and '*L. monticola*' in this area. In '*L. cyreni*', the Bejar female sample appears close to the Guadarrama centroid, but small sample size and poor state of the Bejar specimens prevented from considering the full character set. I would prefer to cluster '*L. cyreni*' from Bejar with their neighbours from Gredos (S^a de Bejar is actually the westernmost part of the Gredos Massif), but its status remains still uncertain.

DISCUSSION

As one can see from the statistical results, the mode of geographical variation is different in the two species.

In '*L. monticola*', there is comparatively great morphological variability at both species and population level. This is expressed by considerable overlap of the confidence regions in the samples studied. Only the two geographically most distant samples deviate slightly from this pattern: (1) S^a de Estrella (representing '*L. monticola monticola*' BOULENGER, 1905) and (2) Picos de Europa. The degree of differentiation in the Picos de Europa sample might have been overestimated because of small sample size. The sample of Estrella is not well defined by ANOVA, but appears as the only well differentiated one in the Canonical Variate Analysis due to the introduction of dichotomous characters (rostral-internasal and postocular-parietal scale contact). The Estrella sample differs from all Cantabric samples by the pattern of variation of the above characters. The Cantabric samples represent a non-homogeneous group (with considerable intrapopulation variation, and some characters showing clinal variation - e. g., dorsalia), which can be assigned to the subspecies '*L. monticola cantabrica*' MERTENS, 1929.

'*L. monticola*' might have originated in the Northwest of the Iberian Peninsula (Galicia and adjacent regions). In this mild and humid area of more or less stable cli-

mate conditions since the Tertiary, many relict forms have survived until now, including '*Chioglossa lusitanica*' and '*Podarcis bocagei*'. The former inhabits an area totally congruent to that of '*L. monticola*'.

The overall variation in '*L. monticola*', as reflected by the Mean Variation Coefficient (MCV), is greater in the western and central samples (Estrella: 1.62; La Coruña: 1.90, Lugo coast: 1.57, Lugo Mts., West Cantabric Mts.: 1.71; Central Cantabric Mts.: 1.8) as compared to the easternmost samples (East Cantabric Mts.: 1.46; Picos de Europa: 1.34).

Rostral-internasal scale contact is largely absent in the Estrella sample but is frequently present in all others (except in the Central Cantabric Mts. sample, where there is just a slight predominance of contact). The absence of supraocular-parietal contact predominates in all populations except in those of the East Cantabric Mts. and Picos de Europa.

There is no doubt that '*L. monticola*' and '*L. cyreni*' are closely related species. Their differentiation from a common ancestor could have started during a Pleistocene interglacial period, by leaving an isolated southern population in the fresh and humid highland refuge of the Sistema Central mountains, whereas other populations survived in the Northwest of the Iberian Peninsula. The former might have given rise to '*L. cyreni*', the latter to '*L. monticola*'. After the end of the Würm

Table 7: '*Lacerta monticola*. Observable variables (characters) and their first two canonical variates (V1, V2) in males and females. For character abbreviations see 'Material and Methods'.

Tab. 7: '*Lacerta monticola*. Die beobachteten Variablen (Merkmale) und ihre ersten beiden kanonischen Variablen (V1, V2) bei Männchen und Weibchen. Abkürzungen der Merkmale siehe 'Material and Methods'.

Character/Merkmal	Males Männchen		Females Weibchen	
	V1	V2	V1	V2
Eigenvalue	11.6	10.5	17.3	8.46
Cumulative %	31.3	59.5	42.5	63.3
GrSr	0.011	-0.246	-0.152	0.012
GrSl	-0.004	-0.173	-0.141	0.110
GUL	-0.065	-0.059	-0.054	0.152
COLL	-0.226	-0.025	0.132	0.269
DORS	-0.436	-0.590	-0.490	-0.080
VENT	0.154	-0.103	-0.117	-0.259
FEMr	0.050	-0.430	-0.329	-0.108
FEMl	0.047	-0.294	-0.152	0.088
LAM	-0.020	-0.051	-0.044	0.294
CircA	0.258	0.061	0.164	0.021
Rost.-Internas. cont.	-0.285	0.461	-0.118	0.613
Postoc.-Pariet. cont.	0.104	0.238	0.312	0.080
VP (present or not)	0.475	0.001	0.381	-0.380
FLL*100/SVL	0.120	0.140	0.044	-0.106
HLL*100/SVL	-0.120	0.007	0.041	0.073
PL*100/PW	0.183	-0.093	-0.269	-0.126
ØM/PaL	0.243	0.159	0.041	-0.208
ØT/PaL	0.077	0.071	0.068	-0.062
AW/AL	-0.109	0.118	-0.040	0.097

Table 9: '*Lacerta cyreni*. Observable variables (characters) and their first two canonical variates (V1, V2) in males and females. For character abbreviations see 'Material and Methods'.

Tab. 9: '*Lacerta cyreni*. Die beobachteten Variablen (Merkmale) und ihre ersten beiden kanonischen Variablen (V1, V2) bei Männchen und Weibchen. Abkürzungen der Merkmale siehe 'Material and Methods'.

Character/Merkmal	Males Männchen		Females Weibchen	
	V1	V2	V1	V2
Eigenvalue	60,9	7,97	17,3	5,63
Cumulative %	88,4	100	61,2	81,1
GrSr	-0.003	-0.082	-0.020	0.186
GrSl	-0.003	-0.033	0.095	0.206
GUL	-0.043	-0.113	0.129	0.320
COLL	-0.066	-0.003	0.131	0.109
DORS	0.061	-0.118	-0.156	0.406
VENT	0.141	-0.447	-0.221	0.108
FEMr	0.023	0.103	0.141	-0.015
FEMl	0.032	0.067	0.191	0.026
LAM	-0.050	0.040	0.039	-0.032
CircA	-0.027	0.481	0.120	-0.174
Rost.-Internas. cont.	-0.466	0.210	0.419	0.206
Postoc.-Pariet. cont.	-0.008	0.002	-0.060	0.038
VP (present or not)	0.282	0.221	-0.455	-0.173
FLL*100/SVL	-0.016	0.045	0.037	0.153
HLL*100/SVL	0.001	0.001	-0.025	0.052
PL*100/PW	0.002	0.056	0.037	-0.028
ØM/PaL	0.024	-0.235	-0.053	0.100
ØT/PaL	0.001	-0.009	-0.018	-0.097
AW/AL	-0.067	-0.095	-0.015	0.041

Table 8: '*Lacerta monticola* and '*Lacerta cyreni*. Canonical coordinates of the centroid (V1, V2) and radius of 90 % confidential region (Rad) of the samples analyzed.

Tab. 8: '*Lacerta monticola* und '*Lacerta cyreni*. Kanonische Koordinaten des Zentroids (V1, V2) und Radius des 90 % Vertrauensbereiches (Rad) der untersuchten Stichproben.

Sample / Stichprobe	Males / Männchen			Females / Weibchen		
	V1	V2	Rad	V1	V2	Rad
<i>'L. monticola</i>						
[S1] Estrella	2.13	-1.77	1.94	0.026	-2.43	1.54
[S2] Coruña	-0.69	0.381	1.5	-0.677	1.23	1.45
[S3] Lugo Coast (Cabarcos)	-1.13	-1	1.37	-2.3	-0.325	2.25
[S4] Lugo Mountains (Incio)	-0.945	-0.234	1.24	-1.66	0.796	1.37
[S5] Sanabria (Truchillas)	-1.27	-0.807	-	-	-	-
[S6] West Cantabric Mts. (Ancares)	0.086	-0.885	1.68	-	-	-
[S7] Central Cantabric Mts. (Somiedo)	-0.181	0.61	1.12	1.28	0.02	1.37
[S8] East Cantabric Mts. (Vegarada, Señales)	-1.07	0.817	1.5	0.762	0.207	1.37
[S9] Picos de Europa	1.8	2.08	2.61	2.56	0.501	2.11
<i>'L. cyreni</i>						
[S1] Estrella (<i>'L. monticola</i>)	6.32	-0.292	2.5	-3.55	-1.52	1.71
[S1.2] Peña de Francia	-0.301	-2.96	-	1.54	0.523	-
[S1.3] Bejar	-5.97	-1.6	-	0.762	-0.472	-
[S1.4] Gredos	-3.86	-1.83	1.64	1.07	1.92	1.1
[S1.5] Guadarrama	-2.46	2.13	2.01	1.72	-1.3	1.43

Table 10: Squared MAHALANOBIS distances between the studied samples in '*Lacerta monticola*' and '*L. cyreni*', respectively. Values of males above, values of females below diagonal.Tab. 10: Quadrate der MAHALANOBIS-Distanzen zwischen den untersuchten Stichproben bei '*Lacerta monticola*' bzw. '*L. cyreni*'. Werte für Männchen oberhalb, für Weibchen unterhalb der Diagonale).

<i>'L. monticola</i>	[S1] Estrella	[S2] Coruña	[S3] Lugo Coast	[S4] Lugo Mts.	[S6] W Cant Mts.	[S7] C.Cant Mts.	[S8] E.Cant Mts.	[S9] Pic. Europa
[S1] Estrella	0	16.6	13.8	14.8	9.85	12.6	18.9	17.1
[S2] Coruña	14.9	0	4.68	4.34	8.58	7.74	10.8	11.1
[S3] Lugo Coast (Cabarcos)	14.6	11.5	0	3.84	7.87	8.19	10.9	19
[S4] Lugo Mountains (Incio)	14.7	5.75	7.62	0	5.13	7.15	8.03	13.9
[S6] W Cantabric Mts. (Ancares)	-	-	-	-	0	7.06	10.4	14.9
[S7] Centr. Cantabric Mts. (Somiedo)	11.7	10.1	18.1	14.1	-	0	3.04	10.7
[S8] E Cantabric Mts. (Vegarada, Señales)	12.9	9.72	14.7	13	-	5.31	0	16.5
[S9] Picos de Europa	18	16.6	27	21.2	-	10.6	12.7	0

<i>'L. cyreni</i>	[S1] Estrella	[S1.2] Francia	[S1.3] Bejar	[S1.4] Gredos	[S1.5] Guadarrama
[S1] Estrella (<i>L. monticola</i>)	0	104	185	106	83
[S1.2] Peña de Francia	40.9	0	82.7	66.7	83.3
[S1.3] Bejar	23.6	17.1	0	37.1	58.8
[S1.4] Gredos	25.7	16.8	11	0	17.6
[S1.5] Guadarrama	30	20.3	11.3	11.5	0

glacial period, the general temperature rise (displacement of vegetation belts in the mountains) could have caused the present isolation of '*L. cyreni*' populations. However, the morphological differentiation of the populations of Gredos, Guadarrama and Peña de Francia has reached subspecific level. The small population of Peña de Francia, despite being undoubtedly '*L. cyreni*' by its color pattern in adults and hatchlings, shows a set of character states which is similar to that of '*L. monticola*' (frequent lack of rostral-supranasal contact, presence of blue ocelli). Maybe the Peña de Francia individuals represent descendants of an ancestral intermediate form from prior to differentiation of '*L. cyreni*' and '*L. monticola*'. However, its *cyreni*-like colour pattern and its small population size presumably connected with high founder effect and genetic drift, fits better to the assumption of a 'conservative' form of '*L. cyreni*'. This form might resemble the ancestor of the species, and may have some characters developed which are now typical to '*L. monticola*'. The sanctuary of the Peña de Francia individuals is restricted to the top of a very pointed and stepped mountain. This situation increases the threat of nega-

tive anthropogenic influence on this small relict population. In Gredos and Guadarrama samples, lack of rostral-internasal contact and presence of blue ocelli is exceptional (but see GARCÍA-PARIS & al. 1989: fig 66).

Between samples of '*L. cyreni*', we find clear morphological differences promoted by the current allopatric distribution of the populations. In the Gredos sample, intrapopulation variation is high (MCV = 1.90) whereas in the Guadarrama sample it is lower (1.62). These results correspond well with the hypothesis of expansion of '*L. cyreni*' along the Spanish Sistema Central in the past, as the geographically most distant populations reveal reduced morphological variability.

In '*L. monticola*', the lowland Coruña male and Central Cantabric female samples show comparable high values of variability. As for the Coruña specimens, the result is plausible, as this area is probably refuge and primitive habitat of '*L. monticola*' after the lizard's almost complete competitive displacement by other lacertid species (*Podarcis bocagei*, *Podarcis hispanica*). The phenomenon of displacement could also explain the presence of '*L. monticola*' in Pleistocene ref-

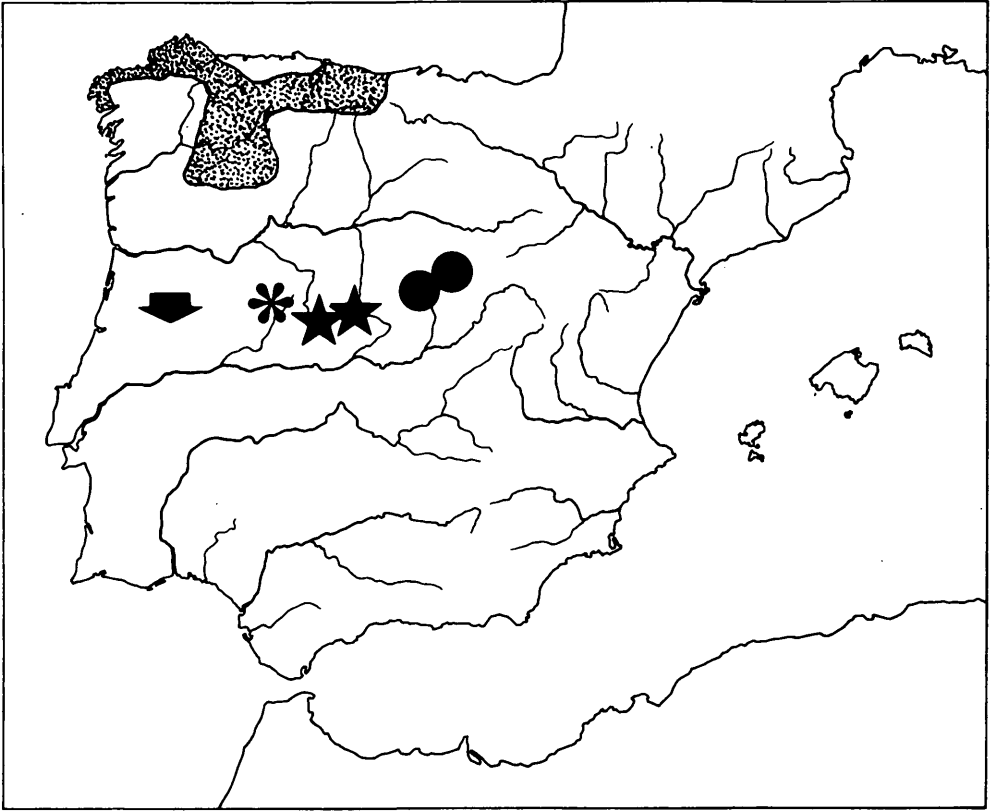


Fig. 1: Distribution of the taxa studied.

Arrow - '*Lacerta*' *monticola monticola*; punctuated area - '*L.*' *monticola cantabrica*; circle - '*L.*' *cyreni cyreni*; star - '*L.*' *cyreni castiliana* ssp. nov.; asterisk - '*L.*' *cyreni martinezricai* ssp. nov.

Abb. 1: Verbreitung der untersuchten Taxa.

Pfeil - '*Lacerta*' *monticola monticola*; punktierte Fläche - '*L.*' *monticola cantabrica*; Kreis - '*L.*' *cyreni cyreni*; Stern - '*L.*' *cyreni castiliana* ssp. nov.; Asterisk - '*L.*' *cyreni martinezricai* ssp. nov.

uges in the lowland areas of Asturias nearby the Central Cantabric Mts. In the East Cantabric Mts. and Picos de Europa, the intrapopulation variability is drastically reduced which probably corresponds to a postglacial extension of the lizard's distribution. However, the hypothesis of the presence of '*L.*' *monticola* in all low altitude parts of Asturias during Pleistocene cannot be rejected, as it still lives there in isolated colonies in the low Sierras de Cuera and Sueva which form the easternmost

part of its distribution area. A scenario of different isolated refuges, with later spreading and introgression, as has been postulated for *Vipera seoanei* in the same area (SAINT GIRONS & al. 1986; BEA & al. 1984) is also imaginable.

Presence or absence of an azygous scale between the prefrontals could serve as a marker for relationship between these '*L.*' *monticola* populations: The frequency of its presence is high in coastal Coruña populations (58%), slightly less in the other

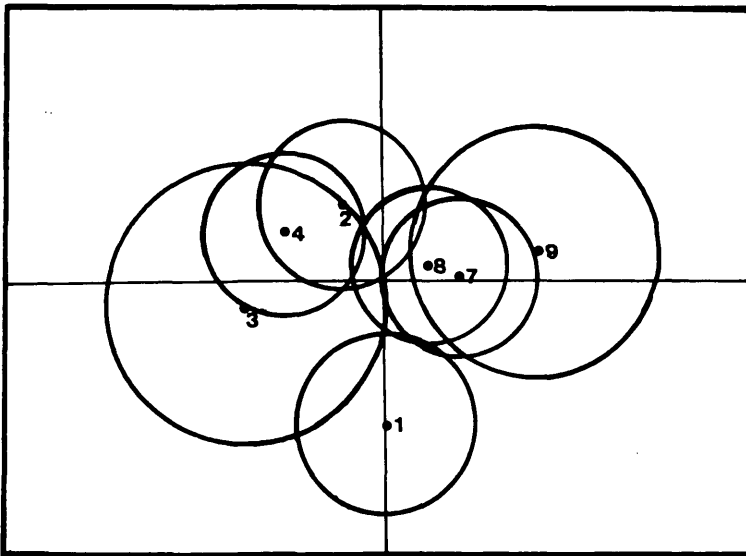
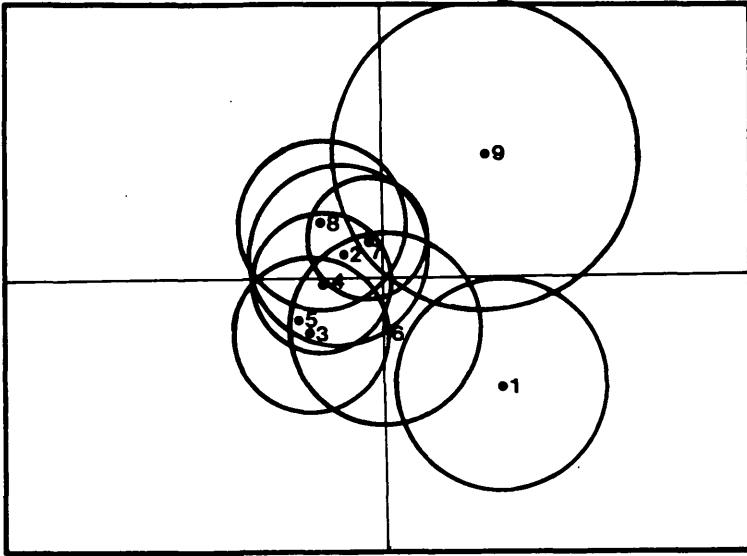


Fig 2: *'Lacerta' monticola*, Canonical Variate Analysis (top: males; bottom: females).

Representation of canonical discriminant functions 1 and 2.

1 - Estrella; 2 - Coruña coast; 3 - Lugo coast; 4 - Lugo Mts.; 5 - Sanabria area; 6 - West Cantabric Mts.; 7 - Central Cantabric Mts.; 8 - East Cantabric Mts.; 9 - Picos de Europa Massif.

Abb 2: *'Lacerta' monticola*, Kanonische Varianzanalyse (oben: Männchen; unten: Weibchen).

Darstellung der Kanonischen Diskriminanzfunktionen 1 und 2.

1 - Estrella; 2 - Coruña Küste; 3 - Lugo Küste; 4 - Lugo Gebirge; 5 - Gebiet Sanabria; 6 - westliches Kantabrisches Gebirge; 7 - zentrales Kantabrisches Gebirge; 8 - östliches Kantabrisches Gebirge; 9 - Picos de Europa.

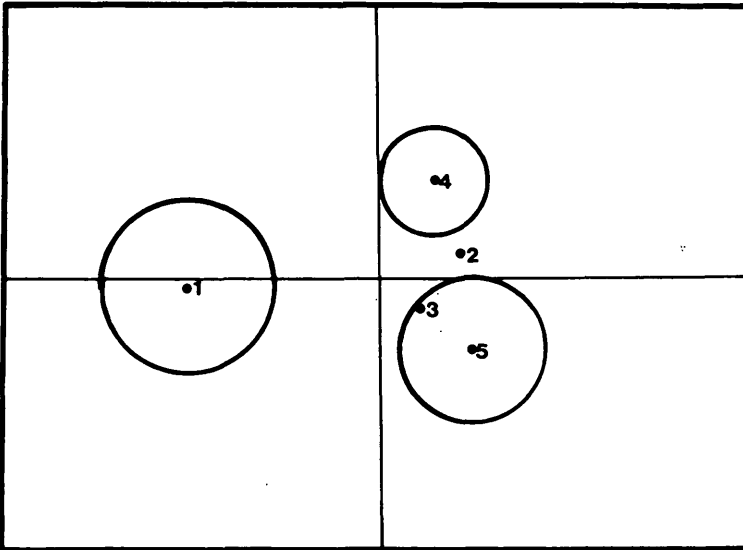
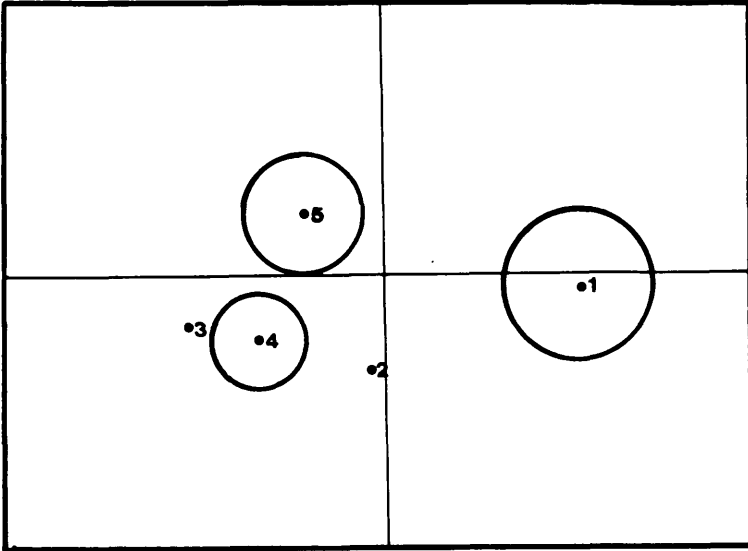


Fig 3: *Lacerta cyreni*, Canonical Variate Analysis (top: males; bottom: females).
Representation of canonical discriminant functions 1 and 2.
1 - Estrella (*L. monicola*); 2 - Peña de Francia; 3 - Bejar; 4 - Gredos; 5 - Guadarrama.
Abb 3: *Lacerta cyreni*, Kanonische Varianzanalyse (oben: Männchen; unten: Weibchen).
Darstellung der Kanonischen Diskriminanzfunktionen 1 and 2.
1 - Estrella (*L. monicola*); 2 - Peña de Francia; 3 - Bejar; 4 - Gredos; 5 - Guadarrama.

Galicia samples (coastal Lugo: 41%; West Cantabric Mts.: 33%) and becomes low towards the east (Central Cantabric Mts.: 12%; East Cantabric Mts.: 16%; Picos de Europa: 25%). On the other hand, in Es-

trella populations, there is a very low percentage of individuals with this anomaly (6%), which is very rare (Gredos: 6%) or absent (Bejar, Guadarrama, Peña de Francia) in the samples of '*L.* cyreni.

TAXONOMIC CONCLUSIONS

'*Lacerta monticola* BOULENGER, 1905

S y n o n y m s: *Lacerta muralis* var. *monticola* BOULENGER, 1905 - Trans. Zool. Soc. London, 17: 365. tab. 24, fig. 11. *Lacerta muralis monticola* MERTENS & MÜLLER, 1928 - Abh. Senck. naturf. Ges. Frankfurt, 41: 36. *Lacerta estrellensis* CYRÉN, 1928 - Göteborg. Vetensk. Handl., (B) 1: 10. Terra typica: Lagoa Comprida, S^a da Estrella, Portugal. *Archaeolacerta monticola* LANZA, CEI & CRESPO, 1977 - Monitore Zool. Ital., (N. S.) 11: 212.

T y p e: Specimens from 'Spain' and 'Estrella' were designated as types by BOULENGER (1920/21) in his second description of the taxon. The terra typica has already been restricted to S^a da Estrella (MERTENS & MÜLLER 1928). The British Museum female specimen from S^a da Estrella of BOULENGER's (1920/21) 'types' could be selected as lectotype.

D i a g n o s i s: A medium-sized robust lizard of the '*Archaeolacerta*' type. Dorsum with various tones of green or brown, frequently with black dots, arranged in one (more rarely two) series all along dorsum length, frequently covering all of its width. Females and young sometimes uniform or scarcely dotted dorsally. Costal band frequently reticulated in males and females, less frequently uniform, dark brown or almost black. Usually some blue ocelli in the shoulder region, more developed in males. Pileus with medium-sized dots, occasionally vermiculated in old specimens. Venter white, green or bluish, more or less spotted. Hatchlings with uniform ('*L.* *m. cantabrica*) or reticulated ('*L.* *m. monticola*) temporal bands, dorsum usually with very few or without marks, tail blue or greenish with few or without spots. Variable rostral-internasal contact (frequently present in Cantabric populations and absent in Portuguese

populations) and variable (more frequently without) postocular-parietal contact. Hemipenial microornamentation crown-shaped (BÖHME 1971). Karyotype: 36 acrocentric macrochromosomes, sex chromosome W euchromatic, NOR in apical position of the telomere of a big pair of chromosomes (ODIERNA & al. 1994, and in press).

D i s t r i b u t i o n see under subspecies.

'*Lacerta monticola monticola* BOULENGER, 1905 (plate 2)

S y n o n y m s: As for the species.

T y p e: As for the species.

D i a g n o s i s: A very big and robust '*L.* *monticola* (up to 84 mm SVL), with striking contrast between the clear greenish, bluish (males) or brownish (females) background tinge and the heavily spotted and reticulate dorsum and flanks in adult specimens. Venter usually heavily spotted in adults. Hatchlings with reticulate temporal bands. Rostral usually not in contact with internasal.

D i s t r i b u t i o n: S^a da Estrella, Portugal.

H a b i t a t: Oromediterranean broom hatlands with meadows and rocky granite - granodiorite outcrops.

'*Lacerta monticola cantabrica* MERTENS, 1929 (plate 3)

T y p e: Male, Senckenberg Museum (SMF 22098) Rodiezmo, León, Spain (J. BERNARDEZ leg.).

D i a g n o s i s: A moderately robust '*L.* *monticola*, very variable in coloration and pattern. This subspecies englobes almost all of the morphological variation of the species diagnosis. Hatchlings with uniform temporal bands. Rostral frequently in contact with internasal. Post-

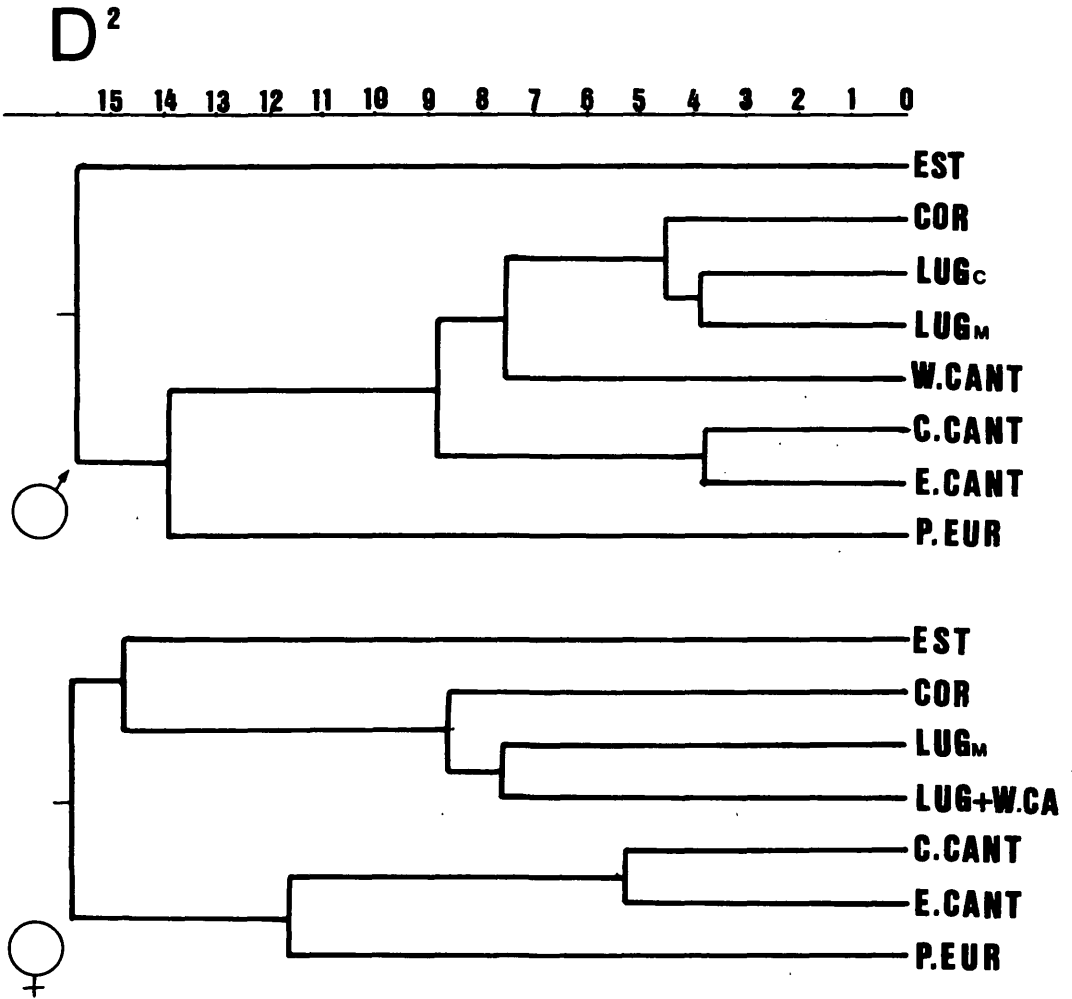


Fig 4: Phenetic relations between '*Lacerta*' *monticola* populations.
(squared MAHALANOBIS distances clustered according to the UPGMA method).
Abb. 4: Phänetische Beziehungen zwischen den Populationen von '*Lacerta*' *monticola*.
(quadierte MAHALANOBIS-Distanzen nach der UPGMA Methode geklustert).

ocular and parietal frequently not in contact.

Distribution: Galicia (isolated populations in very shady and humid valleys from the coast to the upper inland mountains, where it is more common and widespread) and all along the Cantabric Mountains (with a wide altitudinal distribution), as far as Picos de Europa Massif (Cornión=Covadonga Massif) and S^a de Suevo and S^a Cuera in the west. The

Cares river seems to be the eastern limit of the territory of this subspecies in the Cantabric Mts. For Galicia also indicated for San Paio Island (Lugo coast) by GALAN & FERNANDEZ (1993).

Habitat: Present in a wide variety of habitats. Lowland populations inhabit marine cliffs, rocky outcrops, old constructions and stone walls, stream gullies covered with autochthonous deciduous forest ('Fragas' or 'Carballeiras' - *Quercus*

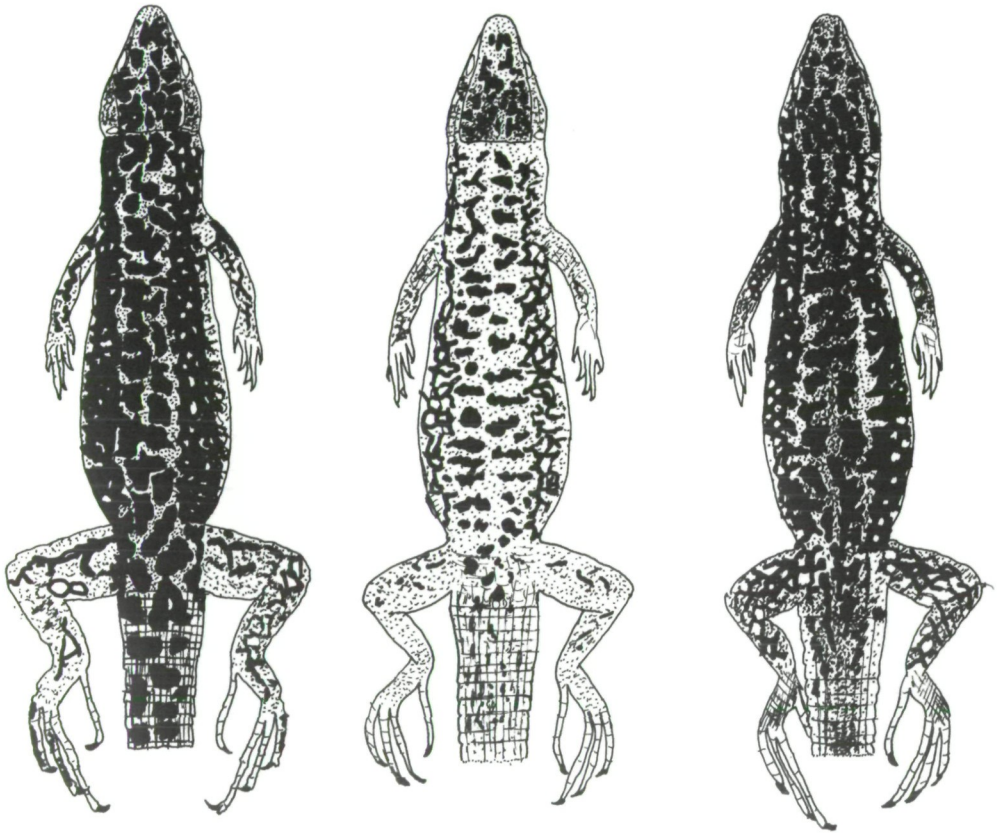


Fig. 5: Pattern variability in '*Lacerta*' *cyreni castiliana* ssp. nov. from Gredos, I.
 Abb. 5: Zeichnungsvariabilität bei '*Lacerta*' *cyreni castiliana* ssp. nov. von Gredos, I.

robur, *Castanea sativa*, *Betula celtiberica*, *Corylus avellana*). In these scarce and endangered autochthonous forests (also habitat of *Chioglossa lusitanica*) the lizard lives near the water edge or in open areas as track talus or rocky outcrops, where sun reaches the ground of the forest. As soon as the humid and closed forest disappears (by fire or by *Eucalyptus* plantation) this species is replaced by more heliophilous lizards as *Podarcis bocagei* or *P. hispanica* (P. GALAN, pers. comm.). In mountainous areas, it also dwells on stone outcrops, talus, rocky boulders, shrub and slopes near open forests (*Quercus petraea*, *Qu. pyre-*

naica, *Fagus sylvatica*, mixed with dispersed stands of *Betula celtiberica*, *Sorbus aucuparia*, *S. aria* and *Crataegus monogyna*) where the lizards predominate in degraded areas covered by shrubland of broom and heath (*Genista legionensis*, *Erica* spp. and *Calluna vulgaris*).

'Lacerta' cyreni
 MÜLLER & HELLMICH, 1937

Synonymy: *Lacerta monticola cyreni* MÜLLER & HELLMICH, 1937 - Zool. Anz. Leipzig, 117: 67.

Type: Male, Zoologische Staats-

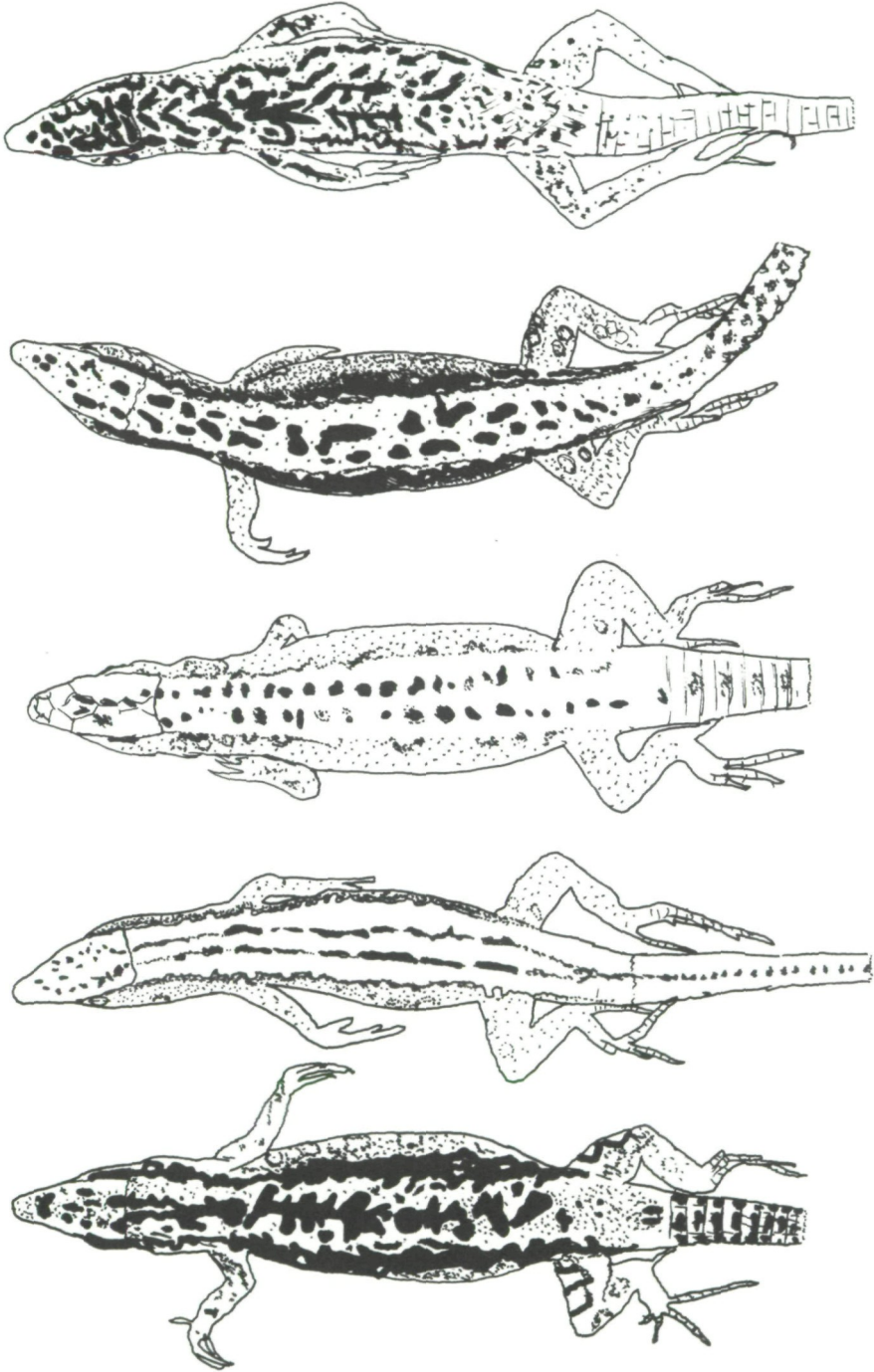


Fig. 6: Pattern variability in '*Lacerta*' *cyreni castiliana* ssp. nov. from Gredos, II.
Abb. 6: Zeichnungsvariabilität bei '*Lacerta*' *cyreni castiliana* ssp. nov. von Gredos, II.

sammlung München (ZSM 2329a) Puerto de Navacerrada, Sierra de Guadarrama. 10-6-1935. W. HELLMICH leg.

Diagnosis: A medium-sized lizard of the '*Archaeolacerta*' type. Characterized by strongly reticulated flanks, sometimes (more frequently in females) by uniform temporal bands (usually with fading medium and lower parts). Vertebral band formed by one or two juxtaposed rows of dots. Greenish and brown individuals in equal proportion and present in both sexes. Almost never blue ocelli in the shoulder region. Ventral punctuation absent in adults, or, at least, reduced in the most external scale rows. Rostral and internasal scales almost always in contact, postocular and parietal scales usually not in contact. Hatchlings with characteristic reticulation of flanks, dorsum and tail heavily spotted, tail greenish. Hemipenial microornamentation crown-shaped (BÖHME 1971). Karyotype: 36 macrochromosomes, with a heterochromatinized (except for a little euchromatic intercalary band) W sex chromosome, NOR in an intercalary (subtelomeric) position of a medium-sized pair of chromosomes.

Distribution: Spanish Sistema Central, with allopatric populations in S^a de Guadarrama, Gredos, Paramera, La Serrota, Bejar and Peña de Francia.

'Lacerta' cyreni cyreni

MÜLLER & HELLMICH, 1937 - comb. nov.
(plate 1)

Synonym: As in the species.

Type: As in the species.

Diagnosis: A *L. cyreni* characterized by a sharply contrasting dark pattern (brownish specimens are more frequent than green ones). Reduced number of ventralia [males: 24.6 (23-26), females: 27.6 (25-29)], increased number of circumanalia [males: 8.46 (7-12), females: 8.5 (8-10)], smaller relative masseteric scale diameter [\emptyset M/PaL - males: 36.17 (30.9-43.75), females: 34.97 (0-50)], slightly reduced numbers of dorsalia [males: 49.9 (45-53), females: 48.3 (43-54)] and gularia [males: 24.23 (21-27), females: 23.85 (19-27)], shorter hindlimbs (in females), as compared to the following subspecies.

Distribution: Sierra de Guadarrama.

Habitat: Oro- and crioromediterranean areas, usually in rocky outcrops with meadows and broom heathlands (*Cytisus balansae*, *Echinopartum barnadesii*).

'Lacerta' cyreni castiliana ssp. nov.
(figs. 5 and 6, plates 1 and 2)

Holotype: Male, CA 86071819, Laguna Grande, Circo de Gredos, Sierra de Gredos. 18-7-1986. O. ARRIBAS & J. GARCÍA leg.

Diagnosis: A '*L. cyreni*' with a more variable pattern, frequently reticulated, reticulation partially fading at the flanks. Green and brown specimens present in equal proportion. Compared to the nominal subspecies: Dark pattern reduced, higher numerical values for ventralia [male: 26.1 (24-29), female: 29 (26-31)], dorsalia [males: 51.3 (46-57), females: 52.25 (47-59)], gularia [males: 25.35 (23-31), females: 25.7 (22-33)], relative masseteric scale diameter [\emptyset M/PaL - males: 42.6 (32.3-53.8), females: 40.1 (25.5-50)], and hindlimb length; less circumanalia [males: 6.47 (5-8), females: 7.17 (5-9)].

Description of holotype: Adult male with broken tail. Snout-vent length: 70.1 mm; forelimb length: 25.5 mm; hindlimb length: 34.6 mm; 4th digit length: 11.7 mm; head height: 8 mm; pileus length: 17.5 mm; pileus width: 8 mm; head length: 19.1 mm; head width: 12.1 mm; parietal length: 6.1 mm; 1st supratemporal: 3.3 mm; masseteric scales: 1/1; masseteric scale \emptyset : 2.7/3 mm; anal plate width: 4.7 mm; anal plate length: 2.6 mm; supraoculars: 4/4; supraciliar granules: 11/10; postnasals: 1/1; loreals: 2/2; supralabials in front of subocular: 4/4; supralabials behind subocular: 3/3; sublabials: 6/6; submaxillars: 6/6; gularia: 23; collaria: 11; longitudinal rows of dorsalia: 52; transversal rows of ventralia: 26; longitudinal rows in 6 series; periventralia (number of dorsal scales in contact with one ventral scale): 2; femoralia: 18/18; lamellae underneath 4th digit: 28/27; scales forming 6th tail ring: 26; inter-femoralia (scales between left and right row of femoral pores): 3; preanalia: 2; circumanalia: 6; supratemporal emarginates the parietal scale; rostral bordering on internasal by a fairly long suture; 1st post-

1 2 3 4 5 6 7

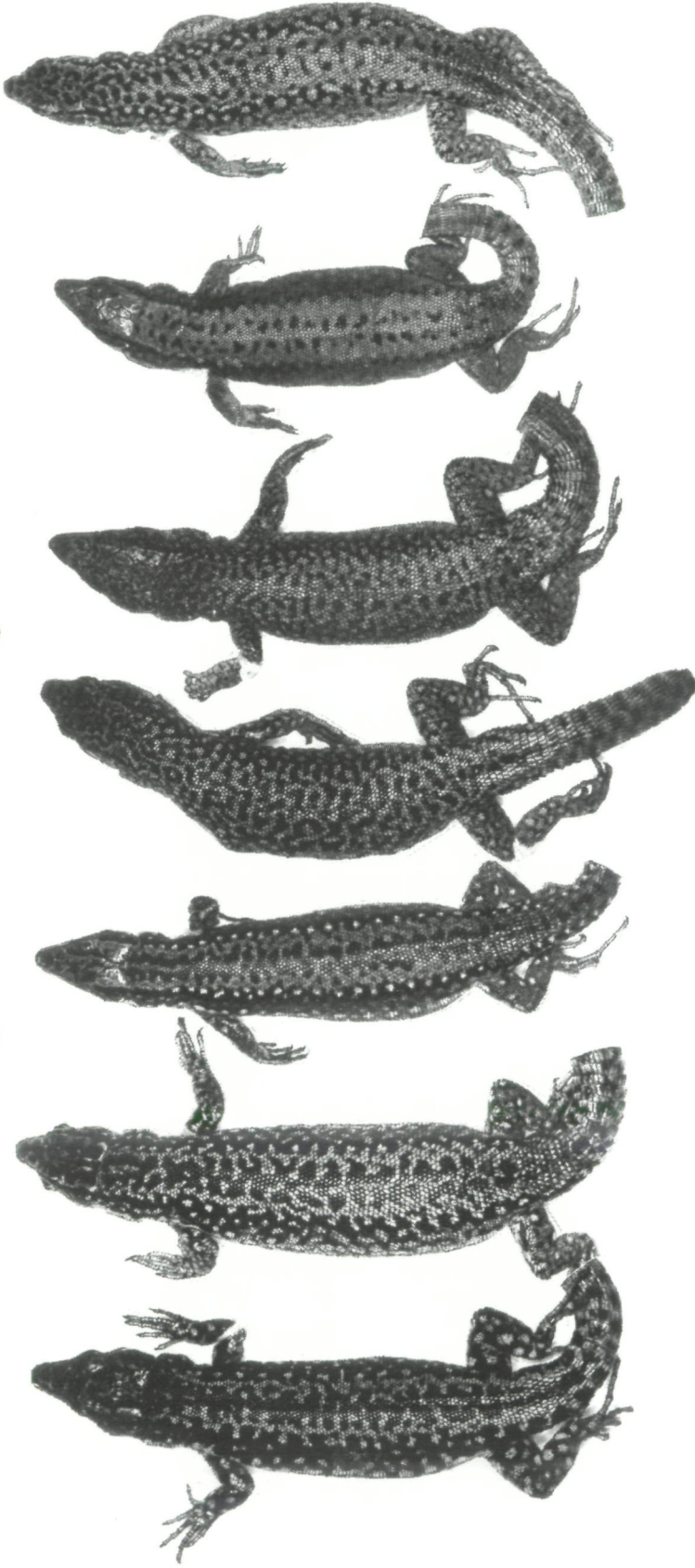


Plate 1: '*Lacerta cyreni cyreni* MÜLLER & HELLMICH, 1937 - Pto. de Navacerrada (Madrid-Segovia, Spain): 1 - CA 93090007 (male); 2 - CA 93090010 (female); 3 - CA 93090009 (female). '*Lacerta cyreni castiliana* ssp. nov. - Circo de Gredos (Avila, Spain): 4 - Holotype CA 86071809 (male); 5 - Paratype CA 86071807 (male); 6 - Paratype CA 86071814 (female); 7 - Paratype CA 86072003 (female).

Tabl. 1: '*Lacerta cyreni cyreni* MÜLLER & HELLMICH, 1937 - Pto. de Navacerrada (Madrid-Segovia, Spanien): 1 - CA 93090007 (Männchen); 2 - CA 93090010 (Weibchen); 3 - CA 93090009 (Weibchen). '*Lacerta cyreni castiliana* ssp. nov. - Circo de Gredos (Avila, Spanien): 4 - Holotypus CA 86071809 (Männchen); 5 - Paratypus CA 86071807 (Männchen); 6 - Paratypus CA 86071814 (Weibchen); 7 - Paratypus CA 86072003 (Weibchen).

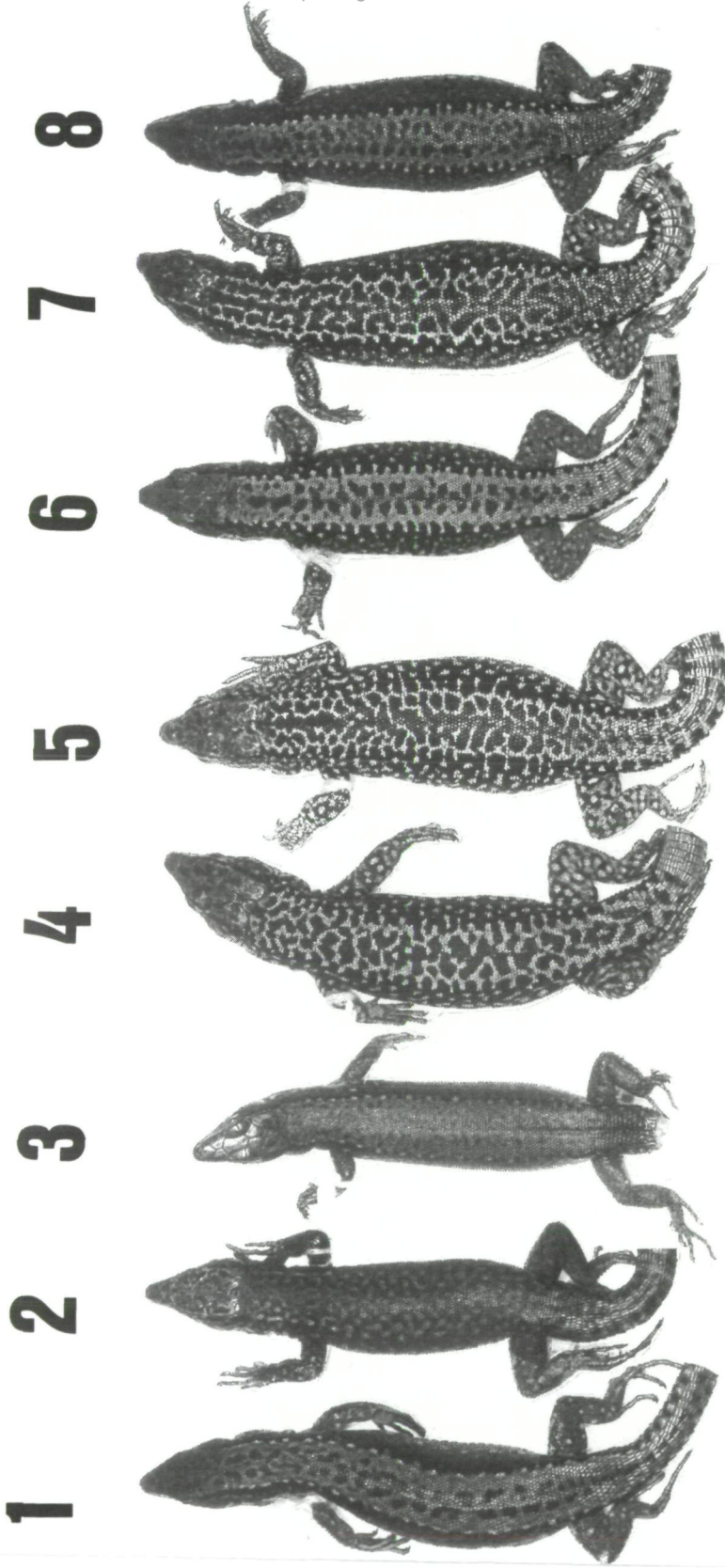


Plate 2: '*Lacerta cyreni castilitana* ssp. nov. - Circo de Gredos (Avila, Spain): 1 - Paratype CA 86071806 (female). '*Lacerta cyreni martinzeircai* ssp. nov. Peña de Francia (Salamanca, Spain): 2 - Holotype CA 3001 (male); 3 - Paratype CA 3002 (female). '*Lacerta monticola monticola* BOULENGER, 1905 - A Torre (Beira Alta, Portugal): 4 - CA 88080422 (male); 5 - CA 88080416 (male); 6 - CA 88080414 (male); 7 - CA 88080412 (female); 8 - CA 88080420 (female).

Tafel 2: '*Lacerta cyreni castilitana* ssp. nov. - Circo de Gredos (Avila, Spanien): 1 - Paratypus CA 86071806 (Weibchen). '*Lacerta cyreni martinzeircai* ssp. nov. Peña de Francia (Salamanca, Spanien): 2 - Holotypus CA 3001 (Männchen); 3 - Paratypus CA 3002 (Weibchen). '*Lacerta monticola monticola* BOULENGER, 1905 - A Torre (Beira Alta, Portugal): 4 - CA 88080422 (Männchen); 5 - CA 88080416 (Männchen); 6 - CA 88080414 (Männchen); 7 - CA 88080412 (Weibchen); 8 - CA 88080420 (Weibchen).

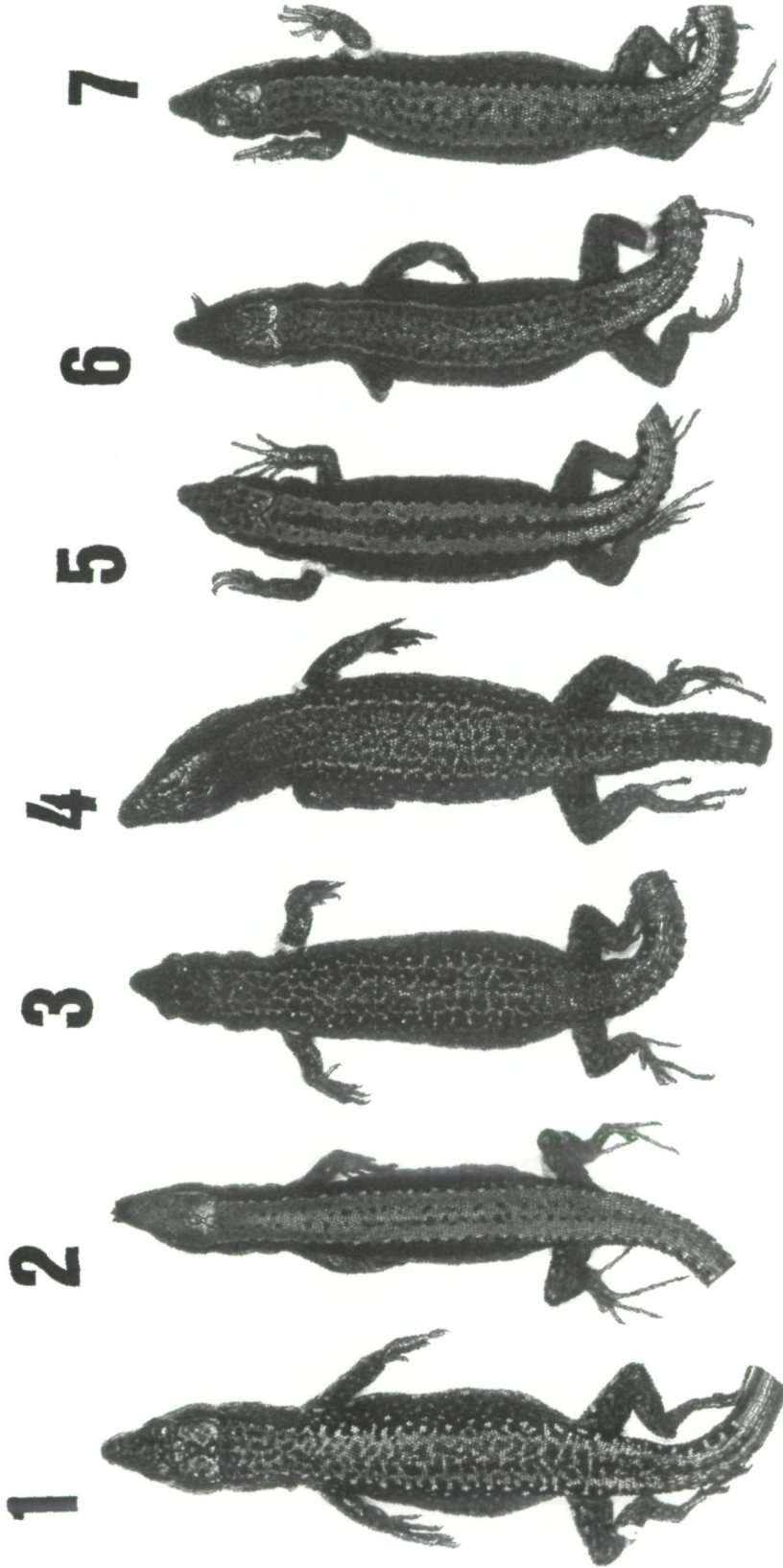


Plate 3: '*Lacerta monticola cantabrica* MERTENS, 1929: 1 - PG 02230285 (male), Caaveiro (La Coruña, Spain); 2 - PG 01040785 (female), Coto del Eume (La Coruña, Spain); 3 - CA 94090002 (female), Lago de la Cueva, Somiedo (Oviedo, Spain); 4 - CA 89032209 (male), Villar de Vildas, Somiedo (Oviedo, Spain); 5 - CA 88080808 (female), Puerto de Vegarada (León-Oviedo, Spain); 6 - CA 89080902 (female), and 7 - CA 89080910 (female), Vega de Enol, Picos de Europa (Oviedo, Spain).

Tafel 3: '*Lacerta monticola cantabrica* MERTENS, 1929: 1 - PG 02230285 (Männchen), Caaveiro (La Coruña, Spanien); 2 - PG 01040785 (Weibchen), Coto del Eume (La Coruña, Spanien); 3 - CA 94090002 (Weibchen), Lago de la Cueva, Somiedo (Oviedo, Spanien); 4 - CA 89032209 (Männchen), Villar de Vildas, Somiedo (Oviedo, Spanien); 5 - CA 88080808 (Weibchen), Puerto de Vegarada (León-Oviedo, Spanien); 6 - CA 89080902 (Weibchen) und 7 - CA 89080910 (Weibchen), Vega de Enol, Picos de Europa (Oviedo, Spanien).

ocular in contact with parietal on the right side, separated on the left side; supranasal not in contact with loreal on both sides, but very close on the left side.

Small black dots all over the green dorsum. Temporal band reticulated, fading towards its lower edge. Lower lateral line not markedly expressed, fused with the lateral network. The animal appears all reticulated, including the limbs. Pileus profusely spotted with medium sized sharply contrasting black spots. Venter immaculate green.

Paratypes: (57 specimens) 1 female CA 86071701 Plataforma de Gredos, Avila, España, 17-7-1986, O. ARRIBAS leg.; 6 males, 15 females CA 860718 (01-18, 20-22) Circo de Gredos, Avila, España, 18-7-1986, O. ARRIBAS & J. GARCÍA leg.; 8 males, 14 females CA 860719 (01-22) Circo de Gredos, Avila, España, 19-7-86, O. ARRIBAS & J. GARCÍA leg.; 5 males, 6 females CA 860720 (01-11) Circo de Gredos, Avila, España, 20-7-86 O. ARRIBAS & J. GARCÍA leg.; 1 female CA 89071901 Portilla de los Machos, Gredos, Avila, España, 19-7-89 O. ARRIBAS leg.; 1 male EBD 4241 Puerto de Angosturas, Gredos, Avila, España 15-6-1959 A. COBOS leg. Paratypes CA 86071701 - female, CA 86071817 - female, CA 86071907 - female, CA 86071917 - male will be stored in Naturhistorisches Museum Wien (NMW 35098:1-4), CA 86072008 - female, and CA 86071811 - female in the scientific collection of EBD.

Derivatio nominis: Castiliana, latin adjective of Castilia (Castile), ancient kingdom and region of central Spain which this lizards inhabits.

Distribution: Sierra de Gredos (eastern, central and western massifs, the latter also known as S^a de Bejar). Populations of the parallel small S^a de La Serrota and S^a Villafranca very probably belong to this subspecies.

Habitat: See under species.

'Lacerta' cyreni martinezricai ssp. nov.
(plate 2)

Holotype: Male, CA 3001, Peña de Francia, Salamanca, España, without further data, M. MEUJIDE leg.

Diagnosis: A *'L.'* *cyreni*

with very variable pattern, characterized by the presence of blue ocelli in the shoulder region both in males and females. Rostral scale frequently separated from internasal. Hatchlings heavily reticulated, with blue reticulate tail.

I decided to establish this *monticola*-like taxon because of its above mentioned outstanding features in association with the sharply limited distribution area even though its description had to be based on the unusual small sample size of three specimens. Further specimens were examined but not preserved. I have seen less than a dozen of these lizards in nature and their population probably does not exceed 50 individuals.

Description of holotype: (in parentheses data from paratypes - adult female/hatchling): Adult male, SVL 63.07 (63.98//28.05); forelimb length: 22.24 (18.12//); hindlimb length: 33.60 (26.83 //); pileus length: 15.95 (13.42//); pileus width: 7.47 (6.38//); parietal length: 5.40 (4.21//); masseteric scale Ø: 2.10 (1.39//); tympanic scale Ø: 1.85 (1.35//); anal plate width: 3.58 (3.21//); anal plate length: 2.28 (2.05//); supraciliar granula: 14/13 (8/10// 10/11); gularia: 28 (27//23); collaria: 11 (11//10); dorsalia: 53 (50//52); ventralia: 24 (29//29); femoralia: 18/17 (18/17//17/17); 4th digit lamellae: 28 (23//25); circumanalia: 6 (6//7); rostral separated from internasal (in contact// separated), postocular separated from parietal, and supranasal separated from loreal (both separated // both separated).

Dorsum and flanks with brown background colour, completely reticulated; two blue ocelli in the shoulder region. Some black dots on the outermost lateral ventral scale row. Venter white in life.

Paratypes: An adult female and a hatchling. CA 302-3. Collecting data and pholidosis see under holotype.

Derivatio nominis: Dedicated to Dr. JUAN PABLO MARTINEZ RICA, for his outstanding and serious contributions to the study of the Iberian herpetofauna, in particular the Pyrenean one.

Distribution, habitat: S^a de la Peña de Francia (Salamanca). A very small population restricted to the uppermost 100 m of this abrupt cone-shaped mountain whose summit is covered by an

anthropogenous construction. This strongly threatened population is completely sur-

rounded by *Podarcis hispanica*. Captures must be totally avoided.

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