

Taxonomic revision of the Iberian 'Archaeolacertae' II: Diagnosis, morphology, and geographic variation of '*Lacerta aurelioi* ARRIBAS, 1994 (Squamata: Sauria: Lacertidae)

Taxonomische Revision der iberischen 'Archaeolacerten' II: Diagnose, Morphologie
und geographische Variabilität von '*Lacerta aurelioi* ARRIBAS, 1994
(Squamata: Sauria: Lacertidae)

OSCAR J. ARRIBAS

KURZFASSUNG

Auf Grundlage allen verfügbaren Materials werden neben einer umfangreiche Diagnose (Biometrie, Pholidose, Osteology, Karyotyp, Allozymdifferenzen, Hemipenismorphologie) Angaben zu Verbreitung, Sexualdimorphismus und geographischer Variabilität von '*Lacerta aurelioi* ARRIBAS, 1994 vorgelegt. Pholidotische und metrische Merkmale werden dabei mit uni- und multivariaten statistischen Methoden untersucht.

'*Lacerta aurelioi* is in einem kleinen Bereich der östlichen Zentralpyrenäen endemisch. Die Art bewohnt die spanischen Gebirgsmassive Montroig und Pica d'Estats i. w. S. (inklusive Serrat de Capifonts) sowie NW-Andorra (Gebirgsstöcke Coma Pedrosa und Tristaina), wo sie zwischen 2100 m bis fast 2940 m Höhe gefunden wird. Dort kommt die Eidechse hauptsächlich auf kambrio-ordovizischen quarzitischen Schiefen und Phylliten, aber auch auf schwach metamorphosierten Staurolitschichten und schiefrigem Cordierit und Andalusit vor.

Morphologisch zeigen die untersuchten Populationen nur schwache Unterschiede auf infrasubspezifischem Niveau. Auch lassen sich keine Korrelationen zwischen Differenzierungsgrad und geographischer Lage oder Entfernung der Populationen feststellen: Die Subpopulationen eines Gebirgsstockes (verschiedener benachbarter Hänge) sind häufig untereinander stärker verschieden als gegenüber Subpopulationen anderer Gebirgsstöcke, sodaß geographisch weiter voneinander entfernte Populationen einander morphologisch stärker ähneln können als geographisch nahe Populationen.

Ein denkbare Szenario der Artbildung, das pleistozene Überleben und die Ausbreitung sowie die gegenwärtige Verbreitung der Art werden diskutiert. Die heutige Verschiedenheit der Populationen wird auf ihre holozäne Isolation zurückgeführt. Die Südhänge des Montroig Massives werden als ein wümrzeitliches Refugium angesehen, von dem aus die Art ihr gegenwärtiges Verbreitungsgebiet, in dem die verschiedenen Populationen isoliert wurden, besiedelte.

ABSTRACT

Based on all individuals available, a comprehensive diagnosis (biometry, pholidosis, osteology, karyotype, allozyme differences, hemipenis morphology), and data on distribution, sexual dimorphism, and geographic variation of '*Lacerta aurelioi* ARRIBAS, 1994 are presented. Pholidosis and biometric characters are analyzed by means of univariate and multivariate statistical methods.

'*Lacerta aurelioi* is an endemite of a small section of the eastern central Pyrenees. It inhabits the Spanish massifs of Montroig, Pica d'Estats s. l. (Serrat de Capifonts included) and NW Andorra (massifs of Coma Pedrosa and Tristaina), where the species is found from 2100 m up to almost to 2940 m a.s.l. There, the lizard occurs mainly upon cambro-ordovician quartzitic slates and phyllites, but also on slightly metamorphized rock facies of staurolite, cordierite and andalusite schists.

Morphological analysis reveals slight differences between the populations studied which, however, have to be considered as infrasubspecific variations. Moreover, there is no apparent correlation between differentiation and geographic position or distance of populations: The subpopulations of a massif (various neighbouring slopes) are frequently more different from each other than from subpopulations of other massifs. In other words, geographically most distant populations may be morphologically more similar than geographically closer populations.

The probable scenario of speciation, the pleistocene survival and spread, and the present range of the species are discussed. It is concluded that the present divergence among populations probably arose from their Holocene isolation. The southern slopes of the Montroig massif are postulated to have been the Würmian refuge from which the species spread into its present territory, in which the various populations became isolated.

KEY WORDS

Sauria, Lacertidae, '*Lacerta aurelioi*'; morphology, diagnosis, geographic variation, distribution, taxonomy, speciation, biogeography, Iberian Peninsula, Pyrenees

INTRODUCTION

'Lacerta' aurelioi ARRIBAS, 1994 is a small lizard species, endemic to a small area in the eastern central Pyrenees (three mountain massifs only) in which this species appears restricted to sheltered and well insulated localities in alpine environments from 2100 m up to almost 2940 m (ARRIBAS 1996 b, 1997). *'Lacerta' aurelioi* was discovered in the field in 1991 and described three years later (ARRIBAS 1994). These populations were absolutely unknown to scientists and never included in other taxa formerly. Until now, *'L. aurelioi*

was studied in detail for external morphology (ARRIBAS 1994), genital morphology, microornamentation, and osteology (ARRIBAS 1998), karyology (ODIERNA & al. 1994, 1995, 1996, and in press) and allozyme differentiation (MAYER & ARRIBAS 1996). All these aspects as well as the lizard's habitat and geographic distribution are reviewed in ARRIBAS (1996 b).

The aim of this paper is to analyze the geographic variation of this taxon in detail and to provide a diagnosis which covers the whole range of the species.

MATERIALS AND METHODS

Field prospection

From 1989 until 1997 included, a total of 70 U.T.M. (Universal Transverse Mercator) grids (10 km x 10 km squares) which - at least in part - cover alpine areas, were prospected all along the Pyrenean range, from Pico de Arlás in the west as far as the Puigmal massif in the east. Only six U.T.M. grid units out of these contained populations of *'L. aurelioi* (fig. 1).

Geographic terms used in this paper (catalan = english): coll = pass; estany, llac = lake; ribera, vall = valley; pic, pica = peak, summit; circ = cirque.

Specimens studied

In total, 242 specimens (139 males and 103 females) were studied. For biometric characters and indexes, only specimens longer than 45 mm (snout-vent length) were included to avoid bias due to allometric effects. All preserved specimens are stored in the author's scientific collection (CA) at Universidad Autónoma de Barcelona (Barcelona, Spain).

Characters studied

Biometry: Snout-vent length (SVL); forelimb length (FLL); hindlimb length (HLL) (both from the insertion of the limb to the tip of the longest toe); pileus length (PL); pileus width (PW); parietal scale length (PAL); masseteric scale diameter (DM); tympanic scale diameter (DT); anal

scale width (AW); anal scale length (AL).

All linear measurements were made with digital callipers to the nearest 0.01 mm, and by one person (author) to avoid inter-observer variability.

Pholidosis (counts): Supraciliary granulae (GRS) of right (r) and left (l) side; gularia along a median line (GUL); collaria (COLL); longitudinal series of dorsalia (DORS); transversal series of ventralia (VENT); femoralia (FEM) of right (r) and left (l) side; lamellae underneath 4th toe (LAM); circumanal (CIRCA).

Scale contact: Frequencies of rostral-internasal (= frontonasal), supranasal-loreal, and postocular-parietal scale contact.

In general, only specimens where the full set of characters was available were used in the numerical analyses. If only one character was missing, it was estimated by linear regression approximation (biometric characters) or substitution by the population mean (meristic characters).

Measurements were transformed into the following more informative and non-dimensional ratios: FLL/SVL; HLL/SVL; PL/PW; DM/PAL; DT/PAL; AL/AW. Metric and meristic characters were log-transformed, ratios were arcsine-square root transformed.

Statistical procedures

Statistical analyses performed in the present study are basically the same as in ARRIBAS (1996a, 1996b).

Univariate statistics: De-

scriptive statistics (mean, range, standard deviation and coefficient of variation) were calculated for all meristic characters and ratios.

Biometric and meristic characters were compared between populations by means of one-factor ANOVA. As SVL was not statistically different among populations (Males: $F_{2,136} = 1.10$, $p > 0.05$; Females: $F_{2,100} = 0.78$, $p > 0.05$), ANCOVA was not applied for interpopulational comparisons. Wherever significant differences occurred among samples, Scheffé's post-hoc test was run. The frequencies of contact among scales were compared by Chi-square tests. All calculations were done separately for males and females (SOKAL & ROHLF 1969), to consider sexual dimorphism (see below).

Multivariate analyses: MANOVA and Canonical Variate Analysis

(CVA) were done to represent the global differences between populations. Initially, dendrograms (UPGMA) and Minimum Spanning Trees (MST) based on Mahalanobis distances (D^2) were calculated from the main samples (SNEATH & SOKAL 1973). D^2 scores of very small samples (e. g., isolated specimens) frequently appeared very exaggerated and clusters were created according to sample size rather than by similarity (ARRIBAS 1996 b). For this reason, later, exclusively MST was applied to ascertain the closest relationship of single specimens to the greater samples.

The following criteria were used to evaluate the distinctiveness of populations: (i) percentage of correct classification from the Canonical Variate Analysis, and (ii) number of significant differences in the ANOVA F-values.

RESULTS

Distribution

'*Lacerta aurelioi*' has been found in six 10 km x 10 km U.T.M. grid units only (fig. 1). All localities known are based on the author's field work and listed in table 1.

This lizard is an endemite of the eastern central Pyrenees where it is restricted to three mountain massifs of the Pyrenean

axis (Montrouig, Pica d'Estats, and Coma Pedrosa-Tristaina) in the region where France, Spain, and Andorra adjoin with each other. The main distribution area is situated within the Spanish territory (Pallars Sobirà, Lérida province) and in Andorra, where the Pyrenees are more extended and their slopes are exposed to the south. A comprehensive description of the overall distribution, habitat, and ecology of

Table 1: Localities where '*L. aurelioi*' has been found.
Tab. 1: Fundorte von '*L. aurelioi*'.

UTM grid / UTM Raster	Location (altitude) (region) (source) / Fundort (Höhe) (Gebiet) (Quelle)
CH52	Estany de la Gola-Estany de Calberante (2340-2500 m) (Lérida) (ARRIBAS 1996 b) Pic de la Gallina Vt. S. (2400 m) (Lérida) (ARRIBAS 1996 b) Estany de la Gallina (2280 m) (Lérida) (ARRIBAS 1996 b) Estany Llavera (2280 m) (Lérida) (ARRIBAS 1996 b)
CH53	Estanys de la Gallina (2280 m) (Lérida) (ARRIBAS 1996 b)
CH61	Serrat de Capifonts (2268-2649 m) (ARRIBAS 1996 b)
CH62	Estany de Sotllo-Estany d'Estats (2100-2500 m) (Lérida) (ARRIBAS 1994 a, 1996 b) Estany Fons (2480 m) (Lérida) (ARRIBAS 1994 a, 1996 b) Estany de Baborte (2340 m) (Lérida) (ARRIBAS 1996 b) Coll de Sellente (2485 m) (Lérida) (ARRIBAS 1996 b)
CH71	Pic de Coma Pedrosa (2756-2942 m) (Andorra) (ARRIBAS 1996 b) Pic de Cataverdis (2200-2400 m) (ARRIBAS 1996 b)
CH72	Coma del Forat-Port de Rat, Ordino-Arcalis (2352-2539 m) (Andorra-Ariège) (ARRIBAS 1996 b) 1.5 Km au sud de Orrys des Estrets (2100-2120 m) (Ariège) (CROCHET & al. 1997) Estanys de Tristaina (2100-2600 m) (Andorra) (ARRIBAS 1996 b) Estany de Creussans (2441 m) (Andorra) (ARRIBAS 1996 b)

this species is given in ARRIBAS (1997). The westernmost localities lie in the Montroig massif (Estany de La Gola and Estany de Calberante; 2340 to 2500 m). These localities are situated in the uppermost part of La Guingueta Valley, along the southern slopes of the Montroig peak (2866 m). In the eastern slopes of the Montroig peak (Estanys de La Gallina) I found this species only in a single small southwesterly facing place at 2280 m which is separated from these latter localities by a high pass (2600 m). In the near Estany Llavera (2280 m), '*L. aurelioi*' is also present but scarce. The species seems to be absent in apparently suitable areas prospected in the southern spurs of this massif, e.g. the uppermost parts of the Ribera d'Estañ Valley, the Estanys de Campirme, Estanys de Soliguera, and Coll de Finestres (from 2200 up to almost 2600 m).

Immediately east of Montroig, the lizard seems to be absent from areas which appear geologically and ecologically suitable [Estany de Mariola (2300 m), Estany de Port (2000 m)] as well as from unsuited formations of granites and granodiorites [Llac de Certascan (2240 m), Estany de Naorte (2160 m), Estany de Romedo de Baix (2020 m), and Estanys d'Aguiló (2204 m)]. All prospection remained fruitless in these latter places, even in sites where the substratum was appropriate.

Further to the east, '*L. aurelioi*' appears again in the Pica d'Estats massif and probably (unconfirmed observations) occurs in the westerly oriented Circ de Broate. It is also found in the southern slopes of Pic de Baborte (Estanys de Baborte - 2340 m; Coll de Sellente - 2485 m; Coll de Baborte - 2618 m). The species is present in the southward slopes of Pic de Sotllo (3075 m) and Pica d'Estats (3115 m) (at the Circs de Sotllo and Estats which have lakes at 2352 m and 2471 m, respectively) from 2100 up to almost 2500 m and at the more westerly oriented Estany Fons (2480 m), maybe also in the neighbouring Estanys de Areste (2400 m) and Port Vell, which have not yet been investigated.

More to the south, the lizard seems to be absent from the prospected areas of the Monteixo massif which is separated from the former by the uppermost parts of the Vallferrera Valley. But it appears again in

the most meridional locality known for this species, Serrat de Capifonts (from 2268 to 2649 m), a spur of the Pic de Salòria massif in which, however, the species is apparently absent from all other prospected localities (e.g., Pic de Covil - 2400 to 2538 m). This latter locality is separated from the main Pyrenean axis by the Port de Cabús (2328 m), where the species was not found as well.

The Andorran populations appear to be relatively isolated despite their close vicinity to the Pica d'Estats massif from which they are separated by the wide Videssos Valley. In this valley, '*L. aurelioi*' is present only in the upper reaches, on the slopes of the Coma Pedrosa massif (almost up to the summit, seen at 2756 and 2942 m), and its northern spurs (ARRIBAS, 1996 b, 1997; ODIERNA & al. 1996; CROCHET & al. 1997). Slightly east of this area, the lizard was found in the southern slopes of the Tristaina massif: Pic de Coma Pedrosa (2756 - 2942 m), Pic de Cataverdis or Cataperdis (2200 - 2400 m), Coma del Forat - Port de Rat (2352 - 2539 m), Estanys de Tristaina (2100 - 2600 m), and finally, in the Estany de Creussans (2441 m) which constitutes the easternmost known locality. More to the west, all search for '*L. aurelioi*' remained fruitless (e. g., uppermost parts of Ransol Valley; Port d'Envalira area; also in Andorra).

From all known localities, density of '*L. aurelioi*' is highest upon cambrio-ordovician quartzitic slates and phyllites, while it is less on slightly metamorphosed rock facies of staurolite, cordierite and andalusite schists (as in Circ de Tristaina), maybe due to the lower degree of fissuration (worse or less refugia) (see ZWART 1979; ZANDVLIET 1979 for a geologic description of these areas). For the area of Coma Pedrosa, CROCHET & al. (1997) erroneously reported this lizard to inhabit granite boulders which probably were confused with one of the abovementioned metamorphic rocks. In the Port de Cabús area, an otherwise apparently suitable location formed by devonian limestones is inhabited by *Podarcis muralis* (LAURENTI, 1768) and separates the main (axial) area of '*L. aurelioi*' from the Capifonts locality. The species also lacks granite areas like the Certascan massif (see above).

Table 2: Male *L. aurelioi* ARRIBAS, 1994. Descriptive statistics (Mean, standard deviation, coefficient of variation, Minimum, Maximum) of three samples including ANOVA results. Abbreviations of measurement parameters are explained under "Materials and Methods".

Tab. 2: Männchen von *L. aurelioi* ARRIBAS, 1994. Beschreibende Statistiken (Mittelwert, Standardabweichung, Variationskoeffizient, Minimum, Maximum) von drei Stichproben einschließlich der ANOVA Ergebnisse. Die Abkürzungen der Meßparameter sind in "Material und Methoden" erklärt.

Parameter	1 = MONTROIG (n = 13)					2 = PICA D'ESTATS (n = 48)				
	Mean	Stdv	CV	Min	Max	Mean	Stdv	CV	Min	Max
SVL	51.99	1.67	0.032	49.1	54.18	52.03	3.21	0.06	44.06	57.18
GRS-r	5	2.2	0.44	2	8	4.52	1.86	0.41	1	9
GRS-l	5	2.07	0.414	2	7	4.7	2.23	0.48	0	9
GUL	24.5	1.3	0.053	23	26	24.88	2.07	0.08	21	30
COLL	11.5	0.75	0.065	10	12	10.02	1.13	0.11	7	12
DORS	47.37	1.06	0.022	46	49	44.31	2.79	0.06	37	51
VENT	26.62	1.18	0.044	25	28	26.86	0.92	0.03	25	29
FEM-r	12	1.51	0.12	10	14	11.15	1.14	0.1	9	13
FEM-l	12	1.51	0.125	9	14	11.38	1.18	0.1	9	14
LAM	24.87	1.24	0.05	23	27	24.29	1.42	0.06	21	27
CIRCA	7.25	0.7	0.097	6	8	7.88	0.81	0.1	6	10
FLL*100/SVL	35.35	0.01	0.039	33.6	37.27	34.68	0.02	0.07	24.28	38.83
HLL*100/SVL	49.88	0.01	0.035	46.43	51.81	49.43	0.02	0.05	44.91	55.51
PL*100/PW	203.46	0.07	0.034	191.1	213.6	201.01	0.05	0.03	188.1	215.3
DM*100/PAL	32.28	0.06	0.19	22.3	40.14	35.5	0.06	0.19	20	52.77
DT*100/PAL	25.56	0.02	0.11	21.26	29.32	29.25	0.05	0.18	10.55	41.66
AL*100/AW	51.84	0.03	0.075	46.25	57.97	48.84	0.05	0.11	37.97	62.83
Scale contacts / Schuppenkontakt		no/nein	yes/ja				no/nein	yes/ja		
Rost.-Internas.		2	11				3	45		
Postoc.-Pariet.		12	1				43	5		
Supranas.-Lor.		0	13				2	46		

Parameter	3 = ANDORRA (n = 68)					ANOVA		Significant Differences		
	Mean	Stdv	CV	Min	Max	F	p	1-2	1-3	2-3
SVL	52.07	3.44	0.066	38.71	65.25	1.1	0.33			
GRS-r	8.27	2.44	0.295	1	14	33.86	0	**		***
GRS-l	8	2	0.25	3	12	34.43	0	**		***
GUL	24.75	1.8	0.073	21	30	1.21	0.3			
COLL	10.97	1.15	0.105	8	14	16.47	0	***		***
DORS	47.51	1.81	0.038	44	52	29.21	0	***		***
VENT	27.38	0.91	0.033	25	29	8.29	0		**	**
FEM-r	12.52	1.28	0.102	10	16	20.31	0	*		***
FEM-l	12.57	1.22	0.097	10	16	13.78	0	*		***
LAM	25.85	2.92	0.113	23	47	8.1	0			***
CIRCA	7.58	0.83	0.109	6	10	4.91	0.01	*		
FLL*100/SVL	35.69	0.01	0.051	29.5	42.03	4.15	0.02			
HLL*100/SVL	50	0.02	0.043	43.41	55.97	1.75	0.18			
PL*100/PW	205.24	0.06	0.032	185.7	217.8	2.59	0.08			
DM*100/PAL	31.76	0.06	0.218	12.75	42.62	5.7	0			**
DT*100/PAL	29.78	0.04	0.163	18.3	40.05	1.45	0.24			
AL*100/AW	53.07	0.07	0.139	41.4	82.1	4.9	0.09			**
Scale contacts / Schuppenkontakt		no/nein	yes/ja			Chi-Sq	p			
Rost.-Internas.		0	78			9.0934	0.01	*		
Postoc.-Pariet.		71	7			0.1195	0.94			
Supranas.-Lor.		6	72			1.5567	0.46			

Sexual dimorphism

Since the sexes differed significantly in SVL (ANOVA: $F_{240,1} = 23.54$; $p < 0.0001$) in that females were longer than males, biometric characters were subject to ANCOVA using SVL as a covariate. As a result, the species is significantly dimorphic in all biometric characters analyzed except for AL (anal length: $F_{240,1} = 0.56$; $p > 0.05$).

In males, all dimorphic metric characters under study are proportionately longer than in females ($p < 0.0001$ in all cases): FLL ($F_{240,1} = 125.73$), HLL ($F_{240,1} = 279.11$), PL ($F_{240,1} = 837.95$), PW ($F_{240,1} = 277.13$), PAL ($F_{240,1} = 280.46$), DM ($F_{240,1} = 21.95$), DT ($F_{240,1} = 39.17$), AW ($F_{240,1} = 62.48$). Thus, males have proportionately longer limbs and heads than females, as is usual in lacertids.

Pholidosis counts were compared by means of ANOVA. Only the number of ventralia (VENT: $F_{240,1} = 284.47$, $p < 0.0001$) shows highly significant sexual differences, being greater in females. The numbers of CIRCA ($F_{240,1} = 5.54$, $p < 0.05$) and LAM ($F_{240,1} = 4.86$, $p < 0.05$) are significantly greater in males. All other counts are slightly but insignificantly ($p > 0.05$) increased either in males [GRS-r ($F_{240,1} = 2.61$), GRS-l ($F_{240,1} = 3.57$), GUL ($F_{240,1} = 2.80$), DORS ($F_{240,1} = 2.04$), FEM-r ($F_{240,1} = 1.12$), FEM-l ($F_{240,1} = 2.39$)] or in females [COLL ($F_{240,1} = 0.39$)].

It is interesting to see that indexes behave different from linear measurements in the intersexual comparison: Differences are highly significant between sexes in FLL/SVL ($F_{240,1} = 150.40$, $p < 0.0001$), HLL/SVL ($F_{240,1} = 296.85$, $p < 0.0001$), PL/PW ($F_{240,1} = 11.03$, $p < 0.001$), and AL/AW ($F_{240,1} = 40.08$, $p < 0.0001$), while they are not in DM/PAL ($F_{240,1} = 0.88$, $p > 0.05$), and DT/PAL ($F_{240,1} = 2.56$, $p > 0.05$). In the Pyrenean mountain lizards (globally taken), the variables DM, DT, and AL are highly independent from both each other and from other variables like SVL, FLL, HLL, PL, PW, PAL, AW which, for their part, are positively correlated with a general body size or growth factor (ARRIBAS 1996 b, in press).

Geographic variation

Several partial analyses were performed to compare single specimens from isolated localities with the larger samples of Montroig, Pica d'Estats, and Andorra. From these analyses resulted a very particular pattern of differentiation among the populations studied (see discussion).

Males

ANOVA: Descriptive statistics of biometric indexes and pholidosis characters are shown in table 2.

The greatest number of differences is observed between the samples of Pica d'Estats massif (Baborte plus Estats) and Andorra. They differ significantly (at $p < 0.001$) from each other in the variables GRS-l, GRS-r, COLL, DORS, FEM-l, FEM-r, and LAM and (at $p < 0.01$) in the variables VENT, DM/PAL, and AL/AW. MANOVA finds highly significant differences between these populations ($F_{32,210} = 6.2780$, $p < 0.0001$; Wilks' Lambda = 0.2612).

The samples Pica d'Estats (Estats plus Baborte) and Montroig (Gola plus La Gallina) differ from each other significantly (at $p < 0.001$) in the variables COLL and DORS, and (at $p < 0.05$) in the variables FEM-r, FEM-l, and CIRCA. MANOVA finds significant differences between the populations of Gola, Gallina, Baborte, and Estats ($F_{48,122} = 1.6172$; $p < 0.05$; Wilks' Lambda = 0.2328).

Finally, the samples Montroig and Andorra differ significantly (at $p < 0.01$) in the variables GRS-r, GRS-l, and VENT. MANOVA finds significant differences between the populations of Andorra, Capi-fonts, and La Gola plus Gallina ($F_{32,148} = 2.0208$, $p < 0.005$; Wilks' Lambda = 0.4843).

Concerning the frequency of contact among rostral and internasal, there are significant differences between the samples of the three massifs ($\chi^2_2 = 9.09$, $p < 0.05$). Over all specimens, scale contact is found in 99.1%. The Montroig sample is characterized by the highest proportion of scale separation (due to the presence of an additional azygous scale between the supranasals in some specimens) while in the well

represented Andorran sample, scale contact is the rule (100 %).

Usually, there is lack of contact between postocular and parietal (93.3 %) without differences among massifs ($\chi^2_2 = 0.11$, $p > 0.05$) and contact between supranasal and loreal (97.5 %) without differences among massifs ($\chi^2_2 = 1.55$, $p > 0.05$).

Canonical Variate Analysis of six samples (Baborte, Estats, Gallina, Gola, Capifonts, Andorra; $n = 136$ specimens) and 16 characters (all pholidotic characters and indexes) shows the relation of these samples based on their morphological similarity (fig 2). The samples differ significantly (MANOVA: $F_{80,55.7} = 3.2283$, $p < 0.0001$; Wilks' Lambda = 0.1602). The loadings of the three first canonical axes explain 100 % of the inter-sample variability.

The first axis (explaining 57.53 % of the variance) has loadings from COLL (0.4423), DORS (0.4005), FEM-r (0.3470), FEM-l (0.2995), GRS-l (0.2973), and GRS-r (0.3798) and separates the samples of Andorra, Gola, Capifonts, and (to a lesser degree) La Gallina (characterized by higher values of COLL, DORS, FEM and GRS) in its positive part, from the samples of Estats and Baborte (characterized by lower values of these characters) in the negative part of the axis.

The second axis (explaining 26.16 % of the variance) has loadings from GRS-l (0.5636), CIRCA (0.4428), HLL/SVL (0.3091), COLL (-0.2700), FLL/SVL (0.2065), and VENT (0.2097) and separates the samples of Baborte and Andorra

(characterized by higher values of GRS-l, CIRCA, HLL/SVL, FLL/SVL, and VENT), in its positive part from the samples of La Gallina, Gola, Estats, and Capifonts (with high values of COLL and lower values of the other abovementioned variables) in its negative part.

The third axis (explaining 16.31% of the variance) has loadings from FLL/SVL (0.4573), DORS (-0.4229), GUL (0.4224), DT/PAL (-0.3832), and FLL/SVL (0.3547) and separates La Gola and (to a lesser degree) Capifonts and Baborte (with higher values of HLL/SVL, GUL, and FLL/SVL and lower of DORS, and DT/PAL) in its positive part from the samples of Estats, Andorra, and (to a lesser degree) La Gallina (characterized by contrary values in these characters) in its negative part.

The three-dimensional representation of the sample centroids (fig. 2) shows the close vicinity of La Gola and Capifonts. Andorra is their nearest neighbour while Estats and Baborte appear distant from this group and from each other. La Gallina mediates between Gola-Capifonts and Estats, Baborte is most distant from all others. Coordinates of centroids and 95 % confidence radii of the samples studied are shown in table 3, Mahalanobis distances between centroids are represented in table 4.

If the two isolated specimens of La Gallina and Capifonts are excluded from the analysis, there is a clear discrimination between samples (lack of overlap in all 95% confidence spheroids). However, the assignment of these two specimens is problematic.

Table 3: Canonical Variate Analysis (CVA) of six samples of male *Lacerta aurelioi*. Coordinates of the centroids in the first three axes (V1, V2, V3) and 95 % confidence radii.

Tab. 3: Kanonische Varianzanalyse (CVA) von sechs Stichproben männlicher *Lacerta aurelioi*. Zentroidkoordinaten auf den ersten drei Achsen (V1, V2 V3) und 95 % Vertrauensradien.

Sample / Stichprobe	Coordinates of Centroids / Zentroidkoordinaten			95 % Confidence Radius / 95 % Vertrauensradius
	V1	V2	V3	
La Gola	0.9634	-0.8612	0.9150	1.614
La Gallina	0.0356	-1.5470	-0.2968	0.000
Baborte	-1.2430	1.1860	0.4976	2.795
Estats	-1.4160	-0.9178	-0.6852	0.884
Capifonts	0.5184	-0.4935	0.4803	0.000
Andorra	1.6950	0.5928	-0.7274	0.633
Eigenvalue	7.351	3.343	2.083	
% of Variance explained / % Varianz erklärt	57.53	26.16	16.31	

Table 4: Mahalanobis distances between centroids (coordinates see table 3) of six samples of male '*Lacerta aurelioi*' which were subject to CVA.

Tab. 4: Mahalanobisdistanzen zwischen den Zentroiden (Koordinaten siehe Tab. 3) von sechs, einer kanonischen Varianzanalyse unterzogenen Stichproben männlicher '*Lacerta aurelioi*'.

	Gol	Gall	Bab	Est	Cap	And
Gol	0					
Gall	17.68	0				
Bab	9.234	24.62	0			
Est	8.224	17.54	5.856	0		
Cap	9.142	27.95	14.54	13.90	0	
And	5.347	22.40	10.49	11.96	12.64	0

As their Mahalanobis distances appear very exaggerated (table 4), the smallest distances computed by means of the MST (Minimum Spanning Tree) were taken for a tentative description of their relationships (table 5).

Curiously, the lowest distance corresponds to two geographically more distant populations (La Gola and Andorra), whereas the spatially closer samples of La Gola and Capifonts are more distant in the threedimensional representation. La Gola also connects with Estats (and this latter with Baborte, as can be expected from their geographic closeness). As can be seen from figure 2, there are two populations with three connections in this minimum spanning tree (La Gola and Estats) where La Gola is the most central sample in that the sum of its distances to all other populations is smallest.

The connection between La Gallina and Estats is not well established. MST suggests to approach the single specimen of La Gallina to the Circ d'Estats sample ($D^2 = 17.54$), but its distance to the geographically neighbouring population of La Gola (both in Montroig massif) is very similar ($D^2 = 17.68$), and this latter seems to be the more plausible relationship. The male of Capifonts appears closest to the La Gola sample ($D^2 = 9.1420$) but is also not much different from the population of Andorra ($D^2 = 12.64$) or even Pica d'Estats massif [Circs d'Estats ($D^2 = 13.90$) and Baborte ($D^2 = 14.54$)]. These results suggest that there is independent differentiation among populations rather than much correlation between morphological similarity and spatial distance.

Discriminant analysis: Dis-

Table 5: The smallest Mahalanobis distances between the populations are the basis for the MST (Minimum Spanning Tree).

Tab. 5: Die kürzesten Mahalanobis Distanzen zwischen den Populationen bilden die Grundlage des MST (Minimum Spanning Tree).

Samples linked by MST Durch MST verbundene Stichproben	Mahalanobis Distance	
Gola	Andorra	5.347000
Gola	Estats	8.224000
Estats	Baborte	5.856000
Gola	Capifonts	9.142000
Estats	Gallina	17.540000

criminant analysis misclassifies only 20 out of 136 males (probability of wrong classification: 0.1493).

Out of 12 specimens of the Montroig massif (La Gola) studied, 11 are correctly classified, and one is assigned to the Andorran sample (91.66% of correct classification). But only 50% of all specimens classified as belonging to the La Gola population really belong to it. The Montroig sample is confused mainly with Andorran specimens.

The four males from Baborte (Pica d'Estats massif) are correctly classified (100 % of correct classification), but from all specimens classified as belonging to this population, only 36 % really belong to it. The Pica d'Estats sample is confused mainly with specimens from Estats (the nearest locality in the same massif) and Andorra.

From all 40 males studied from Estats (Pica d'Estats specimens included), 33 are correctly classified while seven are assigned to other samples (2 to La Gola, 4 to Baborte - a neighbouring population, 1 to Andorra). This means that 82.5 % of the Estats specimens are classified correctly. From all specimens classified as belonging to this population, 100 % really belong to it. In total, 78.72 % of the specimens of the whole Pica d'Estats sample were classified correctly.

Out of 78 Andorran specimens studied, 66 are correctly classified and 12 are assigned to other samples (9 to La Gola, 3 to Baborte). This is 84.6 % of correct classification of the true Andorran specimens. From all specimens classified as belonging to this population, 97 % really belong to it.

Table 6: Female *L. aurelioi* ARRIBAS, 1994. Descriptive statistics (Mean, standard deviation, coefficient of variation, Minimum, Maximum) of five samples including ANOVA results. Scale contacts of the Pica d'Estats and Capifonts samples are treated together. Abbreviations of measurement parameters are explained under "Materials and Methods". Levels of significance: * < 0.05; ** < 0.01; *** < 0.001.

Tab. 6: Weibchen von *L. aurelioi* ARRIBAS, 1994. Beschreibende Statistiken (Mittelwert, Standardabweichung, Variationskoeffizient, Minimum, Maximum) von fünf Stichproben einschließlich der ANOVA Ergebnisse. Die Schuppenkontakte der Stichproben von Pica d'Estats und Capifonts sind gemeinsam behandelt. Die Abkürzungen der Meßparameter sind in "Material und Methoden" erklärt. Signifikanzniveaus: * < 0.05; ** < 0.01; *** < 0.001.

Parameter	1 = (Gola - Gallina) MONTROIG (n = 26)					2 = (Sotllo - Estats) PICA D'ESTATS (n = 16)				
	Mean	Stdv	CV	Min	Max	Mean	Stdv	CV	Min	Max
SVL	53.98	3.45	0.064	45.02	59.7	55.45	3.63	0.07	49	62
GRS-r	5.28	1.83	0.348	2	9	4.71	2.05	0.44	2	8
GRS-l	4.96	1.69	0.341	2	9	4.21	2.42	0.58	1	9
GUL	25.12	1.66	0.066	22	29	24.23	1.73	0.07	21	27
COLL	11.56	0.86	0.075	10	13	10.5	1.87	0.18	8	15
DORS	45.88	1.66	0.036	44	49	44.57	3.1	0.07	38	50
VENT	28.88	0.83	0.028	28	31	29.14	0.86	0.03	28	31
FEM-r	12.08	1.22	0.101	10	14	10.35	1.59	0.15	7	13
FEM-l	12.04	1.42	0.118	10	15	10.85	1.16	0.11	9	13
LAM	24.8	0.86	0.035	24	26	24.23	1.16	0.05	22	26
CIRCA	7	0.95	0.136	6	8	7.71	0.91	0.12	6	9
FLL*100/SVL	32.48	0.01	0.039	30.72	35.94	31.89	0.01	0.04	29.83	34.66
HLL*100/SVL	44.77	0.02	0.054	40.41	50.01	41.26	0.11	0.29	40.5	0.4741
PL*100/PW	197.25	0.05	0.027	187.61	209.09	195.7	0.04	0.02	189.2	201.88
DM*100/PAL	33.16	0.08	0.24	15.8	45.39	35.74	0.14	0.4	0	53.12
DT*100/PAL	27.21	0.04	0.166	18.28	39.94	29.61	0.05	0.19	17.94	39.39
AL*100/AW	57	0.04	0.076	48.41	63.68	56.07	0.04	0.09	47.36	64.86
Scale contacts / Schuppenkontakt		no/nein	yes/ja				no/nein	yes/ja		
Rost.-Internas.		10	16				0	30		
Postoc.-Pariet.		22	4				27	3		
Supranas.-Lor.		2	24				3	27		

Parameter	2 = (Baborte) PICA D'ESTATS (n = 10)					CAPIFONTS (n = 4)				
	Mean	Stdv	CV	Min	Max	Mean	Stdv	CV	Min	Max
SVL	52.88	3.72	0.07	44.43	56.28	57.5	2.11	0.04	55.97	60.64
GRS-r	4.4	1.42	0.324	2	6	6.5	1	0.15	5	7
GRS-l	4.4	1.26	0.287	2	6	5.25	1.5	0.29	4	7
GUL	24.2	1.39	0.057	21	26	25.25	1.5	0.06	24	27
COLL	10.3	0.01	0.121	9	12	10.75	0.95	0.09	10	12
DORS	44.2	2.14	0.048	41	48	45.25	0.95	0.02	44	46
VENT	28.7	1.7	0.059	15	32	28.75	1.25	0.04	27	30
FEM-r	11.1	1.37	0.123	9	14	12.5	1.29	0.1	11	14
FEM-l	10.9	1.59	0.146	9	14	12.75	1.5	0.12	11	14
LAM	23.6	1.17	0.049	21	25	25.75	0.5	0.02	25	26
CIRCA	7.4	1.17	0.158	6	9	7.5	1	0.13	6	8
FLL*100/SVL	32.45	0.01	0.051	30.2	35.13	31.9	0.02	0.02	30.99	32.85
HLL*100/SVL	44.38	0.02	0.046	41.66	46.92	44.32	0.02	0.01	43.93	44.6
PL*100/PW	200.13	0.04	0.022	193.02	206.73	199.4	0.06	0.03	190.4	206.17
DM*100/PAL	39.28	0.1	0.273	14.28	51.56	37.37	0.02	0.08	33.94	40.8
DT*100/PAL	31.72	0.05	0.177	21.76	38.13	26.63	0.05	0.19	19.47	30.89
AL*100/AW	58.59	0.05	0.093	51.28	65.74	59.08	0.1	0.17	50.79	73.82

Table 6 (continued): Female '*L. aurelioi*' ARRIBAS, 1994. Descriptive statistics (Mean, standard deviation, coefficient of variation, Minimum, Maximum) of five samples including ANOVA results. Scale contacts of the Pica d'Estats and Capifonts samples are treated together. Abbreviations of measurement parameters are explained under "Materials and Methods". Levels of significance: * < 0.05; ** < 0.01; *** < 0.001.

Tab. 4 (Fortsetzung): Weibchen von '*L. aurelioi*' ARRIBAS, 1994. Beschreibende Statistiken (Mittelwert, Standardabweichung, Variationskoeffizient, Minimum, Maximum) von fünf Stichproben einschließlich der ANOVA Ergebnisse. Die Schuppenkontakte der Stichproben von Pica d'Estats und Capifonts sind gemeinsam behandelt. Die Abkürzungen der Meßparameter sind in "Material und Methoden" erklärt. Signifikanzniveaus: * < 0.05; ** < 0.01; *** < 0.001.

Parameter	3 = ANDORRA (n = 43)					ANOVA		Significant Differences		
	Mean	Stdv	CV	Min	Max	F	p	1-2	1-3	2-3
SVL	54.16	5.65	0.104	33.93	62.21	0.45	0.64			
GRS-r	7.35	2.25	0.306	2	11	15.39	0		**	***
GRS-l	7.4	2.53	0.342	2	13	16.68	0		***	***
GUL	24.08	1.84	0.076	20	28	1.75	0.18			
COLL	10.54	0.9	0.085	9	13	8.9	0	**	**	
DORS	46.94	2.35	0.05	42	51	7.83	0			***
VENT	29.64	0.75	0.025	27	31	5.93	0		*	*
FEM-r	12.27	1.14	0.093	9	15	13.7	0	***		***
FEM-l	12.18	1.02	0.083	10	14	10.88	0	**		***
LAM	24.64	1.37	0.055	22	27	3.74	0.03	*		
CIRCA	7.45	1.01	0.136	6	9	2.99	0.05			
FLL*100/SVL	32.83	0.02	0.061	28.29	36.68	0.93	0.4			
HLL*100/SVL	45.43	0.02	0.057	40.7	51.99	1.13	0.33			
PL*100/PW	201.38	0.05	0.028	188.1	214.98	4.19	0.02		*	
DM*100/PAL	27.56	0.08	0.304	8.87	41.98	10.13	0			***
DT*100/PAL	27.84	0.04	0.149	18.08	35.84	3.73	0.03			
AL*100/AW	57.28	0.06	0.112	44.89	70.54	0.54	0.59	*		
Scale contacts / Schuppenkontakt		no/nein	yes/ja				Chi-Sqr	p		
Rost.-Internas.		8	39				14.29	0		
Postoc.-Pariet.		40	6				0.37	0.83		
Supranas.-Lor.		4	41				0.091	0.96		

Females

ANOVA: Descriptive statistics of biometric indexes and pholidosis characters are shown in table 6.

The most different samples are Pica d'Estats (Estats plus Baborte) and Andorra (Andorra plus Capifonts). They differ from each other significantly (at p < 0.001) in GRS-r, GRS-l, DORS, FEM-r, FEM-l, and DM/PAL and (at p < 0.05) in VENT. MANOVA finds highly significant differences between the samples of Pica d'Estats (Estats plus Baborte), Capifonts, and Andorra ($F_{32,118} = 2.6856$, p < 0.0001; Wilks' Lambda = 0.3348).

Pica d'Estats (Estats plus Baborte) and Montroig (Gola plus La Gallina) differ from each other significantly (at p < 0.001) in FEM-r, (at p < 0.01) in COLL, and FEM-l and (at p < 0.05) in LAM and DT/PAL. MANOVA does not find signifi-

cant differences between the samples of these massifs (La Gallina, La Gola, Baborte and Estats) ($F_{48,98} = 1.3379$, p > 0.05; Wilks' Lambda = 0.2259).

Finally, Montroig (La Gola and La Gallina) differ from Andorra (Andorra plus Capifonts) significantly (at p < 0.001) in GRS-l, (at p < 0.01) in GRS-r, and COLL and (at p < 0.05) in VENT, and PL/PW. MANOVA finds highly significant differences between the populations of Montroig, Capifonts, and Andorra ($F_{32,118} = 2.8395$, p < 0.0001; Wilks' Lambda = 0.3192).

Concerning the frequency of contact among rostral and internasal, there are significant differences between the samples of the three massifs ($\chi^2_2 = 14.29$, p < 0.001). Over all specimens, scale contact is found in 82.22 %. The Montroig sample is characterized by the highest proportion of scale separation (10 out of 26 females).

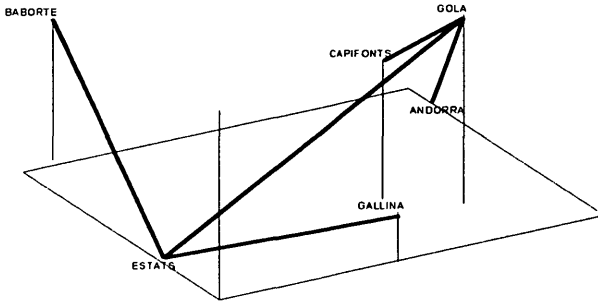


Fig. 2: Threedimensional representation of the population centroids of six samples of male *L. aurelioi* ARRIBAS, 1994. Scores of discriminant functions 1, 2, and 3 explain 100 % of the interpopulation variability. The Minimum Spanning Tree (MST) is superimposed in bold.

Abb. 2: Dreidimensionale Darstellung der Populationszentroide von sechs Stichproben männlicher *L. aurelio* ARRIBAS, 1994. Die Ladungen der Diskriminanzfunktionen 1, 2 und 3 erklären 100 % der Variabilität zwischen den Stichproben. Der Minimum Spanning Tree (MST) ist fett dargestellt.

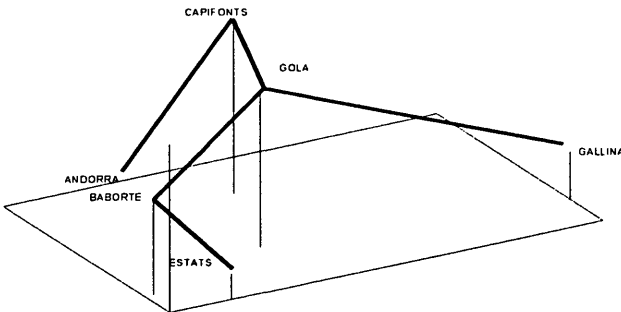


Fig. 3: Threedimensional representation of the population centroids of six samples of female *L. aurelio* ARRIBAS, 1994. Scores of discriminant functions 1, 2, and 3 explain 85.10 % of the interpopulation variability. The Minimum Spanning Tree (MST) is superimposed in bold.

Abb. 3: Dreidimensionale Darstellung der Populationszentroide von sechs Stichproben weiblicher *L. aurelio* ARRIBAS, 1994. Die Ladungen der Diskriminanzfunktionen 1, 2 und 3 erklären 85.10 % der Variabilität zwischen den Stichproben. Der Minimum Spanning Tree (MST) ist fett dargestellt.

Postocular and parietal are usually separated (85.55 %) without significant differences among samples ($\chi^2_2 = 0.36$, $p > 0.05$) while supranasal and loreal are usually in contact (95.5 %) without significant differences among samples ($\chi^2_2 = 0.09$, $p > 0.05$).

Canonical Variate analysis of the six samples (Baborte, Estats, Gallina, Gola, Capifonts, Andorra; $n = 103$ specimens) and 16 characters (all pholidotic characters and indexes) shows a result which is very similar to the situation in males (fig. 3). The samples differ significantly (MANOVA: $F_{80,399} = 2.2798$, $p < 0.0001$; Wilks' Lambda = 0.1633). The first three canonical axes explain 85.10 % of the intersample variability.

The first axis (explaining 47.52 % of the variance) has loadings from COLL (0.3097), FEM-r (0.4316), LAM (0.6074), FLL/SVL (0.3740), HLL/SVL (0.3038), and PL/PAL (-0.3862) and separates the sample of La Gallina (characterized by the greater values of LAM, FEM-r, FLL/SVL, COLL, and HLL/SVL and the lower of LP/PAL) in the positive part, from the samples of Baborte, Estats, Andorra and (to a lesser degree) Gola, and Capifonts (characterized by the lower values of these characters) in the negative part of the axis.

The second axis (explaining 25.57 % of the variance) has loadings from GRS-r (0.4805), GRS-l (0.4160), FEM-r (0.4569), FEM-l (0.3763) and separates populations from Andorra and (to a lesser degree) Capifonts, (with higher values of GRS and FEM) in the positive part, from the populations of Estats, Baborte, La Gallina, and

La Gola (with lower values of the above-mentioned variables) in the negative part of the axis.

The third axis (explaining 12.01% of the variance) has loadings from DM/PAL (0.3819), and VENT (-0.3807) and separates the populations of Capifonts and La Gola (with higher values of DM/PAL and lower of VENT) in the positive part, from the samples of Estats, Andorra and La Gallina (characterized by contrary values in these characters) in the negative part. The Baborte specimens occupy an intermediate position.

The threedimensional representation of these populations (fig 3) shows the close vicinity of Capifonts and La Gola. The small sample of La Gallina seems well isolated from the remaining populations among which Andorra appears somewhat isolated and Baborte and Estats moderately separated. Coordinates of centroids and 95 % confidence radii of the samples studied are shown in table 7, Mahalanobis distances between centroids are represented in table 8.

There is a clear discrimination between populations (95% confidence spheroids do not overlap) when the small samples of Capifonts and La Gallina are not considered.

As in the analysis of the males, these two small samples (La Gallina and Capifonts) show somewhat exaggerated Mahalanobis distances to their neighbours. The smallest distances computed by means of the Minimum Spanning Tree (MST) are indicated in table 9.

Table 7: Canonical Variate Analysis (CVA) of six samples of female '*Lacerta aurelioi*. Coordinates of the centroids in the first three axes (V1, V2, V3) and 95 % confidence radii.

Tab. 7: Kanonische Varianzanalyse (CVA) von sechs Stichproben weiblicher '*Lacerta aurelioi*. Zentroidkoordinaten auf den ersten drei Achsen (V1, V2 V3) und 95 % Vertrauensradien.

Sample / Stichprobe	Coordinates of Centroids / Zentroidkoordinaten			95 % Confidence Radius / 95 % Vertrauensradius
	V1	V2	V3	
La Gola	-0.0975	-0.1966	0.7446	1.206
La Gallina	2.5250	-0.5297	-0.3373	3.340
Baborte	-1.3980	-0.6723	0.1244	1.829
Estats	-0.8389	-1.0350	-0.5586	1.446
Capifonts	0.2871	0.8785	0.8402	2.893
Andorra	-0.4773	1.5550	-0.8134	0.844
Eigenvalue	9.352	5.033	2.363	
% of Variance explained / % Varianz erklärt	47.52	25.57	12.01	

Table 8: Mahalanobis distances between centroids (coordinates see table 7) of six samples of female '*Lacerta aurelioi*' which were subject to CVA.

Tab. 8: Mahalanobisdistanzen zwischen den Zentroiden (Koordinaten siehe Tab. 7) von sechs, einer kanonischen Varianzanalyse unterzogenen Stichproben weiblicher '*Lacerta aurelioi*'.

	Gol	Gal	Bab	Est	Cap	And
Gol	0					
Gal	9.006	0				
Bab	3.910	15.92	0			
Est	4.989	12.75	3.357	0		
Cap	4.069	9.317	7.523	7.192	0	
And	6.048	13.67	7.248	8.057	5.036	0

As in the MST of the males, La Gola is the sample with the highest number of connections (fig. 3), in that it is linked to three other samples to which it is the most similar: La Gallina (geographically closest), Capifonts (related also to Andorra), and Baborte (related also to Pica d'Estats).

Discriminant analysis: Discriminant analysis misclassifies 29 out of 103 specimens (probability of wrong classification = 0.2816).

Out of 23 La Gola specimens, 16 are classified correctly, and 7 are assigned incorrectly (3 to Baborte, 1 to Estats, 2 to Capifonts, and 1 to Andorra). 69 % of the specimens originating from La Gola were correctly classified while 69.56% of the specimens assigned to this population by the analysis really originated from La Gola. La Gola specimens are confused both with individuals from Pica d'Estats and Andorra-Capifonts.

All three specimens (100 %) of La Gallina are correctly classified, but only 60 % of the individuals assigned to this population really belong to this sample (confusion with Capifonts and Andorra).

Four out of ten Baborte specimens studied, are misclassified (2 as La Gola, 1 as Estats, and 1 as Andorra). 60 % of the specimens originating from Baborte were

Table 9: The smallest Mahalanobis distances between the populations are the basis for the MST (Minimum Spanning Tree).

Tab. 9: Die kürzesten Mahalanobis Distanzen zwischen den Populationen bilden die Grundlage des MST (Minimum Spanning Tree).

Samples linked by MST Durch MST verbundene Stichproben		Mahalanobis Distance
Gola	Baborte	3.910000
Baborte	Estats	3.357000
Gola	Capifonts	4.069000
Capifonts	Andorra	5.036000
Gola	Gallina	9.006000

correctly classified while 46.15 % of the specimens assigned to this population by the analysis really originated from Baborte (confused mainly with Estats specimens).

Nine out of 16 specimens from Estats are classified correctly, while 7 are misclassified (4 as Baborte, 1 as La Gola, 1 as Capifonts, and 1 as Andorra). 56.25 % of the Estats specimens are classified correctly, while 75 % of the individuals assigned to this sample really belong to it. If the two Pica d'Estats massif populations (Estats and Baborte) were pooled, correct classification would increase to 64.51 % (confused mainly with La Gola specimens).

One out of four Capifonts specimens is misclassified (as belonging to the La Gallina sample). 75 % of the Capifonts specimens are classified correctly, but only 27.27 % of the individuals assigned to this population really belong to this sample (mainly confused with Andorra specimens).

10 out of 47 Andorran females are misclassified: (4 as La Gola, 1 as La Gallina, 1 as Estats, and four as Capifonts) 78.72 % of the Andorran specimens are classified correctly, while 94.87 % of the individuals assigned to this population really belong to the Andorra sample.

DISCUSSION

As can easily be seen from the above results, all samples studied are more or less different from each other. However, the differences are small and morphological trends among populations which could be related to their geographic position were not detected. From a morphological point

of view, it is therefore not reasonable to describe the populations as subspecies (see also comments in CIRER 1981, 1987a, 1987b; BÖHME & CORTI 1993). The differences observed among these populations of '*L. aurelioi*' can be considered as the result of a recent (Holocene) fragmentation of a for

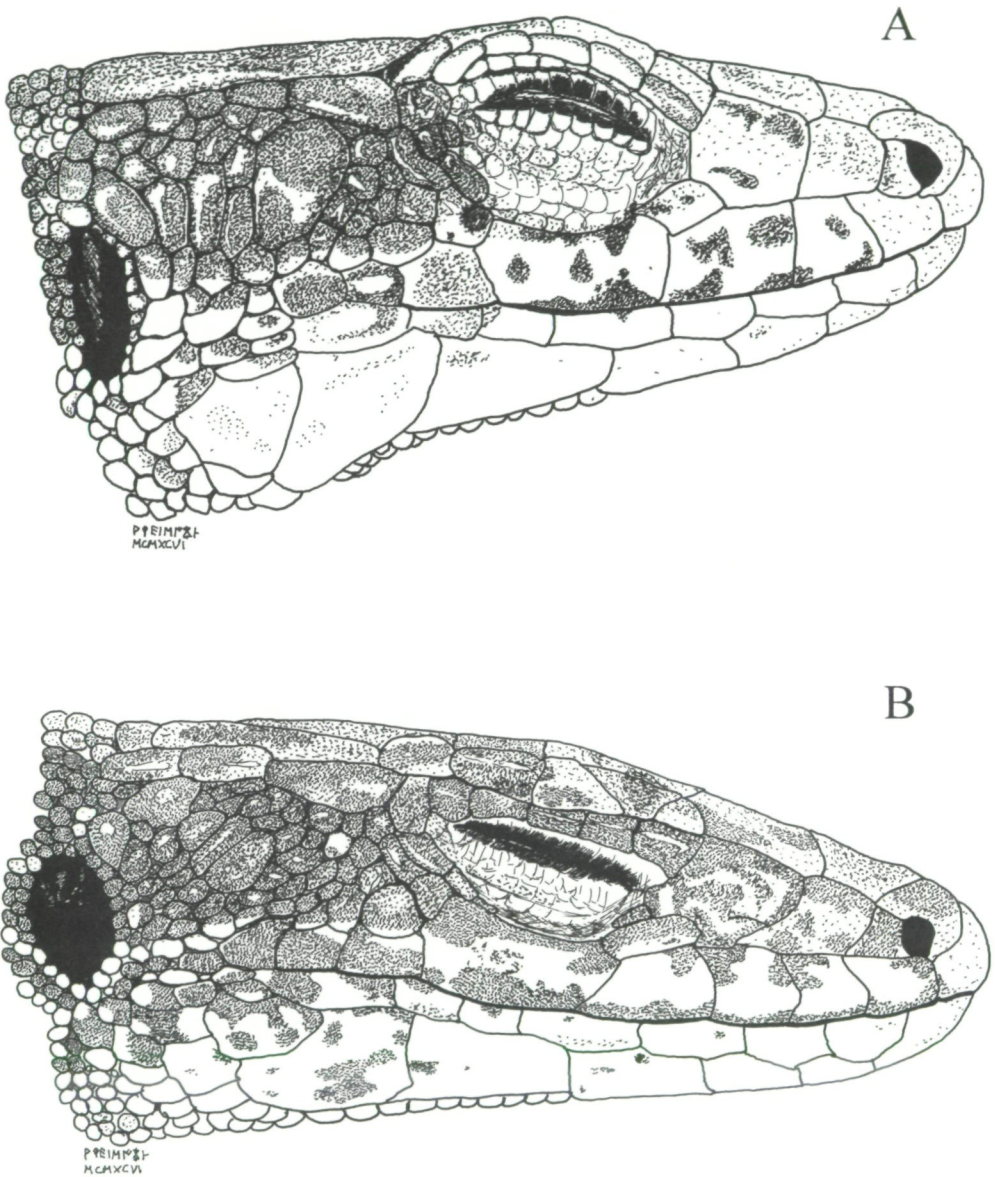


Fig. 4: '*L. aurelioi*' ARRIBAS, 1994. Head in lateral view, showing the variability in the arrangement of the temporal plates (see also ARRIBAS 1994: fig 1).

A - Male from Estany de La Gola (Massif de Montroig, Lérida);

B - Male from Estany de Creussans (Massif de la Coma Pedrosa, Andorra).

Abb. 4: '*L. aurelioi*' ARRIBAS, 1994. Kopf in Seitenansicht, zur Darstellung der Variabilität der Anordnung der Temporalschilder (siehe auch ARRIBAS 1994: Abb 1).

A - Männchen von Estany de La Gola (Montroig-Massiv, Lérida);

B - Männchen von Estany de Creussans (Coma Pedrosa - Massiv, Andorra)

merly more continuous range, probably a single Würmian refuge.

During the last glacial period, the valleys surrounding the massifs which are now inhabited by *L. aurelioi* were occupied by large glaciers with wide ice platforms, cirques and long glacial tongues in the upper reaches. Some of these glaciers are among the longest of the Pyrenees. The Noguera Pallaresa river valley glacier, which was 52 km in length and deposited its terminal moraines at heights of 700 to 800 m. a.s.l., was the longest glacier of the southern Pyrenean slopes (NUSSBAUM 1956; NUSSBAUM & HAZERA 1980; BRU & al. 1985; BORDONAU 1992; PEÑA-MONNÉ et al. 1998). In the Pyrenean north side slopes, which are shorter and more stepped (and thus, less suited to represent a Würmian refuge for this lizard), the glaciers were also well developed (Riberot glacier - 18 km long, Garbet glacier - 12 km, Ariège glacier - the Pleistocene aspect of which has been compared with that of the 52 km long Baltoro glacier in the Karakorum; see BARRÈRE 1963; TAILLEFER 1969; RITTER, 1988). Notwithstanding their barrier effect, these north side glaciers did not immediately affect the differentiation of the species. Although these glaciers did not form a continuous ice barrier, several valleys must have been isolated even during the withdrawal phases since the lower parts of the valleys were impassable because of melting water lakes (VILAPLANA 1984). The ridges above the cirques and glaciers were covered by permanent snow caps (the line of permanent snow was at altitudes between 1700 m and 2100 m; BARRÈRE 1963; TAILLEFER 1969; VIERS 1969; RITTER, 1988; PEÑA-MONNÉ & al. 1998) and must have

presented a "dendritic" or stellate aspect in aerial view, owing to intermediate areas which were more or less free of snow, depending upon their altitude and orientation. During Pyrenean Tardiglacial, forests reached up the mountains approximately as high as 1500 m (northern slopes) or 1800 m (southern slopes), giving space to a belt of alpine habitat which was only 200 to 300 m wide, free of snow in summer and probably suitable for this species, along the meridional slopes (ARRIBAS 1996 b, from data by MONTSERRAT-MARTÍ 1992).

The current full allopatry of the various Pyrenean mountain lizard species indicates lack of contact from the time of their vicariance on. The karyological and morphological uniformity of *L. aurelioi* speaks in favour of a recent common origin of the currently known populations. This mountain lizard seems to have survived the Würm glacial period more or less "in situ", in a single refugium of unknown localization and extension (as probably was the case in the other two Pyrenean high mountain lizard species '*L. aranica*' ARRIBAS, 1993, and '*L. bonnali*' LANTZ, 1927).

It is difficult to determine the location of the primitive refuge that gave origin to the current species' distribution, especially when working on an infrasubspecific level. However, it has been postulated that MST is a good method to analyze evolutive relations, assuming that the neighbour-joining relationship is the most parsimonious relationship. When this method is applied to the analysis of different species, it is likely to be affected by ecotypic character variation which distorts possible similarities over great geographic distances. But within a taxon and under spatial restriction as in

Figs. 5 - 8 (opposite page) / Abb. 5 - 8 (gegenüberliegende Seite)

Fig. 5: Hatchling of *L. aurelioi* ARRIBAS, 1994 from Ordino-Arcalis (Andorra).

Observe the brightly colored green tail.

Abb. 5: Schlüpfling von *L. aurelioi* ARRIBAS, 1994 von Ordino-Arcalis (Andorra).

Man beachte die leuchtend grüne Schwanzfärbung.

Fig. 6: *L. aurelioi* ARRIBAS, 1994 from Estany de Creussans (Andorra). Typical pattern of a male individual.

Abb. 6: *L. aurelioi* ARRIBAS, 1994 von Estany de Creussans (Andorra). Typische Zeichnung eines Männchens.

Fig. 7: *L. aurelioi* ARRIBAS, 1994 from Ordino-Arcalis (Andorra). Typical pattern of a male individual.

Abb. 7: *L. aurelioi* ARRIBAS, 1994 von Ordino-Arcalis (Andorra). Typische Zeichnung eines Männchens.

Fig. 8: *L. aurelioi* ARRIBAS, 1994. Male from Estany de Sotllo (Lérida, Spain).

A more unusual design, with somewhat marbled costal bands.

Abb. 8: *L. aurelioi* ARRIBAS, 1994. Männchen von Estany de Sotllo (Lérida, Spanien).

Ein weniger häufiges Zeichnungsmuster mit etwas marmorierten Flankenstreifen.



6 8



5 7



'*L. aurelioi*', one can assume that environment affects all populations equally, making this method available for the assessment of interpopulation relationships, and evolutive inference. In '*L. aurelioi*', the MST results speak in favour of the southern slopes of the Montroig massif being the most primitive area for this species (Montroig ist the sample with the smallest overall distance to all other samples). This point of view is supported by the fact that - among all '*L. aurelioi*' localities - Montroig is closest to the territory of the other two Pyrenean high mountain lizard species.

A map of the glaciers of the high Noguera Pallaresa drainage (NUSSBAUM in HAZERA 1980) shows a large mountainous area in the southern slopes of the Montroig massif between the Noguera Pallaresa and Ribera de Cardós glaciers (Serres de Pilàs, Campirme and Aurati), suited to have been the possible refuge area from which the species spread. In its lower parts, this ridge connects with other ridges that diverge (valleys included) in a radial manner, in which the primitive Montroig population could have spread towards Pica d'Estats and the Capifonts area, and from there to Andorra (see also analogous maps in ZANDVLIET 1960 and RITTER 1988:213). This fits well together with the MST results. The route would also explain the distributional hiatus of the species in the Certescan massif. To date, this massif which was heavily glaciated during Würm and difficult of access from the aforementioned route, it is not inhabited by the species due to unsuited granitic substrate.

In the Pyrenees (and in other south European mountain ranges), the Würmian climate deviated somewhat from the usual

image of hard climatic conditions during the glacial ages and allowed for an early expansion of the mountain species from their refugia.

When we analyze this postglacial spreading period, it is important to know that chronology of the last Pyrenean glacial period is different from the glaciation of other European areas (as the Alps or northern Europe). In the Pyrenees, the glacial maximum was reached about 50-45,000 years b.p. (versus 20-18,000 years b.p. in the Alps; see e. g. BORDONAU 1992; BORDONAU & al. 1992; SERRAT 1992; MONT-SERRAT-MARTÍ 1992; JALUT & al. 1992) and deglaciation began soon afterwards. The first glacial withdrawal, has been dated from before 38,000-35,000 years b.p. which is clearly earlier than 25,000-24,000 years b.p., when glaciers disappeared from the Pyrenean piedmont and withdrew into the higher parts of the mountains. This approximately coincided with the glacial maximum in the Alps and the dry period registered in Europe about 15,000 b.p. (ANDRIEU & al. 1988; JALUT 1992; JALUT & al. 1992).

The comparatively mild climate and the increased insolation to the southern slopes, should sufficiently explain the survival of these lizards together with a considerable number of other well documented relicts of the Tertiary fauna (paleomontane and primitive oromediterranean taxa) and flora (e. g., arcto-tertiary taxa) in so-called "nunataker", or "refuge massifs" (sensu HOLDHAUS 1954). Almost all highest summits (massifs) were partially free of snow (at least in one of their slopes) allowing for "in situ" survival of many animal and plant species during the coldest periods of the

Figs. 9 - 12 (opposite page) / Abb. 9 - 12 (gegenüberliegende Seite)

Fig. 9: '*L. aurelioi*' ARRIBAS, 1994. Heavily pigmented male from Estany de Sotllo (Lérida, Spain).

Abb. 9: '*L. aurelioi*' ARRIBAS, 1994. Ein stark pigmentiertes Männchen von Estany de Sotllo (Lérida, Spanien).

Fig. 10: Male '*L. aurelioi*' ARRIBAS, 1994. Ventral colour-pattern. Ordino-Arcalis (Andorra).

Abb. 10: Männchen von '*L. aurelioi*' ARRIBAS, 1994. Ventrale Färbung und Zeichnung. Ordino-Arcalis (Andorra).

Fig. 11: Female '*L. aurelioi*' ARRIBAS, 1994. Typical pattern. Ordino-Arcalis (Andorra).

Abb. 11: Weibchen von '*L. aurelioi*' ARRIBAS, 1994. Typische Zeichnung. Ordino-Arcalis (Andorra).

Fig. 12: '*L. aurelioi*' ARRIBAS, 1994. Old female from Estany de Sotllo (Lérida, Spain).
Paratype (OA 91070108).

Abb. 12: '*L. aurelioi*' ARRIBAS, 1994. Altes Weibchen von Estany de Sotllo (Lérida, Spanien).
Paratypus (OA 91070108).



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glaciations (see JEANNEL 1936; GARCÍA-SAINZ 1947; VANDEL 1949; GAUSSEN & BARRUEL 1957; MARCUZZI 1973; VILLAR 1977; MARGALEF 1986). The "refuge massif" concept (CHODAT & PAMPANINI 1902; HOLDHAUS 1902, 1906, 1954) according to which mountain species survived the glaciations in unglaciated areas at the border of the Alps, has been proved for a number of paleoendemic invertebrates and was discussed recently in the cases of *Salamandra atra aurorae* TREVISAN, 1982 and *Salamandra lanzai* NASCETTI, ANDREONE, CAPULA & BULLINI (see GROSSENBACHER 1994). These salamanders were not very successful postglacial colonists and remained restricted to very small areas ("mountain islands"), which is probably also the case in the Pyrenean mountain lizards.

The following considerations refer to the spatial and evolutionary separation of *L. aurelioi* from the other two Pyrenean mountain lizards. *Lacerta aurelioi* and *L. bonnali* (the sister species of *L. aurelioi* - MAYER & ARRIBAS 1996; ARRIBAS 1996, and in press) - evolved from their common ancestor probably during the Middle Pleistocene (ARRIBAS 1996 b). *Lacerta bonnali* is present in the Sant Maurici-Aigüestortes area, west of *L. aurelioi*. The bottom of the Noguera Pallaresa river valley, which separates the area of the two species was and still is occupied by supra-mediterranean vegetation. This vegetation was probably well developed during the Holsteinian (Mindel-Riss) and Eemian (Riss-Würm) interglacials but not during the cold Riss and Würm periods when the valley was occupied by a great glacial tongue preventing contact between the two arising species. The hypothesis of their possible sympatry in the past is contra-

dicted by the apparent absence of *L. bonnali* in the Beret and Marimanha massifs, which represent a natural pass between the areas of the two species in the upper reaches of the Noguera Pallaresa river valley.

The separation of *L. aranica* from the common ancestor of *bonnali*-plus-*aurelioi* seems to date back to the beginning of the plio-pleistocenic climate deterioration. Notwithstanding the current allopatry of *L. aurelioi* and *L. aranica*, the particular smallness of the hemipenes of *L. aurelioi* has been interpreted as a prezygotic isolation mechanism (as can also be the case in the return of a fully developed ventral coloration in *L. aurelioi* - acting as a key character in sex recognition. This mechanism might have arisen during a hypothetical past sympatry (or parapatry) between these species along the continuous, relatively narrow, low crested, and excentric Montvallier massif that connects the Mauberme and Montroig massifs (see ARRIBAS 1996 b). Previous to the last glacial maximum (45 to 50,000 years b.p. in the Pyrenees - BORDONAU 1992; MONT-SERRAT-MARTÍ 1992), this crest, however, could have been higher and wider, representing the remains of a formerly more developed wall that was deepened by the glaciers situated in its slopes. To our present knowledge, there is a 15 km hiatus between the two species' ranges, that would be lesser if lizards sighted at high altitudes in the Montvallier massif turned out to belong to one of these species (see BERTRAND & COCHET 1992; ARRIBAS 1993; CROCHET & al., 1997). However, careful field prospection in suitable areas near this massif (e.g., Coma Gireta, Port de Aulà, Port de Salau, Tuc de Mill) remained fruitless so far.

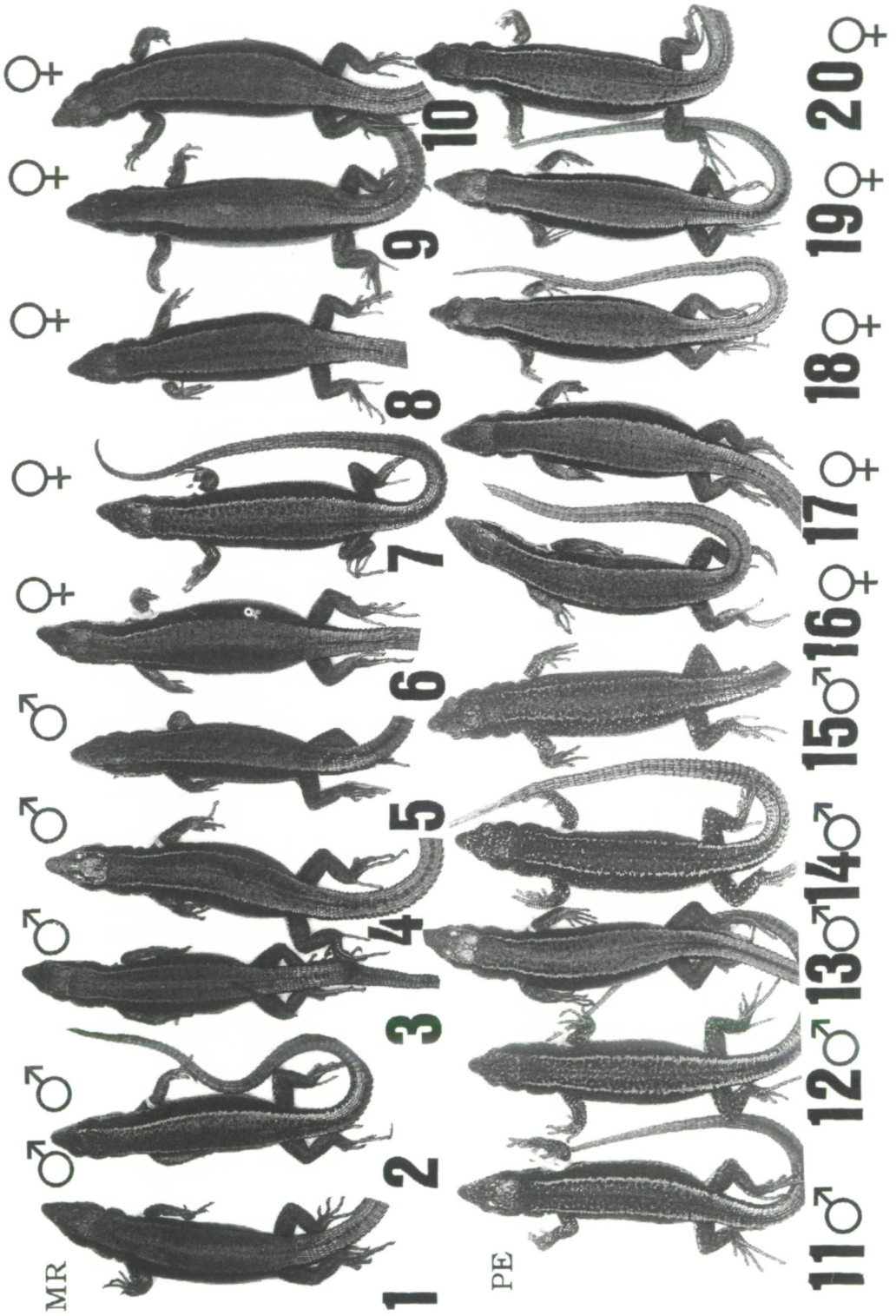
Plate 1 (opposite page): *L. aurelioi* ARRIBAS, 1994. Dorsal pattern variability. M - Male; F - Female.

Tafel 1 (gegenüberliegende Seite): *L. aurelioi* ARRIBAS, 1994. Variabilität der Rückenzeichnung.

M - Männchen; F - Weibchen.

MONTROIG: 1 - Estany de la Gola (M) CA 93080701; 2 - Estans de la Gallina (M) CA 95072601; 3 - Estany de Calberante (M) CA 95070611; 4 - Estany de la Gola (M) CA 93080702; 5 - Estany de la Gola (M) CA 93080711; 6 - Estany de la Gola (F) CA 95070604; 7 - Estans de la Gallina (F) CA 95072602; 8 - Estany de la Gola (F) CA 96061408; 9 - Estany de la Gola (F) 93080706; 10 - Estany de la Gola (F) CA 93080714.

PICA D'ESTATS: 11 - Estany de Sotillo (M) CA 93070405; 12 - Estany de Sotillo (M) CA 93070401; 13 - Estany de Sotillo (M) CA 93081001; 14 - (M) Estany de Sotillo CA 93070409; 15 - Estany de Sotillo (M) CA 93070410; 16 - Estany de Sotillo (F) CA 93081005; 17 - Estany de Baborte (F) CA 95081201; 18 - Estany de Baborte (F) CA 93061207; 19 - Estany de Baborte (F) CA 93061202; 20 - Estany de Baborte (F) CA 95081202.



DIAGNOSIS of '*Lacerta aurelioi*

Morphology: The range of the values of various pholidotic and biometric characters is indicated in tables 2 and 6, with the means in parentheses. Sexually dimorphic characters are given separately for males and females and marked by an asterisk (*).

Biometry: Snout vent-length (SVL*): On the average, SVL of '*L. aurelioi*' is longer in females (54.32 mm) than in males (52.05 mm) although the biggest specimen found was a male (SVL = 65.25 mm) and the maximum SVL in females was 62.21 mm.

Masseteric and tympanic scales are relatively small, especially the tympanic scale.

Forelimb length (FLL*): 24.28 to 42.03 % (35.3 %) of snout vent-length in males and 28.29 % to 36.68 % (32.5 %) in females. **Hindlimb length (HLL*):** 43.41 % to 55.97 % (49.78 %) of snout vent-length in males and 40.70 % to 51.99 % (45.22 %) in females. **Pileus length (PL*):** 1.85 to 2.17 (2.03) times longer than pileus width in the males, and 1.87 to 2.14 (1.99) times longer than pileus width in females. **Masseteric scale diameter (DM):** 8.8 to 53.12 % (32.36%) of parietal scale length. **Tympanic scale diameter (DT):** 10.55 to 41.66 % (28.98 %) of parietal scale length. **Anal scale length (AL*):** 37.97 to 82.1 % (51.43) of its width in males, and 44.89 to 73.82 (57.24) of its width in females.

Pholidosis: **Supraciliar granules (GRS):** 1 to 14 (6.5) in the right side, and 0 to 13 (6.38) in the left side. **Gularia (GUL):** 20 to 30 (24.69). **Collaria (COLL):** 7 to 15 (10.76). **Longitudinal series of dorsal scales (DORS):** 37 to 52 (46.21). **Transversal rows of ventral scales (VENT*):** 25 to 29

(27.14) in males, and 25 to 32 (29.21) in females. **Femoral pores (FEM):** 7 to 16 (11.93) in the right side, and 9 to 16 (12.08) in the left side. **Lamellae underneath fourth toe (LAM):** 21 to 29 (24.87). **Circumanalia (CIRCA):** 6 to 10 (7.56).

Rostral and internasal plates usually in contact (90.49 % of specimens); postocular and parietal usually separated (89.21 % of specimens); supranasal and loreal usually in contact (92.91 % of specimens). There is a great variability in the pholidosis of the temporal region (fig. 4) and a very high frequency of cephalic scale anomalies (usually abnormal fragmentation of scales) (figs. 5, 8, 9, 11).

Coloration: The basic dorsal colour-pattern in '*L. aurelioi*' is represented by two dark costal bands on a brown background color, sometimes with an olivaceous shine in recently shedded specimens. The costal bands usually extend to the proximal third of the tail. On the yellow-coloured ventral background, there is a marked dark pattern of transverse bands which are more developed towards the belly and anal region. Within these bands, the dark pigmentation is restricted to the proximal part of the scales. There are sex-dependent modifications to this basic pattern, which is typical to subadults and young females (plates 1 and 2).

The dorsum of hatchlings (first calendar year) is of largely uniform brown colour, sometimes with barely visible dark spots; the ventral side is white or slightly yellowish; the tail is of bright green colour (fig. 5). At the end of the first year (second calendar year), the yellow colour of the venter is clearly visible.

Plate 2 (opposite page): '*L. aurelioi*' ARRIBAS, 1994. Dorsal pattern variability. M - Male; F - Female.

Tafel 2 (gegenüberliegende Seite): '*L. aurelioi*' ARRIBAS, 1994. Variabilität der Rückenzeichnung. M - Männchen; F - Weibchen.

CAPIFONTS: 1 - Serrat de Capifonts (F) CA 95060703; 2 - Serrat de Capifonts (F) CA 95060705; 3 - Serrat de Capifonts (F) CA 95060704; 4 - Serrat de Capifonts (F) CA 95060701; 5 - Serrat de Capifonts (M) CA 95060702.

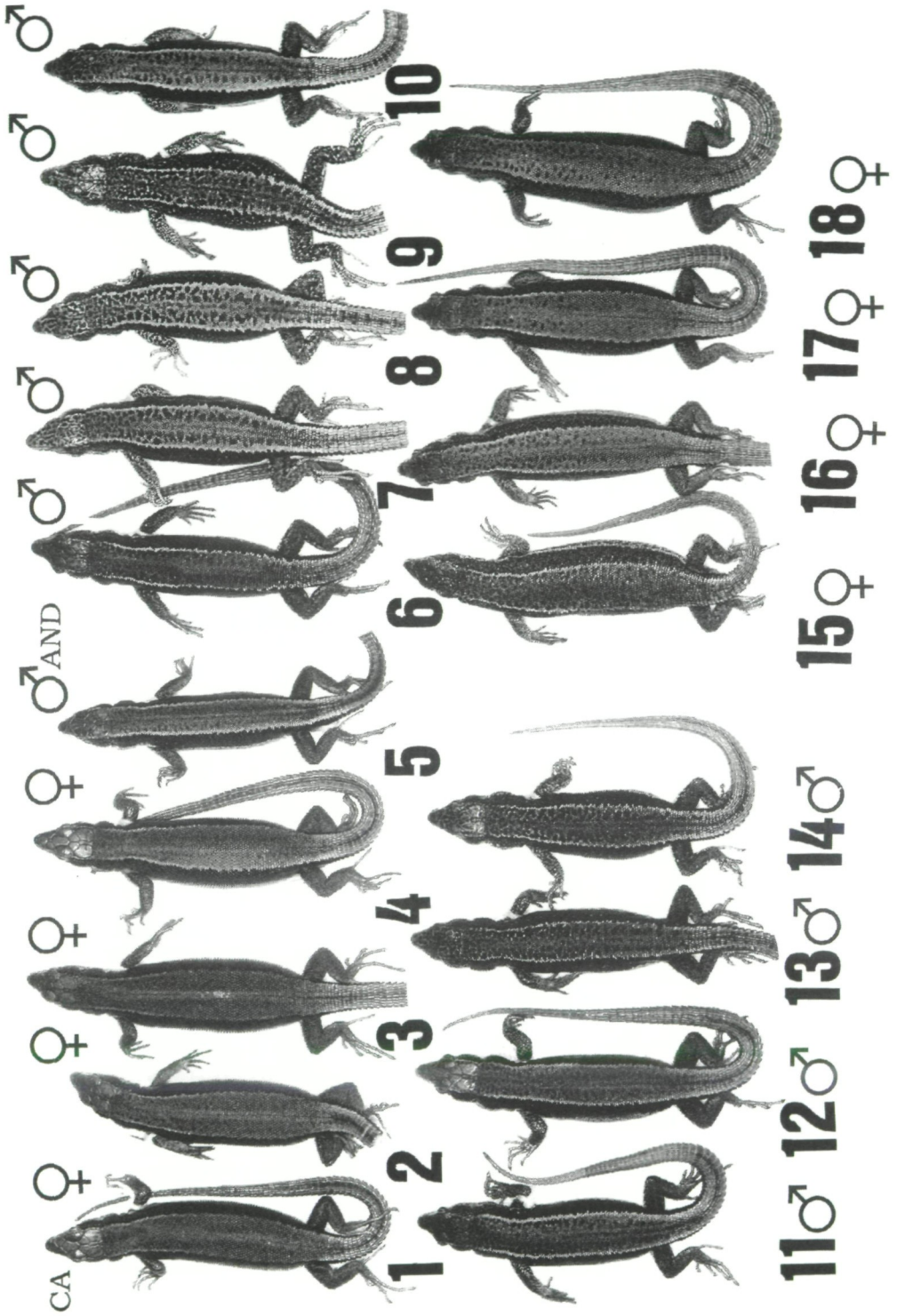
ANDORRA: 6 - Port de Rat (M) CA 95082801; 7 - Port de Rat (M) CA 94081101; 8 - Port de Rat (M)

CA 94081109; 9 - Circ de Tristaina (M) CA 95072201; 10 - Coma del Forat (M) CA 94081105; 11 - Coma del

Forat (M) CA 94060621; 12 - Port de Rat (M) CA 95082806; 13 - Coma del Forat (M) 94081106; 14 - Coma del

Forat (M) CA 94090608; 15 - Coma del Forat (F) CA 95061703; 16 - Coma del Forat (F) CA 94071002;

17 - Port de Rat (F) CA 95082805; 18 - Pic de Coma Pedrosa (F) CA 95081002.



Subadults (third calendar year) may or may not have greenish tails (if present, the green is less bright than in hatchlings) (see ARRIBAS 1994: photo 8). Otherwise, their coloration is similar to the above-mentioned basic pattern.

Adults (from fourth calendar year to an unknown age) present a sexual colour dimorphism. Males develop numerous dark spots on their back and pileus, and usually also on the dorsal face of the tail (figs. 6, 7, 8). Occasionally, strongly pigmented specimens can be seen (fig. 8). The dark lower lateral band is usually discontinuous and formed by dots. The yellow colour of the belly and the chest, and the transverse dark bars across the ventrals (also present on the ventral side of the tail - fig. 10) are more pronounced in males than in females. Occasionally, a greenish tinge, reminiscent of the brightly colored tail of the hatchling, can still be seen in some "young" males (ARRIBAS 1994: photo 5). Females are less pigmented and more similar to the aforementioned basic pattern, but can also develop a ventral color-pattern and - more frequently - some sort of dorsal pattern, although less developed than in males (fig. 11).

Old specimens are strongly pigmented, both males and females (figs. 9, 12, and ARRIBAS 1994: photos 6, 7). Concerning the colour of the ventral side, old females preserve the yellow colour rather than old males and the vivid yolky yellow can turn into an orange yellow. Head and neck are white underneath, whereas the breast, the belly, and the ventral sides of the legs and calves, and even the tail (this latter only in females) are yellow (ARRIBAS 1994: photos 1, 2).

Among adults, almost all specimens have more or less spotted venters; only 4.54 % of the specimens lack spots. In 8.67 % a well developed pattern is restricted to the outermost longitudinal row of the ventrals, in 18.59 % to the two outermost rows, while in the majority of 68.18 % all six rows of ventral plates are spotted. In the dorsal side, adults (especially males) have narrow clear dorsolateral stripes, not sharply differentiated and usually more developed in the anterior half of the dorsum.

Osteology: Anterodistal process of postfrontal and anteromedial process of

the postorbital absent by secondary reduction (the former being an autapomorphy). Postorbital bone longer than postfrontal. Seven premaxillary teeth; processus nasalis slender and subparallel; 15 to 17 (average 15.9) maxillary teeth; 16 to 22 (average 19.6) dentary teeth. The majority of the teeth is bicuspid rather than monocuspid. Males have usually 26 presacral vertebrae, and females 27. The third vertebra is usually associated with a bony rib. Sternal-xiphisternal formula (3+2). Sternal fontanelle oval (occasionally one or two very small foramina), but very frequently secondarily reduced. Clavicles usually closed (emarginated); interclavicle of typical cruciform shape (ratio of length of anterior / posterior branch: 0.22 to 0.35, average 0.29). Usually six short posterior dorsal ribs (ARRIBAS 1994, 1996 b, 1998). Proximal preautotomic caudal vertebrae with perpendicular processes only in their anterior part (A-type in ARNOLD 1973, 1989). Osteological data are taken from ARRIBAS 1994, 1996 b, 1998)

Karyotype: 26 chromosomes (10 metacentric, 16 acrocentric) in the males, and 25 (11 metacentric or submetacentric and 14 acrocentric) in the females. Sex chromosome system Z_1Z_2W . C-banding shows centromeric bands well marked in the acrocentric chromosomes and weakly marked in the metacentric or submetacentric chromosomes. Pericentromeric bands very faint in the three first pairs of these banded chromosomes. NOR in a telomeric position in the long arm of the third pair of banded chromosomes. Specimens from Andorra, Pica d'Estats (two localities) and Montroig have been studied, without detecting geographic variability (ODIERNA & al. 1994, 1995, 1996 and in press; ARRIBAS 1996 b).

Allozyme data: No autapomorphic allele was found in the electrophoretic analysis of the Iberian mountain lizards. '*L. aurelioi*' differs from '*L. bonnali*' (its sister species) in one allele (PGM-2), and from '*L. aranica*' in three alleles (AK, GOT-1 and MDH-1) (MAYER & ARRIBAS 1996).

Hemipenis: Typical of a lacertid, with moderately narrow sulcal lips, but clearly smaller than in the other Ibero-pyrenean species of mountain lizards. With respect to the small size of the hemipenes, a

preceding contact with *'L. aranica* has been postulated (ARRIBAS 1996 b). This contact could have promoted a character displacement serving as a pre-zygotic reproduction barrier. Hemipenial microornamentation crown-shaped (ARRIBAS 1994, 1996 b).

Distribution: Endemite of a

small area in the eastern central Pyrenean axis: massifs of Montrouig, Pica d'Estats (s.l.) and NW Andorra (massifs of Coma Pedrosa and Tristaina). The slight differences among the populations of this monotypic species probably arose from their Holocene isolation.

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Corresponding editor: Heinz Grillitsch

AUTHOR: Dr. OSCAR J. ARRIBAS, Avda. Fco. Cambó 23, E-08003 Barcelona, Spain.