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Taxonomic revision of the Iberian 'Archaeolacertae' IV. Diagnosis, morphology and geographic variation of *Iberolacerta aranica* (ARRIBAS, 1993)
(Squamata: Sauria: Lacertidae)

Taxonomische Revision der iberischen 'Archaeolacerten' IV: Diagnose, Morphologie und geographische Variabilität von *Iberolacerta aranica* (ARRIBAS, 1993)
(Squamata: Sauria: Lacertidae)

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KURZFASSUNG

Iberolacerta aranica (ARRIBAS, 1993) ist ein Endemit der Zentral-Pyrenäen, der ausschließlich das Maubèrme Massiv und dessen Ausläufer zwischen Val d'Aràn (Spanien) and Ariège (Frankreich) bewohnt. Vorkommen der Art sind in fünfundzwanzig 1 km x 1 km U.T.M. Rasterfeldern nachgewiesen; das mögliche Verbreitungsgebiet bedeckt maximal 36 derartige Rasterfelder. Die Eidechse bewohnt Schutthalden, Geröllfelder und steiniges Grasland (meist auf paläozoischen Schiefern und Kalken) im alpinen Vegetationsgürtel zwischen 1940 m (1900 m) und 2668 m Seehöhe.

Alle untersuchten Populationen mit Ausnahme derer von Orlá scheinen untereinander mehr oder weniger in Kontakt zu stehen. In Abhängigkeit vom bewohnten Gesteinsuntergrund bestehen populationstypische Unterschiede in der Rückengrundfarbe. Tiere von Maubèrme ähneln jenen von Liat sehr; beide stehen den Serra d'Armeros Populationen (Barrados und Pica Palomera) nahe. Im allgemeinen dominieren in letzeren Populationen dunkle Farbtöne, während bei Exemplaren von Maubèrme und Liat intermediäre oder hellere Grundfarben vorherrschen. Estany de Güerri ist ein Vorkommen am äußersten Ende der Serra d'Armeros, und das einzige von dort untersuchte Exemplar scheint morphologisch den Tieren von Armenos nahezustehen.

Nur die Exemplare von Orlà unterscheiden sich deutlich von allen übrigen. Sie besitzen eine hellere Rückengrundfarbe mit deutlicher dunkler Fleckung. Pholidotisch unterscheiden sie sich von den übrigen Populationen an der Körperunterseite (vor allem ihre größeren Gularia und Ventralia) sowie durch kleinere Masseterica und Analia; auch haben sie relativ längere Hinterbeine. Die Unterschiede in den Extremitätenproportionen könnten in Zusammenhang mit der gut ausgebildeten Kletterfähigkeit und dem bewohnten Gesteinstyp gesehen werden. Die Populationen von Orlà sind entweder tatsächlich isoliert oder sie stehen mit Maubèrme Tieren über einen sehr schmalen Korridor in Verbindung.

ABSTRACT

Iberolacerta aranica (ARRIBAS, 1993) is a central Pyrenean endemism which exclusively inhabits the Maubèrme Massif and its spurs, between the Val d'Aràn (Spain) and the Ariège (France). The species has been located in twenty-five 1 km x 1 km U.T.M. grids; its potential range covers a maximum of thirty-six 1 km^2 U.T.M. grids. The lizard inhabits boulders, talus screes and stony grasslands with rock debris (mainly on paleozoic slates, schists, and limestones) in the alpine belt from 1940 m (1900 m) to 2668 m a.s.l.

All studied populations - with exception of the Orlà populations - seem to be more or less in contact. The populations differ in the background colour tones related to the type of rocks inhabited. Maubèrme specimens are very similar to Liat specimens and both agree well with the Serra d'Armeros populations (Barrados and Pica Palomera). In general, dark tones are predominant in these latter populations, whereas in Maubèrme and Liat, intermediate or lighter tones predominate. Estany de Güerri is located at the peripheral end of the Serra d'Armeros ridge and the only specimen studied from there appears closely related to those of Armeros.

The specimens of the Orlà population are clearly different from all others. They have a lighter background tone with conspicuous black dots. Pholidotic differences in respect to the remaining samples concern the lower side of the body (mainly their greater gularia and ventralia) and their smaller masseteric and anal plates; they also have relatively longer hindlimbs. The differences in proportional limb length could be linked to increased climbing capabilities related to the rock type inhabited. It is not absolutely clear wether the populations of Orlà are really isolated or communicate with Maubèrme populations along a very narrow strip.

KEY WORDS

Reptilia: Squamata: Sauria: Lacertidae: *Iberolacerta aranica*, morphology, diagnosis, geographic variation, distribution, taxonomy, biogeography, Aran valley, Iberian Peninsula, Pyrenees.

INTRODUCTION

Iberolacerta aranica (ARRIBAS, 1993) was described as *Lacerta bonnali aranica*, based on 45 males, 56 females and 26 juveniles from several localities of the Maubèrme Massif. The lizards were captured by the author from 1989 to 1993 in the framework of a study on the natural history of which was supposed then to be *L. monticola bonnali* LANTZ, 1927.

The first comparative insights on the external morphology of these individuals showed that they were different (stouter, shorter legged and headed, with bigger and fewer numbered scales and with a very particular disposition of plates in the temporal area) from other Pyrenean "*bonnali*-like" populations. Upon the recognition of *I. bonnali* as a full species (ARRIBAS 1993a) and the revision of its geographical variability, *L. bonnali aranica* was described (ARRIBAS 1993b). Also a third lizard species - *I. aurelioi* - was discovered in the Pyrenees: (ARRIBAS 1994a).

Evidence pointing towards the specific status of *I. aranica* appears very soon this same year, as karyotype differs notably both from *I. bonnali* and from *I. aurelioi* (ODIERNA et al. 1994, 1995, 1996). Also important osteological (ARRIBAS 1998a) and genetic (MAYER & ARRIBAS 1996) differences were discovered which indicate that *I. aranica* is not only a different species, but also that is fairly differentiated and the sister group of the clade composed by the other two Pyrenean taxa (ARRIBAS 1997a, 1999b). Notwithstanding this, before these discoveries, the species was treated and included inside *I. bonnali* in the first papers (ARRIBAS 1993a, 1994a, 1994b); thus, some photographs in these early papers show *I. aranica* instead of *I. bonnali*.

Iberolacerta aranica has been studied in detail for its external morphology (ARRIBAS 1993b), osteology (ARRIBAS 1998a), karyology (ODIERNA et al. 1994, 1995, 1996, in press) and allozyme differentiation (MAYER & ARRIBAS 1996). Its geographic distribution and habitat are described in ARRIBAS (1997b). All these aspects were reviewed in ARRIBAS (1997a).

The aim of this report is to present the results of exhaustive field prospection and to give a detailed analysis of the geographic variation and a final diagnosis of the species.

Table 1: Records of *Iberolacerta aranica*, grouped according to UTM grids (see also figure 1).
Tab. 1: Nachweise von *Iberolacerta aranica* nach UTM-Rastern gruppiert (siehe auch Abb. 1).

CH23	Coll de Barradós (= Coret de Varradòs) (2000 m) (Lérida) (ARRIBAS 1993b, 1994a)
	Coll dera Ansa Caudera (2300 m) (Lérida) (this paper)
	Serra d'Armeros Tuc des Armeros (2000-2516 m) (Lérida) (ARRIBAS 1993b, 1994a, 1994b)
	Upper parts of the Riu Unyola (1978-2400 m) (Lérida) (this paper)
	Estanhons de Baish (2300 m) (Lérida) (this paper)
	Cabana des Calhaus (1900 m) (Lérida) (this paper)
	Tuc de Crabes (southern slopes) (2023-2328 m) (Lérida) (this paper)
CH24	Estany de Liat (2130 m) (Lérida) (VIVES BALMAÑA 1990; ARRIBAS 1993b, 1994a)
	Tuc Crabera (2000-2630 m) (Lérida-Ariège) (ARRIBAS 1994a)
	Tuc dera Pica (2034 m) (Lérida-Ariège) (ARRIBAS 1993b, 1994a)
	Tuc Blanc deth Portilhon (2300 m) (Lérida) (this paper)
	Port de Tartareu (2000-2200 m) (Lérida) (this paper)
	Tuc de Maubèrme (2000-2668 m) (Lérida) (ARRIBAS 1993b, 1994a)
	Lac de Bentaillou (2300 m) (Ariège) (CROCHET obs.)
	Estahn Nere de Güerri (2200-2300 m) (Lérida) (this paper)
(?)	"Canejan, en zona alpina" (Canejan, in alpine heights) (Estación Biológica de Doñana Collection - Sevilla, J. CASTROVIEJO leg.)
CH33	Ribera del Port d'Orlà (2000-2318 m) (Lérida) (ARRIBAS 1993b, 1994a)
	Coma d'Orlà-Port d'Orlà (2000-2318 m) (Lérida-Ariège) (ARRIBAS 1993b, 1994a)
	Port d'Urets (2000-2512 m) (Lérida) (ARRIBAS 1993b, 1994a)
CH34	Malh de Bolard (= Mall de Bulard) (2000-2749 m) (Lérida-Ariège) (this paper)
Other localities	The Montvallier locality (BERTRAND & COCHET 1992) (which should correspond to *I. aranica*) also referred to in ARRIBAS (1993b, 1994a) probably corresponds to an erroneous identification (ARRIBAS 1997a). "Sierra de Guarbes" references (ARRIBAS 1993b, 1994a, 1994b) refer to a small section only (the Serra de Pica Palomera) in the westernmost part of the Sierra de Guarbes.

MATERIALS AND METHODS

Field prospection

From 1989 until 2000, a largely alpine area covering 70 U.T.M. (Universal Transverse Mercator) squares (each 10 km x 10 km in size) was prospected along all the Pyrenean range, from Pico de Arlás in the west as far as the Puigmal Massif in the east. *Iberolacerta aranica* has been localized only in 4 U.T.M. squares (fig. 1). A list of the localities is provided in ARRIBAS (1997a) and in table 1.

English meaning of Catalan, Castilian, Aragonese, Occitane or French geographic terms: Coll, port = pass; Estany, llac, = lake; Ribera, vall = valley; Pic, pica, soum, mahl, mall, tuc, tuca = peak, summit; Circ, circo = cirque.

Specimens and characters studied

In total, 240 specimens (81 males, 132 females, 27 juveniles) were studied. The specimens are stored in the Collection OSCAR ARRIBAS (OA).

Biometry: Snout-vent length (SVL); forelimb length (FLL); hindlimb length (HLL) (both from the anterior 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). For AS see "transformation of measurements into ratios" below.

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

Pholidosis (counts): Supraciliar 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 rigth (r) and left (l) side; lamellae underneath 4th toe (LAM); circumanalia (CIRCA).

Scale contact: Frequencies of rostral-internasal (=frontonasal) (ROST-INT), supranasal-loreal (SN-LOR), and postocular-parietal (POST-PAR) scale contacts. Frequencies of SN-LOR and POST-PAR scale contacts were counted on both sides of the specimens under study (n' = 2n).

Measurements were transformed into the ratios: FLL*100/SVL; HLL*100/SVL; PL*100/PW; DM*100/PAL; DT*100/PAL; AL*100/AW; 100*√(AL*AW)/SVL (coded as AS/SVL).

Metric and meristic characters were log-transformed, and ratios arcsine square-root transformed.

Statistical procedures

Statistical analyses performed in the present study are basically the same as in ARRIBAS (1996a, 1997b and 1999a).

Univariate analyses: Descriptive statistics (mean, range and standard deviation) were calculated for all meristic characters and ratios.

ANOVA / ANCOVA calculations were done only among the two main samples: Barrados (including the samples of the Serra d'Armeros, Liat, and Maubèrme areas which presumably form a continuous) and Orlà (in the peak regions of the Forcall Valley) presumably forming an isolate or almost an extreme of the main species area.

As SVL was statistically different between sexes ($T_{209} = 4.82$, $p < 0.0001$), all calculations were done separately for males and females (SOKAL & ROHLF 1969). ANCOVA was used for comparisons of dimorphism in body measuremens, and ANOVA for scalation characters. The frequencies of contact among plates were compared by Chi-square tests.

Multivariate analyses: MANOVA and Canonical Variate Analysis (CVA) were done for representation of the global differences among populations and isolated individuals.

Dating and terminology of the Pyrenean Pleistocene events follow the system used for the Alps. Even assuming some discrepancy between these two mountain ranges in dating the last glacial maximum and evaluating the eco-geographic conditions (see discussion), far reaching parallelism between the phenomena is assumed (see CALVET 1997 for a discussion on the history of the Pyrenean glacial chronology).

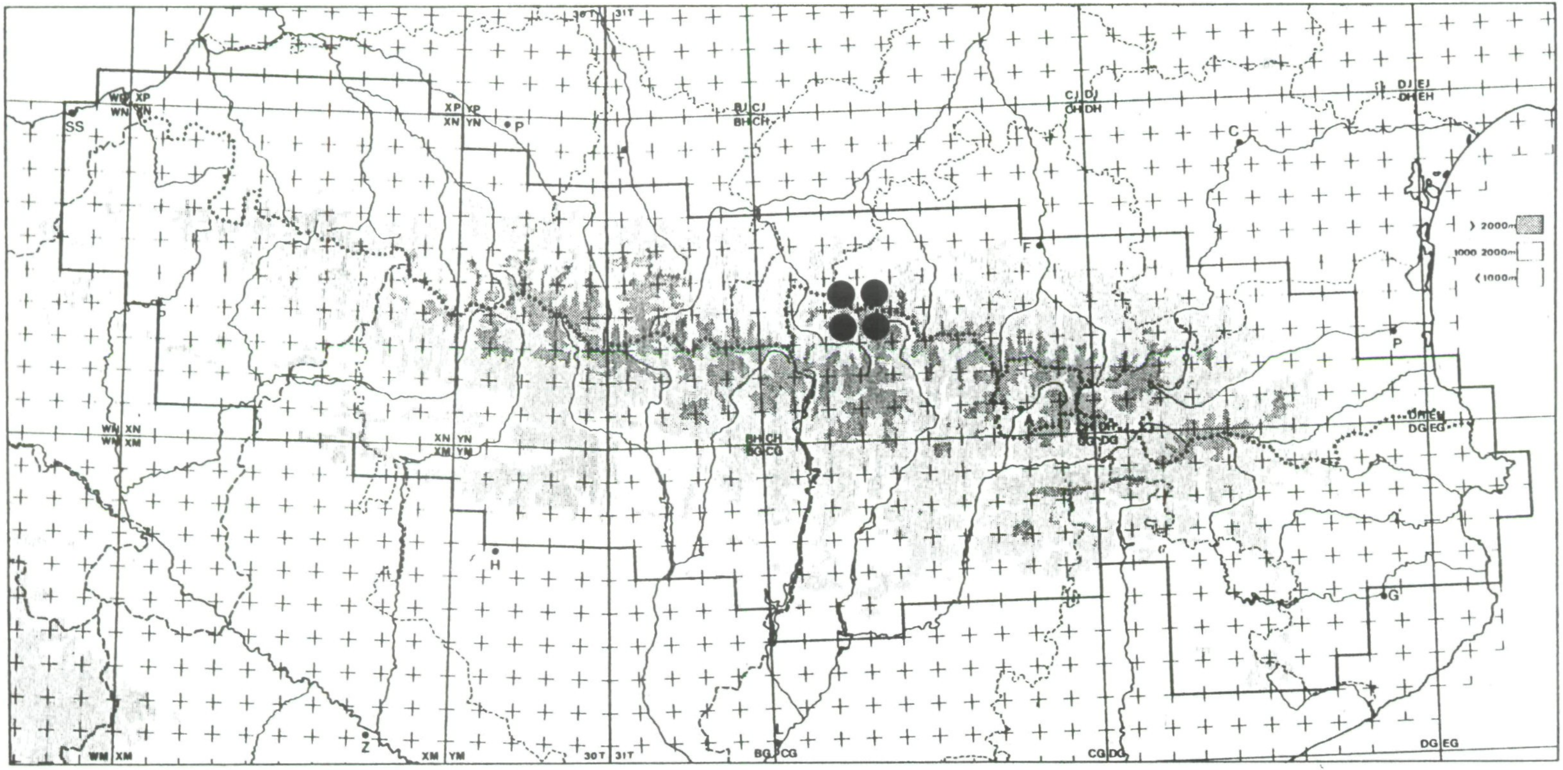


Fig. 1: U.T.M. grid map (grid size 10 km x 10 km) of the Pyrenees. Dots indicate grids in which *Iberolacerta aranica* (ARRIBAS, 1993) was found.

Abb. 1: U.T.M. Rasterkarte (Rastergröße 10 km x 10 km) der Pyrenäen. Die dunklen Punkte bezeichnen die Raster mit Vorkommen von *Iberolacerta aranica* (ARRIBAS, 1993).

RESULTS

Distribution

Iberolacerta aranica is a central-Pyrenean endemism. It exclusively inhabits the Maubèrme Massif and its spurs, between Val d'Aràn (Aran Valley) and Ariège.

Iberolacerta aranica is common or locally abundant within its tiny range. It has been located to date in twenty-five 1 km x 1 km U.T.M. grids and its potential range, after a precise survey, covers a maximum of 36 U.T.M. grids. Nearly 90% of its range lie within the Spanish territory (Val d'Aràn, Catalonia) and the rest in France (Ariège).

The nucleus of its distribution is the Tuc de Maubèrme. From here, it spreads towards NW along the Spanish-French border to Tuc de Crabèra (2630 m a.s.l.) and towards the south, passing along the Estany de Liat cirque as far as the Serra de Armeros and Serra de Pica Palomera axis, from where the species reaches the Coll de Barrados (type locality). The westernmost known locality in this axis is Estany Negre de Güerri (Es Estanhons area). The southern limit of the species passes by the Coll de Barrados not going below 1900 m in the Unhola river valley, where the species descends as far as Cabana des Calhaus. From here, the species occurs in a northeasterly direction, towards Arriu des Calhaus as far as the surroundings of Lac de Montoliu. To the east, along an unprecise line, even a discontinuity, it reappears in the Mahl de Bolard and on the left side of the Ribera d'Orlà valley (Port d'Orlà). The eastern limit of the species lies somewhere between Port d'Orlà and Tuc de Mill, where the species is already missing (see ARRIBAS 1997a, 1999a). The fault which passes through Trauc de Lesca (Port d'Esca) with its geological material discordance may constitute its natural limit on this narrow crest (see ARRIBAS 1999a: 174).

Within this range, the lizard's distribution is localized and discontinuous. It inhabits boulders, talus screes, or stony grasslands with rock debris (mainly slates, schists and limestones, all dating back to the Paleozoic age, see discussion).

Thoroughly sympatric, and occasionally syntopic with *Zootoca vivipara* (JACQUIN, 1787) in the stony grassland areas. It may also be found occasionally next to *Podarcis muralis* (LAURENTI, 1768) in the lower and upper altitudinal boundaries respectively of both species, in the zone between 1900 m (lower limit of *I. aranica*) and 2160 m (highest registered *P. muralis* in this area).

Altitudinally, *I. aranica* is a typical inhabitant of the Alpine belt, with all its characteristics (see ARRIBAS & MARTINEZ-RICA 1997; ARRIBAS 1997a), however, in some places of its range it is difficult to distinguish between the true alpine and the deforested subalpine grasslands used for pasture. The species has definitely been found from 1940 m (possibly 1900 m) to 2668 m (very close to the summit of the Tuc de Maubèrme which is 2880 m).

Today, the natural lower limit of the Alpine belt in this area is towards 2100-2350 m (CARRERAS et al. 1996) although it has been considerably lowered by the destruction of the forest due to trees being felled, fires and grazing (for instance, the upper part of Unhola valley was burnt down in the first half of the 20th century to deprive wolves of their habitat). Locally, *I. aranica* reaches lower heights, even slightly below than 2000 m but we cannot ascertain if it is a result of the anthropogenic destruction of forests or reflects local climatic or substrate conditions such as high oceanity or natural corridors of the cold wind from the valley, and the frequent presence of fog, which can lower the natural forest limits locally.

Iberolacerta aranica is strictly protected and classified as "endangered" in the Spanish National Catalogue of Endangered Species due to its extremely small range. The inhabited areas present easy access in several sites, with notable summer overfrequentation and traffic of vehicles even off the field paths. The ease of access and the acquaintance of some locations could favour the illegal gathering of specimens and the general degradation of some zones. On the other hand, the extremely tiny world wide range of *I. aranica* is threatened in two sites by projects for ski resorts. One of them, on the French side, in the Haut Biros; and the other, in the Val d'Aràn, that would cover the upper parts of the Barradós valley, affecting the type locality and approximately a sixth of the species' total range. Moreover, the greatest ski-resort in the Pyrenees (Baqueira-Beret) is very near its range and expands each year, being now at the limit of the species' range. Also, climatic changes might cause it to become extinct, due to the specialized habitat and the lower height (and therefore lesser "buffer" capacity in the face of the change of the belts of vegetation) of the mountain tops in the region. In fact *I. aranica* is certainly the rarest lizard in mainland Europe. Reserves need to be designated for the protection of the habitat of this species and in order to avoid the development of projects that threaten these areas. It precarious situation and tiny range suggest its inclusion in the category "Critically Endangered".

Sexual dimorphism

As both sexes differ significatively in SVL ($T_{209,1}$ = - 4.82, $p < 0.0001$) being females greater than males, ANCOVA was run with the biometric characters using SVL as a covariate.

The species is statistically significantly dimorphic in all biometric characters. All these dimorphic measurements are comparatively greater in males than in females: FLL ($F_{208,1} = 37.39$, $p < 0.0001$), HLL ($F_{208,1} = 47.45$, $p < 0.0001$), PL ($F_{208,1} = 93.80$, $p < 0.0001$), PW ($F_{208,1} = 101.53$, $p < 0.0001$), PAL ($F_{208,1} = 135.31$, $p < 0.0001$), DM ($F_{208,1} = 90.49$, $p < 0.0001$), DT ($F_{208,1} = 25.05$, $p < 0.0001$), and AW ($F_{208,1} = 53.54$, $p < 0.0001$). The unique character greater in females is AL ($F_{208,1} = 6.84$, $p = 0.0089$). Thus, males have proportionally greater limbs and heads than females, as is usual in the lacertids.

Scalation characters were compared by means of ANOVA. Only VENT ($F_{208,1} = 342.48$, $p < 0.0001$), GUL ($F_{208,1} = 5.68$, $p = 0.0171$), FEMr ($F_{208,1} = 8.75$, $p = 0.0031$) and FEMl ($F_{208,1} = 9.17$, $p = 0.0025$) show significant differences, the first two being greater in females, and FEM greater in males.

The ratios behave very similar to the ANCOVA results on the raw measurements: FLL/SVL ($F_{208,1} = 63.74$, $p < 0.0001$), HLL/SVL ($F_{208,1} = 75.39$, $p < 0.0001$), DM/PAL ($F_{208,1} = 23.27$, $p < 0.0001$) are highly significant and AS/SVL ($F_{208,1} = 3.97$, $p = 0.0462$) is significantly different between sexes and greater in males while AL/AW ($F_{208,1} = 66.00$, $p < 0.0001$) is significantly greater in females. DT/PAL ($F_{208,1} = 0.47$, $p = 0.4933$) and PL/PW ($F_{208,1} = 1.44$, $p = 0.2245$) are not different between sexes.

Presence and absence of contact between the pairs of scales considered do not show significant differences between sexes: POST-PAR ($\chi^2_2 = 2.34$, $p = 0.31$, NS), SN-LOR ($\chi^2_2 = 0.52$, $p = 0.77$, NS), ROST-INT contact was present in all specimens.

Colour pattern. Presence of blue dots in the outermost ventral scale rows is rare and probably atavistic, as in *I. bonnali* (LANTZ, 1927). It seems to be more frequent in males, however not significantly ($\chi^2_1 = 0.20$, $p = 0.65$, with Yates' continuity correction factor, NS; 2 cases out of 77 males and one out of 131 females studied). Specimens bearing blue ocelli could be-underrepresented in the alcohol-preserved material studied.

The degree of dark pigmentation on the ventral side shows significant differences between sexes ($\chi^2_3 = 38.87$, $p = 4.3 * 10^{-7}$) in that males are more pigmented than females: Males (32.9 % in all six ventral rows; 22.8 % in the outermost four rows; 24.1 % in the outermost two rows, 20.3 % completely unpigmented), females (9.1% in all the six ventral rows; 12 % in the outermost four; 15 % in the outermost two rows, 62 % completely unpigmented).

Geographic variation in males

Several partial analyses were run to compare single specimens and poorly represented samples with the main populations.

* ANOVA results. Descriptive statistics from biometric indexes and scalation characters of the samples are shown in table 2.

Armeros (Barrados, Liat and Maubèrme) specimens differ from those of Orlà in several scalation characters: GUL ($F_{77,1} = 6.01$; $p = 0.0165$); VENT ($F_{77,1} = 20.72$; $p < 0.0001$) and CIRCA ($F_{77,1} = 36.90$; $p < 0.0001$). All these counts except CIRCA are higher in Orlà specimens.

Concerning the biometric measurements, Orlà specimens have longer hindlimbs (HLL/SVL: ANOVA, $F_{77,1} = 6.29$; $p = 0.0142$; HLL in ANCOVA with SVL as a covariate, $F_{76,1} = 5.62$; $p = 0.0203$), smaller

Table 2: *Iberolacerta aranica* (ARRIBAS, 1993). Males (for parameters see text). Descriptive statistics (mean, standard deviation, minimum, maximum) and ANOVA results of the two samples studied. For Postocular-Parietal and Supranasal-Loreal scale contacts, both sides are considered. For intersample comparison of the Chi-square results, see text.

Tab. 2: *Iberolacerta aranica* (ARRIBAS, 1993). Männchen (Parameter siehe Text). Deskriptive Statistiken (Mittelwert, Standardabweichung, Minimum, Maximum) und ANOVA Ergebnisse der beiden untersuchten Stichproben. Die Schuppenkontakte von Postoculare-Parietale und Supranasale-Loreale wurden beidseitig registriert. Zum Stichprobenvergleich der Chi^2 Ergebnisse siehe Text.

Sample	BA - Barrados (n = 62)				MA - Maubèrme (n = 6)				OR - Orlà (n = 13)				ANOVA		
Populations Clustered	(Pica Palomera + Armeros)				(Maubèrme + Liat)								Significance of differences Signifikanz der Unterschiede		
Parameter	Mean	Stdv.	Min.	Max.	Mean	Stdv.	Min.	Max.	Mean	Stdv.	Min.	Max.	*F*	*p*	BA - OR
SVL	53.79	3.42	45.4	61.8	55.65	2.82	51.8	59.64	51.75	4.95	45.65	60.12	0.51	0.479	
GRS-r	3.51	1.75	0	7	2.5	1.04	1	4	2.92	1.18	1	4	0.63	0.43	
GRS-l	3.59	1.69	0	8	3	1.78	1	6	3.15	2.19	0	8	0.23	0.6355	
GUL	20.8	1.34	18	24	21	1.67	19	23	22.15	1.99	19	25	6.01	0.0165	*
COLL	10.7	0.85	9	13	11.66	1.03	10	13	11	0.57	10	12	0.17	0.6847	
DORS	39.17	1.6	36	43	40.66	3.38	37	46	38.46	1.71	36	42	1.29	0.2591	
VENT	24.61	0.96	22	27	24.83	0.75	24	26	26	0.81	25	27	20.72	0	***
FEM-r	12.45	1.06	10	15	12.5	1.37	11	14	12.15	1.51	10	15	0	0.99	
FEM-l	12.72	1.04	11	16	12.83	0.98	12	14	12.23	1.23	10	15	1.79	0.1905	
LAM	26.17	1.92	19	30	26.66	1.86	24	29	26.69	1.11	25	29	0.3	0.5869	
CIRCA	7.91	0.6	7	9	8.16	1.17	7	10	7	1.41	6	10	36.9	0	***
FLL*100/SVL	33.02	0.018	28.31	37.88	45.13	0.02	39.32	50.45	33.71	0.02	30.5	38.52	0.66	0.4179	
HLL*100/SVL	45.13	0.02	39.32	50.45	46.51	0.03	43.58	53.47	47.23	0.02	43.51	50.03	6.29	0.0142	*
PL*100/PW	197.4	0.13	183.1	283.63	197.63	0.04	193.51	204.31	200.18	0.094	183.04	213.37	0.85	0.3606	
DM*100/PAL	46.66	0.05	34.84	57.5	45.5	0.04	39.71	51.52	42.61	0.1	35.84	49.27	5.99	0.0167	*
DT*100/PAL	45.21	0.05	35.29	60.29	47.39	0.03	43.26	53.88	43.78	0.12	31.56	50.49	0.16	0.6908	
AL*100/AW	58.79	0.06	40.42	71.94	60.93	0.06	50	66.66	66.97	0.08	55.73	84.71	12.73	0.0006	***
AS/SVL	619.23	0.42	525.62	702.45	646.25	0.53	659.7	707.16	586.73	0.42	536.87	687.41	5.06	0.0273	*
Scale contacts	No/Nein	Yes/Ja							No/Nein	Yes/Ja					
ROST-INT	0	67	n=68						0	11					
POST-PAR	45	91	n'=136						3	19	n'=22				
SN-LOR	7	129							1	21					

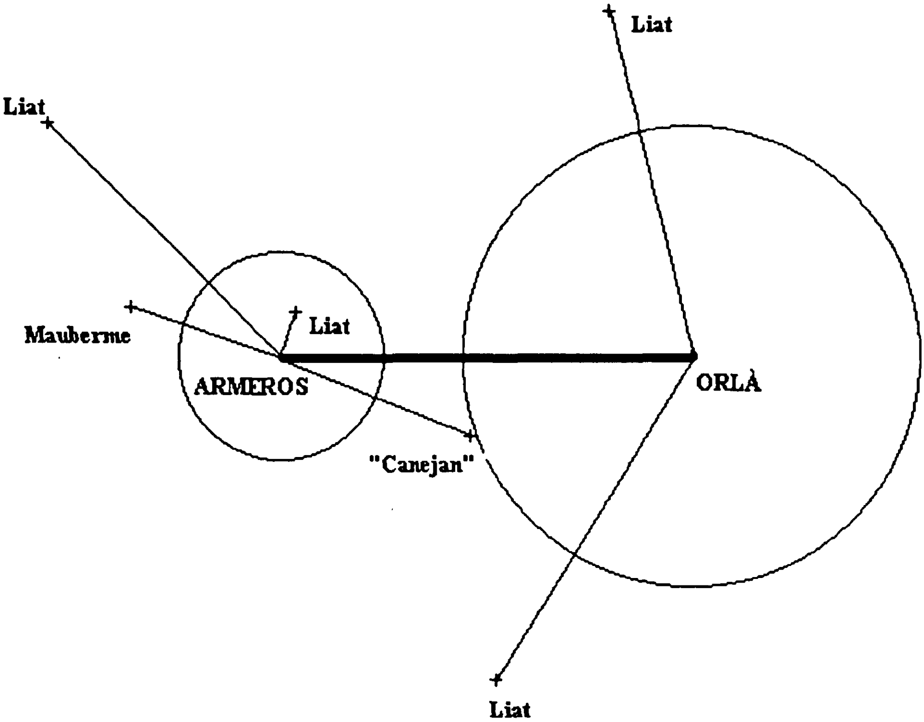


Fig. 2: Bidimensional representation of the population centroids of all *Iberolacerta aranica* male samples studied. The first axis explains 100 % of the interpopulation variability. The relative relationships are shown by the Minimum Spanning Tree (MST) superimposed.

Abb. 2: Zweidimensionale Darstellung der Zentroide aller untersuchten Stichproben männlicher *Iberolacerta aranica*. Die erste Achse erklärt 100 % der Variabilität zwischen den Populationen. Die Beziehungen werden durch den darübergelegten Minimum Spanning Tree (MST) veranschaulicht.

masseteric plates (DM/PAL: ANOVA: $F_{77,1}$= 5.99; p = 0.0167; DM in ANCOVA with SVL as covariate, $F_{76,1}$= 7.86; p = 0.0064); and proportionately smaller anal plates (AL/AW: ANOVA, $F_{77,1}$= 12.73; p = 0.0006) due to their narrowness (AW: ANCOVA with SVL as covariate, $F_{76,1}$= 20.86; $p < 0.0001$; whereas the length of the plate is equivalent, AL: ANCOVA $F_{76,1}$= 0.09; p = 0.7678, NS). Also AS/SVL appears significantly different (ANOVA, $F_{77,1}$= 5.06; p = 0.0273).

None of the scale-contact characters differ significantly between the two populations studied: In all specimens from the two main samples, rostral and internasal plates are in wide contact. In both samples, contact between postocular and pariertal scales (each side of the head treated independently) is observed almost twice as much than separation (χ^2_1= 2.53 with Yates' continuity correction factor, p = 0.1117, NS). Supranasal and loreal scales are almost always in contact (χ^2_1 = 0.16, p = 0.6857, NS).

Blue ocelli are very rare or exceptional in both samples (one specimen in Armeros and in Orlà among 68 and 11 individuals respectively) (χ^2_1 = 0.21 with Yates' continuity correction factor, p = 0.6467, NS). Dark pigmentation in the ventral side does not differ significantly among the studied populations (χ^2_3 = 3.93, p = 0.2683, NS).

* Canonical Variate Analysis of the male samples (n = 82 specimens) and 17 characters (counts and indexes) shows the relative relationships among the two

main samples and the isolated specimens from other localities. MANOVA shows the existence of significant differences among them ($F_{119 \& 388}$ = 1.5439, p = 0.0011; Wilks' Lambda = 0.0799). As only two great populations are involved in the analysis, there is only one significant axis (eigenvalue of 4.68) which explains 100 % of the intersample variability. The second one has an eigenvalue of $0.891 * 10^{-6}$.

The bidimensional representation of the two first axes (fig. 2) explains all variability and separates the Armeros sample in the negative part of the axis from the Orlà sample in the positive part. Both samples are separated by a Mahalanobis' distance of $D^2 = 9.35$ and their confidence radia (95 %) are 0.776 and 1.71, respectively. The Orlà sample is characterized by high values of VENT (0.482), GUL (0.301), AL/AW (0.364) and HLL/SVL (0.338) and lower of CIRCA (-0.379) and DM/PAL (-0.283). Armeros is characterized by contrary values in the above characters.

* The discriminant analysis derived from the first canonical axis misclassifies only two specimens (one in each sample) from a total of 76 (2.63 %).

Concerning the isolated specimens, two out of the Estany de Liat material are closer to the Armeros sample than to the Orlà sample (D^2 = 13.1 versus 33.1, and D^2 = 24.8 versus 33.5), whereas the other two are slightly more similar to the Orlà sample than to the Armeros sample (D^2 = 58.3 versus 64 and D^2 = 31.0 versus 31.5). The Maubèrme specimen appears clearly closer to the Armeros sample (D^2 = 21.5 versus 37.8). The "Canejan" specimen is slighty closer to Armeros than to Orlà (D^2 = 10.7 versus 11.4).

Geographic variation in females

*ANOVA results. Descriptive statistics of biometric indexes and scalation characters from all samples are shown in table 3.

Armeros females differ from those from Orlà in several scalation characters: GUL ($F_{130,1}$= 10.61; p = 0.0014); VENT ($F_{130,1}$= 7.88; p = 0.0058); FEMl ($F_{130,1}$= 5.45; p = 0.0211). FEMr is not far from being significant: $F_{130,1}$= 5.45; p = 0.0705). The values of all these counts except FEM are higher in Orlà specimens.

Concerning the biometric characters, Orlà females have longer hindlimbs (the index does not reveal the difference HLL/SVL: ANOVA, $F_{130,1}$= 0.92; p = 0.3384 while HLL in ANCOVA using SVL as a covariate does, $F_{129,1}$= 6.28; p = 0.0134), smaller masseteric plates (DM/ PAL: ANOVA: $F_{130,1}$= 13.42; p = 0.0004; also in ANCOVA with SVL as covariate, $F_{129,1}$= 13.39; p = 0.0004); and proportionately smaller anal plates (AL/AV: ANOVA, $F_{130,1}$= 9.01; p = 0.0032) due to their narrowness (AW: ANCOVA with SVL as covariate, $F_{129,1}$= 14.51; p = 0.0002; whereas the length of the plate is equivalent, AL: ANCOVA $F_{129,1}$= 0.08; p = 0.7724, NS). Evidently, also AS/SVL appears significantly different, $F_{130,1}$= 5.32; p = 0.0226). Differences are thus, the same as in the male analysis.

None of the scale-contact characters differs significantly between the two populations studied: In all specimens of the two main samples, rostral and internasal plates are in wide contact. In both samples, contact between postocular and parietal scales (each side of the head treated independently) is observed almost three times more than separation (χ^2_1= 1.14 with Yates' continuity correction factor, p = 0.2748, NS). Supranasal and loreal scales are usually in contact (χ^2_1 = 0.06 with Yates' continuity correction factor, p = 0.8068, NS).

Blue ocelli are even rarer than in males, almost exceptional (only one female from Orlà shows them) (χ^2_1 = 0.46 with Yates' continuity correction factor, p = 0.4968, NS). The presence of dark ventral punctuation differs significantly among the studied populations (χ^2_3 = 8.53, p = 0.0362) with relatively fewer specimens being totally unpigmented and a relatively higher degree of Orlà specimens being marked in the outermost scale rows only.

* Canonical Variate analysis of the female samples (n = 134 specimens) reveals significant differences among the studied specimens (MANOVA: $F_{153 \& 881}$ = 1.3771, p = 0.0168; Wilks' Lambda = 0.1797). As in the male analysis, there is only one significant axis (eigenvalue 2.41) which explains 100 % of the intersample variability (fig. 3). The eigenvalue of the second axis is only $0.512 * 10^{-7}$.

The bidimensional representation of the two first axes (fig. 3) explains all of the

Table 3: *Iberolacerta aranica* (ARRIBAS, 1993). Females (for parameters see text). Descriptive statistics (mean, standard deviation, minimum, maximum) and ANOVA results of the two samples studied. For Postocular-Parietal and Supranasal-Loreal scale contacts, both sides are considered. For intersample comparison of the Chi-square results, see text.

Tab. 3: *Iberolacerta aranica* (ARRIBAS, 1993). Weibchen (Parameter siehe Text). Deskriptive Statistiken (Mittelwert, Standardabweichung, Minimum, Maximum) und ANOVA Ergebnisse der beiden untersuchten Stichproben. Die Schuppenkontakte von Postoculare-Parietale und Supranasale-Loreale wurden beidseitig registriert. Zum Stichprobenvergleich der Chi^2 Ergebnisse siehe Text.

Sample	BA - Barrados (n = 96)				MA - Mauberme (n = 7)				OR - Orlà (n = 29)				ANOVA		
Populations Clustered	(Pica Palomera + Armeros)				(Maubèrme + Liat)								Significance of differences Signifikanz der Unterschiede		
Parameter	Mean	Stdv.	Min.	Max.	Mean	Stdv.	Min.	Max.	Mean	Stdv.	Min.	Max.	*F*	*p*	BA - OR
SVL	56.25	4.09	46	66.88	56.73	5.15	48.04	63.73	57.81	4.58	45.99	66.02	2.9	0.0908	
GRS-r	3.96	2.09	0	9	3.71	1.6	2	6	3.2	2.3	0	8	2.79	0.097	
GRS-l	3.71	2.03	0	9	3.85	1.95	1	6	2.96	2.17	0	8	3.11	0.0799	
GUL	21.22	1.49	18	25	22.14	1.06	21	24	22.37	1.91	19	27	10.61	0.0014	***
COLL	10.52	1.38	7	14	10.71	1.49	9	13	10.96	1.05	9	13	2.42	0.1224	
DORS	39.43	2.7	35	48	39.71	2.28	37	42	38.75	1.72	36	42	1.77	0.1857	
VENT	27.39	0.99	25	30	27.57	0.97	26	29	28	1.03	27	30	7.88	0.0058	***
FEM-r	12.05	1.15	10	15	12.42	0.78	11	13	11.65	0.97	10	14	3.32	0.0705	
FEM-l	12.25	1.28	9	16	12.85	1.06	12	15	11.68	1	10	14	5.45	0.0211	*
LAM	25.97	1.2	24	29	26.28	1.38	25	28	27	1.46	24	30	14.01	0.0003	***
CIRCA	7.73	1.07	6	11	8.14	1.06	6	9	7.82	1.13	6	10	0.07	0.7919	
FLL*100/SVL	31.06	0.018	26.98	38.28	30.88	0.014	28.84	32.43	30.57	0.021	22.36	34.13	1.41	0.237	
HLL*100/SVL	42.21	0.03	36.91	52.41	41.92	0.025	37.35	44.37	42.74	0.017	39.9	46.8	0.92	0.3384	
PL*100/PW	195.86	0.063	182.14	212.72	196.2	0.068	184.5	205.08	198.22	0.068	187.88	217.94	2.93	0.0893	
DM*100/PAL	43.6	0.05	25	55	36.15	0.07	21.6	44.2	38.59	0.05	21.48	48.03	13.42	0.0004	***
DT*100/PAL	45.28	0.07	0	61.53	42.79	0.05	38.29	51.73	43.44	0.05	34.14	52.95	1.5	0.2228	
AL*100/AW	67.82	0.076	45.71	84.43	69.53	0.057	62	78.1	72.68	0.07	51.8	85.86	9.01	0.0032	***
AS/SVL	610.51	0.46	479.03	771.49	589.23	0.47	527.44	666.15	587.23	0.37	515.08	672.83	5.32	0.0226	*
Scale contacts	No/Nein	Yes/Ja							No/Nein	Yes/Ja					
ROST-INT	0	103	n=103						0	29	n=29				
POST-PAR	48	158	n'=206						9	49	n'=58				
SN-LOR	10	196							3	55					

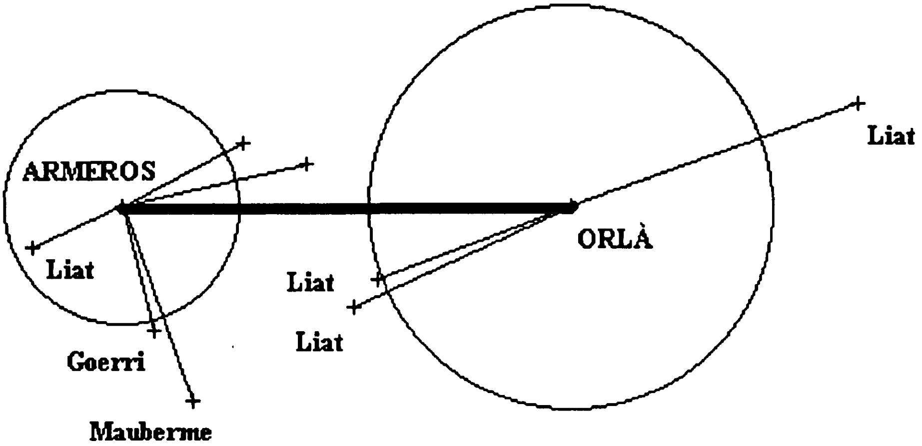


Fig. 3: Bidimensional representation of the population centroids of all *Iberolacerta aranica* female samples studied. The first axis explains 100 % of the interpopulation variability.
The relative relationships are shown by the Minimum Spanning Tree (MST) superimposed.

Abb. 3: Zweidimensionale Darstellung der Zentroide aller untersuchten Stichproben männlicher *Iberolacerta aranica*. Die erste Achse erklärt 100 % der Variabilität zwischen den Populationen.
Die Beziehungen werden durch den darübergelegten Minimum Spanning Tree (MST) veranschaulicht.

variability and separates the Armeros sample in the negative part of the axis from the Orlà sample in the positive part. Both samples are separated by a Mahalanobis distance of D^2 = 4.81 and their confidence radia (95 %) are 0.587 and 1.05, respectively. The Orlà sample is characterized by high values of LAM (0.376), GUL (0.322), VENT (0.283), AL/AW (0.291) and lower of DM/PAL (-0.402) and AS/SVL (-0.250). Armeros is characterized by the contrary values of the above characters.

* The discriminant analysis derived from the first canonical axis misclassifies 16 specimens from a total of 126 (12.7 %). 13 Armeros specimens out of 96 are classified as belonging to Orlà and, on the other hand, 3 Orlà specimens out of 30 as belonging to the Armeros sample.

From the isolated specimens, the Maubèrme specimen is more similar to Armeros than to Orlà (D^2 = 14.2 versus 17.4). Four of the Liat specimens are slightly closer to the Armeros sample (D^2 = 7.26 versus 8.52, D^2 = 21.0 versus 21.5; D^2 = 12.0 versus 18.4 and D^2 = 14.4 versus 16.5), one is equidistant (D^2 = 21.2) and one is more similar to Orlà (D^2 = 30.0 versus 40.9); the Estany de Güerri specimen is more similar to Armeros than to Orlà (D^2 = 29.6 versus 35.3).

DISCUSSION

Hypothesis on the speciation and scenario of the evolution of *I. aranica*

During the Pliocene, the north Pyrenean piedmont was partly occupied by an Atlantic transgression south of the Garonne river from Médoc to the Landes region, penetrating as far as Agen (RITTER 1988) and a Mediterranean transgression in the eastern Pyrenees (Empordà and Rosselló)

(AGUSTÍ & ANTÓN 1997). The mean level of the oceans rose 60 m (AGUSTÍ & ANTÓN 1997).

The vegetation of the Pliocenic Pyrenees was characterized by the presence of tropical plant groups, even in the mountains, together with representatives of modern groups (*Pinus*, *Cedrus*, *Araucaria*). A location close to the Pyrenees (Gurp in Gironde, SW France) presents a Tiglian or pre-Tiglian flora with *Sequoia*, *Taxodium*, *Carya* and *Pinus* (*Haploxylon*), and another one in the eastern Pyrenees (Ille-sur-le Têt) shows *Sciadopitys*, *Sequoia*, *Taxodium*, *Carya*, *Pinus* (*Haploxylon*) and *Tsuga* (SAUVAGE 1965). In Catalonia (southeast of the Pyrenees) the climate in the Pliocene begins with a tropical aspect and evolves towards a temperate-mild climate, similar to the current Mediterranean one in the lower areas, but wetter, with regular precipitations - near 1000 mm, with a few markedly dry seasons - and a mean temperature of about 18-20° C (thus rather more humid than cold), very similar to the current climate in the Canary Islands, Madeira, Azores, SE North America, the northern Caucasus (Colchid and Hyrcanian areas) and the mountains of Tibet (ALIMEN 1967; PONS 1969; SANZ DE SIRIA 1993; ARROYO-GARCÍA 1994). The start of the Ice Age eliminated this dominant tropical flora, remains of which are presently endemic orophyte genera as *Ramonda*, *Iris*, *Saxifraga*, *Petrocoptis*, and *Borderea*, separated from other lowland species also at the end of Tertiary, and constituents of the so-called Arcto-Tertiary flora. The transition from a subtropical climate regime to a drier and glacial one caused a change from an episodic climate regime (with dry and wet seasons) to a temperate one with thermically differenciated periods which reached their extreme in the glacial and interglacial periods (RITTER 1988). This transition proceeded from the Miocene, where the decrease in moisture was mainly marked by two events: 3,2 M.Y. ago, progressive installation of summer dryness and resulting forest clearing; and 2,3 M.Y. ago, first dry period with development of steppe (see SUC 1983). Despite the climatic dropping during the Upper Pliocene, a temperate climate, with not very cold winters was maintained until 1.8 M.Y. ago (AGUSTÍ & ANTÓN 1997).

One can suppose that the ancestor of all lizards of the *Iberolacerta* group was an inhabitant of a mesic habitat, within a mild, even subtropical climate, that characterized large parts of southern Europe, especially the Pyrenees in the early Pliocene. The progressive climatic deterioration should have separated the various lizard populations and restricted them to the mountain piedmonts. The ancestor of *I. horvathi* (MÉHELY, 1904) probably was the first form that was separated from the above mentioned ancestral stock at the beginning of the Plio-Pleistocene climatic deterioration. This isolation could have been caused by factors like a change from a tropical to a more mesic climate and vegetation along with increasing aridity during the Miocene and/or the evolution of the Rhone valley, which - during the Pliocene - was filled by a Mediterranean transgression - "Mer Rhodanienne" - up to the area which now occupies Lyon, and lakes as the so-called "Lac Bressan" (EMBERGER 1968). The ancestor of *I. horvathi* probably retreated eastward to the piedmont of the Alps (perhaps with a very different distribution than today).

On the other hand, the ancestors of the Ibero-Pyrenean group could have been dispersed along the piedmont of the Pyrenean-Cantabric axis mountains. One must bear in mind the presence of a marine transgression during this period (RITTER 1988). Other authors advocate for the presence of marshy areas and lakes in this zone (see e. g., AUBOIN et al. 1981), and support the view that the north Pyrenean piedmond was a more or less straight continuation of the Cantabrian coast, giving the north-Pyrenean slopes (almost as far as the Aran Valley, see above) very mild and oceanic conditions similar to those of the Spanish Cantabrian region. The living conditions of these populations (perhaps still not adapted to the mountains) may be mirrored by the Galician lowland populations of *I. monticola* (see GALÁN 1992, 1999). The isolation between the two main mountain ranges of this Cantabro-Pyrenean axis could have promoted the speciation of the ancestors of the two main groups of these lizards: the Pyrenean (subgenus *Pyrenesaura* ARRIBAS, 1999) and the Iberian clade (subgenus *Iberolacerta* ARRIBAS, 1997 s. str.).

Speciation of *I. aranica* took place at the beginning of the Plio-Pleistocenic climatic deterioration: the end of the genetic flux between *I. aranica* and the common ancestor of *I. aurelioi* (ARRIBAS, 1994) and *I. bonnali* (LANTZ, 1927) - CA[bon+aur] hereinafter - can be traced back to almost 2 million years (D_{NEI} = 0.38, correcting previous data from ARRIBAS 1997a etc. See comments about this and the calibration of the genetic distances in ARRIBAS 1997a, 1998b, 1999a, 1999b, 2000). It should be noted that calibration of divergence times based on genetic distances is very problematic in that genetic distances only indicate the relative divergence from the common ancestor but do not say when this divergence occurred. However, data vary dramatically depending upon which time-divergence equivalent one chooses. In our case, the equivalent used fits acceptably well with the Pleistocenic events that are very probably closely linked with the speciation process in the group. The start of the speciation process could be related to the first cold snaps of the beginning of the Lower Pleistocene (about 2 M.Y. b. p.). No signs of cold were detected in the Pyrenees (for instance in the Lannemezan formation) until the beginning of the Donau age (ALIMEN 1967) which in fact is only a little later than the estimated date of the end of the genetic flux. During this phase considerable fluvial action was registered indicating a humid and perhaps moderately cold climate (ALIMEN 1967).

A certain stock of ancestral populations may have given origin to *I. aranica* on the northern slopes and another one to CA[bon+aur] on the southern slopes of the Pyrenees. During the Tertiary period, the area of the Pyrenees was represented by a plateau of 2,000 - 2,500 m altitude from which summits were rising. This primitive structure was fractured, malformed, carved, and eroded and remains of this plateau can still be found in the Central Pyrenees in a number of places e.g., in the highlands of the Maubèrme massif (RITTER 1988) which offers good living conditions for *I. aranica.* Also, the watershed which surrounds the upper Garonne river was already formed in the Tertiary period (GARCÍA SAINZ 1947; MIANES 1955; MARTÍ-RIBA 1989; VENTURA-ROCA 1989).

During the Lower Pleistocene (comparable to Günz in the Alpine glacial terminology), huge glacier apparatuses developed in the Pyrenees, the young valleys of which were less deep than today.

The climate of the interglacial periods was warm and dry, similar to the present southern pre-Pyrenean climate of the Aquitanian plains. Lauraceous and deciduous forests still of Pliocenic affinity developed (GAUSSEN 1926) including species like *Fagus*, arboreal *Rhododendron*, *Vaccinium* (which ruled out the fir and broadleaved mixed forests during Mindel), *Pinus*, *Carya*, *Pterocarya* (which disappeared in Mindel), *Quercus*, *Alnus*, *Fagus*, and *Betula* in the northern piedmont. Also *Taxus*, *Cupressus*, *Quercus* and the sclerophyllic species *Olea* and *Vitis* (which indicate a hot and dry climate) were registered (RITTER 1988; MORZADEC-KERFOURN 1969).

During Mindel, *Pinus* (ca. 80% of findings), *Abies*, *Quercus*, *Corylus*, *Picea*, and *Alnus* were present. Also Ericaceae and Compositae appeared (almost 6%) in the northern piedmont (ALIMEN 1965; MORZADEC-KERFOURN 1969).

Little is known on the influence of the sea transgressions into the Pyrenean piedmont during the Pliocene and the first interglacial periods. These sea transgressions seem to have been of decreasing intensity in the course of the Pleistocene (ZEUNER 1945; GOMEZ-TABANERA 1980; CHALINE 1982). A shallow sea and later in the interglacial and interstadial periods, the existence of marshy areas or even a shallow sea extending as far as the Adour valley in the south and close to the Garonne river in the east has been postulated (see the map in RITTER 1988). Also the presence of typical coastal birds (e.g., *Stercorarius parasiticus*, *Larus adouinii*, *Larus fuscus*, *Rissa trydactila* and *Alle alle*) in the central Pyrenean paleontological beds (mainly Würmian) (CLOT & MOURER-CHAUVIRE 1984, 1986) testify at least the presence of great swampy areas or lakes in the Pyrenean piedmont. The presence of these lakes (produced by the obstruction of valleys by the frontal moraines) or swamps or shallow seas during warm periods of the Pleistocene, probably implies some considerable climatic asymmetry between the northern (wet and mild) and the southern slopes (warm and drier) of the Pyrenees.

The characteristics (geology, climate and vegetation) of the Pyrenees during the Pleistocene scenario, from Mindel-Riss until the present interglacial period, were already explained in ARRIBAS (1999a, 2000). *Iberolacerta aranica* suffered the same episodic climatic constraints as the other two Pyrenean mountain lizards (ARRIBAS 1997, 1999, 2000) presumably resulting in very limited expansion during interglacial and interstadial periods and retreats to refuge areas during the colder phases. Their presumed range being reduced to a massif on the northern slope of the Pyrenees, it has probably benefited from a slightly milder and more humid climate than on the southern slopes, more continental and drier.

During the last glacial maximum (in the Pyrenees 45,000 to 60,000 years ago; BORDONAU 1992; BORDONAU et al. 1992; SERRAT 1992; MONTSERRAT-MARTÍ 1992; JALUT ET AL. 1992), *I. aranica* could have found "in situ" refuge at the southern slopes of the Maubèrme Massif which extends beyond the surrounding glacial valleys. The existence of permafrost is not really a limiting factor for these mountain lizards (in fact several of the areas occupied today show solifluction due to the periodic freezing and melting of the upper layers of the soil).

The Maubèrme Massif including surrounding areas is a northern exclave of the main axis of the Pyrenees and the only area in the northern part that has south-facing slopes. During several Pleistocene periods it was isolated from the main chain by huge glaciers (Garonne glacier - 66 km, Riberot glacier in the Mont Vallier Massif - 18 km [BARRERE 1963; TAILLEFER 1969; RITTER 1988] and glacial transfluence passes: the Garonne glacier passed over the Pla de Beret and connected with the glacier in the Noguera Pallaresa valley. It has also been suggested that part of the upper Noguera Pallaresa valley was captured by the Garonne glacier).

During this Pyrenean glacial maximum, the pollen spectra of the Barbazan area in the Garonne valley piedmont show the presence of an open landscape dominated by Poaceae, *Artemisia*, Chenopodiaceae, *Helianthemum*, and Compositae with small refugial forests composed of *Pinus* (dominant), *Fagus*, *Picea*, *Abies* and, as relics, also *Quercus* and *Corylus*. The presence of glaciers in the piedmont or in the vicinity of the Garonne valley is certified almost until 21,000 years ago (Barbazan site - JALUT et al. 1992). From 26,000 to 24,000 y.b.p., the process of thawing was accelerated in the Garonne terminal glacial basins. This was paralleled by the increasing development of a climate of the dry type in the Pyrenees (ANDRIEU et al. 1988). Pollen deposits from prior to this event revealed that montane trees (*Fagus*, *Picea* and *Abies*) persisted only in refuges near the still glaciated Garonne axis. The pollen spectra from 26,000 y.b.p. show the development of herbaceous formations with Poaceae, Chenopodiaceae, also with heliophilous taxa associated, as well as several Compositae, *Helianthemum* and *Ephedra*. These communities suggest a low precipitation regime.

From 26,000 until 16-15,000 y.b.p., the glaciers retreated progressively. The lacustrine and fluvioglacial deposits of middle altitudes indicate that the mountains were largely deglaciated, ice being restricted to favourable locations only. On the northern slope, the deglaciation of the higher parts was virtually completed during the dry period of about 15,000 y.b.p. (also coincident with the glacial maximum in the Alps) testified by the increased aridification process in this area (ANDRIEU et al. 1988).

At these times, *I. aranica* spread in a very limited fashion to its current area. During the Holocenic climatic optimum (having its maximum at about 7,000 to 6,500 y.b.p. and its end at about 3,000 y.b.p. - see FRENZEL et al. 1992), the altitudinal limit of the forest was about 100 to 300 m higher than at present reducing the presumed area of *I. aranica* more than today (OZENDA 1985; VEITH & HÖFNER 1993; THEURILLAT 1995; TESSIER et al. 1995).

There is some evidence that there was secondary contact between *I. aranica* and *I. aurelioi* in the past. The particularly small size of the hemipenis in *I. aurelioi* has been interpreted as a mechanism of prezygotic isolation by character displacement (as can be also the case in the reappearance of a fully developed ventral coloration in *I. aurelioi*). This mechanism of isolation might originate from a past phase of sympatry (or parapatry) of these species along a narrow crest zone between the Tuc de Mill massif and Montroig, probably during the last interglacial (or whatever climatically favorable event after the speciation of *I. aurelioi*, see ARRIBAS 1999a).

Hypotheses on the former sympatry among the Pyrenean species of *Iberolacerta* cannot be refuted or verified since at present *I. aranica* does not seem to inhabit any other massif than Maubèrme and its spurs, which presumably have been its postglacial refuge and a place near the the refuge inhabited by this species at least during the last cold pulsation of the Pleistocene.

Although the Maubèrme Massif has been less studied than other nearby massifs, it does not seem to be a primary or secondary centre of speciation in the Pyrenees (even if *I. aranica* originated from the Maubèrme Massif, i. e., "in situ") (ARRIBAS 1999c). As far as known, Maubèrme lacks other endemisms equivalent to these lizards by their vagility (e.g., terrestrial molluscs, alpine Caraboidea, etc..).

The question arises whether *I. aranica* might have existed in places other than the Maubèrme Massif. Is it obvious that *I. aurelioi* and *I. bonnali* are sister species recently derived from a common ancestor which presently share the territory of the Central Pyrenees in a discontinuous manner within allopatric distribution areas while *I. aranica* appears isolated in a massif outside the Pyrenean axis. Could *I. aranica* have withdrawn from the Pyrenean axis because of the presence of CA[bon+aur]? If so, the population of the primitive ancestor of the three Pyrenean species should have been separated into two groups at the beginning of the Pleistocene (about two M. Y. b. p., based on Nei distances). One of these subpopulations gave origin to *I. aranica*, presumably in or near the area inhabited today; and the other, to CA[bon+aur] (developing allopatry due to historical factors and competition since then). If contact between *I. aranica* and CA[bon+aur] had been established secondarily, one could expect that they would appear in sympatry somewhere now, but this is not the case. If this secondary contact had occurred when the lizards had already occupied different niches (e.g., CA[bon+aur] more closely linked to rocks than *I. aranica*) they could co-occur in more or less wide sympatry today, as is known from *Darevskia* species in the Caucasus.

Moreover, one should bear in mind that, when *I. aurelioi* and *I. bonnali* were still conspecific (CA[bon+aur] until some 450.000 years ago, if the calculated Nei distance of 0.09 is close to reality. D_{NEI} = 0.09 corrects data reported in previous papers of ARRIBAS), *I. aranica* was already a taxon of its own the speciation of which dated back to almost one and a half million years at that time.

Nothing speaks against the coexistence of *I. aranica* and CA[bon+aur] in the past, and the presence of the former in other places of the Pyrenean mountain range. However, the lack of evidence of a wide sympatry in the past favours the hypothesis of a more or less "in situ" evolution of *I. aranica* in this north-Pyrenean massif.

Thus, we can conclude that today, *I. aranica* lives in or next to its Upper Pleistocene refuge area, but there is no final evidence to suggest that the species originated (=speciation took place) there.

In the places where the present border lines of the ranges of the three Pyrenean species approach closest, these limits obviously strongly coincide with that of the strongest Pleistocenic glaciation. This emphasizes the importance of these climatically induced physical barriers for the speciation of this species group through the course of the last two million years.

Relationships between populations

Apart from the Orlà population, all other populations of *I. aranica* seem to be more or less in contact and seem to form a network of metapopulations only connected from time to time by pioneer specimens (mainly hatchlings and subadults). However, the migration rate among localities should be sufficiently low in order to permit local differentiations in the lizards' background colour tones. The black dust originating from the meteorization of Paleozoic slates impregnates the scales; even recently shedded specimens are light coloured in limestone and darker on schists and slate substratum.

- Maubèrme and Liat specimens are very similar, and resemble those of the Serra d'Armeros populations (Barrados and Pica Palomera). In the latter localities there are both light (mainly devonian limestones) and very dark (silurian and devonian slates and schists) substrata and the colour of specimens varies within a wide spectrum.

However, in general, dark tones are predominant, whereas in Maubèrme and Liat, intermediate or lighter tones predominate. Estany de Güerri is located at the westernmost end of the species' distribution in the Serra d'Armeros ridge: the only specimen of this location studied appears closely related to the Armeros specimens by its Mahalanobis distance and overall habitus.

- The individuals of the Orlà population are the only specimens which are clearly differenciated from the main group. They live in big blocks of Cambrio-Ordovician sericite-schists and quartzites, largely equivalent to the substratum of the neighboring *I. aurelioi* populations (about 15 km when following the mountain crests). Orlà specimens differ from all others in having a lighter background tone and conspicuous black dots, in pholidotic peculiarities (in the lower side of the body) and, which is more interesting, in biometry (possibly related to their better climbing abilities). The populations of Orlà seem to be isolated from the rest, but the hiatus is narrow and there is one pathway along which communication with the Maubèrme populations could be possible: a narrow and not very suitable strip along the crest of the Serra deth Mahl de Bolard. The species seems to be absent from areas south of the Orlà area (where its presence was *a priori* supposed e.g., in the Tucs de Pedescauç-Closòs axis, the Sarrat de Cardigassos, and even the south facing slopes of the Serra deth Lastoar, very near to known populations) and in all places geographically intermediate between the Orlà region and the other populations of the species.

DIAGNOSIS AND SYNONYMY

Diagnosis of *Iberolacerta aranica*

Biometric and pholidotic key data of the specimens studied is summarized below (mean value in parentheses). See also the data of the two main samples in tables 2 (males) and 3 (females). Sexually dimorphic characters are indicated by an asterisk (*) and treated separately for both sexes.

Biometry. SVL (*): On the average, SVL is longer in females than in males (males: 53.84 mm; females: 56.62 mm). The difference is highly significant. The longest SVL in males was 61.8 mm and in females 66.88 mm. For other measurements see tables 2 and 3.

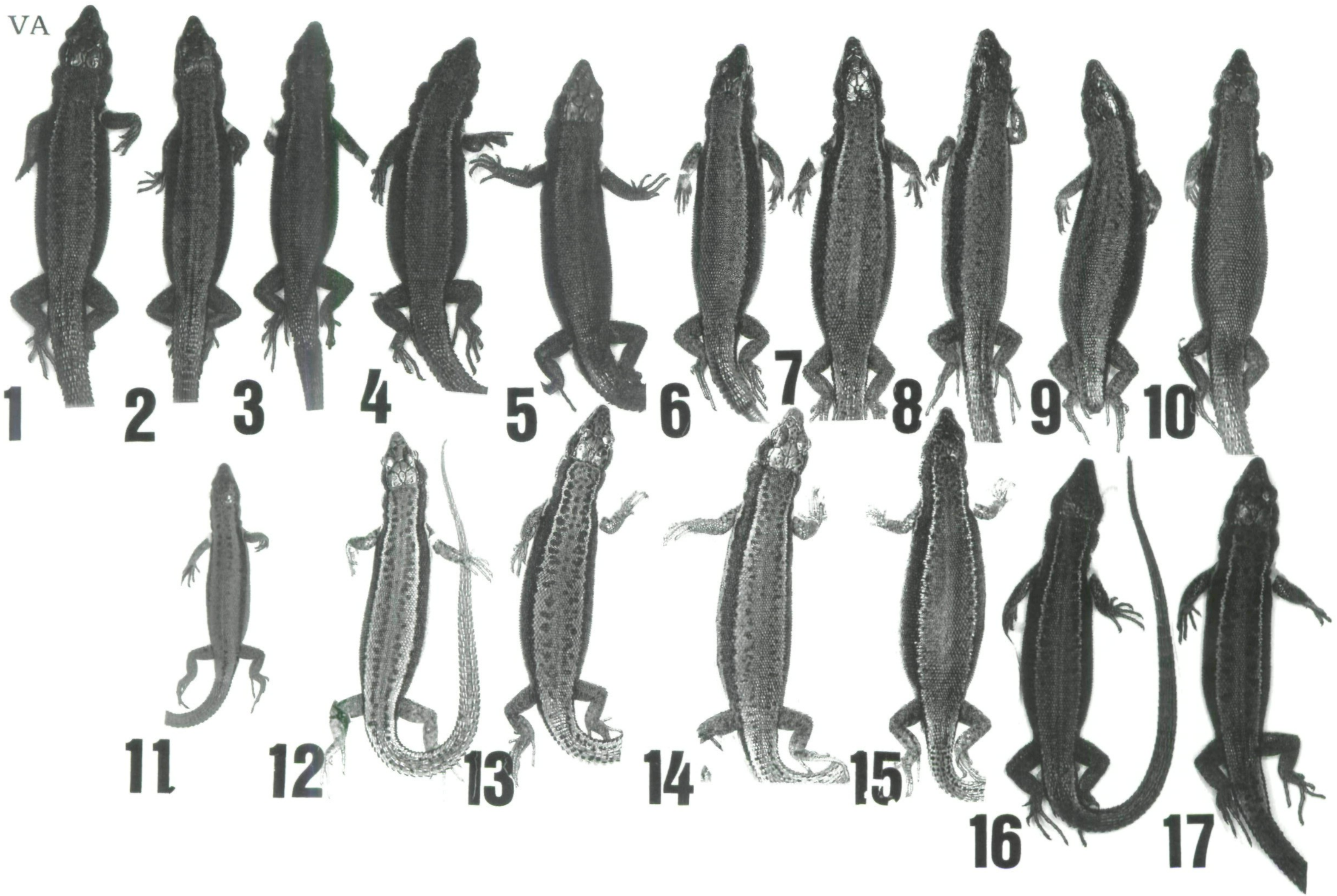
Forelimb length (*): 28.31% - 38.41% (33.13%) of SVL in the males, 22.36% - 38.28% (30.95%) in females. Hindlimb length (*):39.32% - 53.47% (45.50%) of SVL in males, 36.91% - 52.41% (42.31%) in females. Pileus length: 1.82 - 2.83 (1.96) times its width. Masseteric scale (*): 34.84% - 57.5% (46.03 %) of the parietal scale length in males, 21.48% - 55% (42.1%) in females. Tympanic plate: 0% - 61.53% (44.96%) of the parietal scale length. Anal plate length (*): 40.42% - 84.71% (60.11%) of its width in males, 45.71% - 85.86% (68.98%) in females.

Pholidosis. Supraciliar granula: rigth side 0 - 9 (3.63), left side 0 - 9 (3.54); gularia (*): 18 - 25 (20.98) in males, 18 - 27 (21.53) in females; Collaria: 7 - 14 (10.69); dorsalia: 35 - 48 (39.27); transversal rows of ventral scales (*): 22 - 27 (24.82) in males, 25 - 30 (27.53) in females; femoral pores: right side 10 - 15 (12.45), left side 10 - 16 (12.67); lamellae under fourth digit of toe: 19 - 30 (26.23); circumanal scales: 6 - 11 (7.76).

Rostral and internasal plates always in contact (100 % of studied specimens); postocular and parietal usually in contact (70.6% of specimens in both sides, 9% in one side only), supranasal and loreal also usually in contact (91.9% of specimens in both sides, 6.2% in one side only). Usually

Fig. 4 (opposite page): Dorsal pattern variability in *Iberolacerta aranica* (ARRIBAS, 1993).
Abb 4 (gegenüberliegende Seite): Variabilität der Rückenzeichnung bei *Iberolacerta aranica* (ARRIBAS, 1993).

1 - Vall d'Unyola (♂) CA 95081325, 2 - (♂) CA 95081324, 3 - (♂) CA 95081320,
4 - Coll de Barradós (Holotype) (♂) CA 92081007, 5 - (♂) CA 95082703, 6 - (♀) CA 94090003,
7 - (♀) CA 940628SN1, 8 - Vall d'Unyola (♀) CA 95081321, 9 - Coll de Barradós (♀) CA 940628SN2,
10 - (♀) CA 92091108, 11 - Port d'Orlà (♀) CA 98080702, 12 - (♀) CA 92091207, 13 - (♀) CA 92091204,
14 - (♀) CA 92091205, 15 - (♀) CA 95070110, 16 - (♂) CA 98080709, 17 - (♂) CA 99070707.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only one scale between the masseteric and tympanic plates (both well visible). The temporal disposition of these three structures is very peculiar and very similar to that in *Darevskia mixta* (MÉHÈLY, 1909) from the Caucasus. If a similar disposition appears in some *I. bonnali*, the intermediate scale is usually sensibly smaller than the masseteric and tympanic plates. Head scutellation anomalies (plates fused, broken or difform) are very frequent.

The temporal region of the species is represented in ARRIBAS (1993a: fig. b & c; 1993b: fig. 7; 1994b: fig. 1; 1997a).

Colour-pattern. Dorsum grayish-brown, more or less clear or dark according to the colour of the substratum inhabited, occasionally with a light olivaceous reflection, especially in recently shedded individuals. Some males present a malachite-green colour on top of the habitual tones of the dorsum (about 12%). Two dark paravertebral lines along the back (80% of males, 60% of females) (figures 4-7, 9-11).

Belly and breast without conspicuous pattern, usually of various tones of white, occasionally with bluish or greenish reflections (fig. 8). However, the anterior edges of the ventral scales frequently bear black spots, especially in males (90% of males, 30% of females). Blue dots can be found in the more external ventral plates of some males (about 10% of males, exceptionally also in females). The variability of the dorsal pattern of *I. aranica* is shown in figure 4.

Albinism. Unpigmented areas in the body skin were observed in two individuals. They bear small whitish or cream-coloured dots ("pie-balds", partial albinism). In one of the specimens a wide unpigmented band runs along the regenerated tail. Melanism was not observed. Animals which show very pale dorsal background colours and a faint dark pattern (concolor specimens) were found in Port d'Orlà. In fact, two degrees of this fading of the dark pattern were observed (homo and heterozygotes?).

Geographical variation in colour-pattern. The main variation refers to the dorsal background colour, which is clearly associated with colour of the substratum on which the lizards live. In populations which live on limestone rocks, the lizards are frequently very clear (Liat and some restricted areas of Serra d'Armeros) while they are very dark in populations which live on slates and schists (S^a de Armeros). Individuals which inhabit quartzite rocks (as in Port d'Orlà) are also fairly clear.

Ontogenic variation in coloration. Hatchlings (first calendar year). The dorsum is grayish or brownish-gray, usually uniform, with two dark costal bands. Occasionally, very fine paravertebral dark spotting is present. Belly white, with conspicuous dark spots at the anterior edge of the ventral scales, more clearly developed than in adults. Tail usually grayish, like the dorsum (S^a de Armeros, Coll de Barrados) or variable (gray and blue) (Orlà) (see fig. 12).

Figs. 5 - 8 (opposite page): *Iberolacerta aranica* (ARRIBAS, 1993).
Abb. 5 - 8 (gegenüberliegende Seite): *Iberolacerta aranica* (ARRIBAS, 1993).

Fig. 5: Male from Coll de Barrados, Serra d'Armeros (Val d'Aràn, Lleida, Spain). Note the few, big and granular scales in the dorsum, the greenish tinge in the dorsum and the presence of three big scales in the temporal area (masseteric, tympanic and intermediate wedge shaped scale).
Abb 5: Männchen, Coll de Barrados, Serra d'Armeros (Val d'Aràn, Lleida, Spanien). Man beachte die wenigen, großen körnigen Schuppen auf dem Rücken, die grünliche Rückenfärbung und die drei großen Schilde der Temporalregion (Massetericum, Tympanicum, intermediäres keilförmiges Schild).

Fig. 6: Female, Estany Negre de Güerri (Val d'Aràn, Lleida, Spain).
Note the stout habitus and the disposition of the temporal scales.
Abb. 6: Weibchen, Estany Negre de Güerri (Val d'Aràn, Lleida, Spanien).
Man beachte den gedrungenen Habitus und die Anordnung der Schilde der Temporalregion.

Fig. 7: Male, Tuc de Maubèrme (Val d'Aràn, Lleida, Spain). Same characteristics as in figure 5.
Abb. 7: Männchen, Tuc de Maubèrme (Val d'Aràn, Lleida, Spanien). Merkmalsausprägungen wie in Abb. 5.

Fig. 8: Male, Coll de Barrados (Val d'Aràn, Lleida, Spain). Ventral view. Note the white belly, the black spots and the presence (usually rare) of blue dots in the outermost ventral plates.
Abb. 8: Männchen, Coll de Barrados (Val d'Aràn, Lleida, Spanien). Ventralansicht. Man beachte die weiße Bauchseite, die schwarzen Flecken und die (selten vorkommenden) blauen Tupfen auf den äußersten Bauchschilden.

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The pattern of young specimens and subadults (third calendar year included) is very similar to the hatchling basic pattern. Any vivid tail colour present will be lost during the second calendar year. The relative size of the dark spots at the anterior edge of the ventral scales decreases progressively. Dorsally, the paravertebral rows of dots and dorsolateral [= supratemporal] stripes (the latter may be present in the anterior half of the body) develop progressively in the subadults (until their third calendar year).

For the pattern of the adults (fourth calendar year or later) see the above general description of the colour-pattern.

Osteology. Different from the other two Pyrenean species. In the skull, the anterodistal process of the postfrontal and the anteromedial process of the postorbitary are well developed. Postorbitary bone slightly longer than or subequal to the postfrontal. Length of the suture between postorbital and squamosal bones almost half the length of the bones. Premaxilla with seven teeth and a slender and subparallel processus nasalis (in some specimens widened, sublanceolate or even with two or three apexes). Number of maxillary teeth 14 - 17 (mean 15.41), of dentary teeth 16 - 20 (mean 18.58). Bicuspid teeth dominant.

Males have usually 26 presacral vertebrae, and females 27. The third vertebra is very frequently associated with a short bony rib. Sternal-xiphisternal formula (3+2). Sternal fontanelle oval or rounded. Clavicles open (marginated) and inter clavicle typically cruciform (ratio anterior / posterior branches 0.20 - 0.35, mean 0.26). Usually six short posterior dorsal ribs (a young male examined from Orlà, has five). First preautotomic caudal vertebrae with perpendicular processes only in their anterior part (type A sensu ARNOLD 1973, 1989). More detailed osteological data in ARRIBAS (1997a, 1998a).

Karyotype. Different from the two other Pyrenean species, both male and female specimens of *I. aranica* have identical numbers of chromosomes: metaphase with 10 biarmed and 16 acrocentric chromosomes, morphologically similar to those of *I. aurelioi*; meiocytes with 13 homologous pairs. Sex chromosomes are not discernible by conventional staining techniques which is also different from what is known from the other two *Pyrenesaura*. *Iberolacerta aranica* should posses a ZW sex-chromosome system of homomorphic and euchromatic sex-chromosomes. This is derived from the assumption that heterogamety (wether or not cytogenetically discernible) is present in all female lacertids (OLMO et al. 1990, 1993, 1995; ODIERNA et al. 1994).

NOR is present in a telomeric position in the long arm of the third chromosome pair (L-type of OLMO et al. 1990, 1993) as in the other *Pyrenesaura*.

The C-banding reveals intense centromeric bands in the uniarmed chromosomes and weak centromeric and pericentromeric bands in the biarmed. The centromeric bands are completely digested by Alu I, while the pericentromeric bands of the three first biarmed chromosomes, the subtelomeric band associated to the NOR and the intense pericentromeric band of the seventh pair (uniarmed) are resistant to this staining. Only this latter band reacted positive to the staining with DAPI.

Figs. 9 - 12 (opposite page): *Iberolacerta aranica* (ARRIBAS, 1993).
Abb. 9 - 12 (gegenüberliegende Seite): *Iberolacerta aranica* (ARRIBAS, 1993).

Fig. 9: Male, Port d'Orlà (Val d'Aràn, Lleida, Spain). Same characteristics as in figure 5.
Abb. 9: Männchen, Port d'Orlà (Val d'Aràn, Lleida, Spanien). Merkmalsausprägungen wie in Abb. 5..

Fig. 10: Gravid female, Port d'Orlà (Val d'Aràn, Lleida, Spain). There are two scales between the masseteric and tympanic scales. Note the heavily spotted dorsum.
Abb. 10: Trächtiges Weibchen, Port d'Orlà (Val d'Aràn, Lleida, Spanien). Exemplar mit zwei Schilden zwischen Massetericum und Tympanicum. Man beachte die starke Rückenfleckung.

Fig. 11: Gravid female, Port d'Orlà (Val d'Aràn, Lleida, Spain). This female is less spotted than that in figure 10 and represents the usual pattern in the population (see also figure 4).
Abb 11: Trächtiges Weibchen, Port d'Orlà (Val d'Aràn, Lleida, Spanien). Das Tier ist weniger gefleckt als jenes in Abb. 10 und repräsentiert den verbreitetsten Zeichnungstyp der Population (siehe auch Abb. 4).

Fig. 12: Hatchlings from two clutches, Port d'Orlà (Val d'Aràn, Lleida, Spain). Note the tail being of the same colour as dorsum. In this population there are also hatchlings with blue tails.
Abb. 12: Schlüpflinge aus zwei Gelegen, Port d'Orlà (Val d'Aràn, Lleida, Spanien). Man beachte die Farbgleichheit von Rücken und Schwanz. In dieser Population kommen aber auch blauschwänzige Jungtiere vor.

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There are no differences in the karyotypes of the two studied populations of *I. aranica* from Orlà and Armeros (ODIERNA et al. 1994, 1995, 1996, in press; ARRIBAS 1997a).

Allozyme data. *Iberolacerta aranica* differs from *I. aurelioi* in three alleles (AK, MDH-1 and GOT-1), and from *I. bonnali* in four alleles (AK, MDH-1, GOT-1 and PGM-2) (MAYER & ARRIBAS 1996).

Hemipenis. The overall hemipenial morphology is almost as in the other two Pyrenaean species. Contrary to *I. aurelioi*, which has small-sized hemipenes (and a rather narrow tail base in males) (ARRIBAS 1999a), *I. aranica* shares the "normal-sized" hemipenes with *I. bonnali*, but is easily distinguished from the latter because *I. aranica* lacks the enlarged lips in the sulcus spermaticus (see ARRIBAS 1999a, 2000).

The microornamentation found in this species is of spiny-like type (ARRIBAS 1993b), although we have observed also some clearly crown-shaped tubercles in one of the specimens studied (ARRIBAS 1997a). All above data refers to male specimens caught before the egg laying time.

Distribution. *Iberolacerta aranica* is a Central Pyrenean endemism which exclusively inhabits the Maubèrme Massif and its spurs, between the Val d'Aràn and the Ariège.

Type specimen. OA 92081007. Male. Coll de Barradós, Viella, Vall d'Aràn, Lleida province, Spain. Collected on 10-8-1992. 2300 m asl. (ARRIBAS 1993 b).

Synonymy

1993 *Lacerta bonnali aranica*, ARRIBAS, Herpetozoa (Wien) 6 (3/4): 135.

1997 *Lacerta aranica*, ARRIBAS, Distribución y biogeografía de los anfibios y reptiles en España y Portugal, Granada. Publ. Universidad de Granada (Granada): 213.

1997 *Archaeolacerta aranica*, ARRIBAS, Morfología, filogenia y biogeografía de las lagartijas de alta montaña de los Pirineos. Publ. Universidad Autónoma de Barcelona (Bellaterra): 3.

1997 *Iberolacerta aranica*, ARRIBAS, Morfología, filogenia y biogeografía de las lagartijas de alta montaña de los Pirineos. Publ. Universidad Autónoma de Barcelona (Bellaterra): 297.

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