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Taxonomic revision of the Iberian 'Archaeolacertae' III: Diagnosis, morphology, and geographic variation of *Iberolacerta bonnali* (LANTZ, 1927)
(Squamata: Sauria: Lacertidae)

Taxonomische Revision der iberischen 'Archaeolacerten' III: Diagnose, Morphologie und geographischen Variabilität von *Iberolacerta bonnali* (LANTZ, 1927)
(Squamata: Sauria: Lacertidae)

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KURZFASSUNG

Iberolacerta bonnali (LANTZ, 1927), ein Endemit der axialen Zentralpyrenäen, bewohnt die Gebirgsstöcke Arriel, Balaitous, Vignemale (oder Comachibosa), Panticosa, Monte Perdido, Punta Suelza, Posets, Maladeta, Ballibierna und die Gebirge des Sant Maurici-Aigüestortes Nationalparks (Besiberris, Muntanyó de Llacs, Peguera und Encantats) samt einer kleinen nördlichen Exklave in den Massiven von Neouvielle und Bigorre. Das Artareal umfaßt das Gebiet zwischen den Pässen von Portalé (im Westen) und Bonaigua (im Osten). Die Eidechse lebt in der alpinen Region, gewöhnlich in Höhen oberhalb 2000 m (zwischen 1700 m und 3062 m) und kommt dort in kleinen bis mittelgroßen, gewöhnlich eng begrenzten Populationen auf unterschiedlichem Gestein (Kalk, Schiefer, seltener und weniger dicht auf Gneis und Granit) und häufig in der Nähe von Seen und Bächen vor.

Die Stichproben von Posets und Maladeta erscheinen als morphologisch zentral bzw. intermediär. An sie lassen sich die übrigen Stichproben aus verschiedenen Richtungen anschließen. Unter den gut repräsentierten Stichproben scheinen die von Bigorre und Ballibierna denen von Maladeta, Monte Perdido und Posets am nächsten zu stehen. Unter den weniger gut vertretenen Samples nähern sich die von Neouvielle und Arriel an Bigorre an. Punta Suelza Exemplare sind intermediär und nahezu nicht von M. Perdido und Posets Tieren unterscheidbar. Die Stichproben Maladeta, Besiberri, Aigüestortes und Ballibierna sind alle gleichermaßen gegenüber den intermediären Populationen differenziert. Insgesamt entsteht der Eindruck, daß die U-förmige Gebirgsformation von Posets, Maladeta und Ballibierna von einer Gruppe "zentraler Populationen" bewohnt ist, von denen sich drei Stichproben morphologisch am stärksten abheben: Bigorre im Norden, M. Perdido westlich und Aigüestortes im Osten. Dieses Modell positioniert einen möglichen Refugialstandort der Art im Würm auf die Südhänge jenes U-förmigen Gebirgskomplexes, doch bleibt die Möglichkeit anderer kleiner Refugialräume, etwa im Gebiet von Aigüestortes. Das Szenario der Ausbreitung aus diesen Refugialräumen am Ende der letzten Vereisung wird dargestellt, eine das Gesamtmaterial einbeziehende vollständige Diagnose von *L. bonnali* wird gegeben.

ABSTRACT

Iberolacerta bonnali (LANTZ, 1927) is an endemic of the axial Central Pyrenees present in the massifs of Arriel, Balaitous, Vignemale (or Comachibosa), Panticosa, Monte Perdido, Punta Suelza, Posets, Maladeta, Ballibierna, and the mountains of the Sant Maurici-Aigüestortes National Park (Besiberris, Muntanyó de Llacs, Peguera, and Encantats massifs) including a small exclave northwards (massifs of Neouvielle and Bigorre). The distribution area is embraced by two passes, Portalé (in the west) and Bonaigua (in the east). The lizard inhabits the Pyrenean alpine region, usually above 2.000 m (1.700 m to 3.062 m) in small or medium sized, usually local colonies on all kind of substratum (limestone, slates, schists, rarer and less dense on gneiss and granites) frequently in the vicinity of lakes and streams.

The morphologically centralmost samples seem to be those of Posets and Maladeta. In different ways the remaining populations appear morphologically connected to these intermediate samples. The well represented samples of Bigorre and Ballibierna seem more closely related to those of Maladeta, Monte Perdido, and Posets. From the less represented samples, Neouvielle and Arriel approach Bigorre. Punta Suelza specimens are intermediate and hardly to be distinguished from those of M. Perdido and Posets. The samples from Maladeta, Besiberri, Aigüestortes, and Ballibierna are more or less equally differentiated. The overall impression is that the"U-shaped" mountain formation of Posets, Maladeta, and Ballibierna, is occupied by a group of "central populations", from which the three most extreme samples are most different: Bigorre in the north, M. Perdido in the west, and Aigüestortes in the east. This model suggests a probable site of the würmian refuge of these species: the southern slopes of this "U-shaped" mountain area, however, the presence of other small refuges (e. g., in the Aigüestortes area) cannot be excluded. From these areas *I. bonnali* expanded at the end of the last glaciation. This scenario and a complete diagnosis of the species are given.

KEY WORDS

Reptilia: Squamata: Sauria: Lacertidae: *Iberolacerta bonnali*, morphology, diagnosis, geographic variation, distribution, taxonomy, biogeography, Iberian Peninsula, Pyrenees

INTRODUCTION

In 1927, *Iberolacerta bonnali* was described by LANTZ under the name *Lacerta* (*Podarcis*) *monticola bonnali*, based on a series of seventeen specimens captured by MARCEL (count of) BONNAL at Lac Bleu in the French Massif of Bigorre in 1922. The taxonomic position of this largely unknown lizard was subject to several changes (see synonymy) varying from a subspecies of *I. monticola* (BOULENGER, 1905) to one of *Podarcis muralis* (LAURENTI, 1768) until it was recognized as a full species by ARRIBAS (1993a) and PEREZ-MELLADO et al. (1993) independently from each other.

In the same year, ARRIBAS (1993b) published a revision of the geographic variability of the species, reporting it for the first time from the Pyrenean massifs of La Maladeta and Posets, and from numerous new locations in other massifs for which only single records were available (compare LANTZ 1927; BECK 1943; MARTINEZ-RICA 1976, 1977, 1983). In the above paper (ARRIBAS 1993b) the subspecies *L. bonnali aranica* was described from the mountains north of the Aran Valley. Later, this taxon (now *I. aranica*) turned out to be specifically different from *I. bonnali* on osteological, genetic, and karyological grounds (ARRIBAS 1997, 1998a; ODIERNA et al. 1995, in press a, b; MAYER & ARRIBAS 1996). At last, a third species was discovered in the Pyrenees, *I. aurelioi* (ARRIBAS 1994 a). Finally, these Pyrenean 'archaeolacertids' were assigned to the new genus *Iberolacerta* (ARRIBAS 1997) based on their morphological features.

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

Unfortunately, lack of knowledge or confusion with then still undescribed Pyrenean taxa led to the fact that the first 'modern' papers on this species (e. g., ARRIBAS 1993a, 1994a, b; PEREZ-MELLADO et al. 1993) provided incomplete diagnoses of the true *I. bonnali* or commingled *I. bonnali* and *I. aranica*. This situation was maintained even in a recent publication (PEREZ-MELLADO 1998) were data from three Pyrenean species were combined.

The present paper presents the results of comprehensive field prospection and detailed studies on the geographic variation of *I. bonnali*, aiming towards a diagnosis covering the entire range of the species.

MATERIALS AND METHODS

Field prospection

From 1989 until 1998, 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. A list of these localities is provided in ARRIBAS (1997) and in table 1. *Iberolacerta bonnali* - for a long period known only from five U.T.M. squares - has been localized now in 26 U.T.M. squares (fig. 1).

English meaning of Catalan, Castilian, Aragonese, Occitane and French geographic terms used: coll, port, puerto, brecha = pass; estany, llac, ibón = lake; ribera, vall = valley; pic, pica, soum, alto, bony = peak, summit; circ, circo = cirque; peña = mountain.

Specimens and characters studied

In total, 358 specimens (175 males, and 183 females) were studied.

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).

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): Supraciliar granulae (GRS) of right (r) and left (l) side; gularia along a median line (GUL);

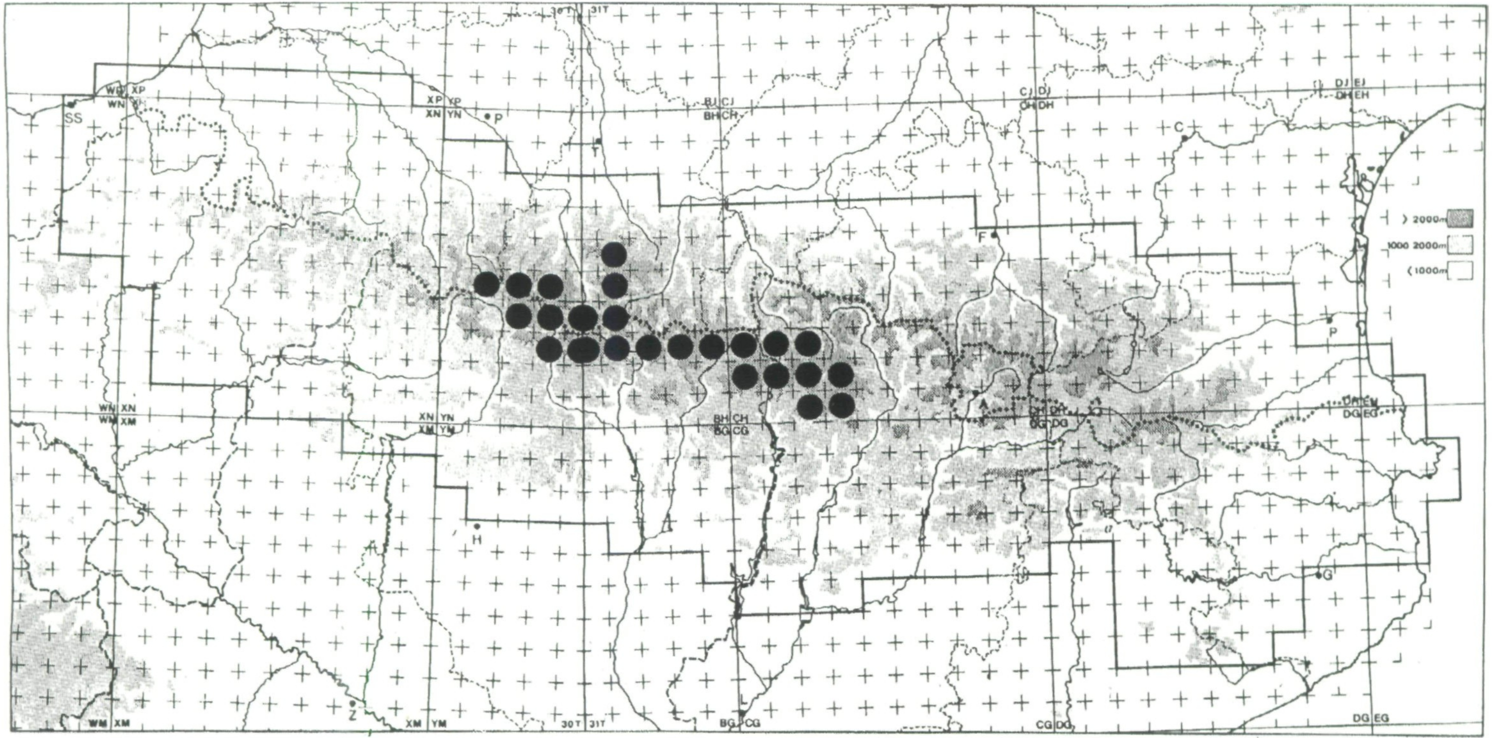

Fig. 1: U.T.M. grid map (grid size 10 km x 10 km) of the Pyrenees. Dots indicate grids in which *Iberolacerta bonnali* (LANTZ, 1927) was found.

Abb. 1: U.T.M. Rasterkarte (Rastergröße 10 km x 10 km) der Pyrenäen. Die dunklen Punkte bezeichnen die Raster mit Vorkommen von *Iberolacerta bonnali* (LANTZ, 1927).

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

YN14	Pic d'Arriel (2824 m) (B. Pyr.) (BECK 1943; ARRIBAS 1997)
	Path from Ibón de Respumoso to Ibones de Arriel (circa 2200 m) (this paper)
	Ibones de Arriel (2350 m) (Huesca) (ARRIBAS 1993b, 1994a, 1997)
	Lac d'Artouste (1991 m) (B. Pyr.) (ARRIBAS 1993b, 1997)
	Col d'Arrious (2259 m) (B. Pyr.) (NAULLEAU 1980; ARRIBAS 1997)
YN23	Picos de Pondiellos. Mallata Alta das Argualás (2500 m) (Huesca) (ARRIBAS 1997)
	Gran Alto de Pondiellos (2900 m) (MARTINEZ RICA 1977; ARRIBAS 1997)
YN24	Ibón superior de Bramatuero (2200 m) (Huesca) (ARRIBAS 1997)
	Path from Ibón de Respumoso to Ibones de Arriel (2100-2200 m) (this paper)
	Ibón de Campo Plano (circa 2178 m) (this paper)
	Ibones de la Facha (2500-2600 m) (R. PUJOL, pers. com.)
	Balaitous (summit). (circa 3140 m) (this paper)
YN32	Peña Tendeñera (hacia los 2300 m) (Huesca) (ARRIBAS 1997)
YN33	Puerto de Bujaruelo (=Col de Bucharo) (2270 m) (Huesca) (ARRIBAS 1993b, 1994a, 1997)
YN34	Ibón de Bramatuero (2316 m) (Huesca) (ARRIBAS 1997)
YN42	Faja de Pelay (1900 m) (Huesca) (ARRIBAS 1993b, 1994a, 1997)
	Circo de Cotatuero (2200) (Huesca) (ARRIBAS 1993b, 1997; PEREZ MELLADO et al. 1993)
YN43	Pto de Bujaruelo (2270) (Huesca) (ARRIBAS 1993, 1994a, 1997)
BH52	Camino al Refugio de Goriz (2000-2200 m) (Huesca) (ARRIBAS 1997)
	Refugio de Goriz (2200 m) (Huesca) (MARTINEZ RICA 1976, 1977; ARRIBAS 1993a, 1993b, 1994a, 1994b, 1997)
	Faja Luenga y camino de Goriz a la Brecha de Rolando (2200-2400 m) (Huesca) (MARTINEZ RICA 1977; ARRIBAS 1997)
	Llano y cuello de Millaris (2400-2500 m) (Huesca) (MARTINEZ RICA 1977; ARRIBAS 1993b, 1997)
	Monte Perdido (MARTINEZ RICA 1976, 1977; ARRIBAS 1993a, 1993b, 1994a, 1994b, 1997)
BH53	Circ d'Estaubé (1670-1700 m) (H. Pyr.) (NAULLEAU 1980; ARRIBAS 1997)
BH62	Puntas Verdes (2621 m) (Huesca) (ARRIBAS 1997)
BH63	La Estiba y Sobreestiva (2300-2500 m) (Huesca) (ARRIBAS 1997)
	Circo de Pineta (2300 m) (Huesca) (ARRIBAS 1993b, 1994a, 1997)
	Petramula (2257 m) (Huesca) (ARRIBAS 1993b, 1997)
	Al E de la Fourche de la Sède (Circ de Troumouse) (2200 m) (H. Pyr) (X. RUFRAY obs., P. A. CROCHET pers. com.; ARRIBAS 1997)
BH64	Lac d'Aubert y Lac d'Aumar, until the Col de Madamette (2212-2500 m) (H. Pyr) (ARRIBAS 1997)
	Clot dets Coubar (2500 m) (Neouv.) (H. Pyr.) (X. RUFRAY obs., P. A. CROCHET pers. com.; ARRIBAS 1997)
	Lac de Cap-de-Long (2200 m) (Neouv.) (H. Pyr.) (P. GENIEZ, S. BOISSINOT,TH. MENUT obs.; ARRIBAS 1997)
	Pic d'Estibères (2000 m) (Neouv.) (H. Pyr.) (R. VOLOT obs., P.A. CROCHET det.; ARRIBAS 1997)
	Val d'Estaragne (2000-2000 m) (Neouv.) (H. Pyr.) (ARRIBAS 1997)
BH65	Lac Bleu de Bigorre (1928-2238) (H. Pyr.) (LANTZ 1927; BECK 1943; LANZA 1963; PEREZ MELLADO et al. 1993; ARRIBAS 1993a, 1993b, 1994a, 1994b, 1997)
	Pic du Midi de Bigorre (2700-2872 m) (H. Pyr.) (ARRIBAS 1997)
	Crête du Tourmalet (2115 m) (H. Pyr.) (ARRIBAS 1997)
	Pic des Quatre Termes (2720) (BECK 1943; ARRIBAS 1997)
BH72	Pico de Urdiceto-Pto. de Urdiceto (= Ordiceto) (2000-2300 m) (Huesca) (ARRIBAS 1997)
BH82	Valle del Clot (o Llardana) (2000-2500 m) (Huesca) (ARRIBAS 1993, 1994a, 1997)
	Barranco de Eriste (2000-2500 m) (Huesca) (ARRIBAS 1997)
BH92	Valle de Montidiego (2300-2400 m) (Huesca) (ARRIBAS 1997)
	Valle de Molseret (2300-2500 m) (Huesca) (ARRIBAS 1997)
CH01	Estany de Llauset (cabecera) (2180-2300 m) (Huesca) (ARRIBAS 1993b, 1995, 1997)
	Lago de Botornás (2300-2400 m) (Huesca) (ARRIBAS 1997)
	Coll de Llauset-P. de Vallhibierna (2400-3062 m) (Huesca) (ARRIBAS 1993b, 1995, 1997)
CH02	Ibón de Cregüeña (2000-2700 m) (Huesca) (ARRIBAS 1995, 1997)
	Portillón de Benasque (1900-2444 m) (Huesca) (ARRIBAS 1997)
	Coll de l'Infern - Port de la Picada (2100-2470) (Lérida-Huesca) (ARRIBAS 1995, 1997)
CH11	Estany de Llauset (2180-2300 m) (Huesca) (ARRIBAS 1993b, 1995, 1997)
CH12	Subida al Coll de l'Infern (2000-2100 m) (Lérida) (ARRIBAS 1997)
	Barranc de Pomero (circa 2000 m) (ex photo) (this paper)
CH20	Port de Filià (2420 m) (Lérida) (ARRIBAS 1997)
	Pic de Filià (from 2420m to the summit, at 2700 m) (M. ARILLA pers. com.)
CH21	Muntanyó de Llacs (2400 m) (MARTINEZ RICA 1976, 1977; ARRIBAS 1993b, 1995, 1997)
	Bony Blanc y Bony Negre (2200-2400 m) (Lérida) (ARRIBAS 1993b, 1995, 1997)
	Llastres de la Morta, Cavallers (1900-2300 m) (Lérida) (ARRIBAS 1997)
CH22	Tossau de Mar (2770 m) (Lérida) (M. VENTURA, S. PLA pers. com.; ARRIBAS 1997)
CH30	Estany Gento-Torrent de Pigaler, Vall Fosca (2400 m) (Lérida) (ARRIBAS 1995, 1997)
	Pic dels Payassos (vt. SE) (2700 m) (this paper)
	Estany de Francí (2350 m) (Lérida) (M. ARILLA, pers. com.)
CH31	Gran Encantat (1800-2747 m) (Lérida) (MARTINEZ RICA 1977; ARRIBAS 1993b, 1994a, 1995, 1997)

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 (ROST-INT), supranasal-loreal (SN-LOR), and postocular-parietal (POST-PAR) scale contact.

Measurements were transformed into the ratios: FLL*100/SVL; HLL*100/SVL; PL*100/PW; DM*100/PAL; DT*100/PAL; AL*100/AW. A new index

$$\frac{100 * \sqrt{(AL * AW)}}{SVL}$$

(coded as AS/SVL) has been introduced and is used as an estimation of scale size in respect to snout-vent length (SVL), whereas AL*100/AW is maintained to describe the general shape of the scale.

Statistical Procedures

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

Since there were significant differences in mean SVL between the females of the four great samples (Bigorre, M. Perdido + Arriel, Posets + Pta. Suelza, and Maladeta + A.Tortes) (Males: $F_{145,3}$ = 2.01, p = 0.1150, NS; Females: $F_{142,3}$ = 6.73, p = 0.0003), ANCOVA was used for comparisons of the body measuremens and ANOVA for the pholidosis characters (tables 2 and 6). ANOVA/ANCOVA calculations include grouped samples only.

MANOVA and Canonical Variate Analysis (CVA) were performed to present the global differences between samples and isolated individuals. For the main samples, MST (Minimum Spanning Tree) and UPGMA trees were calculated on the basis of Mahalanobis distances (D^2) (SNEATH & SOKAL 1973).

Dating and terminology of the Pyrenean Pleistocene events follow the system used for the Alps. In spite of 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).

RESULTS

Distribution

Iberolacerta bonnali is a Central Pyrenean endemic which has been localized within 26 UTM squares extending from the Arriel massif (east of the pass of El Portalé) in the west, to the mountains of the Sant Maurici-Aigüestortes National Park (west of the pass of La Bonaigua) in the east. In west-eastern direction, this lizard inhabits the massifs of Arriel, Balaitous, Vignemale (or Comachibosa), Panticosa, Monte Perdido, Punta Suelza, Posets, Maladeta, Ballibierna, and the mountains of the Sant Mauricio-Aigüestortes National Park (Besiberris, Muntanyó de Llacs, Peguera, and Encantats massifs) from where it extends northward into the massifs of Neouvielle and Bigorre.

Although there are no important discontinuities between the sites on record, the U.T.M grid map (fig. 1) gives a misleading image of the size of the range. In general, this species is restricted to a very small part of each of the 10 x 10 km^2 grids only, which usually corresponds to heights above 2,000 meters where it lives in small colonies, yet locally numerous.

The main distribution is confined to the Pyrenean alpine vegetation belt, i. e. above 2,000 m in the southern and exceptionally lower in the northern slopes: 1,700 m in the cirque of Estaublé (Monte Perdido Massif) and 1,928 m in the Lac Bleu (Bigorre), but 3,062 m in Ballibierna and Balaitous (pers. obs). See also the characteristics of these areas in ARRIBAS & MARTINEZ-RICA (1997).

The habitat is constituted of rocky slopes and outcrops and all their stages of meteorization (rock boulders, stony slopes, etc.) on all kinds of substrate, with higher population densities in well fissurated habitats (slates, schists, limestone clints, etc). The lizard is also present, although in lower densities, in less fissurated habitats (granites and gneisses). It is found frequently in the alpine rock - pasture interface and appears especially abundant in places where the summer hydric deficiency is low (proximity of streams and lakes of glacial origin).

In general, *I. bonnali* is an altitudinal vicariant of *Podarcis muralis* (LAURENTI, 1768). However, at the inferior altitudinal limit of *I. bonnali* both species are sympatric in almost all massifs studied (pers. obs.). Furthermore, *I. bonnali* is sympatric (but usually not syntopic) with *Zootoca vivipara* (JACQUIN, 1787).

The distribution is punctual. Small colonies are embedded in favorable habitats. Limitation to certain massifs and localities is probably of postglacial origin (see discussion). *Iberolacerta bonnali* is locally common or abundant and the prospections carried out allow to suppose the presence of small populations scattered all over the Central Pyrenees. In great parts of the area, the remote habitat protects these saurians from being illegally collected. The species does not seem to be very sensitive to summer tourism, but some threat might arise from habitat destruction around ski resorts. More important may become the reduction of the distribution area due to climatic changes. Models of climatic changes at European latitudes equivalent to the Pyrenees announce an ascent of the vegetation belts of up to 800 m within a little more than a century (e. g., GUISAN et al. 1995).

Iberolacerta bonnali is still frequent in the Central Pyrenees and not subject to special short term threats. Nonetheless, this species is considered as "vulnerable", because its populations are very local, disjunct, and in regression, presumably by natural causes. In some localities, this taxon suffers from severe human interference (ARRIBAS & MARTINEZ-RICA 1997).

Sexual dimorphism

Since SVL is significantly longer in females than in males (ANOVA: $F_{293,1}$ = 39.6; $p < 0.0001$), an ANCOVA of the biometric characters was run using SVL as a covariate. The species is significantly dimorphic in all biometric characters except AL ($F_{293,1}$ = 3.46; $p > 0.05$).

All dimorphic measurements are comparatively longer in males than in females: FLL ($F_{293,1}$ = 81.47; $p < 0.0001$), HLL ($F_{293,1}$ = 196.40; $p < 0.0001$), PL ($F_{293,1}$ = 523.61; $p < 0.0001$), PW ($F_{293,1}$ = 207.95; $p < 0.0001$), PAL ($F_{293,1}$ = 272.29, $p < 0.0001$), DM ($F_{293,1}$ = 44.04, $p < 0.0001$), DT ($F_{293,1}$ = 51.04, $p < 0.0001$), AW ($F_{293,1}$ = 141.84, $p < 0.0001$). Thus, as is usual in lacertids, males have proportionally bigger limbs and heads than females.

Pholidosis characters were compared by means of ANOVA. Only VENT ($F_{293,1}$ = 349.88, $p < 0.0001$) and GUL ($F_{293,1}$ = 11.46, $p < 0.001$) show significant differences, being greater in females.

The ratios FLL/SVL ($F_{293,1}$ = 125.52, $p < 0.0001$), HLL/SVL ($F_{293,1}$ = 224.94, $p < 0.0001$), AL/AW ($F_{293,1}$ = 102.73, $p < 0.0001$), and AS/SVL ($F_{293,1}$ = 12.92, $p < 0.0005$) are significantly different between sexes and greater in males while DM/PAL ($F_{293,1}$ = 1.75, $p < 0.5$), DT/PAL ($F_{293,1}$ = 1.18, $p < 0.5$), and PL/PW ($F_{293,1}$ = 1.37, $p < 0.5$) are not significantly different between males and females.

Contacts between the scales considered do not show significant differences between sexes: ROST-INT (χ^2_1 = 0.15, $p > 0.5$, with Yates' continuity correction factor), POST-PAR (χ^2_2 = 1.76, $p < 0.5$), SN-LOR (χ^2_2 = 3.57, $p < 0.5$).

Concerning the colour-pattern studied, the (rare) presence of blue dots in the outermost ventral scale rows is more frequent in males (8 out of 149) than in females (1 out of 146) (χ^2_1 = 4.0, $p < 0.05$, with Yates' continuity correction factor).

Geographic variation in males

In several partial analyses isolated specimens and some small samples were compared with the main samples.

* ANOVA results. Descriptive statistics from biometric indexes and pholidosis characters of all grouped samples are shown in table 2. Differences at $p < 0.01$ are also indicated it in the table, although $\alpha > 0{,}05$ results are not significant if Bonferroni's correction is applied.

The most deviate sample is that of Bigorre, which shows at least three highly significant differences to all other samples. Compared to the Monte Perdido sample, it differs in FEM-r, FEM-l, LAM, and the variables related to the size of the anal plate (CIRCA, AL*100/AW, AS/SVL). Compared to the Posets sample it differs in GUL, FEM-r and FEM-l and to Maladeta and Aigüestortes in CIRCA, PL*100/PW, and AS/SVL. The

Sample	BIGO - Bigorre (n = 55)				BIGO - Arriel (n = 3)			
Populations Clustered	(Bigorre + Neouvielle)				(Arriel massif)			
Parameter	Mean	Stdv.	Min.	Max.	Mean	Stdv.	Min.	Max.
SVL	52.11	3.19	45.03	58.22	53.77	2.41	51.28	56.01
GRS-r	4.61	2	0	6	4.66	2.31	2	6
GRS-l	4.6	2.17	1	9	3.33	1.15	2	4
GUL	21.98	1.63	18	25	22.33	1.52	21	24
COLL	9.76	2.17	5	15	10	2	8	12
DORS	43.05	2.1	38	47	42.66	3.05	40	46
VENT	26.27	0.78	25	28	25.33	0.57	25	26
FEM-r	14.4	1.44	11	17	14.66	0.57	14	15
FEM-l	14.8	1.23	12	18	14.33	0.57	14	15
LAM	26.67	1.29	24	29	28.33	2.08	26	30
CIRCA	10.26	1.42	7	15	9	1	8	10
FLL*100/SVL	35.51	0.02	30.82	39.17	34.98	0.1	34.12	36.08
HLL*100/SVL	49.93	0.22	44.44	55.2	48.69	0.55	46.13	51.51
PL*100/PW	199.09	0.07	183.58	212.64	197.44	0.06	190.62	201.53
DM*100/PAL	38.63	0.06	24.24	61.33	32.03	0.02	33.81	28.94
DT*100/PAL	42.19	0.05	29.13	55.55	47.03	0.05	42.58	53.29
AL*100/AW	59.05	0.04	48.61	70.56	66.48	0.05	61.22	72.65
AS/SVL	73.56	0.04	63.08	83.68	67.87	0.05	61.99	73.27
Scale contacts	No/Nein	Yes/Ja			No/Nein	Yes/Ja		
ROST-INT	0	55	(asymmetr.: n‘ = n)		0	3	(asymmetr.: n‘ = n)	
POST-PAR	2	108	(symmetr.: n‘ = 2n)		4	2	(symmetr.: n‘ = 2n)	
SN-LOR	4	106	(symmetr.: n‘ = 2n)		0	6	(symmetr.: n‘ = 2n)	

Sample	PERD - Monte Perdido (n = 40)				POSE - Punta Suelza (n = 4)			
Populations Clustered	(Monte Perdido)				(Urdiceto)			
Parameter	Mean	Stdv.	Min.	Max.	Mean	Stdv.	Min.	Max.
SVL	51.87	3.08	45.77	58.14	50.91	0.93	49.57	51.6
GRS-r	4.75	1.73	2	9	4.75	3.09	2	9
GRS-l	5.12	2.22	2	11	4.75	2.87	3	9
GUL	21.07	1.97	17	24	19.25	1.5	17	20
COLL	10.62	1.53	7	14	10.5	1	10	12
DORS	43.42	2.26	38	47	41.5	3	40	46
VENT	26.17	0.74	25	28	26	0.81	25	27
FEM-r	13.02	1.54	9	16	12.75	0.95	12	14
FEM-l	13	1.19	11	15	12	1.63	10	14
LAM	24.95	1.15	23	27	25	1.41	23	26
CIRCA	8.82	1.03	6	11	9.25	1.25	8	11
FLL*100/SVL	36.09	0.19	30.88	41.82	34.37	0.15	33	36.51
HLL*100/SVL	49.27	0.25	44.54	54.76	47.94	0.02	45.25	49.86
PL*100/PW	198	0.06	181.22	213.55	209.8	0.07	203.82	219.96
DM*100/PAL	41.77	0.06	28.97	60.25	36.03	0.07	30	45.26
DT*100/PAL	41.52	0.05	30.55	55	46.28	0.02	42.65	48.04
AL*100/AW	52.11	0.08	31.77	70.94	59.93	0.04	54.27	65.63
AS/SVL	65.65	0.05	55.7	80.16	73.71	0.03	69.55	77.59
Scale contacts	No/Nein	Yes/Ja			No/Nein	Yes/Ja		
ROST-INT	3	37	(asymmetr.: n‘ = n)		0	4	(asymmetr.: n‘ = n)	
POST-PAR	23	57	(symmetr.: n‘ = 2n)		1	7	(symmetr.: n‘ = 2n)	
SN-LOR	1	79	(symmetr.: n‘ = 2n)		0	8	(symmetr.: n‘ = 2n)	

Table 2 (parts 1 and 2 - this and the following page): *Iberolacerta bonnali* (LANTZ, 1927). Males (for parameters and population acronyms see text). Descriptive statistics (mean, standard deviation, minimum, maximum) of eight samples. In the symmetrical postocular-parietal and supranasal-loreal scale contacts, both sides are considered (n' = 2n). For intersample comparison of the Chi^2 results see text.

Sample	POSE – Posets (n = 7)				MALA – Ballibierna (n = 10)			
Populations Clustered	(Posets)				(Llauset)			
Parameter	Mean	Stdv.	Min.	Max.	Mean	Stdv.	Min.	Max.
SVL	50.18	3.58	45.1	54.44	51.82	3.04	48.63	58.12
GRS-r	3.57	2.22	0	6	3.9	2.28	1	7
GRS-l	3.71	3.09	0	9	3.2	2.74	0	6
GUL	20.85	1.77	18	23	22	1.33	20	24
COLL	10	2	7	13	11.2	1.81	7	13
DORS	42.42	2.76	38	46	42.6	2.31	39	46
VENT	26.28	0.75	25	25	26.4	0.96	26	29
FEM-r	13.28	1.38	11	15	13.2	1.03	12	15
FEM-l	13.14	1.34	11	15	13.5	1.58	12	16
LAM	25	2.16	21	28	26	1.05	25	28
CIRCA	9.14	1.34	7	11	8.5	0.52	8	9
FLL*100/SVL	35.21	0.2	32.8	38.7	35.17	0.12	33.33	36.92
HLL*100/SVL	47.84	0.04	38.78	52.55	49.11	0.01	46.63	51.41
PL*100/PW	203.1	0.04	196.42	207.69	201.15	0.06	193.82	215.08
DM*100/PAL	40.06	0.11	18.6	50	41.81	0.05	35.89	53.28
DT*100/PAL	44.79	0.06	35.55	52.94	44.16	0.05	37.47	52.77
AL*100/AW	54.35	0.07	46	64.1	55.98	0.05	49.88	68.23
AS/SVL	67.19	0.04	61.05	73.52	64.63	0.02	59.66	68.75
Scale contacts	No/Nein	Yes/Ja			No/Nein	Yes/Ja		
ROST-INT	0	7	(asymmetr.: n' = n)		0	10	(asymmetr.: n' = n)	
POST-PAR	2	12	(symmetr.: n' = 2n)		12	8	(symmetr.: n' = 2n)	
SN-LOR	0	14	(symmetr.: n' = 2n)		4	16	(symmetr.: n' = 2n)	

Sample	MALA – Maladeta (n = 15)				ATOR – Besiberri (n = 4)			
Populations Clustered	(Picada + Benasque)				(Cavallers)			
Parameter	Mean	Stdv.	Min.	Max.	Mean	Stdv.	Min.	Max.
SVL	52.42	2.55	48.37	55.66	57.16	1.42	55.29	58.73
GRS-r	5.26	2.01	2	9	3.75	0.95	3	5
GRS-l	4.66	2.22	1	8	3	1.41	2	5
GUL	22.26	1.33	21	25	22	1.82	20	24
COLL	9.73	0.88	8	11	9.5	0.57	9	10
DORS	42.2	2.11	39	46	44.75	3.4	40	48
VENT	26.6	0.91	25	28	26.25	0.5	26	27
FEM-r	14	1.3	12	17	15.5	1.29	14	17
FEM-l	14.26	1.03	12	16	14	0.81	13	15
LAM	27.26	1.09	25	29	25.75	1.5	25	28
CIRCA	9.2	0.86	8	11	8.75	0.5	8	9
FLL*100/SVL	35.64	0.13	33.52	37.53	33.91	0.08	32.64	34.69
HLL*100/SVL	49.33	0.01	46.2	51.43	47.03	0.01	45.88	48.32
PL*100/PW	205.59	0.04	200.66	215.63	207.45	0.06	191.39	213.91
DM*100/PAL	42.98	0.03	38.44	50.48	37.92	0.04	31.92	41.95
DT*100/PAL	46.56	0.002	37.04	54.32	43.13	0.03	39.67	47.4
AL*100/AW	56.39	0.05	49.7	68.36	59.69	0.06	50.37	64.95
AS/SVL	69.07	0.03	61.07	74.01	69.42	0.04	64.53	73.6
Scale contacts	No/Nein	Yes/Ja			No/Nein	Yes/Ja		
ROST-INT	0	15	(asymmetr.: n' = n)		0	4	(asymmetr.: n' = n)	
POST-PAR	4	23	(symmetr.: n' = 2n)		2	6	(symmetr.: n' = 2n)	
SN-LOR	1	29	(symmetr.: n' = 2n)		2	6	(symmetr.: n' = 2n)	

Tab. 2 (Teile 1 und 2 – diese und vorangehende Seite): *Iberolacerta bonnali* (LANTZ, 1927). Männchen (Parameter und Populationsbezeichnungen siehe Text). Deskriptive Statistiken (Mittelwert, Standardabweichung, Minimum, Maximum) von acht Stichproben. Die Schuppenkontakte von Postoculare-Parietale und Supranasale-Loreale wurden beidseitig registriert (n' = 2n). Zum Stichprobenvergleich der Chi^2 Ergebnisse siehe Text.

Sample	ATOR - A. Tortes (n = 11)						Significant differences between samples / Signifikante Unterschiede zwischen Stichproben									
Populations Clustered	(Muntanyó + Filià)				ANOVA		BIGO PERD	BIGO POSE	BIGO MALA	BIGO ATOR	PERD POSE	PERD MALA	PERD ATOR	POSE MALA	POSE ATOR	MALA ATOR
Parameter	Mean	Stdv.	Min.	Max.	F	p										
SVL	53.08	3.57	46.6	57.17	2.5	0.0448										
GRS-r	4.63	2.57	0	9	0.39	0.8131										
GRS-l	4.18	2.78	0	9	1.95	0.1048										
GUL	21.9	1.37	20	25	6.72	0		**						*	*	
COLL	11	1.34	9	14	3.34	0.0117										
DORS	42.72	2.76	36	47	2.25	0.0662										
VENT	26.72	0.64	26	28	0.39	0.8136										
FEM-r	13.27	1	11	15	8.17	0	**	**								
FEM-l	13.63	1.68	10	17	13.48	0	**	**					*	*	*	
LAM	28	1.34	26	31	15.73	0	**	*				**	**	*	**	
CIRCA	7.72	0.64	6	8	17.21	0	**	*	**	**					**	
FLL*100/SVL	35.72	0.18	33.42	38.22	1.44	0.2238										
HLL*100/SVL	49.26	0.02	45.08	51.5	3.3	0.0124		*			*					
PL*100/PW	207.36	0.05	201.32	215.09	10.67	0		*	**	**	*	**	**			
DM*100/PAL	35.22	0.08	17.64	46.65	5.48	0.0004							*		*	*
DT*100/PAL	44.1	0.05	35.71	51.35	2.71	0.032										
AL*100/AW	58.6	0.06	49.35	69.56	9.23	0	**						*			
AS/SVL	63.3	0.05	54.26	72.05	15.28	0	**		**	**	*			*		
Scale contacts	No/Nein	Yes/Ja			Chi^2	p										
ROST-INT	0	11	(asymmetr.: n'= n)		8.34	0.08										
POST-PAR	12	10	(symmetr.: n' = 2n)		37.71	0										
SN-LOR	2	20	(symmetr.: n' = 2n)		11.75	0.02										

Table 2 (part 3): *Iberolacerta bonnali* (LANTZ, 1927). Males (for parameters and population acronyms see text). Descriptive statistics (mean, standard deviation, minimum, maximum) of the A. Tortes sample and ANOVA results of the various samples studied. In the symmetrical postocular-parietal and supranasal-loreal scale contacts, both sides are considered (n' = 2n). For intersample comparison of the Chi^2 results see text.

Tab. 2 (Teil 3): *Iberolacerta bonnali* (LANTZ, 1927). Männchen (Parameter und Populationsbezeichnungen siehe Text). Deskriptive Statistiken (Mittelwert, Standardabweichung, Minimum, Maximum) der A. Tortes Stichprobe und ANOVA Ergebnisse aller untersuchten Stichproben. Die Schuppenkontakte von Postoculare-Parietale und Supranasale-Loreale wurden beidseitig registriert (n' = 2n). Zum Stichprobenvergleich der Chi^2 Ergebnisse siehe Text.

Monte Perdido sample differs from Maladeta and Aigüestortes in LAM and relative pileus length while Aigüestortes differs from Posets in LAM and CIRCA.

As far as scale contacts are concerned, differences in rostral-internasal contact do not reach significance level ($\chi^2_4 = 8.34$; $p = 0.0798$) while differences in postocular-parietal contact are highly significant ($\chi^2_4 = 37.841$, $p < 0.0001$), due to a relatively low proportion of absence of contact in the Bigorre sample and a relatively high proportion of contact in that of Aigüestortes. Supranasal-loreal contact also shows significant differences ($\chi^2_4 = 11.749$, $p < 0.0193$) with a slightly decreased number of contacts in the samples of Maladeta and Aigüestortes.

The studied samples do neither mirror significant differences in the frequency of blue dots in the outermost ventral scales ($\chi^2_4 = 5.86$, $p = 0.2097$) nor in the extension of the dark ventral punctuation ($\chi^2_8 = 7.9562$, $p = 0.4378$).

* Canonical Variate Analysis (CVA). Three partial analyses of the male samples were performed in order to ascertain the relative similarity of populations i. e., which populations can be pooled to run a more balanced analysis of well represented (and thus more confident) samples. For this purpose the geographic range of *I. bonnali* was subdivided into three portions (western, central, eastern) in which the well represented populations overlapped and were taken as reference for the assignment of small samples.

- Western massifs. Males from Bigorre (n = 68), Neouvielle (n = 1), Arriel (n = 3) and Monte Perdido (n = 47). MANOVA finds significant differences between the studied samples ($F_{51,295} = 4.7504$, $p < 0.000001$; Wilks' Lambda = 0.1682). The isolated specimen from Neouvielle clusters better with Bigorre ($D^2 = 23.7$) than with Monte Perdido ($D^2 = 30.6$). The same, the three specimens from Arriel cluster better with Bigorre ($D^2 = 16.1$) than with Monte Perdido ($D^2 = 26.9$).

- Central massifs. Males from Monte Perdido (n = 47), Punta Suelza (n = 4), and Posets (n = 9). MANOVA does not find differences between the samples ($F_{34,82} = 1.4321$, $p < 0.1$; Wilk's Lambda = 0.3937). Notwithstanding this result, the geographically intermediate sample from Punta Suelza was preferentially added to Posets ($D^2 = 7.15$) rather than to Monte Perdido ($D^2 = 13.3$).

- Eastern massifs. Males from Ballibierna (n = 10), Maladeta (n = 15), Besiberri (n = 6), and Aigüestortes (n = 11). MANOVA finds significant differences between the samples ($F_{51,66} = 2.6331$, $p < 0.0005$; Wilks' Lambda = 0.0370). Nonetheless, the four populations appear more or less uniformly differentiated, hence, the three best represented samples are selected for final analysis. The Ballibierna population in a southern spur of the Pyrenean axis, is nearly equally different from the other samples ($D^2 = 11.0$ to Besiberri; $D^2 = 12.9$ to Maladeta). The Maladeta sample, originating from the axis of the mountain range, is less different from the spatially closer Ballibierna ($D^2 = 12.9$) than from the other two samples ($D^2 = 17.9$ to Besiberri; $D^2 = 20.2$ to Aigüestortes) originating from the opposite side of the Ribagorzana river valley. Interestingly, the geographically extreme population of Aigüestortes appears more similar to Ballibierna ($D^2 = 12.6$) than to the closer or axial localities ($D^2 = 20.2$ to Maladeta, 22.3 to Besiberri). The above differences suggest a very particular pattern of relationship among these populations.

Finally, 170 male *I. bonnali* represented by the following six samples were subject to CVA: Bigorre (BIGO), Monte Perdido (PERD), Posets + Punta Suelza (POSE), Ballibierna + Besiberri (BALL), Maladeta (MALA), and Aigüestortes (ATOR). MANOVA finds significant differences between these samples ($F_{85,719} = 5.1869$, $p < 0.000001$; Wilks' Lambda = 0.0993).

The canonical axes I, II, and III explain 90 % of the inter-sample variance, giving a fairly good account of the relationships between these main populations.

The first axis (eigenvalue: 11.3) explains 50.4 % of the inter-sample variance. This axis has high positive loadings for CIRCA (0.445), AS/SVL (0.332) and a high negative loading for PL*100/PW (-0.323) and can be interpreted as a display of geographic clinal variation, in that the easternmost representatives (Aigüestortes - in the negative part of the axis) have the longest pileus and the relatively smallest anal plate (with a low number of circumanal scales), while the contrary values (short pileus,

Table 3: Canonical Variate Analysis (CVA) of the grouped male samples of *Iberolacerta bonnali*. Coordinates of the centroids in the first three axes (V1,V2,V3) and 95 % confidence radia.

Tab. 3: Kanonische Varianzanalyse (CVA) der gruppierten Männchen-Stichproben von *Iberolacerta bonnali*. Zentroidkoordinaten auf den ersten drei Achsen (V1, V2, V3) und 95 % Konfidenzradien.

Sample	V1	V2	V3	Confid. Rad.
BIGO	2.06	0.989	-0.394	0.685
PERD	0.692	-1.77	-0.463	0.824
POSE	-0.273	-0.747	1.15	1.57
BALL	-0.352	-0.283	-0.348	1.41
MALA	0.363	1.19	0.514	1.46
ATOR	-2.49	0.622	-0.456	1.70

Table 4: Mahalanobis distances between group centroids (coordinates see table 3) of the grouped male samples of *Iberolacerta bonnali* which were subject to CVA.

Tab. 4: Mahalanobisdistanzen zwischen den Gruppenzentroiden (Koordinaten siehe Tab. 3) der gruppierten Männchen-Stichproben von *Iberolacerta bonnali*, die einer CVA unterzogen wurden.

Sample	BIG	PER	POS	BAL	MAL	ATO
BIGO	0					
PERD	10.4	0				
POSE	10.9	5.38	0			
BALL	8.62	4.84	3.38	0		
MALA	5.55	10.1	6.17	4.89	0	
ATOR	21.1	16.2	9.54	6.74	10.4	0

Table 5: The smallest Mahalanobis distances between the grouped male samples the construction of the MST (Minimum Spanning Tree) is based upon.

Tab. 5: Die geringsten Mahalanobisdistanzen zwischen den gruppierten Männchen-Stichproben, auf denen die Konstruktion des MST basiert.

i	j	Length / Länge
BIGO	MALA	5.5500000
MALA	BALL	4.8900000
BALL	POSE	3.3800000
BALL	PERD	4.8400000
BALL	ATOR	6.7400000

markedly big anal plate surrounded by a greater number of circumanal scales) are found among the Bigorre specimens situated in the positive part of the axis. Ballibierna + Besiberri and Posets + Punta Suelza receive intermediate scores for these characters while the scores of Maladeta and Monte Perdido - although very similar - are slightly higher (rather tending towards Bigorre than towards Aigüestortes). This clinal variation might be caused by abiotic (mainly climatic and geological) factors.

The second axis (eigenvalue: 6.57) explains 29.4 % of the inter-sample variance. This axis has high loadings for LAM (0.646), FEM-I (0.385), and GUL (0.303), all being associated with the positive part of the axis in which the samples of Maladeta, Bigorre, and Aigüestortes are positioned. On the contrary, the Monte Perdido sample appears characterized by the lowest values for these characters. This second axis could be interpreted as reflecting the true path of the postglacial re-colonization process of the Central Pyrenees (see discussion).

The third axis (eigenvalue: 2.28) explains 10.2 % of the inter-sample variance. This axis has an important positive loading for DT (0.467) characterizing Posets, and, to a lesser degree, Maladeta in the positive part. These populations show also the lowest values for GUL (-0.420).

The threedimensional representation of these axes (fig. 2) shows the samples of Ballibierna + Besiberri and Posets + Punta Suelza (to a lesser degree also Maladeta) in an overall intermediate position. Three populations are clearly differentiated from this "central nucleus" and correspond to the geographically extreme samples Bigorre, Monte Perdido, and Aigüestortes, all of them being well differentiated from each other.

The minimum distances between the populations (Minimum Spanning Tree; MST) are given in table 5. Ballibierna + Besiberri (the sample with the highest connectivity) is connected to all other populations except Bigorre which on its side seems to be most similar to Maladeta (fig. 2). Moreover, Ballibierna + Besiberri is the sample with the minimum total distance to all other samples. If all individual samples are entered separately (not clustered according to their partial relationship), the best connected and mimimum distant sample is Posets, followed by its geographical neighbours Ballibierna and Maladeta.

Coordinates of the population centroids in the axes I, II, III are indicated in table 3, Mahalanobis' generalized distances between samples in table 4.

* Cluster analysis of grouped samples (UPGMA method, fig. 3) shows the "central nucleus" (Posets + Punta Suelza and Ballibierna + Besiberri populations: $D^2 = 3.38$), closest related to the

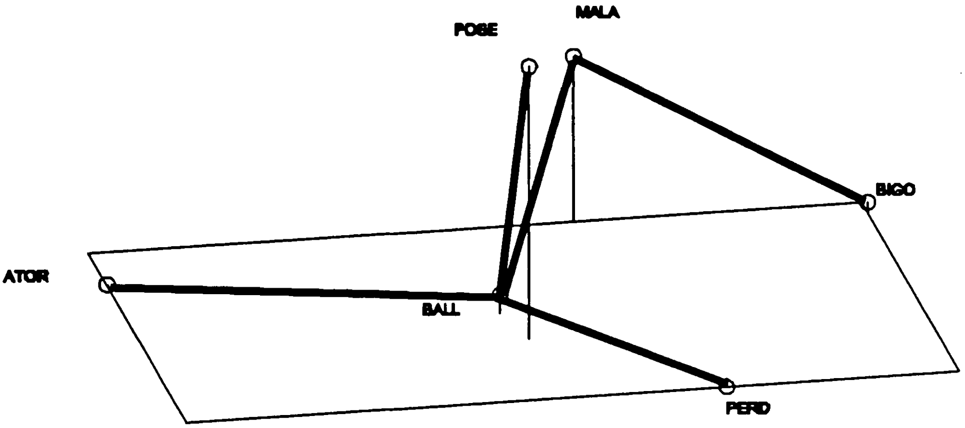

Fig. 2: Threedimensional representation of population centroids of all *Iberolacerta bonnali* male samples studied. The three axes explain 90 % of all interpopulation variance. Minimum Spanning Tree (MST) is superimposed.

Abb. 2: Dreidimensionale Darstellung der Populationszentroide aller untersuchten *Iberolacerta bonnali* Männchen - Stichproben. Die drei Achsen erklären 90 % der Varianz zwischen den Populationen. Der Minimum Spanning Tree (MST) ist darübergelegt.

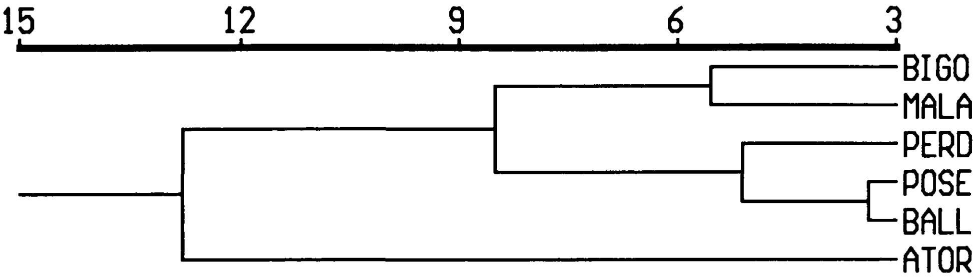

Fig. 3: UPGMA dendrogram based on Mahalanobis distances of grouped samples of male *Iberolacerta bonnali* (see table 4).

Abb. 3: UPGMA Dendrogramm auf Grundlage der Mahalanobisdistanzen zwischen den gruppierten Stichproben von *Iberolacerta bonnali* - Männchen (siehe Tab. 4).

Monte Perdido sample ($D^2 = 5.11$). A second cluster includes Bigorre and Maladeta ($D^2 = 5.55$). These two main clusters join at $D^2 = 8.51$. The most different group is the sample of Aigüestortes (clustering with the rest at $D^2 = 12.79$).

* Discriminant analysis misclassifies 40 specimens out of 170 (23.43 %). From 67 BIGO specimens, 54 are classified correctly; 14 are misclassified and attributed to PERD (5), BALL (2), and MALA (7). Out of 47 specimens from PERD, 35 are classified correctly; 12 are misclassified and attributed to BIGO (1), POSE (2), BALL (5), MALA (3), and ATOR (1). From 13 specimens of POSE, 9 are classified correctly; 4 are misclassified and attributed to PERD (2), BALL (1), and ATOR (1). Out of 16 specimens from BALL, 11 are classified correctly; 5 are misclassified and attributed to BIGO (1), PERD (1), POSE (2), and MALA (1). From 15 MALA specimens, 12 are classified correctly; 3 are misclassified and attributed to PERD (1), BALL (1), and ATOR (1). Finally, from 11 Aigüestortes specimens, 9 are classified correcly; 2 are misclassified and attributed to BALL.

Geographic variation in females

* ANOVA results. Descriptive statistics of biometric indexes and pholidosis characters from all samples are shown in table 6.

As in the males, the most different sample is that of Bigorre, which shows three highly significant differences (FEM-r, CIRCA, DM*100/PAL) to the Monte Perdido sample and one (DM*100/PAL) to the Maladeta population. All other between sample differences are significant only at $p < 0.05$ (not significant if Bonferroni's correction is applied for the number of samples involved in the comparison).

With respect to the scale contacts, differences in ROST-INT do not reach significant levels ($\chi^2_4 = 6.254$; $p = 0.1809$). Differences in POST-PAR are highly significant ($\chi^2_4 = 37.712$, $p < 0.0001$) due to comparatively high absence of contact in the Monte Perdido sample. Differences in SN-LOR are significant ($\chi^2_4 = 18.276$, $p < 0.005$) due to slightly increased absence of contact in the Aigüestortes sample.

The studied samples neither show significant differences in the frequency of blue dots in the outermost ventral scales ($\chi^2_4 = 0.9435$, $p = 0.9108$) nor in the extension of the dark ventral punctuation ($\chi^2_8 = 7.6140$, $p = 0.1068$).

* Canonical Variate Analysis (CVA). As in the male analysis, three partial analyses of the male samples were performed in order to ascertain the relative similarity of populations.

- Western massifs. Females from Bigorre ($n = 84$), Neouvielle ($n = 2$), Arriel ($n = 7$), and Monte Perdido ($n = 40$). MANOVA finds significant differences between the samples studied ($F_{51,337} = 3.7465$, $p < 0.000001$; Wilks' Lambda = 0.2628). The isolated specimen from Neouvielle clusters better with Bigorre ($D^2 = 13.2$) than with Monte Perdido ($D^2 = 15.1$) and best with the small Arriel sample ($D^2 = 12.2$). The specimens from Arriel cluster better with Bigorre ($D^2 = 8.87$) than with Monte Perdido ($D^2 = 10.8$).
- Central massifs. Females from Monte Perdido ($n = 40$), Punta Suelza ($n = 1$), and Posets ($n = 18$). As in the male analysis, MANOVA does not find differences between samples ($F_{34,80} = 1.2598$, $p < 0.2$; Wilk's Lambda = 0.4242). To follow the same criterion as in the males, the sample from Punta Suelza was preferentially added to Posets ($D^2 = 18.9$) rather than to Monte Perdido ($D^2 = 19$).
- Eastern massifs. Females from Ballibierna ($n = 13$), Maladeta ($n = 6$), Besiberri ($n = 3$), and Aigüestortes ($n = 29$). MANOVA finds significant differences between the samples ($F_{51,27} = 2.1291$, $p < 0.05$; Wilks' Lambda = 0.0086). The populations of Ballibierna and Maladeta are closest ($D^2 = 9.98$). Besiberri appears closer to Maladeta ($D^2 = 31.6$) than to the best represented samples Ballibierna ($D^2 = 57.6$) and Aigüestortes ($D^2 = 67.3$); Aigüestortes appears closest to Maladeta ($D^2 = 47.9$). The populations from the axial part of the area (Maladeta) are most similar to the other Central Pyrenean samples which is very conclusive from a geographic point of view.

After excluding or pooling very small samples or isolated individuals, 175 female *I. bonnali* represented by the following seven samples were subject to CVA: Bigorre (BIGO), Monte Perdido (PERD), Posets + Punta Suelza (POSE), Ballibierna

Sample	BIGO – Bigorre (n = 72)				BIGO – Arriel (n = 5)			
Populations Clustered	(Bigorre + Neouvielle)				(Arriel)			
Parameter	Mean	Stdv.	Min.	Max.	Mean	Stdv.	Min.	Max.
SVL	55.5	4.34	45.77	64.75	59.19	3.99	55.38	65.36
GRS-r	5.04	2.19	0	10	4	1.22	3	6
GRS-l	4.55	2.31	0	9	3.8	2.68	1	8
GUL	22.77	1.74	17	27	21.2	0.83	20	22
COLL	9.7	2.03	5	14	11.2	0.44	11	12
DORS	42.85	2.27	37	48	41.6	1.67	39	43
VENT	28.66	0.93	25	31	28.4	0.54	28	29
FEM-r	14.52	1.46	10	18	13.6	0.89	12	14
FEM-l	14.36	1.26	11	17	14	1.22	12	15
LAM	26.45	1.79	20	30	26.6	1.51	25	29
CIRCA	9.61	1.47	7	14	8.8	0.83	8	10
FLL*100/SVL	32.78	0.02	29.15	37.51	31.35	0.01	29.57	33.64
HLL*100/SVL	44.85	0.02	38.58	52.72	42.4	0.02	39.29	45.1
PL*100/PW	198.86	0.06	184.61	216.51	204.96	0.04	212.38	201.68
DM*100/PAL	35.68	0.05	21.62	63.15	40.65	0.03	45	36.34
DT*100/PAL	40.5	0.05	30.05	55.76	48.29	0.01	46.66	49.86
AL*100/AW	66.6	0.06	46.11	79.2	67.92	0.09	58.42	81.73
AS/SVL	68.24	0.04	55.66	76.55	64.04	0.02	61.51	66.2
Scale contacts	No/Nein	Yes/Ja			No/Nein	Yes/Ja		
ROST-INT	0	72	(asymmetr.: n‘ = n)		0	5	(asymmetr.: n‘ = n)	
POST-PAR	4	140	(symmetr.: n‘ = 2n)		5	5	(symmetr.: n‘ = 2n)	
SN-LOR	16	128	(symmetr.: n‘ = 2n)		0	10	(symmetr.: n‘ = 2n)	

Sample	PERD – M.Perdido (n = 32)				POSE - Pta. Suelza	POSE – Posets (n = 17)			
Populations Clustered	(M.Perdido)				(Urdiceto) (n = 1)	(Posets)			
Parameter	Mean	Stdv.	Min.	Max.	Mean	Mean	Stdv.	Min.	Max.
SVL	53.41	3.18	46.91	58.1	53.71	51.45	5.09	45.32	59.94
GRS-r	4.28	2	0	7	1	4.84	3.84	1	15
GRS-l	4.18	2.3	0	8	0	4.7	4.45	0	17
GUL	21.59	1.64	18	25	21	22.15	1.34	20	25
COLL	10.18	1.59	5	14	10	10.53	1.71	6	12
DORS	42.84	1.9	39	47	39	41.69	2.28	39	47
VENT	27.84	1.08	26	29	29	28.17	1.13	26	30
FEM-r	13.12	1.21	10	15	13	13.35	0.99	11	15
FEM-l	12.96	1.06	10	15	12	13.64	0.7	13	15
LAM	24.84	1.16	22	27	26	26	1.96	23	31
CIRCA	8.46	0.98	7	10	9	9.11	0.69	8	10
FLL*100/SVL	34.13	0.02	30.46	38.45	33.77	34.19	0.01	36.87	30.87
HLL*100/SVL	46.07	0.02	43.22	51.88	45.48	46.32	0.02	41.64	51.96
PL*100/PW	197.61	0.05	186.45	207.14	207.11	198.55	0.06	183.09	209.38
DM*100/PAL	41.74	0.05	24.3	52.63	35.58	40.75	0.05	30.2	52.17
DT*100/PAL	43.31	0.05	32.43	54.28	45.19	43.57	0.05	34.21	51.37
AL*100/AW	61.12	0.06	47.72	71.15	52.44	65.43	0.08	53.97	87.5
AS/SVL	66.06	0.05	55.06	77.14	60.67	64.37	0.05	53.69	72.97
Scale contacts	No/Nein	Yes/Ja			Yes/Ja	No/Nein	Yes/Ja		
ROST-INT	2	30	(asymmetr.: n‘=n)		1	1	16	(asymmetr.: n‘=n)	
POST-PAR	23	41	(symmetr.: n‘=2n)		2	5	29	(symmetr.: n‘=2n)	
SN-LOR	2	62	(symmetr.: n‘=2n)		2	0	34	(symmetr.: n‘=2n)	

Table 6 (parts 1 and 2, - this and the following page): *Iberolacerta bonnali* (LANTZ, 1927). Females (for parameters and population acronyms see text). Descriptive statistics (mean, standard deviation, minimum, maximum) of ten samples. In the symmetrical postocular-parietal and supranasal-loreal scale contacts, both sides are considered (n' = 2n). For intersample comparison of the Chi^2 results see text.

Sample	MALA – Ballibierna (n = 6)				MALA – Maladeta (n = 12)				ATOR - Encantats
Populations Clustered	(Llauset)				(Picada + Benasque)				(Gr. Encantat)(n=1)
Parameter	Mean	Stdv.	Min.	Max.	Mean	Stdv.	Min.	Max.	Mean
SVL	60.33	2.84	56.96	64.9	54.4	4.55	48.08	60.9	62.2
GRS-r	4.83	1.83	2	7	5.91	2.46	2	9	1
GRS-l	3.83	1.94	2	7	5.41	2.57	1	8	3
GUL	21.66	1.5	19	23	22.08	2.23	19	27	22
COLL	11.83	1.16	10	13	10.16	1.58	7	12	8
DORS	41.5	1.97	38	44	42.66	2.67	39	47	41
VENT	28	0.89	27	29	28.25	0.96	27	30	26
FEM-r	12.83	0.98	11	14	14.08	1.31	13	17	16
FEM-l	12.33	1.36	11	15	14.08	1.31	12	17	15
LAM	24.5	1.64	22	27	26.08	1.5	23	29	28
CIRCA	8.16	0.98	7	10	9.08	0.79	8	10	8
FLL*100/SVL	31.24	0.01	29.26	35.17	32.39	0.01	29.26	35.17	29.9
HLL*100/SVL	42.2	0.02	39.59	46.71	44.28	0.02	40.26	48.64	47.26
PL*100/PW	204.61	0.11	187.48	219.31	198.77	0.06	186.85	206.98	208.19
DM*100/PAL	45.49	0.07	35.89	52.77	41.2	0.04	32.08	47.7	36.58
DT*100/PAL	43.87	0.02	38.46	46.33	44.87	0.05	33.61	51.94	39.02
AL*100/AW	59.3	0.06	47.18	63.76	63.46	0.03	59.18	69.54	64.28
AS/SVL	65.67	0.04	59.4	70.79	64.02	0.04	57.56	70.51	72.18
Scale contacts	No/Nein	Yes/Ja			No/Nein	Yes/Ja			Yes/Ja
ROST-INT	0	6	(asymmetr.: n'=n)		1	11	(asymmetr.: n'=n)		1
POST-PAR	2	10	(symmetr.: n'=2n)		0	24	(symmetr.: n'=2n)		2
SN-LOR	0	12	(symmetr.: n'=2n)		3	21	(symmetr.: n'=2n)		2

Sample	ATOR – Besiberri (n = 4)				ATOR – A.Tortes (n = 3)			
Populations Clustered	(Caballers)				(Muntanyó + Filià)			
Parameter	Mean	Stdv.	Min.	Max.	Mean	Stdv.	Min.	Max.
SVL	59.94	1.69	58.04	62.17	52.4	2.12	50.9	50.9
GRS-r	4.5	1.29	3	6	7	3	4	10
GRS-l	3.75	2.21	1	6	6	2.64	3	8
GUL	24	1.15	23	25	24.66	2.51	22	27
COLL	7.25	1.7	5	9	11	1	10	12
DORS	45	2.58	42	48	42.33	0.57	42	43
VENT	28.5	1	27	29	27.66	0.57	27	28
FEM-r	14	0	14	14	13.66	1.15	13	15
FEM-l	15	0	15	15	12.33	0.57	12	13
LAM	26.66	1.15	26	28	29.33	0.57	29	30
CIRCA	9.75	0.95	9	11	8	1	7	9
FLL*100/SVL	32.06	0.02	30.07	34.49	33.49	0.01	32.19	34.91
HLL*100/SVL	42.83	0.03	45.62	39.02	48.25	0.02	46.36	50.36
PL*100/PW	205.35	0.09	197.21	219.26	200.91	0.11	191.06	213.46
DM*100/PAL	41.2	0.05	34.97	45.3	35.39	0.07	30.3	43.98
DT*100/PAL	46.23	0.01	44.11	47.79	46.72	0.06	39.89	51.81
AL*100/AW	67.42	0.05	63.39	76.16	69.7	0.002	66.23	73.44
AS/SVL	68.09	0.05	61.19	72.94	62.62	0.06	58.74	70.19
Scale contacts	No/Nein	Yes/Ja			No/Nein	Yes/Ja		
ROST-INT	1	3	(asymmetr.: n'=n)		0	3	(asymmetr.: n'=n)	
POST-PAR	4	4	(symmetr.: n'=2n)		0	6	(symmetr.: n'=2n)	
SN-LOR	5	3	(symmetr.: n'=2n)		0	6	(symmetr.: n'=2n)	

Tab. 6 (Teile 1 und 2 – diese und die vorangehende Seite): *Iberolacerta bonnali* (LANTZ, 1927). Weibchen (Parameter und Populationsbezeichnungen siehe Text). Deskriptive Statistiken (Mittelwert, Standardabweichung, Minimum, Maximum) von zehn Stichproben. Die Schuppenkontakte von Postoculare-Parietale und Supranasale-Loreale wurden beidseitig registriert (n' = 2n). Zum Stichprobenvergleich der Chi^2 Ergebnisse siehe Text.

Parameter	ANOVA F	ANOVA p	Significant differences between samples / Signifikante Unterschiede zwischen Stichproben BIGO PERD	BIGO POSE	BIGO MALA	BIGO ATOR	PERD POSE	PERD MALA	PERD ATOR	POSE MALA	POSE ATOR	MALA ATOR
SVL	5.27	0.0006		*	*	*			*			
GRS-r	1.49	0.2064										
GRS-l	0.42	0.7962										
GUL	4.95	0.0008							*			*
COLL	2.83	0.0262										
DORS	1.35	0.2521										
VENT	3.81	0.0053										
FEM-r	8.56	0	**									
FEM-l	0.56	0.6921										
LAM	3.57	0.0079				*			*		*	*
CIRCA	6.07	0.0001	**									
FLL*100/SVL	4.65	0.0014						*		*		
HLL*100/SVL	3.83	0.0052				*			*		*	*
PL*100/PW	1.04	0.3875										
DM*100/PAL	9.4	0	**	*	**				*		*	*
DT*100/PAL	4.77	0.0011				*						
AL*100/AW	1.92	0.109										
AS/SVL	0.53	0.7171										
Scale contacts	Chi^2	p										
ROST-INT	6.25	0.18										
POST-PAR	37.71	0										
SN-LOR	18.27	0										

Table 6 (part 3): *Iberolacerta bonnali* (LANTZ, 1927). Females (for parameters and population acronyms see text). ANOVA results of the various samples studied. In the symmetrical postocular-parietal and supranasal-loreal scale contacts, both sides are considered (n' = 2n). For intersample comparison of the Chi^2 results see text.

Tab. 6 (Teil 3): *Iberolacerta bonnali* (LANTZ, 1927). Weibchen (Parameter und Populationsbezeichnungen siehe Text). ANOVA Ergebnisse aller untersuchten Stichproben. Die Schuppenkontakte von Postoculare-Parietale und Supranasale-Loreale wurden beidseitig registriert (n' = 2n). Zum Stichprobenvergleich der Chi^2 Ergebnisse siehe Text.

Table 7: Canonical Variate Analysis (CVA) of the grouped female samples of *Iberolacerta bonnali.* Coordinates of the centroids in the first three axes (V1, V2, V3), and 95 % confidence radia.

Tab. 7: Kanonische Varianzanalyse (CVA) der gruppierten Weibchen-Stichproben von *Iberolacerta bonnali.* Zentroidkoordinaten der ersten drei Achsen (V1, V2, V3) und 95 % Konfidenzradien.

Sample	V1	V2	V3	Confid. Rad.
BIGO	-0.0874	0.662	-1.50	0.615
ARRI	0.819	1.27	1.01	2.13
PERD	-1.13	-0.786	-0.323	0.891
POSE	-0.0614	0.105	-0.196	1.33
BALL	-1.32	-0.757	0.906	2.13
MALA	-0.352	0.728	0.139	1.56
ATOR	2.13	-1.22	-0.0445	2.30

Table 8: Mahalanobis distances between group centroids (coordinates see table 7) of the grouped female samples of *Iberolacerta bonnali* which were subject to CVA.

Tab. 8: Mahalanobisdistanzen zwischen den Gruppenzentroiden (Koordinaten siehe Tab. 7) der gruppierten Weibchen-Stichproben von *Iberolacerta bonnali,* die einer CVA unterzogen wurden.

Sample	BIG	ARR	PER	POS	BAL	MAL	ATO
BIGO	0						
ARRI	8.01	0					
PERD	6.17	10.2	0				
POSE	3.78	4.84	3.41	0			
BALL	9.39	9.61	3.77	5.31	0		
MALA	3.88	3.75	4.67	1.91	4.84	0	
ATOR	10.9	9.41	11.9	7.60	13.4	10.4	0

Table 9: The smallest Mahalanobis distances between the grouped female samples the construction of the MST (Minimum Spanning Tree) is based upon.

Tab. 9: Die geringsten Mahalanobisdistanzen zwischen den gruppierten Weibchen-Stichproben, auf denen die Konstruktion des MST basiert.

i	j	Length / Länge
BIGO	POSE	3.780000
POSE	MALA	1.910000
POSE	PERD	3.410000
MALA	ARRI	3.750000
PERD	BALL	3.770000
POSE	ATOR	7.600000

+ Besiberri (BALL), Maladeta (MALA), Aigüestortes (ATOR), and Arriel (ARRI), the latter being additional to the male samples because of sufficient size of the female sample. MANOVA finds significant differences between the samples studied ($F_{102,873} = 2.8625$, $p < 0.000001$; Wilks' Lambda = 0.1932).

The canonical axes I, II, and III explain 85 % of the inter-sample variance, giving a fairly good account of the relationships among these main populations.

The first axis (eigenvalue 8.39) explains 39.9 % of the inter-sample variance. This axis has high loadings for LAM (0.543) in its positive part and a high negative loading for DM*100/PAL (-0.460), separating the samples from Aigüestortes (characterized by high values of LAM and lower for DM*100/PAL), from to the samples of Monte Perdido and Ballibierna (with contrary values).

The second axis (eigenvalue 5.27) explains 25.1 % of the inter-sample variance. This axis has high positive loadings for FEM-I (0.489) and CIRCA (0.530) and separates the small Arriel sample (with high loadings of these characters in its positive part) from the rest of the populations, Aigüestortes, Ballibierna, and Monte Perdido in particular. Compared with Monte Perdido, Aigüestortes and Ballibierna are characterized by their higher numbers of FEM-I and CIRCA.

The third axis (eigenvalue 4.26) explains 20.3 % of the inter-sample variance. In its positive part, this axis separates the samples of Ballibierna and Arriel - both characterized by higher loadings of DT (0.421) and COLL (0.370) - from the sample of Bigorre characterized by the contrary values. The rest of the populations occupies an intermediate position.

The threedimensional representation of these axes (fig 4) shows a group of related populations consisting of Posets + Punta Suelza, Maladeta, Bigorre, Monte Perdido, and Ballibierna + Besiberri, all of them being more or less individually differentiated. As in the male analysis, there are two populations more clearly differentiated from the above "central nucleus". They correspond to the geographically extreme samples of Arriel and Aigüestortes, which are well differentiated from each other.

The coordinates of the population centroids in the axes I, II, III are indicated in table 7, Mahalanobis' generalized distances between samples in table 8.

The minimum distances between the populations (Minimum Spanning Tree; MST) are given in table 9. Posets + Punta Suelza (the sample with the strongest connectivity) is connected with Bigorre, Maladeta, Monte Perdido, and Aigüestortes. From the populations which do not connect directly to

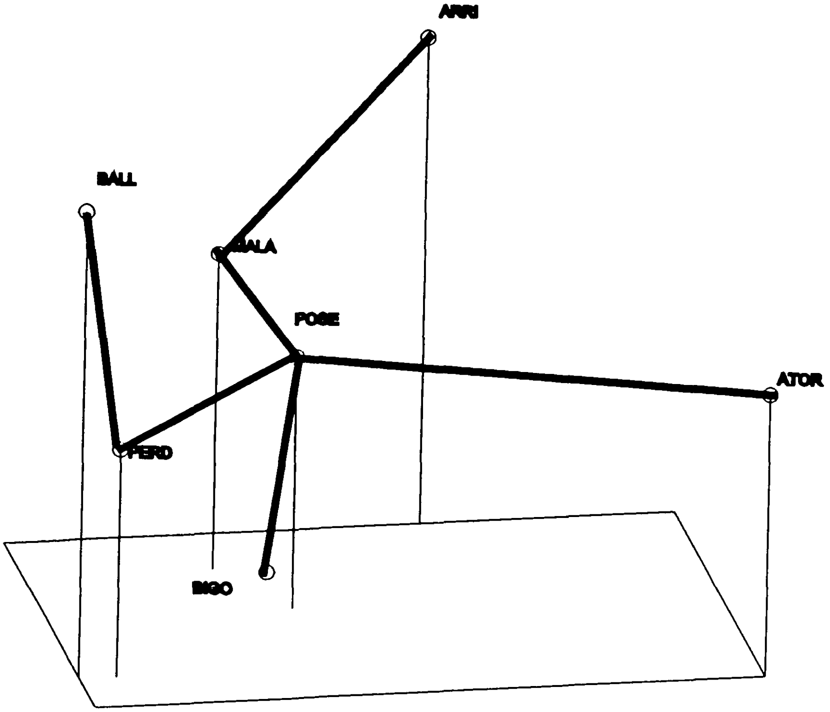

Fig. 4: Threedimensional representation of population centroids of *Iberolacerta bonnali* female samples studied. The three axes explain 85 % of all interpopulation variance. Minimum Spanning Tree (MST) superimposed.

Abb. 4: Dreidimensionale Darstellung der Populationszentroide aller untersuchten Weibchen-Stichproben von *Iberolacerta bonnali*. Die drei Achsen erklären 85 % der Varianz zwischen den Populationen. Der Minimum Spanning Tree (MST) ist darübergelegt.

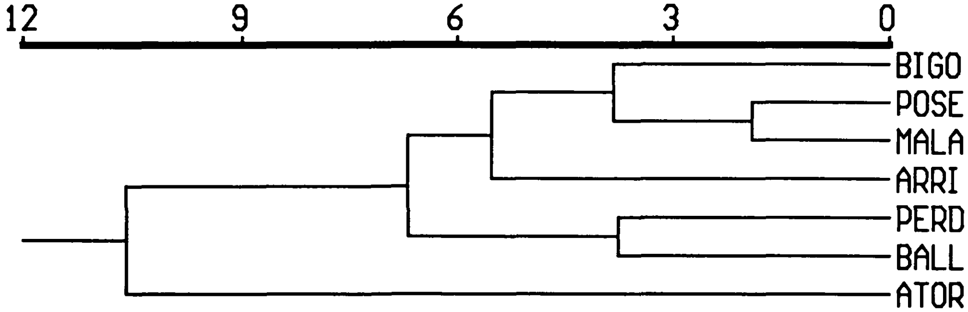

Fig. 5: UPGMA dendrogram based on Mahalanobis distances of grouped female *Iberolacerta bonnali* samples (see table 8).

Abb. 5: UPGMA dendrogram auf Grundlage der Mahalanobisdistanzen zwischen den gruppierten *Iberolacerta bonnali* Weibchen-Stichproben (siehe Tab. 8).

Posets, Ballibierna + Besiberri shows a possibly spurious relationship with Monte Perdido, whereas Arriel appears connected to this geographically close sample. The sample Posets + Punta Suelza shows the lowest total distance to all other samples. If samples are kept separately (not clustered according to their partial relationship), all central Pyrenean samples (Posets, Monte Perdido, Maladeta, Ballibierna) appear closely related, while Bigorre and Aigüestortes (both connected to Posets) are more distant. Punta Suelza appears related to Neouvielle and this latter sample joins Posets which is well in accordance with the geographic position of these massifs. Strange and very probably spurious relationships appear in the underrepresented samples: Arriel connects to Maladeta and Besiberri appears related to Bigorre. Posets is not only the best connected sample but shows also the smallest global distance to all other samples (see discussion).

* Cluster analysis of grouped samples (UPGMA method, fig. 5) shows the "central nucleus" (Posets + Punta Suelza and Maladeta samples: D^2 = 1.91) very closely related. Also closely related to these "central" populations appears Bigorre (D^2 = 3.83) while Arriel (D^2 = 5.53) seems more distant. An odd cluster formed by M. Perdido and Ballibierna (D^2 = 3.77) is clearly separated from all previous samples (D^2 = 6.70). The most different sample is that of Aigüestortes which clusters with the rest of the samples at D^2=10.6.

* Discriminant analysis misclassifies 63 specimens out of 175 (=36 %). From 84 BIGO specimens, 61 are classified correctly; 23 are misclassified and attributed to ARRI (3), PERD (6), POSE (5), BALL (3), MALA (3), and ATOR (3). Out of 7 specimens from Arriel, 5 are classified correctly; 2 are misclassified and attributed to BIGO, and ATOR. From 40 PERD specimens, 22 are classified correctly, 18 uncorrectly and attributed to BIGO (3), ARRI (1), POSE (4), BALL (5), MALA (4), and ATOR (1). Out of 18 POSE specimens, 9 are classified correctly; 9 are misclassified and attributed to BIGO (2), ARRI (1), PERD (1), MALA (4), and ATOR (1). From 7 BALL specimens, 5 are correctly classificated and 2 uncorrectly attributed to PERD and MALA. Out of 13 MALA specimens only 5 are correctly classified; 8 are misclassified and attributed to BIGO (3), ARRI (2), PERD (1), POSE (1), and BALL (1). From 6 Aigüestortes specimens, 5 are classified correctly and one is incorrectly attributed to BIGO.

DISCUSSION

A look at the results leads to the conlusion that the *I. bonnali* populations in the centre of the range of the species are the morphologically most intermediate and probably the most primitive ones. At the end of the last glaciation, this species could have spread from this central area towards the west to Monte Perdido and Neouvielle and from here, using a north Pyrenean passage, to Bigorre, Balaitous, and Arriel. The location of this probably würmian refuge could be derived from the geographic location of the most primitive and original populations as identified by their intermediate morphological positions by means of MST graphs and the minimum global distances to all other populations (see ARRIBAS 1999a).

In our case, the area of the U-shaped complex of mountains which forms the Cinqueta and Esera river watersheds (in the southern slopes of the Maladeta and Punta Suelza massifs of the Pyrenean axis, and the slightly southernly situated Posets and Ballibierna massifs) seems to be the central nucleus from which the species could have expanded into its present area. The whole phase of expansion seems to be postglacial, as in the case of *I. aurelioi* (see ARRIBAS 1999a).

If we analyze the sums of the Mahalanobis' generalized distances of the male samples, the Ballibierna + Besiberri sample appears as the most "central" one (total sum of distances to all other samples: 28.47), followed by Posets + Punta Suelza (35.37), and Maladeta (37.11). Ballibierna + Besiberri is directly connected to all other samples except Bigorre. All abovementioned massifs of Ballibierna, Maladeta, and Posets are located in the upper reaches of the Esera river, jointly situated in the aforementioned U-shaped Pyrenean sector. If all individual samples were treated separately (ungrouped results not presented in this paper), Maladeta would show the lowest global distance to all other populations (sum of 82.37) immediately followed by Ballibierna (83.31) and Posets (86.72). Besiberri would be but slightly more differenciated (91.93), while the other samples were clearly more divergent. Nonetheless, according to the MST, Posets is the best connected individual sample, followed by Maladeta and Ballibierna.

Also in the female analysis, Posets + Punta Suelza is the best connected and most central sample (19.25), followed by Maladeta (29.45). If all individual samples were treated separately, Posets would show the lowest global distances (70.39) followed by Maladeta (77.29). In an ungrouped analysis, Ballibierna would appear more differenciated. As in the analysis of males, the best connected sample is Posets.

Thus, the southern slopes of this U-shaped group of mountains (Posets - Maladeta - Ballibierna) contour the presumed würmian refuge area of *I. bonnali* from which its current distribution area originates. There is, however, the possibility that some of the more differenciated populations, such as Bigorre or Aigüestortes, could go back to additional würmian refuges, from where postglacial spreading and intergradation with the central Pyrenaean populations could have occured. Considering all characters globally (as is done by the CVA and the UPGMA dendrogram), the Bigorre population (although being the sample with most differences in ANOVA) is not markedly differentiated from the central Pyrenean populations. Hence, the more parsimonious assumption should be that the peculiarities of the Bigorre sample (including osteological ones, see ARRIBAS 1998a and diagnosis) go back to founder effects in extreme populations.

Aigüestortes is, both in males and females, the most differentiated population (see figs. 2, 3, 4, 5) among the numerically well represented samples. It cannot be excluded that populations in this area (Filià, Muntanyó de Llacs, Encantats) - where individuals are more scarce and populations apparently more scattered - could be 'in situ' remnants of würmian refuges. The geographical position of these easternmost populations, which are geographically located between *I. aurelioi* and the main part of *I. bonnali*, fits well with the hypothesis of the previous presence of the species in this area and, thus, of the possibility of survival during the würmian colds in this zone. In the present analysis, the sample of Besiberri seems more closely related to the sample from Ballibierna (which is separated by the deep Ribagorzana river valley). But if all populations of this area are considered in detail (see ARRIBAS 1998 b), the most meridional populations (Filià in Aigüestortes, and Llauset in Ballibierna) are closest to each other, whereas Besiberri is closer to the Maladeta (Picada and Benasque) samples. Muntanyó also appears well differenciated (ARRIBAS 1998 b).

Thus, it can be postulated that part of the populations east of the Ribagorzana river valley may be re-imigrants from the Maladeta - Posets refuge (as in the case of Besiberri), while other more eastern populations (see above) could be remnants of another refuge or several refuges where they were isolated for a long time or weakly connected to the Maladeta - Posets population (see ARRIBAS 1998b), a question that deserves a more detailed study.

Hypothesis on the speciation and the scenario of evolution

The end of the genetic flux between *I. bonnali* and *I. aurelioi* can be traced back to the Middle Pleistocene (ARRIBAS 1997, 1999a, b), probably the Mindel-Riss interglacial when the bottom of the Noguera Pallaresa river valley was covered by a belt of supra-mediterranean vegetation, or the beginning of the Riss glaciation when the valley was covered by a glacial tongue (see references in ARRIBAS 1999a). It can be hypothesized that this prevented the populations living at either side of the valley from getting into contact which may have started their independent differentiation then. Applying NEI's (1975) formula (1 distance unit Nei [D_{nei}] = 5 million years) provides a good estimate of the duration of the period between the differentiation of *I. horvathi* and the beginning of the Plio-Pleistocene climatic deterioration (mean D_{nei} in respect to the Ibero-Pyrenean species of 0.48, which corresponds to 2.44 million years) (see ARRIBAS 1997). This date is congruent with a period of progressive aridity and the Alpine glaciation scenario. The differentiation of *I. bonnali* and *I. aurelioi* from their common ancestor (D_{nei} = 0.06) can be tentatively traced back 300.000 years. During this period (Mindel-Riss interglacial), the climate was mild (even milder than today) and wetter (more oceanic) with mixed forests of broadleaved tree species. The vegetation was Mediterranean (southern slopes) and Atlantic (northern slopes). Pine, fir, and oak trees were present in the lowlands, whereas the mountains showed more or less all representatives of the current flora and fir was very restricted while *Pinus uncinata* was more widespread than today (GAUSSEN 1926; RITTER 1988).

During the numerous cold oscillations of the Riss glaciation, important changes occurred in climate (predominantly dry and cold) and flora. Conifers (mainly *Pinus* spp.), birch, and steppe vegetation with bogs and dwarf shrubs dominated the piedmont scenario, while beech trees took refuge in the valleys (GAUSSEN 1926; RITTER 1988). It seems justified to hypothesize that *I. bonnali* survived either in a single refuge area not far from the refuge of its sister species *I. aurelioi* (possibly in the easternmost part of the area inhabited now) or in several places, incompletely isolated from each other since profound morphological differentiations between the recent populations of *I. bonnali* were not detected. Among the recent sites of occurrence, Aigüestortes is closest to the Noguera Pallaresa river valley and certainly was a possible refugial area for *I. bonnali*, although more western refuges (Maladeta, Ballibierna or Posets, in the order of increasing distance and decreasing probability) might also be taken into account. Nonetheless, one particular area could again and again have served as a refuge in the various cold phases of the Riss glaciation.

The Riss-Würm interglacial was a wet and mild period (hotter and wetter than today) (PONS 1969; COOPE 1990; VAN VLIET-LANOE et al. 1991; FRENZEL et al. 1992; GARCIN 1994; RITTER 1998) in which the species could have been distributed in a manner similar as obseved today. Mean temperature during the Riss-Würm interglacial was two to three degrees centigrade higher than today and the upper limit of forests was elevated up to 400 m (OBERMAIER 1925). 120,000 years ago, in the area in question precipitation was at least increased by 300 mm and July, August, and annual mean temperatures were almost 2 °C higher when compared with the conditions of today (FRENZEL et al. 1992). This climate must have favoured the ascent of the vegetation belts (this supports the above estimation of up to 400 m) and caused an increased isolation of the alpine species in the highest parts of the massifs. In this interglacial period there was some oscillation in the extension of oak forests and returning Mediterranean elements (*Quercus ilex*, *Buxus*, *Vitis*, *Olea*, etc.). The northern slopes were dominated by an oceanic temperate vegetation, whereas a Mediterranean vegetation rich in lauraceous plants colonized the southern slopes (RITTER 1988). The end of this interglacial period seems to have been abrupt (WOILLARD 1979; MÜLLER 1979).

The beginning of the Würm glacial - a period of more or less intense cold and drought - favoured a vegetation composed of conifers and betulaceans (GAUSSEN 1926), *Artemisia*, *Ephedra*, *Armeria*, *Galium*, etc (currently still present in dry crests and arid areas) (RITTER 1988). In view of its present differentiation, *I. bonnali* was most likely reduced to one single refuge only (but see above, about the possibility of the existence of several refuges) in the last glacial maximum (45,000 to 60,000 years b. p. in the Pyrenees; BORDONAU 1992; BORDONAU et al. 1992; SERRAT 1992; MONTSERRAT-MARTÍ 1992; JALUT et al. 1992).

During the Würm period, important glacial centers developed in the central Pyrenean range. Most important were those of Panticosa - Vignemale (spatially coinciding with the westernmost part of the present territory of *I. bonnali*) and of Rius - Maladeta - Aneto (close to the presumed Würmian refuge of *I. bonnali*). In general, the importance of ice tongues decreased from the west towards the east, giving space to ice-free areas (possible refuges) rather in the eastern parts of the lizard's range, which accords well with the results of this study (see GARCÍA-SAINZ 1947).

The glaciers of the slopes facing north were generally longer and reached down to 400 m a.s.l. (maximum length given in km:

Aspe (28), Gave d'Ossau (38), Gave de Pau (52), Aure (28), Garona (66) - BARRÈRE 1963; TAILLEFER 1969; RITTER 1988), whereas those of the slopes facing south were shorter and reached down to 800 m a.s.l. only (Gallego (30), Ara (26), Cinca (30), Esera (30), Noguera Ribagorzana (22), Noguera de Tor (22), Flamisell (18), Noguera Pallaresa (51) - PENCK 1885; NUSSBAUM 1935; GARCÍA-SAINZ 1941, 1947; BARRÈRE 1963; RITTER 1988). Their probable aspect has been compared to the Himalayan (RITTER 1988) and the Bernina glaciers at present (GARCÍA-SAINZ 1947).

Several more or less isolated summits in the western part of the Pyrenees seem to have acted as "nunnataker" during this cold period (GARCÍA-SAINZ 1941, 1947; VILLAR 1977; ARRIBAS 1997, 1999a, 1999c), as has been postulated also for the middle and low elevations of the western part of the Pyrenees, where the proximity of Mediterranean areas of complex topography provided numerous plant refuges (references in VISSET et al. 1996). Unfortunately, there is lack of pertinent information on the central parts of the Pyrenees. Nonetheless, a similar situation can be supposed for the southern slopes of the Pyrenees where taxa endemic to the Pre-Pyrenean "sierras" speak in favour of the presence of glacial "nunnataker" or refuge massifs in this area.

Deglaciation and Holocene. With the return of mild conditions at the end of the Würm period, the oak forests returned and so did beech and mountain pine at higher altitudes. The fir tree re-intruded from the easternmost parts of the mountain range, the Scots pine returned from Spain and reconquered medium altitudes (montane and supramediterranean belts) (resumed in RITTER 1988). The beginning of this recomposition of the montane biota has been dated controversially. According to various authors (BORDONAU 1992; BORDONAU et al. 1992; SERRAT 1992; MONTSERRAT-MARTÍ 1992; JALUT et al. 1992), the period of maximum glaciation in the Pyrenees was from 45,000 to 60,000 years b.p. Like other alpine species, *I. bonnali* might have started to spread from its refuges perhaps as early as 25,000 years b.p. when the glaciers disappeared from the Pyrenean piedmont and withdrew into the higher parts of the mountains (about 26,000 years b.p. - ANDRIEU et al. 1988). The vegetation at the Pyrenean piedmont has been supposed to be still an alpine tundra in this period (VAN VLIET-LANOE et al. 1991). Notwithstanding this early withdrawal of the glaciers, palynological data shows us that the great change in vegetation associated with the climatic improvement began only after the so-called "15,000 b.p. event" (REILLE & LOWE 1993). It is clear that if glaciers existed 15,000 years b.p., they had withdrawn to altitudes of at least 1,800 - 1,900 m, since deglaciation was more or less completed most likely about 13,000 years b.p. (ANDRIEU et al. 1988; JALUT et al. 1992). Data on the deglaciation of the northern Atlantic Ocean supports the suggestion that the Pyrenees had their glacial maximum about 20,000 years b.p. - like northern Europe. August and mean annual temperatures in the study area were 8 to 10 degrees centigrade below today during the maximum of this last glaciation, hand in hand with a decrease of annual precipitation of about 500 mm (FRENZEL et al. 1992). Due to the above discrepancies, one should be cautious in dating the beginning of the expansion of *I. bonnali* from its glacial refuge. In fact, the early maximum of the Pyrenean glaciers could be explained by the marked drop in temperature accompanied by a still high precipitation. In later phases of the last Pyrenean glaciation, the decrease in precipitation (a dry period was registred at about 15,000 b.p. - ANDRIEU et al. 1988) induced a slight retreat of the glaciers and stabilization of the climate while - in other parts of Europe and in the Alps - the inertia of the gigantic glacial apparatuses increased their volume and conditioned the local climate (SERRAT 1995). In other words, the early (25,000 years b.p.) retreat of the Pyrenean glaciers, which was not accompanied by corresponding reactions of the vegetation, does not support a scenario of reconstruction of the high mountain biota at that time.

Apart from the abovementioned considerations, the postglacial spreading of *I. bonnali* from its würmian refuge must have been rapid and possibly synchronous with the forest's return to the mountains (yet after the "15.000 b.p. event", see above).

Given that the hypothethic refuge of *I. bonnali* was situated in the east of its current territory, it is not surprising that this species was unable to pass the Arriel and

Balaitous massifs because they constituted a great Pyrenean glacial nucleus and must have been an effective barrier against the westward expansion of central Pyrenean taxa. During the final stages of deglaciation, when the lizard finally arrived there, the upper limit of forests was probably at a level similar to the current one, thus, impeding the colonization of otherwise suitable massifs in the west such as Aspe, Ossau, and Anie. The area of this great glacial nucleus constitutes a clear cut in the current distribution of alpine biota in the Pyrenees (ARRIBAS 1999c).

The presence of the deep Pallaresa and Garona river valleys prevented *I. bonnali* from expanding toward the east, where *I. aurelioi* and *I. aranica* live today. However, postglacial re-colonization of suitable massifs of the southern Pyrenees such as Cotiella or Turbón cannot be excluded. The present absence of *I. bonnali* from the Pre-Pyrenean "Sierras", can be explained by its extinction in these meridional localities during warm and dry holocene periods (most probably the Atlanticum, 7,000 - 5,000 years b.p.) (see ARRIBAS 1999 c) when annual mean temperature was higher (1-2 °C) and precipitation rate lower (about 30 mm) than today (data from 6,000 - 5,500 b.p. - FRENZEL et al. 1992) which favoured the ascent of the forest. The hypsithermic periods in the Riss-Würm interglacial and the postglacial optimum (mainly Atlanticum) should have been as critical for the isolation and survival of this mountain lizard as the glacial periods proper. The species can be considered a "short distance re-imigrant" (sensu HOLDHAUS 1902, 1906, 1954) from a refuge massif.

DIAGNOSIS AND SYNONYMY

Diagnosis of *Iberolacerta bonnali*

Pholidosis and biometric key data of the specimens studied is summarized (mean value in parentheses). See also the data of the various samples in tables 2 (males) and 6 (females). Sexually dimorphic characters are indicated by an asterisk (*).

Biometry. Snout-vent length - SVL (*): Females (55.3 mm) appear to be significantly longer than males (52.17 mm). Longest male 58.73 mm, longest female 65.36 mm. Relative length of forelimb (*): 30.88 % - 41.82 % (35.57 %) of SVL in males, 29.15 % - 38.45 % (33.00 %) in females. Relative length of hindlimb (*): 38.78 % - 52.72 % (49.47 %) of SVL in males, 38.57 % - 52.72 % (44.96 %) in females. Pileus length: 1.81 - 2.19 (2.00) times its width. Masseteric scale: 17.64 % - 63.15 % (39.22 %) of the length of the parietal scale. Tympanic plate: 29.13 % - 55.76 % (42.74 %) of the length of the parietal scale. Anal plate shape (*), length in relation to width: 31.77 % - 72.65 % (56.65 %) in males, 55.06 % - 77.14 (66.83) in females.

Pholidosis: supraciliar granula rigth side: 0 - 15 (4.73), left side: 0 - 17 (4.50). Gularia (*): 17 - 25 (21.64) in males, 17 - 27 (22.34) in females. Collaria: 5 - 15 (10.10). Dorsalia: 36 - 48 (42.81). Transversal ventral scale rows (*): 25 - 29 (26.29) in males, 25 - 31 (28.32) in females. Femoral pores rigth side: 9 -18 (13.87), left side: 10 - 18 (13.88). Lamellae underneath fourth toe: 20 - 31 (26.10). Circumanal scales: 6 - 15 (9.22).

Rostral and internasal plates usually in contact (97.28 % of specimens); postocular and parietal usually in contact (91.23 %), as well as supranasal and loreal (79.42 %). Usually more than one scale between masseteric and tympanic plates which both are well visible. If only one intermediate scale present, then clearly smaller than masseteric and tympanic plates. Anomalies of head pholidosis (plates fused, broken or malformed are very frequent). The temporal region is shown in ARRIBAS (1993a: fig. 1a; 1993b: figs. 4-6; 1998b: fig. 1) and PEREZ-MELLADO (1998: fig. 32).

Colour-pattern. Dorsum greyish or brownish-gray, occasionally with olive reflections especially when shedded recently. Dorsally with or without two paravertebral rows of dots which are more distinguished in the anterior half of the body and more abundant in males, in some of which these dots delimit a darker central zone. In these patterned specimens, the pileus can also show some dots. The dark paravertebral pattern extends back as far as to the tail base. In most cases, clear dorsolateral stripes are not very distinct, or at most, appear very irregular in the foremost part of the dorsum. The lateral bands are of deep dark brown, usually uniform, sometimes inconspicuous. Inferior lateral band present in the form of a row of dots, more marked in males but frequently absent, especially in females.

Belly and breast uniformly white, rarely spotted (without black spotting in 52.9 % of males and 95.2 % of females, with the outermost ventral rows spotted in 43 % of males and 4.1 % of females, and the two outermost ventral rows spotted in the 3.9 % of males and less than 1 % of females) (fig. 11). This black punctuation is clearly less pronounced than in *I. aranica* and *I. aurelioi*. Rarely, the inner part of the calf is of light yellowish colour, probably an atavistic character.

Blue dots in the outermost ventrals are very rare (absent in 96.94 % of specimens; if present, almost only in males). Blue dots seem to be more frequent in Bigorre and Posets specimens, whereas they are totally absent in the samples of Aigüestortes and Monte Perdido.

Albinism was observed in an old female partial albino (Bigorre, Lac Bleu) with ill-pigmented areas of cream colour mainly in the head and upper surface of the tail.

Melanism is expressed in four specimens: one adult female and a juvenile (Bigorre, Lac Bleu) are totally black and the costal bands still discernible; a hatchling ex ovo (Llac de Llauset, Ballibierna) and a melanotic specimen, not seen by the author (Ibón de Respumoso area, Arriel Massif) (R. PUJOL, pers. comm.).

'Concolor' specimens (animals of very pale colour and faint dark pattern) were found in Bigorre (a juvenile) and Ballibierna, Llac de Llauset (an adult female - plate 2, fig. 13).

Geographic variation in colour-pattern. The dorsal background colour is subject to variation depending on the type of rock substrate on which the lizards live. Lizards living on granite or limestone are rather pale (as in Monte Perdido) while they are rather dark on slates and schists (as in Posets). Interestingly, the pale specimens show the most contrasting patterns.

Bigorre. The basic pattern of males and females is represented by two costal (temporal) bands (fig. 8), without further dark elements in the dorsal tract (69.2 % of males, 91.9 % of females) (plate 1, figs. 1-7). A dark vertebral pattern (paravertebral rows of dots) is rare and observed only in the oldest specimens. The dark elements are usually in a rather lateral position, more developed in the anterior half of the body (7 % of males, 8.2 % of females with a conspicuous pattern; 23.1 % of males, 8.21 % of females with very fine and barely distinguishable spotting). Background colour moderately dark. Anal plate frequently distinctively dark edged.

Neouvielle. The few specimens studied seem similar to those of Bigorre (plate 1, figs. 7-8).

Arriel. Similar to Bigorre (plate 1, fig. 9).

Monte Perdido. Males frequently with finely spotted paravertebral dorsal scale rows (plate 1, figs. 10-12), more developed in the anterior half of the body (35 % of specimens), covering the whole dorsal tract (30 % of specimens) or unspotted (35 %). Females less pigmented, only 23.5 % showing a fine dorsal spotting (76.4 % unspotted). The background colour is very bright in all individuals and the dorsal pattern - if present - is very contrasting. There is a tendency of reducing the costal bands which ocassionally appear marbled or faint, especially in females.

Punta Suelza. As in Bigorre (plate 2, fig. 1).

Posets. Similar to Bigorre. Males mainly unspotted (50 %), more rarely finely

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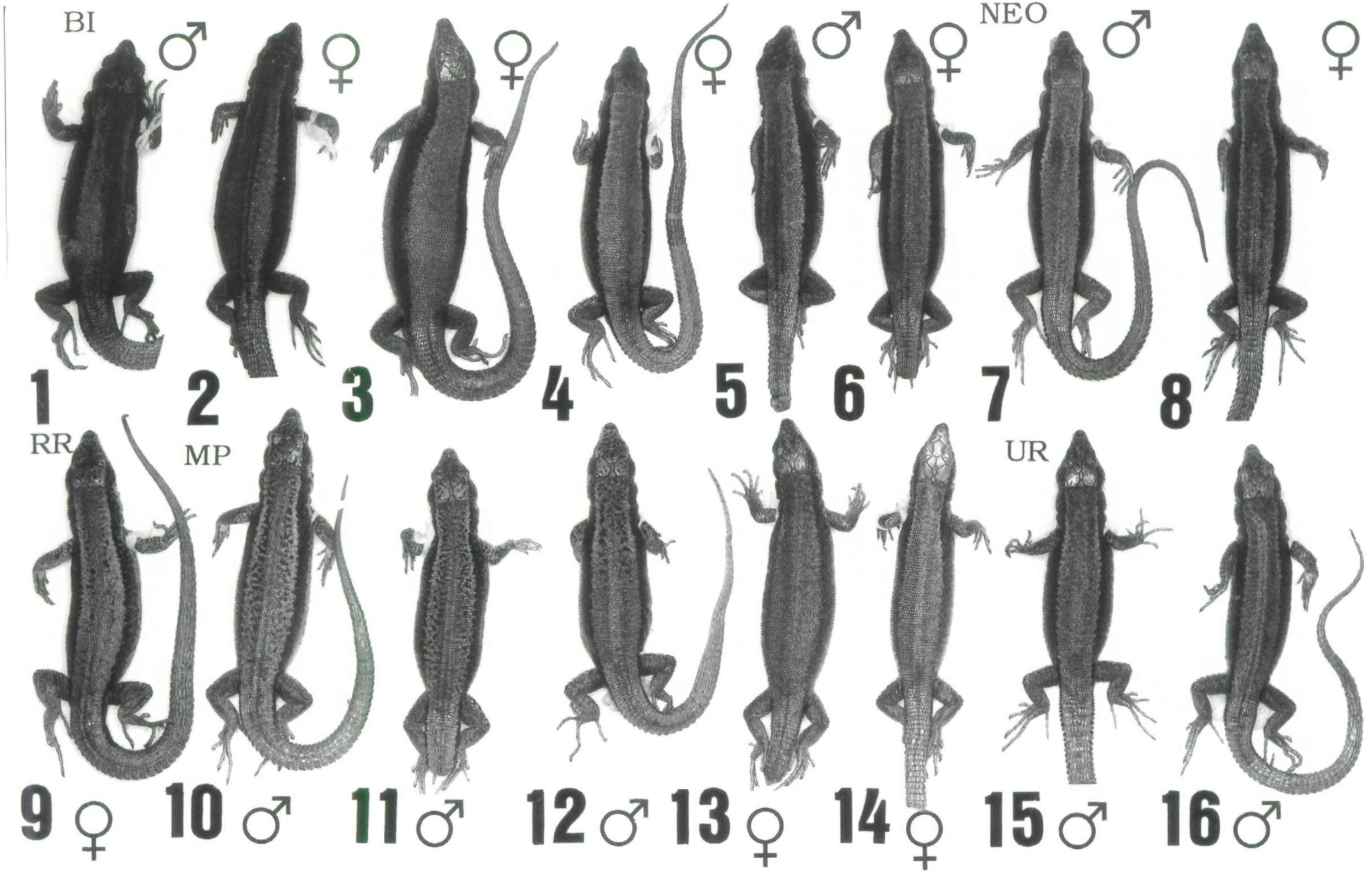
Plate 1 (opposite page): Variability of dorsal pattern in *Iberolacerta bonnali*. (M) - male; (F) - female.
Tafel 1 (gegenüberliegende Seite): Variabilität der Rückenzeichnung bei *Iberolacerta bonnali*. (M) - Männchen; (F) - Weibchen.

Bigorre: 1 - Lac Bleu (M) CA 89080321, 2 - (F) CA 89080318, 3 - (F) CA 94082815, 4 - (F) CA 89070305; 5 - Crete du Tourmalet (M) CA 95071601, 6 - (F) CA 95071602. Neouvieille: 7 - Pic de Madamette (M) CA 95071501, 8 - (F) CA 95071502. Arriel: 9 - Lac d'Artouste (F) CA s.n.. Monte Perdido: 10 - M. Perdido (M) CA93081217, 11 - (M) CA 93071912, 12 - (M) CA 89970506, 13 - (F) CA 92050005, 14 - (F) CA 920504SN. Punta Suelza: 15 - Urdiceto (F) CA 95082603, 16 - (F) CA 95082604.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UR
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16 ♂

spotted in the vertebral area (35.5 %) or well spotted (12.5 %). Females mainly unspotted (70 %) more rarely finely spotted (20 %) or well spotted (10 %). Dorsal background colour very dark in the studied populations (plate 2, figs. 2-4; fig. 10).

Maladeta. Similar to Bigorre. Males mainly unspotted (64.7 %), more rarely finely spotted (23.5 %) or clearly spotted (11.76 %) (plate 2, figs. 5-9).

Ballibierna. Two paravertebral rows of dots are frequently found in adult specimens (33.3 of males, 33.3 % of females). Fine spotting observed in 16.66 % of males, and 50 % of females; 50 % of males and 16.6 % of females unspotted (plate 2, figs. 10-14; fig. 12).

Besiberri. Two paravertebral rows of dots are frequently observed in adult males (33.3 % of males) but not in females. Fine spotting found in 33.3 % of males, and 33.3 % of females; 33.3 % of males; 50.1 % of females unspotted.

Aigüestortes. Similar to Bigorre but of rather bright dorsal background colour. 33.3 % of males and 50 % of females have a fine, barely distinguishable dorsal spotting, whereas 66.6 % of males and 50 % of females are totally unspotted (plate 2, figs. 15-17; figs. 12, 13). Specimens from the area of Muntanyó de Llacs are bright and unspotted, whereas others as from Port de Filià are more distinctly patterned.

Ontogenic variation in coloration. The dorsum of hatchlings (calendar year of hatching) is gray or brownish-gray, usually uniform, with two dark costal bands (fig. 9). Occasionally, a very fine paravertebral dark spotting is present. Venter white, bearing conspicuous (compared to the adults) dark spots on the anterior edge of the ventral scales. Tail usually grayish, as is the dorsum, rarely with an inconspicuous slightly bluish or greenish tinge which is much less developed than in *I. aurelioi* (see ARRIBAS 1999a). Colour-pattern of young and subadults (until third calendar year) very similar to the hatchling basic pattern, without any vivid colour in the tail; the dark spots of the ventral scales are progressively reduced. Adults very similar to the juvenile basic pattern, however the extent of the dorsal dark elements is increased (see above).

Osteology. In the skull, the anterodistal process of the postfrontal is present, while the anteromedial process of the postorbitary is absent by secondary reduction. Postorbitary bone equal or slightly shorter than postfrontal. Premaxilla bears a slender and subparallel processus nasalis and seven teeth. 14 - 18 (mean 15.65) maxillary teeth, 17 - 21 (mean 19.1) dentary teeth, all being usually clearly bicuspid, however intermediate or even monocuspid in some individuals (especially in Monte Perdido where the proportion of mainly monocuspid and mainly bicuspid specimens is almost balanced).

Males have usually 26 presacral vertebrae, females 27. In many cases the third vertebra is associated with a bony rib. Sternal-xiphisternal formula: (3+2). Sternal fontanelle oval. Clavicles open (emarginated), interclavicle typically cruciform (length ratio of anterior branch to posterior branch 0.21 - 0.38, average 0.29). Usually six short posterior dorsal ribs, but occasionally five or seven. The number of five is fixed in Bigorre specimens (ARRIBAS 1997, 1998) while seven may be typical in an isolated population of the Aigüestortes area. First preautotomic caudal vertebrae with perpendicular processes only in their anterior part (A-type sensu ARNOLD 1973, 1989). For detailed osteological data see ARRIBAS (1997, 1998).

Karyotype composed of 24 chromosomes (12 biarmed, 12 uniarmed) in males, and 23 (13 biarmed, 10 uniarmed) in females. Sex chromosome system Z_1Z_2W. W chromosome easily recognizable in be-

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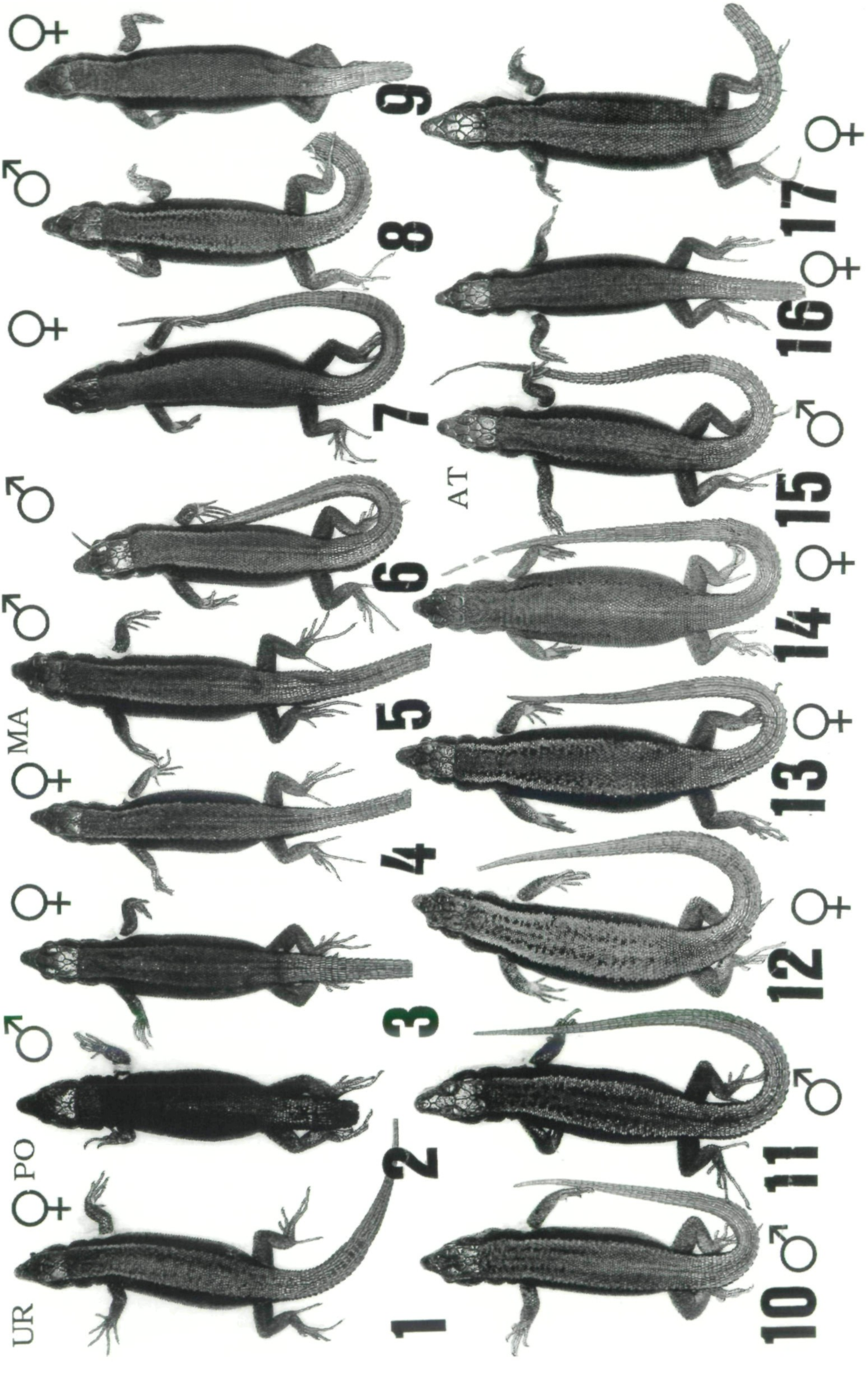
Plate 2 (opposite page): Variability of dorsal pattern in *Iberolacerta bonnali.* (M) - male; (F) - female.
Tafel 2 (gegenüberliegende Seite): Variabilität der Rückenzeichnung bei *Iberolacerta bonnali.* (M) - Männchen; (F) - Weibchen.

Punta Suelza: 1 - Urdiceto (F) CA 95082601. Posets: 2 - Vall del Clot (M) CA 91062701; 3 - Vall de Llardana (F) CA 95070801, 4 - (F) CA 95070801. Maladeta: 5 - Puerto de Benasque (M) CA 95090101, 6 - (M) CA 95090112, 7 - (F) CA 95090107; 8 - Port de la Picada (M) CA 95072404, 9 - (F) CA 95072401; 10 - Estany de Llauset (M) CA 94090501, 11 - (M) CA 94090502, 12 - (F) CA 94071603, 13 - (F) CA s.n., 14 - (F) CA 93071702. Aiguestortes: 15 - Bony Negre (M) CA 93071601, 16 - (F) CA 93071605; 17 - Gran Encantat (F) CA 93062601.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ing the smallest of the biarmed ones and presenting a conspicuous C-band in subtelomeric position in one of the arms. C-banding shows pericentromeric bands faintly marked in the first three biarmed chromosomes which are also resistant to ALU. This enzyme however, reveals an intense telomeric band in a pair of biarmed chromosomes which probably corresponds to the NOR-bearing band. AgNOR stains the telomers of the third pair of homologues. DAPI stains uniformly all chromosomes. NOR in a telomeric position in the long arm of the third pair of biarmed chromosomes (L-type sensu OLMO et al. 1990, 1993) (ODIERNA et al. 1994, 1995, 1996, in press; ARRIBAS 1997).

A sixfold mutant specimen was detected in Posets the karyotype of which was composed of biarmed chromosomes only. In this specimen a complementary robertsonian fusion must have occurred: four pericentric inversions (which explains the presence of an all biarmed karyotype) and a homologous translocation (which explains the presence of an heteromorphic pair of chromosomes). This fact demonstrates that chromosomic evolution is still in process and potentially active in this species, as it is in all species of the karyologically derived subgenus *Pyrenesaura* ARRIBAS, 1999. The karyotype of *I. bonnali* is probably the most derived one among all lacertids so far known (ODIERNA et al. 1994, 1995, 1996, in press; ARRIBAS 1997).

Allozyme data: This species differs from *I. aurelioi* (its sister species) in one allele (PGM-2) and from *I. aranica* in four alleles (AK, GOT-1, PGM-2, MDH-1) (MAYER & ARRIBAS 1996).

Hemipenis. Typical of a lacertid, in that the external lip is well developed (in contrast to *I. aurelioi* and *I. aranica*). Hemipenial microornamentation largely of the spiny type. Occasionally, isolated crown-shaped tubercles can be found suggesting that this spiny situation is derived from the crown-shaped (primitive for the *Pyrenesaura* group) type (ARRIBAS 1994a, 1997). The above description refers to male specimens before egg laying time.

Distribution. Endemic to the Central Pyrenees, from the Arriel massif in the west (Col d'Arrius), to the Sant Maurici-Aigüestortes National Park mountains in the east (Encantats massif). The northernmost locality is Lac Bleu in the French massif of Bigorre and the southernmost is Port de Filià in the Aigüestortes area (Lérida province, Spain). The species is more or less discontinuously present along the Central Pyrenees. Within the monotypic species, there are slight differences between populations, probably arisen from their Holocene isolation and the possible existence of more than one würmian refuge in the easternmost part of their current distribution area.

Type specimens. In his original description based on specimens stored in the Collection L. A. LANTZ (storage place unknown), LANTZ (1927) did not designate a particular type specimen out of 17 specimens available to him; however, he depicted one of them as 'Type' (Collection L. A. LANTZ n° 1209 R"; LANTZ 1927: page 60 figs. 2 and 4).

The only specimen of LANTZ's original material that could be traced (treated as syntype by BRYGOO 1988) is MNHN (Museum national d'Histoire naturelle, Paris) 8530: La 52; Lac Bleu de Bigorre (1960 m); leg. BONNAL (figs. 6, 7 in the present paper). This MNHN specimen should be considered as lectotype of the species.

Synonymy

1927 *Lacerta* (*Podarcis*) *monticola bonnali*, LANTZ, Rev. Hist. nat. appliq., Paris; 8: 10. Type locality: Lac Bleu de Bigorre (1969 m). Pyrenees.

1928 *Lacerta muralis bonnali*, MERTENS & MÜLLER, Abh. senckenberg. naturforsch. Ges., Frankfurt/M.; 41: 35.

1929 *Lacerta monticola bonnali*, MERTENS, Senckenbergiana biol., Frankfurt/M.; 11: 288.

1940 *Lacerta* (*Archaeolacerta*) *monticola bonnali*, MERTENS & MÜLLER, Abh. senckenberg. naturforsch. Ges. Frankfurt/M.; 451: 27.

1993 *Lacerta bonnali*, ARRIBAS, Bol. R. Soc. Española Hist. Nat (Sec. Biol.), Madrid; 90 (1-4): 105.

1993 *Archaeolacerta bonnali*, BÖHME & CORTI, Zoogeography of the lacertids in western Mediterranean basin; p. 21. In: VALAKOS, E. D. & BÖHME, W. & PEREZ MELLADO, V. & MARAGOU, P. (Eds.): Lacertids of the mediterranean region. Athens, Bonn, Alicante (Hellenic Zool. Soc.).

1997 *Iberolacerta bonnali*, ARRIBAS, Morfología filogenia y biogeografía de las lagartijas de alta montaña de los Pirineos. Bellaterra (Publ. Univ. auton. Barcelona), p. 297.

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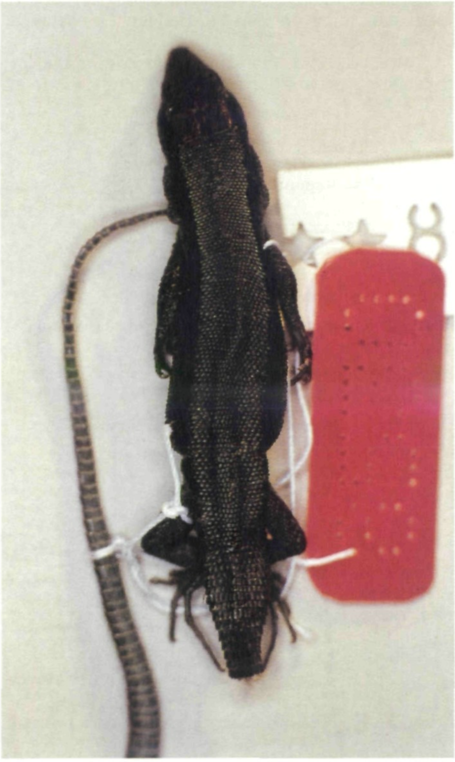
Figs. 6-9 (opposite page): *Iberolacerta bonnali*. / Abb. 6-9 (gegenüberliegende Seite): *Iberolacerta bonnali*.

Fig. 6: Syntype of *Iberolacerta bonnali* (LANTZ, 1927). MHNP 8530: La 52; Lac Bleu de Bigorre (1960 m); leg. BONNAL. Dorsal view.
Abb. 6: Syntypus von *Iberolacerta bonnali* (LANTZ, 1927). MHNP 8530: La 52; Lac Bleu de Bigorre (1960 m); leg. BONNAL. Ansicht von dorsal.

Fig. 7: Syntype of *Iberolacerta bonnali* (LANTZ, 1927). MHNP 8530: La 52; Lac Bleu de Bigorre (1960 m); leg. BONNAL. Ventral view.
Abb. 7: Syntypus von *Iberolacerta bonnali* (LANTZ, 1927). MHNP 8530: La 52; Lac Bleu de Bigorre (1960 m); leg. BONNAL. Ansicht von ventral.

Fig. 8: *Iberolacerta bonnali*. Gravid female, Lac Bleu (Bigorre Massif, Hautes Pyrenees, France). Note the basic pattern of the species - two costal (=temporal) bands.
Abb. 8: *Iberolacerta bonnali*. Trächtiges Weibchen, Lac Bleu (Bigorre Massiv, Hautes Pyrenees, Frankreich). Beachte das Grundmuster der Art - zwei Kostal(=Temporal)bänder.

Fig. 9: *Iberolacerta bonnali*. Yearling, Lac Bleu (Bigorre Massif, Hautes Pyrenees, France). Contrary to *I. aurelioi*, the tail is usually not brightly colored.
Abb. 9: *Iberolacerta bonnali*. Jungtier im ersten Lebensjahr, Lac Bleu (Bigorre Massiv, Hautes Pyrenees, Frankreich). Im Gegensatz zu *I. aurelioi* ist der Schwanz gewöhnlich nicht hell gefärbt.



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Figs. 10-13 (opposite page) / Abb. 10-13 (gegenüberliegende Seite)

Fig. 10: *Iberolacerta bonnali*. Female, Vall del Clot (Posets Massif, Huesca, Spain). In this locality, specimens live among slates and are very dark in coloration.

Abb. 10: *Iberolacerta bonnali*. Weibchen, Vall del Clot (Posets Massiv, Huesca, Spanien). An diesem Fundort leben die Eidechsen zwischen Schiefergestein und sind sehr dunkel gefärbt.

Fig. 11: *Iberolacerta bonnali*. Ventral aspect of a male, Puerto de Benasque (Maladeta Massif, Huesca, Spain). See the white belly which is characteristic to this species.

Abb. 11: *Iberolacerta bonnali*. Ventralansicht eines Männchens, Puerto de Benasque (Maladeta Massiv, Huesca, Spanien). Beachte die für die Art charakteristische weiße Bauchseite.

Fig. 12: *Iberolacerta bonnali*. Adult male, Estany de Llauset (Ballibierna Massif, Huesca, Spain). In this locality, specimens live on granite rocks and are very robust.

Abb. 12: *Iberolacerta bonnali*. Adultes Männchen, Estany de Llauset (Ballibierna Massiv, Huesca, Spanien). An diesem Fundort leben die Eidechsen auf Granitfelsen und sind sehr kräftig gebaut.

Fig. 13: *Iberolacerta bonnali*. Male, Bony Negre (Muntanyó de Llacs Massif, Aigüestortes National Park, Lleida, Spain).

Abb. 13: *Iberolacerta bonnali*. Männchen, Bony Negre (Muntanyó de Llacs Massiv, Aigüestortes Nationalpark, Lleida, Spanien).

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