

Morphological variability of the Cantabro-Pyrenean populations of *Zootoca vivipara* (JACQUIN, 1787) with description of a new subspecies

(Squamata: Sauria: Lacertidae)

Morphologische Variabilität der kantabro-pyrenäischen Populationen von *Zootoca vivipara* (JACQUIN, 1787) samt Beschreibung einer neuen Unterart
(Squamata: Sauria: Lacertidae)

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KURZFASSUNG

Die geographische Variabilität Ibero-Pyrenäischer *Zootoca vivipara* (JACQUIN, 1787) wird untersucht. Multivariate Analysen weisen auf eine Differenzierung zentral- und west-kantabrischer Stichproben, hauptsächlich aufgrund der besonderen Pileuskonfiguration, besonders der Männchen, während die Weibchen beträchtliche morphologische Überschneidungen mit Weibchen anderer Gebiete zeigen. Univariate Statistiken gruppieren Exemplare aus Kantabrien und dem Baskenland (s. lat.) näher beieinander, während die der Pyrenäen sich von diesen etwas abheben, ein Muster, das recht gut mit den Ergebnissen genetischer Studien übereinstimmt.

Die oviparen kantabro-pyrenäischen Populationen werden als neue Unterart beschrieben: *Zootoca vivipara louislantzi* ssp. nov.. Sie unterscheiden sich von anderen Unterarten in mehrerer Hinsicht und sind durch folgende Merkmalskombination gekennzeichnet: morphologisch (verminderte Anzahl von Collaria und Supralabialia, vermehrte Zahl von Subdigitallamellen der 4. Zehe, Fehlen eines diskontinuierlichen breiten, weiß gerandeten Rückenflebens und bei Weibchen jeglicher gelber Pigmentierung auf der Bauchseite), osteologisch (Tendenz zur Reduktion der Präsakralwirbel), karyologisch (W-sex Chromosom einarmig) und genetisch (Nei's genetische Distanz von 0.102 und die diagnostischen Allele ATA-150 und ATA-200 sowie 1,3(±0,5 Standardabweichung)% Sequenzdivergenz in der 16S rRNA und 1.8% (Spannweite: 1-2.6%) im Cytochrom b). Die biometrischen und meristischen Merkmale werden für die neue Unterart insgesamt und getrennt nach den Hauptverbreitungsgebieten angegeben.

ABSTRACT

The geographical variation of Ibero-Pyrenean *Zootoca vivipara* (JACQUIN, 1787) is studied. Multivariate analyses show a differentiation of central and western Cantabrian samples, mainly based on specific pileus scales configuration, especially in males, whereas in females there seems to be a considerable morphological overlap with female specimens of other areas. Univariate statistics clusters Cantabrian and Basque Country (s lat.) specimens more closely, with Pyrenees specimens slightly more differentiated, a pattern fairly coincident with the results of genetic studies.

Oviparous Cantabro-Pyrenean populations are described as a new subspecies: *Zootoca vivipara louislantzi* ssp. nov.. They differ from other subspecies in various traits and are characterized by the following combination of characters: morphologically (decreased collar and supralabial scales counts, increased numbers of lamellae under 4th toe, lack of the discontinuous wide white-bordered vertebral band and also lack of yellow colored bellies in females), osteologically (tendency toward reduction of presacral vertebrae), karyologically (W-sex chromosome uniarmed) and genetically (Nei's genetic distance of 0.102 and the diagnostic alleles ATA-150 and ATA-200; and also 1.3 (± SD 0.5)% of sequence divergence in 16S rRNA and 1.8 % (range: 1-2.6%) in cytochrome b). Biometric and meristic characteristics of the new subspecies as a whole, and separately for its main range areas are given.

KEY WORDS

Squamata: Sauria: Lacertidae; *Zootoca vivipara*, Taxonomy, Pyrenees, Cantabrian Mountains, Iberian Peninsula, scalation, coloration, morphology, geographic differentiation, new subspecies.

INTRODUCTION

The Viviparous Lizard is the reptile species with the widest distribution in the world. It is present from the Cantabrian Mountains and Ireland in the West, across

central France and the British Isles up to the North Cape in Scandinavia, as far to the East as Siberia, Sakhalin Island and Hokkaido in the Pacific Ocean (DELY & BÖHME

1984; BÖHME 1997; MAYER et al. 2000; GLANDT 2001). Despite its extensive range area, this taxon was the paradigm of a monotypic and nearly invariant species for years. Recent studies have shown that the species is represented by a fairly complex array of populations characterized by their karyological and molecular features, as well as in their reproductive mode (KUPRIYANOVA et al. 2006). However, some subspecies had been nominally described in the past:

Zootoca vivipara sachalinensis (PERELSHIN & TERENTJEV, 1963) (Terra Typica Sakhalin Island) is found not only in Sakhalin but also in Hokkaido, Amurland and Ussuriland, and probably extends across Asia to the West as far as the Baltic Sea, central Estonia, eastern Finland, eastern Hungary, parts of Romania and Transcarpathian Ukraine. Both East European populations as well the East Asian ones share an acrocentric/subtelocentric uniarmed W sex chromosome (A-type of KUPRIYANOVA 1990) and correspond to the clade D ("Eastern Viviparous") from SURGET-GROBA et al. (2001, 2006). The name "*sachalinensis*", however, could be a nomen nudum (W. MAYER, pers. com.) and this taxon, thus, in need of another name or a proper description with new authors and data.

Zootoca vivipara pannonica (LÁC & KLUCH 1968) (Terra Typica: Bořany, Kapusansky Forest in Eastern Slovakia) was thought to represent a typical relict taxon from the southeast European steppes ("Puszta") now restricted to the Pannonian Plains (Carpathian Basin). However, this taxon seems to be based on an unlucky historical confusion of populations not related among each other (W. MAYER pers. comm.). Specimens of the type locality (Bořany, Slovakia) do not correspond genetically with specimens from other areas attributed to "*pannonica*", and belong in fact to the clade E, "Western Viviparous" by SURGET-GROBA et al. (2006). Thus, *Z. vivipara pannonica* shall be considered a synonym of the "Western Viviparous" clade. Other "*pannonica*" (sensu Auctt.) belong to other clades (especially "Central Viviparous I" sensu SURGET-GROBA et al. 2006). All these lowland steppe populations of diverse genetic origin are probably ecological representatives of an ancestral (periglacial or early

postglacial) habitat, or a recent colonization by several *Zootoca* haplotypes which invaded a habitat that was almost devoid of lizards.

Zootoca vivipara carniolica MAYER, BÖHME, TIEDEMANN & BISCHOFF, 2000 (Terra Typica: Mt. Snežnik, Slovenia) (non *Lacerta vivipara* var. *carniolica* WERNER, 1897, nomen nudum), a southeastern oviparous form named and correctly described recently as a subspecies. It is distributed in Slovenia, northwestern Croatia, southern Austria and some areas of north Italy (Po Plain, Friuli). In this form males and females were presumed to have 36 chromosomes (35 in females of all the remaining *Zootoca* populations – but see "Central Viviparous II" below) and the W chromosome as small as a microchromosome. This form could deserve species status (BÖHME et al. 1999; MAYER et al. 2000; HEULIN et al. 2000; GHIELMI et al. 2001; ODIERNA et al. 2001); this question is currently under study (W. MAYER, pers. com.). *Zootoca* v. *carniolica* corresponds to the clade A ("Eastern Oviparous") from SURGET-GROBA et al. (2001, 2006).

The remaining populations had been included in *Zootoca vivipara vivipara* sensu lato. However, inside this assemblage, some different lineages have been identified in the last decades:

(a) A "Western Viviparous" (Clade E from SURGET-GROBA et al. 2001, 2006) (= *Z. v. pannonica* [LÁC & KLUCH, 1968]), at the moment unnamed but to which available names (as *oedura* SHEPPARD, 1804, terra typica: "England") could be applied if this taxon proves to be a valid subspecies. Their populations are mainly distributed over Germany, Austria, France, Great Britain, Italy, Poland, Sweden, Switzerland, Germany, Denmark, Bulgaria and are very similar among each other. They correspond to the biarmed (submetacentric) W chromosome (B-type of KUPRIYANOVA 1990). The internal structure of this group may be fairly complex and include diverse subclades (W. MAYER, pers. com.).

(b) Clade C ("Central Viviparous I") from SURGET-GROBA et al. (2001, 2006), a part of the former "false *pannonica*" specimens found in northwestern Hungary, as well as in eastern Austria that belong to the mitochondrial clade "North" (KUPRIYANOVA

et al. 2006). Karyologically they are very similar to the Russian type. This form presents an uniarmed W chromosome (A-type of KUPRIYANOVA 1990). This clade corresponds to the terra typica population of *Z. vivipara* (Schneeberg, Austria) and should bear the nominotypical name: *Zootoca vivipara vivipara*. The "original" description of *Zootoca vivipara* (by JACQUIN in 1783) was not a valid nomenclatural act, being a simple mention of the viviparity of a lizard, and the name should be referred to an other, subsequent author (LICHTENSTEIN, 1823) who really used the name as a binomen (SCHMIDTLER & BÖHME 2006; SCHMIDTLER pers. comm.). If this is accepted, the nomenclatural act will require typification (designation of a Neotype) including restriction of the type locality to "Schneeberg in Austria", in order to link the nominal subspecies to the locality indicated by JACQUIN (1783) and avoid even more confusion.

(c) Clade F ("Central Viviparous II") from SURGET-GROBA et al. (2001, 2006). A singular population of uncertain status was first localized in Ócsa (Hungary) and later found in central Hungary and along the southern Central Alps up to the Italian border (Type "east" in KUPRIYANOVA et al. 2006, table 1) allegedly with the same number of chromosomes in males and females (as in *Z. v. carniolica*), a ZW sex chromosome system (W-shaped as an acrocentric microchromosome) but viviparous. However, in fact this "viviparous variant" of the oviparous *Z. v. carniolica* is part of a completely different haploclade.

Although formerly oviparity was supposed to be the most primitive state and viviparity to be monophyletic having developed only once in *Z. vivipara*, modern chromosomal data suggest the independent appearance of viviparity both in a western population (Western Oviparous Z1Z2W) as well as an eastern one (Eastern Oviparous – *Z. v. carniolica*) (ODIERNA et al. 2004). However, the most parsimonious genetic trees suggest to the contrary a double arousal of oviparity (in *Z. v. carniolica* and the Cantabro-Pyrenean populations) (KUPRIYANOVA et al. 2006).

(d) Clade B ("Western Oviparous") from SURGET-GROBA et al. (2001; 2006) includes the oviparous Cantabro-Pyrenean populations (south of the Garona river),

with acrocentric W sex chromosome in females. This oviparity was first discovered by Louis LANTZ (1927) and later extensively studied by BRAÑA (1986), BRAÑA & BEA (1987), BÖHME (1997) and HEULIN (1988), among others. It constitutes a geographically and biologically well defined and singular (allopatric) group. Inside this group, there seem to exist two main clades, a "Pyrenean" (Pyrenean mitochondrial clade) in the eastern and northern slopes of the Pyrenees up to the Landes department, and a "Cantabrian" (Cantabrian mitochondrial clade) one which occurs in northwestern Spain, from Lugo across the Cantabrian and Basque Mts. up to the Western Pyrenees, entering adjacent France and overlapping with the former (as in Ossau Valley and Gers Department: Gabas, Louvie, Moura de Montrol). Within the "Cantabrian" clade, two subgroups can be distinguished, West and East of Picos de Europa respectively (Western and Eastern Cantabrian mitochondrial subclades, respectively). Their relationships are ("Pyrenees" versus "East Cantabrian + West Cantabrian") following SURGET-GROBA et al. (2001, 2006).

Concerning the intraspecific systematics of *Zootoca*, the most accurate studies rely on maternal inherited traits (W sex chromosome, mtDNA) but sound studies based on a wide range of characters inherited by both parents (nucDNA, morphology, allozymes) are needed for the delimitation of all these forms, especially those connected by a continuous distribution range. The relationships derived from mtDNA study are:

[Eastern Oviparous] [(Central Viviparous I + Central Viviparous II + Western Oviparous) (Eastern Viviparous + Western Viviparous)].

Over the last years, research lines focused mainly on the reproductive modes and genetics (DNA study and karyology), but very little has been done concerning the analysis of the morphology after the classic papers by WERMUTH (1955) and DELY (1981), written long before the recent discoveries about this species. Only recently, ARRIBAS (2001) studied eight scalation characters from a total of 534 specimens (221 males and 313 females) grouped into the clusters (Cantabrian Mts.; Pyrenees;

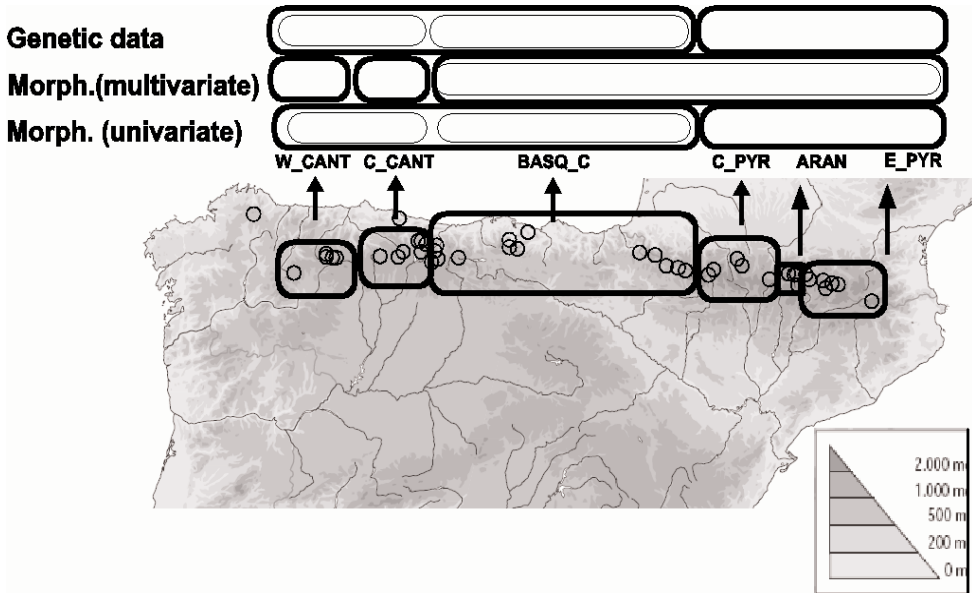


Fig. 1: Localities from which Ibero-Pyrenean *Zootoca vivipara* specimens have been studied (circles). The various groups (for abbreviations see Materials and Methods) as revealed by genetic and morphological (Multivariate and Univariate analyses, this study) studies are presented in frames.

Abb. 1: Fundorte des untersuchten ibero-pyrenäischen *Zootoca vivipara* Materials (Kreise). Eingerahmt sind die jeweils unterschiedlichen Gruppierungen (Abkürzungen erklärt in Materials and Methods), wie sie sich auf der Basis genetischer und morphologischer (multivariater und univariater Merkmalsanalysen, diese Arbeit) Gesichtspunkte darstellen.

British Isles; West and Central Europe; Central European “Puszta” [formerly attributed to *Z. v. pannonica*]; North Balkans [*Z. v. carniolica*]; East Europe plus West Asia; and Sakhalin [*Z. v. sachalinensis*], although with small sample size for some of the populations involved (especially Asiatic ones).

The results were particularly indicative for the discreteness of the oviparous forms. The first and almost unique attempt to find geographic variation patterns within Iberian *Zootoca* was made nearly forty years ago by CASTROVIEJO et al. (1970). The present analysis tries to fill this gap.

MATERIALS AND METHODS

Samples

For the study of the Cantabro-Pyrenean samples, a total of 330 specimens (128 males and 202 females) were measured. Geographic provenance of samples is represented in Fig. 1. Specimens were grouped in function of their geographic origins, considering the physiographic characteristics of the inhabited areas (mountain massifs, natural regions). Grouping into Operational Taxonomic Units (OTUs) has been the following

(localities are followed by the number of specimens, males and females, respectively):

OTU 1. – Eastern Pyrenees (E_PYR, Pyrenean mitochondrial clade, see Introduction): Estans de la Gallina (Lleida, Spain) (1, 0). Estany de Sotllo (Lleida, Spain) (1, 3). Ordino-Arcalis (Andorra) (1, 0). Etang de Prat Matau (Ariège, France) (1, 5). Estany de Soliguera (Lleida, Spain) (2, 1). Ransol (Andorra) (0, 1). Estany d’Estats (Lleida, Spain) (0, 5). Santuari de Nuria (Girona, Spain) (0, 2).

OTU 2. – Vall d'Aran (ARAN, Pyrenean mitochondrial clade): Coll de Barrados (Lleida, Spain) (22, 45). Pla de Beret (Lleida, Spain) (14, 27). Port d'Orla (Lleida, Spain) (1, 2). Estany de Liat (Lleida, Spain) (2, 16). Val de Cabaneta (Lleida, Spain) (1, 0). Estany Redó (Lleida, Spain) (2, 4). Tuc de Pedescaus (Lleida, Spain) (0, 3). Serra de Guarbes (Lleida, Spain) (0, 1).

OTU 3. – Central Pyrenees (C_PYR, Pyrenean mitochondrial clade): Lac Bleu de Bigorre (Hautes Pyrénées, France) (6, 9). Col del Tourmalet (Hautes Pyrénées, France) (2, 18). Puerto del Portalé (=Pourtalet) (Huesca, Spain) (2, 5). Peyragudes sky-resort (Haute Garonne, France) (2, 3). Lac d'Artouste (Basses Pyrénées, France) (0, 1).

OTU 4. – Eastern Pyrenees-Basque Mts.-Eastern Cantabrian Mts. (BASQ_C, Western Cantabrian mitochondrial subclade): Peña Prieta (Palencia, Spain) (2, 1). Sotres (Asturias, Spain) (1, 0). Guarrinza (Huesca, Spain) (1, 1). Pico Corisco (Cantabria, Spain) (0, 2). Pico Arrakogóiti (Navarra, Spain) (0, 1). Braña Vieja sky resort (Cantabria, Spain) (1,3). Polaciones (Cantabria, Spain) (1, 0). Puerto de Roncesvalles (Navarra, Spain) (1, 2). Tresviso (Cantabria, Spain) (1, 3). Puertos de Riofrío (Cantabria, Spain) (0, 1). Puerto de los Tornos (Cantabria-Burgos, Spain) (26, 10). Guriezo (Cantabria, Spain) (3, 0). Portilla de Lunada (Cantabria-Burgos, Spain) (9, 0). Otxogorri (Navarra, Spain) (1, 0). San Roque de Riomiera (Cantabria, Spain) (0, 1). Cantabria (without data, Spain) (2, 3). Fuente Dé (Cantabria, Spain) (1, 1). Portilla de la Sía (Cantabria-Burgos, Spain) (1, 1). Coteroprao (Cantabria, Spain) (0, 1). Barranco de Maze (Navarra, Spain) (0, 1).

OTU 5. – Central Cantabrian Mts. (C_CANT, Eastern Cantabrian mitochondrial subclade): Vega de Enol (Asturias, Spain) (0, 1). Puerto de Vegarada (León, Spain) (3, 1). Collado de Panderrueda (León, Spain) (1, 0). Puerto de las Señales (León, Spain) (4, 6).

OTU 6. – Western Cantabrian Mts. (W_CANT, Eastern Cantabrian mitochondrial subclade): Brañas de los Cuartos, Somiedo (Asturias, Spain) (2, 0). Lago de la Cueva, Somiedo (Asturias, Spain) (0, 1). Lagos de Saliencia, Somiedo (Asturias, Spain) (0, 1). Cofñal (León, Spain) (1, 0). Piornedo de Ancares (Lugo, Spain) (3, 5).

Studied characters

Variables studied for the Ibero-Pyrenean samples were:

* Biometric characters: Snout-vent length (SVL); Forelimb length (FLL); Hindlimb length (HLL); Pileus length (PL); Pileus width (PW). The following indexes have been calculated: FLL/SVL, HLL/SVL and PL/PW and are given multiplied x100 to avoid excessive decimals.

* Scalation characters: Granula Supraciliaria (GRS_r & GRS_l, granules in right and left sides), Dorsalia (DORS, number of transversal dorsal scale rows counted along the middle of the body), Ventralia (VENT, number of transversal rows of ventral scales), Collaria (COLL, number of scales in the collar clearly greater than surrounding ones), Gularia (GUL, number of scales in a straight line from the chin symphysis to the collar), Femoralia (FEM_r & FEM_l, right and left side numbers of femoral pores), Lamellae (LAM, rounded platelets underneath the fourth toe), anterior Loreals (= frenal scales) (LOR_r & LOR_l, number of anterior loreal scales in right and left sides), and Supralabialia previous to the subocular plate (SPRL, sum of both sides), Postnasalia (PN_r & PN_l, number of postnasals in right and left sides). Only specimens greater than 43 mm SVL (adults) were included in analyses. Contact between the supranasal and first loreal plates (SN-LOR) and configuration of the pileus scales (PILCONF), disposition of frontonasals following VOIPIO (1992), coded as: 1 = wide contact ("Median"), 2 = contact in one point ("Cross"), 3 = lack of contact ("Transversal") and 4 = supernumerary scale among prefrontals ("Rectangular").

* Coloration characters: Number of longitudinal ventral scale rows with black spots (PTV).

Statistical Procedures

Statistical analyses used in the morphological study are the same as in ARRIBAS (1996, 1999) and include both Univariate [ANOVA for SVL, scalation characters and indexes, and ANCOVA with SVL as a covariate for the other linear measurements, both of them with post-hoc TUKEY-KRAMER

tests at $p < 0.05$ (* significant) and $p < 0.01$ (**, highly significant) to detect differences among samples], as well as Multivariate techniques (Canonical Discriminant Analysis, CDA). In this later analysis, all specimens appear graphically displayed, but each population can be represented by a centroid (a hypothetical middle individual) from which UPGMA and Minimum-Length Spanning Tree (MST) computed from the Mahalanobis' distance matrix among these centroids, can be calculated. MST helps to detect the nearest neighbors based on their position in the multidimensional space. Cophenetic correlation coefficient was calculated to ascertain the goodness of fit of the UPGMA-derived matrix of cophenetic (ultrametric) distances to the original distance matrix (ROHLF 2000).

Multivariate analyses (CDA) and Univariate statistics were performed with NCSS 2001 (HINTZE 2001) and Mahalanobis' Generalized Distances computed with S-PLUS 2000® (Mathsoft 1999). UPGMA trees and MST were calculated with NTSYS 2.1® (ROHLF 2000).

Osteological study

Specimens cleared and stained for bone study are detailed in Appendix 2. These specimens (alcohol conserved) were skinned and eviscerated, and posteriorly cleared by means of 1% KOH in distilled water. Bones were stained with alizarine red and permanently conserved in glycerine (TAYLOR 1967; DURFORT 1978) (terminology is as in ARRIBAS 1998).

RESULTS

Multivariate Statistics – Males

* Canonical Discriminant Analysis (CDA) conducted with 126 male specimens shows two significant axes that explain 76.1 % of total intersample variation. The two axes together discriminate fairly well the Central and Western Cantabrian samples (all those West of Picos de Europa) from the remaining Ibero-Pyrenean ones (Fig. 2A).

The first discriminant axis (eigenvalue 1.23; 38.6 % of variance explained; $F_{105} = 2.7$, $p = 0.0000$) distributes the samples in a cline without continuity and great overlap from the Pyrenean samples in the most positive scores, progressively towards the Cantabrian in the most negative part, with overlap especially of the Central (French) Pyrenees (OTU 3) with the Eastern Pyrenees-Basque Mts. - Eastern Cantabrian Mts. (Basque Country s. lat. hereinafter) (OTU4). The highest loadings for the positive part have SN-LOR (0.44), LORr (0.39) and LORl (0.21) and for the negative PILCONF (-0.46), FEMl (-0.37), FLL/SVL (-0.25) FEMr (-0.24), DORS (-0.22), and HLL/SVL (-0.21).

The second discriminant axis (eigenvalue 1.19; 37.5 % of variance explained; $F_{80} = 2.2$, $p = 0.0000$) discriminates in their most positive scores both Western and

Central Cantabrian samples with a slight overlap especially with Aran Valley specimens. The Cantabrian populations are characterized by the highest values of PILCONF (0.49), GRSr (0.41), GRSI (0.28), PNr (0.24), PNI (0.18), and the lowest of FEMr (-0.39), FMI (-0.32), DORS (-0.29), and SN-LOR (-0.17).

* Minimum-length spanning tree (MST, not represented) connecting the centroids (hypothetical middle individuals) of each sample is fairly congruent with their geographical position, connecting in general neighboring samples. E_PYR connects with ARAN at a distance of 2.9686, ARAN with C_PYR at 4.1359, C_PYR (the unique sample connected to two others, only one of them geographically closer) with BASQ_C at 3.5327 and with C_CANT at 13.0435, and finally C_CANT with W_CANT at 14.3042.

* UPGMA trees (Fig 2B) based on Mahalanobis' distances among sample centroids cluster geographical neighboring populations in a very similar way as MST, especially in the Pyrenean and Basque samples with very small differences among them. More interesting is the marked differences of the Cantabrian samples West of Picos de Europa (C_CANT and W_CANT). Distances expressed in this tree have a very

good fit ($r > 0.9$; ROHLF 2000) to the original distance matrix (Cophenetic Correlation Index; $r = 0.96$; $t = 2.76$, $p = 0.99$).

Multivariate Statistics – Females

* Canonical Discriminant Analysis calculated with 200 female specimens shows a poor discriminant power among samples. The first two axes explain 71.7% of the total intersample variation, but their eigenvalues are lower than 1. Both axes together produce a relatively bad discrimination of the lizard samples, which largely overlap (Fig. 3A).

The first axis (eigenvalue 0.94; 40 % of variance explained; $F_{105} = 3.7$, $p = 0.0000$) shows a more or less clinal variation (with strong overlap) from samples 1 to 4, which include all the Pyrenean and Basque country s. lat. samples (from the positive to the most negative part), with samples 4 and 5 (again C_CANT and W_CANT) slightly excentric but also widely overlapping with some E_PYR and ARAN specimens. Thus, the first axis shows a gradual cline along Pyrenees, from the Mediterranean extreme of the range in the West up to Picos de Europa. Specimens west of Picos appear morphologically differentiated. The overlap of these latter with some Aran and Eastern Pyrenean specimens is due to their pileus scale configuration (“transverse” type). The positive part of the axis shows high values for PILCONF (0.563137) and GUL (0.301939), and the negative part strong loadings for FEMl (-0.547937), HLL_SVL (-0.436403), FEMr (-0.311495), and VENT (-0.300814).

The second discriminat axis (eigenvalue 0.75; 31.7 % of variance explained; $F_{80} = 2.9$, $p = 0.0000$) slightly separates towards its positive part populations 4 and especially 5 (Central and Western Cantabrian samples), overlapping with the above mentioned E_PYR and ARAN specimens. In the positive part there are high values of PILCONF (0.563137), FEMr (0.439908) and FLL/SVL (0.233596), and in the negative part high loadings of HLL/SVL (-0.436403) and LAM (-0.295927).

* Minimum-length spanning tree (not represented) is fairly similar to that of the males, connecting neighboring

samples. E_PYR is connected with ARAN at 3.8710, ARAN with C_PYR at 2.9855, C_PYR with BASQ_C at 1.6002, however with two anomalies: C_PYR connects with C_CANT at 8.0250 and ARAN appears most similar to W_CANT at 10.2151.

* UPGMA trees (Fig. 3B) based on Mahalanobis’ distances among sample centroids cluster geographical neighboring populations exactly like the dendrogram of the males, all the Pyrenean and Basque samples with very small differences among them, and the two Cantabrian samples West of Picos de Europa (C_CANT and W_CANT) fairly differentiated but not clustering with each other. Distances expressed in this tree also have a very good fit to the original distance matrix (Cophenetic Correlation Index; $r = 0.92$; $t = 2.34$, $p = 0.99$).

Univariate Statistics – Males

The results of the univariate statistics of the three main geographic (and mitochondrially identified) groups (“Pyrenees”, “Basque Country” s. lat. and “Cantabrian Mts.”) are presented in Table 1 (males).

In males, the “Pyrenees” sample accumulates 16 ($p < 0.01$) differences when compared to the other two samples (9 to “Basque Country” s. lat. and 7 to “Cantabrian Mts.”). Basque Country (s. lat.) accumulates 14 ($p < 0.01$) differences (9 to “Pyrenees” and 5 to “Cantabrian Mts.”). Finally, although apparently most strikingly differentiated in CDA, the “Cantabrian Mts.” sample has only the low number of 12 ($p < 0.01$) differences, (7 to “Pyrenees” and 5 to “Basque Country”).

Univariate Statistics – Females

The results of the univariate statistics of the three main geographic (and mitochondrially identified) groups (“Pyrenees”, “Basque Country” s. lat. and “Cantabrian Mts.”) are presented in Table 2 (females).

In females, the “Pyrenees” sample accumulates 13 ($p < 0.01$) differences when compared to the other two samples (8 to “Basque Country” s. lat. and 5 to “Cantabrian Mts.”). Basque Country (s. lat.) accumulates 11 ($p < 0.01$) differences (8 to “Pyrenees” and 3 to “Cantabrian Mts.”). Finally,

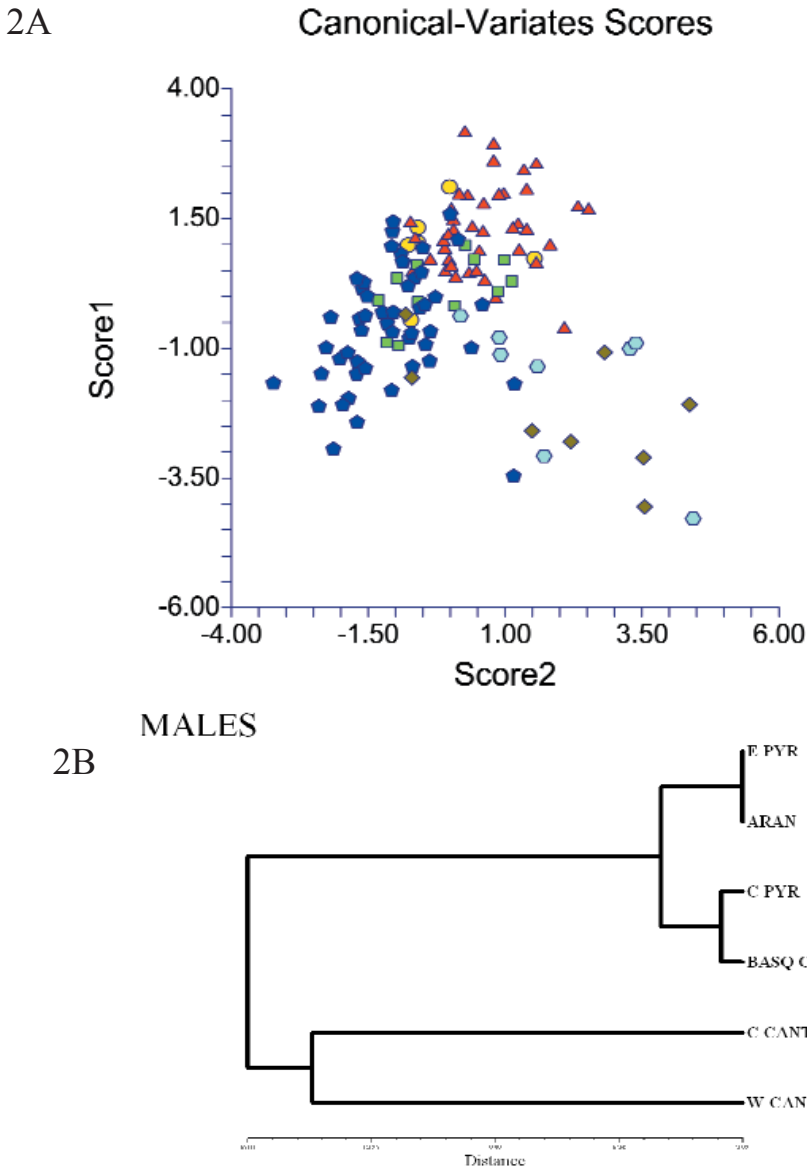


Fig. 2: MALES - CDA plot and UPGMA tree based on the morphology of male Ibero-Pyrenean *Zootoca vivipara* studied (for the coding of OTUs and abbreviations see Materials and Methods). A - CDA plot of the two first two axes (76.1 % of variance explained). Note the distant position of populations 5 (C_CANT) and 6 (W_CANT) is mainly due to their peculiar pileus configuration. B - UPGMA tree (Cophenetic correlation index: $r = 0.96$).

Abb. 2: MÄNNCHEN - CDA Diagramm und UPGMA-Baum auf Grundlage von morphologischen Merkmalen der untersuchten Männchen von iberopyrenäischer *Zootoca vivipara* (Kodierung der OTUs und Abkürzungen siehe Materials and Methods). A - CDA Diagramm der ersten beiden Achsen (76.1 % der Varianz erklärt). Man beachte die abgesonderte Lage der Populationen 5 (C_CANT) und 6 (W_CANT), die wesentlich durch die ungewöhnliche Pileusschild-Anordnung bedingt ist. B - UPGMA-Baum (Cophenetischer Korrelationsindex: $r = 0.96$).

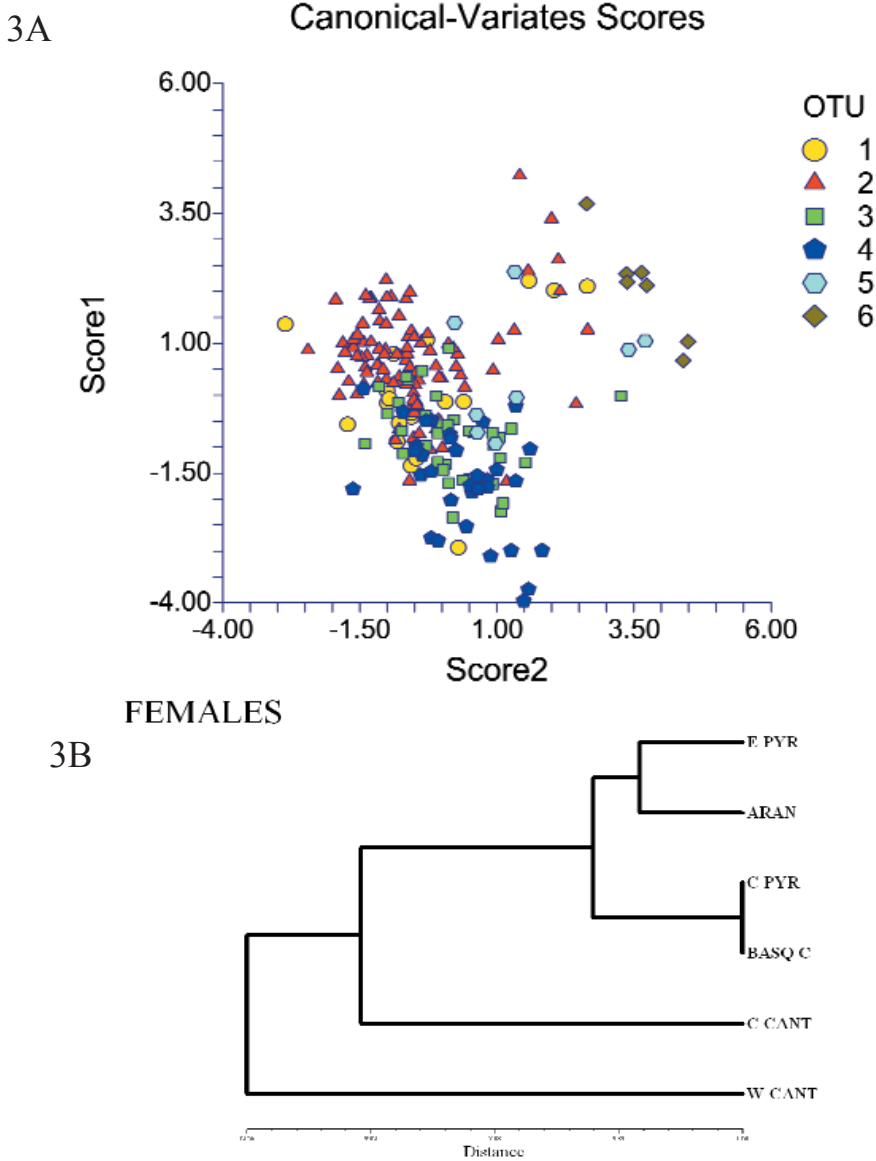


Fig. 3: FEMALES - CDA plot and UPGMA tree based on the morphology of female Ibero-Pyrenean *Zootoca vivipara* studied (for the coding of OTUs and abbreviations see Materials and Methods). A - CDA plot of the two first axes (71.7 % of variance explained). Note that the distant position of populations 5 (C_CANT) and 6 (W_CANT) is not as clearly expressed as in the males due to more overlap with some Pyrenean specimens that share this "rare" pileus scale configuration. B - UPGMA tree (Cophenetic correlation index: $r = 0.96$).

Abb. 3: WEIBCHEN - CDA Diagramm und UPGMA-Baum auf Grundlage von morphologischen Merkmalen der untersuchten Weibchen von iberopyrenäischen *Zootoca vivipara* (Kodierung der OTUs und Abkürzungen siehe Materials and Methods). A - CDA Diagramm der ersten beiden Achsen (71.7 % der Varianz erklärt). Man beachte, daß die abgesonderte Lage der Populationen 5 (C_CANT) und 6 (W_CANT), nicht so deutlich ist wie bei den Männchen und zwar wegen des Auftretens von Pyrenäen-Exemplaren, die auch durch ungewöhnliche Anordnung der Pileusschilde auffallen. B - UPGMA-Baum (Cophenetischer Korrelationsindex: $r = 0.96$).

Table 1: MALES of the Ibero-Pyrenean *Zootoca vivipara* sample studied. Descriptive statistics and ANOVA/ANCOVA results for measurements, counts and indexes. Results are given for the new subspecies as a whole, and individually for three geographical clusters corresponding to the clades and subclades from genetic studies. * - $p < 0.05$ (significant), ** - $p < 0.01$ (highly significant).

Tab. 1: MÄNNCHEN der untersuchten ibero-pyrenäischen *Zootoca vivipara*. Deskriptive Statistiken und ANOVA/ANCOVA Ergebnisse von Meß- und Zählwerten sowie Quotienten. Die Ergebnisse werden für die neue Unterart insgesamt, und einzeln für drei geographische Gruppierungen angegeben, die Clades and Subclades genetischer Untersuchungen entsprechen. * - $p < 0.05$ (signifikant), ** - $p < 0.01$ (hoch signifikant).

<i>Zootoca vivipara louislantzi</i> ssp. nov. MALES	All samples <i>n</i> = 107	(1) Pyrenees (E_PYR+ ARAN+ C_PYR) <i>n</i> = 48	(2) Basque Country (Basque_C) sensu lato <i>n</i> = 47	(3) Cantabrian Mountains (C_CANT+ W_CANT) <i>n</i> = 12	ANOVA ANCOVA <i>F</i>	<i>p</i> value	Inter-sample Comparison		
							1-2	1-3	2-3
SVL	49.71±0.30 3.09-56.72	48.83±0.42 43.24-55.19	50.59±0.41 43.56-56.72	49.82±1.12 43.09-54.76	4.10	0.019312	*		
FLL	14.86±0.11 10.75-17.13	14.21±0.12 10.75-16.28	15.44±0.14 11.62-17.13	15.23±0.35 13.44-17.01	15.75	0.000001	**	**	
HLL	19.81±0.16 15.80-23.57	18.93±0.19 15.78-21.30	20.46±0.23 15.48-23.57	20.79±0.46 18.44-22.46	11.64	0.000028	**	**	
PL	10.11±0.06 8.22-11.38	9.85±0.09 8.22-11.13	10.35±0.07 8.68-11.38	10.28±0.24 8.61-11.29	5.49	0.0054	**	*	
PW	5.81±0.04 4.64-9.37	5.69±0.08 4.95-9.37	5.97±0.04 5.26-6.58	5.67±0.12 4.69-6.10	2.33	0.1025			
GRSr	0.28±0.0 0-3	0.39±0.09 0-3	0.06±0.03 0-1	0.75±0.21 0-2	9.33	0.000187	**		**
GRSI	0.28±0.05 0-2	0.39±0.08 0-2	0.08±0.05 0-2	0.66±0.22 0-2	7.35	0.001033	*		**
GUL	17.00±0.14 13-20	17.16±0.19 13-19	16.76±0.23 13-20	17.25±0.52 14-20	0.99	0.376077			
COLL	7.39±0.10 4-10	7.47±0.16 4-9	7.23±0.14 5-10	7.66±0.22 6-9	1.12	0.329104			
DORS	31.99±0.18 28-38	31.37±0.24 28-35	32.76±0.28 29-38	31.41±0.59 28-35	7.43	0.000961	**		
VENT	24.38±0.14 21-32	24.59±0.15 22-27	24.14±0.23 21-28	24.50±0.73 22-32	1.03	0.359201			
FEMr	10.56±0.12 5-14	9.97±0.18 5-12	11.27±0.15 10-14	10.08±0.38 8-12	15.80	0.000001	**		**
FEMI	10.66±0.10 7-13	10.12±0.12 7-12	11.21±0.13 9-13	10.58±0.25 9-12	17.01	0.000001	**		
LAM	18.26±0.13 15-22	18.00±0.17 16-20	18.34±0.20 15-22	19.00±0.42 17-21	2.84	0.063288			
PNr	1.07±0.03 0-2	1.10±0.04 1-2	0.97±0.04 0-2	1.33±0.01 1-2	5.45	0.005607			**
PNI	1.06±0.03 0-2	1.08±0.05 0-2	1.00±0.05 0-2	1.25±0.13 1-2	2.33	0.102820			
LORr	0.97±0.06 0-6	1.19±0.08 0-2	0.87±0.08 0-2	0.50±0.19 0-2	7.84	0.000678	*	**	
LORI	1.01±0.07 0-4	1.25±0.08 0-2	0.91±0.11 0-4	0.50±0.19 0-2	6.35	0.002498		**	
SUPRLr	3.32±0.05 1-4	3.45±0.09 1-4	3.21±0.06 3-4	3.25±0.13 3-4	2.62	0.077746			
SUPRLI	3.45±0.05 2-5	3.56±0.08 2-5	3.38±0.07 3-4	3.33±0.14 3-4	1.71	0.185189			
SN-LOR	0.69±0.04 0-1	0.81±0.04 0-1	0.68±0.06 0-1	0.29±0.12 0-1	7.91	0.000635		**	*
PILCONF	1.17±0.06 0-4	1.02±0.02 1-2	1.04±0.06 0-4	2.33±0.30 1-4	39.87	0.000001		**	**
PTV	2.88±0.03 0-3	2.95±0.02 2-3	2.80±0.07 0-3	2.91±0.08 2-3	1.71	0.186825			
FLL/SVL	29.92±0.001 24.86-34.94	29.14±0.002 24.86-33.87	30.54±0.002 26.67-34.94	30.61±0.004 27.98-32.98	9.73	0.000133	**	*	
HLL/SVL	39.87±0.002 32.87-44.93	38.83±0.003 32.87-44.06	40.46±0.003 34.35-44.93	41.76±0.005 37.97-44.81	8.95	0.000259	**	**	
PL/PW	174.54±0.009 100.21-189.31	174.05±0.01 100.21-188.71	173.31±0.008 158.44-185.66	181.27±0.01 171.60-181.31	3.58	0.031472		*	*

Table 2: FEMALES of the Ibero-Pyrenean *Zootoca vivipara* sample studied. Descriptive statistics and ANOVA/ANCOVA results for measurements, counts and indexes. Results are given for the new subspecies as a whole, and individually for three geographical clusters corresponding to the clades and subclades from genetic studies. * - $p < 0.05$ (significant), ** - $p < 0.01$ (highly significant).

Tab. 2: WEIBCHEN der untersuchten ibero-pyrenäischen *Zootoca vivipara*. Deskriptive Statistiken und ANOVA/ANCOVA Ergebnisse von Meß- und Zählwerten sowie Quotienten. Die Ergebnisse werden für die neue Unterart insgesamt, und einzeln für drei geographische Gruppierungen angegeben, die Clades und Subclades genetischer Untersuchungen entsprechen. * - $p < 0.05$ (signifikant), ** - $p < 0.01$ (hoch signifikant).

<i>Zootoca vivipara lousilantzi</i> ssp. nov. FEMALES	All samples $n = 178$	(1) Pyrenees (E PYR+ ARAN+ C PYR) $n = 132$	(2) Basque Country (Basque_C) sensu lato $n = 32$	(3) Cantabrian Mountains (C_CANT+ W_CANT) $n = 14$	ANOVA ANCOVA <i>F</i>	<i>p</i> value	Inter-sample Comparison		
							1-2	1-3	2-3
SVL	53.42±0.34 43.06-65.32	53.14±0.38 43.48-65.32	54.86±0.69 49.29-64.51	52.74±1.81 43.06-63.24	1.98	0.141481			
FLL	13.57±0.07 11.18-19.58	13.37±0.08 11.18-19.58	14.27±0.13 12.82-16.60	13.88±0.29 12.32-15.98	10.81	0.000038	**	*	
HLL	18.25±0.09 14.75-22.56	17.89±0.09 14.75-20.94	19.48±0.21 15.96-22.56	18.90±0.42 16.38-21.94	33.37	0.000000	**	**	
PL	9.27±0.04 8.00-10.77	9.17±0.04 8.00-10.66	9.61±0.07 8.90-10.77	9.41±0.22 8.14-10.40	15.10	0.000001	**	**	
PW	5.37±0.02 4.51-6.24	5.32±0.02 4.63-6.24	5.60±0.03 5.23-6.03	5.38±0.14 4.51-6.18	12.62	0.000008	**		
GRSr	0.37±0.04 0-3	0.40±0.05 0-3	0.18±0.10 0-3	0.5±0.85 0-3	1.81	0.166396			
GRSI	0.35±0.05 0-4	0.36±0.05 0-3	0.21±0.14 0-4	0.57±0.17 0-2	1.46	0.234875			
GUL	17.33±0.10 14-21	17.37±0.12 14-21	17.15±0.22 15-20	17.28±0.39 15-20	0.33	0.717653			
COLL	7.25±0.08 3-10	7.30±0.09 3-10	6.90±0.24 3-10	7.57±.25 6-9	2.01	0.137462			
DORS	30.78±0.14 26-37	30.5±0.14 27-34	31.87±0.45 27-37	30.85±0.69 26-35	6.70	0.001573	**		
VENT	27.69±0.09 23-30	27.72±0.11 23-30	27.90±0.17 26-30	26.92±0.39 24-29	3.15	0.045298			**
FEMr	10.11±0.08 8-15	9.84±0.09 8-13	11.03±0.21 9-15	10.64±0.29 9-13	16.96	0.000000	**	*	
FEMI	10.10±0.09 8-14	9.81±0.09 8-13	11.25±0.20 9-14	10.21±0.31 8-12	21.46	0.000000	**	*	
LAM	17.89±0.08 14-21	17.96±0.10 14-21	17.62±0.18 16-21	17.85±0.29 16-20	1.17	0.313174			
PNr	1.03±0.03 0-3	1.06±0.03 0-3	1.00±0.07 0-2	0.92±0.07 0-1	0.86	0.423089			
PNI	1.05±0.03 0-3	1.06±0.03 0-3	0.96±0.07 0-2	1.07±0.12 0-2	0.71	0.493984			
LORr	1.03±0.05 0-4	1.07±0.05 0-2	1.09±0.18 0-4	0.50±0.20 0-2	4.06	0.018900	*	*	
LORl	0.94±0.05 0-3	1.00±0.05 0-3	0.96±0.13 0-2	0.42±0.20 0-2	4.30	0.015029	*	*	
SUPRLr	3.29±0.03 3-4	3.31±0.04 3-4	3.28±0.08 3-4	3.21±0.11 3-4	0.30	0.739654			
SUPRLl	3.31±0.03 3-4	3.28±0.03 3-4	3.43±0.08 3-4	3.35±0.13 3-4	1.54	0.217217			
SN-LOR	0.61±0.03 0-1	0.67±0.03 0-1	0.59±0.08 0-1	0.10±0.07 0-1	10.43	0.000053	**	**	
PILCONF	1.23±0.04 1-3	1.18±0.04 1-3	1.00±0.00 1-1	2.21±0.26 1-3	25.72	0.000000	**	**	
PTV	1.29±0.09 0-3	1.44±0.10 0-3	0.87±0.18 0-3	0.92±0.28 0-3	3.63	0.28526	*		
FLL/SVL	25.49±0.01 20.57-33.20	25.24±0.001 20.57-33.20	26.8±0.002 22.91-29.95	26.51±0.005 23.05-29.88	4.84	0.008957			*
HLL/SVL	34.30±0.001 28.19-41.86	33.80±0.002 28.19-41.86	35.59±0.003 31.28-40.45	36.08±0.006 32.78-40.40	12.10	0.000012	**	**	
PL/PW	172.54±0.004 158.7-191.37	172.5±0.004 158.7-186.03	171.49±0.009 161.65-181.06	175.24±0.02 163.07-191.37	2.23	0.110872			

as in males, “Cantabrian Mts.” samples had only the low number of 8 ($p < 0.01$) differences (5 to “Pyrenees” and 3 to “Basque Country”).

Osteology

A good résumé of the osteological characteristics of *Zootoca* can be found in ARNOLD et al. (2007). The study of specimens from various European origins (see appendix 2) offers few geographically consistent differences between them:

Skull: Often seven premaxillary teeth in adults (from six to eight in our samples). Pterygoid teeth absent; nasal process of premaxilla frequently broad, more or less long (but very short in a Turracher Höhe specimen belonging to the “Central Viviparous II” from SURGET-GROBA et al. 2001, 2006). Frontal bones often without anterior descending processes. Postfrontal and postorbital bones appear fused from embryos (RIEPEL 1992) and continue throughout life (not truly separated, but outlined and visible by transparency in some specimens, as in a male from Moosbrunn, Austria and in a female Cantabrian specimen). Maxillary-jugal suture not stepped. Supraocular osteoderms complete in adults.

Post-cranial skeleton: Usual number of presacral vertebrae is 26 in males (but in Cantabro-Pyrenean specimens 26 and 25 at almost equal frequencies), and 28 in females (more frequently 27 in Cantabro-Pyrenean females) (ranges: 25-27 in males and 26-29 in females of the species). Usually without bony ribs associated to the third presacral vertebrae. Ribs associated to the sixth presacral vertebrae frequently deviate from the usual Lacertini pattern (two segments, the second very short with two small pieces, or only one piece bifurcated as an “antler tip”) in that they are frequently are made up of two or three segments (found only in *Zootoca*, and at least in some *Lacerta* as *L. agilis* LINNAEUS, 1758). Medial loop of clavicle continuous (more frequently) or interrupted posteriorly (more rarely); four to six posterior presacral vertebrae with short ribs (usually five). Lateral arms of interclavicle more or less perpendicular to sagittal axis. Sternal fontanelle oval. Inscriptional ribs sometimes absent (from 0 to 2, more frequently 1). Sternal-parasternal formula usually (3+1), (3+2) and even (2+2). Pattern of caudal vertebrae often A-type, very occasionally B-type (none in the studied sample).

Fig. 4 (opposite page): Dorsal pattern variation in Eurasian *Zootoca vivipara*. The two specimens depicted at the left show the typical pattern of *Zootoca vivipara louislantzi* ssp. nov., male above (from Tresviso, Cantabria, Spain) and female below (from Estany de Sotllo, Lleida, Spain). Rectangles represent a transverse section of the lizards' back (taken from various sources).

Males / Männchen

- First row / Reihe 1: (*Z. vivipara*, “Western Viviparous”)
 1A - Belgium, 1B - United Kingdom, 1C-Alsace (F), 1D-United Kingdom, 1E- Denmark.
 Second row / Reihe 2: (*Z. v. vivipara*, “Central Viviparous I”)
 2A- Czech Republic (formerly “*pannonica*” sensu Auctt.), (*Z. vivipara*, “Central Viviparous II”) 2B -Turracher Höhe (A), 2C- Carinthia (A), (*Z. v. sachalinensis*, “Eastern Viviparous”) 2D - Retezat (RO), 2E - Finland.
 Third row / Reihe 3: (*Z. v. louislantzi* ssp. nov., “Western Oviparous”)
 3A - Somiedo (E), 3B- Ancares (E), 3C - Aran V. (E), 3D - Lac Bleu (F), 3E - Aran Valley (E).

Females / Weibchen

- Fourth row / Reihe 4: (*Z. vivipara*, “Western Viviparous”)
 4A - Denmark, 4B - United Kingdom, 4C - Germany, 4D - Vicenza (I), 4E - United Kingdom.
 Fifth row / Reihe 5: (*Z. v. vivipara*, “Central Viviparous I”)
 5A - Moosbrunn (A) (formerly “*pannonica*” sensu Auctt.), 5B - Illnitz (A), (*Z. v. carniolica*, “Eastern Oviparous”) 5C - Slovenia, 5D - Slovenia, 5E - Risnjak (HR).
 Sixth row / Reihe 6: (*Z. v. sachalinensis*; “Eastern Viviparous”)
 6A - Romania, 6B - Bulgaria, 6C - Altai (RUS), 6D - Japan, 6E - Japan.
 Seventh row / Reihe 7: (*Z. v. louislantzi* ssp. nov., “Western Oviparous”)
 7A - Ancares (E), 7B - Ariège (F), 7C - Hecho valley (E), 7D - Bigorre (F), 7E - Aran valley (E).

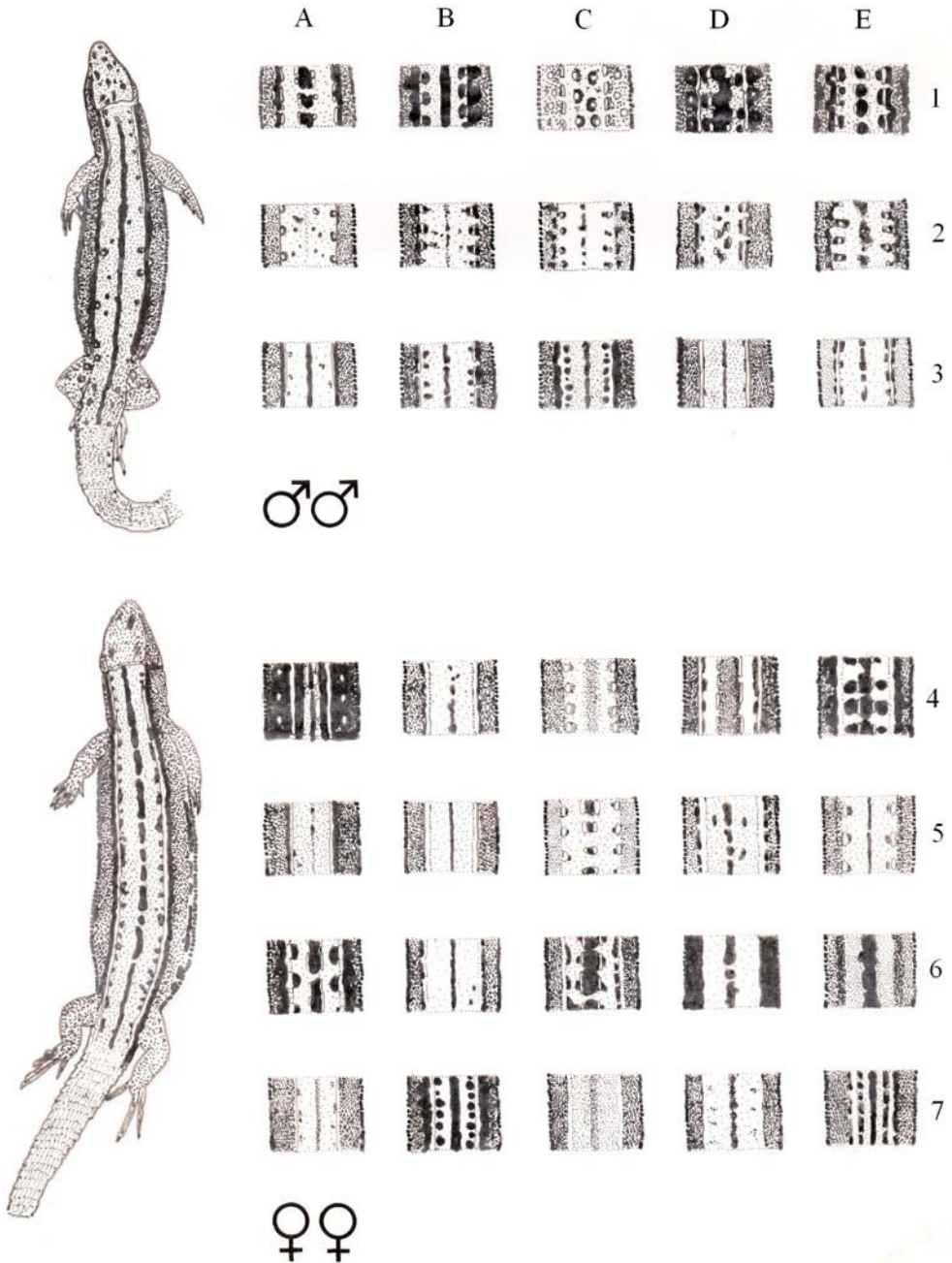


Abb. 4: Variabilität der Rückenzeichnung eurasischer *Zootoca vivipara*. Die beiden Exemplare auf dem linken Bildrand zeigen typisch gezeichnete *Zootoca vivipara louislantzi* ssp. nov.: ein Männchen (oben) von Tresviso, Cantabrien, Spanien) und ein Weibchen (unten) von Estany de Sotllo, Lleida, Spanien. Die Rechtecke repräsentieren Ausschnitte der Rückenzeichnung von Tieren der unterschiedlicher Fundorte (nach verschiedenen Quellen). Die Fundortangaben zu den Rückenzeichnungen finden sich in der englischen Bildunterschrift links.

DISCUSSION

Differences of the
Cantabro Pyrenean populations
relative to other *Zootoca*

ARRIBAS (2001) presented some differences between the oviparous populations (Pyrenees and Cantabrian mountains) and the remaining *Zootoca vivipara*, mainly characterized by lower collar scale numbers and supralabials, and higher counts of lamellae under the 4th toe in the former. Also, a clinal variation in W-E direction among the viviparous populations of the species seems to exist, and may be related to climatic parameters over their wide distribution range. In this paper, Cantabro-Pyrenean populations are regarded an independent subspecific unit within *Z. vivipara*, an opinion also shared by other authors (OSENEGG 1995; GLANDT 2001; ZAWADZKI & BISCHOFF 2006) but not substantiated until now (see appendix 1). ARRIBAS (2001) also pointed to the fact that among the coloration characters, one that distinguishes this new subspecies is the lack of a fairly wide and discontinuous dark vertebral band. Such a band which is contoured by two clear stripes is usually broken up into small clear dots flanking a dark lateral stripe and is very typical in the other *Z. vivipara* from Eurasia and in *Z. v. carniolica* (see MAYER et al. 2000; HEULIN et al. 2000) (Fig 4: 1 A, C-E; 2 D-E; 4 C-D; 5 C; 6 A, C), but absent in the Cantabro-Pyrenean oviparous populations (Fig. 4: 3 A-E and 7 A-E). Also, females of the Cantabro-Pyrenean populations never have any yellow colors on breast and belly (which is however not rare in other well known *Z. vivipara* populations). Yellow pigment on the ventral side is restricted to males in this subspecies, whereas females show a whitish or almost pinkish tinge underneath - a shine caused by physical effects, not a pigment. As to its osteology, there is a tendency toward the reduction of the vertebral counts relative to other *Zootoca* populations, in that the primitive and the derived (i. e. reduced) number are similarly abundant.

Thus, the oviparous Cantabro-Pyrenean *Z. vivipara* populations show morphological (dorsal band and scalation), osteo-

logical and karyological (W chromosome unarmed A-type in KUPRIYANOVA 1990) differentiations. Moreover, they are separated from neighboring allopatric viviparous populations by a Nei's distance of 0.102, diagnostic alleles in ATA dimeric allozymes (ATA-150 and ATA-200) (GUILLAUME et al. 1997) and also by 1.3 (\pm SD 0.5)% of sequence divergence in 16S rRNA (HEULIN et al. 1999) and 1.8% (range: 1-2.6%) in cytochrome b (SURGET-GROBA et al. 2001). This latter divergence is very similar to the difference between some haploclades of European *Zootoca* and *Z. v. sachalinensis* (1.9 %) (but less than between *Z. v. carniolica* and the remaining *Z. vivipara* subspecies with an average of 4.2 % (2.2 to 6.2 %). However the oviparous Cantabro-Pyrenean *Z. vivipara* populations could constitute a differentiable taxon inside within *Z. vivipara*, an opinion yet expressed by OSENEGG (1995) who named it without giving a diagnosis nor description (nomen nudum), and HEULIN et al. (1993) who said "...le degré de différenciation entre souches ovipares et vivipares est probablement subsppécifique". This taxon is named and described in Appendix 1, as a new subspecies of *Z. vivipara* (see below).

When compared to other oviparous *Zootoca*, HEULIN et al. (2000) found that females of Cantabro-Pyrenean lizards were smaller ($p < 0.05$) than those of the oviparous populations belonging to *Z. v. carniolica* (58 ± 4.0 mm; range: 49-67 mm in the Cantabro-Pyrenean, versus 66.5 ± 4.4 ; range 62-74 in *Z. v. carniolica*) which corresponds to lower egg numbers in the clutches of the former (however not significant if SVL effect is extracted). Moreover, Cantabro-Pyrenean lizards seem to lay eggs at a slightly more advanced developmental stage of the embryo (33.1 ± 1.1 , range 30-35 - staging according to DUFAURE & HUBERT 1961) than *Z. v. carniolica* (31.0 ± 0.8 ; range 30-32), also with a shorter incubation period (28.6 ± 2.2 days; range: 25-33 d; versus 34.7 ± 1.8 d, 33-39 d, at 22.5°C) and provided with thinner eggshells (46.3 ± 8.2 μ m, range: 28-62 μ m; versus 72.0 ± 11 μ m, range: 62-94 μ m) (HEULIN et al. 2002). Cantabro-Pyrenean oviparous females produce thicker eggs

($40\frac{1}{4}$ μm) than F1 hybrids (about $25\frac{1}{4}$ μm) when hybridized under lab conditions with the “Western Viviparous” form, which produces very thin eggs upon parturition (less than $10\frac{1}{4}$ μm) (HEULIN 1990; HEULIN et al. 1992). There is a resumé in HEULIN et al. (1993) about the characteristics of the F1 hybrids among viviparous and oviparous Common Lizards.

Geographic variation among the Cantabro-Pyrenean populations

In the Canonical Discriminant Analysis of male samples (Fig. 2A), Central and especially Western Cantabrian samples (West of Picos de Europa) appear characterized by negative loadings of the first and positive loadings of the second axis, caused by low values of SN-LOR (contact between supranasal and first loreal plates), number of loreal scales, dorsalia and high values for “transverse” pileus configuration, femoralia, postnasalia, supraciliaria and proportionately longer forelimbs (FLL) and hindlimbs (HLL). These Central and Western Cantabrian populations appear also well differentiated in the UPGMA tree (Fig. 2B). Considering the ANOVA/ANCOVA results for males (Table 1), the most discriminant characters are FLL, HLL, PL, LORr, and LORl for “Pyrenees”. GRSr, GRSr and FEMr for “Basque Country”, and SN-LOR, PILCONF and, to a lesser degree, PL/PW for “Cantabrian Mts.” with respect to the other two big samples.

In the CDA of females (Fig. 3A) it is also the samples of Central and Western Cantabria that are slightly differentiated, but with a considerable overlap, especially with Aran-Valley specimens (which also have “transverse” pileus scale configurations). These populations are characterized by the high values for transverse pileus scale configuration, gularia, femoralia, ventralia and relative forelimb length (FLL/SVL), and the low loadings for femoralia, lamellae under fourth toe and relative hindlimb length (HLL/SVL). UPGMA tree (Fig. 3B) also separates (but independently among them) the Central and Western Cantabrian samples. Considering the ANOVA/ANCOVA results for females (Table 2), the most

discriminant characters in females are FLL, HLL, PL, FEMr and FEMl, for “Pyrenees”. None for “Basque Country” in comparison with both of the other two samples, and finally, SN-LOR and PILCONF for “Cantabrian Mts.” in respect to the former two big samples.

If PILCONF were not included in the analyses (not shown), the cantabrian samples would lose much of their distinctiveness in the CDA, whereas the hierarchical clustering of UPGMA trees would be very similar to the one shown here (Figs. 2B, 3B) but only with C_CANT as clearly differentiated.

The pileus scales configuration (see material and methods section) is also revealing. The “median” type in which prefrontals are in wide contact is the usual disposition for the species, the other ones are rare and mirror relationships among samples. The “rectangular” pattern is an anomaly closely related to the “transversal” pattern, and is thought to be a pleiotropic by-product of epigenetic instabilities and to develop especially under environmental conditions considered suboptimal for this species (VOIPIO 1968).

Zootoca vivipara populations from West Europe are dominated by this “median” type, which usually makes up over 90%, whereas in Eastern Europe, the percentage falls to 65-70%, similar to some North European populations (64.6% for Finland, but as low as 45.9% in some places) (HEULIN 1986; VOIPIO 1992). In Cantabro-Pyrenean specimens the situation is more or less the same as in other West European populations (average of “median” type is 87.1%, $n = 335$) and in general is near 90% in all populations (E_PYR: 88%, $n = 25$; ARAN: 91.5%, $n = 141$; C_PYR: 95.9%, $n = 49$; BASQ_C: 98.8%, $n = 83$), but there is a considerable deviation in C_CANT (62.5%, $n = 16$) and especially in W_CANT (13.3%, $n = 15$). Specimens from Ancares are practically all of the “transverse” type, whereas in Xistral specimens the situation is less extreme and similar to other C_CANT samples. Despite the suggestion of HEULIN (1986) about possible differences among sexes in the percentage of specimens representing the “transverse” (plus “rectangular”) pileus configuration

type, I did not find significant differences in the Cantabro-Pyrenean samples (7.87% in males, and 9.4% in females; $\chi^2_1 = 0.057$; $p = 0.8117$, NS with Yates' continuity correction factor). As there is a genetic component in this character's inheritance (VOIPIO 1968, 1992), the current situation in the Cantabro-Pyrenean range suggests a shift in the genetic composition of the species resulting in a prevalence of rare founder alleles in the West Cantabrians (an example of REINIG's allele elimination hypothesis; REINIG 1938) with lineage sorting during the species' expansion to the extreme west of its distribution. Here a high proportion of specimens of these rarer variants seem to have been the founders (founder effect) of the current "transverse" pileus type populations. Alternatively, epigenetic disequilibria should favor the occurrence of this character state under suboptimal environmental conditions, as suggested by VOIPIO (1968), but that does not seem to be the case here. Other populations West of Picos de Europa also indicate a shift in this character, but not so marked, reinforcing the idea of this lineage sorting, or a secondary contact with more Eastern populations. However, the populations of *Z. vivipara* west of Picos de Europa as a whole (W_CANT + C_CANT) seem to have a particular PILCONF ("transverse" type: 38.7%, $n = 31$ for the whole area) that could reveal an ancient isolation for all these populations or the presence of a third refuge almost in the later phases of the Pleistocene, different from the main Cantabrian one postulated by GUILLAUME et al. (2000). These rare pileus configurations have effects on neighbouring scales, lowering significantly the percentage of contact among supranasal and first laterals, as in these Western Cantabrian samples.

The results of the univariate (ANOVA/ANCOVA) statistics for both sexes are congruent with those based on mitochondrial or other maternally inherited traits with the "Cantabrian" and "Basque Country" groups being closer (less $p < 0.01$ differences) and the "Pyrenees" more distantly related. ANOVA/ANCOVA statistics for the "Pyrenees" sample is inconsistent with its geographic position (more differences to the neighboring "Basque Country" than to the more distant "Cantabrian"). "Basque Country" (s. lat.) and "Cantabrian" appear,

however, closer and consistent in terms of geographic position and genetic data.

Osteological data: The Pyrenean sample has less premaxillary, maxillary and dentary teeth (average 6.25, 16.64 and 21, respectively) than the Cantabrian one (average 7.25, 18.58 and 21). In the Pyrenean sample, the sternal-parasternal formula is almost always (3+1), whereas the formulae (3+2) and (3+1) are almost equally represented in the Cantabrian samples. All individuals of the Cantabrian and the majority of the Pyrenees samples have closed clavicles, however, some open clavicles are found in the latter. The above results are merely indicative, as the reduced sample impedes to draw firm conclusions.

Genetic data: The electrophoretic study of GUILLAUME et al. (2000) shows that the populations of the two main geographic areas ("Cantabrian Mts." and "Pyrenees") probably are genetically not homogeneous. GUILLAUME et al. (2000) revealed the existence of two genetic types in the Pyrenees based on the study of the mannose-6-phosphate isomerase (MPI) enzymes whose alleles are situated in the W-sex chromosome of females and, thus, maternally inherited like mtDNA. One of them, slow migrating (MPI 190), is widespread among individuals of the Cantabrian Mts. and from southern slopes of the West Pyrenees up to the Tena Valley. The other, fast migrating (MPI 110 or MPI 120), was found among individuals of the northern slopes of the Pyrenees (including Landes department and in the Central and Western Pyrenees). On the other side, HEULIN et al (1999) detected the existence of three mitochondrial haplotypes: OH1, present in the northern slopes of the Pyrenees (Ossau Valley) which largely coincides with the distribution of the allele of the fast migrating MPI 110 or MPI 120; another one (OH2) present also south of Ossau Valley and extending to the west, along the Cantabrian Mts. (more or less coincident with the slow migrating allele MPI 190); and a third one (OH3) only present in the Portalé pass (in the contact area between the Ossau Valley in the northern and the Tena Valley in the southern slopes). Equally for the 16S rRNA, a contact zone among haplotypes was found in the area of the high Ossau Valley (HEULIN et al. 1999).

The study of a 429 bp fragment of cytochrome b and a 23 bp fragment of Glu-tRNA showed a more interesting pattern of differentiation, fairly coincident with the allozymic one. The greater part of the Pyrenean samples (Eastern and Central, up to the Ossau Valley) clusters together (coincident to the "Pyrenees" samples), and are somewhat differentiated from the remaining Cantabrian populations. These latter, cluster in two even closer subgroups, one from the Ossau valley (where the two great groups meet), across Navarra, Basque Country and Cantabria (here "Basque Country" s. lat. samples), and another subgroup west of Picos de Europa including two samples of the Central and Western Cantabrian Mts. (here "Cantabrian" samples) (SURGET-GROBA et al. 2001). Another study of a further 737 bp fragment of cytochrome b and an about 500 bp portion of the 16s rRNA gene, also shows two clusters geographically coincident with the ones outlined above, one in the French (and Eastern) Pyrenees and another in the Cantabrian Mts. (SURGET-GROBA et al. 2006). Thus, the southern slopes of the Western Pyrenees may harbor populations slightly differentiated from those of the Central and Eastern Pyrenees, presumably very similar to the populations of the Cantabrian Mts. that have their own two subclades: east and west of Picos de Europa, as shown in SURGET-GROBA et al. (2001), but not so clear in SURGET-GROBA et al. (2006) who only distinguish a unique Cantabrian clade extending as far as Ossau Valley and a Pyrenean clade from there eastward to the Mediterranean coast (Fig 1).

The multivariate study clearly distinguishes the three units involved in these studies, but their weight and importance is not in accordance with the hierarchy shown by the genetic results (Fig. 1). One cannot distinguish morphologically these two main mitochondrial clades (roughly east and west of Ossau Valley) by means of the CDA, but rather by the number of differences in ANOVA/ANCOVA. The morphological differences are inherited from both parents and their variation seems to be gradual and with great overlapping among them, which suggests a wide gene flow among these mitochondrial clades. Cantabrian populations West of Picos de Europa seem to be more

differentiated morphologically, but this is greatly attributed to their peculiar pileus scales disposition, as there is overlap in CDA with Pyrenean specimens that share this "rare" pileus configuration. A study of true nuclear genes could throw light on this question and be compared with the morphological results, but present results suggest that all the Cantabro-Pyrenean populations are closely related and probably with wide gene flow in their contact areas.

For the West European oviparous *Zootoca vivipara* GUILLAUME et al. (2000) located the glacial refuge during the last glaciation between the Pyrenees and the Cantabrian Mts. In my opinion this may be true, but their differentiation is fairly older than Würmian, and possibly other Pleistocene refugia and subrefugia could have become functional and complicated the current morphological or mitochondrial patterns. *Zootoca* from this area covering Cantabria and Basque Country (here "Basque Country" s. lat. sample) although belonging to the "Cantabrian mitochondrial clade" shows (almost only morphological) signs of intergradation with the Pyrenean clade. Two main refuges can be postulated: One is a Cantabrian refuge and the other may have been in any lowland place close to the northwestern Pyrenees. However, the Cantabrian group could have been split in two refuges in the last cold phases of the Pleistocene, an unknown place between Cantabria and the Bases Pyrenees, and another western one in Asturias or Lugo, in the extreme West of the species' current range area.

The cold hardiness of the species makes it even more difficult to ascertain where it could have taken refuge during the cold Pleistocene phases, as the southern third of what is France today was not glaciated (except mountains) and northern populations of this species currently inhabit without problems even permafrost-grounded areas, and pass over the Arctic Circle (ARRIBAS 2004). Even within a more or less homogenous Würmian area one could assume that the Garona river (of Pliocene origin and also present further north even during the coldest phases of the Würmian glaciation), acted as a barrier for some clades impeding contact with other *Z. vivipara* clades. The presence of the species under glacial or peri-

glacial conditions, as in a number of Würmian localities in Great Britain (Torbryn Caves, Nazeing, Rogers Cave and Cudmore Grove, among others) corresponding to the Oxygen Isotope Stage 2, coincides with the maximum of the late glacial (Würm/Weichselian). Fossil records from other continental localities as Oblazowa 2 (Poland; 33.430±1230 ybp) and Miesenheim II (SW Germany; ca.11.000 ybp) all from Late Pleistocene (HOLMAN 1998; GLEED-OWEN 1998), suggest that *Z. vivipara* in whatever of its forms could have lived in periglacial, probably in part ice-free areas, just as it does

today north of the Arctic Circle, even during the harsher periods of Late Pleistocene.

This possibility of survival in periglacial areas and repeated cycles of area colonization and retraction, could also be responsible for the current complex patterns of haplotype distribution, with some closely related and relictual, fully separated and other more widespread forms (from W. MAYER unpublished data).

The species has not been referred still to Pyrenean or Cantabrian Late Pleistocene localities (ARRIBAS 2004) but certainly was present here.

APPENDIX 1

Zootoca vivipara lousilantzi ssp. nov.

Holotype: MNCN n° 44290 (ex OA 95073001). Adult male. Pla de Beret (Vall d'Aràn, Lleida). Spain. 30-07-95. O. ARRIBAS leg.

Paratypes: (44 specimens) Pla de Beret, Lleida, Spain. 8M, 13F (MNCN 44291-98, ex OA 95071701-08) (NMW 38569, ex OA 95073002; MNCN 44299-00, ex OA 95073002-03) (NMW 38570-79, ex OA 96072201-10) (OA 97090201). Estany de Soliguera, Lleida, Spain. 2M, 1F (OA 95072101-03). Estany de Sotllo, Lleida, Spain. 2M, 3F (OA 91070111, 14, 07; OA 930807, 10). Estany d'Estats, Lleida, Spain. 1M, 5F (OA91081311, 13, 15; OA 92070322, 23; OA 960706SN). Estany Redó, Lleida, Spain. 3M, 4F (OA 93061502, 03, 06, 07, 08, 09; OA 980824). Santuari de Nuria, Girona, Spain. 2F (OA 94061601, 02).

Holotype and nine paratypes deposited in Museo Nacional de Ciencias Naturales (MNCN; Madrid, Spain), eleven paratypes in Naturhistorisches Museum Wien (NMW; Vienna, Austria). Remaining paratypes in the author's herpetological collection.

Diagnosis: When compared to other *Z. vivipara* populations, *Zootoca vivipara lousilantzi* ssp. nov. is morphologically characterized by lower collar and supralabial scale counts and an increased number of lamellae under the 4th toe. Regarding the pattern and coloration characters, it lacks traits which are frequently present and very typical in other *Z. vivipara*

from Eurasia (including *Z. v. carniolica*) such as a wide and discontinuous dark vertebral band contoured by two clear stripes which are usually composed of small clear dots flanking laterally dark wide dots in the vertebral area. Females never present yellow or orange pigment on breast and belly (not uncommon in other *Z. vivipara* populations). Osteologically, males present 25 and 26 presacral vertebrae at equal frequency (predominantly 26 in other forms) and females predominantly 27 (instead of 28). Karyologically they are characterized by a W chromosome of the uniarmed A-type (sensu KUPRIYANOVA 1990), and differ genetically (Allozymes) from neighboring (but allopatric) viviparous populations ("Western Viviparous") by a Nei's distance of 0.102 and diagnostic alleles of the ATA dimeric enzyme (ATA-150 and ATA-200) (GUILLAUME et al. 1997). There is also 1.3 (± SD 0.5)% of sequence divergence in 16SrRNA, and 1.8% (range: 1-2.6%) in cytochrome b. *Zootoca v. lousilantzi* ssp. nov. lays eggs slightly more advanced than the other oviparous ssp. *Z. v. carniolica*, and also has shorter incubation time and thinner eggshells.

Description of the holotype (Fig. 5): Adult male, Snout-vent length (SVL) 52.2 mm, Forelimb length (FLL) 15.2 mm, hindlimb length (HLL) 20.4, Pileus length (PL) 10.3, Pileus width (PW) 5.8, Granula supraciliaria in the right side



Fig. 5: Holotype of *Zootoca vivipara louslantzi* ssp. nov. (MNCN n° 44290). Adult male. Pla de Beret (Vall d'Aràn, Lleida). Spain. 30-07-95. O. ARRIBAS leg.

Abb. 5: Holotypus von *Zootoca vivipara louslantzi* ssp. nov. (MNCN n° 44290). Adultes Männchen. Pla de Beret (Vall d'Aràn, Lleida). Spanien. 30-07-95. O. ARRIBAS leg.

(GRS_r) 1, Granula supraciliaria in the left side (GRS_l) 1, Gularia (GUL) 18, Collaria (COLL) 9, Dorsalia (DORS) 32, Ventralia (VENT) 25, Femoralia right side (FEM_r) 10, Femoralia left side (FEM_l) 10, Lamellae under 4th digit (LAM) 18, Postnasal scales in the right side (PN_r) 1, Postnasal scales in the left side (PN_l) 2, Loreal scales in both sides (LOR) 2, Supralabial scales in the right side (SPRL_r) 4, Supralabial scales in the left side (SPRL_l) 3, Supranasal and first loreal in contact (SN-LOR), Pileus scales

configuration (PILCONF) “median” with wide contact among prefrontals, ventral black punctuation (PTV) in all six scale rows, relative length of forelimbs (FLL/SVL) 0.29, relative length of hindlimbs (HLL/SVL) 0.39, Pileus shape (PiL/PiW) 1.76; color (in alcohol) gray-bluish with dorsolateral clear stripes well visible. Pileus with very few markings, only with five small points in the outer parts of the parietal scales. Dorsal band in the form of a discontinuous row of irregular points, as



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Figs. 6 - 9: Pyrenean specimens of *Zootoca vivipara lousilantzi* ssp. nov.
6 - Female, Coll de Barrados, Viella (Val d' Arán, Lleida, Spain); 7 - Aged female, Lac Bleu de Bigorre (Hautes Pyrénées, France) partially buried for oviposition, note the rare light and contrasting pattern; 8 - Male, Puerto del Portalé (=Pourtalet; Huesca, Spain); 9 - Same specimen as Fig. 8. Underside.
Abb. 6 - 9: *Zootoca vivipara lousilantzi* ssp. nov. aus den Pyrenäen. 6 - Weibchen, Coll de Barrados, Viella (Val d' Arán, Lleida, Spanien); 7 - Altes Weibchen, Lac Bleu de Bigorre (Hautes Pyrénées, Frankreich) zur Eiablage teilweise eingegraben, man beachte die seltene helle Farbe und das kontrastreiche Muster; 8 - Männchen, Puerto del Portalé (=Pourtalet; Huesca, Spanien); 9 - Gleiches Exemplar wie in Abb. 8 von der Bauchseite.



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Figs. 10 - 13: Cantabrian specimens of *Zootoca vivipara lousiantzi* ssp. nov.
10 - Male, Puerto de las Señales (León, Spain); 11 - Female, Puerto de las Señales (León, Spain); 12 - Aged male, Puerto de Vegarada (León, Spain) with a clear and contrasting pattern; 13 - Female, Serra de Xistral (Lugo, Spain), the westernmost locality of the species in continental Europe.

Abb. 10 - 13: *Zootoca vivipara lousiantzi* ssp. nov. aus den Pyrenäen. 10 - Männchen, Puerto de las Señales (León, Spanien); 11 - Weibchen, Puerto de las Señales (León, Spanien); 12 - Altes Männchen, Puerto de Vegarada (León, Spanien) mit hellem, -kontrastreichen Muster; 13 - Weibchen, Serra de Xistral (Lugo, Spain), dem westlichsten Fundort der Art auf dem europäischen Festland.

well as discontinuous dorsolateral black stripes. Temporal (= costal) bands relatively clear, of gray-bluish background color, only delimited by a black irregular line above, and a fairly more discontinuous one in the lower part, continuing along the tail. Inferior lateral stripe decomposed also into small points. Ventral parts of the same gray-bluish tinge (in alcohol), cream-yellow in life, with a heavily black spotted pattern, also in the lower parts of the tail.

Variation: Juveniles have a pattern very similar to adult females, but it is masked by the overall dark brown (black at sight) pigmentation, as in other *Z. vivipara*. Subadults begin to show sexual dimorphism at the age of their second calendar year, when the yellow coloration appears on the belly of males. Adults show only few variation, especially expressed in the continuity or interruption of the pattern stripes (see Fig. 4 – rows 3 and 7 and Figs. 6-13) and in the background color, which is usually darker in moist localities and clearer and more contrasted with the black pattern in drier ones. For scalation and measurements see Tables 1 and 2.

Derivatio nominis: The subspecific epithet *louislantzi* honours Amédée

LOUIS LANTZ (Mulhouse 1886 - Basel 1953), the French herpetologist who was the first to discover oviparity in *Z. vivipara* from above the ville of Gerde (Hautes Pyrénées) in September 8, 1924.

Synonymy: In her unpublished doctoral thesis OSENEGG (1995) termed the Cantabro-Pyrenean population *Lacerta vivipara vasconiae*, which did not constitute a nomenclatural act. Later, GLANDT (2001: 65) used this nomen in his book of the Common Lizard where it represents a nomen nudum.

Distribution¹⁾: Cantabro-Pyrenean axis, with an extension to the Landes department (France) exclusively south of the Garona river that constitutes the northern limit of the range area. In the Pyrenees, it lives from Puigmal Massif in the East, to the west along the mountain range axis (but more widespread in the northern, more humid slopes where it descends to the foothills), across the Basque mountains, and along all the Cantabrian Mts. to the west as far as the Ancares and Xistral mountains (Lugo, Spain). The taxon is more abundant in middle mountain altitudes, but can be found from almost sea level up to 2100 m in Cantabrian Mts. and 2400 m in the Pyrenees.

APPENDIX 2

Additional materials included in the osteology studies

In addition to the Ibero-Pyrenean samples the following materials were included in the osteology studies:

- *Zootoca vivipara* (“Western Viviparous”): Adamello, Western Trentino Alps (Italy) (0,1).

- *Zootoca vivipara* (“Central Viviparous I): Lunz/See (Austria) (0,1); Moosbrunn (Austria) (1,0) (formerly “*pannonica*” sensu auctt.).

- *Zootoca vivipara* (“Central Viviparous II”): Turracher Höhe (Austria) (0,1).

- *Zootoca vivipara louislantzi* ssp. nov. (“Western Oviparous”): Lago de Cerveriz (Spain) (0,1); Puerto de Vegarada (Spain) (0,1); Coll de Barrados (Spain) (2,2); Col del Tourmalet (France) (0,1); Puerto de los Tornos (Spain) (1,0); Puerto de las Señales (Spain) (1,0); Cantabria (Spain) (no data) (1,2).

- *Zootoca vivipara carniolica* (“Eastern Oviparous”): Altopiano Pokljuka (Slovenia) (0,1); Velebit (Croatia) (0,1); Risnjak (Croatia) (0,1).

¹⁾ A small and presumably introduced population of unknown origin south of the Ebro river, in Puerto de Piqueras (Soria-Logroño; Sierra de Cebollera Mts.) has been detected (ARRIBAS unpublished). The animals were probably released in the last years (first detected 2006), as they were found in a well explored locality where various herpetological surveys from 1962 to 1993 did not detect them.

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(Santander, Spain), Sergi PLA (Barcelona, Spain), and others helped in several aspects with some specimens, data or helping in fieldtrips from 1986 onwards. Type specimens were captured under permissions n° 2017 (1991-1992), 1152 (1993), 563 (1994), 516 (1995), 5787 (1996), 106 (1997), 51 (1998) from Generalitat de Catalunya Environmental departments.

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