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Description of a new endemic species of mountain lizard from Northwestern Spain: *Iberolacerta galani* sp. nov. (Squamata : Lacertidae)

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Abstract

A new species of *Iberolacerta* is described from the Montes de León (northwest Iberia). This new species, *Iberolacerta galani* **sp. nov.**, is characterized by its relatively large size, high number of blue ocelli on the shoulders and the relatively frequent contact or near-contact between the supranasal and the first loreal scale, the fairly straight squamosal bone (only curved on its posterior part), a unique karyotype in *Iberolacerta* combining 2n=36 chromosomes, an L-type NOR and differentiated W and Z sex chromosomes, and unique mitochondrial DNA sequences for the cytochrome *b* and 12S rRNA genes.

The correlation analyses show that morphology in general, but especially scalation, is strongly correlated with the amount of precipitation during the months of lizard activity, which suggests that these are not good taxonomic characters, and that other characters apparently independent of the climate like for instance osteological, karyological and DNA features are much more reliable in delimiting species boundaries in *Iberolacerta*.

According to our phylogenetic analyses, *I. galani* nov. is part of a very well supported clade that originated around 2.5 mya and also includes *I. monticola* and *I. martinezricai*. Phylogeny suggests *I.martinezricai* might be the sister taxon to *I. galani* nov. from which it split approximately 2 mya, at the beginning of the Pleistocene. The clade containing *I. galani* nov., *I. martinezricai* and *I. monticola* was probably widely distributed across western Iberia during moderately cool and moist phases of the Pleistocene, but it was probably restricted to its present range as a result of the general temperature increase during the Holocene and competition with other lacertid lizards. *Iberolacerta galani* nov. is endemic to the Montes de León, where it is isolated from the other species of the "monticola-group" by the Duero and Miño-Sil Rivers, but particularly by the Bibei river valley.

Key words: Mountain lizards, speciation, evolution, biogeography, taxonomy, phylogeny, cytochrome b, 12S rRNA

Introduction

The Lacertid lizard genus *Iberolacerta* is among the most widely studied lizard groups in Europe. Following several recent taxonomic revisions using morphological (scalation, morphometry and osteology), karyological and genetic data (allozymes, nuclear DNA and mitochondrial DNA), it is largely accepted that the genus *Iberolacerta* comprises 7 species (Arribas 1993a, b, 1994a, b, 1996, 1997, 1998, 1999; Pérez-Mellado *et al.* 1993; Mayer & Arribas 1996, 2003; Odierna *et al.* 1996; Arribas & Carranza 2004; Carranza *et al.* 2004; Crochet *et al.* 2004; Arribas & Odierna 2005). As a result of their phylogenetic affinities and geographical distribution (see Fig. 1), these can be subdivided in three main groups: 1) Iberian Rock lizards, also known as the "Iberian group" or "monticola-group", which includes *I. cyreni*, *I. martinezricai* and *I. monticola*. The first taxon comprises *I. cyreni cyreni* (Müller & Hellmich, 1937) from the Sierra de Guadarrama, and *I. c. castiliana* (Arribas, 1996) from the Sierra de Gredos, whilst the populations from the Sierra de Bejar and from the Sierras de Avila are of uncertain assignation. *Iberolacerta martinezricai*

(Arribas, 1996) inhabits the Peña de Francia and the Batuecas area and is probably also present in other areas of the Sierra de Francia and Sierra de Gata. Finally, *I. monticola* is divided into *I. monticola monticola* (Boulenger, 1905), restricted to the Serra da Estrela in Portugal, and *I. m. cantabrica* (Mertens, 1929), distributed across a wide area in northwest Spain; 2) Pyrenean Rock lizards, also known as the "Pyrenean group" or "bonnali-group", which belong to the subgenus *Pyrenesaura* Arribas, 1999 and include *I. aurelioi* (Arribas, 1994), present in Spain, France and Andorra at very high altitude (usually above 2000 m) in the massifs of Montroig, Pica d'Estats, Coma Pedrosa, Tristaina and Sarrera; *I. aranica* (Arribas, 1993), only found in a very restricted area of the Maubèrme massif and its spurs to the south and east, situated between the Aran Valley in Spain and the Ariège in France, and *I. bonnali* (Lantz, 1927) with a comparatively large distribution range in the central Pyrenees, stretching from the Midi D'Ossau Massif in the west to close to the Bonaigua Pass in the east; and finally 3) the Horvath's Rock lizard *I. horvathi* (Méhely, 1904), which is found more than 1000 km further east and presents a patchy distribution across the Eastern Alpine and North Dinaric mountain ranges.

Recent phylogenetic analyses suggest that *I. horvathi* is sister to all the remaining representatives of *Iberolacerta*, from which it separated approximately 8 mya (Mayer & Arribas 2003; Carranza *et al.* 2004). These phylogenies show that both Iberian Rock lizards and Pyrenean Rock lizards are reciprocally monophyletic and that they may have originated around 7 mya. Genetic data further suggest that all three species of Pyrenean Rock lizards appeared almost simultaneously in the Pliocene, shortly after the separation between *I. cyreni* and the clade formed by *I. monticola* and *I. martinezricai*, which might have occurred during the Upper Miocene (Mayer & Arribas 2003; Carranza *et al.* 2004; Crochet *et al.* 2004;). *Iberolacerta monticola* and *I. martinezricai* are genetically fairly closely related, but phylogenetic analyses using both nuclear and mitochondrial genes clearly show that they are evolving independently, which is also supported by the clear differences in their morphology and karyotype (Arribas & Carranza 2004; Arribas & Odierna 2005). In the latest phylogenetic analyses published by Mayer and Arribas (2003), Carranza *et al.* (2004), and Arribas & Carranza (2004), the nominal subspecies branches within a much more varied *I. m. cantabrica*, suggesting that the Serra da Estrela was colonized very recently from the north. Interestingly, Carranza *et al.* (2004) also showed that variability within *I. m. cantabrica* is very high. In their study, a sample from Sanabria (southern Montes de León) differed from all the other representatives of *I. m. cantabrica* included in their study in 4.7% of the mitochondrial cytochrome *b* positions sequenced: a genetic distance similar to that which separates *I. monticola* from *I. martinezricai* (Arribas & Carranza, 2004).

Iberolacerta monticola cantabrica presents a continuous distribution along the Cordillera Cantabrica, from Lugo in the west to the Picos de Europa and the Fuentes Carrionas area (north of the province of Palencia) in the east (Fig. 1). Apart from this continuous area, there are also several small, isolated populations within the same

Eurosiberian biogeographic region at low altitude or even at sea level in the provinces of La Coruña and Lugo (Fig. 1). These are thought to be the result of a relatively recent reduction in the distribution range of this subspecies (Galan 1982, 1999). Other isolated and little-known populations inhabit the Mediterranean biogeographical region and are situated between the rivers Miño-Sil and Duero (see Fig. 1). These populations are distributed across two main areas, formed by the so-called Macizo Central Ourensano (Serra da Queixa, Invernadero, etc.) in the west and the populations from the Montes de León (Sierra Segundera, Sierra de la Cabrera Baja, Sierra del Eje and Sierra del Teleno) in the east. These two areas are separated by a minimum distance of approximately 40 km of low mountains and valleys, particularly the Bibei River valley (see Fig. 1). The populations from the Montes de León are also separated by a minimum distance of 45 km from the populations of *I. m. cantabrica* from the Sierra de Caurel, which lie on the northern side of the Sil river valley (see Fig 1). This valley has a forest with a characteristically Mediterranean climate and Mediterranean herpetofauna, where Rock lizards have never been reported. A dubious sighting of *I. m. cantabrica*, which has never been confirmed, was made in the Montesinho Natural Park (Serra da Coroa) in Portugal, close to the border with Galicia, approximately 50 km from both the Montes de León and the Serra da Queixa (Macizo Central Ourensano), to the south west and south east, respectively (Antunes *et al.* 2001).

The first specimen of *I. monticola* from the Montes de León was collected in 1971 in Truchillas, León (Elvira & Vigal 1982) and very few specimens from this interesting area have been studied since.

A sample from Sanabria was pooled together with specimens from Ancares in a univariate and multivariate analysis of scalation (Brown & Pérez-Mellado 1993). In this study, the mixed Sanabria-Ancares sample appeared more closely related to *I. m. monticola* from the Serra da Estrela than to the other *I. m. cantabrica* included in their analysis (all from Galicia), indicating an unsatisfactory subspecific division of *I. monticola*.

Lizards from the Montes de León were mentioned but not included in the most recent revision of the “monticola-group” (Arribas 1996), and until now they have not been studied from a karyological and osteological point of view. As stated above, the single specimen from Sanabria included in the phylogenetic analysis made by Carranza *et al.* (2004) was genetically very different from the remaining populations of *I. m. cantabrica* that were analyzed (see above).

In this work we use univariate and multivariate morphological analyses, together with information from osteology, karyology and a molecular phylogeny inferred using 1041 base pairs of both mitochondrial and nuclear genes from a wide range of species, subspecies and populations of *Iberolacerta*, in order to analyze the taxonomic status of the isolated populations from the Montes de León that are currently assigned to *I. monticola*.

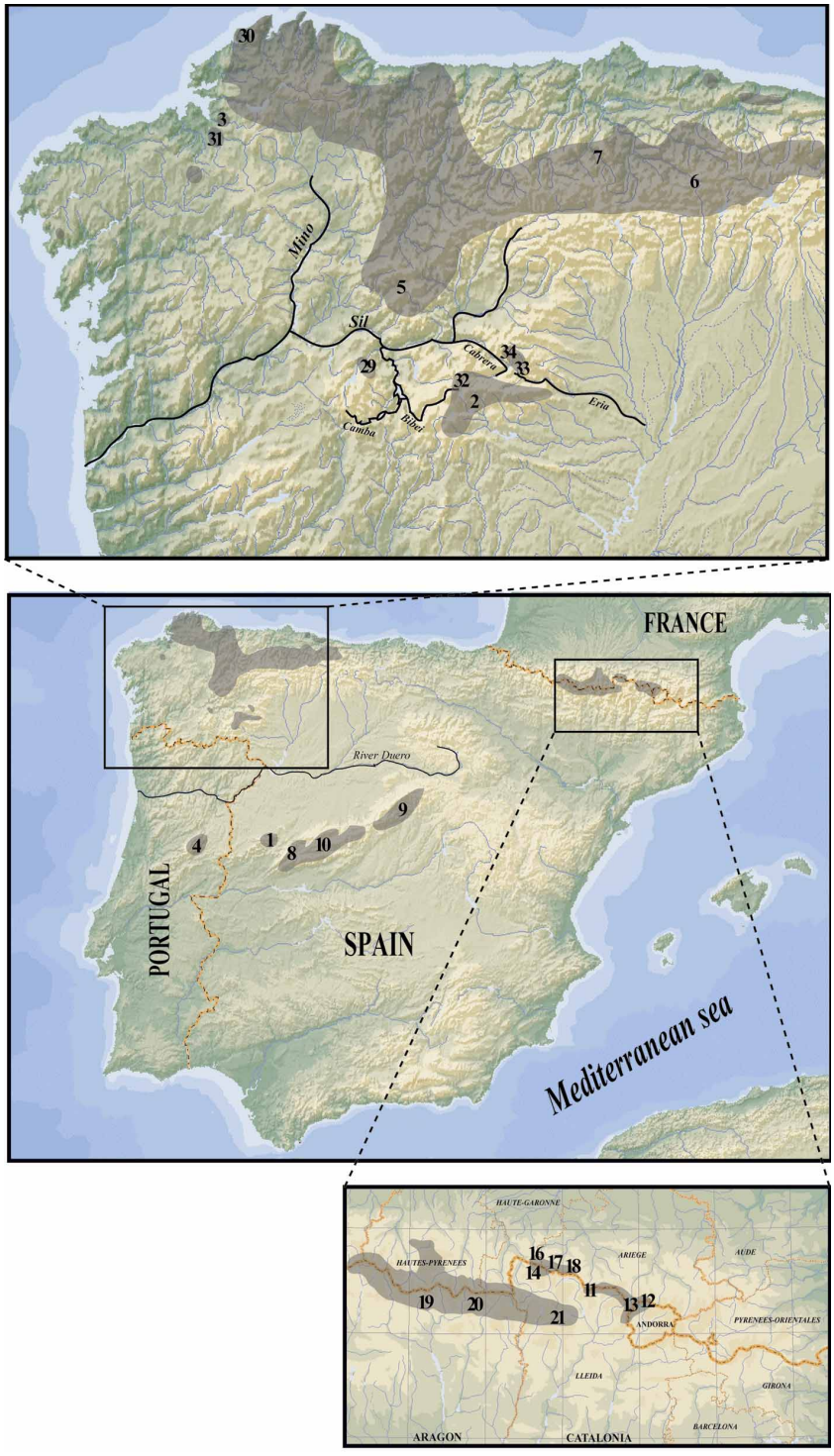

FIGURE 1. Map of the Iberian Peninsula showing the current distribution ranges of all known species and subspecies of *Iberolacerta* (shaded areas). Numbers refer to sampling localities as in Table 1.

Material and methods

Morphology

A total of 621 specimens (303 males and 318 females) from Oscar Arribas' (OA) database, with snout-vent length greater than 45 mm, were included in the univariate (ANOVA) analyses. Of these, 550 specimens (268 males and 282 females) were also included in a multivariate analysis (single isolated or unisex samples were eliminated from the analyses). The specimens studied were mainly from the collections of Pedro Galan (La Coruña, Spain), Manuel Meijide (Soria, Spain), the author (O.A.) — a scientific collection from Barcelona — and the collections of the Estación Biológica de Doñana, C.S.I.C. (Sevilla, Spain). New samples were collected under the corresponding collecting permits issued by the Junta de Castilla y León and Xunta de Galicia.

Acronyms used for the different OTUs included in the morphological multivariate analysis are as follows:

GUAD: Sierra de Guadarrama (Madrid and Segovia provinces, Spain), 32 males and 39 females [*I. cyreni cyreni*]

GRED: Sierra de Gredos (Avila province, Spain), 27 males and 47 females [*I. cyreni castiliana*]

BATU: Sierra de la Peña de Francia/Las Batuecas (Salamanca province, Spain), 23 males and 28 females [*I. martinezricai*]

LEON: Montes de León: Sª Segundera (=Sanabria area), Sª de la Cabrera Baja, Sª del Teleno and Peña Trevinca (Zamora, León and Orense provinces), 20 males and 26 females [Montes de León new taxon, see below]

ESTR: Serra da Estrela (Beira Alta district, Portugal), 15 males and 22 females [*I. monticola monticola*]

GALc: Galician lowland areas (Galician Coast) (La Coruña and Lugo provinces; Spain), 35 males and 24 females [*I. monticola cantabrica*]

GALm: West Cantabrian Mountains (Galician Mountains) (Lugo province, Spain), 35 males and 19 females [*I. monticola cantabrica*]

CANT: Central Cantabrian Mountains (León and Asturias provinces, Spain), 68 males and 68 females. [*I. monticola cantabrica*]

EURO: Picos de Europa and more eastern areas (Asturias and Santander provinces, Spain), 39 males and 36 females [*I. monticola cantabrica*]

A complete list of specimens studied is available from the author.

In general, the numerical analyses included only those specimens for which a full set of characters was available. In cases where only one value was missing, this was estimated using linear regression. Given that these populations present sexual dimorphism (Arribas 1996, 1999), separate analyses were carried out for males and females.

Characters studied

Biometric characters: Snout-vent length (SVL); Forelimb length (FLL); Hindlimb length (HLL); Pileus length (PL); Pileus width (PW); Parietal length (PaL); Masseteric scale diameter (DM); Tympanic scale diameter (DT); Anal width (AW) and Anal length (AL). All linear measurements were made with a digital calliper to the nearest 0.01 mm by O.A. to avoid inter observer variability. These measurements were converted into the following, more informative and non dimensional-dependent ratios: FLL/SVL (relative forelimb length; "FLL index"); HLL/SVL (relative hindlimb length, "HLL index"); PL/PW (pileus shape, "Pileus index"); DM/PaL (relative masseteric plate size, "Masseteric index"); DT/PaL (relative tympanic size, "Tympanic index"); AL/AW (anal plate surface, "Anal form index") and AS/SVL ($\sqrt{}$(AL*AW)*100/SVL, relative anal plate size with respect to total length, "Anal size index") (see Arribas 1996, 2001). Linear measurements and indexes yielded largely similar results. All ratios were given multiplied by 100 to avoid excessive decimal places.

Scalation characters: Supraciliar Granula (GrS) for the right and left sides; Gularia (GUL); Collaria (COLL); Dorsalia (DORS); Ventralia (VENT); Femoralia rigth (FEMr) and left (FEMl); 4th. digit Lamellae (LAM); and Circumanalia (CIRCA). The full presence (2), contact at one point (1) or absence (0) of contact between Rostral-Internasal (R-I), Supranasal-first Loreal contact (Sn-Lor), and Postocular-Parietal contact (Po-Pa) were also studied.

Pattern and coloration: The ranges of pairs of ventral plates (symmetric) with black dots were recorded (PV), as well as the number of blue ocelli on the shoulders (BO). Coloration in life was standardized with a colour code (Kornerup & Wanscher 1967). Methuen codification values are given in parenthesis, and their Munsell Notation equivalent in square brackets [Hue_Value/Chroma]. Ultraviolet photographs followed the methods described in Arribas (2001).

Statistical procedures

Statistical analyses used in the morphological study were the same as in Arribas (1996, 1999) and included both univariate (ANOVA for SVL, scalation characters and indexes, and ANCOVA with SVL as a covariate for the other linear measurements, both with *post-hoc* Tukey-Kramer tests at $p<0.05$ and $p<0.01$ to detect differences among samples) and multivariate techniques (Canonical Discriminant Analysis, CDA). In this latter analysis, each population is represented by a centroid (a hypothetical middle individual). Minimum-length spanning tree (MST) calculated from Mahalanobis' distance matrix is represented superimposed on the CDA, and helps to detect the nearest neighbours based on their position in the multidimensional space. MST representation also avoids a distortion of

trees by the reciprocal pairwise distance recalculation at every stage during the construction of UPGMA trees.

Mahalanobis' (squared) distance matrices were compared using a Mantel Test (with 1000 permutations) with the following matrices constructed using Euclidean (squared) distances: 1.— general climate among localities (mean annual precipitation and temperature); 2.— temperature during lizard activity (from March to October); 3.— temperature during egg incubation (May to August); 4.— precipitation during activity; 5.— precipitation during incubation; 6.— aerial (straight—line) geographical distances; 7.— orographic distances (taking into account mountain relief and the known distribution range). Climatic data (precipitation and temperatures) were extracted from Steinhauser (1970), and sun radiation values from Font-Tullot (1984).

Multivariate analyses (CDA) were performed with CANP and DISC programs from MULTICUA Package (Arenas, Cuadras & Fortiana 1991). MST trees and Mantel test were calculated with NTSYS 2.1© (Rohlf 2000). Univariate statistics were processed with NCSS 2001© package (Hintze 2001).

Genetic study

Samples, DNA extraction and amplification

To test the phylogenetic relationships, biogeography and taxonomy of *Iberolacerta* populations from the northwest Iberian Peninsula, a total of 28 specimens of *Iberolacerta* were sequenced for this study, and combined with sequences from a further 43 specimens downloaded from GenBank (see Table 1). In total, the data set included all the recognised species and subspecies of *Iberolacerta*, two *'Lacerta' oxycephala*, two representatives of the genus *Podarcis*, one *Timon lepidus*, and eight representatives of the Gallotiinae. The Amphisbaenid *Blanus cinereus* was used to root the phylogenetic tree (Townsend, Larson, Louis & Macey 2004). Specimen data are given in Table 1 and localities for some selected specimens are shown in Fig. 1.

Genomic DNA was extracted from tissue samples following standard protocols described elsewhere (Carranza *et al.* 1999, 2000). The primers used in both amplification and sequencing were cytochrome *b1* and cytochrome *b2* (Kocher *et al.* 1989) for the cytochrome *b* (cytb) gene, 12Sa and 12Sb (Kocher *et al.* 1989) for the 12S rRNA gene, and G73 and G74 (Saint, *et al.* 1998) for the nuclear c-*mos* gene. Specific primers were designed to amplify the c-*mos* fragment of some representatives of *Iberolacerta* (IberoCmosF: 5' – TGC AGT AAG AAC CGT TTG GC –3' and IberoCmosR 5' – CAG TGA TGA ATA TGT TGG CAG G – 3'). The three gene fragments were amplified by polymerase chain reaction (PCR) and the resultant DNA was sequenced using the same standard protocols and conditions described in (Carranza *et al.* 1999).

TABLE 1. Details of material and sequences used in the present study. Numbers between brackets after locality names refer to localities shown in Figure 1. All specimens from localities 29-34 with the only exception of *Iberolacerta galani* sp. nov.-3 have been specifically sequenced for this work. All the rest of the sequences used have been downloaded from Genbank and are mainly from Carranza *et al.* (2004); Arribas and Carranza (2004).

TAXA	LOCALITY	ACCESSION NUMBERS Cyt *b* / 12SrRNA / C-*mos*	Codes
Psammodromus algirus-2	Spain	AY151835 / AY151914 / AY151998	Palgi1
Gallotia stehlini	Gran Canaria (Canary Islands)	AY151838 / AY151917 / AY152001	Gst2
Gallotia atlantica atlantica	Lanzarote (Canary Islands)	AY151836 / AY151915 / AY151999	Gatat21
Gallotia intermedia	Tenerife (Canary Islands)	AY151844 / AY151923 / AY152007	Gint1
Gallotia simonyi machadoi	El Hierro (Canary Islands)	AF101219 / AY151924 / AY152008	Gsih16
Gallotia caesaris gomerae	La Gomera (Canary Islands)	AY151842 / AY151921 / AY152005	GagaG1
Gallotia caesaris caesaris	El Hierro (Canary Islands)	AY151843 / AY151922 / AY152006	GagaH1
Gallotia galloti eisentrauti	N. Tenerife (Canary Islands)	AY151839 / AY151918 / AY152002	Gagat1
'Lacerta' oxycephala-1	Bosnia-Herzegovina	AY256651 / AY256656 / AY256659	E230922
'Lacerta' oxycephala-2	Bosnia-Herzegovina	AY256652 / AY256657 / AY256660	E230923
'Lacerta' mosorensis-4	Southern Croatia	AY151905 / AY151985 / AY151995	E2106115
Timon lepidus-1	Spain	AY151899 / AY151979 / AY151994	Llepida
Podarcis hispanica-9	Peña de Francia, Salamanca (Spain)	AY151906 / AY151986 / AY151997	E41025
Podarcis hispanica-2	Andorra	AY134703 / AY134738 / AY151996	E2106121
Iberolacerta horvathi	Northwest Croatia	AY256648 / AY256653 / AY256658	E230921
Iberolacerta martinezricai-1	El Maillo, Peña de Francia, Salamanca (Spain) [1]	AY151895 / AY151975 / AY152009	E2106123
Iberolacerta martinezricai-2	200 m from Sanctuary Peña de Francia, Sa (Spain) [1]	AY683631 / AY683635 / AY683639	E410.26
Iberolacerta martinezricai-3	Sanctuary Peña de Francia, Salamanca (Spain) [1]	AY151897 / AY151977 / AY683640	E410.28
Iberolacerta martinezricai-4	Sanctuary Peña de Francia, Salamanca (Spain) [1]	AY683632 / AY683636 / AY683640	E3107.1
Iberolacerta martinezricai-5	Puerto el Portillo, Salamanca (Spain) [1]	AY683633 / AY683637 / AY683641	E3107.2
Iberolacerta martinezricai-6	Puerto el Portillo, Salamanca (Spain) [1]	AY683634 / AY683638 / AY683642	E3107.3
Iberolacerta m. monticola	Serra da Estrela (Portugal) [4]	AY151870 / AY151950 / AY152012	E140618
Iberolacerta m. cantabrica-2	Rio Eume, La Coruña (Spain) [3]	AY151865 / AY151945 / AY152011	E50614

……to be continued

TABLE 1 (continued).

Iberolacerta m. cantabrica-6	Sierra de Caurel, Lugo (Spain) [5]	AY151857 / AY151937 / AY152013	E4109
Iberolacerta m. cantabrica-7	Sierra de Caurel, Lugo (Spain) [5]	AY151858 / AY151938 / AY152014	E41010
Iberolacerta m. cantabrica-9	Sierra de Caurel, Lugo (Spain) [5]	AY151860 / AY151940 / AY152015	E41012
Iberolacerta m. cantabrica-12	Somiedo (Spain), Asturias [7]	AY151864 / AY151944 / AY152016	E140611
Iberolacerta m. cantabrica-11	Somiedo (Spain), Asturias [7]	AY151856 / AY151936 / AY152017	E50612
Iberolacerta m. cantabrica-19	Somiedo (Spain), Asturias [7]	DQ497099 / DQ497157 / DQ497128	E1009.28
Iberolacerta m. cantabrica-14	Puerto de Vegarada, León (Spain) [6]	AY151861 / AY151941 / AY152018	E41015
Iberolacerta m. cantabrica-20	Puerto de Vegarada, León (Spain) [6]	DQ497100 / DQ497158 / DQ497129	E1009.29
Iberolacerta m. cantabrica-16	Cabeza de Manzaneda, Orense (Spain) [29]	DQ497095 / DQ497153 / DQ497124	E1009.30
Iberolacerta m. cantabrica-17	Cabeza de Manzaneda, Orense (Spain) [29]	DQ497096 / DQ497154 / DQ497125	E1009.31
Iberolacerta m. cantabrica-18	Cabeza de Manzaneda, Orense (Spain) [29]	DQ497097 / DQ497155 / DQ497126	E1009.32
Iberolacerta m. cantabrica-19	Serra da Capelada, La Coruña (Spain) [30]	DQ497093 / DQ497151 / DQ497122	E0709.3
Iberolacerta m. cantabrica-20	Serra da Capelada, La Coruña (Spain) [30]	DQ497094 / DQ497152 / DQ497123	E0709.4
Iberolacerta m. cantabrica-21	Rio Mandeo, La Coruña (Spain) [31]	DQ497092 / DQ497150 / DQ497121	E0709.2
Iberolacerta m. cantabrica-22	Rio Mandeo, La Coruña (Spain) [31]	DQ497098 / DQ497156 / DQ497127	E0709.1
Iberolacerta galani sp. nov.-1	Peña Trevinca, Orense (Spain) [32]	DQ497090 / DQ497148 / DQ497119	E0709.8
Iberolacerta galani sp. nov.-2	Peña Trevinca, Orense (Spain) [32]	DQ497091 / DQ497149 / DQ497120	E0709.9
Iberolacerta galani sp. nov.-3	Laguna de los Peces, Sanabria, Zamora (Spain) [2]	AY151863 / AY151943 / AY152010	E41017
Iberolacerta galani sp. nov.-4	Laguna de los Peces, Sanabria, Zamora (Spain) [2]	DQ497088 / DQ497146 / DQ497117	E1009.18
Iberolacerta galani sp. nov.-5	Laguna de los Peces, Sanabria, Zamora (Spain) [2]	DQ497089 / DQ497147 / DQ497118	E1009.22
Iberolacerta galani sp. nov.-6	Laguna de los Peces, Sanabria, Zamora (Spain) [2]	DQ497086 / DQ497144 / DQ497115	E1009.23
Iberolacerta galani sp. nov.-7	Laguna de los Peces, Sanabria, Zamora (Spain) [2]	DQ497084 / DQ497142 / DQ497113	E1009.20
Iberolacerta galani sp. nov.-8	Laguna de los Peces, Sanabria, Zamora (Spain) [2]	DQ497085 / DQ497143 / DQ497114	E1009.21
Iberolacerta galani sp. nov.-9	Laguna de los Peces, Sanabria, Zamora (Spain) [2]	DQ497087 / DQ497145 / DQ497116	E1009.25
Iberolacerta galani sp. nov.-10	Laguna de los Peces, Sanabria, Zamora (Spain) [2]	DQ497082 / DQ497140 / DQ497111	E1009.17
Iberolacerta galani sp. nov.-11	Laguna de los Peces, Sanabria, Zamora (Spain) [2]	DQ497083 / DQ497141 / DQ497112	E1009.19
Iberolacerta galani sp. nov.-12	Puerto Los Portillinos, Teleno, León (Spain) [33]	DQ497079 / DQ497137 / DQ497108	E0709.5
Iberolacerta galani sp. nov.-13	Puerto Los Portillinos, Teleno, León (Spain) [33]	DQ497078 / DQ497136 / DQ497107	E0709.6
Iberolacerta galani sp. nov.-14	Puerto Los Portillinos, Teleno, León (Spain) [33]	DQ497080 / DQ497138 / DQ497109	E0709.7

……to be continued

TABLE 1 (continued).

Iberolacerta galani sp. nov.-15	Puerto El Morredero, Teleno, León (Spain) [34]	DQ497077 / DQ497135 / DQ497106	E0709.10
Iberolacerta galani sp. nov.-16	Puerto El Morredero, Teleno, León (Spain) [34]	DQ497081 / DQ497139 / DQ497110	E0709.11
Iberolacerta galani sp. nov.-17	Puerto El Morredero, Teleno, León (Spain) [34]	DQ497076 / DQ497134 / DQ497105	E0709.12
Iberolacerta galani sp. nov.-18	Puerto El Morredero, Teleno, León (Spain) [34]	DQ497075 / DQ497133 / DQ497104	E0709.14
Iberolacerta galani sp. nov.-19	Puerto El Morredero, Teleno, León (Spain) [34]	DQ497074 / DQ497132 / DQ497103	E0709.15
Iberolacerta galani sp. nov.-20	Puerto El Morredero, Teleno, León (Spain) [34]	DQ497072 / DQ497130 / DQ497101	E0709.16
Iberolacerta galani sp. nov.-21	Puerto El Morredero, Teleno, León (Spain) [34]	DQ497073 / DQ497131 / DQ497102	E0709.17
Iberolacerta bonnali-3	Ordesa, Huesca (Spain) [19]	AY151890 / AY151970 / AY152032	E210611
Iberolacerta bonnali-4	Posets, Huesca (Spain) [20]	AY151894 / AY151974 / AY152033	E210615
Iberolacerta bonnali-7	Port de Rus, Lleida (Spain) [21]	AY151889 / AY151969 / AY152035	E4108
Iberolacerta aurelioi-1	Montroig, Lleida (Spain) [11]	AY151883 / AY151963 / AY152023	E406110
Iberolacerta aurelioi-2	Sorteny (Andorra) [12]	AY151882 / AY151962 / AY152024	E40619
Iberolacerta aurelioi-3	Circ de Comapedrosa (Andorra) [13]	AY151880 / AY151960 / AY152025	E40617
Iberolacerta aranica-1	Coll de Barrados, Valle de Aran (Spain) [14]	AY151879 / AY151959 / AY152026	E40616
Iberolacerta aranica-3	Serre de Ventaillou (France) [16]	AY151876 / AY151956 / AY152028	E40613
Iberolacerta aranica-5	Combe de Muntanyole (France) [17]	AY151874 / AY151954 / AY152029	E40611
Iberolacerta aranica-6	Muntanyes de Barlongere (France) [18]	AY151873 / AY151953 / AY152030	E4101
Iberolacerta cyreni castiliana-12	Sierra de Gredos, Avila (Spain) [10]	AY151852 / AY151932 / AY152022	E140615
Iberolacerta cyreni ssp-7	Sierra de Bejar, Salamanca (Spain) [8]	AY151849 / AY151929 / AY152019	E41022
Iberolacerta cyreni cyreni-8	Navacerrada, Segovia (Spain) [9]	AY151846 / AY151926 / AY152020	E140613
Iberolacerta cyreni cyreni-9	Navacerrada, Segovia (Spain) [9]	AY151845 / AY151925 / AY152021	E140612

Phylogenetic analyses

DNA sequences were aligned using ClustalX (Thompson *et al.* 1997) with default parameters (gap opening = 10; gap extension = 0.2). All the cytb and c-mos sequences had the same length and therefore no gaps were postulated. Although some gaps were postulated in order to resolve length differences in the 12S rRNA gene fragment, all positions could be unambiguously aligned and were therefore included in the analyses.

Three methods of phylogenetic analysis were employed for the combined dataset, and their results compared. These were: Maximum likelihood (ML), Maximum parsimony (MP) and Bayesian analysis. Modeltest v. 3.06 (Posada & Crandall 1998) was used to select the most appropriate model of sequence evolution for the ML and Bayesian analyses under the Akaike Information Criterion. This was, in the case of the cytb and 12S rRNA gene fragments, the General Time Reversible model (GTR), taking into account the proportion of invariable sites (I) and the shape parameter alpha of the gamma distribution (G), and for the c-*mos*, the Hishino-Kasegawa-Yano (HKY) model of sequence evolution. The ML analysis was performed using PHYML (Guindon & Gascuel 2003) with model parameters fitted to the data by likelihood maximization. Maximum parsimony analyses included heuristic searches with TBR branch swapping and 100 random addition replicates. Transitions and transversions had the same weight and gaps were treated as a fifth state. Reliability of the ML and MP trees was assessed by bootstrap analysis (Felsenstein 1985), performed with 1000 replications.

Bayesian analyses were performed with MrBayes v. 3.0 (Huelsenbeck & Ronquist 2001). For the combined dataset (cytb+12S+c-*mos*), each partition had its own independent model of evolution and model parameters (see above). Four incrementally heated Markov chains with default heating values were used. All analyses started with randomly generated trees and ran for 2 x 10^6 generations, with sampling occurring at intervals of 100 generations producing 20,000 trees. To ensure that the analyses were not trapped in local optima, the data set was run three times independently, each run beginning with a different starting tree. For each independent analysis, the log-likelihood values of all trees saved were plotted against the generation time. After verifying that stationary had been reached both in terms of likelihood scores and parameter estimation, the first 5,000 trees were discarded in all three runs, and three independent majority-rule consensus trees were generated from the remaining (post burn-in) trees. The frequency of any particular clade of the consensus tree represents the posterior probability of that node (Huelsenbeck & Ronquist 2001); only values above 95% were considered to indicate that nodes were significantly supported (Wilcox *et al.* 2002).

Topological incongruence among partitions was tested using the incongruence length difference (ILD) test (Farris *et al.* 1994; Michkevich & Farris 1981). In this test, 10000 heuristic searches were carried out after removing all invariable characters from the dataset (Cunningham 1997).

Estimating divergence times

In order to estimate divergence times between lineages the computer program r8s v1.6.4 was used (Sanderson 1997, 2002). This program implements several methods for estimating absolute rates of molecular evolution, ranging from standard maximum likelihood methods to more experimental semiparametric and nonparametric methods, which relax the stringency of the clock assumptions using smoothing methods. One of the advantages of this program is that, through a cross-validation test, it allows the user to explore the fidelity with which any of these methods explain the branch length variation (Sanderson 2002). This procedure removes each terminal branch in turn, estimates the remaining parameters of the model without that branch, predicts the anticipated number of substitutions on the pruned branch and reports the performance of these predictions as a cross-validation score, which allows the user to select the method that best explains the branch length variation (Sanderson 2002).

To estimate absolute rates, we used a single calibration point based on the assumption that divergence between *Gallotia caesaris caesaris* (Lehrs, 1914) (endemic to the island of El Hierro) and *Gallotia caesaris gomerae* (Boettger & Müller, 1914) (endemic to the island of La Gomera) began approximately 1 mya, soon after El Hierro was formed and rapid colonization from La Gomera by the ancestor of *G. c. gomerae* occurred. These taxa are suitable for use in calibration as they are sister species and each is monophyletic with low intraspecific variability (Maca-Meyer *et al.* 2003). Apart from the assumption that El Hierro was colonised rapidly, factors that could affect clock calibrations include stochastic variation at low levels of sequence divergence and the possibility of extinct or unsampled lineages (Emerson *et al.* 2001; Emerson 2002), although there is no evidence of any of these factors in *Gallotia* (Gonzalez *et al.* 1997; Barahona *et al.* 2000; Maca-Meyer *et al.* 2003)

Karyology

Karyological analyses were performed on two specimens (male and female) from the Montes de León, Sanabria, both in the province of Zamora (Laguna de los Peces, Sierra Segundera), and a female from El Teleno (Puerto El Morredero, León) collected by one of the authors (O.A.). Chromosomes were obtained by the standard air-drying method described in Odierna *et al.* (1994) from intestine, oviducts, spleen, lungs, gonads and kidney. In addition to standard staining methods (5% Giemsa solution in pH 7 phosphate buffer), various banding methods were also performed: Ag-NOR banding (Howell & Black, 1980); chromomycin A_3/methylic green staining (CMA_3) following Sahar & Latt (1980); C-banding according to Sumner's method (1972); and sequential C-banding+CMA_3+DAPI staining as reported by Odierna *et al.* (1999).

Osteological study

For the osteological analyses we used the carcasses of the two specimens from the Laguna de los Peces and the Sierra Segundera included in the karyological study (see above). These were cleared by means of KOH, the bones stained with alizarine red and permanently conserved in glicerine (Taylor 1967; Dufort 1978) (nomenclature as in Arribas 1998).

Results and taxonomy

Morphology

The factorial structures of Canonical Variates for the three first axes are shown in Table 2. Centroid coordinates are shown in Table 3, and Mahalanobis distances in Table 4.

TABLE 2. Canonical structure of the first discriminant axes derived from CDA (males and females). Significative values are indicated with an asterisk (* pp<0.05; ** p<0.01).

	Males			Females		
	axis 1	axis 2	axis 3	axis 1	axis 2	axis 3
Eigenvalue	27,7	8,7	6,87	24,2	9,25	7,17
% variability	49,30%	15,40%	12%	46,80%	17,80%	13,90%
% accumulated	49,30%	64,70%	76,90%	46,80%	64,60%	78,50%
GrS r	0,0932	0,0201	-0,0878	-0,0188	-0,00176	-0,328 **
GrS l	0,0917	-0,0353	0,112	-0,0871	0,129	-0,263
GUL	0,0786	-0,0251	-0,0097	-0,115	0,162	-0,121
COLL	-0,044	0,256	-0,0346	0,00308	0,335 **	0,0935
DORS	-0,247	0,209	0,0221	0,153	0,332 **	-0,582 **
VENT	-0,383 **	0,204	0,013	0,35 **	0,294 *	-0,0188
FEM r	0,0421	-0,125	-0,642 **	-0,135	0,0865	-0,165
FEM l	0,0512	-0,135	-0,068	-0,14	0,151	-0,152
LAM	0,0297	0,159	0,39 **	0,0699	0,433 **	0,158
CircA	0,207	-0,189	0,215	-0,247	-0,253	0,221
R-I	0,242	0,373 **	0,324 **	-0,232	0,447 **	0,177
Po-Pa	0,0101	0,00639	0,152	-0,0215	-0,0328	0,229
Sn-Lor	-0,0344	0,15	-0,206	0,00062	0,213	0,0539

BO	-0,54	**	0,241		0,112		0,419	**	0,168		0,013	
PV	-0,396	**	-0,516	**	0,378	**	0,396	**	-0,449	**	0,173	
FLL/SVL	0,0936		-0,144		0,32	**	-0,166		-0,645	**	-0,0672	
HLL/SVL	0,0568		-0,0151		0,307	*	-0,143		-0,0868		-0,23	
PL/PW	-0,00512		-0,182		-0,0475		-0,075		-0,00201		-0,32	**
DM/PaL	-0,0788		0,152		0,17		0,0865		0,0972		0,314	*
DT/PaL	-0,0946		0,0805		-0,374	**	0,279	*	-0,00262		-0,0173	
AL/AW	0,077		0,0658		-0,0702		0,00345		0,132		-0,0159	
AS/SVL	0,339	**	0,117		0,101		-0,419	**	-0,102		0,277	

TABLE 3. Coordinates of sample centroids in the CDA-derived axes. Males and females independently.

	Males			Females		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
GUAD	3,13	-0,713	0,518	-2,92	-0,821	0,825
GRED	2,35	1,26	-0,497	-2,22	0,953	-0,523
BATU	0,711	-0,892	-1,73	-0,485	-1,06	-1,39
LEON	-2,47	1,29	-0,988	2,17	1,46	0,102
ESTR	-2,21	-1,78	0,128	2,19	-1,73	-0,532
GALc	-0,762	0,739	0,878	-0,342	0,763	-0,418
GALm	-0,609	0,495	1,13	0,364	0,818	-0,666
CANT	-0,0928	0,0427	-0,223	0,595	-0,4	1,32
EURO	-0,045	-0,433	0,583	0,649	0,0169	1,28

TABLE 4. Mahalanobis distance among studied samples derived from CDA. Males above-right diagonal and females below-left diagonal.

F\M	GUAD	GRED	BATU	LEON	ESTR	GALc	GALm	CANT	EURO
GUAD	---------	9.318	13.603	37.304	32.189	21.395	17.904	13.577	13.351
GRED	8.975	---------	12.749	26.277	30.470	15.586	15.4905	11.252	12.808
BATU	12.970	11.908	---------	18.717	15.965	12.752	12.626	9.265	10.517
LEON	32.243	23.832	17.067	---------	12.449	11.416	10.718	9.902	13.292
ESTR	31.364	28.584	13.313	13.852	---------	12.046	11.856	10.729	10.247
GALc	12.486	6.368	6.758	10.314	15.110	---------	3.663	7.100	8.883
GALm	17.348	10.966	10.184	10.308	14.002	4.626	---------	6.805	5.131
CANT	14.807	15.934	10.341	9.784	10.728	6.953	8.833	---------	3.320
EURO	17.120	14.402	12.260	9.355	10.478	6.219	8.521	2.993	---------

TABLE 5. ANOVA/ANCOVA results of the morphometric, scalation and biometric indexes from males of *I.cyreni*, *I. martinezricai*, *I. galani* nov. and *I. monticola*. See text for abbreviations of characters and indexes used in the morphometric analysis.

	I. cyreni (1) (n=77)	*I. martinezricai* (2) (n=18)	*I. galani* **sp. nov.** (3) (n=24)	*I. monticola* (4) (n=184)
SVL	64.00±0.95 45.1–77.38	59.89±1.42 50.69–68.15	60.78±1.38 45.83–69.1	61.05±0.45 45.81–72.69
FLL	22.58±0.30 16.81–27.38	20.61±0.30 18.5–22.5	20.73±0.58 15.4–24.9	21.56±0.15 16.45–26.9
HLL	32.62±0.47 23.1–39.32	29.95±0.66 24.5–33.6	30.3±0.74 22.41–35.09	31.26±0.25 23.3–53.17
PL	15.75±0.3 10.7–29.06	15.20±0.36 13.01–17.77	14.92±0.39 10.7–17.52	15.21±0.11 11.5–18.2
PW	7.30±0.12 5.2–11.9	6.84±0.14 5.91–7.75	6.95±0.15 5.46–8.26	7.21±0.05 5.43–8.7
PaL	5.28±0.10 3.1–7.1	5.12±0.15 4.32–6.23	5.22±0.17 3.39–6.44	5.39±0.05 3.8–7.27
DM	2.17±0.05 0.63–3.38	1.54±0.11 0.76–2.52	2.18±0.08 1.46–2.87	2.14±0.03 0.68–3.2
DT	1.89±0.04 0.93–3	1.87±0.06 1.4–2.51	2.01±0.07 1.13–2.83	1.91±0.02 0.82–3.36
AW	4.68±0.1 2.7–6.87	4.09±0.13 3.06–5.07	4.03±0.12 2.7–5.08	4.09±0.04 2.6–5.5
AL	2.7±0.06 1.4–3.8	2.18±0.10 1.63–3.11	2.11±0.07 1.5–2.68	2.27±0.03 1.35–3.26
GrS r	11.05±0.26 6–18	11.44±0.4 6–14	10.12±0.34 5–13	9.86±0.13 5–15
GrS l	10.98±0.24 7–17	10.55±0.45 6–13	9.79±0.38 6–14	9.94±0.13 5–15
GUL	24.62±0.22 21–31	25.22±0.36 23–28	23.66±0.31 21–26	24.16±0.15 19–31
COLL	10.41±0.12 7–13	11±0.31 8–13	11.33±0.26 9–13	10.77±0.09 8–14
DORS	51.66±0.41 45–64	53.38±0.49 50–59	53.54±0.72 47–59	52.30±0.27 44–62
VENT	25.55±0.14 23–29	25.55±0.23 24–28	26.37±0.26 24–29	26.26±0.07 24–29
FEM r	18.54±0.18 15–24	18.83±0.47 15–24	17.62±0.25 16–20	17.70±0.11 15–23

to be continued.

TABLE 5 (continued).

	I. cyreni (1) (n=77)	*I. martinezricai* (2) (n=18)	*I. galani* **sp. nov.** (3) (n=24)	*I. monticola* (4) (n=184)
FEM l	18.36±0.19 14–24	19.11±0.54 16–25	17.54±0.25 15–20	17.78±0.11 14–24
LAM	25.15±0.20 21–29	24.22±0.36 21–28	25.25±0.36 23–30	25.10±0.12 21–31
CircA	7.39±0.13 5–12	6.88±0.27 5–10	6.58±0.19 5–8	6.85±0.07 5–9
R-I	1.87±0.04 0–2	0.72±0.21 0–2	0.66±0.17 0–2	1.35±0.06 0–2
Po-Pa	0.16±0.04 0–1	0.05±0.03 0–0.5	0.04±0.02 0–1	0.20±0.03 0–1
Sn-Lor	0.03±0.01 0–1	0.05±0.05 0–1	0.18±0.07 0–1	0.005±0.003 0–0.5
BO	0.02±0.01 0–1	0.88±0.11 0–2	2.79±0.49 0–11	1.84±0.07 0–5
PV	0.76±0.08 0–3	1.38±0.14 1–3	1.75±0.12 1–3	1.9±0.05 1–3
FLL/SVL	35.41±0.002 29.22–42.37	34.58±0.005 30.12–38.70	34.06±0.004 27.64–37.16	35.39±0.001 30.14–43.06
HLL/SVL	51.03±0.002 43.93–56.34	50.07±0.005 45.79–53.27	49.83±0.004 45.25–53.46	51.29±0.002 44.47–84.54
PL/PW	215.97±0.002 120.16–338.30	222.53±0.004 200.46–280.72	214.28±0.02 195.97–232.43	211.01±0.006 190.62–232.11
DM/PaL	41.12±0.007 16.57–53.84	30.39±0.02 13.93–44.13	41.89±0.01 31.34–54.45	39.75±0.004 12.27–57.14
DT/PaL	35.89±0.006 21.81–49.18	36.61±0.008 26.96–43.95	39.04±0.01 28.82–53.09	35.60±0.004 17.88–68.57
AL/AW	58.04±0.007 40.81–81.48	53.62±0.02 35.38–73.87	52.44±0.01 43.60–64.11	55.99±0.005 37.44–77.77
AS/SVL	552.24±0.05 439.00–689.68	496.94±0.11 417.18–556.29	477±0.07 404.31–545.5	498.12±0.03 372.98–238.51

to be continued.

TABLE 5 (continued)

	F	p	1–2	1–3	1–4	2–3	2–4	3–4
SVL	4	0.00819			**			
FLL	5.41	0.001226	*	**				*
HLL	2.39	0.069288						
PL	2.47	0.062361						
PW	5.86	0.000673			**			
PaL	24.28	0.000000	*	**	**			
DM	14.98	0.000000	**			**	**	
DT	4.06	0.007506		**	*			
AW	13.12	0.000000		**	**			
AL	23.41	0.000000	**	**	**			
GrS r	9.12	0.000003			**		**	
GrS l	6.53	0.000273		*	**			
GUL	5.91	0.000627						
COLL	4.08	0.007297		**				
DORS	2.26	0.081222						
VENT	9.81	0.000003		**	**		*	
FEM r	7.23	0.000106			**		*	
FEM l	5.75	0.000774			*	*	**	
LAM	1.61	0.187077						
CircA	6.35	0.000348		**	**			
R-I	20.63	0.000000	**	**	**		**	**
Po-Pa	2.18	0.090427						
Sn-Lor	10.99	0.000001		**		**		**
BO	75.69	0.000000	**	**	**	**	**	**
PV	49.21	0.000000	**	**	**		*	
FLL/SVL	3.87	0.009757		*				*
HLL/SVL	2.27	0.080350						
PL/PW	6.15	0.000455			*		**	
DM/PaL	13.97	0.000000	**			**	**	
DT/PaL	2.35	0.072560						*
AL/AW	4.85	0.002602		**				
AS/SVL	28.87	0.000000	**	**	**			

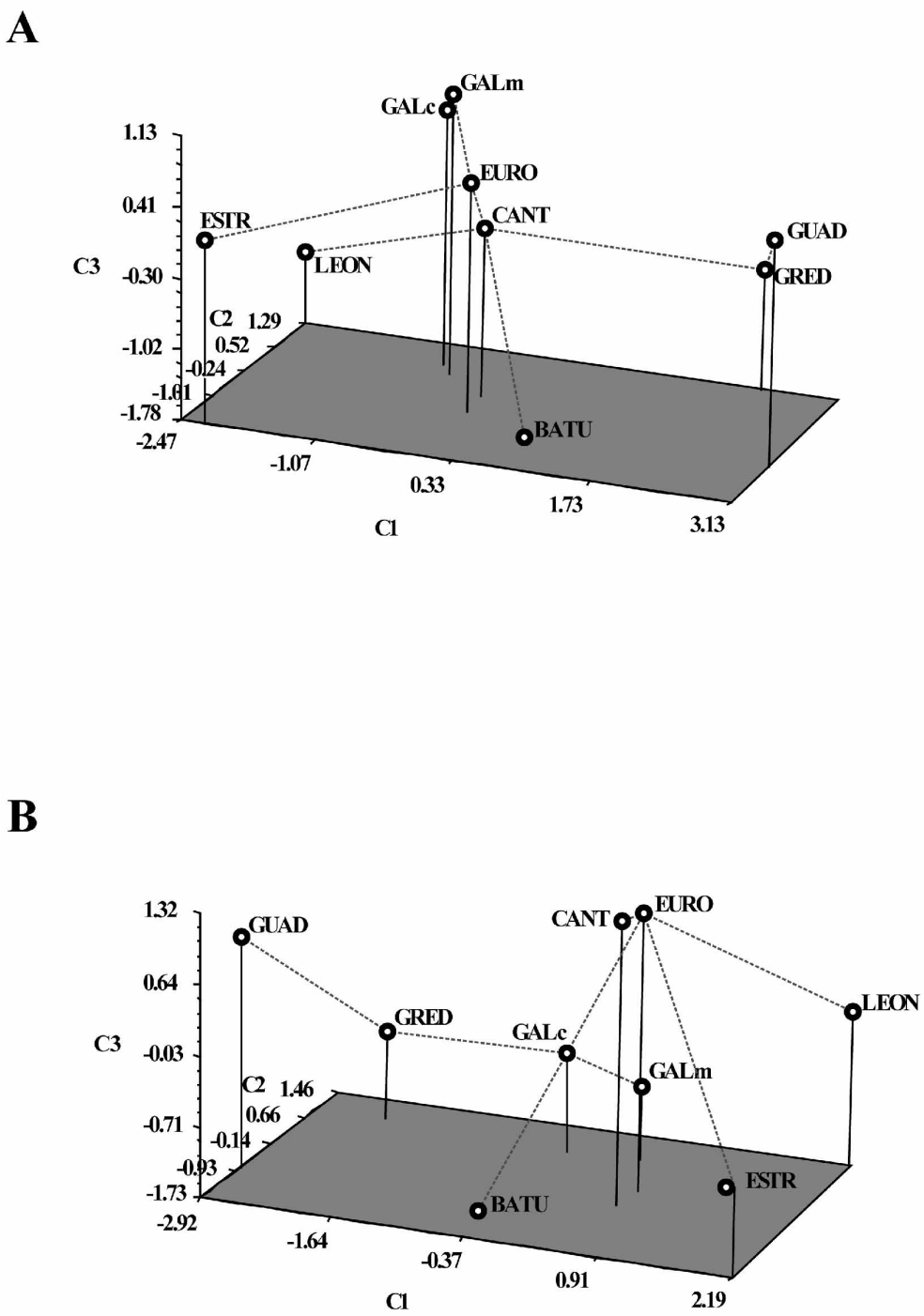

FIGURE 2. Canonical Discriminant Analysis (CDA). Three-dimensional representation of the three first canonical axes. OTUs (same abbreviations as in text) are represented by their centroid. The Minimum-length Spanning Tree (MST) connecting the closest samples is superimposed. A) Male analysis (76.9% of all explained variability). B) Female analysis (78.5% of all explained variability).

Canonical Discriminant Analysis: males

The results of the canonical discriminant analysis including only males are shown in Table 2 and Fig. 2A, and indicate that the difference between all samples analyzed is significant (MANOVA; $F_{176, 2008}$=6.7997; p<0.0000000001, Wilks' Lambda =0.0293). The space defined by the first three axes (Fig 2A) explains 76.9% of the total inter-sample variability, which is considered a fairly good representation. The first axis (Eigenvalue of 27.7) accounts for 49.30 % of the total variability and separates the *I. cyreni* samples (GUAD and GRED) in their positive part, characterized by lower values of BO (-0.54), PV (-0.39) and VENT (-0.383), and a higher value of AS/SVL (0.339) from the remaining samples; LEON (new taxon) and ESTR (*I. monticola*) were the most differing samples on the negative part of the axis. The second axis (Eigenvalue of 8.7) accounts for 15.4% of the total variability and separates LEON (new taxon) and GRED (*I. cyreni*) in their positive part from the remaining samples, which are characterized by higher values of R-I (0.373) and lower values of PV (-0.516). The third axis (Eigenvalue of 6.87) accounts for 12% of the total variability and separates *I. martinezricai* (BATU) in its most negative part, characterized by lower values of LAM (0.39), PV (0.378), R-I (0.324), FLL/SVL (0.32), HLL/SVL (0.307) and higher values of FEM r (-0.642) and DT/PaL (-0.374).

Canonical Discriminant Analysis: females

The results of the canonical discriminant analysis for females are shown in Table 2 and Fig. 2B, which also indicate that there are differences between samples (MANOVA; $F_{176, 2122}$=7.3593; p<0.0000000001, Wilks' Lambda =0.0274). The space defined by the first three axes (Fig 2B) explains 78.5% of the total inter-sample variability, which is even higher than in the male analysis (see above). The first axis (Eigenvalue of 24.2) accounts for 46.8% of the total variability and separates the *I. cyreni* samples (GUAD and GRED) in its negative part from the remaining ones. EST (*I. monticola*) and LEON (new taxon) are also differentiated in the positive part of the axis. As with males, *I. cyreni* females are characterized by lower values of BO (0.419), PV (0.396), VENT (0.35), DT/PaL (0.279) and higher values of AS/SVL (-0.419) from all the remaining samples, but especially from EST and LEON, which present opposite values. The second axis (Eigenvalue of 9.25) accounts for 17.8 % of the total variability and separates LEON (new taxon) from other taxa in its most positive extreme, as well as presenting higher values of R-I (0.447), LAM (0.433), COLL (0.335), DORS (0.332) and VENT (0.294), and lower values of FLL/SVL (-0.645) and PV (-0.449), from ESTR in their most negative part, with extreme opposite values presented for these characters. Finally, the third axis (Eigenvalue of 7.17) accounts for 13.9 % of the total variability and separates BATU (*I. martinezricai*) in the most negative part of the axis from all the remaining samples, which are characterized by higher values of DORS (-0.582), GrS r (-0.328) and PL/PW (-0.32), and lower values of DM (0.314).

ANOVA/ANCOVA

Results of the ANCOVA/ANOVA analyses are shown in Table 5 (males) and Table 6 (females). The LEON (new taxon) sample differs significantly ($p<0.05$; if underlined, $p<0.01$) from its most closely related taxa in the following characters, analyzed independently for males (m) and females (f) (Tables 5 and 6): from *I. cyreni* in FLL (m, f), HLL (f), DT (f), PaL (m), DT (m, f), AW (m, f), AL (m, f), GrS l (m, f), COLL (m, f), DORS (f), VENT (m, f), CircA (m, f), R-I (m, f), Sn-Lor (m, f), BO (m, f), PV (m, f), FLL/SVL (m, f), HLL/SVL (f), DT/PaL (f), AL/AW (f) and AS/SVL(m, f); from *I. martinezricai* in DM (m, f), DT (f), AW (f), COLL (f), VENT (f), FEM l (m), LAM (f), Sn-Lor (m, f), BO (m, f), DM/PaL(m, f), DT/PaL (f); and finally it differs from *I. monticola* in FLL (m), HLL(f), AW (f), COLL (f), DORS (f), VENT (f), LAM (f), CircA (f), R-I (m), Po-Pa (f), Sn-Lor (m, f), BO (m, f), FLL/SVL (m, f), HLL/SVL (f), DT/PaL (m,f), AS/SVL (f).

Minimum Spanning Tree: males

In the MST analysis for males (superimposed on the three dimensional representation of male centroids from Fig. 2A), the LEON sample clusters with *I. monticola* from the Central Cordillera Cantabrica (LEON-CANT at $D^2=9.90$). The two *I. cyreni* samples also cluster together, although they are also relatively well differentiated from a morphological perspective (GUAD-GRED at $D^2=9.31$). Of all the *I. monticola* samples, CANT shows the greatest similarity to both *I. cyreni* and *I. martinezricai* (GRED-CANT at $D^2=11.25$ and CANT-BATU at $D^2= 9.26$). Within *I. monticola*, the most connected sample in the MST analysis is EURO (CANT-EURO at $D^2=3.32$; EURO-GALm at $D^2=5.13$; EURO-ESTR at $D^2=10.24$). The two samples from Galicia are also very similar (GALm-GALc at $D^2=3.66$).

Minimum Spanning Tree: females

In the MST analysis for females (superimposed on the three-dimensional representation of female centroids from Fig. 2B), the LEON sample also clusters with *I. monticola*, but with the sample from the Picos de Europa, and not the central Codillera Cantabrica, as is the case in the analysis including males only (LEON-EURO at $D^2=9.35$). The two *I. cyreni* samples also cluster together (GUAD-GRED at $D^2=9.87$). Both *I. martinezricai* and *I. cyreni* connect with *I. monticola* from the Galician coast (GRED-GALc at $D^2=6.36$; and BATU-GALc at $D^2=6.75$). As for males, within *I. monticola*, EURO is the most connected sample in the MST analysis (GALc-EURO at $D^2=6.21$; EURO-CANT at $D^2=2.99$; EURO-ESTR at $D^2=10.47$). The two samples from Galicia are very similar and also cluster together (GALc-GALm at $D^2=4.62$).

TABLE 6. ANOVA/ANCOVA results of the morphometric, scalation and biometric indexes from females of *I. cyreni*, *I. martinezricai*, *I. galani* nov. and *I. monticola*. See text for abbreviations of characters and indexes used in the morphometric analysis.

	I. cyreni (1) (n=106)	*I. martinezricai* (2) (n=19)	*I. galani* **sp. nov.** (3) (n=26)	*I. monticola* (4) (n=167)
SVL	65.51±0.82	59.77±1.58	64.19±1.94	61.02±0.54
	47.54–81.74	45.46–68.86	48.25–84.42	45.88–79.81
FLL	21.37±0.21	18.39±0.25	19.42±0.42	19.36±0.14
	15.56–25.96	16.27–20.7	15.18–24.05	14.82–24.61
HLL	30.01±0.28	26.47±0.37	27.37±0.53	27.35±0.20
	22.39–36.75	23.18–29.44	22.75–32.98	21.18–35.21
PL	14.10±0.14	12.97±0.21	13.52±0.28	13.15±0.11
	10.95–18.3	10.89–14.53	11.27–16.65	3.66–17.6
PW	6.72±0.07	6.17±0.11	6.62±0.12	6.47±0.04
	5.1–10.8	5.15–6.88	5.6–7.9	5.1–8.6
PaL	4.60±0.05	4.23±0.08	4.50±0.11	4.45±0.03
	3.4–6.3	3.49–5	3.7–5.56	3.37–6.3
DM	1.78±0.03	1.31±0.08	1.77±0.08	1.74±0.02
	0.95–2.52	0.68–1.86	0.86–2.58	0.8–2.8
DT	1.64±0.03	1.60±0.06	1.93±0.06	1.73±0.02
	0.9–2.64	1.1–2.12	1.36–2.63	0.83–2.58
AW	4.62±0.07	3.71±0.13	3.72±0.15	3.79±0.05
	2.88–6.3	2.55–4.59	2.15–5.28	0.4–5.8
AL	2.66±0.04	2.13±0.10	2.18±0.08	2.20±0.03
	1.61–3.82	1.25–2.79	1.52–3.29	1.3–3.57
GrS r	10.49±0.17	10.89±0.60	9.65±0.40	9.85±0.14
	5–17	5–15	6–13	1–18
GrS l	10.61±0.18	10.89±0.45	9.53±0.33	9.67±0.13
	5–16	6–15	5–12	2–16
GUL	24.56±0.22	24.89±0.25	23.88±0.43	23.61±0.17
	19–33	22–27	16–29	18–31
COLL	10.39±0.1	10.21±0.24	11.23±0.27	10.17±0.08
	8–14	9–12	9–14	7–14
DORS	50.25±0.34	51.52±0.65	53.11±0.66	50.20±0.26
	43–59	46–56	48–61	43–59
VENT	28.64±0.12	28.73±0.22	30.65±0.24	29.44±0.08
	25–31	27–30	28–33	26–32

to be continued

TABLE 6 (continued).

	I. cyreni (1) (n=106)	*I. martinezricai* (2) (n=19)	*I. galani* **sp. nov.** (3) (n=26)	*I. monticola* (4) (n=167)
FEM r	17.80±0.16 14–22	17.31±0.29 16–20	17.38±0.34 14–21	16.57±0.10 13–21
FEM l	17.74±0.14 14–22	17.36±0.23 15–19	17.23±0.38 13–21	16.69±0.12 12–25
LAM	24.42±0.16 20–29	22.89±0.42 20–26	25.34±0.40 22–30	24.42±0.11 21–28
CircA	7.61±0.12 5–10	6.57±0.26 5–10	6.23±0.13 5–8	7.03±0.07 4–9
R-I	1.61±0.07 0–2	0.57±0.15 0–2	1.15±0.15 0–2	1.28±0.06 0–2
Po-Pa	0.33±0.06 0–1	0.21±0.07 0–1	0.11±0.05 0–1	0.41±0.03 0–1
Sn-Lor	0.10±0.03 0–1	0±0 0–0	0.29±0.08 0–1	0.04±0.01 0–1
BO	0.009±0.009 0–1	0.68±0.13 0–2	1.96±0.24 0–6	1.02±0.07 0–4
PV	0.39±0.05 0–3	0.63±0.15 0–2	1.03±0.12 0–3	1.36±0.06 0–3
FLL/SVL	32.81±0.002 26.70–39.68	31.05±0.006 25.64–36.13	30.49±0.004 26.75–34.62	31.88±0.001 25.82–38.63
HLL/SVL	46.10±0.003 37.82–52.75	44.64±0.008 39.41–51.76	43.02±0.005 37.06–47.82	45.02±0.002 36.97–55.15
PL/PW	210.36±0.01 132.40–234.69	210.16±0.01 195.35–222.24	203.97±0.01 196.44–219.37	204.38±0.009 150–232.66
DM/PaL	38.53±0.007 18.51–52.44	31.01±0.01 16.83–43.49	39.27±0.01 19.50–50	39.30±0.005 18.43–56.81
DT/PaL	35.34±0.006 22.41–47.21	38.08±0.01 24.4–54.04	42.94±0.01 35.07–59.52	39.14±0.04 17.58–56.09
AL/AW	58.01±0.007 37.25–101.88	57.24±0.01 43.06–63.86	59.39±0.01 48.12–81.86	57.96±0.025 40–76.70
AS/SVL	534.16±0.04 445.33–740.81	468.71±0.11 546.47–179.94	442.40±0.07 366.66–529.88	471.56±0.04 143.33–594.42

TABLE 6 (continued).

	F	p	1–2	1–3	1–4	2–3	2–4	3–4
SVL	8.35	0.000023	*		**			
FLL	27.00	0.000000	**	**	**			
HLL	25.56	0.000000	**	**	**			*
PL	2.78	0.041151			*			
PW	1.83	0.140750						
PaL	3.85	0.009961			*			
DM	8.83	0.000012	**			**	**	
DT	15.58	0.000000		**	**	*		
AW	36.91	0.000000	**	**	**			**
AL	25.79	0.000000	**	**	**			
GrS r	4.04	0.007668			*			
GrS l	7.94	0.000040		*	**		*	
GUL	5.20	0.001611			**			
COLL	6.83	0.000180		**		**		**
DORS	5.98	0.000564		**				**
VENT	24.32	0.000000		**	**	**		**
FEM r	14.36	0.000000			**			
FEM l	9.73	0.000004			**			
LAM	7.87	0.000045	**			**	**	*
CircA	16.08	0.000000	**	**	**			**
R-I	9.95	0.000003	**	*	**		*	
Po-Pa	4.18	0.006396						**
Sn-Lor	8.14	0.000031		**		**		**
BO	62.81	0.000000	**	**	**	**		**
PV	36.50	0.000000		**	**		**	
FLL/SVL	8.77	0.000013	*	**	**			*
HLL/SVL	7.36	0.000088		**	*			*
PL/PW	9.76	0.000004		*	**			
DM/PaL	7.08	0.000128	**			**	**	
DT/PaL	14.19	0.000000		**	**	*		*
AL/AW	0.40	0.751008						
AS/SVL	45.00	0.000000	**	**	**			*

TABLE 7. Correlations (Mantel Test with 1000 permutations) between distance matrices of males and females (r=0.9 among them) and distance matrices for several climatic and geographic parameters. (NF: not significant; * p<0.05; ** p<0.001). A strong correlation is found with climate, especially with the precipitation during the activity months both in male and females. See text for description of the parameters compared.

R T/ p	Orographic distances	Aerial Distances	Climate general	Temp. activity	Temp. incubat.
Males	0.11 0.70/0.22 NS	0.27 1.47/0.08 NS	0.44 1.83/0.05 *	0.04 0.20/0.41 NS	0.04 0.22/0.39 NS
Females	0.14 0.93/0.15 NS	0.11 0.73/0.23 NS	0.54 2.23/0.02 *	-0.16 -0.89/0.74 NS	-0.10 -0.53/0.68 NS

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R T/ p	Precipit. Activity	Precipit. incubat.	Insolation (h/day)	Radiation $Kw.h/m^2$
Males	0.44 1.85/0.05 *	0.28 1.30/0.11 NS	-0.19 -1.06/0.85 NS	-0.19 -1.02/0.84 NS
Females	0.54 2.25/0.01 **	0.17 0.81/0.21 NS	-0.28 1.54/0.96 NS	-0.25 -1.36/0.92 NS

Morphological correlation with climatic and geographic parameters

The correlation between the two distance matrices with the same underlying differentiation process (males and females of the same OTUs) was checked. Whereas the existence of sexual dimorphism implies a low correlation between the strictly biometrical distances (r=0.49), the correlation is higher when scalation (considering only counts: r=0.77 or counts and scale contacts: r=0.82) is taken into account. If all the characters (biometry and scalation) are considered together (as in our multivariate analyses), the correlation between sexes is very high (r=0.9) (normalized Mantel T-test: T=4.09, p=0.001). Therefore, this latter matrix was used for comparisons with several physiographic and climatic parameters, for males and females independently. The results are shown in Table 7 and suggest that both males and females are significantly correlated with the climate (precipitation and temperatures) in general, and particularly with precipitation during the months of activity.

Molecular Phylogenetics

The Incongruence Length Difference (ILD) test (ILD, $P > 0.36$) and the reciprocal 70% bootstrap proportion method showed that the phylogenies derived independently from the three genes were not incongruent. We therefore decided to carry out a combined analysis including 73 specimens in which all three genes were available. In total, the

combined data set included 1041 bp (303 bp of mitochondrial gene cytochrome b, 396 bp of the mitochondrial gene 12S rRNA and 342 bp of the nuclear gene c-*mos*). Of these, 411 positions were variable and 289 were parsimony-informative.

Heterozygotes were detected at position 22 of the 342 bp of the c-*mos* gene fragment sequenced for our study. In this position, all samples have a C, the only exceptions being the *I. monticola* samples, which have a T, and some samples of the new taxon from the Montes de León, which have either a T (samples number 1 from Peña Trevinca, 13 from Puerto Los Portinillos and 15 from Puerto El Morredero, see Table 1) or are heterozygotes (C/T) for this position (samples number 2 from Peña Trevinca, 3 from Laguna del Sotillo, 5–8 11–12 from Laguna de los Peces, and 14, 16 and 17–20 from Puerto El Morredero, see Table 1). All the remaining specimens from the Montes de León have a C at position 22 (samples number 4 and 9–10 from Laguna de los Peces).

The cross-validation test implemented in r8s v1.6 4 (Sanderson 1997, 2002)—see materials and methods—showed that branch length variation is explained with the highest fidelity by the Langley-Fitch (LF) method (Langley & Fitch 1974), which uses maximum likelihood to reconstruct divergence times under the assumption of a molecular clock. As a result, the LF method was run with the Powell algorithm (Gill *et al.* 1981; Press *et al.* 1992; Sanderson 1997, 2002) using a single calibration point (see materials and methods). The inferred dates for the most relevant nodes are shown in Fig. 3.

The results of the combined phylogenetic analyses using three independent methods (ML, MP and Bayesian) are shown in Fig. 3, and indicate that all samples from the Montes de León (the new taxon) form a well-supported clade that originated approximately 2 mya. In the phylogenetic tree this clade is sister to *I. martinezricai*, although with a low bootstrap and posterior probability value. The clade formed by the populations from the Montes de León and *I. martinezricai* is sister to a monophyletic assemblage formed by all the remaining samples of *I. monticola*, including the populations from Cabeza de Manzaneda and Caurel, approximately 40 km to the west and north of the Montes de León respectively.

The remaining phylogenetic relationships depicted in Fig. 3 are congruent with previous phylogenetic analyses (Mayer & Arribas, 2003; Carranza *et al.* 2004; Crochet *et al.* 2004) and support the supposition that all representatives of *Iberolacerta* form a highly supported monophyletic group, which started to diverge approximately 9.4 mya, when *I. horvathi* branched off from the group. This event was followed by the split between the Pyrenean group and the Iberian group, which according to our datings would have occurred approximately 8.7 mya. Speciation within the Pyrenean group did not start until 3.8 mya and according to our analyses all three species of *Pyrenesaura* originated very suddenly (see Fig. 3). Speciation within the Iberian group started 7.5 mya, when *I. cyreni* split from the clade formed by *I. martinezricai*, the populations from the Montes de León and all the remaining *I. monticola* (see above).

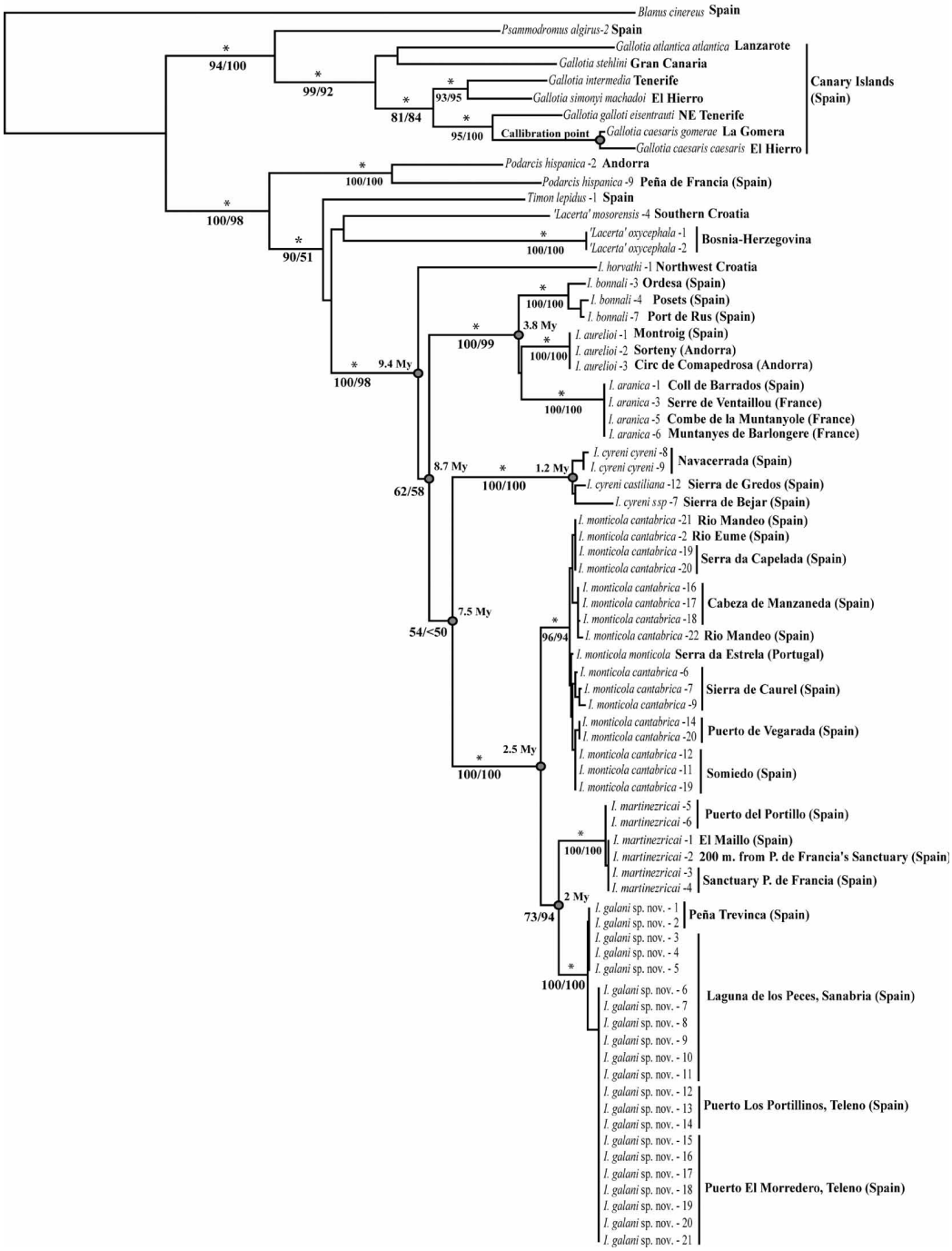

FIGURE 3. Maximum-likelihood tree using 1041 base pairs of the mitochondrial genes cytb and 12SrRNA and the nuclear gene c-*mos*. Support values are presented above the branches (posterior probabilities, only asterisk if value is equal to or above 95%) and below the branches (left bootstrap value for ML and right bootstrap value for MP). Datations are presented for some nodes and are indicated by a dot and a value in My (millions of years).

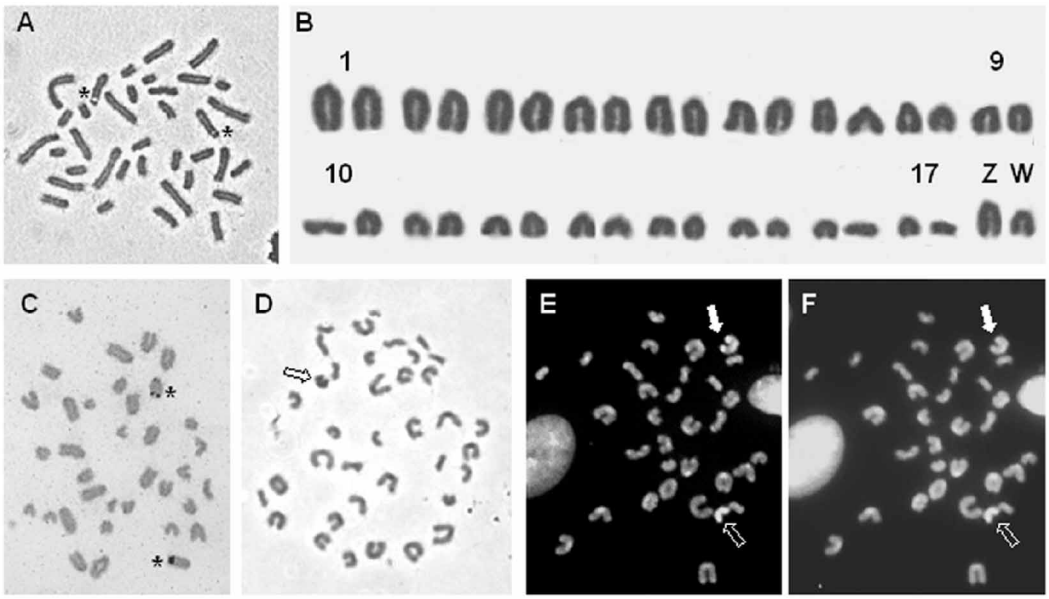

FIGURE 4. Metaphase plates (A, C-F) and karyotype (B) of male (A) and female (B-F) of I. galani from Sanabria, Giemsa stained (A and B), Ag-NOR banded (C), C-banded (D) and sequentially stained with C-banding+CMA3(E)+DAPI(F). Asterisks in A and C point to chromosomes bearing secondary constrictions and Ag-NOR positive spots, respectively; empty and filled arrows in D-F point to W and Z chromosomes, respectively.

Karyology

The three specimens studied from Sanabria (male and female) and Teleno (female) show a karyotype of 2n=36 uniarmed macrochromosomes gradually decreasing in length and NORs in the telomeric position of a large chromosome pair (L pair after Olmo *et al.* 1993), which can be tentatively assigned to the fifth pair (Fig. 4, A–C). The C-banding technique showed the presence of a heteromorphic ZW sex chromosome pair on the metaphase of the studied females from both localities (Fig 4, D–F). Chromosome W is as large as the chromosomes of pairs 10 or 11 and completely imbibed with a CMA_3 and DAPI positive sex heterochromatin. The Z chromosome is as large as the chromosomes of pair 6 and differs from the autosomes in showing a heavy, telomeric, CMA_3 positive C-band. The autosomes show apparently centromeric, CMA_3 and DAPI positive C-bands and light, CMA_3 positive, telomeric C-bands (Fig. 4, D–F). All these characteristics are summarized in Fig. 5 and compared to the karyotypes of the three other species belonging to the “Iberian group”.

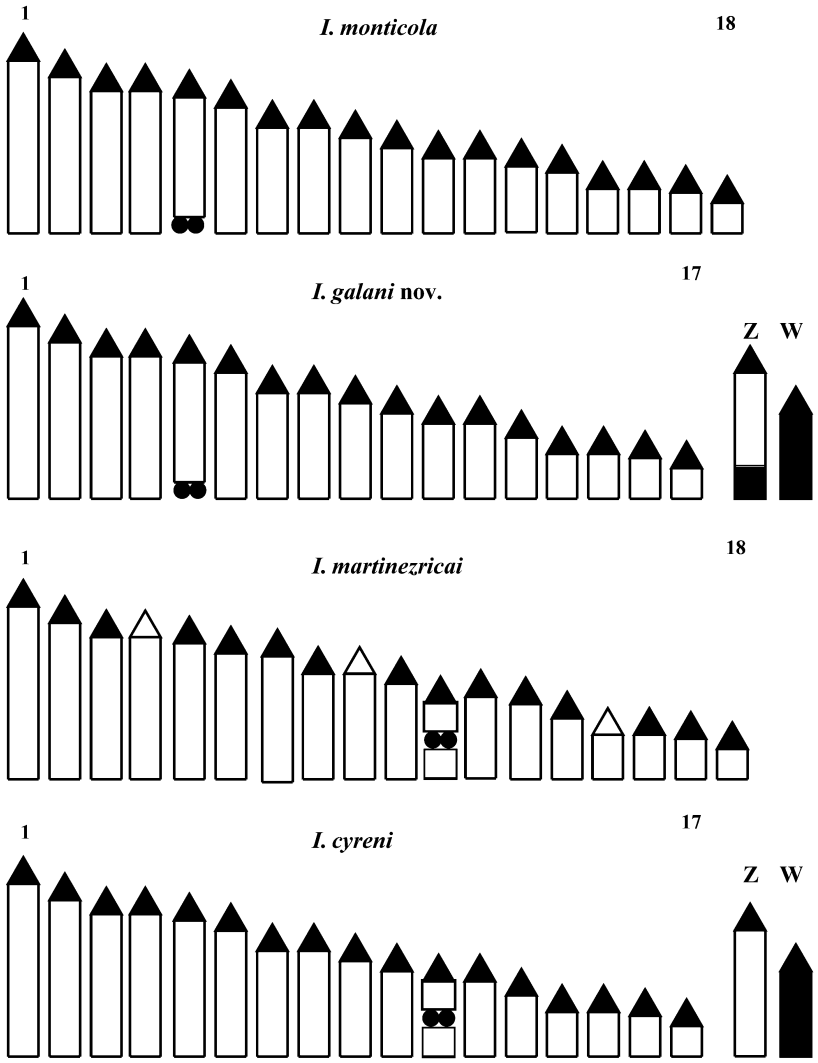

FIGURE 5. Karyograms of Iberian *Iberolacerta* species with 2n=36 chromosomes, showing distribution of heterochromatin (solid black blocks) and localization of NORs (black circles).

Osteology

The two studied specimens (male and female) from Sanabria (Sierra Segundera) have 7 premaxillary teeth and a processus nasalis with sinuose irregular sides of a more or less leaf or arrow-shaped form (clearer in the male). Nasal bones relatively short. Sixteen or 17 maxillary teeth-positions, and 18 to 19 dentary ones, two thirds of them more or less bicuspid, and the remainder monocuspid. Maxillo-jugal suture (margo ocularis) smooth, not stepped. postorbital and postfrontal separated and subequal in length. Anteromedial process of postorbital and anterodistal process of postfrontal both present. The squamosal is fairly straight in comparison with other *Iberolacerta* (see Fig. 6) and is in contact with postocular along nearly a third of its length. There are no ribs associated to the third presacral vertebra. Sternal-xiphisternal costal formula (3+2) and sternal fontanelle nearly

round. Claviculae variable (open—marginated—in the female and closed—emarginated—in the male). Interclavicula cross shaped with very slender lateral branches. These lateral branches were of very similar length to the posterior. Anterior/posterior branches relation from 0.40 (female) to 0.42 (male). The male specimen has 26 presacral vertebrae and the female 28, the last six associated to short ribs. The fifth pre-autotomic vertebrae is of A-type following Arnold (1973).

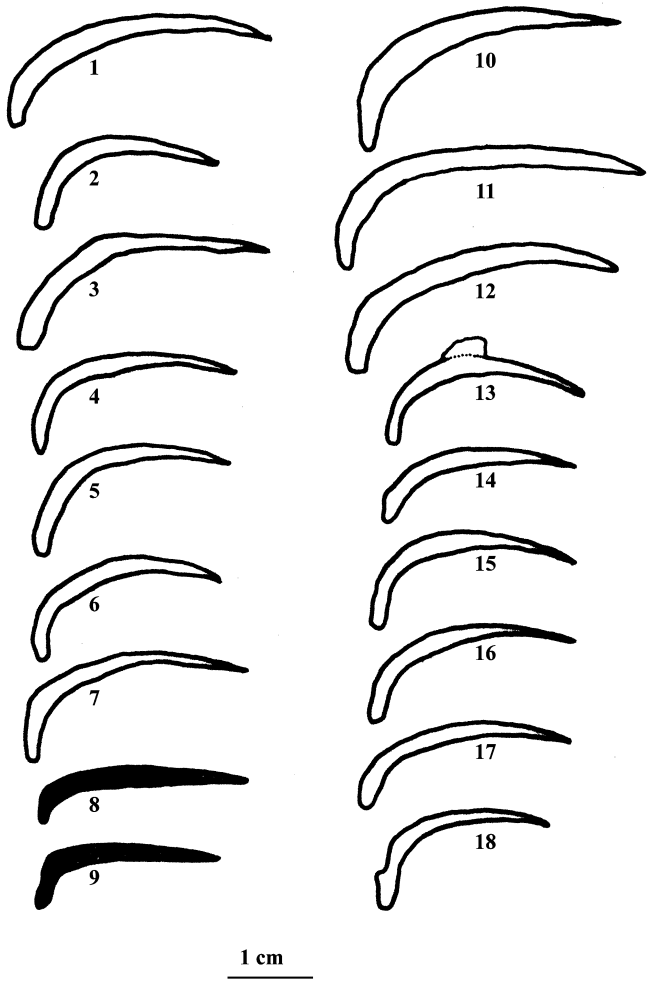

FIGURE 6. Morphology of the squamosal bone in *Iberolacerta*. *Iberolacerta galani* nov. (represented in black) has a fairly straight squamosal in comparison with the more gradually incurved ones of the other *Iberolacerta* spp. 1) *I. monticola* (male) from Sª Estrela; 2) *I. monticola* (female) from Sª Estrela; 3) *I. monticola* (female) from Sª Caurel; 4) *I. monticola* (female) from Pto. de las Señales; 5) *I. monticola* (male) from Somiedo; 6) *I. monticola* (male) from Somiedo; 7) *I. monticola* (female) from Cabeza de Manzaneda. 8) *I. galani* nov. (male) from Sanabria; 9) *I. galani* nov. (female) from Sanabria. 10) *I. cyreni* (male) from Pto. de Navacerrada; 11) *I. cyreni* (male) from Gredos; 12) *I. cyreni* (male) from Gredos; 13) *I. martinezricai* (female) from Las Batuecas.; 14) *I. martinezricai* (female) from las Batuecas; 15) *I. aurelioi* (female) from Coma Pedrosa (Andorra); 16) *I. bonnali* (male) from Bigorre; 17) *I. aranica* (female) from Mauberme massif; 18) *I. horvathi* (female) from Udine (Italy).

Taxonomic account

The data presented above suggests the presence of an undescribed taxon represented by the populations from the Montes de León (see Fig. 1 and Table 1). Despite strong external similarities to *I. monticola*, it is genetically differentiated and also presents a distinctive karyotype.

***Iberolacerta galani* sp. nov.**
[Fig. 8 A–H; Fig 9 A–D]

Synonymy

First nomenclatorial combinations, which include specimens from *Iberolacerta galani* nov. (localities originally referred to are in parenthesis).

Lacerta monticola cantabrica (partim); Elvira & Vigal, (1982), Doñana, Acta Vertebrata, 9: 100, fig 3 (from Truchillas, León and Laguna Vega de Porto, Zamora).

"Lacerta" monticola (partim); Arribas, (1996), Herpetozoa, 9 (1/2): 32 (from Truchillas, León).

Lacerta (Iberolacerta) monticola cantabrica (partim); Carranza et al. (2004), Systematics & Biodiversity 2(1): 61 (from Laguna de Los Peces, Zamora).

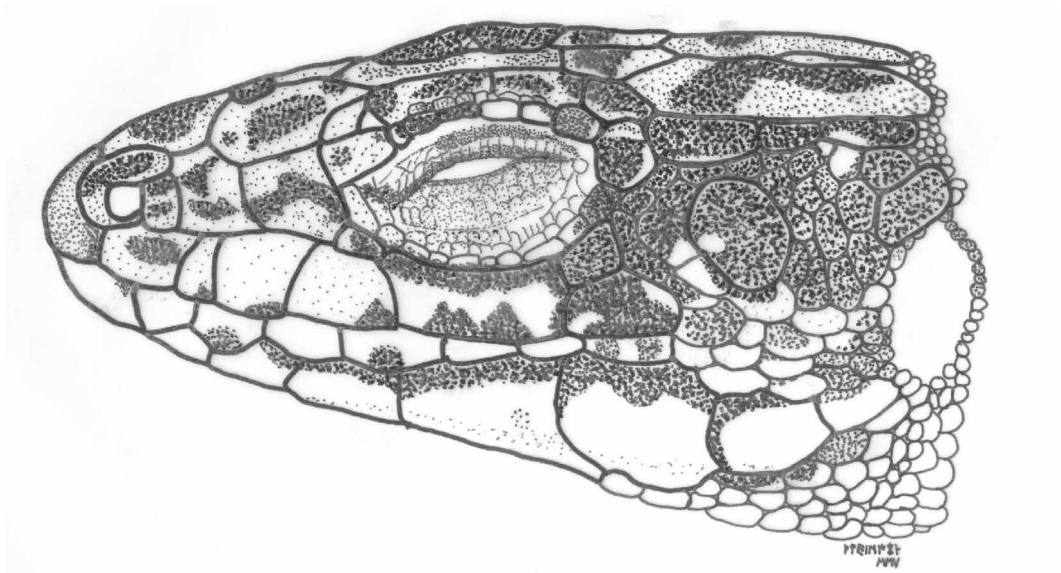

FIGURE 7. Lateral view of the head of the holotype of *I. galani* nov. from the Laguna de los Peces (Sanabria, Zamora), Spain.

Holotype

IPE 4000 Adult male (Fig.7 and 8A–B). Red plastic label attached to left forelimb

with engraved number IPE4000. Also, white cardboard label attached to the left forelimb. Anverse (hand-written): "Laguna de los Peces (Zamora). Sª Segundera. 1700 m. 25-8-04. 2 (encircled). Oscar Arribas". Reverse (hand-written): "*Iberolacerta galani* **sp. nov.**". A red plastic label attached to left hindlimb (in white letters and relief) "HOLOTYPUS". In the I.P.E. collection (Instituto Pirenaico de Ecologia, Jaca, Spain, belonging to the C.S.I.C.).

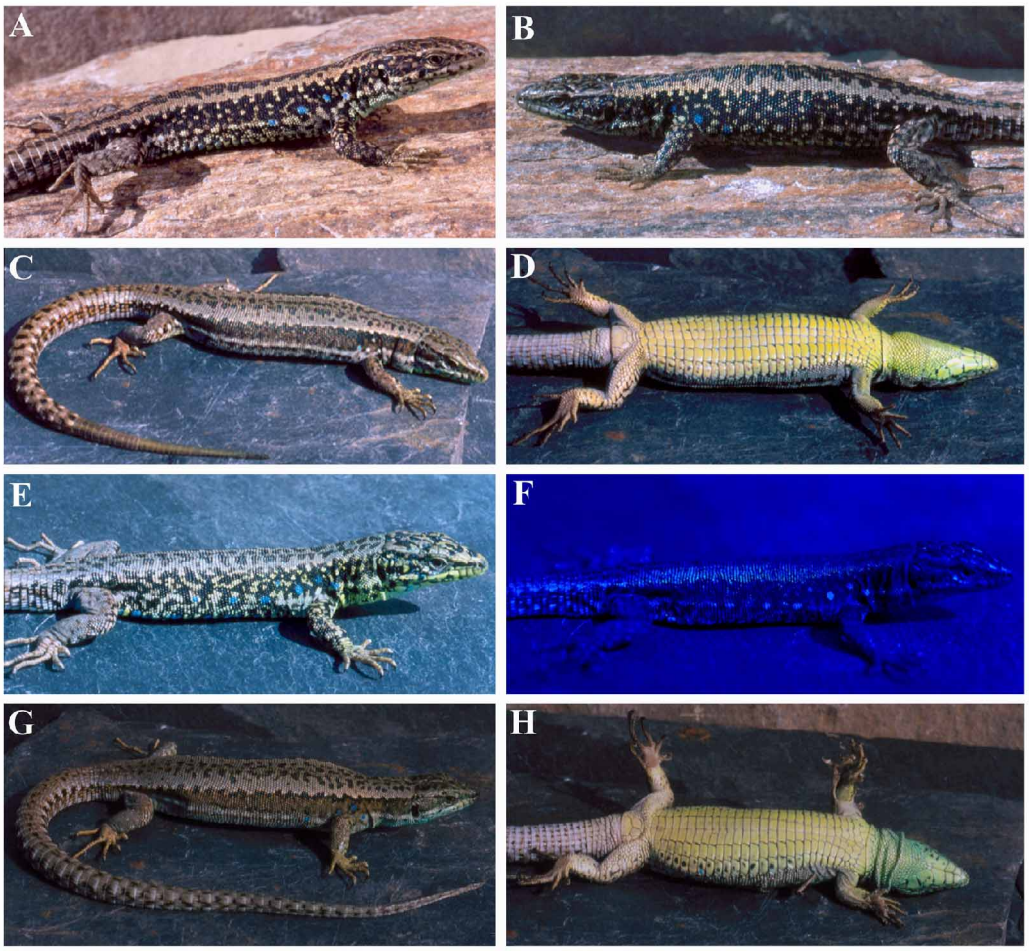

FIGURE 8. Specimens of *I. galani* nov. from several different localities across its distribution range: A–B, male (holotype) from the Laguna de los Peces (Sierra Segundera, Zamora, Spain) viewed from both sides. C, female (paratype) from Puerto del Morredero (Sierra del Teleno, León, Spain). D, female (ventral side) from the same locality as in C, ventral view. E, male (paratype) from Puerto de los Portillinos (Sierra del Teleno, León, Spain). F, same male as in E photographed under ultraviolet light. Notice the highly reflective blue ocelli on the shoulders. G, female (paratype) from the Trevinca Massif (Sierra del Eje, León, Spain). H, same female as in G, ventral view.

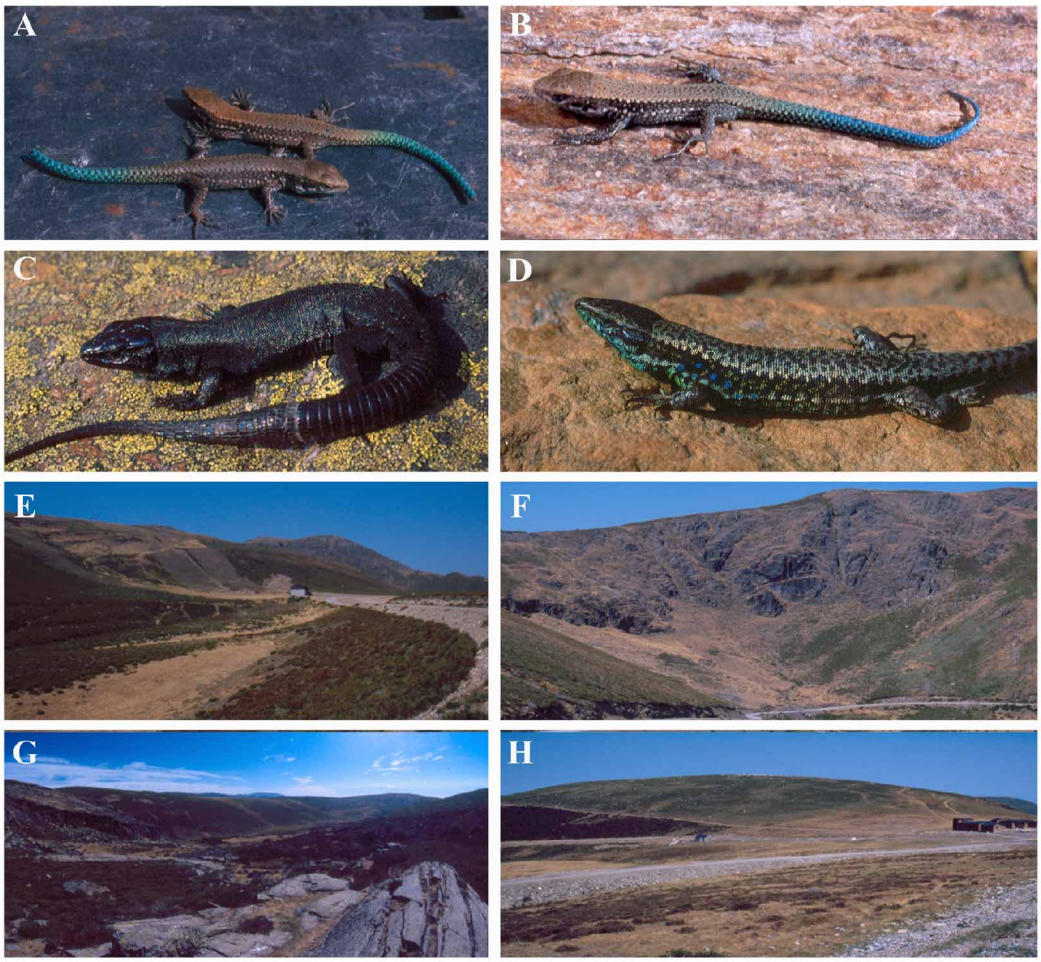

FIGURE 9. Specimens of *I. galani* nov. and pictures of localites across its distribution range: A, hatchlings from Puerto del Morredero (Sierra del Teleno, León, Spain). B, hatchling from the Laguna de los Peces (Sierra Segundera, Zamora, Spain). C, female (paratype) melanistic from Puerto del Morredero (Sierra del Teleno, León, Spain). D, male (paratype) from the Lago de Truchillas (Sierra de la Cabrera Baja, León, Spain). Notice the malachite greenish tinge of the venter and the numerous ocelli on the shoulders. E, Puerto del Morredero (Sierra del Teleno, León, Spain). There is a small ski resort but *I. galani* nov. mainly inhabits the road and track-taluses. F, Puerto de los Portillinos (Sierra de Teleno, León, Spain) is situated near the Puerto del Morredero. In this locality *I. galani* nov. inhabits not only the road taluses but also the extensive rocky (quarzites) outcrops at the higher parts and is syntopic with *Podarcis bocagei*. G, granitoid outcrops surrounded by heathland seen from the dam of the Laguna de los Peces (Sanabria). This is the typical habitat of *I. galani* nov. in Sanabria and is syntopic with *Lacerta schreiberi*. The lizard is especially abundant near the glacial lakes of this area. H, abandoned ski resort in the Peña Trevinca area. *Iberolacerta galani* nov. inhabits the slate slab accumulations by the road and track taluses such as the one seen in the centre of the picture (which constitutes the border between the provinces of León and Orense). It is syntopic with *Podarcis bocagei* in this area.

TABLE 8. Morphometric, scalation and biometric indexes of *Iberolacerta galani* nov. males from different localities. See text for abbreviations of characters and indexes used in the morphometric analysis.

	Teleno (Morredero & Portillinos)	Trevinca (Fonte da Cova)	Cabrera (Lago de Truchillas)	Sanabria (Laguna de los Peces)
	n=3	n=2	n=9	n=10
SVL	58.47±4.15	53.65±7.82	63.28±2.22	60.66±1.84
	53.72–66.75	45.83–61.48	47.11–69.1	51.56–69.05
FLL	20.30±0.76	18.24±2.27	22.33±0.91	19.92±0.88
	19.19–21.76	15.97–20.52	15.87–24.9	15.4–23.8
HLL	29.1±1.58	26.87±3.18	32.34±1.30	29.50±0.90
	27–32.2	23.69–30.06	22.41–35.09	25.21–33.06
PL	14.39±1.02	13.45±1.76	15.82±0.68	14.56±0.52
	13.36–16.43	11.69–15.22	10.7–17.52	11.75–16.89
PW	6.72±0.38	6.34±0.53	7.30±0.26	6.82±0.19
	6.24–7.48	5.81–6.88	5.46–8.26	5.74–7.68
PaL	4.96±0.58	4.59±0.67	5.60±0.29	5.08±0.24
	4.23–6.13	3.92–5.27	3.39–6.44	3.86–6.16
DM	2.15±0.24	2.27±0.6	2.31±0.14	2.06±0.12
	1.78–2.62	1.67–2.87	1.53–2.8	1.46–2.54
DT	2.21±0.21	1.78±0.65	2.05±0.09	1.96±0.10
	1.88–2.61	1.13–2.44	1.8–2.63	1.67–2.83
AW	4.05±0.55	3.79±0.68	4.24±0.23	3.88±0.14
	3.2–5.08	3.11–4.48	2.7–4.9	3.02–4.39
AL	1.98±0.32	1.77±0.25	2.15±0.10	2.17±0.12
	1.53–2.61	1.52–2.03	1.5–2.63	1.68–2.68
GrS r	10±0.57	11±1	10.11±0.51	10±0.68
	9–11	10–12	8–12	5–13
GrS l	9±1	11.5±0.5	10±0.68	9.5±0.61
	8–11	11–12	8–14	6–12
GUL	23±0.57	21.5±0.5	24.33±0.47	23.7±0.49
	22–24	21–22	22–26	22–26
COLL	11±0.57	11±0	11.77±0.36	11.1±0.52
	10–12	11–11	10–13	9–13
DORS	53.66±3.38	54±3	52.66±1.24	54.2±0.92
	47–58	51–57	47–57	49–59

to be continued

TABLE 8 (continued).

VENT	26.33±0.66	26.5±0.5	26.33±0.55	26.4±0.37
	25–27	26–27	24–29	25–28
FEM r	18±0.57	17.5±0.5	17±0.37	18.1±0.43
	17–19	17–19	16–19	16–20
FEM l	17.66±0.66	18.5±0.5	17.11±0.45	17.7±0.39
	17–19	18–19	15–19	16–20
LAM	25.33±0.66	24.5±0.5	25.88±0.69	24.8±0.55
	24–26	24–25	23–30	23–28
CircA	6±1	6±0	6.88±0.35	6.6±0.22
	5–8	6–6	5–8	6–8
R–I	1.33±0.66	1±1	0.11±0.11	0.9±0.27
	0–2	0–2	0–1	0–2
Po–Pa	0±0	0±0	0±0	0.1±0.1
	0–0	0–0	0–0	0–1
Sn–Lor	0.06±0.06	0±0	0.22±0.14	0.25±0.13
	0–0.5	0–0	0–1	0–1
BO	4±1.52	4±1	1.55±0.68	3.6±0.9
	2–7	3–5	0–7	1–11
PV	2±0	1.5±0.5	2.11±0.2	1.4±0.16
	2–2	1–2	1–3	1–2
FLL/SVL	34.89±0.001	34.11±0.007	35.24±0.004	32.27±0.006
	32.59–37.15	33.37–34.84	32.47–37.16	27.64–34.52
HLL/SVL	49.88±0.008	50.29±0.01	51.03±0.006	48.65±0.004
	48.23–51.14	48.89–51.69	47.56–53.46	45.25–50.30
PL/PW	213.62±0.03	211.21±0.10	216.45±0.04	213±14±0.03
	206.81–219.65	201.21–221.22	195.97–232.43	199.09–227.37
DM/PaL	43.50±0.01	48.53±0.05	41.35±0.01	40.57±0.01
	42.08–45.69	42.60–54.45	33.27–46.88	31.34–46.12
DT/PaL	44.88±0.02	37.56±0.08	37.38±0.02	39.07±0.02
	41.50–50.59	28.82–46.29	29.34–53.09	30.35–49.82
AL/AW	48.73±0.01	47.09±0.01	51.24±0.02	55.71±0.01
	47.02–51.37	45.31–48.87	43.60–62.07	45.23–64.11
AS/SVL	480.15±0.38	482.46±0.08	475.59±0.09	477.52±0.11
	411.89–545.5	474.4–490.5	427.18–520.34	404.31–519.23

TABLE 9. Morphometric, scalation and biometric indexes of *Iberolacerta galani* nov. females from different localities. See text for abbreviations of characters and indexes used in the morphometric analysis.

	Teleno (Morredero & Portillinos) n=9	Trevinca (Fonte da Cova) n=3	Sanabria (Laguna de los Peces) n=14
SVL	58.97±2.5	69.04±3.73	66.51±2.9
	48.25–72.18	62–74.71	52.75–84.42
FLL	18.38±0.63	20.01±0.83	19.96±0.62
	15.18–20.42	18.42–21.26	16.25–24.05
HLL	25.86±0.70	28.79±1.13	28.04±0.77
	22.75–29.54	26.63–30.48	24.28–32.98
PL	12.75±0.37	14.16±0.58	13.88±0.41
	11.27–14.83	13–14.9	11.8–16.65
PW	6.29±0.14	7.1±0.32	6.73±0.18
	5.6–6.86	6.5–7.6	5.7–7.9
PaL	4.19±0.13	4.83±0.27	4.63±0.17
	3.7–4.93	4.3–5.2	3.7–5.56
DM	1.85±0.09	1.63±0.07	1.75±0.14
	1.57–2.44	1.49–1.73	0.86–2.58
DT	1.9±0.12	1.98±0.15	1.94±0.04
	1.41–2.5	1.68–2.22	1.36–2.63
AW	3.45±0.24	3.97±0.08	3.84±0.23
	2.15–4.86	3.88–4.14	2.58–5.28
AL	2±0.11	2.31±0.15	2.27±0.12
	1.52–2.53	2.02–2.52	1.79–3.29
GrS r	8.66±0.70	9.66±1.85	10.28±0.45
	6–11	6–12	7–13
GrS l	8.77±0.40	9.66±1.45	10±0.46
	7–11	7–12	5–12
GUL	24.66±0.60	23.66±0.88	23.42±0.67
	23–29	22–25	16–27
COLL	11.77±0.43	11.33±0.66	10.85±0.4
	10–14	10–12	9–14
DORS	52.88±0.88	53±1.15	53.28±1.11
	48–56	51–55	48–61

to be continued

TABLE 9 (continued).

VENT	30.44±0.41	30.33±0.88	30.85±0.34
	28–32	29–32	28–33
FEM r	17.66±0.44	18.33±0.88	17±0.54
	17–21	17–20	14–20
FEM l	17.33±0.57	18.33±0.88	16.92±0.57
	16–21	17–20	13–20
LAM	26.11±0.63	27±2.08	24.5±0.40
	24–30	23–30	22–27
CircA	5.88±0.20	6±0	6.5±0.20
	5–7	6–6	5–8
R-I	0.66±0.28	1.66±0.33	1.35±0.16
	0–2	1–2	0–2
Po-Pa	0±0	0.33±0.33	0.14±0.08
	0–0	0–1	0–1
Sn-Lor	0.22±0.12	0.66±0.33	0.25±0.11
	0–1	0–1	0–1
BO	1.44±0.24	2±0	2.28±0.41
	0–2	2–2	0–6
PV	1.22±0.27	1±0	0.92±0.16
	0–3	1–1	0–2
FLL/SVL	31.29±0.005	29.02±0.003	30.29±0.006
	27.97–34.62	28.45–29.70	26.75–33.87
HLL/SVL	44.10±0.007	41.77±0.006	42.59±0.008
	40.92–47.82	40.79–42.95	37.06–47.48
PL/PW	202.42±0.02	199.68±0.01	205.90±0.012
	197.48–219.37	196.83–202.36	196.44–216.79
DM/PaL	44.11±0.01	33.95±0.004	37.30±0.02
	35.44v49.49	33.52–34.81	19.50–50
DT/PaL	45.29±0.02	41.06±0.01	41.82±0.01
	35.07–59.52	39.25–43.02	35.37–48.05
AL/AW	59.20±0.003	58.08±0.03	59.79±0.01
	48.97–81.86	52.06–64.45	48.12–71.31
AS/SVL	443.46±0.14	439.48±0.09	442.35±0.10
	400.50–523.39	420.15–451.54	366.66–529.88

Paratypes

Eight males and thirteen females from Laguna de los Peces, Sierra Segundera, ca. 1700 m, same data as Holotype (IPE 4001–4005 and OA04082501, 3–18). One male from Lago de Truchillas, Sierra de la Cabrera Baja (León province), 12/04/1990 (nº OA90041201). Eight males from Lago de Truchillas, Sª de la Cabrera Baja, 1390–1750 m (León province), 6/04/1997 (nº OA97040601–08). Six males and five females from Puerto del Morredero (ski resort), Sierra del Teleno, 1762 m (León province), 14/08/2005 (nº OA05081401–09, OA05081412, OA05081416). Two males and four females from Puerto Los Portillinos, Sierra del Teleno, 1820–1957 m (León province), 14/08/2005 (nº OA05081401–06). Two males and three females from "Refugio da Fonte da Cova" (abandoned ski resort), Peña Trevinca, 1860 m (Orense province), 15/08/2005 (nº OA05081501–05). All with plastic red labels attached to their left hindlimbs (with white letters in relief reading "PARATYPUS").

Diagnosis

A large *Iberolacerta*, especially characterized by the following combination of characters: large SVL (females up to 84.42 mm, the largest *Iberolacerta* known to date) with relatively small fore and hindlimbs. High number of blue occelli on the shoulders (UV-reflective, as are the blue spots on the outermost ventral ranges, see Figs. 8 and 9) and contact between supranasal and first loreal contact relatively frequent (full contact in almost a quarter of all specimens analyzed, and near contact in many others; Fig. 7). Frequency of rostral-internasal contact relatively low in males (33 %) but relatively high in females (58 %), higher number of Collaria, Dorsalia and Ventralia and less Circumanalia in comparison with other *Iberolacerta*. Postocular and parietal plates separated. Azygos scale between the prefrontals rare (13 % of specimens). Osteologically, it is characterized by a fairly straight squamosal bone, only incurved in its posterior part (Fig. 6), Karyotype with 36 uniarmed machrochromosomes gradually decreasing in length and NORs in the telomeric position of a large chromosome pair (possibly the fifth chromosome pair; L-Type) (Figs 4 and 5). Sex chromosomes differentiated and heteromorphic. Chromosome Z presents a peritelomeric Chromomycin A_3 heterochromatic band, which is unique among *Iberolacerta* and is as large as the autosome pair 6. Chromosome W is heterochromatinized and as large as autosome pair 10 or 11. Partial mitochondrial DNA sequences for the cytochrome *b* and 12S rRNA genes sequenced for this study are distinct from all the remaining representatives of *Iberolacerta* known to date (Fig. 3).

Description of holotype

Biometry: Adult male with snout-vent length of 69.05 mm. Tail 29.16 mm (autotomized). Forelimb length 23.84 mm. Hindlimb length 33.06 mm. Pileus length 16.8 mm. Pileus width 7.5 mm. Parietal legth 6.16 mm. Masseteric widest diameter 2.54 mm. Tympanic widest diameter 1.87 mm. Anal plate width 4.39 mm. Anal length 2.56 mm.

FLL/SVL (relative forelimb length): 0.345. HLL/SVL (relative hindlimb length): 0.478. PL/PW (pileus shape): 2.252. DM/PaL (relative masseteric plate size): 0.412. DT/PaL (relative tympanic size): 0.303. AL/AW (anal plate surface): 0.583. AS/SVL (relative anal plate size with respect to total length): 4.854.

Scalation

Number of supraciliary granules: 10 (right) and 9 (left). Supralabials: 4 (both sides). Sublabials: 7 (both sides). Submaxillars: 6 (both sides). Gularia: 22. Collaria: 9. Dorsalia: 55. Ventralia: 27. Femoral pores 17, on both sides. Lamellae: 25. Circumanal Plates: 6. Scales on a ring annulus from tail-basis: 27. Rostral in full contact with internasal. Supranasal in contact with first loreal. One postnasal. First postocular separated from parietal plate. An azygos (supernumerary) scale between prefrontals. Occipital and interparietal plates separated by a prolongation of the right parietal, and a supernumerary small scale corresponding to this same anomalous prolongation on the left side. An illustration of a lateral view of the head of the holotype is shown in Fig. 7.

Coloration (in life, outside the breeding period)(Fig 8A–B). Pileus with tiny, vermiculated irregular spotting. Small spots on supralabials, subocular and sublabials. Small spots on the sides of the gular area. Dorsal tract with yellowish-grey (4B2) [2Y 8.1/1.3] to greyish-yellow (4B3) [3.5Y 8.0/2.6] base color in life (same color as in alcohol). Two juxtaposed rows of black spots fused together forming transverse irregular spots that cover approximately half of the dorsal tract width. These black spots get smaller and fainter along the tract towards the tail. Temporal and infratemporal bands fused and reticulated, leaving small whitish (or blue, see below) spots, more developed in the area within these two primitive bands, on the lower part of the flanks. This temporal band starts at the eyes and runs along the sides, where it narrows and appears faintly on the sides of the tail. Four (right side)/five (left side) blue (21A7) [6PB 5.0/12.4] occelli on the shoulders. Small blue dots on the outermost plates of the venter. Venter pastel green (29A4) [6gy 8.7/3.1] on the belly and greenish white towards the limits of the gular area (29A2) [4GY 9.0/1.0] in life. In alcohol, from turquoise white (24A2) [5B 8.7/1.0] on the central plate rows of the venter to light turquoise (24A4) [6.5B 7.7/3.1] towards the outermost ones. The four outermost ventral plate ranges with black spotting (the two outermost well developed, sinuose and placed on the foreborder of the plate, covering near half of its surface; the two inner plate ranges only thin and on the foremost border). Two minute spots on the posterior free border of anal (preanal) plate. Blue occelli on the shoulder UV-reflective, as are the blue spots on the outermost ventral ranges.

Variability

Biometric and scalation values for the whole species, and comparison with the other *Iberolacerta* species from the "monticola-group" are shown in Tables 5 (males) and 6 (females). Intraspecific variability of *I. galani* **sp.** nov. by samples is presented in Tables 8

(males) and 9 (females) (only specimens with SVL>45 mm). The small size of samples precludes any statistical comparisons between them. Pictures of *I. galani* nov. (fig 8A–H & 9A–D) and some *I. monticola* are shown for comparison (Fig. 10, A–H).

FIGURE 10. Photographs of some *I. monticola* specimens from several different localities across its distribution range: A, male (above) and female (below) from Llagu la Cueva, Somiedo (Asturias, Spain). These are perhaps the most common patterns in the main part of the species area. B, young male from the Picos de Europa (Asturias, Spain). Lizards from this area (males and females) take on a vivid green colour during the breeding period. C, young male from Cabeza Grande de Manzaneda (Orense, Spain). D, old female from Cabeza Grande de Manzaneda (Orense, Spain). E, well-grown brown coloured male from Puerto de Vegarada (León, Spain). In some localities where the species inhabits earth taluses instead of rock outcrops, cryptic brown colours seem to be adopted. F, two hatchlings from Puerto de Vegarada (León, Spain). G, old female from Puerto de las Señales (León, Spain). H, adult male from A Torre, Serra da Estrela (Beira Alta, Portugal). Fully-grown specimens from this locality are very patterned, with a greyish, very light brown or more frequently green and occasionally bluish base colour.

Concerning certain singular morphological characters, of nineteen male specimens, fifteen exhibit the common disposition of prefrontals in full contact, whereas two specimens have an azygos scale between them, and another two show separation between these scales, permitting a suture between internasal and frontal plates. Out of twenty-six females, twenty-three exhibit the common disposition of prefrontals in full contact, whereas three have an azygos scale between them. Nine specimens from a total of forty-five (including both sexes) have two masseteric plates instead of one.

Coloration males (breeding period, from Sierra de la Cabrera). In life, dorsal tract from green (28B7 to 28B6) [7.5GY 7.0/7.8 to 7.5GY 7.3/5.7] to greenish grey (28B2) [5GY 8.0/0.8], and to greyish green (28C4) [6GY 6.8/2.5] in the pelvic area and forelimbs. Shoulder occelli vivid blue (22A8) [5PB 4.5/14.2], very numerous, in most cases from two to seven but occasionally up to eleven (Fig 9D). The irregular vertebral band (more barely aligned in two juxtaposed rows) is very developed and finely disgregated, connected to the temporal (=costal) bands giving the specimens a highly reticulated overall appearance. This band connects rapidly and progressively with the costal ones as the specimens grow. Ultraviolet reflective occelli are present in *I. monticola*, *I. martinezricai* and *I. galani* nov. In this latter species (Fig 8E–F), however, blue (and UV reflecting) occelli are more numerous (and are absent in *Podarcis bocagei*, syntopic in some localities). The number and size of UV reflecting occelli increases with age and, presumably, status.

Females (breeding period). Unknown.

Males (outside the breeding period, from Sierra Segundera, Trevinca and Teleno) (Figs 8A, B and E). As in the holotype, yellowish-grey (4B2) [2Y 8.1/1.3] to greyish-yellow (4B3) [3.5Y 8.0/2.6] dorsal tract base color, only slightly darker in specimens close to ecdysis. Specimens that are not yet fully grown (especially those living on slates in Teleno and Trevinca) have a brownish dorsum. Vertebral band with small or medium irregular dots, even elongated and vermiculated, which are barely aligned in two juxtaposed (but distinguishable) rows. These dots or irregular blotches tend to coalesce with age (as in the holotype). Temporal (=costal) bands reticulated, with scalloped upper edge and also fused with the "lateral inferior line", leaving a row of clearer dots among the primitive situation of both, which are a prolongation of the blue occelli of the shoulders. Venter pastel green (29A4) [6gy 8.7/3.1] on the belly and greenish white towards the limits of the gular area (29A2) [4GY 9.0/1.0] in life. The occelli on the shoulders are blue (21A7)[6PB 5.0/12.4]. Usually only the two outermost rows of ventral plates present dark marks. These appear more centrally on the plate in younger males but are bigger and connected to the foreborder in older males. There are a few black dots on the submaxillar plates and especially in the gular sides.

Females (outside the breeding period, from Sierra Segundera, Trevinca and Teleno): (Figs. 8C, D, G and H). Dorsum from pale green (29A3) [6GY 8.9/2.1] to greyish green (29B3 and 29B4) [5GY 8.0/1.8 and 5.5GY 7.9/2.8) in fully-grown animals. Pattern is much less spotted than on males and the degree of development is not correlated with age

(older females may or may not exhibit moderately developed spotting). Usually a dark, irregular spotting or vermiculated in the center of the dorsum, which can either be spread widely across the dorsal tract, or be clearly aligned in two rows. Temporal bands not reticulated but uniform, with marginal areas (especially the upper border) darker (nearly black) and the inner area lighter (brown). Upper edge of this temporal (=costal) band also scalloped, enclosing lighter dots, more visible in younger specimens but also in adults. The rows of lighter dots on the lower part of the sides are less marked, as is the inferior lateral line, which is faint and rarely appears in the form of dots. Venter yellowish green (30A8 and 30A7) [3.5GY 8.5/11.4 and 3.5 8.7/8.6]. Blue occelli as in males. In contrast to the males, black spotting usually appears in the center (or on the rear parts) of the plates of the outermost ventral scale rows, and is often faint. Less frequently, very small dots appear on the second inner row of ventral plates.

A melanic female (the first published case of melanism in the *I. monticola*-group) is depicted in Fig 9C.

Hatchlings (from Sierra Segundera and Teleno): (Figs. 9–A–B). Dorsum with greyish-yellow (2B3 and 2B4) [8Y 8.0/2.5 to 9Y 8.0/4.1] background. Dorsal tract finely spotted with irregular blotches on the vertebral area, which can be very faint and barely distinguishable. Temporal bands slightly reticulated in male hatchlings and more uniform in females (sexual dimorphism from birth). Venter without color pigmentation, with the first (outer) row of ventrals densely spotted, but the inner second and third pairs of rows less marked. Tail is blue (22B7 and 23B7) [5PB 4.9/11.0 and 1PB 5.1/9.2].

Additional material. Additional unnumbered specimens were cleared and stained for the osteological (two from Sanabria) and karyological work (three: two from Sanabria and one from Teleno). Additionally, nine live hatchlings were examined (six from Sanabria and three from Teleno). Almost twenty other adult specimens were examined and released in Sanabria, four adults from Teleno and another subadult from Trevinca.

COMPARATIVE NOTES: (taxa with significant differences to *I. galani* nov. in parenthesis; abbreviations, cyr: *I. cyreni*; mart: *I. martinezricai*; mont: *I. monticola*).

Morphology

MALES of *I. galani* have fewer left supraciliary granules (cyr), greater collaria (cyr), greater ventralia (cyr), small left femoralia (mart), less circumanalia (cyr), low frequency of rostral-internasal contact (cyr, mont), greater supranasal-loreal contact (all other), higher number of blue occelli (all other), greater ventral punctuation (cyr), shorter forelimb length (cyr, mont), shorter parietal length (cyr), greater masseteric plate (cyr, mart), greater tympanic (cyr) and small anal plate (cyr).

FEMALES of *I. galani* nov. have less fewer supracilliary granules (cyr), greater collaria (all other), greater dorsalia (cyr, mont), greater ventralia (all other), less circumanalia (cyr, mont), low frequency of rostral-internasal contact (cyr) supranasal-loreal contact (all other) higher number of blue occelli (all other), ventral punctuation

(cyr), shorter forelimb length (cyr), shorter hindlimb length (cyr, mont), shorter pileus (cyr), greater masseteric plate (mart), greater tympanic size (all other) and smaller anal plate (cyr).

The presence of an azygos scale between prefrontals is rare in *I. galani* nov. (13 %), whereas it is very common in the immediate Galician populations of *I. monticola* (present in more than 50% of the examined specimens from most Galician populations and in all of the examined specimens from the Cabeza de Manzaneda (Orense), the nearest known population to the general area of *I. galani* nov., less than 40 km in a straight line; see Fig. 1).

Osteologicaly, *I. galani* nov. is very similar to the other species in the "Iberian group" (see Fig. 5). However, it differs in the shape of the squamosal bone, which is clearly curved in all the other *Iberolacerta* (including the Pyrenean and Alpine species) but fairly straight in *I. galani* nov. (see Fig. 6). Moreover, in the "Iberian group", *I. cyreni* usually has longer nasal bones and nine premaxillary teeth (seven in the *I. galani* nov. studied); *I. monticola* has a spatuliform or elongated and parallel-sided processus nasalis (only rarely arrow-shaped, more frequent in Galicia and Estrela, also present in *I. galani* nov.); *I. martinezricai* has nine premaxillary teeth, an elongated (parallel-sided, not arrow-shaped as in *I. galani* nov.) processus nasalis, and frequently seven short presacral ribs and a thin triangular medial process in the squamosal, at least in some specimens.

The karyotype of *I. galani* nov. is distinguished from the karyotypes of *I. martinezricai* and *I. cyreni* by the position and location of the NORs (telomeric and on a long chromosome pair in *I. galani* nov. and interstitial and on a medium-large sized pair in *I. martinezricai* and *I. cyreni*). It also differs from the karyotype of *I. monticola* by the presence of differentiated sex chromosomes, Z and W, both heteromorphic and heterochromatic (homomorphic and euchromatic in *I. monticola*) (see Fig 5). It differs from *I. horvathi* (which also has partially heterochromatic W sex chromosome and L-Type NORs) by the fact that in *I. galani* nov., W is fully (not partially) heterochromatic and mainly by the presence of a Z, unique among *Iberolacerta*, in bearing a peritelomeric CMA3 positive heterochromatin.

Derivatio nominis

The specific epithet "galani" is a genitive (possessive) Latin name (g. masculine). This patronym (eponym) honours Dr. Pedro Galán Regalado (Cee, 1955), from A Coruña (Spain), for his lifelong dedication to the study of NW Iberian (especially Galician) herpetofauna and Natural History in general. This is also in recognition of the discovery and long-term study of most of the lowland and sea-level populations of *Iberolacerta monticola* from Galicia.

Distribution

Iberolacerta galani nov. is endemic to the Montes de León (northwestern Iberian Peninsula, see Fig. 1): Sierra Segundera, Sierra de la Cabrera, Sierra del Eje or Peña

Trevinca and Sierra del Teleno between the provinces of León, Zamora and Orense, where it can be found from 1000 to 2000 m, but probably also at higher altitudes. The first two mountain ranges encircle the highland plateau of Sanabria, where as a result of Quaternary glacial activity many lakes were formed. Nearby, *I. galani* nov. is present in the Sierra del Eje or Peña Trevinca, on the border between the provinces of Orense and León, where it has been found from 1700 to 2000 m. It is also present to the north of the Eria and Cabrera rivers, in the neighboring Sierra del Teleno in the province of León, where it has been recorded from 1340 to almost 2000 m, but where it probably reaches the highest peaks of these ranges (Vizcodillo 2122 m, Trevinca 2096 m, and Cerro del Teleno 2185 m) (see Figs. 9E, F, G and H).

The mountain area inhabited has the form of a "V" without vertex, open to the west, formed by the anticlinals of Piornal-Teleno (to the North) and Ollo de Sapo (to the South) and separated in the middle by the synclinal of Truchas. The overall distribution range of *I. galani* nov. borders several lowland areas unsuitable for mountain lizards like *Iberolacerta*. More specifically, its distribution borders with El Bierzo (Sil valley) to the north; with La Maragateria (Duero Valley) to the north east and east; with the Tera valley (draining into the Duero) to the south; and with the Bibei river valley (draining into the Sil) to the west. These lowland areas have either a moderate Atlantic (to the north) or Mediterranean (the remainder) climate (Nieto-Feliner 1985). Further west, on the other side of the dry Mediterranean Bibei river valley, *I. galani* nov. is replaced by *I. monticola*, which inhabits the Serra da Queixa (summit in Cabeza Grande de Manzaneda—1778 m) and the Serra do Invernadeiro (both in Orense province). These *I. monticola* populations lie less than 40 km away from the nearest *I. galani* nov. populations from Peña Trevinca, also in the province of Orense (see Fig. 1).

Iberolacerta monticola is also found very close to the northern part of the distribution range of *I. galani* nov., on the other side of the Sil river valley in the Sierra de Ancares, the Sierra de Caurel, etc. and further to the north east, in the mountainous regions leading to the main axis of the Cordillera Cantabrica (see Fig. 1). The highest pass between the Montes de León (inhabited by *I. galani* nov.) and the spurs of the Cordillera Cantabrica (inhabited by *I. monticola*) is the Puerto del Manzanal (1230 m), where *Iberolacerta* has never been recorded.

Habitat

Within its distribution area, *Iberolacerta galani* nov. inhabits supraforestal habitats, which are characterized by a high-mountain climate and are included in the Oromediterranean and Crioromediterranean bioclimatic stages (Rivas Martinez 1987) (see Figs 9E, F, G and H).

The rocky substrates inhabited are fairly diverse: in Sanabria and the Sierra de la Cabrera it lives upon a small number of fissured igneous rocks ("Ollo de Sapo" and other

sin-cynematic granitoid rocks of uncertain age) (Fig 9G); in Teleno (Fig 9E and F) and Trevinca (Fig 9H) it lives among slabs of black slate from the Middle Ordovician age, highly prized for their use in construction, which could represent a threat to its conservation in some areas; in the highest parts of these sierras (Teleno and Cabrera) it lives among the hard Armorican quartzites that constitute the peaks.

The lower areas currently inhabited by *I. galani* nov. may well have been colonized by the species in historical times, when the forest was cleared for pastures. The species can also inhabit areas of azonal vegetation below its natural limit, in particularly favourable conditions in terms of temperature and moisture such as river canyons. These lower areas are included in the Supramediterranean and altimontane Estrellian, Orensano-Sanabrian and Galaicoportuguese Silicicolous Series of *Betula celtiberica* or birch (*Saxifrago spathularidi-Betuleto celtibericae sigmetum*) and are constituted by the upper limits of the forests, usually destroyed as a result of fires. The regressive stages inhabited by *I. galani* are broom heathlands of *Cytiso striati - Genistetum poligaliphyllae*, which are themselves replaced by heathlands of *Genistello tridentatae - Ericetum aragonensis* (Navarro-Andrés & Valle-Gutierrez 1987; Rivas Martinez 1987).

The main part of the *I. galani* nov. distribution range falls between the Oromediterranean Orensano-Sanabrian, silicicolous series of the dwarf juniper (*Genisto sanabrensis - Junipereto nanae S.*) which are areas with silicicolous, psicroxerophilous and chionophilous oromediterranean shrubs, endemic to the high Orensano-Sanabrian Sierras and belonging to the *Genisto sanabrensis - Juniperetum nanae*, which is its climax series. Covers from 1600m to 2000m. A shrub endemic to the area is *Genista sanabrensis* Valdes-Bermejo, Castroviejo & Casaseca, 1977. Trees are absent from these zones, and the dense scrub has *Juniperus nana, Genista sanabrensis, Cytisus oromediterraneus (=C. purgans)* and *Deschampsia iberica*. The more degraded scrub has *Calluna vulgaris, Cytisus oromediterraneus, Genista sanabrensis* and *Erica aragonensis*. Grasslands contain *Nardus stricta, Agrostis capillaris* and *Phalacrocarpum oppositifolium* (Navarro-Andrés & Valle-Gutierrez 1987; Rivas Martinez 1987).

The upper parts of its altitudinal range (above 2000 m) belong to the Crioromediterranean Orensano-Sanabrian silicicolous series of *Festuca indigesta* (*Teesdaliopsio confertae - Festuceto indigestae S.*), which appears only on those summits above 2000 m, where it forms a mosaic with dwarf shrubs of *Genisto sanabrensis - Junipereto nanae S.* (Navarro-Andrés & Valle-Gutierrez 1987; Rivas Martinez 1987). An exhaustive account of the flora from this area can be found in Nieto-Feliner (1985).

Interestingly, these areas have undergone dramatic changes in their vegetation during the Holocene. Conifers (*Pinus sylvestris* and *Pinus uncinata*), today absent, were present in the Cordillera Cantabrica, Galicia and the Montes de León during the Pleistocene and well into the Holocene, but disappeared very recently (probably during the Subatlantic period, less than 2500 ybp) as a result of oceanic conditions and human influence (there are no conifers in the Cantabric subalpine belt).

Thanks to one of the best pollinic sequences of the Iberian Peninsula (Laguna de las Sanguijuelas, Sanabria, 1000 m, with a time span of nearly 14000 years), the vegetation history of Sanabria is extremely well known and indicates that conifers (*Pinus sp.*) were well represented until very recently and only retreated during Subatlantic, when they were substituted by *Quercus* at low altitude and *Betula* at high altitude (Blanco *et al*. 1996; Arribas 2004).

Endemic zoological species from the Montes de León include mainly coleopters with dispersive capabilities very similar to those of mountain lizards: *Nebria belloti* Franz, 1954 (Trevinca, Segundera and Teleno), *Nebria leonensis* Assmann, Wrase & Zaballos, 2000 (Cabrera baja and Teleno), *Leistus valcarceli* Wrase, Ruiz-Tapiador & Zaballos, 1998 (Cabrera Baja and Teleno), *Zabrus mateui* Novoa, 1980 (Peña Trevinca, Sierra Cabrera Baja, Sierra Segundera and Montes Aquilanos) and *Anchomenidius feldmanni* Wrase & Assmann, 2001 (Teleno) (Alonso *et al.* 1987; Wrase *et al.* 1998; Assmann *et al.* 2000 and our own data). Most of these new species are recent discoveries and, like the lizards of the *I. monticola* group, they belong to the biogeographical "Lusitanian" species groups that are distributed throughout the western Iberian Peninsula, and which spread further into the center and the east along the main mountain ranges, with a high incidence of endemics (Arribas & Carceller 1995; Arribas 2004).

Discussion

Morphology

The results of the correlation analyses (Table 7) indicate that the apparent morphological divergence between different samples is mainly related to precipitation (and thus to evapotranspiration) and is not paralleled by genetic or karyological differentiation. Moreover, lizards share the morphology of their common ancestor and do not change it unless they encounter these geoclimatic factors. When such differences exist, each population shows a scalation value, which is correlated with their position on the geoclimatic gradient.

A low frequency of azygos scale among prefrontals is frequently found in other populations of the different species of the *monticola*-group (Arribas 1996; Arribas & Carranza 2004), but differs greatly from the neighbouring Galician populations of *I. monticola*, where this is a very common occurrence, which might even be used as a diagnostic character for species in that particular area (our own data and P. Galan, pers. comm.).

Contact between supranasal and first loreal plates in *I. galani* nov. appears on both sides in nearly a quarter of specimens, and on only one side or with near-contact in many others (which might explain the existence of some ambiguous records of *I. bonnali* from Sanabria in the raw data for the initial versions of the Spanish Atlas Database, O.A. pers. obsv.). This disposition is either absent or extremely rare in the other species of the

monticola-group (*I. monticola, I. martinezricai* and *I. cyreni*), yet is more frequent in *I. horvathi* (nearly 67% of specimens, and therefore frequently considered as a diagnostic for this species; De Luca 1989) and is present in almost all specimens from the Pyrenean-group (subgenus *Pyrenesaura* Arribas, 1999: *I. aranica, I. aurelioi* and *I. bonnali*).

Other characters such as the relatively large SVL (especially in females), ventralia, etc. and the comparatively short legs can be explained by the elongated body of *I. galani* in comparison to other closely-related species, and the greater dorsalia with its larger body size.

Osteology

With regard to osteology, closely-related species of lacertids do not usually exhibit qualitative differences. Only in very localized populations do certain characters become fixed from time to time, in which case they may be useful as diagnostics. This is probably the case of the diagnostic characters of the three *Pyrenesaura* species and *I. martinezricai*. The fairly straight squamosal bone of *I. galani* nov. (Fig. 6) may be the result of such a process.

Karyotype

The location of NORs in studied specimens of *I. galani* nov. closely relates them to *I. monticola*. Both taxa possess NORs on the L pair, while in the other two Iberian species with 2n = 36 chromosomes, *I. cyreni* and *I. martinezricai*, NORs are on a medium-large (M-type) chromosome pair (11^{th} pair) (Fig. 5) (Odierna *et al.* 1996; Arribas & Odierna 2005). However, the studied specimens can be differentiated from *I. monticola* by the presence of a cytologically detectable ZW sex chromosome system, not found in the latter group (Fig. 5). This sex chromosome system is almost universal among lacertid lizards and the morphology, content and distribution of DNA sequences of the W chromosome are taxonomically informative (Odierna *et al.* 1993; Olmo *et al.* 1987;). However, recent studies have shown that in lacertids, sex chromosomes can appear independently and evolve rapidly in related taxa (Bosch *et al.* 2003; Odierna *et al.* 2004). *Iberolacerta* offers such an example: simple (ZZ/ZW) or multiple ($Z_1Z_1Z_2Z_2/Z_1Z_2W$) sex chromosome systems are present and cytologically detectable in *I. cyreni, I. bonnali, I. aurelioi and I. galani* nov. but not detectable in *I. aranica*, *I. martinezricai* or *I. monticola* (Odierna et al. 1996; Arribas & Odierna 2005). Moreover, differences in the ZW sex chromosome system between *I. galani* nov. and *I. monticola* are significant, particularly the telomeric CMA_3 positive heterochromatin present on the Z chromosome of all studied specimens of *I. galani* nov. This character is unique among all lacertid species investigated to date. Differences in the ZW sex chromosome system might have played an important role in preventing or negatively affecting the chromosome pairing and segregation of the hybrids (e.g. John, 1981; King 1993). Alterations in the morphology and/or heterochromatin content of sex chromosomes, particularly those on the X (or Z) chromosome – as in *I.*

galani nov. – are known to have a negative impact on the fertility of hybrids (Hewitt *et al.* 1989; McKee 1991; King 1993), probably due to the acknowledged involvement in meiotic pairing and segregation of these particular chromosomes (King 1993; McKee *et al.* 2000). As an example, in the rodent *Nesokia indica*, laboratory inbreeding involving specimens of populations with different amounts of the sex chromosome heterochromatin invariably produced unfertile hybrids (Thelma *et al.* 1988).

Karyological results, then, indicate that the studied specimens of *I. galani* nov. are closely related to *I. monticola*, but that the two taxa differ greatly in the presence/absence of a ZW sex chromosome system. This degree of karyologic differentiation points to their specific separation and supports mtDNA and osteological data.

Molecular analyses

Uncorrected genetic distances of the two mitochondrial genes analyzed in this study (cytb and 12S) clearly indicate that *I. galani* nov. is genetically different from its most closely-related taxa, *I. martinezricai* (4.6% for the cytb and 1.8% for the 12S) and *I. monticola* (4.7% for the cytb and 1.9% for the 12S). Although this is in fact lower than the average divergence detected between vertebrate species and between different forms of the lacertid lizard *Podarcis hispanica* (Harris 2002; Harris *et al.* 2002; Harris & Sa-Sousa 2002), it does suggest that these three species have been evolving independently for more than 2 myr. The absence of shared mitochondrial haplotypes between these three closely-related species despite having sequenced a relatively high number of samples (20 *I. galani* nov., six *I martinezricai* and 17 *I. monticola*), together with the fact that all three species present different karyotypes (see Fig. 5), indicates that gene flow between these species is probably very limited. Despite the evidence provided by the mtDNA and karyotypes of some specimens, the presence or absence of gene flow should be tested using an even higher number of specimens and highly variable nuclear markers, such as microsatellites. All specimens of *I. monticola* included in this study and some specimens of *I. galani* nov. are homozygous for a T at position 22 of the c-mos fragment used in our study, rather than the C present in all the other species of *Iberolacerta* (including *I. martinezricai*). Furthermore, several samples of *I. galani* nov. are heterozygotes (C/T) for this position. As a result of the low variability of c-mos, this might indicate that *I. galani* nov. and *I. monticola* are sister species and that the C-T mutation at position 22 occurred in their common ancestor. This contrasts with the phylogenetic tree presented in Fig. 3, in which *I. galani* nov. is sister to *I. martinezricai* and *I. monticola* is sister to them both. Maybe C/T heterozygotes or even homozygotes for a T at position 22 will be discovered in the future in *I. martinezricai* once more sequences from this species have been obtained. Heterozygotes in c-mos have been reported in some previous studies (Jesus *et al.* 2005) and although they provide useful information they can be very difficult to detect if the PCR products are not cloned or the sequences are not very clear and from both directions.

As shown in Table 7 morphology in general, but especially scalation, is strongly correlated with the level of precipitation during the months of lizard activity, but not for the months during which egg-incubation takes place. This suggests that there is an environmental pressure on lizards related to levels of evapotranspiration. Morphological analyses tend to group populations by similar levels of precipitation during their months of activity, which might explain why morphology does not correlate with the mtDNA and karyology in the present work, as is also found in Arribas & Carranza (2004). Although morphological features could help to characterize and identify discriminant characters among discrete populations or taxa, the relative degree of divergence limits their use to assess relationships, especially in the case of the character related to scalation (but also biometric characters, which reflect habitat features such as rock/ground dwelling, climbing, etc.). Essentially, it seems that the morphology of *Iberolacerta* is greatly affected by different geoclimatic conditions (i.e. those conditions that characterize the distinction between the Eurosiberian/Oceanic and Supramediterranean/Continental climatic areas). Aside from the amount of precipitation during the period of activity (directly related to moisture and evapotranspiration and therefore scale counts; see above), these geoclimactic features also include the type of substrate and its steepness, which clearly affects the climbing abilities of the lizards, favouring a certain type of limb morphology and length. Also, overall size can be influenced by thermal or reproductive constraints. As a result of these factors, each population ultimately exhibits the morphology that corresponds to its geographical position within this geoclimatic gradient.

The situation in the NW Iberian Peninsula can be considered a consequence of this scenario and pattern of differentiation. Populations appear ordered by morphology on a geographical gradient, the most differentiated groups being those from the most varied geoclimatic areas (increasingly Supramediterranean in *I. galani* nov., *I. monticola* from Estrela, *I. martinezricai* and *I. cyreni*; *versus* the populations from the Galician and Cantabrian *I. monticola* area of Eurosiberian-Atlantic climate).

Within this framework of degrees of differentiation, in which morphological differences among populations are caused and controlled by differences in their habitat, some of the taxa/populations have developed karyological differences warranting reproductive isolation and a considerable degree of mtDNA differences (for example, *I. martinezricai* and *I. galani* nov.). However, others present only those morphological differences that are geoclimatically induced, and remain karyologically and genetically identical, for instance *I. monticola* from Estrela, which is morphologically different to the rest of the *I. monticola* from Galicia and the Cordillera Cantabrica, but is unchanged in terms of mtDNA and karyotype, probably as a result of its recent isolation.

The existence of *I. galani* nov. reinforces the hypothesis that *I. monticola* originated in the north and indicates that the population from the Serra da Estrela, as well as other isolated populations (Cabeza de Manzaneda, for example) are climatic relicts that became

isolated as a result of an increase in the mean annual temperature of the area since the beginning of the Holocene. The lack of intraspecific variation in *I. monticola* suggests that during the Pleistocene and early part of the Holocene, *I. monticola* was distributed across the lower and more mesic areas of Galicia and northern Portugal. With the progressive climatic amelioration, *I. monticola* was forced to retreat into the most humid areas if remaining in lowland areas (La Coruña, Lugo and Oviedo provinces, north of the Miño-Sil river), or to move high up into the mountain summits (such as Caurel and Ancares in North Galicia, or the whole of the Cordillera Cantabrica in general). Suitable climatic conditions to the south were only found at a relatively high altitude, for instance in the Serra de Queixa (C. de Manzaneda) and Serra do Invernadeiro (Orense province) between the Miño-Sil and Duero rivers, very close to the inland area inhabited by *I. galani* nov. To the south of the Duero, the same occurs in the Serra da Estrela (Beira Alta district), where populations again survive only high in the mountains.

Similarly to the populations of *I. monticola* from the province of Orense, *I. galani* nov. also inhabits the area between the Duero and Miño-Sil rivers, but the two types are separated by the Mediterranean valley of the Bibei river, which might have constituted an important barrier to gene flow, as is suggested by the fact that these populations, although geographically very close, have undergone more than two million years of evolution independently of one another. The Würmian refuge of *I. galani* nov. may have been *in situ*, in any location close to its current area, which was heavily glaciated during Würm. This possible refuge could have been both to the north of its current area (in the Bierzo area, but south of the Sil river, which acts as a barrier) or—more likely—to the south (between the mountains and the Duero River, where thermic areas exist to this day). *Iberolacerta galani* nov. can be considered a "short distance reinmigrant" (sensu Holdhaus 1902, 1906, 1954) originating more or less "in situ", like the other endemic species of the area (see above). A similar scenario has also been suggested for the three closely-related allopatric Pyrenean species (Mayer & Arribas 2003; Carranza *et al.* 2004).

As stated in Llopis & Fontboté (1959), the current raised plain (1700–1900 m) from the Sierra Segundera (Sanabria) originated during the Miocene from a pre-existent relief, the remains of which are still present today in the form of “Monadnocks” in the crests of these Sierras, formed mainly by the hard quartzites mentioned previously. At the end of the Miocene (Antillic phase) the general area rose and the hidrographic network became fitted into the relief, and later, during the Rhodanic phase (clearly Pliocene) the Bierzo graben sank and the Eria and Sil river drainages appeared as they are known today, as occurred with other rivers in Western Iberia (such as the Duero watershed, see Arribas & Carranza, 2004), acting as barriers and causing the virtually simultaneous speciation between *I. galani* nov., *I. martinezricai* and *I. monticola*. In the case of *I. martinezricai*, the basculation to the west of the Iberian Peninsula opened the formerly endorrheic Duero river drainage to the Atlantic Ocean (Arribas & Carranza, 2004), isolating this species to the south. In the case of *I. galani*, this same plate inclination to the west may have led to

the capture of the upper reaches of the Bibei river, which subsequently changed direction and, instead of draining into the Tera river (belonging to the Duero River watershed), moved to the west and later to the north, to the Miño-Sil drainage, thereby cutting off the possible east-west corridor of *Iberolacerta* in the area confining *I. galani* nov. between the Duero and Miño-Sil rivers, and isolating it from other, more western *I. monticola* by the Mediterranean Bibei river valley.

During the Pleistocene, a small inlandsis (or "fjeld") appeared in the highest areas, irradiating ice tongues towards the valleys and making them inhabitable for the lizards. During the Holocene, these previously glaciated mountains have produced a complex of glacial lakes between 1200 and 1600 m asl., where *I. galani* nov. now enjoys suitable habitats.

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