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Systematics of the *Podarcis hispanicus*-complex (Sauria, Lacertidae) I: Redefinition, morphology and distribution of the nominotypical taxon

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Recent genetic works have suggested that the Iberian wall lizard *Podarcis hispanicus* (Steindachner, 1870) *sensu lato* may in fact be a species complex, yet many of its taxa have not been formally described. We redefine the nominotypical *Podarcis* [*hispanicus*] *hispanicus sensu stricto* using univariate and multivariate morphological analyses and pinpoint its geographical distribution. *Podarcis* [*hispanicus*] *hispanicus* is a small wall lizard characterized by a flattened head and body, the general lack of a masseteric shield, a striped dorsal pattern, the frequent bifurcation of the anterior part of the vertebral strip, the belly almost always white and the tail intense blue in young specimens. Its distribution is restricted to the Spanish Levant (provinces of Alicante, Murcia and Almeria).

Key words: morphological analysis, geographical distribution, Reptilia, Spain, wall lizard

INTRODUCTION

Our understanding of the biological diversity of West European amphibians and reptiles is currently changing rapidly, both at the species level and at infra-specific levels (see examples in Crochet & Dubois, 2004). Many of these changes result from the ever more common use of molecular genetics methods in phylogenies and phylogeographic studies. One such case is the Iberian wall lizard *Podarcis hispanicus*, first described by Steindachner (1870) (see Böhme, 1997 and Crochet & Dubois, 2004 for the gender of *Podarcis*). The current systematics of the non-insular Iberian *Podarcis* (excluding the widely distributed *P. muralis* (Laurenti, 1768)) recognizes three species: the widespread *P. hispanicus sensu lato* inhabits most of the Iberian Peninsula and is sympatric with two other species: *P. bocagei* (Seoane, 1884) in the north-western Iberian Peninsula and *P. carbonelli* Pérez-Mellado, 1981 in the western Iberian Peninsula (see, for example, Pleguezuelos et al., 2003; Sá-Sousa, 2001; 2004).

Recent genetic and morphological data (Sá-Sousa, 2000; Harris & Sá-Sousa, 2001, 2002; Harris et al., 2002a, 2002b; Sá-Sousa et al., 2002) indicate that *P. hispanicus* actually consists of several very distinct genetic lineages, which do not form a monophyletic unit relative to *bocagei* and *carbonelli*. *Podarcis bocagei* is the sister taxon of a NW Iberian lineage currently recognized as *P. hispanicus*, and *P. carbonelli* of a SW Iberian *P. hispanicus* lineage. There is thus currently no agreement between genetic divergence and systematics or between phylogeny and systematics. This clearly suggests that many divergent clades in *P. hispanicus* merit a specific rank. Formal changes have until now been proposed for two lineages only: the North African and Southern Iberian taxon *vaucheri* Boulenger, 1905 was given species rank by Oliverio et al. (2000) and Busack et al. (2005), and the north-eastern Spanish form (= "*P. hispanica* morphotype 3" in Pinho et al., 2006) was elevated to species status by Busack et al. (2005) under the name *Podarcis atratus* (Boscá, 1916).

In the case of the Iberian wall lizard, these findings were not totally unexpected as a series of morphological studies (Guillaume & Geniez, 1986; Guillaume, 1987; Geniez, 2001) have identified several units within *P. hispanicus*. Each of these units is distinguished by colour pattern, morphometrics or scalation, and each has a distinct distributional range. These different units were treated as morphological subspecies of *P. hispanicus*. Comparison of the morphological variation and the genetic data suggest that several of the morphotypes identified by Guillaume (1987) and Geniez (2001) correspond to distinct genetic lineages. Similarly, Sá-Sousa et al. (2002) showed that morphological variation and genetic variation coincided among populations of the *P. hispanicus* complex in Portugal, defining two distinct evolutionary units with parapatric distributions in the western Iberian Peninsula.

Whatever the rank afforded to these evolutionary units, naming them in accordance with the principles of zoological nomenclature will be a prerequisite for taking them into account in conservation policies or many scientific analyses of biodiversity. The aim of this paper is to provide the first step in describing and naming biological diversity in the *P. hispanicus* complex by redefining the nominotypical taxon *hispanicus*. We provide a morpho-

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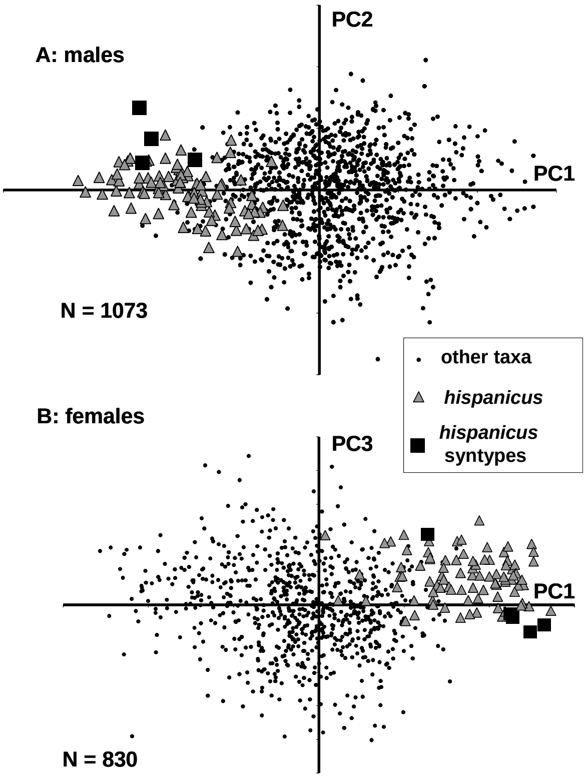

Fig. 1. Bivariate plots of PC1 and PC2 scores (A) or PC1 and PC3 scores (B) of individual specimens from a PCA run on males (A) and females (B) separately, using 16 quantitative and semi-quantitative variables that were available for the type specimens of *Lacerta oxycephala* var. *hispanica*.

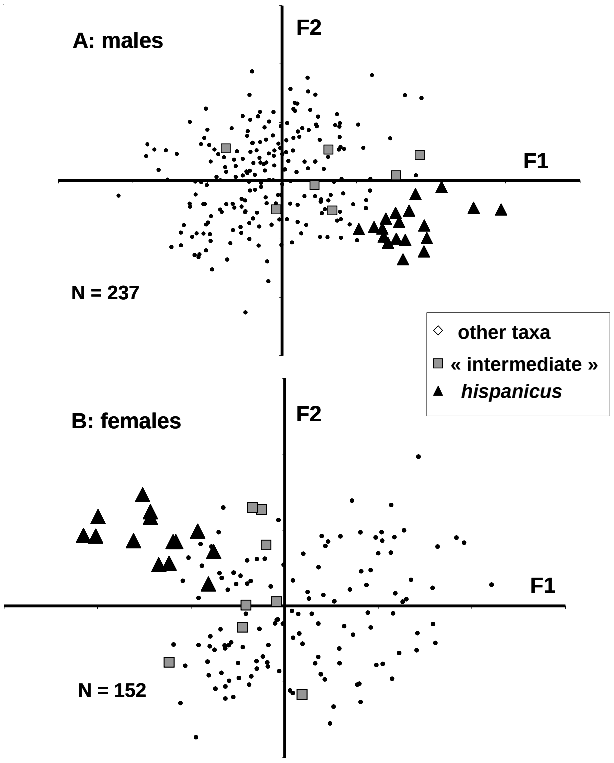

Fig. 2. Bivariate plots of F1 and F2 scores of individual specimens from a Hill & Smith analysis run on males and females separately using 23 quantitative and qualitative variables, including colour variables.

logical diagnosis of this taxon and an updated review of its distribution range, based on our own examination of specimens of the *P. hispanicus* complex in the field and in collections.

MATERIALS AND METHODS

Material examined and specimen identification

The 3152 specimens of the *P. hispanicus* complex examined in this study originate from 270 Spanish, 54 Portuguese and 59 French localities. Among them, 424 specimens measured and released in the field by PSS in Portugal were not used in the multivariate analyses. The other specimens were borrowed from the following collections: Laboratoire de Biogéographie et Écologie des Vertébrés de l'École Pratique des Hautes Etudes, Montpellier, France (BEV); British Museum (Natural History), London, UK (BMNH); Museu Bocage, Lisbon, Portugal (MBL); private collection of Dr Charles P. Blanc in the Laboratoire de Zoogéographie de l'Université Paul Valéry in Montpellier, France (CPB); Estación Biológica de Doñana, Seville, Spain (EBD); Naturhistorisches Museum, Basle, Switzerland (NHMB); Muséum national d'Histoire naturelle, Paris, France (MNHN); Naturistorisches Museum Wien, Austria (NMW); private photographic collection of Philippe Geniez, Vendargues, France (PGe). We examined the complete type series of *hispanicus* (see below) but several type specimens were excluded from the multivariate analyses because they are juveniles (NMW 16088/7 and NMW 16087/2) or are poorly preserved (NMW 16088/8 and NMW 16087/1).

We restricted our analysis to specimens from the European part of the distribution range of the complex (i.e. excluding the North African populations). Since *Podarcis bocagei* and *P. carbonelli* (including *berlengensis* Vicente, 1985) are already treated as specifically distinct from *Podarcis hispanicus* s.l. on the basis of morphological and genetic data (Sá-Sousa & Harris, 2002; Galán, 2003), we did not consider these taxa. Although the Iberian wall lizards of the south of the Iberian Peninsula belong to *P. vaucheri* (Harris et al., 2002a; Busack et al., 2005; Pinho et al., 2006), we have retained European populations of this species as part of *Podarcis hispanicus sensu lato* for the present study, since the distribution range and morphological characters of this species in Spain are still imperfectly known. We also retained the insular taxon *atratus* (Columbretes Islands) because, although it was considered by Castilla et al. (1998) as a distinct species, recent DNA analyses indicate that it is closely related to the Catalonian form of the *P. hispanicus* complex (Carranza et al., 2004; Busack et al., 2005), as also found by Geniez (2001) based on morphological data.

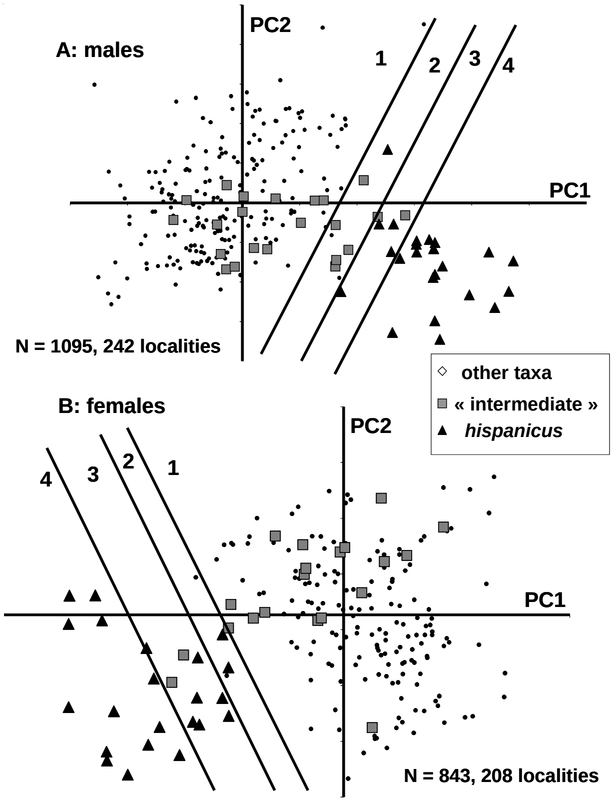

Fig. 3. Bivariate plots of mean PC1 and PC2 scores for each "pooled station" (mean of the PCs scores for each individual in the "pooled station") based on the results of a PCA run for males (A) and females (B) separately using 13 quantitative and semi-quantitative variables. The PC1 X PC2 plan was divided into four zones separated by oblique black lines defining four classes of stations used to produce the maps in Fig. 4.

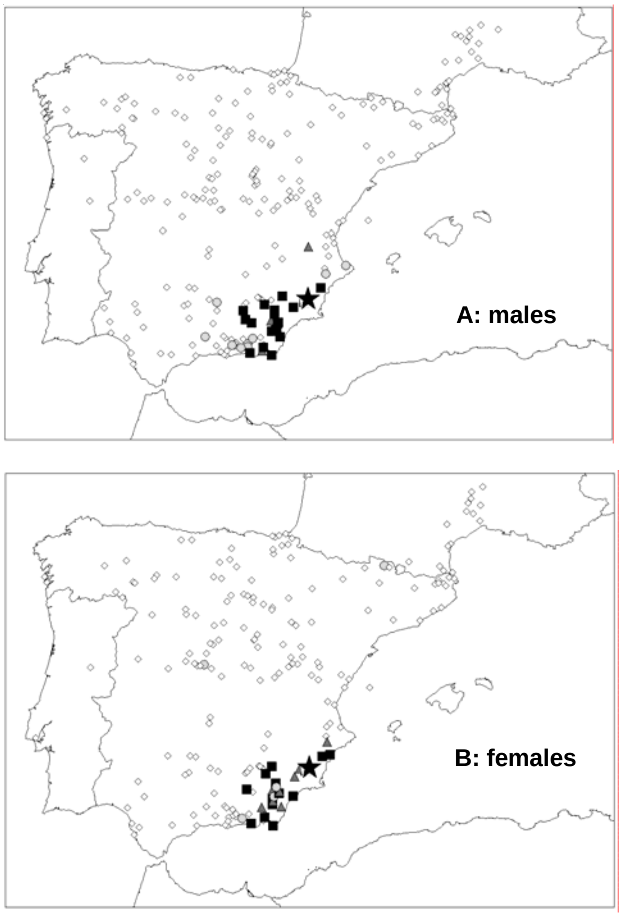

Fig. 4. Maps of the "pooled localities" for males (A) and females (B). Black squares: localities in class 4 on Fig. 3 (typical *hispanicus* morphology); dark grey triangles: localities in class 3 (typical or mostly *hispanicus* morphology); pale grey dots: localities in class 2 (overlap between other taxa, intermediate morphology and *hispanicus* morphology); small white rhombi: localities in class 1 (mainly non-*hispanicus* morphology). The shape and colour of the dots on the map thus depends only on their position in the PCs plan and not on our initial assignment. The star represents the type locality.

Prior to any analysis, the specimens were classified by one of us (PG) into morphotypes based on their external characters following the diagnoses in Guillaume (1987) and Geniez (2001). Three taxonomic units were retained for subsequent analyses: *hispanicus*, "other taxa", and intermediate between *hispanicus* and "other taxa". These intermediate specimens are not necessarily the results of intergradation (although this is one possibility) but they proved difficult to assign on the basis of their external morphology. This *a priori* classification is used in figures for clarity but does not participate in the analyses themselves.

Character analysis

The list of variables used in this study is given in Appendix 1 with their coding. Four categories of characters were measured: quantitative morphometric variables, quantitative pholidosis variables, semi-quantitative variables describing colour pattern that are not modified in preserved specimens and semi-quantitative or qualitative variables related to the coloration of live specimens, not available on preserved specimens. Some of these variables are not available for all specimens. The types of *hispanicus*, for instance, were examined in the late 1980s, and the data for these specimens are not complete. Several variables that do not separate *hispanicus* from the other taxa of the complex were usually excluded from multivariate analyses. All measures and coding were done by the same observer (PG) for all the specimens used in multivariate analyses.

Data analyses

The main analyses used were normalized Principal Component Analysis (PCA) on quantitative and semi-quantitative variables and Hill & Smith Analysis (H&S, Hill & Smith, 1976). The latter enables to analyse qualitative and quantitative variables simultaneously: both quantitative and qualitative characters are processed separately in the first place by respectively normalized PCA and Multiple Correspondence Analysis (MCA) using the same row weights. The Hill & Smith technique then analyses both PCA and MCA statistical triplets and produces a single statistical triplet, allowing

Table 1. Eigenvalues, percent of explained variance and contribution of each variable to the principal components (PC1 and PC2 for males, PC1 and PC3 for females) for the first PCA (with the types).

	PC1	PC2/PC3
Males		
Eigenvalue	3.673	1.869
% explained variance	23	12
Dors	0.3069	-0.6465
Venl	0.1229	-0.2008
Porf	0.3744	-0.3030
Lame	0.3633	-0.5047
ID10	0.534	0.3431
SVL	0.8464	0.1563
PilL	0.8818	0.1097
HeH	0.8659	0.2290
Vert	-0.3254	0.4850
Bif	-0.4689	0.0427
DoLa	-0.2322	-0.2955
Frag	0.0603	-0.6353
SDLa	-0.0032	-0.2908
Pari	-0.5675	-0.1126
Ponc	0.2387	-0.0302
Rond	0.0051	-0.1770
Females		
Eigenvalue	3.838	1.72
% explained variance	24	11
Dors	-0.3518	0.7077
Venl	-0.0950	-0.0033
Porf	-0.3967	0.5134
Lame	-0.3884	0.5607
ID10	-0.4938	-0.5284
SVL	-0.8071	-0.1533
PilL	-0.8626	-0.0508
HeH	-0.8503	-0.1568
Vert	0.5056	-0.2203
Bif	0.5799	0.1750
DoLa	0.2680	-0.1017
Frag	-0.1374	0.3308
SDLa	0.0811	0.0997
Pari	0.5648	0.2842
Ponc	-0.1401	-0.0912
Rond	-0.0818	-0.1152

viewing of all the information analysed on the same axis. Results of these multivariate analyses do not depend on our *a priori* identification. The taxonomic units that we defined (see above) are only used to make the graphic presentation of the results easier to interpret. Only adult specimens were used in multivariate analyses. As preliminary analyses showed great differences among sexes, because of important biometric and coloration differences, males and females were treated separately. All multivariate analyses were implemented with the ADE-4 software package (Thioulouse et al., 1997).

The following analyses were performed: 1) A PCA run on adult males (*n*=1073) and adult females (*n*=830) separately, including all characters that had been measured on the types of *hispanicus* (variables *Dors*, *Venl*, *Porf*, *Lame*, *ID10*, *SVL*, *PilL*, *HeH*, *Vert*, *Bif*, *DoLa*, *Frag*, *SDLa*, *Pari*, *Ponc*, *Rond*). For better clarity of the diagrams, the categories “other *P. hispanicus* taxa” and “morphologically intermediate between *hispanicus* and other taxa” were pooled (see Fig. 1). 2) A Hill & Smith analysis on all adult specimens for which characters of coloration in life were measured; sexes were treated separately (males: *n*=237; females: *n*=152, see Fig. 2). Variables entered as quantitative variables were *Dors*, *Porf*, *Temp*, *TeMa*, *ID10*, *SVL*, *PilL*, *PilW*, *HeH*, variables entered as qualitative variables were *Vert*, *Bif*, *DoLa*, *Frag*, *SDLa*, *Pari*, *Ponc*, *Rond*, *DCol*, *FCol*, *TCol*, *BCol*, *PilP*, *Iris*. 3) A PCA performed on characters that could be measured on preserved specimens except size-related variables (quantitative morphometric variables), sexes treated separately (males: *n*=1,095, 243 localities; females: *n*=843, 208 localities). The variables were *Dors*, *Porf*, *Temp*, *TeMa*, *ID10*, *Vert*, *Bif*, *Frag*, *Pari*, *Ponc*, *Rond*, *DoLa*, *SDLa*, *PilP*.

After this PCA (totally independent of size as only coloration and pholidose variables were included), specimens were grouped by locality and the mean of the PC1 and PC2 scores was calculated for each locality for males and females separately. Mean scores on PC1 and PC2 for each locality were then plotted to produce Figure

Table 2. Eigenvalues and percent of explained variance of the first and second axes of the H & S analysis. Contributions of the quantitative variables to these axes are also given. For contribution of the qualitative variables, see Fig. 5.

	F1	F2
Males		
Eigenvalue	0.20225	0.14949
% explained variance	13	10
Dors	-0.2721	-0.5998
Porf	-0.2780	-0.3420
Temp	0.0608	-0.6677
TeMa	-0.2986	0.5878
ID10	-0.3136	0.7581
SVL	-0.8882	-0.1247
PilL	-0.9150	-0.0752
PilW	-0.9047	-0.0052
HeH	-0.8737	0.1110
Females		
Eigenvalue	3.838	2.179
% explained variance	24	14
Dors	0.3088	0.5940
Porf	0.3335	0.3449
Temp	-0.0242	0.7626
TeMa	0.3651	-0.5258
ID10	0.2621	-0.7525
SVL	0.8632	0.0738
PilL	0.9170	0.0190
PilW	0.8891	-0.0415
HeH	0.8364	-0.1165

Table 3. Eigenvalues, percent of explained variance and contribution of each variable to the principal components for the second PCA (size-independent variables).

	PC1	PC2
Males		
Eigenvalue	2.7685	2.1972
% explained variance	20	16
Dors	0.0805	0.6958
Porf	-0.1323	0.3632
Temp	0.5669	0.4430
TeMa	-0.7872	0.1862
ID10	-0.8606	0.0078
Vert	0.2066	-0.4953
Bif	0.5723	-0.3145
Frag	0.1486	0.6264
Pari	0.6844	-0.2049
Ponc	-0.0387	0.3076
Rond	0.1043	0.1939
DoLa	0.3456	0.1348
SDLa	0.2009	0.3997
PilP	0.1730	0.5113
Females		
Eigenvalue	2.8607	2.2784
% explained variance	20	16
Dors	-0.1187	-0.0258
Porf	0.1091	-0.0127
Temp	-0.4966	-0.2278
TeMa	0.6999	0.3564
ID10	0.7837	0.3554
Vert	-0.4006	0.1082
Bif	-0.6361	-0.1957
Frag	-0.1011	0.2225
Pari	-0.6841	-0.0623
Ponc	-0.1929	0.8408
Rond	-0.2063	0.8237
DoLa	-0.2844	0.2291
SDLa	-0.3645	0.4807
PilP	-0.3836	0.4470

3. Then, based on the position of the localities in the PC1× PC2 plan, four classes of localities were defined: class 1 localities are situated in the portion of the plan where there are no localities of specimens *a priori* classified as *hispanicus* and mainly localities of specimens *a priori* identified as "taxa other than *hispanicus*"; class 4 localities are where there are only localities of *hispanicus*; classes 2 and 3 are situated inbetween, with the limit between classes 2 and 3 set at the limit of the distribution of localities classified as "other taxa" (see Fig. 3). This allowed us to develop a map (Fig. 4) where the localities can be displayed with colour corresponding to their position in the PC1 × PC2 plan, from typical *hispanicus* morphology (black squares, class 4) to typical "other taxa" morphology (white rhombi, class 1). Again, this is based on size-independent variables only.

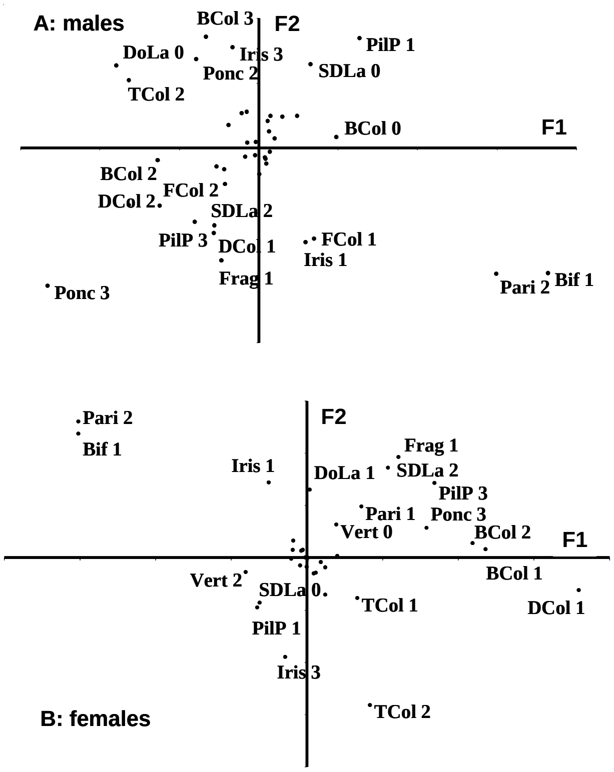

Fig. 5. Contribution of the modalities of the qualitative variables to the first and second axes of the H&S analysis for male (A) and female (B) specimens separately. See Table 2 for the contributions of the quantitative variables.

RESULTS

Morphological variation

Figures 1–4 clearly show that specimens that we call *hispanicus* form a distinct cluster in PCAs and H&S analyses, indicating that they are characterized by peculiar morphological features. The "*hispanicus*" cluster overlaps somewhat with the "other taxa" clusters, as a result of individual morphological variation, but note that most *hispanicus* specimens, including seven of nine type specimens included in the analyses, lie outside the range of variation of the other taxa. The overlap is reduced when coloration characters are also taken into account (Fig. 2). The variables contributing most to the separation of *hispanicus* from the other morphotypes are size (*SVL, PilP, PilW* and *HeH* are all size-related variables), the disposition of the temporal scales (*ID10, Temp* and *TeMA* are all related to this) and some coloration variables (mainly *Pari* and *Bif*) (see Tables 1–3 and Fig. 5, and the diagnosis below). As can be seen from Figure 3, the amount of overlap is even more reduced when specimens are grouped by locality, indicating that most overlap is due to individual, within population, variability. If most overlap was due to introgression, we would expect most intermediate individuals to occur together in populations that would be made of predominantly intermediate individuals, resulting in variability among populations. On the contrary, if most

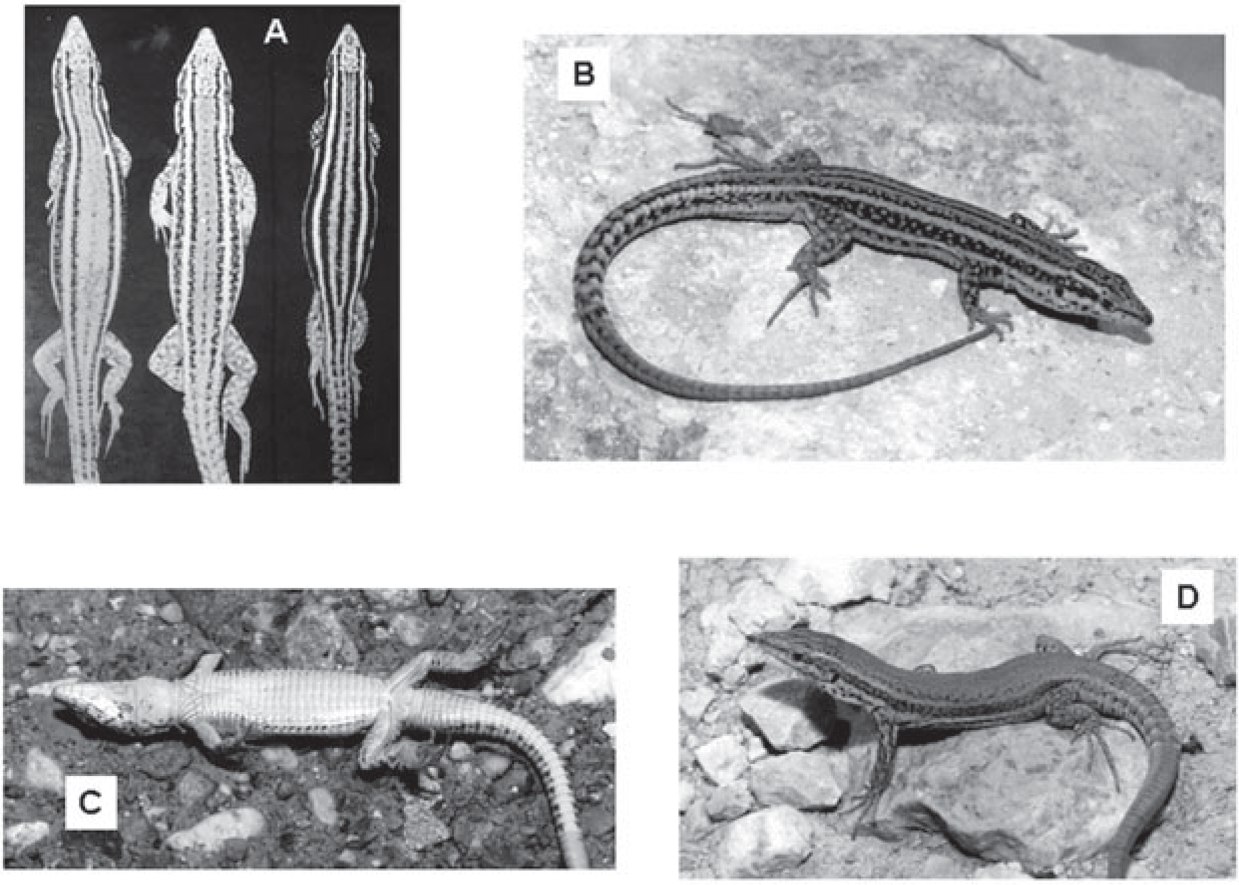

Fig. 6. A) Part of the original type series of *Lacerta oxycephala* var. *hispanica*. From left to right: NMW 16088:6 (female, paralectotype), 16088:1 (male, lectotype) and 16088:11 (female, paralectotype). All from Monte Agudo near Murcia, Spain. B) *Podarcis hispanicus* (adult male, no voucher) from Bullas (Murcia), Spain. Photo P.-A. Crochet. C) *Podarcis hispanicus* (adult male BEV 7337) from 5 km past Santa Maria de Nieva on the road to Vélez Rubio (Almeria). Photo P. Geniez. D) *Podarcis hispanicus* (adult male of poorly patterned coloration, BEV 7338) from 5 km past Santa maria de Nieva on the road to Vélez Rubio (Almeria), Spain. Photo P. Geniez.

overlap is due to individual variation, individuals of intermediate morphology can appear in any population and you do not expect to find populations made of mainly intermediate individuals (hence no intermediate population).

Figure 4 indicates that populations with specimens of typical *hispanicus* morphology (class 4 and 3 in Fig. 3) have a very limited distribution in the south-east corner of the Iberian Peninsula. Although the exact limits of the distribution range of *hispanicus* is difficult to establish in all areas on the basis of our data (incomplete field survey), it is obvious from these maps that *hispanicus* and the other taxa have mostly parapatric distribution at the scale of the Iberian peninsula, with no population of typical "other taxa" morphology being found clearly inside the range of *hispanicus*. The reverse is true, no population of typically or strongly *hispanicus* morphology (class 4 or 3) being found outside of the south-east of the Iberian Peninsula.

Systematic consequences

Our results provide clear evidence that the members of the *hispanicus* complex inhabiting the south-east corner of the Iberian Peninsula are morphologically differentiated from all other populations of the complex and have a well-defined distribution with no or little overlap with these other populations. They thus constitute a clearly defined taxon. Furthermore, the type specimens of *hispanicus* belong to this south-east Iberian taxon. We thus formally restrict the name *hispanicus* (Steindachner, 1870) to the south-east Iberian taxon, for which we provide below a detailed diagnosis. We keep for the time being an open position on the rank of the various taxa in the *hispanicus* complex. We anticipate that many will be ultimately raised to species status but we feel that we have not enough data to assess the rank of *hispanicus* and its neighbouring taxa in this paper (see Discussion). We acknowledge this uncertainty about rank (subspecific or specific) with the use of an interpolated name in square brackets. Names with interpolated names in square brackets are to be interpreted as either a binomen or a trinomen (see e.g. Grillitsch et al., 1993; Crochet et al., 1996 for the use of square brackets).

Podarcis [*hispanicus*] *hispanicus* (Steindachner, 1870)

Lacerta oxycephala Schleg. var. *hispanica* Steindachner, 1870, Sitzungsberichte der Kaiserlichen

Fig. 7. Distribution of *Podarcis hispanicus*. This map is based only on specimens or pictures examined by the authors and judged to be typical specimens of this taxon. See Appendix 3 for the details of all localities.

Akademie der Wissenschaften zu Wien. Mathematisch-Naturwissenschaftliche classe 62: 350, pl. I, figs 3–6.

Name-bearing types. The following specimens are apparently the only syntypes: NMW 16088:1–11 (Monte Agudo) and NMW 16087:1–2 (surroundings of Alicante) (Tiedemann & Häupl, 1980; Tiedemann, pers. comm.). Our examination of the type specimens from Alicante indicate that they certainly do not belong to *hispanicus* as we define it here: both specimens have a well-marked masseteric plate on both sides, the adult specimen (NMW 16087:1) is much larger than the maximum size of *hispanicus* (SVL = 59.2 mm) and lacks its typical pattern, and the juvenile specimen (NMW 16087:2) has no vertebral line although it is not a uniformly coloured animal. Both specimens are apparently referable to the north-east Spanish form. We therefore feel that the designation of a lectotype from the Monte Agudo specimens (which are typical representatives of the Levant taxon) is needed to stabilize the use of the name. We select here the specimen NMW 16088:1 (Fig. 6A) as lectotype of *Lacerta oxycephala* var. *hispanica* Steindachner, 1870.

Type locality. Originally Monte Agudo near Murcia and surroundings of Alicante, in SE Spain, restricted to Monte Agudo here by lectotype designation. Previous type locality restriction to Monte Agudo by Mertens & Müller (1928) is invalid as it is not based on a lectotype designation. It should be noted that neither Alicante nor the Monte Agudo seem to be inhabited by this form today (see Discussion).

Synonyms. Lacerta muralis, subsp. *steindachneri* Bedriaga, 1886, Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 14: 256.

Name-bearing types. This name was based on an assemblage of specimens including the animals described by Steindachner as *L. oxycephala* var. *hispanica*, together with specimens seen by Böttger in Almeria and Cartagena, specimens seen by Bedriaga himself in Alicante and specimens seen by Boscá in Navacerrada and Basco de Avila (Castilia la Vieja) (Bedriaga, 1886). This very wide type locality encompasses the range of several evolutionary units of the *Podarcis hispanicus* complex. Specimens from Almeria, Murcia and Cartagena are referable to *Podarcis* [*hispanicus*] *hispanicus* as understood here, while the Navacerrada, Basco de Avila and (presumably) Alicante specimens, if they belong to the *Podarcis hispanicus* complex, would be members of other taxa. Fixation of the name *steindachneri* by means of a lectotype designation is thus required to stabilize the nomenclature of the *Podarcis hispanicus* complex. Since the name is based partly on the type series of *hispanicus* (which are apparently the only syntypes of *steindachneri* that are still extant), and since most of the localities given in the description correspond to *hispanicus*, we select as lectotype of *Lacerta muralis*, subsp. *steindachneri* Bedriaga, 1886 the specimen NMW 16088:1. As a result, *Lacerta muralis* subsp. *steindachneri* Bedriaga, 1886 becomes an objective junior synonym of *Lacerta oxycephala* var. *hispanica* Steindachner, 1870, with the same type locality.

Diagnosis. A typical member of the *Podarcis hispanicus* complex that can be separated from all other taxa of the complex by the combination of the following characters (see Fig. 6): 1) the continuation of the light dorsolateral stripes and the dark supra-dorsolateral stripes on the parietal plates (in 96% of the specimens; 15.23% in the other taxa, including presumed hybrid specimens with *hispanicus*); 2) the absence of a masseteric plate (5.5% with a small masseteric on one side, only 1.5% with a small masseteric on both sides; 83% of the specimens with one or two masseteric plates in the other taxa); 3) its relatively small adult size (SVL < 50 mm in 99.5%, max = 51.5 mm; SVL ≥50 mm in 66% in adults of the other Iberian wall lizards from Europe); 4) its flattened head and pointed snout (head hight/pileus length <0.46 in 98.5% of the specimens, max = 0.49) and its flattened and delicate body; 5) the frequent presence of the vertebral line (in 83% of the specimens) which is most often bifurcated on the anterior part of the back (in 60.5% of the specimens; 72.5% if only specimens which present a vertebral line are taken into account; in the other Iberian wall lizards from Europe, 0.9%, 1.7% if only specimens which present a vertebral line are taken into account); 6) the disposition of the dark marks on the outer ventral scales in adult males, which are neatly aligned when they are present in *hispanicus* (93%, *n*=15 only) but usually not in the other taxa (20%, *n*=88) where they are irregularly disposed. In addition, there is no clear green coloration on the dorsum (100%, *n*=45), the belly is usually white (97%, *n*=38), never orange or reddish, there is no blue spots on the outer ventral scales of males (93%, *n*=15), the tail is intense blue in juveniles (at most bluish in most other taxa, exceptionally intense blue in some populations), and the iris is pale (creamy, rarely orange, never reddish coloured). The bifurcation of the vertebral line (both sexes), the continuation of the dorsolateral stripes on the parietals (both sexes) and the alignment of the dark mark of the outer ventral scales (males) are nearly diagnostic of *hispanicus* when present, as they are either absent or very rare in all other taxa of the complex.

Description and variation: A relatively small and slender representative of the Iberian wall lizard complex. Head clearly flattened with pointed snout. On the temporal zone, there are numerous small temporal scales, almost always without a distinct masseteric shield. Usually four supralabial scales before the subocular scale, sometimes five. Dorsal scales across midbody: from 44 (mean 53.6) to 68; femoral pores 13 (16.5) 19; gular scales 22 (27.5) 33; lamellae under fourth toe 20 (23.9) 28; temporal scales 56 (91.3) 150.

There are two main types of coloration in *P.* [*hispanicus*] *hispanicus*, with specimens of intermediate coloration: the most common has a contrasted pattern, while the other form is poorly patterned. In the contrasted pattern form, the pileus is light brown with, especially on males, small black punctuations which can be totally absent in females. On the outer edge of the parietal plates, a pale longitudinal stripe is bordered on the inner edge by a black line, which can be continuous or fragmented. These two contrasted lines correspond to the anterior prolongation of the light dorsolateral and black supradorsolateral lines. The ground colour of the dorsum is light brown, sometimes with a bluish hue, especially on juveniles, but never with green tints. A black vertebral line runs on this light background colour. This line can be entire or fragmented into numerous small spots. It usually splits into two or three branches in its anterior part. In some striped specimens, the vertebral line can be very blurred and indistinct. Pale dorsolateral lines are usually almost continuous and well marked, 4–7 scales wide, white or ivory white in juveniles, pale cream in adults. There are usually a few small black dots inside the dorsolateral lines in some adult males. Black supradorsolateral stripes are usually uninterrupted in juveniles and females, but can be made of numerous small punctuations in adult males; they are narrower, equally large or larger than the pale dorsolateral lines. Flanks are dark, bordered below by a pale stripe and a dark stripe along the outer ventral scales. The dark flank stripes are continuous on juveniles and most females, but often made of elongated dark marks in males. The original tail is intense blue in juveniles, light brown or greyish in adults, sometimes with blue or yellowish hues, and with the striped flank pattern extending on the tail.

The throat and belly are generally pure white, rarely with a slight yellowish tint on the throat, on the posterior part of the belly and under the tail. There are frequently some small black dots on the sides of the throat, rarely on the centre. The four central rows of ventral plates are immaculate while the marginal plates generally have a dark spot, round or slightly triangular, clearly aligned and separated by a white area usually narrower than the dark spots, even in adults. This row of aligned dark spots continues under the sides of the tail. Contrary to the other Iberian wall lizards, there is usually no blue coloration on the marginal ventral plates. Iris pale, from whitish grey to light pinkish or pale orange, never reddish.

In some parts of the distribution (e.g. Sierra de Maria de Nieva in the province of Almeria), most of the individuals present a more uniform pattern (see Fig. 6D), the pale dorsolateral lines only being apparent, without prolongation on the parietal plates. The dark spots on the marginal ventral plates are frequently lacking also. These near-concolorous lizards can be identified as *Podarcis hispanicus hispanicus* by their head and body shape, the lack of masseteric, the numerous and small temporal scales, the absence of orange colour below, the pale iris and the typical pattern of the juveniles.

Atypical characters (small masseteric, vertebral line not bifurcated, slight blue tint on the outer ventral plates, yellow colour under the tail) seem more frequent on the periphery of the distribution, suggesting limited morphological intergradation with the other taxa of Iberian wall lizards.

Distribution. Spanish Levant (provinces of Alicante, Murcia, Almeria and Granada). See map in Figure 7 and list of localities in Appendix 2. Figure 7 differs from Figure 4 because it was produced on the basis of all specimens that we attributed to typical *hispanicus* (not only specimens used for the multivariate analyses but also specimens photographed only), and because we excluded some specimens classified by PCA as “*hispanicus* morphology” but that differed in additional characters from typical *hispanicus* (for example, some specimens from Valencia province). These specimens could be atypical members of another taxon, intergrades or even typical *hispanicus*, but are not safely identifiable based on current knowledge and were hence excluded from the map in Figure 7 (see also Discussion).

The distribution of *Podarcis* [*hispanicus*] *hispanicus* extends from the southern slopes of the Sierra Nevada to the region of Alicante, being limited inland by the Sierra Nevada, Sierra de Segura and the border of the Murcia and Alicante province. Most records are from the area between Murcia and the north-eastern and south-eastern slopes of the Sierra Nevada (Hoya de Guadix and Hoya de Baza in the north, Sierra de Gador in the south). Records east of Murcia and Cartagena are scarce (Torrevieja, Elche).

DISCUSSION

The Iberian wall lizards from the Spanish Levant constitute a morphologically well-defined entity; their distinctiveness from all other wall lizards of western Europe is illustrated by the fact that *hispanicus* was the first Iberian wall lizard to be described as distinct from *Podarcis muralis*. Its distribution corresponds to the xerothermomediterranean bioclimatic zone of Emberger et al. (1962) or the southern part of the western zoogeographical district of Alvarez López (1934). It also corresponds to the distribution of *Timon lepidus nevadensis* Buchholz, 1963, which separated from the other Iberian populations of *Timon lepidus* (Daudin, 1802) several millions years ago (Mateo et al., 1996; Paulo, 2001). This area thus appears to have promoted long-term isolation and divergence in Iberian reptiles.

In spite of numerous publications on genetic diversity within the *Podarcis hispanicus* complex, there have been few detailed analyses linking morphologically defined units with genetic lineages (type 1 and type 2 in Portugal: Harris & Sá-Sousa, 2001; *vaucheri*: Busack et al., 2005). Pinho et al. (2006) have suggested that one of their lineages (called “*Podarcis hispanica sensu stricto*”) corresponds to the nominotypical taxon of the complex (i.e. *Podarcis* [*hispanicus*] *hispanicus* for us). Nevertheless, comparison of their Figure 1 with our maps shows that the distribution of their "*Podarcis hispanica sensu stricto*" lineage falls mostly outside the range of *Podarcis* [*hispanicus*] *hispanicus*. On the other hand, their lineage called "*Podarcis hispanica* Galera, SE Iberia" (called "Galera" hereafter) has been sampled in the heart of the distribution of *hispanicus* and not yet outside. We therefore suggest that the typical mtDNA lineage of *Podarcis* [*hispanicus*] *hispanicus* is the lineage called "Galera" in Pinho et al. (2006). Preliminary results from our team (J. Renoult, pers. comm.) as well as from the Portuguese team (C. Pinho, pers. comm.) confirm that the "Galera" mtDNA lineage is the lineage found in most of the *hispanicus* specimens and that it is not found in other taxa.

As we stated above, we prefer not to formally raise to species level any further taxa in the *Podarcis hispanicus* complex in this paper, pending the results of ongoing studied of genetic and morphological variation in contact zones. A specific rank for most evolutionary lineages of the complex might prove more appropriate given 1) the level of genetic divergence between these forms (see Busack et al., 2005 and Pinho et al., 2006 and references herein) and 2) the abrupt transition among morphotypes suggested by our morphological data: pure parental morphotypes come into close contact in most areas of the contact zone. Nevertheless, populations with "intermediate" morphology (class 2 in Figure 3) are preferentially located on the periphery of the distribution range of *hispanicus* for males (see Fig. 4A), as would be expected if introgression occurred (the pattern is less clear for females because there is more overlap between taxa, as shown in Figure 3B).

For example, the non-*hispanicus* specimens from the southern Valencia province often have a delicate build, a flattened head and sometimes no masseteric, as is more typical of *hispanicus*. Conversely, atypical characters (such as presence of a masseteric plate, non-bifurcated vertebral line, robust build) appear to be more frequent in peripheral populations of *hispanicus*. Alternative explanations to introgression are 1) that morphological convergence results from local adaptation to similar climatic and ecological conditions and not from introgression, or 2) that phenotypic plasticity similarly affects the genotypes of both taxa in areas where they come into close contacts. The use of neutral genetic nuclear markers would allow discrimination between these two hypotheses. In the meantime, it is advisable to keep a prudent approach to the rank of the various lineages in the *Podarcis hispanicus* complex.

The distribution of *Podarcis hispanicus sensu stricto* as shown in Figure 7 is still imperfectly known in details due to lack of coverage in some areas. It differs from the maps obtained from PCs scores (Fig. 4) because some specimens that were morphologically close to *hispanicus* (class 3 in PC1 X PC2 scores) were excluded due to atypical characters. For example, the northernmost dark grey dot for males corresponds to a single individual from Cofrentes (Valencia) in the EBD collection that has a distinct masseteric plate, a strong vertebral line that is not bifurcated and triangular dark marks on the outer ventrals (which is extremely rare in *hispanicus*). Despite its position in the PCs scores, this specimen is clearly not a real *hispanicus*.

Some suggestions of range contraction were raised by our recent visit to the Monte Agudo, where our field researches did not reveal any specimens of *P. hispanicus*. We found instead an adult male perhaps belonging to the north-eastern Spanish form (see below) in the village of Monteagudo at the foot of the Monte Agudo itself. While these anecdotal observations are clearly insufficient to draw firm conclusions, it suggests that the range of *Podarcis hispanicus sensu stricto* has contracted during the last century. Systematic confusion has prevented surveys of the range of this distinctive form until recently. The present work should help to recognize this distinctive form and monitor its real status.

As a result of this restriction of the name *hispanicus* to the south-eastern Iberian form, the other populations of the *hispanicus* complex should be designated by other names. In addition to the use of *Podarcis vaucheri* for one north African and southern Iberian lineage (see Introduction), it has recently been suggested that the north-eastern Spanish form should be referred to as *Podacis atratus* (Busack et al., 2005). However, the oldest name available for the north-eastern Spanish form seems to be *liolepis* (Boulenger, 1905) (Guillaume, 1987; Geniez, 2001), which would have priority over *atratus* (Boscá, 1916) (see Salvador, 1986; Alonso-Zarazaga, 1998) if they really apply to the same taxon. Resolving this and other issues related to the nomenclature of the *Podarcis hispanicus* complex is beyond the scope of this paper and will be addressed in subsequent publications.

The present work is thus the first contribution in a series of papers aimed at clarifying the systematics of the Iberian Wall Lizards. Although it has become well known in recent years that the biological diversity of this species group is severely underestimated by current systematic treatments, it was not possible to take into account this diversity as long as these taxa were not named and their morphological characters documented. The situation of the Iberian wall lizards is not unique among European reptiles: recent systematic revisions using morphological and/or genetic methods have often identified "new" species (either taxa that had eluded description for centuries or named taxa of misevaluated status, see Crochet & Dubois, 2004 for many examples). As several authors of the present work experienced during a recent IUCN workshop devoted to the assessment of the conservation status of Mediterranean reptiles, such "new" species cannot be taken into account in conservation policies as long as they have not been formally named in a scientific publication. The naming and description of evolutionary units thus remains an essential step in promoting the recognition, assessment and conservation of biodiversity.

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APPENDIX 1

1) Quantitative morphometric variables

SVL = snout–vent length

HeNe = head length + neck length from the tip of the snout to the insertion of the forelimb

PilL = pileus length

PilW = pileus width

HeH = head height

ALL = forelimb length from its insertion to the tip of the fingers

PLL = hindlimb length from its insertion to the tip of the toes

FooL = foot length from the tibio-tarsal articulation to the tip of the toes

2) Quantitative pholidosis variables

Dors = number of longitudinal rows of dorsal scales at mid-body

Venl = number of transversal rows of ventral plates

Gran = number of supraciliar granules (left side)

Guls = number of gular scales from the foremost part of the throat to the collar

Coll = number of scales in the collar

FPor = number of femoral pores (mean of left and right side)

Lame = number of enlarged scales (infradigital lamellae) under the fourth toe (left side)

Temp = number of temporal scales (including the masseteric shield) (left side)

TeMa = number of temporal scales in contact with the masseteric shield (left side)

ID10 = mean size of the masseteric shields of the two sides as computed from Guillaume (1988).

3) Semi-quantitative variables describing colour pattern that are not modified in preserved specimens

Vert = prominence of the dark vertebral line: 0 = absent, 1 = on part of the back only, 2 = complete (broken or unbroken)

Bif = bifurcation of anterior part of the vertebral line : 0 = no, 1 = yes

DoLa = prominence of the pale dorsolateral stripes: 0 = absent, 1 = weakly prominent, 2 = strongly prominent

Frag = fragmentation of the pale dorsolateral stripes: 0 = no, 1 = yes

SDLa = prominence of the dark supradorsolateral stripes: 0 = absent, 1 = less than 4 scales wide, 2 = 4 scales wide or more

Pari = pale dorsolateral stripes extend on the parietal plates: 0 = no, 1 = weakly, 2 = strongly

Ponc = number of rows of ventral plates with dark sport, from 0 to 3

Rond = 1 if dark spots on the outer ventral plates round, 0 otherwise

Tria = 1 if dark spots on the outer ventral plates triangular, 0 otherwise

PilP = prominence of dark pigmentation of the pileus: 1 = no dark spots, 2 = thin dark spotting, 3 = well marked dark dots

4) Semi-quantitative or qualitative variables related to the colouration of live specimens, not available on preserved specimens

DCol = amount of green on dorsal coloration: 0= no green, 1 = slight green tints, 2 = clear green coloration
FCol = amount of green on flank coloration, same coding as for the back
TCol = throat coloration: 0= white, 1 = yellow, 2 = orange, salmon or brick red
BCol = belly coloration: same coding as throat coloration
Tail = tail coloration: 0 = no blue on the tail, 1 = blue or bluish hues, 2 = clear blue on the tail
Iris = amount of red in iris coloration: 1 = whitish iris, 2 = orangey iris, 3 = reddish iris.

APPENDIX 2

Detailed distribution of *Podarcis hispanicus* based on specimens examined by the authors only. Locality, geographic coordinates [year of collect, origin of the record]. Imprecise localities were deleted from this listing.

Province of Murcia. Monteagudo, near Murcia, 38.020°N/1.097°W [before 1870, NMW-16088/1–11, lectotype and paralectotypes of *Lacerta oxycephala* var. *hispanica* Steindachner]. Aguilas, near the sea, 37.400°N/1.581°W [1968, NMW-19168]. Caravaca de la Cruz, 38.107°N/1.866°W [1984, BEV.3915, PGe.PHH11–13]. Embalse del Argos (north-east of Caravaca de la Cruz), 38.169°N/1.745°W [1984, BEV lost specimens]. Alcantarilla, 37.974°N/1.217°W [1984, EBD.18349–18355]. Inazares, 38.081°N/2.219°W [1980, EBD.80-08-17.4]. Collado Mencheta, Sierra de Espuña, 37.982°N/1.501°W [1967, EBD.3961]. Sanatorio, Sierra de Espuña, 37.853°N/1.537°W [1968, EBD.3083-3084]. 2 km E. Aguilas, Lorca, 37.412°N/1.560°W [1974, EBD.7075]. Casa forestal, Sierra de Espuña, 37.857°N/1.586°W [1967, EBD.3958]. Eastern exit of Albudeite, bridge on the rio Mula, 38.0278°N/1.3819°W [2002, BEV.7330]. Bullas, 38.0519°N/1.6515 [2002, BEV.7331, PGe.PHH10]. La Azohia, 37.549°N/1.169°W [2001, picture of Alain Ravayrol in PGe collection].

Province of Alicante. Embalse de Elche, 38.310°N/0.723°W [1981, EBD without numbers, 6 specimens]. Playa la Mata, Torrevieja, coastal sand dunes, 37.970°N/0.686°W [1981, EBD without number].

Province of Jaén. 2 km N. Tiscar, 37.7739°N/3.0227°W [2002, BEV.7369, 7379–7381].

Province of Almeria. Almeria, 36.842°N/2.467°W [1987 at least, BMNH-86.10.29/1–2, EBD. 23185–23202, 23204–23209, 23211–23215, 23217–23218, 27352, 27356–27359, 27361–27365, 27384–27385, 27388, 27390–27391, 27393]. San José, Gata, 36.766°N/2.118°W [?, EBD.19933–19335, 19858]. Alhama de Almeria, 36.958°N/2.566°W [1961 at least, EBD. 1359, 19857]. Sierra de los Filabres, Albánchez, 37.289°N/2.180°W [1987, EBD.27292–27300, EBD.27383]. Sierra de los Filabres, Gergal, 37.154°N/2.517°W [1987, EBD.27354]. Los Cerricos, Chirivel, Sierra del Saliente, 37.533°N/2.201°W [1987, EBD.27301, 27302, 27304, 27305, 27307, 27308, 27310, EBD.27313–27316]. Pechina, 36.919°N/2.437°W [1959, EBD.1204, 1314–1316, 1314–1320, 1322–1328, 1344–1346]. Cabo de Gata, Vela Blanca, San Jose 36.732°N/2.191°W [1962, EBD.1360]. Barranco de Tartala (=Partala), 10 km N of Almeria, 36.936°N/2.458°W [1962, EBD.4236, 4238, 4327]. Cantoria, 37.355°N/2.195°W [1987, EBD.27373–27374]. Albox, 37.386°N/2.145°W [1980 & 1987, EBD.80-08-15.1, 27355]. Between Albox and Almanzora, 37.369°N/2.130°W [1984, BEV.3892, 3898]. Castle of Vélez Blanco, 37.6903°N/2.0987°W [1987 & 2002, EBD.27389, 27392, 27394–27397, BEV.7345–7350]. Cortijos de Las Juntas, Sierra del Gabar, 37.789°N/2.102°W [1981, EBD without number]. El Ejido, 36.782°N/2.823°W [1960 & 1961, EBD.1355, 1357]. El Gabar (Maria), 37.766°N/2.145°W [1981, EBD without number]. La Hoya, 37.468°N/2.004°W [1959, EBD.1330]. Playa de la Peineta, Cabo de Gata [1981, EBD without number]. Los Gallardos, Bedar, 37.166°N/1.940°W [1981, EBD without number, 3 specimens]. Sierra Larga (Maria Sta), 37.766°N/2.012°W [1981, EBD without number]. Astronomic Telescope, Uleila del Campo, 37.208°N/2.206°W [1987, EBD.27360]. Viator, 36.889°N/2.423°W [1980, EBD.80-10-24.42]. Zurgena, 37.346°N/2.041°W [1961, EBD.1356]. Road C.321, 5 km from Santa Maria de Nieva towards Vélez Rubio, 37.4982°N/1.9887°W [2002, BEV.7336–7342]. Road C.321, 8 km from Santa Maria de Nieva towards Vélez Rubio, 37.5295°N/2.0041°W [2002, BEV.7332-7335]. 6 km before the Sta Maria de Nieva pass from Sta Maria de Nieva, 37.5512°N/1.9962°W [2002, BEV.7343].

Province of Granada. Huescar, road C.330, rio Bravatas, 37.807°N/2.530°W [1984, BEV.3910-3914]. 3 km from Huescar towards Puebla de Don Fadrique, 37.806°N/2.510°W [1986, BEV.4121]. Baza, 37.487°N/2.778°W [1959, EBD.1403]. Embalse del Negratin, 37.5607°N/2.9572°W [2002, BEV.7382-7383]. 7 km from Puebla de Don Fadrique towards Maria, 37.9128°N/2.4001°W [2002, BEV.7353-7356]. 2 km from Hernán Valle between Guadix and Baza, 37.372°N/3.066°W [1984, PGe.PHH2]. 4 km from Berja towards Dalía, 36.83692°N/2.90916°W/435 m [2004, BEV.8520]. 2 km from Dalía towards El Ejido, 36.80507°N/2.85999°W/350 m [2004, obs. Ph. Geniez & M. Cheylan].