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Article

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Systematics of the *Podarcis hispanicus*-complex (Sauria, Lacertidae) II: the valid name of the north-eastern Spanish form

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Abstract

Recent genetic works have suggested that the Iberian wall lizard *Podarcis hispanicus* (Steindachner, 1870) sensu lato is in fact a species complex. Several forms have already been elevated to species rank, including the north-eastern Spanish form alternatively named *Podarcis atratus* (Boscá, 1916) or *P. liolepis* (Boulenger, 1905) in different works. However, a recent study has demonstrated that the province of Valencia, where most individuals of the type series of *Lacerta muralis* var. *liolepis* Boulenger, 1905 originate from, is inhabited by populations that are conspecific with the north-eastern Spanish form. Consequently the nomen *liolepis* has precedence over *atratus* to designate the north-eastern species of the *P. hispanicus* complex which should thus bear the name *Podarcis liolepis*.

Key words: nomenclature, Iberian Wall Lizard, *Podarcis liolepis,* Spain, Reptilia

Introduction

Recent genetic and morphological data indicate that *Podarcis hispanicus* (Steindachner, 1870) as traditionally understood (see for example Pérez Mellado 1986, Pérez Mellado and Gallindo Villardon 1986, Pleguezuelos *et al*. 2003) is actually composed of several genetically distinct lineages, most of which deserve a specific rank (Oliverio *et al*. 2000; Sá-Sousa 2000; Harris and Sá-Sousa 2001, 2002; Harris *et al*. 2002a, 2002b; Busack *et al*. 2005; Pinho *et al*. 2006; Pinho *et al*. 2007, Carretero 2008, Pinho *et al*. 2008, Renoult *et al*. 2009). Few formal systematic changes have been proposed to date, however.

The insular populations from the Columbretes islands have been the first to be formally raised to species rank under the binomen *Podarcis atratus* (Boscá, 1916) (as *Podarcis atrata*, but see Böhme and Köhler 2005 for the gender of *Podarcis*) on the basis of their large amount of genetic divergence (mitochondrial DNA sequences) compared to specimens from the mainland (Castilla *et al*. 1998a, b). Later, the North African and South Iberian taxon *vaucheri* (Boulenger, 1905) has been raised to species rank by Olivero *et al*. (2000) and Busack *et al*. (2005). In the same publication, Busack *et al*. (2005) proposed to treat the north-eastern Spanish form (= "*P. hispanica* morphotype 3" in Pinho *et al*. 2006, TYP3 hereafter) as a distinct species under the nomen *Podarcis atratus*, arguing that the Columbretes populations are conspecific with the mainland specimens of TYP3.

TYP3 corresponds to an evolutionary unit that has been genetically characterised based on specimens from Barcelona (Harris and Sá-Sousa 2002; Pinho *et al*. 2003), Burgos and Medinaceli (Castilla y León) (Pinho *et al*. 2006), Girona, Tarragona and the central southern Pyrenees (Harris and Sá-Sousa 2002), Andorra (Harris *et al*. 2002a) and southern France (unpublished data), and corresponds to the mitochondrial lineage named "*Podarcis hispanica* type 3" in Pinho *et al*. (2006) (called "Type 3" hereafter) and "Liolepis" in Renoult *et al*. (2009). Further south, in the town of Valencia and surroundings, *Podarcis* populations are characterised by a different mitochondrial lineage, named "*Podarcis hispanica* sensu stricto" in Pinho *et al*.

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(2006) and "Valencia" in Renoult *et al*. (2009). We will use this later name here to avoid confusion with the taxon called *Podarcis hispanicus* sensu stricto, most populations of which do not carry this mitochondrial lineage (Geniez *et al*. 2007; Renoult *et al*. 2009). The "Type 3" and "Valencia" mitochondrial lineages diverged several million years ago (Pinho *et al*. 2006). Until recently, it was still unclear whether or not these two lineages correspond to two distinct evolutionary units. Based on a study examining allozyme variation, Pinho *et al*. (2007) first showed that specimens from both lineages were grouped into a single nuclear cluster. Works based on the sequences of two nuclear introns (Pinho *et al*. 2008) subsequently contradicted this result by suggesting an absence of nuclear gene flow between the same two lineages. Renoult *et al*. (2009) re-examined this issue by using nuclear and mitochondrial markers genotyped in the same individuals. They first showed that the distribution of evolutionary units defined with nuclear markers is congruent with the distribution of morphologically defined units. They further demonstrated that the "Valencia" mitochondrial lineage has introgressed into populations that belong to several distinct evolutionary units. Of particular interest are the populations located in the province of Valencia, which possess the "Valencia" mitochondrial lineage but belong to the same evolutionary unit as populations located further north that possess the "Type 3" mitochondrial lineage (Fig. 1). In eastern Spain, the evolutionary unit corresponding to TYP3 thus extends from the Pyrenees to approximately Alicante, some 120 km south of the town of Valencia.

In this article, we do not question that the Columbretes populations are conspecific with TYP3, a conclusion that was already suggested by Geniez (2001) on morphological grounds, but we wish to stress that the oldest available nomen for TYP3 population is *Lacerta muralis* var. *liolepis* Boulenger, 1905, as already pointed out by Guillaume (1987) and Geniez (2001). This name is not in concurrence with *atratus* to designate a taxon limited to the Columbretes islands, but it has precedence over *atratus* if the north-eastern Iberian populations and the Columbretes taxon are united in the same species, as proposed by Busack *et al*. (2005). The syntypes of *Lacerta muralis* var. *liolepis* originate mainly from the town of Valencia and surroundings (see below), and are thus expected to be representative of TYP3 by the light of the results of Renoult *et al*. (2009). However, some evolutionary units within the *Podarcis hispanicus* species complex are known to exhibit discontinuous distribution or to have undergone rapid modification of their distribution range. For example, Geniez *et al*. (2007) report that a single lizard collected recently at the type locality of *Podarcis hispanicus* sensu stricto do not belong to this taxon, even if the type series obtained in the 19th century is clearly identifiable (see also Renoult *et al*. 2010). The assignation of the syntypes of *Lacerta muralis* var. *liolepis* to TYP3 therefore needs to be objectively evaluated before proposing any nomenclatural revision. In this article, we analyse the morphology of the syntypes of *Lacerta muralis* var. *liolepis* and we discuss the nomenclatural consequences of our results.

Material and methods

Reference specimens. Morphological analyses were used to check that the *liolepis* syntypes could be morphologically assigned to one of the lineages of the *P. hispanicus* species complex known to occur in the southern and eastern halves of the Iberian Peninsula. Each lineage was represented by reference specimens which all come from a large database comprising more than 2700 specimens of the *Podarcis hispanicus* complex originating from 270 Spanish, 54 Portuguese and 59 French localities. Most specimens belong to the former collection of the "Biogéographie et Ecologie des Vertébrés" laboratory (BEV) now housed at the Centre d'Ecologie Fonctionnelle et Evolutive (Montpellier, France). Others were borrowed from the Natural History Museum, London, UK (BMNH); Museu Bocage, Lisbon, Portugal (MBL); private collection of Dr Charles P. Blanc (Montpellier, France: CPB); Estación Biológica de Doñana, Seville, Spain (EBD); Naturhistorisches Museum, Bâle, Switzerland (NHMB); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Naturistorisches Museum Wien, Austria (NMW).

In this study, we first excluded from this database specimens with incomplete data, and selected only adult males, as males were more numerous in the type series of *liolepis*. In addition, we excluded specimens that come from vague localities or localities that we were unable to locate. Reference specimens were then selected as follows: we selected specimens located well inside the recognized distribution range of each lineage (Carretero 2008) and typical of these lineages morphologically according to the characters outlined by Geniez (2001), Sá-Sousa *et al*. (2002) and Geniez *et al*. (2007). Most of these specimens have already been submitted to multivariate morphological analyses (Geniez *et al*. 2007; Renoult *et al*. 2009) and for many of them identification is backed by genetic data (Renoult *et al*. 2009). After this selection, a total of 652 reference specimens were analysed: 97 *Podarcis hispanicus* sensu stricto (as redefined in Geniez *et al*. 2007), 160 *Podarcis vaucheri* (Iberian specimens only), 126 *Podarcis hispanicus* type 1 (= TYP1 hereafter), 69 *Podarcis hispanicus* type 2 (= TYP2 hereafter) and 207 TYP3. We did not include *P. bocagei* and *P. carbonelli* in our analyses since they are morphologically well characterized and it is easy to exclude that the syntypes belong to this taxon (see below).

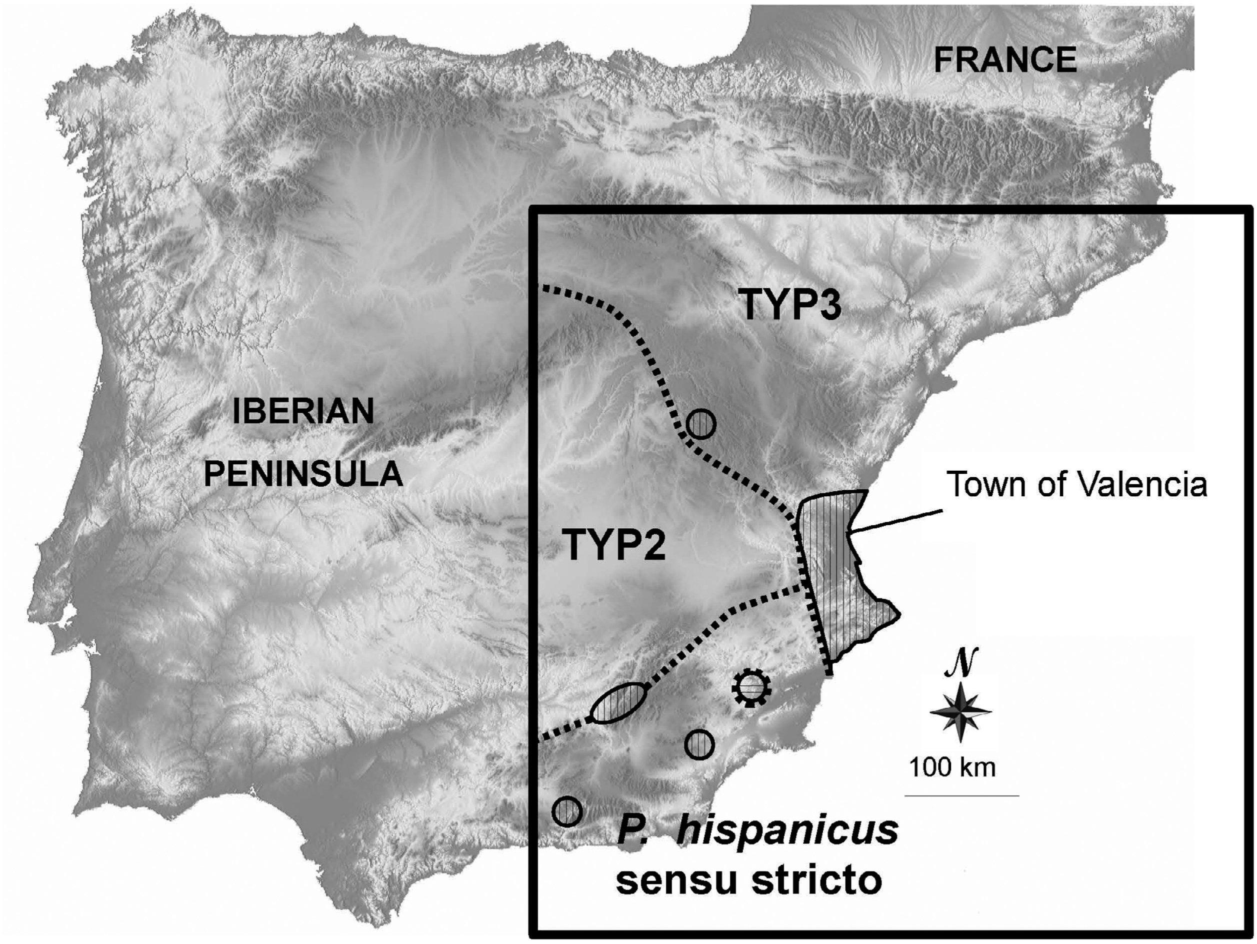

FIGURE 1. Distribution of evolutionary units (modified from Renoult *et al*. 2009) and mitochondrial lineages (modified from Pinho *et al*. 2006; Renoult *et al*. 2009 and unpublished data) of the *Podarcis hispanicus* species complex in south-eastern Spain (inside the box). Four evolutionary units defined by morphology and nuclear data occur in the region (delimited by dashed lines), each one with its own mitochondrial lineage (mtDNA): TYP3 with the "Type 3" mtDNA to the north, TYP2 with the "Type 2" mtDNA to the centre, and *P. hispanicus* sensu stricto (sensu Geniez *et al*. 2007) with the "*P. hispanicus* Galera mtDNA" (sensu Pinho *et al*. 2006) to the south, and an introduced population of *P. vaucheri* with "Vaucheri" mtDNA (Renoult *et al*. 2010) inside the distribution of *P. hispanicus* sensu stricto (horizontal hatching). A fifth mitochondrial lineage ("*P. hispanica* sensu stricto" in Pinho *et al*. 2006 and "Valencia" in Renoult *et al*. 2009; vertical hatching) has introgressed both *P. hispanicus* sensu stricto and TYP3.

Analysed morphological characters. Three categories of characters were measured: (i) 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; *HeH* = head height), (ii) quantitative pholidosis variables (*Dors* = number of longitudinal rows of dorsal scales at mid-body; *Venl* = number of transversal rows of ventral plates; *FPor* = number of femoral pores [mean of left and right side]; *Lame* = number of enlarged scales [infradigital lamellae] under the 4th toe [left side]; *ID10* = mean size of the masseteric shields of the two sides as computed from Guillaume (1988) and (iii) semi-quantitative variables describing colour pattern not modified in the 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]; *PilP* = prominence of dark pigmentation of the pileus [1 = no dark spots, 2 = thin dark spotting, 3 = well marked dark dots].

Morphological multivariate analyses. Principal component analysis is usually well suited to assign individuals to a taxon based on morphology, except when potential taxa are morphologically very close, as is the case within the *Podarcis hispanicus* complex. In this situation, discriminant analysis, which calculates functions maximizing the divergence between reference groups to which studied individuals need to be assigned, has been demonstrated to be appropriate (Renoult *et al*. 2009). Discriminant function analyses were performed using the 16 morphological variables. Reference specimens were active specimens in the analyses, meaning that they were used by the discriminant analyses to compute classification functions. The syntypes were treated as supplementary (non-active) individuals: their position along the discriminant axis was calculated after the analyses but they did not participate in the calculation of the classification functions. Their position was therefore not influenced by any *a priori* assignation.

Renoult *et al*. (2009) showed a gradual variation in TYP3 morphology with the southernmost individuals being smaller, white-bellied, and lacking a distinct masseteric plate. These individuals need to be treated as TYP3 reference specimens as they are part of the variation exhibited by this form, and because their identification was attested with nuclear genetic data. Nevertheless, such specimens may prevent the discriminant analyses from calculating functions that characterize TYP3 reference specimens, if all TYP3 are treated as a whole. We thus performed an additional discriminant analysis by splitting TYP3 into two reference groups according to a geographical limit located some 100 km north of the town of Valencia (based on results presented on Fig. 3B in Renoult *et al*. 2009): 183 northern TYP3 (N_TYP3 hereafter) and 24 southern TYP3 (S_TYP3).

Results

The type specimens of *Lacerta muralis* var. *liolepis* Boulenger, 1905

The central argument developed here is that the majority of the name-bearing types of *liolepis* belong to TYP3. It is therefore crucial to accurately establish which specimens constitute the name-bearing types of *liolepis*. Boulenger (1905) did not list precisely the specimens used for his description but he based it partly on the description made by Bedriaga (1879) of several specimens originating from the town of Valencia. These specimens are thus part of the type series because according to the current edition of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999; the "Code" hereafter), a type series can be defined by bibliographic reference (Art. 72.4.1). Boulenger also assigned to this form specimens from the British Museum collected by Lilford, Boscá and Bolivar: "Among numerous specimens from Valencia in the British Museum (Lilford, Boscá, Bolivar), some agree with Bedriaga's description" (p. 292). Last, he included specimens from Seville received from Prof. Calderon (p. 363). C. J. McCarthy (Natural History Museum, London) examined for us the catalogues of the Natural History Museum and together we were able to establish that the following specimens currently in this collection are part of the original type series: BMNH 1946.9.1.33-35 (formerly 76.2.28.6-8), Valencia, Spain / Lord Lilford; BMNH 86.12.29.1-10 A-H, Valencia, Spain / Prof. E. Boscá; BMNH 1946.9.1.36-45 (formerly 1905.2.27.5-14), Valencia, Spain / Prof. E. Boscá (Madrid museum); BMNH 1920.1.20.321, Valencia, Spain / Prof. E. Boscá

(Lataste collection); BMNH 1905.2.27.15-22, Foyos [= Foios], near Valencia / Prof. E. Boscá (Madrid Museum); BMNH 94.6.1.15-17, Sevilla / Prof. Calderon. Among these, nine were adult males and were thus included in the morphological analyses of this study: BMNH 1946.9.1.33-35, BMNH 86.12.29.1-5, BMNH 86.12.29.1-7.

Bedriaga (1879) does not give a list of the specimens he examined. He explicitly refers to several specimens he saw along the road from Valencia to Dehesa de la Albufera, several of which were collected by himself but died and got rotten before he could measure them, except for one specimen whose measurements are given in his paper. Despite numerous enquiries in various collections, we were unable to locate this specimen or any other *Podarcis* specimen collected by Bedriaga near Valencia. The Bedriaga syntypes are thus probably lost.

Because Valencia and Sevilla are inhabited by different taxa of the *P. hispanicus* complex (see Guillaume 1987; Geniez 2001; Harris *et al*. 2002a; Harris and Sá-Sousa 2002, Pinho *et al*. 2006, Pinho *et al*. 2007, Pinho *et al*. 2008), the name *liolepis* could potentially apply to either of these taxa. Nevertheless, the types of *liolepis* include at least 39 specimens from Valencia and its surroundings but only three specimens from Sevilla. Furthermore, Boulenger (1905) starts the description of *liolepis* by referring to specimens seen at Valencia by Bedriaga, and in a subsequent publication (Boulenger 1921, pp. 402–403, in the appendix) he only lists specimens from Valencia as types. Although this last publication is not the original description, it obviously indicates that Boulenger intended to use the name *liolepis* for the taxon occurring in and around Valencia. This has been followed by Salvador (1986), Guillaume (1987) and Geniez (2001) although none of these authors realised that the type locality actually encompassed Valencia, Foios and Sevilla.

As the Sevilla syntypes are probably *Podarcis vaucheri* (the species currently inhabiting Sevilla and its surroundings; Pinho *et al*. 2006, Pinho *et al*. 2008, pers. obs.) it is necessary to designate a lectotype from the Valencia syntypes to permanently fix the use of the nomen *liolepis*. Among the original syntypes we select here the specimen BMNH 86.12.29.3 (Fig. 2A) from Valencia as lectotype of *Lacerta muralis* var. *liolepis* Boulenger, 1905 (see systematic section below).

Morphological assignation of the type specimens

The examined type specimens (including the lectotype) are easily distinguished from *P. bocagei* and *P. carbonelli* (both highly unlikely in Valencia) by their different head shape, body proportions and coloration (compare Fig. 2 with information in e.g. Galán 2009, Sá-Sousa 2009, Glandt 2010).

Figure 3 shows the results of the discriminant analyses with syntypes from Valencia treated as non-active individuals. In these figures, all lineages differ substantially in morphology, but there is a variable amount of overlap between all morphotypes that were analysed together. Usually, this overlap is due to a few outliers, with most individuals falling outside the bivariate distribution of the vast majority of the specimens of the other morphotypes. The overlap between TYP3 and TYP2 involves more individuals although the majority of specimens have a distinct graphical distribution (Fig. 3A). The lineage that is the most difficult to characterise morphologically seems to be *vaucheri*, whose outliers fall far in the distribution of the TYP1 and TYP3 specimens (Fig. 3B).

All specimens from the type series have a morphology which places them fully within the distribution of TYP3 specimens. Furthermore, they all fall outside the distribution of TYP1 (Fig.3A) *P. hispanicus* sensu stricto (Fig. 3B) specimens. Six out of the nine syntypes fall outside the distribution of TYP2 and the three other syntypes distribute with a few outliers individuals (Fig. 3A). Syntypes are less well discriminated from *vaucheri* specimens, but when the morphological variation within TYP3 is accounted for, with southern TYP3 and northern TYP3 treated as distinct reference groups, all syntypes fall outside the distribution of *vaucheri* but inside the distribution of N_TYP3 (one type) or S_TYP3 (eight types; Fig 3C). In this figure, the seven S_TYP3 individuals with the highest axis 2 score all originate from the *P. hispanicus* sensu stricto-TYP3 contact zone while the other S_TYP3 originate from the town of Valencia. Interestingly, eight types fall within the distribution of the reference specimens originating from the town of Valencia or close surroundings. This result stresses the morphological similarity of *liolepis* syntypes with the TYP3 lizards that currently inhabit the Valencia area.

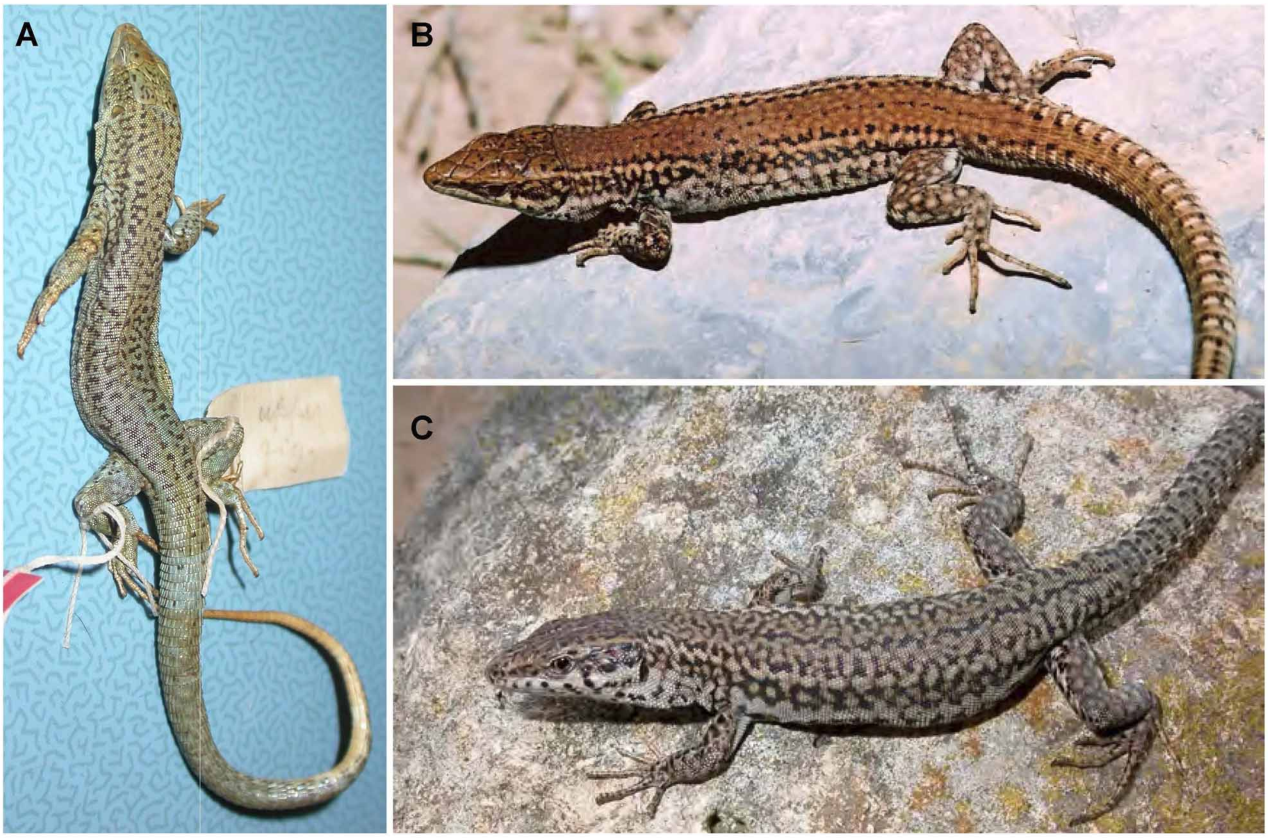

FIGURE 2. Latero-dorsal views of *Podarcis liolepis* (Boulenger, 1905). A. Specimen BMNH 86.12.29.3, lectotype of *Lacerta muralis* var. *liolepis* Boulenger, 1905, Valencia, Spain. Photo C. McCarthy. B. Specimen BEV 9853 with "Valencia" mitochondrial lineage (mtDNA), male, collected in Rafelbuñol, north of Valencia, Spain. Photo PGe. C. Specimen BEV 9815 with "Type 3" mtDNA, male, collected 3 km NW of Miami-Platja along the national road 340, province Tarragone, Spain. Photo PAC. Note the great morphological resemblance of both *Podarcis liolepis* (BEV 9853 and BEV 9815) showing however a deep mitochondrial divergence

Conclusion: the correct name of the north-eastern form of the *Podarcis hispanicus* complex

Busack *et al*. (2005) argued that the TYP3, *i.e*. the north-eastern Spanish form (= "*P. hispanica* morphotype 3" in Pinho *et al*. 2006) is conspecific with the Columbretes populations and proposed to use the binomen *Podarcis atratus* to designate this species. Renoult *et al*. (2009) demonstrated that the populations of the *Podarcis hispanicus* complex originating from the town of Valencia and the surrounding areas belong to the same species as the typical populations of TYP3 located in the north-east of Spain. They also showed that morphological characters constitute a reliable marker of species delimitation for the forms inhabiting the eastern part of the peninsula. In this study, we demonstrated that most original syntypes and the lectotype of *liolepis* belong to TYP3 and thus to the corresponding species. The valid nomen of TYP3 of the *Podarcis hispanicus* complex (= *Podarcis hispanica* type 3) is thus *Lacerta muralis* var. *liolepis* Boulenger, 1905 which has precedence over *Lacerta muralis atrata* Boscá, 1916 when the two nomina are in concurrence to designate a species-rank taxon. Last, since multiple evidence of reproductive isolation between TYP3 and both TYP2 and *P. hispanicus* sensu stricto have been reported recently (Pinho *et al*. 2007; Renoult *et al*. 2009), we concur with Busack *et al*. (2005) and Geniez (2001) that TYP3 should be considered as a full species: *Podarcis liolepis*. The name *P. liolepis* has been already used by several authors in previous publications to refer to TYP3 (e.g. Bour *et al*. 2008, Carretero 2008, Speybroeck and Crochet 2007) but evidence for the use of this name have never been published and as we have shown here, some nomenclatural action is required to formally fix this use.

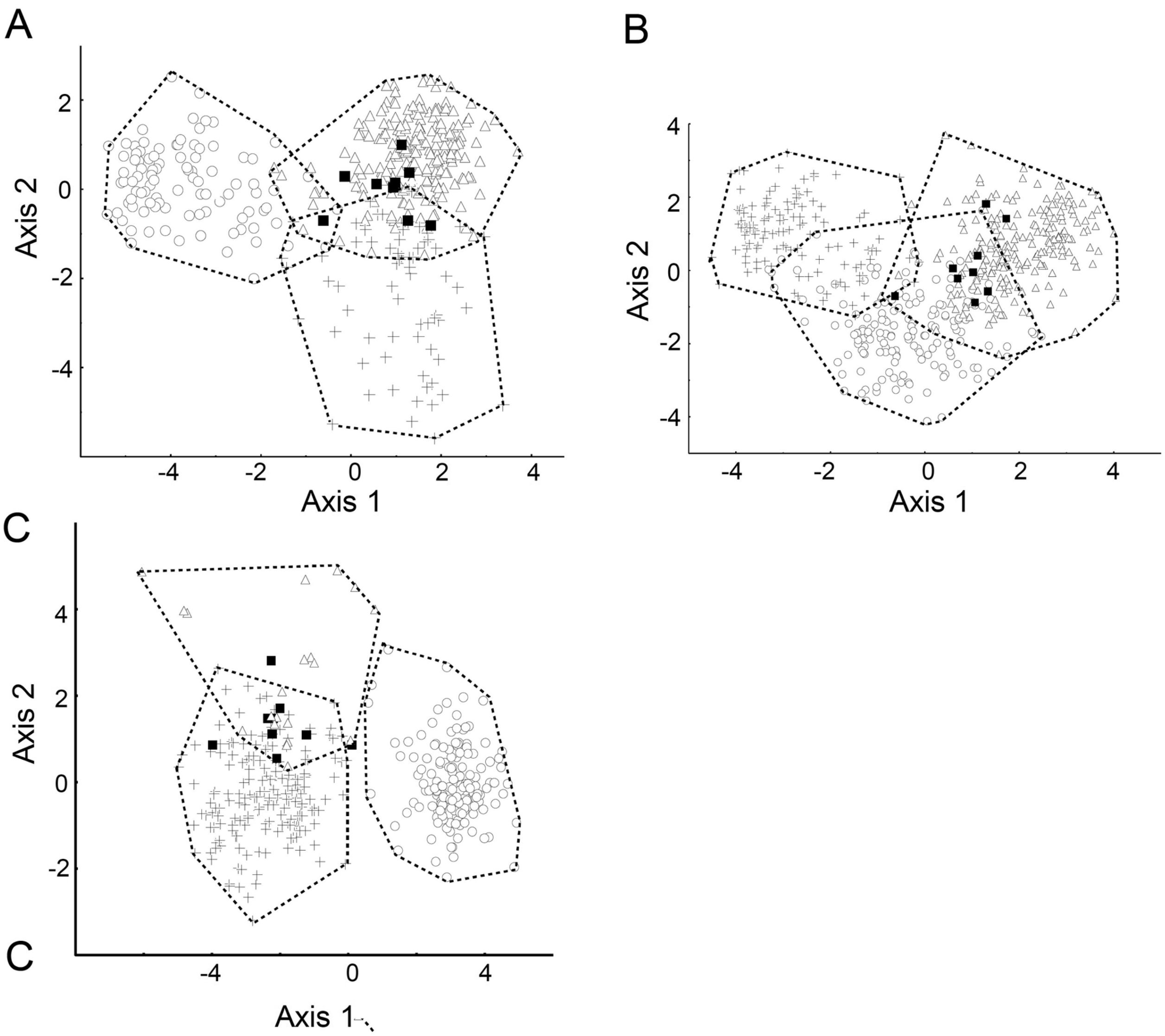

FIGURE 3. First and second components of the discriminant analyses performed with 16 morphological variables on specimens of the *Podacis hispanicus* complex. Specimens from *liolepis* syntypes from the town of Valencia (filled squares) were treated as non-active individuals. We did not include more than three reference lineages in a single analysis to maximise the plot scattering. A. TYP3 (triangles), TYP2 (crosses) and *P. hispanicus* (circles) were active reference specimens. B. TYP3 (triangles), TYP1 (crosses) and *P. vaucheri* (circles) were active reference specimens. C. northern TYP3 (triangles), southern TYP3 (crosses) and *P. vaucheri* (circles) were active reference specimens.

Systematic section

Podarcis liolepis **(Boulenger, 1905)**

Lacerta muralis var. *liolepis*, Boulenger, 1905, Transactions of the zoological Society of London 17: 363. Name-bearing type: Natural History Museum (London) BMNH 86.12.29.3, an adult male from Valencia, coll. or leg by Prof. E. Boscá, lectotype by present designation (see Fig. 2A). The list of the known original syntypes is given above. Type locality: Valencia, Spain, by present lectotype designation. Originally "Valencia", "Foyos" (= Foios) near Valencia, "Sevilla", and along the road from Valencia to Dehesa de la Albufera, Spain.

Junior synonym
Lacerta muralis var. *hesperica*, Schreiber, 1912, Herpetologia europaea. Eine systematische Bearbeitung der Amphibien und Reptilien welche bisher in Europa aufgefunden sind: 943. Name-bearing types: Five syntypes, still extant:

Naturhistorisches Museum Wien NMW 16020 and NMW 16021: 1-4, syntypes (Tiedemann *et al*. 1994). Type locality: Zaragoza, Spain.

Remarks: 1) This nomen was treated as an infrasubspecific nomen by Mertens and Wermuth (1960) and Salvador (1986), and therefore as not available ("nomen illegitimum"). This is clearly a mistake: Schreiber (1912) described *hesperica* as a variety of *Lacerta muralis* (see heading of page 943), treated it as a variety of *muralis* (see page 410). This is confirmed by the original labels of the *hesperica* syntypes in Wien, which writes as: "NMW 16020, *Lacerta bocagei liolepis* Blgr (Lectotypus of *L. muralis* var. *hesperica* Schreib.), Saragossa, Southoff leg, VIII.1912, Coll. Schreiber / NMW 16021:1-4, *Lacerta muralis* var. *hesperica*, Saragossa, Spanien, 1915.II.22E, Coll. Schreiber, Nr. 84,89, leg. Southoff".

2) Despite the mention on the labels that one of the specimen is a lectotype, neither Tiedemann *et al*. (1994) nor ourselves were able to find a published lectotype designation for *hesperica*. The specimens of the original type series thus all remain syntypes.

Proposed status: subjective junior synonym of *Podarcis liolepis*. This nomen would be available for the northern TYP3 populations (carrying the "Type 3" mtDNA lineage) if they were recognised as distinct from the southern TYP3 ones (carrying the south-eastern "Valencia" mtDNA lineage).

A series of other nomina apply to various populations of *Podarcis liolepis*. They are either subjective junior synonyms of *liolepis* (if *Podarcis liolepis* is treated as a monotypic species) or valid nomina for subspecies of *Podarcis liolepis*. As a review of the morphological variation and subspecific systematics of *Podarcis liolepis* is beyond the scope of this paper, we do not address their status here but will do it in a forthcoming work dedicated to the infraspecific systematics of *Podarcis liolepis*.

Diagnosis: a member of the *Podarcis hispanicus* complex characterized by the combination of the following characters: masseteric shield and dark vertebral stripe frequently present but most often discontinuous, dark vertebral stripe never splits near its anterior part, generally lack of yellow coloration on the belly and under tail, pale dorsolateral stripes wider than the dark supradorsolateral stripes except in uniformly coloured individuals. Dorsum generally brown or greyish but often green in some populations from the southernmost parts of the range. Belly and undertail white, salmon-pink or brick red, never yellowish (but females can have yellow under the throat). When present, combination of a dark vertebral stripe and a distinct masseteric shield on one or two sides excludes all other taxa in this complex except *P. carbonelli berlengensis* and some TYP1 specimens (in which the dark vertebral stripe would be limited to the anterior part of the back). In addition, TYP1 (both 1A and 1B lineages, see Pinho *et al*. 2006) differs from *P. liolepis* by contrastingly white or pale dorsolateral stripes (usually less contrasting in *P. liolepis*, rarely white, sometimes absent) which are regularly and strongly dashed in males and some females (less regularly fragmented in *P. liolepis*) or continuous in the other females, and narrower than the black supradorsolateral stripes in both sexes (as wide as or wider than the black supradorsolaterals in *P. liolepis*). Those *P. liolepis* specimens that lack a dark vertebral stripe need to be separated from the other taxa by additional characters. TYP2 (which never shows a dark vertebral stripe) also differs from *liolepis* by the presence of a yellowish coloration on the rear belly and under tail and by wider dark supradorsolateral stripes (which are usually made of scattered marbling in males, more continuous in females) and the typically green or greenish coloration of the dorsum of males in spring. Specimens of *P. hispanicus* sensu stricto lacking a split dark vertebral stripe can be distinguished from small, flattened *P. liolepis* lacking temporal shields by the yellowish coloration on the undertail present in most *P. hispanicus* sensu stricto, by their different head shape with more flattened head and more pointed snout and their paler iris. Iberian populations of *P. vaucheri* (which rarely shows a dark vertebral stripe) often have a yellow or yellowish belly and dark supradorsolateral stripes that are usually either absent or wider than the pale dorsolateral stripes. *P. bocagei* has a blunt, rounder snout and a green dorsum contrasting with brown flanks (males in spring). *P. carbonelli* has a deeper head and more pointed snout and green flanks (often contrasting with brown dorsum) in males in spring. These last two taxa also lack a dark vertebral stripe in most specimens.

Generally, we wish to insist on the difficulty to identify many isolated specimens of the *Podarcis hispanicus* complex on their phenotypic characters only.

Distribution: eastern and northern Spain and parts of southern France (Fig. 4).

FIGURE 4. Distribution of *Podarcis liolepis*.

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