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REVIEW

An integrated assessment of a group with complex systematics: the Iberomaghrebian lizard genus *Podarcis* (Squamata, Lacertidae)

Miguel A. CARRETERO

CIBIO, Reseach Center in Biodiversity and Genetic Resources, Campus Agrário de Vairão, 4485-661Vairao, Portugal

Abstract

A critical review of the evolutionary biology of Iberian and North African lizard members of the genus *Podarcis* (Lacertidae) based on phylogeny, phylogeography, morphometrics, behavior, ecology and physiology is presented. The Iberomaghrebian region is inhabited by at least 12 different evolutionary lineages that group into a monophyletic clade (except *Podarcis muralis*). In contrast to the current taxonomy, the saxicolous '*Podarcis hispanica*' is paraphyletic with respect to *Podarcis bocagei* and *Podarcis carbonelli*, two currently recognized species. Nodes in the phylogenetic tree are deep, resulting from old divergences, clearly preceding the Pleistocene. Nevertheless, more recent range changes as a result of glaciations are also evident. The most plausible evolutionary scenario for this group indicates both vicariant and dispersal events. Although parapatry between lineages is the rule, sympatry and even syntopy are frequent, but usually between ground-dwelling and saxicolous forms. Contacts between forms with similar habitat use are rare and local. Morphological distinctiveness between lineages has been demonstrated, indicating historical constraints. However, other characters have repeatedly evolved under similar environmental pressures independently of the evolutionary lineage. Strong sexual dimorphism derives from sexual selection and is attained before sexual maturity, although developmental restrictions exist. Variation between populations is also important and derives from local variation in both natural (habitat, climate) and sexual (density) selective pressures. Evidence for short-term changes has already been found, particularly in insular populations. Reproductive isolation between syntopic forms and partner recognition are based on male–male competition and on visual and chemical recognition of females by conspecific males. Despite this ancient diversification, most forms maintain a degree of reproductive compatibility. Hybridisation may occur, but is limited, and there is evidence of selection against hybrids. The ecological analysis presented here does not support exploitative competition, but rather behavioral interference between forms. Ecomorph classification of lineages suggests character displacement between those with extensive range overlap. Finally, a critical assessment of the specific status of all lineages is provided and directions for further research are suggested.

Key words: Morphometrics, Mediterranean basin, phylogeny, *Podarcis*, reproductive isolation, speciation.

INTRODUCTION

Evaluating the specific status of organisms requires more than a pure evolutionary and systematic approach, and also involves conservation, management and legisla-

Correspondence: Miguel A. Carretero, CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, 4485-661 Vairão, Portugal.
Email: carretero@mail.icav.up.pt

tion issues, which are mostly based on species lists (Helbig *et al*. 2005). It is a difficult task to determine the number of species comprising a taxonomic group. During the past century many species criteria have been developed (see the reviews by de Queiroz 1998 and Coyne & Orr 2004) and the results of their application are divergent, particularly for those organisms with complex evolutionary trajectories. Nevertheless, two fundamental questions must be addressed (Helbig *et al*. 2005): (i) are such units diagnosable; and (ii) are they likely to retain their genotypic and phenotypic integrity in the future? Under the Biological Species Concept (BSC) (Mayr 1995), probably the most accepted, species are diagnosable in terms of their prezygotic or postzygotic reproductive isolation. Under the Cohesion Species Concept (CSC) (Templeton 1989) diagnosis is based on the phenotypic cohesion of populations. Under the Ecological Species Concept (EcSC) (Van Valen 1976) species are defined by the adaptive zones they occupy. The list could continue, but all these concepts have in common the fact that they consider the retention of such traits into the future as important. In contrast, the Phylogenetic Species Concept (PSC) (de Queiroz & Donogheue 1988) exclusively takes into account the monophyly of each group, but not its further evolutionary trajectory. Given this difference, species defined under this criterion might differ from species defined using other criteria (mainly BSC). For instance, distant groups in the phylogeny can be reproductively compatible (or phenotypically/ecologically similar) while close ones are not. In addition, long-term isolated populations as a result of geographic barriers might potentially merge if they come into contact. In practical terms, multiple genetic markers at population and phylogenetic levels, experimental tests for reproductive isolation, analysis of phenotype, and comparative ecological studies need to be used. As evidence from different sources might be conflictive, it is recommended to approach these problems in a multidisciplinary way (Helbig *et al*. 2005).

The lacertids genus *Podarcis* (Wagler 1830) is a lizard group that evolved and diversified in the Mediterranean Basin (Arnold 1973, 1989; Arnold *et al*. 2007). They represent a relevant herpetofaunal element of Mediterranean ecosystems, where they play a major ecological role in food webs (Carretero 2004). The genus *Podarcis* ranges from Central Europe to the Sahara and from the Iberian Peninsula to the Crimea (Fig. 1): only *Podarcis muralis* (Laurenti 1768) is found in the northern part of the range, whereas the Southern European peninsulas and associated archipelagos harbor the highest degree of endemicity and species richness. Currently, 18 species are considered in the international databases (Uetz *et al.* 2008), two others have recently been added (Lymberakis *et al*. 2008), and more could follow in the near future. Some of these species are critically endangered (Capula *et al.* 2002), while others are successful colonizers through human transport (Corti *et al*. 1999).

As in other groups, the generalization of molecular tools is gradually revealing more evolutionary complexity in *Podarcis* than previously thought. The Iberian Peninsula, a region with high habitat diversity and complex geological history, is no exception. However, there is a risk that phylogenetic works ignore their own taxonomic results or

Figure 1 Distribution of the genus *Podarcis* (modified from Arnold 1973). The lizard in the image is a female *Podarcis liolepis*. The dashed line indicates the estern boundary.

treat them marginally (Padial & de la Riva 2007). In this review, an update of the current knowledge of the evolutionary biology of the Iberian and North African members of this genus is presented using a multidisciplinary approach that integrates evidence from studies on phylogeny, phylogeography, morphometrics, behavior, ecology and physiology. This review does not intend to be another contribution to the species concept debate or a systematic reassessment. Rather, this review aims to provide a critical re-examination of all evidence, either for specific status or not, as well any conflicts that exist in this complex group.

CONTEMPORARY TAXONOMY

The taxonomy of *Podarcis* (Wagler 1830) has been controversial since first described. The genus itself was not widely accepted until its morphological revalidation by Arnold (1973). More recently, its gender is creating considerable nomenclatural debate and instability (e.g. Böhme 1997; Arnold 2000; Lanza & Boscherini 2000; Böhme 2004; Speybroek & Crochet 2007; here the feminine is preferred). Even if one refers only to the changes involving species recognition, the situation remains complex (Table 1).

Regarding the study region, the first classical compilation by Arnold and Burton (1978),incorporated the full recognition of the genus and also the then recently revalidated *Podarcis bocagei* (Seoane 1884), comprising the subspecies *carbonelli* restricted to the West Central System (after Pérez-Mellado 1981a,b). The rest of the Iberian *Podarcis* were assigned to *Podarcis hispanica* (Steindachner 1870) except *Podarcis muralis*, a Central European element. Later, Pérez-Mellado and Galindo-Villardón (1986) confirmed this arrangement, admitting high polymorphism in *P. hispanica* and only separating the North African specimens at the subspecific level (*P. hispanica vaucheri).* In contrast, Guillaume (1987) had suggested that *P. hispanica* should be divided into eight forms/subspecies. More formally, Sá-Sousa (2001a) considered four *Podarcis* to be present in Portugal: *Podarcis bocagei* s.s., *Podarcis carbonelli* (Pérez-Mellado 1981), elevated to the specific level after Sá-Sousa and Harris (2002), and two unnamed morphotypes (1 and 2) of *P. hispanica*. Not only the populations from West Central System, but also many population isolates from the Portuguese coast and Doñana were ascribed to *P. carbonelli* (see also Magraner 1986, Sá-Sousa *et al*. 2001). Almost simultaneously, Geniez (2001) recognised some of the forms of Guillaume (1987) and added others, both in Iberia and North Africa, although they were not formally described. Busack *et al*. (2005) raised *P. vaucheri* (Boulenger 1905) to the species level, but considered it to be present also in the southern tip of the Iberian Peninsula (see also Oliverio *et al*. 2000). These novelties were compiled in the taxonomical synopsis of the Spanish herpetofauna (Montori *et al*. 2005). There, *P. muralis*, *P. bocagei*, *P. carbonelli* and *P. vaucheri* were accepted, whereas *P. hispanica* was considered an artificial assemblage. The status of *Podarcis atrata* (Boscá 1916), endemic to the Columbretes archipelago (East Spain), previously raised to the specific level by Castilla *et al*. (1998b), was considered doubtful. Very recently, Speybroek and Crochet (2007) have restricted the trinomial *P. h. hispanic*a (Steindachner 1870) to south-east Iberia (after Geniez *et al*. 2007) and used *Podarcis liolepis* (Boulenger 1905) for morphotype 3 (sensu Harris & Sá-Sousa 2002) of north-east Iberia and south-east France, also including *P. atrata*.

MOLECULAR PHYLOGENIES

Although other sources of information have been used, recent taxonomical changes mostly derive from the application of molecular techniques. Allozyme analysis was used early in *Podarcis* to assign species (Bea *et al*. 1986; Guillaume 1987), to document phylogeographic patterns within species (Busack 1986; Capula 1994a,b) and to assess species relationships (Mayer & Tiedemann 1980; Capula 1997). However, at the change of the century, phylogenetic studies on *Podarcis* were already based on mitochondrial DNA (mtDNA). Very significantly, all studies (Fu 1998, 2000; Harris *et al*. 1998, 2005; Oliverio *et al*. 1998, 2000; Poulakakis *et al*. 2005; Arnold *et al*. 2007) coincide in recovering the genus as a monophyletic clade, supporting the morphological conclusions of Arnold (1973) and Arnold (1989). Such a clade does not include either *Teira dugesii* (Milne-Edwards 1829) from Madeira or *Scelarcis perspicillata* (Duméril & Bibron 1839) from Morocco and West Algeria, as previously suggested (Böhme 1986), but instead places them as the closest sister group (Arnold *et al*. 2007).

The deep intrageneric relationships are, however, poorly defined probably because of the rapid colonization of the Mediterranean Basin and early diversification (Harris & Arnold 1999), making the geographical origin obscure. Nevertheless, four geographically coherent clades seem to be well supported: the Balkan clade *Podarcis erhadii* (Bedraiga 1882), *Podarcis gaigeae*, (Werner 1830), *Podarcis milensis* (Bedriaga 1882), *Podarcis melisellensis* (Braun 1977), *Podarcis peloponnesiaca* (Bibron & Bory 1833), *Podarcis taurica* (Pallas 1814) and the newly described *Podarcis cretensis* and *Podarcis levendis* (Lymberakis *et al*. 2008); the Italian clade *Podarcis muralis*,

Table 1 Five contemporary systematic arrangements for the Iberian and North African *Podarcis*

Region	Arnold and Burton (1978) Pérez-Mellado and Galindo-Villardón (1986)	Sá-Sousa (2001)	Geniez (2001)	Montori *et al*. (2005)	Speybroek and Crochet (2007)
Pyrennes, Cantabric	*P. muralis*	–	*P. muralis*	*P. muralis*	*P. muralis*
South-east France	*P. hispanica hispanica*	–	*P. hispanica cebennensis*	*P. hispanica* type 3	*P. liolepis*
North-east Iberia	*P. hispanica hispanica*	–	*P. hispanica liolepis*	*P. hispanica* type 3	*P. liolepis*
Columbretes isl.	*P. hispanica atrata*	–	*P. atrata*	*P. atrata* (?)	*P. liolepis*
North Castilian Plateau	*P. hispanica hispanica*	–	*P. hispanica "robusta"*	*P. hispanica* type 3	*P. liolepis*
Eeast Central System	*P. muralis*	–	*P. muralis*	*P. muralis*	*P. muralis*
	P. hispanica hispanica		*P. hispanica "lusitanica"*	*P. hispanica* type 1	*P. hispanicus* type 1
West Central System	*P. bocagei carbonelli*	*P. carbonelli carbonelli*	*P. carbonelli carbonelli*	*P. carbonelli*	*P. carbonelli carbonelli*
			P. hispanica "lusitanica"	*P. hispanica type 1*	*P. hispanicus type 1*
North-west Iberia	*P. bocagei bocagei*	*P. bocagei*	*P. bocagei*	*P. bocagei*	*P. bocagei*
	P. hispanica hispanica	*P. hispanica type 1*	*P. hispanica "lusitanica"*	*P. hispanica type 1*	*P. hispanicus type 1*
Costal Portugal	*P. hispanica hispanica*	*P. carbonelli carbonelli*	*P. carbonelli carbonelli*	*P. carbonelli*	*P. carbonelli*
Berlengas isl.	*P. bocagei berlengensis*	*P. carbonelli berlengensis*	*P. carbonelli berlengensis*	–	*P. carbonelli*
Doñana	*P. hispanica hispanica*	*P. carbonelli carbonelli*	*P. carbonelli "donianensis"*	*P. carbonelli*	*P. carbonelli*
South-west Iberia	*P. hispanica hispanica*	*P. hispanica* type 2	*P. hispanica "virescens"*	*P. hispanica* type 2	*P. hispanicus* type 2
South-east Iberia	*P. hispanica hispanica*	–	*P. hispanica "virescens"*	*P.* "Galera"	*P. hispanicus hispanicus*
Sierra Nevada	*P. hispanica hispanica*	–	*P. hispanica "virescens"*	*P.* "Sierra Nevada"	?
South Iberia	*P. hispanica hispanica*	–	*P. hispanica "virescens"*	*P. vaucheri*	*P. vaucheri*
Rif and Altas	*P. hispanica vaucheri*	–	*P. hispanica vaucheri*	*P. vaucheri*	–
Jebel Sirwah	*P. hispanica vaucheri*	–	*P. hispanica vaucheri*	–	–
Chafarinas isl.	*P. hispanica vaucheri*	–	*P. hispanica "chafarinensis"*	*P. vaucheri*	–
West Algeria	*P. hispanica vaucheri*	–	*P. hispanica vaucheri*	–	–
East Algeria	*P. hispanica vaucheri*	–	*P. hispanica "tunesiaca"*	–	–
Tunisia	*P. hispanica vaucheri*	–	*P. hispanica "tunesiaca"*	–	–

Podarcis sicula (Rafinesque-Schmaltz 1810), *Podarcis rafonei* (Mertens 1958) and *Podarcis wagleriana* (Gistel 1868); the Tyrrhenian–Balearic clade *Podarcis filfolensis* (Bedriaga 1876), *Podarcis lifordi* (Günther 1874), *Podarcis pityusensis* (Boscá 1883), *Podarcis tiliguerta* (Gmelin 1789); and the Iberomaghrebian clade originally *P. atrata*, *P. bocagei* and *P. hispanica*, which is the subject of this review. Although the position of some species is still under debate (i.e. *P. peloponnesiaca*; Harris *et al*. 2005; Poulakakis *et al*. 2005; Arnold *et al*. 2007), the monophyly of the Iberomaghrebian clade itself has not been questioned. Nevertheless, initial phylogenetic studies showed conflicting internal relationships. For instance, Busack (1986) detected low allozyme variation across the Strait of Gibraltar, whereas Capula (1997) using allozymes and Oliverio *et al*. (2000) using mtDNA found the opposite because these authors inadvertently compared either the same or different lineages (see Fig. 2).

More recently, the use of an increasing number of mtDNA markers, covering all known forms, has gradually defined the number of lineages and the internal relationships within this clade (Harris & Sá-Sousa 2002; Sá-Sousa & Harris 2002; Harris *et al*. 2002b; Pinho *et al*. 2006). The region is inhabited by as many as 12 different evolutionary lineages which, except for *P. muralis*, group into a monophyletic clade (Fig. 2). Despite the superficial resemblance, the more saxicolous "*P. hispanica*", as presently considered, is paraphyletic with respect to the ground-dwelling *P. bocagei* and *P. carbonelli* (which are not even sister taxa) and to *P. vaucheri*, the monophyly of which is well supported. Distances between these lineages fall within the values usually attributed to species (Hendry *et al*. 2000). Grouping within this clade is also geographically coherent. Thus, there are two basal elements ranging within East Iberia (*P. liolepis* in the north-east and *P. hispanica* s.s. in the south-east) and two sister subclades, one in West Iberia (*P. bocagei*, *P*. type 1, *P. carbonelli* and *P*. type 2) and the other in south-east Iberia and north-west Africa (the form of Sierra Nevada, *P. vaucheri* in both sides of the Straits of Gibraltar, and two unnamed forms from Tunisia and Jebel Sirwah). The presence of *P. carbonelli* in Doñana, already reported by Magraner (1986) and Sá-Sousa *et al*. (2001), is now confirmed by mtDNA analysis (Harris *et al*. 2002a). More recently, Pinho (2007)

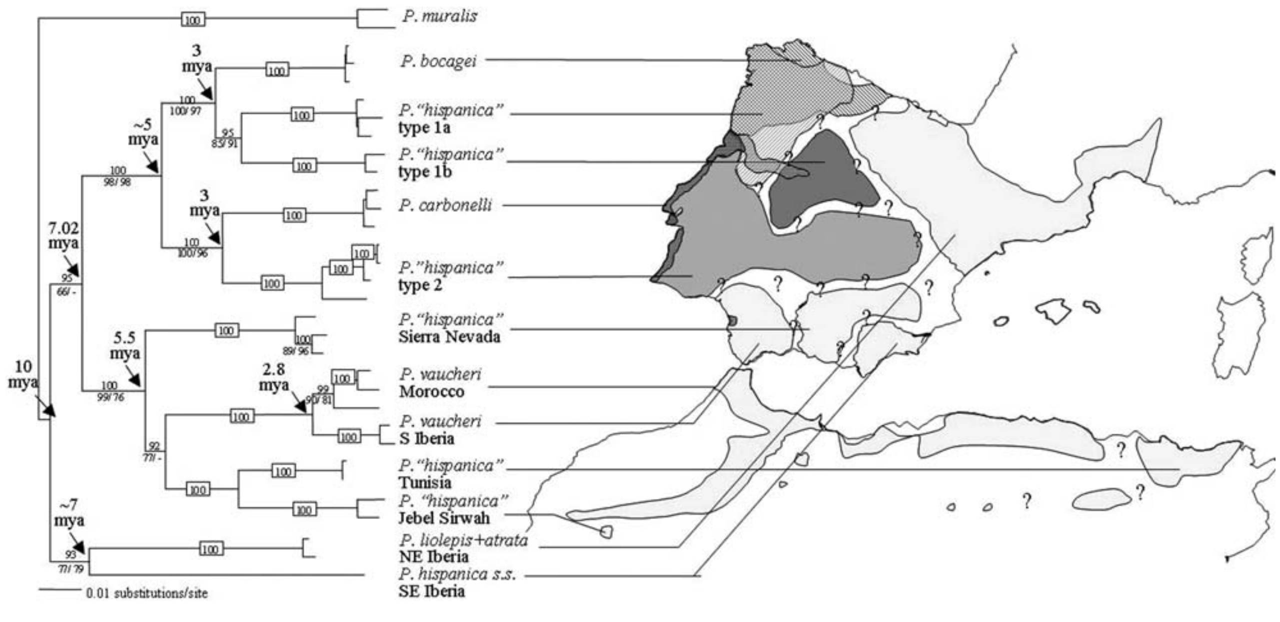

Figure 2 Estimated distribution ranges (after Sá-Sousa 2000, 2001; Pinho *et al*. 2008) and phylogenetic relationships of Iberian and North African *Podarcis* based on five mitochondrial DNA (mtDNA) markers, Cyt-*b*, 12S, 16S, ND4 and control region (after Pinho *et al*. 2006; Geniez *et al*. 2007; Kaliontzopoulou *et al*. 2007). The tree was rooted using *Podarcis muralis*. Bayesian posterior probabilities are given above the nodes, Maximum Likelihood and Maximum Persimony bootstraps, respectively, below the nodes. The numbers and arrows over the main nodes indicate the dates based on a Cyt-*b* calibration (Pinho *et al*. 2006).

has added some Algerian samples to this phylogeny. Whereas those from north-west Algeria clearly belong to *P. vaucheri*, those from the north-east (Algeria A and B in Pinho 2007) fall between the specimens from Tunisia and Jebel Sirwah.

Although this cryptic genetic diversity within the Iberomaghrebian clade seems surprisingly high, the other *Podarcis* groups also reveal more diversity than initially supposed (Poulakakis *et al*. 2003, 2005; Podnar *et al*. 2004, 2005; Harris *et al*. 2005). Nevertheless, not all of the taxa previously described are well supported. Namely, *P. carbonelli belengensis* (Vicente 1985) from the Belenga Islands is not genetically distinguishable from *P. carbonelli* from the adjacent continent (Sá-Sousa *et al*. 2000) and *P. atrata* from the Columbretes Islands is ascribed as *P. liolepis* (Harris & Sá-Sousa 2002; Harris *et al*. 2002) in contrast with previous analyses (Castilla *et al*. 1998a,b).

Nuclear markers have also been used to assess genetic structuring in this species complex. Analyses of protein loci corroborated the major lineages (Pinho *et al*. 2003, 2007a), but the relationships between them were weakly supported, suggesting more rapid diversification than indicated by mtDNA analyses (Pinho *et al*. 2007a). Some misassigned individuals were interpreted as a result of ancestral polymorphism, but others probably derived from limited gene flow between forms (Pinho *et al*. 2007a). A study of two nuclear introns showed discordance between nuclear and mitochondrial DNA, which were better explained by incomplete lineage sorting than by gene flow between forms (Pinho *et al*. 2008). In fact, the only available study of a contact zone (between *P. bocagei* and *P. carbonelli*; Pinho *et al*. in press) indicates that hybridisation was highly localised and bimodal and suggests strong barriers to gene flow. Further intensive studies that are not restricted to closely related taxa are needed to determine the nature of gene flow between other *Podarcis* in contact.

MOLECULAR CLOCKS AND PALEOGEOLOGICAL SCENARIOS

How could this amazing cryptic diversity arise? Are these phylogenies compatible with the compulsive geological history of the Western Mediterranean? For lack of other evidence, it seems reasonable to assume a European origin for this genus and for the Iberomaghrebian group because they are both widespread and diverse there and other related genera also evolved in Europe (Arnold *et al*. 2007). Pinho *et al*. (2006) applied a molecular clock, based on cytochrome-*b* distances, to their robust mtDNA phylogeny (Fig. 2), which does not differ much from that in Carranza *et al*. (2007). Figure 3 shows the paleogeological scenario based on this calibration. The initial split of the Iberomaghrebian group would have taken place during the Late-Middle Miocene in the early Tortonian (10 Mya), almost simultaneously with the radiation of the Balkan group (Poulakakis *et al*. 2005). During this age, the rotational migration of the Balearic, Corsican–Sardinian, Calabrian, Kabylian and Betic–Rifian microplates had already been completed and they occupied their current locations; the Neo-Pyrenees had upraised and the climate was humid and subtropical (Cavazza & Wezel 2003). This was the moment for the earliest diversification of the group, although the vicariant events involved remain obscure. However, the fact that these ancient lineages (*P. liolepis* and *P. hispanica* s.s.) are restricted to East Iberia, together with the presence of lacustrine basins on what are now the Iberian Plateaus (Maldonado 1989), might indicate that West Iberia was colonized later.

The Betic–Rifian arch remained an archipelago not colonizable by land until the end of the Tortonian (7.2 Mya) when the Betic Strait was closed (Duggen *et al*. 2003). The gradual transformation of the Betic channel into a shallow sea lead to the Tortonian salinity crisis, which coincided with a global aridification of the climate (Krijgsman *et al*. 2000), and might have isolated the west and east subclades on both sides of the Iberian Peninsula. In fact, many *Podarcis* are still strongly dependent on humidity (Sá-Sousa 2001b; Kaliontzopoulou *et al*. 2008). Later, because of the intensification of such a trend through the Messinian (7.2–5.3 Mya), forests continued to be replaced by more open landscapes (Favre *et al*. 2007). In consequence, *Podarcis* lizards might have been restricted to isolates, leading to intensive speciation in both groups (Pinho *et al*. 2006). The final closing of the Rifian Strait (7. 2 Mya; Duggen *et al*. 2003), which was responsible for the Messinian salinity crisis and drying of the Mediterranean (Hsü *et al*. 1977), would have allowed the southern subclade to invade the rest of north-west Africa from the Betic–Rifian massif. After the opening of the Strait of Gibraltar and the fast refilling of the Mediterranean at the end of the Messinian (5.3 Mya; Duggen *et al*. 2003), *Podarcis* from North Africa would have become isolated, undergoing separate evolution.

During the Pliocene (5.3–1.8 Mya), the geographic units were not altered, but the climate became cooler, drier and more seasonal (van Dam 2006). In Iberia, separation of the north-west (*P. bocagei* + *P.* type 1) and north-east (*P. carbonelli* + *P.* type 2) subgroups, dated at 5 Mya, reasonably fits this Messinian aridification (Pinho *et al*. 2006). However, the subsequent, simultaneous split of both subgroups into two overlapping lineages at 3 Mya suggests ecological speciation rather than vicariance. Similarly, the separation between the Iberian and Moroccan lineages of *P. vaucheri*, dated at 2.8 Mya, cannot derive from a vicariant event, but rather from transmarine dispersal of *P. vaucheri* from Morocco–West Algeria to south Iberia (Pinho *et al*. 2006). The causes of the separation between *P. vaucheri* and the rest of the African lineages still remain obscure, but could be associated with progressive aridification during the Pliocene (van Dam 2006).

Although all these events clearly predate the Pleistocene, range shifts as a result of Ice Ages are also evident. During glaciations in the Iberian Peninsula, the mountains and the north and central regions were dominated by tundra, steppe and taiga forests (Tarroso 2008), unsuitable for *Podarcis*, which would have been restricted to a few coastal, southern refugia (Gómez & Lunt 2007), whereas most of the territory would become environmentally favorable in the interglacials. Interestingly, the genus *Iberolacerta*, which is a less thermophile, putative competitor of *Podarcis*, radiated simultaneously in Iberia (Arnold *et al*. 2007), but displays the opposite pattern, that is, it expanded during the glacial periods and contracted during the interglacials. (Carranza *et al*. 2004). In Africa, glaciations correspond to humid periods (Prentice *et al*. 2000) allowing *Podarcis* to range widely, whereas the interglacials would have restricted them to the mountains, similar to the present situation (Kaliontzopoulou *et al*. 2008). It is expected that lineages with the northernmost ranges would experience more drastic Pleistocene "pulsations" than those found in more mild situations. Pioneer phylogeographic studies seem to corroborate this hypothesis: *P. bocagei* shows evidence of extreme glacial retraction and postglacial northern expansion; *P. vaucheri* in Morocco displays high genetic diversity, strong geographic substructuring, but no recent expansion; and *P. carbonelli* shows average diversity and both substructure and expansion (Pinho *et al*. 2007b). Interglacials also represent a chance for interaction and introgression between lineages, but glacial retractions do not necessarily imply separation of all lineages. In fact, there is some evidence that some of these lineages could have shared the same glacial refugium (Gómez & Lunt 2007). Moreover, extinctions of some lineages during glaciations and other critical periods are also expected and extremely recent (or human-mediated) colonizations, such as the Iberian *P. vaucheri* in Asilah, Morocco (Busack *et al*. 2005; Kaliontpoulou *et al*. 2007b) or the Moroccan *P. vaucheri* in Almeria, south-east Spain (Renoult 2006), are known to have occurred.

DISTRIBUTION PATTERNS

A quick look at the current distribution patterns of the Iberian and North African *Podarcis* indicates a dominance of parapatric distributions. This is especially true for the saxicolous lineages previously assigned to "*P. hispanica*" and for the North African forms (Fig. 2). In the Western Iberian Peninsula the ranges of type 1 (north-west Iberia) and type 2 (south-west Iberia) are clearly complementary (Sá-Sousa 2000, 2001a). Although both lineages have some differences in their ecological affinities (Sá-Sousa 2000), the almost complete lack of range overlap in the absence of geographical barriers suggests mutual exclusion. Our knowledge of the distribution over the remaining Iberian Peninsula and north-west Africa is not so accurate, but there are indications that other lineages of *P. hispanica* s. l. also substitute each other (Geniez 2001). This is true for *P. liolepis* (north-east Iberia and south-west France), the lineage from Sierra Nevada, *P. hispanica* s.s. (south-east Iberia) and *P. vaucheri* (south Iberia) (Geniez 2001; Geniez *et al*. 2007; Pinho 2007). Similarly, in north-west Africa, *P. vaucheri* ranges from the mountains of Morocco to the west Tellian Atlas (Algeria), but eastwards and southwards it is replaced by a cluster of related lineages successively ranging the east Tellian Atlas (Algeria), north-west Tunisia and the Saharan Atlas (Algeria) and the isolated Jebel Sirwah peak (south Morocco) (Busack *et al*. 2005; Kaliontzopoulou *et al*. 2007b; Larbes *et al*. 2007).

The ranges of the ground dwellers *P. bocagei* and *P. carbonelli* in the Atlantic region of west Iberia are also parapatric (Sá-Sousa 1998, 2001b, 2002; Fig. 2). The only exception was a very small coastal zone of north-west Portugal where strict syntopy between both forms was documented over a very narrow area (Carretero *et al*. 2002; Pinho *et al.* in press). Whereas other similar cases of local contact within saxicolous or ground-dwelling ecotypes may exist, the rule is finding sympatric populations of one representative of each. This is the case for *P*. type 1 and *P. bocagei* in north-west Iberia, the most overlapping pair (Pérez-Mellado 1981a; Sá-Sousa 2001b), for *P*. type 1 and *P. carbonelli* in the Western Central System (Pérez-Mellado 1981b), for *P*. type 2 and *P. carbonelli* in Coastal Portugal (Sá-Sousa 2001b) and even for *P. vaucheri* and *P. carbonelli* in Doñana (Magraner 1986; Sá-Sousa *et al*. 2001; Harris *et al*. 2002). *Podarcis muralis* can be also found in sympatry with *P. liolepis* in the Pyrenees and east Cantabric (Gosá 1985; Llorente *et al*. 1995), with *P*. type 1 in the East Central System (Martín-Vallejo *et al*.

1995) and, locally, with *P. bocagei* in west Cantabric (M. A. Carretero, personal observation). In all these cases, when two *Podarcis* lineages were found in the same site they maintained their identity.

MORPHOLOGICAL EVIDENCE

Podarcis lizards are highly variable in size, shape, scalation and colour pattern, not only between currently recognized species (Arnold & Ovenden 2002), but also between populations and individuals. Moreover, strong sexual dimorphism derived from sexual selection (head and limbs) and selection for fecundity (trunk) is attained before sexual maturity (Kaliontzopoulou *et al*. 2007a, 2008a). All these variations might mask or reinforce eventual differences between lineages. Given this, disentangling the

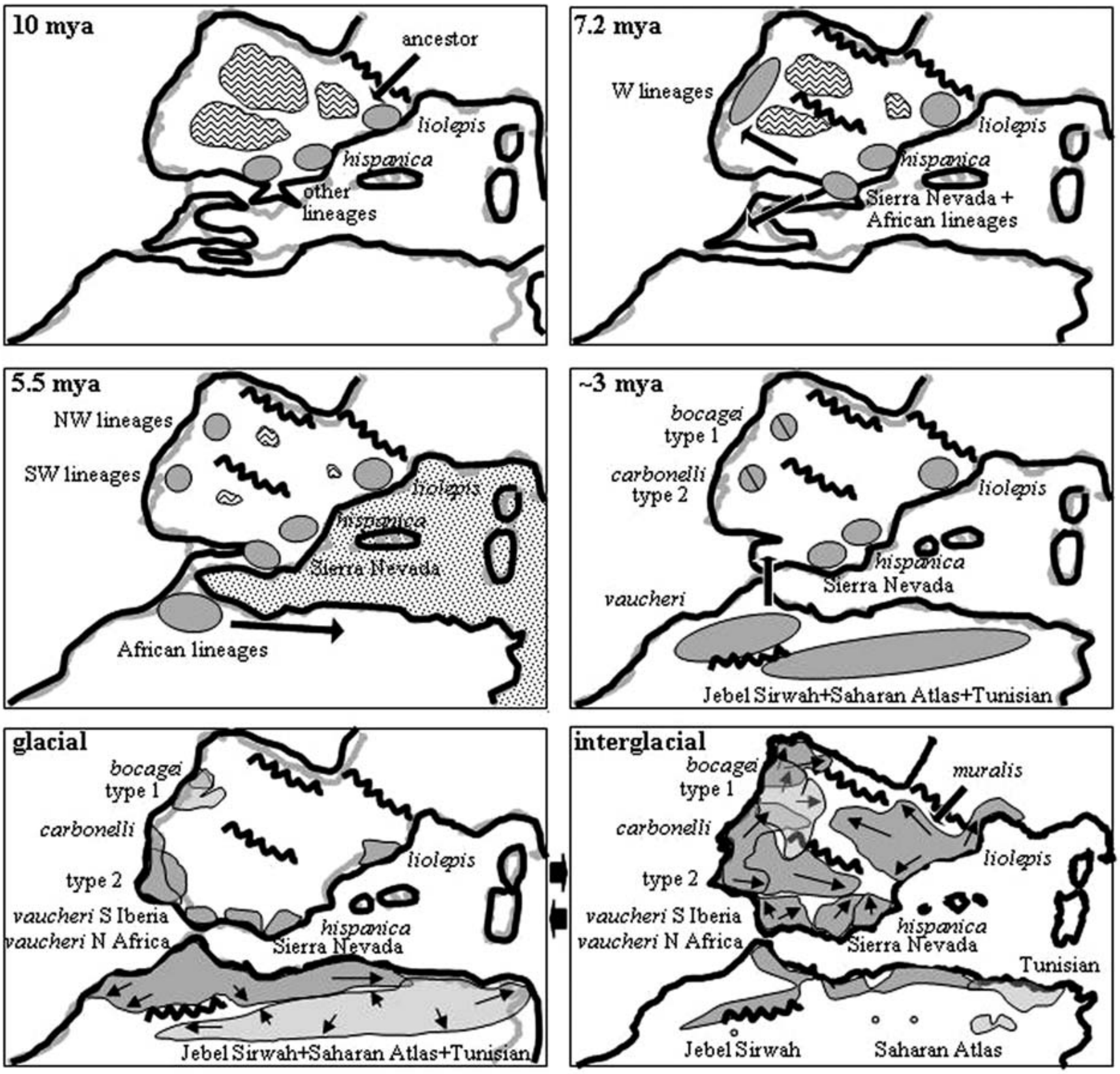

Figure 3 Schematic paleogeographic scenario for the evolution of the Iberian and North African *Podarcis* based on the cyt-*b* calibration by Pinho *et al*. (2006). Previous (black) and current coast lines (grey) are indicated. NW, north-west; SW, south-west; W, west.

track of evolutionary history from the effects of local adaptation or phenotypic plasticity (or finding a cohesive phenotype) can be a difficult task. Morphological distinction between *Podarcis* forms can neither be taken for granted nor necessarily attributed to separate evolution. It is true that the development of multivariate analyses and geometric morphometrics, both exploratory and confirmatory, are increasing the power to detect subtle differences and trends. However, the usefulness of such sophisticated statistics depends on adequate sampling design and hypothesis testing. If the operational taxonomic units (OTUs) (Sneath & Sokal 1973) are to be compared or grouped on the basis of their morphology, they need to be previously defined on the basis of independent evidence (i.e. location, genetic assessment) to prevent circularity. For example, in a morphological analysis of *P. tiliguerta* throughout its range (Bruschi *et al*. 2006), populations not assigned *a priori* to any OTU grouped in accordance to geographical units and genetic markers (Harris *et al*. 2005). This way of working is particularly important when, as in this case, the OTUs themselves are under question.

Unfortunately, such procedures have only been applied recently to the Iberian Peninsula and north-west Africa. Before the development of molecular tools, Galán-Regalado (1986) and Gosá (1985) analysed partial regions of the Iberian Peninsula (north-west and north, respectively) and successfully distinguished *P. muralis*, *P. bocagei* and *P. liolepis* using linear measurements, pholidosis and colour pattern. In such cases, although specimens from all localities were pooled and the species were assigned exclusively on morphology, the strong morphological separation and the restricted geographical area made the OTUs homogeneous, at least according to current phylogenetic knowledge. However, two general studies including all of Iberia and north-west Africa (Pérez-Mellado & Galindo-Villardón 1986; Geniez *et al*. 2007) had to deal with the problem of OTU definition. In both cases, although their criteria were divergent (first, broad and second, restrictive), specimens were pooled by OTUs not defined independently, but rather roughly assigned based on habitat or general range. This might produce either heterogeneous assemblages that are not distinguishable from others (Pérez-Mellado & Galindo-Villardón 1986) or localized morphotypes whose evolutionary significance is questionable (Geniez 2001). In any case, finding significant differences between OTUs does not mean that every specimen (or population) is correctly assigned. The opposite, that is, not finding any difference, also does not necessarily mean that the specimens belong to the same form if the groups compared were heterogeneous assemblages (and, hence, morphological variation was increased).

A different, non-aprioristic approach was taken by Sá-Sousa *et al*. (2002) when studying *P. hispanica* s. l. in Portugal. For both sexes, the populations analyzed clustered in two groups, the so called type 1 (north-west) and 2 (south-west) (Sá-Sousa, 2001a), which were later demonstrated to be distinct in terms of mtDNA (Harris & Sá-Sousa 2001). In the future, this type of analysis should be extended to all ranges of both forms in Spain. In contrast, *P. bocagei* and *P. carbonelli* from environmentally similar localities were morphologically distinct (Harris & Sá-Sousa 2001; Kaliontzopoulou *et al*. 2005) and remained in sympatry (Kaliontzopoulou 2004). In Morocco, agreement between morphology, mtDNA and allozymes belonging to the Iberian and African sublineages of *P. vaucheri* has been found (Busack *et al*. 2005; Kalionzopoulou *et al*. 2007b; Pinho *et al*. 2007a), although the Jebel Sirwah population could not be distinguished using linear morphometrics and pholidosis (Kalionzopoulou *et al*. 2007b). In Algeria, Larbes *et al*. (2007) has detected differences in linear measurements, scalation and pattern between the Algerian populations of the Kabylia and Belezma massifs belonging to different mitochondrial lineages (*P. vaucheri* and *P.* “Algeria A”, respectively, according to Pinho 2007). Furthermore, *P. hispanica* s. s. from south-east Iberia has recently been redefined based on parallel studies of morphology and mtDNA (Geniez *et al*. 2007), although the OTU diagnosis still relies on “expert criterion”. The knowledge of morphological variability of other forms, such as *P. liolepis* and the Sierra Nevada form, is still fragmentary (Geniez 2001; Geniez *et al*. 2007) and awaits further research. Very interestingly, even when hybrids or introgression were detected using molecular markers, individuals with mixed genotypes were not morphologically intermediate (Renoult 2006; Pinho 2007; Pinho *et al*. in press); this is in contrast to what has been described for other *Podarcis* species (Capula 2002).

In general, it appears that morphological distinctiveness between lineages can be demonstrated when properly analyzed. Nevertheless, although some characters reveal strong historical influence (some scalation and pattern traits and head shape), others (size, robustness and background colour) repetitively evolve under the same environmental pressures (Sá-Sousa 2001) independently from the evolutionary lineage. Morphological differences between populations within forms are important, particularly in those species with the largest ranges, and derive from local variation in both natural (habitat and predation pressure and climate) and sexual (density) selective pressures (Tome 2001; Kaliontzopoulou *et al*. 2007a). Both pressures can dramatically change in insularity (decreasing predation, high densities, risk of cannibalism in juveniles, increasing intraspecific competition for food and sexual partners; see Carretero 2004, 2006 and references therein). Because of this, *Podarcis* populations inhabiting small Iberian islets tend to be strikingly distinct from their mainland relatives (Castilla & Bauwens 1997; Sá-Sousa *et al*. 2000; Galán 2003; Arntzen & Sá-Sousa 2007). Such repetitive adaptations, mainly affecting size, robustness and pigmentation, have arisen over a very short time period because the isolation or colonization of most islets dates from the end of the last glacial period and genetic distances from the continent are minimal (Sá-Sousa *et al*. 2000; Harris & Sá-Sousa 2002; Arntzen & Sá-Sousa 2007).

In the future, other internal anatomical traits could be analyzed (Arnold 1973, 1989). For example, Kaliontzopoulou *et al*. (2008b) examined the number of presacral vertebrae that display strong sexual dimorphism, but could not distinguish *P. bocagei* from *P. carbonelli*. Another area where more progress is expected is in distinguishing the effects of adaptation from phenotypic plasticity in morphological variation within forms (Ji & Braña 1999; Braña & Ji 2000).

PHYSIOLOGICAL EVIDENCE

Physiology is seldom taken into account in species evaluations, probably because such phenotypic traits are considered too labile and more likely to result from adaptive pressures than from evolutionary history. However, this is not necessarily the case for all traits. For instance, lacertids are extremely conservative in their thermal physiology. Therefore, although their temperatures in the field vary according to the environment, their preferred body temperatures when free of thermal constraints remain similar within species, even under different climate regimes (Van Damme *et al*. 1990; Tosini & Avery 1993; Gvozdík & Castilla 2001; Carretero *et al*. 2005). This so-called thermal rigidity (Van Damme *et al*. 1989) is not observed between species (Bauwens *et al*. 1995). Even for species belonging to the same genus, body temperatures tend to be distinct and are more related to biogeographic origins than current environmental conditions (Bauwens *et al*. 1995).

Concerning the Iberomaghrebian clade of *Podarcis*, ecological modeling revealed that temperature was a key factor in determining the parapatric distribution of *Podarcis* types 1 and 2 in Portugal (Sá-Sousa 2000). In fact, preliminary research indicates that both forms select different body temperatures in a thermogradient (Amaral *et al*. 2006), suggesting that both perform better in their respective ranges. Similarly, the body temperatures selected by *P. bocagei*, *P. carbonelli*, *P. liolepis* and *P. vaucheri* were distinctive (Amaral *et al*. 2006; Carretero *et al*. 2006a; Veríssimo & Carretero in press). All this evidence points to phenotypic variation in body temperatures associated with phylogenetic inertia.

In the future, other physiological traits could be also incorporated into the analyses. For example, models for the distribution of *P. carbonelli* at geographical (Sá-Sousa 2001) and ecological (Román *et al*. 2006) scales show that this species is highly dependent on humidity, whereas its body temperature is among the highest in the group (Amaral *et al*. 2006). It is tempting to link these findings to the subtropical conditions prevailing in the south-east Iberian Peninsula during the late Miocene when the lineages of *P. carbonelli* and *P.* type 2 deverged from the other lineages (Pinho *et al*. 2006).

REPRODUCTIVE ISOLATION

Determining prezygotic isolation in *Podarcis* not only requires previous knowledge on their reproductive behavior and the mechanisms involved, but the results also need to be placed in an adequate phylogeographic context. Behavioral experiments indicate that *Podarcis* lizards display assortative mating based on male–male competition (López & Martín 2001a, 2002a, 2002b, 2007; López *et al*. 2002) and female recognition by males (López & Martín 2001b). Both chemical and visual stimuli are used. To what extent female choice contributes is still under debate (López & Martín 2001b, 2005, 2006; Barbosa *et al*. 2005, 2006, 2007).

There is experimental evidence that such mechanisms do not only allow for the selection of an adequate partner within the same species but also prevent heterospecific breeding when two *Podarcis* forms are in syntopy. Similarly, mechanisms that allow for the assessment of potential competitors within a species might also prevent allocating efforts in agonistic interactions with heterospecifics. For instance, males (not females) of *P. bocagei* and *P.* type 1, which are sister taxa and widely sympatric in north-west Iberia, were able to mutually discriminate conspecific from heterospecific partners using chemical (Barbosa *et al*. 2006) and visual stimuli (Barbosa *et al*. 2007). Moreover, reproductive interactions were more frequent and intense between conspecific couples than between heterospecifics, while aggressiveness between heterospecific males decreased both in laboratory experiments and in the field (Barbosa *et al*. 2007). Behaviour against chemical stimuli by *P. bocagei* and *P. carbonelli* (Barbosa *et al*. 2005), which are not sister groups, contacting over a narrow area in north-west Portugal displayed the same pattern.

Martín and López (2006a) found chemical differences in the femoral secretions of adult males of *P*. type 1 and type 2, which are parapatric in Central Iberia. Males of both forms successfully distinguished conspecific males from heterospecific males and tended to decrease aggressiveness against the later (Martín & López 2006a, 2006b). Because lizards of both forms did not clearly identify conspecific members of the same sex in laboratory experiments, the results were wrongly interpreted as evidence for incomplete reproductive isolation between them, which would be still undergoing speciation (Martín & López 2006b). On the contrary, from a comparison with an analysis of other syntopic pairs, it seems that a lack of discrimination by females is the rule, with males playing the most active role. Furthermore, because *P*. type 1 and type 2 are not sister taxa (Pinho *et al*. 2006), they cannot be undergoing speciation. Rather, their reproductive interactions are the same as those expected for two lineages that are not directly related and did not evolve together, but rather came into secondary contact at a later stage.

Table 2 Assessment of the specific status of the *Podarcis* forms according to different species criteria

Podarcis form	PSC	CSC	BSC	ESC
muralis	+	+	+	+
liolepis	+	(+)	?	?
atrata	–	(+)	?	–
type 1	+	+	+	+
bocagei	+	+	+	+
carbonelli	+	+	+	+
berlengensis	–	(+)	?	–
type 2	+	+	(+)	+
hispanica	+	+	?	+
Sierra Nevada	+	+	?	+
vaucheri	+	+	(+)	+
Jebel Sirwah	(+)	–	?	+
Tunisia	(+)	?	?	+
West Algeria	(+)	+	?	+

PSC, phylogenetic species concept; CSC, cohesion species concept; BSC, biological species concept; ESC, ecological species concept; +, positive; (+), partially positive; –, negative; ?, doubtful.

Nevertheless, the failure of such behavioral mechanisms is expected when different forms come into contact under certain circumstances (e.g. ecological disturbance; Capula 2002). In such cases, not the occurrence of hybridization itself, but rather the frequency pattern of the hybrids allows for the determination of the eventual existence of post-zygotic isolation mechanisms (Pinho *et al*. in press). In fact, hybridization between unrelated, well-established *Podarcis* species has been reported both in captivity (Bischoff 1973; Galán 2002) and in the wild (Capula 1993, 2002), indicating that most *Podarcis* species have a degree of reproductive compatibility. This is corroborated by the discrepancies between nuclear and mitochondrial phylogeographies (Pinho *et al*. 2007a) and by the presence of individuals with introgressed genotypes discordant from morphology (Geniez *et al*. 2007). However, in a study of the contact zone between *P. bocagei* and *P. carbonelli*, Pinho *et al*. (in press) found a bimodal pattern with scarce hybrids, never F1s, that were phenotypically similar to one of the two parental species, which is expected with strong negative selection against hybrids. Despite this, both species were not reproductively neutral and costs associated with sympatry were detected. Very interestingly, the males of both species displayed increased sperm production when in sympatry (Carretero *et al*. 2006b), suggesting mutual reproductive interference (see Hochkirch 2007 for a similar case in arthropods).

ECOLOGICAL SEGREGATION

Podarcis, including species from Iberia and North Africa, are habitat generalists in comparison with other Mediterranean lacertids (Arnold 1988; Carranza *et al*. 2004). In this region, *Psammodromus* and *Acanthodactylus* are only found on the ground, whereas *Scelarcis* (north-west Africa) and *Iberolacerta* (Iberia) are restricted to steep rocks (Arnold 1988; Schleich *et al*. 1996). In contrast, most *Podarcis* species use either rocks, trunks, vegetation or bare ground for thermoregulation, foraging and shelter. Because this happens in other regions of the Mediterranean Basin, this polyvalence can be considered to be plesiomorphic in the genus (Arnold 1988). Within *Podarcis*, insular populations, in the absence of potential competitors, are particularly eclectic in their habitat use and are difficult to characterize in ecomorphological terms (Arnold 1988; Vanhooydonck *et al*. 2000; Bruschi *et al*. 2006). However, some continental forms show a degree of habitat specialization. For example, *P*. type 1 is very saxicolous (Sá-Sousa 2001a), probably the most specialized within the genus. This is particularly evident when this form is found in sympatry with *P. bocagei*, which behaves as a ground-dwelling specialist (Pérez-Mellado 1981a; Sá-Sousa 2001). Less accentuated segregation is also found between *P.* type 1 and *P. carbonelli* (Pérez-Mellado 1981b). Both ecomorphs are clearly characterized in terms of head (plated *vs* high) and limb (long *vs* short) morphology (Arnold 1988, 1999). Some habitat flexibility depending on the species in sympatry is still possible (i.e. *P. muralis* tends to use rocks in the presence of *P. bocagei* in the León Mountains in north-west Iberia, whereas it is more frequent on the ground when *P. liolepis* occurs in the Pyrenees; M. Carretero, personal observation). However, at least in the case of *P.* type 1 and *P. bocagei*, sister taxa sharing 50% of their respective ranges, such differentiation strongly suggests character displacement. In contrast, other *Podarcis* with parapatric distributions tend to be intermediate in habitat use and morphology (Sá-Sousa 2001). In areas of local contact between *P. bocagei* and *P. carbonelli*, both ground dwellers, Carretero *et al*. (2002) failed to find any other habitat segregation than that attributable to lizard size.

Other aspects of the ecological niche of sympatric *Podarcis* are less elucidative. Differences in the trophic ecology between *P. carbonelli* and *P.* type 1 (Pérez-Mellado 1983) were subsidiary to deferential habitat use (Arnold 1988). In the case of *P. carbonelli* and *P. bocagei*, both ground dwellers, diet differences depended on body size (*P. carbonelli* is smaller), but null models did not reveal evidence of exploitative competition (Marques & Carretero 2007). Helminth fauna in the intestine of both species was also very similar (Galdón *et al*. 2006; Roca *et al*. 2006). Moreover, differences in activity patterns, such as those between *P. carbonelli* and *P.* type 1 in the Central System (Pérez-Mellado 1982), might in fact derive from historical differences in thermal physiology (Amaral *et al*. 2006) and the role that exploitative competition plays in designing the ecological habits of *Podarcis* is probably minute. Nevertheless, interspecific competition based on behavioral interference is now supported not only by field observations (Carretero *et al*. 1991), but also by behavioural experiments (Downes & Bauwens 2002).

CONCLUSION AND PERSPECTIVES

After reviewing all these aspects, it is evident that research on the Iberomaghrebian clade of *Podarcis* is still in progress. However, it is also obvious that, although not free from conflict, the evidence clearly differs from what is currently accepted by taxonomists. Table 2 shows a summary of the application of four species criteria to the different *Podarcis* forms. There is a clear consensus that the genus *Podarcis* (based on morphology and mtDNA) and its Iberomaghrebian clade (based on mtDNA) are well-supported monophyletic units. Moreover, although having part of its range in the Iberian Peninsula, *P. muralis* does not belong to the clade but, instead, evolved elsewhere and penetrated into Iberia during the Pleistocene (Harris & Arnold 1999). Regarding the members of the clade, for *P. bocagei* and *P. carbonelli*, results from morphology, mtDNA, proteins, hybridization pattern in the contact zones, behavioral tests and physiology coincide in supporting their specific distinction. However, *P. hispanica* s.l., as previously considered, did not meet these criteria. Instead, different lineages were artificially grouped under this binomial in a paraphyletic assemblage. Like *P. bocagei* and *P. carbonelli*, the lineages within can be characterized in terms of proteins and mtDNA, and all display genetic distances usually attributed to species. However, evidence for the remaining aspects is incomplete.

Lineage types 1 and 2 are morphologically distinct and show a parapatric distribution in Portugal, but it is not clear that the same occurs in Spain. *Podarcis* type 1 also displays behavioral and ecological segregation with the sympatric *P. bocagei*; the prezygotic mechanisms of reproductive isolation with *P.* type 2 in Central Spain are doubtful because specimens were not genetically assessed and real syntopy was not demonstrated. If reproductive isolation is the case, then lineages 1 and 2 both deserve the same status as *P. bocagei* and *P. carbonelli*.

Evidence for the other Iberian forms is even more deficient and almost exclusively relies on mtDNA. This is the case for *P. liolepis* and for the Sierra Nevada forms. The first corresponds to several morphotypes of Geniez (2001) and the second has not been morphologically characterized. The only exception is *P. hispanica* s.s., recently restricted to south-east Iberia (Geniez *et al.* 2007). As previously mentioned, this form is morphologically well defined, but specimens were assigned to it on the basis of expert criterion. Moreover, extensive introgression with adjacent forms (Sierra Nevada and *P. liolepis*) and discrepancy between mtDNA haplotypes and morphotypes has been found. In contrast, no behavioral tests have been carried out for any of these species. The insular forms *berlengensis* and *atrata* are morphologically distinct, but their characters are attributable to local adaptation. In fact, protein analyses do not distinguish *berlengensis* from *carbonelli*. The molecular evidence for *atrata* is insufficient, although it appears to be allied to *liolepis* and further study is required. For *P. vaucheri*, a satisfactory correspondence between morphology and mtDNA has been found in Morocco and south Iberia, but the form from Jebel Sirwah is not morphologically distinguishable

(Kalionzopoulou *et al*. 2007b). The Tunisian form is not morphologically characterized and the distribution patterns and number of entities in Algeria is unclear, although at least two of them are morphologically distinct.

Furthermore, the analyses of nuclear markers (Pinho *et al*. 2007a) add even more complexity to this complex panorama. Results indicate that most forms, which could otherwise be defined as species under the phylogenetic species concept, still share a degree of reproductive compatibility. Although most of the discordance between nDNA and mtDNA seems to result from ancient polymorphism, the magnitude of introgressive phenomena is unknown except between *P. bocagei* and *P. carbonelli*. If introgression between other species couples was extensive in terms of the geography and genes involved, conflicts between species defined under the phylogenetic and biological species concepts are expected. Nevertheless, such conflicts would affect not only the Iberomaghrebian clade, but also other *Podarcis* because even *P. muralis* is involved. Undoubtedly, more research efforts (involving genetic markers, none aprioristic analysis of phenotype and behavioural experiments) are needed to investigate contact zones.

Finally, a caveat is needed in terms of the degree of knowledge regarding these lizards. The last Iberian lineage was only described in 2006 and new populations in north-west Africa are still being discovered. Even the origin and deep phylogeny of the whole genus are still unresolved, despite the consistent efforts of phylogeneticists. The characterization of their phenotype is partial (morphology) or preliminary (physiology) and the determination of the mechanisms for reproductive isolation is very incomplete. More experimental work is needed, including artificial hybridization and tests for evidencing evoluntionay reinforcement of such mechanisms. Current taxonomy is clearly unsatisfactory, but should be updated at the rate of evidence accumulation. Meanwhile, *Podarcis* lizards will continue to constitute an attractive model organism for evolutionary studies.

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