The Genus Podarcis in the Iberian Peninsula:
A Discussion

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Abstract. In this paper a discussion of the systematics of the Iberian small lizards assigned to the genus *Podarcis* is presented. The existence of a common ancestor close to *Podarcis muralis* is suggested, being supported the Klemmer's model of glacial refuge (1957). It is pled that the Würm's glaciation was the major determinant of the selective pressures that led to the appearance of all the local forms. The constraints imposed by the last glaciation would have caused the geographical isolation of some populational nuclei. These, by means of the founder effect and in the face of different selective pressures, would have originated different genetic units. A mosaic distribution conditioned by a group of selective pressures as the nature of the substratum, altitude, temperature and salinity is suggested for the species of the genus *Podarcis*. Behaviour is presented as a determinant of these lizards' very high morphological variability. Finally, some approaches, which are believed to contribute to clarify this problem, are suggested.

Key words. *Podarcis*, Iberia, systematic, evolution, biodiversity.

Introduction

Three species of small lizards of the genus *Podarcis* are usually referred for Iberia: *Podarcis muralis*, *Podarcis bocagei* and *Podarcis hispanica*.

These three species correspond, in general, to the three following morphotypes:

morphotype 1: head depressed with convex supra ocular plates, longitudinal dark lines on the sub-maxillaries, frequent dark ventral pigmentation; usually associated to mountain habitats, may however be found in coastal and insular biotopes in the Cantabrian region.

morphotype 2: robust, relatively shorter snout, tall head, convex supra-ocular plates; generally associated to coastal and mountain rocky habitats; in humanised areas seems to prefer the soil.

morphotype 3: fragile, relatively sharper snout, flat head, plane supra-ocular plates; usually associated to sandy and plain biotopes; in humanised areas it seems to prefer stone walls; more heliophilous than the previous ones.

In the case of females and of juveniles and sub-adults these criteria become particularly difficult to apply.

To the "morphotype 1" is generally associated the specific restrictive *muralis*, to "morphotype 2", the restrictive *bocagei*, and to "morphotype 3", the restrictive *hispanica*.

History of the Systematic of the Genus

The distribution area of the family Lacertidae is

restricted to the Old World. Its members have diurnal habits and are well adapted to a wide range of habitats, from sandy and rocky coasts to high altitude mountains.

The fossil record of the lacertids is too fragmentary to provide any useful information on the phylogenetic relationships within the family. Therefore, all the speculation about this subject is based on the comparative study of the present forms.

It is Linnaeus who, in 1758, formalises the genus *Lacerta*, with the following characteristics:

corpus tetrapodum, caudatum mudum.
1758 *LACERTA* Linnaeus, Syst. Nat., Ed. 10, 1:200.

Later, in 1830, Wagler differentiates, within the genus *Lacerta*, the subgenus *Podarcis*:

nares in apice canthi rostralis intra suturas trium scutellorum supra primum scutum labiale; tempora Zootocae, reliqua Lacertae; collare. (Dentes palatini nulli.).
1830 *PODARCIS* Wagler, Nat. Syst. Amph., 1:155.

In 1973 Arnold promotes *Podarcis* to genus.

Since last century the systematic of the three Iberian species of small lizards presently included in the genus *Podarcis* has been matter of intense discussion, arousing the growing interest of several generations of naturalists.

Podarcis muralis is described in 1768 by Laurenti:

Seps muralis Laurenti, Synops. Rept.: **61**; Taf. 1, Fig. 4. Terra typica restricta (Mertens & L. Müller 1928): Wien (Mertens and Wermuth, 1960).

Podarcis hispanica is described in 1870 by Steindachner, as a variety of *Lacerta oxycephala*:

Lacerta oxycephala var. hispanica Steindachner, Sber. Akad. Wiss. Wien, math.-naturwiss. Kl., Abt. 1, **62**: 350; Taf. 1, Fig. 3-6. Terra typica restricta (Mertens & L. Müller 1928): Monte Agudo bei Murcia, Südost-Spanien (Mertens and Wermuth, 1960).

However, in 1886, Bedriaga considers it a subspecies of

Lacerta muralis:

Lacerta muralis subsp. *steindachneri* Bedriaga, Abh. senckenberg. naturf. Ges., Frankfurt am Main, **14**(3):256 [240]. - Terra typica restricta (*hoc loco*): Monte Agudo bei Murcia, Südost-Spanien (Mertens and Wermuth, 1960).

Podarcis bocagei is described in 1884 (1885?) by Seoane as a form of *Lacerta muralis*:

Lacerta muralis, Laur. var. Bocagei, nov. var. Comunísimo en toda Galicia. Esta forma, intermedia entre muralis fusca y muralis pytiusensis se diferencia de la primera, por el dorso que es de color verde, y de la segunda por que los flancos son pardos, además de los carácteres que espondré al describirla. Impongo á esta variedad el nombre de mi escelente amigo, el Sr. Barboza du Bocage, Director del Museo zoológico de Lisboa, y actualmente Ministro de Negocios extranjeros del vecino reino.
1884 *LACERTA MURALIS BOCAGEI* Seoane, Id. Lac. Sch.:18-19.

[*Lacerta muralis* var. *bocagei* Seoane, Identid. Lac. schreib.: 18. Terra typica restricta (Mertens & L. Müller 1928): Coruña, Spanien (Mertens and Wermuth, 1960).]

Méhely (1907, 1909 and 1910), working only with the small lacertids commonly named as "wall lizards" by the Anglo-Saxons, separates them into two groups: *Archaeolacertae* and *Neolacertae*.

Boulenger (1916) divides the Palearctic forms of the genus *Lacerta* into five sections or subgenera: *Lacerta s.str., Gallotia, Zooteca, Thetia* and *Podarcis*. In the later subgenus he includes all forms Méhely (*op. cit.*) had placed in both groups, Neo- and *Archaeolacertae*, not accepting that author's classification.

Later researches, however, brought some support to Méhely's division (*op. cit.*). Thus, Boulenger's subgenus *Podarcis* is divided by Mertens in 1921 into two subgenera - *Podarcis s. str.* and *Archaeolacertae*, which are equivalent to, respectively, the *Neo-* and *Archaeolacertae* previously considered.

Due to the high morphological similarity among the species of the subgenus *Podarcis*, it is difficult to establish taxonomic relationships among them. Several subdivi-

sions of the group have been suggested (v.g. Boulenger, 1920; Kopfstein and Wettstein, 1921; Klemmer, 1957), usually based on external morphological characteristics, mainly on colour patterns. However, these characters' diversity may result from polymorphism phenomena, frequently intimately related to the diversity of occupied habitats. Therefore, those may constitute bad indicators of phylogenetic relationships.

In 1957 Klemmer divides the subgenus *Podarcis* into three groups:

I. *muralis* group: *muralis, filfolensis, milensis, tiliguerta* and *wagleriana*;

II. *bocagei* (=*hispanica*) group: *bocagei* (=*hispanica*), *lilfordi, pityusensis* and *dugesii*;

III. *sicula* group: *sicula, erhardii, melisellensis* and *taurica*.

The interest of Klemmer's classification stays in the zoogeographic coherence of the three proposed groups: a western one (II), an eastern one (III) and a third one constituted by a single species which has an extensive circum-Mediterranean distribution area (*muralis*) and four Mediterranean insular forms (I).

Until the publication, by Arnold (1973), of an extensive revision on the Palearctic lacertids' phylogenetic relationships, were accepted as belonging to the subgenus *Podarcis* Wagler 1830 the following 13 species (see v.g. Mertens and Wermuth, 1960):

L. *dugesii* (Madeiran Archipelago)
L. *erahardii* (south of Balkan Peninsula and Greek islands)
L. *filfolensis* (Malta and adjacent islands)
L. *hispanica* (Iberia and NW Africa)
L. *lilfordi* (Balearic Islands)
L. *melisellensis* (Eastern Adriatic)
L. *milensis* (Mílos and adjacent islands)
L. *muralis* - sp. *typica* (South and Central Europe)
L. *pityusensis* (Ibiza and adjacent islands)
L. *sicula* (Italy and coasts of Tyrrhenian and Adriatic seas)
L. *taurica* (Southeast Europe)
L. *tiliguerta* (Corsica and Sardinia)
L. *wagleriana* (Sicily)

Arnold (1973), in an attempt to optimise a natural classification system for the lacertids included in the genera *Lacerta, Algyroides* and *Psammodromus*, elevates *Podarcis* to the generic level, based essentially on osteologic and hemipenis morphological characteristics.

In this genus were placed all species belonging to the previous subgenus *Podarcis*, except *Lacerta dugesii*, which is considered by Arnold (*op. cit.*) to be closer to the genus *Lacerta*, and included in the section named as part II, although he does not consider it very typical. The author also includes in this genus the species *Podarcis peloponnesiaca*, an endemic species of the south of Greece, very close to *Podarcis erhardii*, which Klemmer (1957) had rejected in his classification for having considered it of *incertae sedis*.

Let us now go backwards. In 1920 Boulenger disagrees with the initial proposal from Steindachner (1870), who considered *hispanica* as a variety of *Lacerta oxycephala*, therefore an *Archaeolacertae* in the sense of Méhely (1907). In fact Boulenger (*op. cit.*) considers *hispanica* to be a form closer to *liolepis*, a *muralis* variety. Accordingly, as was said before, Bedriaga (1886) had considered *hispanica* a subspecies of *Lacerta muralis*.

Twenty years later, Mertens and Muller (1940) include the *hispanica* form again in the subgenus *Archaeolacertae*.

Nevertheless, in 1959 Klemmer supports that there is no reason why *Lacerta hispanica* should not be included in the subgenus *Podarcis* and, as was seen before, in 1973 Arnold includes this species in the new genus *Podarcis*.

Still within this genus, Arnold (*op. cit.*) considers the pair *Podarcis hispanica* - *Podarcis muralis* to be the pair of species with more affinities within the group, due to the morphological relationship between the hemipenes, that suggests an intimate phylogenetic relationship and separates them from all other species of the genus. Still based in these two species hemipenian morphology, that approaches them to the genus *Lacerta*, this author suggests that the members of this pair are the most primitives of the genus *Podarcis*.

It is important to point out that Boulenger (1905, 1913, 1920) presented *Podarcis muralis* as an only species,

fragmented into a multitude of varieties, closely related among themselves, and consequently difficult to distinguish.

Let us consider now the form *bocagei*, described in 1884 (1885?) by Victor Lopez Seoane as a variety of *Lacerta muralis*, and accepted as such by Boulenger in posterior works (see v.g. Boulenger, 1905 and 1920).

Cyren (1934) was the first author to attribute it a specific level: *Lacerta bocagii* (sic).

Mertens and Muller (1940) agree with Cyren's classification (op. cit.), as well as Klemmer (1957).

Nonetheless, two years later, Klemmer (1959) states that there are no significant differences between Steindachner's *hispanica* form and Seoane's *bocagei*, and that the only character which would differentiate the two forms would be the Seoane's form green based coloration. Consequently, the highest level that should be attributed to this form would be the subspecific one, therefore *Lacerta hispanica bocagei*.

In 1973, in the already mentioned work by Arnold, this author accepts Klemmer's opinion (1959), not mentioning *Podarcis bocagei* as a good species. Though, in the same work, Arnold refers to a Klemmer's personal communication that indicates that *Podarcis hispanica* may not be simply just one species.

For Guillaume (1976) and Guillaume *et al.* (1976) *Podarcis muralis* and *Podarcis hispanica* are good species, in the face of biochemical criteria.

In fact, Arnold and Burton in 1978 already recognise specific status to *Podarcis bocagei*.

Consequently, *Podarcis muralis* - *Podarcis hispanica* - *Podarcis bocagei* become the triad of largest affinity within the genus *Podarcis*. These species have been considered good species thereafter, and will be referred to from now on in this work as *muralis complex*.

Recently, some authors have described several forms of these three species, to which subspecific status has been attributed (see v.g. Perez-Mellado, 1981; Vicente, 1985; Guillaume, 1987).

Geographical Distribution

Podarcis muralis - European circum-Mediterranean distribution, limited at north by the French and Belgian coasts of the English Channel, to Rhine's mouth. From there, this river, jointly with its tributary Main, become an efficient barrier. Thus, the most northern populations are found in the Bohemia forest, in Sudety, Beskids and Carpathians, to the Black Sea Romanian coast. In the south, this species distribution area extends as far as the Cantabrian system, in Iberia, having from the Pyrenean Mountains to the Black Sea, the Mediterranean coast of continental Europe as border.

Podarcis hispanica - Iberia and Southwest France; Northwest Africa.

Podarcis bocagei - Northwest Iberia, limited at south by the Central System mountains; possibly, some isolated nuclei south of Tagus valley.

Biogeographic Evolution

In Iberia there are not known any fossil records that could be related to the small lizards of *muralis complex*. Consequently, only in the face of the knowledge on the geomorphological and climatic evolution of the Mediterranean region, can their distribution and diversity patterns in Iberia be discussed, and, in a more general way, of the small lizards of the genus *Podarcis* within their overall extensive distribution area.

The geographical identity of Iberia, that results from the presence of very well defined natural barriers, turns the analysis of the evolution of its fauna and flora communities into something extremely interesting. In fact, it can be considered that for the Iberian communities, the rising of natural barriers has played a fundamental role on their evolution.

Iberia constitutes, at least since the Cretaceous, an independent tectonic microplate (Agueda *et al.*, 1977). In Eocene and Oligocene, were already present in Europe many of the now existing families of amphibians and reptiles. Nevertheless, before Eocene's end, there must have existed higher affinity between Iberian and French faunas, due to the fact that the Pyrenees might have not constituted such an important barrier (Crusafont,

1958). For most authors, the most important phenomena in order to explain the Iberian species present distribution, would have taken place in the end of Tertiary, between Oligocene and Pliocene, and during Quaternary (Escriva, 1987).

Thus, all data available points to the *muralis complex* history having taken place mainly after Palaeocene, or, with high probability, in more recent times. Therefore, it is convenient to refer to some important data related to the geomorphological and climatic evolution of the Mediterranean region, in particular of the Iberia.

Geomorphology

According to Salvador (1974), during Eocene the Mediterranean would have been connected to the Atlantic through the Ebro valley and Pyrenean region. Nonetheless, this fact appears not to be completely demonstrated.

Between Eocene and Oligocene would have occurred Alpine movements, inducing a new Pyrenean elevation and, during Miocene, the connection between Mediterranean and Atlantic would have been established, through the Strait of Gibraltar.

At Miocene's end the Iberian Peninsula and the African continent would have been connected again, through the Betica-Ar-Rif mountain range. Only in Pliocene's beginning the separation would have become definitive.

The extension of emersed lands would have been larger during the glaciation peaks than today, in result of the lower sea level, which would have been between 120 and 150 m below the present values (Brown and Gibson, 1983).

Climate

In the beginning of Tertiary the temperature would have been, all over Europe, higher than today. Afterwards a gradual lowering would have taken place and, in Pliocene, the temperature should have been similar to the present ones (Crespo, 1979).

In what refers to humidity, Middle Eocene and Early Miocene should have been humid and Late Eocene, Early Oligocene and Late Miocene should have been arid (Nairn, 1961).

The knowledge of the Quaternary glaciations is fundamental to the understanding of the Palearctic faunas' recent history. The most referred to is the Würm's glaciation. There is unanimity on the fact that the most severe climatic conditions would have taken place during the last glaciation (between 25000 and 13000 BP) (Blondel, 1986). These conditions would have been such that south of the glacial ice cap, which extended as far as Thames, most of Middle Europe would have been covered by open areas and steppes, with rare woody heliophilous (*Pinus, Juniperus, Ephedra*).

Thus, in Quaternary the temperature would have strongly lowered. It is believed that during the last glaciation temperatures were 3 to 7° C lower than today. Precipitation levels would also have been relatively lower - 20 to 60% lower than the present ones (Crespo, 1979).

However, Cheylan (1981), based in the analysis of a multitude of palaeoclimatic indicators of France's Quaternary, concludes that the Würmian coolings should have been more moderate than was thought, or that, at least, during the glaciations peaks some mild climate regional focuses, of the Mediterranean type, would have remained.

In fact, during Würm's glaciation, the Mediterranean region would not have been evenly cold and dry. Recently, the existence of numerous episodes of temperate forest was demonstrated by Beaulieu and Reille (1984). Deciduous forests and associated faunas would have taken refuge at medium altitude, on the mountains that contour the present Mediterranean area and in lower coastal areas today immersed, as well as at river valleys. However, these refuges would still have been spatially limited and relatively few. The existence in all times of Mediterranean vegetation foci, of the maquis type, already suggested by Pons (1981), is also confirmed.

Evolution of *muralis complex*

Given the absence of fossil records assigned to the genus *Podarcis*, almost nothing is known on its evolutionary history. Thus, all the following discussed hypotheses are to be faced as mere speculation.

Therefore, being speculative hypotheses, caution is needed as far as their logical value is concerned. Usually, speculation on evolutionary processes, given the lack of empirical data, is based in the development of mediate inferences, many times formal sequences of the polysyllogistic type, in which partial conclusions become premises of subsequent inferences. It is important to notice that an inference may be formally correct without the premises being necessarily true; obviously, the fact of an inference being correct does not guarantee the truth of the conclusion. Nevertheless, it is to the opposite type of reasoning that the evolutionary theorising is more vulnerable: the errors of the paralogistic type constitute the biggest danger for the evolutionary speculation.

In this discussion we will consider the three species of *muralis complex* and *Podarcis hispanica vaucheri*, which is, according to some authors, a key element on the Iberian *Podarcis* speciation (*see* v.g. Vives-Balmaña, 1980).

In order to briefly discuss some ideas on the evolution of the species of *muralis complex*, it is important to start from the statement of some premises, which, in this context, will assume the logical value of postulates (despite the fact that some of them are discussible):

1. The three Iberian species of *muralis complex* are good species;

2. There is a strong phylogenetic affinity among the three species of *muralis complex*;

3. The homogeneity and continuity of the genus *Podarcis* suggest a recent origin or expansion (Arnold, 1973);

4. About 30% of the Iberian herpetofauna is endemic, fact that can be attributable to two basic reasons:

   a) Pyreneans are in fact an effective barrier, or,

   b) independently of the existence of effective geographical barriers, the ecological specific conditions of Iberia would be enough to induce speciation processes on the local faunas;

   [4 a) and 4 b) are inclusive disjunct propositions]

5. *Podarcis muralis* exists in Europe but not in Africa;

6. *Podarcis bocagei* is endemic;

7. *Podarcis hispanica* exists in Iberia and North Africa;

8. *Podarcis muralis* is a cryophilic and hygrophilous species, and occupies Pyrenean and pre-Pyrenean areas;

9. *Podarcis bocagei* is a frequently a cryophilic and hygrophilous species, usually occupying habitats similar to the ones occupied by *Podarcis muralis*;

10. *Podarcis hispanica* is a typical Mediterranean species, preferring warm and dry climates, although having Pyrenean penetrations in sunny and dry enclaves.

From a formal point of view there are three possible evolutionary proposals:

1. the common ancestor of the present species of *muralis complex* is *Podarcis muralis* or a close form;

2. the common ancestor of the present species of *muralis complex* is *Podarcis bocagei* or a close form;

3. the common ancestor of the present species of *muralis complex* is *Podarcis hispanica* or a close form;

From a logical point of view, these proposals are exclusive disjunct propositions.

Due to the fact that the family Lacertidae is restricted to the Old World, the two following hypotheses (mutually exclusive) referring to the geographical origin of the species of *muralis complex* can be accepted:

1. The *mother-form* would be European;

2. The *mother-form* would be North African.

Let us discuss these two hypotheses on the geographical origin of the *mother-form* of the three species.

If we admit the hypothesis of it being European, then, given its circum-Mediterranean distribution, it should be closer to *Podarcis muralis*. This leads to the first evolutive proposal. Later, *Podarcis hispanica* (or an ancestor) would have passed to the north of Africa, where it would have differentiated into *Podarcis hispanica vaucheri*.

If, on the contrary, the *mother-form* is North African, then, the same reason that previously led to considering it as closer to *Podarcis muralis*, leads now to supposing it as closer to *Podarcis hispanica*. This supports the suggestion that *Podarcis hispanica vaucheri* (or an ancestor) would have invaded the Iberian Peninsula, where something similar to the evolutionary proposal n° 3 could have happened.

Until now we have not considered the hypothesis of an Iberian origin for this group, which, in a merely formal perspective, is equally valid.

The scenery could have been as follows: considering that *Podarcis muralis* and *Podarcis bocagei* seem to constitute the morphologically most coherent pair, from the geographical point of view, *Podarcis muralis* (or an ancestor closer to *Podarcis bocagei*) would have occupied the mountain ranges of the north-east of Iberian Peninsula, penetrating, through Pyrenean Mountains, into the south of France and occupying the whole Mediterranean basin, speciating in the European Mediterranean peninsulas. Towards North Africa, *Podarcis bocagei* or an ancestor, would have crossed the Betica-Ar-Rif Massif during the Pliocene transgression.

However, Crespo (1979) suggests that whole of the species which are common to Iberian Peninsula and Europe had origin out of the Peninsula, pleading that there is nothing that indicates that the Peninsula might have been the centre of origin for any of them. Our agreement with Crespo's suggestion (*op. cit.*) leads us to reject the evolutionary proposal n° 2.

So far, two fundamental questions for the understanding of the phenomena that have been in the origin of the three species of *muralis complex* have been approached:

I. Due to geographical isolation, or to particular ecological conditions, would have existed (and still exist) in the Iberian Peninsula constraints favourable to the occurrence of speciation processes?

II. Is it European or North African the origin of the species of *muralis complex*?

The question I, rose in the premises 4a) and 4b) has implicit factual justification: in fact, 30% of herpetofauna endemisms point in the way of an affirmative answer.

It is also important to notice that the high geotopographical and climatic diversity of the Mediterranean region should have allowed, even during the glaciations' hardest periods, the presence of a mosaic of highly varied plant formations, assuring the local survival of the Mediterranean plant taxa and associations (Blondel, 1986).

During the peak of Würm's glaciation, at Iberia, from Cape Finisterre to the Gulf of Cadiz and Gibraltar there would have existed an extensive area of temperate forest, and the Mediterranean coast of the Peninsula would have been rich in foci of Mediterranean vegetation, as well as Northwest Africa (Flint, 1971; Brown and Gibson, 1983).

Therefore, the proven existence of Mediterranean refuges during Quaternary glaciations should have assured, during each glaciation, the survival of floras and faunas whose distributions were interrupted due to the geographical configuration of the region. The three large peninsulas, Iberian, Ligurian and Balkan, as the Mediterranean large islands, would have constituted disjunct biogeographic entities, within which differentiation would have been possible (Blondel, 1986).

In what concerns the North African or European origin of the genus *Podarcis*, it is important to consider that, although the origin of Squamata would be Permo-Triassic (McFarland et al., 1979) and the "lacertid-like" group, which includes the present teids and lacertids, would have origin in Europe in Jurassic's end, only in the European Palaeocene is found a genus similar

to *Lacerta* (*Plesiolacerta*), appearing *Eolacerta* only in Middle Eocene (Estes, 1978).

It is important to point out that there are not African elements in the Iberian fauna before Miocene (Savage, 1967; Crespo, 1979). This is probably due to the fact that the last previous contacts between Iberian Peninsula and North Africa had been at the end of Jurassic (Glen, 1975).

However, Arnold (1973) points out to the similarity between *Podarcis hispanica* and North African forms of *Lacerta* II, which suggests that *Podarcis hispanica* may be one of the most primitive forms of the genus *Podarcis*. This suggestion of Arnold (*op. cit.*) would lead Vives-Balmaña (1982) to face the hypothesis of a North African origin to the Iberian *Podarcis*, or at least to *Podarcis hispanica*.

This thesis is reinforced by the fact that in all Mediterranean islands, representatives of the genus *Podarcis* are present. This fact may suggest that the initial expansion took place during the regression of Miocene's beginning, which had been the last possibility of connection between the continent and the Mediterranean islands.

Accordingly, *Podarcis hispanica* differentiation, or of an ancestor, would have taken place in NW Africa before the Pliocene transgression, that separated the two continents definitively; it should therefore be attributed, at least, a Miocene origin. European expansion should then have taken place during the Miocene regression, continuing during Pliocene, evolving from populations which would have been total or partially isolated during the transgression of the beginning of this period.

Thus, to accept this hypothesis is to admit that *Podarcis hispanica*, differentiated in NW Africa, would have occupied the Iberian Peninsula during the Pliocene transgression and, during Quaternary, it would have differentiated into *Podarcis bocagei* (possibly in some refuges in Galician coastal areas, which would have allowed its survival during the glaciations peaks). *Podarcis muralis* would also have resulted from the pre-Pyrenean and Pyrenean differentiation of *Podarcis hispanica*, having occupied during Quaternary interglacial periods the whole circum-Mediterranean Europe and differentiating, during the glaciations peaks, in the refuges where the mild climatic conditions allowed its survival (evolu-

tionary proposal nº 3).

However, the great affinity among the three species which constitute *muralis complex* suggests that the differentiation within Iberian Peninsula was more recent than the differentiation in Central Europe, fact that leads to a fourth proposal, also compatible with the *Podarcis hispanica* North African origin, although, in this case, independent of the group *muralis/bocagei*: a common ancestor would have originated in Europe *Podarcis muralis* and in North Africa *Podarcis hispanica*. *Podarcis bocagei* would have resulted from the differentiation of *Podarcis muralis*, with European origin, in Galician refuges during the Quaternary glaciation peaks.

Nevertheless, as Vives-Balmaña (1982) states, the specific differentiation in Europe (and even in the Iberian Peninsula) is higher than between the two sides of Mediterranean, fact that suggests that the European communities are older.

On the other hand, the differences among the three species of *muralis complex* are so little that suggest a very strong affinity among them.

Moreover, it is important to notice that during Early and Middle Miocene the differences, as far as fauna is concerned, between Iberia and North Africa are still quite accentuated, fact that may suggest the lack of a direct relationship between both areas (Hoffstetter, 1961; Hecht *et al.*, 1961). Also, according to Crespo (1979), during Tertiary the passage of North African species into Iberia could only have taken place during a brief period, in Pliocene, before the opening of the Strait of Gibraltar.

Therefore, the hypothesis of European origin of *muralis complex* may be more viable. An expansion would have taken place, as was said, in Miocene's beginning, which is the only way of explaining the Mediterranean insular communities. This expansion would have been of an ancestor form probably much close to *Podarcis muralis*. However, the evolution of the genus would have happened, as pleaded by Klemmer (1957), according to a model of glacial refuge: an European common stem (*Podarcis muralis*) and three groups of species in the Mediterranean peninsular refuges (*Podarcis hispanica* in Iberia, *Podarcis sicula* in Italy and *Podarcis taurica* in Greece and Balkans). Thus,

according to Klemmer (*op. cit.*) the evolution would have taken place in Pleistocene, by isolation in Mediterranean refuges of the *Podarcis muralis* common stem, having occasionally taken place post-glacial expansion of the differentiated forms, to the sympatry with the original form.

It is important to point out that the whole development of these ideas on the evolution of the *muralis complex* is merely a deductive exercise. It is known that evolutionary and taxonomic problems do not always adjust to deductive type reasoning. Thus, the value of this chapter is essentially the value of a model. Formally it does not matter if it is true or false. That question is not relevant. What is important is its capability to generate hypotheses, and it is in that sense that it may or may not be considered operational.

Concluding remarks

Podarcis muralis or an ancestor would have occupied Iberia during the Miocene expansion, having crossed the Betica-Ar-Rif Massif during the Pliocene transgression. Later, during Quaternary glaciations peaks, in refuges with mild climatic conditions, it would have given origin to *Podarcis hispanica vaucheri* in NW Africa, *Podarcis hispanica hispanica* in the south of Iberia and *Podarcis bocagei* in Galicia's coast.

Thus, the glaciations should have influenced the specific and subspecific dispersion, fragmentation and differentiation.

Klemmer's thesis (1957) also agrees with Crespo's proposal (1979) of a fairly generalised invasion of Iberia by European forms, in Middle or Late Miocene.

This hypothesis leads to reconsidering the taxonomic status of *Podarcis hispanica vaucheri*. Due to this form's differentiation being contemporary to *Podarcis hispanica hispanica* and *Podarcis bocagei* differentiation, it should be attributed a specific status, therefore *Podarcis vaucheri*.

The higher morphological similarity among *Podarcis hispanica* and *Podarcis vaucheri* possibly results from the fact that both species are plain morphotypes, subject to very similar selective pressures. *Podarcis bocagei*

(morphologically closer to *Podarcis muralis*) should correspond to a mountain morphotype as *Podarcis muralis*, but subject to predominantly Atlantic climatic conditions.

The proposal of contemporary speciation which results from this model based in the thesis of glacial refuge (*sensu* Klemmer, 1957) leads to reconsidering the taxonomic status of all the forms of *muralis complex*.

If we opt for a phenetic classification model, the current taxonomic structure is formally correct, not being needed any revision.

However, in a phylogenetic perspective in which the classification is expected to reflect the evolutionary history of the group, the attribution of a subspecific status must strictly follow the evolutionary history of the entities that are object of that classification, therefore the temporal sequence. In this context, phenotypic similarity and dissimilarity may only be interpreted as convergence or divergence phenomena, or as result of different speciation rates, product of different "genetic environments" subject to different selective pressures, that is to say, as evolutionary heterochronies.

Accordingly, if one opts for a phylogenetic classification based on Klemmer's model of glacial refuge (1957), that is to say, if the speciation processes were simultaneous (if the great selective pressures which led to the Iberian *Podarcis* differentiation were the glacial isolation, therefore simultaneous), then the current subspecific status are formally incorrect: from a formal point of view (and also biological!), if subspecies exist in Iberia, these will always be phylogenetically closer to *Podarcis muralis* than to *Podarcis bocagei* or *Podarcis hispanica*.

Consequently, for example *Podarcis hispanica robusta*, *Podarcis bocagei carbonelli* or *Podarcis bocagei berlengensis*, or they are good species, therefore *Podarcis robusta*, *Podarcis carbonelli* and *Podarcis berlengensis*, or they are forms phylogenetically closer to *Podarcis muralis*, therefore *Podarcis muralis robusta*, *Podarcis muralis carbonelli* and *Podarcis muralis berlengensis*, Pleistocene forms subject to different selective pressures.

For example, *Podarcis bocagei berlengensis* ancestor would have occupied the island of Berlenga during

Quaternary glaciation peaks, due to the marine regression that would then have happened. Thus, *Podarcis bocagei berlengensis* would be an insular form of *Podarcis muralis* or of a very close form, subject to the selective pressures of a typically Atlantic climate.

Moreover, this model, if accepted, forces all studies that take it into account to use *Podarcis muralis* as reference and not any other species.

Perhaps the biggest challenge and the most interesting conclusion of the model here developed are the opportunity and legitimacy of Boulenger's classifications (1905, 1913, 1916, and 1920).

Perspectives

As was said before, in general *Podarcis muralis* is considered to be the form phylogenetically closer to the *mother-form*. All other forms with more restricted distribution are considered to be populations of recent speciation.

However, observation leads us to believe that, in Iberia, the geographical separation of the possible taxonomic entities is much more complex, the existing proposals appearing to be too simplistic.

It seems perhaps more likely that, if in particular the two taxonomic entities *Podarcis bocagei* and *Podarcis hispanica* are confirmed, these have a mosaic distribution conditioned by certain selective pressures which would be decisive: substratum nature, altitude, temperature and salinity.

Finally, it is also important to refer to behaviour as a very important factor to phenotypic variability of this group of species. The mobility of the small lizards of the genus *Podarcis* is extremely low. The recapture of the same animals in successive years exactly in the same places is proof of that. That strong attachment to the substratum should largely limit gene transference, even at very short distances, and allows the expression of a great diversity of morphotypes in relatively not extensive geographical areas. Even the existence of sexual "satellites" which constitute genetic bridges among reproductive nuclei does not seem to be very effective in determining a "populational genetic unit".

The model presented in the conclusions needs to be tested. Therefore it is fundamental:

a) A deep morphological study, in order to determine and to describe the existing morphotypes;

b) an evaluation of the biodiversity levels of the populations of these animals and of their determinants, at morphological and genetic levels;

c) a morphological analysis considering two types of characters, adaptive and non-adaptive, in order to distinguish eco-morphs from valid taxonomic entities;

d) an intensive geographical covering, aiming at accurately determining the distribution of each of the identified morphotypes;

e) to verify if the western small lizards of the genus *Podarcis* constitute a specific taxonomic unit, or if the taxonomic value of the current species is legitimate;

f) to verify, in case that isolation is not confirmed, if the western small lizards form a specific taxonomic unit with the presumably Cantabrian *Podarcis muralis*;

g) to investigate, independently of the number of specific units detected, the existence of an infra-specific mosaic structure, with the possibility of characterising the units that compose that mosaic (*Boulenger's hypothesis*);

h) to develop ethological studies in order to determine to what extent acts the behaviour, in this group, as a variable that inhibits panmixia;

i) to develop a micro-ecological analysis in a multidimensional perspective, relating micro-habitat choice with morphotype;

j) finally, and related to the previous point, to determine the selective pressures which are eventually related to the process of geographical identity.

By means of crossing these ten approaches, it is possible to contribute to clarify the problem discussed in the present work.

References

Agueda, J., Anguita, F.,Araña, V., Lopez, J. and Sanchez de la Torre, L. (1977): Geologia. Ed. Rueda, Madrid.

Arnold, E.N. and Burton, J.A. (1978): A field guide to the reptiles and amphibians of Britain and Europe. Collins, London.

Arnold, E.N. (1973): Relationships of the paleartic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammodromus*. Bull.Brit.Mus.Zool., 25: 291-366.

Beaulieu, J.L. and Reille, M. (1984): A long upper Pleistocene pollen record from Les Echets, near Lyon, France.Boreas, 13: 111-132.

Bedriaga, J. von (1886): Beiträge zur Kenntnis der Lacertiden-Familie. Abhandlungen der Senckenbergischen natur-forschenden Gesellschaft. Frankfurt a. M., 14: 17-443.

Blondel, J. (1986): Biogéographie Évolutive. Masson, Paris.

Boulenger, G.A. (1905): A contribution to our knowledge of the varieties of the wall lizard (*Lacerta muralis*). Trans.Zool.Soc.London, 17: 351-436.

Boulenger, G.A. (1913): Second Contribution to our knowledge of the varieties of the wall lizard (*Lacerta muralis*). Trans.Zool.Soc.London, 20(3): 135-231.

Boulenger, G.A. (1916): On the lizards allied to *Lacerta muralis*, with an account of *Lacerta agilis* and *Lacerta parva*. Trans.Zool.Soc.London, 21: 1-104.

Boulenger, G.A. (1920): Monograph of the lacertidae. Vol. 1. London (Trustees Brit. Mus.), 352S.

Brown, J.H. and Gibson, A.C. (1983): Biogeography. Mosby, Saint-Louis.

Cheylan, M. (1981): Biologie et 'Ecologie de la Tortue d'Hermann *Testudo hermanni* Gmelin. Thèse. EPHE, Montpellier.

Crespo, E.G. (1979): Contribuição para o conhecimento da biologia dos *Alytes* ibéricos, *Alytes obstetricans boscai* Lataste, 1879 e *Alytes cisternasii* Bosca, 1879 (Amphibia-Salientia): a problemática da especiação de *Alytes cisternasii*. Tese. Universidade de Lisboa. Faculdade de Ciências.

Crusafont, M. (1958): Endemism and pareuropeism in Spain fossil mammalian faunas, with special regard to the Miocene. Comment.Biol., 18: 1-30.

Cyren, O. (1934): Zur Kenntnis der Lacertiden der Iberischen Halbinsel und Makaronesiens. Goteborgs Kgl. Vetensk., vitterh.Samh.Handl. (B), 4 (1): 1-64.

Escriva, L.J. (1987): La guia de INCAFO de los anfibios y reptiles de la Peninsula Iberica, Islas Baleares y Canarias. INCAFO, Madrid.

Estes, R. (1982): The fossil record and early distribution of lizards. Advances in Herpetology and Evolutionary Biology: 365-398.

Flint, R.F. (1971): Glacial and Quaternary Geology. John Wiley & Sons, New York.

Glen, W. (1975): Continental Drift and Plate Tectonics. C. E. Merril, Columbus, Ohio.

Guillaume, C.P. (1976): Étude biomètrique des espèces *Lacerta hispanica* Steindachner, 1870 et *Lacerta muralis* Laurenti, 1768. Bull.Soc.Zool.Fr., 101(3): 489-502.

Guillaume, C.P. (1987): Les petits lacertides du Bassin Mediterranean Occidental (Genera *Podarcis* et *Archaeolacerta* essenciellement): sur quelques problèmes d'ordre systematique et biogeographique. Thèse. Université des Sciences et Techniques du Languedoc, Montpellier. 474 pp.

Guillaume, C.P., Pasteur, N. and Bons, J. (1976): Distinction par électrophorèse sur gel d'amidon des espèces de lézards *Lacerta muralis* Laurenti 1768 et *Lacerta hispanica* Steindachner 1870 dans des populations sympatriques d'Espagne et du Languedoc-Roussillon. C.R.Acad.Sci.Paris,Sér. D, 282: 285-288.

Hecht, M.K., Hoffstetter, R., and Vergnaud, C. (1961): Le gisement de Vertebrés Miocenes de Beni Mellal - Amphibiens. Not.Mém.Serv.Géol.Maroc, 155: 103.

Hoffstetter, R. (1961): Le gisement de Vertebrés de Beni Mellal (Maroc). Squamates. Not.Mém.Serv.Géol.Maroc, 155: 95-101.

Klemmer, K. (1957): Untersuchungen zur Osteologie und Taxionomie der europaischen Mauereidechsen. Abh.Senckenb.Naturf.Ges., 496: 1-56.

Klemmer, K. (1959): Systematishe Stellung und Rassengliederung der spanischen Mauereidechse, *Lacerta hispanica*. Senck.Biol., 40(5-6): 245-250.

Kopfstein, F. and Wettstein, O. (1921): Reptilien und Amphibien aus Albanien. Verth.Zool.Bot.Ges., 70: 387-457.

Laurenti, J.N. (1768): Synopsin Reptilium. Typis Joan. Thomæ nob. de Trattnern, cæs. reg. aulæ typographi, et bibliop., Vienna.

Linnaeus, K. von (1758): Systema Naturae. 10th ed. Laurentii Salvii, Stockholm.

MacFarland, W.N., Pough, F.H., Cade, T.J. and Heiser, J.B. (1979): Vertebrate Life. Macmillan, New York.

Mehely, L. von (1907): Archaeo und Neolacerten (Erwiderung an die Herren G. A. Boulenger, F. R. S. und Dr. F. Verner). Ann.Mus.Nat.Hung., 5: 469-493.

Mehely, L. von (1909): Materialen zur einer Systematik und phylogenie de *muralis* ahnlichen Lacerten. Ann.Mus.Nat.Hung., 7: 409-621.

Mehely, L. von (1910): Weitere Beitrage zur Kenntnis der Archaeo-und Neolacerten. Ann.Mus.Nat.Hung., 8: 217-230.

Mertens, R. (1921): Zur Kenntnis der Reptilienfauna von Malta. Zool.Anz. 53:236-240.

Mertens, R. and Müller, L. (1928): Liste der Amphibien und Reptilien Europas, Abhandlungen der Senckenbergischen naturforschenden Gesellschaft. Frankfurt a. M. 41(1): 1-62.

Mertens, R. and Müller, L. (1940): Die Amphibien und Reptilien Europas. Abhandlungen der Senckenbergischen natur-forschenden Gesellschaft. Frankfurt a. M. 451: 1-56.

Mertens, R. and Wermuth, H. (1960): Die Amphibien und Reptilien Europas. (Dritte Liste, nach dem Stand vom 1, Januar 1960). Verlag Waldemar Kramer, Frankfurt am Main.

Nairn, A.E. (1961): Descriptive Palaeoclimatology. Interscience Publish. Inc., New York.

Perez-Mellado, V. (1981): Nuevos datos sobre la sistematica y distribución de Podarcis bocagei (Seoane, 1884) (Sauria, Lacertidae) en la Peninsula Iberica. Amphibia-Reptilia, 2 (2): 259-265.

Pons, A. (1981): The History of Mediterranean Shrublands. In: F. di Castri, Goodall and Specht (eds). Maquis and Chaparrals, col. Ecosystems of the World. Elsevier, Amsterdam, p. 131-138.

Salvador, A. (1974): Guia de los Anfibios y Reptiles Españoles. ICONA ed., Madrid.

Savage, R.J.G. (1967): Early Miocene Mammal Faunas of the Tethyan Region. In: C. G. Adams and D. V. Ager (eds), Aspects of Tethyan Biogeography. Systematics Association, London: 247-282.

Seoane, V.L. (1884): Identidad de *Lacerta schreiberi* (Bedriaga) y *Lacerta viridis* var. *gadovii* (Boulenger) en Investigaciones Herpetologicas de Galicia. La Coruña. 19p.

Steindachner, F. (1870): Hepetologisch notizen: Uber einige neue oder seltene Reptilian des Wiener Museums. Sber.Akad.Wiss.Wien, 62: 336-350.

Vicente, L.A. (1985): Description d'une nouvelle sous-espèce de *Podarcis bocagei* (Seoane, 1888) (Sauria, Lacertidae) de l' île de Berlenga: *Podarcis bocagei berlengensis*. Bull.Mus.Natn.Hist.Nat.Paris, (4) 7, (A) 1: 267-274.

Vives-Balmaña, M.B. (1980): *Podarcis* Wagler 1830 en Iberie Orientale et l''evolution du groupe en Méditérranée Occidentale. Journées Étud.System.et Biogeogr.Médit. Cagliari: 187-188.

Vives-Balmaña, M.B. (1982): El genero *Podarcis* Wagler 1830 en el NE ibérico: diferenciación especifica y distribución geográfica. P.Cent.pir.Biol.exp., 13: 77-82.

Wagler, J. (1830): Naturliches System der Amphibien mit voranghender Classification der Saugthiere und Vogel. J. G. Cottäschen Buchhandlung, Munchen.

Note. Due to grammatical reasons of genera concordance, the correct latin names for the taxa *Podarcis hispanica*, *Podarcis tiliguerta*, *Podarcis wagleriana*, *Podarcis sicula*, *Podarcis taurica*, *Podarcis peloponnesiaca* and *Podarcis hispanica robusta* should be, respectively, *Podarcis hispanicus*, *Podarcis tiliguertus*, *Podarcis wag!erianus*, *Podarcis siculus*, *Podarcis tauricus*, *Podarcis peloponnesiacus* and *Podarcis hispanicus robustus*.