

*Valakos, Böhme, Pérez - Mellado, Maragou (eds), (1993)*  
*Lacertids of the Mediterranean region, pp. 17-33*

## Chapter 2

# Zoogeography of the lacertid lizards of the western Mediterranean basin

W. Böhme<sup>1</sup> and C. Corti<sup>2</sup>

<sup>1</sup>*Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 150-164, D-53113 Bonn 1, Germany;*

<sup>2</sup>*Museo Zoologico "La Specola", Università di Firenze, Via Romana 17, I-50125 Firenze, Italy*

### Introduction

The objective of this paper is to review the taxonomic groups resp. phylogenetic lineages of lacertid lizards that inhabit the western Mediterranean basin. This review relates their taxonomic and phylogenetic relationships with their geological age as calculated from immunological data and with the evidence from paleogeography. Although the Mediterranean Lacertidae have since long been considered to be of particular zoogeographic importance, (e.g. Mertens, 1916; 1934; Wettstein in Kammerer, 1926, but also very recently: Oosterbroek and Arntzen, 1992), their phylogeny is far from being resolved. There are two modern approaches: 1. a comprehensive paper summarizing earlier research by Arnold (1989) "towards a phylogeny and biogeography of the Lacertidae: relationships within an Old World family derived from

morphology", and 2. a series of chemosystematic, immunological papers by W. Mayer and his coworkers (Mayer and Tiedemann, 1982; Lutz and Mayer, 1984; Lutz, Bischoff and Mayer, 1986; Mayer and Lutz, 1989; 1990). But whereas the approach by Arnold (1989) constructs phylogenetic trees in relative hierarchical successions and not in absolute time spans, the approach by Mayer (op. cit) uses the molecular clock hypothesis (Maxson *et al.*, 1975) for calculating the geological age from the immunological distances found. Therefore only this second approach can be used as a test of paleogeographical hypotheses, or can correspondingly be tested by paleogeographical data. This is why in this paper we mostly rely on the phylogenetic concepts of Mayer (op. cit., see also Fig. 1).

#### Study area and concerned groups

From pragmatic reasons, the western Mediterranean basin is defined here as being delimited by a line following the Adriatic coast of Italy, passing Sicily, Malta and the Galita archipelago to Tunis and following the coast of Tunisia, Algeria and Morocco to the strait of Gibraltar, and then the coastline of Spain and France to Italy. This area is inhabited by the following species groups of lacertids (the taxonomic rank of which - genus/subgenus - is still under debate): *Acanthodactylus*, *Algyroides*, *Archaeolacerta*, *Lacerta* s.str., *Podarcis*, *Psammodromus*, *Teira* and *Timon*. Their distribution is documented in detail in Böhme (1981; 1984; 1986). Although not all of these taxa have been accepted as formal genera, their monophyly has been demonstrated in most cases by morphological as well as biochemical characters (Böhme, 1971; Arnold, 1973; 1983; 1986; 1989; Engelmann and Schäffner, 1981; Mayer and Tiedemann, 1982; Lutz and Mayer, 1984; Lutz *et al.*, 1986; Mayer and Lutz, 1989; 1990). Thus, the most important prerequisite for any biogeographical conclusion, i.e. a sound taxonomic basis, seems relatively well established in this lizard family.

The geological age of these different lacertid lineages can be estimated by immunological techniques (see Lutz and Mayer; Lutz *et al.*; Mayer and Lutz op. cit. as above), their phylogenetic interrelationships, however, remain largely unresolved (see e.g. Arnold, 1989). Only in some instances, sister group relationships have been evaluated, in some cases infragroup relations are known (see below and Fig. 1).

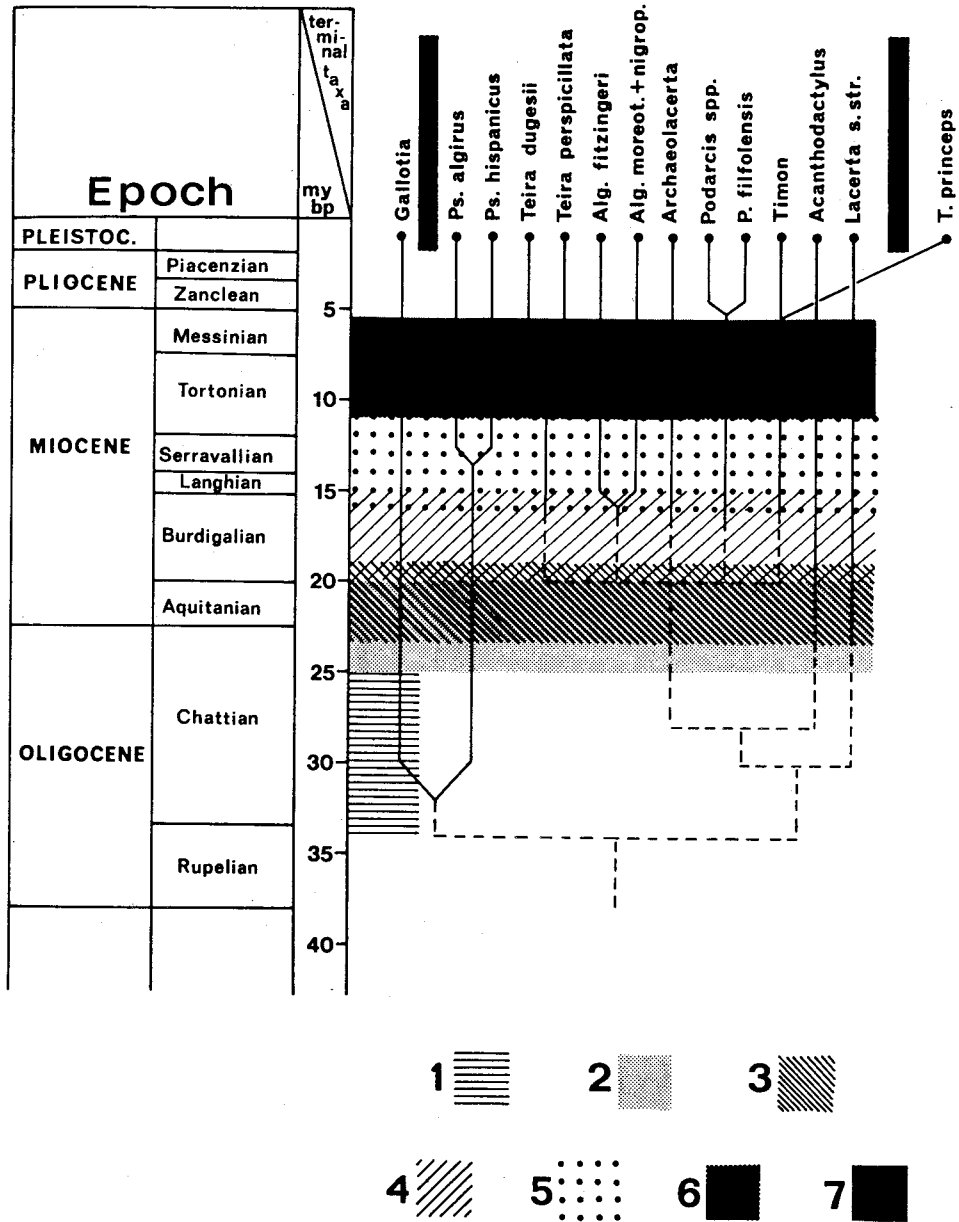


Fig. 1. Correlation of paleogeographic events with phylogeny of lacertid lizards in the western Mediterranean basin. For literature reference see text. 1- formation of the oldest of the Canarian Islands, viz. Fuerteventura; 2 - separation of Tethys and Paratethys by the Balcan/Turkey landmass; 3 - Kabylia block collision forming Great and Tell Atlas; 4 - western Alp connection of Tethys/Paratethys separating Iberia/Italy from Balcan/Turkey; 5 - transmediterranean dispersal possible; 6 - rotation of the Corso-Sardinian microplate; 7 - formation of the strait of Gibraltar.

## Results and discussions

In this section we shall briefly outline and discuss the species content, age, systematic relationships and chorological patterns of the lacertid species groups involved. The species content, i.e. the number of species recognized in each of these groups or lineages refers to the preliminary checklist compiled by Bischoff (1990; 1991 a;b; 1992 a;b). The order of arrangement is alphabetical.

### *Acanthodactylus*

32 species are included, according to the compilation of Bischoff (1990), based on Salvador (1982) and Arnold (1983; 1986). Only one species (*A. erythrurus*) occurs in the region, i.e. can be termed west Mediterranean, although some others, (e.g. *A. savignyi*) may reach the Mediterranean coast of NW Africa (without, however, being Mediterranean faunal elements themselves).

The age of the *Acanthodactylus* lineage is ca. 20 mybp, but in our tree (Fig. 1) it comprises (by implication) also the entire African lacertid radiation to which *Acanthodactylus* belongs, and which is separated from the palearctic clades *Algyroides*, *Archaeolacerta*, *Podarcis*, *Teira* and *Timon* since ca. 24 mybp (Mayer, pers. comm.). The sister group is within the African radiation (Mayer, pers. comm.). Within the genus, the monophyly of which is not under debate, some species groups are recognizable, which differ, however, in their composition according to different viewpoints of Salvador (1982) and Arnold (1983; 1986). The only west Mediterranean species, *A. erythrurus*, occurs in Portugal, Spain, Morocco and Algeria. The Iberian populations are considered subspecifically distinct (*A. e. erythrurus*) from those of North Africa (*A. e. belli*, *A. e. lineomaculatus*) (Salvador, 1981; 1982). The genetic distance (Nei's D) between Spanish and Moroccan lizards is 0,1 (Busack, 1986), thus less expressed than that between the forms of the *Lacerta lepida* complex (see below under *Timon*).

The sister species of *A. erythrurus* (+ *A. savignyi* ?) is not known with certainty. The most probable candidate is *A. schreiberi* from Cyprus and the Levante coast (see Böhme, 1971). Zoogeographically, these fringe-toed lizards may provide another important example of an east-west disjunction in the Mediterranean. The situation of two distinct forms on both sides of the strait of Gibraltar (the formation of which dates back to 7,5 - 5 mybp: Busack, 1986) with a sister taxon of the common ancestor in the eastern Mediterranean is strikingly paralleled by the *Timon* species (see below) and other lizards (e.g. *Blanus*) thus offering a most interesting and well testable hypothesis.

*Algyroides*

Included are 4 species, 2 of them being extralimital, i.e. confined to the eastern part of the Mediterranean. The age of the lineage is 20-18 mybp, and the sister group is uncertain. *Algyroides* belongs to the radiation which gave rise also to *Archaeolacerta*, *Teira*, *Podarcis* and *Timon* (see below and Fig. 1), and their phylogenetic interrelationships are still unknown.

The monophyly of *Algyroides* has been corroborated by Mayer and Lutz (1990). According to them, the first branching within the genus separated the Corso-Sardinian endemic *A. fitzingeri* from the two W Balcanic forms, viz. *A. nigropunctatus* and *A. moreoticus* at about 16 mybp. The phylogenetic position of the Iberian endemic *A. marchi* could not be assessed because only unidirectional values were present for this species. Its putative assertion in the tree of Mayer and Lutz (op. cit.), however, links it with the two Balcan species rather than with the Tyrrhenian species. Apart from the possibility that another and (if so) closer relative of *A. fitzingeri*, viz. *A. hidalgoi*, may exist in Spain (Buchholz, 1964), the hypothesis of Mayer and Lutz (1990) causes problems when compared with paleogeographic evidence. *A. fitzingeri* is said to be older than the rotation of the Corso-Sardinian microplate, which took place between 11,5 and 6 mybp (Alvarez, 1972; Radicati di Brozolo and Giglia, 1973; Alvarez *et al.*, 1974); before this event the microplate, particularly the modern Corsica, was attached to the coast of today Provence and Costa Brava (op. cit.). Therefore, a closer relationship of the Iberian endemic with the two Balcanic forms is more unlikely than the alternative assumption of a separation between the Iberian and the Corso-Sardinian form along with the separation of the Corso-Sardinian microplate from the Iberian landmass.

*Archaeolacerta*

Included are 6 species (*bonnali* of the Pyrenees being recently raised to specific rank by Perez Mellado *et al.*, 1992), 3 of them being extralimital (Balcan). The age of *Archaeolacerta* is 20-18 mybp (Mayer and Lutz 1989), the adelphotaxon is unresolved.

As in *Algyroides* (see the above paragraph) there are two Iberian species, one Corso-Sardinian endemic, and three Balcanic species (one of them extending even to Austria and S Germany: Capula and Luiselli, 1990). In parallel to *Algyroides*, the oldest branching concerns the Corso-Sardinian endemic, i.e. *Archaeolacerta bedriagae*, a conclusion which is, however, based on morphological and hemipenial evidence (Böhme, 1971), as immunological data are ambiguous (Mayer and Lutz op. cit.). There may be a closer relationship of *bonnali* to *horvathi*, exhibiting some Alpine relict chorological pattern

(Nascetti *et al.* in prep.). The relationship of all Iberian forms, however, to *bedriagae* requires further research.

There are, however, some differences between the two similar patterns of *Algyroides* and *Archaeolacerta* in the western Mediterranean, and in particular between the two endemic Corso-Sardinian counterparts.

1. The populations of *Algyroides fitzingeri* on Corsica and Sardinia as well as on some satellite islands are homogenous and taxonomically inseparable (the nominal taxon *logudorensis* being a synonym: Schneider, 1981), whereas *Archaeolacerta bedriagae* has two very distinct populations on Corsica (*b. bedriagae*) on the one hand, and on Sardinia (*b. sardoa* plus *paessleri* and *ferrerae*) on the other.

2. In Iberia there lives only one relict *Algyroides* (*A. marchi*) in SE Spain (Sa. de Cazorla; perhaps another one - *A. hidalgoi* - in the Sa. de Guadarrama?), whereas the Iberian *Archaeolacerta* are much more diverse, inhabiting various mountain ranges: *m. monticola* (Sa. da Estrela), *cantabrica* (Cantabrian Mts.) and *m. cyreni* (Sa. de Guadarrama and Sa. de Gredos). In this group, the monophyly and the phylogenetic position of its generotype *Archaeolacerta bedriagae* has still to be demonstrated until this group can be used as a testing model in paleogeographic terms.

#### *Lacerta* s.str.

*Lacerta* in the strict sense means the "green lizards" *L. agilis*, *L. media*, *L. pamphylica*, *L. schreiberi*, *L. strigata*, *L. trilineata* and *L. viridis* (Bischoff, 1991 a). Of these, only 2 occur in the western Mediterranean region: *L. schreiberi* as an endemic of Iberian mountain ranges, and *L. viridis*, a widely distributed form inhabiting temperate and Mediterranean zones from France eastwards to Turkey. Its range covers also some Tyrrhenian islands. Except the *Gallotia/Psammodromus* lineage (see above) *Lacerta* s. str. is among the oldest evolutionary lineages within the Lacertidae: 24-23 mybp (Mayer and Lutz, 1990).

In the western Mediterranean basin only *L. viridis* inhabits coastal areas and islands: S France, Italy and several Tyrrhenian islands (Elba, Ustica, Marettimo, see Nettmann and Rykena, 1984). These populations are assigned to several subspecies (e.g. *chloronota*, *fejervaryi*) the status of which, however, is unclear. Therefore, they are still useless for any zoogeographic conclusion.

*L. schreiberi* and *L. viridis* obviously invaded the western Mediterranean area rather recently (Plio-/Pleistocene) coming from a clearly eastern group.

*Podarcis*

This is the absolutely dominating group of Mediterranean lacertids. At present 16 species (including the former "*Archaeolacerta*" *graeca*: Mayer and Lutz, 1989) are distinguished. 3 of them are only partially or not at all Mediterranean: *P. bocagei* lives in the central and western Iberian peninsula, *P. muralis* colonized also temperate zones in the north and penetrated the Pontian region in NW Anatolia, *P. taurica* finally likewise penetrated the Pontian region. The age of the lineage is, as in *Algyroides* and *Archaeolacerta*, 20-18 mybp, the sister group relations are unresolved (see Fig. 1).

Within *Podarcis*, several species groups have been defined. Their delimitation, however, is still under debate. The following examples of the area considered here may elucidate the problems:

- Is *Podarcis wagleriana* (Sicily and some surrounding islands) a close relative of the Corso-Sardinian *P. tiliguerta*, along with the Maltese/Pelagian *P. filfolensis* (Klemmer, 1957)? This would imply a zoogeographic linkage between the Sicily/Malta area with Corso-Sardinia, paralleled e.g. by the skink *Chalcides ocellatus* (which is lacking, however, in Corsica).
- Or does *P. wagleriana* belong to the *P. melisellensis*/*P. taurica* clade from the Balcans (indicated by the striking similarity of particularly the females with *P. m. fumana* and *P. t. ionica*) (Böhme, 1986), thus exhibiting a chorological pattern paralleled by e.g. the snake *Elaphe situla*?
- Or is it the sister taxon of *P. sicula* with which it occasionally produces natural hybrids on Vulcano and Marettimo Islands (Capula *et al.*, 1990), thus falsifying both previous hypotheses?
- Is *P. tiliguerta* of Corso-Sardinia a distinct species as first ranked by Klemmer (1957) and biochemically corroborated by Mayer and Tiedemann (1982)? Or is it conspecific with the mainland species *P. muralis*, as suggested by Lanza *et al.* (1977) by likewise biochemical evidence?
- Are the Balearic endemics, *P. lilfordi* and *P. pityusensis* (if not conspecific: see Bischoff, 1973) the sister group of the Iberian *P. hispanica/bocagei* complex, or are they derived from some extinct Messinian ancestor (Alcover and Mayol, 1981, Alcover *et al.*, 1981)?
- What is, finally, the human impact on the distribution of just the wall lizards of the genus *Podarcis* in the Mediterranean? In some instances (*P. sicula* in S Dalmatia and Istanbul, but also in Spain, in the Balearics and Corsica, possibly also Pantelleria; *P. pityusensis* in Mallorca) the anthropogenic origin is obvious, in others not (e.g. *P. hispanica vaucheri* on both sides of the Gibraltar strait, as compared with *Psammodromus algirus* or the *Lacerta (Timon) lepida* complex, see below).

These few examples should suffice to demonstrate the great extent of lacking knowledge prohibiting yet zoogeographical conclusions compatible with those drawn from tipulids, salamandrids and ranids by Oosterbroek and Arntzen (1992) to construct area cladograms and to relate them to paleogeography. This is, unfortunately, not only true for *Podarcis*.

On the other hand, the species of just this genus tend to develop particularly often distinguishable populations on islands and islets. This inspired many authors to describe and to name all of them which in fact made these "varieties" and "races" equally ranking trinominal subspecies. This inflation of infraspecific names, for example just 91 (!) only for *P. sicula* (Henle and Klaver, 1986), 24 for *P. lilfordi* and 43 for *P. pityusensis* (Salvador, 1986 a; b) made gamma-taxonomy an ill-reputed discipline in the eyes of many zoologists, even systematists! The underlying concept, the so called 75 % rule by Mayr, Linsley and Usinger (1953) (see also Mayr, 1975 for "defining" subspecies) is an absolutely arbitrary criterion (Böhme, 1978). Therefore, it is necessary to distinguish between mainland subspecies that can be defined as evolutionary divergent units (a pre-stage of speciation) with often secondary contact zones proving cross fertility and heterosis effects (Böhme op. cit.) and insular/microinsular derivatives of just these mainland forms. This means, that their **lower hierarchical level** must be taken into account. The so called megasubspecies concept of Amadon and Short (1976) provides a possibility to express such hierarchical differences (see Böhme, 1982). One example should elucidate the problem: Mainland *Podarcis sicula campestris* inhabits the northern half of Italy and the Croatian coast down to the Split region. There are many offshore islands and islets along this coast. It is obvious that any of the described insular/microinsular "subspecies" (ranked on the same level as *campestris*) is genetically closer to Croatian mainland ruin lizards than for example to any Tyrrhenian population. Henle and Klaver (1986) dealing with the 91 nominal subspecies of *P. sicula* tried already to form subspecies-groups by listing 24 names with *P. s. campestris*, 20 with *P. s. sicula* and 4 with *P. s. tyrrhenica*. They discussed also the different hypotheses concerning the colonization of the Tuscan archipelago and Corso-Sardinia (Mertens, 1916; 1932; La Greca and Sacchi, 1957; Schneider, 1971; 1972; Hotz, 1973) and correctly concluded that nearly all investigations on this problem suffered from restricting themselves mostly on colour pattern which is not a very reliable character (see e.g. Corti, 1988). Modern statistical analyses are largely lacking. One of the few exceptions has been carried out by Cirer (1981; 1987) on the Pityusas by means of a multivariate, canonical analysis. She correlated her results also with the age of the islands/islets and reduced the number of subspecies in *P. pityusensis* to 7. Another important approach has been made by Corti (op. cit.) who combined a morphological, statistical analysis with a biochemical one. Her



results corroborate the view of Henle and Klaver (1986) and demonstrate a very recent colonization of the Tuscan archipelago islands through only two recognizable forms: *P. s. campestris* which colonized Elba, Cerboli, Pianosa, Formica Grande di Grosseto, Formica di Burano, Sparviero e Montecristo in relatively recent times (mostly also through passive transport), and *P. s. tyrrhenica* which colonized Giglio, Giannutri, Capraia and La Praiola in somewhat earlier times (Upper Pleistocene, 250.000-200.000 years ago (Corti op. cit.).

From all the above comments it should become clear that the use of insular populations of *Podarcis* for biogeographic considerations is - with the exception of the two last mentioned studies - still premature, due to the largely unresolved and instable infraspecific taxonomy. We therefore refrain from discussing the biogeography of the western Mediterranean archipelagos on the still somewhat flimsy basis of *Podarcis* gamma-taxonomy. If these archipelagos resp. islands are to be discussed biogeographically, other reptile or even animal groups (e.g. insects, mammals) may yet provide a safer basis.

#### *Psammodromus*

4 species are included. The age of the lineage is according to Lutz *et al.* (1986) 32 mybp. The sister group relationship with *Gallotia*, a genus endemic to the Canary islands, is corroborated by strong evidence (Lutz *et al.* op. cit., Arnold, 1989). Both together form the oldest branching event within lacertids (Lutz *et al.* op. cit.).

The distribution area of *Psammodromus* is confined to the western part of the area discussed here and covers the Iberian peninsula, the Mediterranean south of France and NW Africa. The most important ingroup speciation event took place 14 mybp (Lutz *et al.* op. cit.) separating *P. algirus* from the smaller sized *P. hispanicus* (and most likely also from *P. blanci* and *P. microdactylus*, *blanci* being ethologically much closer to *hispanicus* than to *algirus*, cf. Bischoff and in den Bosch, 1991), i.e. long before the formation of the strait of Gibraltar (7,5 -5 mybp). The latter event could well correlate with the branching of the Iberian endemic *P. hispanicus* from the North African sister taxa *blanci/microdactylus*, what has to be verified by future research.

The very low genetic distance between Iberian and N African populations of *P. algirus* argues for a recent (anthropogenic) immigration to Spain (Busack, 1986), as does its obvious today expansion in southern France (Böhme, 1981). As an example similar to the situation lined out for *Podarcis* (see above) it should be mentioned that the Galita archipelago off the Tunisian coast harbours an "endemic subspecies" of *P. algirus*, viz. the melanistic *P. a. doriae* (Bedriaga, 1886; Lanza and Bruzzone, 1959). This form, however, is not endemic to the archipelago, but only to Galitone Island, which makes the

"normal" population of Galita itself (*P. a. algirus*) closer to any other one in Algeria, Morocco, Spain or France than to that of the immediately neighbouring island (Böehme, 1981). The absurdity of such concepts is obvious, not only in biogeographic terms.

### *Teira*

Assigned to this informal taxon are 3 species, two of which (*andreanskyi* and *perspicillata*: Mayer, pers. comm.) are confined to NW Africa (the latter being passively transported to Menorca Island in the Balearics). The third one (*dugesii*) is an atlantic endemic of the Selvagens and Madeira archipelagos (introduced also to the Azores). The age of this lineage is 18 mybp (Mayer and Lutz, 1989). The sister group is uncertain. The assumption by Richter (1979) who assigned *Teira* (containing *dugesii* and *perspicillata*) as a subgenus to *Podarcis* was corroborated by Mayer and Lutz (op. cit.) on biochemical grounds but contradicted by Arnold (1989) by morphological arguments. Mayer and Lutz (op. cit.), however, found also "*Lacerta*" *graeca* to be rather close to *Podarcis*, to a similar, but of course independently achieved extent as it is the case in *Teira*. Therefore the hierarchical phylogenetic relationships of *Teira* as a whole and also within *Teira* cannot yet be described. Its atlantic affinities, however, reminding the situation in *Psanmodromus* with its atlantic sister group *Gallotia* are not at all comparable, due to a much younger branching date that has to be postulated between *dugesii* and its two North African con(sub)genera.

### *Timon*

This group, not yet recognized as a full genus, comprises 3 species, 1 being extralimital. The age of the lineage is 20-18 mybp, and the sister group is unclear, possibly *Archaeolacerta* plus *Podarcis* (Lutz and Mayer, 1984). The two west Mediterranean species of *Timon*, i.e. *Lacerta* (*T.*) *lepida* and *L. (T.) pater*, have for many decades been considered to be conspecific. Bischoff (1982) demonstrated partial cross sterility between both and ranked them as (allo-) species. His results were supported by Busack (1987) who calculated their branching date as being 5-4 mybp which coincides with the formation of the Gibraltar strait.

Already Böehme (1971) suggested a relationship of the *lepida* group with the eastern Anatolian/west Iranian *Lacerta princeps*, which was corroborated by Engelmann and Schäffner (1981) and by Lutz and Mayer (1984). The latter authors found a rather small immunological distance between the two, comparable with that found e.g. between *Podarcis erhardii* and *P. taurica* or between *Lacerta* (s.str.) *agilis* and *L. trilineata*. This means a branching date of likewise 5 mybp (see Fig. 1). Busack (1986; 1987) justifiedly claimed that

"while genetic distances computed from different, and differing numbers of loci among representatives of different taxa may not be directly comparable, these data do provide an indication of the range in values expected between biological species within the genus *Lacerta*". Taking into account, however, the much greater morphological distance together with the geographical one, a branching of *princeps* from the *lepida/pater* stock and the separation of *lepida* and *pater* at roughly the same time seems unlikely. One has to postulate that *princeps* diverged earlier from the *lepida* stock than did *pater*, i.e. prior to the formation of the Gibraltar strait and not after it. Due to the biogeographic significance of *Timon* (west/east Mediterranean disjunction, plus transgibraltarian elements) the case should be tested with corresponding chorological groups as e.g. *Acanthodactylus erythrurus* ssp. versus *A. schreiberi*, *Blanus cinereus/mettetalii/tingitanus* versus *B. strauchi*, *Pelobates cultripes/varaldii* versus *P. syriacus*, the west Mediterranean *Discoglossus* radiation vs. *D. nigriventer* etc.

Another open question is the status resp. branching date of *L. (T.) lepida nevadensis*, a phenetically most different form inhabiting the SE of Spain. The characters shared with *pater* (e.g. juvenile dress) are symplesiomorphic. The expressed hybrid belt with *lepida lepida* demonstrates their divergence after the separation of *pater*. *L. lepida nevadensis* offers, however, also examples of insular microevolution. A population inhabiting the small Olla islet off the Spanish coast near Benidorm is significantly smaller (a true dwarf form) and also differently coloured. Nevertheless it is clearly recognizable as being derived from *nevadensis* and not from typical *lepida*. Therefore, it is despite its (taxonomic) distinguishability below the hierarchical level of the subspecies *nevadensis* (Freyhof, Böhme unpubl.). The same arguments are true for some Atlantic ocean microinsular populations of *lepida* and also for the population of the Galita archipelago which is clearly derived from a Tunisian *pater* stock. Again, these microinsular forms are biogeographically not particularly relevant.

### Conclusions

As has been discussed in the previous sections dealing with the single lacertid lineages, several major paleogeographic events have influenced the phylogeny and evolution of these lizards. In the western Mediterranean basin the principal events were (Fig. 1) (1) the formation of the oldest island of the Canarian archipelago, i.e. Fuerteventura; (2) the separation of Tethys and Paratethys by the Balcan/Turkey landmass; (3) the collision of the Kabylia block forming the Great and the Tell Atlas; (4) the Tethys/Paratethys reconnection west of the Alps separating Iberia/Italy from Balcan/Turkey; (5) mid-Miocene regression making transmediterranean dispersal possible; (6) rotation of the Corso-Sardinian microplate; (7) Messinian salinity crisis and

subsequent formation of the strait of Gibraltar (compiled after Álvarez, 1972, Radicati di Brozolo and Giglia, 1973; Alvarez *et al.*, 1974; Hsü *et al.*, 1977; Hsü, 1983; Rögl and Steininger, 1983; Busack and Hedges, 1984; Busack, 1986; Boccaletti *et al.*, 1990 a; b). From these events which we included in our Fig. 1, the lacertids offer the most interesting biogeographic implications connected with the formation of the strait of Gibraltar and the rotation of the Corso-Sardinian microplate. Here also the most striking inconsistencies are to be observed, between the geological age of the lizard lineages as calculated from their immunological distances on the one hand, and the paleogeographical datation on the other. In other instances both datations are fitting. The branching between the endemic Canarian genus *Gallotia* from mainland *Psammodromus* fits well with the origin of the oldest island of the archipelago, viz. Fuerteventura. The early Burdigalian big radiation of several (still polytomic) lineages (*Teira*, *Algyroides*, *Archaeolacerta*, *Podarcis* and *Timon*) fits well with the possible transmediterranean dispersal in that period (Fig. 1).

The obvious inconsistencies/contradictions are:

- The radiation of *Psammodromus* (*P. algirus* vs. the 3 small species) fell into an era where transmediterranean dispersal was possible. Eastern relatives are, however, lacking.
- The even earlier separation of the Corso-Sardinian endemic *Algyroides fitzingeri* from its Balcan relatives (and "officially" also from its Iberian congener!) agrees partly with the western Alp reconnection of Tethys and Paratethys, but disagrees strongly with the much later datation of the beginning rotation of the Corso-Sardinian microplate! The situation of an endemic much older than its area of endemism reminds of the situation of the Galapagos iguanas (Wyles and Sarich, 1983).
- The separation of *Lacerta (Timon) pater* from *L. (T.) lepida* should most likely be due to the formation of the strait of Gibraltar (Busack, 1986; 1987), i.e. 7,5 - 5 mybp according to Hsü *et al.* (1977), Hsü (1983), Busack and Hedges (1984), Busack (op. cit.), when the Atlantic ocean filled the Mediterranean basin again. If, however, the much more diverging *L. (T.) princeps* has also a branching date of 5 mybp (see Lutz and Mayer, 1984), the inconsistency in time seems unresolvable. Furthermore, Rögl and Steininger (1983) give as datation for the desiccation and the salinity crisis (Messinian to upper Pontian) 6,0 - 5,5 mybp which was terminated not before the Pliocene which means even less than 5,5 mybp!

A last remark has to be devoted to the fossil record. Regarding the today diversity and dominance of Mediterranean lacertids, the fossil record is extremely poor. Estes (1983) lists from the Mediterranean region - with the exception of some *L. viridis*- and *L. lepida*- like remains from their recent distribution areas and some doubtful (!) records of *P. sicula* from Poland and

Germany - only Pleistocene *P. erhardii* from Crete. Already Bate (1918) had recorded "*Lacerta sp.*" from the Balearics, which was interpreted as belonging to the "*viridis-ocellata-group*" by Boulenger (1920). Alcover *et al.* (1981) considered this lizard to be the predecessor of the modern species *Podarcis lilfordi* and *P. pityusensis*. Böhme and Zammit-Macampel (1982) identified another "*Lacerta sp.*" sensu Kotsakis (1977) from Sicily as a new species (*L. siculimelitensis*) which they recorded also from Malta. The fossil record so far known is thus far from being sufficient to draw any biogeographical conclusion.

### Summary

The western Mediterranean basin (west of a line from the Adriatic Sea to the Tunisian coast) is inhabited by the following, presumably monophyletic groups (genera/subgenera) of lacertid lizards: *Acanthodactylus*, *Algyroides*, *Archaeolacerta*, *Lacerta s.str.*, *Podarcis*, *Psammodromus*, *Teira* and *Timon*. Each of these groups or lineages is discussed in regard to its geological age (as determined by immunological methods), its putative closest relatives (adelphotaxa) and its chorological pattern in comparison with paleogeographical data. Strong inconsistencies between the latter and the molecular datings were detected. The problems of open taxonomic questions (leading potentially to wrong biogeographical conclusions) and of subspecies concepts in relation to microinsular evolution are particularly stressed.

### Acknowledgements

*We are greatly indebted to Dr. Evstratios Valakos, Athens, for his great work of organizing the "1st International Symposium on the lacertids of the Mediterranean basin" on Lesbos Island, which made this contribution possible. Furthermore, we would like to thank Dr. Werner Mayer, Vienna, for sharing some of his unpublished data with us, Wolfgang Bischoff, Bonn, for constructively commenting on the manuscript, and Ursula Bott, Bonn, for preparing the figure.*

### Literature Cited

- Alcover, J. A. (1981): Espècies relíquies d'amfibis i de rèptils a les Balears i Pitiüses. *Bol. Soc. Hist. Nat. Balears* 25: 151 - 167.
- Alcover, J. A., Moya-Sola, S., Pons-Moya, J. (1981): *Les Quimeres de Passat. Els vertebrats fòssils del Plio-Quaternari de les Balears i Pitiüses*. Ciutat de Mallorca, Ed. Moll.
- Alvarez, W. (1972): Rotation of the Corsica-Sardinia microplate. *Nature Phys. Sci.* 235: 103 - 105.
- Alvarez, W., Cocozza, T., Wezel, F. C. (1974): Fragmentation of the alpine orogenic belt by microplate dispersal. *Nature Phys. Sci.*, 248: 309 - 314.

- Amadon, D., Short, L. L. (1976): Treatment of subspecies approaching species status. *Syst. Zool.* 25: 161 - 167.
- Arnold, E. N. (1973): Relationships of the northern Palaearctic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammodromus* (Reptilia, Lacertidae). *Bull. Brit. Mus. Nat. Hist. (Zool.)* 25: 289 - 366.
- Arnold, E. N. (1983): Osteology, genitalia, and the relationships of *Acanthodactylus* (Reptilia: Lacertidae). *Bull. Brit. Mus. Nat. Hist. (Zool.)* 44: 291 - 339.
- Arnold, E. N. (1986): A key and annotated checklist to the lizards and amphisbaenians of Arabia. *Fauna Saudi Arab.* 8: 385 - 435.
- Arnold, E. N. (1989): Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. *Bull. Brit. Mus. Nat. Hist. (Zool.)* 55: 209 - 257.
- Bate, D. M. A. (1818): On a new genus of extinct muscardine rodent from the Balearic Islands. *Proc. Zool. Soc. London*, 1918: 209 - 222.
- Bedriaga, J. V. (1886): Beiträge zur Kenntnis der Lacertiden - Familie. *Abh. Senck. Naturf. Ges.* 14: 17 - 444.
- Bischoff, W. (1982): Zur Frage der taxonomischen Stellung europäischer und nordwestafrikanischer Perleidechsen (Sauria, Lacertidae, *Lacerta lepida* - Gruppe). *Amphibia - Reptilia* 2: 537 - 367.
- Bischoff, W. (1990): Übersicht der Arten und Unterarten der Familie Lacertidae. 1. Die Gattungen *Acanthodactylus*, *Adolfus*, *Algyroides* und *Australolacerta*. *Die Eidechse* (Internal Circ. AG Lacertiden DGHT) 1: 18 - 23.
- Bischoff, W. (1991 a): Übersicht der Arten und Unterarten der Familie Lacertidae. 2. Die Gattungen *Eremias*, *Gallotia*, *Gastropholis*, *Heliobolus*, *Holaspis* und *Ichnotropis*. *Die Eidechse* (Int. Circ. AG Lacertidae DGHT), 2: 14 - 21.
- Bischoff, W. (1991 b): Übersicht der Arten und Unterarten der Familie Lacertidae. 3. Die Gattung *Lacerta*. *Die Eidechse* (Int. Circ. AG Lacertidae DGHT), 3: 5 - 16.
- Bischoff, W. (1992 a): Übersicht der Arten und Unterarten der Familie Lacertidae. 5. Die Gattung *Podarcis*. *Die Eidechse* (Int. Circ. AG Lacertidae DGHT), 5: 6 - 20.
- Bischoff, W. (1992 b): Übersicht der Arten und Unterarten der Familie Lacertidae. 6. Die Gattungen *Poromera*, *Psammodromus*, *Pseuderemias*, *Takydromus* und *Tropidosaura*. *Die Eidechse* (Int. Circ. AG Lacertidae DGHT) 6: 13 - 17.
- Bischoff, W., in den Bosch, H. A. J. (1991): Zur Kenntnis von *Psammodromus blanci* (Lataste, 1880): Morphologie, Verbreitung, ökologie und Paarungsbiologie. *Salamandra* 27: 163 - 180.
- Boccaletti, M., Ciaranfi, N., Cosentino, D., Deiana, G., Gelati, R., Lentini, F., Massari, F. Moratti, G., Pescatore, T., Ricci Lucchi, F., Tortorici, L. (1990): Palinspastic restoration and paleogeographic reconstruction of the peri-Tyrrhenian area during the Neogene. *Paleogeogr., Paleoclimatol., Paleoecol.* 77: 41 - 50.
- Boccaletti, M., Nicolich, R., Tortorici, L. (1990): New data and hypothesis on the development of the Tyrrhenian basin. *Paleogeogr., Paleoclimatol., Paleoecol.* 77: 15 - 40.
- Böhme, W. (1971): Über das Stachelepithel am Hemipenis lacertider Eidechsen und seine systematische Bedeutung. *Z. zool. Syst. Evolutionsf.* 9: 187 - 223.

- Böhme, W. (1978): Das Kühnelt'sche Prinzip der regionalen Stenözöe und seine Bedeutung für das Subspezies - Problem: ein theoretischer Ansatz. *Z. zool. Syst. Evolutionsf.* 16: 256 - 266.
- Böhme, W. (1981): *Handbuch der Reptilien und Amphibien Europas*. vol. I., Akad. Verlagsges. Wiesbaden.
- Böhme, W. (1982): Das Problem der Hierarchie innerartlicher Gruppierungen. *Vert. Hung.* 21: 47 - 53.
- Böhme, W. (1984): *Handbuch der Reptilien und Amphibien Europas*. vol. II/1, Aula, Wiesbaden.
- Böhme, W. (1986): *Handbuch der Reptilien und Amphibien Europas*, vol. II/2, Aula, Wiesbaden.
- Böhme, W., Zammit-Maempel, G. (1982): *Lacerta siculimelitensis* sp. n. (Sauria: Lacertidae), a giant lizard from the late Pleistocene of Malta.
- Buchholz, K. F. (1964): Zur Kenntnis des Genus *Algyroides* (Reptilia, Lacertidae) in Spanien. *Bonn. zool. Beitr.* 15: 239 - 246.
- Busack, S. D. (1986): Biogeographic analysis of the herpetofauna separated by the formation of the strait of Gibraltar. *Natn. Geogr. Res.* 2: 17 - 36.
- Busack, S. D. (1987): Morphological and biochemical differentiation in Spanish and Moroccan populations of the lizard, *Lacerta lepida*. *J. Herpetol.* 21: 277 - 284.
- Busack, S. D., Hedges, S. B. (1984): Is the peninsular effect a red herring? *Amer. Natur.* 123: 266 - 275.
- Capula, M., Luiselli, L. (1990): Notes on the occurrence and distribution of *Lacerta horvathi* Mehely, 1904 in Federal Republic of Germany. *Herpetol. J.* 1: 535 - 536.
- Capula, M., Nascetti, G., Bullini, L. (1990): Genetic structure of *P. sicula* and *P. wagleriana* (Reptilia: Lacertidae) from Sicily, Egadi and Acolian Islands. *Atti 53 Congr. UZI Palermo*: 321 - 322.
- Cirer, A. M. (1981): La lagartija ibicenca y su círculo de razas. *Cons. Ins. Eivissa Formentera*, 1 - 106.
- Cirer, A. M. (1987): *Revision taxonomica de las subespecies del lacertido Podarcis pityusensis Bosc, 1883*. Ph.D. Thesis Univ. Barcelona.
- Corti, C. (1988): *Ricerche sulla variabilità morfologica e genetica della Podarcis sicula (Rafinesque, 1810) dell'Arcipelago Toscano (Reptilia, Lacertidae)*. Ph. D. Thesis Univ. Firenze.
- Engelmann, W. E., Schöffner, H. (1981): Serologisch - immunologische Untersuchungen zu einigen taxonomischen Problemen innerhalb der Sammelgattung *Lacerta* (Sauria, Lacertidae). *Zool. Jahrb. Syst.* 108: 139 - 161.
- Estes, R. (1983): Sauria terrestria, Amphibia. *Handb. Paläherpetol.*, part 10 A, G. Fischer, Stuttgart.
- Henle, K., Klaver, C. (1986): *Podarcis sicula* (Rafinesque - Schmaltz, 1810) - Ruineidechse. In Böhme, W. (ed.): *Handbuch der Reptilien und Amphibien Europas*, 1: 254 - 342.
- Hotz, H. (1973): Die Amphibien und Reptilien der Inseln Gorgona und Capraia. *Senck. biol.* 54: 15 - 31.
- Hsü, K. J. (1983): *The Mediterranean was a desert*. Princeton Univ. Press, Princeton.

- Hsü, K. J., Montandert, L., Bernoulli, D., Bianca Cita, M., Erickson, A., Garrison, E. E., Kidd, R. B., Mélières, F., Müller, C. Wright, R. (1977): History of the Mediterranean salinity crisis. *Nature* 267: 399 - 403.
- Kammerer, P. (1926): Der Artenwandel auf Inseln und seine Ursachen ermittelt durch Vergleich und Versuch an den Eidechsen der dalmatinischen Eilande, nebst einem Anhang: *Zur Systematik der adriatischen Insel-Eidechsen*. Franz Deuticke, Wien.
- Klemmer, K. (1957): Untersuchungen zur Osteologie und Taxonomie der europäischen Mauereidechsen. *Abh. Senck. Naturf. Ges.* 496: 1 - 56.
- Kotsakis, T. (1977): I resti di rettili i anfibi pleistocenici della grotta di Spinagallo (Siracusa, Sicilia). *Geologica* 16: 211 - 229.
- La Greca, M., Sacchi, C. F. (1957): Problemi del popolamento animale nelle piccole isole mediterranee. *Ann. Ist. Mus. Zool. Univ. Napoli* 9: 1 - 189.
- Lanza, B., Bruzzone, C. L. (1959): Erpetofauna dell' Arcipelago della Galita (Tunisia). *Ann. Mus. Civ. Stor. Nat. Genova*, 71: 41 - 56.
- Lanza, B., Cei, J. M., Crespo, E. G. (1977): Immunological investigations on the taxonomic status of some Mediterranean lizards (Reptilia Lacertidae). *Monit. Zool. Ital.* n.s. 11: 211 - 221.
- Lutz, D., Bischoff, W., Mayer, W. (1986): Chemosystematische Untersuchungen zur Stellung von *Lacerta jayakari* Boulenger, 1887 sowie der Gattungen *Gallotia* Boulenger und *Psammadromus* Fitzinger (Sauria; Lacertidae). *Z. zool. Syst. Evolutionsf.* 24: 144 - 157.
- Lutz, D., Mayer, W. (1984): Albumin-immunologische und proteinelektrophoretische Untersuchungen zur systematischen Stellung von *Lacerta lepida* Daudin und *Lacerta princeps* Blanford (Sauria, Lacertidae). *Zool. Anz.* 212: 95 - 104.
- Maxson, L. R., Sarich, V., Wilson, A. C. (1975): Continental drift and the use of albumin as evolutionary clock. *Nature* 255: 397 - 400.
- Mayer, W., Lutz, D. (1989): Chemosystematische Untersuchungen zur Phylogenie der Sammelgattung *Lacerta* (Reptilia: Sauria: Lacertidae). *Z. zool. Syst. Evolutionsf.* 27: 338 - 349.
- Mayer, W., Lutz, D. (1990): Albumin-immunologische Untersuchungen zur Phylogenie der Gattung *Algyroides* und ihrer systematischen Position gegenüber der Sammelgattung *Lacerta* (Reptilia: Sauria: Lacertidae). *Zool. Anz.* 224: 99 - 105.
- Mayer, W., Tiedemann, F. (1982): Chemotaxonomical investigations in the collective genus *Lacerta* (Lacertidae, Sauria) by means of protein electrophoresis. *Amphibia-Reptilia* 2: 349 - 355.
- Mayer, E. (1975): *Grundlagen der zoologischen Systematik*. Paul Parey, Hamburg.
- Mayer, E., Linsley, E. G., Usinger, R. I. (1953): *Methods and principles of systematic zoology*. New York, Toronto, London.
- Mertens, R. (1916): *Studien zur Systematik der Lacertiden. 1. Teil: Untersuchungen über die Variabilität der italienischen Mauereidechsen (Lacerta muralis Laur. und Lacerta serpa Raf.)*. R. Friedländer u. Sohn, Berlin.
- Mertens, R. (1934): *Die Insel-Reptilien, ihre Ausbreitung, Variation und Artbildung*. E. Schweizerbarth, Stuttgart.
- Nettmann, H.K., Rykena, S. (1984): *Lacerta viridis* (Laurenti, 1768) - Smaragdeidechse). In: Böhme, W. (ed.): *Handbuch der Reptilien und Amphibien Europas*, 2/1: 129 - 180.



- Oosterbroek, P., Arntzen, J. W. (1992): Area-cladograms of Circum-Mediterranean taxa in relation to Mediterranean palaeogeography. *J. Biogeogr.* 19: 3 - 20.
- Perez-Mellado, V., Berbadillo, V.C., Barahona, F., Brown, R. P., Capula, M., Corti, C., Guerrero, F., Lanza, B. (1992): A systematic survey of the Iberian rock lizard, *Lacerta (Archaeolacerta) monticola*. In: Valakos, E., Maragou, P. (eds.); Abstr. *1st International Congress on the lacertids of the Mediterranean basin*. Mytilini, p. 19.
- Radicati di Brozolo, F., Giglia, G. (1973): Further data on the Corsica-Sardinia rotation. *Nature* 241: 389 - 391.
- Rögl, F., Steininger, F. F. (1983): Vom Zerfall der Tethys zu Mediterran und Paratethys. Die neogene Paläogeographie und Palinspastik des zirkum-mediterranen Raumes. *Ann. naturh. Mus. Wien* 85 A: 135 - 163.
- Salvador, A. (1981): *Acanthodactylus erythrurus* (Schinz, 1833) - Europäischer Fransenfinger. In: Böhme, W. (ed.): *Handbuch der Reptilien und Amphibien Europas*, 1: 376 - 388.
- Salvador, A. (1982): A revision of the lizards of the genus *Acanthodactylus* (Sauria: Lacertidae). *Bonn. zool. Monogr.* 16: 1 - 167.
- Salvador, A. (1986 a): *Podarcis lilfordi* (Günther, 1874) - Balearen - Eidechse. In: Böhme, W. (ed.): *Handbuch der Reptilien und Amphibien Europas*, 2/2: 83 - 110.
- Salvador, A. (1986 b): *Podarcis pityusensis* (Bosc, 1883) - Pityusen - Eidechse. In: Böhme, W. (ed.): *Handbuch der Reptilien und Amphibien Europas*, 2/2: 231 - 253.
- Schneider, B. (1971): *Das Tyrrhenisproblem. Interpretation auf zoogeographischer Grundlage, dargestellt an Amphibien und Reptilien*. Ph. D. Thesis. Univ. Saarbrücken.
- Schneider, B. (1972): Variabilitätsanalyse morphognostischer Merkmale bei der Ruineidechse *L. s. campestris* unter besonderer Berücksichtigung der Population von Korsika. *Salamandra* 8: 97 - 100.
- Schneider, B. (1981): *Algyroides fitzingeri* (Wiegmann, 1834) - Tyrrhenische Kieleidechse. In: Böhme, W. (ed.): *Handbuch der Reptilien und Amphibien Europas*, 1: 392 - 401.
- Wyles, J. S., Sarich, V. M. (1983): Are the Galapagos iguanas older than the Galapagos? Molecular evolution and colonization models for the archipelago. In: Bowman, R. I., Leviton, A. S. (eds.): *Patterns of evolution in Galapagos organisms*. Amer. Assoc. Adv. Sci., Pacific Div., San Francisco, 177 - 185.