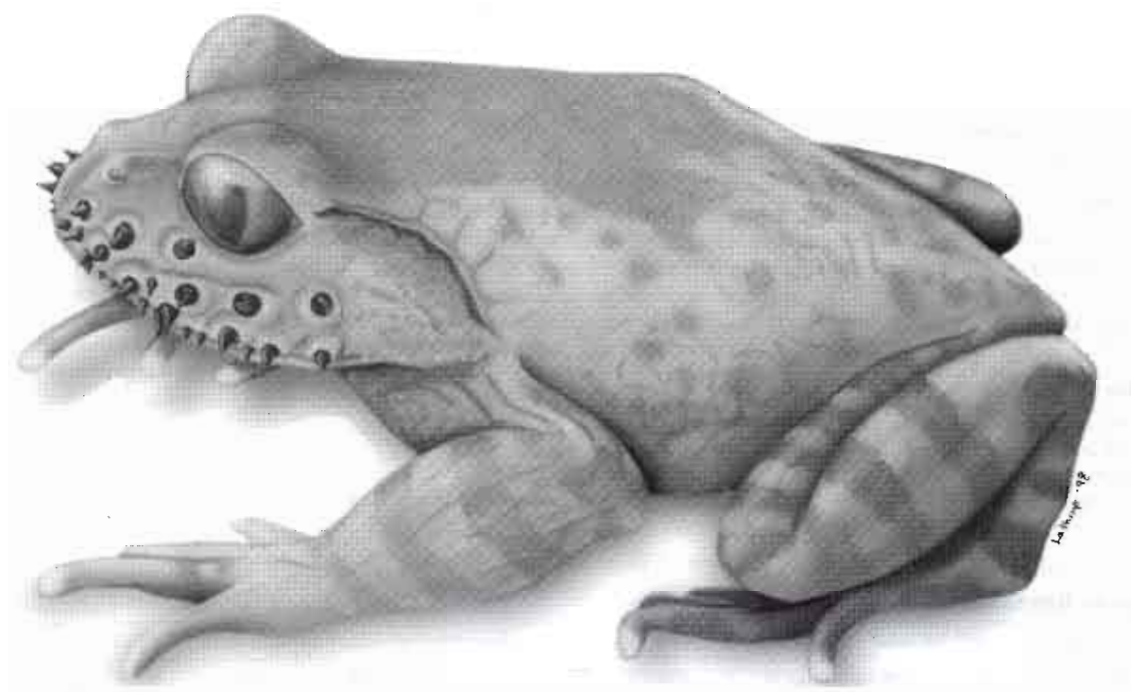# Russian
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PHYLOGENY AND RELATIONSHIPS OF THE MOUNTAIN LIZARDS OF EUROPE AND NEAR EAST (*Archaeolacerta* MERTENS, 1921, *SENSU LATO*) AND THEIR RELATIONSHIPS AMONG THE EURASIAN LACERTID RADIATION

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Archaeolacerta s. l., in the currently utilized sense results to be a polyphyletic taxon, composed of three monophyletic and phylogenetically well differentiated taxa: a) *Archaeolacerta* (s. str.) Mertens, 1921, which includes three species: *A. bedriagae*, *A. oxycephala*, and *A. mosorensis*, distributed by the northern part of the Central Mediterranean (Corsica, Sardinia, and west Balcanic Peninsula). His most related genera seem to be *Teira* (his adelphotaxon in our study), *Apathya*, and *Omanosaura*. b) *Iberolacerta* gen. nov., with two subgenera: *Iberolacerta* s. str. and *Pyrenesaura* subgen. nov. includes six species: *I. monticola*, *I. cyreni*, *I. bonnali*, *I. aranica*, *I. aurelioi*, and *I. horvathi*. They are distributed by the mountains of Western Europe (Iberian Peninsula, Pyrenees, Central and Eastern Alps and the north of the Dinaric Chains). His adelphotaxon are the Caucasian and Near East species of *Darevskia* gen. nov. c) The third taxa is *Darevskia* gen. nov., which includes the species of the "*L.*" *saxicola* complex besides "*L.*" *derjugini*, "*L.*" *praticola*, and "*L.*" *chlorogaster*. They are distributed by Eastern Europe, Caucasus, and Near East. Other clear relationships among some taxa of the Eurasian Radiation [= "Eurasische linie" from (Mayer and Benyr, 1994)] have been found: *Algyroides* seems to be the sister group of the species considered of uncertain phylogenetic relationships belonging to the "*L.*" *danfordi-laevis* group and of *Podarcis*. "*L.*" *brandtii* seems to be a very primitive species within the Eurasian Radiation. *Omanosaura* and *Apathya* appear as sister taxa. "*L.*" *graeca* occupies a very basal position in the sister group of *Podarcis* and relatives (see above). "*L.*" *andreanskyi* is the sister species of the *Darevskia* nov. and *Iberolacerta* nov. clade. The assimilation of "*L.*" *andreanskyi* to *Teira* is very problematic. Also the "*L.*" *parva* group seems to be related to *Timon*. Some groups of species like "*L.*" *brandtii*, "*L.*" *parva-fraasii* and "*L.*" *danfordi-laevis* probably merit generic rank, but it is necessary a more deep study before to take a decision.

Key words: Lacertidae, *Lacerta*, *Archaeolacerta*, *Iberolacerta* gen. nov., *Darevskia* gen. nov., *Pyrenesaura* subgen. nov., Taxonomy, Phylogeny.

INTRODUCTION

The reconstruction of the lacertid phylogeny has met, from their first intents with serious problems, due to the great superficial resemblance between all the groups in study. The methods of approach could be several: morphological, anatomical, genetic (by means of techniques as immunological microcomplement fixation or electrophoresis), karyological, etc.

Data coming from genetic studies can bring measures of distance by means of which we could ascertain the similarities between the different taxa (Arnold, 1993). Other kinds of data as the morphologic and karyological ones, characters can be separated in states (polarities of change from primitive to derived states), which confers to their analysis the advantage that the support to the relationships between two taxa can be analyzed in detail at the light of the consistency and comparative homoplasy of their characters (Arnold, 1993).

Among the methods utilized for the reconstruction of phylogenies in base to characters, the more

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utilized is the cladistic or systematic phylogenetic one (Swofford, 1985; Mayr and Ashlock, 1991).

In the study of the Lacertidae these methods have been employed, even with the difficulty that involves the identification of reliable characters for the phylogenetic reconstruction in this group. The external morphology of the lacertids is very conservative and the characters that help to distinction among species are broadly variable, not only among taxa of the same genus, but even between populations of the same species. Frequently, when groups of Lacertids belonging to different lines enter in similar adaptive zones, this results in the apparition of convergent and parallel answers that bring a considerable level homoplasy. The consequence of this is that to an external and not ever very informative morphology, an abundant number of reversals and parallelisms are added, making appear surprising similarities between groups phylogenetically far away between them. So, for a cladistic approach, enough available characters could not exist, be difficult of identifying in their derived states, present conflict of evidence in their polarity or suffer distortions owed to the included homoplasy, even when this is not apparent (Arnold, 1993). The solution to these problems has been the search for characters previously not utilized, as the osteological (see Arnold, 1973, 1989a; Arribas, 1993b, 1994) and hemipenial ones (Klemmer, 1957; Böhme, 1988, 1993; Böhme and Corti, 1993; Arnold, 1973, 1989a; Arribas, 1993a) that have permitted in the case of the former, to reconstruct the phylogeny at high taxonomic levels of the family, and in the case of the latter, to speculate on the generic relationships of some concrete taxa, usually closely related species.

Within the Lacertidae, the most complete revision by means of these techniques is the one from Arnold (1989a); although some concrete groups have been object of partial revisions, like *Acanthodactylus*, *Adolfus*, *Gastropholis*, *Holaspis*, *Meroles*, and *Pedioplanis*, all they by the same author (Arnold, 1983, 1989a, 1991).

The phylogeny proposed for the group of the Lacertidae (44 studied genera) (Arnold, 1989a), divides the family in two major groups: a) a Palaearctic and Oriental group, paraphyletic and composed of relatively primitive and non-specialized forms, which includes all the taxa here studied; and b) The group of Ethiopian and Saharo-Eurasian advanced taxa, monophyletic, that will be branched among the first. As

the same author indicates (Arnold, 1989a, 1993), while the phylogeny of the second group is quite very well resolved, in the first group it is not this the case.

This phylogeny is contrastable with alternative approaches derived from other techniques (for instance genetic) although in general, in their greater part other approaches have been so far very restricted. Among the genetic studies (immunological and electrophoretic) are the ones from Engelmann (1982), Engelmann and Schäffner (1981), Guillaume and Lanza (1982), Lanza and Cei (1977), Lanza et al. (1977), Lutz and Mayer (1984, 1985), Lutz et al. (1986), Mayer (1981, 1986), Mayer and Tiedemann (1980a, 1980b, 1981, 1982), Mayer and Arribas (1996), Borisov and Orlova (1986), and Busack and Maxon (1987). The recent work from Mayer and Benyr (1994) covers most of the Lacertidae and it is a good source of comparison with Arnold's papers.

From a karyological point of view, the starting of techniques as the chromosome banding and the localization of the NOR, permits a more deep approach to the structure of karyotypes otherwise apparently invariant by means of estandar stains and have permitted in the last years begin to establish models of relationships in the lacertids based on in their chromosomes (Olmo et al., 1991, 1993, 1995; Capriglione, 1995).

So much of the phylogenetic scheme from Arnold (1989a), as the one from Mayer and Benyr (1994), carry basically to very similar conclusions, but they stumble across the problem of the classification of the small lacertids from Europe and Near East. Only progressively is gone succeeding in putting some order and limits to some of their genus (*Algyroides*, *Podarcis*, *Lacerta* s. str.) (Arnold, 1989a), while for others, their formal elevation to the generic level is very recent (*Omanosaura*, *Teira*, *Timon*, *Zootoca*), in press, or still waiting for (Mayer and Bischoff, 1996; also see in Böhme and Corti, 1993). A good group of taxa remains still without systemizing, and between them, the *Archaeolacerta* s. l. group, whose elevation to the generic level (Lanza et al., 1977) stumbles across the difficulty in to establish their limits and relationships. This fact has led to their use in an informal manner (*Archaeolacerta*s or *Archaeolacerta*e in Arnold (1989a) and Arribas (1993a); "*Archaeolacerta* Gruppe" in Mayer and Benyr (1994), etc., although without a clear definition of their limits and contents.

Our objectives are to describe the limits and relationships between the species currently assigned to *Archaeolacerta* s. l. and to sketch the relationships between these species and the remainder taxa of the group of the Eurasian Radiation, ("Eurasische linie" *sensu* Mayer and Benyr 1994) (Largely equivalent to the Palearctic and Oriental group of Arnold, 1989a; see but Mayer and Benyr, 1994).

MATERIAL AND METHODS

Studied Species

All the bisexual species assigned formal or informally to the genus or group of the "*Archaeolacertae*" have been studied, except "*L.*" *defilippi* and "*L.*" *steineri* (the first unavailable for us, and the second recently described from Iran (Eiselt, 1995). For some species as "*L.*" *parva* or "*L.*" *brandtii*, not studied personally for the osteological characters, we have based an opinion on the data of Arnold (1973, 1989a). By this, they present a more tentative position in the general cladogram due to the relatively high number of undetermined characters (coded as missing "?"). *Ophisops, Eremias,* and *Mesalina* (not studied) in the general tree, belong to the Eurasian Radiation Group here treated (fide Mayer and Benyr, 1994) and could be placed perhaps together with *Omanosaura*.

The european species currently assigned to the "*Archaeolacertae*" are named as *Archaeolacerta* in the text. Other species of this group, as the caucasian ones, together with several taxa not closely related to *Lacerta* s. str. are named "*Lacerta.*" *Zootoca, Omanosaura, Teira,* and *Timon* are treated as full genera (see Mayer and Bischoff, 1996).

Methods of Study

The analysis has been carried out by means of HENNIG 86 vers. 1.5 (Farris, 1988). Evolution of characters has been examined subsequently in detail with CLADOS v. 1.2 (Nixon, 1992).

Some taxa alien to the Eurasian Radiation have been studied (*Gallotia, Psammodromus, Lacerta,* and *Zootoca*) in order to study the polarity of characters. Only clear polarities have been used, leaving in many characters, especially in the morphologic ones, the polarity as uncertain ("?" in the outgroup) so that the

algorithm decides the most parsimonious solution in accordance with the characters of clear polarity. Very variable characters within a taxon also have been left as uncertain ("?"). Characters variable in whatever of the terminal taxa (species groups) have been coded in his primitive state, assuming that change occurs in the interior of the given supraspecific taxon.

After a preliminary analysis including the outgroups in order to establish the greater groups, some species like the iberian (*A. monticola* and *A. cyreni*), the pyrenaean (*A. bonnali, A. aranica,* and *A. aurelioi*), and the group of "*L.*" *saxicola* (including "*L.*" *derjugini* and "*L.*" *praticola*) were pooled in groups as terminal taxa, running the definitive analysis of the Eurasian Radiation species.

The option of successive loading has been utilized ("x steps w"). This option provided a method for basing grouping on more reliable characters without having to make a priori decisions on weighting, reducing the number of resultant trees and calculating weights from the better character accesses. The load assigned to each character will rely on the additivity of the same. The successive load is automatically effected until the charge of the character stabilizes and change stops.

The utilized options for the searching of trees have been "mh" and "mh bb" (see Farris, 1988). The first constructs several trees, each one from a simple pass across the data, adding the terminal taxa in several different sequences. The shortest trees are retained. This option proportioned us 3 cladograms equally long, with identical consistency and retention indexes. The second, apply a change of branches to the trees produced by the previous option, retaining all the smallest trees that it could find. This option gives us 72 trees. We choose one of them, coincident in both options, as the preferred cladogram.

Subsequently, we have repeated the analysis for each one of the taxa identified within *Archaeolacerta* s. l. (except for the Caucasian group that has more taxa than variable characters between the nominal species in this study) in order to establish their internal relationships.

Two tests have been utilized in order to examine the strength and consistency of the data: PTP ("Permutation Tail Probability") (Faith, 1991; Faith and Cranston, 1991), and G1 statistics (Sokal and Rohlf, 1995). Both keep in mind the bias in the distribution of the randomly generated trees and their lengths as a

measure of the phylogenetic information from data, being their goodness related to the grade of negative bias of the generated distribution, in our case, for 10,000 trees (Fitch, 1979; Hillis and Huelsenbeck, 1992; Siddall, 1995).

The "Bootstrap" values were also calculated (Felsenstein, 1985; Sanderson, 1989; Garcia-Valdecasas and Sanchiz, 1989) in base to 10,000 randomly generated trees, as a measurement of the comparative consistency and confidence limits of each one of the nodes of the preferred tree. We consider that scores superior to 0.95 reveal statistically significant relationships. All these tests were effected with the program RandomCladistics ver. 3.0 (Siddall, 1995).

Studied Characters

Most of the morphological characters, very variable and homoplastic between groups and species have been left as unordered ("?" in the hypothetical ancestor), as well as polarities of some karyological characters (see Table 1). Osteological data on the taxa come from our own unpublished studies (Arribas, 1998).

Skeletal Characters

Skull.
1. More frequent number of premaxillary teeth: (0) seven (1) nine.
2. Pterygoid teeth: (0) present; (1) absent.
3. Form of the "processus nasalis": (0) slender and undifferentiated; (1) arrow shaped.
4. Postfrontal and postorbital bones: (0) fused; (1) separate.
5. Anterodistal process of the postfrontal: (0) present; (1) absent.
6. Anteromedial process of the postorbitary: (0) present; (1) absent.
7, 8. Comparative lengths of postorbitary and postfrontal: (0, 0) nearly equal; (1, 0) clearly unequal, with Pf > Po; (0, 1) clearly unequal, with Pf < Po.
9. Maxilojugal suture clearly sinuose ("stepped jugal" *sensu* Arnold, 1989a): (0) not; (1) yes.

Vertebral column.
10. Sexual dimorphism in the number of presacral vertebrae: (0) present; (1) absent.
11, 12. Modal number of vertebrae in males: (0, 0) modal number of 26 presacral vertebrae; (1, 0) modal number of 27; (2, 0) modal number of 28; (0, 1) modal number reduced to 25.
13, 14. Modal number of vertebrae in females: (0, 0) 27; (1, 0) 28; (2, 0) 29; (0, 1) 26.
15. Posterior dorsal vertebrae (posterior paraesternal, *sensu* Barbadillo and Sanz, 1983): (0) tendency to re-

tain seven or eight; (1) usually six; (2) tendency to reduce to 5.
16. Presence of ossificated ribs associated at the third vertebra (including Atlas and Axis in the count): (0) yes; (1) not.
17. Form of the associate ribs at sixth vertebra: (0) short and wide; (1) other forms (generally lengthened).
18. Sternal costal formula: (0) (3 + 1) or (3 + 2); (1) (3 + 2) or (3+3).
19–21. Type of caudal vertebrae: (0, 0, 0) A and B types indistinctly; (1, 0, 0) A type only; (0, 1, 0) B and C types; (0, 1, 1) C type only.

Girdles.
22, 23. Form of the clavicles: (0, 0) variable; (1, 0) always closed; (0, 1) always open.
24–26. Sternal fontanelle: (0, 0, 0) oval; (1, 0, 0) faintly or occasionally cordiform; (1, 1, 0) cordiform; (0, 0, 1) reduced or absent.
27, 28. Form of the interclavicle: (0, 0) with the lateral branches more or less perpendicular to the central axis; (1, 0) with the lateral branches directed back; (0, 1) with the lateral branches directed forward.

Hemipenis.
29. Proportions of the hemipenis lobes: (0) apical part greater than the basal one; (1) apical part smaller than the basal one.
30. Presence of pleats ("plicae") in the hemipenis lobes: (0) yes; (1) not.
31. Presence of apical papillae in the hemipenis lobes: (0) not; (1) yes.
32, 33. Hemipenial microornamentation: (0, 0) spiny-like; (1, 0) crown shaped; (0, 1) forked.

Karyotype.
34. Total number of chromatides in macrochromosomes: (0) 38; (1) 36.
35. Presence of microchromosomes: (0) yes; (1) not.
36. Existence of robertsonian fusions: (0) not; (1) yes.
37. Number of robertsonian fusions: (0) none; (n) number of pairs of fused homologues.
38. Sexual heterogamety: (0) ZW (homomorphic or heteromorphic, eu- or heterochromatic); (1)Z1Z2W.
39. Position of NOR (Nuclear Organizer)(character not ordered): (0) m; (1) S; (2) MS; (3) M; (4) L.

Morphologic characters.
40. Contact between the rostral and internasal scales: (0) present; (1) absent.
41, 42. Number of postnasal scales: (0, 0) two; (1, 0) one; (0, 1) three.
43. Supranasal in contact with loreal: (0) not; (1) yes.
44. Usual number of supralabials previous to the subocular scale: (0) usually four; (1) tendency to have five or more.
45. Supracilliary granules: (0) in a complete and uninterrupted row; (1) reduced or absent.
46. Masseteric: (0) present and differentiated; (1) absent by reduction, temporal area composed of granular tiny scales.
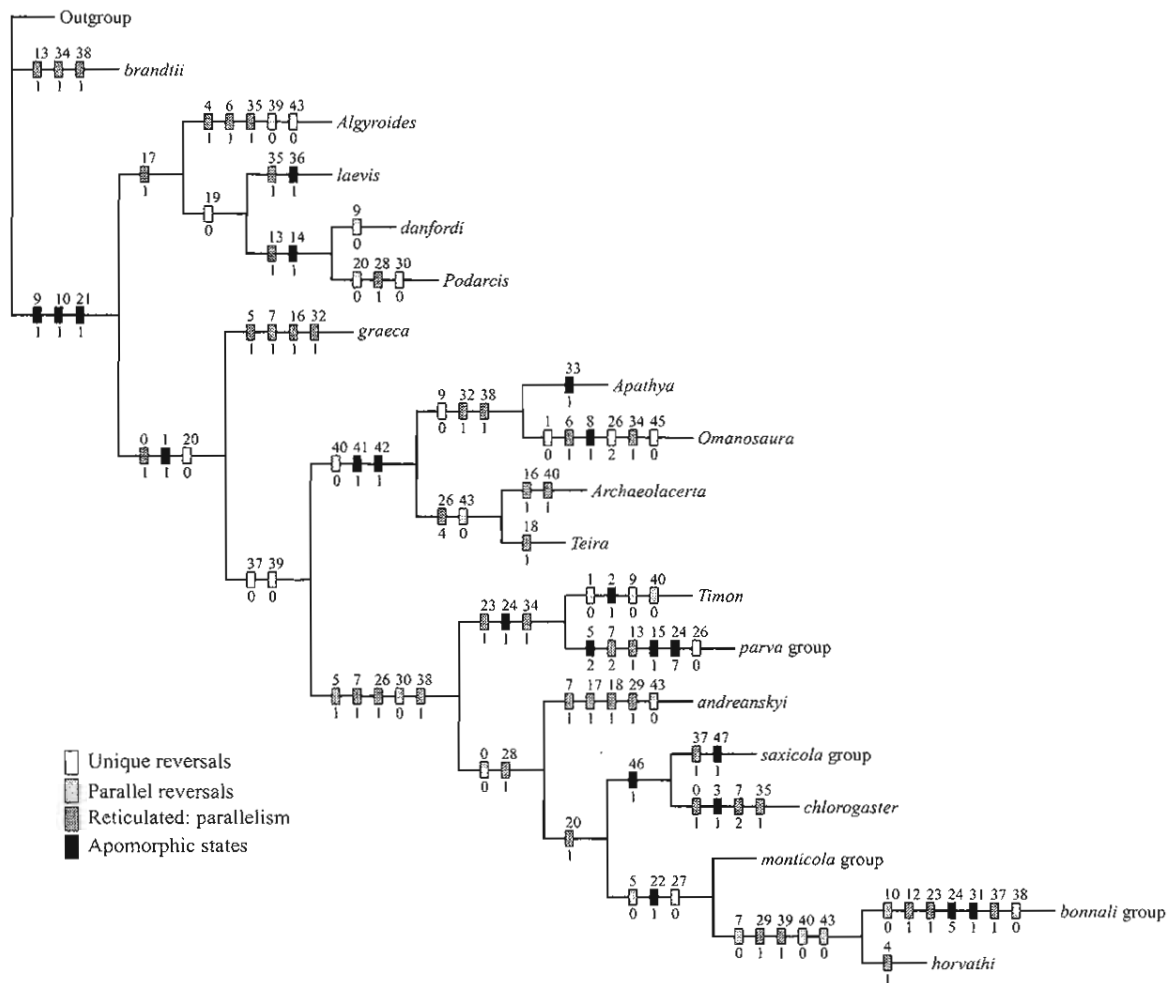47. Ocular window: (0) not developed; (1) developed.

48. Formation of big dorsal scales, probably for coalescence of small ones: (0) absent; (1) present.

49, 50. Form and size of the anal plate: (0, 0) small and single; (1, 0) big and single; (0, 1) divided.

51. Preanal plates: (0) all small and subequal; (1) two developed preanal plates before the anal; (2) only one developed preanal plate before the anal.

52. Collar: (0) present; (1) absent.

53, 54. Number of traverse rows of ventral plates: (0, 0) six rows; (1, 0) eight rows; (0, 1) ten or more rows.

55. 4th. toe subdigital lamellae: (0) not keeled; (1) keeled.

56, 57. Coloration of the throat (if differentiated from the ventral one): (0, 0) not differentiated; (1, 0) blue; (0, 1) red.

58. Ventral coloration of the group of the red (yellow-orange-red): (0) absent; (1) present (yellow-orange, orange or red).

59. Ventral coloration of the group of the green (yellow-green-blue): (0) absent; (1) present (yellow-greenish, green or blue).

60. Ventral pattern (punctuation): (0) absent (1) present.

61. Blue points in the most outer ventral scales: (0) absent; (1) present.

62. Adult dorsal patterns: (0) more or less striated or banded, at fewer in one of the sexes; (1) always reticulate.

63, 64. Juvenile dorsal patterns: (0, 0) with uniform strips or bands; (1, 0) without strips or bands, completely reticulated; (0, 1) patterns based on occelli, with or without other background motives.

65. Blue occelli in the shoulder: (0) absent; (1) present.

66. Occasional presence of a second row of femoral pores: (0) absent; (1) present.

Eto-biological characters.

67. Bite in flank during the courtship: (0) bite in the neck; (1) bite in the flank.

68. Bite in the thigh during the courtship: (0) only in neck or flank; (1) bite in thigh.

69. Type of reproduction: (0) oviparous; (1) viviparous.

70. Formation of clones of parthenogenetic reproduction by hybridization among closely related taxa: (0) absent; (1) present.

RESULTS AND DISCUSSION

Eurasian Lacertid Radiation

In the first analysis, 19 taxa have been included and 48 characters utilized (= 912 entries in the data matrix, from which 12.6%, including the outgroup [with great quantity of nonpolarized characters], are left as missing or variable) (Table 1). From the 48 characters, 28 present homoplasy, while 20 are unambiguous in their change. Nine characters have been considered as autapomorphies by the analysis because they are variable or unknown in any other of the taxa included in the analysis, but they have been left because is possible that they could be variable in some of the missing entrances (coded in both cases as "?").

TABLE 1. Character State Matrix from the Eurasian Lacertid Radiation

Eurasian Radiation	Characters																																															
	01	02	03	07	08	11	12	13	14	15	16	18	19	20	21	22	23	24	27	29	32	34	35	36	37	38	39	40	41	43	44	45	46	47	53	56	57	58	59	60	61	62	63	65	66	67	68	70
Outgroup	0	?	?	0	?	?	0	0	0	0	?	0	?	?	?	?	?	?	?	?	0	0	0	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
monticola	0	1	?	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	4	?	1	0	0	0	0	0	0	0	0	1	?	1	0	0	1	0	1	0	0	
bonnali	0	1	0	0	?	0	0	0	1	0	0	1	0	0	0	0	0	0	1	?	1	1	1	5	?	4	0	1	1	0	1	0	1	0	0	0	0	0	1	0	1	?	0	0	0	0	1	0	0
horvathi	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	4	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0
Archaeo	?	1	0	?	0	0	?	0	?	1	1	0	0	0	0	1	0	0	1	?	1	0	0	0	0	4	?	0	0	1	0	0	0	0	0	0	?	?	?	1	1	1	0	?	1	0	0
saxicola	0	1	0	?	0	1	0	1	0	1	1	0	0	0	0	?	0	?	0	1	1	1	0	0	0	0	4	?	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	1	1	1
chlorog.	1	1	0	1	0	1	0	2	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	?	1	1	0	0	0	0	0	1	0	1	0	1	0	0	1	0	1	0	1	1	0
danfordi	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	1	0	0	0	0	?	1	0	0	1	0	0	0	?	?	?	?	?	?	1	1	?	?	1	0	1	0	0
laevis	?	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	?	1	0	0	1	0	0	0	0	1	1	1	0	1	1	0	0	1	0	1	0	0	
Apathya	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	?	1	0	0	1	0	1	1	0	0	0	0	1	0	0	?	?	1	0	1	0	0	
brandtii	?	0	?	?	?	0	0	0	0	?	?	0	1	0	0	0	0	0	1	1	0	0	0	0	0	?	1	0	0	1	0	0	0	1	0	0	1	1	1	1	0	0	1	0	1	0	0	
Timon	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	4	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0
graeca	1	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	3	1	0	0	1	0	1	0	0	0	0	1	0	1	1	0	0	1	0	1	0	0
Teira	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	4	1	0	0	1	0	?	?	0	0	0	?	0	0	0	?	?	0	0	1	0	0	
andreans	0	1	0	0	0	?	0	2	0	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	?	3	1	1	1	0	0	0	0	0	0	?	?	0	1	0	0	0	0	0	1	0	0
Algyr.	0	?	0	0	1	0	1	0	?	1	1	0	0	0	0	0	0	1	?	1	?	1	0	0	0	0	3	1	0	0	?	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0
Podarcis	0	?	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0	3	1	1	0	0	0	0	0	0	0	0	1	0	?	1	?	?	?	0	1	0	0
parva	?	1	?	?	?	2	0	2	0	1	?	?	0	1	0	1	0	0	0	1	0	1	0	1	7	0	0	1	?	0	0	?	0	0	1	0	0	?	?	0	1	0	0	1	0	1	0	0
Omanos	?	0	?	?	?	0	1	0	1	0	?	?	0	0	0	0	0	0	1	?	1	0	0	0	0	2	1	0	0	1	0	1	0	1	0	0	0	1	0	0	1	1	?	0	0	0	0	

Fig 1. Preferred cladogram of the evolution of the Eurasian Lacertid Radiation. Length = 110 steps, CI = 0.50, RI = 0.51. Each mark in a branch indicates a character state change. In the upper part of these marks is the number of the character following the order of the input matrix and beginning by 0 (total 48 characters), in the lower part the character state adopted in this point.

The chosen cladogram (Fig. 1) has a length of 110 steps (ICI = 50; IRI = 51) that, after elimination the autapomorphic characters (12 characters) which do not add phylogenetic information (Carpenter, 1988), remains reduced to 71 steps (ICI = 53; IRI = 56).

The resulting tree presents a length sensibly minor than if having been generated by chance alone basing on the data matrix (PTP test: $p < 0.0005$). This enables us to consider that the data matrix possesses important phylogenetic information (G1 = -0.277786, $p < 0.001$ for 10,000 randomly generated trees). The output of both tests indicate us that

reliable conclusions could be extracted from the analysis.

The cladogram shows a basal trichotomy between the hypothetical ancestor; "*L.*" *brandtii* (characterized by three parallelisms: presence of vertebrae of B and C types, eight rows of ventral scales, and ventral colorations of the group of the blue) and the clade which contains the remainder of the Eurasian Radiation taxa.

This main clade (the valor of the "Bootstrap," BS hereinafter, is 0.14) is characterized by three synapomorphies (the reduction to six posterior dorsal vertebrae, presence of a fundamental number of 36

chromatides in the macrochromosomes, and the loss of the ribs associated to the third vertebrae [character unknown in "*L.*" *brandtii*]).

At time, this clade divides in two: one which includes *Algyroides*, "*L.*" *danfordi*, "*L.*" *laevis*, and *Podarcis*, characterized by a parallelism (sternal fontanelles cordiform); and another which includes the remainder species, characterized by a synapomorphy (the loss of the pterygoid teeth), a parallelism (9 premaxillary teeth, with abundant reversals in the ingroup) and a parallel reversal (spiny-like hemipenial microornamentation).

Podarcis and relative group

It includes *Podarcis* and related taxa ("*L.*" *danfordi*, "*L.*" *laevis*, and the *Algyroides* species) (BS = 0.98).

Algyroides appears characterized by 3 parallelisms (postfrontal shorter than the postorbitary, differentiated blue colorations in the throat of some species, and reduction to 25 vertebrae in the males), and 2 parallel reversals (disappearance of the spotting in the belly and lost of the blue occelli in the shoulder), constituting the sister group (adelphotaxon) of the remainder of the *Podarcis*-and-relatives clade (BS = 0.63), simultaneously characterized by one reversal (apical part of the hemipenis greater than the basal one), one parallelism (9 premaxillar teeth) and a parallel reversal (spiny-like hemipenial microornamentation).

Within this clade, "*L.*" *laevis* constitutes the species (or group of species) sister of the clade which includes the group of "*L.*" *danfordi* and *Podarcis*.

"*L.*" *laevis* is characterized by an autapomorphy (throat color differentiated from the remainder of the belly, with red tinges) and a parallelism (presence also of blue color in the throat differentiated from the belly color as an alternative to the red, geographically variable).

The "*L.*" *danfordi* plus *Podarcis* clade (BS = 0.95) shows a synapomorphy (clavicles usually closed) and a parallelism (vertebrae of the of C type).

The group of "*L.*" *danfordi* is characterized by a parallel reversal (more than six posterior dorsal vertebrae), while *Podarcis* presents a parallelism (presence of a single postnasal) and two parallel reversals (spiny-like hemipenial microornamentation and reduction to four supralabials previous to the subocular scale).

Main Eurasian radiation clade

The main Eurasian Radiation clade (BS = 0.14) presents "*L.*" *graeca* as sister species of the remainder group. "*L.*" *graeca* appears characterized by four parallelisms (27 vertebrae in the males, 28 vertebrae in the females, clavicles always open and masseteric plate undifferentiated due to secondary reduction).

The remainder group (BS = 0.54) is characterized by only one reversal (the loss of the red group tones differentiated in the belly, with posterior reversal again in some species groups from the Caucasus and Pyrenees) and a parallel reversal (disappearance of the dark spotting of the belly [recovered by parallelism in *A. horvathi* and the group of *A. bonnali*]). All this group is divided in two main clades: a clade with *Omanosaura*, *Apathya*, *Archaeolacerta*, and *Teira* (BS = 0.99), and another that includes the remainder species (BS = 0.55).

The first is characterized by two synapomorphies (dorsal patterns reticulated in the adults and juveniles) and a parallel reversal (disappearance of the blue points in the outermost ventral scales- that are not lost or revert again subsequently, in *Archaeolacerta*), and is divided it in two groups: one Eastern Mediterranean (BS = 0.99), which includes *Omanosaura* and *Apathya*, with a multiple reversal (more than six posterior dorsal vertebrae) and two parallelisms (masseteric plate undifferentiated and green ventral colorations); and other Western Mediterranean, with *Archaeolacerta* and *Teira* (BS = 0.95), characterized by a parallel reversal (loss of blue occelli in the shoulder) and a parallelism (NOR in a L type chromosome).

Omanosaura presents an autapomorphy (26 vertebrae in the females), 2 parallelisms (25 vertebrae in the males and eight rows of ventral scales), 1 parallel reversal (recovery of the pterygoid teeth) and two unique reversals (bite in the neck during the sexual intercourse, and a MS NOR-bearing chromosome [which appears also scattered in other taxa both in the Eurasian Radiation as *A. cyreni* and *T. pater* and is very widespread in the Advanced Saharo-Ethiopian clade, being also present in the outgroup *Z. vivipara*]).

Apathya presents an autapomorphy (existence of an ocular window, which appears in parallel form but structurally different in *Teira*) and a parallelism (vertebrae only of the A type).

Archaeolacerta s. str. is characterized by an autapomorphy (occasional presence of a second row of femoral pores) and two parallelisms (clavicles always open and recovery of the blue points in the outermost ventral scales).

Teira presents a parallelism (interclavicle with lateral branches clearly directed forward [parallel (?) to "*L.*" *andreanskyi*, that however appears in our analysis well separated]).

The clade containing the remainder taxa (BS = 0.55) is characterized by 4 parallelisms (27 vertebrae in the males, 28 vertebrae in the females, NOR in a L type chromosome, and ventral colorations of the group of the green [with loss in the group of *A. bonnali*]) and 1 parallel reversal (to 4 supralabials before to the subocular scale), and is divided in two groups:

a) A clade with *Timon* and the group of "*L.*" *parva* as sister groups (BS = 0.99), with a synapomorphy (one or more robertsonian fusions of chromosomes) and two parallelisms (presence of robertsonian fusions in general [redundant of the above-mentioned character], and eight or more rows of ventral plates).

b) The clade with "*L.*" *andreanskyi*, the caucasian species of the "*L.*" *saxicola* group and the ibero-pyrenaean species (BS = 0.95), defined by a parallelism (a single postnasal) and a parallel reversal (a usual presence of 7 teeth in the premaxillary [reverted in *A. cyreni* and "*L.*" *chlorogaster*]).

Clade of *Timon* and "*L.*" *parva*

Within this clade, *Timon* is characterized by an autapomorphy (nasal process arrow shaped [parallel in *A. cyreni*], and which however appears not very marked in *T. princeps*) and three parallel reversals (recovery of the pterygoid teeth, more than six posterior dorsal vertebrae, and loss of the blue points in the outermost ventral scales).

The group of "*L.*" *parva* ("*L.*" *parva* and "*L.*" *fraasii*) has 3 autapomorphies (7 robertsonian fusions in their karyotypes, clavicles always closed, and 28 vertebrae in the males), 2 parallelisms (caudal vertebrae of B and C types, 29 vertebrae in females) and a unique reversal (NOR bearing chromosome of m type in "*L.*" *parva* [although of L type in "*L.*" *fraasii*]).

Group of Western Palaearctic mountain lizards

The clade that contains the remainder species of the Eurasian Radiation, includes groups in which most of their components are mountain species.

"*L.*" *andreanskyi* appears as the adelphotaxon of all the iberocaucasian species plus *A. horvathi*, assigned previously to *Archaeolacerta* s. l. This species, is characterized by a parallel reversal (lack of blue occelli in the shoulder) and four parallelisms (29 vert. in the females [also in the "*L.*" *raddei* group from the Caucasus], sternal fontanelle slightly cordiform [that also appears in some specimens of the caucasian species], interclavicles with the lateral branches directed forward [although inflected back toward their more distal part], and supranasal in contact with the loreal [like in the pyrenean species and *A. horvathi*]).

Their sister group (BS = 0.87), includes "*L.*" *chlorogaster*, the group of "*L.*" *saxicola*, as well as *A. horvathi* and the groups of *A. monticola* and *A. bonnali*, and is characterized by a unique parallelism (hemipenial microornamentation crown-shaped).

Within this group of species from the Iberian Peninsula, Alps, Caucasus, and Near East, two groups are clearly distinguished: a caucasian one (group of "*L.*" *saxicola*, including "*L.*" *chlorogaster*) (BS = 0.96) and another western european (ibero-pyrenean and alpine), with the groups of *A. monticola*, *A. bonnali*, and *A. horvathi* (BS = 0.98).

The caucasian group is characterized by a synapomorphy (presence of bite to the female in the thigh during the courtship); and includes the group of "*L.*" *saxicola*, characterized by an autapomorphy (formation of parthenogenetic clones by hybridization among his members) and a parallelism (reappearance in their ingroup of ventral colorations of the group of the red), and to "*L.*" *chlorogaster*, characterized by an autapomorphy (postfrontal bone longer that the postocular) and three parallelisms (9 premaxillary teeth, 29 vertebrae in the females and blue color in the throat).

The group of mountain species from Western Europe, which includes the ibero-pyrenean species and *A. horvathi*, is characterized by a synapomorphy (the loss of the microchromosomes in their karyotype), a unique reversal (rostral and internasal plates in contact) and a parallel reversal (to 26 vertebrae in the males). Within this group, the Iberian Group appears to be the sister group of the *A. bonnali* one (Pyrenean

Group) (BS = 0.99) (*A. bonnali*, *A. aurelioi*, and *A. aranica*) plus *A. horvathi*.

The Iberian Group (*A. monticola* and *A. cyreni*) doesn't present any synapomorphy in our analysis, while their sister group (pyrenean plus *A. horvathi*) is characterized by 2 parallelisms (supranasal in contact with the loreal and recovery of the dark pattern in the belly [variable in the group of *A. monticola* since it appears in this but is quite reduced in *A. cyreni*]) and 3 multiple reversals (reduction to 27 dorsal vertebrae in the females, the loss of the blue occelli in the shoulder, and a tendency to the loss of the blue points in the outermost ventral scales).

A. horvathi is characterized by a parallelism (postocular bone greater than the postfrontal), while the group of *A. bonnali* (*A. bonnali*, *A. aranica*, and *A. aurelioi*) remains finally characterized by 2 autapomorphies (supracilliary granules reduced, presence of Z1Z2W sexual chromosome heterogamety in their interior), 3 parallelisms (existence of robertsonian fusions, at fewer five pair of robertsonian fusions in the karyotype, and ventral colorations of the group of the red) and 2 parallel reversals (presence of ossificated ribs associated to the third vertebra, and loss of the green colorations in the belly).

Discussion of the Relationships Among the Taxa of the Eurasian Radiation of the Lacertidae

The preliminary data here obtained gives us some clear groups of taxa, although for obtaining of a more robust phylogeny, would be necessary the study of greater number of characters, due to the high grade of homoplasy and parallelism that appears in the ingroup.

The firmest and important conclusion of the analysis is that *Archaeolacerta* s. l. (in the currently utilized sense) is a polyphyletic assemblage, not a natural taxon, composed, at least, of two holophyletic taxa.

The first of them, *Archaeolacerta* s. str., presents an autapomorphy: the frequent presence of a second row of femoral pores (that seems to be absent, nevertheless, in *A. mosorensis*). Also, is characterized in our general cladogram by two parallelisms (presence of clavicles always open and the recovery of the presence of blue occelli in the outermost rows of ventral scales). If *Omanosaura* doesn't belong to the Eurasian radiation, as postulates Arnold (1989a) and

against the opinion of Mayer and Benyr (1994), the wholly reticulated dorsal patterns of adults and juveniles (occasionally variable or with clear dorsolateral stripes, like in some *Teira*) could also constitute an autapomorphy of this taxon.

The second group, phylogenetically well differentiated from the anterior, is the clade which includes all the mountain species from Western Europe, the Caucasus and the Near East. This group is constituted by two subgroups very defined, which share a parallelism (hemipenial microoornamentation crown-shaped). The valor of BS of this clade is high, but not statistically significant (0.87). Nevertheless, low values of BS not necessarily implicate lacking of confidence in a node, but rather that there are relatively few character changes in that node (Murphy et al., 1996).

The Western European group of mountain lizards is characterized by the loss of microchromosomes (autapomorphy), the presence of contact between rostral and internasal scales (unique reversal) and the reduction to 26 vertebrae in the males (parallel reversal) and seems to constitute a natural group very well defined (BS = 0.98).

The same could be said of the caucasian and Near East species, to which we assimilate "*L.*" *chlorogaster* (BS = 0.96). This latter has been attributed informally to the group, and although it presents some different characters that denote a certain degree of isolation (like the postfrontal longer than the postocular [an autapomorphy], the presence of nine premaxillary teeth, 29 vertebrae in the females, and of blue color in the throat [a parallelism], as well as the keeled scales [present also the "*L.*" *praticola* and probably with ecological significance to the ground life]), any of these characters seem to suppose a consistent impediment in order to unite "*L.*" *chlorogaster* with the rest of the "*L.*" *saxicola* group. On the other hand they share contiguous geographical areas. "*L.*" *chlorogaster* presents in common with the species of the group of "*L.*" *saxicola* a synapomorphy, the possibility of subjection of the female by the thigh during the courtship. On the other hand, "*L.*" *saxicola* presents a satellite DNA (pSHS) that doesn't appear in other genera studied by Capriglione (1995), including *Archaeolacerta* neither *Podarcis*, which guarantees the grade of isolation of this taxon, at fewer concerning to the true *Archaeolacerta*. Moreover is characteristic of this group that, in several of

the species, there has been an extensive hybridization from the end of the Pleistocene, giving place to parthenogenetic clones ("parthenogenetic species": *"L."* *armeniaca,* *"L."* *dahli,* *"L."* *rostombekovi,* *"L."* *unisexualis,* *"L."* *uzzelli,* *"L."* *sapphirina,* and *"L."* *bendimahiensis;* [see Darevsky and Danielyan, 1977; Darevsky et al., 1985; Schmidtler, 1993; Schmidtler et al., 1994]).

We believe that the polyphyly of *Archaeolacerta* s. l. advise to divide this taxon in the three monophyletic taxa above-mentioned.

On the other hand, other associations seem to be quite clear, like the one of the *Algyroides* species and the groups of *"L."* *danfordi* – *"L."* *laevis* (*danfordi, oertzeni, anatolica, laevis, kulzeri* and cf. *kulzeri;* [see Eiselt and Schmidtler, 1986; Hoofien et al., 1990; Bischoff and Franzen, 1993; Bischoff and Schmidtler, 1994]) with *Podarcis* (BS = 0.98). The association of *"L."* *laevis* and *"L."* *danfordi* with *Podarcis* already was pointed out by Arnold (1989a) being based on in the type of tail vertebrae and the presence of big lobes in the hemipenis. However, the order of enbranchment of *"L."* *laevis* proposed in our cladogram is not significant (BS = 0.63).

The relationship between *Omanosaura* (*O. jayakari* and *O. cyanura*), *Apathya* (*A. cappadocica*), *Teira* (*T. perspicillata* and *T. dugesi*), and *Archaeolacerta* s. str. (*A. bedriagae, A. mosorensis,* and *A. oxycephala*) seems to be clear (BS = 0.99). On one hand, differentiate us a centro-occidental mediterranean group, with two genera (*Archaeolacerta* and *Teira*) (BS = 0.95) and on the other hand, another group oriental mediterranean (with *Apathya* and *Omanosaura*) (BS = 0.99), whose relationships appear clear in our analysis and also agree with the opinion of Arnold (1972) (see but, a point of doubt in Leptien and Böhme, 1994).

The relationship between *Timon* (*T. lepidus, T. pater,* and *T. princeps*) and the group of *"L."* *parva* (*"L."* *parva* and *"L."* *fraasii*), although well supported on our tree demands a certain caution due to the fact that it is still necessary a complete osteological study of these latter. Nevertheless, both taxa appear very significantly related in the analysis (BS = 0.99) and it has already been suggested a relationship between *"L."* *parva* and *Timon* based on protein electrophoresis (Engelmann and Guillaume, 1981). The attribution of the generic status for the group of *"L."* *parva* is certain, as indicated by Bi-

schoff (1991), although all the aspects yet unknown of these species should be studied before pronouncing on this topic.

The relationship between *"L."* *graeca* and the species of *Podarcis* have been suggested, so much with immunological (Mayer and Benyr, 1994) and karyological techniques (Olmo et al., 1991, 1993, 1995). It also shares with *Podarcis* a satellite DNA relatively extended (that, nevertheless, also present in *Algyroides* and *Teira* between the taxa studied by Capriglione, 1995). In our cladogram, the position of *"L."* *graeca* is not among the nearest taxa to *Podarcis,* although for their basal position concerning the main Eurasian Radiation clade, their presumed relationship with *Podarcis* could be based on symplesiomorphies.

The relationship of *"L."* *andreanskyi* with the mountain species from Western Europe and Caucasus is a new and significant suggestion in our analysis (BS = 0.95). Usually it has been related to be near *Podarcis* (Arnold, 1973, 1989 a), although other authors approach or include it in *Teira* (Böhme and Corti, 1993; Mayer and Bischoff, 1996), in spite of the fact that their external appearance looks very different to other *Teira* spp. On the other hand, the orientation of their interclavicular branches would merit a more detailed study. Also, their immunological distance is quite high concerning whatever of the groups to those it has been attributed (see Mayer and Benyr, 1994). For their particular characteristics and their position relatively isolated it could deserve a generic or subgeneric appropriate name, but their attribution is still uncertain.

Although remain important gaps in the study of *"L."* *brandtii,* it seems clear that their basal position in the phylogenetic tree indicates a relatively early separation of the main trunk of the Eurasian Radiation. Already Boulenger (1920) considered it one of the most primitive members of the *Lacerta* group. If confirmed this position relatively isolated, endorsed by the presence of a fundamental number of 40 in their karyotype (as in *Gallotia*), it seems logic also the inclusion of this species in his own genus.

Starting from the previous data, it could be observed that there are a good number of phenomenons of vicariancy between both Mediterranean sides:

— *Algyroides* in respect to *"L."* *danfordi* and *"L."* *laevis;* and these last two concerning *Podarcis,* whose more primitive representatives seem to be in

the Iberian Peninsula and nearer areas (*P. bocagei, P. muralis, P. hispanica, P. lilfordi, P. pityusensis,* and *P. tiliguerta*) since they have not acquired the number of 27 vertebrae in the males and 28 in the females, neither the form of insert of the external lips of the "sulcus spermaticus" (Arnold, 1973; 1989 a).

— The group of *Teira* (probably of african origin) and *Archaeolacerta* (european) in the western Mediterranean, concerning *Apathya* (Asia Minor) and *Omanosaura* (Arabian Peninsula) of the eastern Mediterranean.

— The group of "*L.*" *parva* ("*L.*" *parva* in the Near East and "*L.*" *fraasii* in the mountains of the Lebanon) with a pattern of distribution similar to other groups of the same area, like the one of *Daboia xanthina* (Nilson and Andrén, 1986), concerning *Timon*, whose origin could be supposed in Western Europe, where two species (*T. lepidus* and *T. pater*) exist, probably separated from the end of the Messinian time by the Gibraltar strait.

— The caucasian ("*L.*" *saxicola* group and "*L.*" *chlorogaster*) and the western Mediterranean (Ibero-pyrenean species plus *A. horvathi*) groups. Within this latter, *A. horvathi* appears separated at the other side of the Alps very probably due to the effect of the Pleistocene glaciations, in a clear example of the so-called Keilhack's discontinuity (Margalef, 1986).

Some of them, like the relationships between the caucasian and ibero-pyrenean groups of mountain lizards find parallel in another well-known Ibero-Caucasian disjunctions (*sensu lato*), like in *Pelodytes* (*P. punctatus* in Western Europe and *Pelodytes caucasicus* in the Caucasus and Pontic Chains); *Chioglossa lusitanica* in the Iberian Peninsula concerning *Mertensiella* in Turkey (*M. luschani*) and Pontic Chains and Caucasus (*M. caucasica*). Other examples are very numerous (*Blanus, Mauremys,* etc. between the reptiles), *Cechenus* and *Iniopachys* among the *Caraboidea* (*Coleoptera*), *Galemys,* and *Desmana* in Mammals, etc.

In some cases, the disjunction between the eastern and western parts of the Mediterranean is due to the glaciations [Keilhack's discontinuity] in the northern shore of the Mediterranean, while in the southern shore is due to the increasing postglacial aridity of the N. Africa. The affected taxa were in some cases several species of the same genus in both sides of the discontinuity (it is the case of *A. horvathi*

concerning the remainder of ibero-pyrenean species; of *Blanus strauchi* versus *B. cinereus*; *B. mettetali* and *B. tingitanus*; *Mauremys leprosa* versus *M. caspica,* etc). In other cases, like in the above-mentioned in which there are different genus implicated in relation of sister groups, the isolations should be more old, of around 20 million years (see references in Böhme and Corti, 1993; for a synthesis of the vicariant events in several groups see Oosterbroek and Arntzen, 1992).

Taxonomic Revision of the Mountain Lizards from Europe and Near East (*Archaeolacerta* s. l.).

Like we have indicated above, *Archaeolacerta sensu* Auct. is a polyphyletic taxon, which includes almost two monophyletic taxa: the clade of *Archaeolacerta* s. str. on one hand, and the one which includes the Caucasian species and the western european ones (ibero-pyrenean species plus *A. horvathi*) on the other, both phylogenetically well differentiated between them).

The clade that contains as sister groups the Caucasian species and the western european ones, presents an unique synapomorphic character, the parallel apparition of crown-shaped hemipenial microoornamentation. The two groups are differentiated and well characterized, and we believe that they constitute two different genera.

Archaeolacerta s. str. is sustained in an autapomorphy (frequent presence of femoral pores in a second row) and two parallelisms (clavicles always open and presence of blue points in the outermost ventral ranges).

The taxonomy of this genus remains as follows:

Balcanic and Tyrrhenic species

Archaeolacerta Mertens, 1921. *Sensu Novo*

Type species. *Lacerta bedriagae* Camerano, 1885.

Included species. *Archaeolacerta bedriagae* (Camerano 1885), *Archaeolacerta mosorensis* (Kolombatovic, 1886), and *Archaeolacerta oxycephala* (Duméril and Bibron, 1839).

The grade of proximity of the Tyrrhenic species with the other two Balcanic species requires a more deep study.

Diagnosis. Lacertidae of small size, very adapted to the saxicolous life, with very depressed head and bodies, long members and long and narrow

heads. Tail notably long and slender. Dorsal pattern reticulate or break in thick points, without conspicuous blue occelli in the shoulder, but with blue points in the outermost ventral ranges (masked by the blue color of the belly in *A. oxycephala*). Five supralabials previous to the subocular. Two postnasal scales. Clavicles always open. Characterized within the species of the Eurasian Radiation by the occasional presence of a second row (incomplete) of femoral pores. Karyotype with 38 chromosomes (36 macro and two microchromosomes).

Description. Rostral and internasal scales in wide contact or separated. One or two postnasal scales (usually two). Without contact between the supranasal and loreal scales. Usually five supralabials previous to the subocular scale. Supracilliary granules in a complete row. Masseteric plate very variable, from very big until totally reduced and inconspicuous. Palpebral window absent. Dorsal scales small or medium sized, more or less granular and without marked keels. Anal plate of variable size. Six rows of ventral scales. Occasionally a second incomplete row of femoral pores present.

Adults and hatchlings reticulated or at fewer with the design broken up in thick points from the birth. Without blue occelli in the shoulder. Ventral pattern variable (present or absent according to the species). Blue points in the outermost ventral scales usually present.

Seven or nine premaxillary teeth. Nasal process of the premaxilla long and undifferentiated. Postfrontal and postorbitary bones separated and subequal in size or with the first greater that the second. Anteromedial process of the postorbitary and anterodistal of the postfrontal bones developed. Maxilojugal suture not "stepped," without marked inflections.

Sexual dimorphism in the vertebral number. Males present modal numbers of 26 or 25 vertebrae, while the females present 26 to 28. Third presacral vertebra always without developed bony ribs associated. Usually six posterior dorsal vertebrae. Clavicles always open. Interclavicle typical cruciform, with lateral branches perpendicular to the medial axis. Sternal costal formula (3+2). Sternal fontanelle oval, occasionally reduced or absent. Caudal vertebrae of A and B types.

Hemipenis with the typical aspect in the family, with their apical part greater that the basal one. Their lobes profusely plicated and without apical tubercles neither thorns in their more distal part. Hemipenial microornamentation variable, crown-shaped in *A. mosorensis* and *A. oxycephala* or spiny-like in *A. bedriagae*.

Karyotype composed (in the two species in which is known) by 38 acrocentric chromosomes (36 macro and 2 microchromosomes). Nuclear Organizer in a pair of big chromosomes (L type). ZW sex chromosomes.

Courtship with subjection of the female by means of a bite in the flank.

Geographical distribution. Corsica, Sardinia, and Dinaric Mountains (Croatia, Herzegovina, and Montenegro).

Biogeography. The age of the taxon, according to Mayer and Benyr (1994) is of 18 to 20 M.Y. The ancestor of *A. bedriagae* would have reached Corsica and Sardinia during the Messinian time (around 5 M.Y.), remaining subsequently isolated and differentiating from the line that give place to *A. mosorensis* and *A. oxycephala*. From these last, in spite of the fact that we lack genetic data on their differentiation, it could be hypothesized for their notable grade of divergence that they also will have been separated early.

Their probable adelphotaxon is *Teira*. This last genus includes two species: *T. perspicillata* of the NW Africa (introduced also in Menorca); and *T. dugesii* of Madeira and Selvagems islands (introduced in Azores and Lisboa).

Phylogenetic relationships between the species of *Archaeolacerta* s. str. The detailed study of the twelve characters (Table 2) which vary between the three species of this genus, brings us a unique cladogram (Fig. 2) with a longitude of 15 steps (CI = 80 and RI = 50). The tree presents a relationship between the three species congruent from a zoogeographic point of view, with a greater relationship between the two Balcanic species, that form a clade supported in a synapomorphy: the frequent reduction of the number of vertebrae of the males to 25 [a curious and interesting difference between our vertebral counts and the ones from Arnold (1973) exists in this point], and a unique reversal: the reduction of the ventral pattern. *A. mosorensis* is characterized among this genus by an autapomorphy (anal plate of big size), a parallelism (presence of 9 premaxillary teeth, like *A. bedriagae*) and a unique reversal (contact be-

tween the rostral and internasal scales). *A. oxycephala* appears characterized by two autapomorphies (a notably bigger postfrontal than postorbitary, and the frequent reduction in the females to 26 presacral vertebrae), as well as for a unique reversal (disappearance of the ventral colorations of reddish tones) and two parallelisms (ventral coloration of the group of the green [blue in this case] and occasional presence of a second row of femoral pores).

A. bedriagae, that appears as the adelphotaxon of the other two species, presents an autapomorphy (presence of a single postnasal), an unique reversal (spiny-like hemipenial microornamentation) and two parallelisms (occasional presence of a second row of femoral pores and of nine teeth in the premaxilla).

The genetic studies show, nevertheless, that the time of separation between the Balcanic species (only *A. oxycephala* studied) and *A. bedriagae* is quite high. Contradiction exists between the genetic and the karyological-morphologic data, so much for the times of divergence as well for the differentiation degree in respect to other taxa (see comments in Mayer and Arribas, 1996). It is also interesting to underline that the morphological differentiation as well as the degree of genetic divergence between the described subspecies of *A. bedriagae*, are relatively high for a unique species (Guillaume and Lanza, 1982) and perhaps the Tyrrhenic area is inhabited by more than the currently single recognized species. On *A. mosorensis* very few could be said, since it have not been studied neither from a genetic or a karyological point of view (it is the only european species of unknown karyotype).

Phylogenetic relationships among the mountain lizards from western Europe

As we indicate above, within the Eurasian Radiation, the clade of the species characterized by the lack of microchromosomes in their karyotype constitutes a monophyletic group. Also, it is characterized by a parallel reversal and a unique reversal in respect to other taxa: the apparition of the contact between the rostral and internasal scales, and the return to the number of 26 vertebrae in males, respectively. This clade constitutes a monophyletic unnominated taxon that we described now:

Iberolacerta gen. nov.

Type species. *Lacerta monticola* Boulenger, 1905.

Fig. 2. Cladogram (preferred and consensus) from *Archaeolacerta* s. str. species. Length = 15; CI = 0.80; RI = 0.50.

Included species. *Iberolacerta aranica* (Arribas, 1993); *Iberolacerta aurelioi* (Arribas, 1994); *Iberolacerta bonnali* (Lantz, 1927); *Iberolacerta cyreni* (Müller and Hellmich, 1937); *Iberolacerta horvathi* (Méhely, 1904); *Iberolacerta monticola* (Boulenger, 1905).

Diagnosis. Group of lizards of small size and moderately saxicolous. Coloration and pattern typical of the Eurasian Radiation (vertebral stripes, costal bands, etc.). Belly usually spotted. A unique characteristic among all the Eurasian Radiation is the lack of microchromosomes in their karyotype (36 macrochromosomes or less, since a part of the genus presents robertsonian fusions of acrocentric chromosomes to give biarmed ones). They also present four supralabials previous to the subocular scale, rostral frequently in contact with the internasal, and only one postnasal present. Males with 26 vertebrae, females 27 to 29, according to species.

Description. Lizards of small size, moderately saxicolous, with typical dorsal pattern, formed by a vertebral band of thick marks or two arrays of small paravertebral dots. Dark dorsolateral stripes don't exist. Costal bands uniform or reticulated, with their upper border smooth or scalloped. An irregular line of points below the costal band. Background colors brown, gray or greenish, occasionally more clear toward the dorsolateral areas. With or without blue

TABLE 2. Character State Matrix from *Archaeolacerta* s. str.

Archaeolacerta s. str.	Characters											
	0	0	1	1	3	4	4	4	5	5	6	6
	1	7	2	4	2	0	1	9	8	9	0	6
Outgroup	0	0	0	0	1	1	0	0	1	1	1	0
mosorensis	1	0	1	0	1	0	0	1	1	0	0	0
oxycephala	0	1	1	1	1	1	0	0	0	1	0	1
bedriagae	1	0	0	0	0	?	1	0	1	0	1	1

occelli in the shoulder according to the species (*I. monticola* and one ssp. from *I. cyreni* with occelli; the remainder taxa have lost them). Ventral parts with colors of the group of the green (*I. monticola*, *I. cyreni*, and *I. horvathi*) or of the red (*I. aurelioi*). In some species, this coloration has been reduced and only appears occasionally underneath the posterior calves (*I. bonnali* and *I. aranica*). The belly could present points (*I. monticola*, *I. aurelioi*, and *I. aranica*), be reduced to the more external ventral rows (some *I. horvathi* and *I. cyreni*), or be lacking (other *I. horvathi* and *I. cyreni*). Blue points in the outermost ventral ranges could be common (*I. monticola* and *I. cyreni*), be rare (*I. aranica* and *I. bonnali*) or absent (*I. aurelioi* and *I. horvathi*).

Rostral and internasal plates commonly in contact (exceptions frequent in *I. monticola* and rarer in *I. aurelioi*). A single postnasal, that in *I. horvathi* and in the pyrenean species does not contact with the internasal. Usually four supralabials before the subocular scale. Supracilliary granules in a complete or reduced row (this last situation in the pyrenean species). Masseteric and tympanic plates well differentiated and quite big (sometimes reduced in *I. aurelioi*). Without palpebral window. Dorsal scales flat, more or less granular. Six traverse rows of ventral scales. Anal plate of variable size. A semicircle of preanal scales, the more anterior pair of which are generally something more enlarged.

Premaxilla with 7 (*I. aranica*, *I. bonnali*, *I. aurelioi*, *I. horvathi*, and most of *I. m. cantabrica*) or 9 teeth (*I. cyreni*, *I. m. monticola* and some *I. m. cantabrica*). Without pterygoid teeth. Processus nasalis of variable shape: undifferentiated (pyrenean species, *I. horvathi* and a good part of the *I. m. cantabrica*) or arrow shaped (*I. cyreni*, most *I. m. monticola*, and some *I. m. cantabrica*). Postorbitary and postfrontal separated from the birth and with similar lengths (except *I. aurelioi* and *I. horvathi*, in which the first is notably longer than the second). Anterodistal process of the postfrontal present (except in *I. aurelioi*). Anteromedial process of the postorbitary usually present (absent in *I. aurelioi* and *I. bonnali*). Maxilojugal suture not stepped, without marked inflections.

Sexual dimorphism in the vertebral number. Males present 26 vertebrae and females usually 27 (pyrenean species and *I. horvathi*) or 27, 28 or 29 (*I. monticola* and *I. cyreni*). Ribs associated to the third vertebra absent (*I. monticola*, *I. cyreni*, and *I.*

horvathi) or present (pyrenean species). Usually six posterior dorsal vertebrae. Sternal costal formula (3 + 2). Preautotomic caudal vertebrae of A and B types (only A in the pyrenean species and perhaps in *I. horvathi*). Variable clavicles, generally open in some species (*I. horvathi*, *I. aranica*, and *I. bonnali*) and closed in another (*I. m. monticola*, *I. cyreni*, and *I. aurelioi*), or very variable (*I. m. cantabrica*). Sternal fontanelles oval, occasionally reduced or absent (main part of *I. aurelioi*). Interclavicle typical cruciform, with branches perpendicular to their antero-posterior axis.

Hemipenis with the apical part more developed than the basal one, plicated lobes and without apical tubercles or spines. Hemipenial microornamentation usually crown-shaped, although some species present it usually reverted to the spiny-like type (*I. bonnali* and *I. aranica*).

Karyotype exclusively composed of macrochromosomes ($2n = 36$ or less). Microchromosomes absent. Frequently a drastical reduction of the number of chromosomes by robertsonian fusions (pyrenean species). Sexual heterogamety ZW or more rarely Z1Z2W (this latter in *I. bonnali* and *I. aurelioi*). Nuclear organizer of L type and in telomeric position (except in *I. cyreni*, that is of MS type and subtelomeric).

Courtship with subjection of the female by means of a bite in the flank.

Etymology. *Iberolacerta*, of Iberia, the ancient name of the Iberian Peninsula, where inhabit and probably originated most of the species of this genus.

Geographical distribution. Mountains of the central and north of the Iberian Peninsula, Pyrenees, Eastern Alps, and North of the Dinaric Chains.

Biogeography. The age of the taxon is of 15 to 18 M.Y. (although according to Lutz and Mayer [1985], *I. horvathi* would be nearer to *A. bedriagae*) (see for instance Mayer and Arribas, 1996). The genetic data indicate that the more differentiated species is *I. horvathi*. We could postulate a more extensive preglacial distribution of the genus than the current one, that would have been cut in two parts with the beginning of the Plio-Pleistocenic climatic deterioration, leaving *I. horvathi* in their refuge to the eastern Alps and, the other species (probably differentiating already in two groups), in the Pyrenees and Western Iberian Peninsula. The pyrenean group presents a great divergence both morphological and karyologi-

cal and, within it, *I. aranica* would have separated first and subsequently *I. aurelioi* and *I. bonnali* along the Plio-Pleistocene. *I. cyreni* and *I. monticola* would also have been separated during the quaternary glaciations.

I. horvathi, *I. monticola*, and *I. cyreni* are a morphologically, osteologically, and karyologically homogeneous group, and remain as *Iberolacerta* s. str. For the characteristic group of pyrenean mountain lizards we create the subgenus:

Pyrenesaura subgen. nov.

Type species. *Iberolacerta (Pyrenesaura) bonnali* (Lantz, 1927).

Included species. *Iberolacerta (Pyrenesaura) aranica* (Arribas, 1993); *Iberolacerta (Pyrenesaura) aurelioi* (Arribas, 1994); *Iberolacerta (Pyrenesaura) bonnali* (Lantz, 1927).

Diagnosis. Very characteristic group of small lizards with supracilliary granules reduced, ventral colorations [if exist of the group of the red (yolk-yellow or orange), presence of ossificated ribs associated with the third vertebrae, presence in his interior of Z1Z2W sex chromosome system, and karyotypes rich in biarmed chromosomes produced by robertsonian fusions.

Etymology. From Pyrene, daughter from Bebryx, a mythical king from the Bebrices (legendary people from the Cerdanya in the Pyrenees), and lover from Herakles in his tenth legendary work. Seduced and abandoned, was dead by wild animals, and Herakles, contrited, buried her under an enormous amount of rocks which he named Pyrenees (Herodote). In other legend, Pyrene gave birth to a reptile after to death. Sauros (Greek): a lizard.

Geographical distribution. Central Pyrenees, in the supraforestal alpine areas of the different massifs, acting from a biogeographical point of view as insular lizards ligated to these alpine environments. In fact, this particular group constitutes the only truly alpine-dwelling group of lizards (usually 2000 m above sea level) from Europe.

Biogeography. See under *Iberolacerta*.

Phylogenetic relationships between the *Iberolacerta* species

We have performed a detailed analysis within this group in order to find the relationship among the different species, as well as their comparative differentiation. For it, we have utilized 22 characters which present variation in the ingroup (Table 3). The result is two trees of identical length (29 steps, CI = 0.89 and RI = 0.89) that differ in the position of *I. horvathi*, as is reflected in the indetermination of the consensus tree (30 steps, CI = 0.86, RI = 0.86) (Fig. 4). Our preferred cladogram (Fig. 3) is the one which assemble *I. horvathi* with *I. monticola*. Nevertheless, the consensus tree (Fig. 4) is much more short (long: 29 steps, CI = 0.89; RI = 0.89) and presents the relationships of *I. horvathi* as a tricotomy, with the iberian group (*I. monticola* and *I. cyreni*) and the pyrenean group (*I. bonnali*, *I. aranica*, and *I. aurelioi*) separated from it.

The synapomorphic characters that unite *I. horvathi* with the clade of *I. monticola* and *I. cyreni* are the lack of the rib associated to the third vertebra and a unique reversal (the lack of colorations of the group of the red). We parted from the fact that the presence of associated ribs at the third vertebra is the primitive state of the character, since it appear in several of the outgroups employed in the determination of the polarities (f. i. in *Z. vivipara*, *Gallotia* spp., *Psammodromus* spp.) and we considered that the apomorphic state is their reduction. Nevertheless, in the context of

TABLE 3. Character State Matrix from *Iberolacerta* gen. nov.

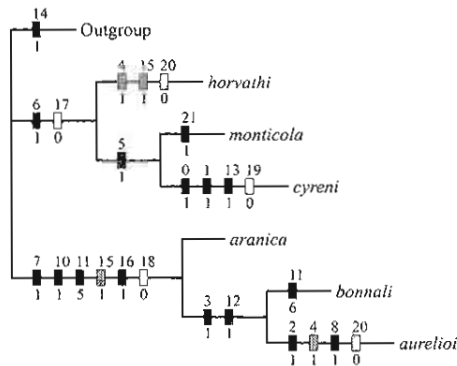| *Iberolacerta* gen. nov.	Characters																					
	0	0	0	0	0	1	1	1	2	3	3	3	3	3	4	4	4	5	5	5	5	6
	1	3	5	6	8	3	6	9	4	2	6	7	8	9	0	3	5	6	7	8	9	3
Outgroup	0	0	0	0	0	0	?	0	0	1	0	0	0	0	1	0	0	1	1	1	1	0
monticola	?	?	0	0	0	1	1	0	0	1	0	0	0	0	?	0	0	0	1	1	1	1
cyreni	1	1	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	1	0	1	?
bonnali	0	0	0	1	0	0	0	1	0	?	1	6	1	0	0	1	1	1	0	1	1	0
aranica	0	0	0	0	0	0	0	1	0	?	1	5	0	0	0	1	1	1	0	1	1	0
aurelioi	0	0	1	1	1	0	0	1	1	1	1	5	1	0	0	1	1	1	0	1	0	0
horvathi	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0

Fig. 3. Preferred cladogram from *Iberolacerta* gen. nov. Length = 29; CI = 0.89; RI = 0.89.
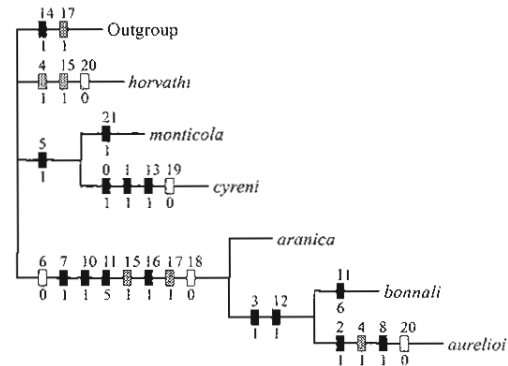

Fig. 4. Consensus tree from *Iberolacerta* gen. nov. Length = 30; CI = 0.86; RI = 0.86.

the general cladogram from the Eurasian Radiation, the third vertebra rib has already disappeared in the ancestors of *Iberolacerta*, for which the more apomorphic state would be the "recovery" of this (which is, therefore, an autapomorphy of the pyrenean group).

I. horvathi appears characterized within *Iberolacerta* by two parallelisms and a multiple reversal. The parallelisms are, on one hand, the possession of a postorbital notably longer than the postfrontal (parallel to *I. aurelioi*) and to present the supranasal scale in contact with the loreal (that also appears in the pyrenean species); the multiple reversal is the loss of the blue points in the outermost ventral ranges (that also fail in *I. aurelioi*, and rarely appear in *I. bonnali* and *I. aranica*).

The iberian group (*I. monticola* plus *I. cyreni*) is sustained in a synapomorphy, the increment in the number of vertebrae in the females (27, 28 or 29, against the 27 almost universal in the other species of the genus). Also, it could be included the number of 9 teeth in the premaxilla, here considered as autapomorphic of *I. cyreni*, but that in monticola appears occasionally, as equally occurs with the processus nasalis arrow-shaped. For their part, *I. monticola* presents an autapomorphy: the generalized presence of blue occelli in the shoulder (that seem to have been lost in *I. cyreni*, except in the ssp. *martinezricai*); while *I. cyreni* appears characterized by 3 autapomorphies (9 teeth in the premaxilla, the arrow-shaped processus nasalis [see comment above], and the type of NOR-bearing chromosome, completely exceptional in this part of the Eurasian Radia-

tion) and a unique reversal (the disappearance of the ventral dark pattern).

The pyrenean group is very well characterized by to present four synapomorphies, a parallelism and a unique reversal. The synapomorphies are the possession of caudal vertebrae only of the A type; the presence of robertsonian fusions (5 in *I. aurelioi* and *I. aranica*, and 6 in *I. bonnali*); possession of ventral colorations of the group of the red (if present any pigment); and reduction of the supracilliary granule rows. The tendency to the reduction on the hemipenial microornamentation could be considered also as a synapomorphy of this group, with posterior reversal in *I. aurelioi*. The parallelism is the presence of contact between the supranasal and the loreal scales (that also appears in *I. horvathi*). Finally, the unique reversal is the disappearance of the ventral colorations of the group of the green.

Within the pyrenean group, *I. aranica* lacks autapomorphies in our analysis and is profiled as the adelphotaxon of the clade that includes *I. bonnali* and *I. aurelioi*. This clade appears defined by two synapomorphies: the reduction of the anteromedial process of the postorbitary and the possession of sexual chromosomes of the Z1Z2W type which makes that the males possess more chromosomes than their corresponding females. *I. bonnali* remains characterized by an autapomorphy, the presence of six robertsonian fusions (that is to say, one more than *I. aurelioi* or *I. aranica*), while *I. aurelioi* possesses two autapomorphies: the disappearance of the anterodistal process of the postfrontal bone and the very frequent occlusion of the sternal fontanelle. This last taxon is

also characterized by a parallelism (a postorbitary longer than the postfrontal) and a multiple reversal (the disappearance of the blue points of the outermost ventral ranges).

Phylogenetic relationships between the mountain lizards of the Caucasus and Near East

The clade that forms "*L.*" *chlorogaster* and the species of the "*L.*" *saxicola* group is defined by a synapomorphy (the grasp of the female by means of a bite in the thigh).

It has been suggested that this group of species could be more or less related to *Apathya* ("*Apathya* s. l.*" in Bischoff, 1991; Mayer and Bischoff, 1996) but, as could be seen in the general cladogram (Fig. 1), both taxa appear very different and present characters very divergent (minor number of vertebrae, spiny-shaped hemipenial microornamentation, different number of supralabials, palpebral window, subdigital lamellae keeled, greater number of postnasals and reticulated pattern, among other distinctive characteristics in *Apathya*). The same could be said concerning *Archaeolacerta* s. str., with which it have been identified, and from which is also distanced.

By their isolation both from *Teira* as from *Archaeolacerta* and their monophyly, we described this unnominated taxon as:

Darevskia gen. nov.

Type species. *Lacerta* saxicola Eversmann, 1834.

Included species. *D. alpina* (Darevsky, 1967); *D. armeniaca* (Méhely, 1909) (parthenogenetic); *D. bendimahiensis* (Schmidtler et al., 1994) (parthenogenetic); *D. caucasica* (Méhely, 1909); *D. clarkorum* (Darevsky and Vedmerja, 1977); *D. daghestanica* (Darevsky, 1967); *D. dahli* (Darevsky, 1957) (parthenogenetic); *D. defilippi* (Camerano, 1877); *D. derjugini* (Nikolsky, 1898); *D. dryada* (Darevsky and Tuniyev, 1997); *D. lindholmi* (Lantz and Cyren, 1936); *D. mixta* (Méhely, 1909); *D. parvula* (Lantz and Cyrén, 1913); *D. portschinskii* (Kessler, 1878); *D. praticola* (Eversmann, 1834); *D. raddei* (Boettger, 1892); *D. rostombekovi* (Darevsky, 1957) (parthenogenetic); *D. rudis* (Bedriaga, 1886); *D. sapphirina* (Schmidtler et al., 1994) (parthenogenetic; *D. saxicola* (Eversmann, 1834); *D. steineri* (Eiselt, 1995); *D. unisexualis* (Darevsky, 1966) (parthenogenetic); *D. uzzelli* (Darevsky and Danielyan, 1977) (parthenogenetic); *D. valentini* (Boettger, 1892).

"*L.*" *moustoufii* seems to be a mere synonym of *D. chlorogaster* (Darevsky, pers. communication).

Diagnosis. Lacertidae of small size, in general moderately saxicolous or more rarely ground dwellers. Coloration and design typical of most of the groups of the Eurasian Radiation. To difference of the other taxa previously included in *Archaeolacerta* s. l., the males present modal numbers of 27-28 vertebrae, and 28-29 in the females. Several of the included species present subjection of the female by the thigh and/or the side during the courtship. Parthenogenetic clones are also produced by hybridization among taxa of the group (a character unique among the Lacertidae). They possess hemipenial microornamentation crown-shaped. Karyotypes of 38 chromosomes (36 macro- and two microchromosomes).

Description. Lizards with typical small lacertid aspect, with lateral bands reticulated or uniform and vertebral band composed by thick dots or paravertebral rows of points. Without dorsolateral dark stripes. A lateral line of thick points below the costal band exists. Colors of the back variable, usually green or brown. Belly of variable color, of the family of the green or of the red, according to the groups of species. Immaculate belly or with marks reduced to the more external ventral rows. Blue occelli in the shoulder and blue points in the outermost ventral ranges frequently present.

Rostral usually separated from the internasal, and the supranasal and loreal also separated (exceptions exist to both). A single postnasal scale. Four supralabials previous to the subocular scale. Rows of supracilliary granules usually complete. Six rows of ventral scales. Palpebral window doesn't exist. Masseteric and tympanic scales well developed, the first of them rarely reduced.

Premaxilla usually with seven teeth (9 in *D. chlorogaster*). Pterygoyd teeth absent. Processus nasalis undifferentiated. Postfrontal and postorbitary bones separated from the birth and of subequal lengths. Anterodistal process of the postfrontal always present. Anteromedial process of the postorbitary bone present or absent (present in some species and variable or reduced in another, like *D. raddei* and *D. mixta*). Maxilojugal suture not "stepped. "

Sexual dimorphism in the vertebral number. Males usually with 27 vertebrae (28 in *D. raddei* and *D. clarkorum*); females with 28 (29-30 in *D. raddei*, *D. clarkorum*, and in the parthenogenetic species,

which proceed from hybridizations of *D. raddei* with other taxa). Third vertebra without associated ossificated ribs (an exception found in the parthenogenetic *D. unisexualis*). Six posterior dorsal vertebrae. Preautotomic caudal vertebrae of A and B types. Sternal costal formula (3 + 2). Open or closed clavicles. Sternal fontanelle oval, not uncommonly cordiform, and rarely reduced. Interclavicle cruciform typical, with branches perpendicular to the central axis (something inclined forward in *D. chlorogaster*).

Hemipenis typical, with the apical part more developed than the basal one. Lobes profusely plicated and without apical spines or tubercles. Hemipenial microornamentation crown-shaped.

Karyotype composed by 38 acrocentric chromosomes (36 macrochromosomes and 2 microchromosomes) (an exception is a homologous from the heteromorphic third pair from *D. rostombekovi* which is submetacentric). Sexual heterogamety of ZW type. NOR in a L type chromosome, in telomeric position.

Several of the species of the group grasp the female by the thigh during the courtship and in a lesser degree also by the belly (*D. saxicola*, *D. raddei*, *D. caucasica*, *D. daghestanica*, *D. alpina*, and *D. praticola*), while anothers make it only by the thigh (*D. nairensis* and *D. chlorogaster*) or by the belly (the remainder of the known species).

Etymology. We dedicated this new genus to the Dr. Ilya S. Darevsky, for their monumental contribution to the knowledge and the systematic of these species in the area of the Caucasus and Near East.

Distribution. Great and Small Caucasus, Transcaucasia and adjacent areas. Towards southwestern through the diagonal mountainous of Anatolia until the Taurus, and along the Pontic Chains until the proximities of the Bosphorous. Towards northwest and west, through the coastal areas of the Black Sea and Crimea, a species (*D. praticola*) occupy parts of Eastern Europe. From the caucasian area, towards the west, through the mountains of the Kurdistan and Elburz Mts., in the north from Iran and Iraq, until Turkmenia. Probably also in the south from Iran (if type locality of "*Lacerta mostoufii*" is correct).

Biogeography. The age of the taxon is of some 15 M.Y. (fide Mayer and Benyr, 1994). Their origin seems to be in the Miocene, when, according to Darevsky (1967), several forms of forest, perhaps similar in their aspect to the current *D. chlorogaster*

which occupies an habitat and area relicts, would have penetrated in the area of the Caucasus.

Their radiation would have given up around the Caucasus. Due to the presence of areas of refuge with subtropical climate and vegetation (Colquid and Talish-hircanian refuges) in their two extremes, or arid in other areas (south of Armenia and Daghestan). The existence of small refuges here and there is testified in the current vegetation (Darevsky, 1967; Tuniyev, 1990; Nilson et al., 1995); and the presence of also a great heterogeneity of habitats, would have favored the successive isolations and contacts between the taxa along the Pleistocene, spreading subsequently following the mountainous chains that today occupy and from the banks of the Black Sea toward the East of Europe. A detailed reconstruction of these events could be found in Darevsky (1967).

Relationships between the species of *Darevskia*

The great number of species of this genus, many of them of recent evolution and of great resemblance among them, disable the realization of a cladistic analysis like in the other genus above-mentioned. There are more terminal taxa than characters differentiating among them in our study.

Nevertheless, some intents of systematization of the group have been carried out until the date:

The first, from Darevsky (1967), expressed in form of evolution tree, shows the opinion from this author on the relationships between the taxa (including the parthenogenetic ones). This author in their outline distinguishes "principal branches": the first includes *D. saxicola* and their subspecies; the second includes *D. raddei* and *D. defilippi*; the third with *D. alpina*, *D. caucasica*, and *D. daghestanica*; the fourth with *D. parvula* and *D. mixta*; the fifth for *D. portschinskii*; and last the sixth that includes a mixture of the current ssp. from *D. rudis* (*tristis* and *bythinica*) together with *D. valentini* (and their ssp.); and finally, the remaining part of the ssp. from *D. rudis* (*rudis*, *obscura*, and *macromaculata*). It is interesting to observe that in spite of the fact that the clusters utilized in this work are not utilized now, an elevated grade of success in many of the groupings of the Darevsky's 1967 classification exists, especially when consciously assembles taxa that the author classifies as different species but that they have resulted to belong to the same group or be very closely related taxa (for instance *D. caucasica*, *D. alpina*, and *D. daghestanica*).

Schmidtler (1993) speaks of *D. mixta, D. raddei* (s. l.), *D. valentini-rudis* complex, and of a *D. portschinskii-parvula* complex, while Grechko et al. (1994) being based on in the study of DNA polymerase chain reaction, they divide the ten species studied by them in two groups: one which contains *D. armeniaca* and *D. dahli* (both parthenogenetic), next to the bisexual *D. portschinskii, D. mixta,* and *D. valentini*; and the second with *D. unisexualis* and *D. rostombekovi* (parthenogenetic) next to *D. raddei* and *D. nairensis* (often considered as ssp. from *raddei,* although probably different).

Mayer and Lutz (1989), in a scheme based on a electrophoretic study, show a position slightly more isolated from *D. parvula,* on one hand, and of *D. praticola* and *D. derjugini,* for another, concerning the general group. The relationship between *D. derjugini* and *D. praticola* with *D. saxicola* was also suggested by Borisov and Orlova (1986).

For our part, and basing us in the available data, we could postulate a position more or less isolated for *D. praticola* (and perhaps *D. derjugini*) and for *D. chlorogaster.* Within the general group, we could find in the "*saxicola* complex" several groups which could be distinguished:

— A *raddei* group: the best defined, characterized by their increment in the vertebral counts (28 instead of 27 as modal number in males, and 29 instead of 28 in females) which includes *D. raddei* (and their ssp., including *D. nairensis*) and very probably also *D. defilippi* and *D. steineri* (Darevsky et al., 1984; Eiselt et al., 1993; Eiselt, 1995). Their possible internal relationships could not be clarified because some of their taxa are still almost completely unknown.

— A *rudis* group: characterized by the presence of a enlarged scale between the circumanal ones, previous to the anal plate; as well as by to present frequently colorations of the group of the red in the belly. It would include *D. rudis, D. valentini, D. portschinskii,* and, maybe in a basal position, *D. parvula* (Darevsky and Eiselt, 1980; Eiselt and Darevsky, 1991; Eiselt et al., 1992; MacCulloch et al., 1995). The position of *D. mixta* is more problematic: Grechko et al. (1994) put it near *D. valentini*; with which also hybridized widely in the past giving place to *D. armeniaca*; also it hybridized with *D. portschiskii* giving place to *D. dahli.* For it, and once discarded their likeness with *D. derjugini* (Uzzell and Darevsky, 1973) seems the more suitable hypothesis to as-

similate it to the *rudis* group. Also *D. mixta* and *D. parvula* are the taxa that show minor genetic differences with the species of the *rudis* group (concerning *D. portschinskii* and *D. valentini* in the study of Uzzell and Darevsky, 1975).

All these species also share the subjection of the female during the courtship only by the side of the belly. Their possible relations are: (*mixta* (*parvula* (*portschiskii* (*rudis* + *valentini*)))).

Murphy et al. (1996) prefer to consider *D. mixta* as the sister species of the clade that includes the groups of *D. raddei* and *D. saxicola.*

— A *saxicola* group: that would include *D. saxicola* and their ssp. (inc. *D. lindholmi* recently elevated to species rank [Ryabinin et al., 1996]) and perhaps *D. clarkorum* and the recently described *D. dryada* too [Darevsky and Tuniyev, 1997]).

— A *caucasica* group: with *D. caucasica, D. alpina,* and *D. daghestanica,* recently studied by Fu et al. (1995) (also see Darevsky, 1984; Roytberg, 1994). Their possible relationships are the following: (*alpina* (*caucasica* + *daghestanica*))

Murphy et al. (1996) bring *D. praticola* near to this group.

As for the relationships between these groups, little could be said basing on the point of grasp of the female during the courtship and the hybridizations that give rise to the parthenogenetic clones. The hybridizations succeeded between taxa of the *rudis* and *raddei* groups, while species of the *saxicola, raddei,* and *caucasica* groups, share the subjection of the female by the tight during the courtship, the same as in *D. praticola* and *D. chlorogaster.* It could be postulated that the subjection by the tight is a synapomorphy of the genus *Darevskia* and that subsequently has suffered a reversal in the *rudis* group, so that the subjection by the flank is a symplesiomorphy that does not indicate us relationships within the genus. Nevertheless it should exist a close relationship between the *raddei* and *rudis* groups. A tentative relation among groups could be: (*chlorog.* (*pratic.* (*g. caucasica* + *g. saxicola* (*g. rudis*+ *g. raddei*)))).

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