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1430

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ABSTRACT

DNA sequence indicates the Lacertidae contain two subfamilies, Gallotiinae and Lacertinae, the latter comprising two monophyletic tribes, the Eremiadini of Africa and arid southwest and central Asia, and the Lacertini of Europe, northwest Africa and southwest and east Asia. Relationships within the 108 species of Lacertini are explored using mtDNA (291 bp cytochrome b; 329 bp 12S rRNA for 59 nominal species, and reanalysis of the data of Harris *et al*. 1998, and Fu 2000). The morphology of the tribe is reviewed and 64 of its characters (equivalent to 83 binary ones) also used to assess relationships. The Lacertini are assigned to 19 monophyletic units of 1 to 27 species, recognised here as the following genera (contents are indicated in brackets): *Algyroides, Anatololacerta* gen. nov. (*L. danfordi* group), *Apathya* (*L. cappadocica* group), *Archaeolacerta* (*L. bedriagae*), *Dalmatolacerta* gen. nov. (*L. oxycephala*), *Darevskia (L. saxicola* group), *Dinarolacerta* gen. nov. (*L. mosorensis*), *Hellenolacerta* gen. nov. (*L. graeca*), *Iberolacerta* (*L. monticola* group), *Iranolacerta* gen. nov. (*L. brandtii* and *L. zagrosica*), *Lacerta* s. str. (sand and green lizards, *L. agilis* group), *Parvilacerta* gen. nov. (*L. parva* and *L. fraasii*), *Phoenicolacerta* gen. nov. (*L. laevis* group), *Podarcis (*wall lizards), *Scelarcis* (*L. perspicillata), Takydromus* (Asian grass lizards*), Teira* (*L. dugesii*), *Timon* (ocellated lizards, *L. lepida* group) and *Zootoca* (*L. vivipara*). Both mtDNA and morphology indicate that *Lacerta* and *Timon* are sister taxa, and DNA suggests further possible relationships among genera (Fig. 1, p. 6). Neither DNA nor morphology indicates that the archaeolacertas (sometimes formalised as *Archaeolacerta* sens. lat.) form a clade. Instead, they are representatives of an ecomorph associated with living on rock exposures and using the narrow crevices that these contain.

The Lacertidae probably arose in the European area, with the Gallotiinae later reaching Northwest Africa and the Canary Islands, and the ancestor of the Eremiadini invading Africa in the mid-Miocene. The Lacertini spread through much of their present European range and diversified, perhaps largely by repeated vicariance, around 12–16 My ago, producing the ancestors of the present mainly small-bodied genera, which then underwent often modest speciation. Three units spread more widely: the *Lacerta-Timon* clade of large-bodied lizards probably dispersed earliest, followed by *Algyroides* and then *Podarcis*. Overall, European Lacertidae show a pattern of repeated spread, often accompanied by restriction of previous groups. Expansion of Lacertini may have displaced earlier lacertid lineages from all or much of Europe; while spread of *Podarcis* may have restricted many other genera of Lacertini. The earlier expansion of the *Lacerta-Timon* clade probably did not have this effect, as difference in adult body size restricted competitive interaction with other forms. Several invasions of more distant areas also occurred: of East Asia by *Takydromus* over 10 My ago, and more recently of northwest Africa by *Podarcis*, *Scelarcis* and *Timon,* and Madeira by *Teira.*

Relationships within the Eremiadini estimated from both mtDNA, and nDNA differ considerably from those based on morphology. They indicate relatively mesic forms may have diversified widely across Africa and given rise to at least three independent invasions of arid habitats. MtDNA also indicates that *Lacerta andreanskyi* belongs in the Eremiadini and may occupy a basal position there. It is assigned to a further new genus, *Atlantolacerta* gen. nov.

Key words: Taxonomy, Lacertini, Eremiadini, Lacertidae, systematics, phylogeny, evolution, mitochondrial DNA

INTRODUCTION

This paper deals with the systematics of the Lacertini, a clade of at least 108 species of lacertid lizards that is the predominant lizard group in Europe and some mainly neighbouring areas. The grounds for its recognition are discussed and evidence for its internal relationships considered. This consists of both DNA sequence and morphological characters, and previous phylogenetic analyses of such data sets are supplemented here by further ones. As a preliminary to its analysis, morphological variation in the Lacertini is reviewed. There then follows a formal systematic treatment in which 19 component genera are recognised and described, of which seven are new. Finally, the history of the Lacertini is discussed.

The Lacertidae. The lizard family Lacertidae Oppel, 1811 consists of about 280 species and is found widely in Eurasia and Africa. Recent molecular analyses using DNA sequences suggest it may be the sister-group of the Amphisbaenia, the worm lizards (Townsend *et al.* 2004; Vidal & Hedges 2004). Otherwise, its nearest relatives are the now exclusively American Teiioidea, which is made up of the Teiidae and the Gymnophthalmidae (Estes *et al*. 1988; Arnold 1989a)**.** Lacertidae plus Teiioidea have been assigned to a more inclusive grouping, Lacertoidea. But, if the sister group relationship of Lacertidae and Amphisbaenia is corroborated, and the latter is included in the grouping, the name of this would be Amphisbaenia Gray, 1844. Lacertids are defined as a clade by a number of mainly exclusive synapomorphies. As many of these involve features not usually apparent in fossils, they define the crown-group of Lacertidae rather than the family in its entirety. They include: lack of downgrowths on the parietal bone (Estes *et al*. 1988); supratemporal fenestra largely or wholly filled by postfrontal bone (a feature shared with Scincidae), usual presence of sexual variation in the number of presacral vertebrae; bodenaponeurosis divided into two lobes caudally, and a parasagittal vertical sheet connecting the quadrate aponeurosis to the temporal fascia (Rieppel 1980); abdominal fat-bodies largely outside the peritoneum (Arnold 1989a); either the lobes of the hemipenis invested by the retractor penis magnus muscle, or the lobes usually complexly folded and the erect hemipenis supported by an elaborate cartilaginous supporting structure, termed an armature (Arnold 1973, 1986, 1989a). To these features can probably be added presence of a microornamentation on the epidermis of the hemipenial lobes consisting of individual cells that are typically hook-shaped spines or crown-shaped tubercles (Klemmer 1957; Böhme 1971; Arnold 1973, 1986, 1989a); this epidermis is also distinctive in growing continuously during the breeding season, and its outer layers and their microornamentation may be shed very frequently, sometimes even daily (In den Bosch 2001). However the possible presence of these striking characteristics of the hemipenial epithelium have yet to be fully investigated in other lizard families. Additional putative synapomorphies of the Lacertidae, involving the scaling of the posterior dorsal surface of the head, such as widespread presence of an occipital scale, have also been put forward (Borsuk-Bialynicka *et al*. 1999).

The main groupings of lacertids

The 280 or so species of lacertids are presently placed in from 24 to about 30 genera (see for instance Arnold 1973, 1989a, b, 1991, 1997; Bischoff 1990, 1991a, b, c, 1992a, b, 1993, 1995a, b, 1996, 1998, 2001; Mayer & Bischoff 1996; Arribas 1997). Most of the genera that have been recognised appear to be clades on the basis of their morphology (Arnold 1989a), with the exception of the paraphyletic central African *Adolfus* (Arnold 1989b) and *Lacerta* sensu lato of Europe, SW And N Asia and northwest Africa. Several attempts to group the lacertids into bigger phylogenetic units have been made. Parsimony analysis of a relatively large morphological data set (84 characters, equivalent to 112 binary ones) recognised a Palaearctic and Oriental group of relatively primitive forms, and a more certainly monophyletic one consisting of Afrotropical and advanced Saharan and Eurasian taxa (Arnold 1989a). Perceived intergeneric relationships within the Palaearctic and Oriental group were very poorly supported by morphology, with the exception of the association between West Mediterranean *Psammodromus* and the Canary Island *Gallotia*. This last relationship is also supported by protein electrophoresis and albumin immunology (Lutz *et al*. 1986; Mayer & Benyr 1994).

DNA sequences have provided further evidence about the higher relationships of lacertids. The most important studies to date are as follows. Some 1049 base pairs (bp) of fragments of the mitochondrial genes cytochrome b, 12SrRNA and 16S rRNA, for 49 taxa (Harris *et al*. 1998); 4708 bp of the mitochondrial genes, cytochrome b, 12SrRNA, 16SrRNA, and COI, for 26 taxa (Fu 2000); 1600 bp of the nuclear genes RAG-1 and c-mos for 43 taxa (Mayer & Pavličev 2005). The two mitochondrial data sets are reanalysed here (Appendix I and Fig. 1). All data sets strongly indicate that *Gallotia* + *Psammodromus* is sister to the remaining Lacertidae. The reanalysis of Fu's mtDNA data and the results of the nDNA analyses by Mayer & Pavličev (2005) both support two well substantiated clades within the latter. One contains the Afrotropical and advanced Saharan and Eurasian taxa, and the other nearly all the Palaearctic and Oriental ones. The only exception is *L. andreanskyi,* which groups with very high support with the former assemblage in the reanalysis of Fu's data set, the only one to contain this species.

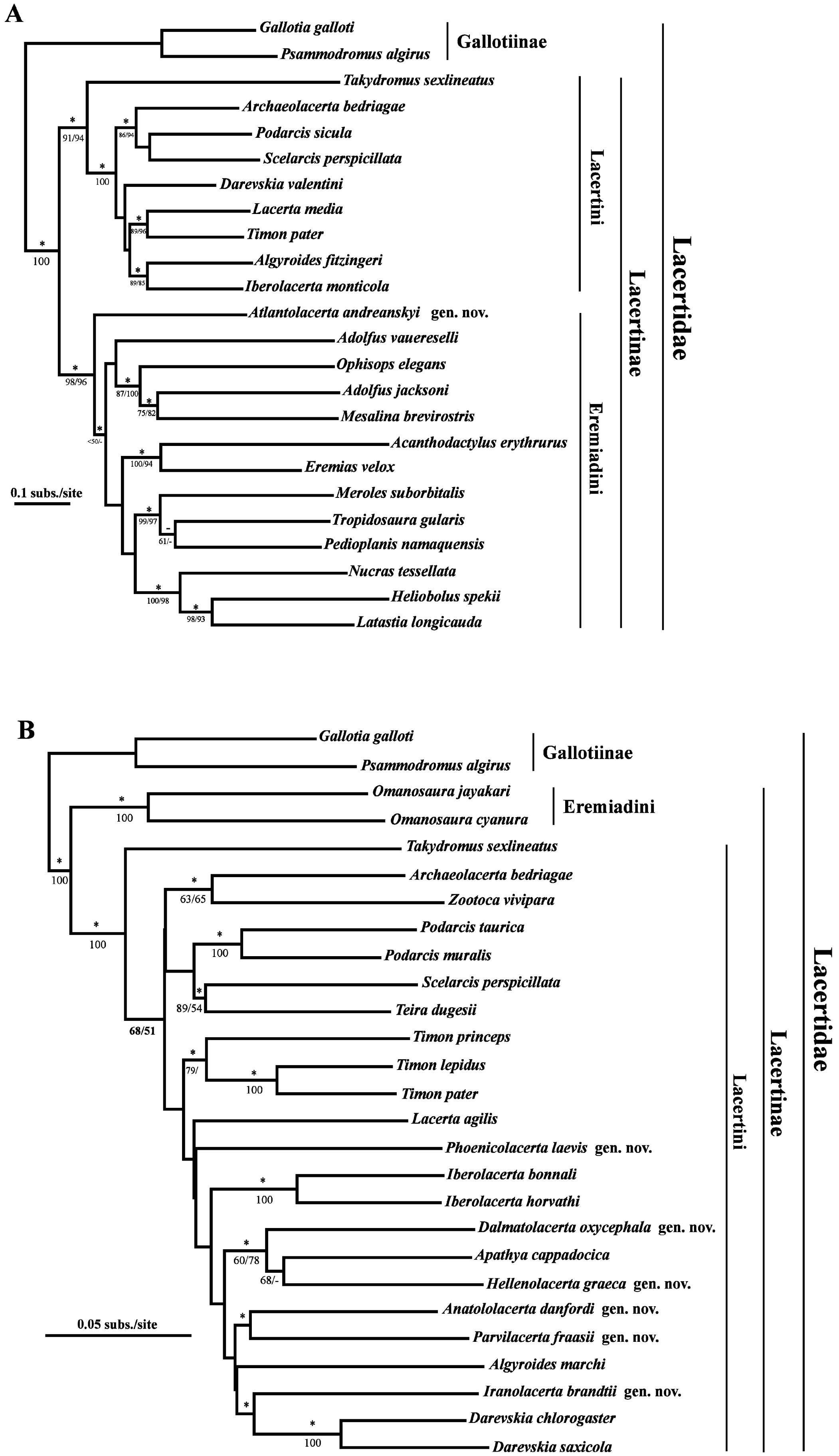
A
Gallotia galloti
Psammodromus algirus
Gallotiinae
Takydromus sexlineatus
Archaeolacerta bedriagae
Podarcis sicula
Scelarcis perspicillata
Darevskia valentini
Lacerta media
Timon pater
Algyroides fitzingeri
Iberolacerta monticola
Atlantolacerta andreanskyi gen. nov.
Adolfus vauereselli
Ophisops elegans
Adolfus jacksoni
Mesalina brevirostris
Acanthodactylus erythrurus
Eremias velox
Meroles suborbitalis
Tropidosaura gularis
Pedioplanis namaquensis
Nucras tessellata
Heliobolus spekii
Latastia longicauda
Lacertini
Eremiadini
Lacertinae
Lacertidae
* 100
* 91/94
* 100
* 86/94
* 89/96
* 89/85
* 98/96
* <50/-
* 87/100
* 75/82
* 100/94
* 99/97
- 61/-
* 100/98
* 98/93
0.1 subs./site
B
Gallotia galloti
Psammodromus algirus
Gallotiinae
Omanosaura jayakari
Omanosaura cyanura
Eremiadini
Takydromus sexlineatus
Archaeolacerta bedriagae
Zootoca vivipara
Podarcis taurica
Podarcis muralis
Scelarcis perspicillata
Teira dugesii
Timon princeps
Timon lepidus
Timon pater
Lacerta agilis
Phoenicolacerta laevis gen. nov.
Iberolacerta bonnali
Iberolacerta horvathi
Dalmatolacerta oxycephala gen. nov.
Apathya cappadocica
Hellenolacerta graeca gen. nov.
Anatololacerta danfordi gen. nov.
Parvilacerta fraasii gen. nov.
Algyroides marchi
Iranolacerta brandtii gen. nov.
Darevskia chlorogaster
Darevskia saxicola
Lacertini
Lacertinae
Lacertidae
* 100
* 100
* 100
68/51
* 63/65
* 100
* 89/54
* 79/
* 100
* 100
* 60/78
68/-
*
*
* 100
0.05 subs./site

FIGURE 1. —Relationships of Lacertidae indicated by DNA sequences. A. ML tree of a reanalysis of the mtDNA data set of Fu (2000), based on 4522 bp (1026 bp of cytochrome b, 1048 bp of cytochrome oxidase I and 2448 bp of the ribosomal genes 12S rRNA + 16S rRNA). B. ML tree of a reanalysis of the mtDNA data set of Harris *et al*. (1998), based on 1014 bp (293 bp of cytochrome b, 313 bp of 12S RNA and 406 of 16S rRNA). See Appendix I for methods and other relevant information. Posterior probability values 95 or higher, resulting from Bayesian analysis, are indicated by an asterisk, *, above the nodes. Below the nodes are bootstrap values for the ML (left) and MP (right) analyses. When relationships vary with different methods of analysis, a dash, -, indicates that the method concerned does not support the topology shown. When only a single number below the nodes is given it means that bootstrap values for the ML and MP analyses are identical. Boostrap values below 50 and posterior probability values below 95 are not shown. Generic allocations are those recognised in this paper.

Most members of each of the three main groups of lacertids share distinctive non-molecular features. Species in the *Gallotia-Psammodromus* clade are singular in regularly vocalising and most have a patch of large soft spines on the hemipenis near the lobe bifurcation (Arnold 1989a). Nearly all the members of the Afrotropical and advanced Saharan and Eurasian clade are characterised by a derived state of the ulnar nerve (first noted by Julien & Renous-Lécuru 1972), and by usually possessing hemipenes with an armature and complexly folded lobes in the retracted organ, genital features that are rare among other lacertids. The primitive Palaearctic clade has a number of features that are rare or absent in the Afrotropical and advanced Saharan and Eurasian clade, although they do not occur universally and some included taxa only have a minority of them. They are: 1. medial loop of the clavicle interrupted posteriorly in at least some individuals of most species; 2. B-pattern tail vertebrae in at least some individuals of most species; 3. an enlarged masseteric scale often present; 4. parietal scale reaching edge of parietal table only posteriorly; 5. hemipenis without an armature and 6. hemipenis regressing in size outside breeding season and losing the distinctive microornamentation on the lobes. However some of these also occur in one or two probably basal units of Eremiadini (at least 1–3 and 5 in *L. andreanskyi* and 1–2 in *Omanosaura).* This suggests the shared features are primitive in the common ancestor of Eremiadini and Lacertini, especially as 3–5 occur in the Gallotinae as well.

As with many of the synapomorphies of the Lacertidae as a whole, very few of the non-molecular features, which help to distinguish the living assemblages of the family that constitute its crown-group, are likely to be usually preserved in most fossils. The only exceptions are the ones involving the clavicle and tail vertebrae, which are common in the primitive Palearctic clade but not exclusive to it. So, assigning the usually fragmentary remains of ancient lacertids to the particular crown-group assemblages will not generally be possible. This is likely to apply even to amber-preserved specimens. These often exhibit external detail but, if so, usually fail to show internal structure.

Names for the main crown-group clades of Lacertidae

The subfamily name Gallotiinae Cano, Baez, López-Jurado & Ortega, 1984 is available for the *Gallotia-Psammodromus* clade (it was originally proposed in the form Gallotiidae, as it was intended for a family containing only *Gallotia*). Similarly, Eremiadinae Shcherbak, 1975 is available for the Afrotropical and advanced Saharan and Eurasian clade. This name is mis-spelt as Eremiainae in Shcherbak's paper. *Eremias* is a Greek noun meaning a solitary devotee, and is related to *Eremia*, signifying an isolated place or desert. The genitive form of *Eremias* is *Eremiados*, so the stem to use in forming a family-group name is Eremiad- (following article 29.3.1 of the International Code of Zoological Nomenclature (International Commission for Zoological Nomenclature 1999)). The name for a subfamily would consequently be Eremiadinae, and for a tribe Eremiadini.

The two subfamily names Gallotiinae and Eremiadinae have been used together with a third, Lacertinae, the last being employed for the primitive Palearctic forms excluding the Gallotiinae (Harris *et al*. 1998). While convenient, this arrangement does not take into account that Gallotiinae is sister to a clade containing the units named above as Eremiadinae and Lacertinae. If a hierarchical classification is required, the clades named as Eremiadinae and Lacertinae cannot have the same rank as Gallotiinae, and must be downgraded to tribes, as Eremiadini Shcherbak, 1975 and Lacertini Oppel, 1811. The unit that forms the sister group of Gallotiinae, which contains both of these tribes, would then take the subfamily name Lacertinae. The resulting classification is summarised below and used in the rest of this paper.

- Lacertidae
  - Gallotiinae (2 genera, 17 species)
  - Lacertinae
    - Lacertini (4–10 currently recognised genera, about 108 species)
    - Eremiadini (18 genera, about 155 species)

Present assessments of relationships within the Lacertini

Taxonomic treatment of the species now assigned to Lacertini has varied considerably over time, but a number of assemblages are now commonly recognised, something which in most cases was initially based on their morphology. Among them are the following (with the exception of *Algyroides* and *Takydromus*, they contain species that were placed in *Lacerta* until quite recently): *Algyroides* (4 species), *Darevskia* (the *L. saxicola* group of the Caucasus and neighbouring areas, 27 species), *Iberolacerta* (the Iberian and eastern Alpine rock lizards, 8 species), *Lacerta* s. str. (the *L. agilis* group, 8 species), *Timon* (the *Lacerta lepida* group plus *L. princeps*, 4 species), *"Parvilacerta"* (*L. parva* and *L. fraasii*), *Podarcis* (the wall lizards, 19 species), *Takydromus* (the Asian grass lizards, 18 species), *Teira* (*L. dugesii* and *L. perspicillata*, the latter being referred to *Scelarcis* by some authors), and *Zootoca* (*L. vivipara*). In addition, *Apathya* has sometimes been used for *L. cappadocica* etc. and *Archaeolacerta* for *L. bedriagae* and a varying selection of other rock lizards. Other assemblages that have no formal names are the *Lacerta danfordi* group (*L. danfordi*, *L. anatolica*, *L. oertzeni*) and the *L. laevis* group (*L. laevis*, *L. cyanisparsa*, *L. kulzeri* and *L. troodica*). Finally, a number of well-defined species are not convincingly associated with other forms. Many of the units that have formal names have sometimes been viewed as self-standing genera but most of them have also been regarded as subgenera within *Lacerta* sensu lato (Harris & Carretero 2001). This has inevitably led to confusion and instability in nomenclature. As a foundation for a more rational and comprehensive system of names for groups of Lacertini, we use new and old evidence for relationships within the group, based both on DNA sequences and morphology.

Phylogenetic analyses of Lacertini based on DNA sequence

Groups within the Lacertini. The mitochondrial studies of Harris *et al*.(1998) and Fu (2000), and reanalyses of their data presented here, support many of the recognised groupings within the Lacertini that have more than one species, although the number of each included in these analyses was quite low (26 and 10 species respectively). More recent investigations with better species representation corroborate the clade status of *Iberolacerta*, *Podarcis,* and *"Parvilacerta"* (Carranza *et al*. 2004). A further study presented here (Fig. 2), using mitochondrial gene fragments (291 bp cytochrome b; 329 bp 12S rRNA) of 96 individuals belonging to 59 nominal species, provides strong corroboration for these units and equally strong support for some others, among them *Darevskia*, *Lacerta* s. str., *Takydromus*, one including *L. danfordi* and *L. anatolica,* and additional ones made up respectively of *L. laevis* and *L. kulzeri*, and of *L. brandtii* and *L. zagrosica*. All these units are supported by bootstrap values between 72 and 100 in both maximum likelihood (ML) and maximum parsimony (MP) analyses and Bayesian posterior probability values of 100. Details of the analysis on which the tree is based are given on APPENDIX I and of the material used in APPENDIX II. In all, 19 units were recognised which molecular clocks suggest separated 12–15 My ago (see Fig. 2 and APPENDIX I). These include the assemblages just mentioned and several units consisting of single nominal species.

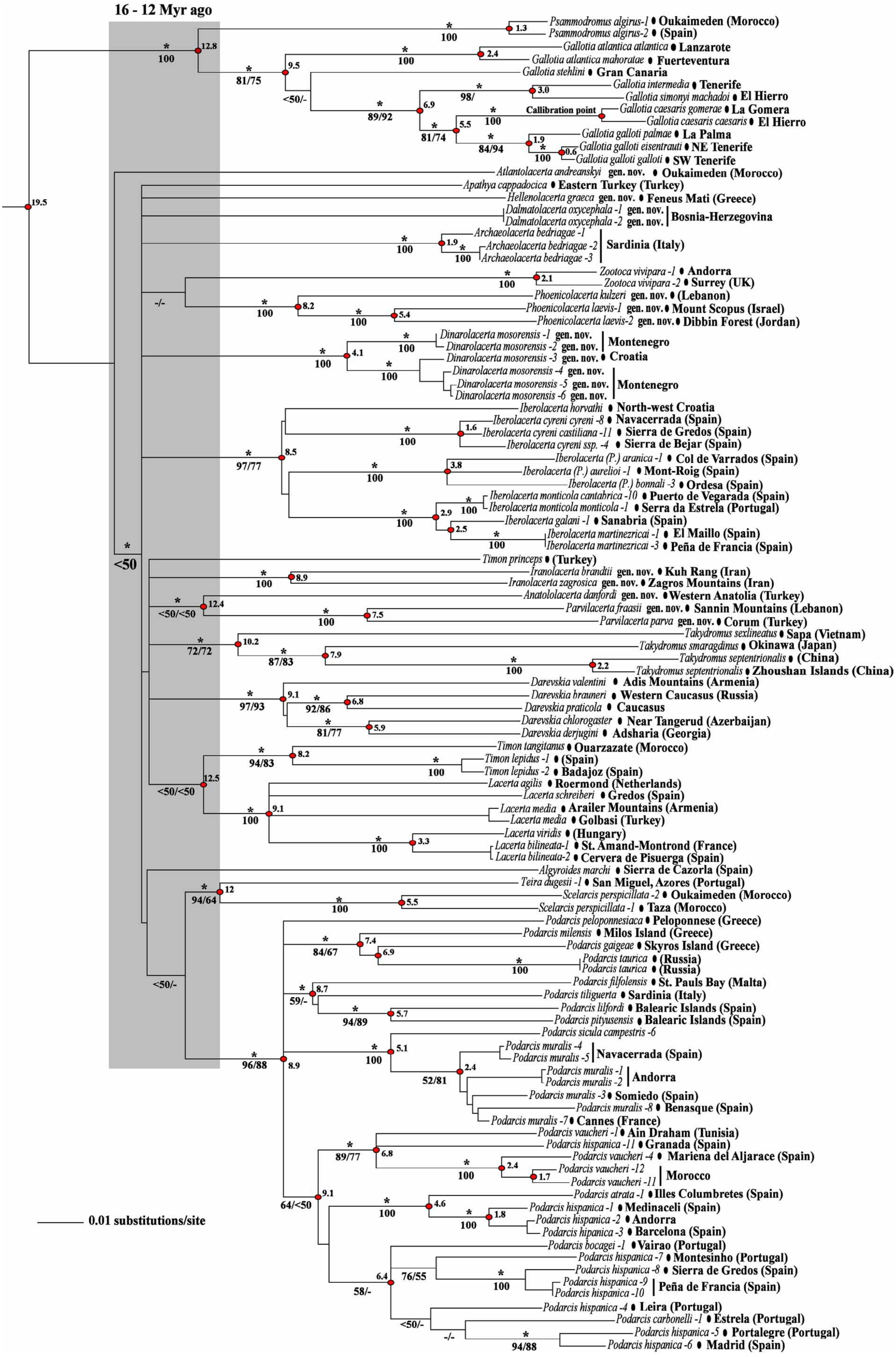
16 - 12 Myr ago
19.5
12.8
* 100
1.3
* 100
Psammodromus algirus-1 ● Oukaimeden (Morocco)
Psammodromus algirus-2 ● (Spain)
9.5
* 81/75
2.4
* 100
Gallotia atlantica atlantica ● Lanzarote
Gallotia atlantica mahoratae ● Fuerteventura
Gallotia stehlini ● Gran Canaria
<50/-
3.0
* 98/
Gallotia intermedia ● Tenerife
Gallotia simonyi machadoi ● El Hierro
6.9
* 89/92
Callibration point
* 100
Gallotia caesaris gomerae ● La Gomera
Gallotia caesaris caesaris ● El Hierro
5.5
* 81/74
1.9
* 84/94
Gallotia galloti palmae ● La Palma
0.6
* 100
Gallotia galloti eisentrauti ● NE Tenerife
Gallotia galloti galloti ● SW Tenerife
Atlantolacerta andreanskyi gen. nov. ● Oukaimeden (Morocco)
Apathya cappadocica ● Eastern Turkey (Turkey)
Hellenolacerta graeca gen. nov. ● Feneus Mati (Greece)
Dalmatolacerta oxycephala -1 gen. nov.
Dalmatolacerta oxycephala -2 gen. nov.
Bosnia-Herzegovina
1.9
* 100
Archaeolacerta bedriagae -1
Archaeolacerta bedriagae -2
* 100
Archaeolacerta bedriagae -3
Sardinia (Italy)
-/-
2.1
* 100
Zootoca vivipara -1 ● Andorra
Zootoca vivipara -2 ● Surrey (UK)
8.2
* 100
Phoenicolacerta kulzeri gen. nov. ● (Lebanon)
5.4
* 100
Phoenicolacerta laevis-1 gen. nov. ● Mount Scopus (Israel)
Phoenicolacerta laevis-2 gen. nov. ● Dibbin Forest (Jordan)
4.1
* 100
* 100
Dinarolacerta mosorensis -1 gen. nov.
Dinarolacerta mosorensis -2 gen. nov.
Montenegro
* 100
Dinarolacerta mosorensis -3 gen. nov. ● Croatia
Dinarolacerta mosorensis -4 gen. nov.
Dinarolacerta mosorensis -5 gen. nov.
Dinarolacerta mosorensis -6 gen. nov.
Montenegro
8.5
* 97/77
Iberolacerta horvathi ● North-west Croatia
1.6
* 100
Iberolacerta cyreni cyreni -8 ● Navacerrada (Spain)
Iberolacerta cyreni castiliana -11 ● Sierra de Gredos (Spain)
Iberolacerta cyreni ssp. -4 ● Sierra de Bejar (Spain)
3.8
* 100
Iberolacerta (P.) aranica -1 ● Col de Varrados (Spain)
Iberolacerta (P.) aurelioi -1 ● Mont-Roig (Spain)
Iberolacerta (P.) bonnali -3 ● Ordesa (Spain)
2.9
* 100
* 100
Iberolacerta monticola cantabrica -10 ● Puerto de Vegarada (Spain)
Iberolacerta monticola monticola -1 ● Serra da Estrela (Portugal)
Iberolacerta galani -1 ● Sanabria (Spain)
2.5
* 100
Iberolacerta martinezricai -1 ● El Maillo (Spain)
Iberolacerta martinezricai -3 ● Peña de Francia (Spain)
* <50
Timon princeps ● (Turkey)
8.9
* 100
Iranolacerta brandtii gen. nov. ● Kuh Rang (Iran)
Iranolacerta zagrosica gen. nov. ● Zagros Mountains (Iran)
12.4
* <50/<50
Anatololacerta danfordi gen. nov. ● Western Anatolia (Turkey)
7.5
* 100
Parvilacerta fraasii gen. nov. ● Sannin Mountains (Lebanon)
Parvilacerta parva gen. nov. ● Corum (Turkey)
10.2
* 72/72
Takydromus sexlineatus ● Sapa (Vietnam)
7.9
* 87/83
Takydromus smaragdinus ● Okinawa (Japan)
2.2
* 100
Takydromus septentrionalis ● (China)
Takydromus septentrionalis ● Zhoushan Islands (China)
9.1
* 97/93
Darevskia valentini ● Adis Mountains (Armenia)
6.8
* 92/86
Darevskia brauneri ● Western Caucasus (Russia)
Darevskia praticola ● Caucasus
5.9
* 81/77
Darevskia chlorogaster ● Near Tangerud (Azerbaijan)
Darevskia derjugini ● Adsharia (Georgia)
12.5
<50/<50
8.2
* 94/83
Timon tangitanus ● Ouarzazate (Morocco)
* 100
Timon lepidus -1 ● (Spain)
Timon lepidus -2 ● Badajoz (Spain)
9.1
* 100
Lacerta agilis ● Roermond (Netherlands)
Lacerta schreiberi ● Gredos (Spain)
Lacerta media ● Arailer Mountains (Armenia)
Lacerta media ● Golbasi (Turkey)
3.3
* 100
Lacerta viridis ● (Hungary)
Lacerta bilineata-1 ● St. Amand-Montrond (France)
Lacerta bilineata-2 ● Cervera de Pisuerga (Spain)
<50/-
Algyroides marchi ● Sierra de Cazorla (Spain)
12
* 94/64
Teira dugesii -1 ● San Miguel, Azores (Portugal)
5.5
* 100
Scelarcis perspicillata -2 ● Oukaimeden (Morocco)
Scelarcis perspicillata -1 ● Taza (Morocco)
8.9
* 96/88
Podarcis peloponnesiaca ● Peloponnese (Greece)
7.4
* 84/67
Podarcis milensis ● Milos Island (Greece)
6.9
Podarcis gaigeae ● Skyros Island (Greece)
* 100
Podarcis taurica ● (Russia)
Podarcis taurica ● (Russia)
8.7
* 59/-
Podarcis filfolensis ● St. Pauls Bay (Malta)
Podarcis tiliguerta ● Sardinia (Italy)
5.7
* 94/89
Podarcis lilfordi ● Balearic Islands (Spain)
Podarcis pityusensis ● Balearic Islands (Spain)
Podarcis sicula campestris -6
5.1
* 100
Podarcis muralis -4
Podarcis muralis -5
Navacerrada (Spain)
2.4
52/81
Podarcis muralis -1
Podarcis muralis -2
Andorra
Podarcis muralis -3 ● Somiedo (Spain)
Podarcis muralis -8 ● Benasque (Spain)
Podarcis muralis -7 ● Cannes (France)
9.1
64/<50
6.8
* 89/77
Podarcis vaucheri -1 ● Ain Draham (Tunisia)
Podarcis hispanica -11 ● Granada (Spain)
2.4
* 100
Podarcis vaucheri -4 ● Mariena del Aljarace (Spain)
1.7
Podarcis vaucheri -12
Podarcis vaucheri -11
Morocco
Podarcis atrata -1 ● Illes Columbretes (Spain)
4.6
* 100
Podarcis hispanica -1 ● Medinaceli (Spain)
1.8
* 100
Podarcis hispanica -2 ● Andorra
Podarcis hipanica -3 ● Barcelona (Spain)
6.4
58/-
Podarcis bocagei -1 ● Vairao (Portugal)
76/55
Podarcis hispanica -7 ● Montesinho (Portugal)
* 100
Podarcis hispanica -8 ● Sierra de Gredos (Spain)
Podarcis hispanica -9
Podarcis hispanica -10
Peña de Francia (Spain)
<50/-
Podarcis hispanica -4 ● Leira (Portugal)
-/-
Podarcis carbonelli -1 ● Estrela (Portugal)
* 94/88
Podarcis hispanica -5 ● Portalegre (Portugal)
Podarcis hispanica -6 ● Madrid (Spain)
0.01 substitutions/site

FIGURE 2.— Bayesian phylogenetic tree of the Lacertini based on 620 bp of mitochondrial DNA sequence (291 bp of cytochrome b and 329 bp 12S rRNA). The phylogenetic tree is rooted using the amphisbaenian *Blanus cinereus* (not shown). Posterior probability values higher than 95 are indicated with an asterisk, *, above the nodes. Below nodes are bootstrap values for the ML (left) and MP (right) analysis. All three methods of analyses gave similar results and support the existence of 19 independent units within the Lacertini, which originated in the Mid-Miocene (between 12 and 16 My ago). *Atlantolacerta andreanskyi* gen. nov., a member of the Eremiadini, is sister to the Lacertini. Comparison among the three different methods of analysis indicate that some phylogenetic relationships between the 18 main clades vary depending on the method. When this happened a symbol "-" was inserted instead of the boostrap or posterior probability value to indicate that this particular method did not support the topology presented in Fig. 2. When only a single number below the nodes is shown it means that bootstrap values for the ML and MP analyses are identical.

Relationships of groups within the Lacertini. None of the available DNA studies (Harris *et al.* 1998, and Fu 2000, and the reanalyses of their data presented in Fig. 2; and Mayer & Pavličev 2005) provide a fully resolved hypothesis of relationships of the main groups in the Lacertini. However, each data set shows strongly supported relationships among members of some of them (Fig. 1 shows cytb + 12S rRNA mtDNA). In most cases these involve different taxa in each data set and all relationships are congruent with each other. The fact that different relationships occur in each data set is partly due to differences in taxon coverage. The studies also vary in the genes involved and the total amount of sequence.

Phylogenetic analyses of Lacertini based on morphology and other non-molecular features

As already noted, a previous morphological analysis, based on 112 binary characters, of all lacertid genera recognised at the time and many informal species groups, uncovered no well supported relationships among the main groups of Lacertini (Arnold 1989a). This was probably partly because the number of features varying among the 18 units of Lacertini that were included was quite small (about 50 binary characters) and turned out to be markedly homoplasious. Also, appropriate rooting of the Lacertini was not possible, as its boundaries and relationship to other lacertids were not known. A new analysis was consequently carried out that was confined to the 19 units of Lacertini recognised using mitochondrial DNA sequences. This also employed more characters (64 characters, equivalent to 83 binary ones), and used appropriate outgroups for rooting. The methods of analysis used are given in APPENDIX I, a comprehensive list of characters with their descriptions in APPENDIX III and the morphological data set used in APPENDIX IV.

The use of different outgroups to root the Lacertini (Gallotiinae, Eremiadini, or both) altered the resultant topology to a limited extent, but analysis of morphology gave relatively little well supported structure. The strict consensus tree (Fig. 3) shows only one relationship, that between *Lacerta* and *Timon*, with a high bootstrap support (99). This relationship is likely to be real for it is also well supported by the reanalysis of Fu's (2000) mitochondrial DNA data (see Fig. 1A). Also, the 17 non-molecular features these taxa share (Fig. 4) occur at most in a small minority of other lacertids and are often likely to be derived. It might be thought that many of the features are functional concomitants of large adult size and might consequently have been acquired independently in *Lacerta* and *Timon*. But many are absent from other lacertids that have independently evolved large body-size, namely *Gallotia* in the Gallotiinae, and *Omanosaura jayakari* in the Eremiadini. The number of features shared by *Lacerta* and *Timon* that also occur in both these taxa is quite limited.

Evidence for relationships from hybridization

Hybridization sometimes occurs between species of Lacertini, especially in captivity, and has been extensively reviewed (Mertens 1950, 1956, 1964, 1968, 1972; Arnold 1973). It provides some further evidence for the coherence of the units of Lacertini concerned, and their separation from others. Many hybridizations have been reported between species of *Podarcis*, but not between these and members of other genera, and the same is true of species of *Darevskia. Lacerta* s. str. is also similar except that one case of hybridization is known between captive *Lacerta trilineata* and *Timon lepidus* (R. Piley, personal communication). However, although the parent animals produced one superficially normal offspring that grew to maturity, other embryos were very deformed (photographs deposited in the Lower Vertebrates library of the Natural History Museum, London). As noted, there is morphological and mtDNA evidence that *Lacerta* and *Timon* are closely related. Apart from this particular case, there are no other reliable reports of hybridization between the 19 units of Lacertini recognised here.

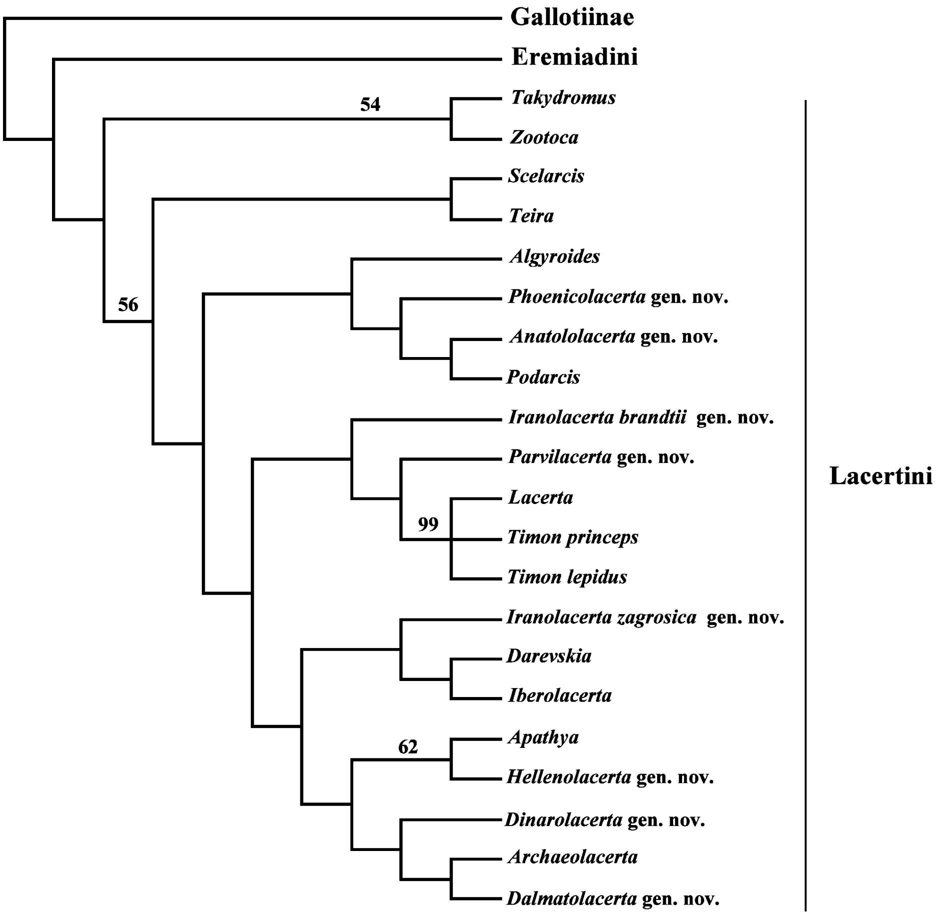

FIGURE 3.— Strict consensus of 2 most parsimonious trees of 311 steps. The phylogeny was based on a total of 64 morphological characters (58 parsimony-informative); equivalent to 83 binary characters. Consistency Index = 0.669; Retention Index = 0.519. Figures above the nodes indicate bootstrap support. Generic allocations are those recognised in this paper.

Taxonomic treatment

Recognising the 19 units as genera inevitably involves name changes for those species given completely new generic names, but there are only about a dozen of these. Possible alternative courses that are rejected are as follows: 1. The 19 units could all be regarded as subgenera of *Lacerta*, but this would mean that *Algyroides Podarcis* and *Takydromus*, long treated as full genera, would cease to be so and their 42 species would be placed in *Lacerta* sensu lato with consequent change in their binomials. Also, Lacertini and *Lacerta* would have the same content, making the lower taxonomic category redundant. 2. Another possibility is an entirely pragmatic arrangement in which *Algyroides*, *Podarcis* and *Takydromus* are retained as genera but the other units regarded as subgenera of *Lacerta*. This course has been advocated, for instance by Harris *et al*. (1998) and Harris and Carretero (2003), on the grounds that relationships in the Lacertini were uncertain at the time these authors wrote, so use of many generic names was likely to be unstable, with associated confusing change in binomials. It is now more certain that Lacertini contain many well supported but separate groups, making such a course redundant. There may be objections to recognising so many monotypic genera. But, as will be seen from the accounts of these in the systematic section of this paper, there is evidence that most of them really consist of more than one species. It might also be argued that there is increasing evidence that some of the 19 units are related to each other (Fig. 1), so fewer generic names are necessary. But these results based on DNA sequences show that all 19 units are old lineages that originated during the mid-Miocene, within a relatively short timespan. Possible relatives identified to date are also often morphologically quite distinct. For example, *Apathya* (*Lacerta cappadocica*) and *Dalmatolacerta* (*L. oxycephala*) exhibit at least 16 anatomical differences, and *Anatololacerta* (*L. danfordi* group) and *Parvilacerta* (*L. parva* and *L. fraasii*) exhibit at least 22. Such levels of morphological differentiation and genetic divergence (all relatives mentioned above have been evolving as independent lineages for the last 12 My) often exceed those between taxa in the Lacertini that are already treated as full genera as for instance *Timon* and *Scelarcis*, which also have identifiable close relatives (*Lacerta* sensu stricto in the case of *Timon* and *Teira* in the case of *Scelarcis*).

Apart from reflecting their distinctness, there are further advantages in clearly recognising 19 genera within the Lacertini. Species names might well be more stable in the future. Naming and diagnosing these clades and defining them phylogenetically also makes it easier for future workers to concentrate on them, knowing that other forms can safely be excluded from consideration. This narrowing of perspective means that more attention is likely to be given to relationships within the genera and their internal taxonomy, biogeography and evolution.

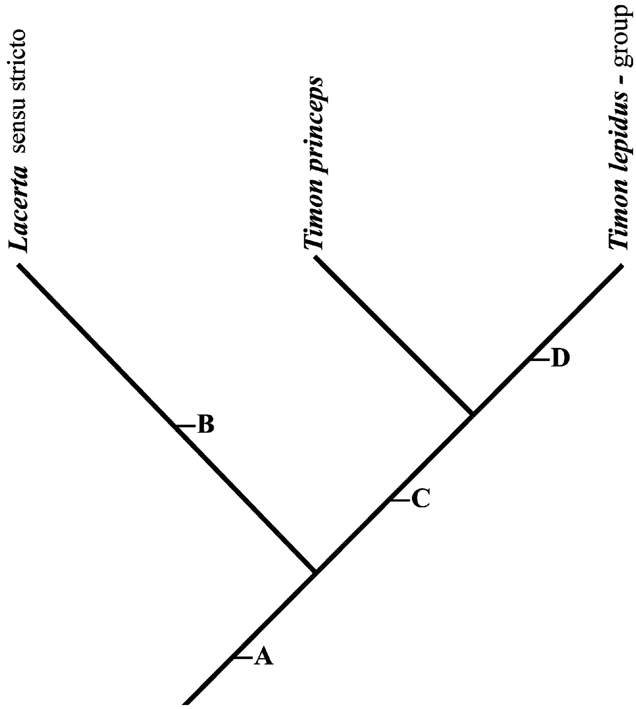

FIGURE 4.— Morphological and other evidence for relationships between the members of *Lacerta* and *Timon*. Features supporting particular nodes are as follows: A. Large size, deep robust head, nasal process of premaxilla broad, pterygoid teeth present, sometimes a depression on snout, presacral vetebrae 27 in males and 28 in females, number of posterior presacral vertebrae with short ribs often reaching seven, serrated collar, ventral scales overlapping posteriorly and with sloping sides, sometimes broad occipital scale, preanal scale surrounded by two or more rows of smaller scales, often overall green colouring, no bright contrasting colour on belly, no lateral septum on the bodenaponeurosis, retractor lateralis anterior muscle does not reach mid-line in front of vent, lateral surfaces of hemipenial lobes often with a microornamentation of elongated spines, hatchlings embryonic in form. B. Maxillary-jugal suture often stepped; frequently narrow light stripes in pattern. C. Occipital scale more frequently large, blue ocelli frequent on flanks; distinctive chromosomes with a single Robertsonian fusion. D. very large body size; sometimes a second nucleolar organiser present. Reanalyses of the data sets of Harris *et al.* (1998) and Fu (2000) shows that mitochondrial DNA provides further support for the relations indicated (see Fig. 1).

MORPHOLOGICAL AND OTHER NON-MOLECULAR VARIATION IN THE LACERTINI

To make this section more easily accessible for future readers, new generic names are used in it that are formally introduced in the next, systematic part of the paper. Among published sources for general morphology of Lacertini, including external morphology, skeleton and hemipenes are Arnold (1973, 1984, 1986, 1989a, 1989b, 1997, 1998a, 1998b, 2002), Arribas (1997, 1998, 1999, 2001), Boulenger (1905, 1916, 1920), Klemmer (1957) and Böhme (1971, 1988, 1993). These and other papers have been supplemented by our own unpublished data.

Compared to Eremiadini, the only other large assemblage of lacertids, the overall range of morphological variation in Lacertini is quite restricted. In particular they lack many of the features found in derived Eremiadini that are exclusively ground-dwelling in arid environments (Arnold 1989a, 2004). There is however considerable variation within taxa of Lacertini. Some features are polymorphic in many species, including the shape of the clavicle and the pattern of transverse processes on the autotomic tail vertebrae. The number of presacral vertebrae differs between the sexes, often varying within each of them and also between species. Many details of scaling and colouring also frequently vary.

Size and shape

Body size. Adults of most Lacertini species are around 55–90 mm from snout to vent (exceptionally over 90 mm in *Podarcis*). A few forms are smaller including some *Algyroides* (*A. fitzingeri* not more than about 45 mm and *A. moreoticus* often under 50 mm). In contrast, *Lacerta* and *Timon* are generally much larger than other Lacertini, with respective adult sizes of about 70–175 mm and 100–210 mm from snout to vent or more. Adult males are usually larger than females, but not in some *Darevskia* species and in *Lacerta*, *Iberolacerta*, *Takydromus* and *Zootoca*.

Body shape. The head and body is fairly deep in most Lacertini but particularly so in *Lacerta*, *Timon* and *Zootoca*. In contrast, a number of species that regularly use crevices as refuges are moderately to very depressed. They include *Algyroides marchi*, *Apathya*, *Archaeolacerta*, *Dalmatolacerta*, many *Darevskia*, *Dinarolacerta*, *Hellenolacerta*, *Iberolacerta*, *Iranolacerta zagrosica*, some *Podarcis* (members of the *P. hispanica* complex and to a lesser extent some populations of *P. muralis*). Overall these two conditions form a continuum. Head size also varies and often shows sexual dimorphism, being larger in males, especially those of *Phoenicolacerta laevis*, *Podarcis peloponnesiaca* and the *Timon lepidus* group. Relative limb and tail length is also variable, something that is often correlated with spatial niche (Arnold 1998a). Tails are especially long in some species of *Takydromus*. Again, sexual differences are usual, males having longer extremities than females. Digits vary considerably in shape, tending to be cylindrical and fairly straight in ground-dwelling forms, and laterally compressed in those that climb regularly. In the latter forms, toes 3–5 on the hind foot are often markedly kinked in the vertical plane (see Arnold 1998a for functional interpretation of these features). Climbing forms also tend to have shorter, deeper and more recurved claws than ground dwelling ones.

Skull (Fig. 5)

Teeth. The premaxilla bears teeth with single cusps and their number usually varies from seven to nine in adults of different species, occasionally reaching ten, for example in *Apathya*, *Lacerta* and *Phoenicolacerta;* the number is regularly 8–10 in *Takydromus.* Teeth on the maxillae and dentaries are often bicuspid at least posteriorly, although they are frequently tricuspid in *Takydromus* and in juveniles of some other taxa. On all these bones tooth number usually increases ontogenetically and with body size, so juveniles have lower counts than mature animals, and smaller species lower ones than their bigger relatives. Additional teeth on each pterygoid bone may be present or absent, and this feature may sometimes vary intraspecifically. Pterygoid teeth are most commonly found in forms with deep, relatively robust skulls.

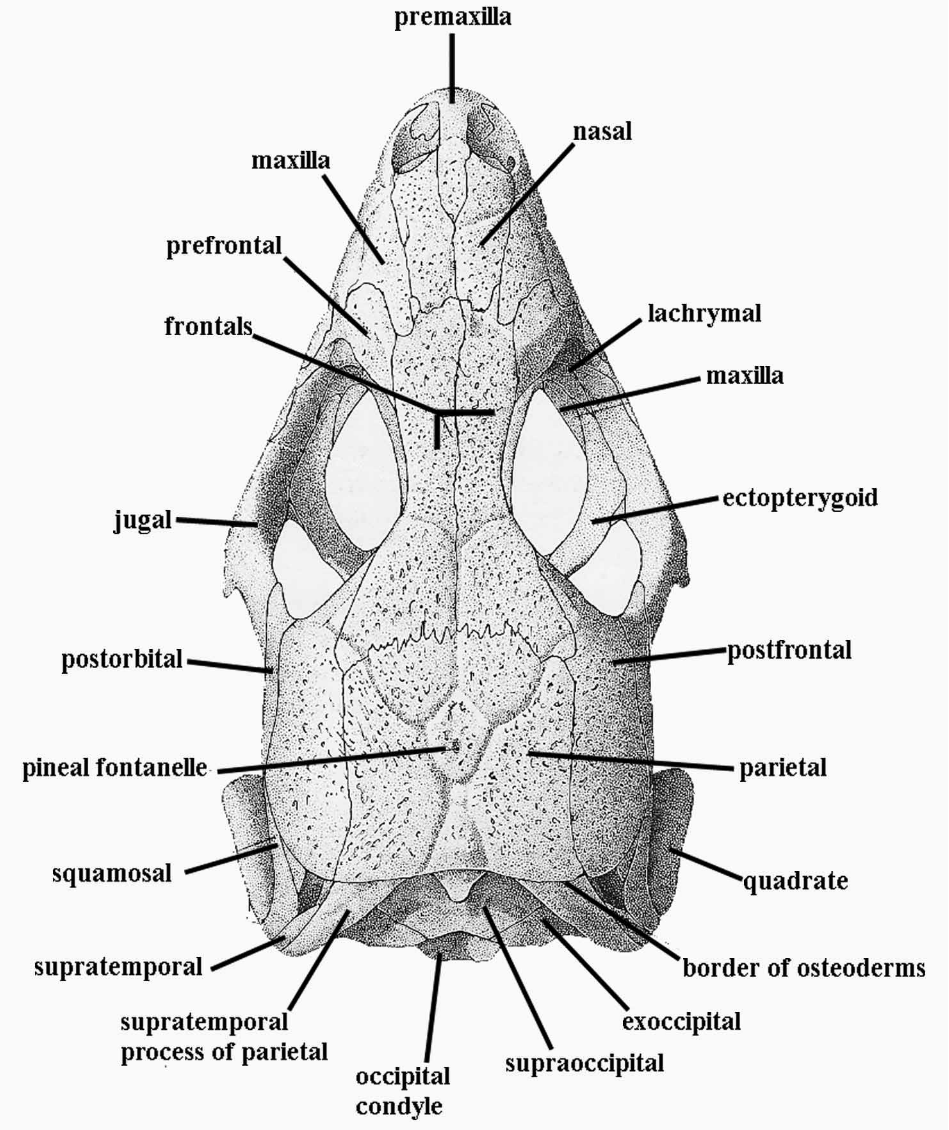

FIGURE 5.—Skull of a member of the Lacertini (*Podarcis taurica*) with thick osteodermal layer in which sutures of the head scales appear as grooves, showing principal dorsal bones but not the palpebral bones or suparaocular osteoderms (From Arnold 1989a).

Nasal opening. The nasal opening of the skull is usually relatively small but is large in many forms with depressed heads (see for example figures in Méhely 1909).

Nasal process of premaxilla. The nasal process of the premaxilla is typically quite slender but it is often broader in *Lacerta*, *Timon* and *Zootoca,* in some Iberian *Iberolacerta* and in *Takydromus.*

Septomaxilla (Fig. 6). The septomaxilla is usually convex above with at most slight anterior and posterior projections, but these are much better developed in at least some *Parvilacerta* and *Iranolacerta brandtii.*

Medial depression on snout. The upper surface of the snout of Lacertini usually has a smooth profile in transverse section, but there may be a slight medial depression in *Iranolacerta brandtii* and *Parvilacerta* and in some *Lacerta* and *Timon.*

Frontal bones. There is usually a descending anterior processes on each frontal bone, but they are absent in *Takydromus* and some *Zootoca.*

Palpebral bone. This element, lying dorsally at the front of the orbit under the supraocular osteoderms, is exceptional in having an elongate posterior process on its lateral edge in *Takydromus.*

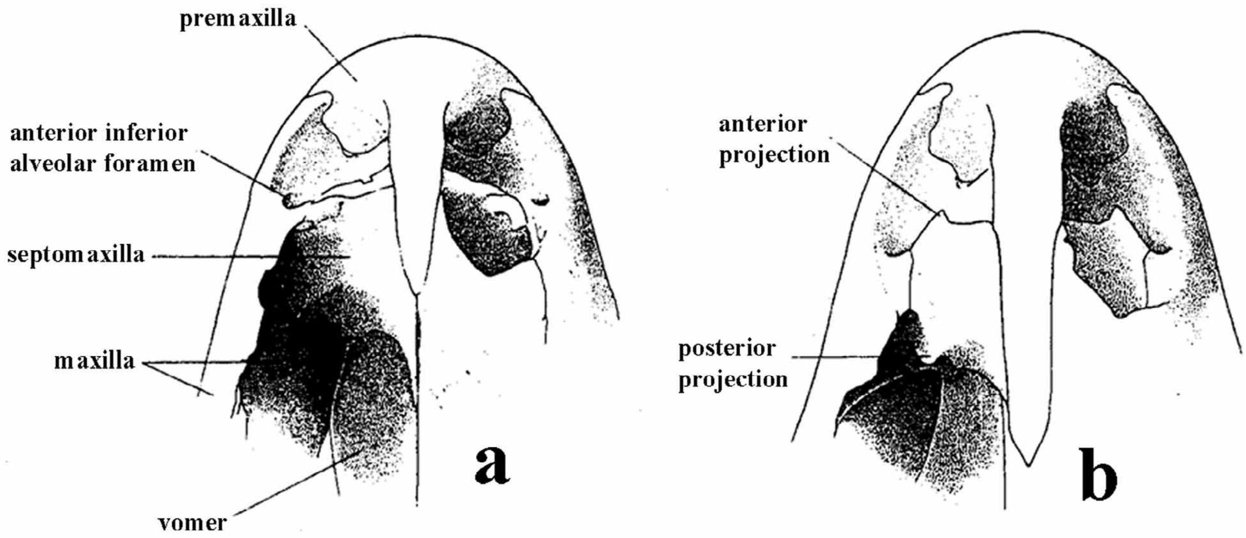

FIGURE 6.—Snouts of lacertid skulls with left nasal cavity opened to show variation in septomaxilla. (a) septomaxilla with rounded upper surface; (b) septomaxilla with anterior and posterior projections (From Arnold 1989a).

Postfrontal and postorbital bones (Fig. 5). These are usually separate at hatching, but are fused at this stage in *Lacerta schreiberi*, *Takydromus* and *Zootoca*. In some other cases, the bones appear to coalesce during life, or at least become tightly joined and covered by a continuous layer of osteoderm. For example, this occurs in many individuals of *Lacerta*, the *Timon lepidus* group and *Teira*. The postfrontal bone usually has an anterolateral process and the postorbital bone an anteromedial one (Fig. 7). But the former is absent in *Darevskia mixta*, *D. raddei*, the parthenogenetic species derived from them, and in *Iberolacerta aurelioi* and *I. bonnali*. Usually, the postfrontal and postorbital bones are subequal in length, but the postorbital may be shorter, for example in some *Algyroides*, *Dalmatolacerta*, *Iranolacerta zagrosica*, *Parvilacerta fraasii*, some *Darevskia* and *Phoenicolacerta*. In contrast it is longer in *Iberolacerta horvathi* and *I. aurelioi*.

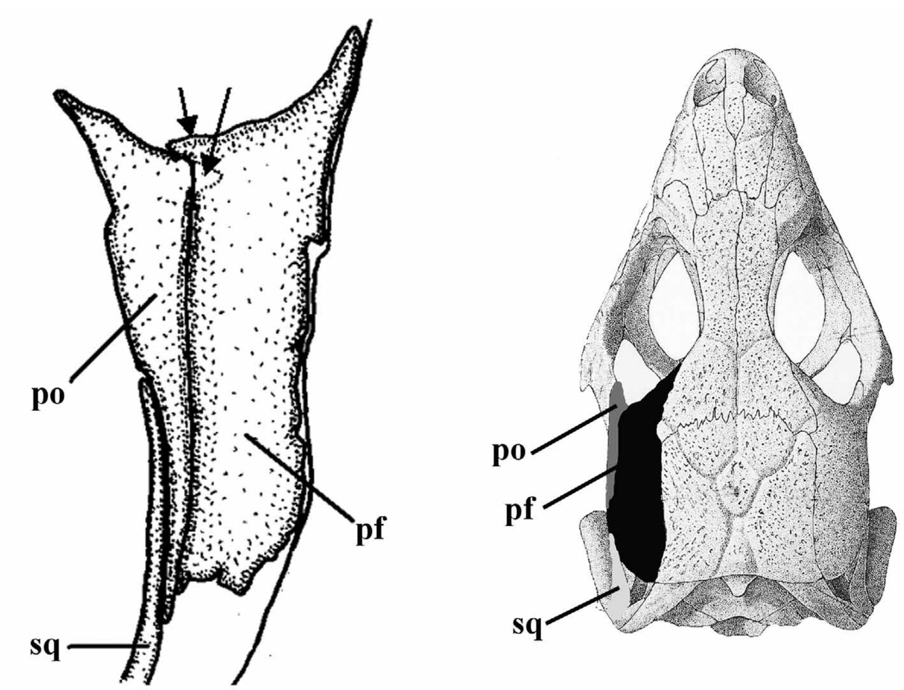

FIGURE 7.— Postorbital and postfrontal bones showing anterior processes (anteriomedial and anterolateral, respectively) (arrows). Po—postorbital; pf—postfrontal; sq—squamosal.

Maxillary-jugal suture (Fig. 8). The suture between the jugal and maxillary bones on the side of the skull is relatively smooth in most taxa but, in many *Lacerta* and *Podarcis* and *Darevskia brauneri darevskii*, it is distinctly stepped, so its course is sinuous.

Subocular foramen (Fig. 9). This foramen is situated beneath the eye and surrounded by the maxillary, palatine, pterygoid and ectopterygoid bones. It is typically quite small and roughly triangular, but is bigger and more rounded in forms like *Dalmatolacerta* and *Dinarolacerta*, and, to a lesser extent, in many other crevice-using species.

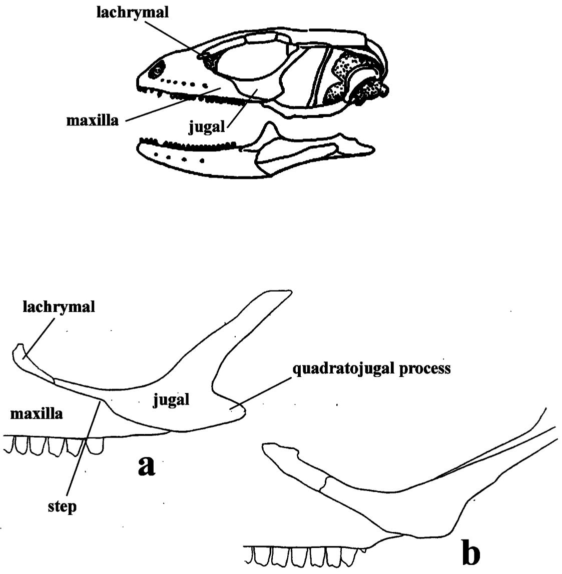

FIGURE 8.—Suborbital area of lacertid skull in lateral view showing: (a) stepped (sinuose) suture between maxillary and jugal bones, frequent in *Lacerta* and *Podarcis*; (b) absence of a step. From Arnold (1989a).

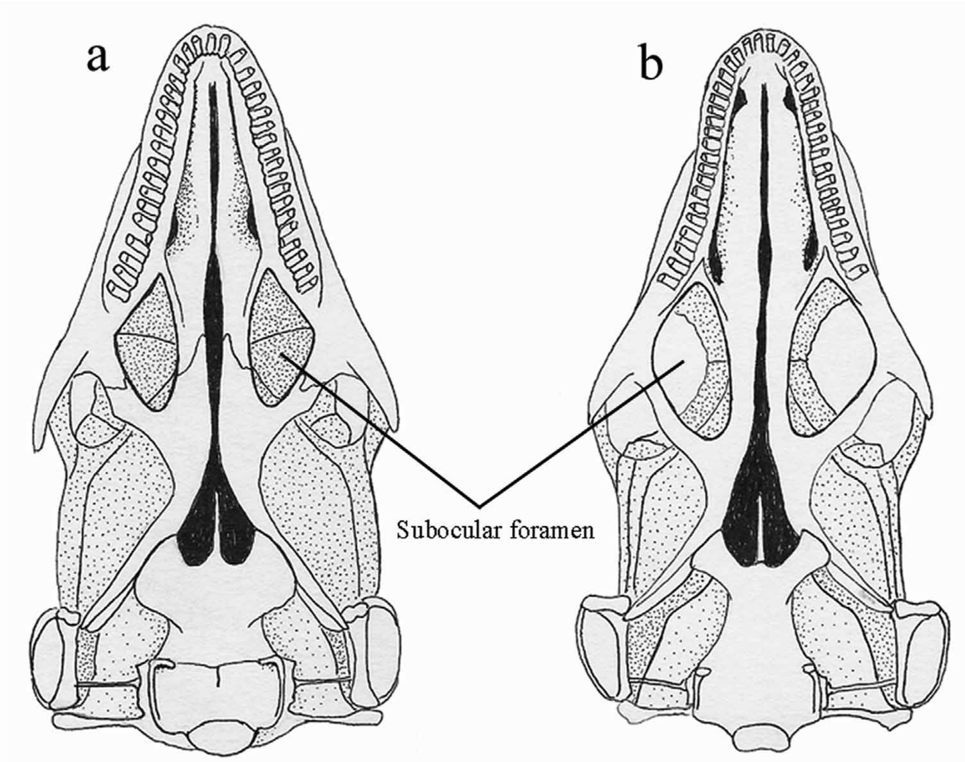

FIGURE 9.—Ventral views of skulls showing differences in shape of subocular foramen. (a) *Podarcis taurica*, foramen relatively small and triangular; (b) *Dalmatolacerta oxycephala*, foramen large and more rounded.

Osteoderms. The layer of osteoderms, that covers the dorsal bones of the skull in lacertids and is closely attached to them, is usually quite well developed in Lacertini, being exceptionally thick in *Lacerta* and *Timon*, *Phoenicolacerta laevis*, and *Podarcis peloponnesiaca.* The series of four separate osteoderms in the skin above the eye (supraocular osteoderms—Fig. 10) frequently ossify completely by maturity, but this process may be incomplete, leaving a fenestra in which the skin remains flexible. This is found in *Algyroides fitzingeri, A. marchi, Apathya, Archaeolacerta, Dalmatolacerta,* many *Darevskia* (not *D. chlorogaster, D. praticola, D. dryada* and *D. clarkorum), Dinarolacerta, Iberolacerta* (not in some *I. monticola), Iranolacerta zagrosica, Parvilacerta fraasii,* some members of the *Podarcis hispanica* complex and some female *Teira.* A tendency in this direction also occurs in *Hellenolacerta.* Fenestrated supraocular osteoderms occur especially in forms that regularly take refuge in crevices. The temporal scales on the side of the head, which cover the main adductor jaw muscles, are usually largely unossifed but regularly contain osteoderms in most adult *Lacerta* (not *L. agilis*), *Podarcis peloponnesiaca*, and *Timon*.

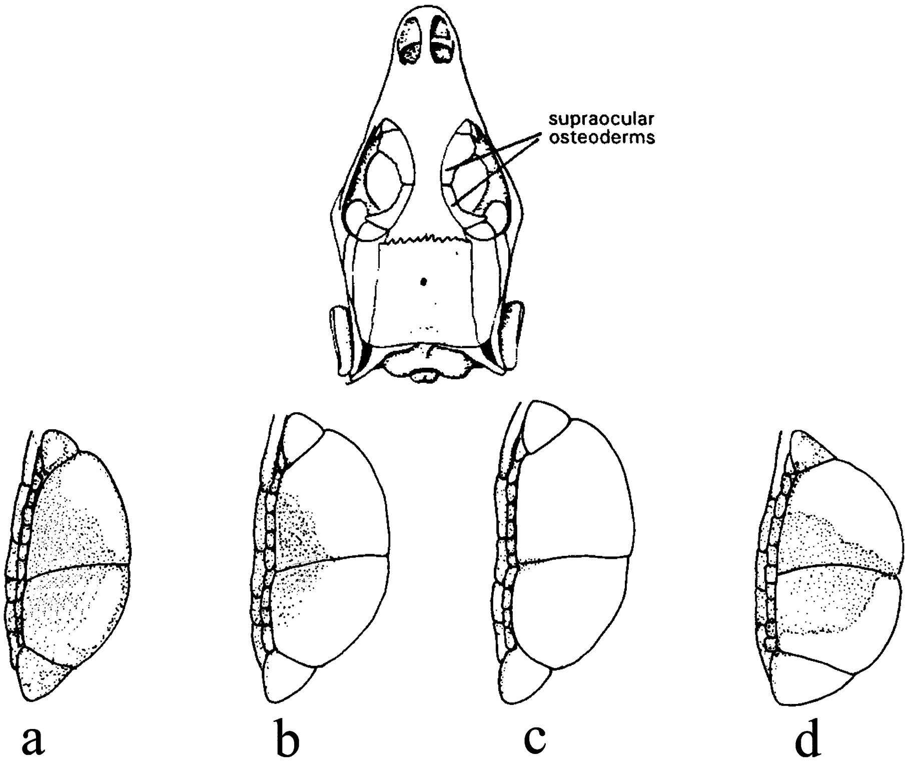

FIGURE 10.—Supraocular osteoderms (unossified areas stippled). a–c. Ontogenetic series showing development of fully ossified condition in adult *Podarcis muralis* d. adult *Dalmatolacerta oxycephala* showing retention of an unossifed fenestra.From Arnold (1998b).

Post-cranial skeleton

Presacral vertebrae. Counts in Lacertini usually vary from 25 to 29, with extremes of 24 and 30. In most species, females have, on average, about one more presacral vertebra than males. Occasionally, the difference is rather larger but is always less than two vertebrae. Counts in each sex of a species can vary by three (exceptionally four) vertebrae. The usual number in males of many species is 26 but it is 27 or more in *Hellenolacerta, Lacerta, Parvilacerta, Darevskia,* and *Timon*, some species of *Podarcis* and some *Scelarcis*. Conversely the number is 25 in *Algyroides* (except *A. fitzingeri*), *Dalmatolacerta,* and in some *Dinarolacerta* and *Takydromus*. In the last genus, the vertebrae of the mid and hind body, including the pygal ones, have neural spines that are laterally compressed and blade-like.

Posterior presacral vertebrae with short dorsal ribs. The number of posterior presacral vertebrae with dorsal ribs that are clearly shorter than the preceding ones varies, often intraspecifically. In many individuals it is usually six, often with occasional deviations, but seven occurs quite frequently in many genera. The highest counts are in *Apathya*, which nearly always have seven vertebrae with short ribs, and *Anatololacerta* where the number is usually seven or eight. In contrast, five vertebrae with short ribs is not uncommon in *Zootoca* and in some individuals there may only be four, while the number is just three to five in *Takydromus*.

Ossified ribs on third presacral vertebrae. In Lacertini, pairs of ribs are regularly present on the fourth presacral vertebra and all more posterior ones, but they may occasionally also occur on the third vertebra. However, ribs are never consistent here, being present only in a small minority of individuals, frequently very small, and often only discernible on one side. Among the groups in which they have been recorded are *Apathya*, the Pyrenean species of *Iberolacerta*, some parthenogenetic *Darevskia*, *Iranolacerta brandtii*, *Lacerta*, *Podarcis* and *Zootoca*.

Clavicle (Fig. 11). The clavicle of lacertids usually has an expanded loop of bone medially. In most forms the loop is continuous, but in Lacertini this is only always so in *Parvilacerta*, and in *Takydromus* where the posterior edge may be very broad. In other Lacertini, the loop is interrupted posteriorly in at least some individuals of each species. The relative proportions of the two conditions are very variable: for instance, in most *Lacerta* species, the interrupted condition is relatively uncommon, but it is apparently universal in *Archaeolacerta*, *Dalmatolacerta*, *Hellenolacerta* and *Scelarcis*.

Interclavicle (Fig. 11). The interclavicle of Lacertini is cross-shaped, as in nearly all other lacertids. In the majority of forms, the lateral arms are usually more or less perpendicular to the sagittal axis or angled slightly forwards, but in *Scelarcis* and *Teira*, they are directed obliquely backwards. In *Takydromus*, the interclavicle may be flanged.

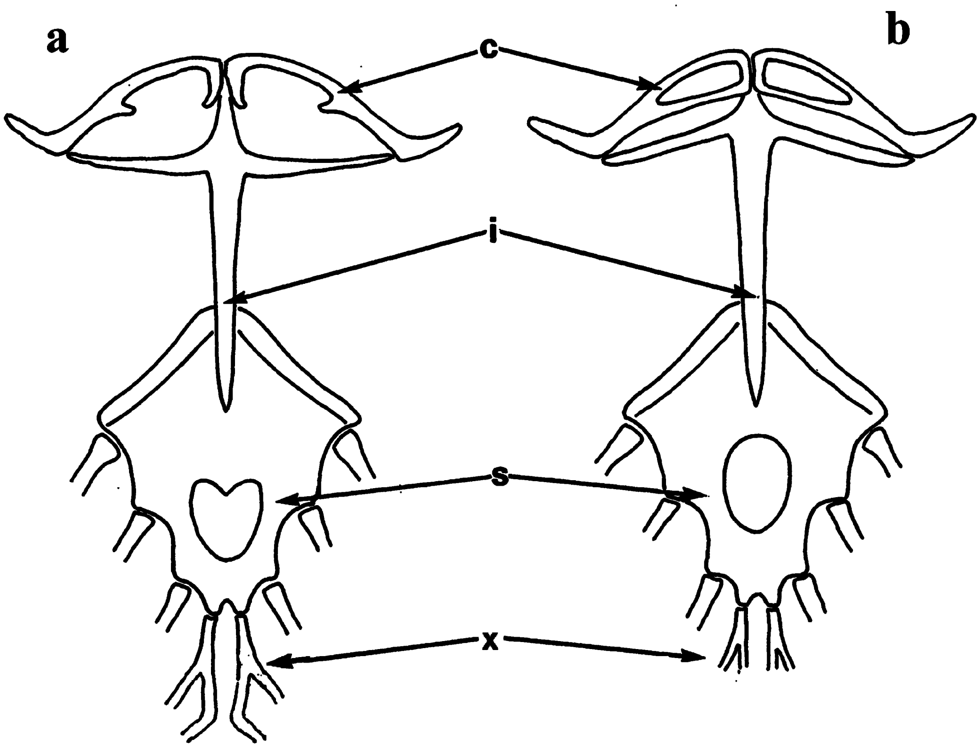

FIGURE 11.—Pectoral girdles of Lacertini, illustrating variable features: c—clavicle; i—interclavicle; s—sternal fontanelle; x—xiphisternum. (a). Medial loop of clavicle interrupted posteriorly, interclavicle with arms roughly perpendicular to sagittal axis or directed slightly forwards, sternal fontanelle heart-shaped. (b). Medial loop of clavicle intact, interclavicle with arms clearly directed obliquely backwards, sternal fontanelle oval. From Arnold (1973).

Sternal fontanelle (Fig. 11). In most Lacertini, this opening in the sternum is oval, the longer axis being sagittal. But in at least some adults of a number of forms, the fontanelle is to some extent heart-shaped. Included among these are *Algyroides marchi* and *A. moreoticus*, *Anatololacerta*, *Dinarolacerta* and some species of *Darevskia*, *Phoenicolacerta* and *Podarcis.* The fontanelle is most strongly heart-shaped in many members of the last genus.

Sternal and xiphisternal ribs (Fig. 11). In nearly all cases, there are three pairs of ribs that run ventrally to attach directly to the sternum, and two more joining this indirectly via the xiphisternum, giving a sternal: xiphisternal formula of 3:2. Exceptionally there may be three xiphisternal pairs of ribs; this condition being recorded in some *Algyroides*, *Darevskia*, *Lacerta*, *Podarcis*, *Timon* and *Takydromus.*

Inscriptional ribs. These are characterised by running ventrally posterior to the xiphisternum but do not join this. Inscriptional ribs are usually present in *Archaeolacerta*, *Iranolacerta zagrosica***,** some *Lacerta*, *Takydromus* and *Timon*, in some species of *Darevskia*, *Iberolacerta*, *Podarcis* and often in *Zootoca.* In other Lacertini genera they occur at low frequencies or not at all. Two pairs are present in some *Takydromus* and up to three in some *Lacerta* and *Timon*.

Pattern of tail vertebrae (Fig. 12). Transverse processes on the anterior autotomic tail vertebrae of Lacertini vary considerably in form (Arnold 1973). *Apathya* and *Takydromus* have an A-type pattern characterised by a single pair of processes anterior to the autotomy plane on each vertebra, the processes being directed more or less perpendicular to the sagittal axis. This condition is also found in most Eremiadini. The majority of other Lacertini have some individuals like this, but others have a B-type pattern of caudal vertebrae in which some have two parallel pairs of processes, the more posterior, which lies behind the autotomy plane, being relatively short. In *Anatololacerta* and *Podarcis* the C-type pattern occurs in which again anterior autotomic vertebrae have two pairs of processes, but they diverge instead of being parallel and the posterior one is longer. *Iranolacerta brandtii* and *Parvilacerta* have patterns in which some vertebrae may be of the B or C-type and others intermediate.

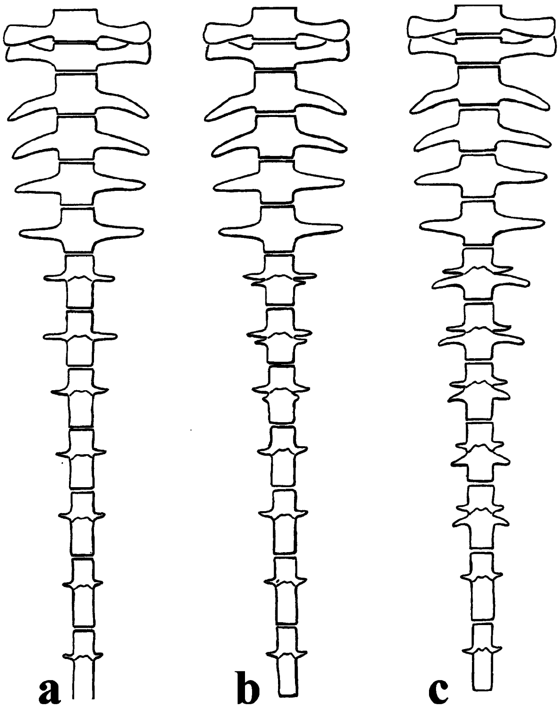

FIGURE 12.—Tail vertebrae of lacertines, showing principal variations in transverse processes of anterior autotomic vertebrae. (a) Type-A pattern – a single anterior pair of processes; (b) Type-B pattern – an anterior pair of processes followed by a parallel shorter pair; (c) Type-C pattern – an anterior pair of processes followed by a longer posterior pair that diverge backwards. The BC-pattern is intermediate between B and C: some vertebrae may be of B and C-types while in others the posterior processes diverge posteriorly but are not longer than the anterior ones. From Arnold (1973).

Scaling on head (Fig. 13)

Rostral-frontonasal contact (Fig. 13, 14a). Usually, the rostral scale is separated from the frontonasal scale by the supranasals, but the two are consistently in contact in *Dinarolacerta* and often so in some Sardinian populations of *Archaeolacerta*, in *Iberolacerta*, *Takydromus amurensis* and some *Darevskia*.

Supraocular scales (Fig. 13). There are usually four of these on each side, but the number is reduced to three in some *Takydromus.*

Supraciliary granules (Fig. 13). A complete and continuous row of granules is usually present between the supraocular and supraciliary scales, but may be reduced in *Darevskia caucasica vedenica*, Pyrenean *Iberolacerta*, and some *Iranolacerta brandtii*, *Lacerta*, *Parvilacerta*, *Phoenicolacerta*, *Takydromus*, *Timon* and *Zootoca*. Granules may be entirely absent in the last genus, and this is also true of *Lacerta agilis*, *Takydromus khasiensis* and *T. sexlineatus.*

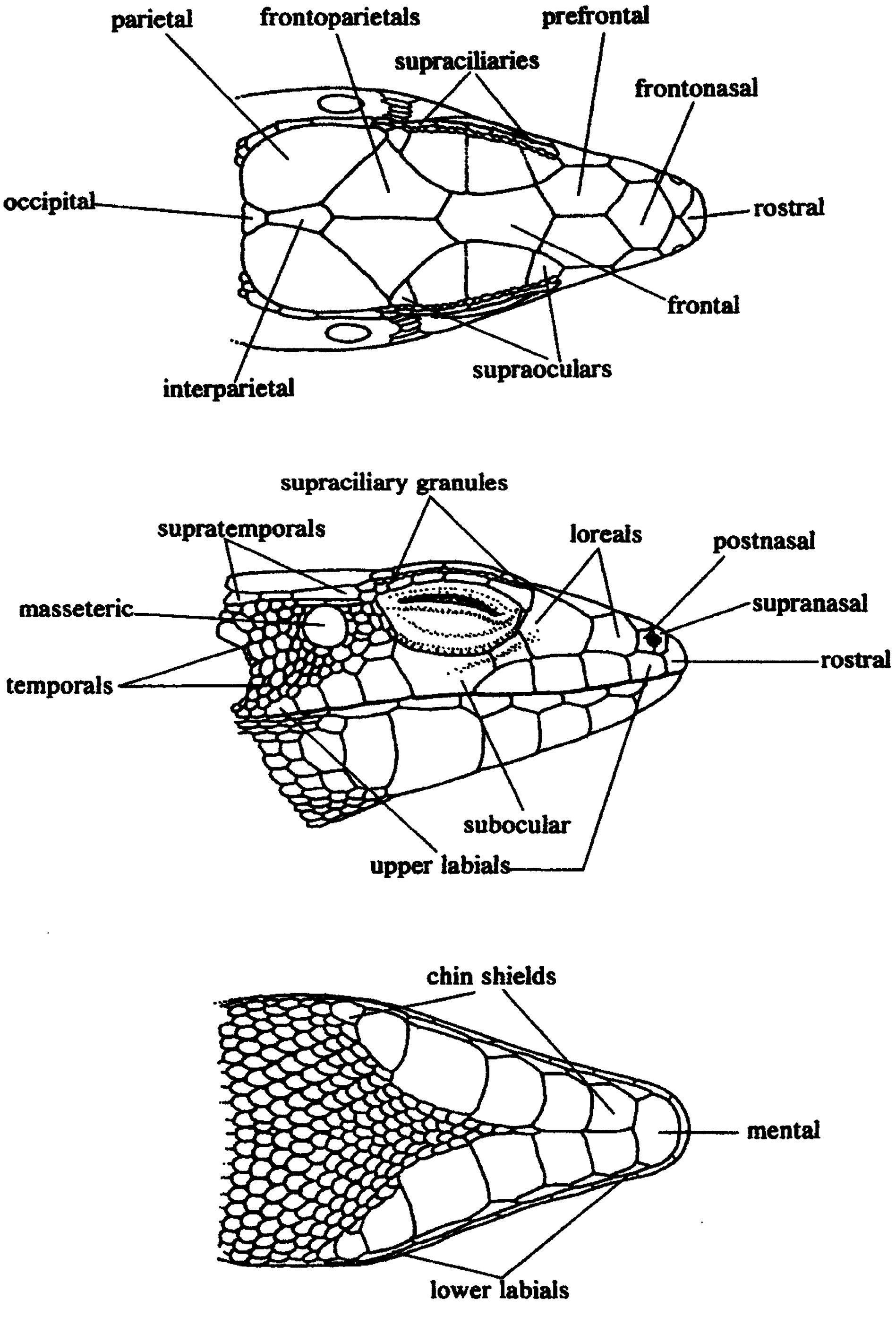

FIGURE 13.—General head-scaling of Lacertini. From Arnold & Burton (1978).

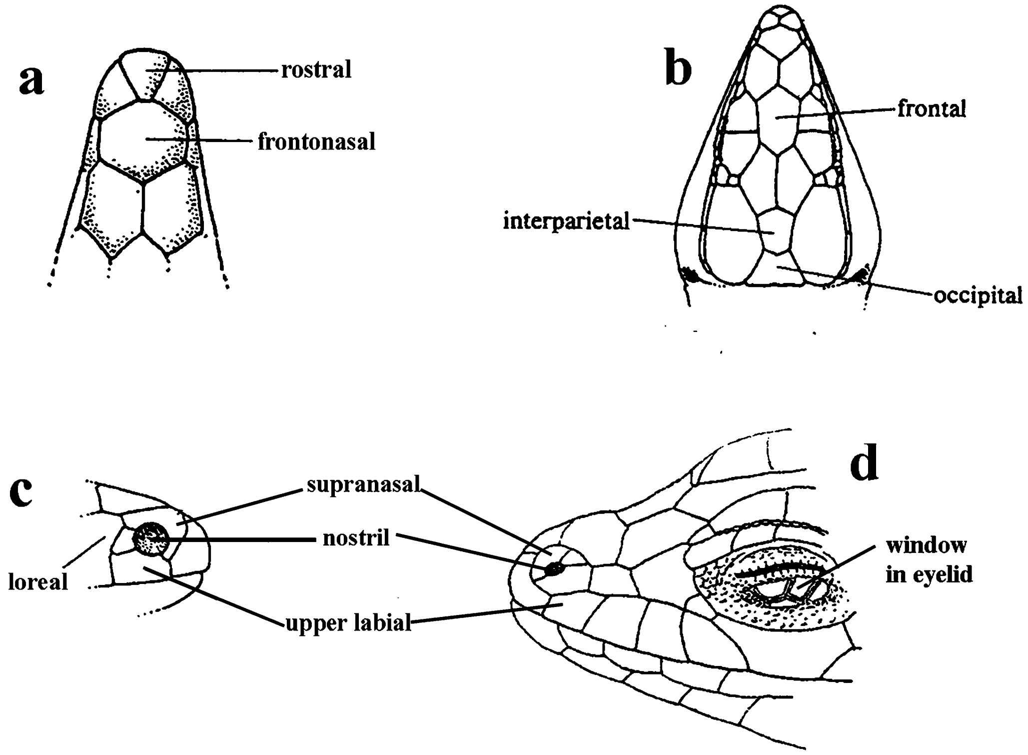

FIGURE 14.—Minority head-scale conditions in Lacertini. (a). Rostral contacting frontonasal scale (e.g. *Dinarolacerta*). (b). Occipital scale as broad as posterior border of frontal scale (e.g. some *Timon*). (c). Supranasal scale contacting anterior loreal scale (e.g. most *Iberolacerta*) (d). window of black-edged scales in lower eyelid. (a–c from Arnold & Burton 1978; d from Méhely 1909)

Position of the outer edge of the parietal scale (Fig. 15). There is a varying relationship between the outer edge of the parietal scale and the lateral border of the parietal table, the latter comprising the edges of the squamosal and postorbital bones. In *Apathya*, *Iranolacerta*, *Lacerta* and *Timon*, the scale does not reach the border of the table at all, while in the majority of Lacertini it does so only posteriorly. However, in some *Archaeolacerta*, *Phoenicolacerta*, and in *Algyroides marchi*, *Podarcis*, *Scelarcis* and *Teira*, the scale reaches or closely approaches the border of the table both posteriorly and anteriorly.

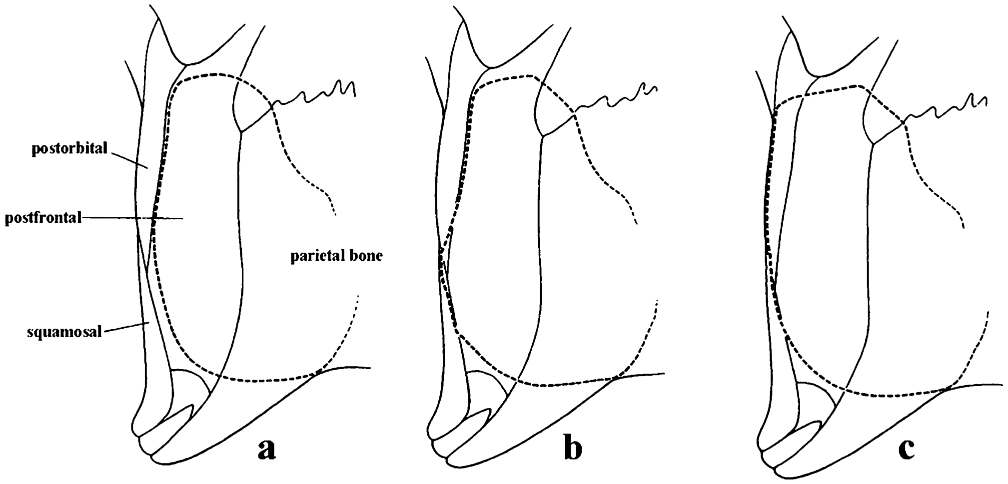

FIGURE 15.—Relationship between the outer margin of the left parietal scale (indicated by a broken line) and the underlying bones of the skull. (a). Parietal scale margin not approaching edge of the parietal table (made up of the outer margins of the postorbital and squamosal bones); (b). Parietal scale margin approaching edge of table posteriorly; (c). Parietal scale margin approaching edge of table posteriorly and anteriorly. From Arnold (1989a)

Size of occipital scale (Fig. 14b). This scale is quite variable in size but is especially large in some individuals of *Lacerta* and more commonly in *Phoenicolacerta* and *Timon.* In these forms it may be as wide as, or wider than, the posterior border of the frontal scale in adults.

Scaling around nostril. Posterior to the nostril there may be two superposed postnasal scales, or a single scale (Fig. 13), which is the usual condition in *Archaeolacerta*, *Darevskia*, *Iberolacerta*, *Iranolacerta zagrosica*, *Lacerta agilis*, *Parvilacerta fraasii*, *Podarcis,* and *Zootoca*. Either one or two postnasals are commonly present in *Dinarolacerta* and *Takydromus,* and in some other forms both conditions exist but one is sporadic. Thus, two scales may occasionally occur in some *Podarcis* and one scale in *Algyroides*. *Apathya* is exceptional in sometimes having three postnasal scales and occasionally three loreal scales instead of two. *Lacerta agilis* and *Zootoca vivipara* also show considerable variation in the scaling of this region. In most Lacertini, the supranasal scale is separated from the anterior loreal scale, but it extends above a single postnasal to make contact with the loreal in *Darevskia derjugini*, *D. dahli* and often in *Iberolacerta*, *Takydromus* and *Zootoca* (Fig. 14c).

In nearly all cases, the nostril is bordered below by the first upper labial scale, but in *Parvilacerta, Scelarcis* and some *Iranolacerta brandtii* and *Zootoca* this is prevented by contact between the supranasal and lower postnasal scales (Fig. 13). In *Apathya* separation may be produced by an additional small scale.

Upper labial scales. The usual number of upper labial scales in front of the subocular scale is often four but is four or five in some cases, such as *Archaeolacerta*, *Dinarolacerta* and some *Podarcis* and *Takydromus*, and regularly five in others, among them *Anatololacerta, Apathya*, *Dalmatolacerta*, *Hellenolacerta*, *Iranolacerta, Phoenicolacerta*, *Scelarcis* and *Teira*. *Takydromus* and *Zootoca* occasionally have only three upper labial scales in front of the subocular.

Lower eyelid (Fig. 14d). In small Lacertini, the centre of the lower eyelid is often transluscent and in some cases the scales in this region are enlarged. In *Apathya* the enlarged scales are black-edged but otherwise fully transparent so they form a window. *Scelarcis* also has a window but this consists of a single large scale.

Temporal scales (Fig. 13). The first upper temporal (suparatemporal) scale is often large and deep compared with other upper temporals. This differentiation is less pronounced in forms like *Podarcis* where the parietal scale extends to the edge of the parietal table anteriorly. Many Lacertini have an enlarged masseteric scale in the temporal region that is not found in other lacertids, with the exception of *Atlantolacerta* and most *Gallotia*. Among Lacertini where it occurs, there is considerable variation in the size of the scale and in whether it is consistently present or not. It is small in some *Algyroides, Dalmatolacerta*, *Parvilacerta*, *Podarcis* and *Phoenicolacerta kulzeri,* and absent in *Apathya*, *Hellenolacerta*, *Scelarcis*, *Takydromus*, *Teira* and some *Anatololacerta. Takydromus* is singular in having temporal scales that are often clearly keeled.

Chin shields (Fig. 13). There are usually six pairs of chin shields in Lacertini, but only three or four pairs in *Takydromus*. In contrast, there may be an additional small scale on each side posteriorly in *Dinarolacerta*, and two such scales on each side in *Iranolacerta zagrosica*.

Scaling on body, limbs and tail

Dorsal body scales. The body is usually covered above and on its flanks by small scales that are not as large as those on the tail. The number of scales in a transverse row across the mid-body is often 40–80 but figures may reach or even exceed 100 in some populations of the *Timon lepidus* group, or be as low as 25 in some *Zootoca*. Dorsal scales are frequently lightly keeled and more strongly so in forms like *Lacerta, Parvilacerta parva, Podarcis taurica*, *Timon princeps* and many *Zootoca.* However, keeling is absent in many forms and, in ones that regularly use crevices as refuges, such as *Dalmatolacerta, Dinarolacerta* and *Iberolacerta horvathi*, the scales themselves are flattened. *Algyroides* and most *Takydromus* differ from all other Lacertini in having dorsal scales that are much bigger than those on the tail. These large scales, which are keeled, are usually blunt and confined to the mid-back, but in *Algyroides moreoticus* and *A. fitzingeri* they are pointed and strongly overlapping and extend onto the flanks as well. In these two species transverse counts at mid-body are as low as 13–24. In many *Takydromus* the large dorsal scales are arranged in regular longitudinal rows and the keels form continuous longitudinal ridges.

Scale microornamentation. Epidermal microornamentation on the dorsal scales of Lacertini usually consists of flattened, strap-shaped 'cells' with overlapping posterior borders (Arnold 2002a). These cells may occasionally bear scattered small pits, as in at least some *Apathya* and *Iranolacerta brandtii*. The only really marked deviations are in *Algyroides* and *Takydromus*. Microornamentation in the former consists of strap-shaped cells with raised posterior borders that are interspersed with large 'pustules', a pattern found elsewhere only in the Central African *Adolfus africanus*. *Algyroides moreoticus* is further distinguished by having the raised edges of the cells denticulated. *Takydromus* also has strap-shaped cells with raised posterior borders and these are combined with a series of coarse anastomosing longitudinal ridges.

Collar (Fig. 16). Nearly all Lacertini have a well-developed collar, although in some *Takydromus* it is weakly differentiated or even absent. Usually the collar is a backwardly-directed skin fold on the lower surface of the neck, just anterior to the lateral arms of the interclavicle, which is covered by a transverse series of large scales. The posterior margins of these scales may form a regular continuous line (collar smooth) or may project backwards to form a free serration (collar serrated). Markedly serrated collars occur especially but not entirely in mainly ground-dwelling forms. They are found in *Algyroides,* some ground-dwelling *Darevskia* species, *Lacerta*, *Parvilacerta*, *Podarcis taurica*, *Takydromus, Timon* and *Zootoca.*

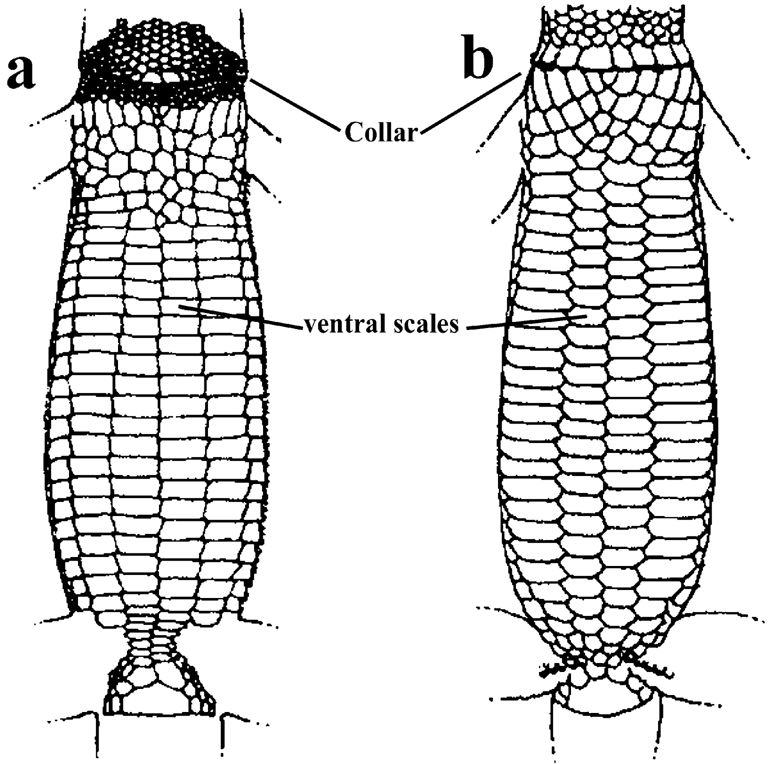

FIGURE 16.—Undersides of Lacertini showing differences in scaling. (a). Collar smooth and ventral scales rectangular with little or no posterior overlap. (b). Collar serrated, and ventral scales trapezoidal with sloping sides and marked posterior overlap.

Ventral scales (Fig. 16). The enlarged ventral scales of Lacertini are arranged in regular transverse and longitudinal rows. Most frequently the usual number of longitudinal rows is six, but it may sometimes be eight in *Anatololacerta* and *Apathya,* and regularly so in *Iranolacerta*, *Parvilacerta* and some *Lacerta*, *Takydromus* and *Timon* species. Other *Timon* have ten longitudinal rows of ventrals and in *Scelarcis* the number is ten or twelve. *Iranolacerta zagrosica* may also sometimes have ten rows, but the outer rows are very short. The ventral scales themselves are often rectangular with little posterior overlap, especially in rock-climbing forms. In other mainly ground-dwelling ones, the scales have obliquely sloping sides with marked posterior overlap, a condition best developed in *Lacerta* and *Timon princeps*, and to a lesser extent in *Zootoca*, *Parvilacerta*, *Podarcis taurica* and some *Darevskia* such as *D. derjugini* and *D. praticola*. *Takydromus* is unique in many species having at least the more lateral ventral scales pointed and keeled; keeling also occurs on the gular scales.

Preanal region (Fig. 17). The preanal scale itself is usually large and bordered by a semicircle of smaller scales (circumanalia) the most anterior one or two of which may be enlarged. The semicircle may also sometimes be incomplete, being interrupted anteriorly. In some cases the preanal scale is smaller and may then be bordered by more rows of scales. There may be either one or two rows, for example in *Algyroides*, *Dinarolacerta*, *Hellenolacerta*, *Iranolacerta zagrosica*, *Scelarcis*, *Teira* and some *Lacerta*; and two or more rows in *Anatololacerta*, *Apathya*, other *Lacerta* and in *Timon*. Some *Takydromus* are distinctive in having keels on the preanal scale, which may also be divided longitudinally.

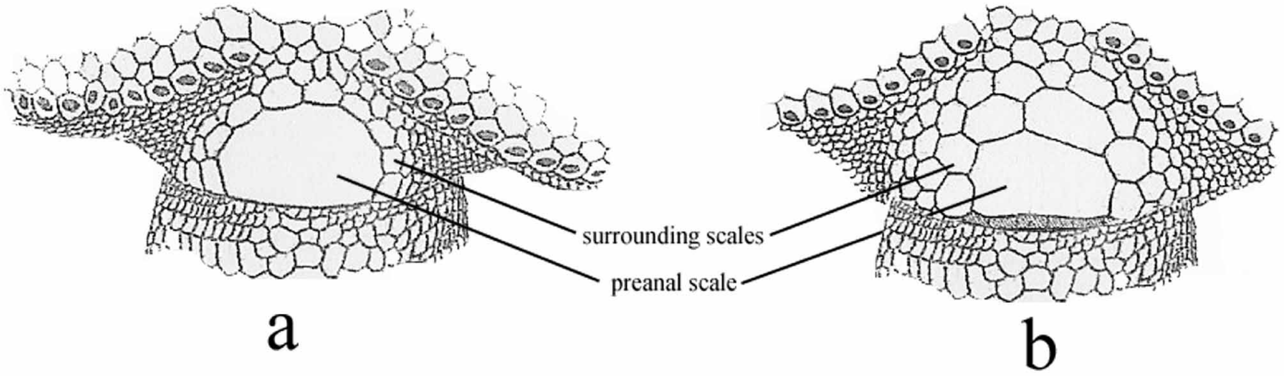

FIGURE 17.—Vent regions of Lacertini showing variation in size of the preanal scale and the number of semicircular rows of scales surrounding it. (a) Large, one row. (b) Small, several rows. From Méhely (1909).

Femoral pores. The femoral pores under the thigh are arranged in most Lacertini in a row numbering 7–31, beginning close to the midline of the body. Normally the row extends to the knee, but it is sometimes shortened distally, for example in *Darevskia derjugini* and some members of the *Lacerta trilineata* group. *Takydromus* is exceptional in often having just one or two femoral pores on each side or sometimes none at all; the maximum number found in this genus is five.

Toes. The toes of Lacertini usually have one or two rows of unkeeled tubercular lamellae beneath, but the lamellae bear a single row of subdigital keels in *Apathya* and sometimes a faint double row in *Parvilacerta parva*.

Tail. The tail scales are arranged in regular whorls, two to each vertebra. The whorls may be subequal in length but are sometimes alternatively markedly longer and shorter. The scales bordering the ventral mid-line of the tail are usually about the same width as neighbouring ones, but they are markedly expanded in *Dalmatolacerta* (Fig. 18) and to a lesser extent in some *Hellenolacerta.*

Colouring

As noted, Lacertini exhibit considerable variation in their colouring and there are often extensive intraspecific differences, both between and within different populations.

Sexual dimorphism. Some species show little difference between males and females in their dorsal colouring, but sexual dimorphism is sometimes well developed, and is usual in *Podarcis*. It also occurs to varying extents in *Algyroides moreoticus*, some *Lacerta* populations (particularly well developed in *L. schreiberi* and *L. agilis*), and some populations of *Hellenolacerta*, *Darevskia*, *Iberolacerta* and in *Teira*.

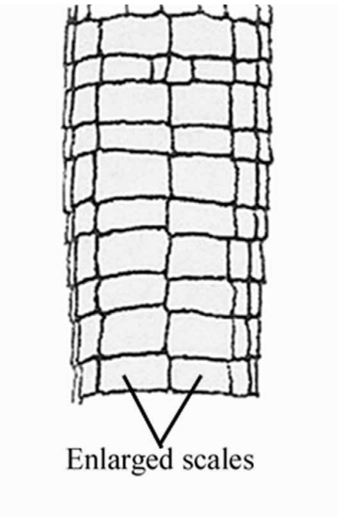

FIGURE 18.—Enlarged scales bordering ventral mid-line of tail in *Dalmatolacerta* (from Arnold & Burton 1978).

Dorsal pattern. Most hatchling Lacertini have a pattern of longitudinal stripes or series of spots on the upper parts. The main elements that may be found are shown in Fig. 19. The juvenile pattern may be retained but often becomes less clear with growth and the stripes may break up or be replaced by reticulation. A number of forms often have narrow pale longitudinal stripes in the pattern, especially those that spend some time among grassy vegetation with dead pale stems. They include *Lacerta*, some *Parvilacerta*, many *Podarcis* and *Zootoca*. Some other Lacertini have broad dorsolateral stripes that are lighter than the flanks and mid-dorsum but sometimes consist of ground colour rather than being lighter than this; they occur in some *Anatololacerta*, *Apathya*, *Scelarcis*, *Takydromus* and *Teira*. Absence of striping in juveniles is uncommon but is found in *Archaeolacerta*, *Dalmatolacerta*, *Timon* and some *Dinarolacerta*, *Podarcis*, *Scelarcis* and many *Takydromus*. In these cases, animals are spotted or reticulated from hatching. Dorsal ground colour is often various shades of brown, buff or grey but it may be at least transiently bright green in many *Lacerta* and *Timon* and a wide though sporadic range of other forms. Melanism occurs sporadically in some taxa, but is especially common in *Podarcis* populations on small islands and in *Dalmatolacerta* at high altitudes. It arises in three different ways: general darkening of the ground colour (the commonest), increase in the number of dark markings, and the spread of those markings already present. These conditions were respectively named melanismus, abundismus and nigrismus, by Reinig (1937).

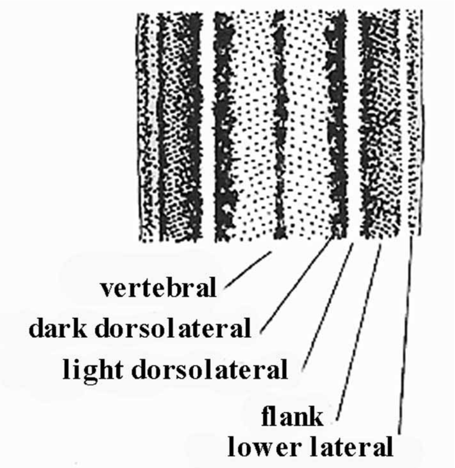

FIGURE 19.—Common elements of patterning in lacertines: mid-back showing frequent positions of longitudinal stripes or rows of spots. From Arnold & Burton (1978).

Concolor morph. In some species a proportion of individuals are abruptly different from the rest in having no dark or light dorsal markings, or virtually none. This phase is known as the concolor morph and occurs in several *Podarcis* species. In *Podarcis melisellensis* and *P. sicula* at least, concolor individuals are homozygous for the recessive allele causing this condition (Kramer 1941). Similar disjunct marked and plain morphs occur in *Scelarcis*, sometimes in *Dalmatolacerta* and *Dinarolacerta*, and sporadically in *Lacerta*, *Zootoca*, *Darevskia*, *Iberolacerta aranica* and *I. bonnali*. In this last genus, in addition to strongly marked and plain individuals, there are ones with faint markings that may possibly be heterozygotes (Arribas 2001).

Presence of ocelli. A number of taxa often have one or more prominent blue ocelli in the shoulder region including some or all species of *Apathya*, *Darevskia*, *Hellenolacerta*, *Iberolacerta*, *Iranolacerta*, *Parvilacerta* and *Podarcis.* Ocelli may be more extensive, occurring especially on the flanks. Usually these widespread ocelli are bigger and more numerous in males than in females where they are sometimes absent, and their number may increase with age. In *Zootoca*, *Lacerta agilis* and juvenile *Lacerta schreiberi*, they have pallid centres, but in *Apathya*, *Hellenolacerta*, some *Iranolacerta*, *Parvilacerta*, *Takydromus sexlineatus ocellatus* and *Timon*, at least some of them are often blue. Blue pigment may also be extensive on the flanks of some *Lacerta* but is not usually arranged in discrete ocelli.

Juvenile tail colour. Usually the upper surface of the tail is relatively sombre, but it is brightly coloured (usually blue or green) in juveniles of some populations, including many or all *Apathya*, *Archaeolacerta*, *Dalmatolacerta*, *Darevskia*, *Dinarolacerta*, *Hellenolacerta*, *Iberolacerta*, some *Podarcis* species and *Scelarcis*. In some cases bright tail colour may be retained by adults, for instance in *Dalmatolacerta* where the tail is also banded with black.

Colouring of underside. Many Lacertini have bright colouring on the belly in at least some breeding adult males, which contrasts with the often more sombre dorsum and usually the flanks as well. The colour often increases in intensity with age and, when present in both sexes, tends to be stronger in males. It may be red, orange, yellow, bright green or sometimes blue, and occasionally more than one colour may be involved, as in *Iranolacerta brandtii*. Such contrasting bright belly pigmentation is absent from a few taxa, including *Apathya*, *Lacerta*, *Scelarcis*, *Takydromus*, and *Timon.* The throat is also often brightly coloured and in some cases it may contrast with the belly. The underside frequently bears varying amounts of dark spotting, although this is usually absent in *Algyroides*, *Apathya*, *Dalmatolacerta*, *Darevskia*, some *Lacerta*, *Scelarcis*, *Takydromus*, *Teira* and *Timon*. Many taxa frequently have blue spots on the lateral edges of some of the outermost ventral scales, although these are missing in most *Algyroides* and in *Apathya*, *Lacerta*, *Scelarcis*, *Takydromus*, *Teira*, *Timon* and *Zootoca*; they are also not apparent in *Dalmatolacerta*, in which they could possibly be masked by the general blue colouring of the underside.

Soft-part characters

Nasal vestibule (Fig. 20). This, the anterior part of the nasal tract, is a small chamber in most Lacertini that is separated from the principal nasal cavity by a ventral ridge. In *Timon* and some *Podarcis* and *Lacerta*, the vestibule is more elongate posteriorly and this trend is emphasised in *Iranolacerta brandtii* and *Parvilacerta* where the posterior border of the vestibule overhangs the most anterior part of the principal nasal cavity.

Bodenaponeurosis. This is the large aponeurosis that attaches to the coronoid bone of the mandible of lizards and on which the large external adductor muscles of the jaw insert. In many lizards, including the great majority of Lacertini, the bodenaponeurosis has a lateral septum on its outer surface that divides the superficial and medial layers of the muscles, but in *Lacerta* and *Timon* it is absent (Rieppel 1980). This absence also occurs in some members of the Gallotiinae, namely *Gallotia* and *Psammodromus algirus*.

Thoracic fascia. A fascia lying just under the skin of the anterior trunk, which is absent in most Lacertini, but is present laterally in the *Timon lepidus* group (Arnold 1989a).

Anterior extent of kidney. In Lacertini, usually less than half the kidney is situated in front of the sacrum, but the proportion is greater in *Apathya* and *Parvilacerta*, where the anterior portion may also be expanded.

This may possibly be related to the problems of excretion in arid habitats, as enlarged kidneys also occur in advanced Eremiadini from dry situations (Arnold 1989a).

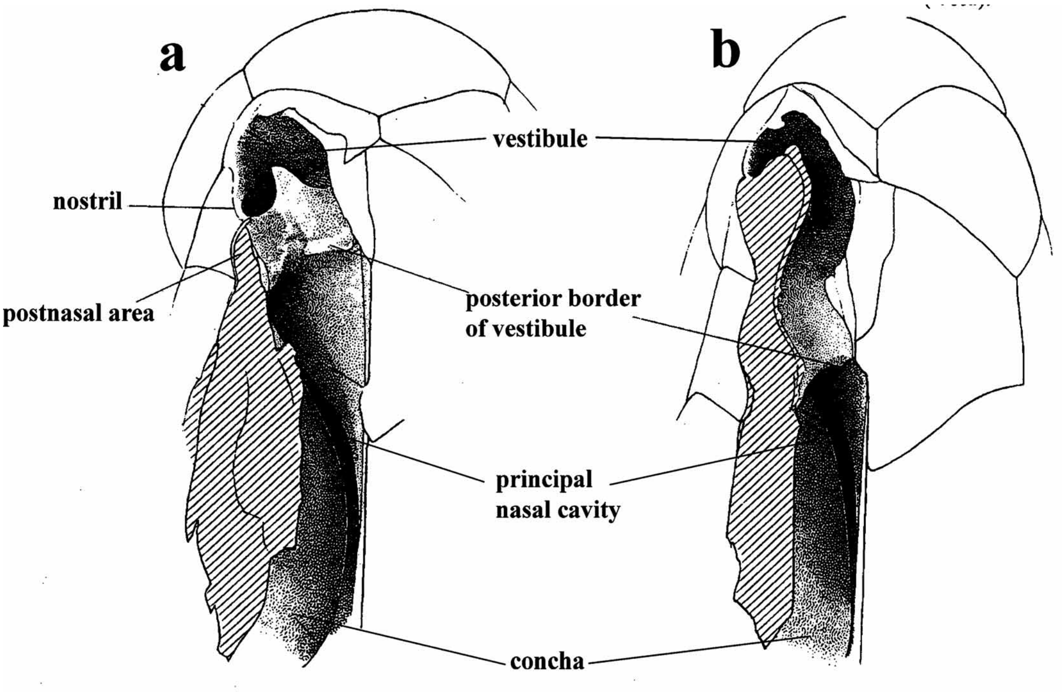

FIGURE 20.—Snouts of lacertids with left nasal cavity opened to show variation in length of the nasal vestibule. Most Lacertini have a short vestibule similar to that shown in (a), while *Iranolacerta brandtii*, *Parvilacerta*, and to a lesser extent *Timon* and some *Lacerta* and *Podarcis* approach the condition shown in (b). although their vestibules are not as long as indicated here. From Arnold (1989a).

Retractor lateralis anterior muscle. In lacertids, this muscle usually originates on the dorsal wall of the hemipenial sheath, or from the transverse processes of the caudal vertebrae and associated horizontal longitudinal septum; it inserts largely or entirely in front of the vent (Arnold 1984). In the majority of Lacertini, insertion is close to the midline but it is more lateral in *Archaeolacerta*, at least some *Darevskia*, in *Dinarolacerta*, *Iranolacerta brandtii*, *Lacerta*, *Phoenicolacerta*, *Teira* and *Timon*. Usually this distal area of the muscle is narrow but, in *Anatololacerta*, *Apathya*, *Takydromus* and *Zootoca*, it is broad with some fibres extending backwards to the region of the anterior lip of the vent. In at least *Apathya*, *Archaeolacerta*, *Dalmatolacerta* and *Hellenolacerta*, other fibres insert on to the base of the hemipenis.

Female genital sinus and oviducts. As in Gallotiinae, and a minority of Eremiadini the female genital sinus of Lacertini is almost always bilobed, but it is unlobed in *Parvilacerta*, as is the case in the majority of Eremiadini. The oviducts normally join the genital sinus on its ventral side some way from its anterior extremities, but in *Podarcis*, they insert near the tips of the lobes.

Hemipenis (Fig. 21)

General form and seasonal variation. Usually the lobes of the hemipenis are relatively thin-walled in Lacertini. In many forms, the organ regresses considerably outside the breeding season, becoming reduced in size and losing the characteristic microornamentation on the lobe plicae, although this feature has not been checked for all taxa. *Takydromus* is distinctive in having thick-walled lobes and no obvious seasonal variation.

Armature and complex lobe folding. The hemipenis of Lacertini have lobes of more or less equal size. Most lizards have hemipenes that are supported hydrostatically while in use, walls being engorged with blood and lymph**.** This is the situation in Gallotiinae and most Lacertini, but among the latter, *Zootoca* is like most Eremiadini in having a distinctive discrete internal cartilaginous supporting structure, the armature, which also becomes engorged during copulation (Arnold 1973, 1986). These forms are also distinctive in their hemipenial lobes having especially thin walls, which are complexly folded when the hemipenis is retracted. *Apathya* has these features weakly developed, possessing a small but definite armature and limited folding of the lobes. The latter feature also occurs in *Hellenolacerta* and this genus may sometimes have traces of an armature, as may *Scelarcis.*

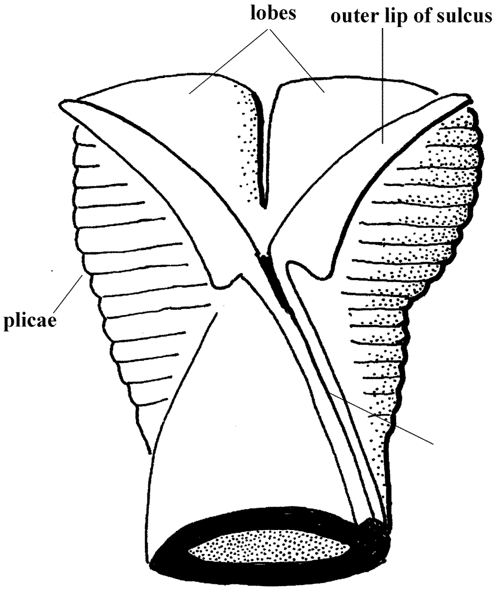

FIGURE 21.—Approximately lateral view of a naturally everted hemipenis of *Lacerta agilis* showing basic structure in Lacertini. From Arnold (1986); after Wöpke (1930).

Proportions of hemipenial lobes (Fig. 22). The hemipenial lobes of Lacertini can be divided into a basal section proximal to their bifurcation and a distal one. In most, the distal section is shorter than the proximal one, but it is longer in *Anatololacerta*, *Iranolacerta zagrosica*, *Podarcis* and often in *Takydromus*. This may also be true, although to a lesser extent, in *Phoenicolacerta.*

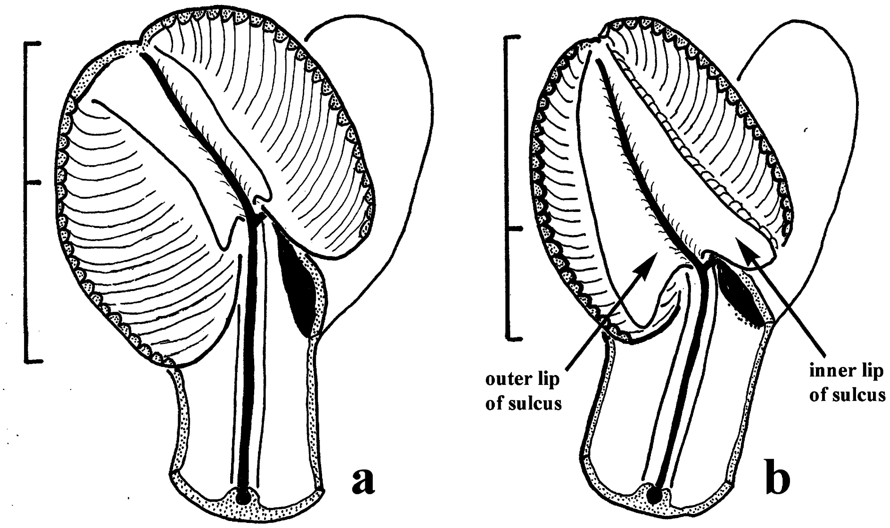

FIGURE 22.—Some variations in hemipenis structure in Lacertini. Diagrams represent retracted organs viewed from below and opened by an incision along the stem and one lobe which is spread outwards. Lines at sides indicate relative lengths of apical and basal sections of the lobes. (a) Widespread pattern, with relatively small sulcal lips and short apical sections to the lobes. (b) Alternative conditions found in *Podarcis* and elsewhere: large sulcal lips and apical sections of lobes relatively long. From Arnold (1973).

Presence of plicae (Fig. 21). In nearly all Lacertini, the outer faces of the hemipenial lobes are covered laterally by hollow plicae separated by grooves that run approximately circumferentially. But these are absent in *Parvilacerta* where the lateral lobe surface is characterised by longitudinal folds and flaps.

Lips of the sulcus spermaticus (Fig. 22). The sulcus spermaticus, the groove along which semen runs during impregnation, usually forks to produce separate branches on each lobe, although these are often absent in *Takydromus*. Where present, the sulcal branches are bordered by reflected lips in most taxa. Usually these are free but they are attached to the lobe wall in most *Podarcis* (but not the *P. hispanica* group or *P. muralis*). Lips are usually small, being exceptionally so in *Algyroides*, but are large in *Anatololacerta*, *Phoenicolacerta*, *Podarcis*, *Scelarcis* and some *Takydromus*.

Hemipenial microornamentation (Fig. 23). The lobe epithelium of Lacertini, at least in the breeding season, bears a microornamentation consisting of tubercles made up of single cells that are largely confined to the plicae (Klemmer 1957; Böhme 1971; Arnold 1973). As in most other lacertids, the tubercles may be hook-shaped spines, being pointed and curved towards the base of the lobes. Instead, they may be more rod-like in *Takydromus*, although still often recurved at their tips. In many other forms the tubercles are crown-shaped, being blunt but with a number of spinules at their tips. *Parvilacerta* is distinctive in having a proportion of tubercles that are forked. In *Lacerta* the lobe flanks are covered by long fairly straight projections that end in a point or in a series of spinules (Böhme 1971). These are also found in *Timon princeps*, but here the projections tends to curve towards the base of the organ.

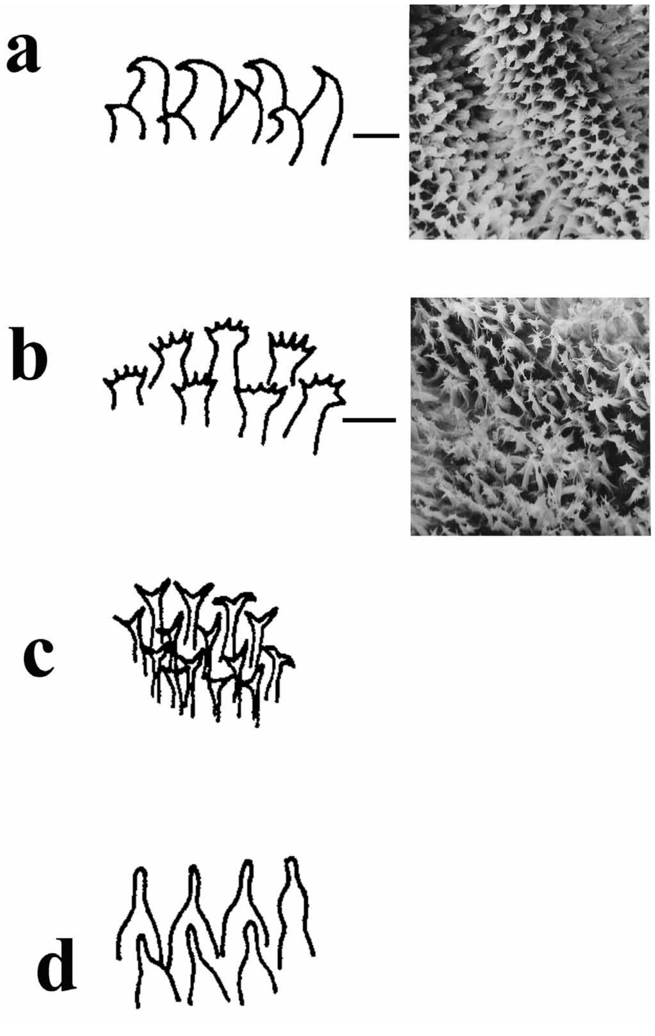

FIGURE 23.—Different patterns of hemipenial microornamentation in Lacertini. (a), hook-like spines; (b). crown-shaped tubercles; (c). bifid tubercles found in *Parvilacerta*; (d). long spinous tubercles on flanks of lobes in *Lacerta* and *Timon princeps*. Line drawings from Böhme (1971) and scanning electron micrographs from Arnold (1984).

Chromosomes (Fig. 24)

Available information on lacertid chromosomes is summarised by Olmo and Signorino (2005). Other relevant publications include Arribas and Odierna (2004), In den Bosch *et al.* (2003), Odierna *et al.* (1996, 1998, 2004), Odierna and Arribas (2005), Olmo *et al.* (1990, 1993, 2001), Volobouev *et al.* (1990).

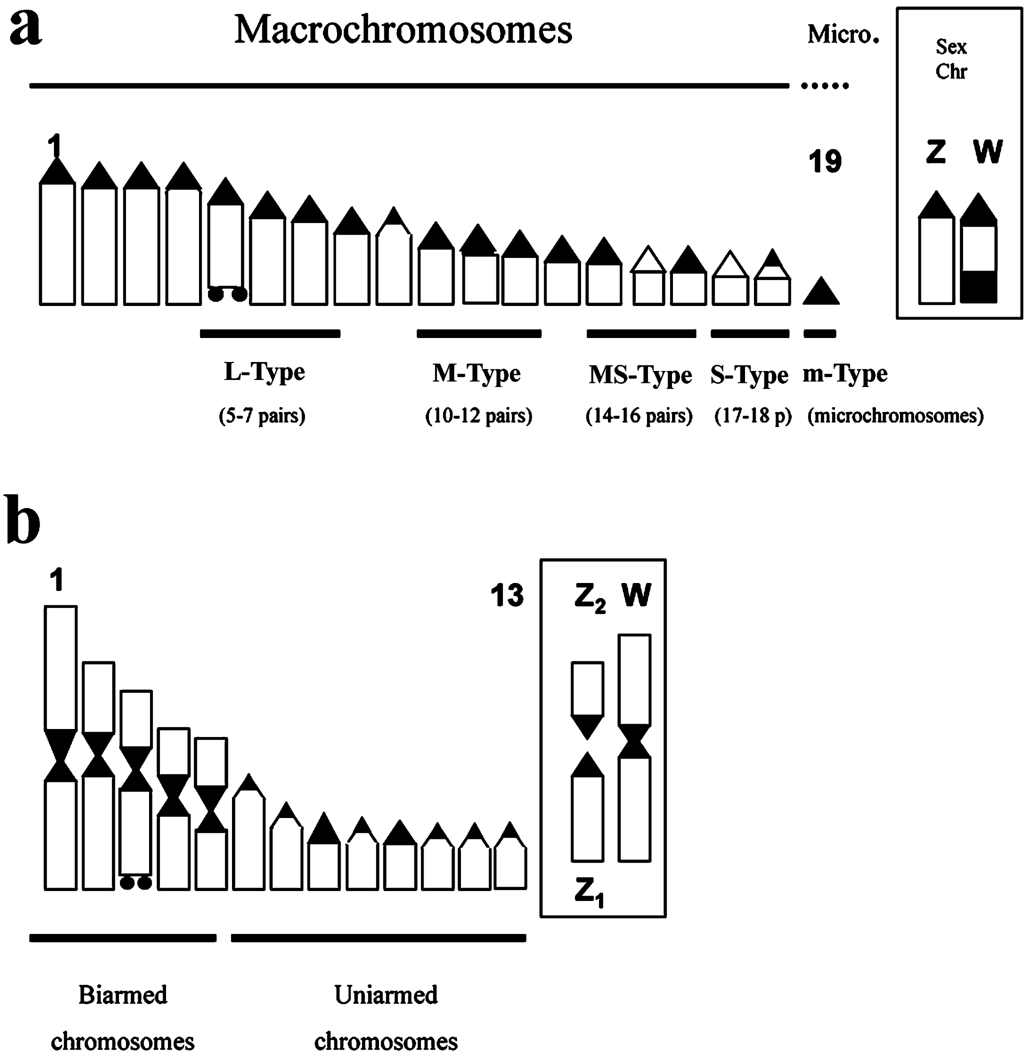

FIGURE 24.—Diagramatic representations of lacertine karyotypes (a single chromosome of each homologous pair is represented). (a) Common haploid condition with 18 single armed (that is uniarmed or acrocentric macrochromosomes) and one microchromosome, producing a diploid number of 38. The box on the right illustrates the sex chromosomes, which are part of the usual complement of chromosomes illustrated to the left but revealed in cytological preparations by specific dyes; in this case they are of the ZW type, where males have ZZ and females ZW in the diploid state. Chromosomes where the nucleolar organiser (NOR) may be situated are marked by horizontal bars and organisers are assigned to categories based on the size of these: if the NOR is situated in a macrochromosome this may be large (L-type), medium (M-type), medium-small (MS-type) or small (S-type); nucleolar organisers may also occur on the microchromosomes (m-type). In the present case the nucleolar organiser, indicated by two small black dots, is L-type. (b) Derived haploid condition with many double armed (that is biarmed, metacentric or submetacentric) chromosomes, based here on *Iberolacerta aurelioi*, but similar conditions occur in other Pyrenean *Iberolacerta* and in *Parvilacerta*. The five double-armed chromosomes appear to have each been produced by fusion of two chromosomes (Robertsonian fusions). The sex chromosome system is Z_1Z_2W, in which males have Z_1Z_1 Z_2Z_2 and females Z_1Z_2W. Here the W chromosome is bi-armed as a result of Robertsonian fusion of two chromosomes, giving females one fewer chromosome than males.

Macro- and micro-chromosomes. The diploid number of chromosomes in Lacertini is usually 38, consisting of 36 single-armed macrochromosomes (otherwise known as uniarmed, acrocentric or subtelocentric) and two microchromosomes. The total number of chromosome arms is termed the Fundamental Number (FN), which is usually 38 in Lacertini. Conditions in other lacertids suggest this overall pattern is the primitive state in this tribe. *Iranolacerta brandtii* is distinctive in having a different arrangement of macrochromosomes, with 34 single-armed ones and a pair that are double-armed (metacentric). With the two microchromosomes, this may indicate a Fundamental number of 40 (2n =38, FN =40), which is also found in some Gallotiinae (*Gallotia* —2n =40, FN =40; most *Psammodromus algirus* —2n = 38, FN =38, but others reported as 2n = 40, FN = 40). *Takydromus* has diploid numbers of 38 to 42, with 36 macrochromosomes and 2–6 microchromosomes. The diploid number is reduced to no more than 36 in *Zootoca* and *Iberolacerta* by loss of the microchromosomes, A similar degree of reduction in chromosome number occurs in *Timon* but here there has apparently been fusion (Robersonian fusion) of two pairs of the single-armed macrochromosomes resulting in one pair of two-armed macrochromosomes. A greater degree of reduction is found in some Pyrenean *Iberolacerta*, resulting in diploid numbers of 26 or 24 in males and 26, 25 or 23 in females, the last being the lowest chromosome number known in lacertid lizards. In male *Iberolacerta* with reduced chromosome numbers, there are 16 or 12 single-armed macrochromosomes and 10 or 12 double-armed ones. Similarly, in *Parvilacerta* the diploid number is reduced to 24 by seven fusions so that there are eight single-armed macrochromosomes, 14 double armed ones and two microchromosomes. In *Darevskia*, hybrids between sexual males and parthenogenetic females may be triploid with 3n=57 chromosomes.

Sex chromosomes. Specific chromosomes among the total complement described above determine the sex of individual lizards. In the widespread ZW system, males have two Z chromosomes (ZZ in the diploid cells) and females one Z and one W chromosome (ZW in the diploid cells). In *Iberolacerta* with reduced chromosome numbers, the sex chromosome system is Z_1Z_2W, in which males have $Z_1Z_1Z_2Z_2$ and females Z_1Z_2W. Populations of *Zootoca* exhibit a range of conditions, including the primitive ZW one in *Z. vivipara carniolica* and some Hungarian populations still considered as *Z. v. vivipara* (Odierna *et al.* 2004), and the Z_1Z_2W system across most of the vast distribution of the genus, from the egg-laying Iberian populations to the Pacific coast of Siberia and Sakhalin island (*Z. v. sachalinensis*). In the Z_1Z_2W system, females have a total chromosome number of 35 chromosomes rather than the 36 usual in males. The W chromosome of *Zootoca* is double-armed in some populations but has single-armed by heterochromatinization and loss of chromosome fragments in others.

Nucleolar organiser. This is situated in chromosomes of different sizes in different species. It may occur in large (L-type), medium (M-type), medium-small (MS-type) or small (S-type) macrochromosomes, or in a microchromosome (m-type). Details are given in Fig. 24. As, L-type nucleolar organisers are known in the Lacertini but are so far unrecorded from other lacertids, they are likely to represent a derived condition. In some individuals or populations of *Timon lepidus* group, a second nucleolar organiser may occur.

Reproduction

Parthenogenesis. In the great majority of Lacertini both sexes are present, but all-female ‘species’ (sometimes known as parthenoclones or agamic, parthenogenetic or unisexual species) occur in *Darevskia*, namely *D. armeniaca*, *D. bendimahiensis*, *D. dahli*, *D. rostombekowi*, *D. sapphirina*, *D. unisexualis* and *D. uzzelli*. These forms originated by hybridisation between members of the *D. raddei*-group and other species of *Darevskia*, particularly *D. valentini* and *D. mixta*. Some of them comprise two or more clones which result from separate hybridisations between their parent species.

Copulatory posture. As in nearly all Eremiadini, males of the great majority of Lacertini grip the side of the body of the female with their jaws during copulation, often leaving one or more bite marks. Exceptions occur in *Parvilacerta parva* and some species of *Darevskia* where males may, in the course of mating, bite the thigh as well as the side of the body; other species of *Darevskia* seem to bit the thigh alone.

Mode of reproduction. Nearly all Lacertini lay eggs, the only exceptions being most populations of *Zootoca vivipara*, which give birth to fully formed young. Even this species produces eggs in some regions, specifically north Spain and the French Pyrenees, and a more eastern area in the northwest Balkan Peninsula and adjoining Alps that includes part of north Italy, Croatia, Slovenia and southern Austria (Odierna *et al*. 2004). When laid, these *Zootoca* eggs enclose an already partly developed embryo and, as a consequence, the time to hatching is shortened. This also occurs to varying extents in *Dinarolacerta*, *Iberolacerta* and in some *Takydromus*.

Shape of hatchlings. Although newly hatched Lacertini are relatively big-headed and long legged in comparison to adults, newly hatched *Timon* and *Lacerta* have an exaggerated 'embryonic' shape with extremely large rounded heads and relatively short extremities (Arnold 1989a). This characteristic morphology does not occur in hatchlings of other large lacertids such as the big species of *Gallotia*, or *Omanosaura jayakari* in the Eremiadini.

SYSTEMATIC ACCOUNT OF LACERTINI

Family Lacertidae Oppel, 1811. Ordn. Fam. Gatt. Rept.: 33. Type genus: *Lacerta* Linnaeus, 1758.
Subfamily Lacertinae Oppel, 1811
Tribe Lacertini Oppel, 1811

Lacertinae (part) Mayer & Benyr, 1994; Ann. Naturhist. Mus. Wien 96 B: 621 & 641.
Lacertinae Mayer & Benyr, 1994; sensu Harris, Arnold & Thomas, 1998; Proc. R. Soc. Lond. B (1998) 265: 1947.

Diagnosis

A large clade of lacertid lizards indicated by mitochondrial and nuclear DNA sequences (Harris 1998; Fu 2000; Mayer & Pavličev, 2005; Fig. 1). The following distinctive morphological features are rare or absent in other lacertids but widespread in Lacertini, although they are not found in all its members: medial loop of the clavicle interrupted posteriorly in at least some individuals of most species; B-pattern tail vertebrae in at least some individuals of most species; an enlarged masseteric scale often present; parietal scale reaching edge of parietal table only posteriorly; hemipenis usually regressing in size outside breeding season and losing the distinctive microornamentation on the lobes.

Diagnoses of genera

In the following generic accounts, the information given in the diagnoses is essentially morphological but the genera are also corroborated by DNA sequences (Fig. 2). This often confirms the marked divergence of genera from each other and helps determine the species that should be included in them.

Allocation of species to genera

An alphabetical list of currently recognised species assigned to the Lacertini, and their proposed generic allocations, is given in APPENDIX V.

Algyroides Bibron & Bory de Saint-Vincent, 1833

Type species. *Algyroides moreoticus* Bibron & Bory de Saint-Vincent, 1833.
Synonymy.
—*Algyroides* Bibron & Bory de Saint-Vincent, 1833, in Bory de Saint-Vincent, Expéd. sci. Morée, 3 (1) Rept.: 67 [*Algyroides moreoticus*].
—*Notopholis* Wagler, 1830 (part); Wiegmann, 1834. Herpetol. Mexic.: 10. [*Notopholis fitzingeri*].
—*Algiroides* Duméril & Bibron, 1839. Erpétol. Gén., 5: 174 (unjustified enmendation).
—*Lacerta* Linnaeus, 1758 (part); Duméril & Bibron. 1839. Erpétol. gén., 5: 190. [*Lacerta nigropunctata*].

—*Tropidopholis* Wagler, 1843. Syst. Rept., 1: 21. Fitzinger, 1843. Syst. Rept. 21 (fide Nomenclator Zoologicus). [*Tropidopholis nigra* (nomen nudum) = *Algyroides fitzingeri*].

—*Tropidophorus* Duméril & Bibron, 1839 (partim). Wretschko in Fitzinger, 1867. Bild. Atl. Wirbelth. 3, Fig. 54. [*Tropidophorus nigra* = *Algyroides fitzingeri*].

Species included. *Algyroides fitzingeri* (Wiegmann, 1834); *Algyroides marchi* Valverde, 1958; *Algyroides moreoticus* Bibron & Bory, 1833; *Algyroides nigropunctatus* (Duméril & Bibron, 1839).

Distribution. Southern Europe: southeast Spain; Corsica and Sardinia; Adriatic coastal region from northeast Italy to southern Greece and Ionian islands (Fig. 25e).

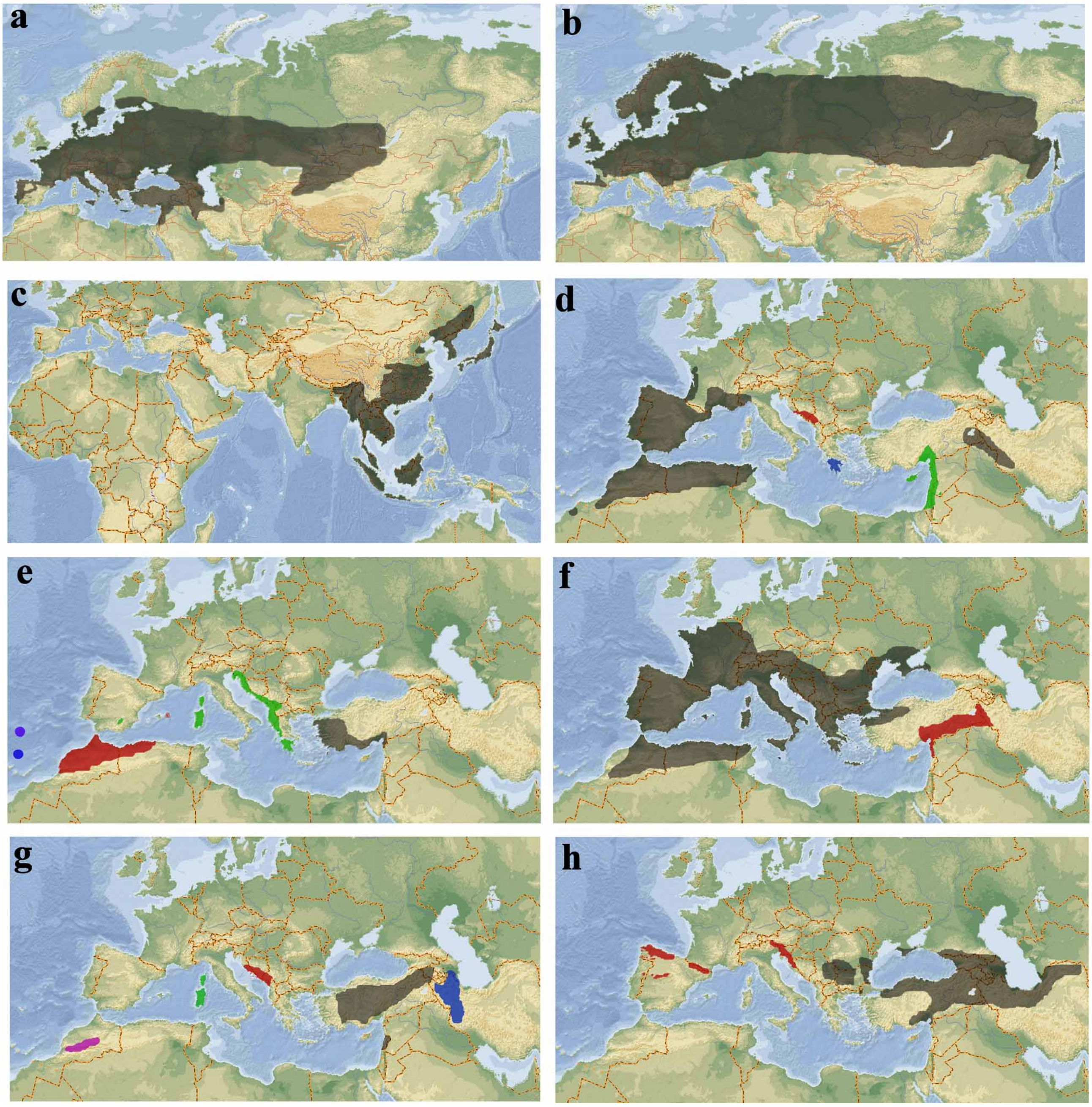

FIGURE 25.—Distribution maps of the 19 genera of Lacertini, and of *Atlantolacerta* (Eremiadini): (a) *Lacerta*; (b) *Zootoca*; (c)*Takydromus*; (d) *Timon* (black), *Dinarolacerta* gen. nov. (red), *Hellenolacerta* gen. nov. (blue), *Phoenicolacerta* gen. nov. (green); (e) *Teira* (blue), *Scelarcis* (red), *Algyroides* (green), *Anatololacerta* gen. nov. (black), (f) *Podarcis* (black), *Apathya* (red); (g) *Archaeolacerta* (green), *Dalmatolacerta* gen. nov. (red), *Parvilacerta* gen. nov. (black), *Iranolacerta* gen. nov. (blue); *Atlantolacerta* (purple); (h) *Iberolacerta* (red), *Darevskia* (black).

Diagnosis. Unique among Lacertini in its very large dorsal body scales with oblique keels and a distinctive microornamentation of raised cell borders and pustules: also exceptional in sulcal lips on hemipenial lobes being very small. Other features found only in a minority of other Lacertini include: often small body-size, usual number of presacral vertebrae 25–26 in males, and sombre dorsal colouring. Other more widely distributed features include: head and body depressed or not, supraocular osteoderms fenestrated in adults of some species, 7–9 premaxillary teeth in adults, inscriptional ribs sometimes present, tails of hatchlings not brightly coloured, hemipenial microornamentation of crown-shaped tubercles or hook-shaped spines.

Description.

Size and shape. Small to very small Lacertini, adults 45–70 mm from snout to vent; adult males often larger than females; head and body markedly depressed or not.

Skull. From seven (*A. fitzingeri*) to nine (*A. nigropunctatus*) premaxillary teeth in adults; pterygoid teeth usually present (*A. moreoticus* and *A. nigropunctatus*) or absent (*A. fitzingeri* and *A. marchi*); nasal process of premaxilla slender; postfrontal and postorbital bones separated and postorbital sometimes relatively long; maxillary-jugal suture not stepped. Supraocular osteoderms complete in adults of *A. moreoticus* and *A. nigropunctatus*, but fenestrated in *A. fitzingeri* and *A. marchi*.

Postcranial skeleton. Usual number of presacral vertebrae 25–26 in males and 26–27 in females (ranges 24–27 and 25–28 respectively); often six posterior presacral vertebrae with short ribs; medial loop of clavicle continuous or interrupted posteriorly; lateral arms of interclavicle more or less perpendicular to sagittal axis; sternal fontanelle oval or sometimes more or less heart-shaped (most commonly in *A. moreoticus* and *A. marchi*); inscriptional ribs present or absent; pattern of tail vertebrae A- or B-type.

Scaling. Rostral separated from frontonasal scale; row of supraciliary granules complete; outer edge of parietal scale reaching lateral border of parietal table posteriorly (also approaching it anteriorly in *A. marchi*). Usually two postnasal scales (occasionally one, especially in *A. moreoticus*); no contact between supranasal and anterior loreal scales above nostril; usually four (*A. fitzingeri* and *A. moreoticus*) or five (*A. nigropunctatus* and *A. marchi*) upper labial scales in front of subocular; first upper temporal scale large; masseteric scale often present but frequently small. Dorsal body scales very large (larger than tail scales) and obliquely keeled, either pointed and extending on to flanks (*A. fitzingeri* and *A. moreoticus*) or truncated and replaced on flanks by small granular scales (*A. marchi* and *A. nigropunctatus*); only 13–28 dorsal scales in a transverse row across mid-body; microornamentation of dorsal scales consisting of raised posterior edges of cells, and of pustules. Collar serrated; six longitudinal rows of ventral scales; preanal scale large, bordered by one (rarely two) semicircles of smaller scales; scales beneath toes smooth or tubercular; whorls of scales on tail alternately longer and shorter, or subequal in length.

Colouring. Basically brown or bronze-brown above. A dark band on each flank usually well developed in *A. marchi* and most *A. moreoticus*, but very faint or absent in *A. fitzingeri* and *A. nigropunctatus*. A dark vertebral line present on body in *A. marchi* and some *A. fitzingeri* and interrupted dark dorsolateral stripes in *A. moreoticus*. Males usually more strongly marked above than females and in *A. moreoticus* sexual difference is more pronounced, with males having pale dorsolateral stripes lateral to the dark ones and mottled flanks. No blue ocelli in shoulder region. Underside whitish, red, orange or yellow, with a contrasting throat in male *A. nigropunctatus* (blue, but green in *A. n. kephallithacius* outside breeding season) and *A. marchi* (white); blue spots present on lateral edges of outer ventral scales only in *A. nigropunctatus*; tails of hatchlings not brightly coloured.

Distinctive internal features. None.

Hemipenis. Lobes with plicae, apical section of each shorter than basal one, their sulcal lips very small; no armature, or folding of lobes in retracted hemipenis; microornamentation consisting of hook-shaped spines in *A. nigropunctatus* and *A. moreoticus*, and crown-shaped tubercles in *A. fitzingeri* and *A. marchi*, although tubercles rather spinous in last species.

Chromosomes. Diploid number (2n) = 38; 36 single-armed macrochromosomes and 2 microchromosomes; sex chromosomes ZW-type; nucleolar organizer in a medium-sized macrochromosome (M-type).

Reproduction. Males bite flank of females during copulation; clutches consisting of 2–6 (usually 2–4) eggs.

Ecology. Often associated with semi-shaded woodland habitats, frequently with fallen timber and abundant litter and sometimes near water. Also occurs in deforested areas and, on Corfu, *A. nigropunctatus* is abundant around human habitations.

Remarks. Mitochondrial DNA sequences and morphology indicate the western *A. marchi* and *A. fitzingeri* are a sister pair related to *A. moreoticus* with *A. nigropunctatus* basal to all of these (Harris & Arnold 1999a).

Anatololacerta gen. nov.

Type species. *Zootoca danfordi* Günther, 1876 [=*Anatololacerta danfordi* (Günther, 1876)].
Etymology. A feminine name derived from Anatolia, the region in which the genus is found, and *lacerta*, a lizard.
Synonymy.
—*Zootoca* Wagler, 1830 (part); Günther, 1876. Proc. Zool. Soc.: 818. [*Zootoca danfordi*].
—*Lacerta* Linnaeus, 1758 (part); Bedriaga, 1879. Bull. Soc. Nat. Mosc.: 30. [*Lacerta danfordi*].
—*Archaeolacerta* Mertens, 1921 (part); Mertens & Müller, 1928. Abh. Senck. Naturf. Ges., Frankfurt am Main 45: 27. [*Lacerta (Archaeolacerta) anatolica*].

Species included. *Anatololacerta anatolica* (Werner, 1900) **comb. nov.**; *Anatololacerta danfordi* (Günther, 1876) **comb. nov.**; *Anatololacerta oertzeni* (Werner, 1904) **comb. nov.**

Distribution. Western and southern Asiatic Turkey and some neighbouring Aegean islands including Samos, Ikaria and Rhodes (Fig. 25e).

Diagnosis. Lizards possessing the following features found only in a minority of other Lacertini: 7–8 posterior presacral vertebrae with short ribs, sternal fontanelle often weakly heart-shaped, pattern of tail vertebrae C-type, often five upper labial scales in front of subocular, masseteric scale frequently small or absent, preanal scale relatively small and bordered by more than one row of smaller scales, broad pale dorsolateral stripes often present, hemipenial lobes relatively long with large outer sulcal lips on lobes. Other more widely distributed features include head and body not strongly depressed, seven premaxillary teeth in adults, usual number of presacral vertebrae in males 26, inscriptional ribs frequently absent, tail brightly coloured in hatchlings; hemipenial microornamentation of crown-shaped tubercles.

Description.

Size and shape. Small Lacertini up to about 75 mm from snout to vent; adult males often larger than females; head and body not very strongly depressed.

Skull. Seven premaxillary teeth in adults; pterygoid teeth absent; nasal process of premaxilla slender; postfrontal and postorbital bones separate, subequal in length; maxillary-jugal suture not stepped. Supraocular osteoderms usually complete in adults or nearly so.

Post-cranial skeleton. Usual number of presacral vertebrae 26 in males and 27 in females (range in males 26–27); seven or eight posterior presacral vertebrae with short ribs; medial loop of clavicle continuous or interrupted posteriorly in all species; lateral arms of interclavicle more or less perpendicular to sagittal axis; sternal fontanelle oval, often faintly or sometimes clearly heart-shaped; inscriptional ribs often absent; pattern of tail vertebrae C-type.

Scaling. Rostral separated from frontonasal scale; row of supraciliary granules complete; outer edge of parietal scale reaching lateral border of parietal table only posteriorly. Two postnasal scales; no contact between the supranasal and anterior loreal scales above nostril; often five upper labial scales in front of subocular; first upper temporal scale large; masseteric scale frequently small or absent. Dorsal body scales small and smooth, about 50–65 in a transverse row at mid-body. Collar smooth-edged; six or eight longitudinal rows of ventral scales; preanal scale very small, bordered by two or more semicircles of small subequal scales and separated from the vent by other smaller scales; scales under toes tubercular; caudal scale whorls subequal in length.

Colouring. More or less striated or banded, frequently with pale fairly broad dorsolateral stripes separating vertebral and lateral bands that may be reticulate, particularly in males. Background colour light bluish-green to light brown with scattered small black spots and white flecks. No blue ocelli in shoulder region. Underside usually whitish or bluish, but throat often reddish especially in males and subadults; chin and throat often with dark spots; blue spots present on outer row of ventral scales; tail bright green-blue in hatchlings.

Distinctive internal features. Insertion of retractor lateralis anterior muscle in front of vent thick.

Hemipenis. Lobes with plicae, apical section of each longer than the basal one, their sulcal lips large; no armature, or folding of lobes in retracted hemipenis; microornamentation consisting of crown-shaped tubercles.

Chromosomes. Unknown.

Reproduction. Males bite flank of females during copulation; clutches consisting of 3–8 eggs.

Ecology. Frequently climbing on rock exposures and their anthropogenic equivalents.

Remarks. The systematics of *Anatololacerta* based on morphology has been reviewed by Eiselt and Schmidtler (1987).

Apathya Méhely, 1907

Type species. *Lacerta cappadocica* Werner, 1902 [= *Apathya cappadocica* (Werner, 1902)].
Synonymy.
—*Lacerta* Linnaeus, 1758 (part); Werner, 1902. Sitzb. Ak. Wien, 111:1086. [*Lacerta cappadocica*].
—*Apathya* Méhely, 1907. Termész. Koslon, Budapest, 85: 26. [*Apathya cappadocica*].
—*Latastia* Bedriaga, 1884 (part); Boulenger, 1907. Ann. Mag. N.H.(7) 20: 45. [*Latastia cappadocica*].

Species included. *Apathya cappadocica* (Werner, 1902); *Apathya yassujica* (Nilson, Rastegar-Pouyani, Rastegar-Pouyani & Andrén, 2003) **comb. nov**.

Distribution. Southeastern Turkey, northern Iraq, and west Iran. (Fig. 25f).

Diagnosis. Unique among Lacertini in having clear single keels on scales beneath toes, a transparent window in the lower eyelid consisting of several black-edged scales, and variable scaling on the side of the snout that may involve up to three postnasal and three loreal scales and sometimes an additional scale between the rostral and the nostril. Also possessing the following features found only in a minority of other Lacertini: 9–10 premaxillary teeth, often 7–8 posterior presacral vertebrae with short ribs, outer edge of parietal scale not reaching lateral border of parietal table, often five upper labial scales anterior to subocular, no masseteric scale, in some populations eight longitudinal rows of ventral scales; preanal scale often very small, bordered by two or more semicircles of smaller scales; often broad light dorsolateral stripes on dorsum; blue ocelli often present on flanks; bright colouring on underside absent, at least posteriorly, no blue spots on outer ventral scales, kidney expanded anteriorly and more than half its length in front of sacrum, hemipenis with traces of an armature and its retracted lobes coarsely folded. More widely distributed features among Lacertini include head and body markedly depressed and supraocular osteoderms fenestrated in adults, usual number of presacral vertebrae in males 26, inscriptional ribs usually absent, tail brightly coloured in hatchlings, hemipenial microornamentationn of hook-shaped spines.

Description.

Size and shape. Small Lacertini up to 83 mm from snout to vent, adult males often larger than females; head and body usually quite depressed.

Skull. Nine or ten premaxillary teeth; pterygoid teeth absent; nasal process of premaxilla slender; postfrontal and postorbital bones separate, subequal in length; maxillary-jugal suture not stepped. Supraocular osteoderms incomplete with a fenestra in adults.

Post-cranial skeleton. Usual number of presacral vertebrae 26 in males and 27 in females (range in males 25–26); often 7–8 posterior presacral vertebrae with short ribs; medial loop of clavicle continuous or interrupted posteriorly; lateral arms of interclavicle more or less perpendicular to sagittal axis; sternal fontanelle oval; inscriptional ribs often absent; pattern of tail vertebrae A-type.

Scaling. Rostral separated from frontonasal scale; row of supracilliary granules complete; outer edge of parietal scale not reaching lateral border of parietal table. Two or three postnasal scales and one to three anterior loreals; sometimes an additional scale between the rostral and the nostril; no contact between the supranasal and anterior loreal scales above nostril; usually five upper labial scales in front of subocular; lower eyelid with transparent window made up of 5 (*A. yassujica*) or 6 to 8 (*A. cappadocica*) large black-edged scales; first upper temporal scale long; masseteric scale absent and temporal area covered by very small granular scales. Dorsal body scales small and smooth, about 50–75 in a transverse row at mid-body. Collar smooth; six or eight longitudinal rows of rectangular ventral scales; preanal scale often very small, bordered by two or more semicircles of small subequal scales; scales under toes with clear single keels; whorls of scales on tail subequal in length.

Colouring. Adult dorsal patterns in *A. cappadocica* more or less striated, banded or reticulated, often with fairly broad, light coloured dorsolateral stripes, the precise pattern varying geographically; *A. yassujica* is often plain above. Background colour bluish-green to greyish. Blue ocelli often present in shoulder region and over rest of flanks. Whole underside without strong pigmentation in *A. cappadocica*, being whitish sometimes with a blue-green tinge, but throat and adjacent thoracic region yellowish-orange in *A. yassujica*; throat and chin of both species often with dark spots; no blue spots on outer row of ventral scales. Juveniles similar to adults but pattern more contrasting and tail blue.

Distinctive internal features. Anterior kidney expanded and over half of organ in front of sacrum; insertion of retractor lateralis anterior muscle in front of vent thick.

Hemipenis. Lobes with plicae, apical section of each shorter than basal one, their sulcal lips small; a poorly developed armature present, and lobes coarsely folded in the retracted hemipenis; microornamentation consisting of hook-shaped spines.

Chromosomes. Diploid number (2n) = 38; 36 single-armed macrochromosomes and 2 microchromosomes; sex chromosomes of ZW-type; position of nucleolar organizer unknown.

Reproduction. Males bite flank of females during copulation; clutches consisting of 3–7 eggs.

Ecology. Often found climbing on rock exposures.

Remarks. Systematics of *Apathya* based on morphology is reviewed by Eiselt (1979); see also Nilson *et al.* (2003).

Archaeolacerta Mertens, 1921

Type species. *Lacerta reticulata* Bedriaga, 1881. [=*Archaeolacerta bedriagae* (Camerano, 1885)].
Synonymy.
—*Podarcis* Wagler, 1830 (part); Bonaparte, 1839, Mem. r. Acad. sc. Tor. (ser. 2), 2: 385. [*Podarcis oxycephala* Bonaparte, not Duméril & Bibron, 1839 = *Archaeolacerta bedriagae*].
—*Lacerta* Linnaeus, 1758 (part); Bedriaga,1881, Bull. Soc. nat. Mosc. 3: 82. [*Lacerta oxycephala* var. *reticulata*].
—*Archaeolacerta* Mertens, 1921 (part). Zool. Anz. 53: 238. [*Lacerta (Archaeolacerta) reticulata*].

Species included. *Archaeolacerta bedriagae* (Camerano, 1885).

Distribution. Corsica and Sardinia (Fig. 25g).

Diagnosis. Lizards possessing the following features found only in a minority of other Lacertini: medial loop of clavicle always interrupted behind, outer edge of parietal scale extending to lateral border of parietal table posteriorly and sometimes anteriorly, one postnasal scale, usually five upper labial scales in front of subocular, dorsal colouring without longitudinal stripes or series of spots and more or less reticulate even in young. Other more widely distributed features among Lacertini include: head and body often strongly depressed and supraocular osteoderms fenestrated in adults, frequently nine premaxillary teeth, usual number of presacral vertebrae in males 26, inscriptional ribs often present, tail brightly coloured in hatchlings, hemipenial microornamentation of hook-shaped spines.

Description.

Size and shape. Small Lacertini up to about 80 mm from snout to vent; adult males often larger than females; head and body markedly depressed.

Skull. Frequently nine premaxillary teeth in adults; pterygoid teeth absent; nasal process of premaxilla slender; postfrontal and postorbital bones separated, subequal in length; maxillary-jugal suture not stepped. Supraocular lamellae usually incomplete with a fenestra in adults.

Post-cranial skeleton. Usual number of presacral vertebrae 26 in males and 27 in females (ranges 25–27 and 26–27 respectively); usually six or seven posterior presacral vertebrae with short ribs; medial loop of clavicle always interrupted posteriorly; lateral arms of interclavicle more or less perpendicular to sagittal axis; sternal fontanelle oval; inscriptional ribs often present; pattern of tail vertebrae A or more commonly B.

Scaling. Rostral usually separated from frontonasal scale in Corsican populations, but often in contact in Sardinian ones; row of supraciliary granules complete; outer edge of parietal scale reaches lateral border of the parietal table posteriorly and sometimes anteriorly as well. One postnasal scale; no contact between supranasal and anterior loreal scales above nostril; four or five upper labial scales in front of subocular; first upper temporal scale sometimes large; masseteric scale usually present but sometimes small and the rest of the temporal area covered by small granular scales. Dorsal scales small, flattened and unkeeled, about 57–88 in a transverse row at mid-body. Collar smooth; six longitudinal rows of rectangular ventral scales; preanal scale relatively large, bordered by single semicircle of smaller subequal scales; a second row of femoral pores exceptionally present; scales under toes smooth or tubercular; whorls of scales on tail alternately longer and shorter.

Colouring. Usually with a dark reticulation above, even in juveniles; background colour may be shades of yellow, grey, brown or green. No blue ocelli in shoulder region. Underside whitish, greyish-yellowish, greenish, reddish or red, the throat not differentiated; dark spotting often present, especially on throat; blue spots occur on outer row of ventral scales; tail often bright blue-green in juveniles.

Distinctive internal features. Insertion of retractor lateralis anterior muscle in front of vent lateral, away from mid-line.

Hemipenis. Lobes with plicae, apical section of each shorter than basal one, their sulcal lips small; no armature, and lobes not folded in retracted hemipenis; microornamentation consisting of hook-like spines.

Chromosomes. Diploid number (2n) = 38; 36 single-armed macrochromosomes and 2 microchromosomes; sex chromosomes ZW-type: nucleolar organiser in a large macrochromosome (L-type).

Ecology. Climbing lizards, often found on rocks and boulders in mountain areas although *Archaeolacerta* occurs at sea level in some places.

Reproduction. Males bite flank of females during copulation; cluches consisting of 3–6 elongate eggs.

Remarks. Archaeolacerta bedriagae is not homogeneous and animals in most of Corsica are morphologically different from those in the extreme south of the island and in Sardinia. There is also considerable variation in mitochondrial DNA and more than one species may be present.

Dalmatolacerta gen. nov.

Type species. *Lacerta oxycephala* Duméril & Bibron, 1839 [=*Dalmatolacerta oxycephala* (Duméril & Bibron, 1839)].
Etymology. A feminine name derived from Dalmatia, the region bordering the east coast of the Adriatic Sea now mainly

in Croatia where the genus occurs, and *lacerta*, a lizard.

Synonymy.

—*Lacerta* Linnaeus, 1758 (part); Duméril & Bibron, 1839. Erp. Gén. 5: 235. [*Lacerta oxycephala*].

—*Archaeolacerta* Mertens, 1921 (part); Mertens & Müller, 1928. Abh. Senck. Naturf. Ges., Frankfurt am Main 41: 28. [*Lacerta* (*Archaeolacerta*) *oxycephala*].

Species included. *Dalmatolacerta oxycephala* (Duméril & Bibron, 1839) **comb. nov.**

Distribution. Dalmatian region: southern Croatia including many offshore islands, southern Bosnia-Herzegovina and Montenegro (Fig. 25g).

Diagnosis. Unique among Lacertini in having a particularly sharply pointed snout, the two medial longitudinal scale rows under the tail much more laterally expanded than neighbouring ones, and a pattern of alternating blue-green and blackish bands on the tail (except in melanic animals). Also possessing the following features found only in a minority of other Lacertini: head and body very strongly depressed, usual number of presacral vertebrae 25 in males, medial loop of clavicle always interrupted posteriorly, five upper labial scales in front of subocular, dorsal colouring without longitudinal stripes or series of spots and more or less reticulate even in young, no obvious blue spots on outer ventral scales. Other more widely distributed features include: supraocular osteoderms fenestrated in mature animals, seven premaxillary teeth in adults, inscriptional ribs usually absent, brightly coloured tail in hatchlings, hemipenial microornamentation of crown-shaped tubercles.

Description.

Size and shape. Small Lacertini, adults up to about 65 mm from snout to vent; little size difference between sexes; snout especially pointed, head and body very strongly depressed, toes relatively short and numbers 3–5 on hind feet particularly strongly kinked in vertical plane.

Skull. Seven premaxillary teeth in adults; pterygoid teeth absent; nasal process of premaxilla slender; postfrontal and postorbital bones separate and postorbital relatively short; maxillary-jugal suture not stepped. Supraocular osteoderms incomplete with a large fenestra in mature animals.

Postcranial skeleton. Usual number of presacral vertebrae 25 in males (occasionally 26), and 26 in females; usually six (sometimes seven or even five) posterior presacral vertebrae with short ribs; medial loop of clavicle always interrupted posteriorly; lateral arms of interclavicle more or less perpendicular to sagittal axis; sternal fontanelle oval; inscriptional ribs usually absent; pattern of tail vertebrae A- or B-type.

Scaling. Rostral separated from frontonasal scale; row of supraciliary granules complete; outer edge of parietal scale reaches lateral border of parietal table only posteriorly. Two postnasal scales; no contact between the supranasal and anterior loreal scales above nostril; five upper labial scales in front of subocular; first upper temporal scale usually large; masseteric scale usually present but often small and occasionally absent. Dorsal scales small, flat and rounded, about 59–76 across mid-body. Collar smooth; six longitudinal rows of ventral scales; preanal scale short and wide, bordered by a semicircle of smaller scales, the two most anterior of these often enlarged, a second incomplete row occasionally present; toes strongly compressed and numbers 3–5 on hind foot strongly kinked in the vertical plane, scales under toes tubercular; whorls of tail scales alternately longer and shorter; the two medial longitudinal scale rows under the tail much wider than those adjoining them.

Colouring. Body of juveniles and adults often buffish grey above (greenish or bluish in some lights) with a reticulated pattern; unregenerated tail usually with numerous alternate turquoise green and blackish transverse bands. Without blue occelli in the shoulder region. Ventral coloration blue, often very vivid in breeding males, the throat undifferentiated; without dark spotting or distinguishable blue spots on lateral edges of the outermost belly. In highland areas and on some islands some or all animals may be very dark; in such cases, the reticulation of the upper parts is still usually apparent, but some individuals are uniformly black. Young animals like adults but tail often more vividly coloured.

Distinctive internal features. None.

Hemipenis. Lobes with plicae, apical section of each shorter than basal one, their sulcal lips small; no armature present and lobes not folded in the retracted hemipenis; hemipenial microornamentation consisting of crown-shaped tubercles.

Chromosomes. Diploid number (2n) = 38; 36 single-armed macrochromosomes and 2 microchromosomes; sex chromosomes ZW-type; position of nucleolar organizer unknown.

Reproduction. Males bite flank of females during copulation; clutches consisting of 2–4 (usually 3–4) elongate eggs.

Ecology. Nearly always associated with rock surfaces or anthropogenic equivalents (walls, parapits, etc), where it takes refuge in often narrow crevices.

Darevskia Arribas, 1997

Type species. *Lacerta saxicola* Eversmann, 1834 [=*Darevskia saxicola* (Eversmann, 1834)].

Synonymy.

—*Lacerta* Linnaeus, 1758 (part). Eversmann, 1834. Lacertae Imperii Rossici. Nouv. Mém. Soc. Nat. Moscou, 3: 349. [*Lacerta saxicola*].

—*Podarcis* Wagler, 1830 (part); Camerano, 1877. Atti. Acad. Torino. 13: 90. [*Podarcis defilippi*].

—*Zootoca* Wagler, 1830 (part); Eichwald, 1841. Fauna Casp.-Caucas.: 73. [*Zootoca chalybdea* = *Darevskia praticola*?].

—*Archaeolacerta* Mertens, 1921 (part); Mertens & Müller, 1928. Abh. Senck. Naturf. Ges., Frankfurt am Main 41: 29. [*Lacerta* (*Archaeolacerta*) *saxicola*].

—*Darevskia* Arribas, 1997. Morf., Filog., Biogeo. Lagart. Alta Mont. Pirineos. Pub. Univ. Aut. Barcelona (Tesis doct.): 4. [*Darevskia saxicola*].

—*Caucasilacerta* (nomen nudum) Harris, Arnold & Thomas, 1998. Proc. R. Soc. Lond. B 265: 1947. [*Lacerta* (*Caucasilacerta*) *saxicola*].

Species included. *D. alpina* (Darevsky, 1967); *D. armeniaca* (Méhely, 1909); *D. bendimahiensis* (Schmidtler, Eiselt & Darevsky, 1994); *D. brauneri* (Méhely, 1909); *D. caucasica* (Méhely, 1909); *D. chlorogaster* (Boulenger, 1908); *D. clarkorum* (Darevsky & Vedmerja, 1977); *D. daghestanica* (Darevsky, 1967); *D. dahli* (Darevsky, 1957); *D. defilippi* (Camerano, 1877); *D. derjugini* (Nikolsky, 1898); *D. dryada* (Darevsky & Tuniyev, 1997); *D. lindholmi* (Lantz & Cyren, 1936); *D. mixta* (Méhely, 1909); *D.* (*raddei*) *nairensis* (Darevsky, 1967); *D. parvula* (Lantz & Cyrén, 1913); *D. portschinskii* (Kessler, 1878); *D. praticola* (Eversmann, 1834); *D. raddei* (Boettger, 1892); *D. rostombekowi* (Darevsky, 1957); *D. rudis* (Bedriaga, 1886); *D. sapphirina* (Schmidtler, Eiselt & Darevsky, 1994); *D. saxicola* (Eversmann, 1834); *D. steineri* (Eiselt, 1995); *D. unisexualis* (Darevsky, 1966); *D. uzzelli* (Darevsky & Danielyan, 1977); *D. valentini* (Boettger, 1892).

Distribution. Caucasus region, Crimea and north and east Asiatic Turkey, eastwards to Alborz mountains of Iran and to Kopet Dagh on Iran-Turkmenistan border; one species (*D. praticola*) reaching the eastern Balkan peninsula (Fig. 25h).

Diagnosis. Lizards possessing the two following features found only in a minority of other Lacertini: 27–28 presacral vertebrae in males, one postnasal scale. Other more widely distributed features include: supraocular osteoderms fenestrated or intact in adults, usually seven premaxillary teeth, inscriptional ribs present in some species, tail often brightly coloured in hatchlings, hemipenial microornamentation of crown-shaped tubercles. A few species of *Darevskia* are parthenogenetic, and males of some bite the thigh of the female during copulation.

Description.

Size and shape. Small Lacertini, adults up to about 50–85 mm from snout to vent; adult males usually larger than females, but not in *D. alpina*, *D. caucasica*, *D. derjugini*, *D. mixta*, *D. praticola* and *D. valentini*; head and body markedly depressed or not.

Skull. Usually seven premaxillary teeth in adults (often nine in *D. chlorogaster*); pterygoid teeth absent;

nasal process of premaxilla slender; postfrontal and postorbital bones separate, usually subequal but postorbital sometimes shorter; anteromedial process of postorbital absent in *D. raddei*, *D. mixta*, and the parthenogenetic species of *Darevskia* which are derived from them; maxillary-jugal suture usually not stepped (sometimes so in *D. brauneri darevskii*). Supraocular lamellae incomplete with a fenestra in adults of many species, variable in *D. derjugini*, and more or less complete in some forms with relatively undepressed heads, including *D. chlorogaster, D. clarkorum*, *D. dryada* and *D. praticola.*

Post-cranial skeleton. Usual number of presacral vertebrae 27 in males and 28 in females, but respectively 28 and 29 in the *D. raddei* group (total range about 26–29 in males and 27–30 in females); often six posterior presacral vertebrae with short ribs (five occur quite frequently in some species, and seven in others such as *D. dahli*, *D. portschinskii* and *D. rostombekowi*); medial loop of clavicle continuous or interrupted posteriorly; lateral arms of interclavicle more or less perpendicular to sagittal axis; sternal fontanelle oval or occasionally slightly heart-shaped; inscriptional ribs present in some species; pattern of tail vertebrae A- and B-types.

Scaling. Rostral usually separated from frontonasal scale but sometimes in contact (for example in *D. alpina* and *D. unisexualis*); row of supraciliary granules usually complete (some exceptions, for instance *D. caucasica vedenica*); outer edge of parietal scale reaching lateral border of parietal table posteriorly. One postnasal scale; typically no contact between supranasal and anterior loreal scales above nostril (present in *D. dahli* and *D. derjugini*); usually four upper labial scales in front of subocular; first upper temporal scale large in most species; masseteric scale present. Dorsal body scales small and often smooth (but keeled in some forms including *D. chlorogaster* and *D. praticola*), about 35–70 in a transverse row at mid-body. Collar smooth or serrated; six longitudinal rows of ventral scales; preanal scale moderate or large, bordered by a single semicircle of smaller scales, the most anterior one or two of which sometimes enlarged; scales under toes smooth or tubercular; whorls of tail scales alternately longer and shorter.

Colouring. Little sexual dimorphism in colouring; basic dorsal pattern consisting of longitudinal streaks or bands, and flanks may be reticulated. Ground colour brown, grey or green. Blue occelli often present in shoulder region. Underside often brightly coloured, and may be yellow, orange or red (as in *D. parvula*, *D. portschinskii*, *D. valentini* and *D. defilippi*) or greenish-yellow or green (as in *D. raddei*, *D. rudis*, *D. caucasica*, *D. alpina*, *D. chlorogaster*, *D. derjugini* and *D. praticola*); bright ventral colour usually reduced or absent in parthenogenetic populations; throat colour may be differentiated from belly; dark ventral spotting usually absent; blue spots generally present on outer row of ventral scales; juveniles often with brightly coloured, greenish or bluish tails.

Distinctive internal features. Insertion of retractor lateralis anterior muscle in front of vent sometimes lateral, away from mid-line.

Hemipenis. Lobes with plicae, apical section of each shorter than basal one, their sulcal lips small; no armature, or folding of lobes in retracted hemipenis; hemipenial microornamentation consisting of crown-shaped tubercles.

Chromosomes. Diploid number (2n) = 38; usually 36 single-armed macrochromosomes and 2 microchromosomes (in the parthenogenetic *D. rostombekowi*, one macrochromosome double-armed, probably being submetacentric as a result of pericentric inversion); sex chromosomes ZW-type; nucleolar organiser in large macrochromosome (L-type).

Reproduction. Some species of *Darevskia* are parthenogenetic and result from hybridisation between sexual species. These are *D. armeniaca*, *D. bendimahiensis*, *D. dahli*, *D. rostombekowi*, *D. sapphirina*, *D. unisexualis* and *D. uzzelli*, a number of which are made up of more than one clone. Males of the majority of species bite only flank of females during copulation, others bite both the flank and the thigh (*D. alpina*, *D. brauneri*, *D. caucasica*, *D. daghestanica*, *D. lindholmi*, *D. praticola*, *D. raddei* and *D. saxicola*), or just the thigh alone (*D. chlorogaster* and *D. nairensis*). Clutches usually consisting of about 2–8 eggs.

Ecology. Many species live mainly on rock exposures and use crevices as refuges, but *D. chlorogaster* is often associated with fallen and standing timber (Anderson, 1999), as is *D. brauneri darevskii*, while *D. derjugini*, *D. clarkorum*, *D. dryada* and *D. praticola* are largely ground-dwelling, often in and around herbaceous vegetation; some species are exclusively montane.

Remarks. It has been suggested that *Darevskia clarkorum* and *D. dryada* might be conspecific (Schmidtler *et al*. 2002). Some recognised taxa, such as *D. praticola* may really comprise more than one valid species and, in parts of Turkey, species boundaries are probably not fully resolved in some other forms. Systematics and biology of many *Darevskia* were extensively reviewed by Darevsky (1967); a partial phylogeny based on DNA sequences is given by Fu and Murphy (1997) and Murphy *et al*. (1996, 2000).

Lacerta mostoufi Baloutch, 1977 was described from material allegedly coming from arid East Iran, some 500 km away from the nearest localities for other Lacertini. It has been regarded as being based on *Darevskia chlorogaster* (Eiselt 1995; I. S. Darevsky, pers. comm., quoted by Arribas 1999). The type in the Teheran museum is apparently lost, but a paratype in the Paris Museum is a *Darevskia praticola praticola* (In den Bosch, 1999). It is highly unlikely that either of these mesic species would have been present at the supposed type locality of *L. mostoufi* (Anderson 1999).

Dinarolacerta gen. nov.

Type species. *Lacerta mosorensis* Kolombatovic, 1886 [=*Dinarolacerta mosorensis* (Kolombatovic, 1886)].

Etymology. A feminine name, derived from that of the Dinaric Mountains on the east coast of the Adriatic Sea where the genus occurs, and *lacerta*, a lizard.

Synonymy.

—*Lacerta* Linnaeus, 1758 (part); Kolombatovic, 1886. Imen-Kralj. Dalmac. 2: 26. [*Lacerta mosorensis*].

—*Archaeolacerta* Mertens, 1921 (part); Mertens & Müller, 1928. Abh. Senck. Naturf. Ges., Frankfurt am Main 41: 28. [*Lacerta* (*Archaeolacerta*) *mosorensis*].

Species included. *Dinarolacerta mosorensis* (Kolombatovic, 1886) **comb. nov.**

Distribution. Southern Croatia (north to Split), southern Bosnia–Herzegovina, Montenegro and extreme north Albania (Fig. 25d).

Diagnosis. Lizards possessing the following features found only in a minority of other Lacertini: head and body very strongly depressed, usual number of presacral vertebrae 25–26 in males, median loop of clavicle often interrupted posteriorly, rostral scale usually contacting frontonasal scale, sometimes five upper labial scales in front of subocular, embryos partly developed at egg-laying. Other more widely distributed features include: supraocular osteoderms fenestrated in adults, nine premaxillary teeth in adults, inscriptional ribs usually absent, tail often brightly coloured in hatchlings, hemipenial microornamentation of crown-shaped tubercles.

Description.

Size and shape. Small Lacertini up to about 70 mm from snout to vent, with little size difference between the sexes; head and body strongly depressed.

Skull. Nine premaxillary teeth in adults; pterygoid teeth absent; nasal process of premaxilla slender; postfrontal and postorbital bones separate and subequal in length; maxillary-jugal suture not stepped. Supraocular osteoderms incomplete with a fenestra in adults.

Post-cranial skeleton. Usual numbers of presacral vertebrae 25–26 in males and 26–27 in females (ranges 25–27 and 27–28 respectively); usually six posterior presacral vertebrae with short ribs; medial loop of clavicle often interrupted posteriorly; lateral arms of interclavicle more or less perpendicular to sagittal axis; sternal fontanelle oval, occasionally rather heart-shaped; inscriptional ribs usually absent; pattern of tail vertebrae A- or B-type.

Scaling. Rostral usually in contact with frontonasal scale; row of supraciliary granules complete, outer edge of parietal scale reaches lateral border of parietal table posteriorly. Usually two postnasal scales (occasionally one); no contact between supranasal and anterior loreal scales above nostril; four or five supralabial scales in front of the subocular; first upper temporal scale large in most cases; masseteric scale usually large. Dorsal body scales flattened and unkeeled, about 36–42 in a transverse row at mid-body. Collar smooth; six longitudinal rows of rectangular ventral scales; preanal scale large and bordered by a semicircle of smaller scales; scales under toes smooth or tubercular; scale whorls on tail alternately longer and shorter.

Colouring. Flanks often darker than back, which may be generally mottled or spotted with dark pigment or with a vertebral band of spots. In some animals the sides are also spotted but are more or less uniform in others. No blue ocelli in shoulder region. Underside often yellow or orange, the throat not differentiated, dark spots often occur; blue spots present on outer row of ventral scales. Juveniles similar to adults but often with a blue or greenish tail.

Distinctive internal features. Insertion of retractor lateralis anterior muscle in front of vent lateral, away from mid-line.

Hemipenis. Lobes with plicae, apical section of each shorter than basal one, their sulcal lips small; no armature or folding of lobes in retracted hemipenis; microornamentation consisting of crown-shaped tubercles.

Chromosomes. Diploid number (2n) = 38; 36 single-armed macrochromosomes and 2 microchromosomes; sex chromosomes ZW-type; nucleolar organiser in medium-small macrochromosome (MS-type).

Reproduction. Males bite the flank of female during copulation; clutches often consisting of 4 eggs but sometimes up to 8. Embryos well developed in newly laid eggs, which often hatch in 17–20 days compared with the 40 or more days usual in small Lacertini.

Ecology. Rock climbing in mountainous areas with high rainfall and often found in more shady situations than *Dalmatolacerta*.

Remarks. Dinarolacerta mosorensis as presently understood is heterogeneous, and may consist of more than one species. In animals from Durmitor in Montenegro the usual number of presacral vertebrae is 25 in males and 26 in females (Arribas 1998), while those from further north usually have 26 in males and 27 in females (Arnold 1973). There is also substantial divergence in mitochondrial DNA sequence (see Carranza *et al*. 2004, and Fig. 2).

***Hellenolacerta* gen. nov.**

Type species. *Lacerta graeca* Bedriaga, 1886. [= *Hellenolacerta graeca* (Bedriaga, 1886)].
Etymology: A feminine name derived from the Latin adjective hellenicus, meaning ‘from Greece’, and *lacerta*, a lizard.
Synonymy.
—*Lacerta* Linnaeus, 1758 (part); Bedriaga, 1886. Abh. Senckenberg naturf. Ges. 14: 290 [274]. [*Lacerta graeca*].
—*Archaeolacerta* Mertens, 1921 (part); Mertens & Müller, 1928. Abh. Senck. Naturf. Ges., Frankfurt am Main 41: 28. [*Lacerta* (*Archaeolacerta*) *graeca*].

Species included. *Hellenolacerta graeca* (Bedriaga, 1886) **comb. nov.**

Distribution. Peloponnese region of southern Greece (Fig. 25d).

Diagnosis. Lizards possessing the following features found only in a minority of other Lacertini: often 27 presacral vertebrae in males, median loop of clavicle always interrupted posteriorly, medial longitudinal scale rows under the tail often a little more laterally expanded than adjoining ones, frequently some sexual dimorphism in dorsal colouring; hemipenis often with traces of an armature. Other more widely distributed features include: head and body markedly depressed but supraocular osteoderms usually complete in adults, nine premaxillary teeth in adults, inscriptional ribs usually absent, tail often brightly coloured in juveniles, hemipenial microornamentation of hook-shaped spines.

Description.

Size and shape. Small Lacertini up to about 80 mm from snout to vent; adult males often larger than females; head and body relatively long and distinctly depressed.

Skull. Nine premaxillary teeth in adults; pterygoid teeth absent; nasal process of premaxilla slender; postfrontal and postorbital bones separate and subequal in length; maxillary-jugal suture not stepped. Supraocular osteoderms usually complete in adults or nearly so.

Post-cranial skeleton. Usual number of presacral vertebrae 27 in males and probably 28 in females (ranges 26–27 and 27–28 respectively); six or seven posterior presacral vertebrae with short ribs; medial loop of clavicle interrupted posteriorly; lateral arms of interclavicle more or less perpendicular to sagittal axis; sternal fontanelle oval; inscriptional ribs usually absent; pattern of tail vertebrae A- or B-type.

Scaling. Rostral separated from frontonasal scale; row of supraciliary granules complete; outer edge of parietal scale reaches lateral border of parietal table posteriorly. Two postnasal scales; no contact between the supranasal and anterior loreal scales above nostril; five upper labial scales in front of the subocular; first upper temporal scale usually larger than others; masseteric scale very small or absent, the temporal region otherwise covered by very small granular scales. Dorsal body scales small and smooth, about 45–70 in transverse row at mid-body. Collar smooth; six longitudinal rows of rectangular ventral scales; preanal scale quite large, bordered by a semicircle of smaller scales and separated from the vent by a row of granules; scales under toes smooth or tubercular; scale whorls on tail usually subequal in length; two medial longitudinal rows of subcaudal scales often a little more expanded laterally than neighbouring ones.

Colouring. Males with dark flanks, usually with light spots, and irregular dark blotches on back; females usually more lightly marked. Background colour often glossy grey-brown but sometimes yellowish. Blue ocelli often present in shoulder region and spots on the flanks of males may also be blue. Underside often yellow to deep orange, the throat not differentiated, and dark spots usually occur, especially on throat; blue spots present on outer row of ventral scales. Juveniles similar to adults but often with bright blue tails.

Distinctive internal features. None.

Hemipenis. Lobes with plicae, apical section of each shorter than basal one, their sulcal lips small; traces of an armature often present but no folding of lobes in retracted hemipenis; microornamentation consisting of hook-like spines.

Chromosomes. Diploid number (2n) = 38; 36 single-armed macrochromosomes and 2 microchromosomes; sex chromosomes ZW-type; nucleolar organizer in medium-sized macrochromosome (M-type).

Reproduction. Males bite flank of females during copulation; clutches consisting of 1–6 (usually 3–4) eggs.

Ecology. Often climbs on rock exposures and other stony surfaces.

Iberolacerta Arribas, 1997

Type species. *Lacerta muralis, var. monticola* Boulenger, 1905. [*Lacerta monticola* Boulenger, 1905] [=*Iberolacerta monticola* (Boulenger, 1905)].

Synonymy.

—*Lacerta* Linnaeus, 1758 (part); Boulenger, 1905. Tr. Zool. Soc. 17: 365. [*Lacerta muralis, var. monticola*].

—*Archaeolacerta* Mertens, 1921 (part); Mertens & Müller, 1928. Abh. Senck. Naturf. Ges., Frankfurt am Main 41: 28. [*Lacerta* (*Archaeolacerta*) *horvathi*].

—*Iberolacerta* Arribas, 1997. Morf., Filog., Biogeo. Lagart. Alta Mont. Pirineos. Pub. Univ. Aut. Barcelona (Tesis doct.): 4. [*Iberolacerta monticola*].

—*Iberolacerta* (*Pyrenesaura*) Arribas, 1999. Russ. J. Herpetol. 6: 15. [*Iberolacerta* (*Pyrenesaura*) *bonnali*].

Species included. *Iberolacerta aranica* (Arribas, 1993); *Iberolacerta aurelioi* (Arribas, 1994); *Iberolacerta bonnali* (Lantz, 1927); *Iberolacerta cyreni* (Müller & Hellmich, 1937); *Iberolacerta galani* Arribas, Carranza & Odierna, 2006; *Iberolacerta horvathi* (Méhely, 1904); *Iberolacerta martinezricai* (Arribas, 1996); *Iberolacerta monticola* (Boulenger, 1905).

Distribution. Disjunct in mainly mountain areas of western Europe: central Portugal, central and northern Spain and French Pyrenees; northwest Croatia, Slovenia and adjoining northeast Italy and Austria (Fig. 25h). Presence in Germany is controversial and might be the result of human introduction. *I. horvathi* was reported from localities in extreme southern Germany but has not been found subsequently.

Diagnosis. Lizards possessing the following features found only in a minority of other Lacertini: rostral and frontonasal scales frequently in contact, one postnasal scale, supranasal and anterior loreal scales often contacting each other, no microchromosomes, number of macrochromosomes 36 or fewer, reduced in some cases to 26 or 24 in males and 25 or 23 in females, embryos often partly developed at egg-laying. Other more widely distributed features include: head and body depressed and supraocular osteoderms often fenestrated in adults, seven to nine premaxillary teeth, usual number of presacral vertebrae 26 in males; inscriptional ribs present or absent, tail brightly coloured in hatchlings, hemipenial microornamentation consisting of crown-shaped tubercles or hook-shaped spines.

Description.

Size and shape. Small Lacertini, up to about 85 mm from snout to vent; adult females larger than males. Head and body moderately depressed.

Skull. Seven to nine premaxillary teeth; pterygoid teeth absent; nasal process of premaxilla usually slender but broad and more or less arrow shaped in *I. cyreni* and *I. galani*; postfrontal and postorbital bones separate and subequal in length in most species (postfrontal shorter in *I. horvathi* and to a lesser degree in *I. aurelioi*), anterolateral process of postfrontal absent in *I. aurelioi* and anteromedial process of postorbital absent in *I. aurelioi* and *I. bonnali;* maxillary-jugal suture not stepped. Supraocular osteoderms usually incomplete with a fenestra in adults, but complete in some *I. monticola*.

Post-cranial skeleton. Usual number of presacral vertebrae 26 in males, 27 in females of *I. aranica*, *I. aurelioi*, *I. bonnali* and *I. horvathi*, and frequently 28 in females of *I. monticola*, *I. galani*, *I. martinezricai* and *I. cyreni* (total ranges for genus 25–26 in males and 26–29 in females); usually six (occasionally five or seven) posterior presacral vertebrae with short ribs; small ossified ribs often present on third presacral vertebra of *I. aranica*, *I. aurelioi* and *I. bonnali*; medial loop of clavicle either continuous or interrupted in all species (most usually continuous in *I. aurelioi* and I. *cyreni*); lateral arms of interclavicle more or less perpendicular to sagittal axis; sternal fontanelle oval (occasionally very small or even absent); inscriptional ribs present or absent; pattern of tail vertebrae A- or less commonly B-type.

Scaling. Rostral often in contact with frontonasal scale (frequently separated in *I. martinezricai*); row of supraciliary granules complete or incomplete (Pyrenean species); outer edge of parietal scale reaching lateral border of parietal table posteriorly; one postnasal scale; contact between supranasal and anterior loreal scales above nostril frequent (almost universal—92%—in the Pyrenean species, very frequent—67%—in *I. horvathi* and also found—25%—in some *I. galani*); usually four upper labial scales in front of subocular; first upper temporal scale often large; masseteric scale present (although sometimes very reduced, as in *I. aurelioi*). Dorsal body scales small and smooth or feebly keeled, about 35–64 in a transverse row at mid-body. Collar more or less smooth; six longitudinal rows of ventral scales; preanal scale often large and broad, bordered by a semicircle of smaller scales of which most anterior pair sometimes enlarged; scales under toes smooth or tubercular; whorls of tail scales alternately longer and shorter.

Colouring. Dorsal pattern of stripes and bands, often including dark flanks and a dark vertebral stripe or two series of spots. Dorsal ground colour often brown or grey but sometimes green or even bluish. Sexual dimorphism in colouring present in some forms with males often having reticulated flanks and green dorsal colouring (*I. cyreni*, *I. galani*, *I. monticola)*. Blue ocelli sometimes present in shoulder region (*I. monticola, I. galani*, *I. martinezricai)*. Underside whitish, pale yellow, deep orange yellow or green (occasionally blue or with pinkish tinge); throat colour usually not differentiated (although in *I. aurelioi* and *I. horvathi*, white throat may contrast with otherwise yellow underside, specially in the former); dark spotting present or absent; blue spots present on outer row of ventral scales (except in *I. aurelioi*). Tail of juveniles often bright, green or blue.

Distinctive internal features. None.

Hemipenis. Lobes with plicae, apical section of each shorter than basal one, their sulcal lips small; no armature or folding of lobes in retracted hemipenis; microornamentation usually consisting of crown-shaped tubercles but of hook-like spines in *I. aranica* and *I. bonnali* from the Pyrenees.

Chromosomes. Diploid number (2n) never more than 36, as a result of loss of microchromosomes. If 36 then all chromosomes single-armed; males of Pyrenean species may have diploid number of 26 or 24, made up of 16 or 12 single-armed chromosomes and 10 or 12 double-armed ones. Sex chromosomes ZW-type in *I. aranica*, *I. monticola*, *I. cyreni*, *I. martinezricai*, *I. galani* and *I. horvathi*, and Z_1Z_2W-type in *I. aurelioi* and *I. bonnali*, the latter type correlated with lower chromosome numbers in females (25 compared with 26 in *I. aurelioi* and 23 compared with 24 in *I. bonnali*). Nucleolar organizer in large macrochromosome (L-type—*I. aranica, I. aurelioi*, *I. bonnali, I. monticola, I. galani*, *I. horvathi*) or in a medium-sized one (M-type—*I. cyreni and I. martinezricai*).

Reproduction. Males bite flanks of females during copulation; clutches consisting of 3–10 eggs. Embryos often partly developed in newly laid eggs. This occurs to some extent in *I. monticola* (Braña 1991) and is very marked in the Pyrenean species of *Iberolacerta* (Arribas 2004; Arribas & Galan 2005). Here embryos may have already reached stages 30 to 33 (Dufaure & Hubert 1961) at laying, about the same degree of development as in the newly laid eggs of oviparous *Zootoca vivipara*. As in this species, *Dinarolacerta* and some *Takydromus* times to hatching are short, at least in captivity (*I. bonnali* 31–36 days, *I. aurelioi* 31–34 days, *I. aranica* 23–34 days).

Ecology. Usually more or less rock dwelling, although sometimes found among scree rather than being associated with more continuous surfaces. Most taxa occur exclusively in mountain areas and frequently at high altitudes (but not always in *I. monticola* in northwest Spain, where some populations live at sea level in humid valleys and sea cliffs).

Remarks. The subgenus *Pyrenesaura* Arribas, 1999 includes the three species of *Iberolacerta* found in the Pyrenees Mountains, namely *I. aranica, I. aurelioi* and *I. bonnali*. It is characterised by strong reduction in chromosome number resulting from Robertsonian fusions. *Pyrenesaura* can be distinguished from other southwest European *Iberolacerta* by almost universal contact between rostral and frontonasal scales, as well as contact between the supranasal and first loreal scales above the nostril; usually a greater number of mid-line scales separating the rows of femoral pores under each hind leg (4 to 9, compared with 1 to 4 in other *Iberolacerta*); absence of blue ocelli in shoulder region; females nearly always with only one presacral vertebra more than males, and more frequent vestigial ribs on third vertebra. Phylogeny and history of *Iberolacerta* has recently been discussed (Arribas 1997, 1999; Carranza *et al*. 2004; Arribas & Carranza 2004); see also Fig. 2 and Mayer and Arribas (2003).

Iranolacerta gen. nov.

Type species. *Lacerta brandtii* De Filippi, 1863 [=*Iranolacerta brandtii* (De Filippi, 1863)].

Etymology. A feminine name derived from Iran, the country where most populations of the genus occur, and *lacerta*, a lizard.

Synonymy.

—*Lacerta* Linnaeus, 1758 (part); De Filippi, 1863. Arch. Zool. 2: 387. [*Lacerta brandtii*]

Species included. *Iranolacerta brandtii* (De Filippi, 1863) **comb. nov.**; *Iranolacerta zagrosica* (Nilson, Rastegar-Pouyani, Rastegar-Pouyani & Andrén, 2003) **comb. nov.**

Distribution. West Iran and Southeast Azerbaijan (Fig. 25g).

Diagnosis. *Iranolacerta brandtii* and *I. zagrosica* occur in the same geographical area and are placed in the same genus on the basis of their strongly supported sister-relationship in DNA phylogenies (Fig. 2). Morphologically they are very different and share few distinctive features. This is probably functionally associated with their divergent life modes, *I. brandtii* being ground dwelling while *I. zagrosica* is found on rock surfaces and in crevices in these. *Iranolacerta brandtii* is distinctive among Lacertini in having a pair of double-armed macrochromosomes among the usual lacertid diploid complement of 38 chromosomes, but the karyotype of *I. zagrosica* has not yet been investigated. Among features found only in a minority of other Lacertini, the two members of *Iranolacerta* share just the following: outer edge of parietal scale not reaching lateral border of parietal table, five upper labial scales in front of subocular, at least eight longitudinal rows of ventral scales, ocelli often present on flanks at least of males. Other more widely distributed shared features include: usual number of presacral vertebrae 26 in males and hemipenial microornamentation of crown-shaped tubercles.

Description.

Size and shape. Small Lacertini up to about 70 mm from snout to vent; adult males larger than females; head and body not depressed in *I. brandtii*, but strongly so in *I. zagrosica* in which the toes are also strongly compressed.

Skull. About seven premaxillary teeth in adults; pterygoid teeth present in *I. brandti*, which may have anterior and posterior projections on the septomaxilla and a slight medial depression on the snout; nasal process of premaxilla slender; postfrontal and postorbital bones separated, postfrontal short in *I. zagrosica*; maxillary-jugal suture not stepped. Supraocular osteoderms complete in adult *I. brandtii*, incomplete and fenestrated in *I. zagrosica*.

Postcranial skeleton. Usual number of presacral vertebrae 26 in males and 27 in females (range in female *I. brandtii* 26–27); usually six or seven posterior presacral vertebrae with short ribs; medial loop of clavicle continuous or interrupted posteriorly; lateral arms of interclavicle more or less perpendicular to the sagittal axis (occasionally directed slightly forwards); sternal fontanelle oval; inscriptional ribs usually absent in *L. brandtii* and present in *I. zagrosica*; pattern of tail vertebrae BC-type in *L. brandtii* and AB-type in *I. zagrosica*.

Scaling. Rostral separated from frontonasal scale; row of supraciliary granules complete; outer edge of parietal scale not reaching lateral border of parietal table. Nostril seprated from first upper labial scale in some *I. brandtii*; two postnasal scales in *I. brandtii* and one in *I. zagrosica*; no contact between supranasal and anterior loreal scales above nostril; five upper labial scales in front of subocular; first upper temporal scale large; masseteric scales present. Dorsal scales small and smooth, about 50–61 in transverse row across mid-body. Collar smooth; at least eight longitudinal rows of ventral scales (a short additional row on each side rasing the maximum nuber of ventral scales across belly to ten in at least some *I. zagrosica*); preanal scale relatively wide and short, bordered by one or two semicircles of smaller scales; scales under toes smooth or tubercular, often only a single row directed ventrally in *I. zagrosica*; whorls of tail scales subequal in length.

Colouring. Adult dorsal patterns more or less banded in *I. brandtii* with dark flanks and often two series of dark spots along back; mid-back markings of *I. zagrosica* more dispersed. Dorsal ground colour brown or green (especially in breeding season in *I. brandtii*). Ocelli present in shoulder region and often along flanks at least in males. Underside of *I. brandtii* white, yellow or greenish, with posterior belly and undersides of hind legs and tail-base orange or reddish in breeding males; underside of *I. zagrosica* blue; throat undifferentiated and dark spots usually occur on underside, especially anteriorly in *I. zagrosica;* blue spots present on outer row of ventral scales; tails of hatchlings not brightly coloured, at least in *I. brandtii*.

Distinctive internal features. Nasal vestibule elongated and overhanging principal nasal chamber posteriorly in *I. brandtii*; this species also has the insertion of retractor lateralis anterior muscle in front of vent lateral, away from mid-line.

Hemipenis. Lobes with plicae, the apical section of each shorter than the basal one in *I. brandtii*, longer in *I. zagrosica*, sulcal lips on lobe sulci small; no armature or folding of lobes in the retracted hemipenis; micro-ornamentation consisting of crown-shaped tubercles.

Chromosomes. Known only in *I. brandtii*. Diploid number (2n) = 38; 34 single-armed macrochromosomes, 2 double-armed macrorochromosomes and 2 microchromosomes; sex chromosomes ZW-type; nucleolar organiser in large macrochromosome (L-type).

Reproduction. Almost unknown; males bite flank of females during copulation.

Ecology. *I. brandtii* is largely gound-dwelling in relatively dry places, while *I. zagrosica* occurs on rock surfaces and cliffs at high altitudes (over 2000m).

Remarks. General biology of *I. brandtii* is discussed by In den Bosch (1996), and the phylogenetic position of *I. zagrosica* by Arnold *et al.* (in press).

Lacerta Linnaeus 1758

Type species. *Lacerta agilis* Linnaeus, 1758; by subsequent designation of Fitzinger, 1843:20.

Synonymy.

—*Lacerta* Linnaeus, 1758. Syst. Nat., ed.10, 1:200. [*Lacerta agilis*].
—*Seps* Laurenti, 1768. Spec. Med. Synops. Rept.: 58. [*Seps argus = Lacerta agilis argus*; *Seps sericeus* and *Seps viridis = Lacerta viridis*].
—*Lacertus* Lacèpede, 1788 in Buffon (ed.), Hist. Nat. Gen. Part. Rept., 37. [not available; supressed by ICZN opinion 1463].
—*Ameiva* Meyer, 1795 (part); Synops. Rept.: 28. [*Ameiva agilis = Lacerta agilis*].
—*Podarcis* (part); Fitzinger, 1864 in Herber, Verh. Zool.-Botan.Ges. Wien, 14: 703. [*Podarcis michahellesii = Lacerta trilineata*; nomen oblitum].

Species included. *Lacerta agilis* Linnaeus, 1758; *Lacerta bilineata* Daudin, 1802; *Lacerta media* Lantz & Cyren, 1920; *Lacerta pamphylica* Schmidtler, 1975; *Lacerta schreiberi* Bedriaga, 1878; *Lacerta strigata* Eichwald, 1831; *Lacerta trilineata* Bedriaga, 1886; *Lacerta viridis* (Laurenti, 1768).

Distribution. Europe, Asiatic Turkey and the Caucasus region, western Syria, Israel, western Jordan, and north and west Iran; one species *Lacerta agilis* also extending eastwards into central Asia as far as Lake Baikal (Fig. 25a).

Diagnosis. Sharing with *Timon* the following combination of features that mainly occur elsewhere only in a minority of other Lacertini and are sometimes restricted to the two genera: large body size, head and body deep, nasal process of premaxilla often broad, nine or more premaxillary teeth in adults, usually 27 presacral vertebrae in males; often seven posterior presacral vertebrae with short ribs; occipital scale frequently relatively broad, collar strongly serrated, ventral scales with sloping sides and strong posterior overlap, preanal scale often surrounded by more than one semicircle of smaller scales, frequently green above and underside without bright contrasting colour except sometimes on throat, no blue spots on outer ventral scales, bodenaponeurosis without a lateral septum, retractor lateralis anterior muscle inserting in front of vent laterally away from midline, hatchlings ‘embryonic’ with very large head and short extremities compared to those of other Lacertini. Other more widely distributed features include: supraocular osteoderms complete in adults, inscriptional ribs present, and tail not brightly coloured in hatchlings.

Differs from *Timon* in smaller adult body sizes (70 to 175 mm from snout to vent); maxillary-jugal suture often stepped, dorsal body scales always keeled; 3–5 narrow light stripes in many juveniles and some females, no well defined blue ocelli on flanks of adults, hemipenial microornamentation usually of crown-shaped tubercles but with longer spines on sides of lobes (latter also present in *Timon princeps*). Also lacks distinctive karyology of *Timon* and is not associated with it by albumin immunology (Lutz & Mayer 1984).

Description.

Size and shape. Medium-sized Lacertini adults about 70–175 mm from snout to vent; adult females often longer than males; head and body robust and deep.

Skull. Usually nine premaxillary teeth in adults (occasionally ten); pterygoid teeth present; nasal process of premaxilla generally broad; postfrontal and postorbital bones usually separate at hatching (with the exception of *L. schreiberi*) but often give the appearance of coalescing during life, subequal in length; maxillary-jugal suture often stepped. Supraocular osteoderms complete in adults, and temporal osteoderms well developed in mature animals (not *L. agilis*).

Post-cranial skeleton. Usual number of presacral vertebrae 27 in males and 28 in females, but often 28 in males and 29 in females of *L. agilis* (total range in genus 26–28 in males and 27–30 in females); usually six or seven posterior presacral vertebrae with short ribs; medial loop of clavicle often but not always continuous; lateral arms of interclavicle more or less perpendicular to sagittal axis; sternal fontanelle oval; one, two or even three inscriptional ribs present; pattern of tail vertebrae A- or B-type.

Scaling. Rostral separated from frontonasal scale; row of supraciliary granules often complete but may be reduced (frequently absent in *L. agilis*); outer edge of parietal scale not reaching lateral border of parietal table; occipital scale sometimes quite broad. Usually two postnasal scales (often one and on rare occasions three in *L. agilis*, in which postnasals may be barely distinguishable from loreals); no contact between supranasal and anterior loreal scales above nostril; usually four upper labial scales in front of subocular; typically two large deep upper temporal scales (occasionally more); masseteric scale present but often barely distinguishable from other large temporal scales. Dorsal body scales small, raised and keeled, about 33–60 in a transverse row at mid-body. Collar deeply serrated; six or eight longitudinal rows of ventral scales with sloping sides and strong posterior overlap; preanal scale relatively small and wide, usually bordered by two or more semicircles of smaller scales the more anterior of which may be relatively large; scales under toes smooth or tubercular; whorls of tail scales subequal in length.

Colouring. Adults quite often wholly or partly green above, especially males. Some juveniles and females with narrow pale dorsolateral and lower lateral stripes or rows of spots, a vertebral one also sometimes present, other individuals more uniform; black-edged pale ocelli may be present, especially on flanks of young *L. agilis* and *L. schreiberi*. No blue occelli in shoulder region. Belly without bright contrasting colour, usually green or yellowish or, more rarely, bluish; throat frequently blue in males and some old females, especially during breeding period when blue also sometimes present on flanks (some *L. media* and *L. pamphylica*); extensive black spotting may occur, especially in *L. agilis* and *L. schreiberi*. Tails of hatchlings usually not brightly coloured, although may be orange in *L. schreiberi*.

Distinctive internal features. Nasal vestibule sometimes weakly elongated; no lateral septum on bodenaponeurosis; insertion of retractor lateralis anterior muscle in front of vent lateral, away from mid-line.

Hemipenis. Lobes with plicae, apical section of each shorter than the basal one, their sulcal lips small; no armature, or folding of lobes in retracted hemipenis; microornamentation usually consisting of crown-shaped tubercles, with long spines on lobe flanks.

Chromosomes. Diploid number (2n) = 38; 36 single-armed macrochromosomes and two microchromosomes; sex chromosomes ZW-type; nucleolar organiser in a large macrochromosome (L-type).

Reproduction. Males bite flank of females during copulation; clutches consisting of 4–30 eggs; hatchlings ‘embryonic’ with very large heads and short extremities compared to those of most other hatchling Lacertini.

Ecology. Adults of *Lacerta* eat larger prey than most other Lacertini. Most species are found in and around dense bushy vegetation in which animals may climb, but also sometimes occur in other habitats.

Remarks. Mitochondrial and nuclear DNA sequences of *Lacerta* have been analysed by Godinho *et al.* (2005). This work suggests that *L. pamphylica* is situated within *L. trilineata* and possibly *L. bilineata* within *L. viridis*, other species relationships not being resolved.

Parvilacerta gen. nov.

Type species. *Lacerta parva* Boulenger, 1887 [=*Parvilacerta parva* (Boulenger, 1887)].

Etymology. A feminine generic name derived from the trivial name of the type species, *parva* meaning small, and *lacerta*, a lizard.

Synonymy.

—*Lacerta* Linnaeus, 1758 (part); Boulenger, 1887. Cat. Liz. III: 22. [*Lacerta parva*].
—*Parvilacerta* Harris, Arnold & Thomas, 1998 (nomen nudum). Proc. R. Soc. Lond. B 265: 1947.

Species included. *Parvilacerta fraasii* (Lehrs, 1910) **comb. nov**; *Parvilacerta parva* (Boulenger, 1887) **comb. nov.**

Distribution. East and central Asiatic Turkey and Armenia (*P. parva*), and disjunctly in Lebanon (*P. fraasii*) (Fig. 25g).

Diagnosis. Unique among Lacertini in following features: medial loop of clavicle never interrupted posteriorly, plicae on hemipenial lobes replaced by longitudinal flaps and folds, hemipenial microornamentation of often bifid tubercles, female genital sinus unlobed, only 24 chromosomes (8 single-armed and 14 double-armed macrochromosomes and 2 microchromosomes). Also possessing the following features found only in a minority of other Lacertini: pterygoid teeth present, septomaxilla with anterior and posterior projections, slight medial depression on snout, elevated number of presacral vertebrae (usually 27–28 in males, 29 in females), BC-type tail vertebrae, nostril separated from first upper labial scale, collar serrated, eight longitudinal rows of ventral scales, preanal scale bordered by two or more semicircles of smaller ones, often blue or green ocelli on flanks of males, nasal vestibule markedly elongated with overhanging posterior border, kidney expanded and more than half its length in front of sacrum. Other more widely distributed features include: head and body not strongly depressed, seven or eight premaxillary teeth, inscriptional ribs usually absent, tail not brightly coloured in hatchlings.

Description.

Size and shape. Small Lacertini up to about 65 mm from snout to vent; adult males not much larger than females; head and body not strongly depressed.

Skull. Usually seven or eight premaxillary teeth in adults; pterygoid teeth present; nasal process of premaxilla slender; septomaxilla with anterior and posterior projections; slight medial depression on snout; postfrontal and postorbital bones separate, nearly equal in length in *P. parva* and postfrontal longer than postorbital in *P. fraasii*; maxillary-jugal suture not stepped. Supraocular osteoderms in adults either complete (*P. parva*) or modestly fenestrated (*P. fraasii*).

Post-cranial skeleton. Usual number of presacral vertebrae 27 (*P. parva*) or 28 (*P. fraasii*) in males and 29 in females (ranges 27–29 in males and 28–29 in females); six or seven posterior presacral vertebrae with short ribs; medial loop of clavicle always continuous; lateral arms of interclavicle more or less perpendicular to sagittal axis or directed slightly forwards; sternal fontanelle oval; inscriptional ribs usually absent; pattern of tail vertebrae BC-type.

Scaling. Rostral separated from frontonasal scale; row of supraciliary granules complete or reduced (in some *P. parva*); outer edge of parietal scale reaching lateral border of parietal table posteriorly. Nostril separated from first upper labial scale; postnasal scales two (*P. parva*) or one (*P. fraasii*); no contact between supranasal and anterior loreal scales above nostril; usually four upper labial scales in front of subocular; first upper temporal scale usually large**;** masseteric scale present, but sometimes not clearly differentiated from other relatively big temporal scales. Dorsal body scales small, mainly smooth (*P. fraasii*) or strongly keeled (*P. parva*), about 30–45 in a transverse row at mid-body. Collar serrated; eight longitudinal rows of ventral scales with sloping sides and some posterior overlap; preanal scale sometimes relatively short and broad (*P. fraasii*) or small (*P. parva*), usually bordered by two semicircles of smaller scales, the most anterior one in the inner semicircle often markedly enlarged in *P. fraasii*; scales under toes smooth or tubercular, sometimes with two faint keels in *P. parva*; whorls of tail scales subequal in length.

Colouring. More or less striated; often two rows of dark blotches on back, though these may not be apparent; narrow light dorsolateral and lower lateral stripes frequently present in *P. parva.* Often blue ocelli in shoulder region; flanks also frequently with blue or green ocelli in males and whitish ones in females. Underside brightly coloured at least in males, often yellow or green, especially strong in outer ventral area of *P. fraasii*; throat colour not differentiated; dark spotting present on outermost ventral scales in *P. fraasii;* blue spots on outer row of ventral scales; tails of hatchlings not brightly coloured.

Distinctive soft-part features. Nasal vestibule elongate, its posterior edge overhanging anterior border of principal nasal cavity; anterior part of kidney expanded and more than half its length in front of sacrum; female genital sinus unlobed.

Hemipenis. Lobes without plicae but surface irregularly folded with longitudinal flaps, apical section of each lobe shorter than basal one, their sulcal lips small; no armature, or folding of lobes in retracted hemipenis; microornamentation consisting of often bifid tubercles.

Chromosomes. Diploid number (2n) = 24; 8 single-armed macrochromosomes, 14 double-armed macrochromosomes and 2 microchromosomes; sex chromosomes ZW-type; nucleolar organizer in a microchromosome (m-type - *P. parva*) or a large macrochromosome (L-type - *P. fraasii*).

Reproduction. Males bite flank of females during copulation, and also the thigh in at least *P. parva;* clutches consisting of 2–5 eggs.

Ecology. Ground dwelling, usually in relatively dry mountain situations.

Remarks. The name *Parvilacerta* was used as a subgenus of *Lacerta* by Harris, Arnold and Thomas (1998), for the morphologically similar species *L. parva* and *L. fraasi,* a decision also based on the distinctive mtDNA of these forms. However, the name was not accompanied by a formal diagnosis nor type species designation, which would make *Parvilacerta* a nomen nudum according to articles 13a and 13b of the third edition of the 1985 edition of the International Code of Zoological Nomenclature (International Commission for Zoological Nomenclature, 1985), the one in force at the time. As the name has already been used in the literature, it is preserved here as a full genus, by providing a diagnosis, formal description and type species designation.

Phoenicolacerta gen. nov.

Type species. *Lacerta laevis* Gray, 1838 [=*Phoenicolacerta laevis* (Gray, 1838)]

Etymology. A feminine name derived from the Latin word, Phoenice, used for the land of the Phoeniceans, on the east Mediterranean coast, where many populations of the genus occur, and *lacerta*, a lizard.

Synonymy.

—*Lacerta* Linnaeus, 1758 (part). Gray, 1838. Ann. N.H. 1: 279. [*Lacerta laevis*].
—*Podarcis* Wagler, 1830 (part); Camerano, 1877. Atti. Acc. Torino. 13: 92. [*Podarcis judaica* = *Ph. laevis*].

Species included. *Phoenicolacerta cyanisparsa* (Schmidtler & Bischoff, 1999) **comb. nov.**; *Phoenicolacerta kulzeri* (Müller & Wettstein, 1932) **comb. nov.**; *Phoenicolacerta laevis* (Gray, 1838) **comb. nov.**; *Phoenicolacerta troodica* (Werner, 1936) **comb. nov.**

Distribution. Southeast Asiatic Turkey, Cyprus, northwest Syria, Lebanon, Israel, west and southwest Jordan (Fig. 25d)

Diagnosis. Lizards possessing the following features found only in a minority of other Lacertini: pterygoid teeth sometimes present, sternal fontanelle occasionally weakly heart-shaped, occipital scale often broad; five upper labial scales in front of subocular, apical sections of hemipenial lobes longer than basal ones, their sulcal lips large. Other more widely distributed features include: head and body not or moderately depressed, seven to eleven premaxillary teeth in adults, usual number of presacral vertebrae 26 in males, inscriptional ribs frequently absent, tail not brightly coloured in hatchlings; hemipenial microornamentation of crown-shaped tubercles.

Description.

Size and shape. Small to medium-sized Lacertini up to about 90 mm from snout to vent; adult males larger than females. Head and body not or moderately depressed and head very large in male *P. laevis.*

Skull. Seven to eleven premaxillary teeth; pterygoid teeth sometimes present; nasal process of premaxilla slender; postfrontal and postorbital bones separate and postorbital often relatively short; maxillary-jugal suture not stepped. Supraocular osteoderms often complete in adults, occasionally fenestrated.

Post-cranial skeleton. Usual number of presacral vertebrae 26 in males and 27 in females (ranges 25–26 and 26–28 respectively); usually six posterior presacral vertebrae with short ribs; medial loop of clavicle often continuous but sometimes interrupted posteriorly; lateral arms of interclavicle more or less perpendicular to sagittal axis; sternal fontanelle oval or sometimes weakly heart-shaped; inscriptional ribs frequently absent; pattern of caudal vertebrae A- or B-type.

Scaling. Rostral separated from frontonasal scale; row of supraciliary granules often complete but not always so; outer edge of parietal scale reaching lateral border of parietal table posteriorly, and sometimes also anteriorly in *P. kulzeri*; Two postnasal scales; no contact between supranasal and anterior loreal above nostril; five upper labial scales in front of subocular; first upper temporal scale large; masseteric scale often but not always present (absent in some *P. kulzeri*). Dorsal body scales small but clearly keeled, especially in males. Collar more or less smooth, six or eight longitudinal rows of ventral scales; preanal scale relatively large, bordered by one semicircle of smaller subequal scales; scales under toes smooth or tubercular; whorls of scales on tail often more or less subequal.

Colouring. Flanks often dark, sometimes with pale spots, and the back plain or dark-speckled with these markings sometimes confined to a broad vertebral band. Dorsal ground colour often brown. No blue occelli in shoulder region. Underside white, green, greenish-blue or red; throat colour sometimes differentiated; dark spotting frequent ventrally; blue spots often present on outer row of ventral scales; tail not brightly coloured in hatchlings.

Distinctive internal features. Insertion of retractor lateralis anterior muscle in front of vent lateral, away from mid-line.

Hemipenis. Lobes with plicae, apical section of each longer than basal one (less so than in *Podarcis*), their sulcal lips large; no armature or folding of lobes in retracted hemipenis; microornamentation consisting of crown-shaped tubercles.

Chromosomes. Diploid number (2n) = 38; 36 single-armed macrochromosomes and 2 microchromosomes; sex chromosomes ZW-type; nucleolar organizer in a medium-small macrochromosome (MS-type).

Reproduction. Males bite flank of females during copulation; clutches consisting of about 2–6 eggs.

Ecology. Often climbing on rocks, walls, and sometimes trees; some taxa montane.

Remarks. Recent studies show considerable diversity within *Phoenicolacerta*, in morphology, karyotypes and DNA sequences (Schmidtler & Bischoff 1999; Tosunoglu *et al*. 1999; Beyerlein & Mayer 1999; In den Bosch *et al*. 2003).

Podarcis Wagler, 1830

Type species. *Seps muralis* Laurenti, 1768. [= *Podarcis muralis* (Laurenti, 1768)].

Synonymy.

—*Lacerta* Linnaeus, 1758 (part); Latreille, 1802. In Sonnini y Latreille, Hist. Nat. Rept., 1: 229. [*Lacerta muralis*].
—*Seps* Laurenti, 1768 (part). Spec. Med. Synops. Rept.:58. [*Seps muralis*].
—*Podarcis* Wagler, 1830. Nat. Syst. Amph.: 155. [*Podarcis muralis*].
—*Podarces* Wiegmann, 1834. Herpetol. Mex.: 9. (not available).

—*Zootoca* Wagler, 1830 (part); Gray 1838. Ann. Mag. Nat. Hist., 1 (4): 279. [*Zootoca muralis*].

—*Alsodromus* Fitzinger, 1843. Syst. Rept.1: 20. (not available).

—*Phenax* Fitzinger, 1843 (not Germar, 1833). Syst. Rept.1: 20. [*Phenax taurica*].

—*Archaeolacerta* Mertens, 1921 (partim); Mertens & Müller, 1940. Abh. Senckenb. Naturf. Ges. 451: 27. [*Lacerta* (*Archaeolacerta*) *hispanica*].

Species included. *Podarcis atrata* (Boscá, 1916); *Podarcis bocagei* (Seoane, 1884); *Podarcis carbonelli* Pérez-Mellado, 1981; *Podarcis erhardii* (Bedriaga, 1876); *Podarcis filfolensis* (Bedriaga, 1876); *Podarcis gaigeae* (Werner, 1930); *Podarcis hispanica* (Steindachner, 1870); *Podarcis lilfordi* (Günther, 1874); *Podarcis melisellensis* (Braun, 1877); *Podarcis milensis* (Bedriaga, 1882); *Podarcis muralis* (Laurenti, 1768); *Podarcis peloponnesiaca* (Bibron & Bory, 1833); *Podarcis pityusensis* (Boscá, 1883); *Podarcis raffonei* (Mertens, 1952); *Podarcis sicula* (Rafinesque-Schmaltz, 1810); *Podarcis taurica* (Pallas, 1814); *Podarcis tiliguerta* (Gmelin, 1789); *Podarcis vaucheri* (Boulenger, 1905) and *Podarcis wagleriana* Gistel, 1868.

Distribution. Europe north to southern Netherlands, Rhine Valley, Czech Republic, Slovakia, Hungary, Roumania and Crimea; northwest Africa (Morocco, north Algeria, Tunisia); northwest Asiatic Turkey; islands in the Mediterranean Sea eastward to the Cyclades (Fig. 25f).

Diagnosis. Possibly the only Lacertini to have the oviducts inserting into the genital sinus near the tips of the lobes. Also possessing the following features found only in a minority of other Lacertini: maxillary-jugal suture often stepped, usual numbers of presacral vertebrae 26–27 in males, sternal fontanelle quite strongly heart-shaped in most cases, pattern of tail vertebrae C-type, nearly always a single postnasal scale, outer edge of parietal scale reaching lateral border of parietal table both posteriorly and anteriorly, sexual dimorphism in dorsal colouring usually marked, with narrow light stripes often present in females, hemipenial lobes long with large outer sulcal lips. Other more widely distributed features include: head and body often not strongly depressed (although exceptions exist), usually seven premaxillary teeth in adults, inscriptional ribs often present, tail occasionally brightly coloured in hatchlings, hemipenial microornamentation of hook-shaped spines.

Description.

Size and shape. Small Lacertini usually about 50–80 mm from snout to vent but occasionally over 90 mm; adult males larger than females; head and body not strongly depressed in most cases, but exceptions in some populations of *P. muralis* and especially the *P. hispanica* species group.

Skull. Usually seven premaxillary teeth in adults, exceptionally eight; pterygoid teeth present or absent in many species, but appear to be consistently present in most *P. milensis* and *P. taurica*, and consistently absent in *P. lilfordi* and *P. wagleriana* (fide Klemmer, 1957); nasal process of premaxilla slender; postfrontal and postorbital bones separate, usually subequal in length; maxillary-jugal suture often stepped. Supraocular osteoderms usually complete in adults, but with a fenestra in some depressed members of the *P. hispanica* species group; temporal osteoderms widespread in adults of *P. peloponnesiaca*.

Post-cranial skeleton. Usual number of presacral vertebrae 26 in males and 27 in females in *P. filfolensis*, some members of the *P. hispanica* group including in *P. bocagei*, *P. lilfordi*, *P. pityusensis* and *P. tiliguerta*; 26 in males and 27–28 in females in *P. muralis*; and 27 in males and 28 in females in the remaining species (total ranges for males and females respectively 25–28 and 26–29); usually six or seven posterior presacral vertebrae with short ribs (total range 5–8; 6 commonest number in *P. filfolensis,* 6 and 7 both common in *P. hispanica* group, *P. melisellensis, P. taurica* and *P. tiliguerta*, 7 often commonest in remaining species); medial loop of clavicle continuous or interrupted posteriorly (nearly always interrupted in *P. filfolensis* and *P. muralis*); lateral arms of interclavicle more or less perpendicular to sagittal axis (occasionally angled slightly backwards, especially in *P. wagleriana*); sternal fontanelle often quite strongly heart-shaped; frequently one pair of inscriptional ribs present; pattern of tail vertebrae C-type.

Scaling. Rostral separated from frontonasal scale; row of supraciliary granules nearly always complete; outer edge of parietal scale reaches or closely approaches lateral border of parietal table both posteriorly and anteriorly. One postnasal scale in the great majority of individuals of all species; no contact between supranasal and anterior loreal scales above nostril; usually four upper labial scales in front of subocular (occasionally five, for instance in some *P. peloponnesiaca*); upper temporal scales often distinguishable but rather narrow, the first often longest but sometimes not clearly differentiated from other upper temporals; masseteric scale usually present and differentiated, occasionally small and the rest of the temporal region covered by very small granular scales. Dorsal body scales small, usually smooth or weakly keeled (more strongly so in *P. melisellensis*, *P. sicula*, *P. taurica* and *P. wagleriana*), about 40–90 in a transverse row across mid-body. Collar usually smooth-edged (distinctly serrated in *P. taurica* and occasionally elsewhere); six (rarely eight) longitudinal rows of more or less rectangular ventral scales with limited posterior overlap; preanal scale relatively wide and short, bordered by one or more rarely two semicircles of smaller plates, the two most anterior scales of which often slightly enlarged; scales under toes smooth or tubercular; whorls of tail scales subequal in length.

Colouring. Sexual dimorphism in colouring marked; adult and juvenile dorsal patterns consisting of longitudinal bands, streaks or rows of spots, especially in females which often have narrow pale dorsolateral and lower lateral stripes; pattern of males more broken up and sometimes forming a reticulation; occasionally reticulation may occur in both sexes and in juveniles, for example in some populations of *P. filfolensis*, the *P. hispanica* group and *P. muralis* on islands off northwest Italy. Ground colour may be brown, grey or sometimes bright green (rarely blue) in adults. Green is sometimes seasonal and best developed in spring**.** In some species dorsal colouring is polymorphic with some individuals abruptly different from the rest in lacking dark markings (the concolor morph, a recessive condition in at least *P. melisellensis* and *P. sicula*; Kramer 1941); this occurs in some populations of *P. erhardii*, *P. filfolensis*, the *P. hispanica* group, *P. melisellensis*, *P. muralis*, *P. sicula*, *P. taurica* and *P. wagleriana*; incidence of concolor morph may vary greatly in different populations of the same species (being absent in some and predominant in others), and often appears commonest in relatively hot dry localities. Very dark colouring (melanism) occurs in some populations on small islands, especially in *P. filfolensis*, *P. lilfordi*, *P. muralis*, *P.pityusensis*, *P. sicula* and *P. tiliguerta*; this may be produced by darkening of ground color, increase in number of dark markings, or spread of the ones already present. Blue ocelli often although not always present in shoulder region. Underside often brightly coloured especially in males, frequently red, orange or pink but sometimes yellow, or blue (especially in melanistic populations); bright ventral colour absent in most populations of *P. sicula* and very restricted in *P. milensis* and some populations of *P. peloponnesiaca*; throat colour may be differentiated; dark ventral spotting frequent and sometimes very strong, for example in *P. bocagei*, *P. milensis* and some *P. muralis*, but virtually absent in at least some populations of *P. erhardii*, *P. melisellensis*, *P. sicula* and *P. taurica*; blue spots often present on outer row of ventral scales. Juveniles of some populations with contrasting tails, coloured grey, or vivid green or blue.

Distinctive internal features. Nasal vestibule occasionally weakly elongated.

Hemipenis. Lobes with plicae, apical section of each longer than basal one, their outer sulcal lips large; no armature, and lobes not folded in retracted hemipenis; sulcal lips free in *P. muralis* and the *P. hispanica* group, as in most Lacertini, but attached to lobe wall in other species and especially broad in *P. erhardii* and *P. peloponnesiaca*; microornamentation consisting of hook-shaped spines.

Chromosomes. Diploid number (2n) =38; 36 single-armed macrochromosomes and 2 microchromosomes; sex chromosomes ZW-type; nucleolar organiser in medium-sized macrochromosome (M-type).

Reproduction. Males bite flank of female during copulation; clutches consisting of 1–12 eggs.

Ecology. Podarcis tends to occur in rather drier and warmer situations than other small-bodied Lacertini within its range (*Archaeolacerta*, *Dalmatolacerta*, *Dinarolacerta*, *Hellenolacerta*, *Iberolacerta*, *Zootoca*), although this is less obvious in *P. muralis* outside lowland Italy and Mediterranean France. Structural niche is quite varied, ranging from climbing on rock exposures and taking refuge in crevices, as in some populations of the *P. hispanica* group, to living largely on the ground often in and around herbaceous vegetation, as in *P. taurica* (Arnold 1987).

Remarks. *Podarcis* has been regarded as feminine for most of its long history, but it has recently been suggested that this generic name should be masculine, which would result in alteration of the endings of several species and subspecies names from *–a* to *–us* (Böhme 1997, 1998, 2005). Some arguments against this change are made elsewhere (Arnold 2000; Lanza & Boscherini 2000; Mayer 1998).

Investigations of mitochondrial DNA sequences are rapidly changing previously accepted systematics and relationships within *Podarcis*. Relevant publications include the following. General relationships—this paper (Fig. 2); Harris and Arnold (1999); Harris *et al*. (2005a); Carranza *et al*. (2004). Species found in Balkan Peninsula—Poulakakis *et al*. (2005). *P. erhardii*—Poulakakis *et al*. (2003). *P. melisellensis*—Podnar *et al*. (2004). *P. sicula*—Podnar *et al*. (2005). *P. tiliguerta*—Harris *et al*. (2005a). *P. raffonei* and *P. wagleriana*—Harris *et al*. (2005b). *P. hispanica* group—Harris and Sá-Sousa (2005). From this work it appears that: *P. erhardii* is paraphyletic, one section being more closely related to *P. peloponnesiaca*; *P. sicula* may be better regarded as two species and *P. tiliguerta* as more than two; the *P. hispanica* group of southwest Europe and northwest Africa contains additional species to the ones already recognised which are *P. atrata*, *P. bocagei*, *P. carbonelli*, *P. hispanica* and *P. vaucheri*.

Scelarcis Fitzinger, 1843

Type species. *Lacerta perspicillata* Duméril & Bibron, 1839 [= *Scelarcis perspicillata* (Duméril & Bibron, 1839)].
Synonymy.
—*Lacerta* Linnaeus, 1758 (part); 1839. Duméril & Bibron. Erpétol. Gén., 5: 249. [*Lacerta perspicillata*].
—*Scelarcis* Fitzinger, 1843. Syst. Rept. 1: 20. [*Scelarcis perspicillata*].
—*Tethia* Gray, 1845. Cat. Spec. Liz. Coll. Brit. Mus.: 32. [*Tethia perspicillata*].
—*Podarcis* Wagler, 1830 (part); Richter, 1986. In Böhme (ed.): Handb. Rept. Amph. Europas, 2 (2):399. [*Podarcis perspicillata*].

Species included. *Scelarcis perspicillata* (Duméril & Bibron, 1839).

Distribution. Northwest Africa, in north Morocco and coastal Algeria; also on Menorca in the Balearic Islands where probably introduced (Fig. 25e).

Diagnosis. The only genus in the Lacertini with a transparent window in the lower eyelid consisting of a single scale. Also possessing the following features found only in a minority of other Lacertini: usual number of presacral vertebrae 26–27 in males, medial loop of clavicle always interrupted posteriorly, lateral arms of interclavicle directed obliquely backwards, hemipenis with large sulcal lips on lobes, outer edge of parietal scale reaching lateral border of parietal table both posteriorly and anteriorly, nostril separated from first upper labial scale, five or more upper labial scales in front of subocular; no enlarged masseteric scale, 10–12 longitudinal rows of ventral scales, preanal scale often bordered by two semicircles of smaller scales, some animals without markings and others with broad dorsolateral stripes; no blue spots on lateral edges of the outer ventral scales. Other more widely distributed features include: head not strongly depressed, usually seven premaxillary teeth in adults, inscriptional ribs usually absent, tail brightly coloured in hatchlings, hemipenial microornamentation of hook-like spines.

Description.

Size and shape. Small Lacertini up to about 60 mm from snout to vent; adult males usually larger than females; body quite depressed but head relatively robust.

Skull. Usually seven premaxillary teeth in adults; pterygoid teeth absent; nasal process of premaxilla slender; postfrontal and postorbital bones separate, subequal in length; maxillary-jugal suture not stepped. Supraocular osteoderms complete in adults.

Postcranial skeleton. Number of presacral vertebrae usually 26–27 in males and 27–28 in females; six or seven posterior presacral vertebrae with short ribs; medial loop of clavicle always interrupted posteriorly; lateral arms of interclavicle distinctive in being directed obliquely backwards; sternal fontanelle oval; inscriptional ribs usually absent; pattern of tail vertebrae A- or B-type.

Scaling. Rostral separated from frontonasal scale; row of supraciliary granules complete; outer edge of parietal scale reaches lateral border of parietal table both anteriorly and posteriorly. Two postnasal scales; nostril separated from first upper labial scale by ventral contact between supranasal and postnasal; no contact between supranasal and anterior loreal scales above nostril; five or more supralabial scales in front of subocular; lower eyelid with a transparent window consisting of a single scale; upper temporal scales often small and not clearly differentiated, especially posteriorly; masseteric scale absent and temporal area covered with very small granular scales. Dorsal scales on body small and granular, about 37–50 in a transverse row at mid-body. Collar smooth; ten or twelve longitudinal rows of rectangular ventral scales; preanal scale fairly small and bordered by one or two semicircles of smaller subequal scales; scales under toes smooth or tubercular, scale whorls on tail alternately longer and shorter.

Colouring. Dorsal patterns of adults and young very variable, sometimes with disjunctly different patterns at one locality Animals may be reticulated all over, or with this pattern interrupted by broad pale dorsolateral stripes, or entirely uniform (similar to concolor morph in some *Podarcis* species). Juvenile patterns like to those of adults. No blue occelli in shoulder region. Underside white sometimes with a greenish or bluish gloss, throat colour not differentiated, dark spotting absent; no blue spots on outer row of ventral scales; tail bright blue, green or yellow in hatchlings.

Distinctive soft-part features. None.

Hemipenis. Lobes with plicae, apical section of each shorter than basal one, their sulcal lips large; sometimes traces of an armature, but lobes not folded in retracted hemipenis; microornamentation consisting of hook-like spines.

Chromosomes. Diploid number (2n = 38); 36 single-armed macrochromosomes and 2 microchromosomes; sex chromosomes ZW-type; nucleolar organizer in a large macrochromosome (L-type).

Reproduction. Males bite flank of females during copulation; clutches consisting of 1–3 eggs.

Ecology. Frequently climbs on rocks and anthropogenic equivalents such as walls and exposures in quarries; sometimes also on the boles and branches of trees.

Remarks. DNA sequence indicates that *Scelarcis perspicillata* as presently understood comprises more than one well differentiated lineage and is likely to consist of two or more species (Harris *et al*. 2003).

Takydromus Daudin, 1802

Type species. *Takydromus quadrilineatus* Daudin, 1802 [= *T. sexlineatus* Daudin, 1802].

Synonymy.

—*Takydromus* Daudin, 1802. Hist. Nat. Rept.,3: 251. [*Takydromus quadrilineatus* = *T. sexlineatus*].
—*Tachidromus* Latreille, 1804. Nouv. Dict. D’Hist. Nat. XXIV: 63. (Emendation).
—*Tachydromus* Froriep, 1806. Dumeril‘s Anal. Zool.: 83. (Emendation).
—*Takysaurus* Gray,1845. Cat. Spec. Liz.: 52. [*Takysaurus tachydromoides*].
—*Platyplacopus* Boulenger, 1917. Mem. Asiat. Soc. Bengal 5: 231. [*Platyplacopus kuehnei*].
—*Apeltonotus* Boulenger, 1917. Mem. Asiat. Soc. Bengal 5: 233. [*Apeltonotus dorsalis*].

Species included. *Takydromus amurensis* Peters, 1881; *Takydromus dorsalis* Stejneger, 1904; *Takydromus formosus* Boulenger, 1894; *Takydromus hani* Chou, Truong & Pauwels, 2001; *Takydromus haughtonianus* Jerdon, 1870; *Takydromus hsuehshanensis* Lin and Cheng, 1981; *Takydromus intermedius* (Stejneger, 1924); *Takydromus khasiensis* Boulenger, 1887; *Takydromus kuehnei* Van Denburgh, 1909; *Takydromus sauteri* Van Denburgh, 1909; *Takydromus septentrionalis* Günther, 1864; *Takydromus sexlineatus* Daudin, 1802; *Takydromus smaragdinus* Boulenger, 1887; *Takydromus stejnegeri* Van Denburgh, 1912; *Takydromus sylvaticus* Pope, 1928; *Takydromus tachydromoides* (Schlegel, 1838); *Takydromus toyamai* Takeda and Ota, 1996; *Takydromus wolteri* Fischer, 1885.

Distribution. Japan, extreme southeastern Russia (Maritime Province), China, Ryukyu Islands, Taiwan, Vietnam, Laos, Cambodia, Thailand, Myanmar, Assam, Malaya, Borneo, Natuna Islands, Sumatra, Bangka and Java (Fig. 25c).

Diagnosis. *Takydromus* differs from all other Lacertini in a range of mainly derived features: lateral teeth sometimes tricuspid in adults; palpebral bone with long posterior process; only 3–5 posterior presacral vertebrae with short ribs; neural spines from mid-body to pygal region laterally compressed and blade-like, clavicles and interclavicle usually flanged, temporal scales usually keeled, at least some ventral body scales keeled, only 0–5 (usually 0–3) femoral pores on each side; lobes of hemipenis thick-walled and often without sulcal branches, hemipenial microornamentation of spines or rods sometimes recurved at the tips; hemipenis and its microornamentation apparently not regressing outside breeding season; extra microchromosomes sometimes present. *Takydromus* also possesses several features that occur only in a minority of other Lacertini: 9–10 premaxillary teeth, frontal bones without anterior descending processes, postorbital and postfrontal bones fused, medial loop of clavicle always continuous; pattern of caudal vertebrae always A-type; sometimes contact between supranasal and anterior loreal scale above nostril, outer edge of parietal scale reaching lateral border of parietal table posteriorly and sometimes anteriorly, no masseteric scale, sometimes broad pale dorsolateral stripes on body, underside without bright contrasting colour and tail not brightly coloured in hatchlings, embryos often partly developed at egg-laying. Other features more widely distributed in Lacertini include: head and body not strongly depressed, usual number of presacral vertebrae in males 25 or 26 in males, one or more pairs of inscriptional ribs.

Description.

Size and shape. Small lacertids; adults up to about 75 mm from snout to vent; females usually rather larger than males; head and body not markedly depressed in most species; body slender and tail often long (in some cases 4–5 times length of head plus body).

Skull. Usually nine or ten premaxillary teeth in adults; pterygoid teeth often absent or few; nasal process of premaxilla slender or broad; frontal bones without anterior descending processes; palpebral bone with elongate posterior process; postorbital and postfrontal bones fused throughout life; maxillary-jugal suture not stepped. Supraocular osteoderms usually complete in adults.

Postcranial skeleton. Usually 25–26 presacral vertebrae in males and 26–27 in females (ranges respectively 24–27 and 25–28); three to five posterior presacral vertebrae with short ribs; neural spines on vertebrae of mid-and hind-body and on pygal vertebrae laterally compressed and blade-like; medial loop of clavicle always continuous; lateral arms of interclavicle sometimes directed obliquely forward; clavicles and interclavicle usually flanged; sternal fontanelle oval; one or more pairs of inscriptional ribs; pattern of tail vertebrae A-type.

Scaling. Rostral usually separated from frontonasal scale (not in *T. amurensis*); supraocular scales sometimes reduced from four to three, supraciliary scales also sometimes reduced; row of supraciliary granules usually complete but absent in *T. khasiensis* and *T. sexlineatus*; outer edge of parietal scale reaches lateral border of parietal table posteriorly and sometimes anteriorly as well. One or two postnasal scales, if one then supranasal and anterior loreal scales often in contact above it; usually four upper labial scales in front of subocular (occasionally three or five); first upper temporal scale often bigger than others but not in all cases; masseteric scale absent and temporals usually keeled; only three or four pairs of chin shields. Dorsum usually with several longitudinal series of large flat scales along mid-back with keels that form continuous longitudinal ridges, scales on flanks small and granular (in *T. dorsalis* and *T. sylvaticus* entire dorsum covered with small, strongly keeled scales); about 25–50 scales in a transverse row at mid-body; dorsal scales with microornamentation of raised posterior edges of cells and coarser anastomosing longitudinal ridges. Gular scales keeled; collar serrated, sometimes only weakly differentiated or even absent; 6–8 longitudinal rows of ventral scales, at least the outermost row often keeled and pointed; preanal scale often large, occasionally divided longitudinally, bordered by a semicircle of smaller scales that may be broadly interrupted anteriorly; scales under thigh often large; 0–5 femoral pores on each side, not extending to knee; scales under toes smooth or tuberculate; scale whorls on tail subequal in length.

Colouring. Often more or less uniform above; pale dorsolateral stripes sometimes present in adults, at least anteriorly, but not young; ground colour usually brown or green. Blue ocelli on flanks only found in *T. sexlineatus ocellatus*. Underside without contrasting bright colour, often whitish or greenish with little or no dark spotting, throat colour not markedly differentiated; no blue spots on outer ventral scales; tail not brightly coloured in hatchlings.

Distinctive internal features. Insertion of retractor lateralis anterior muscle in front of vent thick.

Hemipenis. Lobes thick-walled, with plicae, apical section of each usually longer than basal one; sulcus often without branches running on to each lobe but, if present, branches have small lips, or larger ones that extend basally as flaps; no armature present and no folding of lobes in retracted hemipenis; microornamentation consisting of spines or rods, sometimes recurved at the tips.

Chromosomes. Diploid number (2n) = 38–42; 36 single-armed macrochromosomes, and 2–6 microchromosomes; sex chromosomes ZW-type; nucleolar organiser in microchromosome (m-type).

Reproduction. Males bite female on flank during copulation; clutches consisting of 1–2 to 4–9 eggs in different species. Embryos of some species well developed when eggs layed and period of incubation consequently short.

Ecology. Primitive spatial niche of genus *Takydromus* appears to involve climbing in grass and other flimsy vegetation. This behaviour occurs to varying extents in different species and some have secondarily become largely ground-dwelling or live on tree boles. The primitive spatial niche of the genus is functionally associated with a syndrome of morphological features, some of which have evolved independently in members of the Eremiadini, including *Gastropholis*, *Philochortus* and especially *Poromera* (Arnold 1989a, b, 1997).

Remarks. A further, as yet undescribed species of *Takydromus* occurs in western Myanmar and adjoining India (J. Vindum & M. Koo, pers. comm.). A hypothesis of the relationships of the species of *Takydromus* based on morphology has been presented (Arnold 1997) but, subsequently, better supported phylogenies derived from mitochondrial DNA sequence have appeared, which indicate significantly different patterns of relationships (Ota *et al*. 2002; Lin *et al*. 2002; Tang & Chen 2006). These also corroborate the clade status of *Takydromus.*

Teira Gray 1838

Type species. *Teira punctata* Gray, 1838 [= *Teira dugesii* (Milne-Edwards, 1829)]
Synonymy.
—*Lacerta* Linnaeus, 1758 (part); 1829. Milne-Edwards, 1829. Ann. Sc. Nat. 16: 71, 84. [*Lacerta dugesii*].
—*Teira* Gray, 1838. Ann Mag. Nat. Hist., (1), 1: 280. [*Teira punctata = Teira dugesii*].
—*Podarcis* Wagler, 1830 (part); Richter, 1986. In Böhme (ed.): Handb. Rept. Amph. Europas, 2 (2):388. [*Podarcis dugesii*].

Species included. *Teira dugesii* (Milne-Edwards, 1829).

Distribution. Islands in northeastern Atlantic Ocean: Madeira, Porto Santo, Desertas, and Selvages; introduced to the Azores and to Lisbon, Portugal (Fig. 25e).

Diagnosis. Lizards possessing the following features found only in a minority of other Lacertini: lateral arms of interclavicle directed obliquely backwards, outer edge of parietal scale reaching lateral border of parietal table both posteriorly and anteriorly, usually five upper labial scales in front of subocular, preanal scale bordered by one or two semicircles of smaller scales, some sexual dimorphism in colouring, broad pale dorsolateral stripes frequent in dorsal pattern, hemipenial microornamentation of hook-like spines, which may have slender projections at their tips. Other more widely distributed features include head and body not strongly depressed, frequently nine premaxillary teeth in adults, supraocular osteoderms fenestrated in some adult females, usual number of presacral vertebrae 26 in males, inscriptional ribs absent in most cases, tail not brightly coloured in hatchlings.

Description.

Size and shape. Small Lacertini up to about 80 mm from snout to vent; adult males larger than females; head and body not strongly depressed.

Skull. Usually nine premaxillary teeth in adults; pterygoid teeth absent; nasal process of premaxilla slender; postfrontal and postorbital bones separate, but may coalesce during life, subequal in length; maxillary-jugal suture not stepped. Supraocular osteoderms complete in males, and some females but fenestrated in others.

Postcranial skeleton. Usual number of presacral vertebrae 26 in males and 27 in females (ranges 25–26 and 26–27 respectively); six or seven posterior presacral vertebrae with short ribs; lateral arms of interclavicle directed obliquely backwards; sternal fontanelle oval; inscriptional ribs usually absent; Pattern of caudal vertebrae A- or B-type.

Scaling. Rostral separated from frontonasal scale; row of supraciliary granules complete; outer edge of parietal scale reaches lateral border of parietal table both posteriorly and anteriorly. Two postnasal scales; no contact between supranasal and anterior loreal scales above nostril; usually five upper labial scales in front of subocular; upper temporal scales not differentiated; no masseteric scale and temporal area covered by very small granular scales. Dorsal body scales small and smooth or very faintly keeled, usually 55–80 in a transverse row at mid-body. Collar smooth, six (rarely eight) longitudinal rows of rectangular ventral scales; preanal scale often large, bordered by one or two semicircles of smaller subequal scales; scales under toes smooth or tubercular; whorls of scales on tail alternately longer and shorter.

Colouring. In females and young the centre of the back is often dark-speckled and the sides dark with light flecks, the two areas separated by broad pale dorsolateral stripes; males are also speckled and flecked but are more uniform overall. Ground colour often grey, brown, green or blackish. No blue ocelli in shoulder region. Underside often cream or yellowish but orange or red with a blue throat in some males, sometimes dark spots present; no blue spots on outer row of ventrals. Bright belly colour is said to sometimes fade within seconds when lizards are disturbed (Crisp *et al*. 1979); this needs to be corroborated but if so, this would be a unique feature among lacertids. Tail not brightly coloured in hatchlings.

Distinctive soft-part features. Insertion of retractor lateralis anterior muscle in front of vent lateral, away from mid-line.

Hemipenis. Lobes with plicae, apical section of each shorter than basal one; their sulcal lips small; no armature, or folding of lobes in retracted hemipenis; microornamentation consisting of hook-shaped spines, sometimes with several slender projections towards their tips.

Chromosomes. Diploid number 2n = 38; 36 single-armed macrochromosomes and 2 microchromosomes; sex chromosomes ZW-type; nucleolar organiser in large macrochromosome (L-type).

Reproduction. Males bite flank of female during courtship; clutches usually consisting of 2 (rarely three) eggs.

Ecology. Like many other lizards in depauperate reptile communities on oceanic islands, *Teira* is abundant and found in a very wide range of habitats, occurring on the ground in all sorts of situations, but also climbing extensively.

Remarks. Most of the island populations of *Teira dugesii* show strong divergence in their DNA sequence, and some in morphology, indicating they may deserve separate species status (Brehm *et al*. 2003; Jesus *et al*. 2005).

Timon Tschudi, 1836

Type species. *Lacerta lepida* Daudin, 1802. [=*Timon lepidus* (Daudin, 1802)].
Synonymy.
—*Lacerta* Linnaeus, 1758 (part); Daudin, 1802. Hist. Nat. Gén. Part. Rept., 3: 204. [*Lacerta lepida*].
—*Timon* Tschudi, 1836. Isis von Oken, 29: 551.[*Timon lepidus*].
—*Thimon* Bonaparte, 1840. Mem. R. Accad. Sci. Torino, (2), 2: 419. [*Thimon ocellatus*].
—*Chrysolamprus* Fitzinger, 1843. Syst. Rept.1: 20. [*Chrysolamprus ocellatus*].

Species included. *Timon lepidus* (Daudin, 1802); *Timon pater* (Lataste, 1880); *Timon princeps* (Blanford, 1874); *Timon tangitanus* (Boulenger, 1881).

Distribution. Iberian peninsula, southern France, extreme northwest Italy and northwest Africa (Morocco, Western Sahara, north Algeria and Tunisia), with one species (*T. princeps*) occurring disjunctly in eastern Turkey, northeast Syria, north Iraq and southwest Iran (Fig. 25d).

Diagnosis. Sharing with *Lacerta* the following combination of features that mainly occur elsewhere only in a minority of other Lacertini and are sometimes restricted to the two genera: large body size, head and body deep, nasal process of premaxilla often broad, nine premaxillary teeth in adults, usually 27 presacral vertebrae in males; often seven posterior presacral vertebrae with short ribs; occipital scale often relatively broad, collar strongly serrated, ventral scales with sloping sides and strong posterior overlap, preanal scale often surrounded by more than one semicircle of smaller scales, often green above and underside without bright contrasting colour except sometimes on throat, no blue spots on outer ventral scales, bodenaponeurosis without a lateral partition, retractor lateralis anterior muscle inserting in front of vent but away from midline, hatchlings ‘embryonic’ with very large head and short extremities compared with those of most other Lacertini. Other more widely distributed features include: supraocular osteoderms complete in adults, inscriptional ribs present, and tail not brightly coloured in hatchlings.

Differs from *Lacerta* in larger adult body sizes (100–210 mm or more from snout to vent); maxillary-jugal suture not stepped, medial loop of clavicle more often interrupted posteriorly, occipital scale more frequently very broad, dorsal body scales not always keeled; no narrow light stripes in in dorsal pattern, often well defined blue ocelli on flanks, hemipenial microornamentation of hook-shaped spines, longer spines occurring on the lobe flanks only in *T. princeps*; 32 single-armed and 2 double-armed macrochromosomes and two microchromosomes.

Description.

Shape and size. Large to very large Lacertini, adults from 100–210 mm or more from snout to vent; adult males larger than females; head and body robust and not markedly depressed.

Skull. Usually nine premaxillary teeth in adults; pterygoid teeth present; nasal process of premaxilla broad in *T. lepidus* group, but more slender in *T. princeps*; postfrontal and postorbital bones separate but often give the appearance of coalescing during life, subequal in length; maxillary-jugal suture not stepped; supraocular osteoderms complete in adults and temporal osteoderms well developed in mature animals.

Post-cranial skeleton. Usual number of presacral vertebrae 27 in males and 28 in females (ranges 27–28 and 28–29 respectively); often seven posterior presacral vertebrae with short ribs (range 6–8); medial loop of clavicle continuous or interrupted posteriorly; lateral arms of interclavicle more or less perpendicular to sagittal axis; sternal fontanelle oval; one, two or even three pairs of inscriptional ribs present; pattern of tail vertebrae A- or B-type.

Scaling. Rostral separated from frontonasal scale; row of supraciliary granules complete or reduced; outer edge of parietal scale not reaching lateral border of parietal table: occipital scale trapezoidal and usually very wide posteriorly. Two postnasal scales; no contact between supranasal and anterior loreal scales above nostril; usually four upper labial scales in front of subocular; typically two large, deep upper temporal scales; masseteric scale present but often barely differentiated from other large scales in temporal region. Dorsal body scales small, smooth or feebly or strongly keeled, about 35–100, in a transverse row across mid-body. Collar strongly serrated, eight to ten longitudinal rows of trapezoidal, overlapping ventral scales; preanal scale often relatively small and bordered by two or three rows of smaller scales; scales under toes tubercular; whorls of tail scales subequal in length.

Colouring. Uniform; with black stippling; with a pattern of dark rosettes or white-centred ocelli, the latter in young of the *T. lepidus* group. Ground colour green, grey or brown. Blue ocelli often present in the shoulder region and on the flanks, where several rows may occur. Underside yellowish-green to greenish (*T. lepidus* group) or whitish (*T. princeps*, *T. lepidus nevadensis*), without dark spotting, throat colour often differentiated from venter in males of *T. princeps* (orange or reddish), *T. pater* (yellow) and *T. tangitanus* (pale blue); no blue spots on outer ventral scales. Tail not brightly coloured in hatchlings.

Distinctive internal features. Nasal vestibule sometimes weakly elongated; bodenaponeurosis without a lateral septum; partial thoracic fascia present in *T. lepidus* group; retractor lateralis anterior muscle inserting laterally in front of vent away from mid-line.

Hemipenis. Lobes with plicae, apical section of each shorter than basal one, their sulcal lips small; no armature, or folding of lobes in retracted hemipenis; microornamentation consisting of hook-shaped spines, *T. princeps* also having long recurved spines on lobe flanks.

Chromosomes. Diploid number (2n) = 36; 32 single-armed macrochromosomes, 2 double-armed macrochromosomes and 2 microchromosomes; sex chromosomes ZW-type. In the *Timon lepidus* group,a nucleolar organizer is present in a large chromosome (L-type), and additional one may also exist in some populations and individuals. If so, it occurs in a medium chromosome (M-type) in *T. lepidus*, and in a medium-small one (MS-type) in *T. pater* and *T. tangitanus*.

Reproduction. Males bite flanks of female during copulation; clutches consisting of about 5–22 eggs; hatchlings ‘embryonic’, with a very large head and short extremities compared to those of most other hatchling Lacertini.

Ecology. Like *Lacerta*, adults of *Timon* eat larger prey than most other Lacertini. All species are often found in and around bushy vegetation, but the *T. lepidus* group has a much broader total spatial niche, occurring in a wide range of habitats in which it is active on the ground but also readily climbs.

Remarks. Timon consists of two distinct units: the *Timon lepidus* group of the western Mediterranean region (*T. lepidus*, *T. pater*, *T. tangitanus*) and *T. princeps* of southwest Asia. They appear to be related on the basis of albumin immunology (Lutz & Mayer 1984), mitochondrial DNA sequence (reanalysis of the data set of Harris *et al.* 1998 – see Fig. 1), and some morphological features (Fig. 4). A DNA phylogeny has been presented for the *T. lepidus* group (Paulo *et al*. 2001) and the morphology of *T. princeps* is discussed extensively by Eiselt (1968, 1969).

Zootoca Wagler, 1830

Type species. *Lacerta vivipara* Jacquin, 1787 [=*Zootoca vivipara* (Jacquin, 1787)].
Synonymy.
—*Lacerta* Linnaeus, 1758 (part); Jacquin, 1787. Nova Acta Helvet.1: 33. [*Lacerta vivipara*].
—*Zootoca* Wagler, 1830: Nat. Syst. Amph.: 67. [*Zootoca vivipara*].
—*Atropis* Glükselig, 1851. Lotos 1(7): 138. [*Atropis nigra* = *Zootoca vivipara*].

Species included. *Zootoca vivipara* Jacquin, 1787.

Distribution. From Norway, the British Isles and northwest Spain east across Europe and Palaearctic Asia to its Pacific coast, Sakhalin island, and Hokkaido in Japan. In Europe also extending south to northern Italy, Macedonia and Bulgaria (Fig. 25b).

Diagnosis. The only genus of Lacertini with a hemipenis that has a fully developed armature and complexly folded lobes, in which fully-formed young are produced over most of the geographic distribution, and which is also characterised by small short head, short limbs and thick short tail. Also possessing the following features found only in a minority of other Lacertini: nasal process of premaxilla often broad, postorbital and postfrontal bones fused throughout life, posterior presacral vertebrae with short ribs frequently five, row of supraciliary granules reduced or even absent, outer edge of parietal scale reaching the lateral border of parietal table both posteriorly and anteriorly, single postnasal scale, frequent contact between supranasal and anterior loreal scales above nostril, few dorsal body scales (25–37 across mid-back), serrated collar, imbricate ventral scales, no blue spots on outer ventral scales, insertion of retractor lateralis anterior muscle in front of vent thick, 36 macrochromosomes in males and often 35 in females, no microchromosomes, usually Z_1Z_2W-type sex chromosomes. Other more widely distributed features include head and body not strongly depressed and supraocular osteoderms complete in adults, usually seven premaxillary teeth in adults, usual number of presacral vertebrae 26 in males, inscriptional ribs sometimes absent, tail with bright colouring in juveniles of some populations (although largely masked by darker pigment), hemipenial microornamentation of crown-shaped tubercles.

Description.

Size and shape. Small Lacertini up to about 65 mm from snout to vent; adult females larger than males; head and body undepressed, head small and, like the legs and tail, relatively short.

Skull. Often seven premaxillary teeth in adults; pterygoid teeth absent; nasal process of premaxilla frequently broad; frontal bones often without anterior descending processes; postfrontal and postorbital bones fused throughout life; maxillary-jugal suture not stepped. Supraocular osteoderms complete in adults.

Post-cranial skeleton. Usual number of presacral vertebrae 26 in males, and 28 in females (ranges 25–27 and 27–29 respectively); five or six posterior presacral vertebrae with short ribs; medial loop of clavicle continuous or interrupted posteriorly; lateral arms of interclavicle more or less perpendicular to sagittal axis; sternal fontanelle oval; inscriptional ribs sometimes absent; pattern of caudal vertebrae often A-type, occasionally B-type.

Scaling. Rostral nearly always separated from frontonasal scale; supraciliary granules reduced to four or fewer, or even absent; outer edge of parietal scale reaching lateral border of parietal table both posteriorly and anteriorly. Nostril sometimes separated from first upper labial scale; one postnasal scale (occasionally fused with first loreal scale); frequent contact between supranasal and anterior loreal scales above nostril; usually four upper labial scales in front of subocular (sometimes three, at least on one side); upper temporal scales variable; masseteric scale present but frequently similar to other large scales in the temporal area. Dorsal scales relatively large and coarse, varying from flat and smooth to convex and strongly keeled, about 25–37 in transverse row at mid-body. Collar serrated; six, occasionally eight, longitudinal rows of fairly imbricate ventral scales; preanal scale relatively small, often bordered by two semicircles of smaller scales, the anterior pairs of each frequently enlarged; scales under toes smooth or tubercular, scale whorls on tail alternately longer and shorter.

Colouring. Adult dorsal patterns often consisting of longitudinal stripes, frequently including dark flanks and vertebral streak and light streaks especially dorsolateral ones; sometimes scattered light or dark spots or ocelli, especially in males. Background colour brown, occasionally grey or olive, rarely greenish. No blue ocelli in shoulder region. Underside often whitish, yellow, orange or red, usually dark-spotted (especially in males), the throat frequently contrasting whitish or with bluish gloss especially in males; no blue spots on outer row of ventral scales. Juveniles have similar patterns to adults but obscured by dark bronzy pigment, so they often appear blackish-bronze when first born; tail of hatchlings sometimes with a bluish tone but almost entirely obscured by dark pigment.

Distinctive internal features. Insertion of retractor lateralis anterior muscle in front of vent thick.

Hemipenis. Lobes with plicae, apical section of each shorter than basal one, their sulcal lips large; a large well-developed armature present and lobes complexly folded in retracted hemipenis; microornamentation consisting of crown-shaped tubercles.

Chromosomes. Diploid number (2n) often 36, but 35 in females of many populations; all macrochromosomes single-armed or one double-armed, no microchromosomes. Sex chromosomes ZW-type in *Zootoca vivipara carniolica* of Slovenia and neighboring areas, associated with 2n = 36 chromosomes in both sexes, and Z_1Z_2W-type in other populations where males have four sex chromosomes ($Z_1Z_1Z_2Z_2$) and females three (Z_1Z_2W), associated with 2n = 36 chromosomes in males and 35 in females. W chromosome single-armed in most populations but in viviparous ones it is double-armed over most of Europe. Nucleolar organiser in medium-small macrochromosome (MS-type).

Reproduction. Males bite flank of females during copulation; clutches consisting of 1–13 eggs are produced in north of Iberian peninsula (Cantabrian and Pyrenean mountains) and eastern Alps (Slovenia, south Austria, Croatia and north Italy), but *Zootoca vivipara* gives birth to fully-formed young over the rest of its immense distribution (the largest of any presently recognised lizard species).

Ecology. Essentially ground-dwelling in humid environments, especially among grass and other herbaceous plants and small and dense shrubs in which animals disappear quickly in case of danger, diving among the leaves and stems**.** Frequently montane in south of its range and occurs further north than any other reptile, reaching 70° N in Norway, over 350 km beyond the Arctic Circle.

Remarks. A mitochondrial DNA phylogeny based on a 423 base pair fragment mainly from the cytochrome b gene (Surget-Groba *et al*. 2001) shows a 10% divergence, suggesting differentiation of living populations of *Zootoca* began in the Pliocene. The phylogeny also indicates that Slovenian and other neighbouring egg-laying populations are basal and that viviparous ones are most closely related to the egg-laying populations of Spain and adjoining France. East Asian populations were not sampled but other viviparous animals show a dichotomy between mainly Russian populations and those in the rest of Europe that is likely to have originated in the Pleistocene.

COMMENTS ON THE EREMIADINI

Systematics of *L. andreanskyi*

As noted, mtDNA indicates that *L. andreanskyi* from the Atlas Mountains of Morocco in NW Africa is a member of the Eremiadini and apparently basal within that group. This position would conform with it lacking the synapomorphies that characterize most other Eremiadini, namely a derived condition of the ulnar nerve and the presence of a fully developed armature in the hemipenis, which has folded lobes when retracted. It is also distinctive within the Eremiadini in often possessing an enlarged masseteric scale. Because of its probably basal position without close relationship to any other genus of Eremiadini and distinctive morphology, *L. andreanskyi* is described here as a new genus.

Subfamily Lacertinae

Tribe Eremiadini Shcherbak, 1975

Atlantolacerta gen. nov.

Type species. *Lacerta andreanskyi* Werner, 1929 [= *Atlantolacerta andreanskyi* (Werner, 1929)].

Etymology. A feminine name derived from the Latin adjective atlanticus, which refers to the Atlas Mountains where the genus occurs, and lacerta, a lizard.

Synonymy.

—*Lacerta* Linnaeus, 1758 (part); Werner, 1929. Sitzungsb. Acad. Wiss. Abt. 1, 138 (1–2): 4. [*Lacerta andreanskyi*].

Species included. *Atlantolacerta andreanskyi* (Werner, 1929) **comb. nov.**

Distribution. Western and central parts of the High Atlas Mountains of Morocco (Fig. 25g).

Diagnosis. Member of the Eremiadini distinguished from nearly all others by lacking a derived condition of the ulnar nerve, an armature and folded lobes in the hemipenis and from all except *Omanosaura* in possessing a clavicle loop that is sometimes interrupted behind, and A and B-type caudal vertebrae. Other features that in combination help to distinguish it from other genera of Eremiadini and of Lacertini include the following: small body size, often high numbers of presacral vertebrae (26–28 in males, 29 in females), sternal fontanelle sometimes weakly heart-shaped, edge of parietal scale reaching lateral border of parietal table both posteriorly and anteriorly, one postnasal scale, supranasal scale contacting anterior loreal above nostril; narrow light supraciliary stripes often present; no blue spots on outer ventral scales; outer sulcal lips on lobes of hemipenis large. Other more widely distributed features in Eremiadini and Lacertini include: head and body not strongly depressed and supraocular osteoderms complete in adults, seven premaxillary teeth in adults, inscriptional ribs often present, tail brightly coloured in hatchlings, hemipenial microornamentation of hook-shaped spines.

Description.

Size and shape. Small Eremiadini up to about 55 mm from snout to vent; adult females often larger than males; head and body not strongly depressed.

Skull. Seven premaxillary teeth in adults; pterygoid teeth absent; nasal process of premaxilla slender; postfrontal and postorbital bones separate, subequal in length; maxillary-jugal suture not stepped. Supraocular lamellae complete in adults.

Postcranial skeleton. Number of presacral vertebrae 26, 27 or 28 in males and 29 in females; six or seven posterior presacral vertebrae with short ribs; medial loop of the clavicle continuous or interrupted posteriorly; lateral arms of interclavicle more or less perpendicular to the sagittal axis; sternal fontanelle oval or weakly heart-shaped; inscriptional ribs often present; pattern of tail vertebrae A- and B-type.

Scaling. Rostral separated from frontonasal scale; row of supraciliary granules complete; outer edge of parietal scale reaching lateral border of parietal table both posteriorly and anteriorly. One postnasal scale; supranasal scale in contact with anterior loreal above nostril; four upper labial scales in front of subocular; first upper temporal large**,** masseteric scale usually well developed. Dorsal scales small and smooth, about 36 to 42 in a transverse row at mid-body. Collar fairly smooth; six longitudinal rows of ventral scales; preanal scale broad and of moderate size, borderd by a semicircle of smaller scales; scales under toes smooth or tubercular; whorls of scales on tail subequal in length.

Colouring. Often with a clear pattern of longitudinal stripes, including a dark vertebral stripe and flanks and narrow light dorsolateral stripes, although pattern may be reduced to spots in some adult males which may be faintly reticulated. Background colour brown or greyish. No blue ocelli in shoulder region. Underside whitish sometimes with a greenish tinge, the throat not differentiated, some dark spotting often present; no blue spots on outer ventral scales. Juveniles have greenish-blue tails.

Distinctive internal features. Partial thoracic fascia present; insertion of retractor lateralis anterior muscle in front of vent lateral, away from mid-line.

Hemipenis. Lobes with plicae, apical section of each not longer than basal one, their sulcal lips large; no armature, or folding of lobes in retracted hemipenis; microornamentation consisting of recurved spines.

Chromosomes. Diploid number (2n) = 38; 36 single-armed macrochromosomes and 2 microchromosomes; sex chromosomes ZW-type; position of nucleolar organizer unknown.

Reproduction. Males bite flank of females during copulation; clutches consisting of 1–3 (usually 2) eggs.

Ecology. Mainly ground-dwelling in a variety of mountain situations: screes and areas with boulders, meadows, among low clump-forming shrubs, and in places without plant cover; frequently found in the vicinity of small watercourses.

Remarks. The relatively large and apparently disjunct range of *Atlantolacerta* with populations occurring on isolated ‘mountain islands’ suggests it may not be a single species. The correct spelling of the name of the one species of *Atlantolacerta* recognised to date is *andreanskyi*, as used in the type description (Werner 1929), rather than *andreanszkyi* (with a “z”). This latter spelling is closer to the real name of the Hungarian botanist, Baron Gábor Andreánzsky (1895–1967), to whom the species was dedicated, and was used subsequently by the describer (Werner 1931), but it does not have priority. Also, it is clear that *andreanskyi* is not a lapsus calami, as Werner uses this spelling more than once in his original paper and misspells Andreánszky’s name in a similar way.

Relationships within Eremiadini

In the Eremiadini, recent independent phylogenetic analyses of mtDNA (data from Fu 2000 – Fig. 1) and nDNA sequence (Mayer & Pavličev 2005) show considerable resemblance to each other at some well-substantiated nodes. The analyses indicate that there are two Afrotropical groups: a South African one containing *Tropidosaura*, *Pedioplanis*, *Meroles* and *Ichotropis*; and another made up of *Nucras* of south and east Africa plus a clade consisting of *Latastia*, *Heliobolus* and *Philochortus*. This will be referred to as the Northeast African group, as it has most diversity in that region. In the nDNA tree (Mayer & Pavličev 2005) both these groups form a monophyletic unit which also includes the West African *Poromer*a. The remaining Eremiadini form a separate clade in the nDNA tree. Here, *Adolfus* and *Holaspis* are weakly associated, in agreement with their membership of the Equatorial African group of Eremiadini, which is characterised by several morphological synapomorphies and also includes *Gastropholis* (Arnold 1989b). Also present are the east Arabian *Omanosaura* and four genera mainly found in North Africa and southwest Asia, namely *Acanthodactylus*, *Eremias, Ophisops* and *Mesalina.*

The relationships of the Eremiadini have previously been estimated using 78 binary morphological characters (Arnold 1989a), producing a tree in which many nodes have substantial heuristic support (Harris *et al*. 1998, p. 1944). In contrast to the DNA trees, the morphological one is highly pectinate, with a main lineage from which most genera arise in sequence. The principal exception is the Equatorial African group of genera which arises relatively basally. When gross habitat is reconstructed on the morphological tree, there is one transition spread over more than one node from relatively mesic to increasingly xeric environments. This is associated with the appearance of many (more than 15) derived anatomical features that are widely distributed through the body and include aspects of the nostrils and nasal tract, frontal and quadratojugal bones, eye-size, xiphisternal ribs, body shape, limb, foot and kidney structure. A case can be made that they are functionally related to the problems of surviving in dry habitats with which they are associated (Arnold 1989a, 1993, 2004).

In the DNA estimates of phylogeny, shift to xeric conditions may have occurred more than once, as noted by Mayer and Pavličev (2005). This applies to many of the extensive associated anatomical changes, and there may have been at least three shifts: in the South African group (*Meroles*, *Ichnotropis* and *Pedioplanis* xeric), Northeast African group (*Latastia*, *Philochortus* and *Heliobolus* xeric), and the North African-Eurasian assemblage (*Acanthodactylus*, *Eremias*, *Mesalina* and *Ophisops* xeric). This would inevitably involve a great deal of morphological parallelism. A single shift to xeric conditions with this topology would be even less parsimonious in terms of morphological change, as several reversals to mesic habitats and morphology would be involved. If a multiple shift to xeric conditions and anatomy were accepted, the separate cases would be representatives of an ecomorph, a pattern of morphology that has been acquired independently by different ecological analogues (Williams 1972, 1983). Ecomorphs are a common phenomenon and resemblance may be very striking if the independent cases evolved from forms that, while separate, had similar anatomy. Such resemblance may extend even to the order in which different features are assembled in parallel (Arnold 1994).

Ecomorphs are sometimes detected in morphological data sets and many are already recognised in the Lacertidae on this basis (Arnold 1989a, 1993, 2004). As here, such cases are often confirmed, or at least not refuted, by DNA-based phylogenies when these become available, and further cases may also be revealed. This has recently happened in *Myotis* bats (Ruedi 2001), *Anolis* lizards (Losos *et al*. 1998), toad headed agamids *(Phrynocephalus* and *Bufoniceps*, on the phylogenetic evidence of Macey *et al.* 2006), and in skinks assigned to the genus *Sphenops* (Carranza & Arnold unpublished data). Such cases involve detailed morphological resemblances and contrast with ones where the lineages entering similar selective regimes are initially morphologically quite diverse. Here, anatomical and other solutions to problems may be different and they may be assembled in different orders (Arnold 1994).

The numerous examples of ecomorphs with detailed resemblance mentioned above make it more credible that Eremiadini could have become xeric at least three times. This is especially so as the relationships that indicate this possibility are supported independently by both mitochondrial and nuclear genes involving a total of no less than 6300 bp of sequence. If a tripartite shift into xeric conditions is accepted as a hypothesis, it can be tested further by improving taxon coverage for all available gene fragments and incorporating them into a single analysis of DNA sequence.

It is interesting to note that, although Eremiadini and Lacertini are sister groups and so the same age, branch lengths are generally much longer in the Eremiadini, in both the mtDNA and nDNA trees. This may possibly be because Eremiadini, being found in warmer areas, tend to breed sooner after hatching. They may consequently have had more generations in their history than most lineages of Lacertini, and so might evolve at a faster rate.

Relationships in the northeast African group. Distinctive non-molecular features are present in the Northeast African clade of Eremiadini, which have not been used in previous mainly morphological analyses. Firstly the hemipenis is often thin-walled with the stem inserting dorsal to the basal parts of the lobes, the sulcus often divides before the bifurcation of the organ and its outer lips in the lobes are frequently flap-like and cartilaginous (Arnold 1986). The hemipenis of *Pseuderemias*, which is also found in northeastern Africa, is similar. Secondly, at least some *Heliobolus*, *Philochortus* and *Pseuderemias* have a distinctive way of digging burrows, in which only the forelimbs are used (S. Baha el Din & E. N. Arnold unpublished data). Finally, *Pseuderemias* and *Heliobolus* share additional morphological features (Arnold 1989a). These characters suggest relationships in Nucras and the Northeast African group as a whole are:
Nucras (*Latastia* (*Philochortus* (*Heliobolus*, *Pseuderemias*))).

DISCUSSION

History of Lacertidae

The history of lacertid lizards has been discussed elsewhere (Arnold 1989a, 2004; Carranza *et al*. 2004). The Lacertidae are probably an essentially west Palaearctic group that was originally confined to Europe and perhaps adjoining areas to the southwest. The family has a long fossil history in Europe extending back at least to the Lower Eocene, about 50 My ago. Amber-preserved material of *Succinilacerta* from the mid-Eocene already show the distinctive head and body scaling found in modern lacertids (Borsuk-Bialynicka *et al*. 1999; Böhme & Weitschat 1998, 2002). Parsimony suggests that two of the three extant main groups of lacertids are European in origin, namely the Gallotiinae and the Lacertini (Fig. 26). A molecular clock based on mitochondrial DNA sequences (see Fig. 2 and Appendix I) indicates that separation of the Gallotiinae and Lacertinae perhaps occurred around 20 My ago, in the early Miocene, although albumin immunology suggests it was earlier, about 30–35 My ago in the later Oligocene (Mayer & Benyr 1994). Phylogeny indicates that the Eremiadini separated from the Lacertini at a later date. As already noted, there are few or no features of the three main groups of lacertids that are likely to be usually preserved in fossils, so these are unlikely to help date separations.

If Europe is the source area for modern lacertids, there must have been several invasions of other regions. If the Gallotiinae are European in origin, the age of the deepest dichotomies within *Gallotia* suggest its ancestor invaded the Canary Islands from there over 12 My ago (Fig. 2). This movement must have been wholly or partly transmarine. It could have occurred via northwest Africa but there is no direct evidence for this. Given the pattern of oceanic currents in the Atlantic, invasion may possibly have been direct from western Europe. Northwest Africa was invaded by members of the *Psammodromus hispanicus* group, to produce *P. blanci* and *P. microdactylus*. A molecular clock (Carranza *et al*. 2006) suggests this movement may also have been transmarine, as it appears to have occurred long before the contact of Europe and Northwest Africa at the Strait of Gibraltar in the Messinian, 5.6 My ago. *Psammodromus algirus* also invaded Northwest Africa across water, but at a much later date, perhaps around 2 My ago (Carranza *et al*. 2006). A further likely spread from the European region into Africa was of the Eremiadini, which is considered in the next section.

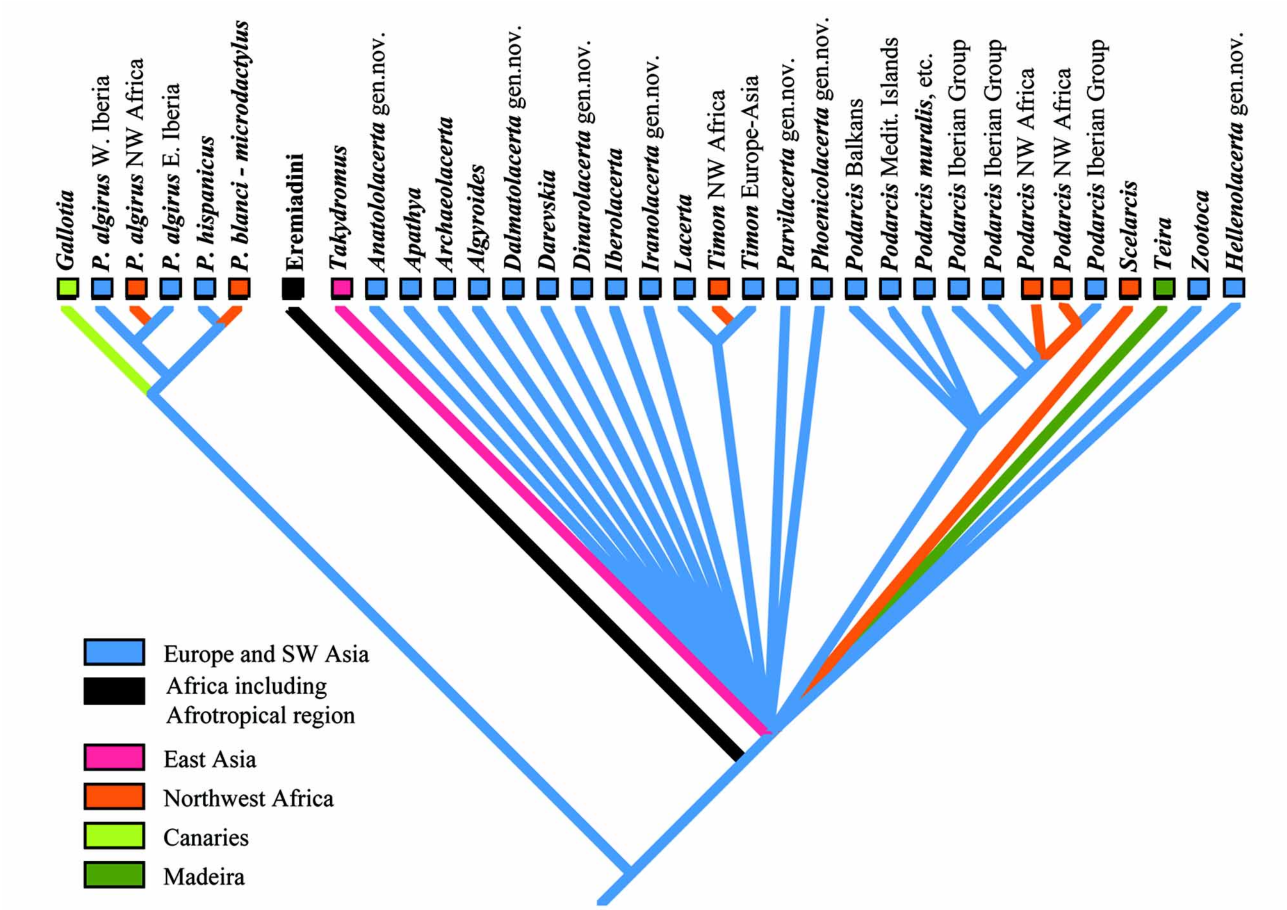

FIGURE 26.—Area cladogram for the Lacertidae. Parsimony analysis using the MacClade program (Maddison & Maddison 1998) indicates an origin for the family in Europe with a minimum of nine movements to other areas (1 to Tropical Africa, 1 to East Asia, 5-6 to Northwest Africa, 1 to the Canaries and 1 to the archipelago of Madeira and Selvages).

History of Eremiadini

Separation of the Eremiadini from the Lacertini may have been around 16 My ago in the mid-Miocene (Fig. 2). This could have been associated with movement into Africa, as invasion of this continent from Europe became easier in the middle of this period 15–19 My ago, when the African-Arabian plate made more or less permanent contact with western Eurasia, specifically between the Arabia and Turkey (Adams *et al*. 1983; Rögl 1999). This event was followed by considerable faunal exchange, including reptiles (Roček 1984). The northwest African distribution of *Atlantolacerta*, which probably occupies a basal position in the Eremiadini could be taken as indicating the tribe entered the continent by this route, perhaps by island-hopping across the Betic islands lying between Africa and southwest Europe at the time. However, phylogenetic topology provides no evidence that this route was actually taken.

As noted, *Atlantolacerta* lacks the distinctive derived features of nearly all other Eremiadini, namely a derived condition of the ulnar nerve and the presence of a fully developed armature in the hemipenis which has folded lobes when retracted. This suggests these features evolved after the Eremiadini arrived in Africa. Once established in the continent, mesic forms appear to have spread widely, reaching east Arabia (*Omanosaura*), the Equatorial region (*Poromera* and the ancestor of the species of *Adolfus*, *Holaspis* and *Gastropholis*), southern Africa *(Australolacerta* and *Tropidosaura*). As already discussed, there may have been three transitions from mesic to xeric habitats, or even more, with substantial parallelism in the evolution of functionally associated features. One set of xeric forms, namely *Eremias*, *Acanthodactylus*, *Ophisops* and *Mesalina,* also extends into southwest and central Asia.

History of Lacertini

The molecular clock used here indicates that the Lacertini split into most of its component living genera 12–16 My ago, so they underwent quite rapid speciation at this time. Most genera in the Lacertini have largely allopatric and often disjunct ranges, which may mean that initial spread of the group was followed or accompanied by multiple vicariance (see Fig. 25). A few units do not fit this pattern and have large ranges that overlap with several other taxa, although these too may have began as vicariant isolates with small ranges and then spread. They are *Lacerta*-*Timon* (Fig. 25d), *Algyroides* (Fig. 25e) and *Podarcis* (Fig. 25f).

The substantial differences in mitochondrial DNA sequences between *Lacerta* and the two parts of *Timon* suggest this unit underwent early divergence and spread. The species of *Lacerta*-*Timon* have far larger body-sizes than other Lacertini and adults often eat larger prey, so contact with these smaller forms may not have affected these deleteriously, permitting long-term coexistence without strong competition. Certainly, fossils indicate large-bodied lacertids have a long history in Europe (Estes 1983; Bailón 2004), although it is rarely certain that they belong to the *Lacerta-Timon* clade. *Algyroides* also has a relatively wide range, and a distinctive niche being often found in cool wooded situations but, unlike *Lacerta*-*Timon*, its range is now disjunct and the total area it covers is small.

Podarcis, like *Lacerta*-*Timon* has a very large subcontinuous range, but in contrast to these lizards it appears to impinge on other small-bodied taxa with which it is in contact, there often being evidence of competition. *Podarcis* may have been responsible for restricting other small-bodied lacertid genera, including *Algyroides, Iberolacerta*, *Archaeolacerta*, *Dinarolacerta*, *Dalmatolacerta* and *Hellenolacerta* (Arnold 1981, 2004; Carranza *et al*. 2004). Although *Podarcis* is an old group that diverged around 9 My ago and spread widely in Europe and mesic northwest Africa, it has not penetrated far to the east. Here it reaches only northwest Asiatic Turkey and has an essentially parapatric distribution with *Anatololacerta* among the islands of the Aegean Sea.

Lacertini have made several incursions outside their original mainly European distribution. The ancestor of *Takydromus* reached East Asia and diversified there (Fig. 25c), the cytochrome b and 12S rRNA sequences of mitochondrial DNA used here suggesting that divergence began at least 10 My ago (see Fig. 2). Ota *et al.* (2002) also showed that genetic divergence within *Takydromus* is very high, with values up to 20% for combined 12SrRNA and 16SrRNA gene fragments. There is no certain fossil record of this genus, but the poorly known *Miolacerta* Roček, 1984 of the mid-Miocene of central Europe shows some resemblance (Arnold 1997). Spread from Europe to the Far East has also occurred in the ancestor of the salamandrid genus *Tylototriton* (Titus & Larson 1995; Carranza & Arnold 2004; Carranza & Wade 2004), and in that of *Cynops*, *Pachytriton* and *Paramesotriton* (Weisrock *et al.* 2005). Molecular divergence within these groups also suggests invasion of the Far East was a long time ago.

Scelarcis may possibly have reached Northwest Africa soon after the main divergence of the Lacertini. *Teira* made the 600–800 km transmarine journey to the Madeira archipelago as much as 12 My ago, arriving first on the oldest island, Porto Santo, moving on to invade Madeira itself and then the neighbouring Desertas and Selvages islands (Jesus *et al.* 2005). Assuming it was originally in southwest Europe, *Timon* reached Northwest Africa around the time of the Messinian salinity crisis or somewhat before, perhaps around 8 My ago (Fig. 2; Paulo 2001). The *Podarcis hispanica* group might have invaded this region twice: once about the time of the salinity crisis and again more recently (Harris *et al.* 2002) or, according to Pinho *et al.* (2006), just once during the salinity crisis, followed by a recent back-colonization into south Iberia. Finally, *Lacerta agilis* appears to have spread eastwards into Central Asia (Fig. 25a), and *Zootoca* across the whole of Eurasia to the Pacific coast and Sakhalin and Hokkaido islands (Fig. 25b), perhaps in the Pleistocene (Surget-Groba *et al*. 2001). In the Mediterranean, some islands may have been invaded by *Podarcis* during the Messinian salinity crisis, the isolation caused by subsequent rise in sea level being followed by divergence. For example in the Balearics, *P. lilfordi* and *P. pityusensis* split at this time (see Fig. 2) and in the Aegean, the differentiation of *P. milensis* and *P. gaigae* from each other and from the mainland *P. taurica* may have been similar (Fig. 2; Poulakakis *et al*. 2005).

Archaeolacertas

A range of Lacertini exhibit a distinctive syndrome of morphological features, including flattened heads and bodies, fenestrated supraocular osteoderms in adults, often unkeeled dorsal body scales and little posterior overlap of the ventral ones, slender and fragile tails and, frequently, dorsal patterns in which longitudinal striping is reduced or absent. These features are developed in, among other groups, *Archaeolacerta*, *Apathya*, some *Dalmatolacerta*, *Darevskia*, *Dinarolacerta*, *Hellenolacerta*, *Iberolacerta*, *Iranolacerta zagrosica*, some *Phoenicolacerta*, some members of the *Podarcis hispanica* group, and *Scelarcis*. Méhely (1909) was among the first to comment on these features and called lacertids bearing them archaeolacertae, a term often modified to archaeolacertas in English and also formalised as *Archaeolacerta* Mertens, 1921. This was initially used as a subgenus of *Lacerta* sensu lato, but later sometimes as a genus with varying content.

In fact, there is no real evidence that archaeolacertas form a clade. Their distinctive features appear to be very labile, all sorts of morphological intermediates occurring between archaeolacertas and other Lacertini. In fact the syndrome of features found in archaeolacertas appears to be an ecomorph functionally related to the problems of living on rock exposures and using the narrow crevices in these for refuge and other purposes (Arnold 1973, 1989a, 1998b, 2004). In agreement with this, molecular phylogenies based on DNA sequence do not support an *Archaolacerta* clade (Carranza *et al.* 2004). They also confirm that there are several instances in which archaeolacertas and Lacertini lacking their characteristic syndrome of morphological traits are closely related, indicating that shift between these two states can take place easily. Cases include *Darevskia*, *Iranolacerta*, *Phoenicolacerta*, *Podarcis*, and *Scelarcis* plus *Teira*.

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APPENDIX I
Material and methods for analysis of molecular and morphological data

Samples, DNA extraction and amplification

Data set 1

To assess the high level phylogenetic relationships within the family Lacertidae, a data set of 24 specimens was assembled with sequences from Genbank (U88603, U88611, AF206528-616; Fu 2000) and analysed. The data set consisted of two individuals of the subfamily Gallotiinae (genus *Psammodromus* and *Gallotia*), 13 individuals of the tribe Eremiadini (corresponding to 12 different genera, including *Atlantolacerta andreanskyi*), 9 individuals of the tribe Lacertini (corresponding to 9 of the genera recognised in this paper)

Data set 2

Data set 2 was assembled to assess the high level phylogenetic relationships within the tribe Lacertini and included 27 specimens. All sequences were downloaded from Genbank (AF80268 – AF80388; Harris 1998) and analysed. The data set consisted of two individuals of the subfamily Gallotiinae (genus *Psammodromus* and *Gallotia*), two individuals of the tribe Eremiadini (*Omanosaura jayakari* and *Omanosaura cyanura*) and 23 individuals of the tribe Lacertini (corresponding to 18 of the genera recognised in this paper).

Data set 3

To assess the phylogenetic relationships within the Lacertini a total of 107 representatives of the Lacertidae were included in the analyses. Of these, 93 individuals belong to the Lacertini itself (56 species representing all the main groups), one to the Eremiadini (*Atlantolacerta* gen. nov.) and 12 individuals to the subfamily Gallotiinae. An amphisbaenian, *Blanus cinereus* was used as outgroup as likely to represent the sister taxon of the Lacertidae (Towsend *et al*. 2004; Vidal & Hedges 2004). Material used in the analyses and Genbank accession numbers are shown in APPENDIX II. DNA extraction, PCR amplification of the cytochrome b and the ribosomal 12S rRNA mitochondrial genes, and sequencing of the PCR fragments was performed using the same procedures, primers and conditions described by Carranza *et al*. (2000, 2004).

Phylogenetic analyses of the DNA data

Data set 1

Molecular data set 1 included 4522 base pairs (1026 bp of cytochrome b, 1048 bp of cytochrome oxidase I and 2448 bp of the ribosomal genes 12S rRNA+16SrRNA). Of these, 2430 positions were variable and 1972 parsimony-informative.

Data set 2

Molecular data set 2 included 1014 base pairs (293 bp of cytochrome b, 318 bp of 12S rRNA and 403 bp of 16S rRNA) of these, 473 positions were variable and 376 parsimony-informative.

Data set 3

The molecular data set included 620 base pairs (291 bp of the cytochrome b and 329 bp of the 12S rRNA) of mitochondrial DNA sequences. Of these, 324 positions were variable and 269 parsimony-informative.

All three data sets were aligned using ClustalX (Thompson *et al.* 1997) with default parameters (gap opening = 10; gap extension = 0.2). All the cytochrome b and cytochrome oxidase I sequences had the same length and therefore no gaps were postulated for these genes, although some were used to resolve length differences in the 12S rRNA and 16S rRNA gene fragment. All positions from both data sets were included in the analyses. Three methods of phylogenetic analysis were employed and their results compared. These were: Maximum likelihood (ML), Maximum parsimony (MP) and Bayesian analysis. Modeltest v. 3.06 (Posada & Crandall 1998) was used to select the most appropriate model of sequence evolution for the ML and Bayesian analyses under the Akaike Information Criterion. This was for all the independent gene partitions of all three data sets and for all three combined analyses the General Time Reversible model (GTR), taking into account the proportion of invariable sites (I) and the shape parameter alpha of the gamma distribution (G). The ML analysis was performed using PHYML (Guindon & Gascuel 2003) with model parameters fitted to the data by likelihood maximization. Maximum parsimony analyses included heuristic searches with TBR branch swapping and 1000 random addition replicates. Transitions and transversions had the same weight and gaps were treated as a fifth state.

Reliability of the ML and MP trees was assessed by bootstrap analysis (Felsenstein 1985), performed with 1000 replications. Bayesian analyses were performed with MrBayes v. 3.1.2 (Huelsenbeck & Ronquist 2001). In all the analyses each partition had its own independent model of evolution and model parameters. Four incrementally heated Markov chains with default heating values were used. All analyses started with randomly generated trees and ran for 1.5 x 10^6 generations, with sampling occurring at intervals of 100 generations producing 15,000 trees. After the analyses, the log-likelihood values of all trees saved from both runs were plotted against the generation time. After verifying that stationarity had been reached both in terms of likelihood scores and parameter estimation, the first 1,500 trees for all three data sets were discarded in all two runs, and independent majority-rule consensus trees were generated from the remaining (post burn-in) trees. The frequency of any particular clade of the consensus tree represents the posterior probability of that node (Huelsenbeck & Ronquist 2001); only values 95% and above were considered to indicate that nodes were significantly supported (Wilcox *et al.* 2002).

Phylogenetic analyses of the morphological data

A data set of 64 morphological and other non-molecular characters (equivalent to 83 binary ones) was assembled for 21 taxa of Lacertini (see APPENDIX III and IV). These were mainly the genera recognised in this paper, but for *Iranolacerta* and *Timon*, which include species disparate in morphology or DNA sequence, more than one unit was included. Phylogenetic analysis included heuristic searches with TBR branch swapping and 1000 random addition replicates. Multiple states of characters were interpreted as polymorphic. The analyses were performed with a backbone constrained tree in which Gallotiinae separated from all other Lacertidae first, and Eremiini was sister to the Lacertini. This forced topology was based on the available molecular data derived from both mitochondrial and nuclear genes (reanalysis of data of Fu 2000; and results of Mayer & Pavličev 2005).

Estimating divergence times

Divergence times were estimated for the different lineages recovered by the analysis of Data set 3 using the computer program r8sb v1.6.4 (Sanderson 1997, 2002). This program implements several methods for estimating absolute rates of molecular evolution, ranging from standard maximum likelihood ones to more experimental semiparametric and nonparametric methods, which relax the stringency of the clock assumptions using smoothing methods. One of the advantages of this program is that, through a cross-validation test, it allows the user to explore the fidelity with which any of these methods explain the branch length variation (Sanderson 2002). This procedure removes each terminal branch in turn, estimates the remaining parameters of the model without that branch, predicts the anticipated number of substitutions on the pruned branch and reports the performance of these predictions as a cross-validation score, which allows the user to select the method that best explains the branch length variation (Sanderson 2002). To estimate absolute rates, we used a single calibration point based on the assumption that divergence between *Gallotia caesaris caesaris* (Lehrs, 1914) (endemic to the island of El Hierro) and *Gallotia caesaris gomerae* (Boettger & Müller, 1914) (endemic to the island of La Gomera) began approximately 1 mya, soon after El Hierro was formed, and rapid colonisation from La Gomera by the ancestor of *G. c. gomerae* occurred. These taxa are suitable for use in calibration as they are sister species and each is monophyletic with low intraspecific variability (Maca-Meyer *et al.* 2003). Apart from the assumption that El Hierro was colonised rapidly, factors that could affect clock calibrations include stochastic variation at low levels of sequence divergence and the possibility of extinct or unsampled lineages (Emerson *et al.* 2001; Emerson 2002), although there is no evidence of any of these factors acting in *Gallotia* (Gonzalez *et al.* 1997; Barahona *et al.* 2000; Maca-Meyer *et al.* 2003).

APPENDIX II

Table 1.—Details of material and new sequences used in Fig. 2 of the present study. Eleven specimens were sequenced specifically; all the rest have been downloaded from GenBank and are mainly from investigations by Harris *et al*. (1998); Carranza *et al*. (2004); Arribas and Carranza (2004).

TAXA	**LOCALITY**	**ACCESSION NUMBERS Cyt *b* / 12SrRNA**	**Codes**
SEQUENCES PRODUCED FOR THIS STUDY			
Darevskia derjugini	Adsharia (Georgia)	EF422420 / EF422431	E2303.5
Darevskia praticola	Caucasus	EF422419 / EF422430	E2303.11
Phoenicolacerta laevis-2	Dibbin forest (Jordan)	EF422429 / EF422440	E2303.6
Parvilacerta parva	5Km E. of Corum (Turkey)	EF422423 / EF422434	E2303.10
Timon princeps	7 Km from Tuveh (Iran)	EF422422 / EF422433	E2303.12
Lacerta bilineata	St. Amand-Montront (France)	EF422426 / EF422437	E2303.3
Lacerta media	Golbasi (200 Km northest of Adana)	EF422424 / EF422435	E2303.15
Lacerta bilineata	Cervera de Pisuerga (Spain)	EF422427 / EF422438	E2303.18
Lacerta schreiberi	Gredos (Spain)	EF422425 / EF422436	E2303.14
Iranolacerta zagrosica	Zagros Mountains (Iran)	EF422421 / EF422432	E11036.1
Podarcis taurica-2	(Russia)	EF422428 / EF422439	E2303.25
SEQUENCES DOWNLOADED FROM GENBANK			
Psammodromus algirus-1	S. of Tizi Chika, High Atlas (Morocco)	AF080309 / AF080308	Harris *et al*. (1998)
Psammodromus algirus-2	(Spain)	AY151835 / AY151914	Palgi1
Gallotia stehlini	Gran Canaria (Canary Islands)	AY151838 / AY151917	Gst2
Gallotia atlantica atlantica	Lanzarote (Canary Islands)	AY151836 / AY151915	Gatat21
Gallotia atlantica mahoratae	Lanzarote (Canary Islands)	AY151837 / AY151916	Gatmaj1
Gallotia intermedia	Tenerife (Canary Islands)	AY151844 / AY151923	Gint1
Gallotia simonyi machadoi	El Hierro (Canary Islands)	AF101219 / AY151924	Gsih16
Gallotia caesaris gomerae	La Gomera (Canary Islands)	AY151842 / AY151921	GagaG1
Gallotia caesaris caesaris	El Hierro (Canary Islands)	AY151843 / AY151922	GagaH1
Gallotia galloti palmae	La Palma (Canary Islands)	AY151841 / AY151920	GagaP2
Gallotia galloti galloti	S. Tenerife (Canary Islands)	AY151840 / AY151919	Gagat2
Gallotia galloti eisentrauti	N. Tenerife (Canary Islands)	AY151839 / AY151918	Gagat1
Iberolacerta m. cantabrica-10	Puerto de Vegarada, León (Spain)	AY151861 / AY151941	E41015
Iberolacerta m. monticola –1	Serra da Estrela (Portugal)	AY151870 / AY151950	E140618
Iberolacerta galani-3	Laguna de los Peces, Sanabria (Spain)	AY151863 / AY151943	E41017
Iberolacerta bonnali-3	Ordesa, Huesca (Spain)	AY151890 / AY151970	E210611
Iberolacerta aurelioi-1	Mont-Roig, Lleida (Spain)	AY151883 / AY151963	E406110
Iberolacerta aranica-1	Coll de Barrados, Valle de Aran (Spain)	AY151879 / AY151959	E40616
Iberolacerta cyreni ssp-4	Sierra de Bejar (Spain)	AY151851 / AY151931	E41024
Iberolacerta cyreni castiliana-11	Sierra de Gredos (Spain)	AY151854 / AY151934	E140617
Iberolacerta cyreni cyreni-8	Navacerrada, Segovia (Spain)	AY151846 / AY151926	E140613
Iberolacerta horvathi	Northwest Croatia	AY256648 / AY256653	E230921
Iberolacerta martinezricai-1	El Maillo, Peña de Francia, (Spain)	AY151895 / AY151975	E2106123
Iberolacerta martinezricai-3	Sanctuary Peña de Francia, (Spain)	AY151897 / AY151977	E410.28
Iranolacerta brandtii	Kuh Rang (Iran)	AF080320 / AF080319	Harris *et al*. (1998)
Anatololacerta danfordi	Western Anatolia (Turkey)	AF080323 / AF080322	Harris *et al*. (1998)
Parvilacerta fraasii	Sannin Mountains (Lebanon)	AF080317 / AF080316	Harris *et al*. (1998)
Takydromus sexlineatus	Sapa (Vietnam)	AF206533 / AF206589	Fu (2000)
Takydromus septentrionalis	(China)	AY217817 / AY218021	Whiting et al.(2003)
Takydromus septentrionalis	Zhoushan Island (China)	AF112290 / AF080337	Harris *et al*. (1998)
Takydromus smaradignus	Okinawa (Japan)	AF080269 / AF080268	Harris *et al*. (1998)
Darevskia valentini	Adis Mountains (Armenia)	AF206173 / AF206597	Harris *et al*. (1998)
Darevskia brauneri	Western Caucasus (Russia)	AF080282 / AF080281	Harris *et al*. (1998)
Darevskia chlorogaster	Near Tangerud (Azerbaijan)	AF080285 / AF080284	Harris *et al*. (1998)
Dinarolacerta mosorensis-1	Prokletije Mt. (Montenegro)	AY151902 / AY151982	E2106111
Dinarolacerta mosorensis-2	Prokletije Mt. (Montenegro)	AY151903 / AY151983	E2106112
Dinarolacerta mosorensis-3	Mount Biokovo (Croatia)	AY151904 / AY151980	E210617
Dinarolacerta mosorensis-4	Lovcen Mt. (Montenegro)	AY151905 / AY151985	E2106120
Dinarolacerta mosorensis-5	Prekornika Mt. (Montenegro)	AY151901 / AY151981	E210619
Dinarolacerta mosorensis-6	Lovcen Mt. (Montenegro)	AY151900 / AY151984	E2106117
Phoenicolacerta laevis-1	Mount Scopus, Jerusalem (Israel)	AF080332 / AF080331	Harris *et al*. (1998)

Phoenicolacerta kulzeri		AF112295 / AF112294	Harris *et al*. (1998)
Zootoca vivipara-1	Andorra	AY151913 / AY151993	E21061-30
Zootoca vivipara-2	Surrey (UK)	AF080335 / AF080334	Harris *et al*. (1998)
Archaeolacerta bedriagae -1	Foret d'Ospedale (Corsica)	AF080326 / AF080325	Harris *et al*. (1998)
Archaeolacerta bedriagae -2	Corsica (France)	AY256649 / AY256654	E911021
Archaeolacerta bedriagae -3	Corsica (France)	AY256650 / AY256655	E911022
Dalmatolacerta oxycephala -1	Bosnia-Herzegovina	AY256651 / AY256656	E230922
Dalmatolacerta oxycephala -2	Bosnia-Herzegovina	AY256652 / AY256657	E230923
Hellenolacerta graeca	Feneus Mati (Greece)	AF080272 / AF080271	Harris *et al*. (1998)
Apathya cappadocica	Eastern Turkey (Turkey)	AF080329 / AF080328	Harris *et al*. (1998)
Atlantolacerta andreanskyi	Oukaimeden, High Atlas (Morocco)	AF206537 / AF206603	Harris *et al*. (1998)
Timon tangitanus	Ouarzazate (Morocco)	AF080294 / AF080293	Harris *et al*. (1998)
Timon lepidus	(Spain)	AY151899 / AY151979	Llepida
Timon lepidus	Badajoz (Spain)	Z48049 / Z48050	Gonzalez *et al*. (1996)
Lacerta agilis	Roermond (Netherlands)	AF080299 / AF080298	Harris *et al*. (1998)
Lacerta media	Arailer Mountains (Armenia)	U88603 / AF206590	Fu *et al*. (1997)
Lacerta viridis	(Hungary)	AF373034 / AF179962	
Algyroides marchi	Sierra de Cazorla (Spain)	AF080307 / AF080306	Harris *et al*. (1998)
Teira dugesii	San Miguel, Azores (Portugal)	AF080314 / AF080313	Harris *et al*. (1998)
Scelarcis perspicillata-2	Oukaimeden, High Atlas (Morocco)	AF080304 / AF080303	Harris *et al*. (1998)
Scelarcis perspicillata-1	Taza (Morocco)	AY151898 / AY151978	E16081.12
Podarcis peloponnesiaca	Peloponnese (Greece)	AF133452 / AF133451	Harris *et al*. (1998)
Podarcis milensis	Milos Island (Greece)	AF133450 / AF133449	Harris *et al*. (1998)
Podarcis gaigeae	Skyros Island (Greece)	AF133445 / AF133444	Harris *et al*. (1998)
Podarcis taurica-1	(Russia)	AF080280 / AF080279	Harris *et al*. (1998)
Podarcis filfolensis	St. Pauls Bay (Malta)	AF133443 / AF133442	Harris *et al*. (1998)
Podarcis tiliguerta	Sardinia (Italy)	AF133457 / AF133456	Harris *et al*. (1998)
Podarcis lilfordi	Balearic Islands (Spain)	AF052639 / AF133447	Harris *et al*. (1998)
Podarcis pityusensis	Balearic Islands (Spain)	AF052640 / AF133453	Harris *et al*. (1998)
Podarcis sicula campestris		AF133455 / AF133454	Harris *et al*. (1998)
Podarcis muralis-4	Navacerrada, Madrid (Spain)	AY151910 / AY151990	E2106126
Podarcis muralis-5	Navacerrada, Madrid (Spain)	AY151911 / AY151991	E2106127
Podarcis muralis-1	Andorra	AY151908 / AY151988	E2106124
Podarcis muralis-2	Andorra	AY151909 / AY151989	E2106125
Podarcis muralis-3	Somiedo, Asturias (Spain)	AY151912 / AY151992	E2106128
Podarcis muralis-8	Benasque (Spain)	AF206572 / AF206600	Fu (2000)
Podarcis muralis-7	Near Cannes (France)	AF080278 / AF080277	Harris *et al*. (1998)
Podarcis vaucheri-1	Ain Draham (Tunisia)	AY134700 / AY134735	E30057
Podarcis hispanica-11	Granada (Spain)	AF469428 / AF469427	Pod12
Podarcis vaucheri-4	Mairena del Aljarace (Spain)	AY134684 / AY134719	E16084
Podarcis vaucheri-11	N. of Oukaimeden (Morocco)	AY134683 / AY134718	E16081
Podarcis vaucheri-12	15Km S.W. of Zinat (Morocco)	AY134688 / AY134723	E29053
Podarcis atrata-1	Columbretes Islands (Spain)	AF052636 / AF133439	Harris *et al*. (1998)
Podarcis hispanica-1	Medinaceli (Spain)	AF469436 / AF469435	Med1
Podarcis hispanica-2	Andorra	AY134703 / AY134738	E21061-21
Podarcis hispanica-3	Barcelona (Spain)	AF469432 / AF469431	Bar1
Podarcis hispanica-7	Montesinho (Portugal)	AF469449 / AF469448	Mon3
Podarcis hispanica-8	Sierra de Gredos (Spain)	AY134704 / AY134739	E21061-22
Podarcis hispanica-9	Pena de Francia (Spain)	AY151906 / AY151986	E41025
Podarcis hispanica-10	Pena de Francia (Spain)	AY151907 / AY151987	E41027
Podarcis hispanica-4	Leiria (Portugal)	AF469458 / AF469457	Pod13
Podarcis hispanica-5	Portalegra (Portugal)	AF372086 / AF469456	Pod15
Podarcis hispanica-6	Madrid (Spain)	AF469460 / AF469459	MadrB
Podarcis bocagei-1	Vairao (Portugal)	AF372087 / AF469421	Pbb5
Podarcis carbonelli-1	Estrela (Portugal)	AF372079 / AF469418	Pcc1

APPENDIX III

Morphological and other non-molecular characters used in the phylogenetic analysis shown in Fig. 3.

Size and shape

1.—Usual adult body size, from snout to vent. Up to 55mm (0); 50-90mm (1); 100-210mm (2).

2.—Head and body shape. Not markedly depressed (0); markedly depressed (1).

Skull

3.—Premaxillary teeth in adults. Seven (0); seven to nine (1); nine to eleven (2).

4.—Pterygoid teeth. Usually absent (0); usually present (1).

5.—Nasal process of premaxilla. Slender (0); often broad (1).

6.—Septomaxilla. Simply convex above with at most slight anterior and posterior projections (0); with distinct and widely separated anterior and posterior projections (1).

7.—Slight depression on mid-line of snout. No (0); yes (1).

8.—Anterior descending processes of frontal bone. Present and well developed (0); reduced or absent (1).

9.—Postorbital and postfrontal bones. Separate at hatching (0); fused throughout life (1).

10.—Maxillary-jugal suture. Not markedly stepped (0); often markedly stepped (1).

11.—Supraocular osteoderms. More or less complete in adults (0); markedly fenestrated (1).

12.—Ossification of temporal scales in adults. Little or none (0); extensive (1).

Post-cranial skeleton

13.—Usual number of presacral vertebrae in males. 25 or fewer (0); 26 (1); 27 or more (2).

14.—Number of posterior presacral vertebrae with short ribs. Often five or fewer (0); often six (1); often seven or more (2).

15.—Medial loop of clavicle. Always intact (0); intact or interrupted (1); always interrupted (2).

16.—Lateral arms of interclavicle. Directed laterally or obliquely forwards (0); directed obliquely backwards (1).

17.—Sternal fontanelle. Oval (0); slightly or markedly heart-shaped (1).

18.—Inscriptional ribs. Often present (0); often absent (1).

19.—Tail vertebrae. A-pattern only (0); A-and B-patterns (1); BC-pattern (2); C-pattern (3).

Scaling on head

20.—Contact between rostral and frontonasal scales. Not usual (0); usual (1).

21.—Outer edge of parietal scale. Not reaching lateral border of parietal table (0); reaching lateral border of parietal table only posteriorly (1); reaching lateral border of parietal table both posteriorly and anteriorly (2).

22.—Occipital scale. Normal (0); broad, as wide as posterior border of frontal scale in some adults (1).

23.—Number of postnasal scales. Usually two (0); usually one (1)

24.—Contact between supranasal scale and anterior loreal scale above single postnasal scale. Not usual (0); usual (1).

25.—Nostril separated from the first upper labial scale by contact between the postnasal and supranasal scales below it. Not usually (0); usually (1).

26.—Usual number of upper labial scales in front of sublabial scale. Four (0); five (1)

27.—Lower eyelid. No transparent window (0); with a transparent window of one or more scales (1).

28.—Enlarged masseteric scale in temporal region. Absent (0); often or always present (1).

Scaling on body and tail

29.—Dorsal scales on body larger than those on upper surface of tail. No (0); yes (1).

30.—Posterior edge of collar. More or less smooth (0); clearly serrated (1).

31.—Number of longitudinal rows of ventral scales. Usually six (0); usually eight (1); ten or more (2).

32.—Shape of ventral scales. Rectangular without little posterior overlap (0); with slightly sloping slides and overlapping posteriorly (1); with strongly sloping sides and strongly overlapping posteriorly (2).

33.—Anterior semicircles of enlarged scales around preanal scale. Nil to one (0); sometimes two (1); two to three (2).

34.—Scales bordering ventral mid-line of tail base. Narrow, not much wider than adjoining scales (0); broad, wider than adjoining scales (1).

Colouring

35.—Dorsal sexual dimorphism. None or weak (0); moderate or strong (1).
36.—Narrow light stripes often present in dorsal pattern. No (0); yes (1).
37.—Dorsum with broad light dorsolateral stripes. No (0); yes (1).
38.—Dorsal pattern of longitudinal streaks or rows of markings in young. Usual (0); no, young often plain, spotted or reticulate from hatching (1).
39.—'Concolor' morph with few or no dark dorsal markings. Absent (0); present (1).
40.—Blue ocelli on shoulder region. No (0); yes (1).
41.—Numerous ocelli on flanks. No (0); yes, usually pale (1); yes, often blue (2).
42.—Tail brightly coloured, blue to green in young. No (0); yes (1).
43.—Bright belly colour often present that contrasts with dorsum. No (0); yes (1).
44.—Blue spots present on outermost ventral scales. No (0); yes (1)

Miscellaneous soft-part characters

45.—Nasal vestibule. Short (0); some posterior elongation (1); more posterior elongation so vestibule overhangs posteriorly (2).
46.—Lateral septum on bodenaponeurosis. Present (0); absent (1).
47.—Thoracic fascia. Absent (0); present (1).
48.—Anterior extent of kidney. Less than half length of kidney in front of sacrum (0); more than half in front of sacrum and anterior section usually expanded (1).
49.—Insertion of retractor lateralis anterior muscle in front of vent. Near mid-line (0); more laterally (1).
50.—Size of retractor lateralis anterior muscle in front of vent. Narrow, with no fibres extending to region of vent lip (0); broad, with some fibres extending posteriorly to region of vent lip (1).
51.—Some fibres of retractor lateralis anterior muscle reaching base of hemipenis. No (0); yes (1).
52.—Female genital sinus. Bilobed (0); unlobed (1).
53.—Exit of oviducts into genital sinus. Ventrally, some way from tip(s) of sinus (0); at or near tips (1).

Hemipenis

54.—Hemipenial armature. Absent (0); traces (1); strongly developed (2).
55.—Cross section of lobes in retracted hemipenis. Simple (0); limited folding (1); complex folding (2).
56.—Distal section of hemipenial lobes longer than proximal section. No (0); yes (1).
57.—Size of outer lips on sulci of hemipenial lobes. Small or very small (0); large (1).
58.—Hemipenial microornamentation on distal lobes. Hook-shaped spines (0); crown-shaped tubercles (1), bicuspid tubercles (2).
59.—Hemipenial microornamentation on sides of lobes made up of long spines. No (0); yes (1).

Chromosomes and reproduction

60. Number of single-armed macrochromosomes (acrocentric). 36 or more (0); reduced to 34 (1), reduced to 26 or fewer (2).
61.—Number of microchromosomes. Two (0); none (1).
62.—Kind of chromosome housing nucleolar organiser. Large macrochromosome (0); medium macrochromosome (1); medium-small macrochromosome (2); small macrochromosome (3); microchromosome (4).
63.—Shape of hatchlings. Relatively small-headed and long-limbed (0);'embryonic' with large heads and short extremities (1).
64.—Embryos markedly or fully developed at oviposition. No (0)

APPENDIX IV

Morphological data set used for the phylogenetic analysis. Numbers in first column refer to the 64 morphological characters listed in Appendix III. Columns A to W give the character states of all 22 taxa included in the phylogenetic analysis. A.—*Algyroides*; B—*Anatololacerta* gen. nov.; C.—*Apathya*; D.—*Archaeolacerta*; E.—*Dalmatolacerta* gen. nov. F.—*Darevskia*; G.—*Dinarolacerta* gen. nov.; H.—*Hellenolacerta* gen. nov.; I.—*Iberolacerta*; J.—*Iranolacerta brandtii* gen. nov.; K.—*Iranolacerta zagrosica* gen. nov.; L.—*Lacerta*; M.—*Parvilacerta* gen. nov.; N.—*Phoenicolacerta* gen. nov.; O.—*Podarcis*; P.—*Scelarcis*; Q.—*Takydromus*; R.—*Teira*; S.—*Timon princeps*; T.—*Timon lepidus;* U.—*Zootoca*; V.—Gallotiinae; W.-Eremiadini. In Eremiadini entries refer mainly to more primitive taxa including *Atlantolacerta, Adolfus, Australolacerta Omanosaura* etc.

Characters with multiple states have been represented with a forward slash between the different states. A question mark (?) indicates this particular feature has not been checked on this taxon.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W
1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	2	2	1	0/1/2	0/1
2	0	0	1	1	1	0/1	1	1	1	0	1	0	0	0	0/1	0	0	0	0	0	0	0	0/1
3	1	0	2	2	0	0	2	2	1	0	0	2	1	1	0	0	0/1/2	2	2	2	0	0/1/2	0/1/2
4	0/1	0	0	0	0	0	0	0	0	1	?	1	1	0/1	0/1	0	0/1	0	1	1	0	0/1	0/1
5	0	0	0	0	0	0	0	0	0/1	0	0	1	0	0	0	0	0/1	0	1	1	1	?	0
6	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0
7	0	0	0	0	0	0	0	0	0	1	0	0/1	1	0	0	0	0	0	0/1	0/1	0	0	0
8	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	1	0	0	0	0/1	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0/1
10	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
11	0/1	0	1	1	1	0/1	1	0	1	0	1	0	0/1	0	0	0	0	0/1	0	0	0	0	0/1
12	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0/1	0
13	0/1	1	1	1	0	2	0/1	2	1	1	1	2	2	1	1/2	1/2	0/1	1	2	2	1	1	0/1/2
14	1	2	2	1/2	1	1	1	1/2	1	1/2	1	1/2	1/2	1	1/2	1	0	1/2	1/2	2	0	1/2	0/1/2
15	1	1	1	2	2	1	1	2	1	1	1	1	0	1	1	2	0	1	1	1	1	0	0/1
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
17	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0/1
18	1	1	1	0	1	0/1	1	1	0/1	1	0	0	1	1	0/1	1	0/1	1	0	0	0/1	0/1	0/1
19	1	3	0	1	1	1	1	1	1	2	1	1	2	1	3	1	0	1	1	1	1	3	0/1
20	0	0	0	0/1	0	0/1	1	0	0/1	0	0	0	0	0	0	0	0/1	0	0	0	0	0	0
21	1	1	0	1/2	1	1	1	1	1	0	0	0	1	0/1	2	2	1/2	2	0	0	2	2	0/2
22	0	0	0	0	0	0	0	0	0	0	0	0/1	0	1	0	0	0	0	1	1	0	0	0
23	0	0	0	1	0	1	0/1	0	1	0	1	0/1	0/1	0	1	0	0/1	0	0	0	1	1	0/1
24	0	0	0	0	0	0	0	0	0/1	0	0	0	0	0	0	0	0/1	0	0	0	0/1	0	0/1
25	0	0	0	0	0	0	0	0	0	0/1	0	0	1	0	0	1	0/1	0	0	0	0/1	0/1	0/1
26	0/1	1	1	0/1	1	0	0/1	1	0	1	1	0	0	1	0	1	0	1	0	0	0	0	0/1
27	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
28	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0	1	1	1	0	0/1
29	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0/1
30	1	0	0	0	0	0/1	0	0	0	0	0	1	1	0	0	0	1	0	1	1	1	0/1	0/1
31	0	0/1	0	0	0	0	0	0	0	1	1/2	0/1	1	0	0	2	0/1	0	2	1/2	0	2	0
32	0/1	0	0	0	0	0/1	0	0	0	0	0	2	1	0	0/1	0	1/2	0	2	2	1	0/1	0
33	1	2	2	0	0	0	0	1	0	0	1	2	2	0	0	0/1	0	1	2	2	2	0/1/2	0/1/2
34	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	1	0/1	0	0	1	0	0	1	0	0	1	0	0	0	0/1	0
36	0	0	0	0	0	0	0	0	0	0	0	1	0/1	0	1	0	0/1	0	0	0	1	0/1	0/1
37	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
38	0	0	0	1	1	0	0	0	0	0	?	0	0	0	0	0/1	0	0	0	0	0	0	0
39	0	0	0	0	1	0	0	0	0/1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
40	0	0	1	0	0	1	0	1	1	1	1	0	1	0	1	0	0	0	0/1	1	0	0/1	0
41	0	0	2	0	0	0	0	2	0	0	1	0/1	2	0	0	0	0	0	2	2	0/1	0/2	0
42	0	0	1	1	1	1	0/1	0/1	1	0	?	0	0	0	0/1	1	0	0	0	0	0/1	0	0/1
43	1	1	0	1	1	1	1	1	1	1	0	0	1	1	1	0	0	1	0	0	1	0/1	0/1

44	0/1	1	0	1	0	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0/1	0/1
45	0	0	0	0	0	0	0	0	0	2	0	0/1	2	0	0/1	0	0	0	1	2	0	2	0
46	0	0	0	0	0	0	0	0	0	0	?	1	0	0	0	0	0	0	1	1	0	0/1	0
47	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0/1	0	0	1	0	0	0/1
48	0	0	1	0	0	0	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	0
49	0	0	0	1	0	0/1	1	0	0	1	?	1	0	1	0	0	0	1	1	1	0	0	1
50	0	1	1	0	0	0	0	0	0	0	?	0	0	0	0	0	1	0	0	0	1	0	0
51	0	0	1	1	1	?	?	1	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	0/1
53	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0/1	0/1
54	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0/2
55	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0/2
56	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	?	1	0/1
57	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	?	0	0/1
58	0/1	1	0	0	1	1	1	0	0/1	1	1	1	2	1	0	0	0	0	0	0	1	0	0
59	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
60	0	?	0	0	0	0	0	0	0/2	0	?	0	2	0	0	0	0	0	1	1	0	0	0
61	0	?	0	0	0	0	0	0	1	0	?	0	0	0	0	0	0	0	0	0	1	0	0
62	1	?	?	0	?	0	2	1	0/1	0	?	1	0/4	2	1	0	0	0	0	0	2	0	0
63	0	0	0	0	0	0	0	0	0	0	?	1	0	0	0	0	0	0	1	1	0	0	0
64	0	0	0	0	0	0	1	0	1	0	?	0	0	0	0	0	0	0	0	0	1	0	0

APPENDIX V

Alphabetical list of species of Lacertini with their proposed generic allocations.

agilis, Lacerta
alpina, Darevskia
amurensis, Takydromus
anatolica, Anatololacerta
aranica, Iberolacerta
armeniaca, Darevskia
atrata, Podarcis
aurelioi, Iberolacerta
bedriagae, Archaeolacerta
bendimahiensis, Darevskia
bilineata, Lacerta
bocagei, Podarcis
bonnali, Iberolacerta
brandtii, Iranolacerta
brauneri, Darevskia
cappadocica, Apathya
carbonelli, Podarcis
caucasica, Darevskia
chlorogaster, Darevskia
clarkorum, Darevskia
cyanisparsa, Phoenicolacerta
cyreni, Iberolacerta
daghestanica, Darevskia
dahli, Darevskia
danfordi, Anatololacerta
defilippi, Darevskia
derjugini, Darevskia
dorsalis, Takydromus
dryada, Darevskia
dugesii, Teira
erhardii, Podarcis
filfolensis, Podarcis
fitzingeri, Algyroides
formosus, Takydromus
fraasii, Parvilacerta
gaigeae, Podarcis
galani, Iberolacerta
graeca, Hellenolacerta
hani, Takydromus
haughtonianus, Takydromus
hispanica, Podarcis
horvathi, Iberolacerta
hsuehshanensis, Takydromus
intermedius, Takydromus
khasiensis, Takydromus
kuehnei, Takydromus
kulzeri, Phoenicolacerta
laevis, Phoenicolacerta
lepidus, Timon
lilfordi, Podarcis
lindholmi, Darevskia
marchi, Algyroides
martinezricai, Iberolacerta
media, Lacerta

melisellensis, Podarcis
milensis, Podarcis
mixta, Darevskia
monticola, Iberolacerta
moreoticus, Algyroides,
mosorensis, Dinarolacerta
muralis, Podarcis
nairensis, Darevskia
nigropunctatus, Algyroides
oertzeni, Anatololacerta
oxycephala, Dalmatolacerta
pamphylica, Lacerta
parva, Parvilacerta
parvula, Darevskia
pater, Timon
peloponnesiaca, Podarcis
perspicillata, Scelarcis
pityusensis, Podarcis
portschinskii, Darevskia
praticola, Darevskia
princeps, Timon
raddei, Darevskia
raffonei, Podarcis
rostombekowi, Darevskia
rudis, Darevskia
sapphirina, Darevskia
sauteri, Takydromus
saxicola, Darevskia
schreiberi, Lacerta
septentrionalis, Takydromus
sexlineatus, Takydromus
sicula, Podarcis
smaragdinus, Takydromus
steineri, Darevskia
stejnegeri, Takydromus
strigata, Lacerta
sylvaticus, Takydromus
tachydromoides, Takydromus
tangitanus, Timon
taurica, Podarcis
tiliguerta, Podarcis
toyamai, Takydromus
trilineata, Lacerta
troodica, Phoenicolacerta
unisexualis, Darevskia
uzzelli, Darevskia
valentini, Darevskia
vaucheri, Podarcis
viridis, Lacerta
vivipara, Zootoca
wagleriana, Podarcis
wolteri, Takydromus
yassujica, Apathya
zagrosica, Iranolacerta