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(Squamata: Lacertidae: Lacertinae),
with descriptions of eight new genera**

E. NICHOLAS ARNOLD, OSCAR ARRIBAS & SALVADOR CARRANZA



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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 Opeel, 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