



Cryptic diversity within the *Anatololacerta* species complex (Squamata: Lacertidae) in the Anatolian Peninsula: Evidence from a multi-locus approach



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ABSTRACT

The rapid development of innovative molecular tools for characterizing biodiversity is leading to an extensive and sometimes unexpected renovation of taxonomic classifications. Particularly, for species having allopatric or parapatric distributions or resulting from recent speciation processes, the absence of clear phenotypic differentiation may hinder the recognition of closely related taxa, while intraspecific polymorphism may be confused with the presence of more than one single species. In the present work, we apply different phylogenetic methods in order to infer relationships within the genus *Anatololacerta*, and to assess the taxonomy of this morphologically diversified group of lizards endemic to western and southern Anatolia and some neighboring Aegean islands. According to morphology, three species have been recognized (*Anatololacerta anatolica*, *A. oertzeni* and *A. danfordi*) as well as several subspecies, but small variation at immunological markers led some authors to join all the populations into one single taxon, *A. danfordi*. By selecting both mitochondrial and nuclear informative markers, we tested the effectiveness of classical “gene tree” (i.e. Bayesian Inference) vs. innovative (i.e. coalescent-based) “species tree” methods in resolving the *Anatololacerta* taxonomic enigma, as a case in point for similar studies on species complexes resulting from non-obvious and cryptic diversification patterns. According to our results, the gene tree method failed in resolving phylogenetic relationships among clades, whereas the multi-locus species tree approach, coupled with species delimitation methods, allowed the identification of four well distinct species. These species probably diversified in different allopatric refugia located in southern and western Anatolia, where isolated populations may have persisted during Pleistocene glacial cycles.

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1. Introduction

The recent emergence of modern molecular techniques for studying biodiversity is revealing that traditional taxonomy and systematics today require an extensive and sometimes unexpected renovation (e.g. Mallet and Willmott, 2003; Wilson, 2003; Wiens, 2007; de Carvalho et al., 2008). One of the most important outcomes of molecular studies is indeed the awareness that morphological approaches to species identification often fail to resolve the specific identity of closely related taxa, which generally look very similar. Particularly, while the study of morphological variation seems to be informative in delimiting boundaries among syntopic species, the distinction of allopatric or parapatric sibling taxa

generally appears to be problematic (e.g. Bruna et al., 1996; Fernandez et al., 2006; Ibáñez et al., 2006). Most cryptic species also result from recent speciation processes, so that morphological or other diagnosable traits have not yet evolved or become evident (Saez and Lozano, 2005; Kaliontzopoulou et al., 2012). Moreover, intraspecific polymorphism, sometimes resulting from random processes or local adaptation of populations, has been historically confused with the existence of distinct species (Darwin, 1859; Mayr, 1963). Finally, in addition to resolving the true phylogenetic relationships among taxa and to shedding light on their taxonomy, ecology, biogeography and evolution, assessing the real extent of species diversity is essential for conservation purposes.

In this framework, and with the use of ever-increasing multi-locus genetic data, coalescent-based methods for species delimitation are being developed and applied to the recognition and delimitation of unknown diversity (Pons et al., 2006; O'Meara, 2010;

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Ence and Carstens, 2011; Yang and Rannala, 2010; Fujita et al., 2012). Indeed, a growing number of studies is revealing that gene tree approaches, such as Maximum Likelihood (ML) and Bayesian Inference (BI), may infer the genealogical pathway of individuals rather than the true evolutionary relationships among species (e.g. Nichols, 2001; Rannala and Yang, 2008). In contrast, multi-locus coalescent methods (i.e. species tree, Edwards, 2009) have been proven to be more effective in delimiting species (Knowles and Carstens, 2007; Carstens and Dewey, 2010), allowing for reliable estimation of species divergence, while taking into account the uncertainties associated with gene tree inference, such as incomplete lineage sorting (ILS, Heled and Drummond, 2010). For this reason, the multi-species coalescent method has now become the default option for phylogenetic and phylogeographic investigations, especially when dealing with non-obvious and cryptic diversification patterns such as those characterizing species complexes.

The lizard family Lacertidae includes about 44 genera and 318 species widely distributed in Eurasia and Africa (Arnold et al., 2007; Uetz, 2014), divided into two subfamilies, Gallotinae and Lacertinae; the latter comprises two main tribes, the Eremiadini and the Lacertini. As a result of the high level of morphological similarity and convergence among different groups, the systematics of Lacertini has been particularly controversial, with most of the taxa being lumped for decades under the paraphyletic genus “*Lacerta*” (see Arnold et al., 2007 for a review). This systematic confusion was resolved with the description of eight new genera of Lacertini using a combination of molecular and morphological data, thus reconciling phylogeny and taxonomy and highlighting the diversity of this group (Arnold et al., 2007). Although molecular data have not been able to resolve the phylogenetic relationships between the different genera of Lacertini (Arnold et al., 2007; Pavlicev and Mayer, 2009; Kapli et al., 2011), DNA sequences have been very useful in resolving the phylogenetic relationships, and

especially in uncovering high levels of cryptic diversity within some genera (e.g. Carranza et al., 2004; Pinho et al., 2007; Ahmadzadeh et al., 2013a,b). However, with the only exception of Ahmadzadeh et al. (2013b), which used a species tree approach, all the phylogenetic analyses of the Lacertini carried out to date have been done with gene trees.

The genus *Anatololacerta* was erected by Arnold et al. (2007) and refers to a small group of lizards endemic to western and southern Anatolia and some neighboring Aegean islands, including Samos, Ikaria, Rhodes and a few other small islets (Fig. 1). Although this genus originated approximately 12 Ma (Arnold et al., 2007), phylogenetic relationships with other Lacertini are still poorly resolved, and only sister relationships with *Parvilacerta* have been suggested based on mitochondrial (Carranza et al., 2004) and nuclear data (Mayer and Pavlicev, 2007). According to previous studies based on morphological characters (Eiselt and Schmidtler, 1986), the genus consists of three species with parapatric distributions: *Anatololacerta danfordi* (Günther, 1876), *A. anatolica* (Werner, 1900), and *A. oertzeni* (Werner, 1904). Populations of *A. anatolica* occur in northwestern Anatolia (north of Büyük Menderes river; nominal form) and in Samos Island (ssp. *aegaea* Eiselt and Schmidtler, 1986). *A. oertzeni* is distributed in southwestern Turkey, from Büyük Menderes river to Anamur area (ssp. *budaki*, *finikensis*, *ibrahimi*, all of them described by Eiselt and Schmidtler, 1986), with insular populations inhabiting Ikaria (nominal form), Rhodes (ssp. *pelasgiana* Mertenz, 1959) and the surrounding islets of Symi (ssp. *quandtaylori* Börner, 1974) and Pentanisos (ssp. *pentanisiensis* Wettstein, 1964). The remaining populations belong to *A. danfordi*, which is spread across the central and eastern portion of the Taurus Mountains from Acıgöl (in Burdur province) to Mersin (ssp. *bileki* Eiselt and Schmidtler, 1986) and in the Bolkar Dağları (nominal form) (Fig. 1). However, the existence of some cases of partial range overlap between taxa, e.g. between *A. oertzeni*

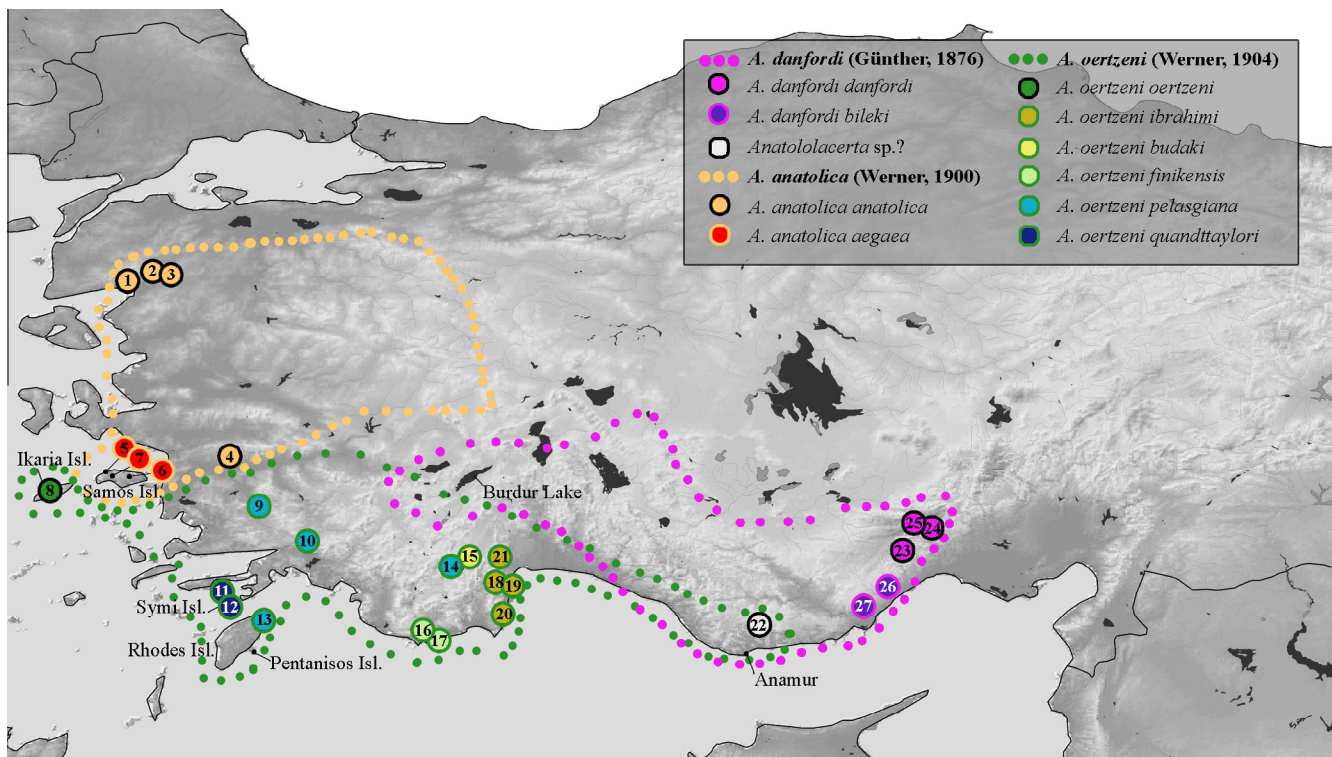


Fig. 1. Sampling localities considered in this study (circles), and approximate range (dotted lines) of the *Anatololacerta* morphospecies according to Eiselt and Schmidtler (1986); orange, *A. anatolica*; green, *A. oertzeni*; purple, *A. danfordi*. Alternative colors identify distinct morphological subspecies, whose correspondence are detailed in the box at right. Within circles, numbers refer to locality codes listed in Supplementary Table S1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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