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Research paper

# The evolutionary history of two lizards (Squamata: Lacertidae) is linked to the geological development of Iran

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ABSTRACT

The Iranian Plateau is an area of highly complex landscape and incredibly diverse habitats, from salt deserts to temperate forests. Such a heterogeneous environment, at the crossroads of Asia, Europe, and Africa, fuels the high diversity and uniqueness of the Iranian fauna and flora. Nevertheless, our understanding of the historical processes that shaped the Iranian biodiversity remains limited. In this context, we revisit the evolutionary history of the two most widespread lizard species on the Iranian Plateau (*Eremias persica* and *Mesalina watsonana*) to explore whether these two taxa of similar ecology have been subjected to similar historical processes. To achieve that, we performed a series of phylogenetic analyses and thoroughly tested all possible alternative topologies based on available mitochondrial sequences (cytochrome *b* and 12S ribosomal RNA). Additionally, we estimated the number of mitochondrial clusters based on a novel single-locus delimitation method and the time of their divergence, using recently inferred evolutionary rates for lacertid species. The results indicate that the two taxa have been shaped by similar physiographic and climatic barriers since both phylogenies split into similar geographical clusters. However, *E. persica* has twice as long evolutionary time on the Iranian Plateau than *M. watsonana*. The first divergence of *E. persica* was estimated in the Middle Miocene (~13 Mya), at the time of the major uplift of the Zagros mountain range. The Upper Miocene tectonic rearrangement that resulted in the uplift of the Alborz mountains coincides with the original split in *M. watsonana* (~6.6 Mya) and several contemporaneous splits within *E. persica.*

## 1. Introduction

The Iranian Plateau is a unique geological formation of Western Asia, located among the continental plates of Eurasia, Arabia, and India. A series of tectonic movements among these plates resulted in the gradual uplift of the Plateau and the extensive mountain system surrounding it (Crawford, 1972; Sborshchikov et al., 1981). Most of the estimates for the initial collision among Arabia and Eurasia range between 35 and 20 Mya (Khadivi, 2010; McQuarrie and Van Hinsbergen, 2013; Van Hinsbergen et al., 2012). At about the same time [25 to 20 Million years ago (Mya)], a "hard" collision episode is presumed to have occurred between the Indian and the Eurasian plates (Van Hinsbergen et al., 2012). Eventually, the combined tectonic movements led to the uplift of the four mountain ranges around Iran, i.e., the Zagros on the west border of the Plateau neighboring Iraq and Turkey, the Alborz range along the coast of the Caspian Sea, the Kopet Dagh on the border of Iran and Turkmenistan, and finally, the mountain ranges of Makran in the southeast (Fig. 2). There has been a broad spectrum of estimates for the initial uplift of the Zagros (Alavi, 1994; Berberian and King, 1981; Jassim and Goff, 2006), but the most recent findings suggest a Middle Miocene (~14Mya) onset of the deformation of the High Zagros (Mouthereau et al., 2012). Nevertheless, the major orogeny did not occur before 12.4 Mya, after which both the Zagros Mountains and the Iranian Plateau were rapidly uplifted in less than 5 My (Khadivi, 2010). During the same period, deformation is also reported in the Alborz (Guest et al., 2007; McQuarrie and Van Hinsbergen, 2013) and the Kopet Dagh mountains (Hollingsworth

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et al., 2010; McQuarrie and Van Hinsbergen, 2013). Later, at the Miocene-Pliocene border, the latest major tectonic activity shaped the area into its current configuration. During this period, the Alborz Mountains and the entire Plateau were uplifted to their current elevations (Allen et al., 2004; Axen et al., 2001).

The geographical position of Iran at the crossroads of Asia, Africa, and Europe, as well as the surrounding mountains that filter the dispersal in and out of the Plateau, has fueled the high biodiversity and endemicity in the area (Anderson, 1999; Bernor, 1986; Firouz, 2005; Frey and Probst, 1986; Madjnoonian et al., 2005). In addition to the vast mountain systems, the diverse habitat synthesis, from (semi-) arid to temperate (Madjnoonian et al., 2005 and references therein) interrupted by the non-habitable deserts of the Dasht-e Kavir and Dasht-e Lut (Blanford, 1876; Hedge and Wendelbo, 1978) create a dynamic mosaic environment that further reinforces the richness and uniqueness of the Iranian fauna and flora.

In spite of the extensive bibliography regarding the tectonics and paleogeography of the area, the systematic studies on the Iranian fauna lag behind, and our understanding of its phylogeography and biodiversity remains limited (Ahmadzadeh et al., 2013). In this study, we attempt to gain insight into the main biodiversity patterns of the Iranian Plateau by studying the historical biogeography of two of its most widely distributed lizards, *Eremias persica* Blanford, 1876, and *Mesalina watsonana* (Stoliczka, 1872). The two lacertids overlap extensively in the Central Plateau and partially in Pakistan and Afghanistan, however, their congeneric species are distributed allopatrically. West of Iran, *Mesalina* Gray, 1838 is found up to Morocco (Schleich et al., 1996), with a typical Saharo-Arabian distribution while *Eremias* Fitzinger, 1834 occurs east of Iran into central Asia (Sindaco and Jeremčenko, 2008). Several phylogenetic studies on the lacertid family acknowledge the two genera as sister taxa (Fu, 2000; Harris et al., 1998; Mayer and Pavlicev, 2007). Nonetheless, the relationships of the family remain significantly unresolved (Kapli et al., 2011; Mayer and Pavlicev, 2007; Mendes et al., 2016), but see (Pyron et al., 2013). Both *M. watsonana* and *E. persica* are assumed to form species complexes, revealing much higher genetic divergence than expected among congeneric lacertid species (Kapli et al., 2015; Pouyani et al., 2010; Šmíd and Frynta, 2012). The two complexes exhibit similar ecological requirements, occurring in the lowlands and mountain hills of the Iranian Plateau (except very high elevations) in arid and semi-arid habitats (Anderson, 1999; Ebrahimi et al., 2013). Recent estimates (Kapli et al., 2015) suggest that the initial divergence within *Mesalina* occurred in early Miocene and resulted in two lineages east (*M. watsonana*) and west (the rest of the *Mesalina* species) of Zagros. However, the first split within *M. watsonana* was estimated in late Miocene (Kapli et al., 2015) [~7 Mya (Kapli et al., 2015; Šmíd and Frynta, 2012)]. The initial split in the *E. persica* complex was estimated earlier, ca. 11 Mya (Pouyani et al., 2010). However, a later study on the phylogeny of the entire *Eremias* genus placed the event much later, ca. 6 Mya (Guo et al., 2011), an estimate much closer to the equivalent for *M. watsonana*.

In this study, we aim to identify whether the evolutionary history of the two lizard species has been subjected to similar historical process on the Iranian Plateau. In this framework, we perform a series of phylogenetic analyses to reconstruct the evolutionary relationships of the two taxa based on Maximum Likelihood and Bayesian Inference. Additionally, we estimate the number of mitochondrial clusters based on single-locus delimitation methods, and the time of their divergence using recently inferred evolutionary rates for lacertid species (Carranza and Arnold, 2012). The comparative analysis of the two taxa under the same assumptions and methods allows us to evaluate previous findings, identify similarities in their evolutionary history and associate them with the most plausible paleogeographic events in the area.

## 2. Material and methods

### 2.1. Sequences

We assembled two sequence datasets for the Iranian *E. persica* and for *M. watsonana* by retrieving sequences from NCBI (www.ncbi.nlm.nih.gov). For *E. persica* we relied on two mitochondrial markers [12S ribosomal RNA (12S) and cytochrome *b* (cyt *b*) sequences] which were originally published in Pouyani et al. (2010). Out of the 129 sequences, 125 belonged to the *E. persica* complex (*E. persica*, *E.* sp., *E. nigrolateralis*, *E. montanus*) and four of them corresponded to three outgroup taxa (*E. velox*, *Ophisops elegans*, and *Mesalina brevirostris*). For the dataset of *M. watsonana*, we combined the cyt *b* sequences produced in two previous phylogenetic studies, one aiming at resolving the relationships of the genus *Mesalina* (Kapli et al., 2015) and the other one focusing on *M. watsonana* (Šmíd and Frynta, 2012). The combined dataset consisted of 29 *M. watsonana* samples that covered the distribution of the species and eight sequences belonging to outgroup taxa (*Eremias brenchleyi*, *Gallotia caesaris*, *G. galloti*, *G. stehlini*, *G. atlantica*, *M. guttulata*). The choice of the outgroup was based on the original articles (Kapli et al., 2011; Pouyani et al., 2010; Šmíd and Frynta, 2012).

### 2.2. Phylogenetic inference

All alignments were performed with MAFFT (Katoh and Standley, 2013) under the default settings. The best-fit model of DNA substitution for each gene was chosen with jModelTest 2.1.1 (Darriba et al., 2012), under three substitution schemes and accounting for base frequencies, gamma shape and invariable sites (excluding the combination of invariable sites and $\Gamma$ distribution). For each dataset, we performed all the analyses, including and excluding the outgroup taxa.

Phylogenetic inference for each of the assembled datasets was carried out with Bayesian Inference (BI) and under the Maximum Likelihood (ML) criterion. For both analyses, the alignment sites were used as discrete, unordered characters. We performed three independent BI analyses with the software MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003), for $5^*10^6$ generations and four chains, and a sampling frequency of 0.01. Subsequently, we assessed the performance of each run with Tracer v1.5 (Drummond and Rambaut, 2007) and discarded 10% of the posterior samples as 'burn-in.' From the remaining trees, we calculated the majority rule consensus topology and the posterior probabilities [($\geq$ 95% indicated significant support according to Huelsenbeck & Ronquist (2001)]. The ML analysis was carried out with RAxML v. 8.0.20 (Stamatakis, 2014) for each dataset under the GTR + $\Gamma$ evolutionary model. For *M. watsonana* there was only one partition, while for *E. persica* the alignment was partitioned into the two loci (12S and cyt *b*) and a distinct substitution model was assigned to each. To assess the confidence of the ML topology, we performed 1000 bootstrap searches under the GTR + $\Gamma$ model.

### 2.3. Single-locus species delimitation

Several previous systematic studies of the two taxa assume a "species complex" status for both *M. watsonana* and *E. persica* (Kapli et al., 2015; Pouyani et al., 2010; Šmíd and Frynta, 2012). So far, however there has been no attempt to draw the limits among the independently evolving lineages involved in each phylogeny. Here, we make a first attempt by quantify the number of mitochondrial clusters for *E. persica* and *M. watsonana* using the recently introduced, single-locus species delimitation method, "multi-rate Poisson Tree Processes model" (mPTP, Kapli et al., 2017). The (m)PTP model attempts to identify the shifting point from the speciation to the coalescent processes, assuming that the