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Molecular phylogeny and biogeography of the genus *Acanthodactylus* Fitzinger, 1834 (Reptilia: Lacertidae) in Iran, inferred from mtDNA Sequences

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Abstract

Phylogenetic relationships of Iranian *Acanthodactylus* species were investigated using 1407 bp of mitochondrial DNA including 606 bp of cytochrome b and 801 bp of NADH dehydrogenase subunit 4 (ND4). Analyses done with maximum parsimony, maximum-likelihood, and Bayesian inference included 67 specimens from 27 geographically distinct localities in Iran. Our molecular results proposed three clear and geographically isolated clades by their phylogenetic positions and genetic differences. These three major clades are: (1) *A. micropholis*+ *A. grandis*+ *A. khamirensis;* (2) *A. blanfordi*+ *A. schmidti*+ *Acanthodactylus sp*$_1$, (3) *A. nilsoni*+ *A. boskianus* + *Acanthodactylus sp*$_2$. The phylogenetic analyses of the genus did not group *A. grandis* with the remaining species of the *A. boskianus* group and clustered it along with *A. khamirensis* within the *A. micropholis* group. In addition, phylogenetic results revealed a monophyletic status for *A. schmidti* and *A. micropholis* groups. Molecular clock approach indicated that the most recent divergence event splits *A. micropholis* from *A. khamirensis* about 2 MYA and results of dispersal-vicariance analyses showed that this diversification occurred by dispersal event rather than vicariance. Results of Reconstruct Ancestral State in Phylogenies (RASP) showed that Most Recent Common Ancestor (MRCA) of *A. micropholis*, *A. blanfordi* and *A. sp*$_1$ originated in eastern Iran. The first diversification of the genus in Iran most likely occurred between 8.5–9 MYA corresponding with the hypothesis that the genus has entered Iran long after the complete uplifting of the Zagros Mts. (10–12 MYA) which limited its dispersal only to the Persian Gulf shores and western slopes of the Zagros Mts.

Key words: Lacertidae *Acanthodactylus*, Mitochondrial genes, Cytochrome b, ND4, Phylogeny, Biogeography, Iran

Introduction

Nine genera and 41 species of lacertid lizards occur in Iran (Rastegar Pouyani *et al.* 2008; Ahmadzadeh *et al.* 2012; Heidari *et al.* 2013). One of these genera is *Acanthodactylus*, which is Saharo-Sindian in its distribution (Anderson, 1999). Of these, so far, seven species have been documented from Iran: *Acanthodactylus blanfordi* Boulenger, 1918, *A. boskianus* (Daudin, 1802), *A. grandis* Boulenger, 1909, *A. micropholis* Blanford, 1874; *A. nilsoni* Rastegar-Pouyani, 1998, *A. schmidti* Haas, 1957, and recently, *A. khamirensis* Heydari, Rastegar-Pouyani, Rastegar-Pouyani and Rajabizadeh, 2013. Current distribution pattern of *Acanthodactylus* species in Iran shows a great potential role of the Zagros Mountains in forming and diversifying its species to a great extent, especially along western slopes of the mountain chain. This mountain chain has played a pivotal role in modeling distribution patterns of various taxa from its emergence to present day (Macey *et al.* 1998, 2000; Rastegar-Pouyani, 1999a, b, c; Rastegar-Pouyani & Nilson 2002; Rastegar-Pouyani *et al.* 2009). The effect of the Zagros Mountains in modeling the evolutionary history of taxa distributed in its western and eastern slopes is a prominent biogeographic question that should be addressed by studying distributional patterns of different species in the area.

The Zagros mountainous ecosystem can be a major physical barrier to the distribution of species that are not rock dwellers and thus unable to live in this type of habitat. Fringed-toed lizard genus, *Acanthodactylus,* is an interesting case to address the influence of this mountainous ecosystem on the phylogeography and taxonomy of its

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the genus *Acanthodactylus* from Africa and the Middle East towards Iran would have happened after the uplifting of the Zagros Mountains. With this hypothesis, we can date back the entrance of the genus into Iran during the Late Miocene, around 10–12.4 MYA. Similar dispersal events have occurred during the late Miocene (9–10 MYA) in accordance with the geological event of the uplifted Zagros Mts. The agamid *Paralaudakia erythrogastra* was formed and originated from the main lineage of *P. caucasia* (Macey *et al.*, 1998, 2000), and in the *Eremias persica* complex, the uplifting of the Zagros Mts. has created two eastern and western clades along the sides of the mountains around 10–11 MYA (Rastegar-Poyani *et al.*, 2008). Specialized animals have less ability to disperse and this may explain why *Acanthodactylus* dispersed across the western and southern margins of the Zagros Mountains along shorelines of the Persian Gulf and did not disperse towards the central Iranian Plateau (through the Zagros Mts.), We suggest that the eastern taxa of the genus *Acanthodactylus* in Iran have originated from western Iran.
The most suitable scenario for the distribution and evolution of the Iranian species of the genus *Acanthodactylus* is by dispersal after uplifting of the Zagros Mts. Other alternative scenarios regarding the occurrence of this genus in Iran cannot be supported here because the species of the genus are absent in the opposite slope of the Zagros Mts. (the eastern slopes), and the high diversity of species in the western and southwestern parts of Iran and the southern slopes of the Zagros Mts. Since dispersal to new and restricted ecological niches in western and southern Iran, the genus has radiated into several species (currently there are about seven defined species in the western towards southern parts of Iran). These processes may have been forced by ecological divergence, competition for acquiring habitats among populations and then by acquiring reproductive isolations (Rundell & Price, 2009). Diverse ecological environments and existing different habitats (sandy hills with soft and hard substrates; plains at low and high elevations) in these regions have facilitated the speciation process of the genus in Iran.

Combined molecular and morphological analyses by Harris and Arnold (2000) suggested that the genus *Acanthodactylus* originated in southwestern Asia and Middle East during the mid-Miocene connection between Asia and Africa and later invaded North Africa on several occasions. Accordingly, it can be suggested that eastward invasion from southwestern Asia occurred during the lower Pliocene. Therefore, the extant species of the genus in Iran and along the shores of Persian Gulf and Oman Sea, towards Pakistan and northwestern India (*A. cantoris*), may be descendants of these lineages, which then led to the establishment of *A. micropholis*, *A. blanfordi*, *A. khamirensis, Acanthodactylus sp$_1$, Acanthodactylus sp$_2$*, and *A. nilsoni*. The current interspecific and intraspecific genetic and morphological variation and divergence of *Acanthodactylus* lineages in Iran may be due to the long time from the initial dispersal of the main lineages from western Iran towards the east to Pakistan, Afghanistan and northwestern India.

Among these 10 out of 42 species of *Acanthodactylus*, it seems that *A. nilsoni* (western Iran), *Acanthodactylus sp$_1$* (Southeastern Iran), *A. khamirensis* (southern Iran) and *Acanthodactylus sp$_2$* (southern Iran) are endemic species for different parts of Iran.

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