Zootaxa 4441 (1): 046–058
http://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4441.1.2
http://zoobank.org/urn:lsid:zoobank.org:pub:C6EAF677-192A-4BDD-9404-123719C54D65

A phylogenetic assessment of the meadow lizard *Darevskia praticola* (Eversmann, 1834) from Iran

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Abstract

The meadow lizard *Darevskia praticola* (Eversmann, 1834) displays a wide distribution range from the Western Balkans and Caucasus to the Hyrcanian forest in Iran. Based on previous studies, four subspecies have been described (*D. p. praticola, D. p. pontica, D. p. hyrcanica* and *D. p. loriensis*), but molecular evidence suggests two main phylogenetic lineages, Balkan and Caucasus. In this study we incorporated geographic records and analysed new samples from Alborz Mountains (Gilan Province, Iran), exploring their phylogenetic affinities using two mitochondrial markers (Cyt *b* and ND4). For the first time, Iranian samples are included in a molecular phylogeny. Our results meet the previous suggestions regarding the presence of a nuclear mitochondrial DNA fragment (numt) in Cyt *b*, causing misleading phylogenetic inferences since it renders the species paraphyletic. In contrast, the ND4 genealogy groups the species into a monophyletic clade, as expected. Samples attributed to *D. p. hyrcanica* (Azerbaijan and Iran) and *D. p. loriensis* (Armenia) are settled in a single clade with minute genetic distance, suggesting synonymisation.

Key words: Meadow lizard, *Darevskia praticola*, Iran, Phylogeny, mtDNA, Alborz Mountains, Numt gene

Introduction

The lizard family Lacertidae comprises 43 genera (Arnold *et al*. 2007; Mendes *et al*. 2016; Uetz & Hošek 2017) divided into two subfamilies, Gallotinae and Lacertinae. *Darevskia* is one of the largest genera within the Lacertinae subfamily, consisting of at least 31 species that range from the Caucasus and adjacent regions, as well as in the Balkans (Arnold *et al*. 2007; Tarkhnishvili 2012; Ahmadzadeh *et al*. 2013; Uetz & Hošek 2017). Most of the species are associated with rocky habitats, but some are ground dwellers and all have small body sizes (Arnold *et al*. 2007). Since the seminal work of Darevsky (1967), the genus has attracted high scientific interest in terms of biogeography, ecology, evolution and systematics (e.g., Fu *et al.* 1997; MacCulloch *et al.* 2000; Arnold *et al*. 2007; Tarkhnishvili 2012; Freitas *et al*. 2016a&b). Remarkably, some sexual species of the genus can produce parthenogenetic lineages via hybridization events, while others produce normal hybrids. In the first case, some parthenogenes may even backcross with bisexual males producing polyploid individuals (Danielyan *et al.* 2008). In these cases, hybrids and backcrosses do not always present intermediate morphologies (Carretero *et al.* 2018), while mtDNA flow across species is expected (Freitas *et al*. 2018), making it challenging to infer its evolutionary history. Nevertheless, this knowledge is still highly incomplete, particularly for those species not involved in hybridization events, and peripheral to the main genus range.

In Iran, eight *Darevskia* species have been reported, which occupy complex habitats in high mountain rocky habitats and grasslands in the north, and the northwestern part of the country (Ahmadzadeh *et al.* 2013). However, the biogeographic knowledge of the genus in Iran is far from complete; for example, the occurrence and status of the meadow lizard, *Darevskia praticola,* remain poorly documented. *Darevskia praticola* sensu lato occurs in two

Accepted by S. Carranza: 10 May 2018; published: 26 Jun. 2018

highly disjunct subranges, the Balkans and the Caucasian Isthmus (Anderson 1999; Sos *et al.* 2012; Tuniyev *et al.* 2013; Šmíd *et al*. 2014; Freitas *et al.* 2016a). Contrary to many *Darevskia* species, it has ground dwelling habits and is usually associated with well-conserved deciduous forest and, hence, vulnerable to forest degradation (Doronin 2015; Ćorović *et al.* 2018). Also, due to its elusive behavior, it may have remained undetected, even in well surveyed areas (Ćorović *et al*. 2018).

Regarding taxonomy, Eversmann firstly described *D. praticola* in 1834 from Nardzana in Russia. Some morphological differences among the specimens within the Caucasian Isthmus, led to the identification of two subspecies; *D. p. pontica* (six pairs of chin shields, three of which form a median suture) and *D. p. praticola* (five pairs of chin shields with two pairs forming a median suture) (see Tuniyev *et al.* 2011 and references therein). On the other hand, Sobolevsky (1930) described *D. p. hungarica* from the Transylvanian Alps in Romania, which was later synonymized with *D. p. pontica* (Mertens & Wermuth 1960; Fuhn & Vancea 1961; Bannikov *et al.* 1977; Orlova 1978; Ananjeva *et al*. 2006). Further morphological studies indicated additional variation in the Caucasus (Tuniyev *et al*. 2011, 2013), and led to the description of two more subspecies, i) *D. p. hyrcanica* from the Talysh foothills and the Western Alborz (Azerbaijan Republic and Iran), and ii) *D. p. loriensis* from Armenia (Tuniyev *et al.* 2013). All four subspecies have allopatric and disjunctive distributions (see Fig. 3a, Tuniyev *et al*. 2011); 1) *D. p. praticola* is reported from Greater Caucasus and Transcaucasia; 2) *D. p. pontica* is considered to occur in the Greater Caucasus and Balkan Peninsula, making it sometimes to be considered as a separate species with imprecise boundaries in the Central Ciscaucasia (Tuniyev *et al*. 2011; Uetz & Hošek 2017); 3) *D. p. hyrcanica* is described from the southwest of the Caspian Sea (Talysh Mountains and west of Alborz Mountains); and finally, 4) *D. p. loriensis* is described from Armenia. This purely morphological taxonomy has, however, been challenged by molecular evidence which only supports two main clades, one in the Balkans and the other in the Caucasus (Freitas *et al.* 2016a).

According to Anderson (1999), *D. praticola* sensu lato occurs in a small region of northwest Iran, in the Talysh Mountains. The first Iranian specimens were collected by Lantz in 1912 in Kheyran (correctly Heyran) on the road between Astara and Ardebil. Further lizards were later captured in Sharferud (Sharif Rud), Enzeli Bay of Gilan Province (Młokosiewicz 1913). Both Lantz and Młokosiewicz's samples were deposited in the Zoological Institute, Russian Academy of Sciences (ZISP) (Tuniyev *et al*. 2011, 2013). Orlova's report (1978) is the only available published record on the occurrence of this species in Iran, which was probably based on the aforementioned museum collection, meaning that no new record of this species is available from the country (see Anderson 1999). Additionally, a paratype of *Lacerta mostoufi* Baloutch, 1977 described from Southeastern Iran of an unknown locality (Baloutch 1977), has been identified as a mislabeled *D. praticola* (Bosch 1999). In previous studies, samples from Talysh and southwestern parts of the species distribution, namely from Azerbaijan (Kidov *et al*. 2009; Kidov 2010; Freitas *et al.* 2016a). However, there is a complete lack of molecular evidence for the Iranian *D. praticola* and of its placement within the broader phylogeny of the species (Fu *et al.* 1997; Arnold *et al*. 2007; Freitas *et al.* 2016a).

In this study, we analyze new samples of *D. praticola* from Talysh, widening the knowledge of this species in Iran. We used two mitochondrial molecular markers to determine the phylogenetic relationships between these Iranian specimens and other available samples, covering the remaining distribution of *D. praticola* sensu lato. After this evidence, we will infer on the phylogeographic events that have shaped the diversity of Iranian specimens, and reassess their taxonomic status.

Materials and methods

We collected five individuals of *D. praticola* from the Talysh Mountain in the Gilan Province of Iran (latitude: 37.55647 N and longitude: 48.72562 E). For each of the individuals, we preserved small fragments of tail tissues in ethanol 96% and stored them at -20ºC in the Molecular Ecology Laboratory at Shahid Beheshti University. For the extraction of DNA, we used a standard high-salt method (Sambrook & Russel 2001), and subsequently amplified two mitochondrial markers; NADH dehydrogenase subunit 4 (ND4) and Cytochrome *b* (Cyt *b*) using the Leu/ND4 (Arevalo *et al*. 1994) and L14910/H16064 (Burbrink *et al.* 2000) primers, respectively. PCR conditions were performed on a total of 25 µL, including 12.5 µL Mastermix Red (Ampliqon, Copenhagen, Denmark), 0.5 µl (of 10 µmol/µl) of each primer, 1 µl template DNA and 10.5 µl dd H_2O. PCRs consisted of an initial denaturation at 93°C for 2min, followed by 35–40 cycles of second denaturation at 92°C for 30”, annealing at 51–53°C for 40” and extension at 72°C for 72”. Successfully amplified samples were then sent for sequencing to an external sequencing facility (Macrogene, Seoul, Korea). The retrieved DNA sequences were edited with Codon Code Aligner v.6.0.2.X program (CodonCode Corporation, Dedham, MA, USA), and submitted to GenBank (Appendix I).

To obtain solid understanding of the evolutionary placement of the Iranian samples in the *Darevskia* phylogeny, we retrieved 94 sequences from GenBank (Appendix I), corresponding to 65 sequences (Accession numbers pending) from Freitas *et al.* (2016a), and 29 sequences from Ahmadzadeh *et al*. (2013). Also, *Lacerta bilineata* was considered as the outgroup. All sequences were aligned with Clustal W as implemented in MEGA6 (Tamura *et al.* 2013), and the best-fitting model of nucleotide substitution selected by Akaike’s Information Criterion (Akaike 1974) was estimated with jModelTest (Darriba *et al.* 2012). The best model for both genes (Cyt *b* and ND4) was the GTR+I+G. For each marker, we estimated the Maximum Likelihood (ML) phylogeny using RAxML v.7.2 software (Stamatakis 2006), under the GTR+G model. The proportion of invariable sites (P-invar) was not incorporated into the analysis, as suggested by the author of the software (Stamatakis 2008). To assess the robustness of the ML phylogeny we employed 1,000 pseudo-replicates of the alignment, and estimated the ML trees for each. Similarly, for each gene, we conducted Bayesian Inference (BI) analyses with Mrbayes (v.3.2) (Huelsenbeck & Ronquist 2001). Each analysis was run for 10^6 generations with five chains and sampling frequency of 100, which resulted in 10,000 samples, out of which 2,500 were discarded as burn-in. Since previous studies reported a nuclear copy within Cyt *b* in some species of lacertids including *D. praticola* (Podnar *et al.* 2007; Freitas *et al.* 2016a), we analyzed separately and carefully the evaluated inference from both markers. Our results showed that there is a nuclear copy within Cyt *b* in our samples too (see below). Therefore, we did not consider the gene for subsequent analysis. Hence, we used the ND4 gene for statistical parsimony networks constructed with TCS v.1.21 (Clement *et al*. 2000). This analysis was implemented considering a 95% probability. To infer the relatedness among populations, we used the “Population Analysis with Reticulate Trees” software (Popart, Leigh & Bryant 2015), hence, creating a median joining network and then switched to map. Uncorrected genetic distances (P-distance) were estimated within *D. praticola* sensu lato just for ND4, implemented in MEGA6.

Results

For both mitochondrial genes, the Iranian samples were nested within other samples identified as *D. praticola* sensu lato. However, the placement differed between the two genes. The Cyt *b* topology was identical for the ML and the BI analyses, and surprisingly placed the Iranian species as sister clade to the Balkan lineage. The other *D. praticola* samples, all from the Caucasus, were recovered as a distinct, non-sister clade to the Balkan, rendering the species paraphyletic (Fig. 1).

The inferred topology of both ML and BI differed between the ND4 and Cyt *b* markers. *D. praticola* as well as all other species were found to be monophyletic, and the Iranian samples were recovered as sister to the Caucasus clade along with the Talysh samples (Fig. 2). The ND4 tree further reveals that the Iranian samples are a sister clade to the Armenian samples assigned to *D. p. loriensis.*

Uncorrected distances showed low genetic divergence between Armenian, Azerbaijani and Iranian samples ≈0.5–0.7% (Appendix II). In fact, samples from Armenia attributed to *D. p. loriensis,* were nested within Iran and Azerbaijan samples (Fig. 2).

The ND4 TCS network showed that the Transcaucasia clade (Iranian, Armenian and Azerbaijani samples), formed a single haplogroup with Iranian samples being the ancestral haplotype (Fig. 3b). Also, the median joining haplotype network results were in agreement with the TCS results. Both haplotype networks recovered four haplotypes in Transcaucasia clade, and both Iranian and Armenian samples settled in one haplotype, but Azerbaijan specimens were located in two haplotypes (Figs 3a, 3b).

Discussion

The present study is the first molecular assessment of Iranian *D. praticola* specimens, contributing to clarify the intraspecific relationships within the eastern part of this species complex distribution range. Remarkably, the two

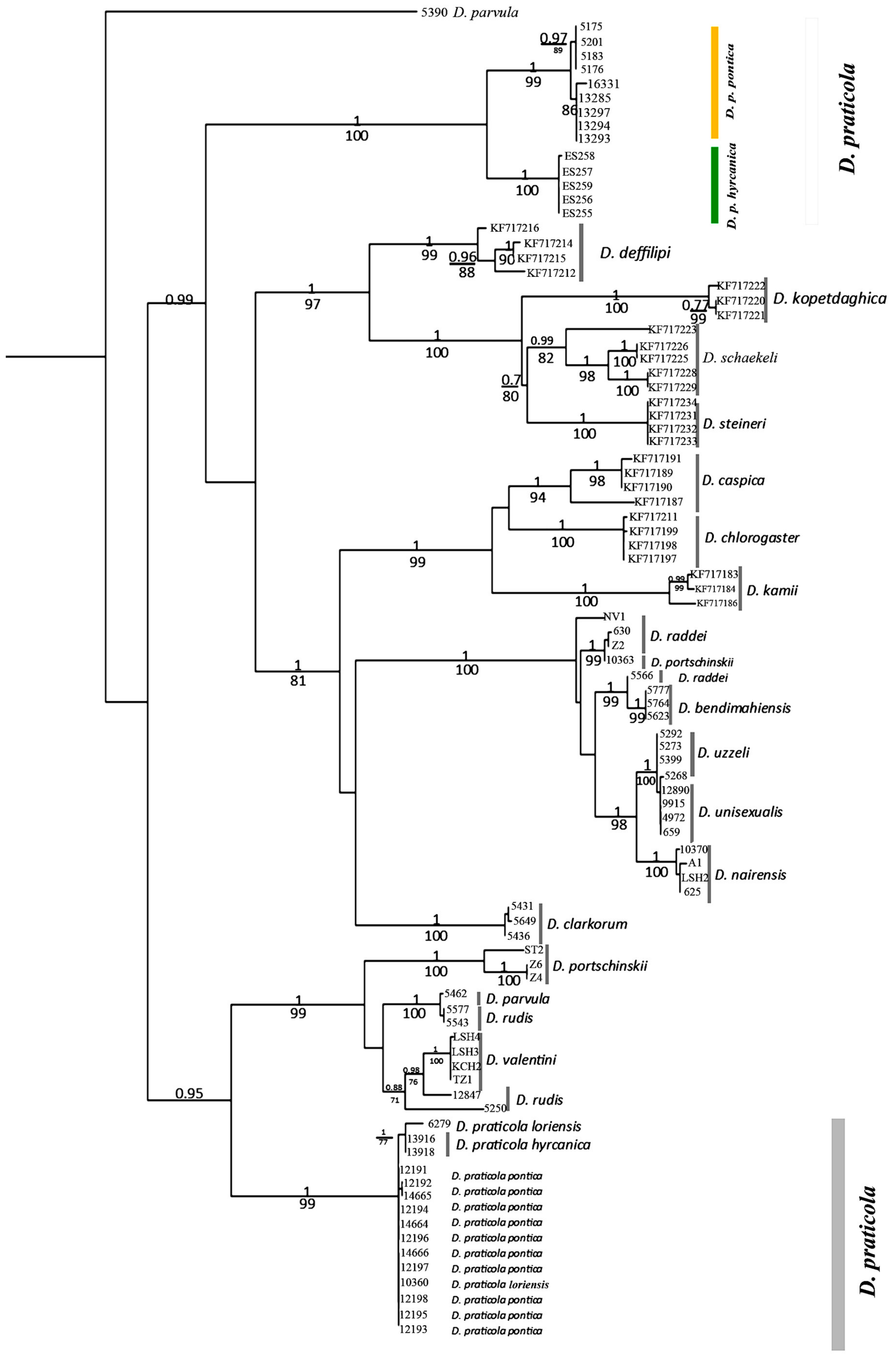

FIGURE 1. Phylogenetic tree for Cyt *b* gene, as Bayesian and ML analyses show similar tree topologies only the ML tree is presented. Numbers on branches are bootstrap support values for ML (below) and posterior probability values for Bayesian (above) analyses. Only values greater than 70 and 0.7, respectively, are shown

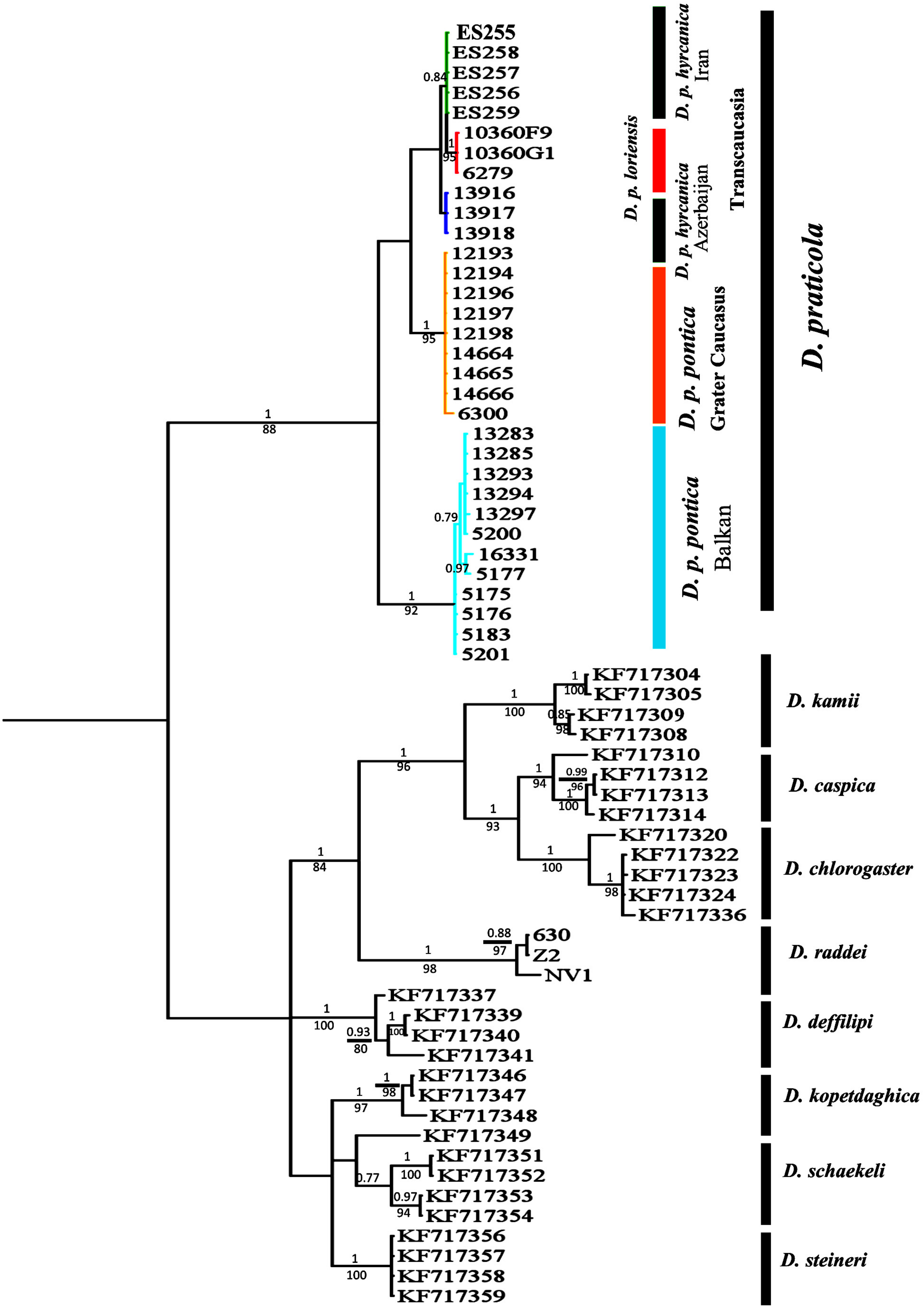

FIGURE 2. Phylogenetic tree for ND4 gene, as Bayesian and ML analyses show similar tree topologies only the ML tree is presented. Numbers on branches are bootstrap support values for ML (below) and posterior probability values for Bayesian (above) analyses. Only values greater than 70 and 0.7, respectively, are shown

mitochondrial markers (Cyt *b* and ND4) used in the study showed contrasting genealogies. Cyt *b* resulted in a paraphyletic arrangement with the Iranian specimens surprisingly settled within the Balkan clade, while ND4 recovered a monophyletic unit with two major clades, the Balkan and the Caucasus. The latter is divided into two sister clades: i) Greater Caucasus, and ii) Transcaucasia. The Iranian samples from Gilan Province placed in the Caucasus clade in the subclade of Transcaucasia. According to the results obtained from the ND4 gene, the Iranian population is closely related to *D. p. loriensis* and to the Talysh population in the Republic of Azerbaijan. As the distance matrix displayed, all these samples are closely related and low genetic divergence exists among specimens ascribed to *D. p. hyrcanica*, *D. p. loriensis*, and the Iranian samples (Appendix II). Also, the haplotype network did not show any shared haplotype among the Iranian samples (Talysh Mountain), Armenia and the ones from Talysh (Republic of Azerbaijan).

This fits the results that were recently published by Freitas *et al.* (2016a), who also studied the intraspecific phylogenetic relationship of the meadow lizard using both ND4 and Cyt *b*. They recovered two divergent clades within ND4: i) the "Lineage A-Balkans" that consists of *D. p. pontica* from the Balkans, and ii) "Lineage B-Caucasus" including specimens theoretically ascribed to *D. p. pontica* from northwestern of Caucasus, *D. p. hyrcanica* from Talysh-Azerbaijan and *D. p. loriensis*. For ND4, the analyzed Iranian samples fell within "Lineage A" *sensu* Freitas *et al.* (2016a). For Cyt *b, D. praticola* appears as paraphyletic, as already indicated by Freitas *et al.* (2016a). Nevertheless, other Iranian species of the genus were recovered as monophyletic using Cyt *b* (see Miraldo *et al*. 2012; Ahmadzadeh *et al.* 2013; Freitas *et al.* 2016a). To explain this pattern, Freitas *et al*. (2016a) suggested that in *D. praticola* this gene is likely a numt (i.e. nuclear mitochondrial DNA fragment). This gene transposition has been reported for other lacertid lizards (Podnar *et al*. 2007). The results of this study further corroborate that a numt copy within Cyt *b* is the most likely explanation for the observed phylogenetic pattern. After the present results, we can infer that most likely, numt appeared in the Caucasus, and was then extended further by gene flow, but never attained the Balkans or Alborz, probably due to geographic isolation. These numt alleles have already been reported to be responsible for other bursts of polymorphism in mitochondrial genes in lizards (Miraldo *et al*. 2012).

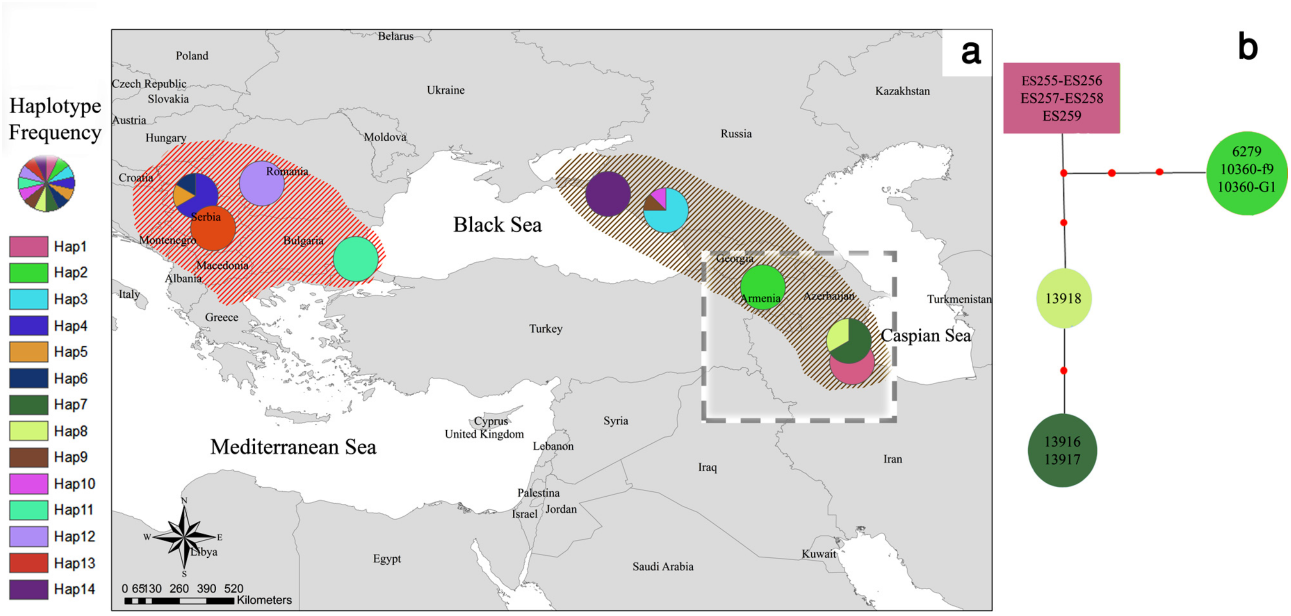

FIGURE 3. Haplotype network of *D. praticola* sensu lato. a) The median joining network graph shows nine haplotypes in all subspecies of *D. praticola*. There were four haplotypes in the Transcaucasia (encompassed by dashed line). b) The statistical parsimony network illustrates that the Transcaucasia samples stay at one haplogroup showing Iranian specimens as ancestral haplotype

Based on morphological traits, Tuniyev *et al.* (2011) placed the Iranian samples with *D. p. hyrcanica*. Two years later, they recorded new subspecies (*D. p. loriensis*) from Armenia, and reported that the samples from North Caucasus, Talysh and Armenia were distinct (Tuniyev *et al.* 2013). Remarkably, our results do not confirm the morphological evidence from Tuniyev *et al.* (2011). *D. p. hyrcanica* and *D. p. loriensis* represent the two less divergent mtDNA lineages (uncorrected P-distance less than 0.8%; see also Fig. 2), and share nuclear haplotypes, and, consequently, should not be considered as distinct subspecies (Freitas *et al*. 2016a). As a taxonomic conclusion, it seems more reasonable to merge the two subspecies, *D. p. hyrcanica* and *D. p. loriensis* with the name *hyrcanica*, since it is the oldest trinomen.

Darevskia praticola complex provides an interesting evolutionary pattern, including segregated distributions (Balkan and Caucasus). Most likely, a major glaciation happened at end of Pliocene (Hays *et al*. 1976) that caused the divergence of the two main clades from each other (Freitas *et al.* 2016a). It seems that other climatic fluctuations have also been leading populations of *D. praticola* to be divided into current fragments. During the Pleistocene glaciation cycles, several species were fragmented and settled in different refuges (Seddon *et al*. 2002; Waltari *et al*. 2007; Kehl 2009). Alborz Mountains and southern coast of the Caspian Sea are considered as refugia (Veith *et al*. 2003; Ahmadzadeh *et al.* 2013; Tarkhnishvili 2014), and some populations of meadow lizard found shelter in Alborz Mountains during glaciations. Then, the populations probably expanded during interglacial periods into Armenia, Republic of Azerbaijan and north of Iran.

As to the taxonomic implications, we provisory suggest that *D. p. loriensis* should be considered a synonym of *D. p. hyrcanica.* Also, the new Iranian population was analyzed here and their situation was determined within *D. praticola*. However, further taxonomical studies are needed for this species complex, namely, if there are putative contacts between *D. p. praticola* and *D. p. pontica* in Central Ciscaucasia. Overall, we await a complete reassessment of the whole *D. praticola* complex based on an extended marker dataset and geographic sampling.

Acknowledgement

We are would like to thank S. Freitas for sharing datasets. We would also like to thank Dr. Paschalia Kapli for reviewing and providing valuable comments on previous versions of the manuscript. MAC is supported by project NORTE-01-0145-FEDER-000007.

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APPENDIX I. Specimens used for phylogenetic analyses with Isolate code, Country, Origin of samples from Ahmadzadeh *et al.* 2013, Freitas *et al.* 2016a and this study

Isolate	Species	Country	Origin	GenBank accession number	
				ND4	Cyt *b*
DB6317	*Darevskia deffilipi*	Iran	Ahmadzadeh *et al*. 2013	KF717337	KF717212
DB6303	*Darevskia deffilipi*	Iran	Ahmadzadeh *et al*. 2013	KF717339	KF717214
DB6304	*Darevskia deffilipi*	Iran	Ahmadzadeh *et al*. 2013	KF717340	KF717215
DB6200	*Darevskia deffilipi*	Iran	Ahmadzadeh *et al*. 2013	KF717341	KF717216
DB13797	*Darevskia kopedaghica*	Iran	Ahmadzadeh *et al*. 2013	KF717346	KF717220
DB13798	*Darevskia kopedaghica*	Iran	Ahmadzadeh *et al*. 2013	KF717347	KF717221
DB6319	*Darevskia kopedaghica*	Iran	Ahmadzadeh *et al*. 2013	KF717348	KF717222
DB13806	*Darevskia schaekeli*	Iran	Ahmadzadeh *et al*. 2013	KF717349	KF717223
DB6218	*Darevskia schaekeli*	Iran	Ahmadzadeh *et al*. 2013	KF717351	KF717225
DB6219	*Darevskia schaekeli*	Iran	Ahmadzadeh *et al*. 2013	KF717352	KF717226
DB13808	*Darevskia schaekeli*	Iran	Ahmadzadeh *et al*. 2013	KF717353	KF717228
DB13810	*Darevskia schaekeli*	Iran	Ahmadzadeh *et al*. 2013	KF717354	KF717229
DB6111	*Darevska steineri*	Iran	Ahmadzadeh *et al*. 2013	KF717356	KF717231
DB6112	*Darevska steineri*	Iran	Ahmadzadeh *et al*. 2013	KF717357	KF717232
DB6113	*Darevska steineri*	Iran	Ahmadzadeh *et al*. 2013	KF717358	KF717233
DB6114	*Darevska steineri*	Iran	Ahmadzadeh *et al*. 2013	KF717359	KF717234
DB13818	*Darevskia kamii*	Iran	Ahmadzadeh *et al*. 2013	KF717304	KF717183
DB13819	*Darevskia kamii*	Iran	Ahmadzadeh *et al*. 2013	KF717305	KF717184
DB6165	*Darevskia kamii*	Iran	Ahmadzadeh *et al*. 2013	KF717308	_
DB6166	*Darevskia kamii*	Iran	Ahmadzadeh *et al*. 2013	KF717309	KF717186
DB6170	*Darevskia caspica*	Iran	Ahmadzadeh *et al*. 2013	KF717310	KF717187
DB6180	*Darevskia caspica*	Iran	Ahmadzadeh *et al*. 2013	KF717312	KF717189
DB6181	*Darevskia caspica*	Iran	Ahmadzadeh *et al*. 2013	KF717313	KF717190
DB13820	*Darevskia caspica*	Iran	Ahmadzadeh *et al*. 2013	KF717314	KF717191
DB13825	*Darevskia chlorogaster*	Iran	Ahmadzadeh *et al*. 2013	KF717320	_
DB13816	*Darevskia chlorogaster*	Iran	Ahmadzadeh *et al*. 2013	KF717322	KF717197
DB13813	*Darevskia chlorogaster*	Iran	Ahmadzadeh *et al*. 2013	KF717323	KF717198
DB13814	*Darevskia chlorogaster*	Iran	Ahmadzadeh *et al*. 2013	KF717324	KF717199
DB13824	*Darevskia chlorogaster*	Iran	Ahmadzadeh *et al*. 2013	KF717336	KF717211
KCH2	*Darevskia valentini*	Armenia	Freitas *et al.* 2016a	_	MH271056
LSH3	*Darevskia valentini*	Armenia	Freitas *et al.* 2016a	_	MH271058
LSH4	*Darevskia valentini*	Armenia	Freitas *et al.* 2016a	_	MH271059
TZ1	*Darevskia valentini*	Armenia	Freitas *et al.* 2016a	_	MH271062
5268	*Darevskia uzzeli*	Turkey	Freitas *et al.* 2016a	_	MH271037
5273	*Darevskia uzzeli*	Turkey	Freitas *et al.* 2016a	_	MH271038
5292	*Darevskia uzzeli*	Turkey	Freitas *et al.* 2016a	_	MH271039
5399	*Darevskia uzzeli*	Turkey	Freitas *et al.* 2016a	_	MH271041
659	*Darevskia unisexualis*	Armenia	Freitas *et al.* 2016a	_	MH271053
9915	*Darevskia unisexualis*	Armenia	Freitas *et al.* 2016a	_	MH271054
12890	*Darevskia unisexualis*	Armenia	Freitas *et al.* 2016a	_	MH271034

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APPENDIX 1. (Continued)

Isolate	Species	Country	Origin	GenBank accession number	
				ND4	Cyt *b*
4972	*Darevskia unisexualis*	Armenia	Freitas *et al.* 2016a	_	MH271035
5250	*Darevskia rudis*	Turkey	Freitas *et al.* 2016a	_	MH271036
5543	*Darevskia rudis*	Turkey	Freitas *et al.* 2016a	_	MH271066
5577	*Darevskia rudis*	Turkey	Freitas *et al.* 2016a	_	MH271046
12847	*Darevskia rudis*	Georgia	Freitas *et al.* 2016a	_	MH271033
630	*Darevskia raddei*	Nagorno-Karabakh Republic	Freitas *et al.* 2016a	MH271004	MH271052
5566	*Darevskia raddei*	Turkey	Freitas *et al.* 2016a	_	MH271045
NV1	*Darevskia raddei*	Armenia	Freitas *et al.* 2016a	MH271005	MH271060
Z2	*Darevskia raddei*	Nagorno-Karabakh Republic	Freitas *et al.* 2016a	MH271006	MH271063
10363	*"Darevskia portschinskii"*	Armenia	Freitas *et al.* 2016a	_	MH271031
ST2	*Darevskia portschinskii*	Armenia	Freitas *et al.* 2016a	_	MH271061
Z4	*Darevskia portschinskii*	Nagorno-Karabakh Republic	Freitas *et al.* 2016a	_	MH271064
Z6	*Darevskia portschinskii*	Nagorno-Karabakh Republic	Freitas *et al.* 2016a	_	MH271065
5390	*Darevskia parvula*	Turkey	Freitas *et al.* 2016a	_	MH271040
5462	*Darevskia parvula*	Turkey	Freitas *et al.* 2016a	_	MH271044
625	*Darevskia nairensis*	Armenia	Freitas *et al.* 2016a	_	MH271051
10370	*Darevskia nairensis*	Armenia	Freitas *et al.* 2016a	_	MH271032
A1	*Darevskia nairensis*	Armenia	Freitas *et al.* 2016a	_	MH271055
LSH2	*Darevskia nairensis*	Armenia	Freitas *et al.* 2016a	_	MH271057
5431	*Darevskia clarkorum*	Turkey	Freitas *et al.* 2016a	_	MH271042
5436	*Darevskia clarkorum*	Turkey	Freitas *et al.* 2016a	_	MH271043
5649	*Darevskia clarkorum*	Turkey	Freitas *et al.* 2016a	_	MH271048
5623	*Darevskia bendimahiensis*	Turkey	Freitas *et al.* 2016a	_	MH271047
5764	*Darevskia bendimahiensis*	Turkey	Freitas *et al.* 2016a	_	MH271049
5777	*Darevskia bendimahiensis*	Turkey	Freitas *et al.* 2016a	_	MH271050
12191	*Darevskia praticola pontica*	Russia	Freitas *et al.* 2016a	_	MH271008
12192	*Darevskia praticola pontica*	Russia	Freitas *et al.* 2016a	_	MH271009
12193	*Darevskia praticola pontica*	Russia	Freitas *et al.* 2016a	MH270979	MH271010
12194	*Darevskia praticola pontica*	Russia	Freitas *et al.* 2016a	MH270980	MH271011
12195	*Darevskia praticola pontica*	Russia	Freitas *et al.* 2016a	_	MH271012
12196	*Darevskia praticola pontica*	Russia	Freitas *et al.* 2016a	MH270981	MH271013
12197	*Darevskia praticola pontica*	Russia	Freitas *et al.* 2016a	MH270982	MH271014
12198	*Darevskia praticola pontica*	Russia	Freitas *et al.* 2016a	MH270983	MH271015
13283	*Darevskia praticola pontica*	Serbia	Freitas *et al.* 2016a	MH270984	_
13285	*Darevskia praticola pontica*	Serbia	Freitas *et al.* 2016a	MH270985	MH271016
13293	*Darevskia praticola pontica*	Serbia	Freitas *et al.* 2016a	MH270986	MH271017
13294	*Darevskia praticola pontica*	Serbia	Freitas *et al.* 2016a	MH270987	MH271018
13297	*Darevskia praticola pontica*	Serbia	Freitas *et al.* 2016a	MH270988	MH271019

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APPENDIX 1. (Continued)

Isolate	Species	Country	Origin	GenBank accession number	
				ND4	Cyt *b*
14664	*Darevskia praticola pontica*	Russia	Freitas *et al.* 2016a	MH270992	MH271022
14665	*Darevskia praticola pontica*	Russia	Freitas *et al.* 2016a	MH270993	MH271023
14666	*Darevskia praticola pontica*	Russia	Freitas *et al.* 2016a	MH270994	MH271024
6300	*Darevskia praticola pontica*	Russia	Freitas *et al.* 2016a	MH271003	_
16331	*Darevskia praticola pontica*	Turkey	Freitas *et al.* 2016a	MH270995	MH271025
5175	*Darevskia praticola pontica*	Romania	Freitas *et al.* 2016a	MH270996	MH271026
5176	*Darevskia praticola pontica*	Romania	Freitas *et al.* 2016a	MH270997	MH271027
5177	*Darevskia praticola pontica*	Serbia	Freitas *et al.* 2016a	MH270998	_
5183	*Darevskia praticola pontica*	Romania	Freitas *et al.* 2016a	MH270999	MH271028
5200	*Darevskia praticola pontica*	Serbia	Freitas *et al.* 2016a	MH271000	_
5201	*Darevskia praticola pontica*	Greece	Freitas *et al.* 2016a	MH271001	MH271029
6279	*Darevskia praticola loriensis*	Armenia	Freitas *et al.* 2016a	MH271002	MH271030
10360-F9	*Darevskia praticola loriensis*	Armenia	Freitas *et al.* 2016a	MH270977	MH271007
10360-G1	*Darevskia praticola loriensis*	Armenia	Freitas *et al.* 2016a	MH270978	_
13916	*Darevskia praticola hyrcanica*	Azerbaijan	Freitas *et al.* 2016a	MH270989	MH271020
13917	*Darevskia praticola hyrcanica*	Azerbaijan	Freitas *et al.* 2016a	MH270990	_
13918	*Darevskia praticola hyrcanica*	Azerbaijan	Freitas *et al.* 2016a	MH270991	MH271021
ES255	*Darevskia praticola hyrcanica*	Iran	This study	MG922582	MG922588
ES256	*Darevskia praticola hyrcanica*	Iran	This study	MG922583	MG922590
ES257	*Darevskia praticola hyrcanica*	Iran	This study	MG922584	MG922589
ES258	*Darevskia praticola hyrcanica*	Iran	This study	MG922585	MG922591
ES259	*Darevskia praticola hyrcanica*	Iran	This study	MG922586	MG922587

APPENDIX II. Uncorrected genetic distances among *D. praticola* subspecies. These p-distances show slight genetic differences between samples

	ES255	ES256	ES257	ES258	ES259	10360_F9	10360_G1	12193	12194	12196	12197	12198	13283	13285	13293	13294	13297	13916	13917	13918	14664	14665	14666	16331	5175	5176	5177	5183	5200	5201	6279	6300
ES255																																
ES256	0.000																															
ES257	0.000	0.000																														
ES258	0.000	0.000	0.000																													
ES259	0.000	0.000	0.000	0.000																												
10360_F9	0.005	0.005	0.005	0.005	0.005																											
10360_G1	0.005	0.005	0.005	0.005	0.005	0.000																										
12193	0.033	0.033	0.033	0.033	0.033	0.036	0.036																									
12194	0.033	0.033	0.033	0.033	0.033	0.036	0.036	0.000																								
12196	0.033	0.033	0.033	0.033	0.033	0.036	0.036	0.000	0.000																							
12197	0.033	0.033	0.033	0.033	0.033	0.036	0.036	0.000	0.000	0.000																						
12198	0.033	0.033	0.033	0.033	0.033	0.036	0.036	0.000	0.000	0.000	0.000																					
13283	0.055	0.055	0.055	0.055	0.055	0.057	0.057	0.055	0.055	0.055	0.055	0.055																				
13285	0.055	0.055	0.055	0.055	0.055	0.057	0.057	0.055	0.055	0.055	0.055	0.055	0.000																			
13293	0.056	0.056	0.056	0.056	0.056	0.059	0.059	0.056	0.056	0.056	0.056	0.056	0.001	0.001																		
13294	0.055	0.055	0.055	0.055	0.055	0.057	0.057	0.055	0.055	0.055	0.055	0.055	0.000	0.000	0.001																	
13297	0.057	0.057	0.057	0.057	0.057	0.060	0.060	0.057	0.057	0.057	0.057	0.057	0.002	0.002	0.001	0.002																
13916	0.005	0.005	0.005	0.005	0.005	0.007	0.007	0.033	0.033	0.033	0.033	0.033	0.055	0.055	0.053	0.055	0.055															
13917	0.005	0.005	0.005	0.005	0.005	0.007	0.007	0.033	0.033	0.033	0.033	0.033	0.055	0.055	0.053	0.055	0.055	0.000														
13918	0.004	0.004	0.004	0.004	0.004	0.006	0.006	0.032	0.032	0.032	0.032	0.032	0.053	0.053	0.055	0.053	0.056	0.001	0.001													
14664	0.034	0.034	0.034	0.034	0.034	0.037	0.037	0.001	0.001	0.001	0.001	0.001	0.056	0.056	0.055	0.056	0.056	0.032	0.032	0.033												
14665	0.033	0.033	0.033	0.033	0.033	0.036	0.036	0.000	0.000	0.000	0.000	0.000	0.055	0.055	0.056	0.055	0.057	0.033	0.033	0.032	0.001											
14666	0.033	0.033	0.033	0.033	0.033	0.036	0.036	0.000	0.000	0.000	0.000	0.000	0.055	0.055	0.056	0.055	0.057	0.033	0.033	0.032	0.001	0.000										
16331	0.055	0.055	0.055	0.055	0.055	0.057	0.057	0.055	0.055	0.055	0.055	0.055	0.005	0.005	0.006	0.005	0.007	0.055	0.055	0.053	0.056	0.055	0.055									
5175	0.052	0.052	0.052	0.052	0.052	0.055	0.055	0.052	0.052	0.052	0.052	0.052	0.002	0.002	0.004	0.002	0.005	0.052	0.052	0.051	0.053	0.052	0.052	0.005								
5176	0.052	0.052	0.052	0.052	0.052	0.055	0.055	0.052	0.052	0.052	0.052	0.052	0.002	0.002	0.004	0.002	0.005	0.052	0.052	0.051	0.053	0.052	0.052	0.005	0.000							
5177	0.053	0.053	0.053	0.053	0.053	0.056	0.056	0.053	0.053	0.053	0.053	0.053	0.004	0.004	0.005	0.004	0.006	0.053	0.053	0.052	0.055	0.053	0.053	0.004	0.004	0.004						
5183	0.052	0.052	0.052	0.052	0.052	0.055	0.055	0.052	0.052	0.052	0.052	0.052	0.002	0.002	0.004	0.002	0.005	0.052	0.052	0.051	0.053	0.052	0.052	0.005	0.000	0.000	0.004					
5200	0.055	0.055	0.055	0.055	0.055	0.057	0.057	0.055	0.055	0.055	0.055	0.055	0.000	0.000	0.001	0.000	0.002	0.055	0.055	0.053	0.056	0.055	0.055	0.005	0.002	0.002	0.004	0.002				
5201	0.052	0.052	0.052	0.052	0.052	0.055	0.055	0.052	0.052	0.052	0.052	0.052	0.002	0.002	0.004	0.002	0.005	0.052	0.052	0.051	0.053	0.052	0.052	0.005	0.000	0.000	0.004	0.000	0.002			
6279	0.005	0.005	0.005	0.005	0.005	0.000	0.000	0.036	0.036	0.036	0.036	0.036	0.057	0.057	0.059	0.057	0.060	0.007	0.007	0.006	0.037	0.036	0.036	0.057	0.055	0.055	0.056	0.055	0.057	0.055		
6300	0.036	0.036	0.036	0.036	0.036	0.038	0.038	0.005	0.005	0.005	0.005	0.005	0.057	0.057	0.059	0.057	0.060	0.036	0.036	0.034	0.006	0.005	0.005	0.057	0.055	0.055	0.056	0.055	0.057	0.055	0.038	