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Reevaluation of the intraspecific variability in *Darevskia parvula* (Lantz & Cyren, 1913): an integrated approach using morphology, osteology and genetics (Squamata: Lacertidae)

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Abstract

The intraspecific variability of *Darevskia parvula* (which has two classical subspecies easily identifiable by external characteristics, *D. p. parvula* and *D. p. adjarica)*, was studied using various approaches including morphology (scalation and biometry), multivariate analyses (PCA, CDA, ANOSIM, UPGMA and MST), osteology, and molecular techniques. High mitochondrial distance, differences at the nuclear level and morphological distinctiveness warrant the specific status of both taxa, *Darevskia parvula* (Lantz & Cyrén, 1913) and *Darevskia adjarica* (Darevsky & Eiselt, 1980) **stat. nov.** A lectotype for *D. parvula*, originally described with syntypes of both species -*D. parvula* and *D. adjarica*- is designated. The uncorrected genetic distance between *D. parvula* and *D. adjarica* in the cytochrome *b* mitochondrial gene is 14.4% ± 1.9%. Intraspecific variability within *D. parvula* is very small (1.5% ± 0.5%), and was not detected in our samples of *D. adjarica*. The two species further differ by two mutations in the nuclear melano-cortin 1 receptor (*mc1r*) gene. Interestingly, past introgression of *D. parvula* mitochondrial haplotypes (5% ± 1% different to those currently known) into some *D. adjarica* has been detected in one locality; all the studied specimens of *D. adjarica* with mtDNA of *D. parvula* are unmistakably *D. adjarica* at the morphological and nuclear levels.

Morphologically, there is almost no overlap between *D. parvula* and *D. adjarica*. These results are corroborated by CDA, MST and UPGMA trees. Specimens of the inland high mountain population of Ardahan (clearly *D. adjarica* in CDA, MST and UPGMA trees) occupy a somewhat intermediate position between both taxa in the PCA (when specimens and not populations as a whole are considered), but this morphological closeness may be attributed to the influence of climatic factors (continental conditions) on scalation of the specimens. Males appear to be more differentiated than females. Overlap among samples within each species is very marked; none can be separated clearly from its conspecifics. This is even more marked in *D. parvula*, which has a fairly small area compared to *D. adjarica*.

Darevskia parvula and *D. adjarica* samples appear to be homogeneously clustered within species and well separated between the two species in the UPGMA trees. In males and females all the *D. parvula* samples are very similar and moderately differentiated. In males of *D. adjarica*, the most differentiated seems to be adjBorçka, the others all being clustered together, with adjÇaykara showing slightly more differentiation from the rest (adjOrtacalar, adjArdahan, adjIkizdere and adjÇermik).

Darevskia adjarica females are also similarly distributed into two subgroups, one including Borçka, Çermik and Ardahan and the other including Ortacalar, Ikizdere and Çaykara. In both sexes, the inland Ardahan sample clearly belongs to *D. adjarica.*

From the most connected MST samples, speculations can be made about areas of origin and expansion of the different taxa. Ortacalar (*D. adjarica*) and Hatila (*D. parvula*) are the most connected (morphologically more "central" in both taxa); in fact, both populations are relatively close, living on the northern (Black Sea) and southern (Anatolian) facing slopes, respectively of the Doğu Karadeniz Mountains (Kaçkar Mountains). This highlights these mountains, which rise from sea level up to nearly 4000 m asl. and have wide buffering possibilities against climate changes, as a zone of refuge and posterior dispersion of this species, and even of the original splitting into two taxa adapted to these different conditions, *D. adjarica* on the coast and *D. parvula* on the continental slope.

Osteologically *D. parvula* and *D. adjarica* are very similar, although Georgian specimens from an isolated population (Atskuri) have closed clavicles not found in Turkish *D. adjarica*. Also, inland Ardahan *D. adjarica* have an extra vertebra in both males and females, compared to the other studied specimens from both species.

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The present study indicates that the situation in Turkey is that *D. parvula* is well differentiated and lives around the Çoruh River Valley, contoured by *D. adjarica* populations on the coastal-facing slopes of the Doğu Karadeniz Mountains on one side, and the Yalnızçam Mountains on the other side, where *D. adjarica* enters from Georgia as the opposite extreme of a geographic distribution. The attribution of more inland ranges to *D. parvula* or *D. adjarica*, as well as the detailed genetic structure of both taxa may be confirmed with more specific studies.

Key words: *Darevskia parvula, D. adjarica* ***stat. nov.,*** caucasic rock lizards, distribution, morphometry, meristic scalation characters, multivariate analyses, CDA, PCA, ANOSIM, MST, UPGMA, osteology, genetic differentiation, northeastern Anatolia, Turkey, Georgia.

Introduction

Darevskia parvula was first described as *Lacerta saxicola* Eversmann *var. parvula nova*, based on specimens collected in the area of Artvin (Çoruh Valley), Kjatib-chan (between Borçka and Artvin), Ardanuç-Artvin and Borçka (Çoruh Valley) in Turkey (Lantz & Cyrén 1913). In many papers, even classic works, the authorship date appears erroneously as "Lantz & Cyren, 1936", probably as Darevsky in his seminal work on the group (Darevsky 1967) confused the date of the description with that of Lantz & Cyren's early revision paper of the "*Lacerta saxicola*" forms (Lantz & Cyren 1936). It appears erroneously dated in Darevsky 1967, Franzen 1990, Baran & Atatür 1998, Baran *et al.* 2004, Szczerbak 2003 and Ananjeva *et al.* 2006, among others.

The species is distributed over west and southwest Georgia and northeastern Turkey (Darevsky 1967; Darevsky & Eiselt 1980; Baran & Atatür 1998; Sindaco *et al.* 2000) and is a Pontic endemism.

It includes two subspecies that were split as recently as 1980, *D. p. parvula* and *D. p. adjarica* (Darevsky & Eiselt, 1980). The nominate subspecies lives around Artvin, Ardahan and Bayburt [Artvin, Borçka and Ardanuç, *fide* Darevsky 1967], while the distribution range of *D. p. adjarica* includes the coast of Rize and Artvin in Turkey and the adjoining areas of Georgia (Darevsky and Eiselt 1980, Baran & Atatür 1998, Sindaco *et al.*, 2000). As Lantz & Cyren (1913) do not designate a type specimen and some of the syntypes come from an area (Artvin Vilayet) also inhabited by *D. p. adjarica* (they are not sympatric, but live so closely that they coexist in the same Turkish province ["vilayet"]), the type locality must be restricted in the current study, as Darevsky & Eiselt (1980) did not restrict it.

Prior to its description, specimens of this species were included by other authors in *L. saxicola* f. typ. (Mehely 1909; Nikolsky 1910, 1913; Nesterov 1912). According to Bodenheimer (1944), *L. s. parvula* is one of the subspecies of *L. saxicola* inhabiting Anatolia. Darevsky (1967) stated that the specimens obtained from northeast Anatolia (Çoruh Valley, now *D. parvula* s. str.) show important differences in terms of meristic pholidotic characters from specimens collected from other areas within the distribution range (Adzharia and Abastumani, in Georgia, now *D. p. adjarica*), all of which were previously considered *Lacerta saxicola parvula*. According to his results, he argued that these differences could represent a cline among the populations of this subspecies. He showed differences in many of the key characters in Lacertid taxonomy including the Dorsalia, Gularia, Femoralia, Supralabialia, Tibialia, temporal scales and Supratemporalia, and also highlighted some interesting differences in the Supralabial scales (frequently 5 in *parvula*, but usually 4 in *adjarica*). In the same work, it was reported that *D. parvula* hybridizes in the field with *D. rudis* and *D. derjugini*.

Clark & Clark (1973) found a new locality for *L. s. parvula*, 15 km E of Artvin in Turkey. They also stated that specimens of *L. s. parvula* completely differed from other rock lizard specimens obtained from same locality (also included in this work as a subspecies of a comprehensive *L. saxicola*) and therefore should be accepted as a different species.

According to Başoğlu & Baran (1977), the distribution zone of *L. saxicola parvula* includes Anatolia and Caucasia. They also give a detailed distribution map of *L. saxicola parvula* in Turkey.

Darevsky & Lukina (1977) reexamined Clark & Clark's rock lizard specimens collected from Anatolia and attributed them to 5 different species, still leaving some of them inside the collective *L. saxicola* subspecies group. They attributed 3 specimens captured from 5 km W of Hopa (Artvin) to *L. parvula.* Three specimens collected from 15 km E of Artvin and Arsin (Trabzon) were accepted as a hybrid form of *L. parvula* and *L. rudis* (Darevsky & Lukina 1977). Orlova (1978) also commented on the existence of these natural hybrids between *D. parvula* and *D. derjugini*.

Darevsky & Eiselt (1980) describe the divergent specimens from the Mestia Region of Georgia mentioned by Darevsky (1967) as a new subspecies, *Lacerta parvula adjarica* (type locality: Abastumani, Georgia), and include in this subspecies the populations of the Pontic coast of NE Turkey.

Baran *et al.* (1997) examined the *L. parvula* specimens collected from Çamlıhemşin (Rize) in terms of pholidotic features and morphometric measurements and attributed them to the subspecies *L. p. adjarica*.

Arribas (1997, 1999) stated that Caucasian rock lizard species (the former *Lacerta saxicola* group) were different from other species groups of the collective genus *Lacerta* (*Lacerta* part II, sensu Arnold 1973) with respect to certain morphological (pholidosis characters and colour-pattern features), osteological, karyological and behavioural features. He therefore attributed the rock lizard species to a newly erected genus, *Darevskia* (Arribas, 1997).

The diagnostic characters of *D. parvula parvula* and *D. parvula adjarica* are summarized in a very simplified way in Szczerbak (2003) as being 51-69 scales at mid-body and 18–26 femoral pores in ssp. *parvula* and 50–66 (mid-body) and 15–22 (femoral) in ssp. *adjarica*. The latter also differs in having a triangular sixth submaxillar scale (more rounded in *parvula* s. str.).

Ilgaz (2009) studied *D. parvula* specimens collected from some previously known and new localities in Turkey (Yusufeli and Kılıçkaya, Artvin), evaluating their morphological features compared to those collected from the known distribution area of northeast Anatolia and enlarged distribution area of the species. The two existing subspecies were also compared morphologically with the help of univariate statistical tests and diagnostic characters checked. Contrary to Darevsky & Eiselt (1990), Ilgaz considers the Anatolian inland populations (such as Ardahan) to be *D. p. adjarica*.

Arribas (2012) pointed to the fact that *D. parvula* shares with the Iranian *D. defilippii* (also of uncertain position in the group) a brick-red colored belly, and to a possible basal relationship between these two species, which live in the extremes of the Caucasian Isthmus, constituting a disjunction between the Colchis and Hircanian (Talish) refuges. Osteologically, both share several characters, but these are primitive and widespread, and are uninformative about their true relationship.

Genetic approaches have so far only included Georgian specimens of *D. p. adjarica*, never Turkish specimens of this same subspecies or of the nominate *D. p. parvula*. Murphy *et al.* (1996) studied allozyme data and found *D. parvula* to be sister taxon to the *rudis*-group (*D. rudis*, *D. portschinskii* and *D. valentini*). Also, Fu *et al.* (1997), using Maximum Parsimony with mtDNA (cytochrome *b*), found that *D. parvula* was relatively isolated and sister taxon to other *Darevskia* groups. The same results (tentatively sister taxon to the *rudis*-group or sister taxon to all the *Darevskia* groups) were shown in subsequent papers on the subject (Fu 1999, 2000). A complete phylogeny of the Caucasian rock lizard (genus *Darevskia*) was inferred using mitochondrial DNA sequence and alloyzme data together (Murphy *et al.* 2000). These authors placed all fifteen bisexual rock lizard species into three major clades, namely *caucasica*, *saxicola* and *rudis*. According to the results of the present study, *D. parvula* is sister taxon to the *rudis* clade.

Other complementary techniques have been applied to the group. Grechko *et al.* (1997) found that *D. parvula* was sister taxon to all the other *Darevskia* when studied using "DNA Taxonprints" (Restriction endonuclease analyis of Highly Repetitive DNA). Ciobanu *et al.* (2002, 2003) and Grechko *et al.* (2006) also studied Satellite DNA in *Darevskia* and found a relatively isolated position of *D. parvula* in which only one type of Satellite DNA predominate (CLsatIII), and as inhabitants of one of the glacial refuges in the extremes of the Caucasus (as *D. clarkorum/dryada*) in the west and *D. chlorogaster* in the southeast, they argue that possibly they resemble the ancestors of the group. The presence of these same microsatellites in the "*mixta*-group" (*clarkorum*, *caucasica*, *daghestanica, dryada*) casts some doubts on the basal association of *D. parvula* with the *rudis* group as stated by means of mtDNA (see above). For Grechko *et al.* (2006), *D. parvula* would be outside these two clades, but hybridized in an early instance of its diversification with the ancestors of both clades.

In this paper, samples of *Darevskia parvula* from northeastern Anatolia were evaluated using morphological, osteological and molecular data and taxonomic assessments were performed.

Materials and methods

Morphology. A total of 213 specimens, collected from 10 localities in 2001 and 2002, were used (see

Supplementary Appendix 1 for locality data, sample sizes and sample acronyms—localities are the same as in Ilgaz 2009). Acronyms include information of the taxon to which they are ascribed and the name of the nearest locality (e.g. "adjArdahan" is a sample of *D. p. adjarica* from the surroundings of Ardahan). The study area covered the northeastern part of Turkey (Fig. 1) and Georgian specimens were used for osteological comparison. Color slides of the specimens were taken and specimens were then fixed with 5% formaldehyde in 70% ethanol and preserved in 70% ethanol according to the method described by Başoğlu & Baran (1977). The specimens were incorporated into the collection of ZDEU (Zoology Department, Ege University) and kept in the Zoology Lab of the Department of Biology at the Science Faculty, Buca, İzmir, Turkey. Cleared and stained specimens for bone studies are in Oscar Arribas' scientific collection (Barcelona, Spain).

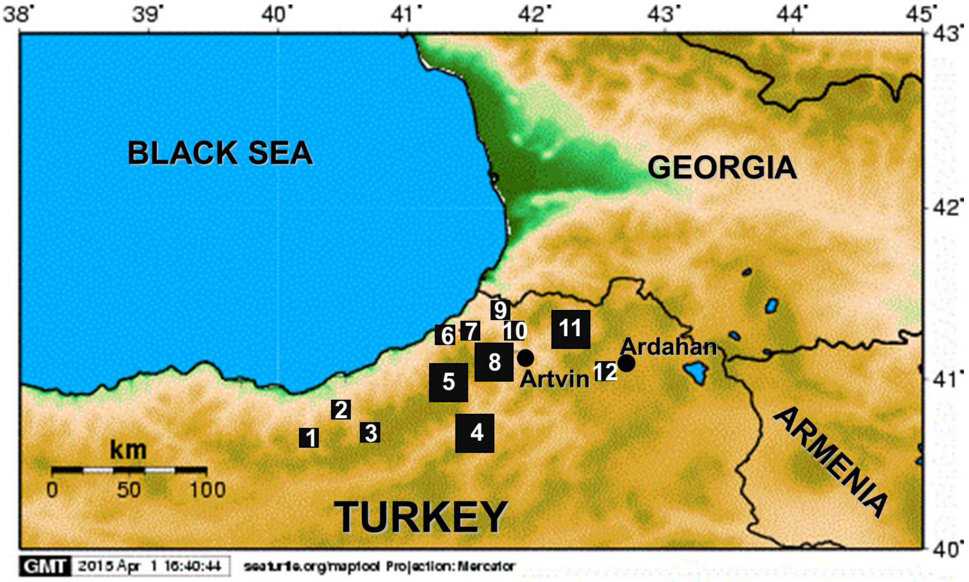

FIGURE 1. Map showing the localities of the samples studied. BIG SQUARES: *Darevskia parvula* (Lantz & Cyren, 1913). SMALL SQUARES: *Darevskia adjarica* (Darevsky & Eiselt, 1980). 1.10 km N of Çaykara. 2.Güneyce, Rize. 3. 12 km SE of İkizdere. 4. Between Kılıçkaya and Karadağ. 5.30 km SW of Yusufeli. 6. Between Arhavi and Güneşli Village 2. km., Arhavi, Artvin 7. 24 km W of Ortacalar. 8. Hatila Valley, Artvin. 9. 10 km E of Borçka. 10. 10 km W of Çermik. 11.15 km W of Şavşat. 12.19 km W of Ardahan. Taxon names correspond to changes proposed in this paper.

The following metric dimensions were taken using dial calipers with accuracy to the nearest 0.01 mm: Snout-vent length (SVL): tip of snout to anal cleft. Tail length (TL): anal cleft to tip of tail. Pileus width (PW): at widest point between parietal plates. Pileus length (PL): tip of snout to posterior margins of parietals. Head width (HW): at widest point of head. Head length (HL): tip of snout to posterior margin of ear opening. Furthermore, morphometric indexes were calculated, Pileus Index (PI) [(PL / PW) X 100] and Head Index (HI) [(HL / HW) X 100].

Meristic scalation characters considered here consisted of the following counts: supraciliar granules (left-right) (SCGa-SCGb), supraciliar plates (left-right) (SCPa-SCPb), supralabial plates (left-right) (SRLa-SRLb), sublabial plates (left-right) (SLa-SLb), transversal series of gular scales between inframaxillar symphysis and collar (MG), collaria (Coll), supratemporal scales (Sptmp), temporal scales 1 (transversal rows of temporal scales between masseteric and tympanic) (left-right) (TS1a-TS1b), temporal scales 2 (longitudinal rows of temporal scales between tympanic and parietal) (left-right) (TS2a-TS2b), temporal scales 3 (longitudinal rows of temporal scales between supratemporal and masseteric) (left-right) (TS3a-TS3b), postemporal plates (left-right) (POTa-POTb), ventral plates (transversal and longitudinal) (TVP and LVP), preanals 1 (number of preanals located anterior of anals) (PA1), preanals 2 (number of preanals surrounding anals) (PA2), femoral pores (left-right) (FPa-FPb), longitudinal rows of scales on ventral surface of thigh between the femoral pores and the outer row of enlarged scales (left-right) (LSa-LSb), subdigital lamellae in the 4th toe (left-right) (SDLa-SDLb), tibial scales (scales lying on dorsal surface of ankle between the large scales (TS) and transversal series of dorsal scales at the midtrunk (DS). The bilateral scales were combined in only one, non-redundant variable (the same acronyms, but without "a" and "b"). The shapes of the submaxillar were also examined and codified as 1 (narrower, more parallel, smooth and rounded scale: types A, B, C from Eiselt & Darevsky 1980) or 2 (more angulate, subtriangular scale: types: D, E, F from these same authors; Fig 2, see also Fig 10) (SBXTypx). Rostral-Internasal (R-I) and Postocular-Parietal (Post-Par) contacts were also examined and codified as 0 (no contact) and 1 (contact).

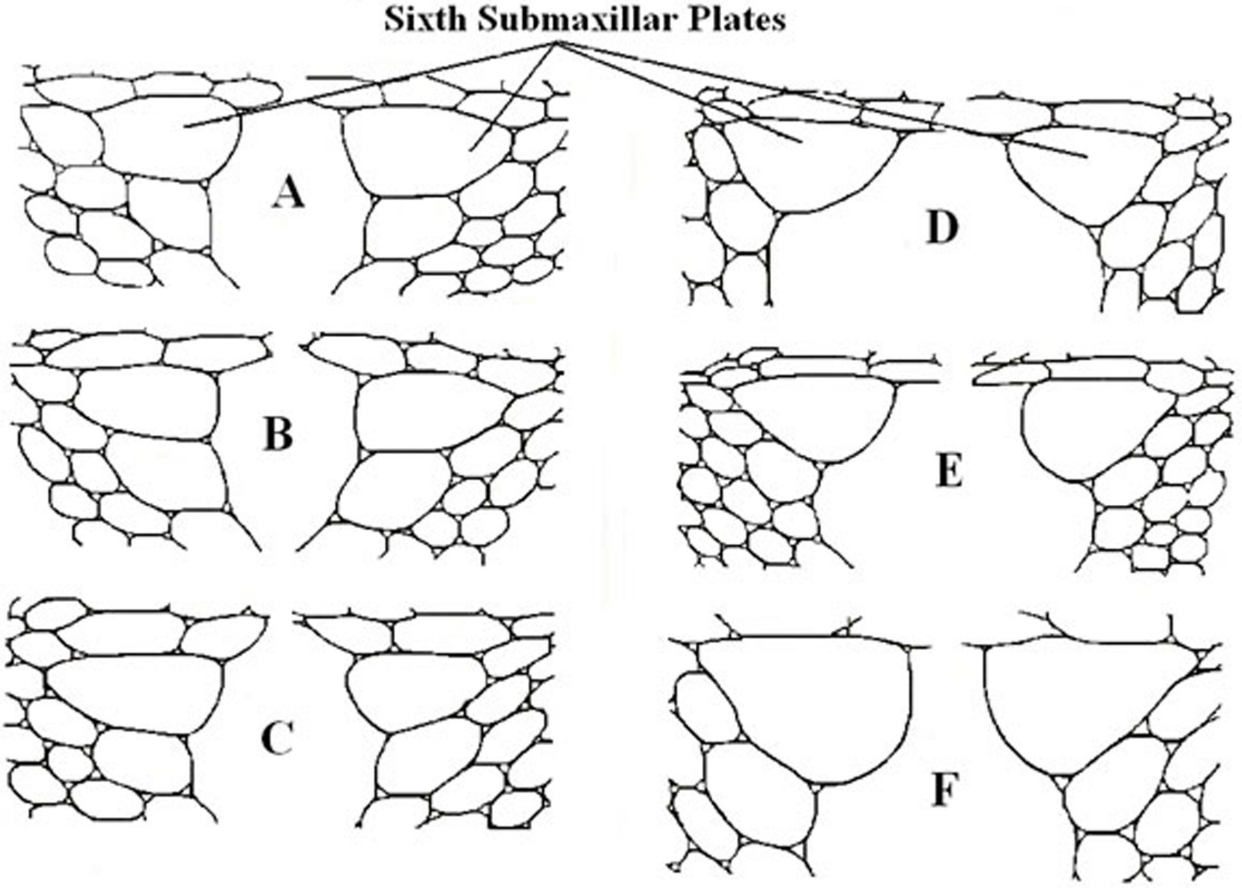

FIGURE 2. Variation of the 6th submaxillar plates, an easy diagnostic characteristic between both taxa (A–C, *D. parvula*; D–F, *D. adjarica*) (left–right). Note the subtriangular shape of the scale in *D. adjarica*, whereas it is fairly smooth shaped and rounded (even subquadrangular) in *D. parvula* (see also Fig. 10) Modified from Darevsky and Eiselt (1980). Taxon names correspond to changes proposed in this paper.

Statistical procedures. As a result of the sexual dimorphism in biometry and scalation presented by all the species of *Darevskia* (see for instance Darevsky 1967), morphological analyses were carried out separately for males and females.

Statistical analyses used in the morphological study were the multivariate techniques of Principal Components Analysis (PCA) and Canonical Discriminant Analysis (CDA) (Sokal & Rohlf 1969; Blackith & Reyment 1971; Legendre & Legendre 1998, and online help in the statistical programs utilized, see below).

Firstly, a PCA was conducted in which every specimen was considered independently, without a priori assignation to any group (population or taxon), retaining, however, the passive information of to which population they belonged (Henderson & Seaby 2007). Here, diverse overlap was observed between the different OTUs, and this was used together with the ANOSIM results to define different groups (those used in the Canonic Discriminant Analysis (CDA)) to confirm the differences between the nominal taxa and calculate the group centroids (hypothetical middle individuals of each group) and their Mahalanobis' distances for UPGMA trees and MST graph representations (Rohlf 2000).

Minimum-length Spanning Tree (MST) and UPGMA dendrograms were computed from the Mahalanobis' distance matrices (D^2) derived from CDA. MST detects the nearest neighbors based on position in multidimensional space. The most connected samples may be interpreted as the "central" ones of the species; in theory, the most primitive. In contrast, UPGMA trees show the global relationships among the samples (Arribas *et al.* 2006; Arribas 2010).

As mentioned above, an Analysis of Similarity (ANOSIM) (Clarke 1988, 1993) was carried out to test the significance of the differences between the samples. This tests whether the assigned groups are meaningful, that is, more similar within groups than between samples from different groups (see more details in Arribas 2010). To check for significance, pseudo-replication tests (1000 randomizations) were run to test if the given results could occur by chance. If the value of R is significant, there is evidence that the samples within groups are more similar than would be expected by random chance. The most useful feature of this test is that pairwise tests among populations allow significance testing of the differences among the groups concerned and detect which ones are really different from the others. However, if samples are small, this should be interpreted with caution.

In addition, Mantel tests were computed to test the correlation among matrices of morphological (Mahalanobis, D^2) distances (males and females separately) with geographical distance and altitude differences among localities.

CDA was calculated with NCSS 2007© (Hintze 2007). Mahalanobis' distances among sample centroids and their coordinates in CDA were calculated with DISC075S from the MULTICUA package (Arenas, Cuadras & Fortiana, 1991). MST, UPGMA trees and Mantel tests were calculated with NTSYS 2.1© (Rohlf 2000). PCA and ANOSIM analyses were performed with Community Analysis Package 4.0© (Henderson & Seaby 2007).

Osteological study. Previously fixed and alcohol preserved specimens were cleaned by means of 1% KOH in deionized water and bones stained with alizarin red. They were posteriorly differentiated and the excess of pigment eliminated with Mall solution (80% of the previous cleaning solution plus 20% glycerol), and preserved permanently in glycerol following the procedures of Taylor (1967) and Durfort (1978). Osteological nomenclature is as in Arribas (1998). Information about the studied specimens and their localities is in Supplementary Appendix 2.

Molecular analyses. A total of 11 specimens of *Darevskia* including 6 *D. p. parvula* and 5 *D. p. adjarica* were used in the molecular analyses (see Supplementary Appendix 3 and Fig. 1). *Archaeolacerta bedriagae* (Camerano, 1885) was used to root the phylogenetic tree. A list of all the specimens with their GenBank accession numbers and other relevant information is presented in Supplementary Appendix 3 (GenBank accession number *Archaeolacerta bedriagae* GQ142126). Genomic DNA was extracted from ethanol-preserved tissue samples using the Qiagen DNeasy Blood & Tissue Kit. All specimens were sequenced for the mitochondrial gene cytochrome *b* (*cytb*) and four specimens for the nuclear gene melano-cortin 1 receptor (*mc1r*). Primers, PCR conditions and source references for the amplification of the mitochondrial and nuclear markers are as in Carranza & Arnold (2012). Chromatographs were checked manually, assembled and edited using Geneious v. 5.3.6 (Biomatters Ltd.). Alignment of the mitochondrial and nuclear markers was unambiguous. Gene fragments were translated into amino acids and no stop codons were observed. For the nuclear loci, *mc1r* heterozygous individuals were identified based on the presence of two peaks of approximately equal height at a single nucleotide site and coded with the appropriate IUPAC ambiguity code. The *cytb* dataset was analyzed with the maximum likelihood (ML) method. The best-fitting model of sequence evolution was inferred using jModeltest v.2.1.3 (Guindon & Gascuel 2003; Darriba *et al.* 2012) under the Akaike Information Criterion (AIC) (Akaike 1973). The ML analysis was performed on RAxML v.7.4.2 (Stamatakis 2006) as implemented on raxmlGUI (Silvestro & Michalak 2012) with 100 random addition replicates, using the GTR+G model of sequence evolution and independent model parameters for each gene partition. Reliability of the ML tree was assessed by bootstrap analysis (Felsenstein 1985) including 1,000 replications. Uncorrected genetic distances were calculated using MEGA 5 (Tamura *et al.* 2012).

Results

Morphology. Descriptive statistics of scalation characters and biometrical dimensions obtained from specimens used in the present study is given in Supplementary Tables 1–4.

Principal components analysis (PCA). PCA was used to explore the differences among the samples while recovering the information about the procedence of the specimens after the analysis. Every specimen was used in the calculations, in comparison with all the others.

Males: [Fig. 3] The two first axes of the PCA account for 33.7% of the total variability. The first axis (Eigenvalue 5.12; 23.3% of variance explained) separates the populations ascribed to *D. p. parvula* in the negative part of the axis (characterised by higher values of POT (-0.32), DS (-0.31), FP (-0.31), TS2 (-0.26), LS (-0.25), SDL (-0.23), SRL (-0.23), TS (-0.19), TS3 (-0.19) ,TS1 (-0.17), and Coll (-0.07) and lower values of SBXTyp

(0.35) and R-I (0.14)) from populations of *Darevskia parvula adjarica,* which are situated towards the positive part and have contrary values for these parameters. The second axis (Eigenvalue 2.30; 10.46% of variance explained) is characterized on its positive part by SDL (0.34) and POT (0.26), and its negative part mainly by TS (-0.42), TS1 (-0.37) and TS3 (-0.30), allowing for distinction of samples inside the same taxon (*parvula* or *adjarica*).

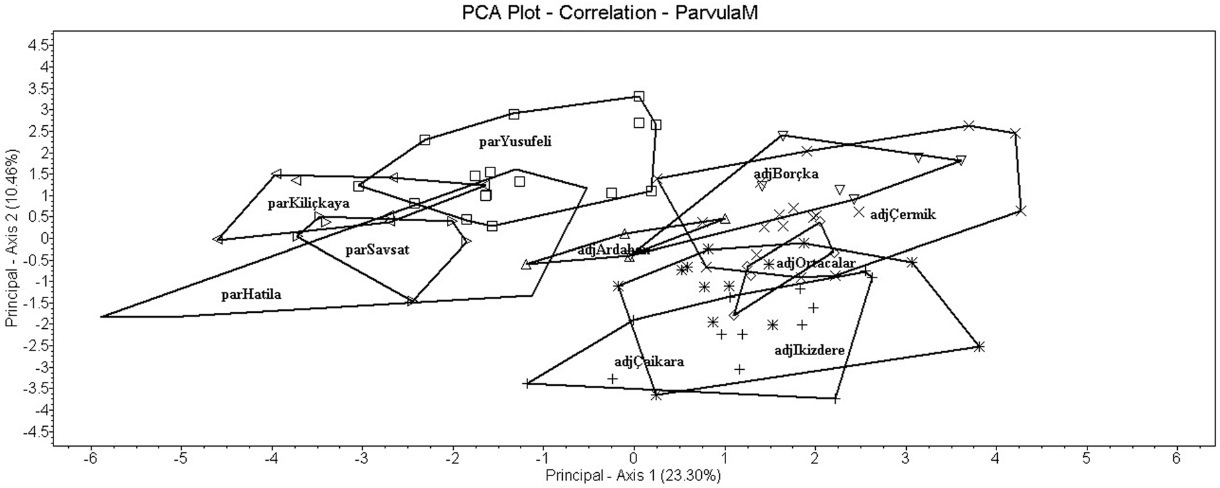

FIGURE 3. PCA plot of the biometric and scalation characteristics of MALES of *D. parvula* and *D. adjarica.* See text for explanation of the results.

There is almost no overlap between taxa on the first axis, but the adjArdahan sample occupies an intermediate position on the graph. There is considerable overlap of adjÇermik+adjBorçka (towards the positive part of the second axis) and of adjÇaykara+adjIkizdere (towards the negative part of second axis), with adjOrtacalar having an intermediate position. In *D. p. parvula*, parŞavşat and parHatila overlap in great part, with very moderate coincidence with parKılıçkaya and especially parYusufeli, which is more differentiated towards the positive part of the second axis.

Females: [Fig. 4] The two first axes of the PCA account for 33.9% of the total variability. The first axis (Eigenvalue 4.82; 21.94% of variance explained) separates the populations ascribed to *D. p. parvula* on the negative part of the axis (characterized by higher values of POT (-0.35), TS2 (-0.31), DS (-0.29), FP (-0.29), SDL (-0.25), SRL (-0.25), TVP (-0.20), TS3 (-0.21), TS1 (-0.14) and SCG (-0.13) and lower values of SBXTypx (0.36), Sptmp (0.12), and Post-Par (0.11)) from *D. p. adjarica* on its positive part, with contrary values for all these parameters.

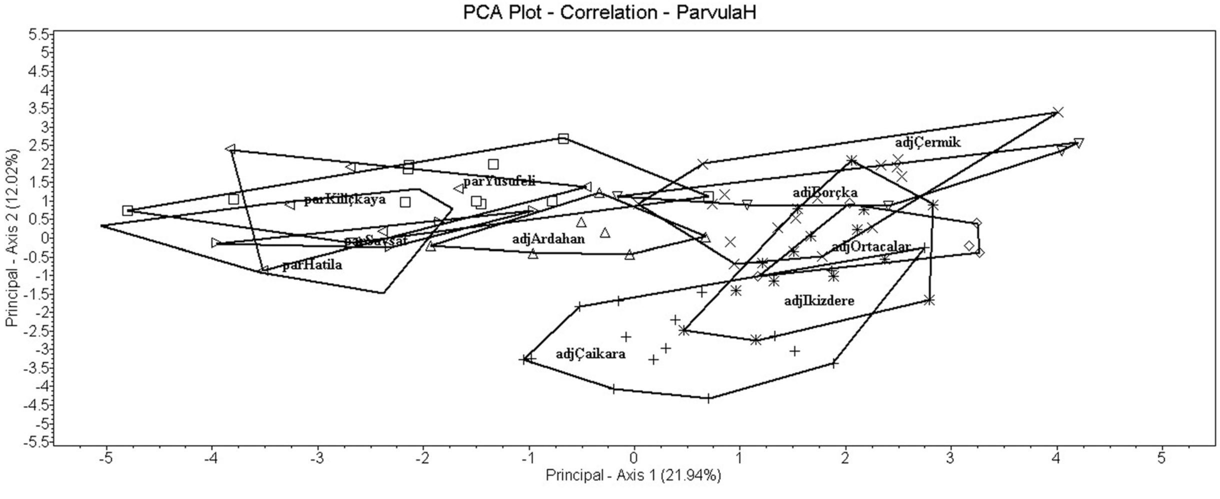

FIGURE 4. PCA plot of the biometric and scalation characteristics of FEMALES of *D. parvula* and *D. adjarica.* See text for explanation of the results.

The second axis (Eigenvalue 2.64; 12.02 % of variance explained) is characterized on its positive part by SDL (0.36), SCG (0.30), DS (0.25) and Post-Par (0.20); and on its negative part by TS1 (-0.39), TS3 (-0.38), Sptmp (-0.31) and TS (-0.26). There is considerable overlap of all the populations studied (both of *parvula* and *adjarica*) on this axis, and only adjÇaykara is clearly differentiated towards the negative part.

There is almost no overlap between *Darevskia parvula parvula* and *D. p. adjarica* in the bidimensional space defined by these two axes, with one notable exception. The adjArdahan females appear in an intermediate position on the graph and almost without overlap with other samples, but are clearly more associated with *D. p. parvula* samples than with *D. p. adjarica* along the first axis. As in males, there is overlap of adjÇermik+adjBorçka and adjOrtacalar+adjIkizdere; the latter partly overlaps with adjÇaykara. In *D. p. parvula* there is considerable overlap between all four samples.

ANOSIM tests. *Males:* ANOSIM tests were significant and confirmed that there were differences among males of the studied populations (R-statistic = 0.55966, $P < 0.001$ with 1000 randomizations). Populations were usually different from each other. There were, however, some paired samples which had no differences (that is, their specimens were more similar to each other than within their own population). There were no differences between the "intermediate" population of Ardahan (adjArdahan) and adjÇermik, adjIkizdere, or parYusufeli (all $P > 0.1$). In addition, there were no differences between adjOrtacalar, adjÇermik and adjIkizdere ($P > 0.1$). Within *D. p. parvula*, there were no differences between parHatila and parKılıçkaya ($P>0.2$), between parHatila and parŞavsat ($P>0.7$), or between parKılıçkaya and parŞavşat ($P>0.1$).

Females: As in males, ANOSIM tests were significant and confirmed differences among females in the studied populations (R-statistic = 0.5657, $P < 0.001$ with 1000 randomizations). As in the male analysis, there were usually differences between samples. In *adjarica*, there were no differences between adjOrtacalar and adjIkizdere ($P > 0.3$); in *parvula*, parŞavsat was no different from parHatila ($P > 0.7$) or parKılıçkaya ($P > 0.1$).

Canonical Discriminant Analysis (CDA). Once the relationships between the isolated specimens had been studied and information of the dispersion of the different geographic samples had been recovered, a CDA analysis was performed for entire populations, searching for differences between them in order to find clearer discriminating characters.

Males: [Fig. 5]: The first axis (Eigenvalue 37.65; 79.7% of variance explained; $F_{198} = 6.2$, $P < 0.0001$; Wilk's Lambda = 0.000111) separates *D. p. parvula* on its positive part (characterized by greater values of TVP (0.33) POT (0.26) FP (0.23) PA2 (0.18) SL (0.13) DS (0.11), and lower values of SBXTypx (-0.98), TS2 (-0.14), Coll (-0.13), Post_Par (-0.12), Sptmp (-0.10)) from *D. p. adjarica* on the negative part, characterized by contrary values.

The second axis (Eigenvalue 3.74; 7.9 % of variance explained; $F_{168}=3.6$, $P< 0.0001$; Wilk's Lambda = 0.004304) separates the populations of *D. p. adjarica* in a series with overlap among them, with adjBorçka at one extreme and adjÇaikara at the other. Populations of *D. p. parvula* are scarcely differentiated, with a wide overlap and intermediate scores. The negative scores (with adjBorçka) are characterized by greater values of TS3 (0.53), TS (0.49), TS1 (0.31), Sptmp (0.30), MG (0.25), TS2 (0.23) and lower values of DS (-0.59) and SDL (-0.49). *Darevskia p. adjarica* populations are ordinated in a gradient from adjBorçka on the negative part of the axis to adjÇaykara at the extreme positive part, characterized by contrary values on the abovementioned characters.

The third axis (Eigenvalue 1.2; 4.1% of variance explained; $F_{140} = 2.9$, $P < 0.0001$; Wilk's Lambda = 0.020407) separates the populations of both taxa along two independent gradients. In *D. p. parvula*, populations appear ordinated (from negative to positive) from parYusufeli, to parHatila and parŞavsat up to parKılıçkaya. However, the centroids are in the order of parŞavşat, parKılıçkaya + parYusufeli and parHatila. In *D. p. adjarica* the gradient runs from the negative part of the axis, adjÇermik, to adjÇaykara+adjArdahan and adjOrtacalar up to adjIkizdere and adjBorçka on the positive extreme (centroids: adjÇaykara adjBorçka, adjIkizdere, adjÇermik, adjOrtacalar, adjArdahan). The negative part is characterized by greater values of DS (-0.36) and TS2 (-0.33), and lower values of TVP (0.83), SDL (0.53), Post_Par (0.43), TS1 (0.40) and PA2 (0.39).

Females: [Fig. 6] The first axis: (Eigenvalue 9.65; 56.2% of variance explained; $F_{198} = 3.9$, $P < 0.0001$; Wilk's Lambda = 0.000811) separates *D. p. parvula* on the positive part from *D. p. adjarica* on the negative. Both taxa show less discrimination than in the male analysis. They do not overlap, but are very close in their values, especially between the adjArdahan sample and the *D. p. parvula* ones. The *parvula* samples are characterized by greater values of POT (0.60), SDL (0.35), DS (0.22), TVP (0.18), FP (0.16), SRL (0.15) and Post_Par (0.14) and lower values of SBXTypx (-0.57), TS1 (-0.22), LS (-0.21), Sptmp (-0.19) and TS (-0.19). *Darevskia p. adjarica* is characterized by contrary values for these characters.

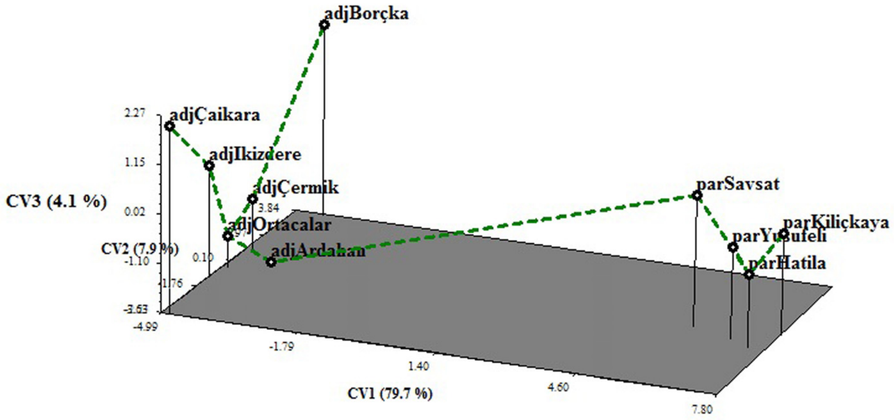

FIGURE 5. Three-dimensional CDA plot and MST superimposed of the biometric and scalation characteristics of MALES of *D. parvula* and *D. adjarica.* See text for explanation of the results. Taxon names correspond to changes proposed in this paper.

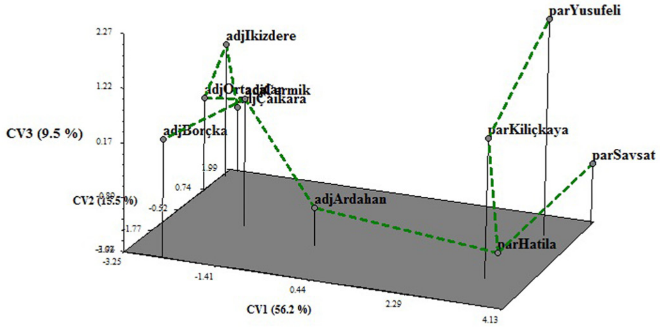

FIGURE 6. Three-dimensional CDA plot and MST superimposed of the biometric and scalation characteristics of FEMALES of *D. parvula* and *D. adjarica.* See text for explanation of the results. Taxon names correspond to changes proposed in this paper.

The second axis: (Eigenvalue 2.66; 15.5% of variance explained; $F_{168} = 2.8$, $P < 0.0001$; Wilk's Lambda = 0.008640) separates the populations of both taxa on a gradient, especially the *D. p. adjarica* ones, but with considerable overlap. *Darevskia p. parvula* values (positive values) range from the very blended parŞavşat, parYusufeli and parHatila, up to the extreme of parKılıçkaya. *Darevskia p. adjarica* samples are more spread along this axis. From the positive to the negative part of the axis appear adjÇaykara, adjIkizdere, adjOrtacalar, adjÇermik and adjBorçka. adjArdahan overlaps in part with adjÇermik, but is closer to the *D. p. parvula* specimens. The positive parts of the axis had greater values for TS1 (0.46), SRL (0.37), POT (0.28), PA1 (0.27), FP (0.25), SL (0.22), TS2 (0.22) and MG (0.21) and lower values for SDL (-0.72), DS (-0.36), TVP (-0.36), Coll (-0.21), R_I (-0.16) and LS (-0.14).

The third axis: (Eigenvalue 1.63; 15.5% of variance explained; $F_{140} = 2.3$, $P < 0.0001$; Wilk's Lambda = 0.031624) is not very discriminatory and shows much overlap among the samples. However, centroids of parYusufeli and parKılıçkaya stand out on the positive part of the axis, away from parŞavşat and especially parHatila. The negative part (parHatila) is more defined by lower values of TS (-0.57), DS (-0.56), TVP (-0.38), and the positive part (parYusufeli) by SCP (0.35), SCR (0.34) and LS (0.32).

UPGMA. UPGMA trees were constructed separately for males and females from the matrices of Morphological (Mahalanobis) squared distances.

Both male and female trees yield very similar results and are in fact highly correlated (good fit: 0.9 < r < 0.8; Rohlf 2000; normalized Mantel test, r = 0.8134; Mantel test with 250 pseudoreplications: t = 5.4324, P = 1).

Males: [Fig. 7] The two nominal taxa *D. p. parvula* and *D. p. adjarica* appear to be homogeneously clustered and well separated from each other. There is little differentiation among *D. p. parvula*. In *D. p. adjarica*, the most differentiated seems to be adjBorçka, the others all being clustered together, with adjÇaykara showing slightly more differentiation from the rest (adjOrtacalar, adjArdahan, adjIkizdere and adjÇermik).

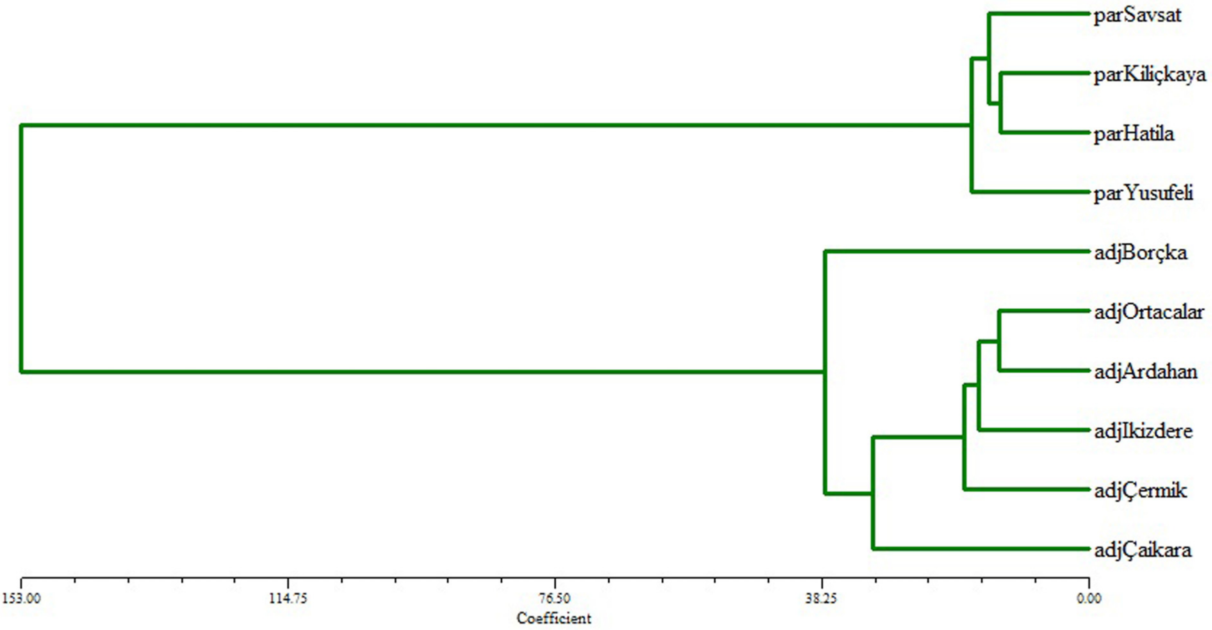

FIGURE 7. UPGMA-tree constructed from Mahalanobis' distances based in the biometric and scalation characteristics of MALES of *D. parvula* and *D. adjarica* populations studied.See text for explanation of the results.

The matrix of ultrametric distances derived from this tree matches very well (very good fit: 0.9 < r; Rohlf, 2000) with the original distances of the Mahalanobis distances matrix (Cophenetic Correlation Coefficient: r = 0.97893; Mantel test t = 6.2485, P = 0.0010). This means that the tree represents their true relationships very accurately.

Morphological differentiation has no correlation with either geographical distances (normalized Mantel test, r = -0.06347; Mantel test with 250 pseudoreplications: t = -0.4490, P = 0.3267) or altitude differences (normalized Mantel test, r = -0.10617; Mantel test with 250 pseudoreplications: t =-0.7404, P = 0.2295).

Females: [Fig. 8] The degree of population differentiation in the female analysis is similar to that found in the male analysis, but the two nominal taxa are less different than in the males. The two nominal taxa are equally homogeneous. *Darevskia p. parvula* samples are similarly differentiated. *Darevskia p. adjarica* are also similarly distributed between two subgroups: one including adjBorçka, adjÇermik and adjArdahan and the other including adjOrtacalar, adjIkizdere and adjÇaykara.

The matrix of ultrametric distances derived from this tree also matches very well (good fit: 0.9 < r < 0.8; Rohlf, 2000) with the original distances of the Mahalanobis distances matrix (Cophenetic Correlation Coefficient: r =

0.84334; Mantel test with 250 permutations, t = 5.629, P = 0.0010). Thus, the tree represents their true relationships very accurately.

As in the male analysis, morphological differentiation has no correlation with either geographical distances (normalized Mantel test, r = 0.01759; Mantel test with 250 pseudoreplications: t = 0.1152, P = 0.5459) or altitude differences (normalized Mantel test, r = -0.19071; Mantel test with 250 pseudoreplications: t =-1.2524, P = 0.1052).

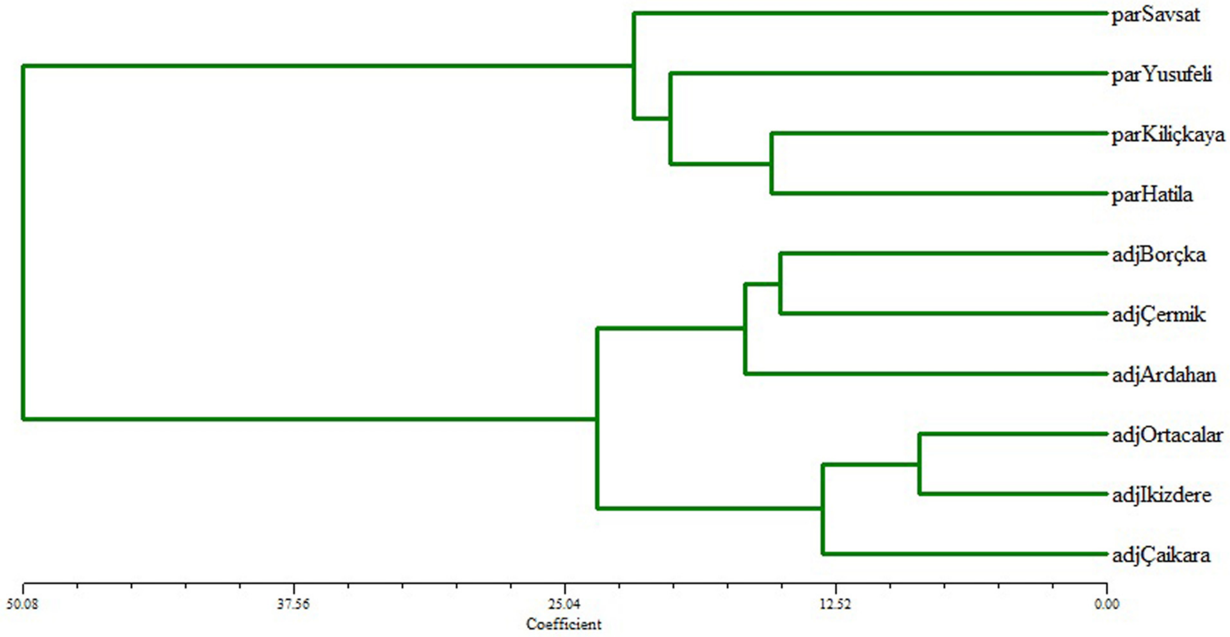

FIGURE 8. UPGMA-tree constructed from Mahalanobis' distances based in the biometric and scalation characteristics of FEMALES of *D. parvula* and *D. adjarica* populations studied. See text for explanation of the results.

Minimum Spanning Tree (MST). In addition to the results of the UPGMA trees and their high Cophenetic Correlation Coefficients (indicating that trees are very similar to the original distances matrix), an MST tree was run to find the closest neighbors for each population, find which are the closest among the two nominal taxa, and finally which are the most connected to the others and are thus more central and theoretically, the most primitive.
Males: [Fig. 5, superimposed to CDA] MST clusters the two nominal taxa (distances are greater in males than in females, as is usual in Lacertini studies), confirming adjArdahan as an *adjarica* population, which although very well separated, is the closest one to *parvula* s. str. In *D. p. adjarica,* the most connected sample is adjOrtacalar, oscillating the intrataxon distances between 12.8 and 26.9. In *D. p. parvula,* the most connected is parHatila, oscillating the intrataxon distances between 12.7 and 14.7. As previously mentioned, the most related intertaxa samples are adjArdahan and parŞavşat (distance 118.0).

Females: [Fig. 6, superimposed to CDA] On the female MST, adjÇermik and parHatila are the most connected of their respective taxa. In *D. p. adjarica*, distances among populations oscillate between 8.69 and 18.7. In *D. p. parvula* the distances range from 15.5 to 18.3. The closest intertaxa relationship is between adjArdahan and parHatila (18.2), no greater than some of the intrataxa distances.

Osteology. The osteology of *Darevskia parvula* is very similar to other *Darevskia*, characterized mainly by primitive and widespread characters among the group. The two nominal taxa are very similar, if not virtually identical, as is usual between closely related lizards. There are, however, some characters shared by all *D. parvula,* which are interesting when tracing their relationships with other *Darevskia* spp. See Supplementary Appendix 2 for the samples studied.

For comparison, the Turkish *D. p. parvula* and *D. p. adjarica* were treated separately, as well as the Georgian *D. p. adjarica* and the adjArdahan sample, which has some interesting differences.

Turkish *D. p. parvula* has an average of 7 premaxillary teeth, 17.7 maxillary teeth, 21.6 dentary teeth, 27 presacral vertebrae in males and 28 in females (6 short ones in the lumbar area). There is no trace of short vertebrae associated with the third presacral vertebrae. Tail autotomic vertebrae are type A (Arnold 1973; Arnold *et al.*

1997). All the clavicles studied are open (marginated). Interclavicle is typically cruciform and rounded, oval or irregularly cordiform. Costal formula is (3+2) with one or no inscriptional rib in similar proportion of occurrence. Postorbital bone is clearly shorter than the Postfrontal. More usually (proportion 4:1), anteromedial process of Postocular is present, but small and frequently very reduced. Anterodistal process of the Postfrontal is present. Squamosal and postocular overlap along one third of the length of the latter (from 1/2 to 1/5, but usually around 1/3).

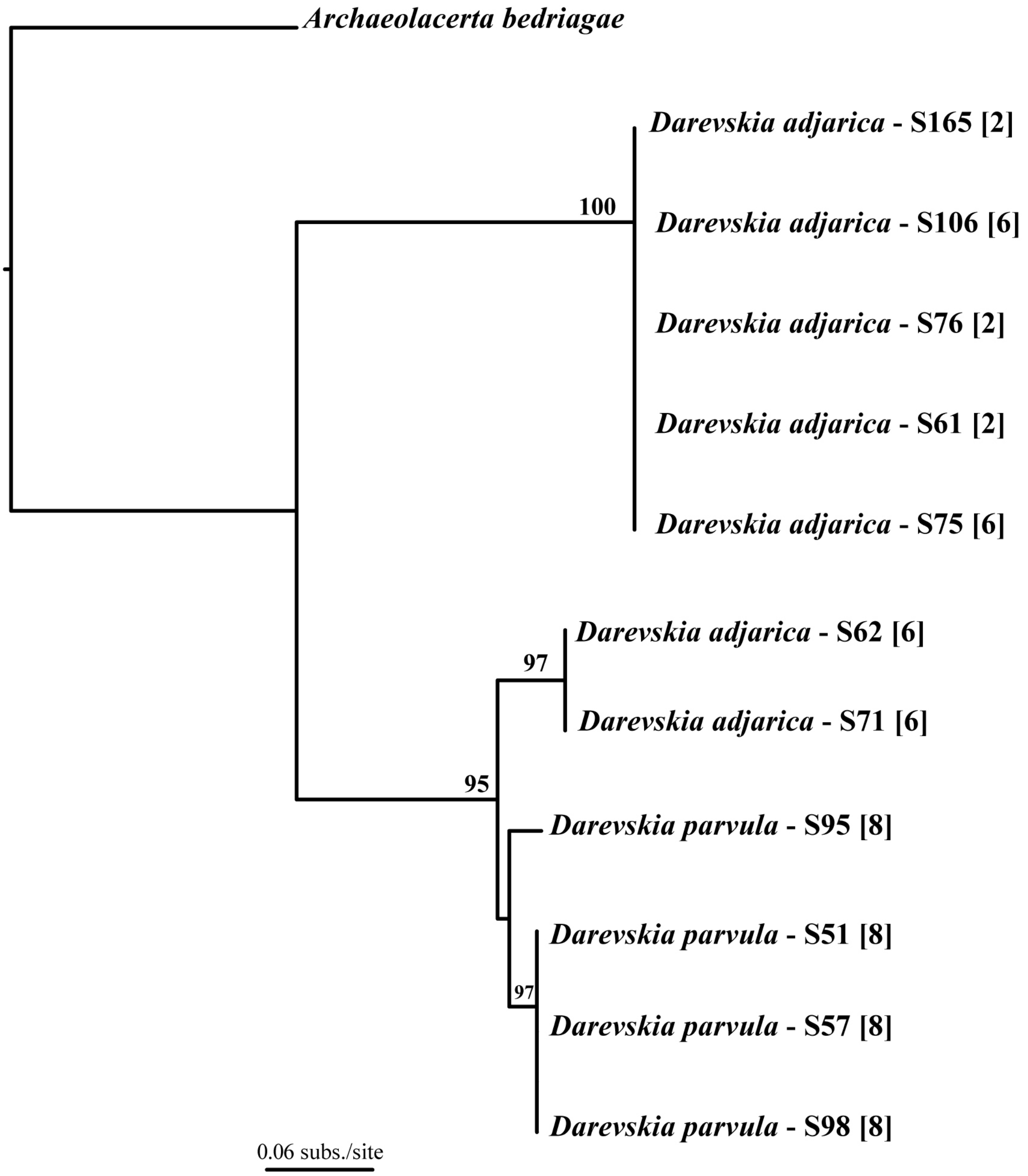

FIGURE 9. Maximum-likelihood tree inferred using the mitochondrial *cytb* gene. Specimen codes are shown after species names and numbers between square brackets indicate code specimens and locality numbers from Supplementary Appendix 3 and Fig. 1 (Map), respectively. Bootstrap values higher than 70% are indicated above the corresponding nodes.

Turkish *D. p. adjarica* (excluding the inland ones from Ardahan) are similar and have an average of 7 premaxillary teeth, 17.16 maxillary teeth, 21.19 dentary teeth, 26.8 presacral vertebrae in males (only one of the studied had 26, the rest 27), and 28 in females (6 short ones in the lumbar area in both sexes). There is no trace of short vertebrae associated with the third presacral vertebrae. Tail autotomic vertebrae are type A (Arnold, 1973; Arnold *et al.* 1997). All the clavicles studied are open (marginated). Interclavicle is typically cruciform and rounded, oval or irregularly cordiform. Costal formula is (3+2) with one or no inscriptional rib in similar proportion of occurrence. Postorbital bone is clearly shorter than the Postfrontal. More usually (proportion 2:1) anteromedial process of Postocular is present, but small or very reduced. Anterodistal process of the Postfrontal is present. Squamosal and postocular overlap along one third to one quarter of the length of the latter.

Georgian specimens of *D. p. adjarica* are also very similar, with an average of 7 premaxillary teeth, 17 maxillary teeth, 20.1 dentary teeth, 27 presacral vertebrae in males and 28–29 in females (6 short ones in the lumbar area - 7 on one side of an asymmetrical male). There is no trace of short vertebrae associated with the third presacral vertebrae. Tail autotomic vertebrae are type A, but also some of type B (Arnold, 1973; Arnold *et al.* 1997). All the clavicles studied are open (marginated) except one (unilaterally) in one specimen. Interclavicle is typically cruciform and rounded or slightly oval. Costal formula is (3+2) with or without one inscriptional rib in half of the specimens. Postorbital bone is clearly shorter than the Postfrontal. More usually (proportion 4:1) anteromedial process of Postocular may exist, be very reduced (half of specimens) or even absent. Anterodistal process of the Postfrontal is present. Squamosal and postocular overlap along one third to one quarter of the length of the latter.

Finally, the high mountain population from Ardahan (above 2000 m) merits special mention. Its characteristics are similar to other *D. parvula*, but specimens are outstanding as they have extra presacral vertebrae (28 instead of 27 in males and 29 instead of 28 in females). Also, in the females there are 7 short lumbar ribs (the normal number, 6, appear in the males).

Molecular analyses. The *cytb* dataset included 306 base pairs (bp), of which 54 were variable (excluding the outgroup). The results of the phylogenetic analyses are presented in Fig. 9 and indicate the presence of two reciprocally monophyletic groups. One clade includes *D. p. adjarica* specimens from Güneyce (Rize, Northeastern Anatolia, 3 specimens) and from an area between Arhavi and Güneşli (Artvin, Northeastern Anatolia, 2 specimens), all morphologically "*adjarica*". All five specimens present identical sequences despite the relatively large distance between the two localities (90 km) (see Fig. 1). The second clade includes *D. p. parvula* specimens from a locality between Artvin and Hatila Valley (Artvin, Northeastern Anatolia, 4 specimens; Fig. 1) and two specimens morphologically classified as *D. p. adjarica* from the abovementioned locality "between Arhavi and Güneşli" (Artvin, Northeastern Anatolia). The uncorrected genetic distance between the two main clades is 14.4% ± 1.9% and the distance between *D. p. parvula* and the two mitochondrially closely related *D. p. adjarica* specimens is 5% ± 1 %. Genetic variability within *D. p. parvula* is very small (1.5% ± 0.5%). In order to clarify the strange phylogenetic position of the two specimens of *D. p. adjarica* (S62 and S71) which are more closely related to *D. p. parvula* than to the other two specimens of *D. p. adjarica* from exactly the same locality (S75 and S106), sequences of the nuclear gene *mc1r* were obtained and visually compared for specimens S61, S75 and S62 (all of them morphologically classified as *D. p. adjarica*) and specimen S95 (*D. p. parvula*). The results of the comparison indicate that specimen S62 of *D. p. adjarica* (mitochondrially closely related to *D. p. parvula*) is identical to specimens S61 and S75 (*D. p. adjarica)* and these three samples differ by five mutations from specimen S95 of *D. p. parvula*.

Discussion and conclusions

Taxonomic consequences. High mitochondrial distance, nuclear differences and morphological distinctiveness warrant the specific status of both taxa: *Darevskia parvula* (Lantz & Cyrén, 1913) and *Darevskia adjarica* (Darevsky& Eiselt, 1980) **stat. nov.**

Darevskia parvula has been described with syntypes from the area of Artvin (Çoruh Valley), Kjatib-chan (between Borçka and Artvin), Ardanuç-Artvin and Borçka (Çoruh Valley) in Turkey (Lantz & Cyrén 1913) which represent a mixture of both taxa (Artvin-*parvula*; between Borçka and Artvin-*adjarica*; Ardanuç-*parvula* and Borçka-*adjarica*). To avoid taxonomic or nomenclatorial problems, in the present study, the taxon name has been fixed to only one of these localities, and one of the true nominate *D. parvula* syntypes from Lantz & Cyrén (1913) has been chosen as the lectotype of the species: a female deposited in the Naturhistoriska Museet Göteborg (GNM 2862), from Artvin (photographed in Darevsky & Eiselt 1980; Abb. 3 Fig. 3, nr. 7).

Genetic differentiation. The uncorrected genetic distance between *D. parvula* and *D. adjarica* clades is 14.4% ± 1.9%. Moreover, both taxa appear very close now, almost parapatric, and their mtDNA has introgressed in the past, producing *parvula*-like haplotypes (5% ± 1% different to the currently known ones) in some *D. adjarica* (witness specimens S62 and S61; Fig. 9). The differences between these *parvula*-related haplotypes and the true *D. parvula* ones should be interpreted as long-term independent divergence of these *parvula* haplotypes introgressed into *D. adjarica* in respect to the main mtDNA genetic pool of the true *D. parvula*.

The genetic variability within *D. parvula* is very small (1.5% ± 0.5%), and *D. adjarica* also seems to be very uniform as distant localities (90 km) share the same haplotype.

The nuclear gene *mc1r* of these *D. adjarica* with *parvula*-like haplotypes (S62 and S71) show that they are true *D. adjarica*, indistinguishable from their syntopic true *adjarica*-haplotype specimens (S75 and S106). All the *D. adjarica* are nucleally identical and differ from *D. parvula* by two mutations.

Morphological differentiation. As can be seen from the PCA results, there is almost no morphological overlap between *D. parvula* and *D. adjarica*. These results are corroborated by CDA, MST and UPGMA trees.

When specimens are not assigned a priori to any population, specimens of the inland high mountain population adjArdahan occupy an intermediate position between both nominal taxa on the first PCA axis, which is the most informative one. In the analysis of females, adjArdahan appears more associated with *D. parvula* samples than with true *D. adjarica*, but is also intermediate. This morphological closeness may be attributed to the influence of climatic factors in scalation. Inland *D. adjarica* from continental climate areas are more similar in their scalation to the *D. parvula* which live in continental climates than they are to the populations of *D. adjarica* from coastal ranges with mild oceanic climates.

In this PCA without population assignation and within each nominal taxon, for *D. parvula*, parŞavşat and parHatila overlap in great part, with very moderate coincidence with parKılıçkaya and especially parYusufeli, which is more differentiated. In the female analysis, the overlap among all the populations is very marked. In any case, all these *D. parvula* populations are very similar. In *D. adjarica* males there is considerable overlap of adjÇermik+adjBorçka and of adjÇaykara+adjIkizdere; adjOrtacalar has an intermediate position. Among females adjÇermik+adjBorçka and adjOrtacalar+adjIkizdere are grouped, the latter overlapping in part with adjÇaykara. All these populations are taxonomically fully assimilable.

ANOSIM was not very resolutive as some of the samples were reduced. It confirmed, however, that there were differences among the different populations (in males and females), but even more informative were some paired samples which had no differences (that is, they were more similar to each other than to other specimens within their own populations). There were no differences between the “intermediate” population of Ardahan (adjArdahan) and adjÇermik, adjIkizdere, or parYusufeli. In addition, there were no differences between adjOrtacalar, adjÇermik and adjIkizdere in males or females. These results highlight the fact that adjArdahan is a *D. adjarica*, despite its somewhat intermediate position in the PCA. Within *D. parvula*, parHatila, parKılıçkaya and parŞavşat are largely equivalent in both sexes.

CDA separated fairly well (by a priori discrimination into concrete samples) the two nominal taxa *D. parvula* and *D. adjarica* (more different in males than in females, as is usual in Lacertini studies), confirming adjArdahan as a *D. adjarica* population, as indicated by Ilgaz (2009) and contrary to Darevsky & Eiselt (1990), but see below. This adjArdahan is the closest *adjarica* to the *parvula*, but there is still a great distance between them.

Darevskia adjarica as a species is differentiated from *Darevskia parvula* in both sexes, particularly by a lower number of posttemporals, dorsals, femoral pores, subdigital lamellae, supralabials, longitudinal rows of temporal scales between the tympanic and parietal, longitudinal rows of temporal scales between the supratemporal and masseteric and higher value of SBXTyp (the subtriangular types) (Fig 10). In addition, males of *Darevskia adjarica* have a lower number of longitudinal rows of scales on the ventral surface of the thigh between the femoral pores and the outer row of enlarged scales and transversal rows of temporal scales between the masseteric and tympanic. Finally, female samples of *Darevskia adjarica* show differences from *Darevskia parvula* females in having less longitudinal ventral plate rows (see Supplementary Appendix 4).

Population relationships derived from morphology. In the male MST, the most connected sample is adjOrtacalar, which appears as the morphologically most intermediate one (for *D. parvula*, this is parHatila); the intertaxa most related samples are adjArdahan and parŞavşat. In the female MST, adjÇermik and parHatila are the most connected, and the intertaxa relationship is between adjArdahan and parHatila. In any case, adjArdahan is the *D. adjarica* closest to the *D. parvula* samples from a morphological point of view.

UPGMA trees derived from Mahalanobis distances yield very similar results for males and females. In both cases, the two nominal taxa *D. parvula* and *D. adjarica* appear homogeneously clustered and well separated from each other. In females, as occurs with the other analyses performed, the degree of differentiation is smaller, but

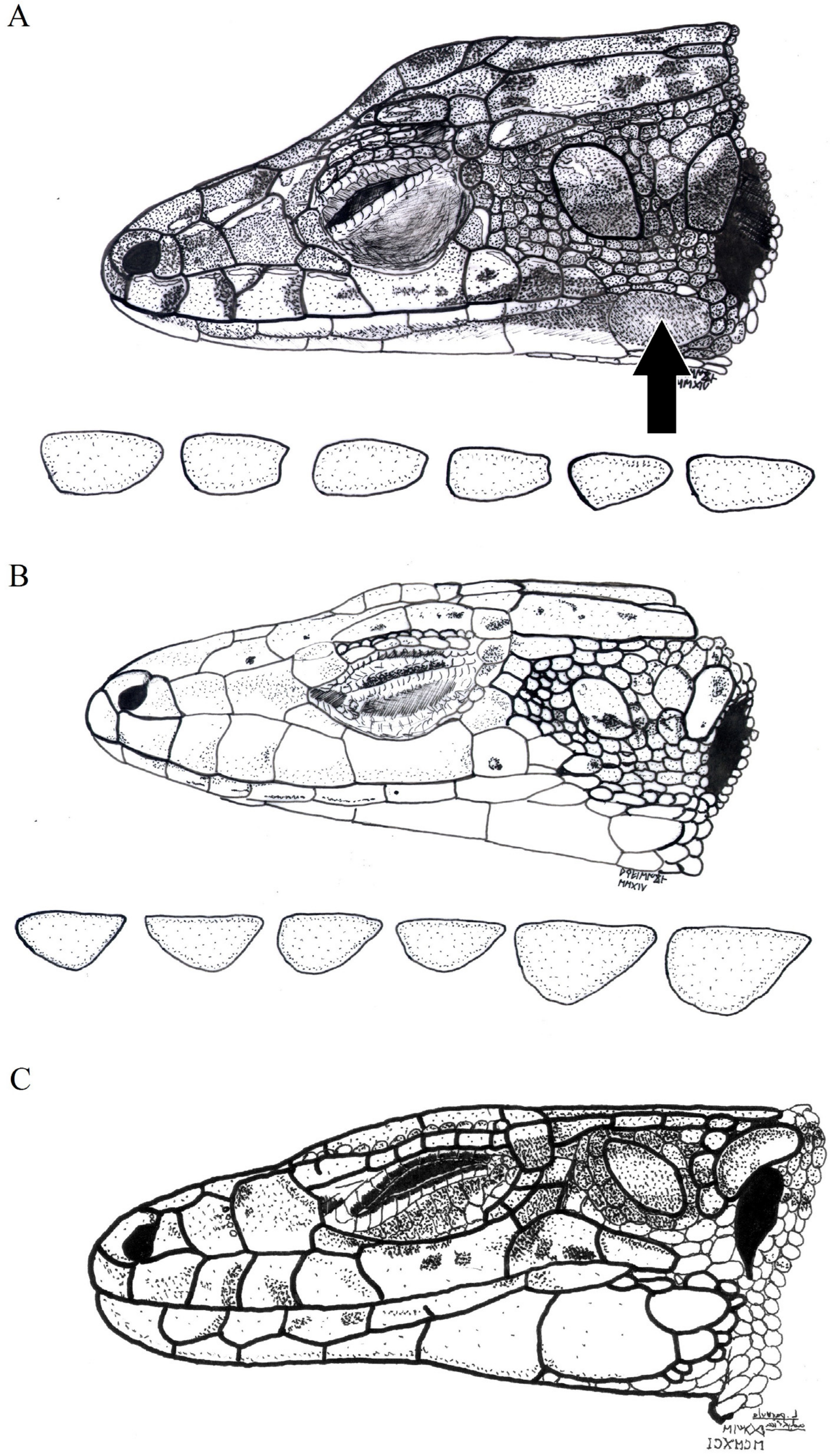

FIGURE 10. Head profiles of A) *Darevskia parvula* (Lantz & Cyrén 1913), "Between Artvin and Hatila, 17 km from Artvin (Turkey)". B) *Darevskia adjarica* (Darevsky & Eiselt, 1980) "9 km West of Ardahan (Turkey)", an inland (continental climate) population of *adjarica*. C) *Darevskia adjarica* (Darevsky & Eiselt, 1980) "Atskuri (Georgia)". Below A and B, respectively appears represented the variability of the the 6th submaxillar plates in *D. parvula* and *D. adjarica*, respectively (position showed by the black arrow in A). Taxon names correspond to changes proposed in this paper.

parallels that of the males. In males and females, all the *D. parvula* samples are very similar and moderately differentiated. In males of *D. adjarica*, the most differentiated seems to be adjBorçka, the others all being clustered together, with adjÇaykara showing slightly more differentiation from the rest (adjOrtacalar, adjArdahan, adjIkizdere and adjÇermik). *Darevskia adjarica* females are also similarly distributed between two subgroups, one including adjBorçka, adjÇermik and adjArdahan and the other including adjOrtacalar, adjIkizdere and adjÇaykara. In both sexes, adjArdahan clearly belongs to *D. adjarica*.

From MST most connected samples, one can speculate about the area of origin and expansion of the two taxa: adjOrtacalar and parHatila are the most connected (morphologically more "central" in both taxa); in fact, both populations live relatively nearby on the northern (Black Sea) and southern facing (inland) slopes, respectively, of the Doğu Karadeniz Mountains (Kaçkar Mountains). These mountains, which rise from sea level up to nearly 4000 m asl. and have wide buffering possibilities against climate changes, may have served as a zone of refuge and posterior dispersion of this species, and even of the original splitting into two taxa adapted to these different conditions, *D. adjarica* on the coast and *D. parvula* on the continental slope. This coastal area of the Black Sea has long been known as a refuge for fauna, an area called the Colchide or Colchis (see a synthesis in Tuniyev 1990).

Among *D. adjarica*, the most differentiated on the UPGMA is adjBorçka, which is on the other side of the Çoruh River from the other samples, but the closer samples are more similar. In the PCA, adjIkizdere and adjÇaykara are more similar, as are adjÇermik and adjBorçka. There seems to be a relationship between geographical proximity and similarity within *D. adjarica*. This is not preserved when all samples are treated together, probably due to the two different taxa and evolutionary histories concerned. All the *D. parvula* are very similar to each other and distributed along the Karadeniz (Kaçkar) Mountains, the middle Çoruh River and its tributaries.

The presence of close relationships in the morphological analyses between samples of the two taxa from relatively close populations (adjArdahan-parŞavşat in males, and adjArdahan-parHatila in females) could be interpreted in two ways:

There are genetic similarities and in the past, genetic flux or contact between the two forms existed; these closer localities still show traces of this, having the most similarities between the two nominal taxa. However, there is no trace of this morphological similarity in the locality where the past introgression of a *parvula*-haplotype inside a *D. adjarica* population has been found; therefore, this seems doubtful. Moreover, other samples from the area included in the multivariate analysis (such as Ortacalar) also fall clearly into *D. adjarica* morphologies.

The closer similarity is due to epigenetic causes, namely, the influence of climatic conditions on scalation. Close localities have similar climatic characteristics and thus their scalations converge. It has been suggested repeatedly that climate almost certainly has an influence on scalation (Schmidtler 1986; Schmidtler *et al.* 2002; Arribas *et al.* 2006).

The fact that despite this relative closeness, morphological distances are well marked (very great in males, moderate in females; see MST results and Supplementary Table 5) made us more inclined to assume a bioclimatic influence than a genetic one. To conclude, adjArdahan is a *D. adjarica* with a scalation modelled by a continental high mountain climate, rather similar to that of *D. parvula*.

There are also small differences across the extense area of *D. adjarica*. In the Turkish *D. adjarica* studied, there were no closed clavicles, but they were present in Georgian specimens. This is relatively common in a lot of Lacertini species, but both may appear in similar proportions. In other species, the closed or open model is fixed in a given taxon. Thus, the open clavicle model seems to be predominant in *D. adjarica*, but in the Atskuri (Georgia) sample, the other model still appears. This is not surprising as Atskuri is one of the isolated populations in the lateral tributaires of the Kura River (Fig 10 C). Small and isolated populations frequently fix uncommon osteological characters (Arribas & Odierna 2004).

Osteological differences. Osteologically, *D. parvula* and *D. adjarica* are very similar, without categorical discriminating characters, as is usual in close congeneric species (Arribas 1998; Arribas & Odierna 2004; Arribas *et al.* 2006), the differences being small and quantitative, not qualitative. However, adjArdahan specimens merit a comment, as they are similar to other *D. parvula* and *D. adjarica* (Turkish and Georgian), but differ in having an extra vertebra in both males and females. All the genus *Darevskia* have an extra vertebra in respect to other typical Lacertini genera (27 instead of 26 in males, and 28 instead of 27 in females; Arribas 1998, 1999; Arnold *et al.* 2007), and among *Darevskia* the *D. raddei* group (*D. raddei raddei*, *D. r. vanensis*, *D. nairensis*) also have an extra vertebra (for males, 28 instead of 27 in other *Darevskia*; 29 instead of 28 in females). These adjArdahan specimens have the increased number typical of this *D. raddei* group. This phenomenon recalls the Jordan's rule in fish, which correlates cold with an increased number of vertebrae (and miotomes) in specimens inhabiting colder localities (Lincoln *et al.* 1998) and also merits in-depth study of the *D. raddei* related forms. However, other mountain or subarctic lizards (such as *Iberolacerta* or *Zootoca*) have the same vertebral numbers that correspond to their more mesic and temperate climate conspecifics.

The status of the inland populations of *D. adjarica*. The distribution of *D. adjarica* runs along the coastal slopes of the Doğu Karadeniz Mountains to the other shore of the Çoruh River, enters Georgia (Adjaria) along the Adzarisckali River, the Meschetskij range and passes through the Caspian watershed to the Kura River drainage (northern slopes of the Trialetskij range) along the Kura River. From this Georgian area of distribution, *D. adjarica* enters inland Turkey again along the Yalnızçam Mountains, from which adjArdahan is an example. Darevsky & Eiselt (1980) attribute some even more inland localities to *D. p. parvula*: in the Güllü and Allahüekber Mountains (Erzurum, 25 km WSW Horasan, Zandzak and-with doubts- Sarıkamış), and also in the Oltu River Valley (Oltu, Tausker). The identification and attribution to *D. parvula* of these populations would merit more in-depth study. These same authors (Darevsky & Eiselt 1980) attribute a sample of Ardahan (ZIL 17890, two specimens, "Around Ardagan"(sic.) in the English translation, presumably Ardahan; Darevsky 1978) to the nominal *parvula*, whereas our sample is clearly related to *D. adjarica* (Ilgaz, 2009, and the present paper) (Fig 10 B). Darevsky & Eiselt (1980) attribute all known inland populations to the nominal *D. parvula* (possibly with scarce samples or simply references). It is not impossible that D. *parvula* is also present on the other side of the Yalnızçam Mountains, on the eastern slopes of this range or near Ardahan and the two taxa meet here.

The present study indicates that the situation in Turkey is that *D. parvula* is well differentiated and lives in the Çoruh River Valley, contoured by *D. adjarica* populations on the coastal-facing slopes of the Doğu Karadeniz Mountains on one side, and the Yalnızçam Mountains on the other side, where *D. adjarica* enters from Georgia as the opposite extreme of a geographic distribution and perhaps with clinal variation. The attribution of more inland ranges to *D. parvula* or *D. adjarica* may be confirmed with more specific studies. Although a wider survey on the genetic variation across the whole distribution area of both forms is needed, our preliminary molecular analyses suggest that *D. adjarica* is fairly uniform over wide distances in its area. *Darevskia parvula* presents some variation within its smaller distribution area. Morphologically, both have a very discrete variability. The possible variation of the inland *D. adjarica* (Ardahan area) and other similar localities remains unknown.

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Zootaxa

SUPPORTING INFORMATION

Reevaluation of the intraspecific variability in *Darevskia parvula* (Lantz & Cyren, 1913): an integrated approach using morphology, osteology and genetics (Squamata: Lacertidae)

Oscar Arribas, Çetin Ilgaz & Yusuf Kumlutaş

APPENDIX 1.

Data of localities and samples of specimens studied in Morphological Multivariate Analyses (PCA, CDA, UPGMA, MST). Taxon names correspond to changes proposed in this paper.

Specimens studied (morphology)

Darevskia parvula (Lantz & Cyren, 1913) (N = 82)

1. **[parSavsat]** ZDEU 149/2001. 6 males, 4 females, 2 juveniles, 15 km W of Şavşat, Artvin, Turkey 04.07.2001, Leg. Y. KUMLUTAŞ, K. OLGUN, Ç. ILGAZ, A. AVCI, F. İRET [41°18'7.66"N; 42°14'13.07"E; 1200 m]

2. **[parYusufeli]** ZDEU 90/2002. 16 males, 12 females, 30 km SW of Yusufeli, Artvin, Turkey, 06.07.2002, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, A. ÖZDEMIR [40°59'4.54"N; 41°24'31.99"E; 1600 m]

3. **[parKılıçkaya]** ZDEU 98/2002. 7 males, 8 females, 4 juveniles, between Kılıçkaya and Karadağ, Artvin, Turkey, 07.07.2002, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, A. ÖZDEMIR [40°43'28.81" N; 41°33'5.01" E; 1970 m]

4. **[parHatila]** ZDEU 101/2002. 13 males, 10 females, Hatila Valley, Artvin, Turkey, 08.07.2002, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, A. ÖZDEMIR [41°10'50.24" N; 41°41'57.68" E; 742 m]

Darevskia adjarica (Darevsky & Eiselt, 1980) (N = 139)

1. **[adjArdahan]** ZDEU 152/2001. 4 males, 7 females, 2 juveniles, 19 km W of Ardahan, Turkey, 06.07.2001, Leg. Y. KUMLUTAŞ, K. OLGUN, Ç. ILGAZ, A. AVCI, F. İRET [41°03'43.34"N; 42°30'47.99"E; 1850 m]

2. **[adjBorçka]** ZDEU 157/2001. 7 males, 5 females, 10 km E of Borçka, Artvin, Turkey, 07.07.2001, Leg. Y. KUMLUTAŞ, K. OLGUN, Ç. ILGAZ, A. AVCI, F. İRET [41°23'57.59"N; 41°44'10.36"E; 427 m]

3. **[adjÇermik]** ZDEU 115/2002. 19 males, 16 females, 10 km W of Çermik, Artvin, Turkey, 12.07.2002, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, A. ÖZDEMIR[41°18'26.1"N; 41°50'19.6"E; 831 m]

4. **[adjOrtacalar]** ZDEU 125/2002. 5 males, 5 females, 2 juveniles, 24 km W of Ortacalar, Artvin, Turkey, 13.07.2002, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, A. ÖZDEMIR [41°17'5.10"N; 41°26'41.72"E; 750 m]

5. **[adjIkizdere]** ZDEU 140/2002. 13 males, 15 females, 12 km SE of İkizdere, Rize, Turkey, 06.09.2002, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, A. AVCI [40°41'50.9"N; 40°41'06.0"E; 1650 m]

6. **[adjÇaikara]** ZDEU 152/2002. 13 males, 16 females, 1 juvenile, 10 km N of Çaykara, Trabzon, Turkey, 08.09.2002, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, A. AVCI.[40°40'46.11"N; 40°15'17.14"E; 620 m]

APPENDIX 2

Data of localities and samples of specimens studied in the Osteological Analysis. Taxon names reflect the changes proposed in this paper.

SPECIES	LOCALITY	NUMBER
Darevskia parvula	Between Kılıçkaya and Karadağ, Northeastern Anatolia. TURKEY [40°43'28.81" N; 41°33'5.01" E; 1970 m]	5 (3 males - 2 females)
Darevskia adjarica	19 km W of Ardahan, Northeastern Anatolia. TURKEY [41°03'43.34"N; 42°30'47.99"E; 1850 m]	4 (2 males - 2 females)
Darevskia adjarica	10 km W of Çermik, Artvin, Northeastern Anatolia. TURKEY [41°18'26.1"N; 41°50'19.6"E; 831 m]	5 (3 males - 2 females)
Darevskia adjarica	10 km E of Borçka, Artvin, Northeastern Anatolia. TURKEY [41°23'57.59"N; 41°44'10.36"E; 427 m]	4 (2 males - 2 females)
Darevskia adjarica	Atskuri. GEORGIA [41º57'36"N; 45º21'48"E; 620 m]	4 (2 males - 2 females)

APPENDIX 3

Localities, sample codes and GenBank accession numbers of the studied specimens in the molecular analyses. Taxon names correspond to changes proposed in this paper.

SPECIES	LOCALITY	CODE	GenBank Cytb/MC1R
Darevskia parvula	Between Artvin and Hatila Valley 17. km., Artvin, Northeastern Anatolia	AH-1 to AH-4	
	[41°10'12.5"N; 41°42'54.5"E; 916 m] **[FIG 1, Loc 8]**	**[S95]**	MH636558/MH636562
		[S98]	MH636557/ -
		[S57]	MH636556/ -
		[S51]	MH636555/ -
Darevskia adjarica	Between Arhavi and Güneşli Village 2. km., Arhavi, Artvin, Northeastern Anatolia	AG-1 to AG-4	
		[S62]	MH636553/MH636560
	[41°18'31.2"N; 41°19'59.4"E; 237 m] **[FIG 1, Loc 6]**	**[S75]**	MH636549/MH636561
		[S71]	MH636554
		[S106]	MH636551
Darevskia adjarica	Güneyce, Rize, Northeastern Anatolia	G-1 to G-3	
	[40°49'45.2"N; 40°28'06.3"E; 500 m] **[FIG 1, Loc 2]**	**[S61]**	MH636548/MH636559
		[S76]	MH636550
		[S165]	MH636552

Table 1. Descriptive statistics of scalation characters obtained from *Darevskia parvula* specimens studied. For abbreviations, see the text (N: number of specimens; min: minimum value; max: maximum value; SD: standard deviation; SE: standard error of the mean). Taxon names correspond to changes proposed in this paper.

	Overall						Males						Females					
Characters	**N**	**Mean**	**min**	**max**	**S.D.**	**S.E**	**N**	**Mean**	**min**	**max**	**S.D.**	**S.E**	**N**	**Mean**	**min**	**max**	**S.D.**	**S.E**
SCGa	82	11.86	10.00	14.00	1.07	0.12	42	11.88	10.00	14.00	1.06	0.16	34	11.82	10.00	14.00	1.09	0.19
SCGb	82	11.87	10.00	14.00	0.91	0.10	42	11.88	10.00	14.00	0.94	0.15	34	11.85	10.00	14.00	0.89	0.15
SCPa	82	6.11	5.00	7.00	0.35	0.04	42	6.17	6.00	7.00	0.38	0.06	34	6.03	5.00	7.00	0.30	0.05
SCPb	82	6.09	5.00	8.00	0.44	0.05	42	6.17	6.00	7.00	0.38	0.06	34	6.00	5.00	8.00	0.49	0.08
SRLa	82	4.43	4.00	5.00	0.50	0.06	42	4.43	4.00	5.00	0.50	0.08	34	4.44	4.00	5.00	0.50	0.09
SRLb	82	4.41	4.00	5.00	0.49	0.06	42	4.36	4.00	5.00	0.48	0.07	34	4.47	4.00	5.00	0.51	0.09
SLa	82	6.14	5.00	7.00	0.39	0.04	42	6.19	6.00	7.00	0.40	0.06	34	6.09	5.00	7.00	0.38	0.07
SLb	82	6.16	5.00	7.00	0.40	0.05	42	6.17	6.00	7.00	0.38	0.06	34	6.15	5.00	7.00	0.44	0.07
MG	82	26.99	23.00	31.00	1.77	0.20	42	26.64	23.00	30.00	1.46	0.23	34	27.41	24.00	31.00	2.03	0.35
STP	82	2.74	2.00	4.00	0.53	0.06	42	2.83	2.00	4.00	0.49	0.08	34	2.62	2.00	4.00	0.55	0.09
TS2a	81	2.67	2.00	4.00	0.60	0.07	41	2.66	2.00	4.00	0.53	0.08	34	2.68	2.00	4.00	0.68	0.12
TS2b	81	2.75	2.00	4.00	0.57	0.07	41	2.68	2.00	4.00	0.53	0.08	34	2.82	2.00	4.00	0.63	0.11
TS1a	82	2.93	2.00	5.00	0.77	0.09	42	2.88	2.00	5.00	0.80	0.12	34	3.00	2.00	4.00	0.74	0.13
TS1b	82	2.96	2.00	5.00	0.76	0.09	42	2.88	2.00	5.00	0.80	0.12	34	3.06	2.00	4.00	0.70	0.12
TS3a	82	1.76	1.00	3.00	0.59	0.07	42	1.71	1.00	3.00	0.55	0.09	34	1.82	1.00	3.00	0.63	0.11
TS3b	82	1.76	1.00	3.00	0.59	0.07	42	1.71	1.00	3.00	0.55	0.09	34	1.82	1.00	3.00	0.63	0.11
POT	82	5.95	4.00	8.00	0.83	0.84	42	5.95	4.00	7.00	0.79	0.12	34	5.94	4.00	8.00	0.89	0.15
TVP	82	6.00	6.00	6.00	0.00	0.00	40	6.00	6.00	6.00	0.00	0.00	34	6.00	6.00	6.00	0.00	0.00
LVP	82	25.33	23.00	29.00	1.44	0.16	42	24.43	23.00	26.00	0.83	0.13	34	26.44	23.00	29.00	1.24	0.21
PA1	82	1.93	1.00	2.00	0.25	0.03	42	1.90	1.00	2.00	0.30	0.05	34	1.97	1.00	2.00	0.17	0.03
PA2	82	6.34	4.00	9.00	0.97	0.11	42	6.33	4.00	9.00	1.12	0.17	34	6.35	5.00	8.00	0.77	0.13
FPa	82	20.47	17.00	25.00	1.74	0.20	42	20.67	17.00	25.00	2.03	0.31	34	20.24	17.00	23.00	1.28	0.23
FPb	82	20.18	16.00	25.00	1.76	0.20	42	20.26	16.00	25.00	2.10	0.32	34	20.09	18.00	23.00	1.26	0.22
LSa	82	5.04	4.00	6.00	0.62	0.07	42	5.12	4.00	6.00	0.55	0.08	34	4.94	4.00	6.00	0.69	0.12
LSb	82	5.04	4.00	6.00	0.62	0.07	42	5.12	4.00	6.00	0.55	0.08	34	4.94	4.00	6.00	0.69	0.12
SDLa	82	30.14	26.00	33.00	1.65	0.19	42	30.21	27.00	33.00	1.57	0.24	34	30.06	26.00	33.00	1.77	0.30
SDLb	82	30.18	26.00	39.00	1.90	0.22	42	30.12	27.00	33.00	1.47	0.23	34	30.26	26.00	39.00	2.34	0.40
TS	82	15.74	13.00	19.00	1.31	0.15	42	15.93	13.00	19.00	1.40	0.22	34	15.50	13.00	17.00	1.16	0.20
DS	82	58.93	52.00	71.00	3.44	0.39	42	59.26	52.00	71.00	3.66	0.57	34	58.53	54.00	66.00	3.15	0.54

Table 2. Descriptive statistics of the biometrical dimensions from *Darevskia parvula*. As in Table 1.

	Overall						Males						Females					
Characters	**N**	**Mean**	**min**	**max**	**S.D.**	**S.E**	**N**	**Mean**	**min**	**Max**	**S.D.**	**S.E**	**N**	**Mean**	**min**	**max**	**S.D.**	**S.E**
PL	76	11.92	9.42	13.94	1.22	0.14	42	12.72	9.74	13.94	0.90	0.14	34	10.93	9.42	13.64	0.75	0.13
PW	76	6.12	4.76	7.56	0.69	0.08	42	6.57	4.92	7.56	0.55	0.08	34	5.56	4.76	6.42	0.37	0.06
HW	76	7.10	5.76	8.64	0.79	0.09	42	7.61	5.78	8.64	0.66	0.10	34	6.46	5.76	7.20	0.37	0.06
HL	76	12.94	10.40	14.98	1.29	0.15	42	13.84	10.66	14.98	0.95	0.15	34	11.84	10.40	12.82	0.61	0.10
SVL	76	52.24	41.20	59.92	4.32	0.50	42	53.66	41.20	59.92	3.82	0.59	34	50.50	41.66	56.60	4.32	0.74
TL	17	108.06	85.00	130.00	13.24	3.21	9	115.33	92.00	130.00	12.73	4.24	8	99.88	85.00	114.00	8.41	2.97
TBL	17	160.66	128.70	187.42	16.91	4.10	9	170.30	142.52	187.42	14.68	4.89	8	149.81	128.70	168.94	12.38	4.38
PI	76	51.33	41.79	56.42	2.35	0.27	42	51.63	46.59	56.42	2.14	0.33	34	50.95	41.79	56.22	2.57	0.44
HI	76	54.81	49.78	59.70	2.02	0.23	42	54.98	49.78	59.70	2.24	0.34	34	54.60	51.64	59.41	1.71	0.29
PLI	76	22.83	19.83	27.14	1.57	0.18	42	23.72	21.18	27.14	0.97	0.15	34	21.72	19.83	25.65	1.46	0.25
PWI	76	11.71	10.05	13.53	0.86	0.10	42	12.24	10.89	13.53	0.57	0.09	34	11.05	10.05	12.86	0.68	0.12
HWI	76	13.58	11.43	15.58	0.95	0.11	42	14.19	12.51	15.58	0.65	0.10	34	12.84	11.43	14.27	0.71	0.12
HLI	76	24.79	21.47	28.28	1.61	0.18	42	25.81	23.56	28.28	0.89	0.14	34	23.54	21.47	26.52	1.39	0.24
TLI	17	205.61	171.90	232.64	18.01	4.37	9	210.24	171.90	232.64	22.30	7.43	8	200.39	186.44	213.06	10.71	3.79

Table 3. Descriptive statistics of scalation characters obtained from *Darevskia adjarica* specimens. As in Table 1.

	Overall						Males						Females					
Characters	**N**	**Mean**	**min**	**max**	**S.D.**	**S.E**	**N**	**Mean**	**min**	**max**	**S.D.**	**S.E**	**N**	**Mean**	**min**	**max**	**S.D.**	**S.E**
SCGa	139	11.11	4.00	15.00	1.54	0.14	61	11.18	4.00	15.00	1.79	0.23	64	11.05	8.00	14.00	1.25	0.16
SCGb	139	11.21	4.00	16.00	1.66	0.15	61	11.16	4.00	16.00	1.82	0.23	64	11.25	8.00	15.00	1.50	0.19
SCPa	139	5.91	4.00	7.00	0.60	0.05	61	5.93	4.00	7.00	0.54	0.07	64	5.89	4.00	7.00	0.65	0.08
SCPb	139	5.94	4.00	7.00	0.39	0.03	61	5.98	5.00	7.00	0.22	0.03	64	5.91	4.00	7.00	0.50	0.06
SRLa	139	4.09	3.00	5.00	0.30	0.03	61	4.02	3.00	5.00	0.22	0.03	64	4.00	3.00	5.00	0.36	0.04
SRLb	139	4.02	3.00	5.00	0.30	0.03	61	3.98	3.00	5.00	0.29	0.04	64	4.06	3.00	5.00	0.30	0.04
SLa	139	6.02	5.00	8.00	0.39	0.03	61	6.02	5.00	7.00	0.39	0.05	64	6.03	5.00	8.00	0.40	0.05
SLb	139	6.03	5.00	7.00	0.40	0.04	61	6.05	5.00	7.00	0.46	0.06	64	6.02	5.00	7.00	0.33	0.04
MG	139	25.62	21.00	30.00	1.79	0.16	61	25.56	21.00	30.00	1.96	0.25	64	25.69	21.00	29.00	1.63	0.20
STP	139	3.10	2.00	4.00	0.48	0.04	61	3.10	2.00	4.00	0.47	0.06	64	3.09	2.00	4.00	0.50	0.06
TS2a	139	2.06	1.00	5.00	0.63	0.06	61	2.10	1.00	3.00	0.57	0.07	64	2.03	1.00	5.00	0.69	0.09
TS2b	139	2.07	1.00	5.00	0.65	0.06	61	2.08	1.00	3.00	0.56	0.07	64	2.06	1.00	5.00	0.73	0.09
TS1a	139	2.71	1.00	5.00	0.96	0.09	61	2.56	1.00	5.00	0.94	0.12	64	2.86	1.00	5.00	0.96	0.12
TS1b	139	2.73	1.00	5.00	0.91	0.08	61	2.59	1.00	5.00	0.94	0.12	64	2.86	1.00	5.00	0.87	0.11
TS3a	127	1.57	1.00	4.00	0.65	0.06	55	1.51	1.00	3.00	0.54	0.07	58	1.62	1.00	4.00	0.75	0.10
TS3b	127	1.57	1.00	4.00	0.65	0.06	55	1.51	1.00	3.00	0.54	0.07	58	1.62	1.00	4.00	0.75	0.10
POT	139	3.50	2.00	6.00	0.80	0.07	61	3.43	2.00	6.00	0.87	0.11	64	3.58	2.00	6.00	0.73	0.09
TVP	139	6.00	6.00	6.00	0.00	0.00	61	6.00	6.00	6.00	0.00	0.00	64	6.00	6.00	6.00	0.00	0.00
LVP	139	24.53	21.00	28.00	1.71	0.15	61	23.33	21.00	26.00	1.22	0.16	64	25.67	23.00	28.00	1.26	0.16
PA1	139	1.75	1.00	2.00	0.43	0.04	61	1.70	1.00	2.00	0.46	0.06	64	1.80	1.00	2.00	0.41	0.05
PA2	139	6.40	4.00	8.00	0.84	0.08	61	6.34	5.00	8.00	0.77	0.10	64	6.45	4.00	8.00	0.91	0.11
FPa	139	18.56	13.00	22.00	1.62	0.15	61	18.61	13.00	22.00	1.70	0.22	64	18.52	14.00	22.00	1.56	0.19
FPb	139	18.49	14.00	23.00	1.65	0.15	61	18.48	14.00	23.00	1.71	0.22	64	18.50	14.00	22.00	1.60	0.20
LSa	139	4.75	4.00	6.00	0.59	0.05	61	4.70	4.00	6.00	0.61	0.08	64	4.80	4.00	6.00	0.57	0.07
LSb	139	4.75	4.00	6.00	0.59	0.05	61	4.70	4.00	6.00	0.61	0.08	64	4.80	4.00	6.00	0.57	0.07
SDLa	139	27.73	22.00	33.00	2.08	0.19	61	27.95	22.00	33.00	2.20	0.28	64	27.52	24.00	31.00	1.95	0.24
SDLb	139	27.74	22.00	33.00	2.05	0.18	61	27.97	22.00	33.00	2.14	0.27	64	27.53	24.00	31.00	1.95	0.24
TS	139	15.60	13.00	20.00	1.24	0.11	61	15.64	13.00	20.00	1.35	0.17	64	15.56	14.00	19.00	1.13	0.14
DS	139	54.41	47.00	62.00	3.13	0.28	61	54.66	47.00	62.00	3.44	0.44	64	54.17	47.00	60.00	2.81	0.35

Table 4. Descriptive statistics of metric dimensions obtained from *Darevskia adjarica*. As in Table 1.

	Overall						Males						Females					
Characters	**N**	**Mean**	**min**	**max**	**S.D.**	**S.E**	**N**	**Mean**	**min**	**max**	**S.D.**	**S.E**	**N**	**Mean**	**min**	**max**	**S.D.**	**S.E**
PL	125	11.96	9.24	15.62	1.21	0.11	61	12.71	10.80	15.62	1.02	0.13	64	11.25	9.24	13.84	0.93	0.12
PW	125	6.39	5.00	8.44	0.71	0.06	61	6.76	5.80	8.44	0.60	0.08	64	6.04	5.00	7.88	0.63	0.08
HW	125	7.49	5.60	10.05	0.93	0.08	61	7.93	6.58	10.05	0.90	0.11	64	7.06	5.60	8.88	0.75	0.09
HL	125	12.87	10.38	16.43	1.24	0.11	61	13.66	11.72	16.43	1.06	0.14	64	12.11	10.38	14.46	0.88	0.11
SVL	125	51.89	41.52	62.28	3.76	0.34	61	52.85	45.50	62.28	3.42	0.44	64	50.97	41.52	60.92	3.87	0.48
TL	30	104.00	82.00	121.00	10.15	1.85	17	107.76	94.00	121.00	7.73	1.87	13	99.08	82.00	119.00	11.09	3.07
TBL	30	156.26	127.78	179.92	13.17	2.40	17	160.32	142.50	176.26	9.80	2.38	13	150.95	127.78	179.92	15.40	4.27
PI	125	53.41	42.92	63.64	2.65	0.24	61	53.16	48.58	58.03	1.98	0.25	64	53.65	42.92	63.64	3.16	0.40
HI	125	58.14	45.66	68.53	3.61	0.32	61	58.00	45.66	67.41	3.74	0.48	64	58.26	49.56	68.53	3.50	0.44
PLI	125	23.05	20.09	26.76	1.51	0.13	61	24.04	21.34	25.28	1.02	0.13	64	22.10	20.09	26.76	1.27	0.16
PWI	125	12.30	10.14	14.21	0.93	0.08	61	12.78	10.81	14.21	0.67	0.09	64	11.85	10.14	14.08	0.91	0.11
HWI	125	14.42	11.35	17.93	1.28	0.11	61	14.99	12.60	17.93	1.16	0.15	64	13.87	11.35	17.89	1.15	0.14
HLI	125	24.80	21.54	27.87	1.59	0.14	61	25.85	23.07	27.87	1.24	0.16	64	23.80	21.54	27.07	1.20	0.15
TLI	30	199.29	161.23	236.22	15.79	2.88	17	205.65	167.20	236.22	16.05	3.89	13	190.98	161.23	200.00	11.28	3.13

Table 5. Pairwise morphological distances (Mahalanobis'; D2) among samples. Males above diagonal and females below.

MAHALANOBIS' (MORPHOLOGICAL) DISTANCES (D^2) AMONG SAMPLES										
Females\Males	**parŞavşat**	**parYusufeli**	**parKılıçkaya**	**parHatila**	**adjBorçka**	**adjOrtacalar**	**adjArdahan**	**adjÇermik**	**adjÇaykara**	**adjIkizdere**
parŞavşat	-	20	15.1	13.4	126	128	118	131	138	**130**
parYusufeli	21.4	-	15.5	14.7	154	154	137	148	159	**155**
parKılıçkaya	25.8	18.7	-	12.7	168	170	153	177	185	**172**
parHatila	18.3	21.7	15.5	-	169	160	147	160	171	**162**
adjBorçka	72.4	59.3	45.1	48.2	-	36.1	35.5	26.9	57.1	**33.4**
adjOrtacalar	65.1	58.3	57.2	49.0	22.8	-	12.8	15.7	30.1	**12.8**
adjArdahan	39.0	33.6	24.6	18.2	18.2	24.2	-	17.1	38.2	**18.7**
adjÇermik	47.9	45.5	35.8	39.8	15.1	14.8	15.3	-	36.8	**20.6**
adjÇaykara	65.1	58.3	61.4	51.6	33.0	15.7	26.2	23.4	-	**19.0**
adjIkizdere	62.5	53.1	57.8	53.1	27.1	8.69	25.6	15.1	10.5	**-**