Monograph

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Revising the taxonomy of *Darevskia valentini* (Boettger, 1892) and *Darevskia rudis* (Bedriaga, 1886) (Squamata, Lacertidae): a Morpho-Phylogenetic integrated study in a complex Anatolian scenario

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Table of Contents

Abstract

Revealing biodiversity allows the accurate determination of the underlying causes of many biological processes such as speciation and hybridization. These processes contain many complex patterns, especially in areas with high species diversity. As two of the prominent zoogeographic areas, Anatolia and Caucasus are also home to the genus *Darevskia*, which has a complex morphological structure and parthenogenetic speciation. *Darevskia valentini* and *D. rudis* are two largely distributed taxa of this genus, both of which have a controversial taxonomic delimitation. Here we performed both a highly detailed morphological comparison and a molecular evaluation for the populations in both species groups. The most comprehensive taxonomic revision of this complex was carried out to determine the cases where the data obtained were compatible or not with each approach. As a result of the obtained outputs, it seems that *D. spitzenbergerae* **stat. nov.**, *D. mirabilis* **stat. nov.** and *D. obscura* **stat. nov.** should be accepted as the species level, this later with subspecies *D. o. bischoffi* **comb. nov.** and *D. o. macromaculata* **comb. nov.**. Also, we propose two new taxa: *D. josefschmidtleri* **sp. nov.** and *D. spitzenbergerae wernermayeri* **ssp. nov.**. It has also been shown that "*lantzicyreni*" subspecies belong to *D. rudis* instead of *D. valentini*. The extensive revision has contributed to subsequent studies to more accurately understand the past histories of species in the genus *Darevskia*.

Key words: *Darevskia*, morphology, phylogeny, taxonomy, Anatolia, Caucasus

INTRODUCTION

Spatial isolation has been accepted as one of the most important steps of speciation since it was first defined (Darwin 1859; Mayr 1982). It is known that both genetic and ecological separation which arises with spatial isolation triggers speciation by causing reproductive isolation (Prohl *et al.* 2010). It is a common phenomenon in nature that species can adapt to environmental conditions in this way by occupying different environments and adopting different ecological niches (Dobzhansky 1937). In addition to this, some other processes like hybridization also can play a key role in the emergence of species (Tarkhnishvili *et al.* 2013). Anatolia, located between temperate and subtropical regions with mountainous range systems which create a wide variety of climates, ecosystems, and habitats, provides suitable conditions for the prominent speciation processes such as spatial isolation and adaptation (Şekercioğlu *et al.* 2011). Additionally, it has hybrid zones between closely related amphibian and reptile species, which contributes to understanding the different causes underlying species diversity (Dufresnes *et al.* 2019; Tarkhnishvili *et al.* 2020a; Karakasi *et al.* 2021). Thanks to this unique feature, it harbors numerous members of herpetofauna (Baran *et al.* 2021; Yaşar *et al.* 2021), some of which are related to a concept known as cryptic species, highly divergent phylogenetic lineages with morphological similarity, found recently in many studies (Sindaco *et al.* 2014; Tamar *et al.* 2015; Kornilios *et al.* 2018; Kotsakiozi *et al.* 2018; Mendes *et al.* 2018; Jablonski *et al.* 2019; Karakasi *et al.* 2021; Yousefabadi *et al.* 2021). Detection of cryptic species is widespread in the genus *Darevskia* (Ahmadzadeh *et al.* 2013; Freitas *et al.* 2016a; Candan *et al.* 2021; Rato *et al.* 2021; Arribas *et al.* 2022).

The genus *Darevskia* Arribas, 1999 (Lacertidae), which currently contains 35 species (Uetz, Freed & Hošek 2022), is one of the prominent lizard groups part of Anatolian species richness with its unprecedented traits involving hybridization events among relatively far forms and consequent parthenogenetic reproduction of the hybrids (Freitas *et al.* 2016b; Tarkhnishvili *et al.* 2020a; Candan *et al.* 2021). The taxonomic positions of the species within the genus have always been conflicting (Gabelaia *et al.* 2018; Candan *et al.* 2021), due to the insufficiency of morphological characters for the separation of the species (Darevsky 1967; Tarkhnishvili *et al.* 2013). On the flipside of the coin, there is a consensus that three big monophyletic lineages are in *Darevskia*: "*rudis*", "*caucasica*" and "*saxicola*" and perhaps other minor ones of species not included in the concerned studies (Murphy *et al.* 2000; Tarkhnishvili 2012).

Darevskia valentini (Boettger, 1892), which belongs to the "*rudis*" clade, is one of the 15 *Darevskia* species distributed in Turkey (Baran *et al.* 2021), and its distribution area also includes Georgia, Armenia, Azerbaijan and Iran (Candan *et al.* 2021). As a result of previous morphological assessments, it is assumed that *D. valentini* includes three subspecies: *D. valentini valentini* (Boettger, 1892) (Type locality: Bazarkent, Armenia), *D. valentini lantzicyreni* (Darevsky & Eiselt, 1967) (Type locality: Erciyes Mountain, Kayseri, Turkey) and *D. valentini spitzenbergerae* (Eiselt, Darevsky & Schmidtler, 1992) (Type locality: Cilo Mountain, Hakkari, Turkey).

Although many partial morphological studies to compare these taxa had been conducted (Darevsky 1967; Darevsky & Lukina 1977; Eiselt *et al.* 1992), it was not until after its molecular phylogenetic reconstruction we realized that there is insufficient information about the complexity of the group (Candan *et al.* 2021). What the genetic markers showed us are new outputs that potentially change the taxonomy of the group. Candan *et al* (2021) stated that *D. valentini* has undescribed genetic lineages which were hitherto not identified as distinct. These new lineages, which were morphologically related to *D. v. lantzicyreni*, have monophyletic positions in respect to other members of the "*rudis*" clade, which means that they are isolated. As a result of the phylogenetic approaches, these are clearly in conflict with the currently accepted (morphological) taxonomy (Eiselt *et al.* 1992). Additionally, it seems that *D. valentini* and *D. rudis* are very closely related species. This sister-clade situation has a puzzling pattern in some geographic areas, giving a polytomy, which makes it difficult to distinguish populations genetically (Candan *et al.* 2021).

A similar conception within "*rudis*" clade has occurred for *D. rudis* (Bedriaga, 1886), suggesting that there are four distinct genetic lineages (Rato *et al.* 2021). Main results based on phylogenetic construction showed that both sister species, *D. valentini* and *D. rudis* are paraphyletic, and that *D. bithynica* (Méhely, 1909) is separated from them as a distinct species due to the possible effect of a geographic barrier system (Kızılırmak River, Turkey). Indeed, *D. rudis* has also several subspecies, the systematic positions of them are controversial (Arribas *et al.* 2013; Koç *et al.* 2017; 2021; Rato *et al.* 2021). In a detailed taxonomic revision, two new subspecies were described as *D. r. mirabilis* from Ovit Pass (Kaçkar Mountains, Turkey) and *D. r. bolkardaghica* from Bolkar Mountain (Central Taurus Mountains, Turkey) (Arribas *et al.* 2013). One of them, *D. r. bolkardaghica*, appears to be genetically closer to *D. r. rudis* and *D. v. lantzicyreni*, while *D. r. mirabilis* appears in a relatively isolated clade (Candan *et al.* 2021).

Because of both reasons, being relatives of each other and the unresolved taxonomic situation of some

populations, both species *D. valentini* and *D. rudis*, should be evaluated together to reach robust conclusions. The aim of the study is (1) to make the most detailed morphological comparison including both *D. valentini* and *D. rudis* to detect certain species-specific characteristics, (2) to re-analysis their phylogenies using a large-scale dataset which includes *D. v. spitzenbergerae* for the first time, (3) to test the validity of entire subspecies scheme within the group, and (4) to describe two new taxa (at a species and subspecies level) from Turkey.

MATERIAL AND METHODS

External morphology and osteology

A total of 850 adult specimens (444 males and 406 females) were used for the morphological study (see Appendix 1 for locality data). Acronyms include information of the taxon to which they are ascribed and the name of the nearest locality (e.g. "spitzmergan1" is the specimen nr. 1 of the taxon *spitzenbergerae* from the Mergan Plateau). The study area covers a great part of Anatolia (Fig. 1) including the rarest and remote populations. Color slides of the specimens were taken and specimens were then fixed with 5% formaldehyde in 70% ethanol or 96% ethanol, and preserved in 96% 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, Science Faculty, at Dokuz Eylül University, Buca, İzmir, Turkey.
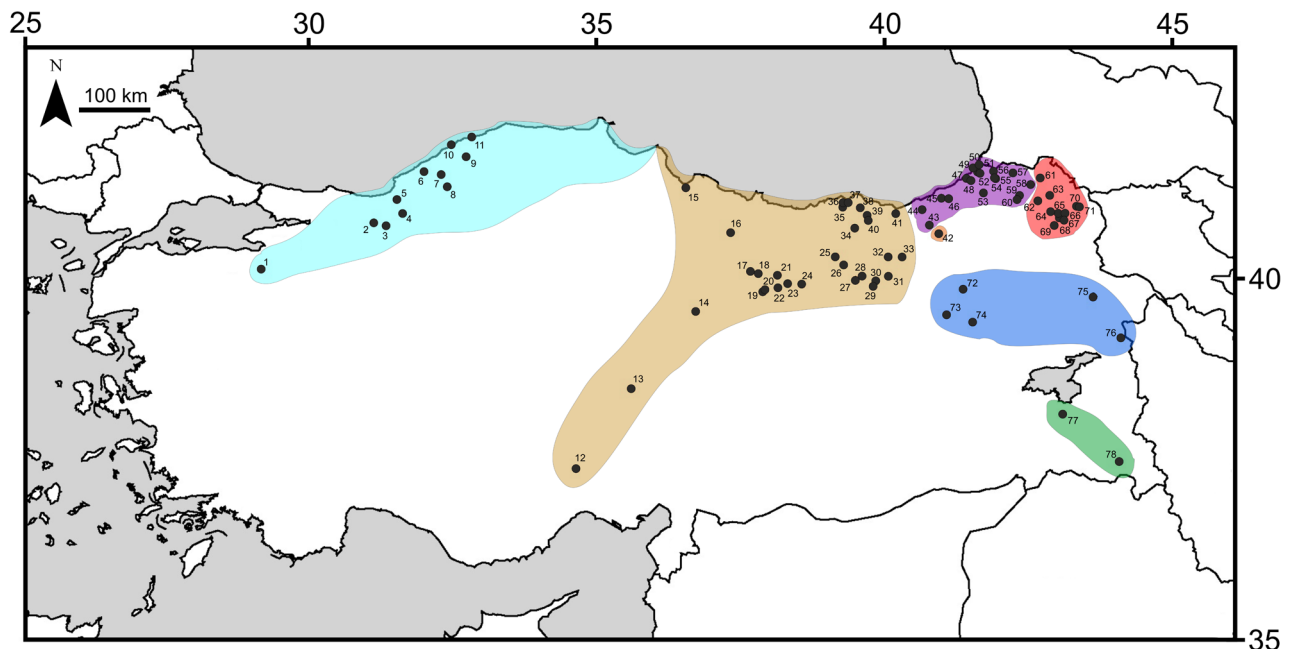
FIGURE 1. Map showing both the localities of populations examined in morphology part and the possible distribution range for each taxa. Only the Turkish areas of the taxa are depicted. Numbers refer to population codes (Map ID) given in Appendix 1. Colors are lineage-specific which were identified in phylo-trees (see Figure 9).

The following metric dimensions were taken using digital calipers with accuracy to the nearest 0.01 mm: Snout-vent length (SVL): from the tip of snout to anal cleft. Tail length (TL): from anal cleft to the tip of the tail. Pileus width (PW): at the widest point between parietal plates. Pileus length (PL): from the tip of snout to the posterior margins of parietals. Head width (HW): at the widest point of the head. Head length (HL): from the tip of snout to posterior margin of the ear opening. Anal Width (AW): width of the anal or preanal plate. Anal Length (AL): longitude of the Anal plate. Hindlimb Length (LL): Longitude of the Hindlimb, from groin to the longest toe tip. Furthermore, morphometric indexes were calculated, Pileus Index (PI) [PL / PW], Head Index (HI) [HL / HW], Anal Index (AI) [AW/AL], Head Relative length (HRL) [HL/SVL], Hindlimb Relative length (LRL) [LL/SVL].

Meristic scalation characters considered here consisted of the following counts: supraciliar granules (left-right) (GR_S), supraciliar plates (left-right) (SUPRAC_PL), supralabial plates (left-right) (SUPRALAB-PL),

sublabial plates (left-right) (SUBLAB_PL), transversal series of gular scales between inframaxillar symphysis and collar (GULARIA), collaria (COLLARIA), supratemporal scales (Supratemporal Left) in left side, temporal scales 1 (transversal rows of temporal scales between masseteric and tympanic) (left-right) (TEMP1), temporal scales 2 (longitudinal rows of temporal scales between tympanic and parietal) (left-right) (TEMP2), Ventral plates (transversal) (VENTRALIA), Number of enlarged circumanals located anterior of the anal plate (PREANALIA), Number of preanals surrounding the big anal plate (CIRCUMANALIA), Number of femoral pores (left-right) (FEMORALIA), Longitudinal rows of scales on ventral surface of thigh between the femoral pores and the outer row of enlarged scales (left-right) (FEMUROUTER), Subdigital lamellae in the 4th toe, left-right (LAMELLAE), Tibial scales lying on dorsal surface of crus (ankle or calf) between the large scales (TIBIALIA), and Transversal series of dorsal scales at the midtrunk (DORSALIA). The bilateral scales were combined in only one, non-redundant variable (the same acronyms, but without "a" and "b") for calculations.

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. The genetic results (see below and Candan *et al.* 2021) and current nomenclature were used to define the different OTUs.

Statistical analyses used in the morphological study were both univariate (ANOVA) and multivariate (Canonical Discriminant Analysis, CDA). ANOVA was run for SVL, scalation characters, and biometric indexes, with posthoc Scheffé tests at $p < 0.05$ (*) and $p < 0.01$ (**) to detect differences among samples. In Canonical Discriminant Analysis (CDA), Chi-square and Wilks' Lambda were used to test the significance of each axis. If the groups have different scores, then the models discriminating between the groups and axes are significant. Bartlett's Sphericity Tests prove if the variables are uncorrelated, a prerequisite for successful discriminant analysis (Sokal & Rohlf 1969; Blackith & Reyment 1971; Legendre & Legendre 1998, and online help in the statistic programs utilized, see below). In this Canonical Discriminant Analysis, each population is represented by a centroid (a hypothetical middle individual).

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 overall most primitive from a morphological point of view. In contrast, UPGMA trees show the global relationships among the samples (Arribas 1999; 2010; Arribas *et al.* 2006).

Analysis of Similarity (ANOSIM) (Clarke 1988; 1993) was carried out to test the significance of the differences between the samples. ANOSIM 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 significant testing of the differences among the groups concerned and detect which ones are different from the others.

ANOVA was calculated with NCSS 2007© (Hintze 2007). CDA and ANOSIM analyses were performed with Community Analysis Package 6© (Seaby & Henderson 2019). MST and UPGMA trees were calculated with NTSYS 2.1© (Rohlf 2000).

Osteological examinations

Previously fixed and alcohol preserved specimens were cleared with 1% KOH in deionized water and bones stained with alizarin red. They were posteriorly differentiated, and the excess of pigment was eliminated with Mall solution (80% of the previous clearing solution plus 20% glycerol) and preserved permanently in glycerol following the procedures of Taylor (1967) and Durfort (1978). Osteological nomenclature follows Arribas (1998). Information about the new specimens studied and their localities are given in Appendix 2. Also, specimens from Arribas (1998) and Arribas *et al.* (2013) were used together with the newly studied ones.

Molecular phylogenetic examinations

Laboratory procedure, datasets, phylogenetic reconstructions

To reach a robust conclusion for phylogenetic relationships of the studied group, we used two independent gene markers (*Cyt-b* from mitochondrial and *MC1R* from nuclear DNA) which are created by combining from two different publications related to *D. valentini* and *D. rudis* complexes, separately (Candan *et al.* 2021; Rato *et al.* 2021). Besides, the sequences of *D. v. spitzenbergerae* subspecies were added to datasets for detection of its true taxonomic position for the first time. For these samples, we followed to same protocols of DNA isolation and PCR conditions, which were described previously by Candan *et al.* (2021). DNA isolation was performed using PureLink (Invitrogen, Thermo Fisher Scientific, https://www.thermofisher.com/order/catalog/product/K182001). To obtain DNA sequences, we amplified isolated samples by Polymerase Chain Reaction (PCR) and PCR products were sequenced with an ABI PRISM 3700 (PE Applied Biosystems, Forster City, CA, USA). All sequenced DNA information has been submitted to GenBank for deposition. Finally, the total number of samples included in our phylo-analyses was 205 (see details in Appendix 3).

All DNA sequences in the datasets were aligned with MAFFT v7 (Katoh & Standley 2013). The number and diversity of haplotypes for each genetic marker belonging to all individuals were determined using DnaSP v6 (Rozas *et al.* 2017). The uncorrected genetic distances (p-distances) among the main groups considered as distinct species in our phylogeny were calculated in MEGA X (Kumar *et al.* 2018). ModelFinder (Chernomor *et al.* 2016; Kalyaanamoorthy *et al.* 2017) implemented in the IQTREE webserver (Trifinopoulos *et al.* 2016; http://iqtree.cibiv. univie.ac.at) was used for both determining the most suitable nucleotide evolution model and deciding the most appropriate partition strategy for *Cyt-b*. The analysis showed that it should be considered as a single partition with TPM2u+G and HKY+G as the most suitable models for applying in phylo-analyses ML and BI, respectively.

Phylogenetic tree topology was created by performing different approaches based on Maximum Likelihood (ML) and Bayesian Inference (BI) with the *Cyt-b* dataset. ML analysis was conducted using IQ-TREE, with the appropriate partition scheme and model. Statistical support of the nodes was tested with SH-aLRT tests with 10,000 replicates (Guindon *et al.* 2010), 10,000 ultrafast bootstrap alignments (Minh, Nguyen & Haeseler 2013) and 100 standard bootstrap alignments (Felsenstein 1985). BI analysis was carried out twice using MrBayes v3.2.6 (Ronquist *et al.* 2012) with eight chains and 2×10^7 generations each, and with tree and log files recorded every 100 generations. The average standard deviation value of the discrimination frequencies (<0.01), was used as a measure to ensure that convergence had been reached. After a 25% burn-in, a majority-rule consensus tree was created from the remaining trees.

Single-locus species delimitation and multilocus coalescent-based species tree

For determination of possible species boundaries, we tested different approaches: (i) The ML phylogenetic tree obtained for *Cyt-b* dataset was used as input files in the multi-rate Poisson tree processes model (mPTP; Kapli *et al.* 2017; - https://mptp.h-its.org/#/tree) (two runs, 10^8 generations, a thinning of 10^4 and a burn-in of 10%). (ii) The statistical parsimony analysis was conducted in TCS 1.21 (Clement *et al.* 2000) under the 90% connection limit of parsimony to construct independent haplotype networks, which were considered distinct evolutionarily significant units (ESUs) (Fraser & Bernatchez 2001). (iii) We used the Bayesian version of GMYC (Reid & Carstens 2012), bGMYC v.1.0.2 in R Studio, implementing 50,000 MCMC steps with 40,000 steps as burn-in and a thinning of 100 steps. As input, we used 1,000 posterior (ultrametric) trees of *Cyt-b* haplotypes constructed with BEAST v1.10.4 (Drummond *et al.* 2012). The analysis was carried out with two independent runs for 3×10^7 generations. Other settings were as follows: Relaxed Uncorrelated Lognormal Clock, Yule tree prior, random starting tree. We determined whether the analyses had reached convergence with Tracer v1.7.1 (Rambaut *et al.* 2018). For the bGMYC analysis, we used a conservative posterior-probability threshold of 0.5 to identify putative species, compared to higher values that could overestimate the species' number. (iv) We performed the Species Tree and Classification Estimation, Yarely – STACEY v.1.2.5 (Jones 2017), in BEAST2 v.2.6.0 (Bouckaert *et al.* 2019) by using both loci, *Cyt-b* from mtDNA and *MC1R* from nDNA. We grouped main clusters for species' assignments (7 clusters; see Fig. 9). Two runs of 10^9 generations were conducted, with an uncorrelated lognormal relaxed clock and a Yule tree prior [CollapseHeight = 0.001; CollapseWeight = beta (1.1) around (0.1); bdcGrowthRate = lognormal (M = 4.6, S = 1.5); pop-PriorScale = lognormal (M = − 7, S = 2); relative death rate = beta (1.1)]. For the species-delimitation analysis, we applied equal ploidy for the nDNA and mtDNA loci as a more robust approach that avoids the disproportionate influence of mtDNA data (Busschau *et al.* 2019). We used SpeciesDelimitationAnalyser (Jones 2015) to process output files and examine the clusters of species assignments.

Haplotype diversity and networks

Heterozygous positions for the *MC1R* gene region were phased with the Bayesian algorithm of Phase 2.1 (Stephens *et al.* 2001; Stephens & Scheet 2005) implemented in DnaSP (Rozas *et al.* 2017), with 1,000 iterations after a burn-in of 100. All haplotypes were estimated with high probabilities (1.0 for *MC1R*). Thus, a haploid dataset that was used in networks was created from these diploid sequences for the nuclear gene region. Haplotype networks were created for each marker separately (*Cyt-b* and *MC1R*) under the statistical parsimony algorithm of TCS (Clement *et al.* 2000) using PopART v1.7 (Leigh & Bryant 2015).

RESULTS

Morphology

Canonical discriminant analysis (MALES)

Discriminant Analysis (CDA) maximizes the discrimination of the samples, especially between the first two significant axes (with eigenvalues greater than one; Chi-square 3508.54 [276 d.f.; $P = 0.001$] and 2370.84 [242 d.f.; $P = 0.001$] for the first and second axes, respectively). The bidimensional plot (see Fig. 2) is a plane defined by the first axis (Eigenvalue 13.58; 51.6 % of the variability explained) and the second axis (7.67; 29.1 % explained) that separates the samples with reduced overlap between them. Both axes together explain 80.3 % of the total variability. Wilks Lambda is 0.000257338 ($F_{276} = 18.63$, $P = 0$). As $P < 0.05$, this demonstrates the existence of significant differences among the samples analyzed. Bartlett's Sphericity Tests further proved that the variables were uncorrelated, a prerequisite for successful discriminant analysis (Bartlett's Chi-Squared Test Statistic = 3512.68, 276 degrees freedom; $P = 0.001$).

As shown in Fig. 2, the first axis (51.6 % of variability explained) separates *D. bithynica* (*bithynica* and *tristis*) males in the positive part of the axis, from the remaining samples of the *rudis* and *valentini* complexes in the negative one. These *D. bithynica* taxa appear very different and are characterized by greater values of head index (0.71), head relative length (0.69), SVL (0.32), hindlimb relative length (0.25); and the smaller scores of pileus index (-0.30). In this first axis, *D. bithynica* and the other taxa are well distinguished, as the former has longer heads both concerning its length as well as relative to their body length, but not in their pilei because other species (especially of the *rudis* complex) had smaller (overall size and length) but very wide heads.

The second axis (29.1 % of variability explained) (Fig. 2) separates in its positive part the samples of the *valentini* complex from the *rudis* complex ones in the central and the negative part of the axis. The *valentini* complex forms (positive part) are characterized by greater hindlimb relative length (0.49), tibialia (0.47), ventralia (0.28), dorsalia (0.25), and the smaller values of head relative length (-0.38), SVL (-0.29) and femurouter (-0.29). This means that the *valentini* complex samples had comparatively longer limbs, a greater number of scales in the crus (which in this case correspond also to smaller sized and no or almost-no keeled ones), and less markedly, a greater number of ventral and dorsal scales. Also, *valentini* complex had comparatively smaller heads, and less markedly smaller sizes and number of scales in the outer part of the crus. Among the *rudis* complex, the extreme values are for *D. r. bischoffi* (Böhme & Budak, 1977) (with the most contrary values respect the *valentini* complex) and *D. r. bolkardaghica* (the taxon with less negative values and thus more similar to the *valentini* complex and *D. bithynica*). Among the *valentini* complex, there are very few differences in this axis.

There would be no real overlap between the OTUs of the *rudis* complex and those of the *valentini* complex if it were not for the fact that some of the *D. r. bolkardaghica* individuals are displaced (that is, have morphological characteristics) from *D. v. lantzicyreni*, an interesting issue in which we will recall later.

The third axis (only 8 % of variance explained; eigenvalue of 2.22) [Chi-square 1453.64, with 210 d.f.; $P = 0.001$] slightly separates in its positive part *D. rudis* s. str. from the other *rudis* complex forms (and also from *D. bithynica* and in a great part of the *valentini* complex ones), especially characterized by greater values of dorsalia (0.95). Among the *valentini* complex forms, this axis orders them clinally from *D. v. lantzicyreni* (with the greater dorsalia) up to *D. v. valentini* (with the smaller values), with clade A, clade B, and *D. v. spitzenbergerae* in more intermediate positions.
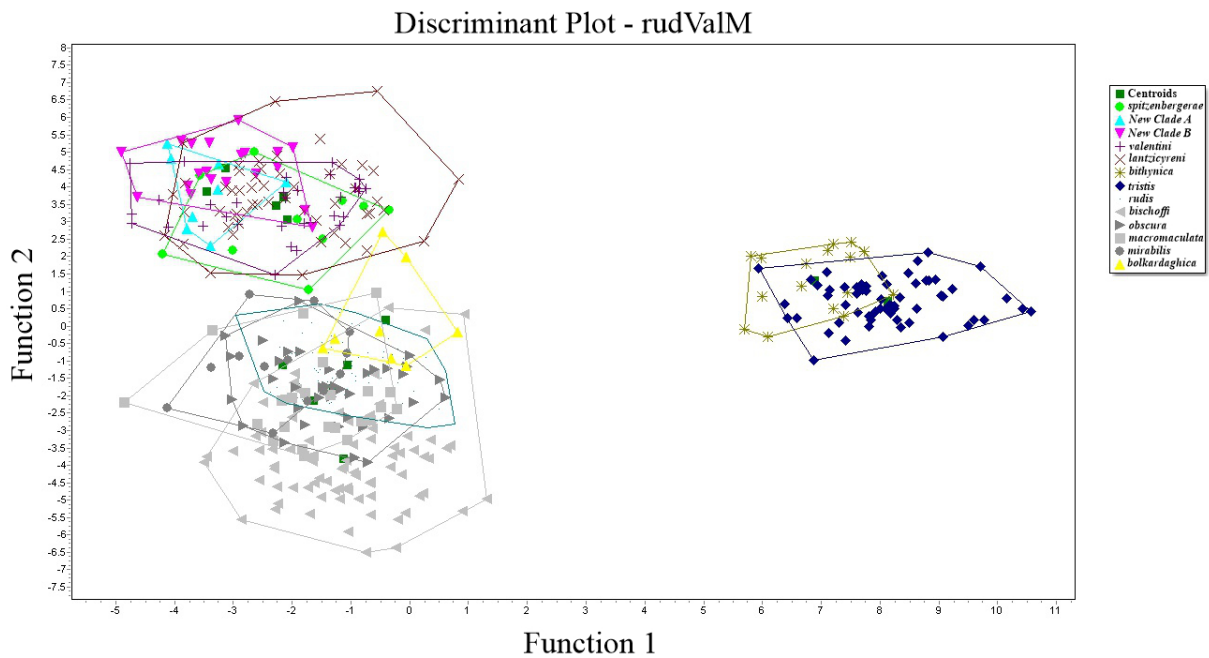
FIGURE 2. Canonical Discriminant Analysis (CDA) plot for MALES. Specimens, sample centroids, and group perimeters are represented. Green circle: ***D. v. spitzenbergerae***; Clear blue triangle: **"Clade A" from Candan *et al.* 2021**; Inverted violet triangle: **"Clade B" from Candan *et al.* 2021**; Cross: ***D. v. valentini***; Blade: ***D. v. lantzicyreni***; Asterisk: ***D. b. bithynica***; Diamond: ***D. b. tristis***; Minute dot: ***D. r. rudis***; Side inclined clear gray triangle: ***D. r. bischoffi***; Side inclined dark gray triangle: ***D. r. obscura***; Clear gray square: ***D. r. macromaculata***; Gray circle: ***D. r. mirabilis***; Yellow triangle: ***D. r. bolkardaghica***. These two first axes explain together 80.3 % of the total variability.

A fourth axis (in the edge, but still significant, with eigenvalue 1.02, 3.8% of variability; Chi-square 957.122, with 180 d.f.; $P = 3.87 \cdot 10^{-6}$) discriminated *D. r. mirabilis* Arribas, Ilgaz, Kumlutaş, Durmuş, Avcı & Üzüm, 2013 in its extreme negative part, characterized by the smaller values of SVL (0.43), femoralia (0.32) and Hindlimb relative length (0.32).

The three-dimensional representation of these axes (Fig. 3) (the three axes together explain 89.1 % of all the variability) shows the MST (Minimum Spanning Tree) superimposed on the three-dimensional representation of the position of the centroids. This MST can be considered as an unrooted NJ and connects each centroid with its closest one. The lowest distances between OTUs are those of clade A and clade B (0.73), as well as between *D. r. obscura* (Lantz & Cyrén, 1936) and *D. r. macromaculata* (Darevsky, 1967) (0.95). The greatest minimum distances are between *D. r. bolkardaghica* and *D. bithynica bithynica* (7.47). In general, all the populations of the *rudis* complex, as well as the *D. bithynica* or the *D. valentini* complex are related with others within each one of these three groups, except the one already mentioned as the greatest, interspecific, distance (*bithynica-bolkardaghica*) or the one between *D. v. spitzenbergerae* and *D. r. bolkardaghica* (3.34) which is the one that relates the *valentini* and the *rudis* complexes. Within the *rudis* complex, the relatively high distance between *D. r. macromaculata* and *D. r. bolkardaghica* (2.62) is also noteworthy. Distances between male centroids can be seen in Table 1 (below diagonal).

Three OTUs are the most connected in the MST: *spitzenbergerae*, *bolkardaghica* and *macromaculata*, with three connections each. Being the most connected could have two explanations; the first being a primitive population from which several lines have diverged (or from a common ancestor of its characteristics) with which it appears closely connected (the idea of "centrality", see for instance Arribas, 1999, 2010), or that it is a population of mixed origin, which appears together with those that gave rise to it. It is not easy to distinguish which may be the case, but genetically almost *D. v. spitzenbergerae* or *D. r. bolkardaghica* do not seem to be introgressed, thus can be considered as more primitive forms.

It is interesting that the two most meridional and isolated forms of both groups (*D. r. bolkardaghica* and *D. v. spitzenbergerae*), are the ones that relate both different lines with the smaller distance, even when other taxa in close contact seem to have introgressed in some places.

The three first axes of the CDA warrant the discrimination of 87.6 % of the specimens, very high. In general, all are above 75 %, except *D. r. macromaculata* (only 70.8 %), reaching even 100 % in clade A (Table 3).
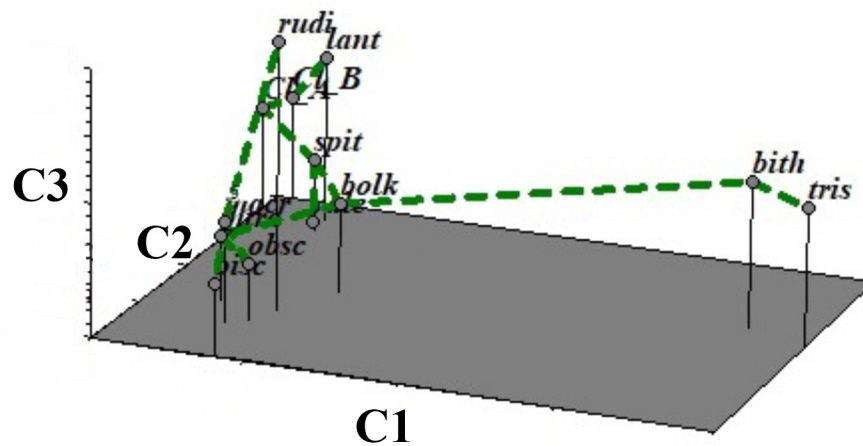
FIGURE 3. The three-dimensional representation of MALE centroids (bidimensional of samples and centroids in Fig 2) shows the MST (Minimum Spanning Tree) superimposed on the three-dimensional representation of the position of the centroids. The three axes together explain 89.1 % of all the variability. This MST can be considered equivalent to an unrooted NJ and connects each centroid with its closest relative. See text for explanation.
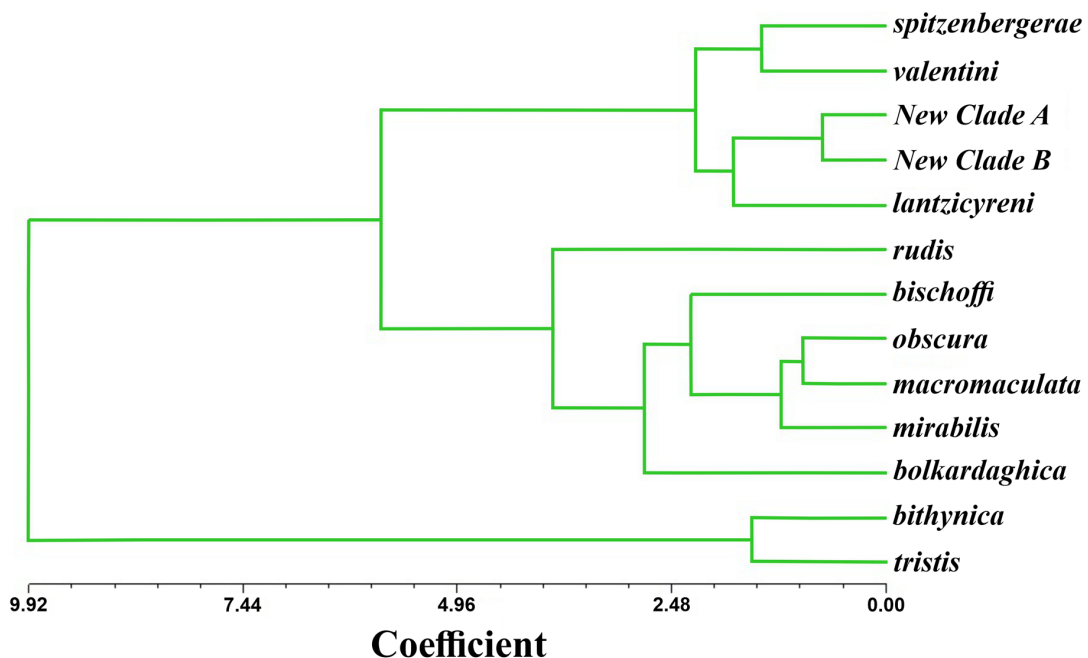
FIGURE 4. UPGMA tree derived from the matrix of distances (Table 1) among MALE samples, showing three great groups: a basal one, well different, with *D. bithynica* (inc. ssp. *tristis*) , and two more closer groups that include the former *rudis* and *valentini*-complexes. See the text for an explanation of the results. The tree, derived from the calculation of ultrametric distances calculated in UPGMA, reflects very well the relationships in respect to the original distanced matrix (see Table 1). Its Cophenetic Correlation Index, r = 0.95, shows that the obtained dendrogram has a very good fit (r > 0.9; Rohlf 2000).

UPGMA tree (Fig. 4) derived from the matrix of distances (Table 1) shows three groups: a basal one, well different, with *D. bithynica* (inc. ssp. *tristis*), and two more closer groups that include the *rudis* complex and the *valentini* complex. In the first, *rudis* s. str. is basal to the other taxa, whereas, in the *valentini* complex, *valentini* s. str. is closer to the *D. v. spitzenbergerae*, and clade A, clade B, and *lantzicyreni* are more closely related among them. The tree, derived from the calculation of ultrametric distances calculated in UPGMA, reflects very well the relationships in respect to the original distanced matrix (see Table 1). Its Cophenetic Correlation Index, r = 0.95, shows that the obtained dendrogram has a very good fit (r > 0.9; Rohlf 2000).

ANOSIM (MALES)

Analysis of Similarity (ANOSIM) of the males sample data show a good taxa assignation (R-statistic = 0.527101, $P < 0.001$, 1000 randomizations). As the general test is significant, the different samples differ more between themselves than internally. In general, all pairs of samples compared are significantly different ($P < 0.01$), except *bithynica-tristis*, and *macromaculata-obscura* (see Table 2) that are not different (their partial tests are close to zero and even negative, so the probability of misclassification among them is very high). *Darevskia v. spitzenbergerae* and clade A are significantly different, but close to the threshold of significance ($P = 0.044$).

Canonical discriminant analysis (FEMALES)

Discriminant Analysis (CDA) maximizes the discrimination of the samples between the three significant axes (Eigenvalues greater than one; Chi-square 3220.71 [276 d.f.; $P = 0.001$] and 2198.83 [242 d.f.; $P = 0.001$] for the first and second axes, respectively). The bidimensional plot (see Fig. 5) is a plane defined by the first axis (Eigenvalue 13.06; 49.8 % of the variability explained) and the second axis (7.98; 30.4 % explained) that separates the samples in a similar way to the males, although with a slightly less clear separation between the *rudis* and the *valentini* complexes. Both axes together explain 79.8 % of the total variability. Wilks Lambda is 0.000240447 ($F_{276} = 17.11$, $P = 0$). As $P < 0.05$, this demonstrates the existence of significant differences among the samples analyzed. Bartlett's Sphericity Tests further proved that the variables were uncorrelated, a prerequisite for successful discriminant analysis (Bartlett's Chi-Squared Test Statistic = 3224.88, 276 degrees freedom; $P = 0.001$).

As shown in Fig. 5, as an occurred in the male's analysis, the first axis (49.8 % of variability explained) separates *D. bithynica (*sspp. *bithynica* and *tristis*) females in the positive part of the axis, from the remaining samples of the *rudis* and *valentini* complexes in the negative one. As in male analysis, *D. bithynica* appears very different and characterized by greater values of head index (0.83), head relative length (0.51), SVL (0.29), hindlimb relative length (0.39); and the smaller scores of pileus index (-0.37) in respect to the *rudis* and *valentini* complexes, with the same explanation as in males (see above).

The second axis (30.4 % of variability explained) (Fig. 5) separates in its positive part the samples of the *valentini* complex from the *rudis* complex ones in the central and the negative part of the axis. The *valentini* complex forms (positive part) are characterized by greater tibialia (0.58), hindlimb relative length (0.35), head index (0.34), and dorsalia (0.27), and the smaller values of head relative length (-0.54), femurouter (-0.28) and SVL (-0.27). In the females, the *valentini* complex samples had comparatively longer limbs, a greater number of scales in the crus (which in this case correspond also to smaller sized and no or almost-no keeled ones) and less markedly, a greater number of ventral and dorsal scales. Also, *valentini* complex had comparatively smaller and narrow heads, and less markedly smaller sizes and scales in the outer part of the crus. In the extreme of the *rudis* complex, with the contrary scores to the *valentini* complex, outstands *D. r. bischoffi*, with the extreme contrary values.

The distinction is very similar to the case of males, with an overlap in these two dimensions of the taxa of the *rudis* complex with each other, and the *valentini* complex with each other, with hardly any overlap between both groups. Interestingly, this little overlap occurs between *rudis* s. str. and *lantzicyreni*, and could correspond to difficult to classify or hybrid specimens.

The third axis (only 8.6 % of variance explained; eigenvalue of 2.25) hardly contributes to discrimination. Within the large group of *rudis* and *valentini* complexes, *D. rudis* s. str. stands out a little (but with a lot of overlap) towards the positive part (with the greater values of dorsalia), while towards the negative *D. valentini* s. str. appears in the other extreme with the lower dorsalia.
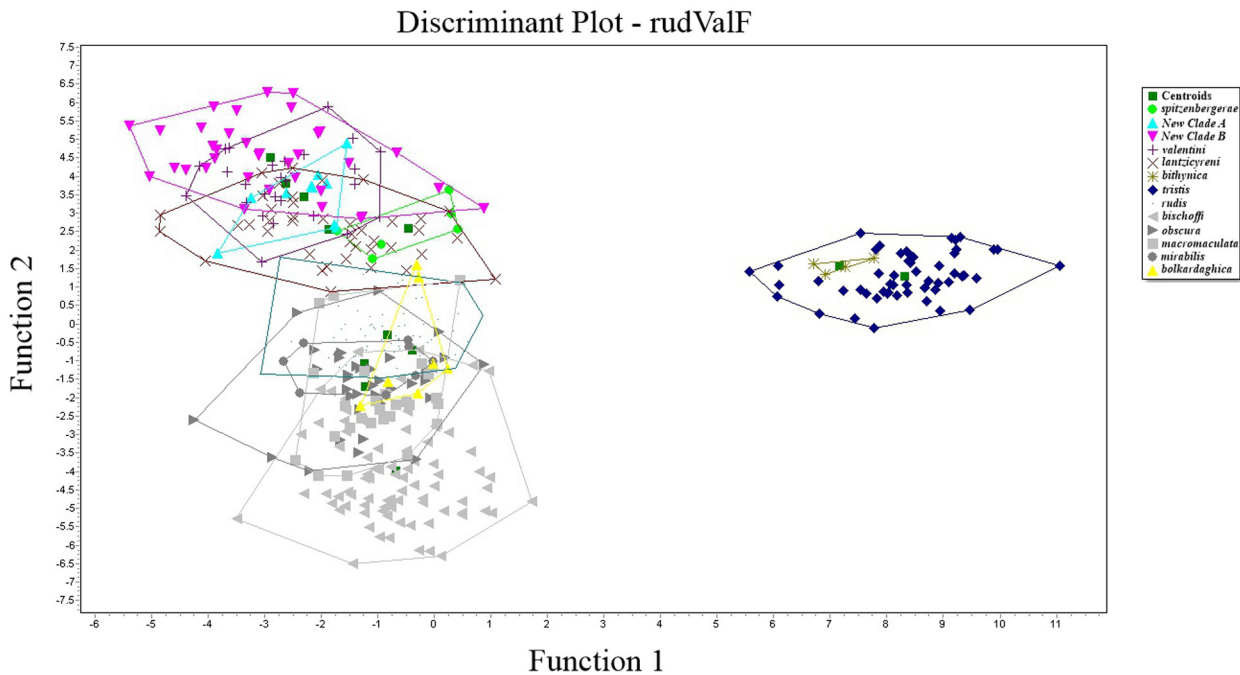
FIGURE 5. Canonical Discriminant Analysis (CDA) plot for FEMALES. Specimens, sample centroids, and group perimeters are represented. Green circle: ***D. v. spitzenbergerae***; Clear blue triangle: **"Clade A" from Candan *et al.* 2021**; Inverted violet triangle **"Clade B" from Candan *et al.* 2021**; Cross: ***D. v. valentini***; Blade: ***D. v. lantzicyreni***; Asterisk: ***D. b. bithynica***; Diamond: ***D. b. tristis***; Minute dot: ***D. r. rudis***; Side inclined clear gray triangle: ***D. r. bischoffi***; Side inclined dark gray triangle: ***D. r. obscura***; Clear gray square: ***D. r. macromaculata***; Gray circle: ***D. r. mirabilis***; Yellow triangle: ***D. r. bolkardaghica***. These two first axes explain together 79.8 % of the total variability.

The fourth axis has an eigenvalue lower than 1, but very close (eigenvalue 0.95, 3.6% of variability; Chi-square 893.835, with 180 d.f.; $P = 3.92 \cdot 10^{-6}$) and discriminates especially clade A and in a lesser degree *D. v. spitzenbergerae* towards its positive part, characterized by higher values of lamellae (0.51), preanalia (0.44) and femoralia (0.36).

The three-dimensional representation of these axes (Fig. 6) (the three axes together explain 88.4 % of all the variability) shows the MST (Minimum Spanning Tree) of females superimposed on the three-dimensional representation of the position of the centroids. The lowest distances between OTUs are those of *D. r. mirabilis* and *D. r. obscura* (0.95), as well as between *D. r. bolkardaghica* and *D. r. mirabilis* (0.99). The greatest minimum distances are between *D. v. spitzenbergerae* and *D. bithynica* s. str. (8.16), probably the geographically farthest populations here studied. As occurred in males, all the populations of the *rudis* complex, as well as the *D. bithynica* or the *D. valentini* complex are related with others within each one of these three groups, except the one already mentioned as the greatest distance (*bithynica-spitzenbergerae*) that connect the *valentini* complex with *D. bithynica*, or the one between *D. v. spitzenbergerae* and *D. r. bolkardaghica* (3.33) that connects the *valentini* and the *rudis* complexes (as occurred in males). Distances between centroids can be seen in Table 1 (above diagonal).

Three OTUs are the most connected in the MST are clade A and *D. r. obscura* with three connections each. As in the male analysis, it is interesting that there are two extreme populations and displaced towards the south of both groups (*D. r. bolkardaghica* and *D. v. spitzenbergerae*) result to be the ones that connect the *rudis* and the *valentini* complexes. The three first axes of the CDA warrant the discrimination of 88.67 % of the females, very high and near-identical to males. All the correct reclassifications are above 77 %, reaching even a 100 % in *D. v. spitzenbergerae*, clade A, *D. valentini* s. str., *D. bithynica* s. str., *D. r. mirabilis* and *D. r. bolkardaghica* (Table 3).

UPGMA tree (Fig. 7) derived from the matrix of distances (Table 1) is similar to the males one and shows three groups: a basal one, well different, with *D. bithynica* (inc. ssp. *tristis*), and two more closer groups that include the *rudis* complex and the *valentini* complex. In the first, *D. rudis* s. str. is basal to the other taxa, whereas, in the *valentini* complex, *D. valentini* s. str. is basal, whereas *D. v. spitzenbergerae* appears closer to *D. v. lantzicyreni*. Clades A and B are paired between them. As in the males, the tree reflects very well the relationships in respect

to the original distanced matrix (see Table 1). Its Cophenetic Correlation Index, r = 0.94, shows that the obtained dendrogram has a very good fit (r > 0.9; Rohlf 2000).
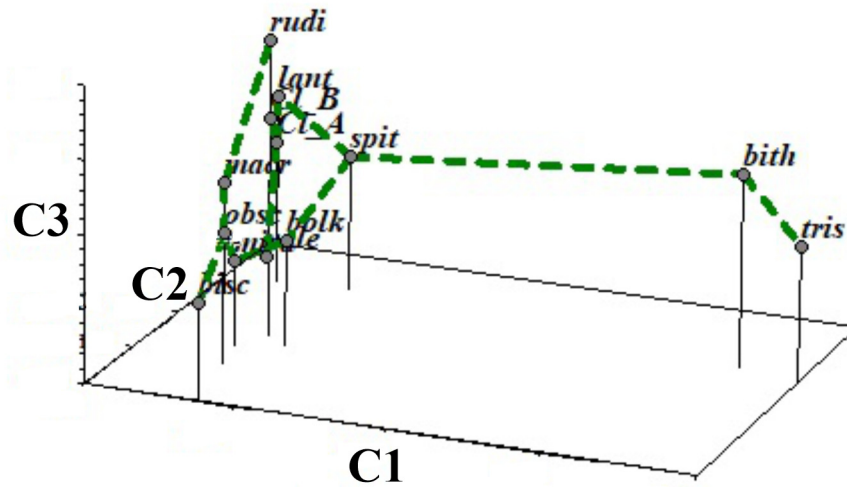
FIGURE 6. The three-dimensional representation of FEMALE centroids (bidimensional of samples and centroids in Fig 5) shows the MST (Minimum Spanning Tree) superimposed on the three-dimensional representation of the position of the centroids. The three axes together explain 88.4 % of all the variability. This MST can be considered equivalent to an unrooted NJ and connects each centroid with its closest relative. See text for explanation.
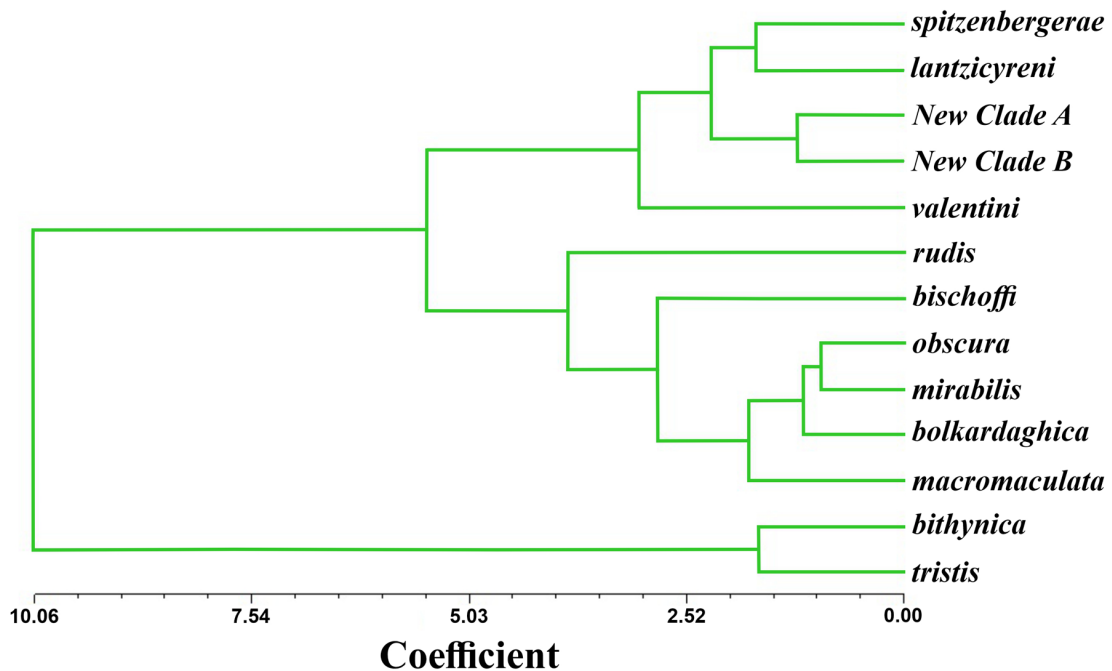
FIGURE 7. UPGMA tree derived from the matrix of distances (Table 1) among FEMALE samples, as in the males one, shows three groups: a basal one, well different, with *D. bithynica* (inc. ssp. *tristis*), and two more closer groups that include the former *rudis* and *valentini*-complexes. See the text for an explanation of the results. The tree, derived from the calculation of ultrametric distances calculated in UPGMA, reflects very well the relationships in respect to the original distanced matrix (see Table 1). Its Cophenetic Correlation Index, r = 0.94, shows that the obtained dendrogram has a very good fit (r > 0.9; Rohlf 2000).

ANOSIM (FEMALES)

Analysis of Similarity (ANOSIM) of the females sample data show a good taxa assignation (R-statistic = 0.479062, $P < 0.001$, 1000 randomizations). The general results are similar to the male analysis and in general, the great majority of samples are statistically different ($p < 0.01$) (Table 2). Among the *valentini* complex, clade B and *D. v. spitzenbergerae* are not significantly different (P = 0.105). In the *rudis* complex, *D. r. bischoffi* and *D. r. macromaculata* (P = 0.23), *D. r. macromaculata,* and *D. r. obscura* (P = 0.48) and *D. r. obscura* and *D. r. bolkardaghica* (P = 0.34) are also not different. Finally, also *D. b. bithynica* and *D. b. tristis* (P = 0.85) are not different. However, some of these female samples (i.e. *bithynica* s. str., *bolkardaghica* and *mirabilis*) are relatively short and results are less reliable than in male analysis.

ANOVA

Descriptive statistics and ANOVA results can be seen in Tables 3, 4 and 5. A graphic display of the degree of significant differences ($p < 0.01$) among the different OTUs is represented in Fig. 8. As can be seen, the overall representation is similar to the current taxonomy. However, *D. r. rudis* appears fairly differentiated to the remaining of the *rudis* complex (with *D. r. obscura* and *D. r. macromaculata* almost identical, and also *D. r. bolkardaghica* and *D. r. mirabilis* successively related to the former ones). *Darevskia b. bithynica* and *D. b. tristis* (Lantz & Cyrén, 1936) appear related and well-differentiated from the remaining OTUs. In the *valentini* complex, *D. v. spitzenbergerae* is almost identical (biometry and scalation) to clade A, and both successively related to clade B, *D. v. lantzicyreni,* and *D. v. valentini*. The discordant note is the presence among this group of *D. r. bischoffi*, probably due to the differences accumulated by its strong size and allometry that distort the results in respect to other *rudis* complex OTUs.
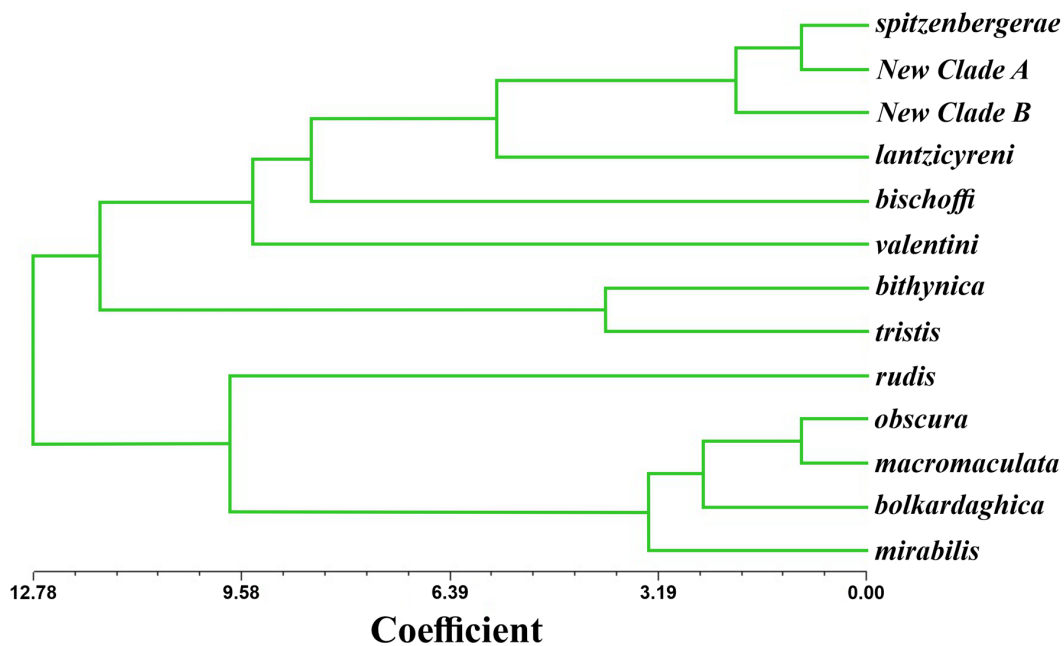
FIGURE 8. A graphic display of the degree (number) of significant differences ($p < 0.01$) among the different OTUs (MALES and FEMALES together). As can be seen, the overall representation is similar to the "old" (only morphological) taxonomy. See text for details.

Among the findings in ANOVA (Tables 4 and 5) (M: males; F: females) are noteworthy:

-Low supraciliar granula (M, F) and gularia (M), and higher circumanalia (M) counts in *D. r. mirabilis*, especially the first, are distinctive of this taxon.

-Higher ventralia counts in *D. v. spitzenbergerae*, clade A, and clade B (M) and in general, in all the *valentini* complex (F) than in *D. bithynica* or the *rudis* complex taxa.

- Preanalia is higher in clade A and strongly characterizes it (M, F).

-Lamellae are characteristically lower in *D. r. bolkardaghica* (M, F).

-Tibialia (M, F) is distinctive with higher counts (and smaller scales size) in the *valentini* complex (and *D. b. bithynica*), appearing the lower counts in part of the *rudis* complex (*D. r. bischoffi*, *D. r. obscura,* and *D. r. macromaculata*). *Darevskia r. rudis*, *D. b. tristis*, *D. r. bolkardaghica* and *D. r. mirabilis* appear in intermediate scores (but in scale size and aspect are similar to the lower scored ones, the *rudis* complex). This can be seen in Fig. 9. There are two morphologies: small and feebly keeled (*valentini* complex and *D. bithynica* ssp.), or very big and strongly keeled scales (most of the *rudis* complex taxa).

-Dorsalia is smaller in a great part of the *rudis* complex (except *D. r. rudis*) than in the *valentini* complex (except in *D. v. valentini* that has lower scores similar to the main *rudis* complex) and *D. bithynica* ssp..

-Temporalia1 is somewhat smaller in *D. r. macromaculata* and *D. r. obscura* (M, F).

-Temporalia2 is a bit lower in *D. v. valentini* (M,F).

-SVL (size) is clearly greater in *D. r. bischoffi* (M, F).

-Pileus index, head index and head relative size are greater (longer pilei and comparatively bigger heads) in *D. bithynica* sspp. (M, F).

-Anal index, a bit greater (comparatively wider) in *D. valentini* than in *D. bithynica* or the *rudis* complex.

-Hindlimb relative length is comparatively smaller in all the *rudis* complex than in the *valentini* complex. The greater scores (greater hindlimbs related to climbing) appear in *D. bithynica* sspp.

Size and keeling of crus area scales

Another qualitative characteristic studied and indirectly expressed in tibialia (see above), is the scale size and keeling of the shin (upper part of the crus or shank) area in the *rudis* and *valentini* complexes (See Fig. 9). Scale size (great, medium, small) and keeling development (weak keeling, medium keeling, strong keeling) are different among the different forms. Often, are compared with the size of the dorsal scales (as in Darevsky, 1967: but there the sense of the different subspecies –i. e. *rudis* s. str.- was different and the size estimation a bit different from ours). We have compared size with dorsal scales from the lumbar part of the animal, in its widest part, not far from hindlimbs.

Darevskia v. lantzicyreni has a medium scale size with medium keeling in the shin, and is similar or a few smaller than dorsum ones.

Darevskia v. "clade B" from Candan *et al.* (2021) has a small scale with weak keeling, that are also smaller than the dorsal ones.

Darevskia v. spitzenbergerae has a small scale size with weak keeling that are smaller than dorsal ones.

Darevskia v. "clade A" from Candan *et al.* (2021) has a medium scale size with weak keeling, smaller than dorsal ones.

Darevskia v. valentini has a medium-scale size with weak keeling, smaller than dorsal ones.

Darevskia b. bithynica has a small scale size and weak keeling, smaller than dorsal ones.

Darevskia b. tristis has a medium-scale size with weak keeling, smaller than dorsal ones.

Darevskia r. bischoffi has a great scale size with strongly keeling, greater than dorsal scales.

Darevskia r. obscura has great scale size and strongly keeling, similar or a bit smaller than dorsal scales.

Darevskia r. macromaculata has a great scale size with strongly keeling, similar or a bit smaller than dorsal ones.

Darevskia r. bolkardaghica has medium scale size and medium keeling, similar or a bit smaller than dorsal ones.

Darevskia r. rudis has a medium scale size with medium keeling, similar or a bit smaller than dorsal ones.

Darevskia r. mirabilis with medium scale size and medium keeling, similar or a bit smaller than dorsal ones.

The strong size and keeling are associated with the *rudis* complex (*D. rudis* and its former subspecies), whereas small size and feebly or near null keeling with the *valentini* complex. However, as can be seen in this work, the assignation of the different taxa to one or other species is far from being clear, and the situation in the shin keeling also shows many intermediate situations between both extremes. One taxon, *D. r. bischoffi*, has very big and strong keeled scales. *Darevskia r. obscura* and *D. r. macromaculata* had scales not so big (medium) but also strongly keeled. *Darevskia v. lantzicyreni*, *D. r. bolkardaghica*, *D. r. mirabilis* and *D. r. rudis* had marked keeling, not so strong, in medium-sized scales. Medium or small-sized scales with feeble keeling (even barely visible) appear in *D. valentini* s. str., *D. v. spitzenbergerae*, clade A, clade B, *D. b. bithynica* and *D. b. tristis*.

Osteology

Osteological characteristics were similar to other *Darevskia*, including its derived increase of vertebral numbers (Arribas 1998; Arnold *et al.* 2007). Characteristics of *D. v. valentini* are here described, and following, the variation of the other forms so far related to *D. valentini* and comments about other taxa of the *D. rudis* complex (see Table 6).

Darevskia v. valentini - Skull: Seven, very rarely eight premaxillary teeth, ever unicuspid. Specimens have 16 to 20 maxillary teeth in each side (average 18), and from 18 to 25 in dentary (average 22), with bicuspid ones more numerous than the monocuspid. Postfrontal and postorbital bones are separated from birth, with the anterodistal process of the postfrontal and anteromedial process of the postorbital present (the latter, present in all the taxa of the so-called *rudis* group), very rarely the latter can be fairly small. Postfrontal is more or less equal in length than postorbital, rarely smaller. Squamosal bone overlaps with postorbital in a third (rarely from only in one fourth to a maximum of a half) of the length of the latter.

Vertebral column: The number of presacral vertebrae shows sexual dimorphism. Males have 27 presacral vertebrae. Females have 29 (from 28 to 30 presacral vertebrae). In males is accompanied by 6 posterior dorsal vertebrae, but in females, there is an increase of presacral vertebrae, from 27 to a range of 28-30, and usually appears an extra short rib, counting seven or eight in total). The third vertebra without associated ossified ribs. Sternal costal formula: (3+2). A-Type (rarely some tendency to B-Type) of pre-autotomic caudal vertebrae (from Arnold, 1973) are present.

Girdles: Clavicles open (very rarely closed). Sternal fontanel is oval (rarely irregular oval tending to irregular cordiform). Interclavicle with the lateral branches perpendicular to the central axis (cruciform), but can be slightly inclined towards the rear. Sternal-xiphisternal formula [3+2]1, thus is, three ribs connected to the sternal plate, two to xiphisternum, and one inscriptional rib (free).

Darevskia v. lantzicyreni has 7 premaxillary teeth, 17.6 (17-18) maxillary teeth, and 22.3 (21-23) dentary ones, more bicuspid than unicuspid. Males have the 27 presacral vertebrae typical of *Darevskia* (rarely reduced to 26 and extremely rare to 25) with 6 or 7 short ribs, and females 28 (rarely 27 in parallel to male's reduction) with six short ribs. Without rib associated to the third vertebrae. Tail vertebrae A-type. Clavicles open (more rarely closed). Interclavicle cruciform or with branches slightly directed backward. Sternal fontanelle oval. Sternal-xiphisternal formula [3+2]1. Postorbital and postfrontal are similar in length (more rarely the first slightly smaller), with the anteromedial process of the postorbital present. Postorbitary overlaps with squamosal in one-third (1/12-1/9) of its length.

Darevskia v. spitzenbergerae has 7 premaxillary teeth, 17.25 (16-18) maxillary teeth, and 21 (20-23) dentary ones, more bicuspid than unicuspid. Males have 27 presacral vertebrae with 6 short ribs, and females 29 with 6 or 7 short ribs. Without rib associated to the third vertebrae. Tail vertebrae A-type. Clavicles open (very rarely closed). Interclavicle with branches slightly directed forwards. Sternal fontanelle oval (more rare irregular cordiform). Sternal-xiphisternal formula [3+2]0/1, more rare [3+1]1. Postorbital greater than postfrontal, more rare similar in length, with the anteromedial process of the postorbital present. Postorbitary overlaps with squamosal in one-third (rarer 1/2) of its length.

Clade A (from Candan *et al.* 2021) has 7 premaxillary teeth, 20.5 (19-21) maxillary teeth, and 23.5 (23-24) dentary ones, more bicuspid than unicuspid (very rare more or less in equal proportion). Males have 27 presacral vertebrae with 6 short ribs, and females and 29 with 6 short ribs. Without rib associated to the third vertebrae. Tail vertebrae A-type. Clavicles open or closed. Interclavicle with branches slightly directed forward or backward. Sternal fontanelle oval. Sternal-xiphisternal formula [3+2]1. Postorbital greater or equal than postfrontal, with the anteromedial process of the postorbital present (sometimes fairly reduced). Postorbitary overlaps with squamosal in one-third (rarer 1/2) of its length.

Clade B (from Candan *et al.* 2021) has 7 premaxillary teeth, 17 (15-18) maxillary teeth, and 21.25 (20-22) dentary ones, more bicuspid than unicuspid. Males have 27/28 presacral vertebrae with 6 or 7 short ribs respectively, and females and 29 with 7 short ribs (which suggest strongly the existence of females with 28/6). Without rib associated to the third vertebrae. Tail vertebrae A-type. Clavicles open, more rarely closed. Interclavicle cruciform or with branches slightly directed backward. Sternal fontanelle oval. Sternal-xiphisternal formula [3+2]1. Postorbital equal than postfrontal, with the anteromedial process of the postorbital present. Postorbitary overlaps with squamosal between 1/3 and 1/2 of its length.

Data about the *rudis* complex taxa are in Arribas *et al.* (2013). The most apparent differences between the large groups (species or complexes) within the *rudis* group [*rudis* and *valentini* complexes, together with *D. portschinskii* (Kessler, 1878)] are:

Usually, the number of bicuspid teeth is higher than that of unicuspids in the dentary and maxilla, but our specimens of *D. portschinskii* are more or less equal (sometimes a little higher, sometimes a little less).

The number of presacral vertebrae in males is usually 27 (the typical number in *Darevskia*), but there can be an increase to 28. There may also be a reduction in this number to 27 in some specimens of *D. v. lantzicyreni*, *D. r. bischoffi*, *D. r. obscura,* or *D. r. mirabilis,* and even more rare down to 25 in a single specimen of *D. v. lantzicyreni*.

The same in females, the base number is 28, but there may be greater abdominal elongation related to egg carrying, with an increase to 29 and even 30, accompanied by a greater number of short ribs in the lumbar area. Also, there may be a reduction of the vertebral number in some specimens (parallel to that of the males) as occurs in a single specimen of *D. v. lantzicyreni* and *D. r. rudis* with 27.

The presence of an (almost partially) ossified rib associated with the third vertebra occasionally appears as an atavistic character in Lacertini, usually in small and marginal populations. In this group, we have only seen them in some specimens of *D. r. bolkardaghica* and are extremely rare or barely visible in *D. r. obscura* and *D. r. bischoffi*.

The pattern of pre-autotomic caudal vertebrae is A type in all except some *D. v. valentini* some of which show any of the processes as the type B and very rarely also in *D. bithynica* sspp.

Claviculae can be open or closed and both models coexist dominating one or the other.

The basic interclavicle is cruciform, but the lateral branches slope forward or backward in many individuals. Pure cruciforms are especially dominant throughout the *rudis* complex and *D. bithynica* ssp., *Darevskia portschinskii*, *D. valentini* s. str., clade B, *D. v. lantzicyreni*, *Darevskia r. bischoffi*, *D. r. macromaculata* and *D. r. chechenica* (Eiselt & Darevsky, 1991) have them cruciform, coexisting with branches somewhat backward. With the lateral branches inclined forward appears *D. v. spitzenbergerae* (with only this model) and in "clade A" (coexisting with branches backward). It also appears in Georgian specimens of *D. r. obscura*.

The sternal fontanelle is oval, but can vary (elongate, irregular in shape) until recalling the irregular cordiform shape, be reduced or absent (as in *D. bithynica* s. str.), or adopt particular shapes, as sand-clock, irregular cordiform, or trilobate in forepart (*D. r. bolkardaghica*).

The sternal-xiphisternal formula is usually 3 + 2, that is, three ribs join the sternum and two the xiphisternum. There is usually an inscriptional rib. These inscriptional ribs may rarely be missing (frequently in our *D. portschinskii*), or increase by one, although the variations are frequently but not always at the expense of a xiphisternal one.

Postorbital and postfrontal usually have similar lengths. In the *valentini* complex are similar or the first is a bit longer. The exception is *D. v. lantzicyreni* in which is also subequal or the first is smaller than the second. In the *rudis* complex (including *D. bithynica* ssp.) are subequal or the postorbital is a bit smaller (what is equal or with the contrary tendency to the *valentini* complex). In *D. portschinskii* is as in *D. valentini* but with postocular greater or equal than postfrontal, in similar proportions. Anterolateral process of the postfrontal is ever-present, and the anteromedial of the postorbital also, but can be, more rarely, reduced [*D. bithynica* ssp., *D. r. obscura*, *D. r. macromaculata*, *D. r. svanetica*, *D. r. chechenica* and *D. r. rudis*]. In *D. v. valentini* and *D. v.* "clade A" can be (but rarely) reduced.

Squamosal and postorbital overlap around one-third of the length of the latter. Sometimes with a bit more (around 1/2) or less (1/4) overlap. The 1/2 is the common ratio in *D. bithynica* ssp. and the most common in *D. r. bolkardaghica*. Very rarely extreme reduced overlap appears in isolated teratological specimens (up to only 1/9 in a single *D. v. lantzicyreni* or even no contact in a specimen of *D. r. bischoffi*).

Molecular analyses

Mitochondrial phylogenetic trees

A partial of 711 bp of *Cyt-b* gene fragment was used both in ML and BI analyses. Due to the topological similarity of the resulting phylogenetic trees, we present the ML tree with the bootstrap and posterior probability (pp) values obtained from both analyses (Fig. 9). One of the prominent results obtained from the analyses is that two basal clades separated clearly from the remaining taxa within the *D. valentini*/*D. rudis* complexes with high bootstrap and pp values. One of them (clade A) is related to *D. v. spitzenbergerae*, while the other (clade B) represents a new lineage that Candan *et al.* (2021) has identified for the first time. The status of *D. r. mirabilis* (clade C) is also apparent by locating in a separate branch than the other taxa. This monophyletic clade has also high bootstrap and pp values, which help to accept its true position. Considering the remaining taxa, it seems that internal nodes have low bootstrap and pp values pave the way for polytomy by messing up the tree topology, while external nodes with higher values have

supported each taxon as monophyletic. While the three defined species, *D. valentini* (clade F), *D. bithynica* (clade E) and *D. obscura* (clade G), clearly differ from each other, a group including *D. v. lantzicyreni*, *D. r. rudis* and *D. r. bolkardaghica* (clade D) exhibits an overlapping complex structure, which is also well-documented in Candan *et al.* (2021).
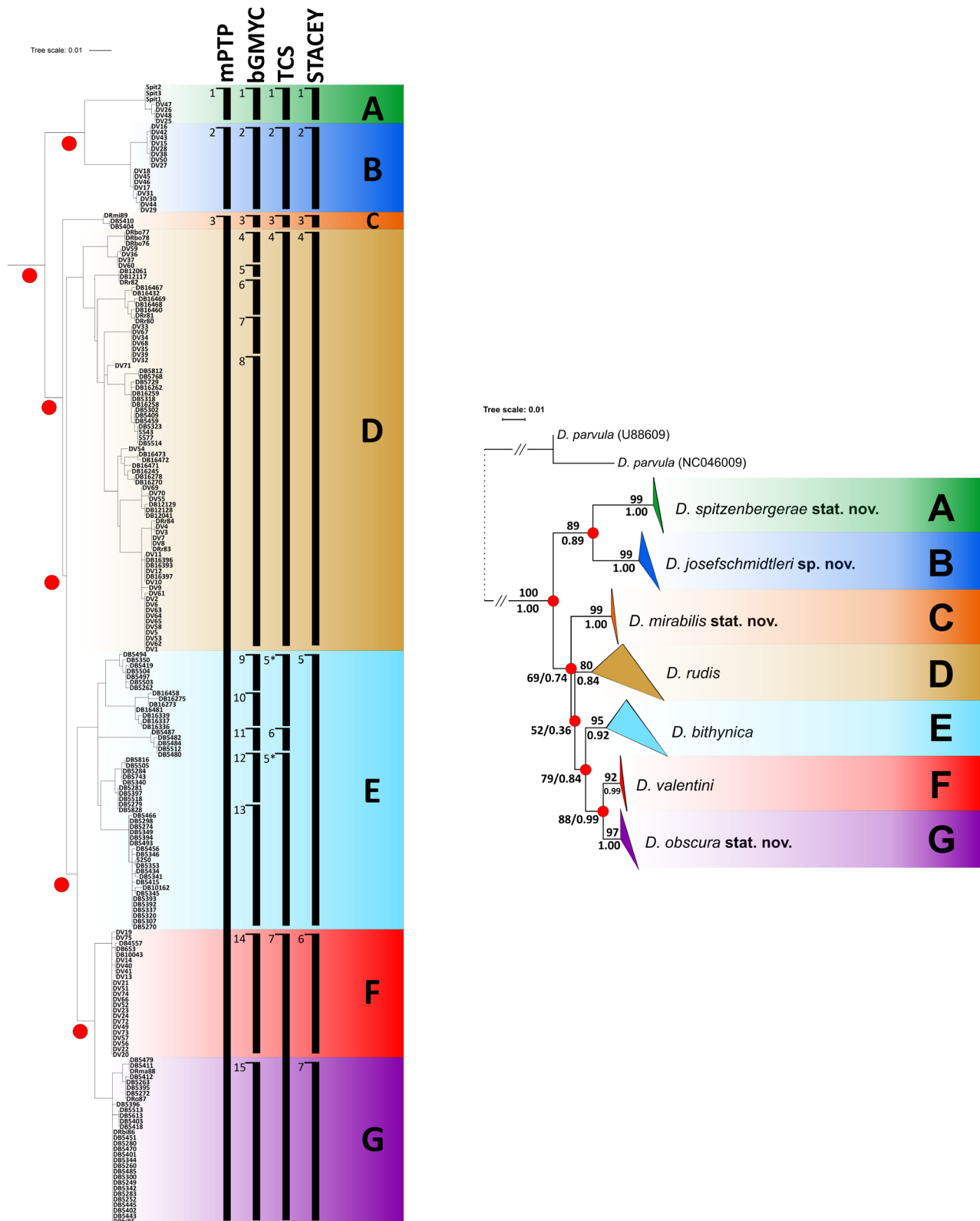
FIGURE 9. Maximum Likelihood (ML) tree (left) and collapsed one for the same tree (right) are given. Numbers on branches indicate the bootstrap and posterior probability (pp) values (ML/BI). Each species delimitation result is shown, and a vertical bar represents each cluster obtained from the analysis. Red circles indicate the internal nodes of each OTUs. The new nomenclature proposed in the text is used.

Species delimitation approaches

Here, we preferred to apply different approaches based on both single- and multi-locus species delimitation to detect species boundaries. Although entirely obtained results of single-locus gave us different outputs, there are overlapping findings in the definition of new species groups (Fig. 9). All analyses support that clades A and B are distinct taxa. *Darevskia r. mirabilis* (clade C) is also supported by all analyses except mPTP as a separate species. Interestingly, bGMYC constitutes a fragmented profile inside *D. valentini*/*D. rudis* complex (clade D) and *D. bithynica* (clade E), while the same situation occurs for *D. bithynica* only in TCS. Finally, *D. valentini* (clade F) and *D. obscura* (clade G) are supported by only bGMYC within single-locus approaches.

A multi-locus species delimitation, STACEY, runs a total of 15,001 different models for the number and composition of species within the dataset including *Cyt-b* and *MC1R*. The prevailing model, supported by 99% of the posterior distribution of samples, showed that entire species groups studied here are valid.

Haplotype networks and genetic distances

The network analysis showed independent results for each gene region as expected due to different sources: mitochondrial *Cyt-b* and nuclear *MC1R* (Fig. 10). Detected haplotypes were 86 for *Cyt-b* and 37 for *MC1R*. Haplotype diversities were as follows: 0.979 (± 0.004) for *Cyt-b* and 0.812 (± 0.013) for *MC1R*. Considering the result of *Cyt-b*, it seems that all putative species groups do not share any haplotypes. As an interesting point, clades A and B link with *D. r. obscura* (clade G) rather than *D. valentini* (clade F). The *MC1R* gene region, on the other hand, exhibits a more complicated pattern, which is associated with its diploid nature, with sharing haplotypes. Clade A has only one haplotype (Hap16), sharing with clades B, C and G. Clade B also finds in Hap26, sharing with clade D. Clade C is distributed in three separate haplotypes as Hap1, Hap16 and Hap18. For detailed information see Fig. 10 and Appendix 3.

The genetic distance values for *Cyt-b* were determined, which can be considered sufficient for species discrimination, while they were insignificant for nuclear one. Although the nuclear marker seems to contribute to the genetic positions of some clades in the haplotype network, it can not help us to understand the genetic distinctiveness between/within species, because non-informative sites emerged from slower substitution rates. Considering mitochondrial genetic distances, there appear to be relatively close values among all groups ranging from 3.2 to 6.1 except only one as 1.6 between *D. valentini* (clade F) and *D. obscura* (clade G). Genetic distances, within and among the main groups, are given in Appendix 4.

Taxonomic implications

Considering our findings based on both morphology and phylogenetic, we accept that a new taxonomic reconstruction is inevitable, and suggest the following taxonomy.

Clade B from Candan *et al.* (2021) and this study, is described as distinct species.

Darevskia josefschmidtleri **sp. nov.**
(Appendix 5; Fig. 12e).

Synonymy/Chresonymy:

Lacerta valentini "Zwischenpopulation"(intermediate population); Eiselt, Darevsky & Schmidtler, 1992. (from "Çaldıran"-sic.!-)
Darevskia valentini "Clade B"; Candan *et al.* (2021) (same locality as this study)
ZooBank registration (http://zoobank.org): urn:lsid:zoobank.org:act:56CFE08E-164E-485B-8F4C-94EA76293128.

Holotype: ZDEU220/2016 (n.2). ♂, Başeğmez Village, Çaldıran, Van, Turkey. leg. Kamil Candan, Nurettin Beşer and Mehmet Kürşat Şahin, 24.06.2016. Conserved in ZDEU collection.
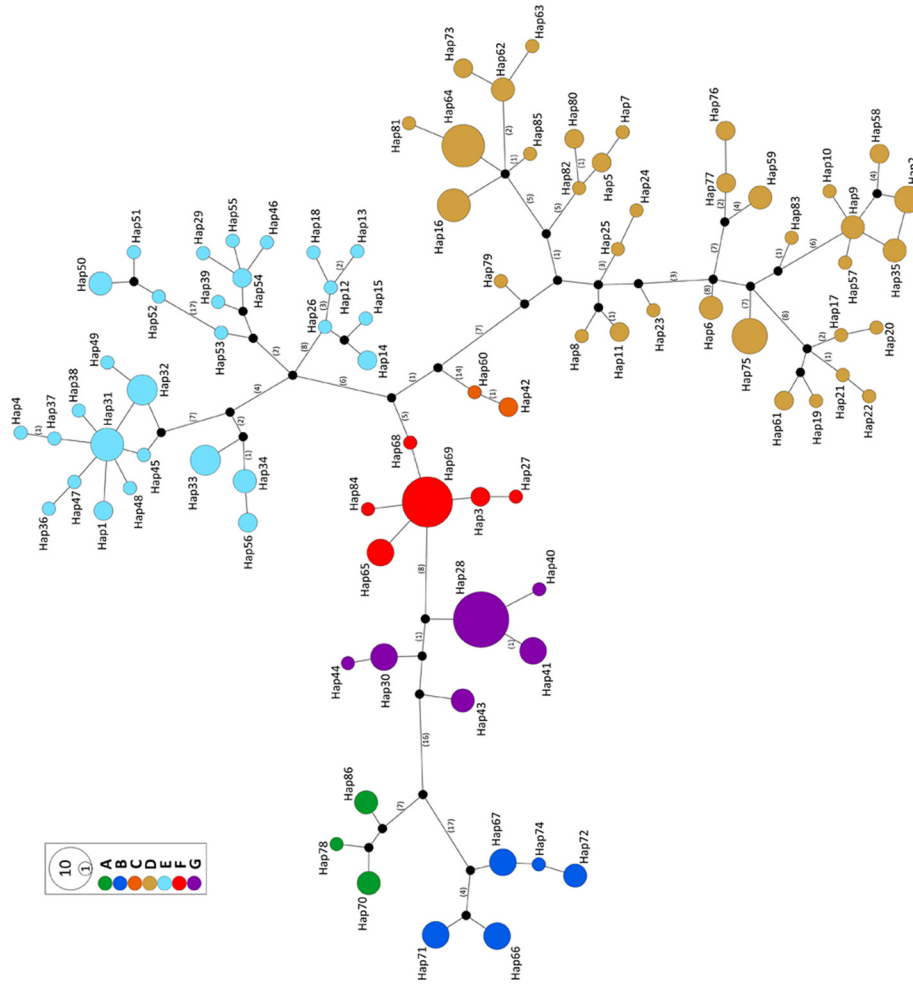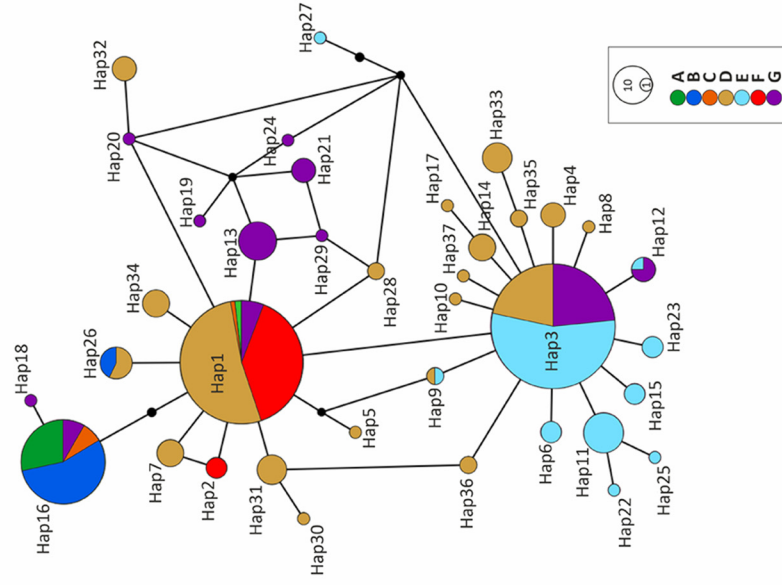
FIGURE 10. Parsimony networks corresponding to *Cyt-b* (A) and *MC1R* (B) represent reconstruction of the studied group. Numbers within parentheses represent a mutational step, black circles missing haplotypes, and colored circles haplotypes. The circle area is proportional to the number of individuals. The new nomenclature proposed in the text is used.

FIGURE 11. Escalation of the calf area in the *rudis* and *valentini* complexes. Scale size (great, medium, small) and keeling development (weak keeling, medium keeling, strong keeling). The new nomenclature proposed in the text is used. *D. r. lantzicyreni* **comb. nov.** (medium scale size, medium keeling); *D. josefschmidtleri* **sp. nov.** (small scale size, weak keeling); *D. s. spitzenbergerae* **stat. et comb. nov.** (small scale size, weak keeling); *D. s. wernermayeri* **ssp. nov.** (medium scale size, weak keeling); *D. valentini* (medium scale size, weak keeling); *D. b. bithynica* (small scale size, weak keeling); *D. b. tristis* (medium scale size, weak keeling); *D. o. bischoffi* **comb. nov.** (great scale size, strongly keeling); *D. o. obscura* **stat. et comb. nov.** (great scale size, strongly keeling); *D. o. macromaculata* **comb. nov.** (great scale size, strongly keeling); *D. r. bolkardaghica* (medium scale size, medium keeling); *D. rudis* (medium scale size, medium keeling); *D. mirabilis* **stat. nov.** (medium scale size, medium keeling.

Paratypes: 8 ♂♂, 8 ♀♀, 2 subadult ♀♀. Same locality, date and collectors as holotype. ZDEU221/2016, 6 ♂♂, 12 ♀♀, 1 juvenile, Çirişli Village, Çat, Erzurum, Turkey. leg. Kamil Candan, Nurettin Beşer, Mehmet Kürşat Şahin, 22.06.2016. ZDEU222/2016, 5 ♂♂, 8 ♀♀, 1 juvenile, Palandöken Mountain, Erzurum, Turkey. leg. Kamil Candan, Nurettin Beşer, Mehmet Kürşat Şahin, 01.07.2016. ZDEU119/2015, 1 ♂♂, 3 ♀♀, 2 ♀♀ subadults, Balık Lake, Taşlıçay, Ağrı, Turkey. leg. Kamil Candan, Elif Yıldırım Caynak, 26.07.2015. ZDEU121/2015, 2 ♂♂, 4 ♀♀, Güzeldere Village, Hınıs, Erzurum, Turkey, leg. Kamil Candan, Elif Yıldırım Caynak, 25.07.2015.

Derivatio nominis: The specific epithet refers to Josef Friederich Schmidtler (born 1942), for his remarkable work on the knowledge of Turkish herpetofauna and its rich diversity.

Comparative diagnosis (Morphology): *Darevskia josefschmidtleri* **sp. nov.** is a medium sized species (adults SVL: 53.25–67.95 mm). It is characterized by medium or small-sized scales with feeble keeling (even barely visible). *Darevskia josefschmidtleri* **sp. nov.** differs from *D. valentini* in that there is a higher number of lamellae (46–59 vs. 42–53) and dorsals (47–58 vs. 41–52); *Darevskia josefschmidtleri* **sp. nov.** males have a higher number of preanal than *D. valentini* (1–3 vs. 1) while females have different collar scores (8–12 vs. 7–10) and gulars (23–31 vs. 21–29). It also differs from *D. valentini* in having a greater head relative length (0.18–0.23 vs. 0.16.–0.21) for males. *Darevskia josefschmidtleri* **sp. nov.** differs from *D. spitzenbergerae spitzenbergerae* **stat. et comb. nov.** (see below) in that there is higher number of tibials (16–24 vs. 15–19) and dorsals (48–58 vs. 44–53) for males. Also, it differs from *D. spitzenbergerae spitzenbergerae* in having a shorter head relative length (0.18–0.23 vs 0.19–0.24). *Darevskia josefschmidtleri* **sp. nov.** differs from "Clade A" from Candan *et al.* (2021) (described below as *D. spitzenbergerae wernermayeri* **ssp. nov.**) in that there is a lower number of ventrals (26–29 vs. 26–31), temp 2 (2–6 vs. 4–6) in males and preanals (1–3 vs. 2–3) in females. *Darevskia josefschmidtleri* **sp. nov.** differs from *D. valentini* in that there is a lower number of maxillary (15–18 vs. 16–20) and dentary teeth (20–22 vs. 18–25). *Darevskia josefschmidtleri* **sp. nov.** differs from Clade A (*D. spitzenbergerae wernermayeri* **ssp. nov.** see below) in that there is a lower number of maxillary (15–18 vs. 19–21) and dentary teeth (20–22 vs. 23–24).

Diagnosis (Molecular): It can be distinguished from other former *D. valentini* populations by unique nucleotide combination located on the mitochondrial gene *Cyt-b* and nuclear loci *MC1R*. The consensus sequence (*Cyt-b*) for *Darevskia josefschmidtleri* **sp. nov.** is found in Appendix 6, together with the respective sequence for the *D. valentini* s. str. In this Table, the thirty simple nucleotide diagnostic characters between the consensus sequences are highlighted. Similarly, the molecular diagnostic characters for *Darevskia josefschmidtleri* **sp. nov.** regarding the nuclear loci are shown in Appendix 6.

Description of holotype: An adult male. Tail in regeneration process. Fixed with ethanol and conserved in 96% ethanol.

Scalation: Rostral not in contact with the nostril. Single postnasal on each side. Width of frontonasal (internasal) plate subequal to length, not contact with rostral. Sutures between prefrontal plates and frontal plate straight. Parietal plates in contact with postorbital plates on each side. Supraciliar granules 9 on each side, interrupted series on right, not on left side. Supraciliar plates 6 on each side. Supralabial and sublabial plates 4 and 6 on each side, respectively. Plates in supratemporal region 3 on left, 4 on right. The first supratemporal plate large, narrow towards the back, ends bluntly. Masseteric large, in one piece on each side, separated from the first supratemporal plate by a row of small scales. Tympanic obvious, in two pieces on the left and one piece on right, separated from masseteric by three and two rows of small scales on the left and right, respectively. Eight flat and smooth collaria. Gularia 27. Ventralia contains 6 longitudinal and 28 transverse rows of plates. Preanal scale in two pieces, surrounded by 6 rows of plates. Femoral pores 21 on left, 20 on right side. Subdigital lamellae 27 on left, 26 on right. Tibial scale 19. Dorsalia 53.

Biometry: SVL 64.68 mm., pileus width 6.79 mm, pileus length 13.27 mm, head width 8.13 mm, head length 13.14 mm. Length of forelimb 18.39 mm, length of hindlimb 27.90 mm. Anal plate width 4.69 mm, length 1.71 mm.

Coloration and pattern (in alcohol): The ground color of the dorsum is greenish brown. Dorsal tract with a wide vertebral band composed of fairly irregular transverse spots nost covering almost its complete width. Similar dark spotting is present on each side of the body (temporal or lateral band) that appears reticulated. Between these two dark spots, located both in the middle of the dorsum and flanks, a paler double line extends from the nape to the base of the tail (Appendix 5). There are few pale spots inside the reticulate on dark bands on flanks, with more in the forelimb. A few light bluish spots near the forelimb basis. Belly, along with head and neck, whitish (see photos in Appendix 5), with dark and blue spots in the outermost rows of ventrals. Background color of head plates brownish, with few scattered and small black spots on it.

Variations of paratypes: Descriptive statistics and variation range of the morphometric and scalation characters are given in Table 7. Frontonasal (internasal) rarely is in contact with rostral. Sutures between the prefrontal and

frontal are usually slanted. Parietal is rarely in contact with postorbital. Masseteric is sometimes divided into two pieces. Tight scales are feeble-keeled, smaller than dorsal ones. In one specimen, transverse dark spots on ground color combined with spots on each side, do not form two separate rows. In addition, transverse dark spots, longitudinally above ground color, are faint in ten specimens. In four samples, pale spots on the forelimb base were not blue (white). Belly, along with head and neck, yellowish in nine specimens. In fourteen samples, no spotting on head plates.
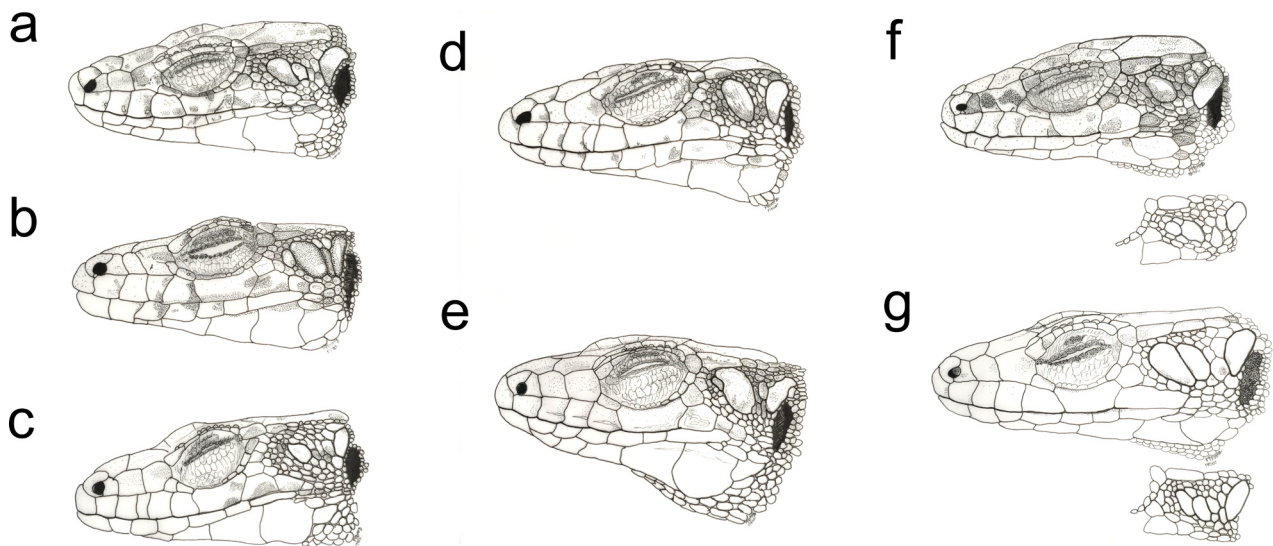
FIGURE 12. a) *Darevskia spitzenbergerae wernermayeri* **ssp. nov.** (Paratype; nº 12, Male; Başeğmez Village, Çaldıran, Turkey); b) *Darevskia mirabilis* **stat. nov.** (Paratype; nº 5, Female; Ovit Pass, Kaçkar Mountains, Rize, Turkey); c) *Darevskia rudis bolkardaghica* (Paratype; nº 1, Male; Karagöl, Ulukışla, Niğde, Central Anatolia, Turkey); d) *Darevskia rudis lantzicyreni* **comb. nov.** (nº 23, male; Kümbet Village, Zara, Turkey); e) *Darevskia josefschmidtleri* **sp. nov.** (Paratype; nº 20, Male; Yukarınarlıca Village, Çatak, Van, Turkey); f) *Darevskia valentini* (nº 9, Male; Tepeler Village, Ardahan, Turkey) and temporal area of an Armenian specimen (Karvansaray, Martuni District, Armenia); g) *Darevskia spitzenbergerae spitzenbergerae* **stat. et comb. nov.** (nº 1, Male; Cilo Sat Mountains, Hakkari, Turkey)- Also, temporal area of other specimen from the same locality. The new nomenclature proposed in the text is used.

Distribution: Confirmed localities draw an area around Çaldıran (Van) located in the east of Van Lake, around Balık Lake (Ağrı), Palandöken Mountain and around Çat and Hınıs (Erzurum) which is in the south of this massif, all in Turkey. Probably also in intermediate areas among these localities.

Habitat: Subalpine-like vegetation from Irano-Turanian Region, in rocky and stony areas near 2000 m or higher: 2095 m. (Çaldıran), 2270 m. (Balık Lake), 2429 m. (Palandöken), 1946 m. (Çat), 2643 m. (Hınıs). *Darevskia unisexualis* was found sympatric in the Palandöken Mountain, while no other reptile species were detected in the same and other localities of the area.

Comments: This new taxon seems to be the parental species that gave origin by hybridization to the parthenogenetic *D. unisexualis*, *D. sapphirina* and *D. bendimahiensis* according to Z-chromosome inheritance (Yanchukov *et al.* 2022).

Darevskia spitzenbergerae **(Eiselt, Darevsky & Schmidtler, 1992) stat. nov.**
(Fig. 12g). Type Locality: Mergan Plateau, Cilo Mountain, Hakkari, Turkey.

Distribution: It is known from only two locations: Mergan Plateau, Hakkari, Turkey and Narlıca Valley, Van, Turkey (this study).

Comments: It includes one of the subspecies of *D. valentini* previously described and a population from Narlıca Valley (called the New Clade A in Candan *et al.* 2021). Since they are morphologically distinct and *D. s. spitzenbergerae* **s**tat. et comb. nov. is so singular in pattern, we think it may be subspecifically different.

Clade A is described as subspecies of *Darevskia spitzenbergerae* **s**tat. nov.

Darevskia spitzenbergerae wernermayeri **ssp. nov.**
(Appendix 5; Fig. 12a).

Synonymy/Chresonymy:

Lacerta valentini lantzicyreni; Eiselt, Darevsky & Schmidtler, 1992. (from "Yukarı Narlıca"-sic.!-).
Darevskia valentini "Clade A"; Candan *et al.* (2021). (same locality as this study)
ZooBank registration (http://zoobank.org): urn:lsid:zoobank.org:act:927894FD-EEFD-450A-81D9-0A68188EDC3B.

Holotype: ZDEU123/2015 (n.3). ♂, Yukarınarlıca Village, Çatak, Van, Turkey. leg. Yusuf Kumlutaş, Çetin Ilgaz, 29.07.2015.

Paratypes: 7 ♂♂, 10 ♀♀. Same locality, date and collectors as holotype.

Derivatio nominis: The specific epithet refers to Dr. Werner Mayer (1943-2015), for his remarkable work on the knowledge of lacertid genera relationships and species taxonomy.

Diagnosis: *Darevskia spitzenbergerae wernermayeri* **ssp. nov.** differs from nominate form (*D. s. spitzenbergerae*) in having a higher number of supraciliar granules (18-31 vs. 14-23), supratemporal (4-6 vs. 3-6), ventrals (29-31 vs. 26-30) (females), preanals (1-3 vs. 1-3), tibial scales (16-21 vs. 15-19), temporal scales 1 (5-7 vs. 2-6) and temporal scales 2 (4-6 vs. 2-6). *Darevskia s. wernermayeri* **ssp. nov.** has a relatively smaller head relative length (0.18-0.21 vs. 0.19-0.24). It also differs by a characteristic color pattern of the body. The main osteological diagnostic characters that differ from the nominate form can be specified as follows: The higher number of maxillary (19-21 vs. 16-18) and dentary teeth (23-24 vs. 20-23). Postorbital greater or equal than postfrontal (greater, rarely equal in *D. s. spitzenbergerae*).

Description of holotype: An adult male. Tail regenerated (see Appendix 5c). Fixed with ethanol and conserved in 96% ethanol.

Scalation: Rostral not in contact with the nostril. Single postnasal on each side. Width of frontonasal (internasal) plate subequal to length, not in contact with rostral. Sutures between prefrontal plates and frontal plate straight. Parietal plates in contact with postorbital plates on each side. Supraciliar granules 13 and 12, interrupted series on left, continuous on right. Supraciliar plates 6 on each side. Supralabial and sublabial plates 4 and 6 on each side, respectively. Plates in supratemporal region 6 on left, 5 on right side. The first supratemporal plate large narrows towards the back, and ends bluntly. Masseteric large, in one piece on left and two pieces on right, separated from the first supratemporal plate by three longitudinal scales on each side. Tympanic obvious, separated from masseteric by three and two rows of small scales on left and right, respectively. Nine flat collaria. Gularia 33. Ventralia contains 6 longitudinal and 28 transverse rows of plates. Preanal scale singular, surrounded by 6 rows of plates. Femoral pores 20 on each side. Subdigital lamellae 28 on each side. Tibialia 20. Dorsalia 51.

Biometry: SVL 63.57 mm. Pileus width 6.90 mm, pileus length 12.96 mm, head width 8.26 mm, head length 13.74 mm. Length of forelimb 22.02 mm, length of hindlimb 31.37 mm. Anal plate width and length are 4.12 mm and 1.84 mm, respectively.

Coloration and pattern (in alcohol): Ground color of dorsum greenish-brown, with two irregular paravertebral rows of dark spots. Similar dark spotting is present on each side of the body, that show the reminiscent of a reticulate pattern reduced to only isolated irregular spots. Between these two areas of dark spots, located both in the middle of the dorsum and flank, a paler and spot-free double strip area extends from nape to base of the tail (see photos in Appendix 5). There are few pale spots on dark bandings on the flanks, and more on the forelimb. A few spots near the basis of the forelimb are bluish. The belly, along with the head and neck, is whitish (Appendix 5). The background color of head plates is brownish, with a few scattered and small black spots. The first longitudinal row of ventral plates has dark spots on each side.

Variations of paratypes: Descriptive statistics and variation range of the morphometric and scalation characters are given in Table 8. Frontonasal rarely contacts with rostral. The suture between the prefrontal and frontal is usually slanted. The Parietal is in contact with the postorbital in general. Supraciliar granules sometimes are double rows. Tight scales are feeble-keeled. In four specimens, transverse dark spots on ground color are combined with spots on each side, do not form two separate rows. In seven samples, paler spots on the forelimb base are not blue. Belly, along with throat and neck, whitish in seven specimens. In three samples, no dotting on head plates. In fifteen samples, the first longitudinal row of ventral plates contains bluish spots on each side.

Distribution: Around Narlıca Valley, Çatak (Van) in the south of Van Lake, Turkey.

Habitat: Subalpine-like vegetation of Irano-Turanian Region, on rocky and stony areas, 2363 m. No other reptile species could be identified in the area during study.

Darevskia mirabilis **Arribas, Ilgaz, Kumlutaş, Durmuş, Avcı & Üzüm, 2013. stat. nov.**
(Fig. 12b).Type Locality: Ovit Pass, Kaçkar Mountains, Rize, Turkey.

Distribution: It is known from the southern parts of Rize and Trabzon, especially around Kaçkar region.

Comments: Distinctiveness of it already mentioned in other previous genetic studies (Rato *et al.* 2021; Candan *et al.* 2021), and whose isolated presence in the Kaçkar mountains, without contact with other forms, has made its classification oscillate between *rudis* and cf. *valentini*, and that has been genetically revealed in another distant locality (Sarıkamış, Kars, Turkey), a question that will be more deeply studied.

Darevskia rudis rudis seems to be distinct from other forms that have been assigned to *rudis* s. lat., and that shall be considered now as nominally belonging to another taxon different from *D. rudis*: *D. obscura* **stat. nov.** (see below)**.** *Darevskia rudis* would have as subspecies *Darevskia rudis lantzicyreni* (Darevsky & Eiselt, 1967) **comb. nov. (Fig. 12d)** and *D. r. bolkardaghica* **(Fig. 12c).**

Darevskia bithynica, together with *Darevskia b. tristis*, perhaps paraphyletic and harboring more than one taxon within, or perhaps the results (paraphyly) are due to an ancient introgression that obscures its homogeneity.

Darevskia valentini (s. str.) **(Fig. 12f)**, monotypical, without any of its former subspecies (*latzicyreni* or *spitzenbergerae*) that belong to other species or are taxa on its own.

Darevskia obscura (Lantz & Cyrén, 1936) **stat. nov.**, including *D. obscura bischoffi* **comb. nov.** and *D. obscura macromaculata* **comb. nov..** The latter seems to be identical in the different analyses done and could be synonymous with *obscura* s. str. (almost the Turkish populations). Must be mentioned that *D. obscura* has been postulated as a species on its own by other authors (Gabelaia *et al.* 2018 – by geometric morphometrics; Tarkhnishvili *et al.* 2020b - by head shape morphometrics-; Gabelaia 2019).

It remains to clarify the status of the two forms of the Greater Caucasus (*D. r. chechenica*, and *D. r. svanetica*): independent from the others or probably closer to *D. obscura*, but not to the true *D. rudis*. This point has to be confirmed, however.

DISCUSSION

Phylogenetic reconstruction

The complex structure of the studied group, *D. valentini*, *D. rudis*, and their relatives, has been recognized from the first studies to the present (Lantz & Cyren 1936; Darevsky & Eiselt 1967; Darevsky 1967; 1972; Darevsky & Lukina 1977; Eiselt *et al.* 1992; Arribas *et al.* 2013; Rato *et al.* 2021; Candan *et al.* 2021). This complexity has always been attractive to researchers who apply both kinds of markers, morphology and/or more recently genetics trying to solve it. Elaborated recent assessments using genetic markers point out that there are more lineages within the *D. valentini*/*D. rudis* complexes than the previously suspected (Candan *et al.* 2021; Rato *et al.* 2021). In this study, we aimed to increase the knowledge of the status of the currently recognized genetic lineages by creating the largest datasets, including a remote subspecies not studied so far – *D. v. spitzenbergerae* – for the first time, to use in both morphological and molecular analyses to clarify the problem. Our phylogenetic results show the presence of several monophyletic clades that reveal themselves as different species (Fig. 9). Of these distinct clades, some had been well-documented for the first time in a recently published study (Candan *et al.* 2021), and the authors have accepted that *D. valentini* s. lat. has more genetic lineages than previously suspected, two of which have been presented there as they should have to be described and named. However, two important shortcomings that we have tried to eliminate here prevented them from their taxonomic description: the lack of morphological study for diagnoses and the absence of samples of one of the up to now two unique subspecies of *D. valentini* (*D. v. spitzenbergerae*), whose study was unavoidable to make taxonomic decisions.

As seen from the tree topology obtained here, genetically divergent lineages, clades A and B, were detected as monophyletic (Fig. 9). The occurrence of these two highly divergent monophyletic lineages is not only confirmed by the tree topology but also the species delimitation analyses revealed both clades as different species, which is one of the most important factors that paved the way for the here proposed taxonomic revision. Network analyses

based on both genetic markers also supported this distinction. In *Cyt-b*, all clades were placed into their unique positions and they did not share any haplotypes (Fig. 10A). In *MC1R*, which is a nuclear marker and has slower substitution rates, an agreement relatively with a more complex structure was showed. Clade A is represented by a single haplotype (Hap16), while clade B appears to have two haplotypes (Hap16 and Hap26) (Fig. 10B). Although these results were suggested by Candan *et al.* (2021), a definite conclusion could not be made due to the absence of subspecies *D. v. spitzenbergerae*, a problem now solved. Considering sampling data used in our phylogenetic construction, clade A consists of both *D. s. spitzenbergerae* from Mergan Plateau (type locality of this relevant and geographically extreme subspecies) and *D. s. wernermayeri* **ssp. nov.** from Narlıca Valley as sister taxa (Fig. 9). Although the population located in Narlıca Valley (Van, Turkey) is morphologically included in *D. v. lantzicyreni* (Eiselt *et al.* 1992), it is genetically more closely related to *D. s. spitzenbergerae* than to the former. In addition to this, the populations, which were assimilated to *D. v. lantzicyreni* according to morphology (Eiselt *et al.* 1992), represent a completely different lineage (clade B) according to genetics. Such discordant patterns called cryptic speciation are often shown in the lizards (Ahmadzadeh *et al.* 2013; Kornilios *et al.* 2018; Karakasi *et al.* 2021; Arribas *et al.* 2022).

Another major point is the status of *D. r. mirabilis* (clade C). This subspecies was first described by Arribas *et al.* (2013) from Ovit Pass, a very isolated geographic region in Kaçkar Mountains. Its phylogenetic position is obvious here and reveals that it should be a species as different as clades A and B (Fig. 9). The genetic difference of this taxon was demonstrated by two independent studies. Firstly, Rato *et al.* (2021) suggested that a clade, called Trabzon-Rize in their study, is genetically distinct and that it should be considered one of the four main lineages of *D. rudis*. Since they did not distinguish any subspecies, they could not determine that this clade belongs to *D. r. mirabilis*. The fact that the *D. rudis* specimens used in their study share the same branch with a specimen we know for certain to be *D. r. mirabilis*, undoubtedly proves that this clade is a new taxon and the corresponding samples of Rato *et al.* (2021) belong to it. Secondly, Candan *et al.* (2021) has also mentioned that it has isolated genetic structure and that its distribution area may be wider than expected because a datum retrieved from GenBank (Tarkhnishvili *et al.* 2013), which is located around Sarıkamış (Kars, Turkey), clustered with *D. r. mirabilis* in the same branch.

Similar to Candan *et al.* (2021), one of the interesting results obtained within *D. valentini*/*D. rudis* complexes is that the specimens belonging to *D. r. rudis*, *D. r. bolkardaghica* and *D. v. lantzicyreni*, cluster together with overlapping. This unexpected pattern makes it difficult to engage the complexity of the group, which unables to apply the current nomenclature and difficulties understanding the main processes underlying genetic variation. Considering the genetic (Fig. 9) and morphological (see results section) evidence together, the most possible scenario seems to accept that *D. v. lantzicyreni* is really a subspecies of *D. rudis*, not from *D. valentini*. Thus, nominal form of *D. valentini* is only limited to northeast Anatolia (with areas of Georgia, Armenia and Azerbaijan), while the distribution of *D. rudis* sensu novo, extends from the northeastern Black Sea region to the inner Anatolia and from there to the south up to the Bolkar Mountains.

Finally, the status of some former subspecies of *D. rudis* also inevitably needs revision. The claim that a member of this group, *D. r. obscura*, is different has been put forward in a previous study including phenotypic comparison (Gabelaia *et al.* 2018; Tarkhnishvili *et al.* 2020b). The phylogenetic results strongly support these morphological findings (clade G, Fig. 9). Above all, *D. r. obscura* has a phylogenetic position quite closely related to other two former *D. rudis* subspecies: *D. r. bischoffi* and *D. r. macromaculata*. Considering all these results, it seems that accepting the first described form, *D. saxicola obscura* Lantz & Cyren 1936, as a species: *D. obscura* will contribute positively to the clarification of this group.

Morphology derived structure

Considering the studied complex group it seems that there are three large groups, which obviously coincide with the current taxonomy based on morphology (we still use here the old nomenclature to refer them). The most different includes *D. bithynica* s. str. and *D. b. tristis*, which had longer heads both concerning its width, and also about their body length, but not in their pilei because other species (especially of the former *rudis* complex) had smaller (in size and length) but very wide heads. Similarly, the scales that cover the upper part of the crus are small and barely keeled. Also, they had comparatively longer hindlimbs (are the more climbing, based on this characteristic). Osteologically, they have very rarely any B-Type pre-autotomic vertebrae. The sternal fontanelle is frequently reduced or absent in *D. b. bithynica*. Postorbital and postfrontal are subequal or the postorbital is a bit smaller (different to *D. valentini*,

clade B and *D. v. spitzenbergerae*). Squamosal and postorbital overlap commonly in half of the second's length (as also in *D. r. bolkardaghica*), more usually than in other forms of the group. *Darevskia b. bithynica* and *D. b. tristis* are identical in ANOSIM. This species is also recovered by genetics. Genetics indicates the possibility that *tristis* is paraphyletic as presently understood.

The former *valentini* complex has a broad overlap among the different forms in CDA. These *valentini* complex samples had comparatively longer limbs, comparatively smaller heads, a greater number of scales in the crus (which in this case corresponds also to smaller scale size, and are no or almost-none keeled), and less markedly, a greater number of ventral and dorsal scales. Anal index, a bit greater (scale comparatively wider) in *D. valentini* than in *D. bithynica* or the former *rudis* complex. One of their supposed taxa, *D. v. lantzicyreni*, perhaps due to its wide dispersal and the presence of isolated populations, appears somewhat heterogeneous. *Darevskia v. lantzicyreni* overlaps a few with *D. r. bolkardaghica* (in males, and even more in females, which would be in agreement with the genetic results and the taxonomic changes proposed above). In turn, *D. v. lantzicyreni* has the higher dorsalia among the former *valentini* complex and is the closer of this complex to *D. rudis* s. str., which would also agree with the genetic analysis (see above) and its relation as conspecific.

Darevskia r. bolkardaghica is characterized by low lamellae (in males and females), and osteologically is characterized because not infrequently shows a weakly ossified rib associated to the third vertebra (an extremely rare character, probably atavistic, associated to small and isolated populations), and the sternal fontanelle adopt singular shapes in sand-clock, irregular cordiform or trilobate in its forepart. Also its squamosal and postorbital bones overlap commonly in half of the second's length (as in *D. bithynica*). Genetically, it is related to *D. v. lantzicyreni* and *D. r. rudis* (all three are proposed here as subspecies of *D. rudis*)

Darevskia v. spitzenbergerae, clade A (here treated as the nominal ssp. of *D. spitzenbergerae*), and clade B (here described as a new species) (in males) and in general, as all the former *valentini* complex (in females) have higher ventralia counts than in *D. bithynica* or the former *rudis* complex taxa. Osteologically, this singular form (*spitzenbergerae*) has the interclavicle lateral branches inclined forwards (with only this model in typical *D. s. spitzenbergerae*) and in "clade A" (coexisting with some branches backward). Postorbital and postfrontal are subequal or the postorbital is a bit greater (as in *D. valentini* s. str. or clade B). Nominal taxa *spitzenbergerae*+clade A, and clade B are recovered as two different species by genetics. *Darevskia spitzenbergerae* and clade A are primitive forms, among the closely related to *D. rudis* (sensu novo) and their subspecies (*lantzicyreni* and *bolkardaghica*, especially this latter).

Darevskia valentini s. str. seems to be a different taxon (genetics) without its formerly assigned subspecies (is nominotypical). It has Temporalia2 a bit lower than in related taxa. In *D. valentini* s. str. not infrequently appear some B-Type autotomic vertebrae. Postorbital and postfrontal are subequal or the postorbital is a bit greater (as in clade B or *D. spitzenbergerae*).

Darevskia rudis complex is characterized by smaller dorsalia in a great part of the *rudis* complex (except in *D. r. rudis* –yet indicated in Arribas *et al.* 2013, that also is recovered as a different species in genetic analyses), than in the former *valentini* complex and *D. bithynica* ssp. (except in *D. v. valentini* that has lower scores similar to the main former *rudis* complex). Hindlimb relative length is also comparatively smaller when compared with the former *valentini* complex and even more with *D. bithynica*. These differences shall be considered as characteristic of *D. obscura* and their newly assigned subspecies, which are very few differentiated. *Darevskia r. obscura* and *D. r. macromaculata* are near the same by morphology, as suggested in Arribas *et al.* (2013). They are so similar in all analyses (including non-significant differences in ANOSIM) that they appear to be the same (increased pigmentation in typical Georgian *macromaculata*, but perhaps not in Turkish specimens, a question to be studied in future). Temporalia1 is somewhat smaller in *D. r. macromaculata* and *D. r. obscura* (M, F), and SVL (size) is greater in *D. r. bischoffi* (M, F).

Paradoxically, *D. rudis* s. str. is morphologically extreme and a differentiated form within "its" former complex, and is distinguished from the other former *rudis* complex taxa (now *D. obscura* sspp.) by its greater values of dorsalia. Also, it is basal to the group in UPGMA. Osteologically, in *D. rudis* s. str. postorbital and postfrontal are subequal or the first is smaller than the second (as in *D. obscura* and *D. bithynica*).

The two extreme populations displaced towards the south of both classical complexes (*D. rudis bolkardaghica* and *D. valentini spitzenbergerae*) result in the ones that connect morphologically the former *rudis* and *valentini* complexes. This may be because they are the most primitive in both groups, or because of an ecoclimatic convergence in their scalation. Both live on calcareous substrates (siliceous, even volcanic in the other forms), so they have a lighter background color than other forms (darker).

Concordance of genetic and morphological results

a)   The classic morphological groupings/species (*rudis* and *valentini* complexes) seem to be no longer valid, due to newly discovered "intermediate" taxa, recent speciation, and multiple past and present introgression. The situation is fairly more complex than previously expected.

b)   The above-mentioned morphological characteristics of *D. bithynica* are valid for this species.

c)   The above-mentioned morphological characteristics of *D. rudis* complex are valid for *D. obscura* (and its sspp. *macromaculata* and *bischoffi*).

d)   As stated above *D. rudis* s. str. is distinguished from the other former *rudis* complex taxa (hereinafter *D. obscura* sspp.) by its greater values of dorsalia. Also, it is basal to the group in UPGMA.

e)   *Darevskia r. lantzicyreni* **comb. nov.** and *D. r. bolkardaghica* are subspecies of *D. rudis*.

f)   *Darevskia spitzenbergerae* is a different taxon. The fourth axis of females analysis (at the limit of significance) discriminates specially clade A (*D. s. wernermayeri* **nov. ssp.**) and in a lesser degree *D. v. spitzenbergerae* (that genetically cluster together and are very similar in ANOVA), characterized by higher values of lamellae, preanalia and femoralia. Inside this *spitzenbergerae* genetic clade, preanalia is higher in clade A (*D. s. wernermayeri* **nov. ssp.**) and strongly characterizes it (M, F) concerning near all the taxa studied here (and if the Tukey-Kramer multiple comparison test is used instead of the much stricter of Scheffe, is significantly different to all the taxa, including the nominal *D. s. spitzenbergerae*)

g)   *Darevskia mirabilis* is another taxon, genetically singular, and only moderately differentiated in its morphology within the former *rudis* complex (morphologically seems more related to *D. o. obscura* or *D. r. bolkardaghica* –Anatolian diagonal effect? -), and longtime approached to *D. valentini* by its pattern, but well isolated genetically. In ANOVA, very low supraciliar granula (M, F) (especially distinctive of this taxon) and gularia (M), and higher circumanalia (M) counts are the most diagnostic characters.

h)   The number (tibialia), size and keeling of the crus scales was formerly used to distinguish between the forms assigned to "*rudis*" and "*valentini*" (sensu auctt.) and is distinctive with higher counts (and smaller scales size and keeling) in the former *valentini* complex (and *D. b. bithynica*), appearing, to the contrary, the lower counts (with big size and strong keeling) in part of the former *rudis* complex (*D. o. obscura*, *D. o. bischoffi* and *D. o. macromaculata*). However, *D. r. rudis*, *D. b. tristis*, *D. r. bolkardaghica* and *D. mirabilis* appear in intermediate scores (but in scale size and aspect are more similar to the lower scored ones, the former *rudis* complex: *D. obscura* sspp.). This can be seen in Fig. 11.

There is dissociation between the results based on morphology (more similar to the former taxonomy) and those based on genetics. We believe this difference is due to three factors:

a)   They are taxa of very recent differentiation. Speciation in the group is very recent, and although some lineages constitute phylogenetic species and biological species (different niches in sympatry, see for example the excellent work of Tarkhnishvili *et al.* 2013), their genetic distances are very low and phylogenies can be obscured also by this reason.

b)   In many places, they are involved in extensive hybridization and introgression phenomena. The presence of numerous hybrids (even hybrid swarms) between the different forms, intermediate animals and that carry mitochondrial haplotypes that are not related to their nuclear reality, as can be seen in Rato *et al.* (2021) and Candan *et al.* (2021).

c)   There are new taxa recently described or in the process of description in this study, some of them barely known up to now, that present intermediate, less well-defined, or mosaic characteristics, and that have been forcibly wedged between previously defined groups in former studies.

For these reasons, morphology is useful for the diagnosis of the different taxa and even the study of their intraspecific variability, but not so much for phylogenetic reconstruction.

CONCLUSION

Some geographical regions in the world are very important both in terms of species diversity and the history of the emergence of this biodiversity. Anatolia and Caucasus, which are valuable geographical regions in terms of both these phenomena, host many extraordinary living creatures, from what the genus *Darevskia* is one of the best examples due to its complex structure, phylogenetic radiation and the parthenogenesis phenomenon. Here,

we performed the most comprehensive morphological evaluation as well as a complete molecular phylogenetic evaluation (without any representative taxa excluded) of a group of *Darevskia* whose taxonomic positions have been discussed for many years. The molecular results showed that the so called *rudis* group (from Murphy *et al.* 2000) contains more genetic lineages than anticipated, one of them identified as new species (*D. josefschmidtleri* **sp. nov.**). Morphological comparisons, on the other hand, contributed also to the definition of a new subspecific taxon (as *D. s. wernermayeri* **ssp. nov.**).

Based on both morphology and molecular markers, the taxonomic structuring of the studied group is proposed as follows:

-*Darevskia valentini* (Boettger, 1892)
-*Darevskia josefschmidtleri* **sp. nov.**
-*Darevskia spitzenbergerae* (Eiselt, Darevsky & Schmidtler, 1992) **stat. nov.**
    -*D. spitzenbergerae spitzenbergerae* (Eiselt, Darevsky & Schmidtler, 1992) **comb. nov.**
    -*D. spitzenbergerae wernermayeri* **ssp. nov.**
-*Darevskia mirabilis* Arribas, Ilgaz, Kumlutaş, Durmuş, Avcı & Üzüm, 2013 **stat. nov.**
-*Darevskia rudis* (Bedriaga, 1886)
    -*D. rudis rudis* (Bedriaga, 1886)
    -*D. rudis lantzicyreni* (Darevsky & Eiselt, 1967) **comb. nov.**
    -*D. rudis bolkardaghica* Arribas, Ilgaz, Kumlutaş, Durmuş, Avcı & Üzüm, 2013
-*Darevskia obscura* (Lantz & Cyrén, 1936) **stat. nov.**
    -*D. obscura obscura* (Lantz & Cyrén, 1936) **comb. nov.**
    -*D. obscura bischoffi* (Böhme & Budak, 1977) **comb. nov.**
    -*D. obscura macromaculata* (Darevsky, 1977) **comb. nov.**
-*Darevskia bithynica* (Méhely, 1909)
    -*D. bithynica bithynica* (Méhely, 1909)
    -*D. bithynica tristis* (Lantz & Cyrén, 1936)

This classification can be completed in future studies with the analysis of more informative genetic markers than the single-copy nuclear markers used here, such as microsatellite DNA or genomic SNPs.

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST

We declare that we have no conflict of interest.

ETHICS

To realize this study, the ethical committee document numbered 11/04/2016 was received from the Dokuz Eylül University Faculty of Medicine Animal Experiments Local Ethics Committee at the meeting dated 23.02.2016 and decided. In addition, the necessary application for the realization of the study was approved by the General Directorate of Nature Conservation and National Parks within the Ministry of Agriculture and Forestry, Turkey on 05.04.2016.

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TABLE 1. Mahalanobis' distances among samples. Males below and females above diagonal.

	D. v. spitzenbergerae	D. v. "Clade A"	D. v. "Clade B"	D. v. valentini	D. v. lantzicyreni	D. b. bithynica	D. b. tristis	D. r. rudis	D. r. bischoffi	D. r. obscura	D. r. macromaculata	D. r. mirabilis	D. r. bolkardaghica
D. v. spitzenbergerae	**0**	1.96	3.02	3.49	1.7	8.16	9.36	4.17	6.65	4.32	4.77	3.84	3.33
D. v. "Clade A"	1.7	**0**	1.23	2.39	1.5	10.06	11.25	5.08	7.6	5.18	5.71	4.62	4.51
D. v. "Clade B"	1.91	0.73	**0**	2.56	2.43	10.87	12.07	6.04	8.78	6.36	6.87	5.81	5.73
D. v. valentini	1.44	2.29	2.37	**0**	3.78	10.97	11.9	7.05	8.13	5.98	6.86	5.16	5.27
D. v. lantzicyreni	1.85	1.77	1.75	3.11	**0**	9.48	10.79	3.63	6.89	4.44	4.69	4.13	3.88
D. b. bithynica	9.23	10.69	10.56	9.79	9.35	**0**	1.67	8.81	10.04	9.37	9.27	9.34	8.37
D. b. tristis	10.48	12.01	11.89	10.94	10.75	1.55	**0**	10.21	10.78	10.35	10.35	10.27	9.35
D. r. rudis	5.57	6.3	6.72	6.84	5.26	8.61	9.82	**0**	5.3	3.57	2.81	4.07	3.65
D. r. bischoffi	6.92	8.05	8.6	7.48	7.78	9.61	10.32	4.52	**0**	2.45	2.54	3.03	3.34
D. r. obscura	4.91	6.12	6.64	5.44	5.92	8.95	9.83	3.97	2.04	**0**	1.19	0.95	1.31
D. r. macromaculata	5.24	6.29	6.85	5.95	5.99	9.23	10.16	3.29	1.82	0.95	**0**	2.11	2.09
D. r. mirabilis	4.16	5.2	5.77	4.72	5.17	9.48	10.47	3.9	2.89	1.08	1.35	**0**	0.99
D. r. bolkardaghica	3.34	4.8	5.15	4.13	4.18	7.47	8.56	3.58	4.05	2.26	2.62	2.21	**0**

TABLE 2. Analysis of Similarity (ANOSIM) results (with 1000 randomizations). Males below and females above diagonal. The number above is the R-statistic pairwise comparison extending from 1 (perfect discrimination) to -1 (total mixing) of the two concerned samples. Below are the test probability results among each of the two populations (significant results indicated with asterisks).

♂♂/♀♀	D. v. spitzenbergerae	D. v. "Clade A"	D. v. "Clade B"	D. v. valentini	D. v. lantzicyreni	D. b. bithynica	D. b. tristis	D. r. rudis	D. r. bischoffi	D. r. obscura	D. r. macromaculata	D. r. mirabilis	D. r. bolkardaghica
D. v. spitzenbergerae	0	0.69 0.001 **	0.14 0.105 n s	0.57 0.001 **	0.18 0.031 *	0.73 0.009 **	0.54 0.001 **	0.42 0.001 **	0.46 0.001 **	0.40 0.004 **	0.52 0.001 **	0.43 0.003 **	0.48 0.002 **
D. v. "Clade A"	0.16 0.044 *	0	0.29 0.001 **	0.82 0.001 **	0.33 0.001 **	1 0.001 **	0.88 0.001 **	0.62 0.001 **	0.70 0.001 **	0.77 0.001 **	0.83 0.001 **	0.88 0.001 **	0.97 0.001 **
D. v. "Clade B"	0.38 0.001 **	0.43 0.002 **	0	0.41 0.001 **	0.19 0.001 **	0.48 0.001 **	0.69 0.001 **	0.60 0.001 **	0.62 0.001 **	0.62 0.001 **	0.66 0.001 **	0.72 0.001 **	0.66 0.001 **
D. v. valentini	0.83 0.001 **	0.97 0.001 **	0.58 0.001 **	0	0.44 0.001 **	0.64 0.001 **	0.82 0.001 **	0.79 0.001 **	0.63 0.001 **	0.56 0.001 **	0.67 0.001 **	0.61 0.001 **	0.51 0.001 **
D. v. lantzicyreni	0.42 0.001 **	0.41 0.001 **	0.19 0.001 **	0.61 0.001 **	0	0.33 0.002 **	0.60 0.001 **	0.42 0.001 **	0.51 0.001 **	0.54 0.001 **	0.57 0.001 **	0.65 0.001 **	0.59 0.001 **
D. b. bithynica	0.60 0.001 **	0.75 0.001 **	0.56 0.001 **	0.90 0.001 **	0.34 0.001 **	0	-0.13 0.854 n s	0.52 0.001 **	0.34 0.016 *	0.25 0.036 *	0.37 0.028 *	0.62 0.001 **	0.59 0.003 **
D. b. tristis	0.67 0.001 **	0.76 0.001 **	0.66 0.001 **	0.74 0.001 **	0.58 0.001 **	-0.005 0.743	0	0.50 0.001 **	0.51 0.001 **	0.64 0.001 **	0.63 0.001 **	0.84 0.001 **	0.67 0.001 **
D. r. rudis	0.70 0.001 **	0.70 0.001 **	0.68 0.001 **	0.84 0.001 **	0.43 0.001 **	0.43 0.001 **	0.55 0.001 **	0	0.37 0.001 **	0.48 0.001 **	0.46 0.001 **	0.62 0.001 **	0.48 0.001 **
D. r. bischoffi	0.61 0.001 **	0.68 0.001 **	0.61 0.001 **	0.66 0.001 **	0.55 0.001 **	0.43 0.001 **	0.56 0.001 **	0.36 0.001 **	0	0.14	0.03 0.235 n s	0.36 0.001 **	0.21 0.032 *
D. r. obscura	0.54 0.001 **	0.76 0.001 **	0.90 0.001 **	0.50 0.001 **	0.61 0.001 **	0.51 0.001 **	0.58 0.001 **	0.54 0.001 **	0.27 0.001 **	0	0.05 0.042 *	0.24 0.004 **	0.03 0.342 n s
D. r. macromaculata	0.55 0.001 **	0.81 0.001 **	0.70 0.001 **	0.76 0.001 **	0.64 0.001 **	0.63 0.001 **	0.59 0.001 **	0.54 0.001 **	0.19 0.003 **	-0.002 0.485	0	0.41 0.001 **	0.32 0.009 **
D. r. mirabilis	0.43 0.001 **	0.66 0.001 **	0.84 0.001 **	0.84 0.001 **	0.70 0.001 **	0.70 0.001 **	0.76 0.001 **	0.66 0.001 **	0.53 0.001 **	0.41 0.001 **	0.43 0.001 **	0	0.25 0.012 *
D. r. bolkardaghica	0.34 0.002 **	0.66 0.001 **	0.66 0.001 **	0.88 0.001 **	0.55 0.001 **	0.65 0.001 **	0.62 0.001 **	0.54 0.002 **	0.40 0.001 **	0.40 0.001 **	0.48 0.001 **	0.35 0.005 **	0

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TABLE 3. Post-Hoc reclassification of specimens derived from CDA (males and females).

MALES	Original D. v. spitzenbergerae	Original D. v. "Clade A"	Original D. v. "Clade B"	Original D. v. valentini	Original D. v. lantzicyreni	Original D. b. bithynica	Original D. b. tristis	Original D. r. rudis	Original D. r. bischoffi	Original D. r. obscura	Original D. r. macromaculata	Original D. r. mirabilis	Original D. r. bolkardaghica	No. Correct	% Correct
Predicted D. v. spitzenbergerae	9	0	1	0	2	0	0	0	0	0	1	1	0	9	90
Predicted D. v. "Clade A"	1	8	1	0	1	0	0	0	0	0	0	0	0	8	100
Predicted D. v. "Clade B"	0	0	17	0	2	0	0	0	0	0	0	0	0	17	85
Predicted D. v. valentini	0	0	0	32	0	0	0	0	0	0	0	0	0	32	96.9697
Predicted D. v. lantzicyreni	0	0	1	1	48	0	0	1	0	0	0	0	0	48	90.566
Predicted D. b. bithynica	0	0	0	0	0	14	8	0	0	0	0	0	0	14	87.5
Predicted D. b. tristis	0	0	0	0	0	2	52	0	0	0	0	0	0	52	86.6667
Predicted D. r. rudis	0	0	0	0	0	0	0	75	0	0	0	0	0	75	92.5926
Predicted D. r. bischoffi	0	0	0	0	0	0	0	0	67	1	0	0	0	67	83.75
Predicted D. r. obscura	0	0	0	0	0	0	0	1	7	31	3	1	0	31	81.5789
Predicted D. r. macromaculata	0	0	0	0	0	0	0	4	0	5	17	0	0	17	70.8333
Predicted D. r. mirabilis	0	0	0	0	0	0	0	0	6	1	3	11	0	11	84.6154
Predicted D. r. bolkardaghica	0	0	0	0	0	0	0	0	0	0	0	0	8	8	100
Total	10	8	20	33	53	16	60	81	80	38	24	13	8	389	87.6126

TABLE 3. (continued)

FEMALES	Original D. v. spitzenbergerae	Original D. v. "Clade A"	Original D. v. "Clade B"	Original D. v. valentini	Original D. v. lantzicyreni	Original D. b. bithynica	Original D. b. tristis	Original D. r. rudis	Original D. r. bischoffi	Original D. r. obscura	Original D. r. macromaculata	Original D. r. mirabilis	Original D. r. bolkardaghica	No. Correct	% Correct
Predicted D. v. spitzenbergerae	6	0	1	0	0	0	0	0	0	0	1	0	0	6	100
Predicted D. v. "Clade A"	0	10	3	0	2	0	0	0	0	0	0	0	0	10	100
Predicted D. v. "Clade B"	0	0	27	0	2	0	0	0	0	0	0	0	0	27	77.1429
Predicted D.v. valentini	0	0	1	26	1	0	0	0	0	0	0	0	0	26	100
Predicted D. v. lantzicyreni	0	0	3	0	36	0	0	4	0	0	1	0	0	36	87.8049
Predicted D. b. bithynica	0	0	0	0	0	4	4	0	0	0	0	0	0	4	100
Predicted D. b. tristis	0	0	0	0	0	0	49	0	0	0	0	0	0	49	92.4528
Predicted D. r. rudis	0	0	0	0	0	0	0	61	0	0	0	0	0	61	88.4058
Predicted D. r. bischoffi	0	0	0	0	0	0	0	0	74	1	0	0	0	74	88.0952
Predicted D. r. obscura	0	0	0	0	0	0	0	2	4	27	1	0	0	27	77.1429
Predicted D. r. macromaculata	0	0	0	0	0	0	0	1	0	4	24	0	0	24	88.8889
Predicted D. r. mirabilis	0	0	0	0	0	0	0	1	6	1	0	9	0	9	100
Predicted D. r. bolkardaghica	0	0	0	0	0	0	0	0	0	2	0	0	7	7	100
Total	6	10	35	26	41	4	53	69	84	35	27	9	7	360	88.67

TABLE 4. Descriptive statistics and ANOVA from MALES. Descriptive statistics of each taxon: mean, standard error, minimum and maximum scores from scalation and biometrical characters and indexes. ANOVA and pairwise comparisons among the taxa (* p < 0.05; ** p < 0.01).

MALES	D. v. spitzenbergerae N=10 (1)	D. v. "Clade A" N=8 (2)	D. v. "Clade B" N=20 (3)	D. v. valentini N=34 (4)	D. v. lantzicyreni N=53 (5)	D. b. bithynica N=16 (6)	D. b. tristis N=60 (7)	D. r. rudis N=89 (8)	D. r. bischoffi N=82 (9)	D. r. obscura N=38 (10)	D. r. macromaculata N=24 (11)	D. r. mirabilis N=17 (12)	D. r. bolkardaghica N=9 (13)
GR_S	19.1±0.75 / 14-22	23.37±1.47 / 18-31	23.1±0.98 / 14-30	18.94±0.55 / 11-25	21.32±0.58 / 12-32	23.31±0.76 / 19-31	23.15±0.37 / 13-29	21.50±0.29 / 10-26	21.8±0.45 / 12-28	20.97±0.52 / 10-26	20.04±0.79 / 10-25	14.52±1.13 / 8-22	20.44±0.95 / 15-24
SUPRAC_PL	10.4±0.47 / 8-12	10.62±0.37 / 9-12	12.2±0.13 / 11-14	12.14±0.18 / 10-15	12.58±0.19 / 6-15	12.06±0.26 / 10-14	11.73±0.19 / 8-18	12.06±0.12 / 7-15	12.34±0.13 / 9-16	11.76±1.56 / 7-14	11.75±0.28 / 8-15	12.35±0.32 / 9-15	12.11±0.38 / 11-14
SUPRALAB-PL	8.1±0.23 / 7-10	8.25±0.31 / 7-10	7.95±0.05 / 7-8	8.02±0.05 / 7-9	8.16±0.06 / 8-10	8.31±0.12 / 8-9	8.31±0.08 / 7-10	8.06±0.05 / 6-10	8.20±0.06 / 7-10	7.95±0.07 / 6-9	8.08±0.08 / 8-10	7.94±0.10 / 7-9	8.33±0.23 / 8-10
SUBLAB_PL	12±0 / 12-12	12±0 / 12-12	12±0 / 12-12	12±0 / 12-12	12±0 / 12-12	13.12±0.22 / 12-15	13.15±0.11 / 12-15	12.24±0.06 / 11-14	12.37±0.09 / 10-15	12.21±0.1 / 11-14	11.91±0.1 / 10-13	11.94±0.16 / 10-13	12±0.28 / 11-14
COLLARIA	9.4±0.22 / 8-10	9.25±0.25 / 9-11	9.45±0.19 / 8-11	8.58±0.12 / 7-10	9.94±0.12 / 8-12	8.56±0.18 / 7-10	8.6±0.13 / 6-11	9.31±8.83 / 7-12	9.34±0.10 / 7-11	9.57±0.15 / 8-11	9.5±0.24 / 6-11	9.70±0.35 / 7-11	9.22±0.14 / 9-10
GULARIA	27±0.57 / 24-30	27.62±0.84 / 25-33	26.75±0.37 / 23-30	24.05±0.27 / 21-27	29.13±0.31 / 25-34	27±0.42 / 24-32	26.38±0.26 / 19-31	28.57±0.25 / 23-35	26.79±0.28 / 21-33	25.55±0.41 / 21-31	25.87±0.45 / 21-30	23.70±0.43 / 20-26	26.22±0.4 / 24-28
Supratemporal (Left)	4±0.39 / 3-6	4.62±0.74 / 4-6	3.6±0.15 / 3-5	2.97±0.07 / 2-4	4.15±0.11 / 3-6	3.5±0.12 / 3-4	3.63±0.07 / 2-5	3.86±0.06 / 3-5	3.91±0.09 / 2-6	3.76±0.15 / 2-7	3.87±0.15 / 2-5	3.17±0.19 / 2-5	3.22±0.22 / 2-4
VENTRALIA	28.5±0.60 / 26-32	28.37±0.65 / 26-31	28±0.19 / 26-29	26.58±0.20 / 25-30	26.39±0.19 / 24-30	23.56±0.28 / 21-26	23.61±0.13 / 21-26	23.50±0.16 / 22-29	23.04±0.12 / 20-25	23.92±0.24 / 21-27	24.08±0.24 / 22-27	25.35±0.36 / 23-28	25.11±0.48 / 23-27
PREANALIA	1.5±0.16 / 1-2	2.37±0.32 / 1-3	1.6±0.18 / 1-3	1±0 / 1-1	1.09±0.04 / 1-2	1.25±0.11 / 1-2	1.31±0.07 / 1-3	1.21±0.04 / 1-3	1.18±0.04 / 1-3	1.07±0.05 / 1-3	1.04±0.04 / 1-2	1.26±0.11 / 1-20	1.66±0.16 / 1-2
CIRCUMANAL.	7.6±0.26 / 6-9	7.12±0.22 / 6-8	6.4±0.15 / 5-7	6.79±0.11 / 5-8	6.60±0.12 / 5-8	7±0.13 / 6-8	7.1±0.11 / 5-9	6.96 / 5-9	6.64±0.11 / 4-9	6.57±0.14 / 5-8	7.79±0.19 / 6-9	8.13±0.32 / 6-10	7.44±0.17 / 7-8
FEMORALIA	38.3±0.57 / 36-41	38.75±0.99 / 36-44	39.95±0.46 / 35-44	36.17±0.45 / 30-44	39.86±0.44 / 31-46	39.93±0.83 / 34-47	38.45±0.42 / 30-45	38.50±0.32 / 29-46	41.41±0.38 / 38-52	37.21±0.46 / 31-42	37.62±0.63 / 33-45	36.94±0.59 / 33-42	39.88±0.82 / 36-42
FEMUROUTER	4±0 / 4-4	4±0 / 4-4	4.2±0.11 / 4-6	3.47±0.09 / 2-4	4.32±0.07 / 3-5	4.31±0.11 / 4-5	4.56±0.06 / 4-5	5.15±0.08 / 3-6	4.86±0.09 / 3-6	4.39±0.14 / 3-6	4.37±0.15 / 3-6	4.70±0.20 / 3-6	4.22±0.14 / 4-5
LAMELLAE	53.1±0.43 / 50-55	53.12±0.66 / 50-56	53.2±0.32 / 50-56	47.61±0.38 / 42-53	51.66±0.38 / 45-58	52.93±0.47 / 50-57	51.73±0.31 / 46-56	52.46±0.32 / 46-58	53.53±0.41 / 46-64	48.42±0.43 / 43-55	50.87±0.65 / 45-57	50.29±0.58 / 47-56	44.77±0.87 / 42-50
TIBIALIA	17.3±0.36 / 15-19	18.37±0.46 / 16-20	20.2±0.45 / 16-24	18.29±0.19 / 16-20	18±0.19 / 14-21	17±0.27 / 15-19	15.98±0.12 / 14-18	15.84±0.14 / 12-19	13.01±0.17 / 10-19	14.5±0.19 / 12-17	13.5±0.15 / 12-15	16.17±0.26 / 14-19	15.11±0.53 / 13-18
DORSALIA	49±0.85 / 44-53	50.87±0.76 / 47-54	52.35±0.65 / 48-58	45.79±0.39 / 41-52	54.13±0.44 / 47-63	54.43±0.52 / 49-57	51.9±0.36 / 46-58	55.79±0.43 / 44-65	44.10±0.31 / 38-52	44.81±0.46 / 38-50	46.25±0.57 / 41-51	45.58±0.71 / 38-50	48.88±0.85 / 45-53

......*Continued on the next page*

TABLE 4. (continued)

MALES	D. v. spitzenbergerae N=10 1	D. v. "Clade A" N=8 2	D. v. "Clade B" N=20 3	D. v. valentini N=34 4	D. v. lantzicyreni N=53 5	D. b. bithynica N=16 6	D. b. tristis N=60 7	D. r. rudis N=89 8	D. r. bischoffi N=82 9	D. r. obscura N=38 10	D. r. macromaculata N=24 11	D. r. mirabilis N=17 12	D. r. bolkardaghica N=9 13
TEMP1	4.5±0.45 2-6	5.62±0.26 5-7	5.5±0.26 4-9	4.73±0.15 3-6	5.67±0.17 4-8	4.37±0.27 2-6	4.06±0.10 2-6	5.03±0.12 2-8	4.37±0.12 2-8	3.73±0.20 2-6	3.58±0.18 2-5	4.11±0.39 2-9	5±0.33 4-6
TEMP2	4±0.51 2-6	4.75±0.31 4-6	2.9±0.28 2-6	2±0 2-2	3.62±0.16 2-6	3.62±0.32 2-6	3.23±0.15 2-6	3.85±0.13 2-6	3.56±0.12 2-6	2.60±0.18 2-6	2.70±0.18 2-4	3.05±0.21 2-4	4±0.47 2-6
SVL	60.14±1.68 49.95-65.24	63.68±1.13 60-67.95	62.75±1.25 50.7-76.87	62.15±0.96 51.2-71.56	65.86±0.82 53.62-79.41	64.68±0.66 60.5-68.56	63.49±0.47 52.38-72.84	65.05±0.49 50.72-75.5	74.30±0.84 54.4-88.66	64.16±0.93 50.64-74.34	63.32±1.03 54.9-75	61.10±1.30 50.52-70.3	61.40±1.45 55.12-68.22
Pileus Index (PI) [PL / PW]	2.03±0.03 1.8-2.19	1.94±0.02 1.84-2.06	2.01±0.02 1.81-2.23	2.04±0.02 1.70-2.23	2.06±0.02 1.86-2.30	2.08±0.01 2-2.25	2.13±0.01 1.83-2.52	1.95±0.01 1.78-2-24	1.98±0.01 1.73-2.29	1.96±0.01 1.78-2.28	1.97±0.02 1.75-2.26	1.89±0.03 1.68-2.26	2.01±0.03 1.88-2.12
Head Index (HI) [HL / HW]	1.70±0.02 1.54-1.83	1.59±0.01 1.51-1.66	1.67±0.02 1.54-1.81	1.67±0.01 1.49-1.79	1.71±0.01 1.51-1.97	2.27±0.03 2.02-2.65	2.38±0.01 2.13-2.71	1.72±0.01 1.30-2	1.69±0.01 1.53-1.99	1.73±0.01 1.56-1.91	1.69±0.01 1.49-1.80	1.68±0.02 1.52-1.90	1.81±0.02 1.72-1.90
Anal Index (AI) [AW/AL]	2.21±0.04 1.93-3.04	2.23±0.13 1.96-3.1	2.52±0.05 1.84-3.01	2.41±0.07 1.69-3.22	2.49±0.05 1.7-3.66	2.29±0.04 1.86-2.55	2.18±0.05 1.66-4.89	2.04±0.03 1.36-2.87	2.06±0.03 1.31-3.06	2.00±0.07 1.42-3.65	1.96±0.05 1.50-2.39	2.18±0.11 1.77-3.15	1.90±0.05 1.62-2.13
Head Relative length (HRL) [HL/SVL]	0.22±0.006 0.19-0.24	0.20±0.003 0.18-0.21	0.20±0.002 0.18-0.23	0.22±0.002 0.18-0.24	0.22±0.002 0.19-0.26	0.33±0.003 0.29-0.35	0.34±0.002 0.28-0.36	0.26±0.01 0.21-0.28	0.26±0.001 0.21-0.31	0.25±0.003 0.21-0.28	0.25±0.003 0.22-0.27	0.24±0.004 0.21-0.26	0.25±0.05 0.23-0.269
Hindlimb Relative length (LRL) [LL/SVL]	0.46±0.01 0.42-0.53	0.47±0.001 0.44-0.52	0.46±0.007 0.37-0.53	0.46±0.01 0.33-0.58	0.50±0.01 0.33-0.77	0.53±0.007 0.45-0.58	0.54±0.004 0.44-0.59	0.37±0.004 0.29-0.59	0.35±0.006 0.27-0.7	0.33±0.004 0.27-0.45	0.35±0.01 0.31-0.54	0.35±0.01 0.28-0.5	0.35±0.02 0.29-0.47

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TABLE 4. (continued)2

	F	P	1-2	1-3	1-4	1-5	1-6	1-7	1-8	1-9	1-10	1-11	1-12	1-13	2-3	2-4	2-5	2-6	2-7	2-8	2-9	2-10	2-11	2-12	2-13	3-4	3-5	3-6	3-7	3-8	3-9	3-10	3-11
GR_S	9.65	0.000000																						**									
SUPRAC_PL	3.99	0.000007				*																											
SUPRALAB-PL	2.03	0.010209																															
SUBLAB_PL	14.6	0.000000						**											*									**	**				
COLLARIA	7.97	0.000000																															
GULARIA	18.06	0.000000																															
Supratemporal (Left)	7.43	0.000000														*																	
VENTRALIA	56.46	0.000000					**	**	**	**	**	**	**	**	**			**	**	**	**	**	**	*	*		**	**	**	**	**	**	**
PREANALIA	8.61	0.000000														**	**	**	**	**	**	**	**	**									
CIRCUMANAL.	7.45	0.000000																								*							*
FEMORALIA	9.12	0.000000																															
FEMUROUTER	16.54	0.000000							*							*														**			
LAMELLAE	19.16	0.000000			**									**	**	*									**						**		
TIBIALIA	82.83	0.000000		**	**					*	**	**	**			**	**	**	*		**	**	**	*	*	*	**	**	**	**	**	**	**
DORSALIA	82.49	0.000000		**	**	**	**	**	**	**	**		**			**	**	**	**	**	**	**	**	**		*	**	**	**	**	**	**	**
TEMP1	11.89	0.000000				**	**										**	**	**		**	**	**	**				**	**		**		**
TEMP2	9.97	0.000000			**	**		**							**	**					**	**	**	**									
SVL	21.89	0.000000					**		**	**											**				**						**		
Pileus Index (PI) [PL/PW]	12.07	0.000000											**					**	**										*				
Head Index (HI) [HL/HW]	248.44	0.000000				**		**									**	**	**	**	**	**	**		**			**	**	**	**	**	
Anal Index (AI) [AW/AL]	10.77	0.000000																												**	**	**	**
Head Relative length (HRL) [HL/SVL]	235.17	0.000000	**				**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
Hindlimb Relative length (LRL) [LL/SVL]	87.50	0.000000												*		**				**	**	**	**	*					**	**	**	**	**

TABLE 4. (continued)3

GR_S	3-12	3-13	4-5	4-6	4-7	4-8	4-9	4-10	4-11	4-12	4-13	5-6	5-7	5-8	5-9	5-10	5-11	5-12	5-13	6-7	6-8	6-9	6-10	6-11	6-12	6-13	7-8	7-9	7-10	7-11	7-12	7-13
	**																	**							**						**	
SUPRAC_PL																																
SUPRALAB-PL																																
SUBLAB_PL				*	**							*	**								*						**	**	**	**	**	*
COLLARIA			**									*	*															*	*			
GULARIA			**		*	**	**						**	**	**	**	**	**			*						*					
Supratemporal			*			**	**							*																		
(Left) VENTRALIA	**	**	**	**	**	**	**	**	**			**	**	**	**	**	**								*						**	
PREANALIA																																
CIRCUMANAL.	**		**	**	**	**	**			*			**				**	**														
FEMORALIA			**	**	*	**	**																				*	**				
FEMUROUTER			**	**	**	*	**	**	*	**					**						*	**					*					
LAMELLAE	**	**	*	*	*	**								**		**	**	**	**			**	**		**	**		**	**		**	**
TIBIALIA	**	**	**	**	**	**								**	**	**	**	**	**		**	**	**	**		**		**	**	**	**	**
DORSALIA	**	**	**	**	**	**							**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
TEMP1	**	**	**	**	**			**	**			**	**	**	**		**	**			**		**				**					
TEMP2		**	**	**	**	**				**	**				**	**	**				**		**				**	**	**		**	**
SVL			**				**											**	**			**						**	**			
Pileus Index (PI)	**			*	**	**	**	**	**	**		**	**		**	**	**	**	**		**	**	**	**	**	**	**	**	**	**	**	**
[PL/PW] Head Index (HI)		**	**	**	**	**	**	**	**	**	**	**	**	**	**	**			**	**	**	**	**	**	**	**	**	**	**	**	**	**
[HL/HW] Anal Index (AI)	**	**	**			**	**	**	**	**	**	**	**		**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
[AW/AL] Head Relative length (HRL)	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
[HL/SVL] Hindlimb	**	**	**	*	**	**	**	**	**	**	**			**	**	**	**	**	**		**	**	**	**	**	**	**	**	**	**	**	**
Relative length (LRL)[LL/SVL]																																

TABLE 4. (continued)4

	8-9	8-10	8-11	8-12	8-13	9-10	9-11	9-12	9-13	10-11	10-12	10-13	11-12	11-13	12-13
GR_S				**				**			**			**	
SUPRAC_PL															
SUPRALAB-PL															
SUBLAB_PL															
COLLARIA	**	**	**	**	*										
GULARIA															
Supratemporal (Left)															
VENTRALIA				**				**							
PREANALIA															
CIRCUMANAL.				*			**	**		**	**				
FEMORALIA	**	**				**	*	**		**	**				
FEMUROUTER	*	**	*												
LAMELLAE		**			**	**			**					**	*
TIBIALIA	**		**			**					**		**		
DORSALIA	**	**	**	**	**	**									
TEMP1	**	**	**	**		**	**					**		**	
TEMP2	**	**	**	**		**	**					**			**
SVL	**			**		**	**	**	**						
Pileus Index (PI) [PL / PW]								**							
Head Index (HI) [HL / HW]									**					**	**
Anal Index (AI) [AW/AL]															
Head Relative length (HRL) [HL/SVL]						**		**	**						
Hindlimb Relative length (LRL) [LL/SVL]				*							**		**		

TABLE 5. Descriptive statistics and ANOVA from FEMALES. As in Table 4.

FEMALES	D. v. spitzenbergerae N=6 (1)	D. v. "Clade A" N=10 (2)	D. v. "Clade B" N=35 (3)	D. v. valentini N=25 (4)	D. v. lantzicyreni N=42 (5)	D. b. bithynica N=4 (6)	D. b. tristis N=54 (7)	D. r. rudis N=72 (8)	D. r. bischoffi N=86 (9)	D. r. obscura N=35 (10)	D. r. macromaculata N=27 (11)	D. r. mirabilis N=16 (12)	D. r. bolkardaghica N=9 (13)
GR_S	19.5±0.84 / 17-23	21.6±0.71 / 18-26	27.73±0.7 / 14-33	21.12±0.68 / 14-29	21.45±0.47 / 15-26	24.75±0.63 / 23-26	23.07±0.40 / 13-30	22.25±0.28 / 16-28	21.45±0.47 / 8-28	20.8±0.58 / 12-27	20.07±0.86 / 9-27	16.81±0.90 / 11-25	20.56±1.14 / 16-28
SUPRAC_PL	10.16±0.65 / 8-12	10.6±0.26 / 10-12	11.25±0.19 / 9-13	12.44±0.25 / 10-15	12.78±0.19 / 11-16	11.75±0.25 / 11-12	11.9±0.16 / 9-15	12.31±0.14 / 10-16	12.61±0.10 / 10-15	11.65±0.22 / 8-14	11.25±0.18 / 9-13	12.87±0.41 / 9-16	11.33±0.33 / 10-13
SUPRALAB-PL	8.16±0.16 / 8-9	8.2±0.13 / 8-9	8.2±0.08 / 8-10	8.12±0.08 / 8-10	8.14±0.07 / 7-10	8.25±0.25 / 8-9	8.33±0.09 / 8-10	8.13±0.06 / 6-10	8.11±0.05 / 7-10	7.97±0.07 / 6-9	7.92±0.09 / 6-9	7.93±0.23 / 6-10	8.22±0.22 / 8-10
SUBLAB_PL	12±0 / 12-12	12±0 / 12-12	12±0 / 12-12	12±0 / 12-12	12±0 / 12-12	13±0.4 / 12-14	12.74±0.11 / 11-14	12.11±0.06 / 10-14	12.16±0.08 / 9-14	12.17±0.10 / 11-14	12.25±0.10 / 1-13	12±0.15 / 11-14	12.11±0.11 / 12-13
COLLARIA	9.33±0.33 / 8-10	9±0 / 9-9	9.77±0.15 / 8-12	8.56±0.16 / 7-10	9.88±0.14 / 8-12	9±0.40 / 8-10	8.7±0.12 / 6-10	9.34±0.12 / 6-11	9.19±0.10 / 7-11	9.45±0.20 / 7-13	9.59±0.14 / 8-14	9.75±0.28 / 8-12	9.88±0.26 / 9-11
GULARIA	25.6±0.34 / 26-28	27.3±0.44 / 24-29	26.94±0.29 / 23-31	24.6±0.4 / 21-29	28.45±0.31 / 25-33	27±0.40 / 26-28	26.75±0.24 / 23-31	28.62±0.23 / 25-34	26.98±0.29 / 21-35	25.88±0.36 / 22-31	25.92±0.39 / 21-30	23.25±0.33 / 20-26	26±0.40 / 23-27
Supratemporal (Left)	3.66±0.21 / 3-4	4.9±0.23 / 4-6	3.82±0.12 / 2-6	2.8±0.12 / 2-4	4.16±0.13 / 2-6	3.75±0.25 / 3-4	3.75±0.07 / 3-5	3.72±0.07 / 2-5	3.96±0.06 / 3-6	3.74±0.14 / 2-6	3.74±0.15 / 1-5	4±0.18 / 3-5	3.33±0.16 / 3-4
VENTRALIA	28.83±0.6 / 26-30	30.1±0.17 / 29-31	30.97±0.23 / 28-33	29.72±0.22 / 27-31	28.14±0.24 / 25-31	26.5±0.28 / 26-27	26.03±0.15 / 23-29	25.79±0.15 / 23-29	25.18±0.13 / 21-28	26.42±0.20 / 24-28	25.51±0.24 / 24-29	26.87±0.55 / 21-30	26.55±0.44 / 25-29
PREANALIA	1.83±0.31 / 1-3	2.8±0.13 / 2-3	1.54±0.11 / 1-3	1±0 / 1-1	1.28±0.09 / 1-3	1±0 / 1-1	1.44±0.08 / 1-3	1.4±0.06 / 1-2	1.31±0.05 / 1-3	1.17±0.07 / 1-3	1.03±0.03 / 1-2	1.27±0.14 / 1-2	1.77±0.14 / 1-2
CIRCUMANAL.	7.66±0.33 / 7-9	7.44±0.26 / 6-9	6.68±0.14 / 5-8	6.92±0.15 / 5-8	7.09±0.17 / 5-10	7±0.4 / 6-8	7.46±0.10 / 6-10	7.19±0.11 / 5-10	7.11±0.10 / 5-9	6.88±0.16 / 5-9	7.96±0.20 / 6-10	6.81±0.4 / 5-9	7.66±0.23 / 7-9
FEMORALIA	37±0.36 / 36-38	39.2±0.87 / 35-43	36.85±0.48 / 29-42	34.68±0.60 / 30-40	38.57±0.39 / 33-44	38.75±0.85 / 37-41	36.81±0.28 / 32-41	37.68±0.32 / 30-44	39.34±0.33 / 32-48	35.91±0.49 / 31-43	35.74±0.53 / 30-40	36.25±0.62 / 32-42	36.66±0.84 / 33-40
FEMUROUTER	4±0 / 4-4	4.2±0.13 / 4-5	3.82±0.07 / 3-5	3.64±0.11 / 3-5	4.07±0.07 / 3-5	4±0 / 4-4	4.35±0.06 / 4-5	4.8±0.08 / 4-6	4.70±0.08 / 3-6	4.22±0.13 / 3-6	4.44±0.13 / 3-5	4.31±0.23 / 3-6	4.22±0.14 / 4-5
LAMELLAE	53.5±0.61 / 51-55	52.7±0.93 / 47-0.93	52.42±0.47 / 46-59	46.92±0.49 / 43-51	50.95±0.48 / 44-59	50.5±0.28 / 50-51	51.53±0.36 / 44-58	51.73±0.31 / 46-56	52.51±0.29 / 47-59	48.08±0.54 / 43-57	51.55±0.47 / 46-55	49.87±0.78 / 44-54	43.77±0.92 / 40-48
TIBIALIA	17.5±0.34 / 16-18	18.5±0.40 / 17-21	20±0.23 / 18-23	18.52±0.28 / 16-22	17.38±0.23 / 14-20	15.75±0.75 / 15-18	16.11±0.13 / 14-18	15.61±0.13 / 13-18	12.51±0.17 / 10-17	13.8±0.23 / 11-17	13.03±0.21 / 11-16	16.5±0.30 / 14-19	15.33±0.47 / 13-17
DORSALIA	49.16±0.54 / 47-51	49.1±0.78 / 44-52	51.11±0.34 / 47-56	45.64±0.51 / 41-51	52.61±0.55 / 44-62	53.5±0.95 / 52-56	51.5±0.40 / 46-58	54.86±0.37 / 48-62	42.83±0.29 / 38-50	44.11±0.46 / 39-51	45.85±0.39 / 42-51	44.93±0.68 / 40-50	44.44±0.81 / 41-49

TABLE 5. (continued)

FEMALES	D. v. spitzenbergerae N=6 — 1	D. v. "Clade A" N=10 — 2	D. v. "Clade B" N=35 — 3	D. v. valentini N=25 — 4	D. v. lantzicyreni N=42 — 5	D. b. bithynica N=4 — 6	D. b. tristis N=54 — 7	D. r. rudis N=72 — 8	D. r. bischoffi N=86 — 9	D. r. obscura N=35 — 10	D. r. macromaculata N=27 — 11	D. r. mirabilis N=16 — 12	D. r. bolkardaghica N=9 — 13
TEMP1	4.5±0.34	5.8±0.13	5.48±0.20	5.4±0.24	5.45±0.13	4±0	4.37±0.11	5.25±0.12	4.09±0.12	3.62±0.20	3.62±0.20	4.06±0.38	4.22±0.14
	4-6	5-6	4-8	2-8	4-7	4-4	3-6	3-8	2-9	2-6	2-6	2-8	4-5
TEMP2	4.16±0.54	5.2±0.24	3.31±0.18	2.12±0.22	3.52±0.21	2.5±0.5	3.18±0.14	4.37±0.14	3.39±0.15	3.05±0.21	2.74±0.18	2.81±0.27	2.66±0.28
	2-6	4-6	2-6	0-4	2-6	2-4	1-6	2-8	2-6	2-6	2-4	2-5	2-4
SVL	59.98±1.58	59.57±0.82	62.99±1.00	68.82±1.00	64.82±0.93	61.35±1.34	62.64±0.70	62.11±0.56	72.46±0.84	65.67±0.67	64.52±0.99	62.21±1.22	61.93±1.9
	55.8-64.94	53.25-62.76	50.41-74.96	60.43-77.39	52.34-77.27	57.92-64.48	50.94-73.42	51.76-73.56	51.4-89.16	57.66-73.68	52.62-74.78	49.22-70.84	55.94-68.44
Pileus Index (PI) [PL / PW]	2.00±0.01	1.85±0.01	1.96±0.01	1.88±0.02	2.01±0.02	2.21±0.02	2.07±0.01	1.99±0.01	1.97±0.01	1.94±0.02	1.94±0.02	1.91±0.03	2.03±0.03
	1.96-2.08	1.75-1.93	1.77-2.12	1.73-2.07	1.73-2.36	2.16-2.26	1.81-2.30	1.81-2.31	1.76-2.27	1.71-2.18	1.73-2.36	1.70-2.12	1.90-2.16
Head Index (HI) [HL / HW]	1.74±0.03	1.57±0.02	1.60±0.01	1.59±0.01	1.63±0.02	2.49±0.07	2.51±0.02	1.77±0.01	1.70±0.008	1.74±0.01	1.74±0.02	1.65±0.01	1.80±0.01
	1.65-1.88	1.38-1.70	1.38-1.88	1.43-1.75	1.40-1.92	2.33-2.68	1.55-2.8	1.50-2.12	1.54-1.91	1.57-1.95	1.56-2.01	1.56-1.74	1.67-1.88
Anal Index (AI) [AW/AL]	2.41±0.22	1.96±0.09	2.10±0.05	2.11±0.09	2.29±0.07	1.91±0.29	1.96±0.02	1.74±0.03	1.89±0.03	1.83±0.04	1.87±0.05	1.92±0.07	1.90±0.14
	1.90-3.42	1.59-2.54	1.25-2.73	1.55-3.66	1.30-3.83	1.02-2.24	1.42-2.30	1.20-2.54	0.89-2.83	1.16-2.42	1.36-2.46	1.56-2.25	1.42-2.86
Head Relative length (HRL) [HL/SVL]	0.21±0.006	0.18±0.001	0.18±0.002	0.17±0.003	0.20±0.003	0.29±0.002	0.30±0.001	0.23±0.001	0.24±0.001	0.22±0.001	0.23±0.002	0.22±0.002	0.23±0.002
	0.20-0.24	0.18-0.19	0.16-0.22	0.16-0.21	0.16-0.24	0.28-0.29	0.26-0.33	0.20-0.30	0.20-0.28	0.20-0.26	0.20-0.26	0.20-0.23	0.22-0.29
Relative length (LRL) [LL/SVL]	0.45±0.01	0.45±0.004	0.42±0.005	0.43±0.01	0.46±0.01	0.47±0.01	0.46±0.003	0.33±0.007	0.34±0.007	0.31±0.007	0.32±0.007	0.35±0.001	0.33±0.02
	0.4-0.53	0.44-0.49	0.36-0.53	0.36-0.55	0.32-0.66	0.44-0.49	0.39-0.52	0.23-0.53	0.24-0.06	0.20-0.51	0.28-0.48	0.28-0.54	0.27-0.46

TABLE 5. (continued)2

	F	P	1-2	1-3	1-4	1-5	1-6	1-7	1-8	1-9	1-10	1-11	1-12	1-13	2-3	2-4	2-5	2-6	2-7	2-8	2-9	2-10	2-11	2-12	2-13	3-4	3-5	3-6	3-7	3-8	3-9	3-10	3-11
GR_S	5.49	0.000000																															
SUPRAC_PL	9.75	0.000000				*				*			*				**				*		*	*			**						
SUPRALAB-PL	1.44	0.145186																															
SUBLAB_PL	6.17	0.000000																											**				
COLLARIA	6.02	0.000000														*										*			*				
GULARIA	13.97	0.000000																						*									
Supratemporal (Left)	7.61	0.000000														**				*					*								
VENTRALIA	67.10	0.000000						*	**	**		**				**	**	*	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
PREANALIA	10.21	0.000000						**							**	**	**	**	**	**	**	**	**	**									
CIRCUMANAL.	3.79	0.000018																															**
FEMORALIA	8.95	0.000000																															
FEMUROUTER	10.53	0.000000																		**										**	**		
LAMELLAE	17.26	0.000000			**									**		**						*		**	**	**					**		
TIBIALIA	107.19	0.000000								**	**	**							**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
DORSALIA	90.06	0.000000							*	**									**	**	**	*				**				**	**	**	**
TEMP1	15.17	0.000000						**											**		*	**	**						*		**	**	*
TEMP2	9.78	0.000000														*			*			*	**	*									
SVL	17.09	0.000000								*											**										**		
Pileus Index (PI) [PL / PW]	9.10	0.000000																**	**										*				
Head Index (HI) [HL / HW]	251.61	0.000000					**	**										**	**	**	*			*				**	**	**	*	*	*
Anal Index (AI) [AW/AL]	8.36	0.000000							*																					*			
Head Relative length (HRL) [HL/SVL]	172.86	0.000000		**			**	**	**	*	**	**						**	**	**	**	**	**	**	**		**	**		**	**	**	
Hindlimb Relative length (LRL) [LL/SVL]	44.75	0.000000		**							**	**					**		**	**	**	**	**					*	*	**	**	**	**

TABLE 5. (continued)3

	3-12	3-13	4-5	4-6	4-7	4-8	4-9	4-10	4-11	4-12	4-13	5-6	5-7	5-8	5-9	5-10	5-11	5-12	5-13	6-7	6-8	6-9	6-10	6-11	6-12	6-13	7-8	7-9	7-10	7-11	7-12	7-13
GR_S	**																														**	**
SUPRAC_PL																	**															
SUPRALAB-PL																																
SUBLAB_PL					**								**														**	**				
COLLARIA			**										**																			
GULARIA	**		**				*									**	*	**									*				**	
Supratemporal (Left)			**	*	**	**	**	*	*	*																						
VENTRALIA	**		*		**	**	**	**	**	**	**		**	**	**	**	**															
PREANALIA																																
CIRCUMANAL.																																
FEMORALIA		*	**	*	*	**																						**				
FEMUROUTER						**	**							**	*																	
LAMELLAE		**	**						**										**										**		**	**
TIBIALIA	**	**			**	**	**	**	**	*	*		*	**	**	**	**					*						**	**	**		
DORSALIA	**	**	**	*	**	**	**	**	**						**		**	*	**			**	**	*	**	**	**	**	**	**	**	**
TEMP1							**	**	**				*		**	**	**	*									*					
TEMP2						**																					**					
SVL																												**				
Pileus Index (PI) [PL / PW]			*	**	**																				*			**	**	*		
Head Index (HI) [HL / HW]		*		**	**							**	**								**			**	**	**	**	**	**	**	**	
Anal Index (AI) [AW/AL]													*			**	*															
Head Relative length (HRL) [HL/SVL]	**	**	**	**	**	**	**		**	**	**	**	**	**	**	**	**	**			**	**	**	**	**	**	**	**	**	**	**	**
Hindlimb Relative length (LRL) [LL/SVL]						**	**	**	**		*	**		**	**		**		**	*	*	*	**	**		**	**	**	**	**	**	*

TABLE 5. (continued)4

	8-9	8-10	8-11	8-12	8-13	9-10	9-11	9-12	9-13	10-11	10-12	10-13	11-12	11-13	12-13
GR_S				**				*							
SUPRAC_PL							**								
SUPRALAB-PL															
SUBLAB_PL															
COLLARIA															
GULARIA	*	**	**	**				**							
Supratemporal (Left) VENTRALIA						*		*							
PREANALIA															
CIRCUMANAL.															
FEMORALIA						**	**								
FEMUROUTER															
LAMELLAE		**			**	**			**	*				*	**
TIBIALIA	**	**	**					**	**	*	**		**		
DORSALIA	**	**	**	**	**		*								
TEMP1	**	**	**												
TEMP2	*	**	**												
SVL	**					**	**	**	*						

Pileus Index (PI) [PL / PW]
Head Index (HI) [HL / HW]
Anal Index (AI) [AW/AL]
Head Relative length (HRL)
[HL/SVL]
Hindlimb Relative length
(LRL) [LL/SVL]

TABLE 6. Condensed information about the osteological characteristics of all the *rudis*-group (*rudis* and *valentini* complexes, plus *D. portschinskii*) taxa studied. To the new specimens studied, also data from Arribas (1998) and Arribas *et al.* (2013) have been used. M is males, F females; A bar (/) OR A "=" means equally probable states; Greater, smaller, or equal signs (<>=) mean relative dispositions of bone proportions; A parenthesis "()" a rare character state or value; a double parenthesis "(())" a very rare or exceptional state; (red.) means reduced (but still present); Ciphers among brackets "[ ]" are sternal-xiphisternal formulae, and numbers following them, inscriptional ribs.. From left to right, Taxa; Number of premaxillary teeth; Maxillary teeth (average and range); Dentary teeth (average and range); Teeth shape (Un=unicuspid; Bi=bicuspid; Tr=tricuspid); Total presacral vertebra; ossified ribs on third presacral vertebra; Claviculae typus (O=open, C=closed); Interclavicle typus (†=directed forwards; Ψ= directed forwards; ⋔=directed backwards); Sternal fontanellae (O=oval, C= cordiform, IC=irregular cordiform, IO=irregular oval); Sternal-xiphisternal formula and postorbital relative legths (see above), Postfrontal anterolateral process (presence or absence); Postorbital anteromedial process (presence/absence); Squamosal overlap with postorbital (approx. percentage of overlap).

TAXA	N	Premaxillary teeth	Maxillary teeth	Dentary teeth	Teeth (Unicuspid/Bicuspid)	Total Presacral vertebrae	Short Presacral vertebrae	Ossified ribs on third presacral vert.	Pattern of Tail vertebrae	Claviculae typus	Interclavicle †Ψ⋔	Sternal Fontanellae	Sternal-Xiphisternal formula	Postfrontal-Postorbital lengths	Postfrontal anterolateral process	Postorbital anteromedial process	Squamosal –Postorbital overlap
Darevskia valentini valentini	10	7 (8)	18 [16-20]	22 [18-25]	Bi>Un	M 27 / F29 (28-30)	M 6 / F 7/8	NOT	A(B)	O(C)	†⋔	O (IO/IC)	[3+2]1	Po=Pf (>)	YES	YES ((red))	1/3 (1/2-1/4)
Darevskia valentini "Clade A"	6	7	20.5 [19-21]	23.5 [23-24]	Bi>Un ((=))	M 27 / F 29	M 6 / F 6	NOT	A	O/C	⋔Ψ	O	[3+2]1	Po>=Pf	YES	YES ((red))	1/3(1/2)
Darevskia valentini "Clade B"	6	7	17 [15-18]	21.25 [20-22]	Bi>Un	M 27-28 / F 29	M 6-7 / F 7	NOT	A	O(C)	†⋔	O	(3+2)1	Po=Pf	YES	YES	1/2-1/3
Darevskia v. lantzicyreni	8	7	17.6 [17-18]	22.3 [21-23]	Bi>Un	M 27 (26)(25)) / F 28 (27)	M 6-7 / F 6	NOT	A	O(C)	†⋔	O	(3+2)1	Po=Pf (<=)	YES	YES	1/3 (1/2-1/9)
Darevskia v. spitzenbergerae	3	7	17.25 [16-18]	21 [20-23]	Bi>Un	M? / F 29	M? / F 6-7	NOT	A	O((C))	Ψ	O(IC)	(3+2)0/1 (3+1)1	Po>Pf (=)	YES	YES	1/3 (1/2)
Darevskia rudis rudis	6	7	17.6 [15-19]	21.5 [19-24]	Bi>Un	M27/28 / F28 (27,29)	M 6 / F 6	NOT	A	O	†	O	[3+2] ((4+1)) 1(0)	Po<Pf	YES	YES (red)	1/3 (1/4)

......Continued on the next page

TABLE 6. (continued)

TAXA	N	Premaxillary teeth	Maxillary teeth	Dentary teeth	Teeth (Unicuspid/Bicuspid)	Total Presacral vertebrae	Short Presacral vertebrae	Ossified ribs on third presacral vert.	Pattern of Tail vertebrae	Claviculae typus	Interclavicle †Ψ𝕞	Sternal Fontanellae	Sternal-Xiphisternal formula	Postfrontal-Postorbital lengths	Postfrontal anterolateral process	Postorbital anteromedial process	Squamosal–Postorbital overlap
Darevskia r. bischoffi	6	8/7	18 [16-21]	21.8 [20-23]	Bi>Un	M 26/27 F28 (29)	M 6 F 6-7	NOT ((yes))	A	O ((C))	† 𝕞	O (elong)	[3+2] ((3+3))	Po<Pf	YES	YES	1/3-1/4 ((0))
Darevskia r. obscura	8	7	17.2 [16-20]	21.2 [20-24]	Bi>Un	M 26/27	M 6	NOT ((yes))	A	O (C)	†	O	2/1 [3+2]	Po=Pf	YES	YES	1/3 (1/4)
Darevskia r. macromaculata	6	7/8 (6) ((8))	17.9 [15-20]	22.1 [20-26]	Bi>Un	M 27/28 F 28/29	M 6/7 F 6(7)	NOT	A	O (C)	(Ψ Ge) † 𝕞	O (IO, IC)	1(0) [3+2]	Po=<Pf	YES	(red) YES	1/3
Darevskia r. mirabilis	4	7	16.1 [15-17]	20.5 [18-23]	Bi>Un	M 26/27 F 28/29	M 6 F 6-7	(yes)	A	O (C)	†	O	[3+2] ((2+2)) ((2+3))	Po=Pf (<)	YES	(size variab) YES	1/3 (1/2) (1/2)
Darevskia r. svanetica	2	7	18 [17-19]	20.5 [20-21]	Bi>Un	M 27 H 29	M 7 F 6	NOT	A	C (O)	†	O (IO)	1(2) [3+2] (3+1)	Po=Pf	YES	YES (red)	1/3
Darevskia r. chechenica	2	7	15.5 [15-16]	21 [20-22]	Bi>Un	M 27 F 29(28)	M 6 F 7(6)	NOT	A	O	† 𝕞	O	1 [3+2]	Po=Pf	YES	YES	1/3
Darevskia r. bolkardaghica	3	7	18.25 [17-19]	22.25 [21-23]	Bi>Un	M 27 F 28/29	M 6 F 6/7	NOT/YES	A	O	†	IO/IC	2/1 [3+2]	(<) Po=Pf	YES	YES	½(1/3)
Darevskia bithynica bithynica	4	7	16.5 [15-18]	21.16 [20-23]	Bi>Un	M 27	M 6	NOT	A((B))	C ((O))	†	O/red	([3+1]) 1/2 [3+2]	Po=Pf	YES	YES	½
Darevskia b. tristis	6	7	17.75 [16-19]	20.9 [17-23]	Bi>Un	M 27 F 28/29	M 6/7 F 6/7	NOT	A((B))	O (C)	†	O ((IO))	1(0) [3+2]	(=) Po=Pf	YES	(red) YES	½
Darevskia portschinskii	4	7	16.3 [15-18]	20.75 [19-22]	Bi=Un (><)	(28) 29 M 27 F 29	M 6 (5) F 7	NOT	A	O	†𝕞	O	1 (2) [3+2]0 ([3+2]1)	(<) Po>=Pf	YES	(red) YES	1/3-1/4

ARRIBAS *ET AL.*

TABLE 7. Descriptive statistics of *Darevskia josefschmidtleri* **sp. nov.** considering all the type series. N: number of samples; S.D.: Standard deviation; S.E.: Standard error of the mean; the abbreviations of characters are given in Materials and Methods.

Characters	N	Mean	Minimum	Maximum	S.D.	S.E.
GR_S (left)	57	11.74	7	16	2.17	0.29
GR_S (right)	57	11.86	6	17	2.24	0.30
SUPRAC_PL (left)	57	5.82	4	7	0.69	0.09
SUPRAC_PL (right)	57	5.81	4	7	0.55	0.07
SUPRALAB-PL (left)	57	4.05	4	5	0.23	0.03
SUPRALAB-PL (right)	57	4.05	3	5	0.29	0.04
SUBLAB_PL (left)	57	6.05	5	7	0.29	0.04
SUBLAB_PL (right)	57	6.05	5	7	0.29	0.04
COLLARIA	57	9.70	8	12	0.89	0.12
GULARIA	57	26.88	23	31	1.69	0.22
SUPRATEMPORAL (left)	57	3.77	2	6	0.71	0.09
SUPRATEMPORAL (right)	57	3.74	1	5	0.84	0.111
VENTRALIA	57	29.91	26	33	1.86	0.25
PREANALIA	57	1.53	1	3	0.73	0.10
CIRCUMANALIA	57	6.61	5	8	0.82	0.11
FEMORALIA (left)	57	18.75	14	22	1.50	0.20
FEMORALIA (right)	57	19.16	15	22	1.68	0.22
FEMUROUTER	57	3.98	3	6	0.52	0.07
LAMELLAE (left)	54	26.48	23	30	1.31	0.18
LAMELLAE (right)	55	26.36	23	30	1.41	0.19
TIBIALIA	57	20.07	16	24	1.62	0.22
DORSALIA	57	51.46	47	58	2.46	0.33
TEMP1 (left)	57	2.77	2	5	0.68	0.09
TEMP2 (left)	56	1.61	1	3	0.65	0.09
TEMP1 (right)	57	2.74	2	4	0.61	0.08
TEMP2 (right)	56	1.55	1	3	0.60	0.08
masseteric (left)	57	1.05	1	2	0.23	0.03
masseteric (right)	57	1.11	1	2	0.31	0.04
tympanic (left)	57	1.16	1	2	0.37	0.05
tympanic (right)	57	1.18	1	2	0.38	0.05
SVL	57	62.12	46.00	76.87	6.55	0.87
PW	57	6.10	5.05	7.60	0.56	0.07
PL	57	12.11	10.32	14.96	1.23	0.16
HW	57	7.33	5.82	8.95	0.72	0.10
HL	57	12.00	9.70	14.77	1.37	0.18
LL	57	27.33	20.60	36.21	3.27	0.43
AW	57	3.97	2.55	5.56	0.70	0.09
AL	57	1.97	1.15	11.99	1.39	0.18

TABLE 8. Descriptive statistics of *Darevskia spitzenbergerae wernermayeri* **ssp. nov.** considering all the type series. N: number of samples; S.D.: Standard deviation; S.E.: Standard error of the mean; the abbreviations of characters are given in Materials and Methods.

Characters	N	Mean	Minimum	Maximum	S.D.	S.E.
GR_S (left)	17	11.29	9	16	1.76	0.43
GR_S (right)	17	10.94	8	15	1.64	0.40
SUPRAC_PL (left)	17	5.12	4	6	0.70	0.17
SUPRAC_PL (right)	17	5.41	5	6	0.51	0.12
SUPRALAB-PL (left)	17	4.12	3	5	0.49	0.12
SUPRALAB-PL (right)	17	4.12	4	5	0.33	0.08
SUBLAB_PL (left)	17	6.24	6	7	0.44	0.11
SUBLAB_PL (right)	17	6.24	6	7	0.44	0.12
COLLARIA	17	9.12	9	11	0.49	0.12
GULARIA	17	27.12	24	29	1.27	0.31
SUPRATEMPORAL (left)	17	4.71	4	6	0.69	0.17
SUPRATEMPORAL (right)	17	4.82	4	6	0.64	0.15
VENTRALIA	17	29.41	26	31	1.54	0.37
PREANALIA	17	1.82	1	3	0.10	0.23
CIRCUMANALIA	17	7.35	6	9	0.70	0.17
FEMORALIA (left)	17	19.35	17	22	1.46	0.35
FEMORALIA (right)	17	19.59	18	22	1.54	0.37
FEMUROUTER	17	4.12	4	5	0.33	0.08
LAMELLAE (left)	17	26.47	24	29	1.33	0.32
LAMELLAE (right)	17	26.24	23	28	1.20	0.29
TIBIALIA	17	18.35	16	21	1.22	0.30
DORSALIA	17	49.82	44	54	2.51	0.61
TEMP1 (left)	17	2.82	2	3	0.39	0.10
TEMP2 (left)	17	2.41	2	3	0.51	0.12
TEMP1 (right)	17	2.94	2	4	0.43	0.10
TEMP2 (right)	17	2.53	2	3	0.51	0.13
masseteric (left)	17	1.29	1	2	0.47	0.11
masseteric (right)	17	1.00	1	1	0.00	0.00
tympanic (left)	17	1.06	1	2	0.24	0.06
tympanic (right)	17	1.06	1	2	0.24	0.06
SVL	17	61.27	53.25	67.95	3.59	0.87
PW	17	6.16	5.63	7.02	0.39	0.10
PL	17	11.69	10.45	13.88	0.99	0.24
HW	17	7.42	6.45	9.26	0.77	0.19
HL	17	11.69	10.33	14.00	1.07	0.26
LL	17	28.46	25.67	34.26	2.42	0.59
AW	17	3.95	3.09	4.70	0.46	0.11
AL	17	1.93	1.35	2.35	0.29	0.07

Appendix 1. Detailed information for specimens were used for morphological comparisons.

Darevskia spitzenbergerae spitzenbergerae **stat. et comb. nov. 10(M), 6(F)**

1. ZDEU 1/2020. (N=16), Mergan Plateau, Hakkari, Turkey, 15.08.2020, Leg. C. YILMAZ [Map ID: 78].

Darevskia spitzenbergerae wernermayeri **ssp. nov. 8(M), 10(F)**

1. ZDEU 123/2015. (N=18), Yukarınarlıca Village, Çatak, Van, Turkey, 29.07.2015, Leg. Y. KUMLUTAŞ, Ç. ILGAZ [Map ID: 77].

Darevskia josefschmidtleri **sp. nov. 20(M), 35(F)**

1. ZDEU 108/2015. (N=4), Balık Lake, Taşlıçay, Ağrı, Turkey, 19.05.2015, Leg. K. CANDAN, E. YILDIRIM CAYNAK [Map ID: 75].

2. ZDEU 121/2015. (N=6), Güzeldere Village, Hınıs, Erzurum, Turkey, 25.07.2015, Leg. K. CANDAN, E. YILDIRIM CAYNAK [Map ID: 74].

3. ZDEU 220/2016. (N=17), Başeğmez Village, Çaldıran, Van, Turkey, 24.06.2016, Leg. K. CANDAN, M.K. ŞAHİN, N. BEŞER [Map ID: 76].

4. ZDEU 221/2016. (N=18), Çirişli Village, Çat, Erzurum, Turkey, 22.06.2016, Leg. K. CANDAN, M.K. ŞAHİN, N. BEŞER [Map ID: 73].

5. ZDEU 222/2016. (N=10), Palandöken Mountain, Erzurum, Turkey, 01.07.2016, Leg. K. CANDAN, M.K. ŞAHİN, N. BEŞER [Map ID: 72].

Darevskia valentini **34(M), 25(F)**

1. ZDEU 218/2016. (N=4), Aygır Lake, Susuz, Kars, Turkey, 29.06.2016, Leg. K. CANDAN, M.K. ŞAHİN, N. BEŞER [Map ID: 67].

2. ZDEU 120/2015. (N=2), Taşbaşı Village, Arpaçay, Kars, Turkey, 04.07.2015, Leg. K. CANDAN [Map ID: 71].

3. ZDEU 116/2016. (N=1), Lavaş Lake, Arpaçay, Kars, Turkey, 28.07.2015, Leg. K. CANDAN, E. YILDIRIM CAYNAK [Map ID: 70].

4. ZDEU 56/2016. (N=17), Boğatepe Village, Susuz, Kars, Turkey, 17.07.2016, Leg. Ç. ILGAZ, K. CANDAN [Map ID: 68].

5. ZDEU 2/2018. (N=7), Tepesuyu Village, Ardahan, Turkey, 23.04.2018, Leg. K. CANDAN, S. GÜL [Map ID: 63].

6. ZDEU 4/2018. (N=8), Tepeler Village, Ardahan, Turkey, 23.04.2018, Leg. K. CANDAN, S. GÜL [Map ID: 62].

7. ZDEU 3/2018. (N=7), Yağmuroğlu Village, Göle, Ardahan, Turkey, 27.04.2018, Leg. K. CANDAN, S. GÜL [Map ID: 64].

8. ZDEU 1/2018. (N=2), Çatköy Plateau, Hanak, Ardahan, Turkey, 30.05.2018, Leg. K. CANDAN, S. GÜL [Map ID: 61].

9. ZDEU 108/2013. (N=5), Akdere Village, Kars, Turkey, 23.07.2013, Leg. Y. KUMLUTAŞ [Map ID: 69].

10. ZDEU 92/2013. (N=2), Büyükçatak Village, Susuz, Kars, Turkey, 23.07.2013, Leg. Y. KUMLUTAŞ [Map ID: 65].

11. ZDEU 6/2011. (N=4), Kurugöl Village, Susuz, Kars, Turkey, 01.07.2011, Leg. Y. KUMLUTAŞ [Map ID: 66].

Darevskia mirabilis **stat. nov. 17(M), 16(F)**

1. ZDEU 142/2014. (N=11), Ovit Pass, Rize, Turkey, 06.08.2014, Leg. Y. KUMLUTAŞ, Ç. ILGAZ [Map ID: 42].

2. ZDEU 145/2002. (N=22), Ovit Pass, Rize, Turkey, 06.09.2002, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, A. ÖZDEMİR [Map ID: 42].

Darevskia rudis lantzicyreni comb. nov. 53(M), 42(F)

1. ZDEU 105/2015. (N=3), Balıklı Village, Kelkit, Gümüşhane, Turkey, 05.05.2015, Leg. K. CANDAN, S. GÜL [Map ID: 27].

2. ZDEU 115/2015. (N=4), Firdevs Hatun Türbesi, Şiran, Gümüşhane, Turkey, 05.05.2015, Leg. K. CANDAN, S. GÜL [Map ID: 26].

3. ZDEU 109/2015. (N=3), Mahmatlı village, Kelkit, Gümüşhane, Turkey, 05.05.2015, Leg. K. CANDAN, S. GÜL [Map ID: 28].

4. ZDEU 107/2015. (N=8), Yukarı Kulaca Village, Şiran, Gümüşhane, Turkey, 06.05.2015, Leg. K. CANDAN, S. GÜL [Map ID: 25].

5. ZDEU 103/2015. (N=11), Kırkpınar Village, Bayburt, Turkey, 30.07.2015, Leg. K. CANDAN, E. YILDIRIM CAYNAK [Map ID: 32].

6. ZDEU 110/2015. (N=1), Bayburt, Turkey, 25.05.2015, Leg. K. CANDAN, E. YILDIRIM CAYNAK [Map ID: 33].

7. ZDEU 109/2011. (N=2), Akçainiş, Sivas, Turkey, 09.06.2011, Leg. Y. KUMLUTAŞ [Map ID: 14].

8. ZDEU 108/2011. (N=6), Yaylacık, İmranlı, Sivas, Turkey, 10.06.2011, Leg. Y. KUMLUTAŞ [Map ID: 22].

9. ZDEU 223/2016. (N=19), Erciyes Mountain, Kayser, Turkey, 20.06.2016, Leg. K. CANDAN, M.K. ŞAHİN, N. BEŞER [Map ID: 13].

10. ZDEU 21/2017. (N=6), Otlukbeli Lake, Erzincan, Turkey, 18.05.2017, Leg. K. CANDAN, S. GÜL [Map ID: 31].

11. ZDEU 58/2014. (N=1), Doğanşar, Sivas, Turkey, 19.06.2014, Leg. Y. KUMLUTAŞ [Map ID: 17].

12. ZDEU 68/2014. (N=1), Armutçayırı Village, Zara, Sivas, Turkey, 19.06.2014, Leg. Y. KUMLUTAŞ [Map ID: 18].

13. ZDEU 3/2011. (N=1), Çilhoroz Village, Çayırlı, Erzincan, Turkey, 28.06.2011, Leg. Y. KUMLUTAŞ [Map ID: 29].

14. ZDEU 197/2014. (N=10), Çamur Village, Kelkit, Gümüşhane, Turkey, 13.07.2014, Leg. Y. KUMLUTAŞ [Map ID: 30].

15. ZDEU 9/2017. (N=4), Kümbet Village, Zara, Sivas, Turkey, 18.07.2017, Leg. Y. KUMLUTAŞ [Map ID: 19].

16. ZDEU 69/2011. (N=1), Sucak, Zara, Sivas, Turkey, 10.06.2011, Leg. Y. KUMLUTAŞ [Map ID: 20].

17. ZDEU 114/2013. (N=2), Yukarıboğaz, İmranlı, Sivas, Turkey, 20.06.2013, Leg. Y. KUMLUTAŞ [Map ID: 23].

18. ZDEU 78/2014. (N=2), Karalar Village, Suşehri, Sivas, Turkey, 11.07.2014, Leg. Y. KUMLUTAŞ [Map ID: 21].

19. ZDEU 68/2016. (N=10), Gemecik Village, Refahiye, Erzincan, Turkey, 25.06.2016, Leg. K. CANDAN [Map ID: 24].

Darevskia rudis rudis 89(M), 72(F)

1. ZDEU 200/2014. (N=10), Karacaören Village, Başçiftlik, Tokat, Turkey, 18.06.2014, Leg. Y. KUMLUTAŞ [Map ID: 16].

2. ZDEU 99/2013. (N=2), Tekkeköy, Samsun, Turkey, 02.08.2013, Leg. Y. KUMLUTAŞ [Map ID: 15].

3. 1 ZDEU 43/2014. (N=7), Şalpazarı, Trabzon, Turkey, 04.08.2014, Leg. Y. KUMLUTAŞ, Ç. ILGAZ, K. CANDAN [Map ID: 35].

4. ZDEU 133/2014. (N=4), Zigana Pass, Gümüşhane, Turkey, 04.08.2014, Leg. Y. KUMLUTAŞ, Ç. ILGAZ, K. CANDAN [Map ID: 34].

5. ZDEU 2/2010. (N=23), Between Sürmene and Köprübaşı 8.km., Trabzon, Turkey, 17.07.2010, Leg. Y. KUMLUTAŞ, Ç. ILGAZ, A. AVCI, N. ÜZÜM, B. ÜZÜM [Map ID: 41].

6. ZDEU 40/2010. (N=23), Maçka, Trabzon, Turkey, 18.07.2010, Leg. Y. KUMLUTAŞ, Ç. ILGAZ, A. AVCI, N. ÜZÜM, B. ÜZÜM [Map ID: 40].

7. ZDEU 60/2010. (N=27), Between Akçaabat and Düzköy 14.km., Trabzon, Turkey, 18.07.2010, Leg. Y. KUMLUTAŞ, Ç. ILGAZ, A. AVCI, N. ÜZÜM, B. ÜZÜM [Map ID: 38].

8. ZDEU 50/2003. (N=19), Zigana Pass, Trabzon, Turkey, 10.07.2003, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, C.V. TOK, F. İRET [Map ID: 34].

9. ZDEU 51/2003. (N=20), Between Sümele and Maçka 10.km., Trabzon, Turkey, 10.07.2003, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, C.V. TOK, F. İRET [Map ID: 39].

10. ZDEU 53/2003. (N=10), Between Beşikdüzü and Şalpazarı 7.km., Trabzon, Turkey, 11.07.2003, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, C.V. TOK, F. İRET [Map ID: 36].

11. ZDEU 54/2003. (N=16), Between Tonya and Vakfıkebir 10-15.km., Trabzon, Turkey, 11.07.2003, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, C.V. TOK, F. İRET [Map ID: 37].

Darevskia rudis bolkardaghica 9(M), 9(F)

1. ZDEU 4/2017. (N=7), Karagöl, Ulukışla, Niğde, Turkey, 13.05.2017, Leg. Ç. ILGAZ, K. CANDAN, E. YILDIRIM CAYNAK [Map ID: 12].

2. ZDEU 36/2009. (N=11), Karagöl, Ulukışla, Niğde, Turkey, 19.07.2009, Leg. Y. KUMLUTAŞ [Map ID: 12].

Darevskia obscura obscura stat. et comb. nov. 38(M), 35(F)

1. ZDEU 43/2016. (N=7), Kutul Plateau, Ardahan, Turkey, 18.07.2016, Leg. Ç. ILGAZ, K. CANDAN [Map ID: 59].

2. ZDEU 17/2010. (N=22), Kutul Plateau, Ardahan, Turkey 14.07.2010, Leg. Y. KUMLUTAŞ, Ç. ILGAZ, A. AVCI, N. ÜZÜM, B. ÜZÜM [Map ID: 59].

3. ZDEU 156/2001. (N=44), Between Geçitli Village and Bilbilen Plateau, Ardanuç, Artvin, Turkey, 06.07.2001, Leg. Y. KUMLUTAŞ, K. OLGUN, Ç. ILGAZ, A. AVCI, F. İRET [Map ID: 60].

Darevskia obscura macromaculata comb. nov. 24(M), 27(F)

1. ZDEU 35/2010. (N=51), Sahara National Park, Ardahan, Turkey, 13.07.2010, Leg. Y. KUMLUTAŞ, Ç. ILGAZ, A. AVCI, N. ÜZÜM [Map ID: 58].

Darevskia obscura bischoffi comb. nov. 82(M), 86(F)

1. ZDEU 38/2015. (N=7), Cankurtaran Pass, Hopa, Artvin, Turkey, 23.07.2015, Leg. Y. KUMLUTAŞ, Ç. ILGAZ [Map ID: 51].

2. ZDEU 201/2014. (N=2), Maden village, Artvin, Turkey, 23.07.2014, Leg. Y. KUMLUTAŞ [Map ID: 57].

3. ZDEU 7/2010. (N=15), Balcılar Village, Borçka, Artvin, Turkey, 15.07.2010, Leg. Y. KUMLUTAŞ, Ç. ILGAZ, A. AVCI, N. ÜZÜM, B. ÜZÜM [Map ID: 55].

4. ZDEU 6/2010. (N=16), Between Borçka and Hopa 8.km., Artvin, Turkey, 15.07.2010, Leg. Y. KUMLUTAŞ, Ç. ILGAZ, A. AVCI, N. ÜZÜM, B. ÜZÜM [Map ID: 52].

5. ZDEU 31/2010. (N=10), Between Arhavi and Güneşli Village, 2.km., Artvin, Turkey, 15.07.2010, Leg. Y. KUMLUTAŞ, Ç. ILGAZ, A. AVCI, N. ÜZÜM, B. ÜZÜM [Map ID: 47].

6. ZDEU 4/2010. (N=11), Between Çamlıhemşin and Ayder Plateau 3.km., Rize, Turkey, 16.07.2010, Leg. Y. KUMLUTAŞ, Ç. ILGAZ, A. AVCI, N. ÜZÜM, B. ÜZÜM [Map ID: 46].

7. ZDEU 25/2010. (N=19), Hemşin, Rize, Turkey, 16.07.2010, Leg. Y. KUMLUTAŞ, Ç. ILGAZ, A. AVCI, N. ÜZÜM, B. ÜZÜM [Map ID: 45].

8. ZDEU 10/2010. (N=17), Between İkizdere and İspir, 19.km., Rize, Turkey, 17.07.2010, Leg. Y. KUMLUTAŞ, Ç. ILGAZ, A. AVCI, N. ÜZÜM, B. ÜZÜM [Map ID: 43].

9. ZDEU 158/2001. (N=9), Between Borçka and Camili 10-21.km., Artvin, Turkey, 07.07.2001, Leg. Y. KUMLUTAŞ, K. OLGUN, Ç. ILGAZ, A. AVCI, F. İRET [Map ID: 56].

10. ZDEU 116/2002. (N=16), Between Borçka and Balcılar, Artvin, Turkey, 12.07.2002, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, A. ÖZDEMİR [Map ID: 54].

11. ZDEU 130/2002. (N=13), Between Rize and Küçükçayır 18.km., Rize, Turkey, 14.07.2002, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, A. ÖZDEMİR [Map ID: 44].

12. ZDEU 124/2002. (N=16), Between Ortacalar and Dülgerli 16-24.km., Artvin, Turkey, 13.07.2002, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, A. ÖZDEMİR [Map ID: 48].

13. ZDEU 163/2001. (N=3), Esenkıyı Village, Hopa, Artvin, Turkey, 07.07.2001, Leg. Y. KUMLUTAŞ, K. OLGUN, Ç. ILGAZ, A. AVCI, F. İRET [Map ID: 49].

14. ZDEU 105/2000. (N=6), Çamurköy, Sarp, Artvin, Turkey, 24.04.2000, Leg. K. OLGUN [Map ID: 50].

15. ZDEU 102/2002. (N=8), Between Artvin and Hatila Plateau 35.km., Artvin, Turkey, 09.07.2002, Leg. İ. BARAN, Y. KUMLUTAŞ, Ç. ILGAZ, A. ÖZDEMİR [Map ID: 53].

Darevskia bithynica bithynica 16(M), 4(F)

1. ZDEU 15/2009. (N=20), Kirazlı Plateau, Uludağ, Bursa, Turkey, 23.06.2009, Leg. Y. KUMLUTAŞ, Ç. ILGAZ [Map ID: 1].

Darevskia bithynica tristis 60(M), 54(F)

1. ZDEU 12/2009. (N=15), Güzeldere Village, Düzce, Turkey, 24.06.2009, Leg. Y. KUMLUTAŞ, Ç. ILGAZ [Map ID: 2].

2. ZDEU 6/2009. (N=23), Samandere Waterfall, Düzce, Turkey, 24.06.2009, Leg. Y. KUMLUTAŞ, Ç. ILGAZ [Map ID: 3].

3. ZDEU 10/2009. (N=6), Between Yığılca and Bolu 30.km., Bolu, Turkey, 27.06.2009, Leg. Y. KUMLUTAŞ, Ç. ILGAZ [Map ID: 4].

4. ZDEU 14/2009. (N=11), Between Yığılca and Alaplı 12.km., Bolu, Turkey, 27.06.2009, Leg. Y. KUMLUTAŞ, Ç. ILGAZ [Map ID: 5].

5. ZDEU 16/2009. (N=19), Between Zonguldak and Gökçebey 15.km., Zonguldak, Turkey, 28.06.2009, Leg. Y. KUMLUTAŞ, Ç. ILGAZ [Map ID: 6].

6. ZDEU 13/2009. (N=8), Yenice, Karabük, Turkey, 28.06.2009, Leg. Y. KUMLUTAŞ, Ç. ILGAZ [Map ID: 8].

7. ZDEU 11/2009. (N=8), Between Safranbolu and Bartın 14.km., Bartın, Turkey, 29.06.2009, Leg. Y. KUMLUTAŞ, Ç. ILGAZ [Map ID: 7].

8. ZDEU 17/2009. (N=5), Ulus, Bartın, Turkey, 29.06.2009, Leg. Y. KUMLUTAŞ, Ç. ILGAZ [Map ID: 9].

9. ZDEU 7/2009. (N=7), Amasra, Bartın, Turkey, 29.06.2009, Leg. Y. KUMLUTAŞ, Ç. ILGAZ [Map ID: 10].

10. ZDEU 9/2009. (N=12), Kapısuyu, Kurucaşile, Bartın, Turkey, 30.06.2009, Leg. Y. KUMLUTAŞ, Ç. ILGAZ [Map ID: 11].

Appendix 2.

Samples ID	Sex	Country	Province	Locality	Species	Subspecies
1	male	Turkey	Hakkari	Cilo Mountain	*Darevskia valentini*	*spitzenbergerae*
2-3	female	Turkey	Hakkari	Cilo Mountain	*Darevskia valentini*	*spitzenbergerae*
4	male	Turkey	Kars	Boğatepe Village, Susuz	*Darevskia valentini*	*valentini*
5	female	Turkey	Kars	Boğatepe Village, Susuz	*Darevskia valentini*	*valentini*
6	male	Turkey	Ardahan	Tepeler Village	*Darevskia valentini*	*valentini*
7	female	Turkey	Ardahan	Tepeler Village	*Darevskia valentini*	*valentini*
8-9	male	Turkey	Van	Yukarınarlıca Village, Çatak	Clade A (Candan *et al.* 2021)	
10-11	female	Turkey	Van	Yukarınarlıca Village, Çatak	Clade A (Candan *et al.* 2021)	
12	male	Turkey	Van	Başeğmez Village, Çaldıran	Clade B (Candan *et al.* 2021)	-
13	female	Turkey	Van	Başeğmez Village, Çaldıran	Clade B (Candan *et al.* 2021)	-
14	male	Turkey	Erzurum	Palandöken	Clade B (Candan *et al.* 2021)	-
15	female	Turkey	Erzurum	Palandöken	Clade B (Candan *et al.* 2021)	-
16	male	Turkey	Erzurum	Çirişli Village, Çat	Clade B (Candan *et al.* 2021)	-
17	female	Turkey	Erzurum	Çirişli Village, Çat	Clade B (Candan *et al.* 2021)	-
18	male	Turkey	Kayseri	Erciyes Mountain	*Darevskia valentini*	*lantzicyreni*
19	female	Turkey	Kayseri	Erciyes Mountain	*Darevskia valentini*	*lantzicyreni*
20	male	Turkey	Sivas	Yaylacık, İmranlı	*Darevskia valentini*	*lantzicyreni*
21	female	Turkey	Sivas	Yaylacık, İmranlı	*Darevskia valentini*	*lantzicyreni*
22	male	Turkey	Sivas	Kümbet Village, Zara	*Darevskia valentini*	*lantzicyreni*
23	female	Turkey	Sivas	Kümbet Village, Zara	*Darevskia valentini*	*lantzicyreni*
24	male	Turkey	Gümüşhane	Çamur Village, Kelkit	*Darevskia valentini*	*lantzicyreni*
25	female	Turkey	Gümüşhane	Çamur Village, Kelkit	*Darevskia valentini*	*lantzicyreni*

Appendix 3. Information regarding all the samples used in this study: accession numbers, sample and population IDs, locations, haplotypes for each nuclear marker analysed.

Sample ID	Group	Country	Province	Locality	Species	Subspecies	Cyt-b	MC1R	Haplotype Cyt-b	Haplotype MC1R	Source
Spit1	A	Turkey	Hakkari	Mergan	*Darevskia valentini*	*spitzenbergerae*	ON036177	ON036180	Hap86	Hap16-Hap16	This study
Spit2	A	Turkey	Hakkari	Mergan	*Darevskia valentini*	*spitzenbergerae*	ON036178	ON036181	Hap86	Hap16-Hap16	This study
Spit3	A	Turkey	Hakkari	Mergan	*Darevskia valentini*	*spitzenbergerae*	ON036179	ON036182	Hap86	Hap16-Hap16	This study
DV1	D	Turkey	Gümüşhane	Balıklı Village, Kelkit	*Darevskia valentini*	*lantzicyreni*	MN613800	MN613983	Hap64	Hap1-Hap33	Candan *et al.* 2021
DV2	D	Turkey	Gümüşhane	Balıklı Village, Kelkit	*Darevskia valentini*	*lantzicyreni*	MN613811	MN613994	Hap64	Hap3-Hap34	Candan *et al.* 2021
DV3	D	Turkey	Gümüşhane	Firdevs Hatun Türbesi, Şiran	*Darevskia valentini*	*lantzicyreni*	MN613822	MN614005	Hap73	Hap7-Hap35	Candan *et al.* 2021
DV4	D	Turkey	Gümüşhane	Firdevs Hatun Türbesi, Şiran	*Darevskia valentini*	*lantzicyreni*	MN613833	MN614016	Hap73	Hap3-Hap32	Candan *et al.* 2021
DV5	D	Turkey	Gümüşhane	Mahmatlı Village, Kelkit	*Darevskia valentini*	*lantzicyreni*	MN613844	MN614027	Hap64	Hap3-Hap33	Candan *et al.* 2021
DV6	D	Turkey	Gümüşhane	Mahmatlı Village, Kelkit	*Darevskia valentini*	*lantzicyreni*	MN613855	MN614038	Hap64	Hap1-Hap33	Candan *et al.* 2021
DV7	D	Turkey	Gümüşhane	Yukarıkulaca Village, Şiran	*Darevskia valentini*	*lantzicyreni*	MN613866	MN614049	Hap62	Hap32-Hap35	Candan *et al.* 2021

Sample ID	Group	Country	Province	Locality	Species	Subspecies	Cyt-b	MC1R	Haplotype Cyt-b	Haplotype MC1R	Source
DV8	D	Turkey	Gümüşhane	Yukarıkulaca Village, Şiran	*Darevskia valentini*	*lantzicyreni*	MN613873	MN614056	Hap62	Hap1-Hap26	Candan *et al.* 2021
DV9	D	Turkey	Bayburt	Kırkpınar Village	*Darevskia valentini*	*lantzicyreni*	MN613874	MN614057	Hap85	Hap7-Hap14	Candan *et al.* 2021
DV10	D	Turkey	Bayburt	Kırkpınar Village	*Darevskia valentini*	*lantzicyreni*	MN613801	MN613984	Hap16	Hap14-Hap33	Candan *et al.* 2021
DV11	D	Turkey	Bayburt	City Center	*Darevskia valentini*	*lantzicyreni*	MN613802	MN613985	Hap16	Hap7-Hap34	Candan *et al.* 2021
DV12	D	Turkey	Bayburt	City Center	*Darevskia valentini*	*lantzicyreni*	MN613803	MN613986	Hap16	Hap26-Hap34	Candan *et al.* 2021
DV13	F	Turkey	Kars	Aygır Lake, Susuz	*Darevskia valentini*	*valentini*	MN613804	MN613987	Hap65	Hap1-Hap1	Candan *et al.* 2021
DV14	F	Turkey	Kars	Aygır Lake, Susuz	*Darevskia valentini*	*valentini*	MN613805	MN613988	Hap65	Hap1-Hap1	Candan *et al.* 2021
DV15	B	Turkey	Ağrı	Balık Lake, Taşlıçay	*Darevskia valentini*	Clade B (Candan *et al.* 2021)	MN613806	MN613989	Hap66	Hap16-Hap16	Candan *et al.* 2021
DV16	B	Turkey	Ağrı	Balık Lake, Taşlıçay	*Darevskia valentini*	Clade B (Candan *et al.* 2021)	MN613807	MN613990	Hap66	Hap16-Hap16	Candan *et al.* 2021
DV17	B	Turkey	Erzurum	Güzeldere Village, Hınıs	*Darevskia valentini*	Clade B (Candan *et al.* 2021)	MN613808	MN613991	Hap67	Hap16-Hap16	Candan *et al.* 2021
DV18	B	Turkey	Erzurum	Güzeldere Village, Hınıs	*Darevskia valentini*	Clade B (Candan *et al.* 2021)	MN613809	MN613992	Hap67	Hap16-Hap16	Candan *et al.* 2021
DV19	F	Turkey	Kars	Taşbaşı Village, Arpaçay	*Darevskia valentini*	*valentini*	MN613810	MN613993	Hap68	Hap1-Hap1	Candan *et al.* 2021
DV20	F	Turkey	Kars	Taşbaşı Village, Arpaçay	*Darevskia valentini*	*valentini*	MN613812	MN613995	Hap69	Hap1-Hap1	Candan *et al.* 2021
DV21	F	Turkey	Kars	Lavaş Lake, Arpaçay	*Darevskia valentini*	*valentini*	MN613813	MN613996	Hap69	Hap1-Hap1	Candan *et al.* 2021
DV22	F	Turkey	Kars	Lavaş Lake, Arpaçay	*Darevskia valentini*	*valentini*	MN613814	MN613997	Hap69	Hap1-Hap1	Candan *et al.* 2021
DV23	F	Turkey	Kars	Boğatepe Village, Susuz	*Darevskia valentini*	*valentini*	MN613815	MN613998	Hap69	Hap1-Hap1	Candan *et al.* 2021
DV24	F	Turkey	Kars	Boğatepe Village, Susuz	*Darevskia valentini*	*valentini*	MN613816	MN613999	Hap69	Hap1-Hap1	Candan *et al.* 2021
DV25	A	Turkey	Van	Yukarınarlıca Village, Çatak	*Darevskia valentini*	Clade A (Candan *et al.* 2021)	MN613817	MN614000	Hap70	Hap16-Hap16	Candan *et al.* 2021
DV26	A	Turkey	Van	Yukarınarlıca Village, Çatak	*Darevskia valentini*	Clade A (Candan *et al.* 2021)	MN613818	MN614001	Hap70	Hap16-Hap16	Candan *et al.* 2021
DV27	B	Turkey	Van	Başeğmez Village, Çaldıran	*Darevskia valentini*	Clade A (Candan *et al.* 2021)	MN613819	MN614002	Hap71	Hap16-Hap16	Candan *et al.* 2021
DV28	B	Turkey	Van	Başeğmez Village, Çaldıran	*Darevskia valentini*	Clade A (Candan *et al.* 2021)	MN613820	MN614003	Hap71	Hap16-Hap16	Candan *et al.* 2021
DV29	B	Turkey	Erzurum	Çirişli Village, Çat	*Darevskia valentini*	Clade A (Candan *et al.* 2021)	MN613821	MN614004	Hap72	Hap1-Hap1	Candan *et al.* 2021
DV30	B	Turkey	Erzurum	Çirişli Village, Çat	*Darevskia valentini*	Clade A (Candan *et al.* 2021)	MN613823	MN614006	Hap72	Hap16-Hap26	Candan *et al.* 2021
DV31	B	Turkey	Erzurum	Palandöken	*Darevskia valentini*	Clade A (Candan *et al.* 2021)	MN613824	MN614007	Hap74	Hap16-Hap16	Candan *et al.* 2021
DV32	D	Turkey	Sivas	Akçainiş	*Darevskia valentini*	*lantzicyreni*	MN613825	MN614008	Hap75	Hap1-Hap3	Candan *et al.* 2021
DV33	D	Turkey	Sivas	Akçainiş	*Darevskia valentini*	*lantzicyreni*	MN613826	MN614009	Hap75	Hap1-Hap3	Candan *et al.* 2021
DV34	D	Turkey	Sivas	Yaylacık, İmranlı	*Darevskia valentini*	*lantzicyreni*	MN613827	MN614010	Hap75	Hap1-Hap1	Candan *et al.* 2021
DV35	D	Turkey	Sivas	Yaylacık, İmranlı	*Darevskia valentini*	*lantzicyreni*	MN613828	MN614011	Hap75	Hap3-Hap31	Candan *et al.* 2021
DV36	D	Turkey	Kayseri	Erciyes Mountain	*Darevskia valentini*	*lantzicyreni*	MN613829	MN614012	Hap76	Hap1-Hap1	Candan *et al.* 2021
DV37	D	Turkey	Kayseri	Erciyes Mountain	*Darevskia valentini*	*lantzicyreni*	MN613830	MN614013	Hap77	Hap1-Hap1	Candan *et al.* 2021
DV38	B	Turkey	Van	Başeğmez Village, Çaldıran	*Darevskia valentini*	Clade B (Candan *et al.* 2021)	MN613831	MN614014	Hap71	Hap16-Hap16	Candan *et al.* 2021
DV39	D	Turkey	Sivas	Yaylacık, İmranlı	*Darevskia valentini*	*lantzicyreni*	MN613832	MN614015	Hap75	Hap1-Hap1	Candan *et al.* 2021
DV40	F	Turkey	Kars	Aygır Lake, Susuz	*Darevskia valentini*	*valentini*	MN613834	MN614017	Hap65	Hap1-Hap1	Candan *et al.* 2021
DV41	F	Turkey	Kars	Aygır Lake, Susuz	*Darevskia valentini*	*valentini*	MN613835	MN614018	Hap65	Hap1-Hap1	Candan *et al.* 2021
DV42	B	Turkey	Ağrı	Balık Lake, Taşlıçay	*Darevskia valentini*	Clade B (Candan *et al.* 2021)	MN613836	MN614019	Hap66	Hap16-Hap16	Candan *et al.* 2021
DV43	B	Turkey	Ağrı	Balık Lake, Taşlıçay	*Darevskia valentini*	Clade B (Candan *et al.* 2021)	MN613837	MN614020	Hap66	Hap16-Hap16	Candan *et al.* 2021
DV44	B	Turkey	Erzurum	Çirişli Village, Çat	*Darevskia valentini*	Clade B (Candan *et al.* 2021)	MN613838	MN614021	Hap72	Hap16-Hap26	Candan *et al.* 2021
DV45	B	Turkey	Erzurum	Güzeldere Village, Hınıs	*Darevskia valentini*	Clade B (Candan *et al.* 2021)	MN613839	MN614022	Hap67	Hap16-Hap26	Candan *et al.* 2021
DV46	B	Turkey	Erzurum	Güzeldere Village, Hınıs	*Darevskia valentini*	Clade B (Candan *et al.* 2021)	MN613840	MN614023	Hap67	Hap16-Hap16	Candan *et al.* 2021
DV47	A	Turkey	Van	Yukarınarlıca Village, Çatak	*Darevskia valentini*	Clade A (Candan *et al.* 2021)	MN613841	MN614024	Hap78	Hap16-Hap16	Candan *et al.* 2021
DV48	A	Turkey	Van	Yukarınarlıca Village, Çatak	*Darevskia valentini*	Clade A (Candan *et al.* 2021)	MN613842	MN614025	Hap70	Hap16-Hap16	Candan *et al.* 2021

Sample ID	Group	Country	Province	Locality	Species	Subspecies	Cyt-b	MC1R	Haplotype Cyt-b	Haplotype MC1R	Source
DV49	F	Turkey	Kars	Boğatepe Village, Susuz	*Darevskia valentini*	*valentini*	MN613843	MN614026	Hap69	Hap1-Hap1	Candan *et al.* 2021
DV50	B	Turkey	Van	Başeğmez Village, Çaldıran	*Darevskia valentini*	Clade B (Candan *et al.* 2021)	MN613845	MN614028	Hap71	Hap16-Hap16	Candan *et al.* 2021
DV51	F	Turkey	Kars	Taşbaşı Village, Arpaçay	*Darevskia valentini*	*valentini*	MN613846	MN614029	Hap69	Hap1-Hap1	Candan *et al.* 2021
DV52	F	Turkey	Kars	Akdere Village	*Darevskia valentini*	*valentini*	MN613847	MN614030	Hap69	Hap1-Hap1	Candan *et al.* 2021
DV53	D	Turkey	Erzincan	Otlukbeli Lake	*Darevskia valentini*	*lantzicyreni*	MN613848	MN614031	Hap64	Hap1-Hap31	Candan *et al.* 2021
DV54	D	Turkey	Sivas	Doğanşar	*Darevskia valentini*	*lantzicyreni*	MN613849	MN614032	Hap79	Hap34-Hap36	Candan *et al.* 2021
DV55	D	Turkey	Sivas	Armutçayırı Village, Zara	*Darevskia valentini*	*lantzicyreni*	MN613850	MN614033	Hap80	Hap3-Hap36	Candan *et al.* 2021
DV56	F	Turkey	Kars	Büyükçatak Village, Susuz	*Darevskia valentini*	*valentini*	MN613851	MN614034	Hap69	Hap1-Hap1	Candan *et al.* 2021
DV57	F	Turkey	Kars	Kurugöl Village, Susuz	*Darevskia valentini*	*valentini*	MN613852	MN614035	Hap69	Hap1-Hap1	Candan *et al.* 2021
DV58	D	Turkey	Erzincan	Çilhoroz Village, Çayırlı	*Darevskia valentini*	*lantzicyreni*	MN613853	MN614036	Hap64	Hap3-Hap33	Candan *et al.* 2021
DV59	D	Turkey	Kayseri	Erciyes Mountain	*Darevskia valentini*	*lantzicyreni*	MN613854	MN614037	Hap76	Hap1-Hap1	Candan *et al.* 2021
DV60	D	Turkey	Kayseri	Erciyes Mountain	*Darevskia valentini*	*lantzicyreni*	MN613856	MN614039	Hap77	Hap1-Hap1	Candan *et al.* 2021
DV61	D	Turkey	Gümüşhane	Çamur Village, Kelkit	*Darevskia valentini*	*lantzicyreni*	MN613857	MN614040	Hap81	Hap1-Hap1	Candan *et al.* 2021
DV62	D	Turkey	Gümüşhane	Çamur Village, Kelkit	*Darevskia valentini*	*lantzicyreni*	MN613858	MN614041	Hap64	Hap3-Hap33	Candan *et al.* 2021
DV63	D	Turkey	Gümüşhane	Çamur Village, Kelkit	*Darevskia valentini*	*lantzicyreni*	MN613859	MN614042	Hap64	Hap1-Hap34	Candan *et al.* 2021
DV64	D	Turkey	Erzincan	Otlukbeli Lake	*Darevskia valentini*	*lantzicyreni*	MN613860	MN614043	Hap64	Hap3-Hap31	Candan *et al.* 2021
DV65	D	Turkey	Erzincan	Otlukbeli Lake	*Darevskia valentini*	*lantzicyreni*	MN613861	MN614044	Hap64	Hap3-Hap31	Candan *et al.* 2021
DV66	F	Turkey	Ardahan	Tepesuyu Village	*Darevskia valentini*	*valentini*	MN613862	MN614045	Hap69	Hap1-Hap1	Candan *et al.* 2021
DV67	D	Turkey	Sivas	Kümbet Village, Zara	*Darevskia valentini*	*lantzicyreni*	MN613863	MN614046	Hap75	Hap1-Hap1	Candan *et al.* 2021
DV68	D	Turkey	Sivas	Sucak, Zara	*Darevskia valentini*	*lantzicyreni*	MN613864	MN614047	Hap75	Hap1-Hap1	Candan *et al.* 2021
DV69	D	Turkey	Sivas	Yukarıboğaz, İmranlı	*Darevskia valentini*	*lantzicyreni*	MN613865	MN614048	Hap82	Hap1-Hap37	Candan *et al.* 2021
DV70	D	Turkey	Sivas	Karalar Village, Suşehri	*Darevskia valentini*	*lantzicyreni*	MN613867	MN614050	Hap80	Hap1-Hap31	Candan *et al.* 2021
DV71	D	Turkey	Erzincan	Gemecik Village, Refahiye	*Darevskia valentini*	*lantzicyreni*	MN613868	MN614051	Hap83	Hap1-Hap3	Candan *et al.* 2021
DV72	F	Turkey	Ardahan	Tepesuyu Village	*Darevskia valentini*	*valentini*	MN613869	MN614052	Hap69	Hap1-Hap1	Candan *et al.* 2021
DV73	F	Turkey	Ardahan	Tepeler Village	*Darevskia valentini*	*valentini*	MN613870	MN614053	Hap69	Hap1-Hap1	Candan *et al.* 2021
DV74	F	Turkey	Ardahan	Yağmuroğlu Village, Göle	*Darevskia valentini*	*valentini*	MN613871	MN614054	Hap69	Hap1-Hap1	Candan *et al.* 2021
DV75	F	Turkey	Ardahan	Çatköy Plateau, Hanak	*Darevskia valentini*	*valentini*	MN613872	MN614055	Hap84	Hap1-Hap1	Candan *et al.* 2021
DRbo76	D	Turkey	Niğde	Karagöl, Ulukışla	*Darevskia rudis*	*bolkardaghica*	MN613787	MN613971	Hap59	Hap1-Hap1	Candan *et al.* 2021
DRbo77	D	Turkey	Niğde	Karagöl, Ulukışla	*Darevskia rudis*	*bolkardaghica*	MN613788	MN613972	Hap59	Hap1-Hap1	Candan *et al.* 2021
DRbo78	D	Turkey	Niğde	Karagöl, Ulukışla	*Darevskia rudis*	*bolkardaghica*	MN613789	MN613973	Hap59	Hap1-Hap28	Candan *et al.* 2021
DRr80	D	Turkey	Tokat	Karacaören Village, Başçiftlik	*Darevskia rudis*	*rudis*	MN613793	MN613977	Hap61	Hap1-Hap30	Candan *et al.* 2021
DRr81	D	Turkey	Tokat	Karacaören Village, Başçiftlik	*Darevskia rudis*	*rudis*	MN613794	MN613978	Hap61	Hap1-Hap31	Candan *et al.* 2021
DRr82	D	Turkey	Samsun	Tekkeköy	*Darevskia rudis*	*rudis*	MN613795	MN613979	Hap6	Hap3-Hap3	Candan *et al.* 2021
DRr83	D	Turkey	Trabzon	Şalpazarı	*Darevskia rudis*	*rudis*	MN613796	MN613980	Hap62	Hap32-Hap32	Candan *et al.* 2021
DRr84	D	Turkey	Trabzon	Zigana Pass	*Darevskia rudis*	*rudis*	MN613797		Hap63		Candan *et al.* 2021
DRbi85	G	Turkey	Artvin	Maden Village, Şavşat	*Darevskia rudis*	*bischoffi*	MN613785	MN613969	Hap28	Hap21-Hap29	Candan *et al.* 2021
DRbi86	G	Turkey	Artvin	Cankurtaran Pass, Hopa	*Darevskia rudis*	*bischoffi*	MN613786	MN613970	Hap28	Hap1-Hap3	Candan *et al.* 2021
DRo87	G	Turkey	Artvin	Kutul Plateau, Ardanuç	*Darevskia rudis*	*obscura*	MN613792	MN613976	Hap30	Hap3-Hap16	Candan *et al.* 2021
DRma88	G	Turkey	Artvin	Sahara Forest, Şavşat	*Darevskia rudis*	*macromaculata*	MN613790	MN613974	Hap43	Hap3-Hap3	Candan *et al.* 2021
DRmi89	C	Turkey	Erzurum	Ovit, İspir	*Darevskia rudis*	*mirabilis*	MN613791	MN613975	Hap60	Hap16-Hap16	Candan *et al.* 2021
5250	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MH271036		Hap1		Rato *et al.* 2021

Sample ID	Group	Country	Province	Locality	Species	Subspecies	Cyt-b	MC1R	Haplotype Cyt-b	Haplotype MC1R	Source
5577	D	Turkey	north-eastern Anatolia		*Darevskia rudis*		MH271046		Hap2		Rato *et al.* 2021
5543	D	Turkey	north-eastern Anatolia		*Darevskia rudis*		MH271066		Hap2		Rato *et al.* 2021
DB10043	F	Armenia	Gegharkunik		*Darevskia valentini*		MW142902	MW142683	Hap3	Hap1-Hap2	Rato *et al.* 2021
DB653	F	Armenia			*Darevskia valentini*		MW142903		Hap3		Rato *et al.* 2021
DB4557	F	Armenia	Gegharkunik		*Darevskia valentini*		MW142904	MW142682	Hap27	Hap2-Hap2	Rato *et al.* 2021
DB5249	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142905	MW142732	Hap28	Hap1-Hap3	Rato *et al.* 2021
DB5252	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142906	MW142701	Hap28	Hap3-Hap3	Rato *et al.* 2021
DB5280	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142907	MW142743	Hap28	Hap3-Hap13	Rato *et al.* 2021
DB5283	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142908	MW142703	Hap28	Hap3-Hap3	Rato *et al.* 2021
DB5300	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142909	MW142744	Hap28	Hap3-Hap13	Rato *et al.* 2021
DB5451	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142910	MW142747	Hap28	Hap3-Hap13	Rato *et al.* 2021
DB5485	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142911	MW142721	Hap28	Hap3-Hap3	Rato *et al.* 2021
DB5396	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142912	MW142746	Hap40	Hap3-Hap13	Rato *et al.* 2021
DB5418	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142913	MW142751	Hap41	Hap20-Hap21	Rato *et al.* 2021
DB5513	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142914	MW142755	Hap41	Hap3-Hap24	Rato *et al.* 2021
DB5263	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142915	MW142769	Hap30	Hap12-Hap12	Rato *et al.* 2021
DB5272	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142916	MW142770	Hap30	Hap3-Hap12	Rato *et al.* 2021
DB5479	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142917	MW142757	Hap43	Hap3-Hap16	Rato *et al.* 2021
DB12041	D	Turkey	Anatolia		*Darevskia valentini*		MW142918		Hap5		Rato *et al.* 2021
DB12128	D	Turkey	Anatolia		*Darevskia valentini*		MW142919		Hap5		Rato *et al.* 2021
DB12129	D	Turkey	Anatolia		*Darevskia valentini*		MW142920		Hap7		Rato *et al.* 2021
DB16245	D	Turkey	Ordu		*Darevskia rudis*		MW142921		Hap8		Rato *et al.* 2021
DB16270	D	Turkey	Ordu		*Darevskia valentini*		MW142922	MW142725	Hap11	Hap3-Hap4	Rato *et al.* 2021
DB16278	D	Turkey	Ordu		*Darevskia valentini*		MW142923	MW142694	Hap11	Hap1-Hap5	Rato *et al.* 2021
DB16471	D	Turkey	Ordu		*Darevskia rudis*		MW142924	MW142756	Hap23	Hap3-Hap10	Rato *et al.* 2021
DB16472	D	Turkey	Ordu		*Darevskia rudis*		MW142925	MW142726	Hap24	Hap3-Hap4	Rato *et al.* 2021
DB16473	D	Turkey	Ordu		*Darevskia rudis*		MW142926	MW142731	Hap25	Hap1-Hap3	Rato *et al.* 2021
DB16393	D	Turkey			*Darevskia valentini*		MW142927		Hap16		Rato *et al.* 2021
DB16397	D	Turkey			*Darevskia valentini*		MW142928	MW142729	Hap16	Hap7-Hap8	Rato *et al.* 2021
DB16396	D	Turkey			*Darevskia valentini*		MW142929	MW142686	Hap16	Hap1-Hap7	Rato *et al.* 2021
DB12061	D	Turkey	Anatolia		*Darevskia rudis*		MW142930	MW142696	Hap6	Hap3-Hap3	Rato *et al.* 2021
DB12117	D	Turkey	Anatolia		*Darevskia rudis*		MW142931	MW142697	Hap6	Hap3-Hap3	Rato *et al.* 2021
DB16258	D	Turkey	Erzurum		*Darevskia valentini*		MW142932	MW142687	Hap9	Hap1-Hap1	Rato *et al.* 2021
DB16259	D	Turkey	Erzurum		*Darevskia valentini*		MW142933		Hap9		Rato *et al.* 2021
DB5318	D	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142934	MW142735	Hap9	Hap14-Hap14	Rato *et al.* 2021
DB16262	D	Turkey	Erzurum		*Darevskia valentini*		MW142935	MW142688	Hap10	Hap1-Hap1	Rato *et al.* 2021
DB5729	D	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142936	MW142790	Hap57	Hap26-Hap26	Rato *et al.* 2021
DB5302	D	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142937	MW142734	Hap35	Hap1-Hap14	Rato *et al.* 2021
DB5323	D	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142938	MW142691	Hap2	Hap1-Hap1	Rato *et al.* 2021
DB5514	D	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142939	MW142692	Hap2	Hap1-Hap1	Rato *et al.* 2021
DB5459	D	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142940	MW142785	Hap35	Hap1-Hap1	Rato *et al.* 2021

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Sample ID	Group	Country	Province	Locality	Species	Subspecies	Cyt-b	MC1R	Haplotype Cyt-b	Haplotype MC1R	Source
DB5768	D	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142941		Hap58		Rato *et al.* 2021
DB5812	D	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142942	MW142754	Hap58	Hap1-Hap28	Rato *et al.* 2021
DB16432	D	Turkey	Ordu		*Darevskia rudis*		MW142943		Hap17		Rato *et al.* 2021
DB16467	D	Turkey	Ordu		*Darevskia rudis*		MW142944	MW142730	Hap20	Hap1-Hap3	Rato *et al.* 2021
DB16468	D	Turkey	Ordu		*Darevskia rudis*		MW142945	MW142689	Hap21	Hap1-Hap1	Rato *et al.* 2021
DB16469	D	Turkey	Ordu		*Darevskia rudis*		MW142946	MW142762	Hap22	Hap4-Hap9	Rato *et al.* 2021
DB16460	D	Turkey	Ordu		*Darevskia rudis*		MW142947	MW142727	Hap19	Hap1-Hap4	Rato *et al.* 2021
DB10162	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142948	MW142695	Hap4	Hap3-Hap3	Rato *et al.* 2021
DB5353	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142949	MW142713	Hap1	Hap3-Hap3	Rato *et al.* 2021
DB5270	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142950	MW142702	Hap31	Hap3-Hap3	Rato *et al.* 2021
DB5307	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142951	MW142706	Hap31	Hap3-Hap3	Rato *et al.* 2021
DB5393	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142952	MW142772	Hap31	Hap3-Hap15	Rato *et al.* 2021
DB5320	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142953		Hap31		Rato *et al.* 2021
DB5392	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142954	MW142714	Hap31	Hap3-Hap3	Rato *et al.* 2021
DB5346	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142955	MW142710	Hap38	Hap3-Hap3	Rato *et al.* 2021
DB5345	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142956	MW142709	Hap37	Hap3-Hap3	Rato *et al.* 2021
DB5415	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142957		Hap45		Rato *et al.* 2021
DB5274	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142958	MW142771	Hap32	Hap3-Hap12	Rato *et al.* 2021
DB5298	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142959	MW142705	Hap32	Hap3-Hap3	Rato *et al.* 2021
DB5493	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142960	MW142723	Hap32	Hap3-Hap3	Rato *et al.* 2021
DB5341	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142961	MW142708	Hap36	Hap3-Hap3	Rato *et al.* 2021
DB5434	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142962	MW142715	Hap47	Hap3-Hap3	Rato *et al.* 2021
DB5281	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142963	MW142777	Hap33	Hap3-Hap11	Rato *et al.* 2021
DB5828	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142964	MW142780	Hap33	Hap11-Hap11	Rato *et al.* 2021
DB5284	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142965	MW142704	Hap34	Hap3-Hap3	Rato *et al.* 2021
DB5340	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142966	MW142707	Hap34	Hap3-Hap3	Rato *et al.* 2021
DB5505	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142967		Hap56		Rato *et al.* 2021
DB5262	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142968	MW142775	Hap29	Hap3-Hap11	Rato *et al.* 2021
DB5497	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142969	MW142781	Hap54	Hap11-Hap23	Rato *et al.* 2021
DB5494	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142970	MW142784	Hap53	Hap11-Hap22	Rato *et al.* 2021
DB16273	E	Turkey	Sinop		*Darevskia rudis*		MW142971		Hap12		Rato *et al.* 2021
DB16458	E	Turkey	Sinop		*Darevskia rudis*		MW142972	MW142761	Hap18	Hap3-Hap9	Rato *et al.* 2021
DB16275	E	Turkey	Sinop		*Darevskia rudis*		MW142973	MW142699	Hap13	Hap3-Hap3	Rato *et al.* 2021
DB16337	E	Turkey	Bartın		*Darevskia rudis*		MW142974	MW142700	Hap14	Hap3-Hap3	Rato *et al.* 2021
DB16339	E	Turkey	Bartın		*Darevskia rudis*		MW142975	MW142765	Hap15	Hap3-Hap6	Rato *et al.* 2021
DB16481	E	Turkey	Kastamonu		*Darevskia rudis*		MW142976	MW142766	Hap26	Hap3-Hap6	Rato *et al.* 2021
DB16336	E	Turkey	Bartın		*Darevskia rudis*		MW142977	MW142763	Hap14	Hap3-Hap6	Rato *et al.* 2021
DB5480	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142978	MW142719	Hap50	Hap3-Hap3	Rato *et al.* 2021
DB5484	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142979	MW142773	Hap50	Hap15-Hap15	Rato *et al.* 2021
DB5482	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142980	MW142720	Hap51	Hap3-Hap3	Rato *et al.* 2021
DB5260	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142982		Hap28		Rato *et al.* 2021

Sample ID	Group	Country	Province	Locality	Species	Subspecies	Cyt-b	MC1R	Haplotype Cyt-b	Haplotype MC1R	Source
DB5342	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142983	MW142733	Hap28	Hap1-Hap3	Rato *et al.* 2021
DB5344	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142984	MW142745	Hap28	Hap3-Hap13	Rato *et al.* 2021
DB5401	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142985		Hap28		Rato *et al.* 2021
DB5402	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142986	MW142748	Hap28	Hap3-Hap13	Rato *et al.* 2021
DB5443	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142987	MW142752	Hap28	Hap1-Hap21	Rato *et al.* 2021
DB5445	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142988	MW142753	Hap28	Hap3-Hap21	Rato *et al.* 2021
DB5470	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142989	MW142750	Hap28	Hap13-Hap13	Rato *et al.* 2021
DB5403	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142990	MW142749	Hap41	Hap3-Hap13	Rato *et al.* 2021
DB5613	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142991	MW142693	Hap41	Hap1-Hap1	Rato *et al.* 2021
DB5395	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142992	MW142740	Hap30	Hap3-Hap3	Rato *et al.* 2021
DB5412	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142993	MW142759	Hap44	Hap16-Hap16	Rato *et al.* 2021
DB5411	G	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142994	MW142789	Hap43	Hap13-Hap19	Rato *et al.* 2021
DB5409	D	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142995	MW142736	Hap35	Hap1-Hap17	Rato *et al.* 2021
DB5404	C	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142996	MW142758	Hap42	Hap1-Hap16	Rato *et al.* 2021
DB5410	C	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142997	MW142760	Hap42	Hap16-Hap18	Rato *et al.* 2021
DB5337	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142998		Hap31		Rato *et al.* 2021
DB5456	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW142999		Hap48		Rato *et al.* 2021
DB5349	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW143000	MW142738	Hap32	Hap3-Hap3	Rato *et al.* 2021
DB5394	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW143001	MW142739	Hap32	Hap3-Hap3	Rato *et al.* 2021
DB5466	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW143002	MW142718	Hap49	Hap3-Hap3	Rato *et al.* 2021
DB5279	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW143003	MW142776	Hap33	Hap3-Hap11	Rato *et al.* 2021
DB5397	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW143004	MW142778	Hap33	Hap11-Hap11	Rato *et al.* 2021
DB5518	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW143005	MW142782	Hap33	Hap3-Hap25	Rato *et al.* 2021
DB5743	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW143006	MW142774	Hap34	Hap3-Hap27	Rato *et al.* 2021
DB5816	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW143007	MW142724	Hap56	Hap3-Hap3	Rato *et al.* 2021
DB5504	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW143008	MW142779	Hap54	Hap11-Hap11	Rato *et al.* 2021
DB5419	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW143009		Hap46		Rato *et al.* 2021
DB5503	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW143010	MW142783	Hap55	Hap23-Hap23	Rato *et al.* 2021
DB5512	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW143011	MW142741	Hap50	Hap3-Hap3	Rato *et al.* 2021
DB5487	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW143012	MW142722	Hap52	Hap3-Hap3	Rato *et al.* 2021
DB5350	E	Turkey	north-eastern Anatolia		*Darevskia rudis*		MW143016	MW142711	Hap39	Hap3-Hap3	Rato *et al.* 2021

Appendix 4. Sequence divergences, as % uncorrected genetic distance values (p-distances), among the species of studied group for mitochondrial *Cyt-b* (below diagonal) and nuclear *MC1R* (above diagonal). Values in diagonal are genetic divergences within each species (*Cyt-b/MC1R*).

| Species	1	2	3	4	5	6	7
1. A (*D. spitzenbergerae*)	**0.3/0.0**	0.1	0.1	0.5	0.5	0.3	0.5
2. B (*D. josefschmidtleri*)	4.6	**0.7/0.1**	0.1	0.4	0.5	0.3	0.5
3. C (*D. mirabilis*)	5.8	4.5	**0.2/0.2**	0.4	0.5	0.3	0.5
4. D (*D. rudis*)	5.2	6.0	4.3	**2.4/0.2**	0.2	0.2	0.3
5. E (*D. bithynica*)	6.1	5.4	4.1	4.6	**2.2/0.1**	0.2	0.3
6. F (*D. valentini*)	5.3	5.8	3.6	3.2	3.5	**0.1/0.0**	0.2
7. G (*D. obscura*)	4.4	6.1	3.8	3.6	3.7	1.6	**0.4/0.3**
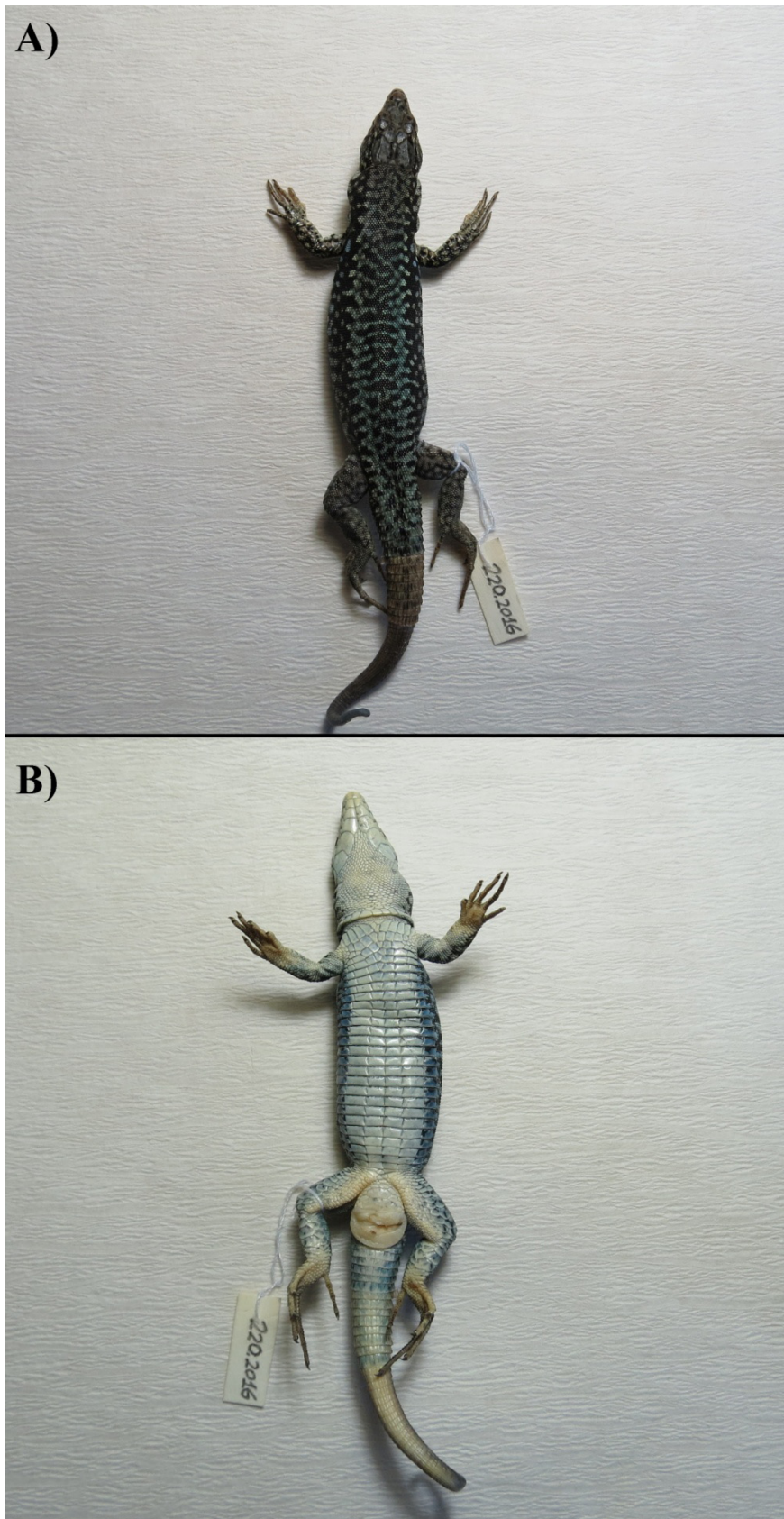
Appendix 5a. Holotype specimen of *Darevskia josefschmidtleri* **sp. nov.** A) dorsal and B) ventral view.

Appendix 5b. The habitat of *Darevskia josefschmidtleri* **sp. nov.**
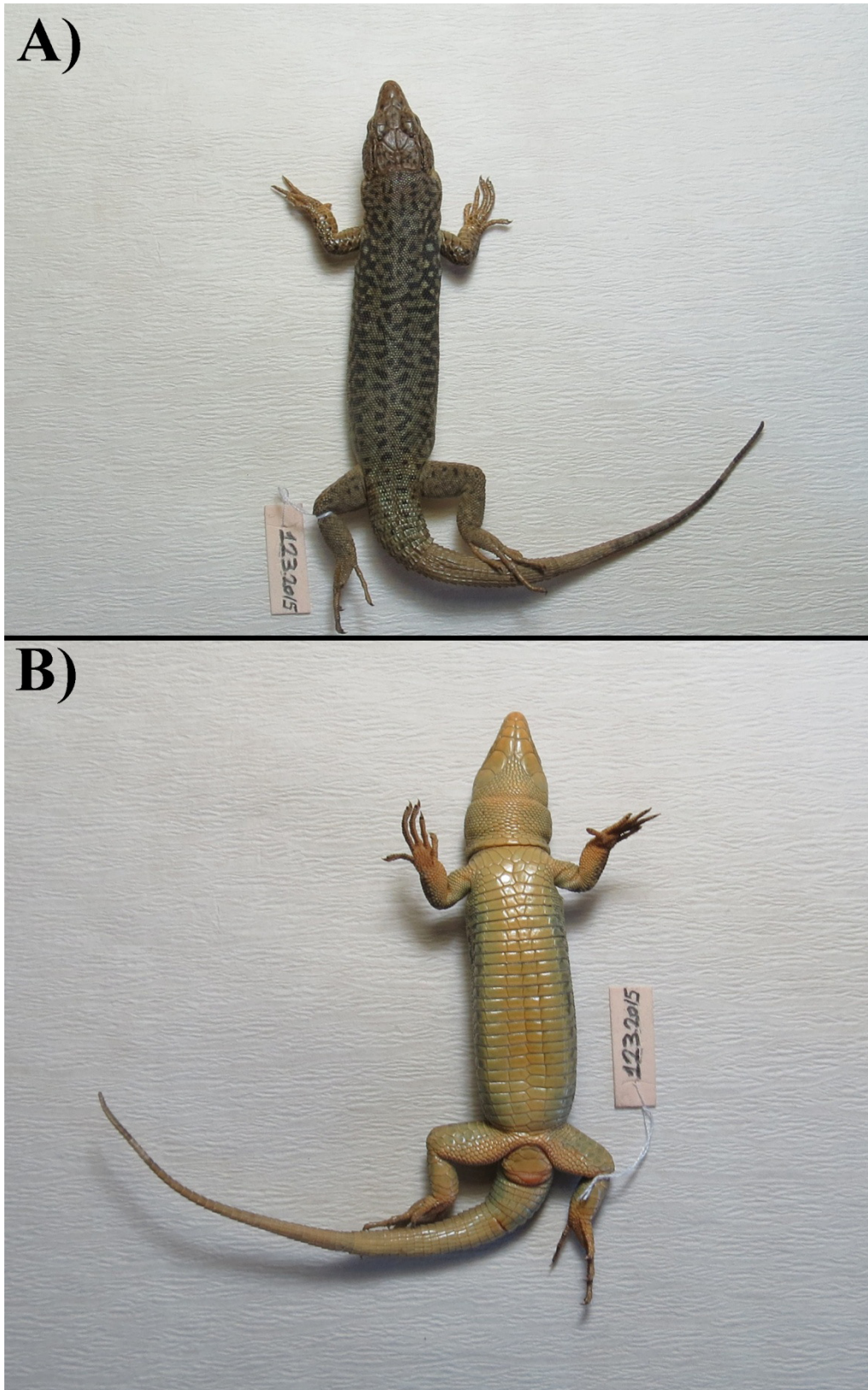
Appendix 5c. Holotype specimen of *Darevskia spitzenbergerae wernermayeri* **ssp. nov.** A) dorsal and B) ventral view.

Appendix 5d. A) The habitat of *Darevskia spitzenbergerae wernermayeri* **ssp. nov.** B) A free specimen in its natural state.

Appendix 6a. The consensus *Cyt-b* sequences of the new species which are presented in this study with currently recognized *D. valentini*. The diagnostic molecular characters are highlighted (yellow background: differences compared with *D. valentini*).

Darevskia josefschmidtleri **sp. nov.**

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Darevskia valentini

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ggcctcctcttcctagccctctttttcacccaacctcctaggagacccagaaaa
```

Appendix 6b. The molecular diagnostic characters for *D. josefschmidtleri* **sp. nov.** compared with *D. valentini* regarding the nuclear locus. Numbers refer to the position of the aligned loci.

Locus	Diagnostic characters with position in alignment of the reference sequence	
	Darevskia josefschmidtleri **sp. nov.**	*Darevskia valentini*
MC1R	63 G; 84 G	63 A; 84 C