



## Phylogenetic signals in scale shape in Caucasian rock lizards (*Darevskia* species)

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### ABSTRACT

The genus *Darevskia* comprises over 20 species of small-bodied lizards, mainly occurring in the Caucasus Mountain Region. They show differences in body size, scalation and coloration, however, fully diagnostic characters that could separate the species with a high confidence level are still lacking. The early phylogenetic hypothesis of this group was based on 'traditional' analysis of morphology, based on multiple body and head measurements and scalation traits. Later, a molecular phylogeny of the genus rejected some of the proposed topology based on morphological traits. In this paper, we used quantitative morphological data (outline-based shape data) to test phylogenetic similarities, as proposed by these earlier hypotheses. We analyzed the pileus shape and the anal area of more than 200 individuals, representing six species of *Darevskia*, using outline based elliptic Fourier analysis. The analysis did confirm a clustering of the individuals and species (using UPGMA) from the same mitochondrial DNA clade. Hence, the phylogenetic affinity of the major clades in *Darevskia* could be identified using both molecular methods and outline analysis, whereas a traditional quantitative morphological analysis could not.

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### 1. Introduction

Caucasian rock lizards of the genus *Darevskia* Arribas, 1999 are a highly diverse, monophyletic clade, mostly found in the Greater and the Lesser Caucasus (Tarkhnishvili, 2012). There are recent debates on the validity of the name *Caucasilacerta* Harris et al., 1998, a senior synonym of the same group according to Busack et al. (2016). However, considering the disputable taxonomic arguments (Arribas, 2016), we follow the widely used application of the name *Darevskia*.

*Darevskia* lizards occupy mostly the same type of habitats: rocks along rivers and roads, stony or break constructions, and pebbled river banks. The exceptions are *D. derjugini* Nikolsky, 1898 and *D. praticola* Eversmann, 1834; which prefer open soil or forest litter (Tarkhnishvili, 2012).

The ranges and habitats of a number of species are overlapping. This overlap has been shown in some cases to lead to interspecific hybridization and gene introgression (Darevsky, 1967; Murphy et al., 1996, 2000; Tarkhnishvili, 2012). Most of them are small

lizards (SVL 50 mm–88 mm), their scalation patterns are variable and strongly overlap across the species.

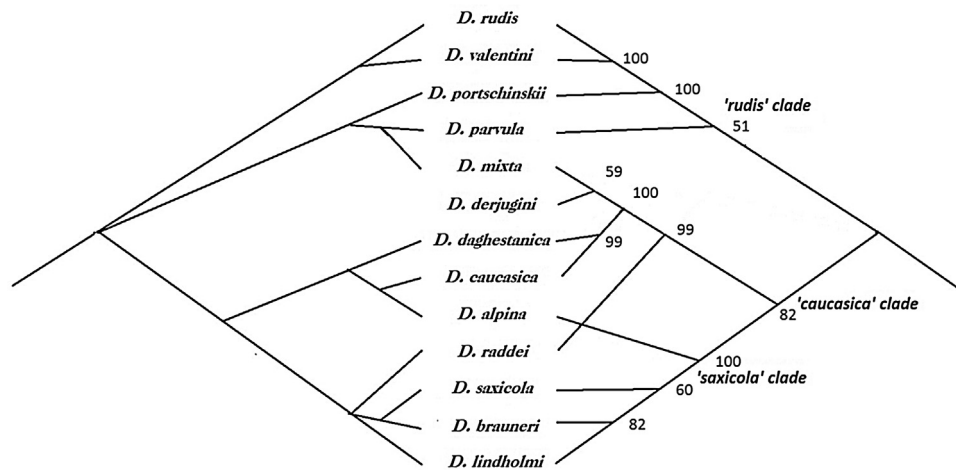
The phylogenetic relationships among *Darevskia* species using molecular data was first studied by Murphy and Moritz (Murphy et al., 1996; Moritz et al., 1992). Later, Murphy et al. (2000) attributed bisexual species of *Darevskia* to three monophyletic clades using mtDNA analysis and allozyme electrophoresis: '*caucasica*', '*saxicola*' and '*rudis*' (Murphy et al., 2000). These studies lead to a taxonomic revision of *Darevskia*, as well as a re-evaluation of their phylogenetic relationships, so far only based on morphological traits (qualitative traits of scalation pattern) in Darevsky's study (1967) (Fig. 1).

Darevsky (1967) identified only six bisexual forms as nominal species: *D. praticola*, *D. derjugini*, *D. saxicola* Eversmann, 1834; *D. caucasica* Méhely, 1909; *D. mixta* Méhely, 1909 and *D. rudis* Bedriaga, 1886 (some of them with several subspecies). He also reconstructed their phylogenetic relationships using 'traditional' morphometrics. Murphy and Moritz, on the other hand, identified 15 bisexual nominal species based on molecular data (Murphy et al., 1996; Moritz et al., 1992; Murphy et al., 2000) leading to an important taxonomic regroupings and revision of their phylogenetic relationships.

According to Darevsky (1967), *D. rudis* and *D. valentini* Boettger, 1892 were attributed to a clade different from the one including *D. portschinskii* Kessler, 1878 and *D. parvula* Lantz and Cyren, 1936;

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**Fig. 1.** Phylogenetic hypotheses of *Darevskia*: topology based on qualitative traits of scalation pattern, according to Darevsky (1967) (on the left) and topology based on the parsimony analysis of molecular data (mtDNA), according to Murphy et al. (2000) (on the right). Numbers indicate bootstrap values.

while the mtDNA analysis grouped those four species into a single clade. Also *D. mixta*, which was grouped with *D. parvula* in Darevsky's analysis, was re-grouped into the 'caucasica' clade based on mtDNA. As a result, it was considered that phylogenetic relationships cannot be reconstructed based on qualitative, morphological traits of *Darevskia* lizards (Fu et al., 1997; MacCulloch et al., 2000; Murphy et al., 2000; Tarkhnishvili, 2012; Tarkhnishvili et al., 2013).

Considering that geometric morphometric approaches are more powerful in capturing shape variation than traditional morphometrics that rely on more qualitative traits (Zelditch et al., 2004; Breno et al., 2011; Maderbacher et al., 2008; Abdel-Rahman et al., 2009; Bernal, 2007; Blanco and Godfrey, 2006), we aimed to study whether interspecific phenotypic patterns (quantified using outline based geometric morphometrics) correspond with the molecular phylogenetic divergence pattern suggested by Murphy et al. (2000). Six species of *Darevskia* lizards, belonging to two clades – 'caucasica' and 'rudis', have been chosen for the study. These two clades were selected for this study because of their conterminous distribution across the Caucasus and the northeastern Turkey. This is important as it is known that the phenotypic variation may depend on the environmental conditions, such as altitude and climate (Darevsky, 1967). Comparing individuals of different species from the same geographic areas minimizes the influence of the environment. In contrast, the third clade 'saxicola' is found exclusively in the western Greater Caucasus, with its range almost not overlapping with that of the other two clades. (Fig. 1): (1) 'caucasica' clade: *D. mixta* and *D. derjugini* and (2) 'rudis' clade: *D. valentini*, *D. rudis*, *D. portschinskii* and *D. parvula*. Although *D. parvula* is associated with the clade 'rudis', it is genetically quite distant from the rest of the species within this clade (Murphy et al., 2000). We analyzed to what degree shape variation in scalation patterns in the studied species reflect phylogenetic signals. We chose two areas: anal scale and pileus (dorsal head scales structure), as both were used by Darevsky for reconstructing the phylogenetic relationships of *Darevskia* species and both are highly suited for outline analysis. We tested whether scale shape can be linked to sex, and the most important, to what degree it reflects phylogenetic relationships between species and clades.

## 2. Material and methods

### 2.1. Selected species

All species selected for this study are rock dwelling, except for *D. derjugini* (Fig. 2), which is a ground dwelling species. It has a rounder

**Table 1**

Sample sizes in the study.

Species	Anal scale	Pileus
<i>D. portschinskii</i>	27♀25♂	20♀21♂
<i>D. valentini</i>	21♀12♂	20♀14♂
<i>D. rudis</i>	40♀32♂	23♀21♂
<i>D. derjugini</i>	11♀11♂	10♀10♂
<i>D. mixta</i>	14♀16♂	14♀16♂
<i>D. parvula</i>	20♀24♂	17♀19♂

head and body, different from rock dwelling lizards, which have a flattened head and body shape (Murphy et al., 2000; Tarkhnishvili, 2012) (Fig. 2).

### 2.2. Sampling

The distribution range for the species used in this study varies per species. Two species have a wide range: *D. rudis* is found throughout most of the Caucasus and Turkey, and *D. derjugini* inhabits forests throughout the western part of the Caucasus Region. The other species have much narrower ranges: Georgian endemic *D. mixta* is found in the Central Greater Caucasus and Central Lesser Caucasus, *D. parvula* occurs in the Central and Western Lesser Caucasus and black sea mountains in Turkey, *D. valentini* in the Southern Lesser Caucasus and *D. portschinskii* in the Eastern Lesser Caucasus (Tarkhnishvili, 2012). The sampling locations are shown in Fig. 3.

During 2009–2014, the research team of Ilia State University photographed the lizards with capture-release method during the field studies throughout Georgia, using a Canon PowerShot SX510 HS with 30× zoom lens. Digital images of anal and pileus (dorsal side of the head) areas were used in our study. In total, 253 anal scale and 205 pileus images of adult individuals throughout Georgia were analyzed (Table 1, Fig. 3).

### 2.3. Outline analysis

The outlines of the study areas (digitization error, which amounted 5% for both analysis, was checked according to the protocol by Adriaens, 2007 – <http://www.fun-morph.ugent.be/Miscel/Methodology/Morphometrics.pdf>) were traced in Coreldraw Graphics Suite x7 (Corel corporation) (Fig. 4), after which they were subjected to an elliptic Fourier analysis using the Shape Software (Iwata and Ukai, 2002). The software extracts the contour from the outline images as a chain-code, then normalizes size,

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