Article

External morphology and osteology of *Darevskia rudis* (Bedriaga, 1886), with a taxonomic revision of the Pontic and Small-Caucasus populations (Squamata: Lacertidae)

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Abstract

A broad sample of *Darevskia rudis* from the main part of its range was reviewed with regard to external morphology (discriminant, UPGMA, MST and ANOVA analyses) and osteology. *Darevskia bithynica* is raised to species rank, with two subspecies: *D. b. bithynica* and *D. b. tristis*. The other subspecies are fairly similar (*D. r. rudis* being the most different). Two singular populations are described as subspecies: *D. r. mirabilis* **ssp. nov.** from Kaçkar Mountains, geographically adjoins the otherwise different *D. r. bischoffi* and *D. r. bolkardaghica* **ssp. nov.**, which is geographically isolated but that seems to be very closely related to *D. r. obscura*.

Key words: Morphometry, osteology, discriminant analysis, Turkey, *Darevskia*, *D. rudis*, *D. bithynica*, species rank, *mirabilis* **ssp. nov.**, *bolkardaghica* **ssp. nov.**

Introduction

Camerano (1877) first described *Podarcis depressa* Camerano, 1877, an obscure synonymy that included several species, from Trabzon, Turkey and Tiflis, Georgia (in part, *Darevskia rudis*). *Darevskia rudis* (Bedriaga, 1886) was first described as *Lacerta depressa var. rudis* from the samples collected from Batumi. Boettger (1892) described the samples obtained from Batumi and Tbilisi as *Lacerta muralis* var. *depressa f. modesta* Boettger, 1892. Boulenger (1904) interpreted this taxon as *Lacerta muralis* var. *rudis*, an incorrect point of view also adopted by Nikolsky (1905).

Werner (1902) included the samples collected from Uludağ, Turkey in the species *Lacerta depressa*. The researcher also pointed out the significant similarity between these samples and the Tbilisi and Batumi samples studied by Bedriaga (1886). The samples from Uludağ were assigned to *Lacerta muralis* var. *chalybdea* by Boulenger (1904). In the research conducted by Mehely in 1909, the presence of *Lacerta saxicola* [now *D. saxicola* (Eversmann, 1834) sensu lato, hence including several other currently valid *Darevskia* taxa] species, which was first described by Eversmann (1834) and which was not accepted until then since it was interpreted as conspecific with *L. muralis* [now *Podarcis muralis* (Laurenti, 1768)] (Boettger 1892; Boulenger 1904)*,* was pointed out and the *rudis* form was interpreted as a subspecies of *L. saxicola*. Mehely (1909) also indicated that the samples obtained from Amasya and Uludağ were different to the known forms and defined *Lacerta saxicola bithynica* Mehely, 1909. Boulenger (1913a, 1920) combined the subspecies *L. s. bithynica* and *L. s. armeniaca* Mehely, 1909 described by Mehely (1909) and interpreted them as *Lacerta muralis var. chalybdea.* Nikolsky (1913) was also mistaking in

combining Mehely's *armeniaca* and *bithynica* under the name *chalybdea*. Boulenger (1920) considered all the above as varieties of *L. muralis*. Bodenheimer (1944) provided a map showing the distribution zone of *Lacerta rudis* between the provinces of Sinop, Trabzon and Rize, Turkey.

Lantz and Cyren (1936) used new study material (640 specimens) and a direct knowledge of the area to recognize up to 13 different taxa (most treated as subspecies), describing for the first time *Lacerta saxicola obscura* Lantz & Cyren, 1936 (= *D. rudis obscura*), *Lacerta s. tristis* Lantz & Cyren, 1936 (= *D. r. tristis*) and *L. s. mehelyi* Lantz & Cyren, 1936 (= *D. v. lantzicyreni*). This scheme was largely followed in the next decades by multiple authors, who contributed to the delimitation of areas and forms (e.g. Mertens 1952; Darevsky 1965 concerning Turkey). This was followed by the seminal work of Darevsky (1967), who considered *Lacerta rudis* as a species (with the nominal *rudis*, *obscura* and a new subspecies, *macromaculata* Darevsky, 1967 inside it). He did not consider (mainly due to the lack of good comparative material) the pontic subspecies that remained in *Lacerta saxicola* (*tristis* and *bithynica*).

Böhme and Budak (1977) included the populations of *L. rudis* in the east and northeast of Trabzon in the nominal form, but pointed out that the *L. rudis* populations west of Kızılırmak (*L. r. bithynica* and *L. r. tristis*) probably differed from this nominal form. The researchers also interpreted the *L. rudis* samples studied from Arhavi, Kanlıdere Village (Hopa) and Düzhan Village (Borçka), Artvin, Turkey, as a new subspecies named *Lacerta rudis bischoffi* Böhme & Budak, 1977. They regarded the samples obtained from Köprüköy, Çamlıhemşin and around Rize as intergradations with the nominal form. Importantly, the study emphasized that the terra typica of the nominal form is not Batumi as stated by Darevsky (1967), but Trabzon.

Darevsky (1972) evaluated the pholidosis characteristics of the samples belonging to *L. rudis* species obtained from Hopa in detail and concluded that these samples should have been included in the nominal form. Clark and Clark (1973) described the rock lizard forms they obtained from different regions of Anatolia as *L. saxicola* without making any taxonomic differentiation.

Darevsky and Lukina (1977), in their research on rock lizard samples collected by Clark and Clark (1973), stated that these samples were included in 5 different species or subspecies. They also included 43 rock lizard samples collected 40, 45, 50, 55 and 60 km west of Ardahan, 15 km east of Artvin, 20 km west of Borçka (Artvin), and 5 km south of Hopa (Artvin) and Fındıklı and Arsin (Trabzon) in *L. r. rudis*.

Budak and Böhme (1978) determined that *L. r. obscura*, which had been known only from Transcaucasia until then, was present also in Kutul-Ardanuç (Artvin, Turkey). They interpreted the samples of *L. rudis* obtained from Hopa, Kanlıdere Village (Hopa, Artvin, Turkey) and Düzhan Village (Borçka, Artvin, Turkey) as the nominal form, while they interpreted the samples from Çangal (Sinop), Ilgaz Passage, Isırganlık (Kastamonu), Gerede (Bolu) and 15 km south of Kastamonu as *L. r. tristis*.

Darevsky and Eiselt (1980), in a study on the samples of *L. rudis*, defined the subspecies *Lacerta rudis svanetica* Darevsky & Eiselt, 1980. They stated that the new taxon inhabits the southern slopes of the central parts of northeast Georgia and northwest Abkhazia.

Schmidtler *et al.* (1990) interpreted the systematic status of the rock lizard samples they obtained from the subalpine region in the Bolkar Mountains (southern Anatolia) as *Lacerta cf. rudis.* Taurus specimens (Karagöl, Aladağ and Hasan Dağı) have been considered as *D. valentini lantzicyreni* (Darevsky & Eiselt, 1967) (Nilson & Flärdh 1988) or as *D.* cf. *rudis* [assuming an uncertain relationship with *D. valentini* (Boettger, 1892) or *D. rudis*] by Schmidtler *et al.* (1990) and Schmidtler (1998). Eiselt and Darevsky (1991), in their morphological examinations on Chechnya samples of *L. rudis*, concluded that the examined population differed from the previously known taxa and described a new subspecies as *Lacerta rudis chechenica* Eiselt & Darevsky, 1991.

Arribas (1997, 1999) stated that the rock lizard species included in the "*Lacerta saxicola*-group" from the Caucasian and surrounding areas were different from other species of the genus *Lacerta* with respect to certain morphological (pholidosis characters and color-pattern features), osteological, karyological, and behavioral features. He therefore assigned these rock lizard species to a newly erected genus: *Darevskia* Arribas, 1997.

A phylogeny of Caucasian rock lizards (genus *Darevskia*) was inferred using mitochondrial DNA sequences and allozyme data (Murphy *et al.* 2000). Murphy *et al.* (2000) placed all 15 bisexual rock lizard species into 3 major clades: *caucasica*, *saxicola* and *rudis*. According to the results of that study, *D. rudis* was included in the *rudis* clade, together with *D. portschinskii* (Kessler, 1878) *D. valentini* and *D. parvula* (Lantz & Cyren, 1913).

Torsten Panner (http://www.lacerta.de/AS/Species.php?Species=322; Last accessed 18/09/2012) considers the Ovit past populations, living according to his opinion under very different (wet) conditions than other *valentini* (sic!) forms, as of uncertain classification but inside this species. Milto (2010) discussed the specific status of *D. r. tristis* based on morphology (scalation) and ecology (more mesophilic, instead of the sclerophilic habitat of *D. rudis*), arguing for a possible closer relationship with *D. raddei* (Boettger, 1892). Ryabinina *et al.* (2003), in a genetic revision of *D. raddei*, questioned the separation of *bischoffi* and *obscura*, also included in the study. Grechko *et al.* (2007) studied the genetic distance between *D. rudis tristis* (from Adapazarı, Turkey) and *D. r. obscura* (Borjomi, Georgia).

The present study evaluates the samples from the distribution area of the species of *D. rudis* in Anatolia (including northern Anatolia and the Middle Taurus Mountains) in the light of morphological and osteological data. Our results point to taxonomical consequences based on the examination of the geographic variation in the morphological traits of *D. rudis.*

Material and methods

Morphology. A total of 307 male specimens and 273 female specimens of *D. rudis* from Turkey with snout-vent length greater than 50 mm (only adults, in order to avoid allometric shape change), were included in the univariate (ANOVA) and multivariate (Discriminant) analyses.

Specimens were collected from different localities in Turkey (in 2001, 2002, 2009 and 2010). The specimens were incorporated into the collection of ZDEU (Zoology Department of Ege University) and are kept in the Zoology Lab of the Department of Biology at Buca Education Faculty, Buca, İzmir, Turkey.

Given that lacertids exhibit sexual dimorphism (Arribas 1996, 1999; Arribas *et al.* 2006), analyses were carried out for males and females separately.

Samples studied were (see Fig. 1):

Darevskia rudis macromaculata

20 M + 23 F. Between Ardahan and Şavşat, Ardahan, northeastern Anatolia (13-VII-2010), (N 41°13'471"–E 42°27'044").
Darevskia rudis obscura
12 M + 10 F. Kutul Plateau, Ardanuç, Artvin, northeastern Anatolia (14-VII-2010), (N 41°04'333"–E 42°12'361").
22 M + 22 F. Between Geçitli Village and Bilbilen Plateau, Ardanuç, Artvin, northeastern Anatolia (6-VII-2001), (N 41°02'152"–E 42°13'133").
Darevskia rudis bischoffi
4 M + 11 F. Balcılar Village, Borçka, Artvin, northeastern Anatolia (15-VII-2010), (N 41°18'261"–E 41°50'196").
9 M + 7 F. Between Borçka and Hopa 8. km., Artvin, northeastern Anatolia (15-VII-2010), (N 41°22'367"–E 41°33'399").
3 M + 7 F. Between Arhavi and Güneşli Village, 2. km., Artvin, northeastern Anatolia (15-VII-2010), (N 41°18'312"–E 41°19'594").
7 M + 4 F. Between Çamlıhemşin and Ayder Plateau 3. km., Rize, northeastern Anatolia (16-VII-2010), (N 41°02'440"–E 41°01'339").
10 M + 9 F. Hemşin, Rize, northeastern Anatolia (16-VII-2010), (N 41°03'080"–E 40°53'579").
10 M + 7 F. Between İkizdere and İspir, 19. km., Rize, northeastern Anatolia (17-X-2010), (N 40°41'432"–E 40°41'335").
6 M + 3 F. Between Borçka and Camili 10–21. km., Artvin, northeastern Anatolia (7-VII-2001), (N 41°24'154"–E 41°48'168").
8 M + 8 F. Between Borçka and Balcılar, Artvin, northeastern Anatolia (15-VII-2002), (N 40°19'186"–E 41°49'178").
6 M + 7 F. Between Rize and Küçükçayır 18. km., Rize, northeastern Anatolia (14-VII-2002), (N 40°53'758"–E 40°33'832").
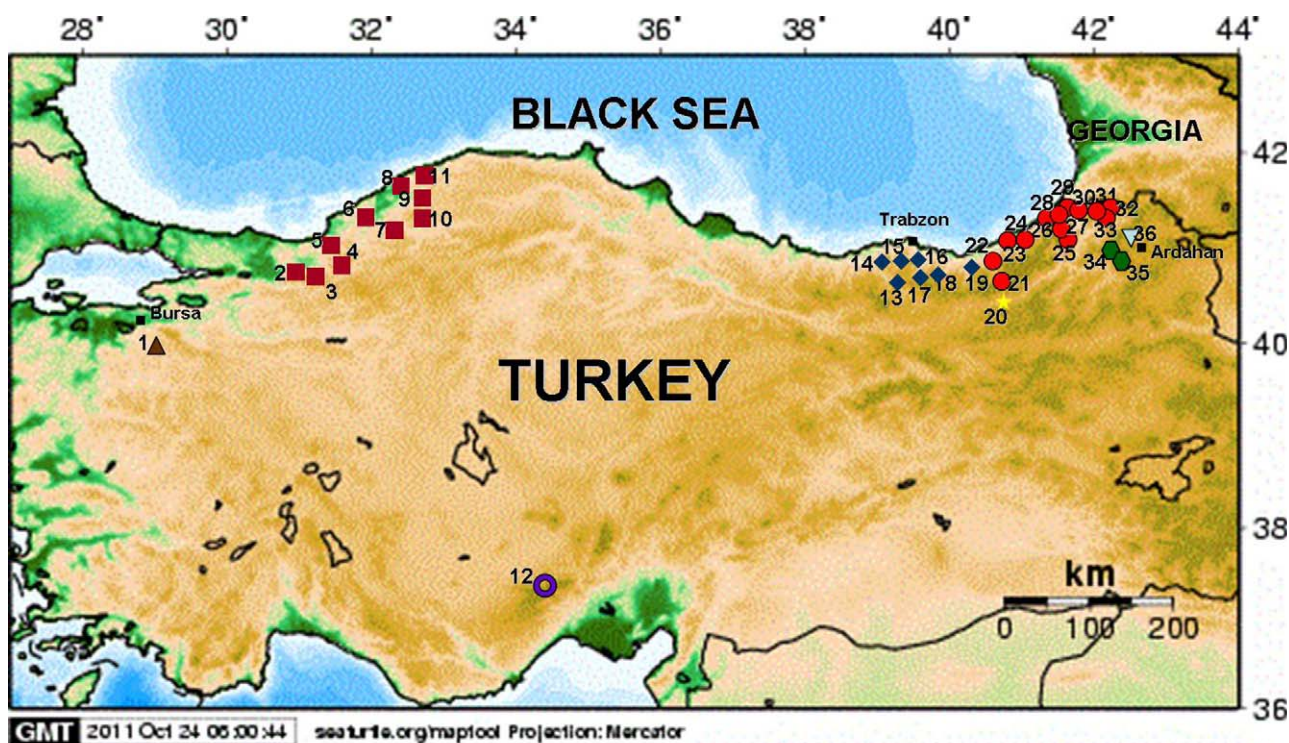
FIGURE 1. Map showing the localities from where specimens have been studied. (Symbol in map, taxon, locality and coordinates North and East). **1. TRIANGLE.** *[D. r. bithynica.* Kirazlı Plateau, Uludağ, Bursa, northwestern Anatolia. (40:06 N, 29:02 E)]. **2.- SQUARES.** *[D. r. tristis.* Güzeldere Village, Düzce, northwestern Anatolia (40:43 N, 31:02 E). **3.** Samandere Waterfall, Düzce, northwestern Anatolia (40:41 N, 31:15 E). **4.** Between Yığılca and Bolu 30. km., Bolu, northwestern Anatolia (40:51 N, 31:33 E). **5.** Between Yığılca and Alaplı 12. km., Zonguldak, northwestern Anatolia (41:02 N, 31:27 E). **6.** Between Zonguldak and Gökçebey 15. km., Zonguldak, northwestern Anatolia (41:24 N, 31:55 E). **7.** Yenice, Karabük, northwestern Anatolia (41:12 N, 32:19 E). **8.** Amasra, Bartın, northwestern Anatolia (41:44 N, 32:23 E). **9.** Ulus, Bartın, northwestern Anatolia (41:35 N, 32:38 E). **10.** Between Safranbolu and Bartın 14. km., Bartın, Northwestern Anatolia (41:21N, 32:42 E). **11.** Kapısuyu, Kurucaşile, Bartın, northwestern Anatolia (41:50 N, 32:44 E)]. **12.- RING.** [*D. r. bolkardaghica* **ssp. nov.** Karagöl, Ulukışla, Niğde, Central Anatolia (37:24 N, 34:33 E)]. **13**. **DIAMOND.** *[D. r. rudis.* Zigana Pass, Trabzon, northeastern Anatolia (40:39 N, 39:24 E). **14.** Between Beşikdüzü and Şalpazarı 7. km., Trabzon, northeastern Anatolia. (40:59 N, 39:12 E). **15.** Between Tonya and Vakfıkebir 10–15. km., Trabzon, northeastern Anatolia. (40:59 N, 39:16 E). **16.** Between Akçaabat and Düzköy 14. km., Trabzon, northeastern Anatolia (40:55N, 39:29 E). **17.** Maçka, Trabzon, northeastern Anatolia (40:49 N, 39:36 E). **18.** Between Sümela and Maçka 10.km., Trabzon, northeastern Anatolia (40:45 N, 39:37 E). **19.** Between Sürmene and Köprübaşı 8. km., Trabzon, northeastern Anatolia (40:51 N, 40:06 E)]. **20. STAR.** [*D. r. mirabilis* **ssp. nov.** Ovit Pass, Rize, northeastern Anatolia (40:37 N, 40:49 E)]. **21. CIRCLE.** *[D. r. bischoffi* Between İkizdere and İspir, 19. km., Rize, northeastern Anatolia (40:41 N, 40:41 E). **22.** Between Rize and Küçükçayır 18. km., Rize, northeastern Anatolia. (40:53 N, 40:33 E). **23.** Hemşin, Rize, northeastern Anatolia (41:03 N, 40:53 E). **24.** Between Çamlıhemşin and Ayder Plateau 3. km., Rize, northeastern Anatolia (41:02 N, 41:01 E). **25.** Between Artvin and Hatila Plateau 35. km., Artvin, northeastern Anatolia (41:07 N, 41:37 E). **26.** Between Arhavi and Güneşli Village, 2. km., Artvin, northeastern Anatolia (41:18 N, 41:19 E). **27.** Between Ortacalar and Dülgerli 16–24. km., Artvin, northeastern Anatolia (41:16 N, 41:24 E). **28.** Esenkıyı Village, Hopa, Artvin, northeastern Anatolia (41:26 N, 41:27 E). **29.** Çamurköy, Sarp, Artvin, northeastern Anatolia (41:29 N, 41:33 E). **30.** Between Borçka and Hopa 8. km., Artvin, northeastern Anatolia (41:22 N, 41:33 E). **31.** Between Borçka and Camili 10–21. km., Artvin, northeastern Anatolia (41:24 N, 41:48 E). **32.** Between Borçka and Balcılar, Artvin, northeastern Anatolia (41:19N, 41:49 E). **33.** Balcılar Village, Borçka, Artvin, northeastern Anatolia. (41:18 N, 41:50 E)]. **34. HEXAGON.** *[D. r. obscura.* Kutul Plateau, Ardanuç, Artvin, northeastern Anatolia (41:04 N, 42:12 E). **35.** Between Geçitli village and Bilbilen Plateau, Artvin, northeastern Anatolia (41:02 N, 42:13 E)]. **36. INVERTED TRIANGLE.** *[D. r. macromaculata.* Between Ardahan and Şavşat, 32. km, Ardahan, northeastern Anatolia (41:13 N, 42:27 E)].

7 M + 9 F. Between Ortacalar and Dülgerli 16–24. km., Artvin, northeastern Anatolia (13-VII-2002), (N 41°16'548''–E 41°24'514'').

1 M + 2 F. Esenkıyı Village, Hopa, Artvin, northeastern Anatolia (7-VII-2001), (N 41°26' 432''–E 41°27'398'').

4 M + 2 F. Çamurköy, Sarp, Artvin, northeastern Anatolia (24-IV-2000), (N 41°29'155''–E 41°33'178'').

5 M + 3 F. Between Artvin and Hatila Plateau 35. km., Artvin, northeastern Anatolia (9-VII-2002), (N 41°07'090"–E 41°37'515").

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9 M + 14 F. Between Sürmene and Köprübaşı 8. km., Trabzon, northeastern Anatolia (17-VII-2010), (N 40°51'021"–E 40°06'373").

16 M + 7 F. Maçka, Trabzon, northeastern Anatolia (18-VII-2010), (N 40°49'186"–E 39°36'559").

13 M + 14 F. Between Akçaabat and Düzköy 14. km., Trabzon, northeastern Anatolia (18-VII-2010), (N 40°55' 250"–E 39°29'236").

10 M + 9 F. Zigana Pass, Trabzon, northeastern Anatolia (10-VII-2003), (N 40°39'854"–E 39°24'888").

16 M + 4 F. Between Sümela and Maçka 10.km., Trabzon, northeastern Anatolia (10-VII-2003), (N 40°45'376"–E 39°37'402").

6 M + 4 F. Between Beşikdüzü and Şalpazarı 7. km., Trabzon, northeastern Anatolia (11-VII-2003), (N 40°59'144"–E 39°12'156").

8 M + 8 F. Between Tonya and Vakfıkebir 10–15. km., Trabzon, northeastern Anatolia (11-VII-2003), (N 40°59'248"–E 39°16'298").

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16 M + 4 F. Kirazlı Plateau, Uludağ, Bursa, northwestern Anatolia (23-VI-2009), (N 40°26'002"–E 29°02'219").

Darevskia rudis tristis

8 M + 8 F. Güzeldere Village, Düzce, northwestern Anatolia (24-VI-2009), (N 40°43'355"–E 31°02'396").

10 M + 13 F. Samandere Waterfall, Düzce, northwestern Anatolia (24-VI-2009), (N 40°41'847"–E 31°15'344").

3 M + 3 F. Between Yığılca and Bolu 30. km., Bolu, northwestern Anatolia (27-VI-2009), (N 40°51'455"–E 31°33'771").

8 M + 3 F. Between Yığılca and Alaplı 12. km., Bolu, northwestern Anatolia (27-VI-2009), N 41°02'129"–E 31°27'684").

9 M + 10 F. Between Zonguldak and Gökçebey 15. km., Zonguldak, northwestern Anatolia (28-VI-2009), (N 41°24'777"–E 31°55'481").

4 M + 4 F. Yenice, Karabük, northwestern Anatolia (28-VI-2009), (N 41°12'128"–E 32°19'163").

6 M + 2 F. Between Safranbolu and Bartın 14. km., Bartın, northwestern Anatolia (29-VI-2009), (N 41°21"420"–E 32°12'487").

2 M + 3 F. Ulus, Bartın, northwestern Anatolia (29-VI-2009), (N 41°35'415'–E 32°38'579").

3 M + 4 F. Amasra, Bartın, northwestern Anatolia (29-VI-2009), (N 41°44'577"–E 32°23'309").

8 M + 4 F. Kapısuyu, Kurucaşile, Bartın, northwestern Anatolia (30-VI-2009), (N 41°50'597"–E 32°44'378").

Darevskia "cf. *valentini"*. *D. v. lantzicyreni* (partim, sensu Darevsky, 1967).

13 M + 9 F. Ovit Pass, Trabzon, northeastern Anatolia (06-IX-2002), (N 40°37'158"–E 40°49'144").

Darevskia "cf. *rudis*" (sensu Schmidtler, Eiselt & Sigg, 1990; Schmidtler, 1998; Panner, 2000).

6 M + 5 F. Karagöl, Ulukışla, Niğde, central Anatolia (19-VII-2009), (N 37°24'378"–E 34°33'356").

Characters studied

Biometric characters: The following measurements were taken from specimens: a) Snout-vent length (SVL—Tip of snout to anal cleft); b) Pileus width (PW—At the widest point between the parietal plates); c) Pileus length (PL—Tip of snout to posterior margins of parietals); d) Head width (HW—At the widest point of head, from cheek to cheek); e) Head length (HL—Tip of snout to posterior margin of ear opening); f) Forelimb length (FLL—Shoulder joint to tip of toe); g) Hindlimb length (HLL—Pelvic joint to tip of toe); h) Anal wide (AW) and i) Anal length (AL). All linear measurements were made with a digital caliper (precision 0.02) to the nearest 0.01 mm. These measurements were transformed to the following more informative and not dimensional-dependent ratios: A) FLL/SVL (relative forelimb length; "FLL index"); B) HLL/SVL (relative hind limb length, "HLL index"); C) PL/PW (pileus shape, "Pileus index"); D) HL/HW (relative head length; "head index"); E) AL/AW (anal plate surface, "Anal shape"index) and AS/SVL ($\sqrt{(AL*AW)}*100/SVL$, relative anal plate size with respect to the total length, "Anal size" index) (see Arribas 1996, 2001).

Scalation characters: These characters were taken from the studied specimens: 1) Supraciliar granules (right-left); 2) Supraciliar plates (right-left); 3) Supralabial plates (right-left); 4) Sublabial plates (right-left); 5) Collar scales; 6) Gular scales; 7) Supratemporal scales (right-left); 8) Ventral plates (transversal); 9) Ventral plates (longitudinal); 10) Preanal-1 (enlarged preanals before anal plate); 11) Preanal 2 (circumanal scales, entire semicircle of preanals); 12) Femoral pores (right-left); 13) Scales between femoral pores and outer plates_left; 14) Subdigital lamellae (right-left); 15) Tibial scales_left; 16) Dorsal scales; 17) Temporal scales-1 (temporals between masseteric and tympanic plates) (left-right); 18) Temporal scales-2 (Temporals in the shortest row between 1st supratemporal and masseteric plates) (left-right); 19) Supralabial plates (right-left).

Some of these variables were almost invariable, were extremely correlated, or even duplicated (as bilateral characters) and gave singular matrixes during calculations of CDA, being progressively deleted from the posterior analyses (bilateral characters were added in a single value, and correlated and invariant ones deleted after a SIMPER analysis for detecting these problems). This analysis breaks down the contribution of each species (or other variable) to the observed similarity (or dissimilarity) between samples. It allows to identify the samples and variables that are most important in creating the observed pattern of similarity using the Bray-Curtis measure (Henderson & Seaby 2007).

Characters used in the final CDA analyses were (numbers and letters identify them in the original dataset): 1) Supraciliaria: Supraciliar granules (right+left); 5) Collaria: scales in the collar; 6) Gularia: Gular scales; 8) Ventralia: Longitudinal rows of ventral plates; 12) Femoralia: Femoral pores (right+left); 14) Lamellae: Subdigital lamellae (right-left); 16) Dorsalia: Number of dorsal scales in a row across middle body. a) FLL/SVL (relative forelimb length; "FLL or forelimb index"); b) HLL/SVL (relative hind limb length, "HLL or hindlimb index"); c) PL/PW (pileus shape, "Pileus index"); d) HL/HW (relative head length; "head index"); e) AL/AW (anal plate surface, "Anal form index") and AS/SVL ($\sqrt{(AL*AW)}*100$/SVL, relative anal plate size with respect to the total length, "Anal size index").

Transformation of the data: Data were transformed [(log (x+1)] for measurement and scalation characters, and arcsine SqRoot for indexes.

Statistical Procedures: Statistical analyses used in the morphological study included both Univariate (ANOVA for SVL, scalation characters and biometric indexes, with *post-hoc* Tukey-Kramer tests at $P < 0.05$ and $P < 0.01$ to detect differences among samples) as well as Multivariate techniques (Canonical Discriminant Analysis, CDA). Chi-square and Wilks' Lambda were used to test the significance of each axis of the CDA. If the groups have different scores, then the models discriminating between the groups and axes are significative. Bartlett's Sphericity Tests prove if the variables are uncorrelated, a prerequisite for a successful discriminant analysis (Sokal & Rohlf 1969; Blackiht & 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 their position in the multidimensional space. The most connected samples can be interpreted as the "central ones" of the species and, in theory, the most primitive. In contrast, UPGMA trees also show the global relationships among the samples.

To test the significance of the differences among pre-established groups (the different *D. rudis* subspecies) we conducted an Analysis of Similarity (ANOSIM) (Clarke 1988) that tests whether the assigned groups are meaningful, that is, more similar within groups than with samples from different groups (see more details in Arribas 2010). To check for significance, resampling tests (1000 randomizations) were run to test whether the given results can 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. Even more important, pair-wise tests among populations allow to test the significance of the differences among the concerned groups and to detect which ones are really different from the others.

Multivariate (CDA, SIMPER and ANOSIM) analyses were performed with Community Analysis Package 4.0© (Henderson & Seaby 2007). MST and UPGMA trees were calculated with NTSYS 2.1© (Rohlf 2000). Univariate statistics were processed with NCSS 2001© package (Hintze 2001).

Osteological study: Previously fixed and alcohol preserved specimens were cleared by means of 1 % KOH in deionized water, and bones stained with alizarin red, being posterior differentiated and pigment excess eliminated with Mall solution (80% of the previous clearing solution plus 20% glycerol) during several months, and preserved

permanently in glycerol following procedures by Taylor (1967) and Durfort (1978). Osteological nomenclature follows Arribas (1998).

Four to six specimens from every studied population and for both sexes were studied, when possible. Moreover, four *D. r. chechenica* from Khvarshi (Daghestan, Russia), six extra *D. r. obscura* (Achaldaba, Georgia), a pair of *D. valentini valentini* (Mt. Legli and Aragatz, Armenia) and *D. valentini* cf. *lantzicyreni* (Yukarı Narlıca, Turkey) studied in Arribas (1998) were also included in the comparisons.

Results

External morphology

Canonical Discriminant Analysis. In the male analysis (Fig. 2a), the first two dimensions were meaningful (Eigenvalue > 1). The main part of the variability was concentrated in the first axis (Eigenvalue of 8.39 and 69.12% of variance explained; Canonical Correlation 0.94), whereas the second one had less importance (Eigenvalue 2.65 and 21.8 % of variance explained; Canonical Correlation 0.85).

Both axes were significant (first axis: Chi-sq. $_{91}$ = 1305.16; P < 0.001; second axis: Chi sq. $_{72}$ = 646.4; P < 0.001) and separate the Turkish *D. rudis* into two very different groups. There were very significant differences among centroids (Wilks' Lambda = 0.0118039; F = 20.44, 91 d.f., P < 0.001; Bartlett's Test = 1307.38, 91 d.f. P < 0.001) and the axes explained together 90 % of the total intersample variability.

The first axis separated *D. r. bithynica* and *D. r. tristis* in their positive part from the remaining *D. rudis* ssp., which were in the negative part. The two aforementioned taxa were characterized by (standardized coefficients within parentheses) greater values for the Head Index (0.92) and Dorsalia (0.42), and lower values for the Supraciliaria (0.19), Anal Size Index (0.16) and Ventralia (0.13). Also, these two taxa had lower scores for Anal Shape Index (-0.14) and Femoralia (-0.11).

The second axis separated the nominate *D. r. rudis* in their positive part from the other subspecies of the main group, the latter largely overlapping among themselves. *Darevskia r. rudis* was characterized by higher Dorsalia (0.94) and Anal Size Index (0.1), and lower Head Index (-0.38), Femoralia (-0.33), Collaria (-0.15) and Forelimb Index (-0.11). In contrast, this axis did not differentiate between *D. r. bithynica* and *D. r. tristis*.

Fig. 2a shows the presence of completely different groups: *D. r. bithynica* and *D. r. tristis* on one side, and the remaining samples on the other side. In the first group, the results do not enable discrimination between *D. r. bithynica* and *D. r. tristis*. In the second group, nominotypical *D. r. rudis* is different and almost without overlap with the remaining samples, which form a completely overlapping group (including Ovit and Karagöl samples).

The female analysis (Fig 2b) totally paralleled that of the males. As in the males, only the first two dimensions were meaningful (Eigenvalues > 1) and most of the variability was concentrated in the first axis (Eigenvalue of 11.48 and 74.5% of variance explained; Canonical Correlation 0.96). The second axis was of limited importance (Eigenvalue 2.82 and 18.3 % of variance explained; Canonical Correlation 0.86).

Both axes together were significant (first axis: Chi-sq. $_{91}$ = 1211.16; P < 0.001; second axis: Chi sq. $_{72}$ = 572.45; P < 0.001) and, as in the male analysis, separated two very different groups. There were very significant differences among centroids (Wilks' Lambda = 0.00833568; F = 19.49, 91 d.f., P < 0.001; Bartlett's Test = 1213.56, 91 d.f., P < 0.001) and explained 92.8 % of the total variability.

The first axis separated *D. r. bithynica* and *D. r. tristis* in their positive part, with respect to the remaining *D. rudis* ssp., which remained in the negative part. The two aforementioned taxa were characterized by a higher Head Index (0.94), Dorsalia (0.22) and Anal Size Index (0.11).

The second axis separated the nominate *D. rudis rudis* in their positive part, with very limited overlap with the other subspecies of the main group, which overlapped extensively among themselves. *Darevskia r. rudis* was characterized by higher Dorsalia (0.98) and lower Head Index (-0.32), Femoralia (-0.29) and Collaria (-0.10). This axis, however, did not differentiate *D. r. bithynica* and *D. r. tristis*. *Darevskia r. macromaculata, D. r. obscura* and *D. r. bischoffi* also largely overlapped in this axis, as did the Karagöl and Ovit samples.

Fig. 2b shows that the results did not totally parallel those obtained with males, with *D. r. bithynica* and *D. r. tristis* being indistinguishable but completely different from the remaining samples. Among the latter, nominotypical *D. r. rudis* were different from the remaining ones, which were completely overlapping among themselves (including Ovit and Karagöl).
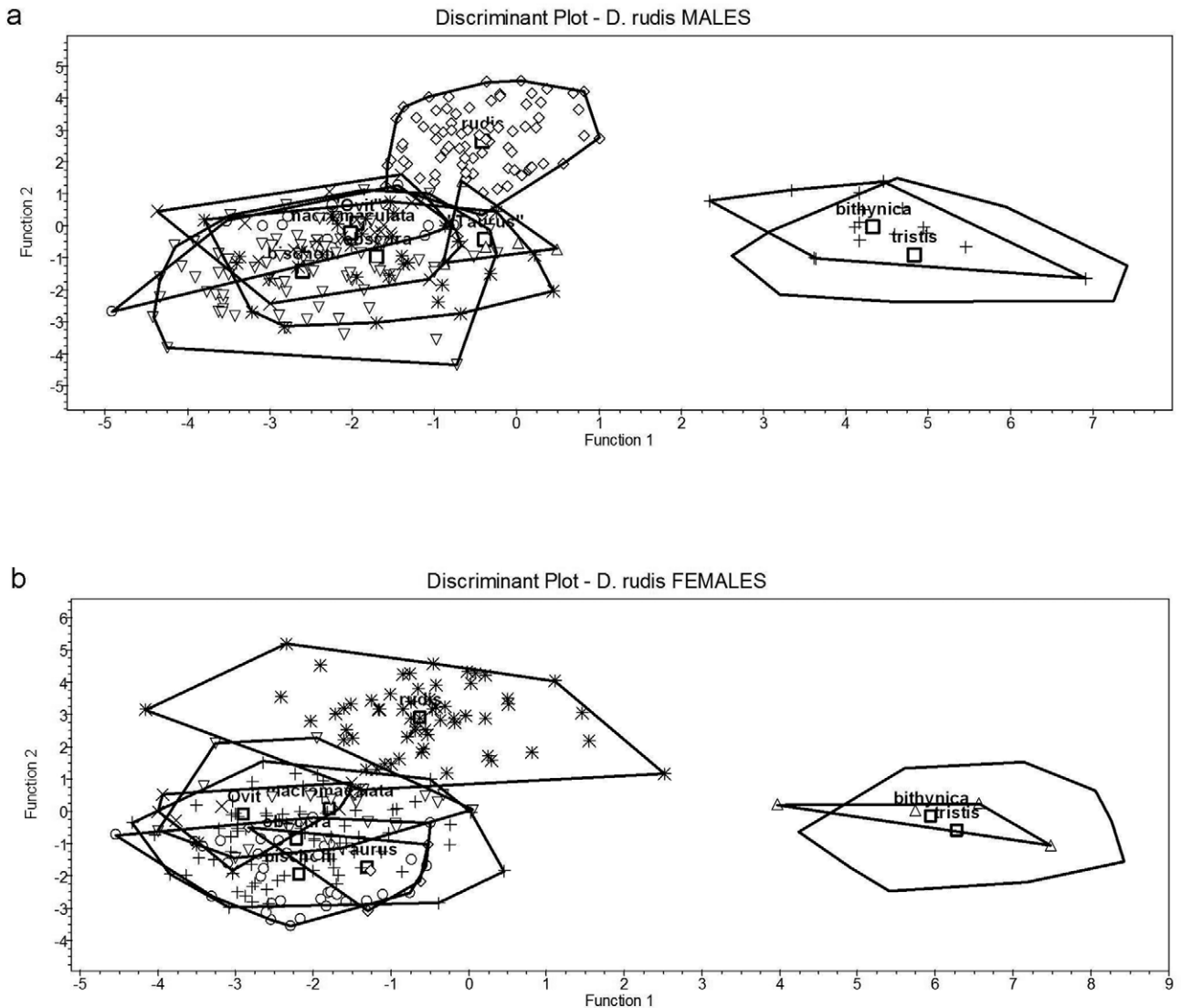
a

b

FIGURE 2. Canonical Discriminant Analysis (CDA) plots for a. males (above) and b. females (below). Specimens, sample centroids and group perimeters are represented. For details, percentage of variance explained, etc. see text.

Analysis of Similarity (ANOSIM). The results of the intersample comparisons are given in Table 1 (males above diagonal, females below).

The ANOSIM of the male data showed a fairly good group assignation: the test value is positive and relatively high (R-statistic = 0.523343, $P < 0.001$; 1000 randomizations). Most of the samples differed from one another, thus warranting differences and underlining taxonomic validity. The ANOSIM of the female data showed a fairly good results too, although slightly less significant than in males (R-statistic = 0.474412, $P < 0.001$; 1000 randomizations).

From the pairwise comparison analyses, *D. r. bischoffi* differed from all the other samples in both sexes. *Darevskia r. bithynica* differed from all the other samples except from *D. r. tristis* (both in males and females) (the lack of difference to *D. r. rudis* females probably reflected the small *D. r. bithynica* female samples). *Darevskia r. macromaculata* was not different from *D. r. obscura* specimens (both sexes) and the small Taurus samples (males). All three were fairly similar, particularly *obscura* and *macromaculata*. *Darevskia r. obscura* did not differ from *D. r. macromaculata* and Taurus specimens in both sexes. Nominotypical *D. r. rudis* were different from all the other samples (not from the very small sample of *D. r. bithynica*, which is certainly an artifact). *Darevskia r. tristis* differed from all the samples, except from *D. r. bithynica*, with which it was largely equivalent. Ovit-pass

specimens were different from all the other samples, both in males and females (females did not differ from Taurus ones, but the latter sample size was very small). Taurus (Karagöl) specimens were not different from *D. r. obscura* (both sexes) and *D. r. macromaculata* (only in males, but the female samples consisted of only 5 specimens), and from Ovit (females).

Dendrograms (UPGMA and MST trees). Mahalanobis distance matrices for males and females are given in Table 2 (males above, females below diagonal). These distances were grouped by the UPGMA method and the resulting dendrograms represented in Figure 3a–b. Corresponding to the CDA representation, in the male dendrogram *D. r. bithynica* and *D. r. tristis* were very different from the other studied samples. From these latter, *D. r. macromaculata*, *D. r. obscura* and *D. r. bischoffi* were very similar; slightly more differentiated were "Taurus", "Ovit" and the nominotypical *D. r. rudis,* the latter being the most different. In females, the result was exactly the same. Both matrices of relationships were totally parallel (cophenetic correlation coefficient among male and female distance matrices: r = 0.98).
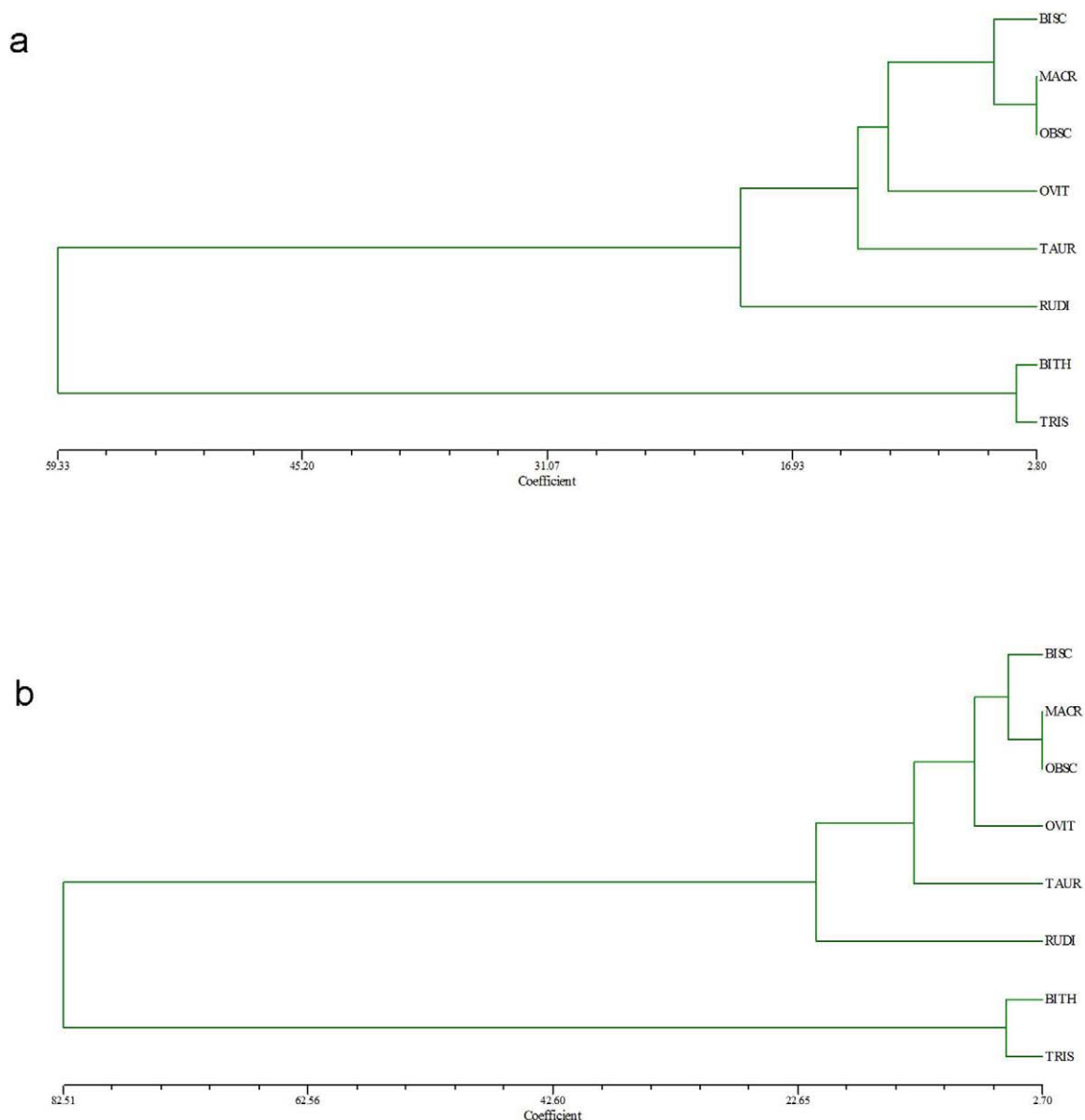

FIGURE 3. UPGMA trees derived from Mahalanobis' distances among sample centroids. See text for interpretation. a. Males. b. Females.

TABLE 1. ANOSIM. Analysis of Similarity (ANOSIM) results (with 1000 randomizations). Males above diagonal and females below. The number above is the R-statistic pairwise comparation, 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 in bold).

MALES FEMALES	Ovit Pass Kaçkar Mts.	Karagöl Taurus Mts.	D. rudis bischoffi	D. rudis bithynica	D. rudis macromaculata	D.rudis obscura	D. rudis rudis	D. rudis tristis
Ovit Pass Kaçkar Mts.	--	**0.34**	**0.52**	**0.87**	**0.23**	**0.27**	**0.91**	**0.71**
	--	0.007	0.001	0.001	0.003	0.001	0.001	0.001
Karagöl Taurus Mts.	0.15	--	**0.34**	**0.87**	0.05	-0.008	**0.82**	**0.48**
	0.133	--	0.004	0.001	0.302	0.485	0.001	0.001
D. rudis bischoffi	**0.53**	**0.34**	--	**0.59**	**0.13**	**0.21**	**0.77**	**0.57**
	0.01	0.017	--	0.001	0.012	0.001	0.001	0.001
D. rudis bithynica	**0.75**	**1**	**0.76**	--	**0.57**	**0.7**	**0.19**	0.001
	0.001	0.008	0.001	--	0.001	0.001	0.007	0.422
D. rudis macromaculata	**0.33**	**0.32**	**0.29**	**0.50**	--	0.04	**0.65**	**0.46**
	0.002	0.021	0.001	0.006	--	0.175	0.001	0.001
D.rudis obscura	**0.29**	0.04	**0.09**	**0.50**	-0.05	--	**0.81**	**0.56**
	0.001	0.335	0.012	0.001	0.84	--	0.001	0.001
D. rudis rudis	**0.87**	**0.93**	**0.90**	0.06	**0.65**	**0.66**	--	**0.41**
	0.001	0.001	0.001	0.32	0.001	0.001	--	0.001
D. rudis tristis	**0.77**	**0.87**	**0.81**	-0.13	**0.46**	**0.50**	**0.27**	--
	0.001	0.001	0.001	0.841	0.001	0.001	0.001	--

TABLE 2. Mahalanobis' distances among samples. Males above and females below diagonal. Samples are ordered alphabetically. BISC—*D. r. bischoffi*, BITH—*D. r. bithynica*, TAUR—Taurus sample (*D. r. bolkardaghica* **ssp. nov**.), OVIT—Ovit pass sample (*D. r. mirabilis* **ssp. nov**.), MACR—*D. r. macromaculata*, OBSC—*D. r. obscura*, RUDI—*D. r. rudis*, TRIS—*D. r. tristis*.

F\M	BISC	BITH	MACR	OBSC	OVIT	RUDI	TAUR	TRIS
BISC	.000	60.9	4.36	6.15	16.0	22.4	18.6	72.5
BITH	90.3	.000	53.1	53.8	69.2	42.2	43.7	3.95
MACR	4.73	79.0	.000	2.80	4.98	13.3	12.9	65.3
OBSC	6.11	74.9	2.70	.000	7.77	18.7	6.92	61.2
OVIT	11.8	103.0	8.05	10.1	.000	24.3	16.3	81.4
RUDI	23.6	65.9	12.1	16.7	22.4	.000	31.0	58.7
TAUR	16.4	74.2	10.0	5.90	18.0	20.8	.000	50.0
TRIS	92.5	5.61	79.5	77.8	102.0	73.0	78.0	.000

The MST tree in males (not represented) showed *D. r. macromaculata* being the most connected sample (to four of the other samples), with small distances to *D. r. obscura* (2.80) and *D. r. bischoffi* (4.36)—all three seemed very closely related—and slightly greater distances to "Ovit" (8.05) and to *D. r. rudis* (13.30). Taurus males seemed more related to *D. r. obscura* (5.90). *Darevskia r. bithynica* and *D. r. tristis* were very different from the other samples (distance of 42.40 to nominal *rudis*), but very close (the closest samples) to each other (3.95).

The female MST is totally parallel to that of the males. *Darevskia r. macromaculata* was also the most connected sample (to four of the other samples), with small distances to *D. r. obscura* (2.70), to *D. r. bischoffi* (4.73) and to "Ovit-pass" (4.98), all of which were closely related, and greater distance to *D. r. rudis* (12.10). The "Taurus" sample found its closest relative in *D. r. obscura* (6.92). *Darevskia r. bithynica* and *D. r. tristis* were also very different from the other samples (65.90 to their closest sample, *D. r. rudis*), but were very similar to each other (5.61).

Relationship between morphologic differentiation and geographic distances. Both male and female distance matrices were related in general to their geographic distances. In males there was a significant correlation (= normalized Mantel statistic Z) of r = 0.67361 (Approximate Mantel t-test: t = 3.1349; Prob. random Z < obs. Z: p = 0.9991; out of 10000 random permutations: 9814 were < Z, 0 were = Z, and 186 > Z). The female matrix also had a significant correlation of r = 0.71709 (Approximate Mantel t-test: t = 3.3067; Prob. random Z < obs. Z: p = 0.9995; out of 10000 random permutations: 9889 were < Z, 0 were = Z, and 111 > Z). The conspicuous differences were the high differences compared to their geographical distance in *D. r. bithynica* and *D. r. tristis* and the comparatively small difference of Taurus specimens in reference to their great separation from other known *D. rudis*. In some cases, the difference was comparatively striking (although moderate) considering the almost null geographical separation (for example between the Ovit-pass sample and *D. r. bischoffi*).

ANOVA. Descriptive statistics of each sample are given in Table 3-A (males) and 4-A (females). Analysis of variance results and pairwise comparisons are also separated by sexes in Table 3-B (males) and 4-B (females).

The number of pairwise significant differences (*P* < 0.01) among the samples was graphically expressed (for both sexes together, as a distance or difference degree) in Fig. 4. Clearly, the most different group was formed by *D. r. bithynica* and *D. r. tristis*, which accumulate the greatest number of differences to the remaining samples, which in turn are fairly similar.

Of the remaining samples, *D. r. bischoffi* was the most different, mainly due to its large size compared to the other populations (this difference was not expressed in UPGMA trees derived from CDA analyses, as SVL was not included in them); also fairly different was the nominotypical *D. r. rudis*. The remaining samples clustered together with scarce differences. *Darevskia r. macromaculata* had only one highly significant (and also two significant, *P* < 0.05) differences from Ovit-pass specimens. *Darevskia r. obscura* was somewhat more different, and even more so the Taurus (Karagöl) specimens. Apart from the increase of the *D. r. bischoffi* difference due to the inclusion of SVL in the ANOVA, all the dendrograms were fairly parallel and largely equivalent in the different approaches.

TABLE 3A. Descriptive statistics of each sample. a. (males) and b. (females). Mean, standard error, minimum and maximum scores from morphometric, scalation and biometrical indexes. See Material and Methods text for abbreviations of characters and indexes used in the morphometric analysis.

MALES	bithynica (n = 16)	tristis (n = 61)	rudis (n = 78)	bischoffi (n = 79)	obscura (n = 34)	macromaculata (n = 20)	mirabilis ssp. nov. Ovit pass (n = 13)	bolkardaghica ssp. nov. Karagöl (n = 6)
	1	2	3	4	5	6	7	8
SUPRACILIARIA	11.56±0.40	11.80±0.21	10.85±0.15	10.78±0.25	10.38±0.32	10.15±0.36	7.53±0.7	10.00±0.57
Supraciliar granulae	9-15	5-15	7-14	4-14	5-13	6-12	4-12	8.12
COLLARIA	8.56±0.18	8.55±0.14	9.26±0.09	9.35±0.10	9.61±0.17	9.45±0.28	9.61±0.44	9.33±0.21
Collar scales	7-10	6-11	7-12	7-11	8-11	6-11	7-11	9-10
GULARIA	27.00±0.42	26.36±0.26	28.96±0.20	26.8±0.29	25.79±0.43	26.05±0.53	23.84±0.46	26.50±0.22
Gular scales	24-32	19-31	24-35	21-33	21-31	21-30	25-26	26-27
VENTRALIA	23.56±0.28	23.55±0.14	23.02±0.09	22.98±0.12	23.82±0.26	23.85±0.24	24.84±0.33	25.00±0.63
Ventral scales	21-26	20-26	22-25	20-25	21-27	22-26	23-27	23-27
PREANALIA	1.25±0.11	1.31±0.07	1.21±0.05	1.17±0.04	1.02±0.03	1.05±0.05	1.23±0.12	2.00±0.00
Preanal plates	1-2	1-3	1-3	1-3	1-2	1-2	1-2	2-2
CIRCUMANALIA	7.00±0.13	7.08±0.11	6.9±0.1	6.62±0.11	6.61±0.15	7.80±0.21	8.20±0.36	7.66±0.21
Circumanal scales	6-8	5-9	5-9	4-8	5-8	6-9	6-10	7-8
FEMORALIA	20.37±0.44	19.21±0.21	19.42±0.17	20.70±0.19	18.5±0.24	19.10±0.36	17.79±0.23	19.30±0.42
Femoral scales	17-24	15-23	15-24	17-26	15-21	17-23	17-19	18-21
LAMELLAE	26.68±0.25	25.77±0.16	26.55±0.16	26.70±0.21	24.2±0.20	25.55±0.37	24.76±0.32	22.16±0.4
Subdigital lamellae	25-29	23-28	23-29	23-32	22-27	23-29	23-27	21-23
DORSALIA	54.46±0.52	51.85±0.36	56.61±0.38	44.15±0.32	44.94±0.49	46.55±0.64	46.00±0.83	47.66±0.84
Dorsal scales	49-57	46-58	48-65	38-52	38-50	41-51	38-50	45-51
SVL	64.68±0.66	63.52±0.46	65.9±0.40	74.26±0.80	64.42±1.01	63.38±1.23	61.13±1.55	63.70±1.28
Snout-vent lengt	60.50-68.56	52.3-72.84	59.1-75.5	54.4-88.54	50.6-74.3	54.9-75	50.5-70.3	59.6-68.2
PL/PW	2.08±0.017	2.13±0.013	1.93±0.007	1.97±0.014	1.95±0.017	1.95±0.031	1.82±0.022	1.99±0.04
Pileus index	2.00-2.25	1.83-2.52	1.78-2.06	1.73-2.29	1.78-2.28	1.75-2.26	1.68-1.95	1.88-2.12
HL/HW	2.27±0.033	2.38±0.05	1.72±0.007	1.69±0.009	1.73±0.017	1.68±0.016	1.64±0.019	1.82±0.022
Head index	2.02-2.65	2.13-2.71	1.60-1.98	1.53-1.99	1.57-1.91	1.49-1.80	1.53-1.75	1.73-1.88
FLL/SVL	0.338±0.004	0.351±0.02	0.343±0.002	0.347±0.003	0.331±0.004	0.336±0.002	0.332±0.011	0.319±0.011
Forelimb index	0.289-0.360	0.293-0.38	0.292-0.383	0.268-0.470	0.277-0.367	0.315-0.360	0.288-0.443	0.292-0.356
HLL/SVL	0.536±0.007	0.541±0.004	0.524±0.003	0.537±0.005	0.501±0.006	0.522±0.006	0.478±0.015	0.486±0.020
Hindlimb index	0.449-0.585	0.443-0.590	0.426-0.582	0.403-0.73	0.417-0.554	0.462-0.555	0.402-0.604	0.413-0.555
AL/AW	0.438±0.008	0.468±0.007	0.498±0.007	0.495±0.007	0.533±0.016	0.530±0.014	0.471±0.021	0.551±0.017
Anal shape	0.391-0.536	0.204-0.6	0.360-0.734	0.326-0.760	0.385-0.699	0.429-0.663	0.317-0.563	0.504-0.614
AS/SVL	5.235±0.07	5.166±0.05	5.025±0.05	4.917±0.05	4.867±0.07	5.247±0.09	5.403±0.18	4.92±0.113
Anal size	4.815-6.072	4.33-6.70	4.035-6.072	3.884-5.969	3.689-5.936	4.578-6.218	4.039-6.368	4.617-5.466

TABLE 3B. Descriptive statistics of each sample. a. (males) and b. (females). Mean, standard error, minimum and maximum scores from morphometric, scalation and biometrical indexes. See Material and Methods text for abbreviations of characters and indexes used in the morphometric analysis.

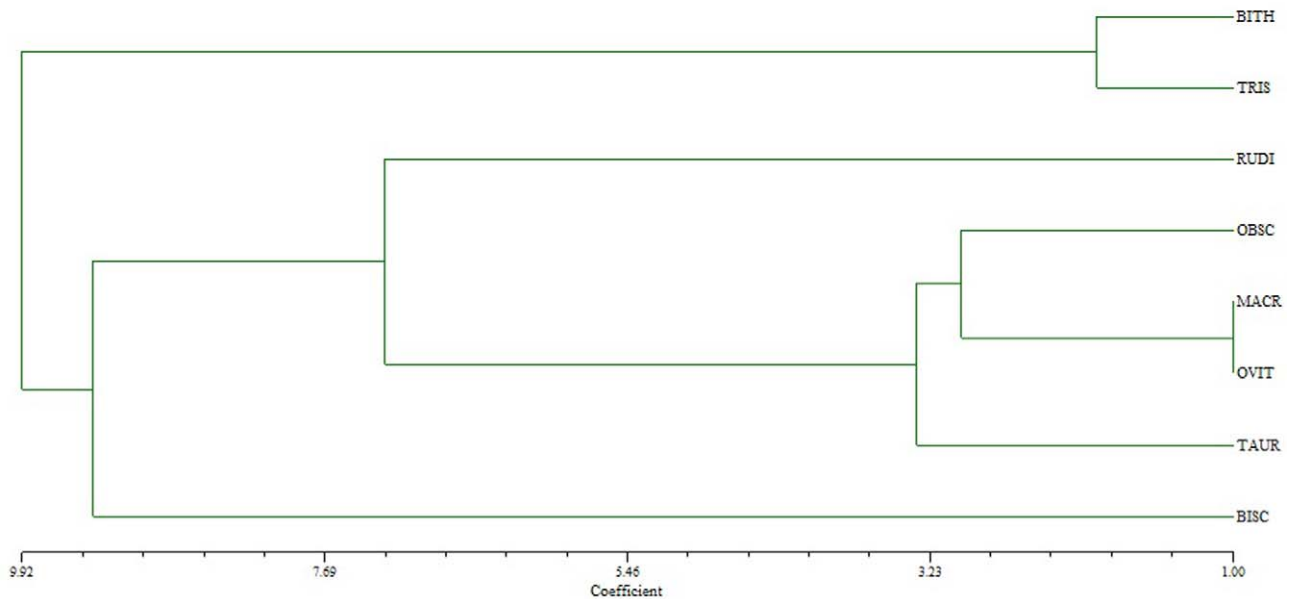| FEMALES	bithynica (n = 4)	tristis (n = 54)	rudis (n = 60)	bischoffi (n = 79)	obscura (n = 32)	macromaculata (n = 23)	mirabilis ssp. nov. Ovit pass (n = 9)	bolkardaghica ssp. nov. Karagöl (n = 5)
	1	2	3	4	5	6	7	8
SUPRACILIARIA	12.25±0.25	11.57±0.24	10.96±0.15	10.83±0.28	10.65±0.31	10.39±0.46	8.66±0.6	9.40±0.67
Supraciliar granulae	12-13	5-16	8-15	2-14	5-14	4-14	6-12	7-11
COLLARIA	9.00±0.40	8.70±0.12	9.3±0.14	9.20±0.10	9.46±0.21	9.65±0.16	10.11±0.42	9.60±0.24
Collar scales	8-10	6-10	6-11	7-11	7-13	8-11	8-12	9-10
GULARIA	27.00±0.40	26.75±0.24	28.46±0.26	26.78±0.29	25.96±0.37	26.04±0.43	23.44±0.37	25.60±0.67
Gular scales	26-28	23-31	25-34	21-33	22-31	21-30	22-26	23-27
VENTRALIA	26.50±0.28	26.03±0.15	25.48±0.12	25.06±0.13	26.28±0.20	25.17±0.18	25.55±0.69	25.60±0.24
Ventral scales	26-27	23-29	23-28	21-27	24-28	24-27	21-27	25-26
PREANALIA	1.00±0.00	1.44±0.08	1.41±0.06	1.29±0.05	1.15±0.08	1.04±0.04	1.33±0.16	1.60±0.24
Preanal plates	1-1	1-3	1-2	1-3	1-3	1-2	1-2	1-2
CIRCUMANALIA	7.00±0.40	7.46±0.10	7.16±0.11	7.16±0.11	6.90±0.17	7.95±0.22	7.00±0.44	7.20±0.20
Circumanal scales	6-8	6-10	5-9	5-9	5-9	6-10	5-9	7-8
FEMORALIA	20.00±0.57	18.37±0.16	18.66±0.17	19.73±0.19	18.06±0.27	18.00±0.47	18.11±0.56	18.40±0.67
Femoral scales	19-21	15-21	15-22	16-24	16-22	10-21	16-20	17-20
LAMELLAE	25.00±0.00	25.8±0.19	25.80±0.19	26.21±0.16	24.15±0.29	25.60±0.26	24.33±0.60	21.40±0.60
Subdigital lamellae	25-25	22-29	23-29	23-30	22-28	23-27	22-27	20-23
DORSALIA	53.50±0.95	51.40±0.40	55.01±0.40	42.68±0.31	44.40±0.46	46.04±0.42	45.33±0.98	42.80±0.58
Dorsal scales	52-56	46-58	48-62	38-50	40-51	42-51	40-50	41-44
SVL	61.35±1.34	62.64±0.7	61.94±0.58	72.12±0.86	65.84±0.72	64.49±1.15	64.12±1.16	64.33±1.63
Snout-vent lengt	57.94-64.48	50.94-73.42	51.76-73.56	51.40-89.16	57.66-73.68	52.62-74.78	61.06-70.84	59.34-68.44
PL/PW	2.21±0.02	2.07±0.01	1.96±0.01	1.95±0.02	1.94±0.02	1.91±0.02	1.81±0.02	1.97±0.03
Pileus index	2.16-2.26	1.81-2.30	1.81-2.19	1.76-2.22	1.71-2.18	1.73-2.10	1.71-1.89	1.90-2.08
HL/HW	2.49±0.07	2.53±0.01	1.77±0.01	1.71±0.008	1.74±0.01	1.73±0.02	1.64±0.02	1.810±0.08
Head index	2.33-2.68	2.27-2.80	1.50-2.12	1.54-1.91	1.57-1.95	1.58-1.88	1.56-1.73	1.67-1.88
FLL/SVL	0.315±0.007	0.303±0.002	0.309±0.003	0.322±0.002	0.300±0.004	0.310±0.004	0.306±0.003	0.294±0.006
Forelimb index	0.296-0.333	0.271-0.336	0.230-0.373	0.248-0.443	0.208-0.341	0.281-0.353	0.288-0.322	0.279-0.313
HLL/SVL	0.476±0.01	0.467±0.003	0.467±0.004	0.499±0.005	0.452±0.0004	0.465±0.005	0.451±0.01	0.429±0.01
Hindlimb index	0.445-0.499	0.396-0.527	0.384-0.587	0.386-0.635	0.413-0.515	0.420-0.517	0.351-0.473	0.396-0.457
AL/AW	0.583±0.13	0.514±0.007	0.592±0.01	0.545±0.01	0.558±0.08	0.560±0.01	0.524±0.02	0.601±0.08
Anal shape	0.449-0.980	0.434-0.702	0.393-0.436	0.352-1.116	0.411-0.861	0.430-0.733	0.444-0.64	0.467-0.700
AS/SVL	4.71±0.45	4.91±0.05	4.70±0.06	4.90±0.06	4.65±0.08	4.93±0.07	4.89±0.16	4.85±0.20
Anal size	3.45-5.43	4.17-5.99	3.63-6.16	3.50-6.95	3.70-5.72	4.15-5.57	4.18-5.88	4.39-5.60

FIGURE 4. ANOVA-differences (*P* < 0.01) derived tree, combined males and females. See text for interpretation.

Osteology. Osteological characteristics were similar to other *Darevskia*, including the derived increase of vertebral numbers (Arribas 1998; Arnold *et al.* 2007). The characteristics of *D. r. rudis* are here described, followed by the variation of the other forms compared to the nominal taxon.

Darevskia r. rudis - Skull: Seven premaxillary teeth. Processus nasalis is slender, slightly widened and overlapping nasal bones. Samples have 15 to 19 maxillary teeth in each side (average 17.6), and from 19 to 24 dentary teeth (average 21.5). Maxilojugal suture is smooth. Postfrontal and postorbitary bones are separated from birth, with anterodistal process of the postfrontal and anteromedial process of the postorbitary present, but the latter fairly small, sometimes barely distinguishable. Postfrontal is longer than postorbitary. Squamosal bone overlaps with postorbitary in one third (rarely only in one fourth) of the length of the latter. Supraocular lamellae are partially reduced and fenestrated.

Vertebral column: The number of presacral vertebrae shows sexual dimorphism. Males have 27 (rarely 28) presacral vertebrae. Females have 28 (rarely 27 or 29 presacral vertebrae). Usual number in males and females is accompanied by 6 posterior dorsal vertebrae (if there is an increase of presacral vertebrae—from 27 to 28 in males, or from 28 to 29 in females, there usually appears an extra short rib, yielding seven in total). Third vertebra without ossified ribs. Sternal costal formula: (3+2). A-Type of preautotomic caudal vertebrae is present (Arnold 1973).

Girdles: Clavicles open. Sternal fontanelle is oval. Interclavicle with the lateral branches is more or less perpendicular to the central axis (cruciform).

Darevskia r. bithynica has 16 (15–18) maxillary teeth and 21.16 (20–23) dentary ones. Females have 28 (with 6 short ribs) and 29 (with 7 short ribs) presacral vertebrae, with both configurations being equally common. Clavicles are closed (very rarely open). Postfrontal is shorter (rarely subigual) than the postorbitary. Anteromedial process of postorbitary is fairly small. Postorbitary overlaps with squamosal along half of its length.

Darevskia r. tristis has 17.35 (16–19) maxillary teeth, and 20.9 (17–23) dentary ones. Females have 28 (with six short ribs) or 29 (with 7 short ribs) presacral vertebrae, but the later number is more common. Clavicles are more commonly open, but some are also closed. Postfrontal and postorbitary bones are subigual (rarely postfrontal is shorter than the postorbitary). Anteromedial process of postorbitary is small. Postorbitary overlaps with squamosal along half of its length (rarely along one third).

Darevskia r. bischoffi has a tendency to increase the number of premaxillary teeth from seven to eight, whereby both values are represented in fairly equal proportions (average 7.5; 7–8). This increase is probably related to its big size. Also, it has 18 (16–21) maxillary teeth and 21.8 (20–23) dentary ones. Males have 27 presacral vertebrae (rarely reduced to 26). Females have 28 (with seven, rarely with six short ribs) or more rarely 29 (with 7 short ribs) presacral vertebrae. Clavicles are open, rarely closed. Interclavicle cruciform, as usual, but some specimens with lateral branches progressively slightly inclined backwards. Sternal fontanelle is oval, but

conspicuously elongated (perhaps related to increased size). Postfrontal is longer than postorbitary. Anteromedial process of postorbitary present. Postorbitary overlaps with squamosal along one third to one quarter of its length.

Darevskia r. obscura has 17.2 (16–20) maxillary teeth and 21.2 (20–24) dentary ones. Males have 27 (rarely 26) presacral vertebrae. Females have 29 (less common 28) presacral vertebrae. Clavicles are variable (more frequently open). Interclavicle is typically cruciform (in some Georgian specimens with lateral branches slightly inclined forwards or medial part forwards and tips backwards). Postfrontal and postorbitary are subequal (one or the other can be slightly longer than the other). Anteromedial process of postorbitary present (occasionally fairly small). Postorbitary overlaps with squamosal along one third (rarely towards one quarter) of its length.

Darevskia r. macromaculata has a surprisingly high variation in the number of premaxillary teeth, from 6 to 9 (average 7.1). It has 17.9 (15–20) maxillary teeth and 22.1 (20–26) dentary ones. Males have 27 (6 short ribs) or 28 (7 short ribs) in similar proportions. Clavicles are variable (more frequently open). Interclavicle is typically cruciform, but in half of the specimens slightly directed backwards. Postfrontal and postorbitary are subequal, or the first is longer that the latter, both conditions in nearly equal proportions. Anteromedial process of postorbitary present (with size fairly variable). Postorbitary overlaps with squamosal along one third (and sometimes up to nearly one half) of its length.

Darevskia r. chechenica (from Arribas 1998) has 15 or 16 maxillary teeth and 20 to 22 dentary ones. Males have 27 and females have 29 (probably also 28) presacral vertebrae. Clavicles are open. Interclavicle is cruciform or slightly inclined backwards. Postfrontal and postorbitary are subequal or the latter slightly longer than the former. Anteromedial process of postorbitary present. Postorbitary overlaps with squamosal along one third of its length.

Ovit-pass specimens have 16.1 (15–17) maxillary teeth and 20.5 (18–23) dentary ones. Males have 26 or 27, and females have 28 (6 short ribs) and 29 (7 short ribs) presacral vertebrae. Clavicles are open (more rarely closed). Postfrontal and postorbitary are subequal (or postfrontal is slightly longer than postocular). Anteromedial process of postorbitary present. Postorbitary overlaps with squamosal along one third (rarely up to nearly one half) of its length.

Taurus (Bolkar Dağı) specimens have 18.25 (17–19) maxillary teeth and 22.25 (21–23) dentary ones. Males have 27 and females have 28 (6 short ribs) or 29 (7 short ribs) presacral vertebrae. Clavicles are open. Sternal fontanelle with odd and irregular shapes (sand-clock, nearly cordiform, etc.). Sternal-Xiphisternal formula is (3+2; 3+1 in one specimen). Postfrontal and postorbitary are subequal, with their respective processes present. Postorbitary overlaps with squamosal along nearly one half of its length.

Discussion and conclusions

The present morphological studies (biometry, scalation and osteology) enable taking some taxonomic decisions regarding the *D. rudis* polytypical species.

Genetic evidence is scarce and in some cases a bit confusing. Mayer and Lutz (1989) compared a sample (*D. rudis* ssp.) that they attributed to an "intergrade zone" between *D. r. rudis* and *D. r. tristis*, following Böhme and Bischoff (1984). In our opinion, this area is a true *D. rudis* or in any case, similar to it, presumably the nominotypical subspecies, almost as currently considered. Its Nei Distance with *D. r. bithynica* was 0.15 (2 of 14 allozyme variants). This difference is, comparatively, the same as between *D. rudis* and *D. valentini*, or *D. rudis* and *D. mixta* (Mehely, 1909), and a bit smaller than with *D. portschinskii* (D = 0.29; 3.5 out of 14 allozyme variants). Considerably smaller distances (although every set of allozymes is different) are considered among other species-pairs [such as *D. daghestanica* (Darevsky, 1967) and *D. caucasica* (Mehely, 1909), D = 0.07–0.08; Fu *et al.* (1995)]. In this same paper, a surprisingly high divergence was found among *D. r. obscura* and *D. rudis* ssp. (presumably *rudis*, as stated above).

Other studies, for example MacCulloch *et al.* (1995), Murphy *et al.* (1996), Fu *et al.* (1997) and Murphy *et al.* (2000), simply situated *D. rudis* as the sister species of *D. valentini* and both as sister species in respect to their basal *D. portschinskii*. The distance between *D. valentini* and *D. rudis* (*obscura*, from Achaldaba) was 0.12–0.15, whereas *D. portschinskii* had greater ones (0.36–0.48) (MacCulloch *et al.* 1995).

Grechko *et al.* (2007) found a distance (Nei-Li) between *D. r. tristis* (from Adapazarı) and *D. r. obscura* (Borjomi) of 0.45, and between *D. rudis* (*obscura* and *tristis*) and *D. raddei* of 0.6–0.7.

All these studies are congruent with a species status for West Pontic populations (*D. r. bithynica* and *D. r. tristis*).

Species status for *D. rudis bithynica* and *D. r. tristis*: *Darevskia r. bithynica* (Mehely, 1909) and *D. r. tristis* (Lantz & Cyren, 1936) were described as subspecies of *L. saxicola*, and still appear under this species name in Darevsky's book (Darevsky 1967), not associated to *D. rudis,* which is elevated to full rank species with some subspecies (*obscura* and *macromaculata*) in the same work. Böhme and Bischoff (1984) assigned these Pontic forms to *D. rudis* as its subspecies, more in line at that time with their geographical location and the absurdity of conserving them inside the very distant and content-reduced *L. saxicola*.

Our multivariate approach (CDA and UPGMA trees derived from distances among populations) shows a very pronounced difference of these forms (*D. r. bithynica* and *D. r. tristis*), with neither intermediate nor closer specimens to the true *rudis* subspecies. Despite a small gap in our sampling, distances (differences) are so radical and samples so homogeneous that we can be confident about the consistency of the differences among them. These taxa are well discriminated in CDA (Fig. 2a–b), completely different with enormous distances in UPGMA trees (Fig. 3a–b) and well differentiated in ANOSIM analysis. *Darevskia r. bithynica* differs from all the other samples except from *D. r. tristis*—both in males and females—(the lack of significance with *D. r. rudis* females, which does not appear in any of the other analyses, probably reflects the few females in the *D. r. bithynica* samples). Also, this taxon reveals a considerable number of differences in ANOVA to all the other *rudis* populations (Fig. 4).

If we consider *D. r. bithynica* and *D. r. tristis* together, they are characterized by subegual in length postfrontal and postorbitary; and postorbitary overlapping to nearly half of its length with the squamosal bone. Only Ovit-pass specimens (where postorbital and squamosal overlap only in one third of its length instead of one half) and Taurus specimens (equivalent in these two characteristics, but with other osteological differences—see below) also have subequal bones.

Accordingly, we raise *D. r. bithynica* to rank species: *Darevskia bithynica* (Mehely, 1909) **stat. nov.**

Despite the lack of discrimination with *D. r. tristis* (see particularly Fig. 2a–b) and the extremely poor discrimination in ANOVA (Table 4), we prefer at this time not to fully synonimize *D. r. tristis* because it is currently totally allopatric with *D. bithynica*, and consider it as a ssp., as *Darevskia bithynica tristis* (Lantz & Cyren, 1936) **comb. nov.** The nominal subspecies becomes *Darevskia bithynica bithynica* (Mehely, 1909) **comb. nov.**

Our results confirm the affirmations of Milto (2010) concerning the specific differences of *D. r. tristis* in respect to other *D. rudis* ssp. Moreover, these differences are the same for *D. r. bithynica,* and this latter taxon has nomenclatorial priority over *D. r. tristis*. Accordingly, the name shall be *D. bithynica* and not *D. tristis*. Concerning the possible relationship of *D. bithynica tristis* (and possibly *D. b. bithynica*) and *D. raddei* (following Milto 2010 and, previously, I. Darevsky pers. com., and Grechko *et al.* 2007), our osteological results do not confirm such a relationship. *Darevskia bithynica* has the usual number of presacral vertebrae as other *Darevskia* species, whereas *D. raddei* (including *nairensis* and *vanensis*) have a higher number (28 and 29 in males and females, respectively, instead of the usual 27 and 28 in the other *Darevskia*). Although a basal position of *D. bithynica* (without the *raddei*-autapomorphy) to the *D. raddei*-complex cannot be rejected outright, this relation seems very doubtful because, genetically, *D. raddei* pertains to the *caucasica*-group and *D. rudis* to the so-called *rudis*-group (Murphy *et al.* 1996). Grechko *et al.* (2007), however, found a distance (Nei-Li) between *D. b. tristis* (from Adapazarı) and *D. r. obscura* (Borjomi) of 0.45. This is slightly smaller than in respect to *D. raddei* (0.6–0.7), which, however, belongs to a different species-group inside the genus *Darevskia*.

Darevskia bithynica as a species is characterized in our analyses (species diagnosis) by having comparatively longer heads (Head index), Dorsalia and Anal Size Index (relatively bigger anal plates) in both sexes. Subigual postfrontal and postorbitary bones, whereby the latter overlap up to half of their length with the squamosal bone.

The status of the nominotypical *D. rudis* (Bedriaga, 1886): The nominotypical *D. rudis* appears well differentiated in CDA with very limited or no overlap with other samples. Also, in ANOVA, one of the most different samples is *D. rudis* sensu novo. Nonetheless, in lack of other evidence (e.g. genetic) to the contrary, we prefer to maintain it associated to the other subspecies situated south or east of the current *D. r. rudis* area. If *D. r. rudis* proves to be different from the other subspecies, then these other ones (including those described here—see below—and the Great Caucasus ones) must be combined under the name "*obscura*", which has nomenclatorial priority. Lacking other evidence, however, we refrain from considering *D. r. rudis* as a species different from other subspecies of *D. rudis* s. str. (sensu this paper). In ANOSIM analysis, *D. r. rudis* differed from all the other samples

TABLE 4A. ANOVA and pairwise comparisons among samples. a. (males) and b. (females). See Material and Methods text for abbreviations of characters and indexes used in the morphometric analysis.

MALES Pairwise comparisons	F $_{7,299}$	P	1-2	1-3	1-4	1-5	1-6	1-7	1-8	2-3	2-4	2-5	2-6	2-7	2-8	3-4	3-5	3-6	3-7	3-8	4-5	4-6	4-7	4-8	5-6	5-7	5-8	6-7	6-8	7-8
SUPRACILIARIA	9.83	0.000000						**			*	**	**	**					**				**					**	**	**
Supraciliar granulae																														
COLLARIA	6.22	0.000001				*				**	**	**	*																	
Collar scales																														
GULARIA	14.39	0.000000		*			**	**		**	**		**	**		**	**	**	**			**	**	**				**		*
Gular scales																														
VENTRALIA	9.19	0.000000			**			*					**	**		*	**	**	**	**	**	*	**	**						
Ventral scales																														
PREANALIA	4.74	0.000046							**			*			**				**				**		**	**				**
Preanal plates																														
CIRCUMANALIA	8.64	0.000000			**			*					**					**			**	**	**		**	**	**			
Circumanal scales																														
FEMORALIA	11.78	0.000000			*	**	**	**		**	**		*			**			**		**	**	**			**				
Femoral scales																														
LAMELLAE	18.33	0.000000		*	**	**	*	*	**	*	**	**	**	**	**	**	**	**	**	**	**	*	**	**	*			**	**	*
Subdigital Lamellae																														
DORSALIA	128.0	0.000000	*	**	**	**	**	**	**	*	**	**	**	**	**	**	**	**	**	*	*	*								
Dorsal scales																														
SVL	31.45	0.000000		**		**	**	**		**	**	**	**			**			*		**	**	**	**						
Snout-vent length																														
PL/PW	26.92	0.000000	**	**	*	**	**	**	**	**	**	**	**	*					**		**	**	**		**	**		**	*	**
Pileus index																														
HL/HW	418	0.000000	**	**	**	**	**	**	**	**	**	**	**	**	**		**				*	**	*	**	*	*		*	*	**
Head index																														
FLL/SVL	4.35	0.000130										**		*							*									
Forelimb index																														
HLL/SVL	8.33	0.000000			**			**		**	**	**	**	*					**		**		**	*				*		
Hindlimb index																														
AL/AW	6.26	0.000001		*	*	**	**		*			**	**							*										
Anal shape																														
AS/SVL	4.46	0.000098									*	*	**										**							
Anal size																														

TABLE 4B. ANOVA and pairwise comparisons among samples. a. (males) and b. (females). See Material and Methods text for abbreviations of characters and indexes used in the morphometric analysis.

FEMALES Pairwise comparisons	F $_{7,258}$	P	1-2	1-3	1-4	1-5	1-6	1-7	1-8	2-3	2-4	2-5	2-6	2-7	2-8	3-4	3-5	3-6	3-7	3-8	4-5	4-6	4-7	4-8	5-6	5-7	5-8	6-7	6-8	7-8
SUPRACILIARIA Supraciliar granulae	3.55	0.001175												**					*				*							
COLLARIA Collar scales	4.11	0.000264								*		*	**	**																
GULARIA Gular scales	9.27	0.000000								**			**	**		**	**	**	**				**			*				
VENTRALIA Ventral scales	6.47	0.000000	**	**							**	**	*			*	*				**	**								
PREANALIA Preanal plates	2.70	0.010240											*																	
CIRCUMANALIA Circumanal scales	3.23	0.002697																*				**			**					
FEMORALIA Femoral scales	7.34	0.000000									**					**					**	**								
LAMELLAE Subdigital Lamellae	13.66	0.000000			**	**	**	**	**			**	**	**	**		**			**	**	**	**	**		**		**	**	
DORSALIA Dorsal scales	119.9	0.000000			**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**		**							
SVL Snout-vent lengt	20.20	0.000000			**	**					**					**	*				**	**	**							
PL/PW Pileus index	17.11	0.000000	**	**					**		**			**		*		**	**				**			*				
HL/HW Head index	467.5	0.000000	**	**	**	**	**	**	**	**	**	**	**	**	**	**		**	**	**										
FLL/SVL Forelimb index	5.47	0.000007														*		*			**									
HLL/SVL Hindlimb index	9.94	0.000000									**					*					**	**	**	**						
AL/AW Anal shape	3.29	0.002280													**															
AS/SVL Anal size	1.86	0.076111																												

(but not from a very small *bithynica* female sample, which is certainly an artifact). Its osteological characteristics are very similar to *D. r. macromaculata*, *D. r. obscura*, *D. r. bischoffi* and *D. r. chechenica*.

Darevskia r. rudis is characterized in both sexes particularly by larger Dorsalia, Gularia and smaller Head Index (shorter heads), Femoralia, Collaria and smaller Forelimb Index (comparatively shorter forelimbs).

Status and relationships of the other *D. rudis* subspecies: All the following taxa or samples are largely equivalent in CDA (and their derived UPGMA trees), and is impossible to clearly discriminate among them. Both in UPGMA and MST, *D. r. macromaculata*, *D. r. obscura* and to a lesser degree *D. r. bischoffi* are very similar and difficult to separate.

Darevskia r. bischoffi is different from all the other samples in ANOSIM for both sexes, even if its characteristically large size was not considered in the multivariate analysis (CDA & UPGMA). In ANOVA (see also Fig. 4) it is the taxon (apart from *bithynica* and *tristis*) with the most significant differences accumulated ($P < 0.01$), but most of these are in SVL. It also has a tendency to increase the number of premaxillary teeth, their sternal fontanelles are somewhat elongated, and the overlap between the postorbitary and squamosal is frequently reduced to one fourth. All of these characters are probably linked to its larger size. Its status as a valid (morpho) subspecies is indisputable.

Darevskia r. macromaculata is not different in ANOSIM from the small Taurus sample (males, but not in the more numerous female sample) and, more importantly, from *D. r. obscura* specimens (both sexes). The differences in ANOVA are also minimal, and both subspecies (*D. r. obscura* and *D. r. macromaculata*) may be synonyms. The striking spotting of *D. r. macromaculata* from the type locality (Akhalkalaki, Georgia) is less developed in the Turkish specimens, or these Turkish ones are not true *D. r. macromaculata* (which is very improbable because the localities are contiguous)—or the dense and extensive spotting of Georgian *D. r. macromaculata* is a substrate-related coloration. *Darevskia r. macromaculata* is the most connected sample in MST, with fairly small differences with *D. r. obscura, D. r. bischoffi* and the Ovit-pass population. This connectivity, together with the small distances and the greater variation in osteological characters, suggests that *D. r. macromaculata* is the most primitive taxon in the species and perhaps related with its original spreading point.

Our *D. r. macromaculata* are very similar to our *D. r. obscura*, but these taxa are not so related in Eiselt and Darevsky (1991). Also, our *obscura* exhibit scalation differences compared with those of Eiselt and Darevsky (1991). The variation inside *D. r. obscura* merits a detailed future study due to its potential synonymy with *D. r. macromaculata*.

Darevskia r. obscura does not differ in ANOSIM from Taurus specimens or *D. r. macromaculata* in both sexes. In the first case, although the animals look very different, they are probably fairly related, whereby the different dorsal tones are linked to the type of rocks inhabited. The second case is explained above. Probably, *D. r. obscura* and *D. r. macromaculata* are synonyms.

Darevskia r. chechenica was not included in this study, but based on its osteological data (Arribas 1998 and this paper) and the data in Eiselt and Darevsky (1991) seems to be a true *D. rudis*, not very different from other subspecies. Its relationship with *D. r. svanetica* (Darevsky & Eiselt 1980), which has a nearly continuous area with it and is a large-sized subspecies, recalls and parallels the case of *D. r. bischoffi* in respect to the other *D. rudis* from Small-Caucasus studied in this paper. Great and Small Caucasus have their respective "small inland" and "giant sea-close" populations. North of Georgia, in the Great Caucasus, *D. r. svanetica* inhabits an area perhaps connected with coastal areas during colder periods, whereas inland areas are occupied by *D. r. chechenica*. In Eastern Pontic Chains and the Small Caucasus, coastal areas are occupied by the big-sized *D. r. bischoffi*, and inland mountainous areas by *D. r. obscura*, *D. r. macromaculata* and a new form here described. This parallelism between these two mountain areas, with a large-sized subspecies closer to the Black Sea and a smaller one inland is an interesting phenomenon worthy of further study.

Kaçkar-range alpine lizards (Ovit Pass): Ovit pass specimens are different in ANOSIM from all the other samples, both with regard to males and females (females are not different from Taurus ones, but this latter sample is very small). This population inhabits alpine environments and is clearly different from the neighboring *D. rudis* populations inhabiting lower areas (*D. r. bischoffi*). It has been considered as belonging to *D. valentini lantzicyreni* based on BMNH specimens (Darevsky 1967) (although his text about this taxon included a notable blend of localities and probably different taxa): "Pass through Rize range from İkizdere (in İspir)" and "road from İkizdere in İspir to the Pass, vilayet Rize" [BMNH 1964 383 (1)] (Darevsky 1967). Photos of this taxon are in www.lacerta.de as "*D.* cf. *valentini*". Our morphological results, however, clearly show that these specimens are

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specifically not different from other *D. rudis* populations. In fact, they are very similar to *D. r. macromaculata* (and *D. r. obscura*) and cannot be considered as a different species (i.e. belonging to *D. valentini*).

Another problem is the true relationship of the nominal taxon *lantzicyreni* and even of *D. valentini* to *D. rudis*. Their relationships and even the pertinence of some of their attributed populations (particularly of *lantzicyreni*) to *D. rudis* instead to *D. valentini* is a question to be studied in the future. *Darevskia v. valentini* (Boettger, 1892) and *D. r. macromaculata* are almost sympatric in Akhalkalaki, Georgia; and with *D. r. obscura* in Atensk Gorge, Georgia (Darevsky 1967), which, in principle, warrants its different specific status.

Ovit specimens have low supraciliaria and, correspondingly, usually interrupted rows of supraciliar granula (prevalent situation in *D. r. chechenica*, but reduced in the other subspecies to less than half and even more, usually less than one third of specimens). In *D. v. lantzicyreni,* continuous (uninterrupted) rows dominate, whereas in *D. v. valentini* discontinuous (interrupted) rows are dominant. *Darevskia v. spitzembergerae* (Eiselt, Darevsky & Schmidtler, 1992) has an intermediate situation. Rostral and frontonasal (internasal) scales are frequently in contact (nearly 50% of specimens), a geographically widely present but low-percentage situation in other *D. rudis* and *D. valentini*.

The masseteric plate is larger than the tympanic plate, and is usually separated by only one temporal scale. Two such scales are the usual condition in other *D. rudis* and *D. valentini*.

Ovit-pass specimens have osteological characteristics very similar to other *D. rudis*, but with postfrontal and postorbitary being subequal (or postfrontal only slightly longer than postocular). This character appears also in *D. bithynica* (*bithynica* and *tristis*) but very rarely in other *D. rudis* apart from the Taurus specimens. In *D. valentini* (*valentini* and cf. *lantzicyreni*) it is not infrequent that lateral branches of the interclavicle are slightly rear incurved towards their tips. This character is not present in the Ovit specimens studied by us, but has been reported in other *D. r. obscura*, *D. r. bischoffi* and *D. r. macromaculata*. This argues against a very close relationship of Ovit specimens with *D. valentini* as suggested previously, but not of other *D. rudis* ssp. with this latter taxon.

This population is described as a new subspecies below.

Taurus populations (Bolkar Dağları): Bolkar Dağ (Karagöl) specimens have a very particular coloration and appearance, with very clear background tone and contrasted black pattern, but are not different from *D. r. obscura* (both sexes in ANOSIM) and from *D. r. macromaculata* (in males, but female samples consists of only 5 specimens). *Darevskia r. obscura* is also closest in MST (males and females), a reason to consider them closely related and the differences (particularly in coloration) due to their particular rock substrate differences (crystalline and dark-toned in *obscura*, and very clear-toned limestone in Bolkar Dağ ones). Based on its coloration, osteology and allopatric distribution, we are fairly confident of their distinctiveness as a ssp. of *D. rudis*. At the same time, it is not very different from *D. r. obscura* and is clearly less strongly different than its apparently different habitus leads us to believe. In resume, they are not very different from other *D. rudis* ssp., discarding its pertinence to another species and confirming the statements of Schmidtler (Schmidtler *et al.* 1990; Schmidtler 1998) that it is a *D. rudis* (*D.* cf. *rudis* in Schmidtler papers).

Bolkar Dağı specimens have continuous (uninterrupted) rows of supraciliar granula (typical situation in *D. rudis* ssp., except *D. r. chechenica*). In *D. v. lantzicyreni,* continuous (uninterrupted) rows also dominate, whereas in *D. v. valentini* the situation is the inverse and in *D. v. spitzenbergerae* intermediate. Rostral and frontonasal (internasal) scales are separated, typical of *D. rudis* and *D. valentini*. The masseteric plate is usually smaller than the tympanic plate and is separated by more than 2 temporal scales. Two scales is the usual condition in *D. rudis* and *D. valentini*.

Taurus (Bolkar Dağı) specimens have relatively high maxillar and dentary teeth counts for their size. The sternal fontanelle has odd, irregular shapes (sand-clock, nearly cordiform, etc, but probably anecdotal, perhaps due to endogamy, bottlenecks, or other such phenomena). The postfrontal and postorbitary are subequal (as in *D. bithynica,* Ovit pass specimens—see above—but also not infrequently in their close relative *D. r. obscura*—see above). The postorbitary overlaps with the squamosal along near one half of its length (as commonly occurs in *D. bithynica*).

This population is also described as a second new subspecies below.

Taxonomic Descriptions

Darevskia rudis mirabilis ssp. nov.

(Fig. 5a–b)

Holotype. ZDEU 145/2002 (n 9). Ovit-pass, Trabzon, northeastern Anatolia. Sample number 4. 06-IX-2002. Adult male. leg. İ. Baran, Y. Kumlutaş, Ç. Ilgaz, A. Avcı. Conserved in ZDEU collection.

Paratypes. 12 males, 9 females, 2 juveniles. Same locality, date and collectors as holotype. All in ZDEU collection except 6 (including the cleared and stained specimens for bone study) in the O. Arribas scientific collection.

Derivatio nominis. The subspecies name is feminine and means wonderful, amazing, unique and miraculous in Latin. The name refers to its vivid and beautiful coloration in respect to other *D. rudis* subspecies.

Diagnosis. A *Darevskia rudis* is characterized by having rostral and frontonasal plates either in contact or separated (in contact in 50% specimens). Supraciliar granula almost always in an interrupted row. Masseteric plate longer than the tympanic one, separated only by a single row (rarely more) of scales. Tibial scales moderately keeled. Relatively high (for *D. rudis*) values for dorsalia, circumanalia, and relative anal-plate size. Relatively low values for femoralia and hindlimb length as well as short head. Postfrontal and postorbitary subequal (or postfrontal only slightly longer than postocular). Interclavicle cruciform, with tips not incurved.

Description of the holotype: An adult male. Tail autotomized. Fixed with ethanol and formaline. Conserved in alcohol (ethanol).

Coloration and pattern (in alcohol): Dorsal tract greenish-gray, with black or dark brownish (more towards sides) dark pattern. Pileus, especially in its hind-half, with medium-sized dark spots, most being well defined and others fainter. Vertebral (occipital) dark band composed of transversal, relatively narrow spots, sometimes decomposed in two or more independent spots at each vertebral side. This band does not occupy the entire dorsal tract, but leaves narrow areas without dark pattern along this band and the lateral (temporal) bands. This band continues along the dorsal part of the tail basis. Lateral (temporal) bands extend from the temporal area of the head along the sides until the tail. The upper edges of the lateral bands very scalloped (irregular, serrated), encircling round whitish spots that give the band a slightly reticulated aspect. The lower limit is more faint and difficult to discern. The belly is whitish with slight traces of the yellow color that it has in life. No spotting on the belly, either in the gular or submaxillar area.

Scalation: Number of supraciliar granules left side, 4 (interrupted series); supraciliar granules right side, 4; supraciliar plates left side, 6; supraciliar plates right side, 6; supralabial plates left side, 4; supralabial plates right side, 4; sublabial plates left, 5; sublabial plates right side, 6; collaria, 7; gularia, 25; supratemporal scales left side, 3; ventralia, 27 transversal rows; ventral plates (longitudinal rows), 6; enlarged circumanal (preanal) scales, 1; circumanalia (all preanal scales), 10; femoral pores left side, 18; femoral pores right side, 18; scales between femoral pores and outer plates left side, 5; subdigital lamellae left side, 27; subdigital lamellae right side, 24; tibials left side, 16; dorsalia, 45; temporals-1 left side, 2; temporals-1 right side, 2; temporals-2 left side, 2; temporals-2 right side, 2.

Rostral and frontonasal scales are in contact. An azygos (supernumerary) scale is presents among prefrontals, frontal and frontonasal scales. Masseteric scale present and of intermediate size. Supraciliar granula are totally interrupted. Tight scales are weakly or moderately keeled, but tail ones are very strongly keeled, as in other *rudis*.

Biometry: Snout-vent length (SVL), 63.9 mm; pileus width, 7.56 mm; pileus length, 13.44 mm; head width, 8.96 mm; head length, 14.36 mm; forelimb length, 19.10 mm; hindlimb length, 27.60 mm; anal wide, 4.14 mm; anal length, 2.16 mm.

Intrasubspecific variation. Descriptive statistics and variation range of the morphometric and scalation characters are given in Table 3a–b. Rostral and frontonasal plates can be in contact or separated. Supraciliar granula almost always in a clearly interrupted row. Masseteric plate is larger than the tympanic one, both separated by only a single or more rarely two rows of scales. Tight scales are moderately keeled.

Specimens of the type series show variations in the dorsal pattern. Adult males can have the vertebral band dots less well individualized and transversal, but more irregular and interconnected. In others, the vertebral band can be totally separated into two paravertebral rows of dots (n. 19), with a clear (background colour or slightly darker) stripe between them. One male shows a vermiculated dorsal tract and two dorsolateral stripes, more clear than the general dorsal tract, only distinct in the first half of the dorsum (n. 11). In life, lizards show diverse tones

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of greens (green, malaquite green, grass green) with blue axillar occelli and abundant blue points in the outer ventrals, both in males and females (Fig. 6a–b). Females are very similarly patterned to the males. Usually as the holotype, some more irregular. Also two paravertebral rows (n. 16).

Young specimens are basically similar to adults but with less contrasted patterns and less vividly green tones (greenish brown, brownish and brownish-gray) with whitish or yellowish axillar occelli. Undersides are unspotted in both sexes and subadults. In life, the underside is yellow in both sexes, occasionally with white throats. The upper side of the tail is greenish brown or brownish gray.

Colour photographs of these lizards can be seen at: (http://www.lacerta.de/AS/Bildarchiv.php?Species=322&Kind=1&RegioId=727&Regio=Türkei / Ovit-Pass. Last accessed 18/09/2012).

Habitat and ecology. The specimens were captured under stones on slopes of a hill covered by grass vegetation. The altitude at which the sampling was conducted was 2550 m a.s.l. The specimens were collected during sunny conditions and at temperatures between 15 and 22ºC. The collection locality was close to a stream fed by snowmelt that is habitat of *Rana macrocnemis* Boulenger, 1885. There are no tree formations on the habitat, which includes grass such as *Carex glauca, Geranium dissectum, Campanula tridenta* and *Veronica gentianoides*.

Distribution. Few sites are known. Currently known from the higher parts of the Kaçkar mountains (Ovit Pass and surrounding areas) above 2000 m, in alpine environments with wet meadows and rocks. Probably a more extended range in these mountains, perhaps also at lower altitudes in concrete habitats.

Darevskia rudis bolkardaghica ssp. nov.
(Fig. 5c–d)

Holotype. ZDEU 144/2009 (n. 6). An adult male. Karagöl, Ulukışla, Niğde, Central Anatolia, 19-VII-2009, leg. Y. Kumlutaş. Fixed and conserved in alcohol (ethanol). Deposited in the ZDEU collection.

Paratypes. ZDEU 144/2009. 5 males, 5 females, 2 juveniles, Karagöl, Ulukışla, Niğde, Central Anatolia, 19-VII-2009, leg. Y. Kumlutaş. Eight specimens in the ZDEU collection and four (including the cleared and stained for bone study) in the O. Arribas scientific collection.

Derivatio nominis. From the name of the mountains where the lizards were collected: Bolkar Dağı (also spelled Bulghar Dagh) in the Taurus Mountains.

Diagnosis. A dorsally very clear-toned *D. rudis* characterized by separated rostral and frontonasal scales. Supraciliar granula series are usually complete and uninterrupted. The massseteric plate is smaller or similar to the tympanic plate. The number of scales between masseteric and tympanic range from 2 to 4. Scales are tight and moderately keeled. Numerous dorsalia and relatively long heads (head index). Low values for femoralia, lamellae, hindlimb length, circumanalia and anal size. Relatively high maxillar and dentary teeth counts for its size. Sternal fontanelle with odd, irregular shapes (such as sand-clock or nearly cordiform). Postfrontal and postorbitary subequal. Postorbitary overlaps with squamosal along near one half of its length.

Description of Holotype. An adult male. Tail tip autotomized and regenerating. Fixed and conserved with ethanol.

Coloration and pattern (in alcohol): Dorsal tract gray, with very small and faint dots all over the dorsum (less in the neck area). No vertebral band. Pileus almost unspotted. Lateral (temporal) bands very decomposed, forming a faint reticule from which only some black dots and a faint interconnecting network remain. This band is more present in the fore halves of the flanks, where black-surrounded occelli encircle vivid blue spots. Outermost ventral scales with conspicuous blue points that form a continuous line. Belly whitish and totally unspotted.

Scalation: Number of supraciliar granules left side, 9; supraciliar granules right side, 10; supraciliar plates left side, 6; supraciliar plates right side, 5; supralabial plates left side, 4; supralabial plates right side, 4; sublabial plates left, 6; sublabial plates right side, 6; collaria, 9; gularia, 26; supratemporal scales left side, 3; ventralia, 24 transversal rows; ventral plates (longitudinal rows), 6; enlarged circumanal (preanal) scales, 2; circumanalia (all preanal scales), 8; femoral pores left side, 19; femoral pores right side, 20; scales between femoral pores and outer plates left side, 5; subdigital lamellae left side, 23; subdigital lamellae right side, 22; tibials left side, 16; dorsalia, 48; temporals-1 left side, 3; temporals-1 right side, 3; temporals-2 left side, 2; temporals-2 right side, 2. Rostral and frontonasal scales are separated. Left parietal and frontoparietal are eroded. Maseteric scale is present and of intermediate size. Supraciliar granula series are complete and continuous. Tight scales are almost not keeled, but tail ones very strongly keeled, as in other *rudis*.
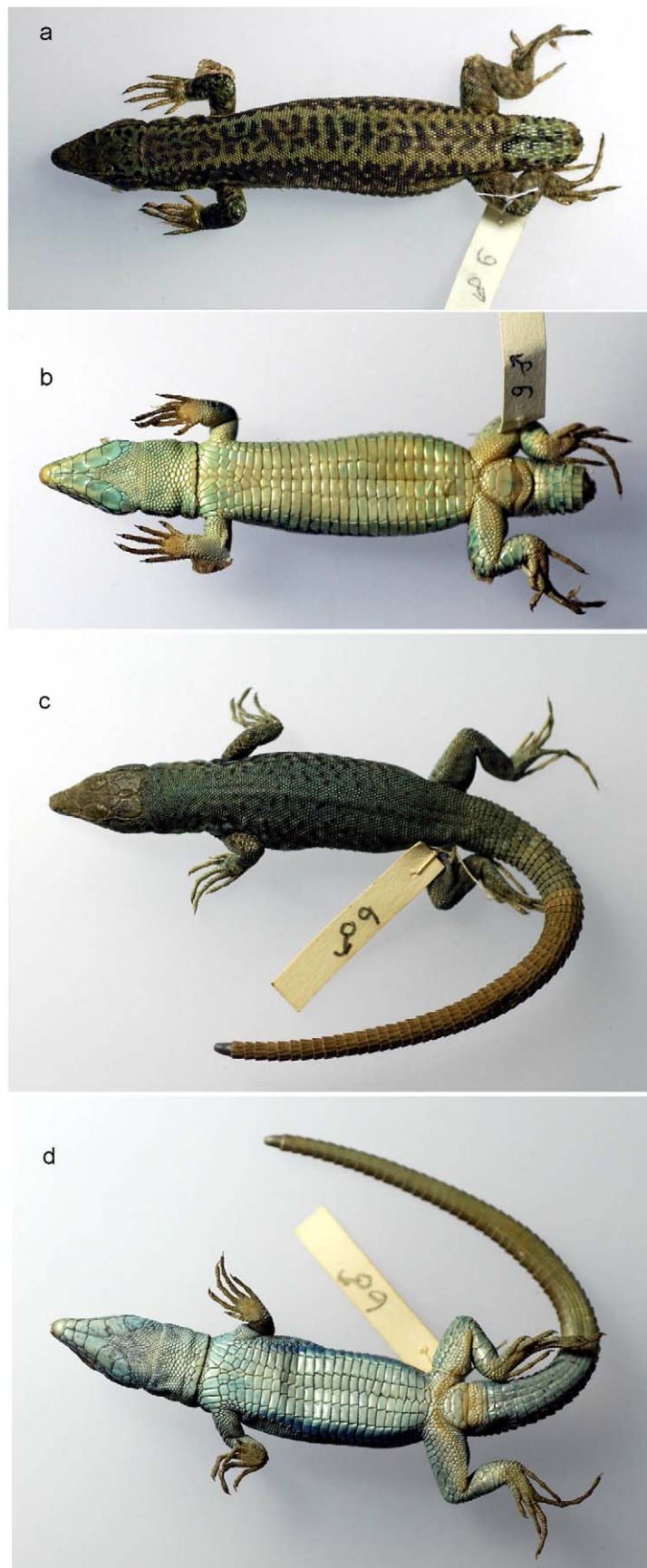
FIGURE 5. a. *Darevskia rudis mirabilis* **ssp.nov.** Holotype. Dorsal view. **b.** *D. r. mirabilis* **ssp. nov.** Holotype. Ventral view. **c.** *Darevskia rudis bolkardaghica* **ssp. nov.** Holotype. Dorsal view. **d.** *D. r. bolkardaghica* **ssp. nov.** Holotype. Ventral view.

FIGURE 6. a. *Darevskia rudis mirabilis* **ssp.nov.** Male dorsal coloration in life. Dorsal view. **b.** *D. r. mirabilis* **ssp. nov.** Male ventral coloration. **c.** Photograph of the type locality of *Darevskia rudis bolkardaghica* **ssp. nov.**

Biometry: Snout-vent length (SVL), 59.68 mm; pileus width, 6.5 mm; pileus length, 12.88 mm; head width, 8.4 mm; head length, 15.84 mm; forelimb length, 21.28 mm; hindlimb length, 33.18 mm; anal wide, 4.16 mm; anal length, 2.10 mm.

Intrasubspecific variation. Descriptive statistics and the variation range of the mophometric and scalation characters are given in Table 3a–b. Rostral and frontonasal scales are separated. Supraciliar granula series are usually complete and uninterrupted. The massseteric plate is smaller than tympanic. The number of scales between masseteric and tympanic is 2 to 4. Tibial scales are moderately keeled. Specimens of the type series show variations in the dorsal pattern. Adult males can have better developed spots than the holotype, but without forming any band in the dorsum in the type series, as much, the spotting approaches to a faint network. Other specimens can have a vertebral band composed of big transverse dots, as in other *rudis*, and even less well-patterned specimens exist. Lateral bands can also be more developed, but always composed of spots. The fore parts of the band are always more distinct marked than the rear parts. The belly is white or grayish-gray. Females have, in general, the best distinct patterns, with big spots. Blue occelli are less numerous than in males, and the blue points in outermost ventrals less developed. Hatchlings as well as adults clear background-toned, with very distinct very scarce pattern. Green tails, contrary to other *rudis* ssp. Photographs of this subspecies can be found in Schmidtler *et al.* (1990) and Panner (2000).

Habitat and ecology. The specimens were captured on rocks while they were sunning themselves. The altitude at which the sampling was conducted was 2560 m a.s.l. The specimens were collected during sunny conditions and a temperature of 15ºC. The collection locality was close to Karagöl. The biotope has alpine characteristics but lacks tree formations. The alpine vegetation mainly includes *Astragalus plumosus*, *A. angustifolius*, *Acantholium ulicium* and *Onobrychis cornuta* (Fig. 6c).

Distribution. Above 2000 m, almost up to 2800 m on rocks of Oromediterranean xerophylic pastures and near mountain lakes. Bolkar Dağı and Aladağ. Other populations such as the Hasan Dağı one (Schmidtler *et al.* 1990) could pertain to this form, but this extreme remains to be studied.

Remarks. Our lizards belong undoubtedly to *D. rudis* and are very similar to *D. r. obscura*. The striking pattern differences are due, in our opinion, due to the inhabited substrate (very clear toned recifal limestone in the case of *D. r. bolkardaghica*), whereas northern Turkey subspecies generally inhabit dark-toned acid rocks. The relationships of the nominal *D. valentini lantzicyreni* (Loc. Typ: Erciyes Dağı) will be studied more deeply: they could belong to *D. rudis* rather than *D. valentini*.

The reproduction of this form has been described in captivity by Panner (2000). He reports an extremely long duration of the copula (max. 2 h and 4 min). The clutch consists of two to four very elongated eggs and seems to be laid towards mid July (own data). A case of siblings is known (Panner 2000).

Anatolia is a predominantly mountainous area whose diverse geomorphology produces many different climatic regions and vegetation types. These characteristics and the geomorphology of Anatolia were described by Sindaco *et al.* (2000) in a checklist study of Anatolian herpetofauna. Anatolian mountains have played an important role in speciation and in the definition of biogeographical subregions. These mountains have been defined as "hotspots" of biodiversity for many different organisms (Çıplak 2003, 2004). The eastern part of Pontic mountain range situated in North Anatolia is high, continuous and lies close to the Black Sea. According to Sindaco *et al.* (2000), northern mountains including Pontic Mountains are one of the main relief regions for reptile and amphibian species in Anatolia. Veith *et al.* (2003) stated that Pontic Mountains are the refugium for Anatolian mountain frogs. They also pointed that Anatolian mountain frogs spread from the Pontic refugium to other sides of Anatolia in the Pleistocene. According to Billing *et al.* (1990), Pontic Mountains might have been an important dispersal route for many Euro-Siberian snakes such as *Coronella austriaca* Laurenti, 1768, *Zamenis longissimus* (Laurenti, 1768) and *Vipera transcaucasiana* Boulenger, 1913. Our present results also suggest that this area has played an important role in the speciation and differentiation of the *D. rudis* complex, with one species (D. *bithynica*) in their western parts, and several well-differentiated subspecies of *D. rudis* in the east, such as *D. r. mirabilis* ssp. nov.. The Bolkar Mountain is the central part of the Taurus region which rises along the southern edge of the Anatolia Plateau. Based on rates of endemism among amphibians and reptiles, Schmidtler (1998) described five centers of endemism in the Taurus Mountains: Lycia, Pamphylia/Isauria, Bolkar, Antitaurus, and Eastern Taurus. The Bolkar and the Antitaurus are well known for their endemic reptile and amphibian subspecies such as *Anatololacerta danfordi danfordi* (Günther, 1876), *Ablepharus chernovi ressli* Schmidtler, 1997, *Eirenis aurolineatus* (Venzmer, 1919), *Montivipera bulgardaghica* (Nilson & Andren, 1985), *Rana holtzi* Werner, 1898

and now *D. r. bolkardaghica* ssp. nov. (Nilson & Andren 1985; Eiselt & Schmidtler 1987; Schmidtler 1993; Schmidtler 1997; Schmidtler 1998). Sindaco *et al.* (2000) stated that the richest unit with 43 reptile species is located mainly in the Adana, Kayseri and Niğde provinces including the Bolkar Mountains in Turkey.

Acknowledgements

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