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Darevskia praticola **(Eversmann, 1834)**
Orlovsky Forest, Stavropol Krai, Russia
May 26, 2010.
Photo by Konstantin Yu. Lotiev

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NEW DATA ON THE POSTCRANIAL SKELETON AND SYSTEMATICS OF CAUCASIAN ROCK LIZARDS (LACERTIDAE: *Darevskia*)

Igor V. Doronin,[1]* Anastasia V. Lishchuk,[1] and Lyudmila F. Mazanaeva[2]

Submitted August 30, 2025.

Anatomical and morphological features of the postcranial skeleton of nine rock lizard taxa of the genus *Darevskia* Arribas, 1999 belonging to *Darevskia* (superspecies *praticola*) and *Darevskia* (superspecies *rudis*) were studied based on representative samples. The study involved type specimens, topotypes, and collections made as close as possible to their type localities. A comparison was made between the complexes within *Darevskia* and the taxa within them. Also, the postcranial skeleton of *D. caucasica* vedenica sample from Dagestan and the recently described species *D. arribasi* were studied. According to our data, *D. pontica* and *D. praticola* differ in the lower limit of the number of presacral vertebrae, the occurrence of B-type caudal vertebrae, the oval type of the sternal fontanelle, and the closed type of the clavicles; *D. r. obscura* differs from other representatives of *Darevskia* (*rudis*) in the lower limits of the number of presacral vertebrae. The following anomalies were found in the studied sample: asymmetric structure of the ribs and/or transverse processes of the vertebrae; reduction of the ribs; anomalies of the Sternal/xiphisternal costal formula; fusion, increase in the number, or reduction of the vertebrae. Anomalies were found most often in representatives of *Darevskia* (*rudis*). The greatest diversity of anomalies was, however, observed among the representatives of *Darevskia* (*praticola*). A *Graminilacerta* subgen. nov. is described, which differs from other subgenera of Caucasian rock lizards in a set of morphological features, ecology and range.

Keywords: Sauria; Lacertini; *Darevskia*; anatomical-morphological differences; systematics; postcranial skeleton; new subgenera.

INTRODUCTION

A significant part of the rock lizard genus *Darevskia* Arribas, 1999 (about 40 species in total) is endemic to the Caucasus (about 27 species) (www.lacerta.de). Despite a long history of study and hundreds of publications devoted to their phylogeny and systematics, a number of taxa have a controversial taxonomic status. To a large extent, this applies to the *Darevskia* (superspecies *caucasica*), *Darevskia* (superspecies *praticola*), *Darevskia* (superspecies *rudis*) and *Darevskia* (superspecies *saxicola*) (the name of these species complexes is given in accordance with Article 6.2 of the International Code of Zoological Nomenclature; ICZN, 1999). The study of the postcranial skeleton of lizards is an important component in the study of the systematics of lacertid lizards (Lacertini) (Arnold et al., 2007; Arribas, 2024). Thus, to substantiate the independent generic status of Caucasian rock lizards, previously included in the subgenus *Archaeolacerta* Mertens, 1921, a set of 70 features was used, 28 of which related to the characteristics of the skeleton, and the main diagnostic feature was the number of vertebrae (27 – 28 in males and 28 – 29 in females) (Arribas, 1999).

In the last decade, researchers have paid special attention to representatives of the *Darevskia* (*rudis*). This is due to the wide distribution of these rock lizards in the Caucasus (Greater Caucasus and Transcaucasia) and Asia Minor (they inhabit a significant part of Turkey), the uniqueness of their morphological features (the largest rock lizards) and their great variability. Until recently (Arribas et al., 2013; Doronin, 2017), the following taxa were considered as valid in this complex: *D. r. rudis* (Bedriaga, 1886), *D. b. bithynica* (Méhely, 1909), *D. b.*

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tristis (Lantz et Cyrén, 1936), *D. r. obscura* (Lantz et Cyrén, 1936), *D. r. macromaculata* (Darevsky, 1967), *D. r. bischoffi* (Böhme et Budak, 1977), *D. r. svanetica* (Darevsky et Eiselt, 1980), *D. r. chechenica* (Eiselt et Darevsky, 1991), *D. r. mirabilis* Arribas, Ilgaz, Kumlutaş, Durmuş, Avci et Üzüm, 2013 and *D. r. bolkardaghica* Arribas, Ilgaz, Kumlutaş, Durmuş, Avcı et Üzüm, 2013. Arribas et al. (2022) published a taxonomic revision based on an integrative approach, describing new taxa and reconsidering the status of a number of previously described taxa. According to these authors, *Darevskia* (*rudis*) is represented in Anatolia and adjacent territory by the following taxa: *D. mirabilis*, *D. r. rudis*, *D. r. lantzicyreni* (Darevsky et Eiselt, 1967), *D. r. bolkardaghica*, *D. o. obscura*, *D. o. bischoffi*, *D. o. macromaculata*, *D. b. bithynica*, and *D. b. tristis*. The phylogenetic position of *D. r. svanetica* and *D. r. chechenica* remains unexplored. It can be recognized that the revision of the system of the complex is not complete and requires further study.

Currently, the most complete work devoted to the osteology of rock lizards is a monograph by Arribas (2024), which is based on the study of about 300 rock lizard specimens. The author used 20 osteological characters: his list includes 16 characters (8 skull and 8 postcranial skeleton characters). Based on the data obtained, this author raised the taxonomic status of many complexes to subgeneric rank, describing 7 subgenera. These are: *Colchiodarevskia*, including *D.* (*C.*) *caucasica*, *D.* (*C.*) *daghestanica* (Darevsky, 1967), *D.* (*C.*) *derjugini* (Nikolsky, 1898), *D.* (*C.*) *mixta* (Méhely, 1909), *D.* (*C.*) *clarkorum* (Darevsky et Vedmederja, 1977) and *D.* (*C.*) *dryada* (Darevsky et Tuniyev, 1997). In his new subgenus *Patrodarevskia* he included taxa of the *Darevskia* (*rudis*), viz. *D.* (*P.*) *valentini* (Boettger, 1892), *D.* (*P.*) *josefschmidtleri* Arribas, Candan, Kornilios, Ayaz, Kumlutas, Gül, Yilmaz, Yildirim-Caynak et Ilgaz, 2022, *D.* (*P.*) *spitzenbergerae* (Eiselt, Darevsky et Schmidtler, 1992) and *D.* (*P.*) *portschinskii* (Kessler, 1878). The nominatypic subgenus included the *Darevskia* (*saxicola*) (*D.* (*D.*) *arribasi* Tuniyev, Petrova et Lotiev, 2023, *D.* (*D.*) *brauneri* (Méhely, 1909), *D.* (*D.*) *lindholmi* (Szczerbak, 1962), *D.* (*D.*) *saxicola* (Eversmann, 1834), and *D.* (*D.*) *szczerbaki* (Lukina, 1963)); moreover he included *Darevskia* (*D.*) (*praticola*) *pontica* (Lantz et Cyrén, 1918), *D.* (*D.*) (*p.*) *praticola* (Eversmann, 1864) and *D.* (*D.*) (*p.*) *hungarica* (Sobolevsky, 1930) (three taxa with controversial systematic status) and also *D.* (*D.*) *alpina* (Darevsky, 1967). This decision is questionable as the aforementioned lizards of this subgenus are significantly distant in morphological and ecological characteristics.

The material of Arribas (2024) did not include some taxa; some samples consisted of two or three specimens. This made it impossible to study skeletal differences between males and females, individual variability, or variability between samples from different locations.

For a long time, the systematic position of the *Darevskia* (*praticola*) remained controversial. Based on the study of external morphology, partly osteology, the structure of the epithelium of the male hemipenis and the morphology of chromosomes, most authors placed this species in the subgenus *Zootoca* Wagler, 1830 (Boulenger, 1920; Mertens and Müller, 1940; Böhme, 1971; and others). Borisov (1981) published data on the study of interspecific differences in the electrophoretic spectra of some proteins of representatives of the genus *Lacerta* s. l., according to which *D. praticola* s. l. was placed in the subgenus *Archaeolacerta* together with the Caucasian rock lizards. In the publication of Borisov and Orlova (1986), the close relationship of *D. praticola* s. l. to the rock lizards was also shown using immunology.

Murphy et al. (1996) considered *D. praticola* s. l. as a sister taxon to the "*D. caucasica* group" based on allozyme data. Using this conclusion, Roitberg (1999) attempted to estimate their degree of relationship using canonical analysis. He suggested that the ancestral species in this group was *D. daghestanica*, from which *D. praticola* and *D. caucasica* have diverged in the postglacial period.

In a publication by Fu et al. (1997), when analyzing mitochondrial DNA, *D. praticola* was used as an outgroup in relation to other Caucasian rock lizards, including representatives of the "*saxicola*" and "*caucasica*" groups. Subsequently, Fu (1999) and Murphy et al. (2000) included these lizards in their "*saxicola*" clade. In subsequent publications (Arnold et al., 2007; Freitas et al., 2016, 2022; Murtskhvaladze et al., 2020) this has been repeatedly confirmed. Here it is necessary to cite a publication by Kupriyanova and Odierna (2002): based on the study of the chromosome structure, *Darevskia* (*praticola*) and *Darevskia* (*saxicola*) were assigned to their so-called "advanced clade."

The discovery of *D. caucasica vedenica* (Darevsky et Roitberg, 1999) in new biotopes for this lizard on the southern slope of the Andy (= Kisten) Range (Dagestan) (Doronin et al., 2022) and the description of *D. arribasi* Tuniyev, Petrova et Lotiev, 2023 from the eastern range of *Darevskia* (*saxicola*) (Tuniyev et al., 2023) raises new questions in the study of the variability and systematics of these complexes. *Darevskia arribasi* was described based on a genetic analysis and was included in the same clade with *D. saxicola* and *D. szczerbaki*, according to the molecular genetic study by Tuniyev et al. (2023). The morphological diagnosis of this species given in the de-

scription does not allow a reliable identification of specimens. The osteological information can well be used to study the phylogenetic relationships of the taxa involved.

Previously, we began to study the skeleton of rock lizards on with large samples, which allowed us to obtain new information on the *Darevskia* (*caucasica*) and *Darevskia* (*saxicola*) (Lishchuk et al., 2024; Lishchuk and Doronin, 2025). In this publication, we are expanding the sample size, adding new populations and unstudied taxa for which there is no anatomical and morphological characteristic of the skeleton. Particular attention is paid to the systematic status of the *Darevskia* (*praticola*).

MATERIAL AND METHODS

We studied 386 specimens of lizards fixed in ethanol or formalin from the collection of the Zoological Institute of the Russian Academy of Sciences (ZISP): 13 specimens of the *Darevskia* (*caucasica*) from 1 locality, 219 specimens of the *Darevskia* (*praticola*) from 35 localities, 144 specimens of the *Darevskia* (*rudis*) from 11 localities, 10 specimens of the *Darevskia* (*saxicola*) from 1 locality (see *Appendix*). Material from our previous publications was also used (538 specimens) (Lishchuk et al., 2024; Lishchuk and Doronin, 2025). It is important to note that the work used type specimens (holotypes, paratypes, lectotypes, paralectotypes) and topotypes (Table 1). In this publication, we use the nomenclature of the *Darevskia* (*rudis*) without amendments from Arribas et al. (2024).

To obtain X-ray images, we used the multifunctional mobile installation PRDU-2021, provided by the Core Facilities Centre "Taxon" at the ZISP (http://www.ckp-rf.ru/ckp/3038/?sphrase_id=8879024). The samples were placed in the apparatus box and imaging was performed (75 kV, 90 μA; exposure time 3 sec). Each picture took about 5 sec on average. Digital images were displayed on the screen of a computer connected to the remote control in the basic program of the device. To obtain more complete information about some characters, samples were photographed from both dorsal and ventral sides; some specimens were also photographed in a lateral projection.

When studying the images for each individual according to the scheme proposed by Arnold et al. (2007), the total number of presacral vertebrae and the number of last presacral vertebrae with short ribs were counted, the presence or absence of ossified ribs in the third (cervical) presacral vertebra was determined, the Sternal/xiphisternal costal formula (3 + 1, 3 + 2, or 3 + 3), the shape of the sternal fontanelle (oval or heart-shaped), the form of the clavicles (opened or closed), the shape of the ribs at the sixth presacral vertebra (wide shortened or otherwise), the type of transverse processes of the caudal vertebrae (A-type — single, B-type — forked, the second pair is shorter than the first) were documented. It is important to note that the characters are noted in both adult and immature lizards.

In order to analyze the occurrence of anomalies in the studied specimens of rock lizards, we used the scheme developed by Borkin et al. (2012). It includes the following statistical indicators that make it possible to describe the diversity of anomalies in natural populations: partial frequency of anomaly (A_p, %) — the number of specimens with a given anomaly (N_{as}) as a percentage of all (normal and abnormal) specimens in the total sample (N); relative occurrence of anomaly (A_{ra}, %) — proportion of the sum of all registered cases of anomalies in the sample (N_a); individual spectrum of anomalies (S_{ai}) — the ratio of N_a to N_{as}.

From a methodological point of view, information about the difficulties that inevitably arise in the course of conducting research based on museum collections is important. For example, some juvenile specimens were too small (less than 2 cm) to be X-rayed on an existing installation. Several specimens were damaged due to the presence of a wire inside the body connecting the parts of the broken tail. Overly concentrated formalin, which was used to fix some of the samples, also negatively affected the condition of the specimens, including skeletal structures. A number of specimens lacked tails, or the tail vertebrae were replaced by cartilage due to autotomy, which made it impossible to determine their type. Such samples were excluded from the analysis based on signs that could not be diagnosed in the images. In addition, due to

TABLE 1. Summary of the Number of Studied Specimens of Lizard *Darevskia* (*caucasica*), *Darevskia* (*praticola*), *Darevskia* (*rudis*), and *Darevskia* (*saxicola*) Species

Taxon	Number	Used type specimens and topotypes
***Darevskia* (*praticola*)**		
D. caucasica vedenica	13	Holotype and paratypes
D. pontica	99	Lectotype and paralectotypes
D. praticola hyrcanica	19	Paratypes and topotypes
D. praticola loriensis	11	Paratypes
D. p. praticola	90	—
***Darevskia* (*rudis*)**		
D. r. chechenica	42	Paratypes
D. r. macromaculata	19	Holotype and paratypes
D. r. obscura	56	Lectotype and paralectotypes
D. r. svanetica	27	Holotype and paratypes
***Darevskia* (*saxicola*)**		
D. arribasi	10	Paratypes
Total	386	

the postmortem displacement of the edges relative to their axis and the lack of diagrams/photographs in the literature demonstrating the differences, it is difficult in some cases to judge their shape only from textual descriptions.

The free software Stattictica 10 (https://statistica.software.informer.com/10.0) is used for statistical processing of the data.

RESULTS

1. Description of the postcranial skeleton of the *Darevskia* (*praticola*)

Based on the data obtained, descriptions of the postcranial skeleton were compiled for the taxa included in the complex and for the entire complex as a whole (Tables 2, 3; Fig. 1).

***Darevskia pontica*.** Usually 27 presacral vertebrae in males and 29 in females; limits: 26 – 29 in males and 28 – 31 in females. The number of the last presacral vertebrae with short ribs is usually 6 in both males and females; limits: 5 – 7 in males and 6 – 7 in females. At the third (cervical) vertebra, ossifying ribs were found in 6 specimens (1 male and 5 females – 6.1%). Sternal/xiphisternal costal formula: 3 + 2, in one male 3 + 3 were found (1%). The shape of the ribs at the sixth presacral vertebra is "wide shortened"; the sternal fontanelle is usually cordate, less often oval (12.6%); the form of the clavicles is more often "closed clavicles" than not "open clavicles" (22.4%). The type of tail vertebrae is B-type in more than half of the samples, A-type in the rest (35.3%).

Darevskia praticola hyrcanica. Usually 28 presacral vertebrae in males and 29 in females; limits: 27 – 28 in males and 29 – 30 in females. The number of the last presacral vertebrae with short ribs is 6 in both males and females, 5 were found in one male (12.5%); limits: 5 – 6 in males, only 6 in females. At the third (cervical) vertebra, ossifying ribs were found in 2 specimens (1 male and 1 female – 13.3%). Sternal/xiphisternal costal formula: 3 + 2, 3 + 1 were found in one male (7.2%). The shape of the ribs at the sixth presacral vertebra is "wide shortened"; the sternal fontanelle is usually oval, heart-shaped was found in 2 females (18.2%); form of the clavicles is merged ("the clavicles are closed"). The type of tail vertebrae is A-type.

TABLE 2. Number of Presacral Vertebrae in *Darevskia* (*praticola*) Species

Taxon	min – max, $M \pm m$ (n)			t	P
	all specimens	males	females		
D. pontica	26 – 31 28.24 ± 0.12 (95)	26 – 29 27.28 ± 0.08 (49)	28 – 31 29.27 ± 0.1 (44)	1.98	<0.05
D. praticola hyrcanica	27 – 30 28.35 ± 0.22 (14)	27 – 28 27.75 ± 0.16 (8)	29 – 30 29.16 ± 0.16 (6)	2.18	<0.05
D. praticola loriensis	28 – 30 28.72 ± 0.23 (11)	28 – 29 28.16 ± 0.16 (6)	29 – 30 29.5 ± 0.29 (4)	2.30	<0.05
D. p. praticola	27 – 31 28.96 ± 0.09 (90)	27 – 29 28.23 ± 0.07 (48)	29 – 31 29.81 ± 0.07 (42)	1.98	<0.05
Complex as a whole	26 – 31 28.58 ± 0.07 (210)	26 – 29 27.77 ± 0.07 (111)	28 – 31 29.51 ± 0.06 (96)	1.97	<0.05

Note. Here and below, in all tables, the data are given without taking into account individuals with vertebral anomalies and damaged bone structures

TABLE 3. Number of Posterior Presacral Vertebrae with Short Ribs in *Darevskia* (*praticola*) Species

Taxon	min – max, $M \pm m$ (n)			t	P
	all specimens	males	females		
D. pontica	5 – 7 5.87 ± 0.05 (85)	5 – 7 5.66 ± 0.07 (45)	6 – 7 6.1 ± 0.05 (40)	1.99	<0.05
D. p. hyrcanica	5 – 6 5.92 ± 0.07 (13)	5 – 6 5.88 ± 0.12 (8)	6 6.0 ± 0.0 (5)	2.20	>0.05
D. p. loriensis	6 – 7 6.18 ± 0.12 (11)	6 – 7 6.16 ± 0.16 (6)	6 – 7 6.25 ± 0.25 (4)	2.30	>0.05
D. p. praticola	5 – 7 5.95 ± 0.03 (81)	5 – 6 5.95 ± 0.03 (41)	5 – 7 5.95 ± 0.06 (40)	1.99	>0.05
Complex as a whole	5 – 7 5.92 ± 0.03 (190)	5 – 7 5.82 ± 0.04 (98)	5 – 7 6.03 ± 0.04 (89)	1.97	<0.05

Darevskia praticola loriensis. Usually 28 presacral vertebrae in males, in females both 29 and 30 are equally common; limits: 28 – 29 in males and 29 – 30 in females. The number of the last presacral vertebrae with short ribs is usually 6 in both males and females; limits: 6 – 7 in both sexes. There are no ossifying ribs at the third (cervical) vertebra. Sternal/xiphisternal costal formula: 3 + 2. The shape of the ribs at the sixth presacral vertebra is "wide shortened"; the sternal fontanelle is oval; form of the clavicles is not merged ("clavicles are open"). The type of caudal vertebrae is A-type.

Darevskia praticola praticola. Usually 28 presacral vertebrae in males and 30 in females; limits: 27 – 29 in males and 29 – 31 in females. The number of the last presacral vertebrae with short ribs is usually 6 in both males and females; limits: 5 – 6 in males, 5 – 7 in females. At the third (cervical) vertebra, ossifying ribs were found in 15 specimens (9 males and 6 females — 15%). Sternal/xiphisternal costal formula: 3 + 2. The shape of the ribs at the sixth presacral vertebra is "wide shortened"; the sternal fontanelle is more often cordate (63.1%) than oval; form of the clavicles is merged ("closed clavicles"), or not merged ("open clavicles"), both options are found almost equally (50.6% and 49.4%, respectively). The type of tail vertebrae is mainly A-type, in 5 specimens B-type was found (3 males and 2 females — 6.3%).

Characteristics of the entire complex. Usually 28 presacral vertebrae in males and 30 in females; limits: 26 – 29 in males and 28 – 30 in females. The number of the last presacral vertebrae with short ribs is usually 6 in both males and females; limits: 5 – 7 in both males and females. At the third (cervical) vertebra, ossifying ribs were found in 23 specimens (11 males and 12 females — 10.5%). Sternal/xiphisternal costal formula: usually 3 + 2, in one male 3 + 3 (0.5%), in one male 3 + 1 (0.5%). The shape of the ribs at the sixth presacral vertebra is "wide shortened"; the sternal fontanelle is more often heart-shaped (69.2%) than oval; Form of the clavicles is merged ("closed clavicles"), less often not merged ("open clavicles") (35.8%). The type of caudal vertebrae is usually A-type, to a lesser extent B-type (31.4%).

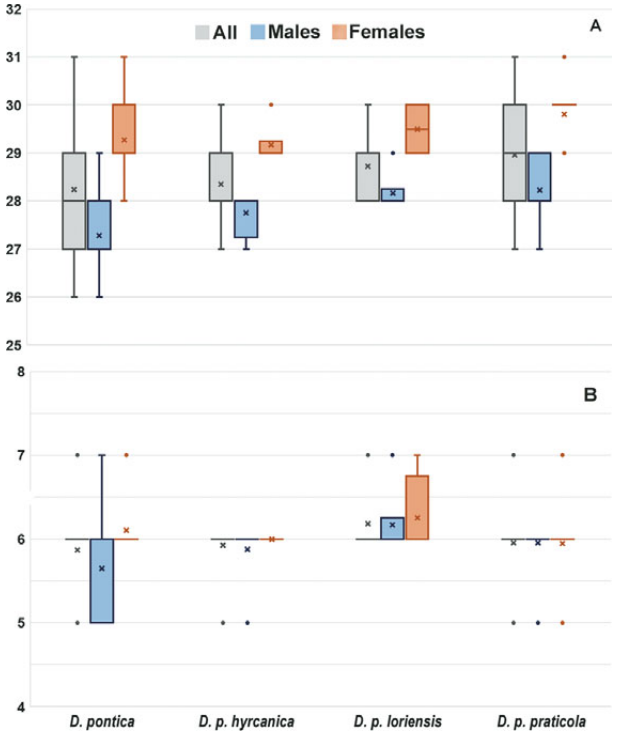

Fig. 1. Box plot of the number of presacral vertebrae (A) and the number of last presacral vertebrae with short ribs (B) in taxa of *Darevskia* (*praticola*).

2. Description of the postcranial skeleton of the *Darevskia* (*rudis*)

Based on the data obtained, descriptions of the postcranial skeleton were compiled for the taxa included

TABLE 4. Number of Presacral Vertebrae in *Darevskia* (*rudis*) Species

Taxon	min – max, $M \pm m$ (n)			t	P
	all specimens	males	females		
D. r. chechenica	27 – 30 28.39 ± 0.12 (41)	27 – 28 27.76 ± 0.12 (13)	28 – 30 29.0 ± 0.08 (18)	2.04	<0.05
D. r. macromaculata	27 – 29 27.73 ± 0.2 (19)	27 – 29 27.56 ± 0.2 (16)	28 – 29 28.66 ± 0.33 (3)	2.10	<0.05
D. r. obscura	26 – 29 27.26 ± 0.1 (53)	26 – 28 26.91 ± 0.07 (37)	27 – 29 28.33 ± 0.18 (12)	2.01	<0.05
D. r. svanetica	27 – 29 27.79 ± 0.15 (24)	27 – 28 27.09 ± 0.09 (11)	28 – 29 28.3 ± 0.15 (10)	2.09	<0.05
Complex as a whole	26 – 30 27.76 ± 0.07 (138)	26 – 29 27.22 ± 0.07 (77)	27 – 30 28.63 ± 0.08 (44)	1.98	<0.05

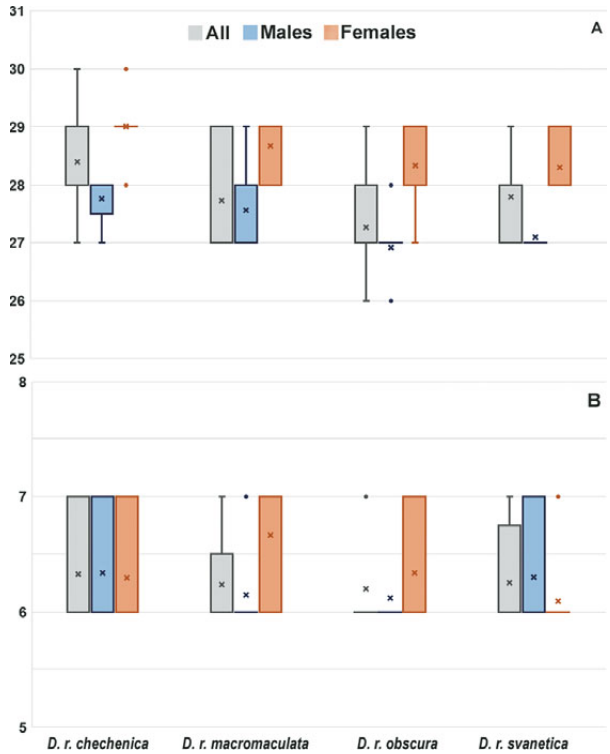

Fig. 2. Box plot of the number of presacral vertebrae (A) and the number of last presacral vertebrae with short ribs (B) in taxa of *Darevskia* (*rudis*).

in the complex and for the entire complex as a whole (Tables 4, 5; Fig. 2).

***Darevskia rudis chechenica*.** Usually 28 presacral vertebrae in males and 29 in females; limits: 27 – 28 in males and 28 – 30 in females. The number of the last presacral vertebrae with short ribs is usually 6 in both males and females; limits: 6 – 7 in both sexes. At the third (cervical) vertebra, ossifying ribs were found in one female (2.4%). Sternal/xiphisternal costal formula: 3 + 2. The shape of the ribs at the sixth presacral vertebra is "wide shortened"; the sternal fontanelle is oval; form of the clavicles is not merged ("clavicles are open"). The type of caudal vertebrae is A-type.

***Darevskia rudis macromaculata*.** Usually 27 presacral vertebrae in males and 29 in females; limits: 27 – 29 in males and 28 – 29 in females. The number of the last presacral vertebrae with short ribs is usually 6 in males and 7 in females; limits: 6 – 7 in both sexes. There are no ossifying ribs at the third (cervical) vertebra. Sternal/xiphisternal costal formula: 3 + 2. The shape of the ribs at the sixth presacral vertebra is "wide shortened"; the sternal fontanelle is oval; form of the clavicles usually is not merged ("clavicles open"), less often is merged ("clavicles closed") (26.3%). The type of caudal vertebrae is A-type.

***Darevskia rudis obscura*.** Usually 27 presacral vertebrae in males and 28 in females; limits: 26 – 28 in males and 27 – 29 in females. The number of the last presacral vertebrae with short ribs is most often 6 in both males and females; limits: 6 – 7 in both sexes. At the third (cervical) vertebra, ossifying ribs were found in 4 specimens (2 males, 1 female, and 1 subadult individual of indeterminate sex – 7.1%). Sternal/xiphisternal costal formula: 3 + 2, in one subadult individual of indeterminate sex – 3 + 1 (1.9%). The shape of the ribs at the sixth presacral vertebra is "wide shortened"; the sternal fontanelle is oval; form of the clavicles usually is not merged ("clavicles open"), less often is merged ("clavicles closed") (14.9%). The type of tail vertebrae is A-type, in 3 females B-type was found (5.8%).

***Darevskia rudis svanetica*.** Usually 27 presacral vertebrae in males and 28 in females; limits: 27 – 28 in males and 28 – 29 in females. The number of the last presacral vertebrae with short ribs is most often 6 in both males and females; limits: 6 – 7 in both sexes. At the third (cervical) vertebra, ossifying ribs were found in almost half of the examined specimens (4 males and 6 females – 48.1%). Sternal/xiphisternal costal formula):

TABLE 5. Number of Posterior Presacral Vertebrae with Short Ribs in *Darevskia* (*rudis*) Species

Taxon	min – max, $M \pm m$ (n)			t	P
	all specimens	males	females		
D. r. chechenica	6 – 7 6.32 ± 0.07 (37)	6 – 7 6.33 ± 0.14 (12)	6 – 7 6.29 ± 0.11 (17)	2.05	>0.05
D. r. macromaculata	6 – 7 6.23 ± 0.1 (17)	6 – 7 6.14 ± 0.09 (14)	6 – 7 6.66 ± 0.33 (3)	2.13	>0.05
D. r. obscura	6 – 7 6.2 ± 0.05 (50)	6 – 7 6.11 ± 0.05 (34)	6 – 7 6.33 ± 0.14 (12)	2.01	>0.05
D. r. svanetica	6 – 7 6.25 ± 0.09 (24)	6 – 7 6.09 ± 0.09 (11)	6 – 7 6.3 ± 0.15 (10)	2.09	>0.05
Complex as a whole	6 – 7 6.25 ± 0.03 (129)	6 – 7 6.15 ± 0.04 (71)	6 – 7 6.34 ± 0.07 (43)	1.98	<0.05

3 + 2. The shape of the ribs at the sixth presacral vertebra is "wide shortened"; the sternal fontanelle is oval; form of the clavicles is merged ("the clavicles are closed"), less often is not merged ("the clavicles are open") (12%). The type of caudal vertebrae is A-type, in one male and one female, B-type was found (7.4%).

Characteristics of the entire complex. Usually 27 presacral vertebrae in males and 29 in females; limits: 26 – 29 in males and 27 – 30 in females. The number of the last presacral vertebrae with short ribs is usually 6 in both males and females; limits: 6 – 7 in both males and females. At the third (cervical) vertebra, ossifying ribs were found in 18 specimens (12.5%). Sternal/xiphisternal costal formula: usually 3 + 2, in one immature individual of indeterminate sex 3 + 1 (0.8%). The shape of the ribs at the sixth presacral vertebra is "wide shortened"; the sternal fontanelle is oval; form of the clavicles usually is not merged ("the clavicles are open"), less often is merged ("the clavicles are closed") (25.8%). The type of tail vertebrae is usually A-type, in 5 specimens B-type was found (1 male and 4 females – 3.6%).

3. Description of the postcranial skeleton of *Darevskia arribasi*

Usually 27 presacral vertebrae in males and 28 in females; limits: 26 – 28 in males and 27 – 28 in females. The number of the last presacral vertebrae with short ribs is usually 6 in males, 6 in females; limits: 5 – 6 in males, only 6 in females. There are no ossifying ribs at the third (cervical) vertebra. Sternal/xiphisternal costal formula: 3 + 2. The shape of the ribs at the sixth presacral vertebra is "wide shortened"; the sternal fontanelle is usually oval (60%), but heart-shaped also occurs; form of the clavicles is more often "open clavicles" (70%). The type of caudal vertebrae is A-type.

4. Description of the postcranial skeleton of a sample of *Darevskia caucasica vedenica* from Dagestan

Usually 27 presacral vertebrae in males and 28 in females. The number of the last presacral vertebrae with short ribs is 5 and 6 in males (there were only 2 males in the sample), more often 6 in females; limits: 5 – 6 in both sexes. There are no ossifying ribs at the third (cervical) vertebra. The Sternal/xiphisternal costal formula is 3 + 2, with 3 + 3 found in one male. The shape of the ribs at the sixth presacral vertebra is "wide and shortened"; the sternal fontanelle is usually oval; form of the clavicles is merged ("the clavicles are closed"). The type of caudal vertebrae is A-type.

5. Anomalies of the postcranial skeleton

During the study of the material, rare and common anomalies of the postcranial skeleton were found in 76 specimens, both mature and immature (16.4% of the total sample of 462 specimens). The following groups of anomalies were identified:

1. Asymmetrical structure of the ribs and/or transverse processes of the vertebrae.

1.1. Anomaly of the sacral vertebrae.

1.1.1. Anomaly of the symmetry of the processes of the sacral vertebrae. The 27th, 28th, 29th, or 30th vertebra has a rib on one side and a transverse process of the sacral vertebra on the other, the next vertebra is a normal sacral, the one following it has a transverse process of the sacral vertebra on one side and a transverse process of the caudal vertebra on the other. *D. pontica* ZISP 18966, 22853, *D. p. hyrcanica* ZISP 26604, *D. p. praticola* ZISP 16307, *D. r. chechenica* ZISP 18781, *D. r. obscura* ZISP 17172, *D. r. svanetica* ZISP 17814/17875 were identified.

1.1.2. Anomaly in the shape of the processes of the sacral vertebrae. One individual of *D. p. praticola* (ZISP 23562.4) has an atypical shape of the processes of the first sacral vertebra.

1.2. Rib anomaly in a presacral vertebra.

1.2.1. The 21st, 22nd, 23rd, or 24th vertebra has a long rib on one side and a short one on the other. Found in *D. pontica* (ZISP 18966, 19112, 22223), *D. p. hyrcanica* (ZISP 26606, 30056), *D. p. praticola* (ZISP 16307, 22125, 23562, 25763, 26532), *D. r. chechenica* (ZISP 17882, 17878, 18781, 19545), *D. r. macromaculata* (ZISP 17440), *D. r. obscura* (ZISP 17171, 17172).

1.2.2. The presence of two ribs on one vertebra. On the left side on the 25th vertebra in one individual of *D. r. obscura* (ZISP 17171).

1.2.3. Fusion of two ribs of adjacent vertebrae. Fusion of ribs of the 11th and 12th pairs was found on the right side in one individual of *D. r. obscura* (ZISP 17057), interestingly, this led to the appearance of a secondary anomaly — asymmetry of the costal formula.

2. Reduction of ribs. Reduction of ribs on the 4th presacral vertebra was found in one individual of *D. pontica* (ZISP 19112).

3. Sternal/xiphisternal costal formula anomalies.

More ribs can be attached to the xiphoid process on one side (*D. r. chechenica* ZISP 18374, *D. r. svanetica* ZISP 17814/17875) than on the other. Part of the sternum becomes part of the xiphoid process (*D. c. vedenica* ZISP 17744), or vice versa — part of the xiphoid process is fused with the sternum (*D. p. loriensis* ZISP 17075, *D. r. chechenica* ZISP 17878, 19545). One rib from a pair (or the entire pair) is attached not to the xiphoid process, but to the sternum (*D. r. obscura* ZISP 17171, *D. r. svane-*

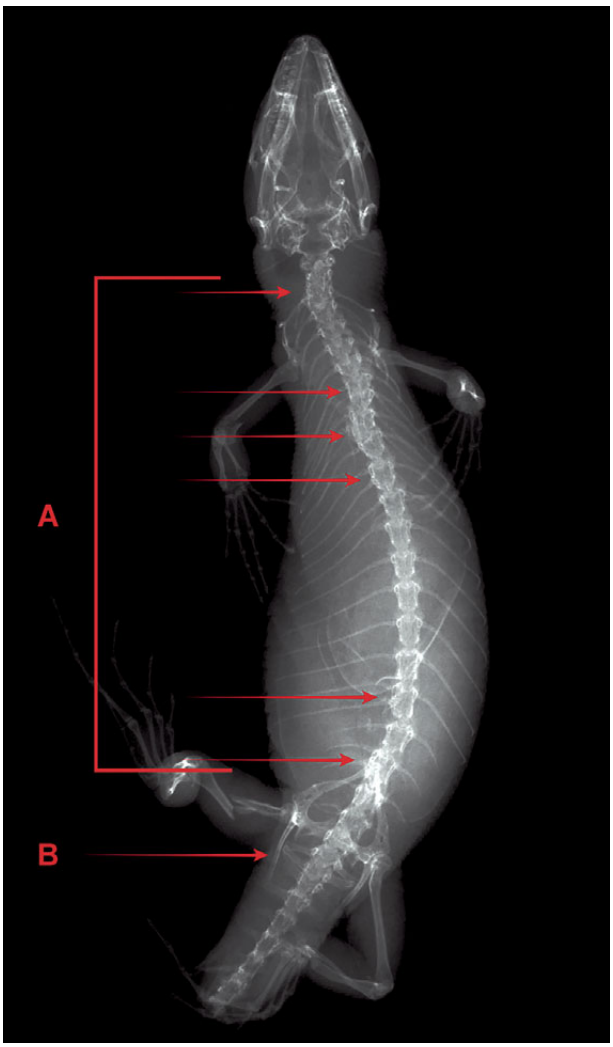

Fig. 3. Fusion of vertebrae in *D. pontica* (ZISP 22852): multiple fusions of vertebrae (A) and presence of three sacral vertebrae (B).

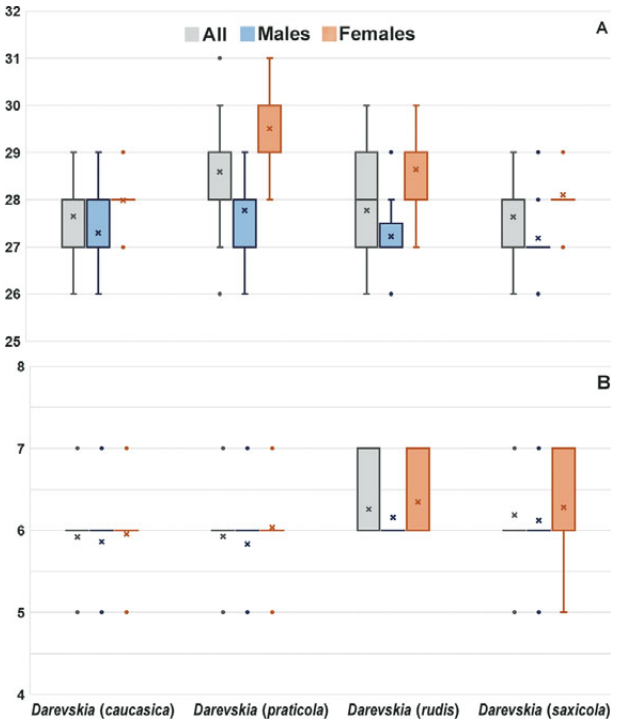

Fig. 4. Box plot of the number of presacral vertebrae (A) and the number of last presacral vertebrae with short ribs (B) of *Darevskia* (*caucasica*), *Darevskia* (*praticola*), *Darevskia* (*rudis*) and *Darevskia* (*saxicola*).

tica ZISP 17814/17875). The formerly free 8th pair of ribs gains contact with the sternum, forming an atypical formula (4 + x) (*D. r. chechenica* ZISP 18374). Asymmetry of the costal formula occurs due to the fusion of two ribs on one side (*D. r. obscura* (ZISP 17057). Asymmetry of the formula and/or an increase in the number of ribs in contact with the sternum can occur due to several factors present simultaneously: the appearance of contact between the 8th pair of ribs and the sternum, the disappearance of contact between the 9th and/or 11th pair and the sternum, the disappearance of contact between the 13th pair and the xiphoid process, and other similar aberrations, which, in essence, represent a cascade displacement of contacts between the ribs and the sternum/xiphoid process (*D. pontica* ZISP 18966, 22223, *D. p. praticola* ZISP 25764, 31625, *D. r. obscura* ZISP 17171).

4. Fusion, increase in the number or reduction of vertebrae.

4.1. Fusion of vertebrae. Fusion of 8 and 9 as well as 11 and 12 vertebrae (*D. r. obscura* ZISP 17057). A unique case of multiple fusions was found in one individual of *D. pontica* (ZISP 22852, Fig. 3A): 3 – 5, 10 – 11, 12 – 13, 15 – 16, 23 – 24, and 26 – 27 vertebrae were fused.

4.2. Increase in the number of vertebrae. In one individual of *D. pontica* (ZISP 22852), in addition to numerous fusions, an extra sacral vertebra was found (Fig. 3B). Usually there are 2 of them, but this specimen has 3.

4.3. Reduction of vertebrae. In one individual of *D. pontica* (ZISP 18966), one of the vertebrae, from the second to the sixth, was reduced, since a shift by one segment occurred, leading to a change in the alternation of rib types.

DISCUSSION

1. A characterisation of the postcranial skeleton

Differences in the morphology of the postcranial skeleton were revealed both between the four complexes

TABLE 6. Comparison of the Postcranial Skeleton of *Darevskia* (*caucasica*), *Darevskia* (*praticola*), *Darevskia* (*rudis*), and *Darevskia* (*saxicola*) Species

Characteristics	*Darevskia* (*caucasica*)		*Darevskia* (*praticola*)		*Darevskia* (*rudis*)		*Darevskia* (*saxicola*)	
	males	females	males	females	males	females	males	females
Number of presacral vertebrae min – max, $M \pm m$ (*n*)	26 – 29 27.29 ± 0.05 (134)	27 – 29 27.99 ± 0.04 (131)	26 – 29 27.77 ± 0.07 (111)	28 – 31 29.51 ± 0.06 (96)	26 – 29 27.22 ± 0.07 (77)	27 – 30 28.63 ± 0.08 (44)	26 – 29 27.18 ± 0.04 (102)	27 – 29 28.09 ± 0.06 (92)
Number of posterior presacral vertebrae with short ribs min – max, $M \pm m$ (*n*)	5 – 7 5.86 ± 0.04 (131)	5 – 7 5.95 ± 0.04 (122)	5 – 7 5.82 ± 0.04 (98)	5 – 7 6.03 ± 0.04 (89)	6 – 7 6.15 ± 0.04 (71)	6 – 7 6.34 ± 0.07 (43)	5 – 7 6.12 ± 0.04 (98)	5 – 7 6.27 ± 0.05 (86)
Type of the first autotomic tail vertebrae, % (*n*)	(131)	(129)	(107)	(82)	(75)	(46)	(102)	(88)
A-type	98.5	97.7	66.4	70.7	98.7	91.3	89.2	92.1
B-type	1.5	2.3	33.6	29.3	1.3	8.7	10.8	7.9
Sternal/xiphisternal costal formula, % (*n*)	(133)	(133)	(110)	(99)	(72)	(44)	(104)	(94)
3 + 1	1.5	3.7	0.9	0	0	0	0	2.1
3 + 2	96.2	95.6	98.2	100	100	100	100	97.9
3 + 3	2.3	0.7	0.9	0	0	0	0	0
Ossified ribs at the third cervical vertebra, % (*n*)	(137)	(138)	(115)	(101)	(79)	(47)	(104)	(95)
Missing	92.0	92.0	90.4	88.1	92.4	83.0	99.0	100
Available	8.0	8.0	9.6	11.9	7.6	17.0	1.0	0
Clavicle type, % (*n*)	(136)	(134)	(106)	(95)	(75)	(43)	(103)	(92)
Open	10.3	11.9	39.6	29.5	69.3	81.4	55.3	56.5
Closed	89.7	88.1	60.4	70.5	30.7	18.6	44.7	43.5
Type of sternal fontanelle, % (*n*)	(117)	(121)	(94)	(85)	(60)	(39)	(73)	(79)
Heart-shaped	50.4	38.8	70.2	68.2	0	0	11.0	35.4
Oval	49.6	61.2	29.8	31.8	100	100	89.0	64.6

(Table 6; Fig. 4) and between the taxa included in them. The increase in the number of studied individuals in the *Darevskia* (*saxicola*) compared to our previous publication (Lishchuk et al., 2024) allowed us to establish a new lower limit for the number of presacral vertebrae and update the information related to the *Darevskia* (*caucasica*) and *Darevskia* (*saxicola*), since these two groups were previously well distinguished by their lower limit (Lishchuk et al., 2024). Now, both are characterized by limits of 26 – 29 presacral vertebrae. Also, a more detailed study of the specimens revealed the presence of a heart-shaped sternal foramen in these complexes, and not only an oval one.

The postcranial skeleton of the *Darevskia* (*praticola*) and *Darevskia* (*rudis*) differs significantly from previous studies complexes. For example, among the taxa of the *Darevskia* (*praticola*), individuals with type B caudal vertebrae and a cordate sternal fontanelle are much more common. In the *Darevskia* (*rudis*), individuals with ossified ribs at the level of the third vertebra are most common, the open type of clavicles predominates, and the cordate type of sternal fontanelle is absent (Arribas, 2024) indicated the presence of individuals with a cordate form in *D. r. macromaculata*). These two complexes are also characterized by a greater number of presacral vertebrae. Interestingly, in the *Darevskia* (*rudis*), the lower scores is 6 presacral vertebrae with short ribs, in contrast to 5 in all the others.

In all complexes, individuals with the B-type caudal vertebrae variant were found, most of them in the *Darevskia* (*praticola*) — 31.4% and 1.7 – 8.3% in the other complexes. The most common Sternal/xiphisternal costal formula variant among the rock lizards considered is 3 + 2, the 3 + 1 variant is extremely rare, but is found in all complexes. 3 + 3 is observed only in the *Darevskia* (*caucasica*) and *Darevskia* (*praticola*). Individuals with ossified ribs on the third (cervical) vertebrae are rare, they are found in all complexes, however, among *Darevskia* (*praticola*) and *Darevskia* (*rudis*) they are more common — 10.5% and 12.4%, respectively that of *Darevskia* (*caucasica*) — 8%, and of *Darevskia* (*saxicola*) — 0.4%.

Interesting results were shown by the study of clavicle types: in *Darevskia* (*caucasica*) and *Darevskia* (*praticola*) the closed type clearly predominates, in that of *Darevskia* (*rudis*) — the open type, and in *Darevskia* (*saxicola*) the percentage ratio of the two variants was di-

vided almost equally, with a slight advantage in favor of the open type (55.5%).

The proportion of specimens with different types of sternal fontanelle varies across all complexes. In that of *Darevskia* (*caucasica*), the distribution is almost equal — 47.7% with a cordate opening and 52.3% with an oval opening. In that of *Darevskia* (*praticola*), those with a cordate opening predominate, while in the *Darevskia* (*saxicola*), those with an oval opening are more common. In the *Darevskia* (*rudis*), those with a cordate type are completely absent.

According to our data, *D. pontica* and *D. praticola* differ in the lower limit of the number of presacral vertebrae (26 and 27, respectively), the occurrence of B-type caudal vertebrae (64.7% and 6.3%), the oval type of the sternal opening (12.6% and 36.9%), the dominance of closed clavicles in *D. pontica* (77.6%), while closed and open clavicles are almost equally common in the *D. praticola* sample; *D. r. obscura* differs from other representatives of the *Darevskia* (*rudis*) in the lower limits of the number of presacral vertebrae: 26 – 28 males, 27 – 29 females. These are the minimum values for the complex.

TABLE 7. Comparison of the Postcranial Skeleton of *Darevskia caucasica vedenica* from the Kezenoyam Lake Area (ZISP 32587 – 32599) and Type Series (ZISP 17744)

Characteristics	ZISP 32587 – 32599	ZISP 17744
Number of presacral vertebrae min-max, $M \pm m$ (n)	27 – 28 27.66 ± 0.14 (12)	26 – 29 27.75 ± 0.09 (40)
Number of posterior presacral vertebrae with short ribs min-max, $M \pm m$ (n)	5 – 6 5.72 ± 0.14 (11)	5 – 6 5.52 ± 0.07 (40)
Type of the first autotomic tail vertebrae, % (n)	(13)	(40)
A-type	100	100
B-type	0	0
Sternal/xiphisternal costal formula, % (n)	(13)	(39)
3 + 1	0	0
3 + 2	92.3	97.4
3 + 3	7.7	2.6
Ossified ribs at the third cervical vertebra, % (n)	(13)	(40)
Missing	100	100
Available	0	0
Clavicle type, % (n)	(12)	(39)
Open	0	0
Closed	100	100
Type of sternal fontanelle, % (n)	(12)	(34)
Heart-shaped	25.0	29.4
Oval	75.0	70.6

The sample of *D. c. vedenica* from Dagestan (ZISP 32587 – 32599) is almost completely identical to the type series (ZISP 17744) in postcranial features (Table 7). The only difference in the considered sample lies in the limits of the number of presacral vertebrae. The lower one contains 27, the upper one 28 vertebrae. The limits of the type series are wider, 26 – 29 presacral vertebrae. It was also found that males of the studied population have only 27 presacral vertebrae, while females have only 28. However, no significant differences were found according to the results of the two-sample t-test (Table 8).

The study of the skeleton of *D. arribasi* revealed differences from closely related species. This taxon is the only one in the *Darevskia* (*saxicola*) with a lower limit of 26 presacral vertebrae (Table 9; Fig. 5). The upper limit of 28 vertebrae is also lower than in *D. brauneri*, *D. saxicola* and the entire complex. The average value of the number of presacral vertebrae is lower (27.3 ± 0.21) than in *D. brauneri* (27.94 ± 0.12), *D. saxicola* (27.86 ± 0.12) and the entire complex (27.64 ± 0.04). There is also a difference in the average number of presacral vertebrae with short ribs, as well as in the upper limit: *D. arribasi* has an average of 5.88 ± 0.11 and an upper limit of 6 vertebrae, while *D. brauneri* has 6.16 ± 0.09 and an upper limit of 7 vertebrae, *D. saxicola* has 6.23 ± 0.07 and an upper limit of 7 vertebrae. Unlike closely related species, *D. arribasi* lacks B-type caudal vertebrae, the closed type of clavicle clearly predominates (70%), and the heart-shaped type of sternal opening is slightly more common.

2. Anomalies of the postcranial skeleton

A study of large samples of Caucasian rock lizards showed are characterized by various anomalies of the postcranial skeleton: asymmetric structure of the ribs and/or transverse processes of the vertebrae, reduction of the ribs, anomalies of the sternal/xiphisternal costal formula, fusion, increase in the number or reduction of the vertebrae. Among them, the atypical costal formula is especially interesting: it was found that changes in the formula can be associated with asymmetric attachment of

TABLE 8. Results of Two-Sample *t*-Test for Quantitative Traits when Comparing *Darevskia caucasica vedenica* from the Kezenoyam Lake Area (ZISP 32587 – 32599) and Type Series (ZISP 17744)

All specimens		Males		Females	
t	*P*	*t*	*P*	*t*	*P*
Number of presacral vertebrae					
2.01	>0.05	2.13	>0.05	2.05	>0.05
Number of posterior presacral vertebrae with short ribs					
2.01	>0.05	2.13	>0.05	2.05	>0.05

the ribs, with the structure of the sternum and/or xiphoid process, and — in rare cases — with fusion of the ribs.

The most common anomalies are the asymmetry of processes of sacral vertebrae (a total of 30 specimens were found among 12 taxa) and the anomaly of ribs in presacral vertebra, in which vertebra 21 – 24 has a long rib on one side and a short one on the other (a total of 59 specimens were found among 16 taxa) (Table 10). Anomalies are most often found in *Darevskia* (*rudis*): the number of abnormal specimens is 19.3% of the sample, while *D. r. chechenica* is the taxon with the largest number of abnormal specimens in relation to normal ones (26.2%) (Table 11). The greatest diversity of anomalies is observed among representatives of the *Darevskia* (*praticola*) — 8, in the *Darevskia* (*rudis*) and *Darevskia* (*saxicola*) 6 each, in that of the *Darevskia* (*caucasica*) — 4. The same complex has the highest S_{ai} index. The leader in the frequency of occurrence of anomalies is the *Darevskia* (*rudis*). The smallest number of anomalies was found in *D. arribasi*, *D. p. hyrcanica*, *D. p. loriensis*, and *D. r. macromaculata* (Table 12).

The most common anomaly is the asymmetrical structure of the ribs at the 21st, 22nd or 23rd presacral vertebra, the rarest are the reduction or increase in the number of vertebrae, atypical form of the processes of the sacral vertebrae, reduction of the ribs at the 4th presacral

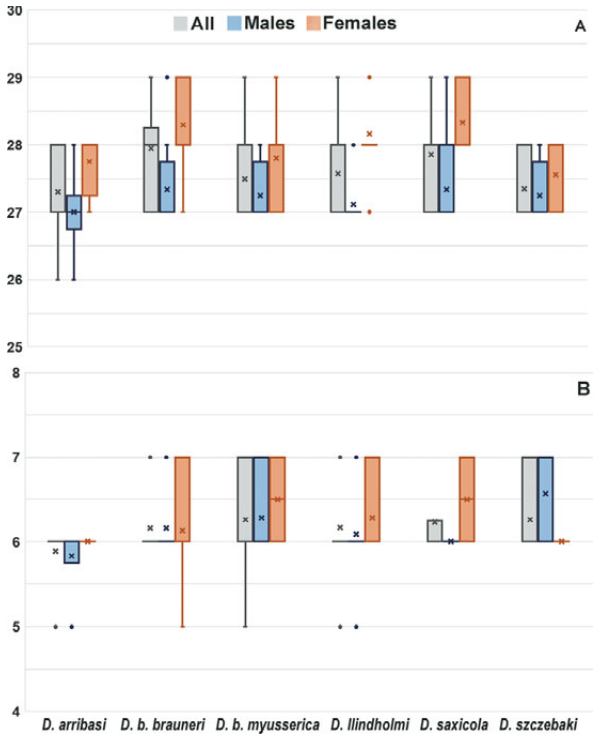

Fig. 5. Box plot of the number of presacral vertebrae (A) and the number of last presacral vertebrae with short ribs (B) in taxa of *Darevskia* (*saxicola*).

TABLE 9. Comparison of the Postcranial Skeleton of Taxa of *Darevskia* (*saxicola*)

Characteristics	*D. arribasi*	*D. b. brauneri*	*D. b. myusserica*	*D. lindholmi*	*D. saxicola*	*D. szczerbaki*
Number of presacral vertebrae min-max, $M \pm m$ (n)	26 – 28 27.3 ± 0.21 (10)	27 – 29 27.94 ± 0.12 (34)	27 – 29 27.5 ± 0.11 (28)	27 – 29 27.57 ± 0.06 (103)	27 – 29 27.86 ± 0.12 (36)	27 – 28 27.35 ± 0.11 (20)
Number of posterior presacral vertebrae with short ribs min-max, $M \pm m$ (n)	5 – 6 5.88 ± 0.11 (9)	5 – 7 6.16 ± 0.09 (31)	5 – 7 6.25 ± 0.11 (27)	5 – 7 6.16 ± 0.03 (101)	6 – 7 6.23 ± 0.07 (34)	6 – 7 6.26 ± 0.10 (19)
Type of the first autotomic tail vertebrae, % (n)	(10)	(32)	(18)	(99)	(39)	(19)
A-type	100	93.75	55.6	97.98	84.6	100
B-type	0	6.25	44.4	2.02	15.4	0
Sternal/xiphisternal costal formula, % (n)	(9)	(35)	(18)	(105)	(39)	(20)
3 + 1	0	0	5.6	0	2.6	0
3 + 2	100	100	94.4	100	97.4	100
3 + 3	0	0	0	0	0	0
Ossified ribs at the third cervical vertebra, % (n)	(10)	(36)	(28)	(106)	(39)	(20)
Missing	100	100	100	100	97.4	100
Available	0	0	0	0	2.6	0
Clavicle type, % (n)	(10)	(35)	(18)	(99)	(38)	(20)
Open	30.0	60.0	77.8	44.4	78.9	50.0
Closed	70.0	40.0	22.2	55.6	21.1	50.0
Type of sternal fontanelle, % (n)	(10)	(34)	(16)	(76)	(32)	(16)
Heart-shaped	40.0	32.4	37.5	32.9	25.0	25.0
Oval	60.0	67.6	62.5	67.1	75.0	75.0

vertebra, fusion of the ribs, and the presence of two ribs on one side of the vertebra. It can be assumed that the appearance of anomalies is associated with the embryonic morphogenesis. However, in some cases, the influence of trauma on the disruption of the structure of skeletal structures (post-traumatic morphogenesis) cannot be excluded.

3. Taxonomic conclusions

If we summarize the data we obtained from the skeleton of *Darevskia* (*praticola*) and the available information on the biology of these lizards (Orlova, 1978; Stugren, 1984; Ljubisavljevic et al., 2006; Tuniyev et al., 2011, 2013; Doronin, 2015; Arribas, 2024), then it is necessary to revise the taxonomic status of the complex by describing a new subgenus. This does not contradict the logic in the publication of Arribas (2024).

TABLE 10. Rock Lizards of *Darevskia* (*praticola*) and *Darevskia* (*rudis*) with Occurrence of Anomalies of the Postcranial Skeleton

Taxon	Number of specimens	Number of specimens with anomalies, %
***Darevskia* (*praticola*)**		
D. pontica	99	19 (19.2)
D. praticola hyrcanica	19	3 (15.8)
D. praticola loriensis	11	1 (9.1)
D. p. praticola	90	15 (16.7)
The whole complex	219	38 (17.4)
***Darevskia* (*rudis*)**		
D. r. chechenica	42	11 (26.2)
D. r. macromaculata	19	2 (10.5)
D. r. obscura	56	10 (17.9)
D. r. svanetica	27	5 (18.5)
The whole complex	144	28 (19.4)

TABLE 11. Individual Spectrum of Anomalies of the Postcranial Skeleton of Rock Lizards of *Darevskia* (*praticola*) and *Darevskia* (*rudis*)

Taxon	Total number of anomalies found	Number of anomalies in one specimen (S_{ai}) min – max	Average number of anomalies per specimen (S_{ai})
***Darevskia* (*praticola*)**			
D. pontica	21	1 – 3	1.11
D. praticola hyrcanica	3	1 – 1	1
D. praticola loriensis	1	1 – 1	1
D. p. praticola	17	1 – 2	1.13
The whole complex	42	1 – 3	1.11
***Darevskia* (*rudis*)**			
D. r. chechenica	11	1 – 1	1
D. r. macromaculata	2	1 – 1	1
D. r. obscura	11	1 – 2	1.1
D. r. svanetica	5	1 – 1	1
The whole complex	29	1 – 2	1.04

Graminilacerta subgen. nov.

https://zoobank.org/6EA31197-B52F-4F66-B9D5-56D9C8F1F012

Type species. *Lacerta praticola* Eversmann, 1834 [= *Darevskia praticola* (Eversmann, 1834)]. Included: *Darevskia* (*Graminilacerta*) *pontica* (Lantz et Cyrén, 1918), comb. nov.; *Darevskia* (*Graminilacerta*) *praticola praticola* (Eversmann, 1834) comb. nov.; *Darevskia* (*Graminilacerta*) *praticola hyrcanica* Tuniyev, Doronin, Kidov et Tuniyev, 2011 comb. nov., *Darevskia* (*Graminilacerta*) *praticola loriensis* Tuniyev, Doronin, Tuniyev, Aghasyan, Kidov et Aghasyan, 2013 comb. nov.; *Darevskia* (*Graminilacerta*) *hungarica* (Sobolevsky, 1930) comb. nov. (Fig. 6).

Diagnosis. Females are larger than males. Head is not flattened, muzzle is short. Postorbital and postfrontal bones are equal in length. Length of contact between postorbital and squamosal bones is a significant value of postorbital bone length (one half or one third). Usually 28 presacral vertebrae in males, and 30 in females with the largest limit of presacral vertebrae (31). They are distinguished by the presence of thin lamellar expansions on the clavicles in their more lateral part, while in other species of the genus these are significantly less developed or only indicated. Significantly high number with B-type caudal vertebrae (1/3 of all studied specimens). Predominantly with cordate sternal fontanelle and closed type of clavicles. Dorsal scales are relatively large, elongated, hexagonal or rhombic, with ribs (scale ribs are absent only on several rows adjacent to ventral scutes). Around the middle of the body there are 30 – 48 scales (in representatives of the nominotypical subgenus *Darevskia* s. s. 47 – 74). The upper side of the body is light brown, brownish-gray, brown or beige with small black spots and dots; there is no green color. There are no blue occelli of the shoulder region. The tail color of most juveniles lacks greenish-blue tones (Fig. 7).

Etymology. A composite name from the "*gramen*, *graminis*" (Latin), meaning grass, grassy, and "*lacerta*" (Latin), meaning lizard. The name refers to the habitat confinement of the lizards of the new subgenus. The name is feminine.

Distribution. Lizards of the subgenus can be found in a region stretching from the Caucasus (Abkhazia, Armenia, Azerbaijan, Georgia, Iran, Russia, and South Ossetia) including the western part of Alborz in the Gilan Province of Iran, to the south of the East European Plain

TABLE 12. Partial Frequency of Anomaly and Relative Occurrence of Anomaly (A_p/A_{ra}) of the Postcranial Skeleton of Rock Lizards of *Darevskia* (*praticola*) and *Darevskia* (*rudis*)

Taxon	Asymmetrical structure of the ribs and/or transverse processes of the vertebrae					Reduction of ribs at the 4th vertebra level	Anomalies of the sternal: xiphisternal costal formula	Fusion, increase in number or reduction of vertebrae		
	Anomaly of symmetry of the processes of the sacral vertebrae	Anomaly of the shape of the processes of the sacral vertebrae	The 21st, 22nd, 23rd, or 24th vertebra has a long rib on one side and a short one on the other	Two ribs on one side of a vertebra	Fusion of two ribs of adjacent vertebrae			Fusion	Increase	Reduction
					***Darevskia* (*praticola*)**					
D. pontica	3% (3 out of 99)/14% (3 out of 21)	—	11.1% (1 out of 99)/52.4% (11 out of 21)	—	—	11.1% (1 out of 99)/4.8% (1 out of 21)	3% (3 out of 99)/14.3% (3 out of 21)	1% (1 out of 99)/4.8% (1 out of 21)	1% (1 out of 99)/4.8% (1 out of 21)	1% (1 out f 99)/4.8% (1 out of 21)
D. praticola hyrcanica	5.3% (1 out of 19)/33.3% (1 out of 3)	—	10.5% (2 out of 19)/66.7% (2 out of 3)	—	—	—	—	—	—	—
D. praticola loriensis	—	—		—	—	—	9.1% (1 out of 11)/11.8% (2 out of 17)	—	—	—
D. p. praticola	4.4% (4 out of 90)/23.5% (4 out of 17)	1.1% (1 out of 90)/5.9% (1 out of 17)	11.1% (10 out of 90)/58.8% (10 out of 17)	—	—	—	2.2% (2 out of 90)/11.8% (2 out of 17)	—	—	—
Complex as a whole	3.7% (8 out of 219)/19% (8 out of 42)	0.5% (1 out of 219)/2.4% (1 out of 42)	10.5% (23 out of 219)/54.8% (23 out of 42)	—	—	0.5% (1 out of 219)/2.4% (1 out of 42)	2.7% (6 out of 219)/14.3% (6 out of 42)	0.5% (1 out of 219)/2.4% (1 out of 42)	0.5% (1 out of 219)/2.4% (1 out of 42)	0.5% (1 out of 219)/2.4% (1 out of 42)
					***Darevskia* (*rudis*)**					
D. r. chechenica	2.4% (1 out of 42)/9.1% (1 out of 11)	—	9.5% (4 out of 42)/36.4% (4 out of 11)	—	—	—	14.3% (6 out of 42)/54.5% (6 out of 11)	—	—	—
D. r. macromaculata	—	—	10.5% (2 out of 19)/100% (2 out of 2)	—	—	—	—	—	—	—
D. r. obscura	3.6% (2 out of 56)/18.2% (2 out of 11)	—	7.1% (4 out of 56)/36.4% (4 out of 11)	1.8% (1 out of 56)/9.1% (1 out of 11)	1.8% (1 out of 56)/9.1% (1 out of 11)		5.4% (3 out of 56)/27.3% (3 out of 11)	1.8% (1 out of 56)/9.1% (1 out of 11)	—	—
D. r. svanetica	11.1% (3 out of 27)/60% (3 out of 5)	—	—	—	—	—	7.4% (2 out of 27)/40% (2 out of 5)	—	—	—
Complex as a whole	4.2% (6 out of 144)/20.7% (6 out of 29)	—	6.9% (10 out of 144)/34.5% (10 out of 29)	0.7% (1 out of 144)/3.5% (1 out of 29)	0.7% (1 out of 144)/3.5% (1 out of 29)	—	7.6% (11 out of 144)/37.9% (11 out of 29)	0.7% (1 out of 144)/3.5% (1 out of 29)	—	—

Fig. 6. Male of *Darevskia p. praticola*, Staropavlovskaya Village, Stavropol Krai, Russia, 04.05.2015, photo by I. V. Doronin (A); female of *D. p. praticola*, on the road from Maryinskaya village to Zolskoye Village, Stavropol Krai, Russia, 05.08.2018, photo by I. V. Doronin (B); male of *D. pontica*, Afipsip Village, Adygea, Russia, 15.06.2013, photo by I. V. Doronin (C); male of *D. hungarica*, Thrace, Greece, 11.05.2011, photo by T. Panner (D).

(Russian Plain) in the Rostov Oblast of Russia, with an isolated population in the Balkans (Bulgaria, Greece, Kosovo, Romania, Serbia, and Turkey) that is the only representative of the genus there — a unique range among Caucasian rock lizards. This is the longest range in the genus: from west to east approximately 2500 km and from north to south approximately 1400 km. These lizards are not sclerophilous, preferring well-sunny places in foothills, floodplains and mountain forests (mainly deciduous), sometimes entering meadows and steppes bordering forests (Fig. 8). They inhabit also anthropogenically transformed landscapes: gardens, orchards, wastelands, cemeteries in populated areas, or artificial forest plantations. The altitudinal distribution ranges from 0 to 2000 m a.s.l.

Remarks. The composition of the new subgenus is given according to the publications of Tuniyev et al. (2011, 2013) and Doronin (2016). We designate the Balkan populations as *D. hungarica* based on the differences found in publications of Freitas et al. (2016, 2022). Our study did not include specimens of *D. hungarica* [the lectotype and two paralectotypes from the ZISP have not been found at present (Doronin, 2016)], but the taxonomic conclusions can certainly be extended to this taxon. At present, we cannot accept the conclusion of Saberi-Pirooz et al. (2018) about the synonymisation of *D. p. loriensis* with *D. p. hyrcanica*, and the subspecific status of *D. pontica*. The study of these authors did not include the nominotypical subspecies *D. p. praticola*, which is crucial for systematic decisions. The genetic distances between *D. pontica* and *D. praticola* are comparable with the distances between other recognised species of rock lizards.

The phylogenetic closeness of the *Graminilacerta* subgen. nov. and *Darevskia* subgen. s. s., which differ sharply in ecology and morphology, is noteworthy. This is an example of a change of stations and the emergence of new morphological adaptations, as well as the emergence of morphological features similar to those of an unrelated taxon living in similar conditions. *Darevskia*

Fig. 7. Juvenile *Darevskia p. praticola*, Staropavlovskaya Village, Stavropol Krai, Russia, 14.08.2025, photo by I. V. Doronin.

caucasica is similar in skeletal features (predominance of closed clavicles and a significant proportion with a cordate opening of the sternum, the presence of a variant of the 3 + 3 costal formula), larger size of females, proportions of the body and limbs, pholidosis, and coloration. It should be noted that in terms of habitat parameters in the genus with representatives of the new subgenus, *D. c. vedenica* shows the greatest similarity. It adheres to overgrown places of boulders and rock fragments in the sole part of rock outcrops, forest edges, clearings, roadsides, gullies, river beds and streams, and it penetrates the depths of the forest, where it can be found on the trunks of fallen trees (Lotiev and Doronin, 2011). In general, Caucasian rock lizards are characterized by the adaptation to a wide range of biotopes. Thus, for the xerophilous and sclerophilic *D. daghestanica*, a transition to life habits towards a mesophilic forest biotope without rock outcrops was described (Doronin et al., 2021).

The experimental protocols were approved by the Bioethics Commission of the Zoological Institute of the Russian Academy of Sciences (conclusion No. 1-3/15-06-2021).

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Fig. 8. Biotope of *Darevskia pontica* — edge of an ash-hornbeam forest on Strizhament Mount, Stavropol Krai, Russia, 5.08.2012 (A); biotope of *Darevskia p. praticola* — roadside in oak-ash forest "Safonova Dacha," Stavropol Krai, Russia, 12.08.2015 (B), photo by I. V. Doronin.

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Appendix

TABLE 1. Detail of the Specimens of Lizards of *Darevskia* (*caucasica*), *Darevskia* (*praticola*), *Darevskia* (*rudis*), and *Darevskia* (*saxicola*) Species Used in Our Study of the the Postcranial Skeleton

Collection numbers	Number of specimens	Taxon/locality	Geographical coordinates N, E	Collector (-s)	Date of collecting
		Darevskia* (*caucasica*)** ***Darevskia caucasica vedenica			
ZISP 32587 – 32599	13	Russia, Dagestan, Botlikhsky District, watershed of the Okholitlau and Khulhulau Rivers	42°50′55.9″ 46°10′42.4″	L. F. Mazanaeva	28.08.2022
		Darevskia* (*praticola*)** ***Darevskia pontica			
ZISP 22853 lectotype	1	Abkhazia, vicinity of Gagra	43°18′03.6″ 40°15′51.1″	S. F. Tzarevsky	06.1911
ZISP 22852 paralectotypes	2	Abkhazia, Gudauta	43°06′12.2″ 40°38′08.5″	—»—	07.1911
ZISP 5278	1	Abkhazia, Sukhum-Kale (= Sukhum, Sukhumi)	43°01′50.2″ 41°01′16.0″	V. N. Czerniavsky	1879
ZISP 5279 paralectotype	1				
ZISP 5280 paralectotypes	5				
ZISP 22223	16	Russia, Adygea, Maykopsky District, vicinity of Dakhovskaya Village, Nickel Village	44°14′18.2″ 40°12′27.4″	K. D. Milto	16.06 – 04.07.2000
ZISP 19112	11	Russia, Adygea, Takhtamukaysky District, between Enem and Afipsky	44°54′15.1″ 38°52′59.9″	O. P. Bogdanov	02.03 – 01.04.1972
ZISP 22854 paralectotype	1	Russia, Krasnodar Krai, Sochi, Khosta District, Mountain Bol′shoi Akhun	43°33′01.4″ 39°49′09.8″	N. S. Dorovatovsky	10.06.1912
ZISP 15204	1	Russia, Krasnodar Krai, Mostovskoy District, Caucasian Biosphere Reserve, on the road from the Veriyut (= Nikitino Village) on the Malaya Laba River to the Malyi Pambak Mount	43°53′05.6″ 40°31′40.8″	A. N. Bartenef	15.07.1930
ZISP 18966	56	Russia, Krasnodar Krai, Seversky District, Krepostnaya Village	44°42′34.2″ 38°40′24.2″	Kazakova	22 – 25.07.1972
ZISP 32068 – 32069	2	Russia, Rostov Oblast, Azovsky District, vicinity of Sonino Village on the bank of an oxbow lake of the Eya River	46°38′15.7″ 39°00′37.5″	N. G. Smirnova	01.05.2022
ZISP 31623 – 31624	2	Russia, Stavropol Krai, Shpakovsky District, Tatarka Village	44°57′46.5″ 41°56′42.2″	N. V. Klyushnikova	01.07.2021

Collection numbers	Number of specimens	Taxon/locality	Geographical coordinates N, E	Collector (-s)	Date of collecting
		Darevskia praticola hyrcanica			
ZISP 12632 – 12633 paratypes	2	Azerbaijan, Astara District, Kaladagna Village	38°32′25.8″ 48°49′10.6″	Baldamus	30.03.1912
ZISP 26601 – 26606 topotypes	6	Azerbaijan, Astara District, Talysh Ridge, Natural Boundary of Gada-Zyga-Hi	38°28′00.0″ 48°35′00.0″	A. A. Kidov	18.08.2009
ZISP 29826 – 29828 topotypes	3		38°47′03.8″ 48°35′56.6″	—»—	04.2014
ZISP 32945 topotype	1		38°31′09.3″ 48°43′30.5″	S. N. Litvinchuk	02.11.2018
ZISP 12301 paratype	1	Azerbaijan, Lankaran District, Lerik	38°46′32.2″ 48°25′21.0″	N. A. Kirichenko	14.05.1909
ZISP 30056	1	Azerbaijan, Lerik District, vicinity of Veri Village	38°40′17.2″ 48°30′08.7″	D. Rakimov	16.08.1953
ZISP 30057 – 30058	2	Azerbaijan, Lerik District, vicinity of Siev Village	38°40′14.9″ 48°35′51.8″	—»—	22.07.1953
ZISP 12630 paratype	1	Iran, Gilan Province, Sharferud (= Sharif Rud, Sefid-rud) River, Anzali Gulf	37°27′02.9″ 49°55′38.3″	L. F. Młokosiewicz	13.09.1913
ZISP 12634 paratype	1	Iran, Gilan Province, Heyran between Astara and Ardabil	38°24′30.2″ 48°35′51.0″	L. A. Lantz	05.04.1912
ZISP 12635 paratype	1	Iran, Gilan Province, Elburs Mountain (= Ridge), vicinity of Ardebil	37°35′09.2″ 49°00′45.7″	—»—	
		Darevskia praticola loriensis			
ZISP 17075 paratypes	11	Armenia, vicinity of Vanadzor (= Karakilisa)	40°49′35.0″ 44°27′44.3″	I. S. Darevsky	23.06.1956
		Darevskia praticola praticola			
ZISP 29845 – 29846	2	Russia, Kabardino-Balkaria, Nalchik	43°28′02.1″ 43°35′33.3″	I. V. Doronin	14.09.2017
ZISP 7203	1	Russia, North Ossetia-Alania, vicinity of Vladikavkaz, Tarskaya (= Il) Mount	42°59′28.8″ 44°43′35.6″	A. N. Ananov	1886
ZISP 23562	10	Russia, Stavropol Krai, Budyonnovsky District, floodplain of the Kuma river, Orlovka Village	44°40′43.0″ 44°09′13.7″	K. Yu. Lotiev, K. D. Milto	30.06.2005
ZISP 26532 – 26534	3	Russia, Stavropol Krai, Georgievskiy District, vicinity of Krasnokumskoe Village, State Botanical Reserve ″Safonova Dacha″	44°11′08.9″ 43°30′34.6″	I. V. Doronin	01.08.2012
ZISP 16307	50	Russia, Stavropol Krai, Pyatigorsk	44°03′44.6″ 43°00′49.7″	—	1911
ZISP 31625	1	Russia, Stavropol Krai, Kirovsky District, Staropavlovskaya Village	43°50′31.4″ 43°38′26.4″	M. A. Doronina	08.07.2021
ZISP 25761 – 25765	5	Russia, Stavropol Krai, Predgorny District, Lysaya Mountain	44°06′04.0″ 43°12′05.8″	I. V. Doronin	23.07.2006
ZISP 32121	1	Russia, Stavropol Krai, Predgorny District, cordon of the Bolshoy Essentuchok Nature Reserve	44°00′40.6″ 42°42′22.7″	—»—	06.07.2022
ZISP 31088	1	Russia, Stavropol Krai, Predgorny District, Nizhneetoksky Village	44°00′12.3″ 43°22′18.9″	—»—	29.05.2020
ZISP 22125	15	Russia, Stavropol Krai, Sovietsky, Georgievsky and Mineralovodsky Districts, the floodplain of the Kuma River from the town of Zelenokumsk to the town of Mineralnye Vody	43°55′18.5″ 42°43′08.8″; 44°16′00.5″ 43°41′48.1″; 44°13′53.0″ 43°15′06.5″; 44°13′16.0″ 43°11′06.0″	—	2000
ZISP 31538	1	South Ossetia, Dzau District, Magkota Village	42°28′01.0″ 43°42′53.0″	K. Yu. Lotiev, K. D. Milto, P. A. Dzhelali	27.05.2021

Collection numbers	Number of specimens	Taxon/locality	Geographical coordinates N, E	Collector (-s)	Date of collecting
		Darevskia* (*rudis*)** ***Darevskia rudis chechenica			
ZISP 19545 paratypes	15	Russia, Dagestan, Tlyaratinsky District, Tlyarata Village	42°06′29.0″ 46°21′18.0″	Seryogin, M. M. Alkhasov	10 – 12.09.1972
ZISP 17878 paratypes	13	Russia, Ingushetia, Dzheyrakhsky District, gorge of the Armhi (= Makaldon) River in 8 km above the confluence of the Terek River	42°49′03.0″ 44°41′48.0″	I. S. Darevsky	18.08.1965
ZISP 18374 paratypes	5	Russia, Ingushetia, Dzheyrakhsky District, vicinity of Armhi resort	42°48′49.0″ 44°42′34.0″	—»—	7.07.1973
ZISP 18781 paratypes	6	Russia, Chechnya, Shatoysky District, vicinity of Sovetskoye (= Shatoy) Village	42°52′00.0″ 45°41′00.0″	—»—	21.09.1976
		Darevskia rudis macromaculata			
ZISP 17440 paratypes	18	Georgia, Samtskhe-Javakheti Region, Gorge of the Akhalkalakichay (= Akhalkalak-Chay, Paravani) River lower (south) of the Akhalkalaki	41°51′48.8″ 44°21′07.7″	I. S. Darevsky	21.07.1959
ZISP 17940.6 holotype	1	Georgia, Samtskhe-Javakheti Region, vicinity of Akhalkalaki	41°23′00.0″ 43°29′00.0″	—»—	24.06.1961
		Darevskia rudis obscura			
ZISP 17059 paralectotypes	3	Georgia, Samtskhe-Javakheti, Borjomi, Banis-Tskhevi (= Bonis-Hevi) River Valley	41°46′28.0″ 43°14′43.0″	L. A. Lantz	27.05.1914
ZISP 14436 paralectotype	1	Georgia, Samtskhe-Javakheti, Borjomi, Borjomka (= Borjomula) River Valley	41°50′14.1″ 43°23′19.9″	—»—	28.05.1914
ZISP 15402 paralectotype	1			—»—	
ZISP 17058 paralectotypes	2			—»—	
ZISP 17172 paralectotypes	15			—»—	
ZISP 14440 paralectotype	1	Georgia, Samtskhe-Javakheti, Borjomi, road to Akhaltsikhe	41°49′38.5″ 43°20′55.0″	—»—	28.05.1914
ZISP 14435 paralectotype	1			—»—	30.05.1914
ZISP 14437 paralectotype	1			—»—	
ZISP 14438 paralectotype	1			—»—	
ZISP 16290 paralectotype	1			—»—	
ZISP 17057 paralectotypes	3			—»—	
ZISP 17171.1 lectotype	1			—»—	
ZISP 17171.2 – 26 paralectotypes	25			—»—	
		Darevskia rudis svanetica			
ZISP 17875.1 holotype	1	Georgia, Samegrelo-Zemo Svaneti Region, vicinity of Mestia	43°03′00.0″ 42°45′00.0″	I. S. Darevsky	13.08.1965
ZISP 17875 paratypes	26			—»—	
ZISP 17814 paratypes		Georgia, Samegrelo-Zemo Svaneti Region, the gorge of the Inguri River at the confluence of the Nakra (= Neukra) River	43°02′49.0″ 42°22′52.0″	—»—	29.06.1964
		Darevskia* (*saxicola*)** ***Darevskia arribasi			
ZISP 19433 paratypes	10	South Ossetia, Dzau District, upper reaches of the Kvirila River, Tsonskoe Gorge, vicinity of Ertso Lake	42°28′01.2″ 43°45′03.2″	I. S. Darevsky	07.08.1979