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The osteology of the lacertid genus *Darevskia* Arribas, 1999 (Squamata, Lacertidae)

OSCAR ARRIBAS*
IES Castilla. Junta de Castilla y León. 42003 Soria. Spain
oscar.arramo@educa.jcyl.es; *https://orcid.org/0000-0003-4613-5237*
**Corresponding author*

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OSCAR ARRIBAS
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Abstract

A total of 230 cleared and alizarin stained and 136 radiographed specimens of *Darevskia* belonging to 47 nominal taxa (species, subspecies or singular clades) including the seven parthenogenetic ones and a triploid hybrid were studied. Sixteen osteological characters in all the tried species were analyzed. These characters by corporal regions were: skull characters: 1.—number of premaxillary teeth; 2.—number of maxillary teeth; 3.—number of dentary teeth; 4.—teeth morphology; 5.—presence of anterolateral process in the postfrontal bone; 6.—presence of anteromedial process in the postorbital bone; 7.—comparative lengths of the postorbital and postfrontal bones; 8.—overlap degree between the postorbital and the squamosal bones. Postcranial characters: 9.—existence of visible (ossified) ribs associated with the third presacral vertebrae; 10.—sternal/xiphisternal costal formula and presence of inscriptional ribs; 11.—number of presacral vertebrae; 12.—number of posterior dorsal vertebrae (short presacral ribs); 13.—presence and form of the sternal fontanelle; 14.—form of the clavicles (emarginated or marginated); 15.—interclavicle form; 16.—morphology of first autotomic vertebrae of the tail.

Our goals were to characterize osteologically the different species of *Darevskia*, to contrast their relationships traced from osteological traits with the available genetic-derived phylogenies of the group, to compare the osteological characteristics of the parthenogenetic species with their bisexual parental species, and to comment on their parentage and character polarity. Finally, we aimed to search for osteological characteristics of the different groups within *Darevskia*, diagnosing them for the first time. The results, commented on by characters, are available in the main text, and taxa characteristics are easily consultable and condensed in Table 1.

Osteological characteristics of *Darevskia*, together with available phylogenetic trees, have permitted us to define some new groups within *Darevskia* (*raddei*, *chlorogaster*, *defilippi*, and *parvula* new groups) (Appendix 3), which are reciprocally monophyletic and have diagnostic characteristics. All of them are diagnosed and named as subgenera to be used if necessary, instead of the partial, old and not always comprehensive groups.

Key words: Sauria, Lacertini, *Darevskia*, Caucasus, Anatolia, Osteology, teeth, skull, vertebrae, ribs, clavicle, interclavicle, sternal fontanelle, systematics, taxonomy, parthenogenetic species, character polarity, species groups, new subgenera

Introduction

Osteology brings a set of complementary morphological characters hidden inside the lizard's bodies. As there are few useful for field identification or quick diagnosis of specimens, this morphological discipline is little studied nowadays and perhaps abandoned in favor of genetics or the classic approach of external morphology, which is easier if you have the right equipment and provides faster results. Moreover, although it is not very complex to access the bones, it requires a good amount of experience and a certain "touch of art" to obtain good results in the clearing or skeletonization processes, and especially a lot of expertise to interpret and compare the results.

Apart from mentions in publications about classic general osteology of reptiles, like those from Camp (1923) and Romer (1956), very little attention has been devoted to the osteological variations in the Lacertidae for taxonomic purposes. Most of the classical works on the subject are nearly a century old. Skull morphology was thoroughly studied by Mehely (1907, 1909, 1910), where the careful morphological study also accompanies the description of the skull, paying special attention to the form of the postorbital, postfrontal, premaxillary teeth number, maxilla, dentary, etc. Other authors, like Mehely's rival G.A. Boulenger, did not use osteological characteristics as he didn't want to damage specimens but instead counted teeth by passing carefully a pin along the throat (Adler, 1989). Likewise, Klemmer's work (Klemmer, 1957) is also noteworthy, as it pays special attention to the sexual dimorphism in the development of the skull osteoderms (*crusta calcarea*) and the different degrees of platycephaly in different species as a function of their more or less saxicolous habitat. More recently, Barahona & Barbadillo (1997, 1998) and Barahona *et al.* (1998) did excellent osteological work on several Spanish lizards. Concerning the vertebral column, the classic works of Siebenrock (1894), Kühne (1913), and Hoffstetter & Gasc (1969) are outstanding, and related to the caudal region, the work of Etheridge (1967).

In recent years, the works of Arnold (1973, 1989) reviewed a good number of osteological characters within a wide spectrum of species (many of which find their first and only osteological reference there until the comprehensive work of Arribas, 1998 for the European and Caucasian mountain lizards), using this information together with others from morphological origins for the inference of phylogenies of the Lacertidae and the delimitation and diagnosis of some of its genera (Arribas 1999). The last exponent of the usefulness of osteology as a diagnostic character in groups of notable convergence and parallelism can be found in Arnold *et al.* (2007), in their complete revision of the

Lacertini. Recently published is the noteworthy paper about skull identification of a fairly complete representation of the main Lacertidae and other Sauria genera from Europe (Villa & Delfino, 2019) aimed at paleontological diagnosis. Other references to the use of osteological characters for specific species studies appeared in Barbadillo & Sanz (1983), Perez-Mellado *et al.* (1993), Arribas (1993, 1994, 1997, 1999, 2012), Barbadillo & Martinez Solano (2002), Müller (2002), Arribas & Odierna (2005), Arribas *et al.* (2006, 2013, 2018), Ljubisavljevic *et al.* (2007), and the very good paper on *Lacerta* s. str. from Čerňansky & Syromyatnikova (2019). For Eremiadini, Arnold (1983), Dubke *et al.* (2018), and Khosravani *et al.* (2011) are equally interesting references.

The genus *Darevskia* Arribas, 1999 (Type species: *Lacerta saxicola* Eversmann, 1834 [=*Darevskia saxicola* (Eversmann, 1834)]) is a genus with more than 40 species (seven of them parthenogenetic clonal "species") distributed in the Caucasus region, Crimea, and mountain areas of Anatolia, eastwards to the Alborz mountains in Iran and Kopet Dagh on the Iran-Turkmenistan border; with one species (*D. praticola*) reaching the eastern Balkan peninsula (Arnold *et al.* 2007). See Appendix 1 (Taxonomic Remarks) for nomenclatural issues and species criteria chosen. *Darevskia* is characterized by the following combination of characters: 27–28 presacral vertebrae in males, with only one postnasal scale. Other more widely distributed features include: head and body depressed or not, supraocular osteoderms fenestrated or intact in adults, usually seven premaxillary teeth, inscriptional ribs present in some species, tail often brightly colored in hatchlings, hemipenial microornamentation of crown-shaped tubercles. A few species are parthenogenetic, and males of some species bite the thigh of the female during copulation, alone or together with the more usual belly grasping (Arnold *et al.*, 2007). *Darevskia* species constitute a monophyletic group within the Lacertini and possess a tandemly repeated (satellite) DNA family named CLsat, and nuclear DNA markers from the SINE family named Squam1-34, both exclusive to the genus (Grechko *et al.*, 1999; Rudykh et al, 1999, 2002; Ciobanu *et al.* 2003, 2004; Kosushkin & Grechko, 2013).

Darevskia is a difficult group that seems to have had a rapid and explosive speciation process, sometimes perhaps still incomplete and very recent, with numerous species frequently separated by relativelly low genetic distances. Moreover, hybridization occurs and had occurred frequently, which converts its phylogenetic reconstructions (especially the mitochondrially based ones) into a minefield with a kind of phylogenetic "wormholes" that "transport" specimens to distant parts of their respective phylogenies due to mtDNA flux between taxa. These specimens with mtDNA from other species, together with the possibility of confusion in the identification of a sample, mean that here and there in phylogenetic reconstructions can be misleading specimens, which can lead to serious errors in the location of some taxa (see Appendix 1: Taxonomic Remarks for several examples of this).

Ingroup systematics and biology of many *Darevskia* were extensively reviewed by several authors from Morphology and especially Genetics. See Appendix I (Taxonomic Remarks) for details about these reconstructions. Several groups can be distinguished among *Darevskia* (see especially Murphy *et al.*, 2000). The different authors have tried to fit their results between Murphy's groups, although since not all the significant taxa were represented in all the analyses, the results in the delimitation of these groups have been uneven. In reality, these discrepancies are because there are more monophyletic groups within *Darevskia* than those defined in Murphy *et al.* (2000). These groups and their diagnoses can be seen in Appendix 3 (*Darevskia* groups) where they are named as subgenera, but we will not use these "new" groups in the text to facilitate the correct interpretation of the results that lead to their definition. A good indication that these groups belong to the same genus is that they hybridized with each other occasionally, as well in the past giving rise to the parthenogenetic species.

For an outline of the ecology, biology, and speciation of *Darevskia*, the works of Darevsky (1967) and Tarkhnishvili (2012) are strongly recommended. Likewise, and without giving rise to new parthenogenetic species, the species of the genus *Darevskia* hybridize widely, and the cases described are very numerous (see these hybridizations and their references in Appendix 2: Hybrids).

Materials and Methods

2.1. Studied Specimens

The numbers of studied specimens, as well as their origin localities, are indicated in Appendix 4. The first number represents the specimens cleared and alizarin stained, while the second number (in parentheses) refers to those studied using X-rays. The species included and their osteological traits are summarized in Table 1, which contains all the osteological information and serves as the core consultable data in this study.

TABLE 1. Condensed information about the osteological characteristics of all the taxa studied. M is males, F females; a bar (/) OR a "=" mean equally probable states; greater, smaller, or equal signs (< > =) mean relative dispositions of bone proportions; a parenthesis "( )" a rare character state or value; a double parenthesis "(( ))" a very rare or exceptional state; (red.) means reduced (but still present); Ciphers among brackets "[ ]" are sternal-xiphisternal formulae, and numbers following them, inscriptional ribs. From left to right, Taxa; Number of premaxillary teeth; Maxillary teeth (average and range); Dentary teeth (average and range); Teeth shape (Un=unicuspid; Bi=bicuspid; Tr=tricuspid); Total presacral vertebrae; ossified ribs on third presacral vertebra; Claviculae type (O=open, C=closed); Interclavicle type († pure cruciform; Ψ= directed forwards; ⋔=directed backwards); Sternal fontanelle (O=oval, C= cordiform, IC=irregular cordiform, IO=irregular oval); Sternal-xiphisternal formula (see above), Postfrontal and postorbital relative lengths (see above); Postfrontal anterolateral process (presence or absence); Postorbital anteromedial process (presence/absence); Squamosal overlap with postorbital (approximated percentage of overlap).

TAXA	Pre-maxil-lary teeth	Maxil-lary teeth	Dentary teeth	Teeth (Unicus-pid/Bicus-pid)	Total Presacral vertebrae	Short Presacral vertebrae	Ossified ribs on third presacral vert.	Pattern of Tail verte-brae	Cla-vicu-lae typus	Inter-clavi-cle †Ψ⋔	Sternal Fonta-nellae	Sternal-Xi-phisternal formula	Postfron-tal and Postorbit-al relative lengths	Postfron-tal an-terolateral process	Postorbital antero-medial process	Squamosal overlap with Postorbital	N
Darevskia clarkorum	7	16.8 [15–18]	20.7 [17–22]	Un=Bi	M 27/28 F 28/29	M 5–6 F 6	NOT (yes)	A (B)	O = C	†	O (red)	[3+2] 1	Po<<Pf (<=)	YES	YES	>1/3 <1/4	12
Darevskia mixta	7	17.6 [16–19]	23 [22–25]	Bi>Un	M 27 F 28/29	M 6 F 5/6	NOT	A (B)	O = C	† = Ψ	IC (O)	[3+2] 1	Po<<Pf	YES	NOT (red)	1/3–1/4	4
Darevskia dryada	7	17.25 [15–20]	24 [22–26]	Un<=Bi	M 27 F --	M 5–6 F --	NOT	A (B)	O = C	†⋔	O	[3+2] 1	Po<<Pf	YES	YES	1/3–1/6	2
Darevskia derjugini	7 (8)	17.3 [15–20]	21 [19–24]	Un=Bi	M 27 (26) F 28 ((29/27))	M 5/6 F 6	NOT ((yes))	A ((B))	O ((C))	† (Ψ)	O/C/IC	[3+2] 0/1/2	Po<=Pf	YES	NOT (red.)	1/2–1/3	6
Darevskia daghestanica	6/7 (4/5)	15 [12–17]	17.2 [13–21]	Un=Bi	M 27 F 28/29	M 6 F 6/7	NOT ((yes))	A ((B))	O = C	† (Ψ)	O/I/C	[3+2] 1/0 (([3+3]))	Po<=Pf	YES	NOT ((very small))	1/3–1/4	8
Darevskia c. caucasica	6/7	16.3 [14–18]	20.8 [19–23]	Bi>Un	M 26/27 F 28	M 5 H 6	NOT	B ((A))	C (O)	†Ψ⋔	O	[3+2] 1/0	Po<=Pf	YES	YES	1/3 (1/2–1/4)	3
Darevskia caucasica vedenica	7	16.5 [15–18]	21.5 [21–22]	Bi>Un	M 27 F 28	M 5/6 F 6	NOT	A ((B))	C	⋔	O	[3+2] 2	Po=Pf	YES	YES (red.)	1/3–1/2	2
Darevskia chlorogaster	9 (10)	18.3 [16–20]	23.3 [20–27]	Bi>Un	M 27 ((26/28)) F 28/29	M 6 F 7	NOT ((2 & 3 cart))	A (B)	O (C)	Ψ (†) ((⋔))	O/IO	[3+2] 1(0)	Po<Pf	YES	YES	1/3 (1/2–1/5)	6

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TABLE 1. (Continued)

TAXA	Pre-maxillary teeth	Maxillary teeth	Dentary teeth	Teeth (Unicuspid/Bicuspid)	Total Presacral vertebrae	Short Presacral vertebrae	Ossified ribs on third presacral vert.	Pattern of Tail vertebrae	Clavicu-lae typus	Inter-clavicle †Ψ⋔	Sternal Fonta-nellae	Sternal-Xiphisternal formula	Postfrontal and Postorbital relative lengths	Postfrontal anterolateral process	Postorbital antero-medial process	Squamosal overlap with Postorbital	N
Darevskia raddei raddei	7	17.3 [17–18]	22 [21–23]	Bi>Un	M 28 F 29–30	M 6 F 6–7	NOT ((yes))	B (A)	O	†	O	[3+2] 1(0)	Po<<Pf	YES	YES (red.)	1/4 (1/3–1/5)	5
Darevskia raddei vanensis	7	18 [17–19]	20.5 [20–21]	Bi>Un	M 28 F 29	M 6 F 7	NOT	B	O	⋔	O	[3+2] 1	Po<=Pf	YES	NOT	1/3	2
Darevskia nairensis	7	18 [17–19]	22.5 [21–24]	Bi>Un	M 28 F 29	M 5–7 F 6	NOT	A (B)	O	Ψ⋔	O(IO)	[3+2] 1/0	Po<=Pf	YES	YES	1/3 (1/4)	2
Darevskia defilippii	7 (6)	15.3 [13–17]	19.8 [19–20]	Bi>Un	M 27 F 28	M 6 F 6	NOT	A	O	Ψ	O(IO)	[3+2] 0/1	Po=Pf (<)	YES	YES	1/3	3
Darevskia brauneri	7	18.4 [17–20]	23 (21–26)	Bi>>Un	M 27 F 28	M 6 F 6	NOT (cart.)	A	O	† Ψ ⋔	O ((C))	[3+2] 1/0	Po<<Pf	YES	YES (red.?)	<1/3 ((1/10))	5
Darevskia lindholmi	7	17.5 [17–18]	22 [21–23]	Bi>Un	M 27 F 28	M 6 F 6	NOT (cart.)	A (B)	O	Ψ	O	[3+2] 1	Po<<Pf	YES	YES	>1/5	2
Darevskia szczerbaki	8	19	21	Bi>Un	M 27 F 28(¿)	M 6 F 6(¿)	NOT	A	O	†	O	[3+2] 1	Po<Pf	YES	YES	1/6	1
Darevskia saxícola	7 (9) ((4))	17.3 [16–18]	21.5 [19–24]	Bi>Un	M 27 F 28	M 6 F 6	NOT	B (A)	O	† ⋔	O	[3+2] 1	Po<<Pf	YES	Red. (NOT)	1/10<1/5<1/4	3
Darevskia alpina	7	17.2 [16–18]	21 [18–25]	Bi>Un (tri)	M27(26) F28(29)	M 6 F 6 (7)	NOT ((cart))	A(B)	O/C	† (Ψ)	O/C	[3+2] 1((2))	Po<Pf	YES	YES	1/4 [1/10–1/5]	7
Darevskia (p.) praticola	7	15 [14–16]	20 [19–21]	Bi>Tr>Un	M 27 F 30	F 6	NOT	A(B)	C	†	O	[3+2] 1	Po=Pf	YES	YES	1/3–1/2	1
Darevskia (p.) pontica	7	17.1 [16–20]	23 [22–25]	Bi>Un ((tri))	M 27 F 28/29/30	M 5/6 F 6	NOT	A/B	O/C	Ψ (†)	O (C)	[3+2] 1	Po>=Pf (=)	YES	YES	1/2–1/3	5
Darevskia (p.) hungarica	7/8	17.75 [17–18]	21.25 [20–23]	Bi>Un (tri)	M 27 F 29	M 5 F 6	NOT	A	O (C)	†	O	[3+2]1 (3+1)1	Po=Pf (><)	YES	YES (red)	1/3	2

......*continued on the next page*

TABLE 1. (Continued)

TAXA	Pre-maxillary teeth	Maxillary teeth	Dentary teeth	Teeth (Unicuspid/Bicuspid)	Total Presacral vertebrae	Short Presacral vertebrae	Ossified ribs on third presacral vert.	Pattern of Tail vertebrae	Clavicu-lae typus	Interclavicle †Ψ⋔	Sternal Fontanellae	Sternal-Xiphisternal formula	Postfrontal and Postorbital relative lengths	Postfrontal anterolateral process	Postorbital antero-medial process	Squamosal overlap with Postorbital	N
Darevskia valentini	7/8	17.75 [16–19]	22 [18–25]	Bi>>Un	M 27 F 28/29/30	M 6 F 7/8	NOT	A(B)	O (C)	†	O/C (IO)	[3+2]1	Po=Pf (>)	YES	YES (red)	1/3 (1/2–1/4)	10
Darevskia s. spitzenbergerae	7	17.25 [16–18]	21 (20–23)	Bi>Un	M? F 29	M? F 6–7	NOT	A	O ((C))	Ψ	O (IC)	(3+2)0/1 (3+1)1	Po>Pf (=)	YES	YES	1/3 (1/2)	3
Darevskia s. wernermayeri	7	20.5 [19–21]	23.5 [23–24]	Bi>Un ((=))	M 27 F 29	M 6 F 6	NOT	A	O/C	⋔ Ψ	O	[3+2]1	Po>=Pf	YES	YES ((red))	1/3(1/2)	6
Darevskia josefeiselti	7	17 [15–18]	21.25 (20–22)	Bi>Un	M 27–28 F 29	M 6–7 F 7	NOT	A	O(C)	† ⋔	O	(3+2)1	Po=Pf	YES	YES	1/2–1/3	6
Darevskia r. rudis	7	17.6 [15–19]	21.5 [19–24]	Bi>Un	M27/28 F28 (27,29)	M 6 F 6	NOT	A	O	†	O	[3+2] ((4+1)) 1((0))	Po<Pf	YES	YES (red)	1/3 (1/4)	6
Darevskia r. lantzicyreni	7	17.6 [17–18]	22.3 [23–24]	Un>Bi	M 27 (26)((25)) F 28(27)	M 6–7 F 6	NOT	A	O(C)	†⋔	O	[3+2]1	Po=Pf (<=)	YES	YES (red)	1/3 (1/2–1/9)	8
Darevskia r. bolkardaghica	7	18.25 [17–19]	22.25 [21–23]	Bi>Un	M 27 F 28/29	M 6 F 6/7	NOT/ YES	A	O	†	IO/IC	[3+2] ([3+1]) 1/2	Po=Pf	YES	YES	½(1/3)	3
Darevskia o. obscura	7 ((8))	17.2 [16–20]	21.2 [20–24]	Bi>Un	M 26/27 F 28/29	M 6 F 6(7)	NOT ((yes))	A	O (C)	† (Ψ Ge)	O	[3+2] 1(0)	Po=Pf	YES	YES (red)	1/3 (1/4)	8
Darevskia o. bischoffi	8/7	18 [16–21]	21.8 [20–23]	Bi>Un	M 26/27 F28 (29)	M 6 F 6–7	NOT ((yes))	A	O ((C))	† ⋔	O (elong)	[3+2] ((3+3)) 2/1	Po<Pf	YES	YES	1/3–1/4 ((0))	6
Darevskia o. macromaculata	7/8 (6)	17.9 [15–20]	22.1 [20–26]	Bi>Un	M 27/28 F 28/29	M 6/7 F 6/7	NOT	A	O (C)	† ⋔	O (IO, IC)	[3+2] 1((2))	Po=<Pf	YES	YES (size variab)	1/3 (1/2)	6

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TABLE 1. (Continued)

TAXA	Pre-maxillary teeth	Maxillary teeth	Dentary teeth	Teeth (Unicuspid/Bicuspid)	Total Presacral vertebrae	Short Presacral vertebrae	Ossified ribs on third presacral vert.	Pattern of Tail vertebrae	Clavicu-lae typus	Interclavicle †Ψ⋔	Sternal Fontanellae	Sternal-Xiphisternal formula	Postfrontal and Postorbital relative lengths	Postfrontal anterolateral process	Postorbital antero-medial process	Squamosal overlap with Postorbital	N
Darevskia 'r.' chechenica	7	15.5 [15–16]	21 [20–22]	Bi>Un	M 27 F 29(28)	M 6 F 7(6)	NOT	A	O	† ⋔	O	[3+2] 2/1	Po=Pf (<)	YES	YES	1/3	2
Darevskia 'rudis' svanetica	7	18 [17–19]	20.5 [20–21]	Bi>Un	M 27 H 29	M 7 F 6	NOT	A	C (O)	†	O (IO)	[3+2] (3+1) 1	Po=Pf	YES	YES (red)	1/3	2
Darevskia mirabilis	7	16.1 [15–17]	20.5 [18–23]	Bi>Un	M 26/27 F 28/29	M 6 F 6–7	NOT (yes)	A	O (C)	†	O	[3+2] ((2+2)) ((2+3)) 1(2)	Po=Pf (<)	YES	YES	1/3 (1/2)	4
Darevskia bithynica bithynica	7	16.5 [15–18]	21.16 [20–23]	Bi>Un	M 27 F 28/29	M 6 F 6/7	NOT	A ((B))	C ((O))	†	O/red	[3+2] 1(0)	Po<Pf (=)	YES	YES (red)	½	4
Darevskia b. tristis	7	17.75 [16–19]	20.9 [17–23]	Bi>Un	M 27 (28) 29	M 6/7 F 6/7	NOT	A ((B))	O (C)	†	O ((IO))	[3+2] 1 ((2))	Po=Pf (<)	YES	YES (red)	½	6
Darevskia portschinskii	7	16.3 [15–18]	20.75 [19–22]	Bi=Un (><)	M 27 F 29	M 6 (5) F 7	NOT	A	O	†⋔	O	[3+2]0 ([3+2]1	Po>=Pf	YES	YES	1/3–1/4	4
Darevskia parvula	7	17.7 [16–19]	21.6 [20–24]	Bi>Un	M 27 F 28	M 6 F 6	NOT	A	O	† (Ψ)	O/C	[3+2]1/0	Po<<Pf	YES	YES ((red))	1/3 (1/2–1/5)	5
Darevskia adjarica (Georgia)	7	17 [14–19]	20.1 [16–24]	Bi>Un	M 27 F 28	M 6 F 6	NOT	A	O	† Ψ	O	[3+2]1/0	Po<<Pf	YES	YES (red)	1/3–1/4	4
Darevskia adjarica (Turkey)	7	17.16 [16–19]	21.19 [19–23]	Bi>Un	M 27(26) F 28	M 6 F 6	NOT	A	O	† (Ψ⋔)	O/C	[3+2]1/0	Po<<Pf	YES	NOT (YES)	1/3–1/4	9

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TABLE 1. (Continued)

TAXA	Pre-maxillary teeth	Maxillary teeth	Dentary teeth	Teeth (Unicuspid/Bicuspid)	Total Presacral vertebrae	Short Presacral vertebrae	Ossified ribs on third presacral vert.	Pattern of Tail vertebrae	Clavicu-lae typus	Inter-clavicle †Ψ⋔	Sternal Fontanellae	Sternal-Xiphisternal formula	Postfrontal and Postorbital relative lengths	Postfrontal anterolateral process	Postorbital antero-medial process	Squamosal overlap with Postorbital	N
Darevskia tuniyevi (Ardahan, Turkey)	7	16 [14–18]	20.5 [18–23]	Bi>Un	M 28 F 29	M 6 F 7	NOT	A	O	† Ψ	O	[3+2]1/0	Po<<Pf	YES	NOT (red)	1/3	2
Darevskia armeniaca (p)	7	18 [17–19]	21.2 [20–22]	Bi>Un	29 (28)	6 (7)	NOT (cart) (2ªcart!)	A ((B))	O	† (⋔)	O (IC)	[3+2]1 (0) ([4+2]0)	Po=Pf	YES	NOT /red	1/3	7
Darevskia dahli (p)	7	17.8 [17–19]	22.6 [21–24]	Bi>Un	29/30	7 (6)	NOT	A	C (O)	† (⋔)	O (C)	[3+2]0/1	Po=/>Pf ((<))	YES	NOT /Red	1/3	5
Darevskia rostombekowi (p)	7	17 [16–18]	21.14 [19–23]	Bi>Un	28/29	6/7	NOT	A	O	† (Ψ)	O (IC)	[3+2]0/1 ((2))	Po>=Pf (Po<Pf)	YES	NOT (red)	1/4 (1/3)	7
Darevskia unisexualis (p)	7	18 [15–20]	21.6 [19–23]	Bi>Un	28	6	YES (not)	A	O	†	O	[3+2]1/0 ([3+1])1 ([4+1])1	Po<=Pf (Po=Pf)	YES	NOT	¼	8
Darevskia unisexualis x D. nairensis (Triploid)(p)	7	19.5 [19–20]	24 [24–24]	Bi>Un	28	6	YES/ NOT (unilat)	B	O	†	C	[3+2]1	Po>=Pf	YES	NOT	1/3	1
Darevskia uzzelli (p)	7	18.5 [17–20	22 [21–23	Bi>Un	29 (28)	7 (6)	YES/ NOT	B (A)	O	† ⋔	O (C)	[3+2]1	Po<=Pf (Po>=Pf)	YES	NOT (yes)	1/3–1/4	4
Darevskia sapphirina (p)	7 (5,6,7)	16.25 [12–21]	20.5 [17–23]	Bi>Un (Bi=Un maxilla)	28/29	6/7	NOT (yes unilat or cart)	A	O ((C))	⋔ (†)	IO	[3+2]1 ([3+2]0)	Po=Pf (><)	YES	NOT (yes)	1/3	4
Darevskia bendimahiensis (p)	7	16.6 [15–18]	20.5 [19–21]	Bi>Un	28/29	6/7	NOT	A	O (C)	⋔ (†)	IO	[3+1]/[2+2] ([2+2]) 1 (0)	Po>Pf	YES	NOT	1/3–1/2	3

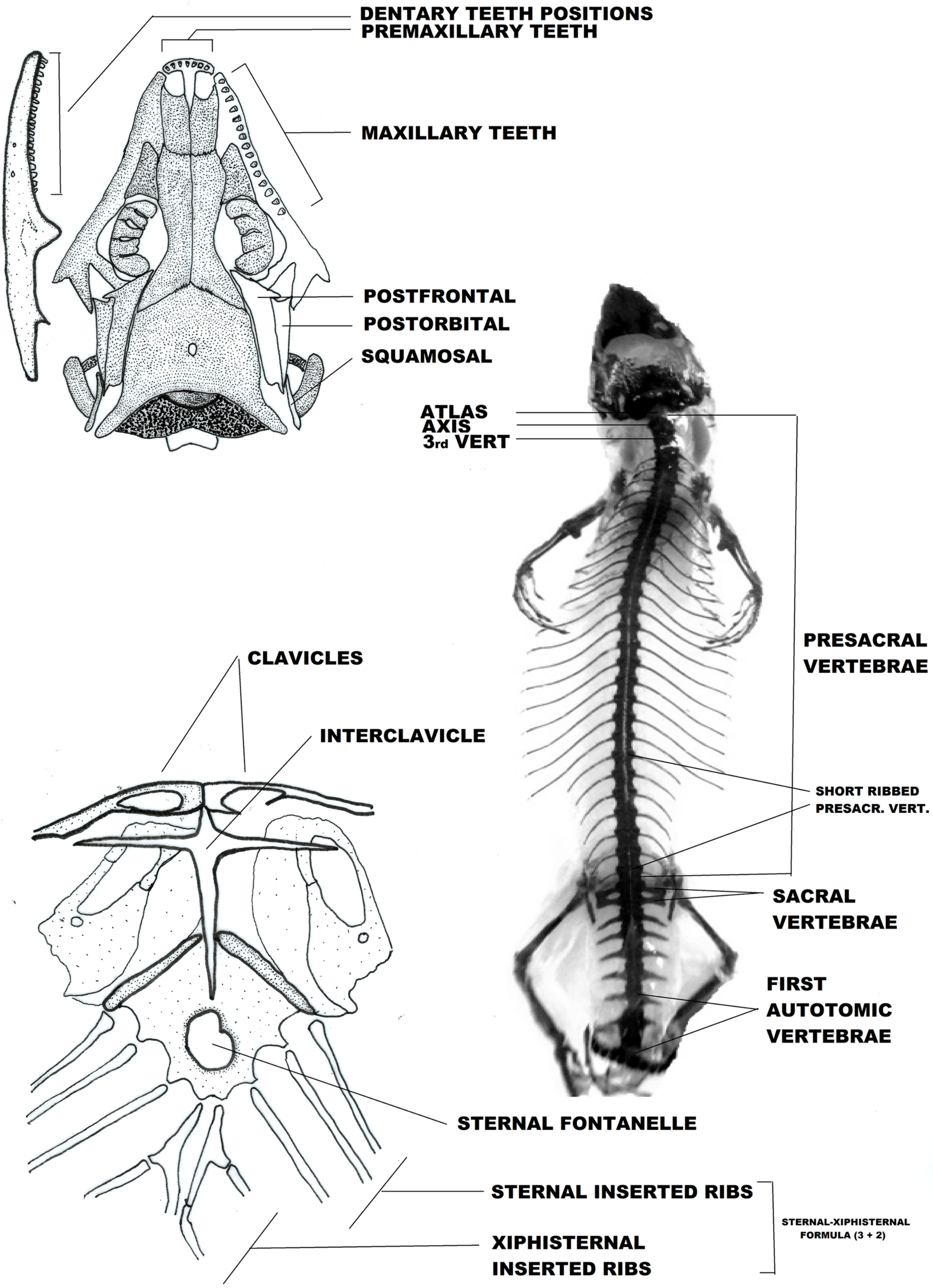

FIGURE 1. Cranial and skeleton characters studied. Top left: Skull of *Darevskia uzzelli* (original). Bones with characters studied are left in white, and teeth positions (hidden in the inferior part, indicated). At the left side of the skull, a jaw of *Darevskia clarkorum* (original) showing dentary teeth. Bottom left: Scapular girdle of *Darevskia derjugini* (original) showing in white the bones mentioned in the text. Right side: Skeleton of *Darevskia uzzelli* (a cleared and stained specimen) showing the different vertebral characters studied in the text.

2.2. Methods

Previously fixed and alcohol-preserved specimens (almost 24 to 72 hours, but preferably long-term conserved in alcohol) were cleared using 1% KOH in deionized water (from 24 to 72 hours until some bones became visible through muscle). Bones were stained with alizarin red (0.1% alizarin in the previously mentioned 1% KOH solution, from 12 to 24 hours), then differentiated and the excess pigment eliminated with Mall solution (80% of the previous clearing solution plus 20% glycerol) until the muscles were completely transparent. This process can last several weeks and even a few months to be well cleared, depending on the fixation strength of the specimens and the presence of formalin. The Mall solution is progressively replaced by glycerol: 10 days in 5% glycerol, 10 days in 25%, and then preserved permanently in glycerol. If the reactive strength (concentration) is lower, processing times can be longer; if stronger, there is a risk that muscle can disintegrate and bones become disarticulated (from Taylor 1967; Durfort 1978, modified). Osteological nomenclature follows Arribas (1998) and Arnold *et al.* (2007).

X-ray plates were performed with a Philips Super 100 cp apparatus. The best results were obtained with a capacity of 40 Kv, an intensity of 4 milliamperes per second, and an exposure of 19 milliseconds. These X-ray plates allowed us to study the number of presacral vertebrae of many animals without destroying the specimens. This method has been successfully employed by other authors such as Arnold (1973).

Lacertid species show a small amount of variability in vertebral numbers (see Arnold 1973; Arribas 1998; Kaliontzopoulou *et al.* 2008). To perform statistics on vertebral numbers would require destroying dozens of specimens. This is often not feasible as some species are rare in collections or nature, and it is not ethically acceptable to sacrifice this number of specimens solely for such a study. If cleared and stained specimens are used, this would entail killing or destroying a significant number of conserved museum specimens. Radiography, depending on the apparatus used, may render the cardboard label of the specimen more opaque to X-rays than the lizard vertebrae, possibly causing extra presacral vertebrae to remain undetected, leading to counting errors (own experience). The first vertebrae (atlas, axis, and third presacral vertebra) are very difficult to discriminate in radiographs. Therefore, radiography is a less reliable method for vertebrae and rib counts. Lizards have a modal (“normal”) trait and a few deviant specimens. Studying a small sample is sufficient to determine the modal (or most common) number or character state in a given taxon, providing a reasonable approach to the description of species osteology based on a smaller number of specimens.

2.3. Studied Characters

We studied a total of 20 osteological characters in all the species (Table 1; Figure 1). These characters, grouped by body regions, are:

2.3.1. Skull Characters:

1. Number of premaxillary teeth.
2. Number of maxillary teeth (dental tooth positions in the maxillary bone).
3. Number of dentary teeth (dental tooth positions in the dentary bone).
4. Unicuspid, bicuspid, or tricuspid teeth (teeth morphology).
5. Presence of an anterolateral process in the postfrontal bone.
6. Presence of an anteromedial process in the postorbital bone.
7. Comparative lengths of the postorbital and postfrontal bones.
8. Overlap degree between the postorbital and the squamosal bones.

2.3.2. Postcranial Characters:

9. Existence of visible (ossified) ribs associated with the third presacral vertebrae.
10. Sternal/xiphisternal costal formula and presence of inscriptional ribs.

11. Number of presacral vertebrae.
12. Number of posterior dorsal vertebrae (short presacral ribs).
13. Presence and form of the sternal fontanelle.
14. Form of the clavicles (emarginated or marginated).
15. Interclavicle form.
16. Morphology of the first autotomic vertebrae of the tail (see Arnold, 1973, 1989).

A general description of *Darevskia* osteology (*D. parvula* and *D. adjarica*) that can serve as a basis for the whole genus is provided by Yildirim *et al.* (2019). Skulls of some species are depicted in Mehely (1909), and some bones in Arribas (1998), which also gave the first osteological data for many of these taxa. Darevsky (1967) describes skull shapes and provides specific cranial measurements for most *Darevskia* species. For other Lacertid genera, we use data from Arnold (1983, 1989), Arribas (1998), Barahona *et al.* (1998), Arnold *et al.* (2007), and our unpublished data.

We use the term "group" to refer to several species or species-complexes that cluster together (monophyly) inside *Darevskia* (as in Murphy *et al.* 2000, or Arribas 1999) (Appendix 3: *Darevskia* groups). Within these groups, we use the term "complex" to designate closely related species (sometimes recently split, or in some cases former subspecies or close taxa of disputed status). Several complexes can exist within a group, and several groups constitute the entire genus *Darevskia*. The term "parental" refers to both parents (without distinguishing sex) that gave rise to a parthenogenetic species through hybridization; "paternal" refers to the male of that cross, and "maternal" to the female.

2.4. Objectives

It is not possible to use these osteological characters to reconstruct an independent phylogeny due to high variability, homoplasy, and reversals. There are more taxa than characters studied. However, these characters can be useful for mapping onto a robust phylogeny, as they help diagnose groups and understand certain evolutionary processes.

Our goals are:

a) To characterize osteologically the different species of *Darevskia* and contrast their relationships derived from osteological traits with the available genetic-derived phylogenies of the group.
b) To compare the osteological characteristics of the parthenogenetic species with their bisexual parental species, known from previous genetic studies.
c) To search for osteological characteristics of the different groups within *Darevskia* (see Appendix 3: *Darevskia* groups) to diagnose them (including some new ones) and name them as subgenera within *Darevskia*.
d) To attempt to assign some scarcely known species (not included in previous phylogenies) within the other more studied bisexual taxa, based on their osteological characters.

Results and Discussion

The results from the study of the sixteen characters indicated above are summarized in Table 1 for all the taxa studied and discussed character by character in the following pages. Character differences are noted for the taxa of *Darevskia*, and also for other Lacertini and Lacertidae in general to add valuable information and ascertain their character state polarity.

3.1. Skull Characters

3.1.1. Number of Premaxillary Teeth

The premaxilla has unicuspid teeth, and their number generally varies from seven to nine in adults (it may be fewer in offspring or subadults of the same species). In *Darevskia*, the usual number is 7, more rarely 8 (as in the only studied specimen of *D. szczerbaki*) or 9 (7 but rarely 9 in *D. saxicola*), or 6 in very small species (6 and 7 in similar proportion appear in *D. daghestanica* and *D. caucasica*), 7 or 8 in *D. (p.) hungarica*, *D. valentini*, *D. obscura bischoffi*, *D. o. macromaculata*, or surprisingly variable in the small parthenogenetic *D. sapphirina* (7 in two cases, but also 5 and 6 in a kind of premaxilla atrophy). At the other extreme, *D. chlorogaster* has 9 or even 10.

It is difficult to determine the primitive number of premaxillary teeth in the Lacertini. The two most common numbers, 7 and 9, appear more or less mixed in Lacertini ("Eurasian radiation of the Lacertidae" from Arnold, 1989). This number can be up to ten, for example, in *Apathya* and *Lacerta* s. str., 9 (but up to 11) in *Timon*, or between 8 and 10 in *Takydromus*. In the Gallotiinae there are 7 in *Gallotia* and 9 in *Psammodromus*. In some Eremiadini ("Ethiopian and advanced Saharo-Eurasian assemblage" from Arnold, 1989), such as *Acanthodactylus* or the basal *Atlantolacerta*, the usual number is 7. The case of *Gallotia* is interesting. Although some species reach a large size, in some characters, such as the number of premaxillary teeth or their reduced clutch size, they behave like small lizard species, despite being overgrown. This seems to confirm the hypothesis of Rocek (1980) that "the number of premaxillary and maxillary teeth does not seem to be so subjected to these ontogenetic variations" (referring to the increase in number when growing), but this number is best conserved only for premaxilla, as in maxilla and dentary the number of teeth increases frequently ontogenetically, so that juveniles have lower numbers than mature animals, as smaller species tend to have fewer than their larger relatives.

3.1.2. Number of Maxillary Teeth (Dental Tooth Positions, Dental Loci)

Even more markedly than in the premaxilla, in the maxilla and the dentary, the number of teeth increases frequently ontogenetically, so that juveniles have lower numbers than mature animals, and smaller species tend to have fewer than their larger relatives. The counts for this character in *Darevskia* can be seen in Table 1. However, there are no significant intrageneric differences between large and small species for these counts. Pterygoid teeth, an additional tooth patch on each pterygoid bone, seem to be absent from the studied *Darevskia* but appear in its sister genus *Iranolacerta* (*I. brandtii*).

In general, they are associated with deep and robust skulls (as in *Lacerta* s. str., *Gallotia*, *Psammodromus algirus*, *Omanosaura jayakari*, *Phoenicolacerta*, and some East Mediterranean *Podarcis* -*milensis*, *taurica*, *peloponnesiaca*-).

3.1.3. Number of Dentary Teeth (Dental Tooth Positions)

As with the maxillary teeth, the number of dentary teeth is greater in large-jawed species and smaller in smaller-sized ones. The lower values (Table 1) are found in small species such as *D. daghestanica* (average 17.2; from 13 to 21), while the higher ones appear in *D. dryada* (24, 22–26), *D. chlorogaster* (23.3; 20–27), *D. brauneri* (but due to the big-headed *D. b. darevskii*; 23; 21–26) and *D. s. wernermayeri* (23.5, 23–24). See Table 1 for a detailed account of each taxon.

Within each species, there seems to be a clear relationship between the general size of the individual and its number of dentary teeth. Therefore, growing individuals and large adults show small differences in the number of teeth, with higher values in the latter (see, for example, Rocek, 1980). Furthermore, according to the superior allometric growth of the head that males of almost all species reach, these *Darevskia* (and most small *Lacertini*) can be divided into two groups, with obvious intermediate cases: one that develops allometrically large heads (with more teeth) and a second with short or small heads (with fewer teeth). These differences seem to correlate between similar (related) species and appear to have some phylogenetic validity. For example, they are conserved in larger forms, such as *Gallotia simonyi*, whose number of teeth does not differ significantly from those of other smaller species (a curious aspect already mentioned regarding the premaxilla; large *Gallotia* species seem actually "small but overgrown lacertids”). On the other hand, the number of premaxillary and maxillary teeth does not seem to be so subject to these ontogenetic variations, according to Rocek (1980). It is more likely a matter of “grain” in the appreciation, since the greater the number of teeth, the better the differences in that number are appreciated, as is the case of the counts in the dentary bone.

3.1.4. Unicuspid, Bicuspid, or Tricuspid Teeth

In all the *Darevskia*, uni- and bicuspid teeth coexist in similar numbers, sometimes with one shape slightly dominating over the other, especially bicuspids over unicuspids. In *D. alpina*, we have observed some very rare tricuspid teeth. Strikingly, in the unique *D. (p.) praticola* specimen studied, tricuspid teeth were visible and not rare, less abundant than bicuspids but more abundant than unicuspids. In *D. (p.) hungarica*, some rare tricuspid teeth are insinuated, and in our *D. (p.) pontica*, they are even rarer. All these taxa belong to the *saxicola* group of Murphy *et al.* (2000).

In *Lacertini*, the teeth in dentary and maxillary bones are often bicuspid at least in their posterior half, with the remaining (and especially the front ones) unicuspid. They are frequently tricuspid in *Takydromus* and are a majority in juveniles of other taxa, such as juveniles of *T. lepidus* and *L. schreiberi*, in which they become bicuspid (and also dominant over unicuspid) when growing to adults. In Gallotiinae (*Gallotia* spp.), tricuspid teeth are also present and can become dominant.

3.1.5. Presence of anterolateral process in the postfrontal

The anterolateral process of the postfrontal is present in all the *Darevskia* species (Figures 2–6).
This postfrontal process is very rarely absent in Lacertini. It is obviously absent in species that have the postfrontal and postorbital bones fused from birth, such as *Lacerta schreiberi, Takydromus* spp.*, Zootoca vivipara,* and *Z. carniolica*. In species with both bones individualized, this absence occurs, for example, in the Pyrenean *Iberolacerta aurelioi* (Arribas, 1998).

3.1.6. Presence of anteromedial process in the postorbital

Within *Darevskia*, this process is absent in *D. mixta, D. r. vanensis, D. rostombekowi* (sometimes still visible but reduced), *D. unisexualis,* and *D. uzzelli* (rarely indicated). It is also absent or greatly reduced in *D. daghestanica, D. derjugini, D. saxicola, D. armeniaca, D. dahli, D. bendimahiensis,* and *D. sapphirina* (in which it can also rarely appear). It is present (and rarely reduced) in *D. caucasica vedenica, D. raddei raddei, D. nairensis, D. brauneri, D. (p.) hungarica, D. s. wernermayeri, D. rudis rudis, D. o. obscura, D. ‘r.’ svanetica, D. bithynica bithynica, D. b. tristis, D. adjarica*, and present but very rarely absent in *D. parvula*. In other taxa, it is always present (almost in our samples).

The presence of this process is much more subject to variation than the anterodistal process of the postfrontal (see Figures 2–6). The normal situation is for it to be present and developed, as is frequent in all the Lacertini in which the postfrontal and postorbital bones are separated from birth (the vast majority except those mentioned in the previous section). This process is absent or appears reduced in some species that belong to different phyletic lines. For instance, it can appear developed but is frequently reduced and even absent in the *raddei* complex (Figure 2).

3.1.7. Comparative lengths of postorbital and postfrontal

In *Darevskia*, both bones can be subequal in length, but there is a marked tendency for the postorbital to be shorter than the postfrontal (Figures 2–6). With similar length or the postorbital tending to be slightly shorter than the postfrontal are *D. derjugini, D. daghestanica, D. c. caucasica, D. c. vedenica, D. chlorogaster, D. raddei vanensis, D. nairensis, D. defilippi, D. szczerbaki, D. alpina, D. b. bithynica, D. b. tristis, D. rudis* ssp. (incl. *D. r. lantzicyreni*), *D. obscura* sspp.*, D. armeniaca, D. unisexualis, D. uzzelli,* and *D. sapphirina* (in the latter, it is surprisingly variable for a clonal taxon: it can be equal, slightly smaller, or greater). Interestingly, *D. r. lantzicyreni*, recently changed

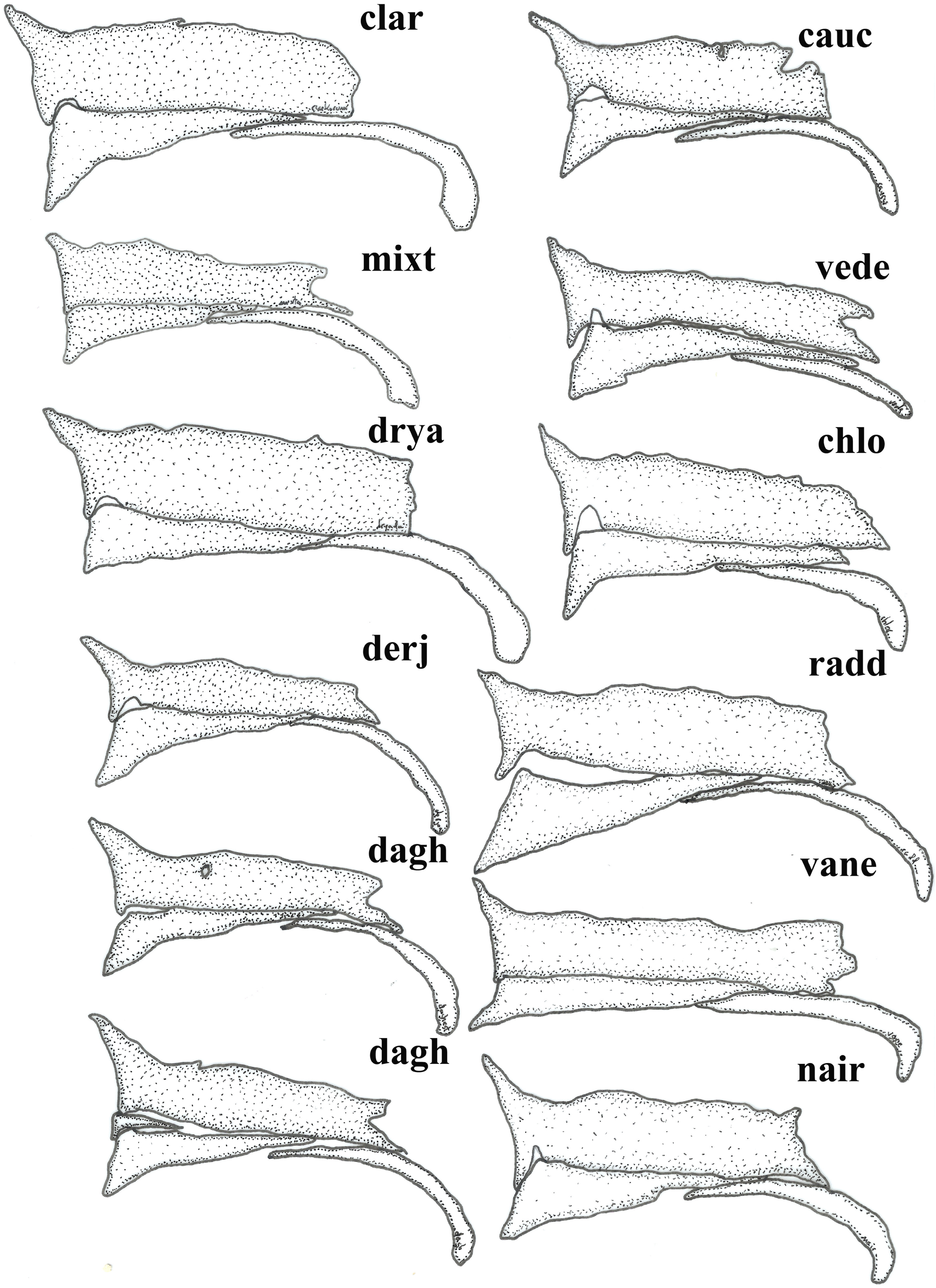

FIGURE 2. Postfrontal, postorbital and squamosal shapes, processes and overlaps among them. The anteromedial process of the postorbital, hidden under the postfrontal, is showed outlined and without stippled. Left side (from top to bottom): *Darevskia clarkorum* **(clar)**, *D. mixta* **(mixt)**, *D. dryada* **(drya)**, *D. derjugini* **(derj)**, *D. daghestanica* **(dagh)**, *D. daghestanica* **(dagh)** (variation: note the presence of a supernumerary postorbital), Right side (from top to bottom): *D. caucasica* **(cauc)**, *D. c. vedenica* **(vede)**, *D. chlorogaster* **(chlo)**, *D. raddei* **(radd)**, *D. r. vanensis* **(vane)**, *D. nairensis* **(nair)**.

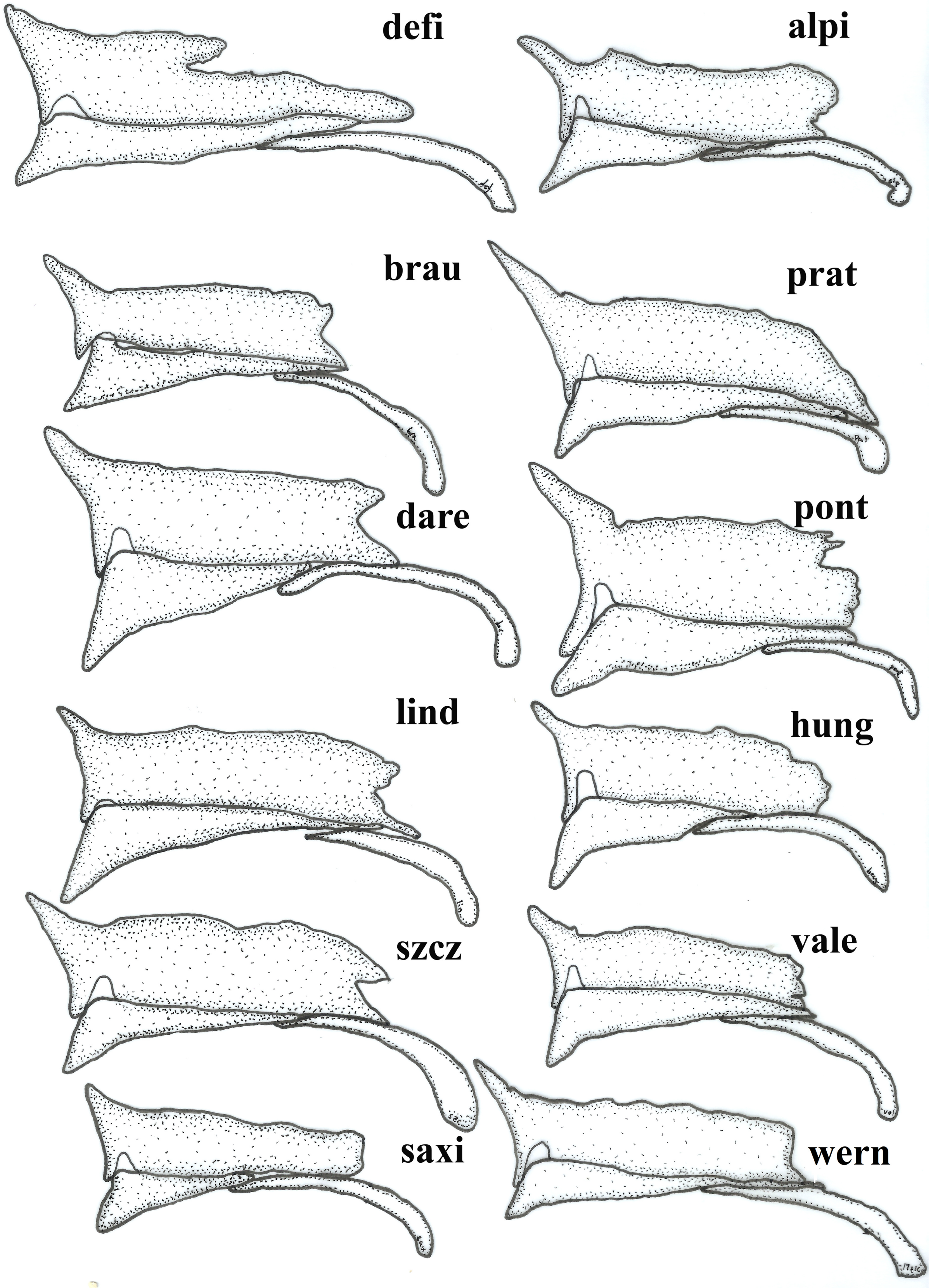

FIGURE 3. Postfrontal, postorbital and squamosal shapes, processes and overlaps among them. The anteromedial process of the postorbital, hidden under the postfrontal, is showed outlined and without stippled. Left side (from top to bottom): *Darevskia defilippi* **(defi)**, *D.b. brauneri* **(brau)**, *D. b. darevskii* **(dare)**, *D. lindholmi* **(lind)**, *D. szczerbaki* **(szcz)**, *D. saxicola* **(saxi)**, Right side (from top to bottom): *D. alpina* **(alpi)**, *D.(p.) praticola* **(prat)**, *D.(p.) pontica* **(pont)**, *D. (p.) hungarica* **(hung)**, *D. valentini* **(vale)**, *D. s. wernermayeri* **(wern)**.

from *D. valentini* to *D. rudis* as a ssp., has it as the other *rudis* and different from the *D. valentini* and related forms, thus it is equal or shorter. Postorbital much shorter than the postfrontal appears in *D. clarkorum, D. mixta, D. dryada, D. r. raddei, D. saxicola, D. brauneri, D. lindholmi, D. parvula,* and *D. adjarica*. Finally, the rarest trend is the situation in which the postorbital is (subequal or) greater than the postfrontal, as in *D. (p.) praticola, D. (p.) pontica, D. (p.) hungarica, D. v. valentini, D. s. spitzenbergerae, D. s. wernermayeri, D. portschinskii,* and frequently in *D. dahli, D. rostombekowi,* and *D. bendimahiensis*. We have even seen a supernumerary postorbital in a specimen of *D. daghestanica* (see Fig. 2).

In general, in the Lacertini both bones have more or less equivalent lengths (primitive character state), although secondarily, variations of this primitive proportion occur in some species (for example, when there is a reduction in cranial ossification related to a saxicolous life with general head flattening). The postfrontal and postorbital bones are generally separated from birth in most Lacertini, but appear fused in *Lacerta schreiberi, Takydromus* spp*.,* and *Zootoca spp*. They are also fused in the Gallotiinae (*Gallotia* and *Psammodromus*). In Eremiadini the situation is variable but in the case of being two separate bones, they are in principle subequal in length (they are fused in *Eremias, Meroles, Ichnotropis, Philochortus, Gastropholis, Bedriagaia,* and *Adolfus*; separated in *Holaspis guentheri*, and variable in *Acanthodactylus* and *Pedioplanis*—fused only in *P. lineoocellata* and *P. laticeps*). In some other cases, the bones apparently "fuse" during the life of the animal, but in reality, they are only tightly bonded and covered with a continuous layer of osteoderms. The more robust the skull, the more noticeable is this apparent fusion, as occurs, for example, in many individuals of *Lacerta* s. str., *Timon lepidus*, or *Teira dugesii*. In the case of *Zootoca*, it seems that the fusion is secondary, a derived character, as although usually fused from birth, in some very rare specimens the two bones are partially separated or almost slightly individualized (a single *Z. v. louislantzi* and *Z. v. pannonica* in our studied specimens). The postorbital can be shorter, for example in *Dalmatolacerta*, *Iranolacerta zagrosica*, *Parvilacerta fraasii*, some *Darevskia* spp. above mentioned and *Phoenicolacerta*. On the contrary, it is longer (the rarest situation) in some *Algyroides* and some *Iberolacerta* (*I. horvathi* and *I. aurelioi*).

3.1.8. Overlap degree between the postorbital and the squamosal

In the studied *Darevskia*, the longitudinal overlap between the squamosal and the postorbital usually runs between a third (1/3) and a quarter (1/4) of the postorbital length (Figures 2–6). Overlap tends to be greater (towards half of the postorbital length) in *D. (p.) pontica, D. s. spitzenbergerae, D. s. wernermayeri, D. josefschmidtleri, D. bithynica (*and its ssp. *tristis)*. On the contrary, it can be less than a third in very big-headed species such as *D. dryada, D. szczerbaki* (up to 1/6), and some very big *D. brauneri* (ssp. *darevskii*, up to 1/10) being very variable in our *D. saxicola* sample (one of them up to near 1/10). In the species studied, the length of the contact between the squamosal and the postorbital varies along a continuum that goes from a quarter of the length of the latter to a third or even a half of its length. In general, within the same species, the variation remains within some reasonable limits and it is possible to quantify whether it is more or less than a half or a third of the comparative lengths of both bones in a given taxon. The most widespread morphology implies approximately a third of superposition, the reason why we can consider it as the primitive state of the character, being the other states derived.

3.2. Postcraneal characters

The vertebral column can be divided into the following different subregions (Siebenrock 1894; Kühne 1913):

- *Cervical*: all the vertebrae preceding the first with ribs associated to the sternum (includes an atlas, axis, the third presacral vertebrae—with or without a small associated rib—) [see Figure 1], fourth to sixth vertebrae (short and with a wide insertion), and seventh and eighth, with longer ribs that do not join the sternum.
- *Sternal*: five vertebrae with long ribs that join the sternum (usually 3) and xiphisternum (usually 2).
- *Parasternal* (= dorsal): the remaining ones, 13 to 16 vertebrae, with associated ribs that can be divided into parasternal anterior (with long and free ribs, 7 to 9, rarely 10); and parasternal posterior (with short and free ribs, 5 to 8 depending on the lacertid group concerned).

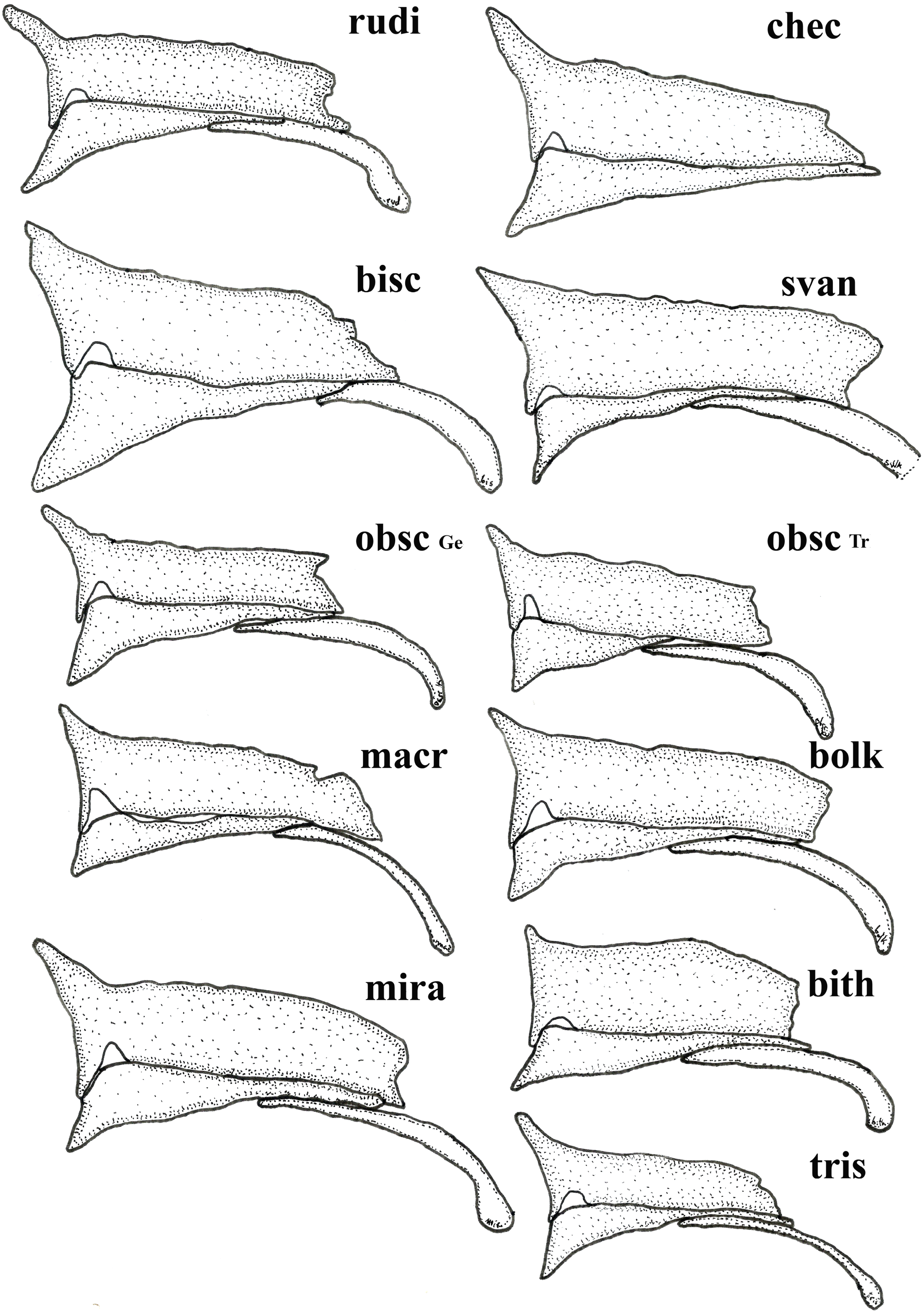

FIGURE 4. Postfrontal, postorbital and squamosal shapes, processes and overlaps among them. The anteromedial process of the postorbital, hidden under the postfrontal, is showed outlined and without stippled. Left side (from top to bottom): *D. r. rudis* **(rudi)**, *D. o. bischoffi* **(bisc)**, *D. o. obscura* (Georgia) **(obsc Ge)**, *D. o. macromaculata* **(macr)**, *D. mirabilis* **(mira)**, Rigth side (from top to bottom): *D. 'r.' chechenica* **(chec)**, *D. 'r.' svanetica* **(svan)**, *D. o. obscura* (Turkey) **(obsc Tk)**, *D. r. bolkardaghica* **(bolk)**, *D. b. bithynica* **(bith)**, *D. b. tristis* **(tris).**

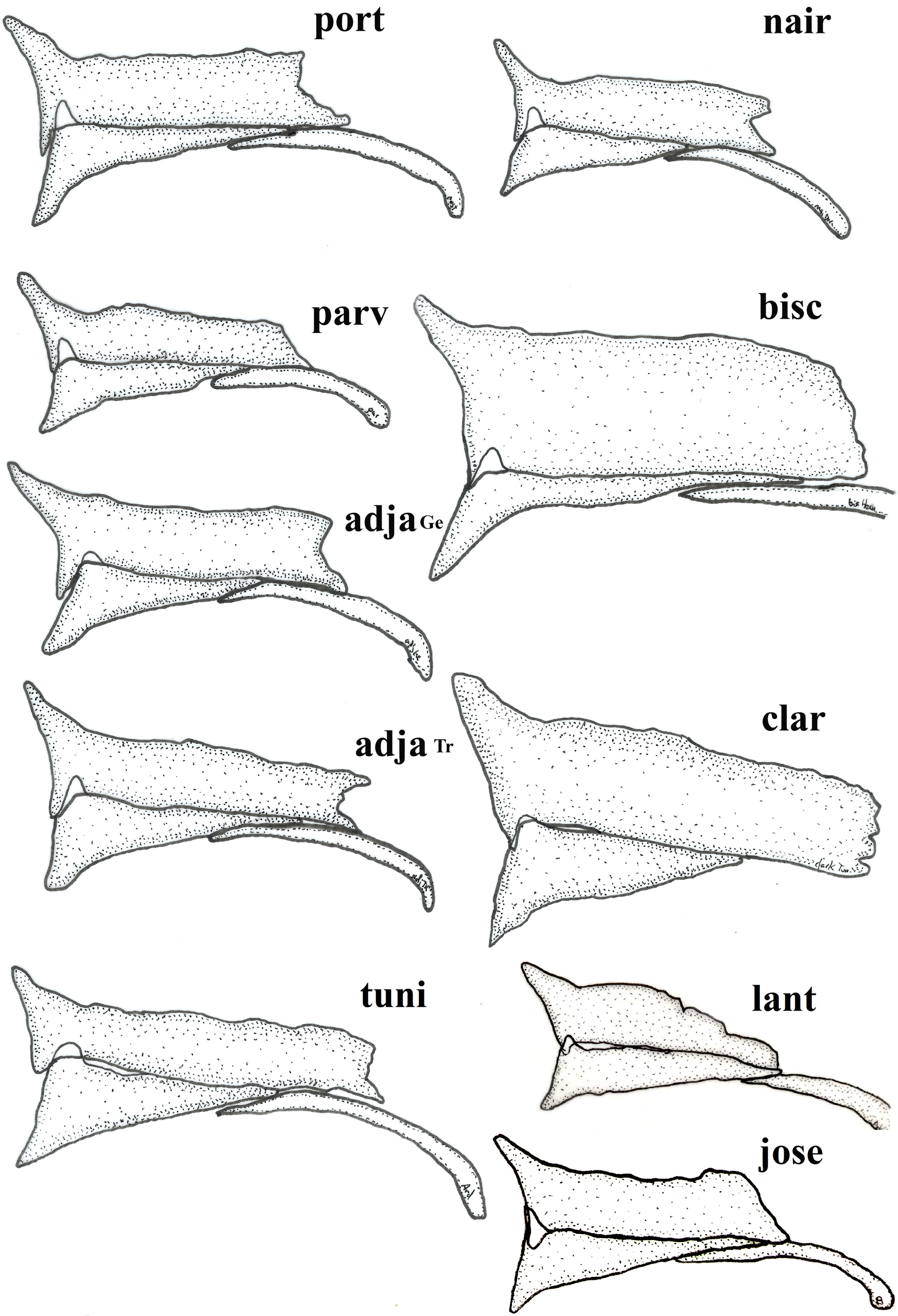

FIGURE 5. Postfrontal, postorbital and squamosal shapes, processes and overlaps among them. The anteromedial process of the postorbital, hidden under the postfrontal, is showed outlined and without stippled. Left side (from top to bottom): *D. portschiskii* **(port)**, *D. parvula* **(parv)**, *D. adjarica* (Georgia) **(adja Ge)**, *D. adjarica* (Turkey) **(adja tr)**, *D. tuniyevi* (Ardahan, Turkey) **(tuni)**, Right side (from top to bottom): *D. nairensis* **(nair)**, *D. o. bischoffi* **(bisc)**, *D. clarkorum* **(clar),** *D. r. lantzicyreni* **(lant),** *D. josefschmidtleri* **(jose)**.

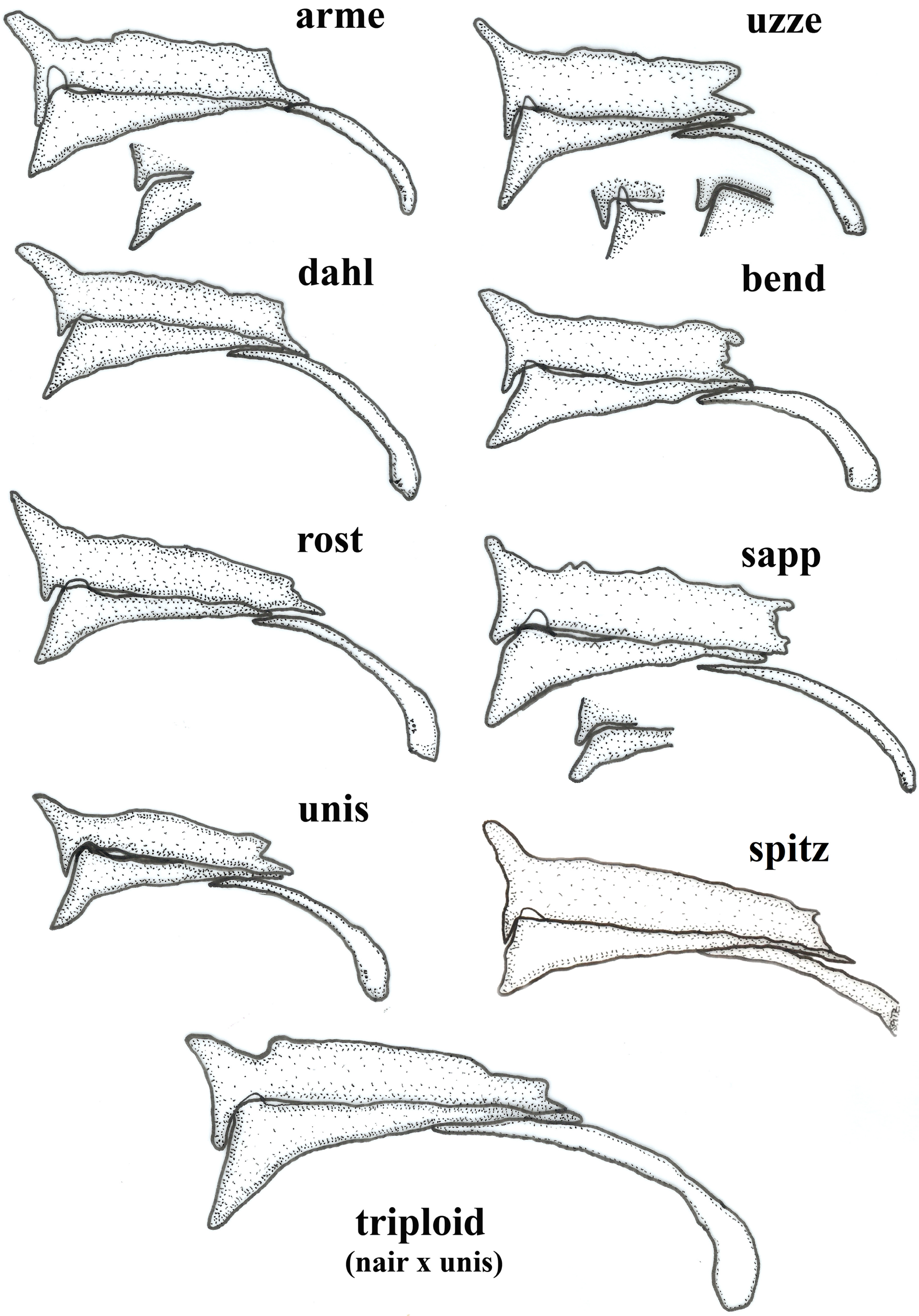

FIGURE 6. Parthenogenetic species. Postfrontal, postorbital and squamosal shapes, processes and overlaps among them. The anteromedial process of the postorbital, hidden under the postfrontal, is showed outlined and without stippled. Left side (from top to bottom): *D. armeniaca* **(arme)**, *D. dahli* **(dahl)**, *D. rostombekowi* **(rost)**, *D. unisexualis* **(unis)**, Right side (from top to bottom): D. uzzelli **(uzze)**, *D. bendimahiensis* **(bend)***, D. sapphirina* **(sapp)**, *D. s. spitzenbergerae* **(spitz)**. Bottom (in the middle): Triploid specimen (*D. nairensis* x *D. unisexualis*) **[triploid (nair x unis)]**.

For practical reasons, for our study, we are going to differentiate between the total number of presacral vertebrae (including atlas and axis) (see 3.2.1) and the number of posterior vertebrae with short ribs (=parasternal posterior) (see 3.2.2).

3.2.1. Existence of visible (ossified) ribs associated with the third presacral vertebrae

In *Darevskia*, as in other Lacertini, the appearance of a rib associated with the third vertebra is a numerically very rare but widespread phenomenon. That is, it may appear scattered and rarely in some individuals of most taxa. By this, it is not necessary to make a distinction between taxa in which we have not seen a single case and those in which it is very rare (one specimen among all studied). Neither among those that have this rudimentary rib already ossified nor those in which it can be appreciated but appears hyaline and constituted of cartilage. In *D. chlorogaster*, these ribs are generally absent, but we have studied a specimen that not only had a short one in the third, but also a small rudiment in the second vertebra. The same occurred in a *D. armeniaca* specimen. In parthenogenetic species, *D. armeniaca* does not have them (although it may be insinuated and cartilaginous); it is also missing in *D. dahli* and *D. rostombekowi*. On the contrary, it is generally present in *D. unisexualis* (and in the only specimen of its triploid hybrid with *D. nairensis* studied by us, in which it is present only on one side of the vertebra while it is not indicated on the other). In *D. uzzelli*, it may or may not be present, with similar frequencies, and in *D. sapphirina* or *D. bendimahiensis*, it is not present but it may appear rarely or in the form of cartilage in some rare specimens of the first species.

In Lacertini, pairs of ribs are regularly present in the fourth presacral vertebra and all the posterior ones, but occasionally they can also appear from the third vertebra (see, for example, Barbadillo and Sanz, 1983). However, the ribs are never very large nor well-developed, being present only in a small minority of individuals, often very small, and even only discernible on one of the sides. In the most primitive lacertids (e.g., Gallotiinae), there are small bony ribs associated with this vertebra. In the remaining species belonging to more modern groups (Lacertini), these ribs also frequently exist but are not noticeable because they are very small or cartilaginous (not ossified) and are often reduced only to their most proximal part. Thus, the presence of bony ribs associated with the third vertebra is common not only in *Gallotia* and *Psammodromus*, but they also appear relatively frequently or occasionally in *Zootoca vivipara* (and *Z. carniolica*), *Lacerta agilis*, *Apathya cappadocica*, *Iranolacerta brandtii*, *Podarcis lilfordi*, as well as in the three *Iberolacerta* (*Pyrenesaura*) species, although they are generally absent in the vast majority of Lacertini genera (or appear only in some very rare specimens, perhaps as an atavistic character). A certain correlation is noted between the development of this third rib and the presence of strong necks in ground-dwelling species with robust heads and necks, and also with species of much-reduced distribution and perhaps inbreeding, with fixation of these rare or atavistic characters.

3.2.2. Sternal/Xiphisternal costal formula and presence of inscriptional ribs

The usual sternal-xiphisternal formula in the *Darevskia* studied is [3 + 2], deviating from this a specimen of *D. (p.) hungarica* [3 + 1], a rare specimen of *D. r. rudis* [4 + 1], another of *D. o. bischoffi* [4 + 1], two *D. mirabilis* [2 + 2] and [2 + 3], one *D.'r.' svanetica* [3 + 1], another *D. r. bolkardaghica* [3 + 1], and among the parthenogenetic, a *D. armeniaca* [4 + 2], in *D. unisexualis* rarely [3 + 1] and exceptionally [4 + 1], and [2 + 2] in half of the *D. bendimahiensis* studied. In one specimen of the latter (Fig. 11 I), there was bilateral asymmetry in the sternal/xiphisternal formula (3 + 1 and 2 + 2).

The sternal-xiphisternal formula is represented as [x + y], where x and y are the number of ribs with sternal and xiphisternal insertion, respectively. Within Lacertidae, there are three more usual formulas: [3 + 1], [3 + 2], and [3 + 3]. The second is the most common, but some species could present two of these formulas at the same time, for example, generally [3 + 2] and more rarely [3 + 1], as in *Gallotia* and *Zootoca* (primitive character status). Other species have [3 + 2] and sometimes [3 + 3], as in the remaining taxa of Lacertini. In Lacertini, normally there are three pairs of ribs running from the dorsum to the ventral part, to join directly to the sternum, and two more to join indirectly through the xiphisternum, giving a sternal + xiphisternal formula of [3 + 2]. Exceptionally, there can be three pairs of xiphisternal ribs, as occurs in some *Algyroides*, *Darevskia* (see above), *Lacerta*, *Podarcis*, *Timon*, and

Takydromus. In the Eremiadini, a total of 5 ribs (3 + 2) is the most usual formula, although it can be reduced to a total of 4 or 3 in some species of *Meroles*, *Pedioplanis*, etc.

Regarding the inscriptional ribs, the basic number in *Darevskia* is 1. More frequently absent in *D. portschinskii*. They can vary between 0, 1, or 2 in *D. derjugini*; or be absent (1 and 0) in some *D. daghestanica*, *D. caucasica*, *D. defilippi*, *D. brauneri* (in our *D. b. ssp. darevskii* specimens), *D. chlorogaster*, *D. raddei*, *D. nairensis*, *D. s. spitzenbergerae*, *D. r. rudis*, *D. o. obscura*, *D. b. bithynica*, *D. parvula*, *D. adjarica*, and among the parthenogenetics in some *D. armeniaca*, half of the *D. dahli*, *D. rostombekowi*, *D. unisexualis*, *D. sapphirina*, or *D. bendimahiensis*. Also, the number can be increased from 1 to 2 in some *D. alpina*, *D. o. bischoffi*, *D. mirabilis*, *D. 'r.' chechenica*, *D. 'r.' svanetica*, *D. r. bolkardaghica*, and *D. b. tristis*.

These inscriptional ribs are situated after the sternal/xiphisternal ones and are characterized by running ventrally towards the xiphisternum but without joining it, remaining further back and free. These inscriptional ribs appear in *Archaeolacerta*, *Atlantolacerta*, *Iranolacerta zagrosica*, some *Lacerta* s. str., *Takydromus* and *Timon*, and in some specimens or species of *Darevskia* (see above), *Iberolacerta*, *Podarcis*, *Algyroides*, and frequently in *Zootoca* spp. In other genera of Lacertini, they appear very rarely or are always missing. Often they are a single pair, but two pairs are present in some *Takydromus* and up to three in some *Lacerta* s. str. and *Timon*. Their number is variable in Gallotiinae (variable in *Gallotia*, and frequently present in *Psammodromus algirus*, but not usual in *Ps. hispanicus*). Mostly absent in the Eremiadini (but present in some *Nucras*, and usually present in the genera *Gastropholis*, *Bedriagaia*, *Adolfus*, etc.). The most usual sum of Sternal + Xiphisternal + inscriptional ribs is 6, in the form [3 + 2] 2, more rarely 5, and still more rare other numbers.

3.2.3. Number of presacral vertebrae

The *Darevskia* studied usually have 27 vertebrae in males and 28 in females. Deviations from these numbers are mainly observed in the *raddei* complex (*D. raddei raddei*, *D. r. vanensis*, and *D. nairensis*), where males have 28 and females 29 or even 30 (the latter observed in a female *D. r. raddei*). In *D. clarkorum*, males alternate between 27 and 28, and similarly 28 and 29 in females. *D. caucasica* shows the usual 27 as well as a reduction to 26. Within the *praticola* complex, males usually have 27, while females of *D. (p.) pontica* have 28, 29, or 30 vertebrae; *D. (p.) praticola* has 30; and *D. (p.) hungarica* has 29.Partial deviations from these basic numbers are also seen in the *rudis* group: *Darevskia valentini* females have 28, 29, or 30 vertebrae (27 in males); *D. s. wernermayeri* males have 27–28 and females 29. *Darevskia r. rudis* and *D. o. macromaculata* males typically have 27, with almost half showing 28 (females show 28 and occasionally 29). *Darevskia o. bischoffi* have 27, with some reduced to 26 (females have 28 and rarely 29). *Darevskia o. obscura* and *D. 'r.' chechenica* have 26 and 27 (females have 28 and 29). *Darevskia adjarica* (from coastal Turkey) typically has males with 27 and rarely 26, whereas *D. tuniyevi* (inland Anatolia: Ardahan, Turkey) have 28 in males and 29 in females (Arribas *et al.*, 2018, 2022).

Parthenogenetic species maintain the female number of vertebrae, yet despite being clones, they exhibit considerable variation. *Darevskia armeniaca* has 28, rarely 29; *D. dahli* shows 29 or 30; *D. rostombekowi* has 28 or 29; *D. unisexualis* and its triploid hybrid have 28 (consistent in our sample); *D. uzzelli* has 29 and rarely 28; and *D. sapphirina* and *D. bendimahiensis* show 28 or 29 in similar proportions. In a specimen of *D. clarkorum*, asymmetry was observed between both sides of the body, resulting in an extra vertebra on one side compared to the other (Fig. 11 A). Similar asymmetries were detected in specimens of *D. saxicola* (Fig. 11 B) and *D. portschinskii* (Fig. 11 C).

Lacertidae exhibit sexual dimorphism in the number of presacral vertebrae (a primitive character state). This dimorphism is secondarily lost in *Gallotia* and in some *Acanthodactylus* species where males and females have identical numbers. Generally, females have one to three more vertebrae than males (typically one more). The counts in each sex of a species can vary up to three (exceptionally four) vertebrae. The usual number in males of many Lacertini species is 26, whereas it is 27 or more in *Hellenolacerta, Lacerta, Parvilacerta, Darevskia, Timon*, some *Podarcis,* and *Scelarcis* species. Some genera like *Algyroides* (except *A. fitzingeri*), *Dalmatolacerta*, and some *Dinarolacerta, Apathya,* and *Takydromus* often exhibit a reduction to 25 vertebrae in males. In *Takydromus*, the middle and posterior body vertebrae have laterally compressed neural spines, contributing to body stiffness related to their lifestyle.

The lizards considered as sister group to Lacertini, the Gallotiinae, typically have 26 vertebrae in males (*Gallotia* and *Psammodromus*), which is considered the plesiomorphic number. The reduction to 25 or increase to 27 or 28 vertebrae in males as observed in *Darevskia,* and even higher counts in *Parvilacerta* (*P. parva* and *P. fraasi*; 28 in males and 29 in females), are considered independent and apomorphic character states. In Eremiadini, except for some *Acanthodactylus* species with the same number in males and females, most other *Acanthodactylus* and other genera exhibit sexual dimorphism in vertebral numbers. Males typically have 26–27 vertebrae, with some genera showing reductions to 25 or increases to 29. In the basal *Atlantolacerta*, males have 26, 27, or 28 vertebrae, and females have 28 or the modal number of 29.

According to Arnold (1983), there is a general but imprecise correlation between vertebral numbers and habitat preference: species with higher vertebral counts tend to occupy relatively more mesic habitats, while lower numbers are found in species from more arid, open, and less vegetated environments. This might be related to the need for greater body inflection to navigate through vegetation, where a higher number of vertebrae facilitate movement. Alternatively, another theory proposed by Arnold suggests that additional vertebrae increase female body volume, potentially aiding in clutch size. The conservation of vertebral numbers across phylogenetically related taxa suggests a significant phylogenetic background to this trait, with minimal variation within closely related groups, even in clonal parthenospecies.

3.2.4. Number of posterior dorsal vertebrae (with short presacral ribs)

Darevskia species generally exhibit 6 short ribs on the posterior part of the vertebral column (posterior parasternal region), although variations of 5 or 7 are occasionally observed as individual variations. The presence of 7 short ribs often accompanies specimens with an increased vertebral count, while the reduction to 5 is associated with a lower than usual vertebral number. Thus, variability in the number of dorsal vertebrae primarily occurs through the addition or subtraction of vertebrae in the posterior parasternal zone (e.g., *D. daghestanica, D. alpina, D. chlorogaster* females with 29 vertebrae and 7 short ribs; *D. josefschmidtleri* male and females, *D. s. spitzenbergerae* females with 29 vertebrae and 6 or 7 short ribs; female *D. raddei* with 30 presacral vertebrae accompanied by 7 short ribs). This phenomenon is more pronounced in *D. valentini* females, where 28, 29, or 30 vertebrae are observed alongside 6, 7, or even 8 short ribs. However, this parallelism is not always observed: *D. r. lantzicyreni* has 27 (rarer 26, and extremely rare 25) with 6 or 7 short ribs.

In parthenogenetic species, *D. armeniaca* exhibits 6 or 7 short ribs, with both numbers present in specimens with 29 presacral vertebrae (and the only one with 28 having 6). *D. dahli* has 29 or 30 vertebrae, including 7 short ribbed ones (one with 6). *D. rostombekowi*, with both 28 and 29 presacral vertebrae, can have 6 or 7 short ribbed ones. All *D. unisexualis* specimens had 28 vertebrae with 6 short ribbed ones (like their triploid hybrid), and finally, *D. uzzelli, D. sapphirina,* and *D. bendimahiensis* all had 28 (6) or 29 (7) in similar proportions.

Posterior dorsal vertebrae refer to the last presacral vertebrae that have short ribs associated with them ("parasternal posterior" vertebrae or region). Their number varies, typically ranging from 7 or 8 (the primitive state of character in Lacertidae), as observed in *Gallotia* (other Gallotiinae, like *Psammodromus algirus*, exhibit 6, 6+0, or 7). Variability is also noted in the Eremiadini, where most genera have 7 or more (*Acanthodactylus, Eremias, Meroles, Pseuderemias, Heliobolus, Ichnotropis, Latastia, Philochortus, Omanosaura,* and variable counts in *Nucras* and *Poromera*). In Lacertini, 6 or 7 are common numbers (with 7 being the derived state), but some species exhibit reductions to five (e.g., most *Zootoca* with 5 or 4+0 in *Z. vivipara* sspp., and two out of three *Z. carniolica* studied, with the third having 6, representing an even more derived state). *Takydromus* typically exhibits only three to five vertebrae with short ribs.

Arnold (1989) compared the number of these posterior vertebrae ("number of short free dorsal ribs") with the number of anterior dorsal ribs (with long ribs), although he considered the reverse polarity compared to our criteria. The presence of both states in the external group and the frequent occurrence of a larger number of short vertebrae as a character state in African Eremiadini complicate determining the polarity of this character.

3.2.5. Presence and form of the sternal fontanelle

In the *Darevskia* studied, oval fontanelles are more frequent (we will not distinguish between irregular and regular oval or round fontanelles) but frequently coexist with the cordiform model (Figures 7–10). Irregular cordiform models appear together with the oval ones in some *D. derjugini*, some *D. r. bolkardaghica* (frequently very odd-shaped; Fig. 11 G), some *D. parvula*, rare *D. daghestanica* (Fig. 11 E), some *D. adjarica* (coastal Turkey), some *D.*

mixta (Fig. 11 G), and some *D. s. spitzenbergerae*. Shaped cordiform ones appear (together with oval ones) in part of the *D. daghestanica*, *D. alpina*, and *D. valentini*; some rare *D. brauneri*, *D. (p.) pontica*, and a few and rare *D. o. macromaculata*. In *D. b. bithynica* it is frequently obliterated and reduced to a very small hole, if at all; and it is also reduced in some *D. clarkorum*.

Among the parthenogenetic species, in *D. armeniaca* it is oval, but some rare specimens have irregular cordiform; in *D. dahli* it is oval and rarely cordiform; in *D. rostombekowi* it is oval and rarely irregular cordiform; in *D. unisexualis* it is oval, but in the triploid hybrid with *D. nairensis* it is cordiform (Fig. 11 F); in *D. uzzelli* it is oval and rarely cordiform; and finally, in *D. sapphirina* and *D. bendimahiensis* it is irregular oval.

The sternal fontanelle is an opening present from birth in the sternal plate of most lacertids. Its shape is variable: it can be rounded, more or less oval (the most extended model), slightly heart-shaped (sometimes quite asymmetrical), or cordiform (as in *Podarcis*, see Arnold, 1973, 1989). The rounded or oval models, scarcely differentiated and very extended, are the primitive ones; and the cordiform morphologies are derived (Arnold, 1973, 1989), although it seems that they appear here and there in well-separated groups, so they would be a convergent model or with numerous reversions to the supposed primitive model (the oval or round).

In other Lacertini genera, the oval (or rounded) model is the most widespread. Exceptions are *Podarcis*, *Phoenicolacerta*, *Anatololacerta*, some *Algyroides* (*A. moreoticus* and *A. marchi*), and the *Darevskia* cited above that have them more or less cordiform. The fontanelle is oval in the Gallotiinae (*Gallotia* and *Psammodromus*) and many Eremiadini (but it is cordiform in *Atlantolacerta*, *Ophisops*, *Mesalina*, *Acanthodactylus*, *Eremias*, *Pedioplanis*, and in only some *Meroles* and *Aporosaura*).

3.2.6. Form of the clavicles (emarginated or marginated)

In *Darevskia* both models (open and closed) appear mixed in many of the species, sometimes with a dominance of one or the other (Figures 7–10). Always open appear in the *raddei* complex (*D. r. raddei*, *D. r. vanensis*, and *D. nairensis*), and possibly also (with doubts by the scarce sample) in *D. defilippi*, the *saxicola* complex (*D. saxicola*, *D. brauneri*, *D. szczerbaki*, and *D. lindholmi*), *D. portschinskii*, and the *parvula* complex (*D. parvula*, *D. adjarica*, and *D. tuniyevi*). The clavicles of the *D. praticola* complex are outstanding by the presence of a thin laminar expansion well developed in their more lateral part (Figure 8), also present but fairly smaller in *D. brauneri* and only weakly indicated in other species. Seem particularly few developed or absent in the *rudis* group.

In parthenogenetic species such as *D. armeniaca*, *D. unisexualis* (and its triploid hybrid), *D. rostombekowi*, and *D. uzzelli*, the clavicle is ever open. *Darevskia bendimahiensis* and *D. sapphirina* usually show it also open, and rarely or very rarely closed. Some parthenogenetic had the laminar expansion of the distal part of the clavicle indicated or moderately developed (*D. armeniaca*, *D. dahli*, *D. unisexualis*, *D. sapphirina*, and the triploid hybrid *D. unisexualis x D. nairensis*) whereas it is almost indiscernible or absent in others (*D. rostombekowi*, *D. uzzelli*, and *D. bendimahiensis*) (Figure 10).

The clavicle of the lacertids has an expansion towards its medial part, with an internal opening that is between the two clavicular branches (called anterior and posterior) (is the model of clavicle emarginated or closed). In addition, the posterior branch may be missing, leaving the clavicle open (marginated or open clavicle). Anatomically, the closed model seems to be the primitive one, but both types of clavicles appear very frequently mixed in the same species (in fact, the rare case is that only one model exists in a given taxon). Some species such as the external group (Gallotiinae) present ever-closed models (*Psammodromus*, *Gallotia*), almost in adults, but is very interesting that is open in juveniles and posteriorly becomes closed in adults (Barahona *et al.*, 1998). The Eremiadini also have almost universally closed clavicles (except *Holaspis*—open-, and *Atlantolacerta* or *Omanosaura*—variable-).

In the Lacertini, the situation is variable. Are almost always closed in most *Lacerta*, *Zootoca* (*Z. vivipara* sspp., and in *Z. carniolica*) species, and even we have observed a specimen with the interior gap obliterated by a thin bone plate, and also in *Parvilacerta* and in *Takydromus*, in which the posterior edge of the clavicle is fairly wide. It is variable in the great part of the *Darevskia* above mentioned, as in *Iberolacerta*, *Apathya*, *Podarcis*, and *Teira*. Is almost ever (or universally) interrupted (open) in *Archaeolacerta*, *Dalmatolacerta*, *Dinarolacerta*, *Hellenolacerta*, *Scelarcis*, and *Timon*. For this reason, some authors such as Arnold (1989) consider in practice the presence of both models mixed as the primitive situation and the presence of one or the other exclusively, as a derived condition.

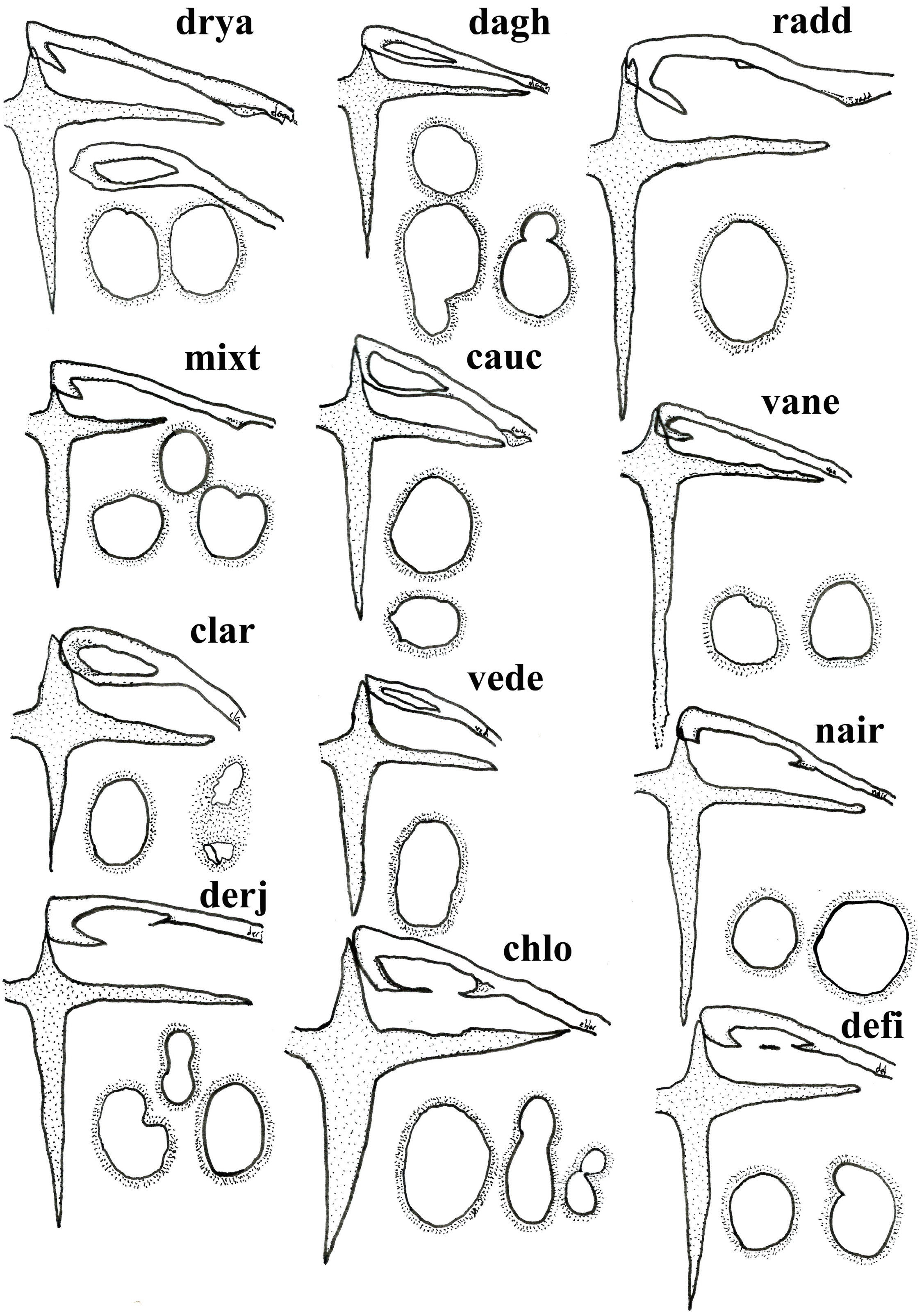

FIGURE 7. Left clavicle, interclavicle (right side not represented) and sternal fontanelle shape variation. The sternal fontanelles are represented to the right and below the interclavicle, not in their anatomical position (towards the tip of the posterior branch of the interclavicle—see Fig. 1—). Left column (from top to bottom): *D. dryada* **(drya)**, *D. mixta* **(mixt)**, *D. clarkorum* **(clar)** and *D. derjugini* **(derj)**. Central column (top to bottom): *D. daghestanica* **(dagh)**, *D. c. caucasica* **(cauc)**, *D. c. vedenica* **(vede)**, *D. chlorogaster* **(chlo)**. Right column (top to bottom): *D. r. raddei* **(radd)**, *D. r. vanensis* **(vane)**, *D. nairensis* **(nair)**, *D. defilippi* **(defi)**.

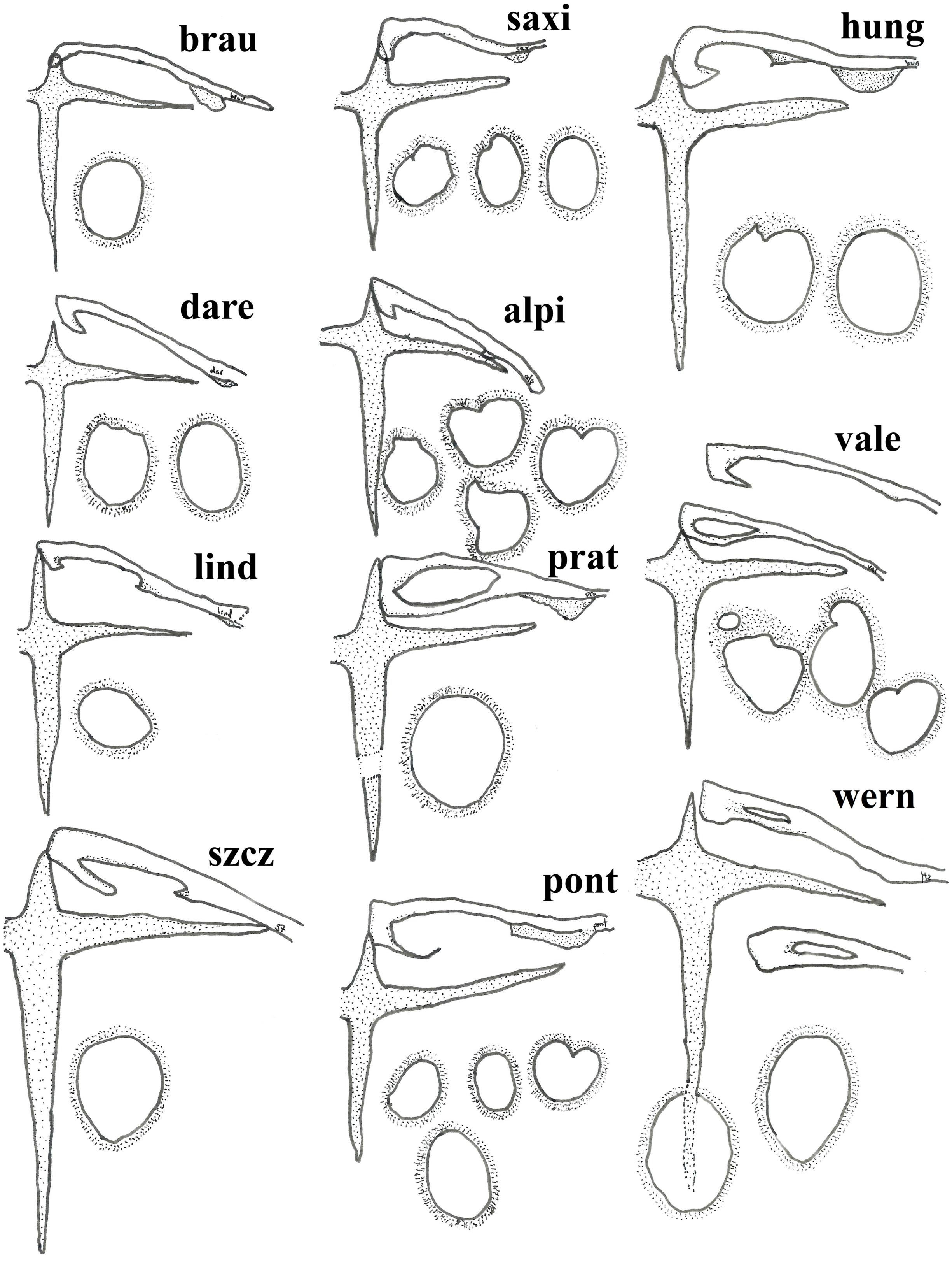

FIGURE 8. Left clavicle, interclavicle (right side not represented) and sternal fontanelle shape variation. The sternal fontanelles are represented to the right and below the interclavicle, not in their anatomical position (towards the tip of the posterior branch of the interclavicle—see Fig. 1—). Left column (from top to bottom): *D. b. brauneri* **(brau)**, *D. b. darevskii* **(dare)**, *D. lindholdmi* **(lind)**, *D. szczerbaki* **(szcz).** Central column (top to bottom): *D. saxicola* **(saxi)**, D. alpina **(alpi)**, *D. (p.) praticola* **(prat)**, *D. (p.) pontica* **(pont).** Right column (top to bottom): *D. (p.) hungarica* **(hung)**, *D. valentini* (and variation on clavicle shape) **(vale)**, *D. s. wernermayeri* **(wern)**.

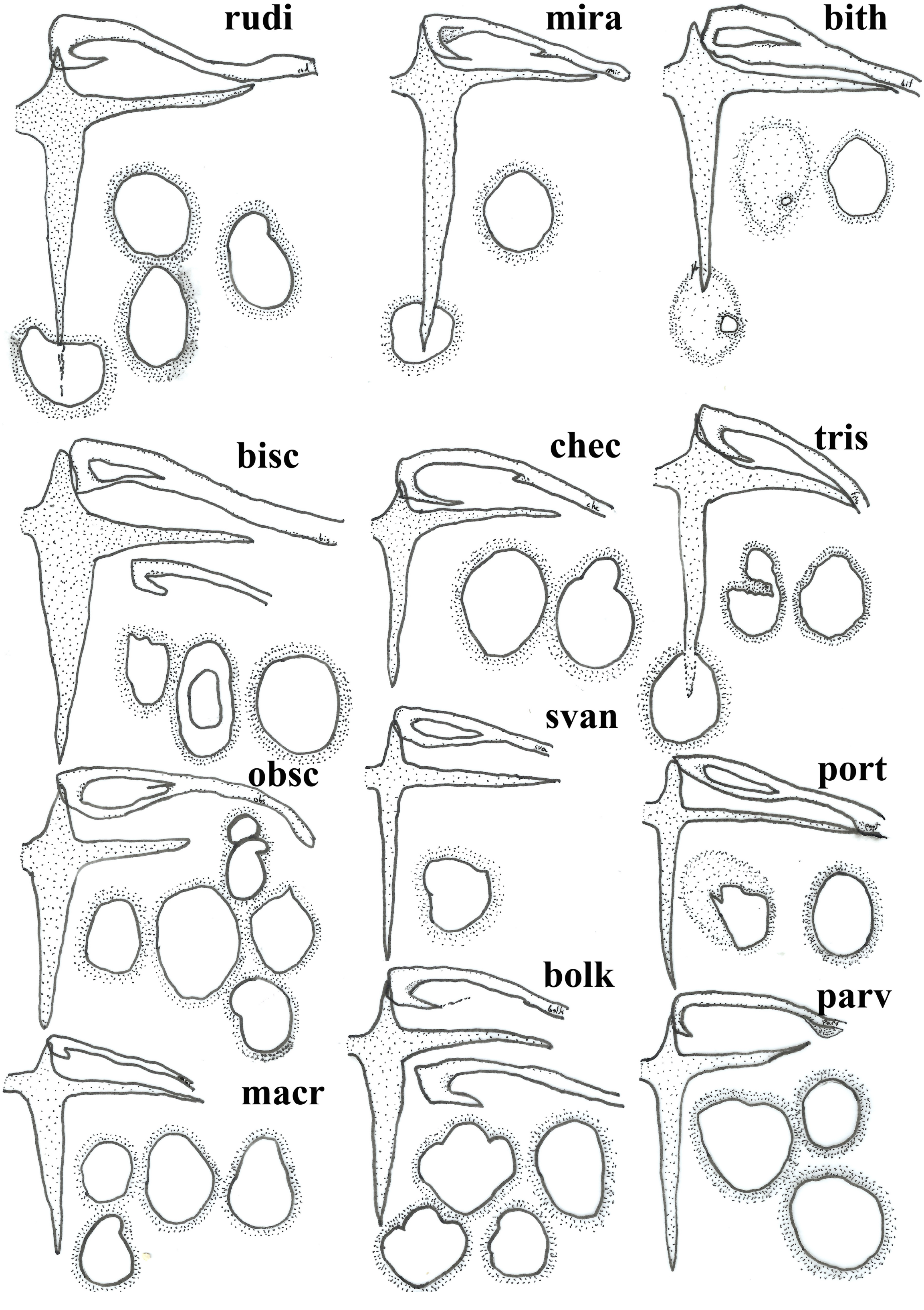

FIGURE 9. Left clavicle, interclavicle (right side not represented) and sternal fontanelle shape variation. The sternal fontanelles are represented to the right and below the interclavicle, not in their anatomical position (towards the tip of the posterior branch of the interclavicle—see Fig. 1—). Left column (from top to bottom): *D. r. rudis* **(rudi)**, *D. o. bischoffi* **(bisc)**, *D. o. obscura* **(obsc)**, *D. o. macromaculata* **(macr).** Central column (top to bottom): *D. mirabilis* **(mira)**, *D. 'r.' chechenica* **(chec)**, *D.'r.' svanetica* **(svan)**, *D. r. bolkardaghica* **(bolk)**. Right side (top to bottom): *D. b. bithynica* **(bith)**, *D. b. tristis* **(tris)**, *D. portschinskii* **(port)**, *D. parvula* **(parv)**.

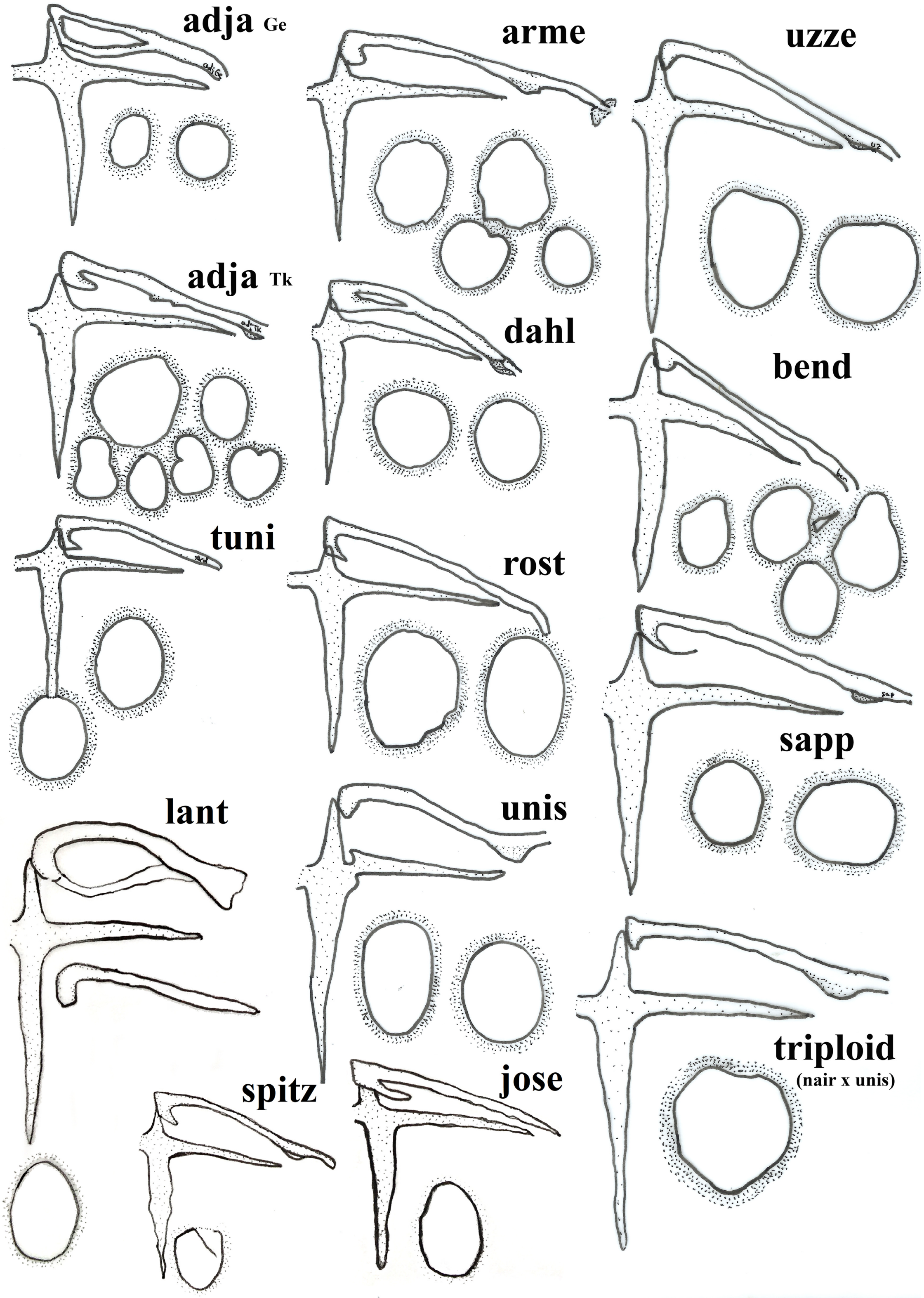

FIGURE 10. Left clavicle, interclavicle (right side not represented) and sternal fontanelle shape variation. The sternal fontanelles are represented to the right and below the interclavicle, not in their anatomical position (towards the tip of the posterior branch of the interclavicle—see Fig. 1—). Left (from top to bottom): *D. adjarica* (Georgia) **(adja Ge)**, *D. adjarica* (Turkey) **(adja Tk)**, *D. tuniyevi* (Ardahan, Tk.) **(tuni),** *D. r. lantzicyreni* s. str **(lant)**, *D. s. spitzenbergerae* **(spitz)**. Central (top to bottom): *D. armeniaca* **(arme)**, *D. dahli* **(dahl)**, *D. rostombekowi* **(rost)**, *D. unisexualis* **(unis)**, *D.josefschmidtleri* **(jose)**. Right column (top to bottom): *D. uzzelli* **(uzze)**, *D. bendimahiensis* **(bend)**, *D. sapphirina* **(sapp)**, Triploid (*D. nairensis* x *D. unisexualis*) **[triploid (nair x unis)].**

3.2.7. Interclavicle form

In *Darevskia*, the basic model is cruciform (cross-shaped), but many species also present specimens where the lateral branches, especially the most distal parts, can be inclined slightly forward or backward. We recommend seeing Table 1 for each particular taxon (and Figures 7–10).

Only cruciform models (with lateral branches perpendicular to the sagittal axis) appear in *D. clarkorum* and the specimens studied of *D. szczerbaki*, *D. (p.) praticola*, *D. (p.) hungarica*, *D. valentini*, *D. r. rudis*, *D. mirabilis*, *D. 'r.' svanetica*, *D. r. bolkardaghica*, and *D. bithynica* sspp. The most strongly inclined forward appear in *D. chlorogaster*, as stated in Arribas (1998) (Fig. 11 D). Only slightly inclined forward in the few studied specimens of *D. defilippi*, and only slightly backward in the few specimens examined of *D. c. vedenica*, *D. r. vanensis*, and *D. s. spitzenbergerae*. Usually cruciform, but with some rare specimens pointing forward are in *D. derjugini*, *D. daghestanica*, *D. alpina*, *D. parvula*, *D. o. obscura* (cruciform in specimens from Turkey, but pointing forward in Georgian ones). Usually cruciform but also pointing backward, appear in *D. dryada*, *D. saxicola*, *D. o. bischoffi*, *D. o. macromaculata*, *D. 'r.' chechenica*, *D. josefschmidtleri*, *D. r. lantzicyreni*, and *D. portschinskii*. In *D. mixta* there are as many cruciforms as slightly pointing forward. Even the three models can appear (moderately inclined) coexisting in variable proportions among the same taxon, as have appeared in *D. caucasica*, *D. brauneri*, and *D. adjarica* (from coastal Turkey).

Concerning parthenogenetic ones (Figure 10), *D. armeniaca* and *D. dahli* have them cruciform (and rarely inclined backward). *Darevskia uzzelli* has it cruciform and inclined backward in similar proportions, and in *D. sapphirina* and *D. bendimahiensis* the slightly backward model is more abundant than the cruciform one. In *D. rostombekowi* both models, cruciform and forward appear, while in *D. unisexualis* and its triploid hybrid with *D. nairensis*, there are only cruciform ones.

The interclavicle in Lacertidae is cross-shaped in all species (cruciform), with a very short anterior branch relative to the posterior, having moderately long lateral branches. In general, the lateral branches are more or less perpendicular to the anteroposterior axis, sometimes slightly inclined forward or backward, or slightly variable in either direction. The primitive state of the character is the possession of a cruciform interclavicle (cross-shaped), with the lateral branches more or less perpendicular to the axis of the body, as it appears in the Gallotiinae species, the vast majority of Eremiadini (except *Holaspis*), being also the most widespread form in all Lacertini. Branches moderately directed forward appear in *Dalmatolacerta* and some *Darevskia* (see above). On the contrary, in *Teira* and *Scelarcis* the interclavicular branches are directed backward, and less clearly in our specimens, in *Atlantolacerta* (see Arnold, 1973, 1989; Arribas, 1998 and own data). Both situations can be considered derived. In *Takydromus*, the interclavicle may be flanged (as in some rare Eremiadini as *Poromera* and is variable in *Ophisops*) (Arnold, 1989; Arnold et al, 2007).

3.2.8. Morphology of first autotomic vertebrae of the tail

Darevskia species generally bear autotomic vertebrae type A, often coexisting with rarer cases of type B, which frequently appear interspersed in the same specimen. We have found more type B than type A in *D. caucasica*, *D. r. raddei*, *D. r. vanensis*, *D. saxicola*, and among the parthenogenetic *D. uzzelli*. The triploid hybrid (♀ *D. unisexualis* -type A- x ♂ *D. nairensis* -type A, rarely type B-) shows type B (see below). All the other parthenogenetics have type A. It is striking that all *D. rudis* sspp. and most of the *D. valentini* related forms (except *D. valentini* itself) show only type A (but in the closer *D. bithynica* some rare type B also appear), as occurs in *D. portschinskii* and the entire *D. parvula* complex.

Arnold (1973, 1989) and Arnold *et al.* (1997) distinguish three models of autotomic vertebrae at the base of the tail: the first one only presents perpendicular processes in its anterior part (type A). The second model has two pairs of processes, one before and one after, with the first being greater than the second (type B). The third model also has two pairs of processes, but the later ones are greater than the previous ones (type C). Types A and B frequently appear together and are widespread among the Eurasian radiation groups of Lacertidae (Lacertini), including all species of genera such as *Archaeolacerta*, *Dalmatolacerta*, *Dinarolacerta*, *Iberolacerta*, *Apathya*, *Phoenicolacerta*, *Zootoca*, *Takydromus*, *Timon*, etc. Type A also appears in the vast majority of the Eremiadini (except *Acanthodactylus*, see below) and sometimes coincides with type B as in *Atlantolacerta*—type A and also some of the *B* type—or in *Omanosaura*. Type B is also very widespread in the Eremiadini (except *Acanthodactylus*).

Type C appears in *Podarcis*, some species from the Near East (*Anatololacerta*), and in species of the external group, the subfamily Gallotiinae (*Gallotia*, *Psammodromus*), and in rare Eremiadini (such as *Acanthodactylus*). In *Parvilacerta* (*P. parva*, *P. fraasi*) and *Iranolacerta* (*I. brandtii*), intermediate models between types B and C are present, according to Arnold (1989). All our studied *Zootoca* spp. had only type A.

Although Arnold (1989) considers that types A and B are the primitive models because they are the most widespread, we believe, based on data from the external group and at least the existence also in the Eremiadini (such as *Acanthodactylus*), that the primitive model could also be type C. However, the polarity and homology between the different models are not at all clear.

3.3. Parthenogenetic species and their bisexual relatives: osteological comparison

The parental species considered for the different parthenogenetic species are (Uzzell & Darevsky, 1975; Darevsky & Danielyan, 1977; Darevsky *et al.*, 1985, 1986; Kupriyanova, 1989; Moritz *et al.*, 1992; Freitas *et al.*, 2016; Tarkhnishvili *et al.*, 2020b):

Darevskia armeniaca [*D. mixta* ♀ x *D. valentini* (*valentini*) ♂] (see however Tarkhnishvili *et al.*, 2017, 2020b for the possible participation of *D. portschinskii* in this parthenogenon). *Darevskia dahli* [*D. mixta* ♀ x *D. portschiskii* ♂]. *Darevskia rostombekowi* [*D. raddei* ♀ x *D. portschinskii* ♂]. *Darevskia unisexualis* [*D. nairensis* ♀ x *D. josefschmidtleri* ♂]. *Darevskia uzzelli* [*D. nairensis* ♀ x *D. valentini* ♂]. *Darevskia sapphirina* [*D. raddei* (*vanensis*) ♀ x *D. josefschmidtleri* ♂]. *Darevskia bendimahiensis* [*D. raddei* (*vanensis*) ♀ x *D. josefschmidtleri* ♂].

Darevskia armeniaca is composed of at least five distinct genetic groups of comparable size (McCulloch *et al.*, 1995; Korchagin *et al.*, 2007; Girnyk *et al.*, 2018). In other species, genetic variability is lower due to their restricted areas or their limited population sizes (Fu *et al.*, 2000a), but they also contain several genetic variants, probably different clones: *D. dahli* (Murphy *et al.*, 1997; Davoyan *et al.*, 2007; Vergun *et al.*, 2014), *D. unisexualis* (McCulloch *et al.*, 1995; Korchagin *et al.*, 2007) and in *D. uzzelli*, *D. sapphirina*, and *D. bendimahiensis* (Fu *et al.*, 2000b). *Darevskia rostombekowi* by the moment is considered to be a unique original clone with posterior mutations (Ryskov *et al.*, 2017), and Vergun *et al.* (2020) also postulate for a single clone for *D. unisexualis*. From the point of view of microsatellites study, *D. rostombekowi* and *D. unisexualis* are considered to be a unique original clone with posterior microsatellite mutations (Ryskov *et al.*, 2017; Vergun *et al.*, 2020); and *D. dahli* and *D. armeniaca* are considered to be three original clones with posterior microsatellite mutations (Vergun *et al.*, 2014; Girnyk *et al.*, 2018).

Parthenogenetic species inherit their characteristics from the bisexual species that gave rise to them by hybridization, in a single or frequently in multiple events, during the past. It is interesting to compare if the parthenogenetic species resemble both parents; are more similar to the females of any of the taxa that originated them; or in some circumstances show some different characteristics to both parental species, and what is the possible interpretation to this. In the case of triploid hybrids between a parthenogenetic and a bisexual species, the hybrids are closer to their parthenogenetic maternal form in coloration and the major scalation characters than to the bisexual paternal form (Darevsky, 1967), and there are concurrently a few hybrid features formed distinctly under the paternal influence (Darevsky & Kulikova, 1962).

Osteologically, parthenogenetic species could look more frequently like the females of the cross that gave origin to them (Arribas, 1998) or, if they are different, show characteristics that can be used to determine the evolutionary polarity of these characters. It is generally accepted that the traits of parents are expressed in hybrids in two typical ways: The hybrids can be intermediate (especially in quantitative characters) or be a mosaic of characters from the two parents, in which case the dominant ones are expressed in the hybrid (McCarthy, 2006). We hypothesize that, when two different genomes (of the parental species) come together, the part common to both is expressed and, if they appear different from the parentals, the primitive character by atavism is shown in the hybrid phenotype.

This appearance in parthenogenons of characters alien to the genus *Darevskia*, interpreted as reappearances of atavistic features, is well known in the external morphology of these parthenogenetic species (Darevsky, 1967). The arrangement of the temporal area in *D. armeniaca*, the presence of two postnasals in *D. dahli*, the contact between the rostral and the internasal plates in *D. unisexualis*, etc., are very rare or absent in the bisexual species of *Darevskia*, but they do appear in a very characteristic way in other species of Lacertini. The following lines aim to test this atavistic hypothesis or the dominance of the maternal species traits (as stated in Arribas, 1998). On the other hand, the comparison with the parental species can help determine a parent species in some cases where there are still doubts.

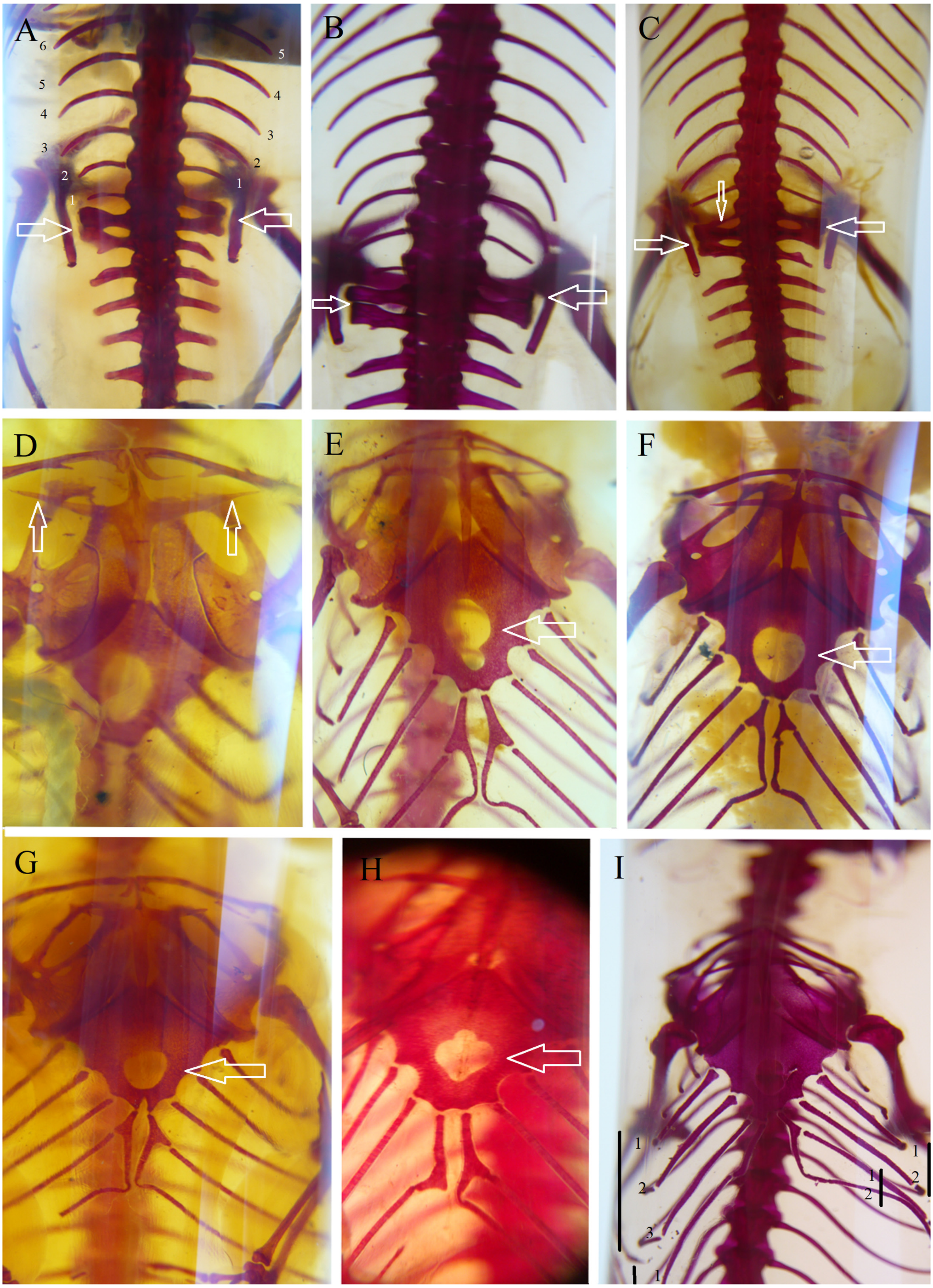

FIGURE 11. Details of cleared and stained specimens. A) Asymmetry in the vertebral column, with sacral processes in different vertebrae that lead to a different presacral count in right and left sides in *D. clarkorum*. B) As A, but in *D. saxicola*. C) As A and B but in *D. portschinskii.* D) Forward directed lateral branches of the interclavicle in *D. chlorogaster*. E) Irregular sternal fontanelle in *D. daghestanica*. F) Cordiform sternal fontanelle in a triploid hybrid (*D. unisexualis* x *D. nairensis*). G) Cordiform sternal fontanelle in *D. mixta*. H) Odd shaped irregular cordiform sternal fontanelle in *D. r. bolkardaghica*. I) Bilateral asymmetry in the sternal/xiphisternal formula (3+1 and 2+2) in *D. bendimahiensis*.

Another surprising aspect revealed in this study is the relatively high variability of these parthenogenetic taxa in many osteological characters, given that they are supposed to be clones (and they are in fact, although in reality almost all except *D. rostombekowi* have been shown to be several clones; Murphy *et al.*, 1997; Vergun *et al.*, 2014; Ryskov *et al.*, 2017; Osipov *et al.*, 2018; Girnyk *et al.*, 2018; Freitas *et al.*, 2019, among others) and they are expected to have less variability than bisexual species, as Darevsky *et al.* (1985) and recently Tarkhnishvili *et al.* (2020a) demonstrated for morphological traits. The parentage question is still open as recently Vergun *et al.* (2020) postulated a single hybridization event for the origin of *D. unisexualis*. Also, Tarkhnishvili *et al.* (2020b) found that genotypes at multiple loci were shared frequently between different parthenogenetic species, especially *D. sapphirina* + *D. bendimahiensis* and *D. dahli* + *D. armeniaca*, and less often between other parthenogens. These authors postulate the attractive hypothesis that these pairs of parthenogenetic species come from a single initial hybridization event, and later the hybridization of the first hybrid with other bisexual lizards (i.e., *D. valentini* for *D. armeniaca*; see also Tarkhnishvili *et al.*, 2017) explains its current differences.

Teeth numbers: Teeth numbers offer few characteristics since, as expressed above, they can be influenced by the size of the individuals and the taxa in general. The extreme variation of premaxillary teeth in *D. sapphirina* is striking, as being a clone, its number of premaxillary teeth can be seven but also five or six. The two parental species (*D. josefschmidtleri* and *D. raddei vanensis*) have the common number of seven (rarely 8). Only a determining factor due to the very small size constraining teeth number in the premaxilla or some unknown instability between the parental genomes could explain this phenomenon (however, the parental species are the same as in *D. bendimahiensis* and partly in common with other parthenogenons). The only bisexual species in which we have found such variation is in *D. saxicola* (seven, rarely 9, and one specimen with only 4-teratological?-).

Teeth shape: The ratio of bicuspid to unicuspid teeth is quite a labile character during the growth of the lizards, the reason why only adult animals shall be compared. For example, in *D. dahli* more bicuspid than unicuspid teeth appear, as in their maternal species *D. mixta*, while in the paternal (*D. portschinskii*) although variable, the proportion is usually very similar between both types. Something similar occurs in *D. uzzelli*, with more bicuspid than unicuspid teeth, such as the maternal (disputed between *D. raddei vanensis* and *D. nairensis*) and the entire *raddei* complex, while the paternal *D. valentini* has also more bicuspid than unicuspid. The situation in *D. bendimahiensis* is the same, more bicuspid than unicuspid as in the maternal *D. r. vanensis*, and also in the paternal *D. josefschmidtleri*. Also, *D. sapphirina* and *D. bendimahiensis* have more bicuspid than unicuspid teeth, as their maternal species (*D. raddei vanensis*) and the paternal one *D. josefschmidtleri*. In this character, in case of discrepancy, the hybrids seem to be more similar to their maternal species.

Anterolateral process in the postfrontal: All parthenogenetic species have the anterolateral process of the postfrontal developed, as in their parental ones and in general, all the *Darevskia*.

Anteromedial process in the postorbital: As we have indicated above in the general description of this character, some species present the process reduced or absent. In parthenogenetic, it is frequently absent due to the influence of maternal species of the *raddei* complex or *D. mixta*, in which it is frequently absent. In *D. armeniaca* situation is very variable, it is missing or is very reduced but even can be present, as in its maternal *D. mixta* (in which it is usually absent) more than in the paternal species (*D. valentini*, who has it well developed or is somewhat reduced). In *D. dahli* the same occurs, is absent or rarely only reduced, as in *D. mixta*, the maternal species, whereas the paternal species *D. portschinskii* has it developed. More interesting is the case of *D. rostombekowi* who does not present the process (or had them reduced) while his parents theoretically had it developed (in *D. raddei*, the maternal is present but sometimes reduced; and in *D. portschinskii*, the paternal, is developed). Interestingly, in other taxa of the *raddei* complex is variable, but *D. r. vanensis* that in principle is not maternal of *D. rostombekowi*, also lack the process (could be other *raddei* complex form the maternal of *D. portschinskii*, or this trait is inherited from the part of the *raddei* complex species that now lacks it?). *Darevskia unisexualis* lacks the process but its maternal *D. nairensis* usually has it, as occurs also in the paternal *D. josefschmidtleri* (that very rarely presents it reduced). The same occurs for his triploid hybrid with *D. nairensis*, which has the same situation as the maternal *D. unisexualis* (absent). Seems strange but even if present, seems to be a tendency to the reduction in size in most of the *raddei* complex. Of particular interest is the case of *D. uzzelli*, who usually lacks the process (can be present with diverse degrees of reduction) while his alleged parents (paternal *D. valentini*, maternal *D. r. raddei*) have it developed, although on rare occasions reduced. *Darevskia sapphirina* does not present it (very rarely can be present, again another example of this strange variability of this specific taxon of hybrid origin), and the same for *D. bendimahiensis*, in both cases as their maternal species (*D. r. vanensis*) which also lacks it, since they differ from their paternal (*D. josefschmidtleri*) which has it developed (rarely reduced). It may be that when both bones originated, the process obviously did not existed, and then, its absence today is the apparition here and there by atavism of a primitive character.

Comparative lengths of postorbital and postfrontal: As discussed above, postorbital and postfrontal bones have similar lengths; one or the other can be longer, but not very dissimilar. In *D. armeniaca* both are of equivalent lengths, in this case as in his paternal species (*D. valentini*), while in the maternal *D. mixta* the postorbital is notably shorter than the postfrontal. In *D. dahli* the postorbital is equal to or shorter than the postfrontal, as well as in the paternal species (in this case, *D. portschinskii*), while in the maternal (*D. mixta*) is shorter. In *D. rostombekowi*, the situation is similar, more similar to the paternal species, but somewhat more confusing, since the postorbital is usually greater than or equal to the postfrontal, but also rarely shorter (again, a surprising variability in a parthenogenon). In the paternal species (*D. portschinskii*) it is, as in the previous cases, greater or equal (as in *D. rostombekowi*), and in the maternal (*D. r. raddei*) it is shorter (shorter than, or equal, in the other taxa studied of the *raddei* complex). *Darevskia unisexualis* has the postorbital shorter than or equal to the postfrontal, as its maternal species (*D. nairensis*) and also the paternal one (*D. josefschmidtleri*, equal or more rarely greater), but as some *D. r. lantzicyreni*. More interesting is its triploid hybrid with *D. nairensis*, which has it greater than or equal, while the parents (*D. unisexualis* and *D. nairensis*) have it the opposite, shorter than or equal. Of the three genomes present in the triploid, two of them have the opposite character to the triploid specimen itself, shorter than or equal, and in the third one (from *D. josefschmidtleri*) is equal or more rarely greater. The persistence of this “greater or equal“ suggests that it is more primitive (especially the “equal”) than the shorter one, despite being in minority among the genomes present. *Darevskia uzzelli* has it shorter or equal (rarely greater than or equal), more similar to the maternal species (*D. r. raddei*, clearly shorter; and shorter or equal in the other taxa studied of the *D. raddei* complex) and compatible with the state in the paternal species (more or less equal in *D. josefschmidtleri*). *Darevskia sapphirina* has them more or less of the same length (rarely one or the other somewhat greater) while each of the parents can have it in one different proportion (smaller or equal in the maternal, *D. r. vanensis*; more or less equal in all our studied *D. josefschmidtleri*). Finally, *D. bendimahiensis* has a greater postorbital than the postfrontal, different from the paternal (more or less equal in *D. josefschmidtleri*) and the maternal (smaller or equal to in *D. r. vanensis*). It is interesting the difference with *D. sapphirina*, as both share the same parents. The more or less similar lengths seem to be the primitive character, while the deviations, are an effect of the asymmetric reduction of the cranial bones in parallel to the increasing platycephaly and adaptation to fissuricolous life.

Overlap between the postorbital and the squamosal: There are no remarkable differences in the parthenogenetic species in respect to their bisexual parents.

Ribs associated with the third presacral vertebrae: The presence of ribs (bone or cartilaginous) associated with the third presacral vertebra seems to be an atavistic character that appears here and there in species at a low or very low frequency (Arribas, 1998). *Darevskia armeniaca* can have ribs rarely present at the third presacral vertebra (but even a rudiment in the second presacral, somewhat exceptional), although we have not found it in its parental species. *Darevskia unisexualis* usually has it (rarely absent) while its parents do not, suggesting that it is a primitive (atavistic) character that reappears when the two different genomes combine. The triploid hybrid presented it on one side in a form more similar to the maternal species (*D. unisexualis*) than to the parental one (*D. nairensis*) from which it, nevertheless, has two genomes. *Darevskia uzzelli* may or may not have them, more similar in this case to the maternal *raddei* complex (*D. r. raddei*) that can rarely have it, than to the paternal (*D. valentini*, which does not present it at a detectable frequency). We have not detected it in other species of the *raddei* complex such as *D. nairensis* or *D. r. vanensis*, although they could exist at very low frequencies, as in most species. *Darevskia dahli*, *D. rostombekowi*, *D. sapphirina* and *D. bendimahiensis* and their parental species do not have these ribs (or exist at such a low frequency that we have not detected it).

Sternal/Xiphisternal costal formula and inscriptional ribs: There are no remarkable differences in this character in the parthenogenetic species in respect to their bisexual parents.

Number of presacral vertebrae: The numbers of presacral vertebrae in parthenogenons (unisexual) usually coincide roughly with the corresponding one in their parental (bisexual) species (more considering that there may be undetected variability in our sample), but in some cases, the variability (range) in the parthenogenetic species exceeds that of the parental ones. In *D. dahli* the numbers can be 29 and 30. The latter is higher than those known in the females of the parental species (*D. mixta* and *D. portschinskii*). On the contrary, in *D. rostombekowi* is just the opposite, it has 28 and 29, while in the females of the parental taxa is generally higher (in the paternal, *D. portschinskii* females have 29; and in the maternal *D. r. raddei* 29 or 30), although in this case and given that *D.*

portschinskii males have 27, maybe also the number of 28 presacral vertebrae exists undetected in females of this species). In the case of *D. sapphirina* and *D. bendimahiensis* the number is 28 or 29 as in the females of the parental species (*D. josefschmidtleri* and *D. raddei vanensis*). Something similar occurs in *D. unisexualis*, which has 28 presacral vertebrae, while the parental species females have more (females of the paternal, *D. josefschmidtleri* 28, and the maternal *D. nairensis*, 29). It seems that the hybrid shows the primitive character (common) to both parents, that is, without the vertebral (apomorphic) increase of the *raddei* complex. Furthermore, in the triploid hybrid between *D. unisexualis* and a male of *D. nairensis* (which therefore has two genomes of *D. nairensis* and one of *D. josefschmidtleri*) there are also 28 presacral vertebrae, as in *D. unisexualis*, without the increased number characteristic of the *raddei* complex and despite to have two genomes of *D. nairensis*, which has 29 and belongs to this group.

Posterior dorsal vertebrae (short presacral ribs): Concerning the posterior presacral vertebrae bearing short ribs, *D. armeniaca* has 6 or more rarely 7, and in this case, they perhaps look somewhat more like the females of the paternal species (*D. valentini*) that have 6, 7 or 8, and different to the maternal (*D. mixta*, who have 5 or 6). *Darevskia dahli* has 7 (more rarely 6), also somewhat more similar to her paternal species *D. portschinskii*, in which is 7, than to the maternal *D. mixta*, which has only 5 or 6. Others like *D. rostombekowi*, *D. uzzelli*, *D. bendimahiensis* or *D. sapphirina* are like their parents. Probably this is also the case in *D. unisexualis*, which has 6 as its maternal species (*D. nairensis*, which can also have 7) although this number also appears in its paternal species (*D. josefschmidtleri* which has usually 7, but in males also appear 6). The triploid hybrid has also 6 as in *D. unisexualis* and *D. nairensis*, their parents. It is interesting the influence of *D. portschinskii* (6 short ribs in males and 7 in females) as a paternal taxon into their derived taxa *D. dahli* (7, rarer 6) and *D. rostombekowi* (6 or 7 in similar proportion). Six seems to be the primitive number in the genus.

Sternal fontanelle: (Figure 10) *Darevskia armeniaca* has the fontanelle oval (rarely irregular cordiform), the latter as in its maternal species (*D. mixta*) while in the paternal (*D. valentini*) is both oval and more rarely cordiform. In *D. dahli* it is oval or more rarely cordiform, compatible with its parents (irregular cordiform or rarely oval in the maternal *D. mixta*, oval in *D. portschinskii*). In *D. rostombekowi* is oval (or rarely irregular cordiform), compatible with its two parents that have it oval (*D. portschinskii* and *D. r. raddei*). In *D. unisexualis* it is also oval and corresponds to the parental shapes (oval in *D. josefschmidtleri* and *D. nairensis*). In *D. uzzelli* it is oval as in its maternal species (*D. r. raddei* and also all the raddei complex; as in the paternal *D. valentini*), and both *D. sapphirina* and *D. bendimahiensis* have it more or less oval (irregular) as their parents who also have it oval and *D. raddei vanensis* and *D. josefschmidtleri*). It is striking the triploid hybrid (*D. unisexualis* x *D. nairensis*) has it perfectly cordiform, although its parthenogenetic maternal is oval (of parents also mainly oval), and its paternal also oval. Could the cordiform shape, that appears in the triploid, be an atavistic and primitive character in respect to the common oval or rounded ones?.

Form of the clavicles (emarginated or marginated): (see Figure 10) The shape of the clavicles is more similar to their maternal species than to the paternal ones. In *Darevskia dahli* the clavicles are closed (rarely open), rather like the maternal (*D. mixta*, which has both open and closed) and different from the paternal (*D. portschinskii*, always open). *Darevskia uzzelli*, *D. sapphirina*, and *D. bendimahiensis* also have open clavicles as their maternal species (all of the *raddei* complex) and the paternal one (*D. josefschmidtleri*, usually open, rarely closed). *Darevskia armeniaca*, *D. rostombekowi*, *D. unisexualis* (and their triploid hybrid) have open clavicles, as is dominant or unique in their parental species. Concerning the presence of the laminar expansion in the distal part of the clavicle, it is partly indicated or moderately developed (*D. armeniaca*, *D. dahli*, *D. unisexualis*, *D. sapphirina*, and the triploid hybrid *D. unisexualis x D. nairensis*), and almost indiscernible or absent in others (*D. rostombekowi*, *D. uzzelli*, and *D. bendimahiensis*), whereas their paternal group (all of the *D. rudis* group in general) and the maternal one (*D. raddei* complex) have it very reduced or absent. In this case, our interpretation is also that it is a primitive (atavistic) character that reappears in these hybrid-origin species.

Interclavicle form: (see Plate 10) The interclavicle has a cruciform shape, with slight deviations of the lateral branches forward or backward. In *Darevskia armeniaca* it is purely cruciform (simply "cruciform", with perpendicular lateral branches), and rarely with branches slightly turned backward. Its parental species also had it cruciform or slightly backward (*D. valentini*) or cruciform and forward in similar proportions (*D. mixta*), but not backward, which is frequent in *D. portschinskii*, which according to Tarkhnishvili *et al.* (2017, 2020b) would have played a primary role in hybridization with *D. mixta*, with this hybrid later hybridizing with *D. valentini*. *Darevskia dahli* has it cruciform or rarely backward, more similar to its paternal species (*D. portschinskii*, cruciform or backward) than to the maternal species (*D. mixta*, cruciform or forward). In *D. rostombekowi*, on the contrary, it is cruciform or rarely forward. In the former species (*D. dahli*), it resembles its parents, but in the latter (*D. rostombekowi*), it differs from both parental species (paternal, *D. portschinskii*, cruciform or backward; maternal, *D. raddei*, cruciform, and also in *D. r. vanensis* it is backward, and in *D. nairensis* forward or backward). *Darevskia unisexualis* always has it cruciform, as does its paternal species (*D. josefschmidtleri*—rarely slightly backward—), but different from the maternal (*D. nairensis*, forward or backward directed), hence the most primitive state is the cruciform (in the triploid, it is also cruciform, as in *D. unisexualis*, and different from *D. nairensis*, despite having two genomes of this). In *D. uzzelli*, it is cruciform or directed backward, as in the parental species (*D. valentini*, backward or pure cruciform), and in *D. nairensis* (the maternal species). *Darevskia sapphirina* and *D. bendimahiensis* have lateral branches backward or are rarely cruciform, which is the shape of their two parents (backward in some *D. josefschmidtleri*, and *D. r. vanensis*), or the primitive character (cruciform) in other *D. josefschmidtleri*.

First autotomic vertebrae of the tail: In general, parthenogenetic species have these first autotomic vertebrae as in the parental species, normally type A and extremely rare some of type B. *Darevskia armeniaca* (type A and very rarely type B), *D. rostombekowi* (A), *D. unisexualis* (A), *D. sapphirina* (A), and *D. bendimahiensis* (A). *Darevskia uzzelli* presents type B vertebrae and more rarely type A, more like its maternal species (*D. raddei*, with B and rarely A; *D. nairensis* A and rare B, and *D. r. vanensis* B in our few samples, although surely there will also be A), while the paternal is type A (*D. valentini* and *D. josefschmidtleri*). Finally, the situation of the triploid (*D. unisexualis x D. nairensis*) is striking, as it has vertebrae type B, while its maternal *D. unisexualis* has type A and the second genome of its paternal *D. josefschmidtleri* also has type A (the triploid has two genomes from *D. nairensis* and one from *D. josefschmidtleri*). The question arises: will type B be more primitive than type A?

Conclusions

4.1. Osteological characters

1. There is great variability in osteological characters, not only within the genus but also among species and individual specimens.
2. Almost concerning the premaxilla, a specific taxon that belongs to a group of small sized species, even if being big-sized, retains teeth numbers similar to the small species
3. *Darevskia chlorogaster* (and probably its recently splitted taxa) stands out due to its increased premaxillary tooth counts (9 and even 10, instead of the usual 7).
4. There is an imperfect correlation between taxon size and the number of teeth in the maxillary and especially dentary bones.
5. The anteromedial process of the postorbital bone is absent or extremely reduced in some species of the *caucasica* group (such as *D. mixta* and *D. derjugini*), although it is generally present in the main part of the *saxicola* complex, and there is a tendency toward reduction in size (even disappearance) throughout all of the *raddei* complex.
6. Initially, the postorbital and postfrontal bones have similar lengths. A shorter postorbital compared to postfrontal is observed in a well-defined cluster within the *caucasica* group (*D. clarkorum*, *D. mixta*, and *D. dryada*). This occurs also in the *saxicola* complex (except the specimen of *D. szczerbaki* studied here) and in the *parvula* complex. The inverse relationship, with postorbital longer (often subequal) than postfrontal, appears in the *praticola* complex and within the *rudis* group only in *D. valentini* + *D. portschinskii* binomial (Interestingly, *D. r. lantzicyreni* shows it as in other *rudis*, thus equal or smaller).
7. There is greater overlap than usual between the lengths of the squamosal and postocular bones in some dispersed taxa (*D. bithynica* spp., *D. s. spitzenbergerae*, *D. s. wernermayeri*, *D. josefschmidtleri*, or *D. (p.) pontica*), and less overlap than normal in the taxa of larger size (*D. b. darevskii*, *D. szczerbaki*, and *D. dryada*), as if the bones do not reach sufficient overlap in these “overgrown” taxa.
8. The presence of inscriptional ribs tends to increase from one to two in the *rudis* complex (except in *D. r. rudis* and *D. o. obscura*, including *D. b. tristis* but not in our studied *D. b. bithynica*).
9. A synapomorphy, perhaps the most important of the *Darevskia* genus, is the modal increase in the number of presacral vertebrae from 26 to 27 in males and from 27 to 28 in females. Reduction from this basic number is very rare and occurs in some specimens of the *D. rudis* complex (*D. o. obscura*, *D. o. bischoffi*, *D. ‘r.’ chechenica*), and a unique specimen of *D. bendimahiensis*.

10. A further increase in this modal numbers of 27/28 in males and females respectively, appears in the *raddei* complex (both in males with 28, and in females with 29), as well as partially, only in the females of the *praticola* complex (27 males, but 28/29/30 en females) and in *D. valentini* (27 in males, but 28/29/30 in females). Also in some particular species such as *D. clarkorum* (with a tendency to increase from 27 to 28 in males and from 28 to 29 in females) and *D. tuniyevi* from the Lesser Caucasus spurs (28 in males and 29 in females).
11. The number of short presacral ribs corresponding to posterior dorsal vertebrae is usually six, with some variability to five or seven, which in small populations may become dominant or diagnostic of a given taxon by small population size and inbreeding. Typically, the increase within a species in the number of presacral vertebrae parallels a greater number of short ribbed ones (as in females of *D. valentini*, up to 7 and 8) and appears more frequently than normal (considering as normal the proportion in bisexual ones) in various parthenogenetic taxa (see the corresponding section above or conclusions for parthenogenetic below).
12. Usually, both types of clavicles (open and closed) coexist in the same species, being the presence of only one type of these, a derived character. Only open clavicles appear in the *raddei* complex, *saxicola* complex, *parvula* complex, and *D. portschinskii*.
13. The taxa of the *Darevskia praticola* complex are outstanding by the presence in their clavicles of thin laminar expansions in their more lateral part, fairly less developed or only indicated in other species. May be this morphology is related to their ground dwelling.
14. The interclavicle is cruciform with lateral branches more or less perpendicular to the central axis, sometimes slightly inclined forward or backward. The only species with branches very inclined forward is *D. chlorogaster*, and similar but with slightly less inclined branches *D. defilippi*, although we do not know if it is characteristic of its entire complexes of recently described species.
15. Being the A-model the most abundant autotomic vertebrae type and frequently the only one present, often both models coexist in the same individual, that normally presents type A and some rare type B interspersed. In the *raddei* complex, type B is dominant over A (except in *D. nairensis* that has both, but we have found more type A than B). In *D. caucasica* and *D. saxicola* we have found slightly more type B than A. In the *rudis* complex, we have only found type A (although some rare type B appear in *D. b. bithynica* and intermingled in *D. valentini*).
16. The parthenogenetic species present marked characteristic features of their parental species, particularly of the females of the original crossing which gives origin to them.
17. It is striking the variability in the parthenogenetic *D. sapphirina* with an extreme variation of premaxillary teeth number, as being a clone, its number of premaxillary teeth can be seven but also six or even five. Also has the postorbital and postfrontal more or less of the same length (but one or the other can be longer than the other). This variation does not exist in *D. bendimahiensis* that share the same parental taxa.

4.2. What do parthenogenetic species tell us about character polarity and their inheritance?

a) Osteological traits in parthenogenetic species seem to be surprisingly variable, which might seem like a contradiction since they are believed to be morphologically less variable than bisexual ones. It must be caused by instability (or heterozygosity) between the two different genomes of the progenitor species.
b) Teeth shape: in case of discrepancy, the hybrids seem to be more similar to their maternal species.
c) Postorbital process: In the parthenogenetic species, the anteromedial process of the postorbital is frequently absent due to the influence of maternal species of the *raddei* complex (where it is reduced) or *D. mixta* (where it is frequently absent). In summary, the character appears as in the parental females, or if it is different (sometimes absent but present in the parental taxa), it would represent the appearance of an atavistic character. Moreover, since the process does not exist when the separation of both bones originated, this reinforces the hypothesis that its absence is originally primitive.
d) Comparative lengths of postorbital vs. postfrontal: in general, the comparative longitude of postfrontal and postorbital appears as in their parental species, because originally both bones were of similar lengths (primitive state). Deviations are a by-product of the asymmetric reduction of the cranial bones in parallel to the increasing platycephaly and fissuricolous life.

e) Third vertebra associated ribs: the presence of ribs (bone or cartilaginous) associated with the third presacral vertebra, seems to be an atavistic character that appears here and there in species at a low (or very low) frequency. In the parthenogenetic taxa they do not appear frequently, the same as occurs in their parents, but sometimes appear in some species without having been detected in their parents, which would be the reappearance of an atavistic character. Very rare cases of appearing even in the second presacral vertebrae had been detected.

f) A certain relation is noted between the development (or best, the conservation or reappearance) of a rib in the third presacral vertebra (rare but present hence and there in most Lacertini) and the presence of strong necks in ground-dwelling species (with robust heads and necks). Also, its presence is more frequent in species of much-reduced distribution and inbred, where rare or atavistic characters became fixed and more abundant.

g) Number of presacral vertebrae: is noteworthy the case of *D. unisexualis*, which has 28 presacral vertebrae, while the females of the parental species have more (females of the paternal *D. josefeiselti* 29, and the maternal *D. nairensis*, also 29). It seems that the hybrid shows the primitive character (in common) to both parents, that is, without the vertebral (apomorphic) increase of the *raddei* complex. Furthermore, in the triploid hybrid between *D. unisexualis* and a male of *D. nairensis* (which therefore has two genomes of *D. nairensis* and one of *D. josefeiselti*) there are also 28 presacral vertebrae, as in *D. unisexualis*, without the increase characteristic of the *raddei* complex and despite to having two genomes of *D. nairensis* and one of *D. josefeiselti,* which all have 29. In summary, the numbers of presacral vertebrae in parthenogenetic (unisexual) usually coincide roughly with the corresponding in the parental (bisexual) ones (more considering that there may be undetected variability in our sample), but in some cases, the variability (range) in the parthenogenetic species exceeds that of the parental ones. In case of discrepancy, the primitive character seems to predominate (even if in inferiority with respect the number of genomes).

h) Posterior short ribbed vertebrae: Appear as in parents or especially more like the females of the paternal species, or the females of the maternal one, but the resulting number is almost ever six, that is the primitive number. There is an interesting exception, the paternal influence of *D. portschinskii* (which has 6 in males and 7 in females) into their derived *D. dahli* (usually 7, rarer 6) and *D. rostombekowi* (6 or 7 in similar proportion) that show both the more rare number of 7.

i) First autotomic vertebrae of the tail: In general, parthenogenetic species have these first autotomic vertebrae as in the parental species, normally type A and extremely rare some type B. The triploid (*D. unisexualis* x *D. nairensis*) is striking, as has vertebrae type B, while its maternal *D. unisexualis* has type A and its paternal *D. nairensis* also type A, although with some rare type B intermingled. Will type B be more primitive than the A?. The triploid has two genomes from *D. nairensis* and one from *D. josefeiselti*, in both species the normal model is A (rarely with some rare B intermingled in the former). Thus, B seems to be more primitive than A, although both coexist (type A dominant in number, and type B rarer).

j) Clavicles shape: in the parthenogenetic species as *D. armeniaca*, *D. unisexualis* (and its triploid hybrid), *D. rostombekowi,* and *D. uzzelli*, the clavicle is always open. *Darevskia bendimahiensis* and *D. sapphirina* show it usually also open, and rarely or very rarely closed. In *D. dahli* are more frequently closed. Only *D. dahli* and *D. armeniaca* had *D. mixta* as a maternal species (that had both models: open and closed). The other species had them as in the *raddei* complex (their maternal species), always open. Thus, the shape of the clavicle is as in both parents, or in the case of discrepancy, more similar to maternal species.

k) The laminar expansion in the distal part of the clavicle, that is indicated or moderately developed in *D. armeniaca*, *D.dahli*, *D. unisexualis*, *D. sapphirina*, and the triploid hybrid *D. unisexualis* x *D. nairensis*, is almost indiscernible or absent in others (*D. rostombekowi*, *D. uzzelli* and *D. bendimahiensis*). This expansion is absent or very rare and reduced in all their parental groups. Probably the presence of this expansion well developed is a primitive (atavistic) character that appears also in these hybrid origin species.

l) Interclavicle shape: is as in the parental taxa, but in the case of *D. rostombekowi* (cruciform or rarer slightly inclined forward) it is different from the two parental species (the paternal, *D. portschinskii*, cruciform or backward; the maternal *D. raddei*, simply cruciform, but in *D. r. vanensis* it is backward and in *D. nairensis* forwards or backward). As the parentship of *D. rostombekowi* is not disputed, this can be attributed to undetected variation in their parental species.

m) Sternal fontanelle: is striking that the triploid hybrid (*D. unisexualis* x *D. nairensis*) has it perfectly cordiform, although its parthenogenetic maternal species had it oval (of parents also mainly oval), and in its paternal species is also oval. This triploid has two genomes of *D. nairensis* that have it oval (but also rarely cordiform irregular), and one genome of *D. josefeiselti* that has it also oval. Could the cordiform shape, that appears in the triploid, be an atavistic and primitive character in respect to the common oval or rounded ones?. As stated in Arribas (1998) some irregular cordiform seem to derive from the primitive oval and are difficult to discern from true primitive cordiform. Oval seems to be the primitive and basic model in *Darevskia*, but secondarily cordiform shapes reappear as secondarily derived or as an atavistic character.

4.3. Parentship of parthenogenetic taxa

Although in general the origin of the main part of parthenogenetic species has been well established for a few decades, and the crosses that originated them are known with enough precision, including the implied species and the sex that they were in the original cross (see above), there are still some doubts or controversies that could be considered even as open disputes.

4.3.1. The maternal ancestor of D. uzzelli

Although the present results are not conclusive and much work remains to be done regarding the systematics of the *raddei* complex, there is controversy about the maternal ancestry of *D. uzzelli*. It is usually considered to be *D. raddei*, but Freitas *et al.* (2016) and Yanchukov *et al.* (2022) consider it to be *D. nairensis*, as did Darevsky & Danielyan (1977) in the original description of the species (where they believed *D. parvula* was the paternal taxon, an idea now abandoned), and later Moritz *et al.* (1992) also defended (with doubts). *Darevskia uzzelli* lacks the anteromedial process of the postorbital, contrary to its paternal species *D. valentini*. Concerning the controversial maternal identification, both *D. r. raddei* and *D. nairensis* usually have the anteromedial process of the postorbital developed, but our small sample of *D. r. vanensis* lacks it, as is the case in *D. uzzelli*. It must be investigated if *D. raddei vanensis* or a closely related form could be the maternal taxon for *D. uzzelli*, although geographically, *D. nairensis* is a more probable candidate and recent genetic data seem to point in this direction (Freitas *et al.*, 2016; Tarkhnishvili *et al.*, 2020b; Yanchukov *et al.*, 2022).

4.3.2. The paternal ancestry of D. armeniaca

D. armeniaca is usually considered to have originated from the crossbreeding of a *D. mixta* female with a *D. valentini* male. However, according to Tarkhnishvili *et al.* (2017, 2020b), the initial crossing would have been with a *D. portschinskii* male, and then that hybrid would have subsequently crossed with *D. valentini* when invading the area of this latter species. In *D. armeniaca*, the interclavicle is cruciform (rarely with branches slightly turned backward). Its parental species also had it cruciform (*D. v. valentini*) or cruciform and forward in similar proportions (*D. mixta*), but not backward, which is frequent in *D. portschinskii*. These data are not conclusive but suggest that the Tarkhnishvili *et al.* (2017, 2020b) hypothesis deserves consideration.

The groups of Murphy *et al.* (2000) informally recovered as groups or clades by other authors, along with some new ones, are here redefined, diagnosed with morphological, genetic, and osteological traits, and named as subgenera in Appendix 3. These subgenera names, used when necessary, simplify the verbose explanations of the group's name, the author who defined it, and the subsequent modifications or additions of formerly unstudied taxa to the originally proposed group.

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Appendix 1

Taxonomic Remarks

Although it is difficult to achieve a precise calibration with genetic data (and the following lines show this disparity), the common ancestor of all the subfamily Lacertinae is currently estimated to have existed around 37.55 million years ago (Garcia Porta *et al.* 2019). The separation of the different genera must have occurred due to isolation in various landmasses (Iberia, Balkans, Carpathians, Anatolia, Apennines, etc.) during the Paleogene. The genus *Darevskia* diverged from other groups around 32.59 million years ago, isolated in the Anatolian landmass. *Darevskia* internal divergences (among the major groups) began after the Messinian according to several authors (see below), but were inferred to as far as 18–23 million years ago, following the mitogenome analyses of Murtskhvaladze *et al.* (2020; Fig 6). We will follow the succession of cladogenetic events described in Murtskhvaladze *et al.* (2020), which coincide fairly well with other authors, although their calibrations (not only for *Darevskia* but also for other genera and species in their trees) seem notably overestimated. Therefore, in the following lines, we follow their sequence of events, but the time calibration is only indicative.

The first *Darevskia* group to split was the parvula group (around 20.83 million years ago) (25 million years according to Roquet *et al.* 2014; 11 million years according to Zheng & Wiens 2016; or 15.13 million years according to García-Porta *et al.* 2019), the most divergent in most phylogenies (with varying time calibrations, as can be seen), suggesting that the northeast of the Anatolian landmass and the current Lesser Caucasus was the area where the ancestral lineages of *Darevskia* originated, and where the *parvula* group still largely coexists with the second group to split off, the *rudis* group (Tarkhnishvili 2012; Murtskhvaladze *et al.* 2020).

The second group to split was the *rudis* group (around 18.53 million years ago) (Murtskhvaladze *et al.* 2020) (5.9 million years [5–7.6 at 90% confidence limits], about 5 [3.9, 6.1] million years ago; from Tarkhnishvili 2012 and Freitas 2017, respectively; or 13.43 million years for García-Porta *et al.* 2019), also in the Anatolian plate.

The splitting of the other groups occurred later, from around 16.06 million years ago (Murtskhvaladze *et al.* 2020), 11.59 million years for García-Porta *et al.* (2019), or fairly less, at 5.2–5.4 (4.5–7.4) million years ago (Freitas 2017), probably due to connections and separations of landmasses, increasing aridity, and the configuration of the main river watersheds. Phylogenetically close species diverged within each group even during the Plio-Pleistocene, mostly between 2.5–5.0 (3.1–3.6) million years ago (from Tarkhnishvili 2012 and Freitas 2017).

The separation of the *saxicola* group (mainly represented in the Western Greater Caucasus, from where most other lineages of *Darevskia* are absent) occurred at 14.5–18 million years ago (11.59 million years for García-Porta *et al.* 2019), associated with the first temporal contacts between the Caucasus (then an island to be colonized) with the Anatolian Mainland (Murtskhvaladze *et al.* 2020).

From the remaining groups, splits occurred quickly and in an uncertain order: the *defilippi* group split at 10.69 million years ago (following García-Porta *et al.* 2019); the *raddei* group (see Appendix 3, *Darevskia* groups) split around 12.12 million years ago (dates following Murtskhvaladze *et al.* 2020) (14–18 million years according to Roquet *et al.* 2014 and Zheng & Wiens 2016; 7.78 million years according to García-Porta *et al.* 2019) and is more adapted to the increasingly arid habitats of the Eastern Anatolian Plate. Later, the *chlorogaster* group split at 10.7 million years ago (Murtskhvaladze *et al.* 2020) or 7.78 million years (García-Porta *et al.* 2019), isolated by this increasing aridity in the Hyrcanian areas (Iranian Landmass), from the *caucasica* group (hence distributed in Colchid areas of Eastern Anatolia and Western Great Caucasus). According to García-Porta *et al.* (2019), the *caucasica* group split from the *raddei* + *chlorogaster* groups at 8.76 million years ago, and these latter two split between them at 7.78 million years ago. Within this *caucasica* group, the sister to all the other species is *D. daghestanica*, and from its sister group, *D. derjugini*, a ground-dwelling species with a fairly wide distribution. The remainder of the *caucasica* group differentiated by habitat (forest in *D. mixta* in different forest refuge areas from *D. clarkorum* and *D. dryada*, of uncertain status but not fully identical) and alpine stony grasslands in *D. caucasica* (Tarkhnishvili 2012; Murtskhvaladze *et al.* 2020).

All these differentiations must be linked to successive isolations and contacts of the Iranian Plateau and Eastern Anatolia (the first junction between this and Anatolia, the origin of *Darevskia*, is dated to 13–14 million years ago; Popov *et al.*, 2004), and the increasing aridification of the climate that led to isolation by the appearance of intermediate unsuitable areas. Some of the splits between closely related species of the *saxicola* group, *caucasica* group, and *rudis* group are relatively recent and occurred even in the middle or late Pleistocene (Tarkhnishvili

2012; Murtskhvaladze *et al.* 2020). Extant parthenogenetic *Darevskia* are expected to be relatively recent (~100,000 years; Freitas *et al.* 2016). Even though both hypotheses for their origin (Balance Hypothesis and Phylogenetic Constraint Hypothesis) are not mutually exclusive, the latter better explains the origin of parthenogenetic hybrids and the patterns of gene flow found in this genus (Freitas 2017). According to chromosome Z, which is related to the paternal line (Yanchukov *et al.* 2022), these authors date the origin of *D. armeniaca*, *D. dahli*, *D. uzzelli*, and *D. rostombekowi* to -0.5 to -0.9 million years ago, while *D. bendimahiensis* and *D. sapphirina* would be even older, between 1 and 2 million years ago.

Closely related *Darevskia* species appear today with allopatric or parapatric areas, whereas phylogenetically more distant species may coexist and occur sympatrically (Tarkhnishvili 2012). Sympatry developed after secondary niche differentiation from the common primitive niche of the ancestors of each group. Up to four species can coexist on a single rock face, and up to eight species may occur within an area of 10 km² (Tarkhnishvili 2012), but in these cases, they belong to different groups within *Darevskia* (see Appendix 3: groups). Hybridization is a frequent event, as evidenced by the mitochondrial flux between taxa (see Appendix 2, Hybrids); however, parthenogenetic species appeared only in hybridization events between parental species belonging to different groups within *Darevskia* (see Freitas *et al.* 2016, 2017 for a discussion on these topics). Paternal species of all parthenogenetic *Darevskia* are always species of the *rudis* group, whereas maternal species are always representatives of the groups *caucasica* or *raddei* (the "mixta clade" in Tarkhnishvili 2012). This latter author states that this is not surprising given the larger body size of the lizards from the former clade and that male success is a determinant during pair formation in lizards (Tarkhnishvili 2012).

Genus date and authorship

There was a recent controversy regarding whether the date of the genus *Darevskia* and its correct description corresponded to 1997 (Arribas 1997) or a 1999 paper (Arribas 1999), and even if the valid name should be *Caucasilacerta* Harris, Arnold, and Thomas, 1998 (Busack *et al.* 2016). The case was submitted to the ICZN (Arribas *et al.* 2018a) to choose between validating the microfiche publication (1997), which was valid when published (ICZN 1985) but not valid under the current Code version (ICZN 1999 and updates), or Arribas (1999). Additionally, papers were published explaining in detail why *Caucasilacerta* was a *nomen nudum* (Arribas 2016; Arribas *et al.* 2017). Finally, the International Commission on Zoological Nomenclature has ruled for the preservation of the names *Iberolacerta* and *Darevskia* for two genera of lacertid lizards by confirming their availability from Arribas (1999). The microfiche publication (Arribas 1997) has been confirmed as unavailable and placed on the Official Index of Rejected and Invalid Works in Zoological Nomenclature. The name *Caucasilacerta* Harris, Arnold & Thomas, 1998 is confirmed as a *nomen nudum* and placed on the Official Index of Rejected and Invalid Generic Names in Zoology (ICZN 2020).

Phylogeny of *Darevskia*

The first phylogenetic reconstruction by Darevsky (1967) expressed his opinion in the form of an evolutionary tree. His outline showed some "principal branches" that hinted at some of the groups within the genus. Several of his groupings were later supported by genetic studies, including the *rudis* group, the *caucasica* group, and the *saxicola* group of Murphy *et al.* (2000). However, he wrongly grouped other species such as *D. portschinskii* and *D. parvula*. Darevsky's first group included *D. saxicola* and their subspecies, many of which are now considered separate species; the second included *D. raddei* and *D. defilippi*; the third included *D. alpina*, *D. caucasica*, and *D. daghestanica*; the fourth included *D. parvula* and *D. mixta*; the fifth included *D. portschinskii*; and the sixth included what we now call the *rudis* group (*D. rudis* s. lat., the current *D. bythinica*, etc.) together with *D. valentini* (and their former subspecies); and finally, the remaining part of the subspecies from *D. rudis* (the current *D. rudis*, *D. obscura*, and *D. o. macromaculata*). It is interesting to observe that although the clusters utilized in this work are not used now, there was a high degree of success in many of the groupings in Darevsky's 1967 classification, especially when assembling taxa that the author classified as different species but that have since been found to belong to the same group or to be very closely related. A good general overview of the genus *Darevskia* is also provided by Tarkhnishvili (2012).

Mayer & Lutz (1989), in a scheme based on an electrophoretic study, showed a slightly more isolated position of *D. parvula* on one hand, and *D. praticola* and *D. derjugini* on another, in respect to the general group. The relationship between *D. derjugini* and *D. praticola* with *D. saxicola* was also suggested by Borisov & Orlova (1986).

Schmidtler (1993) mentioned *D. mixta*, *D. raddei* (s.l.), the *D. valentini-rudis* complex, and a *D. portschinskii-parvula* complex. Grechko *et al.* (1993), based on the study of DNA polymerase chain reaction, divided the ten species studied by them into two groups: one containing *D. armeniaca* and *D. dahli* (both parthenogenetic), next to the bisexual *D. portschinskii*, *D. mixta*, and *D. valentini*; and the second containing *D. unisexualis* and *D. rostombekowi* (parthenogenetic) next to *D. raddei* and *D. nairensis* (often considered as subspecies of *raddei*, although probably different).

Murphy *et al.* (1996), based on allozymes, preferred to consider *D. mixta* as the sister species of the clade that included the groups of *D. raddei* and *D. saxicola*. The grouping would be the *saxicola* group, including *D. saxicola* and their former subspecies, and perhaps *D. clarkorum* and the recently described *D. dryada*; the *caucasica* group, including *D. caucasica*, *D. alpina*, and *D. daghestanica*, to which these authors also approached *D. praticola*.

Arribas (1999), based on morphology and other available data, postulated a more or less isolated position for *D. praticola* (and perhaps *D. derjugini*) and also for *D. chlorogaster*. Within the genus, he distinguished a *raddei* group, the best defined, characterized by their increased vertebral counts (28 instead of 27 as a modal number in males, and 29 instead of 28 in females), including *D. raddei*, *D. nairensis*, and very probably *D. defilippi* and *D. steineri* (considered at that time to be close to *D. raddei*); a *rudis* group, characterized by the presence of an enlarged scale between the circumanal ones, previous to the anal plate, as well as by frequently presenting (in almost all included species) red coloration on the belly. It would include *D. rudis*, *D. valentini*, *D. portschinskii*, and perhaps in a basal position, *D. parvula*. The position of *D. mixta* was more problematic. A tentative relationship among groups (now discarded by genetics) was: (*chlorogaster* (*praticola* (g. *caucasica* + g. *saxicola* (g. *rudis* + g. *raddei*)))).

As a general starting scheme, Murphy's one (Murphy *et al.* 2000) is frequently taken, which seems to be the first correct, with modifications (mainly the introduction of taxa not studied in that paper). Murphy *et al.* (2000), studying mtDNA, distinguished three groups (they called them clades): the *caucasica* group (*mixta*, *clarkorum*, *derjugini*, *daghestanica*, *caucasica*, and sister to all of them, *raddei*); the *saxicola* group (*brauneri*, *lindholmi*, *saxicola*, *alpina*, and *praticola*); and the *rudis* group (*valentini*, *rudis*, *portschinskii*, and sister to them, *parvula*).

Brown (2005) analyzed a large subunit of the 16S rRNA. There, *D. raddei* and *D. parvula* appeared as independent groups. Ahmadzadeh *et al.* (2013; Suppl. Table S1.1), when describing new species close to *D. chlorogaster* and *D. defilippi*, also supported *D. raddei* and *D. chlorogaster* as separate groups and placed *D. parvula* as sister to the *rudis* group. Pyron *et al.* (2013), although with little resolution, situated *D. parvula* as an independent group inside *Darevskia*, and *D. praticola*, *D. chlorogaster*, and *D. raddei* relatively isolated from their real groups. Roquet *et al.* (2015) showed a very similar scheme, with *D. chlorogaster* clustering with *D. raddei*, and *D. parvula* as an independent group. Zheng & Wiens (2016) presented a scarcely resolutive tree for this concrete group but showed *D. parvula* as an independent group. Garcia-Porta *et al.* (2019), in a similar scheme to the previously referred, clustered the *raddei* and *chlorogaster* groups, and left *D. parvula* in its own group, sister to the other *Darevskia* groups. Murtskhvaladze *et al.* (2020), studying 16 new mitogenomes of *Darevskia* and employing next-generation sequencing (NGS) of genomic DNA, inferred a phylogeny and found that concatenated 16S RNA and Cytochrome *b* genes generated a robust phylogeny comparable with the complete mitogenome one. The dates of the separations of the different groups are considerably older than in other authors who have dealt with the subject.

Species criteria and some taxonomic comments

Murphy (1999) highlights a notable oversight regarding the original description of *D. rostombekowi* by Darevsky (1957), specifically that it should be spelled with a "w" instead of a "v". Although Darevsky used the original spelling for nearly a decade, his later amendment to "rostombekovi" (as seen in his seminal works on Caucasian lizards, Darevsky 1966, 1967) was an unjustified emendation (Art. 33.2.3) according to ICZN (1999).

The validity of *Darevskia nairensis* as a species is contentious. Omelchenko *et al.* (2016) and Bobyn *et al.* (1996) present conflicting conclusions. Fu (1999) notes that accepting *D. nairensis* as a species renders *D. raddei* paraphyletic. However, *D. nairensis* exhibits unique biological traits, such as female thigh-grasping and a distinct reproductive period. If merged with *D. raddei*, it would be preferable to divide *D. raddei* "*raddei*" into multiple taxa (see Fig. 2 in Freitas *et al.* 2016b). This issue remains unresolved, and a comprehensive revision of this complex is necessary. Recently, two taxa with uncertain status have been described within the *raddei* complex: *D. aghasyani* Tuniyev & Petrova, 2019, and *D. r. chaldoranensis* Rastegar-Pouyani *et al.*, 2011.

Fu (1999) argued that DNA data do not support the species status of *Darevskia dryada* (Darevsky & Tuniyev, 1997). However, he noted that three of his five specimens of *D. clarkorum* were from the geographic range of *D.*

dryada (Tskali gorge, Georgia), with the other two from Mahden (Turkey). He mentioned that these specimens also resembled the diagnostic characters of *D. dryada* (Schmidtler *et al.* 2002; Arribas *et al.* 2021). Two of the supposed *D. dryada* specimens shared identical ATPase 6 sequences with *D. clarkorum*, casting doubt on the species status of *D. dryada*. An unpublished allozyme study found no fixed allele differences between the two species (MacCulloch, pers. comm., in Fu 1999). Arribas *et al.* (2021) showed that *D. dryada* differs morphologically from *D. clarkorum* and that the supposed *D. dryada* from Turkey (Subashi-kaj in the original description) are actually *D. clarkorum*. Until true *D. dryada* specimens from the Charnaly River canyon in Georgia are genetically analyzed, *D. dryada* remains independent, possibly as a subspecies of *D. clarkorum*.

McCulloch *et al.* (2000) studied allozymes and supported the species status for *D. saxicola*, *D. brauneri*, and *D. lindholmi*, placing subspecies *szczerbaki* and *darevskii* within *D. brauneri*. The species status of *D. lindholmi* was also supported by Ciobanu *et al.* (2003). *Darevskia szczerbaki* and *D. saxicola* are sister taxa with a low genetic distance (2.4%), rather than *D. szczerbaki* being the sister of *D. brauneri*. Doronin *et al.* (2013) raised *D. szczerbaki* to species level due to a genetic distance of the whole *sczerbaki*+*saxicola* clade of 4.8–5.6% to the *D. brauneri* clade, which is more typical for species-level distinctions. By this *D. szczerbaki* is treated as an independent taxon due to its paraphyly in respect to the rest of the *brauneri* clade, pending further studies on the group. There are doubts about the differentiation of these taxa (Kosushkin & Grechko 2013), but *D. lindholmi* shows a more pronounced difference (Ryabinina *et al.* 1998; Kosushkin & Grechko 2013). Recently, a species of this group has just been described, *Darevskia arribasi*, from the vicinity of Ertso Lake in South Ossetia. It is the smallest species and has the lower dorsal scales counts of this group, and its status is supported by the result of analysis of the mitochondrial cytochrome b data (Tuniyev *et al.* 2023). *Darevskia brauneri darevskii* was synonymized with *D. brauneri brauneri* because one *D. brauneri brauneri* specimen grouped with the *D. b. darevskii* cluster in Doronin *et al.* (2013). The mitochondrial flux due to hybridization between species and subspecies explains this blend. We note the characteristics of both taxa to retain detailed information, but more research is needed on the *saxicola* complex. Tarkhnishvili *et al.* (2016) suggest the group requires revision and identified almost two divergent undescribed clades and introgressive gene flow between populations of *D. saxicola* and *D. brauneri*.

Ljubisavljevic *et al.* (2006) confirmed the validity of *D. p. praticola* and *D. p. pontica*. Tuniyev *et al.* (2011) identified two morphotypes in the Caucasus and Transcaucasia: *D. pontica* (in the west Caucasus) and *D. praticola* (in the east and Transcaucasia), describing *D. p. hyrcanica* from the Talysh area. Freitas *et al.* (2016a) found two clades: one in the western Caucasus (*pontica*) and one in Transcaucasia (Armenia) and the Talysh Mountains (*hyrcanica*). The deep divergence in mtDNA and nuclear DNA between Balcanic populations attributed to *pontica* (dated to 2.5 Mya) and the split between *praticola* and *pontica* (around 650,000 years ago) was noted. These Balkan populations should be named *D. p. hungarica* (Sobolevsky, 1930) and have been treated as a species by Sos *et al.* (2012). Morphological differences between *praticola* s. str. and *pontica* suggest distinctiveness, and genetic distance supports considering *D. p. hungarica* as a separate taxon. We treat the three major divisions as the *D. praticola* complex: *D. (p.) praticola*, *D. (p.) pontica*, and *D. (p.) hungarica*, as in Arribas (2019).

Kurnaz *et al.* (2019) suggested a third, unpublished, and distinct species within the *D. parvula* complex. They disregarded the lectotypification of *D. parvula* by Arribas *et al.* (2018), which restricts the type locality to Artvin, within the area of the supposed new species. Therefore, the distinct clade is the true *D. parvula* (s. str.), while their "*D. parvula*" is likely "inland *adjarica*," closer to *D. adjarica*, recently described as *D. tuniyevi* (Arribas *et al.* 2022). Osteological data are given separately for *parvula* s. str. (Turkey), *adjarica* s. str. (Georgia), "cf. *adjarica*" (Turkish coast), and *D. tuniyevi* (Inland Turkey, "Ardahan").

Arribas *et al.* (2013) studied the morphology of a broad sample of *Darevskia rudis* from its range, reviewing external morphology and osteology. *Darevskia bithynica* was raised to species rank with two subspecies: *D. b. bithynica* and *D. b. tristis*. Two populations were described as subspecies: *D. r. mirabilis* from the Kaçkar Mountains and *D. r. bolkardaghica* from the Taurus range. Koç *et al.* (2021) studied three microsatellite loci and two mitochondrial genes to evaluate the taxonomic status of *Darevskia rudis* and *Darevskia bithynica*. Their results showed a confusing relationship with a hard polytomy at the base of the phylogeny. Clear differences separated *D. rudis* and *D. bithynica*, but samples classified as *D. b. tristis* showed mixed relations with *D. b. bithynica* and *D. r. bolkardaghica* depending on the gene used. Gabelaia *et al.* (2018) suggested species status for *D. (rudis) obscura*. The contact with sympatry and hybrids described by Darevsky (1967) could support this status. Mayer & Lutz (1989) obtained unexpected electrophoretic results for *obscura*. Rato *et al.* (2020) studied two mitochondrial and two nuclear DNA fragments, with ecological niche modeling. Their samples, mostly from Armenia and the Pontic mountains, lacked all the nominal taxa of the group from more southern Anatolia. *Darevskia rudis* or *D. valentini* appeared paraphyletic and substructured into four clades, which started differentiating during the lower Pleistocene (around 1.3 Mya). *Darevskia bithynica* appeared distinct, with the Kizil River valley proposed as the vicariant barrier explaining its origin by allopatric speciation.

Candan *et al.* (2021) also studied the relationships within *D. rudis* and *D. valentini*, with an almost complete geographical sample representation, using a multi-marker dataset comprised of maternally-inherited mitochondrial and biparentally-inherited nuclear markers. In their study, apart from a pectinate phylogeny that is very difficult to interpret, two previously unrecognized genetically highly divergent lineages were identified (named New Clade A and New Clade B by them). Kurnaz *et al.* (2022) describe a new species allegedly from the *rudis* group but with *parvula* habitus as *Darevskia salihae* from the Altıparmak Mountains (Artvin, Turkey). The mitochondrial fragment studied clusters it close to the *rudis* group samples. However, the habitus and characteristics of the type are more compatible with the *parvula* complex (which, however, is far from this sample in the mitochondrial tree). It could be a *D. parvula* (which inhabits nearby localities) with an ancient introgressed mitochondrial from an old hybridization with a *D. rudis* group ancestor (similar to what is called "mixta2" in Freitas 2017). The analysis of a nuclear gene will clarify not only its position among *Darevskia* but also its species status or, to the contrary, its possible identity with *D. parvula*. Some of the characters invoked as distinctive (such as the lack of blue spots in the outermost ventrals) are present and perfectly visible in the photos of the original description (!).

The complexes of *Darevskia valentini* and *D. rudis* have been thoroughly reviewed by Arribas *et al.* (2022), using the complete dataset of Candan *et al.* (2021) and adding all the singular nominal taxa described from Anatolian relict populations. After a highly detailed morphological and molecular study, *D. spizenbergerae* has been raised to species status (with a new subspecies *D. spitzenbergerae wernermayeri*), as well as *D. mirabilis* and *D. obscura*, the latter with the former subspecies of *D. rudis* (s. lat.), *D. o. bischoffi* and *D. o. macromaculata*. Also, a new species is described: *D. josefschmidtleri*. The taxon *lantzicyreni* is reassigned from *D. valentini* to *D. rudis* (*D. rudis lantzicyreni*).

Finally, another source of confusion is past hybridizations with mitochondrial flux between species or the presence of pseudogenes (mitochondrial genes inserted in nuclear DNAs) that can be amplified with or instead of the mitochondrial copies and can give unexpected and unreliable results. In addition, frequent lateral transfer of genes (interspecific gene flows) through hybridization makes mitochondrial DNA a poorly adequate candidate for phylogenetic studies at the species level. Clearly hybrid or poorly determined specimens appear in published trees and lead to considering the taxon they apparently represent in the wrong position of the taxon that hybridized in the past with them. Some examples of this are:

a) *Darevskia saxicola* ("*Lacerta saxicola*") from Dombay (Murphy *et al.* 1996; Fu *et al.* 1997) seems to belong to the *raddei* group (*D. nairensis* according to Fu) both in its sequence and morphology. This is doubly amazing because Dombai is very far from the current area of *D. nairensis* (or any *D. raddei* group population).

b) *Darevskia alpina* ("*L. alpina*") in Murphy *et al.* (1996) and Fu *et al.* (1997) carries a mitochondrial (by introgression in the past, as they are currently not in contact) of *D. mixta*, while the other two "pure" specimens are grouped in their trees with the *caucasica* group.

c) *Darevskia parvula* in Freitas *et al.* (2016b, fig. 3; 2017, fig. 2.2.3) is surely not a *parvula* (or *adjarica*) as it carries a mitochondrial of the *rudis* group (see also comments about *D. salihae* above). On the contrary, what is called "mixta2" (Freitas 2017) seems to be a member of the *parvula* group (perhaps one of the old known naturally originated populations of hybrid origin between *D. adjarica* and *D. derjugini*? mentioned by Darevsky, 1967-See Appendix 2 for references—or true *D. adjarica*).

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Appendix 2

***Darevskia* hybrids**

HYBRIDS between *Darevskia* (double entry by each parental species in alphabetic order).

(p)=parthenogenetic. (The result of the hybridization between a parthenogenetic female and a bisexual male is a triploid hybrid).

Hybridizations between bisexual species that gave rise to parthenogenetic taxa in the past have not been considered in the list (see main text to see these presumably parental species).

Interspecific hybrids (other than parthenogenetic origin ones) known:

**D. adjarica* x *D. derjugini* (Darevsky 1967; Bischoff 1973; Orlova 1979; Murphy *et al.* 2000; Ciobanu *et al.* 2003) (1).
**D. alpina* x *D. brauneri* (Darevsky 1967; Murphy et al 2000).
**D. alpina* x *D. caucasica* (Darevsky 1967; Fu et al 1995; Murphy *et al.* 2000).
**D. alpina* x *D. mixta* (Fu *et al.* 1997; Murphy *et al.* 2000).
**D. armeniaca* (p) x *D. nairensis* (Bischoff 1973).
**D. armeniaca* (p) x *D. portschinskii* (Darevsky & Kulikowa 1961; Mertens 1964; Bischoff 1973).
**D. armeniaca* (p) x *D raddei* (Darevsky & Kulikowa 1961 Mertens 1964).
**D. armeniaca* (p) x *D. obscura* (Darevsky 1967; Bischoff 1973; Darevsky *et al.* 1985).
**D. armeniaca* (p) x *D. o. macromaculata* (Darevsky 1967; Bischoff 1973).

**D. armeniaca* (p) x *D. valentini* (Darevsky 1966, 1967; Darevsky & Kulikowa 1961, 1962; Darevsky *et al.* 1973; Mertens 1964; Bischoff 1973; Darevsky *et al.* 1985; Freitas 2017).
**D. brauneri* x *D. alpina* (Darevsky 1967; Murphy *et al.* 2000).
**D. brauneri* x *D. saxicola* (Darevsky 1967; Murphy *et al.* 2000).
**D. brauneri brauneri* x *D. b. darevskii* (2) (Darevsky 1967).
**D. b. darevskii* x *D. brauneri brauneri* (2) (Darevsky 1967).
**D. caucasica* x *D. alpina* (Darevsky 1967; Fu *et al.* 1995; Murphy *et al.* 2000).
**D. caucasica* x *D. daghestanica* (Darevsky 1967; Fu *et al.* 1995; Murphy *et al.* 2000).
**D. caucasica* x *D. derjugini* (Orlova 1979; Ciobanu *et al.* 2003).
**D. caucasica* x *D. saxicola* (Darevsky 1967; Murphy *et al.* 2000).
**D. clarkorum* x *D. rudis* (Darevsky & Vedmederja 1977; Ciobanu *et al.* 2003).
**D. daghestanica* x *D. caucasica* (Darevsky 1967; Fu *et al.* 1995; Murphy *et al.* 2000).
**D. dahli* x *D. portschinskii* (Darevsky & Kulikowa 1961; Mertens 1964; Darevsky 1967; Bischoff 1973).
**D. derjugini* x *D. adjarica* (Darevsky 1967; Bischoff 1973; Orlova 1979; Murphy *et al.* 2000; Ciobanu *et al.* 2003)(1).
**D. derjugini* x *D. caucasica* (Orlova 1979; Ciobanu *et al.* 2003).
**D. derjugini* x *D. mixta* (Orlova 1979; Murphy *et al.* 2000; Ciobanu *et al.* 2003).
**D. derjugini* x *D. o. obscura* (Darevsky & Kulikowa 1961; Mertens 1964; Bischoff 1973).
**D. derjugini* x *D. saxicola* (Orlova 1979; Ciobanu *et al.* 2003).
**D. dryada* x *D. rudis* (Darevsky & Tuniyev 1997; Ciobanu *et al.* 2003).
**D. mixta* x *D. alpina* (Fu *et al.* 1997; Murphy *et al.* 2000).
**D. mixta* x *D. derjugini* (Orlova 1979; Murphy *et al.* 2000; Ciobanu *et al.* 2003).
**D. nairensis* x *D. armeniaca* (p) (Bischoff 1973).
**D. nairensis* x *D. unisexualis* (p) (Bischoff 1973; Darevsky *et al.* 1985).
**D. parvula* x *D. rudis* (Darevsky 1967; Murphy *et al.* 2000).
**D. portschinskii* x *D. armeniaca* (p) (Darevsky & Kulikowa 1961; Mertens 1964; Bischoff 1973).
**D. portschinskii* X *D. dahli* (Darevsky & Kulikowa 1961; Mertens 1964; Darevsky 1967; Bischoff 1973).
**D. portschinskii* x *D. raddei* (Darevsky 1967; Murphy *et al.* 2000; Freitas 2017).
**D. portschinskii* x *D. rostombekowi* (p) (Freitas 2017).
**D. raddei* x *D. armeniaca* (p) (Darevsky & Kulikowa 1961; Mertens 1964).
**D. raddei* x *D. portschinskii* (Darevsky 1967; Murphy *et al.* 2000; Freitas 2017).
**D. raddei* x *D. rostombekowi* (p) (Darevsky *et al.* 1973, 1985, 1986).
**D. raddei* x *D. valentini* (Darevsky & Kulikowa 1961).
**D. rostombekowi* (p) x *D. portschinskii* (Freitas 2017).
**D. rostombekowi* (p) x *D. raddei* (Darevsky *et al.* 1973, 1985, 1986).
**D. rudis* x *D. clarkorum* (Darevsky & Vedmederja 1977; Murphy *et al.* 2000; Ciobanu *et al.* 2003).
**D. rudis* x *D. dryada* (Darevsky & Tuniyev 1997; Ciobanu *et al.* 2003).
**D. rudis* x *D. parvula* (Darevsky 1967; Murphy *et al.* 2000).
**D. rudis rudis* x *D. r.lantzicyreni* (Darevsky 1967).
**D. o. macromaculata* x *D. armeniaca* (p) (Darevsky 1967; Bischoff 1973).
* *D. o.macromaculata* x *D. o. obscura* (Darevsky 1967) (3).
**D. o. obscura* x *D. armeniaca* (p) (Darevsky 1967; Bischoff 1973; Darevsky *et al.* 1985).
**D. o. obscura* x *D. derjugini* (Darevsky & Kulikowa 1961; Mertens 1964; Bischoff 1973).
**D. o. obscura* x *D. o. macromaculata* (Darevsky 1967) (3).
**D. saxicola* x *D. brauneri* (Darevsky 1967; Murphy *et al.* 2000).
**D. saxicola* x *D. caucasica* (Darevsky 1967; Murphy *et al.* 2000).
* *D. saxicola* x *D. derjugini* (Orlova 1979; Ciobanu *et al.* 2003).
* *D. unisexualis* (p) x *D. nairensis* (Bischoff 1973; Darevsky *et al.* 1985).
**D. unisexualis* (p) x *D. valentini* (Darevsky 1967; Bischoff 1973; Freitas 2017).
**D. valentini* x *D. armeniaca* (p) (Darevsky 1966, 1967; Darevsky & Kulikowa 1961, 1962; Darevsky *et al.* 1973; Mertens 1964; Bischoff 1973; Darevsky *et al.* 1985; Freitas 2017).
**D. valentini* x *D. raddei* (Darevsky & Kulikowa 1961).

**D. valentini* x *D. unisexualis* (p) (Darevsky 1967; Bischoff 1973; Freitas 2017).
**D. r. lantzicyreni* x *D. rudis rudis* (Darevsky 1967).

(1) By the localities concerned, the "*D. parvula*" of these hybridizations were in fact Georgian *D. adjarica*.

(2) Considered subspecies, or synonyms by Doronin *et al.* (2013)

(3) *D. obscura* is considered a species by Gabelaia *et al.* (2018) and Arribas *et al.* (2022). The strange and unexpected differences found by Mayer & Lutz (1989) could support this species status. However, even in this case, it remains to be resolved the complex internal relationships of the Great Caucasus forms (*svanetica* and *chechenica*) if they belong to *rudis* s. str, are conspecific with *obscura*, or should be considered independent with species status (see Arribas *et al.* 2013).

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Appendix 3

Diagnoses of *Darevskia* groups (new subgenera)

From Murphy onwards, three clades were considered (Murphy *et al.*, 2000; Tarkhnishvili, 2012), but not all the species (particularly the Iranian and Anatolian ones) were included in these analyses. Here, some new groups are separated and defined based on osteology, external morphology, and new genetic studies that complement and complete the limited taxa included in Murphy *et al.* (2000). These new groups, here named as subgenera, are supported by combined diagnostic characteristics different from the rest of the groups in which they were integrated in Murphy *et al.* (2000) (if they were represented) and are monophyletic, leaving the rest of the heterogeneous group in which they were previously integrated also monophyletic. The newly defined groups are the *raddei*, *parvula*, *defilippi*, and *chlorogaster* ones. In Murphy *et al.* (2000), the *raddei* group is sister to the remaining *caucasica* group. The *parvula* group is sister to the *rudis* group, and the remaining two were not included in that study. Although it could be suggested that the new groups of *chlorogaster*, *raddei*, and *defilippi* should be integrated into the *caucasica* group, there are several reasons against this. Only *raddei* had been considered for inclusion in the *caucasica* group, but including any of them would leave the latter extremely heterogeneous and meaningless. In addition to the monophyly of each of these groups, they have different (in one case, the *defilippi* group, unknown) CLsat families but do not share (or have a vestigial) one with the *caucasica* group. This tandemly repeated (satellite) DNA family named CLsat, and nuclear DNA markers from the SINE family named Squam1-34, are both exclusive to the genus *Darevskia*, and there are variants characteristic of different subgeneric groups (Grechko *et al.*, 1999; Rudykh et al, 1999, 2002; Ciobanu *et al.* 2003, 2004; Kosushkin & Grechko, 2013). They also have diagnostic osteological characteristics with respect to the *caucasica* group (see below).

The *parvula* group is the most differentiated among all the *Darevskia* groups, as it is very likely sister to all the other groups (as in García-Porta *et al.*, 2019; Murtskhvaladze *et al.*, 2020, and some trees in Freitas *et al.* 2016a or Freitas 2017—see Appendix 1: taxonomic remarks); sister to the *rudis* group (Ahmadzadeh *et al.*, 2013); or sister to all the other members of the genus *Darevskia* in an unresolved polytomy (Pyron *et al.*, 2013; Roquet *et al.*, 2015; Zheng *et al.*, 2016).

The *raddei* group is sister to the *caucasica* plus *chlorogaster* groups (Pyron *et al.*, 2013; Murtskhvaladze *et al.*, 2020), only to the *caucasica* group (Ahmadzadeh *et al.*, 2013), or sister to the *chlorogaster* group, and both together are sisters to the *caucasica* group (Roquet *et al.*, 2015; García-Porta *et al.*, 2019), or included in an unresolved polytomy with *chlorogaster* and the *caucasica* groups (Zheng *et al.*, 2016).

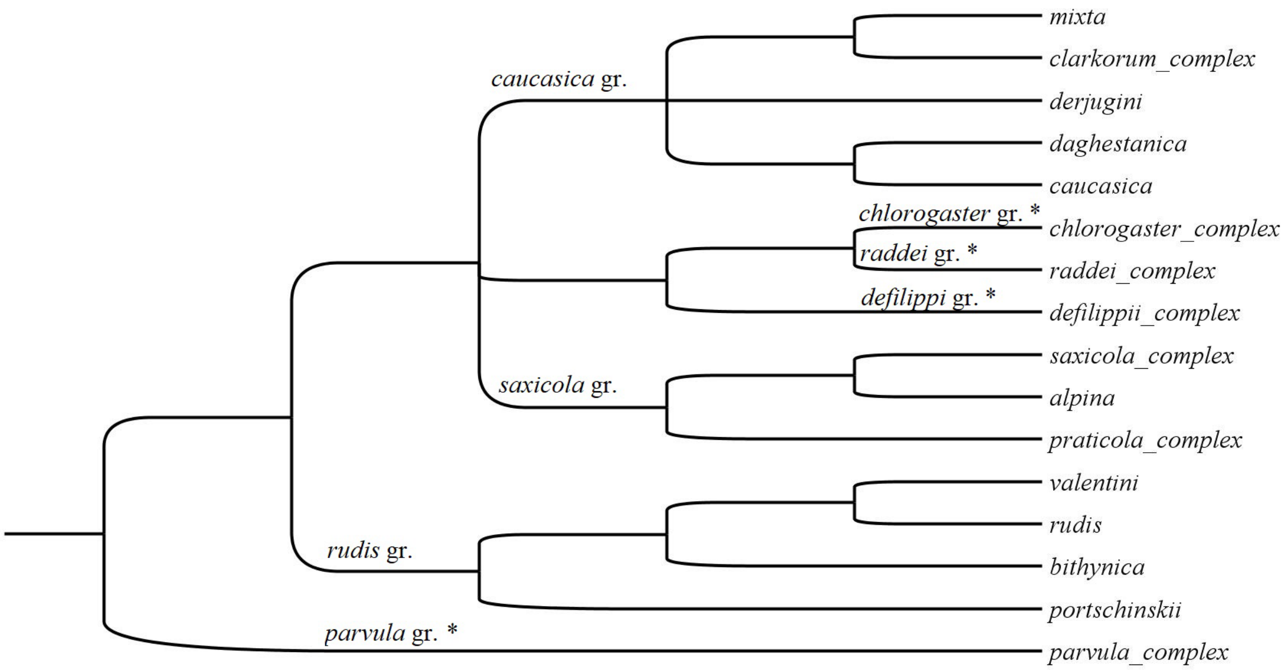
The *chlorogaster* group is sister to the *raddei* group, and both together are sister to the *caucasica* group (Ahmadzadeh *et al.*, 2013; Roquet *et al.*, 2015; García-Porta *et al.*, 2019),only the *chlorogaster* group sister to the *caucasica* group (Murtskhvaladze *et al.*, 2020), or an unresolved polytomy with the *caucasica* group (Pyron *et al.*, 2013; Zheng *et al.*, 2016).

The *defilippi* group has been included in very few studies (and is absent in Murphy *et al.*, 2000). It is sister to the *caucasica*, *raddei*, and *chlorogaster* groups (Ahmadzadeh *et al.*, 2013; García-Porta *et al.*, 2019). It was not included in Pyron *et al.* (2013), Roquet *et al.* (2015), Zheng *et al.* (2016), or Murtskhvaladze *et al.* (2020).

Regarding known hybrids, the vast majority are between components of different *Darevskia* groups. Closely related *Darevskia* species belonging to the same group are frequently allopatric or parapatric, whereas phylogenetically more distant species (different groups or subgenera) may coexist and occur sympatrically, favoring encounters and hybridization. Members of some of these more distant groups hybridize with others from different groups, and the only escape route from sterility they have is via parthenogenesis, while other hybrids or hybrids within closer groups can be theoretically sterile or more likely fertile, becoming diluted again in one of the parental species by backcrosses (see Appendix 2: *Darevskia* hybrids). Parthenogenetic species seem to arise from hybridization between two relatively divergent taxa (not too close) within a specific range of phylogenetic distances (the ‘Balance Hypothesis’) (Freitas *et al.*, 2019).

We describe these very individualized groups (*parvula*, *rudis*, and *saxicola* groups) and others more related (*caucasica*, *raddei*, *defilippi*, and *chlorogaster* groups) as subgenera to be used, if necessary, to refer to these natural clusters of species without cumbersome circumlocutions of their contents and the authors who have used them in a given sense. A tentative scheme of their relationships is in Suppl. Fig 1.

References are in the main text and in Appendix 1 (Taxonomic remarks).



SUPPLEMENTARY FIGURE 1. Tentative scheme of the *Darevskia* relationships.

The defined groups here named as subgenera are:

***Darevskia saxicola* group** (“the saxicola clade” in Murphy et al, 2000) [**Subgenus *Darevskia* Arribas, 1999 nov.** – author and date in correspondence of Art. 43.1 ICZN-; Species Typica: *Lacerta saxicola* Eversmann, 1834 [=*Darevskia saxicola* (Eversmann, 1834)], by nominotypy]. Species included: *D. (D.) saxicola* (Eversmann, 1834)*, D. (D.) brauneri* (Méhely, 1909)*, D. (D.) lindholmi* (Szczerbak, 1962)*, D. (D.) arribasi* Tuniyev, Petrova & Lotiev, 2023, *D. (D.) szczerbaki* (Lukina, 1963)*, D. (D.) alpina* (Darevsky, 1967) and the *D. (D.) praticola* complex [*D. (D.) (p.) praticola* (Eversmann, 1864), *D. (D.)(p.) pontica* (Lantz & Cyrén, 1918) and *D. (D.)(p.) hungarica* (Sobolevsky, 1930)].

Etymology: As the genus, dedicated to Ilya S. Darevsky (1924-2009). The gender is feminine.

Diagnosis: Anal plate surrounded by a semicircle of small scales. There are one or two small preanals, not much greater than the other ones. Belly colorations belong to the family of the red (yellow and orange) or the green (yellow and green). Can appear some tricuspid teeth. Satellite CLsat subfamily CLsatI (and in *D. lindholdmi* the exclusive derived CLsatV)(see above for an explanation of these DNA satellite subfamilies and references).

Other morphological characteristics: Males with dorsal parts of diverse tones of green, more rarely brownish or grayish (ever diverse tones of grayish in the *D. praticola* complex). Females are frequently more brownish or grayish than their respective males. Dorsal part ornate with rows of small spots or blotches along vertebral area, finely stippled in all his width or even more or less faintly reticulated (points remaining). Broad darker bands appear along the mid-dorsal area in the *praticola* complex and *D. daghestanica*, frequently closed by small spots. The sides (temporal or lateral band) uniform, reticulated or faintly reticulated (composed of dots that close clearer centers). Axillary blue ocelli present (more rare or small in *D. alpina*) or absent (*praticola* complex). Belly coloration in reproductive males is white (sometimes bluish –physic color, not pigment–), yellow, orange yellow, greenish yellow or green. Female grasping during copulation both by the belly sides and the thigh.

Origin: the *saxicola* group (mainly represented in the Western Greater Caucasus, from where other lineages of *Darevskia* are almost absent) originated at 14.5–18 mya, associated with the first contacts between the Caucasus (then an island to be colonized) with the Anatolian Mainland (Murtskhvaladze *et al.*, 2020). Its age is lowered to 11.59 by García-Porta *et al.* (2019).

***Darevskia caucasica* group** ("the caucasica clade", *partim*, except the *raddei* group, in Murphy *et al.*, 2000) [**Subgenus *Colchiodarevskia* nov.**; Species Typica: *Lacerta caucasica* Méhely, 1909[= *Darevskia caucasica* (Méhely, 1909)], here designated]. Species included: *D. (C.) caucasica* (Méhely, 1909), *D. (C.) daghestanica* (Darevsky, 1967), *D. (C.) derjugini* (Nikolsky, 1898), *D. (C.) mixta* (Méhely, 1909), *D. (C.) clarkorum* (Darevsky & Vedmederja, 1977) and *D. (C.) dryada* (Darevsky & Tuniyev, 1997).

Etymology: A composite name from the Colchis, an ancient kingdom in the Black Sea shores known to be the destination of Jason and the Argonauts, or in Biogeography the name of a relict biota refuge to which these species belong, and *Darevskia*, the name of the genus. The name is feminine.

Diagnosis: Anal plate with two central small preanals. Belly colorations belong to the family of the green (blue physical color and yellow pigments): white, yellow, yellowish-green or green. Satellite CLsat subfamily CLsatII (and very few I and III).

Other morphological characteristics: Males with dorsum in diverse tones of vivid green, emerald-green (most species), or brown (*D. derjugini*). Females similar to the males, but usually more brownish. Dorsal pattern composed of small spots bands in the vertebral area (vertebral band), or more displaced toward sides (paravertebral bands) closing a broad darker tone band inside. Most species have dark-brown uniform or slightly reticulated temporal bands on the flanks. Axillary blue ocelli present (but scarcely developed: small, few and frequently absent in much specimens) or absent (*D. daghestanica*). Belly coloration in reproductive males is yellow or yellow-greenish in most of the species. Female grasping during copulation only (?) by the belly sides (*D. mixta* and *D. derjugini*), or both by the belly sides and the thigh (other species).

Origin: the *caucasica* group (hence distributed in Colchid areas of Eastern Anatolia) diverged from the *chlorogaster* group 10.7 mya, isolated by this increasing aridity in the Hyrcanian areas (Iranian Landmass) (Murtskhvaladze *et al.*, 2020). For García-Porta *et al.* 2019), the *caucasica* group split from the *raddei* + *chlorogaster* group 8.76 mya.

***Darevskia chlorogaster* group (new)** [**Subgenus *Hyrcanodarevskia* nov.**; Species Typica: *Lacerta chlorogaster* Boulenger, 1908 [= *Darevskia chlorogaster* (Boulenger, 1908)], here designated]. Species included: *D.(H.) chlorogaster* (Boulenger, 1908), *D. (H.) kami* Ahmadzadeh, Flecks, Carretero, Mozaffari, Böhme, Harris, Freitas & Rödder, 2013 and *D. (H.) caspica* Ahmadzadeh, Flecks, Carretero, Mozaffari, Böhme, Harris, Freitas & Rödder, 2013.

Etymology: From Hyrcania, a classical historical region south-east of the Caspian Sea and a relict biota refuge to which these species belong, and *Darevskia*, the name of the genus. The name is feminine.

Diagnosis: Increased number of teeth in premaxilla (usually 9). No platycephaly (no rock crevice life adaptations). Rostral scale usually touching naris. Collar serrated. Anal plate of moderate size and usually two few enlarged preanals before it. Dorsal scales elongated, often hexagonal and clearly keeled. Belly colorations belong to the family of the green (blue physical color and yellow pigments): diverse tones of vivid greens, perhaps with yellow in legs or bluish in throat. Interclavicle lateral branches clearly inclined forward. Almost with none of the CLsat subfamilies known so far (traces of CLsatI).

Other morphological characteristics: Dorsal tract brownish (more in *D. chlorogaster*) or more or less vivid green (*D. chlorogaster* and especially *D. kami* and *D. caspica*). Dorsal pattern composed of rows of small spots, also faintly reticulated or with isolated dots along the entire dorsal tract. Sides (costal bands) reticulated or uniform dark-brown banded. Axillary blue ocelli frequently present. Belly yellowish-green or vivid green. Female grasping during copulation only by the thigh.

Origin: The *chlorogaster* group began its differentiation 10.7 mya, isolated by this increasing aridity in the

Hyrcanian areas (Iranian Landmass), from the *caucasica* group (hence distributed in Colchid areas of Eastern Anatolia) (Murtskhvaladze *et al.*, 2020). According to García-Porta *et al.* (2019) the *caucasica* group split from the ancestor of the *raddei* + *chlorogaster* group 8.76 mya, and the latter two split 7.78 mya.

***Darevskia defilippi* group (new):** [**Subgenus *Persiodarevskia* nov.**; Species Typica: *Podarcis defilippi* Camerano, 1877 [= *Darevskia defilippi* (Camerano, 1877)], here designated]. Species included: *D. (P.) defilippi* (Camerano, 1877), *D. (P.) kopetdaghica* Ahmadzadeh, Flecks, Carretero, Mozaffari, Böhme, Harris, Freitas & Rödder, 2013, *D. (P.) schaekeli* Ahmadzadeh, Flecks, Carretero, Mozaffari, Böhme, Harris, Freitas & Rödder, 2013 and *D. (P.) steineri* (Eiselt, 1995).

Etymology: From Persia, ancient historic area and empire where these lizards spread across its mountains, and *Darevskia*, the name of the genus. The name is feminine.

Diagnosis: Belly colorations belong to the family of the red (red pigment in *D. defilippi, D. kopetdaghica*, *D. schaekeli*) or the green (*D. steineri*; in which all the body is greenish, and perhaps there is no special belly pigment but a physical color). Anal plate medium or small, one (rarely two) small and few conspicuous preanals. Interclavicle lateral branches slightly inclined forward. Satellite CLsat subfamily unknown (not studied).

Other morphological characteristics: Dorsum brown (rarely greenish as in *D. steineri*). Dorsal tract finely stippled or faintly reticulated. Sides (costal bands) reticulated. Axillar ocelli absent (or white among the reticulate, not blue). Belly brick red (rarely pale greenish as in the forestal *D. steineri*). Female grasping during copulation by the belly sides.

Origin: The *defilippi* group split 10.69 mya (following García-Porta *et al.*, 2019).

***Darevskia raddei* group (new)** [**Subgenus *Matrodarevskia* nov.**; Species Typica: *Lacerta saxicola raddei* Boettger, 1892 [= *Darevskia raddei* (Boettger, 1892)], here designated]**.** Species included: *D. (M.) raddei* (Boettger, 1892) (s. lat., with several lineages as *D. (M.) aghasyani* Tuniyev & Petrova, 2019 that probably can be considered different species), *D. (M.) nairensis* (Darevsky, 1967).

Etymology: from matro, derived of mater, meaning mother (Latin), because these species are the maternal of five of the seven parthenogenetic species originated by hybridization, and *Darevskia*, the name of the genus. The name is feminine.

Diagnosis: high vertebral counts (28 instead of 27 as modal number in males, and 29 instead of 28 in females). Two small (*D. raddei*) or two enlarged (*D. nairensis*) preanal scales just previous to the anal plate. Belly colorations belong to the family of the green (physical blue and yellow pigment): white -occasionally bluish-, yellow, yellowish green and green. Grey dorsum (occasionally slightly greenish), with a vertebral band of big dorsal dots or a reticulate dorsal pattern. Microsatellite CLsat subfamily CLsatI.

Other morphological characteristics: Dorsum grey or brownish-gray (sometimes slightly greenish in males). Dorsal pattern with a wide vertebral row of dots, or a well reticulated pattern. Sides (temporal bands) reticulated or almost faintly reticulated. Axillary blue ocelli present, well developed and frequently numerous. Belly usually green or yellowish green (more rarely white or slightly bluish –physical color-).

Female grasping during copulation by the belly sides and thigh (*D. raddei*), or only by the thigh (*D. nairensis*).

Origin: The *raddei* group split at around 12.12 mya (dates following Murtskhvaladze *et al.*, 2020) (14-18 My for Roquet *et al.*, 2014 and Zheng & Wiens, 2016), and is more adapted to the increasingly arid habitats of the Eastern Anatolian Plate (Murtskhvaladze *et al.*, 2020). According to García-Porta *et al.* (2019) *raddei* + *chlorogaster* groups split from the *caucasica* group 8.76 mya, and the latter two split 7.78 mya.

***Darevskia rudis* group** ("the rudis clade", *partim*, except the *parvula* group -see below-, from Murphy et al, 2000) [**Subgenus *Patrodarevskia* nov.**; Species Typica: *Lacerta depressa* var. *rudis* Bedriaga, 1886 [= *Darevskia rudis* (Bedriaga, 1886)], here designated]. Species included: *Darevskia (P.) valentini* (Boettger, 1892), *Darevskia (P.) josefschmidtleri* Arribas, Candan, Kornilios, Ayaz, Kumlutas, Gül, Yilmaz, Yildirim-Caynak & Ilgaz, 2022, *Darevskia (P.) spitzenbergerae* (Eiselt, Darevsky & Schmidtler, 1992), *Darevskia (P.) mirabilis* Arribas, Ilgaz, Kumlutaş, Durmuş, Avci & Üzüm, 2013, *Darevskia (P.) rudis* (Bedriaga, 1886), *Darevskia (P.) obscura* (Lantz & Cyrén, 1936), *Darevskia (P.) bithynica* (Méhely, 1909), and *D. (P.) portschinskii* (Kessler, 1878).

Etymology: patro, from Latin pater meaning father, due to the fact that the species of this group are always the paternal species in all the crosses that give rise to the *Darevskia* parthenogenetic taxa, being the maternal species members of *Matrodarevskia* nov. or *Colchiodarevskia* nov.; and *Darevskia*, the name of the genus. The name is feminine.

Diagnosis: Anal plate with a very characteristic big (unique) preanal scale before the anal one. Belly colorations belong to the family of the red or to the green (yellow and red pigments, and blue physical color): white (occasionally physical bluish)-yellow (yellowish green) and green; or white-yellow-yellowish orange and orange. Female grasping during copulation only by the belly sides. Microsatellite CLsat subfamily CLsatI and CLsat III.

Other morphological characteristics: Dorsum in diverse tones of green (most forms), but also grey in *D. portschinskii and some D.rudis* or greenish-gray in *D. josefschmidtleri*, *D. spitzembergerae*, etc. Dorsal tract very variable, changing with sex and age, but mostly with large dark spots covering the entire dorsum (most *D. rudis, D. obscura* sspp*., D. josefschmidtleri, D. spitzembergerae, D. portschinskii*) or agrupated in the center of the dorsum forming a row of blotches (in *D. valentini, D. bithynica* and in some populations or specimens of *D. rudis* or *D. obscura*), or reticulated (*D. portschinskii, D. josefschmidtleri, D. spitzembergerae, D. rudis lantzicyreni*). Sides (temporal bands) reticulated or faintly reticulated. Axillary blue ocelli present (and sometimes very numerous, i.e. some *D. valentini* but also in the other species). Belly coloration in reproductive males is yellow, yellowish-orange or orange in *D. valentini*; yellow in *D. portschinskii* and *D. mirabilis*; yellow, greenish-yellow (more rarely white bluish or bluish -physic color-) in *D. rudis* and *D. obscura*; or whitish in *D. josefschmidtleri* and *D. spitzembergerae*.

Female grasping during copulation only by the belly sides.

Origin: The second *Darevskia* group to split after the *parvula* group (around 18.53 My) (5.9 My [5-7.6 at 90% confidence limits] following Murtskhvaladze *et al.*, 2020), or about 5 [or from 3.9 to 6.1] My ago from Tarkhnishvili (2012) and Freitas (2017), respectively; or 13.43 for García-Porta *et al.* (2019), also differentiating in the Anatolian plate, the place of origin of the genus.

***Darevskia parvula* group** **(new)** [**Subgenus *Plesiodarevskia* nov.**; Species Typica: *Lacerta saxicola parvula* Lantz & Cyrén, 1913 [= *Darevskia parvula* (Lantz & Cyrén, 1913)], here designated]. Species included: *D. parvula* (Lantz & Cyrén, 1913)*, D. adjarica* (Darevsky & Eiselt, 1980) and *D. tuniyevi* Arribas, Candan, Kurnaz, Kumlutaş, Caynak & Ilgaz, 2022.

Etymology: plesio, from Greek Plesios "nearby to", to significate that very probably is the sister group to all the remaining *Darevskia*, and *Darevskia*, the name of the genus. The name is feminine.

Diagnosis: One or two (variable) moderately enlarged preanals (frequently single, but transversely elongated). Belly colorations belong to the family of the red (red pigment): From white to brick red colorations in both sexes. Female grasping during copulation only by the belly sides. Microsatellite CLsat subfamily CLsatIII.

Other morphological characteristics: Dorsum color grayish, brownish or greenish (males). Dorsal pattern composed of dots forming a wide band, stippled, vermiculated and even faintly reticulate, or two rows of paravertebral spots. Sides with dark-brown bands with clear spots inside or slightly reticulated on the flanks. Axillary blue ocelli sometimes present (but frequently absent or inconspicuous). Belly orange or brick red.

Female grasping during copulation only by the belly sides.

Origin: In genetic studies, this group appears very deeply rooted and sister to the *rudis* group, and frequently also sister to all the other species of the genus *Darevskia*. The *parvula* group split from the rest of *Darevskia* around 20.83 mya (Murtskhvaladze *et al.*, 2020) (25 mya according to Roquet *et al.*, 2014; 11 mya according to Zheng & Wiens, 2016; or 15.13 mya according to García-Porta *et al.*, 2019). This first split of *Darevskia* occurred in the northeast of the Anatolian landmass and the current Lesser Caucasus.

Appendix 4

Localities and number of studied specimens: The first number is the number of specimens cleared and alizarin stained, and the second (in parentheses) is the number of specimens studied using X-ray.

***-Darevskia clarkorum* (Darevsky & Vedmederja, 1977) 12 (2)**

Cankurtaran Gec., Artvin (Turkey). 1 (1) M, 2 (1) F.
"Mountain trial", vicinity of Borçka, Artvin (Turkey). 1 M, 1 F.

Yoldere Village, Hopa, Artvin (Turkey). 2 M, 1 F.
Ayder Plateau, Çamlıhemşin, Rize (Turkey). 1 M.
Ortacalar, Artvin (Turkey). 1 M.
Hatila Plateau, Artvin (Turkey). 1 M, 1 F.

-*Darevskia mixta* (Méhely, 1909) 4 (2)
Zekari (Adjaria, Georgia). 2 M, 2 F
Baniskevi (Georgia). (1) M, (1) F.

-*Darevskia dryada* (Darevsky & Tuniyev, 1997) 2 (1)
Charnali river gorge, Chelvachauri district (Adjaria, Georgia). 2 M. (1) F

-*Darevskia derjugini* (Nikolsky, 1898) 6 (4)
Mlashe (Georgia).(***orlowae*** Bischoff, 1984). 4 (2) M, 2 (2) F.

-*Darevskia daghestanica* (Darevsky, 1967) 8 (22)
Khvarshi (Daghestan, Russia). (10) M, 1 (12) F.
Tpig (Daghestan, Russia). 1 M.
Tlyadal (Daghestan, Russia). 1 M, 3 F.
No locality (Daghestan, Russia). 1 M, 1 F.

-*Darevskia caucasica caucasica* (Méhely, 1909) 3 (5)
Terek River Gorge (Georgia). 1 F
Khvarshi (Daghestan, Russia). 1 (3) M, (2) F.
Pereval (Southern Ossetia). 1 F.

-*Darevskia caucasica vedenica* (Darevsky & Roytberg, 1999) 2 (0)
Vedeno, Andii Range (Chechenia, Russia). 1 M, 1 F.

-*Darevskia chlorogaster* (Boulenger, 1908) 6 (11)
Alexiefska (Azerbaijan). 4 (3) M, 2 (3) F.
Guirkansky Zapoviednik (Azerbaijan). (3) M, (2) F

-*Darevskia raddei raddei* (Boettger, 1892) (s. lat.) 5 (6)
Lichk (Armenia). 1 (3) M, 1 (3) F
Megrinski (Armenia). 1 M, 2 F

-*Darevskia raddei vanensis* (Eiselt, Schmidtler & Darevsky, 1993) 1 (2)
Bendimahi, Muradiye, Van (Turkey). 1 (2) M, (1) F (paratypus).

-*Darevskia nairensis* (Darevsky, 1967) 2 (2)
Agin (Armenia). 1 (1) M, 1 (1) F.

-*Darevskia defilippii* (Camerano, 1877) 3 (1)
Lar valley, Tehran (Irán). 2 M, 1 F.

-*Darevskia brauneri* (Méhely, 1909) 5 (9)
Inguri river Gorge (Georgia). (***brauneri* s. str.).** 1 M, 1 F.
Dagomys, circa Sochi (Russia). (***darevskii* Szczerbak, 1962).** 2 (5) M, 1 (4) F.

-*Darevskia lindholmi* (Szczerbak, 1962) 2 (2)
Bakhchisarai, Crimea (Russia). (1) M, 1 (1) F.

-*Darevskia szczerbaki* (Lukina, 1963) 1 (0)
Anapa (Russia). 1 M.

-*Darevskia saxicola* (Eversmann, 1834) 3 (0)
Kislovodsk, Stavropol (Russia). 2 M, 1 F.

-*Darevskia alpina* (Darevsky, 1967) 7 (7)
Terskol, Mt. Elbrus (Kabardino-Balkariya, Russia). 1 (2) M, 2 (4) F
Mt. Fisht (Krasnodar, Russia). 1 (1) M.
Mt. Aishkha (Russia): 1 M, 2 F.

-*Darevskia* (*praticola) praticola* (Eversmann, 1834) 1 (1)
Stavropol Region (Russia). (1) M, 1 F.

-*Darevskia* (*praticola*) *pontica* (Lantz & Cyrén, 1919) 5 (5)
Kutorskaya (Krasnodar, Russia). 1 (1), 4 (4)..

-*Darevskia* (*praticola*) *hungarica* (Sobolevsky, 1930) 2 (4)
Vrsacki Breg, (Serbia). 2 M, 2 F.

-*Darevskia valentini* (Boettger, 1892) 10 (4)
Karvansaray (Armenia). 1 (1) M, 1 (1) F.
Mt. Legli (Armenia). 1 M.
Gukasyan district (Armenia). 1 (2) F.
Mt. Aragatz (Armenia). 2 F.
Boğatepe Village (Turkey) 1 M, 1 F.
Tepeler (Turkey) 1 M, 1 F.

-*Darevskia spitzenbergerae spitzenbegerae* (Eiselt, Darevsky & Schmidtler, 1992) 3 (0)
Cilo Mountain (Turkey). 1 M, 2 F.

-*Darevskia spitzenbergerae wernermayeri* Arribas, Candan, Kornilios, Ayaz, Kumlutas, Gül, Yilmaz, Yildirim-Caynak & Ilgaz, 2022 6 (3)
Yûkari Narlica, Van (Turkey). 3 (2) M, 3 (1) F.

-*Darevskia josefschmidtleri* Arribas, Candan, Kornilios, Ayaz, Kumlutas, Gül, Yilmaz, Yildirim-Caynak & Ilgaz, 2022 6 (0)
Başeğmez Village, Çaldıran (Turkey). 1 M, 1 F.
Palandöken (Turkey). 1 M, 1 F.
Çirişli Village, Çat (Turkey). 1 M, 1 F.

-*Darevskia rudis rudis* (Bedriaga, 1886) 6 (0)
Maçka, Trabzon, NE Anatolia (Turkey). 3 M, 3 F.

-*Darevskia rudis lantzicyreni* (Darevsky & Eiselt, 1967) 8 (0)
Erciyes Dagh (Turkey). 1 M, 1 F.
Yaylacık (Turkey). 1 M, 1 F.
Kümbet Village (Turkey). 1 M, 1 F.
Çamur Village (Turkey). 1 M, 1 F.

-Darevskia rudis bolkardaghica **Arribas, Ilgaz, Kumlutaş, Durmuş, Avci & Üzüm, 2013 3 (0)**
Karagöl, Ulukışla, Niğde, Central Anatolia (Turkey). 1 M, 2 F.

-Darevskia obscura obscura **(Lantz & Cyrén, 1936) 8 (6)**
Kutul Plateau, Ardanuç, Artvin, NE Anatolia (Turkey). 3 M, 3 F.
Achaldaba (Georgia). 1 (3) M, 1 (3) F.
-Darevskia obscura bischoffi **(Böhme & Budak, 1977) 6 (0)**
Balcılar Village, Borçka, Artvin, NE Anatolia (Turkey). 3 M, 3 F.

-Darevskia obscura macromaculata **(Darevsky, 1967) 6 (0)**
Between Ardahan and Şavşat, Ardahan, NE Anatolia (Turkey). 3 M, 3 F.

-Darevskia 'rudis' chechenica **(Eiselt & Darevsky, 1991) 2 (4)**
Khvarshi (Daghestan, Russia). 1 (2) M, 1 (2) F.

-Darevskia 'rudis' svanetica **(Darevsky & Eiselt, 1890) 2 (0)**
Mestia, Swanetia (Georgia). 1 M, 1 F.

-Darevskia mirabilis **Arribas, Ilgaz, Kumlutaş, Durmuş, Avci & Üzüm, 2013 4 (0)**
Ovit Pass, Trabzon, NE Anatolia (Turkey). 2 M, 2 F.

-Darevskia bithynica bithynica **(Mehely, 1909) 4 (0)**
Kirazlı Plateau, Uludağ, Bursa, Northwestern Anatolia (Turkey). 2 M, 2 F.

-Darevskia bithynica tristis **(Lantz & Cyren, 1936) 6 (0)**
Güzeldere Village, Düzce, NW Anatolia (Turkey). 3 M, 3 F.

-Darevskia portschinskii **(Kessler, 1878) 4 (6)**
Rbemoshuri (Georgia). 2 (3) M, 2 (3) F.

-Darevskia parvula **(Lantz & Cyrén, 1913) 5 (0)**
Kılıçkaya, NE Anatolia (Turkey). 3 M, 2 F.

-Darevskia adjarica **(Darevsky & Eiselt, 1980) 18 (6)**
Guneice, NE Anatolia (Turkey). 1 M.
Adskuri (Georgia). 2 (3) M, 2 (3) F.
Ardahan, Northeastern Anatolia, (Turkey). 2 M, 2 F.
Çermik, Artvin, Northeastern Anatolia (Turkey). 2M, 1 F
Borçka, Artvin, Northeastern Anatolia (Turkey). 2 M, 2 F.
Arhavi, Northeastern Anatolia, (Turkey). 2 M.

-Darevskia tuniyevi **Arribas, Candan, Kurnaz, Kumlutaş, Caynak & Ilgaz, 2022 4 (0)**
19 km W of Ardahan, NE Anatolia (Turkey). 2 M, 2 F.

-Darevskia armeniaca **(Méhely, 1909)** (parthenogenetic) **7 (6)**
Arpalich (Armenia). 3 (6) F
Gei-Gel lake (Azerbaijan). 1 F
Ankavan (Armenia). 3 F

-Darevskia dahli **(Darevsky, 1957)** (parthenogenetic) **5 (6)**
Jodieri, circa Tiflis (Georgia). 2 (6) F
Kodjori (Georgia). 3 F

-Darevskia rostombekowi **(Darevsky, 1957)** (parthenogenetic) **7 (6)**
Zurnabad (Azerbaijan). 3 (6) F
Spitak (Armenia). 1 F
Papanino (Armenia). 3 F

-Darevskia unisexualis **(Darevsky, 1966)** (parthenogenetic) **8 (2)**
Tsomakaberd (Armenia). 1 (2) F.
Aragatz (Armenia). 1 F.
Ankavan (Armenia). 3 F.
Captive-bred (unknown locality). 3 F.

-Darevskia unisexualis **x** ***D. nairensis*** (Triploid hybrid) **1 (1)**
Aragatz Mt., Kutchak (Armenia). 1 (1) F.

-Darevskia uzzelli **(Darevsky & Danielyan, 1977)** (parthenogenetic) **4 (0)**
Horasan (Turkey). 4 F.

-Darevskia sapphirina **(Schmidtler, Eiselt & Darevsky, 1994)** (parthenogenetic) **4 (0) (1)**
Patnos (Turkey). 3 F
30 km NW Ercis (limit Van/ Agri, Turkey). 1 (1)F (Paratypus). 1 F.

-Darevskia bendimahiensis **(Schmidtler, Eiselt & Darevsky, 1994)** (parthenogenetic) **3 (0)**
Bendimahi, Muradiye falls, Van (Turkey). 3 F