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Allium dinaricum (*Amaryllidaceae*), a new species of *A.* sect. *Codonoprasum* from the Balkan Peninsula based on morphology and karyology

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Abstract: *Allium dinaricum* (*Amaryllidaceae*), a new species of *A.* sect. *Codonoprasum* from the NW Balkan Peninsula is described and illustrated. It is a late summer flowering geophyte occurring in several localities of Croatia, Bosnia and Herzegovina, Serbia and Montenegro, where it usually grows in rupestrian calcareous stands from the coastal to mountain belts. The morphological traits, karyology ($2n = 2x = 16$), leaf anatomy, seed micromorphology and ecology of the new species are provided. Possible taxonomic relationships with other species occurring mainly in the E Mediterranean are also examined.

Keywords: *Allium*, *Allium dinaricum*, *Allium* sect. *Codonoprasum*, *Amaryllidaceae*, Balkan Peninsula, Balkans, karyology, morphology, new species, taxonomy

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Introduction

The Balkan Peninsula is one of the main biodiversity centres in Europe with remarkable glacial refugium for many plant species (Thompson 2005; Nieto Feliner 2014; Španiel & Rešetnik 2022). The rich endemic flora of the Balkan Peninsula has been a focus of interest for a long time, and some new integrative approaches in plant taxonomy have been used to resolve relationships within intricate groups of closely related species (e.g. Španiel & al. 2017; Skokanová & al. 2019; Caković & Frajman 2020; Caković & al. 2021; Janković & al. 2019; Rešetnik & al. 2023; Terlević & al. 2023). Recently, within systematic floristic explorations of the W Balkan Peninsula, also known as the Dinaric Alps, many new plant species within different genera have been described new to science e.g. *Allium* L. (Bogdanović & al. 2008, 2009; Jandová & al. 2017), *Campanula* L. (Lakušić & al. 2013; Bogdanović & al. 2014a, 2014b, 2015, 2019; Janković & al. 2016; Stevanovski & al. 2024), *Cardamine* L. (Kučera & al. 2010), *Centaurea* L. (Novaković & al. 2018; Bogdanović & al. 2022), *Goniolimon* Boiss. (Buzurović & al. 2020), and *Knautia* L. (Rešetnik & al. 2023).

The genus *Allium* is considered as one of the species richest genera of vascular plants with more than 1000 species (Govaerts & al. 2021). The first comprehensive study of *Allium* in the Balkan Peninsula was made by Stearn (1978, 1981) who reported 56 species. This number increased significantly during last four decades because of taxonomic studies of the Balkan flora in which many new species of *A.* sect. *Codonoprasum* Rchb. were described, mainly from Greece (Zahariadi 1975; Brullo & al. 1992, 1999, 2003, 2010; Tzanoudakis & Kypriotakis 1993, 2008; Brullo & Tzanoudakis 1994; Biel & al. 2006; Bogdanović & al. 2011; Kalpoutzakis & al. 2012, 2019; Galanos & Tzanoudakis 2017, 2019; Tzanoudakis 2000; Trigas & Bareka 2020; Ionnanidis & Tzanoudakis 2022), Croatia (Bogdanović & al. 2008, 2009; Jandová & al. 2017) and the European part of Turkey (Özhatay & al. 2018).

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Within cytotaxonomic studies on the genus *Allium* in the Balkan Peninsula some interesting populations belonging to *A.* sect. *Codonoprasum* occurring in certain countries of the Dinaric Alps (Croatia, Bosnia and Herzegovina, Serbia, and Montenegro) were investigated here. These plants usually grow in crevices of carbonate rocks, where they form dense tufts associated with several other chasmophytes, many of which are endemic. They flower in late summer (August–September) and are characterized by many rigid and slender leaves, few-flowered inflorescences, erect or slightly divaricate and long spathe valves, greenish yellow perigone tinged with purplish brown, stamens included or slightly exserted from the perigone, with white anthers, and ovary cylindric, minutely tuberculate above. Karyologically, all investigated individuals resulted diploid ($2n = 16$) with metacentric chromosomes. Regarding possible taxonomic relationships, these *Allium* populations show some morphological and karyological similarities with some autumnal *Allium* species occurring in the E Mediterranean area, especially with the E Balkan species *A. fuscum* Waldst. & Kit. that inhabits shaded rocky outcrops in SW Romania, NW Bulgaria and NE Serbia (Brullo & al. 1996; Anačkov 2009; Niketić & Tomović 2018; Vojtěchová & al. 2023b), and according to some authors even in Croatia (Nikolić 2020), Bosnia and Herzegovina (Stupar & al. 2021), and Montenegro (Rohlena 1941–1942). Based on several morphological peculiarities and ecological requirements, the populations at issue are treated here as a species new to science, named *A. dinaricum*.

Material and methods

The morphological investigations on *Allium dinaricum* were carried out on living individuals coming from several Balkan localities and on plants cultivated in the Botanical Garden of Catania. Qualitative and quantitative morphological features were measured and scored on fresh material of c. 50 individuals. Comparison with possibly allied taxa was based on direct surveys from both fresh and herbarium material, as well as on literature data (Table 1). For this morphological study, herbarium specimens from various herbaria, including virtual collections, were examined (B, BEO, BEOU, BUNS, CAT, MA, SARA, ZA and ZAGR). The herbarium acronyms follow Thiers (2024+). Examination was made under a Zeiss Stemi SV8 stereomicroscope at 8–64× magnification. For the leaf anatomy leaf blades of maximum size in their optimal vegetative development taken from cultivated plants were used. Leaf cross-sections were fixed in fresh Carnoy solution (3:1 absolute ethanol and glacial acetic acid) and embedded in paraffin; the transverse sections were doubled stained with ruthenium red and light green. Karyological analyses were performed on mitotic plates from root tip cells of cultivated bulbs, pre-treated 3h with a 0.3% (w/v) colchicine water solution at room temperature, fixed 12 h in Carnoy and stored in 70% ethanol. Then, root tips were hydrolysed in 1N chloridic acid for 7 minutes at 60 °C and stained in Schiff reagent. Microphotographs of good quality metaphase plates were taken using a Zeiss Axioskop 2 microscope equipped with a high-resolution digital camera. The somatic chromosome number and karyotype details were studied in 10 spread metaphase plates from different individuals; mean values were used for the karyotype characterization. Metaphase observations and chromosome measures were made using the image analysis systems Zeiss AxioVision 5.1. Karyotyping was conducted using software CromoLab© 1.1 (Brullo 2002), for the identification of homologues, ordering of chromosome pairs, classification of chromosome, and determination of the karyotype formula based on centromere position (Levan & al. 1964; Tzanoudakis 1983). Karyotype symmetry indices followed Paszko (2006) and Peruzzi & Eroğlu (2013). Mean karyomorphometric parameters are given in Table 2. Seed testa micromorphology was performed on mature and dry material from type specimens using a scanning electron microscope (SEM) Zeiss EVO LS10, according to the protocol reported by Stork & al. (1980), while terminology of the seed coat sculpturing follows Barthlott (1981, 1984) and Gontcharova & al. (2009).

Results

Taxonomy of the new species

Allium dinaricum Bogdanović, Anačkov, Ćato, Borovečki-Voska, Salmeri & Brullo, **sp. nov.** – Fig. 1–6.

Holotype: Croatia, Mt Velebit, above Velike Brisnice, in calcareous rocky crevices along mountain path, 44°46'44.26"N, 14°55'55.9"E, c. 800 m, 13 Sep 2023, *S. Bogdanović & V. Lopac s.n.* (ZAGR 78944!; isotypes: B!, BUNS!, CAT!, ZA!, ZAGR!).

– *Allium fuscum* var. *gracile* Anačkov, Takson. Horol. Roda *Allium* Srbiji: 132. 2009, nom. inval., not effectively published (Turland & al. 2018: Art. 30.9 and 32.1(a)).

Diagnosis — *Allium dinaricum* is similar to *A. fuscum* but differs from the latter in having outer bulb tunics slightly fibrous (vs coriaceous), stems often geminate (vs single), leaf cross-section semi-circular (vs flat), leaf blade narrower, with 2 prominent ribs, spathe valves usually shorter and erect (vs longer and divaricate or reflexed), inflorescence few-flowered (vs many-flowered), tepals smaller, outer stamen filaments shorter, annulus shorter, anther apex apiculate (vs rounded), and ovary smaller.

Description — *Bulb* ovoid to ovoid-subglobose, 8–20 × 6–14 mm, sometimes with some bulbils at base of stem; outer *tunics* slightly fibrous, greyish brown, inner ones membranaceous, whitish. *Stem* 15–40 cm tall, cylindric, glabrous, erect, covered by leaf sheaths for 1/3–1/2 of

Table 1. Main distinguishing characters of *Allium dinaricum* and morphologically similar species.

Character	***A. dinaricum***	***A. fuscum***	***A. istanbulense***	***A. rausii***	***A. therinanthum***
Outer bulb coat	fibrous	coriaceous	coriaceous	coriaceous	coriaceous
Stem	single or geminate	single	single	single	single
Leaf sheaths coverage	1/3–1/2	to 2/3	1/2–2/3	1/3–1/2	2/3–3/4
Leaf number	3–5	3–7	3 or 4	5 or 6	4
Leaf blade in section	semi-circular	flat	flat	semi-circular	semi-circular
Leaf blade spongy tissue	compact or slightly fistulous	fistulous	compact	–	widely fistulous
Leaf blade ribs	2	7	7	–	9
Spathe valves directions	erect or slightly divergent	divaricate or reflexed	reflexed or sub-erect	erect	erect or suberect
Longer spathe valve length (cm)	4–16	10–27	10–21	8–16	8–12
Shorter spathe valve length (cm)	2–6	5–18	4–12	5–12	4–8
Longer spathe nerves	7	7–11	7–9	7–9	7
Shorter spathe nerves	5 or 6	6 or 7	5–7	5–7	5
Inflorescence number of flowers	10–30(–45)	14–140(–160)	10–45	up to 70	20–50
Pedicel length (mm)	7–25	10–37	5–30	15–35	10–30(–60)
Tepal colour	greenish yellow	greenish white to yellowish green	pinkish white	greenish yellow	whitish to straw-coloured
Tepal tinged	purplish brown	purplish brown to brown-green	purplish	brown	purplish
Tepal length (mm)	4.5–5.5	5–6.9	4–5	6–7	5–5.5
Tepal width (mm)	2–2.4	2–3	1.5–2.5	2.5–2.7	2–2.2
Outer stamen filament length (mm)	1.5–2.4	2.5–2.8	1.5–2	2.5–2.7	2.2–2.5
Inner stamen filament length (mm)	2–4	3–4.4	2.2–2.5	3.4–3.6	2.8–3.2
Annulus length (mm)	1–1.2	c. 2	0.5–0.6	c. 1.5	1.5–1.6
Anther colour	white to straw-coloured	whitish	yellow	yellow	yellow
Anther size (mm)	c. 1.5 × 0.7	1–1.7 × 0.6–0.9	c. 1 × 0.8	c. 1.3 × 0.8	c. 1.1 × 0.8
Anther apex	apiculate	rounded	rounded	apiculate	rounded
Ovary shape	cylindric	ellipsoid-cylindric	cylindric-obovoid	obovoid-cylindric	subcylindric
Ovary surface	minutely tuberculate above	tuberculate above	tuberculate above	smooth	roughish above
Ovary length (mm)	3–3.5	3.5–5.3	2.5–3	3.5–4.5	4–4.2
Capsule shape	obovoid	subglobose to obovoid	obovoid	subglobose	obovoid
Capsule size (mm)	4–5 × c. 4	4.5–6.2 × 3.6–6	c. 4 × 3.3–3.5	4.5–6 × 4.5–5	4.5–5.5 × 4.5–5

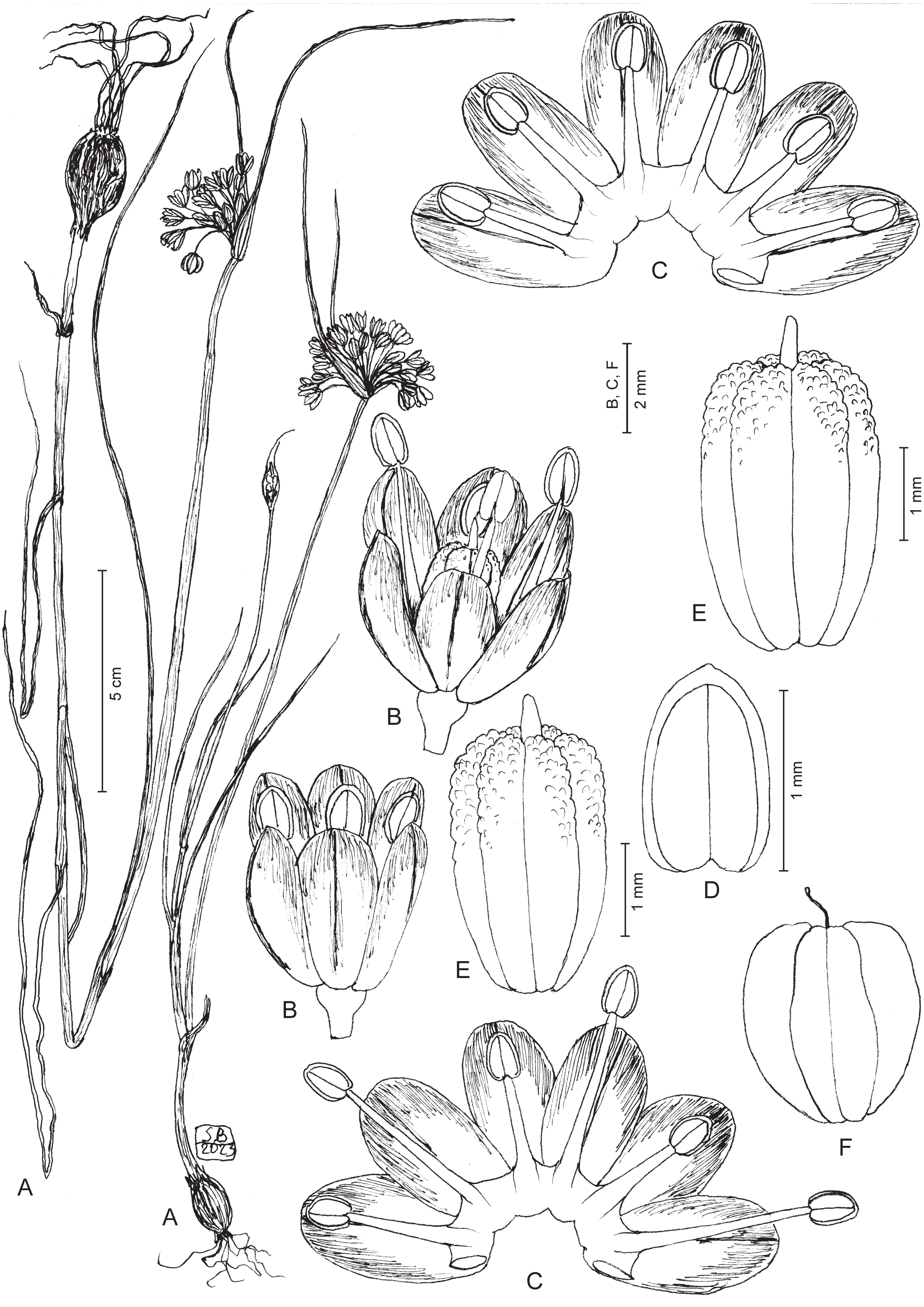

Fig. 1. *Allium dinaricum* – A: habit; B: flowers; C: open perigones with stamens; D: anther; E: ovaries; F: capsule. – A–F from the holotype, *S. Bogdanović s.n.* (ZAGR). – Drawn by S. Brullo.

Table 2. Karyological features of *Allium dinaricum*. Mean values ± standard deviation resulted from 10 good metaphase plates from different individuals from the type locality. Abbreviations: m = metacentric; msm = meta–submetacentric (chromosome nomenclature according to Levan & al. 1964; Tzanoudakis 1983); sat = satellited; TCL = total chromosome length; MCL = mean chromosome length; MAR = mean AR; MCI = mean CI.

Chromosome number	Long arm L (µm)	Short arm S (µm)	Total length CL=L+S (µm)	Relative length RL=CL/TCL (%)	D-value L-S (µm)	Arm ratio AR=L/S	Centromeric index CI=S/CL×100	Type
1	6.75 ± 0.8	4.99 ± 0.7	11.74 ± 1.5	7.41± 0.2	1.76	1.35	42.50	msm
2	6.50 ± 0.7	4.95 ± 0.7	11.45 ± 1.4	7.23 ± 0.1	1.55	1.31	43.23	msm
3	6.04 ± 1.3	5.61 ± 1.0	11.65 ± 2.3	7.33 ± 0.7	0.43	1.08	48.15	m
4	5.78 ± 1.4	5.18 ± 0.9	10.96 ± 2.3	6.88 ± 0.7	0.59	1.11	47.29	m
5	5.73 ± 0.6	4.48 ± 0.5	10.21 ± 1.1	6.46 ± 0.3	1.25	1.28	43.90	m
6	5.54 ± 0.7	4.28 ± 0.5	9.82 ± 1.1	6.22 ± 0.4	1.26	1.29	43.58	m
7	5.78 ± 0.7	4.83 ± 0.7	10.61 ± 1.4	6.70 ± 0.3	0.95	1.20	45.52	m
8	5.53 ± 0.7	4.75 ± 0.5	10.28 ± 1.1	6.50 ± 0.2	0.78	1.17	46.19	m
9	4.93 ± 0.5	4.53 ± 0.3	9.46 ± 0.8	5.99 ± 0.2	0.40	1.09	47.89	m
10	4.86 ± 0.4	4.23 ± 0.2	9.09 ± 0.6	5.77± 0.3	0.63	1.15	46.55	m
11	5.14 ± 0.8	3.87 ± 0.4	9.01 ± 1.2	5.68 ± 0.1	1.27	1.33	42.97	msm
12	4.97 ± 0.9	3.82 ± 0.4	8.79 ± 1.3	5.54 ± 0.2	1.15	1.30	43.44	msm
13	4.62 ± 0.5	4.36 ± 0.4	8.98 ± 0.9	5.68 ± 0.1	0.27	1.06	48.52	m
14	4.54 ± 0.3	4.22 ± 0.4	8.75 ± 0.7	5.55 ± 0.2	0.32	1.08	48.17	m
15	5.09 ± 0.3	3.54 ± 0.6	8.82 ± 0.8	5.59 ± 0.3	1.56	1.44	40.04	msm^{sat}
16	4.86 ± 0.5	3.54 ± 0.6	8.60 ± 0.9	5.45 ± 0.3	1.32	1.37	41.19	msm^{sat}

TCL: 1.58.22 ± 18.4 µm; **MCL**: 9.89 ± 1.1 µm; **MAR**: 1.22; **MCI**: 44.95 ± 2.7; **D-value**: 15.48 µm.
Symmetry indices: **CV_{CL}**: 11.49; **CV_{CI}**: 5.98; **MCA**: 9.87; **Stebbins category**: 1A.

total length, often with 2 stems, one inserted externally to bulb, and second one in centre of leaf sheaths. *Leaves* 3–5, green, glabrous, with blade rigid, semi-cylindric, compact or slightly fistulous, with 2 prominent ribs, 7–25 cm × 1.5–2.5 mm. *Spathe* persistent, with two valves unequal, opposite, erect to slightly divergent at flowering and often divaricate at fruiting, much longer than inflorescence, larger 7-nerved and 4–16 cm long, smaller 5- or 6-nerved and 2–6 cm long. *Inflorescence* lax and hemispherical, 10–30(–45)-flowered; *pedicels* erect or curved, unequal, 7–25 mm long. *Perigone* campanulate, with tepals equal, greenish yellow tinged with purplish brown, elliptic, rounded at apex, 4.5–5.5 × 2–2.4 mm, midrib purplish green. *Stamens* included in perigone or slightly exserted, with simple filament, white or pinkish, unequal, outer ones 1.5–2.4 mm long, inner ones 2–4 mm long, connate below into an annulus 1–1.2 mm high; anthers white to straw-coloured, oblong, c. 1.2 × 0.7 mm, slightly apiculate at apex. *Ovary* cylindric, greenish yellow, minutely tuberculate above, 3–3.5 × 1.7–2 mm; style white, 0.7–2.2 mm long. *Capsule* 3-valved, obovoid, green 4–5 × c. 4 mm.

Phenology — The flowering period of *Allium dinaricum* starts in late July and extends until mid-October, while fruiting is completed in October and November.

Distribution and ecology — Based on field surveys and herbarium investigation, *Allium dinaricum* is distributed across several Balkan countries: Croatia, Bosnia and Herzegovina, Serbia and Montenegro (Fig. 2). It usually grows in rupestrian habitats, primarily on carbonate substrates, occasionally on siliceous and serpentinites rocks. Usually, this species inhabits shaded rock crevices within woodlands, especially in coastal and hilly regions, and also on sunny rocky outcrops in mountainous areas up to an elevation of 1400 m (Fig. 3A, C). In Croatia, *A. dinaricum* is accompanied by many other chasmophytes, many of which are often endemic, such as *Allium horvatii* Lovrić, *Asperula scutellaris* Vis., *Astragalus muelleri* Steud. & Hochst., *Campanula fenestrellata* subsp. *istriaca* (Feer) Damboldt, *Campanula pyramidalis* L., *Centaurea dalmatica* A. Kern., *Centaurea spinosociliata* Seenus, *Inula verbascifolia* Poir., *Iris illyrica* Tomm. ex Vis., *Micromeria croatica* Schott, *Satureja subspicata* Bartl. ex Vis., *Seseli tomentosum* Vis. and *Sesleria juncifolia* Suffren. In Serbia and Montenegro, *A. dinaricum* grows together with other endemics, among them *Allium serbicum* Vis. & Pančić, *Bupleurum karglii* Vis., *Campanula secundiflora* Vis. & Pančić, *Centaurea derventana* Vis. & Pančić, *Euphorbia spinosa* subsp. *glabriflora* (Vis.) Frajman, *Linaria rubioides* Vis. & Pančić, *Ramonda serbica* Pančić, *Reichardia macrophylla* Vis. & Pančić,

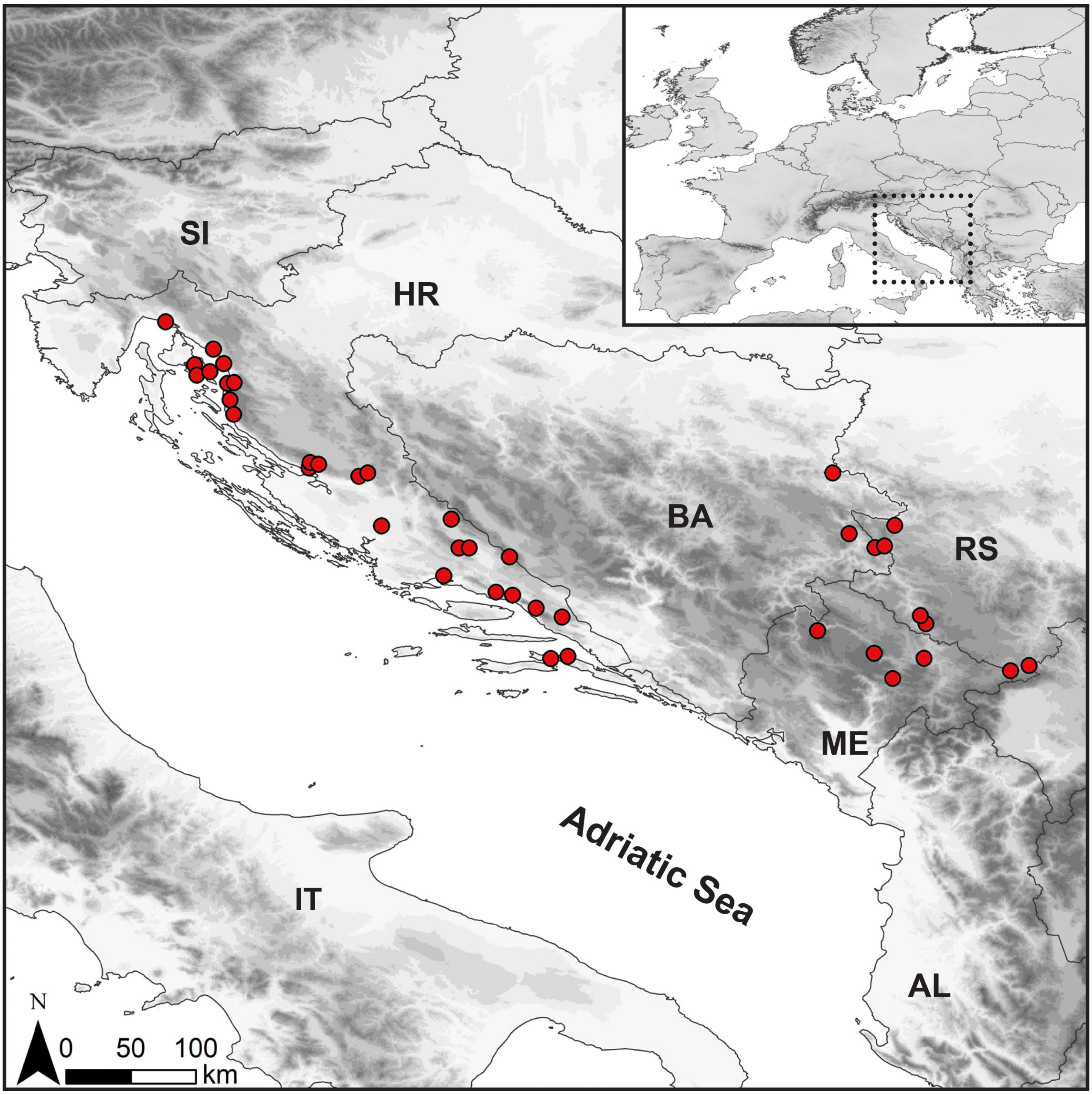

Fig. 2. Distribution map of *Allium dinaricum* (red dots) in the Balkan Peninsula. – AL = Albania; BA = Bosnia and Herzegovina; HR = Croatia; IT = Italy; ME = Montenegro; RS = Serbia; SI = Slovenia.

Silene serbica Adam. & Vierh. and *Stachys anisochila* Vis. & Pančić. Overall, *A. dinaricum* is ecologically well differentiated from the other species within *A.* sect. *Codonoprasum*, especially those with autumnal flowering pattern. *Allium dinaricum* is an obligate chasmophyte, growing almost exclusively on rock faces, whereas the other taxa usually grow in meadows, shrublands, underwood and in salt marshes.

Etymology — The specific epithet refers to the Dinaric Alps, where the new species is distributed.

Leaf anatomy — The leaf cross-section of *Allium dinaricum* exhibits a semi-circular outline, characterized by two prominent ribs in the abaxial surface. The epidermis consists of small cells covered by a thin cuticle, with numerous stomata distributed along the whole leaf surface. The palisade tissue is regular and compact, forming a single external layer with larger cells, while a second layer with smaller cells is present only in the adaxial surface. The spongy tissue is compact in the peripheral part and/or slightly fistulous, constituted by small cells, while it is rather lax in the central part, therefore the mesophyll appears slightly fistulous. Many secretor canals occur beneath the palisade tissue. The vascular bundles are 16 (in the largest leaves), consisting of 13 variable-sized bundles in the adaxial surface, with only 3 small-sized bundles in the abaxial surface (Fig. 4).

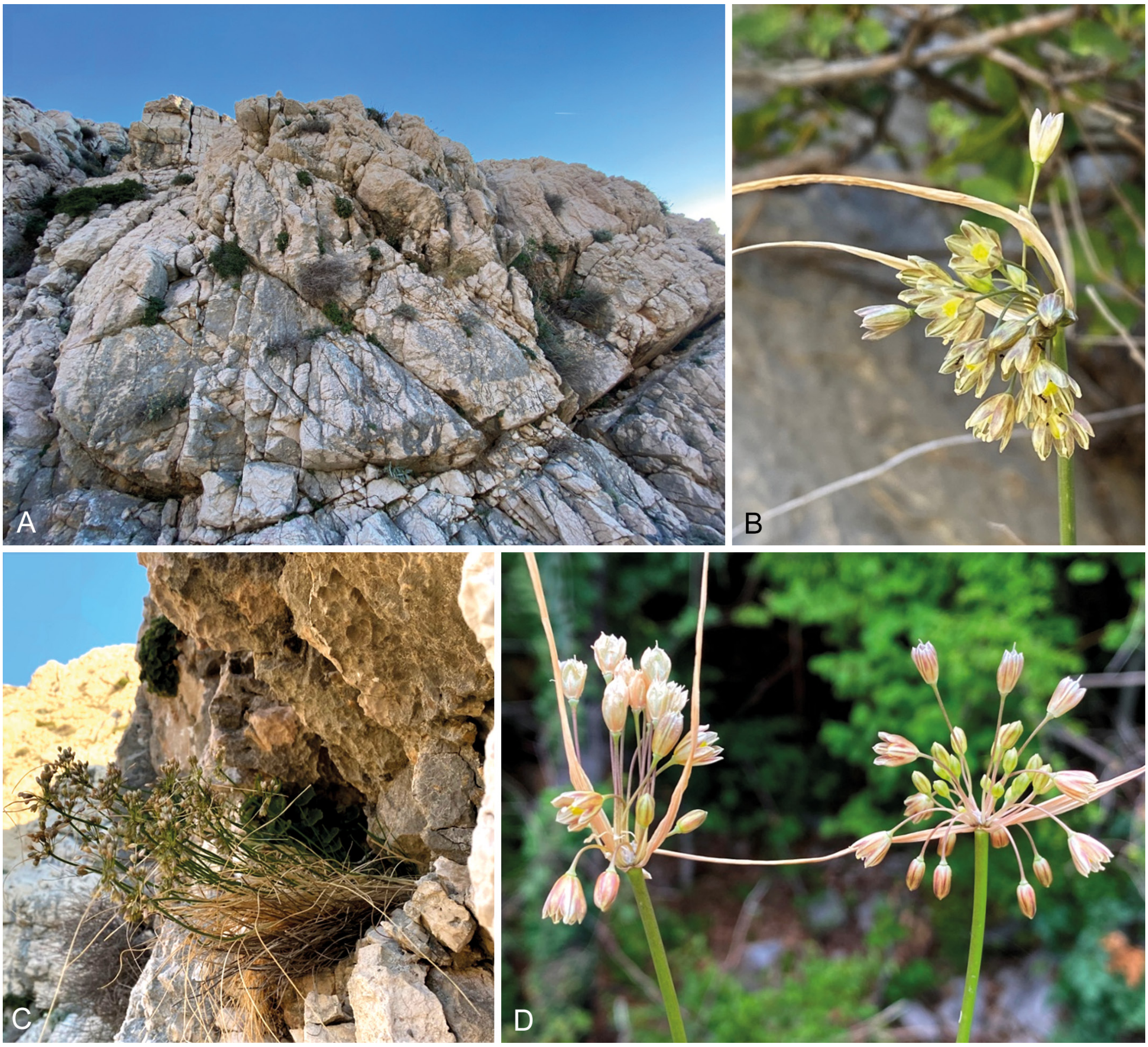

Fig. 3. *Allium dinaricum* – A: rupestrian growth habitat; B, D: inflorescences; C: habit. – A–D: Krk Island, Surbova, 9 Sep 2023, photographs by S. Bogdanović.

Seed morphology and microsculpturing — According to the literature data (Fritsch & al. 2006; Neshati & Fritsch 2009; Celep & al. 2012; Salmeri & al. 2016; Lin & Tan 2017), the microsculpturing of the seed testa in *Allium* is a conservative and stable character, which provides relevant information regarding the taxonomic treatment of this genus. The seeds of *A. dinaricum* are semi-ovoid in outline (3.8–4 × 2–2.1 mm), with a weakly rugose surface (Fig. 5A, B). Observations under SEM at high magnification (500× and 1000×) show irregularly polygonate testa cells, 28–65 µm in diam. (Fig. 5C–F). The anticlinal walls appear flat, straight to curved, and are covered by raised strap-like sculptures forming a widened intercellular region. The anticlinal walls of the seedbed are characterized by a long connection in the form of the Ω-S connection model according to Fritsch & al. (2006). A similar form of undulation is also present in *A. fuscum* and other possibly related species (Anačkov 2009). The periclinal walls are slightly raised, with several granulose verrucae; the central is larger, accompanied by smaller and irregularly shaped verrucae distributed along the cell edges. These micromorphological seed ornamentations closely resemble those observed in other species of *A.* sect. *Codonoprasum* (Češmedžiev & Terzijski 1997; Neshati & Fritsch 2009; Celep & al. 2012; Brullo & al. 2013; Salmeri & al. 2016; Özhatay & al. 2018).

Karyology — *Allium dinaricum* has a diploid chromosome complement with $2n = 16$ (Fig. 6A). The karyotype (Fig. 6B) is regular, composed mainly of metacentric (m) chromosomes, with only three pairs slightly asymmetric and belonging to the meta–submetacentric (msm) type (Tzanoudakis 1983). One msm chromosome pair is microsatellited on the short arm. The karyotype formula can be resumed as $2n = 2x = 16$: 10 m + 4 msm + 2 msm^{sat}. Absolute chromosome length ranges from 11.7 ±

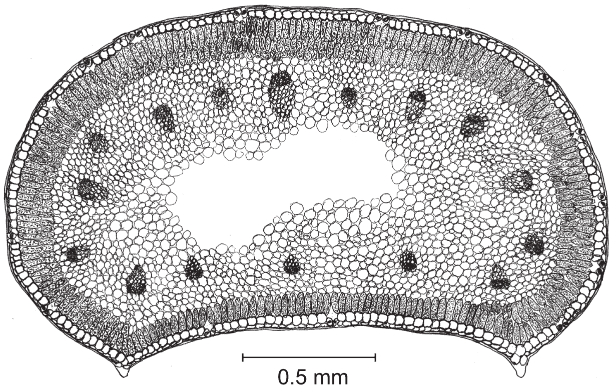

Fig. 4. Leaf cross-section of *Allium dinaricum* from the type locality, *S. Bogdanović & D. Lopac s.n.* (ZAGR 78944). – Drawn by S. Brullo.

1.5 µm for the longest chromosome to 8.6 ± 1 µm for the shortest, while the relative length varies from 7.4 ± 0.2 % to 5.45 ± 0.3%. Chromosome measures and symmetry indices (Table 2) indicate a high degree of homogeneity and symmetry of the *A. dinaricum* karyotype.

Discussion

According to Brullo & al. (1997a), several late-flowering species of *Allium* sect. *Codonoprasum* have been described mainly over the last decades, and are widely distributed throughout the Mediterranean basin, with higher concentration in the eastern part. All W Mediterranean species are tetraploids ($2n = 4x = 32$), usually localized in damp soils of salt marshes or ponds, such as *A. savii* Parl. (Balearic Islands, France, Corsica, Sardinia and N Italy), and *A. telmatum* Bogdanović & al. (Croatia), or in shaded rocks, such as *A. oporinanthum* Brullo & al. (SE Spain and S France), or in undergrowth, such as *A. anzalonei* Brullo & al. (C Italy) (Brullo & al. 1997a, 1997b, 1997c; Bogdanović & al. 2009). The E Mediterranean species are more numerous and predominantly diploid ($2n = 2x = 16$) (Burtt & Davis 1949; Rechinger 1961; Zahariadi 1975; Kollmann & al. 1991; Tzanoudakis & Kypriotakis 1993; Brullo & al. 1999, 2003, 2008, 2010, 2014; Tzanoudakis 2000; Kalpoutzakis & al. 2012, 2019; Galanos 2016; Galanos & Tzanoudakis 2017, 2019; Özhatay & al. 2018; Trigas & Bareka 2020). Among them the following species can be mentioned: *A. autumnale* P. H. Davis (Cyprus), *A. tardans* Greuter & Zahar. (Greece: Kriti and Karpathos islands), *A. rausii* Brullo & al. (Greece: Thessalia), *A. platakisii* Tzanoud. & Kypr. (Greece: Pondikonisi islet), *A. euboicum* Rech. f. (Greece: Evvia island), *A. aegilicum* Tzanoud. (Greece: Antikythira island), *A. archeotrichon* Brullo & al. (Greece: Rodos, Tilos and Symi islands), *A. tardiflorum* Kollmann & Shmida and *A. therinanthum* Brullo & al. (Israel), *A. brussalisii* Tzanoud. & Kypr. (Greece: Sterea Ellas and Peloponnisos), *A. makrianum* Brullo & al. (Greece: Chios island), *A. orestis* Kalpoutz. & al. (Greece: S Peloponnisos), *A. stamatiadae* Trigas & Bareka (Greece: Andros island), *A. panormitisi* Galanos & Tzanoud. and *A. symiacum* Galanos & Tzanoud. (Greece: Symi island) and *A. istanbulense* Özhatay & al. (European Turkey). Based on investigations conducted by Brullo & al. (2003), Biel & al. (2006), Ionnanidis & Tzanoudakis (2022) and Vojtěchová & al. (2023a, 2023b), among these E Mediterranean species there are also two tetraploids ($2n = 4x = 32$), i.e. *A. apolloniense* Biel & al. (Greece: Sifnos island) and *A. dirphianum* Brullo & al. (Greece: Evvia island), and two triploids ($2n = 3x = 24$), i.e. *A. phitosianum* Brullo & al. (C Greece) and *A. goumenissanum* Ionnanidis & Tzanoud. (Bulgaria and N Greece).

Based on literature data (Rohlena 1941–1942; Niketić & Tomović 2018; Nikolić 2020; Stupar & al. 2021) and herbarium investigations, it has been revealed that in the past, populations of *Allium dinaricum* from Croatia, Bosnia and Herzegovina, Montenegro, and from W Serbia were erroneously identified mainly as *A. fuscum* Waldst. & Kit., due to their shared rupestrian habitat and similarities in the gross morphology of the inflorescence and perigone. During taxonomic and chorological investigation of the genus *Allium* in the Serbian flora, Anačkov (2009: 132) noticed some specific morphological characters regarding plant habit and inflorescence in W Serbian populations of *A. fuscum*, and consequently he attributed them to "*A. fuscum* var. *gracile*". According to Brullo & al. (1996) and Vojtěchová & al. (2023b), *A. fuscum* is yet well differentiated from *A. dinaricum* in several features, including the leaf sheaths covering the scape up to 2/3 of its length, leaves flat, (1.7–)2.4–5.7(–7.5) mm wide, inflorescence with more numerous flowers, spathe valves reflexed at anthesis, longer and with more numerous nerves, perigone larger, stamen filaments fused into an annulus c. 2 mm long, anthers larger and rounded at the apex, ovary larger, oblong-obovate, and capsule much bigger (Table 1). From a morphological point of view, *A. dinaricum* shows greater similarities with some diploid species having a summer-autumn cycle occurring in the E Mediterranean, which are characterized at the flowering by more or less erect spathe valves, narrow semi-cylindric glabrous leaves, lax inflorescences and perigone greenish yellow suffused with purplish brown. Among these taxa, *A. istanbulense*, *A. rausii* and *A. therinanthum* are those that show closest similarity with *A. dinaricum* (see Table 1). In particular, *A. istanbulense* is very similar to *A. dinaricum* but differs in having outer bulb tunic coriaceous, stem solitary, covered by leaves sheaths for 1/3–2/3 of its length, leaf blade 1–1.5 mm wide, with 7 prominent scabrous ribs, spathe valves usually reflexed (rarely suberect) and longer, tepals pinkish white, tinged with purplish, the outer ones narrower, annulus shorter, anthers yellow, smaller, and rounded at the apex, ovary cylindric-obovoid, shorter, and capsule smaller. Besides, *A. istanbulense* is a terri-

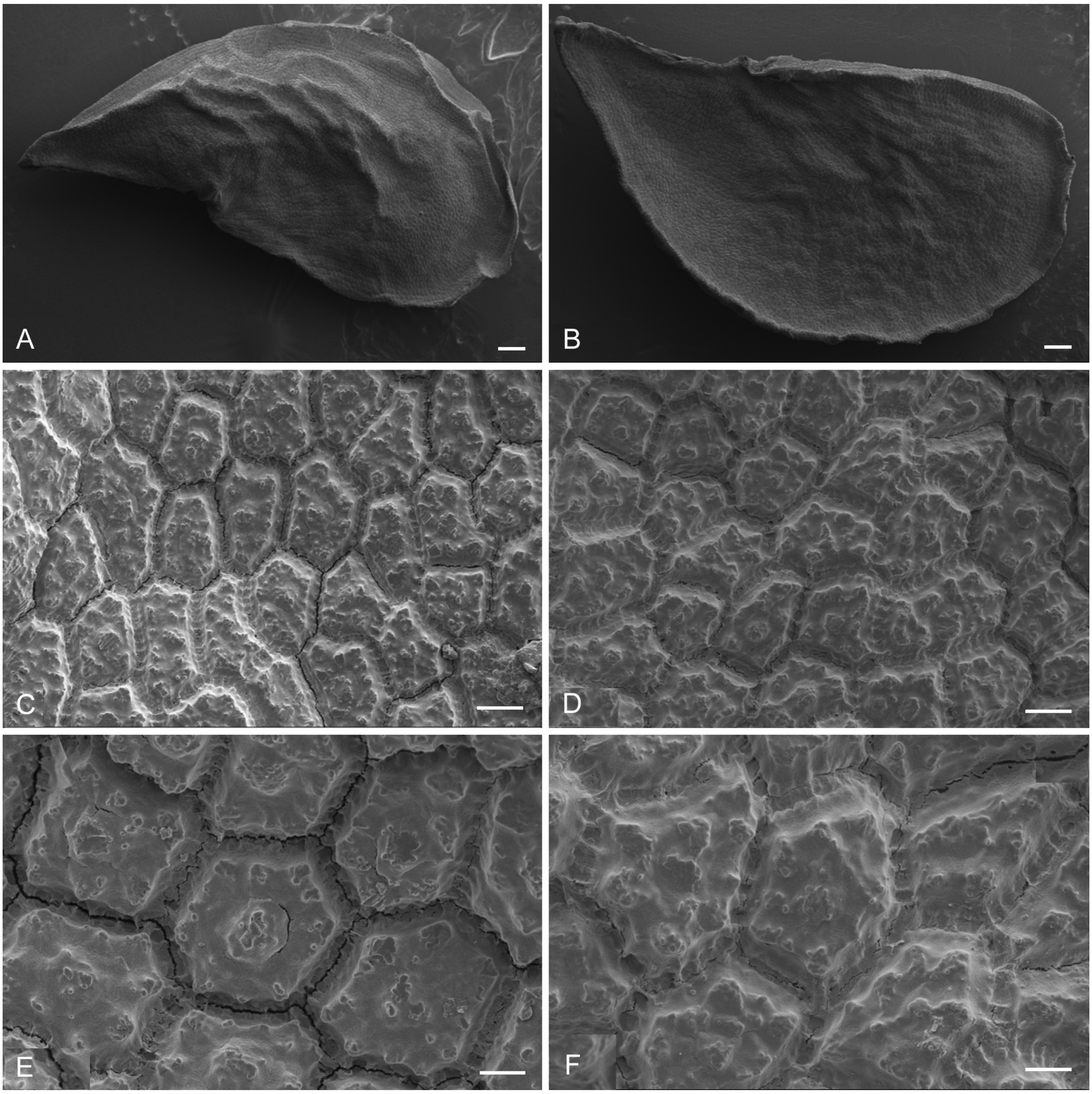

Fig. 5. SEM micrographs of seed coat of *Allium dinaricum*. – A: seed, dorsal face; B: seed, ventral face; C, E: central part of dorsal face; D, F: central part of ventral face. – A–F from the type locality, *S. Bogdanović & D. Lopac s.n.* (ZAGR 78944). – Scale bars: A, B = 200 µm; C, D = 20 µm; E, F = 10 µm.

colous species linked to woodland shady places (Özhatay & al. 2018). As far as *A. rausii* concerns, it also seems quite similar to *A. dinaricum* from which differs in some significant characters such as outer bulb tunics coriaceous, inflorescences with more flowers, tepals longer (6–7 mm), annulus longer (c. 1.5 mm), anthers yellow, ovary longer (3.5–4.5 mm), obovoid-cylindric, smooth, capsule subglobose, narrowed at the base, larger (4.5–6 × 4.5–5.5 mm). In addition, *A. rausii* is well differentiated also for its ecology being a nemoral species occurring on siliceous substrata of deciduous forests (Brullo & al. 2003). Finally, *A. therinanthum* also shows some similarity with *A. dinaricum* but differs in having outer bulb tunic coriaceous, stem covered by leaf sheaths for 2/3–3/4 of its length, leaf blade widely fistulous with several prominent ribs, pedicels longer (to 60 mm), tepals whitish to straw coloured, tinged with purplish, annulus higher (1.5–1.6 mm), anthers yellow, rounded at the apex, ovary longer (4–4.2 mm), roughish above, capsule bigger (4.5–5.5 mm). For its ecological requirements *A. therinanthum* is well distinct from *A. dinaricum*, because it is an orophyte growing at 1500–1700 m of elevation, mainly in underwood of oak forest (Brullo & al. 2014).

Additional specimens examined — ***Allium dinaricum*** — Bosnia and Herzegovina: Dobrun, 43°45'34.63"N,

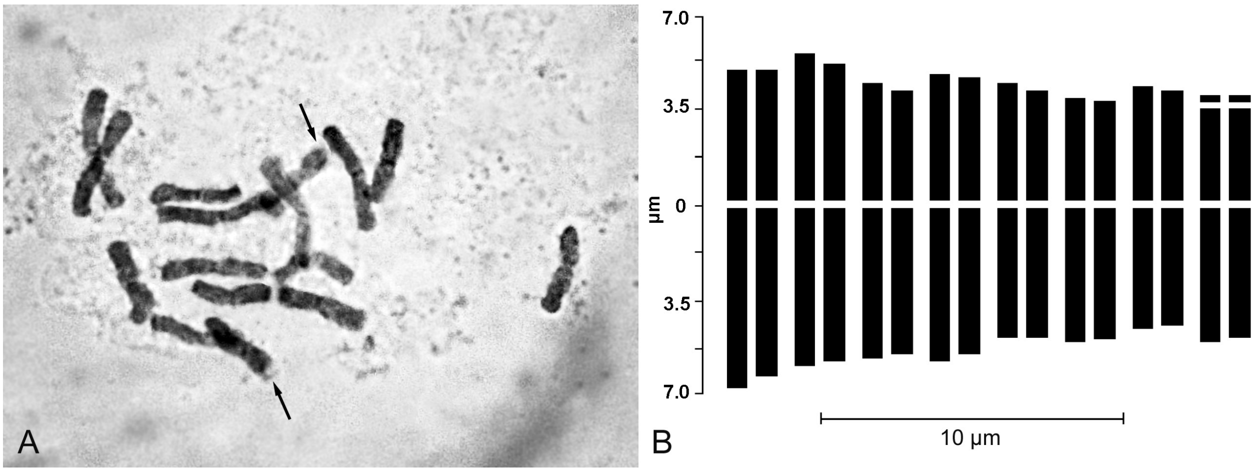

Fig. 6. Chromosome complement (2*n* = 16) of *Allium dinaricum*. – A: mitotic metaphase plate from the type locality, *S. Bogdanović & D. Lopac s.n.* (ZAGR 78944), arrows indicate satellites; B: idiogram.

19°23'53.52"E, 664 m, vertical rocks, 7 Aug 2022, *S. Bogdanović s.n.* (CAT!, ZAGR!); E Bosnia, Vlasenica, Jadar Gorge, limestone rocks, in oak forest, 31 Jul 2022, *G. Anačkov s.n.* (BUNS!); Dobrun (Razdolina), 9 Sep 1949, *Ž. Bjelčić & K. Malý s.n.* (SARA!); In valle Drina prope Milošević-Stari brod, c. 300 m, 18 Sep 1918, *K. Malý s.n.* (SARA!). — Croatia: Velebit, Volarice, rocks along road, 19 Sep 2023, *S. Bogdanović s.n.* (CAT!, ZAGR!); Velebit, above Velike Brisnice, in rocks along mountain path, 13 Sep 2023, *S. Bogdanović s.n.* (CAT!, ZAGR!); Velebit, Biljevine, rocks along road, 27 Jul 2023, *S. Bogdanović s.n.* (CAT!, ZAGR!); Gulf of Kvarner, Bunica, vertical rocks along road, 27 Jul 2023, *S. Bogdanović s.n.* (CAT!, ZAGR!); Dalmatinska Zagora, Zadvarje, 43°25'50.26"N, 16°53'18.65"E, kamenita mjesta u šumi, 28 Jul 2021, *S. Bogdanović s.n.* (ZAGR!); Velebit, Crnopac, c. 1100 m alt., in rocky fissures, 21 Jul 2020, *S. Bogdanović & M. Doboš s.n.* (CAT!, ZAGR!); Mt Svilaja, in rocks near mountain lodge, 28 Jul 2020, *S. Bogdanović & I. Budinski s.n.* (CAT!, ZAGR!); Gulf of Kvarner, island of Krk, Bunculuka, among rocks in *Pinus halepensis* forest, 9 Sep 2023, *S. Bogdanović, Lj. Borovečki-Voska & B. Horvatić s.n.* (CAT!, ZAGR!); Gulf of Kvarner, island of Krk, Vrženica torrent, in rocky crevices, 9 Sep 2023, *S. Bogdanović, Lj. Borovečki-Voska & B. Horvatić s.n.* (CAT!, ZAGR!); Gulf of Kvarner, island of Krk, Surbova torrent, in rocky crevices, 9 Sep 2023, *S. Bogdanović, Lj. Borovečki-Voska & B. Horvatić s.n.* (CAT!, ZAGR!); Gulf of Kvarner, island of Krk, Bay Zala, in rocky crevices near sea, 9 Sep 2023, *S. Bogdanović, Lj. Borovečki-Voska & B. Horvatić s.n.* (CAT!, ZAGR!); Gulf of Kvarner, island of Krk, Vela rika, near waterfall Curak, rocky places in shrubland, 9 Sep 2023, *S. Bogdanović, Lj. Borovečki-Voska & B. Horvatić s.n.* (CAT!, ZAGR!); Gulf of Kvarner, island of Krk, Bunculuka, in *Pinus halepensis* forest, in cult., 15 Dec 2022, *S. Brullo s.n.* (CAT!); Roški slap, in cult., 28 Jul 2022, *S. Brullo s.n.* (CAT!); Roški slap, in cult., 31 Aug 2022, *S. Brullo s.n.* (CAT!); Velebit, Crnopac, in cult., 12 Sep 2023, *S. Brullo s.n.* (CAT!); Velebit, Crnopac, in cult., 15 Jul 2021, *S. Brullo s.n.* (CAT!); In monte Crnopac, 31 Jul 1896, *Lj. Rossi 11.991* (ZA 17871!); Velebit, in monte Zagaljen supra Gračac, 1 Aug 1911, *Lj. Rossi 27.307* (ZA 17873!); Klobučina iznad Krasice, ljuti krš i sastojina sa *Sesleria tenuifolia*, 20 Aug 1983, *M. Randić s.n.* (ZA 17874!); na točilu i stijenovitom grebenu područja Solina – Martinšćica – Rijeka, 7 Sep 1983, *M. Randić s.n.* (ZA 17876!); Dalm., Mte Bikovio bei Macarsca, steinige Orte, 12 Jul 1880, *Th. Pichler s.n.* (B!); Jugoslawien, Velebit, Karlobag, Susanj gegen Ravni Dabar bei Ostarije, 4 Aug 1982, *O. Angerer s.n.* (MA 350434!). — Montenegro: Gornja Dobrilovina, in Tara canyon, on vertical rocks along road, 4 Aug 2022, *S. Bogdanović & D. Caković s.n.* (CAT!, ZAGR!); Sušica canyon, scree along road, 8 Aug 2022, *S. Bogdanović & D. Caković s.n.* (CAT!, ZAGR!); Kolašin, Bakovića klisura, 42.857639°N, 19.522708°E, 910 m, limestone rocks, roadside, in bushes, 4 Aug 2021, *G. Anačkov s.n.* (BUNS!); Bijelo Polje, Kruševo, 42.997044°N, 19.739453°E, 664 m, limestone rocks, roadside, 31 Jul 2022, *G. Anačkov s.n.* (BUNS!). — Serbia: W Serbia, Tara, in saxosis in fauce in Derventa, Jul 1912, *T. Soška s.n.* (BEOU!); N of Potkrš, in Lim canyon, 43°17'24"N, 19°42'49.84"E, on vertical rocks along road, 7 Aug 2022, *S. Bogdanović s.n.* (CAT!, ZAGR!); Tara Mt., Vidikovac, 43.912961°N, 19.535167°E, 918 m, in Fagetum sylvae, steep isolated rocks, 4 Aug 2005, *G. Anačkov s.n.* (BUNS!); Zlatibor Mt Platou, serpentinite rock, 2001, *B. Zlatković & G. Anačkov s.n.* (BUNS!); Zlatibor Mt, Tornik, serpentinite rock, 2001, *B. Zlatković & G. Anačkov s.n.* (BUNS!); Zlatibor Mt, Platou near Ribnica, 1088 m, meadow on a rock field, 28 Jul 2005, *G. Anačkov & L. Barsi s.n.* (BUNS!); Tara Mt., Vidikovac, 43.912961°N, 19.535167°E, 918 m, in *Fagetum sylvae*, steep isolated rocks, 4 Aug 2005, *G. Anačkov s.n.* (BUNS!); Tara Kremna village, 43.5055°N, 19.3403°E, 765 m, near, grassy rockery, 10 Aug 2006, *G. Anačkov s.n.* (BUNS!); Tara Mt., Vidikovac, 43.912961°N, 19.535167°E, 918 m, in *Fagetum sylvae*, steep isolated rocks, 10 Aug 2006, *G. Anačkov s.n.* (BUNS!); Mokra Gora Mt., Kotroman, Beli Rzav Gorge, 43°46'24.2"N, 19°27'47.5"E, 513 m, limestone rocks, thermophilic habitats, 10 Aug 2006, *G. Anačkov & B. Božin s.n.* (BUNS!); Mokra Gora Mt., Kotroman, Beli Rzav Gorge, 513 m, limestone rocks, thermophilic habitats, 27 Jul 2011, *G. Anačkov s.n.* (BUNS!); Tara Mt., Vidikovac, 43.912961°N, 19.535167°E, 910 m, in *Fagetum sylvae*, steep isolated rocks, 5 Aug 2015, *G. Anačkov s.n.* (BUNS!); Novi Pazar, Ribarići (Mehov krš), 42.910307°N, 20.338824°E, 894 m, rocks, 2 Aug 2018, *G. Anačkov s.n.* (BUNS!); Novi Pazar, Ribarići (Crna Reka Monastery), 42.946235°N, 20.467464°E, 1010 m, rocks, 2 Aug 2018, *G. Anačkov s.n.* (BUNS!); Južna Srbija, Ozren (Sjenica), 43.2344389°N, 19.7513905°E, klisura Mrčkovske reke, 30 Jul 2020, *M. Niketić & G. Tomović s.n.* (BEO!).

Allium fuscum — Romania: Rupi ombreggiate di Baile Herculane, 29 Jul 1993, *S. Brullo & F. Scelsi s.n.* (CAT!); Rupi presso Petrosani, 29 Jul 1993, *S. Brullo & F. Scelsi s.n.* (CAT!); Rupi Mt. Mehedinji (Baile Herculane), 29 Jul 1993, *S. Brullo & F. Scelsi s.n.* (CAT!). — Serbia: E Serbia, Montagna di Rtanj, sulle pareti rocciose ombreggiate, 19 Jul 2019, *S. Bogdanović s.n.* (CAT!, ZAGR!); E Serbia, Niš, Seličevica Mt. Kurvingrad, 248 m, termophilic shrub, 17 Aug 2006, *G. Anačkov s.n.* (BUNS!); Niš, Suva planina Mt. Gornja Studena village, 399 m, oak forest, Permian sandstones, 30 Nov 2008, *B. Zlatković & G. Anačkov s.n.* (BUNS!); Niš, Suva planina, Kosmovac, 449 m, 17 Aug 2008, *G. Anačkov s.n.* (BUNS!); W Serbia, Mokra gora, Vigor, 889 m, limestone, s.d., *B. Zlatković s.n.* (BUNS!).

Allium istanbulense — Turkey: European Turkey, Arnavutköy, Terkos (Durusu) Lake, NW end of sea shore among *Quercus* shrubs 27 m, 18 Mar 2017, *S. Brullo, N. Özhatay & E. Özhatay s.n.* (CAT!); A2(A) Istanbul, Princes' Islands, 11 Sep 1986, *S. Brullo s.n.* (CAT!); A2 (E) Istanbul Arnavutköy, Terkos (Durusu) Lake, NW end of sea shore among *Quercus* shrubs 20–30 m, 12 Aug 2017, *N. Özhatay, E. Özhatay & M. Keskin (7654) Ist. Bio 3068* (CAT!).

Allium rausii — Greece: Polidendri, presso Larissa, nel sottobosco di querceti decidui, 30 Aug 1989, *S. Brullo s.n.* (CAT!).

Author contributions

S.Bo. and S.Br. described the new species, elaborated the possible taxonomic relationships and arranged the manuscript. S.Bo., G.A., S.Ć. and Lj.B.-V. performed field and herbarium investigation, C.S. performed karyological analyses. All authors contributed to the text and approved the final version of the manuscript.

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