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Taxonomic review of *Scrophularia* sect. *Tomiohyllum* in Bulgaria and Serbia: the case of *Scrophularia bulgarica*

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Abstract: The taxonomic treatment and geographical distribution of *Scrophularia bulgarica* (\equiv *S. variegata* var. *bulgarica*, *Scrophulariaceae*), a rare and enigmatic taxon in the Bulgarian flora, and application of its name have been revisited. A revised species description and comparison with its closest and nomenclaturally related taxa, *S. rupestris* and *S. heterophylla* subsp. *laciniata*, are given. For the last three decades in the Bulgarian flora, *S. heterophylla* subsp. *laciniata* has been considered within the circumscription of *S. bulgarica* and therefore its presence in Bulgaria was neglected. On the other hand, *S. bulgarica* is newly reported for Serbia, hitherto erroneously identified as *S. laciniata*.

Keywords: Balkan flora, new record, nomenclature, relict species, *Scrophularia*, *Scrophularia bulgarica*, *Scrophularia* sect. *Tomiohyllum*, taxonomic redefinition

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Introduction

Scrophularia sect. *Tomiohyllum* Benth. (*Scrophulariaceae*) was first proposed by Bentham (1846), who divided the genus into three sections: *S. sect. Scorodonia* G. Don, *S. sect. Venilia* G. Don and *S. sect. Tomiohyllum*. To the last section he assigned suffrutescent or herbaceous perennials with ligneous roots, stems branched from the base, non-anastomosing fork-veined leaves and rigid inflorescences. Carlbom (1969) considered *S. sect. Tomiohyllum* as “primitive” due to the xerophilous, subshrubby habit of its representatives and the general lack of polyploidy. In the only comprehensive taxonomic revision of the genus, Stiefel (1910) accepted only two sections: Bentham’s *S. sect. Tomiohyllum* and the new *S. sect. Anastomosantes* Stiefel. He characterized *S. sect. Tomiohyllum* as having species without anastomosing leaf venation and *S. sect. Anastomosantes* with anastomosing venation on the dorsal side. In the present study,

we revealed some more characters for distinguishing the two sections: the representatives of *S. sect. Tomiohyllum* basically have numerous stems and a cuneate to truncate leaf base, while those of *S. sect. Anastomosantes* are with single to few stems and a cordate to rounded leaf base.

According to Scheunert & Heubl (2017), the ancestral range of *Scrophularia* contains an area of SW Asia and Turkey, which corresponds to its present-day primary centre of diversity. Their molecular study concluded that the genus originated around the Oligocene–Miocene boundary (c. 23 million years ago, “mya”), and diversification of major lineages started in the Miocene, within the last c. 15 million years. With regard to *S. sect. Tomiohyllum*, they hypothesized that changes in aridity in its ancestral region during the second half of the Miocene and later (Ballato & al. 2010) had an influence on its divergence (which started c. 8 mya). They indicated two migration routes of *Scrophularia* from the primary centre to Europe: northward through the Caucasus to the NE Black Sea area

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and westward through the mountains of Asia Minor to the Balkans and W Mediterranean. Phylogenetic relationships in the genus revealed that *S.* sect. *Tomiophyllum* is a stable group and is supported as a distinct clade nested within clades of taxa of *S.* sect. *Anastomosantes* (Scheunert & Heubl 2017). Within the group, however, there are still taxa with unclear and confused circumscriptions. One of them is the case of *S. bulgarica* (Stoj.) Peev.

Historical background of the treated taxa

In his *Flora Principatus Serbiae*, Pančić (1874) reported three species from *Scrophularia* sect. *Tomiophyllum*: *S. canina* L., *S. hoppii* W. D. J. Koch and *S. laciniata* Waldst. & Kit. Later Hayek (1931) added to the Serbian flora one more species of that section, *S. variegata* M. Bieb., without a specific record. According to Richardson (1972), the latter is subsequently treated as a misapplied name for *S. heterophylla* subsp. *laciniata* (Waldst. & Kit.) Maire & Petitm. Nevertheless, according to Nikolić (1974), *S.* sect. *Tomiophyllum* is represented in Serbia with the same four abovementioned taxa, with the difference that *S. hoppii* is considered a synonym of *S. juratensis* Schleich. ex Wydler. He indicated *S. variegata* only for the Suva Planina. Most recently, this species is mentioned as an endemic Moesian floral element for the Suva Planina (Randelović & al. 2000). After that, *S. variegata* was not treated in floristic works for Serbia.

According to Velenovský (1891), *Scrophularia* sect. *Tomiophyllum* is represented by two taxa: *S. canina* and *S. variegata* var. *rupestris* (M. Bieb. ex Willd.) Boiss. The identity and circumscription of the latter has varied in time and hitherto remained uncertain. Initially, Neichev (1909) reported it as *S. rupestris* M. Bieb. ex Willd. from the C Stara Planina: Koru Dere (nowadays Sokolna reserve). Later, Stojanov & Stefanov (1925) accepted *S. rupestris* and applied that name in a wider sense, including the populations in the mountains of S Bulgaria. Soon afterward, Stojanov (1926) inferred that the typical *S. rupestris* from Crimea is not present in the Bulgarian flora and he described two new taxa, *S. variegata* var. *bulgarica* Stoj., referring to populations in the C Stara Planina, and *S. laciniata* var. *macedonica* Stoj., referring to populations in the Pirin mountains and C Rhodope mountains. Subsequently, Hayek (1931) accepted Stojanov's first taxon, while he placed the second one in the synonymy of *S. heterophylla* subsp. *laciniata*. Nevertheless, the taxonomic treatment of both taxa described by Stojanov and their geographical delimitation were stably maintained in the next three editions of *Flora bulgarica* (Stojanov & Stefanov 1933, 1948; Stojanov & al. 1967). The major changes of taxonomic treatment took place in *Flora europaea* (Richardson 1972), in which *S. variegata* var. *bulgarica* and *S. laciniata* var. *macedonica* were not present and instead these only *S. heterophylla* subsp. *laciniata* was accepted. The last taxonomic decision was adopted in the Bulgarian flora by Kožuharov (1992), who

accepted in a wider sense *S. heterophylla* subsp. *laciniata*, neglecting *S. variegata* var. *bulgarica*. Finally, in *Flora Reipublicae bulgaricae*, Peev (1995) introduced a new combination, *S. bulgarica* (Stoj.) Peev, thereby restoring the recently neglected *S. variegata* var. *bulgarica*, but he produced a new confusion. Contrary to Kožuharov, Peev considered his *S. bulgarica* in a wider sense and included in its circumscription *S. heterophylla* subsp. *laciniata* sensu Kožuharov (1992). Therefore, the presence of the latter taxon was neglected, and it was omitted from the recent Bulgarian botanical guides (Delipavlov & Cheshmedzhiev 2011; Assyov & al. 2012). However, *S. heterophylla* subsp. *laciniata* is present in the Bulgarian flora according to Euro+Med PlantBase (Marhold 2011) and POWO (2022).

The article aims to clarify the taxonomic and geographical delimitation of *Scrophularia bulgarica* and the related *S. heterophylla* subsp. *laciniata* and the correct application of their names in the Bulgarian and Serbian flora.

Material and methods

The study is based on analysis of the protologues (Willdenow 1800; Waldstein & Kitaibel 1805; Stojanov 1926), relevant literature and type material of *Scrophularia laciniata*, *S. rupestris* and *S. variegata* var. *bulgarica*, examination of selected specimens of *Scrophularia* kept in BEO, BEOU, SO, SOA and SOM (herbarium codes according to Thiers 2021+), the herbarium of the Regional Natural History Museum of Plovdiv and Herbarium Moesiacum Niš (the last two herbaria are not registered in *Index herbariorum*) (Appendix 1). The types of *S. rupestris*, available through the virtual herbarium of LE (LE 01053547 <https://herbariumle.ru/?t=occ&id=117748>; LE 01072987 <https://herbariumle.ru/?t=occ&id=117747>), were examined online. The type specimens of *S. laciniata*, kept in BP, were also retrieved online (<https://gallery.hungaricana.hu/hu/search/results/?list=eyJxdWVyeSI6ICJzY3JvcGh1bGFyaWEgbGFjaW5pYXRhIn0>). Field surveys were carried out in 2016–2018. The collected specimens have been deposited in SOM.

Results and Discussion

Field studies of several populations of *Scrophularia bulgarica* in Bulgaria revealed that those in the Stara Planina (including the type locality) are tangibly and constantly different in a number of morphological features from those in the Pirin mountains. The most prominent differences were in their leaf characteristics and cymes. The plants from the Stara Planina have coriaceous, glaucous, undivided leaves with arcuate secondary veins and ± uniformly toothed, serrate to incised serrate margins, and mostly 1-flowered cymes, while those of the Pirin mountains have ± herbaceous, dark green leaves very variable



Fig. 1. Comparison of *Scrophularia bulgarica* (A: inflorescence; B, C: stems and leaves) and *S. heterophylla* subsp. *laciniata* (D: inflorescence; E, F: stems and leaves). – Photographs by S. Stoyanov and Y. Marinov.

Table 1. Comparison of distinctive characters and habitats of *Scrophularia bulgarica*, *S. rupestris* and *S. heterophylla* subsp. *laciniata*.

Characters	<i>Scrophularia bulgarica</i>	<i>Scrophularia rupestris</i>	<i>Scrophularia heterophylla</i> subsp. <i>laciniata</i>
Stems	grey, 10–30(–40) cm tall, with unclear ridges, indumentum densely farinaceous, yellowish glandular hairy in inflorescence	grey, 10–30 cm tall, with unclear ridges, entirely indumentum densely farinaceous and whitish glandular hairy	mostly purple, 20–70 cm tall, with prominent ridges, indumentum sparsely glandular, white to purple glandular hairy in inflorescence
Cauline leaves	monomorphic, undivided, glaucous, lamina ovate to rhombic, usually cuneate at base, 5–25(–35) × 5–15(–20) mm, ± coriaceous, ± farinaceous, margin mostly serrate or incised serrate, ± uniformly toothed, teeth acute, triangular, upper ones rectangular, secondary veins mostly arcuate, directed upward, yellowish in dried leaves, tertiary veins scanty and unclear	monomorphic, undivided, glaucous, lamina lanceolate to ovate, 15–35 × 5–15 mm, ± coriaceous, densely farinaceous, margins serrate to crenate, ± uniformly toothed, teeth ± acute, secondary veins pinnate to arcuate, yellowish in dried leaves, tertiary veins scanty and unclear	polymorphic, undivided or pinnatifid to bipinnatisect, lamina dark green, 20–60 × 15–30 mm, ± herbaceous, margin mucronate crenate, serrulate-crenate to doubly serrate, irregularly toothed, teeth ± rounded, secondary veins pinnate, directed laterally, purple in dried leaves, tertiary veins clear
Cymes	mostly 1-flowered, rarely lower cymes helicoid to scorpioid, 2–4-flowered	biparous, 3–6-flowered, rarely upper cymes 1-flowered	biparous, 3–8-flowered, rarely upper cymes 1-flowered
Corolla	upper lobes pale reddish to pale purple, lateral and lower lobes yellowish white to whitish	upper lobes reddish, lateral and lower lobes white	upper lobes dark purple to maroon, lateral and lower lobes yellowish white
Stamens	exserted up to 1 mm	exserted almost half of their length	exserted up to 1 mm
Staminodium	yellowish to reddish, spatulate to obcordate	pale reddish, obovate, lanceolate or rhombic	pale purple to brownish, reniform to orbicular
Seeds	dark brown to black, 1–1.3 × 0.6–0.9 mm	light brown to brown, 1–1.3 × 0.5–0.8 mm	brown, 0.8–1 × 0.5–0.7 mm
Habitats	mostly on calcareous and conglomerate rocks and cliffs, 400–1900 m	calcareous rocks, marl and sandstone scree slopes, 0–1500 m	mostly on calcareous scree slopes in high mountains, 400–2500 m

in shape (undivided, pinnatifid to bipinnatisect) with pinnate secondary veins and irregularly toothed, mucronate-crenate to doubly serrate margins, and 3–8-flowered, simple to biparous cymes, rarely 1-flowered. According to Peev (1995), who raised *S. variegata* var. *bulgarica* to the rank of species, the variability of *S. bulgarica* is rather ecological and is due to the different degrees of xerothermicity of habitats. Therefore, he stated that individuals at lower altitudes have pale green, undivided leaves, while those in the highlands (Pirin and Slavyanka mountains) have dark green, deeply divided to pinnatisect leaves. This discrepancy raised suspicion and required analysis of the protologue, original material of *S. variegata* var. *bulgarica* and relevant literature.

Stojanov (1926) described *Scrophularia variegata* var. *bulgarica* based on Neichev's specimens from Koru Dere and the Kupena peak and those of Jordanov from the Chufadaritsa (nowadays Ravnets) ridge, all of them confined to the C Stara Planina. He considered it superficially indistinguishable from the Crimean *S. rupestris*, which differs only in the form of the staminodium. According to the its very scanty diagnosis, *S. variegata* var. *bulgarica* has a spatulate to obcordate staminodium, while that in *S. rupestris* is oblong-ovate, and two to three times as long as

wide. Stojanov definitely believed that the taxon from the Stara Planina was part of the lineage of *S. rupestris*. The treatment of the latter as *S. variegata* var. *rupestris* at that time, as well as the broad species concept used then, probably influenced Stojanov to introduce var. *bulgarica* also within *S. variegata*. While for the other taxon described by him in the same article, *S. laciniata* var. *macedonica*, he considered it as part of the lineage of *S. heterophylla* Willd., and in particular closer to the mountain form of the latter, *S. laciniata*, due to its deeply dentate to pinnatisect leaves. In addition, *S. laciniata* var. *macedonica* has a reniform staminodium and is geographically limited to the Pirin and C Rhodope mountains.

Our examination of syntype material from the Koru Dere and Chufadaritsa localities, as well as our personal study and collecting in the same localities, confirmed Stojanov's treatment and inferred that *Scrophularia variegata* var. *bulgarica* is morphologically closest to *S. rupestris*, especially in the leaf shape and indumentum, but well distinguished from *S. laciniata* var. *macedonica*. *Scrophularia variegata* var. *bulgarica* deserves specific rank as the new combination *S. bulgarica*, but two taxa were tangled in its circumscription sensu Peev (1995). The name *S. bulgarica*, based on *S. variegata* var. *bulgarica*, should be

applied in a narrower sense according to the protologue of the basionym, to the populations from the C Stara Planina. Subsequently, based on a revision of specimens misidentified as *S. laciniata* var. *macedonica*, *S. bulgarica* was found much further west, in the series of high hills between the towns of Montana and Belogradchik (NW Bulgaria) called “Glamite”. Surprisingly, in SOM we came across two specimens of *S. bulgarica* collected in 2002 from the Jerma river gorge, in the territory of Serbia. This locality is c. 60 km S of the closest Bulgarian localities in Glamite. Subsequent field surveys confirmed the occurrence of *S. bulgarica* in several localities in the Bulgarian Glamite and in the Serbian part of the of Jerma river gorge (another part of the same gorge is in Bulgaria and the name of the river there is Erma). The findings from Serbia aroused interest and required revisiting the specimens of *Scrophularia* in the Serbian herbaria in order to clarify the overall distribution of that species. As a result, several more localities of *S. bulgarica* have been added in E and NE Serbia (Gornjačka gorge, Lazareva river canyon, Mali Krš mountain, Sićevočka gorge, Stol mountain, Svrljiške Planine, Tupižnica mountain, Veliki Krš mountain and Veliki Vukan mountain), as well as in W Serbia (Ovčarsko-Kablarška gorge). In these areas, *S. bulgarica* has been mainly confused with *S. laciniata*.

On the other hand, *Scrophularia laciniata* var. *macedonica*, by its dark green, pinnate-veined, deeply dentate to pinnatisect leaves and long-pedicelled, often biparous cymes, is similar to and difficult to distinguish from the very variable *S. laciniata* (nowadays accepted as *S. heterophylla* subsp. *laciniata*), corresponds well to the protologue of that species (Waldstein & Kitaibel 1805) and should be included in its synonymy. *Scrophularia heterophylla* subsp. *laciniata*, which for the last three decades has been a neglected species and erroneously treated within *S. bulgarica* sensu Peev (1995), is now restored to the Bulgarian flora. Its range is restricted to the S Bulgarian mountains of Pirin, C Rhodope and Slavyanka, which were so far indicated for *S. laciniata* var. *macedonica*.

According to the literature data, the main part of the range of *Scrophularia heterophylla* subsp. *laciniata* in Serbia is located in the Balkan mountains and gorges (Suva Planina, Sićevočka gorge, Stol mountain, Veliki Krš mountain, Gornjačka gorge, Zlotska gorge, Jerma river gorge), while the other part is located to the S and W, in the mountains and gorges of the Dinaric and Scardo-Pindic mountain systems (Golija, Kopaonik and Prokletijee mountains and Šar Planina) (Nikolić 1974;



Fig. 2. Habitats of *Scrophularia bulgarica* (A) and *S. heterophylla* subsp. *laciniata* (B). – A: conglomerate cliffs in Sokolna reserve, C Stara Planina; B: calcareous scree slopes, near Orelyak summit, Pirin mountains. – Photographs by S. Stoyanov and Y. Marinov.

Nikolić & al. 1986; Randelović & Stamenković 1986; Lakušić & Niketić 1988; Gajić 1989; Krivošej 1997; Randelović & al. 2000; Bogosavljević & al. 2008). A revision of the herbarium material from these localities revealed that in some localities (mostly Balkan mountains and gorges of E Serbia) records of *S. heterophylla* subsp. *laciniata* were in fact misidentifications of *S. bulgarica*. It was also found that *S. heterophylla* subsp. *laciniata* does not actually grow in E Serbia and its range is confined to C and S Serbia.

Because the description and illustration of *Scrophularia bulgarica* sensu Peev (1995) is confused and more or less corresponds to *S. heterophylla* subsp. *laciniata*, we propose a revised description in accordance with the taxonomic redefinition clarified here.

***Scrophularia bulgarica* (Stoj.) Peev** in Kožuharov, Fl. Reipubl. Bulg. 10: 106. 1995 [excl. syn. *Scrophularia laciniata* var. *macedonica* Stoj.] ≡ *Scrophularia variegata* var. *bulgarica* Stoj. in Izv. Bulg. Bot. Druzh. 1: 78. 1926. – Syntypes: Bulgaria, C Stara Planina, Koru Dere, Jul

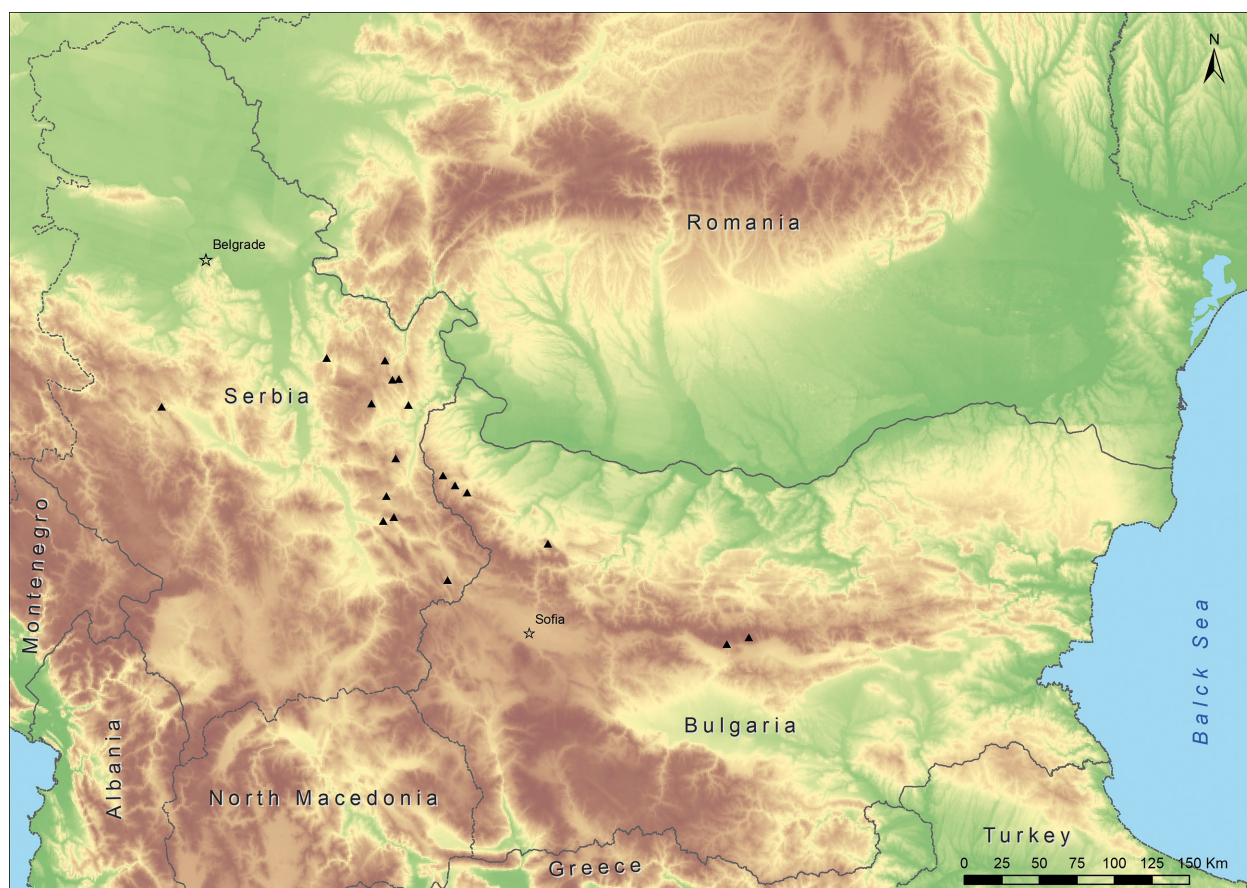


Fig. 3. Distribution map of *Scrophularia bulgarica* (▲) in the Balkans.

1903, I. Neichev (SO 65353, SOM 66958, SOM 66959, SOM 66960, SOM 66961, SOM 66963); Chufadaritsa ridge, on rocks, 24 Jul 1923, D. Jordanov (SO 65354, SOA 10045).

– “*Scrophularia laciniata* var. *laciniata*” sensu Nikolić in Fl. Srbije 6: 169. 1974, non Waldst. & Kit., Descr. Icon. Pl. Hung. 2: 185. 1805.

Description — Perennial herb, 10–30(–40) cm tall, with ligneous roots. Stems numerous, erect to ascending, grey, with unclear ridges, indumentum densely farinaceous, in inflorescence yellowish glandular hairy. *Cauline leaves* opposite, monomorphic, undivided; petiole 2–15 mm long; lamina glaucous, ovate to rhombic, 5–25(–35) × 5–15(–20) mm, ± coriaceous, densely farinaceous-hairy on abaxial surface, sparsely farinaceous to almost hairless on adaxial surface, base usually cuneate, margin serrate, incised serrate to rarely crenate, ± uniformly toothed, with 3–7 pairs of teeth on each side, teeth acute, triangular, upper ones rectangular; secondary veins mostly arcuate, directed upward, rarely pinnate, prominent on abaxial surface, yellowish in dried leaves, tertiary veins scanty and unclear. *Inflorescence* racemose, bracteate, 5–15 cm long; rachis and pedicels densely white to yellowish glandular hairy; cymes mostly 1-flowered, rarely lower ones helicoid to scorpioid,

2–4-flowered; bracts not leaf-like, linear-lanceolate, 2–6 mm long, glandular hairy, margin serrulate to entire; bracteoles whitish, filiform, 1–2 mm long, glandular, margin entire, apex acuminate. *Flowers* zygomorphic. *Sepals* orbicular-ovate, almost equal, 2.5–3.5 × 2–3 mm, farinaceous or sparsely glandular hairy, margin scarious, 0.8–1 mm wide, unevenly dentate, lacerate. *Corolla* urceolate, 5–6 mm long; tube whitish to pale reddish; lobes rounded, unequal, 1–2 mm long, upper lobes pale reddish to pale purple, lateral and lower lobes yellowish white to whitish. *Stamens* 4, fertile ones 5–7 mm long, exerted up to 1 mm; filaments yellowish, densely glandular dotted; anthers pale yellow; staminodium yellowish to reddish, spatulate to obcordate, c. 1 × 1 mm. *Capsule* light brown, spherical to ovoid, 3.5–4.5 × 3–4 mm, glabrous, apex mucronate, mucro c. 0.5 mm long. *Seeds* dark brown to black, ellipsoid to prismatic, 1–1.3 × 0.6–0.9 mm, rugulose-tuberculate.

Note — The taxonomic delimitation of *Scrophularia bulgarica* and *S. heterophylla* subsp. *laciniata* is sometimes difficult on herbarium specimens, especially in cases when both have undivided leaves, but it is much less problematic in the field (Fig. 1). Comparisons of selected, distinctive characters of the three taxa under consideration are given in Table 1.

Current distribution and habitats — A characteristic feature of the entire Neogene flora of Bulgaria (as well as of the Balkans) is that in its development specific processes have taken place that ultimately lead to the emergence of a significant number of new conditionally endemic species and the formation of refugia with relict species (Palamarev 2002). One might speculate that *Scrophularia bulgarica* is a result of a long-lasting divergence and allopatric speciation and its final diversification took place in these “sheltered” habitats.

In the early Pliocene (c. 5–4 mya), the ancestor of *Scrophularia bulgarica* had already reached the Balkans due to the land connection with Asia Minor (Popov & al. 2004). At the same time, glaciers had already appeared in N Eurasia, while the climate in the E Mediterranean (and also in the territory of Bulgaria and Serbia) had remained relatively warm. At the end of the Pliocene a long-lasting cold drought occurred (Boev 2010). Then, probably, *S. bulgarica* found more favourable conditions in the relatively humid habitats of the C Stara Planina and the W Pre-Balkans in Bulgaria and in the deep river canyons in E and NE Serbia. During glaciation in the Pleistocene (c. 2 mya), a part of the thermophilous Tertiary flora died out, but a small part of it was preserved in refugia. *Scrophularia bulgarica* probably also significantly reduced its populations, forced to retreat to the warmer and wetter refugia, where it has survived to the present day along with other Tertiary relicts.

The now existing few small “hot spots”, where *Scrophularia bulgarica* is confined, are characterized by a mild microclimate (probably similar to that in the Tertiary) due to the more heat-retaining calcareous rocks and to the presence of relatively high humidity. The limestones are mostly of Mesozoic age, geologically much older than the time of the emergence of *S. bulgarica* in the Balkans. In some of its localities, the Triassic and Jurassic limestones form complexes with conglomerate rocks from the same epochs (Antonov 1942). The presence of some other Tertiary relict elements is evidence of the refugial nature of these habitats: *S. bulgarica* co-occurs in the E part of its area, in the C Stara Planina, with *Campanula nejceffi* (Hayek) Marinov & Stoyanov, *Clinopodium frivaldszkyanum* (Degen) Bräuchler & Heubl, *Festuca balcanica* subsp. *neicevii* (Acht.) Markgr.-Dann., *Haberlea rhodopensis* Friv., *Jurinea neicevii* (Kožuharov) Greuter and *Seseli bulgaricum* P. W. Ball, while in the W part, in the Glamite hills (Bulgaria) and in the river canyons and mountain cliffs of E and NE Serbia, with *Acanthus balcanicus* Heywood & I. Richardson, *Achillea ageratifolia* subsp. *serbica* (Nyman) Heimerl, *Centaurea chrysolepis* Vis., *Eryngium palmatum* Pančić & Vis., *Ferula heuffelii* Griseb. ex Heuff., *Ramonda serbica* Pančić and *Silene flavescent* Waldst. & Kit.

Scrophularia bulgarica inhabits a very specific habitat: crevices of calcareous and conglomerate rocks and cliffs. It is an obligate chasmophyte and a member of rupestrian community belong to the habitat type “8210 Calcareous rocky slopes with chasmophytic vegetation”

of Directive 92/43/EEC (1992). According to the EUNIS (2012) classification, the habitats of *S. bulgarica* belong to the type “H3.2A13 Balkan Range calcicolous chasmophyte communities” (Fig. 2).

The current distribution range of *Scrophularia bulgarica* includes the following localities: Bulgaria: C Stara Planina (Ravnets ridge and Sokolna reserve), W Stara Planina (Vrachanska Planina) and W Pre-Balkans (Glamite hills above the villages of Replyana, Salash and Varbovo); Serbia: gorges and mountains in E Serbia (Gornjačka gorge, Jerma river gorge, Lazareva river canyon, Mali Krš mountain, Sićevečka gorge, Stol mountain, Svrliške Planine, Tupižnica mountain, Veliki Krš mountain and Veliki Vukan mountain) and the Ovčarsko-Kablarska gorge in W Serbia (Fig. 3).

Conclusion

The study resolved the taxonomic identity of *Scrophularia bulgarica* and found it to be distinctly different from *S. heterophylla* subsp. *laciniata*. By its densely farinaceous leaf and stem indumentum and glaucous, undivided leaves with arcuate secondary veins, *S. bulgarica* probably appeared to be closest to *S. rupestris* and its related species—*S. cretacea* Fisch. ex Spreng., *S. donetzica* Kotov and *S. sareptana* Kleop. ex Ivanina—distributed in the NE Black Sea area (Ukraine, Crimea and SW Russia). In support of this comes the study of phylogenetic relationships in *Scrophularia* (Scheunert & Heubl 2017), according to which the above-mentioned species are well-nested together within an intricate “Tomiophyllum clade”, while *S. heterophylla* subsp. *laciniata* falls within the distinct “Canina subclade”. *Scrophularia bulgarica*, a result of a vicariant event, is a Balkan endemic and a relict species that has survived in the Tertiary refugia of W and C Bulgaria and W and E Serbia.

Author contributions

SS gathered the field data, examined the specimens and wrote the first draft of the manuscript; YM and NAS conducted the field surveys in Bulgarian localities, examined the specimens and prepared the text on habitats and geology; VR and SV analysed the literature data, revised the herbarium records from Serbia and contributed to preparing the manuscript; SS and SV coordinated the study. All authors contributed to the concept and implementation of the study and took part in the final revision and editing of the manuscript.

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- Marinov* (SOM 177330); Sokolna reserve, near springs of Sokolna river, 42.71634°N, 25.10442°E, 1800 m, conglomerate cliff, 18 Jul 2018, *S. Stoyanov & Y. Marinov* (SOM 177331); Sokolna reserve, W slope of valley of Sokolna river, along trail toward Tarnichene village, 42.70774°N, 25.10619°E, 1800 m, conglomerate rocks, 18 Jul 2018, *S. Stoyanov & Y. Marinov* (SOM 177332); Ravnets [Chufadaritsa] ridge, above Kalofer town, 42.67315°N, 24.92517°E, 1640 m, conglomerate rocks, 21 Jun 2018, *S. Stoyanov & Y. Marinov* (SOM 177333, SOM 177334). — W STARA PLANINA: in lapidosis siccis ad Vraca, 1904, *I. Urumov* (SOM 66962, sub *S. rupestris*). — W PRE-BALKANS: Salash village, Belogradchik district, Vedernik ridge, dry calcareous rocks, 2 Jun 1965, *V. Velchev & S. Ganchev* (SOM 154562, SO 102570); above Replyana village, Belogradchik district, N slope of Glamite hills, 22 Jun 1977, *S. Stanev* (SOM 138002, Herbarium Museum Plovdiv 09512, 09513 and 09514, all sub *S. laciniata* var. *macedonica*); above Replyana village, Belogradchik district, N slope of Glamite hills, 43.52276°N, 22.75419°E, 880 m, calcareous cliff, 30 Jul 2017, *S. Stoyanov & N. Apostolova-Stoyanova* (SOM 177335, SOM 177336); above Varbovo village, Belogradchik district, N slope of Glamite hills, 43.56212°N, 22.65257°E, 980 m, calcareous cliff, 29 Jul 2018, *S. Stoyanov & N. Apostolova-Stoyanova* (SOM 177337). — **SERBIA**: NE SERBIA: Gornjačka gorge, 1876, *J. Pančić* (BEOU 7686, sub *S. laciniata*); Gornjačka gorge, rocks, 25 Jun 1906, *leg. ?* (BEO s.n., sub *S. laciniata*); Gornjačka gorge, rocks and scree, from monastery tu Ždrelo, 24 May 1989, *leg. ?* (BEOU s.n., non-determined); Gornjačka gorge, near hermitage at end of gorge, rocks, small scree and scarps, 26 May 1989, *leg. ?* (BEOU s.n., non-determined); Gornjačka gorge, rocks, limestone, 18 Jun 2004, *M. Niketić & G. Tomović* (BEOU 18983, sub *S. laciniata*); Veliki Vukan mountain, 44.29928°N, 21.53833°E, 826 m, limestone rocks, 17 Jun 2010, *D. Lakušić* (BEOU 30377, sub *S. laciniata*); Garvan mountain [Mali Krš mountain], 1871, *J. Pančić* (BEOU 7684, sub *S. laciniata*); Bor, Veliki Krš mountain, 7 Jun 1991, *N. Benić* (BEOU 1458/91, sub *S. alpina*); Stol mountain, Jul 1853, *J. Pančić* (BEOU 7677, BEOU 7678, both sub *S. laciniata*); Slatina, gorge through which Slatinska river passes, Jul 1863, *J. Pančić* (BEOU 7679, sub *S. laciniata*); Bor, Rgotski Kamen, rocky ground, 15 Jun 1973, *V. Nikolić, N. Diklić & M. Bogdanović* (BEO s.n., sub *S. laciniata* var. *umbrosa*); Gaura Lazaru [Lazareva river gorge], 1867, *J. Pančić* (BEOU 7716, sub *S. variegata*, *S. rupestris* and *S. laciniata*); Zlot, 1876, *J. Pančić* (BEOU 7665, sub *S. heterophylla*); Zlot, Jun 1927, *Th. Soška* (BEOU s.n., non-determined); Zlotska river canyon, 25 Jun 1964, *M. Dinkić & Lj. Miladinović* (BEO s.n., sub *S. heterophylla* subsp. *laciniata*); 14 Jun 1965, *N. Diklić* (BEO s.n., sub *S. laciniata*); Zlot, Lazareva river canyon, limestone rock crevices, near Vernjikica, 15 Jul 1982, *V. Stevanović* (BEOU 10407, sub *S. heterophylla* var. *laciniata*?); Zlot, Lazare-

Appendix 1. Selected specimens examined

***Scrophularia bulgarica* — BULGARIA:** C STARA PLANINA: Sokolna reserve, S of Bulkite summit, 42.71841°N, 25.10446°E, 1890 m, calcareous rocks, 23 Jul 2016, *S. Stoyanov & Y. Marinov* (SOM 177327); Sokolna reserve, near springs of Sokolna river, 42.71692°N, 25.10392°E, 1820 m, conglomerate cliff, 7 Jul 2017, *S. Stoyanov & Y. Marinov* (SOM 177328, SOM 177329); Sokolna reserve, west of Chatal Cham summit, 42.71242°N, 25.11794°E, 1590 m, calcareous rocks, 8 Jul 2017, *S. Stoyanov & Y.*

va river canyon, 6 Jun 1983, V. Stevanović (BEOU 1748, sub *S. alpina*); Zlot, vegetation rocks, 12 Jul 1985, *BID* “Josif Pančić” (BEOU 77/85, sub *S. laciniata*); Malinik mountain, Jul 1986, *BID* “Josif Pančić” (BEOU 477/86, sub *S. laciniata* var. *alpina*); Malinik mountain, Lazareva river canyon, 44.02862°N, 21.95322°E, 257 m, limestone rocks, 22 May 2009, S. Vukojević & K. Jakovljević (BEOU 29651, sub *S. laciniata*); Tupižnica mountain, cliff ridge, rocks, 28 Jun 1998, M. Niketić & G. Tomović (BEOU 11382, non-determined). — E SERBIA: Svrljig, in rupestribus, 1869, J. Pančić (BEOU 7680, sub *S. laciniata*); Niševci, 1870, J. Pančić (BEOU 7683, sub *S. laciniata*); Svrljiške Planine, Pleš, 1868, J. Pančić (BEOU 7681, sub *S. laciniata*); Pleš, 12 Jul 1994, V. Randelović & B. Zlatković (Herbarium Moesiicum Niš, sub *S. heterophylla*); Sićevačka gorge, Vis peak, 1880, J. Pančić (BEOU 7661, sub *S. laciniata*). — SE SERBIA: Zvonačka spa, Jerma river gorge, Vlasi village, 18 Jul 1965, V. Nikolić, N. Diklić & M. Rakin (BEO s.n., sub *S. laciniata*); above Dimitrovgrad town, 6 Jun 2002, Zh. Cherneva (SOM 158227); Jerma river gorge, above road toward Poganovo monastery, 6 Jun 2002, Zh. Cherneva (SOM 158228 p.p., mixed sheet, two plants of *S. bulgarica* and one of *S. heterophylla* subsp. *laciniata*); Jerma river gorge, c. 600 m, *Asplenietea rupestris*, limestone, 26 Jun 2006, V. Stevanović, S. Jovanović, D. Lakušić & K. Jakovljević (BEOU 20901, sub *S. laciniata*); Jerma river gorge, calcareous cliff above tunnel between Vlasi village and Poganovo monastery, 42.99323°N, 22.63281°E, 520 m, 29 May 2018, S. Stoyanov (SOM 177338, SOM 177339); Jerma river gorge, S of Poganovo monastery, 42.97253°N, 22.62355°E, 550 m, calcareous rocks, 29 May 2018, S. Stoyanov (SOM 177340). — W SERBIA: Kablar, Jul 1858, J. Pančić (BEOU 7637, sub *S. sp.*); Ovčarsko-Kablarška gorge, limestone, 24 Jun 1978, V. Nikolić, N. Diklić & S. Mladenović (BEO s.n., non-determined).

Scrophularia heterophylla subsp. *laciniata* (all specimens cited below from Bulgaria are deposited under the name *S. laciniata* var. *macedonica* except those of the authors and where expressly indicated) — **BULGARIA:** PIRIN MOUNTAINS: Arnautski Vrah [Sinanitsa summit], Aug 1921, N. Stojanov & B. Stefanov (SOA 10037, SOA 10038, syntypes of *S. laciniata* var. *macedonica*, both sub *S. rupestris*); Banderitsa, rocks, 23 Aug 1915, T. Nikolov (SOA 10036); in saxosis umbrosis supra riv. Banderitsa, 2250 m, 22 Jul 1915, B. Davidov (SOM 66860, sub *S. rupestris*); Kutelo summit, 2700 m, cal-

careous slope, 26 Jul 1932, B. Stefanov & T. Georgiev (SO 65276); in saxosis calcareis ad Orlova Skala [Orelyak summit], 2090 m, 18 Jul 1936, B. Achtarov (SOM 66856); in glareosis calcareis supra Banderitsa, 1900 m, 6 Aug 1938, B. Achtarov (SOM 66854); in glareosis et saxosis calcareis supra Kazana [Kazanite], 2400 m, 7 Aug 1938, B. Achtarov (SOM 66855); in glareosis graniticis riv. Banderitsa, 1850 m, 8 Aug 1938, N. Stojanov (SO 65292); in glareosis gneissis prope lacum Suhodolsko, 2000 m, 31 Jul 1939, N. Stojanov (SO 65282, SO 65286, SO 65293); in fissuris saxis marmoreis ad Bayovi Dupki, 2000 m, 9 Aug 1939, B. Achtarov (SOM 66852); in pascuis saxosis calcareis sub Orlova Skala, 2000 m, 21 Jul 1950, B. Achtarov (SOM 43542); Banderitsa chalet, 27 Jun 1969, B. Kuzmanov (SOM 124284, sub *S. aestivalis*); S of Orelyak summit, 41.56965°N, 23.61311°E, 2060 m, calcareous scree slope, 15 Jun 2017, S. Stoyanov & Y. Marinov (SOM 177341, SOM 177342); along trail between Banderitsa chalet and Kazanite locality, 41.77324°N, 23.42162°E, 2100 m, calcareous scree slope, 3 Aug 2017, S. Stoyanov (SOM 177343, SOM 177344). — C RHODOPE MOUNTAINS: in rupestribus secus viam inter pagia Hvoina et Bela Čerkva, 20 Jul 1909, I. Urumov (SOM 66859, SOM 66861, SOM 66862, syntypes of *S. laciniata* var. *macedonica*, all sub *S. variegata* var. *rupestris*); NE of Trigrad village, Devin district, calcareous rocks, 22 Jul 1938, D. Jordanov (SO 65277); Trigrad village, Devin district, wet rocks above the river, 31 Jul 1940, D. Jordanov (SO 65288); Chervinata Stena reserve, limestone scree slope, 16 Jun 1971, 7 Jun 1978, S. Stanev (Herbarium Museum Plovdiv 7345, 9719 and 9720); Trigrad gorge, near Dyavolskoto Garlo cave, 41°37'N, 24°23'E, 1100–1150 m, limestone, 26 Jul 1997, V. Vladimirov (SOM 155463, sub *S. bulgarica*). — SLAVYANKA MOUNTAINS: above Paril village, rocks, 23 Jun 1923, N. Stojanov (SOA 10039, sub *S. canina*); above Goleshevo village, 28 Jun 1980, B. Kuzmanov (SOM 146859, sub *S. laciniata*); above Paril village, Hambar Dere locality, 1500 m, 27 Apr 1990, I. Pashaliev (SOM 151252). — **SERBIA:** C SERBIA: Kopaonik, J. Pančić (BEOU 15142, sub *S. laciniata*); Tara mountain, in saxosis ad Jagoštica, Jun 1912, Th. Soška (BEOU s.n., sub *S. laciniata*); Tara mountain, Aluge, 24 Jul 1992, D. Lakušić (BEOU 432/92, sub *S. laciniata*). — KOSOVO AND METOHIJA: Šar Planina, Brod village, Gradski Kamen, 30 Sep 1991, M. Niketić (BEOU 2294/91, sub *S. laciniata*); Šar Planina, Kobilica, between Treskavac and Surduk, 42.09822°N, 20.874298°E, 1000 m, rocky ground, Š. Duraki (BEOU 53442, sub *S. laciniata*).

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