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

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**Abstract:** The taxonomic treatment and geographical distribution of *Scrophularia bulgarica* (≡ *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. *Tomiophyllum*, taxonomic redefinition

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### Introduction

*Scrophularia* sect. *Tomiophyllum* 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. *Tomiophyllum*. To the last section he assigned suffrutescent or herbageous perennials with ligneous roots, stems branched from the base, non-anastomosing fork-veined leaves and rigid inflorescences. Carlbom (1969) considered S. sect. *Tomiophyllum* as “primitive” due to the xerophilous, sub-shrubby habit of its representatives and the general lack of polyploidy. In the only comprehensive taxonomic revision of the genus, Stiefelhagen (1910) accepted only two sections: Bentham’s S. sect. *Tomiophyllum* and the new S. sect. *Anastomosantes* Stiefelh. He characterized S. sect. *Tomiophyllum* 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. *Tomiophyllum* 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. *Tomiophyllum*, 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. rupestris* 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 & Petitim. Nevertheless, according to Nikolić (1974), S. sect. Tomiophyllum is represented in Serbia with the same four abovementioned taxa, with the difference that *S. rupestris* 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 Sokolina 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; Assyrov & 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 & Kitaiibel 1805; Stojanov 1926), relevant literature and type material of *Scrophularia lacinia*, *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 Nis (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. lacinia*, kept in BP, were also retrieved online (https://gallery.hungaricana.hu/hu/search/results/?list=eyJxdWVyeSf6ICJzY3JvcGkibGFyaWJgbGFjaW5pYXRhInt0), 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.
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 xerothermic 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* Wild., 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

| Characters | Scrophularia bulgarica | Scrophularia rupestris | Scrophularia heterophylla subsp. laciniata |
|-----------|------------------------|------------------------|------------------------------------------|
| 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 scorpionid, 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 |
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, Sićevačka gorge, Stol mountain, Svrliške Planine, Tupižnica mountain, Veliki Krš mountain and Veliki Vukan mountain), as well as in W Serbia (Ovčarsko-Kablarska 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. *laciniata*.

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, Sićevačka gorge, Stol mountain, Veliki Krš mountain, Gornjačka gorge, Zlotačka 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 & al. 1986; Randelović & Stamenković 1986; Lukić & 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.

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*Nikolić & al. 1986; Randelović & Stamenković 1986; Lukić & Niketić 1988; Gajić 1989; Krivošej 1997; Randelović & al. 2000; Bogosavljević & al. 2008)*.

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**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.
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 pinate, 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 scorpionid, 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 scariosus, 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, exserted 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 nejeffii (Hayek) Marinov & Stoyanov, Clinopodium frivaldszkyanum (Degen) Bräuchler & Heubl, Festuca balcanica subsp. nejevii (Acht.) Markgr.-Dann., Hauberlea rhodopensis Friv., Jurinea nejevii (Kožuhar) 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, Achilles ageratofolia subsp. serbica (Nyman) Heimerl, Centaurea chrysolepis Vis., Eryngium palmatum Pančić & Vis., Ferula heuffelii Griseb. ex Heuff., Ramonda serbica Pančić and Silene flavescens 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 rupestran 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 calciculous chasmophyte communities” (Fig. 2).

The current distribution range of Scrophularia bulgarica includes the following localities: Bulgaria: C Stara Planina (Ravnens 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 gorges, Jermaj river gorge, Lazareva river canyon, Mali Krš mountain, Sicevačka gorge, Stol mountain, Svrljške Planine, Tupižnica mountain, Veliki Krš mountain and Veliki Vukan mountain) and the Ovčarsko-Kablarška gora 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 (Scheuern & Heubl 2017), according to which the above-mentioned species are well-nested together within an intricate “Tomophyllum clade”, while S. heterophylla subsp. laciniata falls within the distinct “Canana subclade”. Scrophularia bulgarica, as 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 in 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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Appendix 1. Selected specimens examined

**Scrophularia bulgarica** — **BULGARIA**: C Stara Planina: Sokolna reserve, near springs of Sokolina river, 42.71634°N, 25.10442°E, 1800 m, conglomerate cliff, 18 Jul 2018, S. Stoyanov & Y. Marinov (SOM 177330); Sokolna reserve, near springs of Sokolina 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 Sokolina 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 PLAINA**: in lapis-dosis siccis ad Vraca, 1904, I. Urumov (SOM 66962, sub. S. rupestris). — **W Pré-Balkans**: Salash village, Belogradchik district, Vedernik ridge, dry calcareous rocks, 2 Jun 1965, V. Velchev & S. Ganchev (SOM 154562, SO 102570); above Repljana 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 Repljana 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. ? (BEO s.n., non-determined); Gornjačka gorge, near hermitage at end of gorge, rocks, small scree and scarp, 26 May 1989, leg. ? (BEO 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 & N. Dinkić (BEO s.n., 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. laciniata); Stol mountain, Jul 1853, J. Pančić (BEOU 7677, BEOU 7678, both sub. S. laciniata); Stolina, gorge through which Slatinska river passes, Jul 1863, J. Pančić (BEOU 7679, sub. S. laciniata); Bor, Rtotski 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-
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. Vukojić & K. Jakovljević (BEOU 29651, sub S. laciniata); Tüpižnica mountain, cliff ridge, rocks, 28 Jun 1998, J. Pančić (BEOU 7680, sub S. laciniata); Niševci, 1870, J. Pančić (BEOU 7683, sub S. laciniata); Svrliške Plaine, Pleš, 1868, J. Pančić (BEOU 7681, sub S. laciniata); Pleš, 12 Jul 1994, V. Randelović & B. Zlatković (Herbarium Moesiacum Niš, sub S. heterophylla); Sićevačka gorge, Vis peak, 1880, J. Pančić (BEOU 20901, sub S. laciniata); above Dimitrovgrad town, 6 Jun 2002, V. Stevanović, S. Jovanović, D. Lakušić & K. Jakovljević (BEOU 20901, sub S. laciniata); Jerma river gorge, above road toward Poganovo monastery, 6 Jun 2002, Zh. Cherneva (BEOU 158277); Jerma river gorge, above road toward Poganovo monastery, 22 May 2018, V. Stevanović, S. Jovanović, D. Lakušić & K. Jakovljević (BEOU 20901, sub S. laciniata); Jerma river gorge, c. 600 m, Asplenieta 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 (BEOU 177338, SOM 177339); Jerma river gorge, S of Poganovo monastery, 42.97253°N, 22.62335°E, 550 m, calcareous rocks, 29 May 2018, S. Stoyanov (BEOU 177340). — W SERBIA: Kablar, Jul 1858, J. Pančić (BEOU 7637, sub S. laciniata); Ovčarsko-Kablarska 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 (BEOU s.n., sub S. laciniata); above Dimitrovgrad town, 6 Jun 2002, Zh. Cherneva (BEOU 158277); Jerma river gorge, above road toward Poganovo monastery, 6 Jun 2002, Zh. Cherneva (BEOU 158228). — EAST SERBIA: in saxosis umbrosis supra riv. V. Vladimirov (Herbarium Museum Plovdiv 7345, 9719 and 9720); Trigrad gorge, near Dyavolskoto Garlo locality, 1500 m, 27 Apr 1990, V. Stevanović (SOM 66861, SO 65286), 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); Chervenata 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. Kazmanov (SOA 146859, sub S. laciniata); above Paril village, Hambar Dere locality, 1500 m, 27 Apr 1990, I. Pashaliev (SOM 151252). — 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 METOHIA: Čar Planina: above Paril village, 22 Jul 1915, B. Davidov (SO 66860, sub S. rupestris); Kutelo summit, 2700 m, calcareous slope, 26 Jul 1932, B. Stefanov & T. Georgiev (SO 65276); in saxosis calcareis ad Orlova Skala [Orelyak summit], 2090 m, 18 Jul 1936, B. Achterov (SO 66856); in glareosis calcareis supra Banderitsa, 1900 m, 6 Aug 1938, B. Achterov (SO 66854); in glareosis et saxosis calcareis supra Kazana [Kazanite], 2400 m, 7 Aug 1938, B. Achterov (SO 66855); in glareosis graniticis riv. Banderitsa, 1850 m, 8 Aug 1938, N. Stojanov (SO 65292); in glareosis gneisseeis prope lacum Suhodolisko, 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. Achterov (SO 66852); in pascuis saxosis calcareis sub Orlova Skala, 2000 m, 21 Jul 1950, B. Achterov (SO 43542); Banderitsa chalet, 27 Jun 1969, B. Kazmanov (SO 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). — C RHODOPE MOUNTAINS: in rupestribus secus viam inter pagia Hvoina et Bela Čerkva, 20 Jul 1909, I. Urumov (SO 66859, SO 66861, SO 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); Chervenata 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. Kazmanov (SOA 146859, sub S. laciniata); above Paril village, Hambar Dere locality, 1500 m, 27 Apr 1990, I. Pashaliev (SOM 151252).