Turkish Journal of Botany

http://journals.tubitak.gov.tr/botany/

Research Article

Turk J Bot
(2023) 47: 388-398
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doi:10.55730/1300-008X.2776

A new *Scrophularia* (Scrophulariaceae) species without staminodes in the enigmatic "*Canina* clade" from the Western Taurus (Türkiye)

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Received: 22.03.2023 • **Accepted/Published Online:** 02.08.2023 • **Final Version:** 26.09.2023

Abstract: The new species of *Scrophularia* was discovered among the screes and stony slopes of the Alakır Valley (Antalya) located in the Western Taurus. The most remarkable morphological feature of the species is its flowers without staminodes. With this feature, the species is unique among the representatives of the "*Canina*" clade in Türkiye. The new species is closely related to *S. floribunda* endemic to Türkiye and East Aegean Islands (Greece) according to our phylogenetic analyses based on the nuclear ITS and chloroplast *trn*L-F regions. Apart from its corollas without staminodes, the new species differs from its morphologically similar species by having densely glandular inflorescence (incl. calyxes), relatively small corollas, corolla lobes with a narrow white border, and very long filaments.

Key words: *Canina* clade, new species, phylogeny, *Scrophularia*, taxonomy, Türkiye

1. Introduction

The genus *Scrophularia* L. (Scrophulariaceae) is represented by more than 250 taxa (species and subspecies) worldwide (Ortega-Olivencia, 2009; Scheunert and Heubl, 2017; Wang et al., 2022a). *Scrophularia*, a genus widely distributed in the temperate zone of the Northern Hemisphere, has centers of diversity in Southwest Asia, Central Asia, the Himalayas, and the Iberian Peninsula, with the Mediterranean region being particularly significant for its high levels of diversity and endemism rate (Scheunert and Heubl, 2014). Without exception, *Scrophularia* species are concentrated in mountainous regions and the genus exhibits a high degree of endemism throughout its range (Vaarama and Hiirsalmi, 1967; Scheunert and Heubl, 2017). Türkiye has an important geographical position for the distribution of the genus and the country hosts 78 taxa (62 species, 1 subspecies, and 15 varieties), 37 of which are endemic to Türkiye (Lall and Mill, 1978; Uzunhisarcıklı et al., 2018; Uzunhisarcıklı et al., 2019), and the endemism rate of this genus is 49% in this country, with the new species described here.

The widely accepted classification of the genus *Scrophularia* was done by Stiefelhagen (1910), who classified the genus into two sections which are Sect. *Anastomosantes* Stiefelhagen (also known as Sect. *Scrophularia*) and Sect. *Tomiophyllum* Bentham, which includes subsections *Farinosae* Stiefelhagen, *Orientales* Stiefelhagen, and *Lucidae* Stiefelhagen (Ortega-Olivencia, 2009). The species that thrive in damp environments are mainly restricted to Sect. *Anastomosantes*, while Sect. *Tomiophyllum* is composed of more xerophytic elements, which are better adapted to arid conditions (Scheunert and Heubl, 2014) as predominantly found in regions of Northwest China and Central Asia (Wang et al., 2022b). Subsequently, during the revision of the genus for the Iberian Peninsula, two sections were delineated which are currently in use as Sect. *Anastomosantes* and Sect. *Canina* G. Don (Ortega-Olivencia and Devesa, 1993).

Scrophularia is a taxonomically difficult and morphologically diverse genus, characterized by a high degree of significant variation (Stiefelhagen, 1910; Lall & Mill, 1978; Hong, 1983; Fischer, 2004). The genus has a complex evolutionary history that involves hybridization and gene flow, which has contributed to the remarkable diversity of *Scrophularia* species in the Western Mediterranean and Macaronesia (Scheunert and Heubl, 2014; Navarro-Pérez et al., 2015; Riahi and Ghahremaninejad, 2019). To gain insight into the intricate evolutionary history of *Scrophularia* lineages, the most comprehensive study to date utilized both the nuclear ribosomal internal transcribed spacer (ITS) region and chloroplast *trn*L(UAA)-F(GAA) regions (Scheunert and Heubl, 2011, 2014, 2017). Nevertheless, relationships among many subclades and infraspecific taxa were weakly supported, and discrepancies were found between the cytoplasmic and nuclear data (Scheunert and Heubl, 2017). Finally, Wang et al. (2022a)

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showed that the entire chloroplast genome contains highly variable regions and distinct microsatellite loci patterns, which can improve the precision of phylogenetic analysis and species identification, particularly in the study of closely related species (Wang et al., 2022b).

The presence, size, and shape of the staminode are taxonomically useful and important characters for the genus. In *Scrophularia*, staminode size is known to be influenced by selection pressure and can rapidly change during periods of environmental change, with implications for the reproductive success of the species (Ortega-Olivencia et al., 2012; Rodríguez-Riaño et al., 2015a, 2015b). For example, staminode size can help protect the nectar from rainwater (Ortega-Olivencia et al., 2012; Rodríguez-Riaño et al., 2015a, 2015b) and promote the success of female reproductive processes (López et al., 2016). The staminode is well-developed in Subsect. *Scrophularia* (Sect. *Scrophularia*), while it is completely absent in Subsect. *Vernales* (Sect. *Scrophularia*) and it is very small or even absent in some species of Sect. *Canina* (in *S. crithmifolia*). As stated by Rodríguez-Riaño et al. (2015a), the staminodes may entirely disappear in some flowers on the same plant of *S. canina* subsp. *canina* (e.g., *Scrophularia canina* subsp. *canina*, Ortega-Olivencia pers. observ.).

The new species described here is distinguished by its flowers without staminodes. With this unique morphological feature, it is similar to *S. crithmifolia* native to Spain and there is no other species in the world that does not have staminodes in the Sect. *Canina*, and it is closely related to *S. floribunda* Boiss. & Balansa endemic to Türkiye and the East Aegean Islands (Greece). Within the scope of the study, we aimed to clarify the phylogenetic position of the new species in the *Canina* clade by using both nuclear and chloroplast sequences and to evaluate the phylogenetic relationships between the new species and its close relatives by molecular studies. Besides, we explained the morphological similarities and differences between the new species and its similar species.

2. Material and methods

2.1. Plant specimens and morphological studies

The specimens of the new species were collected from screes and stony slopes in the Alakır Valley (Kumluca, Antalya) between the years 2019 and 2022. Their morphological characteristics were recorded in both the field and laboratory. The collected specimens were comprehensively evaluated by the use of the relevant literature (Gorshkova, 1950; Greuter and Rechinger, 1967; Carlbom, 1968; Feinbrun-Dothan, 1978; Lall and Mill, 1978; Grau, 1981; Meikle, 1985; Olivencia, 2009; Uzunhisarcıklı et al., 2018) and the specimens present in ANK, E, EGE, G, HUB, and AKDU herbaria (acronyms follow Thiers[1]).

2.2. Isolation of DNA, PCR amplification, and sequencing

Total genomic DNA was extracted from dried tissues using the CTAB method as described by Doyle and Doyle (1990) with minor adjustments such as extra chloroform-isoamyl alcohol and 70% ethanol cleaning steps. DNA quality and quantity were estimated by electrophoresis on 1% agarose gels, and the amount was fixed at 100 ng/μL using lambda DNA as a reference.

Amplification of the nuclear ribosomal ITS regions (ITS-1, 5.8S rDNA subunit, ITS-2) and the chloroplast *trn*L-F region was conducted with the primers of ITS5/ITS4 (White et al., 1990) and c/f (Taberlet et al., 1991), respectively. Polymerase chain reaction (PCR) for both ITS and *trn*L-F regions was performed in 15 μL reaction mixture containing 2 mM of $MgCl_2$, 200 mM of (each) dNTP, 0.4 μM of each primer, 1 U of Taq DNA polymerase (Fermentas Life Sciences, Burlington, Canada) with supplied reaction buffer at 10X concentration, and 40 ng of template DNA. PCR was carried out with the following protocol: initial denaturation step for 5 min at 95 °C, 35 cycles of denaturation for 1 min at 95 °C, annealing for 30 s at 52 °C for ITS, 1 min at 68 °C for *trn*L-F and then a final extension of 5 min at 72 °C. PCR products were loaded onto 1.5% agarose gel and visualized under UV light after staining with ethidium bromide. The products of each sample were purified using the GeneJET Gel Extraction Kit (Thermo Scientific Fermentas, Vilnius, Lithuania). Sequencing was carried out at Macrogen Inc., Europe via BM Laboratories Ltd., as direct sequencing in two directions using the amplification primers. The sequences were submitted to GenBank. Accession numbers of all sequences used in this study are shown in Appendix.

2.3. Phylogenetic analyses

In order to test the phylogenetic position of the new species, Bayesian and maximum likelihood analyses were conducted based on the nuclear ITS and chloroplast *trn*L-F regions. In addition to two newly sequenced *Scrophularia* specimens, representatives of some species groups including "*Canina*" and "*Striata*" groups in the *Canina* clade described by Scheunert and Heubl (2017), and available taxa from Türkiye were obtained from GenBank. *Verbascum thapsus* L. was used as an outgroup.

The raw ITS and *trn*L-F sequences were edited using Unipro UGENE software version 37.0. (Okonechnikov et al., 2012) KY067611 and KC692623 were used as references for ITS and *trn*L-F sequences, respectively. The sequences were then aligned using MUSCLE software v.3.6 (Edgar, 2004). The best substitution models for both regions were selected by MEGA X (Kumar et al., 2018) using the Akaike Information Criterion (AIC). GTR + G and HKY +G models were selected for ITS and *trn*L-F datasets, respectively. Bayesian analyses were conducted using MrBayes 3.2.6 (Ronquist et al., 2012). Two simultaneous runs were performed using Metropolis-coupled Markov Chain Monte Carlo (MCMCMC) sampling for 10 million generations, and one tree was sampled every 1000 generations. Maximum likelihood analyses were carried out in RAxML (Stamatakis, 2006) choosing the rapid bootstrapping option with 1000 bootstrap iterations.

2.4. Phylogenetic networks

In order to visualize phylogenetic conflicts as a result of hybridization events among the *Scrophularia* taxa studied, a NeighborNet analysis was conducted using SplitsTree ver. 4.11.3 (Bryant and Moulton, 2004). Both bootstrap support values and delta scores were computed to check the robustness of the network and the level of the reticulation signal for each taxon respectively.

1Thiers B (2023) onward (continuously updated). Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden'´s Virtual Herbarium [online]. Website: http://sweetgum.nybg.org/ih/ [accessed 20 February 2023].

3. Results

3.1. Taxonomic treatment

Scrophularia tugbae-birhanii **Aykurt, Deniz & M. Gülben** ***sp. nova*** (Figures 1–2)

Type: Türkiye. Antalya: Kumluca, Sarıkaya Wild Life Development Area, Alakır Valley, screes and stony slopes, 1330 m, 29 May 2019, *C. Aykurt 5074* & *H. Sümbül* (holotype: AKDU 6332).

Diagnosis: *Scrophularia tugbae-birhanii* differs from *S. floribunda* by its stems branched from the base (vs. unbranched), densely glandular calyx lobes with scarious margins up to 0.5 mm (vs. glabrous calyx with 0.7–1.2 mm scarious margin), and rather small corollas without staminodes, 2.6–3 mm long (vs. corolla with lanceolate staminodes, 5.5–6 mm long).

Description: Perennial herb. Stem erect, angled, 25–55 cm long, 1.5–3 mm diam, glabrescent to minutely glandular-hairy, branched from base. Leaves pinnatifid to pinnatisect, 1.5–6 × 0.5–1.5 cm; glabrescent, with sessile glands, minutely glandular papillose especially on margins; leaflets with dentate lobes or pinnatifid to pinnatisect, terminal leaflets larger than laterals; petiole 0.1–2 cm long. Basal leaves fleshy; lower cauline leaves opposite to subopposite; upper cauline leaves alternate. Inflorescence aphyllous. Bracts 2–6 mm long, lower deeply pinnatifid, upper becoming linear to lanceolate, entire, densely glandular hairy. Cymes dichasial, usually with 3–7 flowers, alternate, densely glandular hairy; peduncle 2–6 mm long; alar pedicels 1–1.5 mm long, ± equal or slightly shorter than bracteoles. Calyx lobes densely glandular, ovate to oblong, 1.8–2.5 × 1.1–1.8 mm; scarious margin up to 0.5 mm broad, lacerate. Corolla tube 2.1–2.3 mm long, maroon, lobes with white border; upper lips ± 0.5–0.7 mm long. Stamens exserted to usually 1.5–2 ×

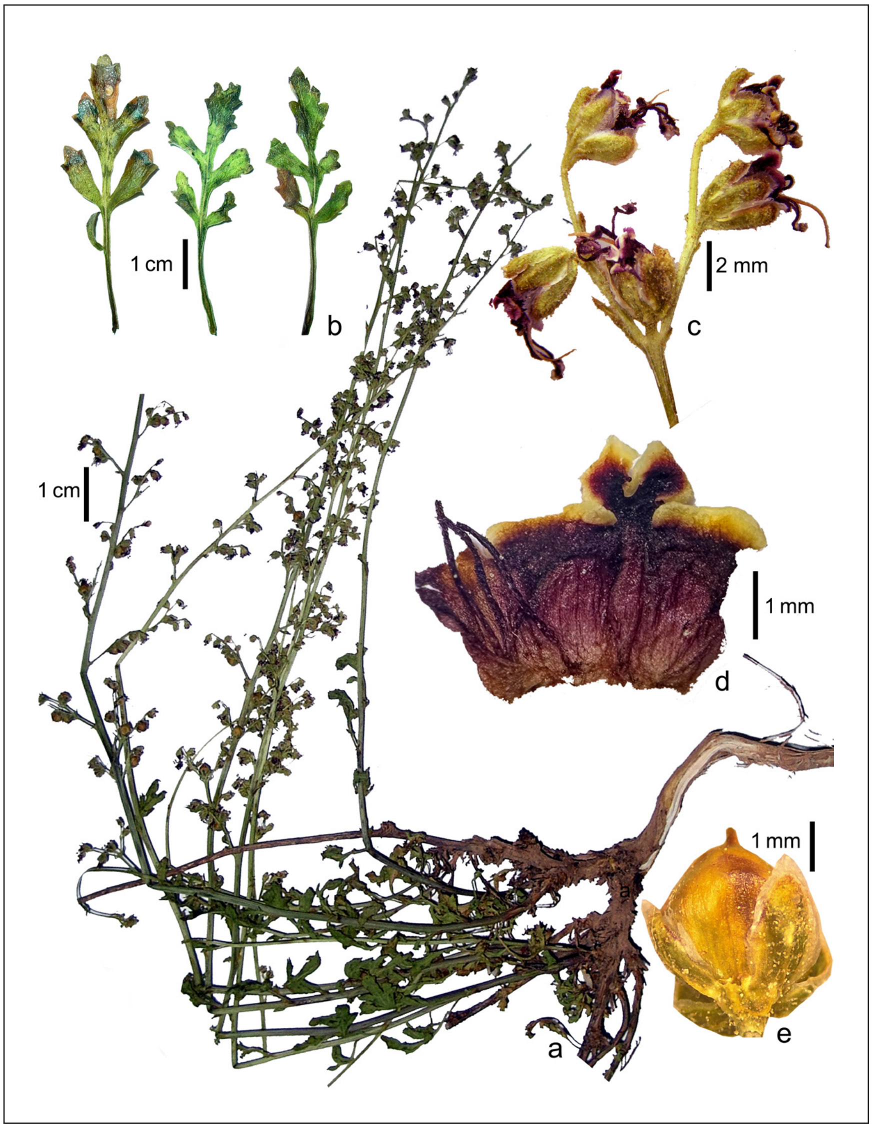

Figure 1. *Scrophularia tugbae-birhanii* from holotype *C. Aykurt* 5074, a- Habit, b- Lower cauline leaves, c- Cymes, d- Inner surface view of corolla, e- Capsule.

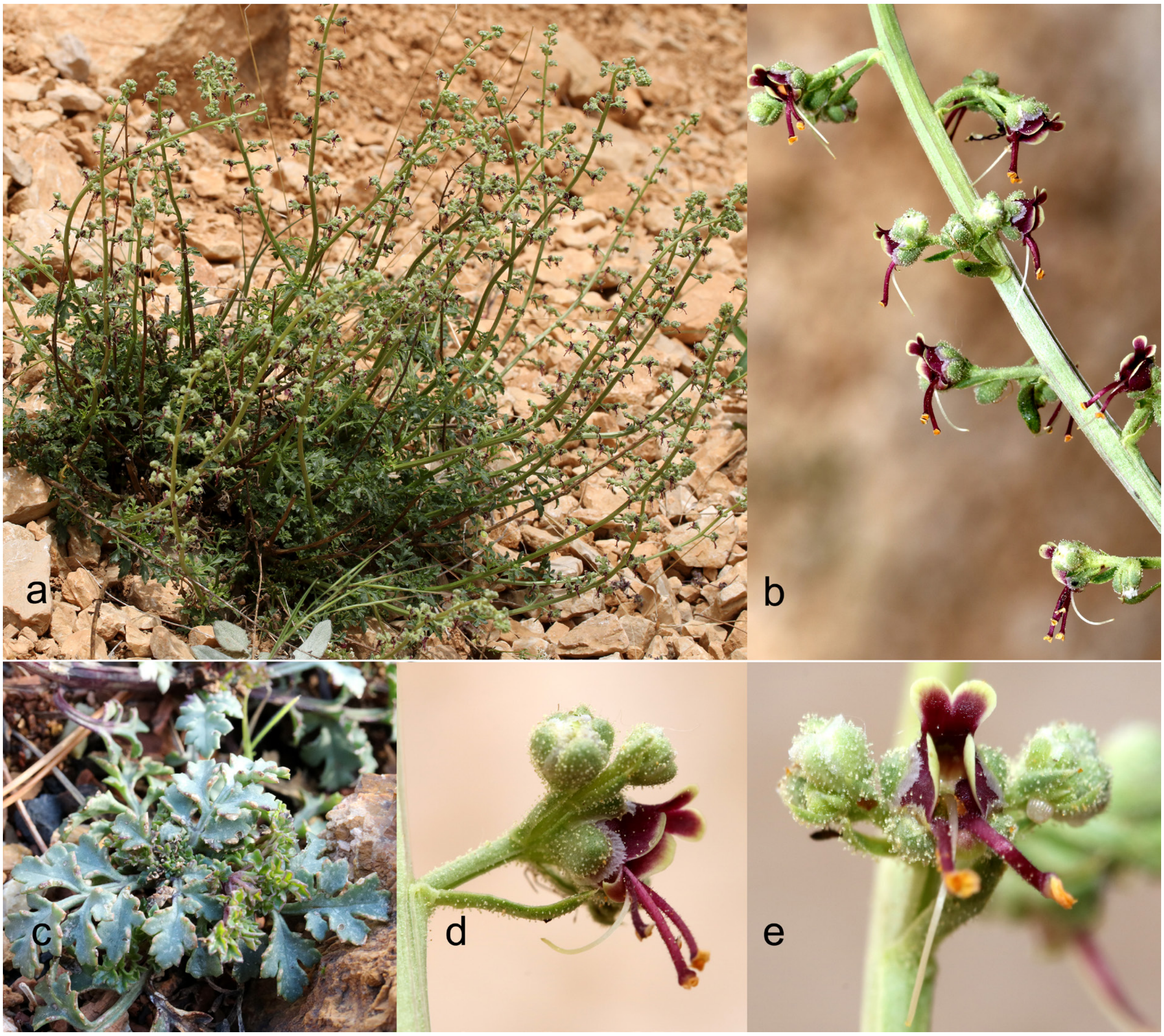

Figure 2. Field photographs of *Scrophularia tugbae-birhanii* from type location, a- Habit, b- A part of inflorescence, c- Basal leaves, d-e- flowers.

length of corolla tube; filaments 4–6 mm long, densely glandular, maroon; anthers ± 0.5–0.6 mm long; staminode absent. Style 4.5–5 mm long, glabrous; ovary 1–1.3 mm long, glabrous. Capsules 2–4 x 2–4 mm, globose, apiculate, pale brown. Seeds alveolate, blackish-brown, oblong to slightly obovoid, 0.7–1.2 × 0.5–1 mm.

Distribution, habitat and ecology: *Scrophularia tugbae-birhanii* is distributed on screes and stony slopes in the Alakır Valley (Kumluca, Antalya) at altitudes ranging between 930 and 1250 m. The species was observed in five different locations, specifically in the southern, eastern, and southeastern aspects of the valley. It occurs in suitable habitats and aspects within the elevation limits specified for the valley. *Muscarimia muscari* (L.) Losinsk. was also recorded in every location with the new species. The new species is associated with plants such as *Plocama calabrica* (L.f.) M.Backlund & Thulin, *Centaurea urvillei* DC., *Pentanema verbascifolium* (Willd.) D.Gut.Larr., Santos-Vicente, Anderb., E.Rico & M.M.Mart.Ort., *Nepeta phyllochlamys* P.H.Davis, *Salvia dorystaechas* B.T.Drew, *Rumex scutatus* L., *Anthemis rosea* Sm. subsp. *carnea* (Boiss.) Grierson, and *Clypeola ciliata* Boiss.

Eponymy: The specific epithet '*tugbae-birhanii*' honors "Tuğba-Birhan", a couple who lives in their own mud house in the Alakır Valley and has devoted their life to the protection of nature.

3.2. Molecular results

The phylogenetic tree obtained from ITS data sets is given in Figure 3, and S. *tugbae-birhanii* falls into a clade with its morphological relative *S. floribunda* along with *S. xanthoglossa*. This clade is supported by PP 0.87 and 60 bootstrap values. Although the close relationship between *S. tugbae-birhanii* and *S. floribunda* is supported by the analysis from *trn*L-F data (Figure 4), *S. xanthoglossa* is placed outside of this clade, but still inside the large polytomic *Canina* clade. The characteristics of the ITS and *trn*L-F datasets are presented in Table 1.

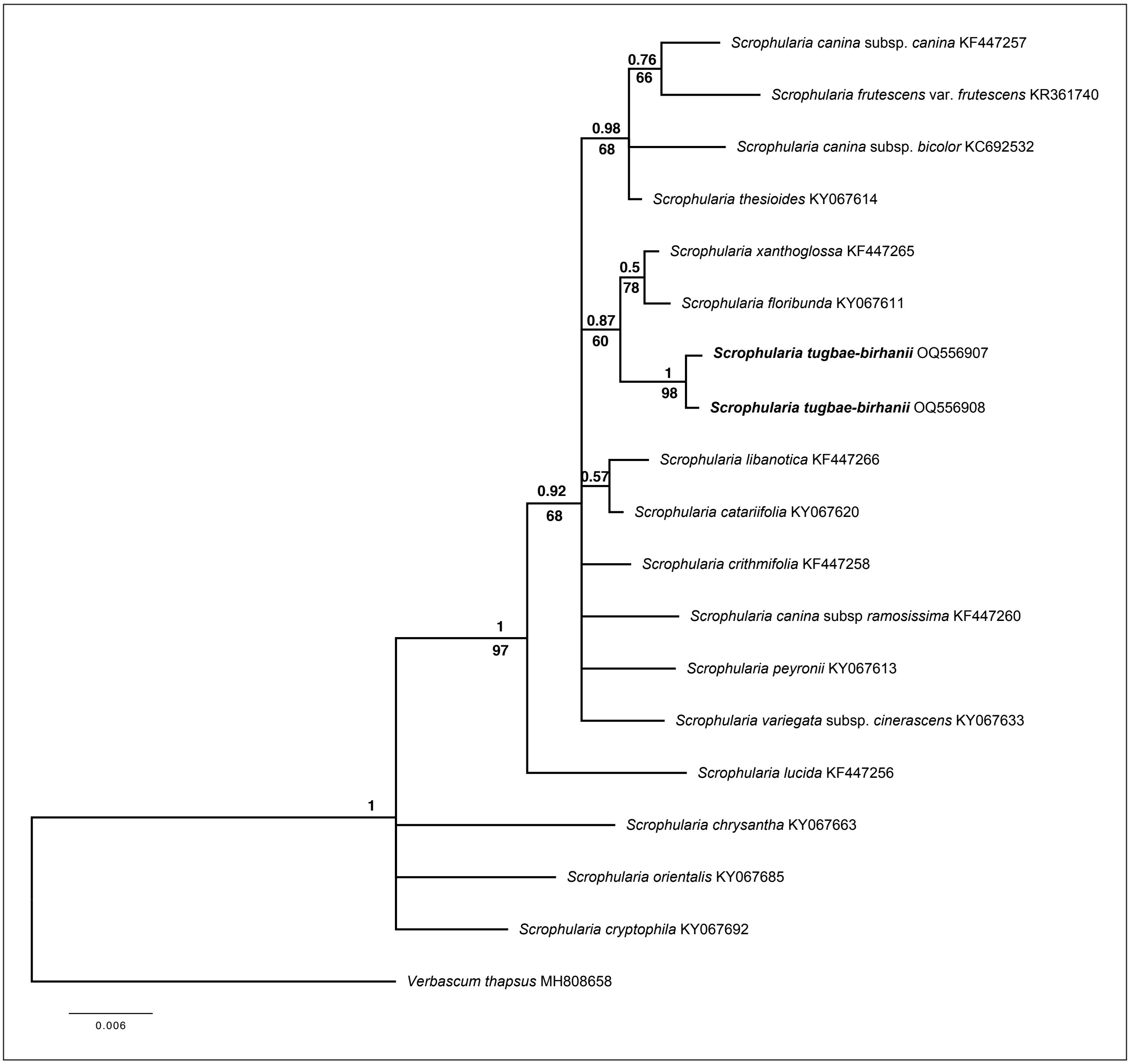

Figure 3. Phylogenetic placement of *Scrophularia tugbae-birhanii* based on internal transcribed spacer (ITS) region. Phylogram is derived from Bayesian analysis. Posterior probabilities (>0.5) and bootstrap values (derived from maximum likelihood analysis) are given above and below the branches, respectively.

The results of the network analysis are shown in Figure 5 as a split graph. The split graph contained 50 splits (bipartitions) and resulted in a NeighborNet network of 132 nodes and 212 edges. The NeighborNet diagram produced is highly congruent with the results obtained with Bayesian and maximum likelihood analyses. The clade including S. *floribunda* and *S. xanthoglossa* along with the newly described species *S. tugbae-birhanii* is easily separated from other species.

4. Discussion

Plant specimens of the new species were collected from Alakır Valley (Kumluca, Antalya) in 2019 for the first time, and subsequently, different populations of the species were observed throughout the valley for four years. It has been observed that *S. tugbae-birhanii* is distributed only on screes and stony slopes of the valley by the field studies carried out between the two valleys of the Beydağlar Mountains (a large part of the Western Taurus range) extending to the sea. The area where the field studies were carried out is known as one of the hottest spots in Türkiye in terms of endemism (Noroozi et al., 2019). The Beydağlar Mountains have an isolated position from other mountain ranges thanks to the Alakır and Akçay Valleys. Since 2016, three new species, which are *Glaucium alakirensis* Aykurt, K. Yıldız & A. Özçandır (Aykurt et al., 2017), *Ricotia candiriana* A. Özçandır,

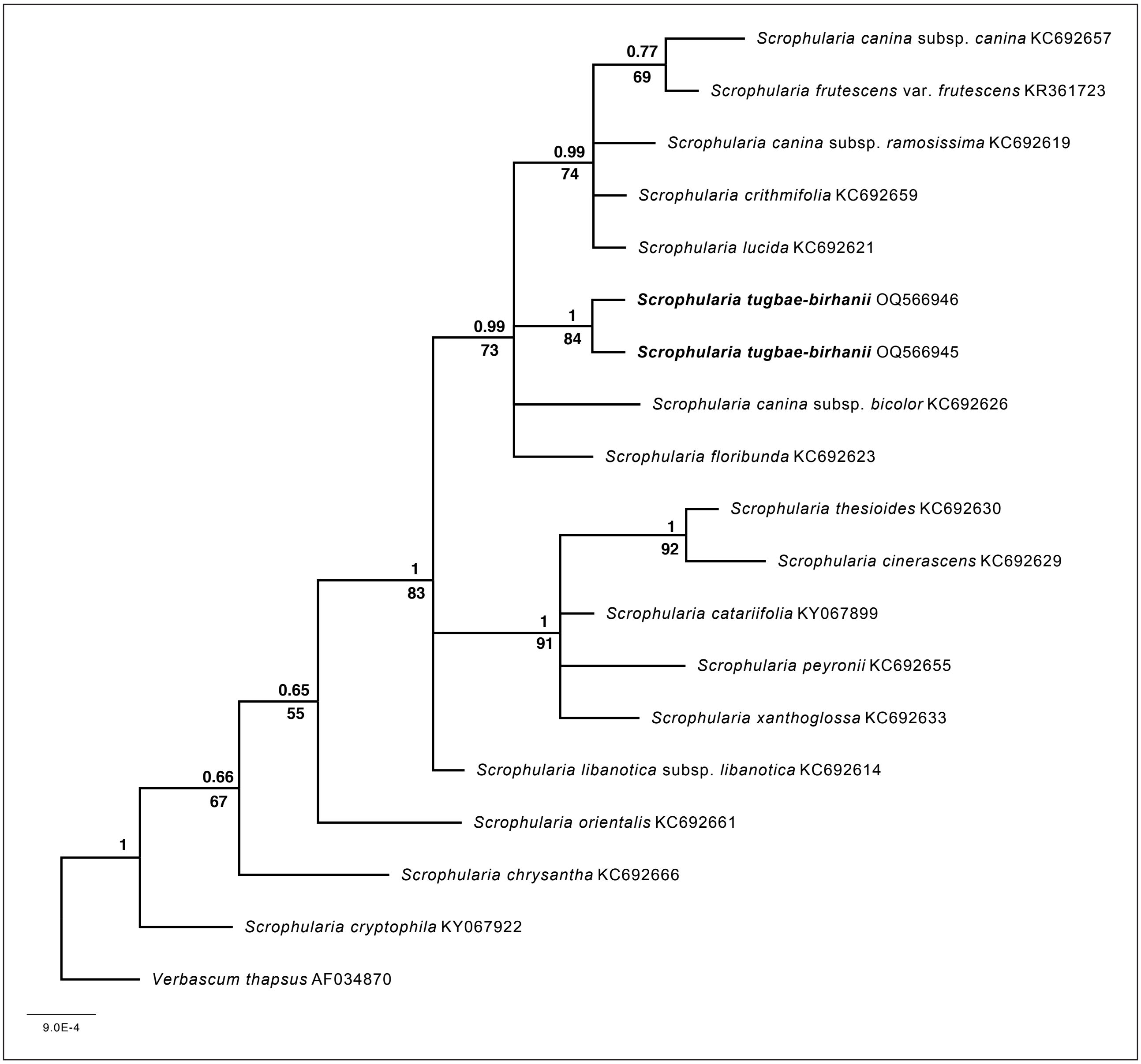

Figure 4. Phylogenetic placement of *Scrophularia tugbae-birhanii* based on *trn*L-F region. Phylogram is derived from Bayesian analysis. Posterior probabilities (>0.5) and bootstrap values (derived from maximum likelihood analysis) are given above and below the branches, respectively.

Aykurt & Özüdoğru (Özçandır et al., 2019) and *Omphalodes nedimeae* Aykurt & Sümbül (Aykurt et al., 2021), have been discovered in this area. The studies conducted on the ancestral area reconstructions (Scheunert and Heubl, 2017) revealed that the genus *Scrophularia* originated in a region comprising Southwestern Asia and Türkiye, which corresponds to its present-day primary center of diversity. As is known, the mountain ranges of the Mediterranean Area provide complex, heterogeneous habitats on small geographical scales, which facilitate adaptive speciation and allopatric divergence (Lobo, 2001; Wen et al., 2014) and can also stabilize new hybrids by isolating them from their parents (Scheunert and Heubl, 2017). The discovery of the new species once again highlights the importance of these areas in terms of the diversification of the genus *Scrophularia*.

Scrophularia is a taxonomically complex genus characterized by frequent natural hybridization, great morphological plasticity, and a variety of polyploid species (Scheunert and Heubl, 2014; Navarro-Pérez et al., 2015; Riahi and Ghahremaninejad, 2019; Scheunert and Heubl, 2017). The genus was divided into two main sections by Stiefelhagen (1910), which are Sect. *Anastomosantes* and Sect. *Tomiophyllum* (= *S.* sect. *Canina*) is mainly based on leaf vein characteristics clearly anastomosing or not. Within the scope of our study, 17 *Scrophularia* taxa, 3 of which are *S. chrysantha*, *S. orientalis* ve *S. cryptophylla* in Sect.

Table 1. Summary statistics of ITS and *trn*L-F regions. N = number of sequences, L = alignment length, V = variable sites, Pi = parsimony-informative characters, C = consistency index, R = retention index.

	N	L	V	Pi	C	R
ITS	19	623	77	24	0.625000	0.666667
*trn*L-F	19	766	27	11	0.923077	0.966667

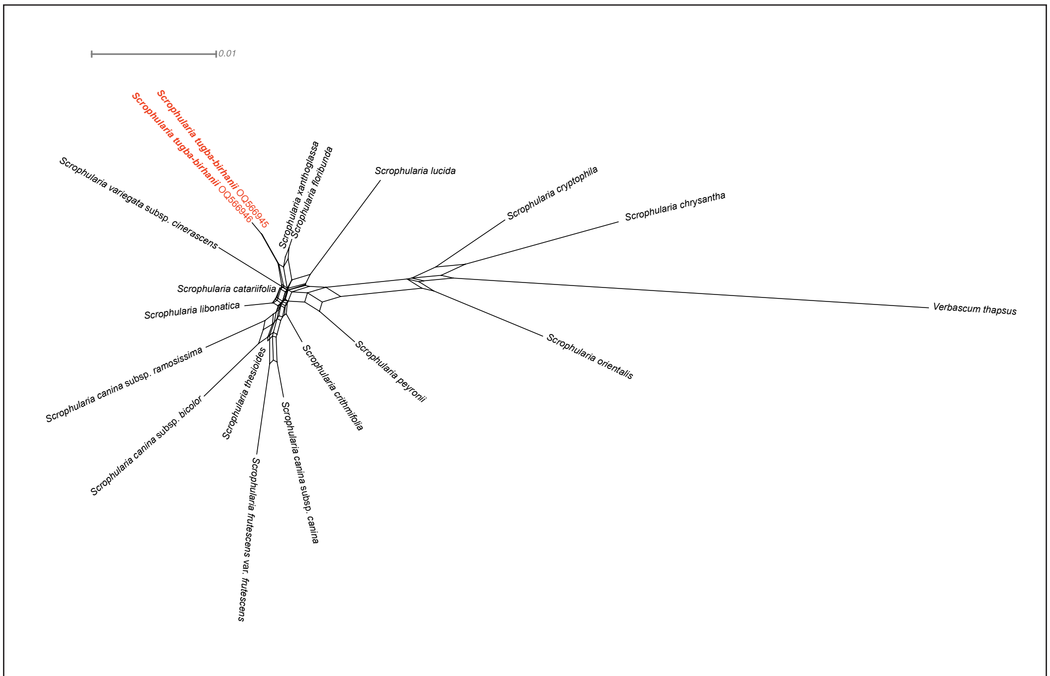

Figure 5. NeighborNet split graph of ITS sequences of *Scrophularia* taxa studied based on SplitsTree program.

Anastomosantes, and 14 taxa in Sect. *Canina*, are included in the phylogenetic analyses. It is assumed that the *Canina* clade has an allopolyploid origin and has reticulation present in its origin (Scheunert and Heubl, 2014). Some species included in the Sect. *Canina* were evaluated by dividing them into species groups by Scheunert and Heubl (2017) by considering the phylogenetic analyses conducted by using nuclear and chloroplast sequences. We focused especially on the "*Canina*" and "*Striata*" species groups to determine the phylogenetic position of the new species and the relationships between its close relatives.

Both ITS and *trn*L-F trees obtained within the scope of the study show that *S. tugbae-birhanii* is a distinct species and easily separated from others (Figures 3 and 4). However, due to the reticulate origin of *Canina* clade (Scheunert and Heubl, 2014), the species is located in different positions in the ITS and *trn*L-F trees. The new species fell into a moderately supported clade (PP 0.87, BS 60) along with a monophyletic subclade consisting of *S. floribunda* and *S. xanthoglossa* and it is a sister to this subclade, according to the ITS tree obtained (Figure 3). The similar relation among these three species can be also seen in the split graph of the ITS sequences (Figure 5). Although *S. floribunda* is morphologically similar to the species included in the *Canina* group, it is close to *S. xanthoglossa* in the ITS tree created by Scheunert and Heubl (2017) and is included in the "*Striata*" species group. However, this close relationship is not supported by the *trn*L-F tree (Figure 4) and the new species and *S. floribunda* are located in a clade with *S. canina*, *S. crithmifolia*, *S. frutescens* from the *Canina* group, whereas *S. xanthoglossa* is placed in a polytomic clade with *S. catariifolia*, *S. peyronii*, *S. cinarescens* and *S. thesioides*. In the *trn*Q-*rps*16 + *trn*L-*trn*F tree by Scheunert and Heubl (2017), *S. xanthoglossa* is still in the *Striata* group, while *S. floribunda* is close to the *Canina* group but separate from this group. This can be explained by the fact that the origin of the *Canina* clade has reticulation, as mentioned before.

In *S. xanthoglossa*, the upper corolla lobes are relatively large, maroon and without a pale border and the corolla have large orbicular and dentate staminodes. Although the corolla of the new species is maroon, the lobes (incl. upper lobes) are with a narrow white border and the corolla is rather small. *Scrophularia tugbae-birhanii* is morphologically similar to *S. floribunda* and *S. canina* subsp. *bicolor* which is the single representative of *S. canina* in Türkiye, in terms of morphological features. The fact that it has particularly long filaments makes the new species morphologically close to *S. floribunda*. The detailed comparison of diagnostic morphological characters of the new species and its close relatives is shown in Table 2. *Scrophularia floribunda* is an endemic species to Türkiye and the East Aegean Islands, and its main distribution area is the Aegean Region of Türkiye, but the limits of its distribution extend to Antalya. This species grows in *Pinus brutia* forests and openings, macchia, calcareous rocky and stony slopes at altitudes between sea level and 1450 m (Lall and Mill, 1978, Uzunhisarcıklı et al., 2018). Some specimens collected by Peşmen and Oflas from Çığlıkara Nature Conservation Area (Elmalı, Antalya), close to the distribution area of *S. tugbae-birhanii*, were evaluated as *S. floribunda* by Lall and Mill (1978). The herbarium material E00713416 belonging to this collection was evaluated within the scope of the study. Interestingly, some flowers without staminodes and some of them having narrowly lanceolate and small staminodes were observed in this sample. A similar situation was also determined in some individuals collected from Bozkaya, near Çığlıkara, during the field studies. The individuals observed in this area, where the distribution areas of the two species converge, were evaluated as transitional forms between *S. floribunda* and *S. tugbae-birhanii*.

Ortega-Olivencia (2009) stated that in most *Scrophularia* species the staminode is represented by an organ which is more or less developed, consisting of a basal zone (the old filament) generally adnate to the corolla upper lip and a free, colored, scale-like distal zone (the old anther), which is glandular on the adaxial side. The differences of flower morphology between the new species without staminode and its closely related species, *S. floribunda* having narrowly lanceolate staminodes, are shown in Figure 6.

Scrophularia crithmifolia within the *Canina* species group (Scheunert and Heubl, 2014, 2017) is so far unique as it is the

Table 2. Comparison of diagnostic morphological characters of the new species and its close relatives.

Characters	*S. tugbae-birhanii*	*S. floribunda* (Lall and Mill 1978)	*S. xanthoglossa* (Lall and Mill 1978)	*S. crithmifolia* (Olivencia 2009	*S. canina* subsp. *bicolor* (Lall and Mill 1978)
Habitus	Perennial herbs	Suffruticose perennials	Perennial (or biennials?) with fleshy to woody stems	Suffruticose perennials	Suffruticose perennials
Stem	25–55 cm long, branched mainly at the base	20–45 cm long, ± unbranched	24–60(–120) cm long, branched mainly at the base	Up to 75 (140) cm long, branched mainly at the base	30–100 cm long or more, many stemmed
Basal leaf shape	1–3 pinnatifid to pinnatisect	2–3 pinnatisect	2–pinnatifid to 3–pinnatisect	2–3 pinnatifid to pinnatisect	1–2 pinnatisect.
Alar pedicels	1–1.5 mm long, ± equal or slightly shorter than bracteoles	1–2 mm long, shorter than bracteoles	0.5–2 mm long, much shorter than bracteoles	(0.5) 1.5–3.5 mm long, generally shorter or less equal than bracteoles	1–2 mm long, shorter than bracteoles
Calyx lobes	Densely glandular; with scarious margin up to 0.5 mm broad, lacerate	Glabrous; with broad (0.7–1.2 mm) scarious margin, lacerate	Glabrous; with scarious margin of 0.3–0.6 mm broad, denticulate to lacerate	Glabrous or sometimes with sessile glands; with a scarious margin of (0.1) 0.2–0.4 (0.6) mm, denticulate	Glabrous; with scarious margin of 0.4–0.5 mm broad, entire to lacerate
Corolla	Maroon, 2.6–3 mm, lobes with a narrow white border	Maroon, 5.5–6 mm; lobes with a white border	Maroon, 5–6 mm; lateral and lower lobes with yellowish-white border	Maroon, 3.4–5.5 (6.5) mm, lateral lobes with whitish border	Maroon, 2.5–5 mm, upper lobes with yellowish–white border
Stamens	Stamens with very long filaments exserted to 1.5–2 × length of the corolla	Stamens with very long filaments exserted to 1.5–2 × length of the corolla	Stamens exserted from corolla tube	Stamens exserted from corolla tube	Stamens exserted from corolla tube
Staminode	Absent	Present / Narrowly linear	Present / Orbicular	Absent	Present / Oblong-lanceolate to narrowly oblong
Capsule	2–4 × 2–4 mm, globose, apiculate, pale brown	3.5–4 mm long, globose, apiculate	4–5 × 3.5–4.5 mm, ovoid to globose, apiculate	(3) 3.5–6 (7) × (3) 3.5–6.5 mm, ovoid or subglobose, apiculate	3.5–4 mm long, globose, apiculate

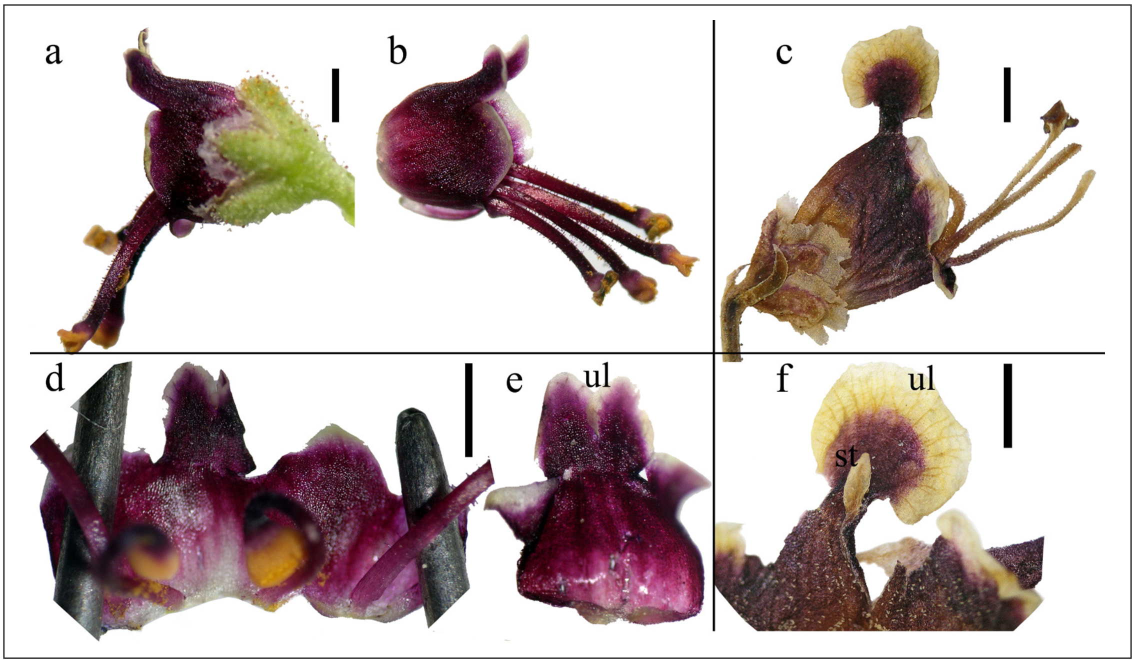

Figure 6. Flower parts photographed under a stereomicroscope of *S. tugbae-birhanii* (*M. Gülben 1025*) (a, b, d, e) and *S. floribunda* (*Davis 41712*) (c, f); (a, c- flower, b- corolla, d- inner surface of corolla, e- close view of inner surface of corolla, f- staminode adnate to the corolla upper lips, st- staminode, ul- upper lips, scale bars: 1 mm).

only species without staminodes. However, the discovery of the new species described here shows that there is also a loss of staminodes in a different lineage in the Sect. *Canina*. Examining the loss of staminodes that occur in phylogenetically close lineages with more detailed studies will make a great contribution to gaining more comprehensive information about the speciation patterns of the genus.

Additional specimens examined:— Paratypes of *Scrophularia tugbae-birhanii*: Türkiye. Antalya, Kumluca, Sarıkaya Wild Life Development Area, Alakır Valley, screes and stony slopes, 1330 m, 7 June 2019, *C. Aykurt 5081, H. Sümbül* and *Z. Öz* (AKDU 6333; HUB); *ibid.*, 30 May 2023, *M. Gülben 1025* (AKDU)*;* Antalya, Kumluca, 3 km west of Kuzca, stony slopes, 900–1100 m, 14 May 2023, *SWLDA 31-2; 34-2; 117-1 (C. Aykurt et al., Obs.)*. ***S. canina:*** Cyprus. Askas: above Askas, 2 km w. of Palekhori, roadside, 950 m, 23 April 1979, *Edmondson 2930 & McClintock* (G 155882); ***S. canina* subsp. *bicolor*:** Türkiye. Kırklareli Elmalı, 5 June 1982, *Oguz & Cetindag* (E00713343); Muğla: 13 km South of Fethiye, by sea, rocks, flowers brown, 16–28 May 1976, *O. Polunin 13929* (E00713349); İstanbul: R. Hissar, Bosphore, 26 June 1918, *B.V.D. Post* (E00713342); İzmir, Bornova, in Ege University, near arable field, 13 March 1966, *H. Peşmen* (E0071344); Eğirdir, around 940 m, 20 May 1966, *Regel* (E0071345); Balıkesir: Edremit, above Mehmet Alan Village, on the Kozdağ Road, May 1967, *H. Peşmen* (E0071346); Muğla: 13 km South of Fethiye, sandy places, 16–28 May 1976, *O. Polunin 13995; 13929* (E0071348; E00713349); Bilecik: Bilecik limestone gorge near station, 300 m, eroded slopes, 2 July 1962, *Davis 36523 & Coode*. (E00713341); Muğla: 1 km west of Muğla, dry, stony soil on the exposed plain, 660 m, *Lambert. & Throp.* (E00713336); İçel: Anamur, Anamur-Kazancı road, Kızılalan, 1400 m, 24 June 1984, *H. Sümbül 3125* (HUB); Konya: Ermenek, Kazancı, 900–1100 m, 19 June 1983, *H. Sümbül 2080* (HUB). ***S. crithmifolia* var. *alpina*** Boiss.: Spain. *Boissier* (type G00343780 photo); ***S. floribunda*:** Türkiye. Antalya: Elmalı-Çığlıkara Forest Enterprise, Sevindik location., around 500 m, 28 April 1968, *H. Peşmen & Oflas* (E00713416; EGE12618); İzmir: Ceşme, 10–50 m, Rocky limestone slopes, 26 April 1965, *Davis41816* (E00713414); İzmir: Kemalpaşa-Karabel, *P. brutia* forest, 21 April 1967, *H. Peşmen & M. Ayder* (E00713417; E00713418; EGE 12593; EGE12617); İzmir: North foot of Samsun Dağ, west of Güzelçamlı, 0–50 m, garigue on limestone, 24 April 1965, *Davis41712* (E00713419); İzmir: Ahmetbeyli, machie, around 700 m, 29 March 1966, *H. Peşmen 474* (EGE6022); İzmir: Kemalpaşa, Nif mountain, 21 May 1980, *Ö. Seçmen 2169* (EGE21491); Muğla: between Milas and Bodrum, Güvercinlik, within the shrubland, calcareous terrain, 0–30 m, 08 April 1981, *A. Güner 3343, B. Yıldız* (ANK; HUB24175); Muğla: near Selimiye, 170 m, temple, *Davis 40722* (E00713415); ***S. lucida*:** Türkiye. Ankara: Kızılcahamam-Soğuksu, National park-in riverbed, 13 November 1966, *Leblebici & Ersoy* (E00655063); Artvin: mountain above Artvin, 1900 m, limestone outcrop, 19 June 1957, *Davis 29810 & Hedge* (E00655068); İzmir: Ödemiş, Bozdag, Gölcük road, around 1000 m, 14 July 1966, *Regel & H. Pesmen* (E00655066); Antalya; Kaş, 22 April 1970, *Ö. Secmen & Aydar* (E00655065). ***S. xanthoglossa:*** Türkiye. Gaziantep: Düllük Baba 7 km, N. of Gaziantep, 1100 m, rocky calcareous slopes, 12 May, 1957 (E00723591 photo); Ankara: Başkent University, South of Bağlıca Campus, behind of Faculty of Science, valley floor and slopes, 30 May 2009, *D. Töre 1777* (HUB); Ankara: Kızılcahamam, Çeltikçi turnout, steep slopes, 9 June 1983, *A. Güner 5014, K. Sorkun* (HUB24720); Nevşehir: Avanos, Kızılırmak riverbank, 28 May 1978, *Ş.Yıldırımlı 1046* (HUB24723); Nevşehir: Ortahisar, 1200 m, 23 May 1989, *M. Vural, Ü. Kol, N. Adıgüzel* (HUB 24484); Isparta: Şakikaraağaç, Kızıldağ National Park, Kıyakdede Mountain, east slopes, 1150 m, 11 May 1995, *B. Mutlu 1332* (HUB 37155); Kahramanmaraş: Göksun, Çardak, Kandil Mountain, *Pinus* woodland, 1500–1800 m, 12 June 1978, *B. Yıldız 2062* (HUB24713); Erzincan: Kemah, Uluçınar village environs, Munzur Mountains, 1500 m, 28 May 1979; *Ş. Yıldırımlı 1651* (HUB24712); Ankara: Güdül, Kimil River Valley, aglomera, rocks, 11 September 2002, *B. Tarıkahya 1486* (HUB); Ankara: Çubuk, Karagöl, volcanic slopes, *S. Erik 220* (HUB24715).

Acknowledgments

We would like to thank The Scientific and Technological Research Council of Türkiye (TÜBİTAK; project no. KBAG-120Z584) and Akdeniz University Scientific Research Projects Unit (Project number: FBA-2018-3773) for financial support of this study. We also would like to thank the curators of the AKDU, ANK, E, EGE, G, and HUB for access to specimens.

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Appendix
Locality data of the taxa used in the phylogenetic analyses for the current study and GenBank accessions numbers.

Taxon	**Locality and reference number**	**Acc. no.**
ITS		
S. tugbae-birhanii	Türkiye, Antalya, *C. Aykurt 5074* (AKDU 6332)	OQ556907
S. tugbae-birhanii	Türkiye, Antalya, *C. Aykurt 5081* (AKDU 6333)	OQ556908
S. canina L. subsp. *bicolor* (Sm.) Greuter	Türkiye, Denizli, *A. Ortega-Olivencia & F.J. Valtueña 89AOO/11* (UNEX 36050)	KC692532
S. canina L. subsp. *canina*	Morocco, Tiznit, D. Podlech 52525 (MSB)	KF447257
S. canina L. subsp. *ramosissima* (Loisel.) Bonnier & Layens	Sardinia, Oristano, *U. Hecker I 774* (MJG)	KF447260
S. catariifolia Boiss. & Heldr.	Türkiye, Hakkari, *P.H. Davis 45685* (M)	KY067620
S. *chrysantha Jaub. & Spach*	CULT., orig.: - *A. Scheunert 022/1-1* (MSB)	KY067663
S. crithmifolia Boiss.	Spain, Malaga, *E. Bayer, J. Grau & G. López González* (M)	KF447258
S. cryptophila Boiss. & Heldr.	Türkiye, Konya, *M. Nydegger 47235* (MSB)	KY067692
S. floribunda Boiss. & Balansa	Türkiye, Izmir, *P.H. Davis 41712* (M)	KY067611
S. frutescens L. var. *frutescens*	Spain, Roquetas de Mar, Punta Entinas-Pta. del Sabinar, *A. Ortega-Olivencia 11AOO/09* (UNEX 35988)	KR361740
S. libanotica Boiss.	Iraq, Sulaymaniyyah, *K.H. Rechinger 10358* (M)	KF447266
S. lucida L.	Greece, Attica, *J. Grau* (M)	KF447256
S. orientalis L.	Azerbaidzhan, Ganja-Qazakh, *A.K. Skvortsov* (M)	KY067685
S. peyronii Post	Syria, Dar'a, *K.H. Rechinger 13009* (M)	KY067613
S. thesioides Boiss. & Buhse	Türkiye, Gümüşhane, *M. Nydegger 46781* (M)	KY067614
S. variegata M.Bieb. subsp. *cinerascens* (Boiss.) Grau	Iran, E-Azerbaijan, *K.H. Rechinger 40378* (M)	KY067633
S. xanthoglossa Boiss.	Israel, Negev, *K. Tielbörger* (M)	KF447265
Verbascum thapsus L.	-	MH808658
***trn*L-F**		
S. tugbae-birhanii	Türkiye, Antalya, *C. Aykurt 5074* (AKDU 6332)	OQ566945
S. tugbae-birhanii	Türkiye, Antalya, *C. Aykurt 5074* (AKDU 6333)	OQ566946
S. canina L. subsp. *bicolor* (Sm.) Greuter	Türkiye, Denizli, *A. Ortega-Olivencia & F.J. Valtueña 89AOO/11* (UNEX 36050)	KC692626
S. canina L. subsp. *canina*	Morocco. TD: puerto de Tizi-n-Nissi, *L. Medina LM3416* (MA 745799)	KC692657
S. canina L. subsp. *ramosissima* (Loisel.) Bonnier & Layens	Italy, Palau, *porto Pollo, M. Navarro 54AOO/10* (UNEX 35911)	KC692619
S. catariifolia Boiss. & Heldr.	Türkiye, Hakkari, P.H. Davis (M)	KY067899
S. *chrysantha Jaub. & Spach*	Armenia, monte Aragat, Ghazaravan, *Medina et al. 2552* (MA 743942)	KC692666
S. cinerascens Boiss.	Armenia, lago Sevan, pr. Tsovazard, *Herrero et al. 2544* (UNEX 35961)	KC692629
S. crithmifolia Boiss.	Spain, Malaga, Álora, a 9 km de Carratraca, *A. Ortega-Olivencia* (UNEX 26214)	KC692659
S. cryptophila Boiss. & Heldr.	Türkiye, Konya, *M. Nydegger 47235* (MA 742218)	KY067922
S. floribunda Boiss. & Balansa	Türkiye, Izmir, Kemalpaşa, Karabel, *A. Ortega-Olivencia & F.J. Valtueña 88AOO/11* (MA 687764)	KC692623
S. frutescens L. var. *frutescens*	Spain, Roquetas de Mar, Punta Entinas-Pta. del Sabinar, *A. Ortega-Olivencia 11AOO/09* (UNEX 35988)	KR361723
S. libanotica Boiss. subsp. libanotica	Türkiye, Gümüshane, road Gümüshane to Bayburt, *S. Nisa* (MA 687764)	KC692614
S. lucida L.	Greece, entre Sofikó y Angelokastro, *T. Rodríguez-Riaño & J. López 106AOO/1* (UNEX 35961)	KC692621
S. orientalis L.	Armenia, *S. Castroviejo et al. 17688* (MA 743942)	KC692661

S. peyronii Post	Türkiye, Sanliurfa, Hilvan, *A. Ortega-Olivencia & F.J. Valtueña 97AOO/11* (UNEX 3605)					KC692655
S. thesioides Boiss. & Buhse	Armenia, c. embalse Azat, c. Landjazat, *C. Navarro 5837* (MA 742276)					KC692630
S. xanthoglossa Boiss.	Israel, Kfar Yehoshua, A. Ortega-Olivencia 43AOO/10 (UNEX 36092)					KC692633
Verbascum thapsus L.	-	-	-	-	-	AF034870