

Research article

Two new chasmophytic species of *Silene* (Caryophyllaceae, sect. *Siphonomorpha*) from IranFarzaneh JAFARI ^{1,*}, Maryam KESHAVARZI ², Moslem DOOSTMOHAMMADI ³ & Mansour MIRTADZADINI ⁴^{1,2} Department of Plant Sciences, Faculty of Biological Sciences, Alzahra University, Vanak, 1993893973 Tehran, Iran.^{3,4} Department of Biology, Faculty of Science, Shahid Bahonar University of Kerman, P.O. Box 76169-133, Kerman, Iran.*Corresponding author: f.jafari@alzahra.ac.ir²Email: m.keshavarzi@alzahra.ac.ir³Email: doost@sci.uk.ac.ir⁴Email: mirtadz@uk.ac.ir

Abstract. Based on morphological and molecular evidence, two new species of *Silene* are recognized and described here, *S. penduliflora* F.Jafari, Keshavarzi & Doostm. sp. nov. and *S. thyrsoniantha* F.Jafari, Mirtadz. & Keshavarzi sp. nov. The newly discovered species are distributed in the central and southeastern parts of Iran, growing in rocky habitats. Relationships among these species and their close relatives are demonstrated using nrDNA ITS and cpDNA *rps16* phylogenies. *Silene ghahremanejadii*, *S. parrowiana*, and *S. shahrudensis* form a clade with these new species. A key to *S. penduliflora* and *S. thyrsoniantha* and their close relatives is provided.

Keywords. cpDNA *rps16*, Iran, nrDNA ITS, *Silene*, *Siphonomorpha*, sp. nov.

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Introduction

Silene L. is the largest genus of Caryophyllaceae Juss., consisting of ca 870 species. It is mainly distributed in the Northern hemisphere with the highest diversity in the Mediterranean region, West and Central Asia (Hernández-Ledesma *et al.* 2015; Jafari *et al.* 2020).

The flora of Iran is rich in *Silene* and in *Flora Iranica*, Melzheimer (1988) recognized 98 species assigned to 21 sections. A more recent taxonomic study indicated ca 120 species, classified in three subgenera and 16 sections (Jafari *et al.* 2019). Habitats in Iran with species of *Silene* range from an alpine zone (Lalezar Mt) to sea level (Bandar Anzali), where they grow on rocky mountain steppes, on grasslands, and sometimes in woodlands (Jafari *et al.* 2020). Species of *Silene* in Iran mainly belong to *S.* sect. *Auriculatae* (Boiss.) Schischk., including 57 perennial species and more than 25 endemics.

Seven new taxa belonging to this section have been described after Melzheimer's (1988) study was published (Edalatiyan *et al.* 2011; Gholipour & Parsa Khanghah 2015; Gholipour 2017, 2021; Jafari *et al.* 2019; Heidari Rican *et al.* 2020). In addition to these seven species, six other taxa in this section have been reported as new to the flora of Iran since 1988 (Edalatiyan *et al.* 2010, 2017; Gholipour *et al.* 2016; Gholipour & Amini Rad 2017; Heidari Rican *et al.* 2019).

Silene sect. *Siphonomorpha* Otth s. lat., as circumscribed by Naciri *et al.* (2017) and Jafari *et al.* (2020), is characterized by a perennial habit (a few biennials are known), often thyrsoid synflorescences, viscid upper stem internodes, tubular or campanulate calyx in the flower and clavate or campanulate in the fruit, corolla with or without coronal scales, and entire to deeply bifid petal limbs. The section comprises 150 perennial diploid species distributed in Europe, West Asia, Middle Asia, East Asia and North Africa, and is one of the largest sections of the genus. Short branches with low resolution in phylogenetic trees (Đurović *et al.* 2017; Naciri *et al.* 2017; Jafari *et al.* 2020) together with a high species diversity may indicate a rapid recent radiation in this section. The traditional classification of *Silene* followed by Melzheimer (1988) did not include *S.* sect. *Siphonomorpha* in the region of the *Flora Iranica*, while a more recent molecular phylogenetic study (Jafari *et al.* 2020) demonstrated that *S. cyri* Schischk. and *S. italica* (L.) Pers., treated as members of *S.* sects. *Otites* (Adans.) Otth and *Paniculatae* (Willk.) Chowdhuri respectively by Melzheimer (1988), belong to *S.* sect. *Siphonomorpha* s. lat. Although *S. nizvana* Melzh. and *S. ruprechtii* Schischk. were assigned to *S.* sects. *Auriculatae* and *Lasiostemones* (Boiss.) Schischk. respectively by Melzheimer (1988), a molecular phylogenetic study did not support that placement; instead, these taxa were also nested within *S.* sect. *Siphonomorpha* s. lat. (Jafari *et al.* 2020).

Silene parrowiana Boiss. & Hausskn. is a perennial and endemic species occurring in the west of Iran, Kermanshah Province. It grows on rocks of the Parrow Mountain from Bisotun to Mianrahan (Jalilian *et al.* 2018). The species is characterized by a dense and slightly capitate paniculate inflorescence and basal leaves remaining alive in autumn and winter (Melzheimer 1988). While Melzheimer (1988) recognized *S. parrowiana* as a member of *S.* sect. *Lasiostemones*, phylogenetic data demonstrated that *S. parrowiana* should be placed in *S.* sect. *Siphonomorpha* s. lat. with other perennial species including *S. shahrudensis* Rech.f. and *S. ghahremaninejadii* Hoseini & Assadi (Bahmani *et al.* 2020). *Silene shahrudensis* and *S. ghahremaninejadii* were described from Shahrud in Semnan Province and Khamin Mountain in Kohgiluyeh and Boyer-Ahmad Provinces, respectively.

During field surveys and in the course of studying the morphology and phylogeny of *Silene* from Iran, we have found two species that cannot be attributed to any of the described species. The two species are here described based on a combination of morphological and molecular phylogenetic data. A key to the two new species is provided, as well as a discussion of phylogenetic relationships and morphological affinities with allied species.

Material and methods

Taxonomic study

We studied specimens deposited at FUMH, GB, HSHU, IRAN, M, MIR, MSB, S, SFAHAN, TARI, and TUH (abbreviations according to Thiers 2022+). Identifications were conducted using *Flora Iranica* (Melzheimer 1988). We used online images on GBIF (2022) (<https://www.gbif.org/>) and JACQ (<https://www.jacq.org/>) to study the type and isotype specimens of *S. parrowiana*, *S. shahrudensis*, and their close relatives. In addition, field studies were carried out to examine species in their natural habitats during the period 2016–2020 in various regions of Iran.

Phylogenetic study

We assembled two datasets including 53 and 49 accessions for both nrDNA ITS and cpDNA *rps16* regions respectively which were extracted from GenBank (see Appendix). The specimens proposed here as new species were sequenced as part of this study. The accessions were selected mainly from *S. sect. Siphonomorpha* s. lat. with representatives belonging to other sections from the subgenera *Behenantha* (Otth) Torr. & A.Gray, *Lychnis* (L.) Greuter, and *Silene*.

DNA was extracted from herbarium specimens using the NucleoSpin Plant DNA extraction kit (Macherey Nagel, Düren, Germany) and the Sinaclon Plant DNA extraction kit (Tehran, Iran) according to the manufacturer's protocols. Polymerase chain reaction (PCR) amplifications were performed in 25 µL reactions, containing 10 µL of deionized water, 12.5 µL of 2X Reddy® to use PCR Master Mix, 0.5 µL of each primer (10 pmol/µL), and 1 µL of template DNA. Amplification of the ITS region was performed using the primers P17 and 26S-82R (Popp & Oxelman 2001). We used the primers *rpsF* and *rpsR2R* for amplification of *rps16* (Oxelman *et al.* 1997). Cycle sequencing was done using the BigDye Terminator ver. 3.1, Cycle Sequencing Kit (Applied Biosystems, Carlsbad, California, USA). DNA samples were sequenced with an ABI3130XL DNA Analyser 16-well capillary sequencer (Applied Biosystems) performed by Niagene Noor (Tehran, Iran).

Sequence alignment was performed in MAFFT ver. 7 (Kuraku *et al.* 2013; Katoh *et al.* 2019) at the web service (<http://mafft.cbrc.jp/alignment/server/>). The default setting was applied for all options. The preliminary alignments were then corrected manually. PAUP* 4.0a169 (Swofford 2022) was used to select the best-fitted model of nucleotide substitutions based on the Akaike information criterion corrected (AICc). The General Time Reversible model with Gamma-shaped rate variation (GTR+G) model was selected for both regions. Maximum likelihood (ML) analyses were conducted in RAxML HPC ver. 8.2.12 (Stamatakis 2014) using the GTRGAMMA model with 1000 pseudo-replicates to evaluate bootstrap support for each node. Bayesian gene tree inference was performed using MrBayes ver. 3.2.7a (Ronquist *et al.* 2012) with 2 million generations for both nrDNA ITS and cpDNA *rps16* datasets. Four Metropolis-coupled chains were run with trees and parameter values saved every 1000th generation in two parallel runs. The first 25% of total trees were discarded as burn-in. All phylogenetic analyses were carried out on the CIPRES science gateway (Miller *et al.* 2010).

Results

Molecular phylogeny

The ITS (Fig. 1) and *rps16* (Fig. 2) phylogenies are concordant, showing a clade with *S. ghahremaninejadii*, *S. parrowiana*, *S. shahrudensis*, and four GenBank accessions of *S. ruprechtii* Schischk. (MN420835 and MK559501 in ITS tree; MN460318 and MN460319 in *rps16* tree) for which we could not confirm the species identification (more details in Discussion below). The specimens from Semirrom and Kerman (Palvar Mountain) proposed here as new species are nested within this clade as well (Fig. 1, PP (Posterior probability)=1, MLB (Maximum likelihood bootstrap)=100%; Fig. 2, PP=0.98). The three accessions of *S. ruprechtii* and *S. saxatilis* Sims form a distinct cluster clearly separate from *S. parrowiana* and its close relatives (Fig. 1, PP=1, MLB=81%; Fig. 2, PP=0.92).

Morphological characters

Silene penduliflora F.Jafari, Keshavarzi & Doostm. sp. nov. and *S. thyrsoniantha* F.Jafari, Mirtadz. & Keshavarzi sp. nov. (see taxonomic treatment) and close relatives including *S. ghahremaninejadii*, *S. parrowiana* and *S. shahrudensis* are perennial endemic taxa that are distributed in southeastern, central and western Iran (Fig. 3). They are characterized by a compact caudex, thyrsoid synflorescences, glabrous, fleshy, and glaucous leaves, a glabrous, coriaceous calyx, and petal claws without coronal scales (Table 1).

The protologue of *S. ghahremaninejadii* (Hoseini & Assadi 2016) and the treatments of *S. parrowiana* and *S. shahrudensis* in the *Flora Iranica* (Melzheimer 1988) defined the inflorescences of these taxa as panicles. We believe these taxa have a determinate inflorescence and we consider the synflorescence as thyrsoid here (Simpson 2006; Staedler & Endress 2009).

We demonstrate that the reduction in the number of flowers in the dichasia and the elongation of pedicels and peduncles are diagnostic features between the new species and *S. parrowiana* (Fig. 4).

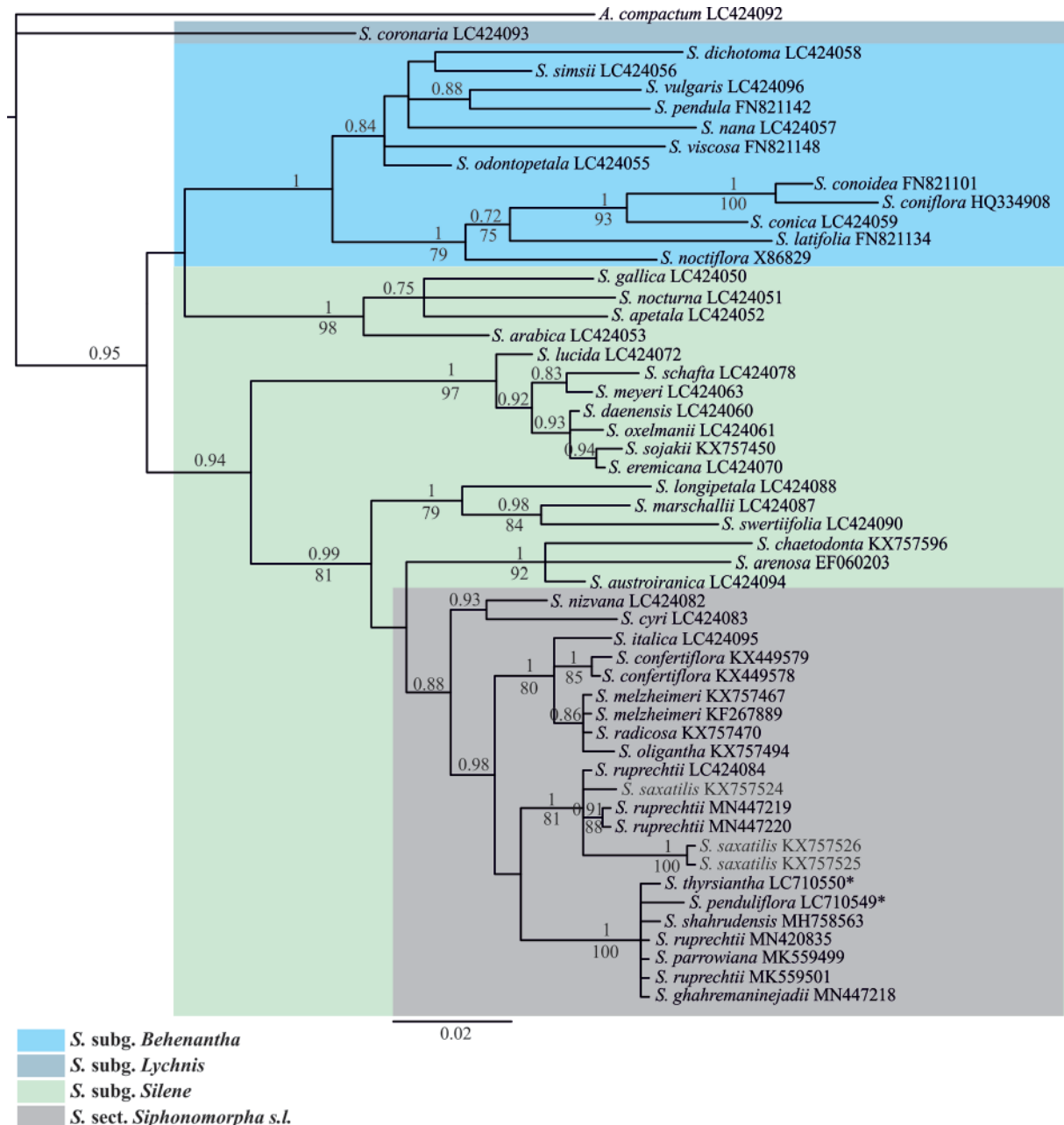


Fig. 1. 50% majority-rule consensus tree obtained from the Bayesian inference analysis of the nrDNA ITS sequences in selected species of *Silene* L. Posterior probabilities (PP) ≥ 0.70 are shown above the branches and Maximum likelihood bootstrap (MLB) values $\geq 70\%$ below. Accessions newly sequenced are indicated by a star. Accessions of *S. ruprechtii* Schischk. (MN420835 and MK559501) are misidentified by Bahmani *et al.* (2020).

Taxonomic treatment

We examined the morphological characters of *S. parrowiana* and its close relatives including *S. ghahremaninejadii* and *S. shahrudensis* together with collections from the Semirom and Palvar Mountains. The morphological differences (Table 1), ITS and *rps16* phylogenies (Figs 1–2) and the geographical distinction (Fig. 3) of these taxa led us to treat collections from the Semirom and Palvar Mountains with the Jupar Mountains as new species.

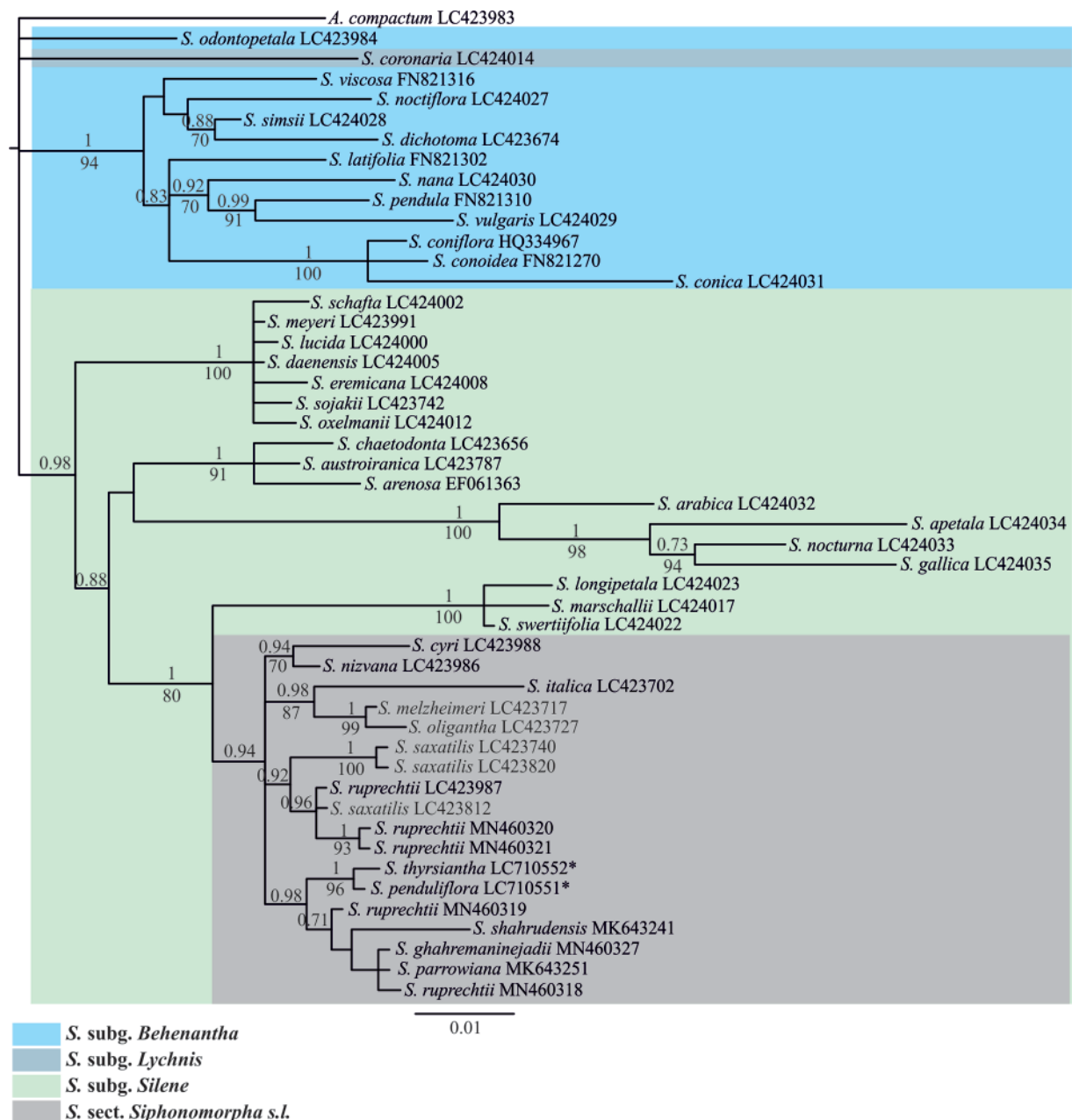


Fig. 2. 50% majority-rule consensus tree obtained from the Bayesian inference analysis of the cpDNA *rps16* sequences in selected species of *Silene* L. Posterior probabilities (PP) ≥ 0.70 are shown above the branches and Maximum likelihood bootstrap (MLB) values $\geq 70\%$ below. Accessions newly sequenced are indicated by a star. Accessions of *S. ruprechtii* Schischk. (MN460318 and MN460319) are misidentified by Bahmani *et al.* (2020).

Key to *S. penduliflora* F.Jafari, Keshavarzi & Doostm. sp. nov., *S. thyrsoniantha* F.Jafari, Mirtadz. & Keshavarzi sp. nov. and close relatives

1. Stems non-viscid; synflorescences densely thyrroid, pedicel <4 mm; calyx <8 mm.....
..... *S. parrowiana* Boiss. & Hausskn.
- Stems viscid; synflorescences laxly thyrroid, pedicel >4 mm; calyx usually >8 mm..... 2
2. Calyx 7–11 mm; pedicel 5–9 mm; capsule 6.5–9×2.5–5.5 mm 3
- Calyx 8–10 mm; pedicel (4.5–)5–16 mm; capsule 4–6×3–4 mm 4
3. Basal leaves 5–32×2–4.5 mm; calyx 7–9 mm; petal limb 2–3 mm; capsule 6.5–7×2.5–3 mm.....
..... *S. ghahremaninejadii* Hoseini & Assadi
- Basal leaves 11–60×2.5–4 mm; calyx 9–11 mm; petal limb 5–6 mm; capsule 7.5–9×4–5.5 mm
..... *S. penduliflora* F.Jafari, Keshavarzi & Doostm. sp. nov.
4. Stem non-thick; pedicel (4.5–)5–16 mm; petal limb ca 5 mm; claw glabrous; seeds 0.8×0.6–0.7 mm;
seed testa cell margins V-shaped; distribution: Isfahan Province.....
..... *S. thyrsoniantha* F.Jafari, Mirtadz. & Keshavarzi sp. nov.
- Stem thick; pedicel 6–12 mm; petal limb 5–5.5 mm; claw ciliate; seeds 1.1×0.8 mm; seed testa cell
margins U-shaped; distribution: Semnan Province *S. shahrudensis* Rech.f.

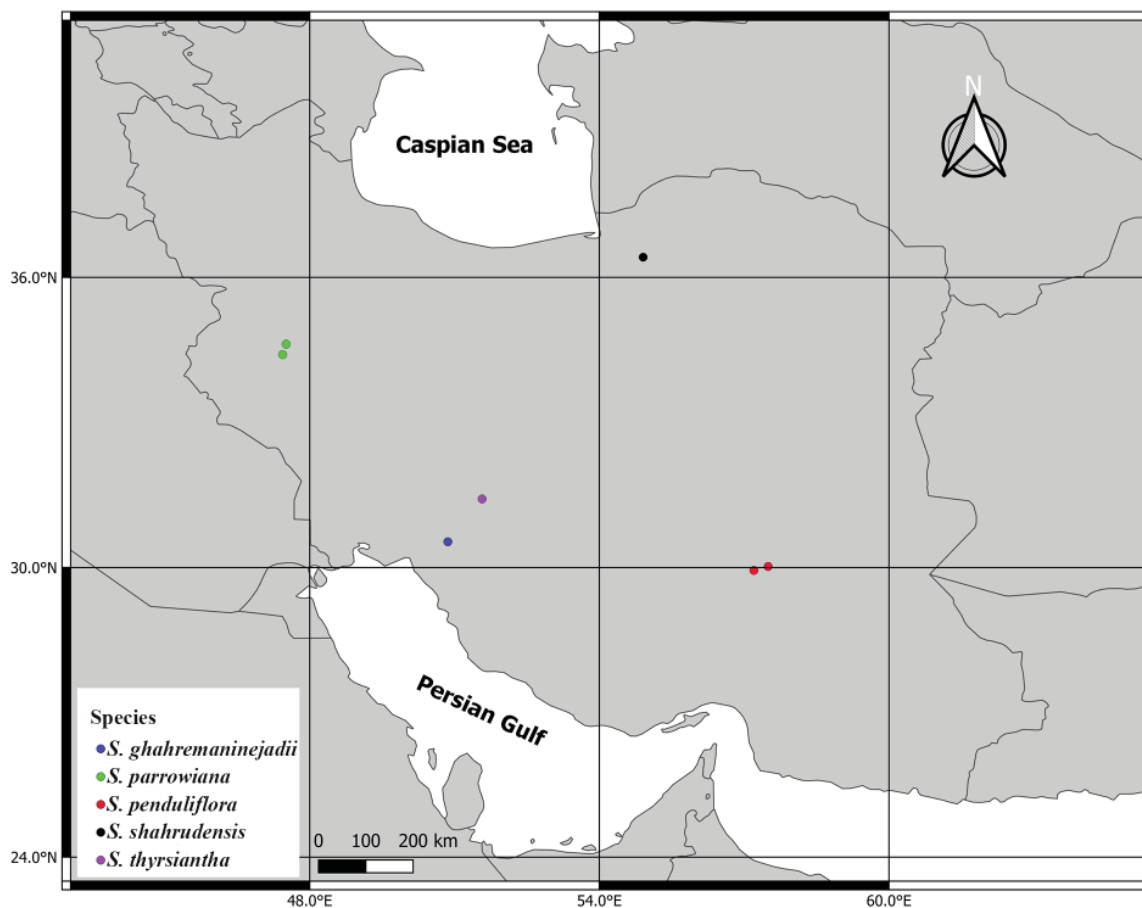


Fig. 3. Distribution map of *S. ghahremaninejadii* Hoseini & Assadi (blue dot), *S. parrowiana* Boiss. & Hausskn. (green dots), *S. penduliflora* F.Jafari, Keshavarzi & Doostm. sp. nov. (red dots), *S. shahrudensis* Rech.f. (black dot), and *S. thyrsoniantha* F.Jafari, Mirtadz. & Keshavarzi sp. nov. (purple dot). The map was made with QGIS ver. 3.22.9.

Table 1. Morphological comparison among *S. penduliflora* F.Jafari, Keshavarzi & Doostm. sp. nov., *S. thyrsoantha* F.Jafari, Mirtadz. & Keshavarzi sp. nov. and close relatives. Distinctive character states are shown in bold.

	<i>S. ghahremaninejadii</i>	<i>S. parrowiana</i>	<i>S. thyrsoantha</i>	<i>S. penduliflora</i>	<i>S. shahrudensis</i>
Plant length	Up to 58 cm	Up to 40 cm	33.5–35.5 cm	29.5–40.5 cm	25–35 cm
Stem	yellowish-green, puberulent with eglandular hairs in lower parts , glabrous and highly viscid above	yellowish-green, subglaucous, glabrous, non-viscid	pale green, glabrous, viscid	pale green, glabrous, viscid	pale green, glabrous, viscid above the middle
Leaf texture	non-fleshy, glabrous	fleshy, glabrous	almost fleshy, glabrous, sometimes ciliate	non-fleshy, glabrous	almost coriaceous, glabrous or scaberulous
Leaf apex	subacute	acute, acuminate	acute, acuminate, shortly mucronate	rounded and acute	rounded and shortly subcartilaginous-mucronate
Basal leaves	5–32 × 2–4.5 mm, linear-lanceolate to broadly lanceolate	35–47 × 5–10 mm, oblanceolate	14–20 × 2.5–4 mm, oblanceolate	11–60 × 2.5–4 mm, oblanceolate	15–35 × 2.5–6 mm, oblanceolate-spatulate
Cauline leaves	lanceolate to broadly lanceolate	oblong to linear	oblanceolate to linear	oblanceolate to linear	narrowly oblanceolate to linear-spatulate
Synflorescence	laxly thyrsoid	densely thyrsoid , subcapitate at top	thyrsoid with few flowers	thyrsoid	laxly thyrsoid
Pedicel length	4–5 mm	1–4 mm, shorter than calyx	4.5–16 mm	5–9 mm	6–12 mm
Calyx length	7–9 mm	(6)7–8 mm	8–10 mm	9–11 mm	8–10 mm
Calyx shape	cylindric	obconic-cylindric	narrow cylindric	cylindric	narrow obconic-cylindric
Calyx texture	subcoriaceous	coriaceous	coriaceous	coriaceous	coriaceous
Calyx teeth	obtuse, scarious margins	ovate, membranous margins	acute, obtuse, or triangular, membranous margins	acute, obtuse, or triangular, membranous margins	acute or triangular, membranous margins
Petal limb length	2–3 mm	ca 4 mm	5–5.5 mm	5–6 mm	ca 5 mm
Claw indumentum	glabrous	ciliate	glabrous	glabrous	ciliate
Anthophore length	2.5–4 mm	2–3 mm	3 mm	3.5 mm	3–4 mm
Capsule	6.5–7 × 2.5–3 mm	4–4.5 × 3–3.5 mm	5.5–6 × 3–3.5 mm	7.5–9 × 4–5.5 mm	4–6 × 3–4 mm

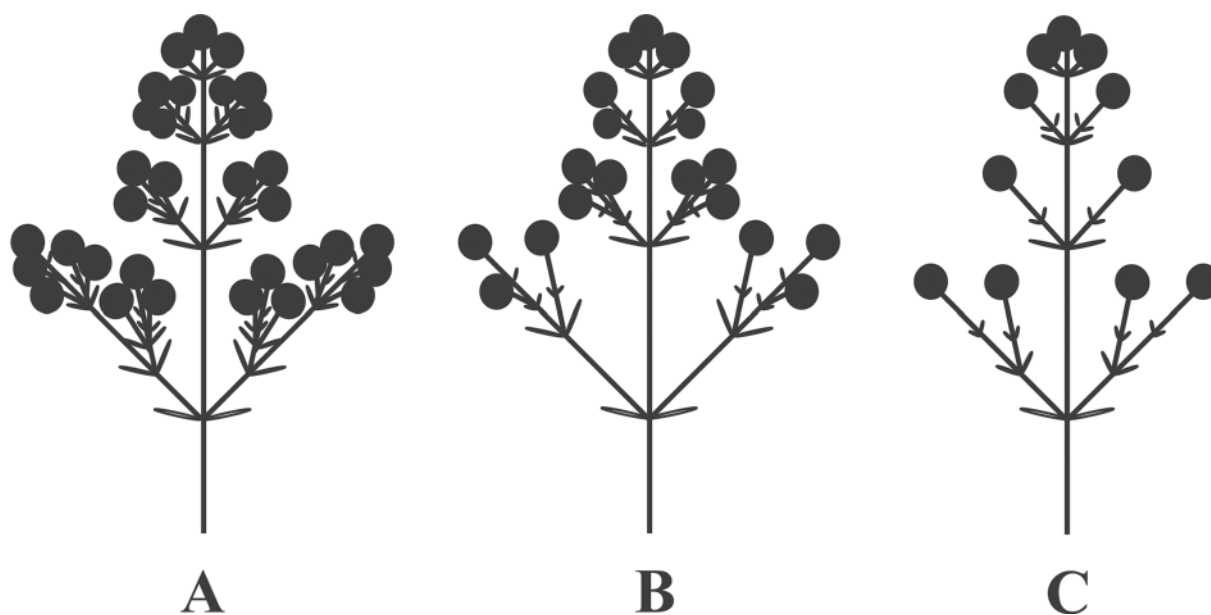


Fig. 4. Thyrsoid synflorescences of the chasmophytic species. **A.** *S. parrowiana* Boiss. & Hausskn., dense form with short pedicels and many flowers. **B.** *S. penduliflora* F.Jafari, Keshavarzi & Doostm. sp. nov., lax form with long pedicels and peduncles. **C.** *S. thyrsoniantha* F.Jafari, Mirtadz. & Keshavarzi sp. nov., reduction in number of flowers.

Taxonomy

Class Magnoliopsida Brongn.
Superorder Caryophyllanae Takht.
Order Caryophyllales Juss. ex Bercht. & J. Presl.
Family Caryophyllaceae Juss.
Genus *Silene* L.
Section *Siphonomorpha* Oth

Silene thyrsoniantha F.Jafari, Mirtadz. & Keshavarzi sp. nov.

urn:lsid:ipni.org:names:77313980-1

Figs 1–3, 5, 6A–C; Table 1

Diagnosis

Silene thyrsoniantha sp. nov. differs from *S. parrowiana* in having viscid stems (vs not viscid), a thyrsoid synflorescence with few flowers, secondary axes mainly with one flower (vs more than three), pedicel length ((4.5–)5–16 mm vs 1–4 mm), calyx length (8–10 mm vs 7–8 mm), and anthophore length (3 mm vs 2–3 mm) (Table 1).

Etymology

The specific epithet refers to the form of the inflorescence: a thyrsoid synflorescence with one-flowered secondary inflorescences.



Fig. 5. *Silene thyrsiantha* F.Jafari, Mirtadz. & Keshavarzi sp. nov. (holotype, M. Mirtadzadini 2089; MIR!).

Material examined

Type

IRAN – **Isfahan** • north of Semirom on the rocks; 31.422412° N, 51.572952° E; alt. 2530 m; 26 Sep. 2014; *M. Mirtadzadini 2089*; holotype: MIR!; isotype: TARI!. Genbank: LC710550 (ITS) and LC710552 (*rps16*).

Description

Perennial plants, glabrous, internode viscid. Stems 33.5–35.5 cm tall, pale green, glabrous, viscid, internodes 14–32 mm long. Basal leaves 14–20 × 2.5–4 mm, oblanceolate, base attenuate, acute, apex shortly mucronate, glabrous, minutely ciliate margins, glaucous; cauline leaves oblanceolate to linear, acute, apex acuminate, 7–20 × 0.5–2 mm, often glabrous. Synflorescence thyrsoid with few flowers, secondary inflorescences with one flower, pedicels (4.5–)5–16 mm long, glabrous. Bracteoles small, lanceolate, 1–1.5 mm long. Calyx narrow cylindrical, 8–10 mm long, glabrous, coriaceous; teeth membranous at margin, triangular, 2 mm long, two teeth acute with narrow transparent margin, other three teeth slightly broader, rounded, and with broad transparent margin. Petals yellowish (when dried), claw 5–5.5 mm long, with broad lateral margins, glabrous, without coronal scales; limb 5–5.5 mm long, linear, bifid to base. Anthophore 3 mm long, puberulent. Mature capsule 5.5–6 × 3–3.5 mm, ovoid-oblong. Seeds 0.8 × 0.6–0.7 mm, basically reniform, seed testa cells elongate with V-shaped margins.

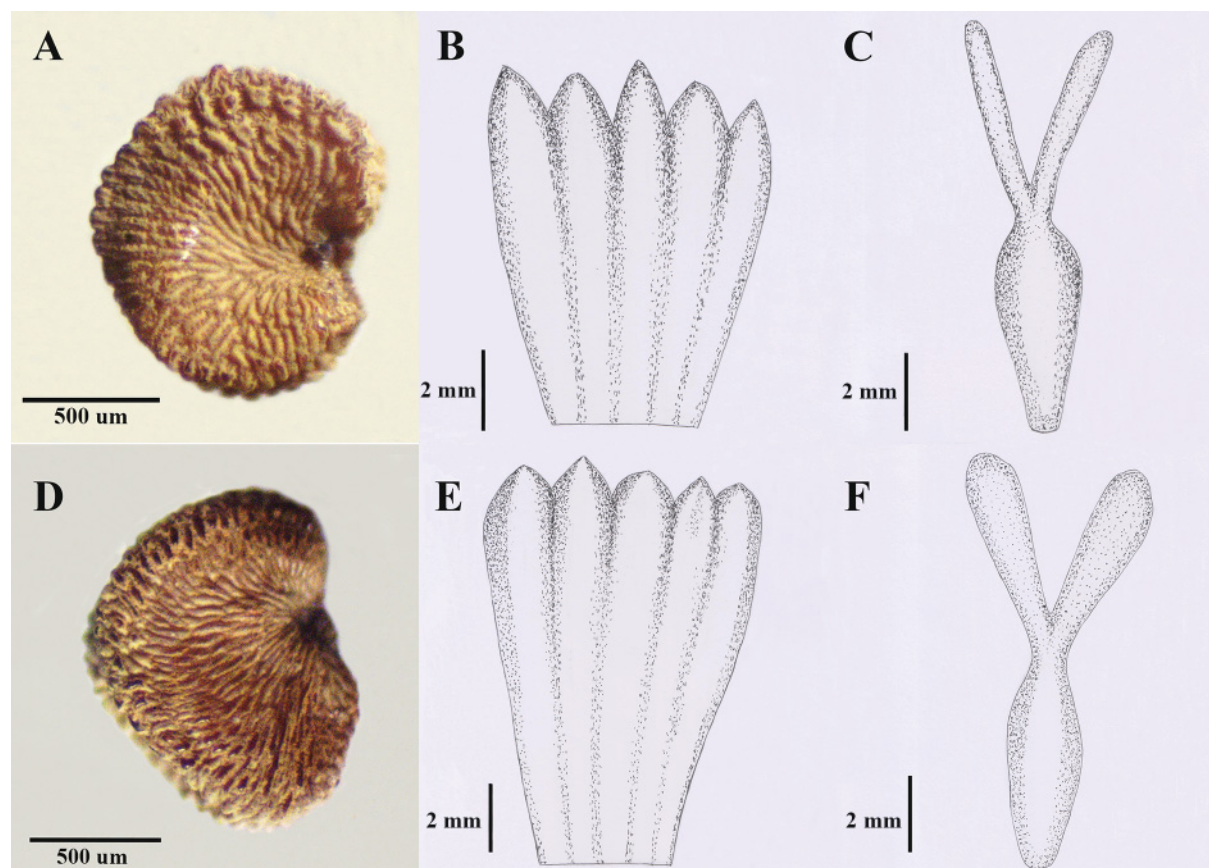


Fig. 6. A–C. *Silene thyrsoniantha* F.Jafari, Mirtadz. & Keshavarzi sp. nov. (*M. Mirtadzadini 2089*; MIR!). A. Seed. B. Calyx. C. Petal. – D–F. *Silene penduliflora* F.Jafari, Keshavarzi & Doostm. sp. nov. D. Seed (*M. Doostmohammadi & A. Ghorbanalizadeh 4054*; MIR!). E. Calyx. F. Petal (*M. Doostmohammadi 4056*; MIR!). Seeds were scanned with a Dino-Lite digital microscope AM413T model.

Distribution and habitat

Silene thyrsoniantha F.Jafari, Mirtadz. & Keshavarzi sp. nov. grows on stony rocks in central part of Iran near Semiron in the Isfahan Province at an altitude of about 2500 m.

Remarks

In the ITS phylogeny, *S. thyrsoniantha* F.Jafari, Mirtadz. & Keshavarzi sp. nov. is a member of a well-supported, but unresolved, group with *S. ghahremaninejadii*, *S. penduliflora* F.Jafari, Keshavarzi & Doostm. sp. nov., *S. ruprechtii* (MK559501, MN420835), and *S. shahrudensis*. The occurrence of single nucleotide polymorphisms (SNPs) leads to the variation of branch length (Fig. 1, PP=1, MLB=100%). However, *S. thyrsoniantha* is the closest relative of *S. penduliflora* sp. nov. in the *rps16* tree (Fig. 2, PP=1, MLB=96%).

Silene thyrsoniantha F.Jafari, Mirtadz. & Keshavarzi sp. nov. and *S. parrowiana* grow in the same rocky habitats. They are similar in having a compact caudex, glabrous stem, thyrsoïd synflorescences and coriaceous calyx. Petal limbs are bifid to base and claws without coronal scales. However, they are different in geographical distribution (Semirom in Isfahan Province is about 650 km away from Bisotun in Kermanshah Province). The stems of *S. thyrsoniantha* are viscid while they are non-viscid in *S. parrowiana*. Both calyx length and pedicel length in *S. thyrsoniantha* are longer than in *S. parrowiana*. The secondary inflorescences in *S. thyrsoniantha* are mainly one-flowered while the number of flowers in the secondary inflorescence are more than three in *S. parrowiana*. The inflorescence looks lax with less flowers in *Silene thyrsoniantha* compared to *S. parrowiana*. Cauline leaves are shorter than leaf internodes in *Silene thyrsoniantha* while they are often larger in *S. parrowiana*.

Silene thyrsoniantha F.Jafari, Mirtadz. & Keshavarzi sp. nov. is distributed in Semirom which is about 300 km from Khamin Mountain in Kohgiluyeh and Boyer-Ahmad Province, and 800 km from Shahrud in Semnan Province. The new species differs from *S. shahrudensis* in leaf apex (acute or acuminate vs rounded), cauline leaf size (14–20 × 2.5–4 mm vs 15–35 × 2.5–6 mm), pedicel length (4.5–16 mm vs 6–12 mm), thyrsoïd synflorescence (thyrsoïd vs lax thyrsoïd; the number of nodes and length of internodes are different), petal limb (linear vs oblanceolate), claw indumentum (glabrous vs ciliate), and seed size (0.8 × 0.6–0.7 vs 1.1 × 0.8 mm; margins of the testa cells V-shaped vs U-shaped). The holotype of *S. ghahremaninejadii* was not available at TARI when the first author visited the herbarium. The morphological comparison between *S. ghahremaninejadii* and *S. thyrsoniantha* was conducted using information from the protologue (Table 1).

Silene penduliflora F.Jafari, Keshavarzi & Doostm. sp. nov.

urn:lsid:ipni.org:names:77313984-1

Figs 1–3, 6D–F, 7–8; Table 1

Diagnosis

Silene penduliflora F.Jafari, Keshavarzi & Doostm., sp. nov. differs from *S. shahrudensis* in basal leaf size (11–60 × 2.5–4 mm vs 15–35 × 2.5–6 mm), calyx length (9–11 mm vs 8–10 mm), petal limb length (5–6 mm vs ca 5 mm), claw indumentum (glabrous vs ciliate), and capsule size (7.5–8.5 × 4–5 mm vs 4–6 × 3–4 mm) (Table 1).

Etymology

The specific epithet refers to the status of the flowers: flowers are pendulous at flowering time in this species.



Fig. 7. *Silene penduliflora* F.Jafari, Keshavarzi & Doostm. sp. nov. (holotype, *M. Mirtadzadini* 2076; MIR!).

Material examined

Type

IRAN – **Kerman** • Jupar Mountain; alt. 3400 m; Jun. 1997; *M. Mirtadzadini* 2076; holotype: MIR!; isotypes: MIR!, TARI!.

Paratypes

IRAN – **Kerman** • Mahan, Palvar Mountain, western slopes; alt. 3300 m; 15 Sep. 2017; *M. Doostmohammadi* 4056; MIR! • same collection data as for preceding; 14 Aug. 2020; *M. Doostmohammadi* & *A. Ghorbanalizadeh* 4054; MIR!. Genbank: LC710549 (ITS) and LC710551 (*rps16*).

Description

Perennial plants, glabrous, internodes viscid. Stems 29.5–40.5 cm tall, pale green, glabrous, viscid, internodes 32–82 mm long. Basal leaves 11–60 × 2.5–4 mm, oblanceolate, base attenuate, apex rounded and acute, glabrous, glaucous; cauline leaves oblanceolate to linear, apex acute, 12.5–41 × 1.5–3.5 mm, often glabrous. Synflorescences laxly thyrsoid, pedicels 5–9 mm long, glabrous. Bracteoles small,



Fig. 8. *Silene penduliflora* F.Jafari, Keshavarzi & Doostm. sp. nov. (paratypes, *M. Doostmohammadi* & *A. Ghorbanalizadeh* 4054; MIR!. *M. Doostmohammadi* 4056; MIR!). **A–B.** Inflorescence at flowering and fruiting times. **C.** Basal leaves and caudex. **D.** Habit and habitat. Photos by: *M. Doostmohammadi*.

lanceolate, 2.5–3 mm long. Calyx cylindrical, 9–11 mm long, glabrous, coriaceous; teeth membranous at the margin, triangular, 2 mm long, two teeth acute with narrow transparent margin, other three teeth slightly broader, rounded, and with broad transparent margin. Petals yellowish, claw 6–6.5 mm long, with broad lateral margins, glabrous, without coronal scales; limb 5–6 mm long, oblanceolate, bifid to base. Anthophore 3.5 mm long, puberulent. Mature capsule 7.5–9 × 4–5.5 mm, ovoid-oblong. Seeds 1–1.1 × 0.7–0.8 mm, basically reniform, seed testa cells elongate with V-shaped margins.

Distribution and habitat

Silene penduliflora sp. nov. is restricted to rocks in southeast Iran on the Jupar and Palvar mountains of Kerman Province at 3300–3400 m altitude.

Remarks

Although *S. penduliflora* F.Jafari, Keshavarzi & Doostm. sp. nov. and *S. shahrudensis* show more morphological resemblance to each other than to other close relatives, neither their ITS nor *rps16* sequences reflect a closer relationship, and *S. penduliflora* and *S. thyrsoniantha* F.Jafari, Mirtadz. & Keshavarzi sp. nov. form a well-supported clade in the *rps16* tree (Fig. 2, PP=1, MLB=96%). *Silene penduliflora* and *S. shahrudensis* differ in pedicel length (5–9 mm vs 6–12 mm), calyx length (9–11 mm vs 8–10 mm), petal limb length (5–6 mm vs ca 5 mm), surface of the claw (glabrous vs ciliate), and capsule size (7.5–9 × 4–5.5 mm vs 4–6 × 3–4 mm) (Table 1). The margin of the seed testa cells is V-shaped in *S. penduliflora* while it is U-shaped in *S. shahrudensis*. Geographically, these two species are also distant. *Silene shahrudensis* is confined to the central and eastern Alborz (north central Iran) while *S. penduliflora* is endemic to the highlands of Kerman in southeast Iran about 1000 km distant.

Despite the affinity of *S. penduliflora* F.Jafari, Keshavarzi & Doostm. sp. nov. and *S. thyrsoniantha* F.Jafari, Mirtadz. & Keshavarzi sp. nov. in the phylogenies, they differ in calyx length (9–11 vs 8–10 mm), secondary axis inflorescence (one flower vs more than one), capsule size (7.5–9 × 4–5.5 vs 5.5–6 × 3–3.5 mm), anthophore length (3.5 vs 3 mm), petal limb shape (oblanceolate vs linear), and seed size (1–1.1 × 0.7–0.8 vs 0.8 × 0.6–0.7 mm). Although their calyx lengths overlap, the calyx in *S. thyrsoniantha* is narrower than in *S. penduliflora* and both the capsules and seeds of *S. thyrsoniantha* are smaller than those in *S. penduliflora*.

Silene penduliflora F.Jafari, Keshavarzi & Doostm. sp. nov. differs from *S. ghahremaninejadii* in the calyx length (9–11 mm vs 7–9 mm), petal limb length (5–6 mm vs 2–3 mm), anthophore length (3.5 mm vs 2.5–4 mm), and capsule size (7.5–9 × 4–5.5 mm vs 6.5–7 × 2.5–3 mm).

Discussion

The ITS phylogeny supports the close relationship of *Silene ghahremaninejadii*, *S. parrowiana*, *S. penduliflora* F.Jafari, Keshavarzi & Doostm. sp. nov., *S. thyrsoniantha* F.Jafari, Mirtadz. & Keshavarzi sp. nov., and *S. shahrudensis*. They are similar in several morphological characters, including compact caudex, glabrous leaves, glabrous calyx, and petal claws without coronal scales. These species also grow in similar rocky habitats. However, they can be clearly distinguished by synflorescence characters, i.e., number of flowers and length of pedicels, peduncles and internodes within main and lateral thyrsoid inflorescences, and features of stem, calyx, petal limb, claw, capsule, and seed. Although the close relationship between *S. penduliflora* and *S. thyrsoniantha* is confirmed by the ITS and *rps16* data, their geographical distributions are very distinct.

The aforementioned taxa form a clade with four GenBank accessions (MN420835 and MK559501 in the ITS tree; MN460318 and MN460319 in the *rps16* tree), named *Silene ruprechtii*, but of which the

species identity could not be confirmed here. We examined two specimens listed in the voucher table of Bahmani *et al.* (2020) (“Iran: East Azarbaijan, protected area between Kalaleh and Mahmoudabad, 2000–2500 m, 73933 TARI!; GenBank: MN420835 (ITS), MN460320 (*rps16*)” and “Iran: East Azarbaijan, protected area, Doghroon mountain, 2700 m, 21904 TARI!; GenBank: MN447220 (ITS), MN460321 (*rps16*)”), and identified them as *S. ruprechtii*. However, comparing information between GenBank, the phylogenetic result, and the voucher table, it seems the accession “MN420835 (ITS)” in Bahmani *et al.* (2020) was incorrectly linked to the specimen “*S. ruprechtii* 73933 TARI!” in the voucher table. Instead, accession “MN420835 (ITS)” belongs to specimen “Iran: Isfahan, Semirum, Siah mountain, 2450 m, 58232 TARI; GenBank MN460319 (*rps16*)”, and the accession “MN447220 (ITS)” belongs to “*S. ruprechtii* 73933 TARI!”. In addition, accession “MN447219 (ITS)” was erroneously linked to specimen “Iran: Kohgiluyeh and Boyer-Ahmad, Sisakht, 13 km from Sisakh to Padena, Dena mountain, Bizhan pass, 3300 m, 14106 IAUH; GenBank: MN460318 (*rps16*)” in the voucher table instead of “Iran: East Azarbaijan protected area, Doghroon mountain, 2700 m, 21904 TARI; GenBank: MN460321 (*rps16*)”. It appears the specimens from “Semirum, Siah Kuh, 58232 TARI” and “Kohgiluyeh and Boyer-Ahmad, Bizhan pass, 14106 IAUH” (voucher table in Bahmani *et al.* 2020) belong to the complex, including the five species, and are distinct from *S. ruprechtii* by phylogenetic data. Since we could not examine the specimens “58232 TARI” and “14106 IAUH”, we could not verify the identity of these collections. *Silene ruprechtii* is different from the five species in both distribution and morphological characteristics; it is distributed in northwestern Iran (East Azarbaijan), about 735 km from the collection sites of any of the five species in the complex, the petal limbs include coronal scales, and the leaves are not fleshy or glaucous. Accessions of *S. ruprechtii* share a 11 bp insertion in *rps16* but this insertion is not found in the complex including the five species. Here, we follow Melzheimer’s treatment by regarding *S. ruprechtii* and *S. saxatilis* as two separate species.

The morphological comparison of the five species shows *Silene parrowiana* is similar to *S. thyrsoniantha* F.Jafari, Mirtadz. & Keshavarzi sp. nov. However, *S. parrowiana* is characterized by a non-viscid stem, a short pedicel and calyx, a dense inflorescence, and a ciliate claw making it different from *S. thyrsoniantha*. *Silene thyrsoniantha* and *S. shahrudensis* differ by features of stem, leaf, petal limb, claw indumentum, and seed. Among the five species, the shortest petal limbs are found in *S. ghahremaninejadii* and the largest calyx and capsule in *S. penduliflora* F.Jafari, Keshavarzi & Doostm. sp. nov. The latter species and *S. shahrudensis* are distinguished by basal leaf size, pedicel length, calyx length, petal limb length, claw indumentum, capsule size, and shape of seed testa cell margins. Morphological differences, geographical distinctiveness, and the phylogenies support separation of *S. penduliflora* and *S. thyrsoniantha* from *S. shahrudensis*.

Based on morphology, the closest relative of the five chasmophytic species could be *Silene manissadjianii* Freyn. They are similar in having a glabrous and coriaceous calyx that is basically conic-cylindric, a petal claw lacking coronal scales, and a puberulent anthophore. Melzheimer (1988) included *S. manissadjianii* Freyn var. *straussiana* Bornm. in his treatment as an incompletely known taxon, noting he was doubtful about the identification of the specimen from Alvand Mountain. He annotated the specimen (JE 00013404!) as *S. marschallii* C.A.Mey. but it shows the following differences with that species: flowering time (August vs June), stem (viscid vs sometimes not at all viscid), caudex (dense vs not dense), leaves (leathery and fleshy vs not leathery and fleshy). Furthermore, a recent phylogenetic study (Jafari *et al.* 2020) showed *S. marschallii* belongs to *S.* sect. *Sclerocalycinae* (Boiss.) Schischk. Based on our morphological observations, it seems *S. manissadjianii* var. *straussiana* could be nested within *S.* sect. *Siphonomorpha* s. lat. and possibly close to the five chasmophytic species. Among them, *S. ghahremaninejadii* is similar to *S. manissadjianii* var. *straussiana*. Detailed taxonomic studies and DNA sequence data are needed to determine the boundaries of *S. manissadjianii* and the five chasmophytic species. More investigation is also needed to determine the status of the specimen from Alvand Mountain; is it really a variety of *S. manissadjianii*, a species described from central Turkey.

Here, the phylogenies do not have enough resolution to show the relationships among the five chasmophytic species. Additional populations of the five species along with *S. manissadjianii* var. *straussiana* and using other markers will improve the resolution of the phylogenies.

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Appendix

Materials used for phylogenetic analyses. Herbarium abbreviations according to Thiers (2022+). Voucher information and missing accessions at GenBank are indicated by –; new sequences are indicated by an asterisk.

Taxon	Voucher	Genbank accession numbers	
		ITS	<i>rps 16</i>
<i>Atocion compactum</i> (Fisch. ex Hornem.) Tzvelev	–	LC424092	LC423983
<i>S. apetala</i> (L.) Willd.	–	LC424052	LC424034
<i>S. arabica</i> Boiss.	–	LC424053	LC424032
<i>S. arenosa</i> K.Koch	–	EF060203	EF061363
<i>S. austroiranica</i> Rech.f., Aellen & Esfand.	–	LC424094	LC423787
<i>S. chaetodonta</i> Boiss.	–	KX757596	LC423656
<i>S. confertiflora</i> Chowdhuri	–	KX449578	–
<i>S. confertiflora</i>	–	KX449579	–
<i>S. conica</i> L.	–	LC424059	LC424031
<i>S. coniflora</i> Nees ex Othh	–	HQ334908	HQ334967
<i>S. conoidea</i> L.	–	FN821101	FN821270
<i>S. coronaria</i> (L.) Clairv.	–	LC424093	LC424014
<i>S. cyri</i> Schischk.,	–	LC424083	LC423988
<i>S. daenensis</i> Melzh.	–	LC424060	LC424005
<i>S. dichotoma</i> Ehrh.	–	LC424058	LC423674
<i>S. eremicana</i> Stapf	–	LC424070	LC424008
<i>S. gallica</i> L.	–	LC424050	LC424035
<i>S. ghahremaninejadii</i> Hoseini & Assadi	–	MN447218	MN460327
<i>S. italica</i> (L.) Pers.	–	LC424095	LC423702
<i>S. latifolia</i> Poir.	–	FN821134	FN821302
<i>S. longipetala</i> Vent.	–	LC424088	LC424023
<i>S. lucida</i> Chowdhuri	–	LC424072	LC424000
<i>S. marschallii</i> C.A.Mey.	–	LC424087	LC424017
<i>S. melzheimeri</i> Greuter	–	KF267889	LC423717
<i>S. melzheimeri</i>	–	KX757467	–
<i>S. meyeri</i> Fenzl ex Boiss. & Buhse	–	LC424063	LC423991
<i>S. nana</i> Kar. & Kir.	–	LC424057	LC424030
<i>S. nizvana</i> Melzh.	–	LC424082	LC423986
<i>S. noctiflora</i> L.	–	X86829	LC424027
<i>S. nocturna</i> L.	–	LC424051	LC424033
<i>S. odontopetala</i> Fenzl	–	LC424055	LC423984
<i>S. oligantha</i> Boiss. & Heldr.	–	KX757494	LC423727
<i>S. oxelmanii</i> Gholipour	–	LC424061	LC424012
<i>S. parrowiana</i> Boiss. & Hausskn.	–	MK559499	MK643251
<i>S. pendula</i> L.	–	FN821142	FN821310
<i>S. penduliflora</i> F.Jafari, Keshavarzi & Doostm. sp. nov.	Iran, Kerman, <i>Doostmohammadi</i> & A. <i>Ghorbanalizadeh 4054</i> , MIR	LC710549*	LC710551*
<i>S. radicata</i> Boiss. & Heldr.	–	KX757470	–
<i>S. ruprechtii</i> Schischk.	–	MN447219	MN460318
<i>S. ruprechtii</i>	–	LC424084	LC423987
<i>S. ruprechtii</i>	–	MK559501	MN460319
<i>S. ruprechtii</i>	–	MN420835	MN460320
<i>S. ruprechtii</i>	–	MN447220	MN460321

Taxon	Voucher	Genbank Accession numbers	
		ITS	<i>rps 16</i>
<i>S. saxatilis</i> Sims	–	KX757524	LC423812
<i>S. saxatilis</i>	–	KX757525	LC423740
<i>S. saxatilis</i>	–	KX757526	LC423820
<i>S. schafta</i> Hohen.	–	LC424078	LC424002
<i>S. shahrudensis</i> Rech.f.	–	MH758563	MK643241
<i>S. simsii</i> F.Jafari, Oxelman & Rabeler	–	LC424056	LC424028
<i>S. sojakii</i> Melzh.	–	KX757450	LC423742
<i>S. swertiifolia</i> Boiss.	–	LC424090	LC424022
<i>S. thyrsoantha</i> F.Jafari, Mirtadz. & Keshavarzi sp. nov.	Iran, Isfahan, <i>Mirtadzadini 2089</i> , MIR	LC710550*	LC710552*
<i>S. viscosa</i> (L.) Pers.	–	FN821148	FN821316
<i>S. vulgaris</i> (Moench) Garcke	–	LC424096	LC424029