

The indumentum of vegetative and reproductive parts of annual species of *Silene* (Caryophyllaceae) in Iran

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ABSTRACT

Large and diverse genera, such as *Silene* need more reliable morphological traits for the credible identification and delimitation of the species. Despite the fact that the type of indumentum among the species of *Silene* had been addressed in most available revisions, monographs and floristic studies, the trichome-based features and their adaptational importance have not been investigated explicitly. In the present study, the trichomes of annual species of *Silene* in Iran are studied. Beside other floral traits and vegetative features, the presence, distribution and mixture of the glandular and eglandular trichomes on stems, leaves, inflorescence axes, pedicels, anthophores, inner and outer surfaces of calyces, petals and styles are proved to be of diagnostic importance in *Silene*. Indumentum of the inner calyx among the studied species is investigated here for the first time. An identification key is performed mainly based on indumentum features. In addition, a putative trichome-based defense strategy is proposed in the examined species.

Keywords: Taxonomy; Trichome; Glandular hairs; Defense strategy; Plant-herbivore interaction.

Introduction

Considered to be one of the largest genera of the family Caryophyllaceae Juss. and the flowering plants, *Silene* L. contains at least 700 species worldwide, many of which are Mediterranean and west Asian elements spreading in northern hemisphere (1, 2). Iran, possessing a wide variety of geological and ecological features, is the homeland of approximately 101 species of *Silene*, at least 28 of which are endemic (2, 3-5).

Morphological features corresponding to reproductive organs, especially the floral parts, have been primarily applied to delimitation of *Silene* taxa due to their intra-specific constancy, on the one hand, and their inter-specific variation, on the other hand (1, 2).

The presence and the type of indumentum on various parts of *Silene* taxa have been considered to have diagnostic importance in several global revisions on the genus or local floras mentioned below.

The presence and type of the indumentum on

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calyces, leaves and stems in *Silene* spp. are backed to "Species Plantarum" by Linnaeus (6). The diagnostic importance of indumentum in *Silene* was also emphasized in monumental works such as: "Flora Orientalis" (7), "Monographie der Gattung *Silene*" (8), "A revision of the genus *Silene*, Linn." (9), "Flora of the USSR" (10), "Studies in the genus *Silene*" (11), "Flora of Turkey and the East Aegean Islands" (12), "Flora Iranica" (2) and Greuter's revision on the Greek *Silene* (1). However, despite their potential importance in species discrimination, trichome features and their variation have been rarely investigated in detail in the genera of Caryophyllaceae. One rare example studied properly is the genus *Gypsophila* L. in which the distribution, density, type and size of the trichomes on various parts of the plants have been proved to be of diagnostic importance (13).

Moreover, Trichomes have important adaptational roles in plant defense against herbivory and nectar-robbing in addition to aiding the pollination and the dispersal of seeds, fruits and propagules (1, 14, 15).

In this study, the characteristics of indumentum on various parts of the annual species of the genus *Silene* in Iran were investigated in detail to evaluate the application of trichome-based traits in determination of these species. In addition, the taxon-specificity of indumentums type as well as the major trichome-based defensive strategies of annual *Silene* in Iran are discussed.

Materials and Methods

Trichomes of 20 species representing eight sections (2) of *Silene* were examined. For each species at least two populations were studied to indicate the possible intraspecific variation (Table 1). Following sections were included: sect. *Melandrifformes* (*S. noctiflora* L.), sect. *Conoimorpha* (*S. conica* L., *S. conoidea* L., *S. coniflora* Nees ex Otth), sect. *Saponarioideae* (*S. nana* Kar. & Kir.), sect. *Compactae* (*S. compacta* Fisch.), sect. *Lasiocalycinae* (*S. dichotoma* Ehrh., *S. gallica* L., *S. apetala* Willd., *S. lagenocalyx* Fenzl ex Boiss.), sect. *Bipartitae* (*S. arabica* Boiss., *S. villosa* Forssk., *S. vivianii* Steud.), sect. *Atocion* (*S. rubella* L., *S. aegyptiaca* (L.) L.f., *S. atocioides* Boiss.), sect.

Rigidulae (*S. microsperma* Fenzl, *S. chaetodonta* Boiss., *S. arenosa* C.Koch, *S. austroiranica* Rech.f., Aellen & Esfand.). In addition, two Mediterranean species which have previously been assumed to present the ancestral lineages in the genus (17), i.e. *S. delicatula* Boiss. and *S. cordifolia* All., were also included in our study.

Trichomes on vegetative and floral parts were studied by means of a Zeiss stereomicroscope and electron microscopy. The stereomicroscope graphs were taken from dried plant parts removed from herbarium specimens without rehydration and by means of a Cannon G10 camera. For electron microscopy the plant parts were mounted directly on aluminum stubs using double-sided adhesive tape and were sputter coated with a thin layer (ca. 25 nm) of gold. The SEM micrographs were taken in a Hitachi SU3500 (Japan) at an accelerating voltage of 15 kV.

Results

The main types of the investigated trichomes among the species studied are summarized in Table 2. Selected stereomicroscope graphs (Fig. 1) and SEM micrographs (Figs. 2-3) of common indumentum types are presented.

any trichome (the glabrous type).

The trichome features of the species studied are summarized in Table 2. The indumentum of the inner calyx is investigated here for the first time in the species studied. The trichome characteristics were constant among various samples of each species with few exceptions. *Silene conica* and *S. conoidea* show, for example, variations in the ratio of glandular to eglandular trichomes on the inflorescence axis and outer calyx. Moreover, the outer calyx of young flowers in *S. austroiranica* is covered by fine eglandular trichomes, while the mature flowers become glabrous with age.

According to our results, the trichome types might vary on different organs. Therefore, we investigated the trichome types on following partitions: 1- shoot (including the vegetative leaves), 2- inflorescence axis (including floral branches, bracts and bracteoles), 3- pedicel, and 4- anthophore (Fig. 4).

Table 1. The voucher specimens studied. The specimens are deposited in the herbaria T, TARI and W.

Taxa	Vouchers
<i>S. noctiflora</i>	Iran: Mousavi 40188 (T), Akhani 11572 (W), Zehzad & Siami 3389 (W), Gauba & Sabeti 2182 (W), Termeh & Matin 33858-E (W), Rechinger 49626 (W), Rechinger 52652 (W); Germany: Wolf 1997-01695 (W), Dörr 1996-02975 (W)
<i>S. conica</i>	Iran: Rostami & Takabi 3086 (T), Termeh & Matin 36850-E (W), Wendelbo 433 (W), Sabeti 173 (W), Rechinger 39597 (W), Rechinger 39586 (W); Greece: Bauer 235 (W), Stamadiados 9857 (W), Rechinger 19774 (W), Pinatzi 2.VI.1958 (W); Macedonia: Rechinger 19714 (W)
<i>S. conoidea</i>	Iran: Abdoli 30155 (T), Samiee 17103 (T), Runemark & Mozaffarian 27228 (TARI), Assadi & Mozaffarian 27581 (TARI), Rajmand & Bazargan 31703 (TARI), Amini & Mousavi 1915 (TARI), Mozaffarian & Nowrozi 34306 (TARI), Assadi & Aboohamzeh 38342 (TARI), Jacobs 6316 (W), Furse 1859 (W), Zarif 2559-E (W), Behboudi & Aellen 1478 (W)
<i>S. confiflora</i>	Iran: Bonvan 9778 (TARI), Sanii 11288 (TARI), Riazi 3883 (TARI), Wendelbo & Foroughi 15838 (TARI, W), Dadashzadeh 25801 (TARI), Rechinger 352 (W), Rechinger 3193 (W), Rechinger 4161 (W), Archibald 1797 (W), Rechinger 50340 (W), Rechinger 50802 (W); Iraq: Anders 1850 (W); Syria: Haradjian 4008 (W)
<i>S. nana</i>	Afghanistan: Lalande R2475-S12-E3 (W); Iran: Rechinger 50670 (W), Rechinger 50902 (W), Rechinger 33222 (W), Rechinger 50653 (W), Rechinger 28936 (W), Rechinger 51596 (W), Rechinger 7281 (W), Rechinger 33225 (W); Turkmenistan: Nikitiin 1920/Iy 57 (W)
<i>S. compacta</i>	Iran: Anonymous 6491 (W), Petrovitz 70 (W), Amini 1324 (W), Termeh 1980-05118 (W), Termeh 14381-E (W), Zehzad & Siami 3333 (W), Rechinger 49620 (W), Rechinger 48712 (W), Siami 3322 (W), Termeh, Mousavi & Tehrani 41623 (W)
<i>S. dichotoma</i>	Iran: Karimi 13421 (T), Runemark & Lazari 26364 (TARI), Rechinger 43274 (W), Mousavi & Karavar 41599 (W), Rioux & Golvan 114 (W), Rechinger 11526 (W), Mirdamadi 2167-E (W), Wendelbo & Assadi 16506 (W), Zehzad & Siami 3432 (W), Rechinger 49609 (W), Rechinger 56736 (W), Rechinger 6327 (W), Rechinger 10161a (W); Iraq: Barkley & Barkley 5752 (W), Field & Lazari 699 (W)
<i>S. gallica</i>	Greece: Dörrler 827 (W), Mayendorf 2005-12339 (W); Iran: Mozaffarian 65151 (TARI); Syria: Makowsky 2005-12258 (W), Makowsky 2005-12260 (W), Makowski 2005-12330 (W)
<i>S. apetala</i>	Afghanistan: Anders 3040 (W), Lalande R738-S5-E3 (W), Lalande R868-S17-E3 (W); Iran: Mashayekhi 32103 (T), Runemark & Mozaffarian 26901 (TARI), Koeie 140 (W), Iranshahr & Termeh 14944-E (W), Iranshahr & Termeh 33682-E (W), Termeh & Iranshahr 34441-E (W), Koelz 14613 (W), Grant 17043 (W), Koelz 14849 (W), Pag 13421-E (W), Iranshahr & Termeh 33674-E (W), Iranshahr & Termeh 14942-E (W), Termeh & Mousavi 34444-E (W), Iraq: Rechinger 13867 (W), Rechinger 14568 (W); Pakistan: Rechinger 30406 (W), Rechinger 8895 (W), Rechinger 9208 (W), Rechinger 12768 (W), Rechinger 13985 (W)
<i>S. lagenocalyx</i>	Iran: Foroughi 3828 (TARI), Rechinger 3419 (W), Sojak 7309 (W), Koeie 367 (W), Koelz 17328 (W), Wendelbo & Foroughi 15827 (W), Archibald 1714 (W), Behboudi 37 (W), Jacobs 6428 (W)
<i>S. arabica</i>	Afghanistan: Rechinger 35317 (W); Iran: Runemark & Mozaffarian 27048 (TARI), Runemark & Mozaffarian 26952 (TARI) Iraq: Rechinger 14143 (W), Rechinger 7280 (W), Rechinger 46644 (W), Rechinger 50218 (W), Rechinger 46306 (W), Rechinger 50667 (W), Rechinger 50534 (W), Rechinger 52072 (W), Rechinger 51577 (W), Rechinger 57446 (W), Rechinger 46157 (W), Rechinger 46288 (W)
<i>S. villosa</i>	Iran: Bornmuller 96 (W), Iranshahr & Termeh 14943-E (W)
<i>S. vivianii</i>	Iran: Behboudi 5532-E (W), Sharif 9558-E (W); Iraq: Barkley and Al-Ani 7198 (W), Anders 1806 (W), Anders 2523 (W), Rechinger 9006 (W), Rechinger 9012 (W), Rechinger 9054 (W), Rechinger 9140 (W), Rawi 12642 (W)
<i>S. rubella</i>	Iran: Terme & Mousavi 34447E (W), Sharif 441 (W), Sharif 5233-E (W), Esfandiari 53-E (W), Koelz 14567 (W), Riedl & Ershad 15862 (W); Iraq: Rechinger 14127 (W)
<i>S. aegyptiaca</i>	Jordan: Walter 7361 (W), Staudinger J1/17 (W); Syria: Haradjian 81 (W), Haradjian 369 (W); Turkey: Rechinger 27032 (W)
<i>S. atocioides</i>	Iran: Termeh 13073-E (W) ; Iraq: Anders 666 (W), Anders 2014 (W), Anders 2444 (W), Rechinger 15676 (W), Rechinger 15687 (W); Turkey: Rechinger 11912 (W), Anders 1281 (W); Turkey: Sorger 63-30-20 (W)
<i>S. microsperma</i>	Turkey: Sorger 69-31-2 (W), Sorger 71-13-12 (W), Sorger 71-40-1 (W), Sorger NT-65-33-46 (W), Fitz & Spitzenberger 964 (W)
<i>S. chaetodonta</i>	Afghanistan: Freitag 34844 (W), Rechinger 34862 (W), Rechinger 35007 (W), Rechinger 34961 (W), Rechinger 34927 (W), Rechinger 34796 (W); Iran: Esmaeeli 3053 (T), Runemark & Mozaffarian 27227 (TARI), Runemark & Mozaffarian 26669 (TARI), Bokhari & Wendelbo 235 (TARI), Pravitz 935 (W), Termeh 13409-E (W), Rechinger 51024 (W), Rechinger 34830 (W), Sojak 5794 (W), Koelz 16096 (W), Koeie 725 (W), Gauba 2160 (W); Iraq: Rechinger 10060 (W), Rechinger 10146 (W), Rechinger 10772 (W)
<i>S. arenosa</i>	Afghanistan: Amsel 6AVIII (W); Armenia: Gabrielian 1971-22876
<i>S. austroiranica</i>	Iran: Rechinger 3386 (W), Rechinger 3261 (W), Rechinger 3785 (W), Rechinger 4014 (W), Rechinger 14579 (W), Rechinger 48236 (W), Rechinger 54676 (W), Koeie 480 (W), Assadi, Edmondson & Miller 2141 (W), Behboudi 472-E (W), Sojak 7319 (W), Jacobs 6977 (W), Iranshahr & Mousavi 15674-E (W), Leonard 5868 (W), Leonard 6262 (W); Iraq: Haines 1973-12248 (W) Rechinger 9627 (W), Rechinger 12134 (W), Rechinger 12327 (W), Rechinger 12731 (W), Rechinger 12739-a (W), Rechinger 11735 (W)
<i>S. delicatula</i>	Turkey: Sorger NT 65-24-10 (W)
<i>S. cordifolia</i>	France: Merxmüller & Zollitsch 26212 (W); Italy: Buchner 2012-07231 (W), Staudinger W5d/2 (W), Horandl et al. 6875 (W), Bernoulli 1974-20181 (W), Vidal 3208 (W), Rönninger 1962-14331 (W), Koch 55/174

Indumentum of annual *Silene*

Table 2. Types of trichomes on various parts of *Silene* spp. El: eglandular long, Es: eglandular short, Gl: glandular long, Gs: glandular short, Gla: glabrous. The styles are short glandular hairy in all species examined.

Taxa/Character	Stem	Leav.	Inflores.	pedicle	Anth.	Out.cal	Inn.cal	Cal.D	filam.	petals
<i>S. noctiflora</i>	El/Gs	El/Gs	El/Gs	El/Gs	Gla	El/Gs	Gla	Es	Gla	Es
<i>S. conica</i>	Es	Es	Es/Gs	El/Gs	Es	Es/Gs	Es	Es	El	Gla
<i>S. conoidea</i>	Es	Es	Es/Gs	Gs	Es	Gs	Es	Es	El	Gla
<i>S. confiflora</i>	Es	Es	Gs	Gs	Gla	Gs	Gla	Es	El	El
<i>S.nana</i>	Gla	El	Gla	Gla	Gla	Gla	Gla	Es	Gla	Gla
<i>S. compacta</i>	Gla	Gla	Gla	Gla	Gla	Gla	Gla	Gs	Gla	Gla
<i>S. dichotoma</i>	El/Es	El/Es	El/Es	El/Es	Gla	El/Es	Gla	Es	Gla	Gla
<i>S. gallica</i>	El/Es	El/Es	Gs/Es	Gs	Es	El/Gs	Gla	Gl	Es	Gla
<i>S. apetala</i>	Es	Es	Es	Es	Es	Es	Gla	Es	Gla	Es
<i>S. lagenocalyx</i>	El/Es	El/Es	El/Es	El/Es	Gla	El/Es	Gla	Es	Gla	Gla
<i>S. arabica</i>	Gs/Es	Gs/Es	Gs	Gs	Es	Gs	Es	Es	Gla	Es
<i>S. villosa</i>	Gs/Es	Gs/Es	Gs/Es	Gs/Es	Gla	Gs/ El	Gla	Gla	Gla	Gla
<i>S. vivianii</i>	Es	Es	Es	Es	Es	Es	Gla/Es	Es	Gla	Es
<i>S.rubella</i>	Es	Es	Es	Es	Es	Es	Gla	Es	Gla	Gla
<i>S. aegyptiaca</i>	El/Es	Es	Es/Gs	Gs/Es	Gla	Gs/Es	Gla	Es	Gla	Gla
<i>S.atocioides</i>	El/Es	Es	Es/Gl	Gl/Es	Gla	Gl/Es	Gla	Es	Gla	Gla
<i>S.microsperma</i>	Es	Es	Gla	Gla	Es	Es	Gla	Es	Es	Gla
<i>S. chaetodonta</i>	Es	Es	Gla/Es	Gla/Es	Es	Es	Es	Es	Gla	Gla
<i>S. arenosa</i>	Es	Es	Gla/Es	Gla/Es	Es	Es	Es	Es	Gla	Gla
<i>S.austroiranica</i>	Es	Es	Gla/Es	Gla/Es	Es	Es/Gla	Es	Es	Gla	Gla
<i>S. cordifolia</i>	Gs	Gs	Gs	Gs	Gla	Gs	Gla	Es	Gla	Gla
<i>S. delicatula</i>	El/Gs	El/Gs	El/Gs	El/Gs	Es	Gl/El	Gla	Es	Gla	Es

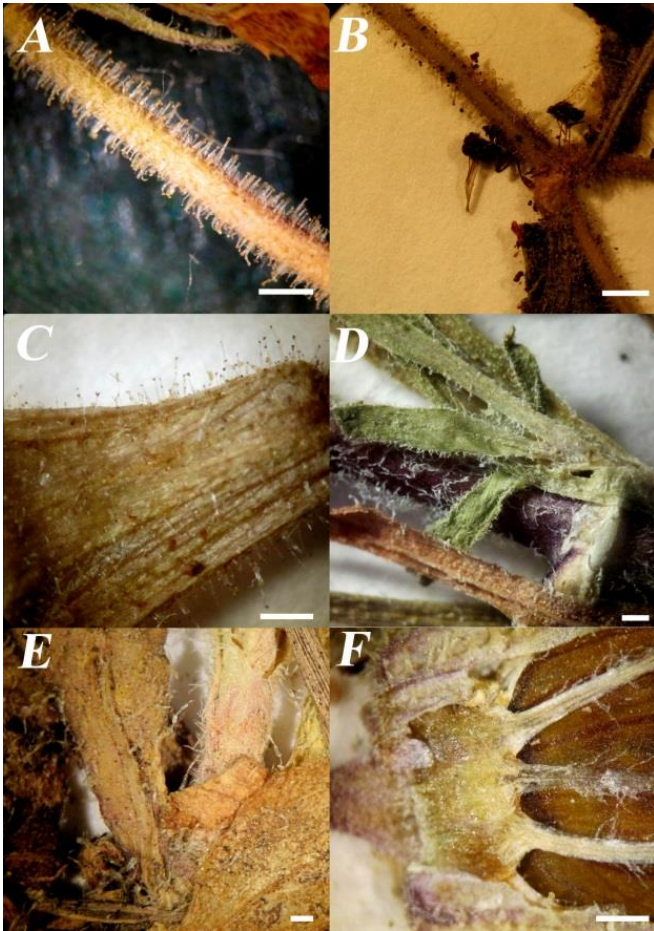


Figure 1. Stereomicroscope images of representative trichome types in selected species of annual *Silene*. A: *S. conoidea*, short glandular trichomes on pedicel. B: *S. delicatula*, short glandular trichomes on inflorescence axis, note the trapped insects. C: *S. atocioides*, outer calyx with long glandular hairs. D: *S. lagenocalx*, long eglandular trichomes on stem. E: *S. gallica*, long and short eglandular hairs on stem. F: *S. coniflora*, long eglandular trichomes on petals and filaments. Scale bars equal to 1 mm.

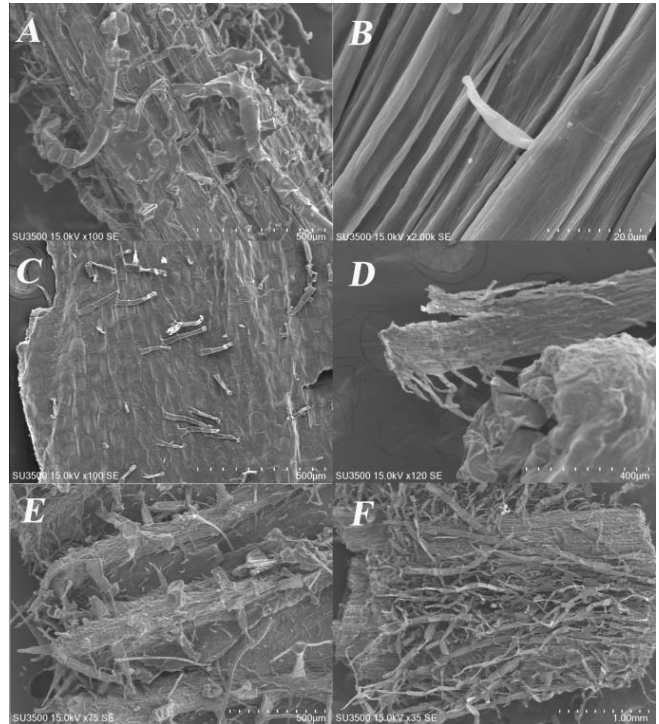


Figure 2. SEM micrographs of trichomes in selected species of annual *Silene*. A: *S. noctiflora*, pedicel with long eglandular and short glandular hairs. B: *S. noctiflora*, petal trichomes. C: *S. conoidea*, hairs on inner calyx. D: *S. coniflora*, hairs on filaments. E: *S. coniflora*, glandular and eglandular hairs on outer calyx. F: *S. gallica*, long eglandular trichomes on the stem.

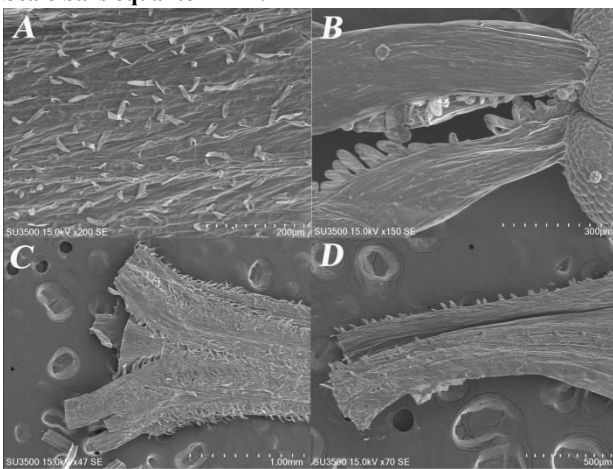


Figure 3. SEM micrographs of trichomes in selected species of annual *Silene*. A: *S. chaetodonta*, hairs on inner calyx. B: *S. austroiranica*, styles, note the trapped pollens. C: *S. vivianii*, anthophore hairs. D: *S. vivianii*, petal hairs.

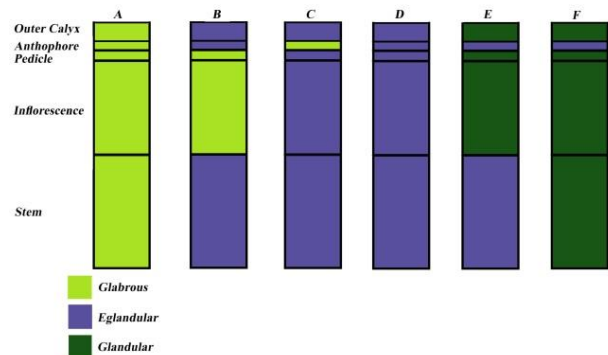


Figure 4. Major distribution patterns of trichomes on main axes of annual *Silene* spp. in Iran.

Two basic types of trichomes can be distinguished: glandular and eglandular ones. Both mentioned types could be composed of short trichomes (the so-called pubescent or puberulent vestiture) which are mostly not longer than 0.25 mm, or long (forming villose vestiture) commonly longer than 0.4 mm. The short hairs might be uni- or multicellular, while the long ones are commonly multicellular (Figs. 1-3). In few species some parts (vegetative or floral) might lack

Discussion

The present study indicates the importance of trichome characters in identification and delimitation of taxa in *Silene*. These characters were mostly constant among different populations of a certain species, so provide valuable source of data in species discrimination. According to these results we are able to perform a determination key based on trichome characters which could be used beside other available morphological keys for the annual species of *Silene* distributed in Iran (see below).

For taxon pairs *S. chaetodonta*-*S. arenosa* and *S. conoidea*-*S. conica* showing same trichome characteristics we were not able to use such characters for discriminating them, so we used gross morphological characters for separating taxa in each pair.

We evaluated also the potential implication of trichome characters in assessing the relationships between taxa. The available molecular phylogenetic trees (17, 19-23) do not support the monophyly of the annual species in *Silene*. The variation in trichome characters also confirms this finding, as the studied species do not show uniformity in these characters. In addition in some cases, as for example in the above mentioned taxon pairs, the trichome features are very similar, reflecting their possible close relationship. We conclude also that the glabrous forms might be raised independently in the genus. For examples, *S. nana* and *S. compacta* are both more or less glabrous on calyx, but have such obvious morphological differences that they are placed in separate sections (sect. *Saponarioideae* Boiss. and sect. *Compactae* Boiss., respectively). In addition, the general trichome profiles in these two species are very similar.

Referring to the available molecular phylogenetic

studies, it seems that similar to gross morphological features, the trichome characters are not trustworthy to represent the inter-specific relationships in *Silene*, although they have high taxonomic value in species delimitation. In such cases, while using morphological traits retain their limited usefulness in discrimination of the species, they are neither sufficient in species identification, nor for the assessing the true evolutionary history in the genus.

Another potential significance of trichome features is their possible defensive role. Plants tend to protect their vegetative and floral parts from herbivory by defensive measures to enhance their survivability. While the elaborate petals and the shape of the calyx tube and corolla could determine the type of the pollinator preferred by the plants (24), trichomes on petals, stamens, inner and outer surfaces of calyx tube and anthophore could prevent the nectar robbery. In addition, the main role of the glandular and eglandular trichomes on the shoots is to defend the plant against insect herbivores (25, 26).

Based on our results, there are two major shifting points on the main axes of the species studied in which the type of the indumentum switches from a type to another. The first shift is between the stem and the inflorescence axis which occurs in most species studied (see below for examples). The second shift is between the pedicel and the anthophore.

Our results allow distinguishing four major trichome-based defense strategies in the species studied: type 1 (represented by patterns C, D and F in Fig. 4) with intense defense of both vegetative and floral parts; type 2 (represented by pattern B in Fig. 4) with more intense defense of vegetative parts compared to floral parts; type 3 (represented by pattern E in Fig. 4) with more intense defense of floral parts compared with vegetative ones; and type 4 (represented by pattern A in Fig. 4) with low investment in defense of both vegetative and floral parts.

Among the studied species *S. noctiflora*, *S. dichotoma*, *S. apetala*, *S. lagenocalyx*, *S. arabica*, *S. villosa*, *S. vivianii*, *S. rubella*, *S. cordifolia* and *S. delicatula* are examples of type 1. The vegetative and outer floral parts in these species are uniformly covered with glandular or eglandular hairs. Species of

type 2 including *S. microsperma*, *S. chaetodonta*, *S. arenosa* and *S. austroiranica* prefer to protect their vegetative parts more sophisticatedly than their floral parts. These species have sometimes their glandular hairs condensed on the lower parts, or the density of hairs on lower parts is higher than the floral parts. Species of type 3 including *S. conica*, *S. conoidea*, *S. coniflora*, *S. gallica*, *S. aegyptiaca* and *S. atocioides* fiercely protect their floral parts and invest more resources (hairs) on them. Species of type 4 represented by *S. nana* and *S. compacta* have intense trichome-based protection neither on vegetative nor on floral parts.

The defense against nectar-robbing could be enhanced by functional hairs on anthophore, outer and inner calyx, petals and filaments, which provide a controlled passage for accepted pollinators (mainly butterflies and moths) to reach the nectariferous region on the distal end of the anthophore. The entrance of unwanted visitors would be prohibited by the trichome-covered defense cylinders (inner calyx

and petal-filament tubes) from inside and trichome-covered pedicel, inner and outer calyx and anthophore by piercing the defensive cylinders from outside.

Major distribution patterns of trichomes on floral parts are summarized in Fig. 5. Although high variation are indicated in the mentioned types, the ideal defense type with outer glandular coverage plus eglandular indumentum on inner parts of the flowers (type G in Fig. 5), had no representative in this study.

While the evolutionary value of trichome-based features in plant-pollinator and plant-herbivore relationships should be considered with greater extent in future studies to provide detailed materials for more complete analyses, the current study did its best to open an outlook to the diagnostic and taxonomic values of such features. It could be assumed that plant strategies for survival, reproduction and seed-dispersal highly shaped their morphology through their own evolutionary history, thus the better understanding of those strategies would lead the taxonomists to get a better classification of the genus.

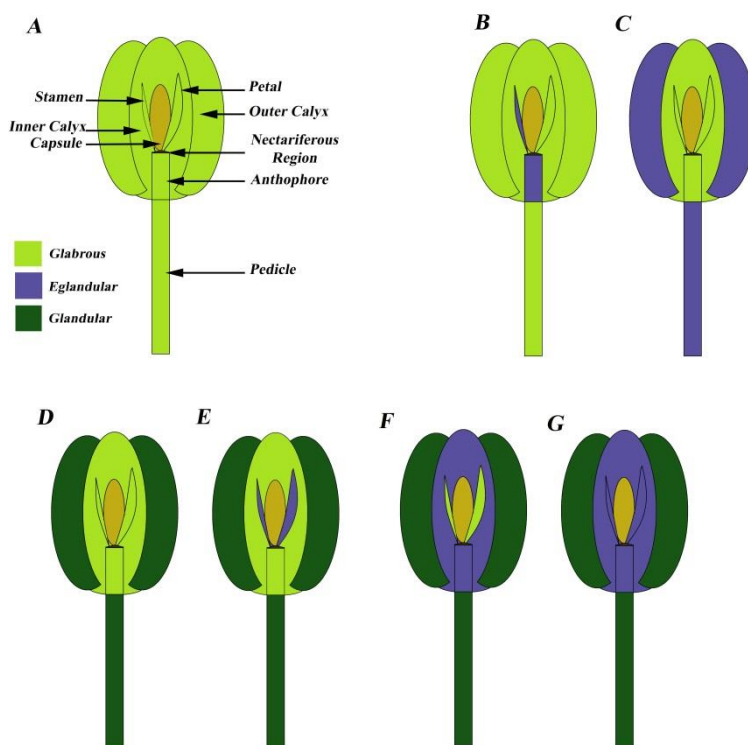


Figure 5. Major distribution patterns of trichomes on floral parts in annual species of *Silene* in Iran. Type G was not identified in Iranian species, but represents the supposed ideal protection against nectar-robbing.

Diagnostic key to annual species of *Silene* distributed in Iran according to trichome features

- 1- Petal glabrous-----2
- Petal hairy -----17
- 2-Filaments glabrous-----3
- Filaments hairy-----14
- 3- Stem glabrous-----4
- Stem hairy-----5
- 4- Leaves glabrous-----*S. compacta*
- Leaves hairy-----*S. nana*
- 5- Stem only with glandular hairs-----*S. cordifolia*
- Stem with glandular/eglandular or just eglandular hairs-----6
- 6- Inner calyx glabrous-----7
- Inner calyx hairy-----12
- 7- Anthophore hairy-----*S. rubella*
- Anthophore glabrous-----8
- 8- Stem with glandular and eglandular hairs-----*S. villosa*
- Stem with just eglandular hairs-----9
- 9- Outer calyx with both glandular and eglandular hairs-----10
- Outer calyx with just eglandular hairs-----11
- 10- Outer calyx with short glandular hairs-----*S. aegyptica*
- Outer calyx with long glandular hairs-----*S. atocioides*
- 11- Anthophore 1-3.5mm-----*S. dichotoma*
- Anthophore 4-5.5mm-----*S. lagenocalyx*
- 12- Calyx hairy at youth and glabrous at maturity-----*S. austroiranica*
- Calyx always hairy-----13
- 13- Calyx teeth more than 3mm-----*S. chaetodonta*
- Calyx teeth less than 3mm-----*S. arenosa*
- 14- Filament hairs long and multicellular-----15
- Filament hairs short and unicellular-----16
- 15- Pedicels with mostly Glandular Hairs-----*S. conoidea*
- Pedicels with both glandular and eglandular hairs-----*S. conica*
- 16- Outer calyx with just short hairs-----*S. microsperma*
- Outer calyx with both long and short hairs-----*S. gallica*
- 17- Petals with long hairs-----*S. coniflora*
- Petals with short hairs-----18
- 18- Inner calyx glabrous-----19
- Inner calyx hairy-----21
- 19- Anthophore glabrous-----*S. noctiflora*
- Anthophore hairy-----20
- 20- Outer calyx with short hairs-----*S. apetala*
- Outer calyx with both long and short hairs-----*S. delicatula*
- 21- Inflorescence with eglandular hairs-----*S. vivianii*
- Inflorescence with glandular hairs-----*S. arabica*

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REFERENCES

1. Greuter, W. (1995) *Silene* (Caryophyllaceae) in Greece: A subgeneric and sectional classification. *Taxon* **44**, 543-581.
2. Melzheimer, V. (1988) Caryophyllaceae: *Silene* L. in: Rechinger, K.H. (Ed.). Flora Iranica, vol. 163, 341-508. Akad. Druck und Verlagsanstalt., Graz, Austria.
3. Hoseini, E. and Assadi, M. (2016) Introducing a new species, *Silene ghahremaninejadii* (Caryophyllaceae), from Iran. *Nova Biol. Reperta*, **3** (2), 131-135.
4. Edalatiyan, M.N., Ghahremaninejad, F., Attar, F. and Joharchi, M.R. (2010) A taxonomic study on the genus *Silene* (Caryophyllaceae) in Iran. *Rostaniha*, **11**(2), 133-149.
5. Edalatiyan, M.N., Joharchi, M. and Ghahremaninejad, F. (2011) *Silene ferdowsii* (Caryophyllaceae), a new species from Iran. *Ann. Bot. Fenn.*, **48**(2), 155-158.
6. Linnaeus, C. (1753) Species plantarum, vol. 1, 416-420. Salvius, Stockholm, Sweden.
7. Boissier. E. (1867) Flora Orientalis, vol. 1, Caryophyllaceae. Geneva et Basieer Aputh. Georg, Bibliopolam, Pp. 567-656.
8. Rohrbach, P. (1868) Monographie der Gattung *Silene*. W. Engelmann. Leipzig, Germany.
9. Williams, F.N. (1896) A revision of the genus *Silene* L. *J. Bot. Linn. Soc.*, **32**, 1-196.
10. Schischkin, B.K. (1936) *Silene* L., in: Schischkin, B.K., and Komarov, V.L. Flora of the USSR, vol. 6, 442-528. Akademi Nauk SSSR, Moskva, Leningrad.
11. Chowdhuri, P.K. (1957) Studies in the genus *Silene*. Notes Roy. Bot. Gard. Edinb., **22**: 221-278.
12. Coode, M.J.E. and Cullen, J. (1967) *Silene* L., in: Davis, P.H. (ed.), Flora of Turkey and the East Aegean Islands, vol. 2, 179-242. Edinburgh University Press, Edinburgh, UK.
13. Nejad Falatoury, A., Assadi, M. and Ghahremaninejad, F. (2015) Taxonomic significance of indumentum in the genus *Gypsophila* L. (Caryophyllaceae). *Nova Biol. Reperta*, **2**, 91-102.
14. Levin, D.A. (1973) The role of trichomes in plant defense. *Quart. Rev. of Biol.*, **48**, 3-15.
15. Prabhakar, M., Kumar, B.V., Ramayya, N. and Leelavathi, P. (1985) Structure, distribution and taxonomic significance of trichomes in some *Indigofera* L. (Fabaceae). *Proc. Plant Sci.*, **95**(5), 309-314.
16. Bringezu, K., Lichtenberger, O., Leopold, I. and Neumann, D. (1999) Heavy metal tolerance of *Silene vulgaris*. *J. Plant Physiol.*, **154**, 536-546
17. Greenberg, A.K. and Donoghue, M.J. (2011) Molecular systematics and character evolution in Caryophyllaceae. *Taxon*, **60**(6), 1637-1652.
18. Thiers, B. (continuously updated) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/>
19. Filatov, D.A., Laporte, V., Vitte, C. and Charlesworth, D. (2001) DNA diversity in sex-linked and autosomal genes of the plant species *Silene latifolia* and *Silene dioica*. *Mol. Biol. Evol.*, **18**(8), 1442-1454.
20. Ingvarsson, P.K., Ribstein, S. and Taylor, D.R. 2003. Molecular evolution of insertions and deletion in the chloroplast genome of *Silene*. *Mol. Biol. Evol.*, **20**(11), 1737-1740.
21. Popp, M., Erixon, P., Eggens, F. and Oxelman, B. (2005) Origin and evolution of a circumpolar polyploid species complex in *Silene* (Caryophyllaceae) inferred from low copy nuclear RNA polymerase introns, rDNA, and chloroplast DNA. *Syst. Bot.*, **30**(2), 302-313.

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22. Rautenberg, A., Hathaway, L., Oxelman, B. and Prentice, H.C. (2010) Geographic and phylogenetic patterns in *Silene* section *Melandrium* (Caryophyllaceae) as inferred from chloroplast and nuclear DNA sequences. *Mol. Phylogenet. Evol.*, **57**(3), 978-991.
23. Rautenberg, A., Filatov, D., Svennblad, B., Heidari, N. and Oxelman, B. (2008) Conflicting phylogenetic signals in the SIX1/Y1 gene in *Silene*. *BMC Evol. Biol.*, **8**(1), 1.
24. Endress, P.K. and Matthews, M.L. (2006) Elaborate petals and staminodes in eudicots: diversity, function, and evolution. *Org. Divers. Evol.*, **6**(4), 257-293.
25. Fürstenberg-Hägg, J., Zagrobelny, M. and Bak, S. (2013) Plant defense against insect herbivores. *Int. J. Mol. Sci.*, **14**(5), 10242-10297.
26. Glas, J.J., Schimmel, B.C., Alba, J.M., Escobar-Bravo, R., Schuurink, R.C., Kant, M.R. (2012) Plant glandular trichomes as targets for breeding or engineering of resistance to herbivores. *Int. J. Mol. Sci.*, **13**(12), 17077-17103.