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Trichome micromorphology and its significance in the systematics of *Convolvulus* L. (Convolvulaceae)

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Abstract: Trichomes of 35 species of the genus *Convolovulus* and one species of the genus *Calystegia* (*C. sepium*) were investigated using light and scanning electron microscopy. The trichomes show a great variation, which provides valuable data for sections and species delimitation in *Convolvulus*. Trichomes of *Convolvulus* are nonglandular, simple, and basifixed or rarely asymmetrically medifixed. Characters of taxonomic interest were the degree of curviness (straight to spiral), orientation relative to the epidermal surface (appressed to erect), and presence of papillae on trichome surface. The trichomes are divided into two basic types: cylindrical and flattened ribbon-like. Our data provide the additional evidence to include *Calystegia* in *Convolvulus*; the former is characterized by glabrous shoots supporting its inclusion in the *Convolvulus* sect. *Convolvulus*. Using the evolutionary framework provided by recent molecular phylogenetic investigations, the following trends can be proposed in *Convolvulus*: long cylindrical trichomes are advanced against the flattened ribbon-like ones, densely papillate trichomes are derived against the nonpapillate or loosely papillate ones, long trichomes are advanced against the short ones, and appressed trichomes are primitive compared with the erect ones. In most investigated species of *Convolvulus*, a mixture of various kinds of trichomes has been detected, and the level of advancement should be determined by a collective approach.

Key words: *Convolvulus*, epidermis, indumentum, Iran, phylogenetics, taxonomy

1. Introduction

Convolvulaceae are a large family, including 59 genera and 1950 species (Staples 2018). They occur in both tropical and temperate regions and exhibit a rich diversity of morphological characteristics. *Convolvulus* L. (Convolvuleae, Convolvulaceae) comprises 190–200 species following its most recent circumscription (William et al., 2014; Wood et al., 2015). The genus includes annual, perennial herbs, subshrubs and shrubs that are widely distributed in dry, sandy and stony and gravelly habitats of temperate biomes. Several centers of diversity have been recognized for the genus in both the Northern and Southern hemispheres. Although the genus is almost absent from East Asia, it is most diverse in the Irano-Turanian region (Wood et al., 2015).

In terms of subgeneric classification, Boissier (1875) based his system on differences in the habit (shrubby, cushion, annual to perennial herbs and prostrate or erect stems, trailing or twinning), spine presence, hairiness of ovary and capsule. He divided the genus into 10 unranked (indicated as "§") groups. Rechinger (1963), treated *Convolvulus* distinct from *Calystegia*, mainly followed Boissier (1875), and divided the genus into nine series. This classification was not followed by Sáad (1967), who revised the genus in the Mediterranean area and western Asia and classified its species in three sections: *C.* sect. *Acanthocladi*, *C.* sect. *Inermes* and *C.* sect. *Convolvulus*. She also recognized 12 subsections in the genus. Wood et al. (2015) presented the most updated monograph of *Convolvulus* based on the phylogenetic framework published by William et al. (2014) and assigned these species to seven morphological and geographical units. They hesitated to present a formal supra-specific classification of the genus given the nature of the morphological variation and high level of homoplasy.

The family Convolvulaceae has been the subject of several molecular phylogenetic studies. The monophyly of the family has been confirmed within Asterids using several

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molecular markers including, all three plant genomes (Stefanović et al., 2002). Referring to this established well-resolved framework, several monophyletic groups were detected supporting the traditional tribal classification of the family, and five well-supported clades were also added, which match with the tribal concept (Stefanović et al., 2002). All these findings have led to lessening the incompatibility of traditional taxonomic classification systems, which have used homoplasious characters as criteria. Moreover, two groups previously considered to represent separate families, viz. genus *Cuscuta* and tribe Dichondreae, were shown to be nested within Convolvulaceae (Stefanović et al., 2003).

Micromorphology and ultrastructural data have provided useful information on the evolution and classification of different genera of seed plants and might play a significant role in modern synthetic classification systems. Trichome micromorphology could provide further evidence to create more natural classifications, particularly at generic and subgeneric levels. Sáad (1967), who presented the most comprehensive monograph of *Convolvulus*, described some features of trichomes, including the shape and length of apical cells (ranging from 0.2 to 5 mm), but she did not use the trichome types for species delimitation. Aykurt and Sümbül (2014) presented a revision of genus *Convolvulus* in Turkey, in which they used the indumentum type as a diagnostic character at the species level. According to Wood et al. (2015), six groups can be distinguished based on trichome size and density on leaves and stems. There are several descriptive studies on single or few species of the genus, without any comprehensive implication. Khokhar et al. (2012) examined six species of the genus *Convolvulus* and distinguished the papillate ornamentations on trichomes of *C. psuedocantabrica* to represent pneumatophores. Trichome density appears to exhibit phenotypic plasticity in drought conditions in *C. chilensis* (Gianoli and González-Teuber, 2005). The genus *Ipomea* L. shows greater variability in trichomes of vegetative organs; Paiva and Martins (2011) detected specialized calycinal (peltate, shortly stalked, and secretory) trichomes located on the calyces of *I. carica* (L.) Sweet, which had been neglected before and showed the function and structure analogous to colleters. Khan et al. (2013) studied the diversity of trichomes of foliar epidermis corresponding to 40 genera and 20 families, including some members of Convolvulaceae in the tropical part of Pakistan, recognizing two main types of trichomes in the family, i.e. attenuate and peltate. Furthermore, Ashfaq et al. (2019) studied the foliar micromorphology of Convolvulaceous taxa, gathered from arid parts of Northern Punjab Pakistan to estimate the hypothesis that glandular trichomes density decreases with high aridity. Other studies in the family detected stellate, capitate, and peltate glandular trichomes in the genera *Evolvulus* L., *Jacquemontia* Choisy and *Merremia* Dennst. ex Endl.), respectively (Buril et al., 2012; Aron et al., 2013; Ketjarun et al., 2016). Ezazi et al. (2019) provided the trichome-based identification key of five species of sect. *Acanthocladi*. None of the previous studies dealt with the systematic importance of trichome characters in Convolvulaceae sufficiently, despite the potential value known for such structures in other dicot families (e.g., Metcalfe and Chalk, 1950; El-Gazzar and Watson, 1970; Abu-Asab and Cantino, 1987; Cantino, 1990).

The present study aims at documenting the trichome micromorphology of *Convolvulus* spp. to evaluate their systematic significance and discuss them on the background of both molecular and traditional classifications. We are going to test the trichome micromorphology in the delimitation of subgeneric taxa or known clades in the genus. Besides, the informative characters which might be useful in determining and distinguishing the species/subspecies in *Convolvulus*, which were primarily based on Iranian taxa, will be explained.

2. Materials and methods

In the present study, trichomes of 35 species of *Convolvulus* (including *Convolvulus sepium* L. = *Calystegia sepium* (L.) R.Br.) were investigated. We used mainly fresh materials collected in 2015–2018 from natural populations. Otherwise, in some cases, the materials were removed from the specimens deposited mainly in the herbarium of Research Institute of Forest and Rangelands, Iran (TARI), the central herbarium of the University of Tehran (TUH) and herbarium of the Iranian Research Institute of Plant Protection (IRAN). A list of voucher specimens examined is provided in Table 1.

Trichomes were obtained from the vegetative parts (stems and leaves) and calyces and investigated with stereo-, light, and scanning electron microscope (SEM). For scanning electron microscopy, small dried pieces (2 × 2 mm) of stem, leaves, and calyces were fixed on aluminum stubs using a double-sided adhesive, which was coated subsequently with gold. The SEM micrographs were taken with a TESCAN FE-SEM scanning microscope at Lorestan University. For measurements, we used an ocular linear applied in the stereomicroscope. Digimizer software[1] was used to measure the exact length of trichomes. The types of trichomes were described and classified according to terminology provided by Payne (1978) as well as Navarro and El Oualidi (2000).

3. Results

The main types of trichomes and their distribution among 35 studied species are described in detail below and summarized in Table 2. Selected SEM micrographs of the

[1] https://www.digimizer.com

Table 1. Collection data of *Convolvulus* spp. distributed in Iran and adjacent countries examined in the present study for trichome characters. Sectional and subsectional concept follows Sáad (1967).

Species	Section/subsection	Collection data and herbarium
C. acanthocladus Boiss. & Kotschy	*Acanthocladi/Acantocladi*	Prov. Bushehr, Khurmuj, H. Khodayari & E. Roudi 2019200 (HSBU)
C. aitchsonii C.B.Clarke	*Acanthocladi/Acantocladi*	Afghanistan, between Alizaiee and Habibkalla, Kurrama valley, 1000-2000m. J. Aitchison 35719 (TARI)
C. ammannii Desr.	*Inermes/Inermes*	Prov. Krasnojrask, Chakassia, V. Reverdatto 3764 (TARI)
C. arvensis L.	*Convolvulus/Convolvulus*	Prov. Semnan, Ray Abad to Hossein Abad Kalpoosh, 1356m, E. Roudi et al. 2019202 (HSBU)
C. betonicifolius Mill.	*Convolvulus/Convolvulus*	Prov. Ilam, Eivan, E. Roudi & M. Arabameri 2019203 (HSBU)
C. calvertii Boiss.	*Inermes/Lanuginosi*	Prov. Semnan, Hossein Abad Kalpoosh to Till Abad, E. Roudi et al. 2019204 (HSBU)
C. cantabrica L.	*Inermes/Oleifolii*	Prov. Semnan, Between Rezvan and Hossein Abad Kalpoosh, E. Roudi et al. 201920 (HSBU)
C. cephalopodus Boiss.	*Inermes/pannosi*	Prov. Bushehr, Khurmuj, H. Kodayari & E. Roudi 2019205 (HSBU)
C. chondrilloides Boiss.	*Inermes/Inermes*	Prov. Lorestan, Lorestan University Campus, H. Khodayari & E. Roudi 2019207 (HSBU)
C. commutatus Boiss.	*Inermes/Lanuginosi*	Prov. West Azarbayjan, Urmia, Shahriar, in the road to Anhar village, Sh. Bahadori & M. Arab Ameri 2019209 (HSBU)
C. dorycnium L.	*Inermes/Inermes*	Prov. Khorasan, Shirvan to Kopedagh, M. Arab Ameri et al. 2019211 (HSBU)
C. elymaiticus Mozaff.	*Inermes/Lanuginosi*	Prov. Ilam, Kaver to Zarrin Abad, E. Roudi & M. Arab Ameri 2019212 (HSBU)
C. eremophilus Boiss. & Buhse	*Inermes/Inermes*	Prov. Semnan, Mayami to Biarjemand, E. Roudi et al. 2019214 (HSBU)
C. fruticosus Pall.	*Acanthocladi/Acantocladi*	Prov. Isfahan to Shahreza, 5 km to Shahreza, Nik Abad, E. Roudi et al. 2019215 (HSBU)
C. gonocladus Boiss.	*Inermes/Pannosi*	Prov. Khuzestan, Behbahan to Borazjan, H. Khodayri & E. Roudi 2019216 (HSBU)
C. glomeratus Choisy	*Inermes/Diffusi*	Prov. Hormozgan, Bandar Abbas, 21 km on road of Bandar Lengeh to Bandar Khamir, V. Mozzafarian 63593 (TARI)
C. kotschyanus Boiss.	*Inermes/Pannosi*	Prov. Hormozgan, Bandar Abbas, 21 km from Bandar Charak to Gavbandi, M. Iranshahr & F. Termeh 13159 (IRAN)
C. lineatus L.	*Inermes/Pannosi*	Prov. Kurdistan, Kamyaran, H. Khodayari & E. Roudi, 2019217 (HSBU)
C. leiocalycinus Boiss.	*Acanthocladi/Acantocladi*	Prov. Bushehr, Kangan to Taheri, H. Khodayari & E. Roudi 2019218 (HSBU)
C. oxyphyllus Boiss.	*Acanthocladi/Spinescentes*	Prov. Ilam, Saleh Abad, Sarney, E. Roudi & M. Arab Ameri 2019219 (HSBU)
C. oxysepalus Boiss.	*Acanthocladi/Serospinescentes*	Prov. Kerman, Jiroft, Dam Area of Halilroud, 1202 m, V. Mozaffarian 88568 (TARI)
C. pilosellifolius Desr.	*Inermes/Diffusi*	Prov. East Azarbyjan, After Eskanlou deviation, 5 km to Kaleibar, E. Roudi et al. 2019220 (HSBU)

Table 1. (Continued).

C. prostratus Frossk.	*Inermes/Diffusi*	Prov. Hormozgan, Charak, Kish Iland, F. Termeh & M. Karavar 25899 (IRAN)
C. pseudocantabrica Schrenk	*Inermes/Inermes*	Prov. Semnan, Abr Forest, Ghatri Mount., E Roudi et al. 2019223 (HSBU)
C. rectangularis Rech.f.	*Inermes/Inermes*	Afghanistan, 35 km NW Urgun, 2200-2400m, K. H. Recshinger 35902 (TARI)
C. reticulatus Choisy	*Inermes/Pannosi*	Prov. Ilam, SalehAbad, Sarney, E.Roudi & M. Arab ameri, 2019222 (HSBU)
C. schirazianus Boiss.	*Inermes/Lanuginosi*	Prov. Kerman, 40km Baft, South of Gugher, A. Ghahraman et al. 28591 (TUH)
C. spinosus Forssk.	*Acanthocladi/Acantocladi*	Prov. Baluchestan, Rask, Pishin village, A.H. Pahlavani et al. 47517 (IRAN)
C. stachydifolius Choisy	*Convolvulus/Convolvulus*	Prov. Lorestan, Lorestan University sight, E. Roudi & H. Khodayari 2019221 (HSBU)
C. stapfii Rech.f.	*Inermes/Pannosi*	Prov. Fars, Shiraz, Baramshur, 750m, A. Dehbozorgi 32683 (TARI)
C. turrillianus Parsa	*Acanthocladi/Serospinescentes*	Prov. Sistan and Baluchestan, Bazman, 1366m., M. Ranjbar et al. 37437.(Bu Alisina University herbarium)
C. urosepalus Pau	*Acanthocladi/Spinescentes*	Prov. Lorestan, Azna, Tyan village, 2700-3300m, M. Iranshahr 13332 (IRAN)
C. virgatus Boiss.	*Acanthocladi/Serospinescentes*	Prov. Baluchestan, Sareh, 1000 m, A. Ghahraman et al. 21578 (TUH)
C. sepium L.	*Convolvulus/Convolvulus*	Prov. Guilan, Rasht, Imamzade Hashem region, E. Roudi 2019224 (HSBU)

common types of trichomes are presented in Figures 1–3. The trichomes in all examined species were nonglandular, simple or bifurcate (medifixed), and unicellular. Among several analyzed criteria of trichomes, characters of taxonomic importance were the size of trichome, surface of trichome (smooth, papillate or articulate), orientation of trichome (erect, subappressed, or appressed), attachment of trichome to the surface (basifixed or medifixed), and the curviness of trichomes (hooked, bent, or twisted). Based on the solidness of epidermal cells, two types of trichomes were recognized, viz. cylindrical and flattened, as the basic trichome types in the investigated species which can be subdivided into six groups (four subtypes in cylindrical type and two subtypes in flattened type, see below) based on variations observed. The cylindrical trichomes included short to extremely long hairs attached to a rounded epidermal cell, and might be appressed or slightly erect, smooth, or papillate on the surface. Based on the variation observed in terms of level of curviness, cylindrical trichomes could be subdivided into four subtypes: 1) acicular: needle-shaped trichomes, subappressed or appressed trichomes with rounded basal epidermal cell and an elongated apical cell slightly folded at base (Figures1a–1c), 2) hooked: erect trichomes abruptly curved or bent at tip (Figure 1e), 3) falcate: evenly curved trichomes (Figure 2e), and 4) spiral: trichomes folding along their entire length, being erect or appressed (Figure 2i). Flattened ribbon-like trichomes ranged from erect (Figure 1l) to appressed (Figure 3i) and from smooth to articulate on the surface (Figure 3c). These trichomes might be divided into basifixed or medifixed subtypes. The basifixed subulate trichomes (Figures 3b and 3c) tapered from a thick base to a sharp point, while the medifixed trichomes (Figure 3i) were shortly stalked and split into two lateral opposite halves forming equal to unequal arms.

The density of trichomes varied among the examined species and different parts of a certain species (Table 2). Acicular trichomes occur in almost all species but vary in density among various species. In some species, both main types of trichomes (simple and medifixed) could simultaneously occur. Indumentum is not distributed uniformly on all parts of the plants, for example, the cylindrical trichomes in *Convolvulus chondrilloides* covered the calyx densely, while they were sparsely distributed

Table 2. Trichome characteristics of examined *Convolvulus* spp. Abbreviations used: C= calyx, L= leaf, 'S= stem; all measurements in µm.

Species/Section	Density	Surface	Size	Cylindrical				Flattened ribbon-like	
Sect. *Acanthocladi*				Acicular	Falcate	Hooked	Spiral	Medifixed	Basifixed
C. acanthocladus	Dense	Smooth	900/657-(1260/38)-1661/57	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, + L, - C, -
C. fruticosus	Dense	Papillate	615/45-(803/65)-919/62	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, +
C. leiocalycinus	Dense	Smooth	758/86-(906/07)-1054/62	S, + L, + C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. oxyphyllus	Dense	Papillate	448/065-(554/8)-761/465	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, + L, - C, -
C. oxysepalus	Dense	Smooth	314/14-(475/549)-620/126	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. spinosus	Sparse	Smooth	106/98-(150/81)-173/96	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. turrilianus	Dense	Smooth	435/60-(683/55)-931/77	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, + L, - C, -
C. urosepalus	Sparse	Smooth	366/595-(610/77)-730/644	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. virgatus	Sparse	Papillate	545/62-(753/55)-962/87	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
Sect. *Inermes*									
C. aitchisonii	Dense	Smooth	515/35-(703/55)-819/52	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. ammani	Dense	Smooth	110/320-(160/324)-219/326	S, + L, + C, -	S, - L, - C, -	S, - L, - C,	S, - L, - C, -	S, - L, - C, -	S, - L, - C, +
C. cephalopodus	Very dense	Smooth	394/98-(526)-868/58	S, + L, + C, +	S, + L, - C, +	S, - L, - C, -	S, + L, + C, -	S, - L, - C, -	S, - L, - C, -
C. calvertii	Dense	Smooth	123/639-(405/166)754/217	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C,-	S, - L, - C, -	S, - L, - C, +
C. cantabrica	Dense	Smooth	96/152-(325/54)-475/93	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -

Table 2. (Continued).

C. chondrilloides	Dense	Smooth	100/764-(339/332)-762/625	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. commutatus	Dense	Smooth	58/43-(435/41)-993/55	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, +
C. dorycnium	Dense	Smooth	128/06-(204/05)-281/69	S, - L, - C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, + L, - C, -	S, + L, - C, +
C. elymaiticus	Very dense	Smooth	764/62-(1159/38)-1246/67	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. eremophilus	Dense	Papillate	402/977-(588/68)-751/561	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, + L, - C, +
C. glomeratus	Sparse	Papillate	317/297-(440/392)-522/198	S, + L, + C, +	S, - L, - C, -	S, + L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. gonocladus	Dense	Smooth	504/98-(726)-1068/58	S, + L, + C, +	S, + L, - C, -	S, - L, - C, -	S, + L, - C, -	S, - L, - C, -	S, - L, - C, -
C. kotschyanus	Dense	Smooth	313/61-(352/9)-380/90	S, + L,+ C, +	S, + L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. lineatus	Dense	Smooth	291/52-(333/15)-378/731	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. pilosellifolius	Dense	Smooth	237/58-(298/76)-361/284	S, + L, + C, +	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. prostratus	Dense	Smooth	800/006-(1159/38)-1561/75	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. pseudocantabrica	Dense	Smooth	98/06-(145/29)-181/69	S, - L, + C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, + L, - C, -	S, + L, - C, -
C. rectangularis	Dense	Smooth	327/85-(394/76)-461/328	S, + L, + C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. reticulatus	Very dense	Smooth	484/95-(1655/76)-2999/87	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. schirazianus	Dense	Papillate	578/86-(686/07)-854/62	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. stapfii	Dense	Smooth	321/152-(449/05)-578/451	+ S, L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -

Table 2. (Continued).

Sect. *Convolvulus*									
C. arvensis	Sparse	Smooth	212/621-(338/53)-465/77	S, + L, + C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. betonicifolius	Sparse	Smooth	312/549-(598/127)-993/552	S, + L, + C, +	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. stachydifolius	Sparse	Smooth	145/31-(257/21)-369/11	S, + L, + C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -
C. sepium (= *Calystegia sepium*)	Very sparse	Smooth		S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -	S, - L, - C, -

on the adaxial and abaxial sides of leaves. The medifixed trichomes show high variability among the examined species, for example, two species of *C.* sect. *Inermes*, i.e. *C. psuedocantabrica* (Figure 3i) and *C. dorycnium* L., were covered densely by medifixed trichomes. The density of indumentum on calyx varies extensively from very sparse to very dense. The calyx shows also considerable variability in trichome types (Table 2). The density and types of trichomes in *C.* sect. *Inermes* show higher variability than the two other sections studied here. *Convolvulus sepium* is nearly glabrous and lacks any trichome that could be correlated to any other studied species.

4. Discussion

This study presents the first comprehensive investigation of trichome micromorphology in the genus *Convolvulus* and reveals significant interspecific variation in trichome characteristics that provide a valuable source of data potentially informative for natural grouping in the genus. It seems that the observed variation is most useful to distinguish the species of the genus, but some characters are also section or subsection specific. Without paying detailed attention to trichome characteristics, some general features of indumentum, have been used in previous studies to discriminate the species of *Convolvulus* (Sáad, 1967; Nowroozi, 2000), for example, pubescent ovary against the glabrous one was mentioned as a diagnostic feature to separate *C. chondrilloides* (with hairy ovary) from *C. leptocladus* (with glabrous ovary). Since the trichome characters have successfully been used in indicating the evolutionary trends in some other families, such as Lamiaceae (Navarro & El Qualidi,1999; Salmaki et al., 2009; Xiang et al., 2010; Eiji and Salmaki, 2015), the observed variability in *Convolvulus* might also be linked with the phylogenetic patterns known in the genus (Stefanivic et al., 2002, 2003). Austin (1973) presented a comprehensive description of trichomes in Convolvulaceae discussing their taxonomic value in recognition of tribes and genera in this family. According to Austin (1973), different types of trichomes might be indicative at generic rank, but the intrageneric variation of trichomes in the genus *Convolvulus* has not been sufficiently addressed. Following previous studies (Austin, 1973; Gianoli and González-Teuber, 2005; Paiva and Martins, 2011; Khokhar et al., 2012; Ashfaq et al., 2019), our results showed that *Convolvulus* spp. lack any branched (except for the medifixed ribbon-like ones) and glandular trichomes. On the contrary, other genera proposed to be related to *Convolvulus*, for example, *Evolvulus, Jacquemontia* and *Merremia* are covered partly by branched trichomes. Members of the genera *Ipomea* and *Maripa* Aubl. differ from *Convolvulus* by having glandular trichomes derived from the simple peltate scales located on the leaf apex (Austin, 1973). Based on the available data (Austin, 1973; Stefanović et al., 2002, 2003), it seems that tribe Convolvuleae including *Calystegia, Convolvulus*, and *Polymeria* RBr. is characterized by nonglandular trichomes, while various kinds of trichomes including the glandular and nonglandular (in some species combined and present together in one individual) ones could be detected in tribe Ipomeeae.

The previous molecular phylogenetic studies provided a framework allowing mapping of the trichome characters and indicating their patterns of evolution (Stefanović et al., 2002, 2003; William et al., 2014). Mapping of trichome characters on these phylogenetic trees indicates that the these characters are too homoplasious to allow determining certain trends in their evolution in *Convolvulus*, as it is the case for indicating clear evolutionary transformation series corresponding to plant habit (William et al., 2014). Thus, the proposed evolutionary trends, suggesting short flattened ribbon-like trichomes to be primitive against the long cylindrical ones (Austin, 1973), are not corroborated by the available data.

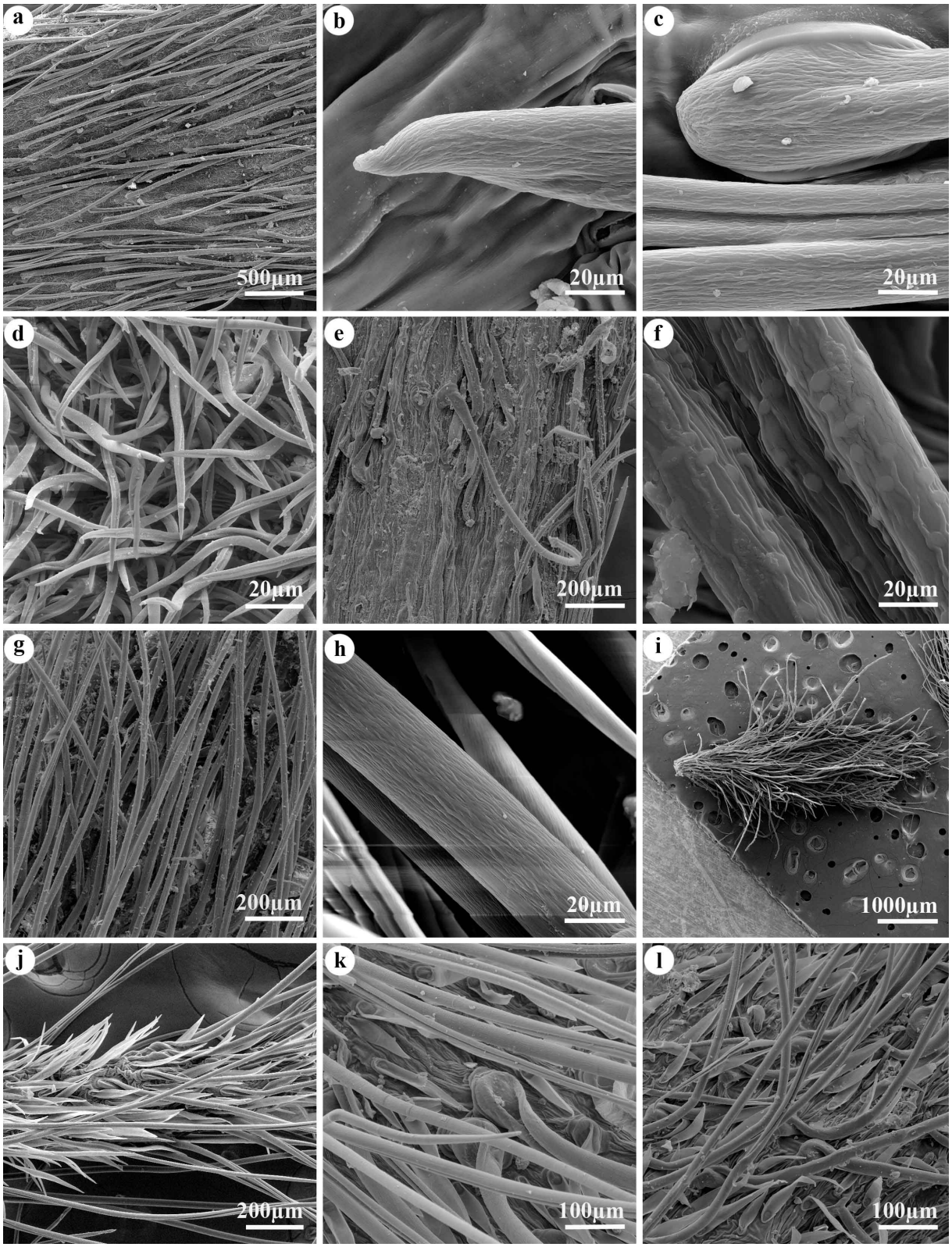

Figure 1. Selected SEM micrographs of *Convolvulus* spp. (a, b, c) acicular trichome in C. *chondrilloides*; (d) dense indumentum in C. *chondrilloides*; (e, f) hooked trichome in *C. glomeratus*; (g) acicular trichome in *C. urosepalus*; (h) nonpapillate trichome in *C. cephalopodus*; (i) calyx indumentum in *C. prostrates*; (j, k) acicular and basifixed trichomes in *C. calvertii*; (l) acicular and flattened trichomes on calyx of *C. oxysepalus*.

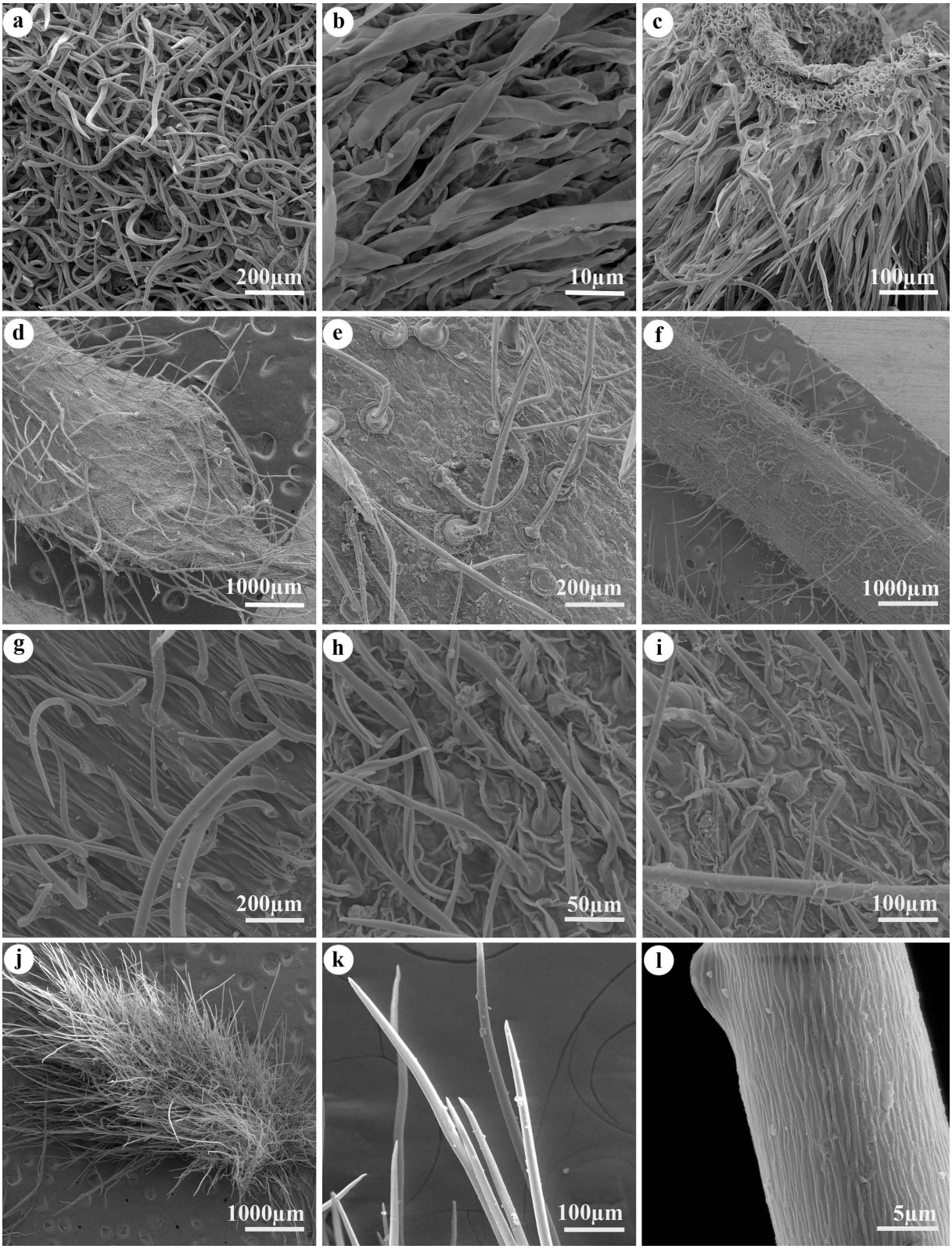

Figure 2. Selected SEM micrographs of *Convolvulus* spp. (a) dense indumentum in *C. oxysepalus*; (b) basifixed trichomes in *C. acanthocladous*; (c) long basifixed trichomes in *C. elymaiticus*; (d, e) falcate trichomes in *C. betonicifolius*; (f, g) falcate trichomes in *C. cephalopodus*; (h, i) spiral trichomes in *C. gonocladous*; (j, k, l) calyx indumentum in *C. reticulatus*.

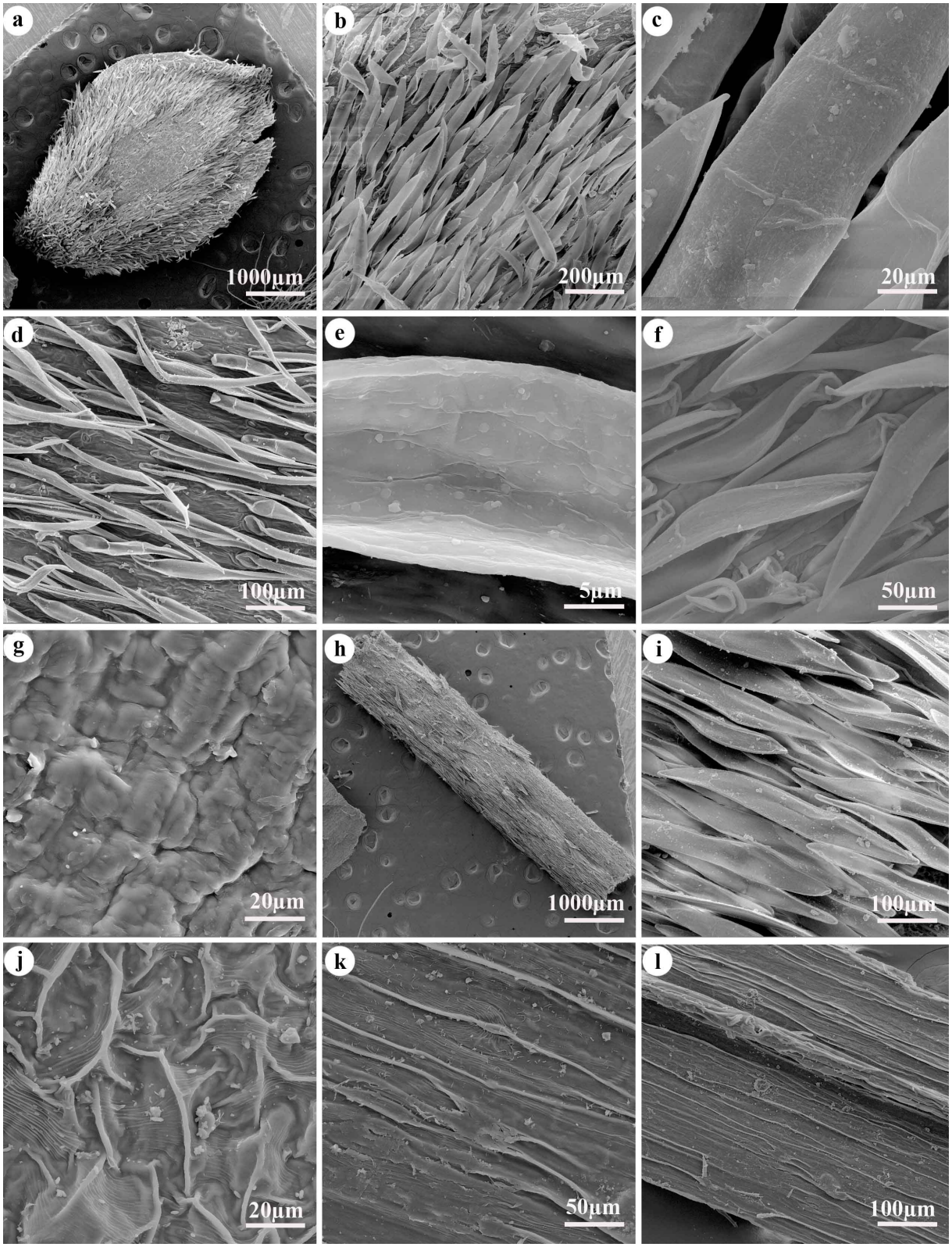

Figure 3. Selected micrographs of *Convolvulus* spp. (a, b, c) erect basifixed trichomes in *C. ammani*; (d, e) basifixed papillate trichomes in *C. fruiticosus*; (f) flattened basifixed trichomes in *C. acanthocladus;* (g) glabrous surface of calyx in *C. leiocalycinus*; (h, i) medifixed trichomes in stem of *C. psuedocantabrica*; (j, k, l) glabrous surface of leave, shoot and calyx in *C. sepium*.

Several previous efforts using trichome characteristics to address the infrageneric classification of *Convolvulus* (formally or informally) applied rather general groupings based on indumentum type. Wood et al. (2015) presented a grouping of *Convolvulus* spp. based on indumentum features of the stem and leaves, defining six informal groups without praising detailed features of individual trichomes: 1- velvety-tomentose, 2- densely sericeous/ canescent, 3- very finely sericeous and often somewhat glabrescent, 4- villous-tomentose, 5- glabrous or nearly so, and 6- sepal indumentum strikingly different from that of stem and leaves. Although the mentioned trichome classification does not support the traditional subgeneric classification of the genus based on morphological features (Sáad, 1967), the villous-tomentose group (group 4) characterized by long trichomes matches well with *C.* sect. *Inermes* as circumscribed by Sáad (1967), predominantly consisting of perennial plants. This finding is partly also in line with our results (for details see below under *C.* sect. *Inermes*). Besides, 'group 5' as defined by Wood et al. (2015) is compatible with *C.* sect. *Convolvulus*, as defined by Sáad (1967) and also matches well with our results in this section.

Grouping of species in the genus *Convolvulus* based on indumentum features may be explained by the geographical distribution patterns (Mitchel et al., 2016). Wood et al. (2015) indicated that nearly all species of *C.* sect. *Acanthocladi* and some members of *C.* sect. *Inermes*, which are distributed widely in the Mediterranean region and the Middle-East, are covered by densely sericeous indumentum and can be classified in the same group based on indumentum type. Although in the large country of Iran which, is occupied by four distinct geographical phytochoria (Zohary, 1973), the trichome features cannot be correlated to the biogeographical patterns known in the country. As an example, in the northern parts of Iran representing the Hyrcanian region, *Convolvulus sepium* (= *Calystegia sepium*), which is related to the members of *C.* sect. *Convolvulus* is frequently distributed, while the other three species of this section in Iran are predominantly distributed in Southwest Iran. A group of closely related species known from North East Iran (Semnan to Khorasan), viz. *C. dorycnium*, *C. eremophilus* and *C. pseudocantabrica*, are morphologically similar, but the cylindrical trichomes are lacking in *C. dorycnium* and *C. pseudocantabrica* and frequent in *C. eremophilus*. Other members of this section, which are distributed in South Iran, are covered mainly by cylindrical trichomes. The indumentum coverage among *Convolvulus* spp. distributed in South Iran was dense, while the species of *Convolvulus*, growing in North Iran, show less indumentum density. Furthermore, the longest trichomes were found in those species of *C.* sect. *Inermes* distributed in Southern parts of the Country.

The foliar indumentum density might have differed as an ecophysiological response to aridity, and has been used often to define infraspecific taxa (see, e.g., Gianoli and González-Teuber, 2005). Recently, based on examining the foliar micromorphology of 18 species of Convolvulaceae in arid habitats of Pakistan, Ashfaq et al. (2019) indicated that the density of glandular trichomes dramatically decreased due to physiological compatibility to drought, while the density and size of nonglandular trichomes particularly in *Convolvulus* spp. was at highest among the investigated genera. It seems that trichome density and type are more strongly affected by the ecological factors than the geographic patterns. Generally, the densely hairy plants are expected to be found in arid areas, while the glabrous or less densely hairy ones in humid habitats (for example in *C. prostratus*, Ashfaq et al., 2019). However, we observed some exceptional cases where the densely hairy populations of *C. pilosellifolius* were distributed in North Iran (Prov. Ardebil, Kaleibar), but the loosely covered populations were found in the South West (Prov. Ilam, Dareshahr).

Trichome micromorphology can potentially provide a basis for evaluating the challenging infrageneric classification of *Convolvulus* as well as some unresolved phylogenetic issues in the genus, but it is known to be very homoplastic at the same time (Austin, 1998b; Manos et al., 2001; Carine and Scotland, 2002). As the next scope of the present research, we are going to test the efficiency of trichome characters in the subgeneric classification of *Convolvulus*. We will also address the traditional classification systems based on morphological characters (Boissier, 1875; Rechinger, 1963; Saad, 1967), even if this traditional concept of sections have not been supported by the recent phylogenetic studies (Williams et al., 2014).

4.1. *C.* sect *Acanthocladi*

The species of this section are characterized by shrubby or subshrubby habit, with branches either ending into spines and upper sterile peduncles or peduncles with falling flowers (Sáad, 1967). This section has been divided into three subsections by Sáad (1967): *C.* subsect. *Acanthocladi* Boiss., *C.* subsect. *Spinescentes* Boiss. and *C.* subsect. *Serospinescentes* Sáad. Most species of *C.* subsect. *Acanthocladi* have densely pilose calyx and sericeous leaves, except *C. leiocalycinus* with glabrous calyx (Figure 3g). According to Wood et al. (2015) the indumentum density could be useful in distinguishing *C. acanthocladus* from *C. iranicus*, the latter being less densely hairy. Ezazi et al. (2019) also used the density and size of leaf trichomes in discrimination of five species of *C.* subsect. *Acanthocladi*. Both main types of cylindrical and flattened appressed trichomes are present in most species of this subsection, while *C. fruticosus* is merely covered by short basifixed and medifixed flattened trichomes, sparsely papillate on the surface of all parts of the plants (Figures 3d).

Convolvulus leiocalycinus is well-characterized by petiolate leaves and also glabrous calyx suggesting its isolated position in the section as deduced according to the molecular phylogenetic findings (William et al., 2014*). Convolvulus oxyphyllus* and *C. urosepalus* (two representatives of *C.* subsect. *Spinescentes*) are characterized by cylindrical (acicular) trichomes sparsely papillate on the surface. Other members of this subsection are, however, characterized by long cylindrical trichomes smooth on the surface mixed with short, flattened semiappressed ones. These two main types of the nonglandular trichomes are observed together and in densely appressed arrangement on the calyx, but the leaves and shoots are covered by the uniform trichomes consisting of one of either type of trichomes. Two endemic species in South Iran, *C. turrillianus*, and *C. oxysepalus* could be discriminated based on leaf and shoot trichomes. Greyish sericeous indumentum is characteristic for *C. turrillianus*, but both species are semiappressed hairy on the calyx with long trichomes up to 2 mm. Phylogenetically, C. *turrillianus* is placed in the Old World clade (William et al., 2014; Mitchel et al., 2016) together with other species characterized by sericeous leaves and shoots. Consequently, we believe that *C. oxysepalus* belongs to the same clade, which needs to be confirmed yet.

4.2. *C.* sect. *Inermes*

The species of this section are characterized by erect and rigid or prostrate shoots covered densely by long trichomes almost uniformly distributed throughout the plants. The members of *C.* sect. *Inermes* were divided into seven subsections, in which representatives of five subsections were examined in our study: *C.* subsect. *Diffusi* Boiss., *C.* subsect. *Inermes* Boiss., *C.* subsect. *Lanuginosi* Peter, *C.* subsect *Oleifolii* Peter, and *C.* subsect. *Pannosi* Boiss. (Sáad, 1967). These subsections could be considered equivalent to informal groups in Boissier's (1875) system, which were defined based on the presence or absence of trichomes on the ovary or elsewhere. Seventeen species of this section were included in our study consisting of the most taxonomically problematic species, *C. eremophilus*, with more than 10 species names considered as its synonyms due to overlapping morphological characters (Wood et al., 2015). The presence of trichome on the ovary could be partly informative for its discrimination from *C. erinaceus* which is characterized by a glabrous ovary (Sáad, 1967).

According to Wood et al. (2015), shoot indumentum also reveals some diagnostic characters of taxonomic interests. As an example, the species of *C.* sect *Inermes* based on the shoot trichome type might be divided into two groups. Flattened basifixed trichomes covered the shoots of *C. dorycnium*, *C. eremophils*, and *C. psuedocantabrica*, which might be informative in discriminating the subspecies. However, most other members of *C.* sect. *Inermes*, viz. *C. bushiricus*, *C. cephalopodus*, *C. chondrolloides*, *C. commutatus*, *C. glomeratus*, *C. rectangularis*, *C. reticulatis*, are covered by cylindrical trichomes. Although other members of *C.* sect. *Inermes* are covered by cylindrical trichomes at least on the calyx, *C. dorycnium* and *C. psuedocantabrica* lack spreading cylindrical long trichomes on the shoots. Moreover, *C. psuedocantabrica* has a cylindrical calyx, which is glabrous. In general, our results indicate that the trichome type could be informative to allow characterizing the subsections (sensu Sáad, 1967). In this section *C. commutatus* and *C. calvertii* which were included in *C.* subsect. *Lanuginosi* by Sáad (1967) are morphologically very similar while they could be distinguished by orientation of the acicular trichomes, which are erect in the latter while appressed in the former. Wood et al. (2015) suggested a close relationship between *C. calvertii*, *C. commutatus*, and *C. elymaiticus* Mozaff. Long cylindrical trichomes densely covering the whole plant is a characteristic feature that supports discriminating the newly described *C. elymaiticus* (Mozaff, 2010) from other mentioned species of this species complex. Although there are many significant morphological differences between *C. reticulatus* (e.g. prostrate habit) and other members of *C. commutatus* alliance (which are erect subshrubs), they have been placed in *C.* sect. *Inermes* by Sáad (1967). In a recent phylogenetic study (William et al., 2014), *C. reticulatus* was not retrieved in the same clade as the members of the *C. commutatus* alliance. Trichome size and density provide additional evidence on separating *C. reticulatus* from the members of *C. commutatus* alliance, as the shoots in the former are covered densely by long spreading trichomes (Table 2 and Figures 2j–2l), while they are acicular and appressed in other members of *C. commutatus* alliance.

Convolvulus gonocladus and *C. kotschyanus* seem to be very similar, through scorpioid cymes, spathulate basal leaves and also very long cylindrical trichomes, covering the whole plant. Recently, *C. gonocladus* was treated as a synonym of *C. kotcshyanus* (Wood et al., 2015). Trichome characteristics examined here confirm this treatment because representatives of both species have the unique falcate type of trichomes, which is not reported in any other species of *Convolvulus.* As another example, *C. bushiricus* had been reduced to subspecific rank under *C. cephalopodus* by Wood et al. (2015). Although the indumentum in both taxa is mainly of the same type (consisting of long cylindrical trichomes), the calyx in *C. cephalopodus* is less hairy than that in *C. bushiricus*, confirming the recent (Wood et al., 2015) taxonomic treatment in this group. *Convolvulus glomeratus*, a Saharo-Sindian element, is less densely hairy compared with other species of *C.* sect. *Inermes*. Two types of trichomes were observed in the species of this section, of which the acicular type is distributed uniformly on all parts of the plants in all studied species, while the hooked trichomes are common in the *C.* subsect. *Diffusi*. Based on a recent phylogenetic investigation (William et al., 2014), *C. glomeratus* is placed

in a different clade isolated from all other species of *C.* sect. *Inermes*. The trichomes in *C. glomeratus* are appressed and distinctly shorter than the other members of the section corroborating its isolate placement in the phylogeny.

4.3. *C.* sect. *Convolvulus*

The members of this section are characterized by twinning branches or twinning shoots (Sáad, 1967). The trichomes in this section are acicular and not papillate on the surface, loosely arranged, uniform and soft. The calyx varies in density among the species of the section ranging from glabrous (*C. arvensis*) to densely hairy. The indumentum density seems to be taxonomically informative in this section and can provide a useful tool in recognition of the species. The presence of pubescent indumentum versus the villous one could be taxonomically valuable in discriminating two members of this section, *C. stachydifolius* var. *stachydifolius* and *C. stachydifolius* var. *villosus* Hallier f. Thus, this character is useful in the delimitation of subspecific rank. The members of the *C.* sect. *Convolvulus* phylogenetically form a subclade in a larger clade consisting of all the Euro-Siberian species of the genus (William et al., 2014). Most of the species representing this section in our study are glabrous (except *C. betonicifolius*, which is covered by spreading trichomes, particularly on the calyx).

4.4. *Calystegia sepium*

In the most recent molecular studies of *Convolvulus* (Stefanović et al., 2002; Carine et al., 2004; William et al., 2014), *Calystegia* nested within the same clade as the representatives of *C.* sect. *Convolvulus*. From a micromorphological point of view, most members of this clade at least on leaves and stems are glabrous. *Calystegia sepium*, as the only representative of the genus, is glabrous, corroborating its close relationship with *C.* sect. *Convolvulus*. Among the species of this section, some species such as *C. scammonia* are also glabrous and similar to *Calystegia*, but morphologically have yellow corolla and smaller bracts enveloping the calyx. Thus, inclusion of *Calystegia* in the genus *Convolvulus* is supported by trichome micromorphology and other morphological characters.

5. Conclusion

The diversity of trichomes in the genus *Convolvulus* is quite low, because of the absence of the glandular and branched trichomes. Two basic types of trichomes are recognized in the genus: the flattened ribbon-like and the cylindrical ones. Both kinds of trichome show variation to some extent, allowing their application for various taxonomical purposes. The present study indicates the importance of trichome micromorphology in the taxonomy of the genus *Convolvulus*, especially in discriminating the sections and subsections. In a few cases, the type of trichomes and their density provide characteristic features in the delimitation of species. Some possible evolutionary trends can be recognized corresponding to trichome features: long cylindrical trichome is advanced against the flattened ribbon-like ones, densely papillate trichomes are derived from the nonpapillate or loosely papillate ones, long trichomes are advanced against the short ones and the appressed trichomes are primitive compared with the erect ones. There are some clear examples of the genus *Convolvulus* in dryer habitats, contradicting the ecological pattern of trichomes expected to be cylindrical, long, and erect. Our results support the inclusion of *Calystegia* in *Convolvulus* and its placement close to the members of *C.* sect. *Convolvulus*.

A diagnostic key to distinguish the sections and subsections in the genus *Convolvulus*:

1a. Glabrous plants or nearly glabrous plants sparsely covered by cylindrical trichomes ..... *C.* sect. *Convolvulus*

1b. Hairy plants covered uniformly or randomly by trichomes on one part or all parts of the plant 2

2a. Plants covered by cylindrical trichomes or both cylindrical and flattened ribbon-like trichomes 3

2b. Plants covered just by flattened ribbon-like trichomes 5

3a. Plants with sericeous indumentum, simultaneously covered by cylindrical and ribbon-like trichomes .... *C.* sect *Acanthocladi*

3b. Plants with certain type of cylindrical trichomes 4

4a. Plants densely covered by erect cylindrical trichomes ..... *C.* subsect *Pannosi*

4b. Plants densely covered by appressed cylindrical trichomes ..... *C.* subsect. *Lanuginisi*

5a. Plants uniformly covered by flattened ribbon-like trichomes on the whole plant 6

5b. Plant randomly covered by flattened ribbon-like trichomes 7

6a. Plants covered densely by flattened ribbon-like appressed trichomes ..... *C.* subsect. *Oleifolii*

6b. Plants sparsely covered by flattened ribbon-like appressed trichomes ..... *C.* subsect. *Acanthocladi*

7a. Plants sparsely covered by flattened ribbon-like trichomes on the shoot; calyx glabrous .... *C.* subsect. *Inermes*

7b. Plants sparsely covered by flattened ribbon-like trichomes on the calyx; shoots nearly glabrous .... *C.* subsect. *Diffusi*

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