

# Foliar trichomes and their systematic relevance in *Solanum* (Solanaceae) species from southern Western Ghats, Kerala

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## Abstract

Morphological features of foliar trichomes have been successfully employed in classification of diverse groups of plants. The present study evaluates the taxonomic value of trichomes in 17 taxa of *Solanum* L. using Scanning Electron Microscopy. Both glandular and non-glandular trichomes were observed on the leaves which showed variations in their density of distribution among the species as well as on the two surfaces of the leaves of the same species. The non-glandular trichomes with 1 to 14 arms often form a dense mat over the leaf surfaces, providing protection. The differential length of the radiating arms also helpful in delimiting the species. The non-glandular trichomes are of two kinds: long and short capitate or ovate forms. Species with sparse non-glandular trichomes showed comparatively more number of glandular trichomes. The micromorphology and distribution patterns of trichomes can be used in the taxonomic delineation of various *Solanum* species.

Keywords: Adaptations, Glandular Hairs, Scanning Electron Microscopy, Stellate Hairs

# Introduction

Plants are adapted to survive under different environmental conditions by morphological modifications. Aerial parts of the plants develop modifications when they are exposed to environmental stress. Trichomes and epidermal features are the main foliar adaptations in response to specific environments (Li et al., 2011). Trichomes are the major morphological marker to analyze the interplay of various developmental events correlated with cellular functions (Edwin-Wosu et al., 2012). Celep et al. (2011) revealed the significance of trichome micromorphology of Lamium species. Trichome specificities effectively delineate taxa within genus or even at family level. Secretory and non-secretory trichomes provide insight on the nature of the secreted phytochemical and their defense against herbivores. Lamiaceae, Brassicaceae, Verbenaceae and Cucurbitaceae display glandular trichomes with potent bioactive molecules with immense economic importance. Hayat et al. (2009) and Dipa & Daniel (2011) provided the significance of foliar trichomes in taxonomic discrimination in Acanthaceae and Artemisia in Asteraceae, respectively.

Solanaceae comprise 98 genera with c. 2700 species (Olmstead & Bohs, 2007). The family includes many economically important vegetable species which are also employed as biological model systems. Adedeji et al. (2007) analyzed the organographic distribution of the trichomes of Solanaceae species and reported two types of trichomes, which showed variations among the species even within the same genus. Phylogeny of species in the family was traced by Sarkinen et al. (2013) in terms of phytochemistry, environmental niche, geographical distribution, ecological parameters and the genomes. Comparing other groups, the studies on trichome micromorphology of Solanum is scanty. Thus, the present study is an attempt to analyze the ultrastructural features of trichomes in Solanum using scanning electron microscopy and their ecological significance.

# Materials and Methods

#### Plant Materials

Leaves of 17 taxa of *Solanum*, viz., *S. americanum* Mill., *S. torvum* Sw., *S. violaceum* (Ortega) subsp. *violaceum*, *S. violaceum* (Ortega) subsp. *multiflorum* (C.B. Clarke) K.M. Matthew, *S. wendlandii* Hook.f., *S. macrocarpon* L., *S. melongena* L. var. *insanum* (L.) Prain, *S. erianthum* D. Don, *S. mauritianum* Scop., *S. giganteum* Jacq., *S. exarmatum* Anil *et al., S. capsicoides* All., *S. seaforthianum* Andrews, *S. mammosum* L., *S. aculeatissimum* Jacq., *S. pseudocapsicum* L. and *S. trilobatum* L. were collected from Western Ghats of Kerala were subjected to Scanning Electron Microscopic examination, and the voucher specimens were later deposited at TBGT.

# Ultrastructural analysis using scanning electronic microscopy (SEM)

The ultramorphological analysis was carried out using Scanning Electron Microscopy with healthy expanded leaf blades, fixed in 3% glutaraldehyde. The samples were kept for 24 hrs and subsequently washed in a 0.05 M potassium phosphate buffer for 30 minutes. After that the leaf blades were dehydrated in ethyl alcohol series followed by critical point drying using CO<sup>2</sup> (Bozzolla & Russel, 1992) and mounted on metallic stubs. Further, the specimens are coated with gold in the Sputter coater (ION 25 SEM). Analysis was done using the scanning electron microscope (SU 6600, Hitachi and Zeiss EVO 18) and images were captured in different magnifications. A minimum of ten leaves per taxon have been analyzed and in all cases, fully expanded leaves are chosen. Very young and older leaves have been excluded from the analysis.

# **Results and Discussion**

Leaves of Solanum species show wide range of variation in micromorphology in terms of distribution, nature and structure. Glandular and non-glandular trichomes were noticed in the Solanum species. The non-glandular trichomes may be stellate or simple while the glandular trichomes may be short or long-stalked. The number of arms in the stellate trichomes showed variations and similarly the number of cells in the stalk and head of the glandular trichomes also displayed variations among the species and sometimes on the two sides of the same leaf. Among the studied taxa, stellate trichomes are found in S. giganteum, S. erianthum, S. mauritianum, S. melongena var. insanum, S. violaceum subsp. multiflorum, S. violaceum subsp. violaceum and S. torvum (Fig. 1a-g). All these species also possess stellate non-glandular trichomes on both upper and lower surfaces of the leaves. However, density, number and nature of radiating arms show considerable variations among these taxa.

The number of radiating arms in most species is 9. Maximum number of radiating arms (up to 18) was observed in the pluricellular stellate trichomes of *S. mauritianum* (**Fig. 1c**). *Solanum aculeatissimum* is found to be distinct from the rest of the species in having stellate non-glandular trichomes along with simple trichomes on the lower surface (**Fig. 1h**).

The radiating arms of S. giganteum were broader and shorter under SEM (Fig. 1a). The stellate trichomes in S. violaceum subsp. violaceum were also comparatively shorter than all others (**Fig. 1f**). Solanum violaceum subsp. multiflorum is distinct from others in having single elongated slender pointed central arm in their stellate trichomes (Fig. 1e). In all other species with stellate trichomes, the slender radiating arms were more or less similar in size. The number of arms in stellate trichomes exhibit variations on both surfaces of the same leaves in the species investigated. In S. erianthum, the stellate trichomes on dorsal leaf surface have 1,3,4,5 and 8 arms (Fig. 2a), a feature not noticed in other species whilst those on lower surface have 8–10 arms (Fig. 1b). Similar stellate trichomes have been reported in S. leprosum (Toledo Picoli et al., 2013) and suggested that these differences are due to ontogenic processes starting at different times. In the present study, similar aged leaves of S. erianthum have been used, but the species showed the difference with respect to the number of arms in trichomes on the two surfaces. In S. *mauritianum*, the dorsal surface had 6–15 radiating arms for the stellate trichomes (Fig. 1c) and the lower leaf surface had mostly 6 arms (Fig. 2b). In S. melongena var. insanum (Fig. 1d) and S. giganteum (Fig. 1a), both the upper and lower surfaces of the leaves had stellate trichomes with 9 arms. It has been noted that in S. violaceum subsp. *multiflorum*, the stellate trichomes were having one much elongated slender pointed central arm with 3 basal protruding arms on the upper surface and with 8 basal protruding arms on the lower surface (**Figs. 1e** & **2c**). Interestingly, the elongated arms were found to have micropappillae or echinate ornamentations (Fig. 2d). According to Barthlott (1981) the cuticular micropappillae are in continuation of the cuticular folding present on the surface of the surrounding epidermal cells. Werker (2000) reported that the outer surface of the foliar trichomes in plants including members of Lamiaceae may be smooth or exhibit micro ornamentations such as micropappillae, warty, reticulate and seriate. In S. aculeatissimum, the lower leaf surface has stellate trichomes with 4 basal arms particularly along the veins and also has



Fig. 1. Non-glandular trichomes of *Solanum* taxa: a. Upper leaf surface of *S. giganteum* Jacq.; b. Lower leaf surface of *S. erianthum* D. Don.; c. Upper leaf surface of *S. mauritianum* Scop.; d. Upper leaf surface of *S. melongena* (L.) var. *insanum* (L.) Prain; e. Upper leaf surface of *S. violaceum* Ortega subsp. *multiflorum* (C.B. Clarke) K.M. Matthew; f. Upper leaf surface of *S. violaceum*; g. Upper leaf surface of *S. torvum* Sw.; h. Lower leaf surface of *S. aculeatissimum* Jacq.



Fig. 2. Non-glandular trichomes of *Solanum* taxa: a. Upper leaf surface of *S. erianthum* D. Don.; b. Lower leaf surface of *S. mauritianum* Scop.; c. Lower leaf surface of *S. violaceum* Ortega subsp. *multiflorum* (C.B. Clarke) K.M. Matthew; d. Micropapillate projections on the trichomes *S. violaceum* Ortega subsp. *multiflorum* (C.B. Clarke) K.M. Matthew.; e. Simple non-glandular trichomes on the upper leaf surface of *S. aculeatissimum* Jacq.; f,g. Simple trichomes on the upper leaf surface of *S. capsicoides* All. and *S. exarmatum* Anil *et al.*; h. Upper leaf surface of *S. mammosum* L.

simple non-glandular trichomes along the veins and leaf surface (**Fig. 1h**). The simple trichomes are mostly two-celled. The upper surface of the leaf bears only two-celled simple trichomes with basal cluster of short cells (**Fig. 2e**).

Species such as S. capsicoides, S. exarmatum (Fig. 2f,g), and S. mammosum (Fig. 2h) have simple non-glandular trichomes. These simple trichomes form dense mat-like covering over the leaf surface in S. mammosum (Fig. 3a). Among the studied taxa, S. mauritianum and S. torvum are having comparatively denser distribution of stellate trichomes as thick mat over the upper leaf surface (Fig. 1c,g). This can be correlated with the specific habitat of Solanum species. Hairy leaves reduce leaf internal temperatures and transpiration (Sandquist & Ehleringer, 2003) whilst inter- and intra-specific variations exist for this feature. There are previous reports regarding the functioning of leaf trichome density as a defensive trait against herbivory among solanaceous species (van Dam & Hare, 1998). In S. giganteum, the leaves are covered with stellate trichomes all over the surface (Fig. 1a). In *S. erianthum*, the lower surface of the leaves has denser distribution of stellate trichomes rather than the upper surface (Figs. 1b & 2a). Hussain et al. (1990) reported that in most of the plant species, trichomes are much denser on the lower surface which tends to diminish the importance of trichomes as a sunshade adaptation. However, based on the stomatal studies conducted on Solanum species (Anil Kumar et al., 2013), it can be inferred that the lower surface of the leaves is having more stomatal frequency (Table 1). The leaf morphological and physiological attributes change with different environmental conditions appear to be consequence of responses to abiotic factors such as soil moisture (Beerling et al., 1996; Sun et al., 1996), air temperature (Panek & Waring, 1995), and atmospheric CO<sup>2</sup> levels (Marshall & Monserud, 1996). For the present investigation, all the specimens have been collected from plants growing in their natural habitats and also in the same season and hence the influence of environmental variations can be neglected in considering trichome morphology as a speciesspecific trait.

*Solanum pseudocapsicum* and *S. trilobatum* lack non-glandular trichomes on either surface of the leaves (**Fig. 3b,c**). This may be due to the relatively low stomatal indices in the taxa (**Table 1**). In *S. americanum*, multicellular non-glandular trichomes with broad base are scattered on the upper surface and margins of leaves (**Fig. 3d**), and are also studded with micropappillae. In *S.* 

seaforthianum, similar type and distribution of nonglandular trichomes could be observed, though the nature of glandular trichomes is different from that of S. americanum (Fig. 3e). Solanum macrocarpon has slender elongated non-glandular trichomes together with glandular trichomes on leaf margins (Fig. 3f), but surfaces of the leaves are devoid of any non-glandular trichomes. Solanum wendlandii has non-glandular trichomes with broad base only on the leaf margins (Fig. **3g**). All these species are not having the protective mat of stellate trichomes. Solanum trilobatum, S. macrocarpon and S. wendlandii are having reflective cuticular layer on the upper surface of their leaves. This feature of glaucousness or waxy bloom on leaves is a boon to maintain high tissue water potential and is therefore considered as desirable trait for drought tolerance (Ludlow & Muchow, 1990). Richards et al. (1986) compared the range of leaf temperature between non-glaucous and glaucous leaves of Triticum and also the rate of leaf senescence. They observed that glaucous leaves were retained longer than non-glaucous leaves in the droughted treatment. Further, S. trilobatum and S. macrocarpon showed comparatively low stomatal indices. It may be because their leaves lack dense trichome mat to protect from excess transpiration. However, comparatively higher stomatal frequencies have been noticed with the lower surface of S. wendlandii and both surfaces of S. seaforthianum. Both these species are without trichome mat and it can be suggested that the habit as well as habitat of these species may be the reason for these variations. Apart from the role of glaucous layer, some additional physiological mechanisms may be operating in the xeric plants like Opuntia (Nerd & Nobel, 1991), and others. This include decline in turgor potential due to water loss from the water storage parenchyma. However, the physiology related to the water stress and glaucousness in Solanum species needs further studies. It has been reported that plants generally limit the number and area of leaves in response to drought stress to reduce the water budget at the cost of yield loss (Schuppler et al., 1998). In S. wendlandii and S. seaforthianum, the leaf area is reduced owing to the dissected nature of leaves. As far as S. americanum is concerned, the species exclusively prefers moist shady habitats with low light and temperature exposure.

Another important strategy of glandular trichome is related with its chemical defense against herbivores (Ascensao *et al.,* 1999) and nonglandular trichomes in mechanical defense and protect the plants from excessive transpiration



Fig. 3. Non-glandular trichomes of *Solanum* species: a. Dense simple trichomes on the lower leaf surface of *S. mammosum* L.; b. Upper leaf surface of *S. pseudocapsicum* L.; c. Upper leaf surface of *S. trilobatum* L.; d. Scattered non-glandular trichomes on the upper leaf surface of *S. americanum* Mill.; e. Upper leaf surface of *S. seaforthianum* Anderws showing scattered non-glandular trichomes; f. *S. macrocarpon* L. showing leaf margin with glandular and non-glandular trichomes; g. Broad based non-glandular trichomes on the upper leaf surface of *S. wendlandii* Hook.f.

Sl. No.	Taxa Studied	Stomatal Index*	
		Upper Epidermis	Lower Epidermis
1.	Solanum aculeatissimum Jacq.	3.92 <sup>h</sup>	8.44 <sup>k</sup>
2.	Solanum americanum Mill.	11.71°	$24.47^{d}$
3.	Solanum capsicoides All.	13.7 <sup>b</sup>	18.01 <sup>g</sup>
4.	Solanum erianthum D. Don	10.93 <sup>d</sup>	26.67 <sup>b</sup>
5.	Solanum exarmatum Anil et al.	5.46 <sup>f</sup>	12.25 <sup>i</sup>
6.	Solanum giganteum Jacq.	5.37 <sup>f</sup>	18.75 <sup>g</sup>
7.	Solanum macrocarpon L.	3.92 <sup>h</sup>	6.2 <sup>1</sup>
8.	Solanum mammosum L.	13.67 <sup>b</sup>	25.17°
9.	Solanum mauritianum Scop.	<b>4.4</b> 4 <sup>g</sup>	22.94 <sup>e</sup>
10.	Solanum melongena L. var. insanum (L.) Prain	6.0 <sup>e</sup>	13.37 <sup>h</sup>
11.	Solanum pseudocapsicum L.	$2.77^{i}$	4.59 <sup>m</sup>
12.	Solanum seaforthianum Andrews	21.51ª	33.88ª
13.	Solanum torvum Sw.	1.02 <sup>j</sup>	12.76 <sup>i</sup>
14.	Solanum trilobatum L.	6.45 <sup>e</sup>	10.15 <sup>j</sup>
15.	Solanum violaceum Ortega subsp. multiflorum	5.37 <sup>f</sup>	13.96 <sup>h</sup>
	(C.B. Clarke) K.M. Matthew		
16.	Solanum violaceum Ortega subsp. violaceum	3.05 <sup>h</sup>	13.48 <sup>h</sup>
17.	Solanum wendlandii Hook.f.	5.69 <sup>f</sup>	$20.02^{f}$

#### Table 1. Stomatal indices of *Solanum* taxa

\*Mean values followed by the same letter in the superscript do not vary significantly based on ANOVA and t-test at  $p \le 0.05$ .

(Corsi & Bottega, 1999). The glandular trichomes vary in morphology, structure and in number per unit area of the epidermis among species and organs (Ascensao et al., 1999). In Solanum, the glandular trichomes on leaves generally belong to two groups, viz., long and short capitate or ovoid glandular trichomes as observed in S. capsicoides, S. exarmatum, S. erianthum, S. aculeatissimum, S. giganteum, S. macrocarpon, S. mauritianum, S. melongena var. insanum, S. violaceum subsp. multiflorum, S. pseudocapsicum, S. trilobatum, S. torvum, S. violaceum subsp. violaceum, S. mammosum and S. wendlandii (Figs. 4a-h & 5a-g). In S. seaforthianum, the heads of glandular trichomes are conical with pointed tips on multicellular long stalk whilst in S. americanum, the heads are elongated ovoid with blunt tips (Fig. 5h,i). The long-glandular trichomes in S. capsicoides and S. exarmatum have globular secreting heads and in S. aculeatissimum, these long-glandular trichomes have ovoid heads (Fig. 4a,b,d). Presence of glandular trichomes is characteristic of the genus Solanum and other members of Solanaceae with

the exception of *Nicotiana glauca* and *Solandra nitida* (Maiti *et al.*, 2002). These types of glandular trichomes identified on the leaves might be responsible for the production, accumulation and release of secondary metabolites such as saponins and steroid alkaloids as reported by Drewes & van Staden (1995). The secondary metabolites secreted from the glandular trichomes of aerial organs are related to defense of plants against the attack of herbivores and pathogens or act as attractants to pollinators or for fruit dispersal (Werker *et al.*, 1994; Heinrich *et al.*, 2002). Like the non-glandular trichomes, the glandular trichomes also show variation in their density and distribution pattern.

In the present investigation, *S. aculeatissimum, S. capsicoides, S. exarmatum* and *S. mammosum* display the presence of glandular trichomes on both surfaces of leaves. Meanwhile, it is restricted to upper surface of the leaves in others, viz., *S. erianthum, S. giganteum, S. macrocarpon, S. mauritianum, S. melongena* var. *insanum, S. pseudocapsicum, S. seaforthianum, S. violaceum* subsp. *violaceum, S.* 



Fig. 4. Glandular trichomes of *Solanum* taxa: a. Upper leaf surface of *S. capsicoides* All.; b. Upper leaf surface of *S. exarmatum* Anil *et al.*; c. Upper leaf surface of *S. erianthum* D. Don.; d. Upper leaf surface of *S. aculeatissimum* Jacq.; e. Upper leaf surface of *S. giganteum* Jacq.; f. Upper leaf surface of *S. macrocarpon* L.; g. Upper leaf surface of *S. mauritianum* Scop.; h. Upper leaf surface of *S. melongena* (L.) var. *insanum* (L.) Prain.



Fig. 5. Glandular trichomes of *Solanum* taxa: a. Upper leaf surface of *S. violaceum* Ortega subsp. *multiflorum* (C.B. Clarke) K.M. Matthew; b. Upper leaf surface of *S. pseudocapsicum* L.; c. Upper leaf surface of *S. trilobatum* L.; d. Upper leaf surface of *S. torvum* Sw.; e. Upper leaf surface of *S. violaceum* Ortega subsp. *violaceum*; f. Lower leaf surface of *S. mammosum* L.; g. upper leaf surface of *S. wendlandii* Hook.f.; h. Upper leaf surface of *S. seaforthianum* Andrews; i. Upper leaf surface of *S. americanum* Mill.

trilobatum, S. macrocarpon, S. americanum and S. wendlandii. Further, a few scattered glandular trichomes are noticed on the lower surface of S. trilobatum and S. wendlandii (Fig. 5c,g). Solanum wendlandii possesses non-glandular trichomes with broad base along the leaf margins but S. trilobatum lacks such non-glandular trichomes. In S. americanum, the glandular trichomes are also found along the margins. Solanum macrocarpon, S. pseudocapsicum and S. seaforthianum lack both non-glandular or glandular trichomes on their lower leaf surface.

Leaves of Solanum species having dense mat of stellate trichomes display reduced number of glandular trichomes and this dense mat of stellate trichomes functions as bioshield against the stresses. On other hand, species with sparse stellate or simple non-glandular trichomes showed more number of glandular trichomes. This can be considered as an acquired defense adaptation of the species to escape from pathogenic invasion as these glandular trichomes have the potential to secrete bioactive defense compounds (Wagner et al., 2004). A striking observation noticed in the present study is that spiny Solanum taxa are having an equidistribution of glandular and nonglandular trichomes, except S. trilobatum. The species without spines namely S. mauritianum and S. erianthum have comparatively low density of glandular trichomes amidst the mat of stellate trichomes which take part in the defense role. The exact phylogeny behind these kinds of adaptive responses is yet to be unraveled.

In the investigated species namely S. giganteum, S. melongena var. insanum, S. violaceum subsp. multiflorum, S. torvum, S. violaceum subsp. violaceum and S. wendlandii are having peltate glandular trichomes on the upper surface of their leaves, though the density of distribution varied drastically (Figs. 4e,h & 5a,d,e,g). Only a scanty number of such trichomes could be observed with S. torvum. In S. mauritianum, ovoid glandular trichomes were observed in lesser density on the upper surface (Fig. 4g). Solanum violaceum subsp. violaceum is different from rest of the species in having peltate glandular trichomes on the lower surface of the leaves also. Interestingly, the stellate non-glandular trichomes are abundant on both surfaces and the rays of adjacent trichomes interlock and form a dense cover and often form two or three layers of flattened multicellular shields. Though ecological variations may affect the distribution of trichomes, the type of trichome is constant in most species (Okpon, 1969). Many researchers have employed the presence or absence and types of trichomes on the epidermal surfaces as key characters for classification (Rollins & Shaw, 1973; Adedeji et al., 2007). It has long been suggested that the types of epidermal trichomes can frequently be used in delimiting species, genera or families (Hayat et al., 2009; Shaheen et al., 2009; Ajmal Ali & Al Hemaid, 2010; Saheed & Illoh, 2010; Kemka & Nwachukwu, 2011; Adedeji, 2012; Al Sheef et al., 2013; Khan et al., 2013; Rashid & Parnell, 2013; Naidoo et al., 2014). The following key has been constructed to easily differentiate the 17 different Solanum taxa found in the southern Western Ghats, Kerala based on the type and distribution of trichomes observed on their leaf surfaces during the present Scanning Electron Microscopic study.

#### Key to taxa

1. Non-glandular and glandular trichomes present ...... 2 1. Non-glandular trichomes absent but glandular trichomes present ..... 16 2. Presence of either simple or stellate nonglandular trichomes ...... 3 2. Presence of both simple and stellate nonglandular trichomes ..... 15 3. Trichomes of exclusively stellate ...... 4 3. Trichomes of exclusively simple ...... 9 4. Dense mat of trichomes present ...... 5 Radiating arms of trichomes shorter, broader 5. and equal-sized ..... S. giganteum 5. Radiating arms of trichomes are slender and equal-sized ..... 6 Glandular trichomes with multicellular stalks 6. ......S. erianthum Glandular trichomes with unicellular stalks .. 7 7. Stellate trichomes on dorsal surface with up to 18 radiating arms ..... S. mauritianum 7. Stellate trichomes on dorsal surface with up to 9 radiating arms ..... S. torvum 8.... Peltate glandular trichomes present on abaxial and adaxial leaf surfaces ..... .....S. violaceum subsp. violaceum 8. Peltate glandular trichomes present on adaxial leaf surface only .. S. melongena var. insanum 9. Leaves with glandular trichomes on both surfaces ..... 10

- 10. Secretory heads of glandular trichomes multicellular and elongated .... S. mammosum
- 10. Secretory heads of glandular trichomes singlecelled and globular ..... 11
- 11. Leaves with long-glandular trichomes amidst short-stalked ones ...... S. capsicoides

- 12. Margins lack glandular trichomes and are confined to leaf blade ...... 14
- 13. Non-glandular trichomes seen amidst glandular ones are without micropappillae...... S. macrocarpon

- 15. Simple and stellate trichomes interspersed and the stellate trichomes studded with micropappillae with one of the arms much longer .........**S. violaceum** subsp. **multiflorum**
- 16. Short-stalked glandular trichomes have peltate head ...... S. trilobatum
- 16. Short stalked-glandular trichomes have ovoid head ...... S. pseudocapsicum

### Conclusion

The trichome morphology of *Solanum* species and distribution pattern of trichomes on leaf surfaces are useful in distinguishing the species. Particularly, this would be helpful for pharmacognosists, archaeobotanists, paleobotanists and agronomists. Occurrence of diverse glandular or non-glandular trichomes reported in the present study reflects the foliar features of studied *Solanum* taxa.

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