

MORPHOLOGY OF FOLIAR EPIDERMIS IN TWO GROUPS OF *SOLANUM* SECTION *GEMINATA* (SOLANACEAE)

Morfología de la epidermis foliar en dos grupos de *Solanum* sección *Geminata* (Solanaceae)

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ABSTRACT

Solanum arboreum, *S. falconense*, *S. gratum*, *S. lucens*, *S. ripense* and *S. tanysepalum* of the *S. arboreum* group; *S. imberbe* and *S. sieberi* of *Solanum deflexiflorum* group were studied in the context of ongoing anatomical research in the *Geminata* section of the genus *Solanum*, in order to identify epidermal features that can be recognized and employed as useful taxonomic characters. Leaf materials were taken from herbarium specimens and treated using conventional anatomical procedures. Qualitative features such as epidermal cell wall shape and thickness; stomata distribution, type and density, and trichome type and distribution were evaluated as well as quantitative traits such as stomatal length and width, stomatal index (SI) and trichome density. Some of the studied epidermal features are of particular interest, especially on the adaxial surface, because they differ conspicuously between species. Polygonal cells are unique in all studied species but *S. lucens* and *S. tanysepalum*. Differences were also found in trichome, distribution (on intercostal areas of *S. imberbe* and *S. sieberi*) as well as trichome type, which proved useful in differentiating some of the studied species. Glandular long and short, branched trichomes were found only on the adaxial epidermis in *S. tanysepalum*. On the abaxial surface only *S. falconense* showed eglandular, long and unbranched trichomes. A key for identification of the species is provided.

Key words. Solanaceae, *Solanum*, Section *Geminata*, foliar epidermis.

RESUMEN

En el contexto de una investigación anatómica foliar en desarrollo, se estudiaron especies de *Solanum* sección *Geminata* pertenecientes al grupo *S. arboreum*: *Solanum arboreum*, *S. falconense*, *S. gratum*, *S. lucens*, *S. ripense* y *S. tanysepalum* y al grupo *S. deflexiflorum*: *S. imberbe* y *S. sieberi*, con la finalidad de explorar rasgos epidérmicos que puedan ser reconocidos y utilizados como caracteres taxonómicos. Se seleccionaron muestras de hojas provenientes de especímenes de herbario, las cuales fueron tratadas utilizando procedimientos anatómicos convencionales. Se evaluaron rasgos cualitativos tales como forma y espesor de las paredes de las células epidérmicas, ubicación, tipo y distribución de los estomas, tipo y distribución de los tricomas y caracteres cuantitativos como el largo y el ancho de los estomas, el índice

estomático (IE) y la densidad de los tricomas. Algunas de las características estudiadas resultaron de interés particular, especialmente los de la superficie adaxial, como las células poligonales en todas las especies, a excepción de *S. lucens* y *S. tanysepalum*. Se observaron otras diferencias en la distribución de los tricomas, localizados en áreas intercostales en *S. imberbe* y *S. sieberi*, así como el tipo de tricomas que resultó útil para diferenciar algunas de las especies estudiadas. Se observaron tricomas glandulares cortos y largos, ramificados sólo en la epidermis adaxial de *S. tanysepalum*. *Solanum falconense* mostró tricomas eglandulares largos y no ramificados en la epidermis abaxial. Se propuso una clave para identificación de las especies estudiadas.

Palabras clave. Solanaceae, *Solanum*, Section *Geminata*, epidermis foliar.

INTRODUCTION

Solanum sect. *Geminata* comprises ca. 130 species of shrubs and small trees ranging from Mexico to Argentina. The species have been divided into 16 groups (Knapp, 2002), twelve represented in Venezuela, with 34 species growing in cloud forest understory, gallery and riparian forest, and disturbed areas.

Literature source about epidermal morphology of *Solanum* sect. *Geminata* is rather scarce, but is well known that in Solanaceae leaves provide many anatomical traits integrated by morphological features to understand relationships between species (Ahmad, 1963; Ahmad, 1975; Juhász, 1968; Patel & Inamdar, 1971; Bessis & Guyot, 1979; Wilkinson, 1979; Karatela & Gill, 1986; Gbile, 1986; De Pasquale *et al.*, 1991; Cosa de Gastiazoro, 1994; Jáuregui *et al.*, 2001; Benítez & Berlingeri, 2003).

At the same time, the use of anatomical features from the leaf has been evaluated in solving different kind of taxonomic problems in several plant families (Solederer, 1908; Carlquist, 1961; Wang *et al.*, 2001; Nazneen Parveen *et al.*, 2000).

For this reason, a description of qualitative and quantitative traits of leaf epidermis in eight species belonging to *Solanum arboreum* group and *Solanum deflexiflorum* group, located in Venezuela: *Solanum arboreum*, *S. falconense*,

S. gratum, *S. lucens*, *S. ripense*, *S. tanysepalum*, *S. imberbe* and *S. sieberi* has been made.

MATERIAL AND METHODS

Eight species from the genus *Solanum* conforming the *Geminata* has been studied; sections were obtained using dry material from the following herbaria: Facultad de Farmacia de la Universidad de Los Andes Mérida (MERF), Missouri Botanical Garden USA (MO), Herbario de la Facultad de Agronomía de la Universidad Central de Venezuela (MY) and Herbario Nacional de Venezuela (VEN) (Table 1).

The sculpture of the adaxial and abaxial epidermal cells was studied on semi-permanent slides and on transverse section of leaf blades taking 1 cm² segments from the middle portion of leaves previously fixed in FAA. Material was macerate in a sodium hypochlorite solution (5.25%) at room temperature (56-58 °C), washed with distilled water, stained with 0.5% aqueous toluidine blue and mounted in a 1:1 solution of water: glycerine for microscopic examination under a Leica DMLS 30 microscope.

The number of analyzed leaves was two on each specimen by species (Table 1). Qualitative traits, stomatal width and length and trichome density were based on 25 measurements on each leaf from different microscopic areas (0.19635 mm²).

Table 1. Origin of the materials used from different herbaria : Herbario de la Facultad de Farmacia de la Universidad de Los Andes Mérida (MERF), Missouri Botanical Garden USA (MO), Herbario de la Facultad de Agronomía de la Universidad Central de Venezuela (MY) y Herbario Nacional de Venezuela (VEN).

Group	Taxa	Specimens
<i>S. arboreum</i>	<i>S. arboreum</i> Dunal	VENEZUELA. Yaracuy . Sierra de Aroa. 1200m. 29-V-1944 Aristeguieta & Pannier 1959 (VEN) VENEZUELA. Bolívar . Sureste de Los Patos, Norte del río Hacha. El Manteco. 400m. 09-VIII-1960 Steyermark 87069 (VEN)
	<i>S. falconense</i> S. Knapp	VENEZUELA. Falcón . El Chorro between La Chapa and Uría, Curimagua. 1300m. 22-V-1994 5152 (MY) VENEZUELA. Falcón . La Soledad, road Curimagua-La Chapa. 1200m. 09-VII-2001 Benítez & al. 6218 (MY)
	<i>S. gratum</i> Bitter	VENEZUELA. Dtto. Federal . Cerro El Ávila, cabeceras del río Arauco. 1200m. 10-VI-1991 Meier W. 6 (MY) VENEZUELA. Dtto. Federal . Los Venados-Boca de Tigre, Cordillera de la Costa. 1300m. 19-III-1971 Morillo G. & al. 813 (MY)
	<i>S. lucens</i> S. Knapp	VENEZUELA. Táchira . La Buenacita. 600m. 19-III-1994 Benítez & al. 5044 (MY) VENEZUELA. Táchira . Between Las Dantas and Buena Vista. 400m. 24-X-1984 Kanpp & Mallet, J. 6832 (MY)
	<i>S. ripense</i> Dunal	VENEZUELA. Mérida . Arriba de la Tomatera de Estanques, Páramo Las Nieves, 2100m. 18-03-2002 Benítez de Rojas & al. 6378 (MY) VENEZUELA. Mérida . Monte Zerpa. 2400m. 30-XII-1983 Molinari L. 83-2 (MERF)
	<i>S. tanysepalum</i> S. Knapp	VENEZUELA. Aragua . Between Costa de Maya and El Rosario. 800m. 30-III-1990 Ruíz & al. 4551 (MY) VENEZUELA. Dtto. Federal . Cerro El Ávila. 1200m. 28-IX-1992 Meier 2817 (VEN)
<i>S. deflexiflorum</i>	<i>S. imberbe</i> Bitter	VENEZUELA. Mérida . La Carmelita, Mucuchíes. 3000m. 19-IV-1967 López-Palacios S. 1638 (MERF) VENEZUELA. Zulia . Machiques. 400m. 09-XI-1982 Bunting 11984 (MO)
	<i>S. sieberi</i> Van Heurck & Müll. Arg.	VENEZUELA. Falcón . 1 km from La Cuevita, road to Agua Salada. 200m. 07-VII-2001 Benítez & al. 6198 (MY) VENEZUELA. Lara . Duaca. 600m. 11-VII-1993 Benitez & al. 4978 (MY)

The microscopic qualitative features on the adaxial and abaxial epidermis which have been considered include: epidermal cell shape and cell wall sinuosity from a front paradermal view; type, location and distribution of stomata; trichomes shape, size and distribution.

Quantitative features considered in this study included stomatal length and width and stomatal index (SI). and trichome density (per mm²) on the adaxial and abaxial epidermis. These quantitative features were measured by using a calibrated reticulated eyepiece with a x100 and x400 magnification. Photographic documentation of the foliar epidermis was obtained through a Leica MPS 30 camera.

Stomatal index and trichome density were calculated using the following equation counting cells from the permanent slides at x100 and x400 respectively (Salisbury, 1927). Areas without stomata were also considered as replicates for the arithmetic mean calculation of SI.

Stomatal Index (SI)

$$SI = S / E + S \times 100$$

S = Stomata number per leaf area unit

E= Epidermal cell number in the same leaf unit

Trichome Density (TD)

$$TD = \text{Trichome number per leaf area unit} / 0.19635 \text{ mm}^2$$

0.19635 mm² = observed leaf area at x400 magnitude

Tables for qualitative traits on both epidermis from the selected species were made in order to compare features that can be used as a taxonomic tool using leaf epidermis from specimens of the two studied groups of *Solanum* section *Geminata*. A key for identification of species using features of the adaxial surface is provided.

RESULTS AND DISCUSSION

The study of the epidermal leaf features from species in this section revealed differences in micro morphological characters, some of them showing interesting interspecific variations.

Observation of leaf segments allowed to register qualitative and quantitative features on adaxial and abaxial epidermis in the studied species (Table 2 and 3), introducing them into a matrix for each epidermis. Based on the data contained in each matrix, differences between species from epidermal leaf features were described.

Epidermal cells-Adaxial surface

Epidermal cells on the adaxial and abaxial surface showed almost the same size and shape. Adaxial surface of most species exhibit polygonal cells (Fig. 1a-h). *S. lucens* and *S. tanysepalum* can be differentiated by sinuous cell walls (Fig. 1d, f) (Table 2). Only *S. lucens* and *S. ripense* show pairs of epidermal cells differing from the rest by a segment of straight cell wall in the adaxial epidermis (Fig. 1d, e), contrasting with the strongly sinuous cell walls in *S. lucens* (d) and differing from *S. sieberi* in which cell shape was polygonal showing more than one straight segment (h).

In most of the studied species, epidermal cell walls on the adaxial surface were thicker than walls on abaxial surface, only *S. tanysepalum* showed thin walls in epidermal cells on both surfaces (Fig. 1f and Fig. 2n).

Epidermal cells-Abaxial surface

On the abaxial surface, epidermal cell walls exhibit a gradation of sinuosity, being strongly sinuous only in *S. lucens* (Fig. 2l) and *S. tanysepalum* (Fig. 2n), and slightly sinuous in the rest of species (Fig. 2i-k and Fig. 2m,o,p).

Table 2. Matrix of qualitative features on adaxial epidermis in the selected species.

Species/Features	1	2	3	4	5	6	7	8
<i>S. arboreum</i>	0	0-0.5	0.5	1	0	1	0	3
<i>S. falconense</i>	0	0.5	0.5	1	0	1	0	1-7
<i>S. gratum</i>	0	-	0.5	0	-	1	0	7
<i>S. lucens</i>	-	0	0.5	1	0-1	1	0	7
<i>S. ripense</i>	0	1	0.5	1	0	1	0	2
<i>S. tanysepalum</i>	-	0	0	1	0-1	1	0	4-6
<i>S. imberbe</i>	0	-	0.5	1	0-1	1	0.5	1
<i>S. sieberi</i>	0	-	0.5	1	0	1	0.5	7

(-) means that the feature was not showed

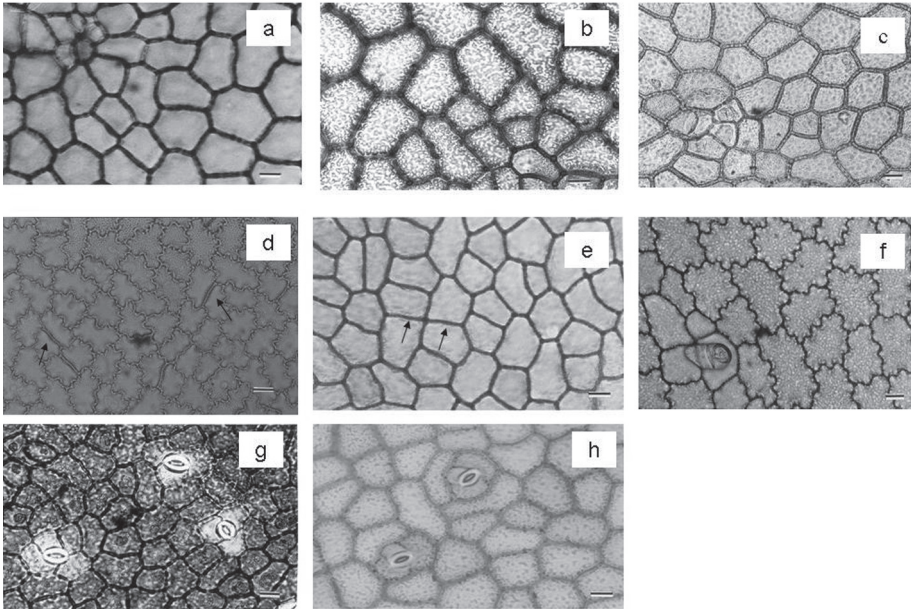
1. Epidermal cell shape: regularly polygonal = 0; irregularly = 1
2. Epidermal cell wall: strongly sinuous = 0; slightly sinuous = 0.5; straight = 1
3. Cell walls thickening: thin = 0; moderately thick = 0.5; thick = 1
4. Stomata: absent = 0; present = 1
5. Type of stomata: anisocytic = 0; staurocitic = 1
6. Trichomes: absent = 0; present = 1
7. Distribution of trichome: costal area = 0; intercostal area = 0.5
8. Trichome type and size: eglandular, long and branched = 0; eglandular, long and unbranched = 1; eglandular, short and branched = 2; eglandular, short and unbranched = 3; glandular, long and branched = 4; glandular, long and unbranched = 5; glandular, short and branched = 6; glandular, short and unbranched = 7

Table 3. Matrix of qualitative features on abaxial epidermis in the selected species.

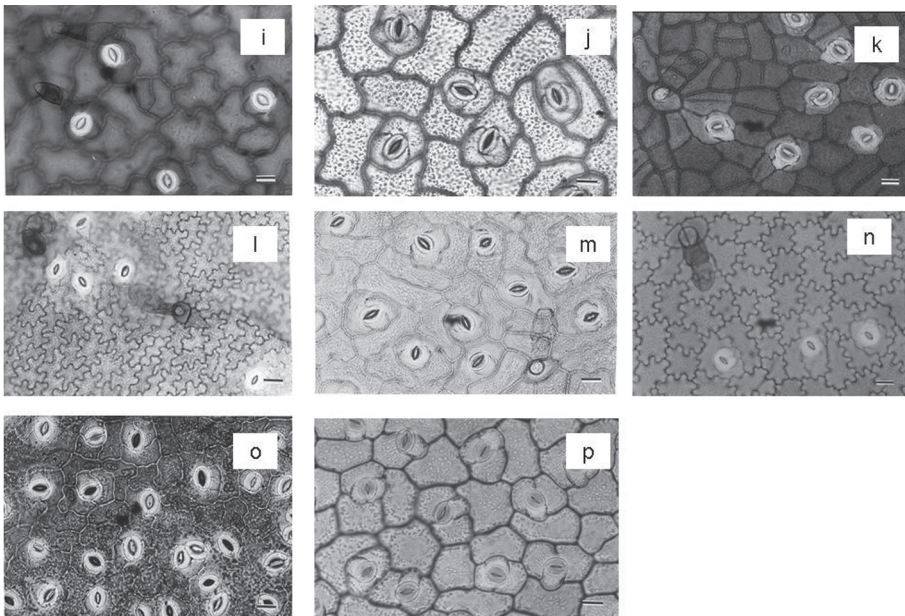
Species/Features	1	2	3	4	5	6	7	8
<i>S. arboreum</i>	-	0.5	0.5	1	0	1	0	3
<i>S. falconense</i>	-	0.5-1	0.5	1	0	1	0	1-5
<i>S. gratum</i>	0	0.5	0	1	0	1	0	7
<i>S. lucens</i>	-	0	0	1	0	1	0	7
<i>S. ripense</i>	-	0.5	0-0.5	1	0	1	0	2
<i>S. tanysepalum</i>	-	0	0	1	0	1	0	7
<i>S. imberbe</i>	-	0.5	0.5	1	0	1	0	5
<i>S. sieberi</i>	0	0.5	0.5	1	0	1	0	7

(-) means that the feature was not showed

1. Epidermal cell shape: regularly polygonal = 0; irregularly = 1
2. Epidermal cell wall: strongly sinuous = 0; slightly sinuous = 0.5; straight = 1
3. Cell walls thickening: thin = 0; moderately thick = 0.5; thick = 1
4. Stomata: absent = 0; present = 1
5. Type of stomata: anisocytic = 0; staurocitic = 1
6. Trichomes: absent = 0; present = 1
7. Distribution of trichome: costal area = 0; intercostal area = 0.5
8. Trichome type and size: eglandular, long and branched = 0; eglandular, long and unbranched = 1; eglandular, short and branched = 2; eglandular, short and unbranched = 3; glandular, long and branched = 4; glandular, long and unbranched = 5; glandular, short and branched = 6; glandular, short and unbranched = 7



Figs. 1. Adaxial epidermis of *Solanum*: (a) *S. arboreum* (Aristeguieta & Pannier 1959); (b) *S. falconense* (Benítez *et al.*, 6218); (c) *S. gratum* (Morillo *et al.*, 813); (d) *S. lucens* (Knapp & Mallet 6832); (e) *S. ripense* (Benítez *et al.*, 6378); (f) *S. tanysepalum* (Meier 2817); (g) *S. imberbe* (López-Palacios 1638); (h) *S. sieberi* (Benítez *et al.*, 6198). Scale= 5 μ m.



Figs. 2. Abaxial epidermis of *Solanum*: (i) *S. arboreum* (Aristeguieta & Pannier 1959); (j) *S. falconense* (Benítez *et al.*, 6218); (k) *S. gratum* (Meier 6); (l) *S. lucens* (Benítez *et al.*, 5044); (m) *S. ripense* (Benítez *et al.*, 6378); (n) *S. tanysepalum* (Meier 2817); (o) *S. imberbe* (López-Palacios 1638); (p) *S. sieberi* (Benítez *et al.*, 6198). Scale= 5 μ m.

In some cases, the shape of epidermal cells can be considered as a good diagnostic feature for the identification of species on the basis of leaf anatomy, as were emphasized by Metcalfe & Chalk (1950), and Sonibare *et al.*, (2005). This was not the case of the studied groups, in which all the species showed polygonal epidermal cells being the sinuosity a differential feature for only two species.

These results are in agreement with those indicated by Benítez (2007), who found polygonal shapes in epidermal cells of the adaxial surface in the studied species of *Solanum nudum* group.

In the eight studied species, epidermal cell walls on the abaxial surface were thinner than those on the adaxial one; this feature was also reported by Benítez (2007) for species in *Solanum nudum* group.

Stomata

Stomata in adaxial and abaxial surfaces of the studied species are anisocytic, with exception of *S. lucens*, *S. tanysepalum* and *S. imberbe* which also showed staurocytic stomata on adaxial surface (Table 2-3). Patel and Inamdar (1971) demonstrated that more than one stomata type could be developed during the life history of one species.

Comparing length of stomata between adaxial and abaxial surface in the same species we found that they are shorter in the abaxial surface. In reference to stomata width, *S. arboreum*, *S. falconense*, *S. lucens* and *S. ripense* have wider stomata on abaxial surface. *S. imberbe*, *S. sieberi* and *S. tanysepalum* showed stomata of similar width on both surfaces (Table 4-5).

Table 4. Measurement of adaxial epidermal features. Each value represent mean \pm standard deviation.

Species/Features	Length of stomata (μm)	Width of stomata (μm)	Stomatal Index (SI)	Trichome density (mm^2)
<i>S. arboreum</i>	157.9 \pm 0.0	106.3 \pm 0.00	2.0 \pm 0.39	1.6 \pm 0.5
<i>S. falconense</i>	266.7 \pm 16.6	160 \pm 11.7	*	1 7 1.6 \pm 0.5 2.1 \pm 0.0
<i>S. gratum</i>	0	0	0	0.95 \pm 0.1
<i>S. lucens</i>	201.3 \pm 0.00	109.3 \pm 0.00	*	7 3.66 \pm 0.74
<i>S. ripense</i>	271.2 \pm 23.1	152.5 \pm 15.5	*	5.45 \pm 1.68
<i>S. tanysepalum</i>	218 \pm 9	132.5 \pm 10.5	*	3.15 \pm 0.41
<i>S. imberbe</i>	170.43 \pm 12.61	117.83 \pm 7.95	3.48 \pm 2.25	1 4.08 \pm 0.43
<i>S. sieberi</i>	165.67 \pm 11.08	122.0 \pm 5.66	4.7 \pm 1.3	7 0.84 \pm 0.13

Bold numbers correspond to type of trichome as described in Table 2.

(*) Represent species with stomata only on costal areas.

Table 5. Measurement of abaxial epidermal features. Each value represent mean \pm standard deviation.

Species/Features	Length of stomata (μm)	Width of stomata (μm)	Stomatal Index (SI)	Trichome density (mm^2)
<i>S. arboreum</i>	141.7 \pm 0.00	108.3 \pm 0.00	10.25 \pm 1.45	6.8 \pm 1.93
<i>S. falconense</i>	255.4 \pm 3.6	180.8 \pm 0.5	127.4 \pm 0.00	1 5 3.46 \pm 0.31 3.66 \pm 0.95
<i>S. gratum</i>	233.9 \pm 3.1	190.5 \pm 8.2	132.6 \pm 12.9	5.77 \pm 1.57
<i>S. lucens</i>	197.2 \pm 0.1	146.5 \pm 2.5	97.1	7 1.79 \pm 1.57
<i>S. ripense</i>	250 \pm 27.7	181 \pm 3.3	101 \pm 38.6	3.35 \pm 2.94
<i>S. tanysepalum</i>	200.7 \pm 1.6	140.2 \pm 19.8	9.16 \pm 0.08	7.13 \pm 1.05
<i>S. imberbe</i>	166.52 \pm 18.25	120 \pm 9.05	21.30 \pm 2.30	5 5.48 \pm 2.33
<i>S. sieberi</i>	161.80 \pm 8.34	117.0 \pm 2.12	16.21 \pm 2.68	7 5.669 \pm 0.9

Bold numbers correspond to type of trichome as described in Table 2.

Stomata location and Stomatal Index (SI)

Regarding stomata location, all but one species, *S. gratum*, are amphistomatic.

It is important to notice that the leaf is an integrated junction of parts (veins and blade), that conform different areas. On adaxial surface differences in stomata location were noticed, observing areas surrounded by veins or intercostals areas, and areas represented by veins or costal areas, where the stomata were present.

These areas were separated in order to calculate SI on this epidermis. In the case of *S. falconense*, *S. lucens*, *S. ripense* and *S. tanysepalum*, stomata were distributed only on costal areas (Fig. 3q, r). Considering that SI represents stomata number per leaf area unit related to epidermal cell number in the same leaf unit, stomata located on costal areas were not considered for SI calculation, because the epidermal cells in these areas are smaller, then originating a smaller SI. It is also important to notice that due to the wide range of plasticity of SI, a higher number of specimens of each species should be studied to think about this index as a valid taxonomic trait for the studied groups of plants.

For this reason, SI on adaxial surface was calculated only for *S. arboretum*, *S. imberbe*

y *S. sieberi* (Table 4). In both groups, SI was always higher in abaxial surface (Table 4-5).

Trichomes

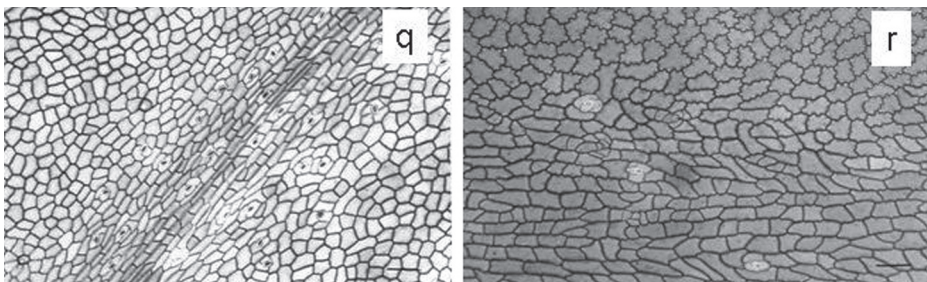
The studied species showed trichomes in both epidermis, *S. arboreum*, *S. falconense*, *S. gratum*, *S. tanysepalum* and *S. sieberi* showed higher trichome density (mm^2) on abaxial surface; only *S. ripense* and *S. imberbe* showed similar trichome density on both surfaces (Table 4-5).

Trichome type and size

Trichome type and size in both leaf surfaces varied from eglandular long, branched and unbranched; eglandular short, branched and unbranched to glandular short, long branched and unbranched (Fig. 2i, k, l, n and Fig. 4s, t).

S. arboreum, *S. gratum*, *S. lucens*, *S. ripense* and *S. sieberi* showed the same trichome type on both epidermis (Table 2-3).

As well as indicated by Benítez (2007) qualitative and quantitative traits of leaf epidermis related to trichomes, can be used to separate the species in the *Solanum nudum* group. In the *Solanum arboreum* and *S. deflexiflorum* group, studied in this work, trichome features also resulted of value to separate species.



Figs. 3. Stomata in adaxial epidermis located only on costal areas (near and on vein surface). (q) *S. ripense* (Benítez *et al.*, 6378); (r) *S. tanysepalum* (Meier 2817). Scale= 70 μm .

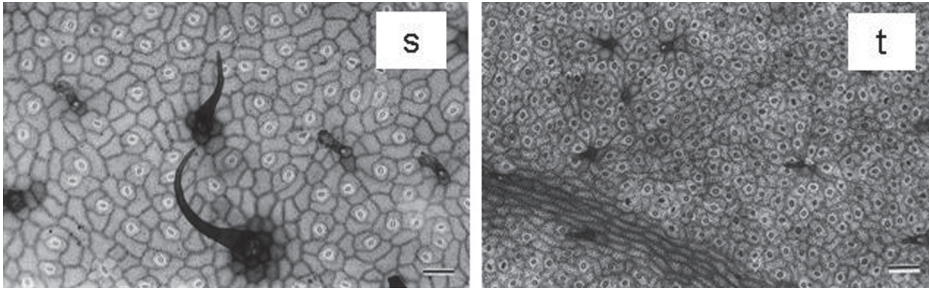


Fig. 4. Trichomes on abaxial epidermis of *Solanum*: (s) *S. falconense* (Benítez *et al.*, 5152); (t) *S. sieberi* (Benítez *et al.*, 5167). Scale= 70 μ m.

Key for identification of species

- 1 Epidermal cell walls straight.....2
- 1' Epidermal cell walls sinuous.....3
- 2 Pairs of epidermal cells differing from the rest by a segment of straight cell wall.....*S. ripense*
- 2' Pairs of epidermal cells absent.....4
- 3 Thin cell walls.....*S. tanysepalum*
- 3' Moderately thick cell walls.....*S. falconense*
- 4 Amphistomatic leaves.....5
- 4' Hypostomatic leaves.....*S. gratum*
- 5 Length of stomata <200 μ m.....*S. lucens*
- 5' Length of stomata <170 μ m.....6
- 6 Glandular trichomes long and branched.....7
- 6' Glandular trichomes long and unbranched.....*S. arboreum*
- 7 Stomata always anisocytic.....*S. sieberi*
- 7' Stomata anisocytic and staurocytic.....*S. imberbe*

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LITERATURE CITED

- AHMAD, K.J. 1963. Cuticular studies with special reference to abnormal stomatal cells in Cestrum. *J. Indian Bot. Soc.* 43:165-177.
- AHMAD, K.J. 1975. Cuticular studies in some Acanthaceae and Solanaceae. *New Bot.* 2:94-100.
- BENÍTEZ, C.E. 2007. Anatomy of the foliar epidermis of the *Solanum nudum* species group of *Solanum* Sect. *Geminata* (Solanaceae). *Acta Hort.* 745:287-293.
- BENÍTEZ, C.E. & K. BERLINGIERI. 2003. Anatomía comparada de la epidermis foliar en el grupo de especies *Solanum sessile* de la Sección Geminata (Solanaceae). *Sida* 20(4):1651- 1661.
- BESSIS, J. & M. GUYOT. 1979. *An attempt to use stomatal characters in systematics and phylogenetic studies of Solanaceae.* In: J.G. Hawkes, R.N. Lester & A.D. Skelding (eds.). pp:321-328. *The Biology and Taxonomy of Solanaceae.* Academic Press, London.
- CARLQUIST, S. 1961. *Comparative Plant Anatomy.* Holt, Rinehart and Winston New York.
- COSA DE GASTIAZORO, M.T. 1994. Estudio morfoanatómico de órganos vegetativos en *Cestroideae* (Solanaceae) II: Tribu Salpiglossideae. *Kurtziana.* 22:47-72.
- DE PASQUALE, A., M.P. FASULO, A.M. FORESTIPRI, S. RAGUSA & G. TUMINO. 1991.

- A survey of foliar features of the genus *Datura* (Solanaceae), section *Datura*. *Plantes medicinale et phytotherapie*. Tome 25(1):23-31.
- GBILE, Z.O. 1986. Epidermal studies in the *Solanum nigrum* complex in Nigeria. In: W. G. D'Arcy (ed.). pp:159-168. Solanaceae, Biology and Systematic. Columbia University Press. New York.
- JÁUREGUI, D., N. RÍOS & C.E. BENÍTEZ. 2001. Estudios anatómicos foliares en Solanaceae de Venezuela. VI: Anatomía foliar de diez especies de *Cestrum* L. *Acta Cient. Venez.* 52:248-260.
- JUHÁSZ, M. 1968. A comparative histological examination of the leaf epidermis of some *Solanum* species. *Acta Biologica (Szeged)*. 14:5-9.
- KARATELA, Y.Y. & L.S. GILL. 1986. Observation on the development studies of stomatal differentiation in the epidermis of Solanaceae. *Feddes Repertorium* 97(5-6):303-311.
- KNAPP, S. 2002. *Solanum* section *Geminata* Solanaceae. *Flora Neotropica*. Monograph. 84:1-404.
- METCALFE, C.R. & L. CHALK. 1950. *Anatomy of the Dicotyledons*. Oxford at the Clarendon Press. Vol. II:1259-1271.
- NAZNEEN PARVEEN, S.K. SRI RAMA MURTHY & T. PULLAIAH. 2001. Leaves epidermal characters in *Crotalaria* species (Papilionoideae) from eastern Ghats. *Phytomorphology* 50(2):205-212.
- PATEL, R.C. & J.A. INAMDAR. 1971. Structure and Ontogeny of stomata in some Polemoniales. *Ann. Botany (London)*. II:25:389-409.
- SALISBURY, E.J. 1927. On the causes and ecological significance of stomatal frequency, with special reference to the woodland flora. *Phil. Trans. Roy. Soc. London*. 216:1-65.
- SOLEDERER, H. 1908. *Systematic anatomy of the dicotyledons*. Clarendon Press. London. 1:575-583.
- SONIBARE, M.A., A.A. JAYEOLA, A. EGUNYOMI & J. MURATA. 2005. A survey of epidermal morphology in *Ficus* Linn. (Moraceae) of Nigeria. *Bot. Bull. Acad. Sin.* 46:231-238.
- WANG, YU-FEI, D.K. FERGUSON, R. ZETTER, T. DENK & G. GARFI. 2001. Leaf architecture and epidermal characters in *Zelkova*, Ulmaceae. *J. Linn. Soc.* 136:255-265.
- WILKINSON, H. P. 1979. The plant surface (mainly leaf). In: Metcalfe and L. Chalk (eds.), *Anatomy of the Dicotyledons*. Ed. 2, Vol., 3. Clarendon Press, Oxford. pp:97-165.

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