Leaf epidermal studies of some *Solanum* (*Solanaceae*) species in Nigeria

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Abstract. Epidermal features of ten Nigerian species of *Solanum* were studied, in order to find useful taxonomic characters. Fresh leaf material was collected and treated by conventional anatomical procedures. Characters that indicate close interrelationships among the investigated species include: presence of anisocytic to anomocytic stomata, amphistomatic leaves and glabrous or pubescent surfaces among others. Stellate trichomes prevailed on pubescent surfaces in all species, except for *S. americanum, S. nigrum* and *S. macrocarpon.* The results of this work, taken along with data from other sources, can be used to enhance the proper taxonomic evaluation of genus *Solanum*.

Key words: amphistomatic, diagnostic, epidermis, stellate trichome

Introduction

The taxonomic value of epidermal morphology is well documented in botanical literature (Jayeola & al. 2001; Adedeji & Illoh 2004; Adedeji & al. 2007; Saheed & Illoh 2010; Ogundare & Saheed 2012). Many of these studies have underlined the reliability of epidermal anatomical characters in resolving taxonomic controversies, especially in such a complex genus as *Solanum* L., type genus of the family *Solanaceae*. This genus is represented in Nigeria by 20 species, 15 of which are indigenous and the remaining five were introduced and are now cultivated (Hutchison & Dalziel 1963; Gbile 1987). Some very important leafy vegetables and edible fruits are among the cultivated species and represent sources of rich proteins, vitamins and minerals (Asaolu & Asaolu 2002; Oboh & al., 2005). Resolving the taxonomic controversy in this important genus is very important to taxonomists, because of the complexity of the genus. For instance, the diversities in overall morphology and eco-geographical distribution of the member species have led to serious confusion among the researchers of this genus (Gbile 1979; Wunderlin & al. 1993; Levin & al. 2005; Yousaf & al. 2006).

It is equally important to point out that many *Solanum* species do not have clearly defined subgeneric or sectional affiliation, in addition to the existing infrageneric groups with yet unknown phylogenetic relationships even in well-characterized species (Bohs & Olmstead 1997). Another reason for this genus complexity is explained by the fact that most of its members are cultivated and cultivated plants are more difficult to classify than the wild plants, because of human interference (Schultze-Motel & Meyer, 2005). Furthermore, taxonomic confusion in the genus could also be attributed to its large size, morphological variations and its predominantly tropical distribution (Gbile 1987; Bohs & Olmstead 1997).

There has been a series of effort aimed at using the anatomical characters in delimiting some *Solanum* species. The early work of Metcalfe & Chalk (1950) described the general anatomy of the family *Solanaceae* and used anatomical characters for

identification of some *Solanum* species. Illoh & Inyang (1998) reported on the use of epidermal and petiole anatomical characters in establishing the taxonomic relationships among six *Solanum* species in the subgenus *Leptostermonum* occurring in Nigeria. Their work led to recognition of four (4) divisions of vascular bundles, shape and arrangement in the petioles. Mbagwu & al. (2007a,b) carried out anatomical studies of *S. macrocarpon* and *S. nigrum* and pointed out that the similarities in leaf epidermal features of the taxa showed reasons for putting them in the same genus, while the differences in the root anatomical structures showed reasons to set them apart as different species. Therefore, this paper explores the stable and discrete leaf epidermal characters of ten Nigerian *Solanum* species and also discusses the extent to which leaf epidermal features might be utilized in the systematic consideration of the *Solanum* species in view of the morphological similarities of their characters.

Material and methods

Ten out of the twenty Nigerian *Solanum* species were used in this study. Specimens were collected from different locations in Ile-Ife, Osun State (Table 1). Identification of the specimen was was done using the information in volume II of the *Flora of West Tropical Africa* by Hutchinson & Dalziel (1963). Comparison with the herbarium specimens was also made for proper identification at the Herbarium of Forestry research Institute (FHI) Ibadan Awolowo University, Ile-Ife, Nigeria (IFE).

Fresh mature leaves of each species were cut from the standard median portion for processing. Epidermal peels of most of the specimens were obtained manually using forceps and dissecting needles. Fragile and delicate material was obtained by the previously described procedure (Adedeji & Jewoola 2008). The peels were stained with 1 % Safranin 'O' solution for about 5-10 minutes, rinsed carefully in several changes of water to remove excess stains and then mounted in dilute (10 %) glycerol solution on a glass slide for further microscopic observation. Microscopic observations of important epidermal characters such as trichome and stomata types, venation patterns and crystal grains distribution were handled by an Olympus BH-2 compound microscope fitted with a JVC KYF70B digital camera; thereafter, the selected images were imported as bitmaps to Corel Draw 12 (Corel Corporation, Ottawa, Canada 2003).

Twenty different measurements were made for each of the measured parameters per species. The values, ± standard error (SE), were later grouped into a range, where applicable. Guard cell area (GCA) was calculated by multiplying the length and width of guard cells

Table 1. Studied *Solanum* species and their locations.

Taxa	Localities	Coordinates
S. torvum	Olatunbosun Str., Olonade, Ile-Ife.	N 07° 30.380, E 004° 32.706
		N 07° 30.493, E 004° 32.775
	Along the new road to O.A.U Teaching Hospital, Ile-Ife.	N 07° 30.761, E 004° 32.926
S. anomalum	At the back of St. Barnabas Anglican Church, off Olonade Str., Ile-Ife.	N 07° 30.364, E 004° 32.652
		N 07° 30.355, E 004° 32.647
		N 07° 30.353, E 004° 32.641
	Gate farm, along road 7, O.A.U, Ile-Ife.	N 07° 30.796, E 004° 32.919
S. melongena	At the back of St. Barnabas Anglican Church, off Olonade Str., Ile-Ife.	N 07° 30.364, E 004° 32.652
		N 07° 30.356, E 004° 32.639
	Gate farm, along road 7, O.A.U, Ile-Ife	N 07° 30.796, E 004° 32.919
S. aethiopicum	At the back of St. Barnabas Anglican Church, off Olonade Str., Ile-Ife.	N 07° 30.356, E 004° 32.639
		N 07° 30.353, E 004° 32.641
	Gate farm, along road 7, O.A.U, Ile-Ife.	N 07° 30.819, E 004° 32.906
S. americanum	At the back of St. Barnabas Anglican Church, off Olonade Str., Ile-Ife.	N 07° 30.355, E 004° 32.647
	Department of Botany, O.A.U, Ile-Ife (cultivated)	N 07° 31.155, E 004° 31.562
		N 07° 31.154, E 004° 31.569
		N 07° 31.156, E 004° 31.567
S. nigrum	Farm gate, along road 7, O.A.U, Ile-Ife.	N 07° 30.819, E 004° 32.906
		N 07° 30.794, E 004° 32.913
	Old Buka, O.A.U. campus, Ile-Ife.	N 07° 31.303, E 004° 31.195
		N 07° 31.308, E 004° 31.186
		N 07° 31.314, E 004° 31.175
S. erianthum	Olatunbosun Str., Olonade Ile-Ife.	N 07° 30.493, E 004° 32.775
		N 07° 30.569, E 004° 32.773
	Security post, road 7 gate, O.A.U., Ife.	N 07° 30.669, E 004° 32.867
	Behind Chemical Engineering Dept. O.A.U, Ife.	N07° 31.149,E 004° 31.678
S. wrightii	All Souls Chapel premises, O.A.U, Ile-Ife.	N 07° 30.720, E 004° 31.092
		N 07° 30.713, E 004° 31.078
		N 07° 30.712, E 004° 31.074
		N 07° 30.694, E 004° 31.090
S. macrocarpon	Faith House, Afeki Road, Opa, Ile-Ife.	N 07° 31.896, E 004° 34.964
		N 07° 31.889, E 004° 34.966
		N 07° 31.842, E 004° 35.006
	Gate farm, along road 7, O.A.U, Ile-Ife.	N 07° 30.788, E 004° 32.930
		N 07° 30.796, E 004° 32.919
S. gilo	Asunle area of Tonkere village, Ile-Ife.	N 07° 31.995, E 004° 31.479
		N 07° 31.996, E 004° 31.477
		N 07° 31.996, E 004° 31.475
		N 07° 31.998, E 004° 31.495

by 0.7854 Franco's constant (Franco 1939). Stomatal number or frequency (average number of stomata per square millimetre of leaf) (SN or SF), as well as the stomatal index (SI), which is a percentage of stomatal number (the guard cell) to the other epidermal cells present on a leaf portion (Dilcher 1974), were also calculated. The stomatal index is obtained by the formula: S. I. = [S/(E+S)] × 100, where S = number of stomata per unit area, E = number of ordinary epidermal cells plus the subsidiary cells in the same unit area.

Results

The quantitative data on the investigated leaf anatomical characters are presented in Table 2 for all species. Qualitative data observed are also presented.

S. torvum Sw. (Fig. 1, a-e)

Epidermal cells on the adaxial surface (Fig. 1, a, b) are polygonal, with straight to wavy anticlinal walls. Stomata are mostly anisocytic, but occasionally brachyparacytic types are encountered and are densely distributed. Non-glandular trichomes of different types are present, densely distributed, which may be unicellular, uniseriate, 2 to 5-armed or rotate-stellate. On the abaxial surface (Fig. 1, c, d), epidermal cells are irregular to polygonal, with wavy to sinuous anticlinal walls. Stomata are anomocytic, more densely distributed than on the adaxial surface. Rotate to stalked multiangulate and 4 to 5-armed stellate types of trichomes are present. Venation (Plate 1, e) shows the major veins as cladodromous, with well formed areoles, variable in size and shape. Druses of calcium oxalate crystals are abundant and are randomly distributed.

S. anomalum Thonn. (Fig. 1, f-j)

Adaxial epidermal cells (Fig. 1, f-h) are polygonal in shape, with wavy anticlinal walls. Stomata are present, they are anisocytic and densely distributed. Non-glandular and glandular trichomes are present and are sparsely distributed. Non-glandular trichomes are of different types, they may be unicellular, uniseriate, 2 to 5-armed and multiangulate stellate trichomes. Abaxial epidermal cells (Fig. 1, i) are polygonal in shape, with straight to wavy anticlinal walls. Stomata are present, they are anisocytic and more densely distributed than on the adaxial surface. Non-glandular trichomes are present, densely distributed; they are of the sessile to stalked multiangulate stellate types, much longer than on the adaxial surface. Major veins (Fig. 1, j) are cladodromous, areoles are well formed and variable in size and shape. Crystal grains and druses of calcium oxalate are present, numerous and randomly distributed.

S. melongena L. (Fig. 1, k-n)

Epidermal cells on the adaxial surface are polygonal in shape (Fig. 1, k-l), with straight to wavy anticlinal walls. Stomata are anisocytic and densely distributed. Glandular and non-glandular trichomes are present; non-gladular stellate types could be rotate to multiangulate, densely distributed, but unicellular and uniseriate types are few. Abaxial epidermal cells (Fig. 1, m) are irregular in shape. Anticlinal walls are deeply sinuous. Stomata are present; anomocytic, densely distributed. Non-glandular trichomes are present; rotate to stalked multiangulate stellate type, more densely distributed than on the adaxial side. Major veins are cladodromous, with well formed areoles (Fig. 1, n) variable in size and shape. Crystals: druses of calcium oxalate are present, with numerous and randomly distributed crystal grains.

Table 2. Summary of the quantitative leaf anatomical characters of the studied *Solanum* species.

	SF (mm-2)		SI (%)		GCA(µm2)			
SPECIES	**AD**	**AB**	**AD**	**AB**	**AD**	**AB**	**VE**	**AA (mm2)**
S. torvum	25.70 ±0.48	47.10 ±0.56	15.12 ±0.32	31.82 ±0.36	329.12 ±15.99	187.62 ±8.16	0–1	54.00 ± 3.39
S. anomalum	28.10 ±0.38	57.00 ±0.51	12.28 ±0.15	25.35 ±0.16	127.97 ±5.60	161.26 ±7.39	0–2	83.85 ±7.22
S. melongena	30.00 ±0.62	42.80 ±0.38	17.92 ±0.30	28.89 ±0.26	173.40 ±5.45	192.48 ±7.59	1	90.62 ± 5.46
S. aethiopicum	23.80 ±0.52	40.10 ±0.57	19.61 ±0.41	33.49 ±0.37	214.67 ± 7.36	224.73 ±13.14	0–2	79.18 ± 3.66
S. americanum	6.06 ±0.27	26.83 ±0.38	12.91 ±0.53	17.72 ±0.21	364.14 ±13.74	254.21 ± 13.31	1–2	170.41 ±10.33
S. nigrum	16.3 ±0.33	27.3 ±0.52	16.90 ± 0.44	17.85 ±0.28	306.58 ±12.04	226.12 ±8.74	1–2	58.84 ±2.64
S. erianthum	19.37 ±0.31	22.93 ±0.52	10.33 ±0.17	12.23 ±0.27	181.73 ±7.22	305.53 ±10.74	1–3	52.91 ±2.18
S. wrightii	17.83 ±0.40	51.77 ±0.44	10.18 ±0.20	31.97 ±0.58	258.72 ±12.66	202.19 ±6.91	1–2	70.52 ±3.07
S. macrocarpon	20.50 ±0.47	37.20 ±0.62	19.55 ± 0.47	23.20 ± 0.91	167.51 ±6.66	184.15 ±6.58	1–3	126.26 ±13.72
S. gilo	42.37 ±0.82	55.6 ±0.73	25.08 ± 0.61	29.34 ± 0.93	177.56 ± 6.11	203.92 ± 8.25	1–2	62.47 ± 2.78

SF = stomata frequency; **SI** = stomata Index; **GCA** = guard cell area; **VE** = veinlet endings per areole; **AA** = areole areas; **AD** = adaxial; **AB** = abaxial.

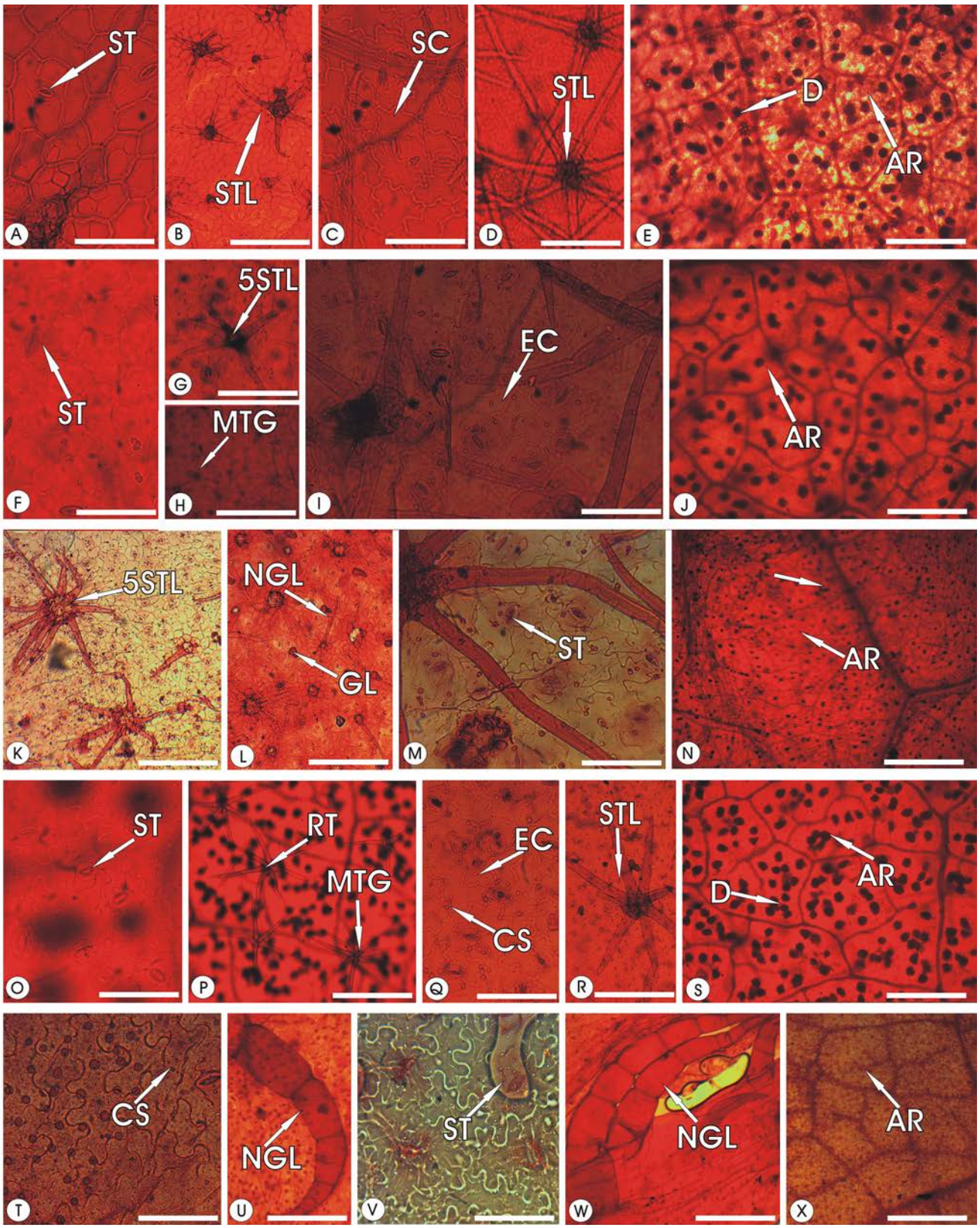

Fig. 1. Adaxial and abaxial epidermal surfaces of the *Solanum* species. *S. torvum* **A-B**) adaxial, **C-D**) abaxial, **E**) venation; *S. anomalum* **F-H**) adaxial, **I**) abaxial, **J**) venation; *S. melongena* **K-L**) adaxial, M) abaxial, **N**) venation; *S. aethiopicum* **O-P**) adaxial, **Q-R**) abaxial, **S**) venation; *S. americanum* **T-U**) adaxial, **V-W**) abaxial, **X**) venation. **ST** – stomata, **EC** – epidermal cell, **SC** – subsidiary cell, **NGL** – non-glandular trichome, **GL** – glandular trichome, **RT** – rotate stellate, **MTG** – multiangulate, **STL** – stellate trichome, **5STL** -5-armed trichome, **AR** – areoles, **CS** – crystal grain, **D** – druses. Scale = 30 μm.

***S. aethiopicum* L.** (Fig. 1, o-s)

Epidermal cells are irregular on the adaxial surface (Fig. 1, o-p), with wavy to sinuous anticlinal walls. Stomata are anisocytic and densely distributed. Non-glandular trichomes are present; they could be unicellular, uniseriate, rotate to multiangulate or, 3 to 5-armed stellate trichomes, sparsely distributed. On the abaxial surface (Fig. 1, q-r), epidermal cells are irregular in shape, with wavy to sinuous anticlinal walls and anomocytic stomata. Non-glandular trichomes are present; rotate to stalked multiangulate or 4 to 5-armed stellate, densely distributed. Major veins are cladodromous, areoles are well formed, and they are variable in size and rectangular to polygonal in shape. Crystals: druses of calcium oxalate and crystal grains are present; they are abundant and randomly distributed.

***S. americanum* Mill.** (Fig. 1, t-x)

Epidermal cells on the adaxial surface (Fig. 1, t-u) are irregular with sinuous anticlinal walls. Stomata are anomocytic and sparsely distributed. Non-glandular trichomes are present, of the multicellular uniseriate type and sparsely distributed. Stellate trichomes are absent. On the abaxial surface (Fig. 1, v-w), the epidermal cells are irregular in shape, with anticlinal walls, deeply sinuous and the stomata are anomocytic. Non-glandular multicellular uniseriate trichomes are present, sparsely distributed. Major veins are brochidodromous, areoles are well formed and rectangular in shape. Crystals: crystal grains are present and randomly distributed.

***S. nigrum* L.** (Fig. 2, a-f)

Adaxial epidermal cells are irregularly shaped, with wavy to sinuous anticlinal walls. Stomata are present, mostly anisocytic, but occasionally paracytic and diacytic types are encountered. Glandular and non-glandular trichomes are present; non-glandular types are multicellular, uniseriate and peltate, with 7 to 8 cell types and sparsely distributed. Stellate trichomes are absent. Abaxial epidermal cells are equally irregularly shaped; the anticlinal walls are deeply sinuous, with anomocytic stomata which occasionally could be brachyparacytic. Non-glandular multicellular uniseriate trichomes are present, sparsely distributed. Short glandular trichomes are also present but moderately distributed (Fig. 2, d, e). Major veins are brochidodromous, with areoles that are well formed and rectangular in shape. Crystals: crystal grains are randomly distributed.

***S. erianthum* D. Don.**
(Syn. *S. verbascifolium*) (Fig. 2, g-j)

Adaxial epidermal cells are polygonal to irregular in shape, with straight to wavy anticlinal walls. Stomata are present and anisocytic, densely distributed. Non-glandular trichomes are present; they are unicellular, multiseriate, and rotate to multiangulate or 3 to 4-armed stellate types, densely distributed (Fig. 2, g, h). On the abaxial surface, the epidermal cells are polygonal to irregular in shape, with straight to wavy anticlinal walls. Stomata are densely distributed, mostly anisocytic; however, paracytic to staurocytic types are also present. Non-glandular trichomes, which are of unicellular, multicellular multiseriate, rotate to multiangulate stellate types, are present and densely distributed. Short glandular trichomes are also present but sparsely distributed (Fig. 2, i). Major veins are brochidodromous and the areoles are not well formed. Crystals: druses of calcium oxalate and crystal grains are present and randomly distributed (Fig. 2, j).

***S. wrightii* Benth.** (Fig. 2, k-o)

The shape of the epidermal cells on the adaxial surface is polygonal with straight anticlinal walls. Stomata are anisocytic, occasionally brachyparacytic and sparsely distributed. Non-glandular trichomes are present; they may be simple unicellular or multiseriate and are densely distributed. Stellate trichomes are absent (Fig. 2, k, l). Abaxial epidermal cells are irregular in shape, with wavy anticlinal walls. Stomata are densely distributed and they are anomocytic to anisocytic in type. Non-glandular trichomes are present; they are of stalked, multiangulate stellate type and densely distributed (Fig. 2, m, n). Major veins are craspedodromous, the areoles are well formed and rectangular to polygonal in shape. Crystals: druses of calcium oxalate and crystal grains are present, numerous and randomly distributed.

***S. macrocarpon* L.** (Fig. 2, p-t)

Epidermal cells are polygonal on the adaxial surface, with anticlinal walls, straight to wavy. Stomata are present; they are mostly anisocytic and occasionally brachyparacytic. Trichomes are present only of the short glandular type, while non-glandular stellate trichomes are absent (Fig. 2, p, q). On the abaxial surface, the epidermal cells are irregular in shape, with sinuous anticlinal walls. Stomata are densely distrib-

uted and anisocytic. Short glandular trichomes are present as on the adaxial surface, but non-glandular stellate trichomes are absent (Fig. 2, r, s). Major veins are cladodromous, the areoles are well formed and rectangular in shape. Crystals: druses of calcium oxalate are present, numerous and randomly distributed.

***S. gilo* Raddi.** (Fig. 2, u-y)

On the adaxial surface, epidermal cells are irregular in shape, with sinuous to wavy anticlinal walls. Stomata are anisocytic and densely distributed. Non-glandular trichomes are present; they may be unicellular, uniseriate, 2 to 5-armed stellate (sessile to stalked and densely distributed) or stalked multiangulate stel-

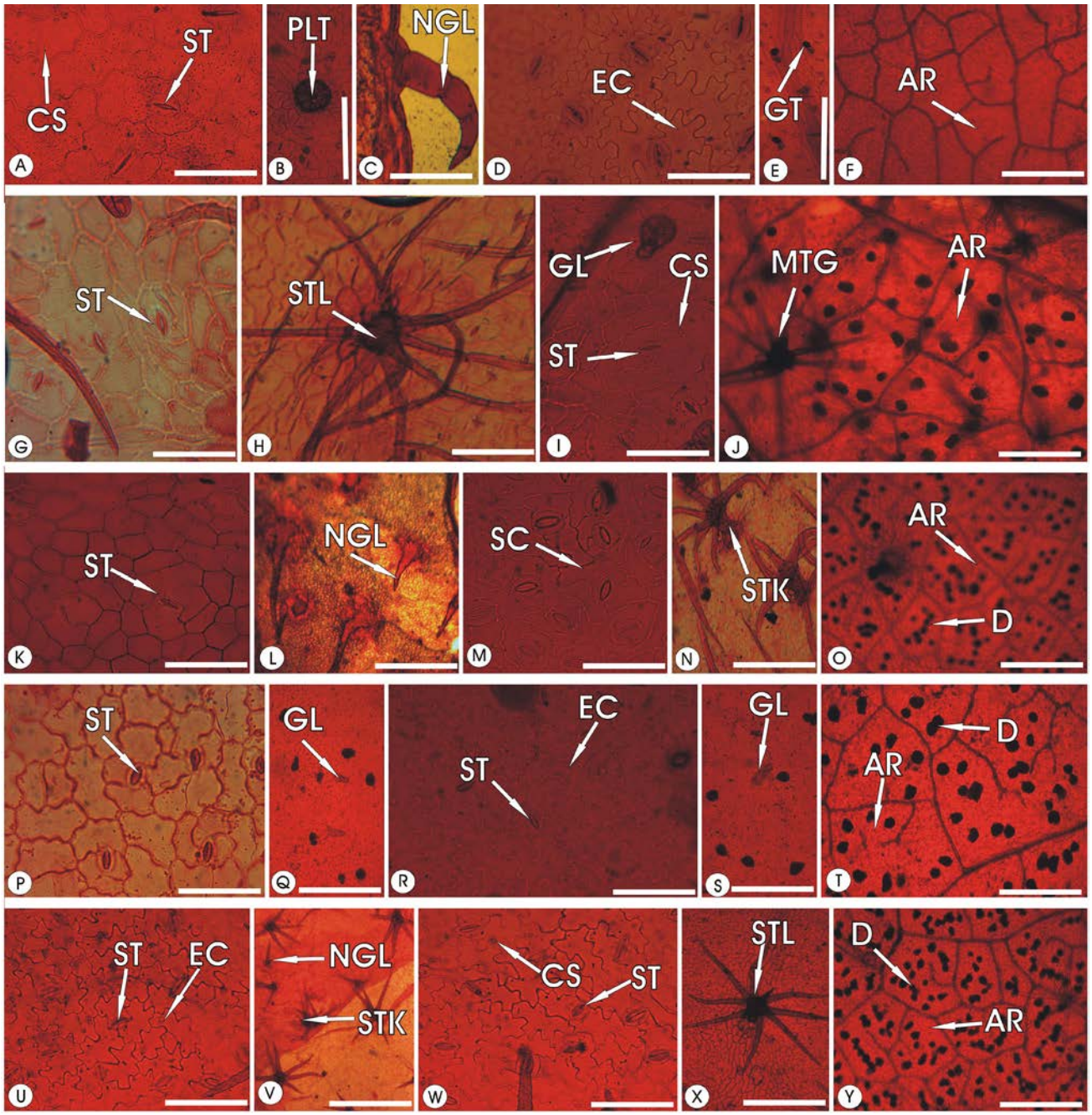

Fig. 2. Adaxial and abaxial epidermal surfaces of *Solanum* species. *S. nigrum* **A-C**) adaxial, **D-E**) abaxial, **F**) venation; *S. erianthum* **G-H**) adaxial, **I**) abaxial, **J**) venation; *S. wrightii* **K-L**) adaxial, **M-N**) abaxial, **O**) venation; *S. macrocarpon* **P-Q**) adaxial, **R-S**) abaxial, **T**) xenation; *S. gilo* **U-V**) adaxial, **W-X**) abaxial, **Y**)venation. **ST** – stomata, **EC** – epidermal cell, **SC** – subsidiary cell, **NGL** – non-glandular trichome, **GL** – glandular trichome, **MTG** – multiangulate, **STK** – stalked stellate, **STL** – stellate trichome, **PLT** – peltate trichome, **AR** – areoles, **CS** – crystal grains, **D** – druses. Scale = 30 μm.

late (few). Short glandular trichomes are also present (Fig. 2, u, v). Abaxial epidermal cells are irregular in shape, with sinuous anticlinal walls. Stomata are densely distributed, mostly anomocytic, but sometimes paracytic types are encountered. Non-glandular trichomes, rotate to stalked multiangulate stellate in type, are present and densely distributed (Fig. 2, w, x). Major veins are cladodromous, the areoles are well formed and rectangular in shape. Crystals: druses of calcium oxalate and crystal grains are randomly distributed.

Discussion

Anatomical characters have been regarded as important in the classification of angiosperms and these characters are known to provide additional features, which along with other characters, are usually of taxonomic value in the classification and identification of plants. Howard (1979) & Khatijah & al. (1992) asserted that anatomical characteristics sometimes show affinity between species and often define the species position. In this study, the observation of morphology of epidermal cells reveals variations among the studied *Solanum* species. The leaves of all studied species are amphistomatic, i.e. stomata are found present on both upper and lower surfaces, but they prevail on the lower epidermis. This is in agreement with the earlier works of Metcalfe & Chalk (1950), Mbagwu & al. (2007) and Adedeji & al. (2007).

The stomata complex types are mostly anisocytic and occasionally anomocytic. Adedeji & al. (2007) have earlier reported more anisocytic to anomocytic stomata types in the species within the genera *Solanum* and *Nicotiana.* Illoh & Inyang (1998) reported the useful presence and combinations of different types of stomata in the classification and delimitation of the *Solanum* species. In addition to the prevailing anisocytic and anomocytic stomata types, some other stomata types were occasionally observed. Brachyparacytic stomata were observed in *S. torvum, S. nigrum, S. macrocarpon,* and *S. wrightii.* Diacytic stomata were observed in *S. nigrum.* A paracytic stomata type was observed occasionally in *S. erianthum, S. nigrum* and *S. gilo.* A staurocytic stomata type was also observed in *S. erianthum.* The presence of staurocytic stomata type has been reported in some *Solanum* species of section *Geminata* by Benitez & Ferrarotto (2009). *Solanum nigrum* was observed to have the highest number of stomata types, thus delimiting it from all the other investigated species.

The stomata index is highly constant for certain species and can be used for their delimitation (Olatunji, 1983 cited by Adedeji & al. 2007). On the adaxial surface, *S. gilo* had the highest stomata index (25.08 %), while the lowest was observed in *S. wrightii* (10.18 %). Similarly, on the abaxial surface, *S. aethiopicum* had the highest index (33.49 %) and the lowest was recorded in *S. erianthum* (12.23 %). Generally, the stomata index was found to be higher on the abaxial surface of all studied taxa. This is in agreement with the earlier work of Benitez and Ferrarotto (2009). The guard cell area, although quantitative, is quite diagnostic (Adedeji et al. 2007). It is lowest on the adaxial (127.97 μm^2) and abaxial (161.26 μm^2) surfaces of *S. anomalum,* and highest on the adaxial surface of *S. americanum* (364.14 μm^2) and abaxial surface of *S. erianthum* (305.53 μm^2).

The use of trichomes as anatomical features for systematic comparisons and delimitation has been underlined by many research workers. Some families can be easily identified by the presence of a particular type of trichome (Adedeji & al. 2007). Non-glandular trichomes have been successfully used for grouping the species of *Hibiscus* in Nigeria (Adedeji & Illoh 2004). Rao & Ramayya (1977) used trichomes to separate the two species of Malvastrum in India. Adedeji (2004) also used trichome morphology in tracing the evolutionary relationships in the genus *Emilia*. Stace (1969) used glandular trichomes for classification of the genus *Combretum* in Africa. Similarly, Isawumi (1992) used the structure and distribution of trichomes to classify the West African species of *Hibiscus.* Inamdar & al. (1990) also reported the structure, ontogeny, organographic distribution, and taxonomic significance of trichomes in the family *Cucurbitaceae*. Trichome characters act as biomarkers to identify medicinal plants even in raw material or powder form (Gohil & al. 2007 cited by Dipa & Daniel 2011).

Stellate trichomes prevail in all species, except for *S. americanum, S. nigrum* and *S. macrocarpon* (Fig. 1 (t-x), 2 (a-f) and 2 (p-t)). Stellate trichomes observed in the studied *Solanum* species are quite characteristic and diagnostic in this family. This agrees with the statement of Arambari & al. (2006) that stellate trichomes are of diagnostic value in *Buddlejaceae, Euphorbiaceae, Malvaceae, Rutaceae, Solanaceae,* and

Tiliaceae. Glandular trichomes are classificatory of *S. macrocarpon* and *S. nigrum,* being the only species with glandular trichomes. *Solanum americanum* and *S. nigrum* were found to contain non-glandular multicellular uniseriate trichomes. An additional spot character is the presence of peltate trichomes on the adaxial surface of *S. nigrum,* which distinguishes this taxon from *S. americanum* and the remaining taxa. However, *S. wrightii* is quite distinct by the absence of stellate trichomes on the adaxial surface. In addition to the stellate trichomes found in the taxa, simple unicellular, uniseriate trichomes are also present on the adaxial surface of all taxa, except in *S. erianthum* and *S. wrightii* which have unicellular, multiseriate trichomes. Simple unicellular to multicellular multiseriate trichomes were also found on the abaxial surface of *S. erianthum*. Glandular trichomes are absent on the surfaces of *S. aethiopicum* and *S. wrightii,* adaxial surface of *S. erianthum* and abaxial surface of *S. anomalum, S. melongena* and *S. gilo. Solanum torvum, S. anomalum, S. aethiopicum,* and *S. erianthum* also contain 2 to 5-armed trichomes.

The cell-wall pattern is one of those epidermal features of taxonomic importance at specific level (Barthlott 1981; Saheed & Illoh 2010). The cell-wall patterns of the epidermis can be taxonomically employed to delimit members of the genus *Solanum*. Of all studied taxa, *S. erianthum* is quite distinct in the surface view of the epidermis, with a straight to wavy anticlinal wall on both surfaces. The same is valid for *S. americanum* with its deeply sinuous wall pattern on both surfaces, and *S. aethiopicum* with wavy to sinuous walls on both surfaces. *Solanum nigrum* and *S. gilo* are characterized by wavy to sinuous anticlinal wall on the adaxial surface, and a sinuous wall pattern on the abaxial surface. *Solanum torvum, S. melongena* and *S. macrocarpon* were found to have straight to wavy anticlinal wall pattern on the adaxial surface, while on the abaxial surface, *S. melongena* and *S. macrocarpon* possess a sinuous wall and *S. torvum* has a wavy to sinuous wall pattern. *Solanum anomalum* has a wavy wall pattern on the adaxial surface and straight to wavy wall pattern on the abaxial surface. However, *S. wrightii* is characterized by a straight wall on the adaxial surface and a wavy wall pattern on the abaxial surface.

Foliar venation has been used by Levin (1986) to provide a new insight into the relationships within subfamily *Phyllanthoidea,* and subsequently recommended similar studies into other subfamilies, which undoubtedly would be illuminating. Perfect areoles were observed in all studied taxa, i.e. the areoles are well formed with the exception of *S. erianthum* with its imperfect areoles (Fig. 2, j). On the basis of the type of veinlet terminating end per areole, the species can be divided into two groups: those with simple or unbranched veinlets, as found in *S. torvum* and *S. melongena;* and those with branched veinlets, as found in the remaining taxa. Areole area is greatest in *S. americanum* (170.41 mm^2) and smallest in *S. erianthum* (52.91 mm^2).

The importance of crystals in taxonomy has been highlighted by Amos (1951 cited by Illoh & Inyang 1998). All studied species were found to have randomly distributed cell inclusions. However, they can be classified into three groups on the basis of the type of cell inclusion: those having only druses, as found in *S. torvum* and *S. macrocarpon;* those having only crystal grains, as in *S. americanum* and *S. nigrum;* and those having both druses and crystal grains, as in *S. anomalum, S. melongena, S. aethiopicum, S. erianthum, S. wrightii,* and S. *gilo.* Taxonomic decisions based on epidermal studies are quite reliable, because of being less susceptible to environmental manipulation (Barthlott 1981; Saheed & Illoh 2010; Ogundare & Saheed 2012). Thus, comparative epidermal studies have been useful in resolving the identity problems among closely related taxa.

In conclusion, in spite of some overlapping characters, which justify the relative closeness of the species in this genus, this work clearly highlights the discerning characters that delimit these species. These characters include the specific types of stomata, stomata index, guard cell area, trichome types, cell-wall pattern, veinlet endings, and types of crystals. Collectively, our data do not support the position that *S. gilo* is a synonym of *S. aethiopicum,* and that *S. nigrum* is a synonym of *S. americanum* in The Plant List (http://www.theplantlist.org/). This is because there are a number of stable and reliable leaf epidermal characters that distinguish these species in this study. However, we are well aware that further data from other taxonomic character sources may tend to strongly suggest otherwise.

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