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

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Received: September 06, 2016 ▷ Accepted: March 20, 2017

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 et 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 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>
<thead>
<tr>
<th>Taxa</th>
<th>Localities</th>
<th>Coordinates</th>
</tr>
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<tr>
<td>S. torvum</td>
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<td>N07°30.380, E004°32.706</td>
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<td></td>
<td>Along the new road to O.A.U Teaching Hospital, Ile-Ife.</td>
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<td>Gate farm, along road 7, O.A.U, Ile-Ife.</td>
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<td>Department of Botany, O.A.U, Ile-Ife. (cultivated)</td>
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<td>S. macrocarpon</td>
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<td>N07°30.816, E004°34.964</td>
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<td>S. gilo</td>
<td>Asunle area of Tonkere village, Ile-Ife.</td>
<td>N07°30.995, E004°31.479</td>
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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:

\[ S.I. = \frac{S}{(E+S)} \times 100 \]

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 multiangular trichomes are present. Veneration (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 multiangular 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 multiangular 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 (Fig. 1, k-l) are polygonal in shape, with straight to wavy anticlinal walls. Stomata are anisocytic and densely distributed. Glandular and non-glandular trichomes are present; non-glandular stellate types could be rotate to multiangular, 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 multiangular 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.**

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>SF (mm²)</th>
<th>SI (%)</th>
<th>GCA(µm²)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>AD</td>
<td>AB</td>
<td>AD</td>
</tr>
<tr>
<td><em>S. torvum</em></td>
<td>25.70 ± 0.48</td>
<td>47.10 ± 0.56</td>
<td>15.12 ± 0.32</td>
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<tr>
<td><em>S. anomalum</em></td>
<td>28.10 ± 0.38</td>
<td>57.00 ± 0.51</td>
<td>12.28 ± 0.15</td>
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<tr>
<td><em>S. melongena</em></td>
<td>30.00 ± 0.62</td>
<td>42.80 ± 0.38</td>
<td>17.92 ± 0.30</td>
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<tr>
<td><em>S. aethiopicum</em></td>
<td>23.80 ± 0.52</td>
<td>40.10 ± 0.57</td>
<td>19.61 ± 0.41</td>
</tr>
<tr>
<td><em>S. americanum</em></td>
<td>6.06 ± 0.27</td>
<td>26.83 ± 0.38</td>
<td>12.91 ± 0.53</td>
</tr>
<tr>
<td><em>S. nigrum</em></td>
<td>16.3 ± 0.33</td>
<td>27.3 ± 0.52</td>
<td>16.90 ± 0.44</td>
</tr>
<tr>
<td><em>S. erianthum</em></td>
<td>19.37 ± 0.31</td>
<td>22.93 ± 0.52</td>
<td>10.33 ± 0.17</td>
</tr>
<tr>
<td><em>S. wrightii</em></td>
<td>17.83 ± 0.40</td>
<td>51.77 ± 0.44</td>
<td>10.18 ± 0.20</td>
</tr>
<tr>
<td><em>S. macrocarpon</em></td>
<td>20.50 ± 0.47</td>
<td>37.20 ± 0.62</td>
<td>19.55 ± 0.47</td>
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<tr>
<td><em>S. gilo</em></td>
<td>42.37 ± 0.82</td>
<td>55.6 ± 0.73</td>
<td>25.08 ± 0.61</td>
</tr>
</tbody>
</table>

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; they could be unicellular, uniseriate, rotate to multiangulate or, 3 to 5-armed stellate trichomes, sparsely 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-

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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 multiangular 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. (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 Dipe & 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. anomalum* 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 sinusous walls on both surfaces. *Solanum nigrum* and *S. gilo* are characterized by wavy to sinusous anticlinal wall on the adaxial surface, and a sinusous 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 sinusous wall and *S. torvum* has a wavy to sinusous 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 mm²) and smallest in *S. erianthum* (52.91 mm²).

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.

**Acknowledgment.** The Authors wish to acknowledge the contribution of Mr. Stephen Ekperemehci towards the collection of plant samples used for this research.
References


