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Systematic significance of foliar epidermis and tendril morphology in three West African genera of Cucurbitaceae: *Momordica* L., *Luffa* Mill. and *Trichosanthes* L

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Momordica, *Luffa* and *Trichosanthes* are important cucurbitaceous plants whose foliar epidermal characters are sparsely documented. A combined investigation of leaf epidermis and tendrils of the species was carried out with the aid of light and scanning electron microscopy, and visual assessment. All *Momordica* species have hypostomatic leaves except *M. balsamina* whose leaves are amphistomatic. This adds to our knowledge of range of stomatal distribution in *Momordica* which hitherto, is reported hypostomatic. It also raises doubt about the naturalness of Sect. *Momordica*. Only *M. multiflora* is glabrous and *M. angustisepala* alone is pubescent on the epidermal surfaces. Epidermis of *Luffa* is amphistomatic and non-cystolithic whereas, it is hypostomatic and cystolithic in *Trichosanthes*. Tendrils branches arise from the base in *Luffa* (3–4 in number) and *Trichosanthes* (2–3 in number) whereas in *Momordica* they may not branch or are bifurcated, with one being vestigial. These comparative data support classifying the three genera in separate tribes. In particular, characters of the leaf epidermis will assist in identifying the species even when the leaf samples are fragmentary, or when there is a mix-up, the usual state of herbal materials in the African markets.

Keywords: Cucurbitaceae; cuticle; leaf epidermis; microscopy; taxonomy; tendrils

Introduction

The infra-familiar and generic composition in Cucurbitaceae has been reviewed at different times and significant amendments were made (Hutchinson and Dalziel 1958; Jeffrey 1962, 1980, 1990, 2005; Ali et al. 2011; Schaefer and Renner 2011). However, inadequate information on distribution pattern, insufficiency of materials for study and variable morphology of some taxa have been reported as responsible for the limited understanding of certain taxa in this family (Hutchinson and Dalziel 1958; Schaefer and Renner 2010, 2011). In addition, some species from domesticated and wild populations are known to hybridize freely (Schaefer and Renner 2010; Bharathi, Munshi et al. 2012; Guo et al. 2012), leading to polymorphism and increased confusion in taxon identification. Reversal from dioecy to monoecy and vice versa in genera such as *Momordica* L., c. 24 dioecious and 23 monoecious species in Africa (Schaefer and Renner 2010) and genera such as *Luffa* Mill. (Schaefer and Renner 2011) and *Bryonia* L. (Volz and Renner 2008) is another important reason for misidentification in this family.

Many studies focused on the problems above, have improved our knowledge of taxon relationships in Cucurbitaceae, e.g. morphology by Hutchinson and Dalziel (1958), Jeffrey (1962, 1980, 1990, 2005), Schaefer and Renner (2010) and Omar (2009); anatomy by Sawhney (1920), Metcalfe and Chalk (1950, 1979), Ali et al. (2011) and, Aguoru and Okoli (2012); cytology by Bharathi et al. (2011) and molecular studies by Zhang

et al. (2006), Kocyan et al. (2007), Ali et al. (2010), Schaefer and Renner (2011), Bharathi, Parida, et al., (2012a) and Guo et al. (2012).

The latest classification by Schaefer and Renner (2011) recognized 15 tribes in the family following the work of Cogniaux (1881) and Jeffrey (2005). *Momordica*, the primary focus of this work, was formerly in the tribe Joliffieae (Jeffrey 2005) but is now placed in the new tribe Momordiceae and recognized as a monophyletic genus (Schaefer and Renner 2011) despite the inclusion of some poorly known species. *Luffa* and *Trichosanthes* L., the secondary concern of the study, are exo-morphologically distinct; but their tribal position is not yet clear. Tribal placement of *Luffa* has been controversial.

Jeffrey (1962, 1980, 1990, 2005) placed *Luffa* in different tribes – Cucurbiteae and Benincaseae at different times but *Trichosanthes* has been consistently placed in Trichosanthaeae. These genera are now placed in an old tribe – Sicyoeae – based on molecular data (Schaefer and Renner 2011). In view of these changes, we considered leaf epidermis and tendril morphology for possible useful taxonomic data that will enhance sharp discrimination of the taxa.

The genera cannot be identified using fragmented leaf samples because of limited information on the subject and lack of materials to be used as an identification guide. In West Africa, there is an old account on morphology (Hutchinson and Dalziel 1958), limited anatomical information (Metcalfe and Chalk 1950, 1979; Aguoru

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and Okoli 2012) and minimal data on leaf epidermal morphology (Kadiri 2003). This situation has hampered the optimal use of the species in crude drug discovery in spite of the high medicinal potency reported in certain folkloric accounts (Oliver 1960; Agoha 1963; Burkhill 1985). Furthermore, when there is mix-up of leaves due to fragmentation (the condition in which medicinal plants are available in African markets), misidentification of taxa persists. This study therefore, reflects the pattern of inter- and intra-generic relationships in the three genera, so as to contribute useful data that can be combined with other data for a meaningful phylogenetic interpretation. The work also attempts to validate the existing infra-generic classification of *Momordica* by Schaefer and Renner (2011). We addressed these concerns using combined data from tendrils and leaf epidermis correlated on the maximum likelihood phylogenetic tree branches of Schaefer and Renner (2011).

The three genera (*Momordica*, *Luffa* and *Trichosanthes*) are either cultivated or grow in the wild. They have pantropical distribution worldwide (Willis 1966; Schaefer and Renner 2010, 2011) and the species have culinary, medicinal and many other commercial values (Oliver 1960; Agoha 1963; Welihinda et al. 1982; Burkhill 1985; Jiratchariyakul et al. 2001; Grover and Yadav 2004).

Materials and methods

Both herbarium and field specimens were used for the study. Provenances of the herbarium samples are shown in Appendix I. Herbarium abbreviations follow Holmgren et al. (1990). For light microscopy, the approach adopted followed Kadiri (2003), Kadiri and Ayodele (2003), Kadiri et al. (2009) with some modifications. A whole leaf or 1- to 5-cm² portions sectioned from the standard median portion of the lamina (i.e. near the mid-rib) were examined in three to five specimens. Dried leaves were swollen by boiling in water for 30 minutes, and then soaked in concentrated trioxonitrate (v) acid (HNO₃) in capped specimen bottles for about 2–5 hours to macerate the mesophyll. Tissue disintegration was indicated by bubbles and the epidermis was transferred into Petri dishes containing water for cleansing, after which the surfaces were separated with a pair of forceps and a mounting needle. Tissue debris was cleared off the epidermis with a fine-hair brush and washed in several changes of water. A few drops of a graded series of 50%, 75% and 100% ethanol were added in turn to dehydrate the cells. The preparations were later stained with Safranin O for about 5 minutes before mounting in glycerine on the glass slide. The uppermost surfaces of the epidermis were viewed after covering them with cover-slips and were ringed with nail varnish to prevent dehydration. Assessment of 20 randomly selected epidermal cells and stomata from 10 different microscope fields was carried out.

Line drawings of the epidermis were obtained using a camera lucida drawing apparatus. Photomicrographs were obtained with a digital camera attached to a CE Olympus compound microscope. Images were produced and edited on the computer. The formula for stomatal index of Cutter (1978) was adopted, namely: Stomatal Index (%) = $(NS \times 100)/(ES + NS)$, where NS is the number of stomata and ES is the number of epidermal cells. Tendrils of all the herbarium specimens were examined while those of other samples were assessed *in situ* in their natural populations. Three morphological characters such as number of branches, point of branching and twisting pattern, whether lax or deep, were studied.

For electron microscopy, small pieces (c. 7 mm²) of the leaf were fixed on scanning electron microscope stubs with double-sided tape and sputter coated with gold. Specimens were examined and photographed in a Jeol JSM 35 scanning electron microscope.

Results

The seven West African species of *Momordica* in the tribe Momordiceae, were investigated. In the genus, the leaves are hypostomatic in all species except *Momordica balsamina* L. which is amphistomatic (Figure 1C, D; Table 1). The leaves of *Momordica multiflora* Hook.f. are glabrous whereas in other species, they are pubescent (Table 1). The anticlinal walls are undulate on the abaxial surface of all species; although a slightly curved pattern may be found in *Momordica charantia* L. (Figure 1G, H; Table 1) and *Momordica cissoides* Planch. ex Benth. (Figures 2A, B, 3G, H; Table 1). Curved, undulate and straight anticlinal walls were found on the adaxial surface of all species (Table 1). The cell shape is irregular on both surfaces of the epidermis in all species except *Momordica cabraei* (Cogn.) C. Jeffrey, which has polygonal cell shape on the adaxial surface (Figure 1E; Table 1). Stomatal type is generally anomocytic in the genus. The trichome types recorded were long or short conical in *Momordica angustisepala* Harms (Figure 5B; Table 1) and *Momordica foetida* Schumach. (Figure 5H; Table 1) on the adaxial surface, and also in *M. cabraei* (Figure 5D; Table 1) on the abaxial surface (Figure 6F; Table 1). Short conical trichomes were found on the abaxial surface of *M. angustisepala* (Figure 5A, Table 1) and *M. balsamina* (Figure 5C; Table 1). Multicellular conical types occurred on the adaxial surface of *M. charantia* (Figure 5E, Table 1), *M. cissoides* (Figure 5F; Table 1) and *M. foetida* (Figure 5G; Table 1) whereas filiform coiled types were recorded in *M. cissoides* on the abaxial surface (Figure 7D).

Mean cell length varied from 25.5 ± 3.5 on the abaxial surface in *M. charantia* (Table 1) to 58.4 ± 4.2 on the adaxial surface in *M. multiflora* (Table 1). Mean width of the cells ranged from 15.3 ± 3.0 in *M. charantia* to 35.7 ± 3.1 in *M. multiflora*, all on the adaxial surface. *Momordica multiflora* has the largest cells in the genus

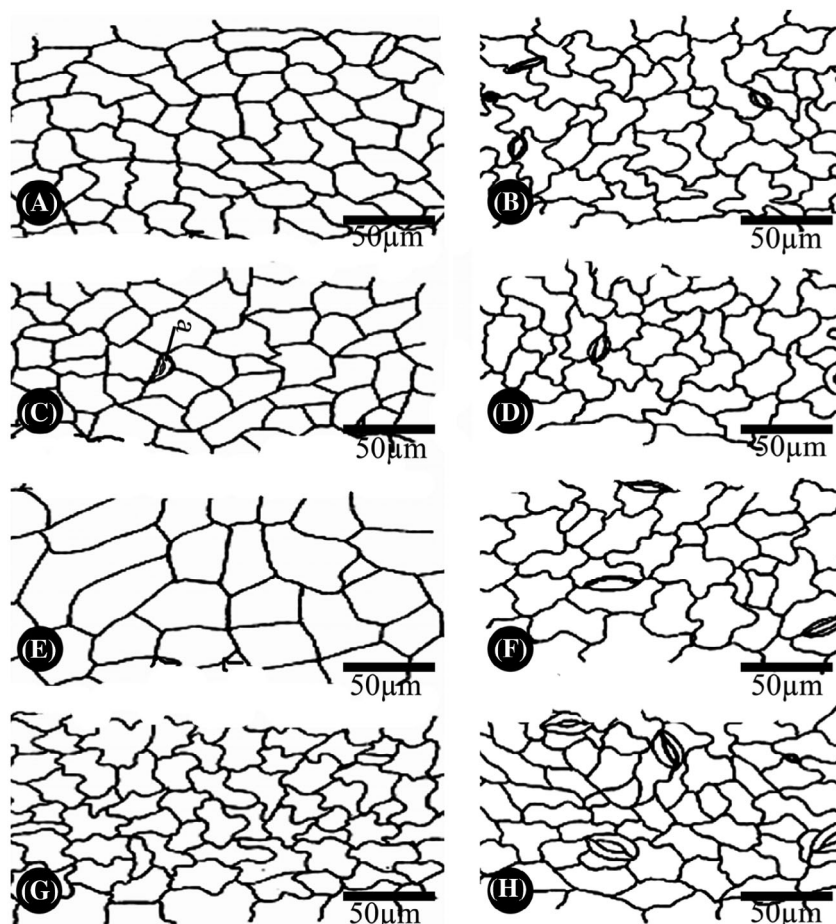


Figure 1. Leaf epidermal characters of West African species of *Momordica*. (A, C, E, G) Adaxial surfaces. (B, D, F, H) Abaxial surfaces. (A, B) *Momordica angustisepala*; (C, D) *Momordica balsamina*, a = stoma on the adaxial surface; (E, F) *Momordica cabraei*; (G, H) *Momordica charantia*.

(Table 1). There are more cells per square millimetre on the adaxial than abaxial surface of the epidermis in *M. balsamina* (Figure 1C, D; Table 1), *M. charantia* (Figure 1G, H; Table 1) and *M. foetida* (Figures 2C, D, 3K, L; Table 1). On the abaxial surface, mean stomatal size varied from 15.2 ± 5.0 by 8.8 ± 1.4 in *M. balsamina* to 23.5 ± 4.0 by 8.6 ± 2.0 in *M. cabraei* (Table 1). On the abaxial surface, the highest number of stomata per square millimetre (173) was recorded in *M. foetida* on the abaxial surface (Table 1) whereas the lowest value of 83 stomata per square millimetre was obtained in *M. balsamina* (Table 1). In the genus, stomatal index varies from 2.1% to 14.3% (Table 1).

The periclinal wall is either conspicuous or inconspicuous. It is conspicuous on both surfaces of *M. charantia* (Figure 6G, Table 2) and *M. multiflora* (Figure 7C, Table 1); inconspicuous on both surfaces of *M. balsamina* (Figure 6C, D; Table 1) and *M. foetida* (Figure 7C, D; Table 1). It may be conspicuous or inconspicuous on either surface of the epidermis of other species (Table 2). The epicuticular wax usually appeared as a continuous thin sheet on the epidermis in most species

(Table 1). In *M. angustisepala*, the wax may be clustered on the adaxial surface (Figure 6A, Table 2) or occur as flakes on the abaxial surface (Figure 6B, Table 2). The stomatal orientation may be sunken as observed in *M. balsamina* (on both surfaces) (Figure 6C, D; Table 1), *M. charantia* (Figure 6H; Table 2), *M. cissoides* (Figure 7B, Table 2) or superficial as recorded in *M. angustisepala* (Figure 6B, Table 1), *M. cabraei* (Figure 6F, Table 2), *M. foetida* (Figure 7D, Table 2) and *M. multiflora* (Figure 7F, Table 2). Cuticular striations are lacking in the species except *M. cabraei* on the abaxial surface (Figure 6F, Table 2) and *M. multiflora* (Figure 7F, Table 2). Peristomatal rim is narrow in all species except in *M. multiflora* (Figure 7F, Table 2) and *M. angustisepala* (Figure 6B, Table 2) where it is wide or narrow to wide, respectively. Cuticular surface is either rough or smooth in the genus (Figures 6 and 7, Table 2).

In Sicyoeae, we only considered the single species of *Luffa* and *Trichosanthes* that are common in West Africa. In *Trichosanthes cucumerina*, cystoliths were encountered (Figure 3D, E). Epidermal cells may be undulate

Table 1. Qualitative and quantitative leaf epidermal characteristics of the West African species of *Momordica*, *Luffa* and *Trichosanthes*.

Species	Anticlinal wall pattern	Epidermal cell shape	Epidermal cell length (µm)	Epidermal cell width (µm)	Mean cell No. / mm ²	Stomatal length (µm)	Stomatal width (µm)	Stomatal No. / mm ²	Stomatal index (%)	Trichomes
<i>M. angustisepala</i> (Ad) (Ab)	Cur Und	Irr Irr	33.6 (44.1±5.0) 54.6 32.0 (39.5±2.0) 47.0	15.0 (23.0±3.0) 30.5 14.8 (16.4±4.0) 25.0	986 1543	— 14.0 (14.8±2.0) 15.5	— 5.3 (7.1±1.8) 8.8	102	— 6.2	LCT SCT
<i>M. balsamina</i> (Ad) (Ab)	Cur Und	Irr Irr	34.8 (41.5±2.0) 48.6 16.0 (36.5±3.0) 55.5	16.0 (17.6±3.0) 19.3 13.5 (22.1±3.0) 30.8	1369 1240	6.4 (6.8±1.1) 7.5 14.0 (15.2±5.0) 16.3	1.8 (2.2±0.6) 2.5 7.0 (8.8±1.4) 10.5	30 83	2.1 6.3	Absent SCT
<i>M. cabraei</i> (Ad) (Ab)	Str Und	Pol Irr	32.0 (47.0±3.0) 62.0 20.0 (28.0±2.0) 36.0	17.5 (24.5±5.0) 31.5 15.5 (22.0±4.0) 28.5	868 1623	— 18.0 (23.5±4.0) 28.0	— 6.8 (8.6±2.0) 9.3	202	— 11.1	Absent LCT
<i>M. charantia</i> (Ad) (Ab)	Und Curv-und	Irr Irr	19.0 (31.3±4.0) 43.5 15.0 (25.5±3.5) 36.0	10.0 (15.3±3.0) 21.5 12.5 (21.4±1.2) 31.2	2088 1832	— 14.0 (20±4.2) 22.0	— 7.0 (8.4±1.2) 9.8	167	— 8.4	MCT Absent
<i>M. cissoides</i> (Ad) (Ab)	Und Cur-und	Irr Irr	25.0 (41.0±3.3) 57.0 15.0 (31.9±6.3) 48.8	14.0 (23.0±3.2) 32.0 12.0 (19.4±4.1) 26.8	1060 1616	— 12.0 (15.2±1.7) 18.3	— 7.0 (8.3±1.5) 9.5	124	— 7.1	MCT Absent
<i>M. foetida</i> (Ad) (Ab)	Und	Irr	21.5 (37.8±2.1) 56.0	11.0 (17.0±3.0) 28.0	1556	—	—	—	—	LCT, MCT
<i>M. multiflora</i> (Ad) (Ab)	Und Cur	Irr Irr	22.5 (36.0±3.0) 48.5 43.8 (58.4±4.2) 73.0	17.5 (26.8±2.1) 36.3 22.8 (35.7±3.1) 48.5	1036 480	12.5 (20.3±1.8) 28.0	7.0 (9.8±2.1) 12.5	173	14.3	Absent Absent
<i>Luffa aegyptiaca</i> (Ad) (Ab)	Und Str	Irr Pol	34.0 (51.2±2.4) 68.4 25.0 (30.0±2.1) 45.0	10.5 (21.5±2.1) 32.0 15.0 (21.0±3.0) 27.0	908 1587	14.0 (22.8±2.8) 31.5 10.0 (13.6±0.8) 17.2	7.0 (7.5±2.1) 8.9 5.0 (6.5±1.1) 8.0	130 227	12.5 12.5	Absent LCT
<i>Trichosanthes cucumerina</i> (Ad) (Ab)	Cur Und	Irr Irr	12.5 (21.0±3.0) 30.0 28.8 (45.1±4.2) 62.0	10.5 (20.0±2.1) 28.3 18.5 (29.0±3.2) 38.5	2381 765	12.5 (20.3±1.8) 28.0	7.0 (9.8±2.1) 12.5	397	14.3	LCT LCT, MCT
	Und	Irr	20.0 (43.0±2.2) 65.4	10.0 (14.0±1.6) 18.0	1661	15.0 (21.8±1.8) 28.7	3.0 (4.1±0.7) 5.3	415	20	LCT, MCT

Notes: Ab, abaxial surface; Ad, adaxial surface; Cur, curved; Cur-und, curved-undulate; Irr, irregular; LCT, long conical trichomes; MCT, multicellular conical trichomes; Pol, polygonal; SCT, short conical trichomes; Str, straight.

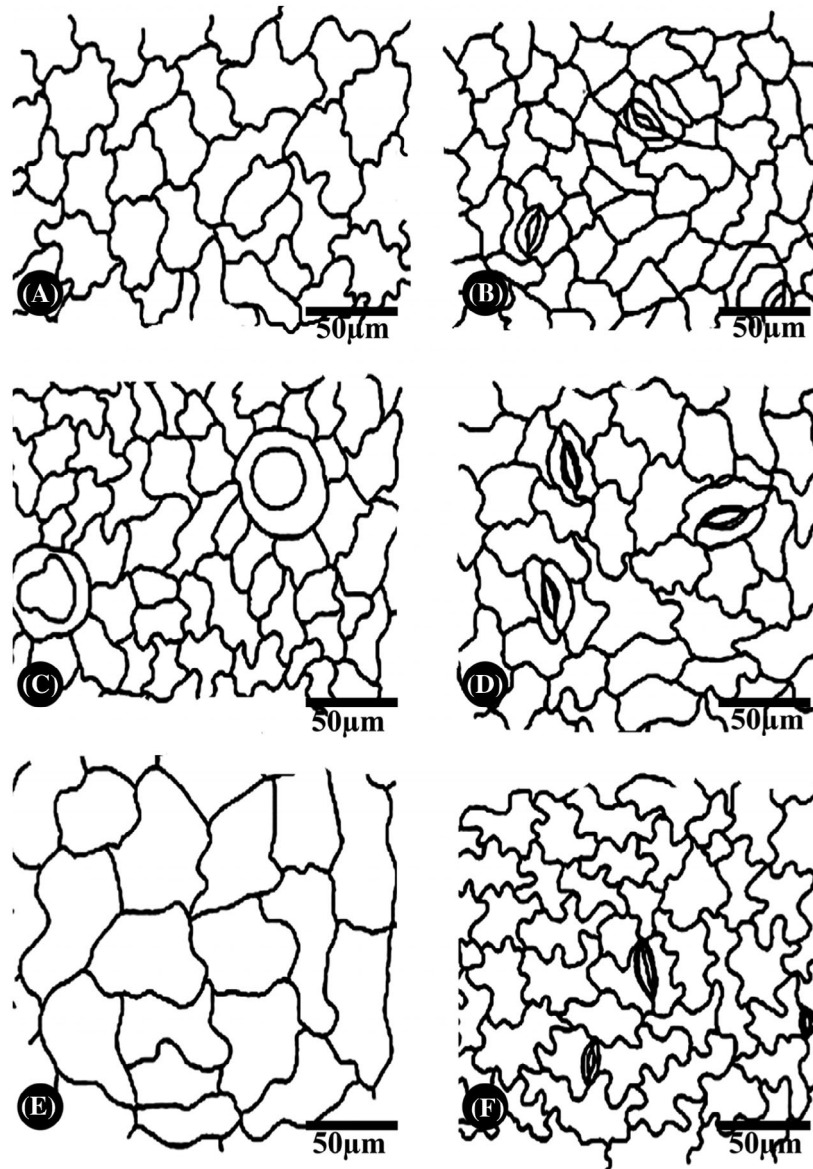


Figure 2. Leaf epidermal characters of West African species of *Momordica*. (A, C, E) Adaxial surfaces. (B, D, F) Abaxial surfaces. (A, B) *Momordica cissoides*; (C, D) *Momordica foetida*; (E, F) *Momordica multiflora*.

on both surfaces of *T. cucumerina* (Figure 3D, E; Table 1) or straight on the adaxial surface and curved on the other layer in *Luffa aegyptiaca* Mill. (Figure 3A, B; Table 1). The cell shape is irregular on both surfaces of the epidermis except in *L. aegyptiaca*, where the adaxial surface has polygonal epidermal cells (Table 1). Larger cells were recorded in *T. cucumerina* L. than *L. aegyptiaca* (Table 1). Generally, there are more epidermal cells per square millimetre on the abaxial than adaxial surface (Table 1). The leaves of *L. aegyptiaca* are amphistomatic (Figure 3A, B; Table 1) but they are hypostomatic in *T. cucumerina* (Figure 3E, Table 1). Stomata are larger in *T. cucumerina* than *L. aegyptiaca* (Table 1). Stomatal index varies from 12.5% to 20% between the two

genera. The two species have conical trichomes which may be long (Figures 5I–K, 7H; Table 1) or bent and warty on the surface (Figure 7G) in *L. aegyptiaca*.

In *Momordica*, the tendrils may be laxly or deeply twisted. They may be branched or not branched (Figures 3 and 4; Table 3). When branched, one of the branches is vestigial; it is morphologically different in size and twisting pattern. This condition was recorded in *M. multiflora* (Figure 4G, Table 3) and *M. cabraei* (Figures 3J, 4C, Table 3). In *L. cylindrica*, the tendrils may have up to four branches emanating from the base and they are laxly twisted (Figure 3C). Tendrils of *T. cucumerina* are deeply twisted, having up to three branches (Figure 3F).

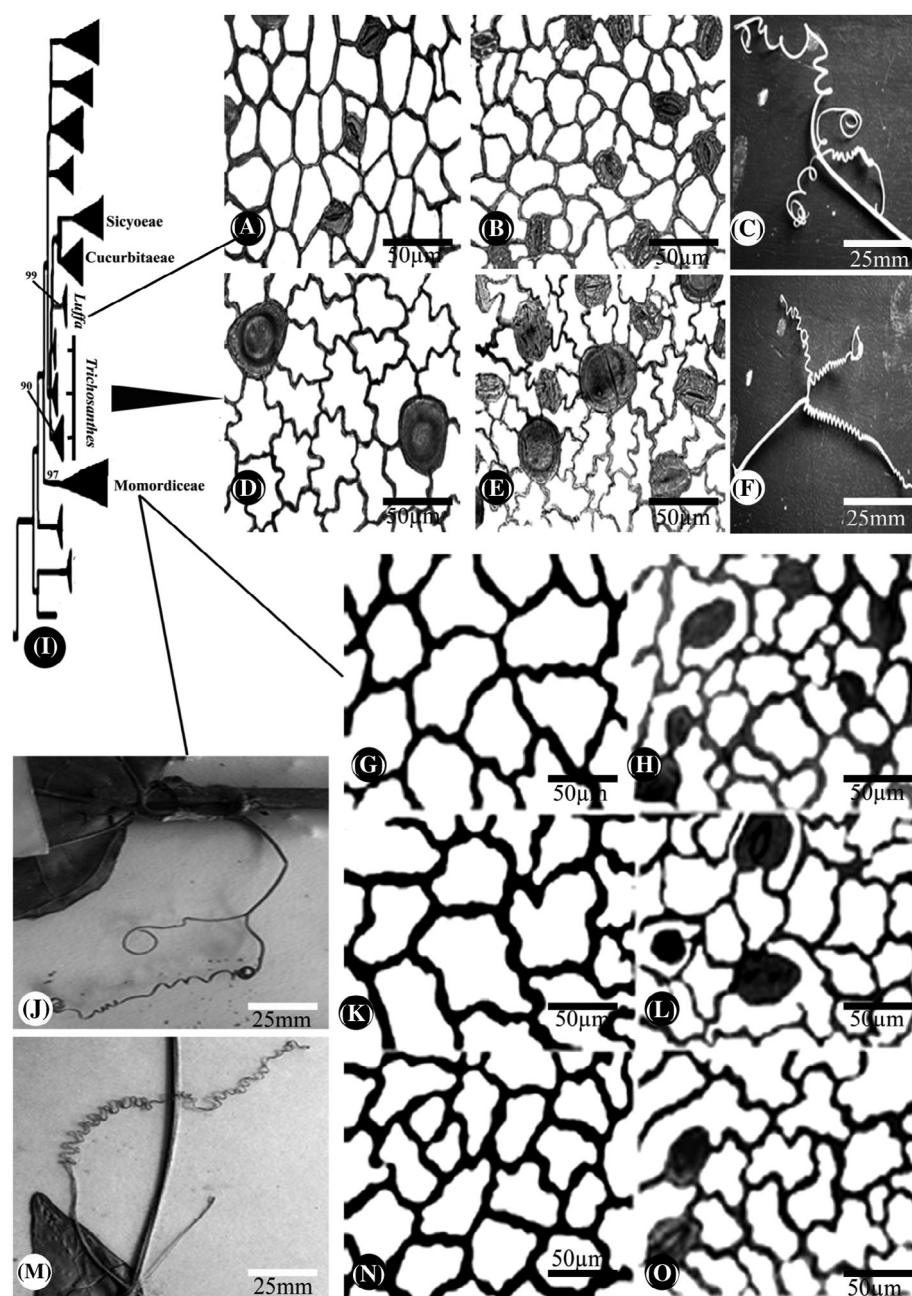


Figure 3. Combined leaf epidermis and tendrils characters correlated on the maximum likelihood phylogenetic tree branches of Schaefer and Renner (2011). (A, D, G, K, N) Adaxial surfaces. (B, E, H, L, O) Abaxial surfaces. (C, F, J, M) Tendrils. (I) Branches of maximum likelihood phylogenetic tree. (A–C) *Loffa aegyptiaca*, (D–F) *Trichosanthes cucumerina*, (G, H) *Momordica cissoides*; (K, L) *Momordica foetida*; (N, O) *Momordica multiflora*. (J, M) Types of tendrils found in *Momordica* (J) *Momordica cabraei*, (M) *Momordica angustisepala*.

Discussion

Some taxonomically useful epidermal features were recorded in the genus *Momordica*. The characters that are good for species diagnosis include amphistomatic leaves found only in *M. balsamina*. This observation opposes the report of Metcalfe and Chalk (1950, 1979), where stomata are reportedly confined to the abaxial surface in the genus. Other diagnostic characters are polygonal cells on the adaxial surface of *M. cabraei*, pubescent adaxial and abaxial surfaces in *M. angus-*

tisepala and, glabrous adaxial and abaxial surfaces in *M. multiflora*. Epidermal features that are useful for generic discrimination include irregular cell shape, anomocytic stomata, inconspicuous periclinal walls on the abaxial surface, epicuticular wax that covers epidermis like a sheet, rough cuticular surface on the adaxial surface and stomatal index that is not more than 20%. Although these features are known to be influenced by some environmental factors, their value in making taxonomic decisions cannot be under-estimated (Davis and

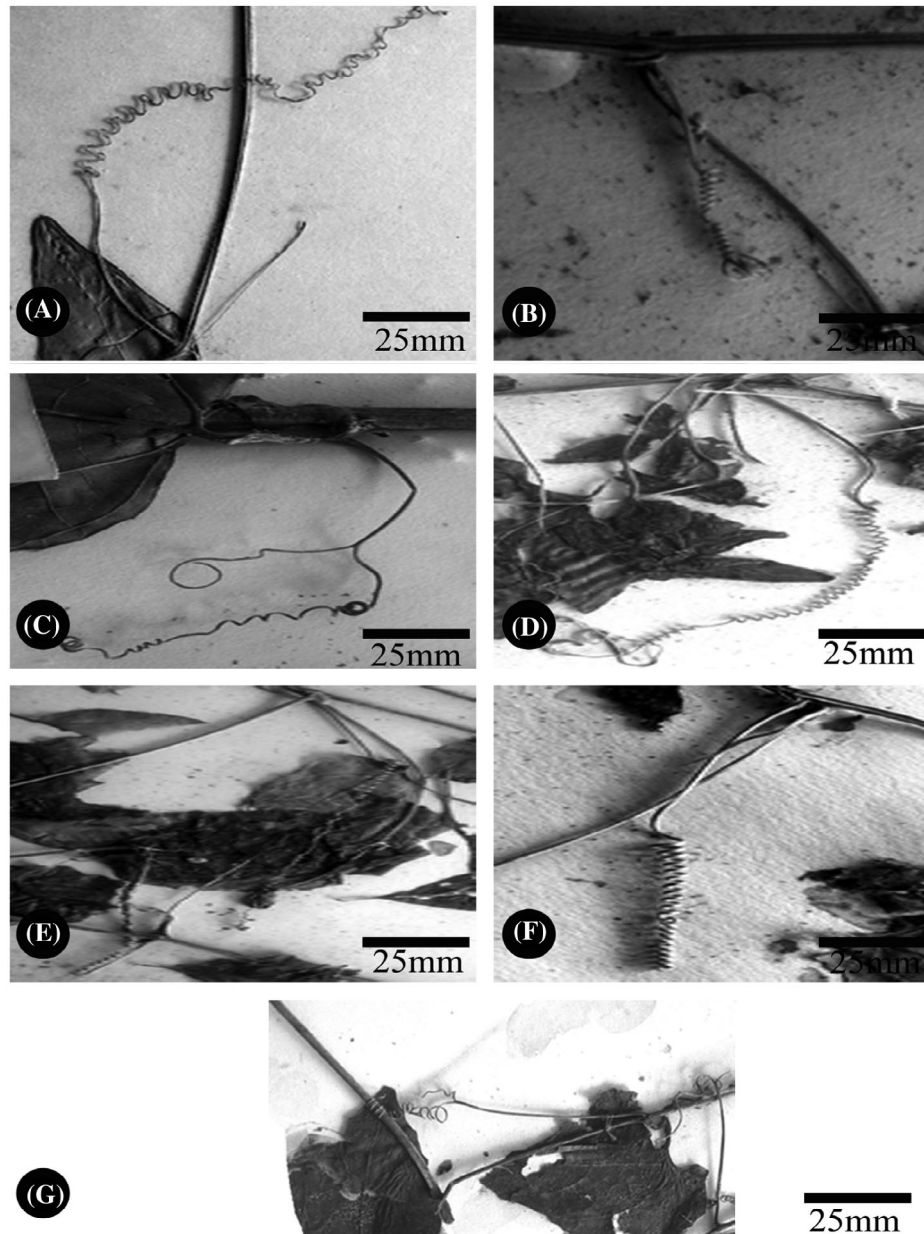


Figure 4. Tendrils of the West African *Momordica* species showing branching patterns. (A, B, D–F) show tendrils without branches. (C, G) show tendrils with branches. (A) *Momordica angustisepala*, (B) *Momordica balsamina*, (C) *Momordica cabraei*, (D) *Momordica charantia*, (E) *Momordica cissoides*, (F) *Momordica foetida*, (G) *Momordica multiflora*.

Heywood 1963; Stace 1965; Inamdar and Gangadhara 1977; Ali and Al-Hemaid 2011). Similarly, the branching and twisting patterns of tendrils may also offer some assistance to generic delimitation. In *Momordica*, tendrils are either intact (i.e. without branching) or bifurcated at the middle. Twisting may be deep or lax in the genus. In *Luffa* and *Trichosanthes*, branching of tendrils is basal but twisting pattern is as found in *Momordica* – deep or lax. Tendrils are known to offer some taxonomically useful characters among arid cucurbitaceous plants (Omar 2009).

In Cucurbitaceae, tendrils are either simple or variously branched. According to Sawhney (1920), they are

thigmotropic structures, which may develop from extra-axillary or any part or all of a stem, leaf or petiole; and they receive their vascular supply from leaf trace and cauline bundles. A combination of both epidermal and tendril characters also supports the sections recognized in *Momordica* by Schaefer and Renner (2011). Section *Momordica* is heterogeneous; it is represented in the study by *M. balsamina*, *M. charantia* and *M. foetida* unlike in the other four sections where one species is represented. *Momordica balsamina* have amphistomatic leaves unlike the other species, which are hypostomatic, the usual type in the genus (Metcalf and Chalk 1950, 1979). *Momordica balsamina* occurs chiefly in the dry

Table 2. Qualitative leaf cuticular characteristics of the West African species of *Momordica*, *Luffa* and *Trichosanthes*.

Species	Periclinal wall pattern	Nature of epicuticular wax	Stomatal orientation	Cuticular striations	Peristomatal rim	Cuticular surface
<i>M. angustisepala</i> Ad.	Conspicuous	Clustered	No stoma	Absent	No stoma	Rough
Ab.	Inconspicuous	Flaky	Superficial	Absent	Wide	Rough
<i>M. balsamina</i> Ad.	Inconspicuous	Thin sheet	Sunken	Absent	Narrow	Rough
Ab.	Inconspicuous	Thin sheet	Sunken	Absent	Narrow	Rough
<i>M. cabraei</i> Ad.	Conspicuous	Thin sheet	No stoma	-	No stoma	Rough
Ab.	Inconspicuous	Thin sheet	Superficial	Present to Absent	Narrow to wide	Smooth
<i>M. charantia</i> Ad.	Conspicuous	Thin sheet	No stoma	Absent	No stoma	Rough
Ab.	Conspicuous	Thin sheet	Sunken	Absent	Narrow	Rough
<i>M. cissoides</i> Ad.	Conspicuous	Thin sheet	No stoma	Absent	No stoma	Smooth
Ab.	Inconspicuous	Thin sheet	Sunken	Absent	Narrow	Smooth
<i>M. foetida</i> Ad.	Inconspicuous	Thin sheet	No stoma	Absent	No stoma	Rough
Ab.	Inconspicuous	Thin sheet	Superficial	Absent	Narrow	Rough
<i>M. multiflora</i> Ad.	Conspicuous	Thin sheet	No stoma	Present	No stoma	Rough
Ab.	Inconspicuous	Thin sheet	Superficial	Present	Wide	Rough
<i>L. aegyptiaca</i> Ad	Inconspicuous	Thin sheet	No stoma	Absent	No stoma	Rough
Ab	NA	NA	NA	NA	NA	NA
<i>T. cucumerina</i> Ad	Inconspicuous	Thin sheet	No stoma	Absent	No stoma	Rough
Ab	NA	NA	NA	NA	NA	NA

Notes: Ab, abaxial surface; Ad, adaxial surface; LCU, long, conical and unicellular; NA, not available; SCG, short curved and glandular; SCT, short conical trichomes. Cuticular data on *Luffa* and *Trichosanthes* were obtained from Ali and Al-Hemaid (2011).

areas of the tropics, found in northern Nigeria and Sudan; and arid areas of India (Hutchinson and Dalziel 1958; Bharathi et al. 2011). Other species in the section occur in moist areas. Distribution of stomata on leaf surfaces is under the influence of environmental factors, yet features of the stomata can still offer useful taxonomic information because their expression is under a strong genetic control (Davis and Heywood 1963; Stace 1965).

Furthermore, *M. balsamina* can be separated from other species by its bracts that closely subtend the flowers and possession of coarsely lobulate–dentate leaves (Hutchinson and Dalziel 1958). Whether or not to retain *M. balsamina* in this section is a future question that would have to be addressed with additional data from gross morphology, anatomy and molecular studies that will use many taxonomically informative genetic markers. Given that other sections have one species each; their sectional grouping is accepted due to lack of conflicting data. Therefore, this work presents some of the features that are characteristic of sections in *Momordica*.

Luffa and *Trichosanthes* are well supported as separate genera based on the examined leaf epidermal and tendril features. Cystoliths and undulate anticlinal walls found on both surfaces of the epidermis of *T. cucumerina* are unique to the species. *Luffa aegyptiaca* has polygonal cells on the adaxial surface and the leaves are amphistomatic; whereas they are hypostomatic in *T. cucumerina*.

Based on the features studied, *Luffa* is closer to *Momordica* than *Trichosanthes*. *Luffa aegyptiaca* has similar features, such as polygonal cells on the adaxial surface with *M. cabraei* and hypostomatic leaves with

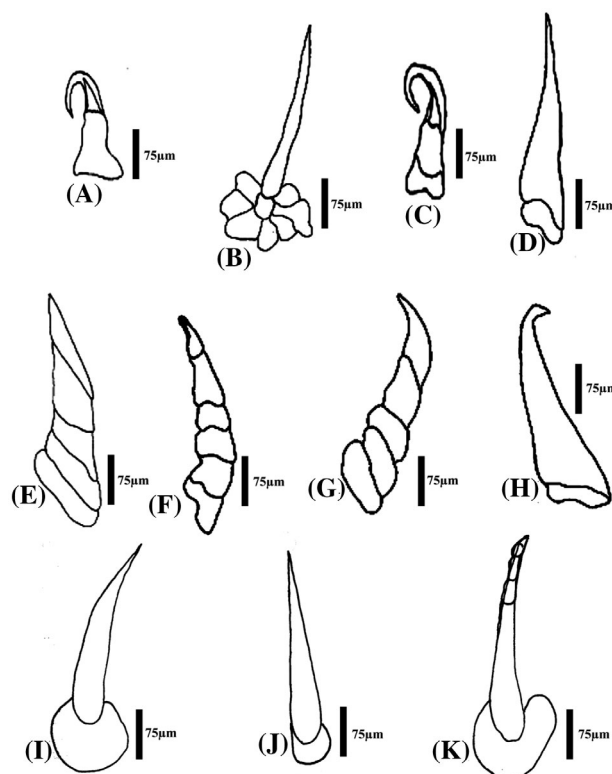


Figure 5. Trichomes types found among the taxa. (A) Abaxial surface and (B) adaxial surface of *Momordica angustisepala*; (C) *Momordica balsamina* (abaxial surface); (D) *Momordica cabraei* (abaxial surface); (E) *Momordica charantia* (adaxial surface); (F) *Momordica cissoides* (adaxial surface); (G, H) *Momordica foetida* (adaxial surface); (I) *Luffa aegyptiaca* (both surfaces); (J, K) *Trichosanthes cucumerina* (Both surfaces).

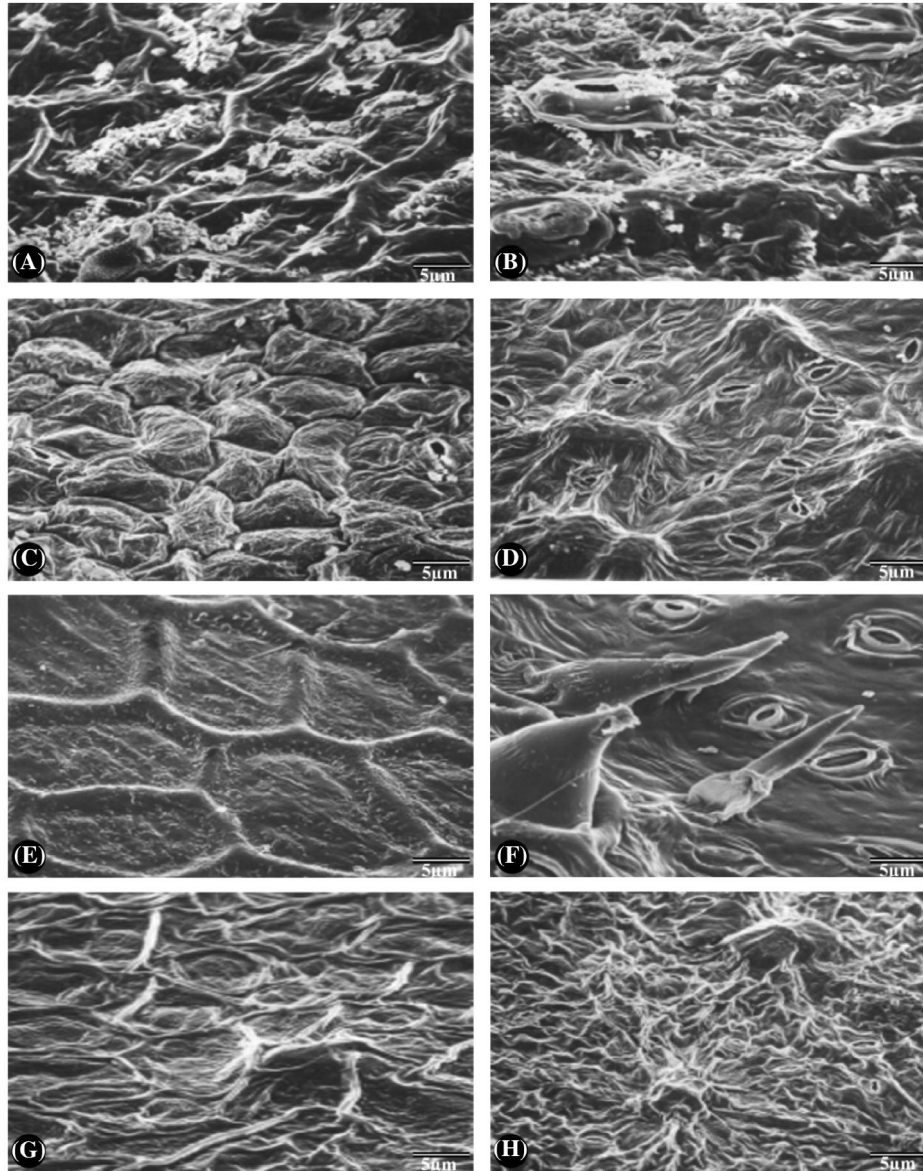


Figure 6. Scanning electron micrographs of leaf epidermis of West African species of *Momordica*. (A, C, E, G) Adaxial surfaces. (B, D, F, H) Abaxial surfaces. (A, B) *Momordica angustisepala*; (C, D) *Momordica balsamina*; (E, F) *Momordica cabraei*; (G, H) *Momordica charantia*.

M. balsamina. But it is different from these species by having a higher number of epidermal cells per square millimetre on both surfaces and higher stomatal index values. It can also be distinguished by the presence of the same type of trichomes: long conical on both surfaces of the epidermis and presence of rough cuticular surface on both surfaces. In addition, tendrils of *Momordica* only divide mid-way if at all; whereas division which may be up to four is basal in *Luffa*. On the other hand, *Luffa* and *Trichosanthes* have tendrils that are branched at the base, three or four branches in *Luffa* and up to three branches in *Trichosanthes*. There are cystoliths on both surfaces of the epidermis of *T. cucumerina* that are lacking in other genera. The leaf epidermis of *Luffa* and *Trichosanthes* shares a suite of

similar characters more than with *Momordica*; e.g. irregular cell shape on the abaxial surface, similar trichome types on both surfaces of the leaf, inconspicuous periclinal walls and rough cuticular surfaces (Ali and Al-Hemaid 2011). Therefore, it is reasonable to conclude that *Momordica* and *Luffa* are distant from each other based on the facts contained herein. In contrast, the closeness of *Trichosanthes* and *Luffa* shown in this work supports the suggestion by Schaefer and Renner (2011) to place them in a single tribe – Sicyoeae – while the differences lend support to the position of Jeffrey (2005) and Kocyan et al. (2007), where the genera are placed in separate tribes. An artificial indented dichotomous key that can be used to delimit the taxa, based on the data reported, is presented below.

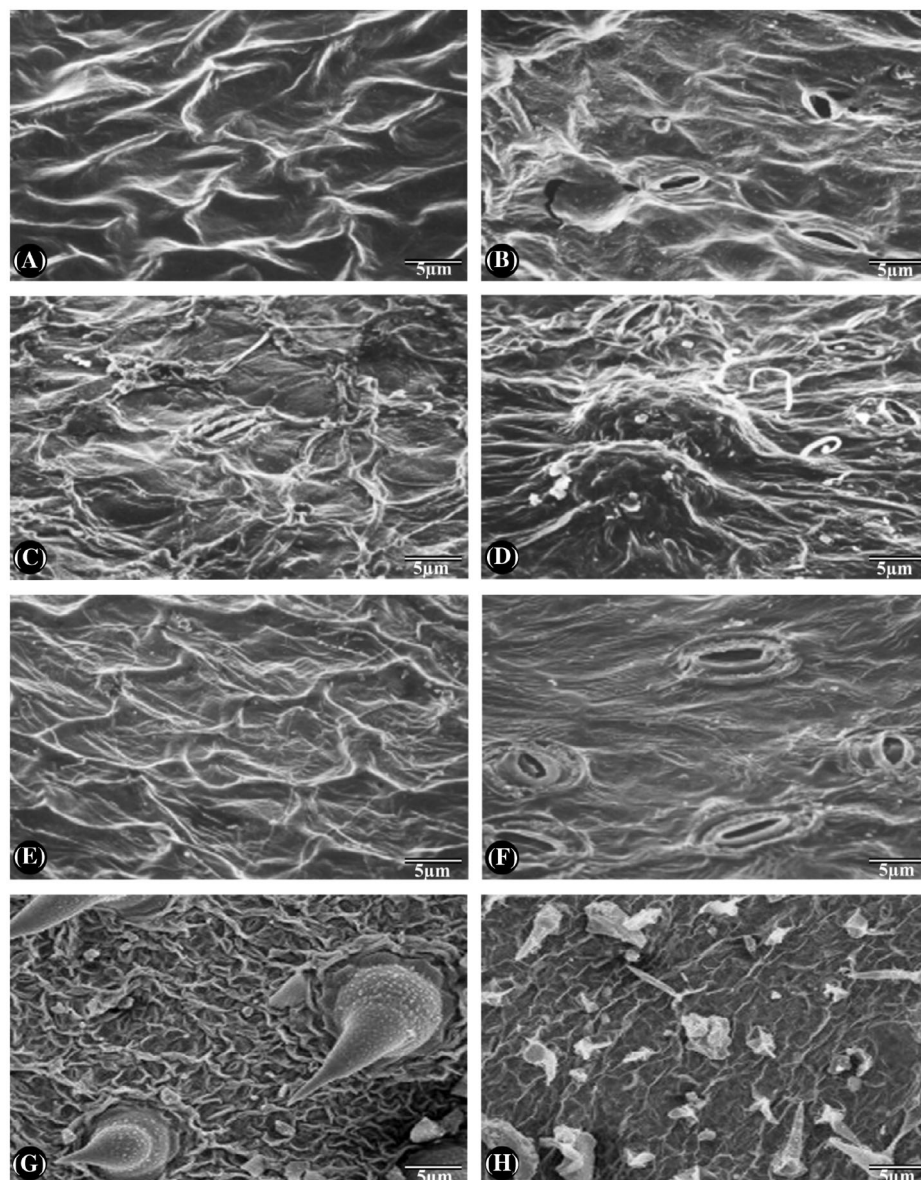


Figure 7. Scanning electron micrographs of leaf epidermis of West African species of *Momordica*, *Lagenaria* and *Trichosanthes*. (A, C, E, G, H) Adaxial surfaces. (B, D, F) Abaxial surfaces. (A, B) *Momordica cissoides*; (C, D) *Momordica foetida*; (E, F) *Momordica multiflora*; (G) *Luffa aegyptiaca*; (H) *Trichosanthes cucumerina*. G and H were obtained from Ali and Al-Hemaid (2011).

1. Tendril branches originating from the base, 2-4 in number.....**Tribe Sicyoeae**
 2. Leaf amphistomatic, cell shape polygonal on the adaxial surface..... *Luffa aegyptiaca*
 2. Leaf hypostomatic, cell shape irregular on the adaxial surface.....*Trichosanthes cucumerina*
 1. Tendril branches arising mid-way, 1-2 in number.....
**Tribe Momordiceae**
 3. Stomata sunken.....4
 4. Leaf amphistomatic.....*M. balsamina*
 4. Leaf hypostomatic.....3
 5. Cuticular surface of epidermis rough on both layers, more cells on the adaxial than abaxi surface.....
*M. charantia*

5. Cuticular surface of epidermis smooth on both layers, more cells on the abaxial than adaxial surface.....
*M. cissoides*
 3. Stomata superficial.....6
 6. Cuticular striations equivocal.....7
 7. Cell shape polygonal on adaxial surface.....*M. cabraei*
 7. Cell shape irregular on adaxial surface.....8
 6. Cuticular striations absent or present.....8
 8. Leaf pubescent.....9
 9. Trichomes present on both surfaces of epidermis.....*M. angustisepala* 9
 9. Trichomes restricted to adaxial surface only..... *M. foetida*
 8. Leaf glabrous.....*M. multiflora*

Table 3. Validation of sectional classification of *Momordica* with some leaf epidermal and tendril characters.

Common features	Section Cissoides	Section Multiflora	Section Angustisepala	Section Momordica	Section Dimorphochlamys
	<i>M. cissoides</i>	<i>M. multiflora</i>	<i>M. angustisepala</i>	<i>M. balsamina</i> <i>M. charantia</i> , <i>M. foetida</i>	<i>M. cabraei</i>
Leaf epidermis	Multicellular conical trichomes, smooth cuticular surface on both sides of the epidermis	Absence of trichomes, presence of cuticular striations on both sides of the epidermis	Trichomes present on both sides of the epidermis	Cell shape is irregular on both sides of the epidermis; more cells are on the adaxial epidermis than the abaxial surface; cuticular surface is rough; narrow peristomatal rim Unlike other species, <i>M. balsamina</i> is amphistomatic	Cell shape is polygonal on the adaxial surface of epidermis; more cells on the abaxial surface than adaxial side of the epidermis; peristomatal rim narrow to wide on the abaxial surface
Tendrils	Lax twisting, no branch	Lax twisting, two branches	Lax twisting, no branch	Deep twisting, no branch	Lax twisting, two branches

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Appendix I. Exsiccate data of the plants samples examined for the study.

Species	Name of collector	Date of collection	Herbarium No.
<i>M. angustisepala</i> Harms	<i>M. G. Latilo</i>	15. 7.1959	FHI 43453
	"	April, 1971	FHI 64749
	<i>Jones and Stapfield</i>	10.7.46	FHI 18837
	<i>C. F. A. Onochie</i>	22.9.44	FHI 7699
	"	20.11.58	FHI 35230
	"	26.4.47	FHI 21986
	<i>L. G. Chizea</i>	1.8.50	FHI 23997
	<i>J. A. Emwiogbon</i>	28.3.69	FHI 23997
	<i>J. F. Redhead</i>	10.8.64	FHI 55957
	<i>R. W. J. Keay</i>	4.7.58	FHI 37672
	"	7.4.45	FHI 8286
	<i>J. B. Hall</i>	22.5.71	FHI 69618
	<i>J. Olorunfemi</i>	7.6.58	FHI 38051
	<i>Kadiri A. B.</i>	27.10.06	LUH 584
	<i>C. F. A. Onochie</i>	18. vi. 1947	FHI 23355
<i>M. balsamina</i> L.	<i>M. C. Clintock</i>	7.12.54	FHI 38960
	<i>P. N. Leeuw., Tuley and Oche</i>	20.3.67	FHI 17909
<i>M. cabraei</i> (Cogn.) C. Jeffrey	<i>C. F. A. Onochie</i>	7. 3.1957	FHI 36482
	<i>R. W. J. Keay and A. P. D. Jones</i>	28.10.45	FHI 13778
	<i>Ogan</i>	22.4.66	FHI 58290
	<i>R. Germain</i>	30.11.48	FHI 18577
	<i>J. Redhead</i>	3.12.62	FHI 45610
	<i>J. Redhead</i>	2.3.63	FHI 47570
	<i>M. G. Latilo</i>	18.12.59	FHI 43812
	<i>A. Binuyo and H. D. Onyeachusim</i>	10.2.66	FHI 57885
	<i>R. W. J. Keay and R. D. Meikle</i>	18.2.50	FHI 25664
	<i>B. O. Daramola</i>	1.2.78	FHI 85204
	<i>J. Olorunfemi</i>	3.1.78	FHI 91922
	<i>T. K. Odewo et al.</i>	8.8.84	FHI 101725
	<i>D. P. Stanfield</i>	21.2.62	FHI 45610
	<i>C. Ayelotan</i>	18. 2. 2008	FHI 108020
	<i>Balogun Akeem</i>	7.2.2004	FHI 106632
<i>M. charantia</i> L.	<i>Adebambo A. A.</i>	25.10.2007	FHI 108176
	<i>Oguntayo and Adejinmi</i>	9.6.77	FHI 83680
	<i>J. Redhead</i>	20.11.62	FHI 46390
	<i>Thomas R. H</i>	17.10.49	FHI 27022
	"	28.10.49	FHI 27037
	<i>C. F. A. Onochie</i>	13.10.55	FHI 34910
	"	June 1955	FHI 38575
	<i>C. F. A. Onochie, Ekwuno and others</i>	15.8.78	FHI 87638
	<i>Tekobo A. M.</i>	8.12.2003	FHI 106489
	<i>Emwiogbon J. A</i>	20.1.65	FHI 55864
	"	18.7.67	FHI 60083
	"	28.6.67	FHI 60113
	"	17.4.72	FHI 33139
	"	21.11.59	FHI 43858
	"	25.8.67	FHI 60107
	<i>Emwiogbon J. A and Osanyinlusi</i>	15.10.77	FHI 87360
	<i>H. J. Killick</i>	Sept. 1955	FHI 39242
	<i>D. P. Stanfield</i>	12.5.60	FHI 52405
	<i>D. W. Lawlor and Hall J. B.</i>	15.8.62	FHI 18456
	<i>Z. O. Gbile</i>	20.4.78	FHI 84263
	<i>J. C. Okafor and J. A. Emwiogbon</i>	7.7.66	FHI 40969
	<i>D. Gledhill</i>	9.5.66	FHI 14305
	<i>G. J. H. Amshoff</i>	22.4.59	FHI 51156
	<i>J. Olorunfemi and Oguntayo</i>	Nov. 1977	FHI 86704
	<i>Olorunfemi and others</i>	19.9.78	FHI 88308
	"	31.10.81	FHI 96535
	<i>J. P. M. Brenan</i>	16.2.48	FHI 39376
	<i>J. Lowe</i>	30.5.25	FHI 77535
	<i>Z. O. Gbile and Oni</i>	18.1.77	FHI 79050
	<i>J. K. Morton</i>	7.11.52	FHI 48659
	<i>A. P. D. Jones</i>	28.5.46	FHI 17333

(Continued)

Appendix 1. (Continued).

Species	Name of collector	Date of collection	Herbarium No.
<i>M. G. Latilo</i>	<i>M. G. Latilo</i>	27.5.69	FHI 62572
	"	17.11.68	FHI 62292
	<i>P. Wit and B. O. Daramola</i>	28.12.71	FHI 64875
	<i>Amachi</i>	July 1958	FHI 3288
	<i>J. Redhead</i>	13.11.62	FHI 46387
	<i>G. Ibhanebhor</i>	21.6.82	FHI 95397
	<i>P. P. C. van Meer</i>	24.8.65	FHI 92351
	<i>Ariwaodo, J. A.</i>	17.5.83	FHI 10042
	<i>A. J. M. Leeuwenberg</i>	10.3.65	FHI 68618
	<i>Adebusuyi and Emwiogbon</i>	24.8.63	FHI 45927
	<i>J. Redhead</i>	28.7.43	FHI 4127
	"	24.10.52	FHI 48670
	<i>Odewo, Ibhanebhor and Oguntayo</i>	9.7.79	FHI 90843
	<i>Daramola and Osanyinlusi</i>	23.4.79	FHI 90209
	<i>L. Lowe</i>	29.5.68	FHI 10781
	<i>B. O. daramola and Kadiri A. B.</i>	2.12.10	LUH 3291
	<i>S. Tamajong</i>	28. iv. 1946	FHI 16925
	<i>Ekwuno et al.</i>	15.9.81	FHI 95973
	<i>J. K. Morton</i>	7.11.52	FHI 48658
	<i>Eimujeze and Oguntayo</i>	28.5.74	FHI 72598
<i>M. cissoides</i> Planch. ex Benth.	<i>Magbagbeola and Ariwaodo</i>	26.6.81	FHI 94733
	<i>J. K. Morton</i>	24. 10.1952	FHI 48668
	<i>J. A Emwiogbon</i>	14.6.83	FHI 94993
	"	7.7.66	FHI 60210
	<i>J. Olorunfemi</i>	12.10.59	FHI 43702
	<i>P. Witt</i>	25.8.71	FHI 26866
	<i>J. Lowe</i>	31.10.73	FHI 69287
	<i>J. J. Bos</i>	31.3.70	FHI 91488
	<i>J.K. Morton</i>	14.2.64	FHI 48668
	<i>Dundas</i>	10.3.47	FHI 20373
	<i>Hall H. R.</i>	11.10.49	FHI 27014
	<i>A. J. M. Leeuwenberg</i>	13.10.65	FHI 69463
	<i>Gbile, Wit and Daramola</i>	11.5.72	FHI 65588
	<i>J. Redhead</i>	13.11.62	FHI 46388
	<i>Kadiri A. B.</i>	26.7.12	LUH 5382
	"	4.8.2007	LUH 603
	"	29.6.09	LUH 225
	<i>C. F. A. Onochie</i>	26. vi.1957	FHI 31240
	"	20.5.57	FHI 38776
<i>M. foetida</i> Schumach.	<i>A. J. M. Leeuwenberg</i>	3.7.65	FHI 69498
	<i>Hall and Agyakwa</i>	27.4.68	FHI 23612
	<i>John Tangbo</i>	23.9.76	FHI 94992
	<i>J. J. Bos</i>	7.7.70	FHI 97428
	<i>Nditaph</i>	30.11.59	FHI 50292
	<i>A. P. D. Jones and R. W. J. Keay</i>	9.10.45	FHI 13718
	<i>M. G. Latilo</i>	18.10.59	FHI 43482
	<i>Ghesquire, J</i>	Sept. 1937	FHI 19207
	<i>J. K. Adebusuyi</i>	22.6.62	FHI 45909
	<i>Ogu</i>	24.8.60	FHI 51283
	<i>Dundas</i>	30.12.45	FHI 13922
	<i>Emwiogbon and Osanyinlusi</i>	4.10.77	FHI 87029
	"	4.10.77	FHI 87030
	"	8.10.77	FHI 87141
	<i>Z. O.Gbile and B. O. Daramola</i>	31.3.70	FHI 62854
	<i>Z. O. Gbile</i>	20.7.70	FHI 67454
	<i>Ariwaodo, J. A.</i>	29.6.83	FHI 101882
	<i>E. E. Zamierowskii</i>	12.8.65	FHI 57568
	<i>J. F. Redhead</i>	4.11.64	FHI 5617
	<i>Eimunjeze V. E and Binuyo A.</i>	28.7.67	FHI 60599
<i>M. multiflora</i> Hook.f.	<i>Olorunfemi and Oguntayo</i>	29.11.77	FHI 86939
	<i>B. O. Daramola and P. Ekwuno</i>	14.7.70	FHI 67313
	<i>Odewo, Ibhanebhor and Oguntayo</i>	16.6.79	FHI 90847
	<i>B. O. Daramola</i>	4.1.78	FHI 84524
	<i>B. O. Daramola</i>	26.7.79	FHI 91196

(Continued)

Appendix 1. (Continued).

Species	Name of collector	Date of collection	Herbarium No.
<i>Luffa aegyptiaca</i>	<i>Gbile, Olorunfemi and Binuyo</i>	7.2.69	FHI 20582
	<i>Oguntayo and Adejinmi</i>	21.6.77	FHI 83340
	”	21.6.77	FHI 90766
	<i>T.K. Odewo</i>	19.8.77	FHI 87969
	”	25.8.77	FHI 91038
	<i>Soladoye and Ekwuno</i>	28.10.77	FHI 84073
	<i>Peter and others</i>	25.6.86	FHI 103443
	<i>Oyayomi and Osanyinlusi</i>	21.6.77	FHI 83396
	<i>Anisere A.</i>	27.9.13	LUH 5919
	<i>Lamidi R.</i>	2.8.13	LUH 5995
	<i>Kadiri A. B.</i>	7.5.2010	LUH 3945
	<i>B. O. Daramola</i>	1.11.2008	LUH 581
	<i>Ogaga A.</i>	12.7.13	LUH 5890
	<i>Tijani G.</i>	21.11.12	LUH 5431
	<i>Anigbogu O. J</i>	2.2.07	LUH 1682
	<i>Jaboro E.</i>		LUH 3034
	<i>Kehinde O.</i>		LUH 582
	<i>Kadiri A. B.</i>	13.12.14	LUH 6354
	”	15.12.14	LUH 6355
<i>Trichosanthes cucumerina</i>	<i>Olowokudejo J. D.</i>	19.11.2009	LUH 6357
	<i>Kadiri A. B.</i>	5.8.07	LUH 710
	”	14.12.09	LUH 2053
	”	9.3.10	LUH 1725
	<i>Azeta O.</i>	10.10.14	LUH 6257
	<i>Kadiri A. B.</i>	18.11.14	LUH 6356