

# Morphological and anatomical characters of the spermoderm of certain taxa of the tribe Solaneae (Solanaceae)

Abd El-Salam Al-Nowaihi\*

and

Magdy M. Mourad

Botany Department, Faculty of Science,  
Ain Shams university,  
Cairo, Egypt

\* E-mail: abdel salamalnowaihi@hotmail.com

Al-Nowaihi A. S. and Mourad M. M. 1999. Morphological and anatomical characters of the spermoderm of certain taxa of the tribe Solaneae (Solanaceae). *Taekholmia* **19** (2): 157-181.

The morphological and anatomical characters of the spermoderm of 49 native and foreign taxa in Wettstein's tribe Solaneae were investigated for their delimitation as well as for a speculation of their phylogenetic status. The observations culminated into the suggestion of an identificatory key. Taxonomic changes including transference (re-allocation) and addition were done for some taxa. Nomenclatural amendments for some other taxa were suggested and a new species, *Atropa lutea*, has been reached at. The phylogenetic status of the studied taxa was speculated relying on the number of the spermoderm layers. Multi-layered spermoderm was considered less advanced than the few-layered one.

**Key words:** Solanaceae, Solaneae, spermoderm anatomy, spermoderm morphology.

## Introduction

Only over the latest few years have seed data been progressively studied by SEM for finer details of the surface micro-characters. Together with macro-morphology and seed-coat anatomy all proved their applicability in the interpretation of several taxonomic and phylogenetic queries. To cite but a few literature, one can refer to the work of Wojciechowska (1972), Dilcher (1974), Gunn and Gaffney (1974), Henderson (1974), Corner (1976), Sharma *et al.*, (1977), Whalen (1979 a, b), Wilkinson (1980), Barthlott (1981, 1984), Edmonds (1983), Farooqui (1983), Farooqui and Bahadur (1984, 1985), and Preisner (1985).

As regards the **Solanaceae**, most of the earlier anatomical investigations on the testa layers and/or its exomorphic peculiarities were investigated by LM (West, 1866; Souégés, 1907; Dnyansagar and Cooper, 1960; Czaja, 1963; Saxena and Singh, 1969; Corner, 1976; Rick, 1978; and several others). Although these studies gave valuable information on the subject yet, and as Jha and Pandey (1989) pointed out, few taxonomists had investigated such characters by SEM. Furthermore, and so far as the present authors are aware no attention has been previously paid to the anatomical characters of the spermoderm as being delimitative. With this in mind, this work was undertaken for more

---

Received 30 June 1999. Revision accepted 27 November 1999.

accurate identification of certain taxa of the tribe **Solaneae** as well as for a speculation of their phylogenetic status.

### ***Material and methods***

Our material represents 49 native and foreign taxa belonging to Wettstein's tribe Solaneae (Table 1). The general features of the spermoderm were studied by light stereomicroscope and M5 scanning electron microscope Jeol JSM 35 C SEM working at an accelerating voltage of 20 kv. For anatomical investigations the seeds were soaked in water for 12 hrs, embedded in paraffin wax microtomed at 12-15  $\mu$ , dehydrated and stained with safranin and light green according to the conventional methods (Johansen, 1940). Drawings were made at bench level by a Camera Lucida.

### ***Results and discussion***

#### ***A. Macro-features of the Spermoderm*** (Table 1)

So far as the present data are concerned, the seed shape shows consistency at both the infra-specific level (cultivars of both *Capsicum frutescens* and *Lycopersicon esculentum*) and at the interspecific level (*Physalis* spp. and *Withania* spp.). At the generic level the seeds of *Solanum* spp. exhibit wide spectrum of shape, thus Souégés(1907), Wojciechowska (1971-1972) and Gunn and Gaffney (1974) relied on it, with other characters, in the delimitation of some taxa of the **Solanaceae**.

As regards the colour, the seeds exhibit various grades between yellow and brown. Although this character was keyed by some earlier workers for some solanaceous taxa (Isely, 1947; Wojciechowska, 1972 and Whalen, 1979 a, b), yet the present authors tend to insert it among the weak characters because its expression in a floral organ, is governed by i) the availability to the plant of the aluminium ions in the soil, and ii) the pH of cell sap; both determining the phenolic compounds formed. The latter give its various degrees from the beginning of maturation to the complete senescence.

Perhaps the hilar characteristics (Plate 1) are the most impressive of the general features.

In this work two aspects of the hilum are studied; the hilar topography viz. levelling relative to the adjacent epidermal cells and the appearance of the latter, and the hilar aperture.

Four cases of topography and two cases of aperture are recorded.

i) As regards topography:

H<sub>1</sub> = Hilum sunken with the surrounding epidermal cells arched (ridged).

H<sub>2</sub> = Hilum sunken with the surrounding epidermal cells at a level.

H<sub>3</sub> = Hilum elevated with the surrounding epidermal cells at a level.

H<sub>4</sub> = Hilum at a level, ridges lacking.

ii) As regards the aperture it is either rounded or slit-like.

Morphological and anatomical characters of certain taxa of Solanaceae

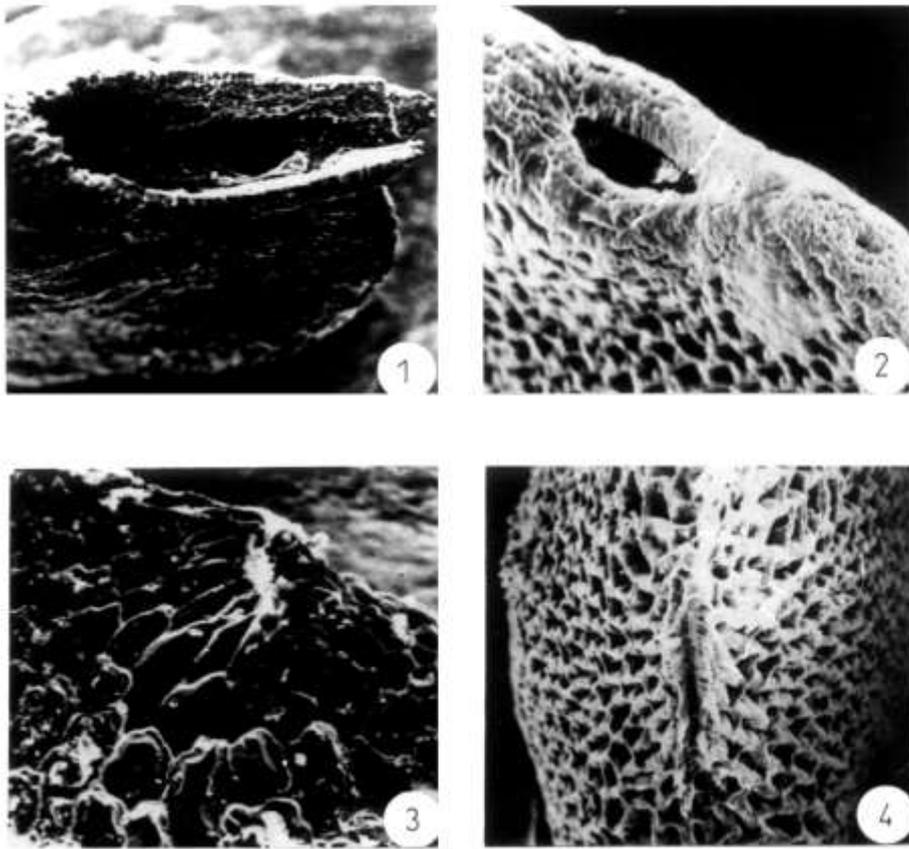


Plate 1- SEM micrographs of hilar shape and topography. Fig.1 *Capsicum frutescens* (H1-type) x50, Fig.2. *Solanum macrocarpon* (H2-type) x200, Fig.3. *Atropa belladonna* (H3-type)x200, Fig.4. *Solanum nigrum* (H4-type)x100.

Table (1) The Morphological Aspects of the Spermoderm

Aspects Taxa	LM		SEM				
	Shape	Colour	Hilum		Surface View of the Spermoderm		
			Shape	Topography	Anticlinal wall Reticulation	Iry wall	Periclinal wall
1- <i>Atropa belladonna</i> L.	Reniform / Subglobose	Brown	Rounded	H <sub>3</sub>	Lobed	+	Gl.deeplyCv
2- <i>A. belladonna</i> var. <i>lutea</i> Doll.	Subglobose	Brown	Rounded	H <sub>4</sub>	Straight	+	Gl.deeplyCv
3- <i>Capsicum annuum</i> L.	Reniform with tapering end	Yellow	Slit Like	H <sub>1</sub>	Lobed-micropap.	-	Gl.-Cv
4- <i>C. frutescens</i> L. cv. California Wonder.	Reniform with tapering end	Yellowish Red	Slit Like	H <sub>1</sub>	Slight-Undulate	-	Gl.-Cv
5- <i>C. frutescens</i> l. cv. Early Jalpino.	Reniform with tapering end	Yellowish Red	Slit Like	H <sub>1</sub>	Slight-Undulate	-	Gl.-Cv
6- <i>C. frutescens</i> L. cv. Elpaso	Reniform with tapering end	Yellowish Red	Slit Like	H <sub>1</sub>	Slight-Undulate	-	Gl.-Cv
7- <i>C. frutescens</i> L. cv. Long Red Cayenne.	Reniform with tapering end	Yellowish Red	Slit Like	H <sub>1</sub>	Slight-Undulate	-	Gl.-Cv
8- <i>Cyphomandra betacea</i> (Cav.) Sendt	Orbicular	Pale Yellow	Rounded	H <sub>2</sub>	Lobed Hairy	-	-
9- <i>Hyoscyamus aureus</i> L.	Oval	Brown	Rounded	H <sub>4</sub>	Lobed	-	Gl.-Cv
10- <i>H. boveanus</i> (Dun.) Asch. & Schweinf.	Oval	Brown	Rounded	H <sub>4</sub>	Lobed	-	Gl.-Cv
11- <i>H. desertorum</i> Asch Ex Bioss.	Oval	Pale Brown	Rounded	H <sub>4</sub>	Lobed	-	Gl.-Cv
12- <i>H. munticus</i> L.	Oval	Brown	Rounded	H <sub>4</sub>	Lobed	-	Gl.-Cv
13- <i>H. niger</i> L.	Oval	Brown	Rounded	H <sub>4</sub>	Slight Undulate	-	Gl.-Cv
14- <i>Lycium chinense</i> Mill.	Orbicular	Yellowish	Rounded	H <sub>4</sub>	Lobed	+	Gl.-deeply Cv
15- <i>L. shawii</i> Roem. Et Sch.	Triangular	Brown	Rounded	H <sub>2</sub>	Lobed-invaginat	-	Gl.-deeply Cv
16- <i>Lycopersicon esculentum</i> Mill.	Oval/tapering end	Straw Yellow	Slit-Like	H <sub>4</sub>	Lobed-Hairy	-	-
17- <i>L. esculentum</i> cv. Bakmor B.	Oval	Pale Rose	Slit-Like	H <sub>4</sub>	Lobed-Hairy	-	-
18- <i>L. esculentum</i> cv. Strain B.	Oval	Pearl Gray	Slit-Like	H <sub>4</sub>	Lobed-Hairy	-	-
19- <i>L. esculentum</i> cv. UC 82.	Oval	Rose	Slit Like	H <sub>4</sub>	Lobed-Hairy	-	-
20- <i>L. esculentum</i> cv. VFN 8.	Oval	Pale Rose	Slit Like	H <sub>4</sub>	Lobed-Hairy	-	-
21- <i>L. esculentum</i> var. <i>pyriforme</i> Alef.	Oval	Tawny Yellow	Slit Like	H <sub>4</sub>	Slight-undulate-Hairy	-	-
22- <i>Mandragora officinarum</i> L.	Reniform	Pale Yellow	Rounded	H <sub>4</sub>	Lobed-micropap.	-	Microret.-Cv
23- <i>Physalis alkekengi</i> L.	Reniform	Yellow	Rounded	H <sub>2</sub>	Lobed	+	Gl.-deeply Cv
24- <i>P. angulata</i> L.	Reniform	Brown	Slit Like	H <sub>4</sub>	Lobed-int.	-	Gl.-deeply Cv
25- <i>P. ixocarpa</i> Brot. ex Hornem.	Reniform	Straw Yellow	Rounded	H <sub>2</sub>	Lobed	+	Gl.-deeply Cv
26- <i>P. peraviana</i> L.	Pear/Reniform	Straw Yellow	Rounded	H <sub>2</sub>	Lobed	+	Gl.-deeply Cv
27- <i>P. prainosa</i> L.	Reniform	Yellow	Rounded	H <sub>2</sub>	Lobed	+	Gl.-deeply Cv
28- <i>Scopalia lurida</i> (Link&Otto.) Dun.	Pear/Reniform	Brown	Rounded	H <sub>4</sub>	Lobed	+	Gl.-deeply Cv
29- <i>S. physaloides</i> Dun in DC.	Pear/Reniform	Yellowish Brown	Rounded	H <sub>4</sub>	Straight	+	Gl.-frat
30- <i>Solanum aviculare</i> G.Farster.	Oval	Pale Brown	Rounded	H <sub>2</sub>	Lobed	-	*
31- <i>S. citrullifolium</i> A.Br.	Oval	Dark Brown	Rounded	H <sub>2</sub>	Lobed	+	Str.deeply Cv
32- <i>S. cornutum</i> Lam.	Reniform	Dark Brown	Rounded	H <sub>2</sub>	Lobed-micropap.	-	Gl.-flat
33- <i>S. dulcamara</i> L.	Oval	Yellow	Slit Like	H <sub>4</sub>	Lobed-micropap.	-	Gl.-Cv
34- <i>S. forsskaolii</i> Ky ex Dun.	Orbicular/deep furrow	Dark Brown	Rounded	H <sub>2</sub>	Straight	-	Gl.-Cv
35- <i>S. incanum</i> L.	Orbicular/Reniform	Dark-Brown	Rounded	H <sub>2</sub>	Lobed-int.	-	*
36- <i>S. indicum</i> var. <i>aldabranse</i> Linn.	Reniform	Yellowish	Slit Like	H <sub>2</sub>	Lobed-micropap.	+	Curled-Cv
37- <i>S. macranthum</i> Dun.	Orbicular	Pale Brown	Rounded	H <sub>2</sub>	Lobed-micropap.	+	Curled Cv
38- <i>S. macrocarpon</i> L.	Pear	Straw Yellow	Rounded	H <sub>2</sub>	Lobed-int.	-	*
39- <i>S. melongena</i> L. cv. Block Beuty.	Orbicular/Reniform	Pale Yellow	Rounded	H <sub>2</sub>	Lobed-int.	-	*

Morphological and anatomical characters of certain taxa of Solanaceae

40- <i>S. melongena</i> cv. Long Purple.	Orbicular/Reniform	Pale Yellow	Rounded	H <sub>2</sub>	Lobed-int.	-	*
41- <i>S. melongena</i> cv. Long White	Orbicular/Reniform	Pale Yellow	Rounded	H <sub>2</sub>	Lobed-int.	-	*
42- <i>S. nigrum</i> L.	Oval	Yellow	Slit Like	H <sub>4</sub>	Lobed-micropap.	-	*
43- <i>S. quitoensis</i> Lam.	Pear/Reniform	Dark Brown	Slit Like	H <sub>2</sub>	Slight-pap.	-	*
44- <i>S. seaforthianum</i> Andrews	Pear/Reniform	Brown	Rounded	H <sub>2</sub>	Slight undulate.- hairy	-	-
45- <i>S. sisymbriifolium</i> Lam.	Orbicular/Reniform	Pale Yellow	Rounded	H <sub>2</sub>	micropap.	-	Curled-Cv
46- <i>S. villosum</i> (L.) Mill.	Oval	Yellow	Slit-Like	H <sub>4</sub>	Lobed-micropap.	-	*
47- <i>S. wrightii</i> Benth.	Oval	Pale Brown	Slit-Like	H <sub>4</sub>	Lobed-invaginate	+	Gl.-flat
48- <i>Withania riebeckii</i> Schweing	Reniform	Brown	Slit-Like	H <sub>2</sub>	Lobed	+	Gl.-deeply Cv
49- <i>W. somnifera</i> (L.) Dun.	Reniform	Pale Brown	Slit-Like	H <sub>2</sub>	Lobed-micropap.	+	Gl.-deeply Cv

+ , Present; - , Absent; Cv , Concave; Gl., Glabrous; int, Intestine ; pap., Papillate ; Str., Striated; \* , Ill – defined.

The hilar characteristics seem to be diagnostic at the generic level (H<sub>4</sub>-*Hyoscyamus*). Martin & Barkley (1961), reached at a similar conclusion where they in addition, took into consideration the seed shape and size. At the infra-specific level (H<sub>1</sub>-*Capsicum* cvs.) the hilar aspect is consistent. In *Solanum*, some species have the H<sub>2</sub>-type and some others have the H<sub>4</sub> - type. The inconsistency in this genus may be one justification to its heterogeneous nature. External evidence for its heterogeneity comes from the numerical study by Al-Nowaihi and Khalifa (1974) on certain members of Solanaceae.

**B- SEM of the spermoderm (Plate 2)**

SEM of the epidermal cells clarifies the texture and reticulation of their anticlinal (radial) walls, the appearance of the outer periclinal walls and the persistency of the primary cell walls.

**i) Reticulation of the anticlinal walls**

The seed surface reticulation is simple with pentagonal-hexagonal epidermal cells having straight anticlinal walls with normal thickening. This pattern is considered here as the basic type and is recorded in *Atropa belladonna* var. *lutea*, *Scopolia physaloides* and *Solanum forsskaolii*. In the remainder taxa, such aspect is disturbed through the elongation to various degrees of the anticlinal walls, their thickening, undulation and the appendages they carry, if any. Taking this into consideration the following cases are recorded for the anticlinal walls: Straight papillate (*Solanum quitoensis*), straight micropapillate (*Solanum sisymbriifolium*), slight undulate either glabrous (species nos. 4, 5, 6, 7 & 13), or hairy (*Lycopersicon esculentum* var. *pyriforme* and *Solanum seaforthianum*), lobed (species nos. 1, 10, 11, 12, 14, 23, 25, 26, 27, 28, 30, 31, & 48), lobed hairy (species nos. 8, 9, 16, 17, 18, 19 & 20), lobed micropapillate (species nos. 3, 22, 32, 33, 36, 37, 42, 46 & 49), lobed with invaginated wall (*Lycium shawii* and *Solanum wrightii*) or lobed with intestine-like wall (species nos. 24, 35, 38, 39, 40 & 41).

**ii) Outer periclinal wall (Table 1)**

In the present work the description is confined to the outer wall since the inner one is best studied through the anatomy of the seed coat. The outer wall is lacking in eight taxa. Dnyansagar and Cooper (1960), Czaja (1963), Saxena and Singh (1969) and Mohan (1970) attributed its absence to the transformation of their corresponding cell contents into mucilage during the formation of 'hairs'. Also Czaja (1963) and Farooqui (1983), stated that the hair-like structures are bands of lignified thickenings on the lateral and basal walls of the outer epidermis.

As regards its shape in surface view, it may be flat (*Scopolia lurida*, and *S. physaloides*; *Solanum cornutum* and *S. wrightii*), concave (species nos..3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13 & 34), concave and curled in *Solanum macranthum* and *S. sisymbriifolium*, concave and microreticulate in *Mandragora officinarum*, deeply concave in species nos..1, 2, 14, 15, 23, 24, 25, 26, 27, 48 & 49, deeply concave and striate in *Solanum citrullifolium* and *S. indicum* var. *aldabranse* and ill-defined in ( species nos..30, 33, 35, 38, 39, 40, 41, 42, 43 & 46).

Morphological and anatomical characters of certain taxa of Solanaceae

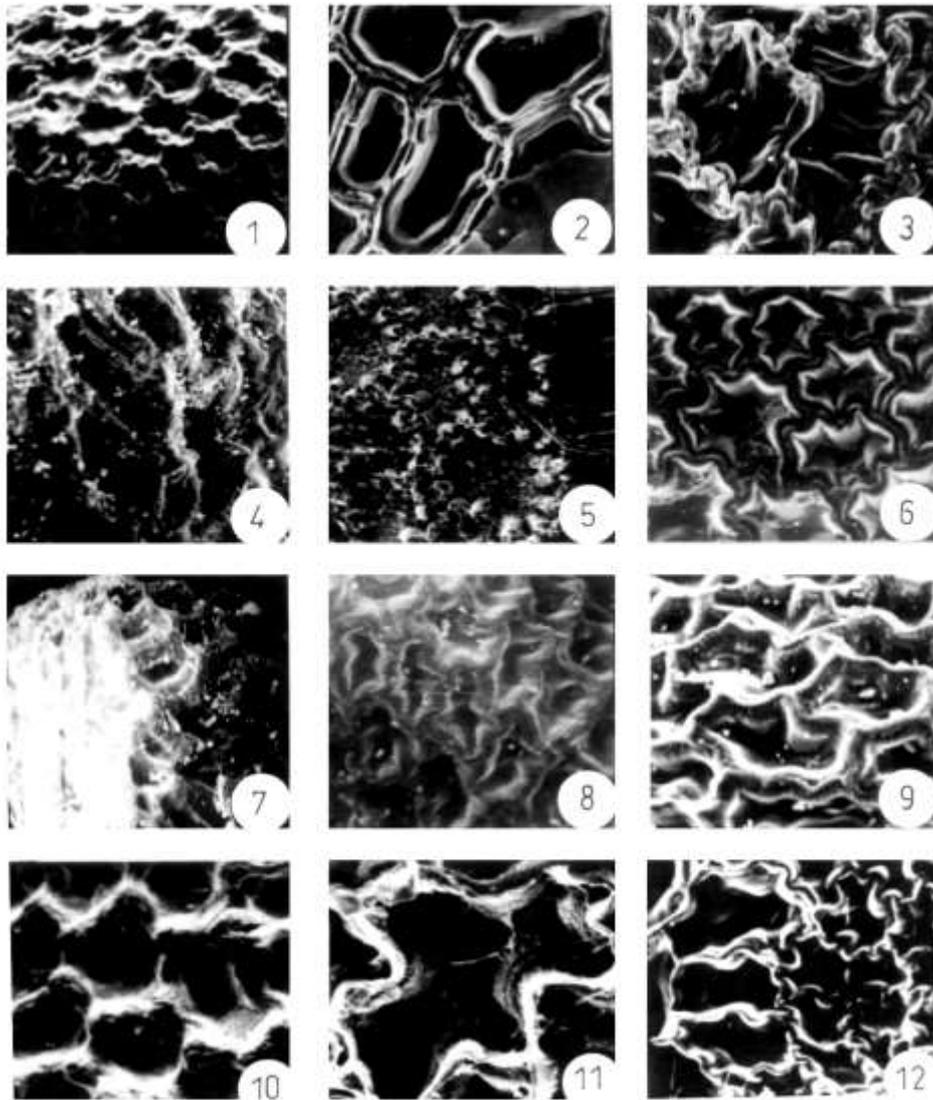


Plate 2- Spermoderm surface under SEM. Fig.1-*Atropa belladonna* x100, Fig.2-*A. belladonna* var. *lutea* x200, Fig.3 *Capsicum annum* x200, Fig.4-*C. frutescens* cvs. X350, Fig.5-*Cyphomandra betacea* x200, Fig.6-*Hyoscyamus aureus* x200, Fig.7-*H. boveanus* x500, Fig.8-*H. desertorum* x200, Fig.9-*H. muticus* x200, Fig.10-*H. niger* x200, Fig.11-*Lycium chinense* x500, Fig.12-*L. shawii* x200

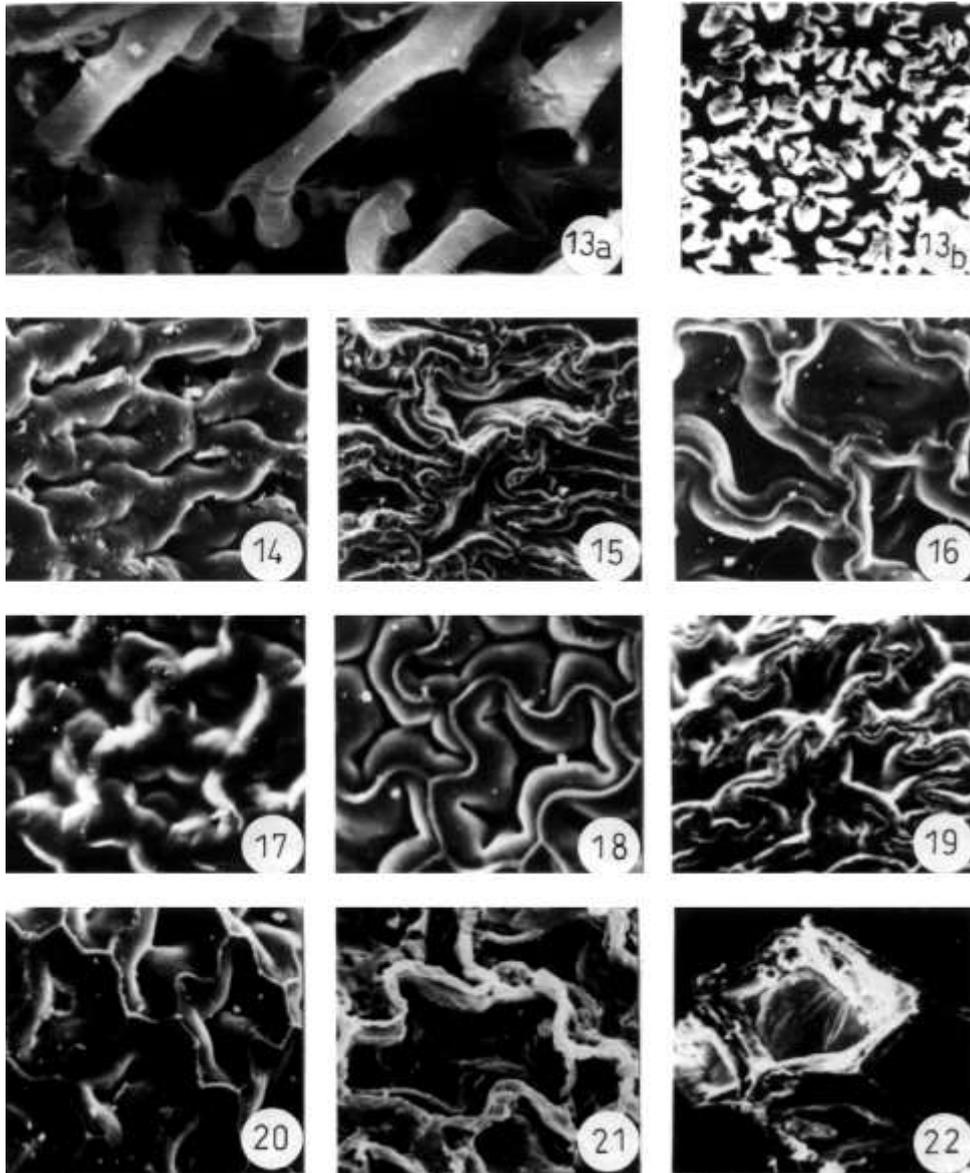


Plate 2- Spermoderm surface under SEM (cont.). Fig.13a- *Lycopersicon esculentum*, a portion of the coat with hairs x500, Fig.13b- The same glabrous x150, Fig.14-*L. esculentum* var. *pyriforme* x500, Fig.15-*Mandragora officinarum* x100, Fig.16-*Physalis alkekengi* x200, Fig.17-*P. angulata* x200, Fig.18-*P. ixocarpa* x200, Fig.19-*P. peruviana* x500, Fig.20-*P. pruinosa* x200, Fig.21- *Scopolia lurida* x 200, Fig.22-*S. physaloides* x 200.

Morphological and anatomical characters of certain taxa of Solanaceae

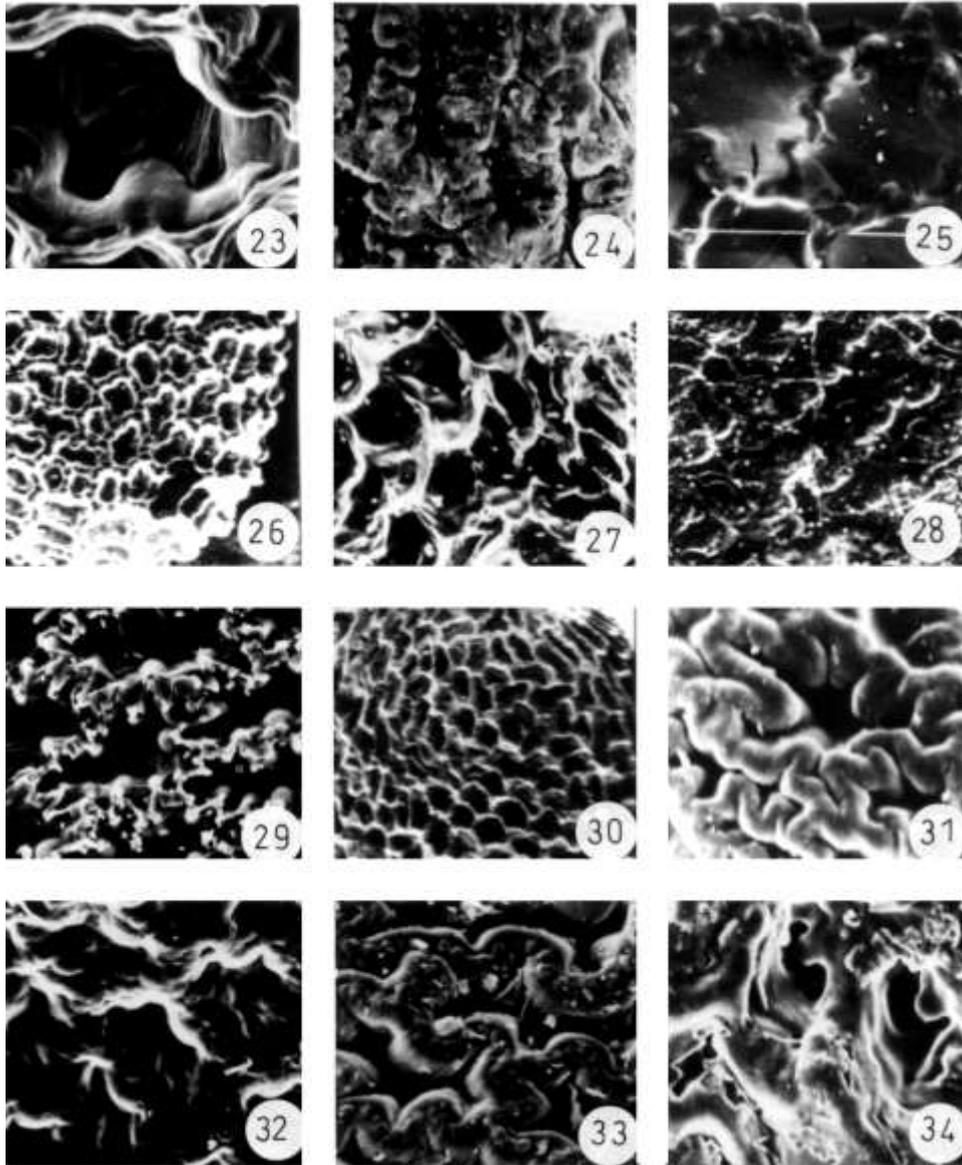


Plate 2- Spermoderm surface under SEM (cont.). Fig.23- *Solanum aviculare* x100, Fig.24-*S. citrullifolium* x500, Fig.25-*S. cornutum* x550, Fig.26-*S. dulcamara* x200, Fig.27-*S. forsskaolii* x200, Fig.28-*S. incanum* x 200, Fig.29- *S. indicum* var. *aldabranse* x500, Fig.30- *S. macranthum* x500, Fig.31-*S. macrocarpon* x200, Fig.32- *S. melongena* cvs. X500, Fig. 33-*S. nigrum* x350, Fig.34- *S. quitoensis* x200.

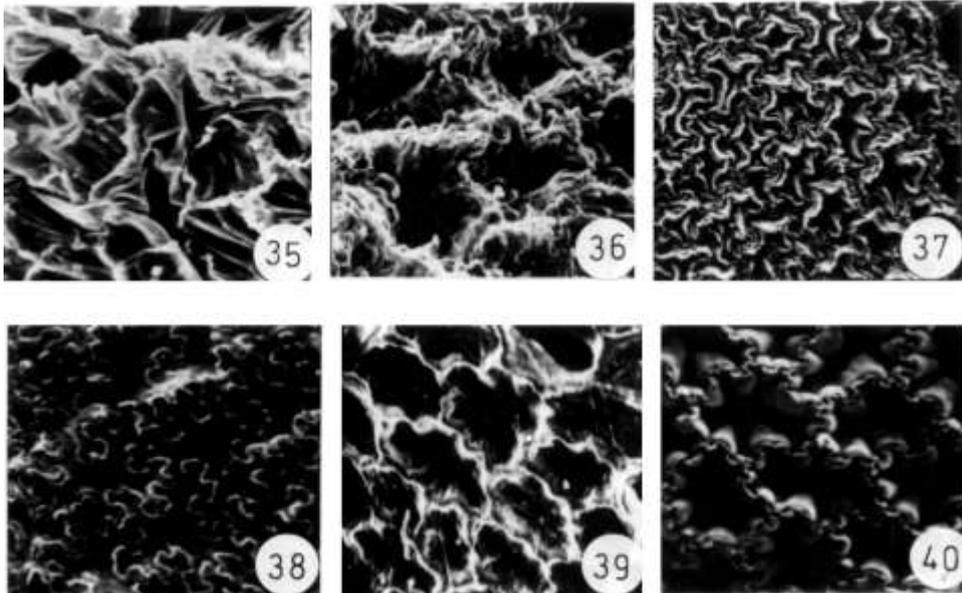


Plate 2- Spermoderm surface under SEM (continued). Fig.35-*S. seaforthianum* x200, Fig.36-*S. sisymbriifolium* x200, Fig.37- *S. villosum* x200, Fig.38-*S. wrightii* x200, Fig.39- *Withania riebeckii* x200, Fig.40- *W. somnifera* x500.

Our observations on the outer periclinal wall seem to be diagnostic at both the generic level (*Physalis*, *Withania*) and the specific level (*Solanum* investigated species.). So far as the available literature is concerned, such characters were not considered by earlier workers.

### *iii) Detection (persistence ) of the primary cell wall*

The primary cell wall is undetectable in 32 taxa, detectable in 15 taxa and more or less detectable in the remaining two taxa. Although, no reference has early been done to this character, yet, in the present work, it is considered to be rather diagnostic (cf.. the proposed artificial key).

### **C. Spermoderm Anatomy (Plate 3)**

Generally, the seed coat is formed of an outer epidermis, an intermediate parenchymatous zone and inner epidermis forming the endothelium. The intermediate zone may be differentiated into an outer parenchymatous layer forming a hypoderm and an inner hyaline layer consists of more or less compressed cells. (Table 2).

In the present study, the endothelium is absent in *Mandragora officinarum*, *Scopolia lurida* and *S. physaloides*. Where the three layers are present, the following variation patterns are recorded:

**1) Outer epidermis** - The shape of the epidermal cells is ill-defined in eight taxa (species nos. 8, 16, 17, 18, 19, 20, 21 & 44). The reasoning put earlier by Hayward (1938), Saxena and Singh (1969) and Mohan (1970) and presented elsewhere in this paper, is that the unclarity is due to the transformation of the outer walls to mucilage during the formation of hairs. In the remainder taxa, the epidermal cells are clearly detected as being radially elongated in 38 taxa, tangentially elongated in eight taxa or tangentially and radially elongated in five taxa. However the different walls of the epidermal cells have the following aspects.

**i) Outer periclinal wall** - Where the outer periclinal wall is persistent and detectable, the following cases are recorded: straight in 24 taxa, straight to concave in six taxa, deeply concave in *Lycium chinense* and *L. shawii*, shallowly-concave in the three cvs. of *Solanum melongena*, concave in five taxa, deeply invaginated with micropapillae in *Solanum sisymbriifolium*. Such variation in straightness and concavity is found to be consistent in *Capsicum*, *Lycium*, *Scopolia* and *Withania*, species, and inconsistent in the investigated *Solanum* species.

**ii) Inner periclinal wall**- These are either thin in *Solanum quitoensis*, thick and even in 25 taxa or comparatively thick with the cell having one-two median papillae in 23 taxa.

**iii) Anticlinal (Radial) wall** -They are thick in all the taxa studied and the thickening differs as regards to whether it is on the entire length of the wall or only on a part of it. The following cases are recorded: the thickening is to the summit of the wall (23 taxa), the thickening is deposited on 3/4 of the wall or the thickening is half-way (five taxa). Edmonds (1983) argued whether the thickening could be taxonomically effective at the generic, sectional and the specific levels, while Souégés (1907) relied upon the shape of thickening. Here, the thickening is consistent at the generic level (*Solanum* excluded) as well as effective as a key character.

**2) Middle layer** -The two zones of the middle layer, viz. the outer parenchymatous and the inner hyaline are recorded in 12 taxa, the outer zone is absent in 13 taxa and both are lacking in the remainder 24 taxa.

**3) Inner epidermis (Endothelium)** - It is ill-defined in *Scopolia lurida*, *S. physaloides* and *Mandragora officinarum.*, it consists of one layer in the other taxa.

Where the endothelium is persistent and detectable, the following aspects are recorded:

**i) Shape**- Either tangentially flattened in eight taxa, rectangular in 30 taxa or squared in eight taxa.

**ii) Thickening**- The endothelial cells are either thin (14 taxa) or thick. Where the thickening is recorded it differs in both universality on all the walls or its restriction to some of them. The following patterns are observed.

1. All walls of the endothelial cells are thick (16 taxa).
2. Only the outer periclinal wall is thin (seven taxa).
3. Only the inner periclinal wall is thin (eight taxa).
4. Only the outer periclinal wall is thick (*Solanum macrocarpon*).

**iii) Pigmentation**-The endothelium is pigmented in 23 taxa, other taxa lack the pigments.

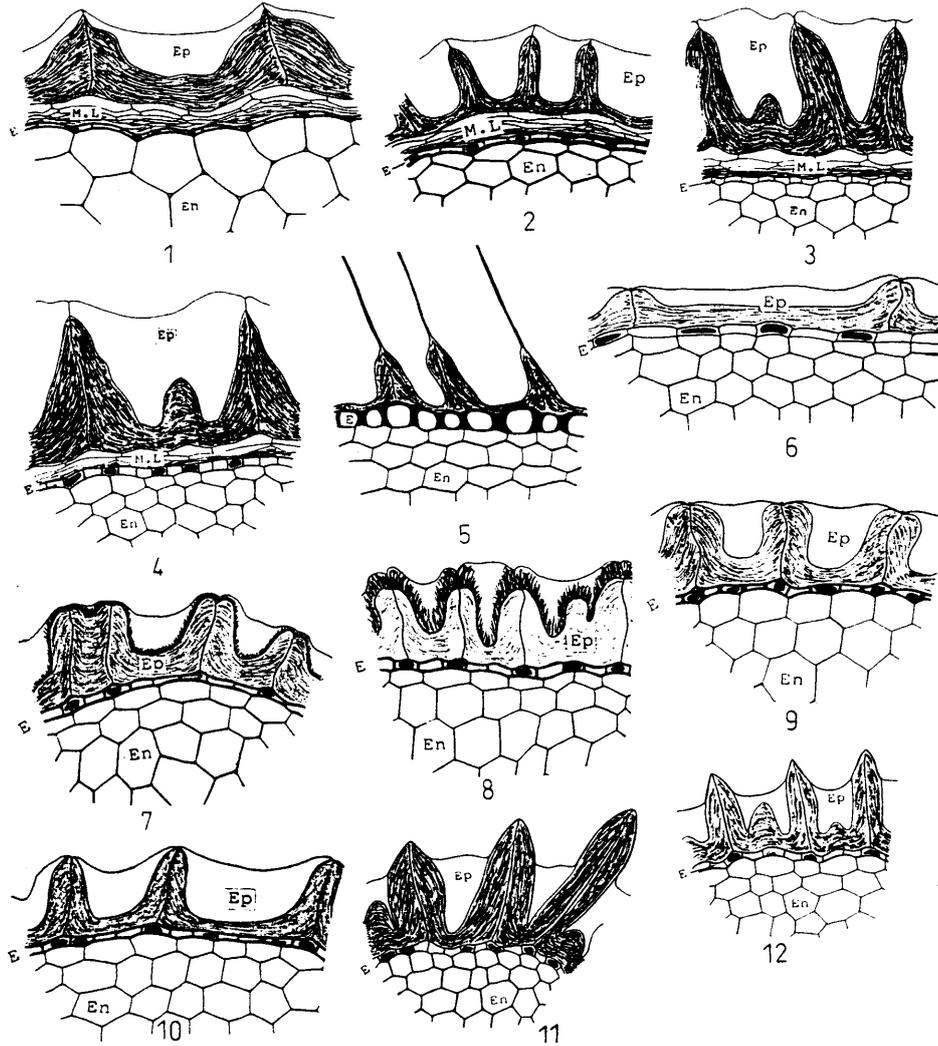


Plate 3- Spermoderm anatomy. Fig.1. *Atropa belladonna*, Fig.2. *A. belladonna* var. *lutea*, Fig.3. *Capsicum annum*, Fig.4. *C. frutescens* cvs., Fig.5. *Cyphomandra betacea*, Fig.6. *Hyoscyamus aureus*, Fig.7. *H. boveanus*, Fig.8. *H. desertorum*, Fig.9. *H. muticus*, Fig.10. *H. niger*, Fig.11. *Lycium chinense*, Fig.12. *L. shawii*. Cu=Cuticle; E=Endosperm; En=Endothecium; Ep=Epidermis; M.L=Middle Layer.

Morphological and anatomical characters of certain taxa of Solanaceae

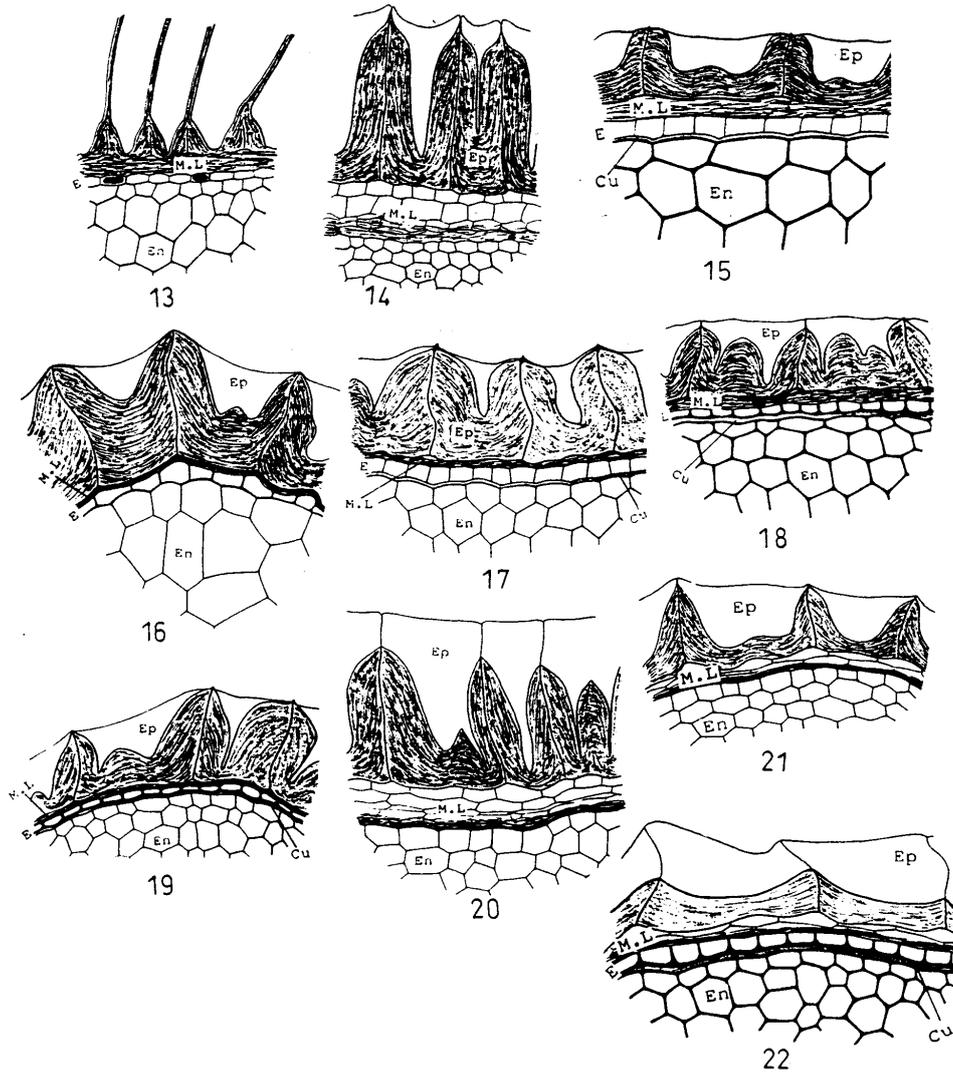


Plate 3. Spermoderm anatomy (cont.). Fig.13. *Lycopersicon esculentum* cvs. and var. *pyriforme*, Fig.14. *Mandragora officinarum*, Fig.15. *Physalis alkekengi*, Fig.16. *P. angulata*, Fig.17. *P. isocarpa*, Fig.18. *P. peruviana*, Fig.19. *P. pruinosa*, Fig.20. *Scopolia lurida*, Fig.21. *S. physaloides*, Fig.22. *Solanum aviculare*. Cu=Cuticle; E=Endosperm; En=Endothecium; Ep=Epidermis; M.L.=Middle Layer.

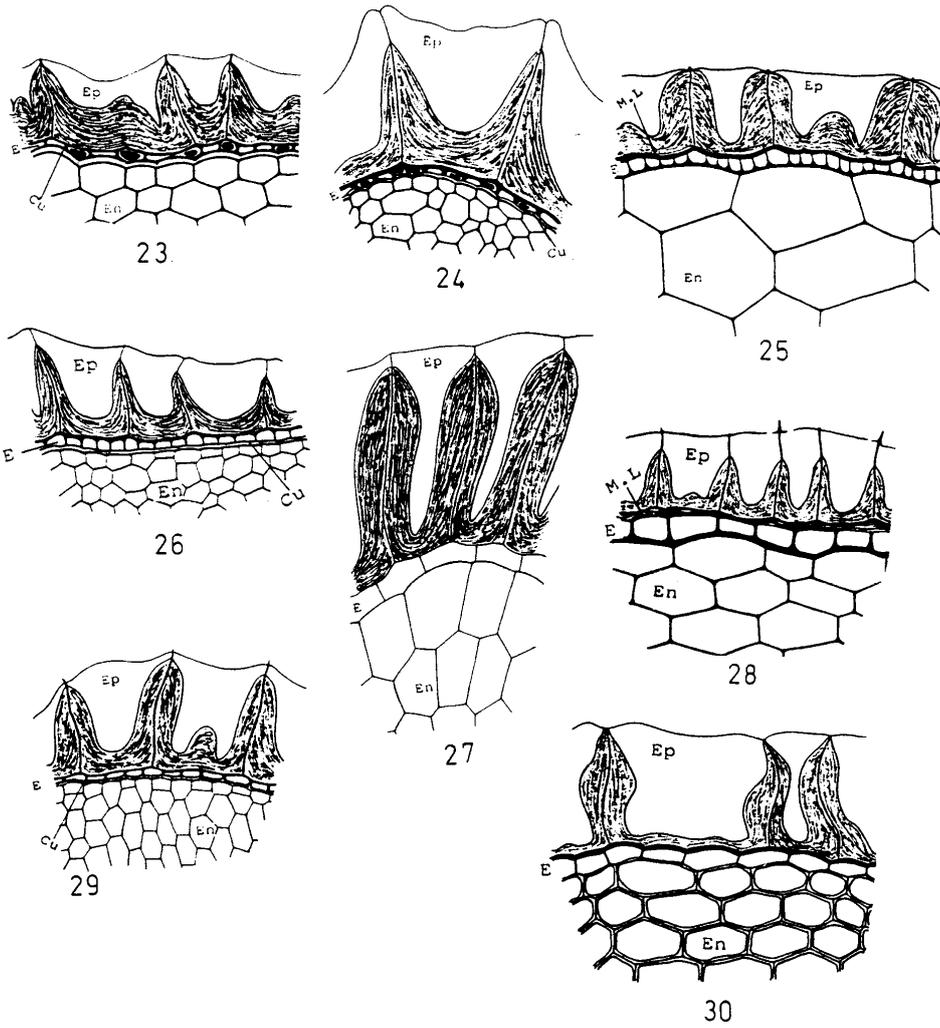


Plate 3- Spermoderm anatomy (cont.). Fig.23. *S. citrullifolium*, Fig.24. *S. cornutum*. Fig.25. *S. dulcamara*, Fig.26. *S. forsskaolii*, Fig.27. *S. incanum*, Fig.28. *S. indicum* var. *aldabranse*, Fig.29. *S. macranthum*, Fig.30. *S. macrocarpon*. Cu=Cuticle; E=Endosperm; En=Endothecium; Ep=Epidermis; M.L=Middle Layer.

Morphological and anatomical characters of certain taxa of Solanaceae

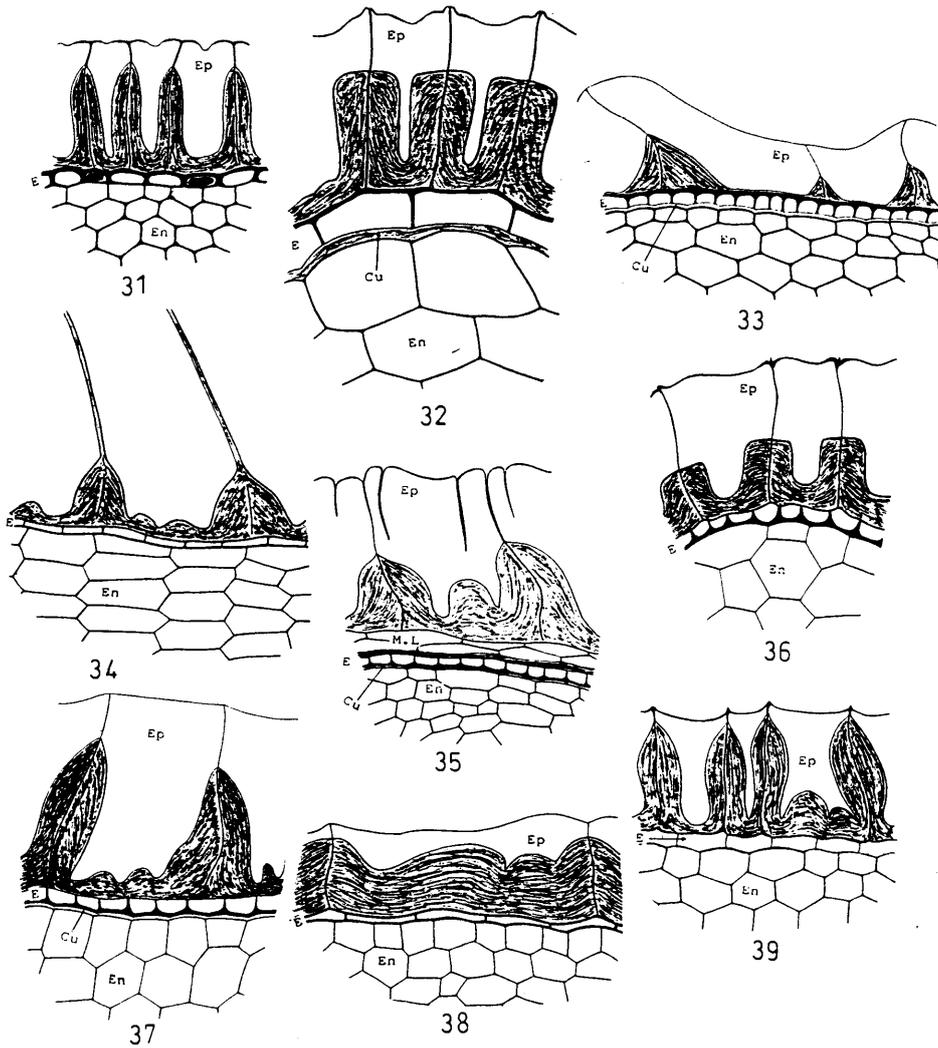


Plate 3- Spermoderm anatomy (continued). Fig.31. *S. melongena* cvs., Fig.32. *S. nigrum*, Fig.33. *S. quitoensis*, Fig.34. *S. seaforthianum*, Fig.35. *S. sisymbriifolium*, Fig.36. *S. villosum*, Fig.37. *S. wrightii*, Fig.38. *Withania riebeckii*, Fig.39. *W. somnifera*. Cu=Cuticle; E=Endosperm; En=Endothelium; Ep=Epidermis; M.L=Middle Layer. =

Table (2) The Anatomical Aspects of the Spermoderm

Aspects	Taxa	Outer Epidermal Cells			Middle Layer		Inner Epidermis (Endothelium)			
		Shape	Wall Thickening			Outer Hypodermal	Inner Hyaline	Shape	Thickness	Pigment
			Outer periclinal	Inner periclinal	Radial wall					
1- <i>Atropa belladonna</i> L.	T	Straight/Cv	K	K ¾	+	+	T	K	+	
2- <i>A. belladonna</i> var. <i>lutea</i> Doll.	R	Straight	K	K ¾	+	+	T	K	+	
3- <i>Capsicum annuum</i> L.	R	Straight	K-papillose	K ¾	+	+	Rectangular	N	-	
4- <i>C. frutescens</i> L. cv. California Wonder.	R	Straight	K-papillose	K ¾	+	+	T	K	+	
5- <i>C. frutescens</i> l. cv. Early Jalpino.	R	Straight	K-papillose	K ¾	+	+	Rectangular	K	+	
6- <i>C. frutescens</i> L. cv. Elpaso	R	Straight	K-papillose	K ¾	+	+	Square	K	+	
7- <i>C. frutescens</i> L. cv. Long Red Cayenne.	R	Straight	K-papillose	K ¾	+	+	Rectangular	K	+	
8- <i>Cyphomandra betacea</i> (Cav.) Sendt.	*	Disintegrating	K	KS	-	-	Square	K-inner N	-	
9- <i>Hyoscyamus aureus</i> L.	T	Straight	K	KS	-	-	Rectangular	N	+	
10- <i>H. boveanus</i> (Dun.) Asch.& Schw einf.	R	Cv	K	KS	-	-	T	K	+	
11- <i>H. desertorum</i> Asch. Ex Bioss.	R	Cv	K-papillose	KS	-	-	Rectangular	K	-	
12- <i>H. munticus</i> L.	R	Straight	K	KS	-	-	T	K	+	
13- <i>H. niger</i> L.	T/R	Straight/Cv	K	KS	-	-	T	K	+	
14- <i>Lycium chinense</i> Mill.	R	Deeply Cv	K-papillose	KS	-	-	Rectangular	N	+	
15- <i>L. shawii</i> Roem. Et Sch.	R	Deeply Cv	K-papillose	KS	-	-	Rectangular	K	+	
16- <i>Lycopersicon esculentum</i> Mill.	*	Disint.	K	KS	-	+	Rectangular	N	+	
17- <i>L. esculentum</i> cv. Bakmor B.	*	Disint.	K	KS	-	+	Rectangular	N	+	
18- <i>L. esculentum</i> cv. Strain B.	*	Disint.	K	KS	-	+	Rectangular	N	+	
19- <i>L. esculentum</i> cv. UC 82.	*	Disint.	K	KS	-	+	Rectangular	N	+	
20- <i>L. esculentum</i> cv. VFN 8.	*	Disint.	K	KS	-	+	Rectangular	N	+	
21- <i>L. esculentum</i> var. <i>pyriforme</i> Alef.	*	Disint.	K	KS	-	+	Rectangular	N	+	
22- <i>Mandragora officinarum</i> L.	R	Cv	K	KS	-	+	-	-	-	
23- <i>Physalis alkekengi</i> L.	T	Straight	K-papillose	KS	+	+	Square	N	-	
24- <i>P. angulata</i> L.	R	Cv	K-papillose	KS	-	+	Rectangular	N	-	
25- <i>P. ixocarpa</i> Brot. ex Hornem.	R	Cv	K-papillose	KS	-	+	Square	N	-	
26- <i>P. peruviana</i> L.	T	Straight	K-papillose	KS	-	+	Rectangular	K-outer N	-	
27- <i>P. prainosa</i> L.	T/R	Straight	K-papillose	KS	-	+	Rectangular	K	-	
28- <i>Scopalia lurida</i> (Link&Otto.) Dun.	R	Straight	K-papillose	K ¾	+	+	-	-	-	
29- <i>S. physaloides</i> Dun in DC.	T	Straight	K	K ¾	+	+	-	-	-	
30- <i>Solanum aviculare</i> G.Farster.	T	Straight	K	K ¾	+	+	Square	K-outer N	-	
31- <i>S. citrullifolium</i> A.Br.	T/R	Straight/Cv	K-papillose	K ¾	-	-	Rectangular	K	+	
32- <i>S. cornutum</i> Lam.	R	Straight	K	K ¾	-	-	Rectangular	K-inner N	+	
33- <i>S. dulcamara</i> L.	T/R	Straight	K-papillose	KS	-	+	Square	K-outer N	-	
34 <i>S. forsskaolii</i> Ky ex Dun.	R	Straight	K	K ¾	-	-	Rectangular	K-inner N	-	
35- <i>S. incanum</i> L.	R	Straight	K	K ¾	-	-	Rectangular	N	-	
36- <i>S. indicum</i> var. <i>aldabranse</i> Linn.	R	Straight	K-papillose	K ¾	-	+	Square	K-outer N	-	
37- <i>S. macranthum</i> Dun.	R	Straight	K-papillose	K ¾	-	-	Rectangular	K	-	
38- <i>S. macrocarpon</i> L.	T/R	Straight	K	KS	-	-	Rectangular	K-outer N	-	
39- <i>S. melongena</i> L. cv. Block Beauty.	R	Invaginated	K	K ¾	-	-	Rectangular	K-inner N	+	
40- <i>S. melongena</i> cv. Long Purple.	R	Invaginated	K	K ¾	-	-	Rectangular	K-inner N	+	
41- <i>S. melongena</i> cv. Long White	R	Invaginated	K	K ¾	-	-	Rectangular	K-inner N	+	

Morphological and anatomical characters of certain taxa of Solanaceae

42- <i>S. nigrum</i> L.	R	Straight/Cv	K	K ½	-	-	Rectangular	K-inner N	-
43- <i>S. quitoensis</i> Lam.	T	Straight/Cv	N	K ½	-	-	Square	K-inner N	-
44- <i>S. seaforthianum</i> Andrews	*	Disint.	K-papillose	KS	-	-	T	K	-
45- <i>S. sisymbriifolium</i> Lam.	R	Papillated	K-papillose	K ½	+	+	Rectangular	K-outer N	-
46- <i>S. villosum</i> (L.) Mill.	R	Straight	K	K ½	-	-	Rectangular	K-outer N	-
47- <i>S. wrightii</i> Benth.	R	Straight	K-papillose	K ¾	-	-	Rectangular	K-outer N	-
48- <i>Withania riebeckii</i> Schweinf.	T	Straight	K-papillose	K ¾	-	-	T	K	-
49- <i>W. somnifera</i> (L.) Dun.	R	Straight	K-papillose	K ¾	-	-	Rectangular	N	-

Cv , Concave; Disint, Disintegrating; K , Thick ; KS , Thickness to the summit; K ¾ , Thickness almost ¾ ; k ½ , Thickness almost to the middle; N , Thin ; R , Radially elongated ; T , Tangentially elongated ; + , Present ; - , Absent; ● , Foreign taxa.

Of all the characters of the endothelium the universality of thickening on its walls and the presence of pigments are found to be fairly diagnostic at the generic level. In *Atropa* species it is pigmented and the thickenings are deposited on all the walls. In *Lycopersicon* species it is also pigmented but all the walls are thin.

### Conclusions

In addition to the identificatory key suggested for the studied taxa, the subsequent salient remarks on the taxonomy and the phylogeny of **Solaneae** are presented.

From the taxonomic view point the shape of the seed is found to be an exclusive character for certain taxa. These are *Lycopersicon* species where the seed is oval and provided with long tubular 'hairs' and *Capsicum* species where it is reniform with tapering ends. Except for the genera *Solanum*, *Physalis*, *Atropa* and *Lycium*, the hilar characteristics are uniform within the remainder examined taxa.

The aspect of the anticlinal walls (undulation, thickening and detection of the primary cell wall) as clarified by SEM showed consistency at the infraspecific level (cvs. of *Lycopersicon esculentum* and *Capsicum frutescens*). Where present, the different aspects of the outer periclinal wall are consistent at the generic level (*Solanum* excluded).

Of the anatomical remarks, the extent of deposition of thickening on the radial walls was consistent at the generic level (*Solanum* excluded).

As regards the purity of the genera, the consistency of the morphological characters in the studied species of *Lycopersicon*, *Lycium*, *Hyoscyamus*, *Physalis* and *Withania* is an indicator to the homogeneity of these genera, whereas the diversity of the same characters in *Solanum* species renders it a heterogeneous one.

However, the totality of the morphological and anatomical data culminated into some taxonomic and nomenclatural changes. In terms of Wettstein's classification (Table 3) the subsequent taxonomic changes are suggested.

Table (3): Part of Wettstein's classification of the tribe Solaneae (1895)

Tribe	Subtribe	Genera	Section	Species	
Solaneae	Lyciinae	<i>Atropa</i>	Brachycope Mesocope Macrocope	<i>L.europaeum, L.arabicum</i>	
		<i>Lycium</i>			
	Hyoscyaminae	<i>Scopolia</i>		Euscopolia	<i>S. lurida</i>
				Anisodus	
		<i>Hyoscyamus</i>		Euhyoscyamus	<i>H. muticus, H. niger, H. albus, H. aureus</i>
				Chlamaehyoscyamus	
	Solaninae	<i>Withania</i>			<i>W. riebeckii, W. somnifera</i>
		<i>Physalis</i>			<i>P. alkekengi, P. ciliata, P. peruviana</i>
		<i>Capsicum</i>		Eucapsicum	<i>C. cannuum, C. frutescens.</i>
				Tubocapsicum	
		<i>Solanum</i>		Pachystemonum	<i>S. dulcamara, S. nigrum, S. villosum</i>
				Lycianthus	
			Leptostemonum	<i>S. melongena</i>	
	Lycopersicon		<i>S. Lycopersicon, S. Pyriforme</i>		
Mandragorinae	<i>Cyphomandra</i>			<i>C. betacea</i>	
	<i>Mandragora</i>			<i>M. officinarum</i>	

### 1- Transference (Re-allocation)

*Hyoscyamus muticus* is better transferred from section **Euhyoscyamus** Wettstein to section **Chlamaehyoscyamus** Wettstein; the latter section contains in addition, *H. aureus*. This may be justified by the sharing of the seed of both species to many morphological characters as well as their keying out.

### 2- Addition:

- a- *Scopolia physaloides*, not mentioned by Wettstein, is added with *S. lurida* in section *Anisodus*.
- b- *Solanum incanum* is added with *S. melongena* in section Leptostemonum.
- c- *Physalis ixocarpa* and *P. pruinosa* were neither mentioned by Wettstein nor assigned to any section. Here, both species are added in the proposed classification, and assigned to two new sections:
  - i) Section **Angulata** containing *P. angulata*
  - ii) Section **Peruviana** containing *P. alkekengi, P. ixocarpa, P. pruinosa* and *P. peruviana*.

With regard to the nomenclatural changes, the following amendments are suggested:

- i) The old name *Solanum bactaceum* Cav. is retained over *Cyphomandra bactacea* Sendt. This is favoured by the pronounced similarity in the morphology and anatomy of the spermoderm of both *Solanum seaforthianum* and *Cyphomandra batacea* which led to

their keying together, as well as being attached with most *Solanum* species as presented in the lay-out of the phylogenetic status.

ii) *Solanum villosum* (L.) Lam. is lowered to the variety rank as suggested early by Linnaeus (1753); thus amended to *Solanum nigrum* var. *villosum* L. An external evidence comes from the work of Wojciechowska (1972) who stated that *S. nigrum* and *S. villosum* were keyed together.

iii) The variety *lutea* of *Atropa belladonna* is raised to the specific rank *A. lutea* Al-Nowaihi & Mourad stat. nov. Table (4) shows the amendments suggested for Wettstein's classification.

Table (4) Proposed modifications to Wettstein's classification of the tribe Solaneae

TRIBE	SUBTRIBE	GENERA	SECTION	SPECIES
Solanaceae	Lyciinae	<i>Atropa</i>		<i>A. belladonna</i> *, <i>A. lutea</i> !
		<i>Lycium</i>	Barchycope Mescope Mescope	<i>L. shawii</i> , <i>L. chinense</i> *
	Hyoscyaminae	<i>Scopolia</i>	Euscopolia Snisodus	<i>S. lurida</i> , <i>S. physaloides</i> *
		<i>Hyoscyamus</i>	Euhyoscyamus	<i>H. albus</i> , <i>H. niger</i> , <i>H. boveanus</i> *
			Chlamaehyoscyamus	<i>H. aureus</i> , <sup>o</sup> <i>H. muticus</i> <sup>o</sup>
	Solaninae	<i>Withania</i>		<i>W. riebeckii</i> , <i>W. somnifera</i>
		<i>Physalis</i>	Angulata• <i>Peruviana</i> •	<i>P. angulata</i> , <i>P. alkekengi</i> , <i>P. peruviana</i> , <i>P. pruinosa</i> *, <i>P. ixocarpa</i> *
		<i>Capsicum</i>	Eucapsicum Tubocapsicum	<i>C. annuum</i> , <i>C. frutescens</i> .
		<i>Solanum</i>	Pachystemonum Lycianthus Lepostemonum Nycterium	<i>S. dulcamara</i> , <i>S. nigrum</i> <i>S. melongena</i> , <i>S. ncanum</i> * <i>S. citrullifolium</i> , <i>S. macrocarpon</i> <i>Solanums</i> *spp. No. 30, 31,33, 35, 36,37,34,44,45 and 47
	Mandragorinae	<i>Lycopersicon</i>		<i>L. esculentum</i>
		<i>Cyphomandra</i>		<i>C. betacea</i> ϕ
		<i>Mandragora</i>		<i>M. officinarum</i>

• New sections proposed; \* Taxa not mentioned by Wettstein; ϕ Taxa amended; ! New Species;

o Taxa transferred to new section

As regards the phylogenetic status of the studied taxa Corner (1976) and Prasad & Singh (1978) relied upon the number of the spermoderm layers as an indicator to the evolutionary status. They considered the multilayered seed coat is less advanced than the few-layered one. Following the same concept the studied taxa are arranged from less advanced to more advanced as shown in Fig. (1). The less advanced multilayered taxa are *Solanum aviculare*, *S. sisymbriifolium*, *Atropa*, *Capsicum*, *Mandragora* and *Scopolia*. In these taxa the three layers are present with the middle layer differentiated into a hyaline zone and a hypoderm. The more advanced few-layered taxa are *Cyphomandra*, *Hyoscyamus*, *Withania*, *Lycium* and some *Solanum* species. In these taxa the middle layer is absent altogether. Intermediate taxa are those in which the middle layer of the seed coat is represented by the hyaline zone while the hypodermal zone is absent. These taxa are *Solanum dulcamara*, *S. indicum* var. *aldabranse*, *Lycopersicon* and *Physalis*.

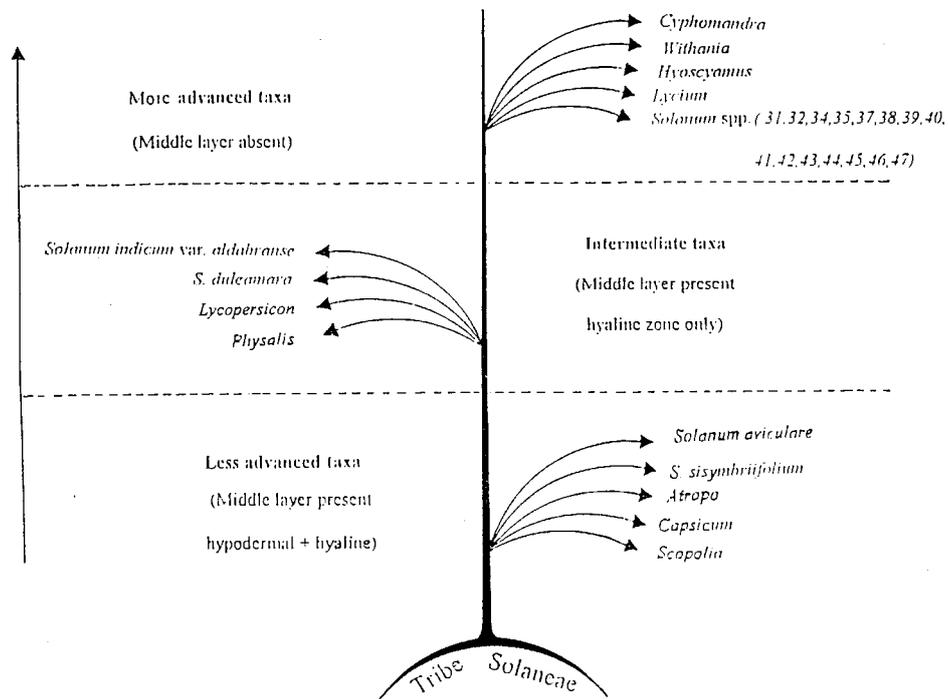


Fig. (1) A proposed phylogenetic status for the studied taxa of tribe Solaneae

**key for the studied taxa of the tribe Solaneae**

- A. Hilum at a level
  - B. Seeds covered with hairs
    - C. Anticlinal walls lobed ..... *Lycopersiconesculentum* cvs.
    - CC. Anticlinal walls slightly undulate .... *Lycopersicon esculentum* var *pyriforme*.
  - BB. Seeds glabrous
    - D. Anticlinal walls straight (s.v)
      - E. Seeds pear to reniform ..... *Scopolia physaloides*
      - EE. Seeds subglobose ..... *Atropa lutea*
    - DD. Anticlinal walls lobed (s.v)
      - F. Thin ..... *Solanum wrightii*
      - FF. Thick
    - G. Hilum aperture slit-like.
      - H. Seeds oval, anticlinal wall micropapillate.
        - I. Endothelial cells square, middle layer of hyaline zone only, inner tangential wall of outer epidermis with papillate thickening ..... *Solanum ulcamara*.
        - II. Endothelial cells rectangular, both middle layer and papillose thickening lacking ..... *Solanum nigrum* & *S. nigrum*. var. *villosum*
      - HH. Seeds reniform, anticlinal wall smooth, intestine like ..... *Physalis angulata*.
  - GG. Hilum aperture rounded
    - J. Seeds oval
      - K. Primary walls detectable (persistent)
        - L. Endothelial cells thin, rectangular ..... *Hyoscyamus aureus*.
        - LL Endothelial cells thick, tangentially flattened ..... *Hyoscyamus muticus*.
      - KK. Primary walls undetectable
        - M Inner tangential wall of the epidermis with papillose thickening, endothelial cells rectangular ..... *Hyoscyamus desertorum*.
        - MM. Inner tangential wall of the epidermis without papillose thickening, endothelial cells tangentially flattened ..... *Hyoscyamus boveanus* & *H. niger*.
    - JJ. Seeds pear to reniform.
      - N. Two zones of middle layer persistent, radial wall thickening to  $\frac{3}{4}$  of its length ..... *Scopolia lurida*.
      - NN. Only hyaline zone of the middle layer persistent, radial wall thickening to the summit ..... *Physalis peruviana*.
    - JJJ. Seeds orbicular ..... *Lycium chinense*.
- AA. Hilum sunken
  - O. with the surrounding epidermal cells arched (ridged).
    - P. Hilum rounded ..... *Mandragora officinarum*.
    - PP. Hilum slit-like.

- Q. Anticlinal walls lobed, micropapillate ..... *Capsicum annum*.  
 QQ. The same slightly undulate, smooth ..... *Capsicum frutescens* cvs.  
 OO. With the surrounding epidermal cells at a level  
 R. Hilum slit-like.  
 S. Anticlinal walls straight, papillate ..... *Solanum quitoensis*.  
 SS. Anticlinal walls lobed, micropapillate  
   T. Endothelial cells thick, square ..... *Solanum indicum* var. *aldabranse*.  
   TT. Endothelial cells thin, rectangular ..... *Withania somnifera*.  
 SSS. Anticlinal walls lobed, smooth ..... *Withania riebeckii*  
 RR. Hilum rounded  
 U. Seeds 'hairy'  
   - Seeds reniform ..... *Solanum seforthianum*  
   = Seeds orbicular ..... *Solanum betaceum*  
 UU. Seeds glabrous.  
 V. Primary wall detectable (persistent)  
   1 W. Seeds reniform.  
     - Endothelial cells thin, square .....  
       ..... *Physalis alkekengi* & *P. ixocarpa*  
     = Endothelial cells thick, rectangular..... *Physalis pruinosa*  
   2 W. Seeds orbicular ..... *Solanum macranthum*  
   3 W. Seeds oval..... *Solanum citrullifolium*  
 VV. Primary wall undetectable  
   1 X. Anticlinal walls lobed, smooth  
     - Seeds triangular ..... *Lycium shawii*.  
     = Seeds oval ..... *Solanum aviculare*.  
   2 X. Anticlinal walls straight.  
     - Wall smooth ..... *Solanum forsskaolii*  
     = Wall micropapillated ..... *Solanum sisymbriifolium*.  
   3 X. Anticlinal walls lobed, intestine-like  
     Y. Seeds pear-like ..... *Solanum macrocarpon*  
     YY. Seeds orbicular to reniform  
       - Endothelial cells thick, pigmented .....  
         ..... *Solanum melongena* cvs.  
       = Endothelial cells thin, not pigmented .....  
         ..... *Solanum incanum*  
   4 X. Anticlinal walls lobed, micropapillate .....  
     ..... *Solanum cornutum*.  
 AAA. Hilum elevated ..... *Atropa belladonna*.

### **Acknowledgement**

We thank Hortus Botanicus Nationalis Belgii, the Herbarium of the Royal Garden, Kew and Botanischer Garten Der universitat, Zurich for providing the seeds of the foreign taxa.

### **References**

- Al-Nowaihi, A.S Khalifa, S.F. 1974. A numerical classification of **Solanaceae** in Egypt. *Ind. Bot. Soc.* **53**:224-248.
- Barthlott, W. 1981. Epidermal and seed surface characters of plants: Systematic applicability and some evolutionary aspects. *Nord. J.Bot.* **1**:345-355.
- ..... 1984. Microstructural features of seed surfaces. In *Current Concepts in Plant Taxonomy*. (eds. V.H. Heywood & D. M. Moore): **95**-105. London: Academic Press.
- Corner, E.J.H. 1976. *The Seeds of Dicotyledons* I. Cambridge, U.K.
- Czaja, A.T.H. 1963. Neue Untersuchungen an der Testa der Tomatensamen. *Planta*, **59**: 262-279.
- Dilcher, D.L. 1974. Approaches to the identification of angiosperm leaf remains. *Bot. Rev.* **40**:1-157.
- Dnyansagar V.R.& Cooper, D.C. 1960. Development of the seed of *Solanum phyreja*. *Am. J. Bot.* **47**:167-186.
- Edmonds, J. M. 1983. Seed coat structure and development in *Solanum* L. section *Solanum* (Solanaceae). *Bot. J. Linn. Soc.* **87** (3): 229-246.
- Forooqui, S. M. 1983. Seed morphology of a *Nicotiana* species *Nicotiana Kowakamii* (Solanaceae). *Indian J. Bot.* **6** (1): 98-99.
- ..... & Bahadur, B. 1984. Seed characters LM and SEM in 3 species of *Nicotiana* L.. *Indian Bot. Rep.* **3** (1): 92-94.
- ..... 1985. Studies on seed morphology LM and SEM of American *Nicotiana* L. (Solanaceae). *Indian J. Bot.* **8** (2): 191-197.
- Gunn, C.R. & Gaffney, F.B. 1974. Seed characters of 42 economically important species of Solanaceae in United States; *U. S. D.A. Technical Bulletin* 1471:-1-3.
- Hayward, H.E. 1938. *The structure of economic plants*. New York: The Macmillan Company.
- Henderson, R J.F. 1974 *Solanum nigrum* L. (Solanaceae) and related species in Australia. *Contributions from the Queensland Herbarium*, **16**:1-78.
- Isely, D. 1947. Investigations in seed classification by family characteristic. *Iowa Agricultural Experiment Station, 28, Agricultural Research Bulletin*, **351**:317-380.
- Jha, S.S.& Pondey, A. K. 1989. Seed coat structure in *Melilotus* (Fabaceae). *Phytomorphogy*, **39** (2,3): 221-229.
- Johansen D.A. 1940. *Plant Microtechnique*, (New York: Mc Graw-Hill).
- Linnaeus. C.1753. *Species Plantarum* ed. 1. (Stockholm).

- Martin, A. C. & Barkley, W.D. 1961. *Seed Identification Manual*. University of California Press, Perkeley, U.S.A.
- Mohan, K. 1970. Morphological studies in Solanaceae. V. Embryology as well as structure and development of seed of *Solanum macranthum* Dun. Agra. University J. of Research (Science), **19**:55-66.
- Prasad, T. & Singh, D. 1978. Gametophytes and seed development in *Nicotiana physaloides*. *J. Indian Bot. Soc.* **7-5(1)**: 76-83.
- Preisner, T.R. 1985. A preliminary light and scanning electron microscope study on the seed coat of six varieties of *Lycopersicon esculentum*. *Proc. Pa. Acad. Sci.* **59(1)** :83.
- Rick, C. M. 1978. *The Tomats. Scientific American.* **239**: 67-76.
- Saxena, T. & Singh, D. 1969. Embryology and seed development of tetraploid form of *Solanum nigrum*. *Linn. J. Ind. Bot.* **48**:148-157.
- Sharma, S.K; Babu, C.R.; Johri, B.M. & Hepworth, A. 1977. SEM studies on seed coat patterns in *Phaseolus mungo radiatus-subloatus* complex. *Phytomorphology* **27**:166-111.
- Souégés, R. 1907. Development et structure du tegument seminal chez les Solanaceae. *Sci Ann.. not. Bot.. Ser.* **9**:1-124.
- West, T. 1866. On the structure of the testa of the seed of Solanaceae. *J. Bot.* **4**: 208.
- Wettstein, R. 1895. Solanaceae in Engler und Prantl. *Die naturalischen pflanzenfamitien IV Abt. 3-b* :4-38. Leipzig, Wilhelm Engelman.
- Whalen, M.D. 1979 a. Speciation in Solanum Section Androceras, in J. G. Hawkes *et al.* (eds). *The Biology and Taxonomy of the Solanaceae*: 581-596- London: Academic Press.
- .....1979 b. Taxonomy of *Solanum* section Androceras. *Gentes Herbarium* **11**: 359-426.
- Wilkinson, H.P 1980. The Plant surface, in *Anatomy of the dicotyledons*, (eds. C.R. Metcalfe & L. Chalk): 97-165. London: Oxford Press .
- Wojciechowska, B. 1971. Diagnostic features of *Solanum aviculare* Forst. and *S. laciniatum* Ait. *Seed. Herb. Polonica* **17**:31-39.
- Wojciechowska, B. 1972. Systematic studies on the seeds of the family Solanaceae Pers. *Monographic Botancia.* **36**: 117-197