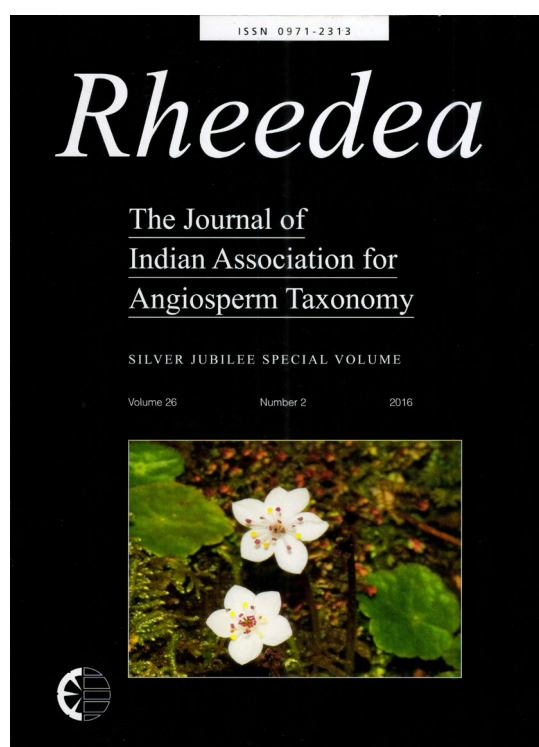




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Significance of architectural patterns of spermoderm in taxonomic studies of *Solanum* species from southern Western Ghats, Kerala, India

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Abstract

Seed micromorphology can provide stable marker characters valuable for authentication at different level of identification in taxonomic hierarchy. Spermoderm sculpturing patterns of 16 taxa of *Solanum* were investigated using Scanning Electron Microscope (SEM) to analyse their unique features useful in taxonomic studies. Considerable diversity was noticed in sculpturing of the outer seed coat and lateral seed coat walls (anticlinal walls) with thickened pyramidal bases topped by varied lignified projections. The sculpturing pattern in different taxa varied from cerebelloid and faintly cerebelloid to reticulate and sometimes without conspicuous cell lumens. Further, *S. seaforthianum* Andrews possesses luxuriant fibrillar or hairy cover on its seed surface. The testal cells also varied from polygonal to isodiametric. In *S. seaforthianum*, cells were not distinctively seen due to fibrillar cover. The distal appendages when present had finger-like lacinations or fibrils. Except in *S. aculeatissimum* Jacq., *S. seaforthianum*, and *S. torvum* Sw. the lateral testal cell walls of all other taxa could be distinctively seen and their pattern ranged from smooth, papillate to tuberculate. The study emphasises the applicability of seed coat architectural patterns in species discrimination.

Keywords: Scanning Electron Microscopy, Seed Morphology, Solanaceae, Taxonomy

Introduction

Scanning electron microscopic analysis of seed morphology provides many potential characters useful for delimiting at species level to taxonomic circumscription including phylogenetic kinship (Mostafavi *et al.*, 2013). The seed coat morphology is usually stable and is less influenced by external environmental conditions as the seeds develop and mature within the fruit (Rajput & Ghate, 2014). Therefore, seed character analysis can provide valuable information in the authentic identification of taxa at any levels. Observations in many plant groups have shown that seed morphology and anatomical features are rather conservative which makes them taxonomically important (Kaya *et al.*, 2011; Khalik & Hassan, 2012; Bona, 2013). In recent years the seed surface features as revealed by SEM studies have been used by several investigators for systematic studies in a number of taxa (Koc *et al.*, 2011; Minuto *et al.*, 2011; Bona, 2013; Khalik, 2013; Mostafavi *et al.*, 2013; Yilmaz, 2013). Categorization at tribal level in Brassicaceae was successfully established using seed morphology (Bona, 2013). *Linum* L. seed morphology was effectively used in

differentiating 18 of its species (Talebi *et al.*, 2012). Seed micromorphology is of remarkable importance in the identification of taxa in Solanaceae from generic to specific levels. *Physalis* L., *Capsicum* L. and *Tubocapsicum* Wettst. are differentiated by seed coat structure. Seed size and compression are phylogenetically significant in *Hyoscyamus* L. and *Physochlaina* G. Don (Zhang *et al.*, 2005). SEM and IR finger printing analysis of *Solanum diphyllum* L. was previously attempted (Anil Kumar *et al.*, 2014). The salient feature of systematic importance in the seed epidermis has been the anticlinal wall which, in many species, is naturally exposed to surface view by disorganization of the outer periclinal wall during the ontogeny of seed. The fully formed anticlinal and inner periclinal walls are unevenly thickened by secondary wall materials providing a pyramidal appearance in sectional view. In addition, random accumulations of secondary wall materials near the outer periclinal walls produce spurious hairs or scales with zigzag orientations. These markers are commonly employed in systematic evaluation of taxa.

Very little information is available on spermoderm patterns of Solanaceae in general and *Solanum*

in particular (Lester & Hasan, 1990; Karihaloo & Malik, 1995; Lester *et al.*, 1999; Zhang *et al.*, 2005). No serious studies have been made so far regarding the seed architectural patterns of *Solanum* species of southern Western Ghats. The present work is an attempt to analyse the seed coat patterns of 16 taxa of *Solanum* from southern Western Ghats of Kerala and their taxonomic significance.

Materials and Methods

Plant Material

Seed characters of 16 taxa of *Solanum* were studied using freshly collected mature seeds (Table 1). Plant specimens with mature fruits were collected from different localities in the Western Ghats of Kerala. The plant specimens were identified at TBGT. A total of 10 to 15 mature seeds of each taxon, manually separated from the fruits and cleaned were used for the scanning electron microscopic studies. For SEM, seeds were mounted with double-stick tape on alloy stubs, coated with gold, and examined at 10 kV with either a Hitachi (Model SU6600) or Ziess (Model EVO 18) SEM. Terminology for seed surface sculpture follows that of Murley (1951) and Barthlott (1984, 1990).

Results and Discussion

Seed morphology and spermoderm features are genetically regulated and are expressed at both intra- and interspecific levels. The *Solanum* species show wide variation in their seed shapes. It is reniform in *S. trilobatum* L., *S. pseudocapsicum* L. and *S. giganteum* Jacq.; winged reniform in *S. capsicoides* All., and *S. exarmatum* Anil *et al.*; ellipsoid in *S. melongena* L. var. *insanum* (L.) Prain; ovoid in *S. mammosum* L.; subovoid-oblong in *S. torvum*; triangular in *S. seaforthianum* and *S. mauritianum* Scop.; ovoid with reniform in *S. violaceum* Ortega subsp. *violaceum*; subglobose in *S. aculeatissimum*; subglobose to subovoid in *S. erianthum* D. Don; compressed ovoid in *S. americanum* Mill.; *S. macrocarpon* L. and obliquely spheroid in *S. violaceum* Ortega subsp. *multiflorum* (C.B. Clarke) K.M. Matthew (Figs. 1–6). Table 1 shows the wide diversity in shape, size and surface sculpturing pattern in the solanaceous seeds.

From the table, it can be seen that among the species studied, *S. capsicoides* and *S. exarmatum* have the largest seeds, measuring 3.73/4.35 to 4.09/4.34 mm in length and breadth (Fig. 1a,b,c,d). *Solanum americanum* (Fig. 1e) is the smallest having a length and breadth dimension of 1.57–1.59 × 1.14–1.16 mm. Typical winged seeds were observed in *S. capsicoides*, *S. exarmatum* and *S. pseudocapsicum*

(Fig. 1a,c,g) while wing-like distensions could be observed in *S. giganteum* (Fig. 2a,b), *S. violaceum* subsp. *violaceum* (Fig. 2c,d), *S. violaceum* subsp. *multiflorum* (Fig. 2e,f) and *S. trilobatum*, making these seeds comparatively larger than the rest (Fig. 2g,h). The size of the seeds has implications for dispersal mechanism. Smaller seeds travel farther than larger seeds and also they possess wings or hairs that favour wind dispersal. Among species with wings or hairs, typically the wing area increase with seed mass. It has also been observed that species with winged seeds such as *S. capsicoides* and *S. exarmatum* produce berries with dry pericarp and the ripened fruits do not fall off; instead they dehisce even while attached to the plant and disperse the seeds. Remarkable diversity in shape and size is reported among the angiosperm taxa. Seeds range from the micro seeds of the Orchidaceae, some saprophytic and parasitic species (around 10⁻⁶ g) to ten orders of magnitude as in the double coconut, *Lodoicea maldivica* (J.F. Gmel.) Pers. (10⁴ g) (Harper *et al.*, 1970). The seed size of a species represents the amount of material investment in an individual offspring or how much “packed lunch” an embryo is provided to initiate germination. Within species, seed size typically spans less than half an order of magnitude – about four fold (Michaelis *et al.*, 1988). There is strong overlap of seed size characters between species growing along different habitats/zones like tropics and the temperate (Lord *et al.*, 1995). But variation within the habitat remains the major component between species variation (Lord *et al.*, 1995). Seed size generally increases from forbs and grasses through shrubs to trees and vines (Leishman *et al.*, 1995). A relationship between seed size and growth form has been well-documented for a variety of species from a range of habitats. Hence, the *Solanum* seeds collected from different localities of southern Western Ghats are attempted to correlate seed size with that of its life form. Interestingly, the present investigation does not support the above findings. For example, among the taxa studied, *S. capsicoides* and *S. exarmatum* have the largest seeds with herbaceous habit. Similarly, *S. mammosum* another herbaceous species has seed size (Fig. 3a,b) close to the larger winged seeds of *S. capsicoides*, *S. exarmatum* and *S. pseudocapsicum*. The larger shrub or smaller tree forms like *S. erianthum* possess seeds with dimension (Fig. 3c,d) close to the smallest seeds of *S. americanum*. It can generally be noticed that fruits with winged seeds are having a dry pericarp and since the seeds are winged, dispersal does not necessarily depend on animals or birds. However, *S. pseudocapsicum* is exceptional in having fruits that are fleshy. Further, dehiscence

Table 1. Seed morphoforms of different *Solanum* taxa

Sl. No.	Plant Name	Shape	Size (mm)	Surface sculpturing
1	<i>S. capsicoides</i> All.	Winged reniform	3.73/4.35 across	Compactly packed irregular cells without conspicuous lumens and muri. The hilum region shows faint lumens and muri.
2	<i>S. exarmatum</i> Anil et al.	Winged reniform	4.09/4.34 across	Surface sculptured with irregular thick fibrils. Conspicuous lumens absent.
3	<i>S. aculeatissimum</i> Jacq.	Subglobose	2.32–2.36 × 1.89–1.92	Wavy irregular fibrillar ridges along the cell boundaries reticulate, without conspicuous lumen.
4	<i>S. giganteum</i> Jacq.	Reniform	3.22–4.29 × 2.73–2.57	Foveate, with conspicuous lumens, distal ends of tangential walls bearing minute fibrillar threads towards the hilum.
5	<i>S. erianthum</i> D. Don	Subovoid	1.54–1.58 × 1.59–1.64	A faintly cerebelloid reticulate pattern with shallow lumens.
6	<i>S. violaceum</i> Ortega subsp. <i>violaceum</i>	Ovoid and roughly reniform	2.73–2.85 × 2.10–2.19	Cell boundaries irregular, lumens shallow, distal ends of tangential walls raised to broader elements.
7	<i>S. violaceum</i> Ortega subsp. <i>multiflorum</i> (C.B. Clarke) K.M. Matthew	Obliquely spheroid	3.69–3.78 × 3.63–3.71	Regularly reticulate with irregularly folded thickenings seen along the cell boundaries with inconspicuous lumens.
8	<i>S. torvum</i> Sw.	Subovoid-oblong	2.14–2.19 × 1.49–1.55	Testal cells with irregular boundaries are compactly packed without lumens or hairs.
9	<i>S. trilobatum</i> L.	Reniform	3.52–3.48 × 2.54–2.51	The surface is roughly reticulate and the fibrillar structures from the distal ends project out and merge laterally. The cell lumens are shallow.
10	<i>S. americanum</i> Mill.	Compressed ovoid	1.57–1.59 × 1.14–1.16	Profuse hairs from the distal ends of the tangential walls and the lumens are irregular.
11	<i>S. seforthianum</i> Andrews	Triangular	3.14–3.19 × 3.10–3.16	The seed surface is profusely and densely hairy. It is hard to see the actual testal surface.
12	<i>S. mammosum</i> L.	Ovoid	3.78–3.84 × 3.24–3.29	The seed surface is apparently even with irregularly raised wavy projections. The lumens not conspicuous.
13.	<i>S. mauritianum</i> Scop.	Triangular	2.08–2.14 × 1.81–1.70	Foveate reticulate, lumens deep and the distal ends of the tangential walls pappillate.

Sl. No.	Plant Name	Shape	Size (mm)	Surface sculpturing
14.	<i>S. macrocarpon</i> L.	Compressed ovoid	3.18–2.84 × 2.68–2.62	The testal surface has irregular ridges with very shallow lumens and the distal ends of the tangential walls are sparsely papillate.
15.	<i>S. pseudocapsicum</i> L.	Reniform	3.96–3.21 × 2.74–2.45	Compactly packed irregularly folded fibrillar thickenings having medium-sized lumens in between.
16.	<i>S. melongena</i> L. var. <i>insanum</i> (L.) Prain	Ellipsoid	2.30–2.35 × 2.09–2.13	Reticulate cerebelloid surface with broad and thick wavy projecting elements along the cell boundaries around shallow lumens in regular pattern.

of the dry fruit also helps in dispersing the seeds to some distance, avoiding crowding at the base of the mother plant. In the case of species having comparatively smaller seeds such as *S. erianthum* (Fig. 3c), *S. torvum* (Fig. 3e,f), *S. mauritianum* (Fig. 3g,h) and *S. americanum* (Fig. 1e), the berries are fleshy and mostly eaten by birds and animals, thus facilitating dispersal. The number of seeds per fruit is also comparatively high in them.

The systematic and diagnostic importance of the seed epidermal patterns in Solanaceae has been established by a number of studies (Bona, 2013; Rajput & Ghate, 2014). Recent investigations have shown that the traits related to seed morphology are of considerable systematic relevance at both generic and specific levels. The main structures of taxonomic interest in the seed epidermis of the Solanaceae are the anticlinal walls and the disintegrated outer periclinal wall during seed development. Enzyme etching is done in cases where a persistent outer periclinal wall is present (Lester & Durrands, 1984). The mature anticlinal walls and inner periclinal walls are unevenly thickened by depositions of secondary wall materials, imparting a pyramidal or triangular appearance in transverse section. Further, uneven depositions near the outer periclinal walls produce appendages such as hairs, spurious hairs, pseudohairs, hair-like structures, scales and zigzag outgrowths (Corner, 1976; Edmonds, 1983). The shapes of the anticlinal walls and their projections have been found to be specific to species or sections of the genus (Edmonds, 1983).

The lateral seed coat walls or the anticlinal walls of spermoderm cells of solanaceous seeds are composed of thickened more or less pyramidal bases topped by a wide variety of elongate lignified

projections (Talebi *et al.*, 2012), which are often connected by thinner membraneous sections of materials called fibrils. Fibrils, common in most species of Solanaceae are found in *S. americanum*, *S. pseudocapsicum*, *S. violaceum* subsp. *violaceum*, *S. trilobatum*, *S. mauritianum*, *S. aculeatissimum* and *S. macrocarpon* though the type, nature as well as the distribution vary obviously (Fig. 1f,h; Fig. 2d,h; Fig. 3g,h; Fig. 4a,b,c,d). The longest and most conspicuous fibrillar hairs were observed in *S. seaforthianum* (Fig. 4e,f). *Solanum americanum* too has short profuse hairs imparting the characteristic surface view to the seeds. In other species, it can be broad fibrillar network as in *S. trilobatum*; and broad finger-like lacinations which become intact towards hilum as in *S. violaceum* subsp. *violaceum*. The cerebelloid pattern in *S. pseudocapsicum* shows broad thread-like fibrillar outgrowths relative to the cell shape. In *S. aculeatissimum*, the distal fibrillar projections are ribbon-like, seen along the boundary of the cells and becoming inconspicuous towards the hilum region. Further, *S. mauritianum* displays small fibrillar projections at the apex of the anticlinal walls, which often organise into a consecutive row. Though the distal projections seen in *S. macrocarpon* resemble that of *S. pseudocapsicum*, they are somewhat broader and faint towards the hilum region. The spermoderm appears to exhibit a cerebelloid pattern in *S. americanum*, *S. pseudocapsicum*, *S. mammosum*, *S. erianthum* and *S. melongena* var. *insanum* (Fig. 1f,h; Fig. 3b,c; Fig. 4h) while *S. violaceum* subsp. *multiflorum* shows a feebly cerebelloid pattern (Fig. 2f). Further, the cerebelloid nature of *S. melongena* var. *insanum* is found to be most conspicuous among other taxa (Fig. 4g,h). A reticulate surface pattern is displayed by species such as *S. capsicoides*, *S. exarmatum*, *S. giganteum*, *S. violaceum* subsp. *violaceum*, *S. trilobatum*, *S.*

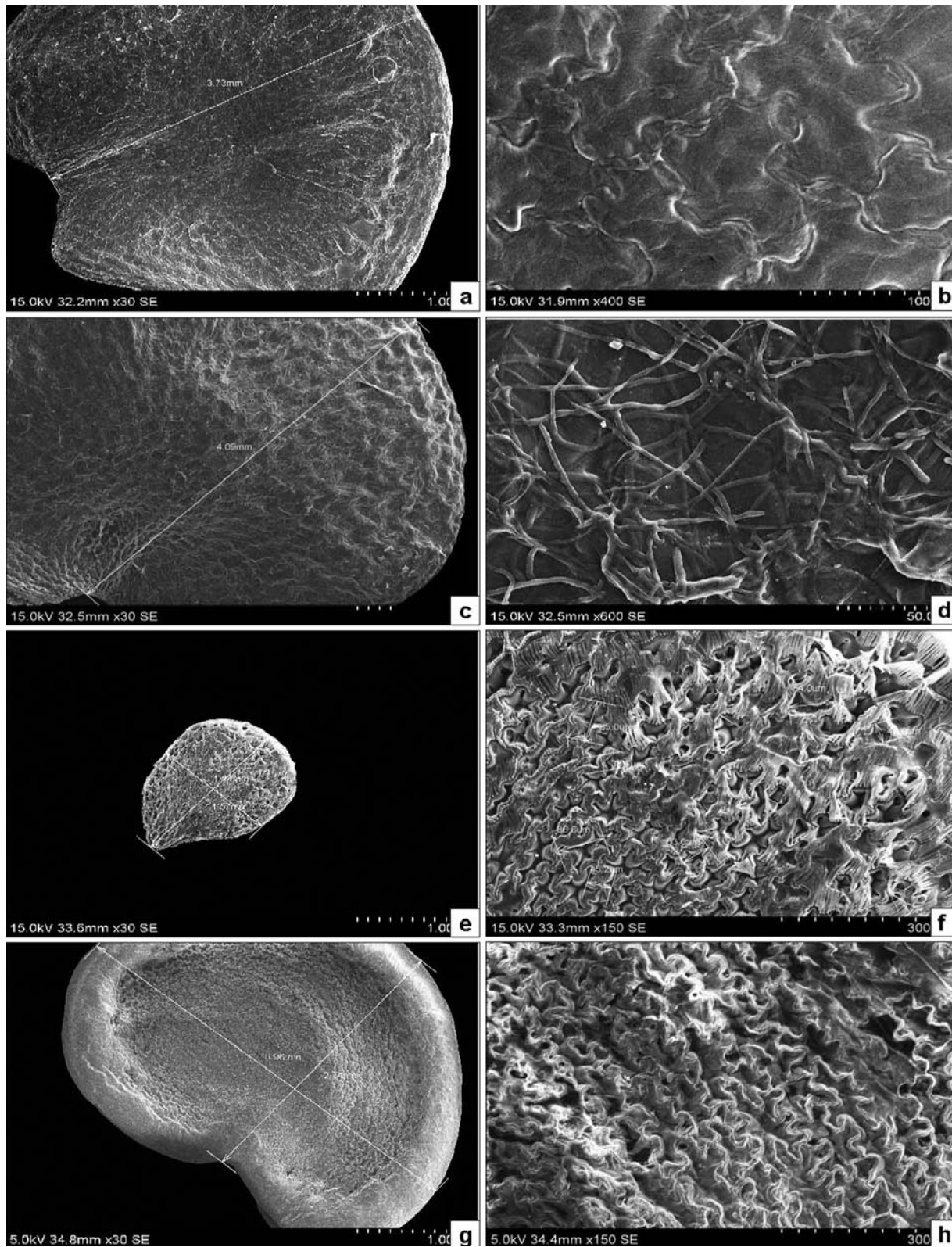


Fig. 1. Scanning electron micrograph of seed surface: a & b. *Solanum capsicoides*; c & d. *S. exarmatum*; e & f. *S. americanum*; g & h. *S. pseudocapsicum*.

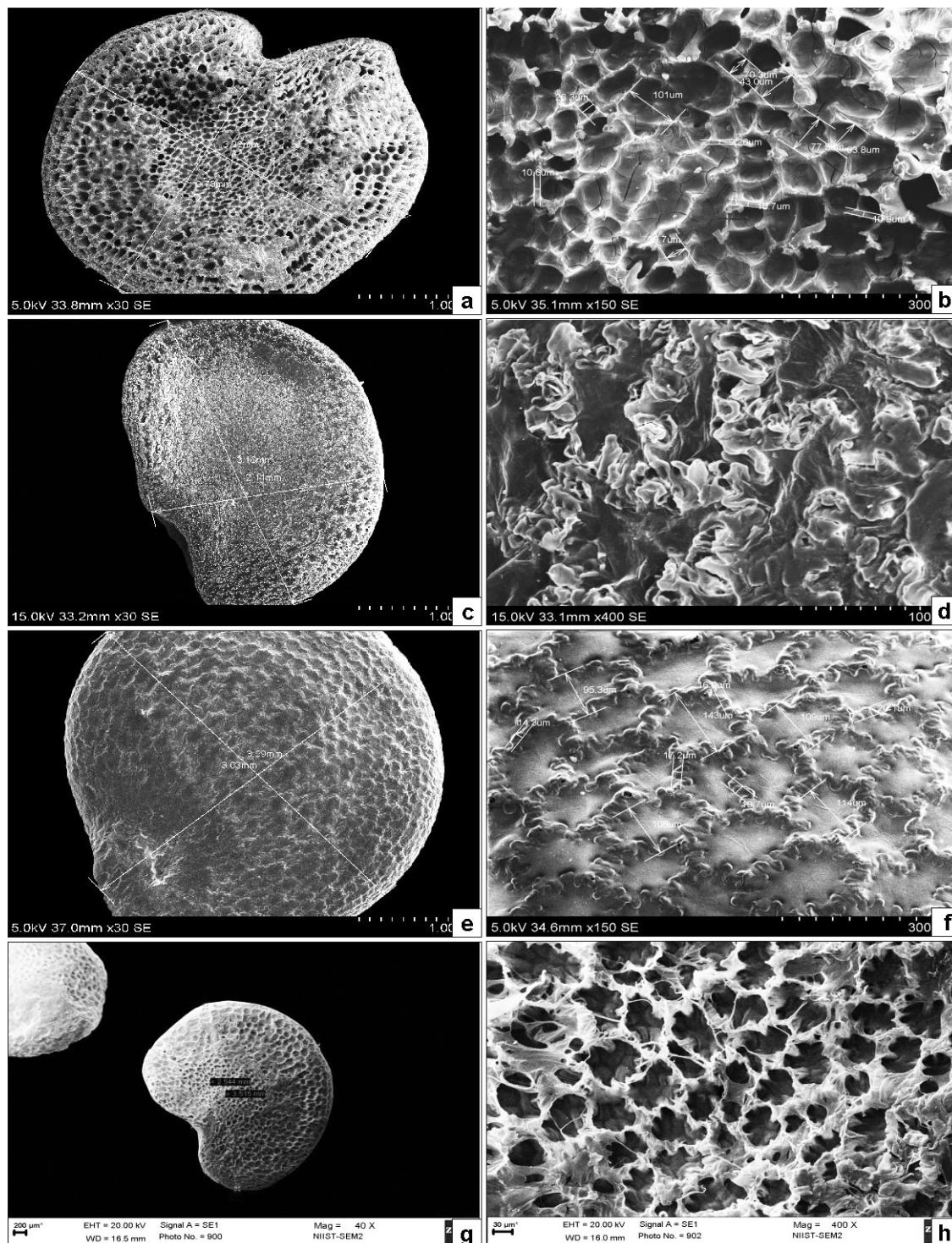


Fig. 2. Scanning electron micrograph of seed surface: a & b. *Solanum giganteum*; c & d. *S. violaceum* subsp. *violaceum*; e & f. *S. violaceum* subsp. *multiflorum*; g & h. *S. trilobatum*.

mauritianum and *S. macrocarpon* (Fig. 1b,d; Fig. 2b,d,h; Fig. 3h; Fig. 4d). It is interesting to note that the spermoderm is devoid of any conspicuous lumen in *S. torvum*, *S. aculeatissimum* (Fig. 3f; Fig. 4b) and in *S. searforthianum*, the actual seed surface is not at all visible due to long fibrils (Fig. 4f). Anil Kumar &

Murugan (2012) have studied the different accessions of *S. capsicoides* and found a few accessions that differ from the proper in having distinct seed surface patterns and other micromorphological features of pollen and trichomes. Later, it was established as a new species, *S. exarmatum* (Anil Kumar *et al.*, 2015).

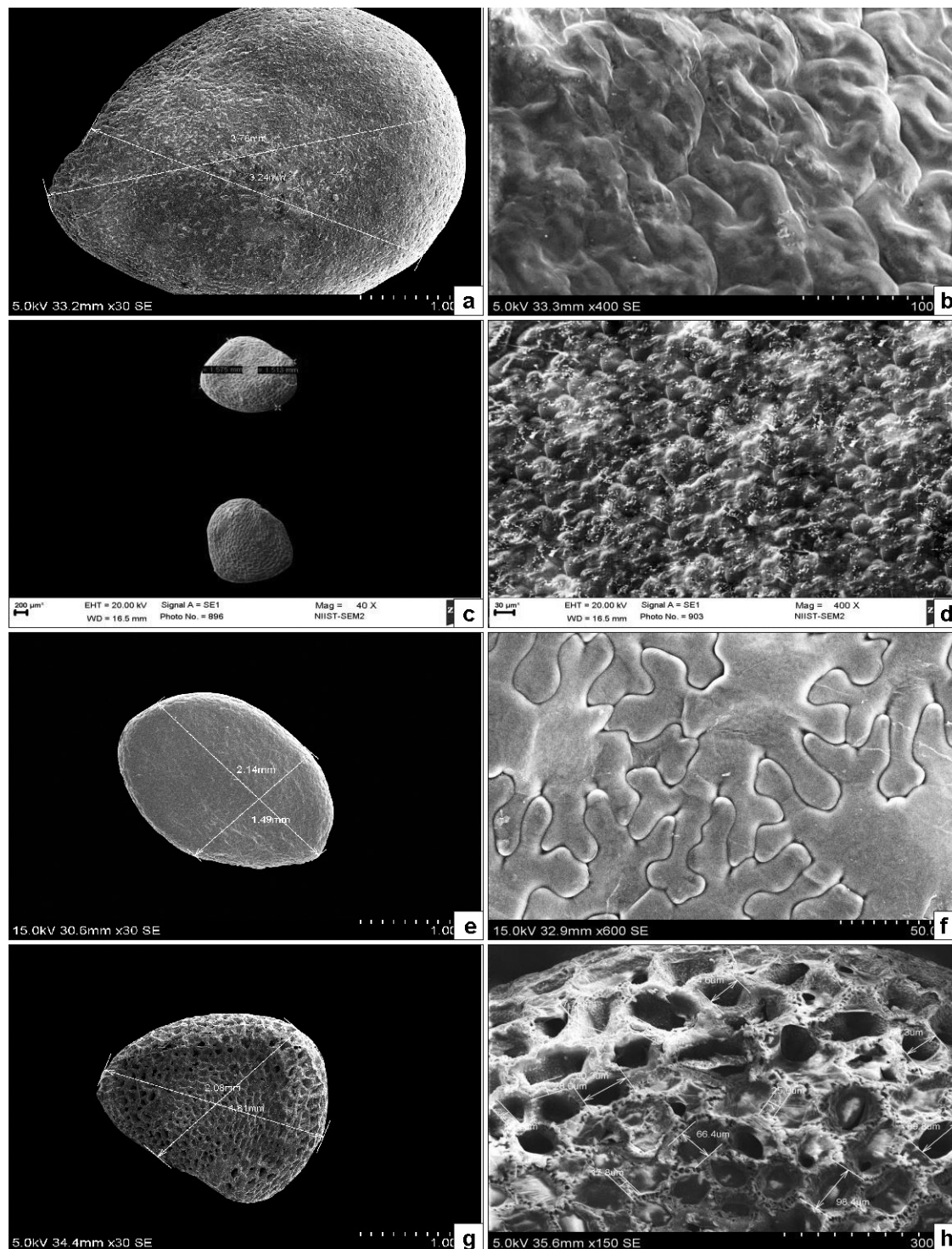


Fig. 3. Scanning electron micrograph of seed surface: a & b. *Solanum mammosum*; c & d. *S. erianthum*; e & f. *S. torvum*; g & h. *S. mauritianum*.

Hilum in most of the studied species was sunken, i.e., concave and subbasal in position (Fig. 5a–h; Fig. 6a). However, hilum is in basal position in species such as *S. capsicoides*, *S. exarmatum*, *S. giganteum*, *S. mauritianum*, *S. trilobatum* and *S. melongena* var. *insanum* (Fig. 6b–g).

Zhang *et al.* (2005) attempted in grouping species based on these spermoderm architectural patterns. Overall appearance of the spermoderm, cell shape, degree of sinuosity of cell wall, distal appendages on the anticlinal cell walls and type of lateral testal cell wall ornamentations are

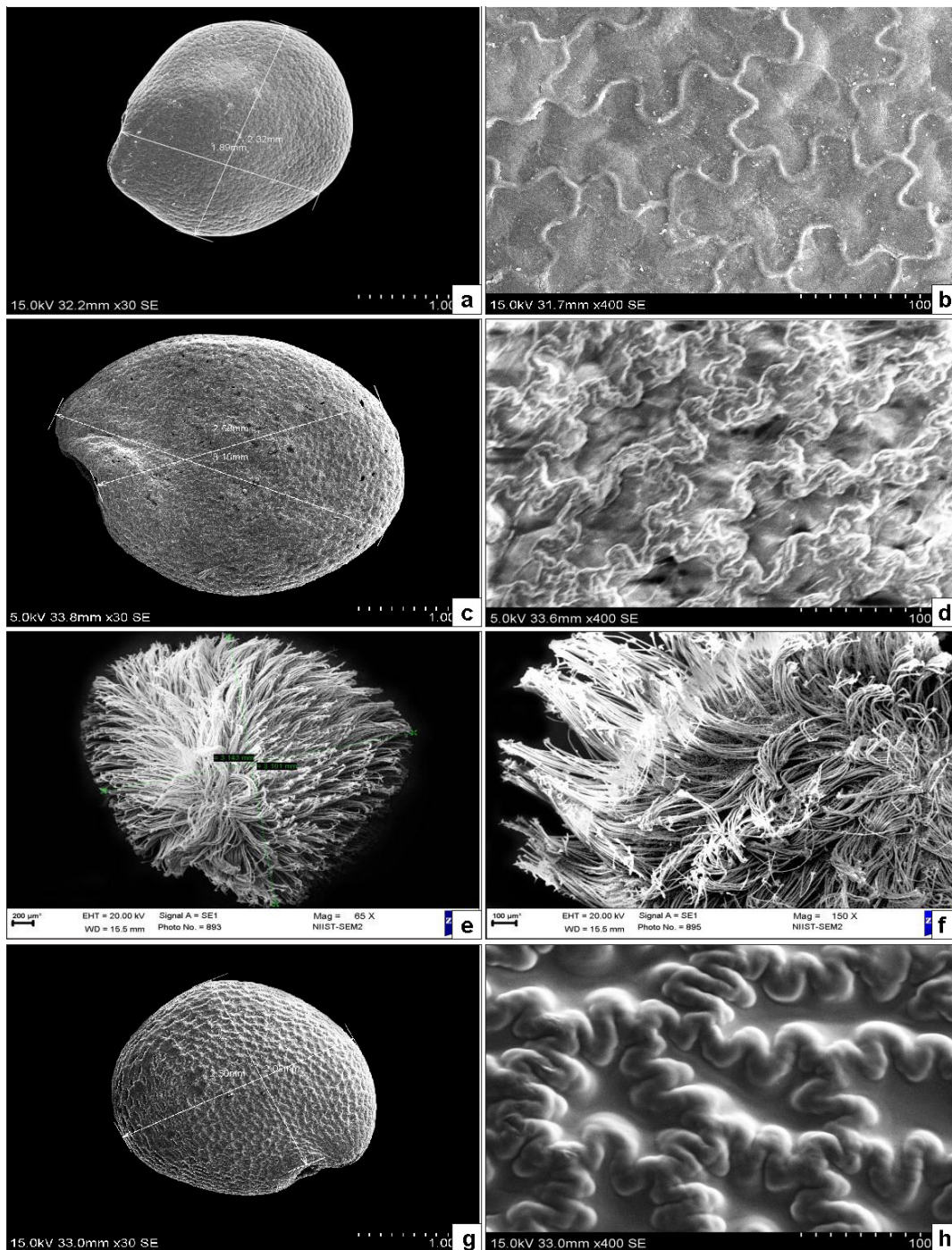


Fig. 4. Scanning electron micrograph of seed surface: a & b. *Solanum aculeatissimum*; c & d. *S. macrocarpon*; e & f. *S. seaforthianum*; g & h. *S. melongena* var. *insanum*.

employed in the present study for discriminating species. The species clustering attempted is as follows:

1. Based on overall appearance of the spermoderm

A. Cerebellod type – *S. pseudocapsicum*, *S. americanum*, *S. melongena* var. *insanum*, *S. mammosum*, *S. erianthum*

B. Faintly cerebellod – *S. violaceum* subsp. *multiflorum*

C. Reticulate – *S. giganteum*, *S. mauritianum*, *S. trilobatum*, *S. capsicoides*, *S. exarmatum*, *S. macrocarpon*, *S. violaceum* subsp. *violaceum*

D. Without conspicuous cell lumen – *S. torvum*, *S. aculeatissimum*, *S. seaforthianum*

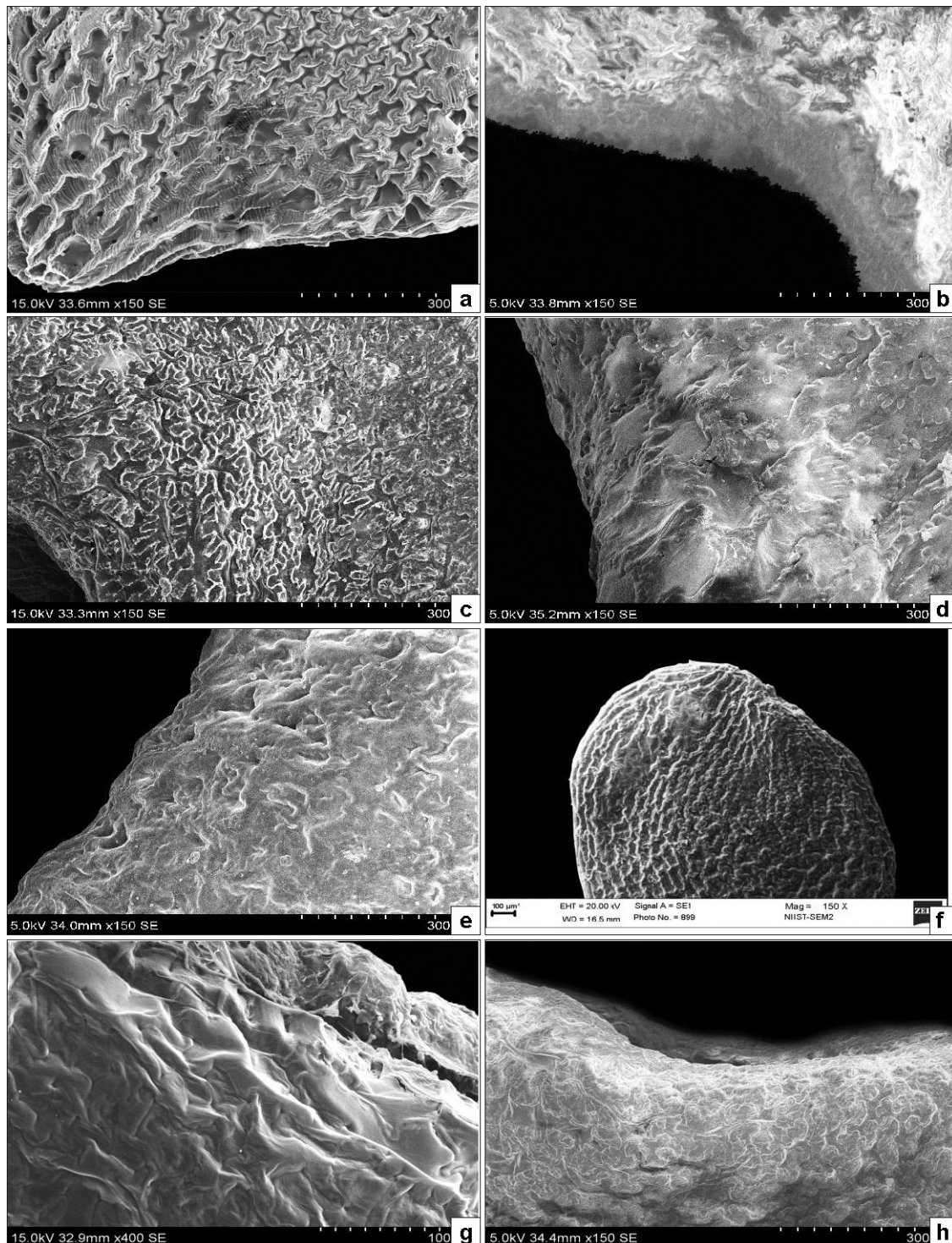


Fig. 5. Scanning electron micrograph of subbasal portion of hilum: a. *Solanum americanum*; b. *S. pseudocapsicum*; c. *S. violaceum* subsp. *violaceum*; d. *S. violaceum* subsp. *multiflorum*; e. *S. mammosum*; f. *S. erianthum*; g. *S. torvum*; h. *S. macrocarpon*.

2. Based on overall cell shape and degree of sinuosity of the cell walls

A. Polygonal to subrounded in shape, isodiametric or nearly isodiametric – *S. mauritianum*, *S. violaceum* subsp. *multiflorum*, *S. trilobatum*, *S. violaceum* subsp. *violaceum*

B. Not isodiametric – *S. giganteum*, *S. pseudocapsicum*, *S. torvum*, *S. americanum*, *S. capsicoides*, *S. exarmatum*, *S. macrocarpon*, *S. aculeatissimum*, *S. melongena* var. *insanum*, *S. mammosum*, *S. erianthum*

C. Cells not distinct – *S. seforthianum* (due to profuse surface hairs)

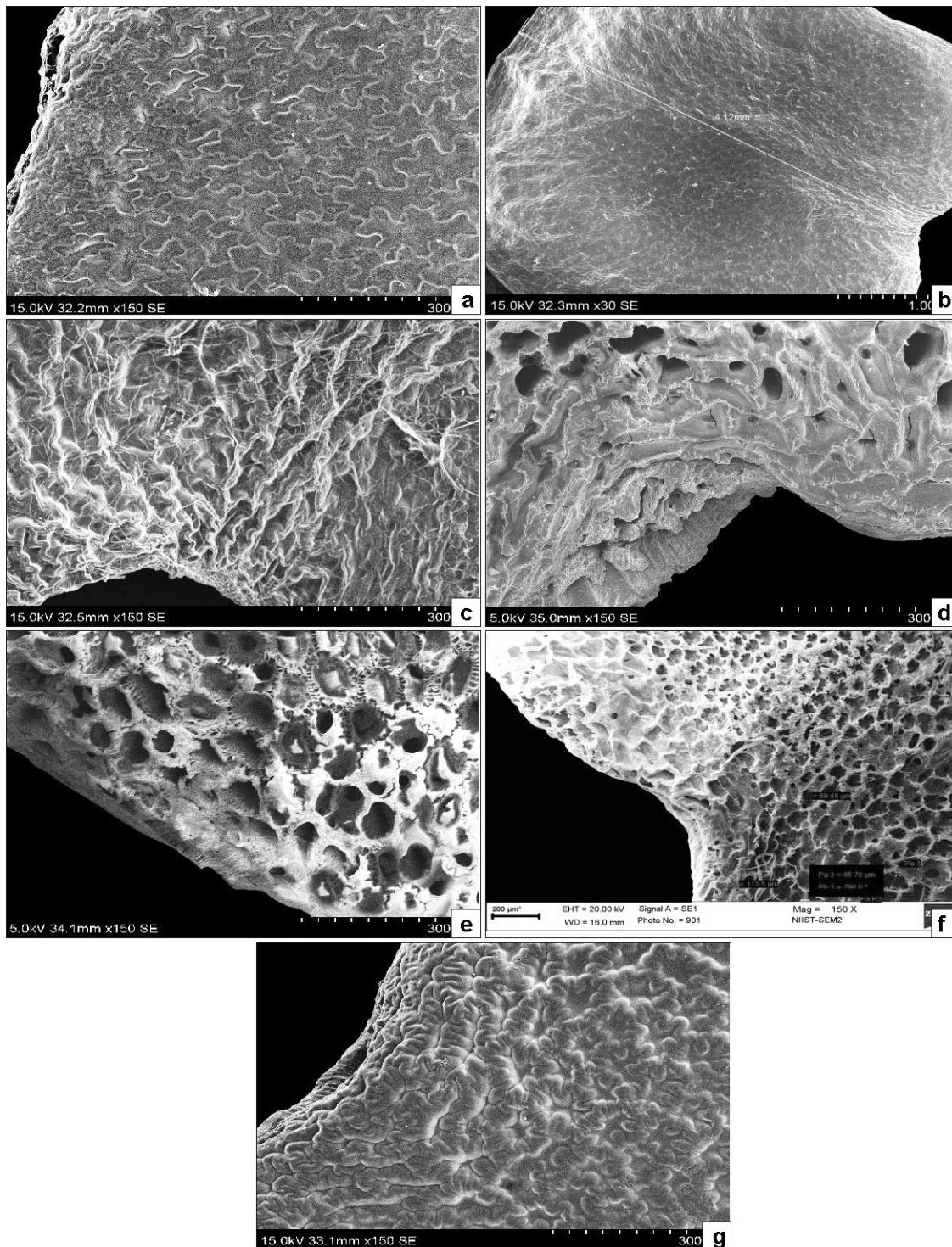


Fig. 6. Scanning electron micrograph of subbasal portion of hilum: a. *Solanum aculeatissimum*; b. *S. capsicoides*; c. *S. exarmatum*; d. *S. giganteum*; e. *S. mauritanum*; f. *S. trilobatum*; g. *S. torvum*; h. *S. melongena* var. *insanum*.

3. Based on distal appendages of the anticlinal cell walls

A. Essentially absent – *S. giganteum*, *S. violaceum* subsp. *multiflorum*, *S. torvum*, *S. capsicoides*, *S. exarmatum*, *S. melongena* var. *insanum*, *S. mammosum*, *S. erianthum*

B. Projections with differentiated finger like lacinia-tions or fibrils – *S. americanum*, *S. aculeatissimum*, *S. pseudocapsicum*, *S. mauritanum*, *S. trilobatum*, *S. violaceum* subsp. *violaceum*, *S. macrocarpon*, *S. seaforthianum*

4. Based on type of lateral testal cell wall ornamentations

- A. Lateral testal cell walls smooth without ornamentations – *S. violaceum* subsp. *multiflorum*, *S. pseudocapsicum*, *S. americanum*, *S. melongena* var. *insanum*, *S. mammosum*, *S. erianthum*
- B. Lateral cell walls smooth but penetrate near the base – *S. mauritianum*
- C. Lateral testal cell walls sparsely or densely papillate or tuberculate – *S. giganteum*, *S. trilobatum*, *S. capsicoides*, *S. exarmatum* (as seen towards the hilum), *S. macrocarpon*, *S. violaceum* subsp. *violaceum*
- D. Lateral testal cell walls not prominent due to inconspicuous lumen – *S. torvum*, *S. aculeatissimum*, *S. capsicoides*, and *S. exarmatum* (as seen on the majority of seed surface).
- E. Lateral testal cell walls not visible and luxuriant growth of long fibrillar hairs cover the seed surface – *S. seaforthianum*

Micromorphology and ultrastructural data have contributed useful information for the modern synthetic systems and classification of angiosperms (Ray et al., 2014). The spermoderm sculpturing features were positively employed at generic level to distinguish *Physalis*, *Capsicum* and *Tubocapsicum* (Zhang & Lu, 1999). In *Solanum*, seed morphology has been useful in distinguishing species groups, closely related species or species complexes (Junlakitjawat et al., 2010). Karihaloo & Malik (1996) explored the surface sculpturing of two *Solanum* species of the subgenus *Leptostemonum* – *Solanum melongena* and *S. violaceum*. SEM data of *Solanum* species suggest that seed coat sculpturing is a useful tool in systematics and can delineate taxa that show apparent phenotypic resemblance. Spermoderm sculpturing pattern helps to segregate *Solanum* species into groups: reticulate, irregularly striate-reticulate, and cerebelloid. The shapes of testal cells in *Solanum* are: irregular, oblong/polygonal or nearly isodiametric.

Ray et al. (2014) evaluated seed micromorphological features of ten accessions of winged bean *Psophocarpus tetragonolobus* (L.) DC. in terms of size, shape, colour, hilum size and surface ornamentation pattern for effective subspecific demarcations. Junlakitjawat et al. (2010) attempted SEM analysis of *Solanum aculeatissimum*, *S. erianthum*, *S. violaceum*, *S. mammosum*, *S. americanum* Mill., *S. sanitwongsei* Craib, *S. spirale* Roxb., *S. stramonifolium* Jacq. and *S. trilobatum* collected from Thailand using primary and secondary wall features. Chakrabarti

et al. (2003) differentiated cultivars of tomato based on pore nature, wall type and hair types. A total of 17 legume species belonging to *Crotalaria* L., *Alysicarpus* (L.) DC. and *Indigofera* L. were examined for seed exomorphic features and resolved problems of systematics at species level. Similarly, 19 species of *Epilobium* are categorised into four groups based on seed characters such as irregular cell walls forming reticulum, seeds with papillae, seeds with ridges and seeds with pits (Saxen, 2011). The present study supports and extends the use of seed coat patterns for species identification.

Conclusion

Micromorphology of seed coat of 16 genotypes of *Solanum* was analysed. The study revealed marked differences in surface architectural patterns that can delineate the species. Various criteria specifically related to spermoderm sculpturing characteristics resulted in grouping of *Solanum* species reflecting their specific seed coat features. The wide variation in spermoderm morphology together with other plant morphological features are very useful in distinguishing different species of *Solanum* and suggests that SEM studies of seed morphology may help to solve taxonomic issues in other taxa.

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