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Pollen morphology of selected taxa of the genus *Solanum* from Southern Western Ghats, Kerala, India

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Abstract

Pollen morphology of 18 taxa of *Solanum* from Kerala has been analyzed on an evolutionary perspective on palynological relationship shared by the wild taxa and the cultivated ones. The exine ornamentation in wild germplasm ranges from spinulose (*S. mauritianum* Scop. and *S. wendlandii* Hook.f) to granulose (*S. giganteum* Jacq. and *S. trilobatum* L.), from synechinulate to striate echinulate in shrubby taxa and from echinulose to granulose in herbaceous forms. But the cultivar germplasm uniformly showed a mammilate – echinulate exine ornamentation with lax distribution of projecting elements. The stragglers and lianas of the germplasm *viz. S. trilobatum, S. seaforthianum* Andr. and *S. wendlandii* showed a tendency for multi-bridging at the colpi region and the trees, *viz. S. giganteum, S. mauritianum* and *S. erianthum* D.Don. showed ornamented colpi with slight tendency for bridging at the region of apertures. Traits like multibridging, compact exine ornamentation and prominent operculum characterize the wild species which makes them better adapted against environmental and biotic stresses. While the wild taxa have well developed aspis and operculum, the domesticated species such as *S. melongena* L. 'Neelima', *S. mammosum* L., *S. macrocarpon* L. and *S. melongena* L. var. *insanum* (L.) Praine. were having only a feebly developed aspis and operculum as an indication of less protection which in turn is an indication for secondary evolution.

Keywords: Pollen morphology; Solanaceae, *Solanum*, Western Ghats, Kerala

Introduction

With great diversity of habitats, morphology and ecological adaptations, the family Solanaceae consists of about 100 genera together with *c.* 2500 representative species (Olmstead & Bohs, 2007) in tropical and temperate regions with the major dispersal centres being Australia and Latin America (Barroso *et al.*, 1991). Plant taxonomic studies successfully incorporate microspore morphology, as the traits of pollen are under the selective forces coupled with the processes of pollination, dispersal and germination (Moore *et al.*, 1991; Stuessy, 1990). Pollen morphology of various members of the family Solanaceae has been studied by different workers from time to time (Natarajan, 1957; Murray & Eshbaug, 1971; Raghuvanshi, 1974; Sharma, 1974; Anderson & Gensel, 1976; Palri & Koch, 1976; Anderson, 1977; Srivastava, 1977; Edmonds, 1984; Gentry, 1986; Plowman, 1998; Persson *et al.*, 1999). Early reports suggest the distribution of tricolporate pollen grains with scabrate tectum as the most common morphology found in the family and the striking variations being assigned to the shape class, apertural types and tectal surface (Lashin, 2012).

The pollen morphology of *Solanum* species had been a subject of interest for various researchers across the globe from time to time (Perveen & Qaiser, 2007; Al-Wadi & Lashin, 2007; Franklim & Esteves, 2008; Lashin, 2012). Palynological approaches have also been attempted in various genera under the family Solanaceae (Punt & Monna-Brands, 1977; Barth & Duarte, 2008; Martins *et al.*, 2013). The investigations on the palynomorphs of genus *Solanum*, (Salgado- Labouriau *et al.*, 1969; Sharma, 1974; Anderson & Gensel, 1976; Symon, 1981; Edmond, 1984; Roubik & Moreno, 1991) suggest a homogeneous morphological pattern to the pollen grains of this genus. Edmonds (1984) made significant contributions to the knowledge of infrageneric taxonomic groups for section *Solanum*.

However, a detailed phylogenetic approach has not been attempted on the pollen morphology of various species of *Solanum*. Indian *Solanum* species have not been given any comprehensive treatment after Clarke (1883) despite the significant contributions on these plants from other parts of the world. Except for the preliminary investigations on the comparative analysis of the size of the grains of six medicinally important species of the genus (Vijayakumari & Vilasini, 2005), very few palynological studies have been carried out in the *Solanum* species of Kerala. It is in this background the present study has been undertaken with a view that the results of pollen analysis could be utilized in clarifying infraspecific taxonomic disputes of the taxa as well as for extracting the evolutionary tendencies with other species or subspecies. The morphological and palynological analysis of *Solanum* species have proved to be of immense assistance in interpreting problems related to taxonomy of different species.

Materials and Methods

The polliniferous materials of 14 species of *Solanum*, 2 subspecies and 1 variety, along with the cultivated *S. melongena* 'Neelima' were collected from Southern Western Ghat region of the state of Kerala, India between 8°30′0″latitude/ 76°55′12″ longitude and 9°51′0″ latitude / 76°56′24″ longitude. Collections were made during the flowering seasons from April to January and mature unopened flower buds were fixed in 70% alcohol. The anthers were carefully removed, crushed in distilled water, centrifuged at 1000 rpm and filtered through fine mesh. The pollen grains were acetolysed (Erdtman, 1958) and were subjected for ultra structural analysis under Scanning Electron Microscope (SU6600, Hitachi and Zeiss EVO 18). Pollen descriptions were made following Punt *et al*., (2007) and Hesse *et al*., (2007) by observing 75 grains under SEM at different magnifications.

Results

The analysis of the pollen morphology of selected species of *Solanum* from Western Ghat region of Kerala revealed inter - specific and intra specific pollen morphological variations. The results showed inter relationships among different species with respect to operculum, multibridging at the colpi and ora as well as ornamentations in the colpi region. Further, an evolutionary tendency in exine sculpturing can also be deduced as there is intense excrescence patterns in the wild germplasm in contrast to the negligent ornamentation patterns displayed by cultivar taxa as well as domesticated germplasm **.**

Domesticated vs Wild genetic resources of *Solanum*

The domesticated germplasm under consideration include the edible *Solanum melongena* 'Neelima' and *S. macrocarpon*, the medicinally potent *S. melongena* var. *insanum* and one ornamental taxa *S. mammosum* L.. The wild taxa included are *S. capsicoides* All., *S. exarmatum* Anil *et al.*, *S. mauritianum, S. giganteum, S. erianthum, S. pseudocapsicum* L., *S. trilobatum, S. wendlandii, S. seaforthianum, S. violaceum* Ortega subsp. *violaceum, S. violaceum* Ortega subsp. *multiflorum* (Clarke) Matthew., *S. aculeatissimum* Jacq., *S. torvum* Sw. and *S. americanum* Mill.

Pollen morphology of wild genetic resources

1. **Solanum aculeatissimum** Jacq.

Grains prolate spheroidal, 19.3–20.4 × 17.8–18.3 μm in polar view, 16.8–17.4 × 15.9–16.8 μm in equatorial view, trizonocolporate, operculate, aspis raised, arch-like and connate. Ornamentation echinate, with ornamented operculum and aspis (**Fig. 1. a–d**).

2. **Solanum americanum** Mill**.**

Grains prolate spheroidal, ranging between 12.1–12.44 × 12.2–12.56 μm in polar view and 12.9–13.42 × 12.9–13.15 μm in equatorial view, trizonocolporate with granulose - micro echinate exine ornamentation. Grains operculate and colpi with minute granules. Ridges are absent (**Fig.1. e –h**).

3. **Solanum capsicoides** All.

Grains heteromorphic, exhibiting trimorphism, triangular obtuse convex and trizonocolporate.

Type 1: Grains suboblate, in polar view it ranges between 20-21.9 μm and equatorially between 19–20.5 × 24.2–25.1 μm, brevicolporate, ora region aspidate, ornamentation echinate. The apocolpium region is with lax echinae. Operculum and aspis feebly developed (**Fig. 2. a–c**).

Type 2: Grains subprolate, equatorially elongated ranging between 21–22.7 × 18.5–19.1 μm, brevicolporate, with lax echinate ornamentation without prominent operculum (**Fig. 2. d**).

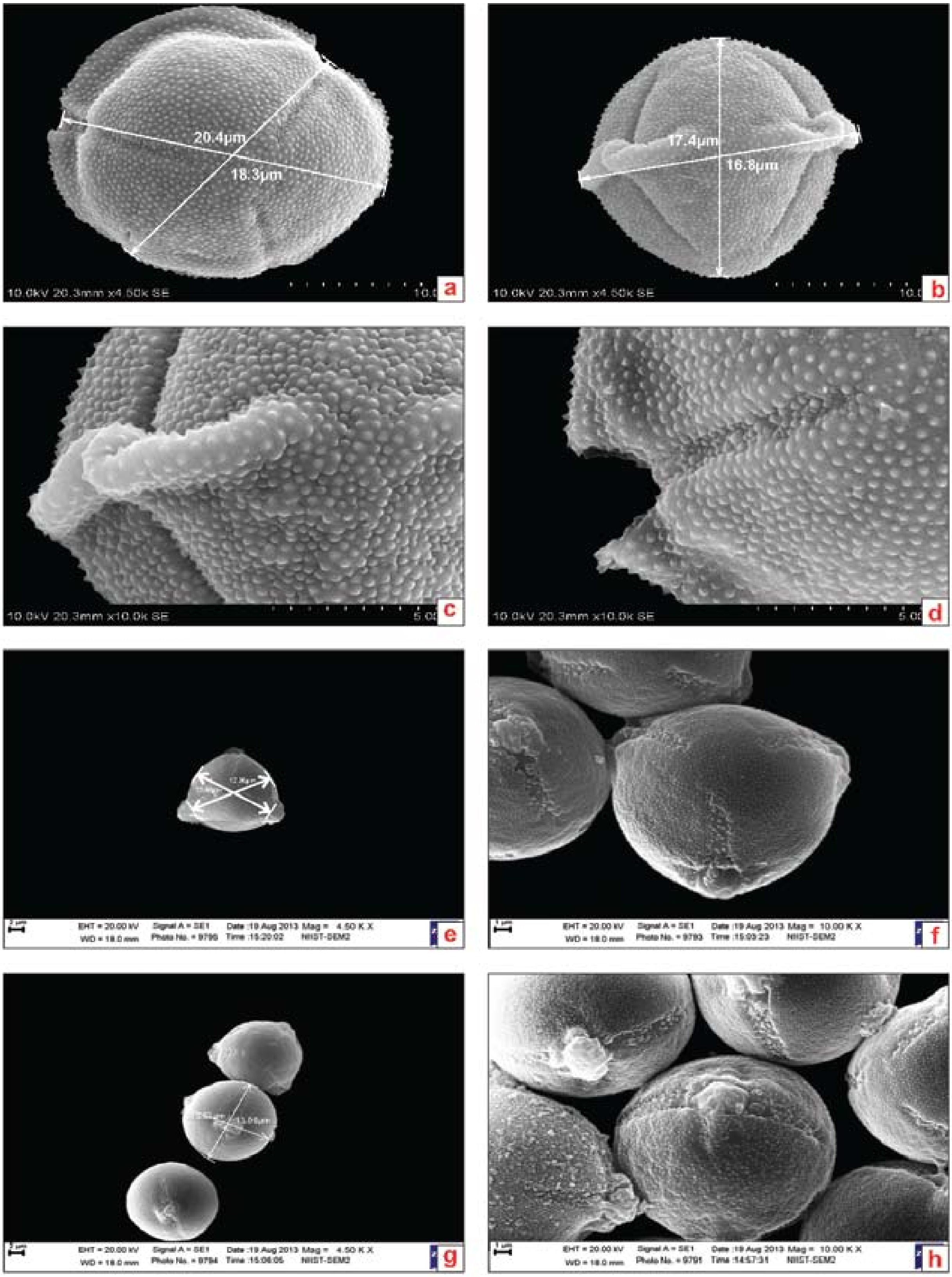

Fig.1. a–d. *Solanum aculeatissimum* Jacq.: **a.** Polar view; **b.** Equitorial view; **c.** Ornamented operculum; **d.** Exine ornamentation; **e–h.** *Solanum americanum* Mill.: **e.** Polar view; **f.** Microechinate exine; **g.** Equitorial view; **h.** Colpus showing minute granules.

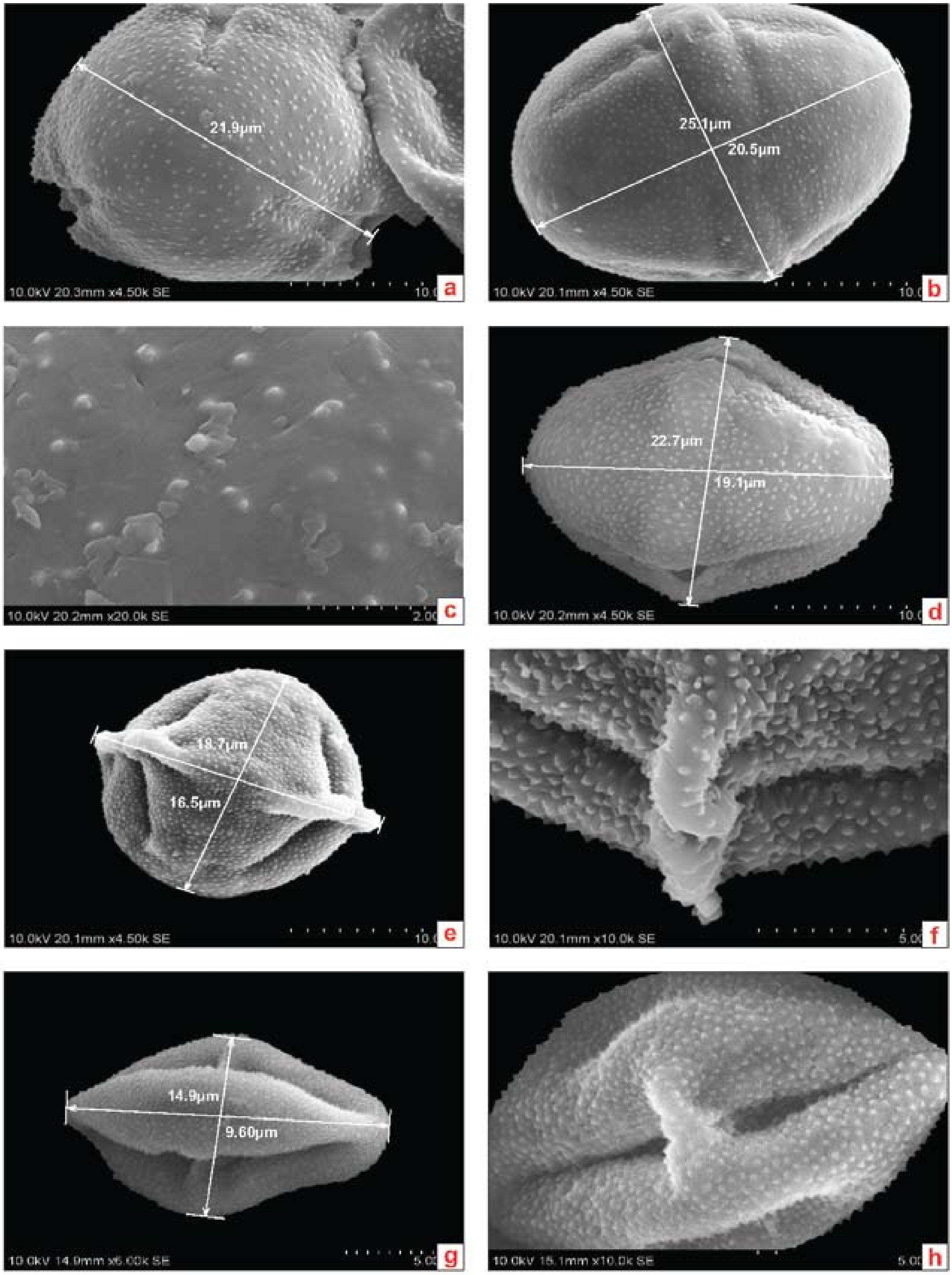

Fig. 2. a–f. *Solanum capsicoides* All.: **a.** Polar view of large grain; **b.** Equitorial view of large grain; **c.** Exine ornamentation of large grain; **d.** Medium sized grain in equitorial view; **e.** Equitorial view of small grain; **f.** Ornamented operculum of the small grain; **g** & **h.** *Solanum erianthum* D. Don.: **g.** Equitorial view; **h.** Colpus region showing ridges and bridging at ora.

Type 3: Grains prolate spheroidal, ranging between 18–18.7 × 15.5–16.5 µm with compact echinules, brevicolporate, having prominent finger like operculum with dense micro echinate ornamentation (**Fig.2. e – f**).

4. **Solanum erianthum** D.Don.

Grains prolate, equatorially elongated ranging between 13.2–14.9 × 8.2–9.5 µm, tri- zonocolporate, micro echinate, ridged, with bridging at the ora region (**Fig.2. g– h; Fig.3. a**).

5. **Solanum exarmatum** Anil, Maya, Soumya & K. Murugan

Grains heteromorphic, exhibiting dimorphism, triangular obtuse convex and trizonocolporate.

Type 1: Grains oblate spheroidal, polar view ranges between 19.5–20.5 µm across, equatorially between 23.5–24.51 × 24.2–25.6 µm, triangular obtuse convex and trizonocolporate, lalongate with thickened and ornamented margo. Ornamentation syn - micro echinate at random with horizontally joining projecting elements. Apocolpium is less ornamented with absence of syn – echinulae. Operculum and aspis feebly developed (**Fig.3. b– f**).

Type 2: Grains prolate spheroidal, 22.5–23.4 × 19.1–20.6 µm in equatorial view. In other traits, it resembles the type 1 (**Fig. 3.g**).

6. **Solanum giganteum** Jacq.

Grains subprolate, triangular in polar view with 20–20.31 × 18.3–18.64 µm across, obovate in equatorial view with 25.5–26.1 × 19.6–20.2 µm, trizonocolporate, ridged with granulose exine ornamentation (**Fig. 3.h; Fig.4. a & b**).

7. **Solanum mauritianum** Scop.

Grains subprolate, 17–17.46 × 16–16.30 µm in polar view and 16.6–16.81 × 14– 14.64 µm in equatorial view, trizonocolporate, exine ornamentation is spinulose. The colpi elongated with operculum and the colpus margin is ornamented (**Fig. 4. c– f**)

8. **Solanum pseudocapsicum** L.

Grains prolate spheroidal, 10.9–11.49 × 10.1–10.50 µm in polar view, 11–11.71 × 11.2–11.43 µm in equatorial view, trizonocolporate, exine with granulose ornamentation. The colpi are with compactly packed granules (**Fig. 4.g & h; Fig.5.a & b**).

9. **Solanum seaforthianum** Andr.

Grains spheroidal and monomorphic, measures between 13.8–14.2 × 13–13.3 µm in polar view and 15.8–16.2 × 15.9–16.2 µm in equatorial view, tetrazonocolporate, colpi fused in pairs, semi syncolpate, ornamentation micro echinate, bridge partial and adnate (**Fig. 5. c & d**).

10. **Solanum torvum** Sw.

Grains prolate spheroidal and mono morphic, 18.5–19.2 × 18.6–19.4 µm in polar view and 20.5–21.4 × 18.4–19.1 µm in equatorial view; trizonocolporate, micro echinate, operculate with connate aspis. Apocolpium with random echinulae, compact echinulae at mesocolpium and colpi margins. Colpi elongate (**Fig.5. e– h**).

11. **Solanum trilobatum** L.

Grains globose, triangular obtuse convex, 22–22.9 × 21–21.8 µm in polar view, trizonocolporate, operculum prominent and globular; Colpus is multi-bridged and aspis is absent; Exine ornamentation is granulate (**Fig.6. a–d**).

12. **Solanum violaceum** Ortega. subsp. **multiflorum** (Clarke) Matthew

Grains prolate spheroidal, 20–20.47 × 18.8–19.95 µm in polar view and 20.5–21.55 × 19.8–20.39 µm in equatorial view, trizonocolporate, ora lalongate and ornamentation is densely micro echinate (**Fig.6.e–g**).

13. **Solanum violaceum** Ortega. subsp. **violaceum**

Accession vise variations were recorded in this species.

Type 1 (VSA 002 – accession from Thiruvananthapuram): Grains prolate spheroidal, 22–22.96 × 20.5–21.64 µm in polar view and 19.5–20.67 × 17.8–18.76 µm in equatorial view; triangular obtuse convex, trizonocolporate, aspis of adjacent colpi united, margo tuberculate, ora circular to elliptic. Ornamentation showed variation from micro echinate to syn micro echinate. Within this accession, some grains are with prominent ridge like operculum along with aspis while most grains are devoid of aspis and operculum (**Fig.6. h; Fig. 7. a–e**).

Type 2 (VSA 29 – accession from Idukki): Grains prolate spheroidal, trizonocolporate, aspis of adjacent colpi united, ora circular to elliptic.

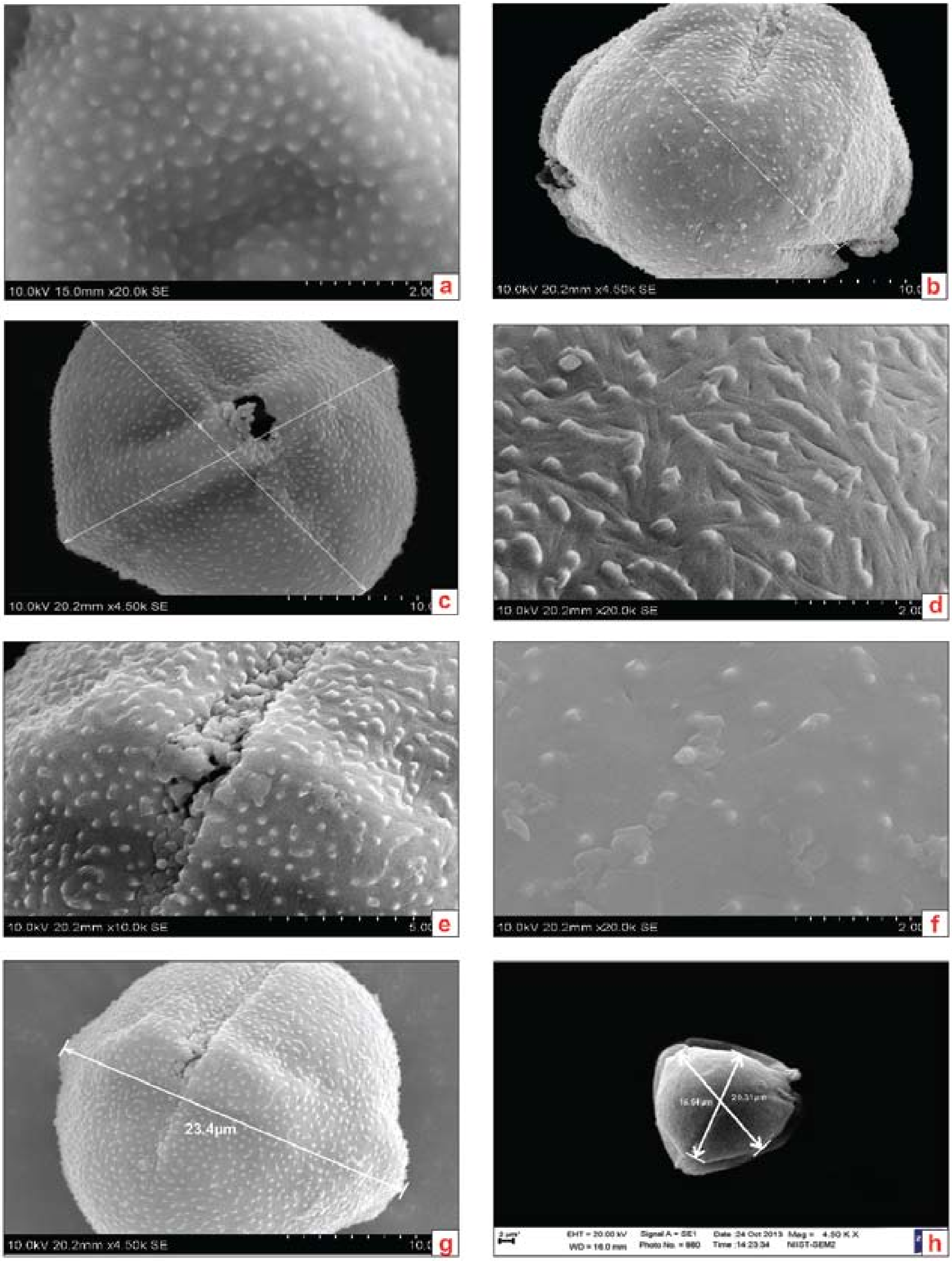

Fig. 3. a. *Solanum erianthum* D. Don.: Apocolpium region; **b–g.** *Solanum exarmatum* Anil *et al.*: (large grain); **b.** Polar view; **c.** Equitorial view; **d** & **e.** Syn microechinate ornamentation showing horizontally joining projecting elements; **f.** Apocolpium showing lax ornamentation; **g.** Medium sized grains. **h.** *Solanum giganteum* Jacq. polar view of grain.

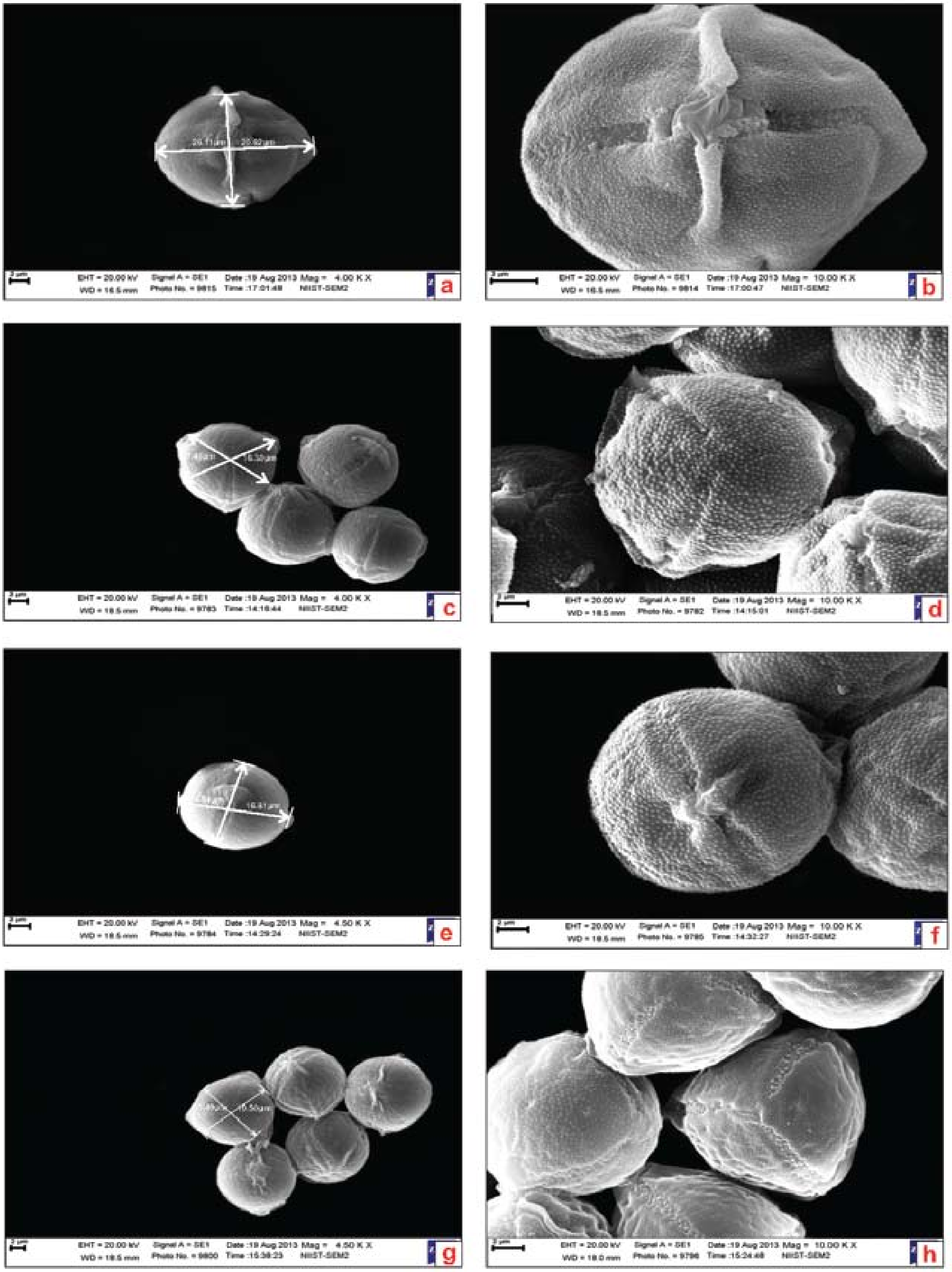

Fig. 4. a–b. *Solanum giganteum* Jacq.: **a.** Equitorial view; **b.** Colpus region with ridges. **c–f.** *Solanum mauritianum* Scop.: **c.** Polar view; **d.** Spinulose ornamentation at the apocolpium; **e.** Equitorial view; **f.** Ornamented colpus and operculum. **g** & **h.** *Solanum pseudocapsicum* L.: **g.** Polar view; **h.** Colpus with compact granules.

Operculum is ridge like and arched. Ornamentation showed variation in this accession from syn micro echinate, echinate, to striate micro echinate. The apocolpium displays triplex joining of projecting elements (**Fig. 7. f – h; Fig.8 a & b**).

14. **Solanum wendlandii** Hook.f.

Grains prolate spheroidal, ranging between 15–15.31 × 14.9–15.20 µm in polar view and 16–16.55 × 15–15.77 µm in equatorial view, trizonocolporate, ornamentation compact spinulose with globose operculum, tendency for multi-bridging for the colpi region (**Fig. 8. c – f**).

Pollen morphology of domesticated germplasm

1. **Solanum macrocarpon** L.

Grains prolate spheroidal, 20–20.72 × 20–20.49 µm in polar view and 20–20.55 × 19.2–19.54 µm in equatorial view, trizonocolporate with connate operculum and ridge at pore region. Exine ornamentation is mammilate - echinate and the distribution of projecting elements are less at apocolpium than at mesocolpium (**Fig. 8. g & h; Fig. 9. a – d**).

2. **Solanum mammosum** L.

Grains subprolate, ranging between 20–20.42 × 19–19.71µm in polar view and 20 – 20.97 × 17–17.18 µm in equatorial view, trizonocolporate with operculum and the colpi are syncolpate at one plane. Exine ornamentation is mammilate with swollen basal cushion overtopped by minute spinules (**Fig. 9. e–h; Fig. 10. a & b**).

3. **Solanum melongena** L.var. **insanum** (L.) Praine.

Grains dimorphic with tri and tetrazonocolporate apertural systems and compact mammilate exine ornamentation.

Type 1: Grains are triangular obtuse convex, tri zono colporate. (18–18.6 × 17–17.83 µm in polar view and 19–20 µm along the equatorial plane). Absence of ridge and aspis is a striking difference from non- cultivars. Grains are with compactly placed mammilate exine ornamentation (**Fig .10. c–h**).

Type 2: Grains are spheroidal, tetrazonocolporate, 23.8–24 × 23–23.5µm across, non operculate with absence of aspis. Ornamentation at mesocolpium is different from apocolpium. At mesocolpium region, clumped masses of projecting elements with horizontal joining at the colpi margin could be observed and the elements are mammilate in appearance (**Fig. 10. g & h**).

4. **Solanum melongena** L.'**Neelima'**

Grains prolate spheroidal, ranging between 21–22 × 19–19.6 µm in polar view and 24–24.5 × 22–22.4 µm in equatorial view. Trizonocolporate, ora lalongate and the connate aspis is not prominent as in other species. Ridge is absent. Exine ornamentation is mammilate - micro echinate (**Fig. 11. a–d**).

Key to *Solanum* species based on SEM images of pollen grains

1. Pollen grains with feebly developed aspis and operculum ………………………………………… **2**
1. Pollen grains with well developed aspis and operculum …………………………………………… **5**
2. Exinemammillate……………….……………..**3**
2. Exine mammillate with spiny projections … **4**
3. Grains tri and tetrazonocolporate ……………… ……………………… **S. melongena var. insanum**
3. Grains trizonocolporate only …………………… ……………………………………… **S. mammosum**
4. Aperture region with a ridge .. **S. macrocarpon**
4. Aperture region without a ridge ……………… …………………………… **S. melongena 'Neelima'**
5. Grains trizonocolporate and heteromorphic .. **6**
5. Grains trizonocolporate and monomorphic .. **7**
6. Heteromorphic grains exhibiting trimorphism ………………………………………… **S. capsicoides**
6. Heteromorphic grains exhibiting dimorphism ……………………………… **S. exarmatum**
7. Aperture with tendency for multibridging .. **8**
7. Aperture without tendency for multibridging ………………………………………………………… **13**
8. Aperture region without ornamentation but with multibridging throughout ……………… **9**
8. Aperture region is ornamented with slight tendency for bridging ……………………… **11**
9. Colpi partially fused forming semi syncolpi with micro echinate ornamentation …………… ……………………………………… **S. seaforthianum**
9. Colpi without fusion ………………………… **10**
10. Grains triangular obtuse convex with granulose exine ………………… **S. trilobatum**
10. Grains prolate spheroidal with compact spinulose exine ………..…….. **S. wendlandii**

11. Width of grains upto 9.5 μm in equatorial plane …………………........… **S. erianthum**
11. Width of grains more than 9.5 μm in equatorial plane ……..….......................................…… **12**
12. Shape of grains triangular in polar view …………………........…………... **S. giganteum**
12. Shape of grains sub prolate in polar view ....…....……… **S. mauritianum**
13. Granules present in the colpi region …....**14**
13. Granules absent in the colpi region ……… **15**
14. Exine ornamentation granulose-micro echinate ……………....……... **S. americanum**
14. Exine ornamentation granulose with compact granules ………........…..... **S. pseudocapsicum**
15. Aspis connate with operculate condition .. **16**
15. Aspis not connate ….…………………........ **17**
16. Ornamentation echinate .. **S. aculeatissimum**
16. Ornamentation micro echinate ..… **S. torvum**
17. Ora circular to elliptic .... **S. violaceum subsp. violaceum**
17 Ora lalongate ………………………...................... ....…… **S. violaceum subsp. multiflorum**

Palynology has been useful in elucidating the probable lines of evolutionary trends (Diaz & Lifante,1991). Critical evaluation of the apertural morphoforms and nature of ora, operculum and aspis observed under present investigation agree with the general fact that the taxa have tri zono colporate apertures. Lashin (2011) made comparative analysis of six species of *Solanum* from Saudi Arabia and suggested that the pollen morphology is isopolar, symmetrical, trizonocolporate and the measurements of species under consideration showed overlapping. The natural lateral hybridization from indiscriminate mating may be operating in this complex and can be the reason for the observed size differences of the pollen grains. Similar observations have been made earlier in *Solanum cardiophyllum* Lindl. subsp *cardiophyllum* (Luna - Cavazos & Gara- Moy, 2002).

Earlier reports by Sharma (1974), Anderson & Gensel (1976), Symon (1981), Edmond (1984) and Roubik & Moreno (1991) stated uniform pollen traits with homogenous distribution among the different species of *Solanum* using light microscopy. But the present analysis of the ultrastructural observations through SEM displayed multi-faceted apertural patterns, exine ornamentations and protection measures for the haploid germplasm of the different species of *Solanum*.

The diverse habits exhibited by the different species of *Solanum* coupled with other features like adaptability to different climatic and edaphic zones, range of habitats, intensity of domestication and intercrossing might have played a key role in the development of typical pollen traits among the different species of the genus. The variability in pollen morphology exhibited by different accessions of *Solanum violaceum* subsp. *violaceum* procured from different geographical zones of Southern Western Ghats, showed the tendency for variation of the germplasm in accordance with the ecological pressure exerted by the habitats coupled with the processes of pollination and dispersal. The accession from Thiruvananthapuram is having pollen grains with and without prominent aspis and operculum, which explains the tendency of pollen evolution within the species i.e., from wild to domestic. While, the accession from Idukki retains the wild trait only i.e., prominently operculate grains having aspis without exhibiting the tendency for any germplasm evolution. Conspicuous operculum can be considered as an indication of developmental response of the germplasm against the imposed stresses and hence greater adaptability.

Moreover, the pollen morphological variability of two different collections of *Solanum capsicoides*, viz. (TBGT 24069 and TBGT 016) is another distinct indication of genetic variation coupled with the distribution of spines and morphology of pollen which resulted in delineating one of the accessions as a new species (Anil Kumar & Murugan, 2012; Anil kumar *et al*., 2015). In the spiny accession (retained as *Solanum capsicoides*), out of the three pollen morphoforms, the suboblate and subprolate grains are having feebly developed aspis and operculum whereas the prolate spheroidal grains are with much prominent operculum and aspis. This can also be considered as a tendency of the taxa to get adapted for domestication through intermediate pollen types. This is further supported by the pollen grains of the lax spiny accession (established as the new species i.e., *Solanum exarmatum*) which are having feebly developed operculum and thus show a tendency for evolution towards domesticated germplasm. It can be correlated with the evolution of a species with marked morphological variations from *S. capsicoides*. A similar feature is shown by *S. americanum* with edible fruits, in which the pollen grains display an inclination towards domestication with less

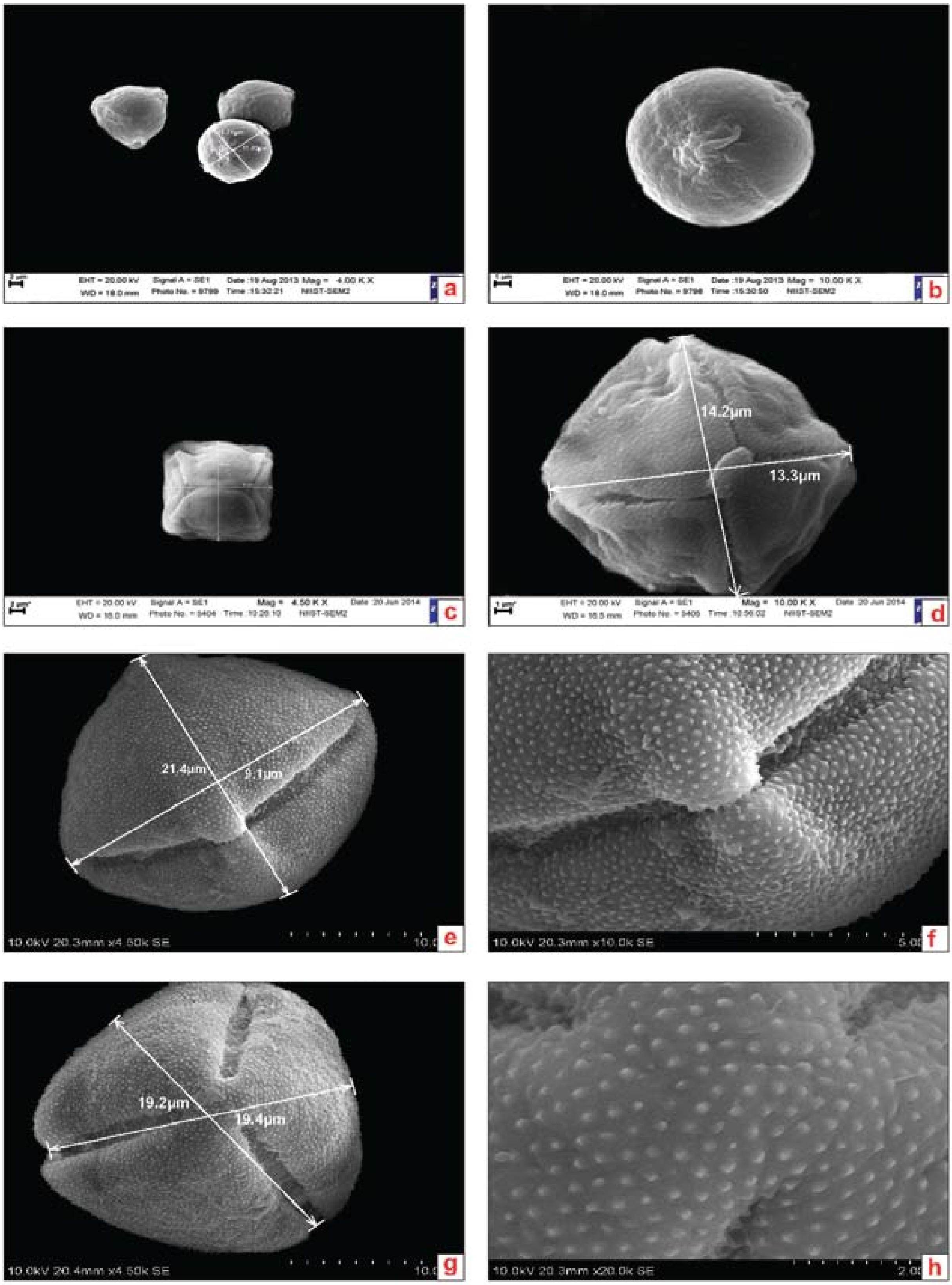

Fig. 5. a–b. *Solanum pseudocapsicum* L.: **a.** Equitorial view; **b.** Equitorial view showing colpus with ornamentation. **c** & **d.** *Solanum seaforthianum* Andr.: **c.** Equitorial view showing fused colpi; **d.** Polar view showing micro echinate ornamentation. **e–h.** *Solanum torvum* Sw.: **e.** equitorial view; **f.** Colpus region; **g.** Polar view; **h.** Apocolpium showing random echinulae.

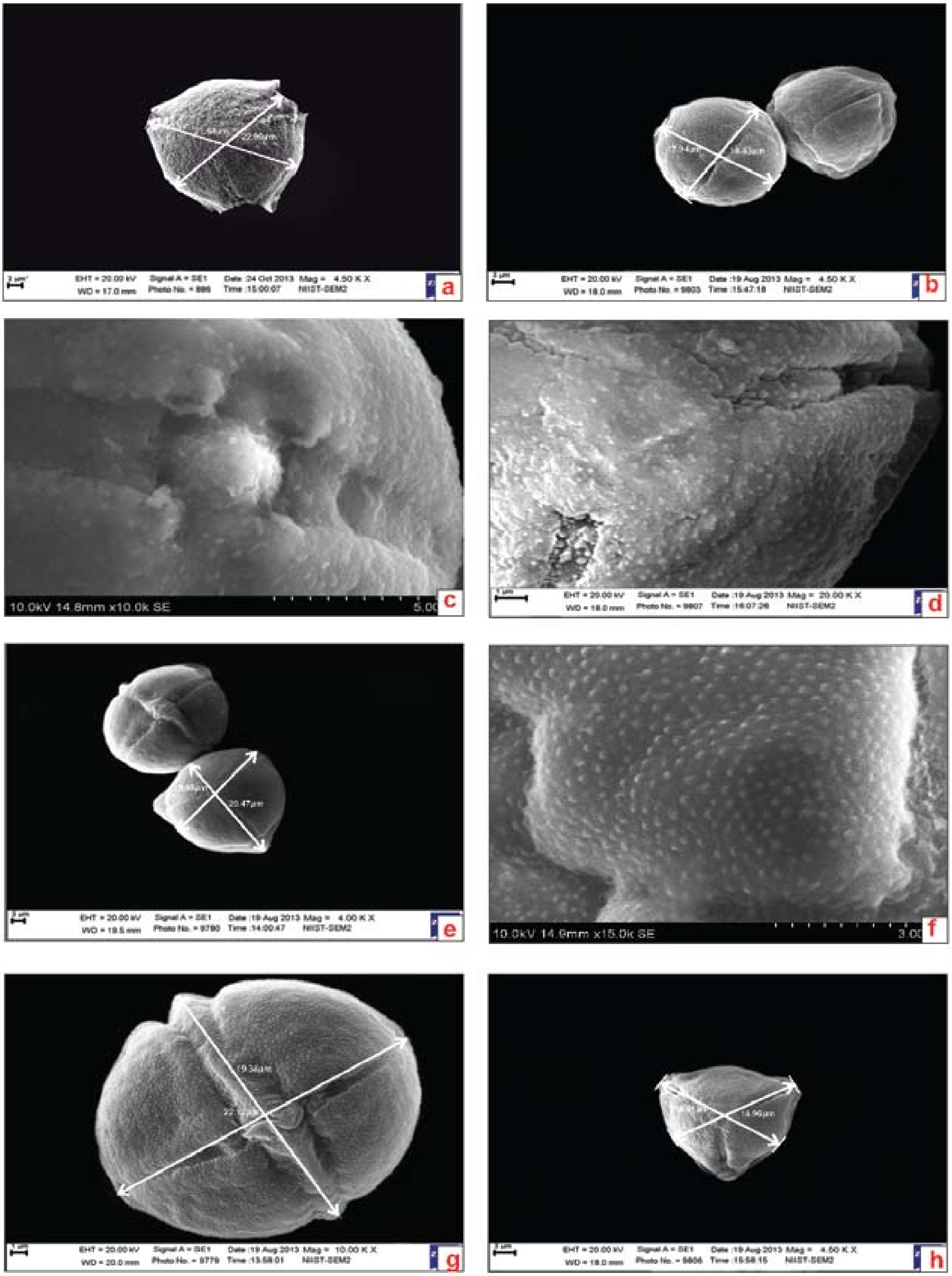

Fig. 6. a–d. *Solanum trilobatum* L.: **a.** Polar view; **b.** Equatorial view; **c.** Colpus region showing multi bridging; **d.** Apocolpium region. **e–g.** *Solanum violaceum* Ortega subsp. *multiflorum* (Clarke) Matthew: **e.** Polar view; **f.** Apocolpium showing micro echinate ornamentation; **g.** Equatorial view; **h.** *Solanum violaceum* Ortega. subsp. *violaceum*: Type 1 grain (accession from Thiruvananthapuram) polar view.

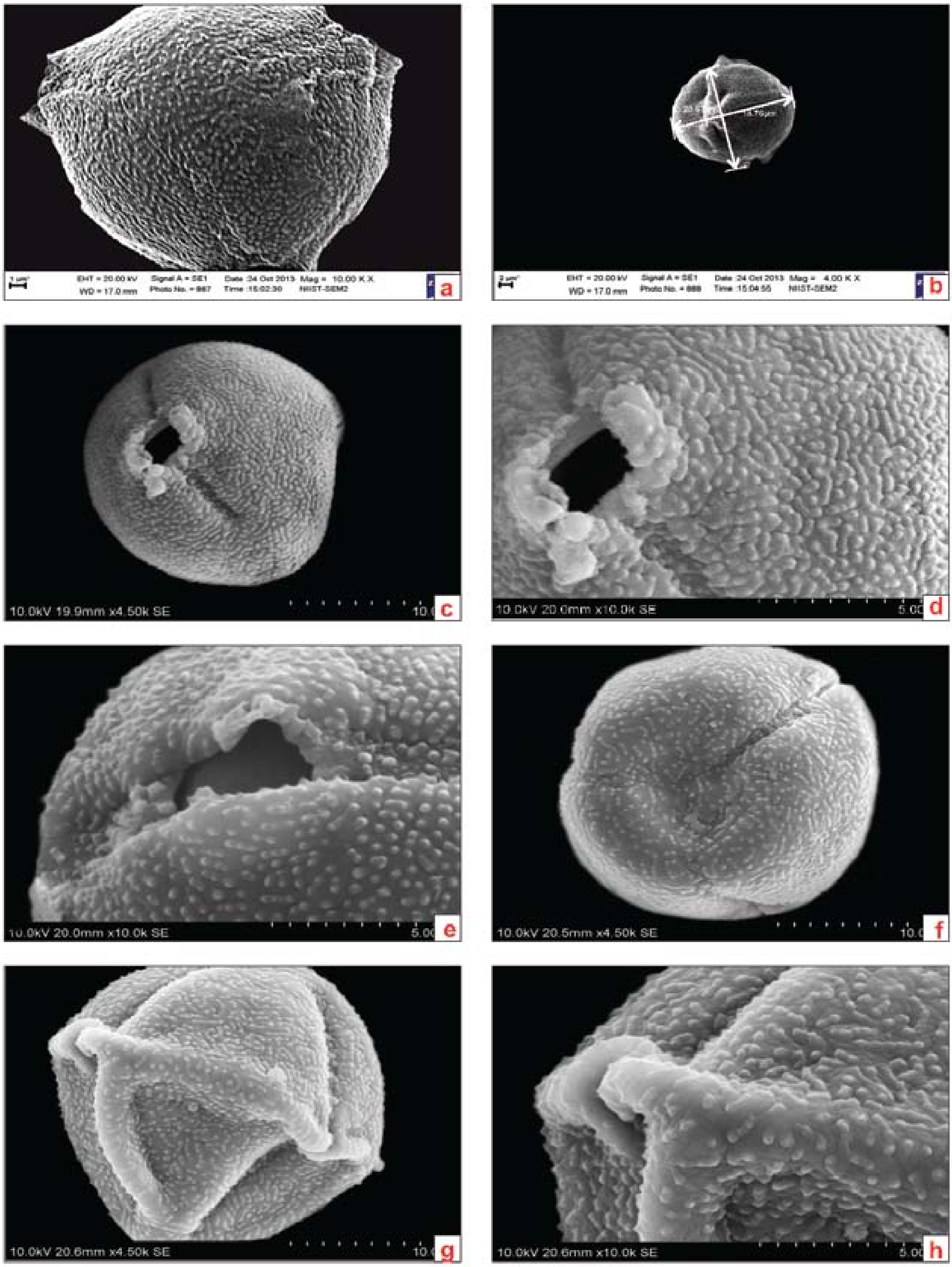

Fig. 7. a–h. *Solanum violaceum* Ortega. subsp. *violaceum* : **a.** Ornamentation of apocolpium; **b.** Equatorial view; **c.** Grain showing circular ora; **d.** Syn micro echinate ornamentation; **e.** Colpus region; **f–h.** Accession from Idukki (Type 2 grain) **f.** Polar view; **g.** Equatorial view; **h.** Operculum region.

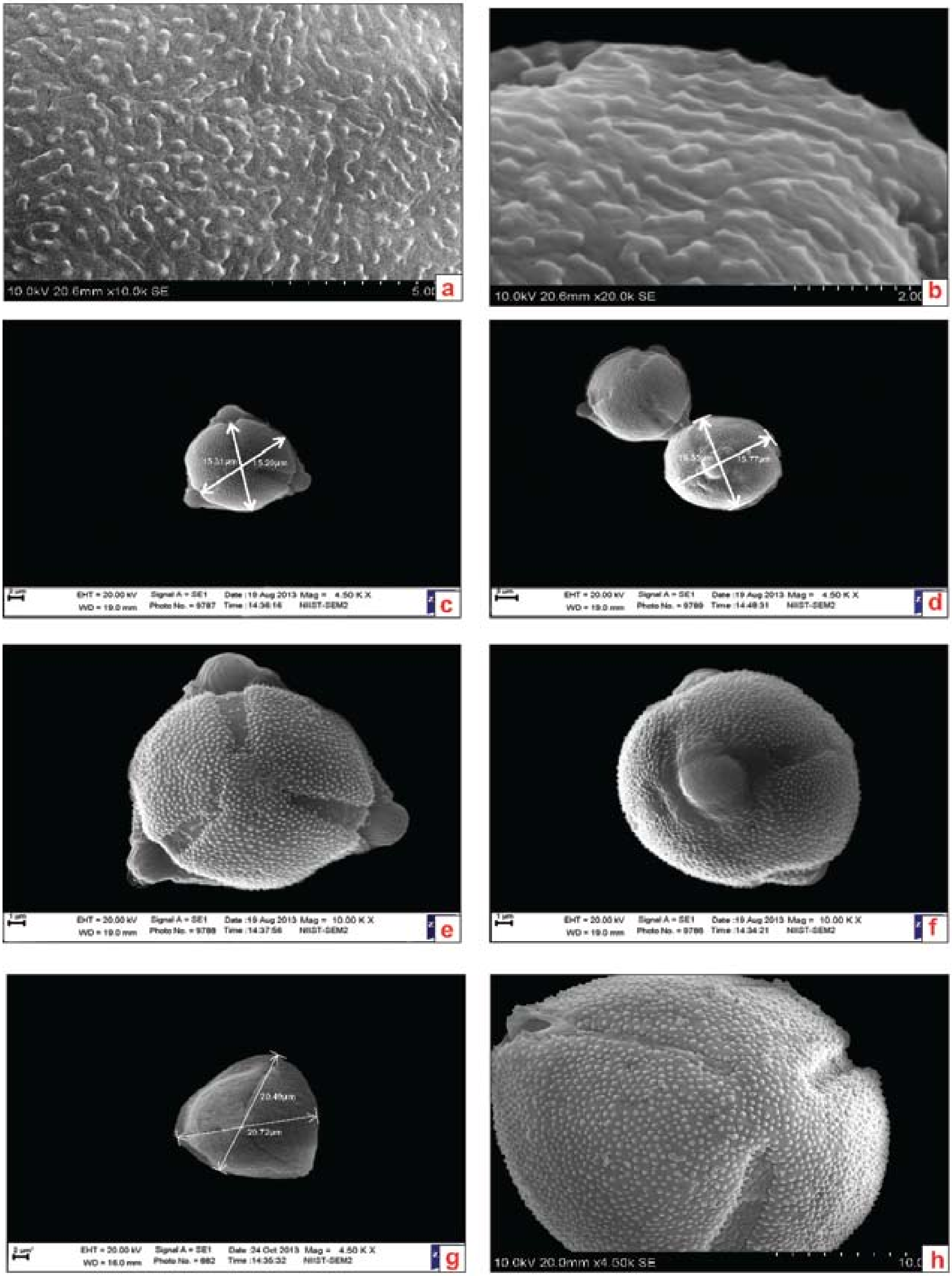

Fig. 8. a & **b.** *Solanum violaceum* Ortega. subsp. violaceum: **a.** Apolcolpium showing triplex joining of elements; **b.** Ornamentation at mesocolpium. **c–f.** *Solanum wendlandii* Hook.f.: **c.** Polar view; **d.** Equatorial view; **e.** Compact spinulose exine ornamentation; **f.** Globose operculum and multi bridging at the colpus; **g** & **h.** *Solanum macrocarpon* L.: **g.** Polar view; **h.** Apocolpium view.

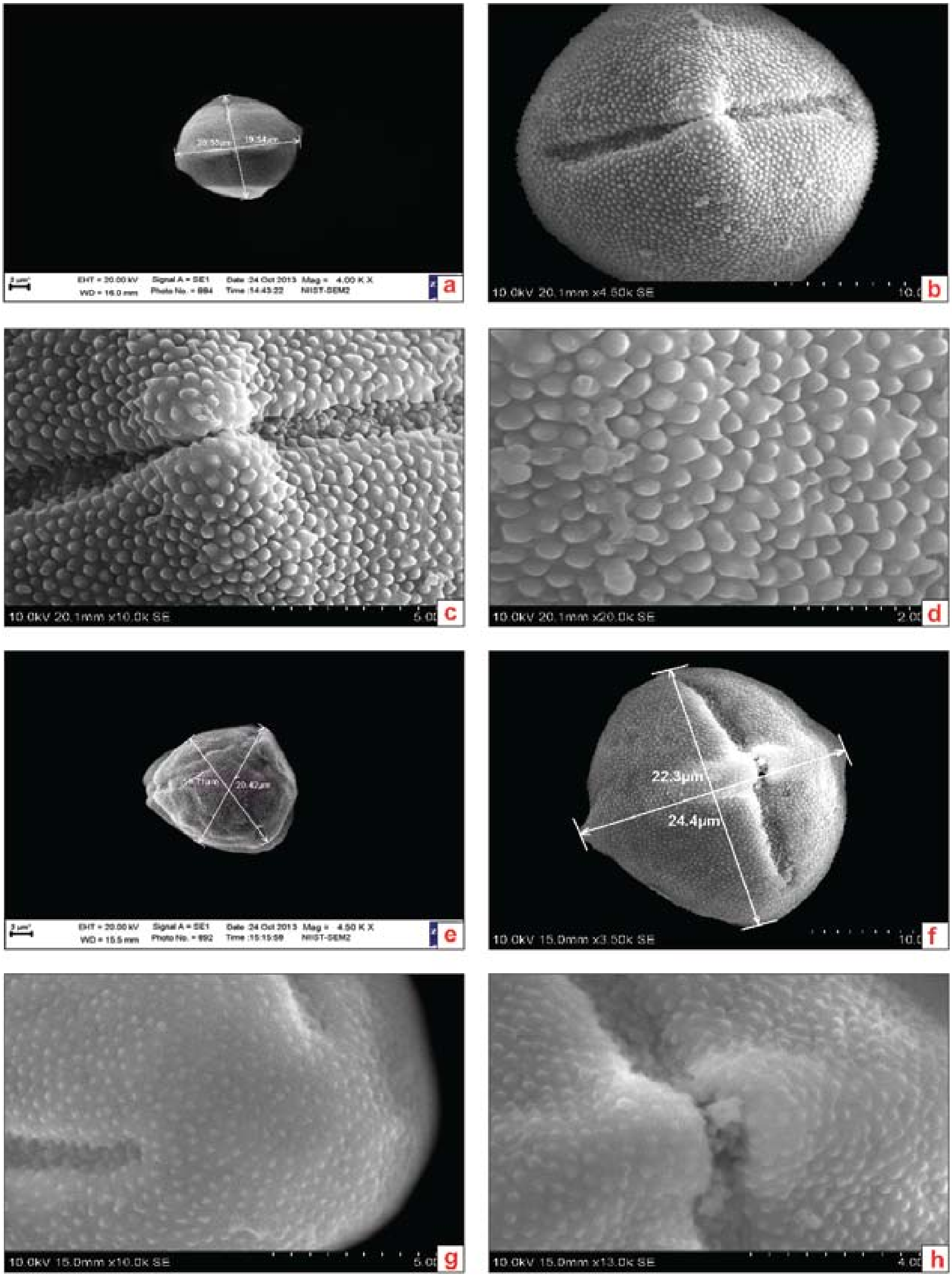

Fig. 9. a–d. *Solanum macrocarpon* L.: **a.** Equatorial view; **b.** Colpus with ridge at the pore; **c** & **d.** Exine ornamentation. **e–h.** *Solanum mammosum* L.: **e.** Polar view; **f.** Equatorial view; **g.** Apocolpium region; **h.** Colpus region.

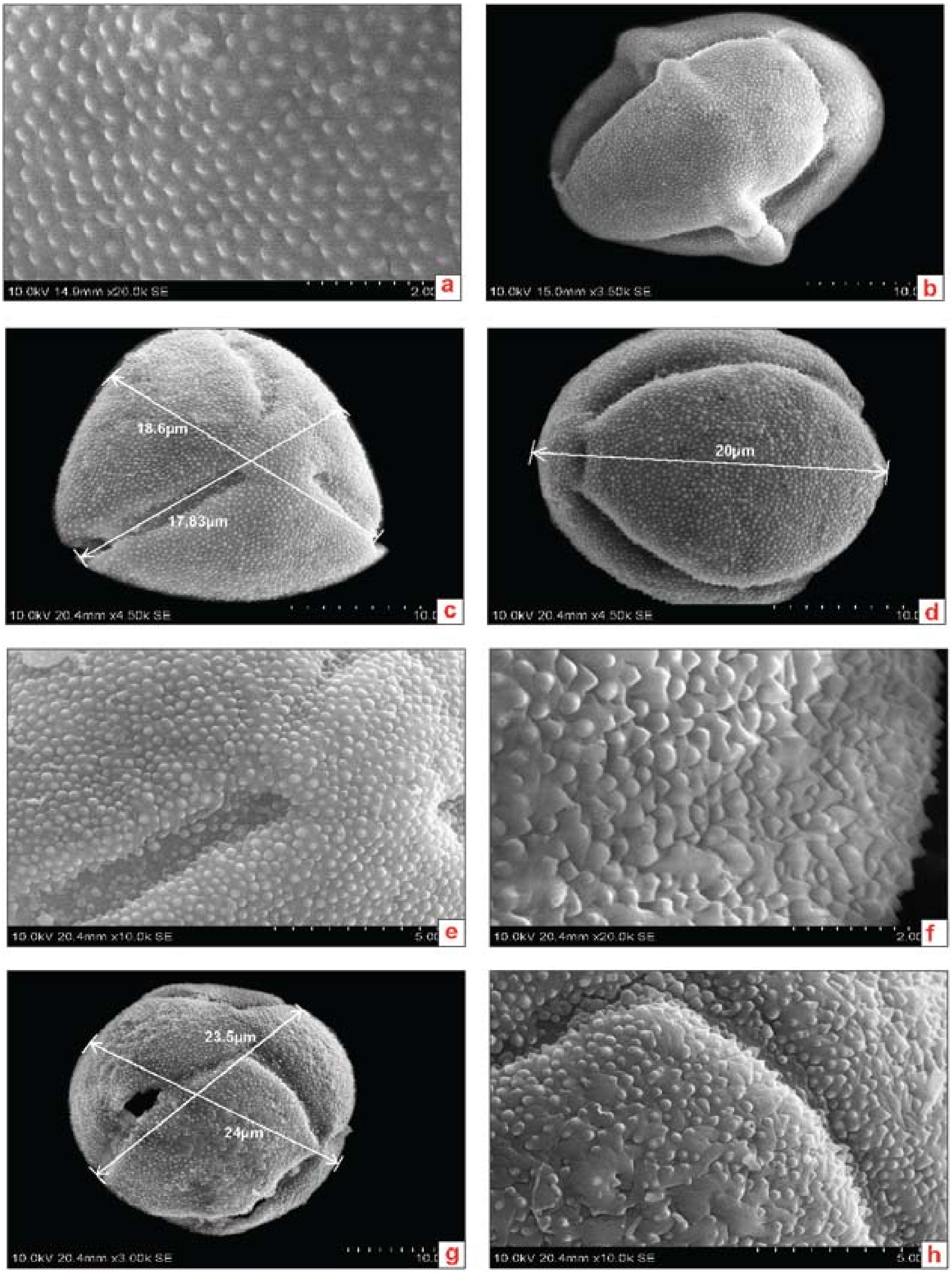

Fig. 10. a & **b.** *Solanum mammosum* L.: **a.** Exine ornamentation; **b.** Syncolpate colpi at one plane. **c–h.** *Solanum melongena* L. var. *insanum* (L.) Praine: (Type 1 grains) **c.** Polar view; **d.** Equatorial view; **e.** Apocolpium showing compact mamillate ornamentation; **f.** Mesocolpium region. **g** & **h.** Type 2 grains., **g.** Tetrazono colporate grains; **h.** Exine ornamentation.

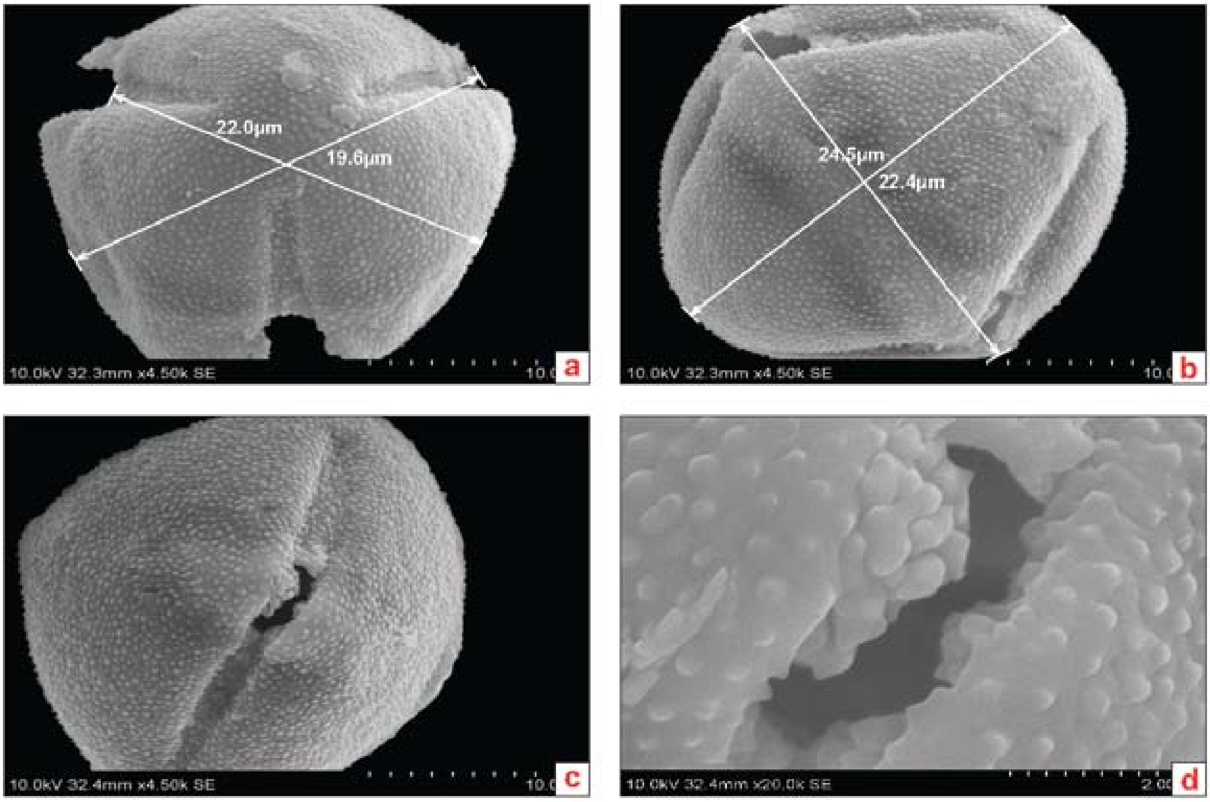

Fig. 11. a–d. *Solanum melongena* L. 'Neelima': **a.** Polar view; **b.** Equatorial view; **c.** Colpus region and exine pattern; **d.** Ora region.

developed aspis. *S. mammosum*, though treated as domesticated ornamental due to its attractive fruits, remnants of wild traits are retained by the pollen grains in having operculum and aspis.

Analysis of pollen traits revealed that the wild taxa have lalongate ora with well developed aspis and operculum which may be the result of primary evolution offering additional protection compared to that of domesticated ones i.e., devoid of aspis and well developed operculum. At the same time, the stragglers and lianas of the germplasm viz. *S. trilobatum*, *S. seaforthianum* and *S. wendlandii* showed a tendency for multi-bridging at the colpi region and the trees, *viz. S. giganteum, S. mauritianum* and *S. erianthum* showed ornamented colpi with slight tendency for bridging at the region of apertures.

Opercula are rare in basal angiosperms with monosulcate pollen. Among monocots, opercula are characteristic of the orders Asparagales, Liliales and Poales that might have undergone evolution due to selection pressures. Opercula protect the pollen grains against desiccation and pathogen invasion. It can be correlated that species coming under Iridaceae and Tecophilaeaceae growing in dry habitats have opercula while species of Alismatales and Zingiberales that prefer to grow in wet habitats lack opercula (Furness & Rudall, 2006). Thus the presence of operculum can be considered as an adaptation of taxa against environmental as well as biotic stresses like desiccation and pathogen invasion. Very often, these adaptations characterize the wild germplasms.

The exine ornamentation in wild germplasm ranges from spinulose (*S. mauritianum* and *S. wendlandii*) to granulose (*S. giganteum* and *S. trilobatum*) from syn echinulate to striate echinulate in shrubby taxa and from echinulose to granulose in herbaceous forms. In herbaceous forms, it ranges from micro echinate to granulose. But the cultivar germplasm uniformly showed mammilate – micro echinate exine ornamentation with lax distribution of projecting elements. Of these, *S. violaceum* subsp. *violaceum* show micro echinate – syn micro echinate exine ornamentation with lalongate apertures and can be considered as a connecting link for the evolution of the domesticated germplasm through *Solanum melongena* var. *insanum* with mammilate exine ornamentation, as the former show tendency to adapt to the cultivable and tamable lands as an escape from wild. Similarly, *S. torvum*, though seen in the wild, shows a lesser degree of similarity with the cultivar *S. macrocarpon*, even though the operculum and aspis are more prominent in the former species. The feebly developed aspis and operculum or their absence is an indication for secondary evolution and may be considered as signal for the recent origin and diversification for the cultivated germplasm of *Solanum*.

Hence, it is pertinent that the polliniferous materials and the methods of protection offered for the haploid germplasm in different species of *Solanum* might have proceeded through two different lines of diversification, one through the wild species in untamed habitats and the second through the domesticated germplasm via cultivars and land races. Further studies are warranted at molecular levels to establish the different lines of evolution among *Solanum* species.

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