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SEM STUDIES OF SEED-COATS IN MALCOLMIA (CRUCIFERAE)

Adelaïde L. STORK and Jean WÜEST ¹

ABSTRACT

The seed-coat and the development of epidermal slime bodies of the following species groups of *Malcolmia sensu lato* were investigated with SEM, viz. *M. maritima* agg. including *M. macrocalyx*, *M. crenulata* agg., *M. africana* agg., and *Torularia* spp. using special techniques (swelling in water and/or in eau de Javel, ultra sonic treatment). The morphology of the epidermal slime bodies is found to be rather uniform within the same species group whereas there are great differences between the different groups. These results are discussed in relation to the taxonomic treatment and subdivision of *Malcolmia sensu lato* suggested by different botanists.

In previous papers (particularly Stork 1971, 1972), the results of testa studies in *Malcolmia sensu lato* (*Cruciferae*) by classical anatomical methods (hand-cut or microtomed preparations examined under a light microscope, LM) have been presented. Special stress was laid on the seed-coat micromorphology and, chiefly, on the form of the epidermal slime columns. The latter were shown to be of great taxonomic value at generic and even at specific level. In these earlier studies scanning electron microscopy (SEM) was used to a limited extent, i.e. for surface views only, but it was felt that SEM observations of the slime bodies be interesting as a complement.

SEM STUDIES OF SEED AND ACHENE SURFACES

Since the real start of SEM techniques in testa studies in the mid-1960's, a great number of short notes or monographs have been published. In a critical review of the use of SEM (Brisson & Peterson 1976) and in an exhaustive bibliography (Brisson & Peterson 1977), covering the period 1967-1976, Brisson and Peterson cite several hundreds of titles and more could now be added.

Because of the economic importance of many Cruciferous plants, special attention has been paid to this group. Among the more recent contributions the following

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authors, using LM and/or SEM techniques, can be cited, viz. Bengoechea & Gomez-Campo (1975), Bouman (1975), Freytag (1958), Godeau (1974), Jonsell (1975), Latowski (1975), Mulligan & Bailey (1976), Prasad (1977), Vaughan (1956, 1959, 1960, 1968) and Vaughan & al. (1976).

Among the many studies of other plant families a few are of special relevance because the internal structure of the epidermis has been investigated, viz. Heyn & Herrnstadt (1977) on *Lupinus* (*Leguminosae*), Hill (1976) on *Mentzelia* (*Loasaceae*), and Walter (1975) on *Carex* (*Cyperaceae*). In general, however, little attention has been given to internal structures and the present authors wish to draw attention to the taxonomic interest of much detailed investigations.

MATERIAL AND METHODS

This paper is restricted to the species groups of *Malcolmia sensu lato* cited in Table 1. However, only the species illustrated in Plates I-V are mentioned. A complete list of species is given in Stork (1972 pp. 432-436; Table 1 follows the arrangement of the taxa and the nomenclature used in this publication).

Three species groups investigated with LM (Stork 1972) are not represented here, viz. *Malcolmia littorea*, *Maresia* and *Eremobium*. This is because the same preparation techniques cannot be used, the morphology and reactions of the seed-coat being quite different.

For each taxon studied, mature seeds were photographed with SEM dry and after diverse treatments (see below). The seeds were glued to SEM supports by means of colloidal silver and coated with gold by diode sputtering. The observations were made in a "Cam Scan III" scanning electron microscope (Cambridge; GB) at the Conservatoire botanique, Geneva.

To study the swelling of the epidermal slime, seeds were immersed in water for at least 5 minutes during which time the slime bodies spread. After water immersion, seeds were immediately dehydrated in graded ethanol, transferred to graded amyl acetate, and dried in CO₂ in a critical point dryer. Some micrographs (Plates IV Figs. 2 and 3; V Figs. 2, 4 and 7) show the good results of this simple treatment.

For detailed studies of the slime bodies seeds were cut or sonicated (ultra sonic treatment) in water or in a water solution (1:1) of commercial eau de Javel (sodium hypochlorite aqueous solution), the duration of this treatment varying from a few seconds to more than 10 minutes (cf. the legends of Plates II-V). The sonicated seeds were rinsed in tap-water, dehydrated in ethanol, transferred to amyl acetate and critical point dried as above.

In the previous seed-coat studies of *Malcolmia* (Stork 1971, 1972) the swollen epidermal slime bodies were observed in a saturated water solution of potassium chlorate (here replaced by the eau de Javel). Some experiments were also made here with this treatment, but no differences in the results were observed between these two liquids.

OBSERVATIONS

1. Surface views

As was shown in Stork (1972) the surface pattern of the testa within a species group is rather uniform. Slight differences were, however, observed between certain closely related species and between subspecies of the same species.

a. *Malcolmia maritima* agg.

Some examples are shown in Plates I and III. Dry seeds of *M. chia* (not illustrated here), *M. flexuosa* (Pl. I Figs. 1-2), *M. maritima* (not illustrated), *M. graeca* (Pl. I Figs. 3-6), and *M. orsiniana* (not illustrated) have a uniformly reticulate-pusticulate or -ocellate surface pattern (for terminology see Stearn 1966 pp. 506 f.). In each cell pustule the top of the slime body is impressed like rings. In the above-mentioned taxa, *M. graeca* subsp. *graeca* (Pl. I Figs. 3-4) has generally bigger and more protruding epidermis cells than the other ones.

M. macrocalyx placed in this aggregate because of its general vegetative and floral morphology and its basic chromosome number ($x = 8$), does not fit into this scheme. The seeds are much bigger and the seed-coat could be described as rugose pustulate-tuberculate, the protuberances being disposed in (secondary) transverse ridges. Furthermore, the impression of the epidermal slime body is quite different, resembling an irregular brain-like clump.

b. *M. crenulata* agg.

The dry testa of *M. crenulata* (the only species illustrated here) has a distinctive appearance. The epidermis cells are big (Pl. III Figs. 5-6), forming a pusticulate-foveate pattern with strongly marked slime body rings and a central crater.

c. *M. africana* agg. and *Torularia*

The dry seed-coat of these two species groups (Plate IV Figs. 7-8; Plate V Fig. 3) has a much "thinner" aspect than that of all the above-mentioned taxa: the radial cell walls form a fine reticulum where the slime bodies are only slightly impressed like low, round warts in the cell middles (reticulate-pusticulate surface).

2. Swelling of the epidermis

Although the swelling cannot be observed continuously with SEM as in LM, different stages in this process can be fixed and easily studied. In Plate IV some micrographs of *M. crenulata* show the surface aspect at different stages of swelling. When the seed is immersed in water the epidermis cells swell into rounded balloons and the surface becomes colliculate. The outer wall layer then breaks and the slime body grows out (cf. different stages of the cell columns in Plates IV Figs. 7-8, and V Figs. 4-5).

3. Slime bodies

In all the taxa studied the ground form of the slime bodies is characteristic of each species group. Slight differences have also been found between closely related

<i>Taxon</i>	<i>Collector, collection No. (Herbarium; voucher No.)</i>	<i>Origin</i>	<i>Fig. No.</i>
The <i>Malcolmia maritima</i> group			
<i>M. chia</i> (L.) DC.	Stork 706001 (S)	Greece, Rhodes	Pl. II/1-2
<i>M. flexuosa</i> (Sm.) Sm.			
subsp. <i>naxensis</i> (Rech. fil.) A. L. Stork	Stork 700601 (S) Stork 704701 B (S)	Greece, Attica Greece, Euboea	Pl. I/1 Pl. I/2; II/3
<i>M. graeca</i> Boiss. & Sprun.			
subsp. <i>graeca</i>	Stork 700201 (S) Stork 705201 (S) Stork 706801 (S)	Greece, Attica Greece, Attica Greece, Attica	Pl. I/3 Pl. I/4 Pl. II/5
subsp. <i>hydraea</i> (Heldr. & Hal.) A. L. Stork	Stork 700901 (S) Stork 701001 (S) Stork 701601 (S)	Greece, Korinthia Greece, Korinthia Greece, Baeotia	Pl. II/6 Pl. I/5 Pl. I/6
subsp. <i>bicolor</i> (Boiss. & Heldr.) A. L. Stork	Stork 701101 (S)	Greece, Argolis	Pl. II/4 & 7
<i>M. macrocalyx</i> (Hal.) Rech. fil.			
subsp. <i>scyria</i> (Rech. fil.) P. W. Ball	Stork 705001 (S)	Greece, Euboea	Pl. III/1-4
The <i>Malcolmia africana</i> group			
<i>M. turkestanica</i> Litw.	Rechinger 4218 (W 42)	Afghanistan, Bala Murghab	Pl. IV/7-8; V/1-2
<i>M. africana</i> (L.) R. Br.			
subsp. <i>africana</i>	leg. ? (GOET 9) Rechinger 1608 (W 16) Rioux & Golvan 175 (W 22)	Caucase Iran, Khorasan Afghanistan, Girishk	Pl. V/3 Pl. V/5-6 Pl. V/4
The <i>Malcolmia crenulata</i> group			
<i>M. crenulata</i> (DC.) Boiss.	Eig s.n., 9.IV.1922 (S; Cren 4) Naftolsky s.n., 14.V.1929 (S; Cren 8) Seeds commun. Feinbrun, 1974 (Cren 1974)	Israel, Negev Israel, Esdraelon Israel, Jerusalem	Pl. IV/1 Pl. III/5; IV/5-6 Pl. III/6; IV/2-4
<i>Torularia</i>			
<i>T. contortuplicata</i> (Willd.) O. E. Schulz	Sintenis 2056 (LD; T 3)	Turkmenistan, Ashkabad	Pl. V/7

Table 1. — Species of *Malcolmia sensu lato* represented in the plates I-V (the nomenclature and arrangement follow Stork 1972: pp. 432-436).

taxa, especially in the *Malcolmia maritima* agg. where the morphology of the slime bodies is particularly suitable for detailed investigation.

a. Malcolmia maritima agg.

As was shown in Stork (1971) two different types of columns are found in this group. *M. chia* (Pl. II Figs. 1-2), *M. flexuosa* (Pl. II Fig. 3), *M. graeca* (Pl. II Figs. 4-7), *M. maritima* (not illustrated), and *M. orsiniana* (not illustrated) have pile-like solid bodies, in the upper half of which discs are clearly visible. The height of these piles as well as the number and form of the free disc edges varies rather constantly from one species to another (cf. Stork 1971 p. 289). Especially striking are the differences between the three subspecies of *M. graeca* (Pl. II Figs. 4-7): subsp. *graeca* having low and broad columns, subsp. *bicolor* extremely long and narrow ones; subsp. *hydraea* cannot be characterised clearly but resembles either one or the other. Thus, the previous observations made with LM are confirmed by SEM.

The slime body pattern of *M. macrocalyx* (Pl. III Figs. 3-4) differs totally. There is no central core and the whole structure forms a spongy network of corrugated lamellae — or a completely corroded clump where only a framework of the ground substance has been left.

b. M. crenulata agg.

The slime bodies found in these species (Pl. IV Figs. 1-6) have the appearance of hollow cones or chimneys with solid walls. In outer form they somewhat simulate those of the *M. africana* group. However, the internal wall stratification and other details observed in LM have not yet been studied with SEM.

c. M. africana agg. and *Torularia*

M. africana and neighbouring East Mediterranean-Oriental species as well as *Torularia contortuplicata* (Plate V Figs. 1-7) have very similar slime structures that grow out like stout flagstaffs ending in a knob. When fully developed these protuberances stand out like pointed teeth covering the whole seed. On the hand-cut sections previously investigated (Stork 1972 Fig. 4 p. 428) a particular internal structuring was found which has not yet been investigated with SEM. However, a broken "tooth" in Pl. V Fig. 2 indicates a characteristic micromorphology.

TAXONOMIC DISCUSSION AND CONCLUSIONS

The difficulties of classifying the homogeneous *Cruciferae* are well known. A general survey of the different approaches has been published recently by Hedge (1976). In *Malcolmia sensu lato*, it is interesting to note how authors of different

floras and monographs consider its subdivision and the systematic position of the different species groups. Boissier (1867) in his "Flora Orientalis" recognizes three series or sections of *Malcolmia*, viz.

§ 1 *Sisymbrioideae* including *M. parviflora* (DC.) DC. [= *M. ramosissima* (Desf.) Thell.] and species often placed in the separate genus *Maresia* (*M. nana*, *pulchella*, *pygmaea*);

§ 2 *Rigidae* comprising all the mainly Oriental species around *Malcolmia africana* placed by certain authors in the genera *Fedtschenkoa* (cf. Dvořák 1970) and *Torularia*;

§ 3 *Eumalcolmia* with the proper *Malcolmia* species including also *M. crenulata* and related taxa. On the other hand, *Eremobium* is kept separate.

The purely West Mediterranean species (*Malcolmia littorea*, etc.) were placed by Rouy & Foucaud (1895) in the series "*Eumalcolmia*" together with *M. maritima*.

In more recent floras, the taxonomic position of all these taxa varies considerably. In "Flora Iranica" (Hedge & Rechinger 1968), for instance, the authors place *Malcolmia*, *Eremobium* and *Maresia* (not treated in direct connection with *Malcolmia*) in the *Hesperideae*, whereas *Torularia* is considered under *Sisymbrieae*. However, in "Flora Europaea" (Ball 1964) all these genera are treated in one sequence (*Malcolmia* — *Torularia* — *Maresia*).

In the most recent floras there seems to be a trend back to Boissier's concept of the group with the same sections, e.g. "Flore de l'Afrique du Nord" (Maire 1977), and "Flora of Cyprus" (Meikle 1977). In the former, however, *Maresia sensu stricto* is kept as a separate genus, whereas Meikle joins *Maresia nana* to *Malcolmia* through *M. ramosissima*.

In his morphological and anatomical analyses of the *Malcolmia* group, Dvořák (1969, 1970, 1972) discusses, apart from the basic *M. maritima* group, the relationships between the different "marginal" taxa and their systematic position. His conclusions are as follows: the mainly West Mediterranean species *Malcolmia ramosissima*, *littorea*, *lacera*, and *arenaria* are transferred to *Maresia* principally because of the anatomical structure of the silique septum. A little later Dvořák (1972) also includes *Malcolmia meyeri*, *crenulata*, and *exacoides* into *Maresia* for the same reason. *Eremobium* is considered as derived from *Maresia*. As to the Mediterranean-Oriental taxa around the species *Malcolmia africana*, he groups them together in the genus *Fedtschenkoa*, because of the form of the floral organs and their basic chromosome number ($x = 7$). He also points out that the anatomical structures of the fruit of *Malcolmia* (*Fedtschenkoa*) *scorpioides* and of *Torularia contortuplicata* are very similar.

If we consider Dvořák's results in the light of the micromorphology of the testa, there are undoubted coincidences. His *Fedtschenkoa* species group and *Torularia contortuplicata* (Plates IV and V) and *T. torulosa* (cf. Stork 1972) have the same

PLATES I-V.

For plant names and collections, see Table 1 p. 232.

All photographs taken by J. Wüest at the Conservatoire botanique, Geneva.

PLATE I

- FIG. 1. — *Malcolmia flexuosa* subsp. *naxensis*. Stork 700601. Dry seed. $\times 60$.
FIG. 2. — *M. flexuosa* subsp. *naxensis*. Stork 704701B. Surface view of dry seed. $\times 500$.
FIG. 3. — *M. graeca* subsp. *graeca*. Stork 700201. Dry seed. $\times 50$.
FIG. 4. — *M. graeca* subsp. *graeca*. Stork 705201. Surface view of dry seed. $\times 500$.
FIG. 5. — *M. graeca* subsp. *hydraea*. Stork 701001. Dry seed. $\times 60$.
FIG. 6. — *M. graeca* subsp. *hydraea*. Stork 701601. Surface view of dry seed. $\times 500$.

PLATE II

- FIG. 1. — *Malcolmia chia*. Stork 706001. Fully developed epidermal slime bodies. Seed immersed in water during 6 hours; then transferred to a water solution (1:1) of commercial eau de Javel for 30 minutes; finally sonicated during 15 seconds in the same liquid. Immediately rinsed in water and then dehydrated (see Methods p. 230). $\times 1000$.
FIG. 2. — *M. chia*. Stork 706001. Fully developed epidermal slime bodies. Seed immersed in water during a few minutes; then transferred to and sonicated in eau de Javel:water (1:1) during 1-2 minutes. $\times 1000$.
FIG. 3. — *M. flexuosa* subsp. *naxensis*. Stork 704701B. Fully developed epidermal slime bodies. Seed treatment as in Fig. 2 above. $\times 750$.
FIG. 4. — *M. graeca* subsp. *bicolor*. Stork 701101. Fully developed epidermal slime bodies. Seed treatment as in Fig. 1 above. $\times 1500$.
FIG. 5. — *M. graeca* subsp. *graeca*. Stork 706801. Fully developed epidermal slime bodies. Seed treatment as in Fig. 1 above. $\times 1000$.
FIG. 6. — *M. graeca* subsp. *hydraea*. Stork 700901. Fully developed epidermal slime bodies. Seed treatment as in Fig. 1 above. $\times 1000$.
FIG. 7. — *M. graeca* subsp. *bicolor*. Stork 701101. Fully developed epidermal slime bodies. Seed treatment as in Fig. 2 above, but sonicated only during 5 seconds. $\times 1000$.

PLATE III

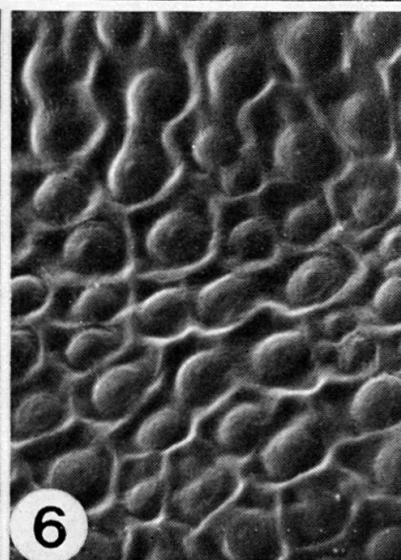
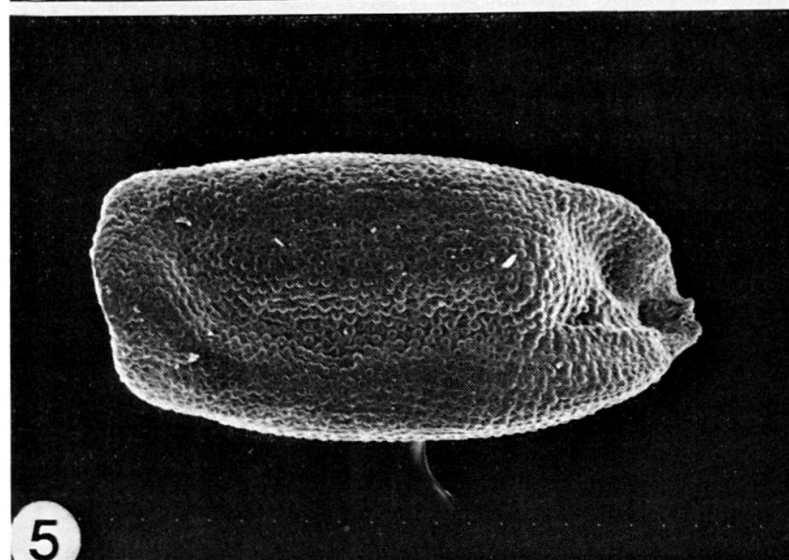
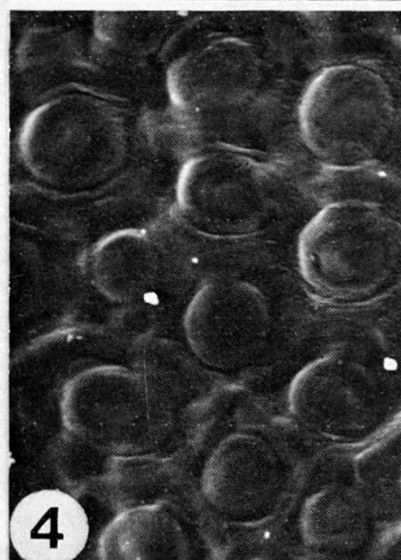
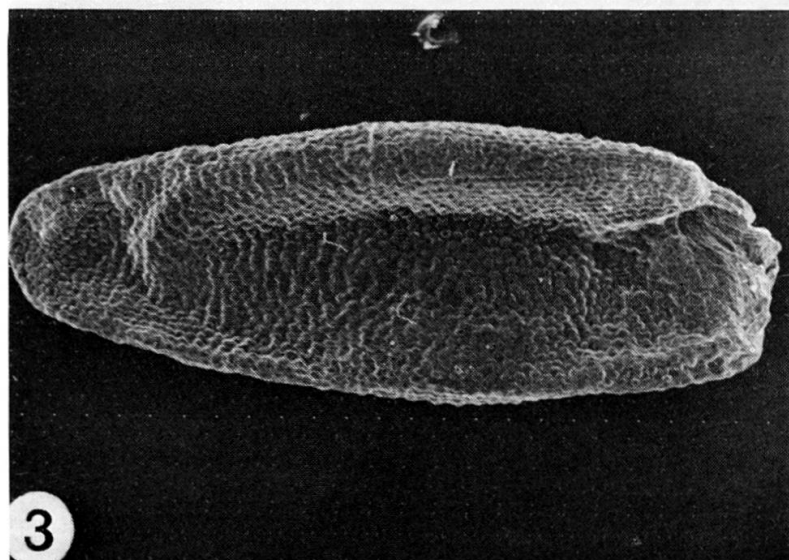
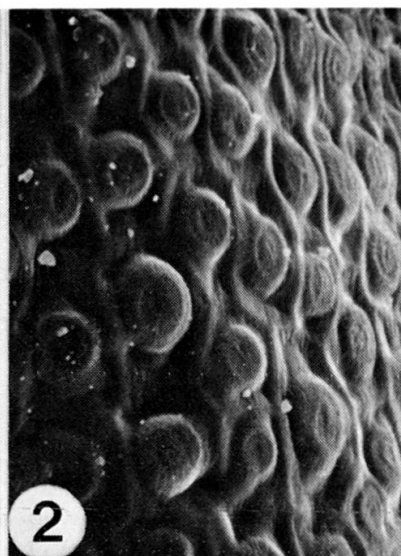
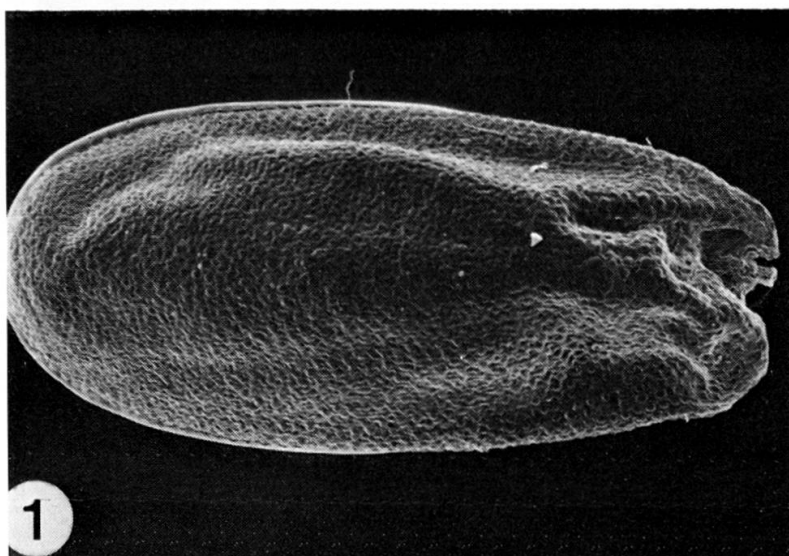
- FIG. 1. — *Malcolmia macrocalyx* subsp. *scyria*. Stork 705001. Dry seed. $\times 40$.
FIG. 2. — *M. macrocalyx* subsp. *scyria*. Stork 705001. Surface view of dry seed. $\times 500$.
FIG. 3. — *M. macrocalyx* subsp. *scyria*. Stork 705001. Fully developed epidermal slime bodies. Seed treatment as in Plate II Fig. 1. $\times 500$.
FIG. 4. — *M. macrocalyx* subsp. *scyria*. Stork 705001. Fully developed epidermal slime body. Seed treatment as in Plate II Fig. 1. $\times 1000$.
FIG. 5. — *M. crenulata*. Cren 8. Dry seed. $\times 60$.
FIG. 6. — *M. crenulata*. Cren 1974. Surface view of dry seed. $\times 500$.

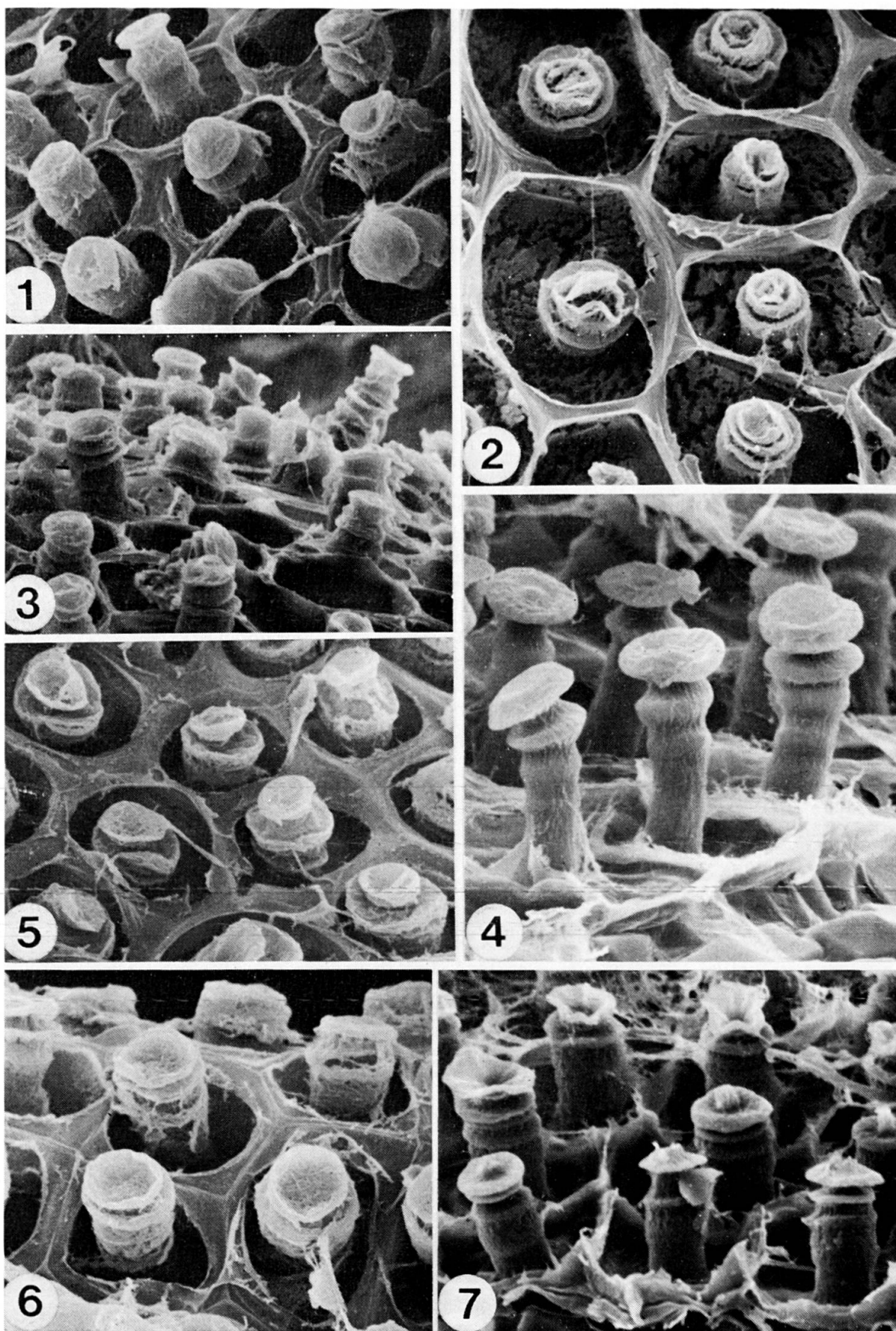
PLATE IV

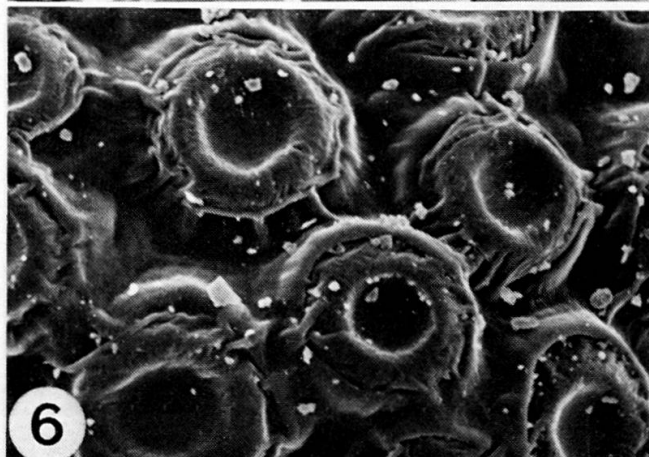
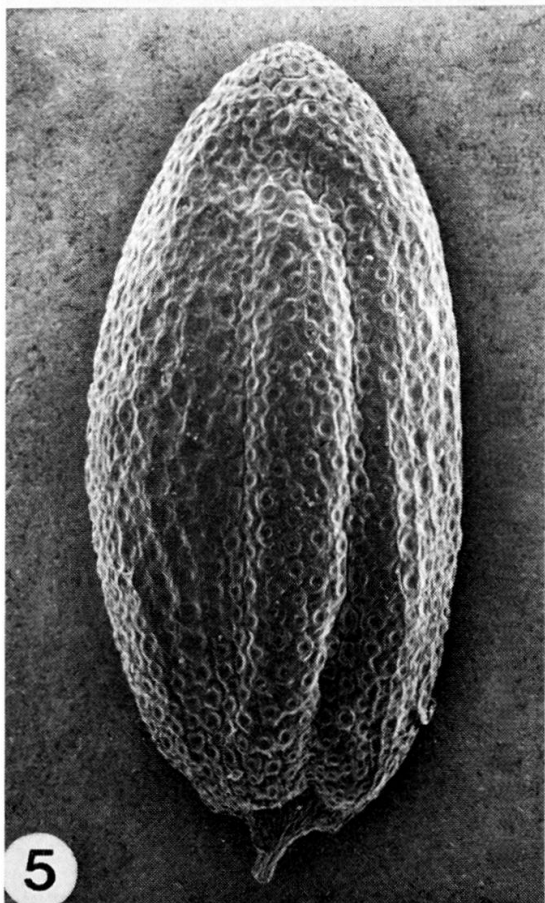
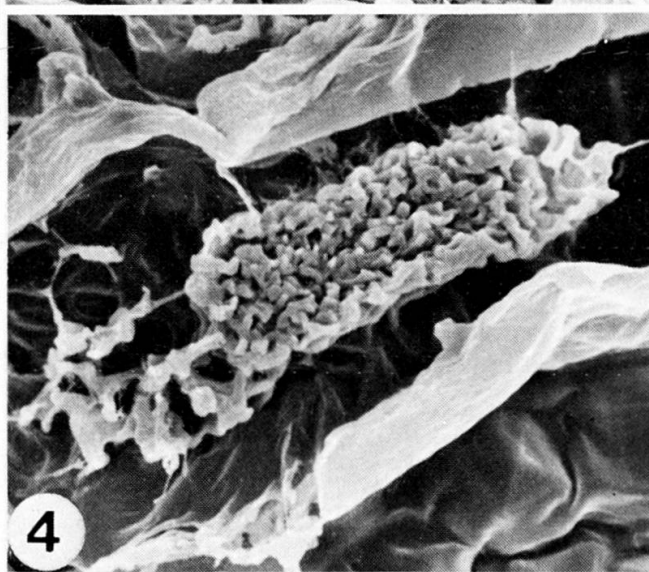
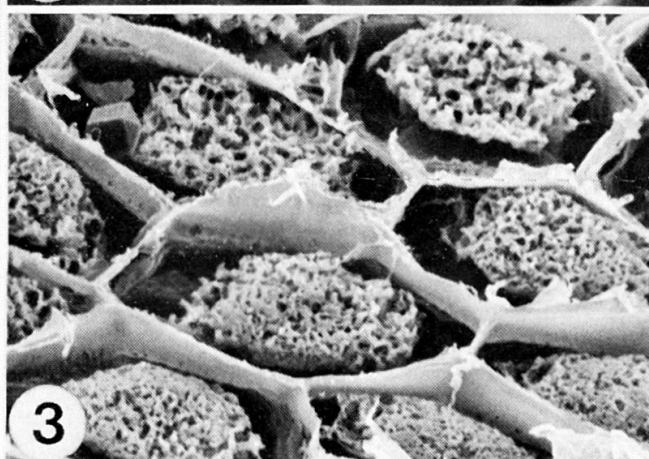
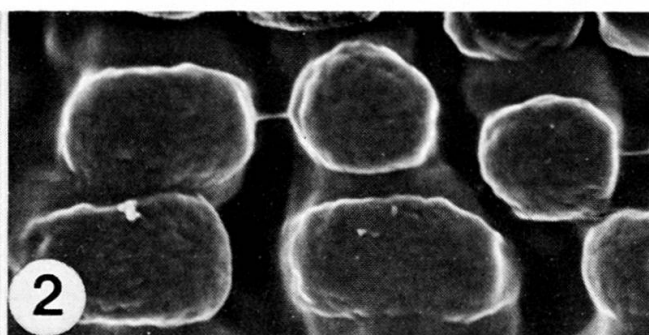
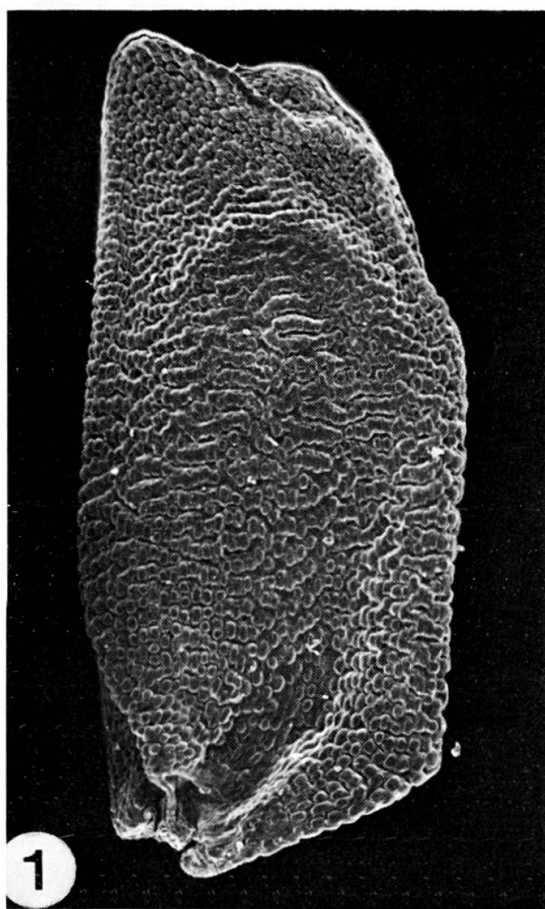
- FIG. 1. — *Malcolmia crenulata*. Cren 4. Swelling seed-coat. Seed sonicated directly in eau de Javel: water (1:1) during 15 seconds. $\times 500$.
FIG. 2. — *M. crenulata*. Cren 1974. Swelling seed-coat. Seed immersed in water during a few minutes, then dehydrated. $\times 500$.
FIG. 3. — *M. crenulata*. Cren 1974. Swelling seed-coat. Seed immersed in water during a few minutes, then dehydrated. $\times 500$.
FIG. 4. — *M. crenulata*. Cren 1974. Fully developed epidermal slime bodies. Seed treatment as in Fig. 1 above. $\times 500$.
FIG. 5. — *M. crenulata*. Cren 8. Fully developed epidermal slime bodies. Seed treatment as in Fig. 1 above. $\times 500$.
FIG. 6. — *M. crenulata*. Cren 8. Fully developed epidermal slime body. Seed treatment as in Fig. 1 above. $\times 1000$.
FIG. 7. — *M. turkestanica*. W 42. Dry seed. $\times 60$.
FIG. 8. — *M. turkestanica*. W 42. Surface view of dry seed. $\times 500$.

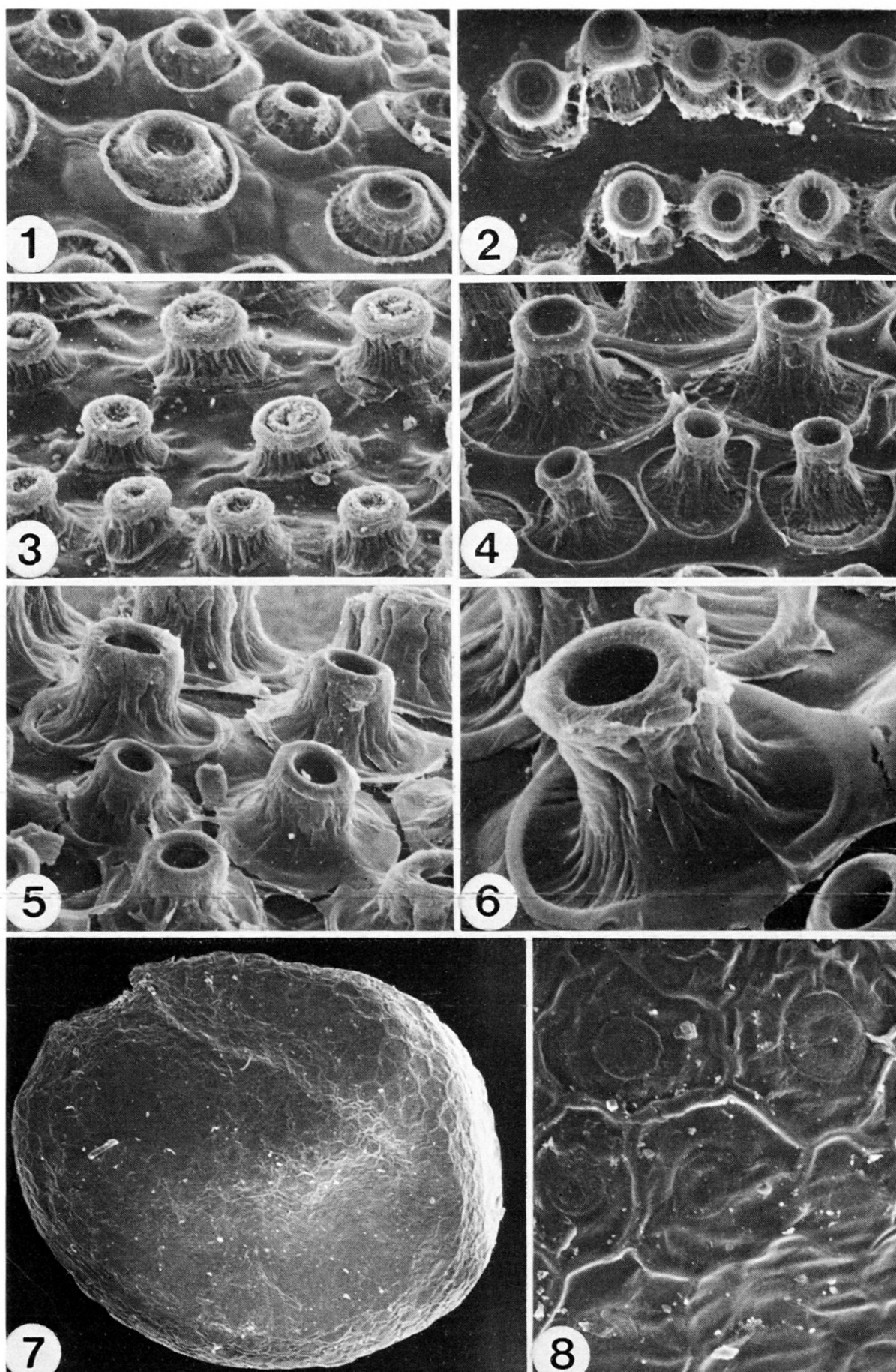
PLATE V

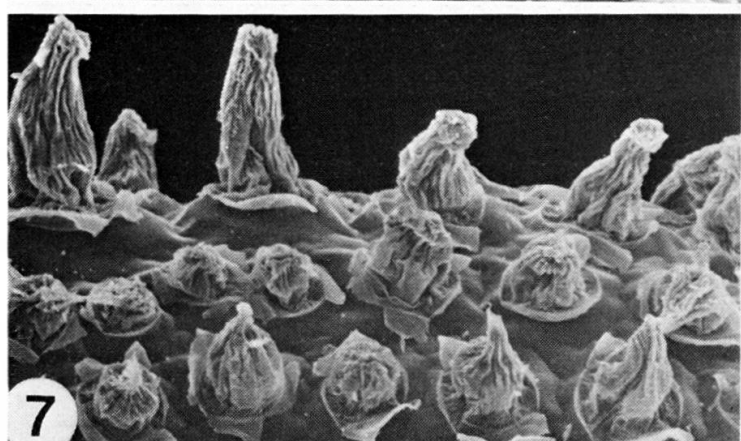
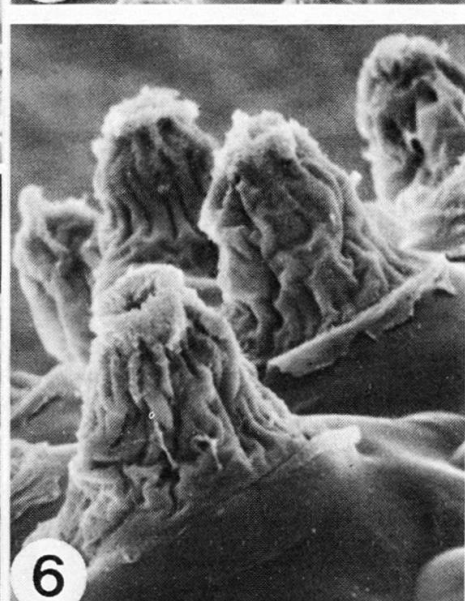
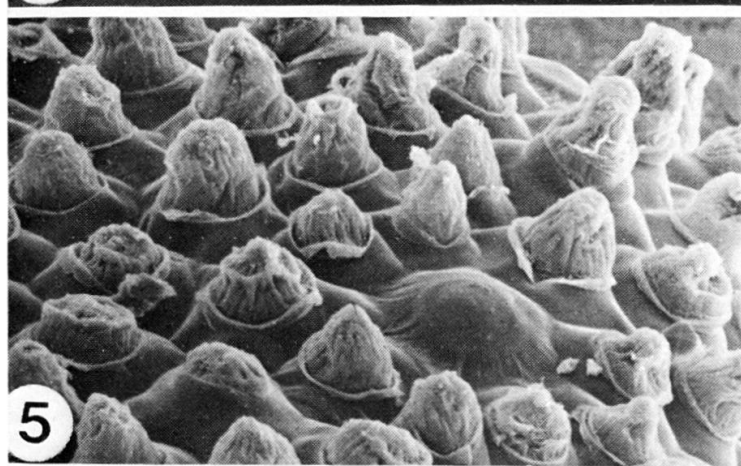
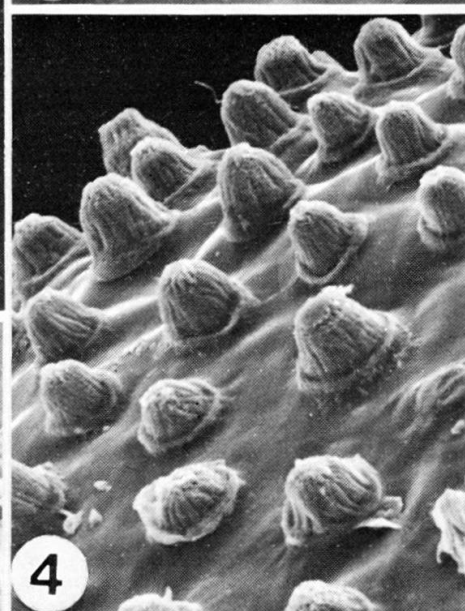
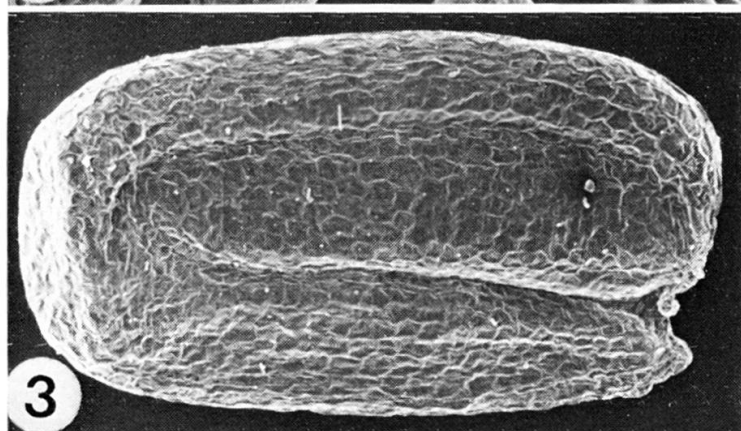
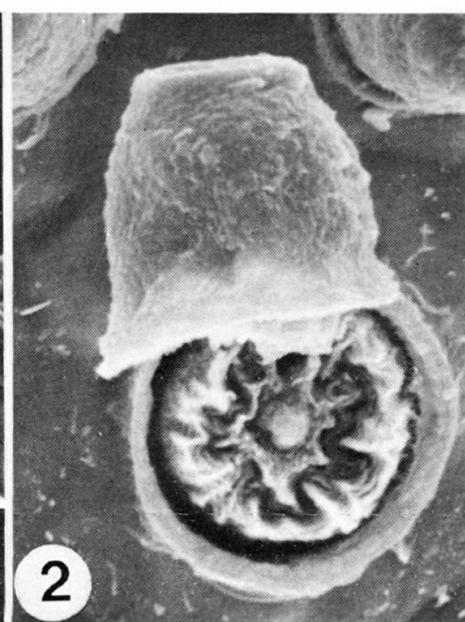
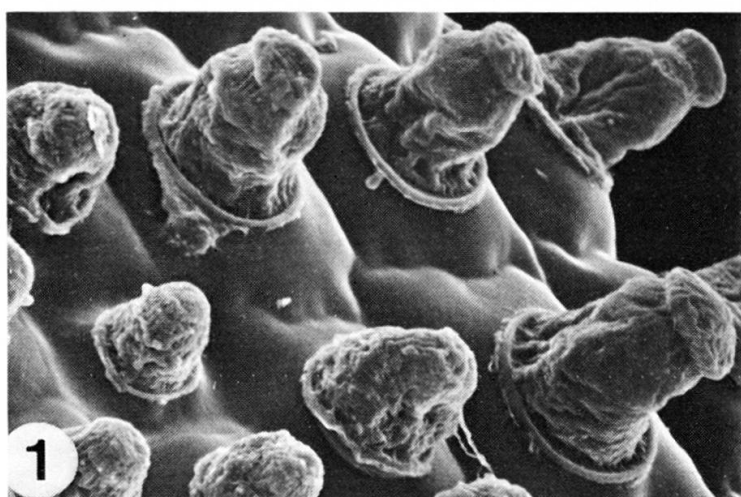
- FIG. 1. — *Malcolmia turkestanica*. W 42. Swelling epidermal slime bodies. Seed sonicated in water during 15 seconds, then dehydrated. $\times 500$.
FIG. 2. — *M. turkestanica*. W 42. A broken swollen slime body showing a transverse section of its base. Seed immersed in water during a few minutes, then dehydrated. $\times 1000$.
FIG. 3. — *M. africana*. GOET 9. Dry seed. $\times 60$.
FIG. 4. — *M. africana* var. *africana*. W 22. Swelling slime bodies. Seed immersed in water during a few minutes, then dehydrated. $\times 500$.
FIG. 5. — *M. africana* var. *africana*. W 16. Swelling seed-coat. Seed treatment as in Fig. 1 above. $\times 500$.
FIG. 6. — *M. africana* var. *africana*. W 16. Fully developed slime bodies. Seed sonicated during 15 seconds in water, then dehydrated. $\times 1000$.
FIG. 7. — *Torularia contortuplicata*. T3. Slime bodies in different stages of swelling. Seed immersed in water during a few minutes, then dehydrated. $\times 250$.











type of epidermal slime bodies and subepidermal structure (Stork 1972 p. 427). Dvořák's *Maresia* taxa (the East Mediterranean *M. crenulata* agg. however not included) also constitute a separate group with a particular slime epidermis "behaviour" and a similar testa anatomy (Stork 1972). Their subepidermal structure resembles very much that of the "*Fedtschenkoa*" taxa. The East Mediterranean *Malcolmia crenulata* group is, however, quite different from *Maresia*. Its testa morphology is rather intermediate between *M. maritima* and *M. africana* but it is quite characteristic and distinct from either of them.

Jonsell (1975) rightly points out that similar morphological or anatomical structures need not indicate close affinities. Furthermore, much detailed investigation of seed-coat micromorphology in *Cruciferae* is still necessary to allow real conclusions about the relationships between the different species and species groups. However, from a purely morphological point of view, the following groups of taxa can be distinguished. If they are kept in *Malcolmia* — as Boissier did and it must be said that he had a profound "taxonomic" sense of plant relationships — or if they are considered as belonging to separate related genera, is a question of hierarchical concept.

a. Taxa with pitcher-like solid slime bodies, made up of a pile of discs (*M. chia*, *flexuosa*, *graeca*, *maritima*).

b. Species with the slime bodies forming a clump-like network (*M. macrocalyx*, conventionally included in *M. maritima* agg.).

c. Taxa with hollow cone-like slime bodies (*M. crenulata* and "*M. conringioides*").

d. Taxa with teeth-like slime columns (*M. africana*, *behboudiana*, *cabulica*, *karelinii*, *longipetala*, *scorpioides*, *spryginioides*, *strigosa*, *taraxacifolia*, *turkestanica*, *Torularia* spp.).

e. Epidermis micromorphology completely different from that of the above-mentioned species (*M. littorea*, *broussonetii*, *lacera* including *patula*, *arenaria* including *biloba*, *Maresia* spp., *Eremobium aegyptiacum*). We are currently completing our study of this group.

GENERAL CONCLUSIONS

The results of the previous LM investigation of seed-coat micromorphology in *Malcolmia* have been amplified by SEM techniques. It is shown that purely surface views of dry seeds complement more detailed investigations, but are not sufficient to distinguish the more relevant internal microstructure of the slime bodies. However, it could be useful to complete our SEM observations with investigations on the internal stratification of the slime bodies.

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