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Seed characters in Brassica section Brassica and some related groups

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RÉSUMÉ

STORK, A. L., S. SNOGERUP & J. WÜEST (1980). Caractéristiques morphologiques des graines du genre *Brassica*, section *Brassica*, et de quelques autres groupes voisins. *Candollea* 35: 421-450. En anglais, résumé français.

La section *Brassica* est définie comme n'incluant que les espèces à $x = 9$, génome caractéristique de *B. oleracea* L. Plusieurs caractères ont été étudiés en microscopie optique et en microscopie électronique à balayage: dimensions des graines, développement des couches de l'enveloppe, structures de surface, cellules à mucilage. Dans la section *Brassica*, nous avons étudié *B. oleracea* L., *B. montana* Pourr., *B. hilarionis* Post, *B. cretica* Lam., *B. insularis* Moris., *B. macrocarpa* Guss., *B. rupestris* Rafin., *B. villosa* Biv.-Bern., *B. incana* Ten. ainsi que plusieurs cultivars comme le chou-fleur, les brocolis, le chou de Bruxelles, les choux potagers et fourragers et le chou géant. Dans les groupes voisins, nous avons observé *B. balearica* Pers., *B. repanda* (Willd.) DC., *B. gravinae* Ten., *B. spinescens* Pomel, *B. napus* L. (colza), *B. rapa* L. (chou chinois), *Sinapis arvensis* L. et *Sinapidendron frutescens* (Ait.) Lowe. Cet article comprend en outre la description des méthodes utilisées, une discussion taxonomique et une liste importante de références bibliographiques.

ABSTRACT

STORK, A. L., S. SNOGERUP & J. WÜEST (1980). Seed characters in *Brassica* section *Brassica* and some related groups. *Candollea* 35: 421-450. In English, French abstract.

Section *Brassica* is defined as including only the species with the $x = 9$ genome characteristic of *B. oleracea* L. A number of seed characters such as seed size, development of testa layers, surface structures and mucilage cells have been studied by means of LM and SEM. The following taxa from Section *Brassica* have

been studied: *B. oleracea* L., *B. montana* Pourr., *B. hilarionis* Post, *B. cretica* Lam., *B. insularis* Moris., *B. macrocarpa* Guss., *B. rupestris* Rafin., *B. villosa* Biv.-Bern., *B. incana* Ten. and a number of cultivars including cauliflower, broccoli, sprouting broccoli, Brussels sprouts, kales, cabbages and giant cabbage. From related groups *B. balearica* Pers., *B. repanda* (Willd.) DC., *B. gravinae* Ten., *B. spinescens* Pomel, *B. napus* L. (oil-seed rape), *B. rapa* L. (Chinese cabbage), *Sinapis arvensis* L. and *Sinapidendron frutescens* (Ait.) Lowe were investigated. Methods are described, taxonomic discussions are included and an extensive list of references is given.

INTRODUCTORY REMARKS ON TAXONOMY

The arrangement of species in genera and infrageneric taxa in *Brassica* and related genera has constituted a problem and different solutions have been proposed. We are aware that new data from cytology and crossing relations have stressed the need to revise the taxonomy at genus and section levels. Pending the results of current investigations, a full reclassification should be postponed. Therefore we have avoided new combinations and descriptions that might later prove unnecessary. Only a few points where we deviate from common usage will be commented on.

We find it necessary to define more precisely Section *Brassica*, on which we have concentrated our studies. In the sense used here, Section *Brassica* includes only the forms with the $x = 9$ genome characteristic of the nomenclatural type, *B. oleracea* L. All its wild members are to some extent interfertile, perennial, and have sepals erect in flower and leaves that are semi-coriaceous in varying degrees. The form and structure of the seed are also shown to be of use in delimiting the section from other sections and genera. Accumulating evidence shows that the formation of a new genomic structure is rare in this group, so that the characteristic genomes provide important characters for the delimitation of higher categories.

The following species are here included in Section *Brassica*: *B. oleracea* L., *B. montana* Pourr., *B. hilarionis* Post, *B. cretica* Lam., *B. insularis* Moris., *B. macrocarpa* Guss., *B. rupestris* Rafin., *B. villosa* Biv.-Bern., *B. incana* Ten. and the cultivated $2n = 18$ forms. According to BORGÉN & al. (1979), *B. bourgeau* (Webb) O. Kuntze must also be included.

Under *B. insularis* Moris., we include material previously known as *B. atlantica* (Coss.) Schultz from Tunisia. The morphological resemblance to the forms from Sardinia is very close and our crossings indicate full interfertility. In this broad sense, *B. insularis* is a good example of a Messinian trans-Mediterranean distribution as discussed by BOCQUET & al. (1978).

The cultivated forms ($2n = 18$) show resemblance to different wild taxa and are probably not of recent common descent (cf. SNOGERUP, 1979, 1980). The situation is further complicated by crossings, accidental as well as intentional and by plant breeding with increasingly more intricate and radical methods. The cultivated forms appear here under English vernacular names.

B. balearica Pers. presents a taxonomic problem, as summarized by GOMEZ-CAMPO & TORTOSA (1974) and BENGOCHEA & GOMEZ-CAMPO (1975). On morphological evidence, we agree with these authors that *B. balearica* is closely related to *B. repanda* and *Sinapidendron*. The known chromosome numbers are for *B. repanda* $n = 10$, and for some *Sinapidendron* species $n = 10$. The correct number for *B. balearica* is $n = 16$, according to DAHLGREN & al. (1971) and counts by Snogerup on the same material. Earlier reports of $2n = 18$ for this species derive from misidentified material. These data together with leaf characters make it probable that *B. balearica* and the similar North African plants described as *B. spinescens* Pomel and *B. scopulorum* Coss. should be recognized as a separate section, but probably not under the genus *Brassica*. WIDLER & BOCQUET (1979) included *B. balearica* together with parts of Section *Brassica* in a new section, *Lignosae*. We consider this disagrees with morphological, experimental and ecological facts.

PREVIOUS WORK ON SEED CHARACTERS

In a series of papers, Vaughan and collaborators deal with the seed-coat morphology and histology of *Brassica* and closely related genera and their taxonomic significance is discussed. Exhaustive bibliographies covering previous studies of this plant group are included. It has been shown that the testa structure in *Brassica* is of value in species identification. It seems, however, not to be sufficient to support the different hypotheses concerning species differentiation (VAUGHAN & al., 1963). Other important contributions to this subject have been published by APPELQUIST & OHLSSON (1972), BERGGREN (1960, 1962), MULLIGAN & BAILEY (1976) and MUSIL (1948).

MATERIAL AND METHODS

In this paper, the testa structure of members of Section *Brassica* is described. A few species belonging to other sections and genera are included for comparison. The material studied is listed in Table 2; the position of localities for the material of Section *Brassica* is indicated in Fig. 1. For the morphological observations of shape, size and colour, entire seed collections were used. For the LM studies of seeds sectioned by hand and observed dry, in water and in an aqueous solution of lactic blue, three to four seeds from each collection were used. Seeds from each taxon were also photographed in SEM dry and after varying treatments (see below). The seeds were fixed to SEM

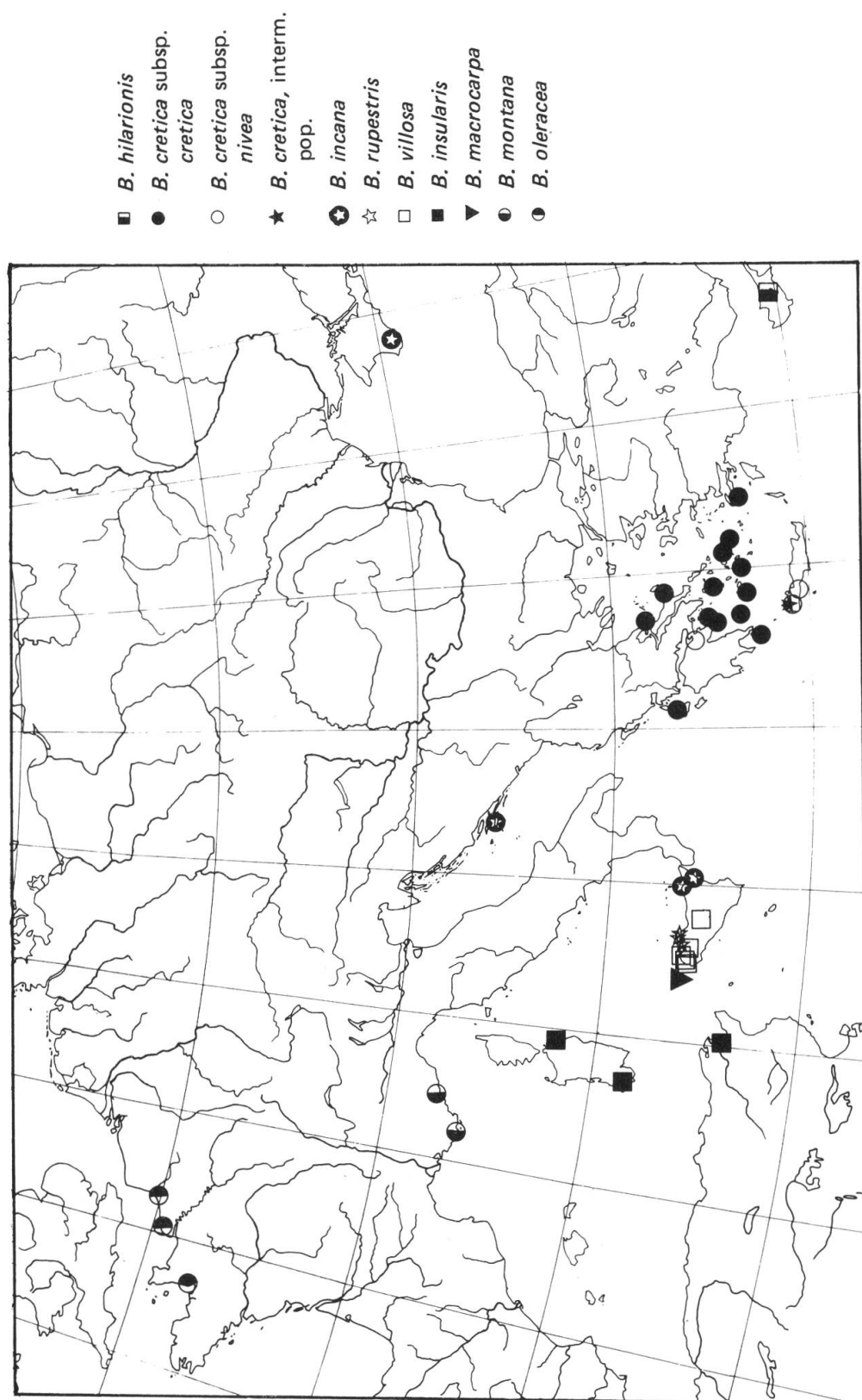


Fig. 1. — Position of localities for the spontaneous material of Section *Brassica*.

supports with nailpolish 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.

For the swelling studies, pieces of seed coat sectioned by hand were observed by LM. For the SEM studies, various pre-treatments of the whole seed have been tried. They were first soaked in tapwater (the effects of tapwater and distilled water on the mucilage production have been thoroughly studied by GRUBERT & HAMBACH, 1972 and GRUBERT & SCHRIEWER, 1972) for periods ranging from about half an hour up to four to six days. In some cases Teepol, a detergent, was added. After this treatment, some seeds were transferred to a 1:1 aqueous solution of commercial eau de Javel (sodium hypochlorite in aqueous solution) and left there for a few minutes up to 24 hours. The best results were obtained after ultrasonic treatment of 5 to 20 seconds in water or in eau de Javel. In a few cases, the sonication was repeated once or twice, which made the structure of the mucilage core easier to observe. The seeds were then rinsed in tapwater, dehydrated in ethanol, transferred to graded amyl acetate and dried in CO₂ in a critical point dryer.

Classical microtome sections were prepared at the Department of Systematic Botany, University of Lund. Some seeds were first softened in 20% formaldehyde for 14 days, then washed in water, dehydrated in graded ethyl alcohol and butyl alcohol, embedded in paraffin, sectioned at 14 µm and stained in safranin-light green. In other cases, dry seeds were embedded directly in paraffin, sectioned and stained as described above.

THE SEED COAT

STORK (1971, 1972) and STORK & WÜEST (1978) have shown that in other cruciferous species, in particular *Malcolmia*, the outer epidermis of the seed coat provides useful diagnostic characters, particularly the epidermal mucilage structures. In *Brassica*, however, the characters of the epidermis itself cannot be used for separating species, though it is characteristic of certain species groups. The epidermal and palisade layers together contribute to the morphological variation (VAUGHAN & al., 1963). The testa structure of *Brassica* and other closely related taxa has been studied by a number of authors, recently by BENGOCHEA & GOMEZ-CAMPO (1975), BERGGREN (1960, 1962), BOUMAN (1975), VON HOFSTEN (1974), MULLIGAN & BAILEY (1976), VAUGHAN (1959), VAUGHAN & al. (1963, 1976), VAUGHAN & WHITEHOUSE (1971).

The seed coat layers of ripe *Brassica* seeds have been described in detail in some of these publications. In particular BOUMAN (1975) has studied their initiation and development in *Brassica nigra* and *Sinapis alba* and found that in both genera the outer integument differentiates into an outer layer of mucilage cells. Large, or "giant", parenchyma cells represent its subepidermal layer.

The sclerotic, or palisade, cells are formed by the inner epidermis of the outer integument. In the ripe seed, the inner integument is to a greater or lesser extent crushed. Only cellular membranes and wall fragments adpressed to the palisade cells can be seen. According to BOUMAN (1975), the most important difference between *Brassica* and *Sinapis* is to be found here, i.e. in the presence in *Sinapis* of a pigment layer derived from one of the cell layers of the inner integument. However, in all the *Brassica* species and cultivated forms investigated by us, a clear pigment layer was also observed. It is true that this layer is thicker in *Sinapis arvensis* than in the species of Section *Brassica* or petsai (*B. rapa* form) or in oil-seed rape, but cells containing a brownish substance are present in these (Plate V/1-4, 6, 7). The cellular structure of this layer is particularly evident in *Brassica gravinae*, *B. repanda* and *Sinapidendron frutescens*. The innermost cell layer, or aleuron layer, is derived from the endosperm.

FORM, SIZE AND COLOUR OF THE SEEDS

In all the taxa studied, the seeds are spherical (Plates I-III) with the exception of *Brassica balearica*, *B. spinescens*, *B. repanda*, *Sinapidendron frutescens* and some seeds of *B. gravinae*. Some seeds deviating from the strictly spherical form were noted in *B. macrocarpa*, *B. rupestris*, *B. villosa*, *B. cretica* and in the cultivated forms where they were the commonest. The axis parallel to the length axis of the radicle and cotyledons is always longer. The seeds of *B. balearica* (Plate IV/3) and *B. repanda* are flat and oval, those of *B. spinescens* flat and circular, those of *B. gravinae* ellipsoidal to spherical, and those of *Sinapidendron frutescens* flat and spool-shaped.

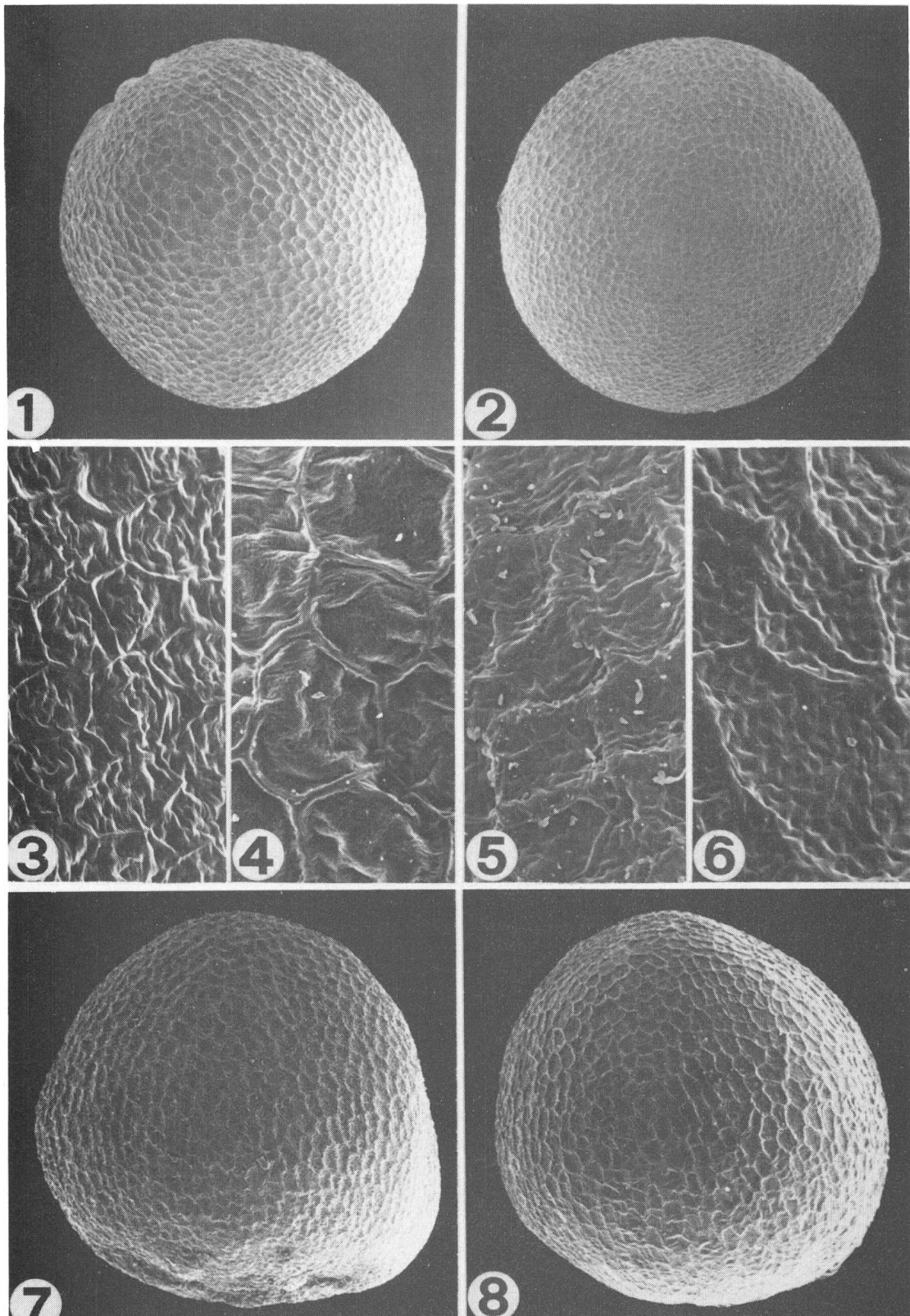
In all the taxa investigated, the cotyledons are folded around the radicle ("Orthoploceae").

The spherical seeds treated in this paper are not winged. A short wing has been found on the flat seeds of *Brassica repanda*, continuing laterally from the tip of the radicle to the upper end of the cotyledons, which are shorter than the radicle. Some seeds of *Sinapidendron frutescens* also bear a short wing which varies in size and position.

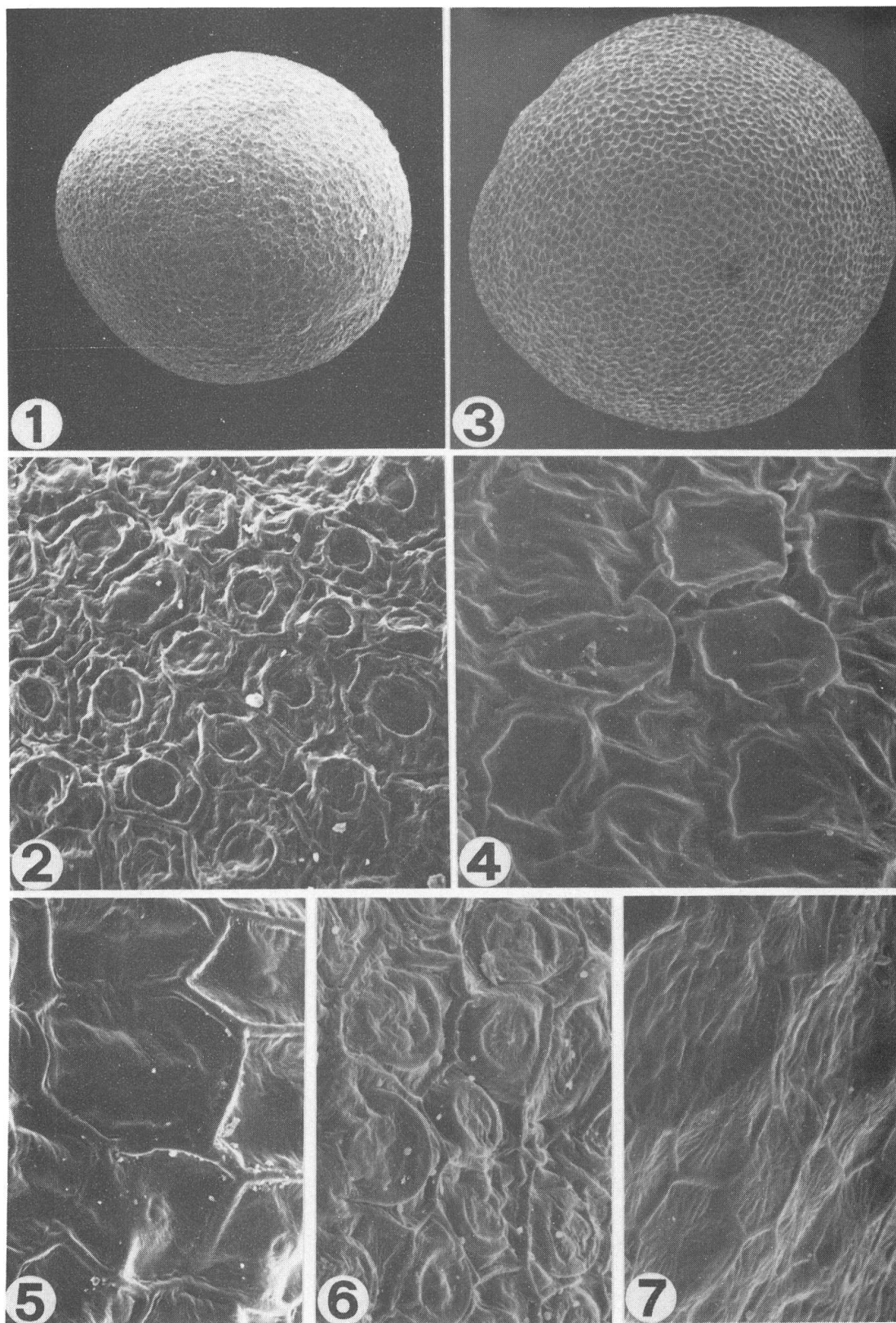
Seed size varies considerably between species as well as between populations, and sometimes between individuals. Under unfavourable conditions, most individuals set few to many seeds which are not fully developed. They are smaller and to a varying degree irregular. From observations on cultivated material, we have found that the percentage of such seeds varies widely in the same individual on different occasions. If seed size is to be used as a character, it is necessary to confine the measurements to the category of well-developed seeds of uniform size which, under favourable conditions, constitute the majority. Our studies have been carried out entirely on such

Plate I. — *Brassica*, SEM micrographs of dry seed surfaces.Fig. 1. — *B. cretica* subsp. *cretica*, Kephallinia, cult. n° 38. $\times 21$.Fig. 2. — *B. cretica* subsp. *cretica*, Skiathos, cult. n° 35. $\times 25$.Fig. 3. — *B. cretica* subsp. *cretica*, Milos, cult. n° 15. $\times 210$. The palisade cells are clearly visible under the epidermis cells in the middle of which the mucilage structures protrude.Fig. 4. — *B. cretica* subsp. *nivea*, W. Crete, cult. n° 01. $\times 275$. The palisade cells are less visible under the epidermis cells than in *B. cretica* subsp. *cretica*.Fig. 5. — *B. cretica*, intermediate form, Crete, cult. n° 28. $\times 210$.Fig. 6. — *B. montana*, Coudon near Toulon (France), cult. n° 88. $\times 210$. The palisades form a network with lower bridges between the main ones.Figs. 7 and 8. — *B. cretica* subsp. *nivea*, same as in Fig. 4 above. $\times 25$. Notice the difference in the surface pattern between seeds from the same seed collection.Plate II. — *Brassica*, SEM micrographs of dry seed surfaces.Figs. 1 and 2. — *B. oleracea*, Fécamp (Seine-Maritime, France), cult. n° 87. 1 = $\times 25$, 2 = $\times 275$. The epidermis aspect is very typical with the central mucilage ring.Figs. 3 and 4. — *B. rupestris*, Sicilia, cult. n° 49. 3 = $\times 21$, 4 = $\times 275$. The epidermis cells form a typical surface pattern.Fig. 5. — *B. insularis*, Isola Frigello off Sardinia, cult. n° 56. $\times 275$. Seed surface with dominating epidermis cells. The underlying palisade cells are not visible.Fig. 6. — *B. hilarionis*, Cyprus, Kyrenia, Kennedy 482, 1936, Herb. K. $\times 275$. Protruding epidermis cells with mucilage structures.Fig. 7. — *B. incana*, Sicilia, cult. n° 57. $\times 275$. The epidermis cells and the palisade ridges are visible.Plate III. — *Brassica*, SEM micrographs of dry seed surfaces.Fig. 1. — Sprouting broccoli, Green Duke 5875 (Suttons). $\times 25$.Fig. 2. — Old Jugoslavian cultivar of kale, cult. n° 73. $\times 25$.Fig. 3. — Giant Jersey cabbage. $\times 275$. The low and diffuse palisade reticulum is typical to the cultivated forms in general.Fig. 4. — Cabbage Delicatesse Prepak 6058 (Suttons). $\times 275$. Epidermal and palisade patterns.Figs. 5 and 6. — Chinese cabbage Sampan 6097 (Suttons). 5 = $\times 25$, 6 = $\times 275$. The secondary palisade network between the main ridges is distinct.Fig. 7. — Oil-seed rape, Gland (VD, Switzerland) n° 3. $\times 190$. Main and secondary palisade network.

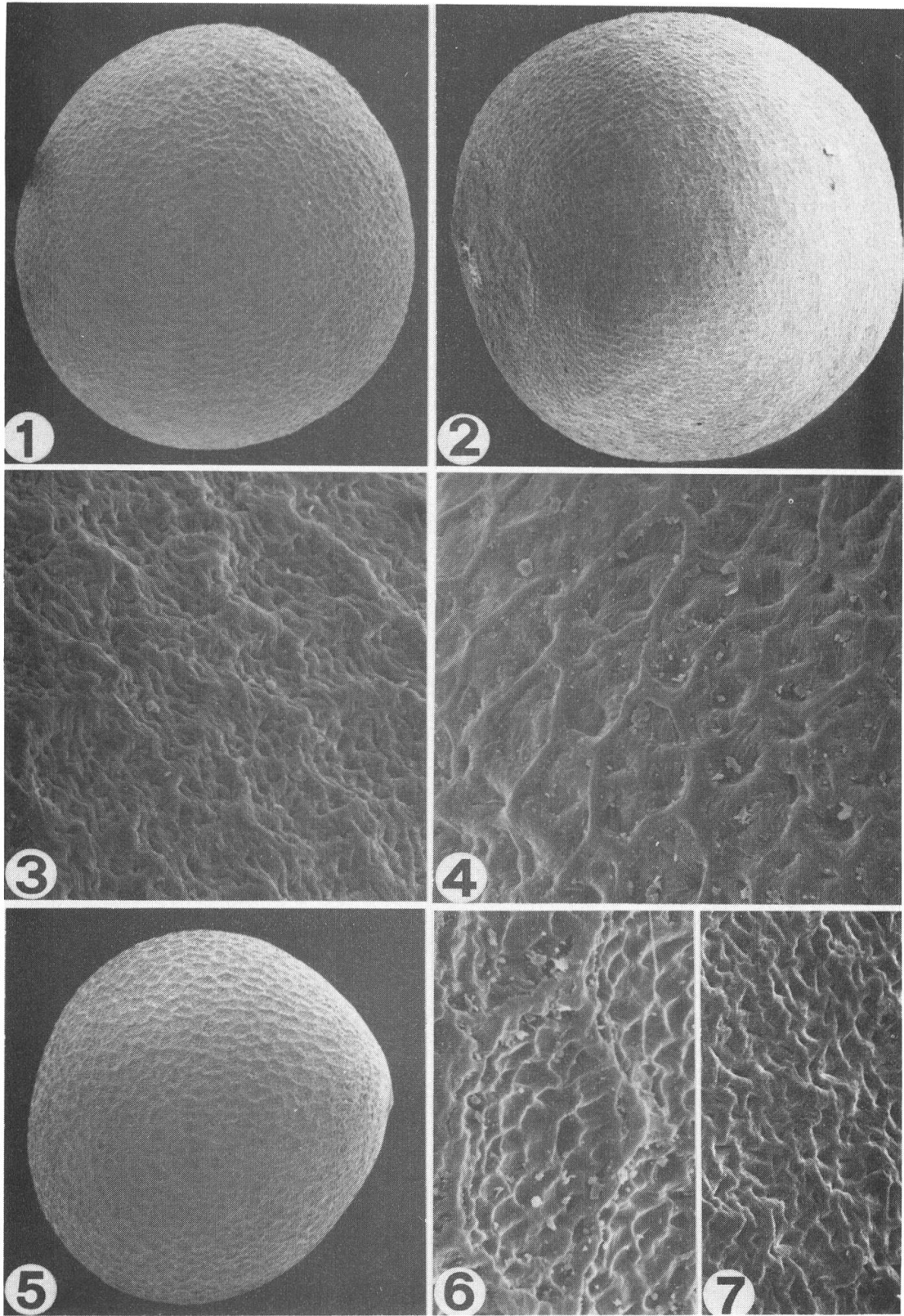
Pl. I



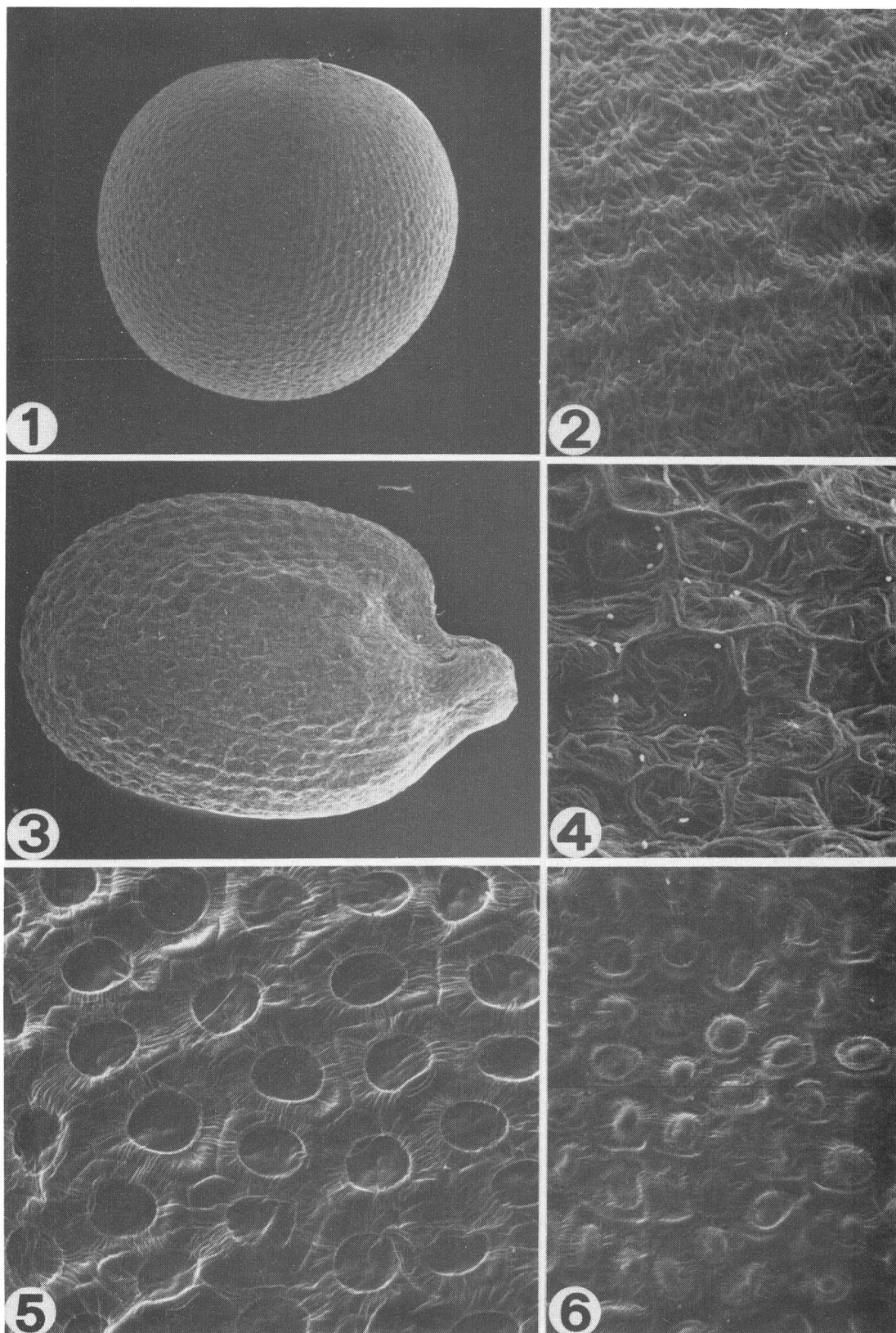
Pl. II



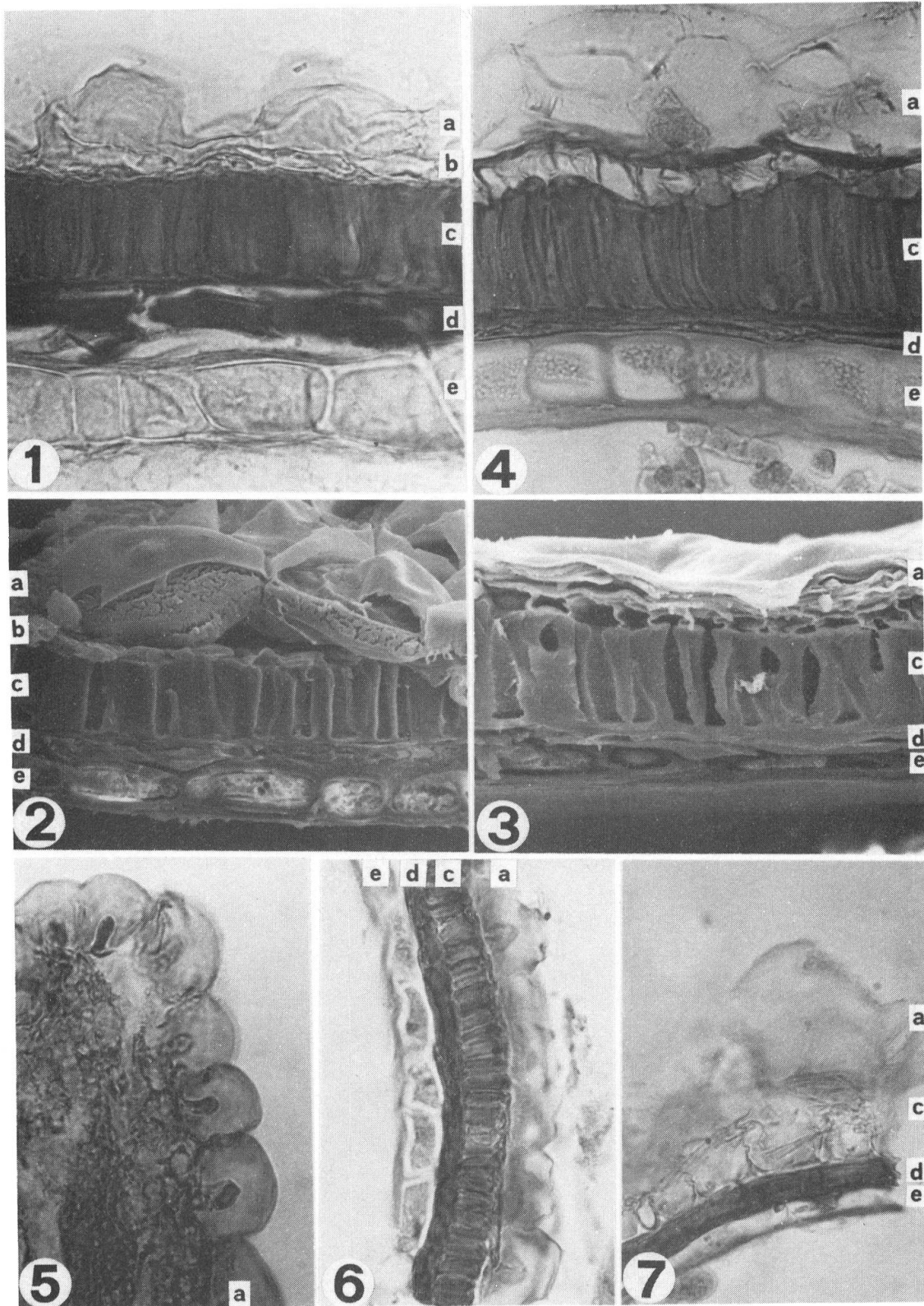
Pl. III



Pl. IV



Pl. V



Pl. VI

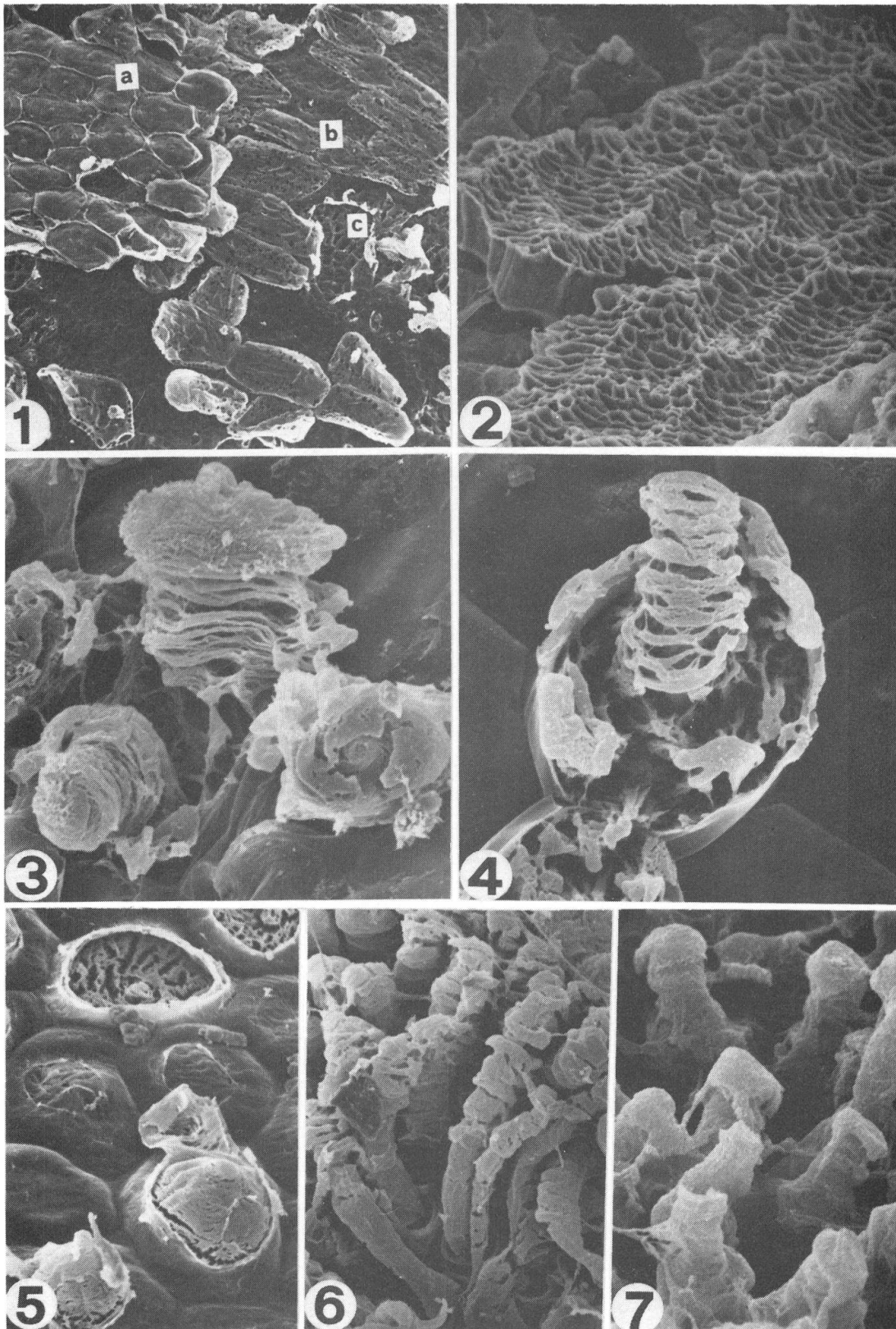


Plate IV. — SEM micrographs of dry seed surfaces.

Figs. 1 and 2. — *Sinapis arvensis*, Gland (VD, Switzerland). 1 = $\times 33$, 2 = $\times 275$. Fig. 2 shows epidermal surface pattern in detail.

Figs. 3 and 4. — *Brassica balearica*, Mallorca, cult. n° 48. 3 = $\times 33$, 4 = $\times 275$. Fig. 4 shows the epidermis cells with their mucilage structures.

Fig. 5. — *Brassica gravinae*, Tunisia, Cosson & al. s.n., 1883, Herb. G. $\times 330$. Epidermis cells with mucilage structures.

Fig. 6. — *Brassica repanda*, Lautaret (Hautes-Alpes, France), Salmeen 1977, Herb. G. $\times 190$. Epidermis cells with mucilage structures.

Plate V. — *Brassica* and *Sinapidendron*, transverse sections of seed-coat.

Figs. 1 and 2. — *B. cretica* subsp. *cretica*, Milos, Ananes, cult. n° 07. 1 = microtome section, LM, $\times 275$. 2 = SEM micrograph of seed immersed in water (4 hours) and sonicated (5 seconds), $\times 330$. *a* = epidermis layer with mucilage; *b* = subepidermal layer of giant cells; *c* = palisade layer; *d* = membranes and pigment layer (notice its cellular structure); *e* = aleuron layer.

Fig. 3. — *B. cretica* subsp. *cretica*, Kephallinia, cult. n° 38. SEM micrograph of water-immersed seed (18 hours). $\times 520$. Cell layers as in Figs. 1 and 2 above.

Fig. 4. — *B. insularis*, Isola Frigello off Sardinia, cult. n° 56. Microtome section, LM. $\times 275$. Cell layers as in Figs. 1 and 2 above. Notice the varying height of the palisade cells, forming the general reticulum.

Figs. 5 and 6. — *B. gravinae*, Algeria, Clavé s.n., 1909, Herb. G. Microtome section, LM. $\times 275$. Seed-coat layers as in Figs. 1 and 2 above. Notice the mucilage cones of the epidermis cells and the thick pigment layer.

Fig. 7. — *S. frutescens*, Madeira, Mandon 16, Herb. G. Microtome section, LM. $\times 275$. Seed-coat layers as in Figs. 1 and 2 above. Notice the particular aspect of the palisade layer and the thick pigment layer.

Plate VI. — *Brassica*. SEM micrographs of seed-coat.

Fig. 1. — Kohlrabi 4315 (Select). Seed immersed in water (36 hours), sonicated in eau de Javel: water (1:1, 15 seconds). $\times 105$. Oblique fracture showing: *a* = bottoms of epidermal cells; *b* = giant subepidermal cells; *c* = tops of palisade cells.

Fig. 2. — *B. macrocarpa*, Isole Egadi, Sicilia, Snogerup & Gustafsson. Seed immersed in water (3, 5 days), in eau de Javel: water (1:1, 1 hour), sonicated (5 seconds), resonicated after one hour in eau de Javel: water (5 seconds), then left in water for 24 hours. $\times 275$. Notice the varying height of the palisade cells.

Figs. 3 and 4. — *B. cretica* subsp. *nivea*, W. Crete, cult. n° 01. Seeds immersed in water (4 hours), sonicated (5 seconds), transferred to eau de Javel: water (1:1, 2 hours), resonicated (5 seconds), 3 = $\times 480$, 4 = $\times 415$. Swollen epidermal slime cones.

Fig. 5. — Cabbage Weisskabies III.4 (Select). Seed immersed in water (36 hours), transferred to eau de Javel: water (1:2, 30 minutes), sonicated (20 seconds). $\times 330$. Swelling epidermis cells.

Fig. 6. — *B. balearica*, Mallorca, cult. n° 48. Seed immersed in water (40 minutes), transferred to eau de Javel: water (1:2) and sonicated repeatedly (three times during 5 seconds with 10 minutes' intervals). $\times 165$. Swollen epidermal slime cones.

Fig. 7. — *B. gravinae*, Tunisia, Cosson & al. s.n., 1883, Herb. G. Seed immersed in water (4 days), sonicated (5 seconds), transferred to eau de Javel: water (1:1, 2 hours), resonicated (5 seconds), 3 = $\times 480$, 4 = $\times 415$. Swollen epidermal slime cones.

selected seed samples. We consider that for meaningful statistic treatment, the seeds must be allowed to develop under uniform, favourable conditions and in a complete absence of pests. More specialized studies on seed sizes are presented by BENGOCHEA & GOMEZ-CAMPO (1975) and BERGGREN (1962).

The largest rounded seeds in the Section *Brassica*, with a diameter of 2.1-2.8 mm, are found in *B. rupestris*, *B. villosa*, *B. macrocarpa*, *B. insularis* and in marrow stem kale. However, in some populations of *B. villosa*, the seeds are only 2.1-2.3 mm. In the few collections of *B. incana* studied, the seeds are small compared with most other material of the *B. rupestris* group, 2-2.4 mm. The seeds of *B. montana* are 1.6-2.3 mm, those of wild *B. oleracea* 1.7-2.2 mm. The seeds of the cultivated $2n = 18$ forms are not always as small as those of the wild *B. oleracea*, but vary from 1.9 to 2.7 mm. In *B. cretica*, there is a variation between populations ranging from 1.7 to 2.8 mm, the smallest seeds being found in populations from Kithnos and Naxos, the largest in a population from an islet close to Milos.

Variation can be great in a sample. In cabbage, for instance, the diameter of the seeds from one and the same commercial seed bag (Weisskabies 1111.4, Pain de sucre, Switzerland) ranges from 1.7 to 2.4 mm.

In other taxa with rounded seeds, those of *Sinapis arvensis* (Plate IV/1), petsai and oil-seed rape are the smallest, 1.6-2.0 mm. The ellipsoidal seeds of *B. gravinae* are 1-1.6 mm. Most flat seeds are small, exceptions being *B. repanda* (1.9-2.1 mm) and *B. balearica* (1.7-2.0 mm). In *B. spinescens*, the flat seeds are circular or nearly so and measure about 1-1.3 mm in diameter.

Some authors such as BERGGREN (1962), VAUGHAN (1959), VAUGHAN & al. (1963) have paid special attention to seed colour. The normal colour of the testa in *Brassica* is brown or purplish to reddish-brown. In *B. cretica*, particularly in subsp. *nivea*, as well as in cauliflower, broccoli and sprouting broccoli, the seeds are parti-coloured, the reticulum ridges being reddish-brown marked with dark-coloured zones and the depressions yellow. Yellow seeds have also been reported for some cultivated Oriental and American varieties of *B. juncea* (VAUGHAN & al., 1963).

GENERAL MORPHOLOGY OF THE SEED SURFACE

Thorough morphological studies of the seed surface in *Brassica* have been published by BERGGREN (1962), MULLIGAN & BAILEY (1976) and VAUGHAN & al. (1963, 1976). In a great number of *Brassica* species, the seed surface is reticulate to reticulate-foveate (STEARN, 1966) on account of the varying height of the palisade cells (Plates I-III, V, VI). The raised network can be very distinct with high narrow ridges, of medium height or diffuse. The meshes are regular or nearly so, sometimes with diffuse ridges between the

main ones (Plate I). The general surface pattern thus varies greatly. This variation is not constant between taxa, seeds of the same collection can differ. BERGGREN (1962) even found differences between parts of one and the same seed.

The depressions between the main ridges are also finely reticulate. Although this can even be observed in a binocular (10×25), it is seen much more clearly on the SEM micrographs (Plates I and III). This feature is particularly pronounced in the petsai or Chinese cabbage and in oil-seed rape (Plate III/5-7). This very fine reticulum is also formed by the palisade cells, the radial, thickened walls of each cell forming the ridges, and the lumen a depression. In certain taxa, there are fewer palisade cells to a main mesh than in others and the diameter of the lumen is greater or smaller. However, these characters are not always constant in a taxon. BERGGREN (1962) even found that the diameter of the palisade lumen can vary in one and the same seed.

In some taxa, the palisade network is less prominent and a distinct epidermal network dominates (Plate II/4). This has been observed, for instance, in some populations of *B. rupestris* from western Sicilia and in some deviating forms of *B. villosa* from the same area. The epidermal cells give the impression of being raised above the general surface. In most other taxa studied, the radial wall and a protruding peripheral or central inner cone-like structure give rise to a characteristic surface pattern, as in *B. hilarionis* (Plate II/6), *B. cretica*, *B. insularis*, *B. rupestris*, *B. oleracea* (Plate II/2), cauliflower and *Sinapis arvensis* (Plate IV/2). A somewhat different pattern with a very diffuse general reticulum and a granulate surface pattern is found in *B. repanda* and *B. gravinae* (Plate IV/5, 6). The reticulum has not always the same appearance. In *B. balearica*, it is coarser with square meshes forming regular lines following the outline of the seed (Plate IV/3). In *B. repanda*, a central disc is evident, whereas in *B. gravinae* the inner part of the epidermis cell is pit-like (Plate IV/5, 6).

THE OUTER INTEGUMENT

In addition to the observations mentioned, small pieces of seed-coat were studied dry and in water. This material was supplemented with tangential and transverse microtome sections. Certain differences in the appearance of the epidermal cells have been found between taxa (Table 1). On dry fragments of seed coat, they are virtually invisible or observed with difficulty in *B. cretica* subsp. *cretica*, *B. montana*, certain varieties of cabbage and Brussels sprouts, certain forms of broccoli and cauliflower, petsai and oil-seed rape. They are visible to varying degrees in *B. cretica* subsp. *nivea*, wild *B. oleracea*, marrow stem kale, certain varieties of cabbage, Brussels sprouts, broccoli, cauliflower, *Sinapis arvensis*, and are distinct in *B. macrocarpa*, *B. insularis*, *B. rupestris*, *B.*

villosa, *B. incana*, *B. hilarionis*, *B. balearica*, *B. spinescens*, *B. repanda*, *B. gravinae*, *Sinapidendron frutescens*, the giant Jersey cabbage and kohlrabi.

When fragments are examined in water, the epidermal cells are more easily observed, the variation in degree of visibility generally being the same as in the dry cells. In a few cases, they are coloured, pale yellow in some *B. cretica* collections and in *B. hilarionis*, yellow in wild *B. oleracea* and *B. montana*, *B. insularis*, *B. macrocarpa*, *B. incana*, some collections of *B. rupestris*, Brussels sprouts, curly kale, marrow stem kale, kohlrabi, some varieties of cabbage and an old cultivar from Yugoslavia.

Under the mucilaginous epidermal layer, there is a layer, or in some cases, presumably two layers of "giant" cells (Plates V/1, 2 and VI/1), the inner periclinal walls of which are reinforced in some taxa with hard seeds — from the outer border trabeculae cross the surface (*B. rupestris*, Table 1).

The next layer is made up of undulating palisade cells (Plates V and VI) which, in some taxa, show through the epidermal cells (Table 1). The thickness of the lower part of the radial walls and the diameter of the lumen vary considerably. In the taxa studied, the palisade cells look the same in all the species with the exception of *B. balearica*, *B. repanda* and *Sinapidendron frutescens* (Plate V/7) in which the radial cell walls are less thickened. The appearance of the main reticulum in tangential view has also been studied. In addition to other seed coat features, it is characteristic of certain taxa. On dry fragments observed under the LM, the seed coat reticulum is obscure and the palisade cells invisible or seen with difficulty in *B. macrocarpa*, *B. rupestris*, *B. villosa*, *B. hilarionis* and most of the cultivated $2n = 18$ forms. Both can be observed to some extent and are sometimes distinct in *B. incana*, oil-seed rape and Chinese cabbage (petsai). In wild *B. oleracea* and *B. montana*, they are more distinct than in the above-mentioned taxa. *B. cretica* is not homogeneous. In its subsp. *cretica*, the dry reticulum and palisade cells are diffuse, both ridges and depressions being brown; in its subsp. *nivea*, the dry palisade cells do not show through the epidermis, but the seed-coat reticulum is distinct and regular with reddish brown ridges and yellow depressions. In some varieties of broccoli and cauliflower, the appearance is the same as in subsp. *nivea*.

In fragments examined in water, the general reticulum and the palisade cells are normally visible. If they were already visible on dry fragments, they become very distinct in water.

The diameter of the palisade lumen varies as follows:

- a) narrow lumen: *B. macrocarpa*, *B. insularis*, *B. montana*, wild *B. oleracea*, Brussels sprouts;
- b) wide lumen: *B. cretica*, *B. rupestris*, cultivated cabbages, kales, cauliflower and broccoli in general, Chinese cabbage, oil-seed rape, *Sinapis arvensis*, *B. villosa*, *B. balearica*;
- c) variable: *B. rupestris*, *B. incana*.

<i>Taxon</i>	<i>Number of collections studied</i>	<i>Seed-coat dry, hard or soft</i>	<i>Epidermis cells dry</i>	<i>Epidermis cells in water</i>	<i>Seed-coat reticulum (= ground net) dry</i>	<i>Palisade cells dry</i>	<i>Palisade cells in water</i>	<i>Lumen. Radial walls of palisade cells</i>
B. cretica subsp. cretica	14	soft	± visible	visible, uncoloured or yellowish	obscure	± visible	very distinct	± big lumen thin wall
B. cretica subsp. nivea	4	soft	± distinct	very distinct, uncoloured or yellowish	distinct	± visible	± visible	big lumen thick wall
B. macrocarpa	3	soft	very distinct	very distinct, yellow	obscure	± distinct	± distinct	± narrow lumen thick wall
B. insularis	4	hard	very distinct	very distinct, yellow	± distinct	± visible	± distinct	narrow lumen thick wall
B. rupestris	4	hard special wall structure	very distinct	very distinct, yellow or uncoloured	invisible	± visible	± visible	narrow or big lumen thick wall
B. villosa	3	hard special wall structure	very distinct	very distinct, yellow or uncoloured	invisible or obscure	invisible	± visible	big lumen
B. incana	5	soft	distinct or very distinct	very distinct, yellow or uncoloured	± distinct	± visible	distinct	narrow or big lumen thick wall
B. montana	3	soft	± visible	visible, yellow or uncoloured	distinct	very distinct	very distinct	narrow lumen thick wall
B. oleracea/wild	5	soft	distinct	distinct, yellow	± distinct	± distinct	very distinct	± narrow lumen ± thick wall
B. hilaricnis	1	soft	very distinct	very distinct, yellowish	obscure	± visible	distinct	thick wall
Cabbages, various sorts	10	soft	± visible to distinct	± visible, yellow or uncoloured	obscure or distinct	± distinct	very distinct	big lumen thin wall
Brussels sprouts	4	soft	± visible to distinct	visible to distinct, yellow or uncoloured	obscure	distinct	distinct	narrow lumen thick wall
Kohlrabi	2	soft	very distinct	distinct, yellowish or uncoloured	obscure	± distinct	distinct	big lumen ± thick wall

Curly kale	1	soft	distinct	± distinct, yellowish	obscure	obscure	± distinct	distinct	big lumen
Marrow-stem kale	3	soft	distinct	distinct, yellow or uncoloured	± distinct, regular	obscure	± distinct	distinct	big lumen
Jugoslavian old cultivar	1	soft	± visible	± distinct, yellowish	distinct, regular	obscure	distinct	very distinct	big lumen
Giant Jersey cabbage	1	soft	very distinct	± distinct, uncoloured	obscure, irregular	obscure	± visible	distinct	big lumen thin wall
Cauliflower	9	soft	± visible to distinct	visible to distinct, uncoloured	± distinct	obscure	± visible to distinct	distinct	big lumen
Broccoli and sprouting Broccoli	10	soft	± visible to distinct	± visible to distinct, uncoloured	± distinct	obscure	± visible	distinct	big lumen
Chinese cabbage (2n = 20)	2	soft	invisible	± visible, uncoloured	obscure or distinct	obscure or distinct	very distinct	very distinct	big lumen
Oil-seed rape	4	soft	± visible	visible to distinct, uncoloured	± distinct	± distinct	± distinct	distinct	big lumen thin wall
B. spinescens	2	± hard	distinct	very distinct	obscure	obscure, coloured zones	invisible	± visible	varying lumen and wall
B. balearica	1	soft	very distinct	very distinct, uncoloured	distinct, coloured zones	distinct	invisible	± visible	big lumen ± thick wall
B. repanda	2	soft	very distinct	distinct, yellowish	invisible	invisible	invisible	invisible	
B. gravinae	3	soft	very distinct	very distinct, yellowish	invisible	invisible	invisible	± visible	big lumen thin wall
Sinapis arvensis	1	soft	± distinct	very distinct, uncoloured	obscure	obscure	± distinct	distinct	big lumen thin wall
Sinapidendron frutescens ..	1	soft	distinct	very distinct, uncoloured	obscure	obscure	± visible	visible	

Table 1. — Some *Brassica*, *Sinapis* and *Sinapidendron* species. Characters observed in small pieces cut by hand of the seed, dry and in distilled water, with LM.

Table 2. — List of material studied. I. *Brassica* Section *Brassica* sens. str.*B. cretica* subsp. *cretica*

Kikladhes, Kithnos: Yavalido Bay, maritime cliffs, 1968, Runemark & Engstrand 37 848, cult. n° 02.

Kikladhes, Kithnos: W. of Stenon Kanalas, maritime cliffs, 1968, Runemark & Engstrand 38 292, cult. n° 03.

Kikladhes, Milos: Ananes islets, the N.W.-islet, 1967, Runemark & Bentzer 29 761, cult. n° 07.

Kikladhes, Milos: Ananes islets, the S.-islet, 1967, Runemark & Bentzer 29 748, cult. n° 15.

Kikladhes, Folegandros: 2 km W. of Pelagia, maritime cliffs, 1967, Runemark & Bentzer 29 518, cult. n° 09.

Kikladhes, Amorgos: the islet of Nikouria, maritime cliffs, 1967, Runemark & Bentzer 30 587, cult. n° 12.

Kikladhes, Naxos: 5 km E. of the town, 200 m, cliff, 1964, v. Bothmer & Strid 21 758, cult. n° 26.

Greece, the S.W. Aegean, the island of Karavi, 1974, Runemark & v. Bothmer 47 171.

Greece, the island of Nisiros: Chochlaki near Mandrakion, 1971, Papatsou 482, cult. n° 37.

Greece, N. Sporades, Skiathos: 4 km N. of the town, maritime cliffs, 1966, Phitos, cult. n° 35.

Greece, the island of Euboea: the islet of Scopulus Prasouda, 1969, Phitos 8888, cult. n° 25.

Greece, the island of Poros: the islet of Modhi, 1974, Runemark & v. Bothmer 47 363.

Greece, the island of Idra: 2 km E. of Ormos Mandraki, 1974, Runemark & v. Bothmer 47 298.

Greece, the island of Kithira, 1973, v. Bothmer.

Greece, the island of Kephallinia, maritime cliffs S. of Assos, 1966, Snogerup 23 668, cult. n° 18.

Greece, the island of Kephallinia, maritime cliffs at Assos, 1971, Phitos, cult. n° 38.

B. cretica subsp. *nivea*

Kriti: 2 km S. of Topolia, 1967, Runemark, cult. n° 01.

Kriti: 1 km S. of Topolia, 1973, Gustafsson, cult. n° 46.

Kriti: Ag. Rumeli, maritime cliffs, 1973, Gustafsson, cult. n° 45.

Peloponnesos: Akrokorinth, N.-exposed cliffs, 1973, Gustafsson, cult. n° 47.

B. cretica, intermediate between subspp.

Kriti: 9 km E.S.E. of Kastelli, S.E. of Rocca, in great gorge, 1964, Snogerup & al. 21 036, cult. n° 28.

B. insularis

Sardinia: Isola Frigello near Olbia, 100 m, 1973, v. Bothmer & Bentzer, cult. n° 56.

Sardinia: Mte S. Giovanni near Iglesias, 300 m, 1973, v. Bothmer & Bentzer, cult. n° 61.

Tunisia: Mt. Ressos, 400 m, 1976, Gustafsson & Knutsson, cult. n° 91.

Tunisia: Bou Kournein, 1976, Gustafsson & Knutsson, cult. n° 92.

B. macrocarpa

Sicilia: Isole Egadi, Favignana, 1 km W. of the harbour, 1973, Snogerup & Gustafsson 1339, cult. n° 53.

Sicilia: Isole Egadi, Favignana, cliffs towards the N.W.-point, 1973, Snogerup & Gustafsson.

Sicilia: Isole Egadi, Marettimo, 1899, Ross 208.

B. rupestris

Sicilia: Capo Zafferano, 50-200 m, 1973, Snogerup & Gustafsson 1330, cult. n° 49.

Sicilia: Mte Pellegrino N. of Palermo, 1973, Snogerup & Gustafsson 1331, cult. n° 59.

Sicilia: Mte Cinisi, 100 m, 1973, Snogerup & Gustafsson 1336, cult. n° 63.

Sicilia: S. part of Partinico, 1973, Snogerup & Gustafsson 1334, cult. n° 55.

B. villosa

Sicilia: N.W. of Castellamare-del-Golfo, 100 m, 1973, Snogerup & Gustafsson 1334, cult. n° 54.

Sicilia: E. part of Mgna Grande, 500 m, 1973, Snogerup & Gustafsson 1343, cult. n° 58.

Sicilia: 2 km E. of Borghetto, 1973, Snogerup & Gustafsson 1346.

Sicilia: S. Giuliano N.E. of Trapani, type loc. of *B. drepanensis* (Car.) Dam., 1973, Snogerup & Gustafsson 1337, cult. n° 50.

Sicilia: Scutari, 50 m, 1973, Snogerup & Gustafsson 1342, cult. n° 51.

Sicilia: Bonagia N.E. of Trapani, 50 m, 1973, Snogerup & Gustafsson.

Sicilia: S. of Pizzolungo, N. of Trapani, 50-200 m, 1973, Snogerup & Gustafsson 1335.

Sicilia: Marianopouli, 1000 m, type loc. of *B. tinei* Lojac., 1973, Snogerup & Gustafsson 1347, cult. n° 52.

B. incana

Sicilia: Castel Morla above Taormina, 400-500 m, 1973, Snogerup & Gustafsson 1300, cult. n° 57.

Sicilia: Capo Tindari, maritime cliffs, 1973, Snogerup & Gustafsson 1308.

Sicilia: Capo Piraino, 50 m, 1973, Snogerup & Gustafsson 1312.

Jugoslavia: Korcula, the islet of Obljak, 1974, Gustafsson & Engstrand, cult. n° 75.

Jugoslavia: Korcula, the islet of Kosor, 1974, Gustafsson & Engstrand, cult. n° 76.

Crimea: 1968, Cockov 506, cult. n° 62.

B. montana

France: Coudon near Toulon, 1975, v. Bothmer & Gustafsson, cult. n° 88. Same loc. 1979, Albert.

France: Gorges-du-Loup near Nice, 1975, v. Bothmer & Gustafsson, cult. n° 89.

B. oleracea, wild

France, Seine-Maritime: Fecamp, maritime cliffs, 1975, v. Bothmer & Gustafsson, cult. n° 87.

France, Seine-Maritime: St.-Pierre-sur-Mer, maritime cliffs, 1975, v. Bothmer & Gustafsson.

France, Seine-Maritime: Les Grandes Dalles, maritime cliffs, 1975, v. Bothmer & Gustafsson.

France, Manche: Roc Granville, maritime cliffs, 1975, v. Bothmer & Gustafsson, cult. n° 86.

France, Somme: Le Treport, 3 km S.W. of the town, maritime cliffs, 1975, v. Bothmer & Gustafsson.

B. hilarionis

Cyprus: Kyrenia, 1100 ft, 1936, Kennedy 482 (K).

Cauliflower

Saxa 4163 (Select).

Stor Dansk (Weibulls), cult. n° 64.

Delfter Markt (Select).

Neckarperle (Select).

Chou-fleur brocoli très tardif d'Anger (without origin; bought in Saumur, France).

Walcheren Winter Thanet (Suttons).

Mechelse Arcturus 6415 (Suttons).

Snow Ball 6437 (Suttons).

Kangaroo 6462 (Suttons).

Broccoli

Green Mountain (Weibulls), cult. n° 85.

Coastal 1102.3 (Select).

Express Corona 5870, Calabrese F₁ hybrid (Suttons).

9 Star Perennial (Thompson & Morgan).

Broccoli de Cicco (Thompson & Morgan).

Sprouting Broccoli

Green Duke 5875, Calabrese F₁ hybrid (Suttons).

Green Lance F₁ hybrid (Thompson & Morgan).

Improved White Sprouting (Suttons).

Purple Sprouting 5931 (Suttons).

Early Purple Sprouting (Thompson & Morgan).

Head-forming cabbages

Vitkål (Weibulls), cult. n° 70.

Kabies Juniriesen (Select).

Weisskabies, Pain de sucre IIII.4 (Select).

Delicatesse Prepak 6058 (Suttons).
 Primo (Thompson & Morgan).
 Shamrock F₁, Big Apple (Thompson & Morgan).
 Savoy Ormskirk Rearguard 6186 (Suttons).
 Savoy King F₁ (Thompson & Morgan).

Brussels sprouts

Chou Bruxelles (Select).
 Roodnerf Vremo Inter 5802 (Suttons).
 Evesham Special (Johnsons).
 Cambridge N^o 5 (Thompson & Morgan).

Kohlrabi

Kohlrabi 4315 (Select).
 Wiener vit (Weibulls), cult. n^o 65.

Marrow Stem Kale

Fodermärgkål P24 (Weibulls), cult. n^o 69.
 Cavalier vert (Truffaut).
 Chou Surmoel (Truffaut).

Green curly kale

Borecole Dwarf Green curled (Thompson & Morgan).

Different non-standard coles

Giant Jersey Cabbage (Etacq Woodcrafts, St. Ouen).
 Cabbage Offenham, Flower of Spring (Carters).
 Wheelers Imperial (Suttons).
 Jugoslavian old cultivar, like marrow stem kale, cult. n^o 73.

II. Other *Brassica* species and related genera.

B. balearica

Islas Baleares: Mallorca, Mount Tossals, 900-1000 m, 1969, Dahlgren & al. 544, cult. n^o 48.

B. repanda

France, Hautes-Alpes: Lautaret, 1850 m, Salmeen 1977 (G).
 France, Hautes-Alpes: Mt. Sécisa, 1500 m, 1900, Girod (G).

B. spinescens

Algérie: falaises du Cap Falcon près d'Oran, 1852, Balansa 657 (G).
 Algérie: Falcon près d'Oran, rochers maritimes, 1932, Faure (G).

B. gravinae

Tunisie: Zaghouan, 1883, Cosson & al. (G).

Algérie: rochers, 1914, Alleizette (G).

Algérie: Constantine, Lambèse, côneau de Bou-Adeloun, 1909, Clavé (G).

B. napus, oil-seed rape

Switzerland: Gland 1. Vaud: between Gland, Vich and Luins, 1979, Stork.

Switzerland: Gland 2. Vaud: 1 km N. Gland, 1979, Stork.

Switzerland: Gland 3. Vaud: between Gland and Bursin, 1979, Stork.

Switzerland: Vaud: Bursin, Möwenpick, 1979, Stork.

B. campestris s.l., Chinese salad cabbage

Sampan 6097, F₁ hybrid (Suttons).

Petsai, F₁ hybrid (Clause).

Sinapis arvensis (= *B. kaber*)

Switzerland: Vaud, Gland, 1979, Stork.

Sinapidendron frutescens

Madeira: in rupibus excelsioribus, Serra d'Agoa et Pico Grande, 1000-1300 m, 1866, Mandon 16 (G).

MUCILAGE CELLS

Mucilaginous seeds or fruits occur in some angiosperm families, genera and species, a comprehensive list of which was published by GRUBERT (1974). In many representatives of the Cruciferae, mucilage is found in the epidermis of seeds of dehiscent fruits. The taxonomic value of the mucilage has not yet been fully investigated, but in the genera hitherto studied, it seems to vary from one group to another, of no significance in *Lepidium* (JONSELL, 1975) or *Morettia* (STORK & WÜEST, 1980), of great interest in certain *Malcolmia* species (STORK, 1971, 1972; STORK & WÜEST, 1978). The possible ecological importance of the mucilage is discussed in GRUBERT (1974), GRUBERT & HAMBACH (1972) and GRUBERT & SCHRIEWER (1972).

In Cruciferae, the type of mucilaginous epidermis of the testa varies considerably. A classification has been presented by VAUGHAN & WHITEHOUSE (1971), and in VAUGHAN & al. (1976). They distinguish fifteen basic categories, but for certain taxa at least, the mucilage pattern is too complex to fit into any of them. This is the case with the *Brassica* species studied by us.

In some cases, the mucilage structures are easy to investigate as in certain *Malcolmia* species, whereas other taxa present great difficulties. The latter is

true for *Brassica*. The mucilage of intact cells (the wall does not burst in water) consists of an inner mass with concentric and/or twisted striations (Plates V and VI). In damaged cells of all species of Section *Brassica*, the mucilage protrudes as rounded lumps. The outer layer forms a frame of loose, bubble-like mucilage. The structure of the inner part of the mucilage lump is more elaborate — the mucilage contains a pile of loose discs (Plate VI/3, 4).

In *B. balearica*, LM and SEM observations reveal a different mucilage pattern (Plate V/6). The longitudinal view of intact, elongated, soaked epidermal cells presents a tree-like structure, a basal central trunk bearing a crown of concentric or twisted concretions. After ultrasonic treatment, the mucilage of soaked seeds takes the form of long narrow columns, the lower part of which is more homogeneous than the upper which seems to be made up of piled-up discs. Such columns have also been observed by BENGOCHEA & GOMEZ-CAMPO (1976).

In dry *B. repanda* and *B. gravinae* seeds, there is a peripheral collar with a central point (Plate IV/5, 6). In water, these structures elongate and in LM give an impression of an outer cup with a central spirally twisted cone. SEM observations after ultrasonic treatment of soaked seeds have not confirmed the presence of an outer collar-like structure. There, we only found a central column arising from a broad platform (Plate VI/7).

LM studies of *Sinapidendron frutescens* show a still simpler spirally twisted mucilage cone. The SEM micrographs are similar to those of *B. gravinae* seeds.

The mucilage of *Sinapis arvensis* is also of a different appearance. In LM a simple conical central structure has been found. This can be compared with the diffuse mucilage column of the cultivated cabbage.

TAXONOMICAL EVALUATIONS OF SOME SEED-COAT CHARACTERS

A. Relations within Section *Brassica*

Some morphological similarities and differences are of taxonomic interest. In all the taxa studied, the seed coat morphology is variable at population and individual levels. The meshes of the surface reticulum can be large or small, the ridges of varying height. The thickness of the radial walls of the palisade cells also varies considerably, even in one and the same taxon or seed collection. Two morphological groups can, however, be distinguished. The one group comprises seeds in which dermal and subdermal

layers are transparent to varying degrees and the palisade network and cells are clearly visible, i.e. *B. cretica*, *B. oleracea*, *B. montana* and the cultivated varieties of the section. In the other group, the seeds have very thick or non-transparent dermal and subdermal layers through which the palisade network and cells are not visible or only faintly so, i.e. *B. insularis*, *B. macrocarpa*, *B. rupestris*, *B. villosa*, *B. incana* and *B. hilarionis*. Within both these groups, some variation has been noted.

In the first group, seeds of *B. cretica*, *B. oleracea* and *B. montana* resemble one another closely, i.e. they are soft, and the palisade reticulum is regular with fairly small meshes and is usually easy to observe. However, each taxon has some distinguishing characters. The most obvious features are the distinct epidermis cells and the yellow reticulum depressions in *B. cretica* subsp. *nivea*, and the distinct and yellow epidermal cells in *B. oleracea* and *B. montana*. However, yellowish dermal and subdermal layers have also been observed in some *B. cretica* populations. The seeds of *B. cretica* subsp. *cretica*, *B. oleracea* and *B. montana* are uniformly reddish-brown. Transverse sections show a slight difference in the shape of the palisade cells which are often high and narrow in *B. cretica* subsp. *cretica*, whereas they are lower and wider in the other taxa. The cultivated $2n = 18$ forms are very variable. On the average, the epidermal cells are more transparent and the surface reticulum is less pronounced than in the wild species, the palisade cells are low and wide and the seed colour is lighter. However, the seed colour can be extremely variable even in one and the same commercial seed bag. The seed coat patterns of some of the forms of cauliflower, broccoli and sprouting broccoli studied correspond to that found in typical *B. cretica* subsp. *nivea*, i.e. the epidermal cells are colourless and more conspicuous, and the reticulum depressions yellow. This is particularly true of the broccolis and sprouting broccolis, which correspond more exactly to the wild *B. cretica* subsp. *nivea* in spite of their long horticultural history. According to BUCK (1956) and SWARUP & CHATTERJEE (1972), cauliflower is probably a later derivative. Seeds of other strains of these cultivars greatly resemble those of cabbages, Brussels sprouts, kales and kohlrabi. The epidermal cells of these forms are often distinct and yellow, the palisade reticulum obscure to indistinct, the colour reddish-brown although very pale seeds also occur. A primitive kale from Yugoslavia with very large seeds and a yellowish epidermis, and the giant Jersey cabbage, which has a colourless epidermis, have a similar morphology.

In the second seed group, the seeds of *B. hilarionis*, *B. macrocarpa* and *B. insularis* have a striking external resemblance in that the yellow epidermis is distinct and non-transparent and the palisade cells do not show through. However, *B. hilarionis* and *B. macrocarpa* have soft seeds, easy to section with a razor blade, and their palisade reticulum is obscure. *B. insularis* has hard seeds and a distinct palisade reticulum can be seen on dry fragments. In *B. rupestris* and *B. villosa*, the seed coat is hard and periclinal wall thickenings have been found in the subdermal layer in several collections of each species. In all collections of these species, the dermal and subdermal

layers have been found to be yellowish and the subdermal cells to be more conspicuous than in other species. The seed coat reticulum is not evident and the palisade cells are high and narrow. The populations of *B. incana* from eastern Sicilia differ in several respects from the above taxa. The seed coat is easily cut, i.e. it is soft, the epidermis is distinct, the dermal and subdermal layers are yellowish, the palisade reticulum is distinct and regular, the palisade cells low. The collections from Yugoslavia and the Crimea observed differ somewhat in the less distinct and more transparent epidermal cells, an obscurer palisade reticulum, and low, broad palisade cells. In the Crimean population, the dermal and subdermal layers are colourless, in the Yugoslavian ones yellow.

B. Other sections and genera

The seed coat morphology of petsai or Chinese cabbage (of the *B. rapa* complex, $2n = 20$) and of the oil-seed rape (*B. napus*, $2n = 38$) slightly differs from the other taxa studied (Plate III/5-7). In addition to the general reticulum which is made up of distinct and regular rows of rhomboidal or hexagonal depressions, the finer network formed by the individual palisade cells, which are low with wide lumina, is more conspicuous than in Section *Brassica*. The dermal layers are colourless, and the epidermis of dry fragments is difficult to distinguish with LM.

The seeds of *Sinapis arvensis* (Plate IV/1, 2) have many features in common with *B. rapa* and *B. napus*, though the epidermal cells are more conspicuous with a central mucilage core of a different shape. The taxonomic position of *S. arvensis* has been discussed in several publications, which are reviewed in VAUGHAN & al. (1976). European authors usually treat it under *Sinapis*, whereas North-American works often refer to it as *Brassica kaber* (DC.) L. Wheeler. The latter arrangement may be preferable, if we are to retain a large genus *Brassica* at all.

The seeds of other *Brassica* species investigated differ entirely in having flat seeds (exception *B. gravinae*) and conspicuous epidermal cells with a characteristic surface (Plate IV/5, 6). In *B. balearica*, the seeds are yellow with darker zones forming a rectangular surface network (Plate IV/3, 4). The epidermal cells are colourless and the outer wall has the appearance of a wrinkled skin, spreading from a central slightly protruding knob. In *B. spinescens* seeds, the epidermis is similar, though they are brown and circular in outline. The isolated position of *B. balearica* has also been pointed out by previous authors (cf. ONNO, 1933). In characters studied by GOMEZ-CAMPO & TORTOSA (1974), such as seedling, particularly cotyledon, and siliqua morphology, this species is characteristic in a way that these authors consider primitive. Together with other species usually classified in Section *Brassicaria* (Godr.) Coss. (such as *B. repanda* and *B. gravinae*), it approaches the Macaronesian *Sinapidendron* species in these characters as well as those

studied by us. The seed morphology and the appearance of the mucilage support the removal of *B. balearica* from Section *Brassica*, or even from the genus.

B. gravinae is an exception to the group. It has spherical seeds as was also pointed out by BENGOCHEA & GOMEZ-CAMPO (1975), and low, wide but typical palisade cells. The appearance of the epidermis is characteristic. The pale yellow cells meet at a very sharp angle. Each cell has a peripheral raised zone and a central pit in the middle of which is a little knob, i.e. the top of a central mucilage cone (Plate IV/5). On the other hand, the seed coats of *Brassica repanda* and *Sinapidendron frutescens* are similar. In transverse section (Plate V/7), the absence of true palisade cells and the presence of a clearly cellular pigment layer are striking. The appearance of the epidermal cells of dry fragments is also characteristic with a protruding broad central mucilage core (Plate VI/7). Both species have short seed wings.

CONCLUDING REMARKS

If we compare the variation pattern in the general morphology of the seed coat and that in the appearance of the epidermal mucilage, obvious similarities can be seen. Section *Brassica* is uniform. Though there are slight variations in the morphology of the seed coat, the appearance of the mucilage is constant. In *B. balearica*, not only the seed form and the seed coat morphology but also the epidermal mucilage structures point to an isolated position. There are also differences between this species and the taxa which are normally included in Section *Brassicaria*. The seed coat morphology of petsai, or Chinese cabbage ($2n = 20$), *Sinapis arvensis* and even more that of oil-seed rape resembles that of Section *Brassica*. The mucilage structures of petsai and oil-seed rape resemble those of Section *Brassica*, whereas the mucilage of *Sinapis arvensis* differs.

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