

The Northwest European Pollen Flora, 20

PAPAVERACEAE

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LITERATURE

Erdtman (1952, 1969), Faegri and Iversen (1975), Henderson (1965), Kuprianova and Alyoshina (1972, 1978), Layka (1975, 1976), Rachele (1974), Sagdullajeva (1959), Tarnavschi and Mitroiu (1960).

INTRODUCTION

The Papaveraceae are distributed, with a few exceptions, throughout the Northern Hemisphere, especially in both eastern Asia and western North America (subfam. Hypecoideae and subfam. Papaveroideae) and in northern Africa and Asia Minor (subfam. Fumarioideae). The plant family is ill represented in NW Europe; only 33 of the more than 800 species are distributed in this area, and only 7 of the 42 genera (Fedde, 1936).

Three surveys on the pollen morphology of Papaveraceae have been written. Erdtman (1952) studied 60 species from 32 genera, and Sagdullajeva (1959) 84 species from 28 genera. Both works are mainly taxonomic and aim to show the variability of pollen types in this family. They are therefore based mainly on non-European species. The recent monograph of Layka (1976), who studied 384 species from all genera is more complete and he included most of the species from NW Europe. His approach is also taxonomic and therefore differs from the present survey, but his results and many photomicrographs are of great interest and will be discussed below.

More authors have studied the morphology of Papaveraceae pollen but only papers concerning NW European species are summarized here. Three pollen floras are dealing with NW European species: that on Romanian species by Tarnavschi and Mitroiu (1960), Rachele (1974) on the Papaveraceae from northeastern North America and Faegri and Iversen (1975) on NW European pollen. The two former papers give short descriptions of the pollen of each species and these are closely in accord with our results. Rachele describes several pollen types and gives a key for their separation. Faegri and Iversen mention in their key to the NW European pollen a type for *Papaver*, one for *Glaucium* and another for *Fumaria*. These correspond in the present paper to the *Papaver rhoeas* type, the *Glaucium flavum* type and, partially, the *Fumaria officinalis* type (*F. densiflora* group see page 220). Faegri and Iversen do not mention other Papaveraceae.

Although most authors have emphasized the differences between the pollen types in the Papaveraceae, they have several characteristics in common:

(1) All the colpate types have a granulate colpus membrane with somewhat coarse granules. In porate pollen, however, the membrane is nudate (*Papaver argemone* excepted).

(2) The inner surface of the nexine is always more or less structured (Layka, 1975). These features are not artefacts and they occur in almost all pollen types of the Papaveraceae. They are therefore an important part of the descriptions which are constant within each species (Layka, 1975) and can be used to distinguish species within a pollen type (see *Papaver rhoeas* type, page 227). The author agrees with Van Campo (1978) that, in this case, the term nexine can not be used according to its definition. (nexine: the inner, non-sculptured part of the exine, Erdtman, 1952). Notwithstanding this consideration the author decided to use the term nexine for the ornamented inner layer of the exine also. This is done for practical reasons.

In Papaveraceae two kinds of nexine structures are distinguishable in LM at a magnification of $1000\times$: (a) The inner surface of the nexine has small ornamentations. They are visible in cross-section as a rough margin to the nexine, and in L-O analysis as "scabrae" below the nexine: cf. "endexine endo-sculptée" (Van Campo, 1971), "endexine en petits plaques" (Layka, 1976), "endosculptures" (Van Campo, 1978). In this article the term **endo-sculptures** has been used. (b) The inner surface of the nexine is divided up by a series of channels. These are visible in cross-section as grooves in the nexine, and in L-O analysis as a negative reticulum below the nexine: "endo-cracks" (Oldfield, 1959) and "channels" (Clarke and Jones, 1977). The remaining parts of the nexine are irregular, angular shaped, and of more or less equal dimensions throughout the grain: cf. "endexine en plaques" (Van Campo, 1971, 1978; Layka, 1975, 1976). In the present article the term **endo-cracks** has been used.

(3) Pollen of Papaveraceae usually lacks endoapertures (*Papaver argemone* excepted).

Each species in the Papaveraceae has a variable number of ectoapertures. Usually the percentage of aberrant pollen is low (about 5%), but percentages up to 50% are found, e.g. in certain *Fumaria* species.

An even more common feature is the existence of a connection between two or more ectoapertures. A sign that this has happened is the existence of one or more colpi in a porate grain (especially in the *Fumaria densiflora* group, see page 220). In colpate pollen this feature causes syncolpate ecto-colpi (especially in the *Corydalis lutea* type, see page 216).

The Papaveraceae in NW Europe is divided into two sub-families: Papaveroideae and Fumarioideae. The pollen grains of the species within each sub-family have certain characteristics in common by which they differ from those in the other subfamily:

	Papaveroideae	Fumarioideae
Pollen class	usually zonoaperturate	usually pantoaperturate
Apertures	usually three ectocolpi	usually six or twelve ectocolpi or ectopori
Ornamentation	tectate, tectum perforatum or reticulate; always with scabrae	verrucate or psilate; no scabrae
Columellae	arranged in curved rows or forming an infra-reticulum	columellae not visible in light microscope

TERMINOLOGY

Syncolpate: In this article the word "syncolpate" has been used as a term, meaning that two or more colpi are connected (Reitsma, 1970). It is not used to define a pollen class in the sense of Faegri and Iversen (1975). Most pollen classes are defined on the number and distribution of the apertures on the grain. The term syncolpate deals only with a different aspect of the morphology: whether or not the colpi are connected. In Papavera-ceae the pollen fall into several pollen classes: zonocolpate, pantocolpate or pantoporate. Within the first two of these classes, the apertures may also be syncolpate. Using syncolpate as a separate pollen class is misleading and has therefore been avoided.

Apocolpium: Area delimited by transverse lines connecting neighbouring ectocolpus ends. The term apocolpium has been redefined in the present paper in order to make it suitable for pantocolpate pollen grains also, and not only for zonocolpate ones. In fact apocolpium and mesocolpium are complementary terms; the apocolpium refers to the area outside the ends of ectocolpi, whereas the mesocolpium is the area in between the ectocolpi.

Mesocolpium (Reitsma, 1970): Area delimited by two adjacent ectocolpi and by transverse lines drawn through the ends of these ectocolpi.

Punctae: Parts of the exine may be pierced by perforations less than 1 μm in diameter which are separated from one another by distances of less than 1 μm . These have been termed punctae (Praglowksi and Punt, 1973).

Endo-cracks (Oldfield, 1959) and *Endosculptures* (Van Campo, 1978): See the Introduction.

SPECIMENS EXAMINED

Subfam. Fumarioideae

Corydalis bulbosa (L.) De Candolle — France: Guinet s.n. (MPU); Germany: Kooper s.n. (U); Switzerland: Kintschi s.n. Fl. Raetica Exsicc. 541 (U).

Corydalis cava (L.) Schweigger et Koerte — syn. *Corydalis bulbosa* (L.) De Candolle.

Corydalis claviculata (L.) De Candolle — England: Cochrane 107 (U); France: De Smidt B 113 (U); The Netherlands: Janssen s.n. (fresh material) (U), Mennega s.n. (U).

- Corydalis densiflora* C. Presl — syn. *Corydalis solida* (L.) Swartz ssp. *solida*.
Corydalis fabacea (Retzius) Persoon — syn. *Corydalis intermedia* (L.) Mérat.
Corydalis halleri Willdenow — syn. *Corydalis solida* (L.) Swartz.
Corydalis intermedia (L.) Mérat — Austria: Traunsteiner 1077 (U); Switzerland: Flüttsch Fl. Raetica Exsicc. 952 (U).
Corydalis lutea (L.) De Candolle — France: Behrendsen s.n. (U); The Netherlands: Dijkstra 1028 (U).
Corydalis ochroleuca Koch — The Netherlands: Went s.n. (U); Yugoslavia: Biol. Exc. 1960-235 (U), Mennega and Baretta 125 (U).
Corydalis pumila (Host) Reichenbach — Germany: Kobus s.n. (L).
Corydalis solida (L.) Swartz ssp. *solida* sensu Flora Europea — Belgium: Van der Burgh s.n. (U), Smit 2009 (U); The Netherlands: s.c. Anno 1961 (fresh material) (U), s.c. Anno 1964 (fresh material) (U), Went s.n. (U).
Fumaria bastardii Boreau — Portugal: Fernandes, Sousa and Matos 3718 (U).
Fumaria boraei Jordan — syn. *Fumaria muralis* ssp. *boraei* (Jordan) Pugsley.
Fumaria caespitosa Loscos y Bernal — syn. *Fumaria parviflora* Lamarck.
Fumaria capreolata L. ssp. *babingtonii* (Pugsley) P.D. Sell — Ireland: Biol. Exc. 1969-152 (U).
Fumaria capreolata L. ssp. *capreolata* sensu Flora Europea — The Netherlands: Oudemans 414 (U).
Fumaria caroliana Pugsley — Switzerland: Allen s.n. (type specimen) (BM).
Fumaria densiflora De Candolle — France: Guinet s.n. (MPU), Hekking 425 (U); The Netherlands: De Boer 567 (U).
Fumaria martinii Clavaud — England: Bucknall s.n. (BM), Sandwith, Sandwith and Ellman s.n. (L), Sandwith and Sandwith s.n. (L).
Fumaria micrantha Lagasca y Segura — syn. *Fumaria densiflora* De Candolle.
Fumaria muralis Sonder ssp. *boraei* (Jordan) Pugsley — The Netherlands: Leemans s.n. (U).
Fumaria muralis Sonder ssp. *muralis* sensu Flora Europea — France: Biol. Exc. 1963-3855 (U); Ireland: Hessel, Klein and Rubers 875 (U).
Fumaria muralis Sonder ssp. *neglecta* Pugsley — England: Pugsley 285 (BM).
Fumaria occidentalis Pugsley — England: Bickham and Viquers s.n. (L), Rilstone s.n. (BM), Sandwith and Sandwith 3579 (L).
Fumaria officinalis L. ssp. *officinalis* sensu Flora Europea — Belgium: Hekking 702 (U); The Netherlands: Van den Burgh s.n. (fresh material) (U), Mennega s.n. (U).
Fumaria officinalis L. ssp. *wirtgenii* (Koch) Arcangeli — Malta: Kramer and Westra 4173 (U); Switzerland: Biol. Exc. 1922 s.n. (U).
Fumaria parviflora Lamarck — France: Leeuwenberg 1341 (U), Germany: Wttewaall van Wickenburg s.n. (U).
Fumaria purpurea Pugsley — England: Sandwith s.n. (L), Sandwith and Sandwith s.n. (L); Ireland: Hessel, Klein and Rubers 1181 (U).
Fumaria schrammii (Ascherson) Velenowski — Germany: Dubian s.n. (U); Spain: Wilmott s.n. (co-type specimen) (BM).
Fumaria vaillantii Loiseleur — Germany: Behrendsen s.n. (U), Biol. Exc. 1965-865 (U).
Fumaria vaillantii Loiseleur ssp. *schrammii* (Ascherson) Haussknecht — syn. *Fumaria schrammii* (Ascherson) Velenowski.
Fumaria wirtgenii Koch — syn. *Fumaria officinalis* L. ssp. *wirtgenii* (Koch) Arcangeli.

Subfam. Papaveroideae

- Chelidonium majus* L. — England: France 908 (U); Ireland: Hessel, Klein and Rubers 1175 (U); The Netherlands: Cult. Hort. Utrecht s.n. Anno 1964 (U) (fresh material), Punt s.n. (fresh material) (U), Uittien 480 (U).
Eschscholzia californica Chamisso — The Netherlands: De Kleuver s.n. (L), Kramer 123 (U); U.S.A. (California): Van Heerdt 494 (U).

- Glaucium corniculatum* (L.) J.H. Rudolph — The Netherlands: Mennega s.n. (U); Spain: Biol. Exc. 1962-1614 (U), Biol. Exc. 1964-741 (U).
- Glaucium flavum* Crantz — England: Wilson 41 (U); France: Van Loon 279 (U), Van Oordt s.n. (U).
- Meconopsis cambrica* (L.) Viguier — England: Biol. Exc. 1968-447 (U); Spain: Bordère s.n. (U), Horreüs de Haas 47 (U).
- Papaver argemone* L. — Belgium: Lejeune et Courtois 353 (U); France: Leeuwenberg 1523 (U); The Netherlands: s.c. Anno 1961 (U) (fresh material), s.c. Anno 1964 (U) (fresh material), De Roon s.n. (U), Van Royen 476 (U).
- Papaver dubium* L. — Ireland: Biol. Exc. 1962-2684 (U); The Netherlands: s.c. Anno 1905 (U), Dijkstra 767 (U), Punt s.n. (fresh material) (U), Lieftinck s.n. (U).
- Papaver hybridum* L. — Germany: s.c. Anno before 1840 (U); Spain: Biol. Exc. 1951-505 (U), Biol. Exc. 1957-453 (U).
- Papaver lecoquii* Lamotte — England: Wilmott 55 VC (BM).
- Papaver oriëntale* L. — The Netherlands: Abeleven s.n. (L), Brand s.n. (L).
- Papaver radicum* Rottboel — Greenland: Daniëls and De Molenaar 311 (U); Iceland: Draaier s.n. (U), Hekking 3743 (U), Oosterveld O. 1366 (U); Spitsbergen: Van Oordt 25 (U).
- Papaver rhoeas* L. — England: Biol. Exc. 1968-163 (U), Biol. Exc. 1968-227 (U); The Netherlands: Dieleman 347 (U), Jonker s.n. (fresh material) (U).
- Papaver somniferum* L. ssp. *somniferum* sensu Flora Europea — The Netherlands: Hekking s.n. (U).
- Papaver somniferum* L. ssp. *setigerum* (De Candolle) Corbière — Belgium: Hekking 697 (U).
- Papaver strigosum* (Boenninghausen) Schur = *P. rhoeas* L. p.p. — France: De Roon s.n. (U); The Netherlands: Van der Aa s.n. (U), Vooren s.n. (U).

KEY TO THE POLLEN TYPES

- 1.a. Pollen grains with ectopori 2
- b. Pollen grains with ectocolpi 3
- 2.a. Ectopori (6–12) with thick, distinct annuli; pore membrane nudate, strongly protruding from the ectopori; endoapertures absent; ornamentation verrucate; pollen spheroidal. *Fumaria officinalis* type
- b. Ectopori (6) without annuli; pore membrane not protruding, with coarse granules forming an ill-defined operculum; faint endoaperture present, congruent with the ectoporus; ornamentation scabrate; pollen cubic *Papaver argemone* type
- 3.a. Pollen zonocolpate 4
- b. Pollen pantocolpate 11
- 4.a. Ornamentation reticulate, micro-reticulate or a tectum perforatum, at least in mesocolpium 5
- b. Ornamentation psilate, scabrate or verrucate 7
- 5.a. Pollen with 5 or 6, rarely with 4 or 7 ectocolpi; ectocolpi narrow; colpus membrane obscure; ornamentation reticulate, with lumina of similar dimensions throughout *Eschscholzia californica* type
- b. Pollen 3-zonocolpate; ectocolpi of medium width or broad; colpus membrane granulate; ornamentation microreticulate or reticulate or a tectum perforatum; if reticulate lumina smaller near the apocolpium 6

- 6.a. Ornamentation micro-reticulate or a tectum perforatum; colpus membrane with small granules *Chelidonium majus* type
- b. Ornamentation reticulate in the mesocolpium; size of lumina decreasing towards the apocolpium; tectum perforate at apocolpium; colpus membrane with coarse granules. . *Glaucium flavum* type
- 7.a. Ornamentation psilate; apocolpium thickened, with few, distinct perforations; pollen 3-zonocolpate *Corydalis claviculata* type
- b. Ornamentation scabrate or verrucate; apocolpium without visible perforations; pollen 3- or 4-zonocolpate 8
- 8.a. Pollen 4-zonocolpate; P/E ratio usually erect 9
- b. Pollen 3-zonocolpate; P/E ratio adequate to semi-erect 10
- 9.a. Ornamentation scabrate *Papaver radicum* type: type A
- b. Ornamentation verrucate *Papaver radicum* type: type B
- 10.a. Ornamentation scabrate; exine usually somewhat thickened in the apocolpium, but sometimes not *Papaver rhoeas* type
- b. Ornamentation verrucate; exine of equal thickness throughout the grain *Corydalis solida* type
- 11.a. Ornamentation psilate 12
- b. Ornamentation scabrate or verrucate 13
- 12.a. Pollen 6-pantocolpate with distinct apocolpium: index ca. 0.25; exine clearly thickened in the apocolpium; pollen cubic *Corydalis claviculata* type
- b. Pollen 6- or 12-pantocolpate usually with syncolpate ectocolpi, rarely with a small apocolpium: index 0.00—ca. 0.10; exine not thickened in the apocolpium; pollen spheroidal or a convex tetrahedron *Corydalis lutea* type
- 13.a. Ornamentation verrucate 14
- b. Ornamentation scabrate 15
- 14.a. Ectocolpi frequently syncolpate, strikingly broad; pollen 6- or sometimes 12-pantocolpate; differentiation between sexine and nexine clear *Papaver radicum* type: type B
- b. Apocolpium present; ectocolpi of medium width or rather narrow; pollen 6-pantocolpate; differentiation between sexine and nexine diffuse *Corydalis solida* type
- 15.a. Diameter of the grain 35—45 μm *Papaver radicum* type: type A
- b. Diameter of the grain 20—30 μm *Papaver rhoeas* type

DESCRIPTION OF THE POLLEN TYPES (ARRANGED IN ALPHABETIC ORDER)

Chelidonium majus type (Plate I)

Pollen class: 3-Zonocolpate.

P/E ratio: Usually more or less adequate, sometimes subtransverse or suberect

Apertures: Ectoaperture — colpus, long, of medium width, hardly sunken; margins indistinct and irregular; margo absent; costae absent; ends subacute or obtuse; colpus membrane with distinct irregular angular granules; on these granules small scabrae of less than 0.5 μm (SEM). Endoaperture — absent.

Exine: Nexine with indistinct endosculptures, visible in cross-section. Sexine as thick as or a little thicker than nexine. Sexine 1 of distinct, slender columellae, thicker than sexine 2. Sexine 2 a tectate or semi-TECTATE layer. Sexine 3 of short scabrae, not or hardly visible in cross-section.

Ornamentation: Microreticulate or a tectum perforatum. Muri simplicolumellate. Lumina or perforations irregular, rounded; not or slightly decreasing towards the apocolpium. Small scabrae on the tectum or on the muri of the microreticulum (SEM). The microreticulum in LM appears to be a tectum perforatum in SEM (compare Plate I,6 and I,1). Columellae arranged in curved rows or circles (infra-reticulum); all similar in outline and diameter.

Outlines: Equatorial view — usually circular or slightly elliptic. Polar view — circular, colpi hardly intruding.

Measurements: Glycerine jelly — P 27–34 μm , E 27–34 μm , P/E 0.90-(1.00)-1.10; Apocolpium index 0.17-(0.19)-0.21 Silicone oil — P 25–30 μm , E 25–30 μm , P/E 0.90-(1.00)-1.10.

Species: *Chelidonium majus*.

Comments

This pollen type is characterized by the microreticulate or tectum perforatum ornamentation, the infra-reticulum, and the granulate colpus membrane. The pollen type most resembles the *Glaucium flavum* type, from which it differs by the microreticulum (compare Plate I,6 and XV,7), the outline (compare Plate I,2 and XVI,1, 2, 3), and the arrangement of the columellae (compare Plate I, 7 and XV, 7). The pollen grains appear to be more constantly spheroidal and the colpi are hardly sunken, whereas in the *Glaucium flavum* type most grains are ellipsoidal and the colpi are more deeply sunken.

We could not confirm the statement of Rachele (1974) that the colpus membrane of *Chelidonium* is not granulate.

Corydalis claviculata type (Plate II)

Pollen class: Mostly 6-pantocolpate, sometimes 3-zonocolpate or 12-pantocolpate.

Apertures: Ectoaperture — colpus, long, of medium width, not or hardly sunken; margins diffuse; margo absent; ends irregularly acute, in 12-pantocolpate grains ectocolpi syncolpate; colpus membrane with small granules, colpi arranged as though on the sides of a tetrahedron. Endoaperture — absent, but there is an elliptic area beneath the ectoaperture where the endocracks are more frequent than elsewhere.

Exine: Nexine thin, interrupted by perforations or deep endocracks; perforations common in meso- and apocolpium, endocracks concentrated near ectocolpus. Sexine thick, much thicker than nexine, thickened in the apocolpium and along ribs between the apocolpia, thus giving the grain a cubic shape. The perforations and the endocracks from the nexine penetrate deeply into the sexine (visible in cross-section, Plate II, 1), but do not reach the outside of the grain (compare Plate II, 3 and II, 2). This causes a slight differentiation in the sexine: a rather thick layer with endocracks and a thinner one without.

The outer layer is thickened in the apocolpium and has a different density of staining (Plate I, 1).

Ornamentation: Psilate with few distinct perforations, especially in the apocolpium. These perforations do not reach the surface of the sexine, but are clear in L-O analysis, about 1 μm in diameter, and rather irregular in outline. Endocracks clearly visible in L-O analysis especially near ectocolpi.

Outlines: Obtusely quadrangular with slightly sunken colpi in each view. Colpi situated between the angles.

Measurements: Glycerine jelly — diameter 35–40 μm ; exine ca. 2 μm thick near the ectocolpi, ca. 3.5 μm thick in the apocolpium; apocolpium index 0.20–0.25. Silicone oil — diameter 34–40 μm .

Species: *Corydalis claviculata*.

Comments

This pollen type is particularly distinct in its shape: the exine is thickened in a rather remarkable way, namely along the sides of a cube, thus causing the grain to be cubic. The six ectocolpi lie diagonally on the sides of the cube, in such a way that they form a tetrahedron within the cube. Grains with this shape do not occur in the other *Corydalis* pollen types, most of which are spherical or convex tetrahedrons (compare Plate II, 2 and III, 1; Plate IV, 2).

The *C. claviculata* pollen type also differs from the *C. lutea* type in the thickened apocolpium (compare Plate II, 1 and V, 1), the apocolpium index (compare Plate II, 2 and III, 1), the thin nexine with prominent endocracks (compare Plate II, 3 and IV, 1), and the clear perforations in the exine (Plate II, 4). From the *C. solida* type it differs in the psilate ornamentation (compare Plate II, 2 and IV, 2), the thickening of the exine (compare Plate II, 1 and V, 2), the apocolpium index (compare Plate II, 2 and IV, 2), and the different nexine structures (compare Plate II, 3 and IV, 4).

Corydalis lutea type (Plate III, Plate IV, 1, Plate V, 1)

Pollen class: 6- or 12-Pantocolpate in about equal amounts and sometimes (about 5%) 3- or 4-zonocolpate or 8- or 9-pantocolpate.

Apertures: Ectoaperture — colpus, long, of medium width, hardly sunken, margins diffuse; margo absent but a faint thickening of the exine parallel to the colpus margin is sometimes visible, particularly in cross-section; costae absent; colpus ends mostly meeting: syncolpate, sometimes with apocolpium and obtuse or indistinct colpus ends; colpus membrane with faint small granules in LM, more distinct in SEM; arrangement of the ectocolpi regular, forming the ribs of an imaginary tetrahedron if 6-pantocolpate, and an imaginary cube if 12-pantocolpate. Endoaperture — absent.

Exine: Nexine with endosculptures, clearly visible in cross-section. These structures continue under the colpus membrane, making it appear granular. Sexine slightly undulating, about twice as thick as nexine, sometimes a little thickened along the colpus margins. No apparant differentiation within the sexine; sometimes a few perforations visible in cross-section.

Ornamentation: Psilate with few perforations, perforations sometimes rather clear, but often hardly visible in L-O analysis. Inner surface of the nexine with endosculptures, clearly visible in L-O analysis as scabrae beneath the exine.

Outlines: Both 6-colpate and 12-colpate grains are spheroidal with more or less circular outlines.

Measurements: Glycerine jelly — diameter 40–47 μm in both 6- and 12-colpate grains; exine ca. 2 μm thick; apocolpium index in not syncolpate grains 0.00–0.10. Silicone oil — diameter 37–43 μm .

Species: *Corydalis lutea*, *C. ochroleuca*.

Comments

This pollen type is characterized by the psilate ornamentation, the 6 or 12 syncolpate ectocolpi and their arrangement, and the prominent nexine structures. It differs from the *Corydalis claviculata* type in the spheroidal shape (compare Plate III, 1 and II, 2) and the syncolpate ectocolpi or low apocolpium index. In addition, the *C. lutea* type differs from the *C. solida* type in the psilate ornamentation (compare Plate III, 1 and IV, 2), and the structure of the nexine (compare Plate IV, 1 and IV, 4).

Corydalis solida type (Plate IV, 2–4; V, 2)

Pollen class: Mostly 6-pantocolpate, but about 5% are 3-, or 4-zonocolpate, or 8-, 9-, or 12-pantocolpate.

Apertures: Ectoaperture — colpus, long, of medium width, hardly sunken, more or less parallel sided, margins clear but irregular; margo absent; costae absent; ends obtuse; colpus membrane with coarse irregular granules; the six ectoapertures arranged as though along the sides of a tetrahedron. Endoaperture — absent.

Exine: Nexine with firm endosculptures separated by more or less distinct endocracks which are clearly visible in cross-section. Sexine undulating, about three times as thick as nexine, of equal thickness throughout. Sexine 1 (columellae) not or hardly visible. Sexine 2 a tectate layer with perforations which are sometimes clearly visible in cross-section. Sexine 3 of low verrucae, thinner than sexine 2.

Ornamentation: Verrucate, the verrucae large, well-defined, irregular to more or less circular in outline; zones between verrucae perforate (LM) and punctate (SEM). Inner surface of nexine with large endosculptures visible in L-O analysis as large verrucae beneath the nexine, mostly more or less congruent with the verrucae on the tectum but sometimes smaller.

Outlines: The overall shape of the 6-pantocolpate grains is a more or less convex tetrahedron or a sphere and therefore the outlines are quadrangular into obtusely convex sides, or circular (with view on a colpus), or obtusely convex triangular or circular (with view on a mesocolpium). The verrucae in cross-section give an undulating margin to the sexine.

Measurements: Glycerine jelly — diameter 30–45 μm ; exine ca. 2 μm thick; apocolpium index ca. 0.15. Silicone oil — diameter 30–40 μm .

Species: Corydalis bulbosa (syn. *C. cava*), *C. intermedia* (syn. *C. fabacea*), *C. pumila*, *C. solida* (syn. *C. halleri*).

Comments

Pollen of the *Corydalis solida* type is characterized by the coarsely verrucate ornamentation, the regular 6-pantocolpate arrangement of the ectocolpi, and the distinct nexine structures.

This type differs from the *C. lutea* type in its verrucate ornamentation (compare Plate IV, 3 and IV, 1) and apocolpium index. It differs from the *C. claviculata* type in its verrucate ornamentation (compare Plate IV, 2 and II, 2), apocolpium index and constant exine thickness (compare Plate V, 2 and II, 1).

Apart from 6-pantocolpate pollen grains, anthers of most specimens of *Corydalis* species also contain pollen with a different number of ectocolpi (Layka, 1976). Within the *C. solida* type 3-zonocolpate pollen grains regularly occur, mostly at a very low percentage but in some flowers up to about 40%. The statement of Tarnavski and Mitroiu (1960) however that all the pollen grains of *C. intermedia*, *C. pumila* and *C. solida* have three colpi, was not confirmed by the present results.

The *C. solida* type includes all NW European representatives of the *Corydalis* Section *Bulbocarpus* (Bernhardi) Koch. There are no striking differences in pollen morphology between the species of this Section. Pollen of *C. bulbosa* may be somewhat larger (36–44 μm) than that of the other species (30–35 μm), but differences in ornamentation and exine measurements, such as those indicated by Layka (1976) were not found in the present material.

Eschscholzia californica type (Plate VI, VII, 1–3)

Pollen class: Usually 5-zonocolpate (about 80%), sometimes 6-zonocolpate (about 15%), rarely (about 5%) 3-, 4-, or 7-zonocolpate.

P/E ratio: Adequate, subtransverse or suberect.

Apertures: Ectoaperture — colpus, moderately long, very narrow, slit-like, not or slightly sunken; margins distinct, irregular; margo absent; costae absent; ends rather diffuse, sometimes (about 10%) syncolpate; colpus membrane invisible. Endoaperture — absent.

Exine: Nexine with indistinct endosculptures visible especially in cross-section. Sexine about as thick as nexine. Sexine 1 of distinct columellae. Sexine 2 a semitectate layer, about as thick as sexine 1, but somewhat variable in thickness. Sexine 3 of short scabrae, not or hardly visible in cross-section.

Ornamentation: Reticulate. Muri simplicolumellate, beset with low scabrae. Scabrae mostly on top of the columellae, sited at the angles of the muri, sometimes one or two scabrae within the lumina (Plate VI). Lumina irregular, angular, of constant size throughout. Tectal floor of the lumina finely punctate, clearly visible in SEM (Plate VI, 3), not or hardly visible in L-O analysis (Plate VII, 2–3). Columellae arranged in an angular pattern under the muri, sometimes one or two under the lumina. Nexine structures not visible in L-O.

Outlines: Equatorial view — circular or elliptic or convex rectangular with obtuse angles. Polar view — mainly five-lobed, the colpi separated by convex mesocolpia.

Measurements: Glycerine jelly — P 29–33 μm , E 29–32 μm , P/E ratio 0.90–(1.00)–1.10; Apocolpium index 0.38–(0.42)–0.45; exine ca. 2 μm thick; lumina 1–3 μm in diameter. Silicone oil — P 28–34 μm , E 28–34 μm , P/E ratio 0.90–(1.00)–1.10.

Species: *Eschscholzia californica*.

Comments

The *Eschscholzia californica* type is distinguished from others in NW European Papaveraceae by the five zonocolpate ectocolpi and the reticulate ornamentation, in which the floor of the lumina is perforate. According to Layka (1976), stephanocolpate pollen is characteristic for the whole tribe Eschscholieae. Layka, who studied 11% of the species of *Eschscholzia*, stated that the ornamentation found in the pollen of *E. californica* is characteristic of the whole genus. He describes this ornamentation as a suprareticulum above a tectum perforatum, but in my opinion the reticulate pattern is formed by the connected capita of the columellae, which thus form solid muri, and the scabrae are superimposed on the angles of the muri. The perforated tectum exists only between the muri of the reticulum.

Fumaria officinalis type (Plate VII, 4; VIII; IX; X; XI; XII; XIII)

Pollen class: 5-(6–12)-14-Pantoporate (see Table I).

Apertures: Ectoaperture — porus, rarely colpus, more or less circular in outline, rarely elliptic, variable in diameter, not sunken; margin clear, irregular, with broad, uninterrupted, thick annulus; porus membrane nudate, strongly protruding from the ectoaperture. Endoaperture — absent, but nexine interrupted by endocracks beneath ectoapertures.

Exine: Thick. Nexine thin with endosculptures under the mesopodium, faintly visible in cross-section, but under the annulus smooth with distinct endocracks continuing into the protruding part. Sexine faintly or strongly undulating, much thicker than nexine. Columellae not visible in LM. Sexine a thick tectate layer sometimes with distinct verrucae.

Ornamentation: Verrucate, the verrucae large, mostly well-defined, sometimes hardly visible or rather diffuse, irregular in outline, sometimes with distinct channels between them; area between the verrucae usually with small puncta (SEM). Columellae not visible in L-O analysis. Inner surface of nexine with more or less distinct endosculptures, appearing as a pattern of fine dots beneath the exine in L-O analysis. Distinct endocracks below the annuli.

Outlines: More or less circular with protruding pori, verrucae in cross-section giving an undulating or crenate margin to the sexine. The 6-pantoporate grains are sometimes more or less convex-cubic with the pori regularly distributed on the sides of the cube (Plate X, 3). In other cases the distribution of the pori is mostly rather irregular.

Measurements: Glycerine jelly — diameter 25-45 μm ; exine 2.5—4.5 μm thick; pore diameter 6—14 μm ; annulus up to 3.5 μm broad, up to 4.5 μm thick.

Silicone oil — diameter 30—55 μm , other dimensions like in glycerine jelly.

Species: *Fumaria bastardii*, *F. capreolata*, *F. caroliana*, *F. densiflora* (syn. *F. micrantha*), *F. martinii*, *F. muralis* ssp. *muralis*, *F. muralis* ssp. *boraei*, *F. muralis* ssp. *neglecta*, *F. occidentalis*, *F. officinalis* ssp. *officinalis*, *F. officinalis* ssp. *wirtgenii*, *F. parviflora* (syn. *F. caespitosa*), *F. purpurea*, *F. schrammii* (syn. *F. vaillantii* ssp. *schrammii*), *F. vaillantii*.

Key to the species groups

(With this key it is almost impossible to identify a single grain with certainty, but the more pollen grains available, the more certain the determination will be.)

- 1.a. Verrucae large, well-defined, angular, separated by distinct narrow channels (Plate VIII, 2; XI, 2); in cross-section giving a crenate margin to the sexine (Plate VII, 4; XI, 1); nexine clearly endosculptured, visible in cross-section and in L-O analysis (Plate IX, 2—3; XI, 3—4) 2
- b. Verrucae faint or ornamentation psilate; verrucae rather diffuse, not separated by distinct channels (Plate X, 1—2; XIII, 1); in cross-section giving an undulating margin to the sexine (Plate X, 3; XII, 2); nexine faintly endosculptured, hardly visible in cross-section or L-O analysis (Plate X, 2; XIII, 3) 3
- 2.a. Pores usually 6, sometimes 7, 8, or 9, diameter 30-(33)-37 μm *Fumaria muralis* group
- b. Pores usually 12, sometimes 8, 10, or 14, diameter 37-(43)-47 μm *Fumaria capreolata* group
- 3.a. Pores usually 6, sometimes 7, 8, or 9; grains frequently abnormal, by having one or two colpi instead of pori in the pantoporate grain (Plate X, 4) *Fumaria densiflora* group
- b. Pores usually 12, sometimes 9, 10, or 11 *Fumaria parviflora* group

Differential characters in the Fumaria officinalis type

Species	Diam. in μm	Number of pori in %							
		5	6	7	8	9	10	11	12
<i>Fumaria capreolata</i> group:									
<i>F. capreolata</i> ssp. <i>capreolata</i> ($2n = 56, 64$)	40—45				10	10	5		75
<i>F. occidentalis</i>	40—46				10				90
<i>F. purpurea</i>	37—47				10				90
<i>F. officinalis</i> ssp. <i>officinalis</i> p.p. ($2n = 14, 28, 32$)	40—46		5		30	5	25	10	25
<i>Fumaria densiflora</i> group:									
<i>F. caroliana</i>	30—35	not known							
<i>F. densiflora</i> ($2n = 28$)	30—34	5	55	25	10	5			
<i>F. officinalis</i> ssp. <i>officinalis</i> p.p.	29—35		75	5	15				
<i>F. officinalis</i> ssp. <i>wirtgenii</i> ($2n = 48$)	25—31		60	5	15			5	10
<i>F. schrammii</i> p.p.	29—35		20	15	15	15	5	5	25
<i>F. vaillantii</i> ($2n = 32$)	25—31	5	35	20	15	10	5		5

Species	Diam. in μm	Number of pori in %							
		5	6	7	8	9	10	11	12
<i>Fumaria muralis</i> group:									
<i>F. bastardii</i> ($2n = 48$)	35–40	45	15	15	10				10
<i>F. martinii</i>	31–35	99							
<i>F. muralis</i> ssp. <i>boraei</i>	30–38	10	80	5	5				
<i>F. muralis</i> ssp. <i>muralis</i> ($2n = 28, 32$)	31–35	25	15	20	5	5	5	20	
<i>F. muralis</i> ssp. <i>neglecta</i>	31–37	99							
<i>Fumaria parviflora</i> group:									
<i>F. parviflora</i> ($2n = 28, 32$)	28–34	5		5		10	5	75	
<i>F. schrammii</i> p.p.	29–35	20	15	15	15	5	5	25	

Comments

This pollen type is rather distinctive. It differs from other pollen types of the Papaveraceae in the area by having strongly annulate ectopori and a nudate porus membrane. Compared with the other pantoporate pollen types it is characterized by the thick, verrucate sexine, the thick annuli and the strongly protruding pore membrane.

The pollen type is rather variable in its ornamentation, number of ectopori, and dimensions. This variation can be found in the anthers of practically all specimens of any species so it is nearly impossible to find differential characters between *Fumaria* species. This confirms the results of Layka (1976), who studied the morphology of pollen in the whole genus.

Nevertheless four species groups could be established in the NW European *Fumaria* species. The species groups are differentiated by features present in at least two-thirds of their pollen grains; it is these features that are used in the key to the species groups.

The *Fumaria* type, as described by Faegri and Iversen (1975) in their key to the NW European pollen types, conforms to the present *F. densiflora* group.

The *F. capreolata* group and the *F. muralis* group include the NW European representatives of *Fumaria* Section *Grandiflorae*. The two groups correspond in their coarsely verrucate ornamentation with deep narrow channels (Layka, 1976, used the term "areolée" for this ornamentation). The groups differ in their dimensions and number of ectopori. This may well be correlated with ploidy level: *F. muralis* ($2n = 28, 32$) pollen has usually 6 pores and a diameter of about $33 \mu\text{m}$; *F. capreolata* ($2n = 56, 64$) pollen has usually 12 pores and a diameter of about $43 \mu\text{m}$. Unfortunately the chromosome numbers of the other species in these groups are not yet known, but polyploidy seems normal in *Fumaria*; Rydberg (1960) considered most *Fumaria* species to be polyploids.

Glaucium flavum type (Plate XIV, XV, XVI)

Pollen class: 3-Zonocolpate.

P/E ratio: Usually suberect but often subtransverse, adequate or semi-erect.

Apertures: Ectoaperture — colpus, long, broad, slightly sunken; margins distinct and regular; indistinct narrow margo, formed by thinning of sexine; costae absent; ends subacute or obtuse, rarely syncolpate; colpus membrane with distinct irregular angular granules, on these granules small scabrae of less than $0.5\ \mu\text{m}$ (SEM). Endoaperture — absent.

Exine: Nexine with indistinct endosculptures visible in cross-section, clearly visible in SEM (Plate XV, 1). Sexine as thick as nexine. Sexine 1 thicker than sexine 2, of distinct, slender columellae. Sexine 2 a semi-tectate layer varying in thickness. Sexine 3 of short scabrae, hardly visible in cross-section.

Ornamentation: In mesocolpium reticulate, in apocolpium a tectum perforatum. Muri simplicolumellate or duplicolumellate. Lumina irregular, angular, clearly decreasing in size towards the apocolpium. Muri beset with scabrae, in SEM clearly visible as short, broadly based micro-echinae (Plate XV, 1). In SEM the reticulum of the mesocolpium appears to be a tectum perforatum. Columellae of the mesocolpium arranged in more or less angular patterns under the muri, arrangement in the apocolpium irregular. Columellae regularly rounded or irregularly angular in outline. Nexine structures slightly visible in polar view as indistinct endocracks; in equatorial view no nexine structures distinguishable.

Outline: Equatorial view — elliptic or circular. Polar view — circular with intruding colpi, rarely obtuse triangular with colpi in the middle of the sides.

Measurements: The dimensions of the pollen in this type are rather variable. Three sizes may be distinguished in the pollen of each specimen of both investigated species (measurements in μm):

Glycerine jelly

<i>G. corniculatum</i> :	P 23–25,	E 20–24,	P/E 0.90-(1.08)-1.18,	exine ca. 2.5
	P 30–35,	E 25–35,	P/E 0.90-(1.11)-1.60,	exine ca. 2.0
	P 40–46,	E 33–40,	P/E 1.00-(1.23)-1.50,	exine ca. 2.0
<i>G. flavum</i> :	P 20–24,	E 17–23,	P/E 0.86-(1.08)-1.27,	exine ca. 2.5
	P 27–29,	E 23–30,	P/E 0.86-(1.08)-1.25,	exine ca. 2.5
	P 35–43,	E 30–35,	P/E 1.00-(1.16)-1.29,	exine ca. 2.5

Silicone oil

<i>G. corniculatum</i> :	P 23–26,	E 19–23,	P/E 1.00–1.30
	P 32–37,	E 24–28,	P/E 1.10–1.35
	P 42–46,	E 30–35,	P/E 1.20–1.45
<i>G. flavum</i> :	P 20–24,	E 20–24,	P/E 1.05–1.30
	P 29–33,	E 28–31,	P/E 1.00–1.25
	P 35–40,	E 32–35,	P/E 1.10–1.30

Species: *Glaucium corniculatum*, *G. flavum*.

Key to the species

- 1.a. Columellae visible, small, regularly rounded in outline, arranged in rows under the muri of the reticulum (Plate XIV, 6); muri mainly duplicolumellate (Plate XIV, 6); lumina $1\text{--}3\ \mu\text{m}$ in diameter (Plate XIV, 5); apocolpium index below 0.25 (Plate XIV, 1) . . *Glaucium corniculatum*

- b. Columellae clearly visible, irregular, angular in outline; capita more or less connected forming the muri of the reticulum (Plate XV, 7). Muri mainly simplicolumellate (Plate XV, 7). Lumina ca. $1\ \mu\text{m}$ in diameter (Plate XV, 6). Apocolpium index above 0.28 . . . *Glaucium flavum*

Comments

The *Glaucium flavum* type is rather heterogenous. Within it six kinds of pollen can be distinguished which differ in various features such as shape and dimensions. Nevertheless, the whole pollen type is characterized by some clear morphological features: the distinct, coarse, angular granules on the colpus membrane (Plate XIV, 2), and the differences in ornamentation between the (reticulate) mesocolpium and the (tectate perforate) apocolpium (Plate XIV, 1).

From the other 3-zonocolpate Papaveraceae, this pollen type is distinguished by its reticulate ornamentation. It most resembles the *Chelidonium majus* type (especially *Glaucium corniculatum*). Pollen of *G. corniculatum* differs from that of *Chelidonium majus* in its reticulum (compare Plate XIV, 5–6 and I, 6–7), duplicolumellate muri (compare Plate XIV, 6 and I, 7), and the indistinct margo. Thus pollen morphology supports the suggestion of Ernst (1962) that *Glaucium* should be placed near *Chelidonium*. Ernst based his conclusions on gross-morphology.

Layka (1976) studying the pollen morphology of the whole genus *Glaucium* found that the pollen of most species was polymorphic. Explaining this phenomenon he pointed to a relationship with floral polymorphism: a variation in the length of the anthers. The two species with long and short anthers have two different pollen types. Species with short, long and intermediate anthers have three different kinds of pollen (found in 7 species including *G. flavum* and *G. corniculatum*). Species with anthers all of the same length have only one kind of pollen (found in 14 species). This polymorphism manifests itself in the dimensions of the pollen and its exine. Short anthers give small pollen, longer anthers give larger grains.

This trimorphism is a striking phenomenon which has been established in all specimens of both species. It manifests itself in the length of P and E and in the P/E ratio (see table of measurements). Differences in the exine as indicated by Layka (1976) such as width of the reticulum and differences in nexine structures, have not been found in the present material.

The statement of Tarnavschi and Mitroiu (1960) that pollen of *G. corniculatum* and *G. flavum* may be separated on the presence of a margo in *G. flavum* is not confirmed.

Papaver argemone type (Plate XVII)

Pollen class: 6-Pantoporate, pores sometimes 7, rarely even more.

Apertures: Ectoaperture — porus, more or less circular in outline, slightly sunken, margin irregular but clear, annulus absent; porus membrane covered with distinct irregular sexine granules forming an ill-defined operculum.

Endoaperture — porus, congruent with the ectoaperture, formed by a thin area of nexine; costae absent. Apertures regularly arranged on the faces of a cube.

Exine: Nexine distinct, smooth in LM, but in SEM with faint endosculptures (Plate XVII, 3), endocracks present below the ectoapertures. Sexine a little thicker than nexine. Sexine 1 of distinct slender columellae, decreasing in length towards the porus; sexine 2 a tectate layer, thinner than sexine 1, with small punctae (SEM); sexine 3 of short scabrae, not usually visible in cross-section.

Ornamentation: Scabrate. Scabrae visible in L-O analysis, crowded, regularly distributed on the tectum and on the granules of the operculum. Columellae clear in L-O analysis, arranged in curved rows, but sometimes without arrangement. Endocracks clear below the ectopori, endosculptures hardly or not visible in L-O analysis.

Outlines: Quadrangular in each view, the sides convex, the angles obtuse.

Measurements: Glycerine jelly — longest diameter 30-(33)-36 μm ; exine ca. 2.0 μm thick; pore diameter 7–9 μm . Silicone oil — longest diameter 30–36 μm .

Species: *Papaver argemone*.

Comments

In NW Europe the pollen of *Papaver argemone* is quite different from that of the other *Papaver* species. The most striking characteristics are: (1) it is the only *Papaver* species with porate pollen; (2) it is the only Papaveraceae pollen type with endo-apertures; (3) the granules on the porus membrane are rather prominent, and form an operculum-like structure in the sense of Clarke and Jones (1977).

The pollen grains in the six specimens of *P. argemone* that we have seen from NW Europe normally have six pores. However, Tarnavski and Mitroiu (1960) and Layka (1976) found, in material from Roumania and Syria, pollen with 6–12 pori and/or colpi. Apparently plants from the eastern part of the range of *P. argemone* show a greater variability in the number and shape of ectoapertures.

Layka (1976) mentions another *Papaver* species with porate ectoapertures, *Papaver virchowii*. This is a Greek species which is closely related to *P. argemone* but not mentioned in Flora Europaea. Layka's description of *P. virchowii* places it in the present *P. argemone* type. According to Layka the pollen morphology of both *P. argemone* and *P. virchowii* is very close to that of the genus *Roemeria* Medicus. The pollen of *P. virchowii* is particularly similar to that of *Roemeria refracta* and Layka (1976) cites this as evidence to support the suggestion that the genera *Papaver* and *Roemeria* are closely related.

Papaver radicum type (Plate XVIII, XIX)

Two different pollen types occur together in the anthers of *Papaver radicum* Rottboel: type A and type B.

Papaver radicum type, type A (Plate XVIII, 1–4)

Pollen class: 4-Zonocolpate and 6-pantocolpate, usually in about equal proportions. Rarely 3-zonocolpate.

P/E ratio: Zonocolpate pollen erect.

Apertures: Ectoaperture — colpus, long, broad, slightly sunken, margins indistinct, diffuse; margo absent; costae absent; ends obtuse, some of the ends are often connected, especially in 4-zonocolpate grains; colpus membrane with distinct, irregular granules. Endoaperture — absent.

Exine: Nexine thin, endosculptures not or hardly visible in cross-section. Sexine thicker than nexine or of about equal thickness, usually thickened in the apocolpium. Sexine 1 of distinct, slender columellae. Sexine 2 a tectate layer, thinner than sexine 1, a little undulating. Sexine 3 of short scabrae, not or hardly visible in cross-section.

Ornamentation: Scabrate. Scabrae crowded, regularly distributed on the tectum, sometimes on top of indistinct verrucae, which are hardly visible in L-O analysis. Columellae visible in L-O analysis, arranged in curved rows, sometimes forming an intrareticulum, or sometimes random. Columellae irregular in outline or more or less circular.

Outlines: 4-Zonocolpate pollen: equatorial view — convex obtuse rectangular or elliptic; polar view — 4-lobed, colpi separated by convex mesocolpia.

6-Pantocolpate pollen: convex obtuse triangular. Syncolpate pollen: more or less circular.

Measurements: Glycerine jelly — 4-zonocolpate pollen: P 40–48 μm , E 30–36 μm , P/E 1.2–1.5; exine ca. 2.5 μm thick; apocolpium index ca. 0.3. 6-Pantocolpate pollen: longest diameter 37–44 μm . Silicone oil — 4-Zonocolpate pollen: P 40–48 μm , E 30–36 μm . 6-Pantocolpate pollen: longest diameter: 35–45 μm .

Species: *Papaver radicum* s.str.

Comments

This pollen type resembles the pollen of most other *Papaver* species (see *P. rhoeas* type), but it differs in the number and distribution of ectocolpi and in the dimensions.

Pollen of most *Papaver* species have a variable number of ectocolpi, mostly both 3 and 6; 4-zonocolpate pollen grains are rare, species with both 4 and 6 colpi are not mentioned in Layka's (1976) monograph. Also the only specimen of *P. radicum* he studied, had mainly 3-zonocolpate grains (69%), 26% 6-pantocolpate grains, and only 5% 4-zonocolpate grains. Judging from his illustrations, they belong to the present type A. The pollen of *P. radicum* from Russia studied by Kuprianova and Alyoshina (1978) is mainly 4-zonocolpate and confirms the present type A. They mention the same pollen type for the closely related species *P. laponicum*.

Papaver radicum type, type B (Plate XVIII, 5; XIX)

Pollen class: Usually 6-pantocolpate, often with some colpus ends connected. Sometimes 4-zonocolpate, or 12-pantocolpate, rarely 3-zonocolpate.

P/E ratio: Zonocolpate pollen erect.

Apertures: Ectoaperture — colpus, long, broad or very broad, hardly sunken, margins indistinct, diffuse; margo absent; costae absent; ends indistinct, often connected; colpus membrane with coarse, irregular granules provided with small scabrae (SEM). Endoaperture — absent.

Exine: Nexine thin, endosculptures not or hardly visible in cross-section. Sexine thicker than nexine. Sexine 1 of indistinct, short columellae. Sexine 2 a tectate layer, distinctly undulating. Sexine 3 of coarse verrucae, thicker than rest of sexine. Sexine 4 of hardly visible scabrae.

Ornamentation: Verrucate. Coarse, irregularly shaped verrucae, beset with faint scabrae (clear in SEM, Plate XIX, 3). Columellae hardly visible in L-O analysis, arrangement random.

Outlines: Irregular. 6-Pantocolpate pollen: more or less circular or obtusely triangular with convex sides. 4-Zonocolpate pollen: as type A. 12-Pantocolpate pollen: more or less circular or obtusely quadrangular with convex sides.

Measurements: Glycerine jelly — 6-pantocolpate pollen: longest diameter 29-(32)-35 μm , 12-pantocolpate pollen: longest diameter 34-(37)-40 μm .

Silicone oil — 6-pantocolpate pollen: longest diameter 28—36 μm ; 12-pantocolpate pollen: longest diameter 33—40 μm .

Species: *Papaver radicum* s.str.

Comments

This pollen type is very different from type A, especially in the ornamentation of the exine which has coarse verrucae beset with faint scabrae (compare Plate XVIII, 2—4 and XIX, 1—2) but also in the short columellae. The number of ectocolpi also differs. Within the genus *Papaver* no other pollen type corresponds with this one. It most resembles the pollen of *Corydalis*, especially those of the *Corydalis solida* type, from which it differs in the broad ectocolpi with diffuse colpus margin, the faint scabrae on the verrucae, and the irregular shape (compare Plate XIX and IV, 2—4).

Comments on Papaver radicum type as a whole

The two different pollen types occur together in all the specimens of *Papaver radicum* s.str. investigated. These pollen types show moreover a great variability, especially in the number of ectocolpi. This variability was to be expected because *Papaver radicum* is an extremely variable plant in other ways. In Norway alone, fourteen subspecies have been described (Morvat and Walters, 1964), and the species is distributed throughout the European Arctic and Greenland. In the present study it was impossible to study the whole *P. radicum* complex in detail, but a further investigation of the complex would be worthwhile.

Five specimens have been studied here: three from Iceland, one from Greenland, and one from Spitsbergen. Both pollen types were found in the flowers of each specimen. In those from Iceland and Greenland type A predominated while in the one from Spitsbergen type B was more common.

Within type A, the Greenland and Spitsbergen plants contained mainly 3- and 4-zonocolpate pollen but the Icelandic plants mainly had 4-zono- and 6-pantocolpate pollen. No 3-zonocolpate grains were found in the plants from Iceland.

Within type B, the Greenlandic and Icelandic plants contained mainly 6-pantocolpate pollen while the Spitsbergen plants had mainly 6- or 12-pantocolpate grains which were frequently syncolpate.

Also Kuprianova and Alyoshina (1978) mention two types in the pollen of *Papaver radicum* from Russia. Judging their illustrations, they belong to the present type A and B. The 4-zonocolpate grains of type A seem predominant.

Papaver rhoeas type (Plate XX—XXV)

Pollen class: 3-Zonocolpate, rarely 2-, 4-zonocolpate or 6-pantocolpate.

P/E ratio: Undamaged grains adequate or suberect, sometimes semi-erect.

Grains with ruptured colpus membrane usually semi-erect or erect.

Apertures: Ectoaperture — colpus, long, of medium width or narrow, not or slightly sunken; margins indistinct or diffuse with irregular granules; margo absent; costae absent; ends diffuse, frequently some colpus ends connected; colpus membrane with distinct irregular granules, easily ruptured. Endoaperture — absent.

Exine: Exine frequently raised above the equatorial area, thus showing a geniculate colpus margin in equatorial view (Plate XXV, 4). Nexine thin with faint endosculptures, or distinct endocracks. Sexine as thick as nexine in mesocolpium. Sexine 1 of usually distinct columellae, usually thickened in the apocolpium. Sexine 2 a tectate layer, thinner than sexine 1, sometimes undulating, sometimes provided with small punctae (SEM, Plate XX, 2 and XXI, 1). Sexine 3 of short scabrae, usually not or hardly visible in cross-section.

Ornamentation: Scabrate. Scabrae densely and regularly distributed, distinct in L-O analysis. Columellae either faint or invisible, but sometimes distinct in L-O analysis. Arranged in curved rows, forming an infra-reticulum.

Outlines: Equatorial view — elliptic or sometimes bisymmetric, with one side slightly obtusely angular and the other side convex. Polar view — circular with the colpi not or hardly intruding, or obtusely triangular with convex sides and apertures situated in the angles (especially in grains with broken colpus membrane).

Measurements: Glycerine jelly — P 20–35 μm , E 20–32 μm , P/E 0.95–1.30 in grains with undamaged colpus membrane, otherwise P/E 1.20–1.40; exine ca. 1.2 μm thick in mesocolpium, 2–2.5 μm in apocolpium; apocolpium index ca. 0.2, rarely 0.3. Silicone oil — P 18–35 μm , E 18–30 μm ; other dimensions like in glycerine jelly.

Species: Meconopsis cambrica, Papaver dubium, P. hybridum, P. oriëntale, P. rhoeas including *P. strigosum, P. somniferum*.

Key to the species

- 1.a. Ectocolpus narrow or slit-like, colpus membrane often ruptured (Plate XXI, 2); exine not thickened in the apocolpium (Plate XXII, 1) *Papaver dubium*
- b. Ectocolpus of medium width, colpus membrane clear, rarely ruptured (Plate XXV); exine sometimes thickened in the apocolpium 2
- 2.a. Exine thickness the same throughout (Plate XXII, 2); apocolpium index ca. 0.3 (Plate XXII, 5–6) *Papaver hybridum*
- b. Exine thickened in the apocolpium; apocolpium index relatively small, ca. 0.2 3
- 3.a. Nexine with endocracks visible throughout the grain in L-O analysis; scabrae not or hardly visible in L-O analysis, if visible then densely crowded (Plate XV, 4) *Papaver oriëntale*
- b. Nexine with endosculptures or with faint endocracks under the apocolpium; scabrae clearly visible in L-O analysis, regularly distributed (Plate XV, 1–3) 4
- 4.a. Columellae only distinct at the apocolpium, not or hardly so in the mesocolpium (Plate XXXIII, 3–7); nexine without endocracks; P/E ratio usually suberect; P 20–27 μm *Papaver rhoeas* incl. *P. strigosum*
- b. Columellae faintly visible throughout the grain; nexine with both endosculptures and endocracks; endocracks only visible under the apocolpium (Plate XIV, 6); P/E ratio usually adequate; P 27–35 μm 5
- 5.a. Ornamentation scabrate; scabrae visible in L-O analysis, but not in cross-section (Plate XXIV, 1–5) *Papaver somniferum*
- b. Ornamentation scabrate but with faint perforations between the scabrae, thus forming an indistinct tectum perforatum in L-O analysis (Plate XX, 3–6); scabrae distinct, also visible in cross-section. *Meconopsis cambrica*

Comments

The distinctive features of the *Papaver rhoeas* type are the three ectocolpi, the scabrate ornamentation, the infra-reticulum caused by the columellae, and the structured nexine. The type comprises most species of *Papaver*.

This pollen type differs from the *P. radicum* type in the number of ectocolpi and the dimensions; and from the *P. argemone* type in having ectocolpi instead of ectopori.

The *P. rhoeas* type differs from the other 3-zonocolpate, scabrate pollen types in its infra-reticulum (Faegri and Iversen, 1975).

Within this pollen type the nexine needs special attention. Both kinds of nexine structures mentioned in the Introduction are present. In *Papaver dubium, P. hybridum, P. rhoeas, P. strigosum* the nexine has endosculptures and in *Meconopsis cambrica, Papaver oriëntale, P. somniferum* the nexine has endocracks especially under the apocolpium. These features are important for the separation of the species within the *P. rhoeas* type. Moreover, these

features distinguish the various sections of the genus *Papaver*. Layka (1976) mentions that all pollen from species in Section *Pilosa* have an "endexine en gros plaques" or endocracks. Judging from the present results as compared with the illustrations of Layka (1976), species from Section *Orthorhoeades* have pollen with endosculptures or "endexine en petits plaques".

In some species within the *P.rhoeas* type the ornamentation needs special attention. SEM-micrographs of *Meconopsis cambrica* (Plate XX, 2), *Papaver dubium* (Plate XXI, 1) and *P.heldreichii* (Layka, 1976) show that the tectum between the scabrae is punctate. This feature is most striking in *M.cambrica*, less distinct in *P.heldreichii*, and least distinct, although certainly present, in *P.dubium*. This feature points to a close relationship between *Meconopsis* and *Papaver* as has been indicated by Henderson (1965) and Layka (1976).

Layka (1976) studied the pollen of half the species of the genus *Papaver*. He distinguished two pollen types: one colpate and the other porate. The colpate pollen type corresponds with the present *P.rhoeas* type about which some remarks can be made:

(1) The number of ectocolpi is usually three, rarely two, four, or six. In my opinion, the variation in the number of ectocolpi is characteristic for most species in *Papaver*, rather than for a number of species in particular Sections.

(2) *Papaver radicum* belongs to a separate pollen type.

(3) Layka mentioned a perforated tectum in *P.dubium*, *P.hybridum* and *P.somniferum*. The SEM shows no perforations in the tectum of *P.hybridum* and *P.somniferum*, and the punctae in the tectum of *P.dubium*, which are mentioned above, are not visible in LM.

(4) According to Layka *Meconopsis cambrica* is practically indistinguishable from certain *Papaver* species. The present investigations corroborate this; *M.cambrica* is here combined with *Papaver* species in the *P.rhoeas* type.

ACKNOWLEDGEMENTS

I wish to express my gratitude to Dr. W. Punt who gave me the opportunity to study the pollen morphology, and for his valuable criticism during this study. I would also like to thank Dr. G.C.S. Clarke for his comments on the manuscript and for correcting the English text. I am thankful to Marcel Grol for the use of his preliminary investigations on this subject. I am grateful to Mr. H. Elsendoorn for printing all photomicrographs.

PLATE DESCRIPTIONS

(all plates \times 2000 except as otherwise stated; all SEM micrographs are made by Dr. W. Punt)

PLATE I (p. 231)

Chelidonium majus L. (fig.1, s.c. s.n.; figs. 2–5, Uittien 480; figs. 6, 7, Hessel, Klein and Rubers 1175)

1. Scanning electron micrograph; polar view.
2. Polar view; cross-section; nexine with endosculptures.
3. Polar view; ornamentation at high focus, scabrae and perforated tectum.
4. Polar view; ornamentation at medium focus.
5. Polar view; ornamentation at low focus, columellae.
6. Equatorial view; ornamentation at high focus, microreticulum.
7. Equatorial view; ornamentation at low focus, columellae arranged in an infra-reticulum.

PLATE II (p. 232)

Corydalis claviculata (L.) De Candolle (figs.1, 3, 4, De Smidt B 113; fig. 2, Menega s.n.)

1. Optical cross-section; thin nexine, inner sexine layer with endocracks near ectocolpi, outer sexine layer thickened in the apocolpiä.
2. Scanning electron micrograph; overall view, psilate tectum, cubic shape.
3. Ornamentation near ectocolpus at low focus; elliptic area beneath ectocolpus with endocracks, mesocolpia with perforations, position of ectocolpus diagonally on the side of the cube.
4. Ornamentation of the apocolpium at medium focus, perforations.

PLATE III (p. 233)

Corydalis ochroleuca Koch (Biol. exc. 1960-235)

1. Scanning electron micrograph; overall view 12-pantocolpate grain; psilate ornamentation.
2. Scanning electron micrograph; inner face of the nexine with endosculptures and perforations (\times 10 000).

PLATE IV (p. 234)

Corydalis lutea (L.) De Candolle (fig.1, Behrendsen s.n.)

1. Equatorial view of a 3-zonocolpate grain; ornamentation at low focus, psilate ornamentation, nexine with endosculptures.

Corydalis bulbosa (L.) De Candolle (fig.2, Kintschi s.n.)

2. Scanning electron micrograph; overall view of a 6-pantocolpate grain; verrucate ornamentation, zones between verrucae punctate.

Corydalis solida (L.) Swartz (figs. 3, 4, Smit 2009)

3. Ornamentation of the mesocolpium at high focus; verrucae and punctae.
4. Ornamentation of the mesocolpium at low focus; nexine with verrucate endosculptures, more or less congruent with verrucae on the tectum.

PLATE V (p. 235)

Corydalis ochroleuca Koch (fig.1, Biol. exc. 1960-235)

1. Optical cross-section; nexine with endosculptures.

Corydalis bulbosa (L.) De Candolle (fig.2, Kintschi s.n.)

2. Optical cross-section; nexine with endosculptures.

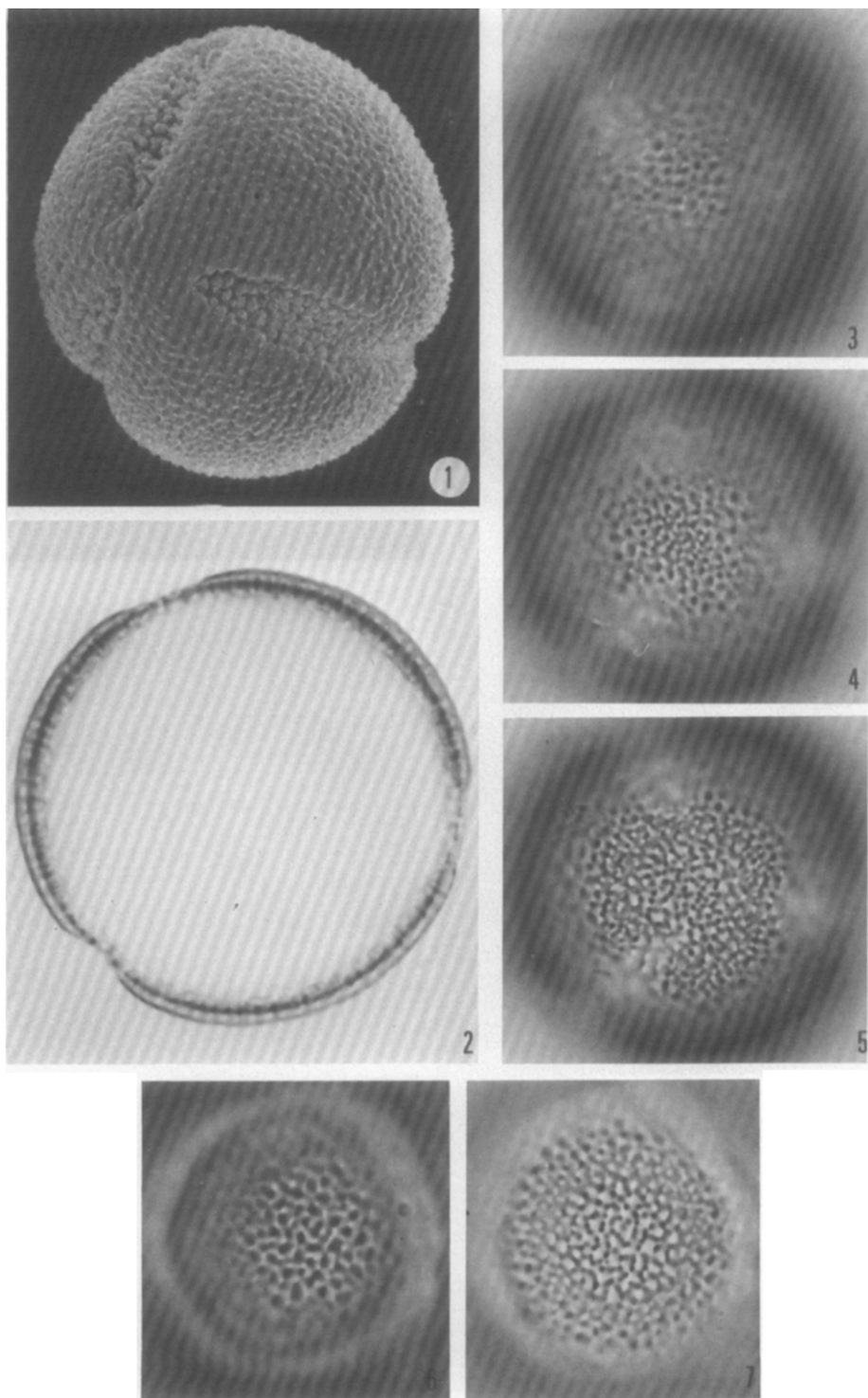
PLATE I (*Chelidonium majus* type)

PLATE II (*Corydalis claviculata* type)

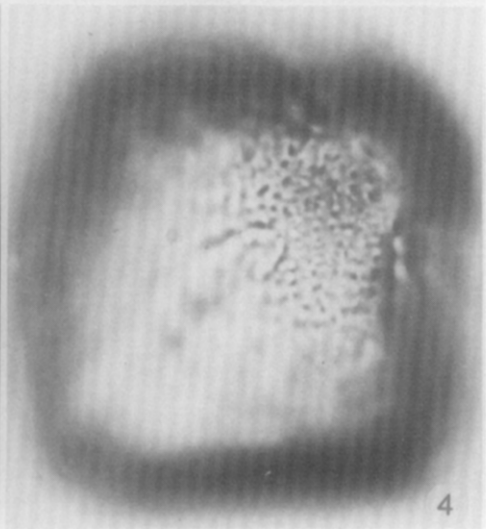
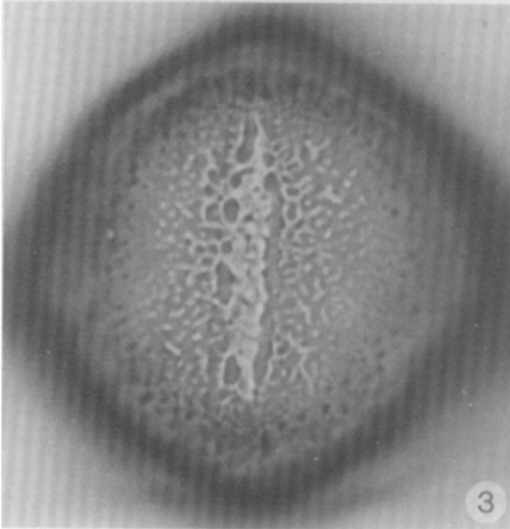
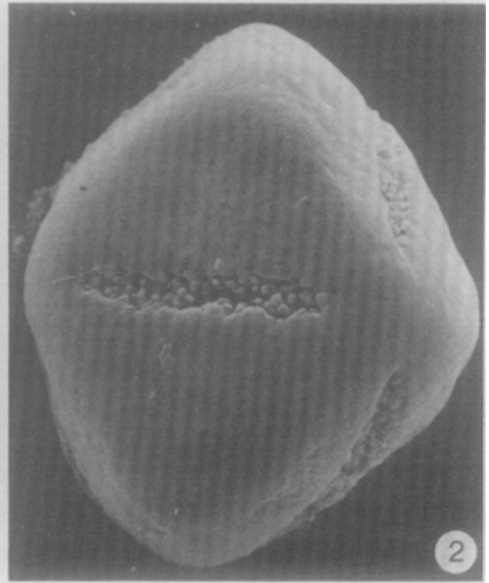
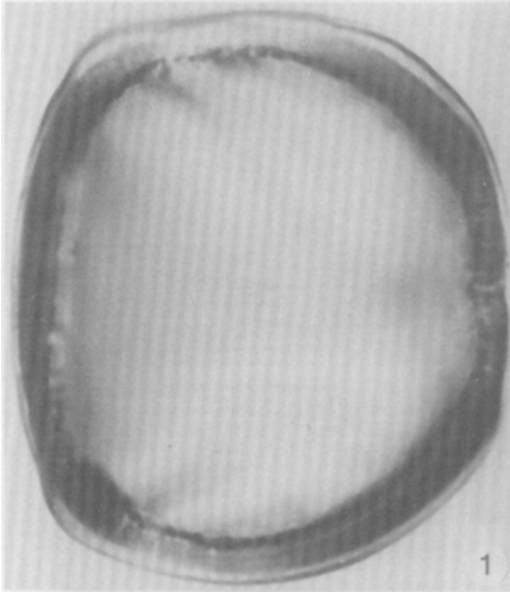


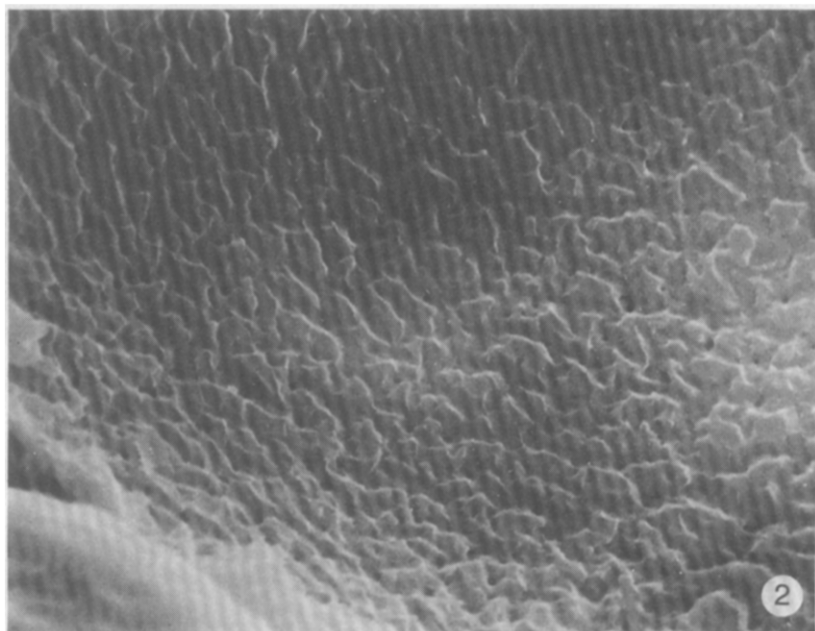
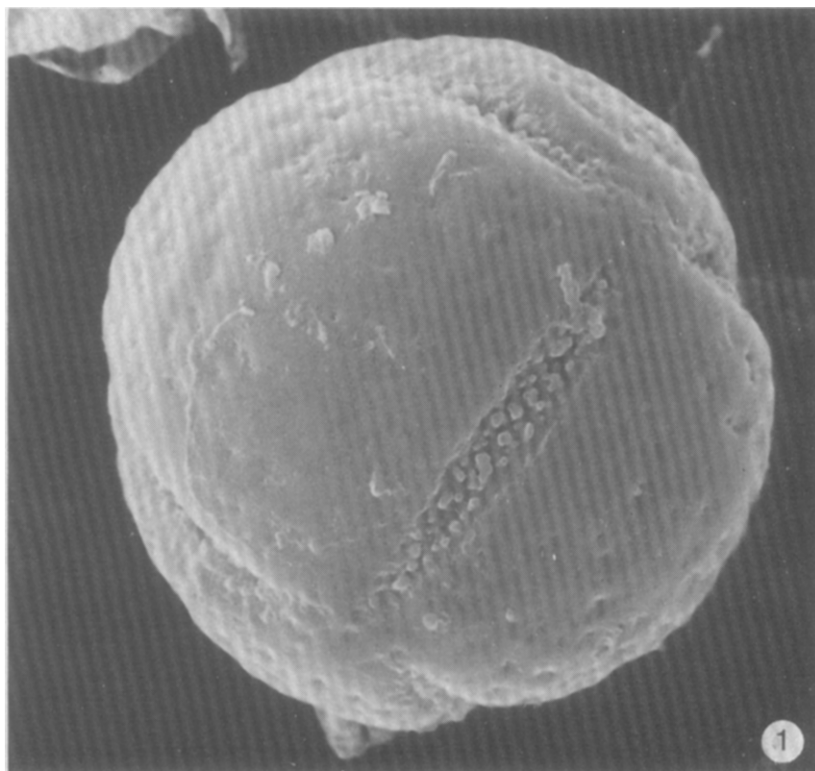
PLATE III (*Corydalis lutea* type)

PLATE IV (*Corydalis lutea* type, 1; *Corydalis solida* type, 2-4)

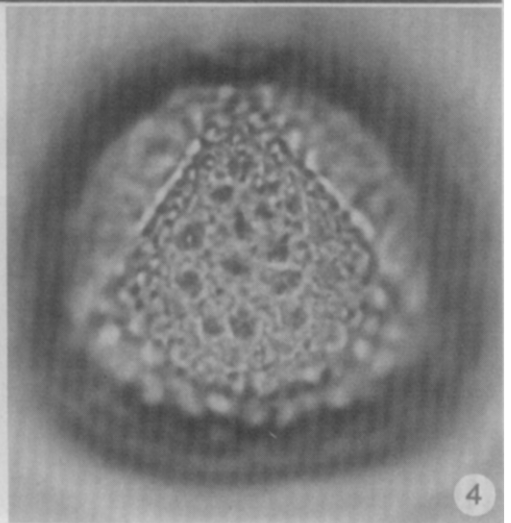
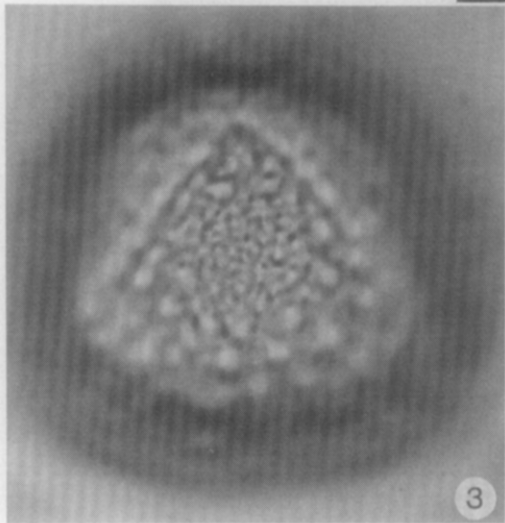
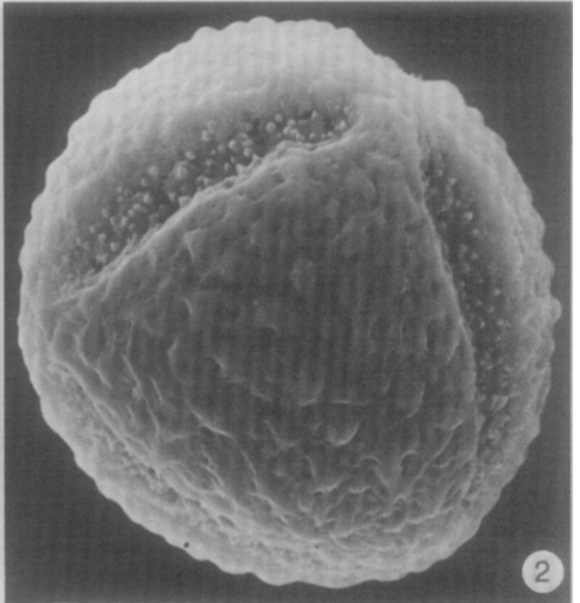
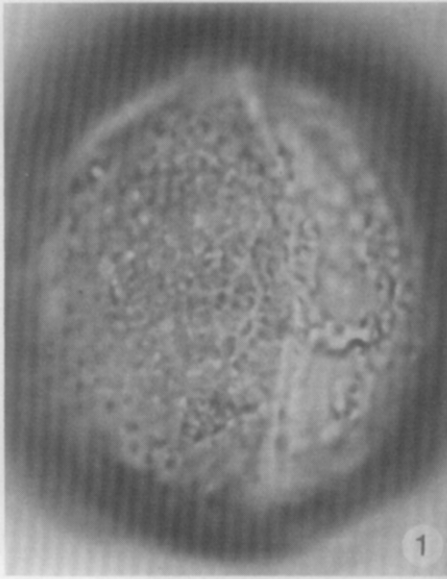


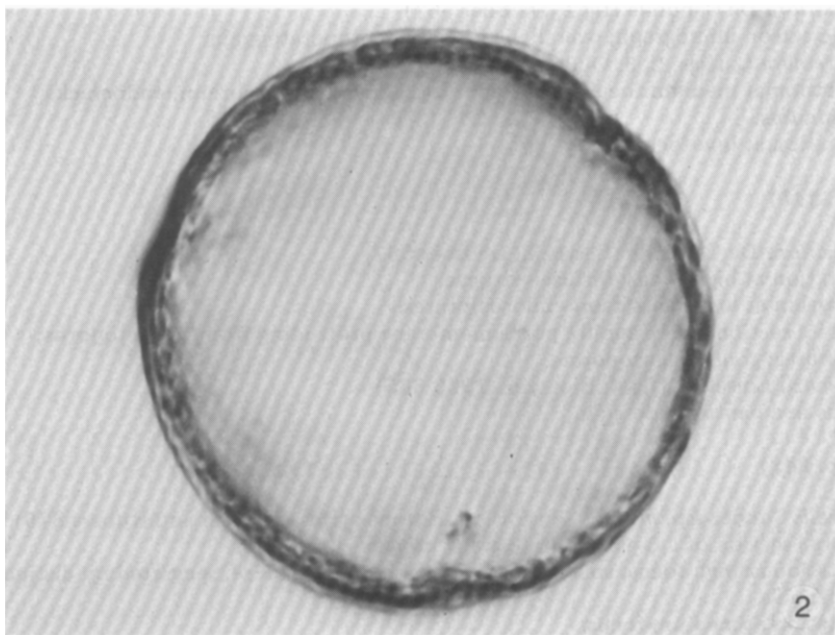
PLATE V (*Corydalis lutea* type. 1; *Corydalis solida* type. 2)

PLATE VI (p. 237)

Eschscholzia californica Chamisso (Kramer 123)

1. Scanning electron micrograph; equatorial view; narrow ectocolpi.
2. Scanning electron micrograph; polar view; five ectocolpi.
3. Scanning electron micrograph; ornamentation, reticulum with a perforated tectum in the lumina ($\times 10\ 000$).

PLATE VII (p. 238)

Eschscholzia californica Chamisso (figs.1—3, Kramer 123)

1. Polar view; cross-section; nexine with indistinct endosculptures.
 2. Equatorial view; ornamentation near ectocolpus at high focus, showing the reticulum with scabrae on the muri and within the lumina.
 3. Equatorial view; ornamentation at low focus.
- Fumaria capreolata* L. (fig.4, Oudemans 414)
4. Optical cross-section; grain 12-pantoporate.

PLATE VIII (p. 239)

Fumaria officinalis L. ssp. *officinalis* sensu Flora Europea (fig.1, Mennega s.n.)

1. Scanning electron micrograph; overall view of a 14-pantoporate grain.
- Fumaria purpurea* Pugsley (fig.2, Sandwith s.n.)
2. Ornamentation at high focus; well-defined, large, angular verrucae, separated by distinct narrow channels.

PLATE IX (p. 240)

Fumaria densiflora De Candolle (fig.1, De Boer 567)

1. Scanning electron micrograph; overall view of a 7-pantoporate grain.
- Fumaria capreolata* L. (figs. 2, 3, Oudemans 414)
2. Ornamentation at medium focus; endosculptures beneath mesopodium, endocracks beneath annulus.
 3. Ornamentation at low focus.

PLATE X (p. 241)

Fumaria densiflora De Candolle (figs.1—3, De Boer 567)

1. Ornamentation at high focus; diffuse verrucae.
 2. Ornamentation at low focus; faint endosculptures.
 3. Optical cross-section; thick annuli; porous membrane protruding from the ectoporus; endosculptures; grain 6-pantoporate.
- Fumaria vaillantii* Loiseleur (fig.4, Biol. exc. 1965-865)
4. Ectocolpus in a pantoporate grain.

PLATE XI (p. 242)

Fumaria muralis Sonder ssp. *muralis* sensu Flora Europea (Hessel, Klein and Rubers 875).

1. Optical cross-section of a 6-pantoporate grain; convex-cubic grain.
2. Ornamentation at high focus; well-defined, large, angular verrucae, separated by distinct narrow channels.
3. Ornamentation at medium focus.
4. Ornamentation at low focus; endosculptures beneath mesopodium, endocracks beneath annuli.

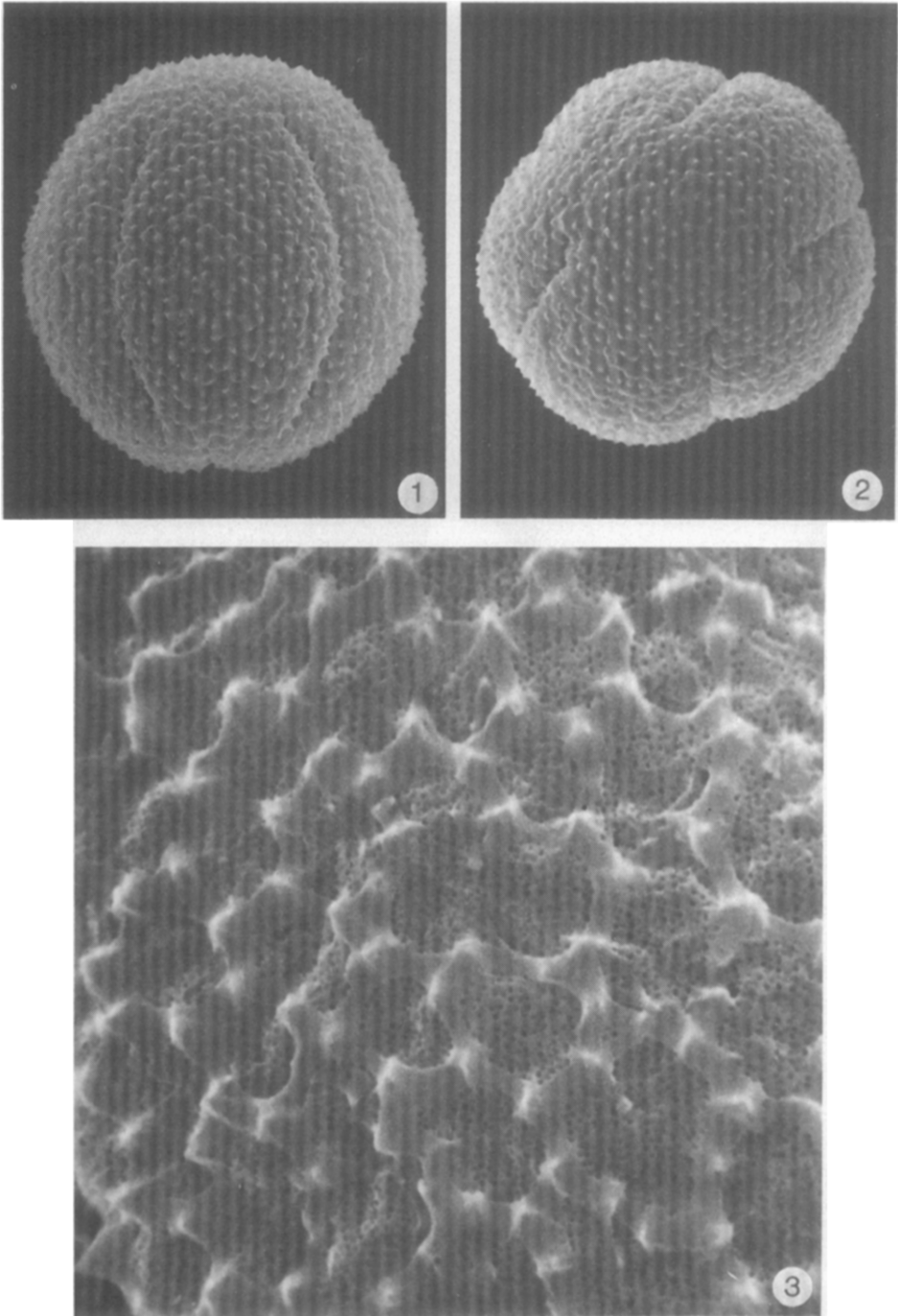
PLATE VI (*Eschscholzia californica* type)

PLATE VII (*Eschscholzia californica* type, 1-3; *Fumaria officinalis* type, 4)

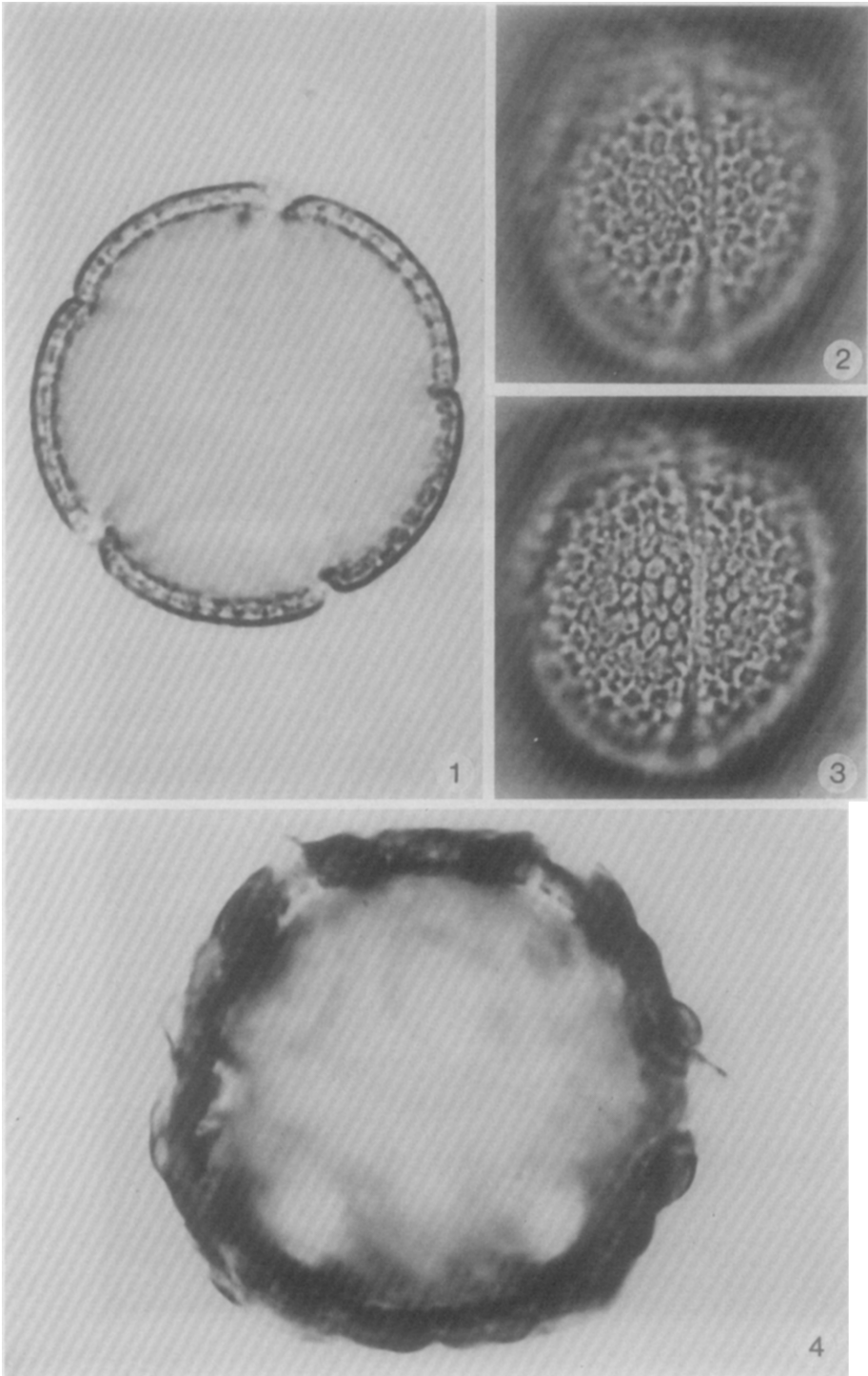


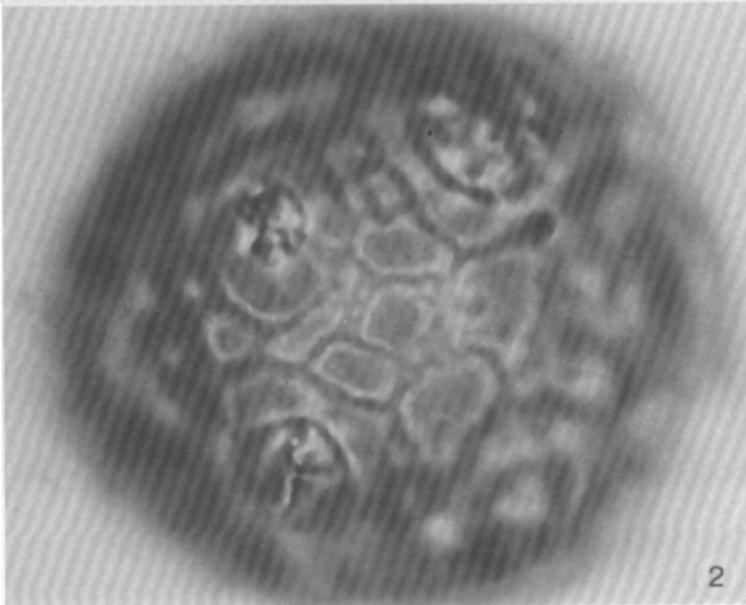
PLATE VIII (*Fumaria officinalis* type: *F. capreolata* group)

PLATE IX (*Fumaria officinalis* type: *F. densiflora* group, 1; *F. capreolata* group, 2-3)

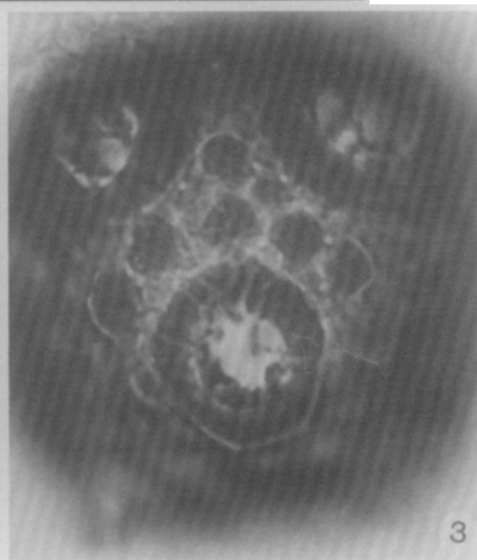
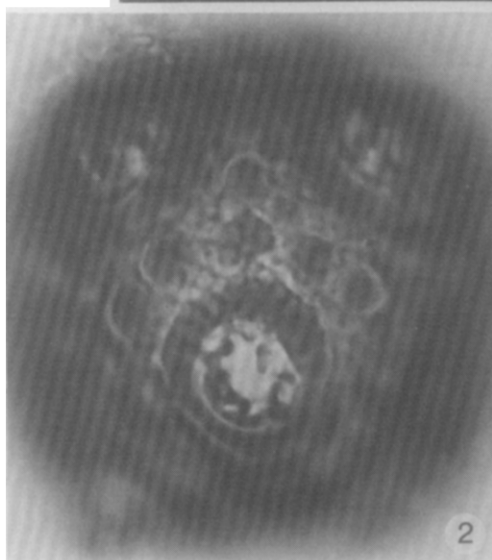
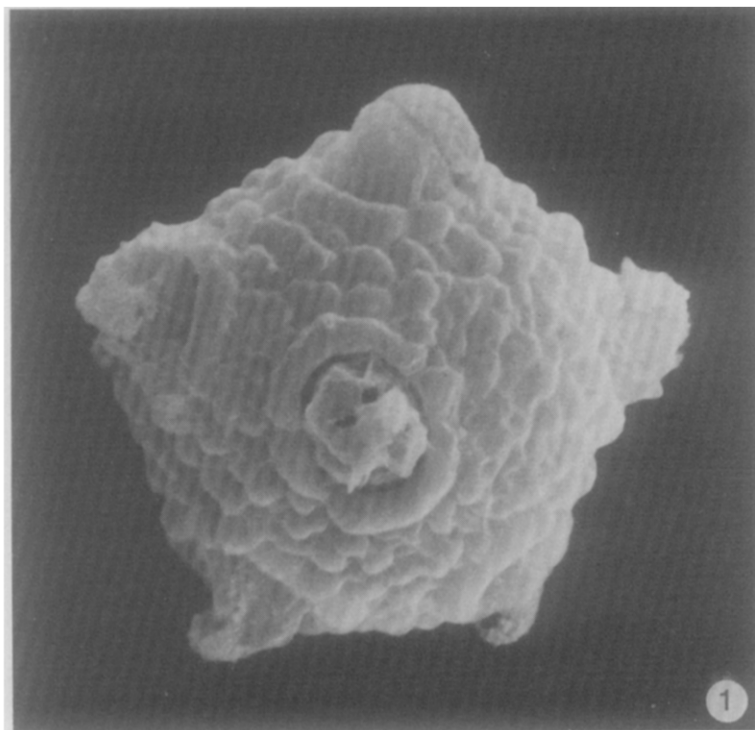


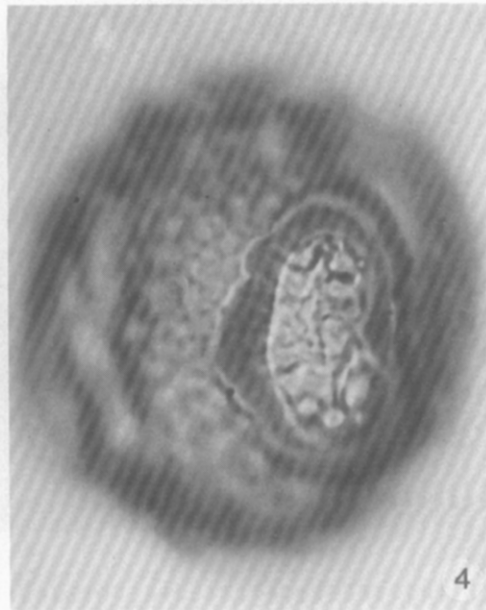
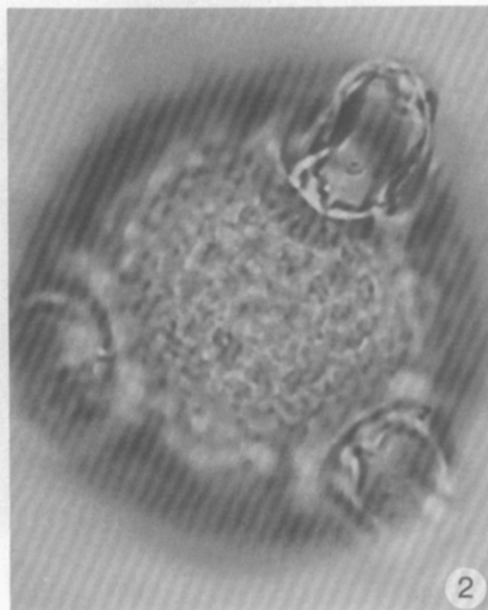
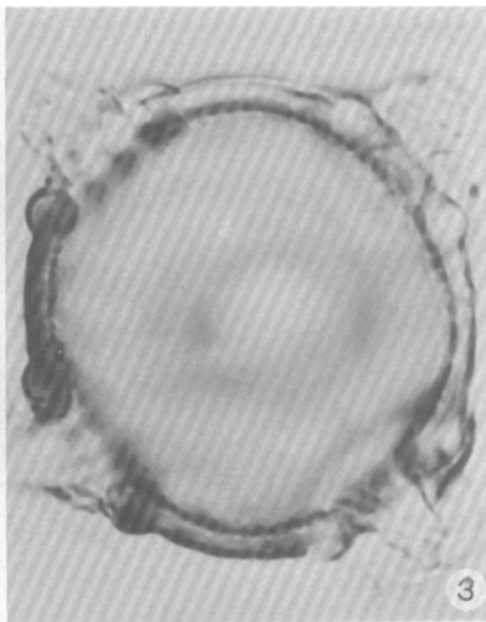
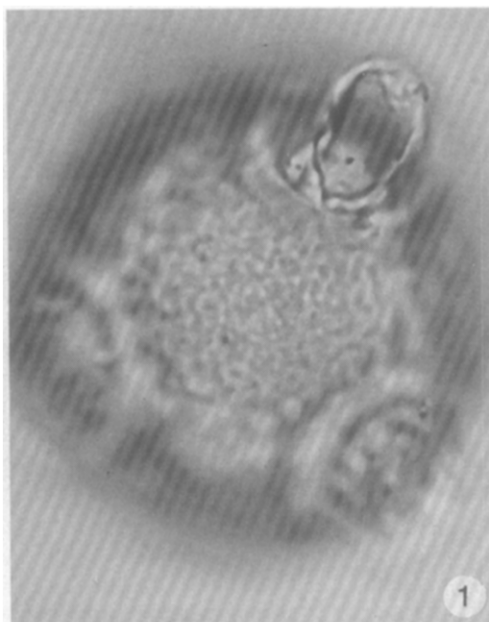
PLATE X (*Fumaria officinalis* type: *F. densiflora* group)

PLATE XI (*Fumaria officinalis* type: *F. muralis* group)

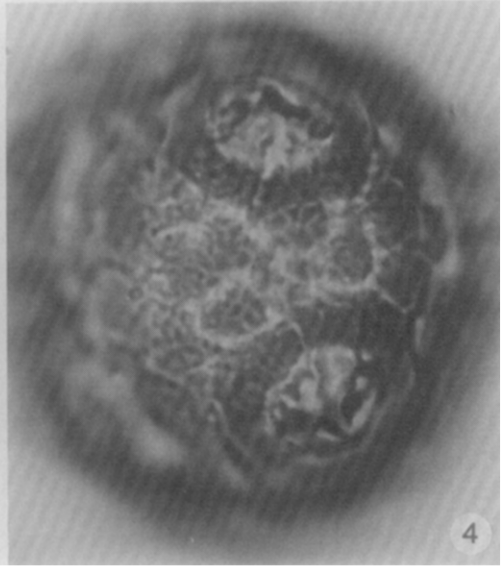
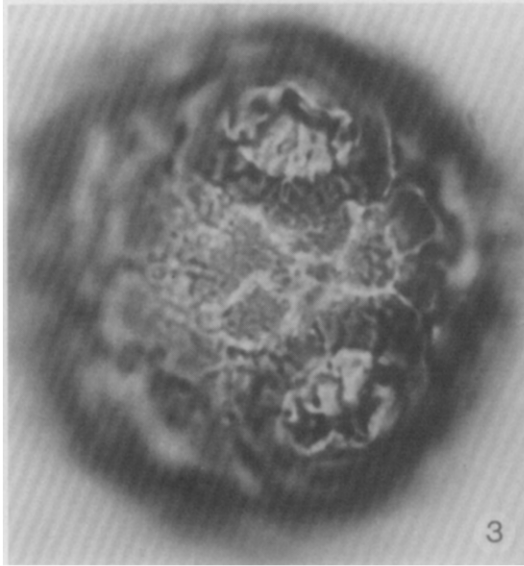
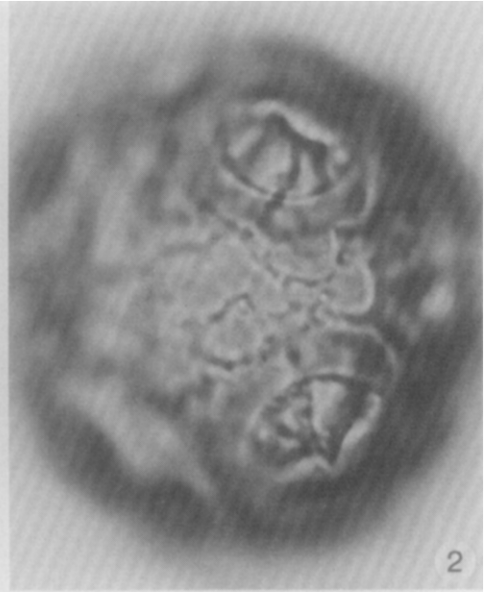
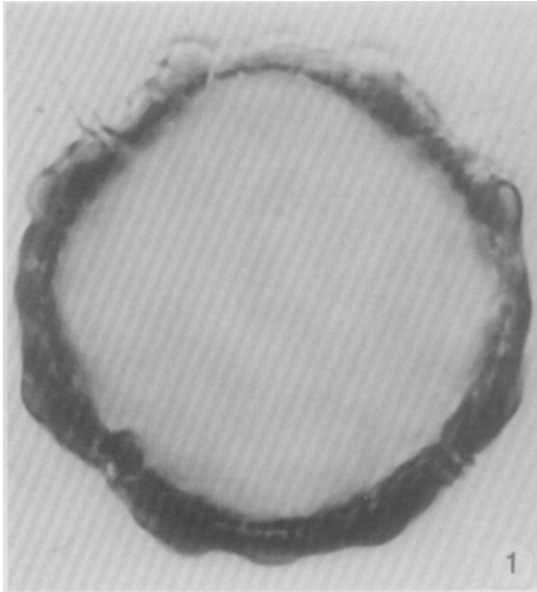


PLATE XII (p. 244)

Fumaria muralis Sonder ssp. *boraei* (Jordan) Pugsley (fig.1, Leemans s.n.)

1. Scanning electron micrograph; overall view of a 6-pantoporate grain.

Fumaria parviflora Lamarck (figs.2, 3, Wittewaall van Wickenburg s.n.)

2. Scanning electron micrograph; overall view of a 12-pantoporate grain.

3. Scanning electron micrograph; inner face of the nexine with endosculptures.

PLATE XIII (p. 245)

Fumaria parviflora Lamarck (Wittewaall van Wickenburg s.n.)

1. Ornamentation at high focus; faint verrucae.

2. Ornamentation at medium focus.

3. Ornamentation at low focus; faint endosculptures beneath mesopodium; endocracks beneath the annuli.

PLATE XIV (p. 246)

Glaucium corniculatum (L.) J.H. Rudolph (Biol. exc. 1962-1614)

1. Scanning electron micrograph; overall view; reticulum decreasing towards the apocolpium.

2. Colpus membrane and ornamentation near ectocolpus; distinct, coarse, angular granules.

3. Ornamentation of the apocolpium at medium focus; columellae rounded in outline.

4. Ornamentation of the apocolpium at low focus; endocracks.

5. Ornamentation of the mesocolpium at high focus; reticulum.

6. Ornamentation of the mesocolpium at medium focus; muri mainly duplicolumellate.

PLATE XV (p. 247)

Glaucium flavum Crantz (Van Oordt s.n.)

1. Scanning electron micrograph; detail of fractured exine, muri beset with short broadly based microechinae, columellae, nexine with endosculptures. ($\times 10\,000$)

2. Scanning electron micrograph; equatorial view.

3. Ornamentation of apocolpium at high focus; tectum perforatum.

4. Ornamentation of apocolpium at medium focus; columellae irregular in outline.

5. Ornamentation of apocolpium at low focus; faint endocracks.

6. Ornamentation of mesocolpium at high focus; capita more or less connected, forming muri of a reticulum.

7. Ornamentation of mesocolpium at medium focus; muri simplicolumellate.

PLATE XVI (p. 248)

Glaucium flavum Crantz (figs.1-3, Van Oordt s.n.)

Trimorphism: optical cross-section in polar view of the three sizes:

1. Large grain.

2. Intermediate grain.

3. Small grain.

Glaucium corniculatum (L.) J.H. Rudolph (figs.4-6, Biol. exc. 1962-1614)

Trimorphism: optical cross-section in equatorial view of the three sizes:

4. Small grain.

5. Intermediate grain.

6. Large grain.

PLATE XII (*Fumaria officinalis* type: *F. muralis* group, 1; *F. parviflora* group, 2-3)

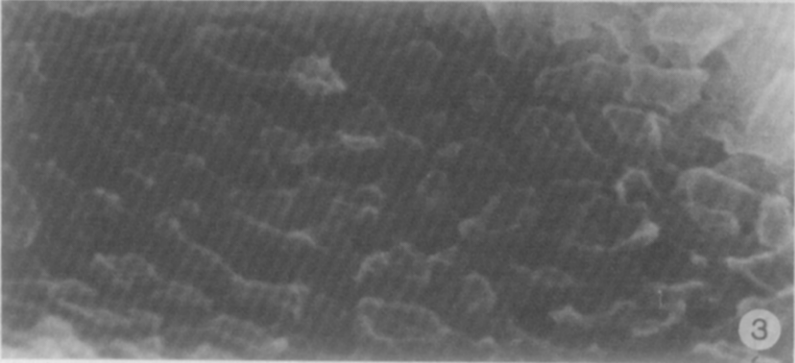
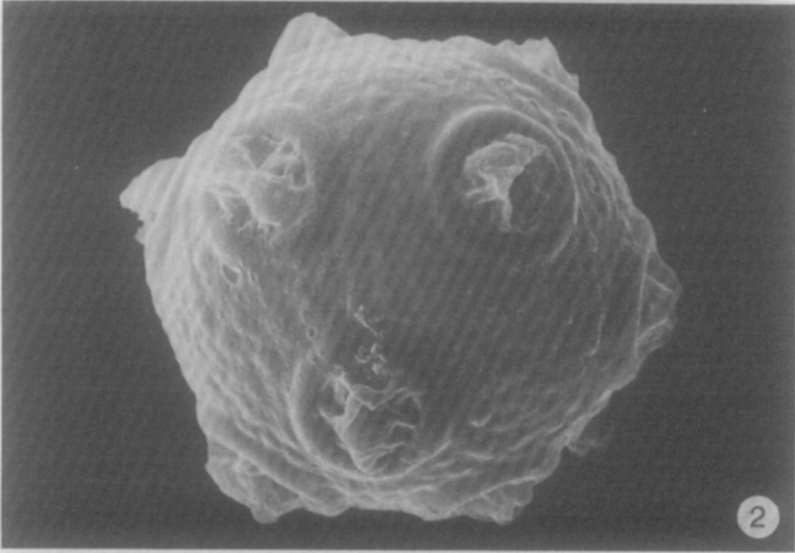
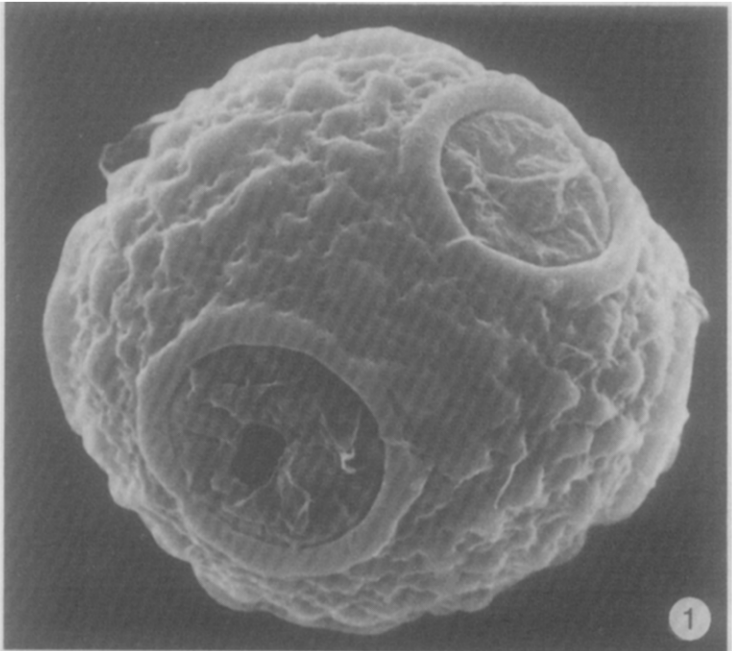


PLATE XIII (*Fumaria officinalis* type: *F. parviflora* group)

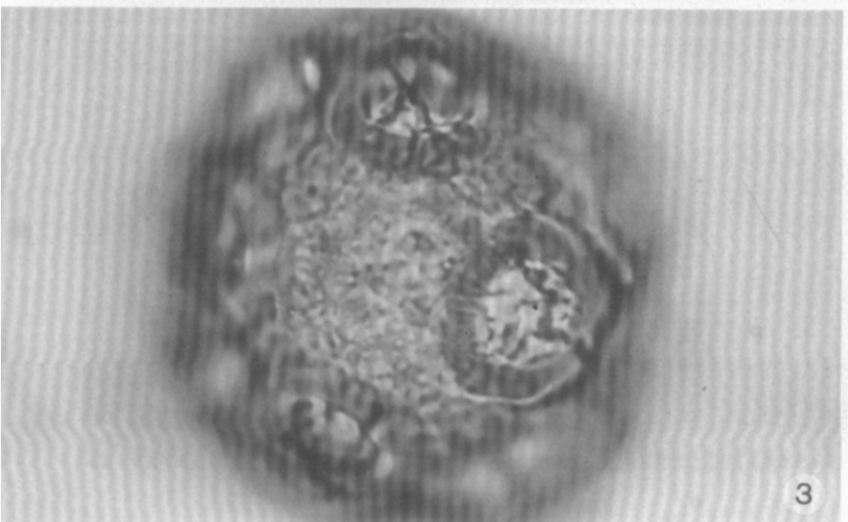
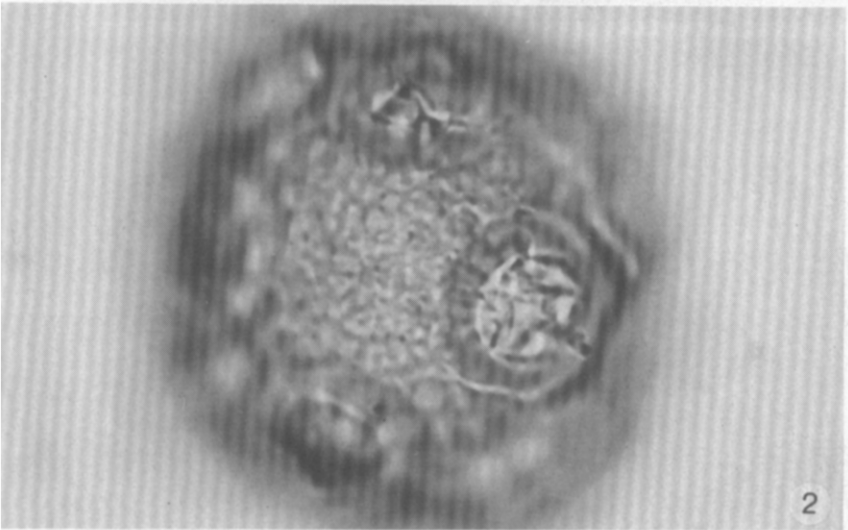
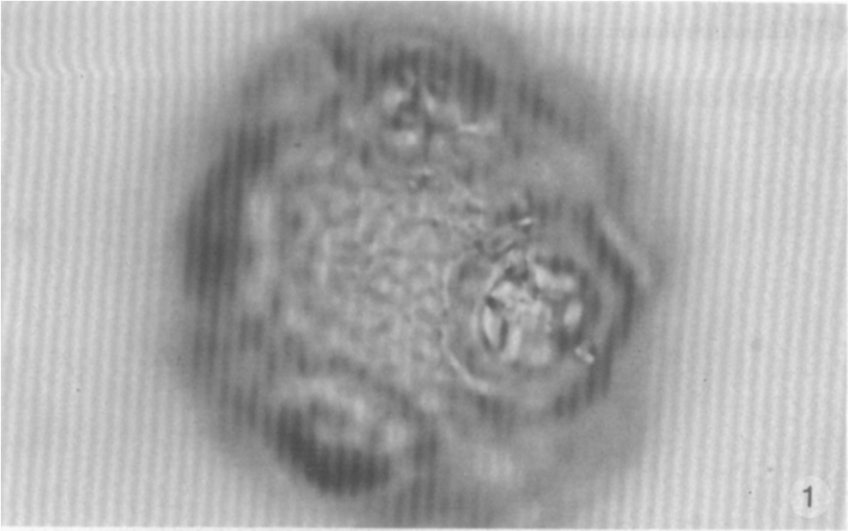


PLATE XIV (*Glaucium flavum* type: *G. corniculatum*)

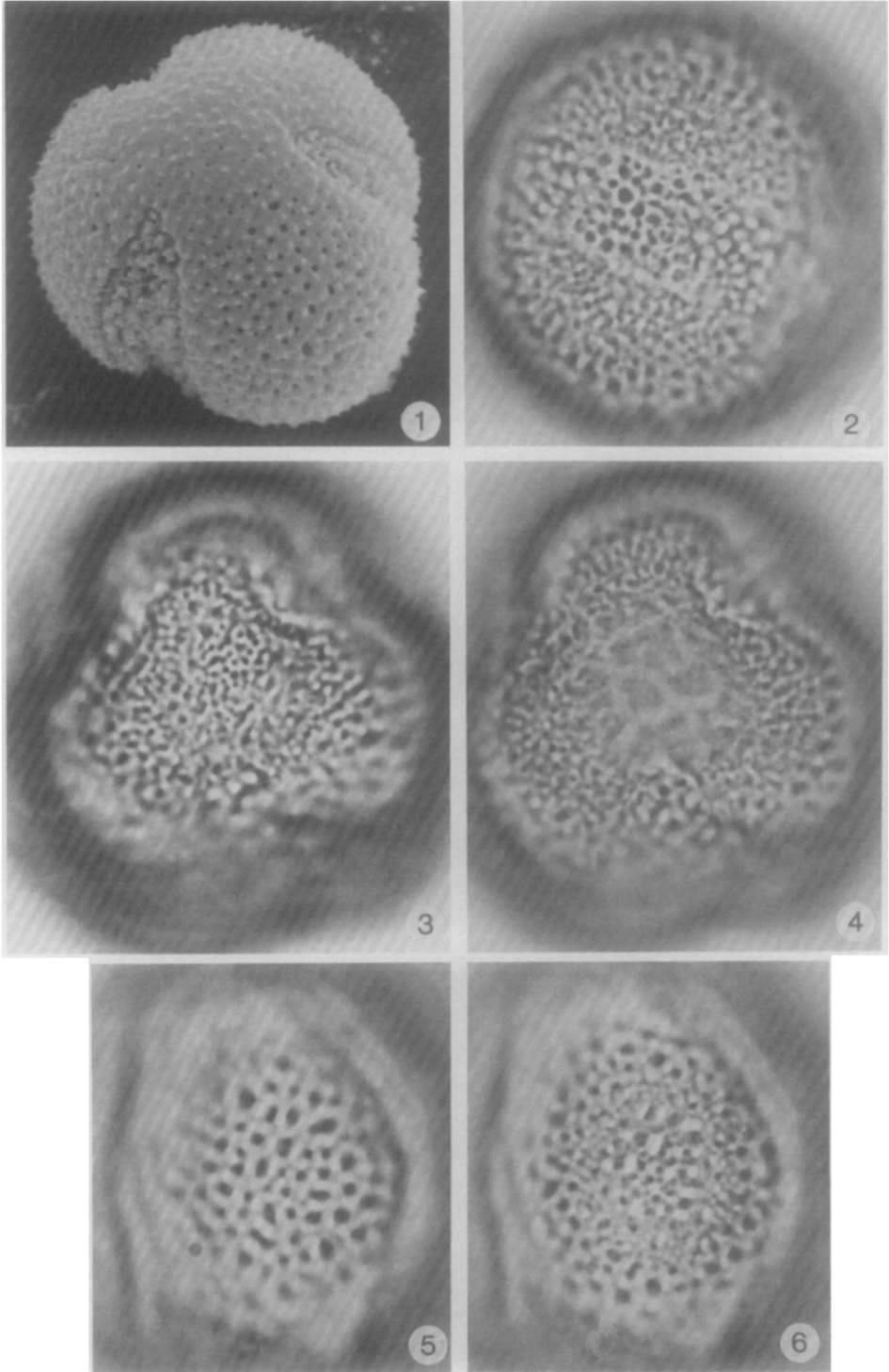


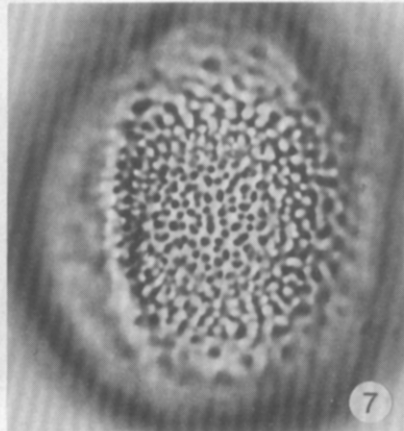
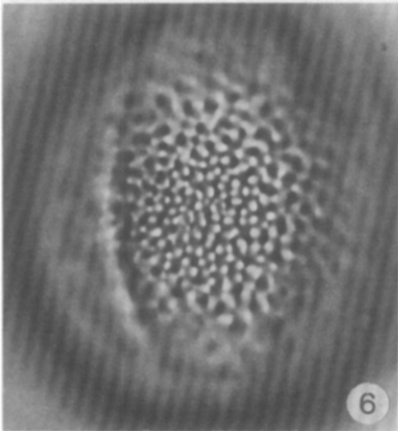
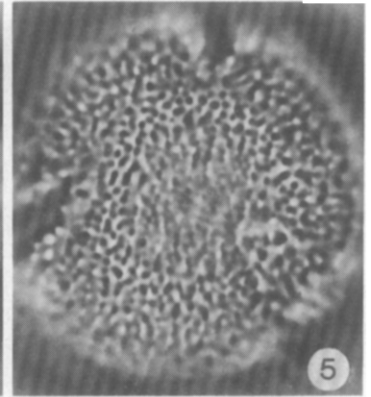
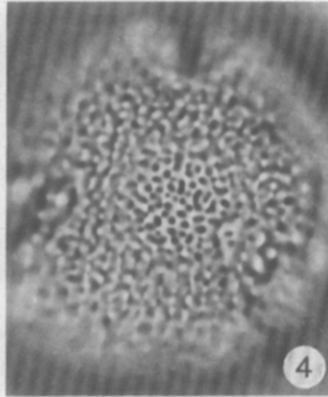
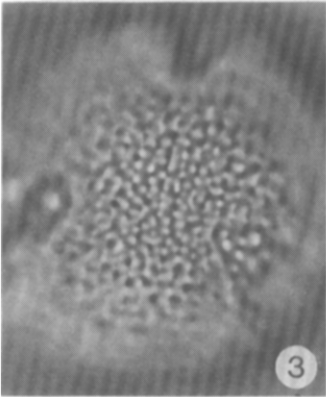
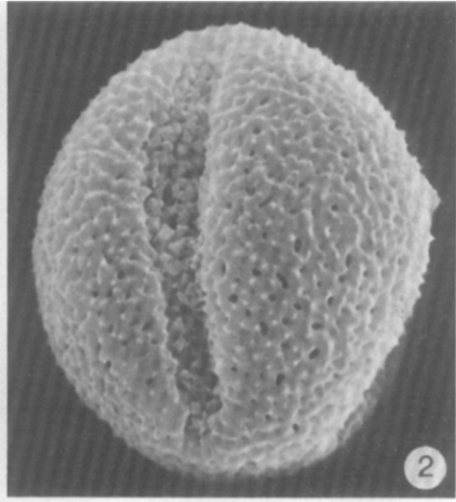
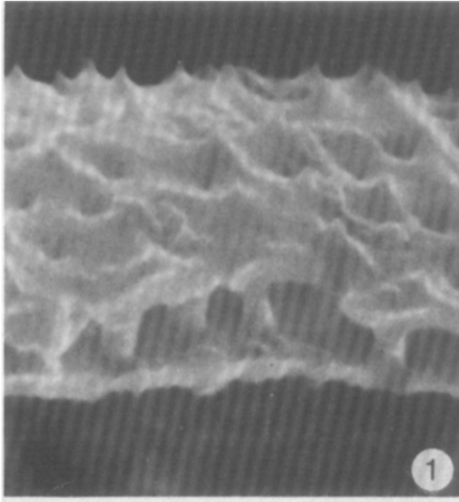
PLATE XV (*Glaucium flavum* type: *G. flavum*)

PLATE XVI (*Glaucium flavum*, trimorphism)

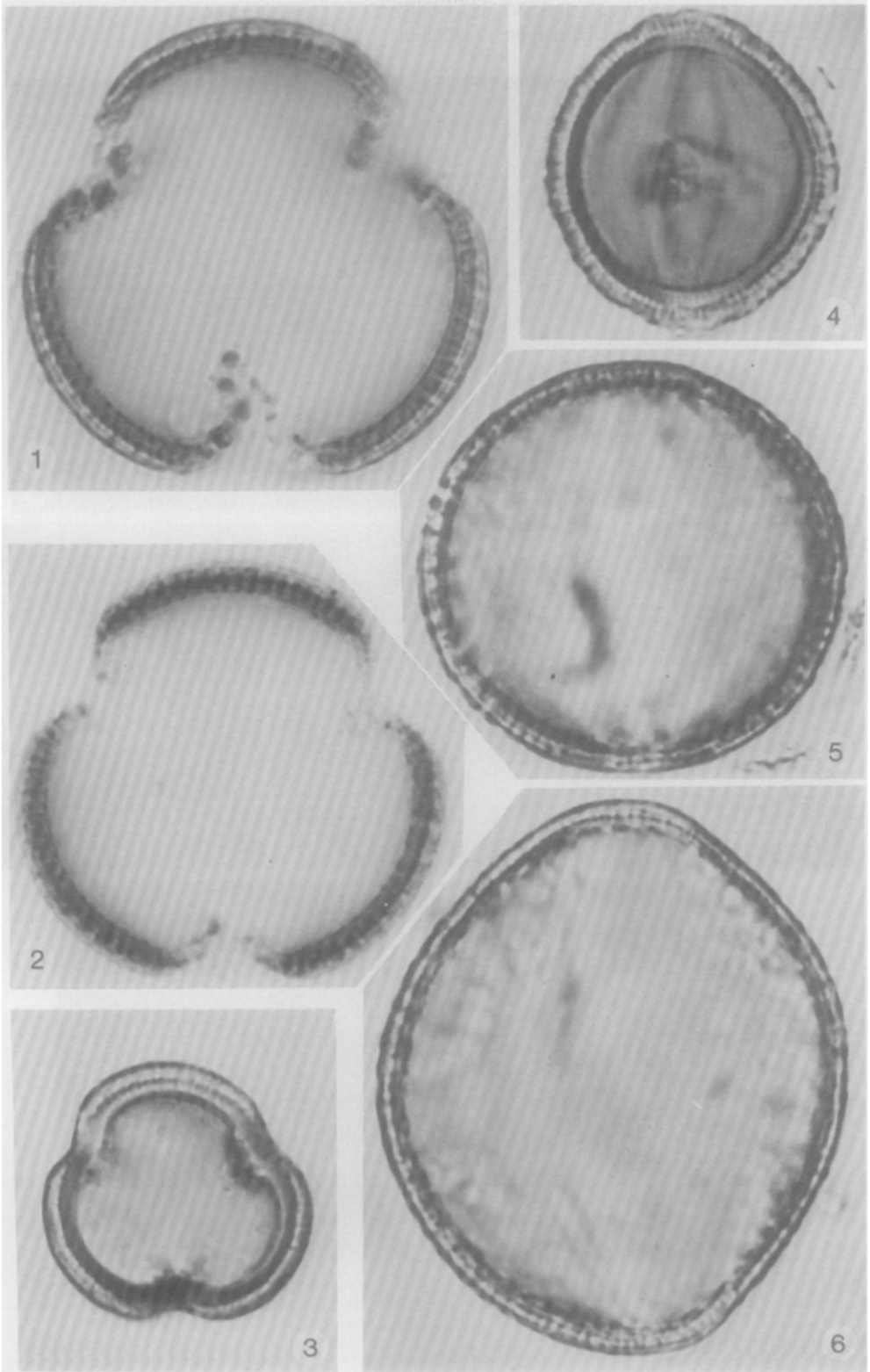


PLATE XVII (p. 250)

Papaver argemone L. (Lejeune and Courtois 353)

1. Optical cross-section; quadrangular outline; thickness of exine decreasing towards apertures.
2. Scanning electron micrograph; overall view, cubic shape; porus membrane with sexine granules, forming an ill-defined operculum.
3. Scanning electron micrograph; detail of fractured exine, nexine with endosculptures, sexine 1 of columellae, sexine 2 a tectate layer with short scabrae ($\times 10\ 000$).
4. Ornamentation and operculum at high focus.
5. Ornamentation and operculum at low focus; columellae in curved rows; distinct irregular granules of the operculum.

PLATE XVIII (p. 251)

Papaver radicum Rottboel (figs.1–4, Oosterveld O.1366; fig.5, Van Oordt 25)

1. Optical cross-section in equatorial view of a 4-zonocolpate grain; convex rectangular outline; tectum smooth or little undulating (type A).
2. Ornamentation of apocolpium at high focus; scabrae (type A).
3. Ornamentation of apocolpium at medium focus; columellae in curved rows.
4. Ornamentation of apocolpium at low focus; endosculptures.
5. Optical cross-section in equatorial view of a 4-zonocolpate grain; coarse verrucae, tectum distinctly undulating (type B, compare fig.1)

PLATE XIX (p. 252)

Papaver radicum Rottboel (figs.1, 2, Oosterveld O.1366, fig.3, Van Oordt 25)

1. Ornamentation of mesocolpium of a 6-pantocolpate grain (type B) at high focus; coarse, irregularly shaped verrucae, beset with scabrae.
2. Ornamentation at low focus.
3. Scanning electron micrograph; detail of apocolpium in a 6-pantocolpate grain (type B); coarse verrucae beset with scabrae, colpus membrane with coarse granules provided with scabrae. ($\times 10\ 000$)

PLATE XX (p. 253)

Meconopsis cambrica (L.) Viguiet (Bordère s.n.)

1. Scanning electron micrograph; equatorial view.
2. Scanning electron micrograph; ornamentation of the mesocolpium; microreticulum with a perforated tectum in the lumina ($\times 10\ 000$).
3. Ornamentation of mesocolpium at high focus; scabrae.
4. Ornamentation of mesocolpium at medium focus; microreticulum.
5. Ornamentation of mesocolpium at medium focus; columellae.
6. Ornamentation of mesocolpium at low focus; endosculptures.

PLATE XXI (p. 254)

Papaver dubium L. (figs.1, 2, 5, s.c. s.n.; figs.3, 4, Lieftinck s.n.)

1. Scanning electron micrograph; detail ornamentation of mesocolpium; scabrae, small punctae between scabrae ($\times 10\ 000$).
2. Scanning electron micrograph; equatorial view, slit-like ectocolpus, small apocolpium.
3. Ornamentation of mesocolpium at medium focus; scabrae, columellae.
4. Ornamentation of mesocolpium at low focus; endosculptures.
5. Scanning electron micrograph; detail of inner side of nexine showing endosculptures and perforations ($\times 10\ 000$).

PLATE XVII (*Papaver argemone* type)

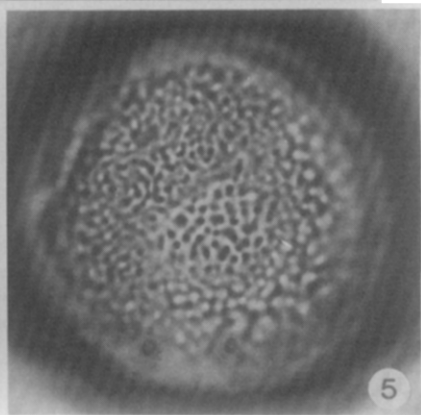
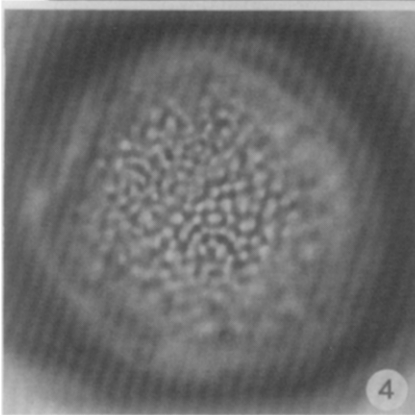
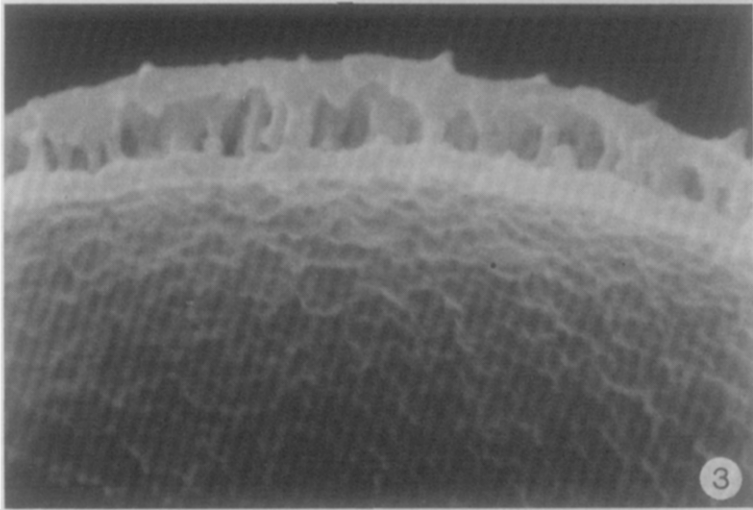
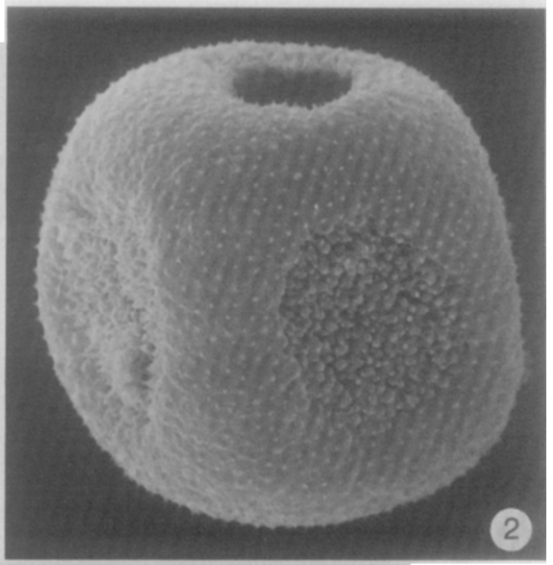
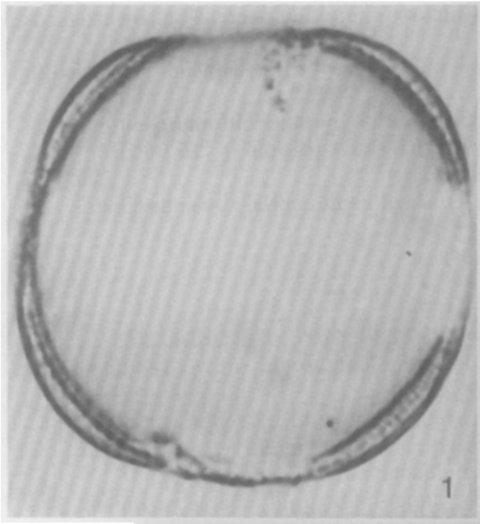


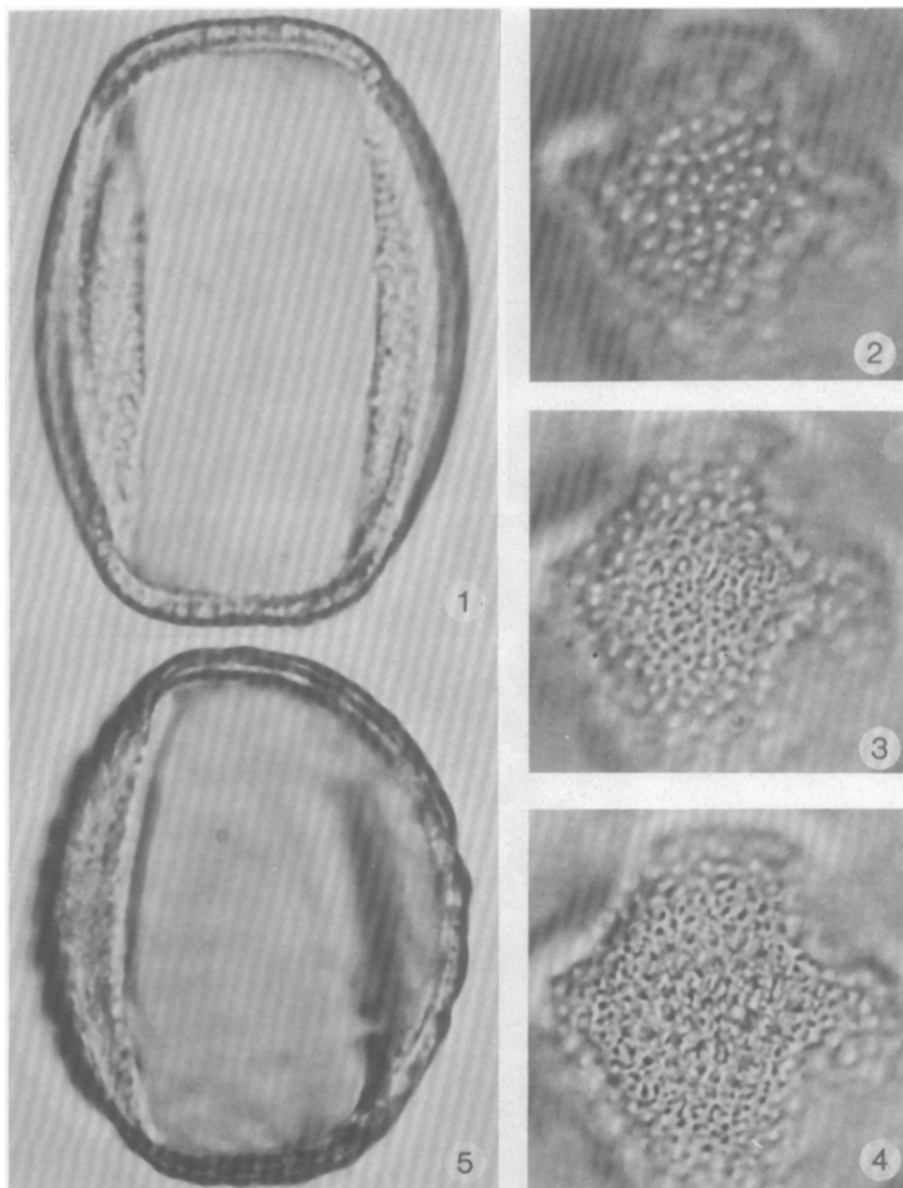
PLATE XVIII (*Papaver radicatum* type: type A, 1-4; type B, 5)

PLATE XIX (*Papaver radicatum* type: type B)

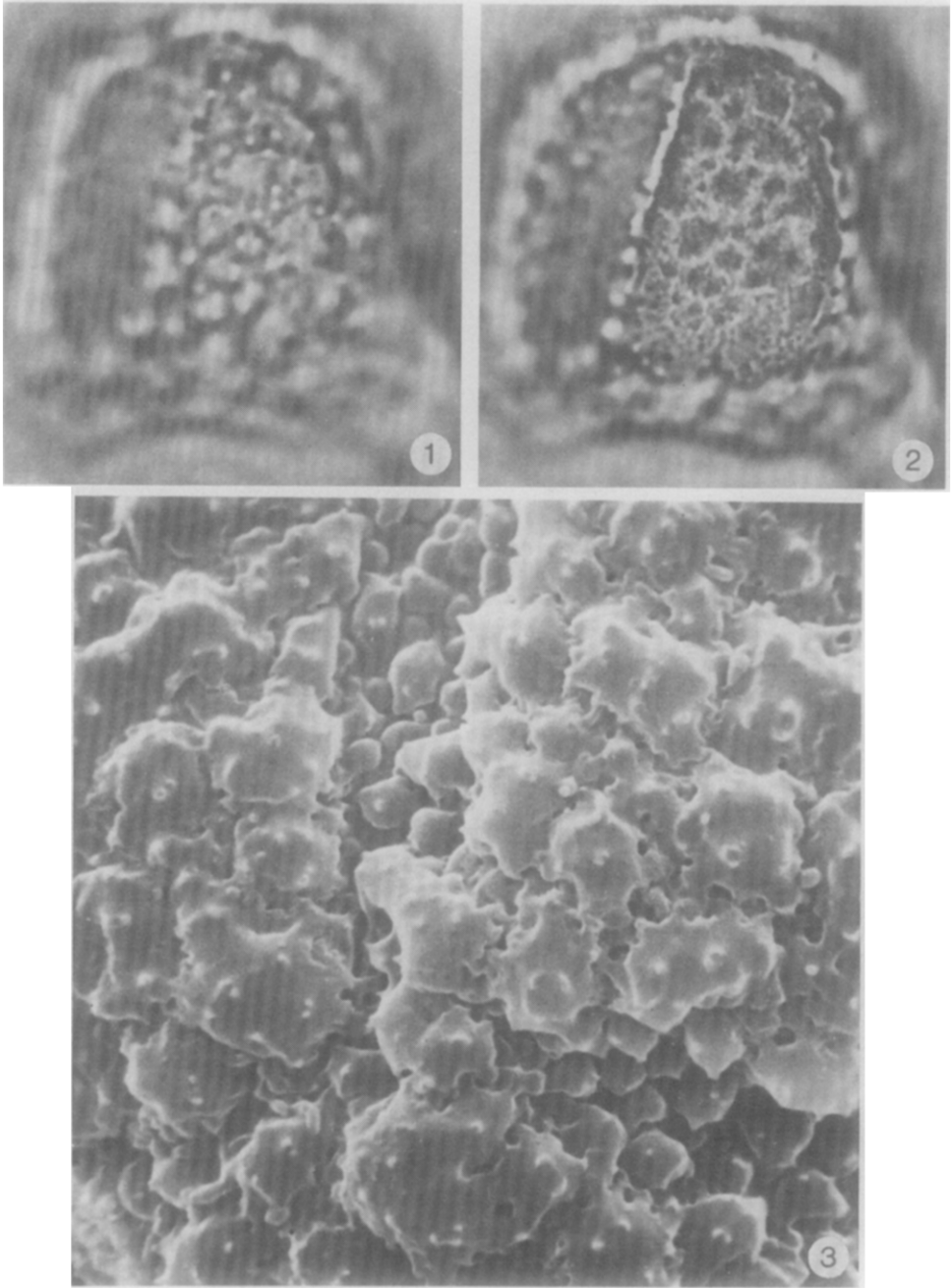


PLATE XX (*Papaver rhoeas* type: *Meconopsis cambrica*)

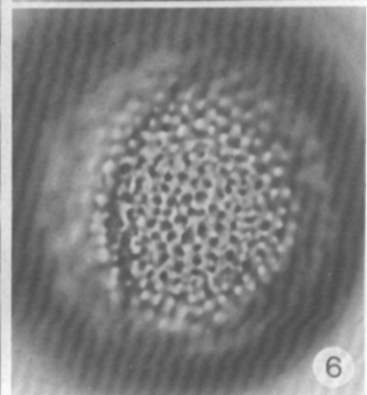
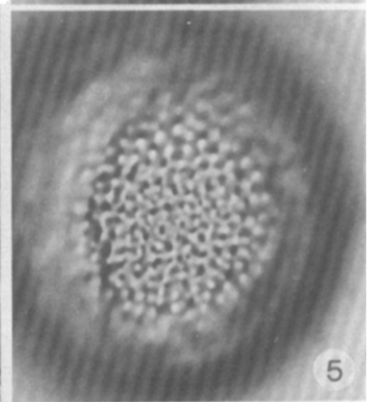
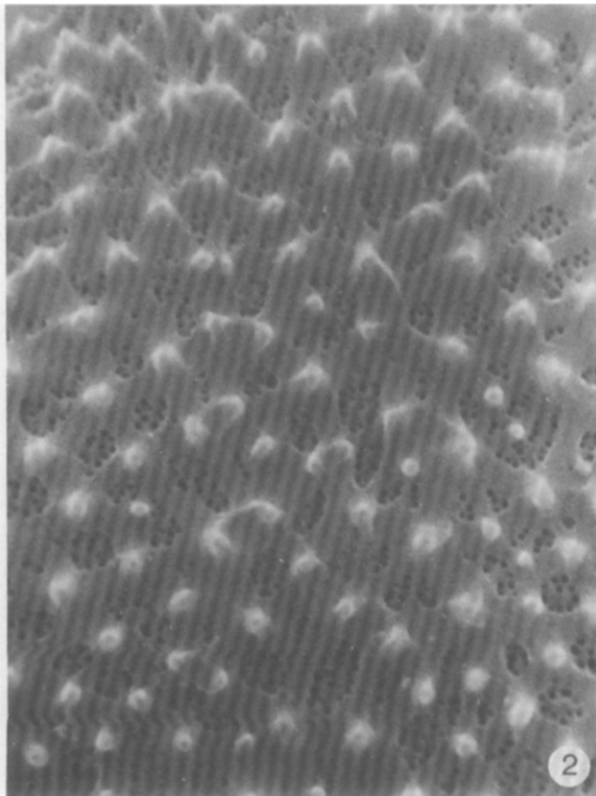
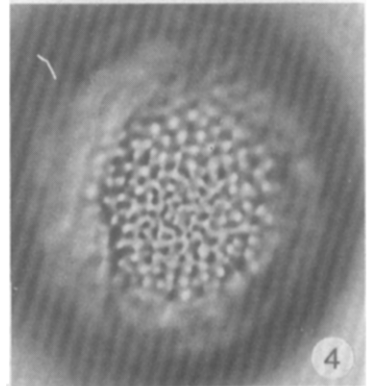
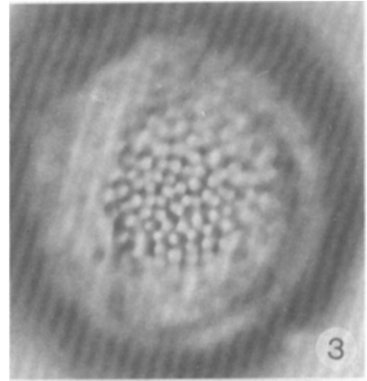
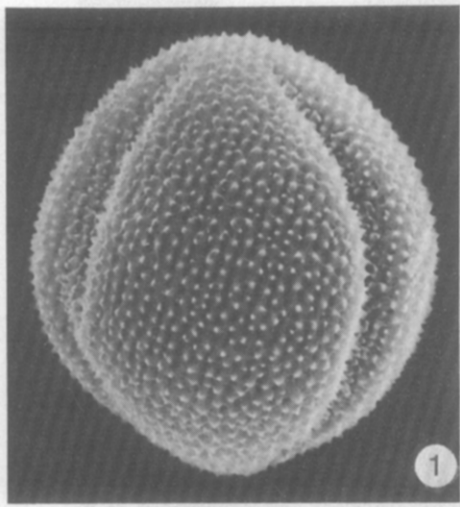


PLATE XXI (*Papaver rhoeas* type: *P. dubium*)

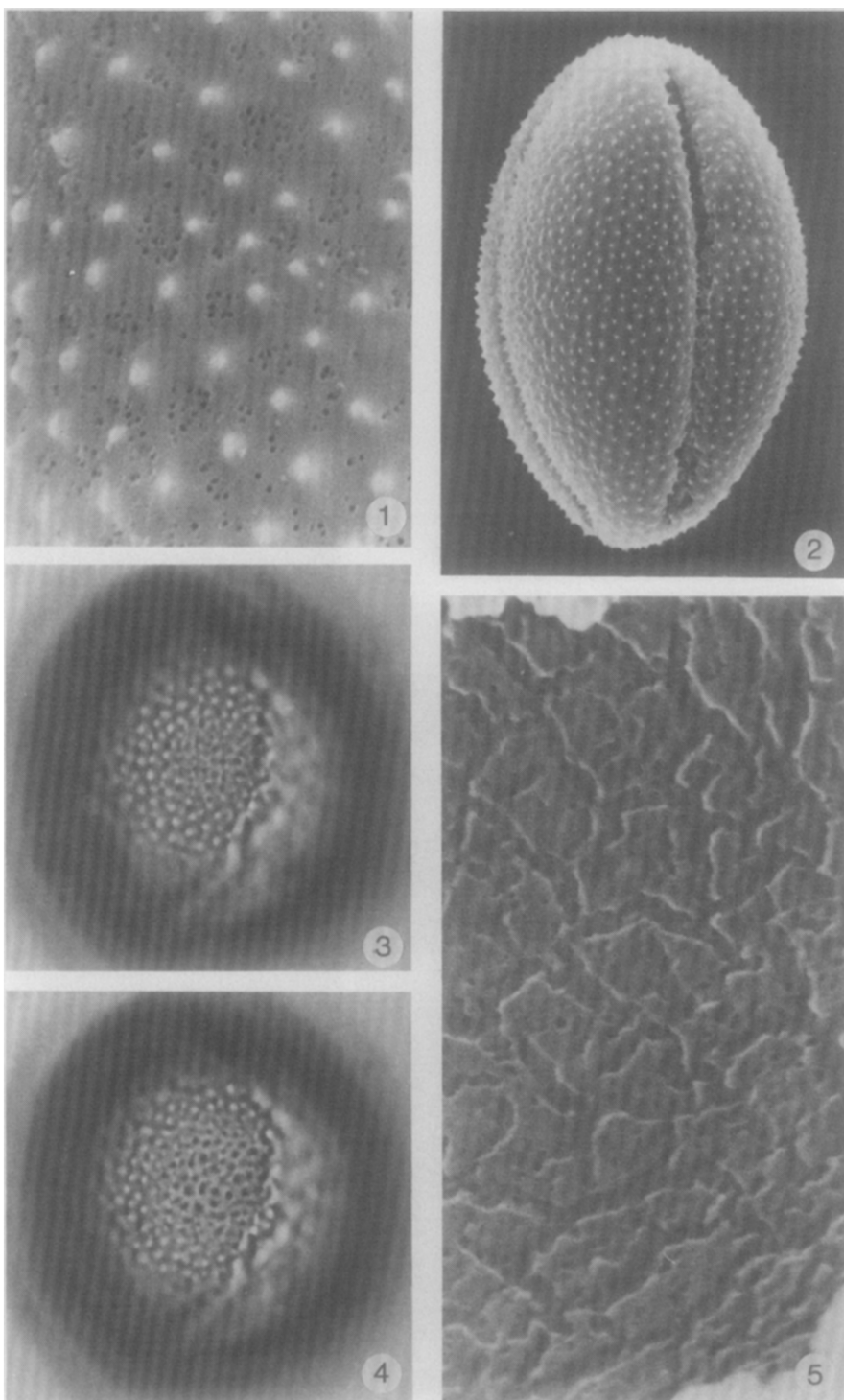


PLATE XXII (p. 256)

Papaver dubium L. (fig.1, Lieftinck s.n.)

1. Optical cross-section in equatorial view of an undamaged grain, exine not thickened in the apocolpium.

Papaver hybridum L. (figs.2–6, s.c. s.n.)

2. Optical cross-section in equatorial view; exine not thickened in the apocolpium.
3. Ornamentation of mesocolpium at high focus; scabrae.
4. Ornamentation of mesocolpium at medium focus, columellae in curved rows forming an infra-reticulum.
5. Ornamentation of apocolpium at medium focus; infra-reticulum.
6. Ornamentation of apocolpium at low focus; endosculptures; relatively large apocolpium.

PLATE XXIII (p. 257)

Papaver rhoeas L. (Dieleman 347)

1. Optical cross-section in polar view.
2. Optical cross-section in equatorial view; exine thickened in the apocolpium.
3. Ornamentation of mesocolpium at high focus; scabrae.
4. Ornamentation of mesocolpium at medium focus; faint columellae forming an infra-reticulum.
5. Ornamentation of mesocolpium at low focus; endosculptures.
6. Ornamentation of apocolpium at high focus; scabrae.
7. Ornamentation of apocolpium at medium focus; distinct columellae forming a distinct infra-reticulum (compare fig.4).

PLATE XXIV (p. 258)

Papaver somniferum L. (figs.1–6, Hekking s.n.)

1. Optical cross-section in equatorial view; exine thickened in the apocolpium, scabrae not visible in cross-section.
2. Optical cross-section in polar view.
3. Ornamentation of the mesocolpium at high focus; scabrae.
4. Ornamentation of the mesocolpium at medium focus; columellae in curved rows forming an infra-reticulum.
5. Ornamentation of the mesocolpium at low focus; endosculptures.
6. Ornamentation of the apocolpium at low focus; endocracks.

Papaver oriëntale L. (fig.7, Abeleven s.n.)

7. Scanning electron micrograph; detail of the inner side of the nexine showing endocracks ($\times 10\ 000$).

PLATE XXV (p. 259)

Papaver strigosum Schur (*P. rhoeas* L. p.p.) (fig.1, Vooren s.n.)

1. Scanning electron micrograph; equatorial view.

Papaver somniferum L. (figs.2, 3, Hekking s.n.)

2. Scanning electron micrograph; polar view.
3. Scanning electron micrograph; equatorial view.

Papaver oriëntale L. (fig.4, Abeleven s.n.)

4. Scanning electron micrograph; equatorial view; densely crowded scabrae.

PLATE XXII (*Papaver rhoeas* type: *P. dubium*, 1; *P. hybridum*, 2-6)

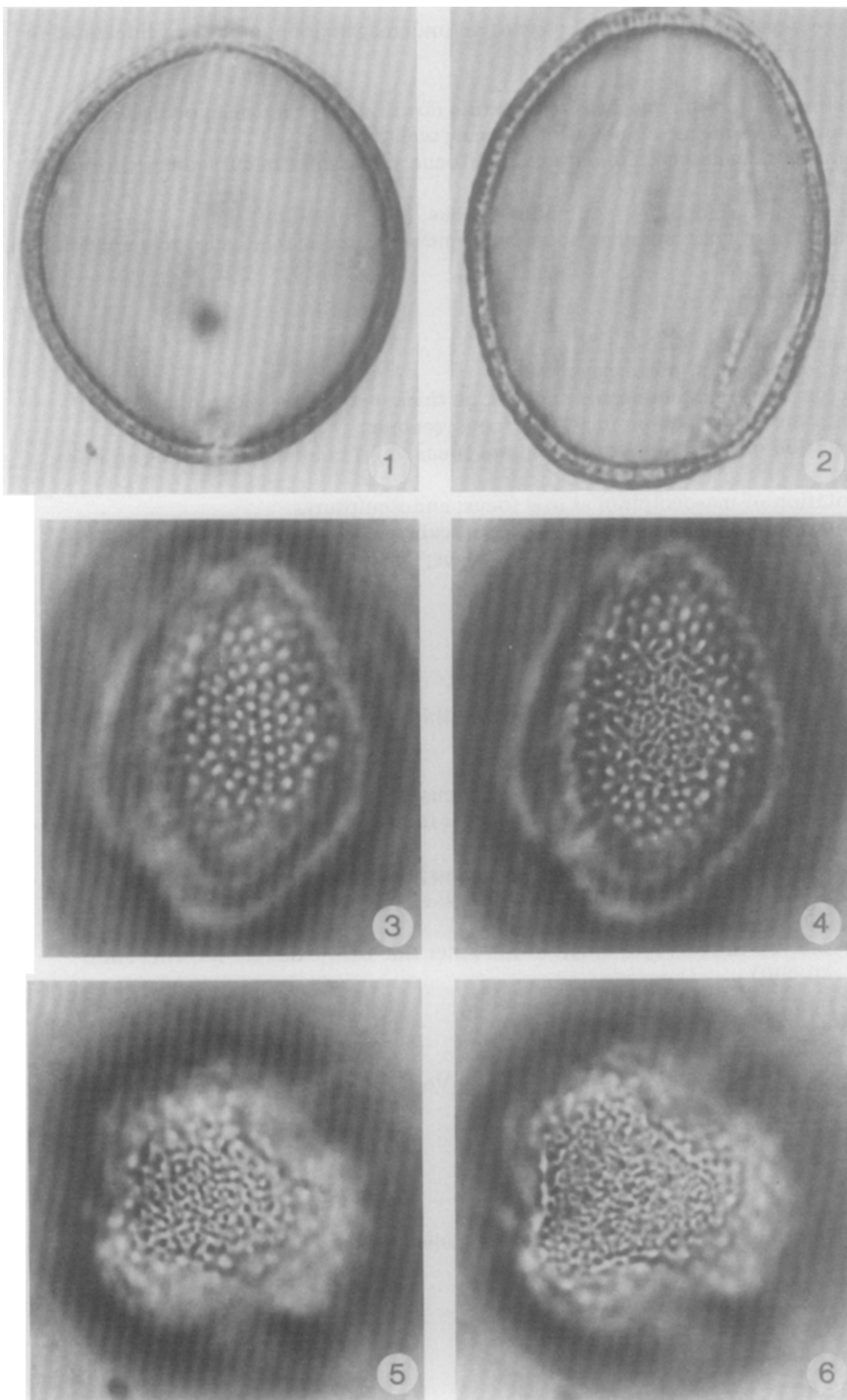


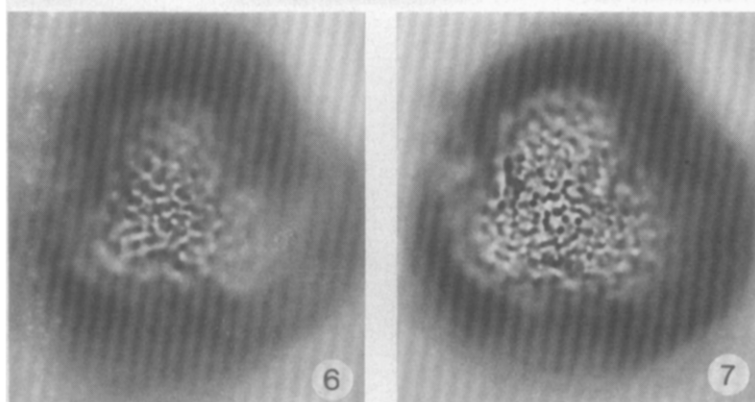
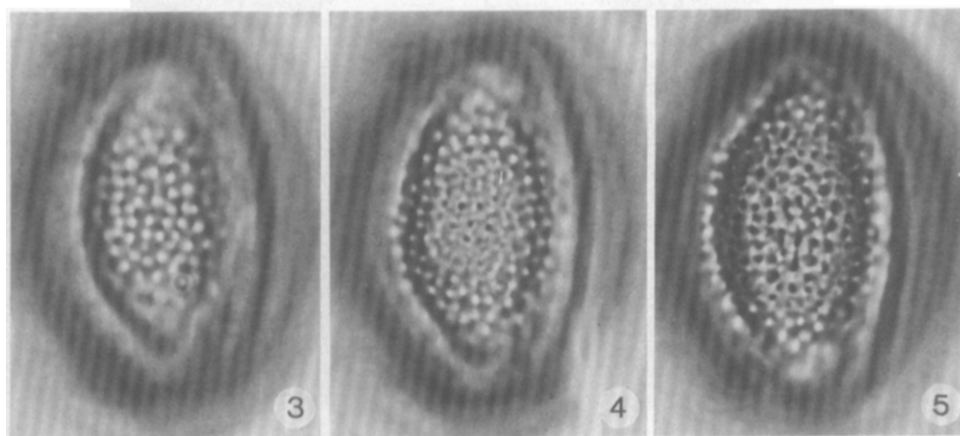
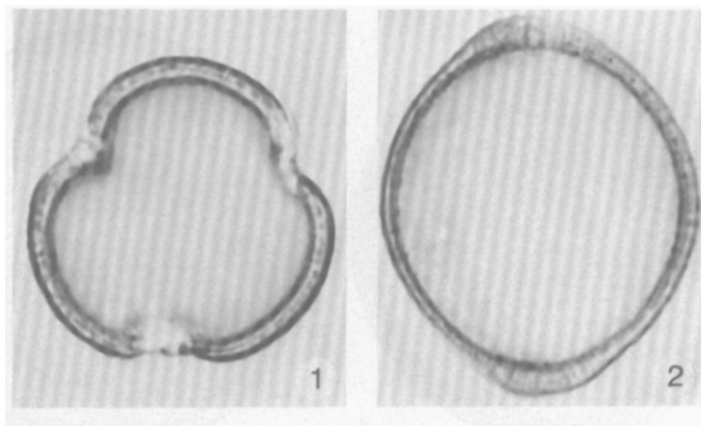
PLATE XXIII (*Papaver rhoeas* type: *P. rhoeas*)

PLATE XXIV (*Papaver rhoeas* type: *P. somniferum*, 1-6; *P. orientale*, 7)

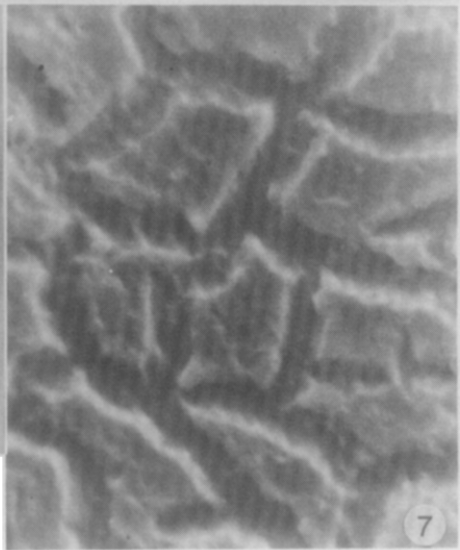
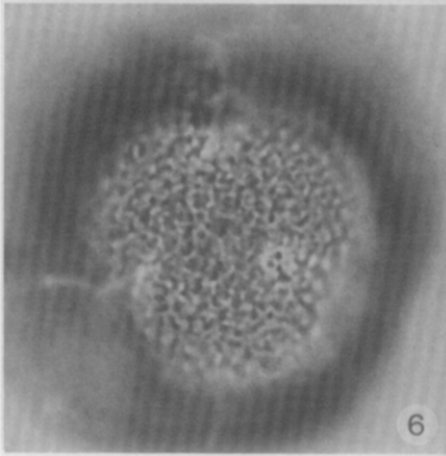
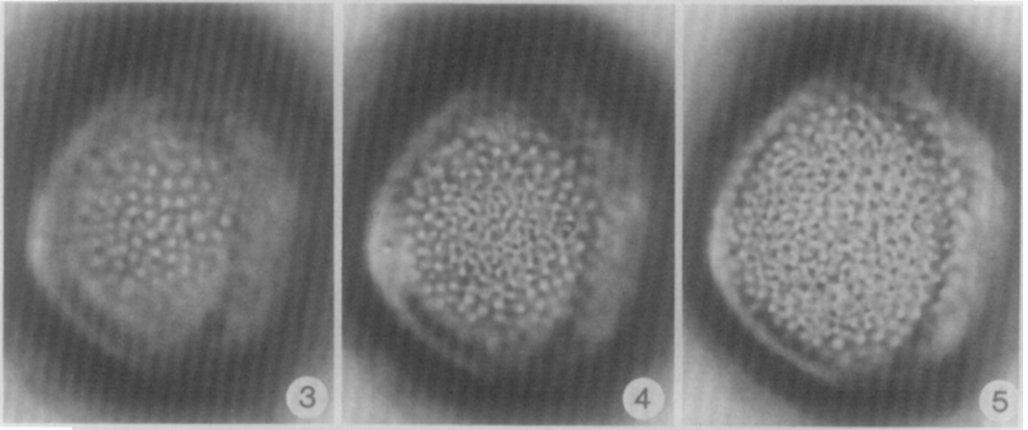
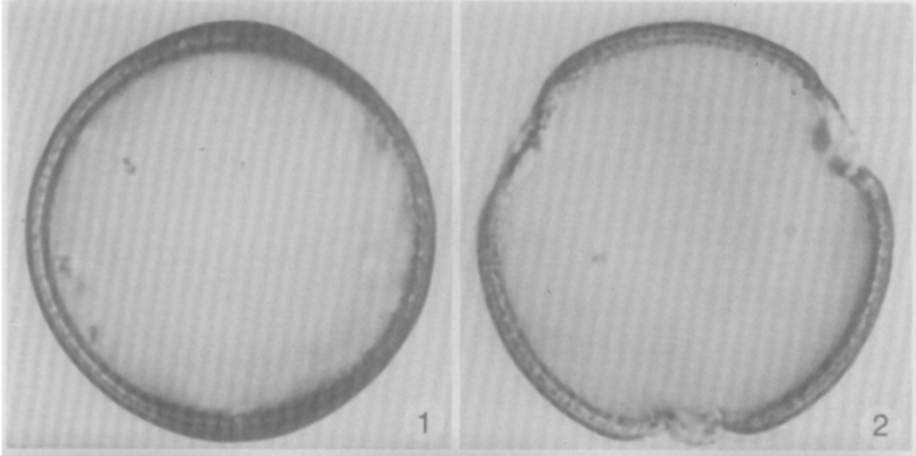
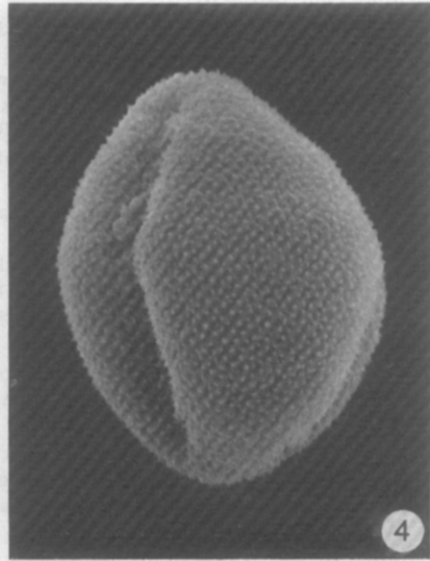
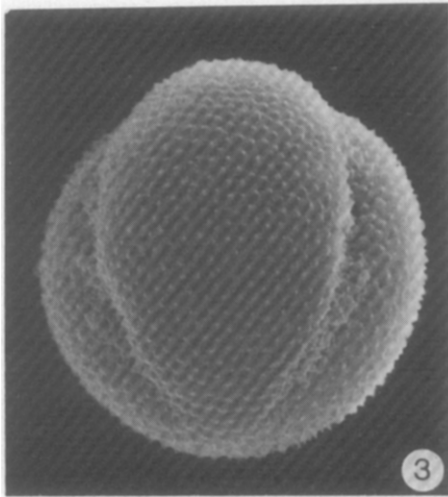
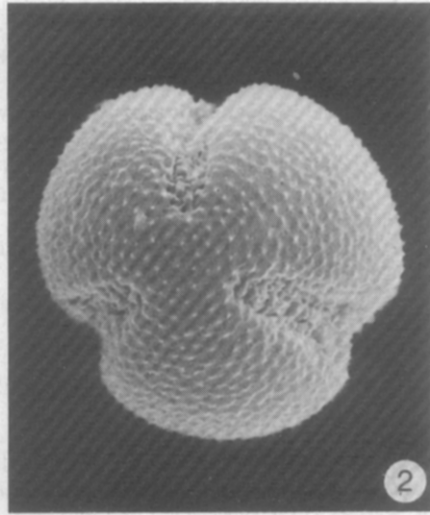
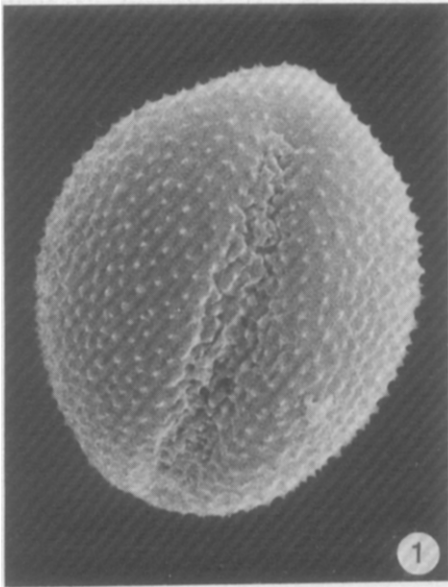


PLATE XXV (*Papaver rhoeas* type)

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