BLUMEA 23 (1977) 301—335

POLLENMORPHOLOGY OF THE GENUS MISCHOCARPUS (SAPINDACEAE)

R. W. J. M. VAN DER HAM
Rijksherbarium, Leiden, The Netherlands

CONTENTS

SUMMARY

The pollen morphology of all 11 species of the genus *Mischocarpus* is studied. All species possess basically the same syntricolpate pollen type. Transitions to the tricolpate type were observed rarely. Within the syntricolpate type, subtypes could be established. For a few species a rather wide range of variability in some characters is described.

Pollen morphology correlates with macromorphology as well as with geography, thus supporting the results, based on macromorphological evidence, concerning infrageneric structure and relationships of *Mischocarpus*.

I. INTRODUCTION

The genus *Mischocarpus* was recently studied taxonomically (Van der Ham, 1977a). To complement this, a pollen morphological study was made in which all species recognized could be investigated.

The data for this study were obtained with the lightmicroscope (LM), scanning electron microscope (SEM), and transmission electron microscope (TEM). The LM studies were made on acetolysed grains with Olympus, model E, H.I. 100 ×, A = 130; photographs were made with Leitz, ApoOel 90 ×, A = 1.32.

The SEM studies were made on acetolysed grains with a Cambridge A II scanning electron microscope at the Geological Institute, Leiden. The method producing the freeze microtome sections of grains for SEM study is described in Muller, 1973. For coating was used the E 5000 diode spottering system.

Two methods were used to study pollen with TEM:

1. preparation of acetolysed grains: *M. sundaicus*; fixation: 2% OsO_4, 1 hour; pre-staining: 5% Uranyl acetate, 2 hours; embedding: Epon 3/7; post-staining: leadcitrate, 10 minutes.

In this preparation the endexine is less electron dense than the ektexine.

2. preparation of non-acetolysed grains: *M. reticulatus*; fixation: 0,1 M glutaraldehyd, 3 days + 0.1% OsO4, 2 hours; embedding: Epon 3/7 or Spurr + 2.5% Phtaal Dibutyl (DBP); staining: 0.5% Uranylacetate; sometimes also with leadcitrate.

In this preparation the endexine is more electron dense than the ektexine.

II. GENERAL MORPHOLOGY

The pollen grains in *Mischocarpus* are single, isopolar or slightly anisopolar (see: ektoapertures), tricolporate, although di- or/and tetracolporate grains occur in some species. A dicolporate grain is shown in Pl. V fig. 6, a tetracolporate grain in Pl. VII fig. 1, and Pl. XII fig. 13.

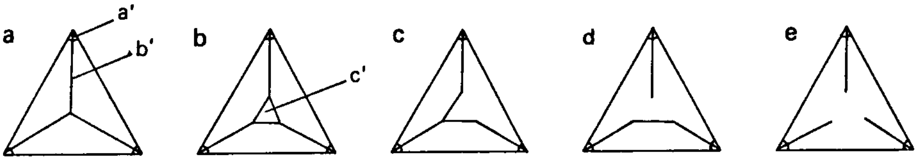


Fig. 1. a. Syncolporate grain; b. parasyncolporate grain; c. and d. pseudo-parasyncolporate grains; e. colporate grain. — a′: endoaperture; b′: ektoaperture; c′: apocolpium.

The grains are syncolporate or parasyncolporate (fig. 1a or b); sometimes they are pseudoparasyncolporate (fig. 1c and d), or rarely colporate (fig. 1e) (see: ektoapertures).

Average size varies between 19 and 33 µm. Shape, as defined by the ratio between the length of the polar axis and the equatorial axis (P/E) varies from peroblate to oblate-spheroïdal, P/E varying from 0.33 tot 0.90.

The equatorial outline is rounded triangular (Pl. X fig. 5) to triangular with convex to straight sides (Pl. VI fig. 4).

With the TEM a study has been made of the structure of the wall in *M. reticulatus* and *M. sundaicus*. As the sample of *M. reticulatus* was not acetolysed the intine could be studied here. This layer, lining the inside of the exine, is more or less homogeneous except at the endoapertures where it is much thickened and where a subdivision in at least three sublayers is visible. Pl. XIV, XV, and XVI fig. 1 show the transition of transverse sections through an ektoaperture (from different grains) from near the pole to at the endoaperture demonstrating the gradual thickening of the intine with the differentiation in its sublayers. The situation at the endoaperture is as follows. The inner sublayer has the same appearance and is continuous with the intine layer as it is developed on the mesocolpia. It is about as thick as, but usually much more folded than on the mesocolpia (Pl. XV fig. 2). The middle sublayer, thinning rapidly towards the centre of the mesocolpia, is characterized by electron dense material, mostly in a regularly spotted, probably trabeculate pattern (Pl. XIV fig. 4; XV fig. 1, 2). In this sublayer, also folds can be observed; they are most distinct near the inner sublayer. The outer sublayer is also thinning rapidly towards the centre of the mesocolpia, homogeneous, thickest at the endoaperture (Pl. XVI fig. 1).

The intine measures about 0.2 µm at the mesocolpia and up to 3 µm at the endoaperture. The thickened intine at the endoapertures can be designated as an oncus.

Observations with LM on the structure of the exine show the presence of an outer structured and an inner non-structured layer. TEM observations indicate that the inner layer is differentiated in two sublayers, contrasting light-dark or dark-light, depending on the way of preparation (see: Introduction).

In Pl. XIV fig. 2 and XVI fig. 2, 3, we can see that the outer sublayer is thickest at the mesocolpia, thinning out near the colpi, finally to be absent at the colpi.

The inner sublayer, which is thinner than the outer one at the mesocolpia, is thickening near the colpi, reaching its greatest thickness at the colpi, especially around the endoapertures. The inner sublayer can be interpreted as endexine *sensu stricto* and will be referred to as endexine. It is rather thinly developed in *M. reticulatus* when compared with *M. sundaicus*: about 0.05 μm at the mesocolpia and 0.5 μm at the colpi, against 0.2 μm and 0.7 μm resp. for *M. sundaicus*. Whether this is due to the method of preparation or to a difference in maturity is not known. The contact between the two differently staining sublayers is the contact between the endexine (*s. str.*) and the ektexine.

The outer sublayer is the footlayer, ektexinous in nature, staining always the same as the outer structured layer of the exine. At the centre of the mesocolpia it measures up to 0.4 μm for *M. reticulatus* and up to 0.6 μm for *M. sundaicus*. Sometimes it is gradually slightly thickening to the colpi, but nearer to the colpi it is fastly thinning out.

As no TEM observations were made on other species, endexine and footlayer could not be studied separately there, but there is no reason to doubt a similar composition for these species.

The endexine at the aperture and the adjoining parts of the mesocolpia can be folded inwards, forming an apertural fold (Pl. IV fig. 4, 5; XI fig. 1), stretching and folding of which reflects harmomegathic functioning of the exine. Possibly also the folds of the intine, most clearly demonstrated in its inner sublayer, is related to this mechanism.

The outer structured layer of the wall is developed as an inner layer of columellae and an outer layer with a characteristic sculpture: the tectum; both are ektexinous in nature.

With LM the columellate layer appears as a thin layer separating tectum and endexine. In mesocolpal surface view the columellae are more or less distinct but in optical section of the grain they may be indistinct because of their small size. Of course with SEM and TEM the columellae are very distinct. Usually they are arranged in conformity with the pattern of sculptural elements of the tectum. Sometimes, as in *M. exangulatus*, they also stand free in the lumina (Pl. II fig. 6). In all species isolated pieces of ektexine are found on the apertural membrane.

In *M. reticulatus* the columellae are up to 0.3 μm high and 0.1—0.4 μm Ø (Pl. XIV—XVI fig. 1); in *M. sundaicus* they measure up to 0.4 μm high and 0.2—0.3 μm Ø (Pl. XVI fig. 2, 3). Generally they measure up to 0.4 μm high (rarely up to 0.5 μm); they are usually shortest near the apertures, the tectum descending to the level of the endexine there.

The sculpture of the tectum could be studied in detail in all species with SEM. Two types of sculpture were observed:

Type 1: In *M. exangulatus* the tectum is a two-dimensional system of muri, showing a reticulate pattern with relatively large, rounded lumina. Muri up to 0.9 μm wide, lumina up to 1.2 μm Ø.

Type 2: In all other species the tectum forms a three-dimensional system of more or less straight ridges, arranged in a regular criss-cross pattern, anastomosing in variable degree. In LM this may appear as a two-dimensional reticulate pattern. The structure of the tectum is loose in general, but especially along the apertures rather dense, having there fewer and smaller lumina and ridges joining in a subparallel pattern. The lumina in the outer part of the tectum are usually more angular and larger than those in the inner part (Pl. I fig. 1). They are relatively small compared with those in type 1, being usually not wider than the ridges. The variation in width of the ridges is 0.20—0.55 μm, in *M. reticulatus* down to 0.10 μm. There is a rather broad variation in the degree of anastomosis between the ridges: when they are less anastomosing, the sculpture has a somewhat rugulate appearance (Pl. V fig. 4, 5); when more anastomosing, the sculpture resembles that of type 1, being more or less two-dimensional, about reticulate, but with smaller lumina and ridges still distinguishable (see *M. reticulatus, M. pyriformis* subsp. *retusus* and *papuanus*).

In some samples, grains occur with an aberrant type of sculpture appearing more or less rugulate-verrucate (see: *M. sundaicus*). Sometimes it seems developed by later deposition of sporopollenine which lacked the normal control mechanism (see *M. anodontus, M. grandissimus*). As within the same sample these aberrant grains were gradually connected with normal grains, no special types have been distinguished.

The total thickness of the exine lies between 0.8 μm near the apertures and 1.6 μm at the centre of the mesocolpia.

In the unacetolysed sample of *M. reticulatus* it was noticed that the surface and cavities of the wall between columellae and on the tectum, could be filled with an electron dense substance which may be 'tryphine' (Pl. XV fig. 3).

The ektoapertures are meridionally oriented. Depending on the state of expansion of the grain they may be nearly closed or they can be open, showing much of the surface of the apertural membrane and endoaperture.

The ektoapertures are syncolpate (fig. 1a) or parasyncolpate (fig. 1b). In the latter situation an apocolpium is present, rather variable in size and shape, between the species, but also within one species and even in one grain. The apocolpium can be large, rounded triangular to triangular, or may consist of a few more or less isolated warts, its relative size, expressed in the ratio A/E (in which A = size of apocolpium and E = size of equatorial axis), varies from 0 to 0.63. When the apocolpium is large enough to contain a few ridges, the sculpture is like that of the mesocolpia. Otherwise it is a small piece of ektexine, more or less smooth, sometimes still with a few small lumina, or it consists of a few warty elements. The apocolpia (and mesocolpia) can be sharply or irregularly defined, in the latter case the edge being more or less warty (compare Pl. V fig. 4 and Pl. III fig. 2).

In a few species the pollen grains are sometimes pseudoparasyncolporate (fig. 1c and d) or, more rarely, colporate (fig. 1e), the apocolpium being connected with one (c), two (d), or three (e) mesocolpia, although the connections are often partial and irregular and the shape of the apocolpium remains more or less distinguishable.

Noteworthy is the occurrence of colporate grains in one sample of *M. sundaicus* in which the sculptural pattern is nearly perfectly continuous from one mesocolpium to another while an apocolpium is absent or hard to distinguish. These grains are connected by transitions with pseudoparasyncolporate grains in the same sample.

When an apocolpium is absent (syncolporate: fig. 1a) connections between mesocolpia were never observed.

Summarizing the condition of the ektoapertures and the apocolpium: the normal condition is syncolpate and, when an apocolpium is present, parasyncolpate. In the latter case connections between apocolpium and mesocolpia can arise, which are very variable, even within one grain, and are thought to be of minor taxonomic importance.

The endoapertures are situated on the equator and are variably developed, mostly approximately elliptic (long axis in equatorial plane) or approximately rounded, sometimes irregularly rounded (Pl. IV fig. 6; Pl. XI fig. 5, 6). Size varies between 2 and 5 μm. The endoapertures are more or less bridged by tectal connections between the adjoining mesocolpia. Possibly, the endexine is sometimes also making part of such a bridge (Pl. XVI fig. 1). The bridging may be complete or the margins of the ektoaperture may approach each other to a varying degree. Sometimes, the endoapertures are constricted-oval because of a protrusion of the endexine (Pl. IV fig. 6; Pl. XI fig. 5). For all species bridging of the endoaperture by tectal connections or by protruding parts of the endexine is a rather variable character.

Sectioned grains of *M. sundaicus* and *M. grandissimus*, and LM observations on all species show that the endoapertures are more or less rounded or elliptic holes, apart from the tectal connections which can bridge the endoaperture situated completely in the endexine (Pl. XVI fig. 1).

Except for TEM and SEM observations of sectioned grains, this description covers all species of the genus. Inter- and intraspecific differences will be described in the following account.

III. SYSTEMATIC DESCRIPTIONS

Mischocarpus anodontus (F. v. M.) Radlk.

Pl. I fig. 1—4; XII fig. 3.

Material studied. Australia: 1) *MEL 55975*; 2) *MEL 55973*; 3) *Betche s.n.* (L) 1896.

P/E 0.50 (0.58) 0.65, equatorial outline triangular with straight to slightly convex sides, number of apertures 3, tetracolporate: up to 1%, size P 13 (14.6) 17 μm, E 21 (24.9) 30 μm. Ektoapertures parasyncolpate, rarely syncolpate. Apocolpium about triangular, sometimes rounded or irregular, size up to 6 μm, A/E up to 0.24, sometimes connected with 1, 2 (pseudoparasyncolporate: fig. 1c and 1d, Pl. I fig. 2), or 3 (colporate: fig. 1e, Pl. I fig. 4) mesocolpia; sculpture as on mesocolpia, somewhat more dense, more or less sharply defined. Endoapertures 3—4 μm. Total exine thickness about 1.3 μm in the centre of the mesocolpia and up to 1.6 μm near the apertures. Columellae in LM more or less distinct, up to 0.3 μm high. Tectum with sculpture of type 2. Ridges are more than moderately anastomosing, 0.25—0.40 μm wide.

Comment. In a few grains of sample 3 an aberrant sculpture was met, somewhat resembling the strange sculpture seen in sample 1 of *M. grandissimus* (compare Pl. I fig. 4 with Pl. III fig. 4—6, and IV fig. 1, 2).

Mischocarpus exangulatus (F. v. M.) Radlk.

Pl. II; XII fig. 1, 2.

Material studied. Australia: 1) *Brass 2345* (BRI) 1932; 2) *Dallachy s.n., NSW 133902*; 3) *MEL 55978*, 1871.

P/E 0.55 (0.65) 0.78, equatorial outline rounded triangular to triangular with slightly convex sides, number of apertures 3; size P 12 (15.7) 18 μm, E 21 (23.8) 27 μm. Ektoapertures syncolpate or parasyncolpate. Apocolpium more or less rounded or warty, size up to 3 μm, A/E up to 0.13; sculpture about as on the margins of the mesocolpia or warty, irregularly defined. Endoapertures 2—4 μm. Total exine thickness about 1.2 μm in the centre of the mesocolpia and up to 1.6 μm near the apertures. Columellae with LM distinctly visible, up to 0.3 μm high, in single, sometimes double row supporting the muri (Pl. XII fig. 2); moreover, sometimes they stand isolated in the lumina, not connected with the muri (Pl. II fig. 6). Tectum with sculpture of type 1. The lumina are rounded and up to 1.2 μm; the muri are up to 0.9 μm wide. Locally, the muri may also resemble the ridges as seen in type 2, then showing a tectum with smaller (up to 0.7 μm) and more angular lumina and muri, more or less three-dimensionally arranged and 0.35—0.50 μm wide (Pl. II fig. 4). Sometimes these muri consist of 2—4 smaller subparallel ridges 0.1—0.2 μm wide (Pl. II fig. 2) (see comment). The sculpture near the apertures is more dense, the lumina being smaller there.

Comment. The compound muri do not occur elsewhere in *Mischocarpus*. It is noteworthy that this character is more distinctly expressed in *Arytera o'shanesiana* and *A. leichhardtii* (Van der Ham, 1977b).

Mischocarpus grandissimus (F. v. M.) Radlk.
Pl. III; IV; XII fig. 14, 15.

Material studied. Australia: 1) *Francis s.n., BRI 071281*, 1932; 2) *Volck 138*, Atherton Forestry Office Herbarium.

P/E 0.52 (0.62) 0.72, equatorial outline triangular with more or less convex sides, number of apertures 3. Size P 11 (13.8) 17 μm, E 19 (22.1) 24 μm. Ektoapertures parasyncolpate. Apocolpium triangular with straight or slightly convex sides, sometimes rounded triangular; size 3—8 μm, A/E 0.13—0.29; sculpture as on mesocolpia, irregularly defined, the edge consisting of warts which are more or less connected with the ridges of the apocolpium. Endoapertures 3—4 μm, Pl. IV (see: General Morphology). Total exine thickness about 1.2 μm in the centre of the mesocolpia and up to 1.6 μm near the apertures. Columellae in LM more or less distinct, up to 0.3 μm high. Tectum with sculpture of type 2. Ridges less than moderately anastomosing, 0.20—0.40 μm wide.

Comment. In sample 1 grains with an abnormally developed tectum were observed. The tectum is covered with huge verrucae up to 6 μm Ø and 4 μm high, consisting of ascending ridge-like elements like the poles supporting a wigwam. These ridge-like elements are 4—8 μm long (Pl. IV fig. 1, 2). All transitions can be found between grains with a normal tectum and grains with a tectum as described above (Pl. III fig. 4—6). The aberrant grains originated from a few anthers which contained hardly a normal grain; most anthers of sample 1 contain only normal grains. The cause of this strange ektexine deposition in some anthers is not known (see also under *M. anodontus*).

Mischocarpus lachnocarpus (F. v. M.) Radlk.
Pl. VI fig. 1, 2; XIII fig. 1, 2.

Material studied. Australia: 1) *Van Altena 3622* (L) 1966; 2) *Bailey 120* (BRI) 1904.

P/E 0.44 (0.53) 0.66, equatorial outline triangular with more or less convex sides, number of apertures 3. Size P 10 (12.5) 16 μm, E 22 (23.2) 25 μm. Ektoapertures parasyncolpate, sometimes syncolpate. Apocolpium mostly present, triangular to irregularly rounded, size up to 4 μm, A/E up to 0.18, sometimes more or less connected with 1 or 2 mesocolpia (pseudoparasyncolporate: fig. 1c, 1d), sculpture as on mesocolpia, somewhat more dense, sharply defined. Endoapertures 3—4 μm. Total exine thickness about 13 μm in the centre of the mesocolpia and up to 1.6 μm near the apertures. Columellae in LM more or less distinct, up to 0.5 μm high. Tectum with sculpture of type 2. Ridges moderately anastomosing, 0.25—0.40 μm wide.

Mischocarpus largifolius Radlk.

Pl. V fig. 4—6; XII fig. 4—6.

Material studied. New Guinea: 1) *NGF 23893* (L) 1965; 2) *NGF 17082* (L).

P/E 0.58 (0.74) 0.90, equatorial outline rounded triangular to triangular with rather convex sides, number of apertures 3; dicolporate: once, Pl. V fig. 6. Size P 13 (16.2) 20 μm, E 19 (21.8) 24 μm. Ektoapertures parasyncolpate. Apocolpium triangular with straight to slightly convex sides, size 5 (9) 12 μm, A/E = 0.23 (0.38) 0.63, sculpture as on mesocolpia, sharply defined. Endoapertures 3—4 μm. Total exine thickness about 1.1 μm in the centre of the mesocolpia and up to 1.6 μm near the apertures. Columellae in LM more or less distinct, up to 0.3 μm high. Tectum with sculpture of type 2. Ridges less than moderately anastomosing, 0.35—0.55 μm wide.

Mischocarpus paradoxus Radlk.

Pl. V fig. 1—3; XII fig. 7, 8

Material studied. New Guinea: 1) *C. T. White 586* (BRI) 1918; 2) *Carr 14265* (L) 1935; 3) *LAE 60073* (L) 1973.

P/E 0.52 (0.60) 0.69, equatorial outline triangular with slightly convex sides, number of apertures 3. Size P 12 (13.8) 16 μm, E 22 (23.2) 24 μm. Ektoapertures parasyncolpate. Apocolpium rounded to triangular, size 2—5 μm, A/E 0.09—0.22, rarely connected with one of the mesocolpia (pseudoparasyncolporate: fig. 1c), sculpture as on mesocolpia, somewhat more dense, sharply defined. Endoapertures 3—4 μm. Total exine thickness about 1.1 μm in the centre of the mesocolpia and up to 1.6 μm near the apertures. Columellae more or less distinct in LM, up to 0.3 μm high. Tectum with sculpture of type 2. Ridges somewhat more than moderately anastomosing, 0.20—0.35 μm wide.

Mischocarpus pentapetalus (Roxb.) Radlk.

Pl. VI fig. 3—6; XII fig. 12, 13

Material studied. 1) India: *Wallich Cat. 9035* (BM) 1829; 2) Thailand: *Kerr 4972* (L); 3) Sumatra: *Forbes 2475* (L); 4) *Junghuhn s.n.* (L); 5) *Van Rossum 64* (L); 6) *De Wilde c.s. 13902* (L) 1972; 7) *Yates 1305* (L); 8) Java: *Zollinger 507* (P); 9) *Meijer 2618* (L) 1954; 10) Sabah: *NBFD/SAN 43029* (L) 1964; 11) *NBFD/SAN 41544* (L) 1966; 12) *NBFD/SAN 56255* (L) 1966; 13) Philippines: *Wenzel 660* (BM) 1914; 14) *Elmer 7271* (K) 1906; 15) *Vanoverbergh 1175* (L) 1914; 16) *BS 45192* (BRI) 1925; 17) *PNH 2482* (A) 1947; 18) *Elmer 9320* (L).

P/E 0.40 (0.52) 0.62, equatorial outline triangular with straight to slightly convex sides, number of apertures 3; dicolporate rarely tetracolporate up to 1% (Pl. XII fig. 13). Size P 11 (13.5) 19 μm, E 21 (25.7) 2.95 μm (once 33 μm). Ektoapertures syncolpate, sometimes more or less parasyncolpate. Apocolpium nearly always absent. In a few samples there is a small apocolpium in up to 10% of the grains, consisting of a few warts which can be more or less connected with one of the mesocolpia (pseudoparasyncolporate: fig. 1c), size up to 2 μm, A/E to 0.08. Endoapertures 3—4 μm. Total exine thickness about 1.3 μm in the centre of the mesocolpia and up to 1.6 μm near the apertures. Columellae rather distinct in LM, up to 0.4 μm high. Tectum with sculpture of type 2. Ridges somewhat less than moderately anastomosing, 0,25—0.45 μm wide.

Comment. Many samples were prepared because this species proved to be macromorphologically rather variable, especially in N. Borneo and the Philippines (Van der Ham, 1977a). Before the taxonomic revision many species were distinguished that are now lumped together. In contrast to the macromorphological characters, pollen turned out to be very homogeneous, which supports the taxonomic decision.

Mischocarpus pyriformis (F. v. M.) Radlk.
Pl. VII; XIII fig. 8—12

Material studied. subsp. *pyriformis*. Australia: 1) *Swain s.n.*, *NSW 133895*, 1910; 2) *NSW 133886*, 1895. subsp. *papuanus* (Radlk.) Van der Ham. New Guinea: 3) *Brass 8508* (L) 1936; 4) *NGF 9180* (L) 1962. subsp. *retusus* (Radlk.) Van der Ham. New Guinea: 5) *NGF 27003* (L) 1965; *NGF 28455* (L) 1966.

P/E 0.50 (0.63) 0.80, equatorial outline rounded triangular to triangular with about straight sides, number of apertures 3; tetracolporate: up to 1% (Pl. VII fig. 1). Size P 13 (14.7) 17 μm, E 20 (24.2) 27 μm. Ektoapertures syncolpate or parasyncolpate. Apocolpium rounded triangular to irregularly rounded, or warty, size up to 5 μm, A/E up to 0.20, sometimes more or less connected with 1 or 2 of the mesocolpia (pseudoparasyncolporate, fig. 1c, d), sculpture rarely as on mesocolpia but more or less smooth or warty, more or less sharply defined. Endoapertures 3—4 μm. Total exine thickness 1.0—1.2 μm in the centre of the mesocolpia and up to 1.6 μm near apertures. Columellae more or less distinct in LM, up to 0.4 μm high. Tectum with sculpture of type 2. Ridges mostly more than moderately anastomosing, 0.20—0.40 μm wide.

Comment. There are a few infraspecific differences:

Equatorial outline in subsp. *pyriformis* is approximately triangular with nearly straight sides; in the other two subspecies it is rounded triangular to triangular with slightly convex sides.

Equatorial axis in subsp. *papuanus* is shorter than in the subsp. *pyriformis* and *retusus* (averages respectively: 21, 25.1, and 25.3 μm), with the same variation in the length of the polar axis resulting in a higher P/E value for subsp. *papuanus* (0.71 against 0.56, and 0.58 resp.).

Apocolpium in subsp. *retusus* nearly always present, rounded triangular to irregularly rounded, rarely warty, sometimes connected with one or two mesocolpia, size up to 5 μm, A/E up to 0.20; while the apocolpium in the other two subspecies is absent or small, size up to 2 μm, A/E up to 0.08, mostly warty, sometimes irregularly rounded, not connected with mesocolpia

Sculpture: ridges in subsp. *papuanus* and *retusus* and sample 1 of subsp. *pyriformis* more than moderately anastomosing; in sample 2 of subsp. *pyriformis* ridges about moderately anastomosing.

It thus appears that here the subspecific distinctions based on macromorphology are, to a certain extent, supported by pollen morphological differences.

Mischocarpus reticulatus (Radlk.) Van der Ham
Pl. VIII; XIII fig. 13, 14; XIV; XV; XVI fig. 1

Material studied. New Guinea: 1) *Hartley 12237* (L) 1963; 2) *Hartley 12534* (L) 1963; 3) *Clemens 3093* (A) 1936.

P/E 0.60 (0.71) 0.80, equatorial outline rounded triangular to triangular with slightly convex sides, the pores sometimes protruding, number of apertures 3; tetracolporate: up to 4%. Size P 18 (19.5) 21 μm, E 25 (27.7) 31 μm. Ektoapertures syncolpate or parasyncolpate, rather narrow. Apocolpium about triangular or irregularly rounded, sometimes warty, size up to 4 μm, A/E up to 0.14, sometimes connected with 1, 2, or 3 mesocolpia (pseudoparasyncolporate: fig. 1c and 1d, or colporate: fig. 1e), sculpture about as on the margins of the mesocolpia, sharply or irregularly defined. Endoapertures 3—5 μm. Total exine thickness 0.8—1.2 μm in the centre of the mesocolpia and up to 1.6 μm near the apertures. Columellae rather distinct in LM, up to 0.3 μm high and 0.1—0.4 μm Ø. Tectum with sculpture of type 2. Ridges mostly strongly anastomosing, sometimes in such a way that separate ridges are hardly distinguishable and the sculpture then has a 2-dimensional, somewhat reticulate appearance with small lumina. The latter is in contrast with *M. exangulatus*, the pollen of which has also a reticulate sculpture but with much larger lumina. At the margins of the mesocolpia the sculpture becomes more dense, the ridges being less wide and the lumina very small or absent. Ridges near apertures and on apocolpium 0.10—0.25 μm wide, and in the centre of the mesocolpia 0.25—0.40 μm wide.

Comments. In all samples the grains are more or less irregularly shaped. There are only few grains with a regular shape. The wall of the grain seems to dent easily and many grains are totally collapsed when being prepared for scanning. This may be caused by the rather thin wall.

Noteworthy is the observation of the presence of a tryphinelike covering of the tectum (Pl. XV fig. 3).

Mischocarpus sundaicus Bl.

Pl. IX; X; XI; XIII fig. 3—7

Material studied. Acetolysed. 1) Thailand: *Geesink 5245* (L) 1973; 2) Vietnam, Tonkin: *Bon 1683* (P) 1882; 3) India: *Helfer 117* (L) 1836—38; 4) Sumatra: *HB 4557* (L); 5) Java: *Saimaendt 32* (L); 6) Philippines: *BS 38759* (BRI) 1920; 7) Flores: *Schmutz 2021* (L) 1968; 8) New Guinea, Biak: *BW 9661* (L) 1959; 9) New Britain: *NGF 26720* (L) 1966; 10) Milne Bay Dist.: *NGF 16846* (L) 1964; 11) Sudest Isl.: *Brass 28207* (L) 1956; 12) Australia: *Brass 19266* (L) 1948.

Not acetolysed. 13) Vietnam, Amman: *Pételot 8863*; 14) *Chevalier 40473*; 15) *Poilane 6019*; 16) Cochinchine: *Pierre 5/1866*; 17) Laos: *Kerr 21296*; 18) Thailand: *Kerr 17374*; 19) *Put 2901*.

P/E 0.54 (0.65) 0.80, equatorial outline rounded triangular to triangular with more or less convex sides, number of apertures 3; rarely dicolporate, tetracolporate: sometimes up to 3%. Size P 13 (15.3) 18 μm, E 20 (22.9) 26 μm. Ektoapertures syncolpate or parasyncolpate, rarely colpate. Apocolpium very variable: from triangular with straight sides to rounded triangular, or irregularly shaped, sometimes warty, size up to 8 μm, A/E up to 0.34. Occasionally, the apocolpium is connected with one or two (pseudoparasyncolporate: fig. 1c and 1d; Pl. IX fig. 5), or three (colporate: fig. 1e; Pl. IX fig. 1—4) mesocolpia. The sculpture of the apocolpium is generally the same as on the mesocolpia, although mostly somewhat more dense. The margins are sharply or irregularly defined. Endoapertures 2—5 μm. Total exine thickness about 1.2 μm in the centre of the mesocolpia and up to 1.6 μm near the apertures. Columellae in LM more or less distinct, up to 0.4 μm high and 0.2—0.3 μm Ø. The tectum is rather variably developed in this species. It mostly occurs as described under type 2, with moderately anastomosing ridges, but also different sculptures are present. Sometimes, ridges are strongly anastomosing (Pl. X fig. 4), the sculpture may be rugulate-verrucate (*Brass 19266*) while ridges are hard to recognize, being shortened and widened. In other cases a more or less warty sculpture is observed, while lumina are much smaller or absent, resulting in a tectum which is nearly or completely closed and covered with warty elements (*BW 9661* and *NGF 16846*; Pl. IX fig. 6; X fig. 5, 6). Ridges in sculpture of type 2 are 0.20—0.45 μm wide; the widened ridges in the aberrant sculpture are up to 0.60 μm wide; the warts sometimes occurring up to 1 μm ⌀. As the aberrantly sculptured grains are connected by transitions with normal grains within the same sample no special type has been recognized for *BW 9661* and *NGF 16846*.

Comment. Noteworthy is the occurrence of colporate grains in *Geesink 5245*. In contrast with all other observations (*M. anodontus*, *M. reticulatus*) of colporate grains, where connections between apocolpium and mesocolpia are irregular or partial, the sculpture is regularly continuous from one to the other mesocolpium, the shape of an apocolpium being not or hardly distinguishable (Pl. IX fig. 1—4). The grains in this sample can therefore be referred to type A (tricolporate) as defined by Muller & Leenhouts (1976).

Infraspecific variation. The pollen of *M. sundaicus* is rather variable in several aspects. Apocolpium: pseudoparasyncolporate and colporate grains occur especially in samples from western parts of the area of distribution of the species (sample 1—6), rarely in eastern regions. The apocolpium is mostly absent or small in western regions and rarely absent, small to large in eastern regions. Sculpture: as already mentioned it is rather variable. It is noteworthy that samples with grains with a sculpture of type 2, with ridges which are moderately anastomosing, mostly come from western regions (also the only sample from Australia has this sculpture, although with more than moderately anastomosing ridges). Samples with grains with a rugulate-verrucate sculpture occur in New Guinea (samples 8—11).

Summarizing, we can recognize certain geographically based trends in the pollen of *M. sundaicus*. In western regions pollen is often pseudoparasyncolporate or colporate, the apocolpium is mostly absent, A/E rarely up to 0.26, the sculpture is of type 2, with moderately anastomosing ridges. In eastern regions pollen is rarely pseudoparasyncolporate and never colporate, the apocolpium is rarely absent, A/E up to 0.34, the sculpture is often aberrant: rugulate-verrucate (New Guinea) or with ridges which are more than moderately anastomosing (Australia).

The trends in pollen morphology are not connected with macromorphological variation.

Mischocarpus triqueter Radlk.

Pl. I fig. 5, 6; XII fig. 9—11

Material studied. Philippines: 1) *BS 21985* (K) 1913; 2) *FB 1871*, 1904.

P/E 0.56 (0.62) 0.70, equatorial outline about triangular with slightly convex sides, number of apertures 3, Size P 13 (14.8) 16 μm, E 22 (23.6) 25 μm. Ektoapertures syncolpate, sometimes more or less parasyncolpate. A small apocolpium is sometimes present, consisting of a few warts which are more or less connected with one of the mesocolpia (pseudoparasyncolporate: fig. 1c), size up to 1 μm, A/E up to 0.04. Endoapertures 3—5 μm. Total exine thickness 1.0—1.2 μm in the centre of the mesocolpia and up to 1.6 μm near the apertures. Columellae more or less distinct in LM, up to 0.3 μm high. Tectum with sculpture of type 2. Ridges moderately anastomosing, 0.25—0.40 μm wide.

IV. THE POLLEN TYPE OF MISCHOCARPUS

When we combine data about variation in shape (P/E), equatorial outline, and apertures, we obtain a general picture of pollen of *Mischocarpus* which is not wholly conform any of the pollen (sub)types distinguished by Muller & Leenhouts (1976) as demonstrated in table 1.

Except for a type of pollen occurring rarely in *M. sundaicus*, which will be discussed later, the pollen of *Mischocarpus* closely agrees with type B, which is widespread in the tribe *Cupanieae*. However, it is neither like subtype B1, for the equatorial outline is never rounded, nor like subtype B2, for the endoapertures are never reduced. Therefore a third subtype, B3, is distinguished for *Mischocarpus*. The possible relations between these subtypes are shown in fig. 2.

The subtype B3 can be syncolporate as well as parasyncolporate. The pseudoparasyncolporate and colporate grains sometimes occurring are transitional with parasyncolporate grains: fig. 2b—e (see also general morphology: apocolpium). The fact that parasyncolporate and syncolporate grains are closely related is demonstrated in some species, samples, or even single grains where both situations occur together. The syncolporate B3 subtype can be most easily connected with subtype B1. There is only a difference in equatorial outline. An important role is played in the diagram figure 2 by one sample of *M. sundaicus: Geesink 5245*, which much resembles pollen type A, as distinguished by Muller & Leenhouts (1976). Here, colporate pollen grains occur in which

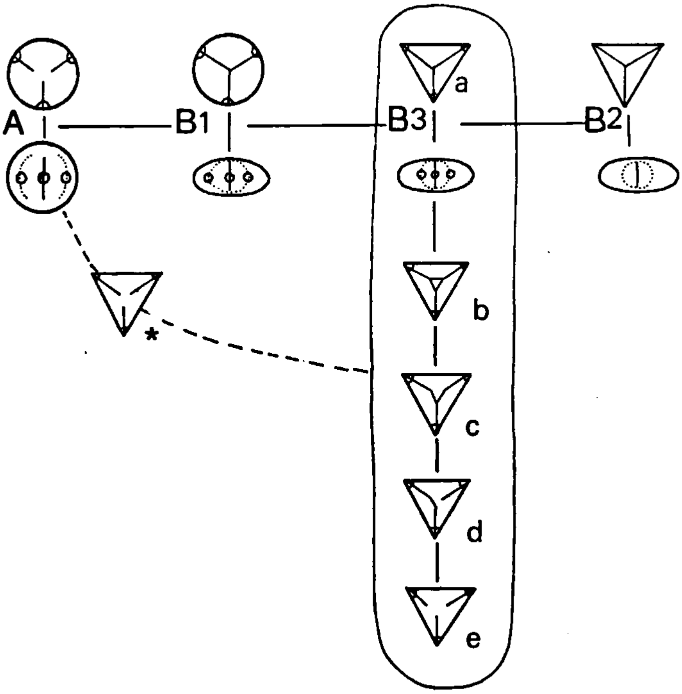


Fig. 2. A, B1, and B2: pollen types as distinguished in Muller & Leenhouts (1976). B3 a—e: pollen type of *Mischocarpus* with subtypes; a. syncolporate; b. parasyncolporate; c and d. pseudoparasyncolporate; e. colporate.: *M. sundaicus, Geesink 5245*, a type transitional between A and B3.

TABLE 1

character \ pollen-type	A	transitional A-B	B1	B2	Mischocarpus
shape	spherical	spherical	oblate	oblate	oblate
ektoapertures	colpate	syncolpate	syncolpate	syncolpate	syncolpate, rarely colpate
endoapertures	not reduced	(not reduced)	not reduced	reduced	not reduced
equatorial outline	rounded	rounded	rounded	triangular	rounded triangular to triangular

TABLE 4. Presence or absence and size of apocolpium

M. pentapetalus	West ↑	in nearly all samples absent; in a few small, warty. A/E up to 0.08
M. triqueter		in each sample sometimes a small, warty apocolpium present. A/E up to 0.04
M. paradoxus		always present. A/E 0.09--0.22
M. largifolius		always present. A/E 0.23 (0.38) 0.63
M. reticulatus		in one sample rarely, in the others mostly present. A/E up to 0.14
M. grandissimus	↓ East	always present. A/E 0.13--0.29

the sculpture at the poles is completely continuous to the three mesocolpia. This is in contrast with colporate pollen observed in *M. anodontus*, *M. reticulatus*, and other samples of *M. sundaicus*, where an apocolpium is still distinguishable because the sculpture at the poles is incompletely continuous to the three mesocolpia. As pseudoparasyncolporate grains occur also in *Geesink 5245*, colporate pollen from this sample can be easily placed in the series b—e (fig. 2). But as colporate pollen in this sample is different from colporate pollen observed in the other samples and much resembles pollen of type A, *Geesink 5245* can be as easily placed in between type A and subtype B3. So, subtype B3 is connected with type A, although only by one sample, as well as with subtype B1. Subtype B2 is more closely connected with subtype B3 than with subtype B1.

V. POLLEN MORPHOLOGY AND GEOGRAPHY

When the pollen characters are arranged in a table, hardly any significant correlation between them can be found. Rather self-evident is a correlation between shape (P/E) and equatorial outline of the grains: in general, species with a P/E value higher than 0.65 have a rounded triangular outline; those in which P/E is lower have an approximately triangular outline. However, a correlation between some characters and geographical data has been observed. This is especially clear when we compare the presence or absence and size of the apocolpium and the sculpture of the grain with the geographical origin as shown in table 2.

From table 2 we see that in the western regions an apocolpium is mostly absent and, when present, it is mostly very small. In the eastern regions, it is generally present in all species. This holds true also for *M. sundaicus* which occurs in both western and eastern regions.

Sculpture. We can recognize groups of species in which the sculpture is very much alike. The pattern of sculpture largely depends on the degree of anastomosing of the ridges and is shown in table 3 in relation to the origin of the samples. In the western regions the ridges are always moderately anastomosing. In the eastern regions sculpture is much more variable in this respect; ridges are from less than moderately anastomosing (approximately rugulate) to reticulate. *M. sundaicus* occurs in both regions; in the eastern regions, the ridges are more anastomosing than in the western regions.

In the eastern regions, sculpture can be aberrant in *M. sundaicus*, *M. anodontus*, and *M. grandissimus* (see: Systematic descriptions). However, the correlation with geography is less distinct for this character than for the preceding one.

Summarizing, we may say that some characters (presence or absence and size of apocolpium, sculpture) are more or less correlated with geography, and a difference between the western and eastern part of the area is apparent. Although both presence or absence and size of apocolpium and sculpture, in the same way are correlated with geography, their mutual correlation is less striking.

VI. POLLEN MORPHOLOGY AND TAXONOMY

In the recent revision of *Mischocarpus* (Van der Ham, 1977a), the following 5 groups, three of which are monotypic, were distinguished:

group 1.	sundaicus-group:	*M. sundaicus*
		M. lachnocarpus

TABLE 2. Presence or absence and size of apocolpium

	western regions: west of New Guinea	
M. sundaicus	in most samples absent, in few small	A/E rarely up to 0.26
M. pentapetalus	generally absent, in a few small, warty	A/E up to 0.08
M. triqueter	in each sample sometimes a small, warty apocolpium present	A/E up to 0.04
	eastern regions: New Guinea and Australia	
M. anodontus	generally present	A/E up to 0.24
M. exangulatus	present or not	A/E up to 0.13
M. grandissimus	always present	A/E 0.13--0.29
M. largifolius	always present	A/E 0.23 (0.38) 0.63
M. lachnocarpus	in one sample always, in the other mostly present	A/E up to 0.18
M. paradoxus	always present	A/E 0.09--0.22
M. pyriformis subsp. pyriformis	absent or small	A/E up to 0.08
subsp. papuanus	absent or small	A/E up to 0.08
subsp. retusus	generally present	A/E up to 0.20
M. reticulatus	in one sample rarely, in the others mostly present	A/E up to 0.14
M. sundaicus	generally present	A/E up to 0.34

group 2. pentapetalus-group: *M. pentapetalus*
M. triqueter
M. largifolius
M. paradoxus
M. reticulatus
M. grandissimus
group 3: *M. pyriformis*
group 4: *M. anodontus*
group 5: *M. exangulatus*

These groups could be phylogenetically related on the basis of more primitive and more advanced character states (cf. Van der Ham, 1977a: Infrageneric structure). However, the groups distinguished on macromorphology find no support in pollen morphology, except for group 5, *M. exangulatus*, which is macromorphologically rather deviating,

TABLE 3. Distribution of sculpture

ridges	species	area of distribution
less than moderately anastomosing (about rugulate)	M. grandissimus	Australia
	M. largifolius	New Guinea
moderately anastomosing	M. sundaicus	West of New Guinea
	M. pentapetalus	West of Moluccas
	M. triqueter	Philippines
	M. lachnocarpus	New Guinea + Australia
	M. paradoxus	New Guinea
	M. pyriformis subsp. pyriformis	Australia
more than moderately anastomosing	M. sundaicus	Australia
	M. pyriformis subsp. pyriformis	Australia
	subsp. papuanus	New Guinea
	subsp. retusus	New Guinea
	M. paradoxus	New Guinea
	M. anodontus	Australia
much more than moderately anastomosing to reticulate	M. reticulatus	New Guinea
reticulate	M. exangulatus	Australia

being one of the most derived groups, and is also pollen morphologically different by its unique reticulate sculpture. Whether this reticulate sculpture is derived cannot be said.

Concerning the relations within the groups, we can say that the clear correlation, found in group 2, between the level of macromorphological development and geography, can also be detected in the pollen morphology of the group. It was already concluded that in the genus there was a correlation between the presence or absence and size of the apocolpium, and geography. Now we take a special look at the species of group 2. In table 4 the species are arranged from west to east.

We see that in the macromorphologically most primitive species, *M. pentapetalus*, the pollen is nearly always syncolporate, while the pollen of the eastern more derived species generally possess a more or less large apocolpium (parasyncolporate), sometimes even very large as in *M. largifolius*.

Aberrant in this series is *M. reticulatus*, since the data about the apocolpium do not fit very well. As macromorphologically *M. reticulatus* is the most derived species of the group, one should expect a constantly present, large apocolpium; it is small and often absent, however. Also in the following characters the pollen of this species is isolated: relatively high percentages of tetracolporate pollen (up to 4%); the largest pollen in the genus, average 27.7 μm (against 25.7 μm for *M. pentapetalus*, the next largest); a relatively thin wall; a different sculpture. Macromorphologically, especially the floral characters isolate this species and suggest a shift to some other pollinator than is usual in the other species. Probably pollen forms an important part in the changed mechanism of pollination, resulting in a number of deviating characters.

Noteworthy is the fact that the pollen of *M. triqueter*, which species largely follows *M. reticulatus* in floral characters, hardly resembles the pollen of the latter. It is, however, very close to pollen of *M. pentapetalus*, to which species *M. triqueter* is geographically closely bound in the Philippines.

Concerning the sculpture we can say that *M. sundaicus* and *M. pentapetalus*, species which were macromorphologically found to be the most primitive in *Mischocarpus*, have a type of sculpture in which the ridges are moderately anastomosing (*M. sundaicus* only as far as the western collections are concerned; the origin of *M. sundaicus* is supposed to lie in western regions!). In species (or groups) which are more derived, and occur in eastern regions, much more variation was noticed in this character: from about rugulate in *M. largifolius* to reticulate in *M. exangulatus*.

Returning now to figure 2, we come to the following interpretation of the diagram: From the results obtained in group 2, in which the most primitive species has syncolporate and the more derived species have parasyncolporate pollen, we can suppose that probably a syncolporate grain is more basal than a parasyncolporate one, within the limits of group 2. The following facts indicate that this conclusion can be applied more generally. *M. sundaicus*, close to the most primitive species of group 2, has mostly syncolporate pollen in western regions; here the primary centre of radiation for group 1 and 2 is supposed to lie (based on macromorphological evidence). In the eastern regions, pollen of *M. sundaicus* and of the slightly more derived *M. lachnocarpus* (group 1) are mostly parasyncolporate.

Also the other groups, 3, 4, and 5, of which 3 and 5 are macromorphologically more derived, have parasyncolporate pollen.

The series b—e in fig. 2 cannot be seen otherwise than as a range of variability, closely connected with the presence of an apocolpium.

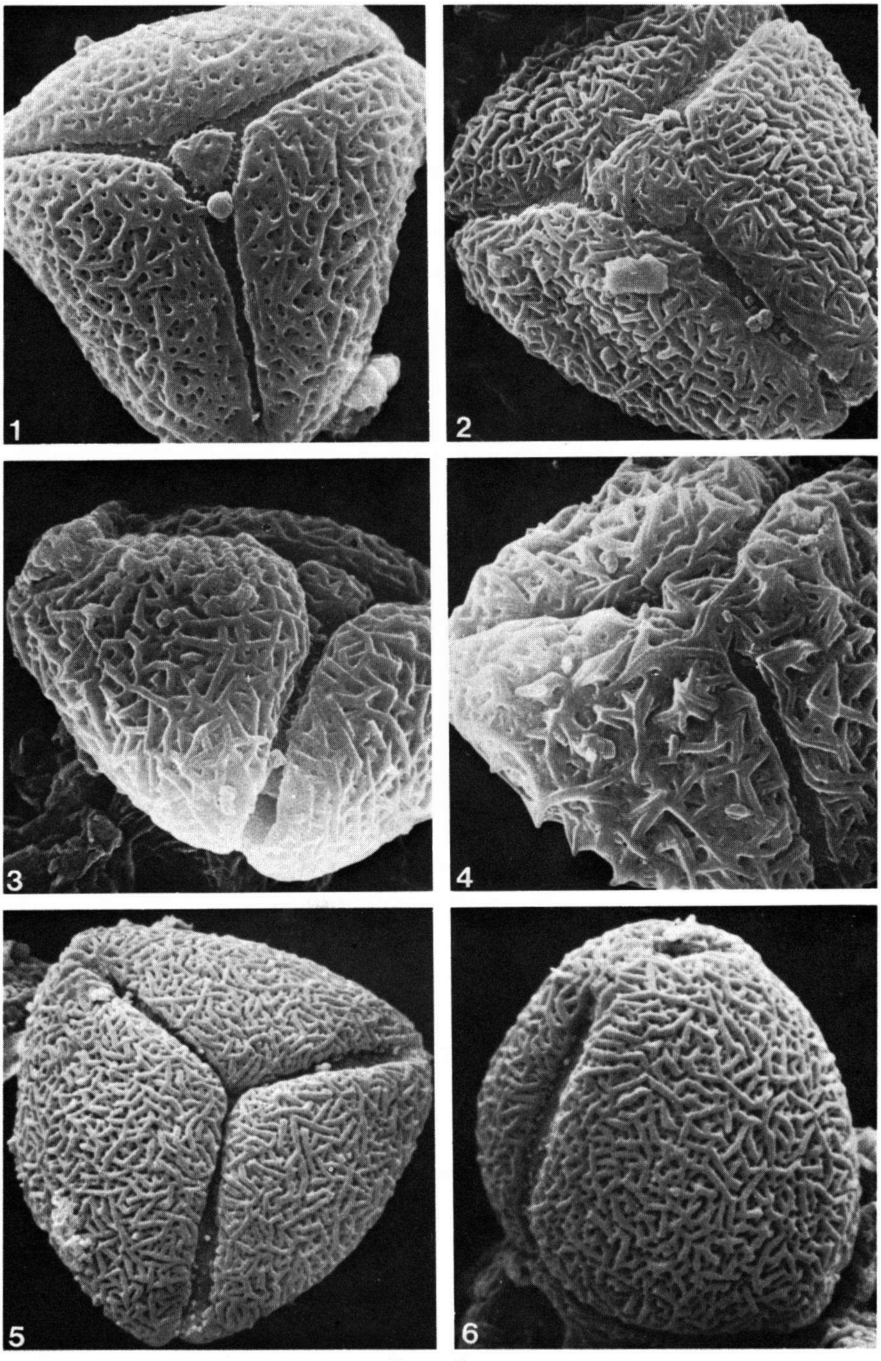


PLATE I

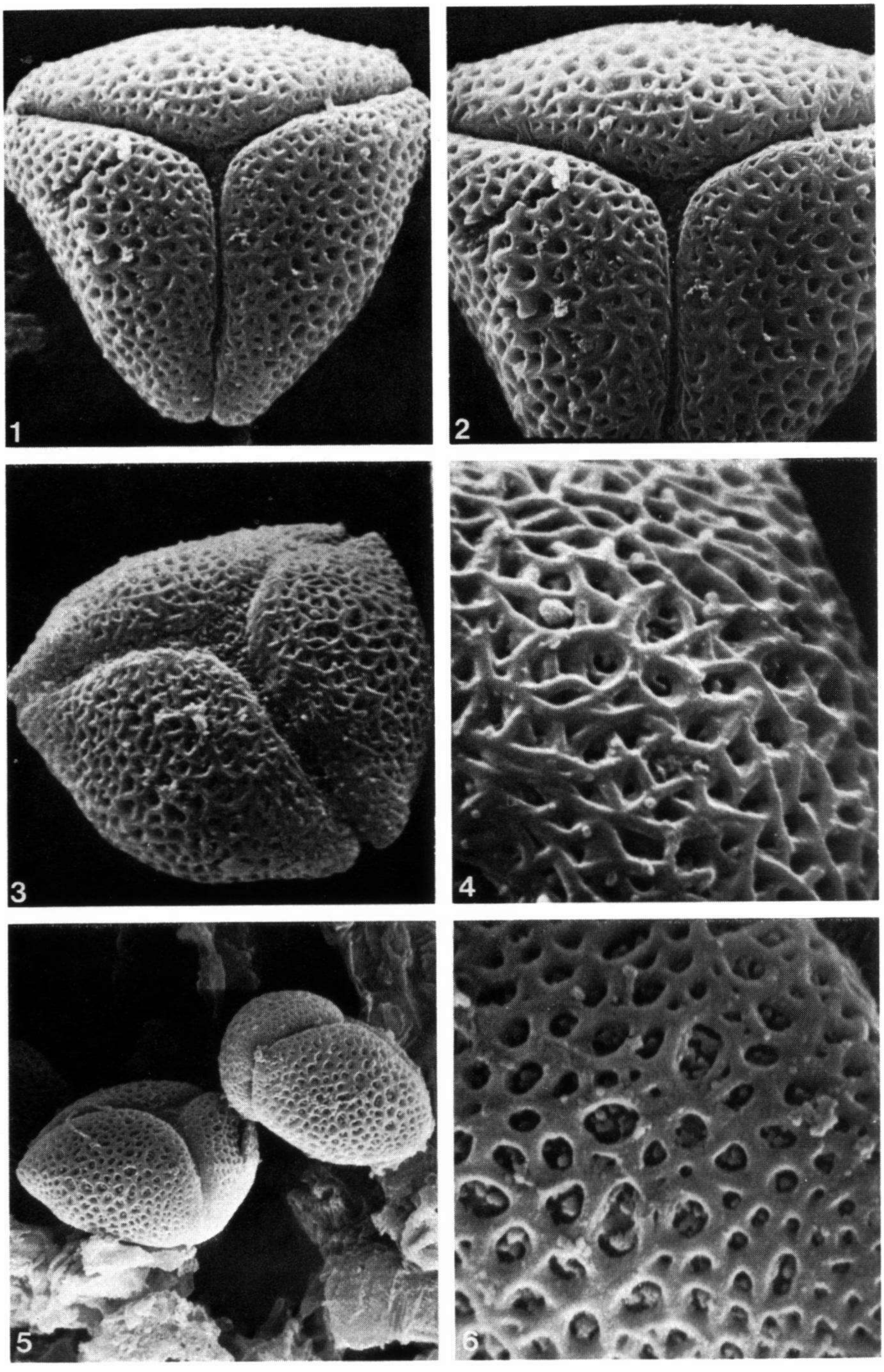
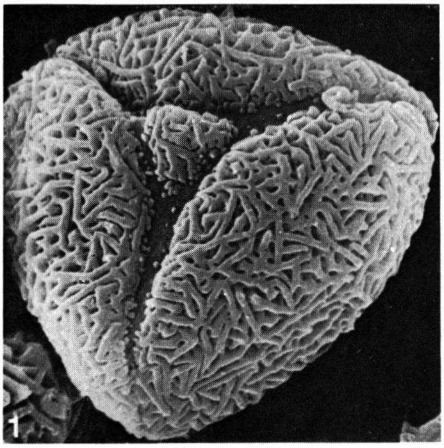
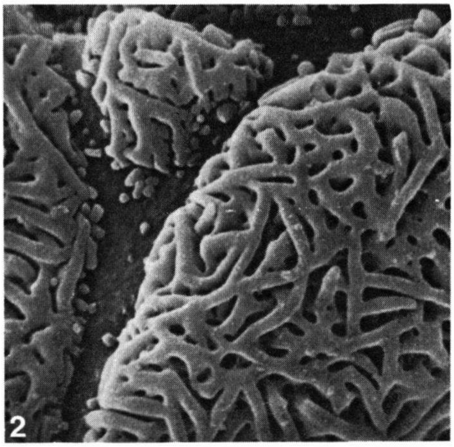
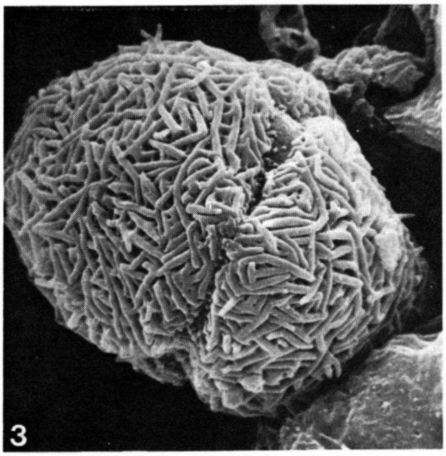
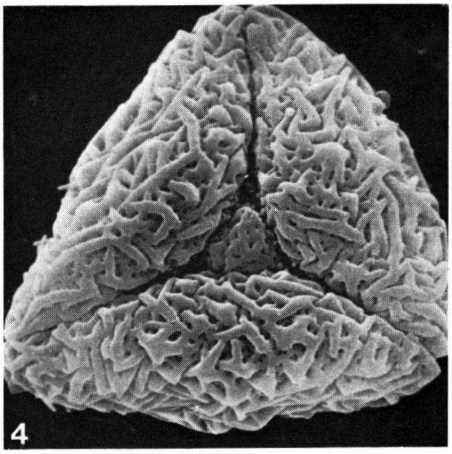


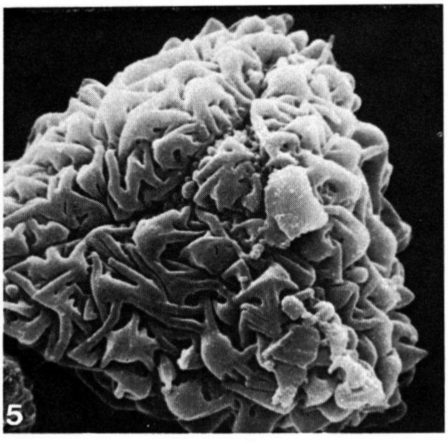
PLATE II











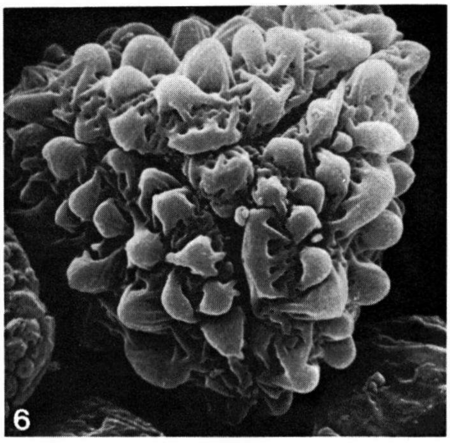


Plate III

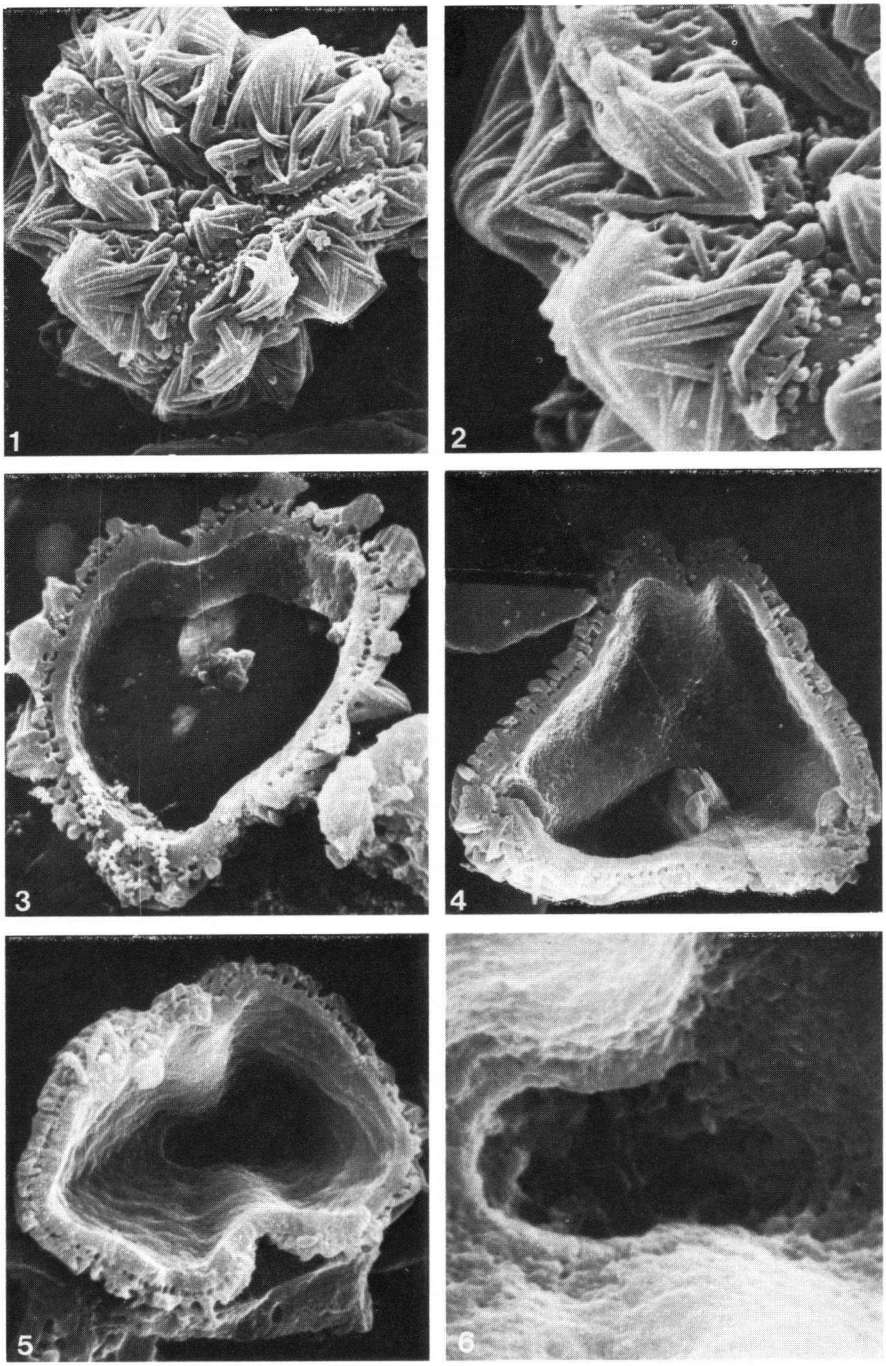
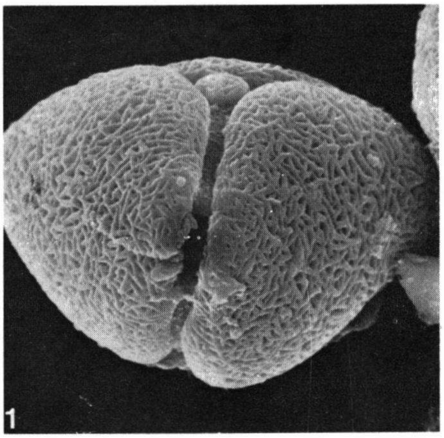
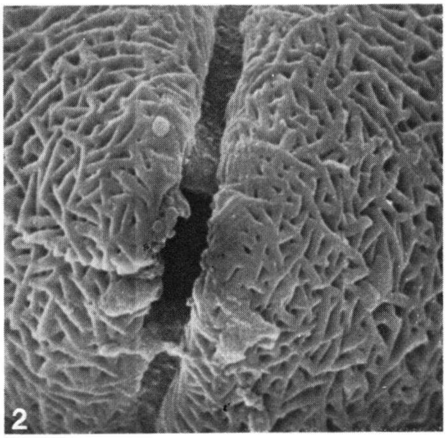


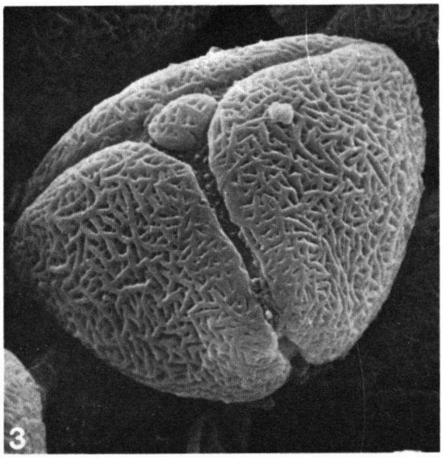
PLATE IV



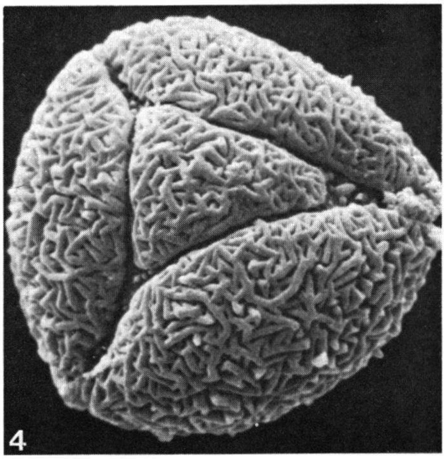
1



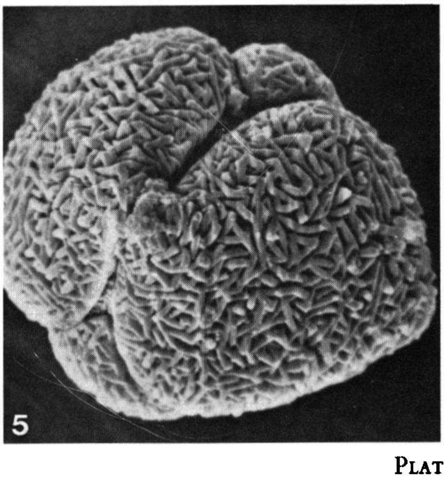
2



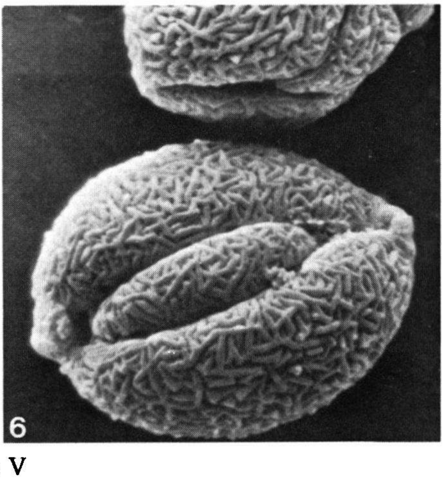
3



4

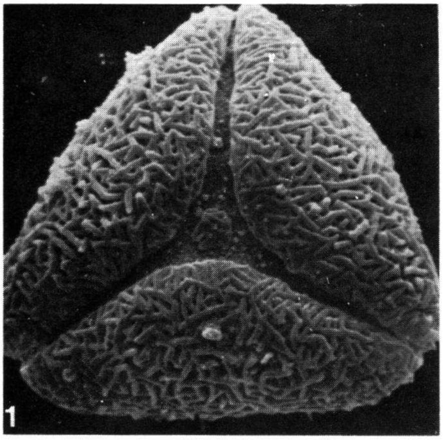


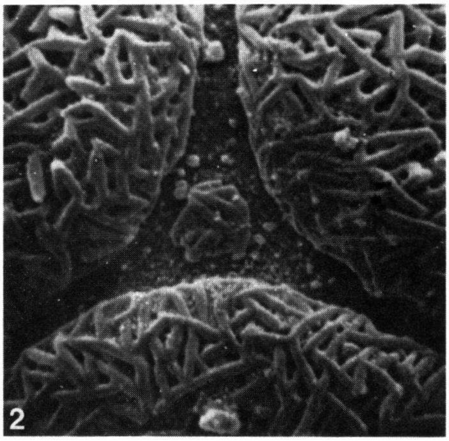
5

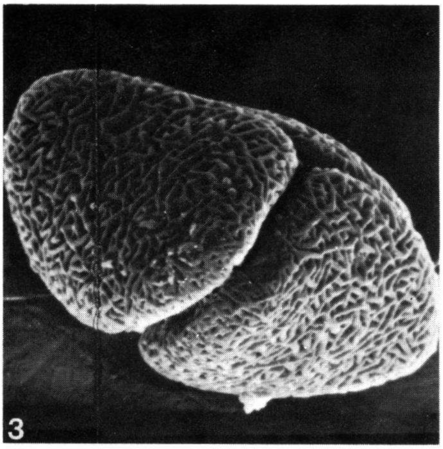


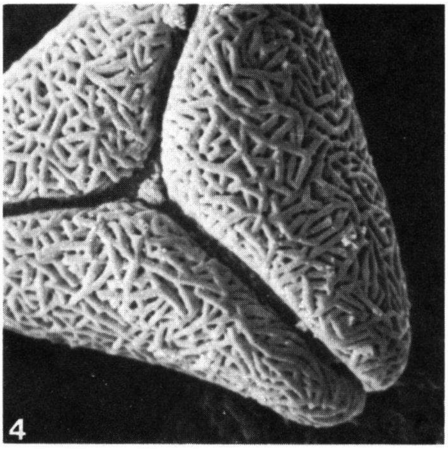
6

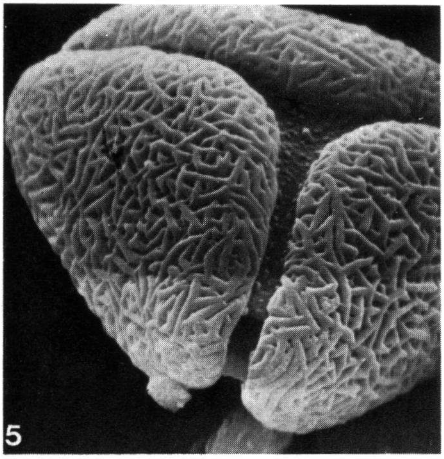
PLATE V











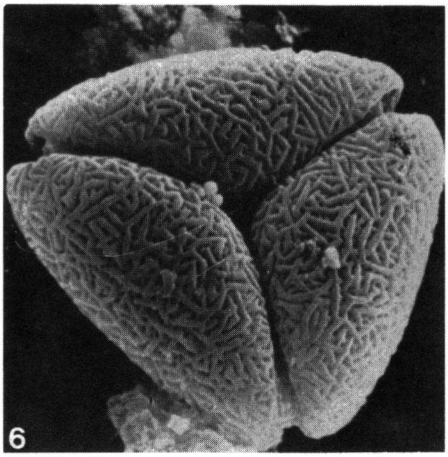
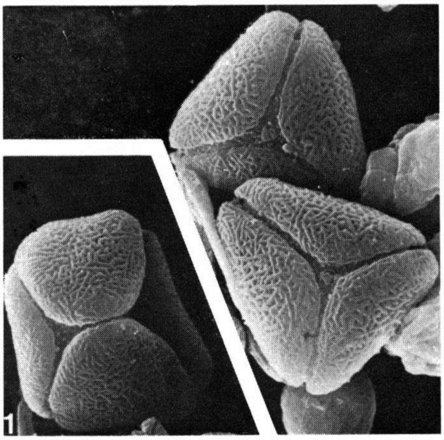
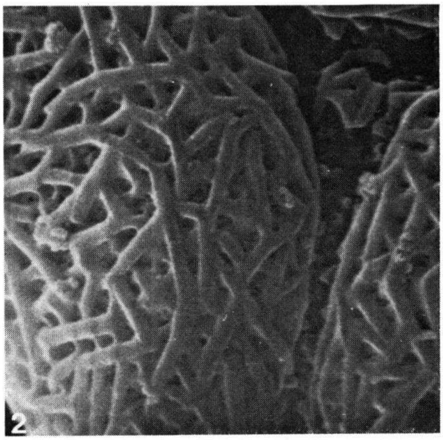
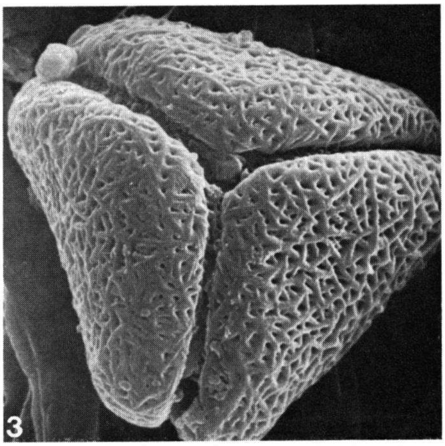
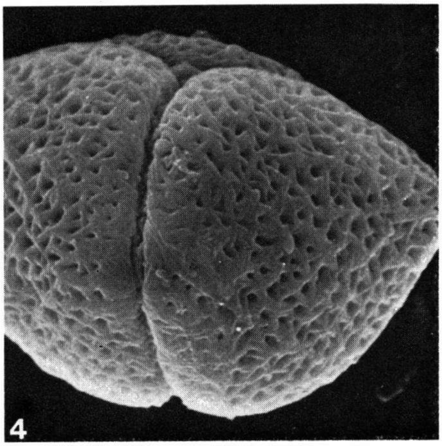


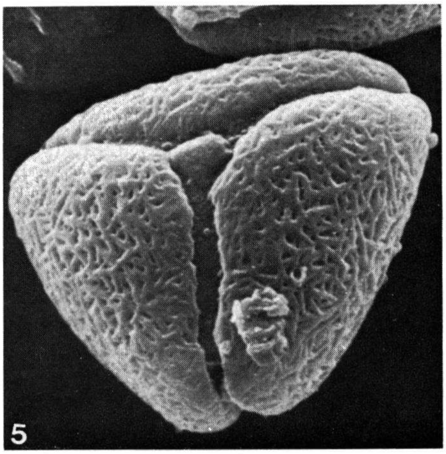
PLATE VI











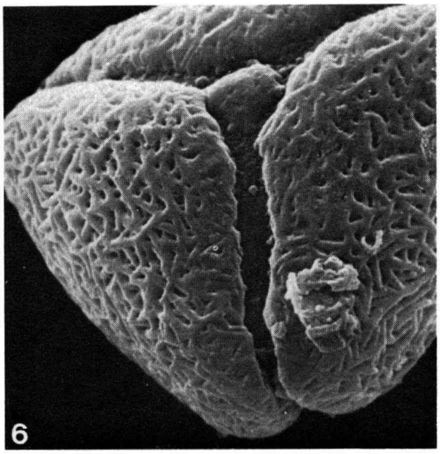


PLATE VII

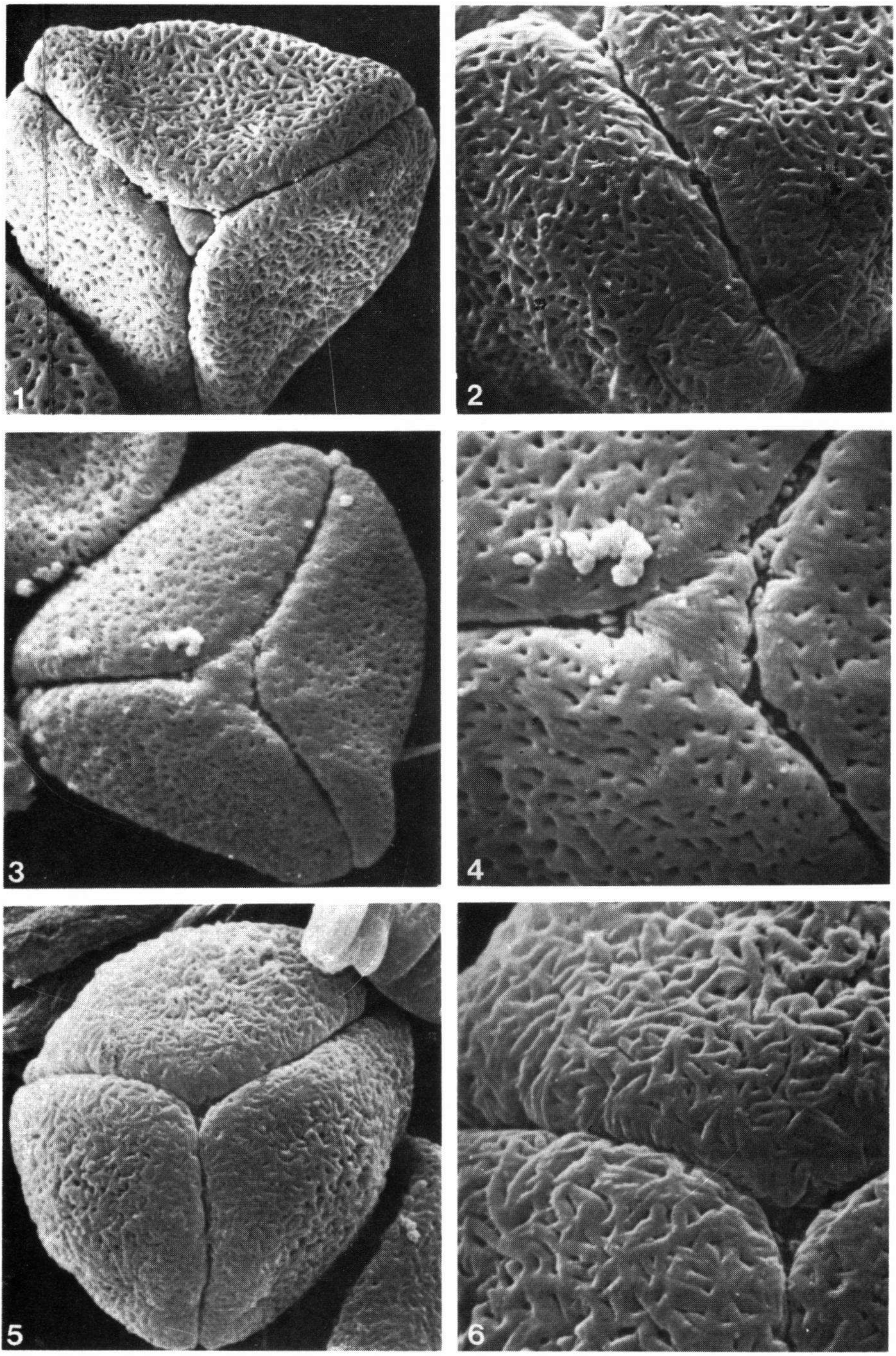
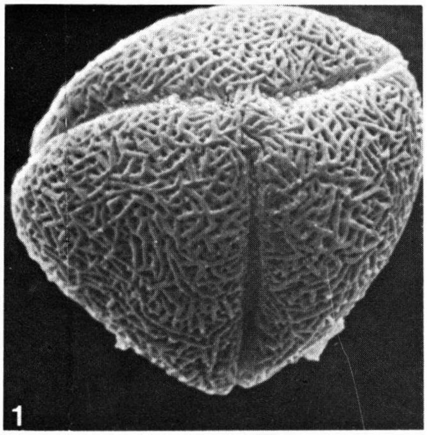
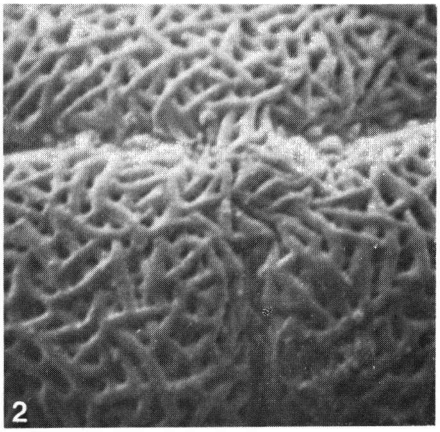
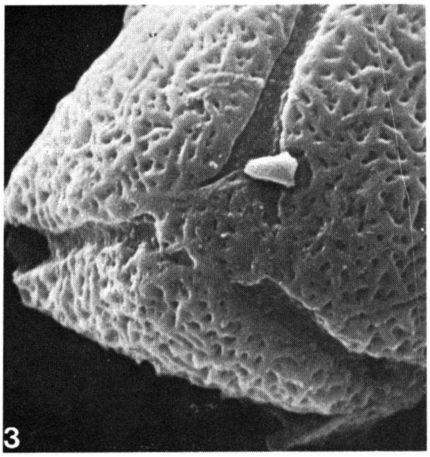
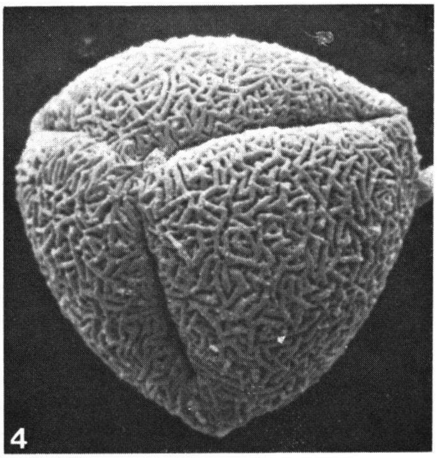


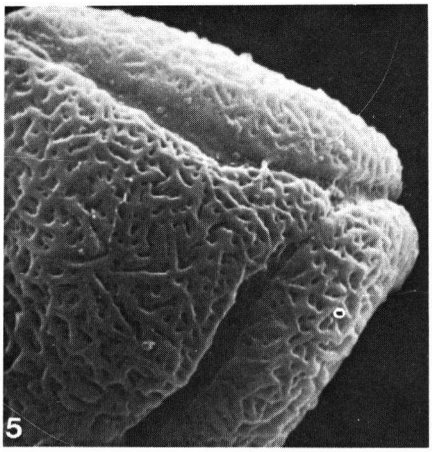
Plate VIII


1


2


3


4


5

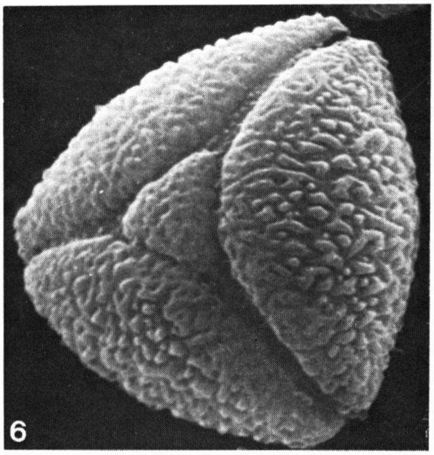

6

PLATE IX

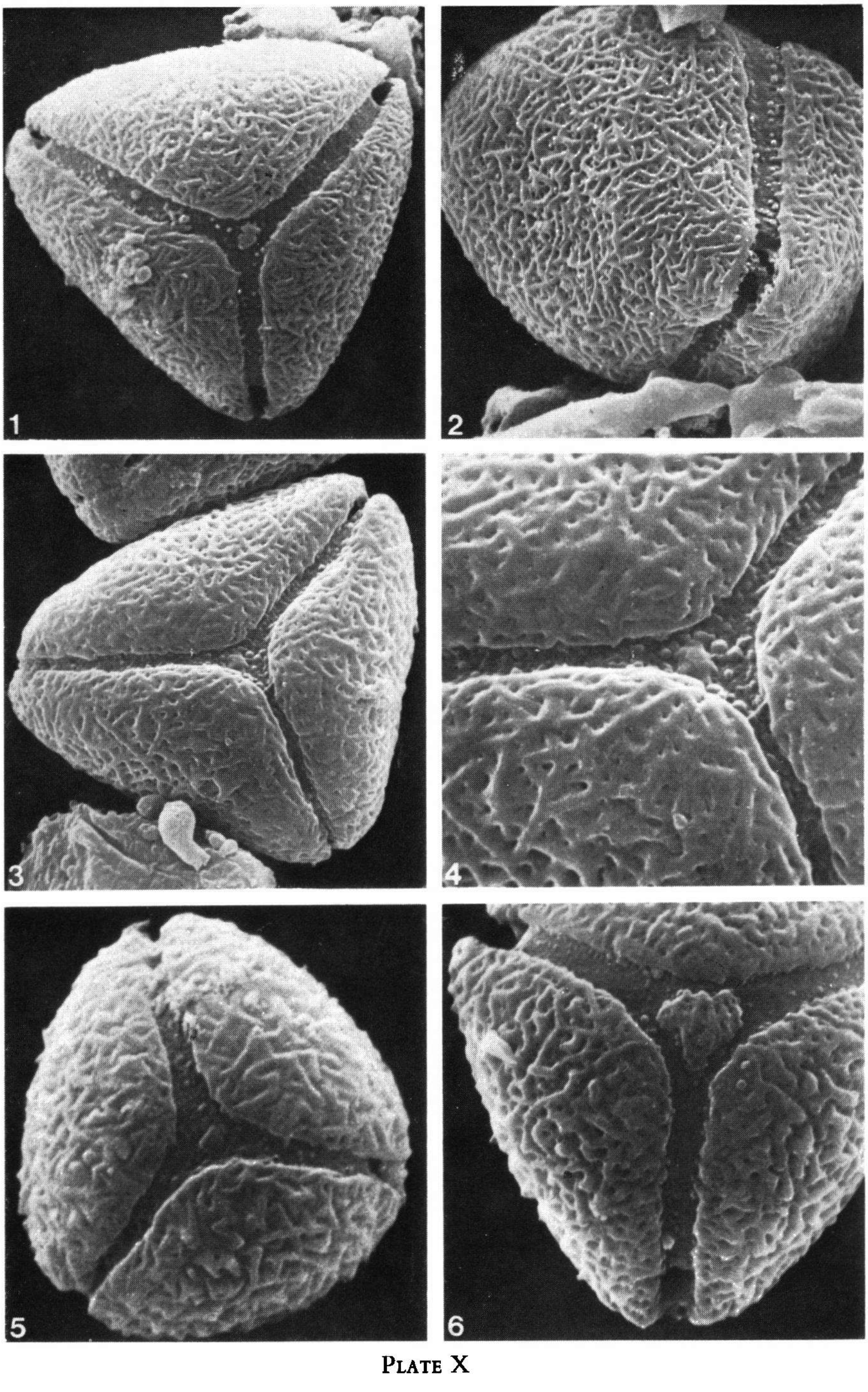


PLATE X

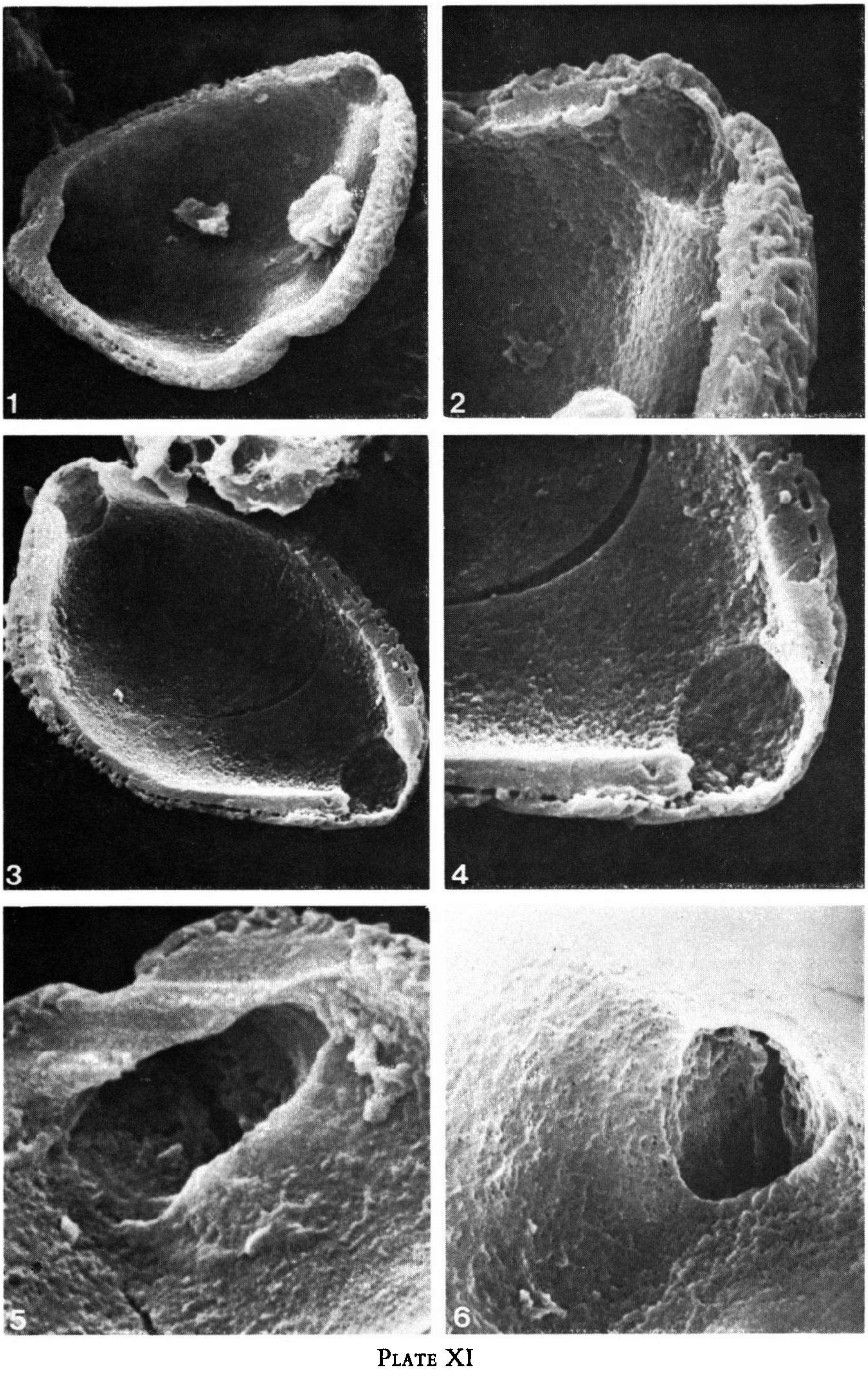


Plate XI

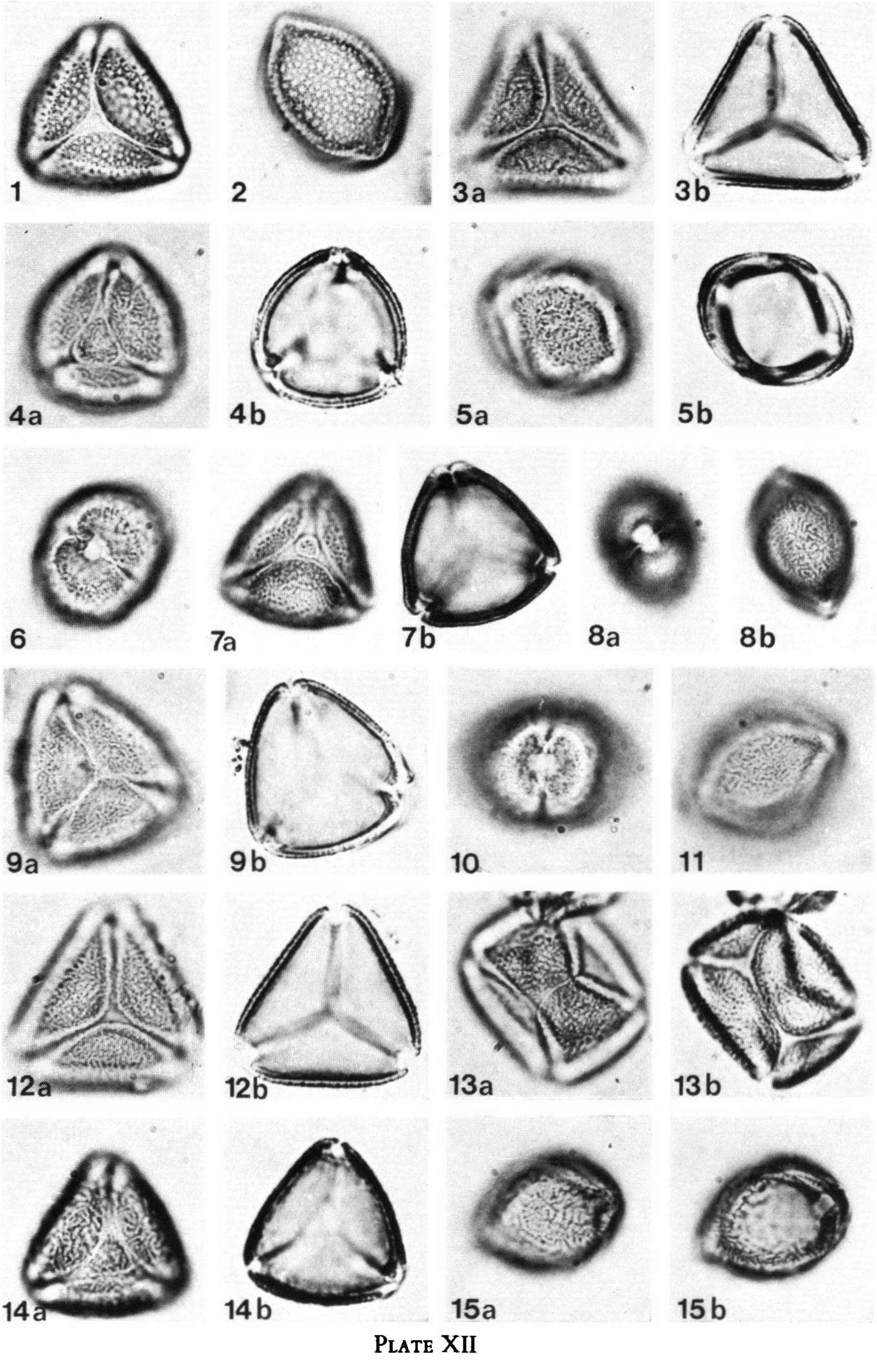

1
2
3a
3b
4a
4b
5a
5b
6
7a
7b
8a
8b
9a
9b
10
11
12a
12b
13a
13b
14a
14b
15a
15b

PLATE XII

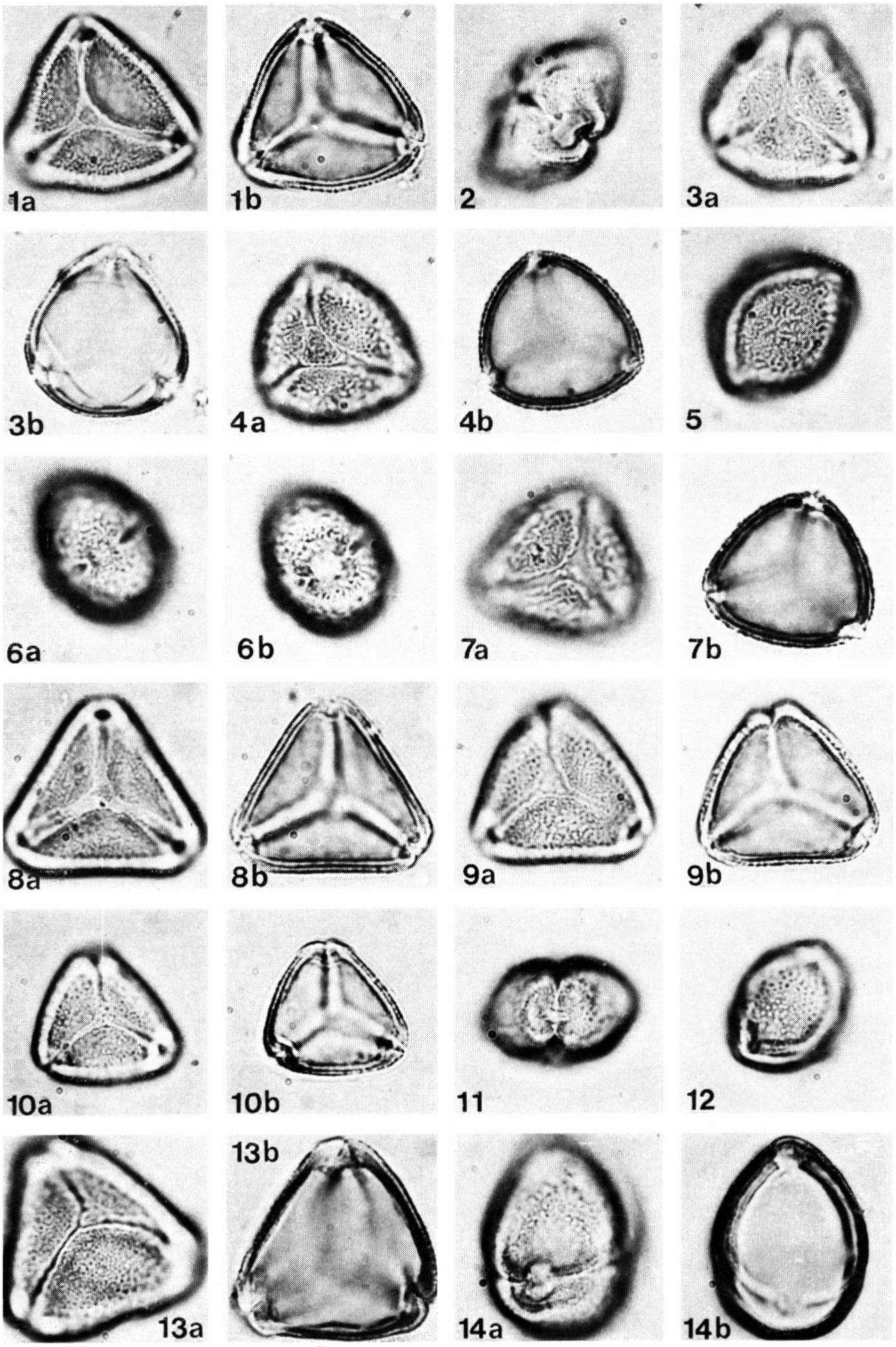

1a
1b
2
3a
3b
4a
4b
5
6a
6b
7a
7b
8a
8b
9a
9b
10a
10b
11
12
13a
13b
14a
14b

PLATE XIII

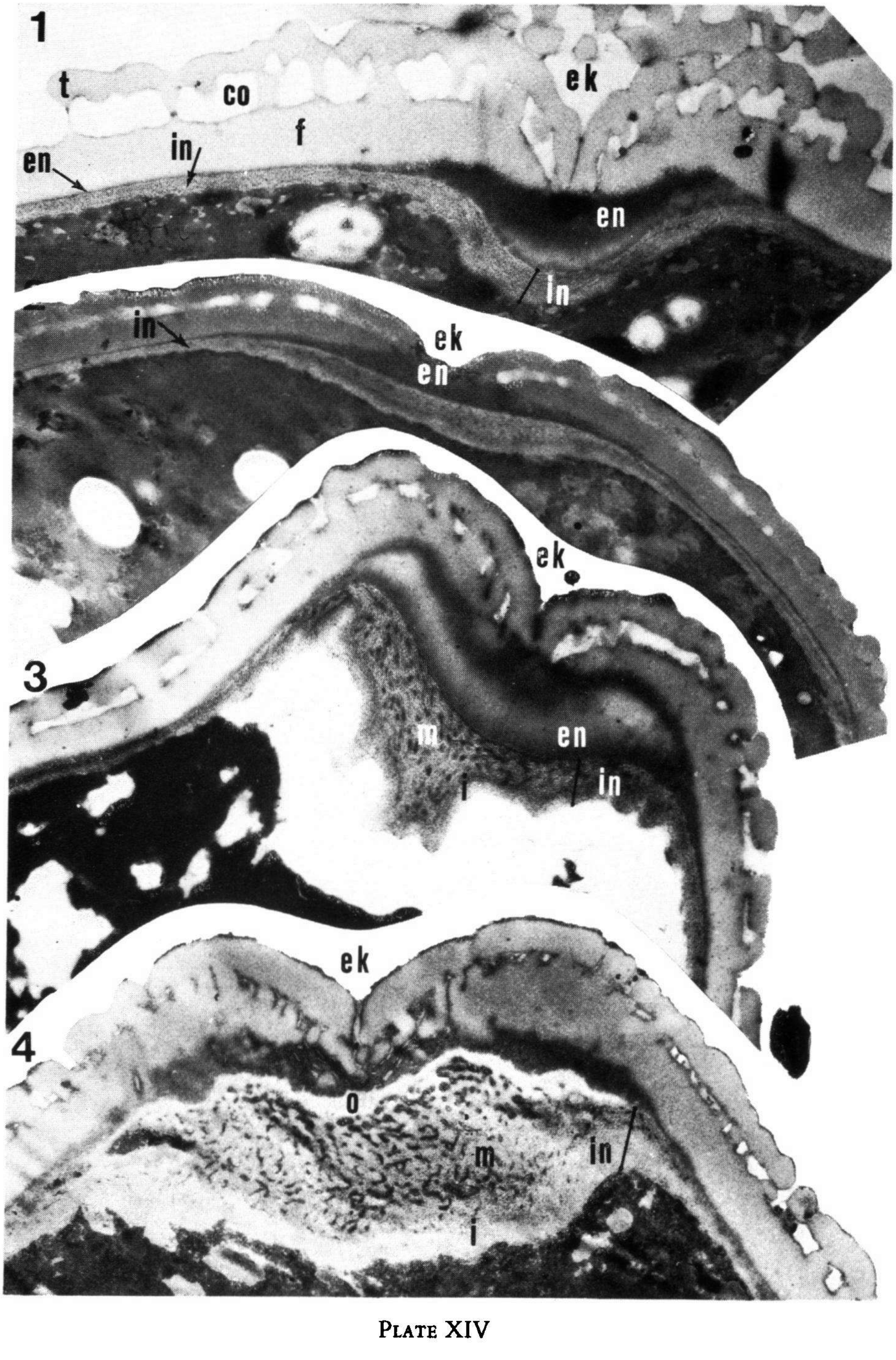


PLATE XIV

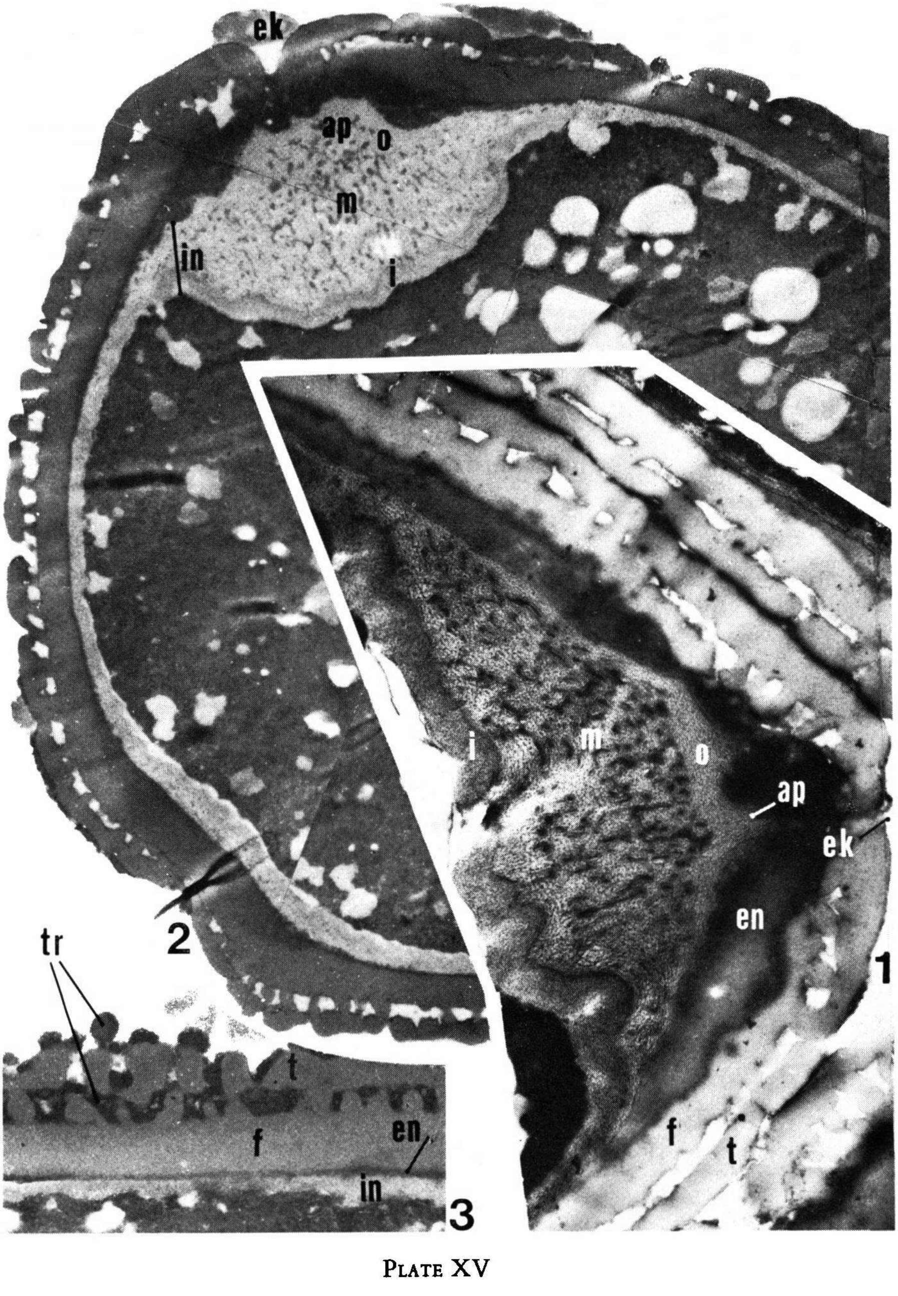


Plate XV

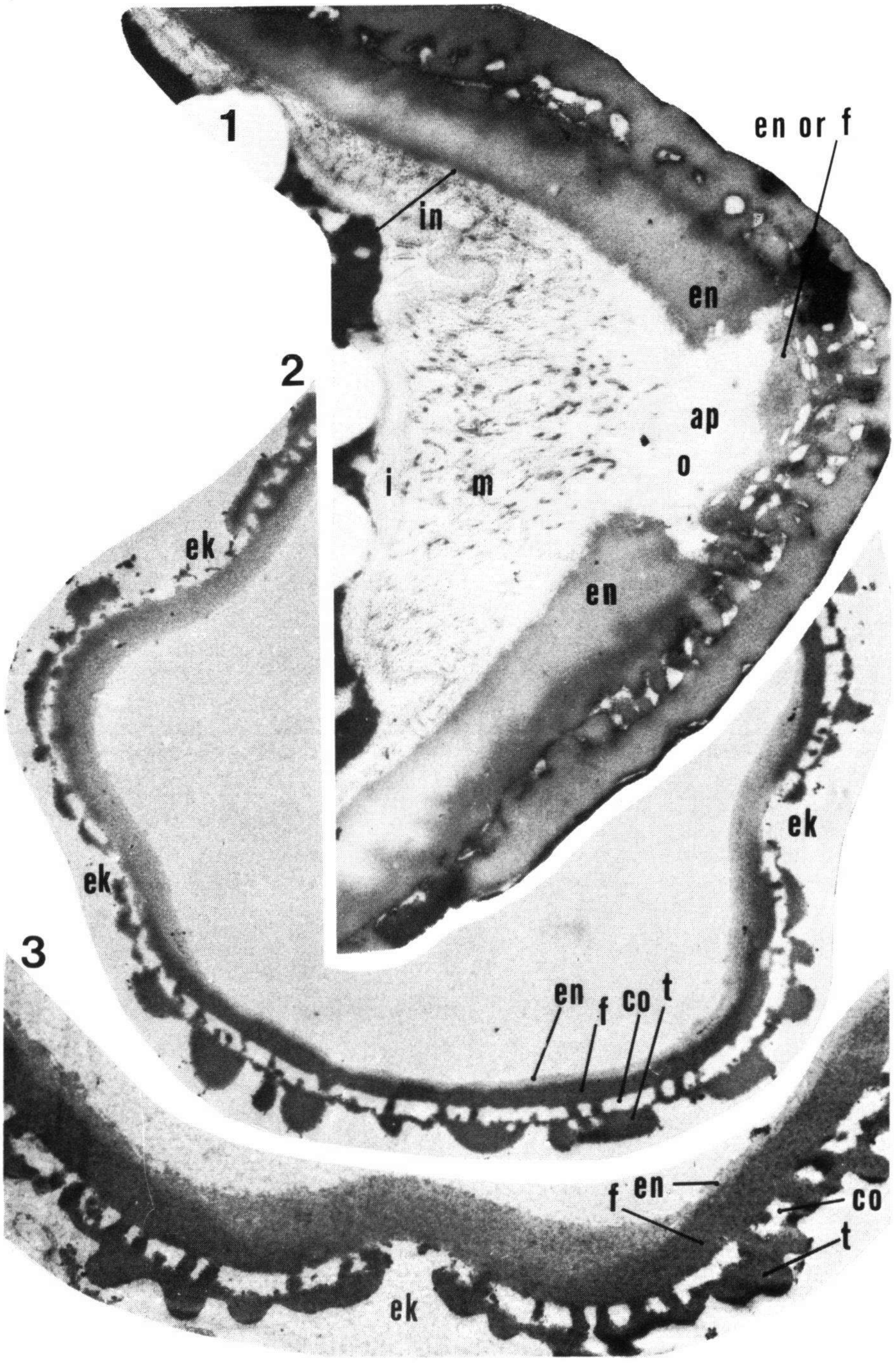


PLATE XVI

The sample *Geesink 5245 (M. sundaicus)*, which shows pollen transitional between type A and subtype B3, comes from SE. Asia, the region where only the most primitive species of *Mischocarpus*, *M. sundaicus* and *M. pentapetalus*, occur and where they probably originated.

The occurrence of a transitional type (A—B3) in *M. sundaicus* in SE. Asia fits very well in the theory that pollen type A is a more basal type and B a more advanced type in *Sapindaceae* (Muller & Leenhouts, 1976).

Final conclusions. Although no subdivision in pollen types could be found correlating with a subdivision based on macromorphology, morphological trends were noticed in pollen, concerning presence or absence and size of apocolpium, and sculpture, which are geographically based. Van der Ham (1977a) discussed a similar correlation between macromorphology and geography. So, it can be concluded that pollen characters join the macromorphological characters here as the same geographically based trends occur in both sets of characters.

In group 2, it is tried to connect certain pollen characters to the macromorphological level of development of the species in which they occur, in order to get insight in the question whether these pollen characters are primitive or derived. From this the conclusion can be drawn that in group 2 syncolporate pollen is more primitive than parasyncolporate pollen because the former dominate in species which are considered macromorphologically primitive. In *M. sundaicus* a pollen type occurs rarely that may be more primitive than the syncolporate type. Macromorphologically, this species is only slightly more derived than *M. pentapetalus*, the most primitive species of *Mischocarpus*.

ACKNOWLEDGEMENTS

The author is much indebted to Mr. W. Star (Rijksherbarium) for producing the TEM photomicrographs; to Mr. H. Kammeraat and Mr. F. van Zanddijk (both Geological Institute, Leiden) for producing the SEM photomicrographs; and to Mr. J. Muller (Rijksherbarium) for guiding this study.

REFERENCES

BERG, R. G. VAN DEN, 1975. Pollen morphology of the genera Pometia, Cubilia, Otonephelium, and Litchi (Sapindaceae). Unpublished report, Rijksherbarium.

HAM, R. W. J. M. VAN DER, 1977a. A revision of Mischocarpus (Sapindaceae). Blumea 23: 251—288.

— 1977b. Notes on Arytera (Sapindaceae). Blumea 23: 289—300.

MULLER, J. 1973. The pollen morphology of Barringtonia calyptrocalyx K. Sch. (Lecythidaceae). Grana 13: 29—44.

—, & P. W. LEENHOUTS, 1976. A general survey of pollen types in Sapindaceae in relation to taxonomy. In: I. K. Ferguson & J. Muller, eds.: The evolutionary significance of the exine. Linn. Soc. Symp. Ser. no. 1: 407—445.

EXPLANATION OF PLATES

Plate I. Fig. 1—4: *Mischocarpus anodontus* (*Betche s.n.*). 1. polar view, × 3300; 2. polar view of pseudoparasyncolporate grain, × 3300; 3. equatorial view, × 3300; 4. polar view of colporate grain with aberrant sculpture, × 3300. — Fig. 5, 6: *M. triqueter* (*BS 21985*). 5. polar view, × 2700; 6. equatorial view, × 2700.

Plate II. Fig. 1—6: *Mischocarpus exangulatus* (*MEL 55978*). 1. polar view, × 2800; 2. detail of 1, × 3800; 3. polar view, × 2650; 4. detail of 3, × 7400; 5. left grain: oblique polar view, right grain: equatorial view, × 1500; 6. detail of 5, left grain; note the isolated columellae in the lumina, × 7600.

Plate III. Fig. 1—6: *Mischocarpus grandissimus* (*Francis s.n.*). 1. polar view, × 3300; 2. detail of 1, × 6600; 3. equatorial view, × 3300; 4—6. transitions between grains with normal and grains with abnormally developed tectum; polar view, × 3300.

Plate IV. Fig. 1—6: *Mischocarpus grandissimus* (*Francis s.n.*). 1. grain with abnormally developed tectum, × 3300; 2. detail of 1, × 6600; 3. section of grain with abnormally developed tectum, × 3500; 4. equatorial section of grain with normal tectum, × 3500; 5. interior equatorial view showing endoaperture and part of ektoaperture, × 3500; 6. detail of 5, × 14,000.

Plate V. Fig. 1—3: *Mischocarpus paradoxus* (*LAE 60073*). 1. equatorial view, × 3300; 2. detail of 1, × 6600; 3. oblique polar view, × 3300; — Fig. 4—6: *Mischocarpus largifolius* (*NGF 23893*). 4. polar view, × 3200; 5. equatorial view, × 3200; 6. syndicolporate grain, × 2200.

Plate VI. Fig. 1, 2: *Mischocarpus lachinocarpus* (*Altena 3622*). 1. polar view, × 2700; 2. detail of 1, × 5400. — Fig. 3—6: *Mischocarpus pentapetalus* (3, 4: *De Wilde c.s. 13902*; 5, 6: *Wenzel 660*). 3. equatorial view, × 3200; 4. polar view, × 3200; 5. oblique polar view, × 3900; 6. polar view, × 2850.

Plate VII. Fig. 1—6: *Mischocarpus pyriformis*. 1, 2: subsp. *pyriformis* (*NSW 133886*). 1. polar view, at left a syntetracolporate grain, × 1500; 2. detail of 1, right grain, × 7200. 3, 4: subsp. *papuanus* (*NGF 9180*). 3. polar view, × 3600; 4. equatorial view, × 3600; 5, 6: subsp. *retusus* (*NGF 27003*). 5. oblique polar view, × 2700; 6. detail of 5, × 3600.

Plate VIII. Fig. 1—6: *Mischocarpus reticulatus* (1, 3, 4: *Hartley 12237*; 2: *Hartley 12534*; 5, 6: *Clemens 3093*). 1. polar view, × 2700; 2. oblique polar view showing colpus from pole to equatorial plane (from upper left to lower right), × 4100; 3. polar view, × 2000; 4. detail of 3, × 5400; 5. polar view, × 2500; 6. detail of 5, × 6800.

Plate IX. Fig. 1—6: *Mischocarpus sundaicus* (1, 2, 4: *Geesink 5245*; 3, 5: *BS 38759*; 6: *NGF 16846*). 1. polar view, × 3200; 2. detail of 1, × 6400; 3. polar view, × 3900; 4. polar view, × 2500; 5. polar view, × 3900; 6. polar view, × 2900.

Plate X. Fig. 1—6: *Mischocarpus sundaicus* (1, 2:*Schmutz 2021*; 3, 4: *Brass 19266*; 5, 6: *BW 9661*). 1.polar view, × 2650; 2. equatorial view, × 3600; 3. polar view, × 3200; 4. detail of 3, × 6400; 5. polar view, × 2850; 6. polar view, × 3800.

Plate XI. Fig. 1—6: *Mischocarpus sundaicus* (*Schmutz 2021*). 1. appr. equatorial section, × 2600; 2. detail of 1, showing endoaperture, × 7100; 3. interior equatorial view showing two endoapertures, × 3500; 4. detail of 3, × 7000; 5. interior equatorial view showing an appr. elliptic endoaperture and part of the ektoaperture, × 7000; 6. interior equatorial view showing an appr. rounded endoaperture and part of the ektoaperture, × 7000.

Plate XII. Fig. 1, 2: *M. exangulatus* (*MEL 55978*) 1. polar view; 2. equatorial view. — 3: *M. anodontus* (*MEL 55975*). polar view. — 4—6: *M. largifolius* (*NGF 23893*). 4. polar view; 5, 6. equatorial view. — 7, 8: *M. paradoxus* (*LAE 60073*). 7. polar view; 8. equatorial view. — 9 —11: *M. triqueter* (*FB 1871*); 9. polar view; 10, 11. equatorial view. — 12, 13: *M. pentapetalus* (*Kerr 4972*). 12. polar view; 13. polar view of syntetracolporate grain. — 14, 15: *M. grandissimus* (*Volck 138*). 14. polar view; 15. equatorial view. All × 1000, O.I.; a = upper focus, b = lower focus.

Plate XIII. Fig. 1, 2: *M. lachnocarpus* (*Altena 3622*). 1. polar view; 2. equatorial view. — 3—7: *M. sundaicus*. 3. *Geesink 5245*, polar view; 4—6. *NGF 16864*. 4. polar view; 5, 6. equatorial view; 7. *BW 9661*, polar view. — 8—12: *M. pyriformis*. 8: subsp. *retusus* (*NGF 28455*), polar view. 9: subsp. *pyriformis* (*NSW 133886*), polar view. 10—12: subsp. *papuanus* (*NGF 9180*). 10. polar view; 11, 12. equatorial view. — 13, 14. *M. reticulatus* (*Hartley 12237*). 13. polar view; 14. equatorial view. All × 1000, O.I.; a = upper focus, b = lower focus.

Plate XIV, XV, and XVI fig. 1: *M. reticulatus*: equatorial sections (except for XVI, fig. 1, which is a meridional section) through an ektoaperture arranged according to the position of cutting; Pl. XIV, fig. 1 beginning near one of the poles, and XVI, fig. 1 ending at the endoaperture (the sections are of different grains). t = tectum; co = columellate layer; f = footlayer; ek = ektoaperture; en = endexine; in = intine; i = inner sublayer of intine; m = middle sublayer; o = outer sublayer; tr = tryphine-like substance; ap = endoaperture.

Pl. XIV. Fig. 1. Intine at the ektoaperture slightly thickened, still undifferentiated, × 11,715. — Fig. 2: At the ektoaperture differentiation of the intine becomes visible, × 9900. — Fig. 3: Intine is clearly differentiated into 2 sublayers: an inner, homogenous one (i), continuous with the intine layer as it is developed on the mesocolpia, and an outer one (m) characterized by electron dense material, × 14,850. — Fig. 4: A third, homogenous sublayer of the intine (o) is now visible here below the endexine, × 11,715.

Pl. XV. Fig. 1, 2: The outer, homogenous sublayer of the intine is protruding in the endoaperture which becomes visible now (fig. 1 × 9900, fig. 2 × 14,850). — Fig. 3: Triphine-like covering of tectum and columellae, × 9900.

Pl. XVI. Fig. 1: Meridional section; the endoaperture is distinct here and the intine is optimally differentiated, the outer sublayer (o) in the endoaperture adjoining the footlayer (endexine?), × 14,850.

Pl. XVI. Fig. 2, 3: *M. sundaicus*. 2. Oblique equatorial section through grain showing endexine and ektexine (respectively light and dark); ek = ektoaperture; en = endexine; f = footlayer; co = columellate layer; t = tectum, × 6600. 3. Detail of one ektoaperture (section at another level of the right ektoaperture of fig. 2), × 11,715.