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POLLEN MORPHOLOGY OF THE GENERA POMETIA, CUBILIA, OTONEPHELIUM, AND LITCHI (SAPINDACEAE-NEPHELIEAE)

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CONTENTS

SUMMARY

The pollen morphology of the nine taxa within the genus *Pometia*, the three subspecies of *Litchi chinensis*, and the species *Cubilia cubili* and *Otonephelium stipulaceum* (*Sapindaceae – Nephelieae*) was studied. Three pollentypes were found:

1) the *Pometia* pollentype, which occurs in all nine taxa of the genus;
2) the *Litchi* pollentype, which can be divided in two subtypes:
    a) characteristic for *Litchi chinensis* subsp. *chinensis*, subsp. *phillippinensis*, and *Otonephelium* and, as could be concluded from a provisional investigation, also for *Xerospermum* and *Nephelium*, and
    b) characteristic for *Litchi chinensis* subsp. *javensis*;
3) the *Cubilia* pollentype.

Possible evolutionary trends in the tribe *Nephelieae* are discussed.

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I. INTRODUCTION

The genus *Pometia* was studied taxonomically by Jacobs (1962). It comprises two species: *P. ridleyi* Radlk. and *P. pinnata* Forst. Within the latter eight formae are distinguished by Jacobs: f. *pinnata*, f. *glabra*, f. *repanda*, f. *acuminata*, f. *alnifolia*, f. *macrocarpa*, f. *tomentosa*, and f. *cuspidata*.

The genus has been studied pollenmorphologically by Wang & Chien (1956), who present illustrations and a description (in Chinese) of *P. pinnata*. Rao & Lee (1970) describe the pollen of *P. alnifolia* (Bl.) King as 3-porate. Huang (1972) calls the pollen of *Pometia* scabrate, 3(4)-porate and presents a key to the genera of the *Sapindaceae*. Since all *Pometia* pollen studied by the present author proved to be reticulate, this key is at least partly erroneous. Martin (1973) mentions *Pometia* as possessing a more or less similar aperture as the fossil pollen genus *Siberiapollis*, together with *Elaeagnaceae* and *Symplocaceae*, but his illustration is not typical for *Pometia*, considering the diameter of 65 µm, which is twice the size of the largest grains found during the present study. The specimen may have been misidentified.

The species *Litchi chinensis* Sonn. is divided by Leenhouts (1978) in three subspecies: subsp. *chinensis*, subsp. *philippinensis*, and subsp. *javensis*. The above mentioned key in Huang (1972) states the tectum of *Litchi* to be reticulate and the author gives an illustration of a large triangular reticulate grain, which does definitely not belong to *Litchi chinensis*.

On the pollen of *Otonephelium stipulaceum* (Bedd.) Radlk. and *Cubilia cubili* (Blanco) Adelb. no literature was available.

It may be added that the pollen of *Litchi*, *Otonephelium*, and *Cubilia* are of the same basic type (type A: Muller & Leenhouts, 1976), which seems to be present throughout the tribe *Nephelieae* with the exception of *Pometia* which has a distinctly more complex pollentype (type C). This raises fundamental questions about the taxonomic place of *Pometia*.

The study of these genera was undertaken in order to acquire insight in the interrelations within the tribe *Nephelieae*. Comparison with the genus *Dimocarpus* (studied macromorphologically by Leenhouts and palynologically by Muller, 1971) proved to be necessary for this aim. Some provisional data on the genera *Nephelium* and *Xerospermum*, which are at present being revised by Dr. Leenhouts, are also included in order to present a general view of pollen morphology in the *Nephelieae*.

II. MATERIAL AND METHODS

In all cases flowers were sampled from herbarium-sheets (Rijksherbarium, Leiden, except *Otonephelium stipulaceum*, which was collected in Kew) and prepared according to standard acetolysis procedure. For lightmicroscopic observation, the grains were mounted in glycerine-jelly and studied with a Leitz microscope (Apo oel 90: 1 A1,32 or Phaco oel 100/1,30). For scanning electronmicroscopic observation, drops of the suspension of acetolysed grains in distilled water were placed on specimen stubs and covered with a thin gold coating, using at first an Edwards Vacuum coating unit Model E12E. Later an E5000 diode Sputtering System became available, which produces superior results. All observations were made with a Cambridge A II scanning electronmicroscope (Geological Institute, Leiden). In order to study wall- and endoaperture-structure, sections were cut on a Leitz freeze-microtome (—30 °C, 15 and 2,5 µm; see Muller, 1973). For transmission-electronmicroscopic observation two methods were followed: 1) using normally acetolysed grains, fixed in 2% $OsO4$ and 0,1 M cacodylate-buffer for one hour, pre-stained with 5% uranylacetate for two hours, dehydrated in a alcohol-series (30—100%), embedded in Epon 3/7, post-stained with Reynold's leadcitrate (in some cases); 2) using non-acetolysed grains following the suggestions of Rowley & Nilsson (1972) to rehydrate herbarium material, fixed in 0,1% OsO4, 0,1 M cacodylate-HCl-buffer, and 0,1 M glutaraldehyde for two hours, pre-stained with 5% uranylacetate for two hours (in some cases), dehydrated in a alcohol-series (30—100%), embedded in Epon 3/7, post-stained with Reynold's leadcitrate or with uranylacetate and leadcitrate (the latter method should produce more difference in contrast, but this was not found). Fixing in 1% Alcian blue +0,1 M glutaraldehyde was tried but failed to produce satisfying results. Sections were cut with a diamond knife.

III. GENERAL MORPHOLOGY OF THE POMETIA POLLENTYPE

The pollengrains of *Pometia* are single, isopolar, and tricolporate (Huang, 1972, gives a photograph of a tetracolporate grain, but these were not found in the present study). Equatorial diameter varies between 28 and 32 μm. Shape is suboblate as defined by the ratio between length of the polar axis and the equatorial diameter (P/E). The equatorial outline is triangular to rounded triangular. The apertures are situated at the angles (Plate I; Fig. 16 and 17). The ectoaperture consists of a narrow meridional groove, about 7—8 μm long (Plate I: Fig. 18 and 19; Plate IV: Fig. 2 and 4). The thickness of the exine is uniform (1.7 μm) except in the apertural areas where a thickening of the inner layer is present. The stratification of the exine is uniform except in the complex structure of the apertural region, to be described in detail below. Some LM-photographs of coupes stained with basic fuchsin show the inner layer to stain darker. TEM-studies failed to show any difference in contrast, however (Plate VII, VIII). Therefore in the exine only a tectum, a layer of columellae, and a nexine, subdivided into nexine-1 and nexine-2, will be distinguished, the presence of a true endexine being very uncertain. The stratification of the exine can be described as follows:

- a reticulate tectum (thickness 0.8 μm). The shape of the lumina is highly variable (isodiametric to irregular) (Plate IV; Fig. 3; Plate V). Towards the ectoapertures the size of the lumina decreases till in the apertural area a closed tectum is present, with at most only a few small perforations (Plate IV: Fig. 4);
- a layer of columellae (0.5 μm thick, columellae 0.2 μm in cross-section) arranged in a reticulate pattern, supporting the muri;
- a nexine-1 (0.6 μm thick) on which the columellae are based;
- a nexine-2 which is present only in the apertural area and has a lamellar structure.

In the mesocolpia only the nexine-1 is present but towards the aperture the nexine-2 becomes apparent: thin lamellae are visible, at first lying parallel to the nexine-1, but bending inward on approaching the apertural opening. The first lamellae are extremely thin (0,04 μm) but closer to the opening they are thicker (0.13—0.20 μm) (Plate VII: Fig. 1). The endoaperture consists of a tubular opening through these lamellae, narrowing towards the outer surface of the grain. The opening is about 3.5 μm wide at the level of the thinnest lamellae and about 2.0 μm at the outer end (Plate VIII: Fig. 1).

Before discussing these structures further, it may be appropriate to consider an alternative for the terminology used in describing the stratification of the exine. As has been explained above the lack of contrast on TEM-photographs of *Pometia* makes it impossible to distinguish ectexine- and endexine-layers with certainty. One solution is to call the tectum and the columellae 'ectexine' and use 'nexine' for the innerlayer(s). The alternative, supported by the lack of contrast, is to state that endexine is not present and that all layers of the exine consist of ectexine. The pollen of *Pometia* thus would lack an endexine-layer, which would make *Pometia* unique if compared with the other genera investigated.

A striking similarity seems to exist between the lamellae in *Pometia* and those found in the pollen of *Elaeagnaceae*. In *Elaeagnus turcomania*, for instance, the following situation is observed (Leins, 1967: 392): '...Die lockere Nexine-2, welche die kegelförmigen aperturdragenden Partien der Pollenkörner auskleidet, präsentiert sich auf den elektronenmikroskopischen Bildern in Form locker angeordneter nach innen vorspringender Lamellen (...). Die Lamellen, deren Dikke 0,03—0,08μm beträgt, scheinen verschieden breit zu sein (...). Auffallend ist eine schmale helle Linie in der Mitte der geschnittenen Lamellen. Demnach handelt es sich also um Doppellamellen (...). Eine Nexine-2 kleidet auch den kugelförmigen Zentralkorper des Pollenkornes aus. Diese ist hier aber sehr dünn (ca. 0,1 μm) und wenig von der Nexine-1 abgegrenzt...) (Translated: The loose nexine-2, that covers the conic aperture-bearing parts of the pollengrain, shows on the electronmicroscopic photographs as loosely arranged, inward bending lamellae (...). The lamellae, whose thickness is 0.03—0.08 μm, seem to differ in width (...). Striking is a narrow bright line in the middle of the sectioned lamellae. Therefore we have to do here with double-lamellae (...). A nexine-2 covers also the spheroid central part of the pollengrain. Here it is very thin (*c.* 0.1 μm), however, and not clearly distinguishable from the nexine-1.)

Sheperdia argentea seems to present the same situation. Here it is observed that the lamellae become thicker toward the ora and also between apertures lamellae are found, the latter running parallel to the wall while those nearer the aperture bend inward as in *Pometia.*

Endoapertural structure in *Elaeagnus* and *Sheperdia* (*Elaeagnaceae*) and in *Pometia* thus looks markedly alike. In *Pometia*, however, no evidence was found of a continuous nexine-2. It would be of interest to study the pollen of *Elaeagnaceae* treated according to the method of Rowley and Nilsson (See Material & Methods) and compare the results with those given below of pollen of *Pometia* prepared according to this method.

In order to study the role of the intine in the structure of the endoapertures unacetolysed grains were sectioned (Plate VIII: Fig. 2). The following observations were made: the intine covers the inside of the exine completely and forms a plug filling the tube-like opening through the endoapertural lamellae. This plug or oncus seems to be pushed into the protoplast under the aperture. According to Erdtman (1969: 46) the intine often consists of two layers. The outer of these has a great capacity for swelling. This swelling produces the thickening underneath the apertures. The TEM-micrographs of the present study give no clear indication of a two-layered intine. The plug does seem comparable with an oncus, however. The material between the lamellae in acetolysed grains could be the remains of the intine (Plate VII: Fig. 2).

This description is valid for both species of the genus *Pometia* and for all formae of the species *P. pinnata*. Variations in size, reticulum-density, form and number of lumina, length of colpi, are present, however. These differences are listed under the systematic descriptions; their importance for classification is discussed in chapter VI.

SYSTEMATIC DESCRIPTIONS

Pometia ridleyi Radlk.

Wong Swee Ming KEP FRI 9452 – Malay Peninsula.

Pollengrains oblate, P/E 0.74, equatorial outline triangular to rounded triangular, always tricolporate. Size: P 15 (19.1) 22 μm, E 22 (25.7) 29 μm. Ectoaperture 8 (8.8) 10 μm. E/c 2.97. Endoaperture circular, 2.0—2.5 μm. Total thickness of exine 2.0 μm. Thickening of nexine-2 around apertures 3.8 μm. Nexine-1 1.0 μm, columellae 0.4 μm, tectum 0.6 μm. Tectum reticulate, lumina-dimensions l 0.81 μm, b 0.38 μm.

Pometia pinnata Forst. f. **pinnata**
Plate I: Fig. 18 and 19; Plate VI: Fig. 1 and 3.

Mauriasi BSIP 12477 – Solomon Is.

Pollengrains suboblate, P/E 0.77, equatorial outline triangular to rounded triangular, always tricolporate. Size: P 16 (20.7) 25 μm, E 23 (26.1) 32 μm. Ectoapertures 6 (7) 8 μm. E/c. 3.80. Endoapertures circular, 2.5—3.5 μm. Total thickness of exine 1.9 μm. Thickening of nexine-2 around apertures 4.5 μm. Nexine-1 0.9 μm, columellae 0.4 μm, tectum 0.6 μm. Tectum reticulate, lumina-dimensions l 0.89 μm, b 0.44 μm.

Pometia pinnata Forst. f. **glabra** Jacobs
Plate I: Fig. 13—17; Plate IV: Fig. 3, 5, and 6; Plate VI: Fig. 2, 4—6; Plate VII; Plate VIII.

bb 29745 – Sumatra; *Hoogland & Craven 10603* – New Guinea.

Pollengrains suboblate, P/E 0.82, equatorial outline triangular to rounded triangular, always tricolporate. Size: P 18 (21.1) 24 μm, E 23 (25.6) 29 μm. Ectoapertures 6 (8.8) 12 μm. E/c 2.96. Endoapertures circular, 2.5—3.0 μm. Total thickness of exine 1.7 μm. Thickening of nexine-2 around apertures 5.2 μm. Nexine-1 0.6 μm, columellae 0.5 μm, tectum 0.6 μm. Tectum reticulate, lumina-dimensions l 0.98 μm, b 0.31 μm.

Pometia pinnata Forst. f. **repanda** Jacobs
Plate V.

Cel. V/239 – Celebes: *Rutten 1847* – Moluccas; *Mahuze BW 5149* – New Guinea.

Pollengrains suboblate, P/E 0.83, equatorial outline triangular to rounded triangular, always tricolporate. Size: P 18 (20.3) 24 µm, E 20 (24.6) 27 µm. Ectoapertures 6 (7.1) 8 µm. E/c 3.54. Endoapertures circular, 2.0—2.5 µm. Total thickness of exine 1.3 µm. Thickening of nexine-2 around apertures 3.8 µm. Nexine-1 0.5 µm, columellae 0.3 µm, tectum 0.5 µm. Tectum reticulate, lumina-dimensions l 1.21 µm, b 0.69 µm.

Pometia pinnata Forst. f. **acuminata** Jacobs
Plate IV: Fig. 1, 2, and 4.

Anderson S 19131, Haviland 134 – Borneo.

Pollengrains suboblate, P/E 0.78, equatorial outline triangular to rounded triangular, always tricolporate. Size: P 14 (17.5) 20 µm, E 19 (22.4) 25 µm. Ectoapertures 4 (5.1) 6 µm. E/c 4.47. Endoapertures circular, 1.5—2.0 µm. Total thickness of exine 2.0 µm. Thickening nexine-2 around apertures 5.1 µm. Nexine-1 0.7 µm, columellae 0.5 µm, tectum 0.8 µm. Tectum reticulate, lumina-dimensions l 1.0 µm, b 0.40 µm.

Pometia pinnata Forst. f. **alnifolia** Jacobs

NIFS 10 T1P11 – Sumatra; *L. L. Forman 519* – Borneo.

Pollengrains suboblate, P/E 0.87, equatorial outline triangular to rounded triangular, always tricolporate. Size: P 20 (21.7) 25 µm, E 24 (24.8) 30 µm. Ectoapertures 6 (7.2) 8 µm. E/c 3.50. Endoapertures circular, 2.0—2.5 µm. Total thickness of exine 2.0 µm. Thickening nexine-2 around apertures 5.8 µm. Nexine-1 1.0 µm, columellae 0.3 µm, tectum 0.7 µm. Tectum reticulate, lumina-dimensions l 1.12 µm, b 0.55 µm.

Pometia pinnata Forst. f. **macrocarpa** Jacobs

B. A. Krukoff 4419 – Sumatra.

Pollengrains suboblate, P/E 0.82, equatorial outline triangular to rounded triangular, always tricolporate. Size: P 18 (24.4) 29 µm, E 26 (29.5) 33 µm. Ectoapertures 5 (6.0) 7 µm. E/c 5.01. Endoapertures circular, 2.0—2.5 µm. Total thickness of exine 2.0 µm. Thickening nexine-2 around apertures 4.6 µm. Nexine-1 0.6 µm, columellae 0.5 µm, tectum 0.9 µm. Tectum reticulate, lumina-dimensions l 1.21 µm, b 0.60 µm.

Pometia pinnata Forst. f. **tomentosa** Jacobs

Achmad 1473 – Sumatra; *Winckel 1809 b* – Java.

Pollengrains suboblate, P/E 0.79, equatorial outline triangular to rounded triangular, always tricolporate. Size: P 23 (25.6) 29 µm, E 29 (32.1) 38 µm. Ectoapertures 6 (6.8) 8 µm. E/c 4.81. Endoapertures circular, 2.5—3.5 µm. Total thickness of exine 1.8 µm. Thickening nexine-2 around apertures 5.9 µm. Nexine-1.07 µm, columellae 0.5 µm, tectum 0.6 µm. Tectum reticulate, lumina-dimensions l 1.17 µm, b 0.54 µm.

Pometia pinnata Forst. f. **cuspidata** Jacobs

De Voogd 1919 – Sumbawa.

Pollengrains suboblate, P/E 0.77, equaorial outline triangular to rounded triangular, always tricolporate. Size: P 20 (21.2) 27 μm, E 25 (27.1) 30 μm. Ectoapertures 5 (7.2) 10 μm. E/c 3.69. Endoapertures circular, 2.0—2.5 μm. Total thickness of exine 1.6 μm. Thickening nexine-2 around apertures 4.9 μm. Nexine-1 0.5 μm, columellae 0.5 μm, tectum 0.6 μm. Tectum reticulate, lumina-dimensions l 1.02 μm, b 0.63 μm.

IV. GENERAL MORPHOLOGY OF THE LITCHI POLLENTYPE

The pollengrains of the *Litchi* type are single, isopolar, and always tricolporate. Equatorial diameter varies between 18 and 20 μm. Shape, as defined by P/E is suboblate to spherical. The equatorial outline is circular to rounded triangular. The ectoaperture consists of a long meridional colpus (Plate I: Fig. 1, 2, 5, 6, 9, and 10; Plate III). The thickness of the exine is greatest in the mesocolpia (1.2 μm). Towards the colpi the exine becomes thinner. The colpi are closed by a thin membrane only (Plate IX: Fig. 3).

The stratification of the exine of the mesocolpium differs from that of the colpus. In the mesocolpium cross-sections show:

- a striate tectum (0.4 μm);
- a layer of columellae (0.2 μm thick, columellae 0.13 μm in cross-section), which are arranged in a striate or striate-reticulate pattern in conformity with the sculptural pattern of the tectum;
- a sole (footlayer) (0.6 μm).

TEM-micrographs show that these three layers have an identical contrast and therefore they will be considered to form the ectexine. As the thickness of the exine decreases toward the colpi, the sole becomes thinner and ultimately disappears beneath the colpus, its place being taken by the endexine, which shows less contrast on TEM-micrographs (Plate IX: Fig. 4). The colpi are thus closed by a membrane consisting of endexine only. Away from the colpus the endexine-layer becomes rapidly thinner (as the sole increases in thickness) and is, as stated above, not visible in the mesocolpial part of the grain. The endexine does not show a lamellar structure.

Small verrucae (presumably consisting of ectexine) are present on the colpusmembrane. The colpi are long (14—17 μm), leaving only small apocolpia at the poles. They are up to 2 μm wide at the equator. The endoapertures are circular, sometimes meridionally elongated, diameter 2—3 μm (Plate III: Fig. 2, 4, and 6).

The tectum is striate in *Litchi chinensis* subsp. *chinensis*, subsp. *philippinenesis*, and *Otonephelium stipulaceum*, or striate-reticulate, as in *Litchi chinensis* subsp. *javensis*. The ridges of the striate tectum are about 0.3 μm wide. In principle they run parallel to each other and to the colpi. At the poles the ridges of the different mesocolpia meet. They can continue into each other, or one ridge can divide into two, each offspring joining ridges of the other two mesocolpia. Furthermore, ridges anastomose at different levels (Plate III: Fig. 1 and 3).

Litchi chinensis subsp. *javensis* shows a different pattern. The ridges are less parallel and small lumina are formed by intersecting ridges, the resulting sculpture being transitional to a reticulate one (Plate III: Fig. 5).

The pollen of *Otonephelium* is very similar to that of *Litchi*, especially to that of the subspecies *chinensis* (Plate II: Fig. 2, 4, and 6). The main difference is in size, *Otonephelium* being smaller. The general description of *Litchi*-pollen applies also to *Otonephelium*, as far as external features are concerned. *Otonephelium* was not studied with TEM-techniques, however, therefore no data on wall-stratification and aperture-structure are available.

The pollen of *Xerospermum* and *Nephelium* has been investigated only provisionally. SEM-observations showed these genera to possess pollen very similar to that of *Otonephelium* and *Litchi chinensis* subsp. *chinensis* and which can be included in the *Litchi* pollentype.

SYSTEMATIC DESCRIPTIONS

Litchi chinensis Sonn. subsp. **chinensis**
Plate I: Fig. 1, 2, 5, 6, 9 and 10; Plate III: Fig. 3. and 4.

Poilane 11991 – Indo-China.

Pollengrains suboblate, P/E 0.83, equatorial outline circular to rounded triangular, always tricolporate. Size: P 12 (15,6) 19 μm, E 16 (18,6) 25 μm. Ectoapertures 14 (15.7) 16 μm. E/c 1.21. Endoapertures circular/elliptical, meridionally elongated, diameter about 2 μm. Thickness of exine 1.2 μm in mesocolpia. Sole 0.6 μm, columellae 0.2 μm, tectum 0.4 μm. Tectum striate. Orientation of ridges not always parallel to the colpi, some (especially in the middle of the mesocolpia) run in equatorial direction.

Litchi chinensis Sonn. subsp. **philippinensis** Leenh.
Plate III: Fig. 1 and 2.

Vidal 722 – Philippines: Luzon.

Pollengrains suboblate, P/E 0.85, equatorial outline circular to rounded triangular, always tricolporate. Size: P 14 (15.4) 18 μm, E 16 (18,0) 20 μm. Ectoapertures 12 (14,3) 16 μm. E/c 1.28. Endoapertures circular/elliptical, meridionally elongated, diameter about 2—3 μm. Thickness of exine 1.3 μm in mesocolpia. Sole 0.7 μm, columellae 0.2 μm, tectum 0.4 μm. Tectum finely striate. The ridges run strictly parallel to each other and to the colpi.

Litchi chinensis Son. subsp. **javensis** Leenh.
Plate III: Fig. 5 and 6.

Unknown collector in herb. L 908.270—267 – Java.

Pollengrains spherical. P/E 0.95, equatorial outline circular, always tricolporate (one abnormal syncolpate grain was found). Size: P 17 (19.9) 23 μm, E 20 (20.9) 23 μm. Ectoapertures 16 (17.4) 20 μm. E/c 1.23. Endoapertures circular/elliptical, meridionally elongated, diameter 2.5—3.0 μm. Thickness of exine 1.0 μm in mesocolpia. Sole 0.4 μm, columellae 0.2 μm, tectum 0.4 μm. Tectum striate/reticulate. No strict parallel orientation of ridges. Small isodiametric lumina are formed by intersecting ridges.

Otonephelium stipulaceum Radlk.
Plate I: Fig. 3, 7, and 11; Plate II: Fig. 2, 4, and 6.

Herb. Hooker, a. 1867 – India.

Pollengrains spherical, P/E 0.98, equatorial outline circular to rounded triangular, always tricolporate. Size: P 13 (15.2) 18 μm, E 14 (15.4) 20 μm. Ectoapertures 10 (12.2) 14 μm. E/c 1.27. Endoapertures circular/elliptical, meridionally elongated, diameter about 2 μm. Thickness of exine 1.6 μm in mesocolpia. Sole 0.8 μm, columellae 0.2 μm, tectum 0.6 μm. Tectum striate, with a pattern similar to that of *Litchi chinensis* subsp. *chinensis*.

V. GENERAL MORPHOLOGY OF THE CUBILIA POLLEN TYPE

The pollengrains in *Cubilia* are single, isopolar, and always tricolporate. Equatorial diameter varies between 11 and 13 μm. Shape as defined by P/E is spherical. Equatorial outline is circular. The ectoaperture consists of a long meridional colpus (Plate I: Fig. 4, 8, and 12; Plate II: Fig. 1, 3, and 5). The thickness of the exine is uniform (0.5 μm) except for a thickening (of the endexine) underneath the colpi. In contrast to *Litchi*, thickness of the exine is greatest at the colpi and not at the mesocolpia; furthermore, the thickness of the exine does not decrease towards the colpi as in *Litchi* (Plate IX: Fig. 1).

The stratification of the exine of the mesocolpium differs from that of the colpus. In the mesocolpium cross-sections show:

- a closed tectum (0.16 μm), carrying micro-echinate processes (up to 0.3 μm high, diameter 0.2 μm). Although the tectum is for the major part closed, near the colpi, especially near the pores, small perforations can be found. A few of these perforations may be present over the surface of the grain;
- a layer of columellae (0.16 μm thick, columellae 0.10 μm in cross-section), regularly distributed. The position of the processes of the tectum does not seem to be correlated with the position of the columellae;
- a sole (0.16 μm).

These three layers show no difference in contrast on TEM-micrographs and therefore they will be considered to form the ectexine. Underlying the colpus there is a thickening of the inner layer which is more transparent to the electron-beam. This would mean that the colpus is closed by an endexineous layer. Away from the colpus this layer becomes rapidly thinner (as in *Litchi*) and is not visible in the mesocolpia. On this membrane micro-verrucae are present.

SYSTEMATIC DESCRIPTION

Cubilia cubili Adelb.
Plate I: Fig. 4, 8, and 12; Plate II: Fig. 1, 3, and 5.

Kostermans 13874 – Borneo; *Merrill 705, Sulit PNH 22872* – Philippines: Luzon; *Koorders 22616β*— Celebes.

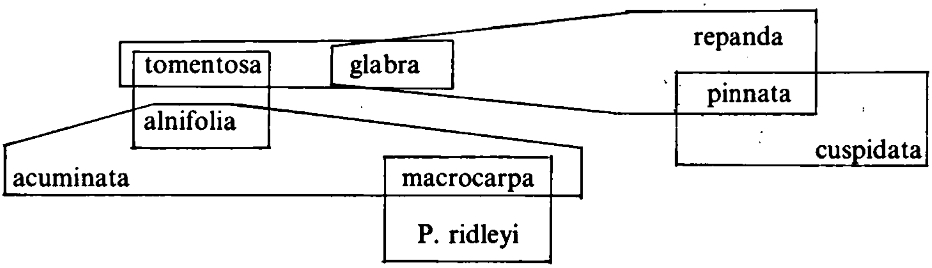
Pollengrains spherical, P/E 0,94, equatorial outline circular, always tricolporate. Size: P 10 (11.8) 14 μm, E 11 (12.4) 15 μm. Ectoapertures circular/irregularly shaped, diameter about 1.5 μm. Thickness of exine 0.5 μm in mesocolpia. Sole 0.16 μm, columellae 0.16 μm, tectum 0.16 μm. Tectum closed (except for a few, small perforations), carrying small (0.3 μm) pointed echinae.

VI. POLLENMORPHOLOGY AND TAXONOMY

Pometia

The taxonomy of *Pometia* was studied by Jacobs (1962), who stated (p. 117): 'Vegetatively there is a resemblance with *Litchi philippinensis* Radlk.; the structure of the inflorescence and of the flowers comes perhaps nearest to that of *Nephelium*.'

From macromorphological data the following relationships within the genus may be postulated (Jacobs, 1962: 118): '... f. *macrocarpa* seems to represent the point were *P. pinnata* and *P. ridleyi* are connected. The widespread f. *glabra* seems closest related to f. *pinnata* and f. *repanda* in the eastern half of the area and to f. *tomentosa* in the western half. The f. *tomentosa* seems closer related to f. *alnifolia* with which the f. *macrocarpa* and f. *acuminata* are associated. The f. *cuspidata* of the Lesser Sunda Islands could have been drived from f. *pinnata*.' These relationships could be pictured as follows:



It seems noteworthy that these formae and combinations of formae are largely restricted to certain geographical regions. The *glabra/repanda/pinnata*-complex, for instance, constitutes the population of Celebes, the Philippines, the Moluccas, and New Guinea. *Glabra/tomentosa* are found in this combination on Java only. Attention should be given to the isolated position of f. *cuspidata* and to the relatively restricted distribution of the mutually related f. *macrocarpa* and *P. ridleyi*. From the scheme of macromorphological resemblance combined with the map of distributions it is evident that differences in pollenmorphology within the genus *Pometia* are more likely to be found between, for instance, *Pometia ridleyi* and *P. pinnata* f. *repanda* than between the formae *pinnata* and *repanda*. However, all pollenmorphological differences proved to be quantitative and are part of a continuous variation. The pollen of the two species in the genus, *P. ridleyi* and *P. pinnata*, shows no significant difference and also between the formae there are few differences.

Let us take a closer look at the variation within *Pometia*: Shape: P/E ranges from 0.74 to 0.87. All formae of *P. pinnata* are suboblate. *P. ridleyi* is oblate but the boundary at 0.75 (0.50—0.75 oblate, 0.75—0.88 suboblate) is arbitrary, and *P. ridleyi* differs too little from *P. pinnata* f. *pinnata* and f. *cuspidata* (which have P/E 0.77) to place them in different form-classes. There is no significant relation of shape to size. P/E does not gradually change with size. F. *alnifolia*, which has the largest P/E (0.87), is only average in size.

Size. Of the nine taxa in the genus *Pometia*, the pollen of f. *acuminata* definitely are smallest, while f. *tomentosa* has the largest dimensions. Small size could denote primitiveness (Muller, 1970: 551). The distribution of the f. *acuminata*, however, (endemic on Borneo) can be explained either as a derived condition or as a relict and so a decision whether the forma is primitive or derived can hardly be taken. It is possible to define arbitrary sizeclasses as follows:

<25 μm – *acuminata, repanda*

>25 μm, <30 μm – *alnifolia, glabra, ridleyi, pinnata, cuspidata*

>30 μm – *macrocarpa, tomentosa*

Relative length of the colpus. This can be expressed in the E/c-ratio. The two largest pollengrains, those of the formae *macrocarpa* and *tomentosa*, have high E/c-ratio's, indicating that these formae posses the longest colpi within the genus. Assuming that the *Pometia* pollentype has ultimately been derived from a tricolporate grain with longer colpi (as will be discussed further in the section on evolutionary trends in the tribe *Nephelieae*), the formae *macrocarpa* and *tomentosa* could be most primitive.

Wall thickness and lumina dimensions. Measurements lead to the conclusion that, also for these characters, it is not possible to assign pollentypes to the different formae. The main conclusion is therefore that pollen-morphologically the formae can hardly be distinguished from each other. While within the genus *Pometia* evolution is hard at work (according to Jacobs, 1962), this process has not yet resulted in a clear pollenmorphological differentiation.

Cubilia

The genus *Cubilia* comprises only one species, *Cubilia cubili*. Macro-morphologically, no further subdivision of this species seems possible, although a clinal variation exists (Borneo – Philippines – Celebes). Such a clinal variation is not found in pollen morphology: in several samples (from Borneo, Luzon, and Celebes) only one pollentype was found. This pollentype with its echinate sculpture of the tectum is rare in general in the *Sapindaceae* and may be unique in the tribe *Nephelieae*.

Litchi

The species *Litchi chinensis* can be divided in three subspecies: subsp. *philippinensis*, subsp. *chinensis*, and subsp. *javensis* (Leenhouts, 1978). The pollengrains of these three subspecies can be discerned by the sculpture of the tectum (Plate III):

1) subsp. *philippinensis:* finely striate. The ridges run strictly parallel to each other and to the colpi. At the poles they join as described in the section on the general pollen morphology of the *Litchi* pollentype. Furthermore, the pollen of this subspecies is the smallest within the species.
2) subsp. *chinensis:* striate. The ridges run less regular. The parallel orientation is less evident. At the poles the pattern of one of the three mesocolpia seems to override the other two.
3) subsp. *javensis:* striate/reticulate or striate/perforate. No strict parallel orientation of ridges. Small isodiametric lumina/perforations are formed by intersecting ridges. The pollen of this subspecies is the largest of the species. Palynology thus supports the opinion of Leenhouts that subsp. *javensis* is not just a cultivated form of subsp. *chinensis*, but a separate taxon. Of the three subspecies subsp. *philippinensis* could be the most primitive because of its small size. In the course of evolution a tendency to diminish the parallel orientation of the striae may have arisen, leading to subsp. *chinensis* and, in another direction, to subsp. *javensis*.

Otonephelium

The genus *Otonephelium* comprises only one species, *Otonephelium stipulaceum*. Only one sample was available. SEM-observation showed this taxon to possess pollen which is very similar to that of *Litchi* and it is considered to belong to the *Litchi* pollentype. Because of the scarcity of the material is was not possible to investigate the presence of any variation within the genus.

Nephelieae

The genera *Pometia*, *Cubilia*, *Litchi*, and *Otonephelium*, together with *Xerospermum* and *Nephelium*, are placed fairly close to each other in the taxonomic system on account of their macromorphological resemblance. Pollenmorphologically, this seems to be valid for *Litchi*, *Otonephelium*, *Xerospermum*, and *Nephelium*, but not for *Pometia* and *Cubilia*.

In the tribe *Nephelieae* two basic pollentypes (A and C according to Muller and Leenhouts, 1976) exist. *Dimocarpus*, *Otonephelium*, *Litchi*, *Cubilia*, *Xerospermum*, and *Nephelium* all possess type A. Only in *Pometia* type C occurs. The pollentypes differ mainly in shape, nature of the apertures, and sculpture of the tectum. Within the *Nephelieae* type A is a small spherical grain with long colpi and a striate or echinate tectum. Type C is large, suboblate with a triangular equatorial outline, and has a well-developed endoaperture but a reduced ectoaperture and a reticulate tectum. If one considers type C derived (which is in accordance with macromorphological data, which show *Pometia* to be most advanced in the *Nephelieae*) and type A primitive, four evolutionary trends could be postulated:
-increasing size of the pollengrain;
-decreasing length of the ectoaperture (colpus);
-tectum from closed via striate/reticulate to reticulate;
-shape from spherical with circular equatorial outline to suboblate with triangular equatorial outline.

According to these trends, of the four genera investigated *Cubilia* would be most primitive, followed by *Otonephelium*, *Litchi* and, finally, *Pometia*. Size steadily increases in this order. It is true that the length of the colpus increases from *Cubilia* to *Litchi chinensis* subsp. *javensis*, but, as grainsize increases also, one must compare the relative values. If the length of the colpus would increase relatively, the value of E/c would decrease. In fact, it does not, indicating that if size increases, the colpus takes up about the same proportion of the grainsurface. The pollengrains of *Pometia* show a substantial increase of the E/c because of the relative decrease in colpus length. The pollen of *Litchi chinensis* subsp. *javensis* would be an exception to the fourth evolutionary trend: it is spherical

The sequence *Cubilia* – *Otonephelium* – *Litchi* – *Pometia*, with *Xerospermum* and *Nephelium* somewhere around *Litchi*, is not an evolutionary one, however. *Otonephelium* and *Litchi* may be closely related, but *Cubilia* with its unique tectum-sculpture, as well as *Pometia* with its different pollentype seem to take rather isolated positions.

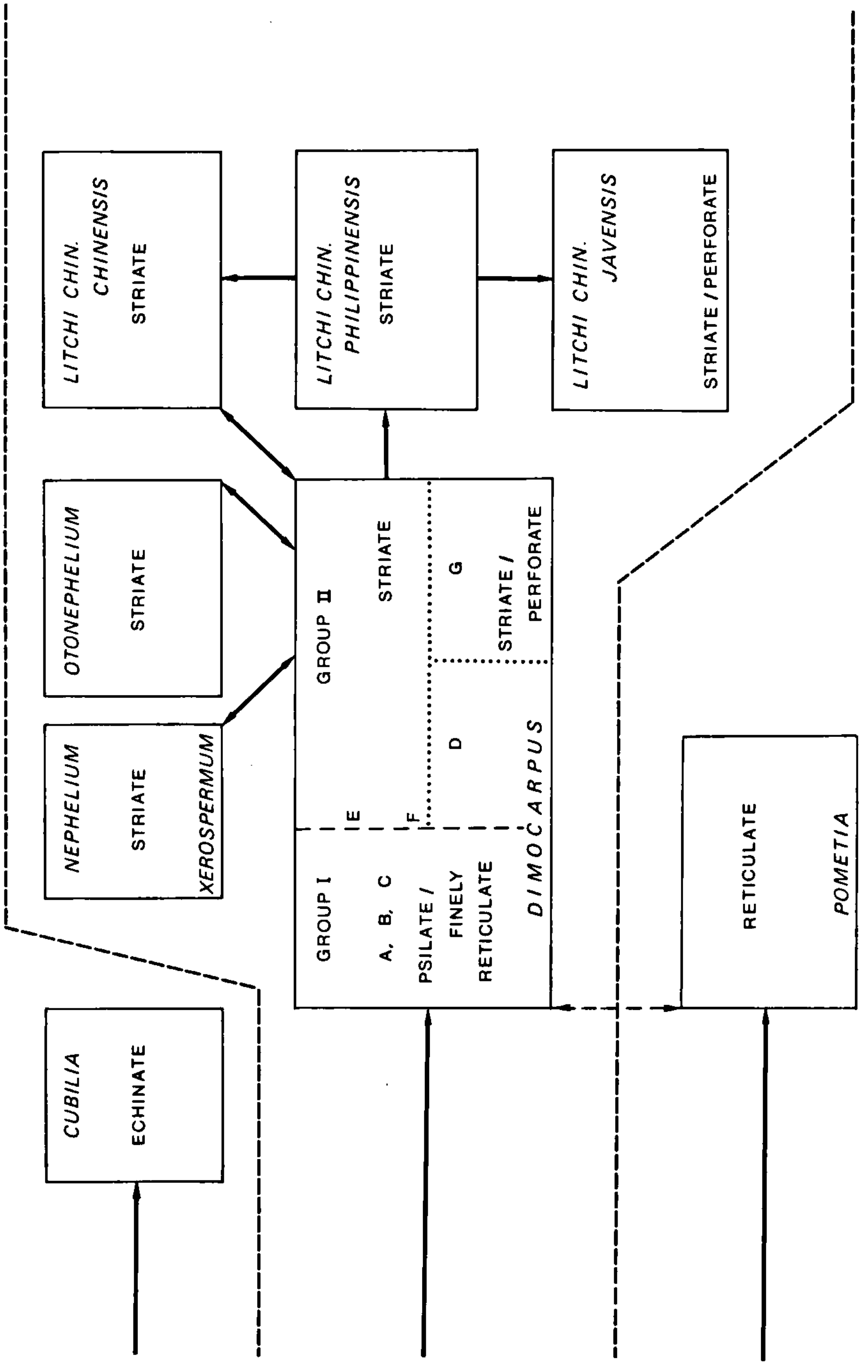
In order to understand the interrelations within the *Nephelieae*, it is necessary to include the genus *Dimocarpus* in the comparison. The present circumscription of *Dimocarpus* is due to a revision by Leenhouts (1971), who combined Radlkofer's genera *Euphoria* and *Pseudonephelium*. The genus appears to occupy a central position in the so called *Dimocarpus*-group of the tribe *Nephelieae* (the other group, the *Pappea*-group, is not discussed here). According to Leenhouts (p. 115): 'The only genus which seems closely related to *Dimocarpus* is *Otonephelium* Radlk. (...) To the wider relationships of *Dimocarpus* belong *Cubilia* and *Litchi*, which seem to be further derived, possibly *Pometia*, whereas *Dimocarpus* itself may have been derived from *Nephelium* or *Xerospermum*.' (see also the scheme of relationships in Leenhouts, 1978).

The pollen morphology of *Dimocarpus* was studied by Muller (1971). It is possible to distinguish seven pollensubtypes (A—G) in the five species of *Dimocarpus*. Muller (p. 143): 'The subtypes can be seperated in group I (A, B, C) which has a simply built, psilate or perforate/reticulate pattern, and group II (D, E, F, G) which has a more or less distinct striate pattern.'

Based on the sculpture of the tectum, the relations between the genera *Nephelium*, *Xerospermum*, *Dimocarpus*, *Cubilia*, *Pometia*, *Otonephelium*, and *Litchi* can be illustrated as in scheme 1. *Nephelium*, *Xerospermum*, *Otonephelium*, and *Litchi* could very well be related to the striate subtypes of group II of *Dimocarpus*. In pollen morphology a parallel development has taken place leading to *Nephelium*, *Xerospermum*, *Otonephelium*, and *Litchi chinensis* subsp. *chinensis* (the latter seems derived from *Litchi chinensis* subsp. *philippinensis*, as does subsp. *javensis*, but in another direction). This is in accordance with macromorphological findings (compare scheme 1 and Leenhouts, 1978).

Cubilia does not seem to be related to *Dimocarpus* too closely. Its echinate tectum is difficult to connect with any of the sculpture-types in *Dimocarpus*. Its small size could denote a not too far advanced state of development and in the macromorphological scheme (Leenhouts, 1978) *Cubilia* appears as an early offspring of the main line in the tribe.

Pometia, finally, on account of its C-pollentype, may be the result of a different line of descent altoghether. Its coarsely reticulate tectum could, tentatively, be connected with the finely reticulate sculpture of group I of *Dimocarpus*, indicating that, if *Pometia* is in some way related to *Dimocarpus*, it bran-



SCHEMA 1: INTERRELATIONS WITHIN THE TRIBE NEPHELIEAE ACCORDING TO POLLEN MORPHOLOGY

A survey of macromorphological characters of the genera treated (inf. Leenhouts)

	Cubilia	Otonephelium	Dimocarpus	Litchi	Pometia
stamens	5 (6)	8	(6—) 8 (—10)	6—11	5 (6)
petals	5	0	0—5(6)	0	5 (0)
scales on petals	—	—	—	—	+/—
	2-merous	2-merous	2 (3)-merous	2-merous	2 (3)-merous
stigma	lobed	lobed	lobed	lobed	grooved
mesocarp	dry	dry	dry	dry	juicy
arilloid	$^1/_2$	$^1/_2$—1	1	$^1/_2$—1	1
embryo	nearly straight	nearly straight	straight	straight	curved
stipules	–	+	–	–	+
aperture-type according to Muller & Leenhouts, 1976	A	A	A	A	C

ched off very early. A further deviating characteristic is the lack of endexine, which could be correlated with the evident reduction of the ectoaperture. Furthermore, there are macromorphological and ecological data to consider. Compared with the closest related genera (*Dimocarpus*, *Otonephelium*, *Cubilia*, and *Litchi*), *Pometia* seems to be derived. It is deviating in possessing a smooth fruit with a juicy mesocarp, a curved embryo, an arilloid completely enveloping the seed, petals with scales on their inside, and a grooved stigma. All other genera mentioned have the fruits more or less densely covered with spines or warts, a straight embryo, no scales on the inside of the petals, and a lobed stigma. In *Dimocarpus* the arilloid covers the seed completely (as in *Pometia*), in *Litchi* and *Otonephelium* the seed is partly or completely enveloped by the arilloid, while in *Cubilia* only the lower half of the seed is covered (this is difficult to verify, however, because the arilloid is slow in developing). According to van der Pijl (1968: 118): 'The last phase in the evolution of dissemination organs is that seeds have lost all independent power of attraction and that this function (when maintained at all) has become entrusted to the pericarp.' In *Pometia* we find that, while the seed still has a thin fleshy arilloid, the mesocarp is juicy and edible. If van der Pijl's opinion is correct, this situation must be considered derived as compared to that found in the other genera of the tribe, where the mesocarp is not juicy, the fruit more or less covered with spines, and only the arilloid around the seed is edible.

There is a great resemblance between *Pometia* and the other genera of the tribe in leaves, inflorescences, number of petals, locules, and ovula, indumentum etc. However, as stated above, *Pometia's* position in the tribe is already comparatively isolated as far as fruit characters etc. are concerned, and palynological evidence places it even further apart. Its triangular suboblate grain with reduced colpi and complex endoapertures is certainly more derived than the small spherical pollen with long colpi and simple endoapertures. Furthermore, between the two types no transitional stages are found (although it must be noted that the fossil record is still unsufficiently known).

The distinct difference in pollen morphology would make one expect differences in flowerbiology, too. This must be studied in the field. The ecological distribution of *Pometia* shows the genus to be very succesful. It occurs in the lower storey as well as the canopy of primary and secundary tropical rain forest, from low to medium altitude, on dry land, on slopes and ridges, on plains, on different soils, and also in temporarily inundated habitats, along rivers and even in swamps. The other genera in the *Nephelieae* show a distinct preference for more specialised habitats. For instance, *Litchi chinensis* subsp. *chinensis* prefers a hot wet climate with short cool and dry seasons without frost, on compact, moist, fertile soils, in contrast with subsp. *javensis* which seems to favor everwet conditions. Likewise, *Cubilia* grows best on poorly aerated, somewhat basic soils.

From the foregoing it is evident that *Pometia* is able to enter many different habitats, not having specialised like *Litchi*, *Dimocarpus*, or *Cubilia*. The large amount of variability found in the macromorphological characters as well as in its pollen is indicative of a flexible young taxon.

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EXPLANATION OF PLATES

Plate I. Fig. 1, 2, 5, and 9. *Litchi chinensis* subsp. *chinensis* (*Poilane 11991*), polar views. Fig. 6 and 10. id. equatorial views. — Fig. 3, 7, and 11. *Otonephelium stipulaceum* (*herb. Hooker*, 1867), polar views. — Fig. 4, 8, and 12. *Cubilia cubili* (*Sulit PNH 22872*), polar views. — Fig. 13—17. *Pometia pinnata* f. *glabra* (*bb 29745*), polar views. — Fig. 18 and 19. *Pometia pinnata* f. *pinnata* (*BSIP 12477*), equatorial views. All magnifications 1000 x.

Plate II. Fig. 1. *Cubilia cubili* (*Sulit PNH 22872*), polar view. — Fig. 2. *Otonephelium stipulaceum* (*herb. Hooker*, 1867), polar view. — Fig. 3. *Cubilia cubili* (*Sulit PNH 22872*), equatorial view. — Fig. 4. *Otonephelium stipulaceum* (*herb. Hooker*, 1867), equatorial view. — Fig. 5. *Cubilia cubili* (*Sulit PNH 22872*), section. — Fig. 6. *Otonephelium stipulaceum* (*herb. Hooker*, 1867), section. All magnifications 2600 x.

Plate III. Fig. 1. *Litchi chinensis* subsp. *philippinensis* (*Vidal 722*), polar view. Fig. 2. id. equatorial view. — Fig. 3. *Litchi chinensis* subsp. *chinensis* (*Poilane 11991*), polar view. Fig. 4. id. equatorial view. — Fig. 5. *Litchi chinensis* subsp. *javensis* (L 908–270.267), polar view. Fig. 6. id. equatorial view. All magnifications 2600 x.

Plate IV. Fig. 1. *Pometia pinnata* f. *acuminata* (*Haviland 134*), polar view, 2600 x. Fig. 2. id., equatorial view, 2600 x. — Fig. 3. *Pometia pinnata* f. *glabra* (*bb 29745*), reticulum, 5200 x. — Fig. 4. *Pometia pinnata* f. *acuminata* (*Haviland 134*), detail ectoaperture, 10400 x. — Fig. 5. *Pometia pinnata* f. *glabra* (*Hoogland & Craven 10603*), section, 1000 x. Fig. 6. id. detail endoaperture, 5200 x.

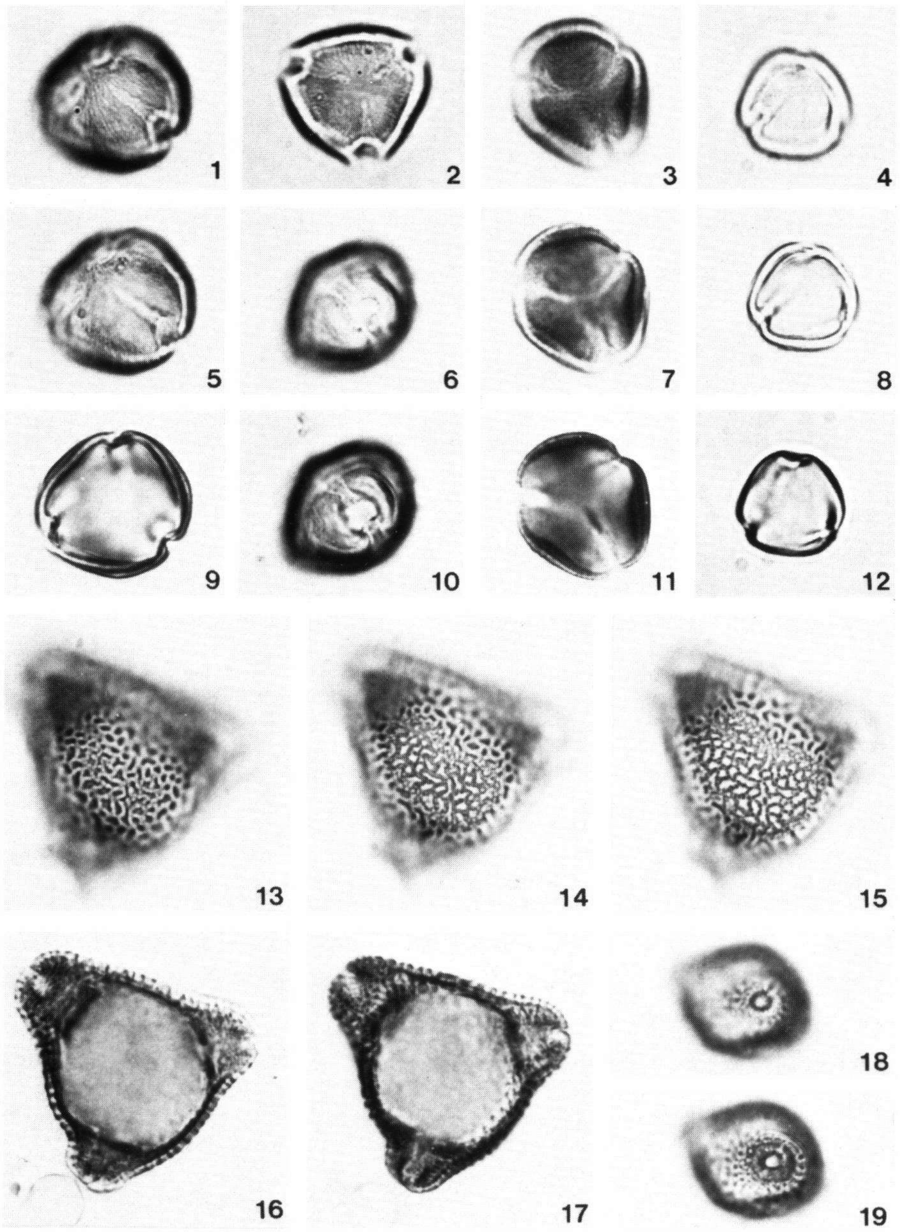
Plate V. *Pometia pinnata* f. *repanda*. Fig. 1. (*V-239*), polar view, 1000 x. Fig. 2. id. reticulum, 5200 x. Fig. 3. (*Mahuze BW 5149*), polar view, 1000 x. Fig. 4 and 5. id. reticulum, 5200 x. Fig. 6. (*V-239*), reticulum, 5200 x.

Plate VI. Fig. 1. *Pometia pinnata* f. *pinnata* (*Mauriasi BSIP 12477*), endoaperture seen from inside, 2600 x. — Fig. 2. *Pometia pinnata* f. *glabra* (*bb 29745*), cross-section through endoaperture, 5200 x. — Fig. 3. *Pometia pinnata* f. *pinnata* (*Mauriasi BSIP 12477*), endoaperture seen from inside, 10400 x. Fig. 4 and 5 id. (*Hoogland & Craven 10603*), cross-section through endo-aperture, 5200 x. Fig. 6. id., 10450 x.

Plate VII. *Pometia pinnata* f. *glabra* (*Kostermans 21620*). Fig. 1. Lamellar structure of endoaperture, 8300 x. Fig. 2. id., detail, 25250 x.

Plate VIII. *Pometia pinnata* f. *glabra* (*Kostermans 21620*). Fig. 1. Cross-section endoaperture, 11500 x. Fig. 2. id. non-acetolysed grain, 4950 x.

Plate IX. Fig. 1. *Cubilia cubili* (*Sulit PNH 22872*), equatorial section, 5000 x. Fig. 2. id. detail aperture, 15000 x. — Fig. 3. *Litchi chinensis* subsp. *chinensis* (*Poilane 11991*), equatorial section, 4100 x. Fig. 4. id. detail aperture, 8950 x.



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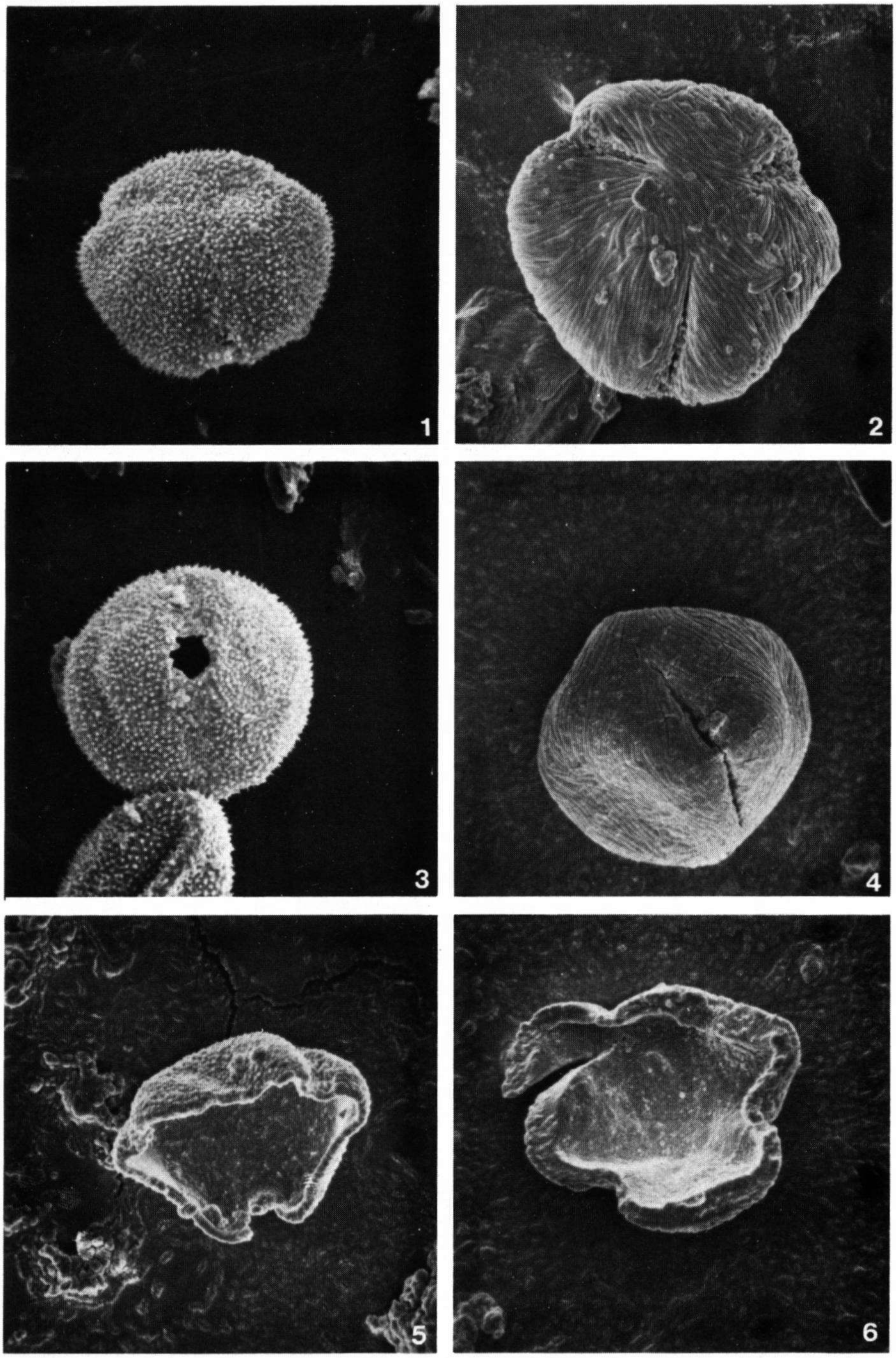

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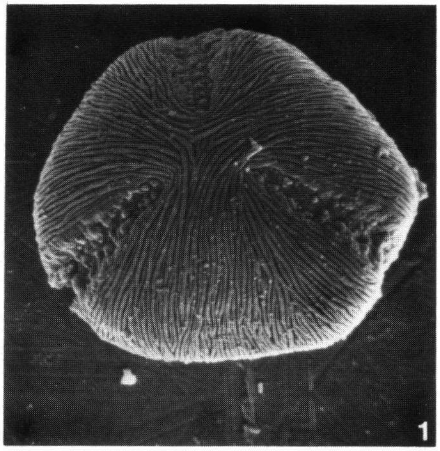

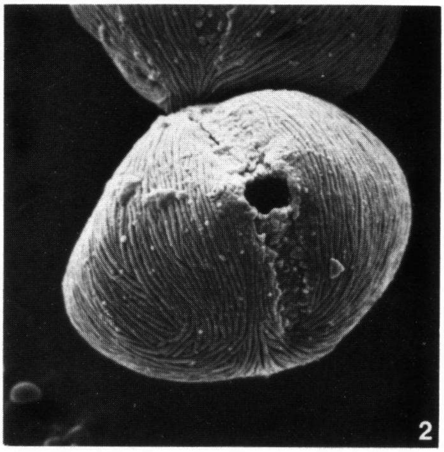

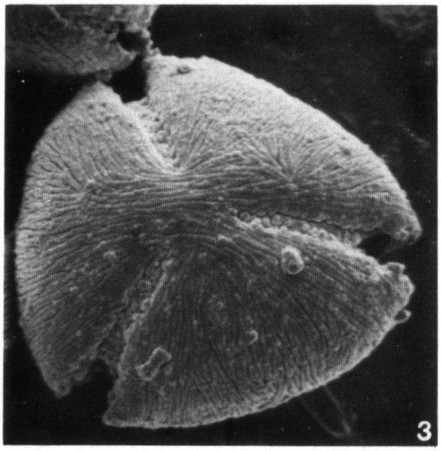

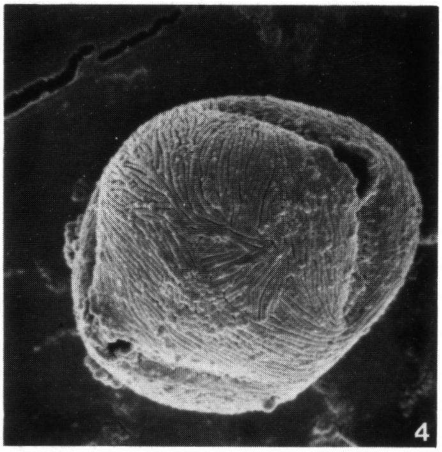

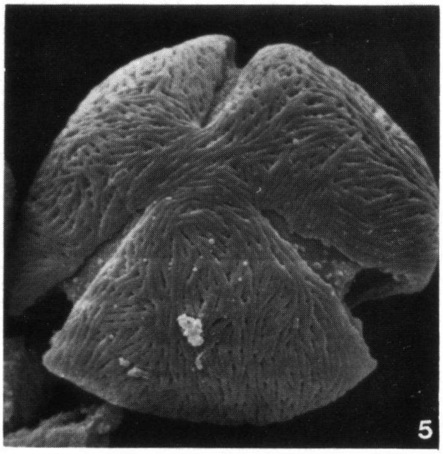

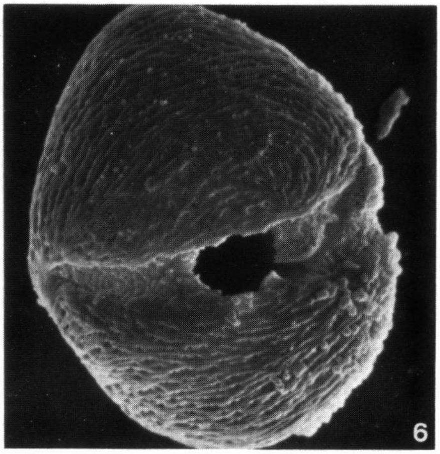

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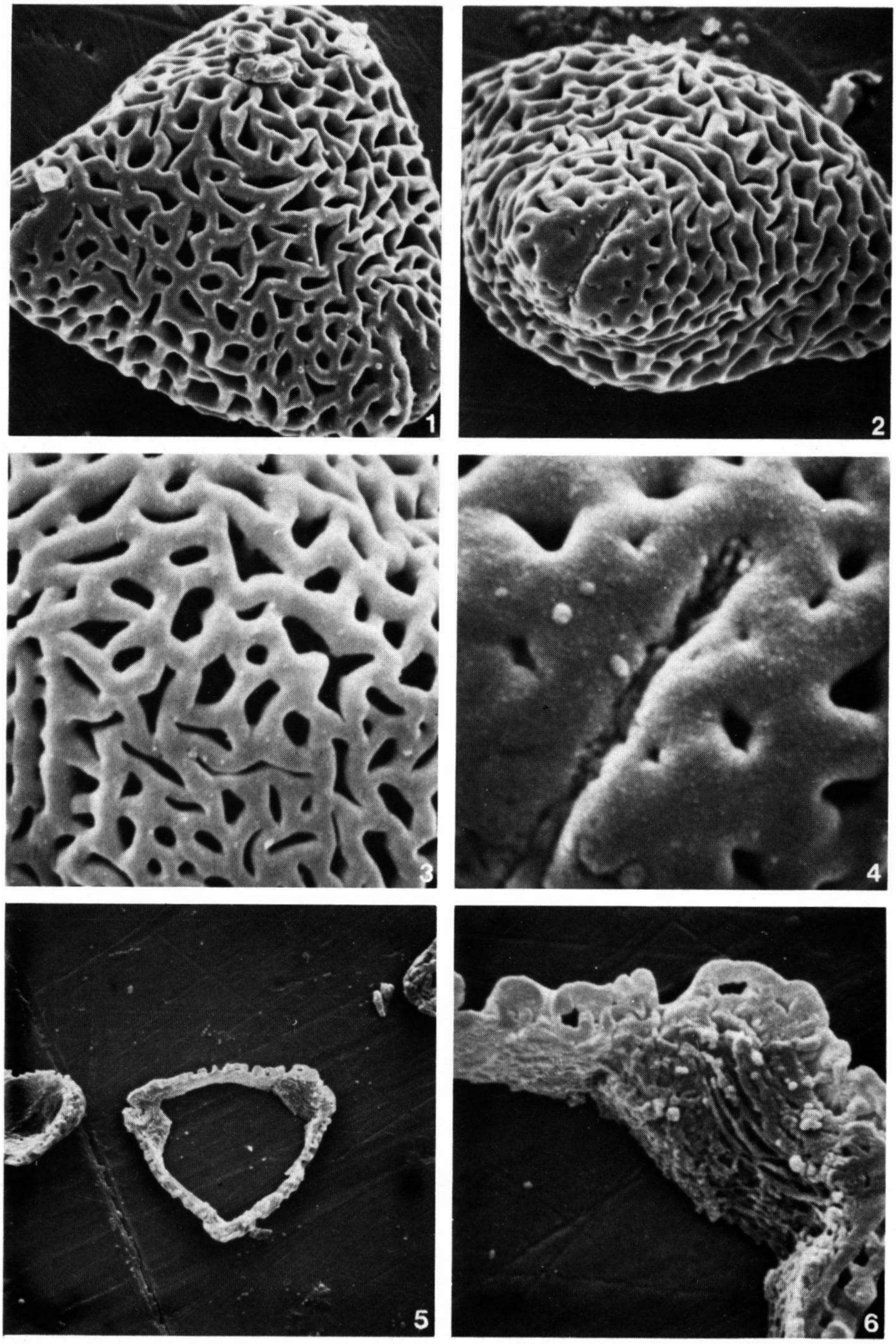

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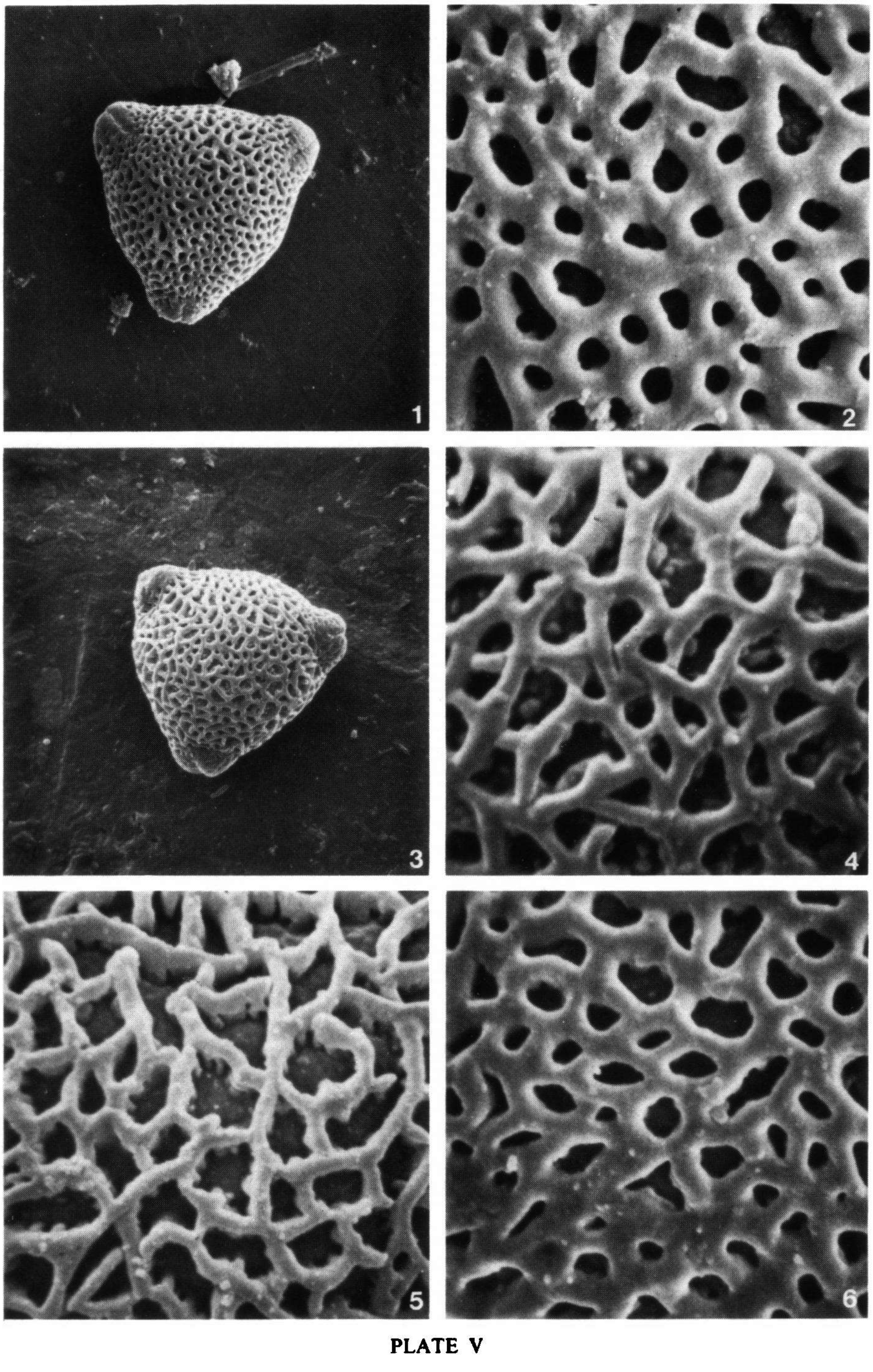

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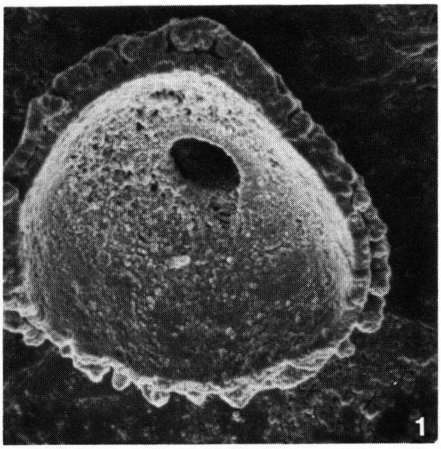
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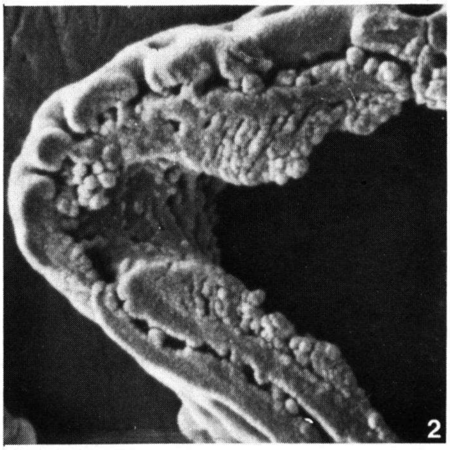
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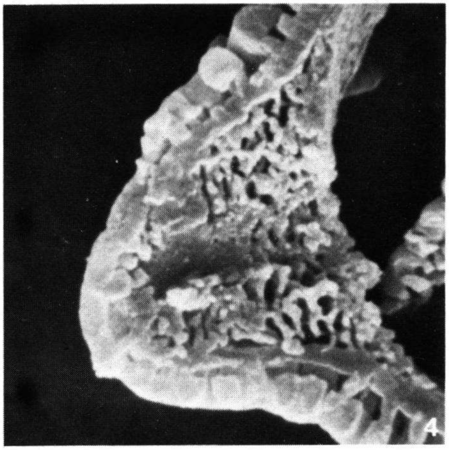
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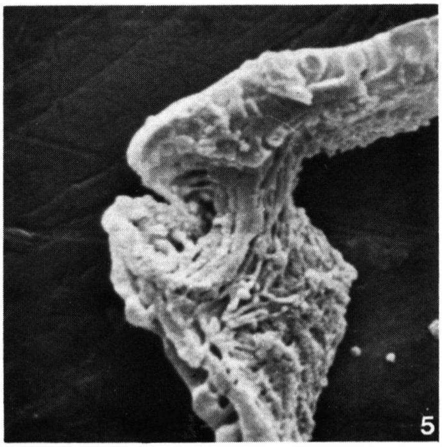
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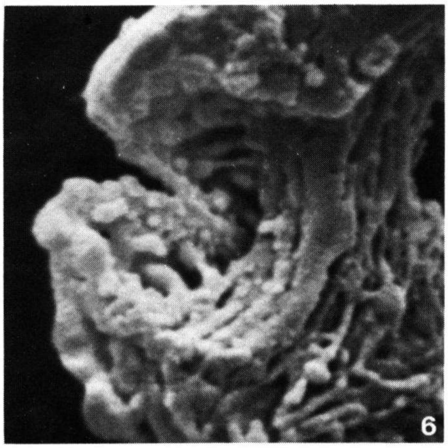
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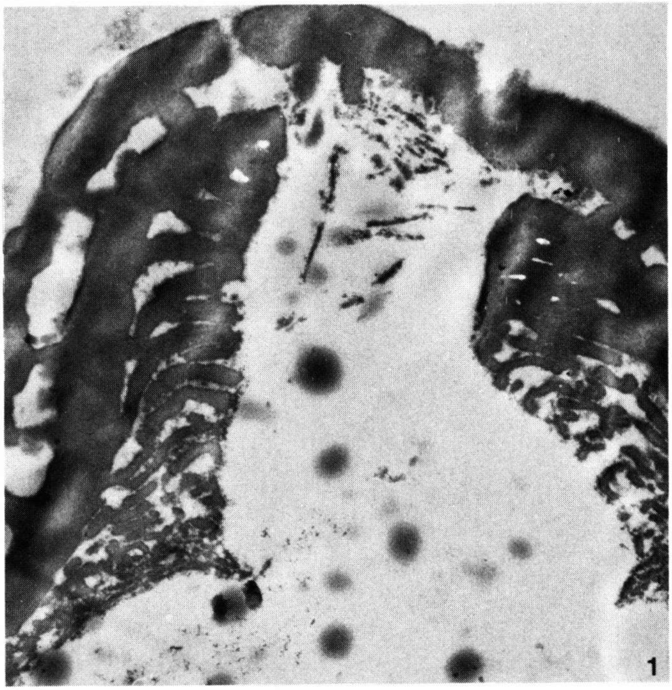
PLATE VI

PLATE VII



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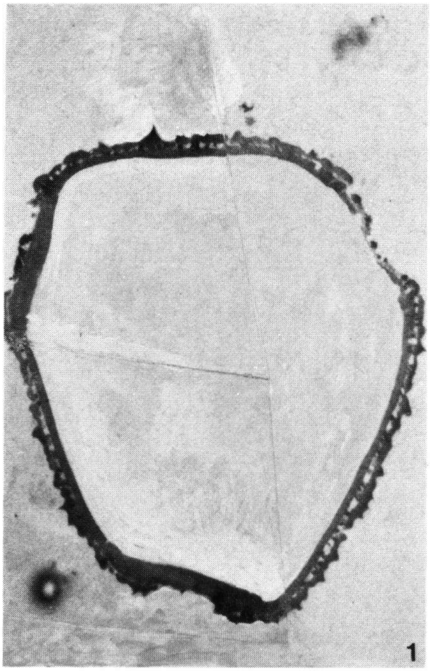

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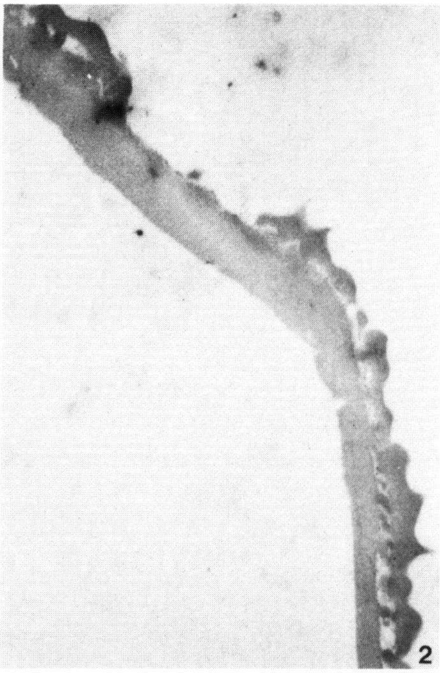

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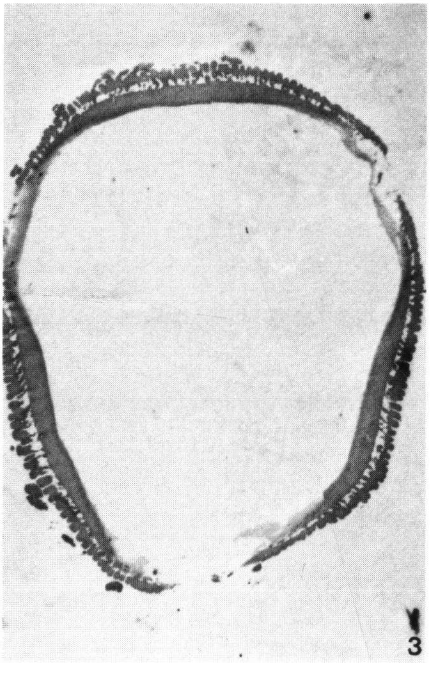

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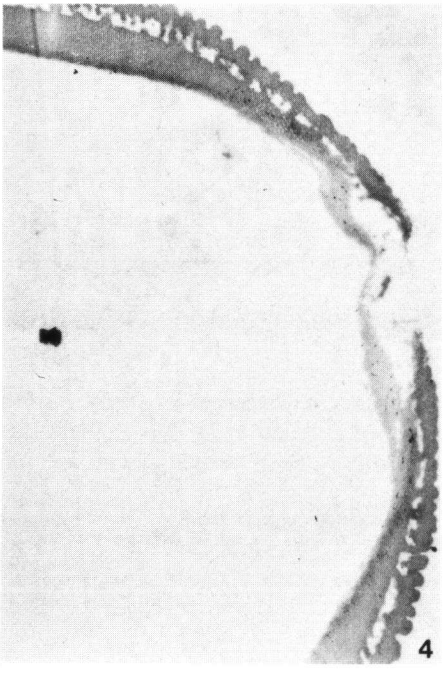

4

PLATE IX