A GENERIC ATLAS OF HAMAMELIDACEOUS POLLENS

A. Linn Bogle[1,2]
C. Thomas Philbrick[2]

The Hamamelidaceae, when considered in the broad sense, i.e., including the subfamily Liquidambaroideae, which is often split off as a segregate family Altingiaceae, presently consists of 28 genera, or 29 if the poorly known segregate genus *Semiliquidambar* H. T. Chang (1962) is admitted.

Among angiosperms the Hamamelidaceae appear to be a relatively ancient family, with a very high proportion of small or monotypic genera having highly restricted or narrowly endemic distributions, and a high concentration of both genera and relatively primitive floral types in Southeast Asia. Concomitant with this phytogeographical evidence of antiquity is a fossil record which, in the form of the readily identifiable periporate pollen grains of *Liquidambar*, extends back at least as far as the Paleocene (Muller, 1970) or possibly even the Cretaceous on the basis of macrofossils of *Liquidambar* (Brown, 1933a, b). But the pollen of *Liquidambar* is relatively specialized within the family. If reliable identification of the more generalized and primitive tricolpate pollens which characterize the large majority of hamamelidaceous genera becomes possible, the microfossil record of the family may be found to extend considerably further back into the Cretaceous.

The pollen morphology of the family has been the subject of several investigations in recent years, but none of these has covered the entire family, and most have considered only a single genus or a few of the more common genera. Several of the more significant studies include the following:

Simpson (1936) categorized the pollen grains of 18 extant hamamelidaceous genera in six morphological groups which he considered convenient, and described fossil pollens of six genera which he attributes to the family from Tertiary lignitic coals of Argyllshire, western Scotland.

Erdtman (1943) provided descriptions of *Hamamelis* and *Liquidambar* as examples of Hamamelidaceae. He later (1946, 1952) provided brief descriptions of the pollen of 18 species from 15 genera, including *Distylium guatemalense* (= *Molinadendron guatemalense* (Radlk. ex Harms) Endress) as representative of the genus *Distylium*, and *Sycopsis dunnii* (= *Distyliopsis dunnii* (Hemsl.) Endress) as representative of the genus *Sycopsis*. In this respect a currently recognized species of *Distylium* is not included in his descriptions, but one of *Sycopsis*

[1]Scientific Contribution Number 1D32 from the New Hampshire Agricultural Experiment Station.
[2]Present address: University of New Hampshire, Botany and Plant Pathology Department, Durham, N.H. 03824.

is by virtue of the fact that he added a description of *Sycopsis griffithiana* Oliv. in 1952. The 1946 descriptions apparently provided the basis for his general description of the pollen morphology of the family (1952).

Ikuse (1956) also provided brief descriptions of the pollen of ten species of six genera native or cultivated in Japan (*Liquidambar, Disanthus, Loropetalum, Hamamelis, Corylopsis, Distylium*).

Lee (1969), in a master's thesis (unpublished) written at the University of Pennsylvania, described the pollen of 22 species of ten genera, and recognized four pollen types: tricolpate, tricolporoidate, tricolporate, periporate.

Several authors have published detailed analyses of the pollen of *Liquidambar* and *Altingia* in relation to considerations of the taxonomic position and evolutionary history of these genera (e.g., C. T. Chang, 1958, 1959; Kuprianova, 1960; Makarova, 1957; Samorodova-Bianki, 1957; Sears, 1930).

The most extensive study to date has been that of C. T. Chang (1964), who examined and described (in Russian) 57 species of 21 genera of the family, including seven species of *Altingia* and *Liquidambar* which he separates in a family Altingiaceae, and 50 species of 19 genera of Hamamelidaceae. His descriptions are accompanied by 21 plates of photomicrographs. Several very rare genera were not included in this study for lack of material, and several new genera have since been recognized in the family.

Hesse (1978) describes the ultrastructural characteristics of the exine and "pollenkitt" of *Hamamelis vernalis, H. virginiana, Corylopsis platypetala*, and *Parrotia persica* in relation to their entomophilous (sticky pollen) or anemophilous (dry pollen) pollination ecology.

Most of these studies preceded the development and widespread use of the scanning electron microscope as a research tool in morphological studies, and were therefore conducted at the level of the light microscope, which is still the basic tool in pollen analysis. However, scanning electron micrographs of pollen grains, because of their three-dimensional appearance and great magnification, are much more useful for illustrating the surface details of grains than are light micrographs, and are increasingly being used in conjunction with light microscope analyses in palynological studies.

Scanning electron micrographs of hamamelidaceous pollen grains are infrequent in the literature, the largest assemblage that we know of being a group of eight photographs appearing in a recent review paper on evolutionary trends in the Hamamelidales-Fagales group (Endress, 1977). The SEM photographs presented here have resulted from a continuing effort to develop descriptions and illustrations of all 28 genera, in the hope that a broader base of data than has previously

been available will facilitate interpretations of intra- and inter-familial relationships and phylogenetic trends.

The genera illustrated here, and their distribution among the subfamilies and tribes of the family, for purposes of this work, are as follows:

Subfamily Liquidambaroideae. *Liquidambar, Altingia.*
Subfamily Rhodoleioideae. *Rhodoleia.*
Subfamily Exbucklandioideae. *Exbucklandia* (syn.: *Bucklandia, Symingtonia*), *Mytilaria, Chunia.*
Subfamily Disanthoideae. *Disanthus.*
Subfamily Hamamelidoideae.
Tribe Hamamelideae: *Maingaya, Ostrearia, Neostrearia, Trichocladus, Dicoryhe, Hamamelis, Tetrathyrium, Loropetalum, Embolanthera.*
Tribe Eustigmateae: *Eustigma.*
Tribe Corylopsideae: *Corylopsis, Fortunearia, Sinowilsonia.*
Tribe Fothergilleae: *Fothergilla, Parrotiopsis, Parrotia.*
Tribe Distylieae: *Sycopsis, Distyliopsis, Histylium, Molinadendron, Matudaea.*

MATERIALS AND METHODS

Pollen samples were taken from specimens collected in the field or in botanic gardens, or from specimens in or on loan from several major herbaria. Both pickled and dried materials were acetolyzed (Faegri and Iversen, 1975). For light microscope examination part of each sample was then mounted in glycerine jelly (Erdtman, 1952) and set aside for a period of at least two weeks to allow the grains to adjust to the mounting medium. Measurements were then made under oil immersion of at least thirty grains in each sample. The equatorial and polar axes were measured as seen in equatorial view. The ratio of the average dimensions of these axes (P/E) was then used to determine the shape classification according to the designations of Erdtman (1952). The magnification bars included in micrographs of whole grains represent lengths of approximately 10 μm, while those in higher magnification pictures of surface details represent approximately 1 μm.

For scanning electron microscopy, acetolyzed grains were washed in two successive distilled water washes, followed by two washes of 100 percent acetone, the first for ten minutes and the second for 30 minutes. The pollen was then transferred to aluminum stubs by means of Pasteur pipettes. The stubs had been previously coated with an acetone-tape adhesive (1 mm length of half-inch double-stick tape

partially dissolved in 10 ml of 100 percent acetone). The stubs were then coated with palladium-gold on a Technics Hummer 2 sputter coater and examined with an AMR 1000 scanning electron microscope at the Museum of Comparative Zoology of Harvard University.

OBSERVATIONS

Size. Pollen size in the family ranges from very small grains, averaging less than 20 μm along the largest diameter, to large grains averaging close to 60 μm along the largest diameter.

In general, the smallest grains among our samples are concentrated among the genera of the tribe Hamamelideae (subfamily Hamamelidoideae), in which flowers are complete, often contain staminodia and/or sterile disc lobes, and are presumably insect-pollinated. Conversely the largest grains appear among those genera which tend toward, or have advanced to, the naked-flowered, wind-pollinated state (Liquidambaroideae, *Chunia* among the Exbucklandioideae, members of tribe Distylieae in the Hamamelidoideae).

In contrast to the small grains of the Hamamelideae are the very large grains of the genus *Eustigma* (Eustigmateae, Hamamelidoideae), which is generally considered closely allied to the Hamamelideae. Although the flowers of *Eustigma* are complete, their petals are small and their styles greatly elongated, with broadly expanded sitgmatic surfaces, suggesting a specialized pollination mechanism which is, as yet, unreported.

Pollen size can also vary significantly among the species of a genus (e.g., *Fothergilla, Corylopsis*), or even among geographical races of the same species (C. T. Chang, 1964).

Among the most morphologically distinct pollen forms in the family are those of the large, nodding, red-flowered pseudanthia of *Rhodoleia* (Rhodoleioideae), which are reported to be bird-pollinated. These grains are small, with a very smooth surface marked only by minute perforations.

Shape. Pollen grain shapes among our samples ranged from oblate, through spheroidal, to prolate, with most of the taxa falling within the subspheroidal categories. Wind-pollinated genera with porate or polyporate grains, such as *Altingia, Liquidambar* and *Sycopsis,* exhibit large spheroidal grains. *Mytilaria* appears to be consistently oblate (C. T. Chang, 1964; Lee, 1969). However, shape designations are based on averages and may not reflect the full range of variation within a genus or species. Grains of the monotypic genus *Parrotiopsis,* for example, vary from oblate to prolate in shape, although the average form falls within the subspheroidal range. Furthermore, it is well-known that grain dimensions may be affected by the mounting medium

used, so one cannot be certain whether differing reports of grain shape are due to natural variation in the plant population, or to technique. For example, the general form of grains of *Loropetalum chinense* in our preparation (acetolysis, glycerine jelly) is subprolate, but C. T. Chang (1964, Methyl green/Glycerine jelly method of Wodehouse, 1935) reports grains of this species to be prolate, and Lee (1969, unacetolyzed grains in aceto-carmine, poly-vinyl alcohol, lactic-triacetin, or Calberla-basic fuchsin) reports them to be oblate-spheroidal. Consequently reports of pollen grain shape should be considered very carefully, and may be of little value from a taxonomic point of view. The general shape classification for our sample of each genus illustrated here is included in the plate caption.

Apertures. A large majority of hamamelid genera are tricolpate, with apertures varying in length, sharpness or bluntness of terminations, margin, and membrane characteristics among the genera. In general, apertures are long, with regular margins and pointed terminations approaching the poles in genera with complete flowers. Apertures become shorter, with blunt to round ends, and indistinct, irregular margins in those genera which tend toward incomplete or unisexual, wind-pollinated flowers. Rugate grains appear in *Chunia, Matudaea, Sycopsis,* and *Distylium,* and polyporate grains appear in *Altingia* and *Liquidambar.* Pore shaped apertures also appear rarely in *Chunia* (C. T. Chang, 1964), and with greater frequency (presumably through modifications of colpi or rugae) in *Distylium, Matudaea* and *Sycopsis.*

It thus appears that rugate to polyporate grains have arisen within three separate lineages within the family, in conjunction with a transition to naked, bisexual or unisexual, wind-pollinated flowers (Liquidambaroideae; *Chunia* among the Exbucklandioideae; *Distylium, Matudaea, Sycopsis* among the Distylieae in the Hamamelidoideae.

Tricolporate or tricolporoidate grains have been reported for a number of genera. Simpson (1936) described some degree of pore structure in the colpus membranes of twelve genera (*Exbucklandia, Corylopsis, Disanthus, Eustigma, Fortunearia, Fothergilla, Hamamelis, Loropetalum, Rhodoleia, Sinowilsonia, Tetrathyrium, Trichocladus*). Lee (1969) also reports tricolporate grains in *Exbucklandia,* and C. T. Chang (1964) for *Rhodoleia.* Tricolporoidate grains are described for *Mytilaria* and *Exbucklandia* by Erdtman (1952), *Chunia* and *Sycopsis* by C. T. Chang (1964) and *Fothergilla* by Lee (1969). Among the photographs included here there is the appearance of central pore-like protrusions in the colpi of *Fothergilla.* This aspect of aperture structure is in obvious need of detailed investigation.

Aperture margins are distinct in most genera and often differentiated as a pronounced margo with even or uneven edges, but margins become

indistinct in *Fortunearia, Sinowilsonia, Parrotia, Distylium, Sycopsis, Distyliopsis* and *Molinadendron*. In *Dicoryphe*, and to a lesser extent in *Embolanthera*, the margins of the apertures consist of the deep muri of the exine reticulum, which, on invagination of the colpus, close over and obscure the aperture.

Aperture membranes range from finely to coarsely granular. In some genera the granules appear to be concentrated in a longitudinal band in the center of the membrane, surrounded by a relatively smooth border. In this sense the membranes of *Disanthus* bear deeply sculptured opercula. In *Parrotia* the coarse granules of the membranes are fused in irregular ornate or vermiform patterns.

Exine. Sculpturing of the exine surfaces is generally reticulate in the family. The overall trend of modification is from a very coarsely reticulate pattern, with deep muri borne on pronounced bacula (e.g., *Dicoryphe*), through reduction of the meshes of the reticulum and depth of the muri, to very finely reticulate (*Chunia, Parrotiopsis, Distylium*), foveolate (*Altingia, Liquidambar, Matudaea*), or scrobiculate (*Rhodoleia*) patterns, with correspondingly shallower muri or a thinner tectum. In general this trend corresponds to the trends of floral modification from complete and presumably insect-pollinated types to incomplete, naked and/or unisexual forms, and is more or less evident among the three genera of Exbucklandioideae (*Exbucklandia, Mytilaria, Chunia*).

In a number of genera the exine reticulum is considerably finer in the polar than in the equatorial regions. This condition is well-developed in *Eustigma*, in which the polar areas may become scrobiculate or partially psilate. The very smooth, scrobiculate grains of *Rhodoleia* may also appear psilate in some cases.

The muri of a number of genera bear verrucae (*Altingia, Liquidambar, Fortunearia, Distylium, Distyliopis, Sycopsis, Parrotia*). These are mostly wind-pollinated taxa but the significance of this structural feature in relation to the pollination mechanism is not known at present.

Unusually variable exine sculpturing, previously unreported, is evident in our samples of *Sinowilsonia* and *Molinadendron*, and is illustrated.

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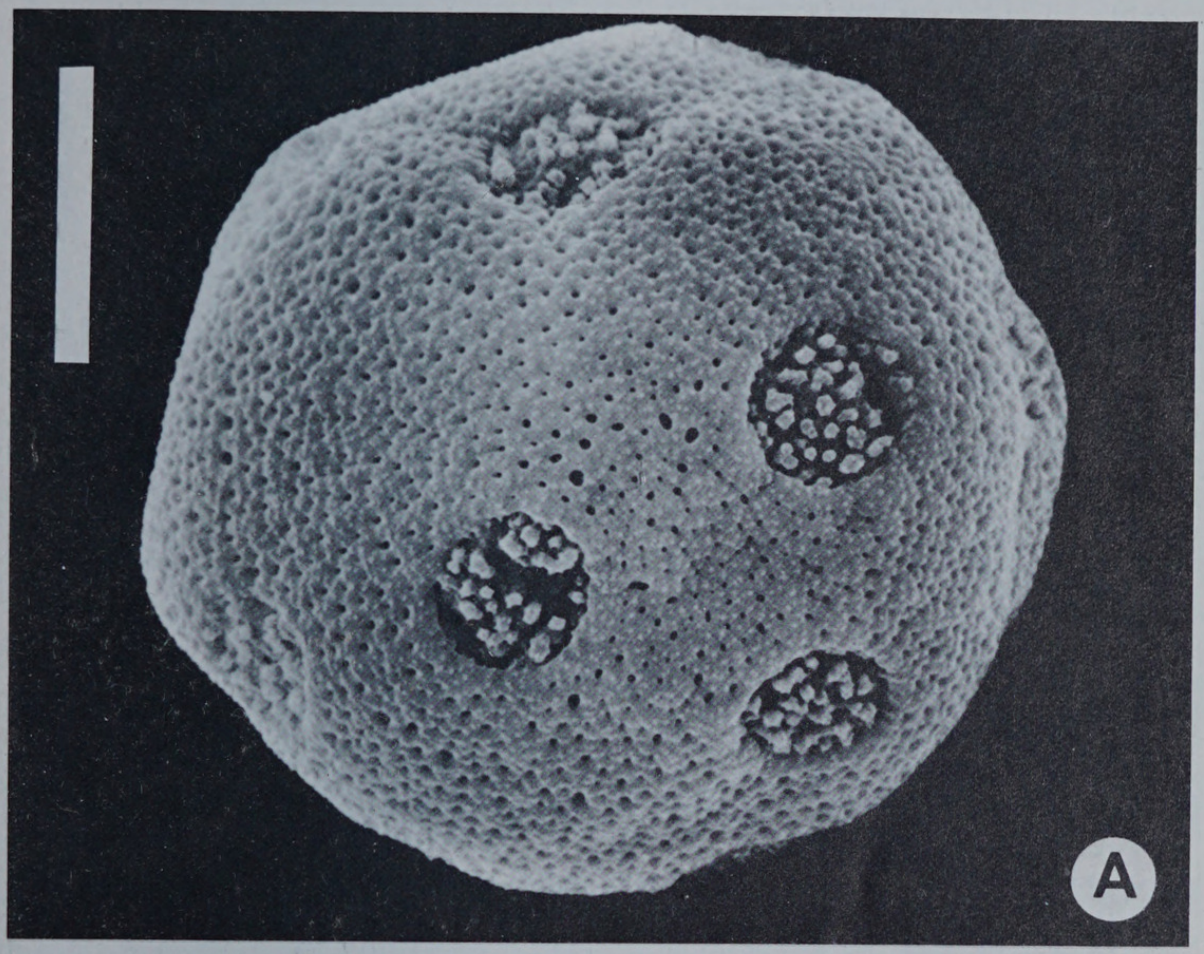
PLATE 1. *Liquidambar* L. (Subfamily Liquidambaroideae)
VOUCHER MATERIAL: *Liquidambar orientalis* Mill.; Bogle 973: from cultivated tree in authors collection (NHA).

A. Somewhat angular, periporate grain with foveolate exine and numerous granules of irregular size and shape on the pore membranes. Note the minute supratectal verrucae scattered on the surface of the tectum, × 2959. Shape: spheroidal. Size range: 32–55 μm. (Bar = 10 μm.)

B. Close up of grain surface showing a rounded aperture with a somewhat irregular margin, the supratectal verrucae, and the verrucate granules of the pore membrane, × 10,000. (Bar = 10 μm.)

A genus of three or four widely disjunct, wind-pollinated species distributed in Southeast Asia (*L. formosana* Hance), southeastern Asia Minor (*L. orientalis* Mill.) and southeastern North America and Central America (*L. styraciflua* L.). The Central American specimens are segregated by some authors as *L. macrophylla* Oerst. The genus has been the subject of several palynological investigations aimed at working out the evolutionary history and taxonomic relationships of the extant species (C. T. Chang, 1958, 1959, 1964; Kuprianova, 1960; Makarova, 1957).

Pore number, shape, diameter and margin characteristics appear to be somewhat variable within and among the species. Pores range from circular to elongate. Pore margins may be more or less even to fissured ("cracked").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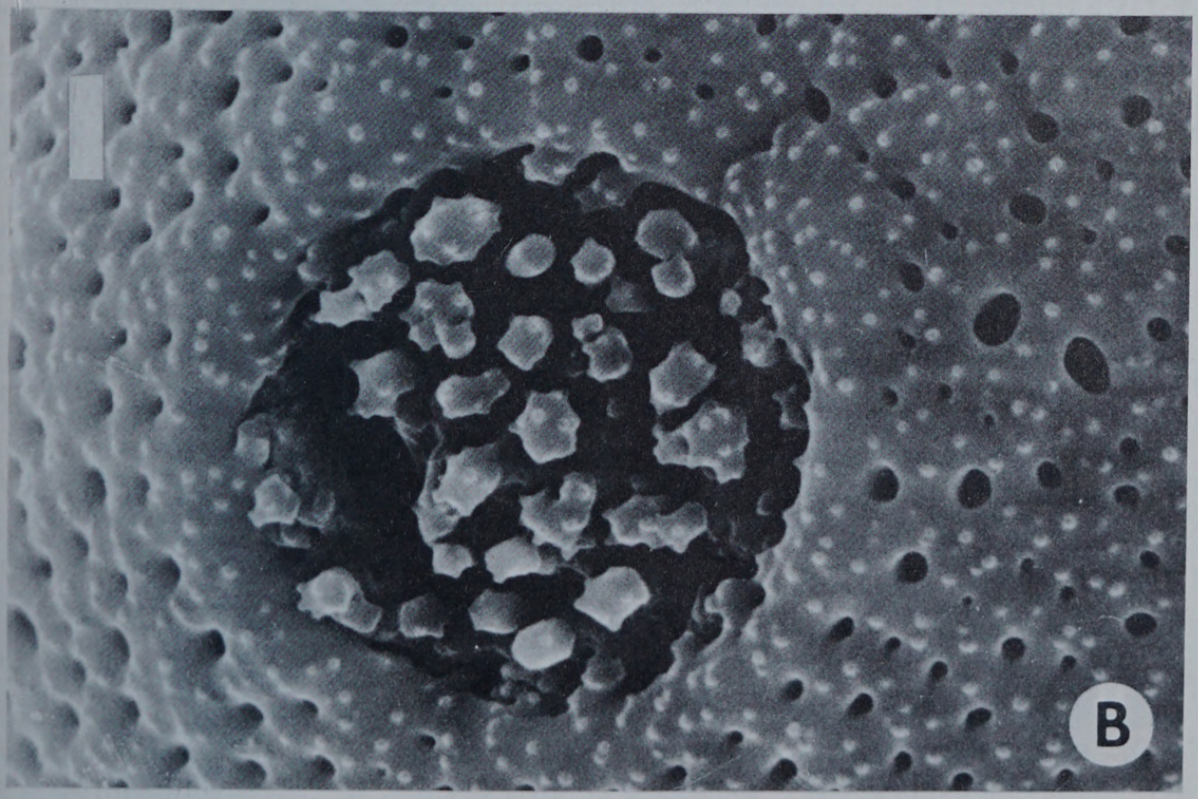
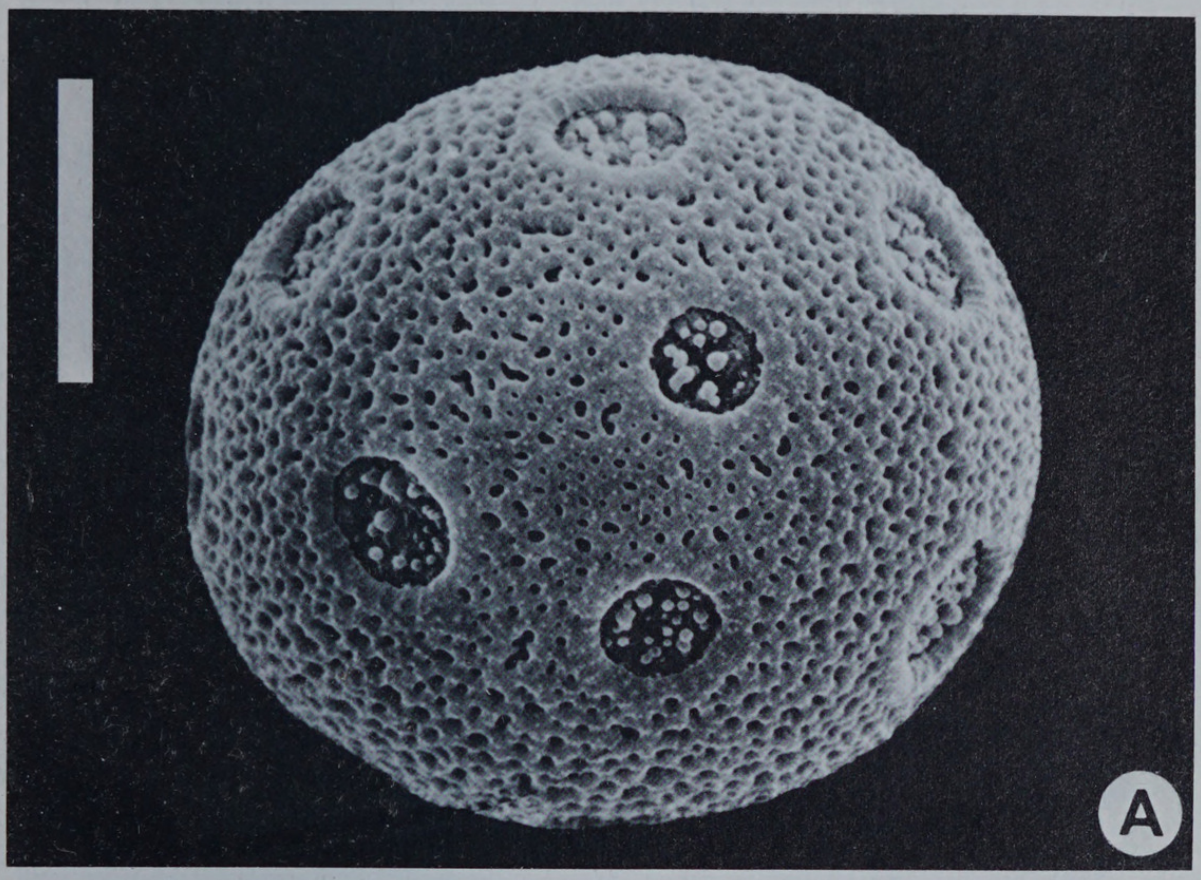

B

PLATE 2. *Altingia* Nor. (Subfamily Liquidambaroideae)
VOUCHER MATERIAL: *Altingia chinense* Oliver ex Hance; Bogle 583: Hong Kong Botanic Garden (NHA); *A. excelsa* Nor. Bogle 313: Mentigi Forest Reserve, Cameron Highlands, Malaya (NHA). *A. obovata* Merr. and Chun; H. Y. Liang 64734: Hainan, China (AA).

A. Periporate grain of *Altingia chinense* with foveolate exine; pore membranes bearing granules of varying size and shape. Note the small supratectal verrucae uniformly distributed over the surface of the tectum and on the membrane granules, × 2780. Shape: spheroidal. Size range: 35–58 μm. (Bar = 10 μm.)

B–D. Close-ups of grains of three species to show sexine, pore margin, pore membrane and membrane granules (some of which bear verrucae). B, *A. excelsa*, × 10,000; C, *A. obovata*, × 10,000; D, *A. chinense*, × 10,000. (Bar = 10 μm.)

Altingia is a genus of one (Vink, 1957) to about 13 species (various authors; see Index Kewensis, H. T. Chang, 1973). The flowers and inflorescences of the genus are similar to those of *Liquidambar*. Pollination is anemophilous. The pollen grains of *Altingia* in our material have characteristically round pores which may vary slightly in diameter, and have a distinct margin which is very nearly regular or even. Figures B–D illustrate the variation, which is apparent also in light microscope observations, of perforation size in the reticulum of the tectum. In this respect *A. excelsa* (B) has many minute, rounded perforations; *A. obovata* (C) exhibits rounded perforations of larger diameter; and *A. chinense* (A, D) has perforations which may vary in shape from rounded to somewhat elongate or irregular. From a taxonomic point of view the significance of this variation is obscure.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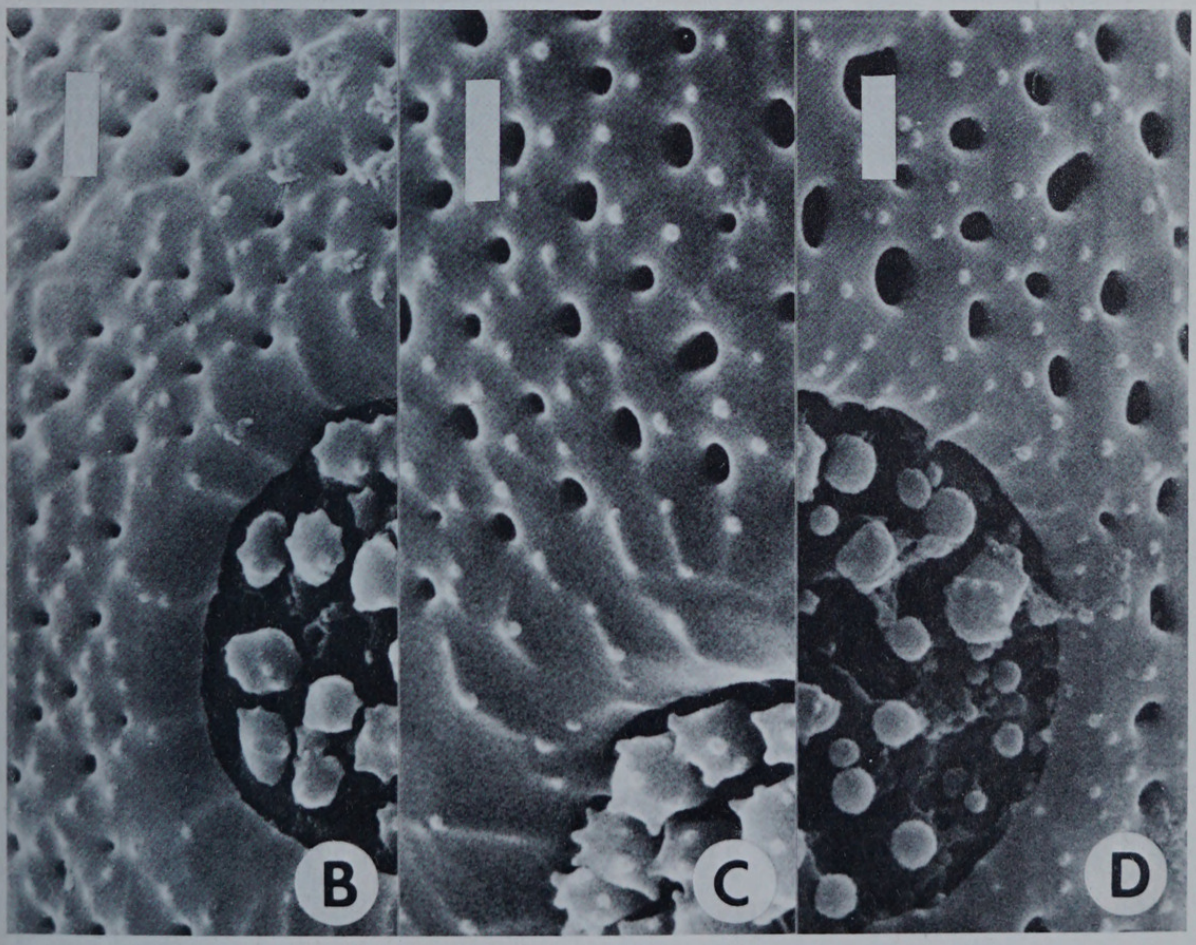

B
C
D

PLATE 3. *Rhodoleia* Champ. ex Hook. (Subfamily Rhodoleioideae) VOUCHER MATERIAL: *Rhodoleia championi* Hook. f.; Bogle 276: Klang Gates, near Kuala Lumpur, Selangor, Malaya (NHA).

A. Oblique view showing relatively smooth, scrobiculate tectum and two invaginated colpi, × 5800. Shape: subprolate. Size range in equatorial view: equatorial axis, 16–26 μm; polar axis, 20–29 μm. (Bar = 10 μm.)

B. Slightly oblique polar view showing very small perforations (lumina) of the tectum and granular sculpturing of invaginated colpus membranes, × 5920. (Bar = 10 μm.)

A genus of one variable species (Vink, 1957; Tardieu-Blot, 1965) or about 7–10 distinct species (see Exell, 1935; H. T. Chang, 1973; discussion in Tardieu-Blot, 1965) distributed from southern China southward through Indochina and Malaya to Sumatra. The pollen grains have been described as being "tricolpate-porate" by C. T. Chang (1964), but a pore is not evident in our scanning electron micrographs. *Rhodoleia* may be unique among hamamelids in being bird-pollinated or at least partially so (D. van Leeuwen, cited in Vink, 1957). The birds may be attracted to nectar reportedly secreted by a cycle of glands inserted between the stamens and the ovary, and the sticky, rather than powdery pollen may represent an adaptation toward ornithophily.


A

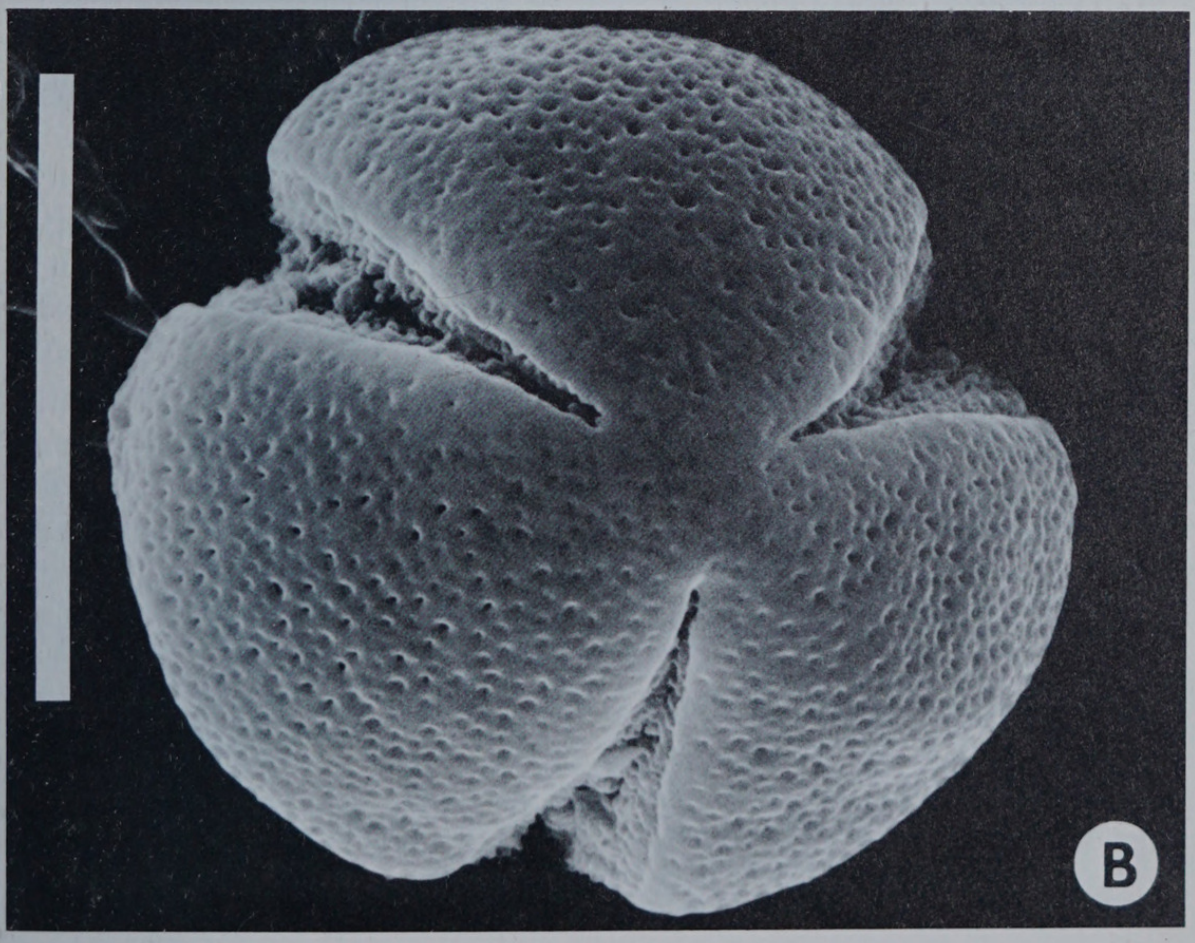
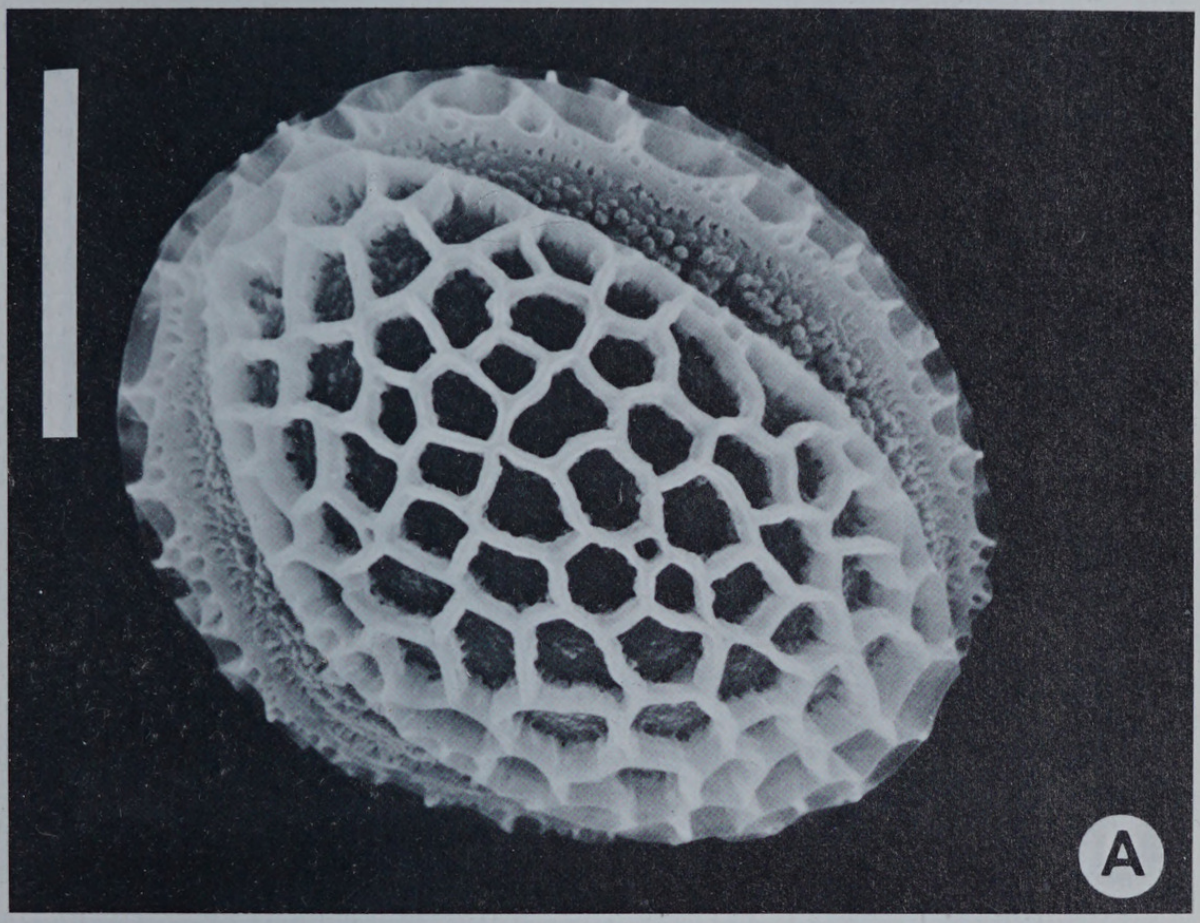

B

PLATE 4. *Exbucklandia* R. W. Brown. (Subfamily Exbucklandioideae)
VOUCHER MATERIAL: *Exbucklandia populnea* (R. Br. ex Griff.) R. W. Brown; Bogle 314: Tanah Rata Village, Cameron Highlands, Selangor, Malaya (NHA).

A. Equatorial view showing the coarse reticulum. Note the large lumina of fairly uniform size but somewhat irregular, angular shape; the margin of very small lumina bordering colpi; deep muri resting on distinct bacula; coarse granules on surface of the nexine; granular colpus membranes, × 3520. Shape: prolate spheroidal. Size range in equatorial view: equatorial axis, 26–32 μm; polar axis, 23–37 μm. (Bar = 10 μm.)

B. Polar view showing coarsely reticulate exine with lumina not differing markedly in size from those of the mesocolpium. Note the colpi with acutely pointed ends reaching nearly to the poles; the distinct bacula subtending the muri; coarse granules on nexine surface, × 3540. (Bar = 10 μm.)

A genus of two (Vink, 1957; Tardieu-Blot, 1965) or three (H. T. Chang, 1973) species ranging from the Sikkim Himalaya to central China, and southward through Indochina and Malaya to Sumatra. The mature flowers of *Exbucklandia* are incomplete, lacking a calyx, and are rather inconspicuous. No published observations on the pollination mechanism are known to us. The pollen structure is similar in its coarsely reticulate exine and tricolpate condition to that of a number of other hamamelidaceous genera with complete and presumably insect-pollinated flowers, including those of *Dicoryphe* (Madagascar), and *Maingaya* (Malaya). The closely related genus *Mytilaria* (Indochina) has a finer reticulum. Simpson (1936) suggests the presence of a pore in a fossil grain he attributes to *Exbucklandia,* while Lee (1969) describes and illustates (Pl. I, Fig. 6; Pl. III, Fig. 2) a pore in the colpus of *Exbucklandia.*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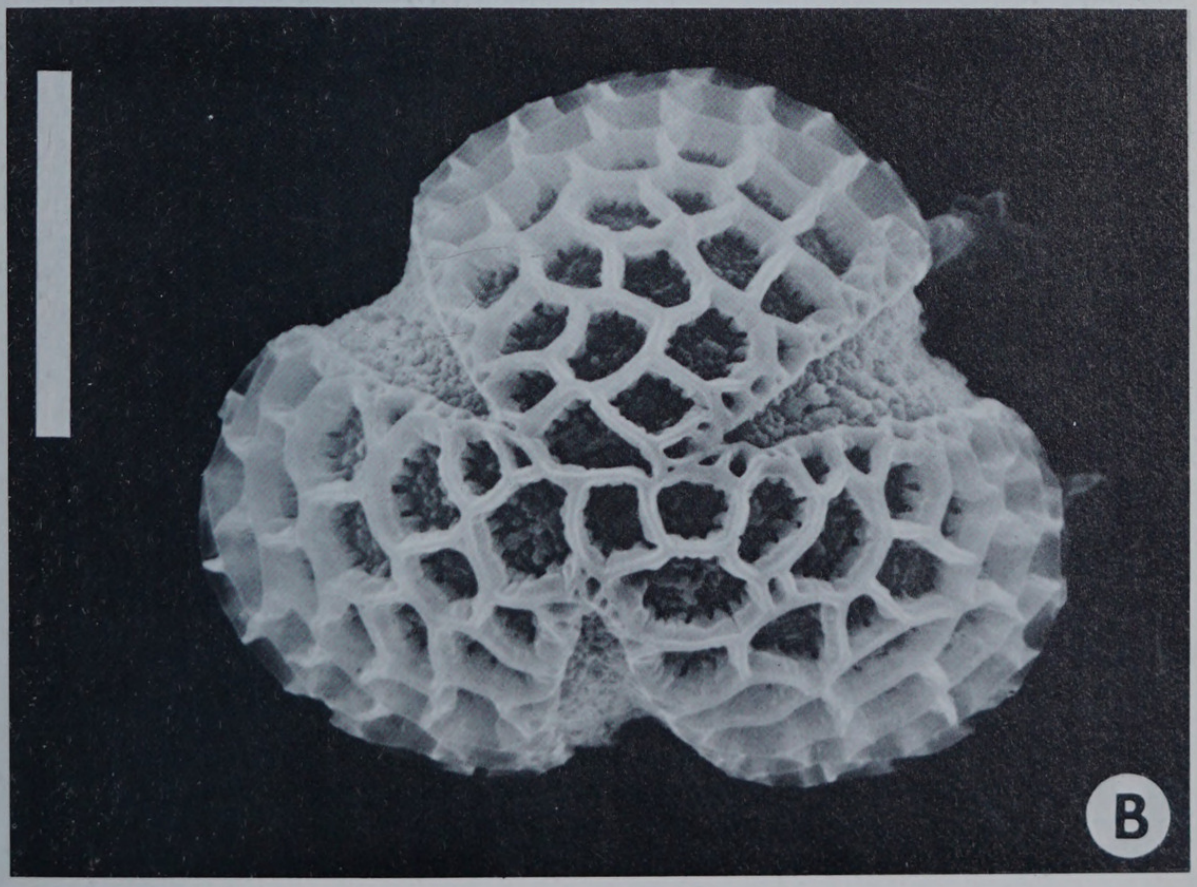
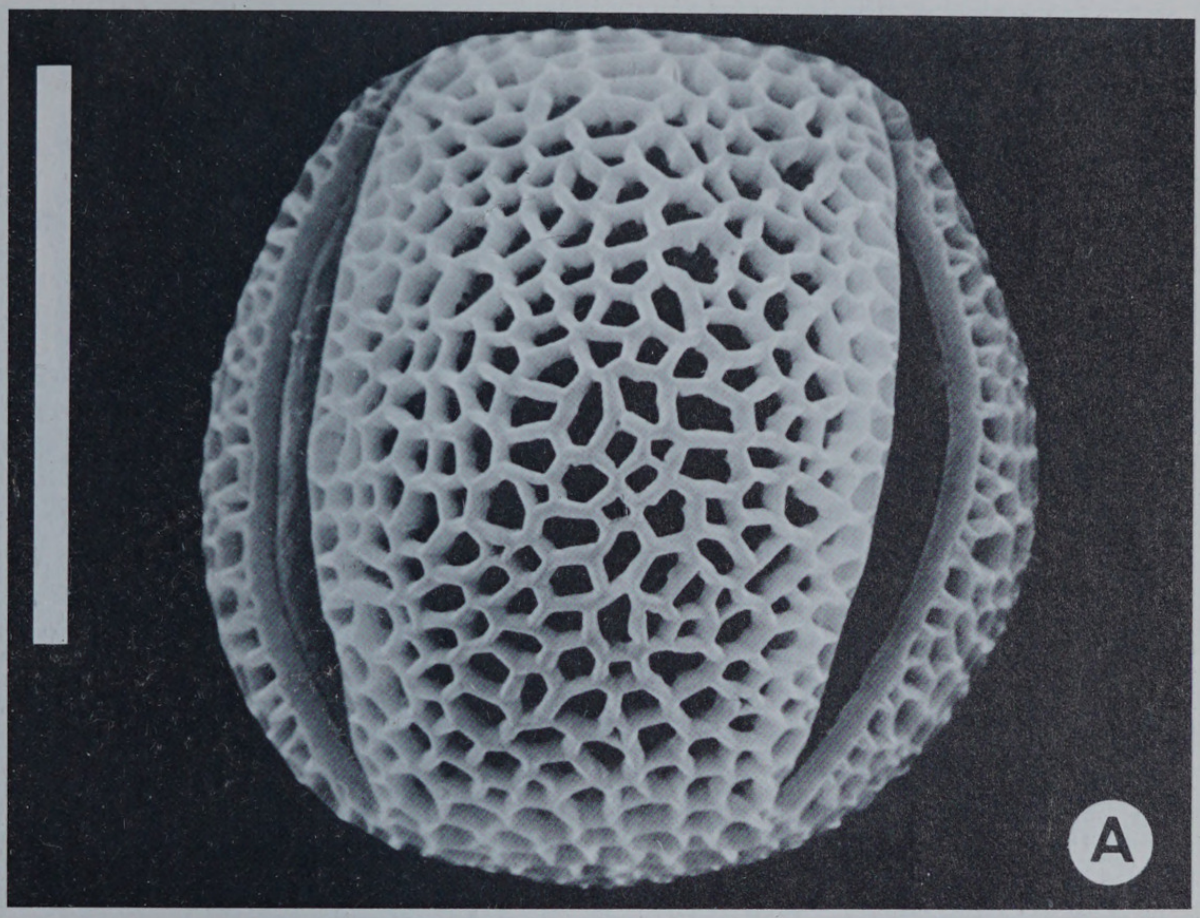

B

PLATE 5. *Mytilaria* Lecomte (Subfamily Exbucklandioideae)
VOUCHER MATERIAL: *Mytilaria laosensis* Lecomte; Ko 55988: Kwangsi, China (AA).

A. Slightly oblique equatorial view showing the coarsely reticulate exine, with deep muri borne on bacula. Lumina more or less isodiametric to elongate; angular in outline; varying in size, but on average smaller and more numerous per unit area than in the closely related *Exbucklandia*, × 5550. Size range in equatorial view not available. (Bar = 10 μm.)

B. Polar view of tricolpate grains. Note the less elongate lumina in the apocolpium as compared with *Exbucklandia*; margo distinct, with associated small lumina surrounding the colpi; colpus membranes appear to be relatively smooth in marginal areas, but finely granular towards the center, × 5830. (Bar = 10 μm.)

A little known monotypic genus found only in southern China and Indochina. It is almost indistinguishable from *Exbucklandia* and *Chunia* vegetatively, but differs strongly in floral morphology. The flowers are complete, with nearly inferior ovaries immersed in a fleshy spike. Ten stamens with horned filaments and hooded antlers are connivent in one cycle over minute styles and stigmas. Grains are oblate according to C. T. Chang (1964) and Lee (1969), or sub-oblate to oblate-spheroidal (Erdtman, 1946). There is no information on the pollination mechanism.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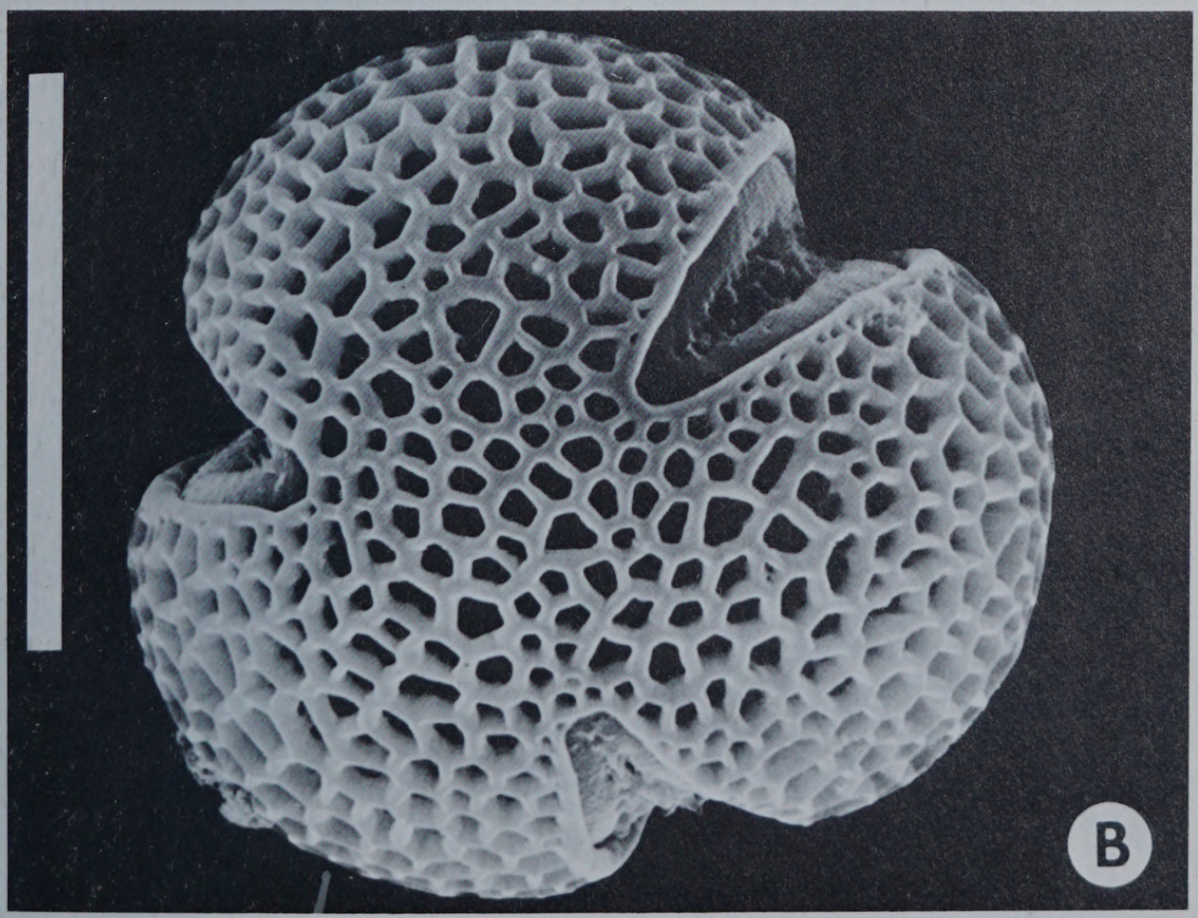
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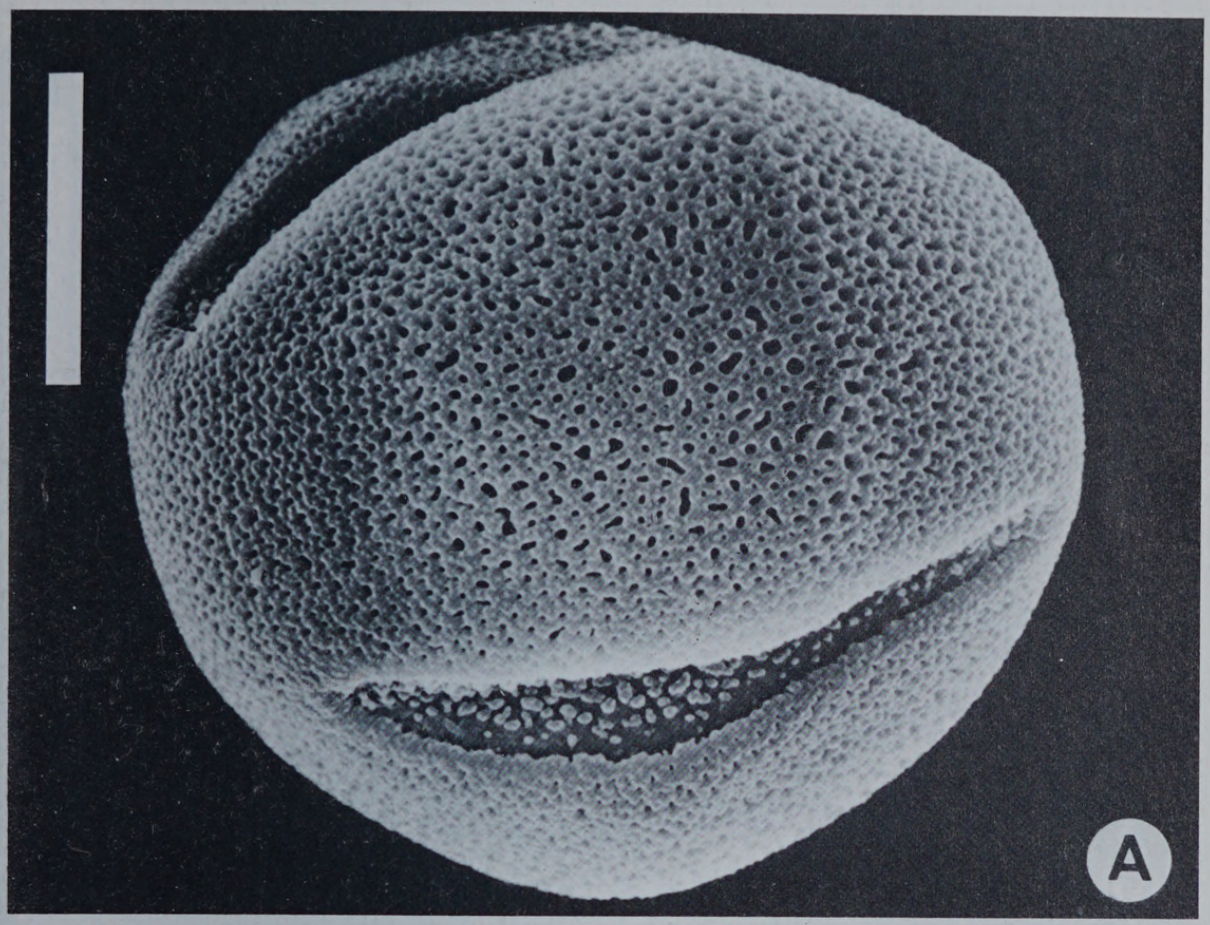
PLATE 6. *Chunia* H. T. Chang (Subfamily Exbucklandioideae)
VOUCHER MATERIAL: *Chunia bucklandioides* H. T. Chang; C. Wang 36075: Hainan, China (AA).

A. Slightly oblique equatorial view of a tricolpate grain, showing the microreticulate sexine with small lumina of variable size and shape, and granular membranes of the colpi. Note also the numerous small supratectal verrucae on the surfaces of the muri, × 2840. Shape: prolate spheroidal. Size range in equatorial view: equatorial axis, 26–37 μm; polar axis, 29–38 μm. (Bar = 10 μm.)

B. Slightly oblique polar view of a tricolpate grain showing the foveolate exine of the apocolpium, with lumina of reduced size and regular shape. Note the distinct margo and bluntly rounded ends of the colpi, the coarse granules of the colpus membranes, and the verrucae of the tectum and margo, × 3820. (Bar = 10 μm.)

Chunia is another poorly known monotypic genus. It is endemic to the island of Hainan, off the southern coast of China. Although vegetatively similar to *Exbucklandia* and *Mytilaria,* its flowers differ by being naked and clustered in short, fleshy spikes that present a "ball" of stamens on elongate filaments at anthesis. The genus has apparently evolved toward wind-pollination. Further evidence of this tendency is the pronounced modification of the exine to a relatively smooth, foveolate condition, as opposed to the coarse reticula of *Exbucklandia* and *Mytilaria,* and a tendency toward an increase in the number of apertures. Grains in our sample range from 3- or 4-colpate to hexarugate (see Plate 7). C. T. Chang (1964) reports 15 per cent hexarugate grains and some polyporate grains in his material of *Chunia.* In our sample 81 per cent of the grains are tricolpate, while 19 per cent have more than three apertures.

These modifications (naked flowers; exserted anthers; increase in aperture number; relatively smooth, foveolate exine) run parallel to similar tendencies in other members of the family which have progressed independently toward anemophily (e.g., Liquidambaroideae; Distylieae of the Hamamelidoideae). However, the minute styles and stigmas of the ovaries in *Chunia* might seem to contradict this list of characteristics which often accompany anemophily.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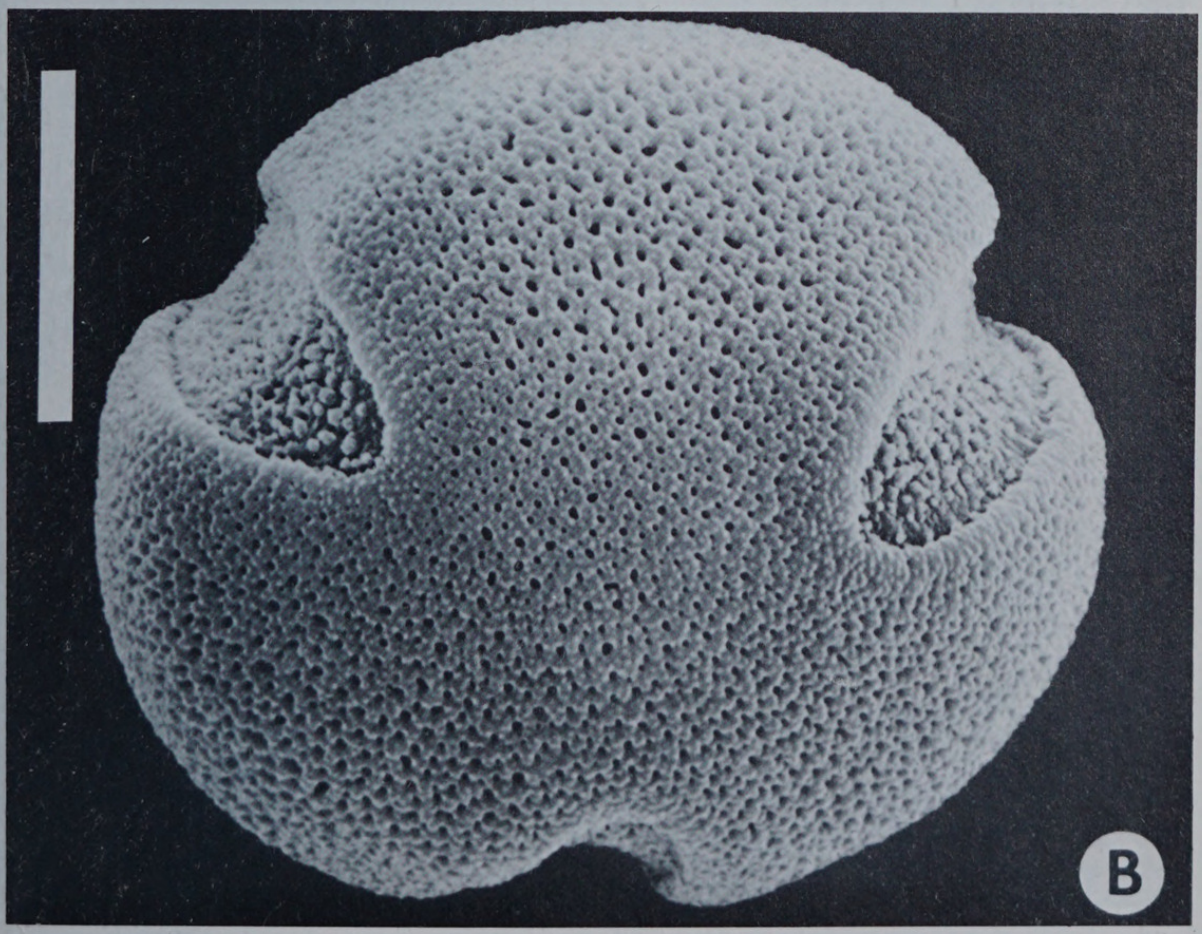
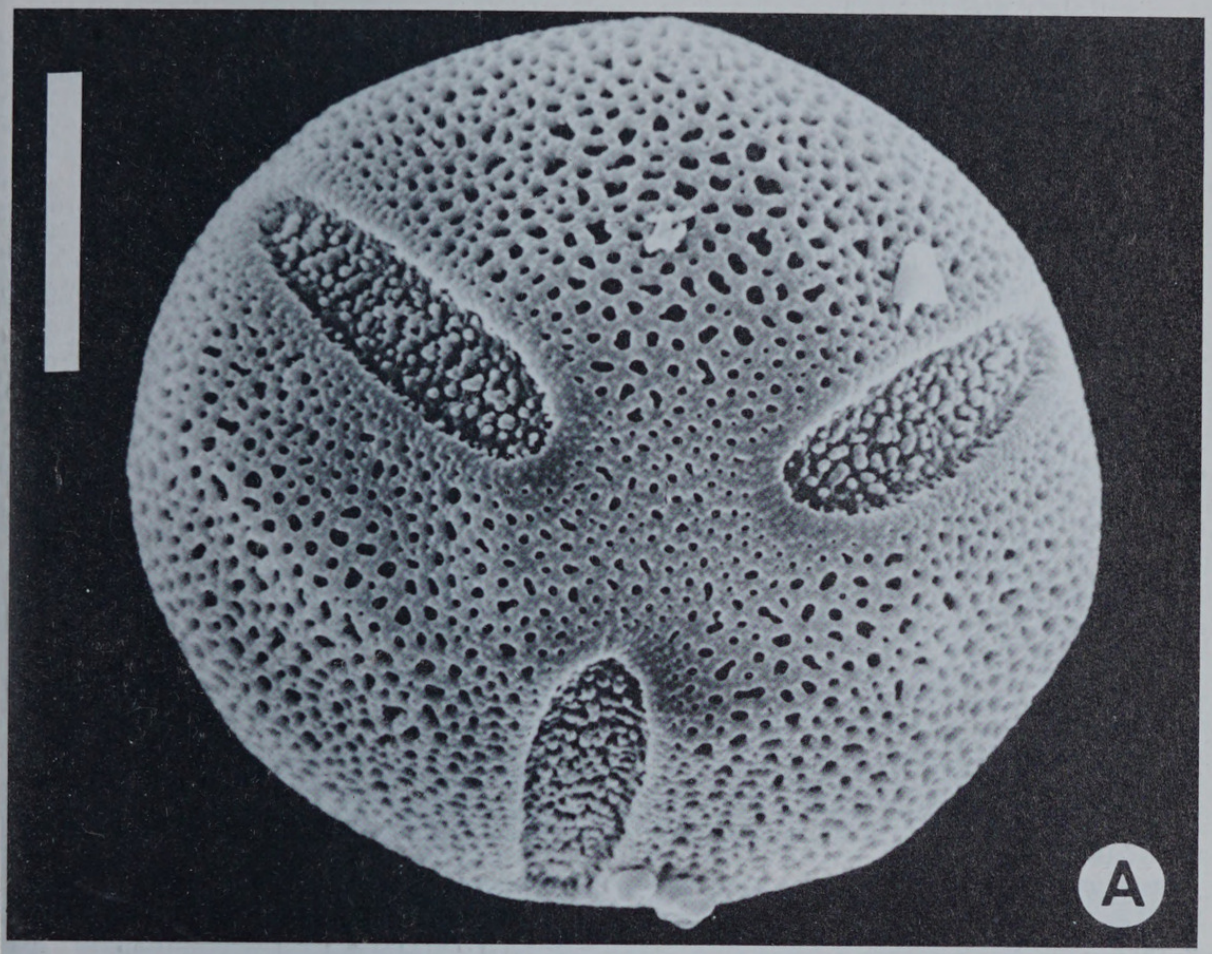

B

PLATE 7. *Chunia* H. T. Chang (Subfamily Exbucklandioideae)
VOUCHER MATERIAL: same as Plate 6.

A. View of hexarugate grain, showing three colpi of shortened length with coarsely granular membranes. Note the finely reticulate exine of the mesocolpium and the reduced size of lumina in the apocolpium, × 3170. Size range for hexarugate grains, 32–43 μm. (Bar = 10 μm.)

B. Tricolpate grain (left) next to hexarugate grain. Note difference in length of the colpi, × 2000. (Bar = 10 μm.)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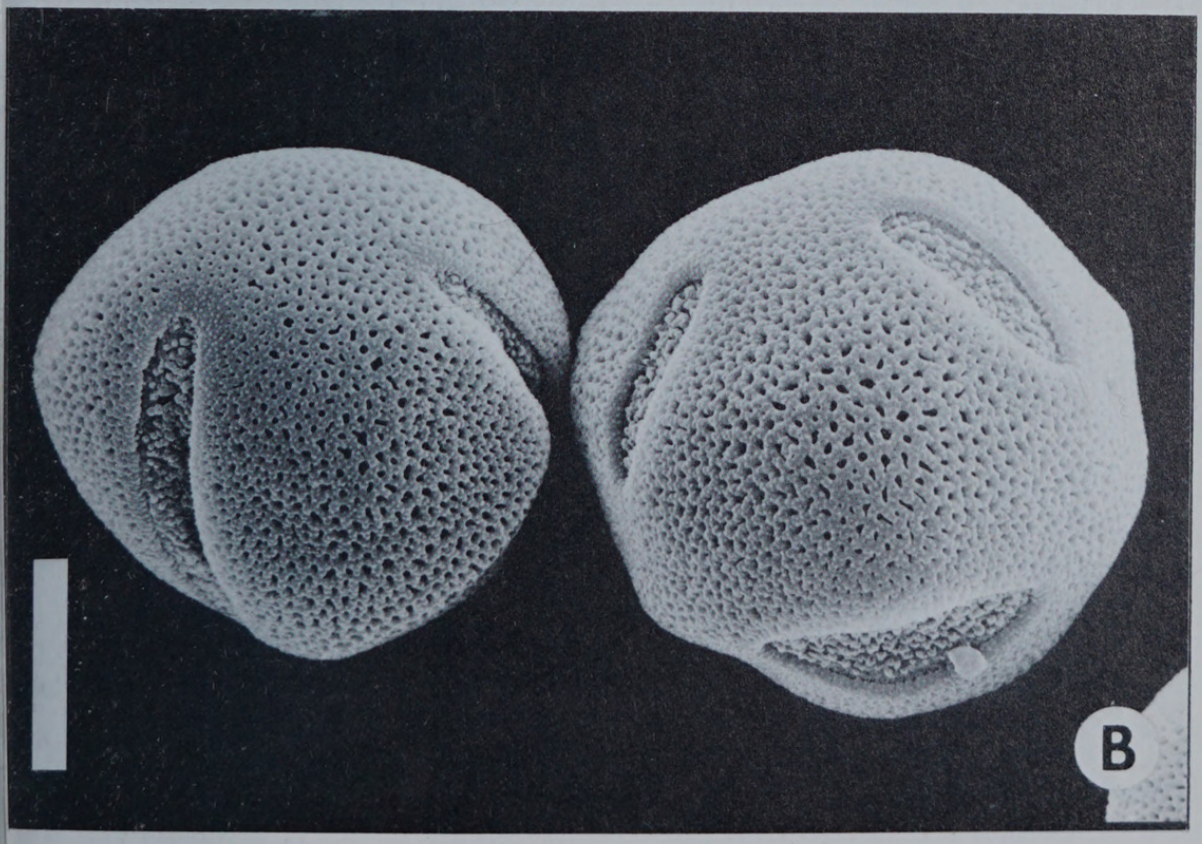
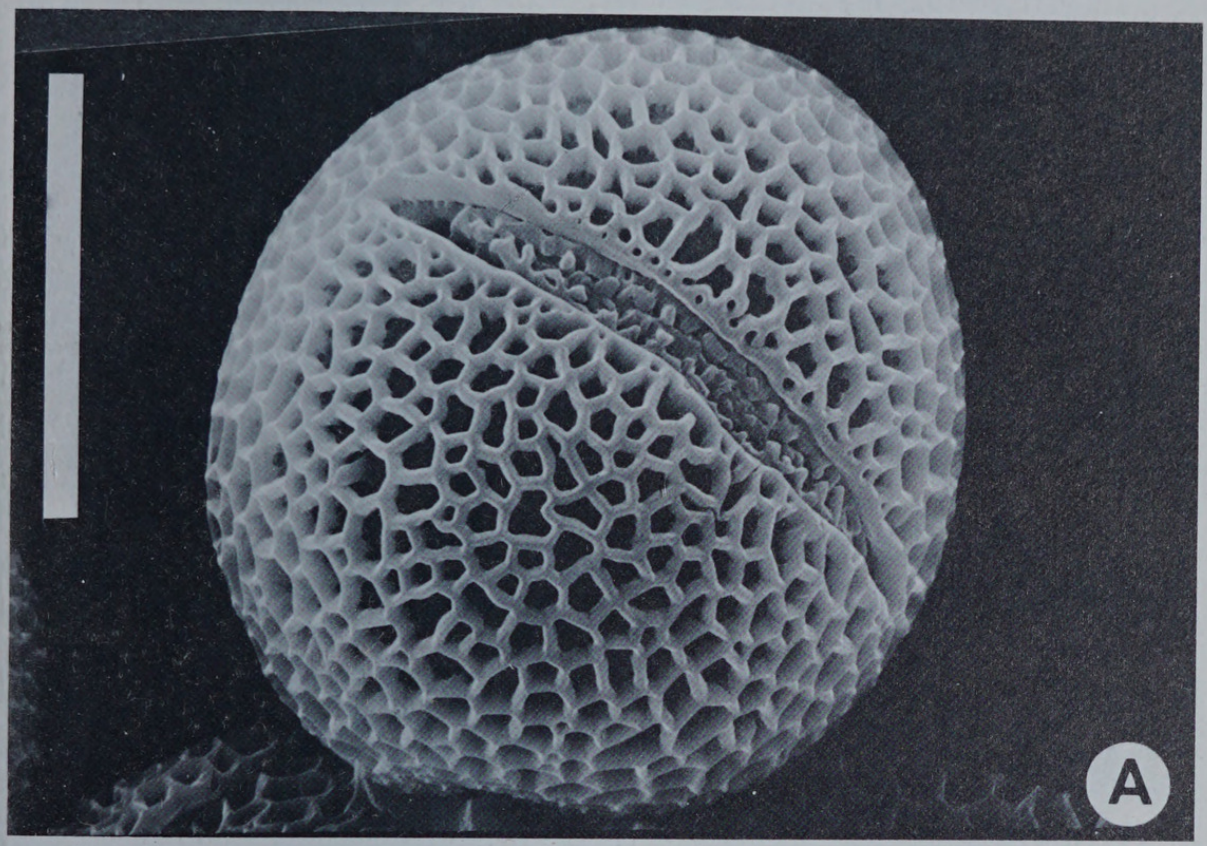

B

PLATE 8. *Disanthus* Maxim. (Subfamily Disanthoideae)
VOUCHER MATERIAL: *Dianthus cercidifolius* Maxim.; Bogle 1268, from M. Mizushima, s.n.: cultivated plant, Japan (NHA).

A. Equatorial view of tricolpate grain, showing reticulate exine, with relatively deep muri borne on short bacula. Note the generally uniform size and angular outline of the meshes, and the occasional small lumina scattered among the larger ones; the border of small lumina along margins of the colpi; the strongly sculptured exine of the colpus membrane, × 4300. Shape: prolate spheroidal. Size range in equatorial view: equatorial axis 22–33 μm; polar axis, 22–33 μm. (Bar = 10 μm.)

B. Polar view showing reticulate exine with slight reduction in size of the lumina in the apocolpium; sharply pointed ends of colpi; operculum-like islands of deeply sculptured exine on colpus membranes. The exine frequently appears tectate along the margins of the opercula, × 3900. (Bar = 10 μm.)

A monotypic genus (and subfamily) distributed in the mountains of Japan and central China, but widespread in cultivation. The presence of opercula on the colpus membranes is distinctive among hamamelidaceous pollens. The pentamerous flowers of *Disanthus* are reported to bear nectaries on the inner face of the petals (Mizushima, 1968) which attract flies as pollinators.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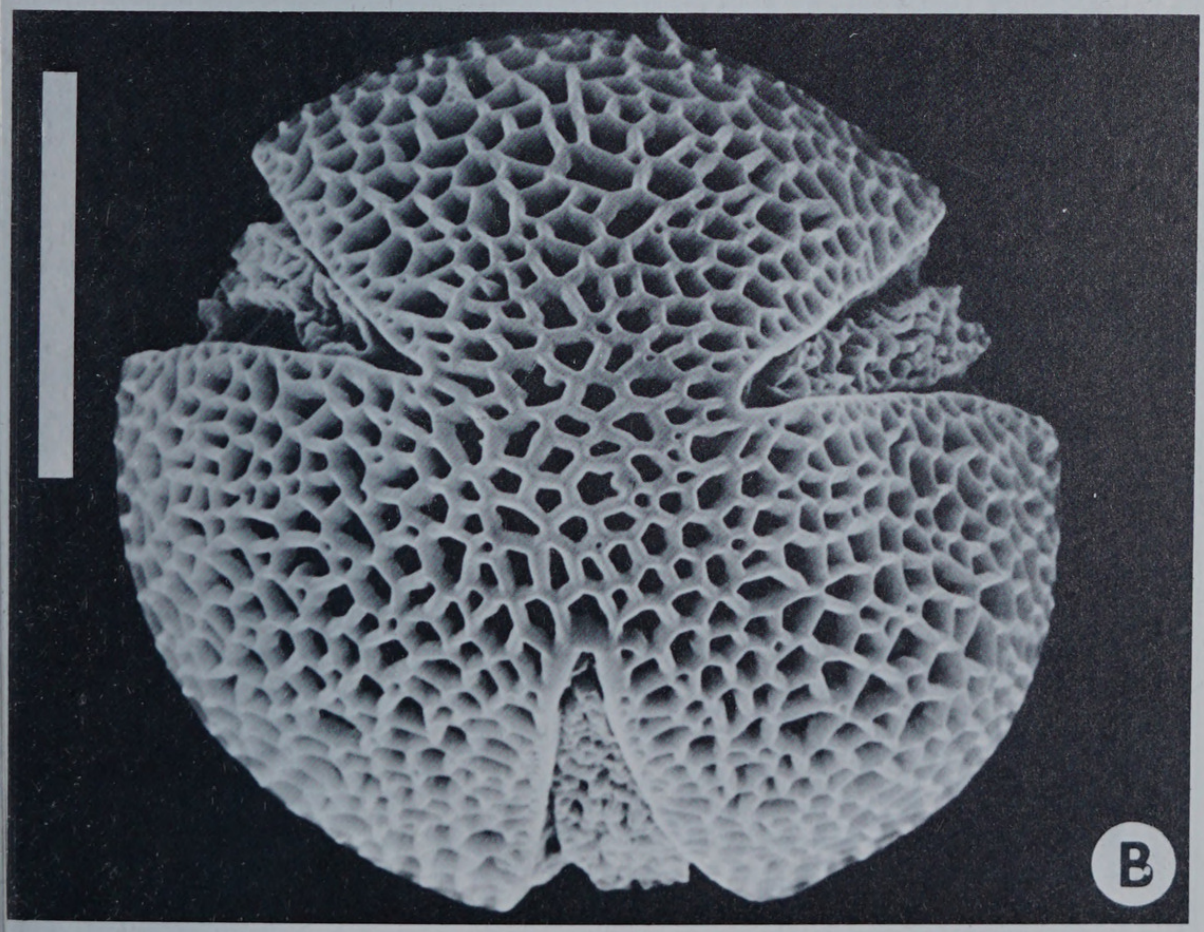

B

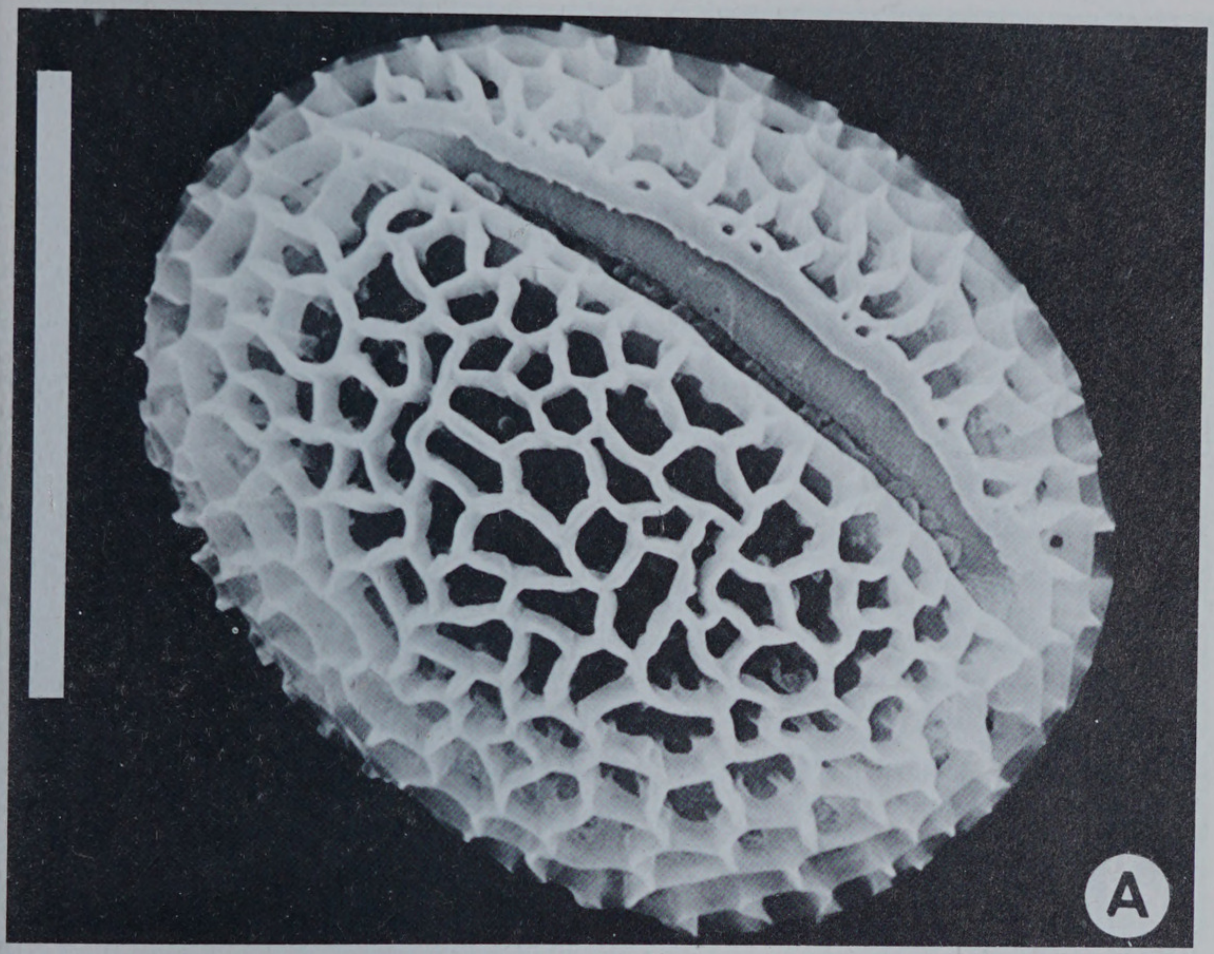
PLATE 9. *Maingaya* Oliver (Subfamily Hamamelidoideae; Tribe Hamamelideae)

VOUCHER MATERIAL: *Maingaya malayana* Oliv.; Burkill 7594: Penang, Malaya (AA).

A. Equatorial view of tricolpate grain, showing the coarsely reticulate sexine, with deep muri borne on relatively long bacula. Lumina of the sexine are irregular in shape and angular in outline. Note the very small lumina along the smooth margin of the colpus; occasional coarse granules on the nexine surface under the exine reticulum; coarsely granular central portion of the colpus membrane, × 5960. Shape: oblate spheroidal. Size range in equatorial view: equatorial axis, 16–23 μm; polar axis, 13–21 μm. (Bar = 10 μm.)

B. Polar view, grain slightly indented at upper right. Lumina of the reticulum reduced slightly in size in the apocolpium. Ends of the colpi sharply pointed, × 5910. (Bar = 10 μm.)

Maingaya is a monotypic genus known only from a very few collections in Perak and Penang, Malaysia.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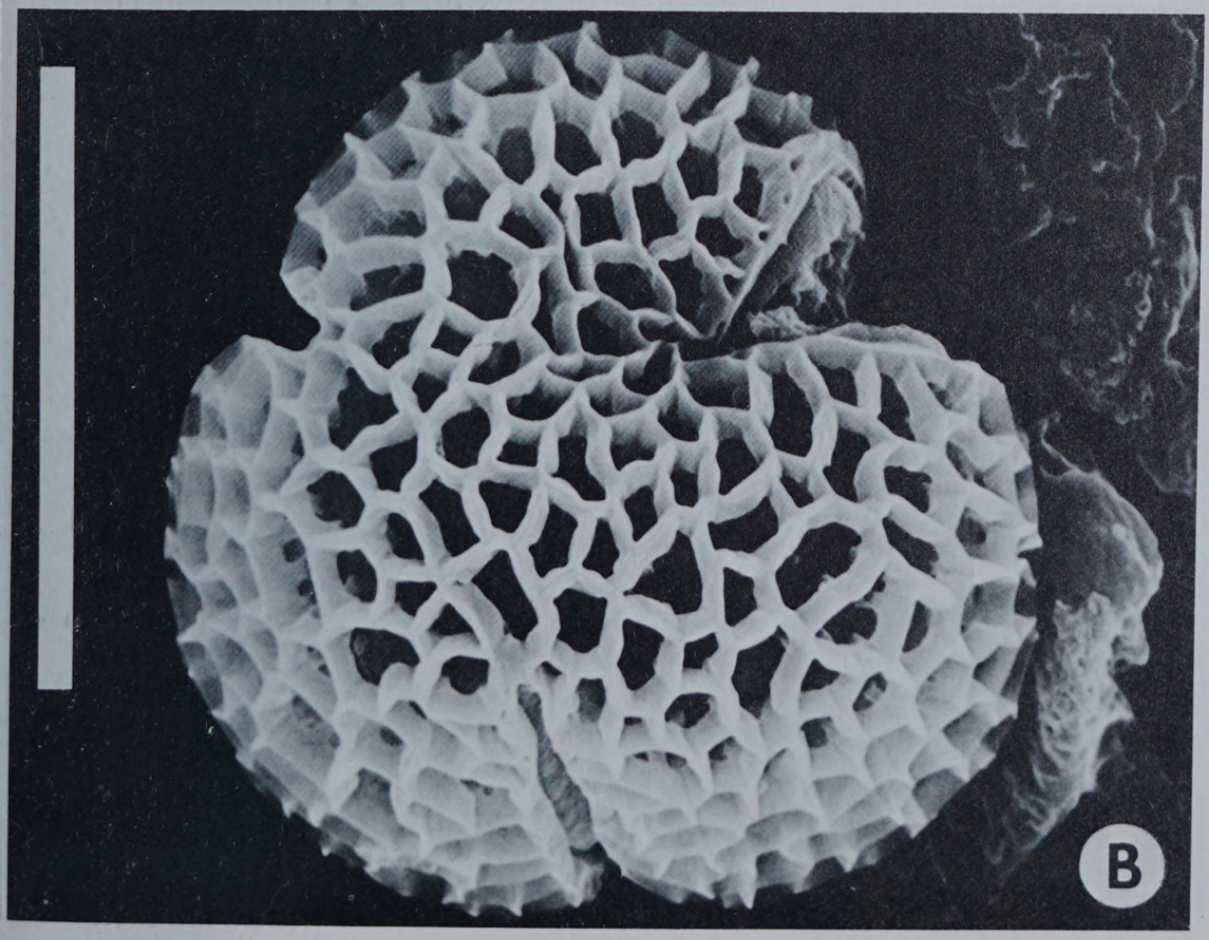
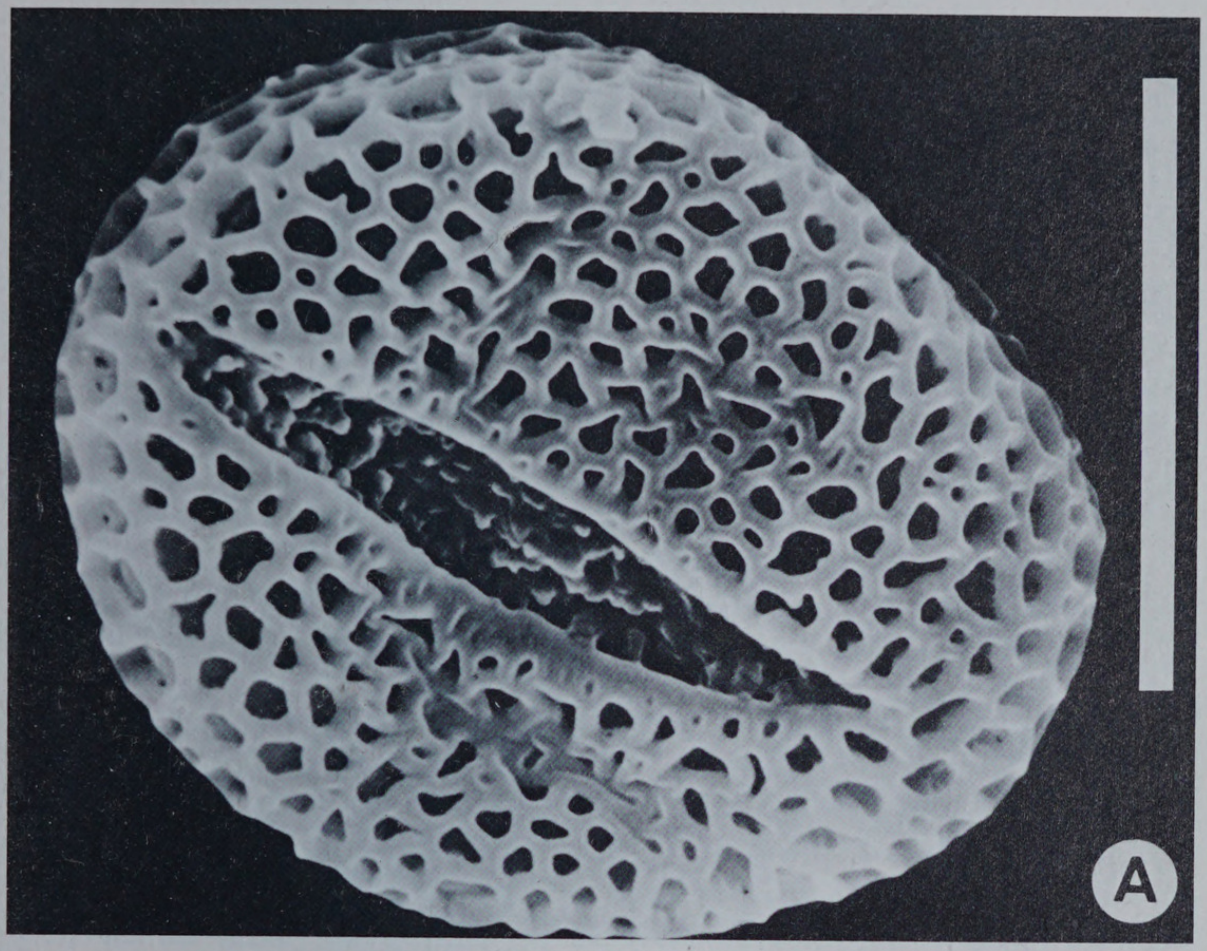

B

PLATE 10. *Ostrearia* Baill. (Subfamily Hamamelidoideae; Tribe Hamamelideae)
VOUCHER MATERIAL: *Ostrearia australiana* Baill.; Brass 20266: Queensland, Australia (AA).

A. Equatorial view of a tricolpate grain (partially collapsed), illustrating the moderately coarse reticulum of the sexine. The lumina vary widely in size and shape. The tectum is supported on short bacula. Note the elongate colpus, the distinct margo with numerous small perforations along the margins, and the granular colpus membrane, × 5700. Shape: prolate spheroidal. Size range in equatorial view: equatorial axis, 17–20 μm; polar axis, 18–21 μm. (Bar = 10 μm.)

B. Oblique polar view. Reticulation of the apocolpium not differing significantly from that of the mesocolpium; short bacula supporting tectum visible in upper and lower left quadrants. Note acute ends of colpi, colpus margins and granular membranes, × 5670. (Bar = 10 μm.)

A monotypic genus endemic to the rain forests of northern Queensland, Australia, and together with *Neostrearia* the only members of the family presently known from that continent. The pollen morphology of the two genera is rather similar, the only obvious differences in our samples being the degree of coarseness of the reticulum, and in the distinctness and evenness of the colpus margins.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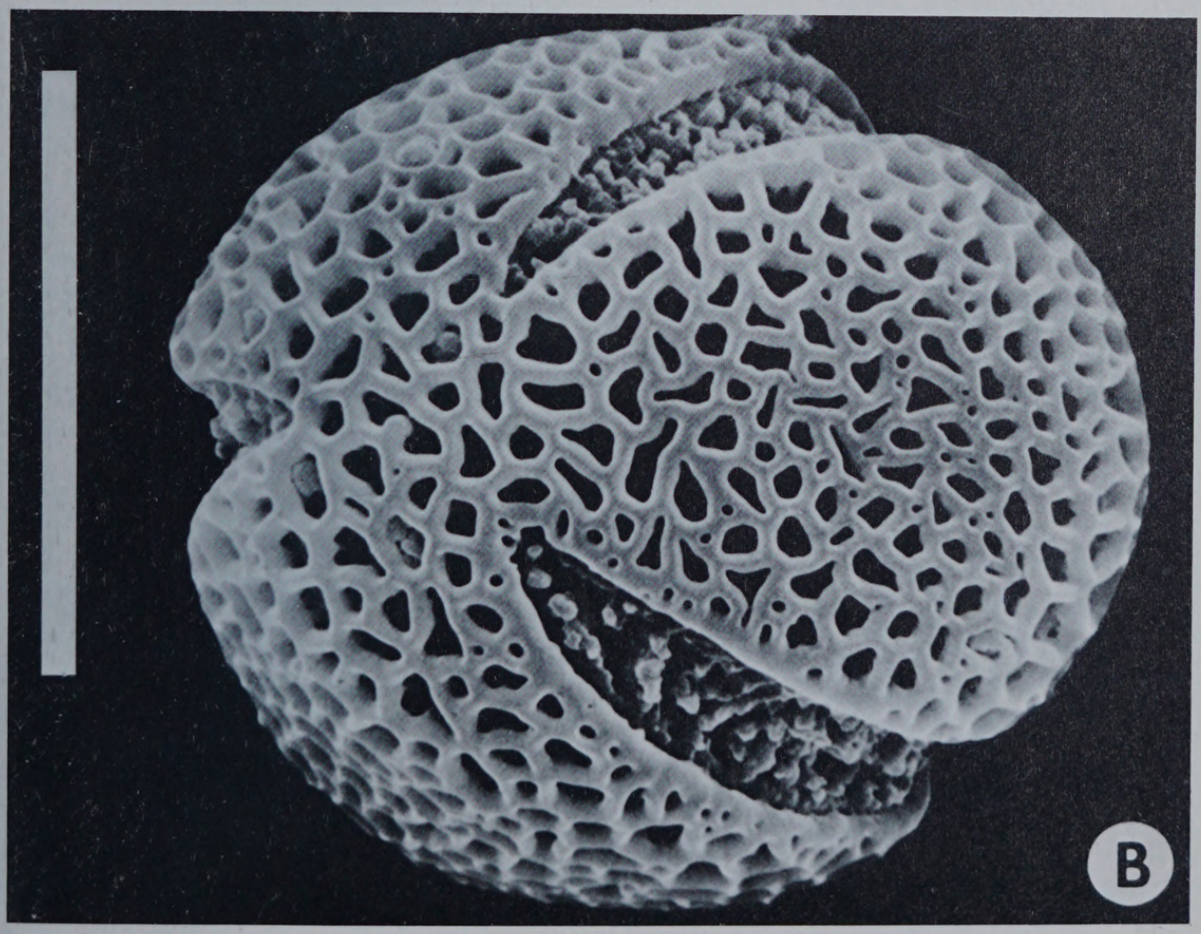
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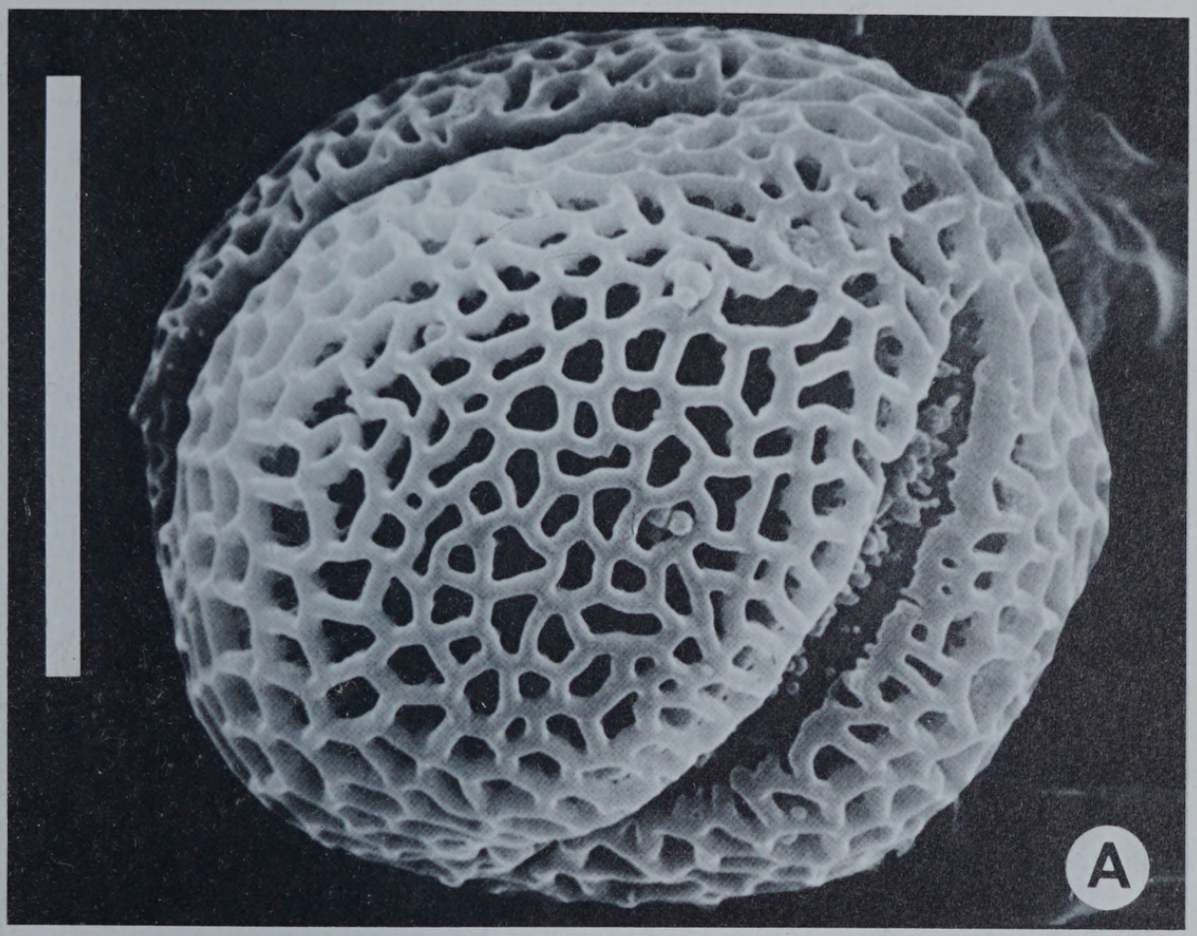
PLATE 11. *Neostrearia* L. S. Smith (Subfamily Hamamelidoideae; Tribe Hamamelideae)
VOUCHER MATERIAL: *Neostrearia fleckeri* L. S. Smith; Brass 2140: Mossman River Gorge, Cook District, Queensland, Australia (AA).

A. Oblique equatorial view of a tricolpate grain showing the irregular and moderately coarse reticulum of the exine. Note the elongate colpi with blunt ends; the degree of irregularity in the size and shape of the lumina; the uneven to "cracked" colpus margins, and the granular colpus membranes, × 5650. Shape: oblate spheroidal. Size range in equatorial view: equatorial axis, 22–25 μm; polar axis, 20–27 μm. (Bar = 10 μm.)

B. Slightly oblique polar view. Lumina of sexine in apocolpium not differing significantly in size from those of the mesocolpium. Note the margins and membranes of the colpi, × 4830. (Bar = 10 μm.)

A monotypic genus endemic to rain forests of northern Queensland, Australia. *Neostrearia* is apparently closely related to *Ostrearia*. The pollen in our sample of *Neostrearia* appears to differ from that of *Ostrearia* in having slightly larger lumina in the reticulum, no distinct margo, and more uneven margins along the colpi.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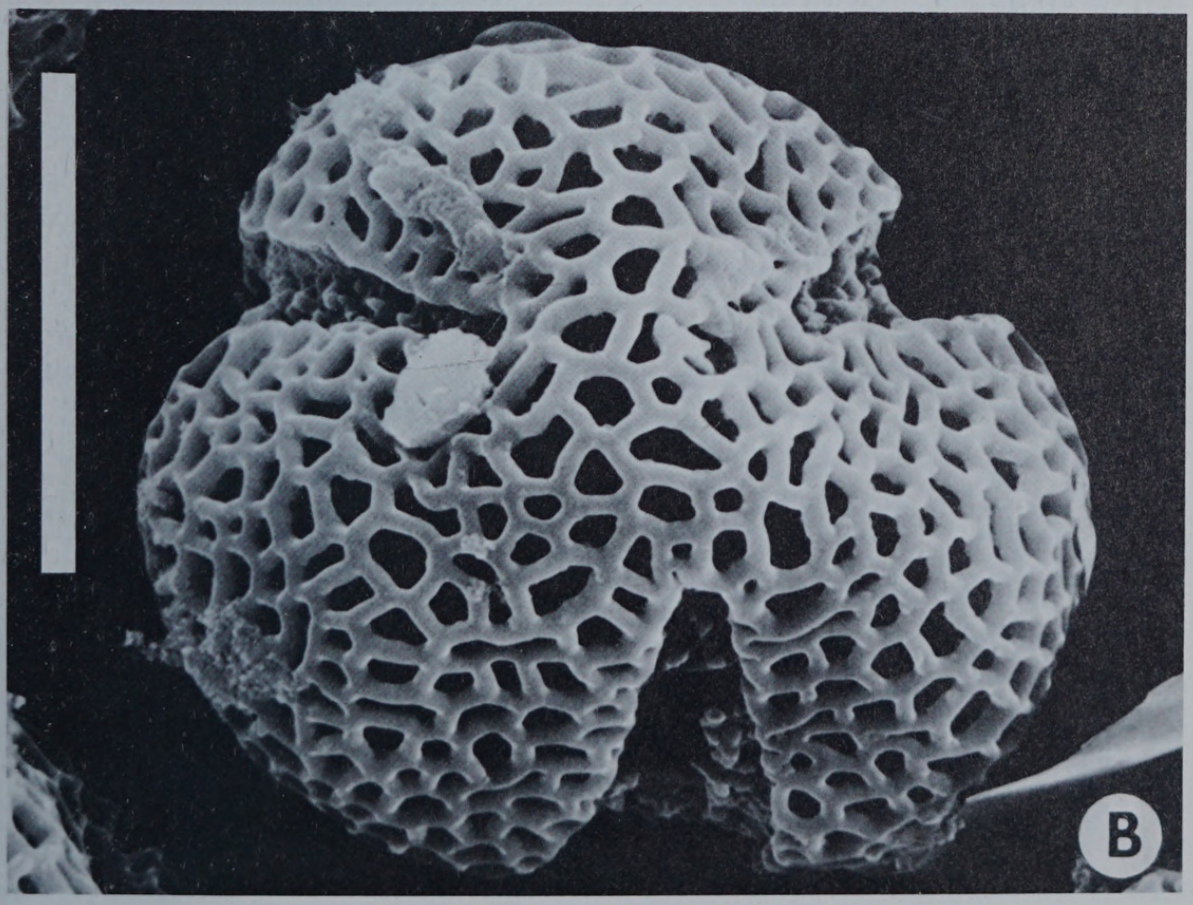
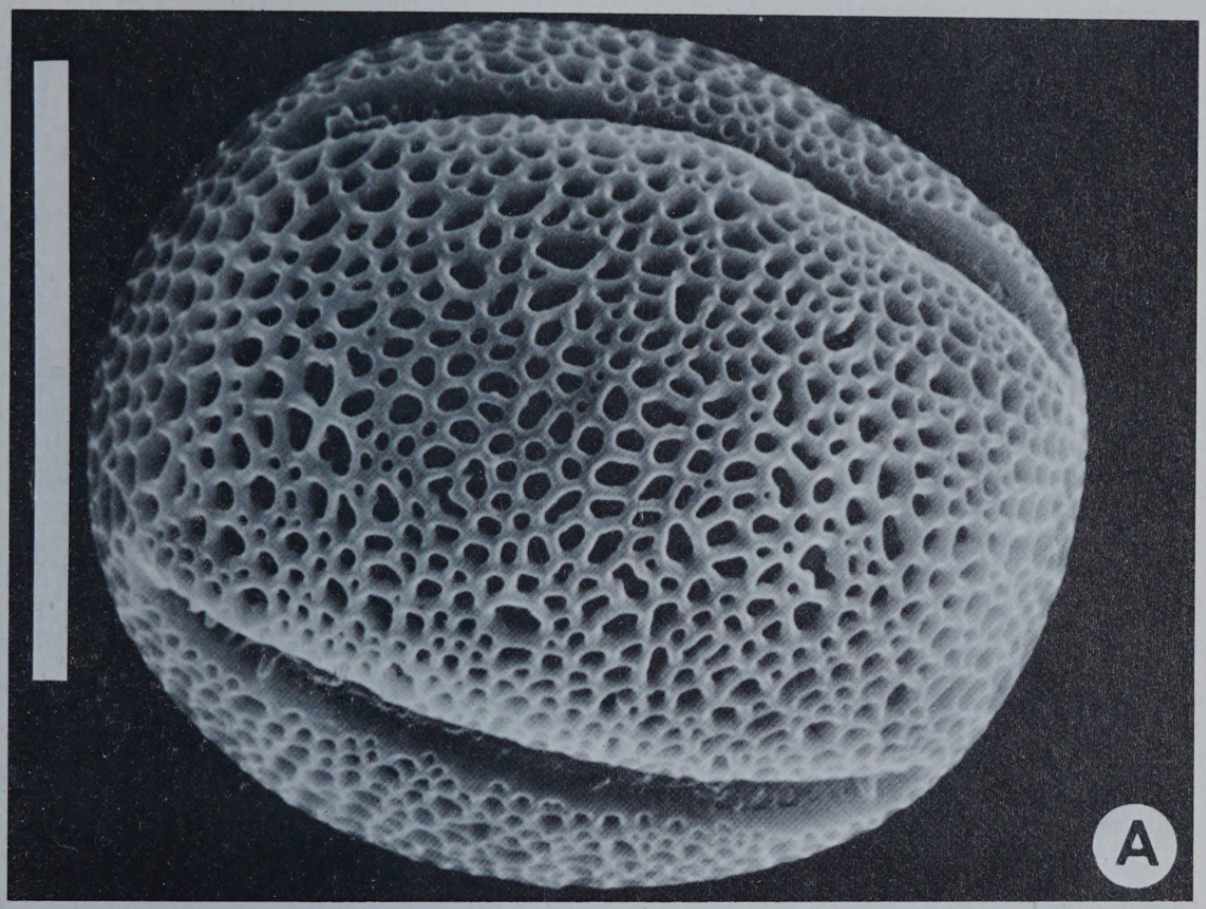

B

PLATE 12. *Trichocladus* Pers. (Subfamily Hamamelidoideae; Tribe Hamamelideae)
VOUCHER MATERIAL: *Trichocladus crinitus* Pers.; S. C. Troughton 180: Swaziland (NHA).

A. Equatorial view of a tricolpate grain showing elongate colpi and the moderately coarse reticulum of the exine. Note the numerous small, rounded lumina scattered among larger meshes of irregular shape; the outline of the lumina is not strongly polygonal or angular, × 6000. Shape: prolate spheroidal to sub-prolate. Size range in equatorial view: equatorial axis, 15–22 μm; polar axis, 18–25 μm. (Bar = 10 μm.)

B. Polar view. The lumina of the apocolpium appear, on average, to be slightly smaller in diameter and more rounded than in the mesocolpium. In the distal portions of the mesocolpium the lumina appear to exhibit a tendency to become aligned in short, curving rows. Note the concentration of small lumina along the narrow margo of the colpi, the even edge of the margin, and the coarsely granular colpus membranes, × 6000. (Bar = 10 μm.)

Trichocladus consists of about five species distributed in eastern Africa, from Ethiopia southward to the Cape of Good Hope, in South Africa. Erdtman (1946) provides a brief description of the pollen of *T. crinitus*, while Bakker (1959) gives descriptions of *T. ellipticus* E. and Z. and *T. grandiflorus* Oliver.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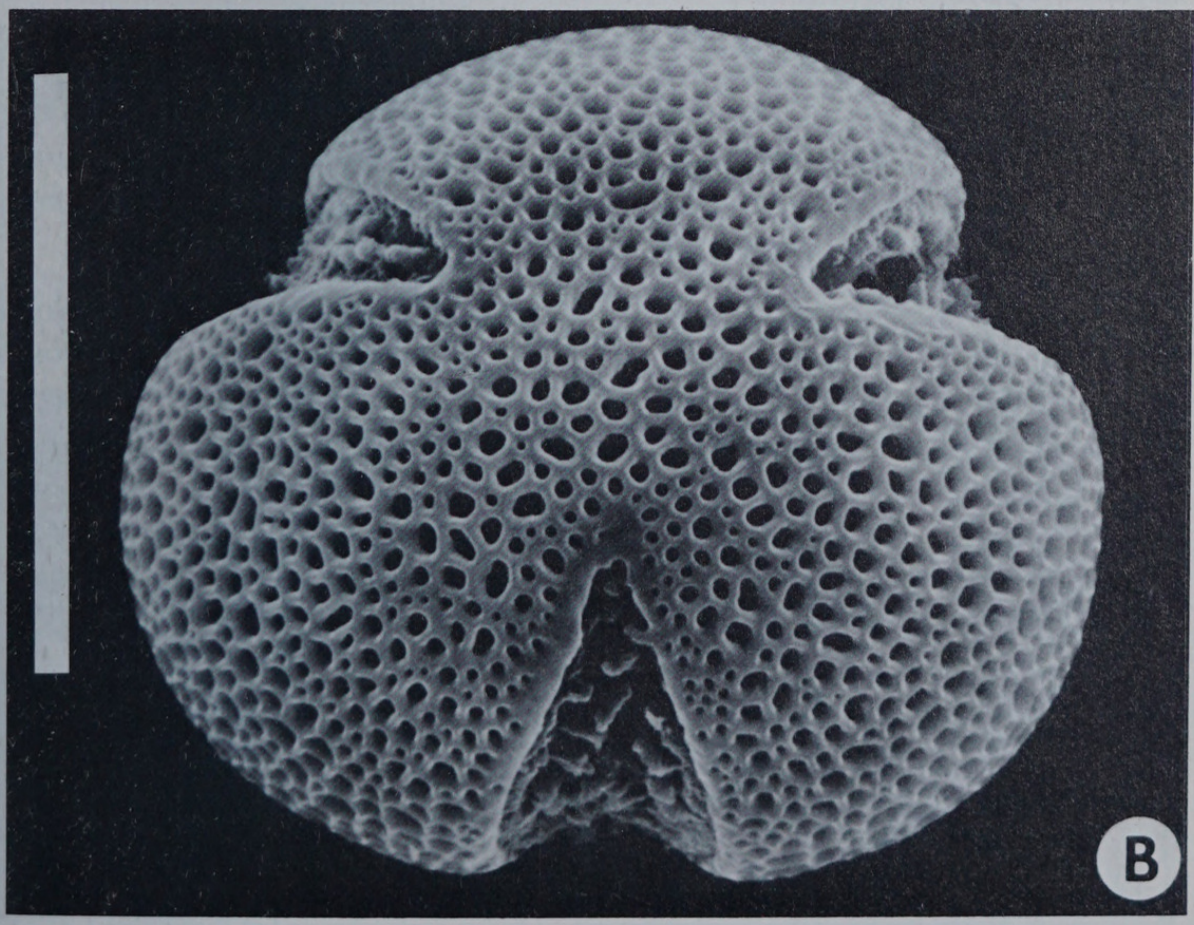
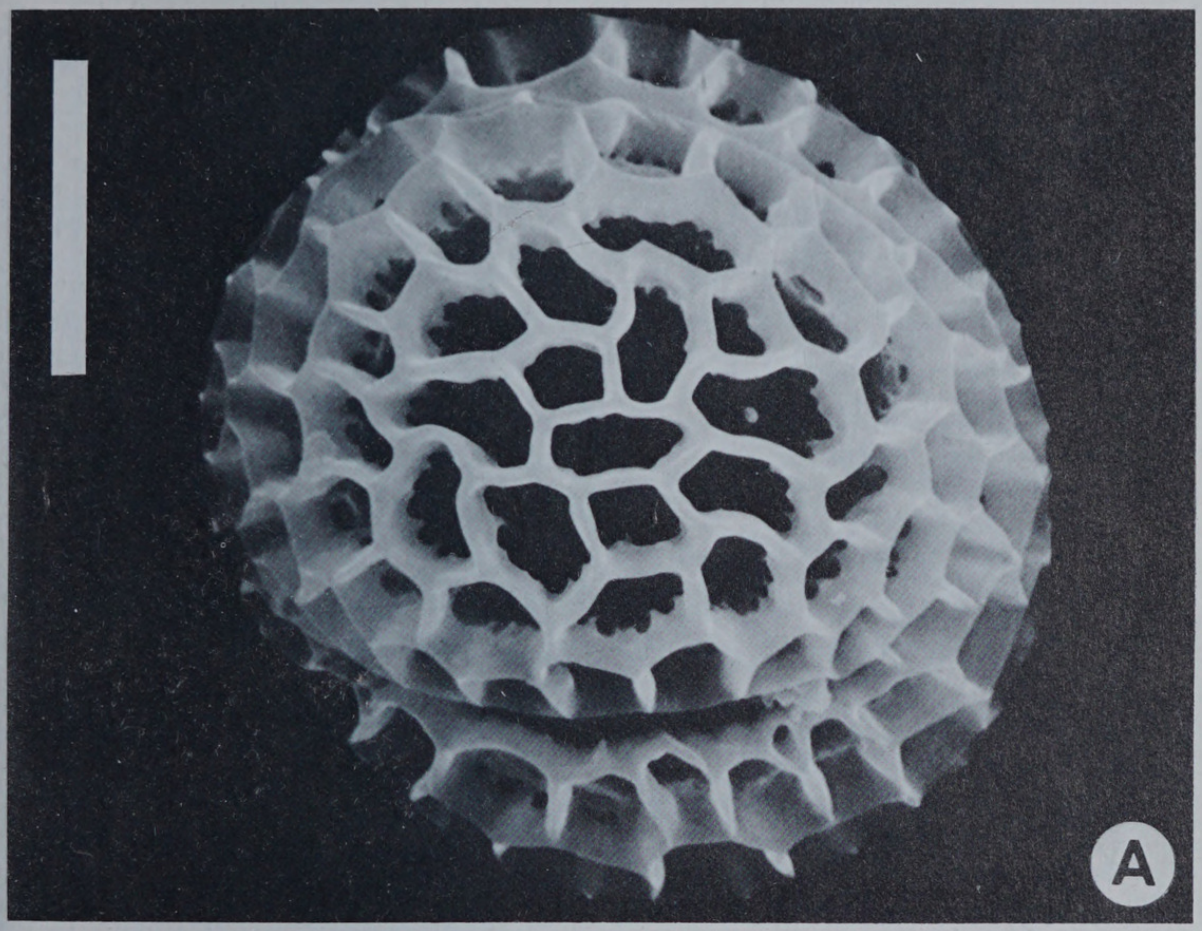

B

PLATE 13. *Dicoryphe* Thou. (Subfamily Hamamelidoideae; Tribe Hamamelideae)
VOUCHER MATERIAL: *Dicoryphe viticoides* Baker; Perrier de la Bathie 239: Ankaratin, Madagascar (P).

A. Slightly oblique view of a tricolpate grain showing the coarsely reticulate exine with deep muri resting on relatively long bacula. The lumina are angular, ranging in shape from regular pentagonal to mostly elongate or curving. Note the margin of the colpus; very small lumina or perforations occur only occasionally along the margins, × 3030. Shape: oblate spheroidal. Size range in equatorial view: equatorial axis, 29–34 μm; polar axis, 27–35 μm. (Bar = 10 μm.)

B. Slightly oblique polar view. The lumina of the apocolpium do not appear to differ significantly in size from those of the mesocolpium. The colpi are slightly shortened. Note that the colpus margins (lower middle) consist of the undulating muri of adjacent large meshes. The projecting angles and indentations of the opposing margins appear to be complimentary, so that the colpi are obscured when invaginated, × 2820. (Bar = 10 μm.)

Dicoryphe is a genus of about 13 species endemic to the island of Madagascar. Little is known of this interesting group apart from the morphological descriptions of the species provided in various taxonomic accounts. Simpson (1936) attributed certain fossil grains in Scottish lignites to *Dicoryphe* on the basis of their coarse reticulum and colpus margin characteristics. Chang (1964) compares *Dicoryphe* with *Exbucklandia* on the basis of their coarse reticula.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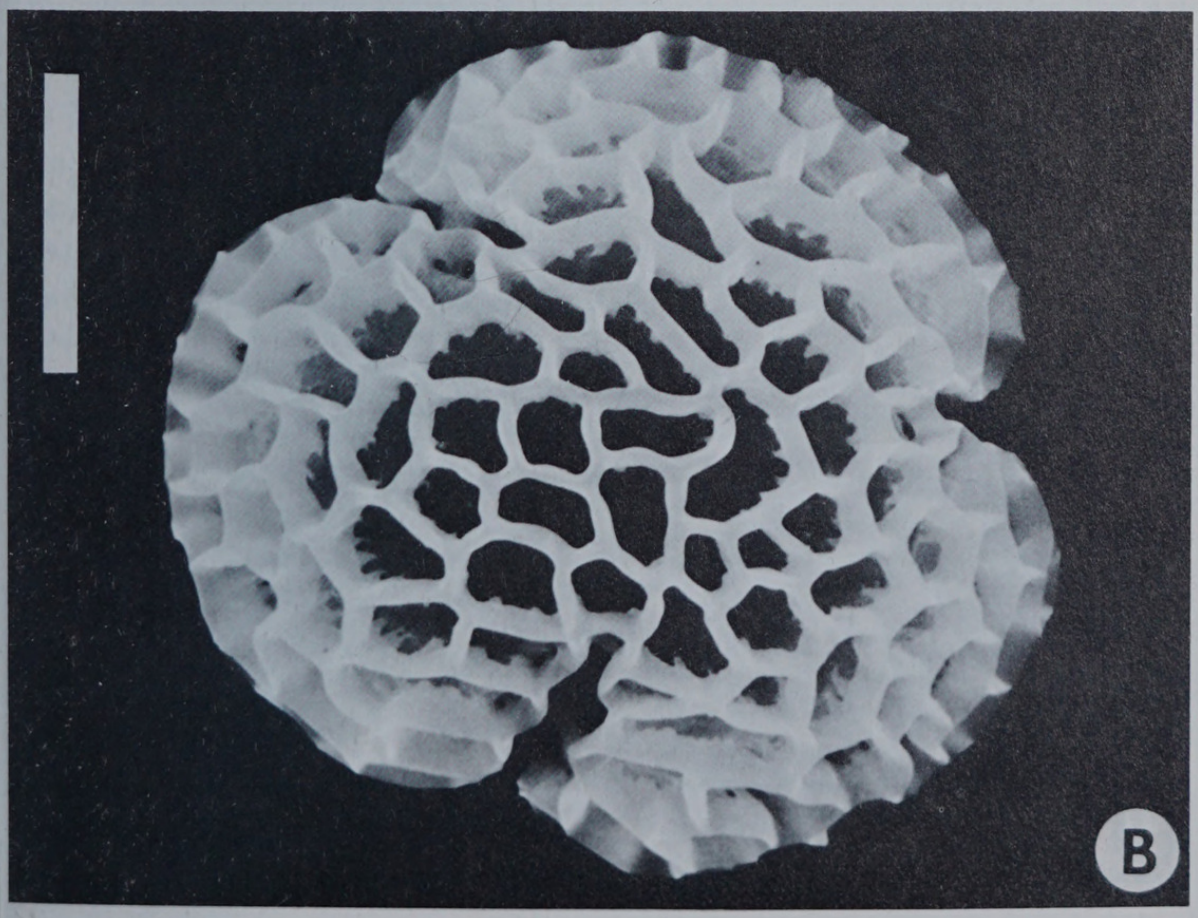
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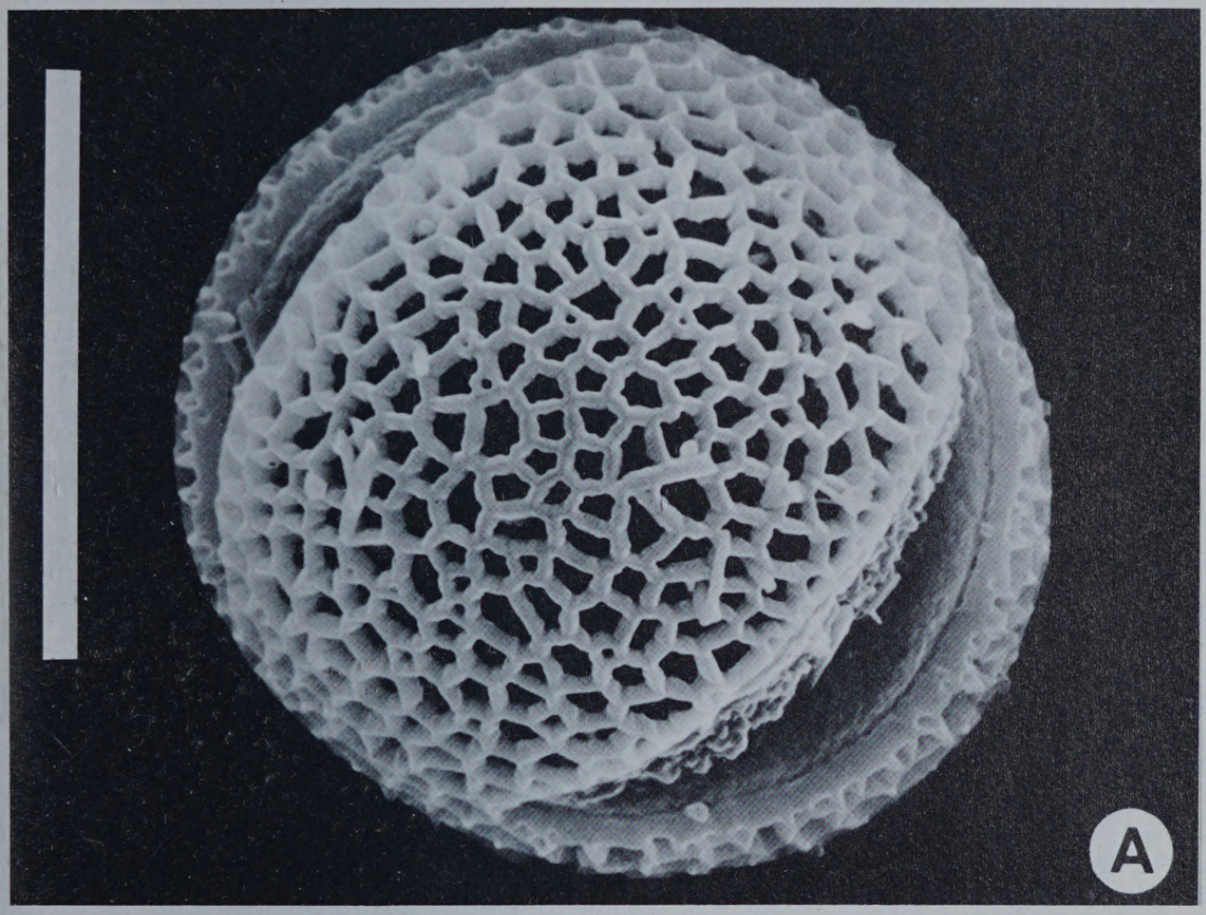
PLATE 14. *Hamamelis* L. (Subfamily Hamamelidoideae; Tribe Hamamelideae)
VOUCHER MATERIAL: *Hamamelis virginiana* L.; Bogle 771: Interstate Park, Polk Co., Wisconsin (NHA).

A. Equatorial view showing the moderately coarse reticulum and muri of moderate depth resting on short bacula, as shown in upper right of photograph. The lumina are polygonal, with pronounced angles. Note the occasional small, rounded perforations scattered among the polygonal meshes. The peripheral region of the colpus membrane appears unsculptured, the central portion granular, × 5710. Shape: prolate spheroidal. Size range in equatorial view: equatorial axis, 15–19 μm; polar axis, 18–22 μm. (Bar = 10 μm.)

B. Slightly oblique polar view, showing the elongate colpi with acutely pointed ends. The reticulum of the apocolpium does not differ significantly from that of the mesocolpium. Note the narrow margo with associated small lumina, the even edge of the margin, and the central granular and peripheral unsculptured portions of the colpus membrane as shown in upper left of photograph, × 6000. (Bar = 10 μm.)

A genus of about nine species distributed in eastern North America, the mountains of Mexico, in Japan and China. The pollen of *Hamamelis* is similar to that of *Loropetalum*. The flowers of the two genera are similar in appearance and share a similar tetramerous floral plan. The two genera were once considered congeneric. Chang (1964) notes minor differences but basic similarity among the species of *Hamamelis* he examined, with the exception of *H. japonica* Sieb. et Zucc., which he reports to be larger in size and to have a thicker exine. Ikuse (1956) also provides brief descriptions of three species of *Hamamelis* (*H. japonica, H. mollis, H. virginiana*) in Japan. The pollen of *H. vernalis* and *H. virginiana* is "sticky," with "pollenkitt" deposited on the exine surface (Hesse, 1978). Small flies are the principal pollinators of *H. virginiana*.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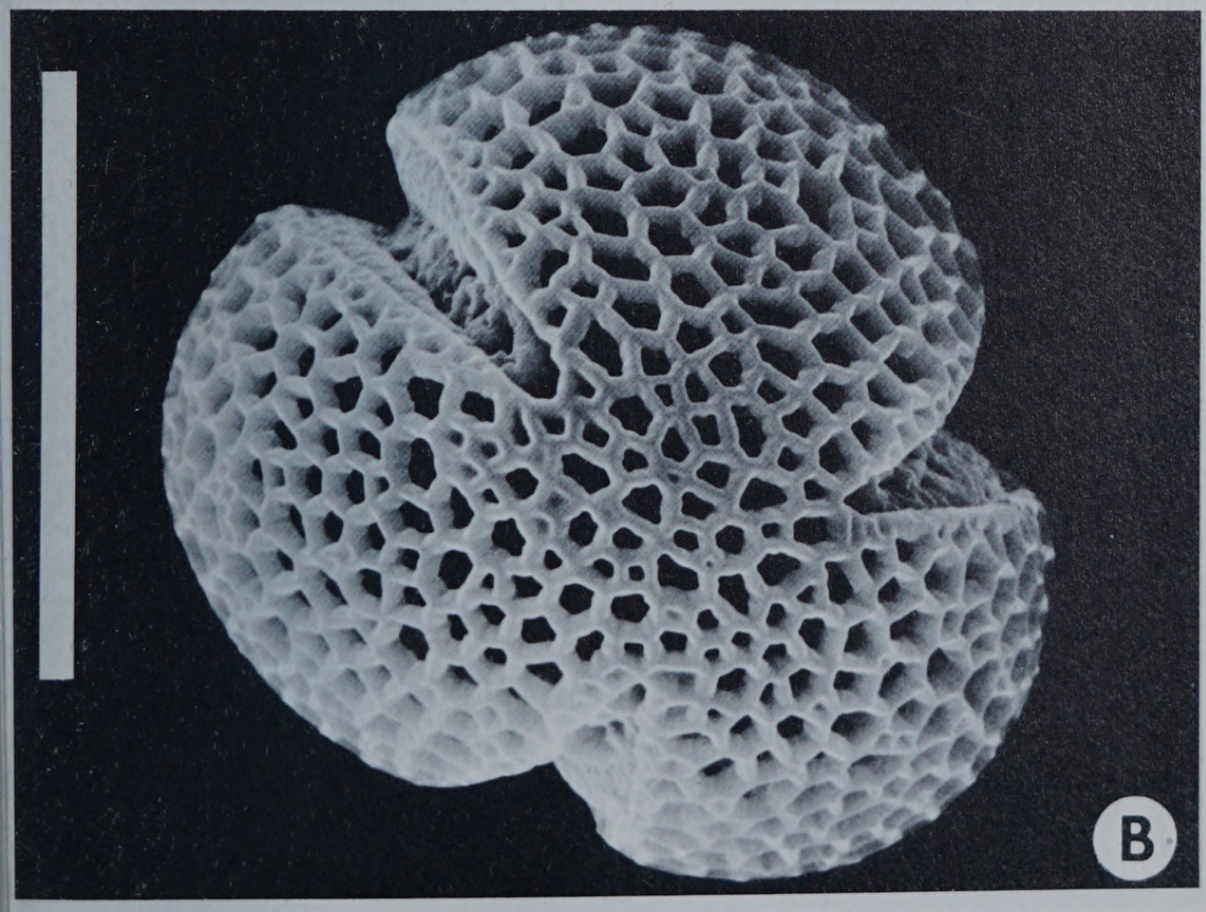
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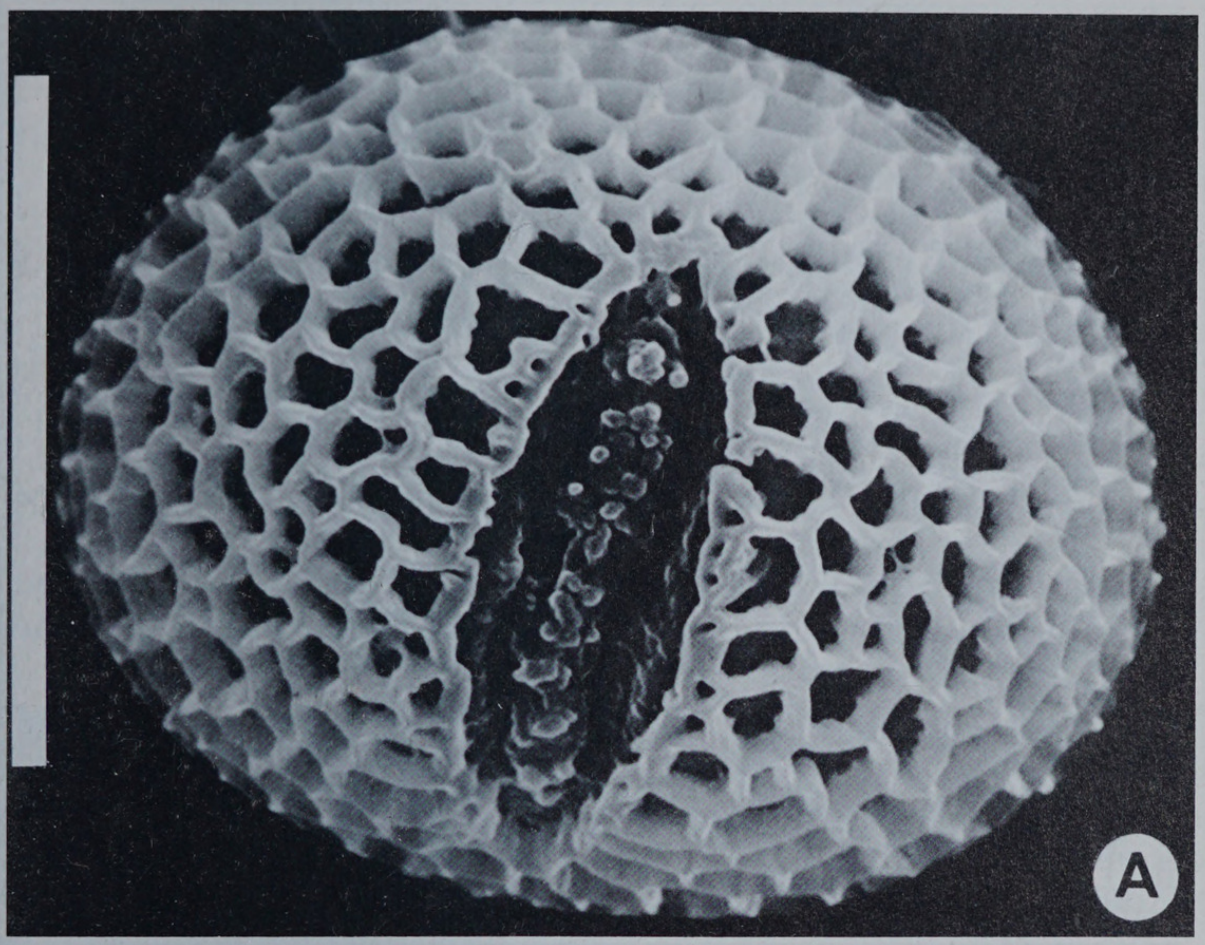
PLATE 15. *Tetrathyrium* Benth. (Subfamily Hamamelidoideae; Tribe Hamamelideae)
VOUCHER MATERIAL: *Tetrathyrium subcordatum* Benth.; Bogle 586: Bowen Road, Victoria, Hong Kong (NHA).

A. Equatorial view of a tricolpate grain showing a slightly expanded colpus with central zone of granular sculpturing and relatively smooth peripheral areas. Note the coarse reticulum of the mesocolpium with irregularly shaped, angular lumina, the relatively deep muri on short bacula, and the distinct but somewhat uneven margins of the colpus, with scattered small lumina along the margin and occasional breaks in the margo, × 6350. Shape: oblate spheroidal. Size range in equatorial view: equatorial axis, 19–26 μm; polar axis, 16–25 μm. (Bar = 10 μm.)

B. Slightly oblique polar view illustrating the reticulum of the apocolpium; the lumina of the reticulum not differing significantly in size from those of the mesocolpium, × 5800. (Bar = 10 μm.)

Tetrathyrium is a monotypic genus which is endemic to Hong Kong. It was once thought to include *Loropetalum,* from which it differs in its pentamerous rather than tetramerous floral plan, in its coarse reticulum, and deeper muri.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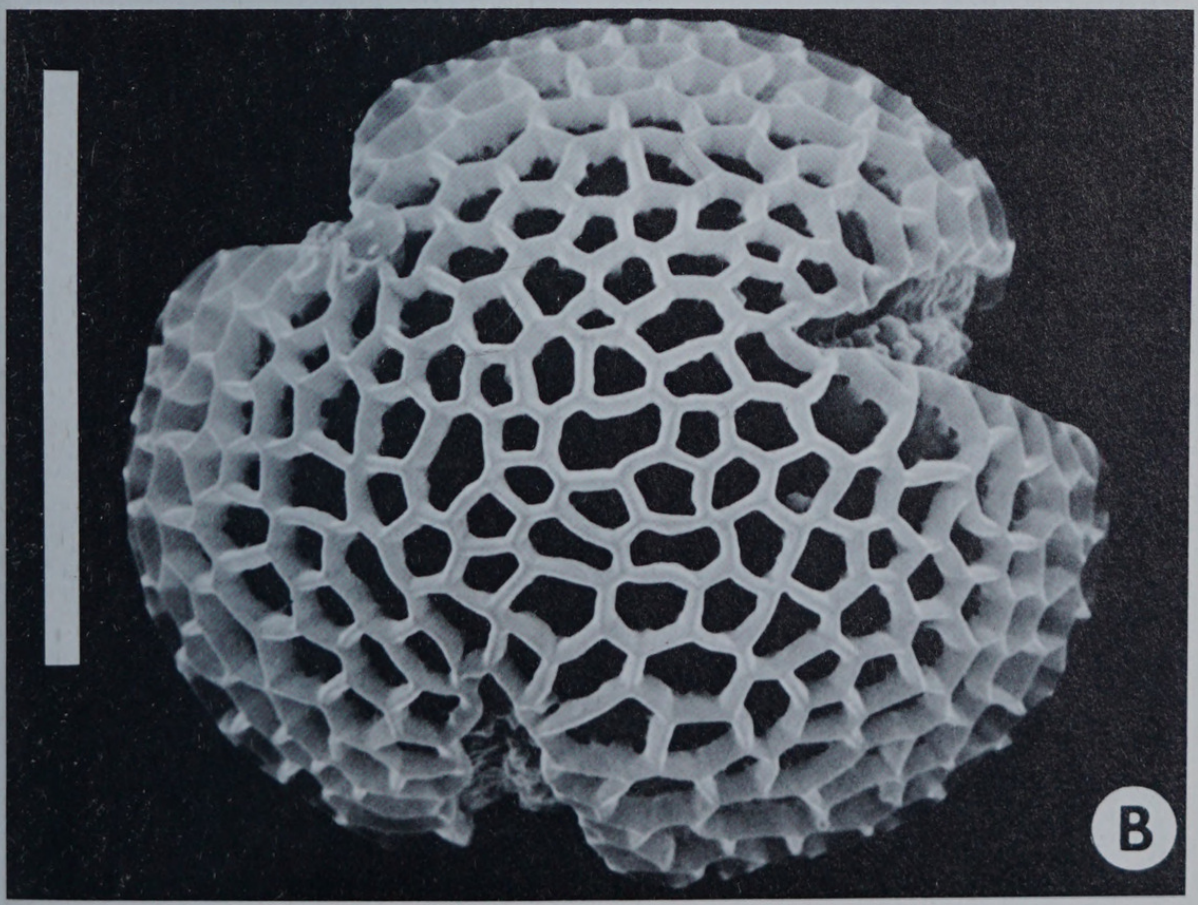
B

PLATE 16. *Loropetalum* R. Br. (Subfamily Hamamelidoideae; Tribe Hamamelideae)
VOUCHER MATERIAL: *Loropetalum chinense* Oliv.; Bogle 776: cultivated plant, U.S.D.A., Plant Introduction Station, Glenn Dale, Maryland (NHA).

A. Slightly oblique equatorial view of a tricolpate grain showing the moderately coarse reticulum of the exine, with muri of moderate depth resting on short bacula, and two elongate colpi. Note the very small, round lumina scattered among the larger, angular meshes, and along the margin of the colpi, × 6090. Shape: subprolate. Size range in equatorial view: equatorial axis, 16–27 μm; polar axis, 19–23 μm. (Bar = 10 μm.)

B. Slightly oblique polar view, showing general reduction in size of the lumina of the apocolpium. Note the acutely pointed ends of the elongate colpi, and the coarsely granular membrane of the colpus (upper right), × 6000. (Bar = 10 μm.)

Loropetalum is a genus of about four species (Index Kewensis; H. T. Chang, 1973) distributed in China, Hong Kong and westward to the mountains of eastern India (Assam). Its tetramerous flowers are similar in appearance to those of *Hamamelis*.

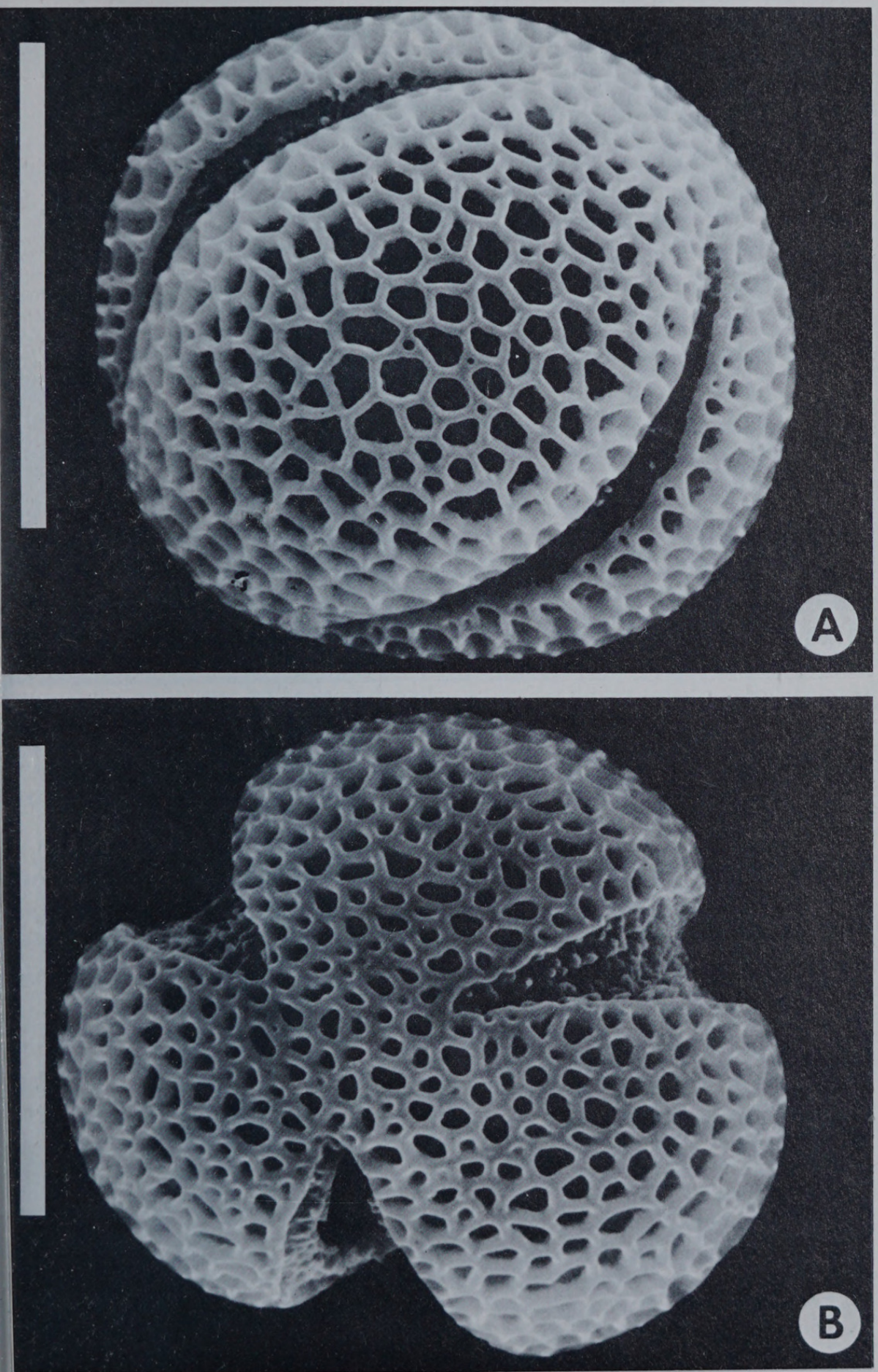
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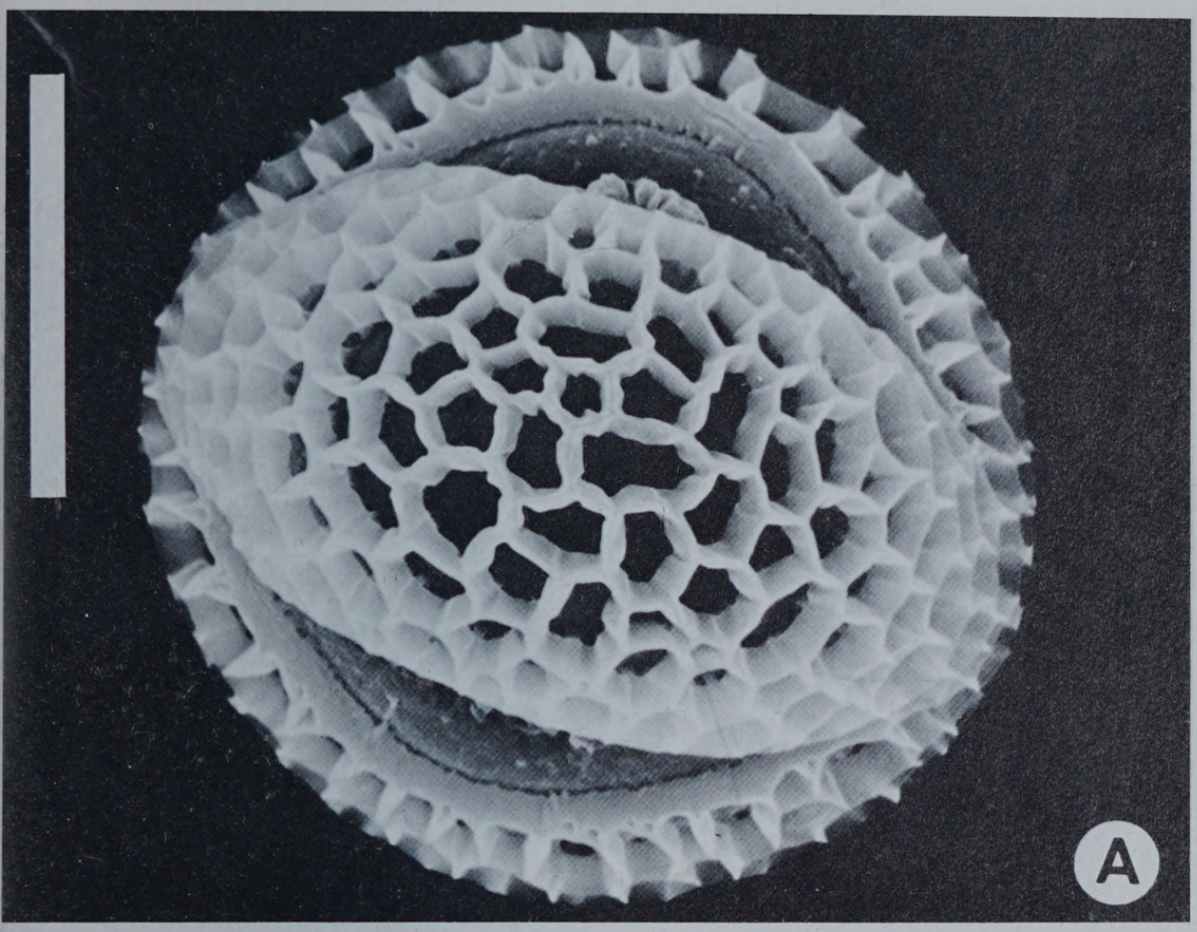
PLATE 17. *Embolanthera* Merr. (Subfamily Hamamelidoideae; Tribe Hamamelideae)
VOUCHER MATERIAL: *Embolanthera spicata* Merr.; Sulit 14791: Palawan, Philippine Islands (AA).

A. Equatorial view of a tricolpate grain, showing the coarse reticulum of the mesocolpium. Note the deep muri borne on short bacula; lumina are of fairly uniform dimensions and angular outline; margins of the colpi are distinct and even, containing a few very small, scattered lumina. The colpus membranes appear smooth peripherally, but bear a central zone of granular exine, × 4140. Shape: prolate spheroidal. Size range in equatorial view: equatorial axis, 18–26 μm; polar axis, 17–25 μm. (Bar = 10 μm.)

B. Slightly oblique polar view. Lumina of the apocolpium appear slightly smaller than in the mesocolpium. Note the margins and membranes of the colpi, × 5250. (Bar = 10 μm.)

Embolanthera is a genus of only two species, one of which is known only from the island of Palawan, in the Philippines, the other from a single location in North Viet Nam (Lee, 1969; Merrill, 1909; Tardieu-Blot, 1965). The genus is considered closely related to *Maingaya* and *Loropetalum*.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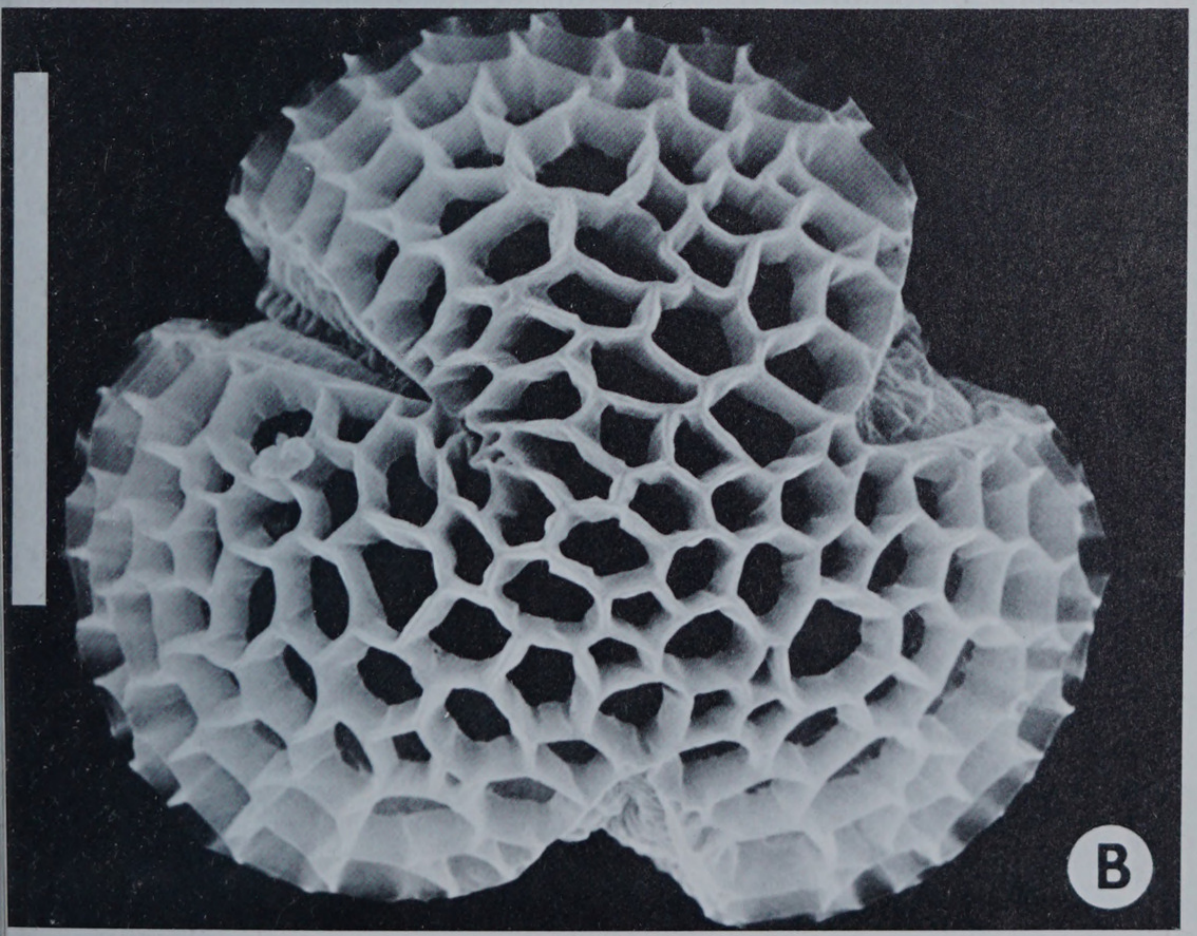
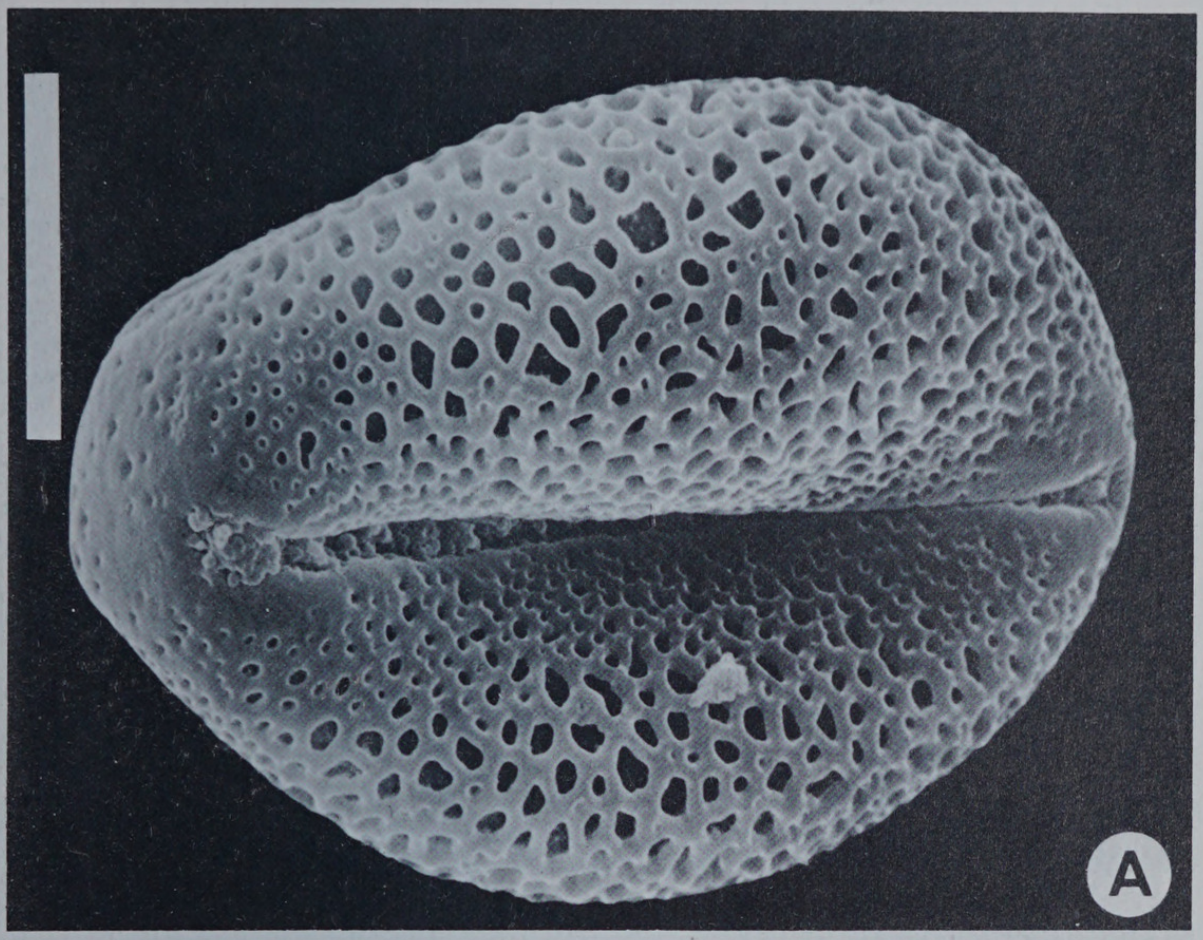

B

PLATE 18. *Eustigma* Gardn. and Champ. (Subfamily Hamamelidoideae; Tribe Eustigmateae)
VOUCHER MATERIAL: *Eustigma oblongifolium* Gardn. and Champ.; Bogle 584: Victoria Peak, Hong Kong (NHA).

A. Oblique view of an invaginated grain showing the irregular reticulum in the mesocolpium, with lumina varying from large and angular to very small and rounded, grading to a scrobiculate or fully tectate condition at the poles, × 3830. Shape: subprolate. Size range in equatorial view: equatorial axis, 39–52 μm; polar axis, 45–61 μm. (Bar = 10 μm.)

B. Oblique polar view showing the reticulate mesocolpium and foveolate to scrobiculate apocolpium. Note the margo, rounded ends, even to slightly ragged margins, and granular membranes of the elongate colpi, × 3440. (Bar = 10 μm.)

A genus of two species distributed in China, Hong Kong, Taiwan (*Eustigma oblongifolium*) and Vietnam (*E. balansae* Oliver). Although it shares many basic similarities in floral morphology with members of the Hamamelideae, *Eustigma* is sufficiently different to merit recognition as the sole member of a separate tribe. Chang (1964) notes the basic similarity of the grains of the two species, but with *E. oblongifolium* he found that pollen grains from plants of Kwangtung, China, exhibit a thicker exine and a coarser reticulum than those from the island of Hainan, off the southern coast of China.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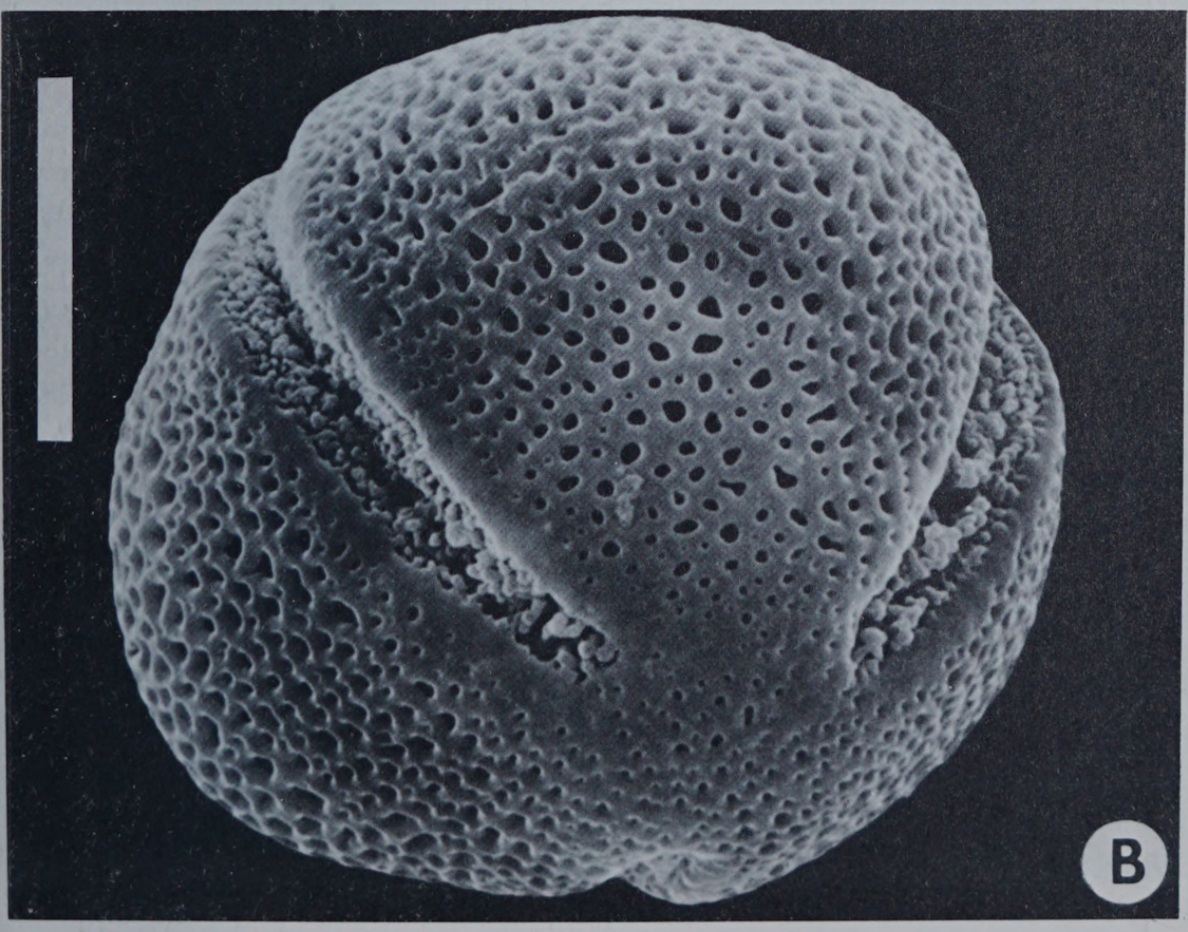
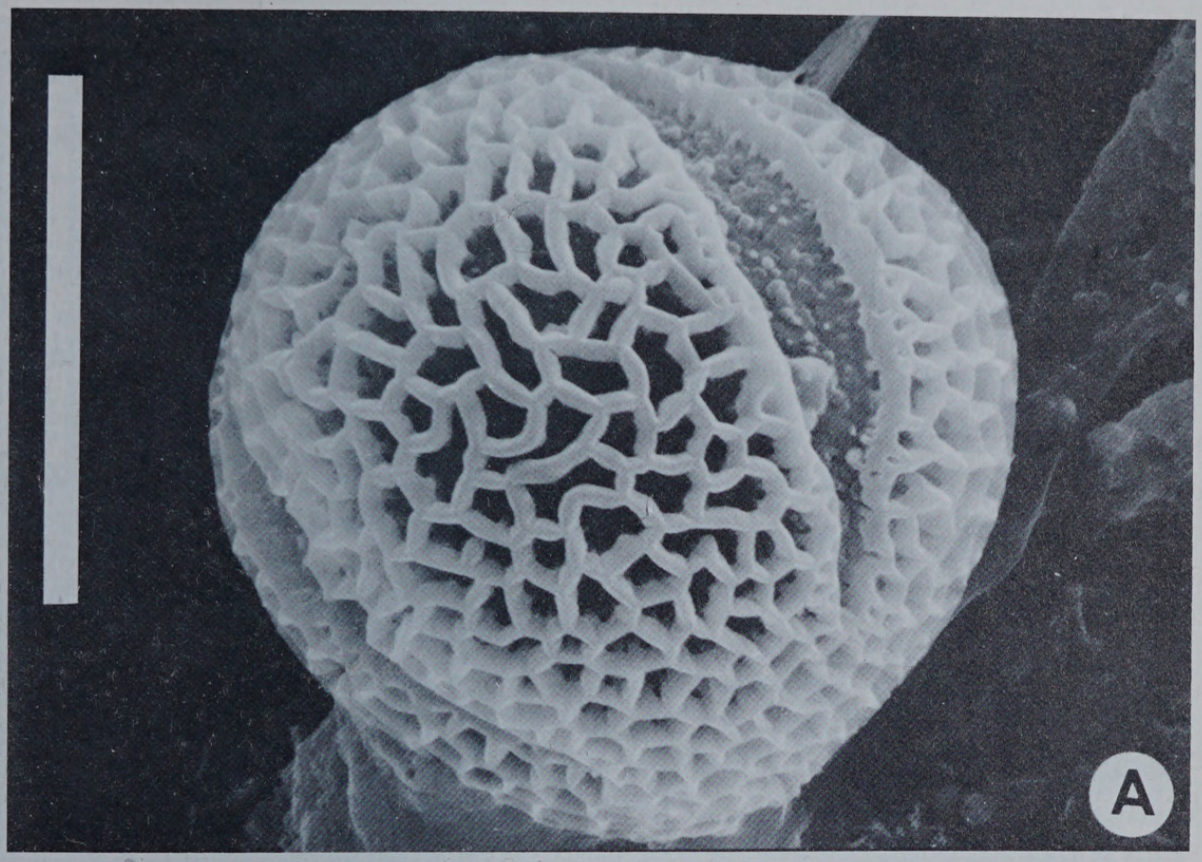

B

PLATE 19. *Corylopsis* Sieb. and Zucc. (Subfamily Hamamelidoideae; Tribe Corylopsideae)
VOUCHER MATERIAL: *Corylopsis platypeta* Rehd. and Wils.; Bogle 963: from a cultivated plant, Arnold Arboretum (NHA).

A. Oblique equatorial view of a tricolpate grain illustrating the coarsely reticulate exine with rather irregular, angular lumina, some of which are highly elongate and curved or constricted, the moderately deep muri borne on short bacula, the margo of the elongate colpus, and the finely granular colpus membrane, × 5000. Shape: oblate spheroidal. Size range in equatorial view: equatorial axis, 19–24 μm; polar axis, 17–21 μm. (Bar = 10 μm.)

B. Oblique polar view, illustrating the reduction in size of the lumina in the apocolpium, and the minute lumina scattered along the margo of the sharply pointed ends of the colpi, × 5640. (Bar = 10 μm.)

Corylopsis is a large and poorly understood genus of at least 36 described species distributed in Korea, Japan, Taiwan, China, and the Himalayas of eastern India (see Index Kewensis; H. T. Chang, 1973). In a recent morphological survey of the genus Morley and Chao (1977) reduced the number of species to seven, while acknowledging that the genus needs intensive study. Lee (1969) reports occasional syncolpate grains in two of the six species he examined; he also failed to find pores in the colpi as reported by Simpson (1936). The flowers are insect-pollinated in cultivation (e.g., honey bees, blow flies, hover flies), but observations in nature are lacking (Morley and Chao, 1977). Hesse (1978) describes the ultrastructure of the sticky "pollenkitt" deposited on the exine surface.


A

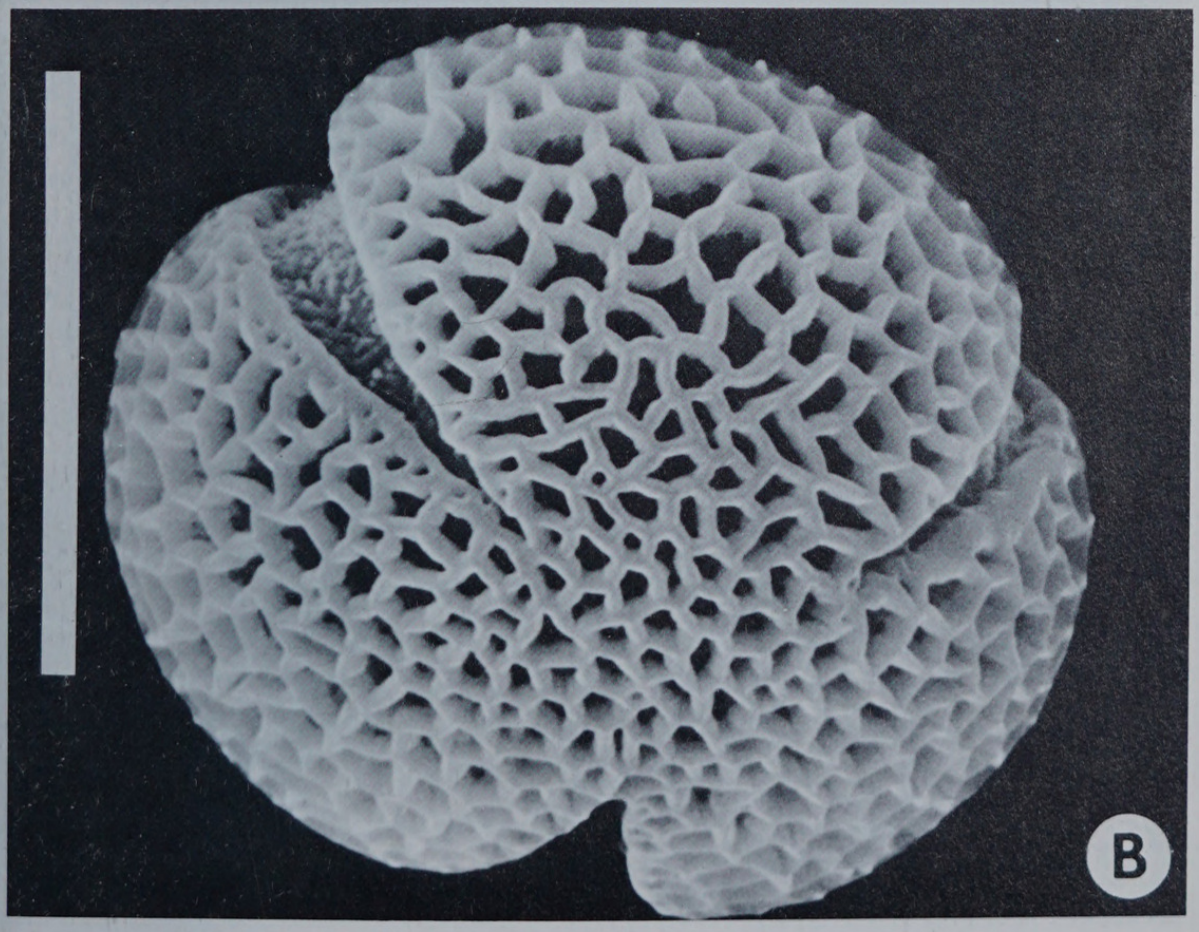
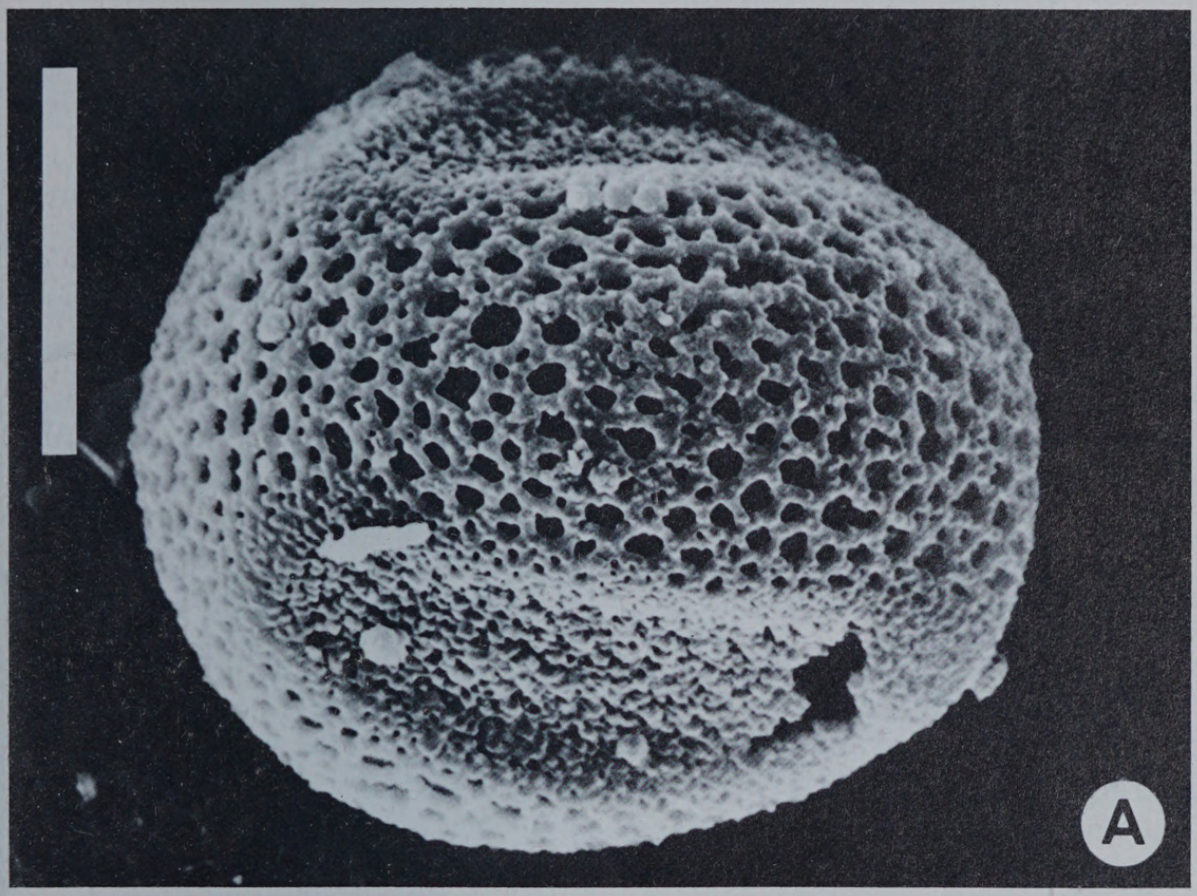

B

PLATE 20. *Fortunearia* Rehd. and Wils. (Subfamily Hamamelidoideae; Tribe Corylopsideae)
VOUCHER MATERIAL: *Fortunearia sinensis* Rehd. and Wils.; Bogle 778: from a cultivated plant, grounds of U.S.D.A., Plant Introduction Station, Glenn Dale, Maryland (NHA).

A. Slightly oblique equatorial view of a tricolpate grain. The reticulum is moderately coarse, with very small, rounded lumina scattered among larger lumina which vary in outline from rounded to triangular or polygonal. The muri are verrucate. The colpi are relatively short, with rounded ends, indistinct margins, and finely granular membranes. The sexine appears here to become modified into a finely perforate and verrucate margo around the colpi, × 3800. Shape: subprolate. Size range in equatorial view: equatorial axis, 18–34 μm; polar axis, 18–40 μm. (Bar = 10 μm.)

B. Oblique polar view. The reticulum of the apocolpium does not differ significantly from that of the mesocolpium. Note the finely perforate and verrucate margo of the colpus, × 3900. (Bar = 10 μm.)

Fortunearia is yet another monotypic genus which is endemic to China, with a very limited distribution in western Hupeh Province. It is vegetatively similar to *Sinowilsonia,* but its pollen is closer to that of *Parrotia,* differing in having a finer reticulum, broader muri, and less coarsely granular membranes. Several other genera, however, show basic similarities in having reticulate-verrucate exines (although with increasingly smaller lumina) and relatively indistinct colpi, rugae or pores with granular membranes, including *Molinadendron, Distylium, Sycopsis* and *Distyliopsis.*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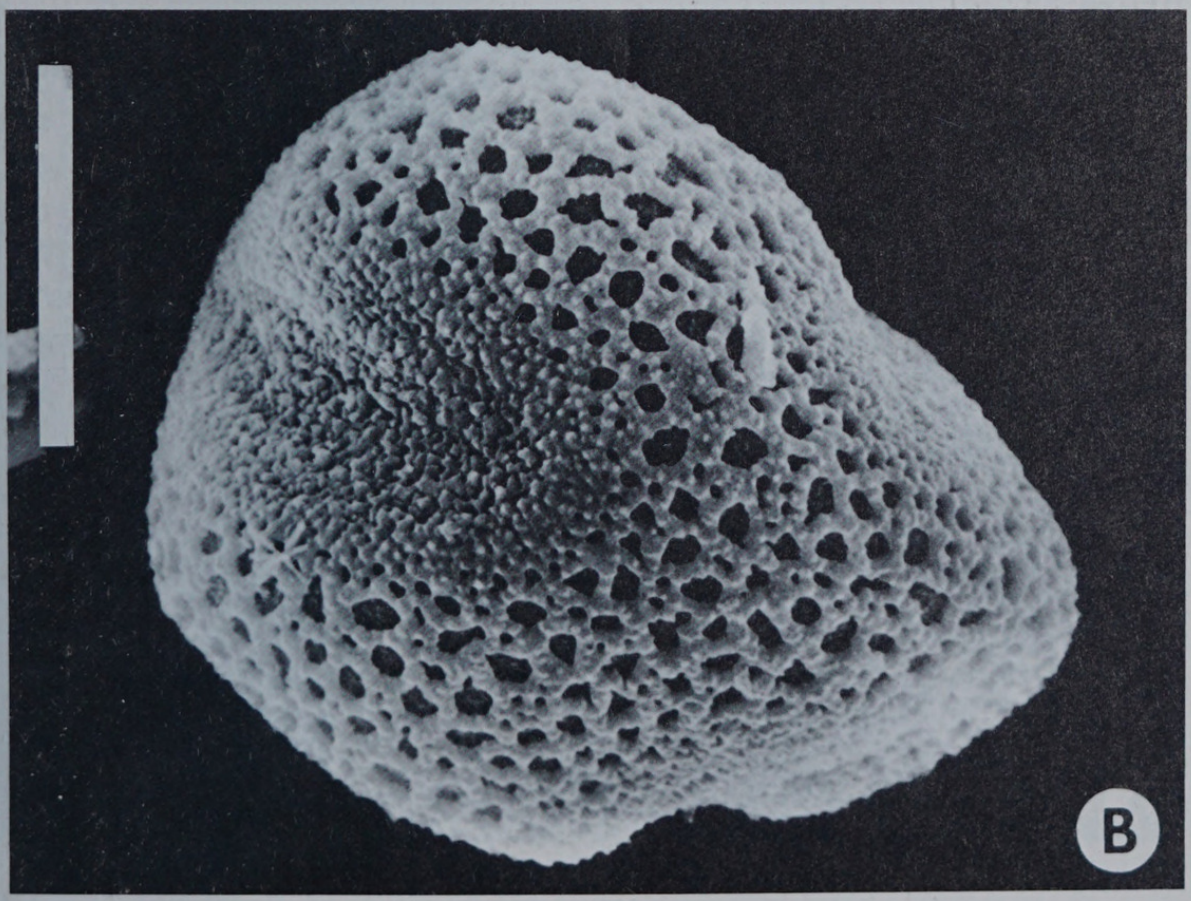

B

PLATE 21. *Sinowilsonia* Hemsl. (Subfamily Hamamelidoideae; Tribe Corylopsideae)
VOUCHER MATERIAL: *Sinowilsonia henryi* Hemsl.; Bogle 970: from a cultivated plant, Royal Botanic Garden, Kew (NHA).

A. Equatorial view of the interapertural area of a tricolpate grain with a moderately coarse reticulum. The lumina range from more or less isodiametric to angular, and show considerable variation in size, with numerous very small lumina occurring singly or in small clusters among the larger meshes. Absence of small segments of murus results in exceptionally large or erratically shaped lumina. The colpi are elongate, approaching the poles, × 2800. Shape: prolate spheroidal. Size range in equatorial view: equatorial axis, 24–41 μm; polar axis, 28–43 μm. (Bar = 10 μm.)

B. Oblique polar view of another grain, illustrating a reduction in the size of the lumina in the polar area. The colpi exhibit a partial margo around their rounded ends, while the lateral margins tend to be less distinct, with numerous small lumina and a ragged to broken edge. The colpus membranes are coarsely granular, × 2600. (Bar = 10 μm.)

Sinowilsonia is a monotypic genus which, like *Fortunearia,* is endemic to Hupeh Province in central China. The two genera are somewhat similar vegetatively, but differ in their floral morphology, and to a certain extent in their pollen morphology. The flowers of *Sinowilsonia* are functionally unisexual, with the staminate and pistillate flowers in separate inflorescences, while the flowers of *Fortunearia* are functionally bisexual. Chang (1964) describes the exine of *Sinowilsonia* as coarsely reticulate. His photomicrographs (op. cit., Plate XII, Figs. 1–7) illustrate a reticulum that appears slightly finer than that illustrated here. However, we found extensive variation in the reticulum of grains taken from flowers of four mature male inflorescences in our material. The sculpturing ranged from relatively coarse to finely reticulate, foveolate, or scrobiculate. Some of this variation is shown in Plate 22. Still other grains exhibited coarsely granular to capillate sculpturing, suggesting an incomplete development of the exine.

In its various forms the reticulum in *Sinowilsonia* approaches that of *Fortunearia* and *Parrotia,* among others, but lacks the supratectal verrucae seen in these genera.

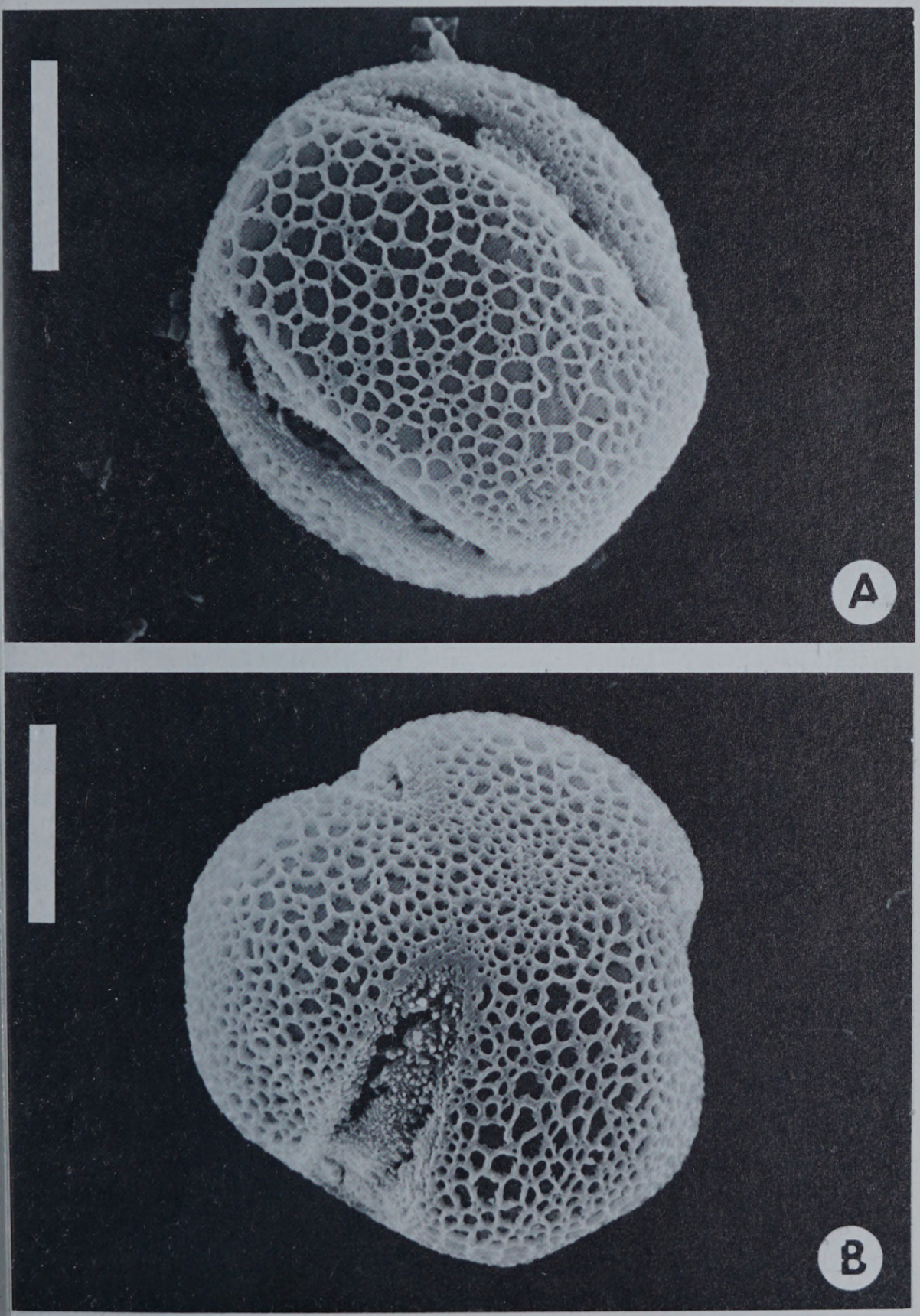

A
B

PLATE 22. *Sinowilsonia* Hemsl. (Subfamily Hamamiledoideae; Tribe Corylopsideae)
VOUCHER MATERIAL: Same as Plate 21.

A. Coarse reticulum and aperture margin of the grain illustrated in Plate 21B. Note the range of size in the lumina and the absence of supratectal verrucae, × 10,000. (Bar = 1 μm.)

B. Close-up view of the reticulum of a variant grain, the exine sculpturing varying from reticulate to vermiform. Note the ragged margin and granular membrane of the colpus, × 10,000. (Bar = 1 μm.)

C. Scrobiculate to vermiculate reticulum of another grain; the lumina varying from small, round perforations to much elongated and erratically curving and branching, surrounded by broad expanses of tectum. Note the erratic colpus margin and granular membrane, × 10,000. (Bar = 1 μm.)

Chang (1964) does not mention variability of this type in the exine of *Sinowilsonia,* but it is so prevalent in our sample that it seemed worthy of note. Further investigation is needed to explain the range of variation. Among the other genera included in this study only *Molinadendron* approaches *Sinowilsonia* in the variability of its sculpturing.

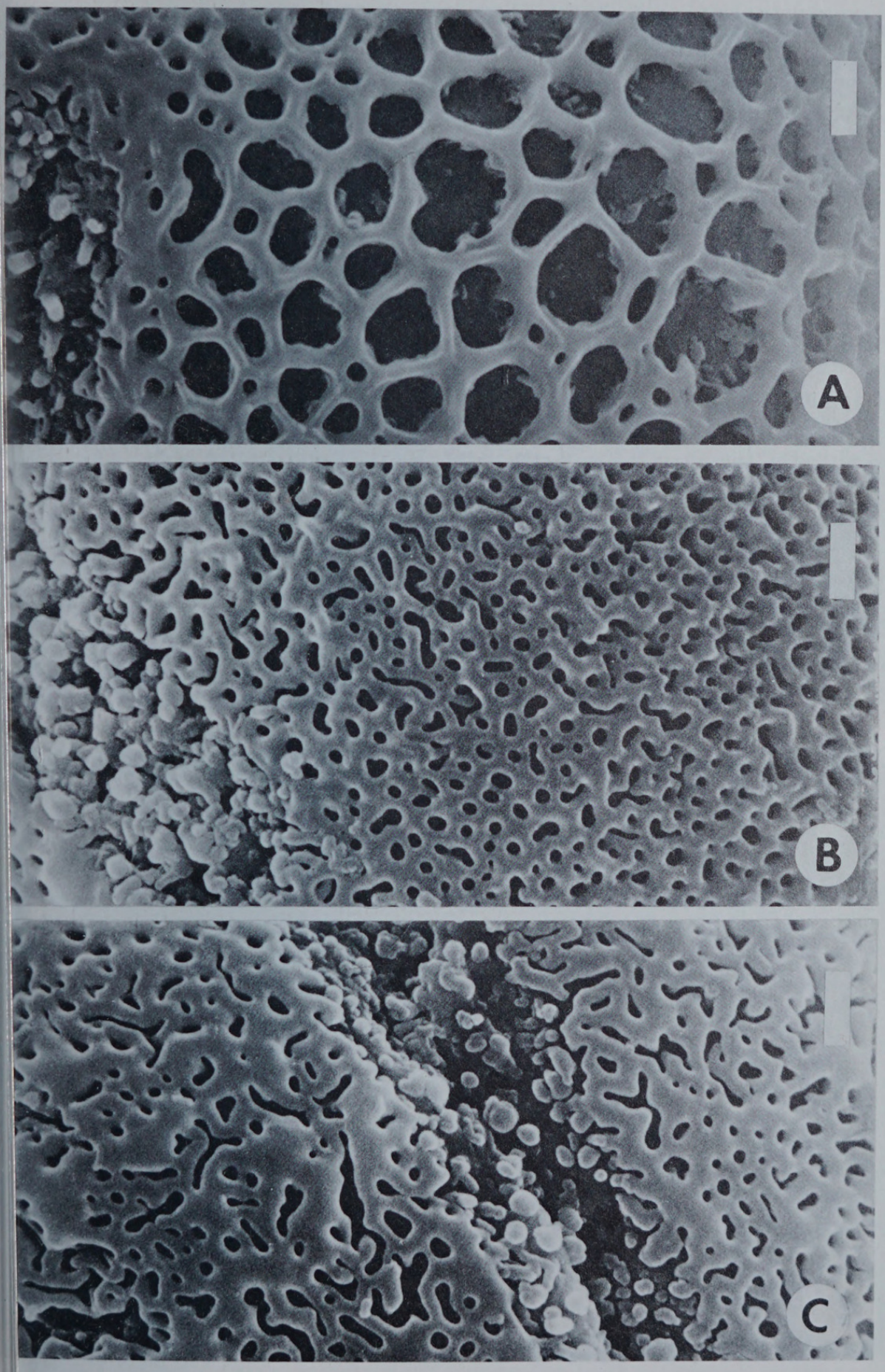
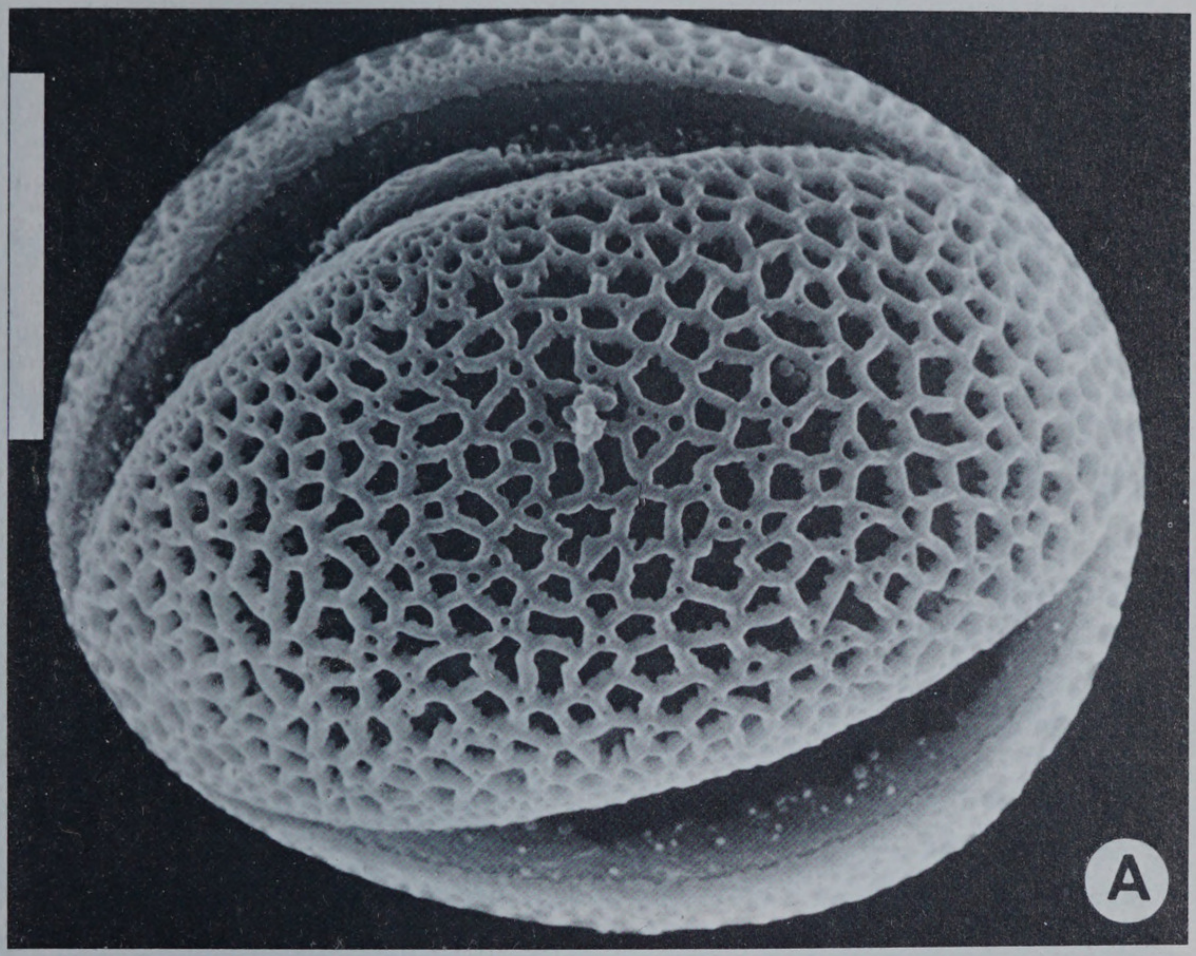

A
B
C

PLATE 23. *Fothergilla* Murr. (Subfamily Hamamelidoideae; Tribe Fothergilleae)
VOUCHER MATERIAL: *Fothergilla major* Lodd.; Bogle 929: cultivated plant in the author's collection (NHA).

A. Equatorial view of a tricolpate grain with elongate colpi. The moderately coarse reticulum contains lumina of highly variable size and shape, with numerous small round perforations scattered among larger lumina of erratic shape. The bacula supporting the tectum are visible to right and left. Note the concentration of small perforations in the margo of the colpus (upper left), the even margin and the sparsely and finely granular to almost smooth membrane. Note also the expanded central region (pore?) of the upper colpus membrane, × 3540. Shape: subprolate. Size range in equatorial view: equatorial axis, 22–36 μm; polar axis, 25–50 μm. (Bar = 10 μm.)

B. View of a hexarugate grain. Note the reduced size of the lumina in the apocolpium, × 2900. (Bar = 10 μm.)

A genus of two (−3) species (Weaver, 1969) distributed in the coastal plains and mountains of southeastern United States. Rugate grains were not seen in our light microscope preparation of this species.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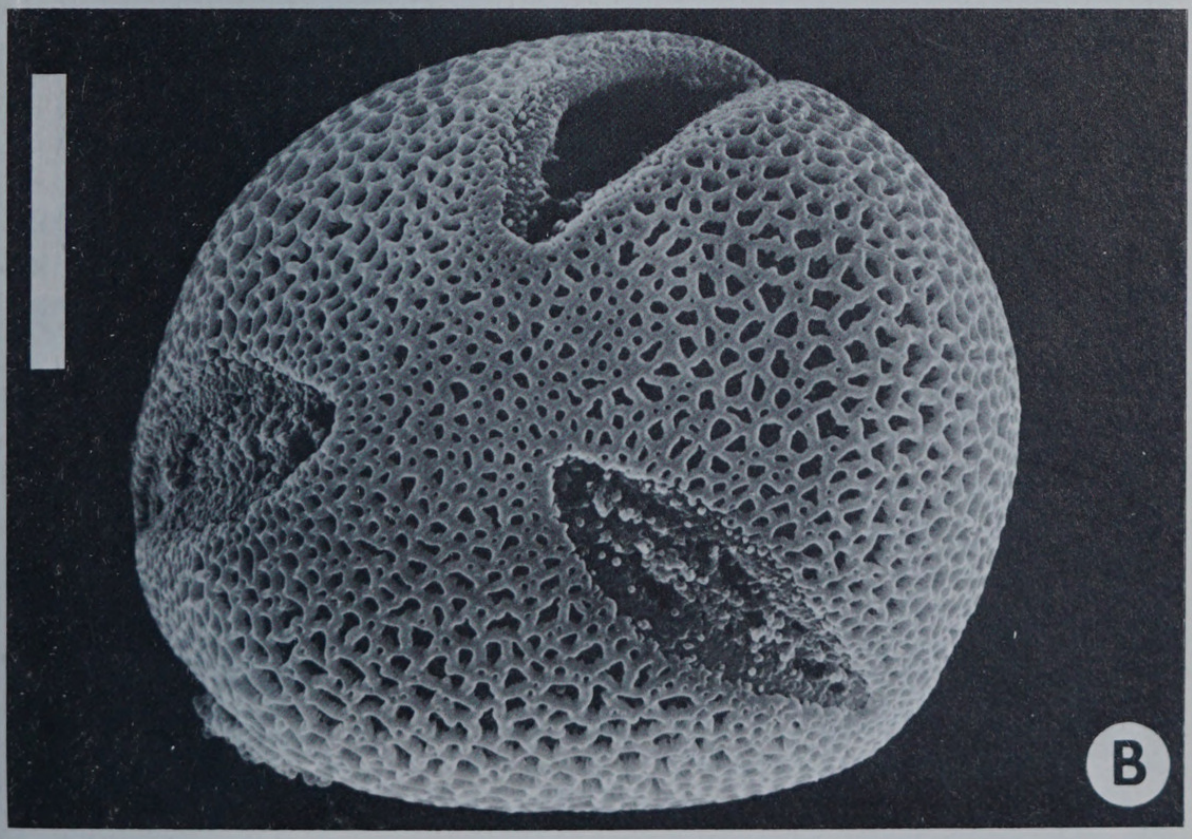
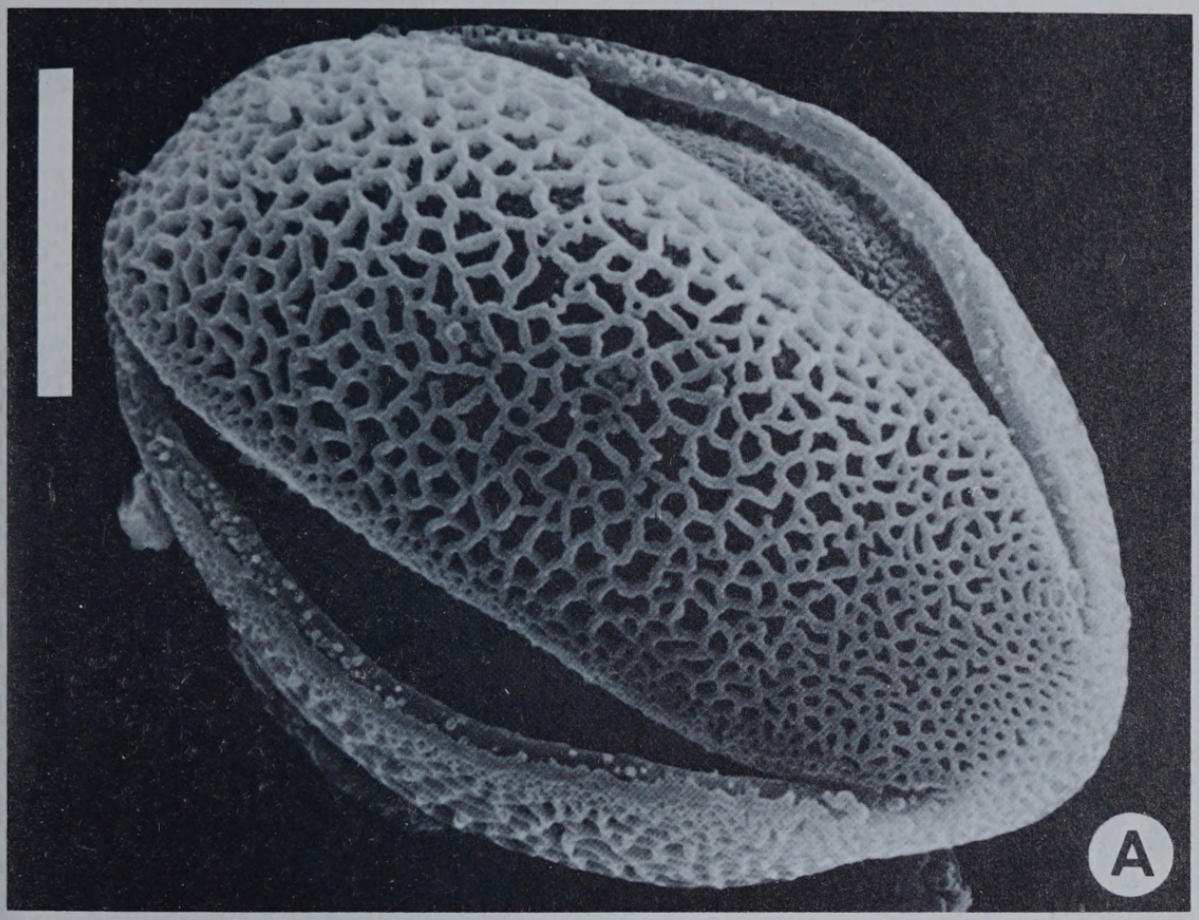

B

PLATE 24. *Fothergilla* Murr. (Subfamily Hamamelidoideae; Tribe Fothergilleae)
VOUCHER MATERIAL: *Fothergilla monticola* Ashe; Bogle 1270: cultivated plant, Arnold Arboretum (NHA).

A. Slightly oblique equatorial view of an invaginated tricolpate grain, with one intact and one ruptured colpus membrane apparent. Note the very small rounded perforations scattered among the larger lumina; the variable shape of the lumina, ranging from rounded to polygonal, elongate or stellate. The size of the lumina is strongly diminished toward the poles, as shown in the lower right. The colpi are long and acutely pointed at the ends, have a distinct margo containing many minute perforations, and finely granular membranes, × 3280. Shape: prolate. Size range in equatorial view: equatorial axis, 27–36 μm; polar axis, 35–53 μm. (Bar = 10 μm.)

B. Slightly oblique polar view. Note the marked decrease in the size of the lumina in the apocolpium, the acutely pointed ends of the long colpi approaching the poles, the distinct and minutely perforated margo, and the granular colpus membranes. A central pore-like protrusion of the aperture membranes can be seen in the upper right and lower right colpi, × 2800. (Bar = 10 μm.)

Fothergilla monticola is considered either as a distinct species or as a variant of *F. major* (see Weaver, 1969, for a review of the genus). The grain figured in (A) exhibits more erratic shape in the lumina of the mesocolpium than is seen in *F. major* (Plate 23, A), through interruption of some muri, producing stubs of muri which project into lumina space. The "bottle brush" inflorescenses of *Fothergilla* are very distinctive within the family. Pollinators are mainly bees and bumble-bees (Endress, 1977). Lee (1969) describes the grains of both *F. gardenii* and *F. major* as "tricolporoidate, pore-like appearance about 4 μm in diameter." Chang (1964) does not describe pores in his analyses of the same species.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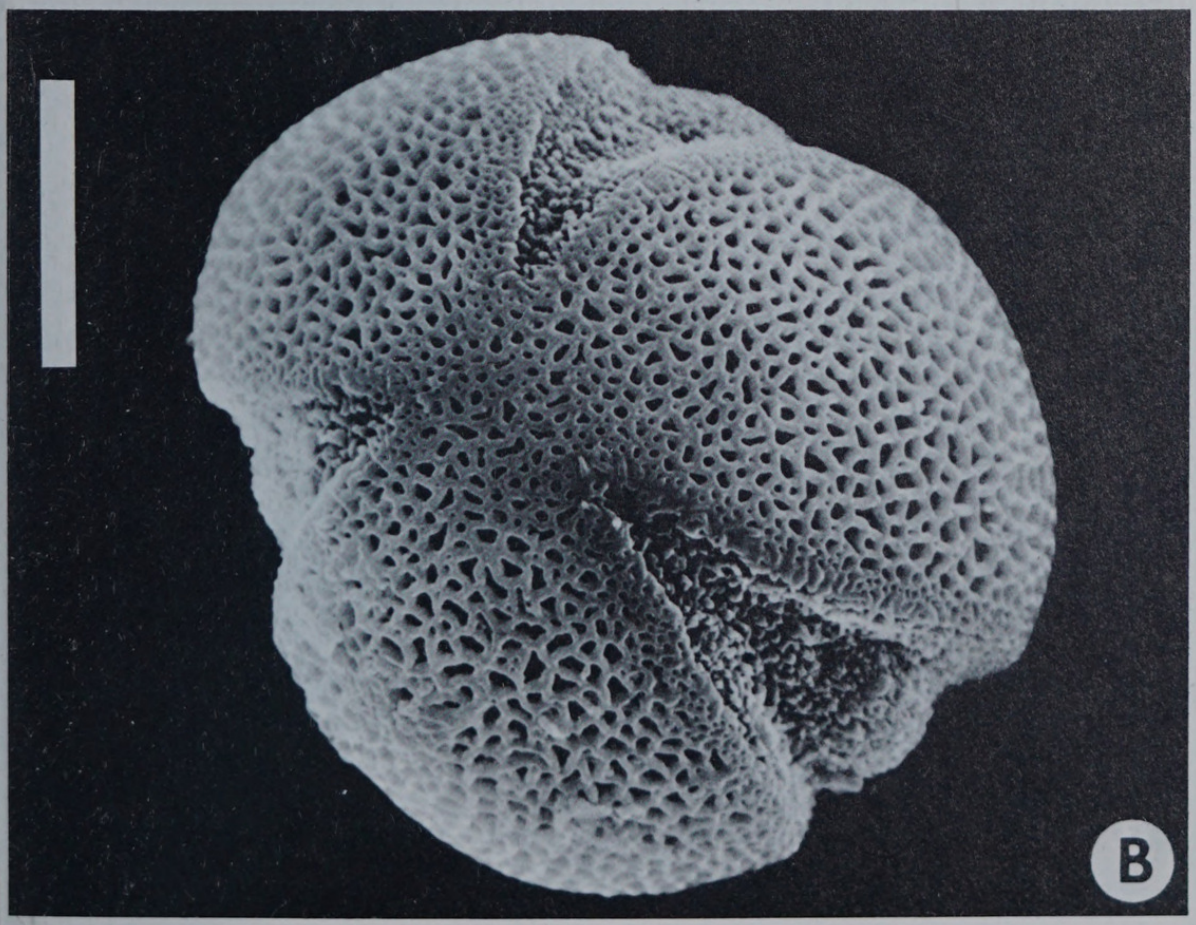
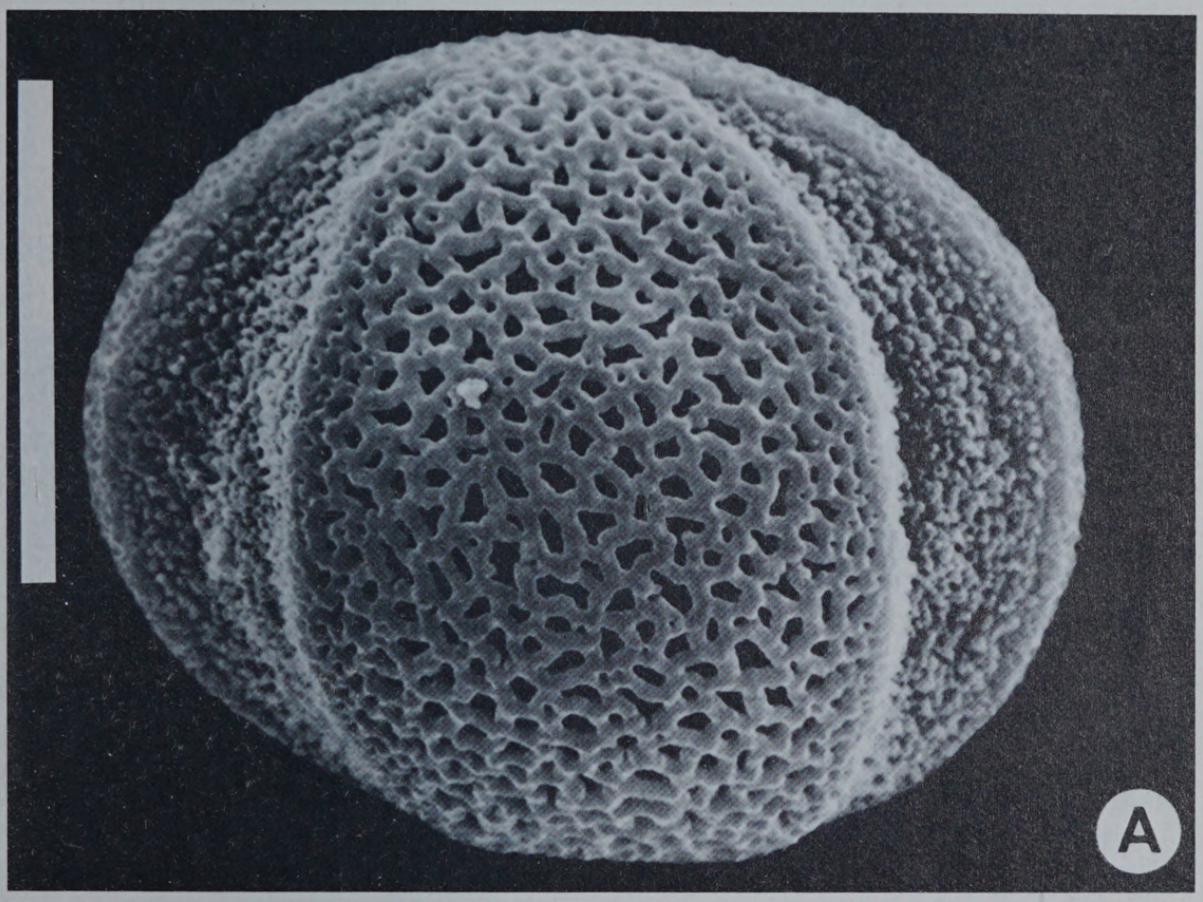

B

PLATE 25. *Parrotiopsis* (Niedenzu) Schneid. (Subfamily Hamamelidoideae; Tribe Fothergilleae)
VOUCHER MATERIAL: *Parrotiopsis jacquemontiana* (Decne.) Rehd.; Bogle 964: cultivated plant in garden of Dr. A. R. Kruckeberg, Seattle, Washington (NHA).

A. Slightly oblique equatorial view of a tricolpate grain. The reticulum of the exine is fine; with minute perforations scattered among larger lumina of irregular size and shape; the width of the larger lumina is about equal to or only slightly larger than the width of the adjacent muri. The surfaces of the muri are very weakly verrucate. The colpus membranes are finely and uniformly granular, × 4840. Shape: subprolate. Size range in equatorial view: equatorial axis, 19–28 μm; polar axis, 26–35 μm. (Bar = 10 μm.)

B. Polar view. Note the reduction in size of the lumina in the distal portion of the mesocolpium and in the apocolpium. The colpi narrow to acutely pointed or rounded ends. A distinct but narrow margo with associated minute perforations and slightly rough margins borders the colpus. (Bar = 10 μm.)

A monotypic genus restricted in distribution to the Himalayan mountains of northern Kashmir, northern West Pakistan, and northeastern Afghanistan. *Parrotiopsis* is apparently closely related to *Parrotia* and *Fothergilla,* but the pollens of the three genera differ, and that of *Parrotiopsis* is closer to *Fothergilla* than to *Parrotia.* Chang (1964) notes pronounced similarities of *Parrotiopsis* with *Corylopsis cordata* Merr. ex Li.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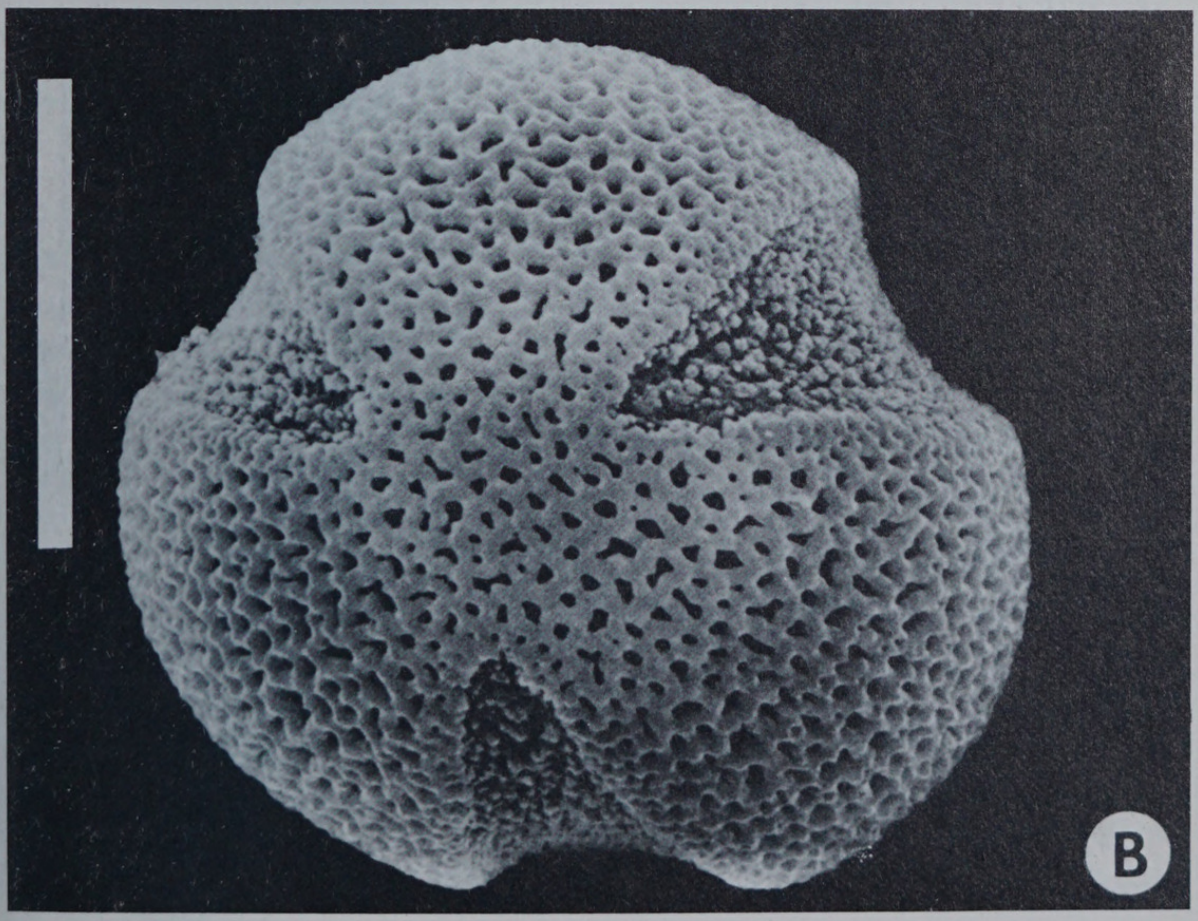
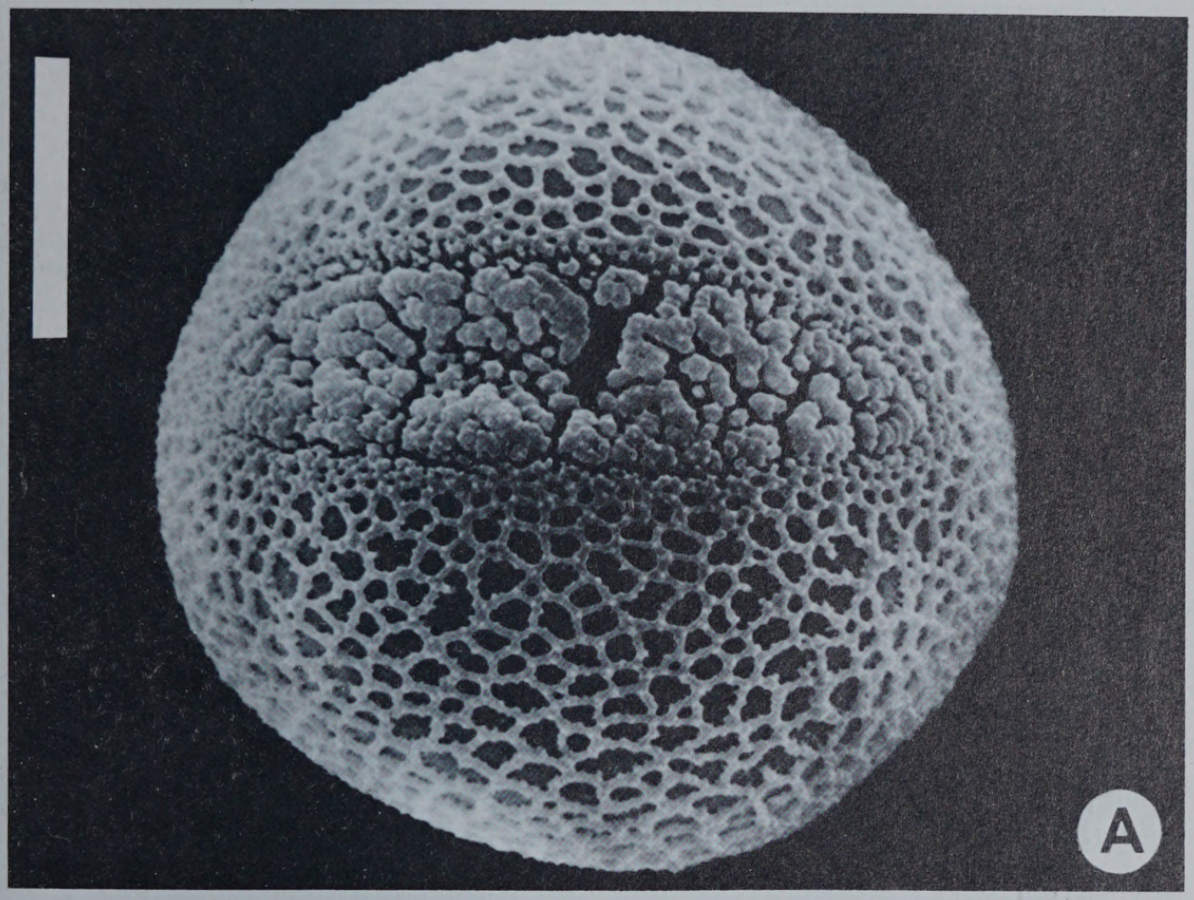

B

PLATE 26. *Parrotia* C. A. Meyer (Subfamily Hamamelidoideae; Tribe Fothergilleae)
VOUCHER MATERIAL: *Parrotia persica* (DC.) C. A. Mey.; Bogle 952: cultivated plant, Morris Arboretum, Philadelphia (NHA).

A. Equatorial view of a tricolpate grain with a moderately coarse reticulum and relatively thin exine. The lumina vary from scattered, small, round perforations to mostly large polygonal, elongate, or irregular meshes with intruding segments of murus. Numerous supratectal verrucae are borne on the muri. The colpi are of moderate length, with bluntly rounded ends, and indistinct, ragged to broken margins consisting of very finely reticulate or perforated exine. The colpus membranes are covered with very coarse, isolated to ornately fused, verrucate granules which in some areas become partially tectate, × 2600. Shape: oblate to subspheroidal. Size range not available. (Bar = 10 μm.)

B. Polar view. The lumina are slightly smaller in the apocolpium than in the mesocolpium. Note the concentration of very small lumina along the margins of the colpi, and the coarse sculpturing of the membranes, × 2570. (Bar = 10 μm.)

Parrotia is a monotypic genus which is narrowly distributed in forests on the southern shores of the Caspian Sea, in northern Iran and southern Russia (C. T. Chang, 1964). The verrucate reticulum and colpi of *Parrotia* in our sample are somewhat similar to, but coarser than, those of *Fortunearia, Molinadendron,* and *Distylium.* The similarity with *Sinowilsonia* cited by Chang (1964) is not apparent in our material. Lee (1969) reports the grains of *Parrotia* to be rarely dicolpate, tetracolpate, or syncolpate. Nair (1965) states that "a lolongate endocolpium is clearly noticed in some grains." Hesse (1978) describes and illustrates the ultra-structure of the pollen wall in *Parrotia* with regard to "pollenkitt" deposition, and the powdery form of the pollen in regard to its anemophilous pollination mechanism.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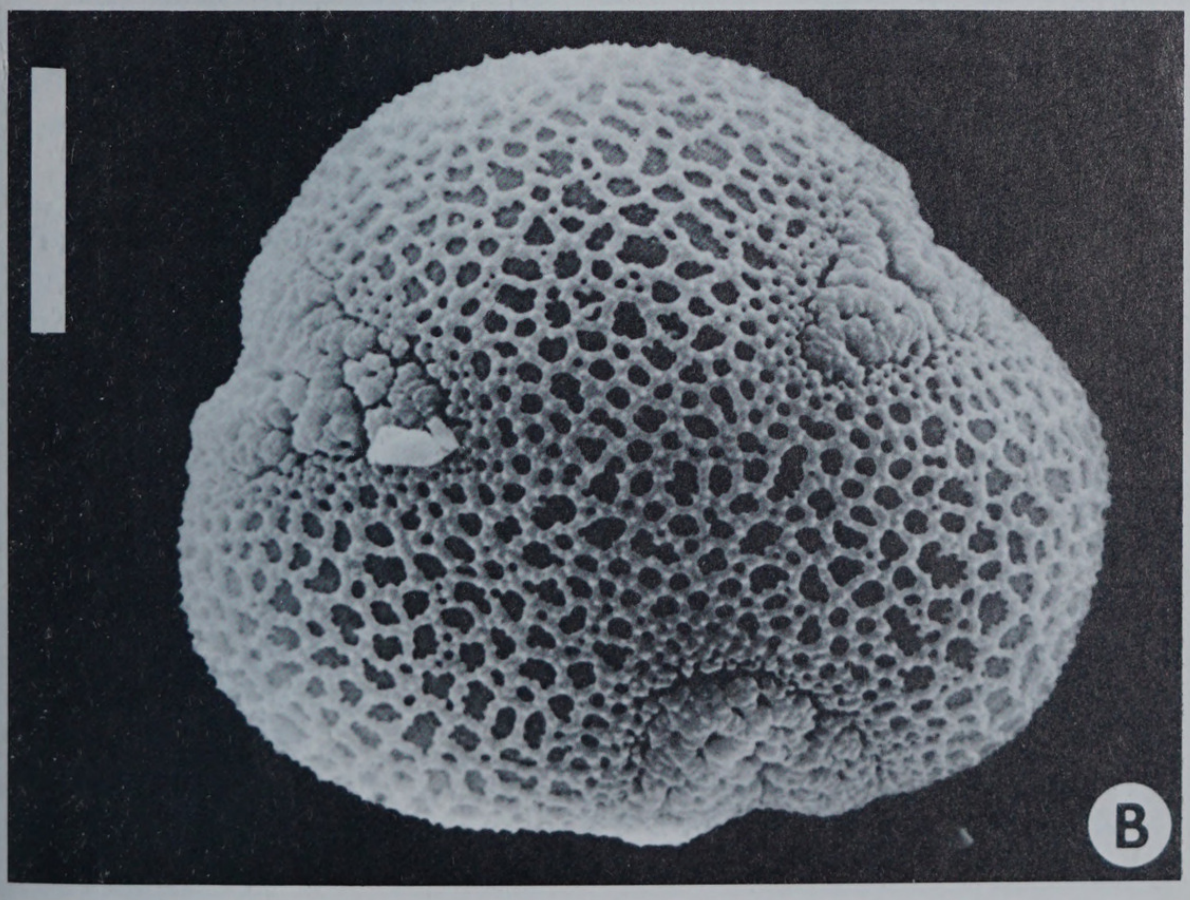
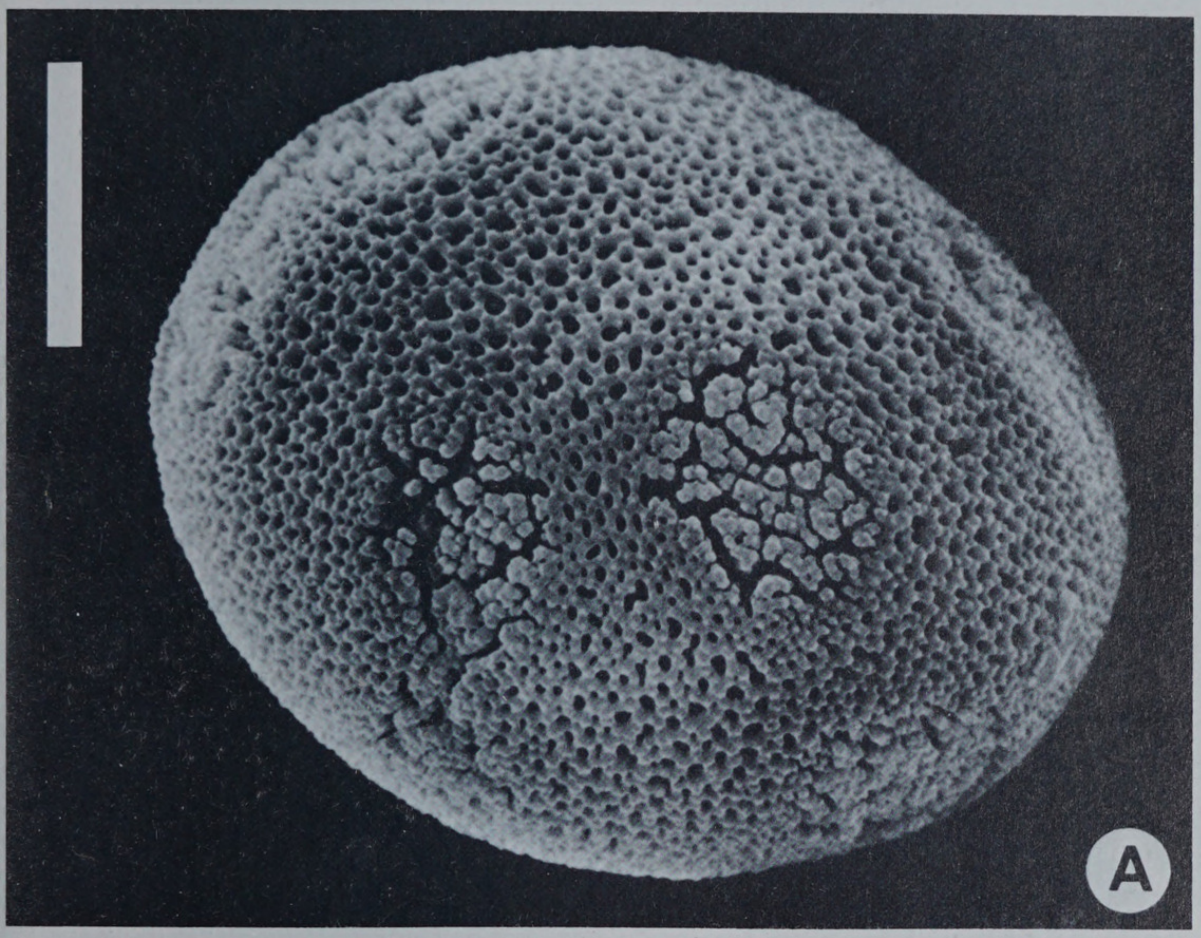

B

PLATE 27. *Sycopsis* Oliv. (Subfamily Hamamelidoideae; Tribe Distylieae)
VOUCHER MATERIAL: *Sycopsis sinensis* Oliv.; Bogle 949: cultivated plant, University of Washington Arboretum, Seattle, Washington (NHA).

A. Entire grain. The exine is finely reticulate, the lumina mostly rounded. Supratectal verrucae are numerous on the muri and on the coarse granules which cover the aperture membranes. The apertures range from more or less oblong rugae to rounded and pore-like. Aperture margins are indistinct, ragged to broken. The coarse granules of the aperture membranes appear to become fused and partially tectate in places, × 2870. Shape: spheroidal. Size range: 34–55 μm. (Bar = 10 μm.)

B. Close-up view of the reticulum, pore margin, and heavily sculptured sexine on the membrane of the pore in middle-right of A (above), × 12,000. (Bar = 10 μm.)

Sycopsis consists of perhaps as many as nine species (cf. Index Kewensis; H. T. Chang, 1973), or 13 if the segregate genus *Distyliopsis* is included. The distribution of the genus (excluding *Distyliopsis*) stretches westward from Taiwan, through south-central China, across the tip of northern Burma into the mountains of Assam. In addition to *Distyliopsis,* the genus is closely related to *Distylium,* and to *Parrotia* of the Fothergilleae. The flowers are apparently wind-pollinated.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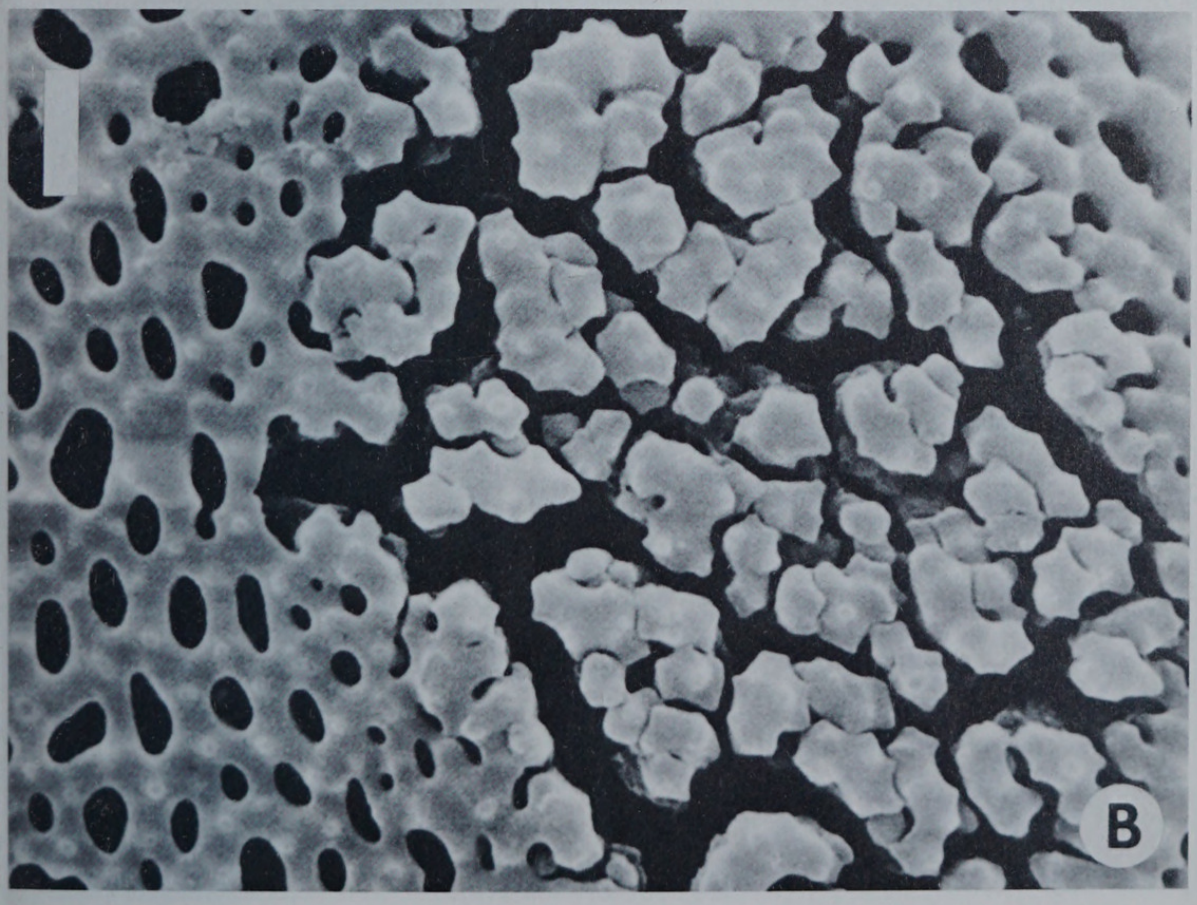

B

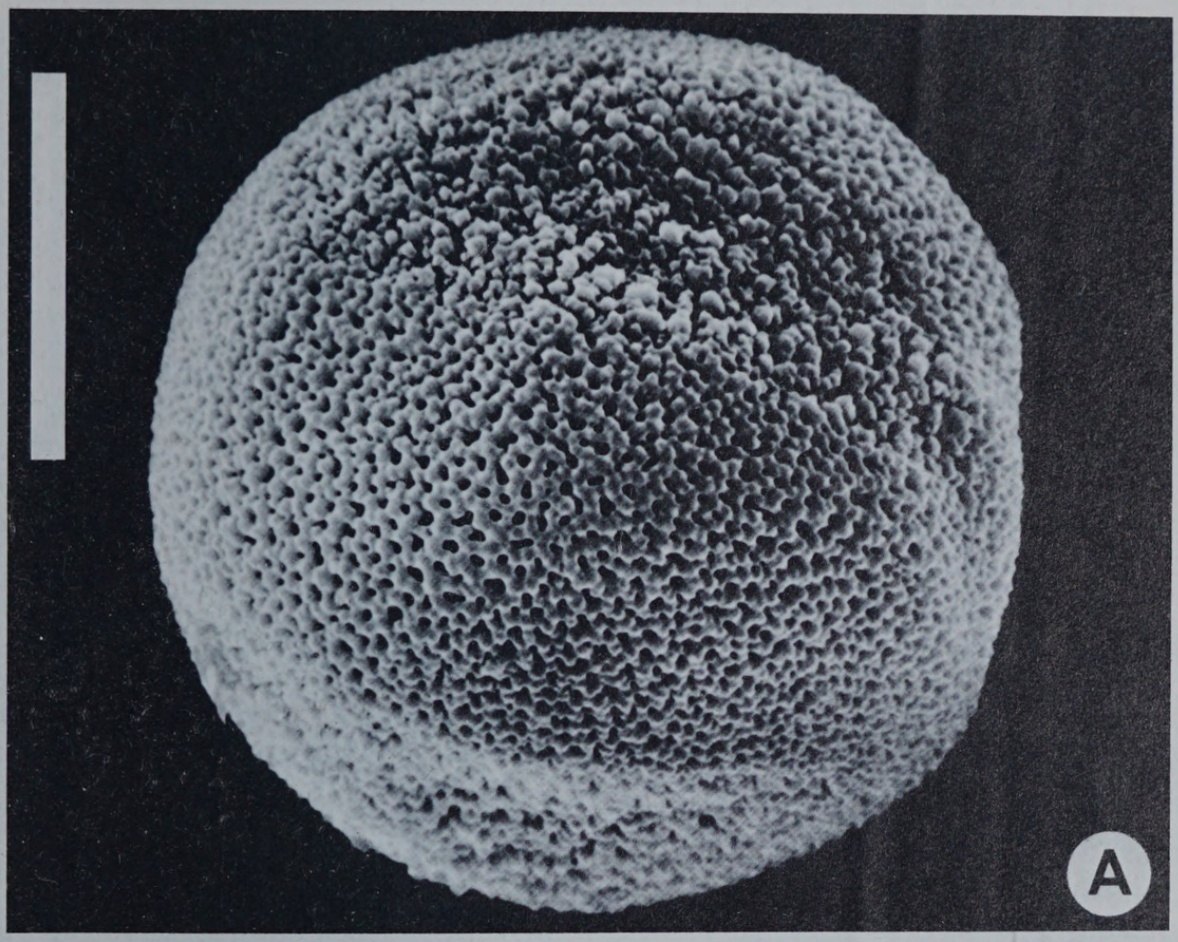
PLATE 28. *Distyliopsis* Endress (Subfamily Hamamelidoideae; Tribe Distylieae)

VOUCHER MATERIAL: *Distyliopsis dunnii* (Hemsl.) Endress; A. Kairo 44090: Yamap, Morobe District, New Guinea (AA).

A. Equatorial view of a tricolpate grain. The colpi are indistinct and of moderate length, with broadly rounded ends, little or no definition of the margins, and membranes covered with coarse verrucate granules. The exine is very finely reticulate, the lumina rounded to slightly elongate in outline, and of approximately the same width as the adjacent muri. Supratectal verrucae are borne on the muri, × 3800. Shape: subprolate. Size range in equatorial view: equatorial axis, 25–36 μm; polar axis, 30–38 μm. (Bar = 10 μm.)

B. Polar view. The lumina of the reticulum are slightly reduced in size in the apocolpium. Note the terminal portions of the three colpi, × 3440. (Bar = 10 μm.)

Distyliopsis consists of about four species segregated from the genus *Sycopsis* (Endress, 1970). The distribution of the genus ranges from Taiwan and southeastern China westward in the mountains to Burma, southward in an arc through the Philippines and Sabah, possibly in Laos (see Tardieu-Blot, 1965), to Malaya and eastern Sumatra, and erratically eastward in Celebes and in the mountains of New Guinea (see map in Endress, 1970). The genus is closely related to *Distylium* and *Sycopsis*. Pollination is anemophilous. Vink (1957) and H. T. Chang (1973) reject *Distyliopsis*.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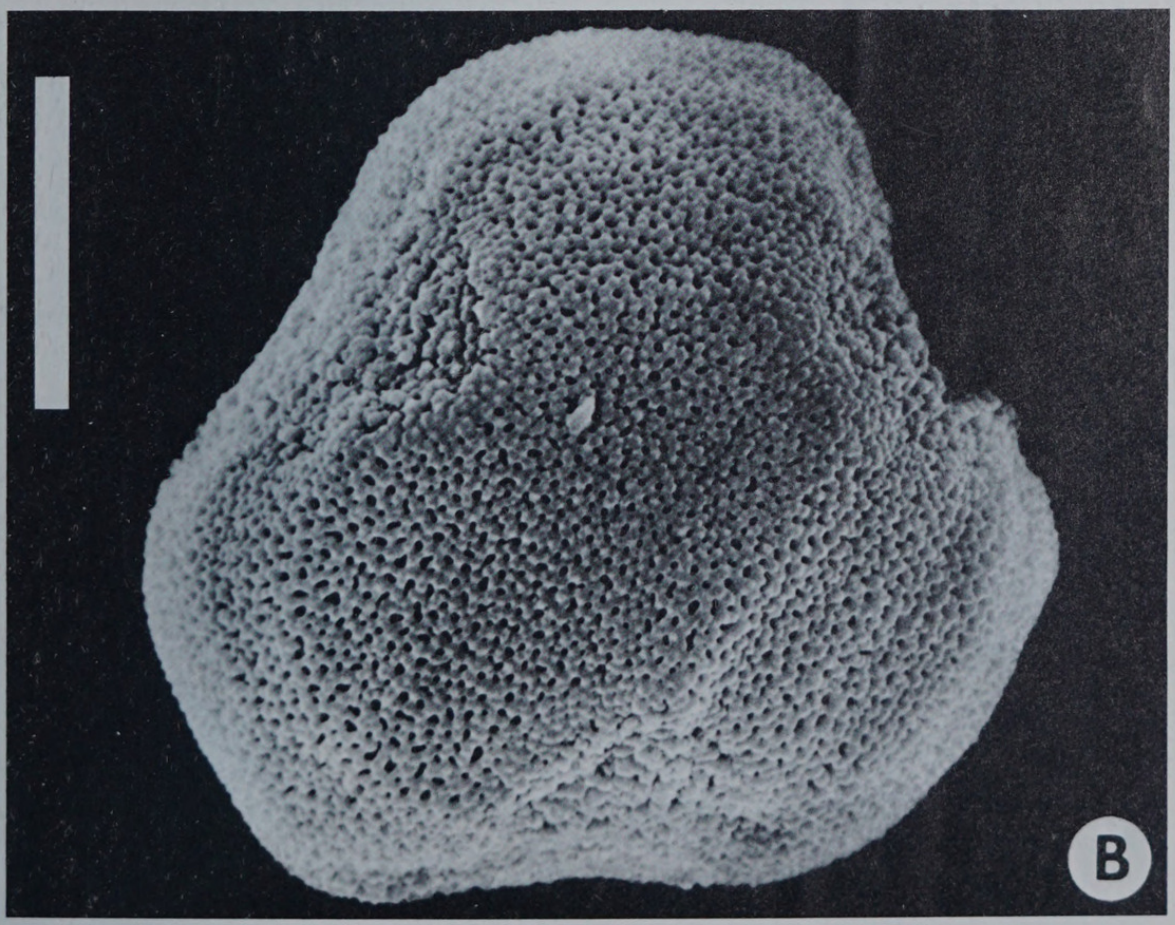

B

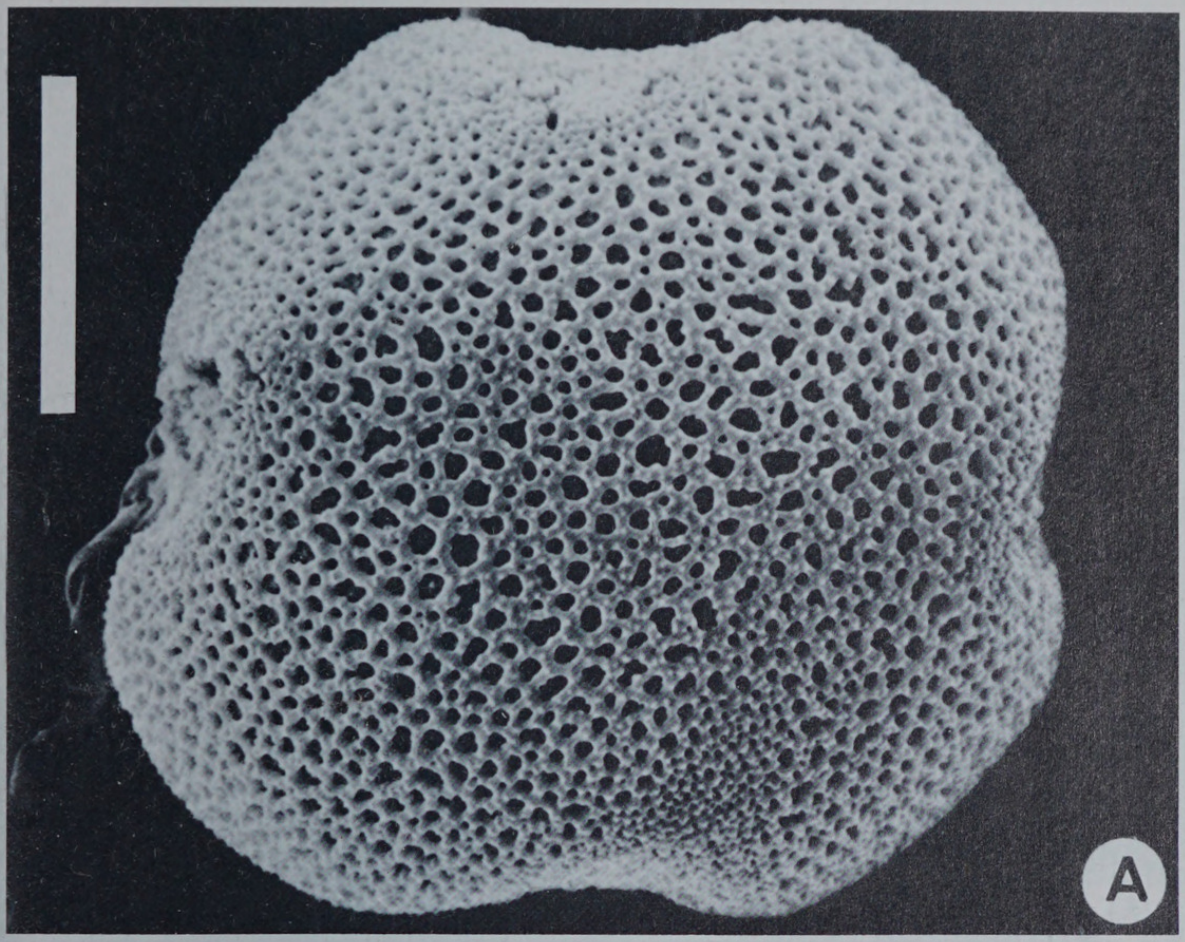
PLATE 29. *Distylium* Sieb. and Zucc. (Subfamily Hamamelidoideae; Tribe Distylieae)

VOUCHER MATERIAL: *Distylium racemosum* Sieb. and Zucc.; Bogle 740: cultivated plant, Dr. Graham's garden, Seattle, Washington (NHA).

A. Polar view of a tetracolpate grain, illustrating the finely reticulate exine. The lumina are rounded to slightly elongate or irregular in outline, and the muri are verrucate. The colpi are shortened, with broadly rounded ends, indistinct margins, and uniformly granular membranes, × 3000. Shape: spheroidal to oblate spheroidal. Size range: 40–53 μm. (Bar = 10 μm.)

B. View of a grain with about ten apertures ranging in shape from rugae (right) to rounded and pore-like. Reticulum of the sexine finer than that in (A) (above), the lumina smaller and perhaps a little more irregular in outline. Aperture membranes coarsely granular, the granules also bearing verrucae, × 3030. (Bar = 10 μm.)

A genus of about 19 described species (see Index Kewensis; H. T. Chang, 1973) ranging from southern Japan and Korea southward and westward through central China to Assam, and southward through Indochina to Malaya, Sumatra, Java and eastward to Flores. The naked flowers are probably wind-pollinated.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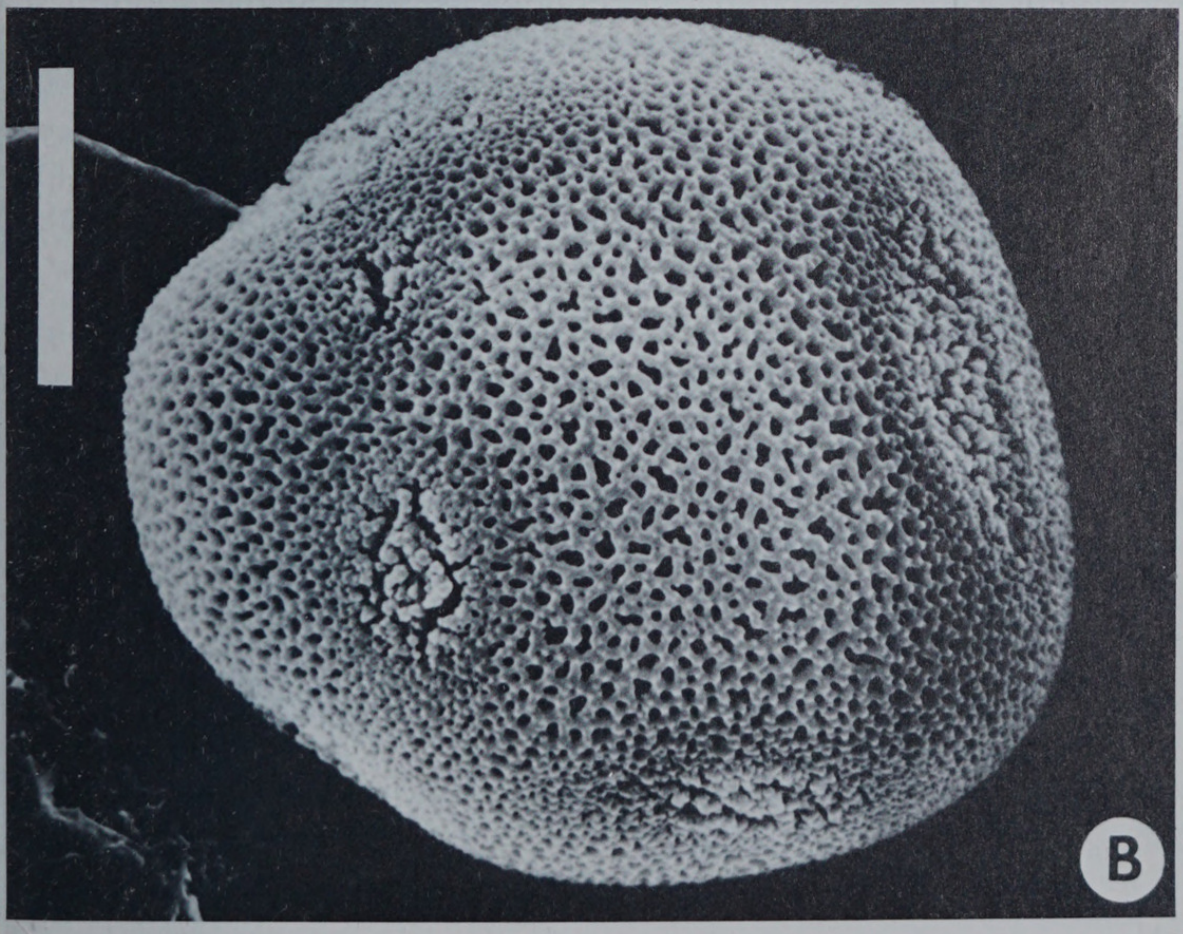
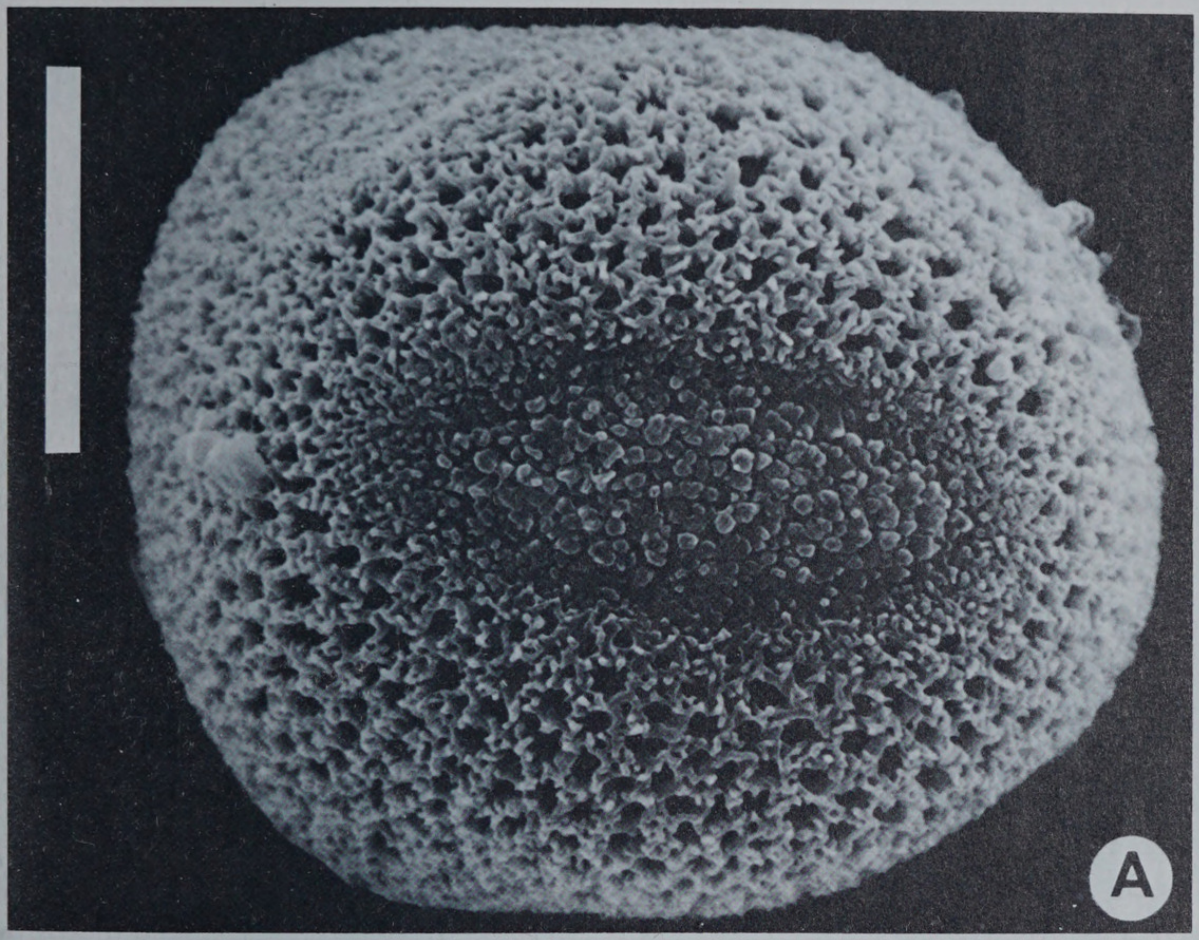

B

PLATE 30. *Molinadendron* Endress (Subfamily Hamamelidoideae; Tribe Distylieae)
VOUCHER MATERIAL: *Molinadendron sinaloense* (Standley and Gentry) Endress; Bogle 860: Sierra Suratato, Sinaloa, Mexico (NHA).

A. Equatorial view of a tricolpate grain. The reticulum is fine, consisting of numerous minute perforations interspersed among larger, rounded to elongate lumina. The muri are complex, often appearing multilayered; appearing to be made up of interwoven strands, some of which produce erect processes which project above the surface of the muri (compare enlargement in Plate 31, B-1), giving the outer surface a verrucate to papillate (as in this figure) appearance. The colpi are somewhat shortened, with bluntly rounded ends, indistinct margins, and coarsely granular membranes, × 3630. Shape: subprolate. Size range in equatorial view: equatorial axis, 22–32 μm; polar axis, 26–41 μm. (Bar = 10 μm.)

B. Slightly oblique polar view of another grain, with processes of the exine more or less elaborated; the shape and variation of the lumina more apparent (compare close-up of exine in Plate 31, B-2), × 3500. (Bar = 10 μm.)

Molinadendron is a Central American genus consisting of three species distributed in the mountains of Mexico, Guatemala and Honduras. These taxa were originally described as species of *Distylium*, but anatomical and morphological evidence support their segregation as a separate genus (Bogle, 1970; Endress, 1969).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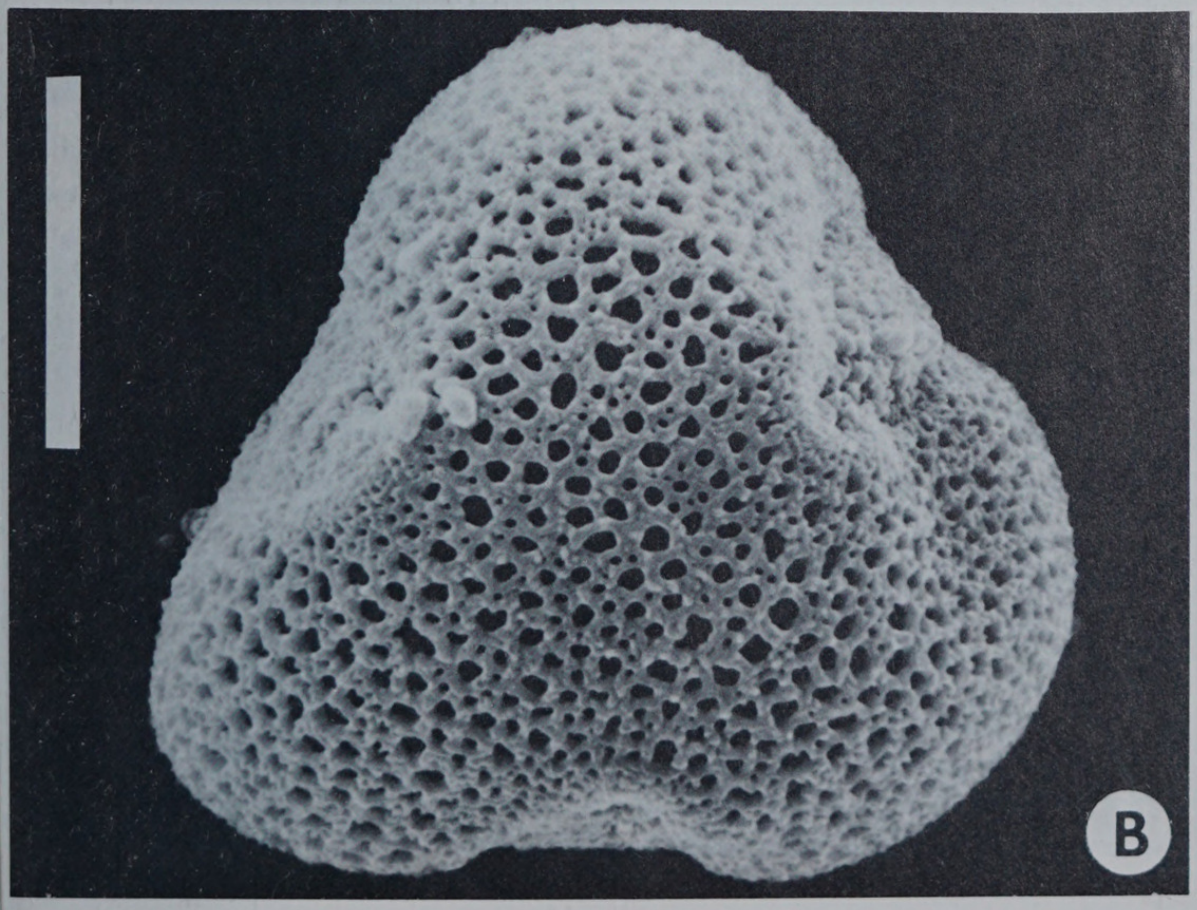
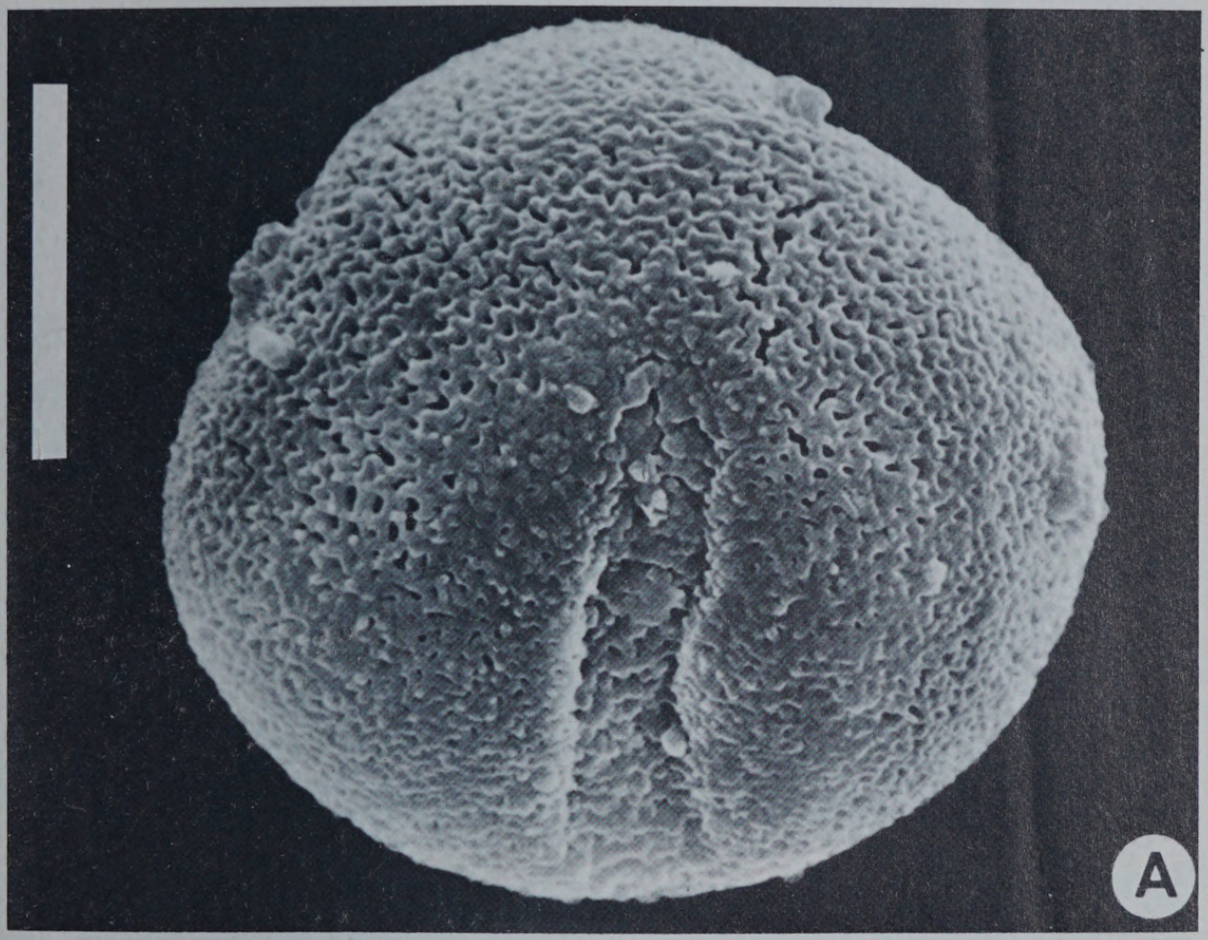
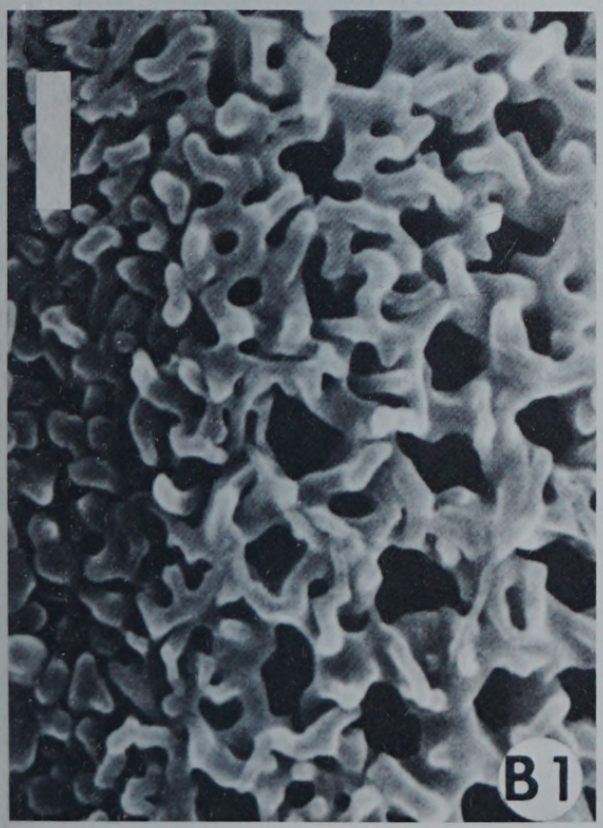

B

PLATE 31. *Molinadendron* Endress (Subfamily Hamamelidoideae; Tribe Distylieae)
VOUCHER MATERIAL: same as Plate 30.

A. A third variant form found in our sample. The lumina are much reduced and rather irregular in shape; the exine appears scrobiculate in some areas, particularly around the colpus, finely foveolate in other areas. The overall appearance is of a more extensive and smoother tectum than in the other grains of this species illustrated here, × 3550. (Bar = 10 μm.)

B. Close-ups of the exine sculpturing of the grains illustrated in Plate 30, (A) and (B). B-1: note the extensive intertwining of the exine strands in the muri, and elaboration of the supratectal processes. The muri often appear double (or even triple) banded in width. The exine grades into the granular pore membrane at left, × 12,500. B-2: less extensive development of processes on the muri, and the more typical conditions seen in our sample. Note the interwoven, over-and-under appearance of the strands making up the muri, and in some areas strands lying side by side in the muri, giving the surface a channeled appearance. Processes less numerous and less protrusive, × 12,780. (Bar = 1 μm.)


A


B1

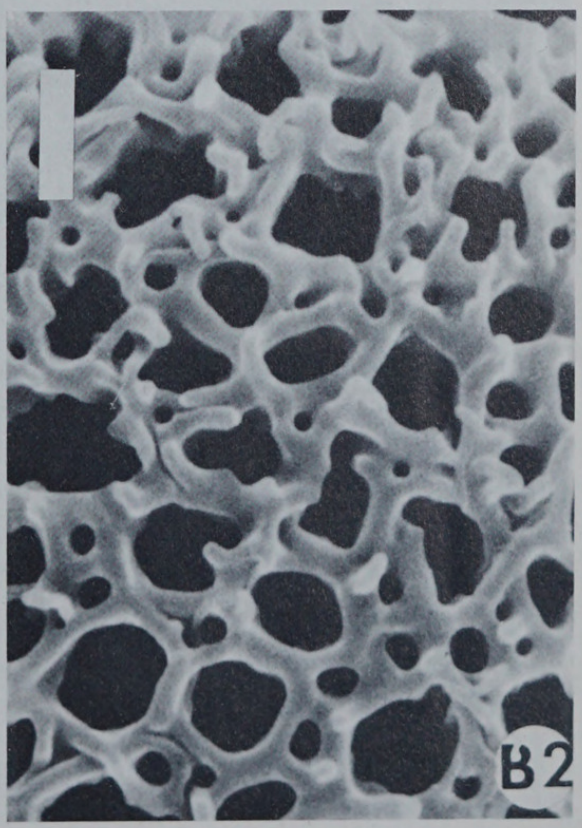

B2

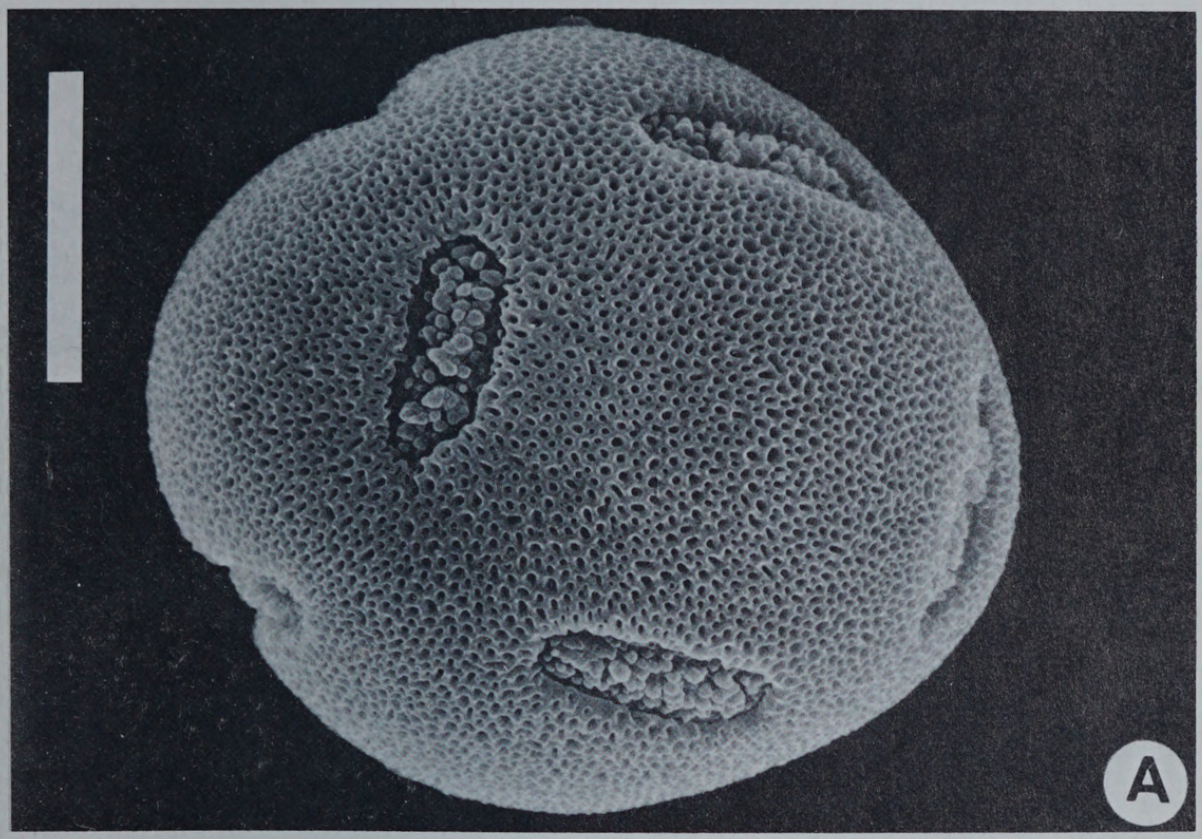
PLATE 32. *Matudaea* Lundell (Subfamily Hamamelidoideae; Tribe Distylieae)

VOUCHER MATERIAL: *Matudaea trinervia* Lundell; Bogle 848: Behucos, Nanchititla, Mexico, Mexico (NHA).

A. View of a rugate grain with six shortened colpi visible. The reticulum of the exine is very finely foveolate. The aperture margins are distinct but uneven, the aperture membranes are coarsely granular, × 3000. Shape: spheroidal to subspheroidal. Size range: 32–45 μm. (Bar = 10 μm.)

B. Another grain with irregular apertures, ranging from shortened colpi to pores. The irregular pores at lower-middle and upper-middle may represent medianly constricted colpi (compare Plate 33, A and B, lower right grain), × 2360. Size range: 32–45 μm. (Bar = 10 μm.)

Matudaea, like *Molinadendron,* is a Central American genus. It contains only two species distributed in mountain forests of Mexico, Guatemala, and Honduras. The number of apertures appears to vary from four (tetracolpate) to as many as 12-rugate. The genus is possibly allied with *Distylium* and *Distyliopsis.* Pollination is apparently anemophilous.


A

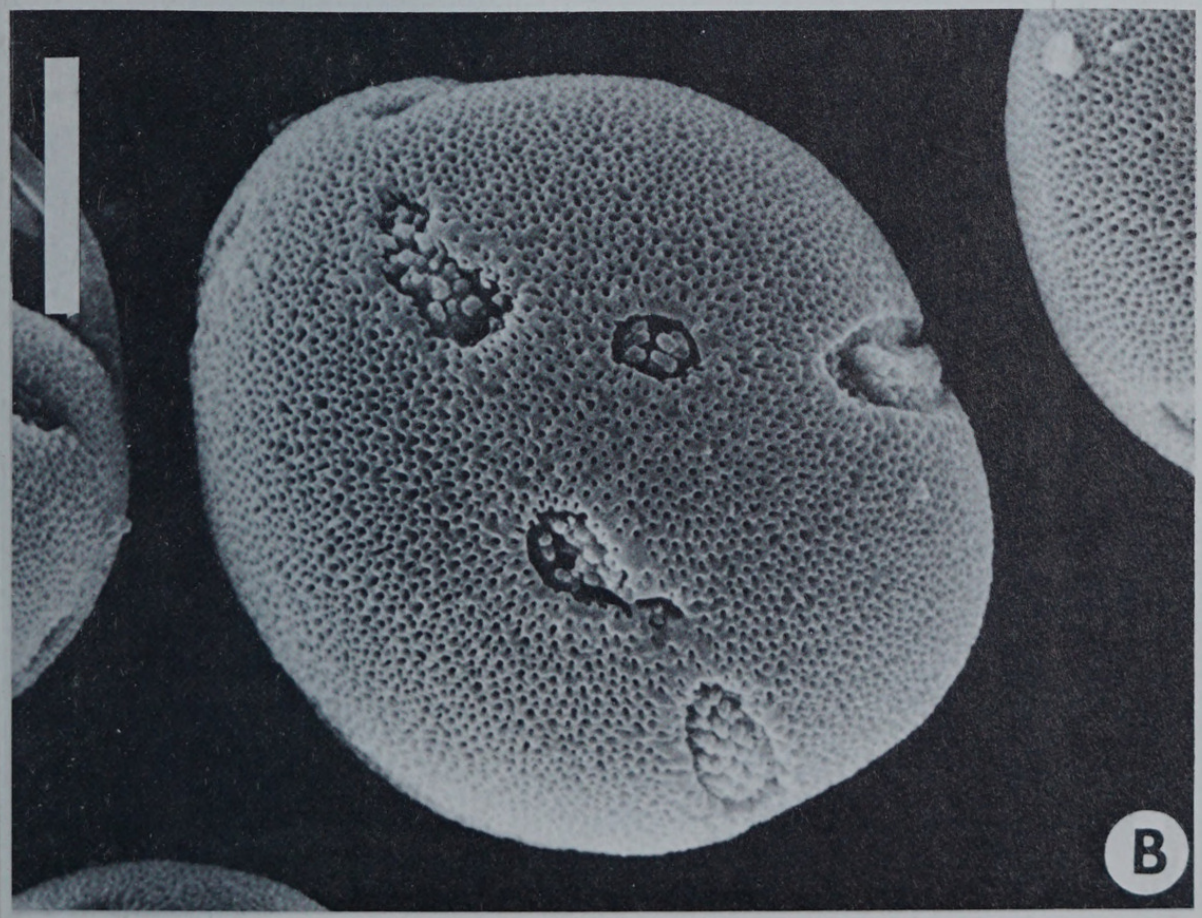
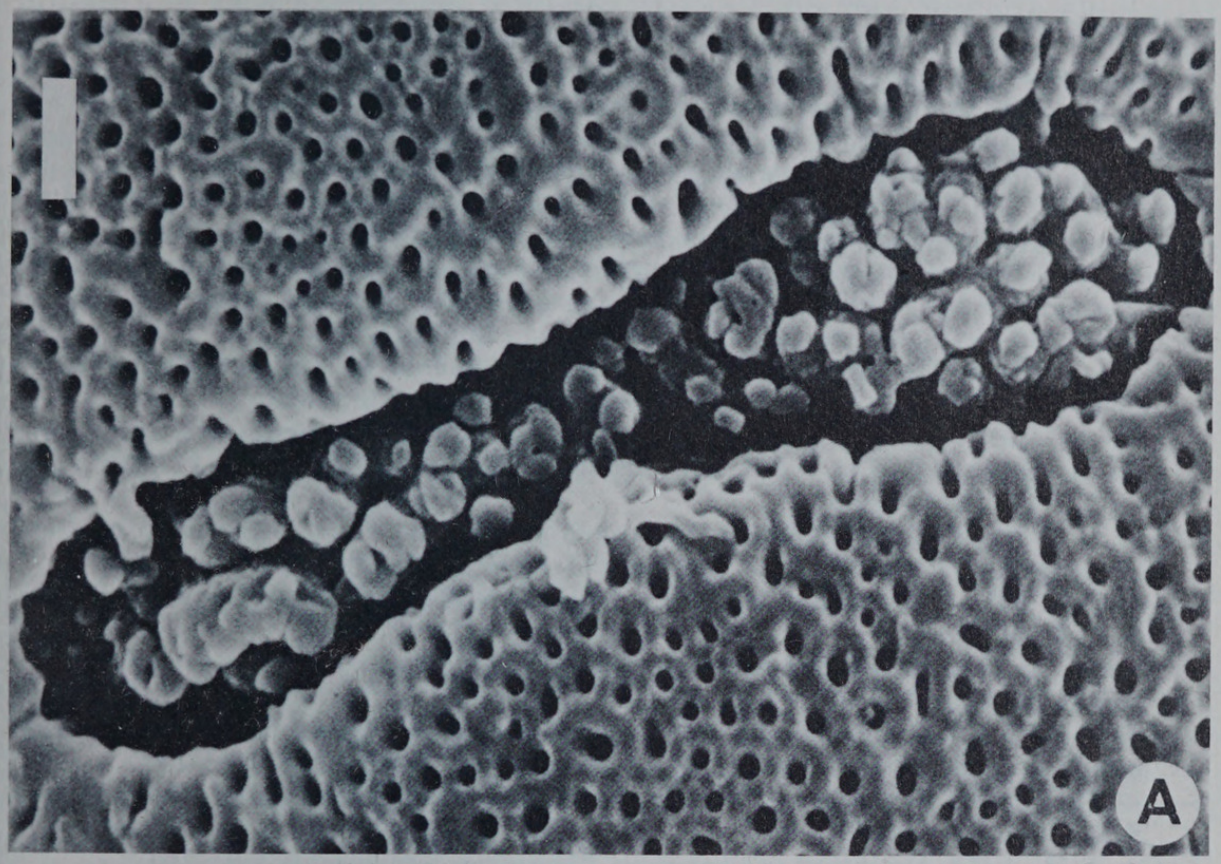

B

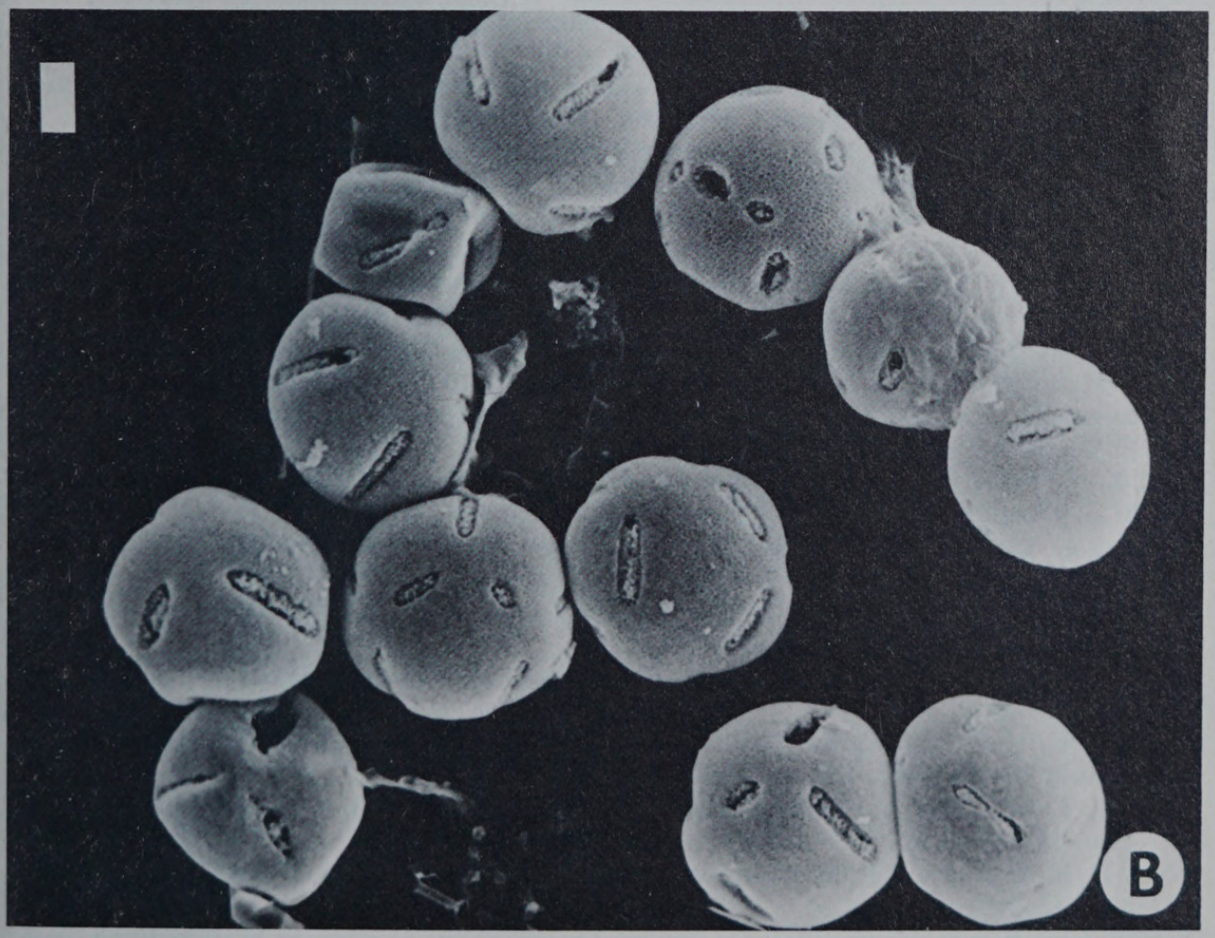
PLATE 33. *Matudaea* Lundell (Subfamily Hamamelidoideae; Tribe Distylieae)

VOUCHER MATERIAL: same as Plate 32.

A. Close-up view of the colpus of a rugate grain, showing an apparent early stage in the median constriction of a colpus which, when carried to the extreme, results in the formation of pore-like apertures. Note the foveolate exine, irregular margins and coarsely granular membranes of the colpus, × 12,500. (Bar = 1 μm.)

B. A group of 12 grains, showing various aperture forms and configurations, × 670. (Bar = 10 μm.)


A


B

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