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POLLEN CHARACTERS IN RELATION TO THE DELIMITATION OF MYRTALES

The University of Oklahoma PH.D. 1982

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GRADUATE COLLEGE

POLLEN CHARACTERS IN RELATION TO THE DELIMITATION OF MYRTALES

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

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VARSHA C. PATEL

1982

POLLEN CHARACTERS IN RELATION TO THE DELIMITATION OF MYRTALES

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POLLEN CHARACTERS IN RELATION TO THE DELIMITATION OF MYRTALES

ABSTRACT

Pollen grains representative of the Lythraceae, Punicaceae, Sonneratiaceae, Trapaceae, Oliniaceae, Combretaceae, Alzateaceae, Penaeaceae, Crypteroniaceae, Melastomataceae, Myrtaceae (including Psiloxylaceae) and Onagraceae, the twelve families constituting the order Myrtales, were examined with scanning (SEM) and transmission (TEM) electron microscopy with major emphasis on SEM. With omission of the Trapaceae, Myrtaceae, and Onagraceae, the remaining families have enough similarities to be grouped together palynologically. Heterocolpate pollen characterizes the Lythraceae, Combretaceae, Oliniaceae, Penaeaceae, Crypteroniaceae and Melastomataceae. In the latter five families pseudocolpi were noted in all taxa examined except Adelobotrys, Allomorphia, Astronia, Bredia, Oxyspora, and Tococa of the Melastomataceae and Buchenavia, Laguncularia, and Strephonema of the Combretaceae. With the exceptions of the latter four genera these taxa possess intercolpar concavities. Pseudocolpi are equal to the number of apertures except in Lythraceae where Ammannia, Nesaea and Crenea have twice the number; intercolpar concavities are also isomerous with apertures. In Oliniaceae the pseudocolpi are located in just one hemisphere and hence considered as half pseudocolpi. The Alzateaceae may have incipient pseudocolpi while the Sonneratiaceae and Punicaceae possess meridional ridges

which alternate with the apertures; they are prominent in the former and weakly defined in the latter. Meridional ridges are also present in some Lythraceae taxa lacking pseudocolpi. Exine sculpturing in the mesocolpia is variable throughout the order with Crypteroniaceae, Alzateaceae, Oliniaceae, and Penaeaceae basically psilate; Melastomataceae basically striate and rugulate; Punicaceae basically granular-microrugulate; Sonneratiaceae basically verrucate-rugulate; Combretaceae echinate, reticulate, rugulate, striate and psilate; and Lythraceae striate, psilate, verrucate and granular. Commonly, the pseudocolpi and colpi have different sculpturing than the mesocolpial regions. Exine structure is essentially of the post and beam construction with the fundamental ektexine and endexine stratification layers. In all Combretaceae and some Melastomataceae the foot layer is strikingly delineated as domes, whereas, in Alzateaceae the columellae layer shows a zig-zag configuration. The Oliniaceae and Penaeaceae are distinct throughout the order with remarkably thickened tectum and foot layer and negligible columellae; Acanathella of the Melastomataceae is somewhat similar, differing only in a better developed columellae layer. In general, the Lythraceae has the most diverse pollen at both sculptural and structural levels; the Combretaceae also have considerable diversity, primarily exomorphically, and Strephonema is the only taxon noted in the order with a reticulate sculpture; the Melastomataceae are diverse exomorphically and Tococa spadiciflora is the only polyad in the order other than Ludwigia (Onagraceae); the Oliniaceae, Penaeaceae, and Crypteroniaceae show rather uniform intrafamilial morphology. The monogeneric Trapaceae with protruding and domed apertures and meridional ridges resulting from exine folds, is totally unique in the Myrtales. Some samples show linked pollen grains suggestive of polyads while sections through the ridge area show an extremely thick endexine and loosely

organized ektexine reminescent of some Onagraceae. The Myrtaceae, with pollen oblate-elliptic in lateral view and triangular in polar view, is also without a counterpart in the Myrtales. Refinement of previous studies indicates three major pollen groups based on the nature of the colpi: (1) longicolpate, (2) syncolpate and parasyncolpate with and without intercolpar concavities, and (3) brevicolpate and brevissimicolpate. Myrtus communis and Psidium littorale occur as tetrads as well as monads and are the only tetrads recorded in the Myrtales other than the Onagraceae. The pollen morphology of Psiloxylon and Heteropyxis, genera of questionable taxonomic placement, appear comfortable within the Myrtaceae. The final family, Onagraceae, is also very distinctive in the Myrtales. The viscin threads, tetrads and polyads, exceptionally thick endexine, essentially spongy-paracrystalline ektexine with columellae absent or greatly reduced, absent foot layer, protruding apertures, and 2-aperturate grains (in Fuchsia) distinguish this family, which, with a few superficial comparisons to Trapaceae and Penaeaceae differs from all others in the Myrtales.

INTRODUCTION

Pollen morphology in the core families of the Myrtales as recognized by Dahlgren and Thorne (in press) has received surprisingly little study. The very extensive reference citations given in the four monumental pollen bibliographic indices of Thanikaimoni (1972, 1973, 1976, 1980) for these families are misleading in that they include all studies in which pollen morphology is mentioned (e.g., atlases; regional and local floras; anatomical and embryological reports; horticultural, agricultural and geological records; chemical systematics), but relatively few of them are actually based on comprehensive pollen investigative research. Of those emphasizing pollen morphology, about 90% are confined to light microscopy. Scanning electron microscopy (SEM) was utilized to a limited degree and remarkably, structural data from transmission electron microscopy (with the exception of Muller 1973, 1975, 1978, 1981; Lugardon and Van Campo, 1978; Gadek and Martin, 1981, 1982; Skvarla, Raven, and Praglowski, 1975, 1976; and Skvarla, Raven, Chissoe, and Sharp, 1978) is virtually non-existent in the order. Furthermore, there are noticeably few modern studies in the three largest families, Melastomataceae, Combretaceae, and Myrtaceae, although the latter is currently under comprehensive examination by Gadek and Martin (1981, 1982, personal communication).

This report is the first in what is contemplated as a series on Myrtales pollen. In it we have attempted to provide a pollen morphologic overview of the

pollen of the major taxa in the core families (i.e., Lythraceae, Punicaceae, Sonneratiaceae, Trapaceae, Oliniaceae, Combretaceae, Alzateaceae, Penaeaceae, Crypteroniaceae, Melastomataceae, Myrtaceae including Psiloxylaceae, and Onagraceae). Our major emphasis is on the exomorphic characters (i.e., sculpture patterns) as revealed by SEM. In an attempt to supplement this data we have provided a limited amount of structural information obtained by TEM. Subsequent reports in this series will concentrate on: (1) exine structure (i.e., TEM) in the cores families, (2) comprehensive SEM-TEM pollen morphologic descriptions of the approximately 30 or so families considered to be closely as well as distantly allied to the Myrtales, and (3) expanded SEM and TEM coverage in some of the families in the Myrtales particularly the Melastomataceae.

MATERIALS AND METHODS

All pollen was treated by the acetolysis method of Erdtman (1960). Pollen for SEM was either critical point dried or air dried from 95% ethanol, sputter coated with gold, and examined with an ISI Super II SEM. For TEM, the acetolyzed pollen was processed according to previously described methods (Skvarla, 1966) and examined with a Philips model 200 TEM. Pollen was examined with LM to determine the nature of colpi and endoapertures.

Table 2 lists taxa examined, collecting information, select morphologic data, pseudocolpi ubiquity, and figure references.

The organization of this report is such that the core families are given individual discussion to include (1) general palynology, (2) specific morphology for taxa listed in Table 2, (3) a brief review of previous studies when relevant, and (4) significant morphological correlations with other core families. Following this

treatment of the individual families an attempt was made to summarize as well as synthesize the data for the entire order.

TERMINOLOGY

The terms used in this study to describe pollen grain morphology are essentially those of Erdtman (1971) for exomorphology and Faegri and Iversen (1975) for endomorphology. Although most of the terms are standard palynological jargon and therefore not in need of clarification, a few are particularly crucial to describing Myrtales pollen and are therefore discussed below.

1. Pseudocolpi. According to Faegri and Iversen (1964, p. 225) "Pseudocolpus (pseudopore): differs from a normal furrow (pore) in that it is not an exit for the pollen tube", while the definition of Erdtman (1971, p. 467), is "Colpoid streaks not functioning as apertures". Pseudocolpi usually have a thinner ektexine than the surrounding mesocolpial areas but in contrast to the colpi, all exine layers are usually represented. Frequently, the thinning of the ektexine is gradual and thus the pseudocolpi often are not as clearly delimited as the colpi, although the endexine is increased in thickness just as in the colpi. Further, the surface sculpture in the pseudocolpi is often different than from that of the colpi. Pseudocolpi function in volume changes of the pollen grain during expansion and contraction in response to moisture content (i.e., harmomegathy of Wodehouse, 1935) and as such have been termed "subsidiary colpi" by Muller (1981). In this study pseudocolpi have been observed in the Lythraceae, Combretaceae, Melastomataceae, Oliniaceae, Penaeaceae, and Crypteroniaceae, characterizing all pollen examined in the latter three families. Other families in which they have been observed are the Acanthaceae, Boraginaceae, Hydrophyllaceae, Leguminosae, and Verbenaceae

(Faegri and Iversen, 1975; Erdtman, 1971; Nowicke and Skvarla, 1974; Ferguson and Skvarla, 1981). Pseudocolpi are either equal to the number of colpi (= isomerous) and alternating with them or there can be additional pseudocolpi, as particularly noted in the Lythraceae.

2. Heterocolpate. This term signifies the presence of pseudocolpi and was originally defined by Faegri and Iversen (1950, p. 129) "Some furrows with, others without pores, free pores absent."

3. Intercolpar concavities. As originally defined by Wodehouse (1928) for pollen in the Compositae tribe Mutisieae "These two species . . . . are unique in the possession of three distinct concavities appearing as the impressions one could make with the thumb in a ball of soft dough. Since these impressions are between the furrows, I shall call them intercolpar concavities, and their position on the equator suggests the further designation of equatorial concavities" (p. 453). We consider them to be structurally and functionally similar to pseudocolpi. In contrast to pseudocolpi they are considerably larger and are easily distinguished from colpi and pseudocolpi. In this study intercolpar concavities are found in some Melastomataceae and many Myrtaceae. They may also be present in the Lythraceae as they appear to be in light photomicrographs of Peplis portula by Guers (1970). In Crypteronia large concavities in the mesocolpia have been considered as pseudo colpoid depressions (Muller, 1975). Intercolpar concavities have also been described in the Calyceraceae (Skvarla et al., 1975) and if our interpretations of Erdtman (1971) are correct, perhaps in Hoplestigmataceae, Verbenaceae, and Olacaceae.

RESULTS AND DISCUSSION

LYTHRACEAE

Pollen is tricolporate (some heterocolpate with either three or six pseudocolpi), radially symmetrical, and isopolar. Great variability exists in shape, surface sculpture, aperture system, and to a lesser extent, exine structure. Apart from Nesaea (Figs. 1A,B) and Ammannia (Figs. 2A,B) which are similar, each genus has a distinct morphology and is described below.

Ammannia: A. robusta (Figs. 2A,B) is heterocolpate with six pseudocolpi, subprolate in lateral view, circular in polar view. The surface is striate. Colpi are long with obtuse ends and with a smooth, slightly granular surface. The endoapertures are circular to slightly elliptic-lalongate. Pseudocolpi are short with a slightly granular surface. Ammannia coccinea, which also has a striate surface and six pseudocolpi, was examined with the TEM (Fig. 5B). The endexine is as thick as the ektexine in the mesocolpial area. The foot layer is thick and often shows irregular channels near its lower margin, columellae are thick, short, and simple and the tectum is very thin and imperforate. In cross section the striae composing the tectum appear deeply grooved and constricted at the base. In the colpal and pseudocolpal regions the endexine is thicker than in mesocolpial regions and the foot layer appears to be continuous as a very thin film. Near the endoaperture, the endexine is granular and continues as a very thin layer over the pore (Fig. 5B).

Crenea: C. surinamensis (Fig. 1F) was examined only with SEM. The pollen is spheroidal to subprolate in lateral view, in polar view the slightly collapsed grains are triangular with meridional ridges forming obtuse corners. Pollen is heterocolpate with six pseudocolpi, the mesocolpia between each pair of pseudocolpi are wide and thick, forming three meridional ridges. Colpi are long and not distinct;

pseudocolpi are shorter than the colpi and also not distinct. Endoapertures are circular and raised. The surface is verrucate-rugulate.

Cuphea: Both C. carthagenensis (Fig. 2C) and C. petiolata (Figs. 2D,E,F) are tricolporate-syncolpate, oblate-suboblate in lateral view, triangular (subtriangular to circular in C. petiolata) in polar view, and goniotreme (i.e., angulaperturate). In C. carthagenensis the surface is psilate with meridional folds or ridges on the mesocolpia toward the pores. Colpi are very narrow and united at the poles. The pores are aspidote, like a cylindrical extension, and open by a vertical splitting of the cylinder. In C. petiolata, the corners are obtuse, the surface is basically striate, but on the equator on each side of the colpus two elliptic areas are delineated in some grains. The size and the sculpture of these patterns is highly variable and range from striate-spinulate to rugulate-striate in grains from the same collection. Colpi have a granular surface and the endoapertures are lalongate.

Cuphea nitidula (Fig. 5D) and C. racemosa (Fig. 5C) were examined with TEM. C. nitidula is oblate-triangular with protruding pores and has a uniform endexine which is thickened at the base of the pores. The foot layer is thin, columellae are simple and extremely short. The tectum is thin and tectal perforations are rare. Tectal ridges are solid. The protruding pore (not shown in figure) has a thin granular endexine, a fragmented and thin foot layer, short columellae, and a very thin but continuous tectum. Cuphea racemosa has suboblate, tricolporate grains (Cos Campos, 1964). In thin section (Fig. 5C), the endexine is thin and uneven, the foot layer is thick, and short columellae are erect, and the tectum is thin with some perforations. However, the endexine is very thick below the colpi and granular near the endoapertures (not illustrated here).

Diplusodon: D. villosus was examined only with SEM (Figs. 3A,B). The tricolpoidorate grains are subprolate in lateral view. Endoapertures are circular.

The surface is verrucate-rugulate with tightly packed verrucae as well as elongate, convoluted rugulate elements. Colpi are very short and have large spherical elements on the surface.

Heimia: H. salicifolia was examined with both SEM and TEM. Tricolporate pollen grains are spheroidal in lateral view and circular in polar view (Figs. 1C,D,E). The surface has irregularly shaped elements with overlapping finger-like branches and irregular gaps between them (Fig. 1E). Blunt spinules are also scattered on the surface (Fig. 1E). Colpi are long, with obtuse ends and a granular surface. Endoapertures are lalongate. Thin section (Fig. 5A) shows a thick endexine, a foot layer which is either as thick as or thinner than the endexine, and simple or branched columellae which are erect and tall but becoming shorter toward the colpi. The lower margin of the tectum is more or less straight while the upper margin is irregular. Tectal perforations are numerous and often large. The endexine is very thick below the colpi; near the endoaperture, its lower margin is granular. The membrane over the endoaperture consists of very thin granular endexine. The granules on the colpi surface (not shown in figure) appear to be solid and constricted at the base or rarely with fine columellae under them.

Lafoensia: L. punicifolia was examined with both SEM and TEM. The tricolpoidorate grains are subprolate in lateral view, and triangular-pleurotreme with obtuse corners and straight sides in polar view (Figs. 3D,E). The three protruding pores are situated midway between the sides of the triangular pollen grain. The three meridional ridges and the apocolpia (polar caps) separate three ellipic, apertural fields. The surface of the apertural fields is granular-verrucate-rugulate; the surface of the ridges and the margins of the apertural fields near the apocolpia is rugulate but coarser than the rest of the apertural fields. The apocolpia

have a psilate surface. The short colpus appears as a slightly depressed area with fewer and smaller granular elements than the surrounding area. The pores are circular, the membrane over them is similar to and continuous with the surrounding area. In TEM (Figs. 5E,F, 6A) the ektexine is thick in the ridge areas and thinner in the apertural fields and at the poles (Fig. 5E). In the ridge areas, the foot layer is thick, with the upper margin often irregular or raised into domes, columellae are tall, erect and simple, and the tectum is thick, but discontinuous due to the rugulate surface. In the apertural fields (Fig. 6A), the columellae are shorter, the foot layer is thinner, and the tectum irregular in thickness and discontinuous but with tightly packed verrucate units. The endexine in the ridge and aperture fields is thick and uniform (Figs. 5E, 6A). At the poles (Fig. 5F) the entire exine is thinner. Here the endexine is very thin, and the foot layer and tectum are thicker than the endexine. The tectum is continuous with a smooth upper margin and an irregular lower margin; the very short columellae are wider at their distal ends and appear to be finely branched (Fig. 5F).

Lagerstroemia: L. speciosa was examined only with SEM. Tricolporate grains are subprolate in lateral view and circular to hexagonal in polar view (Fig. 3C). The surface appears to be microrugulate with cylindrical, often branched and overlapping irregularly compacted elements. On the mesocolpia, a poorly developed meridional ridge with two slightly depressed parallel areas on each side is discernible. Colpi are long with obtuse ends and a granular surface. Endoapertures are circular with a slightly raised membrane over them.

Nesaea: N. schinzii was examined only with SEM (Figs. 1A,B). The tricolporate grains are hetercolpate with six pseudocolpi. They are subprolate in lateral view and circular in polar view. The surface is striate. Colpi are long with

acute ends and a granular surface. Pseudocolpi are shorter than the colpi and have a granular surface.

Rhynchocalyx: Rhynchocalyx lawsonioides was examined with both SEM (Fig. 4C) and TEM (Fig. 6D). Pollen is tricolporate, heterocolpate with three pseudocolpi, radially symmetrical and isopolar. It is spheroidal in lateral view and triangular-hexagonal in polar view. The surface is coarse, with many punctae and irregular channels. Colpi are long, narrow with acute ends, and a granular surface. Endoapertures are lalongate. Mesocolpial extensions are present over the endoapertures. Pseudocolpi are wide and in some grains they appear to be united at the poles. Their surface is similar to that of the mesocolpia. Thin sections (Fig. 6D) show that the foot layer is well developed in the mesocolpial regions; columellae are numerous, erect and branched distally, often forming an infratectal granular layer. The tectum is thick, perforate, with an undulating upper margin that is locally discontinuous and separated into domes. The endexine is very thin and has an irregular lower margin. At the colpi and pseudocolpi the endexine is thick, columellae are shorter, and the tectum and foot layer are thinner than in the mesocolpial areas. In the region of the endoaperture, the endexine is granular, the foot layer tapered and the shorter columellae and thin tectum lie directly on the endexine. Additional comments regarding Rhynchocalyx pollen can be found in the discussion of the Crypteroniaceae below.

Discussion: This report is in agreement with others which indicate that the Lythraceae have the most diverse pollen morphology of the Myrtales, at least, certainly of the core families as established by Dahlgren (Dahlgren and Thorne, in press). Much of this diversity centers on the apertural systems, for example,

tricolporate grains are documented in Physocalymna (Cos Campos 1964), Pemphis, Rotala (Guers, 1970), Heimia (Graham, 1977; this report), Adenaria, Pleurophora, Galpinia, Woodfordia (Erdtman, 1971), and Diplusodon (Muller, 1981; this report); heterocolpate grains with isomerous pseudocolpi are present in Lythrum (Cos Campos, 1964; Guers, 1970; Heusser, 1971), Rotala (Guers, 1970), and Peplis (Heusser, 1971) grains with six pseudocolpi occur in Nesaea, Ammannia (Erdtman, 1952; Cos Campos, 1964; Guers, 1970; Graham, 1977, Lobreau et al., 1969; this report), Crenea (Erdtman, 1952; Muller, 1981; this report), and Lawsonia (Muller, 1981), and grains with three meridional ridges that alternate with apertural fields are present in Lafoensia, Crenea and Lagerstroemia (Muller, 1981; this report).

This pollen diversity is also common at the infrageneric level, for instance, Cuphea with over 250 species, shows a wide variation in morphology with pollen ranging from a basic tricolporate-spheroidal type to a tricolporate-syncolpate-oblate triangular type (Erdtman, 1952; Cos Campos, 1964; Graham et al., 1968; Graham and Graham, 1971; Guers, 1970; this report). Graham et al. (1968) examined the pollen of 153 species of Cuphea in order to determine the extent of diversity among species as well as the potential use of pollen in the systematics of the genus. Starting with a basic oblate, tricolporate, striate, tectate grain, Cuphea was shown to be remarkably eurypalynous with great variation at sectional, subsectional, specific, and varietal levels. Twelve morphological categories representing eight sections and nine subsections were established. Of particular concern was the great number of pollen types present in bud clusters, buds, and individual anthers in pollen of C. crassiflora, C. kockneana, and C. jocullensis. These authors felt it was crucial to the pollen taxonomic data to determine whether the pollen was polymorphic suggestive of heterostyly or if a single basic pollen type with several

variations was produced. As discussed by them (Graham et al., 1968, p. 1087-1088):

> "The term "polymorphisme" has been used to describe the multiple pollen types produced by individual plants or anthers in Cuphea (Cos Campos, 1964), but in our opinion use of the term has been preempted by a different situation existing in certain species of Primula, Lythrum, and other genera. As early as 1841, Vaucher noted three floral forms in Lythrum, and Darwin (1865) made a study of trimorphism in L. salicaria L. According to S. Graham (1964), 'In this species there are three style lengths and three sets of stamens of lengths corresponding to those of the styles. The forms are termed long-, mid-, or short-styled, depending on whether the style exceeds, lies between, or is shorter than the two whorls of stamens. Pollen differs in color, size and amount of stored starch in each of the three stamen lengths. The longest stamens have the largest grains, the anthers are green, and the pollen is filled with starch. The two shorter stamen lengths have yellow anthers and correspondingly smaller pollen containing less starch.' Thus Lythrum salicaria produces three morphologically distinct kinds of pollen and each is consistently associated with another feature of floral structure, viz., stamen length. In Cuphea the multiplicity of pollen types is greater (up to 12 in C. strigulosa, fide Cos Campos, 1964, p. 332), occurs within a single anther, and is not correlated with any other feature of the plant."

Therefore, in order to determine the nature of the multiple pollen types in Cuphea, size studies of single anther lactic acid preparation were conducted (Graham et al., 1968). The statistical data rather definitively gave support to the idea of normal pollen variations rather than to heterostyly.

A very comprehensive light miscroscope study by Lee (1979) included 26 genera and 62 species of Lythraceae pollen. Great emphasis was placed on the number of pseudocolpi and three major pollen groups were established: (1) three-pseudocolpate (Lythrum, Pemphis, Peplis, Physocalymma, Rhynchocalyx); (2) six-pseudocolpate (Ammannia, Capironia, Crenea, Ginoria, Haitia, Lagerstroemia, Lawsonia, Nesaea, Pleurophora, Rotala); and (3) non-pseudocolpate (Adenaria, Alzatea, Cuphea, Decodon, Didiplis, Diplusodon, Galpinia, Grislea, Heimia, Lafoensia, Rotala). Based on number of pseudocolpi this study did not support the

tribal classification of the Lythraceae (Koehne, 1903) into the Lythreae and Nesaeae and their respective subdivisions; all had a mixture of the above three pollen groups. It was also concluded that the non-pseudocolpate pollen of Alzatea, which was originally placed near to Physocalymma and Diplusodon (Lourteig, 1965), is better assigned near to Grislea or Adenaria. Also, the placement of Rhynchocalyx near Lawsonia (Sprague and Metcalfe, 1937) was disputed on the basis of three pseudocolpi and indistinct pores in the former and six pseudocolpi and distinct pores in the latter.

In the most recent study of Lythraceae, pollen of Crenea, Diplusodon, Lafoensia, and Lagerstroemia, as well as Sonneratia (Sonneratiaceae) was compared from a harmomegathic functional standpoint and several structural pollen types were established (Muller, 1981). Starting with a tricolporate, longiax prototype Muller (1981) postulated that the relationship between pollen form and function was indicative of adaptive radiation in the following directions or series: (1) in the first series there is a trend toward increasing the number of colpi (i.e., pseudocolpi), (2) in the second series harmomegathic functions are transferred from individual colpi to flexible apertural fields alternating with meridional ridges, (3) in the third series harmomegathic functioning is transferred to prominent pores, and (4) in the last series harmomegathic functioning is lost in the ecto- and endoapertures.

The usefulness of pollen morphology in the taxonomy of the Lythraceae is summarized by Muller (1981, pp. 121-122) whereby he emphasizes the need:

> ". . . . for ecologic interpretations of function and for detailed ultrastructural studies to uncover those characters which reflect ancient phylogenetic links. This can perhaps best be illustrated by a discussion of possible affinities between the genera Lafoensia, Lagerstroemia and Sonneratia, assuming that it is decided to place the latter in the Lythraceae. If convergences in recent pollen morphology are stressed, Lafoensia would be considered closely related, but

> the differences in ultrastructure and the heterocolpate nature in some pollen types of this genus would argue against affinity with Sonneratia. If fossil evidence is taken into account, the genus Lagerstroemia appears a much stronger candidate, although its present-day types show less similarity with living Sonneratia types, having diverged rather strongly from a postulated common ancestral matrix, although the peculiar granular deposits in the intercolumellar space appear to be present both in Lagerstroemia and Sonneratia".

In a more general sense and concerning the taxa examined in this study (Table 1), Lafoensia is similar to Sonneratia of the Sonneratiaceae (Muller, 1969; 1978; 1981; this report, Fig. 4E); Diplusodon is similar to Duabanga, also of the Sonneratiaceae (Muller, 1981; this report, Fig. 4F); Rhynchocalyx is similar to the Crypteroniaceae s. str. (Muller, 1975; this report, Figs. 21A,B) as well as to some Melastomataceae (e.g., Dissochaeta, Figs. 23F, 26B) and perhaps to some Combretaceae (e.g. Lumnitzera, Fig. 16D); and Lagerstroemia bears resemblance to Punica (Punicaceae, Fig. 4A).

PUNICACEAE

Punica granatum was examined with SEM (Fig. 4A) and TEM (Fig. 6E). The pollen is tricolporate, radially symmetrical, isopolar, subprolate in lateral view, and circular in polar view with slightly angular mesocolpia. Three weakly developed meridional ridges with rugulate surfaces are in the center of the mesocolpia. The surface is granular-microrugulate. Colpi are long, with acute ends and a smooth surface. Endoapertures appear to be circular to slightly oblong and lalongate.

Thin sections show that the foot layer is narrow, often discontinuous, and with vertical channels. The columellae are very short, thick, and numerous. They are branched where the exine is most thickened. The tectum is thick, with a lobed or wavy upper margin. Tectal perforations are present. The prominent endexine

increases in thickness in the colpal regions. Near the endoapertures the endexine is granular. Punica granatum pollen is comparable to Lagerstroemia speciosa (Fig. 3C of this report), Woodfordia and Lawsonia (Guers, 1970), all of the Lythraceae. In these four taxa, indistinct meridional ridges impart a triangular shape to the pollen in polar view.

SONNERATIACEAE

Sonneratia caseolaris and Duabanga moluccana were examined with SEM (Figs. 4E,F). In both, the pollen is triporate, radially symmetrical, and isopolar. In Duabanga the shape is subprolate, elliptic in lateral view, and triangular-hexagonal in polar view. Sonneratia grains are prolate, cylindrical in lateral view, and triangular-hexagonal (?) in polar view. Three well developed, meridional ridges alternating with three, oblong apertural (pore) fields are present in both taxa. The ridges in Sonneratia are more pronounced than those in Duabanga. The surface is verrucate in the apertural fields and verrucate-rugulate on the ridges. Each apertural field has a protruding pore at its center. The surface of the pore membrane is similar to that of the surrounding field. In Sonneratia, in addition to the three large ridges, six smaller ridges are present, two in each apertural field. They are parallel to the larger ridges and have a rugulate surface. The pore is located between the two smaller ridges. In both taxa, the large, triangular polar caps have a psilate surface with a few punctae scattered over them.

Discussion: In a light microscope study (Muller, 1969) the pollen morphology was described for five species and two interspecific hybrids of Sonneratia. Major conclusions from his study were: (1) that S. alba and S. caseolaris pollen showed

great intraspecific variability that is geographically related and considered as genotypic, and (2) the dominent pollen morphology of one parent of the two intraspecific hybrids suggested introgressive hybridization. Later, pollen of S. alba and S. caseolaris was examined by SEM and TEM (Muller, 1978) in order to supplement the morphological data of earlier studies (Muller and Hou-Liu, 1966; Muller, 1969). Since the present study did not include TEM observations, the pollen ultrastructure of Sonneratia is summarized from Muller's studies as follows: the endexine is thin on the polar caps and thick in the equatorial zone. It is granular around the pores. The sole (= foot layer) on the other hand, is thick on the polar caps and thinner in the equatorial zone. In the porate fields of the equatorial zone, short columellae connect the verrucae to the sole. In the meridional ridge areas in S. alba, the columellae are longer and rather widely spaced, and support a tectum. At the polar caps, distinct columellae grading into areolate protrusions of the sole, are present. The tectum is continuous on the polar caps, partially broken up on the ridges (in S. alba) and occurs as separate verrucae over the porate fields. A granulate layer completely or partially fills the infratectal cavities. It was emphasized that in S. alba well formed meridional ridges united with polar caps which markedly delineated apertural or porate fields while in some grains of S. caseolaris the lack of meridional ridges did not confine the pores to fields, and in other grains, indistinct meridional ridges were found. The conclusion was that pollen of S. alba was more advanced in " . . . . controlled harmomegathy than that of S. caseolaris and it is significant in this connection that the latter species has been proven to be phylogenetically older" (Muller, 1978, p. 287-289).

Recognizing the taxonomic problems associated with distinguishing pollen of S. caseolaris from S. alba (Muller, 1969; 1978), our SEM results show that S.

caseolaris (Fig. 4E) is more similar to Muller's SEM of S. alba (Muller 1978, Pl. II, Fig. 1; Muller, 1981, Pl. VI, Fig. 2) than to his SEM of S. caseolaris (Muller, 1978, Pl. 1, Figs. 1,2; Muller, 1981, Pl. VII, Fig. 3). The similarity is seen in the well developed meridional ridges and apertural fields in our S. caseolaris and Muller's S. alba.

In a general comparative sense the pollen of Sonneratiaceae is similar to the Lythraceae with Sonneratia resembling Lafoensia, and Duabanga resembling Diplusodon.

TRAPACEAE

Trapa japonica and T. natans were examined with SEM and TEM. Pollen from both species are basically similar. They are tricolpate, radially symmetrical, isopolar, spheroidal in lateral view; and triangular, goniotreme with obtuse corners, and straight to convex sides in the polar view (Figs. 7,8). There are three meridional ridges on the grains. The surface is granular. The three apertures are protruding and swollen as elongated domes. In T. japonica these domes are better developed than in T. natans. Within them there is an elongated lens-shaped opening or colpus (Erdtman, 1943, pp. 104-105, Fig. 221-223) which is not visible in the scanning electron micrographs as it is covered by the meridional ridge. The meridional ridges are formed by the folding of the ektexine and they are united at both poles where their fused triangular base is greatly enlarged (Figs. 7B; 8B). The ridges are taller at the poles; as they extend toward the equator in a folded, undulating manner their height decreases. The surface at the upper portion of the ridge near the poles is smooth with many channels. The lower portion shows a granular- verrucate surface (Fig. 7C). Toward the equator, the upper portion of the ridge is more

rugulate-verrucate. Over the colpi, the upper portion of the ridge continues as a wide and not very tall, verrucate-granular band. The lower portion spreads over the swollen domes and is continuous with the surrounding interapertural areas (Figs. 8C,D,E). The surface of the domes is granular like that on the mesocolpia. It is not clear how the colpi open, but they appear to do so by an irregular splitting of the exine (Figs. 7A; 8D,F).

One sample of Trapa natans (House 21708) showed clumps of grains (polyads ?) along with free grains (monads). Exinous connections between the members of these "polyads" are present (Figs. 7D,E,F). However, there is no discernible specific arrangement of the polyad members, and the bridges connect different parts of the adjacent grains. This phenomenon is not yet clearly understood.

In T. natans the fine, granular surface of the grain is due to the tightly packed clavate and rod-shaped elements that form a very thin layer as seen in the thin sections (Figs. 9A-C). These clavae are either solid in their entire length, or show a fine, fuzzy granular layer below them. The exine structure of T. japonica (Fig. 9D) is similar to T. natans but the fuzzy layer is not evident. When cut obliquely, the clavate layer appears to be beaded and spongy. The thick, more or less solid layer below the fuzzy layer appears to be the endexine which becomes granular near the pores. The foot layer is difficult to recognize but it is perhaps present as a very thin layer between the fuzzy layer and the solid endexine. On the granular endexine near the pores, such a layer is clearly visible.

Sections passing through the ridge show that it encloses a cavity (star in Fig. 9A). The clavate layer (CL in Fig. 9A) along with the fuzzy granular layer (G in Fig. 9A) lifts to form the ridge wall (Fig. 9A). It continues as such for a short

distance (the granular lower portion of the ridge seen from the outside, the solid star in Fig. 7C) and then becomes a more or less discontinuous, solid layer (the psilate upper portion of the ridge seen from the outside, the open star in Fig. 7C). The inner margin of this solid layer is highly irregular. Clavae at the base of the ridge cavity are large and often appear to be branched. Just above these clavae, the cavity is filled with circular or elongate ektexinous elements.

Discussion: Structurally, the meridional ridge of Trapa is different from that found elsewhere in the order. It is formed by the uplifting and folding of the ektexine and encloses a cavity. However, the ridge found in Punicaceae, Lythraceae (Lagerstroemia, see also Van Campo, 1966) and Onagraceae (Ludwigia) is formed by the increased thickness of the exine. Moreover, the ridge passes over the colpi in Trapa, whereas it alternates with the colpi in the other groups.

The distinctiveness of Trapa pollen was recognized by Erdtman (1971), who examined three species and felt that the genus merited family status. Trapa pollen shows a distant resemblance to Onagraceae pollen in surface sculpture and in the nature of the protruding apertures (see Figs. 38-41 of Onagraceae pollen below). Similarities to Onagraceae are further evident in the very thick endexine and indistinguishable, or at least, very thin foot layer (compare Figs. 9 and 42).

OLINIACEAE

Olinia emarginata, O. radiata, O. rochetiana, O. usambarensis (= O. rochetiana) and O. ventosa (= O. cymosa) were examined with SEM and TEM. Pollen from all of the species is remarkably similar, both at the exomorphological and the endomorphological levels.

Pollen is tricolporate, radially symmetrical, heteropolar, spheroidal to subprolate in lateral view, and circular to triangular in polar view (Figs. 10,11). The surface is usually psilate, or rarely psilate-punctate as in O. radiata (Figs. 10B,C).

The aperture system in Olinia is unique in that the pollen grains have unusual colpi and pseudocolpi. Each colpus is asymmetrical and has a long arm and a short arm. The long arms are on the same hemisphere of the grain (Figs. 10A,F) and they are slightly wider than the short arms (Figs. 11A,F). The surface of the colpi is smooth or granular and the ends are acute. An elliptic, lalongate endoaperture is present on the equator where the two arms of the colpus meet. The endoapertures are covered by extensions of the mesocolpia.

The second unusual character of Olinia pollen is the presence of three half pseudocolpi which do not extend into both hemispheres of the grain. They are present on the hemisphere that has the short arms of the colpi. Their surface is rugulate, with irregular, branched channels (Figs. 10C,D,E; Figs. 11A,D,E,F). They are often wide and therefore tend to resemble intercolpar concavities. This type of aperture system makes the grains heteropolar. However, in some grains a size difference between the two hemispheres, such as illustrated in Fig. 11F, also results in heteropolarity. Rarely, the pseudocolpi extend slightly beyond the equator to the opposite hemisphere.

The ektexine in the mesocolpia consists of a very thick foot layer (Fig. 12) which becomes extremely thick toward the colpi (Figs. 12D,E). From the foot layer arise the thick and short, often prostrate or irregular-mound-like columellae which are often narrower at their distal ends where they form an infratectal granular layer (Fig. 12C). The tectum is thick, uniform and without perforations (except in O. radiata). The upper margin of the tectum is smooth. The endexine is thin but

becomes markedly thickened in the colpi and pseudocolpi regions. The pseudocolpi show a thinner, undulating, often dome shaped tectum (Fig. 12A). The infratectal granular layer is continuous here. The columellae appear as short connections between it and the very thin, discontious foot layer.

In the area of the endoapertures, (Figs. 12D,E), the endexine is granular. The extensions of the mesocolpia show a disrupted thin foot layer, and a thin infratectal granular layer below a slightly thinner tectum.

Discussion: Oliniaceae pollen grains differ from all other groups in their unusual aperture system, i.e. the asymmetrical colpi and the half pseudocolpi (Patel, Skvarla, Raven, in preparation). All species examined are very similar in their exo- and endomorphology and are difficult if indeed, impossible to distinguish. Erdtman (1971) reported that pseudocolpi are absent in O. volkensii (= O. usambarensis, and O. rochetiana). Samples labelled O. usambarensis and O. rochetiana were examined in this study and both show the half pseudocolpi and the asymmetric colpi, and are thus similar to the rest of the species. These half pseudocolpi are very small areas, present only on one hemisphere, differ only slightly in surface sculpturing from the surrounding exine, and are thus extremely difficult to visualize under the light microscope. It is not surprising that their true nature has not been revealed with the light microscope. For example, O. cymosa (= O. ventosa) was reported by Erdtman (1971) as having three pseudocolpi. However, in the light micrograph of O. volkensii by Archangelsky (1971), three half pseudocolpi are clearly visible (Fig. 1, Pl. 20).

Apart from the unusual apertures, the colpi and the half pseudocolpi, the Oliniaceae resemble the Penaeaceae. Pollen from both families compare very well

in the psilate surface as well as in exine structure; that is, there is a very thick foot layer, a thick tectum, and a thin columellae layer with an infratectal granular layer extending over the pseudocolpi (compare Figs. 12A-E to Figs. 20B,D).

COMBRETACEAE

Pollen is tricolporate, mostly heterocolpate (except in Buchenavia Laguncularia and Strephonema), radially symmetrical, and isopolar. The shape of the grains is spheroidal to subprolate in lateral view and circular to hexagonal in polar view. In the heterocolpate species, the colpi are long, with acute ends, and a granular surface. Syncolpate grains are present in Combretum farinosum. Endoapertures are lalongate and elliptic in Combretum cacoucia, Strephonema pseudocola, and Lumnitzera racemosa, circular in Poivrea coccinea (Fig. 16C) and Anogeissus acuminata (Figs. 15D,F), and circular to elliptic in Bucida macrostachya (Fig. 14A) and C. farinosum. Pseudocolpi are wide and often united at the poles in Ramatuella argentea, Terminalia catappa, and Guiera senegalensis (illustrated in Fig. 14E and Fig. 15E).

Diverse surface sculpture patterns are present in the family. They are striate in Combretum laxum, G. senegalensis and P. coccinea. In C. laxum thick striae are separated by short, punctate channels while the surface of the pseudocolpi is striate-rugulate. In Guiera (Fig. 15E) small groups of short striae cross, and the pseudocolpi appear to have a finer, granular, striate surface. Poivrea (Fig. 16C) shows bands of fine, long striae while the pseudocolpi are striate-rugulate.

In Quisqualis indica (Fig. 13F), Ramatuella argentea (Figs. 14E,G), Terminalia edulis (Fig. 14D), and T. catappa (Fig. 14F) narrow, elongated, and branched muri appear tightly interwoven. Punctae are present in the channels

separating the muri. The pattern becomes finer at the margins of the mesocolpia and less so at the poles where it appears to be punctate in Q. indica. The surface of the pseudocolpi is rugulate-granular in Ramatuella (Fig. 14G) and Terminalia. In Quisqualis (Fig. 13F) the pseudocolpi are wider than in the other taxa examined and their surface appears to be similar to the surface on the meso- and apocolpia.

In Combretum farinosum, Bucida macrostachya (Fig. 14A), Pteleopsis myrtifolia (Fig. 14C), and Conocarpus erecta (Fig. 14B), the surface is coarse and punctate with short channels which are more pronounced at the margins of mesocolpia. The pseudocolpi in C. farinosum and B. macrostachya show a coarse, granular-verrucate-rugulate surface. In C. cacoucia (Figs. 13A-C) the surface appears to be finely rugulate.

A rugulate surface is present in Lumnitzera racemosa (Fig. 16D) and Calycopteris floribunda (Fig. 13G). In Lumnitzera the surface of the pseudocolpi appears to be granular, whereas in Calycopteris it is rugulate-verrucate with slightly smaller rugulate elements than on the mesocolpia.

Anogeissus acuminata (Figs. 15D,F) and Thiola inundata (Figs. 13D,E) have an echinate surface with spinules. In Anogeissus, scattered spinules are situated on a smooth surface. They become smaller and more numerous at the margins of the mesocolpia. They are also present on the pseudocolpus and the colpus membrane over the endoaperture. In Thiola, in addition to the spinules, are large punctae and deep channels which also have punctae. Due to the channels the surface appears to consist of more or less fused "plates or islands" (Fig. 13D). The surface of the pseudocolpi also has spinules and punctae. Longer spinules are present on the colpus membrane over the endoapertures.

Buchenavia suaveolens, Laguncularia racemosa, and Strephonema pseudocola are without pseudocolpi. In Buchenavia (Figs. 15A-C) grains are spheroidal in lateral view and triangular in polar view. The surface is echinate, like that in Thiola, with spinules, punctae, and deep channels forming "plates". Colpi are long and narrow. Endoapertures are lalongate. In Laguncularia (Figs. 16E,F), grains are subprolate in lateral view and circular to triangular in polar view. The surface is smooth with minute punctae. Colpi are medium length and have a granular surface. Extensions of mesocolpia are present over the lalongate endoapertures. Strephonema pseudocola (Figs. 16A,B) is subprolate in lateral view and circular to triangular in polar view. The surface is reticulate with large lumina which gradually decrease in size toward the margins of the mesocolpia. The large lumina are filled with rod-like, short elements, some of which are free standing while others extend diagonally and fuse with the muri from below. Colpi are long and wide with obtuse ends and a granular surface. Endoapertures are lalongate and elliptic.

Combretum laxum (Fig. 17A), C. farinosum (Figs. 17B,C), Conocarpus erecta (Fig. 17E), and T. edulis (Fig. 17D) were examined with TEM. In general, in the mesocolpial area the foot layer is well developed, its lower margin is straight and upper margin is curved (convex) so it appears dome-shaped. Columellae are short (less in height than the thickness of foot layer or tectum), erect, and simple (in C. laxum branched just below the tectum). The tectum is thick, with large perforations, its lower margin is straight, and its upper margin is undulating. The endexine is very thin in the mesocolpial area but is very thick below the colpi and pseudocolpi. At the margins of the mesocolpia near the pseudocolpi, the foot layer usually terminates but sometimes appears to continue as a very fine layer over the endexine of the pseudocolpi. In T. edulis and C. laxum, finer and shorter columellae, and a thinner tectum are present in the pseudocolpi region.

Combretum farinosum (Figs. 17B,C) differs from the other three taxa examined with TEM in having a very fine granular matrix in the columellae layer. This matrix fills the spaces between the columellae and is also continuous in the pseudocolpi region. Here, the columellae are shorter, the tectum slightly thinner and often discontinuous as domes forming the granular and rugulate units on the exine surface. The granular matrix is also continuous in the colpi. The columellae are embedded in it with their protruding distal ends forming the granules of the colpus surface. The tectum occurs as a thin film on the matrix (Fig. 17C). Irregular, broken lamellae of ektexinous material (foot layer?) are also present. The thick endexine also appears granular in the vicinity of the endoaperture and is difficult to distinguish from the granular matrix. In C. laxum the endexine is granular near the endoaperture and granular-lamellate in C. erecta and T. edulis.

Discussion: Apparently, there are no modern detailed studies of Combretaceae pollen (see Thanikaimoni, this symposium). The following, therefore, is presented as a brief background of the basic morphology. Erdtman (1971) described Quisqualis indica as having colpi alternating with "pseudocolpoid thin walled areas" and made favorable comparisons with Cacoucia, Combretum and Terminalia. He also described Laguncularia racemosa but did not mention the presence or absence of pseudocolpi. Quisqualis latialata was described as having three pseudocolpi by Lobreau et al (1969). Sowunmi (1974) described pollen of Combretum glutinosum, Terminalia avicennioides, T. glauscens, T. macroptera, and T. superba in general as resembling each other and possessing a characteristic shape, aperture system, and exine. All grains were noted to have "colpoid streaks" (= pseudocolpi) alternating with colpi. Lastly, Guers (1974) and Guers et al (1971) also

showed a fundamental similarity in the pollen of Combretum aculeatum, C. grandiflorum, C. lokele, C. micranthum, C. platypterum, C. smeathnianni, Conocarpus erectus, Pteleopsis diptera, Terminalia glaucescens, T. laxiflora and T. superba. All had colpi alternating with pseudocolpi. The one SEM, that of Combretum aculeatum, is similar to C. cacoucia (Figs. 13A-C, this report).

From a comparative point of view, Erdtman (1971, p. 117) felt that "Pollen grains ± similar to those in Combretaceae occur in Melastomataceae (cf. also Lythraceae and Penaeaceae). The grains in Haloragaceae, Hernandiaceae, Myrtaceae, Punicaceae, Sonneratiaceae, etc. are ± different".

Our SEM observations indicate several rather distinctive groups. Combretum (Figs. 13A-C), Quisqualis (Fig. 13F), Bucida (Fig. 14A), Conocarpus (Fig. 14B), Pteleopsis (Fig. 14C), Terminalia (Fig. 14D), Ramatuella (Fig. 14E), Guiera (Fig. 15E), Poivrea (Fig. 16C), and Lumnitzera (Fig. 16D) comprise the first group and are similar in having colpi alternating with pseudocolpi. Various surface patterns are represented in this group. A second group, characterized by the presence of an echinate surface and pseudocolpi is represented by Thiola (Figs. 13D,E) and Anogeissus (Figs. 15D,F). A third group, consisting only of Buchenavia (Figs. 15A-C) has an echinate surface but lacks pseudocolpi. A fourth group, also consisting of just one taxon, Laguncularia (Figs. 16E,F), has a punctate surface and lacks pseudocolpi. The fifth group, represented only by Strephonema (Figs. 16A,B), also lacking pseudocolpi, is completely different from all other Combretaceae in having reticulate surface. Interestingly, this reticulate surface has not been observed in any member of the Myrtales core families. In contrast to the diverse surface morphology is the TEM data which indicates structural similarities. However, this data at present, is greatly limited.

Generalized comparisons with pollen from the core families essentially agree with Erdtman's (1971) suggestions given above. The pollen included in our first group shows broad resemblances to some Penaeaceae, some Melastomataceae, and some Crypteroniaceae. The Penaeaceae that show these resemblances are, Endonema (Figs. 19A,C), Brachysiphon (Fig. 19D), and Sonderothamnus (Fig. 19E). The Melastomataceae that show these resemblances are, Memecylon (Fig. 21C), Mouriri (Fig. 21D), Trembleya (Fig. 22A), Osbeckia (Fig. 22B), Tibouchina (Fig. 22C), Tristemma (Fig. 22D), Votomita (Fig. 22E), Marumia (Fig. 23A), Dissotis (Figs. 23C,D), Acanthella (Fig. 23E), and Dissochaeta (Fig. 23F). The Crypteroniaceae that show these resemblances are, Axinandra (Fig. 21A) and Dactylocladus (Fig. 21B). The other four groups do not, at least to this time, show resemblances to other Myrtales. In TEM, the very markedly domed foot layer of Combretaceae (Figs. 17A,B,D,F) was recognized also in the Melastomataceae (Tristemma, Fig. 25A; Trembleya, Fig. 25B; Osbeckia, Figs. 25D,E; Marumia, Fig. 26A), and Penaeaceae (Penaea, Fig. 20A; Sonderothamnus, Fig. 20B; Stylapterus, Fig. 20D).

ALZATEACEAE

Alzatea verticellata (the only member of this monotypic family). Pollen is tricolporate, radially symmetrical, isopolar, spheroidal to subpolate in lateral view, triangular, goniotreme with obtuse corners and straight sides in polar view (Figs. 4B,D). The surface is psilate except in the elliptical areas at the middle of the mesocolpia where it is psilate-punctate; these areas are slightly depressed and possibly represent pseudocolpi or intercolpar concavities and give the pollen a triangular shape in polar view. Colpi are long, with obtuse ends, and a smooth surface. A wide, coarse margin is present around the colpus. Endoapertures are lalongate. Extensions of the mesocolpia are present over the endoapertures.

On the sides of the mesocolpia (i.e., around the punctate, elliptic areas) the foot layer is well developed in the form of continous "hills" or "domes" (Fig. 6B). The thick tectum has a smooth, slightly undulating upper margin. Its lower margin corresponds in shape to that of the foot layer, resulting in an undulated or zig-zag columellae-layer between the tectum and the foot layer. The short, erect columellae are unbranched. The endexine is relatively thin. At the middle of the mesocolpia (Fig. 6C), where the surface is punctate, the exine becomes thinner: the foot layer at first becomes thinner and then is present only as wide bases of the columellae; the columellae slightly increase in height and become branched; and the thin tectum has large perforations and an infratectal granular layer. The endexine increases in thickness as it does in taxa with pseudocolpi.

Near the colpi, the endexine is very thick and the foot layer tapers and is either present as a thin layer or is absent. At the margins of the mesocolpia, the very short columellae and the thin tectum with an infratectal granular layer are present on this thick endexine. The endexine is granular in the vicinity of the endoapertures.

Discussion: The punctate areas at the middle of the mesocolpia in Alzatea are suggested as being incipient pseudocolpi by Muller (1975). The exine indeed is thinner in this area as is shown in the TEM (Fig. 6C). As mentioned by Muller, Alzatea pollen is comparable with those species of Rotala that show indistinct pseudocolpi (Guers, 1970). Pollen of this genus has been characterized as (1) three colporate, (2) three colporate with indistinct pseudocolpi, and (3) three colporate with distinct pseudocolpi (Guers, 1970). Further, a spectrum of heterocolpateness also occurs within a single taxon (Cos Campos, 1964). Alzatea pollen may also be

compared with those of Physocalymma (Cos Campos, 1964; Van Campo in Lourteig, 1965). A detailed examination involving electron microscopy of these two Lythraceous genera (i.e., Rotala and Physocalymma) should be instructive.

Alzatea cannot be placed definitively in any family (see Dahlgren, this volume). Muller (1975) treated it in the Crypteroniaceae following the system of Van Beusekom-Osinga and Van Beusekom (1975), as an ancestral tricolporate type, deriving from it the bisyncolporate bilateral Crypteronia-type and the heterocolporate triradiate Dactylocladus-type. In a broad generalized sense, he considered the relatively unspecialized pollen common throughout the angiosperms, particularly the Punicaceae, Lecythidaceae, Rhizophoraceae, Combretaceae and Lythraceae (particularly Adenaria, Pemphis, Pehria, Pleurophora, Physocalymma, Woodfordia, and some Rotala).

Although the pollen of Alzatea is generalized, we feel that it is very similar to that of Chrysobalanus oblongifolius (Chrysobalanaceae) exomorphologically in shape and a smooth-punctate surface. Endomorphologically, similarities are noted in the "zig-zag" nature of the tectum, columellae, and foot layer (unpublished data).

PENAEACEAE

Pollen grains are tricolporate in Brachysiphon (Fig. 19D), Endomema (Figs. 19A-C), and Sonderothamnus (Figs. 19E,F), and tetracolporate in Penaea (Figs. 18A-C) and Stylapterus (Figs. 18D-F); and heterocolpate with isomerous pseudocolpi alternating with the colpi. They are radially symmetrical, isopolar (except some in Penaea and Stylapterus, see below), spheroidal to subprolate in lateral view, and circular to hexagonal (in tricolporate species) or circular to octagonal (in tetra-

colporate species) in polar view. The surface is psilate in Penaea, Brachysiphon, Sonderothamnus, and Stylapterus, with few pits and punctae. In Endonema it is rugulate with punctae.

Colpi are long, with acute (Brachysiphon, Penaea, and Stylapterus) or obtuse (Endonema, Sonderothamnus) ends, their surface is granular with the exception of Brachysiphon where it is smooth. Endoapertures are circular in Penaea and Stylapterus, and lalongate, elliptic with two lateral extensions in Endonema (Fig. 19B) and Brachysiphon. In Endonema, extensions of the mesocolpia are present over the endoapertures. They are either very small or absent in Brachysiphon and are absent in the remaining taxa. In Sonderothamnus the endoapertures are slightly elliptic-lalongate and the colpus membrane often persists as a horizontal bar over the open endoapertures (Fig. 19F).

The pseudocolpi are long and have a granular surface (granular-verrucate in Endonema). They are often united at the poles in Brachysiphon and Sonderothamnus. In Penaea and Stylapterus, the colpi or pseudocolpi are often united in various configurations, for example Fig. 18C of Penaea shows an undulating syncolpus with two pores (also see Figs. 18A,E,F). Thus many grains are heteropolar in these two genera.

In TEM (Fig. 20) the tectum along the mesocolpia is very thick and without perforations in all three species examined. The foot layer is also prominent, thicker than the tectum in Sonderothamnus (Fig. 20B) and Stylapterus (Fig. 20D), and is dome shaped. In Penaea (Fig. 20A) a very thin, undulating gap separates the tectum and the foot layer. The gap contains very short columellae. In Stylapterus (Fig. 20D), the upper margin of the foot layer is irregular, and an infratectal granular layer with problematical columellae is present between the foot layer and the

tectum. In Sonderothamnus (Fig. 20B), the upper margin of the foot layer is also irregular, but in contrast to Stylapterus, very short, thick, and irregular columellae are evident and surrounded by an infratectal granular layer. In all taxa the lower margin of the foot layer is smooth. In the mesocolpia the endexine is well developed and uniform but much thinner than the foot layer and tectum.

Toward the colpi and pseudocolpi, the endexine increases in thickness while the foot layer and tectum taper or decrease. In the pseudocolpus region in Sonderothamnus (Figs. 20B,C), a fragmented, thick foot layer supports an elaborate, granular, spongy layer. This granular layer is a continuation of the infractectal layer of the mesocolpia but is much wider and better developed here (Fig. 20C). The tectum is thin and has an undulating outer margin. In Stylapterus (Fig. 20D) also, the infractectal granular layer continues over the pseudocolpi but is not as well developed as in Sonderothamnus. In Penaea (Fig. 20A) the foot layer continues as a thin, irregular layer and the tectum continues as a thin, undulating layer; the gap between them contains granular elements along with the short columellae. These granular elements were not observed in the mesocolpia. Near the endoaperture, the endexine is very thick and granular in Penaea and Sonderothamnus.

Discussion: Pollen of the seven genera constituting the Penaeaceae are best known through the light microscope studies of Dahlgren (1967 a,b,c, 1968, 1971) as part of the comprehensive biology of the family. While variations in pollen size and shape are common the pollen is fairly uniform and characterized by colpi alternating with pseudocolpi. The only major difference was in the number of apertures which seem to be the most variable in Penaea and Saltera (Dahlgren, 1968, 1971). These observations are also supported in other studies (i.e., Erdtman, 1971; Archangelsky, 1971).

Our results indicate that exomorphologically, Penaeaceae pollen resembles Melastomataceae [compare Endonema (Figs. 19A,C) with Tristemma (Fig. 22D) and Dissotis (Figs. 23C,D)] and Combretaceae [compare Brachysiphon (Fig. 19D) and Stylapterus (Fig. 19E) with Combretum (Fig. 13B)]. Endomorphologically the striking and somewhat unique exine structure in the mesocolpium is close to Oliniaceae (Figs. 12B-E) while the pseudocolpal areas show a somewhat distant similarly to Onagraceae (compare Sonderothamnus, Fig. 20C, with Figs. 42B-D).

CRYPTERONIACEAE

Dactylocladus stenostachys and Axinandra zeylanica were examined only with SEM. Both have tricolporate, heterocolpate, radially symmetrical, and isopolar pollen (Figs. 21A,B). Pollen is spheroidal in lateral view and triangular-hexagonal in polar view. In Axinandra, the surface of the mesocolpia is psilate, with a few scattered punctae. The colpi have acute ends, a smooth appearing surface, and are narrower than those in Dactylocladus. The obscure endoapertures are covered by exine extensions of the mesocolpia. The pseudocolpi are long, sometimes united at the poles. Often, they are wide, appearing like intercolpar concavities. Their surface is punctate. The margin of the mesocolpia around the pseudocolpi is often more punctate than other areas of the pollen grain.

In Dactylocladus the surface is psilate with some punctae and channels on the mesocolpia around the pseudocolpi. The colpi are wide with a granular surface and obtuse ends. The obscure endoapertures are slightly protruding and have extensions of the mesocolpia over them. The pseudocolpi are also wide, with a granular surface, and irregular channels. At the poles the pseudocolpi are united.

Discussion: Muller (1975) described with light and electron microscopy the pollen morphology of Axinandra beccariana, Dactylocladus stenostachys, Crypteronia paniculata, C. cumingii, C. griffithii, Rhynchocalyx lawsonioides, and Alzatea verticillata. The latter two taxa, at least for the purpose of the present report, have been included elsewhere (i.e., Rhynchocalyx in the Lythraceae and Alzatea in the monotypic Alzateaceae). Three pollen types were established: (1) tricolporate Alzatea type, (2) heterocolpate Dactylocladus type which also included Axinandra and Rhynchocalyx, and (3) bisyncolpate Crypteronia type. Muller also presented a detailed TEM structural description of all taxa (except Alzatea) and in the absence of our own TEM data we will present below his interpretations. Crypteronia and Dactylocladus were regarded as fundamentally similar with the exine consisting of the basic endexine and ektexine with foot layer, columellae and tectum. His detailed description follows (Muller, 1975, pp. 276-277):

> "The endexine appears to be thickest near the endoapertures, decreasing in thickness towards the mesocolpia, but it is occasionally also relatively thick under the pseudocolpi. The endexine generally shows a finely granular structure.
>
> The inner boundary of the footlayer is smooth and distinct, but the outer one is rather irregular and can only be arbitrarily delimited from the often broadened basal parts of the columellae. The footlayer is generally thickest on the mesocolpia. Near the colpi it appears to be reduced and changed from a homogeneous structure into a granular (Dactylocladus) or into a lamellar structure (Rhynchocalyx, Crypteronia). It is not quite clear in these genera whether the footlayer is also reduced under the pseudocolpi. In Axinandra the footlayer appears reduced or absent both under colpi and pseudocolpi.
>
> The columellate layer in Axinandra is formed by rather widely and regularly spaced short columellae only, but in Dactylocladus, Rhynchocalyx, and Crypteronia the columellae are variable in shape and size, and are interspersed with and transitional to small granules. These granules are best developed in Dactylocladus and Rhynchocalyx, where they are concentrated in the outer

> zone, partially fusing with the lower tectum surface. In Crypteronia only weak evidence for the presence of granules could be found. Both columellae and granules are reduced or absent on the colpus membranes. On the pseudocolpi they are reduced but probably present over the entire membrane.
>
> The tectum is generally homogeneous with a more or less irregular inner and outer surface. In Axinandra and Dactylocladus it has a rather smooth surface, but in Crypteronia and Rhynchocalyx it is more irregular with perforations centred in the depressions. In Rhynchocalyx the tectum dissolves into separate granules near the apertures. This is less noticeable in Crypteronia, where the tectum is absent on the colpus membrane and dissolved into separate verrucae on the pseudocolpoid areas.
>
> In Axinandra the tectum is probably still present as a very thin membrane on the colpi and clearly present on the pseudocolpi.
>
> In Dactylocladus and Rhynchocalyx the tectum appears to be more or less continuous, although much thicker on the mesocolpia and probably absent in the centre of the colpi.
>
> Detailed studies, preferably of fresh material, are necessary to verify these preliminary observations on the fine structure of the wall. Until then, an evaluation of the differences found between the genera is not advisable."

In a generalized sense, Axinandra and Dactylocladus pollen compare with pollen in Melastomataceae, Combretaceae, Penaeaceae, Oliniaceae, and Lythraceae (Lythrum, Peplis, some species of Ammannia, Nesaea, and Rotala). The Crypteronia-type pollen of Muller relates to Corynocarpaceae, Cunoniaceae, Eucryphiaceae and Saxifragaceae (Muller, 1975; see also Erdtman, 1971).

MELASTOMATACEAE

Pollen of Melastomataceae is tricolporate or triporate (Tococa), radially symmetrical, isopolar (perhaps heteropolar in Tococa stephanotricha). Monads are found in all taxa examined with the exception of Tococa spadiciflora which has polyads. On the basis of exomorphology, three pollen groups can be established: heterocolpate with pseudocolpi, "heterocolpate" with intercolpar concavities, and triporate.

In the heterocolpate group with pseudocolpi, the three colpi (four in Votomita) alternate with three (four in Votomita) elongate, narrow pseudocolpi. This type of pollen is present in Trembleya phlogiformis (Fig. 22A), Tibouchina urvilleana (Fig. 22C), Tristemma littorale (Fig. 22D), Dissotis brazzae (Figs. 23C,D), Marumia nervosa (Figs. 23A,B), Dissochaeta celebica (Fig. 23F), Osbeckia polycephala (Fig. 22B), Acanthella sprucei (Fig. 23E), Memecylon normandii (Fig. 21C), Mouriri glazioviana (Fig. 21D), and Votomita monadelpha (Figs. 22E,F). Grains are spheroidal to subprolate in lateral view with a circular to three lobed or triangular shape in the polar view. The surface sculpture is quite variable. A more or less smooth surface with a few pits and punctae is present in Acanthella (Fig. 23E). In Dissotis (Figs. 23C,D) and Trembleya (Fig. 22D) many channels, pits, and punctae are present on a smooth rugulate surface. In Maurumia (Figs. 23A,B), Dissotis (Fig. 23F), and Memecylon the surface is rugulate-punctate. It is striate-rugulate in Osbeckea (Fig. 22B), with elongate, more or less parallel muri which become shorter and separated at the poles where the surface then becomes verrucate-rugulate. In Trembleya (Fig. 22A), it is striate whereas in Tibouchina (Fig. 22C) it is smooth-punctate with a very faint striate pattern which in some grains is quite prominent at the poles. The surface in Mouriri (Fig. 21D) and Votomita (Figs. 22E,F) is composed of fine, elongate, branched, often overlapping muri that form a compact network with perforations in between.

Colpi are long, (some grains are syncolpate in Dissotis, Acanthella and Dissochaeta) with acute ends, and a smooth surface except in Acanthella, Marumia, and Dissochaeta where the surface is granular. In Votomita the colpus surface is covered with bead-like elements. Endoapertures are lalongate (not clearly defined in Dissochaeta) and elliptic (circular to elliptic in Votomita). Extensions of the

mesocolpia over the endoapertures are present (Figs. 22A,D; 23E). A horizontal bar is often persistent over the open endoapertures (Figs. 22C; 23A,D). Pseudocolpi are long, narrow, and have either a smooth or scabrate or granular surface (Fig. 23B). They are usually shorter than the colpi but in Marumia and Dissochaeta they are as long as or longer than the colpi.

In the second group, "heterocolpate" with intercolpar concavities, there are present on the mesocolpia three intercolpar concavities—large, elliptic, thin walled, depressed areas. The remaining thick walled portion of the mesocolpia forms a more or less narrow band around the intercolpar concavities. This type of pollen is found in Adelobotrys tessmannii (Figs. 24A-C), Allomorphia caudata (Fig. 24D), Oxyspora paniculata (Figs. 24G,H), Bredia hirsuta (Fig. 24F), and Astronia cumingiana (Fig. 24E). The grains are spheroidal in lateral view and circular to triangular or hexagonal (Oxyspora) in polar view. Colpi are long, narrow with acute ends and a more or less smooth surface. Extensions of the mesocolpia are present over the lalongate, elliptic endoapertures (Figs. 24D,E not clearly defined in A. caudata, not examined in A. cumingiana). Adelobotrys differs from the other taxa in having wide colpi which are united at the poles, and by a granular-verrucate surface. The colpus membrane is raised over the endoaperture (Fig. 24B, arrow). This raised membrane is vertically oriented and does not seem to be analogous with an operculum.

The surface of the meso- and apocolpia is variable: psilate in Adelobotrys (Fig. 24A-C), scabrate in Allomorphia (Fig. 24D not very clear), striate-rugulate in Oxyspora (Figs. 24G,H), fine rugulate-verrucate in Bredia (Fig. 24F), and coarse with many channels and pits (rugulate ?) in Astronia (Fig. 24E). The intercolpar concavities differ in their size and surface sculpture. In Bredia and Astronia, their

surface sculpture is similar to that of the rest of the grain except that it is finer. Adelobotrys and Allomorphia have a verrucate surface while Oxyspora has angular, flat, irregularly shaped units on the surface of the intercolpar concavities.

The exine structure is similar in both pollen types. In the meso- and apocolpia the foot layer is well developed and often dome shaped (Figs. 25B,D; 26A; 27A). Here the endexine is less developed, often very thin (Figs. 26A,B). A "white line" between the foot layer and the endexine is often very distinct (Figs. 25B,C; 26A). The columellae are short, erect, and distally branched. The tectum is thick, perforate, and has an undulating outer margin; although in Adelobotrys (Fig. 27A) perforations are rare and the outer margin of the tectum is smooth. Acanthella (Fig. 26D) differs from the other taxa in having a very thick tectum (rarely perforate) and a thick foot layer which are separated by columellae that appear granular and have lateral extensions.

Toward the colpi and pseudocolpi or the intercolpar concavities, the endexine becomes thicker whereas the ektexine layers taper. The foot layer is discontinuous and thinner at the margins of the mesocolpia: on the surface of the colpi, pseudocolpi, and intercolpar concavities, it remains either as a very thin layer (Figs. 26A; 27A,B,D) or is absent. The tectum is thin, the columellae are short and fine, or both units are absent. In the intercolpar concavities the verrucae (or the irregular elements of Oxyspora) show a thin, dome shaped tectum below which one or more very fine columellae are present (Figs. 27A,B,D). In Astronia the tectum is thin and columellae are irregular and short (Fig. 27C).

In the region of the endoaperture, the endexine is thick and granular and often lameliate (e.g., Adelobotrys, Trembleya). The tectum is thinner and the columellae are shorter. The foot layer is tapered leaving the columellae and tectum

directly overlying the granular endexine (Figs. 26D; 27A,C,D). Around the endoaperture in Astronia (Fig. 27C) the columellae and tectum are separated from the endexine.

The third, tricolporate group, is represented only by Tococa stephanotricha which has a rugulate surface and very short colpi (SEM not included in this report). The TEM (Figs. 28B,C) shows that the endexine is uniform in thickness except near the endoapertures where it is thicker, granular and lamellate. The foot layer is also uniform in thickness. The columellae are short, erect or reclining, and rarely branched. The tectum is discontinuous with irregular dome like units in section.

A second species of Tococa, T. spadiciflora, could not be assigned to one of the three groups described above. It consists of polyads, with individual grains having a punctate surface. The nature of the apertures, the occurrence of intercolpar concavities, and the arrangement of polyad members is not clearly understood at present (SEM included elsewhere, Patel, Skvarla, Raven and Almeda, 1982). In TEM (Fig. 28A) the endexine is more or less uniform in thickness except near the endoapertures where it is thicker and granular. The foot layer is uniform in some areas but in others it is highly irregular and discontinuous with many channels and gaps. Columellae are long, thick and erect, at their distal ends they break up into fine, very short branches. The tectum is thick, uniform, and with large perforations. The tectum as well as the columellae show fusion at the points of attachment between members of the polyads.

Discussion: As indicated earlier, Melastomataceae pollen has received little study above the light microscope level. Guers (1974) included scanning electron micrographs of Dicellandra barteri, Calvoa orientalis, and Osbeckia decandra.

These were part of a light microscope study of eight genera and 20 species from tropical Africa. Dicellandra compares favorably with our second pollen group in possessing what we interpret to be intercolpar concavities, in contrast, C. orientalis (triporate) and O. decandra (tricolporate) are heterocolpate.

Within the extremely limited context of this study only those taxa in our first pollen type, that is, the heterocolpate type, show some similarities to other core families. At the SEM level some resemblance is evident with Combretum (Figs. 13A,B), Bucida (Fig. 14A), Conocarpus (Fig. 14B), Pteleopsis (Fig. 14C), Terminalia (Fig. 14D), Ramatuella (Fig. 14E), Guiera (Fig. 15E), Poivrea (Fig. 16C), and Lumnitzera (Fig. 16D) of the Combretaceae; and Sonderothamnus (Fig. 19E) of the Penaeaceae. At the TEM level the striking dome shaped foot layer of the heterocolpate type (Figs. 25,26 except Acanthella Fig. 26D) compares with the Combretaceae (Fig. 17). TEM of Acanthella (Fig. 26D) is notably distinctive in the Melastomataceae, resembling to some extent Penaea (Fig. 20A), Sonderothamnus (Fig. 20B), and Stylapterus (Fig. 20D) of the Penaeaceae; and Olinia (Figs. 12B-E) of the Oliniaceae.

TEM of the other two pollen types (Figs. 27,28) does not reveal any significant comparisons other than those already mentioned in the plate legends and pollen descriptions. Clearly, pollen in this family must be investigated in greater depth.

MYRTACEAE (including PSILOXYLACEAE)

In general, the pollen is tricolporate (triporate in Tristania nereifolia), radially symmetrical, and isopolar or heteropolar. In lateral view the pollen is oblate, elliptic with acute or truncate sides. In polar view it is triangular,

goniotreme with straight or curved sides (convex or concave), and with acute or rounded corners. Colpi vary in length, are either syncolpate or parasyncolpate and generally have a smooth surface. Endoapertures are lalongate. Intercolpar concavities are present in some species. Heteropolar grains are due either to the nature of the colpi (e.g. long on one pole and syncolpate on the other pole), or to the different shapes (concave, convex, straight) of the two hemispheres. In Eugenia capuli, and in some grains of Luma chequen, Chamelaucium unciniatum, Temu divaricatum, and Ugni molinae, one hemisphere is concave (or straight, in Chamaelaucium) and the other is convex. The pollen is free except in Myrtus communis (Fig. 36D) and Psidium littorale (Fig. 34B) where tetrahedral tetrads are present along with the monads.

Based on the nature of colpi, Pike (1956) recognized three pollen types in the Myrtaceae from the southwest Pacific area: (1) longicolpate grains; (2) syn- or parasyncolpate grains, and (3) brevi- or brevissimicolpate grains. All three types are present in the taxa examined in this study.

(1) Longicolpate type:

The colpi are long, "Colporate grains are longicolpate when the colpi are longer than the distance between their apices and the poles" (Pike, 1956, p. 51). Hypocalymna angustifolum (Figs. 32E,G), Myrceugenella apiculata (Fig. 35F), and U. molinae (Figs. 34D,E) belong to this type. In addition to the long colpi, pollen shape is also similar in Myrceugenella and Ugni: the triangular grains have convex sides and slightly protruding apertures in polar view and an elliptic shape with acute ends in lateral view. The surface in Myrceugenella is verrucate-granular with some larger verrucate elements at the poles (Fig. 35F). Ugni shows a unique surface pattern with multiangular units that have acute corners (Fig. 34E). These units are

large and scattered at the poles but become smaller and more tightly packed toward the equator. The surface appears to be granular around the endoapertures. In Hypocalymna the grains are triangular with straight sides in polar view and elliptic with acute corners in lateral view. The surface has a pebbly appearance, with large units of different shapes, separated by deep, narrow spaces. This pattern becomes finer at the margins of the colpi and at the poles. The colpi in all three taxa are very narrow, with a smooth surface except in Myrceugenella which has a granular surface.

(2) Syncolpate and Parasyncolpate type:

In syncolpate grains, the colpi are either straight, that is, meeting at the poles without becoming wider, or curved where they are wider at the poles and form a triangular area. In parasyncolpate grains, the colpi bifurcate and their branches outline a triangular apocolpium. Not all grains are strictly syncolpate or parasyncolpate, some are syncolpate on one pole and parasyncolpate on the other pole (i.e., syn/para), while others also combine with longicolpate grains and result in long/syn and long/para forms. These combinations were found in Myrtus communis, Psidium littorale, Eucalyptus ficifolia (Figs. 30C,D), E. robusta, Heteropyxis natalensis, Temu divaricatum, and Eugena elliptifolia. The taxa included in the syncolpate and parasyncolpate type are further grouped according to the presence or absence of the intercolpar concavities.

Pollen with Intercolpar Concavities.

Since the Myrtaceae pollen examined is oblate in lateral view, the intercolpar concavities are equatorially elongated and elliptic in shape. They are clearly defined in Acmena smithii (Fig. 35B), Callistemon speciosus (Figs. 31B,D), C. teretifolius (Fig. 31A), Eucalyptus ficifolia (Figs. 30C-E), E. robusta (Fig. 30F),

Heteropyxis natalensis (Figs. 30A,B), Melaleuca hypericifolia (Figs. 33A,B), M. rhaphiophylla (Fig. 33E), Tristania conferta (Figs. 29C,D), and T. lactiflua (Fig. 29F). In Cleistocalyx operculata (Fig. 35A), Eugenia elliptifolia (Fig. 35D), Metrosideros nervulosa (Fig. 29B), and M. polycephala (Fig. 29A) they are not as markedly "depressed" as in the above mentioned taxa. In A. smithii, E. ficifolia, E. robusta, and T. lactiflua, the intercolpar concavities have many punctae with fine, irregular channels on a smooth surface while the rest of the mesocolpia is psilate. Similar surface sculpturing is present in E. elliptifolia and Cleistocalyx. Melaleuca hypericifolia has a verrucate-granular surface in the intercolpar concavities and the surrounding areas are scabrate. In C. teretifolius, C. speciosus, and H. natalensis the surface of the mesocolpia is rugulate, and it is rugulate-verrucate in the intercolpar concavities. In M. rhaphiophylla, T. conferta, and perhaps Calothamnus validus (Fig. 31E) it is granular-verrucate in the intercolpar concavities and finely rugulate with fine channels on the mesocolpia. In M. nervulosa and M. polycephala the intercolpar concavities have a coarse, rugulate-verrucate surface. On the mesocolpia, it is finely rugulate in the former and psilate in the latter (Figs. 29A,B). Melaleuca pulchella (Fig. 33G) has a coarse rugulate surface on the entire grain.

Pollen Without Intercolpar Concavities.

Here, the surface is more or less uniform over the entire grain. The surface in M. communis (Figs. 36B-D), P. littorale (Figs. 34A-C), Eremaea pauciflora (Fig. 31F), Melaleuca preissiana (Fig. 33D), and M. decussata (Fig. 33C) is similar: granular-verrucate-rugulate. There are fine, branched, irregular channels separating the surface elements. In M. communis (Fig. 36C) minute lines and dots are seen on the surface elements.

The surface in Luma chequen (Fig. 35E), Pilidiostigma glabrum (Fig. 34F), and Rhodamnia argentea (Fig. 36E) is verrucate-granular. In Luma, the colpi are curved and form a large thin walled triangular area at the poles that has irregularly scattered verrucae and granules on it. In Pilidiostigma, at the parasyncolpate pole, scattered granules form a triangular apocolpium. The surface is smooth near the endoapertures in both of these taxa. In Rhodamnia, larger verrucate elements are present along the margins of the mesocolpia, even near the endoapertures.

Austomyrtus bidwillii (Fig. 36F), Temu divaricatum (Fig. 36A), and Psiloxylon mauritianum (Fig. 33F) show a coarsely rugulate pattern. In Austomyrtus isolated rugulate and verrucate elements are present on the apocolpia. In Psiloxylon the rugulate elements are much taller on the equator. This genus has very large apocolpia and differs from the rest of the parasyncolpate taxa in this respect. Eugenia capuli (Fig. 35C) has a slightly less coarse rugulate surface. In all the rugulate taxa, the surface near the endoapertures is smooth.

The cross section of the Myrtus communis monad (Figs. 37C,D) shows that the endexine is uniform except near the endoapertures where it increases in thickness and becomes granular. The thin foot layer has an irregular upper margin and is discontinuous. The short columellae support a thick, infratectal granular layer. The tectum is also thick, with an irregular upper margin and shows many perforations. The section of the tetrad (Fig. 37A) indicates in places a discontinuous dome shaped tectum with a granular layer below it. Figure 37B shows the fusion of tecta between two members of the tetrad.

(3) Brevicolpate and Brevissimicolpate type:

In the brevicolpate grains the length of the colpi is equal to or less than the distance between their ends and the poles (Erdtman, 1971). In the brevissimicolpate

grains, the colpus length is less than that of the underlying endoaperture (Erdtman, 1971). Chamelaucium uncinatum (Figs. 32F,H) has brevissimicolpate grains. The surface is smooth with minute pits. The ends of the very short colpi are rounded.

Uncertain taxa: Due to the lack of sufficient data the following taxa could not be assigned to any of the above pollen types. Baeckea virgata (Fig. 32A) and Osbornia octodonta (Fig. 34G) appear to have curved syncolpi. However, they are often partially obscured or not well developed and then appear as short colpi which outline a faint triangular thin walled area at the pole. Moreover, Baeckea appears to have intercolpar concavities. Homaranthus wilhelmii (fig. 32B) and Thryptomene calycina (Fig. 32D) seem to be brevissimicolpate. The surface is psilate in both taxa and Thryptomene shows a circular, thin walled area at the pole. Balaustion microphyllum (Fig. 32C) appears to be brevicolpate with a psilate surface and with a circular, thin walled area on the pole. Intercolpar concavities may be present. However, colpi are slightly longer on one hemisphere and rarely one or two of the longer colpi unite with the polar, thin walled area. Tristania nereifolia (Fig. 29E) differs from all the taxa of the family. The triangular pollen has deeply concave sides. The surface is scabrate and the nature of the three apertures is difficult to interpret but the pollen appears to be triporate.

Discussion: Of the 93 genera and over 300 reference citations listed by Thanikaimoni (in press) for the Myrtaceae only three allude to electron microscopy, making it obvious that SEM-TEM investigations are greatly needed in the family although, as discussed below, taxonomic investigations by Gadek and Martin (1981, 1982) are currently in progress. Since our intent in this study is the presentation of

a broad overview of the Myrtales core families we will not attempt a review of the extensive Myrtaceae pollen references, instead, only briefly mention a few of the more recent pertinent ones. The most comprehensive taxonomic light microscope study was that of Pike (1956) which included 71 genera and 300 species from the southwestern Pacific area. Some of the conclusions reached from this study were:

(1) although the pollen in the family is essentially uniform, in some taxa minor differences make it possible to recognize particular genera or species,

(2) within a family (following Niedenzu's classification, in Engler and Prantl, 1893) "There appears to be no particular feature that separates pollen of the Myrtoideae from that of the Leptospermoideae, but pollen of the tribe Chamoelaucieae (placed by Niedenzu in the Leptospermoideae) differs markedly from that of all other tribes in the family" (Pike, 1956, p. 46),

(3) within a tribe the taxa usually are similar ". . . . e.g. Myrtinae, Chamaelaucieae, but it is possible for closely related genera to have quite distinct pollen, e.g. Metrosideros and Spermolepis, Leptospermum and Agonis, Baeckea and Balaustion, Wehlia and Pileanthus. On the other hand, grains of widely separated genera may show certain similarities, e.g. those of Regelia ciliata are difficult to distinguish from those of some species of Eucalyptus, and those of Astartea and Agonis are ± similar" (Pike, 1956, p. 46),

(4) within a genus "Grains of different species of the same genus are usually indistinguishable, e.g. Leptospermum, or they may be similar in general features but show a comparatively large range in size, e.g. Eucalyptus. Rarely is it possible to make specific distinctions as in Regelia" (Pike, 1956, p. 47).

McIntyre (1963) examined the pollen of 18 New Zealand taxa and found that most genera could be recognized. Species within genera also could be recognized to some extent. As concerns fossil identification of Myrtaceae pollen, McIntyre (1963, p. 104) stated:

> "There is little or no difference between the pollen grains of many genera of the Myrtaceae. Identification of living genera and species from fossil pollen, therefore, can only be reliable if there are no grains of similar type, from extinct

> genera and species, in the sample under consideration . . . . .
> When all factors are considered it is obvious that attempted identifications of fossil Myrtaceae pollen on the basis of pollen characters of the indigenous species should be restricted to a period of time where it is reasonably certain that no other species or genera of the family were present . . . . ".

Most recently Gadek and Martin (1981) examined the pollen of 28 species and 7 genera of the subtribe Metrosiderinae with light and SEM. They found a greater range of pollen morphology within the family than was heretofore recognized and in some instances pollen could be identified to the generic and specific levels. With the SEM they were also able to circumscribe three basic exine sculpture types.

Lugardon and Van Campo (1978) examined pollen of Tristania laurina and Myrtus communis with TEM and apparently encountered, at least with the latter, the same problem as we did, that is, a lack of staining contrast between the endexine and the foot layer. They described in both taxa a thick nexine as consisting of a thin often discontinuous foot layer above a "white line" and a thick endexine below it. They further described an infractectal granular layer between the tectum and nexine but did not recognize columellae. In contrast, our section of M. communis (Fig. 37D) indicates very short columellae below the infratectal granular layer. This section also shows a distinct foot layer and endexine. The most definitive TEM study is that of Gadek and Martin (1982, p. 75) in which pollen of Eucalyptus and Tristania were examined in great detail. Their general description for the pollen structure is as follows:

> "The species all show a typical angiosperm exine differentiation consisting of two chemically different layers, an electron dense ektexine and a less dense endexine divided by a very thin electron-transparent lamella. They all differ, however, from the typical angiosperm architecture by the presence of a somewhat unstructured, granulate infratectal

> layer and the presence of a granular/alveolate endexinous layer around the pores. Species differences relate to the granulate/columellate organization of the infratectal layer; the extent or density of tectal perforations; and the presence and thickness of a foot-layer around the grain".

In summary, Myrtaceae pollen as documented with SEM does not appear to have any close similarities to taxa from the other core families of the Myrtales. Perhaps, some superficial similarity exists with Onagraceae pollen but there is no mistaking the two families. Erdtman (1971) suggests similarity to Lythraceae but we have not been able to confirm it in this study. On the other hand, we do not have sufficient data to compare Myrtaceae pollen with families outside of the Myrtales as suggested by Erdtman (1971). It would be of interest to examine pollen of the Cunoniaceae, Proteaceae, Lecythidaceae and Sapindaceae in order to check the validity of Erdtman's (1971) observations. Pollen of the Lecythidaceae and Sapindaceae have been examined in SEM (Muller, 1972, 1973; Muller and Leenhouts, 1976; Mori, Orchard and Prance, 1980) and are not similar to Myrtaceae pollen. However, in the Sapindaceae there are several taxa with triangular, parasyncolpate grains (Muller and Leenhouts, 1976).

The distinct SEM appearance of Myrtaceae pollen is countered by the TEM structure; which basically conforms with a typical post-and-beam organization of angiosperm pollen. The 'granular/alveolate' endexine of Gadek and Martin (1982) does appear somewhat similar to Onagraceae pollen but as further suggested by them it can also be found in other families, thus diminishing the uniqueness of the character. Furthermore, the infratectal granular layer has been observed in a number of core families in this study.

ONAGRACEAE

The SEM Of Onagraceae pollen (Figs. 38-4) is intended to present a general overview of the morphology of the family although only nine of the seventeen genera are included here. Pollen represented by a dominant circular or central body (Praglowski et al., 1982) with markedly protruding apertures is very typical of Fuchsia (Figs. 38A,B), Circaea (Figs. 38C,D), Clarkia (Figs. 39A,B,D), Gaura (Fig. 39H), and Oenothera (Figs. 40A,C). In comparison, the apertural protrusions are less pronounced in Ludwigia (Figs. 41F,H) and Hauya (Fig. 38E) while in Gongylocarpus (Fig. 40D) and Boisduvalia (Fig. 41A) they appear to blend into the central body. The latter two genera tend to have a more triangular outline in polar view. While most Onagraceae is three aperturate, Fuchsia (Fig. 38A) very commonly is two aperturate. In addition to the monad pollen represented in the above figures, tetrad pollen is illustrated here by Boisduvalia (Fig. 41A), Ludwigia goiasensis (Fig. 41D), and L. alternifolia (Fig. 41F). Further, pollen occurring in polyads is represented by L. longifolia (Fig. 41H). The internal bridges (Fig. 41G) connecting adjacent tetrad members and the external bridges (Fig. 41I) (Skvarla et al., 1982) connecting adjacent tetrads appear identical to each other as well as to their respective exine surfaces. All taxa except C. alpina ssp. imaicola (Fig. 38D) are characterized by long ektexinous strands or viscin threads which originate on the proximal polar surface (see especially Hauya, Fig. 38E; Clarkia, Figs. 39A,B,D; Oenothera, Fig. 40A; Gongylocarpus, Fig. 40D). These threads assume different surface patterns such as smooth (Circaea, Fig. 38C; Clarkia, Figs. 39C,F; Boisduvalia, Fig. 41E; Ludwigia, Figs. 41F,H,I), segmented-ropy (Fuchsia, Fig. 38A), segmented-beaded (Hauya, Fig. 38F; Gaura, Figs. 39E,G; Oenothera, Figs. 40B,E), incised-compound (Boisduvalia, Fig. 41B), and tightly-compound-twisted (Boisduvalia, Fig. 41C). Viscin

thread morphology has received intensive study elsewhere (Skvarla et al., 1978). Sculpturing of the exine surface is also pleomorphic and illustrated by circular-globular elements (Hauya, Fig. 38F; Clarkia unguiculata, Fig. 39F; Gaura mutabilis, Fig. 39G), circular and elongate elements (Circaea cordata, Fig. 38C; Gonglyocarpus fruticulosus ssp. glaber, Fig. 40F), rugulate elements (F. michoacanensis, Fig. 38B; Boisduvalia Figs. 41B,C,E), and their combinations (see especially Clarkia speciosa ssp. speciosa, Fig. 39C). Furthermore, the exine surface supporting these elements frequently is highly perforate (G. lindheimeri, Fig. 39E; Oenothera, Fig. 40B; Boisduvalia, Figs. 41B,C,E).

Other surface features of significance are the long colpi (Figs. 41D,F,H) and prominent ridges (Fig. 41F) in Ludwigia. The latter are of two types, meridional, which occur over the polar faces and extend to the equator midway between the apertural protrusions, and equatorial, which occur between the apertural protrusions and join there with the meridional ridges (L. alternifolia, Fig. 41F). Of the two, the equatorial ridges seem to be the most consistent. In contrast, the meridional ridges are prominent in L. alternifolia (Fig. 41F) but poorly developed in L. goiasensis (Fig. 41D) and L. longifolia (Fig. 41H).

Exine structure of the central body as observed in TEM (Fig. 42) as well as in fractured grains in SEM (Fig. 38G) is composed of a spongy-paracrystalline ektexine and a dense, uniform endexine which frequently has a thin, granular, basal component (L. brevipes, Fig. 42B). Most commonly, the ektexine is not divided into tectum, columellae, and foot layer units. The columellae and foot layer are absent and the spongy-paracrystalline tectum is in direct contact with the endexine (F. garleppiana, Fig. 42A; L. brevipes, Fig. 42B; Circaea mollis, Figs. 42D,F). Less commonly, extremely short columellae reside on the endexine (Hauya, Fig. 42C; also

see the SEM of fractured grains of Gaura mutabilis, Fig. 39H and Gongylocarpus fruticulosus ssp. glaber, Figs. 40C,E).

In the apertural protrusions the apertural chamber is usually overlain by spongy ektexine and underlain by thick layers of endexine lamellae (C. mollis, Fig. 42F). Fractured grains through the apertural protrusions also clearly show these endexine lamellae (F. michoacanensis, Fig. 38B; Gaura mutabilis, Fig. 39H). Also note in Fig. 39H that short columellae are present on the apertural protrusion--an important observation in need of further study. Exine structure of Onagraceae pollen has been previously discussed in considerable detail elsewhere (Skvarla et al., 1976).

The viscin threads are of ektexine origin and can be considered as extensions of the ektexine surface (F. garleppiana, Fig. 42A). Sections through groups of threads are often as useful as SEM in revealing thread morphology (Hauya, Fig. 42E).

Discussion: Onagraceae pollen has been the object of studies at the light (Mitroiu, 1961-62; Ting, 1966; Brown, 1967) and electron microscope (Skvarla et al. 1975, 1976, 1978, 1982) levels. They have shown that the pollen of the 17 genera and approximately 650 species all possess the following distinctive features: viscin threads, a spongy-paracrystalline ektexine, apertural protrusions and a large central body; tetrads and/or polyads in certain groups; and an exine surface composed of circular or globular elements. Prior to this study our feeling was that Onagraceae pollen was unique in the angiosperms, easily recognizable and difficult to confuse with other groups. After this survey of Myrtales pollen our ideas have not changed and Onagraceae pollen morphology remains distinctive in the order. In a remote

sense--that is by the extremely thick endexine, surface sculpturing, and protruding apertures--the pollen of Ludwigia resembles Trapa (see discussion in Trapaceae), although there are no difficulties in recognizing these taxa. A remote similarity between Myrtaceae and Onagraceae pollen exists particularly those grains having short colpi (compare Hauya, Fig. 38E; Gongylocarpus, Fig. 40D; and Boisduvalia, Fig. 41A; as well as Lopezia of Skvarla et al., 1976, with Myrtaceae SEM on Figs. 29-36). Further, sections through the pseudocolpus of Sonderothamnus (Fig. 20C) of the Penaeaceae show a remarkable similarity to those Onagraceae taxa having the spongy ektexine residing directly on the endexine. Lastly, although meridional ridges have been observed on Ludwigia pollen (L. alternifolia, Fig. 41F) there is no mistaking this genus from those taxa in the Myrtales also possessing meridional ridges.

POLLEN MORPHOLOGY IN RELATION TO TAXONOMY

Most recent classification systems (Cronquist, 1981; Dahlgren, 1981; Takhtajan, 1980; Thorne, 1981) include the core families described here in the order Myrtales (Table 1). Cronquist (1981) placed the Myrtales in his subclass Rosidae, deriving it from the Rosales. He suggested relationship between the two orders via Cunoniaceae (Rosales) and Crypteroniaceae (Myrtales). Dahlgren (1981), however, included the order Myrtales in the Myrtiflorae along with the Haloragales and Rhizophorales, placing Myrtiflorae near Rosiflorae and Proteiflorae. The superorder Myrtanae of Takhtajan (1981) consists of a single, widely circumscribed order Myrtales, and follows the superorder Rosanae (both superorders in subclass Rosidae). The Myrtales in this system, is derived from the Saxifragales-Cunoniinae, and is divided into four suborders: the Myrtinae with the core families described here; the

Haloragineae with Haloragaceae; the Rhizophorineae with Rhizophoraceae; and the Lecythidineae with Lecythidaceae. Thorne (1981) included the core families in the only order Myrtales of the superorder Myrtiflorae. The latter follows the superorder Rosiflorae. Thus, except for a few minor discrepancies of ranks and alignment, there is a general agreement on the circumscription and relationships of the order. The only classification system that deviates from this agreement is that of Hutchinson (1969, 1973). The division of the dicotyledons into Lignosae and Herbaceae, isolated the herbaceous families Onagraceae and Trapaceae from the other Myrtales. The tentative splitting of the core families into two orders Lythrales and Myrtales s. str. by Briggs and Johnson (1979) was mainly based on seed characters (Corner, 1976), (seeds with a fibrous tegmen, and with or without sclerotic mesotesta in the former, and with sclerotic mesotesta in the latter). Briggs and Johnson have now withdrawn this viewpoint (Johnson and Briggs, in press).

Thorne (1981), who defines ordinal and familial concepts widely, included Punicaceae and Sonneratiaceae in the Lythraceae as subfamilies Punicoideae and Sonneratioideae respectively, along with the Lythroideae. As discussed earlier, the pollen of these two taxa, are similar indeed to some Lythraceous taxa and would support their inclusion in the Lythraceae. It should be remembered, however, that when separate, these two families are placed near the Lythraceae. Punicaceae agrees with Lagerstroemia (Lythraceae) in characters such as stipules, numerous centrifugal stamens, and the pollen morphology. It is distinct from the Lythraceae in having an inferior ovary and fruit with a leathery pericarp. Sonneratiaceae agrees with the Lythraceae in the nature of stipules (dissected and axillary), opposite leaves and embryology. According to Muller (1978) Sonneratiaceae is "a highly specialized offshoot of lythraceous stock".

Crypteroniaceae traditionally includes a single genus Crypteronia (4 species distributed in India, the Philippines, and the Malay Archipelago). Van Beusekom-Osinga and van Beusekom (1975) added Axinandra, Dactylocladus, Rhynchocalyx, and Alzatea to Crypteroniaceae, a system that is not widely accepted. Dahlgren included the three asiatic taxa (Crypteronia, Axinandra, Dactylocladus) in the Crypteroniaceae. Thorne, however, included these three as the subfamily Crypteronioideae in the Melastomataceae along with the Melastomatoideae, Astronioideae, and Memecyloideae.

Crypteronia (not included in this report) has dicolporate, syncolpate pollen that has two, large intercolpar concavities (Muller, 1975). Disregarding the number of apertures (2 vs 3), Crypteronia pollen compares well wtih the Melastomataceae pollen possessing intercolpar concavities. Axinandra and Dactylocladus resemble those Melastomataceae having pseudocolpi. Cunoniaceae to which Crypteronia is sometimes associated (Hutchinson, 1973) also has dicolporate pollen in some taxa (Erdtman, 1971). According to Cronquist (1981), "Although its largely unisexual flowers indicate that it is not on the direct line of descent, Crypteronia does strengthen the case for deriving the Myrtales from the suborder Cunoniinae of the Rosales".

Rhynchocalyx, which resembles Lythraceae in wood anatomy (Van Vliet and Baas, in press) is included in that family by Dahlgren (1981, Dahlgren and Thorne, in press). It was included in the Dactylocladus pollen type by Muller (1975) who described the pollen of Crypteroniaceae (sensu van Beusekom-Osinga and van Beusekom). Van Beusekom-Osinga (1977), based on Muller's work stated "Palynological evidence does not fully sustain the recognition of Crypteroniaceae as a distinct family, it could be accepted, but the evidence may allow other

possibilities". Although Rhynchocalyx has tricolporate pollen with three pseudocolpi (like Axinandra and Dactylocladus), this is a common pollen type of the order, and is also seen in some Lythraceae (Lythrum, Rotala). Ultrastructural data on these Lythraceae taxa would, indeed, be helpful for a better understanding of the relationships of Rhynchocalyx.

Alzatea which lacks distinct pseudocolpi or intercolpar concavities, has an undulating columellae layer which has not yet been noted elsewhere in the order. However, it greatly resembles Chrysobalanus (Chrysobalanaceae, sometimes included in the Rosaceae). Alzatea is also distinct in having trilacunar nodes (found in some Melastomataceae). According to Lourteig (1965), the proper place for Alzatea is in the Lythraceae as all characters except the placentation, are found in different genera of that family. The pollen was compared with that of Physocalymma. It differs from the Lythraceae in many aspects, however, such as the presence of branched foliar sclereids, pentamerous flowers, and parietal placentation. According to Dahlgren (Dahlgren and Thorne, in press) Alzatea is distinctive enough for a separate family status which will probably soon be recognized formally by Alan Graham and Shirley Graham.

Venkateswarlu and Prakasa Rao (1972) isolated Strephonema, as family Strephonemataceae, from the Combretaceae on the basis of anatomical characters such as, the presence of fiber tracheids (libriform fibers in other Combretaceae), diameter and length of vessel elements, and the number of vessels per square mm. Strephonema also differs from other Combretaceae in having a semi-inferior ovary and paracytic stomata (anomocytic and cyclic elsewhere). However, it has the characteristic combretaceous hairs and a unilocular ovary with two pendulous ovules. According to den Outer and Fundter (1976), the separation is not entirely

justified, as the secondary phloem in the presence of druses, small width of rays, and an orderly sequence of elements is combretaceous. Most experts of the family (Excell and Stace, 1966; den Outer and Fundter, 1976; Van Vliet and Baas, in press) agree in retaining it as a separate subfamily Strephonematoideae while placing other taxa in subfamily Combretoideae. The pollen of Strephonema pseudocola is distinct in the reticulate surface sculpturing. However, further investigations may reveal such sculpturing in other taxa of the family.

The recognition of the monotypic Psiloxylaceae consisting of Psiloxylon mauritianum (Croizat, 1961), is supported by Dahlgren (Dahlgren and Thorne, in press, Dahlgren, 1981). It differs from other Myrtaceae in having unisexual, perigynous flowers, a 3-carpellate pistil, three stigmatic lobes, chambered crystalliferous fibers, and cancellate testa. Schmid (1980), in his comparative morphological and anatomical treatment of Psiloxylon and Heteropyxis (a genus sometimes treated as Heteropyxidaceae) with the Lythraceae and other Myrtaceae, formed a new subfamily Psiloxyloideae, along with the Myrtoideae, Leptospermoideae and Chamelaucioideae. The latter is included in the Leptospermoideae in the widely accepted classification of the Myrtaceae by Niedenzu (1893). The inclusion of Heteropyxis in the Leptospermoideae is generally agreed upon. Both Psiloxylon and Heteropyxis resemble other Myrtaceae in gland-dotted, entire, simple leaves; leaf venation; the absence of endosperm in mature seeds; the presence of secretory cavities; druses; wood anatomy; ovule morphology; etc. Their inclusion in the Myrtaceae is also supported by pollen morphology as it is typically Myrtaceous (this report, Schmid, 1980).

The evidence presented in this report shows that palynologically Lythraceae, Punicaceae, Sonneratiaceae, Oliniaceae, Combretaceae, Alzateaceae,

Penaeaceae, Crypteroniaceae, and Melastomataceae, can be grouped together. In general, the pollen in these families is spheroidal, circular, tricolporate, and heterocolpate with pseudocolpi or intercolpar concavities. Pseudocolpi occur in other families of the dicotyledons, but as Dahlgren points out (Dahlgren and Thorne, in press), they are not as prevalent in any other single order as they are here. The palynological similarities indicated under each family description, support the interrelationships of these families as suggested by Takhtajan (1980) and Dahlgren (Dahlgren and Thorne, in press), for example, Melastomatacae to Crypteroniaceae, Penaeaceae to Oliniaceae, Oliniaceae to Melastomataceae, Punicaceae to Lythraceae, and Sonneratiaceae to Lythraceae.

Myrtaceae, Trapaceae, and Onagraceae deviate palynologically, not only from the above mentioned families but also from each other. Myrtaceae, with its typical triangular, angulaperturate, oblate-suboblate pollen is distinct. However, the occurrence of intercolpar concavities, and the exine structure relate it to the families above.

Trapaceae, a monogeneric family of aquatics, has many unusual characters, such as, leaf teeth with double apex; early degeneration of endosperm; haustorial embryosac; unequal cotyledons, one rudimentary, the other massive and storing starch. It has been placed in or near the Onagraceae (Takhtajan, 1980) but is generally related to the Lythraceae by most authors. Miki (1959) based on the fruit morphology of fossil genus Hemitrapa, and living and fossil species of Lythrum and Trapa derived Trapaceae from the Lythraceae and not Oenotheraceae (= Onagraceae). Raven (as cited by Cronquist) also rejects its relationship with Onagraceae. Although it is quite distinct, the pollen of Trapa shows remote resemblance to Ludwigia (Onagraceae).

Palynologically, the most distinct and presumably the most advanced family of the order is Onagraceae. The spongy ektexine with reduced or no columellae, the absence of a foot layer, and the very thick endexine are considered advanced features of the angiosperm pollen wall (Walker, 1976). The nature of apertures, and the presence of elaborate viscin threads also separates this family from the rest of the Myrtales. It differs from other members of the order in having a 4-nucleate, Oenothera type embryosac; Rosoid leaf teeth; and the oxalate raphides. It is considered to be isolated in the order but related to the Lythraceae by most authors (Cronquist, 1981; Takhtajan, 1980; Dahlgren and Thorne, in press).

Thymelaeaceae, Haloragaceae, Rhizophoraceae, and Lecythidaceae are families sometimes referred to the Myrtales. The last three are considered by most authors to be close to the Myrtales. Thymelaeaceae are included in the Myrtales only by Cronquist. Their spheroidal, porate pollen with crotonoid surface (Erdtman, 1971; Archangelsky, 1971) resembles those in the Euphorbiales. Haloragaceae have porate or colpate (3,4, or 5) pollen, with mostly echinate (with spinules) surface. The aperture and exine structure (Praglowski, 1970; Patel, unpublished data) are different from any myrtalean pollen. Rhizophoraceae has tricolporate pollen with psilate-perforate-reticulate or rugulate surface (Muller, 1977; Patel, unpublished data). Lecythidaceae has two basic pollen types: the Planchonia type and the Lecythis type (Erdtman, 1971; Muller, 1972, 1973). The pollen is tricolporate, syncolpate with marginal crests and grooves near colpi in the former, and tricolporate or tricolporate but never syncolpate in the latter. The surface varies from psilate-punctate to reticulate. Pollen of these families does not compare directly with any myrtalean taxa.

Table 1. Comparison of Recent Classification Systems

Family	Cronquist (1981)	Dahlgren (1981)	Hutchinson 1969, 1973	Takhtajan 1980	Thorne 1981
CORE FAMILIES:					
Lythraceae	Myrtales of subclass Rosidae	Myrtales of Myrtiflorae	Myrtales of Lignosae	Suborder Myrtineae of Myrtales	Myrtales of superorder Myrtiflorae
Sonneratiaceae	"	"	"	"	in Lythraceae
Punicaceae	"	"	"	"	in Lythraceae
Trapaceae	"	"	Onagrales of Herbaceae	"	Myrtales
Oliniaceae	"	"	Cunoniales (Lignosae)	"	"
Combretaceae	"	"	"	"	"
Alzateaceae	?	not in 1981 but in Dahlgren and Thorne (in press)	Celastraceae (Lignosae)	?	?
Penaeaceae	Myrtales	"	Thymelaeales (Lignosae)	Myrtineae	Myrtales
Crypteroniaceae	" (only Crypteronia)	"	Cunoniales	"	in Melastomataceae
Melastomataceae	Myrtales	"	Myrtales	"	Myrtales
Psiloxylaceae	"	"	Myrtaceae	?	in Myrtaceae
Myrtaceae	"	"	Myrtales	Myrtineae	Myrtales
Onagraceae	"	"	Onagrales	"	"

(Table 1. Cont.)

OTHER FAMILIES:					
Thymelaeaceae	Myrtales	Thymelaeales of Malviflorae (= Dilleniiflorae)	Thymelaeales	Thymelaeales near Euphorbiales	Euphorbiales of Malviflorae
Haloragaceae	Haloragales of Rosidae	Haloragales of Myrtiflorae	Onagrales	Haloragineae of Myrtales	Cornales (suborder Haloraginae) of Corniflorae
Rhizophoraceae	Rhizophorales of Rosidae	Rhizophorales of Myrtiflorae	Myrtales	Rhizophorineae of Myrtales	Cornales (suborder Rhizophorineae)
Lecythidaceae	Lecythidales of Dilleniidae	Theales of Theiflorae	Myrtales	Lecythidineae of Myrtales	Theales (suborder Lecythidineae)

SUMMARY AND CONCLUSIONS

Pollen morphology of the families that are considered to be the core members of the Myrtales (Dahlgren and Thorne, in press) forms a relatively cohesive group with the exceptions of the Trapaceae, Myrtaceae and Onagraceae. Each family is summarized below.

1. Lythraceae. The 13 taxa examined from this family show the greatest amount of variation in pollen morphology in the entire order, with diversity evident at all levels: (1) shape (in lateral view: oblate-suboblate, spheroidal-subprolate, and spheroidal; in polar view: triangular-goniotreme, triangular-pleurotreme, triangular to hexagonal, and circular); (2) apertures (tricolpoidorate, tricolporate, tricolporate-syncolpate, porate); (3) pseudocolpi (0,3,6); (4) sculpture (striate, striate-spinulate, psilate, verrucate-rugulate); and (5) structure (normal ektexine-endexine layers; highly reduced as well as complex columellae. The taxa which compare with other members of the Myrtales are: Lafoensia with Sonneratia (Sonneratiaceae); Diplusodon with Duabanga (Sonneratiaceae); Lagerstroemia with Punica (Punicaceae); Rhynchocalyx with Dissocheata (Melastomataceae), Lumnitzera (Combretaceae), Axinandra and Dactylocladus (Crypteroniaceae).

2. Punicaceae. The one member examined, Punica granatum, is similar to Lagerstroemia (Lythraceae) in the triangular shape resulting from three meridional ridges. Pseudocolpi are absent.

3. Sonneratiaceae. Sonneratia and Duabanga are characterized by meridional ridges and apertural fields (true pseudocolpi are absent) and, as mentioned above, compare favorably with the Lythraceae.

4. Trapaceae. This family is unique in having colpi hidden within the protruding, swollen aperture domes of sharply triangular pollen grains (in polar view)

and in having three meridional ridges which are united at the poles. The ridges pass over the apertures and in this respect, as well as in structure, they differ from the meridional ridges found elsewhere (e.g., Lafoensia, Lagerstroemia, Ludwigia). Trapa remotely resembles Ludwigia (Onagraceae) in having a granular-beaded surface sculpture and the Onagraceae, in general, in exine structure (very thick endexine and indistinct foot layer and columellae). One sample of T. natans showed linked pollen grains indicating possible polyads.

5. Oliniaceae. The five taxa examined all showed two unique features: asymmetrical colpi with unequal arms extending into the opposite hemispheres and half pseudocolpi which are present on only one hemisphere. Olinia resembles some Penaeaceae in having a psilate pollen surface; it resembles Penaeaceae in exine structure (a very thick foot layer and tectum, and a thin columellae-infratectal granular layer).

6. Combretaceae. The 19 taxa examined have diverse morphology and five groups were recognized: (1) heterocolpate, (2) heterocolpate with a distinct echinate surface sculpture, (3) echinate surface without pseudocolpi, (4) punctate surface without pseudocolpi, and (5) reticulate surface without pseudocolpi. Pollen in the heterocolpate group indicated general similarities to some Penaeaceae, Crypteroniaceae and Melastomataceae.

7. Alzateaceae. Alzatea verticellata is similar to Axinandra and Dactylocladus (Crypteroniaceae) and Rhynchocalyx (Lythraceae). Indistinct pseudocolpi or intercolpar concavities appear to be present. In fine structure some resemblance is shown to Chrysobalanus (Chrysobalanaceae).

8. Penaeaceae. The five taxa examined all are heterocolpate with tri-and tetracolporate pollen. Exomorphic resemblances are with Melastomataceae

(Tristemma, Dissotis) and Combretaceae (Combretum). Endomorphic resemblance is striking with Oliniaceae.

9. Crypteroniaceae. The two taxa examined are heterocolpate and can be favorably compared with Lythraceae, Melastomataceae, Combretaceae, and perhaps with much of the Myrtales.

10. Melastomataceae. The 19 taxa showed three pollen groups: (1) heterocolpate with pseudocolpi alternating with colpi, (2) "heterocolpate" with intercolpar concavities alternating with colpi, and (3) non-heterocolpate. The first group resembles several of the heterocolpate Combretaceae. Tococa spadiciflora occurs as polyads, the only member of the family to the present time to occur this way, and along with some Ludwigia of the Onagraceae (and perhaps Trapa natans as discussed above), the only polyads in the Myrtales.

11. Myrtaceae. An essentially consistent morphology was noted for the 38 taxa examined. The markedly triangular (in polar view) pollen, with modification of earlier work, was placed into three groups using colpus morphology: (1) longicolpate (no intercolpar concavities), (2) syn-and parasyncolpate with and without intercolpar concavities, and (3) brevi- or brevissimicolpate (no intercolpar concavities). Myrtus communis and Psidium littorale were frequently noted as tetrads, the only other record for the Myrtales other than the Onagraceae (some species of Ludwigia, Epilobium, Boisduvalia, Zauschneria, and Camissonia). Psiloxylon was identical to most Myrtaceae pollen. Pollen of the Myrtaceae does not have a true counterpart in the Myrtales.

12. Onagraceae. The pollen of the 23 taxa examined is variable within the family but, like the Myrtaceae, without any close similarity in the Myrtales. The distinctive characters are circular to triangular central body with markedly to

slightly protruding apertures, granular (globular)-rodlike-rugulate (with perforations) surface elements, tetrads and polyads, viscin threads, thick endexine and essentially spongy-paracrystalline ektexine usually lacking columellae and always lacking a foot layer.

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Figure 1. Scanning electron micrographs of Lythraceae pollen. A,B. Nesaea schinzii. A. Lateral view showing granular colpus with circular endoaperture (at center) and two pseudocolpi. The exine surface is striate. X 3,150. B. Polar view X 3,200. Each of the three colpi alternates with two pseudocolpi (arrowheads). Note that all of the nine mesocolpia are equal in size. Comparison should be made with the SEM of N. longipes (Graham, 1977, Figs. 4-6) in which the three mesocolpia that are flanked by pseudocolpi are prominent and larger than the remaining six mesocolpia. C-E. Heimia salicifolia. C. Lateral view. X 2,800. D. Polar view. X 2,900. E. Surface detail. X 15,000. The three colpi have a granular surface. Pseudocolpi are absent. The mesocolpium consists of elongated, branched, often overlapping elements. Comparison with the SEM of Graham (1977, Figs. 1-3) indicates a somewhat different sculptured surface. F. Crenea surinamensis. Lateral view showing two shallow colpi and four pseudocolpi (arrow heads). The mesocolpium (open arrow) between the pseudocolpi is wide and forms a meridional ridge. The exine surface is verrucate-rugulate. X 2,800. This pollen grain (see also SEM of Muller, 1981, Pl. 1, Figs. 1-2) is in marked contrast to other grains with six pseudocolpi (viz. Fig. 1A,B; 2A) in that adjacent colpi and pseudocolpi are not all equidistant. Scales equal 1 μm.

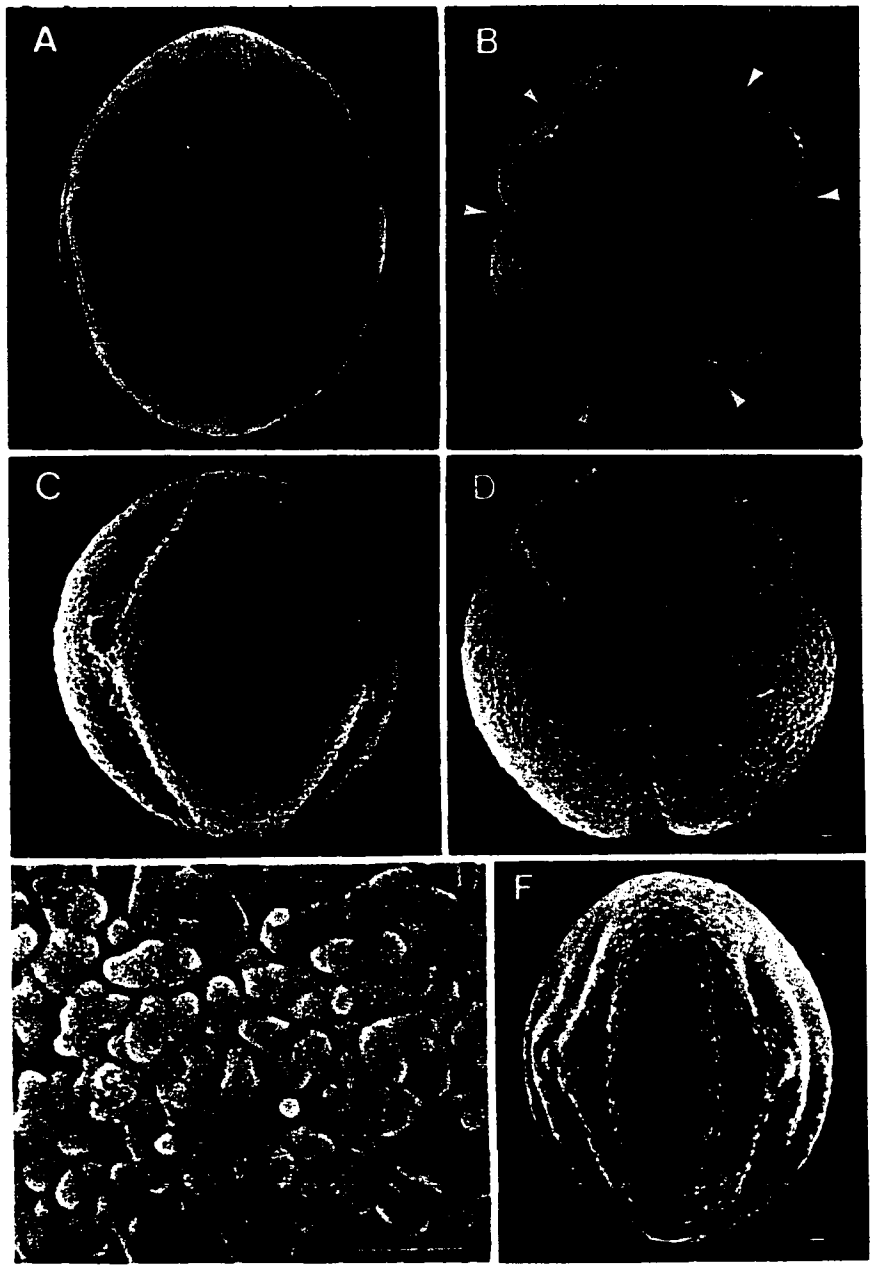
A
B
C
D
F

Figure 2. Scanning electron micrographs of Lythraceae pollen. A,B. Ammannia robusta. A. Lateral view. Each colpus is separated by two pseudocolpi. The exine surface is striate. X 3,000. B. Surface detail near the circular endoaperture (Fig. 2A) which is covered by a granular colpus membrane. X 10,000. C. Cuphea carthagenensis. Polar view. Pores are located in the cylindrical extensions on the three corners; colpi are narrow and united at the pole. The surface is psilate with large ridges (see TEM of C. nitidula, Fig. 5D) near the pores. X 2,900.
D-F. Cuphea petiolata. D. Lateral view with randomly oriented striae in the aperture region. X 3,750. E. Polar view showing syncolpate apertures. X 2,800.
F. View of open endoaperture and surrounding striate surface. X 7,000. See also TEM surface replicas of other species of Cuphea (Graham and Graham, 1968, Figs. 4,5,8). Scales equal 1 μm.

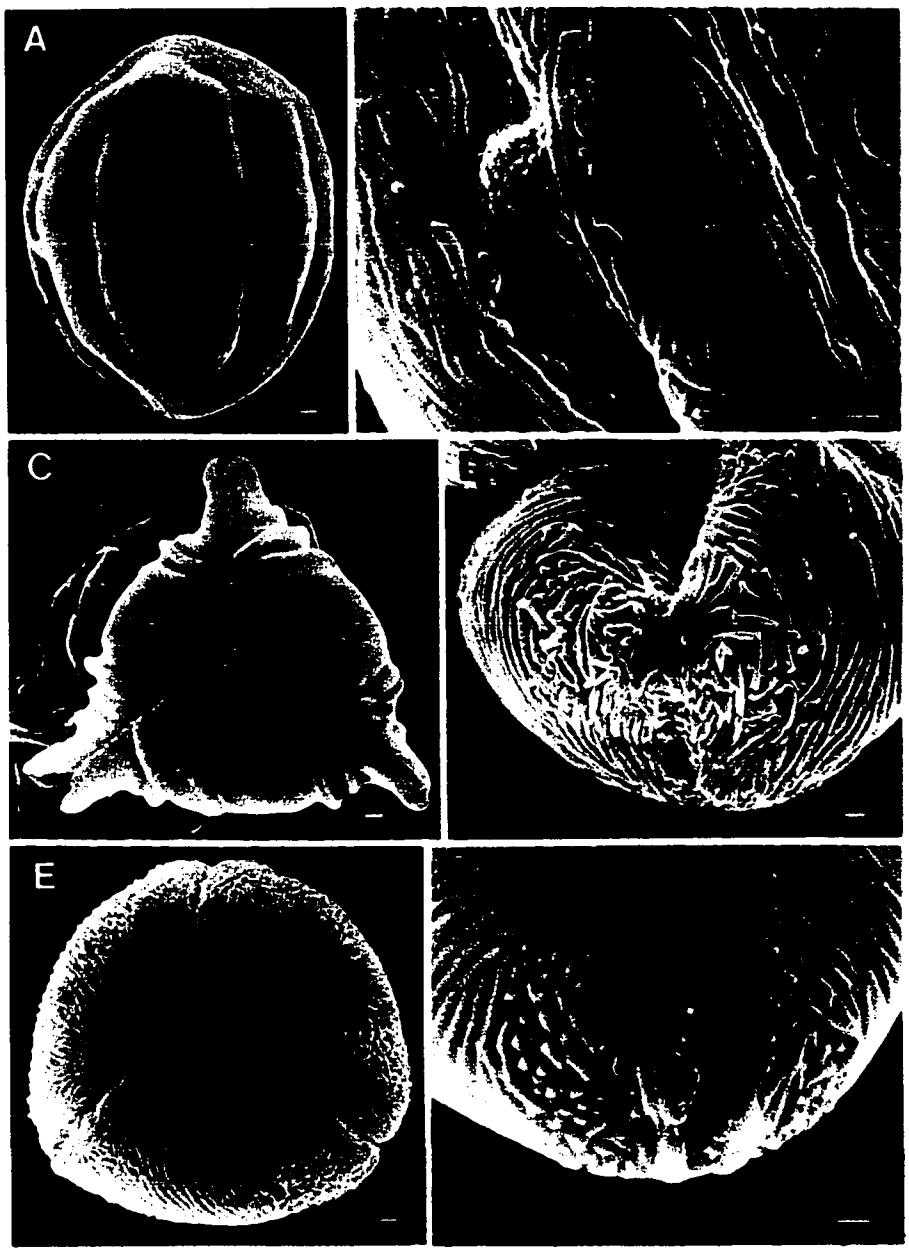
A
C
E

Figure 3. Scanning electron micrographs of Lythraceae pollen. A-B. Diplusodon villosus. A. Lateral view. The aperture system consists of a short colpus and circular endoaperture. X 1,000. B. A verrucate-rugulate surface encompasses the short colpus (arrow) and prominent circular endoaperture. X 2,700.

C. Lagerstroemia speciosa. Polar view showing weakly developed meridional ridges (arrows) between each colpus. X 2,400. This SEM complements the SEM of Muller (1981, Pl. 1, Figs. 3-4) for the same species. D-F. Lafoensia punicifolia. D. Polar view showing prominently psilate polar cap, three protruding apertures and three meridional ridges. X 2,000. E. Lateral view with meridional ridge separating two apertural fields. Arrow indicates colpus. X 1,800. F. The surface of the aperture field surrounding the pore is verrucate-rugulate. A portion of the colpus is indicated by an arrow. X 5,000. These SEM's should be compared with those of Muller (1981, Pl. 7, Figs. 1-2). Scales equal 1 μm.

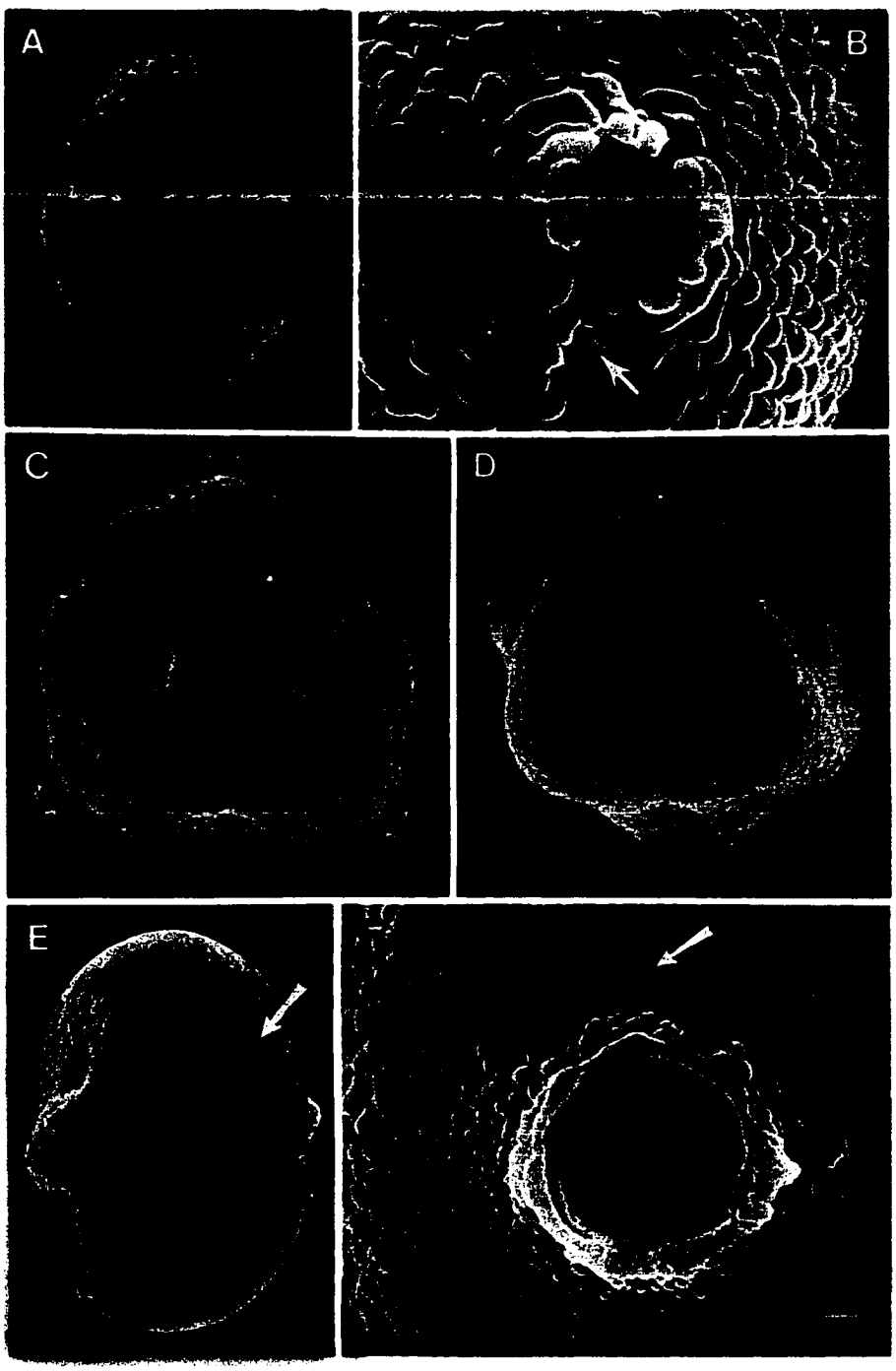
A
B
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Figure 4. Scanning electron micrographs of pollen from Punicaceae (A), Alzateaceae (B,D), Lythraceae (C), and Sonneratiaceae (E,F). A. Punica granatum. Lateral view. Meridional ridge at the middle of the mesocolpium is not well developed but it has a coarser surface (rugulate) than the surrounding granular exine. The grain appears to be slightly collapsed. X 3,600. B,D. Alzatea verticillata. B. Polar view. X 4,000. D. Lateral view. X 4,000. For both figures, the surface is psilate but at the middle of the mesocolpia slightly depressed psilate-punctate areas are noted (open arrows). These have been interpreted as incipient pseudocolpi (see SEM of Muller, 1975, Pl. IV, Figs. 6-9). A distinct margin (solid arrow) is present around the colpus. C. Rhynchocalyx lawsonioides. Polar view. Tricolporate grains have three pseudocolpi that appear to be united (i.e., they are "synpseudocolpate") (arrow) at the pole. X 3,000. See also SEM of Muller (1975, Pl. V, Figs. 7-11). E. Sonneratia caeseolaris. Sublateral view. Polar cap has a psilate surface with a few punctae. The well developed meridional ridge has a rugulate surface. Note the two elliptic apertural fields and the protruding pores which are enclosed by two small ridges (arrowheads). The surface of the apertural fields and the membranes over the pores is verrucate. X 1,250. (See also SEM of Muller, 1978, several plates). F. Duabanga moluccana. Lateral view. The surface is smooth on the polar caps; elsewhere it is verrucate-rugulate. The meridional ridge has a coarser surface than the apertural fields. In contrast to S. caeseolaris (Fig. 4E) polar caps and meridional ridges are less distinct and the protruding pores are without surrounding ridges. Scales equal 1 μm.

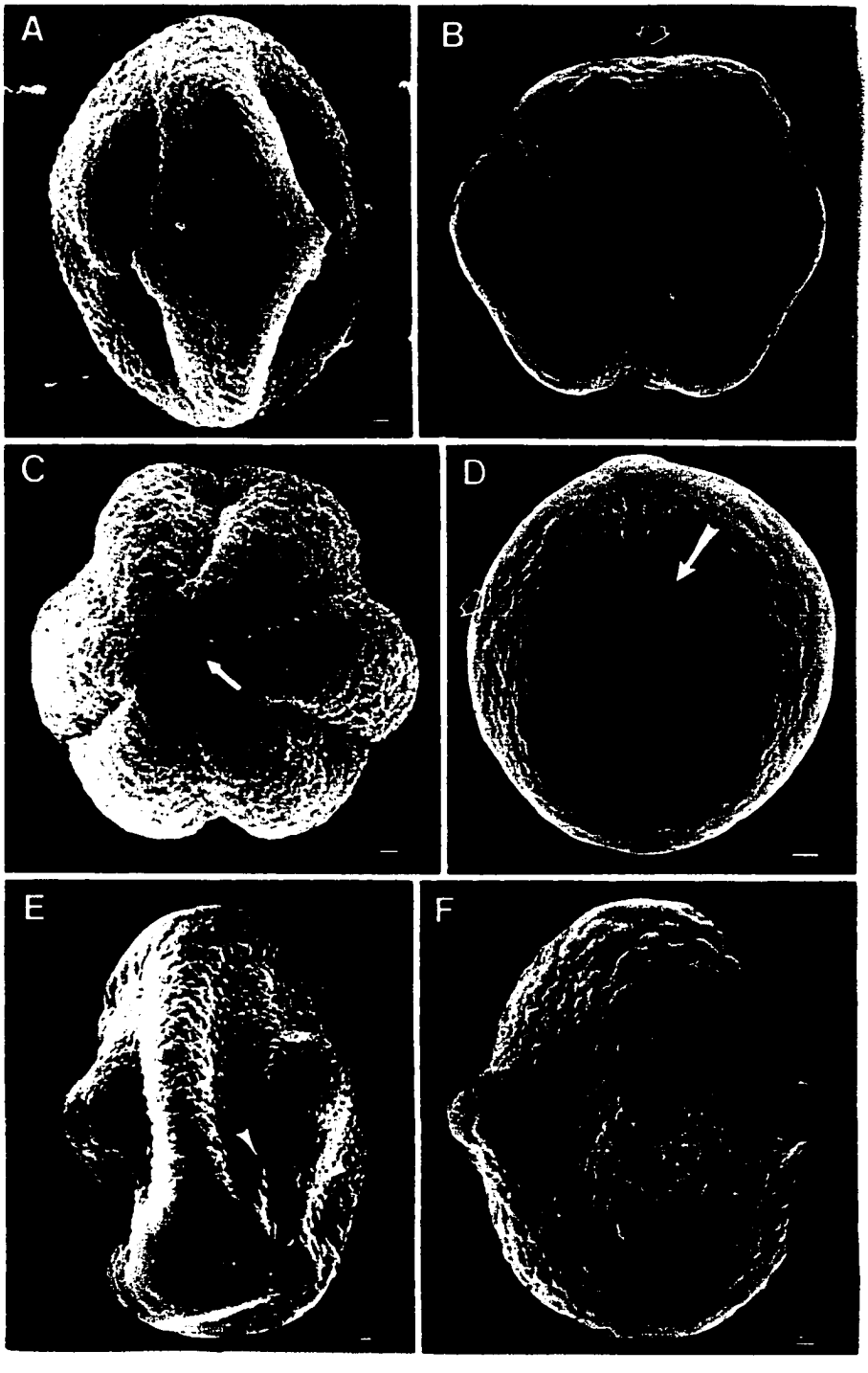
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Figure 5. Transmission electron micrographs of Lythraceae pollen. A. Heimia salicifolia. Section of a mesocolpium with a colpus on each side. X 7,600. B. Ammannia coccinea. Section of a mesocolpium. The striae are cut perpendicularly, are deeply lobed, and are constricted at their bases. The tectum (arrow) is very thin, columellae are short and thick; the foot layer is highly irregular and has some lamellae. The endexine is as thick as the entire ektexine. X 16,200. C. Cuphea racemosa. Portion of a mesocolpium. Note thin, irregular endexine. X 27,000. D. Cuphea nitidula. Section of the mesocolpium near pore (to the right but not included). The ridges (r) (as described in SEM Fig. 2C) are solid, columellae (arrow) are short, and the foot layer is essentially uniform. The endexine increases in thickness toward the pore and is stained darker than the ektexine. X 34,000. E,F. Lafoensia punicifolia. Section perpendicular to mesocolpium and including adjacent pores. The ektexine on the meridional ridge (within arrows) is more prominently developed than on the adjacent apertural fields. The endexine is well developed: under the meridional ridge it is nearly equal in thickness to the ektexine, toward the pores it becomes granular as well as increasing in thickness. X 5,500. This transverse section is in contrast to Fig. 6A which represents a section parallel to the polar axis (i.e., a longitudinal section) and includes part of the polar cap and apertural field. These two different sectioning planes represented in Figs. 5E and 6A explain the disparity in respective endexine thicknesses. See also Muller (1981, Pl. IV) for additional TEM. F. Section of polar cap. In contrast to Figs. 5E and 6A note particularly the smooth, solid tectum and the thick and branched columellae. The uniform foot layer is thicker than the narrow endexine. X 16,000. This section is directly comparable to TEM of Muller (1981, Pl. IX, Fig. 3). Scales equal 1μm.

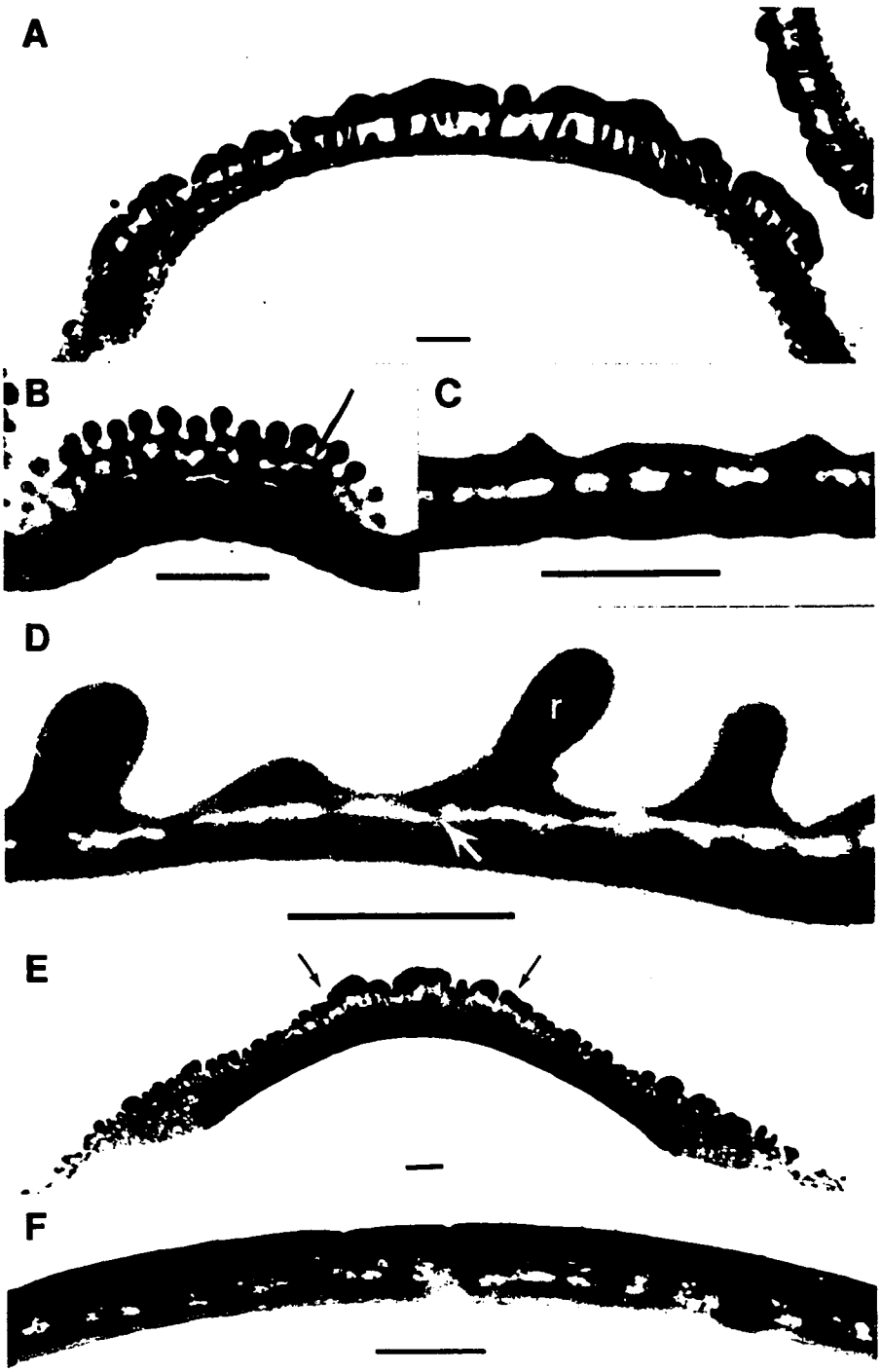
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Figure 6. Transmission electron micrographs of pollen from Lythraceae (A,D), Alzateaceae (B,C), and Punicaceae (E). A. Lafoensia punicifolia. Section through the polar cap (left of bracket) and apertural field. In the apertural field, the verrucae (v) are composed of a thick tectum and short, perpendicular columellae. Between the verrucae the surface granules (g) of SEM (Figs. 3D-F) are supported by columellae. The foot layer is well developed and has an irregular upper margin. The endexine is thick and more densely stained than the ektexine. Toward the polar cap the tectum is continuous and has a finely granular layer below it. The columellae are shorter and the foot layer is thicker than in the apertural field. The endexine decreases in thickness from right to left (i.e. toward the polar cap). X 16,100. (See additional comments to Figs. 5E,F and also Muller, 1981, Pl. IV). B,C. Alzatea verticellata. B. Section of a portion of the mesocolpium. At the extreme right is the colpus. The foot layer is highly irregular and forms "hills" (double arrow) and "valleys". The thickness and shape of the tectum is in direct correspondence with that of the foot layer, between them is a more or less uniform, columellae layer. Near the colpus, the tectum is thin, the columellae are short and the foot layer is extremely thin. The endexine, which is relatively thin in the mesocolpium, is very thick in the colpus. X 21,100. C. A continuation of the section in Fig. B to show the middle portion of the mesocolpium. Here, the entire exine decreases in thickness. The tectum is thinner than the surrounding areas and more perforate. The columellae either remain the same or slightly increase in length and are branched near the base of the tectum. The foot layer is either absent or present only as thickened bases of columellae. The endexine has increased in thickness, although considerably less so than in the colpus region. X 21,100. D. Rhynchocalyx lawsonioides. The section is near the end of a colpus or pseudocolpus and includes

portions of two mesocolpia. The arrow indicates granules at the inner (lower) margin of the tectum (see also Muller, 1975, Pl. VII, Fig. 1-3). X 21,100. E. Punica granatum. Section of a mesocolpium. X 12,900. Scales equal 1 μm.

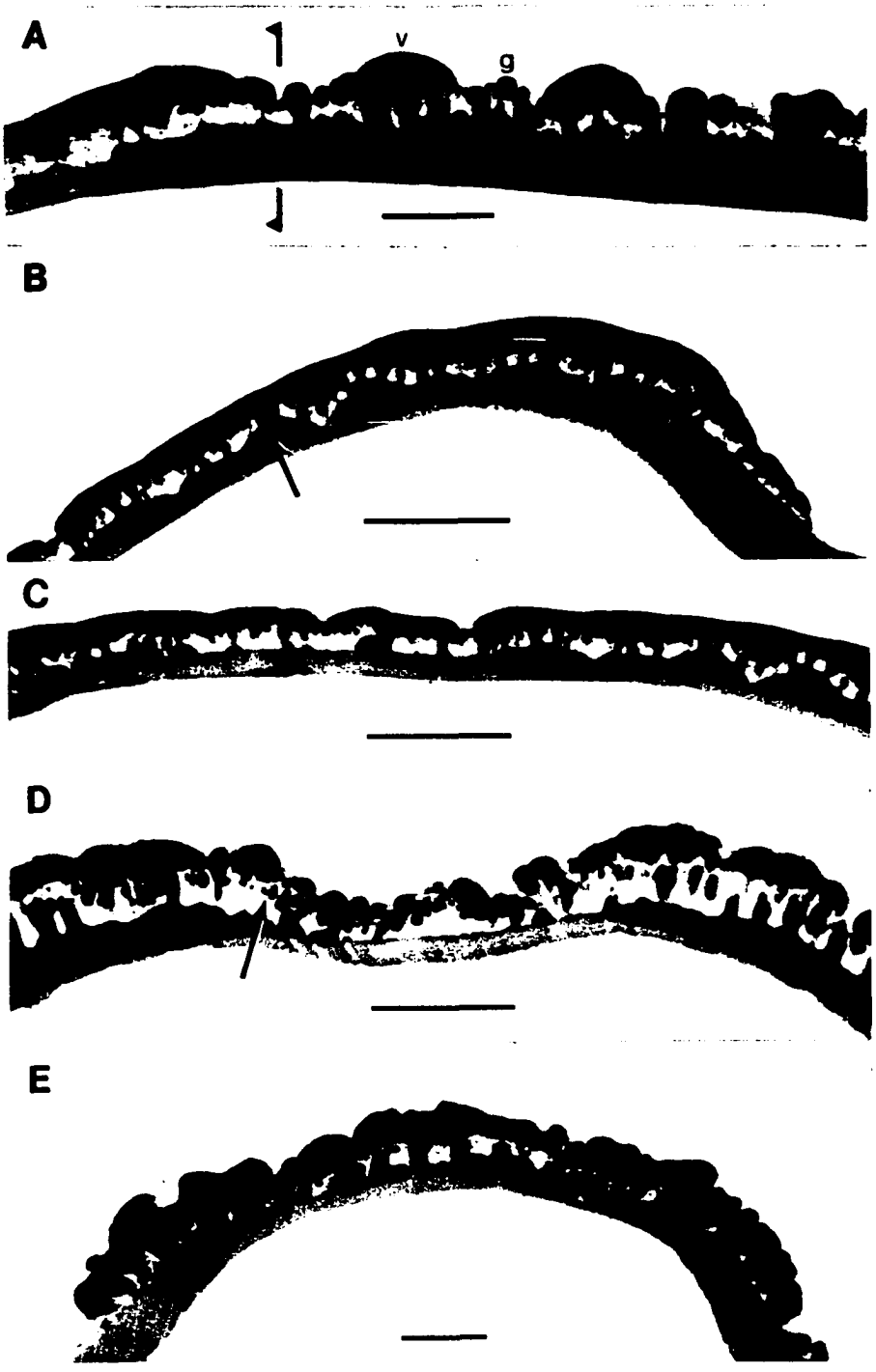
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Figure 7. Scanning electron micrographs of Trapaceae pollen. A-F. Trapa natans. A. (Engelmann s.n.). Lateral view showing three meridional ridges. The vertically cracked area of the dome in the central ridge exposes part of the colpus. X 1,000. B. (Engelmann s.n.). Polar view. The three protruding domes (arrows) are covered by meridional ridges, which in turn, are united at the pole. X 1,000. C. (House 21708). Lateral view of the area between two meridional ridges. Note that the ridges are continuous over the domed areas. The two-part nature of the ridge is indicated by the stars: the open star shows the upper part which is highly folded, the solid star shows the lower part which is granular. X 1,000. D. One sample of T. natans (House 21708) contained numerous fused grains (polyads). A part of such a polyad is shown here. X 800. E. (House 21708). Enlarged area of Fig. 7D showing fusion of two adjacent exine surfaces. X 2,300. F. (House 21708). Extexinous bridges appear to be another mechanism of pollen grain adhesion: the arrow shows a bridge connecting the meridional ridges of two pollen grains. X 1,700. Scales equal 1 μm.

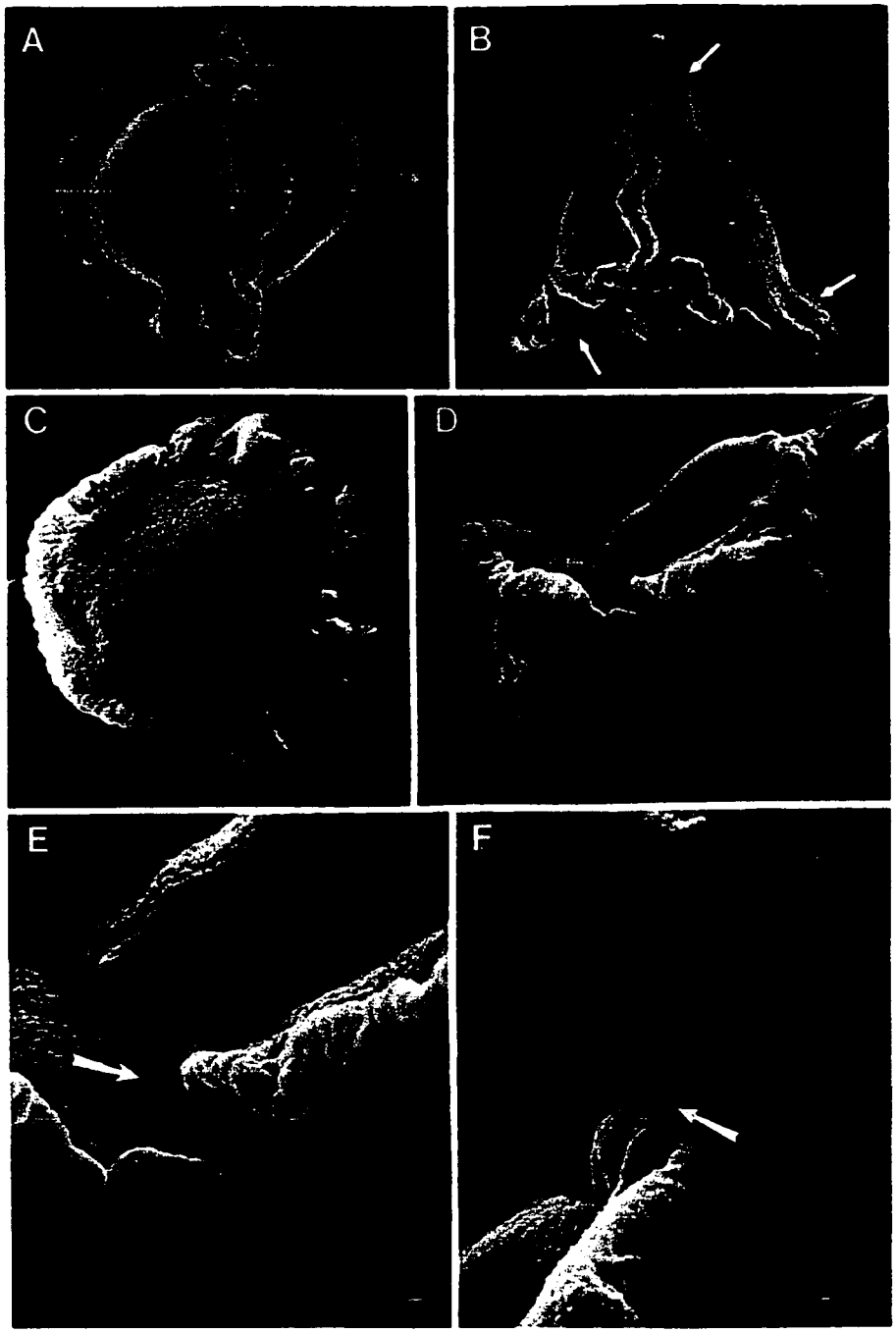
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Figure 8. Scanning electron micrographs of Trapaceae pollen. A-D. Trapa japonica. A. Lateral view with a domed area (arrow) and a meridional ridge that passes over it (in this grain the ridge is discontinuous at the equator). The maximum height of the ridge is at the poles. An elongated lens-shaped colpus is enclosed within this domed area which is only visible with light microscopy (Erdtman, 1943, Pl. XIII, Figs. 221-223). X 760. B. Polar view showing three protruding, domed areas (arrows) and the three ridges that unite at the poles. X 880. C. Surface detail of Fig. 8A. X 1,800. D. Close up of domed area which has split horizontally. X 1,800. E,F. Trapa natans. E. (MO 2532983). Close up of domed area (arrow) which is less prominent than in T. japonica (see Figs. 8A,C,D). The ridge is composed of verrucate, granular elements. X 1,700. F. (Engelmann). View showing irregular splitting of the ridge in the dome area. X 3,000. Scales equal 1 μm.

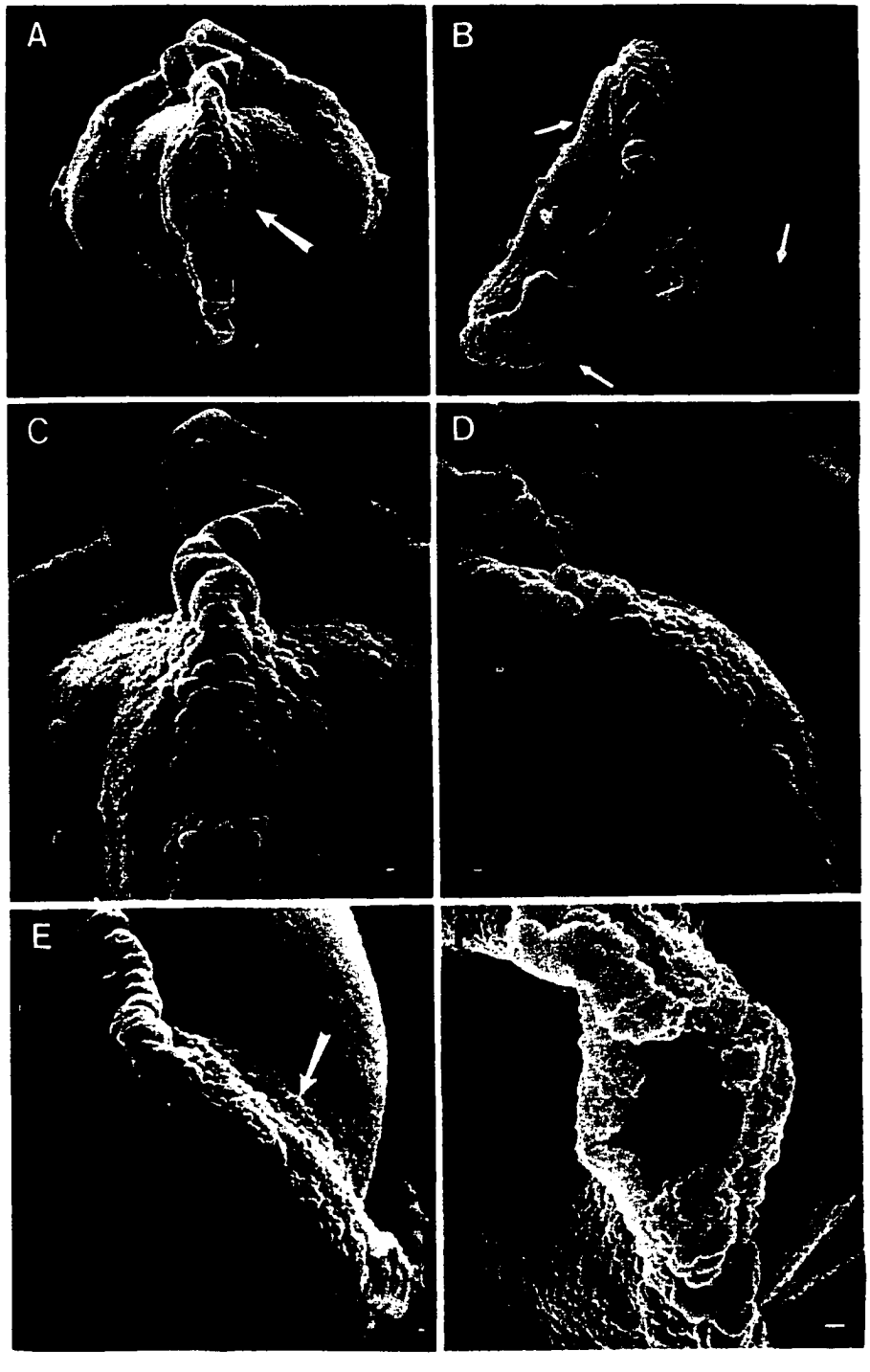
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Figure 9. Transmission electron micrographs of Trapaceae pollen. A-C. Trapa natans. A. (Engelmann s.n.) Section of the meridional ridge with cavity (star) and surrounding area. The upper portion of the ridge (within bracket) is essentially homogeneous; the lower portion has a clavate layer (CL) over an expanded granular layer (G). Large, solid, irregular elements (unlabeled arrow) are present at the base of the ridge cavity. The endexine (en) is extremely thick and uniform. X 10,100. B. (House 21708). Section of colpus. The endexine is thick, granular (star) and finely lamellate. The absence of endexine (bracket) indicates a colpus which is a lens-shaped meridional area (not evident here, see Fig. 8A legend discussion). This area is covered by clavae and a coarsely granular layer (arrow). X 10,100. C. (House 21708). Two sections of the mesocolpium. The ektexine is thin and composed of tightly packed clavae with a "fuzzy" basal layer (arrowhead). The foot layer cannot be readily distinguished and the endexine is thick (significantly thicker than the ektexine). X 7,800. D. Trapa japonica. Section of a mesocolpium. X 13,900. In all TEM preparations of Trapa pollen, the endexine has shown little, if any, difference in electron density from the ektexine. Further studies, particularly with fresh pollen, should help to clarify this exine layer, as well as the presence or absence of the foot layer. Scales equal 1 μm.

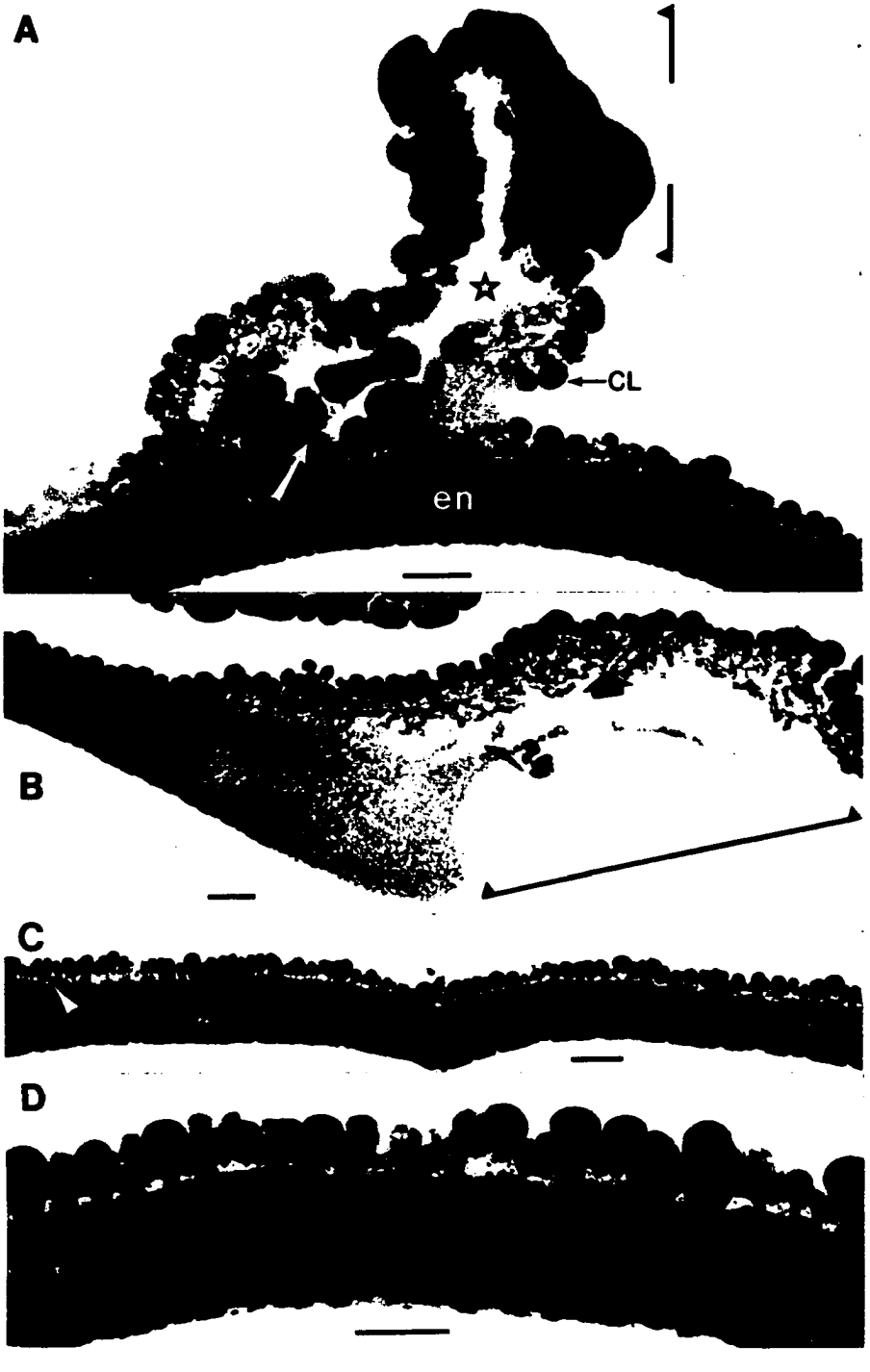
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Figure 10. Scanning electron micrographs of Oliniaceae pollen. A-C. Olinia radiata. A. Polar view showing the hemisphere without pseudocolpi. X 2,000. B. Lateral view. The colpus is asymmetrical with the long arm extending into the hemisphere that does not have pseudocolpi (lower half in this figure) and the short arm extending into the hemisphere that has the pseudocolpi (a pseudocolpus is indicated between arrows). An elliptic, lalongate endoaperture is discernible. X 2,000. C. Polar view showing the hemisphere that has three pseudocolpi alternating with the short arms of the colpi. X 1,600. D-F. Olinia rochetiana. D. Subpolar view. Arrow points to a partially visible pseudocolpus. X 2,000. E. Polar view. Pseudocolpl with a rugulate-granular surface alternate with short arms of the colpi. X 2,100. F. Polar view of the hemisphere that does not have pseudocolpi. X 2,000. Scales equal 1 μm.

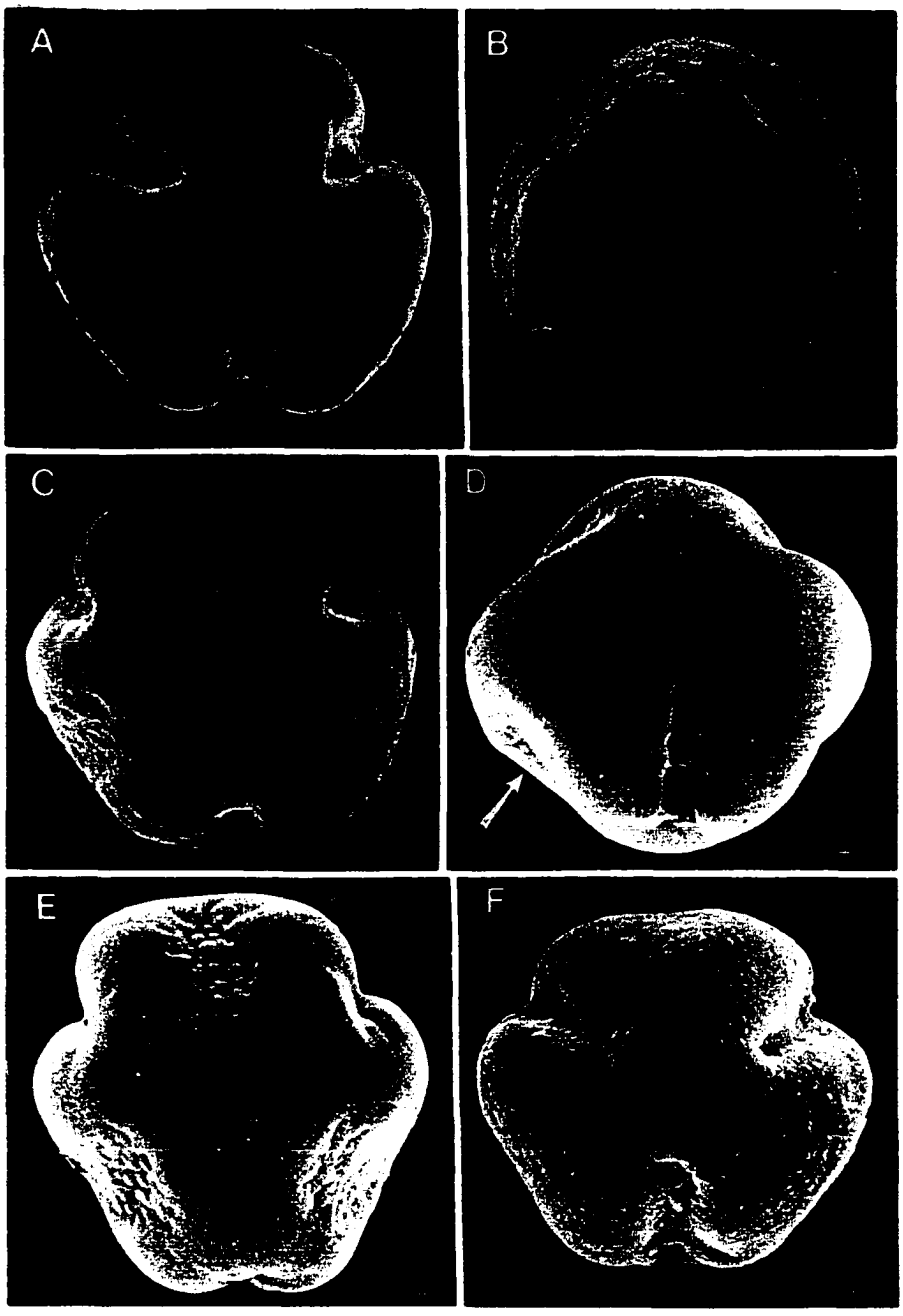
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Figure 11. Scanning electron micrographs of Oliniaceae pollen. A-D. Olinia emarginata. A. Lateral view clearly showing two pseudocolpi (arrows) alternating with the short arm (S) of the colpus on the lower hemisphere. The upper hemisphere has the long arm (L) of the colpus and no pseudocolpi. X 2,000. B. Subpolar view showing the hemisphere that lacks pseudocolpi. The long arms of the three colpi are visible (arrows). X 2,000. C. Details of part of the colpus of Fig. 11A. X 5,000. D. Details of a pseudocolpus showing a rugulate smooth exine surface with irregularly branched channels. X 15,000. E,F. Olinia ventosa. E. View of a pseudocolpus with a rugulate surface. X 7,000. F. Lateral view showing two pseudocolpi, asymmetrical colpus, and psilate exine surface. X 2,000. Scales equal 1 μm.

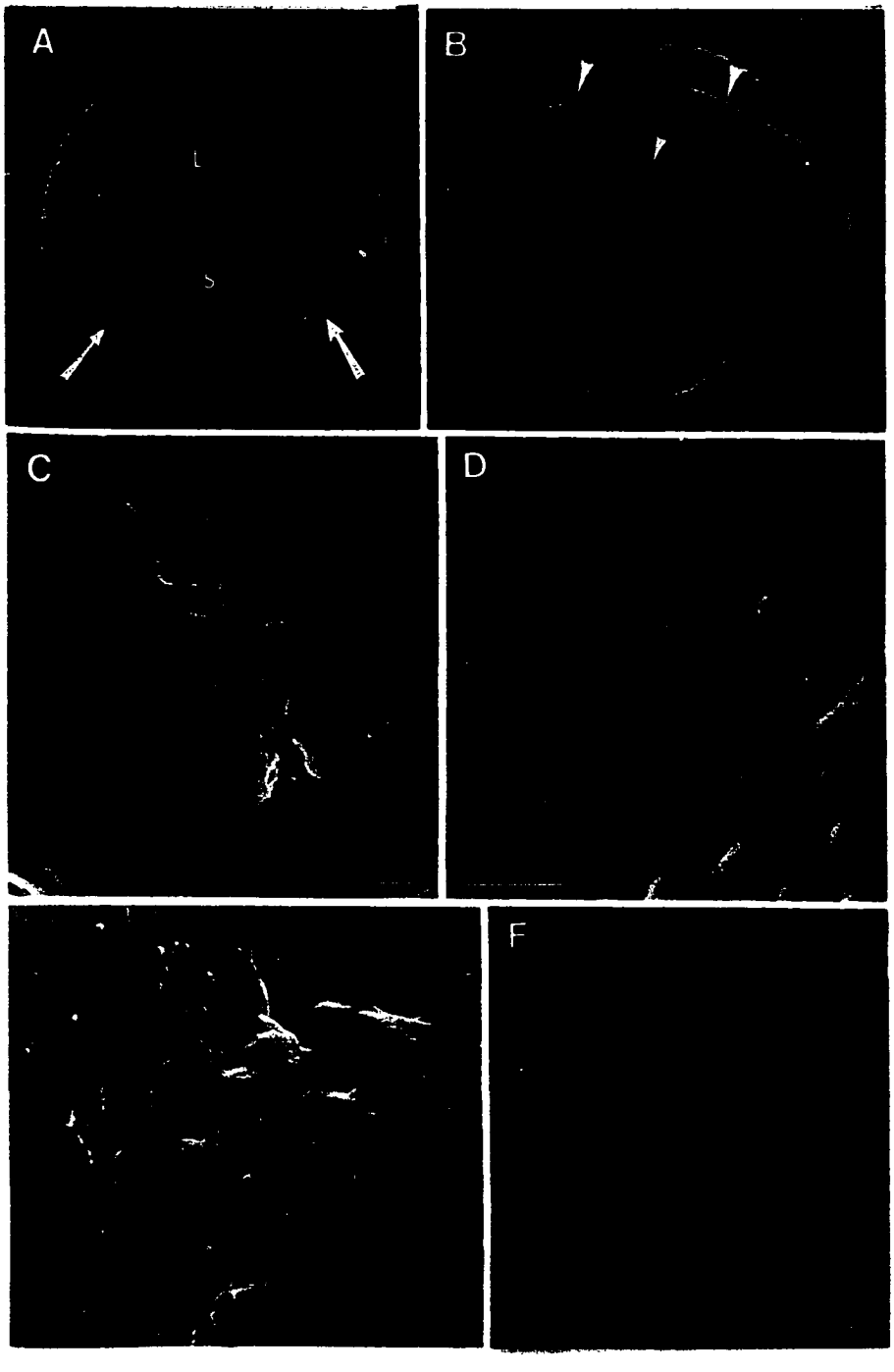
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Figure 12. Transmission electron micrographs of Oliniaceae pollen. A. Olinia rochetiana. Section of pseudocolpus. The rugulate surface elements described in SEM (Fig. 10E) appear in TEM as a dome-shaped tectum below which is an infratectal granular layer. Columellae are absent and the foot layer (arrowhead) is narrow but consistant over the pseudocolpus. The endexine (en) is thick and uniform. X 17,100. B,C. Olinia ventosa. B. Section of a mesocolpium. The tectum is uniform, thick and imperforate. The arrow indicates an infratectal granular layer immediately beneath the tectum. Columellae are extremely short. The foot layer is nearly as thick as the tectum and the underlying endexine is uniform and approximately one half the thickness of the foot layer. X 10,350.
C. Section includes a mesocolpium (right of bracket) and part of pseudocolpus (left of bracket). Note the prominent thickening of the endexine under the pseudocolpus. X 16,000. D. Olinia rochetiana. Section through the aperture region including part of the endoaperture (at the left). The mesocolpial extension over the endoaperture is indicated by the bracket. The thick tectum is gently undulating and imperforate; the infractetal granular layer is prominent and is supported by short but stout columellae. The foot layer (fl) is thickened at the endoaperture margin; similarly, the endexine also is thickened as well as being markedly granular. X 11,900.
E. Olinia emarginata. Section passing through endoaperture. The arrow within the endoaperture indicates free "hanging columellae" and disrupted foot layer typical of this area. Note underlying granular endexine. X 11,300. The sections in Fig. 12 resemble the sections of Penaeaceae pollen in Fig. 20. Scales equal 1 μm.

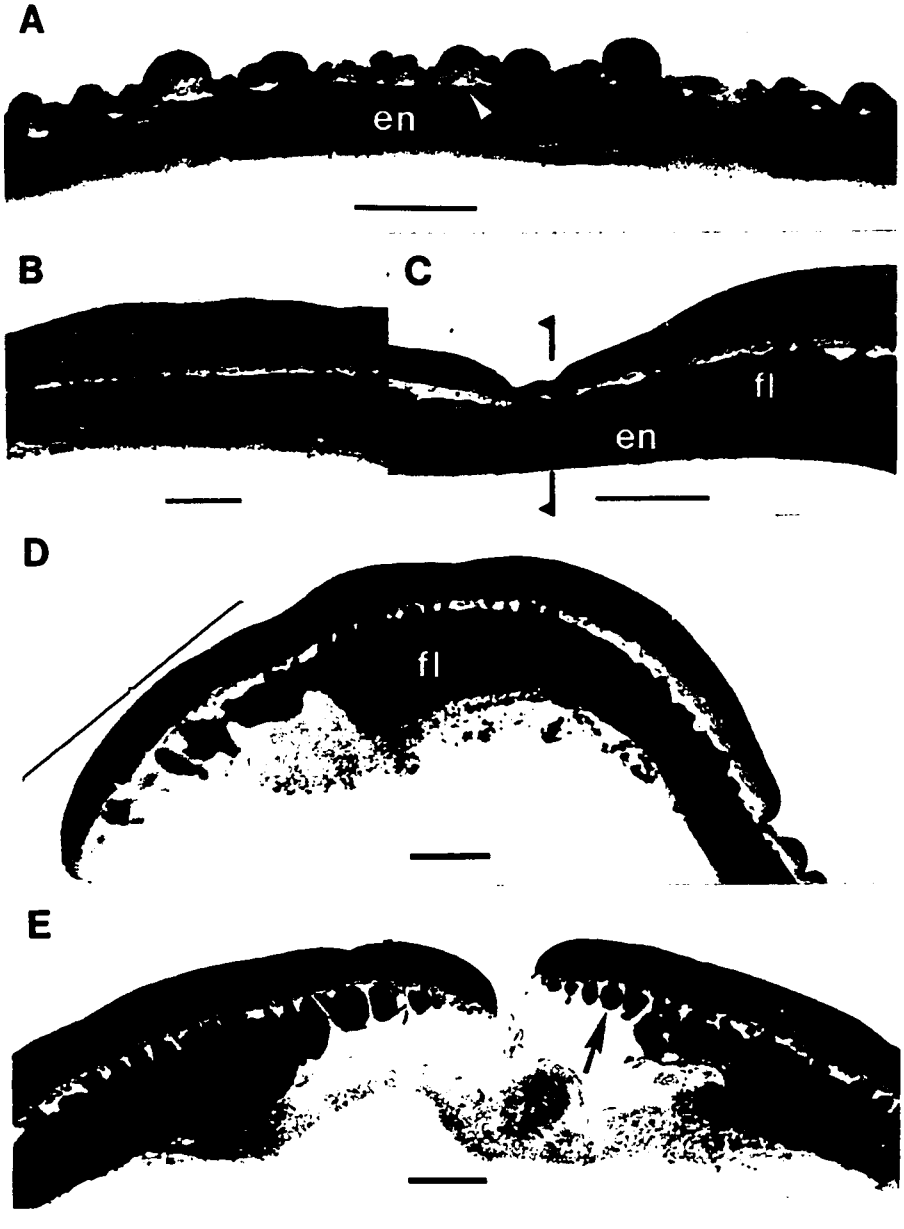
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Figure 13. Scanning electron micrographs of Combretaceae pollen.

A-C. Combretum cacoucia. A. Polar view showing three colpi with extensions of mesocolpia over the endoapertures and three pseudocolpi. X 1,600. B. Lateral view. The endoaperture appears as a wide elliptic shadow. The colpus membrane is granular. Two pseudocolpi are also visible. X 1,600. C. Finely rugulate surface in polar view. X 5,000. D,E. Thiola inundata. D. The exine surface consists of echinate plate-like areas that are delimited by channels and punctae. The colpus has echinae over the endoaperture (arrow). X 10,700. E. Subpolar view showing three apertures and three pseudocolpi. X 3,150. F. Quisqualis indica. Polar view. The three pseudocolpi are wide and appear to be more like intercolpar concavities. X 1,600. G. Calycopteris floribunda. Sublateral view showing a pseudocolpus (center) alternating with colpi. The exine surface is rugulate. X 2,800. Scales equal 1 μm.

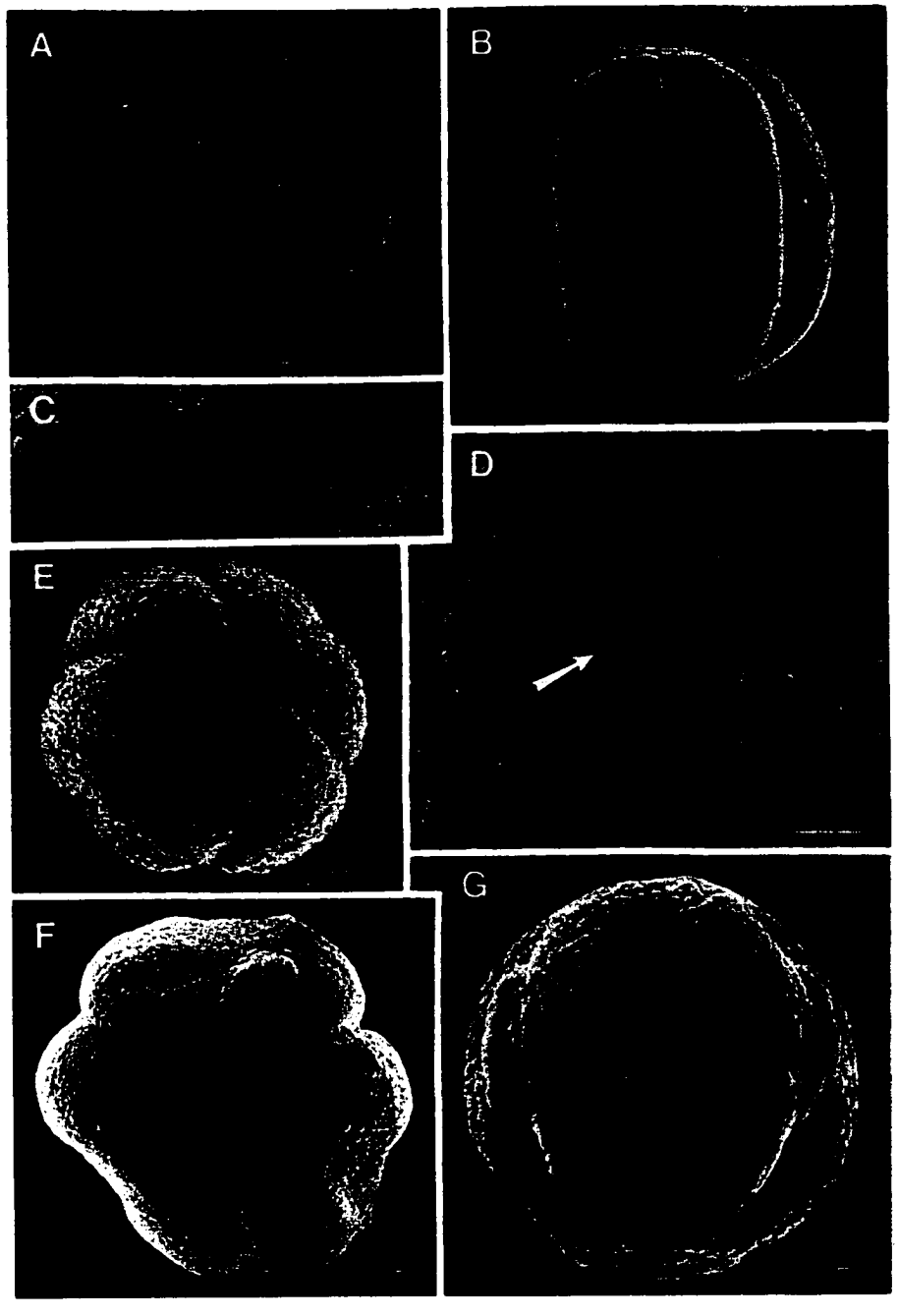
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Figure 14. Scanning electron micrographs of Combretaceae pollen. A. Bucida macrostachya. Lateral view showing a colpus (at center) and two pseudocolpi. X 4,000. B. Conocarpus erecta. Polar view with mesocolpial extensions over the apertures. Also note three pseudocolpi. X 5,000. C. Pteleopsis myrtifolia. Lateral view with a colpus (at center) and two pseudocolpi. X 3,000. D. Terminalia edulis. Lateral view with a colpus (at center) and two pseudocolpi. X 3,000.

E,G. Ramatuella argentea. E. Lateral view with a pseudocolpus (at center) and two colpi. X 3,000. G. Surface detail of a rugulate pseudocolpus. X 21,000.

F. Terminalia catappa. Surface of the mesocolpium near colpus and endoaperture (triangle). Elongate, branched, interwoven elements form the surface sculpture. X 10,000. Scales equal 1 μm.

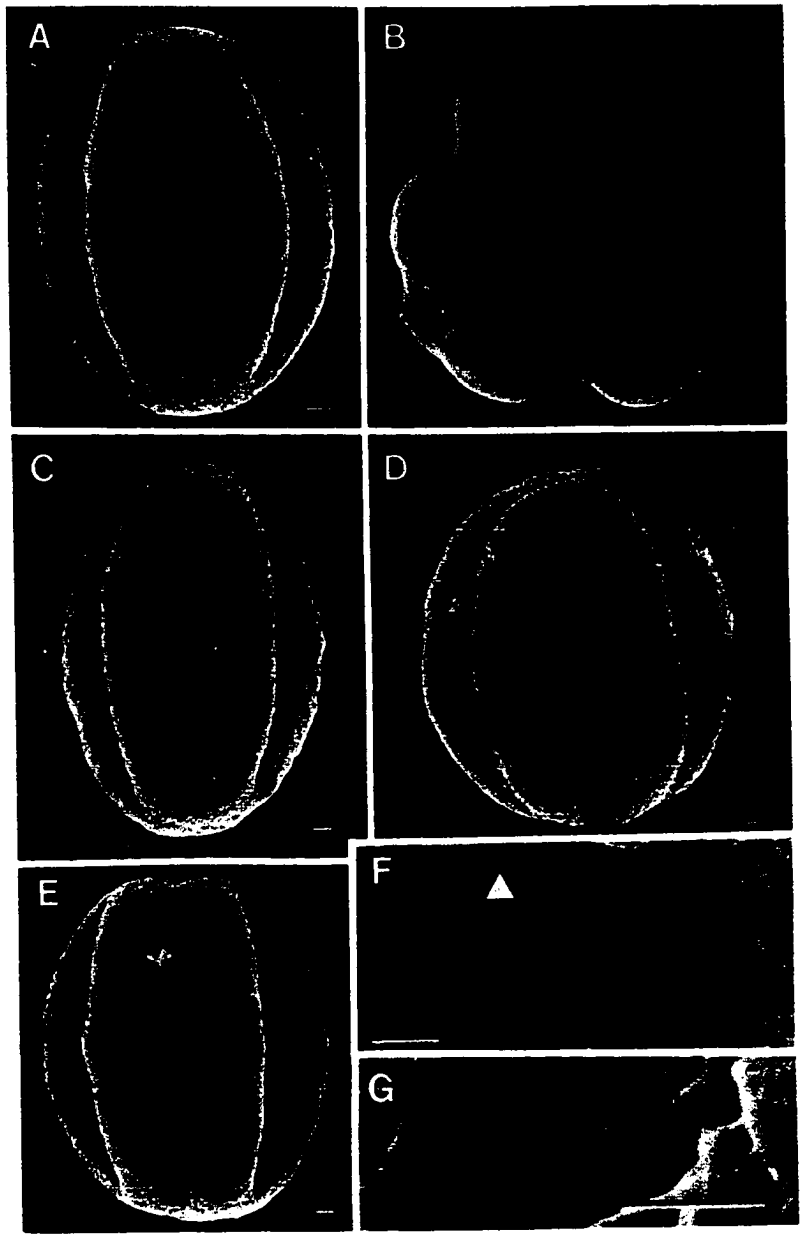
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Figure 15. Scanning electron micrographs of Combretaceae pollen.

A-C. Buchenavia suaveolens. A. Polar view. Colpi are narrow (pseudocolpi are absent) and the surface is echinate. X 4,000. B. Lateral view. X 3,000. C. Details of the echinate-punctate surface. X 17,600. Note similar surface in T. inundata (Fig. 13E). D,F. Anogeissus acuminata. D. Lateral view with a wide and granular pseudocolpus (at center). Two colpi are also evident. The exine surface is echinate. X 4,000. F. Polar view showing colpi alternating with pseudocolpi. X 5,000.

E. Guiera senegalensis. Lateral view with a colpus at center and two pseudocolpi. The exine surface is striate. X 4,000. Scales equal 1 μm.

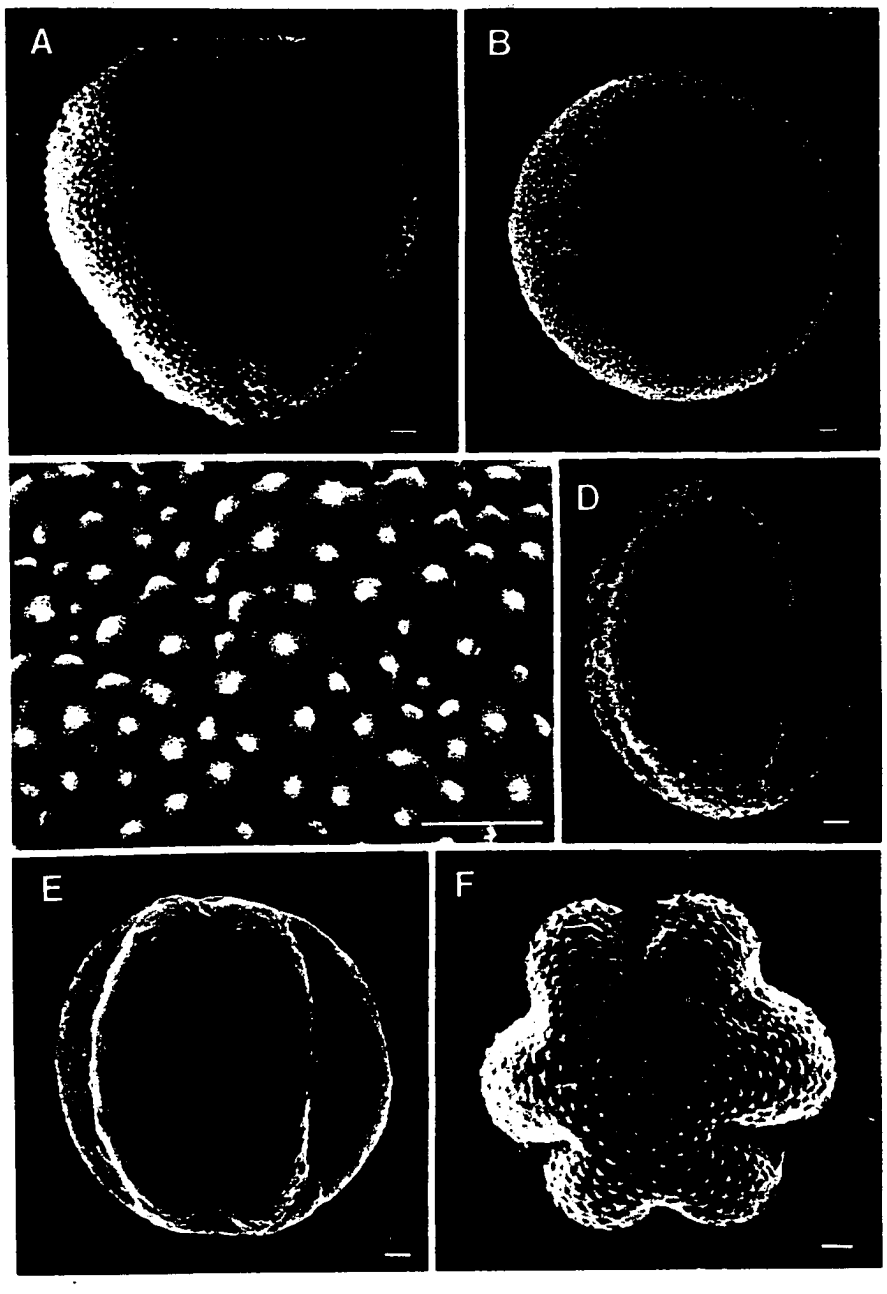
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Figure 16. Scanning electron micrographs of Combretaceae pollen.

A,B. Strephonema pseudocola. A. Lateral view. The exine surface is reticulate with lumina becoming smaller toward the colpus. The partially opened endoaperture is lalongate-elliptic. X 3,000. B. Detail of the surface showing rod-shaped elements in the large lumina. X 10,000. C. Poivrea coccinea. Sublateral view. The circular endoaperture (dark area) is clearly evident through the ektexine. The colpus and pseudocolpus membrane are granular. The surface is striate (cf. with striate surface of G. senegalensis, Fig. 15E). X 3,000. D. Lumnitzera racemosa. Lateral view showing colpus with open endoaperture and two pseudocolpi. The surface is rugulate. X 2,700. E,F. Laguncularia racemosa. E. Lateral view. Colpi are narrow with a granular surface (pseudocolpi are absent). X 2,700. F. Surface detail near an open endoaperture. The surface is punctate. X 7,000. Scales equal 1μm.

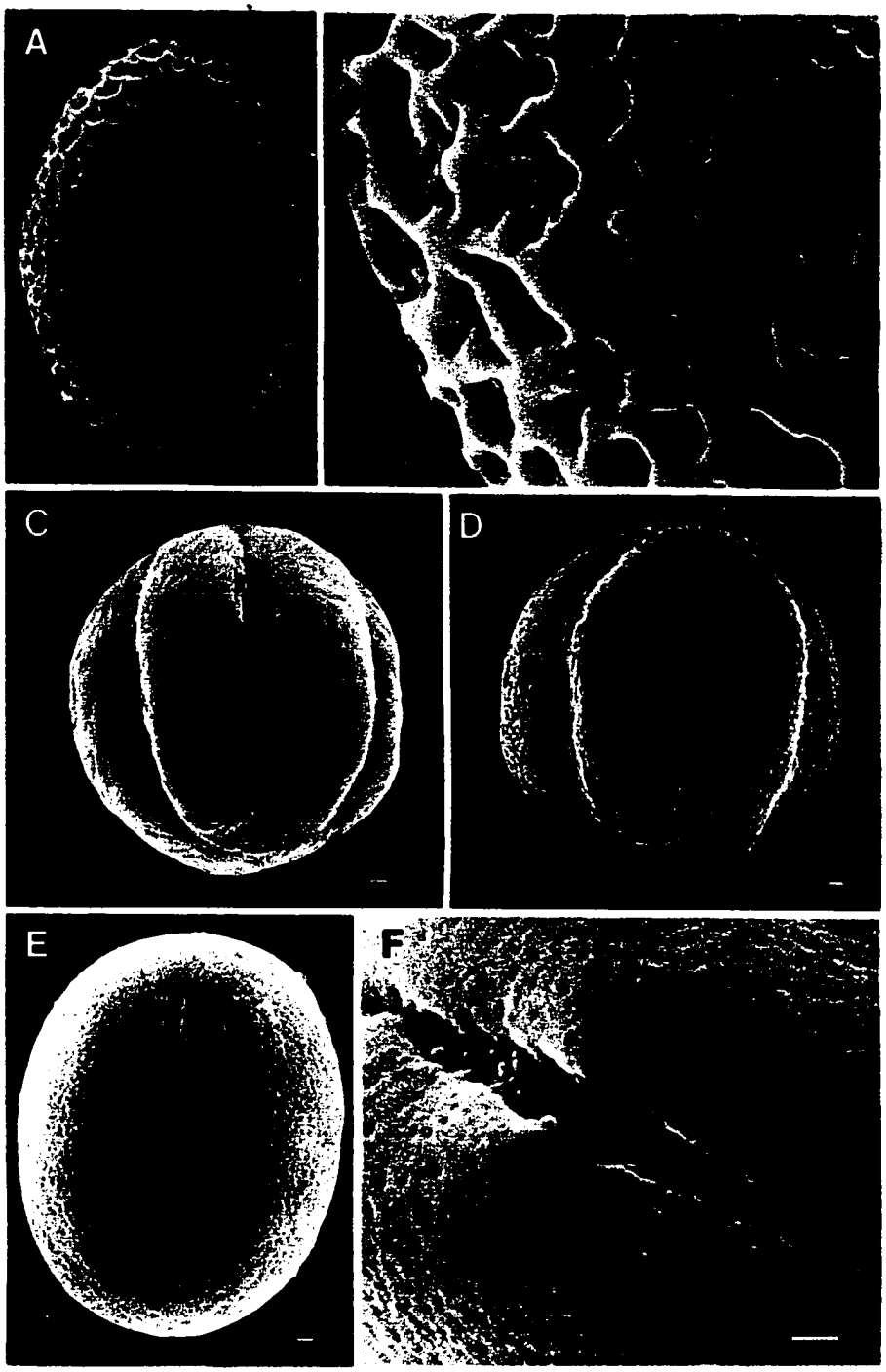
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Figure 17. Transmission electron micrographs of Combretaceae pollen.

A. Combretum laxum. Section of two adjacent mesocolpia and a colpus or pseudocolpus between them. Note the thick, dome-shaped foot layer. The endexine is thicker below the colpus (or pseudocolpus) than below the mesocolpia. X 15,800. B,C. Combretum farinosum. Section through a portion of a mesocolpium (on the right) and a portion of a pseudocolpus (on the left). Note the granular matrix between the columellae. In the pseudocolpus the tectum is thin and discontinuous and the endexine (en) is greatly thickened. At the mesocolpial margin the thick foot layer (fl) tapers toward the pseudocolpus. X 28,400. C. Aperture region showing a thick, granular matrix covered by a fine membrane. Columellae are embedded in the matrix: the lower ends are free and the upper ends protrude as granules on the colpus surface. The foot layer appears to consist of fragmented lamellae. The endexine (arrows) is suggested by a slightly coarser, granular, narrow band at the lower most margin. X 28,400. D. Terminalia edulis. Section includes two mesocolpia and the colpus or pseudocolpus between them. Note the dome-shaped foot layer (identical to C. laxum, Fig. 17A). A "white line" separates the foot layer and endexine. The endexine is thick below the colpus or pseudocolpus and thin elsewhere. X 19,400. E. Conocarpus erecta. Section of two mesocolpia and the pseudocolpus between them. Although the foot layer is thin and discontinuous in this section, other sections show it to be dome-shaped in the mesocolpia (similar to Figs. 17A and 17D). X 20,500. The striking dome-shaped foot layer in Figs. 17A,D is also present in Melastomataceae pollen (see Figs. 25-27). Scales equal 1 μm.

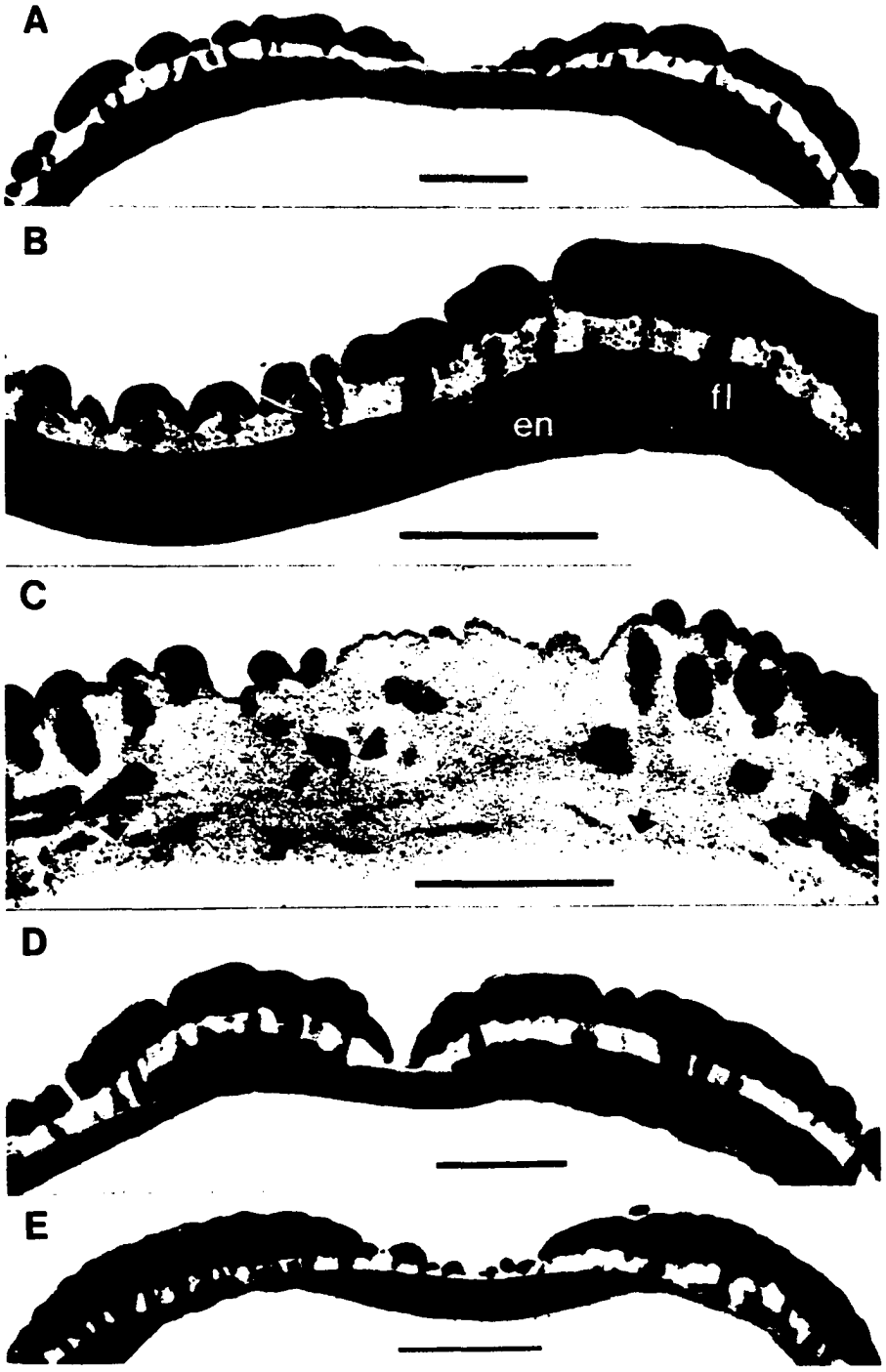
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Figure 18. Scanning electron micrographs of Penaeaceae pollen. A-C. Penaea mucronata. A. Lateral view with colpus at center. Note the irregular development of the pseudocolpi. The pseudocolpus at the left appears to unite with other pseudocolpi at the top pole while at the bottom pole it is free. The pseudocolpus at the right appears to unite with pseudocolpi at both poles. (see also Fig. 19E). The exine surface is psilate; in the colpus and pseudocolpus it is granular. X 1,800.
B. Subpolar view showing portions of four colpi alternating with four pseudocolpi. Note the patch of granular exine at the pole. X 1,800. See also SEM of Dahlgren (1971, Fig. 2). C. Sublateral view showing colpi united to form an undulating syncolpus (arrow). Note the two circular endoapertures as well as fused pseudocolpi (i.e., "synpseudocolpi"). X 1,800. D-F. Stylapterus ericoides. D. Lateral view with a pseudocolpus at center. X 1,800. E,F. Polar views. Four colpi alternate with four pseudocolpi. The pseudocolpi are united at the poles in various combinations. For example, in Fig. 18E the two opposite pseudocolpi are united while in Fig. 18F all four are united. The exine is smooth with few punctae and channels.
E. X 2,000, F. X 2,800. Scales equal 1 μm.

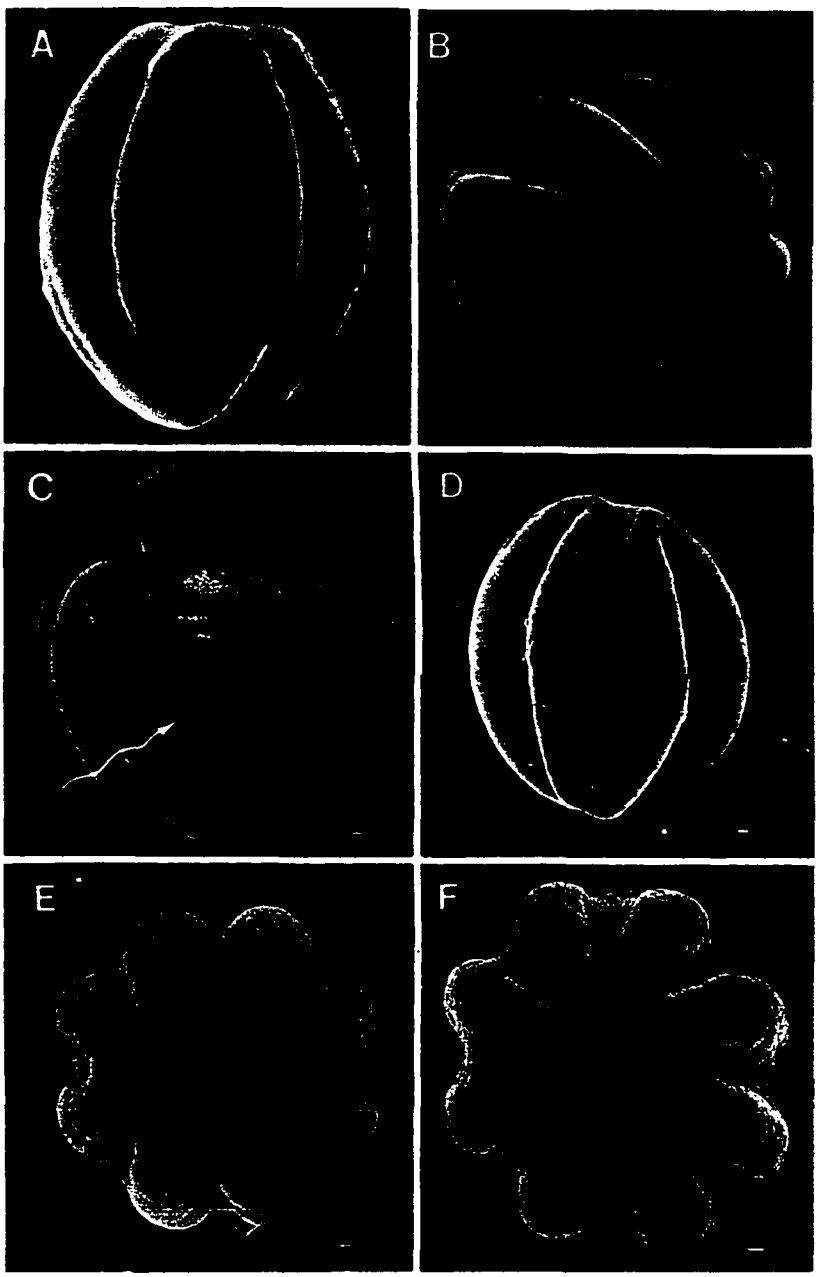
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Figure 19. Scanning electron micrographs of Penaeaceae pollen. A-C. Endonema lateriflora. A. Lateral view. The surface is smooth with many channels and pits while the pseudocolpus has a verrucate-granular surface. X 2,000. B. Elliptic, lalongate endoaperture as viewed from the inside of the pollen grain. The arrows show two lateral extensions of the endoaperture. X 7,000. C. Polar view showing three colpi and three pseudocolpi. Extensions of the mesocolpia are evident over the endoapertures. X 2,000. D. Brachysiphon rupestris. Lateral view with a colpus at the center and two pseudocolpi. The exine surface is psilate while the pseudocolpus is granular. X 2,000. E,F. Sonderothamnus petraeus. E. Lateral view with colpus at center and adjacent pseudocolpi. At the lower pole the two visible pseudocolpi and presumably the pseudocolpus at the back of the pollen grain, appear to be united. At the upper pole the pseudocolpus to the left is not united with other pseudocolpi (see also Fig. 18A). X 1,600. F. View of colpus. An ektexinous bar over the endoaperture gives the false impression of two pores being present within each colpus. Ektexinous bars are also common in some Melastomateceae pollen (see Figs. 22B,C and 23A,C,D). The surface of the mesocolpia is psilate with few pits and channels while the colpus (and pseudocolpus of Fig. 19E) is granular. X 5,000. Scales equal 1 μm.

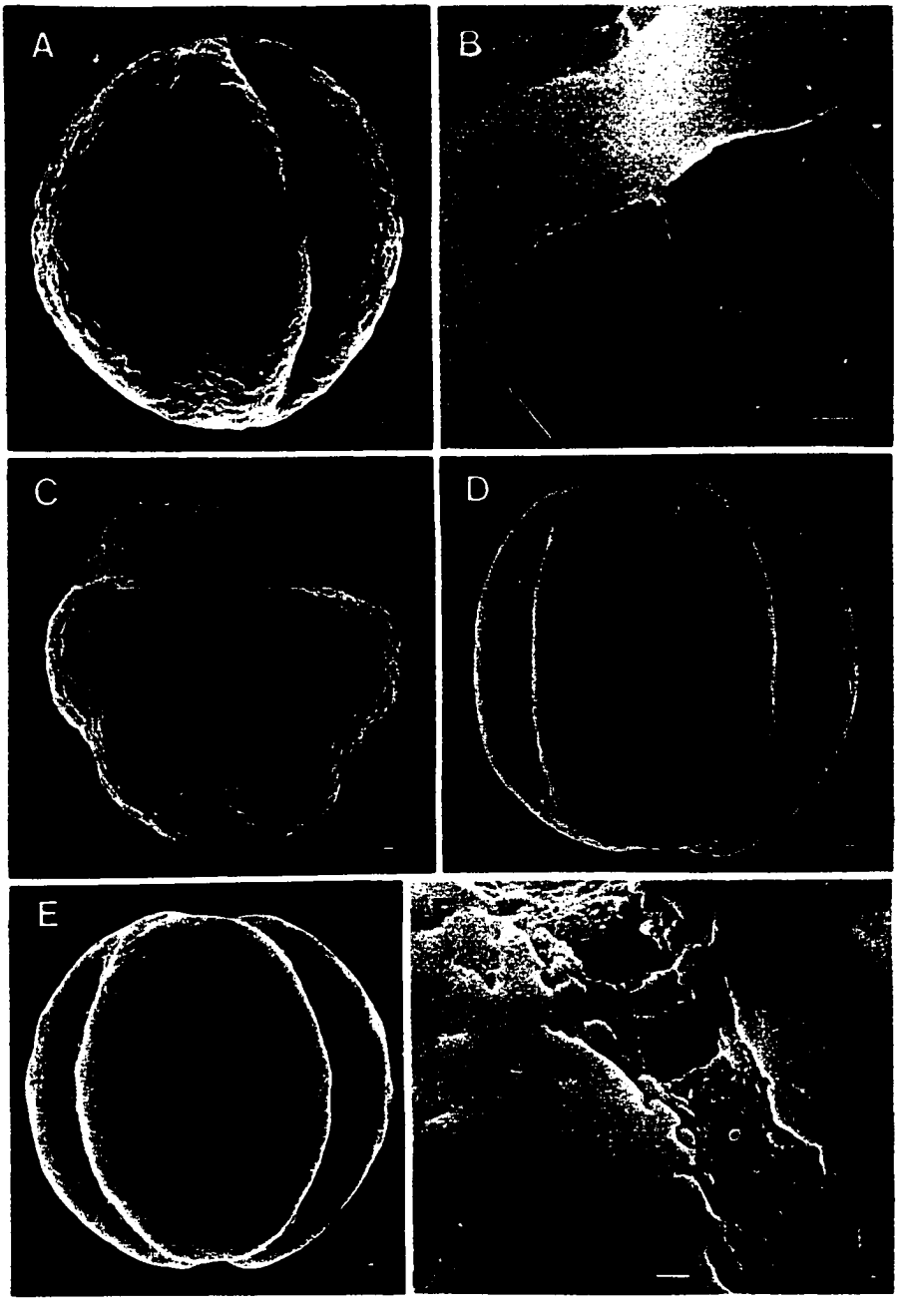
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Figure 20. Transmission electron micrographs of Penaeaceae pollen. A. Penaea mucronata. Section of a mesocolpium with an endoaperture (arrow) on the left and a pseudocolpus on the right. A very thin undulating electron translucent "line" separates the thick tectum from the thick foot layer. Near the endoaperture, both layers are thin and discontinuous; over the pseudocolpus they are extremely thin. The endexine is relatively thin in the middle of the mesocolpium and thick near the pseudocolpus and endoaperture. In the latter area it is also granular. X 14,600. B,C. Sonderothamnus petraeus. B. Section of a mesocolpium. The thick tectum is imperforate. An infratectal granular layer is partially obscurred by osmium precipitate. The foot layer is much thicker than the tectum. The endexine is thin and relatively uniform. X 36,100. C. Section of a pseudocolpus. The tectum is thin with a wavy or lobed outer margin. The infratectal layer is well developed. Immediately below, the foot layer (arrow) appears to be highly disrupted or fragmented. There are no distinguishable columellae. The endexine (en) is as thick or thicker than the ektexine. X 36,100. This section is reminiscent, in a sense, to sections of Onagraceae (See Fig. 42). D. Stylapterus ericoides. Section of a mesocolpium with a pseudocolpus and colpus on either side. Note similarities to Figs. 20A and 20B. The exine sections represented in Fig. 20 should be compared with Oliniaceae sections in Fig. 12. Scales equal 1 μm.

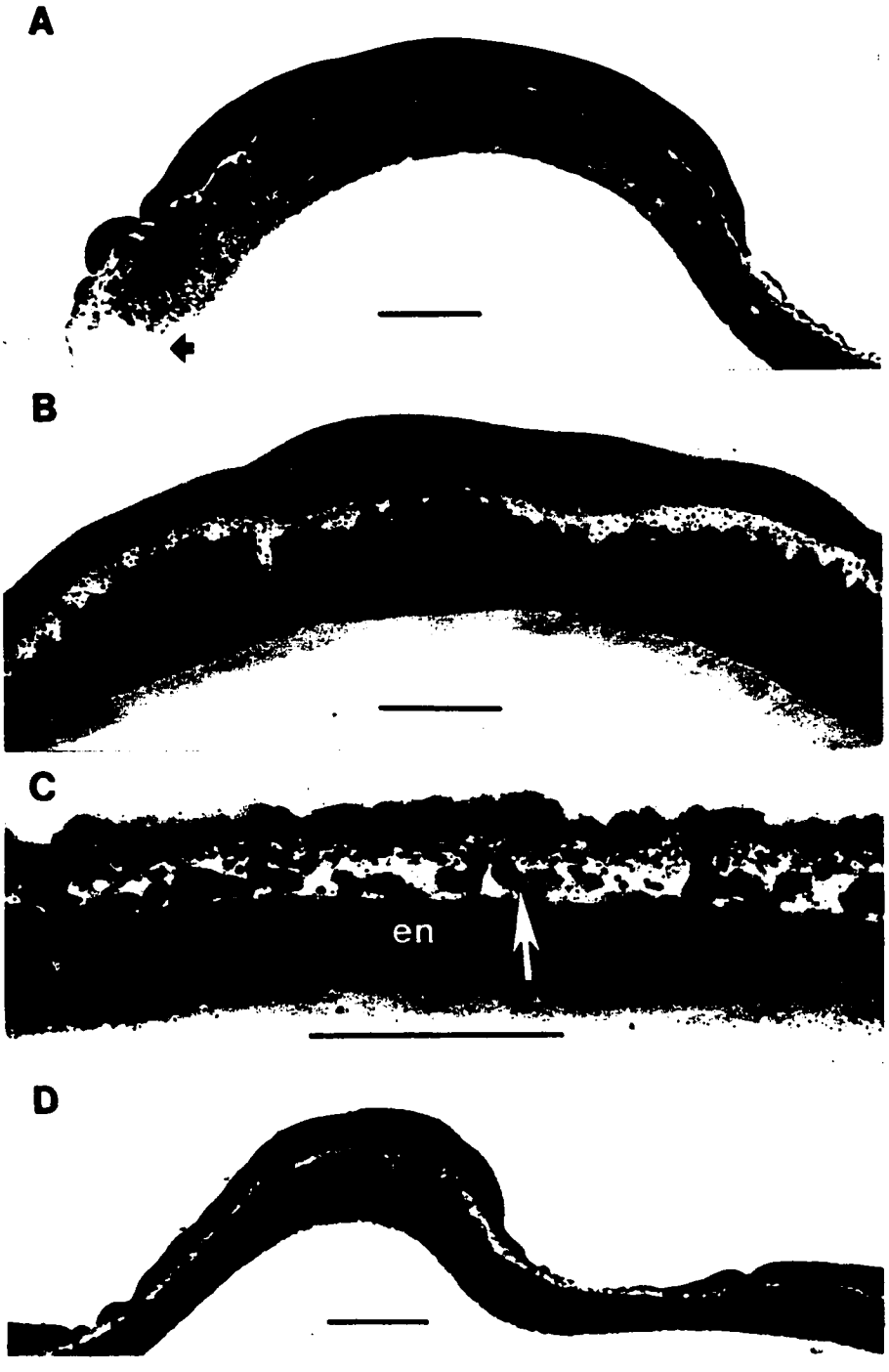
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Figure 21. Scanning electron micrographs of pollen from Crypteroniaceae (A,B) and Melastomataceae (C,D). A. Axinandra zeylanica. Sublateral view. The endoaperture is covered by a raised colpus membrane. X 6,300. B. Dactylocladus stenostachys. Lateral view with a pseudocolpus at the center. The colpus membrane is raised over the endoapertures. The pseudocolpi are united at the poles. X 5,000. Compare also with SEM of Muller (1975, Pl. IV, Figs. 1-3). C. Memecylon normandii. Sublateral view. The surface is rugulate. X 3,800. D. Mouriri glazioviana. Lateral view. Note the elliptic, lalongate, thick-margined endoaperture. The surface is finely rugulate. X 2,300. All pollen grains shown in Fig. 21 have three colpi alternating with pseudocolpi. Scales equal 1 μm.

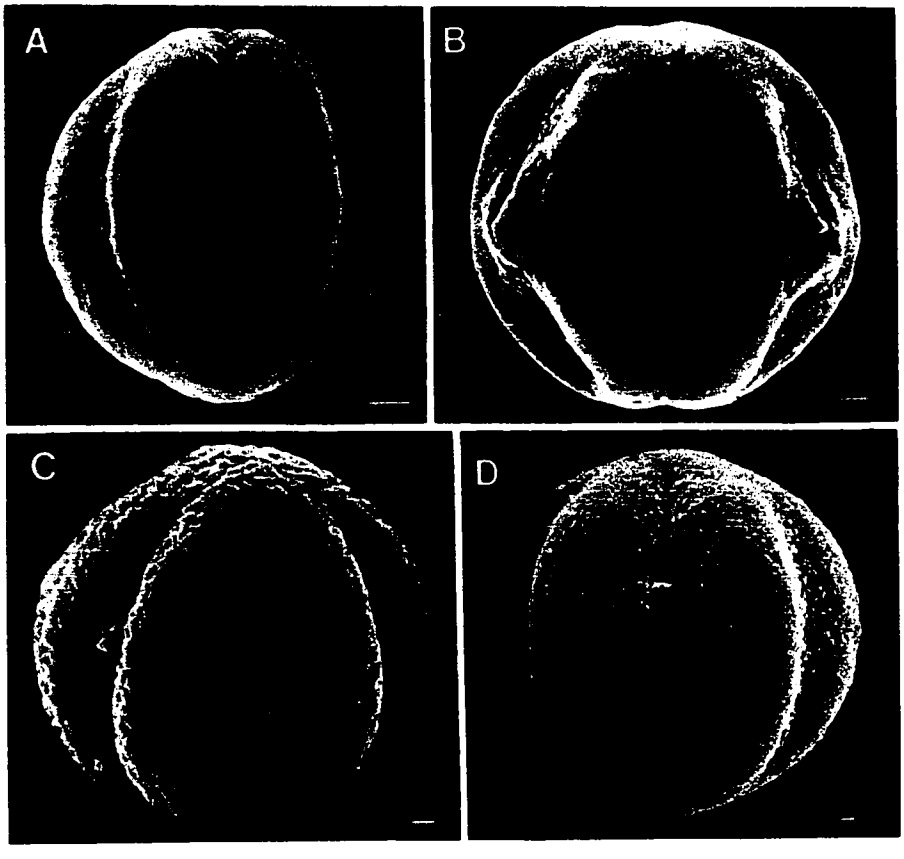
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Figure 22. Scanning electron micrographs of Melastomataceae pollen.

A. Trembleya phlogiformis. Lateral view showing extension of the mesocolpia over the endoaperture (at center) and two pseudocolpi. The exine surface is striate. X 3,000. B. Osbeckia polycephala. Lateral view. The exine surface is rugulate. X 3,000. C. Tibouchina urvilleana. Sublateral view with a pseudocolpus at center. A horizontal ektexinous bar appears to divide the endoapertures into two parts (see legend discussion to Sonderothamnus petraeus, Fig. 19F). X 2,600. D. Tristemma littorale. Polar view. Extensions of mesocolpia are apparent over the endoapertures (arrow). X 4,000. E,F. Votomita monadelpha. E. Lateral view with a pseudocolpus at center. Although not evident in this figure there are four colpi alternating with four pseudocolpi. X 2,000. F. The rugulate surface near the colpus contrasts with bead-like units of the colpus. It also is somewhat similar to the pollen of Boisduvalia (Onagraceae; Figs. 41B,C,E) although it does not appear to be perforate. X 7,000. Scales equal 1μm.

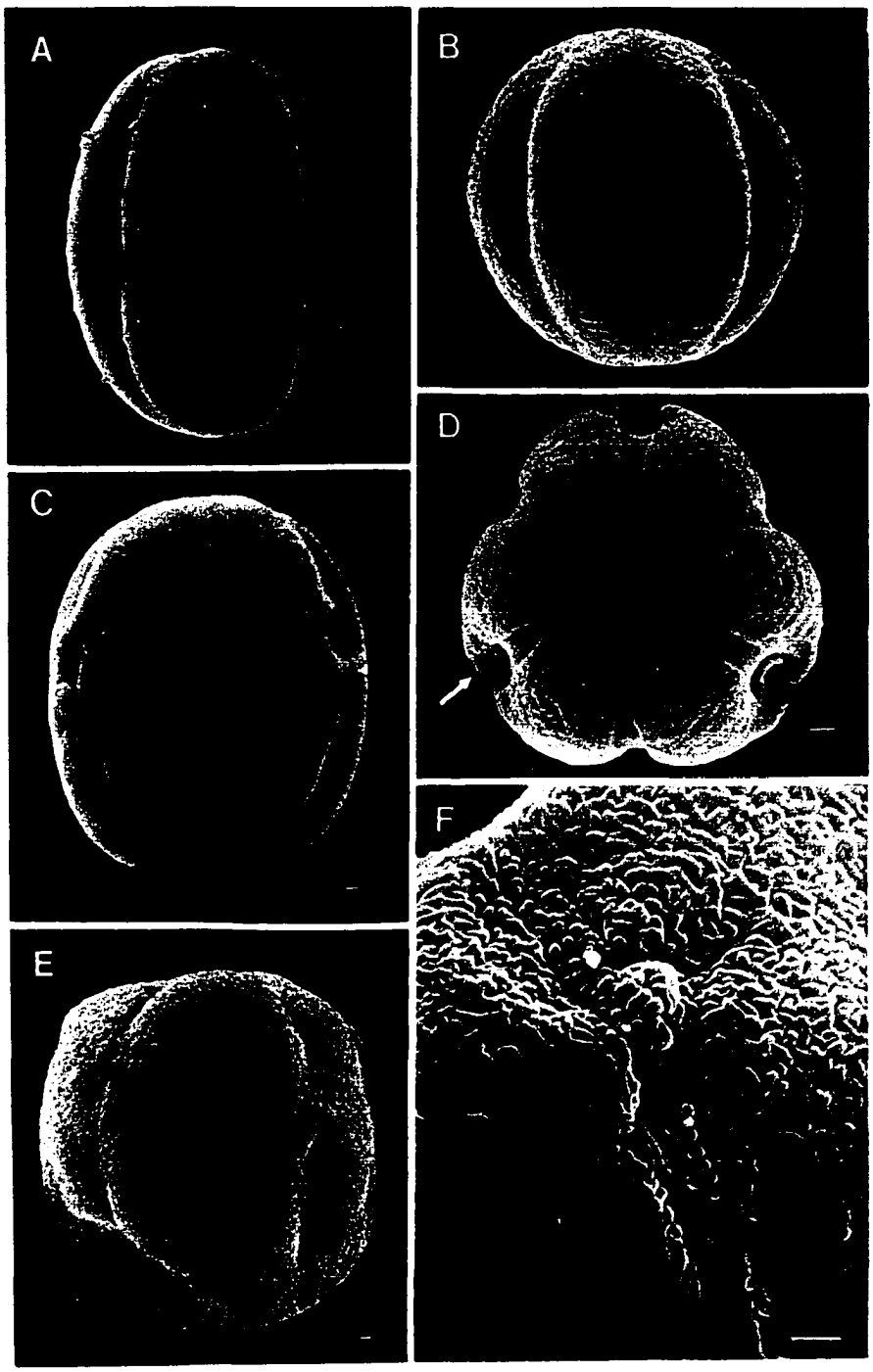
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Figure 23. Scanning electron micrographs of Melastomataceae pollen.

A,B. Marumia nervosa. A. Lateral view showing horizontal bar over endoaperture as described for Fig. 22C. The exine surface is rugulate. X 4,000. B. Details of the granular pseudocolpus and surrounding rugulate mesocolpia. X 10,000.

C,D. Dissotis brazzae. C. Subpolar view. The colpi are united at the pole. The surface is rugulate. X 3,300. D. Lateral view. See discusison to Fig. 22C concerning horizontal bar over endoaperture. E. Acanthella sprucei. Polar view. The surface is smooth with a few channels and pits. Extensions of the mesocolpia over the endoapertures are prominent. X 2,200. F. Dissochaeta celebica. Lateral view. The surface is rugulate. X 5,000. All pollen grains in Figure 23 have colpi alternating with pseudocolpi. Scales equal 1 μm.

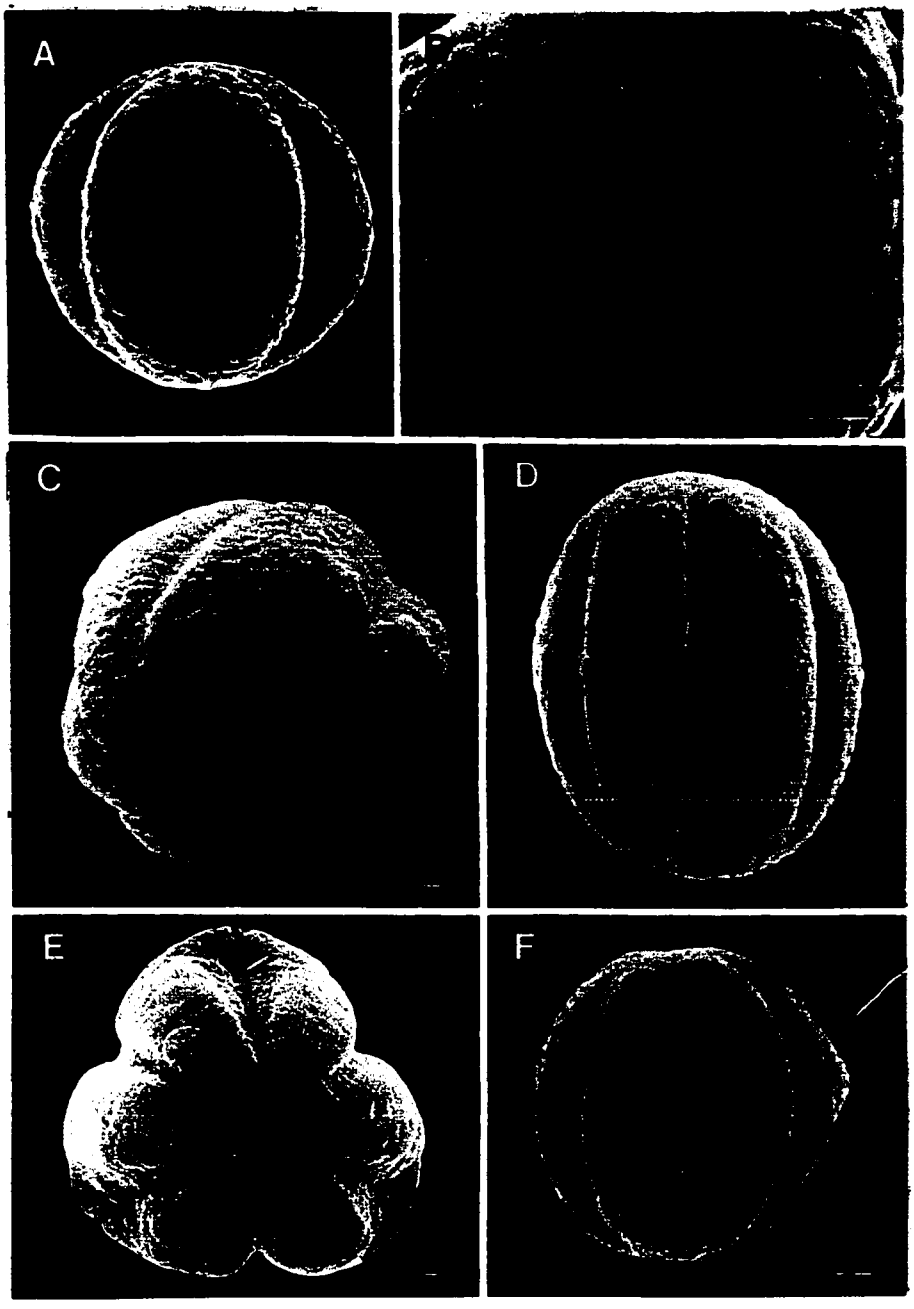
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Figure 24. Scanning electron micrographs of Melastomataceae pollen.

A-C. Adelobotrys tessmannii. A. Lateral view showing an intercolpar concavity with a verrucate surface. The surrounding mesocolpi are narrow and have a psilate surface. The colpi are united at the poles (i.e., syncolpate). X 5,000. B. Lateral view showing a colpus. The colpus membrane is raised over the endoaperture (arrow). X 5,250. C. Polar view showing united colpi with a granular surface. The concave sides of the pollen grain are due to the thin walled intercolpar concavities. In a wet grain they bulge, giving it a circular shape. X 5,100. D. Allomorphia caudata. Lateral view. The colpus is narrow and wide extensions of the mesocolpia are present over the endoaperture. The intercolpar concavities have a verrucate surface. Elsewhere the surface is smooth. X 5,00. E. Astronia cumingiana. Lateral view. The surface is coarsely rugulate. The colpus is very narrow. The surface of the intercolpar concavities is also rugulate but not as coarse as the rest of the grain. X 3,200. F. Bredia hirsuta. Lateral view. The surface is rugulate. The intercolpar concavities are also rugulate but with a finer surface. X 4,050. G,H. Oxyspora paniculata. G. Lateral view. The surface is striate. The colpus is very narrow and long. X 5,000. H. Enlarged view of the intercolpar concavity and the surrounding area. Irregular, flattened elements are present on the surface of the concavity. X 15,000. Scales equal 1 μm.

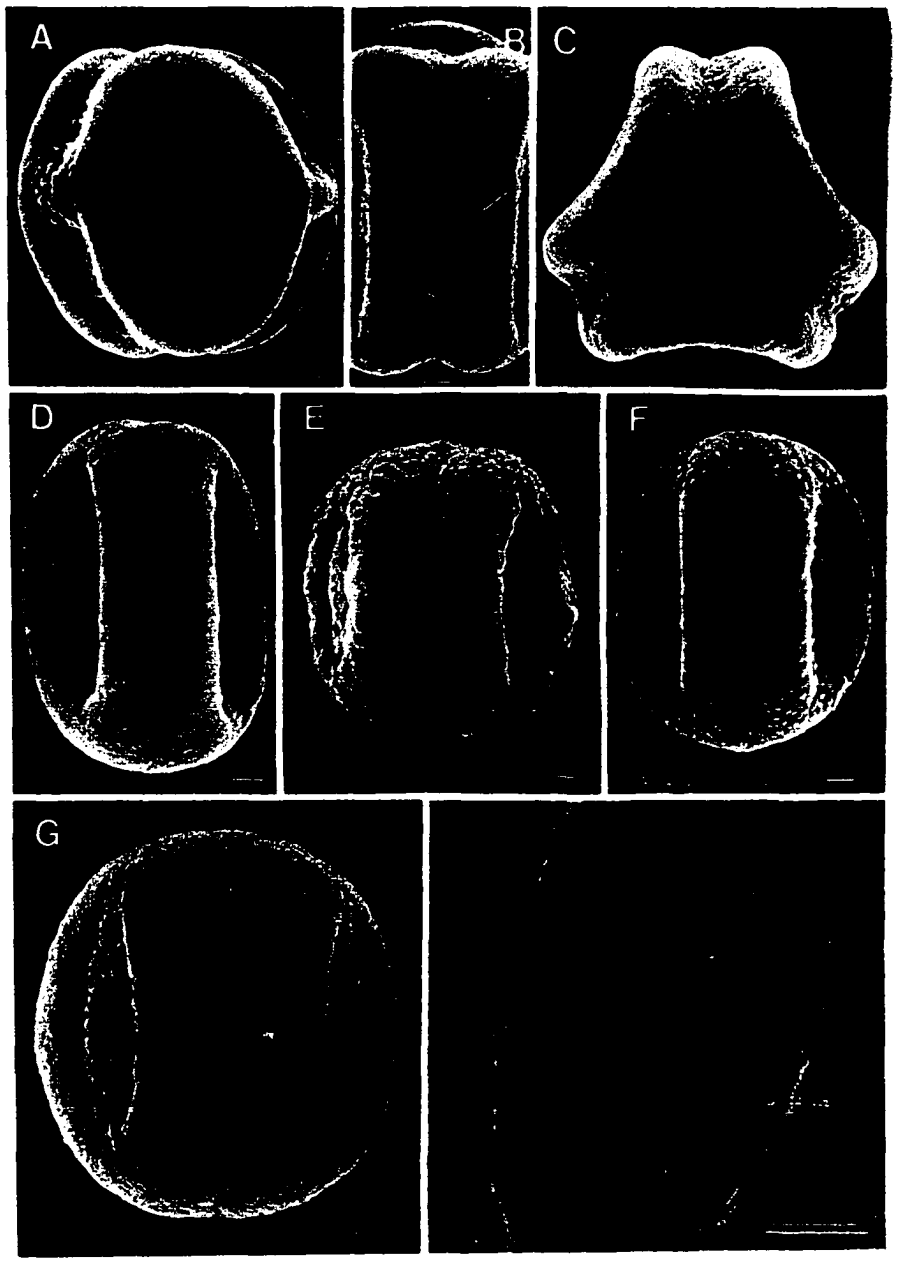
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Figure 25. Transmission electron micrographs of Melastomataceae pollen. A. Tristemma littorale. Section of a mesocolpium. X 19,300. B. Trembleya phlogiformis. An oblique section of a mesocolpium which is folded due to the collapsed grain. The columellae are numerous and markedly branched. X 22,000. C. Tibouchina candolleana. A portion of the mesocolpium near an endoaperture (not included here). The endexine is granular-lamellate. X 29,300. D,E. Osbeckia polycephala. Cross section of an entire grain. Because the section does not include the equator or endoapertures, colpi and pseudocolpi cannot be identified. X 6,700. E. Mesocolpium near an endoaperture. The tectum is deeply lobed due to striae. X 14,000. Scales equal 1μm.

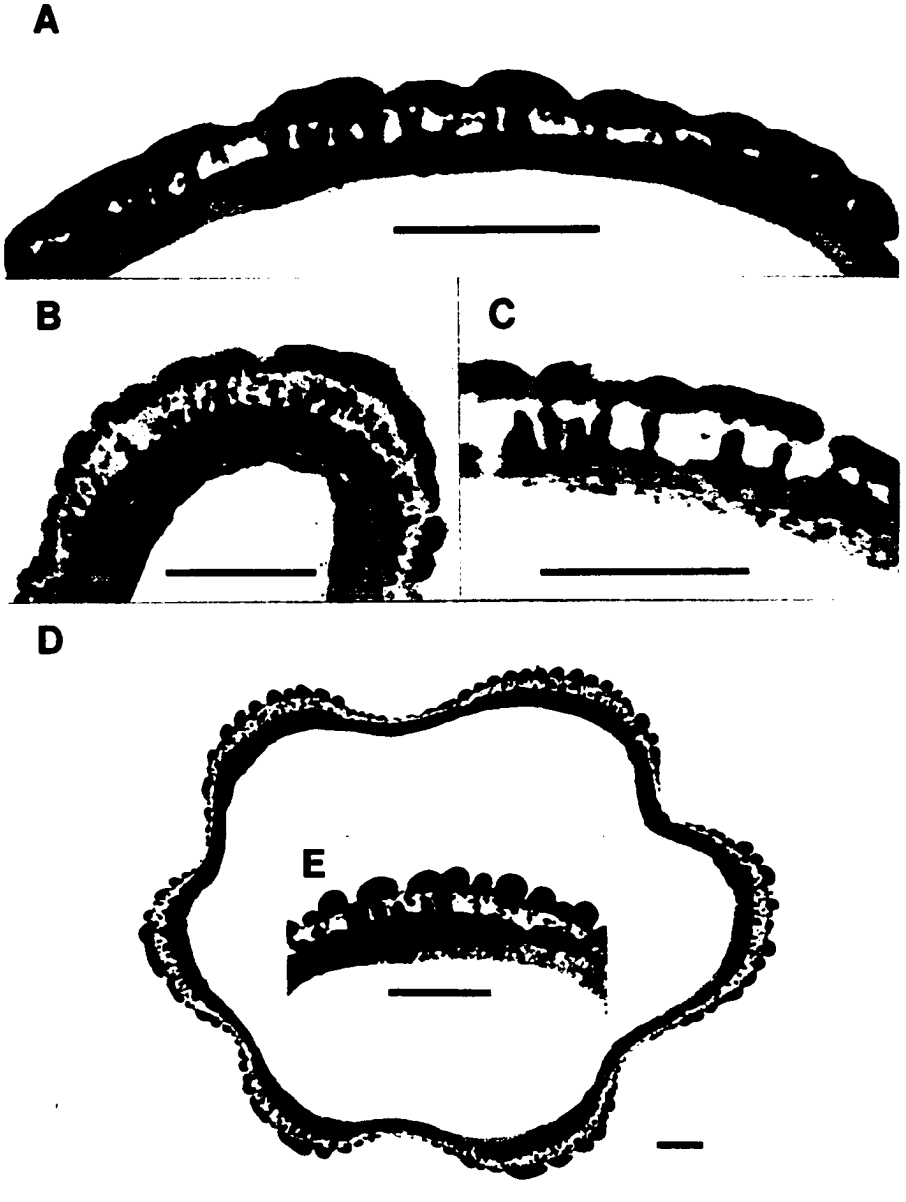
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Figure 26. Transmission electron micrographs of Melastomataceae pollen.

A. Marumia nervosa. Section of two mesocolpia and a colpus or pseudocolpus beween them. The dome-shaped foot layer is similar to Combretaceae pollen (Figs. 17A,B,D,F). X 20,500. B. Dissochaeta celebica. Similar to Fig. 26B. X 26,000.

C. Dissotis brazzae. Similar to Figs. 26B,C. X 16,000. D. Acanthella sprucei. Mesocolpium in the region of an endoaperture. The tectum is very thick with rare perforations. The granular appearing columellae have lateral extensions. Toward the colpus the thick foot layer is reduced while the endexine increases in thickness and becomes granular. Note the general similarity to the pollen of Oliniaceae (Figs. 12B-E) and Penaeaceae (Figs. 20A,B,D). X 16,800. Scales equal 1μm.

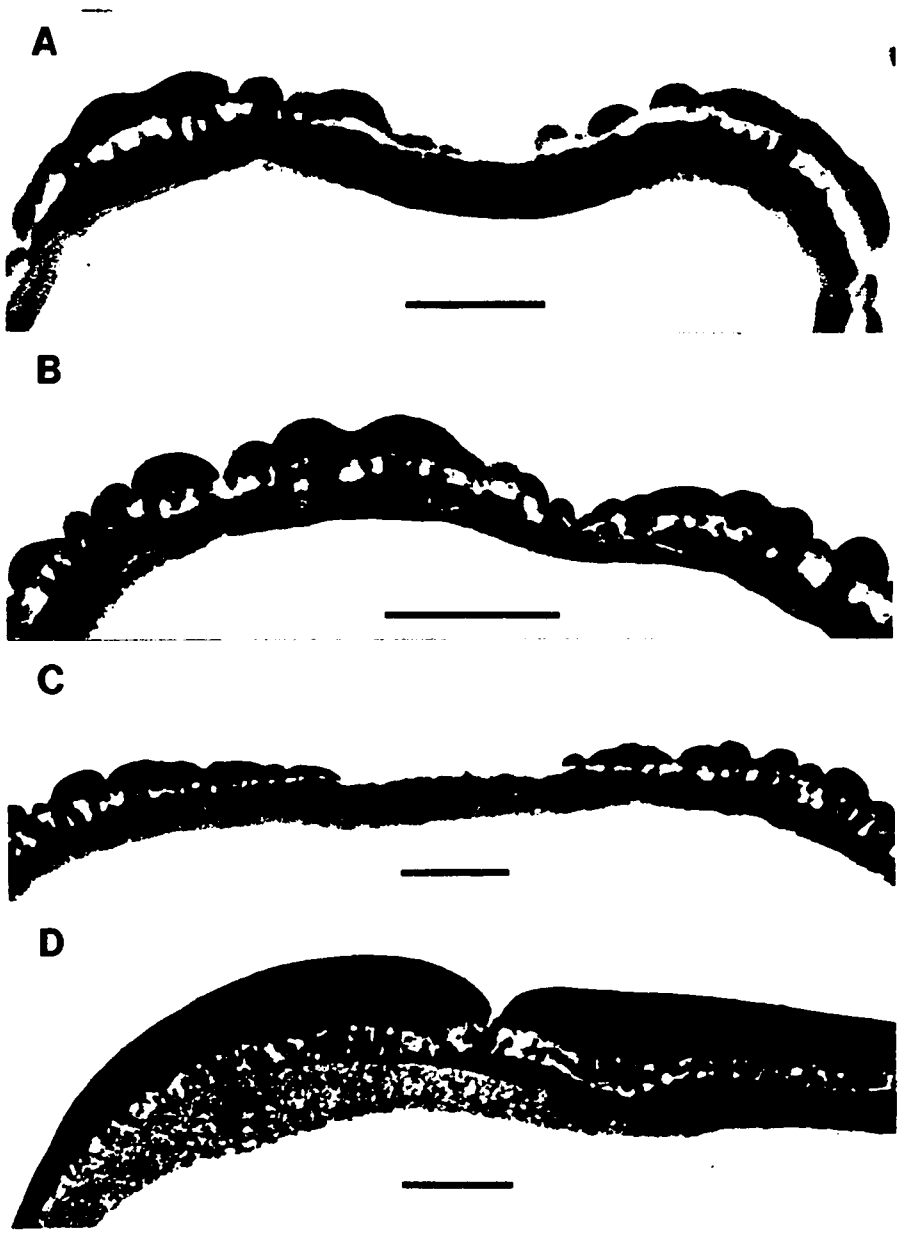
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Figure 27. Transmission electron micrographs of Melastomataceae pollen. A,B. Adelobrotrys tessmannii. A. Section including approximately 1/3 of an entire grain. Colpi and mesocolpia are on the sides of a large intercolpar concavity (between arrows). The mesocolpia consist of a thick imperforate tectum, short columellae, and a thick footlayer. In the intercolpar concavity the verrucae of SEM (Fig. 24A) are dome-shaped and are supported by fine columellae and a thin footlayer. The endexine is thicker below the intercolpar concavity than below the mesocolpia. X 19,800. B. Detail of a portion of the intercolpar concavity as described for Fig. 27A. X 27,000. C. Astronia cumingiana. Section of a mesocolpium near a colpus (right) and an intercolpar concavity (between arrowheads). In the intercolpar concavity the tectum is folded or undulated while columellae and foot layer are not apparent in this plane of section. In the colpus region the area marked with a star is equivalent to the wide mesocolpial extensions noted in SEM (see Fig. 24E). X 18,400. D,E. Oxyspora paniculata. D. Cross section of approximately 1/3 of an entire grain including two colpi (on the sides), two mesocolpia and an intercolpar concavity. X 15,500. E. Enlarged area of a mesocolpium. X 27,000. F. Bredia hirsuta. Section of a mesocolpium. X 59,000. Scales equal 1 μm.

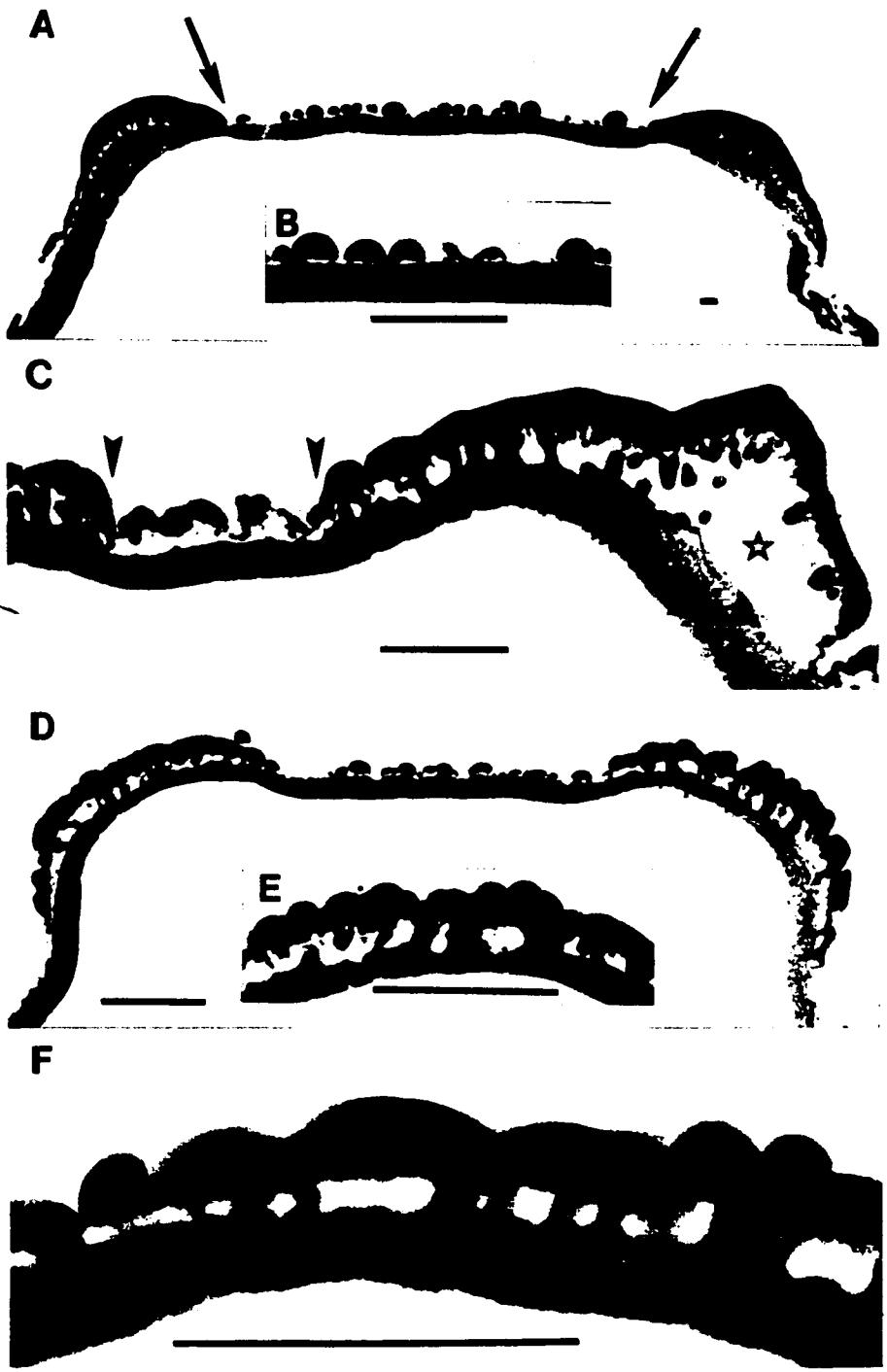
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Figure 28. Transmission electron micrographs of Melastomataceae pollen. A. Tococa spadicifolia. Section of a polyad. Fusion of tecta of two adjacent members (arrowheads). B,C. Tococa stephanotricha. B. Section of an entire grain including two pores. The tectum appears discontinuous due, perhaps, to the verrucate sculpturing. X 4,900. C. Exine at a higher magnification. Note that foot layer and endexine are approximately equal. X 18,600. Scales equal 1μm.

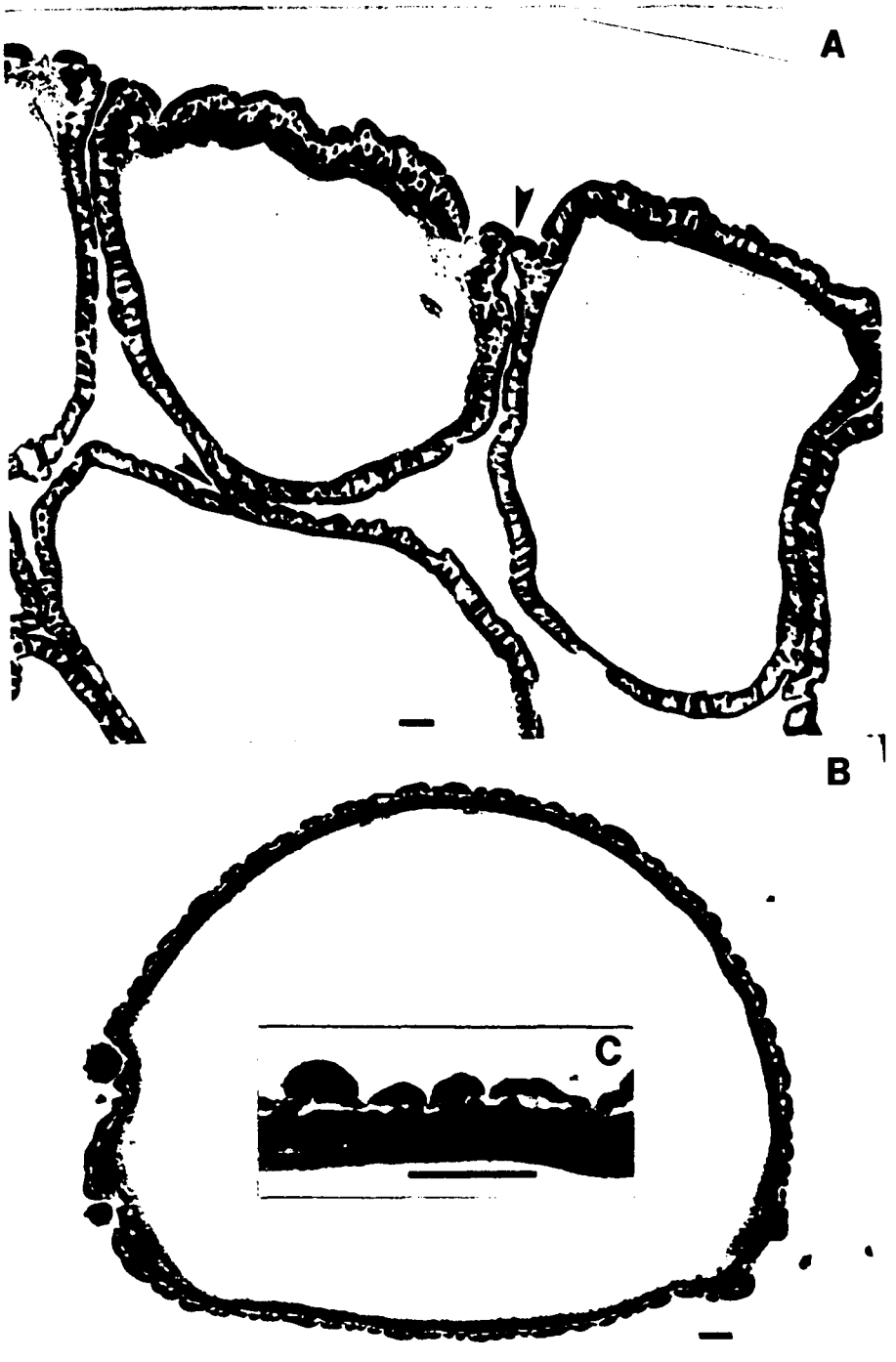
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Figure 29. Scanning electron micrographs of Myrtaceae pollen. A. Metrosideros polycephala. Subpolar view. Colpi are parasyncolpate forming a triangular apocolpium (arrow) at the pole. The intercolpar concavities have a rugulate surface. Elsewhere the surface is smooth. X 3,400. B. Metrosideros nervulosa. Polar view. The apocolpium and the triangular thin walled area formed around it by the parasyncolpate colpi are somewhat collapsed. X 2,900. C,D. Tristania conferta. C. Subpolar view. Syncolpte colpi form a thin walled triangular area at the pole on which are scattered some granular ektexinous elements. X 4,100. D. Lateral view showing the outline of a lalongate, elliptic endoaperture and two intercolpar concavities. X 4,850. E. Tristania nereifolia. Polar view. Note the smooth-scabrate surface. The exine has irregular folds (arrows) over the apertures. X 6,650. Note close agreement with SEM of Gadek and Martin (1981, Fig. 1D). F. Tristania lactiflua. Lateral (left) and subpolar (right) views. The psilate exine has punctae and channels in the intercolpar concavity areas. The grains are syncolpate. X 4,000. Scales equal 1 µm.

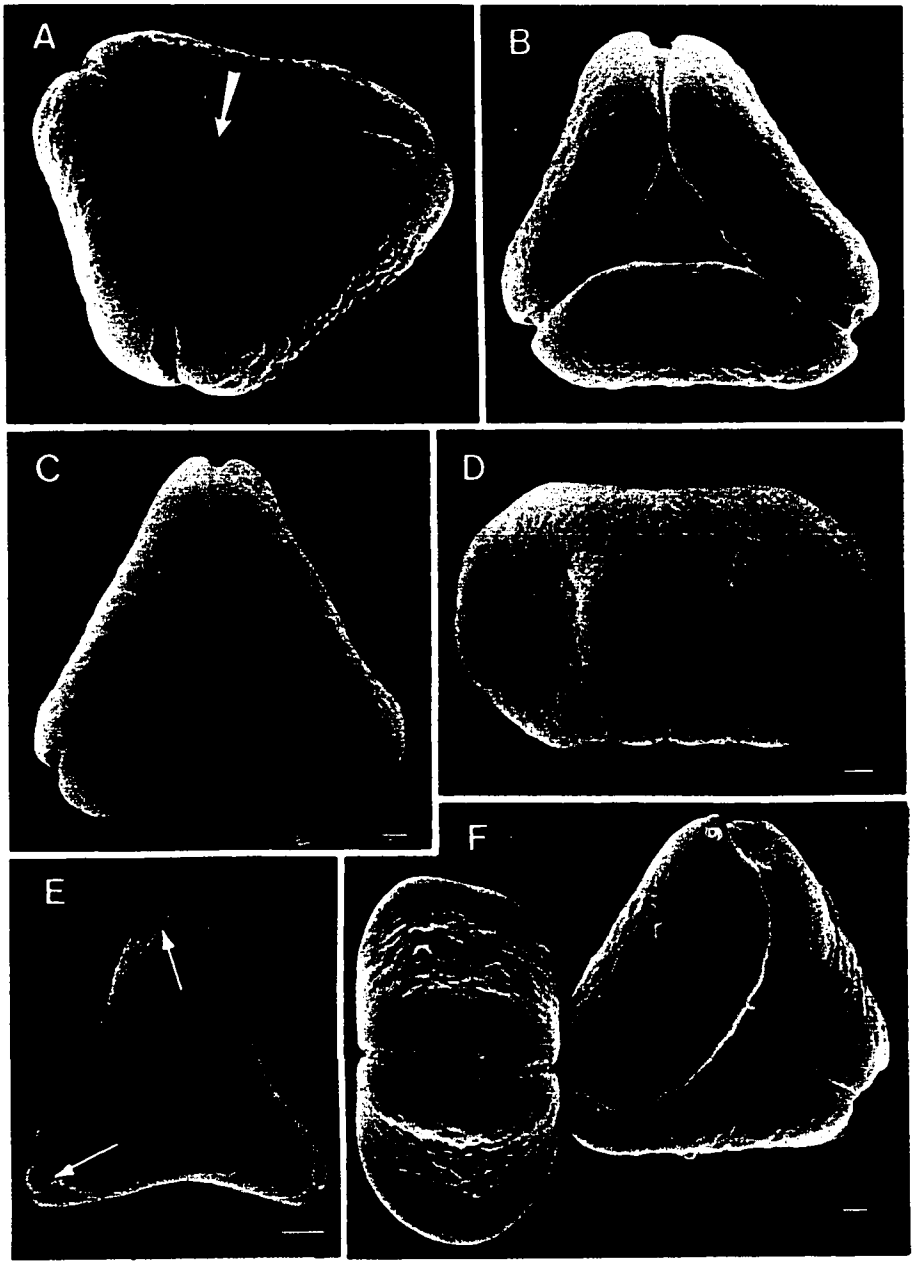
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Figure 30. Scanning electron micrographs of Myrtaceae pollen. A,B. Heteropyxis natalensis. A. Sublateral view. The surface is rugulate on the entire grain. Note distinct intercolpar concavities. The colpus at center is bifurcated at the pole and fused with the other two colpi. The latter colpi do not appear to be united with each other. Different combinations of colpi configurations, that is, syncolpate, parasyncolpate or longicolpate, are found on different grains of Heteropyxis. X 4,000. B. Magnified portion of an apocolpium and surrounding area. In contrast to Fig. 30A, none of the colpi appear to be united at the pole. X 5,200. Fig. 30A is similar to the SEM of Schmid (1980, Fig. 7) except that in the latter the bulging of material at each aperture probably represents the cytoplasmic contents of the unacetolyzed (?) pollen grain. C-E. Eucalyptus ficifolia. C,D. Polar views of two grains from the same sample. In Fig. 30C the grain is syncolpate, in Fig. 30D it is parasyncolpate. C. X 2,000. D. X 2,100. E. Magnified area near the equator (and endoaperture). X 4,500. F. Eucalyptus robusta. Subpolar view. Syncolpate grain. Intercolpar concavities have a granular surface. Elsewhere the surface is smooth. X 3,150. Scales equal 1 μm.

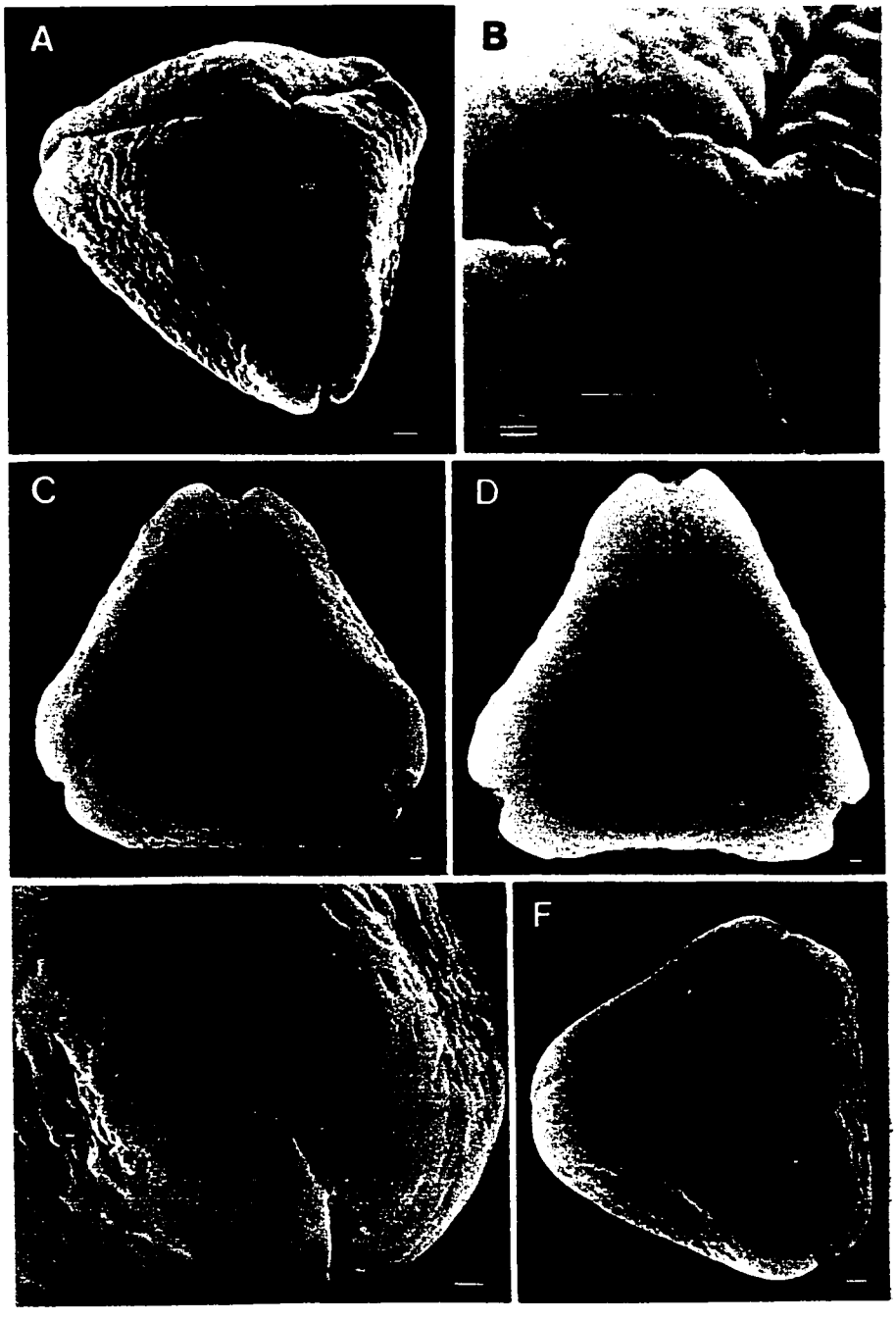
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Figure 31. Scanning electron micrographs of Myrtaceae pollen. A,C. Callistemon teretifolius. A. Polar view. Syncolpate grain. Intercolpar concavities are distinct and have a coarse rugulate-verrucate surface. X 2,800. C. The mesocolpia surrounding the concavities have a fine rugulate-verrucate surface as shown here on an area near the pole. Dark areas on the right are parts of two colpi. X 10,000. B,D. Callistemon speciosus. B. Subpolar view. The surface is rugulate. An intercolpar concavity is clearly visible (at the bottom margin). The triangular apocolpium is connected to the mesocolpium at the right (see also Heteropyxis, Fig. 30A). X 3,400. D. Lateral view showing two intercolpar concavities. X 4,000. E. Calothamnus validus. Polar view. The smooth surface has fine channels. The intercolpar concavities are granular-verrucate. X 3,500. F. Eremea pauciflora. Polar view. Intercolpar concavities appear to be absent. The surface is more or less uniform on the entire grain with fine granular, verrucate, rugulate elements. X 2,900. Scales equal 1 μm.

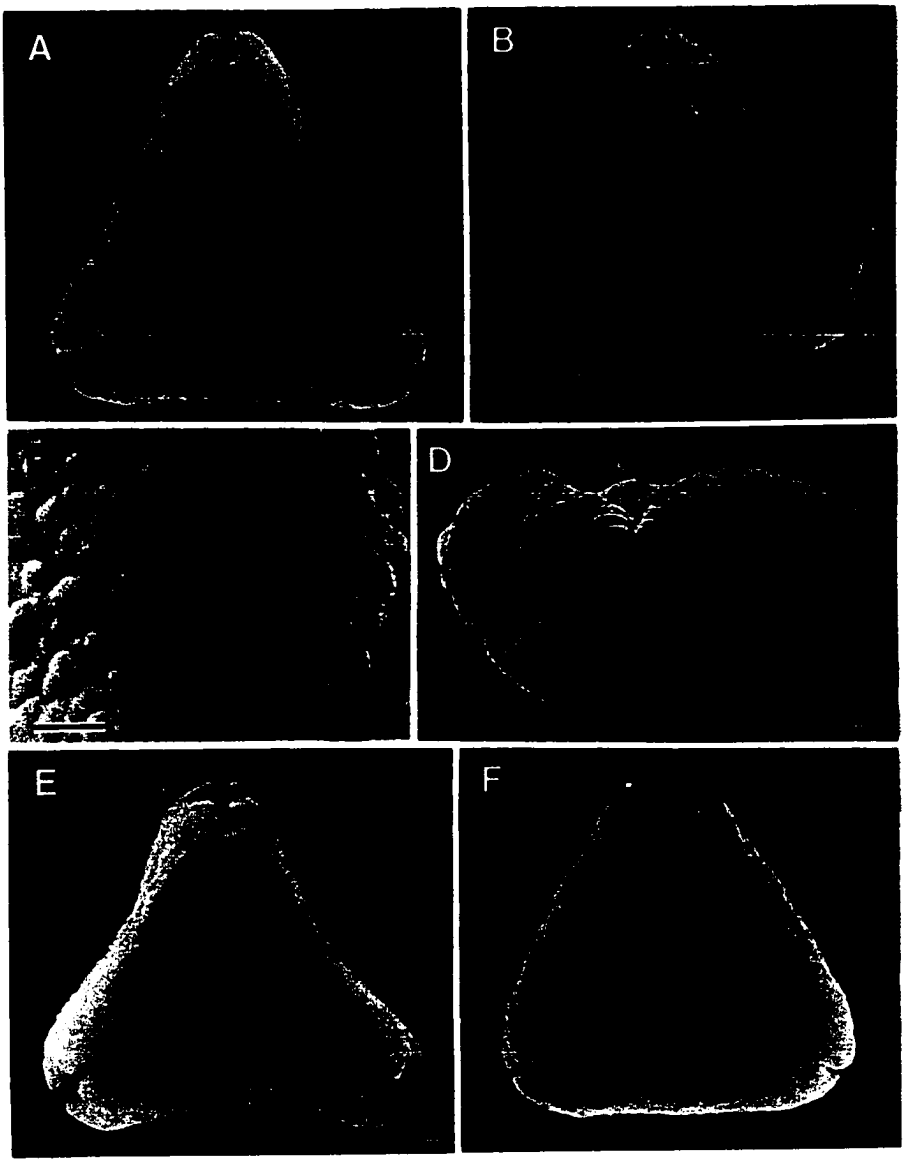
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Figure 32. Scanning electron micrographs of Myrtaceae pollen. A. Baeckea virgata. Sublateral view. The surface is psilate, colpi are short. X 4,200. B. Homoranthus wilhelmii. Polar view showing a psilate surface. X 3,200. C. Balaustion microphyllum. Polar view. Psilate surface, short colpi. Note the circular, thin-walled area at the pole. X 3,150. D. Thryptomene calycina. Polar view. Similar to Fig. 32C. X 4,300. E,G. Hypocalymna angustifolium. E. Lateral view. Surface is pebbly, rugulate-verrucate. X 3,500. G. Polar view. The grain is longicolpate. X 3,000. F,H. Chamelaucium uncinatum. F. Lateral view. The surface is smooth and with pits. The colpus is short and wide. X 2,400. H. Closeup of the aperture. Colpus is shorter than the lalongate, elliptic endoaperture below it. X 4,050. Scales equal 1 μm.

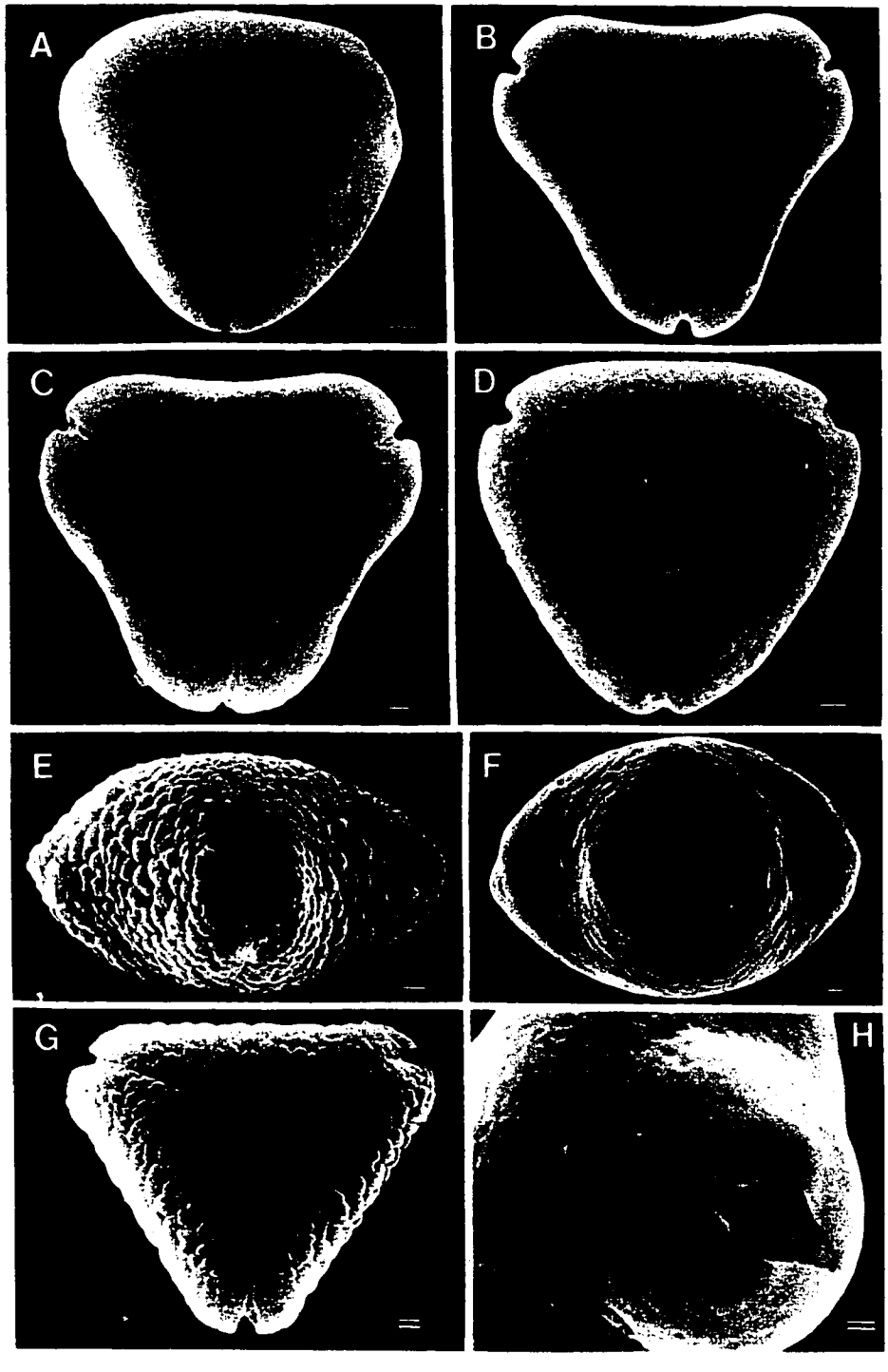
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Figure 33. Scanning electron micrograph of Myrtaceae pollen. A,B. Melaleuca hypericifolia. A. Sublateral view. Distinct intercolpar concavities have a verrucate-granular surface. Elsewhere the surface is psilate. Colpi are curved and united at the pole. X 2,600. B. View near the endoaperture. X 7,000. C. Melaleuca decussata. Polar view. The fine granular-verrucate-rugulate surface sculpture is essentially uniform over the entire grain. In contrast to Fig. 33A the colpi are straight and united at the pole. Intercolpar concavities are absent. X 3,150. D. Melaleuca preissiana. Polar view. The surface is fine granular-verrucate-rugulate and more or less uniform over the entire grain. Colpi are curved (see Fig. 33A). Intercolpar concavities are absent. X 4,200. E. Melaleuca rhaphiophylla. Subpolar view. The intercolpar concavities are not as distinct as in M. hypericifolia. X 2,940. F. Psiloxylon mauritianum. Lateral view. The syncolpi form large apocolpia on both poles. The arrow indicates coarse rugulate (?) elements on the equator: this is not believed to be a regular characteristic as other grains of Psiloxylon have an essentially uniform sculpture. X 3,850. Comparison should be made with the SEM of Schmid (1980, Fig. 5). G. Melaleuca pulchella. Polar view. Surface is rugulate. In this grain intercolpar concavities are not discernible. X 2,400. Scales equal 1μm.

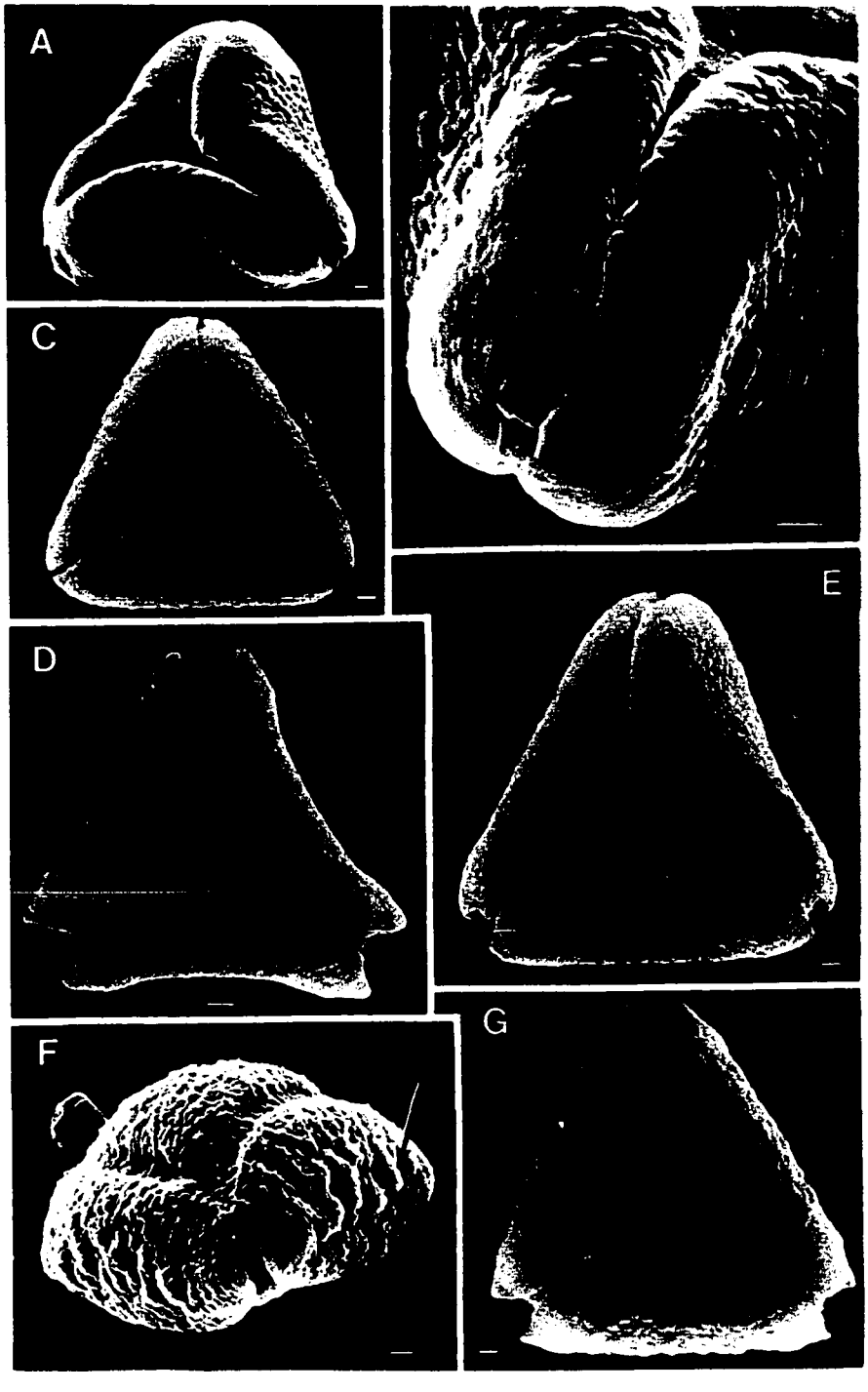
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Figure 34. Scanning electron micrographs of Myrtaceae pollen. A-C. Psidium littorale. A. Subpolar view of a monad. The grain is longicolpate (parasyncolpate and syncolpate grains are also present in sample). Intercolpar concavities are absent. X 3,200. B. A tetrahedral tetrad (fourth grain is at the back). X 1,900. C. Surface details of Fig. 34A near the pole showing the surface to be granular-verrucate-rugulate. X 7,000. D,E. Ugni molinae. D. Lateral view showing elliptic shape. X 4,850. E. Polar view. Colpi are long. Note angular surface elements near the pole. X 4,500. F. Pilidiostigma glabrum. Polar view. The surface is verrucate-rugulate. The arcuate colpi are parasyncolpate. The apocolpium is formed by scattered verrucate, granular elements. X 2,200. G. Osbornia octodonta. Polar view. The surface is scabrate (?), colpi are short and at the pole form a weakly developed thin walled traingular area. X 3,150. Scales equal 1 μm.

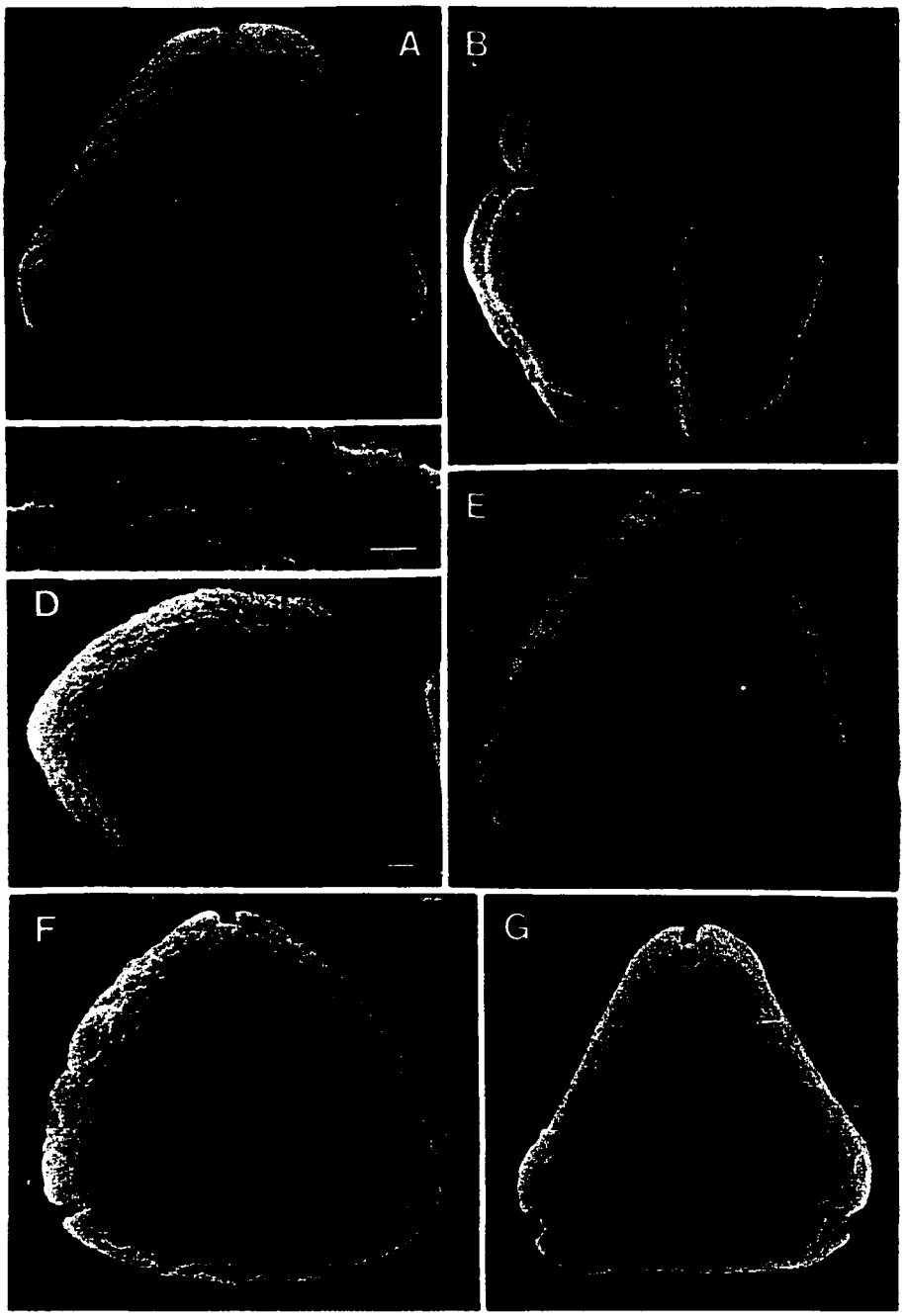
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Figure 35. Scanning electron micrographs of Myrtaceae pollen. A. Cleistocalyx operculata. Subpolar view. The psilate surface has punctae and channels in the shallow and barely discernible intercolpar concavity areas. X 4,900. B. Acmena smithii. Polar view. Surface is psilate; punctae and channels are present in the intercolpar concavities (arrow). X 3,750. C. Eugenia capuli. Polar view of the convex half of the grain, the opposite half is concave. The surface is rugulate. Colpi are united (i.e., syncolpate) but are obscured by rugulate elements at the pole. The pole on the concave side usually has more distinct syncolpi. X 4,000. D. Eugenia elliptifolia. Sublateral view showing syncolpi. The psilate surface becomes coarser and has fine channels and punctae in the intercolpar concavities. X 5,350. E. Luma chequen. Polar (upper) and lateral (lower) views. The surface is smooth to slightly coarse in the area of the endoapertures. Toward middle part of the mesocolpia it becomes granular-verrucate. There is a large thin walled area at the poles that has granules and verrucae scattered over it. The colpi merge with this thin-walled area, thus, the grains are syncolpate. X 2,200. F. Myrceugenella apiculata. Lateral (left) and subpolar (right) views of unacetolysed, gluteraldehyde-fixed pollen. The surface is granular-verrucate. Colpi are long. X 2,500. Scales equal 1 μm.

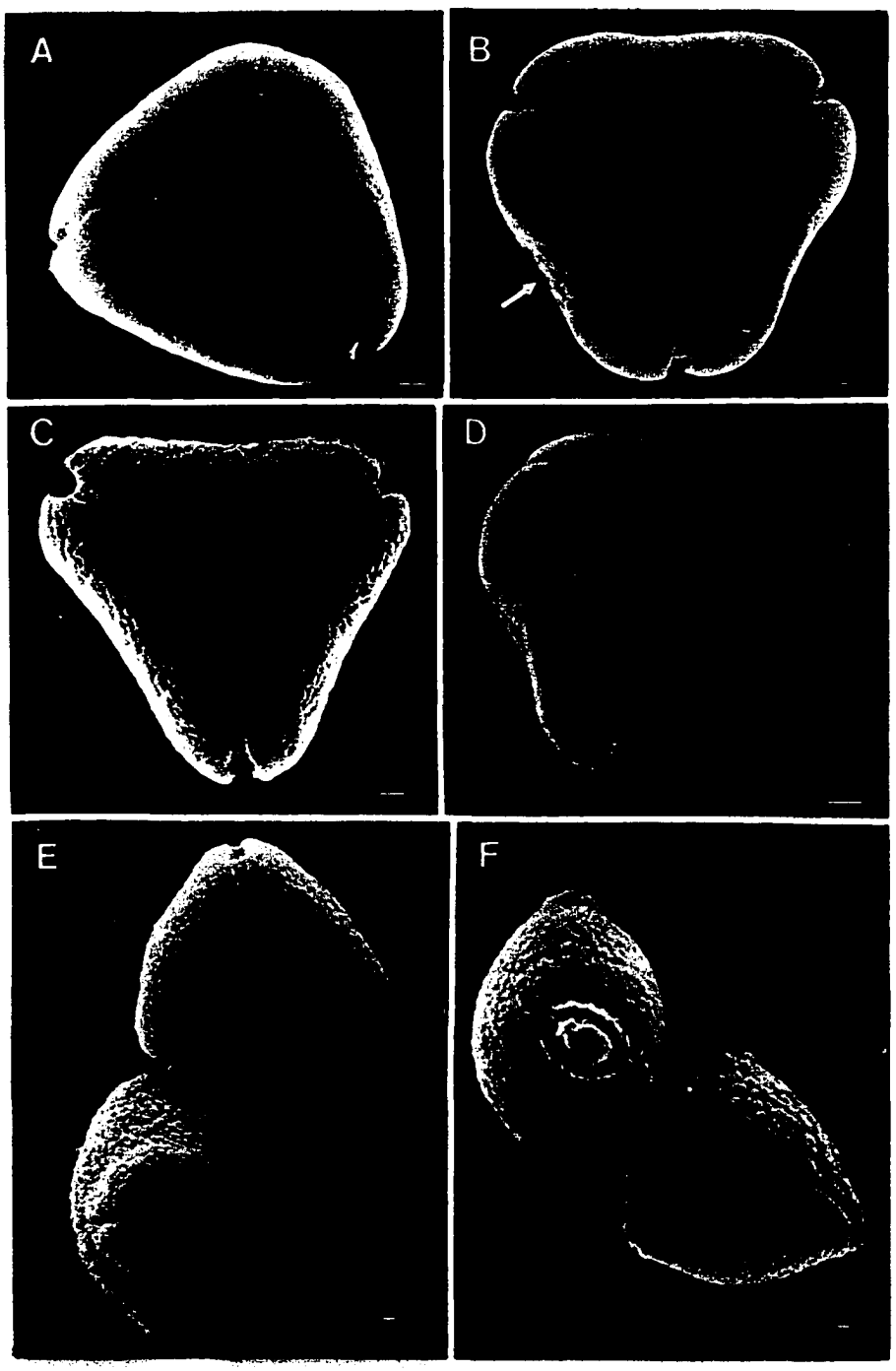
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Figure 36. Scanning electron micrographs of Myrtaceae pollen. A. Temu divaricatum. Polar view of a parasyncolpate grain. Other colpi combinations were found in the same sample. The surface is rugulate. X 3,200. B-D. Myrtus communis. B. Polar view of a monad. All colpi are not united at this pole but different colpi combinations (i.e. parasyncolpate/syncolpate; syncolpate/syncolpate, etc.) are found within the same sample. X 5,250. C. In this enlarged view of the surface, rugulate and verrucate elements contain fine electron dense lines and dots. X 12,600. D. Tetrahedral tetrads are also common in the sample. X 3,150. E. Rhodamnia argentea. Polar view. The syncolpate grain has straight colpi. The surface is verrucate-granular. Large verrucate-rugulate elements are present on colpi margins and at the pole. X 4,900. F. Austromyrtus bidwillii. Subpolar view. Parasyncolpate grain shows rugulate surface. The apocolpoium is formed by separate rugulate and verrucate elements. X 4,300. Scales equal 1 μm.

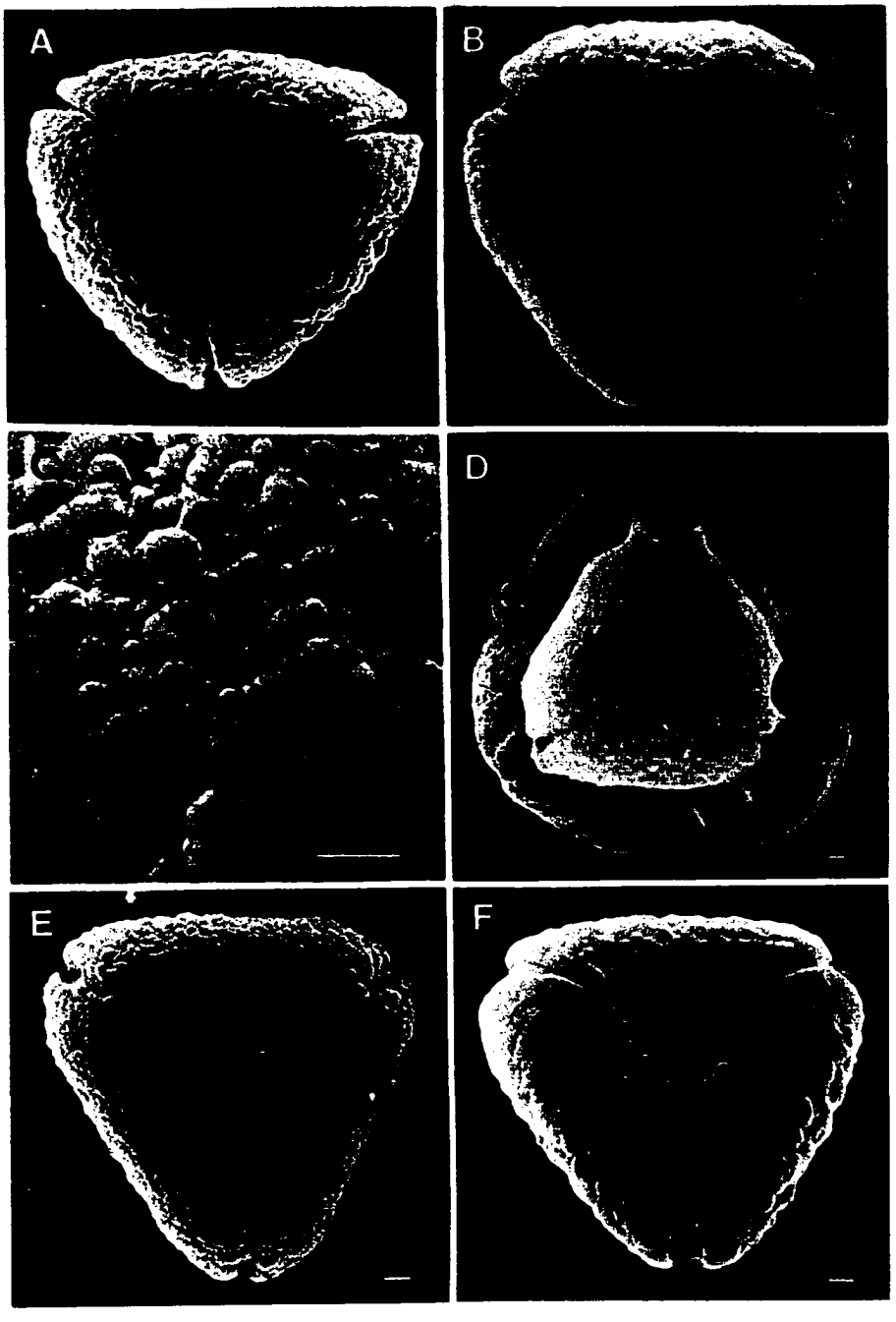
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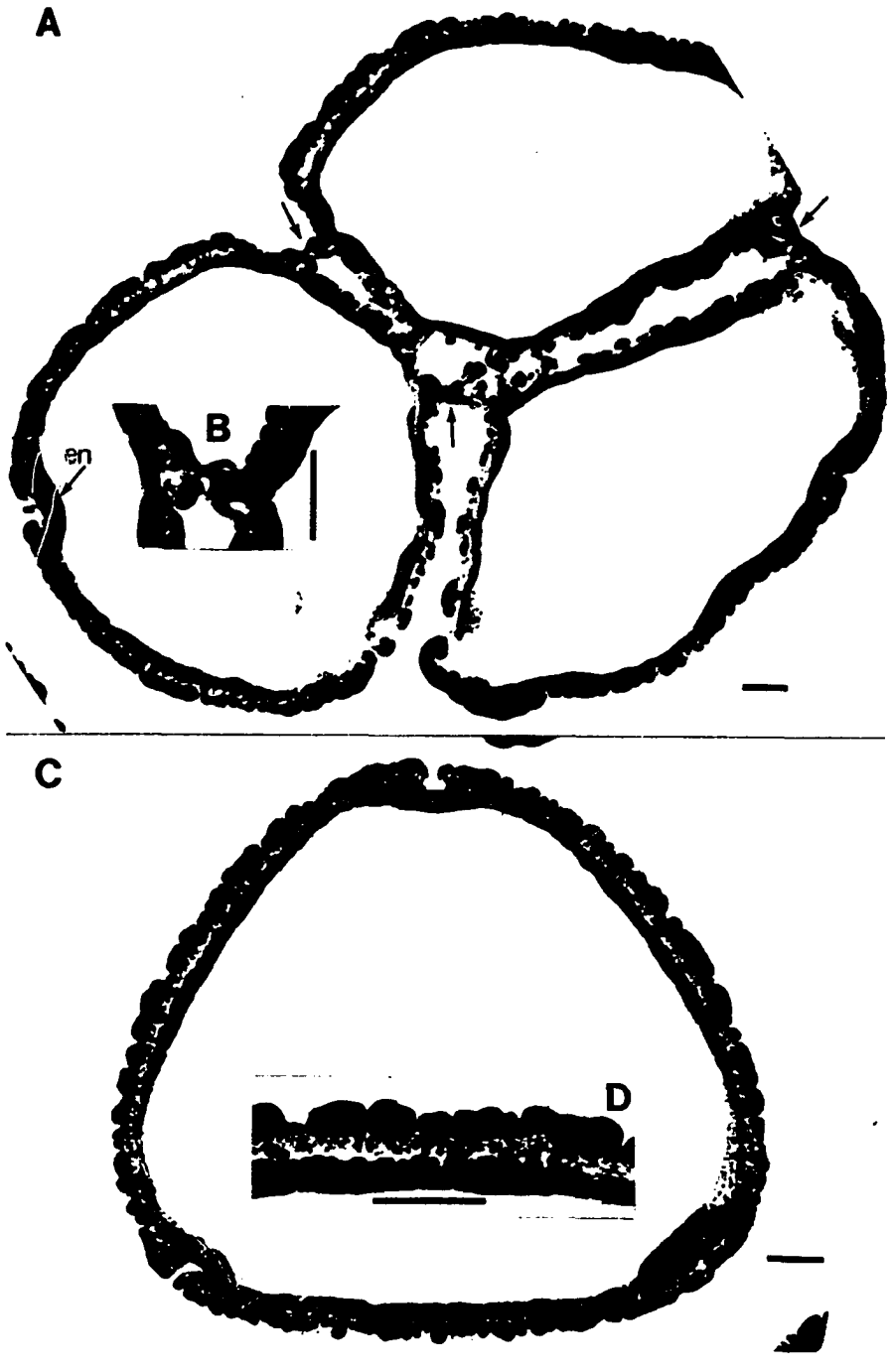
Figure 37. Transmission electron micrographs of Myrtaceae pollen. A-D. Myrtus communis. A. Section of three members of a tetrahedral tetrad. The proximal faces of the grains have a discontinuous tectum (due to verrucate-granular sculpture), while the distal faces show a more or less continuous tectum. In the grain on the left, the apocolpium (the thin walled triangular area where colpi unite) shows a thickened endexine (en). Several ektexinous connections (arrows) between adjacent grains are visible. X 6,300. B. A close-up of a portion of Fig. 37A showing fusion of tecta. X 13,000. C. Cross section of a single grain passing through the three apertures near the equator. X 8,000. D. An enlarged area of Fig. 37C showing a thick tectum, an infratectal granular layer, short columellae, a thin discontinuous footlayer and a well developed endexine. X 17,000. The TEM of Lugardon and Van Campo (1978, Pl. 1, Figs. 1-6) differs from Figs. 37C,D in that columellae were not recognized. Scales equal 1 μm.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D

Figure 38. Scanning electron micrographs of Onagraceae pollen. A. Fuchsia thymifolia ssp. thymifolia. Oblique lateral view with viscin threads associated with the proximal (top) pole. The arrow indicates a thickened area of threads showing a segmented-ropy morphology characteristic of this species (see Skvarla et al., 1978, Pl. 4, Fig. 6). The apertural protrusion (AP) with an irregular pore extends from the central body (CB). A portion of a second apertural protrusion is visible at the upper left. This two-aperturate condition is characteristic for the pollen of most species of Fuchsia. X 1,600. B. F. michoacanensis. Apertural protrusion with crack extending from irregular pore (at right) into the central body. The arrow indicates endexine lamellae. The exine surface is rugulate. X 4,000. C. Circaea cordata. Portion of central body and apertural protrusion with a single smooth viscin thread. The surface is composed of rounded and rod-like elements. X 4,700. D. C. alpina ssp. imaicola. Equatorial view showing three apertural protrusions with an irregular pore on the surface of the central body. Note that the poles are essentially isopolar and in the absence of viscin threads (C. alpina is the only taxon in the Onagraceae without them) it is difficult, if not impossible, to determine the distal and proximal poles. X 1,900. E,F. Two collections of Hauya elegans ssp. elegans. E. (Moran 13387). Two pollen grains in proximal polar view showing masses of viscin threads on the proximal poles. In contrast to the pollen of Fuchsia (Fig. 38A) and Circaea (Fig. 38D) the apertural protrusions are considerably less prominent. X 4,000.

F. (Rzedowski 9294). Two groups of viscin threads exhibiting a segmented to coarsely beaded morphology. Each group consists of several individual threads aligned in parallel fashion. Attachment with the globular elements of the exine surface is partially evident in the thread group at the right. X 10,000.

G. H. elegans ssp. barcenae. Area of a fractured pollen grain showing thick, spongy ("paracrystalline") ektexine (ek) and solid, dense endexine (en). The short, irregular extensions at the lower margin of the ektexine are columellae (see Fig. 42C). The slightly lamellate upper margin of the endexine suggests a foot layer but it has not been confirmed in TEM with any degree of confidence (see Fig. 42C). The separation of ektexine from endexine is artificial,probably a result of processing. X 6,800. The scales equal 1 μm.

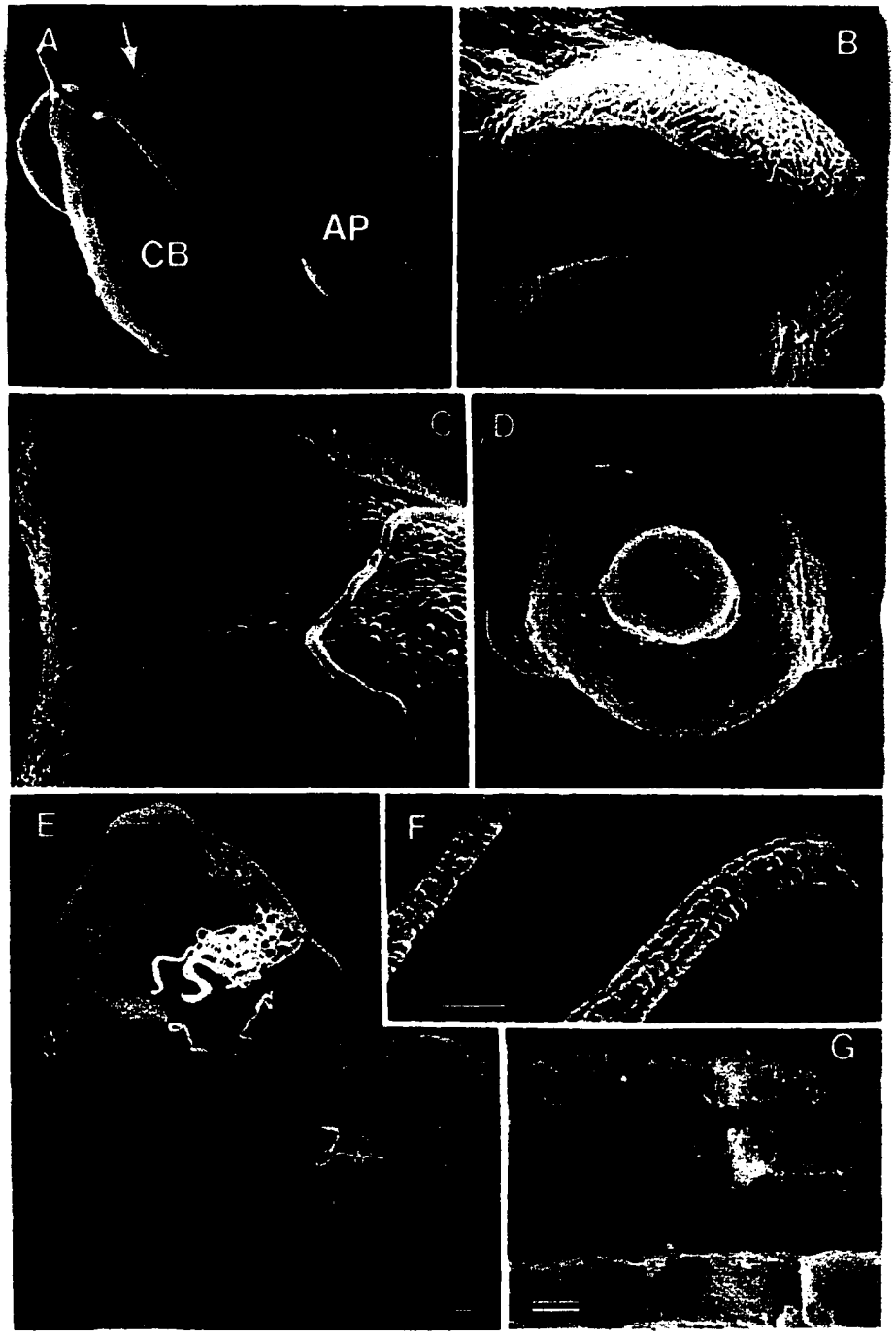
A
CB
AP
B
C
D
E
F
G

Figure 39. Scanning electron micrographs of Onagraceae pollen. A,C. Clarkia speciosa ssp. speciosa. A. Proximal polar view with several viscin threads attached to the exine surface. X 400. C. Viscin threads are smooth and the two groups are attached to the exine surface. Although not clearly indicated, the exine surface is composed of distinct circular and elongate elements. X 5,000.

B,D,F. C. unguiculata. B. Proximal polar view. X 400. D. Equatorial view with viscin threads in association with proximal (top) pole (compare with C. alpina ssp. imaicola, Fig. 38D). X 400. F. View showing circular elements of exine surface and smooth viscin threads. X 10,000. E. Gaura lindheimeri. The segmented-coarsely beaded threads contrast with an exine surface that appears to be rugulate-perforate and have randomly dispersed globular elements. X 20,000. G,H. G. mutabilis.

G. Segmented-beaded viscin threads associated with an exine surface of circular elements on a perforate base. X 10,000. H. Fractured apertural protrusion showing short columellae (arrows) of the ektexine and rows of lamellar endexine within the protrusion. X 1,900. Unless indicated otherwise the scales equal 1 μm.

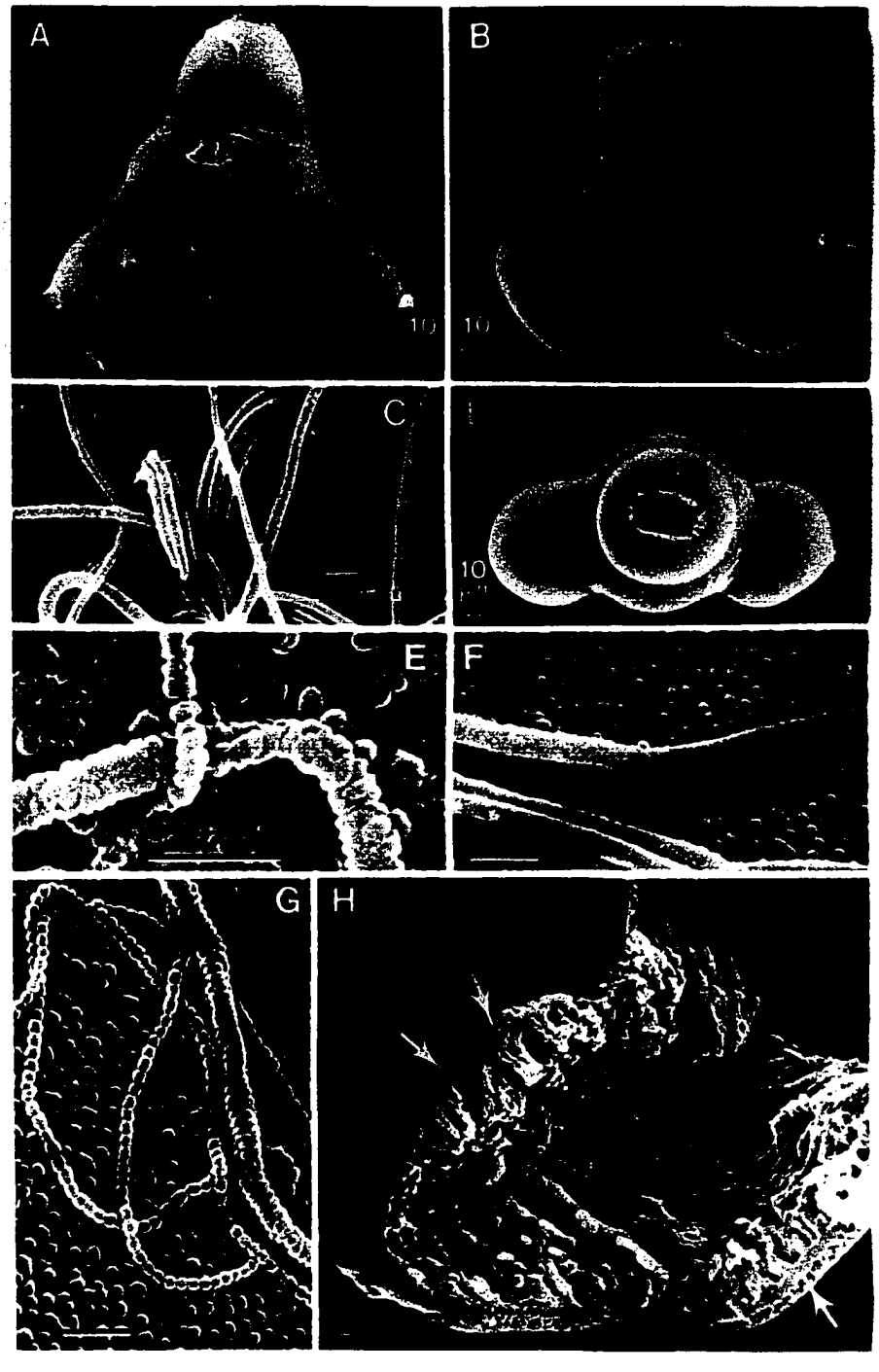
A
B
C
E
F
G
H

Figure 40. Scanning electron micrographs of Onagraceae. A,B. Oenothera brachycarpa. A. Equatorial view similar to Circaea alpina ssp. imaicola (Fig. 38D) and Clarkia unguiculata (Fig. 39D). X 330. B. A group of segmented-beaded viscin threads are attached to a perforate exine surface with circular-elongated elements. X 10,000. C,E. O. texensis. C. The pollen grain is collapsed as well as fractured. The apertural protrusion at the top is mostly covered by exine material of the central body that has been folded back to expose the columellae which appear as white dots. Randomly arranged viscin threads are intermingled with the columellae as well as with the exposed endexine surface of the central body, an artificial association resulting from collapse and fracture of the exine. The bracketed area appears in Fig. 40E. X 800. E. Bracketed area of Fig. 40C emphasizing prominent spongy-perforate columellae and narrow tectum (compare with H. elegans sp. barcenae, Fig. 38G). Several segmented-beaded viscin threads are on the surface of the endexine. X 15,000. D. Gongylocarpus rubricaulis. Proximal polar view showing mass of viscin threads. In contrast to other Onagraceae taxa, apertural protrusions are considerably less conspicuous. X 530. F. G. fruticulosus ssp. glaber. View of exine composed of short rod-like -spherical elements of variable sizes. X 20,000. Unless indicated otherwise the scales equal 1μm.

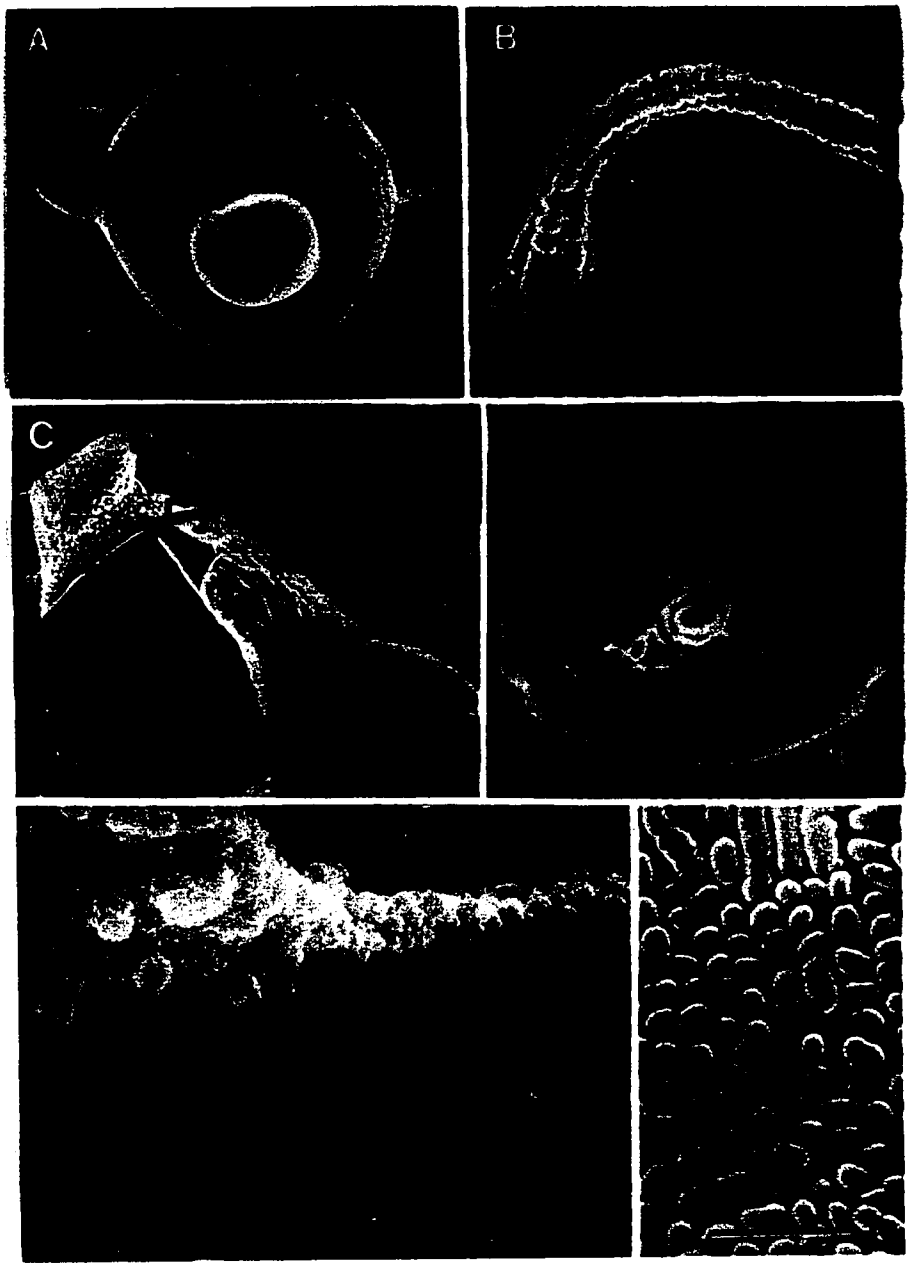
A
B
C

Figure 41. Scanning electron micrographs of Onagraceae pollen. A. Boisduvalia stricta. View of tetrahedral tetrad showing all four pollen members. X 400. B,C,E. B. densiflora. These three SEM's represent different collections and illustrate the diversity in viscin thread morphology which occurs on pollen in some Onagraceae taxa. In Fig. 41B (Piper s.n.), the morphology is clearly incised-compound, in Fig. 41C (Thompson 5099), it appears as tightly compound-twisted, and in Fig. 41E (Heller 12448), it is smooth (see Skvarla et al. 1978 for detailed discussion). In all three examples the associated exine surface appears to be rugulate-perforate. Fig. 41B. X 5,000. Fig. 41C. X 7,000. Fig. 41E. X 10,000. D,G. Ludwigia goiasensis. D. The tetrad (fourth pollen member is not visible) is part of a polyad and is surrounded by parts of other tetrads. The bracketed area is enlarged below in Fig. 41G. Arrowheads indicate colpi. X 800. G. Enlargement of bracketed area in Fig. 41D showing internal bridges (arrows) between adjacent pollen grains of the tetrad. The nature of the globular club-like structure associated with one of the bridges is unknown but may be related to viscin threads. The star represents union of adjacent pollen grain apertures. X 5,000. F. L. alternifolia. Three members of a tetrad. The large open arrows indicate prominent meridional ridges characteristic of several Ludwigia taxa and which bifurcate at the equator to join with the equatorial ridges between the apertural protrusions. In contrast to L. goiasensis (Fig. 41D) and L. longifolia (Fig. 41H) the meridional ridges are best developed in L. alternifolia while the equatorial ridges are of equal prominence in all three species. The short, solid arrows show the colpi. X 800. H,I. L. longifolia. H. Overall view of a polyad with basic tetrad composition. Arrow indicates an external bridge which connects adjacent distal tetrad pollen surfaces and maintains polyad unity. Arrowheads indicate colpi. X 400. I. External bridge (not from Fig. 41H) with portions of adjacent exine surfaces and smooth viscin threads. X 4,000. Unless indicated otherwise the scales equal 1μm.

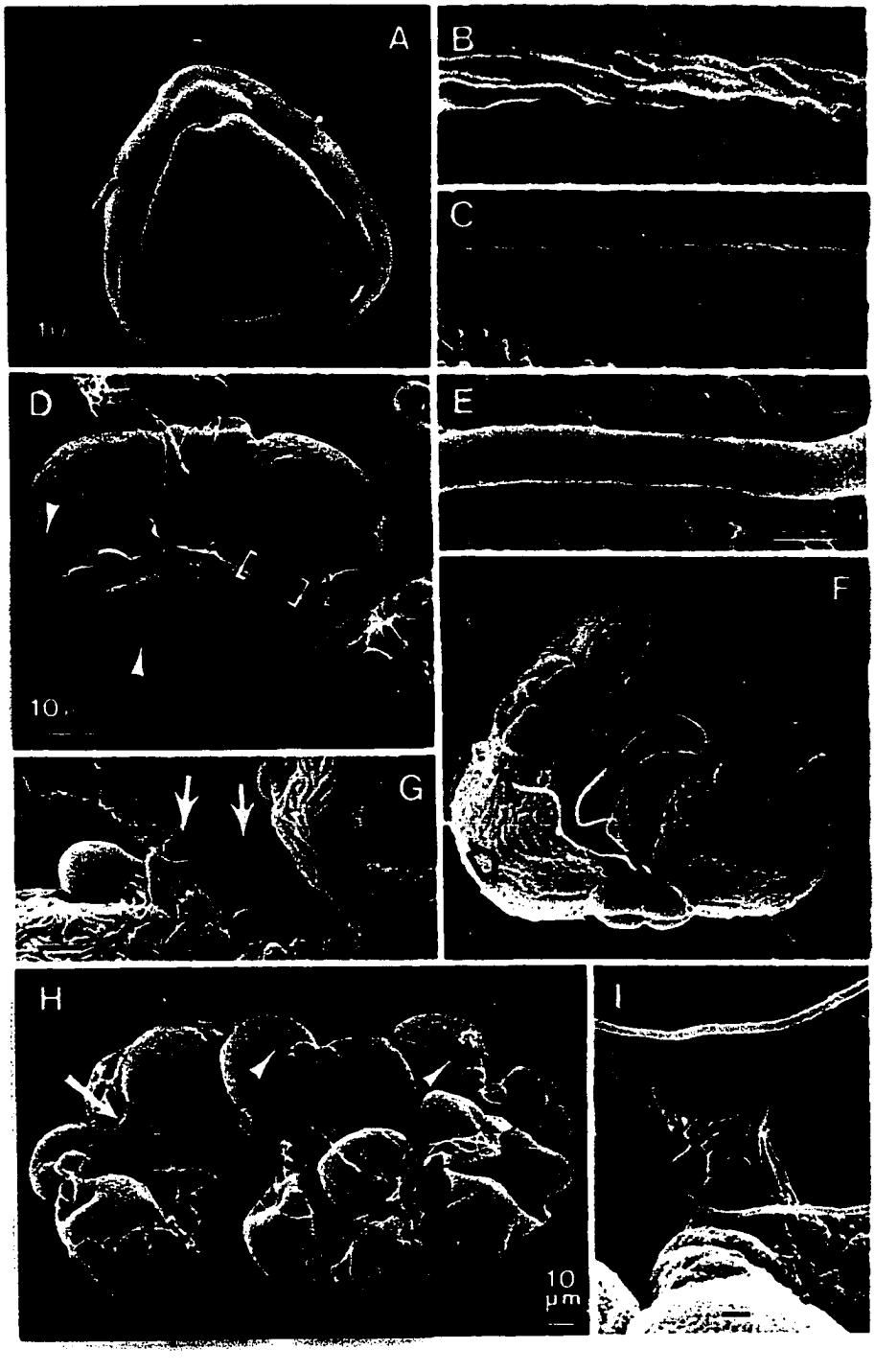
A
B
C
D
E
F
G
H
I
10
μm

Figure 42. Transmission electron micrographs of Onagraceae pollen. A. Fuchsia garleppiana. Section at proximal pole showing irregular spongy-paracrystalline ektexine attached (without columellae) to the uniform and solid endexine. The arrow indicates union of viscin threads (v) with the ektexine. X 21,800.

B. Ludwigia brevipes. Section is through the distal face. The ektexine is massive and spongy-paracrystalline and the surface is markedly undulate. The endexine is uniform and solid and has a thin granular basal area. X 18,900. C,E. Hauya heydeana. C. This sample represents fresh pollen prepared in glutaraldehyde and osmium tetroxide (acetolysis has been omitted). It is very similar to the fractured grain of Hauya elegans ssp. barcenae (Fig. 38G) but clearly emphasizes the short but prominent columellae. The thin, uniform, very dense layer beneath the endexine is probably the intine. The only exine layer that appears to be missing is the foot layer. X 10,300. E. Section through a group of viscin threads showing serrated margins indicative of a segmented morphology (see Plates 20-21 of Skvarla et al. 1978). X 7,500. D,F. Circaea mollis. D. The rugulae on the highly undulate exine surface appear as irregularly shaped isolated islands. X 13,700. F. Section through apertural protrusion showing apertural chamber underlain by a thickened zone of lamellar endexine. X 5,000. Scales equal 1μm.

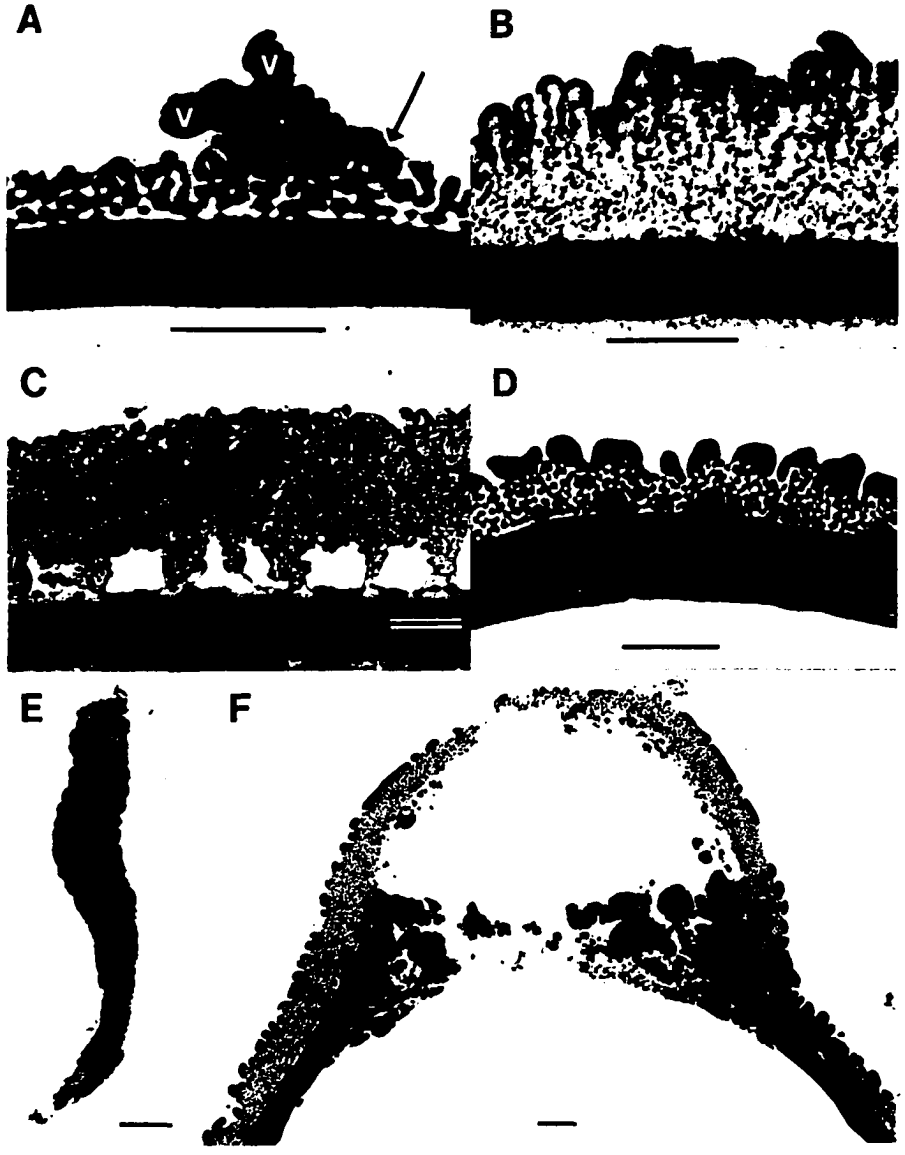
A
V
V
B
C
D
E
F

Table 2. Pollen Examined

TAXON	LOCALITY	COLLECTOR	HERBARIUM	PSEUDOCOLPI	SEM-TEM	FIGURE NO.	REMARKS
LYTHRACEAE							
Ammannia coccinea Rottb.	Kern Co., CA, USA	Twisselman 7983	KE	6	TEM	5-B	
Ammannia robusta Keer & Regel	Oklahoma City, OK, USA	Waterfall 3027	OKL	6	SEM	2-A,B	
Crenea surinamensis L.	Guyana	De La Cruz 3301	MO	6	SEM,TEM	1-F	Meridional ridge
Cuphea carthagenensis (Jacq.) MacBr.	Guatemala	Aguilar 104	OKL	0	SEM	2-C	(Tectal) ridges
Cuphea nitidula HBK.	Mexico	Graham 614	KE	0	TEM	5-D	Tectal ridges
Cuphea petiolata (L.) Koehne	Ozark Nat'l. Forest, Arkansas, USA	Demaree 40737	OKL	0	SEM	2-D,E,F	Variable striate sculpture
Cuphea racemosa (L.f.) Spreng.	Veracruz, Mexico	Graham 689	KE	0	TEM	5-C	
Diplusodon villosus Pohl	Brazil	Irwin et al. 26402	MO	0	SEM	3-A,B	Tricolpoidorate, colpus very short
Heimia salicifolia (HBK.) Link	Mexico	Graham 141	KE	0	TEM	5-A	
" "	Mexico	Ventura A. 2430	MO		SEM	1-C,D,E	Rarely dicolporate and syncolpate
Lafoensia punicifolia DC.	Chiapas, Mexico	Breedlove 40657	MO	0	SEM,TEM	3-D,E;5-E,F 6-A	Meridional ridges, apertural fields and polar caps
Lagerstroemia speciosa (L.) Pers.	Honduras, cultivated	Lent 4	OKL	0	SEM	3-C	Meridional ridges
Nesaea schinzii Koehne	Bulawayo Distr., Rhodesia	Best 395	MO	6	SEM	1-A,B	

Rhynchocalyx lawsonioides Oliv.	Natal, South Africa	Nicholson s.n.	MO	3	SEM	4-C;6-D	
PUNICACEAE							
Punica granatum L.	Iran	Antonio s.n.	OKL	0	SEM	4-A	Weak meridional ridges
" "	Iran	Grant 15704	MO	0	TEM	6-E	
SONNERATIACEAE							
Duaganga moluccana Bl.	Los Banos, Philippines	Elmer 18275	MO	0	SEM	4-F	Triporate, meridional ridges, apertural fields, polar caps
Sonneratia caseolaris Druce	Mahe Island, Seychelles	Sauer 3808	MO	0	SEM	4-E	Triporate, meridional ridges, apertural fields, polar caps
TRAPACEAE							
Trapa japonica Flerov	Japan	Boufford et al. 19962	MO	0	SEM,TEM	8-A,B,C,D; 9-D	Meridional ridges over apertures
Trapa natans L.	------	--------	MO 2532983		SEM	8-E	Meridional ridges over apertures
	Germany	Engelmann s.n.	MO		SEM,TEM	7-A,B;8-F 9-A	Meridional ridges over apertures
	Schenectady Co. NY, USA	House 21708	MO		SEM,TEM	7-C,D,E,F; 9-B,C	Meridional ridges over apertures; polyads
OLINIACEAE							
Olinia emarginata Burtt Davey	Natal, South Africa	Hillard & Burtt 8691	MO	3(½)	SEM,TEM	11-A,B,C,D; 12-E	Asymmetric colpi, half pseudocolpi
Olinia radiata Hofmeyr & Phill.	Zululand	Wylie 8822	K	3(½)	SEM	10-A,B,C	Asymmetric colpi, half pseudocolpi

Olinia rochetiana A. Juss.	Malawi	Chapman 996	MO	3(½)	SEM,TEM	10-D,E,F; 12-A	Asymmetric colpi, half pseudocolpi
Olinia usambarensis Gilg. = O. rochetiana	Mt. Meru, Tanganyika	Greenway & Fitzgerald 14970	MO	3(½)	SEM,TEM	12-D	Asymmetric colpi, half pseudocolpi
Olinia cymosa (L.f.) Thunb. = O. ventosa	Cape Province, South Africa	Fries et al. 660	MO	3(½)	SEM	11-E,F; 12-B,C	Asymmetric colpi, half pseudocolpi
COMBRETACEAE							
Anogeissus acuminata Wall.	Burma	Po Chin 6100	MO	3	SEM	15-D,F	
Buchenavia suaveolens Eichler	Amazonas, Brazil	Gentry & Ramos 12906	MO	0	SEM	15-A,B,C	
Bucida macrostachya Standl.	Chiapas, Mexico	Breedlove 25160	MO	3	SEM	14-A	
Calycopteris floribunda (Roxb.) Poir.	Mysore, India	Saldanha 16363	MO	3	SEM	13-G	
Combretum cacoucia Exell	Stann Creek Distr., Belize	Dwyer et al. 552	MO	3	SEM	13-A,B,C	Spines
Combretum farinosum HBK.	Sinaloa, Mexico	Boke & Florantos 1	OKL	3	TEM	17-B,C	
Combretum laxum Jacq.	Loma Tequerre, Brazil	Duke 10994(3)	MO	3	TEM	17-A	
Conocarpus erecta L.	Sinaloa, Mexico	Waterfall 16249	OKL	3	SEM,TEM	14-B;17-E	
Guiera senegalensis Lam.	Cameroun	Leeuwenberg 7485	MO	3	SEM	15-E	
Laguncularia racemosa (L.) Gaertn.	Costa Rica	Croat 593 A	MO	0	SEM	16-E,F	
Lumnitzera racemosa Willd.	Eastern Province, Sri Lanka	Davidse 7545	MO	3	SEM	16-D	

Polyrea coccinea DC.	Tulear Prov., Madagascar	Croat 31768	MO	3	SEM	16-C	
Pteleopsis myrtifolia (Laws.) Engl. & Diels	Wankie Distr., Zimbabwe	Raymond 130	MO	3	SEM	14-C	
Quisqualis indica L.	Laguna, Philippines	Quisumbing Q-2160	OKL	3	SEM	13-F	
Ramatuella argentia Kunth	Venezuela	Maguire et al. 41879	MO	3	SEM	14-E,G	
Strephonema pseudocola A. Chev.	Tchien Distr., Liberia	Baldwin 8007	MO	0	SEM	16-A,B	
Terminalia catappa L.	Tulear Prov. Madagascar	Croat 30941	MO	3	SEM	14-F	
Terminalia edulis Blanco	Luzon, Philippines	Bernardo 23688	MO	3	TEM	17-D	
" "	Laguna, Philippines	Quisumbing Q-2156	OKL	3	SEM	14-D	
Thiola inundata Ducke	Amazonas, Brazil	Ducke 644	MO	3	SEM	13-D,E	
ALZATEACEAE							
Alzatea verticellata Ruiz & Pav.	Mendoza, Peru	Woytkowski 8331	MO	0	SEM,TEM	4-B,D;6-B,C	
PENAEACEAE							
Brachysiphon rupestris Sond.	South Africa	Dahlgren & Strid 3385	LD	3	SEM	19-D	
Endonema lateriflora (L. f.) Gilg.	South Africa	Dahlgren & Strid 4979	LD	3	SEM	19-A,B,C	
Penaea mucronata L.	Cape Prov., South Africa	Grant 2630	MO	4	SEM,TEM	18-A,B,C;20-A	Tetracolporate
Sonderothamnus petraeus (Sond.) R. Dahlg.	South Africa	Dahlgren & Strid 3654	LD	3	SEM,TEM	19-E,F;20-B,C	

Stylapterus ericoides A. Juss.	South Africa	Dahlgren & Strid 3365	LD	4	SEM,TEM	18-D,E,F;20-D	Tetracolporate
CRYPTERONIACEAE							
Axinandra zeylanica Thw.	Ratnapura Distr. Ceylon	Waas 1210	MO	3	SEM	21-A	
Dactylocladus stenostachys Oliv.	North Borneo	Hassan 732	A	3	SEM	21-B	
MELASTOMATACEAE							
Acanthella sprucei Hook. F.	Amazonas, Venezuela	Davidse 2793	MO	3	SEM,TEM	23-E;26-D	
Adelobotrys tessmannii Markgraf	Huanuco, Peru	Woytkowski 7850	MO	(3)(6)	SEM,TEM	24-A,B,C; 27-A,B	Some grains were cube shaped with 4 colpi and 8 *pseudocolpi* on its edges
Allomorphia caudata (Diels) Li	Yunnan, China	Henry 10761	MO	(3)	SEM	24-D	
Astronia cumingiana Vidal	Sarawak	James et al. S.34401	MO	(3)	SEM,TEM	24-E;27-C	
Bredia hirsuta Bl.	Tokunoshima, Japan	Iwatsuki 523	MO	(3)	SEM,TEM	24-F;27-F	
Dissochaeta celebica Bl.	Johore, Malaya	*Anderson 2667*	MO	3	SEM,TEM	23-F;26-B	
Dissotis brazzae Cogn.	Yala, Zaire	Agnew & Musumba 8572	MO	3	SEM,TEM	23-C,D;26-C	
Marumia nervosa Bl.	Selangor, Malaya	Ahmad S.A. 1080	MO	3	SEM,TEM	23-A,B;26-A	
Memecylon normandii Jacques-Felix	Ghana	Hall & Abbiw s.n.	MO	3	SEM	21-C	
Mouriri cf. *glazioviana* Cogn.	*Minas Gerais, Brazil*	*Anderson 8895*	MO	3	SEM	21-D	
Osbeckia polycephala Naud.	Matale Distr., Sri Lanka	Lazarides 7219	MO	3	SEM,TEM	22-B;25-D,E	

Oxyspora paniculata DC.	Yunnan, China	Henry 9010A	MO	(3)	SEM	24-G,H;27-D,E	
Tibouchina candolleana (DC.) Cogn.	Minas Gerais, Brazil	Williams & Assis 8044	OKL	3	TEM	25-C	
Tibouchina urvilleana (DC.) Cogn.	Cultivated at UCB: native Brazil	Schmid 1980-12	MO	3	SEM,TEM	22-C	
Tococa spadiciflora Triana	Carretera, Colombia	Forero et al. 5703	MO	?	TEM	28-A	Polyads
Tococa stephanotricha Naud.	Marischal Prov., Peru	Schunke 8106	MO	?	TEM	28-B,C	Triporate
Trembleya phlogiformis DC.	Minas Gerais, Brazil	Irwin et al. 19723	MO	3	SEM,TEM	22-A;25-B	
Tristemma littorale Benth.	Lagos State, Nigeria	Brown 938a	MO	3	SEM,TEM	22-D;25-A	
Votomita monadelpha (Ducke) Morley	Brazil	Ducke 18494	K	4	SEM	22-E,F	Tetracolporate
MYRTACEAE							
Acmena smithii (Poir.) Merrill & Perry	Victoria, Australia	Beauglehole & Finck ACB 32281	NSW	(3)	SEM	35-B	
Austromyrtus bidwillii (Benth.) Burret	New South Wales, Australia	W. Bauerlen 584	NSW	0	SEM	36-F	
Baeckea virgata Andrews	Cultivated at UCB; native Australia New Cal.	Schmid 1980-13		0	SEM	32-A	
Balaustion microphyllum C.A. Gardner	Western Australia	A.M. Ashby 312	NSW	0	SEM	32-C	
Callistemon speciosus (Sims) DC.	Cultivated in Berkeley, CA; native Australia	Schmid 1980-11	UC	(3)	SEM	31-B,D	
Callistemon teretifolius F. Muell.	Cultivated at UCB; native Australia	Schmid 1978-198	UC	(3)	SEM	31-A,C	
Calothamnus validus S.L. Moore	Cultivated at UCB; native Australia	Schmid 1980-14	UC	(3)	SEM	31-E	Some tetracolporate

Chamaelaucium uncinatum Schau.	Western Australia	Webster 18570	NSW	0	SEM	32-F,H	Some dicolporate
Cleistocalyx operculata (Roxb.) Merrill & Perry	Darwin, Australia	Byrnes 2786	NSW	(3)?'	SEM	35-A	
Eremaea pauciflora Domin	Western Australia	Coveny 8073	NSW	0	SEM	31-F	
Eucalyptus ficifolia F. Muell.	Cultivated at UCB; native Australia	Schmid 1980-10		(3)	SEM	30-C,D,E	
Eucalyptus robusta Smith	Michoacan, Mexico	Cutler 4044	OKL	(3)	SEM	30-F	
Eugenia capuli (Schl. & Cham.) Berg.	Cayo Distr., Belize	Croat 23525	OKL	0	SEM	35-C	
Eugenia elliptifolia Merrill	Leyte, Philippines	Wenzel 1248	MO	(3)	SEM	35-D	
Heteropyxis natalensis Harv.	Natal, South Africa	Davidson 2642	MO	(3)	SEM	30-A,B	
Homoranthus wilhelmii Cheel	Northern Eyre Peninsula, Australia	Alcock 4038	NSW	0	SEM	32-B	
Hypocalymna angustifolium Schau.	Western Australia	Coveny 8063	NSW	0	SEM	32-E,G	
Luma chequen (Molina) A. Gray	Cultivated at UCB; native Chile	Schmid 1978-194A	UC	0	SEM	35-E	
Melaleuca decussata R. Brown	Cultivated at UCB; native Australia	Schmid 1980-9	UC	0	SEM	33-C	
M. hypericifolia Smith	Cultivated at UCB; native Australia	Schmid 1978-195	UC	(3)	SEM	33-A,B	
M. preissiana Schau.	Cultivated at UCB; native Australia	Schmid 1978-196	UC	0	SEM	33-D	
M. pulchella R. Brown	Cultivated at UCB; native Australia	Schmid 1980-15	UC	0	SEM	33-G	Some grains tetracolporate
M. rhaphiophylla Schau.	Margaret River, West Australia	Earle 70	OKL	(3)	SEM	33-E	

Metrosideros nervulosa C. Moore & F. Muell.	Lord Howe Is., Australia		NSW 108602	(3)?	SEM	29-B	
M. polymorpha Gaud.	Oahu, Hawaii, USA	Chambers 3005	OKL	(3)?	SEM	29-A	
Myrceugenella apiculata DC.	Pucara Peninsula, Argentina	Dawson & Schwabe 203A	OKL	0	SEM	35-F	
Myrtus communis L.	Cultivated in Berkeley CA; native Europe	Schmid 1980-18	UC	0	SEM,TEM	36-B,C,D 37-A,B,C,D	Some tetrahedral tetrads
Osbornia octodonta F. Muell.	Idlers Bay, Papua New Guinea	Womersley NGF 14065	NSW	0	SEM	34-G	
Pilidiostigma glabrum Burret	New South Wales, Australia	Brown 1900	NSW	0	SEM	34-F	
Psidium littorale Raddi	Cultivated at UCB; native trop. Amer.	Schmid 1980-8		0	SEM	34-A,B,C	Some grains tetra-colporate, some tetrahedral tetrads
Psiloxylon mauritianum Baill.			MAU	0	SEM	33-F	Some grains tetra-colporate
Rhodamnia argentea Benth.	New South Wales Australia	Maiden & Boorman s.n.	NSW 138417	0	SEM	36-E	
Temu divaricatum Berg	Valdivia, Chile	Buchtien s.n.	NSW 144644	0	SEM	36-A	
Thryptomene calycina J.M. Black	Grampians, Victoria Australia	Beauglehole ACB 28154	NSW	0	SEM	32-D	
Tristania conferta R. Brown	Cultivated at UCB; native Australia	Schmid 1980-7	UC	(3)	SEM	29-C,D	
T. lactiflua F. Muell.	Western Distr., Papua, New Guinea	Henty & Foreman NGF 49383	MO NGF49383	(3)		29-F	
T. nereifolia R. Brown	New South Wales Australia	Constable 5566	K	0	SEM	29-E	Triporate?
Ugni molinae Turcz	Cultivated at UCB; native central/S. America	Schmid 1980-17	UC	0	SEM	34-D,E	Some grains di- or tetracolporate

ONAGRACEAE

Boisduvalia densiflora (Lindl.) S. Wats.	Washington, Whitman Co.	Piper s.n.	MO	0	SEM	41-B
B. densiflora (Lindl.) S. Wats.	Oregon, Marion Co.	Thompson 5099	MO	0	SEM	41-C
B. densiflora (Lindl.) S. Wats.	California, Shasta Co.	Heller 12448	MO	0	SEM	41-E
B. stricta (A. Gray) Greene	California, Plumas Co.	Jones s.n.	MO	0	SEM	41-A
Circaea alpina L. ssp. imaicola	Tibet, Tse-Kou	Monbeig s.n.	?	0	SEM	38-D
C. cordata Royale	Norway, Oslo	Cultivated at Mo. Bot. Garden	MO	0	SEM	38-C
C. mollis Sieb. and Zucc.	Japan, Kerita, Honshu	Togasi 1797	MO	0	TEM	42-D,F
Clarkia speciosa Lewis and Lewis ssp. speciosa	California, San Luis Obispo Co.	UCB 65.1421	UC	0	SEM	39-A,C
C. unguiculata Lindl.	Univ. Calif. Bot. Garden, cultivated	UCB 59.1244	UC	0	SEM	39-B,D,F
Fuchsia garleppiana Kuntze and Wittmark	Bolivia, Dept. Cochabamba	Linderman 2030	MO	0	TEM	42-A
F. michoacanensis Sesse and Mocino	Todos Santos, Mexico	Melhus & Goodman 3618	OKL	0	SEM	38-B
F. thymifolia HBK. ssp. thymifolia	Mexico, Michoacan	Waterfall 16474	OKL	0	SEM	38-A
Gaura lindheimeri Engelm. and Gray	Cultivated, Univ. of Calif., Los Angeles	Raven (in 1971)	LA	0	SEM	39-E
G. mutabilis Cav.	Mexico, Chihuahua	Jones (in 1903)	DS	0	SEM	39-G,H

Gongylocarpus fruticulosus ssp. glaber (J.H. Thomas) Carlquist and Raven	Mexico, Baja California	Moran 3529	DS	0	SEM	40-F
G. rubricaulis C. and S.	Mexico, Veracruz	Sharp 44846	MO	0	SEM	40-D
Hauya elegans DC. ssp. barcenae (Hensl.) Breedlove and Raven	Mexico, Chiapas	Breedlove 10229	MO	0	SEM	38-G
H. elegans DC. ssp. elegans	Mexico, San Luis Potosi	Moran 13387		0	SEM	38-E
H. elegans DC. ssp. elegans	Mexico, Queretaro	Rzedowski 9294	DS	0	SEM	38-F
H. heydeana Donn. Sm.	Mexico, Chiapas	Breedlove 15653	DS	0	TEM	42-C,E
Ludwigia alternifolia L.	North Carolina, Craven Co.	Peng 3738	MO	0	SEM	41-F
L. brevipes (Long) Eames	South Carolina, Lexington Co.	Godfrey & Tryon 1237	MO	0	TEM	42-B
L. goiasensis		Ramamoorthy 652			SEM	41-D,G
L. longifolia	Argentina, Tucuman	Venturi 2873	MO	0	SEM	41-H,I
Oenothera brachycarpa A. Gray	Mexico, Durango	Anderson 5207 cultivated, Stanford Univ.	MO	0	SEM	40-A,B
O. texensis Raven and Parnell	Texas, Jeff Davis Co.	Parnell s.n.	MO	0	SEM	40-C,E

1. The brackets ( ) in the column for Pseudocolpi mean that intercolpar concavities are recognized

2. Unless stated otherwise, all pollen grains are tricolporate