NEPHELIEAE POLLEN (SAPINDACEAE): FORM, FUNCTION, AND EVOLUTION

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CONTENTS

1. INTRODUCTION

The Sapindaceae have been intensively studied for the last few decades at the Rijksherbarium (Leiden) in the framework of the Flora Malesiana project, especially taxonomically, and to a lesser extent also pollen-morphologically. Although revision of individual genera is nearing its completion many problems, particularly relating to infratribal and intertribal affinities, remained unsolved. Several of these problems concern the Nephelieae. The subdivision of this tribe into groups is based on a few fruit characters only, and the delimitation from the tribe Cupanieae is very weak. Moreover, the infrageneric structure of the two largest genera (viz. *Alectryon* and *Nephelium*) still needs further elucidation. These taxonomic problems, the presence of taxonomic expertise and abundant, reliably identified materials at the Rijksherbarium, and the availability of recent monographs of nearly all genera led to the selection of the tribe Nephelieae as the object of a palynological monograph.

The description of form, the interpretation of function, and the reconstruction of evolution in Nephelieae pollen make up the main purpose of this study. A detailed description of the morphology of the pollen grain wall in the Nephelieae is provided. All genera of Nephelieae are included, even though several of them have been studied before. The improved scanning electron microscope technology permitted more detailed observations, which necessitated the reinvestigation and redescription of formerly studied material. Moreover, exhaustive sampling showed additional variation to occur, enabling extension of most of the previous descriptions. Following the proposal of Rowley (1976) to include ontogenetic studies as an integral part of pollen exploration, particularly if evolution is in question, attention is also paid to the immature pollen grain wall.

Muller (1979) and many others (see Blackmore & Ferguson, 1986) have demonstrated that form and function are closely interrelated in pollen grains. Consequently, interpreting the function of pollen structures is here considered complementary to describing their morphology. Furthermore, because functionally related structures may have evolved together, such an interpretation may shed light on evolution.

On the basis of different sources, including ontogeny, a functional interpretation, the fossil record, pollination biology, and macromorphology, an attempt is made to reconstruct the evolution of Nephelieae pollen. Finally, an evaluation of the results with respect to the taxonomy and phylogeny of the tribe Nephelieae is given.

Taxonomy of the Nephelieae

The tribe Nephelieae was established by Radlkofer (1931–1934) as one of the 14 tribes within the Sapindaceae. At first he included 16 genera in the Nephelieae. Using fruit characters he distinguished two groups (Radlkofer, 1931: 10–12): group A, embracing *Cubilia, Euphoria, Litchi, Nephelium, Otonephelium, Pometia, Pseudonephelium* and *Xerospermum,* and group B, embracing *Alectryon, Cnemidiscus, Heterodendrum, Omalocarpus, Pappea, Podonephelium, Smelophyllum* and *Stad-*

mania. Later (1934: 1498, 1501), Radlkofer joined *Pseudolitchi* to group A, and *Chiarinia* to group B. However, Capuron (1969) reduced *Omalocarpus* to *Deinbollia* (tribe Sapindeae), and *Pseudolitchi* to *Stadmania*. *Euphoria* and *Pseudonephelium* were united to form the genus *Dimocarpus* in the tribe Nephelieae (Leenhouts, 1971). *Cnemidiscus* was reduced to *Glenniea*, tribe Lepisantheae (Leenhouts, 1973, 1975). Ellis (in Sharma et al., 1977) wrongly transferred *Otonephelium* to *Lepisanthes*, tribe Lepisantheae (see chapter 9). The genus *Chiarinia* was reduced to *Lecaniodiscus*, tribe Schleichereae (Friis, 1981), and *Heterodendrum* to *Alectryon* (Reynolds, 1987).

Muller & Leenhouts (1976) maintained Radlkofer's subdivision into two groups, referring to these as the *Dimocarpus* group (group A) and the *Pappea* group (group B). The *Dimocarpus* group was considered as undoubtedly very coherent. Leenhouts (1978) presented a phylogenetic scheme of this group, in which he advanced the supposed interrelations between the genera. Several genera of the *Pappea* group appeared to be closely related too (Muller & Leenhouts, l.c.).

At present, the tribe Nephelieae comprises 12 genera. The revisions on which sampling for the present study was based are:

Alectryon Gaertn. (29)	Reynolds 1982, 1987; Leenhouts, 1987, 1988; Linney, 1988
Cubilia Blume (1)	Leenhouts, 1978
Dimocarpus Lour. (8)	Leenhouts, 1971, 1974; Reynolds, 1982
Litchi Sonn. (1)	Leenhouts, 1978
Nephelium L. (22)	Leenhouts, 1986
Otonephelium Radlk. (1)	Radlkofer, 1932
Pappea Eckl. & Zeyh. (1)	Exell, 1966
Podonephelium Baill. (4)	Radlkofer, 1933
Pometia Forst. (2)	Jacobs, 1962
Smelophyllum Radlk. (1)	Radlkofer, 1933
Stadmania Lam. (6)	Exell, 1964, 1966; Capuron, 1969
Xerospermum Blume (2)	Leenhouts, 1983

The total numbers of species within the tribe is 78. The number of species within each genus is given above between brackets. Infrageneric taxa are listed in chapter 3. The sections, groups and subgenera of *Alectryon* described by Radlkofer (1933) and Leenhouts (1988) have not been distinguished there, as a probably more satisfactory subdivision of the genus is in course of preparation (written comm. G.K. Linney, 1986, 1987, 1988; see also Leenhouts, 1988). This matter will be further discussed in chapter 9.

Distribution and ecology of the Nephelieae

The tribe Nephelieae occurs mainly in tropical and subtropical regions in Africa, Asia and Australia. A few species are found in New Zealand and on a number of smaller islands in the tropical part of the Pacific Ocean (fig. 1). The following list provides the distribution data of the individual genera (listed from west to east according to their westernmost stations).

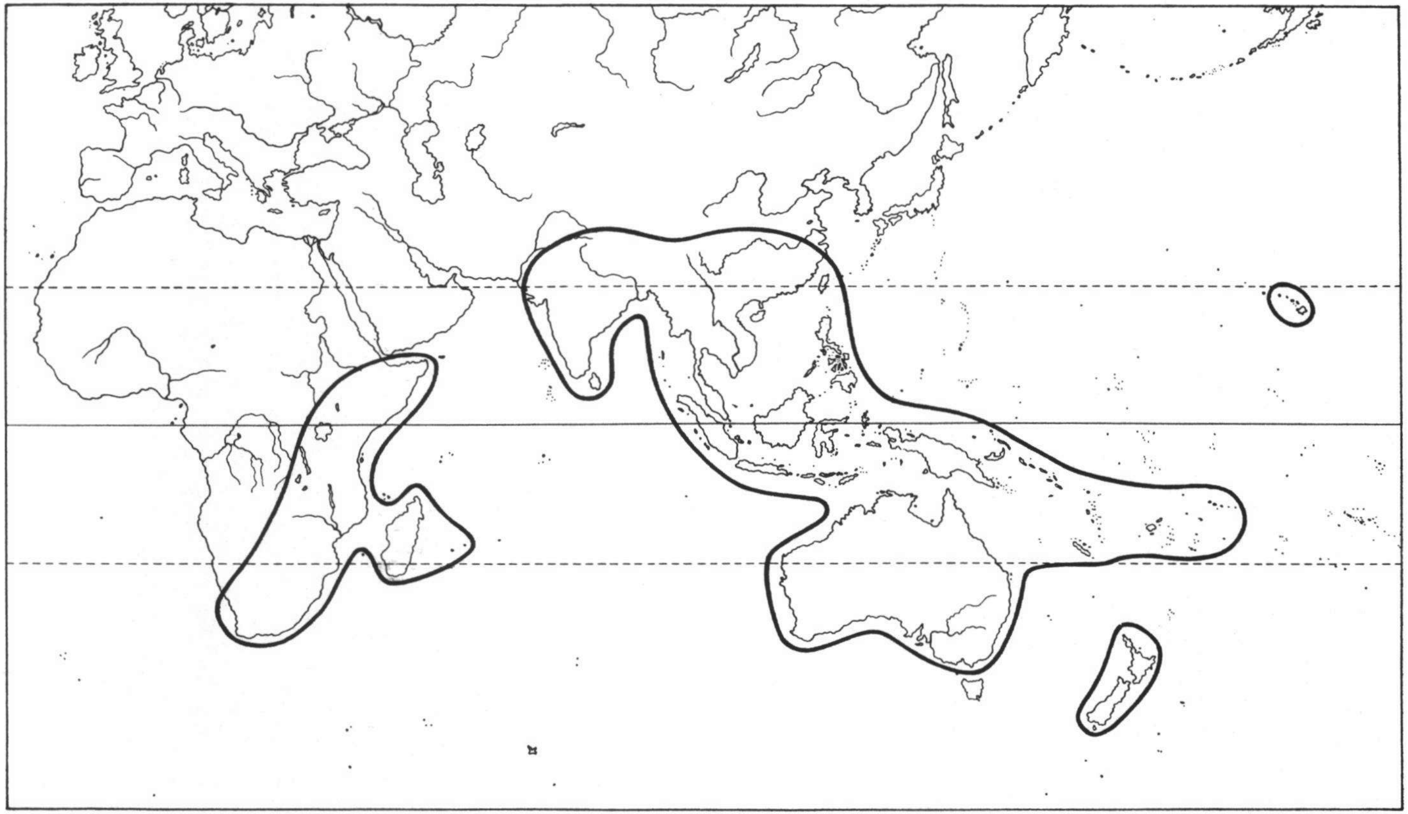


Fig. 1. Distribution of the Nephelieae.

Smelophyllum	S Africa
Pappea	S and continental E Africa
Stadmania	continental E Africa, Madagascar, Mascarene Islands
Otonephelium	S India
Dimocarpus	India, Ceylon, continental SE Asia, W Malesia, NE Australia
Pometia	Ceylon, continental SE Asia, Malesia, Solomon Islands, Santa Cruz Islands, New Hebrides, Fiji, Tonga, Samoa
Litchi	continental SE Asia, W Malesia
Nephelium	continental SE Asia, W Malesia
Xerospermum	continental SE Asia, W Malesia
Cubilia	Philippines, Borneo, Celebes, Moluccas
Alectryon	E Malesia, Australia, New Zealand, Solomon Islands, New Hebrides, New Caledonia, Fiji, Samoa, Hawaii
Podonephelium	New Caledonia

Species of several genera, in particular *Dimocarpus longan* (subsp. *longan* var. *longan*), *Litchi chinensis* (subsp. *chinensis*) and *Nephelium lappaceum* (var. *lappaceum*), are commonly cultivated for their fruits. Due to naturalisation it is difficult now to determine the limits of the natural distribution of such species (Leenhouts, 1971, 1978, 1986).

Nephelieae are trees or shrubs. They grow in a wide range of habitats, including rainforests, savannas and scrubs. Some *Alectryon* species even extend to the margins of deserts.

Nephelieae pollen in literature

Several old publications give data on Sapindaceae pollen. For example, Mohl (1835) distinguished three types, in which he accommodated 12 species belonging to 9 genera: the oblate porate type a, the oblate colporate type b, and the spherical or prolate colporate type c. Two Nephelieae were mentioned: *Litchi chinensis* (as *Euphoria punicea*) and *Nephelium lappaceum*. Both species have type c pollen, which was described as "Sphérique ou ovoïd; trois plis; dans l'eau sphère à trois bandes avec des papilles sur les bandes."

Radlkofer (1932, 1933) was the first to describe Nephelieae pollen in a systematic manner. He included pollen-morphological data in the descriptions of all genera except *Pseudolitchi* and *Smelophyllum*. His original diagnoses are:

Alectryon	pollinis granula subglobosa veltrigono-placentiformia, 3-sulcata, 3-porosa
Cubilia	pollinis granula inter minora (diametro circ. 0.009 mm), trigono-globosa, triporosa
Euphoria	pollinis granula trigono-placentiformia, 3-porosa
Heterodendrum	pollinis granula trigono- vel suborbiculari-placentiformia, 3–4-porosa, laevia vel punctata
Litchi	pollinis granula trigono-placentiformia, 3-porosa
Nephelium	pollinis granula trigono-placentiformia, 3-porosa
Otonephelium	pollinis granula trigono-placentiformia, triporosa

Pappea	pollinis granula trigono-placentiformia, triporosa, quam in *Cubilia* duplo majora
Podonephelium	pollinis granula ellipsoidea, trisulcata, triporosa
Pometia	pollinis granula trigono-placentiformia, 3-porosa, exine subtiliter reticulata
Pseudonephelium	pollinis granula subglobosa, triporosa
Stadmania	pollinis granula trigono-placentiformia, triporosa
Xerospermum	pollinis granula trigono-placentiformia, triporosa

At present *Euphoria* and *Pseudonephelium* form the genus *Dimocarpus*; *Heterodendrum* was reduced to *Alectryon* (see Taxonomy of the Nephelieae).

Radlkofer always mentioned the shape of the pollen grain (usually triangular oblate) and the number of apertures (nearly always three). For *Heterodendrum* and *Pometia* he provided also information about the ornamentation of the outer part of the pollen grain wall. Conscientiously he gave details regarding grain size in *Cubilia,* and he noticed the deviating grain shape in *Podonephelium.* Infrageneric variation was found in *Heterodendrum*: "pollinis granula laevia" in *H. macrocalyx* (= *Alectryon oleifolius* subsp. *canescens*) and "pollinis granula inter majora punctulata" in *H. oleifolius* (= *Alectryon oleifolius* subsp. *oleifolius*). However, he generally failed to recognise the compound nature of the apertures (ectoapertures colpate, endoapertures porate), denoting them mostly as porate. Only for *Alectryon* and *Podonephelium* did he also mention the colpate ectoapertures ("sulcata").

Monographic study of Nephelieae pollen was not undertaken until the early seventies. Muller (1971) reported on the pollen morphology of 5 species of *Dimocarpus.* Pollen of this genus turned out to be rather uniform, justifying only a subdivision into subtypes. Some infraspecific variation was noticed and several evolutionary trends were established and related to taxonomy. Because of increased complexity the striate pollen subtypes (group II) were thought to have originated from the psilate and perforate/reticulate subtypes (group I). An additional observation was that macromorphologically advanced taxa appeared to possess advanced pollen subtypes. Further study, especially of the variable *Dimocarpus longan,* was recommended. Leenhouts (1974) reported on the pollen morphology of the newly described *D. australianus.*

Muller & Leenhouts (1976) presented a survey of sapindaceous pollen types in relation to taxonomy. They distinguished 12 pollen types based on aperture characters. In the Nephelieae two types were found: the colporate type A, which was considered the basic, most primitive type in the family, and the derived type C1 with reduced ectoapertures. The latter type was found only in *Pometia,* the genus that also proved to be macromorphologically the most derived in the tribe. On the basis of its reticulate ornamentation and highly specialised endoapertures a major pollen-morphological gap was determined within the Nephelieae. The (para)syncolporate pollen type B, which is rather common in the family, and which occurs in various *Alectryon* species, was not mentioned for the Nephelieae. This is due to the method of sampling, mostly involving only one or a few species per genus.

Van den Berg (1978) monographed *Pometia* pollen. He suggested that an endexine is absent, thus further consolidating the pollen-morphological gap within the tribe. He also studied pollen of the allegedly related genera *Cubilia, Litchi* and *Otonephelium*. Pollen of *Nephelium* and *Xerospermum* was only provisionally examined. *Cubilia* pollen was found to differ in its small size and echinate ornamentation. *Litchi* pollen showed variation of its striate ornamentation. Finely, regularly striate ornamentation was denoted as possibly more primitive than irregularly striate or striate/reticulate and striate/perforate ornamentation. Van den Berg established three pollen types in the *Dimocarpus* group: the *Pometia* pollen type, including *Pometia* pollen, the *Cubilia* pollen type, including *Cubilia* pollen, and the *Litchi* pollen type, including pollen of *Litchi, Nephelium, Otonephelium* and *Xerospermum*. *Dimocarpus* pollen was not included in one of these types, though the striate *Dimocarpus* subtypes were connected with the similarly striate *Litchi* type. The finely reticulate *Dimocarpus* subtypes were tentatively connected with the reticulate *Pometia* type. According to van den Berg the three pollen types could reflect three different lines of descent in the *Dimocarpus* group. Pollen-morphological relations in the *Dimocarpus* group were considered to be in accordance with the macromorphological relations proposed by Leenhouts (1978).

Muller (1979) discussed the variation of the striate ornamentation in *Litchi chinensis*. In contrast with van den Berg (1978) Muller considered this variation to reflect stages in the evolution from a basically reticulate tectum towards a finely striate tectum. Ridges would probably have developed over a finely reticulate tectum.

Van der Ham (1988), in a short note on Nephelieae pollen, distinguished three harmomegathic types. Type 1 occurs in colporate pollen with long ectoapertures (all genera except *Pometia*), type 2 in colporate pollen with short ectoapertures (*Pometia*), and type 3 in parasyncolporate pollen (*Alectryon,* partly).

Ke et al. (1988a, 1988b) studied the pollen morphology of 11 cultivars of *Dimocarpus longan*. Prominent striate ornamentation was considered derived, whereas less prominent striate ornamentation was denoted to be primitive.

Liang et al. (1988) investigated ornamentation in pollen of 37 cultivars of *Litchi chinensis* subsp. *chinensis*. They reported a wide range of variation, from striate to "pseudo-reticulate", and stated each cultivar to have its own characteristic pattern.

Muller & Schuller (1989) studied pollen of *Stadmania* (except for *S. excelsa*) from Madagascar and the Mascarene Islands. Both striate and perforate ornamentation were found in this genus.

In addition to these monographic studies, abundant literature exists that includes only one or a few species, and usually has a pollen-floristic or melitopalynological nature:

Chang, 1982	*Dimocarpus, Litchi, Nephelium, Pometia*
Chang & Wang, 1965	*Dimocarpus, Litchi*
Chen, 1986	*Dimocarpus, Litchi*
Chen et al., 1986	*Dimocarpus, Litchi*
Cranwell, 1942	*Alectryon*
Cranwell, 1962	*Alectryon*
Erdtman, 1952	*Alectryon*
Erdtman, 1960a	*Pometia*

Erdtman, 1962	*Pometia*
Erdtman, 1969	*Pometia*
Huang, 1968	*Dimocarpus, Litchi, Pometia*
Huang, 1972	*Dimocarpus, Litchi, Pometia*
Liu, 1986	*Pometia*
Macphail, 1981	*Alectryon*
Rao & Lee, 1970	*Pometia*
Rao & Tian, 1974	*Nephelium*
Selling, 1947	*Alectryon*
Wang, 1962	*Dimocarpus, Litchi*
Wang & Chien, 1956	*Dimocarpus, Litchi, Pometia*

Several authors dealt with microsporogenesis and/or pollen germination in vitro in various Nephelieae:

Ha et al., 1988	*Nephelium, Pometia, Xerospermum*
Lim, 1984	*Nephelium*
Liu, 1954	*Litchi*
Mustard et al., 1954	*Litchi*
Singh, 1963	*Litchi*
Singh & Shiam, 1977	*Litchi*

Fossil pollen

Fossil Nephelieae pollen is hardly known. The colporate *Alectryon* cf. *excelsus* pollen was found in the Miocene and Pleistocene of New Zealand (Couper, 1953), and the parasyncolporate *Alectryon macrococcus* pollen in Quaternary samples from Hawaii (Selling, 1947, 1948). However, parasyncolporate *Alectryon* pollen may also have been recorded as *Cupanieidites*. This is a fairly widespread form genus, known from the Turonian onwards (from the Palaeocene in the present distribution of *Alectryon*), and is the oldest fossil pollen attributed to the Sapindaceae (Muller, 1981a). Parasyncolporate pollen is also produced by various representatives of the tribes Melicocceae and Schleichereae (Muller & Leenhouts, 1976). Thus, it appears that the form genus *Cupanieidites* must be assigned a larger taxonomic circumscription within the Sapindaceae than just the tribe Cupanieae. See further chapter 8.

Muller (1964, 1972) mentioned *Pometia* pollen for Tertiary deposits in NW Borneo. Anderson & Muller (1975), Muller (1981a) and Muller & Leenhouts (1976) acknowledged the presence of *Pometia* pollen in (Late) Miocene sediments in (NW) Borneo, and Barré-de Cruz (1982) in Late Miocene and Quaternary sediments in E Borneo. Kedves (1989) noticed the resemblance of *Pometia* pollen with *Atlantopollis,* a form genus in the Normapolles group known from the Upper Cretaceous of N America and W Europe (see further chapter 6.10).

Pollen of *Smelophyllum capense* was found in Quaternary samples from South Africa (Martin, 1968).

2. METHODOLOGY

> *"In fact, the name pollen just means dust. But, as seen with the microscope's eye, it is a vast assemblage of independent organisms. There are hundreds or thousands of them in the least smear of pollen, but each one is an individual and as much entitled to individual consideration as the plant which produced it."*
>
> Wodehouse, 1935

Sampling and observation

The sampling and observation techniques applied in this study are explained in chapter 4. However, a few remarks pertinent to the extent of sampling and observation are of present interest.

Ideally, the whole range of variation occurring in a taxon should be studied. One may not content oneself with random sampling. First, completeness has to be pursued by sampling all available taxa. Next, variation must be traced within these taxa, meanwhile carefully watching intra-individual variation. Much variation was found to occur in Nephelieae pollen, which implied intensive sampling, 454 samples covering 75 species (see chapter 3). *Dimocarpus longan* was most intensively sampled: 80 samples cover 4 infraspecific taxa.

Important pollen features are often beyond the resolution of the light microscope. In such cases the scanning electron microscope furnishes valuable additional information. If variable characters turn out to be involved – obviously, this occurred in Nephelieae pollen – scanning electron microscopy must be regarded as a routine procedure rather than simply a method.

Description

Describing Nephelieae pollen is focused on the level of the tribe and the genus. The pollen of each genus is described in detail. Data pertinent to individual species are given in tables, remarks, and under headings such as Infrageneric variation and Geographical aspects. Ontogeny and function are treated separately. Determining ontogeny and function involves more deduction than describing adult morphologies because they are dynamic processes. In ontogeny a continuous development has to be studied, but only a limited number of stages is known. Studying function is hampered by the lack of living pollen grains. However, careful observation of acetolysed grains combined with simple experiments with unacetolysed material obtained from dried herbarium specimens still provided some information (see chapter 7.1: Harmomegathic types). Actually, as this study did not include living pollen grains, it is more correct to speak of a functional interpretation of form rather than a study or a description of function.

Morphological series and evolutionary trends

In this study several morphological series (transformation series) are deduced from the variation (character states) of various pollen characters (e.g. apertural system, ornamentation). In order to hypothesise the evolution of the characters (polarity of the morphological series) such information may be processed together with other data with a cladistic program, or it may be compared with the results of a cladistic analysis of these data. However, various circumstances are disadvantageous to such a procedure in the Nephelieae. Up to now, only very few cladistic analyses of taxa of Sapindaceae have been undertaken, and none of these pertains to the Nephelieae. An outline cladogram of the family based on suprageneric taxa is also lacking. It was realised too late that the Nephelieae and some of its genera are possibly not monophyletic. Though recent taxonomic revisions of many genera of Sapindaceae are available now, it was considered unfeasible to construct appropriate data matrices and cladograms based on macromorphological features in the framework of the present pollen-morphological study. Cladograms based on pollen-morphological data alone are unfeasible because there are too few characters in proportion to the number of taxa. In addition, most characters show continuous ranges of variation, similarly in several genera.

Therefore a different, more conventional approach was made. Starting from the ranges of variation within single genera and species morphological series were established. Homology of the extreme character states is indicated by the continuity through intermediate forms, which is a morphological criterion, not a phylogenetic one (see Wiley, 1981). Then it was attempted to polarise each morphological series into an evolutionary trend (Punt, 1967, 1975), i.e. to determine which character state of a pair of homologues is the more primitive one (the plesiomorphic state) and which the more derived (the apomorphic state). Hennig (1966) recognised one major criterion and four accessory criteria for polarising a morphological series The major argument is outgroup comparison (if several states of a character occur in a monophyletic group, then the state occurring outside this group is the plesiomorphic state). The four accessory arguments are: geologic character precedence (the older state of a pair of homologues is the plesiomorphic one), chorological progression (plesiomorphic states are found in the centre of origin of a group), correlation of transformation series (two or more morphological series within a single taxon have the same polarity), and ontogenetic precedence (in an ontogeny apomorphies occur later than plesiomorphies). All these criteria have been used in the present study, and data from several other sources of information, including functional pollen morphology and pollination biology, were added. It is realised that the validity of the above criteria is much debated (see e.g. de Jong, 1980; Wiley, 1981, 1987; Williams et al., 1990). For instance, the ontogenetic criterion must be used with great care, as it cannot be supposed that reversals are rare. They may 'easily' originate by paedomorphosis (retention of an ancestral juvenile character by later ontogenetic stages of descendants). The palaeontological criterion must be based on data from the relevant group. Resemblance with 'primitive angiosperm pollen' does not permit the assumption that a certain character state or pollen type represents a plesiomorphy. A general drawback of the fossil pollen record is that simple forms are poorly identifiable. Actually they may belong to many different families (van Steenis, 1986). In Nephelieae pollen the colporate type in particular suffers from this restriction. Nevertheless, it is thought that, for the time being, the applied criteria are useful in reconstructing the evolution of Nephelieae pollen. In due time, the data and ideas presented in this study may be processed according to the transformational approach to phylogenetics, in which polarised morphological series are used to construct cladograms (Hennig, 1966; Weston, 1988), and they may be compared with the results of the pattern approach, in which the polarity of the series follows from the analysis (Nelson & Platnick, 1981; see also Williams et al., 1990).

3. MATERIAL

Of the total number of 78 species in the Nephelieae 75 species were available for sampling of pollen. The following account provides data of the sampled collections. The material mentioned by Muller (1971), van den Berg (1978) and Muller & Schuller (1989), which is revised in the present study, is also included. The names of the taxa are alphabetically arranged.

Whole acetolysed mature grains of nearly all 454 samples were studied with both LM and SEM. The superscript numbers given in addition to the data of a part of the collections refer to the other techniques applied:

1 = sectioned acetolysed mature grains studied with SEM
2 = unacetolysed mature grains studied with TEM
3 = acetolysed mature grains studied with TEM
4 = unacetolysed grains from dehisced anthers studied with LM
5 = acetolysed immature grains studied with LM and SEM
6 = sectioned acetolysed immature grains studied with SEM
7 = unacetolysed immature grains studied with TEM

The collections are kept in the Rijksherbarium, Leiden (L), unless indicated otherwise (see Holmgren et al., 1981 for the explanation of the abbreviations). The pollen preparations are all kept in the Rijksherbarium.

Alectryon Gaertn.

A. affinis Radlk. — New Guinea: Fitzgerald 23 (M), 28^{1} (M).

A. cardiocarpus Leenh. — New Guinea: Brass 1618^{1} (BRI).

A. carinatus Radlk. — New Caledonia: Däniker 2320^{2}, Lécard sh. 949.111-378, MacKee 42151^{1}.

A. connatus (F. Muell.) Radlk. — Australia: Bird s.n. (BRI), Blake 12750 (BRI), 18922 (BRI), Dallachy s.n.^{5} (MEL), Dietrich 1371^{1}, Goodall 11 (BRI), Heinse s.n. (MEL), Leach s.n.^{1,2,4} (BRI).

A. coriaceus (Benth.) Radlk. — Australia: Anon. sh. 1536252 (MEL), Byrnes 3491 (BRI), Durrington 613^{1,2} (BRI), Hyland 9628^{1} (BRI), Irvine 1741^{1} (BRI), Sharpe 2129 (BRI), Sharpe & Durrington 865 (BRI), Simmonds s.n. (BRI).

A. diversifolius (F. Muell.) S. Reyn. — Australia: Clemens s.n.^{1} (K), Mueller s.n. in Herb. Hookerianum^{1} (K).

A. excelsus Gaertn. — New Zealand: Buchanan s.n.^{1} (MEL), Dallachy s.n.^{1} (MEL), Gardner 2607, Goulding 620, van Steenis 22411, Travers s.n. (M), Travers s.n.^{5} (MEL), van Zanten 1301^{2,5}.

A. *ferrugineus* (Blume) Radlk. — New Guinea: Brass 27257, Clemens 698, 1579, Darbyshire 1133, Hoogland 3926 (CANB), LAE 56263, NGF 1668, 15851, 27583[1, 2], 37472.

A. *forsythii* (Maiden & Betche) Radlk. — Australia: Forsyth s.n. (M), Gray 2513 (CANB), Rodd 2458[1, 2] (BRI).

A. *fuscus* Radlk. — Philippines: FB 25472[1] (K).

A. *glaber* (Blume) Radlk. — Java: Koorders 1898[1] (M), Labillardière s.n. in Herb. Webbianum (FI) — Philippines: PNH 80773 — Celebes: van Balgooy 2990.

A. *grandifolius* A.C. Smith — Fiji: Parham, Dept Agric. HI 5835[1, 2] (BISH), Smith 713 (NY), 1055[1] (NY).

A. *grandis* (T. Kirk) Cheeseman: not available.

A. *kangeanensis* Leenh. — Kangean: Backer 29552[1].

A. *kimberleyanus* S. Reyn. — Australia: Beard 8484 (PERTH), Kenneally 8578[1], Tracey 13961 (BRI).

A. *macrococcus* Radlk. var. *auwahiensis* G. Linney — Hawaii: Rock 8642[1] (M); var. *macrococcus* — Hawaii: Degener 9536[1], 10906[1, 2] (NY), 20689 (NY).

A. *myrmecophilus* Leenh. — New Guinea: NGF 4077[1, 2], 5279[2] (BRI), 7406.

A. *oleifolius* (Desf.) S. Reyn. subsp. *canescens* S. Reyn. — Australia: Lothian 3286[4], Smith 6059[1, 2], Speck 1812[1]; subsp. *elongatus* S. Reyn. — Australia: Smith 4520[1]; subsp. *oleifolius* — Australia: Anon. sh. 198223[1, 2].

A. *pubescens* S. Reyn. — Australia: Hockings 17[1] (BRI).

A. *ramiflorus* S. Reyn. — Australia: Zillmann AQ 425108[1], 425109.

A. *repandodentatus* Radlk. — New Guinea: Chalmers s.n.[1] (MEL), Lawrie 29 (BRI), Pullen 6908.

A. *reticulatus* Radlk. — New Guinea (isl. in Gulf of Papua): Anon. s.n.[1] (M) — Australia (isl. in Torres Strait): Hartmann sh. 1537050[1] (MEL).

A. *samoënsis* Christoph. — Samoa: Whistler 20[1] (BISH), 963 (BISH).

A. *semicinereus* (F. Muell.) Radlk. — Australia: Anon. sh. 908.269-1375, Volck 1414[1].

A. *subcinereus* (A. Gray) Radlk. — Australia: Blake 2885, 23747, Floyd 775[1, 2] (BRI), Maiden 1664 (M), Michael 2144 (BRI), Moore s.n. (MEL), NSW 106396[4], White 8566 (BRI).

A. *subdentatus* (Benth.) Radlk. forma *pseudostipularis* Radlk. — Australia: Crawford s.n. (MEL), Forster 1594 (BRI), Hando 138 (BRI), Lam 7632, Williams s.n.[1, 2] (BRI); forma *subdentatus* — Australia: Cambage 3650 (K), Dunn s.n.[5] (K), Longman s.n.[1] (K), Stuart s.n.[1] (M).

A. *tomentosus* (F. Muell.) Radlk. — Australia: Anon. sh. 1537043 (MEL), 1537045 (MEL), Anon. s.n. (M), Blake 2337[1], Gray 372 (BRI), Simmonds s.n. (BRI), Webb & Tracey 13313 (BRI), Williams s.n. (BRI).

A. *tropicum* S. Reyn.: not available.

A. *unilobatus* S. Reyn. — Australia: Hegarty C 3[1] (BRI), Morton 1238[1] (BRI), Webb & Tracey 13390 (BRI).

Cubilia Blume

C. *cubili* (Blanco) Adelb. — Philippines: Elmer 13262, FB 1996 (BO), Merrill Sp. Blanc. 705, PNH 22872[1, 3, 4] — Borneo: Kostermans 13874, SAN 28336, 54920[1] — Celebes: Koorders 22616β, NIFS Cel./V-236[1, 5] — Java: Backer 15203 (BO), Backer s.n. (BO), Hort. Bogor. III-C-18 (BO), Koorders 39421/3 (BO).

Dimocarpus Lour.

D. *australianus* Leenh. — Australia: Gittens 2162, Hyland 2835, Smith 11847[1, 2].

D. *dentatus* Leenh. — Borneo: Endert 5129, 5414, Kostermans 6893[1], SAN 38200[1], 54466[1, 2], 62966.

D. foveolatus (Radlk.) Leenh. — Philippines: BS 7370[1] (M).

D. fumatus (Blume) Leenh. subsp. *fumatus* — Thailand: Geesink & Hattink 6435[1] — Borneo: A 853, Endert 5243, S 23271, SAN 43178, 44665[1,2]; subsp. *indochinensis* Leenh. — Vietnam: Eberhardt 4803[1] (P); subsp. *javensis* (Radlk.) Leenh. — Java: Koorders 11130[1] (BO); subsp. *philippinensis* Leenh. — Philippines: Elmer 15389[1], 15470, PNH 34530.

D. gardneri (Thw.) Leenh. — Ceylon: Cramer 3038[5], Meijer 345[1,5], Thwaites CP 1154[1].

D. leichhardtii (Benth.) S. Reyn. — Australia: Leichhardt sh. 74654[1] (MEL).

D. longan Lour. subsp. *longan* var. *longan* — India: Griffith KD 998, Koelz 25001[1], Kostermans 26018, RTH 26927, Subramanian 1564 — Ceylon: Jayasuriya 1745, Kostermans 25282[1], Waas 1637 — China: Yip 161 — Taiwan: Tanaka & Shimada 10979 (SING) — Hainan: How 70390 — Vietnam: Balansa 3420 (P) — Thailand: Beusekom & Santisuk 2852[5] — Java: Anon. sh. 908.272-802, 908.272-822, Popta 863/210 — New Guinea: Hartley 12197, NGF 17203; var. *longepetiolulatus* Leenh.: not available; var. *obtusus* (Pierre) Leenh. — Vietnam: Pierre 4115 (P), Poilane 127 (P); subsp. *malesianus* Leenh. var. *echinatus* Leenh. — Borneo: SAN 26910 — Philippines: Santos 4124; var. *malesianus* — Burma: Parker 2717 (K) — Vietnam (Con Son): Pierre 4114 — Malaya: Goodenough 1904 (SING), Griffith KD 999, KEP 104556, KEP FRI 8394, 14515, 17981, KL 2856[1], 3268, SF 23885 (SING), Soepadmo & Mahmud sh. 255739[1] — Sumatra: Gusdorf 37, NIFS T 713, Overstreet 512, Posthumus 963 — Borneo: Elmer 21354 (BO), Endert 4716, Kostermans 5331, 6802, 21067, NBFD 5227, NIFS bb 13299, Nooteboom 4250[1], Rahayu 165, S 23044[1], 23086[2,5], 23460, 25025, 26148[1,2,5], 35239, 41214, 43524, SAN 25611, 31095, 31241[5], 31374, 35447, 38203[5], 43034, 54879, 62963[1,2], 66273, 91011[1] — Philippines: ANU 1602[5], BS 16156, 18762, Cuming 1131, Elmer 13482[1], FB 331 (K), PNH 16713, 32819, 37299, 98640, Ridsdale 861, Vidal 221[1], Williams 2899 (K) — Celebes (Muna): NIFS bb 21771.

Dimocarpus spec. (probably new according to a manuscript note by P.W. Leenhouts) — Borneo: S 14972[1,5].

Litchi Sonn.

L. chinensis Sonn. subsp. *chinensis* — India: Gandhe 32 (SING) — Hainan: Lei 465[1] — Thailand: Maxwell 76-27, — Vietnam: d'Alleizette sh. 951.65-553, Poilane 11991[1,3,5], 11994; subsp. *javensis* Leenh. — Java: Anon. sh. 908.270-267[1], Blume sh. 908.270-273[1], Boerlage sh. 908.352-1318; subsp. *philippinensis* Leenh. forma *genuina* Radlk. — Philippines: BS 17429[1,5], FB 2812 (SING), Vidal 722[1]; forma *mindanaensis* Radlk.: not available.

Nephelium L.

N. aculeatum Leenh.: not available.

N. compressum Radlk. — Borneo: Haviland 2270[1,2], 3175[1] (K).

N. costatum Hiern — Malaya: KEP 98852[1], Maingay KD 440.

N. cuspidatum Blume — Thailand: Bunnap 372 — Borneo: SAN 75983; var. *bassacense* (Pierre) Leenh. — Thailand: Kerr 16434[1]; var. *cuspidatum* subvar. *cuspidatum* — Borneo: Endert 2285, Korthals sh. 908.269-1490; subvar. *dasyneurum* (Radlk.) Leenh. — Sumatra: Forbes 2842; var. *eriopetalum* (Miq.) Leenh. — Sumatra: Grashoff 723, Kostermans & Anta 726 — Borneo: Chin See Chung 2774, Endert 4867[1,5], SAN 35848, 89304[2]; var. *multinerve* (Radlk.) Leenh.: not available; var. *ophiodes* (Radlk.) Leenh. subvar. *beccarianum* (Radlk.) Leenh. — Borneo: S 36665; subvar. *ophiodes* — Malaya: King's collector 5481 (MEL), Maingay KD 453; var. *robustum*: not available.

N. daedaleum Radlk. — Borneo: S 36914, SAN 60511[1,2].

N. hamulatum Radlk. — Malaya: KEP 10528[1] (K).

N. havilandii Leenh. — Borneo: Haviland 1862[1,2].

N. hypoleucum Kurz — Burma: Dickason 6802[2], 6861, Kyi 12270 —Thailand: Bunchuai 1604[1], Kerr 11590, Maxwell 76-8, 76-21, 76-36 — Vietnam: Pierre 875, Poilane 2503[2].

N. juglandifolium Blume — Sumatra: Achmad 1275 — Java: Hort. Bogor. III-E-25a[1].

N. lappaceum L. var. *lappaceum* — Thailand: Kerr 11957[1] —Malaya: KEP 99135[1,2], Maxwell 82-94 — Sumatra: de Wilde & de Wilde-Duyfjes 16552 — Java: Anon. sh. 908.269-1398 — Borneo: Haviland 2275, NBFD 3693, SAN 60898 — Philippines: PNH 22998 — Moluccas: Anon. sh. 908.272-61; var. *pallens* (Hiern) Leenh. — Hainan: Lei 431 — Malaya: Soepadmo & Mahmud 1199[1] — Sumatra: Lambach 1295 — Borneo: Korthals sh. 908.269-1400[1], S 36737 — Celebes: NIFS Cel./V-196[1]; var. *xanthioides* (Radlk.) Leenh. — Borneo: Kostermans 12534b[1].

N. laurinum Blume — Malaya: KEP 4752 (K), 17108 (K), Maingay KD 452 (K), Maxwell 80-126[1], SF 28625 (K).

N. macrophyllum Radlk. — Borneo: S 25393[1] (K).

N. maingayi Hiern — Malaya: KEP 527, 10469, Wray 190 — Sumatra: Rahmat si Boeea 8902[1] — Borneo: van Niel 4273, SAN 65365[2].

N. meduseum Leenh. — Borneo: S 37985[1] (K).

N. melanomiscum Radlk. — Borneo: Beccari PB 3918[1] (K).

N. melliferum Gagnepain — Thailand: Put 3570[1] — Vietnam: d'Alleizette 1421[1].

N. papillatum Leenh. — Borneo: SAN 38659[1].

N. ramboutan-ake (Labill.) Leenh. — Malaya: Sinclair sh. 954.167-305 — Sumatra: Meijer 5991 — Java: Blume sh. 908.272-48 — Borneo: A 2733[5], SAN 36302[1] — Philippines: PNH 22808, Rojo 44[1].

N. reticulatum Radlk. — Borneo: Chin See Chung 2794[1].

N. subfalcatum Radlk. — Malaya: KEP FRI 7720 — Sumatra: NIFS T 712[1,2] — Borneo: S 25991[1].

N. uncinatum Leenh. — Borneo: Endert 5069, Kostermans 6376[1], 6527, SAN 69295[2].

Nephelium spec. nov. — Malaya: KEP FRI 19144[1], 19145.

Otonephelium Radlk.

O. stipulaceum (Bedd.) Radlk. — India: Anon. s.n. in Herb. Hookerianum[5,6,7] (K), Pascal 1375[1,5] (HIFP).

Pappea Eckl. & Zeyh.

P. capensis Eckl. & Zeyh. — Ethiopia: Gillett 5058[1] (K) — Somalia: Gillett & Watson 23522 (K) — Uganda: Anon. 346 (K), Eggeling 2346 (K), Jarrett 452 (K) — Kenya: Herlocker 211 (K) — Rwanda: Troupin 4935[1,2] (K) — Tanzania: Semsei 2190 (K) — Zambia: Kemp 721 (MO), Fanshawe 4497 (K) —Zimbabwe: Chase 7671 (K) — Swaziland: Compton 26420 (K) — South Africa: Anon. sh. 898.269-427, Conrath 295 (K), Dyer 1181a[2,5], Hardy & Bayliss 1204[1] (K), Long 233 (K), Rogers 30185 (K).

Podonephelium Baill.

P. concolor Radlk. — New Caledonia: d'Alleizette 1425[3], Vieillard 2395[1] (K).

P. homei (Seem.) Radlk. — New Caledonia: MacKee 3589[5], MacMillan 5057a[2,5], MacPherson 5036; forma *gongrocarpum* Radlk.: not available; forma *homei* — New Caledonia: Vieillard 219[1] (K).

P. parvifolium Radlk. — New Caledonia: MacKee 25665[1].

P. subaequilaterum Radlk. — New Caledonia: Franc 719[1,5] (K).

Pometia Forst.

P. pinnata Forst. — Borneo: NBFD 9087[4], NIFS bb 13329[1], S 38483[5] — New Britain: NGF 21900; forma *acuminata* Jacobs — Borneo: Haviland 134, S 19131[1,5]; forma *alnifolia* Jacobs — Malaya: KEP 77820, KEP FRI 10700, Wray 1336 — Sumatra: NIFS T 1 P 11[1] — Borneo: Forman 519[1], Kostermans 7158, NBFD 4910, NIFS bb 2089; forma *cuspidata* Jacobs — Sumbawa: de Voogd 1919[1]; forma *glabra* Jacobs — Malaya: KL 2520 — Sumatra: NIFS bb 29745[1], de Wilde & de Wilde-Duyfjes 13587 — Java: Anon. sh. 925.250-657 — Borneo: Kostermans 21620[2,3], SAN 25208 — Philippines: Santos 4252 — Moluccas: Kornassi 1226 — New Guinea: BW 12808, Darbyshire 854, Hartley 10514, Hoogland & Craven 10603[1]; forma *macrocarpa* Jacobs — Sumatra: Krukoff 4419[1]; forma *pinnata* — Philippines: Ramos 1702 — Moluccas: Buwalda 5604, NIFS bb 25810 — New Guinea: BW 1286, 5291, NGF 10658, Schodde 2470, 2888 — Solomon Islands: BSIP 2694, 12477[1], Waterhouse 24; forma *repanda* Jacobs — Philippines: PNH 39281 — Celebes: NIFS Cel./V-239 — Moluccas: Rutten 1847 — New Guinea: BW 5149[1], Hoogland 4536, NGF 2722; forma *tomentosa* Jacobs — Sumatra: Achmad 1473[1] — Java: Winckel 301, 1809β, Hort. Bogor. III-K-24.

P. ridleyi Radlk. — Malaya: KEP FRI 9452[1] — Sumatra: Achmad 1400.

Smelophyllum Radlk.

S. capense (Sonder) Radlk. — South Africa: Drège s.n.[2] (K), Wells 3246[1] (K).

Stadmania Lam. section ***Stadmania***

S. oppositifolia Poir. subsp. *oppositifolia* var. *grevei* (Dang. & Choux) Capuron — Madagascar: Bernardi 11305[1,5], Grevé 243[1] (K), 6148-SF (P), 8302-SF (P); var. *oppositifolia* — Tanzania: Bradburne 102[1] (K) — Mascarene Islands: Anon. s.n. in Herb. Hookerianum (K), Person sh. 908.272-91[5]; subsp. *rhodesica* Exell — Zimbabwe: Chase 4733[1,2] (K), 8054[1] (K), Wild & Chase 6279 (K) — South Africa: Brynard & Pienaar 4253 (K).

Stadmania section ***Tricoccodendron*** Capuron

S. acuminata Capuron var. *acuminata* — Madagascar: 8667-SF[1] (P); var. *ambrensis* Capuron: not available.

S. excelsa Capuron — Madagascar: 8969-SF[1] (P).

S. glauca Capuron — Madagascar: 8955a-SF[1] (P).

S. leandrii Capuron — Madagascar: Leandri 2320[1] (P).

S. serrulata Capuron — Madagascar: 16030-SF[1,2] (P).

Xerospermum Blume

X. laevigatum Radlk. subsp. *acuminatum* (Radlk.) Leenh. — Borneo: Haviland & Hose 2080[4], S 8556, 8686[1,2,5], 9801, 12311; subsp. *laevigatum* — Burma: Griffith KD 1006/1 (K) — Thailand: Kerr 17341[1,2,4] — Malaya: KEP FRI 986[1,2], 14628, 20589[5] — Sumatra: Beguin 580 — Borneo: NIFS bb 2138, S 15621, 18096, 36917, 36947.

X. noronhianum Blume — India: Thakur Rup Chand 2941 — Burma: Ba Pe 12085 (K), Kurz 2058 (K), Maung Ba Pe 12929 (K), Muang Mui 2865 (K) — Thailand: Kerr 9850, 12105, Suvarnakoses 2218[5] — Vietnam: Vidal 4940[4] — Anambas: van Steenis 738 — Sumatra: de Wilde & de Wilde-Duyfjes 14822, 15715 — Java: Pl. Jungh. Ined. 386 — Borneo: Jacobs 5252[1,2], SAN 25865.

4. TECHNIQUES

Preferably, ripe male buds or male flowers with undehisced anthers have been sampled. Female flowers have been used reluctantly, as they might yield fewer or less developed grains (see chapter 6.14). Occasionally pollen was obtained from anthers remaining at the bases of fruits (see chapters 6.2, remark 7; 6.6, remark 4; 6.14; 6.15).

In order to study immature grains unripe buds were collected (chapter 6.15); they were processed in the same way as ripe buds.

Acetolysis

For light microscopy (LM) and scanning electron microscopy (SEM) the material was acetolysed according to the following procedure. Anthers or complete buds were soaked in 0.5% Agepon (Agfa-Gevaert, Leverkusen) in order to expand the dried pollen grains (Reitsma, 1969). Then the material was superficially dried, transferred to tubes, ground, and boiled for 2 minutes in an acetolysis mixture prepared according to Erdtman (1960b: 9 volumes acetic anhydride + 1 volume sulphuric acid 95%). Further treatment included washing with acetic acid > 97%, ethyl alcohol 96% and ethyl alcohol 100%. Next, the material was divided into two equal parts, leaving behind coarse remains. One half was used for LM, the other half for SEM.

In order to study harmomegathy, material from dehisced anthers was studied in unacetolysed state in immersion oil (see chapter 7.1: Harmomegathic types).

Mounting for LM

To mount the pollen for LM, glycerin was added to the alcohol/pollen suspension and the alcohol was evaporated for 2 hours at 50°C in an incubator. The pollen grains were mounted in glycerin jelly. Sealing was carried out with Paraplast (Sherwood, St. Louis).

To avoid flattening and swelling of the grains, coverslip supports were added, following the recommendations of Cushing (1961) and Punt (1962). Four small pieces of a clay/Plasticine mixture ensure easy processing of the coverslips and the Paraplast. A slide was placed on a hotplate and the coverslip supports, the glycerin jelly, a drop of the glycerin/pollen suspension (stir), a coverslip (press until it touches the fluid and adjust) and finally the Paraplast (if placed against the coverslip it will slowly run around the suspension) were added successively.

The observations and photography were performed with a Leitz Dialux 20 microscope (NPL Fluotar 100/1.32 oel ICT). Eastman Kodak Panatomic-X Film (FX 135/16°) was used for photography.

Mounting for SEM

To prepare the material for SEM a drop of the alcohol/pollen suspension was placed on an aluminium stub. After evaporation of the alcohol the grains were coated with gold, using a Polaron E 5100 series II sputter-coater. Sectioned grains for SEM were produced with a Leitz freezing microtome according to Muller (1973), and similarly coated.

The observations were carried out with the Jeol JSM 35 at the Rijksherbarium, Leiden. Eastman Kodak Panatomic-X Professional Film (FXP 120/160) was used for photography.

TEM procedures

Preparation for transmission electron microscopy (TEM) included rehydration and fixing of unacetolysed material with 0.1% glutaraldehyde in a 0.1 M sodium cacodylate buffer, pH 7.2 (1, 2 or 3 weeks), followed by fixation with 1% OsO_4 in the same buffer (2 hours); prestaining with 1% or 5% uranylacetate during dehydration; embedding in 3/7 Epon, sometimes in the more easily penetrating Spurr; poststaining with 5% uranylacetate (3 or 5 minutes) and Reynolds' lead citrate (3 or 5 minutes). In preparing acetolysed material of *Podonephelium concolor* the rehydration/fixing step was omitted. Sectioning was performed with a diamond knife on a LKB Ultratome III.

The observations were made with the Philips EM 300 at the Botanical Laboratory, Leiden. Eastman Kodak Fine Grain Release Positive Film 5302 (FRP 426) was used for photography.

Measurements

The polar axis (P) and the corresponding equatorial diameter (E) were measured with LM in equatorial view in ten grains per sample. The distance between two colpus ends (A), and the corresponding equatorial diameter (E) were measured in polar view in about five grains per sample, usually with LM. Generally, three values are given for P, E, P/E and A/E: the minimum, the average (between brackets) and the maximum. The thickness of the exine and its individual layers, and the size of the muri, scabrae, grooves, perforations and lumina were determined with SEM.

The original sets of measurements on which Muller (1971) and van den Berg (1978) based their descriptions of the pollen of *Dimocarpus, Pometia, Cubilia* and *Litchi* were included in the present study. The preparation techniques applied by Muller and van den Berg agree largely with those presented above.

5. GLOSSARY

This glossary explains most pollen-morphological terms used in this study. The terms and their usage were brought as much as possible into line with the proposals drafted by the Terminology Commission (S. Blackmore, S. Nilsson, W. Punt and A. le Thomas) of the Terminology Working Group of the International Federation of Palynological Societies. The meaning of a few terms is narrowed somewhat in order to explain the situation in Nephelieae pollen; it is not intended to affect the general sense of these terms. Intentional aberrant use is sometimes proposed, and is discussed in this glossary.

A (figs. 2, 3): apocolpium size. In a colporate pollen grain A is the distance between two colpus ends. In parasyncolporate grains A represents the maximal diameter of the isolated apocolpia.

A/E: the apocolpium index (apocolpium size/equatorial diameter), which gives the relative apocolpium size.

apocolpium (pl.: apocolpia; figs. 2, 3): each of the two polar areas of a pollen grain. In colporate grains the apocolpia are delimited by imaginary lines between the colpus ends, in parasyncolporate grains by actual connections between the colpus ends. Syncolporate grains do not possess apocolpia (A = 0). Compare with **mesocolpium**.

Punt et al. (1974b) introduced the term apocolpial field for an isolated apocolpium. However, Erdtman (1952) included the isolated condition in his original definition of the term apocolpium: "area at a pole, delimited towards the equator by the polar limits of the mesocolpia", in which the polar limits of the mesocolpia may be imaginary lines but also actual connections between the ends of the adjacent colpi (see his definition of mesocolpium). The examples show completely connected, partially connected and completely isolated apocolpia. He denotes the latter condition as parasyncolpate: "the colpi (or their extensions) are bifurcate and the branches meet ± close to the poles, leaving intact apocolpia of regular shape." In the present study the term apocolpium is used according to Erdtman's original definition. The term pseudoparasyncolporate (van der Ham, 1977b), introduced for parasyncolporate grains that show apocolpia connected with one or two mesocolpia, is considered superfluous.

brevicolporate pollen grain: a pollen grain with compound apertures, the ectoapertures being short colpi (equal to or shorter than the distance between the colpus ends and the poles), and the endoapertures pori. Compare with **colporate**.

callose wall: the layer that develops round the pollen mother cell and, subsequently, round each of the daughter cells. Breakdown of the callose wall results in the release of the four young pollen grains.

colporate pollen grain (fig. 2): a pollen grain with compound apertures (colpori; sing.: colporus), the ectoapertures being free colpi, the endoapertures generally pori. Compare with **syncolporate** and **parasyncolporate**.

colpus (pl.: colpi; figs. 2, 3): an aperture with a length/breadth ratio smaller than 2. In this study colpi are designated as long if $A/E < 0.25$, as fairly long if $A/E = 0.25$ to 0.50, as fairly short if $A/E = 0.50$ to 0.75, as short if $A/E > 0.75$. Compare with **porus**.

colpus membrane: the nexine underlying a colpate ectoaperture.

columella (pl.: columellae): a sexine element between the nexine and the tectum. Columellae constitute the inner part of the sexine. As a whole they are usually designated as the columellate layer (fig. 4).

costa (pl.: costae): a nexine thickening bordering an endoaperture.

duplicolumellate murus: a murus that is supported by two rows of columellae.

E (figs. 2, 3): equatorial diameter, which is the length of the longest equatorial axis of a pollen grain.

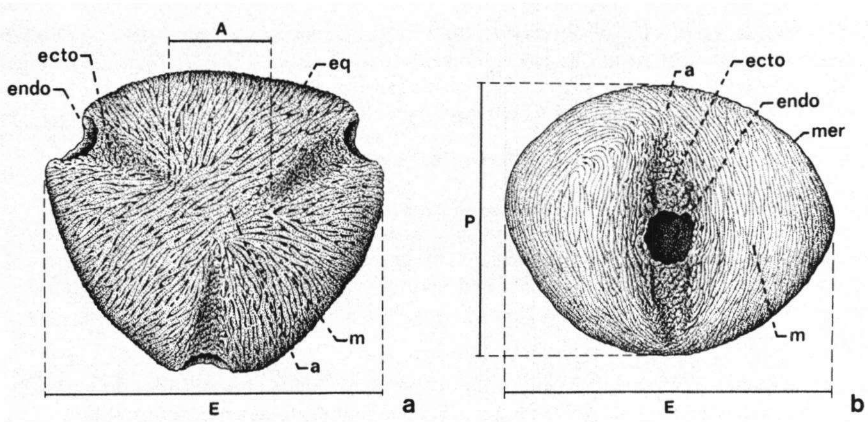


Fig. 2. Colporate grain, × 2200 (*Nephelium hypoleucum, Maxwell 76-36*). a: polar view; b: equatorial view. **a** = apocolpium, **A** = apocolpium size, **E** = equatorial diameter, **ecto** = ectoaperture, **endo** = endoaperture, **eq** = equatorial outline, **m** = mesocolpium, **mer** = meridional outline, **P** = length polar axis.

ectexine (fig. 4): the outer part of the exine, which in TEM photographs contrasts with the inner part, the endexine. The kind of contrast, whether light/dark or dark/light, depends on the method used (see chapter 6.1). Compare with **endexine**.

ectoaperture (figs. 2, 3): an aperture in the sexine. Compare with **endoaperture**.

endexine (fig. 4): the inner part of the exine, which in TEM photographs contrasts with the outer part, the ectexine. Compare with **ectexine**.

endintine (fig. 4): the inner, primarily cellulosic layer of the intine. Generally, it is homogeneous and uniformly thick in TEM photographs. Compare with **exintine**.

endoaperture (figs. 2, 3): an aperture in the nexine. The lateral sides of an endoaperture run perpendicular to the equatorial plane, whereas the polar sides run parallel to it. The meridional size of an endoaperture is the distance between the polar sides, the equatorial size the distance between the lateral sides. Compare with **ectoaperture**.

equatorial axis: a line situated in the equatorial plane. Consequently, many equatorial axes exist in single pollen grain.

equatorial outline (figs. 2, 3): the outline of a pollen grain in polar view. Compare with **meridional outline**.

equatorial plane: the plane that divides a pollen grain into a proximal half and a distal half. The equatorial plane is perpendicular to the polar axis. In Nephelieae pollen the equatorial plane passes through all endoapertures.

exine (fig. 4): the outer, acetolysis-resistant layer of the pollen wall. Compare with **intine**.

exine architecture: the morphology of the exine, including features relating to both structure and sculpture (Walker & Doyle, 1975; Muller, 1979).

exintine (fig. 4): the outer, presumably pectic layer of the intine. It may show numerous dark inclusions in TEM photographs, and it is usually thickened under the endoapertures (see oncus). Compare with **endintine**.

fastigium (pl.: fastigia): a cavity associated with the endoaperture of a colporus, and which results from the separation of the nexine and the domed sexine (Reitsma, 1970). In Nephelieae pollen a fastigium actually consists of two separate cavities, one at either lateral side of the endoaperture; this is clearly visible in equatorial sections, whether physical or optical.

foot layer (fig. 4): the outer, ectexinous part of the nexine.

groove: a supratectal space delimited by muri in striate and rugulate ornamentation.

harmomegathy: the phenomenon that includes changes in shape and volume of a pollen grain as a response to dehydration and rehydration of the protoplasm of the grain during the period between anther dehiscence and germination. Usually it involves folding of apertural and/or non-apertural parts of the pollen wall.

heteropolar pollen grain: a pollen grain with different proximal and distal sides. In this study it pertains to the condition of the apocolpia. Compare with **isopolar** and **subisopolar**.

intine (fig. 4): the inner, acetolysis-nonresistant layer of the pollen wall. Compare with **exine**.

isobilateral tetrad: a tetrad the members of which are arranged in a square (Walker & Doyle, 1975). Compare with **tetrahedral** tetrad.

isopolar pollen grain: a pollen grain with similar proximal and distal sides. In this study it pertains to the condition of the apocolpia. Compare with **heteropolar** and **subisopolar**.

lalongate endoaperture: an about elliptic endoaperture of which the longest axis is perpendicular to the longest axis of the corresponding ectoaperture (which is always meridional in Nephelieae pollen). Compare with **lolongate**.

lolongate endoaperture: an about elliptic endoaperture of which the shortest axis is perpendicular to the longest axis of the corresponding ectoaperture (which is always meridional in Nephelieae pollen). Compare with **lalongate**.

lumen (pl.: lumina): a tectal space delimited by muri in reticulate ornamentation.

margo (pl.: margines): a zone that surrounds an ectocolpus and differs from the central parts of the adjacent mesocolpia by displaying a different kind of ornamentation.

meridional outline (figs. 2, 3): the outline of a pollen grain in equatorial view. If the equatorial outline of the grain is not circular the shape of the meridional outline depends on the position of the endoapertures. In this study meridional outline refers to the outline of a grain of which an equatorial axis through an endoaperture is directed towards the observer. Compare with **equatorial outline**.

mesocolpium (pl.: mesocolpia; figs. 2, 3): an area on a pollen grain delimited by two colpi and imaginary or actual connections between their ends. Compare with **apocolpium**.

micro-echinate ornamentation: a special kind of scabrate ornamentation in which the sexine elements on the tectum are pointed and less than 1 um high (see for example plate 13: 3).

microreticulate ornamentation: the ornamentation type in which the tectum shows perforations, while the muri in between are as wide as or less wide than the perforations.

murus (pl.: muri): a general term for a sexine element, usually elongate, that is situated on the tectum (in case of striate or rugulate ornamentation), or that is part of the tectum (in case of psilate-perforate, microreticulate or reticulate ornamentation).

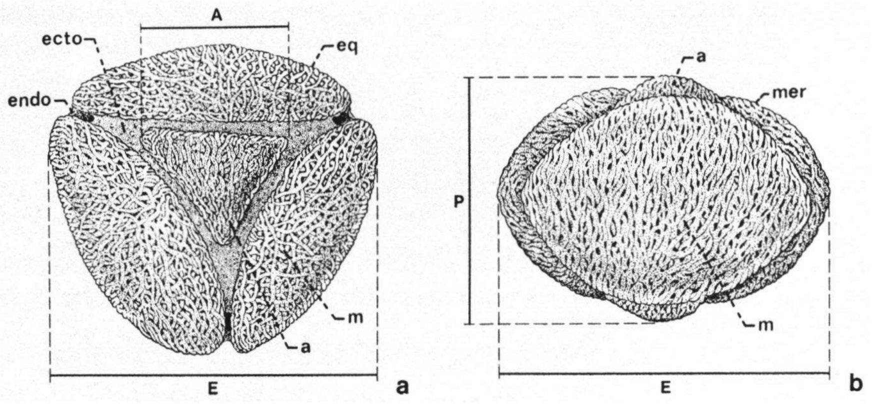


Fig. 3. Parasyncolporate grain, × 2000 (*Alectryon kangeanensis, Backer 29552*). a: polar view; b: equatorial view. **a** = apocolpium, **A** = apocolpium size, **E** = equatorial diameter, **ecto** = ectoaperture, **endo** = endoaperture, **eq** = equatorial outline, **m** = mesocolpium, **mer** = meridional outline, **P** = length polar axis.

nexine (fig. 4): the inner layer of the exine. Using light microscopy this layer displays a more or less homogeneous structure. Compare with **sexine**.

oblate pollen grain: a pollen grain with a P/E ratio between 0.50 and 0.75. See P/E.

oblate spheroidal pollen grain: a pollen grain with a P/E ratio between 0.88 and 1.00. See P/E.

oncus (pl.: onci): the thickened intine underlying an endoapertural area.

ornamentation: the outer, visual aspect of a pollen grain.

P (figs. 2, 3): length of the polar axis.

parasyncolporate pollen grain (fig. 3): a pollen grain with compound apertures (colpori), and connections between the colpus ends that delimitate the apocolpia (van der Ham, 1977b; van der Ham & van Heuven, 1989). Thus, the apocolpia are isolated from the mesocolpia. Compare with **colporate** and **syncolporate**; see also **apocolpium**.

P/E: the ratio of the length of the polar axis and the corresponding equatorial diameter of a pollen grain, which gives an indication of the shape of the grain in equatorial view (Erdtman, 1952). See **(sub)oblate (spheroidal)** and **(sub)prolate (spheroidal)**.

perforate tectum: a tectum provided with perforations, which, in Nephelieae pollen, may be hidden between projecting elements.

perforation: an up to 1 μm wide opening through the tectum.

polar axis: the line that connects the poles of a pollen grain. The polar axis is perpendicular to the equatorial plane.

pole: the central point of an apocolpium. A pollen grain has two poles: a proximal one, which in the tetrad stage faces the centre of the tetrad, and a distal one, which is on the external side of the tetrad.

porus (pl.: pori; figs. 2, 3): an aperture with a length/breadth ratio smaller than 2. Compare with **colpus**.

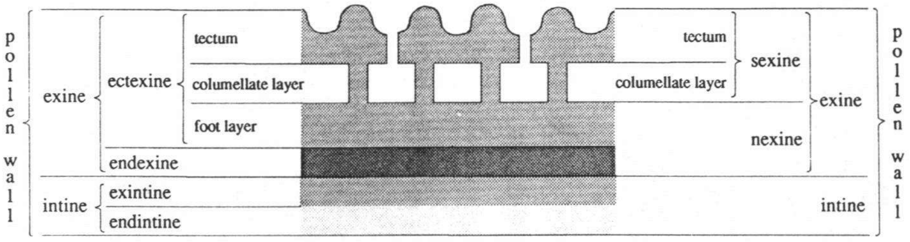


Fig. 4. Wall stratification in Nephelieae pollen. On the left: terms used in LM and TEM; on the right: terms used in LM and SEM.

primexine: the matrix in a tetrad stage grain that contains the receptors for sporopollenin and sporopollenin-like polymers.

prolate pollen grain: a pollen grain with a P/E ratio between 1.33 and 2.00. See **P/E**.

prolate spheroidal pollen grain: a pollen grain with a P/E ratio between 1.00 and 1.14. See **P/E**.

psilate ornamentation: the ornamentation type in which sculptural elements are lacking. See for example plate 18: 4. In Nephelieae pollen perforations may be present (psilate-perforate) or absent (psilate-imperforate). If perforations are present the muri must be wider than 1 µm (compare with **microreticulate**).

reticulate ornamentation: the ornamentation type in which the tectum shows lumina, while the muri in between are as wide as or less wide than the lumina. See for example plate 31: 1.

rugulate ornamentation: the ornamentation type in which elongate muri display a criss-cross arrangement. In Nephelieae pollen perforations may be present (often hidden) in the grooves between the muri. See for example plate 8: 4.

scabra (pl.: scabrae): a variably shaped sexine element on the surface of the exine of less than 1 µm in diameter.

scabrate ornamentation: the ornamentation type that shows scabrae. In Nephelieae pollen perforations may be present (sometimes hidden) between the scabrae. See for example plates 13: 3; 20: 4.

sexine (fig. 4): the outer part of the exine. Usually this layer is distinctly structured and/or sculptured, even if light microscopy is applied. In Nephelieae pollen it consists of an inner columellate layer and an outer tectate layer. Compare with **nexine**.

size of a pollen grain: the maximal diameter of a pollen grain. A grain is small-sized if its maximal diameter is between 10 and 25 µm, and medium-sized if this is between 25 and 50 µm (Erdtman, 1952).

striate ornamentation: the ornamentation type that shows elongate (sub)parallel muri. In Nephelieae pollen perforations may be present (often hidden) in the grooves between the muri. See for example plate 21: 5.

subisopolar pollen grain: a pollen grain with slightly different proximal and distal sides. In this study it pertains to the condition of the apocolpia. Compare with **isopolar** and **heteropolar**.

suboblate pollen grain: a pollen grain with a P/E ratio between 0.75 and 0.88. See **P/E**.

subprolate pollen grain: a pollen grain with a P/E ration between 1.14 and 1.33. See **P/E**.

substriation: a fine lengthwise striate pattern on an individual murus.

syncolporate pollen grain: a pollen grain with compound apertures (colpori) of which the ectoapertures (colpi) are connected at the poles. Compare with **colporate** and **parasyncolporate**.

tectum (fig. 4): the outer layer of the sexine and hence the outermost layer of the pollen wall.

tetrahedral tetrad: a tetrad in which the equatorial planes of the members are arranged according to the faces of a regular tetrahedron.

Ubisch body: a small more or less globular piece of sporopollenin that originates in the tapetum, and that, subsequently, may be found on the outer surface of a pollen grain. Also called orbicule.

6. FORM

6.1. NEPHELIEAE

General morphology

Nephelieae pollen grains are usually isopolar or subisopolar; more or less heteropolar grains were found in *Alectryon, Litchi* and *Xerospermum*. Occasionally tetrads were observed (see chapter 6.15).

Nephelieae pollen is three-aperturate, although grains with two, four (plates 1: 2; 4: 2), five or six apertures may occur in small numbers (< 1% per sample). Liu (1954) and Singh (1963) suggested four-aperturate pollen, which is the commonest of the aberrant forms, to be diploid.

The grains are small or medium-sized (P = 10 (17.7) 32 μm, E = 11 (20.4) 38 μm).

The shape of the grains is oblate to prolate (P/E = 0.50 (0.87) 1.43). Both extreme P/E values occur in *Alectryon*; in this genus P/E value correlates with the morphology of the apertural system. Many individual samples show a wide P/E range too (see chapter 7.1).

The equatorial outline of three-aperturate grains is obtusely triangular to subcircular; the triangular outlines have usually straight to convex sides. *Pometia* pollen may have protruding apertures. The meridional outline is obtusely rhombic, elliptic or subcircular; parasyncolporate *Alectryon* pollen shows a lobed meridional outline. Within a sample the shape of the equatorial and meridional outline probably largely depends on the harmomegathic state of a grain (see chapter 7.1).

Apertures

apertural system

Nephelieae pollen is generally colporate. *Pometia* has brevicolporate pollen. In several *Alectryon* species parasyncolporate pollen was found. Colporate/parasyncolporate intermediates occur commonly in *Alectryon* (see for example plate 3), sometimes in *Stadmania* and *Xerospermum*, and rarely in *Dimocarpus* and *Nephelium*. Colporate/parasyncolporate intermediates are characterised by the presence of broad indistinctly forked colpus ends, depressions between the colpus ends, and/or connections between the colpus ends. Colporate/syncolporate intermediates were occasionally found in *Litchi* (plate 21: 1) and *Xerospermum*. Such intermediates have two or all three colpi connected at one of the two poles.

Muller & Leenhouts (1976) included colporate Nephelieae pollen into their type A. The brevicolporate *Pometia* pollen was placed in type C_1. They did not find their (para)syncolporate type B in the Nephelieae, which is due to their limited sampling. Parasyncolporate *Alectryon* pollen obviously belongs to type B.

ectoapertures

The ectoapertures are usually meridionally oriented long to short colpi; in parasyncolporate pollen cross-connections between the colpus ends form part of the ectoapertural system. The relative apocolpium size (A/E) is 0 to 0.85 (av. 0.70 in *Pometia*, 0.34 in the other Nephelieae).

Ectoaperture width is rather variable in individual samples; much depends on the harmomegathic state of a grain (see chapter 7.1). Uninvaginated ectoapertures are 1 to 5 µm wide in the equatorial zone. Ectoapertures in colporate grains usually taper towards the poles, having obtuse to acute ends. Ectoapertures in parasyncolporate grains and colporate/parasyncolporate intermediates are more or less parallel-sided. The colpus membranes and the membranes of any cross-connections are more or less sunken, the degree of which correlates with ectoaperture width: in wide ectoapertures the membranes are less sunken than in narrow ones. The membranes are smooth to densely covered with scabrae. This cover may be so dense that ectoapertures are hardly perceptible with LM. *Pometia* pollen has no colpus membranes.

endoapertures

The endoapertures have an equatorial position. Meridional and equatorial size are generally between 1 and 7 µm in LM. Using LM the endoapertures are usually lalongate (plate 15: 5) to lolongate pori, occasionally short, lalongate or lolongate colpi. It must be stressed, however, that with LM the shape of an endoaperture is a projection of its three-dimensionally running edge. Van der Ham & van Heuven (1989) demonstrated in pollen of *Guioa* (tribe Cupanieae) that this projection is influenced by the shape of the grain; invagination of the ectoapertures, which makes a grain more prolate, causes the endoapertures to become higher (less lalongate, more lolongate). Using SEM the pori in Nephelieae pollen proved more 'lalongate' than with LM. Thus, also endoaperture shape depends on the harmomegathic state of a grain.

The polar sides of an endoaperture are mostly obtuse; sometimes the edge is meridionally constricted (LM), which is due to the invagination of the colpus membrane at either side. Costae do not occur.

The lateral sides show more variation. They are nearly always distinct in colporate grains, being obtuse or acute to acuminate (plates 30: 3; 26: 3; 58: 9, 13; 59: 23). In parasyncolporate grains they may be indistinct (plates 9: 6; 57: 11); if distinct, they are obtuse. Acute/acuminate lateral sides seem to be important in the harmomegathic functioning of a grain (see chapter 7.1).

A smaller or larger fastigium can mostly be discerned in colporate pollen, at least in SEM sections (see for example plate 12: 5). Parasyncolporate grains never show fastigia.

Sometimes irregularly structured, at least partly acetolysis-resistant material bridges an ectoaperture in the endoapertural area, and/or fills the fastigium. This material may totally obscure the endoapertures in LM. Endoaperture fillings could also be observed with TEM (see for example plate 55: 3, 7), which in addition usually showed some stratification to be present, and probably also with SEM (compare plate 55: 3 with plate 34: 5). Much diversity exists, but three sublayers can mostly be distinguished. The inner one is solid and more or less attached to the nexine; it seems to have an endexinous nature. The middle sublayer has a loose structure and seems to be attached to the nexine as well as the sexine. The outer one is rather solid and seems continuous with the tectum. The middle and outer sublayer have also been found in pollen of other sapindaceous genera (van der Ham, 1977b; Muller, 1985). The inner sublayer is novel. It was observed in a small part of the TEM samples throughout the Nephelieae (see remark 1), usually together with a middle and an outer sublayer. It is variably shaped, being broad and thick in *Alectryon oleifolius,* and small and thin in *Podonephelium homei.*

Because of its diverse morphology and irregular occurrence – also samples belonging to the same species and even grains of a single sample may be different – the taxonomic value of the inner sublayer appears trifling. Possibly, it represents a structure that only occurs in the last stage(s) of maturation of a grain. At the moment its functional significance can only be guessed at (see chapter 7.1).

The endoapertures in *Pometia* pollen are totally different from those of the other genera, being tubular structures of 4 to 6 µm long and 2 to 5 µm in diameter (see further chapter 6.10).

Exine architecture

stratification

Total exine thickness is 0.7 to 2.0 µm in the centres of the mesocolpia. It decreases towards the colpi or it remains about uniform. Near the colpi it mostly increases, which is due to thickening of the nexine. Thus, mostly an oblong relatively thin area exists at either side of a colpus membrane (see for example plates 55: 6, 7; 59: 8, 22). The inner surface of such a thin area is often relatively irregular, being slightly undulate or rough (plates 12: 5; 13: 5; 15: 5; 21: 6; 22: 3; 23: 5, 7; 32: 4; see also *nexine*).

Generally, the thickness of the exine and its sublayers hardly varies between the centres of the mesocolpia and the apocolpia. In a few species of *Alectryon* and *Podonephelium* the apocolpia may be thicker than the mesocolpia, which is due to increasing columella height.

nexine

The nexine is 0.15 to 0.1 µm thick in the central part of a mesocolpium. It thins gradually or strongly towards the colpi, or it remains more or less uniform. Near the colpi it thickens, forming a relatively thick layer (colpus membrane) underlying each colpus and the borders of the adjacent mesocolpia, with an interruption (endoaperture) in the equatorial zone. In *Pometia* pollen the nexine forms a system of lamellae round each endoaperture.

TEM data nearly always show that the nexine consists of an endexine and a foot layer (see plates 44–56). The acceptance of this differentiation is mostly based on the presence of contrast; sometimes slight structural differences (for example with regard to homogeneity) correspond with the subdivision based on contrast. Contrast as well as structural differences may be absent. However, this is not to be regarded as proof for the absence of any differentiation, as both the presence of contrast and structural difference appeared variable even within a single sample. In TEM photographs of unacetolysed grains the contrast between the endexine and the foot layer is usually dark/light (electron-opaque/electron-lucent), occasionally light/dark (plate 47: 3). Absence of contrast may be considered as intermediate. The nexine of acetolysed grains (hardly studied with TEM in the present study) mostly displays a relatively electron-lucent endexine. In addition to the preparation techniques, remnants of the mercury compound in desinfectants formerly used to treat dried herbarium specimens might influence contrast in TEM. The endexine is very thin to rather thick in the central part of a mesocolpium (1/40 to 3/4 of the total nexine thickness). The endexine thickens near the colpi to form the bulk or the whole of each colpus membrane (apertural lamellae in *Pometia*).

The foot layer is always as electron-opaque (or lucent) as the columellate layer and the tectum; together these layers represent the ectexinous part of the exine. The foot layer thins towards the colpi.

The boundary between the endexine and the foot layer is mostly regular or slightly undulate; in *Alectryon* and *Podonephelium* moderately to highly irregular boundaries were found (see for example plates 45: 5; 54: 4). Similar irregular boundaries occur in *Harpullia*, tribe Harpullieae (Muller, 1985, plate VIIb: 1).

Thin (about 10 nm) interbedded electron-lucent lamellae were regularly observed in the outer part of the endexine in the apertural areas, sometimes also in the mesocolpial areas (see for example plates 45: 4; 56: 4). They are often connected with the foot layer. Sometimes narrow zones of relatively electron-opaque material can be seen on each side of these lamellae (plate 45: 1), giving rise to trilamellate structures that are very similar to the tripartite "white line centered lamellae" mentioned in many other studies (see Blackmore & Barnes, 1987).

Muller (1985) provided pictures of similar lamellate structures occurring in *Harpullia* (tribe Harpullieae). On the basis of staining properties and the presence of connections with the foot layer he considered the electron-lucent lamellae within the endexine to consist of incorporated ectexinous material; white line centered structures were supposed to be lacking, because "the endexinal laminae are ± 40 nm thick and do not show a central white line." However, Muller focused on the wrong lamellae:

instead of viewing the electron-lucent lamellae as central white lines, he searched for them within the irregular electron-opaque lamellae separating the electron-lucent ones. Locally in the apertural areas the endexine may show electron-lucent discontinuities that seem to divide this layer into two sublayers, the outer one measuring about as thick as the mesocolpial endexine (plates 44: 2; 46: 1, 2; 55: 1; 56: 1, 4). These irregular discontinuities reach the inner surface of the nexine in the zones where the apertural endexine thins into the mesocolpial endexine. These zones are the oblong areas where the exine is relatively thin, and where the inner surface of the grains was shown to be slightly undulate or rough with SEM (see *stratification*). Probably, this irregular aspect in SEM sections agrees with the outcropping discontinuities observed with TEM. Together with SEM and TEM data of immature grains, in which a colpus membrane seems to be thin, fragmentary or completely lacking, these observations strongly suggest a development of the endexine in two main phases: a first one, in which a thin layer is formed throughout, and a second one, which embraces sporopollenin deposition upon the inner side of this layer under colpi and the mesocolpium borders only (see also chapter 6.15). The discontinuities may be due to interbedding with the intine. Thin electron-lucent lamellae were never found in the inner sublayer.

columellate layer

The columellate layer is 0.1 to 0.6 µm thick in the centre of a mesocolpium. The columellae are broad, isodiametric or oblong, and measure 0.1 to 0.3 µm in diameter. Due to the relatively small grain size and the thick nexine individual columellae are not easily perceptible with LM in most Nephelieae genera. Even the columellate layer as a whole may be difficult to observe.

Columella height decreases gradually or more or less strongly towards the colpi, often down to zero; in several *Alectryon* species it remains about uniform. The height of the apocolpial columellae may exceed that of the mesocolpial ones in *Alectryon* and *Podonephelium*.

Usually the columellae do not exhibit a special arrangement. However, under a reticulate tectum they show a reticulate pattern too, and under wide muri of such a reticulum they may stand in double rows (muri duplicolumellate).

tectum

The tectum is 0.3 to 1.0 µm thick in the centre of a mesocolpium. Mostly, it thins gradually towards the colpi; sometimes it thins strongly or it remains about uniform. Much variation exists with regard to the relative thickness of the tectum. In most genera the tectum is thinner than or as thick as the nexine; in a few it is slightly to distinctly thicker than the nexine.

Two sublayers can usually be distinguished: a basal sublayer, which is perforate (rarely closed or reticulate), and an outer sublayer, which is rather diverse. Together these sublayers form the ornamentation of a grain, although the inner sublayer contributes less to this than the outer one. The outer sublayer may be simple, consisting of scabrae or a single layer of two-dimensionally arranged muri, or more elaborate, displaying a three-dimensional system of wavy, sinuous and intertwining muri (see for example plates 29: 1; 53: 4).

Tectum stratification can also be entirely absent. In such cases projecting elements such as muri or scabrae are lacking (tectum psilate), and ornamentation is only represented by perforations or lumina.

In addition to the sculptured and the psilate condition all intermediate stages were found in Nephelieae pollen. Intermediate forms have low or indistinct projecting elements.

ornamentation

Striate ornamentation is most common in Nephelieae pollen, being widespread or solely present in 10 of the 12 genera. A scabrate/micro-echinate tectum is a characteristic feature of *Cubilia* pollen, while *Pometia* pollen always shows a (micro)reticulate tectum.

6 of the 10 genera in which striate ornamentation occurs, show nonstriate pollen as well, whether restricted to certain species, samples or parts of samples. Rugulate and psilate ornamentation are the commonest nonstriate types. All possible intermediates could be demonstrated between striate, rugulate and psilate.This variation concerns the degree of parallelism of the muri (striate–rugulate), and the prominence of the muri (striate–psilate, rugulate–psilate). Scabrate ornamentation occurs in *Dimocarpus*; it proved variable regarding the prominence of the scabrae (scabrate–psilate), but, contrary to rugulate and psilate ornamentation, it could not directly be connected with striate patterns.

More detailed accounts of ornamentation, in which also several aberrant forms are treated, are included in the generic descriptions. It must be stressed that differentiating ornamentation of Nephelieae pollen is wholly based on SEM data. LM techniques are inadequate to determine tectum patterns in most samples. In particular dense ornamentation, whether prominent or not, and loose nonprominent ornamentation are difficult to assess using LM. A scabrate tectum can only be demonstrated with SEM.

The muri in striate and rugulate ornamentation are generally 0.2 to 0.4 µm wide. In striate forms they show a subparallel, mostly meridional arrangement; in rugulate forms they show a criss-cross pattern. Striate forms have longer muri than rugulate forms. Muri height (or groove depth) determines the prominence of ornamentation. Sometimes muri are rather wide (up to 0.6 µm) and bear a fine, more or less distinct substriation consisting of narrow (0.1 to 0.2 µm) 'submuri' (for example in *Dimocarpus*). Muri are mostly broad-based in cross section; in *Alectryon* and *Podonephelium* pollen muri with a narrowed base occur frequently; locally, they may even be completely separated from the basal tectum sublayer. The muri in the (micro)reticulate *Pometia* pollen measure 0.4 to 1.0 µm wide. Murus width in psilate-perforate exines is very variable, ranging from 0.3 to 2.0 µm.

Scabrae are roughly isodiametric, measuring up to 0.3 µm high and wide, to oblong, measuring up to 1.0 µm long and 0.2 µm wide (see further chapters 6.3 and 6.4).

The grooves in striate and rugulate ornamentation are mostly up to 0.2 µm wide, rarely up to 0.1 µm or up to 0.7 µm. Much depends on the harmomegathic state of a grain (see chapter 7.1). Striate ornamentation has long grooves, whereas they are short and more or less angular in rugulate ornamentation. Grooves are relatively shallow and narrow along colpi.

Perforations are nearly always present, although they may be hidden in densely ornamented grains; only in *Otonephelium* pollen they seem to be totally lacking. Their shape is roughly circular. They measure up to 0.2 µm in diameter. The tectum of *Pometia* pollen shows true lumina, which measure up to 4 µm long and 2 µm wide. Perforations and lumina are usually largest in the centres of the mesocolpia, diminishing towards the colpi and the poles with respect to both number and size. Smooth imperforate margines may occur in indistinctly sculptured or psilate pollen (see for example plate 37: 5).

The edges of the mesocolpia are entire to finely irregularly indented; often they merge into the scabrae on the colpus membranes.

Ubisch bodies and pollenkitt

Ubisch bodies were regularly encountered on grain surfaces, using SEM. Their presence is usually restricted to a small part of a sample. On a single grain they have a local distribution too, being present on one side only (plates 15: 2; 19: 4; 23: 3; 26: 4). Their size is up to about 0.7 µm. Mostly, they are more or less globular or they seem to consist of several fused globules. Sometimes they are sickle-shaped, or ring-shaped. Ring-shaped bodies may consist of two coherent sickle-shaped parts (plate 40: 2). Raj & El-Ghazaly (1987) described ring-shaped bodies in Chloanthaceae; Muller (1979) observed sickle-shaped ones in Dipterocarpaceae.

With TEM, Ubisch bodies were found in all Nephelieae genera (see plates 46, 47, 50, 51, 53–56). In unacetolysed material they are abundantly present in disorganised tapeta and on adjacent grain surfaces, whereas they are lacking elsewhere in the anther sections. This might explain their restricted distribution in samples studied with SEM. Fusion with grain surfaces has never been observed. The Ubisch bodies invariably revealed the same staining properties as the ectexine of the pollen grains in the pertinent sample, being equally electron-lucent or opaque. A relatively electron-lucent central area, or possibly a cavity, is often apparent (see for example plates 53: 5; 54: 4). Such an area, which may extend to the body's surface, is more or less isodiametric to oblong, sometimes linear. The oblong and linear areas seem to subdivide a body into two parts (plate 56: 2).

Ubisch bodies observed with TEM can often be seen in series, whether in partially degraded tapeta or near and against adjacent pollen grain surfaces. Occasionally the oblong/linear central areas of such bodies seem to be aligned as well (plate 56: 2). The linear arrangement of Ubisch bodies may relate to their formation in association with endoplasmatic reticulum running parallel to the inner tangential plasma membrane (see Bhandari, 1984). Sometimes one or several superimposed series were observed (plates 46: 3; 53: 5). According to G. El-Ghazaly (personal comm., 1990) the outer one(s) should be interpreted as (a) collapsed radial series, being formed along the radial parts of the plasma membrane.

The Ubisch bodies as described above measure up to 0.7 µm and are always smooth. Rarely, sculptured bodies of 4 to 8 µm in diameter have been found with

SEM on and amongst grains (see remark 2). The ornamentation pattern is identical to that of the grains in the same sample. The nature of these bodies could not be settled. In view of their aberrant size and surface they are not considered to represent Ubisch bodies.

Using TEM variable amounts of pollenkitt were found covering grains and filling (infra)tectal cavities (plates 48: 4, 5; 49: 2; 50: 2; 53: 2; 55: 7; 56: 2). Pollenkitt is deposited in the last phase of microsporogenesis, probably after the exine is completely formed (Knox, 1984). As this phase may be lacking in part of the samples, no attempt has been made to determine amount, transparency and homogeneity, as Hesse (1979) did for several Aceraceae.

Pollenkitt and tryphine are similar in many respects (see Bhandari, 1984). Because of the absence of distinct tapetum remains, apart from Ubisch bodies if a grain lies near the tapetum, the term pollenkitt is used.

Intine

The intine is the innermost layer of the pollen wall. Due to its pectic/cellulosic nature it generally does not resist acetolysis. The intine has been studied with TEM in 33 species, which belong to 9 of the 12 Nephelieae genera (plates 44–56). No TEM data were available of unacetolysed mature grains of *Cubilia, Litchi* and *Otonephelium*. The intine of *Pometia* pollen and *Xerospermum* pollen has been studied with LM as well (plates 60: 15–17; 61: 15–17).

Intine thickness under the poles and the mesocolpia is 0.06 to 0.55 μm. Towards the colpi it increases slightly. Near and under the endoapertures the intine is usually distinctly thickened, yielding onci of 1.3 to 4.0 μm thick and 5.0 to 8.5 μm in diameter. Relatively thin onci occur in pollen of *Podonephelium homei* and several *Alectryon* species (see remark 3); these species appeared to have a rather thick nonapertural intine.

The inner boundary of the intine is about straight to slightly undulate under the poles and the mesocolpia. Under the endoapertures it is undulate to folded. Often one or two larger folds occur in an oncus, in which the cytoplasm extends towards the endoaperture (see for example plates 48: 3; 56: 5–7). Occasionally such folds, including their contents, were seen to break through the overlying oncus body, reaching the surface of the grain through the endoaperture (plates 49: 1; 56: 7).

stratification

The nonapertural intine is mostly electron-lucent and homogeneous; it may contain a zone of electron-opaque inclusions in the outer part (see for example plates 47: 3; 48: 5).

In an oncus three sublayers can usually be distinguished. The inner one is 0.2 to 0.7 (rarely 2.2) μm thick; it is the continuation of the nonapertural intine or, if this contains dark inclusions, the inner part of it. Often, radially arranged linear extensions of electron-opaque inclusions in the middle sublayer can be observed in the inner sublayer (plates 45: 4; 48: 2; 56: 4). The middle sublayer forms usually the bulk of an oncus, measuring 0.4 to 2.7 μm thick. It thins strongly towards the poles and the mesocolpia. Mostly, it thins out, but sometimes it continues under the poles and the mesocolpia (see above), very distinctly so in *Alectryon* and *Podonephelium* (plates 44–47; 54: 1–4). The middle sublayer is characterised by the presence of numerous electron-opaque inclusions, which are often mutually connected to form a tubular/labyrinthic tract (plate 56: 4). The outer sublayer is thin, being 0.1 to 0.3 μm thick, and homogeneously electron-lucent; occasionally its outer part is relatively electron-opaque (plate 55: 3).

Thickness and stainability of the three sublayers vary considerably. This may be partly due to differences in maturity (Hesse, 1987), conservation (including treatment with desinfectants containing mercury) and age of the material, or possibly preparation technique.

Kress & Stone (1982) summarised the knowledge on intine stratification, and suggested the present terminology. They distinguished an endintine, comprising the inner sublayer adjacent to the cytoplasm, and an exintine, which is formed by the outer intine component. The endintine is generally uniform in thickness and homogeneous in texture throughout, although vesicles and tubules may be present in the apertural areas. It is primarily cellulosic in nature. The exintine is usually thickened under the apertures and may exhibit numerous inclusions. Presumably, it has a pectic nature. Considering these features, the nonapertural intine (or its inner electron-lucent part) and the inner oncus sublayer distinguished in Nephelieae pollen form the endintine, while the middle oncus sublayer, which may extend to under the mesocolpia, and outer oncus sublayer represent the exintine.

Kress & Stone found that, in general, the development of the intine is inversely related to the amount of exine present. Nephelieae pollen seems to confirm this relation. *Alectryon* and *Podonephelium* grains, which mostly have a thin mesocolpial nexine, show a relatively thick mesocolpial intine (see further chapter 7.1).

The intine of *Pometia* pollen deviates markedly from that of the other genera and, consequently, from the general picture presented by Kress & Stone. The nonapertural intine is filled with electron-opaque inclusions almost throughout (plate 54: 5; see also van den Berg, 1978, plate VIII: 2). The onci consist of two sublayers, which are only vaguely delimited; therefore van den Berg (1978) did not subdivide the intine of *Pometia*. The inner sublayer is continuous with the nonapertural intine, being equally filled with electron-opaque material. The outer sublayer contains fewer dark inclusions. It is restricted to the apertures, but it does not seem to proceed into the endoapertural tubes (see also chapter 7.1). A homogeneously electron-lucent inner sublayer could not be demonstrated.

Intine morphology has been studied in a few other sapindaceous genera: *Mischocarpus* (van der Ham, 1977b), *Harpullia* (Muller, 1985; see remark 4) and *Guioa* (van der Ham & van Heuven, 1989). The intines of *Mischocarpus* and *Guioa* proved very similar to those of *Dimocarpus, Nephelium, Pappea, Smelophyllum, Stadmania* and *Xerospermum,* whereas the intine of *Harpullia* resembles that of *Alectryon* and *Podonephelium.* The oncus sublayers i_1, i_2 and i_3 in *Harpullia* pollen are the outer, middle and inner sublayer respectively in the present study. The innermost sublayer i_4 observed by Muller in *Harpullia arborea* is considered to be an artefact due to separation of the intine from the cytoplasm. The same phenomenon has occassionally been observed in Nephelieae pollen too.

intine ghosts

According to Knox (1984) and Hesse & Waha (1989) acetolysis completely destroys the intine. This is a general statement, however, which does not hold for pollen of the Nephelieae and several other taxa in the Sapindaceae and elsewhere. Using LM, acetolysed grains of all Nephelieae genera except *Pometia* may show membranaceous entities inside the exine (see for example plates 57: 20; 58: 8; 59: 17, 22; 60: 2; 61: 11). Continued acetolysis (up to 8 minutes) or other acetolysis and mounting techniques, according to Reitsma (1969) and Andersen (1960) respectively, could not dissolve them. They are considered to represent intine remains (see below). Because of their irregular occurrence, transparent nature, and fluttering appearance when turning the microscope's fine adjustment knob, they have been named intine ghosts. Heslop-Harrison et al. (1986) applied this expression to denote fluorescent cellulosic intines of *Corylus avellana* pollen (Corylaceae) from which the exine, the pectic components of the pollen wall, and the protoplasm had been removed.

An intine ghost in Nephelieae pollen is a continuous membranaceous structure. It is irregularly shaped or it exhibits a specific shape by being more or less attached to the apocolpia and the central parts of the mesocolpia and by largely avoiding the apertural areas (plates 59: 17–19; 61: 11, 12). In the latter shape it closely resembles the endintine. Moreover, small or funnel-shaped evaginations were often found opposite all three endoapertures (plates 61: 11, 12; 59: 20). Such extensions agree with the folds of the endintine that were occasionally observed to break through the overlying exintine to reach the endoapertures (plates 49: 1; 56: 7). As, in addition, the endintine is the only layer found to be always continuous throughout a grain, an intine ghost is regarded as the remainder of that particular part of the intine. Remarkably, the absence in *Pometia* pollen of an electron-lucent inner intine sublayer coincides with the constant absence of intine ghosts.

The cause of the chemical resistance of the intine ghosts is not understood. A negative staining reaction with Fluorescent Brightener 28 of Sigma, St. Louis (= Calcofluor White M2R) demonstrates that the ghosts do not contain cellulose anymore, which is to be expected after acetolysis. Applying PAS (stains cellulosic and/or hemicellulosic intine constituents), alcian blue (stains pectic intine constituents) or basic fuchsin (stains the exine, particularly the ectexine) did not provide a clue either. Obviously, further research is necessary in order to elucidate the nature of the intine ghosts. See Knox (1984) and Kress & Stone (1982) for information as to the usage of the stains mentioned in this paragraph.

Intine ghosts are common in the pollen of *Nephelium, Pappea* and *Xerospermum* particularly, occurring in more than 80% of all studied samples. Within individual samples their presence varies between 1% and 100%. In several samples grains show an intine ghost protruding through an endoaperture. Such observations suggest that in addition to chemical resistance the presence of intine ghosts may be due to ineffective removal of the contents of a grain during acetolysis. Possibly, the removal starts with a cytoplasm protrusion from a specific site opposite an endoaperture due

Table 1. Variation of a number of pollen characters in the Nephelieae.

	P (µm)	E (µm)	P / E	A / E	apertural system
Alectryon	12 (20.4) 29	14 (22.5) 31	0.50 (0.92) 1.43	0.19 (0.36) 0.76	(parasyn)colporate
Cubilia	10 (11.7) 14	11 (12.8) 15	0.73 (0.91) 1.04	0.16 (0.34) 0.44	colporate
Dimocarpus	15 (20.1) 32	17 (22.6) 33	0.66 (0.89) 1.18	0.21 (0.36) 0.75	colporate
Litchi	12 (17.3) 23	16 (20.0) 26	0.70 (0.87) 1.10	0 (0.28) 0.47	colporate
Nephelium	12 (17.0) 25	16 (20.4) 26	0.59 (0.83) 1.06	0.14 (0.29) 0.49	colporate
Otonephelium	14 (15.9) 17	17 (19.5) 21	0.73 (0.82) 0.95	0.26 (0.31) 0.35	colporate
Pappea	14 (16.5) 21	14 (17.7) 24	0.77 (0.93) 1.13	0.19 (0.34) 0.45	colporate
Podonephelium	21 (25.2) 29	19 (22.9) 28	0.92 (1.10) 1.24	0.26 (0.35) 0.46	colporate
Pometia	16 (20.6) 29	20 (26.4) 38	0.67 (0.78) 0.87	0.57 (0.70) 0.85	brevicolporate
Smelophyllum	13 (15.3) 17	18 (21.7) 23	0.66 (0.71) 0.84	0.26 (0.37) 0.49	colporate
Stadmania	14 (18.1) 24	16 (20.3) 29	0.73 (0.89) 1.13	0.10 (0.40) 0.50	colporate
Xerospermum	10 (14.8) 19	14 (18.5) 24	0.62 (0.80) 0.98	0 (0.29) 0.55	colporate
Nephelieae	10 (17.7) 32	11 (20.4) 38	0.50 (0.87) 1.43	0 (0.37) 0.85	

	thickness (µm)*					
	exine	nexine	columellate layer	tectum	endexine/nexine ratio*	ornamentation
Alectryon	0.7 – 1.8	0.15 – 0.9	0.1 – 0.6	0.3 – 1.0	$^{1}/_{10}$ – $^{3}/_{4}$	striate to rugulate
Cubilia	0.7 – 0.8	0.2	0.1 – 0.15	0.3 – 0.4	$^{1}/_{5}$?	scabrate
Dimocarpus	0.9 – 1.6	0.3 – 0.7	0.1 – 0.25	0.3 – 0.7	$^{1}/_{12}$ – $^{1}/_{8}$	striate to psilate to scabrate**
Litchi	0.9 – 1.4	0.4 – 0.6	0.1 – 0.25	0.3 – 0.5	$^{1}/_{20}$	striate to irregularly shallowly striate
Nephelium	0.9 – 1.6	0.4 – 0.7	0.1 – 0.3	0.3 – 0.7	$^{1}/_{15}$ – $^{1}/_{7}$	striate to psilate; striate to rugulate
Otonephelium	1.5	0.8	0.15	0.5 – 0.6	—	striate to irregularly rugulate
Pappea	1.1 – 1.9	0.4 – 0.6	0.1 – 0.2	0.5 – 1.0	$^{1}/_{15}$ – $^{1}/_{10}$	striate
Podonephelium	1.0 – 1.6	0.25 – 0.4	0.25 – 0.5	0.5 – 0.8	$^{1}/_{6}$ – $^{1}/_{3}$	striate
Pometia	1.3 – 2.0	0.5 – 0.9	0.3 – 0.5	0.5 – 0.9	$^{1}/_{20}$ – $^{1}/_{10}$	microreticulate to reticulate
Smelophyllum	1.4	0.6	0.4	0.4	$^{1}/_{40}$ – $^{1}/_{20}$	striate
Stadmania	1.3 – 1.9	0.3 – 1.0	0.15 – 0.4	0.3 – 0.6	$^{1}/_{10}$ – $^{1}/_{6}$	striate to rugulate to psilate
Xerospermum	1.1	0.6	0.1 – 0.15	0.3 – 0.4	$^{1}/_{10}$ – $^{1}/_{6}$	striate to psilate**
Nephelieae	0.7 – 2.0	0.15 – 1.0	0.1 – 0.6	0.3 – 1.0	$^{1}/_{40}$ – $^{3}/_{4}$	

* measured in the centre of a mesocolpium; ** sometimes irregularly or finely or shallowly or indistinctly rugulate.

to pressure on the inside of the intine. This specific site may be determined by the absence of mechanical resistance at the endoapertures (the oncus is supposed to be flexible) and the presence of folds in the inner oncus sublayer. To some degree the process resembles the initial stage of pollen germination as described by Heslop-Harrison et al. (1986), in which a pollen tube tip is defined as a papilla on the inner cellulosic layer opposite an endoaperture.

Intine ghosts occur in other sapindaceous tribes as well. In published photographs they could be noticed in *Diplopeltis*, tribe Dodonaeeae (George & Erdtman, 1969, plate 1: 6, 7), *Lepisanthes*, tribe Lepisantheae (Muller, 1970, plate XIII: 2b), *Mischocarpus*, tribe Cupanieae (van der Ham, 1977b, plate XIII: 3b) and *Harpullia*, tribe Harpullieae (Muller, 1985, plate XVIII: 2).

Similar structures can be observed in the following non-Sapindaceae: *Arabidopsis thaliana*, Cruciferae (Bronckers, 1963, fig. 9), *Bergenia crassifolia*, Saxifragaceae (Verbeek-Reuvers, 1977, plate 1: 2, 7), *Betula nana*, Betulaceae (Erdtman et al., 1961, plate 5: 7, 8), *Calla palustris*, Araceae (Erdtman et al., 1961, plate 3: 12), *Lantana camara*, Verbenaceae (d'Almeida & Roland-Heydacker, 1985, plate 1: 2), *Lonicera xylosteum*, Caprifoliaceae (Punt et al., 1974a, plate 9: 1), *Ostrya carpinifolia*, Corylaceae (Praglowski, 1962, plate 10: 4), *Plagiopteron suaveolens*, Plagiopteraceae (Baas et al., 1979, fig. 2j), *Saxifraga cymbalaria*, Saxifragaceae (Verbeek-Reuvers, 1977, plate 9: 9), *Souroubea peruviana*, Marcgraviaceae (Punt, 1971, plate 5: 6), *Spartium junceum*, Leguminosae (Planchais, 1964, plate 1: 3), *Tilia platyphyllos*, Tiliaceae (Erdtman, 1959, plate 1: 7). This enumeration just mentions a few examples; it is not intended to be a complete list. Apparently, the phenomenon is not rare, but none of the authors mentioned above commented on it.

Table 1 lists the values/states of a number of the above mentioned characters for the individual genera in the Nephelieae.

Remarks

1. An inner sublayer of an endoaperture filling was observed in TEM samples of pollen of *Alectryon oleifolius* subsp. *canescens*, *A. subdentatus* (plate 47: 5), *Nephelium hypoleucum* (only Dickason 6802), *N. subfalcatum* (plate 51: 3), *N. uncinatum* (plate 51: 5), *Pappea capensis* (only Dyer 1181a; plate 53: 1–3), *Podonephelium homei* (plate 54: 3), *Stadmania oppositifolia* (plate 55: 5, 7) and *S. serratula* (plate 55: 3).
2. Sculptured, acetolysis-resistant bodies of 4 to 8 µm have been found in *Dimocarpus longan* (Popta 863/210: several; plate 17: 2), *Nephelium cuspidatum* (Bunnap 372: once) and *Smelophyllum capense* (Wells 3246: once).
3. Relatively thin onci occur in pollen of *Alectryon carinatus*, *A. connatus* (plate 44: 1, 2), *A. ferrugineus* (plate 45: 3), *A. oleifolius* subsp. *oleifolius* (plate 47: 2) and *Podonephelium homei* (plate 54: 1, 3).
4. During the preparation of plate II: 1, 2, 3 in Muller (1985) something went wrong with the labelling of the individual intine sublayers: i_1 has to be i_2, and i_2 is a part of either i_2 or i_3.

6.2. ALECTRYON

(plates 1–12; 44–47; 57: 1–16; figs. 3, 10, 11)

General morphology

Alectryon pollen grains are small or medium-sized (P = 12 (20.4) 29 µm, E = 14 (22.5) 31 µm). Grain shape is oblate to prolate (P/E = 0.50 (0.92) 1.43); the P/E value largely depends on which type of apertural system is represented (see Infrageneric variation). The equatorial outline is obtusely triangular to subcircular. The triangular outlines have slightly convex to convex sides. The meridional outline is obtusely rhombic to subcircular; parasyncolporate pollen shows a more or less lobed meridional outline.

Apertures

Alectryon pollen is generally colporate or parasyncolporate (see remark 1). The colporate and the parasyncolporate condition are not clear-cut, as all intermediate stages between purely colporate (apocolpia entirely connected to the mesocolpia) and purely parasyncolporate (apocolpia completely isolated) also occur in *Alectryon* pollen; these intermediates show depressions between colpus ends, broad forked colpus ends, and partly isolated apocolpia. (see further Infrageneric variation).

Apocolpium size is between 4 and 14 µm (A/E = 0.19 (0.36) 0.76). In parasyncolporate pollen apocolpium size averages higher than in colporate pollen (see Infrageneric variation). Many samples contain more or less heteropolar grains, regarding apocolpium size.

The ectoapertures are free or connected colpi (see remark 1). Free colpi have acute to obtuse ends; sometimes they are broadened and forked (see above). The colpus membranes are slightly to densely covered with scabrae.

The endoapertures are usually lalongate to lolongate pori, rarely lalongate colpi. Meridional size is 1 to 6 µm; equatorial size is 2 to 7 µm. The polar sides of an endoaperture are obtuse; the lateral sides are obtuse to acuminate in colporate grains (plates 12: 6; 7: 5), and obtuse or indistinct in parasyncolporate grains (plate 9: 6). A fastigium can often be discerned in colporate pollen (see for example plates 3: 5; 12: 6).

Exine architecture

stratification

Total exine thickness is 0.7 to 1.8 µm in the centres of the mesocolpia. Usually it is about uniform throughout the greater part of a mesocolpium; sometimes it decreases towards the colpi (see remark 2). Near the colpi it may thicken somewhat. In a few species the exine thickness of the apocolpia exceeds that of the mesocolpia (see remark 3). The colpi and the cross-connections between the colpi in parasyncolporate grains are similar with respect to thickening and thinning of the exine and its individual sublayers.

The nexine is 0.15 to 0.9 µm thick in the central part of a mesocolpium. It thickens near the colpi, forming a relatively thick layer under each colpus (colpus membrane) and the borders of the adjacent mesocolpia (plates 1: 4; 2: 6). With TEM the nexine was shown to consist of an endexine and a foot layer (plates 44–47). The boundary between these two sublayers is regular to highly irregular. The endexine is thin to rather thick in the central part of a mesocolpium (1/10 to 3/4 of the total nexine thickness). A relatively thick irregularly delimited endexine may locally reach the intercolumellar surfaces of the nexine, the columellae often showing ectexinous 'bases' embedded in the endexine (plate 45: 5). The endexine thickens towards the colpi to form the bulk or the whole of each colpus membrane. The foot layer thins towards the colpi. Thin interbedded electron-lucent lamellae occur usually in the outer part of the endexine in the apertural areas and sometimes also in the mesocolpial areas. See also Infrageneric variation.

The columellate layer is 0.1 to 0.6 µm thick in the centre of a mesocolpium. Usually it thins slightly towards the colpi, or it remains about uniform; rarely it thins considerably (see remark 2) or it thins out. Distinct columellae are mostly present along the colpi; this is most obvious in parasyncolporate pollen. Sometimes the polar columellae are taller than the mesocolpial ones (see remark 3). See further Infrageneric variation.

The tectum is 0.3 to 1.0 µm thick in the centre of a mesocolpium, being nearly always distinctly thicker than the nexine (see remark 4). It thins more or less distinctly towards the colpi, or its thickness remains about uniform.

ornamentation

Ornamentation is striate (often irregularly) to rugulate. More or less psilate-perforate grains and shallowly or indistinctly sculptured grains, which occasionally showed up among prominently sculptured ones, are interpreted as immature stages (see chapter 6.15). Both striate and rugulate ornamentation are rather diverse; their appearance is largely determined by the shape, length and variance of direction of the muri, and the shape and width of the grooves between these (see Infrageneric variation). The muri are two, sometimes three-dimensionally arranged; rarely more than two murus layers were observed (see remark 5). Loose three-dimensional ornamentation sometimes shows an inner rugulate pattern and an outer striate pattern (plate 7: 4; see also chapter 6.15). The muri are 0.2 to 0.4 µm wide. Mostly they have a narrowed base; sometimes they seem locally completely isolated from the basal tectum layer (plate 46: 1). Some species show grains with up to 0.5 µm wide bundles of two or three muri, the individual muri measuring 0.1 to 0.2 µm wide (see remark 6). Usually such bundles of muri enclose large isodiametric to slightly oblong lumina, which gives the tectum a reticulate aspect. The grooves between the muri are variously shaped. Long, up to 0.1 µm wide grooves occur in densely striate forms, whereas isodiametric to oblong, often angular up to 0.7 µm wide grooves exist in the more loosely striate and rugulate forms. Perforations are abundantly present and usually very conspicuous; in densely striate and densely rugulate ornamentation they are more or less hidden between the muri. They measure up to 0.3 µm in diameter; occasionally they are up to 0.7 µm in diameter, being congruent with isodiametric to slightly oblong grooves, thus yielding true lumina. The edges of the mesocolpia are usually more or less entire; sometimes they are finely indented, or they merge into scabrae on the colpus membranes.

Table 2 lists the values/states of a number of the above mentioned characters for the individual taxa in *Alectryon.*

Remarks

1. In *Maiden 1664* of *Alectryon subcinereus* a grain devoid of meridional ectoapertures but possessing a circular polar ectoaperture was observed (plate 10: 2); the other pole could not be studied
2. Due to a strongly declining columellate layer total exine thickness decreases from the centre of a mesocolpium towards the colpi in pollen of *A. myrmecophilus* (plates 6: 2; 46: 3, 4).
3. In pollen of *A. carinatus, A. forsythii* and *A. ramiflorus* polar columellae are distinctly taller (up to twice as much) than those in the central part of a mesocolpium, which causes the apocolpial exine to be thicker than the mesocolpial exine.
4. In pollen of *A. fuscus, A. myrmecophilus* and *A. subdentatus* forma *subdentatus* the nexine is thicker than or as thick as the tectum.
5. Grains with a tectum consisting of two to four layers of muri exist in *Smith 6059* (*A. oleifolius* subsp. *canescens*; plate 6: 4).
6. Grains with a tectum consisting of bundles of two or three muri were found in small numbers in samples of *A. connatus, A. forsythii* (plate 4: 4), *A. glaber, A. oleifolius* subsp. *canescens* (plate 6: 4), *A. reticulatus* and *A. unilobatus.*
7. The sample *Anon. s.n.* of *A. reticulatus* consisted of shrivelled anthers obtained from fruit bases (see also chapter 6.14).

Infrageneric variation

Alectryon is outstanding in the Nephelieae because of the occurrence of parasyncolporate pollen, which belongs to type B of Muller & Leenhouts (1976). Initially (p. 410), Muller & Leenhouts distinguished a type B_1 and a type B_2, but in their Systematic discussion they do not differentiate anymore. Indeed, B_1 and B_2 are not distinct (see also van der Ham, 1977b; van der Ham & van Heuven, 1989), and it is not feasible to accommodate parasyncolporate *Alectryon* pollen in either B_1 or B_2.

Besides the parasyncolporate type B *Alectryon* shows the colporate type A of Muller & Leenhouts, while intermediates are fairly abundant. This variation of the apertural system, which is readily and precisely observable if SEM is applied, relates to a greater or smaller degree to grain shape, apocolpium size, endoaperture shape, exine architecture and harmomegathy. Below, an account will be given of the variable condition of the apertural system with regard to apo-/mesocolpium coherence. The various states will be connected with P/E value, A/E value, nexine morphology, relative length of the peripheral columellae of a mesocolpium, and ornamentation; the relation to harmomegathy is dealt with in chapter 7.1.

Pollen characters in *Alectryon* do not display distinct geographical patterns.

Table 2. Infrageneric variation of a number of pollen characters in *Alectryon*.

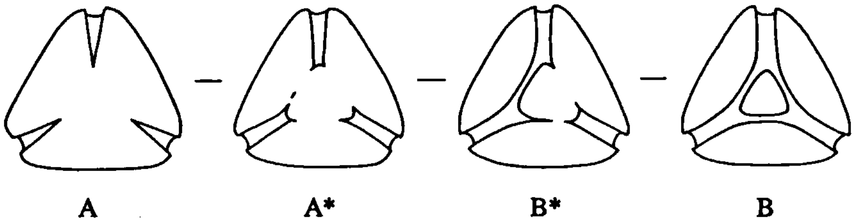
	P (µm)			E (µm)			P / E			A / E		
affinis	16	(19.0)	21	24	(26.4)	30	0.63	(0.72)	0.84	0.33	(0.47)	0.68
cardiocarpus	19	(22.6)	27	19	(19.8)	23	0.95	(1.14)	1.40	0.30	(0.32)	0.34
carinatus	17	(22.0)	26	15	(20.5)	24	0.92	(1.07)	1.35	0.22	(0.29)	0.35
connatus	16	(20.5)	24	20	(24.9)	30	0.65	(0.82)	1.00	0.21	(0.46)	0.70
coriaceus	19	(22.6)	27	19	(23.7)	29	0.77	(0.95)	1.14	0.19	(0.34)	0.40
diversifolius	18	(22.4)	26	20	(22.8)	25	0.83	(0.98)	1.17	0.24	(0.37)	0.48
excelsus	19	(24.4)	29	19	(24.0)	29	0.85	(1.02)	1.15	0.26	(0.32)	0.37
ferrugineus	15	(20.0)	24	18	(21.6)	27	0.83	(0.93)	1.05	0.23	(0.28)	0.30
forsythii	17	(22.4)	26	19	(22.7)	27	0.81	(0.98)	1.25	0.24	(0.27)	0.38
fuscus	16	(18.5)	21	20	(23.0)	27	0.74	(0.76)	0.79	0.23	(0.41)	0.53
glaber	15	(18.8)	25	15	(19.4)	25	0.73	(0.97)	1.25	0.25	(0.32)	0.37
grandifolius	18	(22.6)	28	23	(25.6)	29	0.74	(0.87)	1.08	0.24	(0.33)	0.46
kangeanensis	15	(17.2)	19	23	(24.1)	27	0.64	(0.71)	0.80	0.38	(0.45)	0.50
kimberleyanus	18	(20.0)	22	18	(20.6)	23	0.91	(0.97)	1.05	0.27	(0.31)	0.38
macrococcus	15	(18.6)	23	22	(25.0)	29	0.58	(0.74)	0.88	0.28	(0.43)	0.61
myrmecophilus	17	(21.5)	29	21	(26.1)	29	0.69	(0.82)	1.04	0.42	(0.48)	0.63
oleifolius	19	(21.9)	25	19	(21.1)	26	0.81	(1.04)	1.25	0.28	(0.33)	0.49
subsp. *canescens*	20	(21.6)	24	19	(21.1)	24	0.88	(1.02)	1.25	0.28	(0.38)	0.49
subsp. *elongatus*	21	(22.6)	25	19	(22.8)	26	0.81	(0.99)	1.20	0.24	(0.26)	0.29
subsp. *oleifolius*	19	(21.4)	23	19	(19.3))	21	0.91	(1.11)	1.20	0.20	(0.23)	0.34
pubescens	19	(22.7)	26	21	(22.0)	25	0.91	(1.03)	1.13	0.22	(0.28)	0.41
ramiflorus	14	(18.6)	24	14	(17.8)	23	0.83	(1.04)	1.11	0.24	(0.30)	0.42
repandodentatus	16	(18.6)	21	18	(19.8)	20	0.82	(0.93)	1.10	0.21	(0.26)	0.32
reticulatus A**	14	(16.1)	17	17	(19.3)	21	0.82	(0.83)	0.86	0.28	(0.33)	0.37
" B	18	(19.1)	20	24	(25.4)	27	0.68	(0.75)	0.81	0.35	(0.45)	0.56
samoënsis	15	(16.9)	19	20	(21.8)	24	0.68	(0.78)	0.81	0.39	(0.48)	0.58
semicinereus	17	(21.4)	24	21	(23.2)	26	0.81	(0.92)	1.00	0.25	(0.39)	0.50
subcinereus	12	(18.4)	23	19	(24.5)	31	0.50	(0.76)	1.05	0.25	(0.50)	0.76
subdentatus	16	(19.8)	24	15	(20.7)	26	0.73	(0.96)	1.25	0.20	(0.31)	0.39
f. *pseudostipularis*	16	(19.5)	22	15	(20.7)	24	0.78	(0.94)	1.18	0.20	(0.30)	0.39
f. *subdentatus*	16	(20.1)	24	17	(20.6)	26	0.73	(0.98)	1.25	0.24	(0.32)	0.38
tomentosus	14	(19.1)	23	15	(19.9)	24	0.78	(0.94)	1.43	0.20	(0.29)	0.33
unilobatus	18	(21.2)	22	19	(21.9)	23	0.86	(0.95)	1.05	0.28	(0.36)	0.42
Alectryon	12	(20.4)	29	14	(22.5)	31	0.50	(0.92)	1.43	0.19	(0.36)	0.76

(Table 2 continued)	thickness (µm)*				
	exine	nexine	columellate layer	tectum	ornamentation
affinis	1.1	0.3	0.4	0.4	striate-rugulate
cardiocarpus	1.0	0.2	0.2	0.6	densely striate
carinatus	0.8 – 0.9	0.2 – 0.3	0.1 – 0.2	0.4	densely striate
connatus	1.0	0.3	0.3	0.4	densely striate to striate-rugulate
coriaceus	1.0 – 1.2	0.25 – 0.3	0.15 – 0.3	0.5 – 0.6	densely striate to striate-rugulate
diversifolius	1.3	0.3	0.15	0.8 – 0.9	densely striate to striate-rugulate
excelsus	1.4 – 1.7	0.4	0.4 – 0.5	0.6 – 0.8	densely striate to striate-rugulate
ferrugineus	1.0	0.3	0.2	0.5	densely to loosely striate
forsythii	1.2	0.2	0.2	0.8	loosely striate to striate-rugulate
fuscus	1.3	0.5	0.3	0.5	striate-rugulate to densely rugulate
glaber	0.9 – 1.0	0.2 – 0.3	0.2	0.5	densely striate to striate-rugulate
grandifolius	1.1 – 1.2	0.3 – 0.4	0.3	0.5	densely striate to striate-rugulate to densely rugulate
kangeanensis	1.1 – 1.4	0.3	0.3 – 0.4	0.4 – 0.7	loosely striate to striate-rugulate
kimberleyanus	0.9 – 1.0	0.3 – 0.4	0.2	0.4	densely striate to striate-rugulate
macrococcus	1.1 – 1.3	0.15 – 0.3	0.3 – 0.5	0.5 – 0.7	densely striate-rugulate to densely rugulate
myrmecophilus	1.7	0.6	0.6	0.5	densely striate to densely striate-rugulate
oleifolius	1.1 – 1.7	0.3 – 0.5	0.15 – 0.2	0.6 – 1.0	
subsp. *canescens*	1.3 – 1.4	0.3 – 0.4	0.15 – 0.2	0.7 – 0.8	densely to loosely striate
subsp. *elongatus*	1.7	0.5	0.2	1.0	densely striate
subsp. *oleifolius*	1.1	0.3	0.2	0.6	striate-rugulate
pubescens	1.5	0.4 – 0.5	0.25	0.8	densely striate
ramiflorus	0.8 – 0.9	0.2 – 0.3	0.1 – 0.2	0.4 – 0.5	loosely striate to striate-rugulate
repandodentatus	1.0	0.3	0.2	0.5	densely striate to striate-rugulate
reticulatus A**	0.7	0.15	0.15	0.4	rugulate
" B	1.4	0.3	0.3	0.8	striate-rugulate
samoënsis	1.2	0.3	0.3 – 0.4	0.5 – 0.6	densely to loosely striate-rugulate to rugulate
semicinereus	1.3	0.4	0.2	0.7	densely striate to striate-rugulate
subcinereus	0.9	0.2 – 0.3	0.2 – 0.3	0.3 – 0.4	striate-rugulate to rugulate
subdentatus	0.9 – 1.8	0.25 – 0.9	0.2 – 0.3	0.4 – 0.7	
f. *pseudostipularis*	0.9	0.25	0.2	0.4	densely striate to striate-rugulate
f. *subdentatus*	1.4 – 1.8	0.5 – 0.9	0.3	0.6 – 0.7	densely striate
tomentosus	0.8	0.2	0.2	0.4	densely to loosely striate
unilobatus	0.9 – 1.0	0.2 – 0.25	0.2	0.5 – 0.6	loosely striate to rugulate
Alectryon	0.7 – 1.8	0.15 – 0.9	0.1 – 0.6	0.3 – 1.0	

* measured in the centre of a mesocolpium; ** see remark 7; A: colporate sample, B: parasyncolporate sample (see Apo-/mesocolpium coherence).

Apo-/mesocolpium coherence

Alectryon yields a complete series from purely colporate pollen, via all possible intermediates, to purely parasyncolporate pollen. Purely colporate grains (type A in table 3) show acute colpus ends and apocolpia that are entirely connected to the mesocolpia (see for example plate 11: 5, 6). Intermediately colporate grains (type A* in table 3) show broad more or less distinctly forked colpus ends and/or depressions between the colpus ends (plates 2: 2; 3: 2; 5: 2; 9: 3, 4; 11: 3; 12: 3, 4). Intermediately parasyncolporate grains (type B* in table 3) show apocolpia that are more or less isolated from one, two, or all three mesocolpia (plates 3: 3; 11: 4). Purely parasyncolporate grains (type B in table 3) show completely isolated apocolpia (see for example plate 5: 3). The whole series reads as follows:



Obviously, the boundary between the colporate and the parasyncolporate condition, drawn between intermediately colporate and intermediately parasyncolporate, is a vague one. However, it is usually not difficult to designate a particular sample as either colporate or parasyncolporate. Nearly always either colporate or parasyncolporate grains predominate; only in a few cases intermediate forms make up the whole sample or the greater part of it. Individual samples never contain the whole series from purely colporate to purely parasyncolporate.

Table 3 gives an overview of the variation of the apertural system with regard to apo-/mesocolpium coherence. A few species have been subdivided in order to express infraspecific differences more clearly. The 27 included species offer the following statistics:

- 8 species show exclusively type A grains
- 5 species show type A grains plus (very) small numbers of type A*
- 3 species show type A grains plus usually small numbers of type A* and type B*
- 2 show both type A and type B grains, one of them plus type A* and type B* grains
- 4 species show type B grains plus (very) small numbers of type B*
- 4 species show exclusively type B grains

This explicitly demonstrates the frequency of intermediate forms in *Alectryon*.

The variable degree of apo-/mesocolpium coherence in intermediate forms is most clearly illustrated by three samples belonging to *A. excelsus, A. semicinereus* and *A. unilobatus*. These samples (*Dallachy s.n., Volck 1414* and *Morton 1238* respectively) contain large quantities of intermediate grains.

Table 3. Infrageneric variation of apertural system and ornamentation in *Alectryon* pollen.

Alectryon	apertural system				ornamentation		
					striate	striate-rugulate	rugulate
cardiocarpus	A				+		
carinatus	A				+		
diversifolius	A				+	+	
glaber	A				+	(+)	
kimberleyanus	A				+	+	
ramiflorus	A				+	+	
repandodentatus	A				+	+	
tomentosus	A				+		(+)
forsythii	A	[A*]$^{1/3}$			+	+	
oleifolius	A	[A*]$^{2/5}$			+	+	
pubescens	A	[A*]$^{1/1}$			+		
ferrugineus	A	(A*)$^{2/10}$			+		
grandifolius	A	(A*)$^{2/3}$			+	+	+
coriaceus	A	[A*]$^{2/8}$	[B*]$^{1/8}$		+	+	
subdentatus							
f. *pseudostipularis*	A	[A*]$^{2/5}$			+	+	
f. *subdentatus*	A	(A*)$^{3/4}$	(B*)$^{3/4}$		+		
excelsus (rest)	A	(A*)$^{7/7}$	(B*)$^{1/7}$		(+)	+	
excelsus (Dallachy)	(A)	A*	B*			+	
unilobatus (Hegarty)	A	(A*)			+		
unilobatus (W. & T.)	A	A*					+
unilobatus (Morton)	[A]	A*	B*		+	+	
semicinereus (Anon.)	A	(A*)			+	+	
semicinereus (Volck)		A*	B*	[B]	+	+	
reticulatus (Anon.)	A						+
reticulatus (Hartmann)				B		+	
connatus	A	[A]$^{1/8}$	[B*]$^{5/8}$	B	+	+	+
fuscus			(B*)$^{1/1}$	B		+	+
samoënsis			[B*]$^{2/2}$	B		+	+
subcinereus			[B*]$^{1/8}$	B		+	+
affinis				B		+	
kangeanensis				B	(+)	+	
macrococcus				B		+	+
myrmecophilus				B	+	+	+

A = colporate; A* = intermediately colporate; B* = intermediately parasyncolporate; B = parasyncolporate; ( ) = small number per sample (< 10%); [ ] = very small number per sample (< 1%). The fractions denote the relative numbers of samples in which the pertinent intermediate types were observed (for example, $^1/_3$ = observed in one of the three available samples). See further Apo-/mesocolpium coherence and Apertural system and ornamentation.

Alectryon excelsus — All eight samples of this species show type A (plate 3: 4) and type A* (plate 3: 2); two of them contain also type B* (plate 3: 3). In seven samples type A predominates, whereas in *Dallachy s.n.* it forms the minority. Type A, A* and B* in *Dallachy s.n.* constitute a series of intergrading forms. The transition from A into B* is so gradual that the individual types can hardly be told apart.

Both Travers collections of *A. excelsus* (which do not represent duplicates) revealed a remarkable detail with regard to apo-/mesocolpium coherence: incomplete connections occur especially in immature grains. Moreover, the connections are shorter in the immature stages. Mature grains more frequently have complete connections than immature grains. Possibly, incomplete connections between apocolpia and mesocolpia become complete in a relatively late stage of the development of the exine (see chapter 6.15).

Alectryon semicinereus — Two samples are available of this species. One sample, *Anon. sh. 908.269-1375,* shows type A grains (plate 9: 1) and a small number of type A*. In the other, *Volck 1414,* nearly all grains belong to type A* (plate 9: 2–4) or B*; type B is rare, while type A is lacking. The types A*, B* and B merge into each other. Together with the merging types A and A* of *Anon. sh. 908.269-1375* they constitute a complete series from A to B. Type A* shows depressed zones between the colpus ends (see also *A. unilobatus*).

Alectryon unilobatus — This species is very heterogeneous with regard to apocolpium morphology; all three samples are different (table 3). *Morton 1238* yields a complete series from A to B*, although type A is rare (plate 12: 1–3).

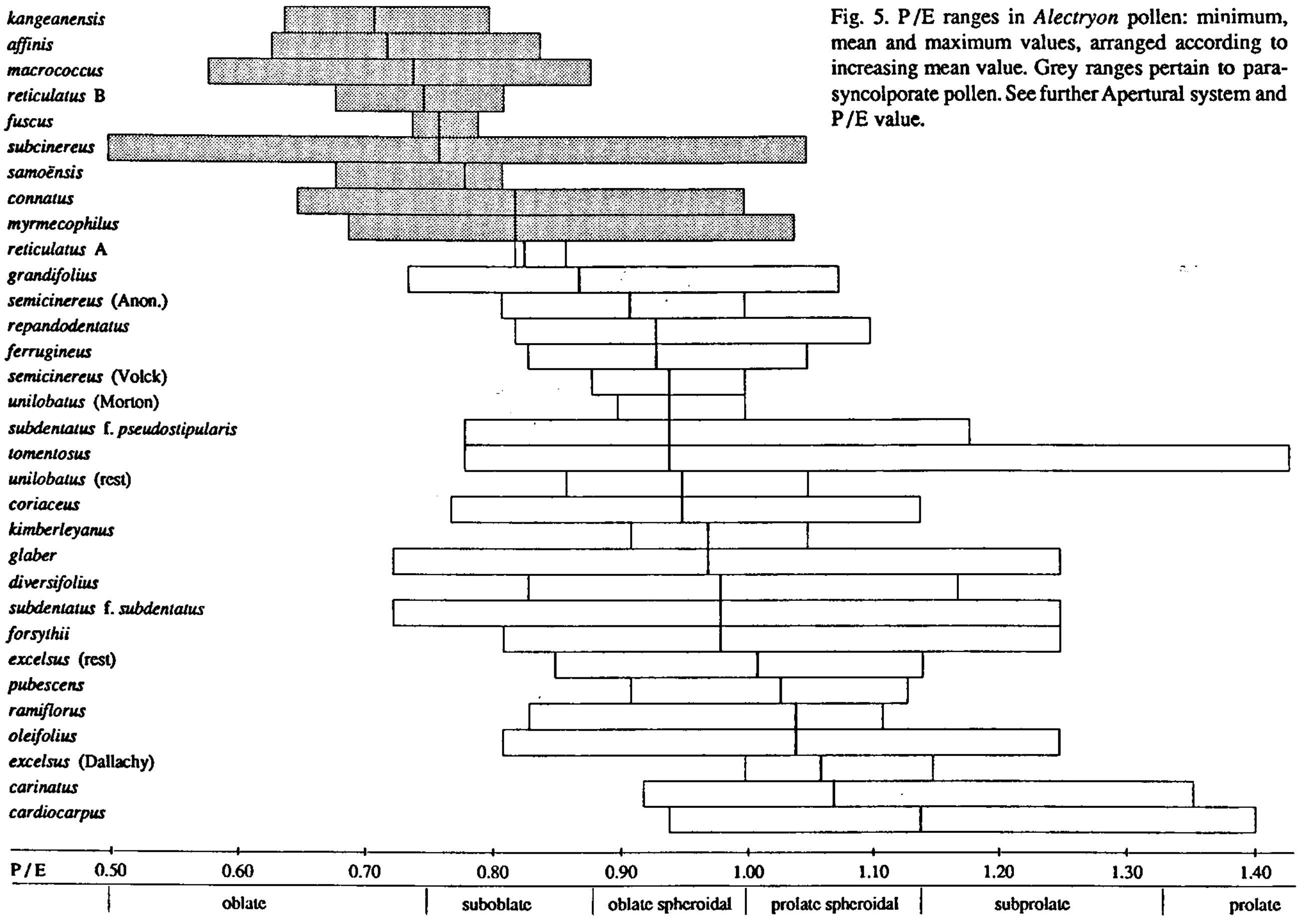
Pollen of *Morton 1238,* in particular type B*, shows much resemblance to that of *Hartmann sh. 1537050,* which belongs to *A. reticulatus* (compare plate 8: 6 with plate 12: 3). The Hartmann sample contains only B type grains; actually it is nearer to *Morton 1238* than to the other sample belonging to *A. reticulatus* (*Anon. s.n.*), which only holds A type grains. Also ornamentation in the two reticulatus samples proved different. *Alectryon reticulatus* is likely to be very rare, being collected only on islands in the Gulf of Papua and the Torres Strait; unfortunately, additional material, which may yield intermediate forms, was not available.

The Morton sample frequently shows grains with fairly well demarcated apocolpia, which, however, are nearly always entirely connected with all three mesocolpia (plate 12: 3). In such cases the demarcation is realised by depressions between the forked colpus ends. These depressed zones correspond to relatively translucent zones between the colpus ends in LM. They are probably due to local thinning or absence of the columellate layer and/or inner tectum (see also chapter 6.15). The same phenomenon was observed in grains of *A. semicinereus* (*Volck 1414*; plate 9: 3, 4) and *A. subdentatus* forma *subdentatus* (*Stuart s.n.*; plate 11: 3, 4).

Apertural system and P/E value

P/E value in *Alectryon* pollen clearly relates to the morphology of the apertural system. Figure 5 gives the P/E ranges of all species, some of these subdivided into

Fig. 5. P/E ranges in *Alectryon* pollen: minimum, mean and maximum values, arranged according to increasing mean value. Grey ranges pertain to parasyncolporate pollen. See further Apertural system and P/E value.



individual samples. Colporate species have higher P/E values than parasyncolporate species. P/E values of samples with many intermediate grains, viz. *Dallachy s.n.* (*A. excelsus*), *Volck 1414* (*A. semicinereus*) and *Morton 1238* (*A. unilobatus*), are similar to those of purely colporate samples. The average P/E in colporate species, including those with samples dominated by many intermediate forms, is 0.97, whereas in parasyncolporate species it is 0.76. Averages of colporate species are ≥ 0.83, those of parasyncolporate species ≤ 0.82.

The type of apertural system of a grain determines to a large extent the way it folds its exine inwards in order to accommodate the volume reduction caused by dehydration of its contents (see also chapter 7.1). Grains with complete connections between the apocolpia and mesocolpia (purely colporate) invaginate their colpi, especially the equatorial parts (fig. 10; plate 3: 4); this makes them more prolate (P/E higher). Complete absence of apo-/mesocolpium connections (purely parasyncolporate) provides a grain with the opportunity to invaginate the colpus membranes round the apocolpia (fig. 11), which causes it to be more oblate (P/E lower).

The presence of apo-/mesocolpium connections is probably the deciding factor in the invagination process. This is illustrated by the samples that show much variation with respect to apo-/mesocolpium coherence (see above); these samples are homogeneous as to other characters, such as apocolpium size and ornamentation. Grains with apocolpia connected to three mesocolpia do not show any invagination, whereas those with apocolpia connected to one or two mesocolpia show partial invagination: only on those sides of the apocolpia where connections are lacking (plates 11: 4; 12: 2). Obviously, apo-/mesocolpium connections hamper easy invagination. Grains with incomplete invagination cannot easily lower their P/E. This explains the fact that the P/E values of the samples with many intermediate grains are similar to those of purely colporate samples, instead of being lower.

Apertural system and A/E value

In addition to P/E value also apocolpium size in *Alectryon* pollen appeared distinctly related to the morphology of the apertural system. Figure 6 shows the A/E ranges of all *Alectryon* species (*A. reticulatus* subdivided into colporate and parasyncolporate). The average A/E value in colporate pollen is 0.32. In parasyncolporate pollen it varies from 0.41 to 0.50 (av. 0.46). Averages of colporate species are ≤ 0.39, whereas those of parasyncolporate species are ≥ 0.41. The minima of all species form a narrower range than the maxima.

The differences between apocolpium sizes of colporate and parasyncolporate pollen are actually still greater than the given A/E values indicate, since E depends on grain shape: prolate and oblate grains of similar size (volume) have different E values. E in colporate grains is 'too low', which results in 'too high' A/E values; E in parasyncolporate grains is 'too high', which produces 'too low' A/E values.

The functional significance of large apocolpium size in parasyncolporate pollen is dealt with in chapter 7.1.

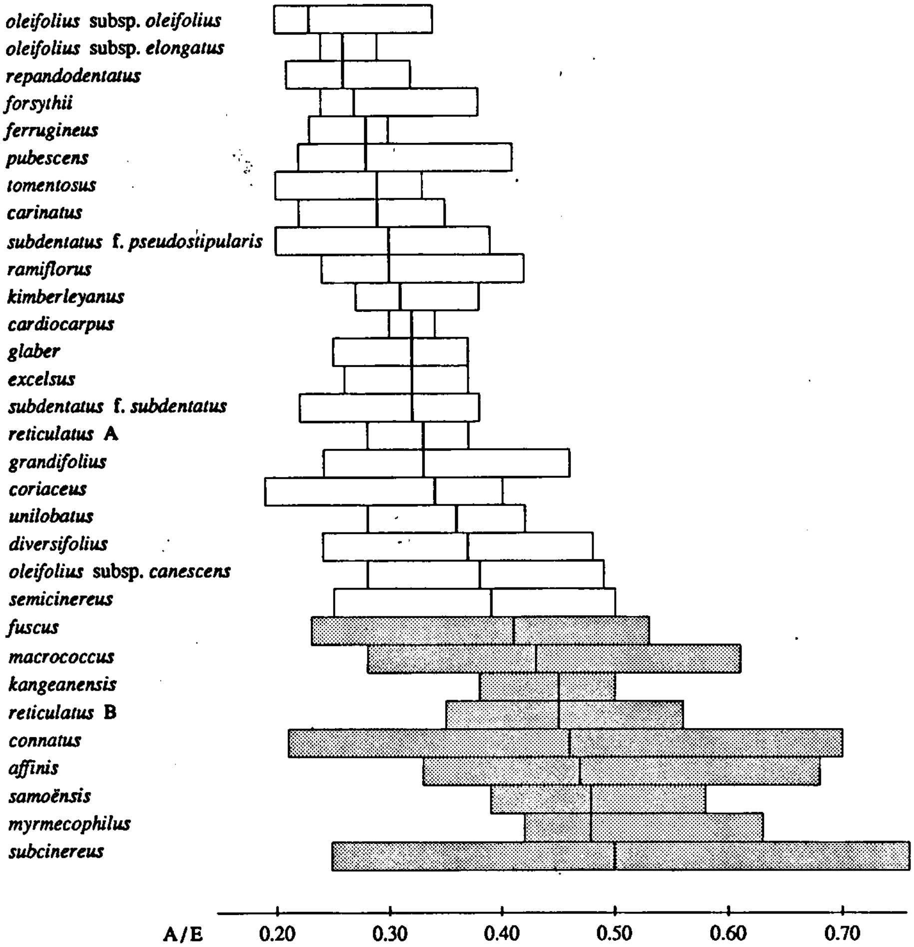


Fig. 6. A/E ranges in *Alectryon* pollen: minimum, mean and maximum values, arranged according to increasing mean value. Grey ranges pertain to parasyncolporate pollen. See further Apertural system and A/E value.

Apertural system and nexine morphology

Pollen of 12 of the 29 *Alectryon* species has been investigated with TEM (table 4). Much variation appeared to exist with respect to the relative thickness and delimitation of the endexine. The contrast between endexine and foot layer is usually distinct, the endexine being more or less darker than the foot layer. In *A. oleifolius* the contrast is sometimes absent or even inverted (plate 47: 2, 3). In *A. connatus* it is totally absent, but the endexine and foot layer are still recognisable due to a slight structural difference: the former is slightly more homogeneous than the latter. Moreover, a very thin electron-lucent 'line' often separates both sublayers (plate 44: 2).

Table 4. Nexine features and columella length in relation to apertural system in *Alectryon* pollen.

Alectryon	prevailing apertural system	boundary endexine/ foot layer	endexine/ nexine ratio/	electron-lucent lamellae		columellae along colpi
				apertural areas	meso-colpia	
carinatus	A	irregular	1/4 – 3/4 (4/4)	+	–	+
coriaceus	A	very irregular	1/2 – 2/3 (4/4)	+	+	++
excelsus	A	rather regular	1/10 – 1/5	+	–	+
ferrugineus	A	irregular	approx. 1/2	+	+	–
forsythii	A	very irregular	1/2 –3/4 (4/4)	–	–	+
grandifolius	A	regular + mix-zone	approx. 1/2 (4/4)	+	+	++
oleifolius	A	irregular or regular + mix-zone	1/3 –1/2	+	–	+
subdentatus	A	irregular	approx. 1/2 (4/4)	+	–	+
connatus	B	regular	1/3 –1/2	–	–	++
macrococcus	B	rather regular	approx. 1/2	+	–	++
myrmecophilus	B	rather regular	1/3 –1/2	+	–	++
subcinereus	B	regular + mix-zone	approx. 1/2	+	+	++

A = colporate; B = parasyncolporate.
Electron-lucent lamellae: + = present, – = absent.
Columellae along colpi: ++ = about equally long as central columellae, or somewhat shorter; + = clearly shorter than central columellae, but still distinct; – = indistinct or absent.
See further Apertural system and nexine morphology, and Apertural system and columella length.

As to relative thickness *A. excelsus* shows a thin mesocolpial endexine (plate 45: 2), whereas several other species possess an endexine that makes up more than half of the total nexine thickness (see for example plate 46: 2, 3). It may reach the intercolumellar surfaces of the nexine in *A. carinatus, A. coriaceus, A. forsythii* (plate 45: 5), *A. grandifolius* (plate 46: 1) and *A. subdentatus.*

The endexine/foot layer contact varies from a regular and sharp boundary to a very irregular mix-zone (compare plates 44: 2; 46: 2, 3 with plates 45: 5; 46: 1). In the apertural areas this mix-zone usually contains thin electron-lucent lamellae (plates 44: 3; 45: 1, 4; 46: 2, 4).

Endexine morphology shows a slight correlation with aperture morphology (table 4): colporate pollen mostly shows an irregular endexine/foot layer boundary, and parasyncolporate pollen usually a more regular one.

Apertural system and columella length

The thinning of the columellate layer from the centre of a mesocolpium towards the colpi has been studied in detail with TEM in 12 species (table 4). Pollen of parasyncolporate species invariably has distinct columellae along the colpi (see for example plates 1: 4; 44: 2; 46: 2, 3); usually (see remark 2), these peripheral columellae of a mesocolpium are as tall as or slightly shorter than the central columellae. The relative length of the peripheral columellae varies in pollen of colporate species. In some species the situation is similar to the parasyncolporate condition (plates 44: 3; 46: 1). Most colporate species have clearly shorter but still distinct columellae along the colpi. In *A. ferrugineus* the columellate layer thins out near the colpi (plate 45: 4). The relative length of the peripheral columellae is possibly an important factor in the harmomegathic functioning of a grain (see chapter 7.1).

In pollen of a few species the polar columellae are distinctly taller than those in the central part of a mesocolpium (see remark 3). The apertural system is colporate in these species.

Apertural system and ornamentation

Ornamentation in *Alectryon* pollen varies from densely striate to densely rugulate. The striate forms show long subparallel muri (plate 4: 1); the rugulate forms show short muri arranged in a criss-cross pattern (plate 8: 4). Between these extremes all possible intermediates exist. Densely striate merges into loosely striate, and densely rugulate into loosely rugulate with somewhat longer and less straight muri. Whether ornamentation is dense or loose depends at least partly on the degree of swelling of a grain (see chapter 7.1). Loosely striate and loosely rugulate intergrade through forms with long sinuous muri that enclose wide grooves with conspicuous perforations.

Sometimes aberrant forms were observed. For instance, one sample of *A. oleifolius* subsp. *canescens* (*Smith 6059*) shows many grains with bundles of muri enclosing true lumina (plate 6: 4); the muri appeared to be arranged into two to four layers.

Ornamentation is always prominent in *Alectryon* pollen. Poorly sculptured grains (plates 39: 1–3; 40: 1, 2, 5, 6), which occasionally occur among prominently sculptured ones, are considered to be immature stages, as they are usually distinctly smaller and have a thinner exine than fully grown grains (see chapter 6.15).

The common forms of ornamentation make up a complete series from densely striate to densely rugulate, which for practical use has been split into three parts: striate, striate-rugulate and rugulate. Striate as well as rugulate comprise both dense and loose forms; striate-rugulate represents the forms with rather long sinuous muri enclosing wide grooves (see for example plate 1: 1–3). Table 3 presents the distribution of the three forms in *Alectryon*. In particular striate and striate-rugulate appear to be common. The distribution of ornamentation forms shows some resemblance to that of apertural types: striate ornamentation predominantly occurs in purely colporate pollen, whereas rugulate ornamentation is mainly found in purely parasyncolporate pollen. Striate-rugulate forms are widespread, being found throughout the range of apertural types.

The functional significance of the correlation between aperture morphology and ornamentation is discussed in chapter 7.1.

Summary

Two main types may be distinguished within *Alectryon* pollen: the colporate type and the parasyncolporate type. These types are not clear-cut, but merge into each other through a complete series of intermediate forms.

The colporate type has usually a colporate apertural system, a high P/E value (av. 0.97), a low A/E value (0.32), and striate to striate-rugulate ornamentation. The parasyncolporate type shows usually a parasyncolporate apertural system, a low P/E value (av. 0.76), a high A/E value (av. 0.46), and striate-rugulate to rugulate ornamentation. In addition, there is some difference in endoaperture and nexine morphology, and the relative length of the peripheral columellae of a mesocolpium. An endoaperture in a colporate grain often shows acute or acuminate lateral sides or a fastigium; these characters were never observed in parasyncolporate grains. Colporate pollen has usually a less regular endexine/foot layer boundary than parasyncolporate pollen. Colporate pollen may have relatively short columellae or no distinguishable columellae at all along the colpi, whereas in parasyncolporate pollen the peripheral columellae are always relatively long.

6.3. CUBILIA

(plates 13; 48: 1; 57: 17–26)

General morphology

Pollen grains of *Cubilia cubili* are rather small (P = 10 (11.7) 14 µm, E = 11 (12.8) 15 µm). Grain shape is oblate to prolate spheroidal (P/E = 0.73 (0.91) 1.04). The equatorial outline is obtusely triangular, with straight to convex sides. The meridional outline is elliptic to subcircular.

Apertures

Cubilia pollen is always colporate. The ectoapertures are long to rather long colpi (A/E = 0.16 (0.34) 0.44). They are usually inconspicuous, especially with LM, which is due to the dense cover of scabrae on the colpus membranes (see also Exine architecture).

The endoapertures are lalongate to isodiametric pori. Meridional size is approximately 1 µm; equatorial size is 1 to 2 µm. The polar sides of an endoaperture are obtuse; the lateral sides are obtuse to acute. A fastigium is absent.

Exine architecture

stratification

Total exine thickness is 0.7 to 0.8 µm and almost uniform throughout the grain.

The nexine is about 0.2 µm thick in the central part of a mesocolpium. Near the colpi it thickens, constituting a twice as thick layer underlying each colpus (colpus membrane) and the borders of the adjacent mesocolpia. TEM data demonstrate the existence of an endexine in the apertural areas. This endexine forms the bulk or the whole of each colpus membrane; it thins towards the mesocolpia. The central part of a mesocolpium does not show any contrast within the nexine, although sometimes a faint and electron-lucent 'line' separates a thin (approx. 1/5 of the total nexine thickness) inner sublayer from a thick outer one (plate 48: 1). Possibly the inner layer represents the mesocolpial endexine (see remark 1).

The columellate layer is 0.1 to 0.15 µm thick in the centre of a mesocolpium. It thins gradually towards the colpi; short columellae still exist along the colpi (see also van den Berg, 1978, plate IX: 1, 2).

The tectum is uniformly 0.3 to 0.4 µm thick (scabrae included).

ornamentation

Ornamentation is variously scabrate (see also Infrageneric variation and geography). The scabrae are more or less isodiametric, measuring up to 0.3 µm high and up to 0.3 µm in diameter, or oblong (see remark 2), measuring up to 1 µm long and about 0.2 µm wide. Low scabrae are obtuse, whereas taller scabrae are more or less acute. In the latter case the tectum may be called micro-echinate. The distance between the scabrae is 0.3 to 0.5 µm. Minute perforations up to 0.1 µm in diameter are usually present between the scabrae. The edges of the mesocolpia merge into the scabrae on the colpus membranes. Sometimes these scabrae look very much the same as the scabrae of the tectum.

Remarks

1. Because of the lack of contrast within the nexine of the central part of a mesocolpium van den Berg (1978) suggested an endexine there to be absent.
2. Oblong scabrae occur locally on grains of *Koorders 22616β*.

Infrageneric variation and geography

Van den Berg (1978) stated that *Cubilia* pollen constitutes a homogeneous and distinct pollen type without any clinal variation. Its scabrate ornamentation was considered as possibly unique in the Nephelieae. Yet, studying additional samples demonstrated the existence of clinal variation with respect to geography. Moreover, the scabrate ornamentation turned out not unique, occuring, although in slightly different shape, in *Dimocarpus* as well.

With regard to ornamentation the available material can be subdivided into three geographical groups:

1. pollen from the Philippines: Luzon and Mindanao (plate 13: 1, 2), which has low obtuse scabrae (up to 0.1 µm high) on the tectum; the colpus membranes are relatively loosely covered with irregularly shaped scabrae (nexine still visible);
2. pollen from Celebes (plate 13: 3, 5), which has obtuse to acute scabrae (up to 0.2 µm high) on the tectum; the colpus membranes are densely covered with irregularly shaped scabrae (nexine obscured);
3. pollen from Borneo (plate 13: 4, 6), which has obtuse to acute scabrae (up to 0.3 µm high) on the tectum; the colpus membranes are densely covered with irregularly shaped scabrae or with elements that closely resemble the acute scabrae on the tectum.

Together these three groups reflect a geographical cline, from the Philippines, via Celebes, to Borneo, in which the scabrae become more prominent, and the cover of the colpus membranes more dense and more like the ornamentation of the tectum.

Van den Berg (1978) provided two illustrations (plate II: 1, 3) of acutely scabrate grains of allegedly Philippine origin. However, checking his data proved these grains to belong to *Koorders 22616β* from Celebes.

As to ornamentation *Cubilia* pollen from the Philippines shows much similarity to the scabrate pollen of several samples of *Dimocarpus longan* subsp. *malesianus*, both possessing low obtuse scabrae (compare plate 13: 1, 2 with plate 19: 1, 2). However, the *Dimocarpus* scabrae are usually more irregularly shaped and more crowded. Fairly large differences exist with respect to grain size and exine stratification.

6.4. DIMOCARPUS

(plates 14–20; 48: 2–5; 49: 1, 2; 58: 1–16)

General morphology

Dimocarpus pollen is small or medium-sized (P = 15 (20.1) 32 µm, E = 17 (22.6) 33 µm). Grain shape is oblate to subprolate (P/E = 0.66 (0.89) 1.18). The equatorial outline is obtusely triangular to subcircular; the triangular outlines have slightly concave to convex sides. The meridional outline is obtusely rhombic to subcircular. The exine of spheroidal grains is often irregularly dented, which is probably due to its flexibility.

Apertures

Dimocarpus pollen is always colporate. The ectoapertures are narrow, long to rather short colpi (A/E = 0.21 (0.36) 0.62). Rarely ectoapertures are short, down to 5 µm (A/E = approx. 0.75) (see remark 1), or rather wide (up to 5 µm) (see remark 2). The ends of the colpi are mostly acute, sometimes obtuse or indistinct. Rarely, broad indistinctly forked colpus ends partly demarcate the apocolpia (see remark 3). The colpus membranes are usually densely covered with scabrae.

The endoapertures are lalongate to lolongate pori, or lalongate (plate 15: 5) or lolongate colpi. Meridional size is 3 to 7 µm; equatorial size is 2 to 7 µm, rarely up to 10 µm. The polar sides of an endoaperture are obtuse (rarely meridionally constricted endoapertures occur); the lateral sides are acute to acuminate. A fastigium can mostly be discerned (see for example plate 16: 5).

Exine architecture

stratification

Total exine thickness is 0.9 to 1.6 µm in the centres of the mesocolpia. It decreases towards the colpi, and it slightly increases again near the colpi.

The nexine is 0.3 to 0.7 µm thick in the central part of a mesocolpium. Usually it thins gradually, sometimes strongly towards the colpi (see remark 4). Near the colpi it thickens again, forming a relatively thick layer under each colpus (colpus membrane) and the borders of the adjacent mesocolpia. With TEM it could mostly be demonstrated to consist of an endexine and a foot layer (plates 48: 2–5; 49: 1, 2; see remark 5). The endexine is thin in the central part of a mesocolpium (1/12 to 1/8 of the total nexine thickness); it thickens towards the colpi to form the bulk or the whole of each colpus membrane. The foot layer thins towards the colpi.

The columellate layer is 0.1 to 0.25 µm thick in the centre of a mesocolpium. It thins gradually towards the colpi; short columellae are usually still visible along the colpi.

The tectum is 0.3 to 0.7 µm thick in the centre of a mesocolpium, being nearly always thinner than the nexine (see remark 6). Its thickness decreases gradually towards the colpi.

ornamentation

Ornamentation is rather diverse. It is usually striate to psilate. The striate ornamentation is sometimes irregular; some irregularly or finely rugulate forms were occasionally found (plate 16: 6, 7). In *D. longan* subsp. *malesianus* several scabrate forms exist (see also Infrageneric variation, and remark 7). The muri in striate and rugulate ornamentation are two-dimensionally arranged (see remark 8), and 0.2 to 0.4 µm, sometimes up to 0.6 µm wide. Several species show wide muri with a fine, more or less distinct substriation ('submuri' 0.1 to 0.2 µm wide; plates 14: 3; 15: 3; 17: 2). The grooves between the muri are up to 0.2 µm, rarely up to 0.5 µm wide. The scabrae are diversely shaped, from roughly isodiametric (plate 19: 2), measuring up to 0.3 µm, to oblong (plate 20: 4), measuring up to 1 µm long and 0.1 to 0.2 µm wide. The isodiametric scabrae do not form a definite pattern; the distance between them varies from 0.1 to 0.6 µm. Oblong scabrae usually show a subparallel arrangement into small groups (grooves approx. as wide as the scabrae), the grains exhibiting a mosaic pattern of finely striate patches. Perforations are nearly always present, although often hidden between the muri or scabrae. They measure up to 0.2 µm, in a few samples up to 0.5 µm in diameter. The edges of the mesocolpia are finely irregularly indented; they often merge into the scabrae on the colpus membranes.

Table 5. Infrageneric variation of a number of pollen characters in *Dimocarpus*.

	P (µm)			E (µm)			P / E			A / E		
australianus	16	(18.8)	24	21	(22.6)	26	0.71	(0.83)	0.96	0.27	(0.31)	0.35
dentatus	21	(23.9)	26	21	(24.9)	31	0.77	(0.96)	1.18	0.35	(0.37)	0.38
foveolatus	19	(21.4)	23	20	(22.7)	25	0.83	(0.94)	1.05	0.26	(0.32)	0.41
fumatus	18	(20.9)	26	19	(21.1)	26	0.83	(0.98)	1.15	0.21	(0.33)	0.56
subsp. *fumatus*	19	(22.5)	26	19	(21.1)	26	0.83	(1.02)	1.15	0.21	(0.36)	0.56
subsp. *indochinensis*	20	(22.1)	25	21	(22.3)	24	0.88	(0.98)	1.14	0.27	(0.32)	0.37
subsp. *javensis*	18	(19.0)	20	19	(20.9)	23	0.86	(0.92)	1.00		0.33	
subsp. *philippinensis*	19	(20.0)	21	19	(20.2)	23	0.83	(0.99)	1.10	0.24	(0.29)	0.32
gardneri	15	(17.3)	20	20	(22.2)	24	0.68	(0.78)	0.90	0.31	(0.40)	0.51
leichhardtii	17	(19.3)	21	20	(22.9)	26	0.78	(0.84)	0.95		0.36	
longan	15	(21.0)	32	17	(24.0)	33	0.66	(0.88)	1.17	0.25	(0.40)	0.62
subsp. *longan*	15	(19.7)	29	17	(22.7)	28	0.68	(0.88)	1.16	0.25	(0.40)	0.54
subsp. *malesianus*	17	(22.3)	32	20	(25.2)	33	0.66	(0.88)	1.17	0.26	(0.39)	0.62
spec.	16	(18.1)	20	19	(20.5)	22	0.74	(0.88)	0.95	0.34	(0.38)	0.41
Dimocarpus	15	(20.1)	32	17	(22.6)	33	0.66	(0.89)	1.18	0.21	(0.36)	0.62

	thickness (µm), measured in the centre of a mesocolpium				
	exine	nexine	columellate layer	tectum	ornamentation
australianus	1.1 – 1.2	0.6	0.1 – 0.2	0.4	striate
dentatus	1.1 – 1.3	0.6	0.1 – 0.2	0.3 – 0.5	striate to indistinctly striate
foveolatus	1.1 – 1.2	0.6	0.2	0.3 – 0.4	psilate
fumatus	0.9 – 1.5	0.3 – 0.6	0.1 – 0.2	0.4 – 0.7	striate to indistinctly striate (see further Infrageneric variation)
subsp. *fumatus*	0.9 – 1.3	0.3 – 0.5	0.1 – 0.2	0.4 – 0.7	
subsp. *indochinensis*	0.9 – 1.0	0.4 – 0.5	0.1	0.4	
subsp. *javensis*	1.2 – 1.3	0.4 – 0.5	0.1	0.6 – 0.7	
subsp. *philippinensis*	1.3 – 1.5	0.6	0.15	0.5 – 0.7	
gardneri	1.0 – 1.2	0.5 – 0.6	0.15	0.4 – 0.5	psilate
leichhardtii	1.1	0.6	0.1	0.4	shallowly striate
longan	1.0 – 1.6	0.5 – 0.7	0.2 – 0.25	0.3 – 0.6	striate to psilate to scabrate; sometimes irregularly or finely or indistinctly rugulate (see further Infrageneric variation)
subsp. *longan*	1.0 – 1.2	0.5 – 0.6	0.2	0.3 – 0.4	
subsp. *malesianus*	1.1 – 1.6	0.5 – 0.7	0.2 – 0.25	0.3 – 0.6	
spec.	1.3	0.7	0.2	0.4	psilate
Dimocarpus	0.9 – 1.6	0.3 – 0.7	0.1 – 0.25	0.3 – 0.7	

Table 5 lists the values/states of a number of the above mentioned characters for the individual species and subspecies in *Dimocarpus*. See Infrageneric variation for differences between the varieties of *D. longan*.

Remarks

1. Short colpi were sometimes observed in *Gusdorf 37, KL 2856* (plate 19: 3) and *S 35239*. In grains with such short colpi the 'usual' position of the colpus ends is often indicated by small (1 to 2 µm) pits in the tectum. Rather short colpi were found in *Nooteboom 4250* and *S 26148* (plate 18: 4). All mentioned samples belong to *D. longan* subsp. *malesianus*.
2. Rather wide colpi exist in *D. australianus, D. fumatus* and *D. longan* subsp. *malesianus*.
3. Partly demarcated apocolpia occur sometimes in immature grains of *D. gardneri* (plate 41: 2; see also chapter 6.15).
4. A rather strongly thinning nexine was found in a few collections of both subspecies of *D. longan*.
5. Most samples of *D. longan* showed very slight or sometimes no contrast at all within the nexine.
6. In a few samples of *D. fumatus* the tectum is as thick as or thicker than the nexine (see further Infrageneric variation).
7. Huang (1972), in a LM study, mentioned a "tectum with scabrate processes" in the description of the pollen of *D. longan*. He also described the sexine to be striate. However, scabrae in Nephelieae pollen are practically unrecognisable using LM, and definitely do not occur in combination with striate ornamentation.
8. Muller (1971) suggested the local presence of a second, superimposed and differently oriented striate system in a striate grain of *PNH 37299* (*D. longan* subsp. *malesianus*). In the present study similar grains were observed in several other samples, for example *Brass 1618* (*Alectryon cardiocarpus*; plate 1: 5) and *van Beusekom & Santisuk 2852* (*Dimocarpus longan* subsp. *longan*; plate 16: 4). Such grains were often found to be more or less dented. Rather than another layer of muri, a superimposed striate system in such grains represents the impression of another striate grain.

Infrageneric variation

Ornamentation in *Dimocarpus* pollen is remarkably variable in comparison with ornamentation in other sapindaceous genera. It appeared still more diverse than it was decribed to be by Muller (1971). Using mainly LM, Muller observed striate (regularly to irregularly) and psilate (finely reticulate, perforate or imperforate) forms. However, applying SEM proved most of his psilate forms, especially those in *D. longan,* to be striate or scabrate. Psilate-perforate ornamentation turned out to be less common than indicated by Muller. Finely reticulate and psilate-imperforate ornamentation could not be demonstrated at all, the former manifesting itself as scabrate (though with crowded perforations), the latter as minutely perforate. In the following sections ornamentation is described for each species separately.

Dimocarpus australianus (plate 14: 1, 2)

Ornamentation striate. Some difference exists between *Gittens 2162* and *Smith 11847* on the one hand and *Hyland 2835* on the other: in the latter sample the muri are approximately 0.2 µm wide, in the other two 0.2 to 0.4 µm. Forms similar to those of *Hyland 2835* occur in *D. longan* subsp. *longan* var. *longan.*

Dimocarpus dentatus (plate 14: 3–5)

Ornamentation striate to indistinctly striate, sometimes slightly irregular. *Endert 5414* and *SAN 54466* are striate, while *SAN 38200* is shallowly or indistinctly striate. *Kostermans 6893* contains striate and shallowly striate forms.

The indistinctly striate grains of *SAN 38200* show muri with a fine substriation ('submuri' approx. 0.1 µm wide). The shallowly striate grains of this sample as well as some grains of *Kostermans 6893* and *SAN 54466* also show this phenomenon, but more locally and less distinctly.

Dimocarpus foveolatus (plate 14: 6)

Ornamentation psilate; perforations not in rows; margines and apocolpia less perforate. The one sample at hand shows only little variation.

Dimocarpus fumatus (plate 15)

Pollen of this species generally has a coarse irregularly shallowly to indistinctly striate ornamentation. This form occurs in subsp. *fumatus* (plate 15: 3–5), subsp. *javensis* and subsp. *philippinensis* (plate 15: 6). Ornamentation in subsp. *indochinensis* is regularly striate and less coarse (plate 15: 1). *Geesink & Hattink 6435* of subsp. *fumatus* contains both forms. The wide muri of the coarsely irregularly striate pollen of *SAN 44665* (subsp. *fumatus*; plate 15: 3) often show a fine substriation.

All collections of *D. fumatus* possess rather wide colpi and large endoapertures. Together with the relatively high P/E value and the usually coarse irregular ornamentation this renders *D. fumatus* pollen a fairly recognisable appearance. In addition, although less easily to observe, pollen of *D. fumatus* generally has a tectum that is as thick as or thicker than the nexine (plate 15: 5); a part of the grains of *Eberhardt 4803* (subsp. *indochinensis*) has a tectum that is thinner than the nexine. Relatively thick tecta appeared to be coarsely irregularly ornamented.

Dimocarpus gardneri (plate 16: 1)

Ornamentation psilate; perforations sometimes locally in rows; margines and apocolpia less perforated. The three samples that are available show only little variation.

Dimocarpus leichhardtii (plate 16: 2)

The sole sample (the species is known from the type specimen only) shows a great deal of variation. Irregularly shallowly striate grains predominate (approx. 90%; plate 16: 2, right-hand grain). The rest of the grains (approx. 4%) is regularly striate, or it has a coarse reticulate pattern of bundles of 'twining' muri (approx. 6%; plate 16: 2, left-hand grain). The bundles in the latter form are up to 1 µm wide, the muri themselves 0.2 to 0.3 µm. The bundles seem to display an anticlockwise 'twining' direction. This can also be noticed in pollen of several other sapindaceous species, e.g. *Arytera foveolata* (chapter 8: fig. 16b) and *Harpullia rhachiptera* (Muller, 1985). Rather straight hardly twining bundles form margines. The depressions enclosed by the bundles are irregularly shaped and measure 0.5 to 2 µm. They contain up to 9 perforations of 0.1 to 0.5 µm in diameter. See also chapter 6.11, remark 1.

Dimocarpus longan subsp. *longan* (plates 16: 3–7; 17: 1–4)

Subsp. *longan* var. *longan* has usually striate pollen; sometimes it is shallowly striate (*Balansa 3420, Kostermans 25282*).

Pollen of *RTH 26927* differs in having a thin tectum with a densely finely rugulate ornamentation, which is sometimes indistinct and has large perforations up to 0.4 µm (plate 16: 6, 7). Intergrading of striate ornamentation and this finely rugulate form could not be demonstrated.

Popta 863/210 shows besides finely striate grains (muri approx. 0.2 µm wide) grains with an incomplete and deviating thin tectum (plate 17: 1, 2; see also Muller, 1971, plate IV: 2, 3). Such grains show patches of isolated columellae (mainly along the colpi), still finer muri (approx. 0.1 µm wide), and faintly striate lumps of sexine material that remind of the striate muri in *Harpullia rhachiptera* (Muller, 1985). In a sense these lumps prove that the incomplete tectum is not an artefact due to acetolysis of a less resistant exine, but rather the outcome of disturbed or 'uncontrolled' tectum formation. The columellae do not seem to be affected. The Popta sample contains a complete series from normal to strongly deviating grains. Two other samples, viz. *Anon. sh. 908.272-802* and *908.272-822,* show the same symptoms, but to a less extent (plate 17: 3, 4). See also chapter 6.11, remark 1.

Chen (1986) found aberrant ornamentation in cultivated *D. longan* (probably subsp. *longan*) from Taiwan. Most of the material studied by Chen is normally striate, but some forms resemble the deviating grains in *Popta 863/210,* and others show wide, more or less separated bundles of muri.

Pollen of subsp. *longan* var. *obtusus* is striate. The muri in *Pierre 4115* are relatively narrow (0.1 to 0.2 µm).

Dimocarpus longan subsp. *malesianus* (plate 17: 5 to plate 20: 5)

Regarding ornamentation subsp. *malesianus* var. *malesianus* is the most variable taxon within the Nephelieae, though individual samples are fairly consistent. Firstly, a complete series of intergrading forms from striate to psilate is represented. Striate ornamentation shows prominent muri (plate 17: 5), whereas psilate ornamentation shows a smooth, more or less perforate tectum (plate 17: 2, 4) or sometimes almost imperforate tectum (plate 18: 5). The intermediate forms may be roughly split into shallowly striate and indistinctly striate forms; distinguishing clearly separate types would be rather arbitrary. Shallowly striate ornamentation has shallower grooves between the muri than striate ornamentation (plate 17: 6). Indistinctly striate ornamentation hardly shows any grooves; at most, faint oblong depressions can be discerned (plate 18: 1). Irregularly striate and irregularly rugulate forms have been occasionally observed in regularly striate samples. Some psilate samples contain also indistinctly rugulate grains.

Secondly, an equally complete series from psilate to scabrate (with more or less isodiametric scabrae) was found (plate 18: 6; 19: 1–3). Less prominently scabrate forms have exposed perforations, whereas these perforations are less conspicuous or hidden in prominently scabrate forms. Further, scabrate with roughly isodiametric scabrae merges into scabrate with oblong scabrae (plates 19: 2–4; 20: 1–4). In several samples (e.g. *Gusdorf 37, KL 2856*) grains with both scabra types have been observed. Pollen of two samples (viz. *S 23044* and *S 23086*, which stem from different trees) contain exclusively the form with oblong scabrae. The grains in these samples display a mosaic pattern of patches of subparallel scabrae (plate 20: 1–4). Oblong patches (0.4 to 0.5 µm wide) of oblong scabrae have an anticlockwise 'twining' aspect (see *D. leichhardtii*).

Putting the three separate series in order, a single continuous range of forms from striate to scabrate with oblong scabrae may be distinguished. Although both extreme forms of this series have oblong elements they do not intergrade in a direct way.

Subsp. *malesianus* var. *echinatus* has scabrate pollen with roughly isodiametric scabrae (plate 20: 5). Within *Dimocarpus* it stands out in having the largest equatorial size (av. 28.8 µm) and a relatively low P/E value (av. 0.78).

Dimocarpus spec. (plate 20: 6)

Ornamentation psilate; perforations sometimes locally in rows; margines less perforated. The sole sample shows only little variation.

Geographical aspects

Striate ornamentation occurs almost throughout the distribution of *Dimocarpus*; it is lacking only in Celebes. Psilate ornamentation is restricted to species with (very) small distributions: *Dimocarpus foveolatus* (one locality in the Philippines), *D. gardneri* (Ceylon) and *Dimocarpus* spec. (one locality in Borneo), or to a part of the distribution of a widespread species: (see *D. longan*). Scabrate ornamentation has a restricted distribution too (see *D. longan*). Two species, viz. *D. fumatus* and *D. longan*, show notable geographical patterns on a infraspecific level.

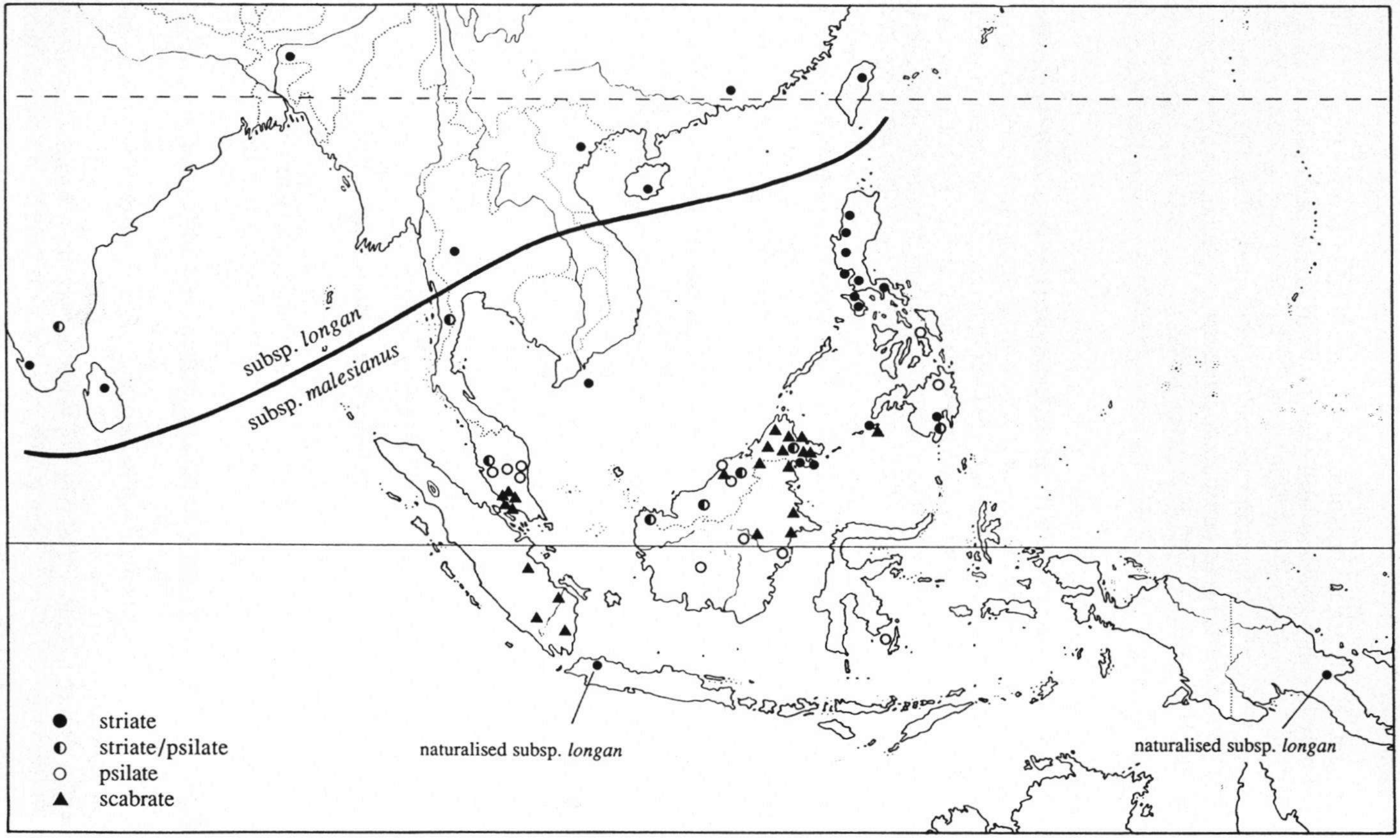


Fig. 7. Distribution of striate, psilate and scabrate ornamentation of *Dimocarpus longan* pollen.

Dimocarpus fumatus

Regular noncoarsely striate ornamentation is confined to continental SE Asia, being found only in subsp. *indochinensis* and in a part of the peninsular Thailand sample of subsp. *fumatus* (*Geesink & Hattink 6435*). Irregular coarsely striate forms occur in peninsular Thailand, Java, Borneo and the Philippines. The Thai sample is considered intermediate between subsp. *indochinensis* and the other three subspecies, pollen-morphologically as well as geographically.

Dimocarpus longan

This species is the most widespread. Subsp. *longan* is often planted as a fruit tree, and its natural distribution is difficult to determine (Leenhouts, 1971). Striate, psilate and scabrate ornamentation show the following geographical pattern (see fig. 7). The striate pollen of subsp. *longan* is spread through India, Ceylon, the northern part of continental SE Asia (including Hainan and Taiwan) and Java. Deviating ornamentation is mainly found in cultivated or naturalised subsp. *longan* from marginal parts of the distribution: *Popta 8031210*, *Anon. sn. 908.272-802* and *908.272-822* from Java, and several collections from Taiwan (see Chen, 1986). Possibly, the aberrant *RTH 26927* from southern India also stems from cultivation. In this connection it may be mentioned that the East Australian *D. leichhardtii*, which also yielded deviating pollen, was suggested to represent a cultivated specimen of *D. longan* (Reynolds, 1982; see also chapter 9).

The striate pollen of subsp. *malesianus* occurs in Vietnam (Con Son), the Philippines (Luzon, Mindanao, Basilan) and NE Borneo. Psilate pollen is present in Malaya, the southwestern part of Borneo, the Philippines (Biliran, Mindanao) and Celebes. Intermediates between striate and psilate come from peninsular Burma, Malaya, NW Borneo and Mindanao. Scabrate pollen of var. *malesianus* appeared to exist in Malaya, Sumatra and the northeastern part of Borneo, that of var. *echinatus* in northeasternmost Borneo and in the Philippines (Basilan). Intermediates between psilate and scabrate occur in Borneo. The scabrate form with oblong scabrae is only found in one locality in NW Borneo (Bukit Mentagai). Intermediates between the two scabrate forms come from Borneo, Malaya and Sumatra.

Summarising the geographical distribution of the various ornamentation forms in *D. longan*:

- striate forms occur in continental SE Asia, northern W Malesia and Java;
- in several regions in W Malesia striate merges into psilate, and in Borneo psilate merges into scabrate ornamentation;
- psilate and scabrate forms are restricted to southern W Malesia, and seem to replace each other there;
- psilate and scabrate ornamentation together more or less replace striate ornamentation in southern W Malesia;
- apparently, Borneo has the widest range of variation regarding ornamentation;
- aberrant forms are mainly found in cultivated or naturalised subsp. *longan* from marginal parts of the distribution.

6.5. LITCHI

(plates 21; 49: 3; 58: 17–20)

General morphology

Pollen grains of *Litchi chinensis* are small (P = 12 (17.3) 23 µm, E = 16 (20.0) 26 µm) (see remark 1). Grain shape is oblate to prolate spheroidal (P/E = 0.70 (0.87) 1.10). The equatorial outline is obtusely triangular to subcircular; the triangular outlines have straight to convex sides. The meridional outline is elliptic to subcircular, sometimes obtusely rhombic (see remark 2).

Apertures

Litchi pollen is usually colporate. Occasionally two or almost three ectoapertures meet, yielding an incomplete syncolporate condition at one pole (see remark 3); wholly syncolporate grains have not been observed.

The ectoapertures are long to fairly long colpi (A/E = 0 (0.28) 0.47) (see remark 2). The ends of the colpi are more or less obtuse, sometimes acute. The colpus membranes are nearly smooth to densely covered with scabrae.

The endoapertures are lalongate to lolongate pori (see remark 2). Meridional size is 3 to 5 µm; equatorial size is 3 to 6 µm. The polar sides of an endoaperture are obtuse; the lateral sides are obtuse to acuminate. A distinct fastigium is present (plates 21: 2, 5, 6; 58: 18).

Exine architecture

stratification

Total exine thickness is 0.9 to 1.4 µm in the centres of the mesocolpia. It decreases towards the colpi, and it slightly increases again near the colpi.

The nexine is 0.4 to 0.6 µm thick in the central part of a mesocolpium. It thins gradually towards the colpi. Near the colpi it thickens slightly, forming a relatively thick layer underlying each colpus (colpus membrane) and the borders of the adjacent mesocolpia. TEM data show the existence of an endexine in the apertural areas (plate 49: 3). This endexine forms the whole of each colpus membrane. It thins towards the mesocolpia, thinning out or becoming very thin (approx. 1/20 of the total nexine thickness) near the central part of each mesocolpium (see remark 4).

The columellate layer is 0.1 to 0.25 µm thick in the centre of a mesocolpium. It thins gradually towards the colpi; short columellae still exist along the colpi.

The tectum is 0.3 to 0.5 µm thick in the centre of a mesocolpium, being at the most as thick as the nexine. It thins gradually towards the colpi.

ornamentation

Ornamentation is striate to irregularly shallowly striate (see Infrageneric variation, and remark 5). The muri are two-dimensionally arranged, and 0.2 to 0.5 µm wide.

Table 6. Infraspecific variation of a number of pollen characters in *Litchi chinensis.*

	P (µm)	E (µm)	P / E	A / E
subsp. ***chinensis***	12 (15.9) 19	16 (19.1) 25	0.70 (0.83) 0.94	0 (0.22) 0.23
subsp. ***javensis***	17 (19.7) 23	20 (22.0) 26	0.78 (0.90) 1.10	0.25 (0.32) 0.47
subsp. ***philippinensis***	14 (16.4) 19	16 (18.9) 21	0.76 (0.87) 0.95	0.21 (0.31) 0.40
Litchi chinensis	12 (17.3) 23	16 (20.0) 26	0.70 (0.87) 1.10	0 (0.28) 0.47

	thickness (µm) *				
	exine	nexine	columellate layer	tectum	ornamentation
subsp. ***chinensis***	1.1	0.5	0.15	0.4	striate
subsp. ***javensis***	1.2	0.6	0.2	0.4	striate to irregularly shallowly striate
subsp. ***philippinensis***	0.9 – 1.4	0.4 – 0.6	0.1 – 0.25	0.3 – 0.5	striate
Litchi chinensis	0.9 – 1.4	0.4 – 0.6	0.1 – 0.25	0.3 – 0.5	

* measured in the centre of a mesocolpium.

The grooves between the muri are up to 0.2 µm wide. Perforations are always present, although often hidden between the muri. They measure up to 0.2 µm in diameter. The edges of the mesocolpia are more or less entire to finely irregularly indented; they often merge into the scabrae on the colpus membranes.

Table 6 lists the values/states of a number of the above mentioned characters for the separate subspecies of *Litchi chinensis.*

Remarks

1. Many samples, including several of subsp. *chinensis* and all three of subsp. *philippinensis,* contain two more or less distinct grain size classes. Liu (1954), studying grain size in a number of cultivars of subsp. *chinensis,* observed this heterogeneity in male flowers and pseudohermaphroditic flowers functioning as males (see chapter 6.14 for the meaning of the term pseudohermaphroditic). In male flowers she noted small nonviable grains (av. diameter 18 µm) and large viable grains (av. diameter 25 µm). In the pseudohermaphroditic males viable grains measure on the average 25 µm, whereas smaller grains without endoapertures were considered nonviable. – In the present study endoapertures were often found indistinct, but their complete absence could never be demonstrated. – In female flowers Liu observed uniform grain size (av. diameter 22.5 µm); the grains appeared normal, but they had a much reduced viability. Liu suggested irregular meioses to be the cause of the differences in grain size and viability in male flowers and pseudohermaphroditic flowers functioning as males (see further chapter 7.2).
2. Irregular grain shape, 4–6-colporate grains, distorted colpi, and nonequatorial endoapertures were relatively often found in subsp. *javensis.*
3. An incomplete syncolporate condition at one pole was observed in about 4% of the grains of *Lei 465* (subsp. *chinensis;* plate 21: 1).
4. Van den Berg (1978) suggested an endexine to be absent in the central part of a mesocolpium.
5. Huang (1972), in a LM study, mentioned a "tectum with scabrate processes" in the description of the pollen of *L. chinensis.* He also described the sexine to be reticulate. Indeed, striate ornamentation may appear reticulate with LM. However, scabrae in Nephelieae pollen are practically unrecognisable using LM, and definitely do not occur in combination with striate or reticulate ornamentation. Besides, the photographs referred to by Huang represent pollen of *Cardiospermum* (tribe Paullinieae).

Infrageneric variation

The differences in ornamentation between the three subspecies of *Litchi chinensis* are not as distinct as they were described to be by van den Berg (1978). He denoted subsp. *philippinensis* as finely striate, subsp. *chinensis* as less regularly striate, and subsp. *javensis* as striate/reticulate or striate/perforate. However, after having studied additional collections murus width proved variable in all subspecies, and regular striate ornamentation appeared not limited to subsp. *philippinensis,* occurring in both other subspecies as well.

Subsp. *philippinensis* shows only regularly striate pollen. *BS 17429* presents one of the most orderly striate forms found in the Nephelieae (plate 21: 5).

Subsp. *chinensis* displays a wide range of variation regarding the degree of parallelism of the muri. In the present study regular (plate 21: 1) and somewhat irregular striate ornamentation were observed. According to Liang et al. (1988), who investigated pollen of 37 cultivars, the pattern varies from "parallel and slightly branched", via "slightly whorled or interwoven", to "sinuous, pseudo-reticulate, striato-reticulate etc."

Subsp. *javensis* is deviating from the other two in having mainly irregular shallowly striate ornamentation. Regular striate ornamentation occurs only in part of the grains of *Blume sh. 908.270-273* (plate 21: 3). Pollen of *Anon. sh. 908.270-267* shows a variable murus width, even within single grains: several narrow muri fuse into a single wide one, and locally wide muri bear a faint substriation. In being relatively prolate and irregularly shallowly striate, sometimes with wide substriated muri, pollen of subsp. *javensis* reminds a lot of that of *Dimocarpus fumatus* (subsp. *fumatus, javensis* and *philippinensis*). Contrary to this, subsp. *javensis* pollen has a tectum that is thinner than the nexine (plate 21: 4).

6.6. NEPHELIUM

(plates 22–27; 50; 51; 59: 1–12; fig. 2)

General morphology

Nephelium pollen grains are small (P = 12 (17.0) 25 µm, E = 16 (20.4) 26 µm). Grain shape is oblate to prolate spheroidal (P/E = 0.59 (0.83) 1.06). The equatorial outline is obtusely triangular, with straight to convex sides; sometimes slightly concave sides or subcircular outlines occur. The meridional outline is usually elliptic, sometimes obtusely rhombic or subcircular.

Apertures

Nephelium pollen is always colporate. The ectoapertures are long to fairly long colpi (A/E = 0.14 (0.29) 0.49). The ends of the colpi are acute to obtuse. Rarely, local depressions between colpus ends partly demarcate the apocolpia (see remark 1). The colpus membranes are usually densely covered with scabrae.

The endoapertures are nearly always lalongate pori; occasionally, lolongate pori or lalongate colpi occur. Meridional and equatorial size are 2 to 7 µm. The polar sides of an endoaperture are usually obtuse (sometimes, meridionally constricted endoapertures occur); the lateral sides are usually acuminate, sometimes acute or obtuse. A fastigium can mostly be discerned (see for example plate 23: 7).

Exine architecture

stratification

Total exine thickness is 0.9 to 1.6 µm in the centres of the mesocolpia. Depending on the degree of thinning of the constituent sublayers it decreases more or less strongly towards the colpi. Near the colpi it increases again.

The nexine is 0.4 to 0.7 µm thick in the central part of a mesocolpium. It thins more or less strongly towards the colpi (see Infrageneric variation). Near the colpi it thickens again, forming a relatively thick layer underlying each colpus (colpus membrane) and the borders of the adjacent mesocolpia. With TEM the nexine was shown to consist of an endexine and a foot layer (plates 50: 2, 4; 51: 2, 3). The endexine is thin in the central part of a mesocolpium (1/15 to 1/7 of the total nexine thickness); it thickens towards the colpi to form the bulk or the whole of each colpus membrane. The foot layer thins towards the colpi. Thin interbedded electron-lucent lamellae occur sometimes in the outer part of the endexine in the apertural areas (see remark 2).

The columellate layer is 0.1 to 0.3 µm thick in the centre of a mesocolpium. It thins more or less strongly towards the colpi (see Infrageneric variation), usually thinning out near the colpi; sometimes short columellae still exist along the colpi.

The tectum is 0.3 to 0.7 µm thick in the centre of a mesocolpium, being at the most as thick as the nexine. Its thickness decreases gradually towards the colpi.

ornamentation

Ornamentation is usually striate or shallowly striate. A few species have indistinctly striate or psilate pollen; several show regularly or irregularly rugulate pollen (see also Infrageneric variation). The muri in striate and rugulate ornamentation are two-dimensionally arranged, and 0.2 to 0.5 µm wide. The grooves between the muri measure up to 0.2, rarely up to 0.4 µm wide (see remark 3). Perforations are probably always present, although often hidden between the muri. They measure up to 0.2, rarely up to 0.4 µm in diameter (see remark 3). The edges of the mesocolpia are mostly finely irregularly indented; usually they merge into the scabrae on the colpus membranes.

Table 7 lists the values/states of a number of the above mentioned characters for the individual species of *Nephelium*. The varieties and subvarieties of *N. cuspidatum* and *N. lappaceum* are not treated separately, as they revealed only minor differences.

Remarks

1. Partly demarcated apocolpia were observed in less than 1% of the grains of *NIFS Cel.IV-196* (*N. lappaceum* var. *pallens*) and *SAN 36302* (*N. ramboutan-ake*).
2. Thin electron-lucent lamellae in the outer part of the apertural endexine were observed in *N. compressum, N. daedaleum* and *N. hypoleucum* (only in *Poilane 2503*).

Table 7. Infrageneric variation of a number of pollen characters in *Nephelium*.

	P (µm)			E (µm)			P / E			A / E		
compressum	13	(15.0)	17	17	(19.4)	21	0.66	(0.78)	0.88	0.21	(0.27)	0.33
costatum	16	(17.9)	20	19	(22.2)	25	0.72	(0.79)	0.85	0.22	(0.28)	0.34
cuspidatum	12	(17.6)	22	17	(20.9)	25	0.59	(0.84)	0.98	0.15	(0.27)	0.39
daedaleum	15	(16.6)	19	17	(21.0)	26	0.65	(0.79)	0.94	0.19	(0.23)	0.28
hamulatum	13	(14.9)	16	18	(19.8)	21	0.68	(0.75)	0.89	0.20	(0.25)	0.31
havilandii	14	(16.0)	19	16	(18.4)	22	0.79	(0.87)	0.90	0.22	(0.29)	0.36
hypoleucum	14	(18.5)	25	17	(21.2)	26	0.68	(0.87)	1.05	0.25	(0.32)	0.40
juglandifolium	17	(18.7)	21	19	(21.1)	23	0.82	(0.89)	0.96	0.27	(0.35)	0.45
lappaceum	13	(18.0)	22	16	(20.8)	26	0.70	(0.86)	0.95	0.23	(0.32)	0.49
laurinum	13	(16.0)	20	17	(19.3)	23	0.71	(0.83)	0.91	0.25	(0.28)	0.32
*macrophyllum****	13	(14.7)	16	18	(19.8)	23	0.62	(0.74)	0.85	0.21	(0.25)	0.29
maingayi	13	(16.6)	20	16	(17.9)	23	0.75	(0.91)	1.06	0.25	(0.32)	0.37
*meduseum****		—			—			—			—	
melanomiscum	13	(15.3)	18	19	(20.3)	22	0.63	(0.75)	0.95	0.23	(0.25)	0.30
melliferum	15	(17.8)	20	20	(21.5)	24	0.71	(0.83)	0.95	0.29	(0.31)	0.33
papillatum	14	(15.2)	18	17	(18.3)	20	0.80	(0.84)	0.90	0.24	(0.27)	0.29
ramboutan-ake	12	(17.2)	23	16	(20.1)	25	0.71	(0.86)	1.00	0.14	(0.28)	0.41
reticulatum	16	(19.7)	22	20	(22.8)	24	0.71	(0.86)	1.00	0.20	(0.26)	0.34
subfalcatum	16	(18.6)	20	19	(21.1)	23	0.81	(0.88)	1.00	0.24	(0.30)	0.33
uncinatum	14	(17.3)	19	17	(19.6)	22	0.81	(0.89)	0.95	0.37	(0.46)	0.49
spec. nov.	19	(19.3)	20	22	(23.5)	24	0.75	(0.82)	0.87	0.32	(0.34)	0.35
Nephelium	12	(17.0)	25	16	(20.4)	26	0.59	(0.83)	1.06	0.14	(0.29)	0.49

(Table 7 continued)

	thickness (µm) *				
	exine	nexine	columellate layer	tectum	ornamentation
compressum	1.3	0.7**	0.2**	0.4	indistinctly striate to psilate
costatum	1.1	0.6	0.1	0.4	shallowly striate
cuspidatum	1.1	0.6	0.1 – 0.15	0.4	striate
daedaleum	1.3	0.7**	0.2**	0.4	indistinctly striate to psilate
hamulatum	0.9	0.4	0.1	0.4	shallowly striate
havilandii	1.1 – 1.2	0.5	0.15 – 0.25**	0.4 – 0.5	striate to rugulate
hypoleucum	1.3	0.6**	0.2**	0.5	striate to rugulate
juglandifolium	1.3	0.6	0.1	0.6	striate
lappaceum	1.2	0.5 – 0.6	0.1 – 0.2	0.5	striate; irregularly rugulate
laurinum	1.0	0.5	0.1 – 0.15	0.3 – 0.4	striate
*macrophyllum****	1.1 – 1.2	0.6**	0.2**	0.3 – 0.4	shallowly striate
maingayi	1.2	0.5	0.15	0.5	striate
*meduseum****	1.4	0.7**	0.2**	0.5	shallowly striate
melanomiscum	1.5	0.7**	0.25 – 0.3**	0.5	shallowly striate
melliferum	1.6	0.7**	0.25**	0.7	striate
papillatum	1.5	0.7**	0.25**	0.5	striate
ramboutan-ake	0.9 – 1.0	0.4	0.1	0.4 – 0.5	striate
reticulatum	1.1	0.5**	0.2**	0.3	shallowly striate
subfalcatum	1.1 – 1.2	0.5	0.1 – 0.2**	0.5	striate; irregularly rugulate
uncinatum	1.0	0.5	0.15**	0.4	striate
spec. nov.	1.5	0.7**	0.25**	0.5	striate
Nephelium	0.9 – 1.6	0.4 – 0.7	0.1 – 0.3	0.3 – 0.7	

* measured in the centre of a mesocolpium; ** strongly decreasing towards the colpi; *** see remark 4.

3. Irregularly shaped grooves up to 0.4 µm wide, containing equally large perforations (thus yielding true lumina), appeared to be present in *N. subfalcatum* (plate 27: 4).
4. The samples of *N. macrophyllum* and *N. meduseum* consisted of shrivelled anthers obtained from fruit bases (see also chapter 6.14).

Infrageneric variation

Nephelium pollen shows a great deal of variation in its ornamentation and in the thickness of the individual sublayers of its exine. Below, special reference is made to the prominence and direction of the muri, and the relative size of the central columellae of a mesocolpium.

Ornamentation

With respect to the prominence of the muri a complete series from striate to psilate was found. Striate ornamentation (see for example plate 24: 5) shows prominent muri, whereas psilate ornamentation (plate 23: 1) shows a smooth more or less perforate tectum (perforations often in rows). Distinguishing separate ornamentation types proved impossible; for the sake of convenience the intermediate forms have been split into: shallowly striate (plates 25: 4; 26: 1), having exposed perforations in shallow grooves, and indistinctly striate (plate 22: 2), showing perforations in faint oblong depressions.

Roughly, three groups of species may be distinguished regarding the prominence of the muri:

1. species that generally have striate (sometimes rugulate) pollen; this group includes 13 species (see table 7);
2. species that mostly have shallowly striate (sometimes shallowly rugulate) pollen; 6 species were included in this group (see table 7);
3. species with indistinctly striate to psilate pollen; this group embraces *N. compressum* and *N. daedaleum* (*Haviland 2270* of the former species, and *SAN 60511* of the latter comprise indistinctly striate, psilate as well as intermediate forms; *Haviland 3175* and *S 36914* of the respective species have indistinctly striate pollen).

As to the direction of the muri a series from regularly striate, via irregularly striate and irregularly rugulate, to regularly rugulate could be established.

Most *Nephelium* species have more or less striate pollen; grains with irregularly striate to irregularly rugulate ornamentation occur, together with regularly striate ones, in *N. cuspidatum* var. *eriopetalum* (*SAN 89304*; plate 22: 6), *N. lappaceum* var. *lappaceum* and var. *pallens* (both several samples), *N. melliferum* (*d'Alleizette 1421*) and *N. subfalcatum* (*NIFS T 712*). *Anon. sh. 908.269-1398* of *N. lappaceum* var. *lappaceum*, and *KEP FRI 7720* of *N. subfalcatum* proved entirely irregularly rugulate. The only sample of *N. havilandii*, and 3 out of the 10 samples of *N. hypoleucum* contain besides regularly striate and irregularly ornamented grains also regularly rugulate grains, thus displaying the full series from striate to rugulate (plates 23: 3, 4; 24: 1, 2).

In contrast with the situation in *Xerospermum* rugulate ornamentation in *Nephelium* is not restricted to the less prominent forms of ornamentation.

Except for those of *N. havilandii* and *N. hypoleucum*, which have very similar pollen, the various rugulate forms in *Nephelium* make up a heterogeneous group.

Columellae

Nephelium pollen shows considerable variation regarding the length of the central columellae of a mesocolpium. In the Nephelieae the central columellae in a mesocolpium are usually the tallest; towards the colpi they shorten. In *Nephelium* long central columellae imply a strong decline towards more peripheral columellae, whereas medium and small-sized columellae manifest a gradual decline. Two groups of species were distinguished as for columella length:

1. species with gradually decreasing columella length towards the colpi (plates 24: 6, 7; 25: 2; 51: 1; 59: 2) and central columellae 0.1 (0.11) 0.2 µm long; this group includes 9 species (see table 7);
2. species with strongly decreasing columella length towards the colpi (plates 22: 3; 23: 6, 7; 50: 3, 4; 51: 4; 59: 8) and central columellae 0.15 (0.21) 0.3 µm long; 13 species were reckoned to this group (see table 7; *N. havilandii, N. hypoleucum, N. macrophyllum* and *N. papillatum* show the strongest decline).

Nephelium subfalcatum showed short (*S 25991*) as well as tall (*KEP FRI 7722, NIFS T 712*) central columellae, and was consequently placed in both groups.

Long strongly declining columellae appeared to be largely associated with a thick similarly declining nexine (see table 7; compare plate 51: 1 with plate 50: 3). Average nexine thickness is 0.52 µm in group 1, and 0.62 µm in group 2. The highest values exist in group 2.

Geographical aspects

Listing the species with shallowly striate to psilate ornamentation and/or a strongly decreasing columellate layer yields a rather distinct geographical pattern (see table 8). Most of the species that possess one or both of these character states appear to be endemics of either Borneo (*N. melanomiscum* also in Mindanao) or Malaya, or Borneo + Malaya + Sumatra; only a few occur outside these regions. The combination of both characters is found only in Bornean species. On the contrary, striate ornamentation and a gradually decreasing columellate layer are common throughout the distribution of *Nephelium* (continental SE Asia, Sumatra, Java, Borneo, Philippines, Celebes).

Being not restricted to the less prominent forms of ornamentation, irregularly striate, irregularly rugulate and regularly rugulate *Nephelium* pollen is found inside as well as outside Borneo. This contrasts with the almost entirely Bornean distribution of irregularly rugulate ornamentation of *Xerospermum* pollen.

Table 8. Ornamentation and columella length in relation to geography in *Nephelium* pollen. See further Geographical aspects.

distribution area	*Nephelium*	strongly decreasing columellate layer	ornamentation shallowly striate to psilate	sometimes irregularly striate, irregularly rugulate or regularly rugulate
widespread	*cuspidatum*			+
	lappaceum			+
	ramboutan-ake			
SE Asia	*hypoleucum*	+		+
	melliferum	+		+
W Malesia	*juglandifolium*			
	laurinum			
	maingayi			
	subfalcatum	+		+
	uncinatum	+		
Malaya	*costatum*		+	
	hamulatum		+	
	spec. nov.	+		
Borneo	*compressum*	+	+	
	daedaleum	+	+	
	havilandii	+		+
	macrophyllum	+	+	
	meduseum	+	+	
	melanomiscum	+	+	
	papillatum	+		
	reticulatum	+	+	

6.7. OTONEPHELIUM

(plates 28; 52; 58: 21–24)

General morphology

Pollen of *Otonephelium stipulaceum* is small (P = 14 (15.9) 17 µm, E = 17 (19.5) 21 µm). Grain shape is oblate to oblate spheroidal (P/E = 0.73 (0.82) 0.95). The equatorial outline is obtusely triangular with straight to slightly convex sides. The meridional outline is elliptic, sometimes subcircular.

Apertures

Otonephelium pollen is always colporate. The ectoapertures are fairly long colpi (A/E = 0.26 (0.31) 0.34). The ends of the colpi are acute. The colpus membranes are densely covered with scabrae; sometimes they are smooth.

The endoapertures are lalongate pori. Meridional size is 2 to 3 µm; equatorial size is 3 to 4 µm. The polar sides of an endoaperture are obtuse; the lateral sides are obtuse to acuminate. A distinct fastigium is present (plates 28: 5, 6; 58: 22).

Exine architecture

stratification

Total exine thickness is approximately 1.5 µm in the centres of the mesocolpia. It decreases towards the colpi. Near the colpi it increases again.

The nexine is 0.8 µm in the centre of a mesocolpium. It thins towards the colpi. Near the colpi it thickens again, forming a relatively thick layer underlying each colpus (colpus membrane) and the borders of the adjacent mesocolpia. TEM data of mature grains are not available. In TEM photographs of immature grains (plate 52) the nexine does not show any subdivision into an endexine and a foot layer. In the apertural areas the nexine is fragmentary or entirely absent. In the tetrad period it is incomplete throughout (see further chapter 6.15).

The columellate layer is about 0.15 µm thick in the central part of a mesocolpium. It thins gradually towards the colpi, thinning out near the colpi.

The tectum is 0.5 to 0.6 µm thick in the centre of a mesocolpium, being always thinner than the nexine. It thins gradually towards the colpi.

ornamentation

Ornamentation is usually striate; sometimes it is irregularly striate or irregularly rugulate (plate 28: 4), particularly in the centres of the mesocolpia. The muri are two-dimensionally arranged, and 0.2 to 0.4 µm wide. The grooves between the muri are up to 0.1 µm wide. Perforations are probably entirely absent. The edges of the mesocolpia are irregularly indented and merge into the scabrae on the colpus membranes.

Remark

The sample *Anon. s.n. in Herb. Hookerianum,* studied by van den Berg (1978), differs considerably from the only other sample *Pascal 1375*:

- the grains are generally smaller (P = 13 (15.2) 18 µm, E = 14 (15.4) 20 µm) and less oblate (av. P/E = 0.98);
- the colpus membranes are relatively thin (plate 28: 2);
- in spite of van den Berg's mention of circular/elliptical meridionally elongated endoapertures of about 2 µm in diameter no distinct endoapertures could be indicated, neither in his slides and photographs nor in newly prepared material; only small to very large (up to half the colpus length) irregular gaps in the thin colpus membranes were observed (plates 28: 2; 42: 3);
- ornamentation is psilate-imperforate in approximately 3% of the grains (plate 42: 3).

All these deviations point to immaturity of the material (see also chapter 6.15). Moreover, checking the herbarium specimen from which it was sampled revealed the inflorescences to be in a very young stage. This supports the view that the pollen grains studied by van den Berg were immature. Therefore the samples from the *Herb. Hookerianum* specimen were used with reservation in compiling the general description of *Otonephelium* pollen. However, they proved very valuable with respect to ontogeny (see chapter 6.15).

6.8. PAPPEA

(plates 29; 53; 59: 13–20)

General morphology

Pollen grains of *Pappea capensis* are small (P = 14 (16.5) 21 µm, E = 14 (17.7) 24 µm). Grain shape is suboblate to prolate spheroidal (P/E = 0.77 (0.93) 1.13). The equatorial outline is obtusely triangular to subcircular; the triangular outlines have convex or sometimes straight sides. The meridional outline is obtusely rhombic to subcircular.

Apertures

Pappea pollen is always colporate. The ectoapertures are long to fairly long colpi (A/E = 0.19 (0.34) 0.45). The ends of the colpi are acute to obtuse. The colpus membranes are nearly smooth to densely covered with scabrae.

The endoapertures are lalongate pori or colpi. Meridional size is 2 to 5 µm; equatorial size is 2 to 8 µm. The polar sides of an endoaperture are obtuse; the lateral sides are usually acute to acuminate, sometimes obtuse. A fastigium can mostly be discerned (plate 29: 4, 5).

Exine architecture

stratification

Total exine thickness is 1.1 to 1.9 µm in the centres of the mesocolpia. Depending on the degree of thinning of the tectum it decreases more or less strongly towards the colpi. Near the colpi it slightly increases again, or it remains about uniformly thick.

The nexine is 0.4 to 0.6 µm thick in the centre of a mesocolpium. It thins gradually towards the colpi. Near the colpi it slightly thickens again. The colpus membranes are hardly or not thicker than the mesocolpial nexine. With TEM the nexine could be shown to consist of an endexine and a foot layer (plate 53: 2, 4, 5). The endexine is thin in the central part of a mesocolpium (1/15 to 1/10 of the total nexine thickness); it thickens towards the colpi to form the bulk of each mesocolpium membrane. The foot layer thins towards the colpi. Thin interbedded electron-lucent lamellae occur sometimes in the outer part of the endexine in the apertural areas (see remark 1).

The columellate layer is 0.1 to 0.2 μm thick in the centre of a mesocolpium. It thins gradually towards the colpi, thinning out near the colpi. The peripheral columellae stand more or less obliquely on the nexine: in an equatorial section and in sections parallel to the equatorial plane the distal columella ends in a single mesocolpium point in convergent directions (plate 53: 2, 4, 5).

The tectum is 0.5 to 1.0 μm thick in the central part of a mesocolpium, being always thicker than the nexine. Its thickness decreases gradually or strongly towards the colpi (see Infrageneric variation and geography).

ornamentation

Ornamentation is usually striate; sometimes it is irregularly striate (see remark 2). The muri are two- or three-dimensionally arranged (see Infraspecific variation and geography). Their width ranges from 0.2 to 0.4 μm. The grooves between the muri measure up to 0.2 μm wide. Perforations are always present, although they may be hidden between the muri. They measure up to 0.2 μm in diameter. The edges of the mesocolpia are finely irregularly indented; mostly they merge into the scabrae on the colpus membranes.

Remarks

1. Thin electron-lucent lamellae in the outer part of the apertural endexine were sometimes observed in both samples studied with TEM.
2. Occasionally a mosaic pattern of striate and psilate-perforate ornamentation was observed in *Anon. 346.*

Infrageneric variation and geography

The samples from the southernmost part of the distribution of *Pappea capensis* possess a somewhat different exine architecture than the others. It concerns *Anon. sh. 898.269-427, Dyer 1181a, Hardy & Bayliss 1204* and *Long 233,* all from the southern part of South Africa. Pollen of these four samples have a relatively thick tectum with deep grooves between the muri (compare plate 29: 1, 2 with 29: 3, and plate 53: 4 with 53: 5). Using TEM it appeared that the tectum in the central part of a mesocolpium consists of a basal layer and two layers of muri (plate 53: 4). The two muri layers do not show a clearly defined boundary, as their muri merge into each other, which results in a truly three-dimensional system of muri. Often the outer muri have a narrowed base; occasionally they seem locally completely separated from the inner muri. Towards the colpi tectum thickness decreases strongly, while the three-dimensional arrangement changes into a two-dimensional one (plates 29: 2; 53: 2).

For the rest it can be stated that *Pappea* pollen is remarkably uniform from Ethiopia to South Africa.

6.9. PODONEPHELIUM

(plates 30; 54: 1–4; 60: 1–8)

General morphology

Podonephelium pollen is small or medium-sized (P = 21 (25.2) 29 µm, E = 19 (22.9) 28 µm). Grain shape is oblate spheroidal to subprolate (P/E = 0.92 (1.10) 1.24). The equatorial outline is obtusely triangular, with straight to convex sides. The meridional outline is obtusely rhombic, elliptic or subcircular.

Apertures

Podonephelium pollen is always colporate. The ectoapertures are fairly long colpi (A/E = 0.26 (0.35) 0.46). The ends of the colpi are acute to obtuse. The colpus membranes are sparsely covered with scabrae.

The endoapertures are lalongate to lolongate pori. Meridional size is 2 to 4 µm; equatorial size is 3 to 5 µm. The polar sides of an endoaperture are obtuse; the lateral sides are obtuse, or sometimes acuminate. A fastigium can mostly be discerned (plate 30: 3).

Exine architecture

stratification

Total exine thickness is 1.0 to 1.6 µm in the centres of the mesocolpia. It decreases towards the colpi, or it remains uniform. Near the colpi it increases again. Sometimes the exine thickness of the apocolpia exceeds that of the mesocolpia (see remark 1).

The nexine is 0.25 to 0.4 µm thick in the central part of a mesocolpium. It thickens near the colpi, forming a relatively thick layer under each colpus (colpus membrane) and the borders of the adjacent mesocolpia. With TEM it was shown to consist of an endexine and a foot layer. The boundary between these two sublayers is regular or rather irregular (compare plate 54: 2 with plate 54: 4). The endexine is rather thick in the central part of a mesocolpium (1/6 to 1/3 of the total nexine thickness); it thickens towards the colpi to form the whole of each colpus membrane. The foot layer thins towards the colpi. Thin interbedded electron-lucent lamellae occur in the outer part of the endexine in the apertural areas (see remark 2).

The columellate layer is 0.25 to 0.5 µm thick in the centre of a mesocolpium. It thins gradually towards the colpi; short columellae still exist along the colpi. The polar columellae may be considerably taller than the mesocolpial ones (see remark 1).

The tectum is 0.5 to 0.8 µm thick in the centre of a mesocolpium, being always thicker than the nexine. Its thickness decreases gradually towards the colpi.

ornamentation

Ornamentation is striate, sometimes irregularly striate (see remark 3). The muri are two-dimensionally arranged and about 0.3 µm wide. Usually they have a narrowed base; sometimes they seem locally completely separated from the basal layer of the tectum (plate 54: 2). The grooves between the muri measure up to 0.1 µm wide. Perforations are abundantly present, although often hidden between the muri. They measure up to 0.2 µm in diameter. The edges of the mesocolpia are usually more or less entire; rarely they are finely indented.

Table 9 lists the values/states of a number of the above mentioned characters for the individual *Podonephelium* species. Pollen of *Podonephelium* reveals only minor infrageneric variation.

Table 9. Infrageneric variation of a number of pollen characters in *Podonephelium*.

	P (µm)	E (µm)	P / E	A / E
concolor	25 (26.5) 29	21 (23.5) 27	1.04 (1.13) 1.21	0.40 (0.43) 0.46
homei	25 (26.8) 29	23 (24.8) 28	0.96 (1.08) 1.19	0.30
parvifolium	21 (23.5) 26	19 (20.9) 23	1.00 (1.12) 1.23	0.26 (0.30) 0.34
subaequilaterum	21 (24.1) 26	20 (22.4) 25	0.92 (1.08) 1.24	0.32 (0.37) 0.42
Podonephelium	21 (25.2) 29	19 (22.9) 28	0.92 (1.10) 1.24	0.26 (0.35) 0.46

	thickness (µm) *				
	exine	nexine	columellate layer	tectum	ornamentation
concolor	1.5 – 1.6	0.3	0.5	0.7 – 0.8	striate
homei	1.1 – 1.2	0.3	0.25	0.5 – 0.6	striate
parvifolium	1.3	0.4	0.4	0.5	striate
subaequilaterum	1.0	0.25	0.25	0.5	striate
Podonephelium	1.0 – 1.6	0.25 – 0.4	0.25 – 0.5	0.5 – 0.8	

* measured in the centre of a mesocolpium.

Remarks

1. In pollen of *Franc 719* (*P. subaequilaterum*) the polar columellae are considerably taller than those in the central part of a mesocolpium, measuring 0.5 µm and 0.25 µm respectively (total exine thickness 1.3 and 1.0 µm). Possibly, taller polar columellae also exist in *P. concolor* (*d'Alleizette 1425*) and *P. homei* (*Vieillard 219*).
2. Thin electron-lucent lamellae in the outer part of the apertural endexine were observed in *P. homei*.
3. About half of the grains in *Franc 719* (*P. subaequilaterum*) bear an irregularly striate tectum (plate 30: 6).

6.10. POMETIA

(plates 31; 54: 5–7; 60: 9–17; fig. 12)

General morphology

Pometia pollen grains are small to medium-sized (P = 16 (20.6) 29 µm, E = 20 (26.4) 38 µm) (see remark 1). Grain shape is oblate to suboblate (P/E = 0.67 (0.78) 0.87). The equatorial outline is obtusely triangular, with concave to convex sides and often more or less protruding apertures. The meridional outline is obtusely rhombic with slightly concave to convex sides.

Apertures

Pometia pollen is always brevicolporate. The ectoapertures are fairly short to short colpi (length = 12 (7.1) 4 µm; A/E = 0.57 (0.70) 0.85). Usually the colpi are nearly or completely closed slits (plate 31: 1, 2, 4); opened colpi (plate 31: 3) are up to 4 µm wide and about elliptic with acute to acuminate ends. There are no colpus membranes; rarely, small parts of the endoapertural lamellae system may be seen near the colpus ends.

The endoapertures are short tubes; they measure 4 to 6 µm long and 2 to 5 µm in diameter. The inner edge of an endoaperture has sometimes one to three (usually two, in the equatorial plane) acute triangular indentations (plate 31: 6). An endoaperture is completely surrounded by a system of lamellae (see Exine architecture). The inner lamellae (near the inner edge) are sometimes more or less separated from the outer lamellae (near the colpi), yielding an indistinct fastigium (plate 31: 5; see also van den Berg, 1978, plate VI: 3). Sometimes a fastigium-like cavity was observed immediately under the borders of the mesocolpia.

Exine architecture

stratification

Total exine thickness varies from 1.3 to 2.0 µm in the centres of the mesocolpia. Apart from the lamellae that surround the endoapertures, exine thickness decreases slightly towards the colpi.

The nexine is 0.5 to 0.9 µm thick in the centre of a mesocolpium. It thins gradually towards the colpi. Near the colpi a number of lamellae split from the main layer. TEM (plate 54: 5, 6; see also van den Berg, 1978) shows the inner lamellae to be thin (approx. 0.05 µm) and irregularly arranged, or indistinct. Towards the colpi they become thicker (up to 0.25 µm), and more regular and distinct. The inner ones are continuous with a thin (approx. 0.05 µm) sparse lamellate/granular and loosely attached layer covering the inner surface of the nonapertural parts of a grain (plate 54: 6, 7). SEM demonstrates the inner side of a grain often to be irregularly rough (plate 31: 5; van den Berg, 1978, plate VI: 1), in particular round the endoapertures. The apertural lamellae and the thin covering of the nonapertural areas are regarded as the endexinous part of the nexine (see remark 2). The main layer of the nexine is considered to represent the foot layer.

The columellate layer is 0.3 to 0.5 µm thick in the central part of a mesocolpium. It thins gradually towards the colpi; short columellae still exist along the colpi.

The tectum is 0.5 to 0.9 µm thick in the centre of a mesocolpium, being thinner to slightly thicker than the nexine. It thins gradually towards the colpi.

ornamentation

Ornamentation is usually reticulate, occasionally microreticulate (see remarks 3 and 4). The muri are 0.4 to 1.0 µm wide; wide muri may be duplicolumellate (plate 60: 9). The lumina are roughly isodiametric and small, measuring up to 1 µm, to oblong irregularly angular and large, measuring up to 4 µm long and 2 µm wide. Their size is largest in the centres of the mesocolpia; distinctly smaller lumina are concentrated round the colpi and sometimes also between the colpus ends and the poles (plate 31: 1, 2). A psilate more or less perforate margo may be present round or at either side of a colpus. The edges of the mesocolpia are entire or finely indented.

Table 10 lists the values/states of a number of the above mentioned characters for each of the two species of *Pometia*. The formae of *P. pinnata* were not included separately, as they revealed only minor differences (see also van den Berg, 1978).

Table 10. Infrageneric variation of a number of pollen characters in *Pometia.*

	P (µm)	E (µm)	P / E	A / E
pinnata	16 (22.1) 29	20 (27.1) 38	0.67 (0.81) 0.87	0.61 (0.75) 0.85
ridleyi	15 (19.1) 22	22 (25.7) 29	0.74	0.57 (0.65) 0.74
Pometia	15 (20.6) 29	20 (26.4) 38	0.67 (0.78) 0.87	0.57 (0.70) 0.85

	thickness (µm) *				
	exine	nexine	columellate layer	tectum	ornamentation
pinnata	1.3 – 2.0	0.5 – 0.9	0.3 – 0.5	0.5 – 0.9	microreticulate to reticulate
ridleyi	1.9	0.9	0.4	0.6	reticulate
Pometia	1.3 – 2.0	0.5 – 0.9	0.3 – 0.5	0.5 – 0.9	

* measured in the centre of a mesocolpium.

Remarks

1. The small sizes noted by van den Berg (1978) for grains of *P. pinnata* forma *acuminata* (P = 14 (17.5) 20 µm, E = 19 (22.4) 25 µm) probably refer to immature grains in *S 19131* (plate 43: 1, 2). The flower buds of this collection proved to be in a very young stage.
2. On the basis of the alleged lack of any contrast within the exine using TEM, van den Berg (1978) eventually suggested an endexine to be absent in *Pometia*. He subdivided the nexine into a nexine-1, representing the main layer of the nexine, and a nexine-2, comprising the lamellate thickenings round the endoapertures. – Van den Berg erroneously applied the terms nexine-1 and nexine-2, which actually are synonyms of foot layer and endexine respectively, pertaining likewise to the presence of contrast. – The nexine-2 was considered absent outside the apertural areas. However, the sparse thin layer covering the nexine in most TEM photographs (including those of acetolysed grains; plate 54: 5, 6, 7) clearly links up the lamellate systems of the three apertural areas. Occasionally TEM showed this layer and the apertural lamellae to be relatively electron-lucent (plate 54: 6). Therefore it is suggested here that the thin layer plus the apertural lamellae constitute the endexine in *Pometia* pollen.

   Van den Berg compared the nexine of *Pometia* with that of several Elaeagnaceae (i.e. *Elaeagnus turcomania* and *Shepherdia argentea*), referring to Leins (1967). Except for the absence of a continuous nexine-2 in *Pometia* both nexines (including the apertural lamellae) were found very similar. Having here suggested an endexine yet to be present, the resemblance gets even stronger. However, fairly great differences still exist with regard to grain size, A/E value, exine thickness, and ornamentation. A remarkable amount of conformity, which for example also includes ornamentation, can be shown for *Pometia* pollen and the fossil *Atlantopollis* (see below). The similarity between *Pometia* pollen and *Tricolporites protrudens* (Erdtman, 1951: Upper Cretaceous and Palaeocene of N and Central Europe) noticed by Erdtman (1960a) is only superficial (see also Batten, 1989).
3. Microreticulate ornamentation occurs in *NIFS Cel.IV-239* (*P. pinnata* forma *repanda*; see van den Berg, 1978, plate V: 1, 2).
4. Huang (1972), in a LM study, mentioned a "tectum with scabrate processes" in the description of pollen of *P. pinnata*. However, scabrae in Nephelieae pollen are practically unrecognisable using LM, and definitely do not occur in combination with reticulate ornamentation.

A comparison between *Pometia* pollen and *Atlantopollis*

Having examined a poster dealing with harmomegathic types in Nephelieae pollen (see van der Ham, 1988), M. Kedves (personal comm. 1987; see also Kedves, 1989) noticed the striking similarity between *Pometia* pollen and *Atlantopollis* Krutzsch, traditionally a form genus in the Normapolles group. The Normapolles group is an assemblage of Late Cretaceous to Eocene form genera that share an oblate grain shape and the presence of brevicolp(or)ate or porate, complex, often protruding apertures (Batten, 1986; Kedves, 1983; Traverse, 1988). According to Muller (1984) Normapolles pollen was produced by plants that should be placed as an extinct family in the Juglandales. Actually, Friis (1983) found Normapolles grains in floral structures of plants that must be considered closely related to extant members of the Juglandaceae. However, Batten (1986, 1989) considered *Atlantopollis* as an atypical member of the Normapolles group that may well have nothing to do with the Hamamelidae (to which subclass the Juglandales belong).

Pometia pollen agrees especially with *Atlantopollis microreticulata* and *A. reticulata*, which have:

- an obtusely triangular oblate shape;
- an equatorial diameter of about 30 µm;
- short colpi (A/E = approx. 0.63);
- a system of lamellae surrounding porate endoapertures;
- fastigium-like cavities under the borders of the mesocolpia;
- an exine thickness of about 2 µm in the centres of the mesocolpia;
- an exine stratification that is very similar to that in *Pometia* pollen (save for the endexine, which could not be demonstrated in *Atlantopollis*);
- a coarse reticulate ornamentation, usually with duplicolumellate muri (lumina in *A. microreticulata* less than 1 µm, in *A. reticulata* more than 1 µm in diameter);
- psilate margines round the colpi.

The differences are actually rather small:

- *Pometia* pollen is less oblate;
- the colpi in *Atlantopollis* are approximately 1 µm wide, have obtuse ends, and show a considerable amount of apertural nexine ('colpus membrane');
- the lamellate systems surrounding the endoapertures are less elaborate in *Atlantopollis*, which results in shorter endoapertural tubes;
- ornamentation in *Pometia* pollen is more regularly reticulate, the muri having a more constant width;
- margines in *Pometia* pollen are usually wider and less distinctly delimited.

In spite of the great resemblance between *Atlantopollis* and *Pometia* pollen, the parent plants of *Atlantopollis* are probably not related to *Pometia* (see also Batten, 1989). *Atlantopollis* is found in N America and W Europe, while *Pometia* is a tropical rainforest genus that occurs from Ceylon to Samoa. Moreover, *Atlantopollis* is known up into the Middle Turonian (Kedves & Párdutz, 1983), or possibly the Lower Coniacian (Zaklinskaja, 1976), whereas *Pometia* pollen does not appear until the Late Miocene (Muller, 1981a). Thus, huge gaps in geography and time, and possibly also in ecology, separate the *Atlantopollis* plants from *Pometia*.

6.11. SMELOPHYLLUM

(plates 32; 55: 1, 2; 59: 21–24)

General morphology

Pollen of *Smelophyllum capense* is small (P = 13 (15.3) 17 μm; E = 18 (21.7) 23 μm). Grain shape is oblate to suboblate (P/E = 0.66 (0.71) 0.84). The equatorial outline is obtusely triangular, with slightly concave to slightly convex sides. The meridional outline is obtusely rhombic to elliptic.

Apertures

Smelophyllum pollen is always colporate. The ectoapertures are fairly long colpi (A/E = 0.26 (0.37) 0.49). The ends of the colpi are acute. The colpus membranes are nearly smooth to densely covered with scabrae.

The endoapertures are lalongate to lolongate pori. Meridional and equatorial size are 3 to 5 μm. The polar sides of an endoaperture are obtuse; the lateral sides are usually acute to acuminate, sometimes obtuse. A distinct fastigium is present (plates 32: 5; 59: 22).

Exine architecture

stratification

Total exine thickness is 1.4 μm in the centres of the mesocolpia. It decreases towards the colpi, and it increases again near the colpi.

The nexine is about 0.6 μm thick in the central part of a mesocolpium. It thins gradually towards the colpi. Near the colpi it thickens again, forming a relatively thick layer under each colpus (colpus membrane) and the borders of the adjacent mesocolpia. With TEM it could be demonstrated to consist of an endexine and a foot layer (plate 55: 1). The endexine is very thin in the central part of a mesocolpium (1/40 to 1/20 of the total nexine thickness); it thickens towards the colpi to form the bulk or the whole of each colpus membrane. The foot layer thins towards the colpi.

The columellate layer is approximately 0.4 μm thick in the centre of a mesocolpium. It thins strongly towards the colpi (plate 59: 22), thinning out near the colpi.

The tectum is about uniformly 0.4 μm thick; it is always thinner than the nexine.

ornamentation

Ornamentation is usually striate; sometimes it is irregularly striate (see remark 1). The muri are two-dimensionally arranged, and 0.2 to 0.4 μm wide; sometimes very narrow muri (approx. 0.1 μm wide) were observed (see remark 2). The grooves between the muri are usually less than 0.1 μm wide (see remark 1). Perforations are nearly always present, although mostly hidden between the muri. They measure up to 0.1 μm in diameter. The edges of the mesocolpia are irregularly indented; mostly, they merge into the scabrae on the colpus membranes.

Remarks

1. Approximately 10% of the grains of *Wells 3246* bear an irregularly striate (plate 32: 2, 3), or an incomplete deviating tectum (plate 32: 4). An incomplete tectum shows lumina of variable size and shape, smooth to finely striate (muri 0.1 to 0.2 µm wide) patches and lumps of sexine material. Sometimes, free columellae and bits of the nexine surface are visible. The sample contains a complete series from regularly striate to strongly deviating grains. The irregularly striate grains resemble the coarsely 'reticulate' grains of *Dimocarpus leichhardtii*, though 'twining' of the muri is lacking (compare plate 32: 2 with plate 16: 2, left-hand grain). The aberrant grains resemble those of *Popta 863/210* (*Dimocarpus longan* subsp. *longan*: compare plate 32: 4 with plate 17: 2 and Muller, 1971, plate IV: 2, 3); likewise they are considered to be the result of disturbed or 'uncontrolled' tectum formation.

   The other sample of *Smelophyllum* pollen (*Drège s.n.*) contains besides normally striate grains only irregularly striate grains (approx. 5%; plate 32: 7).
2. Very narrow muri, approximately 0.1 µm wide, occur together with muri of normal width in most grains of *Drège s.n.*, in regularly striate as well as irregularly striate grains (plate 32: 7).

6.12. STADMANIA

(plates 33–35; 55: 3–7; 61: 1–6)

General morphology

Stadmania pollen grains are small (P = 14 (18.1) 24 µm, E = 16 (20.3) 29 µm). Grain shape is oblate to prolate spheroidal (P/E = 0.73 (0.89) 1.13). The equatorial outline is obtusely triangular, with slightly convex to convex sides; sometimes slightly concave or straight sides occur. The meridional outline is elliptic to subcircular.

Apertures

Stadmania pollen is always colporate. The ectoapertures are long to fairly long colpi (A/E = 0.10 (0.40) 0.50). The ends of the colpi are more or less acute. Sometimes, broad indistinctly forked colpus ends partly demarcate the apocolpium (see remark 1). The colpus membranes are densely covered with scabrae; rarely they are nearly smooth.

The endoapertures are lalongate to lolongate pori. Meridional size is 1 to 6 µm; equatorial size is 2 to 5 µm. The polar sides of an endoaperture are obtuse (see remark 2); the lateral sides are obtuse to acuminate. A fastigium can usually be discerned (plates 33: 2; 34: 5).

Table 11. Infrageneric variation of a number of pollen characters in *Stadmania*.

	P (µm)			E (µm)			P / E			A / E		
acuminata	18	(19.6)	24	21	(23.7)	29	0.73	(0.83)	0.91	0.10	(0.39)	0.46
excelsa	15	(17.2)	18	17	(19.1)	21	0.80	(0.90)	1.06		0.40	
glauca	17	(18.1)	19	18	(19.9)	22	0.82	(0.91)	1.00	0.41	(0.42)	0.43
leandrii	14	(19.3)	24	17	(20.7)	23	0.75	(0.93)	1.04	0.30	(0.37)	0.44
oppositifolia	14	(16.9)	20	16	(19.2)	22	0.75	(0.88)	1.13	0.20	(0.37)	0.50
subsp. *oppositifolia*	14	(17.5)	20	18	(19.7)	22	0.76	(0.89)	0.95	0.33	(0.39)	0.44
subsp. *rhodesica*	14	(16.2)	19	16	(18.6)	21	0.75	(0.88)	1.13	0.20	(0.35)	0.50
serratula	17	(17.7)	18	17	(19.4)	21	0.82	(0.91)	1.00	0.37	(0.42)	0.47
Stadmania	14	(18.1)	24	16	(20.3)	29	0.73	(0.89)	1.13	0.10	(0.40)	0.50

	thickness (µm) *				
	exine	nexine	columellate layer	tectum	ornamentation
acuminata	1.5	0.6	0.3**	0.6	psilate
excelsa	1.5	0.6**	0.3**	0.6	striate
glauca	1.3	0.3 – 0.4	0.35**	0.6	striate to rugulate
leandrii	0.9	0.3 – 0.4	0.15 – 0.2	0.3 – 0.4	psilate
oppositifolia	1.3 – 1.9	0.6 – 1.0	0.25 – 0.4	0.4 – 0.5	
subsp. *oppositifolia*	1.3 – 1.8	0.6**	0.25 – 0.4**	0.4 – 0.6	striate to shallowly rugulate
subsp. *rhodesica*	1.7 – 1.9	0.8 – 1.0**	0.4**	0.5	striate
serratula	1.6	0.8**	0.2**	0.6	striate
Stadmania	0.9 – 1.9	0.3 – 1.0	0.15 – 0.4	0.3 – 0.6	

* measured in the centre of a mesocolpium; ** strongly decreasing towards the colpi.

Exine architecture

stratification

Total exine thickness varies from 1.3 to 1.9 µm in the centres of the mesocolpia. Depending on the degree of thinning of the constituent sublayers it decreases more or less strongly towards the colpi. Near colpi it slightly increases again.

The nexine is 0.3 to 1.0 µm thick in the central part of a mesocolpium. It thins more or less strongly towards the colpi (see Infrageneric variation). Near the colpi it thickens again, forming a relatively thick layer under each colpus (colpus membrane) and the borders of the adjacent mesocolpia. With TEM the nexine was demonstrated to consist of an endexine and a foot layer (plate 55: 3, 5, 7). The endexine is thin in the central part of a mesocolpium (1/10 to 1/6 of the total nexine thickness). It thickens toward the colpi to form the bulk of each colpus membrane; sometimes it is thin throughout (see remark 3). The foot layer thins towards the colpi.

The columellate layer is 0.15 to 0.4 µm thick in the centre of a mesocolpium. It thins more or less strongly towards the colpi (see Infrageneric variation), thinning out near the colpi.

The tectum is 0.3 to 0.6 µm thick in the centre of a mesocolpium, being thicker than, as thick as, or thinner than the nexine. Its thickness decreases more or less strongly towards the colpi.

ornamentation

Ornamentation is usually striate to psilate; several species show irregularly striate and/or rugulate pollen (see Infrageneric variation). The muri in striate and rugulate ornamentation are two-dimensionally arranged, and 0.2 to 0.4 µm wide. The grooves between the muri measure up to 0.2 µm, rarely up to 0.4 µm wide (see remark 4). Perforations are always present, although they may be scarce, or hidden between the muri. They measure up to 0.2 µm, rarely up to 0.4 µm in diameter (see remark 4). The edges of the mesocolpia are entire to finely indented; they often merge into the scabrae on the colpus membranes.

Table 11 lists the values/states of a number of the above mentioned characters for the individual species and subspecies in *Stadmania*. Pollen of var. *grevei* of *S. oppositifolia* subsp. *oppositifolia* is not distinct from that of var. *oppositifolia*.

Remarks

1. Partly demarcated apocolpia are present in up to 10% of the grains of *Brynard & Pienaar 4253*, *Chase 4733* (plate 35: 5) and *Chase 8054* (all *S. oppositifolia* subsp. *rhodesica*).
2. Muller & Schuller (1989) mentioned up to 2 µm thick polar costae. However, the polar sides of the endoapertures are not thickened; Muller & Schuller probably observed invaginated colpus membranes in equatorial view.
3. In a part of the grains of *16030-SF* (*S. serratula*) it was observed that the endexine is also thin in the apertural areas (plate 55: 3). In addition, the middle sub-

layer of the onci in these grains possesses irregular inclusions that are as electron-opaque as the endexine. Possibly, this aberrant morphology reflects 'uncontrolled' deposition of endexinous material, resulting in an irregular displaced inner sublayer of the apertural endexine.

4. Irregularly shaped grooves up to 0.4 µm wide, containing equally large perforations (thus yielding true lumina), appeared to be present in *Bernardi 11305* (*S. oppositifolia* subsp. *oppositifolia*).

Infrageneric variation

The most conspicuous variation in *Stadmania* pollen concerns the ornamentation, and the relative size of the central columellae of a mesocolpium.

Ornamentation

The variation in the ornamentation of *Stadmania* pollen concerns both the direction and the prominence of the muri. A series from striate, via irregularly striate, irregularly rugulate and rugulate, to psilate could be established.

Striate ornamentation occurs in *S. excelsa, S. glauca, S. oppositifolia* and *S. serratula*. Irregularly striate grains were found, together with regularly striate ones, in *S. glauca* and *S. oppositifolia*. The only sample of *S. glauca* contains regular and irregular forms of both striate and rugulate ornamentation; these constitute a series from regularly striate to regularly rugulate (plate 33: 3–5). One sample of *S. oppositifolia* (*Bradburne 102*) yielded only rugulate to shallowly rugulate grains (plate 35: 3, 4), the rugulate pattern being finer and shallower than in the rugulate grains of *S. glauca*. The finely shallowly rugulate grains of *Bradburne 102* can be connected with the almost psilate grains of *S. leandrii* (compare plate 35: 4 with plate 34: 3). Locally, the latter grains 'still' show traces of a finely rugulate ornamentation. The psilate pollen of *S. acuminata* resembles that of *S. leandrii* very much; however, instead of being indistinctly rugulate the tectum is finely irregularly undulate (plate 33: 1).

Shallowly or indistinctly striate intermediates between striate and psilate ornamentation were not found in *Stadmania* pollen. This is in contrast with the situation in *Dimocarpus, Nephelium* and *Xerospermum*.

Columellae

The length of the central columellae of a mesocolpium is rather variable in *Stadmania* pollen. It varies from 0.15 to 0.4 µm. Especially in pollen with long central columellae (0.3 to 0.4 µm; plates 33: 6; 35: 6; 55: 4–7) there appeared to be a strong decline towards the short peripheral ones (see table 11); medium and short-sized columellae (0.15 to 0.25 µm; plate 34: 6) usually show a gradual decline. Both strong and gradual decline occur within pollen of *S. oppositifolia*. That of subsp. *rhodesica* usually has considerably longer central columellae than that of subsp. *oppositifolia*; pollen of one sample of the latter subspecies (*Bernardi 11305*) also has long central columellae.

Just as in *Nephelium*, pollen with long strongly declining columellae possesses relatively often a thick similarly declining nexine (see table 11).

Geographical aspects

Stadmania oppositifolia is the only widespread species in the genus *Stadmania*, all others being confined to Madagascar. It is distributed throughout continental E Africa, Madagascar and the Mascarene Islands. Subsp. *rhodesica*, the southwestern subspecies of *S. oppositifolia* (found in Zimbabwe and northern South Africa), differs from subsp. *oppositifolia* (found in Kenya, Tanzania, Madagascar and the Mascarene Islands) in having usually longer central columellae. In addition, the three samples belonging to subsp. *rhodesica* share the occasional presence of partly demarcated apocolpia (see remark 1).

6.13. XEROSPERMUM

(plates 36–38; 56; 61: 7–20)

General morphology

Xerospermum pollen grains are small (P = 10 (14.8) 19 µm, E = 14 (18.5) 24 µm). Grain shape is oblate to oblate spheroidal (P/E = 0.62 (0.80) 0.98). The equatorial outline is obtusely triangular, with straight to slightly convex sides; sometimes slightly concave sides occur. The meridional outline is obtusely rhombic to elliptic.

Apertures

Xerospermum pollen is usually colporate. Occasionally two or all three ectoapertures meet, yielding an incomplete or complete syncolporate condition at one pole (see remark 1); wholly syncolporate grains have not been observed.

The ectoapertures are long to fairly short colpi (A/E = 0 (0.29) 0.55). The ends of the colpi are acute to obtuse. Sometimes local depressions between the colpus ends, and broad indistinctly forked colpus ends demarcate the apocolpium (see remark 2). The colpus membranes are nearly smooth to densely covered with scabrae.

The endoapertures are lalongate to lolongate pori or lalongate colpi. Meridional size is 1 to 5 µm; equatorial size is 2 to 5 µm. The polar sides of an endoaperture are obtuse; the lateral sides are obtuse to acuminate. A fastigium can usually be discerned (plates 36: 5; 38: 6).

Exine architecture

stratification

Total exine thickness is about 1.1 µm in the centres of the mesocolpia. It decreases towards the colpi and it increases again near the colpi.

Table 12. Infrageneric variation of a number of pollen characters in *Xerospermum*.

	P (µm)			E (µm)			P / E			A / E		
laevigatum	10	(14.7)	18	14	(18.5)	23	0.62	(0.79)	0.98		0.28	
subsp. *acuminatum*	13	(14.5)	17	16	(18.2)	22	0.70	(0.79)	0.88	0.17	(0.31)	0.55
subsp. *laevigatum*	10	(14.8)	18	14	(18.8)	23	0.62	(0.79)	0.98	0	(0.25)	0.36
noronhianum	12	(14.8)	19	15	(18.4)	24	0.68	(0.81)	0.98	0.16	(0.29)	0.44
Xerospermum	10	(14.8)	19	14	(18.5)	24	0.62	(0.80)	0.98	0	(0.29)	0.55

	thickness (µm) *				
	exine	nexine	columellate layer	tectum	ornamentation
laevigatum	1.1	0.6	0.1 – 0.15	0.3 – 0.4	
subsp. *acuminatum*	1.1	0.6	0.15	0.3	indistinctly striate to psilate**
subsp. *laevigatum*	1.1	0.6	0.1 – 0.15	0.3 – 0.4	striate to shallowly striate
noronhianum	1.1	0.6	0.1 – 0.15	0.3 – 0.4	striate to indistinctly striate**
Xerospermum	1.1	0.6	0.1 – 0.15	0.3 – 0.4	

* measured in the centre of a mesocolpium; ** sometimes shallowly or indistinctly rugulate.

The nexine is approximately 0.6 µm thick in the central part of a mesocolpium. It thins gradually towards the colpi. Near the colpi it thickens again, forming a relatively thick layer underlying each colpus (colpus membrane) and the borders of the adjacent mesocolpia. With TEM the nexine could mostly be shown to consist of an endexine and a foot layer (plate 56: 2, 3, 4; see remark 3). The endexine is thin in the central part of a mesocolpium (1/10 to 1/6 of the total nexine thickness); it thickens towards the colpi to form the bulk of each colpus membrane. The foot layer thins towards the colpi. Thin interbedded electron-lucent lamellae occur frequently in the endexine in the apertural areas (see remark 4). Sometimes these lamellae bring about an imbricate structure of the outer endexine.

The columellate layer is 0.1 to 0.15 µm thick in the centre of a mesocolpium. It thins gradually towards the colpi, usually thinning out near the colpi; sometimes short columellae are still visible along the colpi.

The tectum is 0.3 to 0.4 µm thick in the centre of a mesocolpium, being always thinner than the nexine. Its thickness decreases slightly towards the colpi.

ornamentation

Ornamentation is usually striate to psilate; sometimes it is irregularly striate or irregularly rugulate (see also Infrageneric variation). The muri in striate and rugulate ornamentation are two-dimensionally arranged, and 0.2 to 0.5 µm wide. The grooves between the muri are up to 0.2 µm, or rarely up to as wide as the muri themselves. Along the colpi they are relatively narrow and shallow. Perforations are nearly always present, although mostly hidden between the muri. They measure up to 0.2 µm in diameter. The edges of the mesocolpia are mostly finely irregularly indented; usually they merge into the scabrae on the colpus membranes.

Table 12 lists the values/states of a number of the above mentioned characters for the individual taxa in *Xerospermum.*

Remarks

1. An incomplete or complete syncolporate condition at one pole was observed in approximately 1% of the grains of *KEP FRI 986 (X. laevigatum* subsp. *laevigatum*).
2. Partly demarcated apocolpia are present in up to 5% of the grains of *Haviland & Hose 2080* (plate 37: 2, left-hand grain) and *S 8686* (plate 37: 4), both *X. laevigatum* subsp. *acuminatum,* and *NIFS bb 2138,* belonging to *X. laevigatum* subsp. *laevigatum* (plate 36: 2).
3. No subdivision of the nexine could be demonstrated for *X. noronhianum* (however, see chapter 6.1: nexine).
4. Thin electron-lucent lamellae in the outer part of the apertural endexine were observed in both subspecies of *X. laevigatum* (plate 56: 3, 4).

Infrageneric variation

Considerable variation exists within *Xerospermum* with respect to the ornamentation of the exine. A complete series of intergrading forms appeared to be present between striate and psilate. Striate ornamentation shows prominent muri (see for example plate 36: 1), whereas psilate ornamentation shows a smooth, more or less perforate tectum (perforations often in rows; see for example plate 37: 2, 3). The intermediate stages may be roughly referred to as shallowly striate (plates 36: 3, 4; 38: 2) and indistinctly striate (plates 37: 1; 38: 3); distinguishing clearly separate types would be rather arbitrary. Shallowly striate ornamentation has shallower grooves between the muri than striate ornamentation. Indistinctly striate ornamentation hardly shows any grooves; at most, faint oblong depressions can be discerned.

The less prominent the muri, the more conspicuous the perforations. Due to the thinner tectum (which implies shallower grooves) and the lower number and smaller size of the perforations the margines of the colpi usually have a less differentiated architecture than the apocolpia and the centres of the mesocolpia (see for example plate 37: 5).

Besides the variable prominence of the muri two other aspects contribute to the variation of tectum architecture in *Xerospermum* pollen: the direction of the muri and the width of the grooves. Less prominent muri often show a nonparallel arrangement and wide grooves, yielding a number of dissimilar irregularly rugulate forms of ornamentation (plates 37: 6; 38: 5). These merge into members of the striate series, but mutually they do not show any intermediates. Prominently rugulate pollen was not observed in *Xerospermum*.

The ornamentation varies within each of the two *Xerospermum* species. The whole series from striate to psilate occurs within *X. laevigatum*. Pollen of subsp. *laevigatum* is striate to shallowly striate (plate 36: 1, 3, 4), that of subsp. *acuminatum* is indistinctly striate to psilate (plate 37: 1, 3). Pollen of *X. noronhianum* is striate to indistinctly striate (plate 38: 1–3). Irregularly rugulate grains occur, together with indistinctly or shallowly striate grains, in several samples of both *X. laevigatum* subsp. *acuminatum* and *X. noronhianum*, viz. *S 12311* (plate 37: 6), *Jacobs 5252* (plate 38: 5) and *de Wilde & de Wilde-Duyfjes 14822*.

The last mentioned sample represents a notable case of intra-individual variation. Besides shallowly striate, indistinctly striate, irregularly striate and irregularly rugulate grains this sample contains many 'hybrid' grains. The latter combine various forms of ornamentation (including psilate) into a mosaic pattern (plate 38: 4). Rarely grains with a local fine substriation ('submuri' approx. 0.1 μm wide) were observed. The sample reminds of the conspecific *Jacobs 5252*, which also proved rather variable.

Geographical aspects

The variation of the ornamentation exhibits a remarkable geographical pattern: the shallowly striate, indistinctly striate and psilate forms of all three *Xerospermum* taxa are almost only found in Borneo, whereas the striate forms are present throughout the distribution of *Xerospermum* (continental SE Asia, Sumatra, Java, Borneo). In Borneo the striate forms are represented only by *X. laevigatum* subsp. *laevigatum*; they merge into the indistinctly striate and psilate forms of the exclusively Bornean subsp. *acuminata*. In addition, nearly all irregularly rugulate samples originate from Borneo. The Bornean sample *Jacobs 5252* (*X. noronhianum*) is rather variable. Outside Borneo nonstriate shallow to psilate ornamentation was observed only in the very variable Sumatran sample *de Wilde & de Wilde-Duyfjes 14822* (*X. noronhianum*). Obviously, ornamentation in *Xerospermum* has its widest range of variation within Borneo.

6.14. STAMINODIAL POLLEN

Sapindaceae usually have unisexual flowers; truly bisexual flowers are rare. The unisexual flowers contain more or less conspicuous vestiges of the other sex. Therefore female Nephelieae flowers, which have stamens with nondehiscent anthers (staminodes), have been designated as 'hermaphroditic', structurally hermaphroditic (Ha et al., 1988), hermaphroditic functioning as female (Mustard et al., 1954), and even hermaphroditic or bisexual (Appanah, 1982; Lim, 1984; Singh, 1963). Male Nephelieae flowers, which have a nonfunctional pistil, have been called imperfectly hermaphroditic, pseudohermaphroditic and hermaphroditic functioning as male (Liu, 1954; Mustard et al., 1954; Singh, 1963).

Capuron (1969), analysing sex expression in Madagascan Sapindaceae, found anthers in female flowers to be without pollen grains or with deformed pollen grains. Studying pollen of *Lepisanthes* (tribe Lepisantheae) Muller (1970) concluded that female flowers yielded fewer "excellent" pollen samples than male flowers. According to Muller (1985) female Sapindaceae flowers usually produce poorly developed pollen. In *Litchi chinensis* Liu (1954) found the grains from female flowers to be similarly shaped, but on the average smaller and much less viable than those from male flowers. Lim (1984) reported mature grains of male and female *Nephelium lappaceum* flowers to look similar, although most grains from female flowers are devoid of nuclei and hence nonviable. In *Xerospermum noronhianum* a considerable number of staminodial grains abort already in the tetrad stage of the microsporogenesis (Ha et al., 1988). These observations indicate inferior quality of staminodial pollen. Therefore female material has been excluded from the present study as much as possible. Clearly female flowers can be easily avoided, but it is sometimes difficult to determine sex if only buds are available. In view of the shape of unquestionably staminodial pollen (see the last paragraph of this section) it was decided that underdeveloped and collapsed pollen is probably staminodial. Such pollen has not been entered in the descriptions. This procedure does not exclude staminodial pollen completely, because well shaped grains from female flowers become incorporated in this way. This includes the possibility that occasionally differences with respect to, for example, grain size and prominence of ornamentation actually relate to difference in sex.

Although the anthers of female Nephelieae flowers do not dehisce and often yield fewer and/or less developed pollen grains, they may contain a small percentage of viable grains (Appanah, 1982; Ha et al., 1988; Lim, 1984; Mustard et al., 1954; Singh, 1963). According to Appanah (1982) such staminodial pollen can even cause fruit set in *Xerospermum noronhianum*. He observed the slimy breakdown of the indehiscent anthers of the two longest stamens against the stigma, as a result of which pollen was left on the stigma. A similar case was reported by van Welzen et al. (1988): work in Peninsular Malaysia on cultivated female plants of *Nephelium lappaceum* showed fruit and seed set in bagged female flowers. Van Welzen et al. suggested the occurrence of apomixis, but a similar intraflower autogamous mechanism as observed in *Xerospermum noronhianum* may be advocated as well, as Lim (1984) demonstrated viable pollen in indehiscent anthers of female flowers of *Nephelium lappaceum*. In *Xerospermum noronhianum* apomixis was ruled out by Appanah.

The autogamous system observed by Appanah possibly represents an emergency mechanism that must ensure fertilisation in the case that this cannot be achieved by pollen from male flowers through cross-pollination. If the fruits contain viable seeds (Appanah did not provide information concerning seed set), then this is most important for dioecious species of which the individuals grow far apart or grow in areas where the number or movement of pollinators is restricted (Appanah, 1982; Ha et al., 1988; van Welzen et al., 1988; Yap, 1982). It also concerns functionally dioecious species such as (duo)dichogamous species with fully separated male and female phases (see chapter 7.2).

Occasionally, in order to obtain at least some (or some more) pollen data of rare species, material has been collected from fruiting specimens (sometimes shrivelled anthers remain attached at fruit bases). This is true for the following samples: *Anon. s.n.* (*Alectryon reticulatus*; plate 8: 1–5), *S 25393* (*Nephelium macrophyllum*; plate 25: 3, 4) and *S 37985* (*Nephelium meduseum*; plate 25: 6). The grains in these samples are undisputably staminodial. They often turned out to be dented or collapsed. The exine architecture of many grains in the *Alectryon* sample displays clearly juvenile features, which suggests that the pollen of this staminodial sample is partly immature (see further chapter 6.15).

6.15. IMMATURE POLLEN

Microsporogenesis in literature

Ha et al. (1988), Lim (1984) and Singh & Shiam (1977) performed LM studies of the microsporogenesis in *Litchi chinensis*, *Nephelium lappaceum*, *Pometia pinnata* and *Xerospermum noronhianum*. According to Lim and Ha et al. anther formation in these genera agrees with the basic type found in the angiosperms. The submature anther wall consists of an epidermis, an endothecium with radially arranged fibrous bars on the inner tangential cell walls, two or three middle layers, and a glandular (= secretory) tapetum. Before dehiscence the middle layers, the tapetum and the interlocular connective tissue disintegrate.

Pollen mother cell development in *N. lappaceum* conforms to the basic angiosperm type too (Ha et al., 1988). During meiosis generally a tetrahedral tetrad stage proceeds from each pollen mother cell. My own data (see Persistent tetrads) show that the immature pollen grains are arranged according to Fischer's Law (apertures in pairs). "Isobilateral" tetrads have sometimes been observed in *L. chinensis* (Singh & Shiam, 1977) and *N. lappaceum* (Lim, 1984).

Soon after tetrad formation the immature grains separate from each other, due to the degeneration of the callose wall. In this phase the disintegration of the anther wall sets in.

In female flowers of *N. lappaceum*, anther formation and microsporogenesis up to the meiosis appeared essentially the same as in male flowers (Ha et al., 1988). In the tetrad stage, however, many grains abort as a result of protoplasmic degeneration. The interlocular connective tissue does not collapse and the anthers fail to dehisce.

Persistent tetrads

Usually the immature grains that originate from a single pollen mother cell separate from each other soon after tetrad formation. Occasionally, however, the tetrad configuration persists in mature Nephelieae pollen, four grains still being loosely connected to show a tetrahedral arrangement. This phenomenon was observed in *Alectryon excelsus* (*van Zanten 1301*), *Dimocarpus longan* (*SAN 66273*; plate 19: 4, 3/4 tetrad), *Podonephelium subaequilaterum* (*Franc 719*; plate 30: 6), *Stadmania oppositifolia* (*Bradburne 102*; plates 35: 3; 61: 1, 2), *Xerospermum laevigatum* (*S 8686*; plate 37: 5, 3/4 tetrad) and *X. noronhianum* (*de Wilde & de Wilde-Duyfjes 14822*). In *Bradburne 102* approximately 10% of the grains still show the tetrahedral arrangement. Remarkably, pollen of four of the six samples (excluding *Franc 719* and *van Zanten 1301*) have nonstriate ornamentation. Huang (1972) reported the rare occurrence of tetrads in *Dimocarpus longan* and *Litchi chinensis*.

A four-grained unit the members of which represent the offspring of a single pollen mother cell must be considered as a tetrad. Consequently, the tetrahedral units occurring in mature Nephelieae pollen are designated as such. They belong to the acalymmate type of van Campo & Guinet (1961) and Blackmore & Crane (1988), which is characterised by the partial or sometimes extremely tenuous fusion of the four members. The nature of the cohesion in Nephelieae tetrads could not be discovered, so that classification according to Knox and McConchie (1986) is not possible as yet. Knox and McConchie distinguished two types of tetrads: those with simple cohesion (through cohesion of the sexine) and those with cross-wall cohesion (through wall bridges of sexine, nexine and/or intine).

Once (in *S 8686*; plate 37: 4), a single rigid tetrad was encountered. It showed partially obscured sutures as a result of fusion of the tecta of its members. Probably, this aberrant state was caused by an excess of sporopollenin deposition on a more loosely arranged tetrad, as the ectoapertures are partially obscured as well.

Magonia (tribe Harpullieae) is the only sapindaceous genus that invariably has rigid tetrads (Muller & Leenhouts, 1976, plate 4: A). They belong to the acalymmate type, as each member has its own continuous (though proximally reduced) tectum (fig. 8). It fits the simple cohesion type of Knox & McConchie (1986).

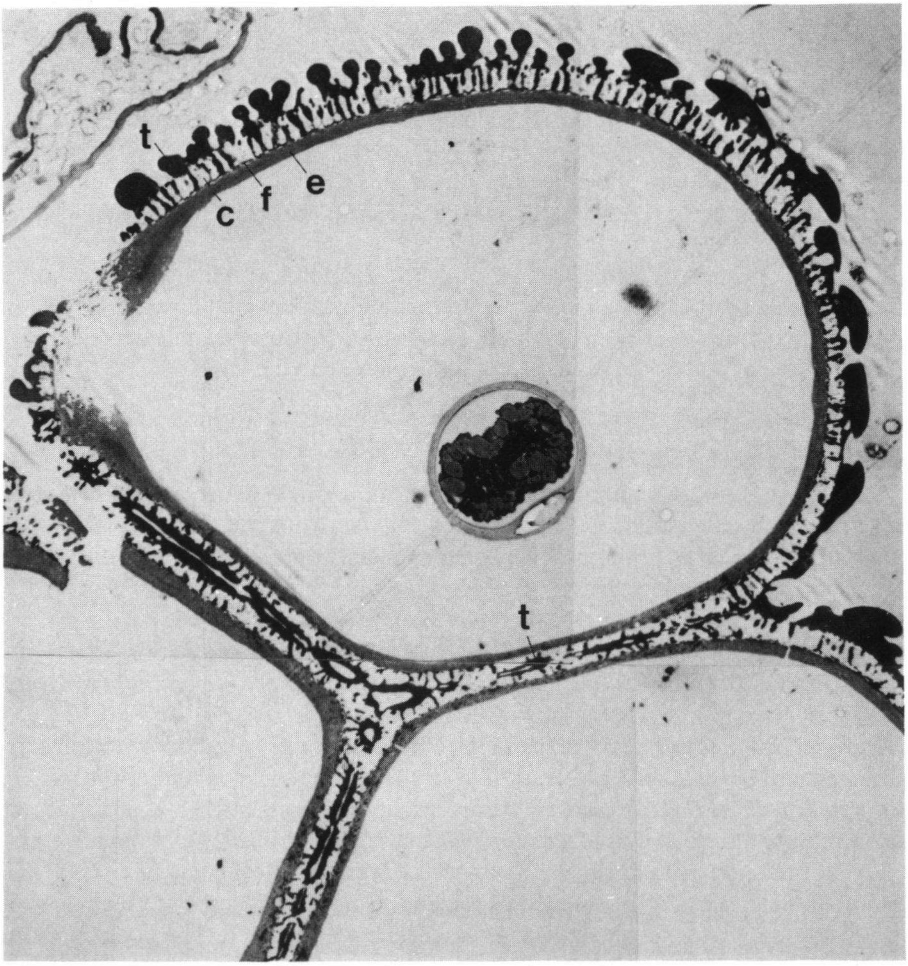


Fig. 8. *Magonia pubescens* St. Hil. (= *M. glabrata* St. Hil.), tribe Harpullieae. Part of TEM section of acetolysed tetrad showing tectum (t; reduced on proximal sides of tetrad members), columellate layer (c), very thin foot layer (f), and thick endexine (e), × 3000. The structure near the centre of the photograph does not belong to the tetrad; possibly it represents a cross section through a fungal hypha. Material: *Ratter & Ramos 267* (U), Brazil. Prepared and photographed for a TEM survey of Sapindaceae pollen carried out by J. Muller; preparation included fixing with 2% OsO_4 (1 hour), prestaining with 5% uranylacetate (2 hours), inbedding in 3/7 Epon, and poststaining with 0.5% uranylacetate (30 minutes) and Reynolds' lead citrate (10 minutes).

In angiosperms the callose wall of a tetrad is generally two-layered, comprising a common part, formed by the pollen mother cell, and individual parts, formed by the daughter cells. The occurrence of tetrads, whether rigid or not, suggests a reduced callose synthesis resulting in deletion of the individual callose walls (Blackmore et al., 1987; Blackmore & Crane, 1988).

SEM and TEM observations on exine growth

Ontogenetic studies may provide valuable clues with regard to the understanding of evolution (Gould, 1977). Stebbins (1974) stated, "The primary effect of genes is on processes of development and metabolism rather than visible characteristics of adult form. We can understand fully the way in which genetic changes can bring about visible differences in form only by discovering more completely the nature of the developmental processes that, in each individual, give rise to its adult form." Rowley (1976) advocated the inclusion of ontogenetic studies as an integral part of pollen exploration, particularly if evolution is concerned.

Heslop-Harrison (1971), Dickinson (1976) and Muller (1979) have acknowledged that pollen grains may acquire resistance to acetolysis in the earliest phase of sporopollenin deposition. Occasionally, small translucent thin-walled, apparently immature grains were noticed with LM in acetolysed Nephelieae samples (plate 57: 7, 8). In order to get some insight in the development of the exine during microsporogenesis, especially with regard to ornamentation, unripe buds of plants belonging to 11 genera (see chapter 3) were collected from herbarium material and subsequently acetolysed and studied with SEM. One *Otonephelium* sample was studied with TEM as well. Usually various bud sizes were treated together as a single sample; a few collections were split up into three bud size classes.

It appeared that small immature grains were readily obtainable in all genera by applying acetolysis on unripe buds. Mostly, they measure one half to two thirds of the average size of the mature grains. Using SEM they are flat or irregularly dented, which is probably due to their thin wall.

With regard to the development of the exine and its ornamentation the results are diverse. In *Alectryon* the smallest immature grains are essentially different from the mature grains. They have a flat shape, a deviating ornamentation and incomplete colpus membranes. It is rather easy to set up a complete series from immature to mature. However, pollen of most other genera hardly shows any essential difference between immature and mature grains. Apart from their irregularly dented shape, only quantitative differences can be observed, the immature grains having narrower muri and grooves, and smaller perforations or lumina. In a few genera (*Dimocarpus, Otonephelium, Pappea* and *Podonephelium*) immature grains displaying a different ornamentation could still be detected, but they are rare, which hampers the formation of series. The following sections offer a more detailed account of the differences between immature and mature Nephelieae pollen.

Alectryon (plates 39, 40)

Unripe buds of three species were collected: *A. connatus, A. excelsus* (two samples) and *A. subdentatus. Van Zanten 1301* (*A. excelsus*) was split up into three bud size classes: small (ø < 1.5 mm, medium (ø < 2 mm) and large (ø > 2 mm). All samples yielded a more or less complete series from immature to mature. Roughly, five stages may be distinguished, which can be characterised as follows:

1. grains small, flat; colpus membranes thin, incomplete or absent; mesocolpial nexine probably discontinuous; exine thin; columellate layer present; ornamentation psilate; perforations absent or inconspicuous; see plates 39: 1; 40: 1;
2. grains small, more or less flat; colpus membranes thin, sometimes perforate or absent; mesocolpial nexine probably continuous; exine thin; ornamentation finely, more or less indistinctly rugulate; muri 0.1 to 0.2 µm wide; perforations conspicuous; see plates 39: 3; 40: 2, 5, 6;
3. grains medium-sized, flat or irregularly dented; colpus membranes complete; exine thin; ornamentation finely shallowly rugulate to striate; muri 0.1 to 0.3 µm wide; perforations conspicuous; see plates 39: 4; 40: 3;
4. grains medium-sized, irregularly dented; colpus membranes complete (probably thicker than in stage 3); exine rather thick; ornamentation striate to striate-rugulate; muri 0.2 to 0.3 µm; perforations present, eventually hidden between muri; see plates 39: 5; 40: 4, right-hand grain;
5. grains large, well shaped; colpus membranes complete; exine thick; ornamentation striate to striate-rugulate; muri 0.3 to 0.4 µm wide; perforations more or less hidden; this stage represents the mature condition; see plates 39: 6; 40: 4, left-hand grain; 40: 6.

These five stages reflect a clear development, in which the exine, including the colpus membranes, is gradually thickened. The psilate-imperforate tectum becomes perforate (possibly by a stretching-process as described by Banerjee et al., 1965; see also Rowley, 1976), and then a rugulate system of narrow muri arises. Next, a system of subparallel narrow muri develops over the rugulate system; sometimes mature, sufficiently loose striate patterns still show a rugulate system of muri underlying the striate one (plate 7: 4); occasionally, old surfaces are detectable with TEM (plate 44: 3). Further development comprises the gradual widening and thickening of at least the muri of the outer system. Meanwhile, the exine has acquired enough strength to resist collapse. In the last stages ornamentation does not change much anymore, but the grain itself then reaches its final size. In *van Zanten 1301* small buds yielded the stages 1 to 5. Medium-sized and large buds contained only stage 5.

The mesocolpia of the smallest immature grains seem to be uniformly thick. By differential growth the tectum becomes somewhat thicker in the central part of a mesocolpium. SEM and TEM photographs of mature grains suggest differential nexine growth under and near the colpi (see chapter 6.1).

Cubilia (plate 41: 1)

Immature and mature *C. cubili* grains show no essential differences. The mature grains are only slightly larger. Immature grains are irregularly dented. The scabrae are crowded and relatively obtuse; similar scabrae cover the colpus membranes. Remarkably, the mesocolpial scabrae seem locally to be arranged on short muri. Perforations are inconspicuous.

Dimocarpus (plate 41: 2–6)

Unripe buds of three species were collected: *D. gardneri* (two samples), *D. longan* (six samples) and *Dimocarpus* spec. Striate, perforate and scabrate ornamentation were included. With a few exceptions immature and mature grains are not essentially different: immature stages of striate pollen are striate, those of perforate pollen perforate, and those of scabrate pollen scabrate. Immature muri are relatively narrow. Considerably different immature grains were found only in the scabrate sample *SAN 31241* of *D. longan* (plate 41: 5, 6). They are small (about 7 µm in diameter), translucent in LM, thin-walled and dented. Their exine is somewhat rough and shows many perforations. Some grains have low crowded scabrae.

Another notable phenomenon was encountered in *S 26148* of *D. longan*. This sample is perforate, mature grains showing many subcircular perforations. In the immature grains these perforations are elongate due to folding of the exine (plate 41: 4). Even short shallow grooves containing several perforations are present, which give some immature grains an indistinct striate appearance.

Litchi (plate 42: 1)

Immature and mature *L. chinensis* grains do not show essential differences. Even very small grains (diameter 8 µm) are distinctly striate, although the muri are narrower than in mature ones.

Nephelium (plate 42: 2)

Unripe buds of two species were collected: *N. cuspidatum* and *N. ramboutan-ake*. Both species have striate mature grains. Immature and mature grains are not essentially different. The striate ornamentation in immature grains is slightly more dense. Immature muri are hardly narrower than mature ones.

Otonephelium (plates 28: 1, 2; 42: 3; 52)

Unripe buds of both available *O. stipulaceum* collections were processed. Apart from being smaller and mostly dented the immature grains in *Pascal 1375* are not essentially different from the mature grains; both are striate, although the immature muri may be somewhat narrower. The other sample, *Anon. s.n. in Herb. Hookerianum,* contains probably only immature pollen (see chapter 6.7). The grains are small, although hardly or not dented. The colpus membranes are thin and do not show distinct endoapertures, but small to large gaps can regularly be seen (plates 28: 2; 42: 3). Most grains are striate; about 3% of the grains show a psilate-imperforate exine (plate 42: 3). The mature exine is probably imperforate as well. No intermediates between the psilate and the striate condition could be detected.

TEM observations

Some very small buds of the *Herb. Hookerianum* specimen were used for a TEM study. Two main stages were encountered: an early stage (plate 55: 1–3), in which the daughter cells are still together in tetrads, and a late stage (plate 55: 4, 5), which shows free grains.

In the early stage the tectum is still incomplete, thin and irregularly thick (0.03 to 0.15 µm). A 0.05 to 0.15 µm thick columellate layer is visible too. The nexine is incomplete, consisting of 0.10 to 0.17 µm thick and variably wide lumps; the nexine is lacking in the apertural areas. Total wall thickness is about 0.35 µm. Total grain size is about 6 µm.

In the free-grain stage the tectum and the nexine are continuous. At first, the tectum, columellate layer and nexine are about equally thick (0.15 to 0.18 µm). The apertural nexine is still absent. In this phase the intine is discernable for the first time, and is already differentiated into thick apertural parts and thin mesocolpial parts. Later, the tectum and nexine are considerably thickened. The tectum is 0.28 to 0.69 µm thick in the centre of a mesocolpium, and it thins towards the colpi. The nexine is 0.44 to 0.65 µm thick in the centre of a mesocolpium. It thins slightly towards the colpi. Apertural nexine is apparent now, but still fragmentary. The columellate layer has not thickened since the early stage. Ornamentation is psilate-imperforate in TEM (plate 52: 5), which confirms the genuineness of the psilate-imperforate pattern observed with SEM (thus ruling out a filmy cover on the pollen wall surface). Total wall thickness is 0.9 to 1.4 µm. Total grain size is 7 to 9 µm.

Pappea (plate 42: 4)

Most immature *P. capensis* grains are not essentially different from the distinctly striate mature ones, although the immature muri are somewhat narrower. A few small flat grains with a psilate to indistinctly striate ornamentation were observed. The muri are about 0.1 µm wide. The centre of a mesocolpium shows a few small perforations.

Podonephelium (plate 42: 5, 6)

Unripe buds of two species were collected: *P. homei* (two samples) and *P. subaequilaterum*. The *P. homei* samples did not yield essentially different immature pollen. Immature grains of *P. subaequilaterum* are irregularly dented and show a fine shallow striate to rugulate ornamentation. The mature grains are prominently striate, and have wider muri.

Pometia (plate 43: 1, 2)

Immature *P. pinnata* grains are irregularly dented, but further they are not essentially different from mature grains.

Stadmania (plate 43: 3, 4)

Only (irregularly) striate *Stadmania* samples have been processed. Immature grains are flat to irregularly dented. Their ornamentation is mostly not essentially different from the mature pattern, although they have narrower muri. Some grains show distinctly shallower grooves, which results in shallow ornamentation.

Xerospermum (plate 43: 5, 6)

Unripe buds of both *Xerospermum* species were collected. Striate and perforate ornamentation were included. Immature grains are not essentially different from mature ones: immature stages of striate pollen are striate, and those of perforate pollen perforate. The muri are relatively narrow, and less prominent in immature striate ornamentation. Perforations are less conspicuous in immature perforate ornamentation.

Discussion

From the data presented above it can be concluded that exine growth in Nephelieae largely conforms to the general pattern of exine development described by Heslop-Harrison (1971): In the tetrad period, wall patterning is initiated. The sporopollenin precursors originate from the grains' protoplasm. During enclosure within the callose wall, grain size hardly increases. On release from the tetrad the grains undergo a rapid expansion by stretching of the whole wall. Further accretion occurs by deposition of sporopollenin derived from the tapetum (see also Dickinson, 1976).

Exine growth in Nephelieae pollen as inferred from the *Alectryon* series proceeds in the following way. At first, a simple psilate exine is present. The nexine is still incomplete, in the apertural areas sometimes even entirely absent. Then ornamentation develops, tectum and nexine thickness increase, and thick colpus membranes are formed. Grain size gradually increases. In the final stages the pattern of ornamentation is fully established, but the muri still pass through a phase of widening and thickening, during which the grain reaches its mature size.

Possibly, the small, more or less psilate-perforate stage found with SEM in pollen of *Alectryon, Dimocarpus* and *Pappea* must be placed in the tetrad period (consequently, the pollen wall in this stage should be referred to as the primexine). Also the absence or incompleteness of the colpus membranes in the earliest stages of *Alectryon* pollen provides an indication for placing these stages in the tetrad period. Colpus membranes in Nephelieae pollen largely consist of endexine, which usually does not develop until after the release of the immature grains from the tetrad configuration (Knox, 1984). It is not easy to determine how far the tetrad period extends in immature Nephelieae pollen as observed with SEM. The available data do not show a special expansion phase as reported by Heslop-Harrison. Neither can the absence/ presence of the basic pattern of mature ornamentation be considered as defining the transition from the tetrad to the free-grain period, as TEM data of *Otonephelium* pollen demonstrate that a simple exine may still occur in the free-grain period. The occasional presence of Ubisch bodies attached on shallowly and indistinctly sculptured exines (plate 40: 1, 2) might also point to the persistence of simple immature ornamentation in the free-grain period. Moreover, mature psilate pollen has a simple tectum throughout its development, and the tetrad configuration occasionally persists in mature pollen. It must be concluded that SEM data do not provide evidence that allows distinguishing the tetrad period from the free-grain period.

As pointed out earlier, all four *Alectryon* samples yielded enough and sufficiently young immature grains to form more or less complete series from a flat thin-walled psilate primexine to a well shaped thick-walled prominently sculptured mature exine. Leaving aside the samples with psilate mature pollen, flat indistinctly sculptured immature grains similar to those in the stages 1 and 2 of the *Alectryon* series were found but exceptionally in a few other genera. The youngest grains observed in the remaining genera are similar to those in stage 3 or 4 of the *Alectryon* series, as they are dented and have complete colpus membranes and an essentially mature ornamentation pattern.

The cause of the absence or rare occurrence of the youngest immature stages in most Nephelieae genera is not understood. At first, it was thought that they might have been destroyed by acetolysis. However, applying the less destructive KOH (potassium hydroxide) method instead of acetolysis, as recommended by Erdtman (1952) for pollen grains with a delicate pollen wall, did not change the results. Possibly, early pollen development is too rapid to be fully sampled. In *Nephelium lappaceum* it was observed that the tetrad period is short indeed (Lim, 1984, "Soon after the tetrads are formed, the microspores separate out ..."). Based upon the generally low frequency of recovery of events between the primexine template period and completely formed tectum and columellae, Rowley (1976) concluded that sporopollenin deposition in the early ontogeny occurs rapidly on the sexine parts of the pollen wall. Therefore, in spite of its absence in most acetolysed samples of unripe buds, it is assumed that a flat thin-walled more or less psilate stage with incomplete colpus membranes exists in an early ontogenetic phase in all Nephelieae. One must ask why early stages can be so easily encountered in *Alectryon* rather than why they are so rare or absent in the other genera. The obvious answer is that early development in *Alectryon* pollen is relatively slow.

Staminodial pollen with juvenile features

In chapter 6.14 it was mentioned that the pollen of *Anon. s.n.* (*Alectryon reticulatus*), which, being collected from fruit bases, is unquestionably staminodial, shows distinctly juvenile characters. Actually the sample contains nearly all developmental stages found in the immature material of *Alectryon connatus*, *A. excelsus* and *A. subdentatus*; only stage 1 seems to be lacking, and the final stage has rugulate instead of striate or striate-rugulate ornamentation (plate 8: 1–4). Exine thickness in stage 3 grains is approximately 0.7 µm (versus 1.4 µm in the mature sample *Hartmann sh. 1537050*). The inner surface of the mesocolpial nexine is densely covered with small pits (plate 8: 5).

A similar case is presented by the pollen of *Whistler 963* (*Alectryon samoënsis*). This sample contains the stages 2 to 4 (plate 10: 5, 6). It consisted of ripe, probably female buds. The other sample of *A. samoënsis* shows well shaped mature pollen (plate 10: 3, 4).

In addition to the *A. reticulatus* sample two others were obtained from fruit bases: *S 25393* (*Nephelium macrophyllum*; plate 25: 3, 4) and *S 37985* (*Nephelium meduseum*; plate 25: 6). The grains in these samples are dented or collapsed. They have a shallow ornamentation too, in *N. macrophyllum* formed by narrow (0.2 to 0.3 µm) muri. However, mature pollen from male flowers is unknown, so that the grains in both samples cannot be designated as resembling immature stages with certainty.

The scarce data provided by the *Alectryon* samples suggest that the morphology of staminodial pollen is immature in comparison with that of pollen from male flowers. Further investigation of developmental differences between pollen from male flowers and staminodial Sapindaceae pollen is recommended. It should include an extensive SEM and TEM study of pollen of undisputedly male and female flowers.

Immature parasyncolporate pollen

With a view to the evaluation of the evolutionary status of parasyncolporate *Alectryon* pollen, special attention has been paid to its immature stages. *Dallachy s.n.* of *A. connatus*, which contains parasyncolporate and intermediately parasyncolporate grains (B and B* respectively; see chapter 6.2) shows several immature stages (plate 40: 5, 6). In addition, occasional immature stages were observed in *Dietrich 1371* (B and B*), *Heinse s.n.* (B and B*) and *Leach s.n.* (B), which belong to *A. connatus* too. The B* grains occur in small or very small numbers in these samples.

It appeared that immature and mature grains are similar with respect to the absence of apo-/mesocolpium connections. Apparently, the parasyncolporate condition is established in a very early stage. In the beginning the isolated apocolpia have the same indistinctly rugulate ornamentation as the mesocolpia. Later, when the more striate pattern of wider muri develops, they mostly become still more clearly isolated, as muri are deposited along and parallel to the separations between an apocolpium and the surrounding mesocolpia. These data demonstrate that the separations do not arise by rupture during ontogeny. It is assumed that they are initiated in the same way as the meridional parts of the ectoapertures, viz.: by persistent plasma membrane/callose wall contact during primexine formation in the tetrad period (Heslop-Harrison, 1971; Blackmore & Crane, 1988). In the Nephelieae the persistence of the plasma membrane/callose wall contact usually provides an effective mechanism to generate long meridionally arranged colpi. Failures were observed only in a few *Dimocarpus* grains (see chapter 6.4, remark 1). However, with regard to the establishment of sexineless zones round an apocolpium in *Alectryon* pollen, the mechanism seems to be much less 'reliable', as the presence and extent of these zones vary considerably.

In parasyncolporate and colporate intermediates in *Alectryon* (B* and A* respectively) the apo-/mesocolpium connections are often entirely or partially depressed. This is clearly visible in *A. semicinereus* (plate 9: 3, 4), *A. subdentatus* (plate 11: 3,

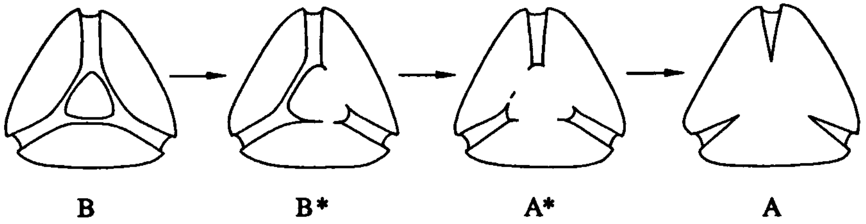


Fig. 9. Hypothetic ontogenetic series from parasyncolporate (B) to colporate (A). B*, A* and A show progressive stages of apo-/mesocolpium coherence by deposition of muri in and over the separations between the apocolpium and the surrounding mesocolpia.

4) and *A. unilobatus* (plate 12: 3). Sometimes it could be perceived that the depressions agree with relatively translucent zones in LM (see chapter 6.2). Being more translucent implies reduced thickness. As the nexine and the outer tectum seem normal, this reduction is probably due to the thinning or absence of the columellate layer and/or inner tectum. Interpreting these observations from an ontogenetic point of view (see fig. 9), the depressions suggest the deposition of muri in and over initially complete separations. In an advanced stage of overgrowth only broad indistinctly forked colpus ends would remain. Further extension of the connections would yield colporate pollen with more or less acute colpus ends. The same process is suggested by pollen of both Travers samples of *A. excelsus*, and some samples of *Dimocarpus, Nephelium, Stadmania* and *Xerospermum* that show depressed apo-/mesocolpium connections and/or broad indistinctly forked colpus ends (see chapter 6.4, 6.6, 6.12 and 6.13 respectively). These samples contain colporate grains and colporate intermediates (A and A* respectively). In those of *A. excelsus* it appeared that incomplete apo-/mesocolpium connections occur mainly in immature grains, whereas the connections are more extensive and more frequently complete in mature grains (see chapter 6.2).

Immature stages of colporate *Alectryon* pollen (A), extensively studied in *Dunn s.n.* of *A. subdentatus,* did not show any traces of incomplete apo-/mesocolpiun coherence.

It has also been tried to find incomplete apo-/mesocolpium connections in immature stages of the colporate pollen of the other Nephelieae genera, particularly those in which pollen with depressed connections and/or broad indistinctly forked colpus ends was observed (see above). Generally, the studied samples failed to show any essential difference between immature and mature grains. Only in one of the *Dimocarpus gardneri* samples (*Meijer 345*) the immature grains sometimes have indistinctly forked colpus ends or depressions between the colpus ends (plate 41: 2), whereas all mature grains are perfectly colporate.

In conclusion, Nephelieae pollen reveals only minor, occasional ontogenetic differences with regard to apo-/mesocolpium coherence.

7. FUNCTION

The primary function of pollen is to transfer male genetic information. Often a secondary function is attributed to pollen: to attract pollinators. Both the transfer aspect and the attractant aspect are discussed in this chapter.

7.1. POLLEN AS MEANS OF TRANSFER: FUNCTION AND FORM

To fulfil its primary function, the transfer of male genetic information, a pollen grain has to satisfy a number of requirements, which particularly relate to the adverse circumstances during the period between anther dehiscence and stigma contact, to the mode of dispersal, and to the recognition phase that precedes germination.

Obviously, the pollen wall plays the most important role during the transfer from anther to stigma, as it represents the interface between the pollen grain and the outside world. Pollenkitt may also have an important function in this respect (Willemse, 1985). Studying exine architecture, Muller (1979) distinguished four main functional aspects: protection, harmomegathy, clustering and storage. Germination can be added to these, particularly if the intine is studied as well. The aspects of pollen wall function may be described in the following way:

- the protective function: sealing off the cell contents in order to prevent desiccation and damage by UV radiation (pollenkitt may contribute);
- the harmomegathic function: accommodating the unavoidable changes in protoplasm volume caused by dehydration before dispersal and rehydration on the stigma;
- the clustering function: sticking together or to a pollinator (often by pollenkitt);
- the storage function: containing pollenkitt with lipids and many other physiologically active substances on infratectal, intratectal and supratectal surfaces;
- the germination function: enabling the formation of the pollen tube, and its passage through the pollen wall.

Although described separately, these functions are by no means independent. They are tightly interwoven by form. Many structures in a pollen grain reflect a compromise between different functional aspects (Muller, 1979): a single structure is involved in several functions, and a single function is performed by several structures, though one function or one structure may dominate. Evidently, the eventual compromise is constrained by history (embodied in ontogenetic processes) and ecological factors (Crane, 1986).

In Nephelieae pollen many aspects of morphology can be related to harmomegathy, and this aspect of function is decribed here in detail.

Harmomegathy

Harmomegathy is envisaged here as the complex of integrated mechanisms in which a number of elements operating together contribute to the accommodation of volume changes of a pollen grain (Blackmore & Barnes, 1986). The pollen wall, being a compromise structure, does not seal off the protoplasm to the same extent in each area; some kind of discontinuity has to allow for the passage of the pollen tube in the germination phase. In order to resist drought and prevent irreversible damage due to plasmolysis the pollen wall follows the shrinking protoplasm, preferably by folding thin parts such as apertures inwards. In the meantime the flexed wall parts build up tension forces that counteract in part the tendency for water loss by creating a negative pressure. Together with the hydrophilic colloids in the protoplasm, pollenkitt filling and covering the grain's outside, and the invagination of thin wall parts, this negative pressure can bring about a state of equilibrium in which there is no further water loss (Payne 1972, 1981; Bolick, 1981), especially since water content is very low now. Aperture morphology during dehydration is aimed at lowering intine exposure (Heslop-Harrison, 1979). Volume reduction in this phase may be considerable. In grains of *Harpullia pendula* (tribe Harpullieae) and *Koelreuteria paniculata* (tribe Koelreuterieae), which roughly resemble pollen of many Nephelieae (three-colporate, spheroidal to subprolate, striate: Muller, 1985 and Nowicke, 1976), Payne (1981) measured 54.9% and 43.3% volume reduction respectively. In 162 species belonging to 84 families volume reduction averaged about 50%.

The ability of the pollen wall to resist tension forces without collapsing or rupturing results from the flexibility of its main constituent, sporopollenin, and from its architectural stability. The large morphological variability of the angiosperm pollen wall, in particular the exinous part of it, can be understood as representing different solutions to the strength and stability problem (Muller, 1979; Payne, 1981; Bolick, 1981). Well known design principles, such as lamination, cellularisation, strutting and arcuation, are frequently evident.

Dehydration generally reaches a maximum within a few seconds after anther dehiscence (Payne, 1981). According to Muller (1979) the exine endures maximal stress during this phase. In the following equilibrium condition a grain may be safely transferred from one flower to another by some vector, either by currents of air or a pollinator. After capture on a receptive stigma the rehydration phase begins. Essentially the same events occur as in the dehydration phase, but their sequence is reversed; aperture morphology is aimed at increasing exposure of the intine (Heslop-Harrison, 1979). Then, after a positive recognition reaction in which substances held in or on the intine or in tectal cavities may play an important role, germination takes place.

Harmomegathic types

In order to enhance comprehension of aperture morphology and function van Campo (1961) recommended the inclusion of hydrated pollen in pollen-morphological studies. An acetolysed grain would just represent "une forme intermédiaire entre celle du pollen turgescente et celle du pollen pulvérulente des étamines" (van Campo, 1966). Also Blackmore & Barnes (1986) emphasised not to rely on a single state of hydration or on acetolysed material alone when studying harmomegathy; experiments with living pollen, ideally using low temperature scanning electron microscopy for observation, should be included. However, living Nephelieae pollen could not be obtained. Therefore the considerations on harmomegathy in this study are completely based on herbarium material, which after all yielded many valuable data.

Using LM and/or SEM it appeared that a single acetolysed sample may demonstrate a wide range of grain shapes due to the different degree of invagination of relatively flexible wall parts (plates 3: 4; 4: 6; fig. 10), though an average shape (the "forme intermédiaire" of van Campo, 1966) usually predominates. It is assumed here that the relatively flexible areas function in living pollen too, and that the range of folding in a sample reflects an important part of the harmomegathic potential of each grain in that sample. Because of the lack of protoplasm in an acetolysed grain a certain bias probably exists. On the one hand it is to be expected that the most inflated shapes (with the most stretched walls) of living grains will not be represented. On the other hand shapes that reflect the most dehydrated condition of the living grains will probably be wanting as well, since there is no protoplasm to retract flexible wall parts as far as possible.

In order to obtain more evidence as to the harmomegathic mechanism inferred from acetolysed grains, additional data were gathered. Pollen was collected from dehisced anthers found on herbarium material (see chapter 3) and then studied with LM in oil (immersion oil suffices). In this way a maximally dehydrated condition of the grains could be observed (plates 57: 13–16, 26; 60: 15–17; 61: 18–20). The associated shape probably approximates the living dehydrated shape. Next, grains from the same anther were studied in a watery wetting agent solution (0.5% Agepon) with LM. Thus, strongly inflated shapes and the stretched condition of the pollen wall could be observed. Unfortunately the latter was difficult to analyse and describe, since LM resolution is too low to determine details in ornamentation of Nephelieae pollen. The most hydrated shapes were invariably found to be spherical or subspherical, with stretched nonapertural exine and fully exposed endoapertures. It is important to use material from dehisced anthers. Undehisced anthers usually yielded irregularly invaginated or collapsed pollen grains.

Applying the above mentioned principles and simple techniques three harmomegathic types can be described in Nephelieae pollen:

1. the colporate type, which attains volume reduction by invaginating particularly the equatorial parts of its ectoapertures (fig. 10; plates 57: 26; 61: 18–20);
2. the parasyncolporate type, which attains volume reduction by invaginating especially the polar parts of its ectoapertures (fig. 11; plate 57: 13–16);
3. the brevicolporate type, which does not exhibit any invagination (fig. 12; plate 60: 15–17).

Blackmore & Barnes (1986) distinguished three distinct elements in the harmomegathy of pollen grains of land plants: folding of the pollen wall (flexibility), contraction and stretching of the wall (elasticity), and compression of internal wall cavities. Folding occurs in the colporate and the parasyncolporate type. Contraction and stretching may contribute to the accommodation of volume changes in each of the three types. The compression element mentioned by Blackmore & Barnes does not occur in the tribe. A fourth, somewhat similar element seems to prevail in the brevicolporate type: invagination of the apertural intine.

In the following sections more detailed descriptions are given of the three harmomegathic types in Nephelieae pollen.

The colporate harmomegathic type

This type has a colporate apertural system with usually fairly long to long ectoapertures. It accommodates volume reduction by invaginating its ectoapertures, especially the equatorial parts. As a result the endoapertural areas are drawn inwards, and the margines of the mesocolpia join and effectively seal the endoapertures and underlying intine parts (onci). Meanwhile, the P/E value of the grain has increased considerably, the meridional outline has become more elongate and the equatorial outline more circular (fig. 10; see also van der Ham, 1988, figs. 11–14).

Fig. 10. The colporate harmomegathic type. Left-hand grain: aperture membranes exposed; right-hand grain: aperture membranes invaginated; the middle grain shows an intermediate state. Material: *Alectryon repandodentatus, Lawrie 29*; × 2500.

The colporate harmomegathic type is found in all Nephelieae genera except *Pometia*. Remarkably, acetolysed material of some genera, in particular *Smelophyllum* and *Xerospermum,* only shows triangular grains with uninvaginated endoapertures and relatively low mean P/E values. In such cases one could easily consider a different harmomegathic system to be present, for instance further lowering of the P/E value or folding of the mesocolpia. However, studying unacetolysed *Xerospermum* grains from dehisced anthers demonstrated the presence of the same colporate harmomegathic system as was found in the other genera (plate 61: 18–20). The forces needed to invaginate the ectoapertures in *Smelophyllum* and *Xerospermum* grains are probably too high to be produced in the absence of shrinking (shrunken) protoplasm. Possibly, the exine in these grains is too rigid (see *The role of the nonapertural exine*).

A similar case is presented by *Cubilia* pollen. Its mesocolpia are relatively thin and often folded inwards in acetolysed state. At first sight, a nonapertural folding mechanism seems to prevail, but studying unacetolysed material from dehisced anthers indicated the colporate type yet to occur (plate 57: 26).

When a colporate grain accommodates volume changes of its protoplasm, not only its shape and P/E value change. Endoaperture shape depends on grain shape (see chapter 6.1), and hence on the harmomegathic state of a grain. Evidently, ectoaperture width depends on it too, as the colpus membranes are the most active harmomegathic structures in a colporate grain. Since contracting and stretching of the exine contributes to the accommodation of volume changes in the colporate type, ornamentation also relates to harmomegathy. In particular the width of the grooves is variable. A stretched striate or rugulate exine may exhibit perforations in wide grooves, whereas in a contracted one these perforations are hidden in narrow grooves (see for example plate 4: 6).

P/E value, equatorial and meridional outline, ectoaperture width, endoaperture shape, and groove width often vary within a single sample. This underlines the close functional interrelations between these pollen characters, and it stresses again (see also Ferguson & Muller, 1981; Ferguson, 1984) the danger of blindly attributing much taxonomic value to characters such as grain shape.

The role of the apertures

Apertures function mainly in harmomegathic and germination processes. The apertural areas of a colporate grain are probably the most dynamic and stressed parts of the exine during dehydration (see also Crane, 1986). In a colporate grain especially the equatorial parts of the ectoapertures invaginate. The degree of invagination depends partly on ectoaperture width. It increases from the apocolpia towards the endoapertural areas; wide colpus membranes (present for instance in several *Dimocarpus* species: chapter 6.4, remark 2) invaginate deeper and more easily than narrow ones (Bolick, 1981).

Colpus membrane motion in Nephelieae pollen is usually not hampered by sexine elements on the membrane; only in *Cubilia* pollen there may be an elaborate sexinous covering (plate 13: 4). The colpus membranes are relatively thick in comparison with nonapertural nexine, but they consist for a much greater part of endexine, which possibly has more flexibility and capacity for contraction and stretching than ectexine (Muller, 1979; Blackmore & Barnes, 1986). However, an invaginating colpus membrane becomes a more or less tubular (plate 61: 18–20) and relatively rigid structure, which contributes to effectively resisting collapse during dehydration, but which may also hamper further invagination. The change in curvature of an ectoaperture is considerable: from strongly curved in roughly spherical hydrated grains to nearly straight in prolate dehydrated grains; achieving such a change is difficult for a groove-shaped or tube-like structure. Obviously, the endoapertural area is the most dynamic area. If the endoaperture is large and completely occupies or exceeds the width of the colpus membrane, flexibility will be optimal, but it may increase water loss. A small endoaperture, on the contrary, will restrict water loss, but it hampers invagination. From this point of view the frequent occurrence of endoapertures with acute to acuminate lateral extensions in colporate Nephelieae pollen can be understood: they represent a compromise between maximal flexibility (harmomegathic function) and small size (protective function). The thought that they have a harmomegathic role is corroborated by the fact that they are missing in parasyncolporate pollen (see The parasyncolporate harmomegathic type: *The role of the endoapertures*). The germination function is probably also involved, but its requirements as to endoaperture shape and size are not known.

Acute/acuminate lateral sides are often very narrow and crack-like (plate 7: 5); sometimes rather sharp edges of the acute/acuminate sides contrast with blunt edges of the rest of the endoaperture border (plate 26: 3). This gives the impression that acute/acuminate lateral sides are sometimes due to rupture, which may have taken place during the short phase of maximal stress following anther dehiscence, or, artificially, during preparation. According to Reitsma (1969) there is a sudden increase in grain size at the moment a pollen grain is brought into contact with the acetolysis mixture. Also the use of a wetting agent solution prior to acetolysis might cause rupture of an apertural area, as onci swell upon hydration. The presence or absence of acute/acuminate lateral sides could not be satisfactorily determined in unacetolysed grains because of the obscuring presence of protoplasm. If occurring, whether naturally or artificially, rupture most clearly demonstrates that the lateral sides of endoapertures are the main stress areas in a colporate grain.

A feature closely associated with endoapertures in colporate grains is the fastigium. A fastigium is a cavity that results from the separation of nexine and sexine at both lateral sides of an endoaperture. Its function is inadequately understood.

Firstly, it may represent a harmomegathic structure that strengthens the apertural area, because it seems to restrict stress and rupture to the lateral endoaperture sides so that the overlying sexine is spared. This view is corroborated by the observation that fastigia are lacking in parasyncolporate pollen (see The parasyncolporate harmomegathic type: *The role of the endoapertures*).

Secondly, it may have a protective purpose, as it is sometimes filled with at least partly acetolysis-resistant material (see chapter 6.1) that possibly counteracts water loss. Especially to the inner sublayer such a function can be attributed; this sublayer might be considered as an internal 'operculum' (plate 55: 3).

Thirdly, it may have a storage function for substances that play a part in pollen-stigma interaction, as was described for exine cavities in general by Heslop-Harrison (1976). In particular the middle, loosely structured sublayer (plate 55: 7) seems appropriate for this function.

Last but not least, its function may be complex, being a combination of the above mentioned possibilities.

The role of the nonapertural exine

The nonapertural exine is distinctly multifunctional, being involved in protection, harmomegathy, clustering and storing.

The nexine has a protective and harmomegathic function. In Nephelieae pollen it is particularly variable as to thickness, thickness differentiation and endexine/ ectexine ratio. *Alectryon* and *Podonephelium* pollen grains usually have thin nexines. A thin nexine also occurs in *Cubilia, Dimocarpus fumatus* subsp. *fumatus, Stadmania glauca* and *Stadmania leandrii.* A thin nexine is more flexible than a thicker one (Bolick, 1981). Pollen of *Dimocarpus fumatus* subsp. *fumatus* combines it with wide ectoapertures and large endoapertures, which yields flexible grains with easily invaginating ectoapertures.

In all Nephelieae the nexine thickens near an ectoaperture, forming a relatively thick layer underlying the ectoaperture itself. In the central part of a mesocolpium nexine thickness is about uniform, for instance in *Alectryon, Cubilia* and *Podonephelium,* or it increases towards the centre of the mesocolpium, for instance in *Litchi,* several *Nephelium* species and *Pappea.* Increasing thickness towards the centre imposes more rigidity to the central part, which can be useful in resisting collapse. Concomitantly, however, a relatively thin oblong area exists at either side of an ectoaperture (see also chapter 6.1). Such a zone is relatively flexible. The whole system is still reinforced by the tectum and columellate layer. Both usually thin towards an ectoaperture; in *Nephelium* and *Stadmania* a thick strongly declining nexine and a thick similarly declining columellate layer are often associated (see chapters 6.6 and 6.12). Such a mesocolpium morphology seems especially aimed at performing the colporate type of harmomegathy (Bolick, 1981).

Alectryon and *Podonephelium* grains show high endexine/ectexine ratios. Endexine is possibly more flexible and elastic than ectexine (Muller, 1979; Blackmore & Barnes, 1986). The presence of a thin nexine (see above) with a thick endexine might explain why *Alectryon* and *Podonephelium* grains show relatively often (compared with for instance *Smelophyllum* and *Xerospermum* grains) invaginated ectoapertures and prolate shapes in acetolysed samples.

The columellate layer as a whole often clearly displays a storage function, showing abundant deposits of pollenkitt between the columellae (see for example plate 56: 3, top left-hand corner).

Columellae in Nephelieae pollen usually stand roughly perpendicular to the nexine. In this position they are optimally suited to resist compression forces (Muller, 1979; Bolick, 1981; Payne, 1981). However, it was noticed that in *Pappea* grains the peripheral columellae of a mesocolpium stand obliquely on the nexine (chapter 6.8; plate 53: 2, 4, 5). This aberrant situation might be understood in the following way. Possibly, due to shear stress (Bolick, 1981), the peripheral columellae are forced in an upright position during dehydration, so that they offer maximal resistance in the flexed state of the mesocolpia. Unfortunately this could not be checked, as invaginated shapes were lacking in TEM and sectioned SEM samples.

The tectum can be attributed all functions already mentioned for the entire nonapertural exine. A thick tectum (*Pappea* from southern South Africa), an imperforate tectum (*Otonephelium*), or a sufficiently sealed perforate tectum may have a protective function. The storage function is illustrated by the presence of pollenkitt on the tectum and in tectal cavities (see for example plates 48: 5; 56: 3). The two other functions, harmomegathy and clustering, require a more detailed account.

Harmomegathy — According to Muller (1979) a meridionally striate tectum particularly fits the colporate harmomegathic system, as it forces folding in one direction. Decreasing thickness towards the ectoapertures promotes this tendency. The long muri in striate ornamentation are economic tensile elements (structures that resist tension; Bolick, 1981). Indeed, colporate Nephelieae grains, which perform the colporate type of harmomegathy, usually possess meridionally striate ornamentation and decreasing tectum thickness towards the ectoapertures. However, several other kinds of ornamentation occur in combination with colporate harmomegathy, such as psilate in *Dimocarpus, Nephelium, Stadmania* and *Xerospermum,* scabrate in *Cubilia* and *Dimocarpus,* and rugulate in for example *Alectryon* and *Nephelium.* These ornamentation types seem to be not optimally adapted to the meridional folding direction of the exine, which suggests that harmomegathy is not the only factor determining ornamentation in Nephelieae pollen. This leads to another function of the tectum:

Clustering — This function is generally fulfilled by pollenkitt covering the tectum, and/or by tectal structures as echini and viscin threads. Echini and viscin threads do not occur in Nephelieae pollen, but pollenkitt has been regularly observed on the tectum. Pollenkitt promotes adherence of a grain to an animal pollen vector (Hesse, 1981), which fits the entomophilous nature of pollination in the Nephelieae. The commonly occurring striate ornamentation may also function well in entomophily. In Araceae, which are mostly pollinated by beetles or flies, Grayum (1986) considered it relatively unspecialised regarding the type of insect.

Many typically anemophilous plants have pollen grains with some kind of microechinate or scabrate tectum (Muller, 1979; Knox, 1984). This could make one think that the scabrate ornamentation in *Cubilia* and *Dimocarpus* possibly relates to anemophily. However, not a single other feature suggests anemophily in the Nephelieae. Their flowers and breeding systems are clearly aimed at entomophily, though *Cubilia* may represent an aberrant case. In this genus the scabrate ornamentation possibly relates to a different mode of pollen transfer, involving other pollinators than social bees that forage for nectar and pollen. *Cubilia* flowers (diameter 2 to 4 mm) are remarkable in having a highly connate calyx with minute lobes that enclose a narrow entrance with only five hardly exserted stamens/staminodes that have stiff broadly band-shaped filaments with small thecae on the inner side. The pistil/pistillode and five woolly petals completely fill up the spaces inside and outside the almost closed circle of filaments. The disc is inconspicuous. Pollen grain size in *Cubilia* is rather small (av. 12.8 µm), and small size may point to some specialised pollination mechanism (Wodehouse, 1935; see also Muller, 1979). Unfortunately field data with respect to pollinators are not available, so that a relation between pollen morphology and a particular pollination type cannot be established as yet. It may be worthwhile to look for insects that oviposit in the flowers, as several collections showed insect larvae between the calyx and the woolly petals. These larvae are almost certainly Diptera (written comm. P.J. van Helsdingen, 1990). They are legless and measure from 0.4 to 1.7 mm long. One female flower (out of a sample of 10) of *PNH 22872* yielded one larva, and two male flowers (out of a sample of 10) of *Elmer 13262* each one larva. One female flower (out of a sample of 20) of *Koorders 22616β* contained three larvae, and another of the same collection a number of elongate 0.2 mm long objects that are possibly insect eggs. The larvae from the Philippines (*PNH 22872, Elmer 13262*) may be similar; those from Celebes (*Koorders 22616β*) are mutually similar, but different from the Philippine ones. One other example of larvae on flowers is known in the Nephelieae. The butterfly *Anthene definita* (Lycaenidae) breeds on the buds and flowers of South African *Pappea capensis* (Palmer & Pitman, 1972). It is a widespread species, occurring in savannas and forest margins from Ethiopia to the Cape (written comm. R. de Jong, 1990). However, it is probably not an essential pollinator, since *P. capensis* is popular with bees too.

Psilate pollen has also been related to anemophily (see for instance Muller, 1979), but according to Grayum (1986) this notion must be seriously reconsidered for tropical floras. Indeed, Nephelieae with psilate pollen (several species of *Dimocarpus, Nephelium, Stadmania* and *Xerospermum*) are distinctly entomophilous. Grayum found psilate pollen in Araceae to be strongly correlated with beetle-pollination. However, beetles play hardly any role in pollen transfer in Sapindaceae. One has to conclude that psilate ornamentation in Nephelieae is sufficiently effective in pollination by bees, which are the main pollinators (chapter 7.2). Then one question remains to be answered: if the pollinators are not different in most Nephelieae, why is pollen ornamentation so diverse in some genera? A possible explanation involves paedomorphosis due to intraflower selfing (see chapter 8).

The parasyncolporate harmomegathic type

This type has a parasyncolporate apertural system. It accommodates volume reduction by invaginating its ectoapertures, especially the polar parts. As a result the margines of the apocolpia and mesocolpia join and seal the underlying aperture membranes; in contrast to folding in the colporate type the endoapertural areas remain superficial. Meanwhile, the P/E value of the grain reduces, the meridional outline

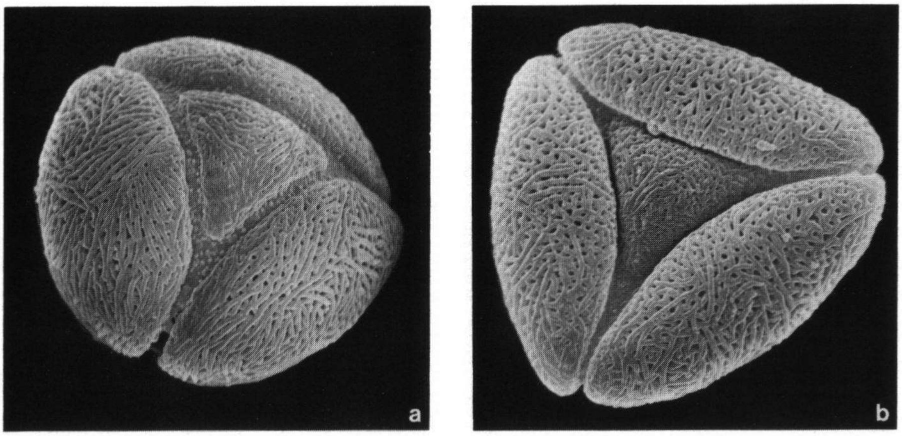


Fig. 11. The parasyncolporate harmomegathic type. a: aperture membranes exposed; b: aperture membranes invaginated. Material: *Alectryon kangeanensis*; × 2500.

becoming broader and the equatorial outline more triangular (fig. 11; see also van der Ham, 1988, figs. 15–18). The apocolpia and the centres of the mesocolpia remain bulging, which contrasts with the inward folding apocolpia and mesocolpium centres in (para?)syncolporate pollen of the Myrtaceae *Eucalyptus cordata* (Blackmore & Barnes, 1986: 143 and figs. 13, 14) and *Eucalyptus spathulata* (Martin & Gadek, 1988: 313 and fig. 6D). The interpretation given above, which is inferred from acetolysed grains, is corroborated by the observations on unacetolysed pollen from dehisced anthers (plate 57: 13–16).

The parasyncolporate harmomegathic type is found in all *Alectryon* species with parasyncolporate pollen. Just as in colporate pollen, P/E value, equatorial and meridional shape, ectoaperture width and groove width in parasyncolporate pollen often vary within a single sample, depending largely on the harmomegathic state of a grain. Several features, such as endoaperture morphology and ornamentation, are different in parasyncolporate pollen. Probably, they are correlated with the parasyncolporate way of performing harmomegathy. Fortunately, the genus *Alectryon* also shows colporate pollen (see chapter 6.2), so that the parasyncolportate harmomegathic type could be directly compared with the colporate type. Comparing the parasyncolporate type with the colporate type of other genera would also involve important differences regarding for instance the nexine (see The colporate harmomegathic type: *The role of the nonapertural exine*), which would reduce the value of the conclusions. Below, aspects of parasyncolporate harmomegathy are described in comparison with colporate harmomegathy in *Alectryon*.

Apertural system and harmomegathy

Colporate as well as parasyncolporate samples show wide P/E ranges, but the averages are clearly different: colporate samples have higher averages than parasyncolporate samples (chapter 6.2). The presence or absence of apo-/mesocolpium connections determines whether a grain will invaginate the polar or the equatorial parts of its ectoapertural system. In a colporate grain polar invagination is hampered, thus the endoapertural areas invaginate, and P/E increases. A parasyncolporate grain invaginates its polar areas, and its P/E ratio decreases.

One may wonder why a parasyncolporate grain does not draw its endoapertural areas inwards. The answer is that possibly the meridional ectoaperture parts are too short for easy invagination, whereas in polar folding the full length of the ectoapertures can be used. Once the polar areas are drawn slightly inwards the grain flattens and the mesocolpia become flexed along the equator, which hampers shape modification in the endoapertural areas still more.

Colporate/parasyncolporate intermediates show partial invagination in the polar areas (chapter 6.2; plates 11: 4; 12: 2). Concomitant equatorial invagination of ectoapertures was not found.

Muller & Leenhouts (1976) mentioned that the thin slit-like ectoapertures in (para) syncolporate Sapindaceae pollen appear to have lost their harmomegathic function. Indeed, such cases are frequently encountered in this family, for example in *Guioa*, tribe Cupanieae (van der Ham & van Heuven, 1989). However, exceptions exist, and parasyncolporate *Alectryon* pollen clearly belongs to this category. Its ectoapertures are never thin and slit-like, but represent distinct harmomegathic structures.

Apocolpium size and harmomegathy

Apocolpium size in *Alectryon* pollen is distinctly correlated with the morphology of the apertural system (chapter 6.2), and hence with harmomegathy. The parasyncolporate harmomegathic type has larger apocolpia (av. A/E = 0.46) than the colporate type (av. A/E = 0.32). Large apocolpia may facilitate polar folding in a parasyncolporate grain. They straighten the ectoapertures along the apocolpia, which reduces stress during folding. At the same time they impede equatorial folding, since the meridional parts are short (see *Apertural system and harmomegathy*). Grains with small apocolpia, or with no apocolpia at all (syncolporate) even show a tendency towards nonapertural folding of the mesocolpia (van der Ham & van Heuven, 1989). Thus, large apocolpia promote polar folding in parasyncolporate pollen. By contrast, harmomegathy in colporate pollen benefits from long ectoapertures and hence small apocolpia. In this way the harmomegathic function helps to explain differences in apocolpium size in *Alectryon*.

The role of the endoapertures

Parasyncolporate pollen, in contrast with colporate pollen, is devoid of fastigia. The endoapertures possess obtuse or indistinct lateral sides (plates 1: 4; 6: 2; 9: 6); crack-like structures could never be demonstrated.

The presence of fastigia and endoapertures with acute/acuminate lateral sides in colporate pollen was tentatively connected with harmomegathy, particularly with equatorial invagination of the ectoapertures (see The colporate harmomegathic type: *The role of the apertures*). Their absence in parasyncolporate grains corroborates the view of a relation being present. Parasyncolporate pollen does not invaginate its endoapertural areas. Consequently stress is lower or absent, and the endoaperture borders do not need fastigia for strengthening or acute/acuminate lateral sides that allow easy invagination.

In comparison with colporate pollen parasyncolporate pollen may possess a lower resistance to water loss, as its endoapertures remain superficial during invagination and lack acute/acuminate lateral sides that reduce their size. Internal 'opercula', which are also attributed a protective function (see The colporate harmomegathic type: *The role of the apertures*), were never observed in parasyncolporate pollen.

The role of the nonapertural exine

Just as in the colporate harmomegathic type the nonapertural exine of parasyncolporate grains is involved in protection, harmomegathy, clustering and storage. No obvious differences with regard to protection, clustering and storage exist between colporate and parasyncolporate pollen in *Alectryon*. Two aspects relating to harmomegathy, namely columella length and ornamentation, deserve a more detailed treatment.

In parasyncolporate pollen the peripheral columellae of a mesocolpium are as tall as or slightly shorter than the central columellae, whereas in colporate pollen they are mostly clearly shorter than the central ones (chapter 6.2). Generally, *Alectryon* pollen has long columellae in comparison with pollen of most other Nephelieae; *Podonephelium* and *Pometia* pollen have long columellae too. Relatively long apocolpial columellae occur in several *Alectryon* and *Podonephelium* species. Undoubtedly, these features relate to particular stress patterns.

Long peripheral columellae in parasyncolporate pollen may be associated with the relative stability of the endoapertural areas. However, other factors, for example storage of pollenkitt, may contribute as well. This makes the matter so complex that assessing the significance of long columellae more precisely is impossible without further data concerning the stress zones and the other functions.

Ornamentation in *Alectryon* pollen is striate, striate-rugulate or rugulate. It may be dense or loose, which partly depends on whether the exine is contracted or stretched. It correlates with aperture morphology (chapter 6.2): meridionally striate ornamentation occurs especially in colporate pollen, whereas rugulate ornamentation is mainly found in parasyncolporate pollen. Striate-rugulate forms are about equally common in both aperture types. Meridionally striate ornamentation can be denoted as an adaptation to the colporate harmomegathic system (Muller, 1979). Therefore it is understandable that parasyncolporate grains are usually not meridionally striate. However, on account of the folding direction of the apocolpium and mesocolpium borders one would expect more or less transversely striate ornamentation. Nevertheless, it is generally striate-rugulate to rugulate; only apocolpia show relatively often more or less striate ornamentation along the ectoapertures (see for example plates 5: 3; 6: 1; 8: 6). Possibly, striate-rugulate to rugulate ornamentation represents some kind of intermediate condition between meridionally and transversely striate. This would correspond with the frequent occurrence of colporate/parsyncolporate intermediates and the versatile nature of *Alectryon* pollen regarding harmomegathy.

The brevicolporate harmomegathic type

This type, which is restricted to the genus *Pometia*, has short colpate ectoapertures and tubular endoapertures. In contrast with the other two types it does not exhibit any invagination (fig. 12). Because of their relative small size and the tubular shape of the underlying endoapertures the ectoapertures are incapable of invagination. The nonapertural exine has a thick nexine and a reticulate system of heavy muri. The grain as a whole displays the phenomenon of peristasy, which is based on the principle of the geodesic dome (Muller, 1979; Payne, 1981). Muller introduced the term peristasy in order to indicate uniform distribution of stress in pollen grain walls. Generally, peristatic types are characterised by reduced folding structures, a relatively thick ectexine and a coarsely reticulate tectum. A spherical shape was also mentioned by Muller. At first sight the protruding apertural areas of *Pometia* pollen may seem weak elements in the dome construction, but internally they appear to be rigid bearing points for a more or less spherical inner nexine.

The relative stability of grain shape in *Pometia* pollen was inferred from the small amount of variation in grain shape in acetolysed samples, and from the observations on unacetolysed pollen from dehisced anthers (plate 60: 15–17). Van der Ham (1988)

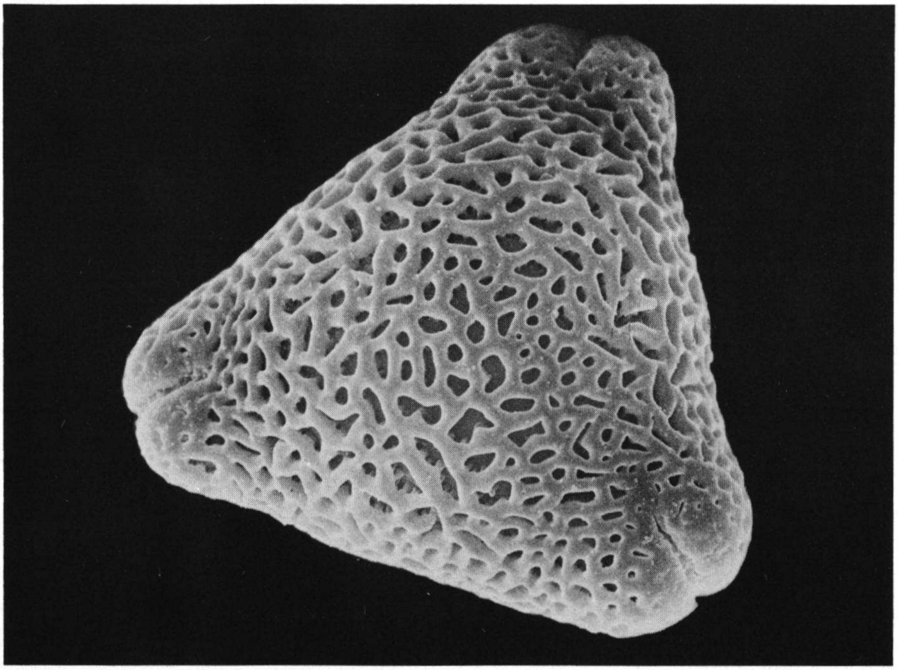


Fig. 12. The brevicolporate harmomegathic type. This type does not show any invagination. It provides a good example of peristasy. Material: *Pometia pinnata* forma *glabra, NIFS bb 29745*; × 3000.

proposed a nonapertural folding mechanism in which the central parts of the mesocolpia fold inwards, producing a lobate grain shape. However, this was based on acetolysed material only. The shrunken and lobate shapes shown by van der Ham are now considered to represent the result of collapse.

One may wonder about the way *Pometia* pollen manages to accommodate volume changes of its protoplasm. In the dehydrated state of the unacetolysed grains from dehisced anthers studied with LM (plate 60: 16), and often in TEM sections as well (plate 54: 5), it could be observed that the apertural intine is drawn inwards by the protoplasm. Consequently the endoapertural tube and the underlying area are 'empty' (van den Berg, 1978, plate VIII: 2) or filled with foreign matter (plate 54: 5). When studying dehydrated grains in oil with LM, often air staying behind in these spaces can be noticed (plate 60: 15). Possibly the invagination of the apertural intine provides the necessary accommodation of the volume change due to dehydration. Further water loss through the apertures is prevented by closure of the ectoapertures (plate 31: compare 3 with 4).

Intine invagination resembles the compression mechanism mentioned by Blackmore & Barnes (1986) in so far that the change is accommodated within the grain. Both mechanisms are peristatic (see also Muller, 1979). They differ in the location of the accommodating areas: within and underneath the endoapertures in *Pometia* pollen, within the mesocolpial exine in the compression mechanism (distinct in pollen of many Compositae; Blackmore et al., 1984).

Pollen with reduced ectoapertures occurs in several other sapindaceous tribes, but up to now peristasy could only be demonstrated in *Harpullia,* tribe Harpullieae (Muller, 1979, 1985).

In chapter 6.10 the close resemblance between *Pometia* pollen and the fossil *Atlantopollis* is dealt with. The apparently oblate shape of *Atlantopollis* grains does not fit peristasy. Batten (1986) commented on the functional significance of exine architecture in Normapolles pollen, including *Atlantopollis.* Normapolles plants were considered to be anemophilous, but the *Atlantopollis* stock was regarded as an exception. According to Batten the open sexine of *Atlantopollis* grains suggests a storage function, which could point at entomophily. Such a function might be attributed to the similar sexine of *Pometia* pollen too.

The Wodehouse effect

Wodehouse (1935), studying pollen types in Polygonaceae, suggested that pollen grain size and shape influence harmomegathy: because small grains have a large surface in proportion to their volume the elasticity of the pollen wall suffices to accommodate volume changes, whereas larger grains with their relatively small surface need additional mechanisms such as invaginating ectoapertures. Prolate grains have a higher surface/volume ratio than spherical ones, and consequently would need less elaborate mechanisms too.

Muller (1979) considered Wodehouse's thoughts on Polygonaceae pollen as universal principles, and described them as the Wodehouse effect: "any increase in size needs a larger reduction in diameter to accommodate a given percent of volume re-

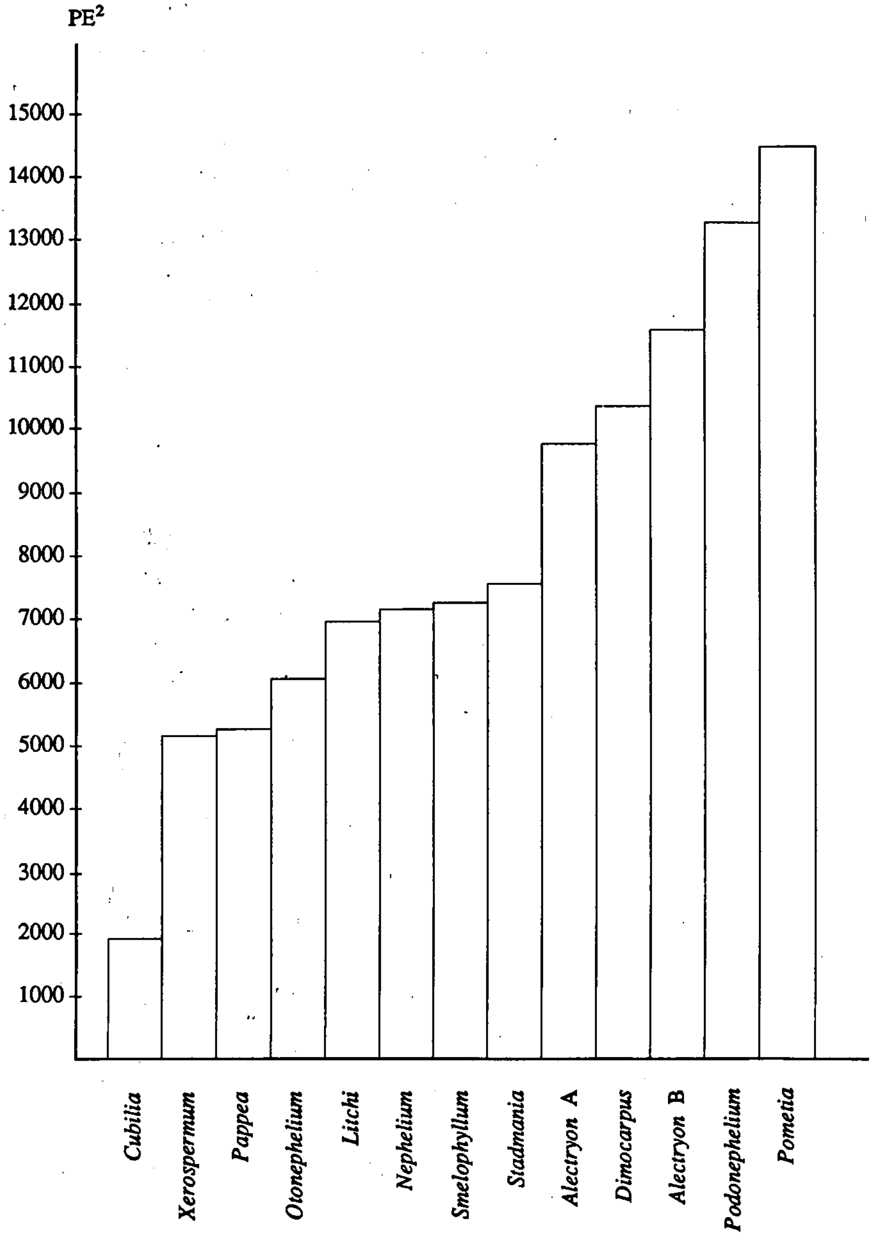


Fig. 13. PE^2 averages in Nephelieae pollen. PE^2 is taken as an approximate measure for comparing grain volumes. *Alectryon* A = colporate *Alectryon* pollen; *Alectryon* B = parasyncolporate *Alectryon* pollen (see figs. 6 and 7).

duction and hence more elaborate harmomegathic structures to accommodate the larger stresses" and "for the same volume a change from a sphere to a more cylindrical, prolate shape needs a smaller reduction in diameter to achieve a given percent of volume reduction and therefore less elaborate harmomegathic structures to accommodate the smaller stresses." Later, the Wodehouse effect was referred to by Batten (1986) and Crane (1986).

The Wodehouse effect seems an attractive explanation for the relative simple architecture of small grains. Thus it was applied in an attempt to interpret the presence of aberrant harmomegathic types in the Nephelieae, namely the parasyncolporate and the brevicolporate type. Parasyncolporate *Alectryon* grains and brevicolporate *Pometia* grains belong to the largest size class of Nephelieae pollen. For example, a *Pometia* grain is about 7.5 times larger (in volume!) than a *Cubilia* grain (fig. 13). Especially the parasyncolporate *Alectryon* pollen seems to display a more elaborate apertural system than the colporate type, owing to the increased amount of ectoaperture length capable of invagination. Colporate Nephelieae pollen of large size (occurring in *Alectryon, Dimocarpus* and *Podonephelium*) appeared to have wide and/or easily invaginating ectoapertures.

However, it was realised that the Wodehouse effect cannot explain deviating harmomegathic mechanisms in large grains, because its premise is invalid. A pollen grain that has to accommodate a given percent of volume reduction (say 50%) needs a fixed percent of surface decrease (37%) and circumference (or diameter) decrease (21%), whether it is small or large (table 13). If the elasticity of the pollen wall is sufficient in the smaller grain, it will be so in the larger; elasticity does not depend on the total amount of surface present. Neither do larger grains need more volume reduction than smaller grains. Payne (1981) measured volume reduction rates varying from 4.2% to 77.6% (average about 50%) in 162 species belonging to 84 angiosperm families, but there was no link between the percent of volume reduction and grain size (Payne, 1981, fig. 1).

Nevertheless, there is a factor that may yield differences between small and large pollen: the thickness of the wall. Large grains usually have thicker walls than small grains (Lee, 1978). A thick wall resists stretching forces more than a thin wall does.

Table 13. Volume, surface and circumference of spherical pollen grains with various (hypothetic) equatorial diameters (E). Between brackets: values after 50% volume reduction.

diameter E	volume $1/6\,E^3\pi$	surface $E^2\pi$	circumference $E\pi$
1	1/6 n (1/12 π)	n (0.63 π)	n (0.79 π)
2	8/6 n (4/6 π)	4 n (2.52 π)	2 n (1.59 π)
3	64/6 n (32/6 π)	16 n (10.08 π)	4 n (3.18 π)
	reduction: 50%	reduction: 37%	reduction: 21%

But, if thicknesses are to be compared in order to assess stretching capacity, one should also involve other important architectural differences, such as endexine/ ectexine ratio, nexine/sexine ratio, relative thickness of the columellate layer and ornamentation. Evaluating the influence of all relevant factors together is too hard with the available data (see also Crane, 1986), and beyond the scope of this study.

The role of the intine

Hesse (1987) stressed the necessity of studying the intine in addition to the exine, as this may yield important data regarding harmomegathy and germination. Therefore a TEM study of the intine of a number of Nephelieae was executed.

The intine in Nephelieae pollen appeared particularly variable with respect to thickness and to the presence of electron-opaque inclusions in its nonapertural parts (chapter 6.1). Much of the variation may be due to differences in maturity of the material (Hesse, 1987), but the distribution of some features is consistent with taxonomy.

Pollen of *Alectryon* and *Podonephelium* show a relatively thick nonapertural intine with many electron-opaque inclusions in the exintine. In *Pometia* pollen the inclusions fill almost the whole nonapertural intine, which is relatively thin. Pollen of all other genera has a relatively thin nonapertural intine with few or no inclusions at all.

Pollen of all Nephelieae shows electron-opaque inclusions in its onci. An oncus, in particular the exintine (Heslop-Harrison, 1979; Heslop-Harrison et al., 1986), plays an important role in the harmomegathy and germination processes of a pollen grain. The presence of the numerous electron-opaque inclusions, which seem to form a complex tubular/labyrinthic system, possibly relates to the ability of the exintine to regulate dehydration and redydration. They are relatively rich in proteins (Kress & Stone, 1982; Knox, 1984). The radially arranged linear extensions into and through the endintine found in several Nephelieae (see for example plate 56: 4) might represent communication canals between this system and the protoplasm. The extension of a thick exintine under the mesocolpia in *Alectryon* and *Podonephelium* pollen suggests that the nonapertural intine has a role in regulating outflow and inflow of water plus dissolved substances too. In those species where relatively thin onci occur (chapter 6.1, remark 3) one might speak of a partial transfer of function.

The supposition of an increased harmomegathic function of the nonapertural intine in *Alectryon* and *Podonephelium* pollen is corroborated by the fact that the nexine in these genera is much thinner than in the other Nephelieae genera. It is known that water plus dissolved substances can permeate through a grain's exine (see Rowley, 1988). A thick, harmomegathically active nonapertural intine may benefit from a thin nexine. This might be the functional significance of the inverse relation between intine thickness and amount of exine found by Kress and Stone (1982) in several unrelated groups of plants. In *Alectryon* and *Podonephelium* pollen the relatively thick endexine, often provided with irregular protrusions that may reach the intercolumellar nexine surfaces, possibly relates or contributes to this effect. Within *Alectryon* there seems to be no correlation between intine morphology and aperture type (colporate vs. parasyncolporate).

A comparable situation is found in *Harpullia* (Muller, 1985; see for example plate VIIb: 1 and plate IX). Here, the possibly higher activity of the nonapertural intine may be connected with the reduced harmomegathic and communication function of the apertures noticed by Muller.

In *Pometia* pollen the presence of numerous dark inclusions in the nonapertural intine does not coincide with a thin nexine, although an endexine is virtually absent. Actually intine morphology as a whole is aberrant (chapter 6.1). *Pometia* pollen certainly has an aberrant harmomegathic system too, but this is not obviously related to intine morphology. The only feature worth noticing is the fact that the intine does not seem to be adnate to the inside and the inner edge of the tubular endoaperture. This enables the intine to withdraw freely.

7.2. POLLEN AS ATTRACTANT

Breeding systems

Sapindaceae flowers are mostly unisexual (see chapter 6.14). Male and female flowers may be found on the same plant (monoecious species) or on different plants (dioecious species). In monoecious species the different sexes occur frequently in two or three phases (dichogamy and duodichogamy respectively), which causes them to be actually dioecious (van Welzen, 1989). Usually the first phase is male (pistil reduced), the second female (anthers well developed, but indehiscent), and the third again male (pistil well developed, but nonfunctional). A second cycle may occur. Breeding in the Sapindaceae seems to be aimed at cross-pollination, either by dioecy or (duo)dichogamy. Self-incompatibilty seems less important, as successful fruit set from interflower selfing (geitonogamy) may readily occur, in the Nephelieae for example in *Dimocarpus longan* (written comm. S.K. Yap, 1988), *Nephelium lappaceum* (van Welzen et al., 1988) and *Pometia pinnata* (Ha et al., 1988).

In some species in the Nephelieae breeding has been thoroughly studied, for instance in *Litchi chinensis, Nephelium lappaceum, Pometia pinnata* and *Xerospermum noronhianum (X. intermedium)*; but in most others observations are scarce or lacking. The following data regarding the distribution of the sexes in the Nephelieae could be gathered.

Alectryon	usually monoecious, but flowers in the former *Heterodendrum* species mostly bisexual (Reynolds, 1982)
Cubilia	monoecious (ms. P.W. Leenhouts)
Dimocarpus	probably monoecious (Leenhouts, 1971)
Litchi	monoecious (Liu, 1954; Mustard et al., 1954)
Nephelium	probably mostly dioecious, sometimes monoecious (Leenhouts, 1986)
N. costatum	dioecious (Yap, 1982)
N. cuspidatum	dioecious (Yap, 1982)
N. lappaceum	monoecious, but male plants occur as well (Ha et al., 1988)
	dioecious (Lim, 1984)
	dioecious (Uji, 1987)
	dioecious, but female plants with a limited number of male flowers may occur (van Welzen et al., 1988; van Welzen & Verheij, 1989)

N. ramboutan-ake	dioecious (Yap, 1982)
Otonephelium	probably monoecious
Pappea	monoecious (Exell, 1966; Palmer & Pitman, 1972)
Podonephelium	monoecious (ms. P.W. Leenhouts)
Pometia	monoecious (Jacobs, 1962; Ha et al., 1988)
Smelophyllum	flowers bisexual (Palmer & Pitman, 1972)
Stadmania oppositifolia	monoecious (Capuron, 1969; Exell, 1966)
S. sect. *Tricoccodendron*	dioecious (Capuron, 1969)
Xerospermum	dioecious (Appanah, 1982; Charlesworth, 1984; Ha et al., 1988; Leenhouts, 1983; Yap, 1982)

However, the records of bisexual flowers (in *Alectryon* and *Smelophyllum*) may actually refer to male or female flowers with conspicuous vestiges of the other sex (see chapter 6.14).

Pollination

Sapindaceae flowers are generally pollinated by insects (entomophily), frequently by bees belonging to the genera *Trigona* (a group of stingless bees) and *Apis* (honeybees), less frequently by danaid butterflies and many uncommon other visitors (Appanah, 1982; Bawa, 1977; Gondim, 1984; Hawkeswood, 1983; Subba Reddi et al., 1983; Uji, 1987; van Welzen et al., 1988). Wind-pollination (anemophily) is rare in Sapindaceae. The genus *Dodonaea* (tribe Dodonaeeae) yields the only well documented case (Keighery, 1982; West, 1982, 1984). The easily released allergenic pollen of *Dodonaea viscosa* is a common constituent of the airborne pollen flora of different parts of India (Subba Reddi et al., 1980). *Distichostemon,* a genus closely related to *Dodonaea,* is probably also wind-pollinated (personal comm. J.G. West, 1988).

In entomophilous Sapindaceae both nectar and pollen are usually abundantly produced, and foraged for by bees. Nectar is the universal food source in bee colonies. It is basically sugar water, but small amounts of amino acids, proteins and several other substances occur as well (Appanah, 1982; Barth, 1985; Heß, 1983; Subba Reddi et al., 1983). In Sapindaceae it is secreted by an extrastamin(odi)al disc. Khoo & Yong (1987) pictured a *Trigona* bee foraging for nectar on female *Nephelium* flowers.

Pollen is gathered in particular as food source for the youngest larvae, being rich in proteins, fats, starches and many vitamins (Barth, 1985; Heß, 1983). The bees may be attracted by odour from the grains (von Frisch, 1977), which arises from the pollenkitt cover of the exine (Knox, 1984; Willemse, 1985), but odours from other flower parts may contribute. Appanah (1982) determined high ratios of domestic to foreign pollen in corbicular loads of trigonid bees visiting male *Xerospermum noronhianum* plants in Malaya (see next section). Chen et al. (1984) found high percentages of *Dimocarpus longan* and *Litchi chinensis* pollen in samples of commercial Longan honey (45–88% *D. longan* grains in 85 samples) and Lychee honey (75–86% *L. chinensis* grains in 3 samples) from Taiwan. These examples indicate intentional pollen foraging by bees in Nephelieae.

Pollen in Sapindaceae: a pollinator attractant?

Because male and female flowers in Sapindaceae are usually separated, either by dioecy or (duo)dichogamy, one may not simply attribute an attractant function to the pollen. According to von Frisch (1977) individuals of the honeybee (*Apis mellifera*) concentrate fully on either nectar or pollen. Little is known of specialisation regarding nectar and pollen foraging in Sapindaceae by trigonid bees, which are probably the commonest pollinators in the family. Appanah (1982) found that *Trigona* individuals visiting male flowers of *Xerospermum noronhianum* may forage for both nectar and pollen. They were never sighted selectively collecting pollen alone, though it is probably stored separately in the nest (see Khoo & Yong, 1987). On female flowers the bees foraged only for nectar; they did not break the anthers of the staminodes. A mean pollen load of 3636 *Xerospermum* grains (ratio domestic to foreign pollen 2870 : 1) was determined for individuals on male plants, whereas the mean load was very low, only three *Xerospermum* grains per individual (ratio domestic to foreign pollen 1 : 12.3), for visitors of female plants. Only 6 of the 13 *Trigona* species involved were found on both male and female plants. These data suggest that pollen foragers do not visit female plants, and that pollination is brought about by nectar foragers visiting male and female plants. This implies that, as far as the data of Appanah are concerned, pollen has no role in attracting potential pollinators. Producing so much pollen seems particularly aimed at enhancing the chance of successful cross-pollination by nectar gatherers. In addition, it may indirectly benefit pollination, as large quantities of pollen help to sustain colonies of potential pollinators, if indeed the pollen foragers and the pollinators belong to the same species. Sequential support (early flowers feed pollinators for late flowers) is necessary for the maintenance of colonies of social insects (Rathcke, 1983). Bee species that visit only one sex must be regarded as 'robbers' that merely exhaust the floral rewards without providing the benefit of pollination.

There is one other interesting datum with respect to the attractivity of the male sex. Bawa (1977), studying the reproductive biology of *Cupania guatemalensis* (tribe Cupanieae), found that two of the *Trigona* species visiting female flowers usually attempted to collect pollen from the staminodes. These observations demonstrate that staminodes (rather than the pollen contained by them) may have an attractant function in pollination in Sapindaceae. Probably, much depends on which trigonids are available. There are many *Trigona* species and they show a wide range of foraging behaviour (Appanah, 1982; Appanah et al., 1986; Barth, 1985; Bawa, 1977; Johnson & Hubbell, 1975; von Frisch, 1977).

Bawa (1977) attributed a mimicking function to the staminodial anthers in the female flowers of *Cupania guatemalensis*, as they are attractive but indehiscent. Pollen from staminodia of Sapindaceae flowers appears normal at first sight, but it is usually largely sterile. The production of large amounts of sterile pollen that cannot be reached by pollen foragers seems superfluous. However, the presence of a small percentage of viable pollen may prove more important than the redundancy of the larger sterile part, as some observations suggest that viable staminodial pollen in Sapindaceae occasionally plays a direct role in pollination by means of an intraflower autogamous mechanism (chapter 6.14). Such a mechanism requires possibly fewer pollen grains than interflower mechanisms, in which losses due to foraging and random transfer by insects have to be built in.

The advantage of being (duo)dichogamous

As pointed out earlier, many Sapindaceae are (duo)dichogamous: usually the first flower phase is male, the second female, and the third male again. A second cycle in which the first male phase is lacking may occur. One may wonder about the profit that can be derived from such a breeding system, particularly from the first male phase. As receptive stigmas do not yet occur, insect visits during the first phase do not benefit the plant with respect to its own pollination; it is a food source and its pollen may effectuate cross-pollination in other plants. However, in the second phase, when receptive stigmas do occur, there may be a delayed pollination advantage for the plant itself.

It is well known by now that bees can learn. Honeybees (*Apis* spp.) may at the same time retain such diverse information as odour, colour, form, time and relative geographical position (Barth, 1985; Heß, 1983; von Frisch, 1977). Moreover, they can communicate odour and geographical data. Learning behaviour is also known in *Trigona* species. Martinez del Rio & Eguiarte (1987) reported flower recognition for *Trigona* in Mexico, while Appanah et al. (1986) presented data indicating memory for food sites, the ability to recruit new bees to the site, time sense, and foraging distances of at least 63 m from the nest for *Trigona* in Malaya. Recruitment can be achieved by marking the route with odour signals, presenting odour to inactive workers, giving off arousing sound signals, and piloting the recruits along the marked route to the food source (Barth, 1985; von Frisch, 1977). The almost complete absence of foreign pollen on *Trigona* bees visiting wild male plants of *Xerospermum noronhianum* (Appanah, 1982) also points at flower constancy and learning. The high percentages of *Dimocarpus longan* and *Litchi chinensis* pollen in Longan honey and Lychee honey found by Chen et al. (1984) are less relevant, since the pollen was probably gathered from plantation trees.

Because of the ability of bees to concentrate on a particular plant species and to retain and communicate geographical information, the first flower phase in (duo)dichogamous Sapindaceae might, in addition to being a pollen and food source, represent an economic advertisement of nectar announcing the coming female phase. Its flowers are numerous, but all possess a reduced pistil, which may be advantageous in terms of energy budgets (Bertin, 1982). As soon as the female phase has arrived, bees (partly recruited by first phase visitors) carrying pollen from other plants plus the information to trace the site can bring about pollination. This allows the 'expensive' female phase to be relatively short, which indeed holds for the (duo)dichogamous Sapindaceae that have been thoroughly studied in the field: *Cupania guatemalensis* (Bawa, 1977), *Litchi chinensis* (Mustard et al., 1954) and *Sapindus emarginatus* (tribe Sapindeae; Subba Reddi et al., 1983). Early advertising is important for (duo)dichogamous Sapindaceae with a low population density, and that grow in habitats with little intertree movement of pollinators, such as the understorey of forests. Actually many Sapindaceae are understorey trees and trigonid bees show little intertree movement. High interspecific competition for the pollinator fauna by a large number of tree species in the understorey (Appanah, 1982) may increase the advantage of advertising early.

An advertising function of the first phase might explain why in *Litchi chinensis* and *Sapindus emarginatus* in the second flowering cycle the first phase is usually lacking: by then the plant is probably known well enough to the bees.

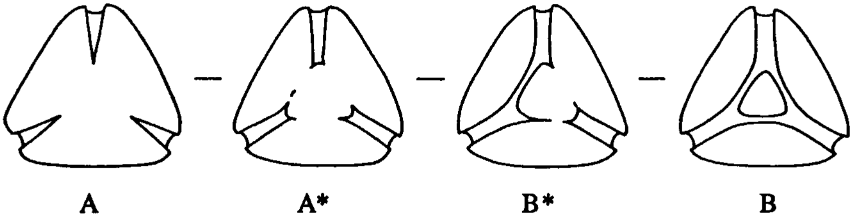
In *Litchi chinensis* Liu (1954) and Mustard et al. (1954) demonstrated that first phase anthers contain considerably more inviable small grains than third phase anthers. This phenomenon may be due to factors relating to cultivation, but it would also fit the advertisement view, as small grains are probably 'cheaper' than large grains. The latter option, however, would imply a reduced role of the first phase in cross-pollination.

8. EVOLUTION

Two major morphological series can be deduced from the variation in Nephelieae pollen. These concern features of the apertural system and of the ornamentation. On the basis of different sources, including ontogeny, the fossil record, a functional interpretation, pollination biology, and macromorphology, an attempt is made to reconstruct evolutionary development. In addition the evolutionary status of a few other features, and of the two rather isolated pollen types, namely *Cubilia* pollen and *Pometia* pollen, will be considered.

Apertural system

The morphological series evident in the apertural systems includes colporate pollen (type A) on the one hand and parasyncolporate pollen (type B) on the other. The intermediate states that link the extremes are denoted as intermediately colporate (type A*) and intermediately parasyncolporate (type B*), the series being:



The full series occurs in *Alectryon* (see chapter 6.2). Type A* was sometimes found in *Stadmania* and *Xerospermum*, rarely in *Dimocarpus* and *Nephelium*, which all generally have type A (see chapters 6.4, 6.6, 6.12, 6.13).

Type A and type B are both common in the Sapindaceae.[1] The former occurs in all 13 tribes recognised by Muller & Leenhouts (1976), the latter in four of them: the

Cupanieae, the Melicocceae, the Nephelieae and the Schleichereae, which all belong to the subfamily Sapindoïdeae. The tribe Cupanieae is closely related to the Nephelieae and Schleichereae. According to Muller & Leenhouts it is the more primitive group of these three tribes. Type B occurs in at least 30 of its 46 genera (see Macromorphological evidence). Several of them, such as *Arytera* (van der Ham, 1977a) and *Elattostachys* show both types. Intermediates similar to those decribed in *Alectryon* were found in many Cupanieae, for example in *Guioa* (van der Ham & van Heuven, 1989) and *Mischocarpus* (van der Ham, 1977b).

Ontogeny

Ontogeny (see chapter 6.15) yields a small amount of evidence regarding the evolutionary status of parasyncolporate *Alectryon* pollen. Immature and mature stages in parasyncolporate samples do not show any difference as to apo-/mesocolpium coherence. However, some observations on samples with abundant intermediates (A*, B*) suggest that during ontogeny intermediates or even colporate pollen can develop from parasyncolporate pollen by overgrowth of the separations between apocolpia and mesocolpia. In one *Dimocarpus* sample immature grains sometimes showed, in contrast with the colporate mature grains, indistinctly forked colpus ends and depressions between colpus ends (type A*). All other colporate samples studied did not reveal any difference between immature and mature grains with respect to apo-/mesocolpium coherence, not even those containing mature intermediates.

Thus the mature parasyncolporate stage is not preceded by an intermediate or colporate stage, but incomplete apo-/mesocolpium connections may possibly become more complete during the growth of the grain. These data indicate that, from an evolutionary point of view, type A might have originated from type B in *Alectryon*. If type A is considered derived in this genus, than the depressed apo-/mesocolpium connections and forked colpus ends that frequently occur in some species, and that characterise type A*, may be regarded as remains of a former (ancestral) parasyncolporate condition (type B). The same may be advanced for the similar features in the A* type grains of *Dimocarpus, Nephelium, Stadmania* and *Xerospermum*.

Fossil evidence

Muller & Leenhouts (1976) distinguished 12 pollen types in the Sapindaceae. They regarded type A as the most primitive type. It embraces colporate, more or less spherical grains with long ectoapertures; all colporate Nephelieae and Cupanieae pollen was attributed to type A. The other 11 types, including both (para)syncolporate types B_1 and B_2, were considered to be probably derived from A. The difference between B_1 and B_2 is very slight. Together with type B_3 described by van der Ham (1977b) they will be treated here as type B. Parasyncolporate *Alectryon* pollen, unknown to Muller & Leenhouts, is included too.

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1) Here, as in Muller & Leenhouts (1976), type B includes both parasyncolporate and syncolporate pollen.

Table 14. Distribution of *Cupanieidites* (Turonian-Quaternary) and Recent (para)syncolporate (type B) Sapindaceae pollen.

				GONDWANA											
		Europe	North America	South America	Africa	Madagascar	India	Antarctica	Indian Ocean	New Zealand	Australia	New Guinea	Malesia	continental SE Asia	Pacific
QUATERNARY			X	X		X	X				X	X	X	X	X
TERTIARY	Pliocene										X	X			
	Miocene		X	X	X		X			X	X	X			
	Oligocene	X					X		X	X	X				
	Eocene	X	X		X		X			X	X				
	Palaeocene		X							X	X				
UPPER CRETACEOUS	Maastrichtian		X	X	X			X							
	Campanian		?	?	X										
	Santonian			X	X		X								
	Coniacian				X										
	Turonian				X										
	Cenomanian														

Sources — **Europe:** Hochuli, 1978 (Eo); Kedves, 1974 (Eo); Krutzsch, 1959 (Eo, Ol). **North America:** Chmura, 1973 (Ca/Ma, Pa); Drugg, 1967 (Ma, Pa); Elsik, 1968 (Pa); Elsik & Dilcher, 1974 (Eo); Fairchild & Elsik, 1969 (Eo); Farabee & Canright, 1986 (Ma); Frederiksen, 1980a (Eo); Graham, 1976 (Mi); Krutzsch, 1959 (Eo); Leffingwell, 1970 (Ma, Pa); Norton & Hall, 1969 (UC, Pa); Oltz, 1969 (Ma); Radlkofer, 1933 (Q: Recent); Srivastava, 1966 (UC); Taylor, 1989 (Eo); Tschudy & van Loenen, 1970 (Eo). **South America:** Graham, 1988 (Mi, Q); Herngreen, 1975 (Ca/Ma); Krutzsch, 1959 (UC); Muller et al., 1987 (Co/Sa, Ca/Ma, Ma); Radlkofer, 1933 (Q: Recent); Stough, 1968 (Ma). **Africa:** Belsky et al., 1965 (UC); Boltenhagen, 1980 (Tu–Ma); Bratzeva, 1988 (Eo); Coetzee & Muller, 1984 (UC, Mi); Krutzsch, 1959 (Co). **Madagascar:** Radlkofer, 1933 (Q: Recent). **India:** Radlkofer, 1933 (Q: Recent); Ramanujam & Reddy, 1984 (written comm. C. Tissot, 1989: Eo; see also Srivastava, 1988); written comm. C. Tissot, 1988 (Q); Venkatachala & Rawat, 1972 (Eo); Venkatachala & Rawat, 1973 (Ol–Mi); Venkatachala & Sharma, 1974 (Co/Sa). **Antarctica:** Askin, 1989 (Ma). Indian Ocean: Kemp & Harris, 1977 (Ol). **New Zealand:** Couper, 1960 (Pa–Mi); Mildenhall, 1989 (Mi); Pocknall, 1989 (Eo, Eo/Ol). **Australia:** Cookson & Pike, 1954 (Eo–Pl); Harris, 1965 (Pa); Hekel, 1972 (LT, Ol, Mi); Milne, 1988 (Eo); Radlkofer, 1933 (Q: Recent); Stover & Evans, 1973 (Eo); Stover & Partridge, 1973, 1982 (Eo–Mi); Truswell et al., 1987 (Ol–Q); Truswell & Owen, 1988 (Eo). **New Guinea:** Cookson & Pike, 1954 (Pl); Radlkofer, 1933 (Q: Recent); Truswell et al., 1987 (Mi–Q). **SE Asia:** Radlkofer, 1933 (Q: Recent). **Pacific:** Radlkofer, 1933 (Q: Recent); Selling, 1947, 1948 (Q).

Ca = Campanian, **Co** = Coniacian, **Eo** = Eocene, **LT** = Lower Tertiary, **Ma** = Maastrichtian, **Mi** = Miocene, **Ol** = Oligocene, **Pa** = Palaeocene, **Pl** = Pliocene, **Q** = Quaternary, **Sa** = Santonian, **Tu** = Turonian, **UC** = Upper Cretaceous.

Thanikaimoni (1986) listed the derivation of a syncolporate from a colporate apertural system as a general evolutionary trend in angiosperm pollen. Muller & Leenhouts (1976) mentioned several arguments for regarding type A as basic and type B as derived in the Sapindaceae. The general argument was that type A is relatively simple and unspecialised. In addition they acknowledged that parasyncolporate pollen appears later in the fossil record than colporate pollen. Within the angiosperms type B is probably derived indeed. This might even hold for the family Sapindaceae, as type B is lacking in the subfamily Dodonaeoïdeae, the outgroup of the subfamily Sapindoïdeae. However, this does not inevitably mean that the A type that occurs in the latter is primitive. In view of the ontogenetic data mentioned in the previous section the possibility that type B reversed to type A must be considered too. Unfortunately the fossil record can hardly provide any evidence in this matter. The (para)syncolporate type B is probably represented by *Cupanieidites* Cookson & Pike emend. Chmura[2], which is known from the Turonian onwards (table 14), but it is very difficult to identify fossil colporate type A Sapindoïdeae pollen. Actually fossil colporate Sapindaceae pollen is hardly, if at all, distinguishable from fossil pollen of many other families (see also Muller, 1984; van Steenis, 1986). Therefore, and not necessarily because of a more recent origin, the oldest reliable record of type A Sapindaceae pollen, *Alectryon* cf. *excelsus* from the Miocene of New Zealand (Couper, 1953), is much younger than the oldest *Cupanieidites* material.

Cupanieidites sensu Chmura (1973) is largely equivalent to the *Cupaniopsis* type of Muller (1981a). This is supposed to represent fossil Cupanieae pollen. Obviously it may have been produced also by some representatives of the Melicocceae, Nephelieae and Schleichereae. The *Cupaniopsis* type of Muller excludes the "non-syncolpate" forms (ectoapertures "extend toward the poles but do not reach the poles") and very indistinctly sculptured forms described by Chmura. However, "non-syncolpate" forms as well as not or very indistinctly sculptured forms were found in several modern (para)syncolporate Sapindaceae genera, for example in *Guioa* (van der Ham & van Heuven, 1989). The "imperfectly parasyncolpate" condition, distinguished by Chmura to indicate apo-/mesocolpium coherence, and which fades into "non-syncolpate", is even common. It is similar to the colporate/parasyncolporate condition (A*, B*) de-

[2] Krutzsch (1969) attributed a myrtaceous affinity to a part of *Cupanieidites* and to *Duplopollis* Krutzsch, which was combined with *Cupanieidites* by Chmura (1973). However, because of the great resemblance with (para)syncolporate pollen of extant Sapindaceae *Cupanieidites* sensu Chmura is here considered to represent fossil Sapindaceae pollen, following Chmura (1973) and Muller (1976, 1981a). According to J.M. Chalson and H.A. Martin (personal comm., 1988) Myrtaceae pollen and (para)syncolporate Sapindaceae pollen are at least in Australia sufficiently different, and it is unlikely that Australian records of *Cupanieidites* pertain to Myrtaceae.

Knowledge of pollen of Myrtaceae and Sapindaceae has been steadily increasing (see for example Patel et al., 1984 and Muller & Leenhouts, 1976) and much has been added to the fossil pollen record since Krutzsch (1969) revised fossil (para)syncolporate pollen (see table 13 for *Cupanieidites*). A new revision, using EM techniques and including material of fossil (para)syncolporate pollen (not only *Cupanieidites* and *Duplopollis*, but also *Myrtaceidites* Cookson & Pike and *Syncolporites* van der Hammen) as well as pollen of recent Myrtaceae and Sapindaceae, is therefore recommended. It will be a huge task to organise the material, but it is regarded as the only way to settle affinities more definitely.

scribed in the present study. Chmura recorded colporate/parasyncolporate intermediates in a rich and highly variable *Cupanieidites* complex from the Upper Cretaceous (Campanian/Maastrichtian) of California (see for instance the photographs of her *C. innexisulcatus*). They were found to be associated and connected by transitional forms with parasyncolporate and syncolporate type B pollen. Such intermediates are not known from the oldest (Turonian–Santonian) deposits with *Cupanieidites*. The Late Cretaceous intermediates from California may represent a starting-point of a development towards colporate pollen, which is a reversal within the Sapindaceae.

Aperture evolution and climate

In view of the abundant presence of type B in Late Cretaceous microfloras of Africa Muller & Leenhouts (1976) wondered about the absence of type B in the Recent flora, though three genera with type B pollen survive in Madagascar (table 14; see also chapter 10: fig. 18). The youngest material from the continent is reported from the Lower Miocene of South Africa (Coetzee & Muller, 1984). These authors suggested unstable, less humid climatic conditions to have been the cause of the disappearance from the fossil record. Indeed, humid forest evidently covered nearly all of Africa until the Miocene, and spreading drought, probably starting near the close of the Oligocene, may have caused the great impoverishment of the African flora (Raven & Axelrod, 1974; Axelrod & Raven, 1978). However, the tribe Cupanieae, considered as the main producer of the B type, probably did not disappear. Several Cupanieae genera as well as genera of the closely related tribes Nephelieae and Schleichereae, all with type A pollen, still exist in the Recent continental African flora. A number of these are known to grow and to flower under dry conditions. For example, the Nephelieae genus *Pappea* grows in dry or arid parts of E and S Africa: Kenya (Battiscombe, 1936), Rwanda (personal comm. C. Ntaganda, 1987), South Africa (Palmer & Pitman, 1972; van Wyk et al., 1988). The persistence of the B type in Madagascar fits the general picture given by Leroy (1978): this island was hardly modified in the course of time, at least since the Early Cretaceous. Its flora did not suffer as much as the similar flora that occupied continental Africa. Madagascar appears to be a centre of survival for archaic autochthonous African taxa.

Similar reasoning can be advanced with regard to North and Central America, Australia plus New Zealand, and Europe. Actually the Early Tertiary was one of the warmest periods of the Phanerozoic, and the subsequent cooling and aridification was a global one. Relatively recently several worldwide stages of 'ice age aridity' occurred (Raven & Axelrod, 1974).

Axelrod (1979) described a climatic trend in SW North America from well watered Late Cretaceous/Early Tertiary conditions to progressively drier regimes in the Late Tertiary and Quaternary (see also Truswell & Harris, 1982). In the Late Eocene and Early Oligocene the climate became very rapidly cooler and possibly also drier in the Gulf Coast region (Frederiksen, 1980b). In Central America the temperature dropped significantly in the Late Eocene and again in the Middle Miocene (Graham, 1989). The abundance of *Cupanieidites* in the Upper Cretaceous and Lower Tertiary of North America contrasts with the scantiness in the Upper Tertiary and Quaternary (at present only in the southernmost part and in the Caribbean: *Cupania, Matayba*). Type A is unknown in modern North American Cupanieae, but it occurs in Central America in *Blomia* and *Dilodendron*. Only little is known of the ecology of these genera. *Blomia* grows in evergreen forest. One *Dilodendron* species is found in moist forest with a strong dry season, a second grows in wet forest, while the third species is known from dry areas in Peru, Boliva and Central plus SE Brazil (Gentry & Steyermark, 1987).

During the Tertiary, type B occurred throughout the greater part of southern Australia and New Zealand (Cookson & Pike, 1954; Couper, 1960; Mildenhall, 1989; Pocknall, 1989; Stover & Partridge, 1973, 1982; Truswell et al., 1987). Nowadays, type B (Cupanieae and Nephelieae) is restricted to the rainforests in the northeast, and it is absent in New Zealand. Type A exists in the Australian rainforests too, in a few Cupanieae genera and in *Alectryon* of the Nephelieae, but in addition it is found in several *Alectryon* species from dry or arid regions. For example, *A. oleifolius* extends to the margins of deserts (Reynolds, 1987). Cupanieae are absent in New Zealand today. Of the only known Nephelieae, *Alectryon excelsus* and the closely related *A. grandis* (Cranwell, 1962), the former generally has type A pollen (sometimes A* and B*); pollen of the latter is unknown. In the course of the Tertiary, Australia and New Zealand were involved in a widespread aridification due to breaking away from Antarctica and drifting northwards, which caused rainforests to retreat (see for example Barlow, 1981; Beard, 1977; Christophel & Greenwood, 1989; Martin, 1978; Pocknall, 1989; Truswell & Harris, 1982).

In Central Europe paratropical conditions prevailed during the developmental optimum of evergreen forests in the Middle and Late Eocene. In the course of the Late Oligocene a definite climatic cooling and continentalisation occurred and temperate and deciduous elements invaded, which resulted in the retreat and gradual decline of the paratropical vegetation (Mai, 1989). In contrast with Africa, America and Australia plus New Zealand no evergreen Sapindaceae survived in Europe. Only *Koelreuteria* (tribe Koelreuterieae), a deciduous element with A type pollen, was found at the outset of the cooler period.

Apparently, *Cupanieidites* (type B) disappeared when climatic conditions deteriorated. However, this does not imply that the plants that produced it also vanished. Taking into account the present-day occurrence of several Cupanieae and Nephelieae under dry or arid conditions, it may be considered that a part of the *Cupanieidites* plants adapted to the new circumstances. The disappearance of type B due to a drier climate, and the presence of type A in some Nephelieae known to grow in dry regions suggest that transformation of type B to type A was a major element of the presumed adaptation. Unfortunately, as pointed out earlier (see Fossil evidence), the fossil record cannot provide evidence (as yet), but a functional interpretation of such a transformation may support this view.

A functional interpretation

In chapter 7.1 it is explained that type A and type B have different harmomegathic systems. One aspect of the difference concerns the position of the endoapertures before and after invagination of the ectoapertures. In type A the endoapertural areas are deeply drawn inwards and at the same time sealed by the margins of the mesocolpia. By contrast, the endoapertural areas in type B (including syncolporate pollen: see van der Ham & van Heuven, 1989) remain superficial. Although experimental evidence is lacking (and would be hard to obtain) it is assumed that the different positions of the endoapertures in the dehydrated state have different protective values, grains with superficial endoapertures being more susceptible to desiccation. This might be the relevance of the transformation of type B to type A under drier climatic conditions suggested above. Such a relation between harmomegathic type and climate would justify the distinction of mesomorphic and xeromorphic pollen. Type B would represent a more mesomorphic type and type A a more xeromorphic type. Attributing a protective function to strong invagination of endoapertures may also explain why type A occurs in dry as well as wet places: if it provides enough protection in dry circumstances, it will certainly do so under wet conditions. Blackmore & Barnes (1986) discussed the concept of mesomorphic and xeromorphic pollen, but they concluded that there is only little evidence for such a distinction.

In conclusion, a functional interpretation of the difference between type A and type B involving ecological factors supports the view that in the subfamily Sapindoïdeae type B may have reversed to type A. It would be a widespread trend, occurring in many groups of the Sapindoïdeae. This may be due to the widespread aridity in the course of the Tertiary. The presence of apo-/mesocolpium coherence, apparent as early as the Late Cretaceous and present in many Recent genera as well, may have been an advantage in surviving under dry conditions. The possibility that forms with apo-/mesocolpium coherence (A*, B*) are more primitive than either A or B is excluded here, because apo-/mesocolpium coherence does not seem to yield a major and successful harmomegathic system (see chapters 6.2, 7.1). Usually it occurs in only a small part of a sample. Moreover, type A* and B* appear later in the fossil record than type B.

One may question the adaptive value for a pollen grain of having a (para)syncolporate apertural system, if a colporate system provides more protection. This question especially affects the origin of type B in the Sapindaceae. To answer it the principle of transfer of function can be invoked (see also Muller 1979, 1981b; Blackmore & Barnes, 1986). In the colporate A pollen, endoapertures mainly function in harmomegathy and germination processes. The endoapertural area is the most dynamic area during invagination. In the (para)syncolporate B pollen the endoapertural areas are relatively rigid, and invagination occurs in the apocolpial/polar areas. This allows the endoapertural areas to be simple without being susceptible to rupture. Endoapertural areas in (para)syncolporate Sapindaceae pollen are simple indeed. They are devoid of the fastigial structures that frequently occur in the colporate pollen of the family (chapter 7.1). Transfer of the main invagination points from the equator to the polar areas might result in an increase of vulnerability in the latter, especially in syncolporate pollen and in parasyncolporate pollen with small apocolpia. This may explain why such pollen often shows a nonapertural harmomegathic system (van der Ham & van Heuven, 1989; see also chapter 7.1: The parasyncolporate harmomegathic type). In parasyncolporate pollen with large apocolpia stress is probably sufficiently spread over the apocolpial areas.

The transfer of invagination from the equator to the poles in type B results in a superficial position of the endoapertures. If this indeed increases the chance of desiccation it may be postulated that the (para)syncolporate B type of the Sapindaceae originated in a humid environment, such as rainforest. According to the stratigraphical and geographical distribution of *Cupanieidites* (table 14) this happened in the Late Cretaceous in Gondwana (see further chapter 10: Geographical aspects).

Pollen of *Eucalyptus* (Myrtaceae) might offer a puzzling combination, being (para)-syncolporate but generally occurring under most xeric conditions. However, Heslop-Harrison & Heslop-Harrison (1990) presented evidence for the existence of a special outer oncus layer that prevents desiccation. They interpreted this layer as an adaptation to a xeric environment.

Macromorphological evidence

Muller & Leenhouts (1976) compared the distribution of type A and type B with the number of derived states of macromorphological characters in 34 Cupanieae genera. The macromorphological characters all concern flower features. From an evolutionary point of view these are generally much more closely related to pollen than for example wood or leaf features (Muller, 1984). Flower structure and pollen morphology are bound together by the pollination mode, and climate may affect pollen morphology (as discussed above) as well as pollination mode (Keighery, 1982) and hence flower structure. This justifies to make comparisons between trends in flower structure and pollen-morphological trends.

Muller and Leenhouts distinguished three macromorphological classes: 0–1, 2–3 and 4–6 derived character states. They determined a positive correlation between a high number of derived states and the presence of type B pollen: 59% of the genera with 0 or 1 derived state have type B, whereas this is 86% in those with 4 to 6 derived states. However, studying more genera (43) and more species of genera already included produces a different picture (table 15): type B is now more or less equally distributed, being present in 60–65% of the genera (data about the number of derived states in the added genera were supplied by P.W. Leenhouts).

Table 15. Cupanieae genera arranged according to pollen type and number of derived states of macromorphological characters (macromorphological classes delimited as by Muller & Leenhouts, 1976).

pollen type	number of derived states of macromorphological characters		
	0–1	2–3	4–6
A	6 (= 40%)	7 (= 35%)	5 (= 38%)
B	9 (= 60%)	13 (= 65%)	8 (= 62%)

Table 16. Cupanieae genera arranged according to region, pollen type and number of derived states of macromorphological characters.

region	pollen type	number of derived states of macromorphological characters						
		0	1	2	3	4	5	6
America	A	*Diplokeleba*	*Dilodendron* *Pseudima*			*Tripterodendron*	*Blomia*	
	?		*Allosanthus*	*Scyphonychium*				
	B	*Cupania*	*Matayba*	*Pentascyphus* *Vouarana*				
Africa	A		*Laccodiscus*	*Aporrhiza* *Blighia*	*Eriocoelum*	*Lychnodiscus* *Neotina**	*Blighiopsis*	
	B		*Molinaea**	*Tina**		*Neotina**		
Asia / Australia / Pacific	A	*Cupaniopsis**	*Lepiderema**	*Arytera*	*Dictyoneura* *Elattostachys* *Lepidopetalum*			
	?				*Gongrospermum*			
	B	*Cupaniopsis** *Rhysotoechia*	*Gloeocarpus* *Gongrodiscus* *Lepiderema* *Mischocarpus**	*Arytera** *Paranephelium** *Pavieasia* *Sarcotoechia* *Storthocalyx*	*Amesiodendron* *Elattostachys* *Guioa** *Synima* *Toechima**	*Euphorianthus** *Jagera** *Sarcopteryx* *Trigonachras*	*Sisyrolepis* *Phyllotrichum*	*Diploglottis*

* = intermediates (A*, B*) present in small percentages. *Blighia* includes *Phialodiscus*, and *Dilodendron* includes *Dipterodendron*.

Splitting into geographical regions and subdividing the macromorphological classes shows some interesting facts (table 16). In America and Africa type B is absent or rare in the genera with the highest numbers (3–6) of derived states. In Asia, Australia and the Pacific type B predominates in every class; type A occurs in a few genera with 0 to 3 derived states, mostly in relatively few samples or species only. In the most 'primitive' genera type A is present in *Diplokeleba* and in a few *Cupaniopsis* species. However, the genus *Diplokeleba* is a doubtful Sapindaceae (personal comm. P.W. Leenhouts, 1987). A cladistic analysis of *Cupaniopsis* demonstrated type B to be a plesiomorphy in this genus and type A a synapomorphy or autapomorphy (personal comm. F.A.C.B. Adema, 1989). In *Guioa* a higher degree of apo-/mesocolpium coherence correlates with more or less psilate ornamentation, which is almost limited to one of the groups with most advanced character states (van der Ham & van Heuven, 1989; van Welzen, 1989; see also Ornamentation). In conclusion, there is no macromorphological evidence that type A is a primitive character state in the Cupanieae. Some evidence exists that type B represents the primitive state.

The phylogenetic relations between the eight tribes of the Sapindoïdeae as outlined by Muller & Leenhouts might indicate that type B is the primitive state in the whole subfamily. The Cupanieae have a basal position within group B (Cupanieae, Nephelieae, Schleichereae). Type B is uncommon in the derived tribes Nephelieae (only *Alectryon*) and Schleichereae (only *Schleichera*). Group C (Thouinieae, Paullinieae), which is considered to be derived from group B, does not contain type B pollen, though remains of a former syncolporate condition may be present, for example in *Cardiospermum* (see *Pometia* pollen) and *Serjania* (Muller & Leenhouts, 1976, plate 12: D). Within group A (Melicocceae, Lepisantheae, Sapindeae), which may be considered as the outgroup of group B + C, the tribe Melicocceae takes a basal position, and is the only one of group A to show type B pollen (in *Castanospora, Tristira, Tristiropsis*; *Melicocca* and *Talisia* have type A).

Conclusion

On the basis of fossil evidence, palaeo-ecological and macromorphological data, and a functional interpretation it is hypothesised that within the subfamily Sapindoïdeae (para)syncolporate pollen (type B) is plesiomorphic and frequently developed into colporate pollen (type A). The trend B → A represents a reversal within the Sapindaceae, since the ancestral stock of the subfamilies Sapindoïdeae and Dodonaeoïdeae is supposed to have possesed type A pollen.

The trend B → A is assumed to hold true in *Alectryon* of the Nephelieae as well. Pollen ontogeny provides some circumstantial evidence. The A type of the other Nephelieae genera is regarded as derived too. The forked colpus ends and depressed apo-/mesocolpium connections occurring in *Alectryon, Dimocarpus, Nephelium, Stadmania* and *Xerospermum,* and that characterise type A* and type B*, are considered to indicate an ancestral parasyncolporate condition.

Alectryon embraces groups of species that largely have type B or type A (see chapter 9). A cladistic analysis may be rewarding in elucidating the evolutionary status of both types in this genus. The same holds true for *Arytera* of the Cupanieae (van der Ham, 1977a), assuming that this genus is monophyletic.

A careful study of the A type pollen of the Sapindoïdeae and the allegedly more primitive Dodonaeoïdeae, and establishing a fossil record of the A type might also help to evaluate the hypothesis presented above. However, as already pointed out by Muller & Leenhouts (1976), type A of the Sapindaceae is relatively simple (see also chapter 9). Therefore it may eventually turn out inevitable to rely heavily on macromorphological evidence in order to unravel its history.

Ornamentation

The morphological series in ornamentation includes consecutively the following major states: rugulate and striate (ornamentation consisting of muri in a criss-cross or parallel arrangement), psilate (projecting elements as muri and scabrae absent) and scabrate (ornamentation consisting of scabrae). All possible intermediate states between rugulate and striate, between striate and psilate, and between psilate and scabrate occur. In addition the scabrate condition shows an intergrading series of forms with roughly isodiametric and oblong scabrae. Scabrate ornamentation with oblong scabrae is always prominent, but, by the lack of intermediates, it cannot be connected with the striate or rugulate state. Several rugulate/psilate intermediates occur. However, they do not form a continuous series and do not come from a single sample, species or group of related species. The whole series reads as follows:

rugulate	—	striate	—	psilate	—	scabrate scabrae isodiametric	—	scabrate scabrae oblong

The series comprises several aspects of variation:

- arrangement of muri (rugulate — striate)
- prominence of muri (striate — psilate)
- prominence of scabrae (psilate — scabrate)
- shape of scabrae (isodiametric — oblong)

Probably, different mechanisms underlie this diversity. With respect to the reconstruction of the phylogeny of ornamentation it is justified to split up the major series, and to treat its parts (the aspects mentioned above) separately.

Fossils are of little use in studying the evolution of ornamentation in the Nephelieae. The available data (almost only LM) do not provide enough information.

Rugulate—striate

Striate ornamentation is present in 10 of the 12 Nephelieae genera (all but *Cubilia* and *Pometia*). Rugulate ornamentation (including less prominent and irregular forms) occurs in 6 of these 10: *Alectryon, Dimocarpus, Nephelium, Otonephelium, Stadmania* and *Xerospermum*. However, only in *Alectryon* it makes up a substantial part. In the other genera its presence is marginal, being restricted to a minor part of the samples of a species, or to a part of the grains in a sample. The complete series from rugulate to striate is found in *Alectryon, Nephelium* and *Stadmania.*

In *Alectryon* striate ornamentation is found especially in colporate pollen, and rugulate ornamentation mainly in parasyncolporate pollen, which is functionally significant with regard to harmomegathy (chapter 7.1). The same holds true in the tribe Cupanieae[3]. In the first part of this chapter (Apertural system) it is hypothesised that within *Alectryon* parasyncolporate pollen (type B) is primitive and colporate pollen (type A) derived. On account of the functional relationship between type B pollen and rugulate ornamentation the latter is considered primitive too. Circumstantial evidence is provided by the ontogenetic development of the tectum in *Alectryon* (chapter 6.15): rugulate ornamentation precedes striate ornamentation, though the width of the muri in both types differ. Early stages have narrower muri than older stages. In pollen with rugulate ornamentation in mature grains the muri become wider but their arrangement remains criss-cross, whereas in pollen that is striate in the mature stage growth is accompanied by a change from a criss-cross to a (sub)parallel pattern. In the ontogeny of *Alectryon* pollen striate ornamentation may be regarded as a terminal addition (in the sense of Gould, 1977; see also Hideux & Abadie, 1986).

The colporate pollen of the other Nephelieae genera is considered as derived too. Occasionally occurring forked colpus ends and depressed apo-/mesocolpium connections would represent remains of an ancestral parasyncolporate condition. Similarly, the casual rugulate ornamentation in *Dimocarpus, Nephelium, Otonephelium, Stadmania* and *Xerospermum,* which does not fit the harmomegathy of colporate grains, is interpreted as ancestral. It is possibly due to some kind of failure or lower expression of the genetic information coding for (sub)parallel arrangement. In contrast with the situation in *Alectryon,* rugulate ornamentation could only once be demonstrated in an immature stage of striate pollen (chapter 6.15: *Podonephelium subaequilaterum*). It is lacking in all other samples with immature stages of striate pollen studied, which may be attributed to a more rapid development in the early ontogeny. In an evolutionary context this can be described as the principle of condensation (Gould, 1977): the length of an ontogeny is limited, and earlier stages are shortened ("acceleration") or eliminated ("deletion") to make room for new features (i.e. terminal additions, apomorphies).

Remarkably 4 of the 5 genera with occasional rugulate ornamentation also show psilate ornamentation. In *Xerospermum* and sometimes in *Dimocarpus* they are even connected, rugulate ornamentation being here shallow or indistinct. This is readily understood if the 'complete' ontogeny of *Alectryon* is studied: psilate and rugulate are successive stages.

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3) One of the very few available SEM photographs of fossil Sapindaceae pollen (*Cupanieidites orthoteichus*) included in a study of Eocene palynomorphs from Tennessee (Taylor, 1989), shows a grain with a parasyncolporate apertural system and rugulate-reticulate ornamentation. The fossil probably belongs to the Cupanieae, since parasyncolporate pollen of Melicocceae, Nephelieae and Schleichereae has rugulate to striate-rugulate ornamentation. Moreover, American parasyncolporate Melicocceae are unknown, and the Nephelieae and Schleichereae are completely restricted to the Old World.

A rugulate (or psilate) tectum is not correlated with forked colpus ends or depressed apo-/mesocolpium connections. These features were mainly found in striate pollen.

Striate—psilate

As mentioned in the foregoing section, 10 of the 12 Nephelieae genera show striate pollen. Psilate ornamentation occurs in 4 of these genera, *Dimocarpus, Nephelium, Stadmania* and *Xerospermum,* in more or less close association with rugulate ornamentation. However, psilate ornamentation is much more constant in comparison with rugulate ornamentation. It characterises whole samples or species. The complete series from striate to psilate is found in all 4 genera, in *Dimocarpus* and *Xerospermum* even within single species.

In chapter 7.1 (see The colporate harmomegathic type) it is argued that harmomegathy does not offer a sound explanation for the presence of psilate ornamentation in Nephelieae pollen. Anemophily or beetle-pollination, which sometimes accounts for psilate ornamentation, could not be demonstrated in the Nephelieae. However, a special pollination mode that may explain psilate ornamentation is known: the intraflower autogamous mechanism observed in *Xerospermum noronhianum* (Appanah, 1982). Through this mechanism staminodial pollen reaches without help of any insect the stigma of the same flower, germinates, and causes fruit set. This is important for (functionally) dioecious species of which the individuals grow far apart or grow in areas where the number or movement of pollinators is restricted (chapter 6.14). Chapter 6.15 provides some data which suggest that staminodial pollen is immature compared with pollen of male flowers, having among other things a less prominent ornamentation. Possibly, less prominent ornamentation, including psilate and all psilate/striate intermediates, was (several times) introduced in the character set of Nephelieae pollen as a result of successful pollination and fruit set with staminodial pollen. If harmomegathy and the possibilities of transfer by insects are not affected too seriously (as seems to hold true: see chapter 7.1), it may be advantageous, since mechanisms (including receptors) for the elaboration of distinct muri can be discarded. In the autogamous mechanism the pollen grains do not need ornamental structures for harmomegathy or transfer, since they can reach the stigma in a sludge of anther remains (Appanah, 1982).

A psilate tectum was found to be the earliest ornamentation phase in pollen of several Nephelieae, and it is assumed that a more or less psilate stage occurs in the early ontogeny of all Nephelieae pollen (chapter 6.15). Psilate ornamentation in mature grains can be interpreted as the effect of absence of murus differentiation during sporopollenin deposition, and indistinct and shallow ornamentation as the effects of less differentiation due to prolongation of the period of indifferential growth. No indications were found that psilate, indistinct and shallow ornamentation can arise by indifferential deposition on or filling up of an earlier formed more prominent pattern. Therefore the presence of these less prominent ornamentation forms in Nephelieae pollen is denoted here as paedomorphic. Paedomorphosis is Garstang's term for retention of an ancestral juvenile character by later ontogenetic stages of descendants (see Gould, 1977; McNamara, 1989). Gould (1977) distinguished two kinds of paedomorphosis: neoteny, produced by retardation of somatic development, and progenesis, produced by precocious sexual maturation of an organism still in a morphologically juvenile stage. McNamara (1989), explaining paedomorphosis with salamanders, distinguished between "moving slower" and "finishing earlier". Moving slower is: the rate of development is slow, but the animal continues to grow bigger, becoming sexually mature while retaining a 'child-like' body. Finishing earlier is: the sexual system matures precociously and growth stops when the animal is still small and looks like a juvenile. There is no evidence in Nephelieae pollen that less prominent ornamentation results from a ceasing of sporopollenin deposition in a premature stage; mature psilate exines have about the same thickness range as prominently ornamented exines. The grain is full-sized and exine development is complete; only its ornamentation has a juvenile nature. Consequently psilate and shallowly or indistinctly sculptured pollen may be considered neotenous (moving slow), and hence derived, with respect to ornamentation. If the staminodial pollen that causes fruit set in *Xerospermum noronhianum* (Appanah, 1982) is indeed small and immature in comparison with pollen from male flowers, it may be designated as an example of progenesis (finishing early).

Viable staminodial pollen was also found in *Litchi* and *Nephelium*. Actually, if searched for, it may be still commoner. Autogamy with staminodial pollen would be particularly significant in dioecious species. Less prominent ornamentation, alleged to be the effect of autogamy with staminodial pollen, indeed mainly occurs in dioecious taxa (see chapter 7.2: *Nephelium, Stadmania* sect. *Tricoccodendron, Xerospermum*); *Dimocarpus* seems to be monoecious. Remarkably the monoecious section *Stadmania* of the genus *Stadmania* mostly shows prominently ornamented pollen, whereas the dioecious section *Tricoccodendron* contains two species with psilate pollen. Dioecy seems to be derived in the Sapindaceae (van Welzen, 1989). If indeed true, this would corroborate the view that psilate ornamentation in the Nephelieae is a derived state.

Rugulate and rugulate/psilate ornamentation do not form a coherent series in the Nephelieae. However, in *Guioa* (tribe Cupanieae) rugulate is the common ornamentation type, and a full series from rugulate to psilate could be established. More or less psilate ornamentation is almost restricted to one of the groups with most advanced character states: *G. pubescens* plus a number of Philippine species. It correlates with a higher degree of apo-/mesocolpium coherence, which is considered derived too (see Apertural system). Nothing is known of the viability of staminodial pollen in *Guioa,* but nevertheless striate—psilate in the Nephelieae and rugulate—psilate in *Guioa* may be regarded as convergent evolutionary trends. In *Cupaniopsis* (tribe Cupanieae) psilate ornamentation is probably a synapomorphy of a group of New Caledonian species (personal comm. F.A.C.B. Adema, 1989).

Psilate ornamentation was found, usually as a minor form, in a few other Cupanieae genera (*Aporrhiza, Diploglottis, Jagera*: fig. 14, *Laccodiscus, Pseudima*) and in most other sapindaceous tribes as well (Lepisantheae: *Lepisanthes*; Melicocceae: *Talisia*; Paullinieae: *Paullinia, Serjania*; Sapindeae: *Deinbollia*; Schleichereae: *Camptolepis, Plagioscyphus*; Thouinieae: *Allophylus, Athyana*). It is known from all tribes of the Sapindoïdeae; the Dodonaeoïdeae, which may be viewed as the outgroup of the Sapindoïdeae (Muller & Leenhouts,1976), do not show psilate pollen. Because of its simplicity and predominance in the earliest fossil angiosperm pollen types Muller (1970, 1971, 1979, 1985) considered psilate ornamentation (including imperforate, perforate and microreticulate patterns) as a primitive character in Sapindaceae pollen. On account of the data now available it represents instead a widespread reversal to the condition in early angiosperms. Another example of advanced psilate ornamentation was provided by Grayum (1986), who concluded that psilate pollen is derived within the Araceae, being a specialisation for beetle-pollination.

Psilate — scabrate

Four Nephelieae genera show psilate ornamentation (see above). In one of them, *Dimocarpus,* scabrate ornamentation as well as all intermediates between psilate and scabrate were also found. The series is restricted to *D. longan* subsp. *malesianus.* Similar scabrate ornamentation occurs in *Cubilia* (see *Cubilia* pollen).

The scabrate ornamentation of *D. longan* subsp. *malesianus* is unique. It does not occur in related taxa, neither in the Nephelieae nor in other Sapindaceae. Therefore, applying the outgroup rule, it is regarded as an autapomorphy in *Dimocarpus.*

Although both scabrate and striate ornamentation are common in *Dimocarpus* no intermediate forms could be demonstrated. Neither do rugulate/scabrate intermediates exist, and scabrae never stand on striate or rugulate patterns. If scabrate ornamentation is to be connected with striate, then the series necessarily runs via psilate. Ontogenetically, the direction is from more or less psilate or indistinctly scabrate towards more prominently scabrate, without any striate phase inserted (chapter 6.15). This leads to the conclusion that scabrate ornamentation is derived from psilate ornamentation, and that it developed only after the full establishment of adult psilate pollen. If it originated from some ontogenetic stage of striate pollen, one would expect to find striate/scabrate intermediates. When the continuous series from striate to scabrate is considered, the second part (psilate—scabrate) may be looked upon as the reversed version of the first part (striate—psilate) with respect to prominence of the projecting elements on the tectum.

The nature of the factor that induced the development from psilate towards scabrate can only be guessed at. In the foregoing section it is argued that psilate ornamentation was selected for by an autogamous pollination mechanism, and that the absence of any projecting tectum elements does not affect the normal transfer by insects too much. It is speculated here that scabrate ornamentation in *Dimocarpus* reflects the restoration of a sculptured tectum and the optimum conditions for transfer by the usual pollinators.

The geographical distribution of psilate and scabrate ornamentation confirms the scenario just outlined. Psilate pollen is found connected with striate pollen in several regions in the area of *D. longan* subsp. *malesianus,* striate—psilate forming a broad cline (chapter 6.4). On the contrary, psilate/scabrate intermediates occur only in Borneo. Scabrate and striate do not merge, not even in places where they coexist (northeastern Borneo and Basilan). In this view Borneo emerges as the centre of origin of scabrate *Dimocarpus* pollen. According to Leenhouts (1971) Borneo indeed seems to be the youngest centre in the area of *Dimocarpus*. It is the region where *D. longan* is most polymorphic.

Scabrae isodiametric—scabrae oblong

This series regards the shape of the scabrae. However, the order aspect is relevant too, since oblong shape of the elements coincides with subparallel arrangement. Typical scabrate pollen with oblong scabrae (plate 20: 1–4) is known only from Bukit Mentagai in NW Borneo, whereas intermediates come from the whole distribution of scabrate ornamentation. It is considered as the most derived scabrate form, being the last terminal addition (Gould, 1977) to the series psilate—scabrate.

No reasonable suggestion can be made as to the cause of the development towards oblong scabrae and the origin of the orderly pattern of finely striate patches as shown by the Bukit Mentagai samples.

Evolutionary status of some other features

Substriation

The muri in striate tecta are usually from 0.2 to 0.4 µm wide, and have an even surface. However, sometimes they show a fine, more or less distinct lengthwise substriation that consists of 0.1 to 0.2 µm wide 'submuri'. This was found in a few samples of *Dimocarpus dentatus, D. fumatus* subsp. *fumatus* and *Litchi chinensis* subsp. *javensis* (chapters 6.4 and 6.5). Remarkably the ornamentation in these samples is shallow to indistinct and usually irregular too. These aspects remind strongly of the ornamentation found in immature Nephelieae grains (see chapter 6.15).

Two alternative explanations can be put forward. Female material may have been used (see chapter 6.14). If not, it might be interpreted as another example of paedomorphic ornamentation, the substriation being a retained juvenile state.

Tendency to reticulate ornamentation

Some *Alectryon* species occasionally show grains with bundles of two or three muri enclosing isodiametric to oblong lumina (chapter 6.2, remark 6). Such grains occur in striate, striate-rugulate and rugulate samples. The pattern gives them a reticulate aspect, which is indistinguishable from genuine reticulate ornamentation if observed with LM. It is regarded as a deviation within *Alectryon*, but it is worthwhile to remember it in explaining the reticulate pollen of *Pometia* (see *Pometia* pollen).

Relatively thin mesocolpium margins

Several Nephelieae genera show considerable differences in exine thickness between the centres and the margins of the mesocolpia. This results from a strongly decreasing tectum, columellate layer or nexine, or from a combination of these features. *Smelophyllum* has a strongly declining columellate layer. Some genera, such as *Alectryon, Nephelium, Pappea* and *Stadmania,* show infrageneric variation.

In chapter 7.1 it is suggested that thickness variation within a mesocolpium may relate to the harmomegathic functioning of a grain. Relatively thin mesocolpium margins particularly promote the colporate type of harmomegathy. Indeed, parasyncolporate pollen shows much less variation as to exine thickness within a mesocolpium (see also van der Ham, 1977b; van der Ham & van Heuven, 1989). In *Alectryon* pollen the length of the peripheral columellae is correlated with aperture type. Colporate Nephelieae pollen is considered to be derived from parasyncolporate pollen, and on account of the functional relationship between a colporate apertural system and relatively thin mesocolpium margins, the latter feature is regarded as derived too.

Irregularly delimited endexine

An irregularly delimited endexine occurs in several *Alectryon* and *Podonephelium* species (chapter 6.2: Apertural system and nexine morphology; chapter 6.9). In *Alectryon* an irregular endexine/foot layer boundary is usually shown by colporate pollen, whereas it is more regular in parasyncolporate pollen (table 4). In view of this relation an irregular boundary is considered derived. In the Nephelieae it has a restricted occurrence. In the related tribes Cupanieae and Schleichereae it has never been found. Muller (1985) observed highly irregular boundaries in an advanced section of *Harpullia* (tribe Harpullieae).

Cubilia pollen

On account of its scabrate ornamentation van den Berg (1978) regarded *Cubilia* pollen as probably unique in the Nephelieae. Now, scabrate ornamentation is known from *Dimocarpus* too, but in spite of this, *Cubilia* pollen remains isolated within the tribe. The combination of a scabrate tectum, thin mesocolpial nexine and small grain size is not found elsewhere, neither in the Nephelieae nor in other Sapindaceae, and intermediates between *Cubilia* pollen and other pollen types could not be detected.

Scabrate ornamentation is rare within the Sapindaceae. Within the subfamily Sapindoïdeae it occurs only in *Cubilia* and *Dimocarpus,* and in *Jagera* (tribe Cupanieae), in the latter genus together with shallowly to indistinctly rugulate and psilate ornamentation (fig. 14). In the subfamily Dodonaeoïdeae it is commoner, though very heterogeneous and connected with several echinate types. In *Harpullia* (tribe Harpullieae) it is restricted to the advanced pollen types (Muller, 1985). Probably, scabrate ornamentation has to be considered as an autapomorphy in most Sapindaceae genera.

A thin mesocolpial nexine was occasionally observed in pollen of *Dimocarpus* and *Stadmania.* In pollen of *Alectryon* and *Podonephelium* it is a constant feature of most species, but the nexine substructure is usually wholly different from that of *Cubilia* pollen.

Small-sized grains occur occasionally in samples of other Nephelieae genera, but on average *Cubilia* pollen is probably the smallest in the Sapindaceae. Van den Berg (1978) mentioned *Cubilia* as most primitive with respect to grain size among the four

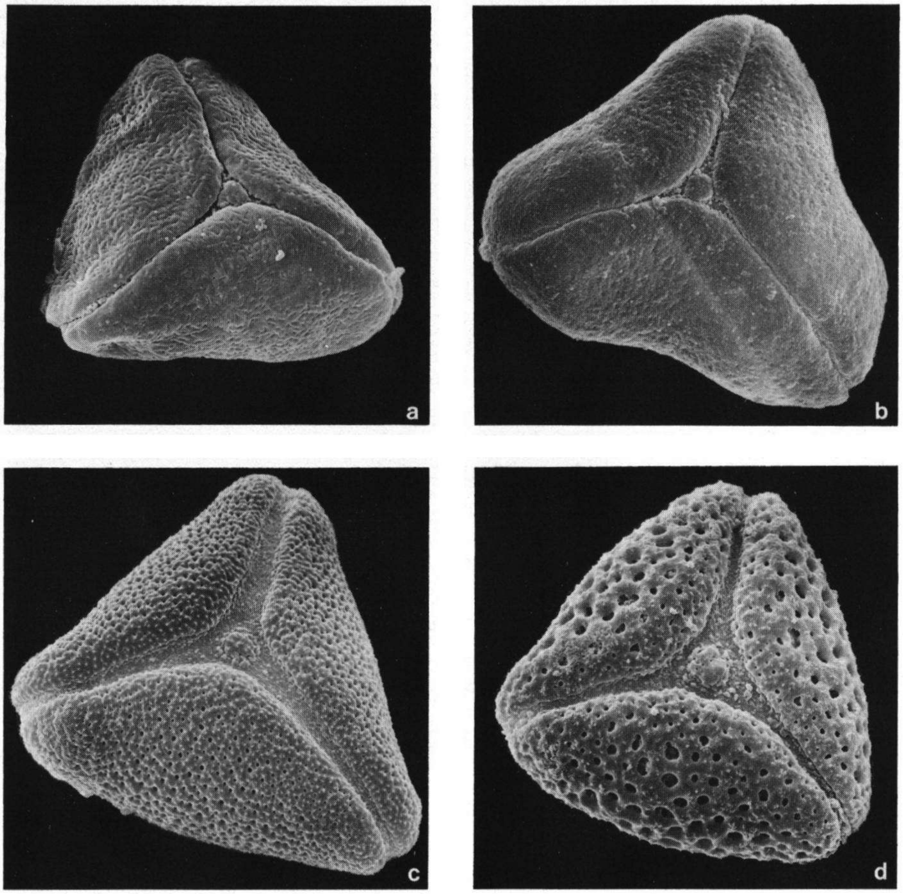

Fig. 14. *Jagera*, tribe Cupanieae. a: *J. discolor* S. Reyn., shallowly rugulate ornamentation, x 2500; b: *J. discolor*, psilate ornamentation, x 2500; c: *J. javanica* (Blume) Kalkman subsp. *javanica*, scabrate ornamentation with small perforations, x 2000; d: *J. javanica* subsp. *australiana* Leenh., scabrate ornamentation with large perforations, x 2000. Material: a: *NGF 21918* (L), New Britain; b: *Hartley 10765* (L), New Guinea; c: *Brass 3587* (L), New Guinea; d: *Gray 1455* (L), Australia.

Nephelieae genera studied (*Cubilia, Litchi, Otonephelium* and *Pometia*). However, his evolutionary trend of "increasing size" cannot be accepted as a general one.

Paedomorphic features

All aberrant character states in *Cubilia* pollen might be explained by the assumption of paedomorphosis (see Ornamentation: Striate—psilate). Mature *Cubilia* grains are only slightly larger than immature ones (chapter 6.15). Moreover, they are similarly sized to immature grains of several other Nephelieae that do show large size differences, for instance those of *Dimocarpus* (compare plate 41: 1 with 41: 3, 5).

Just as all immature Nephelieae grains *Cubilia* grains have a thin mesocolpial nexine, which may be partly caused by the lack of an endexine. The apertural endexine in *Cubilia* pollen is more or less normally developed.

Scabrate ornamentation can be associated with paedomorphosis too. In *Dimocarpus* pollen it is supposed to have originated from paedomorphic psilate ornamentation (see Ornamentation: Psilate—scabrate). Also in *Jagera* it occurs together with psilate ornamentation that may be looked upon as paedomorphic (fig. 14). Psilate pollen was not found in *Cubilia,* though in the Philippines the scabrae are clearly less prominent than in Celebes and Borneo.

Paedomorphosis is suggested in Nephelieae pollen for several ornamental features, including a psilate tectum and substriation. The scabrate ornamentation in *Dimocarpus* pollen is interpreted as an autapomorphy and an indirect result of paedomorphosis. This may hold in *Cubilia* pollen too. In addition, as suggested above, *Cubilia* pollen also shows nonornamental paedomorphic features (small size, thin mesocolpial nexine). Thus it would display a mixture of apomorphic and paedomorphic features. McNamara (1989) stated this to be a common phenomenon.

Origin of the *Cubilia* pollen type

It seems attractive to derive *Cubilia* pollen from scabrate *Dimocarpus* pollen through paedomorphosis of nonornamental features. However, the immature stages of *Cubilia* and *Dimocarpus* pollen differ considerably (compare plate 41: 1 with 41: 6). Also the mature scabrate patterns are only superficially alike, and small grain size and a thin mesocolpial nexine do not occur in mature scabrate *Dimocarpus* pollen. Actually, immature stages of pollen of any other Nephelieae genus than *Dimocarpus* may serve as a starting-point. Therefore the descent of *Cubilia* pollen is thought independent from that of scabrate *Dimocarpus* pollen. A probable origin of the lineage cannot be given as yet, though there is no reason to presume a (para)syncolporate origin. Macromorphology does not provide a decisive answer either. The position of *Cubilia* is somewhat uncertain according to Leenhouts (1978), but the genus seems distinctly to belong in the alliance of *Dimocarpus, Litchi, Otonephelium* and *Pometia.*

The aberrant morphology of *Cubilia* pollen cannot be judged apart from the flower morphology, which is quite deviating too, and certainly derived. The five stamens with their stiff broadly band-shaped filaments and small introrse thecae are particularly peculiar. In chapter 7.1 (see The colporate harmomegathic type: *The role of the nonapertural exine*) it is suggested that other insects than social bees are involved in pollination. Possibly, flower structure and pollen morphology evolved in a close relationship in the ancestors of *Cubilia,* both responding to a change in pollination. Determination of the pollination mode could clarify much of the intriguingly aberrant flower and pollen morphology of *Cubilia.*

Pometia pollen

Pometia pollen is morphologically fairly isolated, within the Nephelieae as well as within the whole family (chapters 6.1, 6.10; see also Muller & Leenhouts, 1976 and van den Berg, 1978). Its apertural system, including short colpate ectoapertures and tubular endoapertures surrounded by a system of lamellae, has not been observed in any other sapindaceous taxon[4]. Yet, the genus *Pometia* is a truly sapindaceous genus, and it seems to be rightly placed in the Nephelieae. Leenhouts (1978) considered it especially related to *Dimocarpus*. The pollen of *Pometia* is certainly advanced, having complex specialised apertures, a strongly reduced mesocolpial endexine, an aberrant intine structure, and a unique harmomegathic system. The strong macromorphological relationship of *Pometia* with the Nephelieae challenges pollen morphology to connect the *Pometia* pollen type with a pollen type occurring in some related genus or tribe.

Origin of the *Pometia* pollen type

Muller & Leenhouts (1976) considered that a major pollen-morphological gap exists between *Pometia* and the other Nephelieae. Van den Berg (1978) stressed that no transitional types were found. – These authors did not know the parasyncolporate type of *Alectryon*, but probably it would not have changed their opinion. – Indeed, not a trace of *Pometia* apertures can be demonstrated in the other genera. Only pollen of *Cardiospermum* (tribe Paullinieae) is reminiscent of *Pometia* pollen. Both are rather large, triangular and have short ectoapertures and a reticulate ornamentation, often with duplicolumellate muri (compare plates 31 and 60: 9–14 with fig. 15). However, instead of a lamellate system a much less elaborate, granular covering surrounds the endoapertures (Muller & Leenhouts, 1976, plate 11: E), and the mesocolpial endexine is well developed in *Cardiospermum*. Pollen of *Cardiospermum* is probably highly derived within the Paullinieae, as is *Pometia* pollen within the Nephelieae. Macromorphologically, the two genera have little in common, which hampers connecting their pollen types. Yet, *Cardiospermum* pollen offered the clue to a possible derivation of *Pometia* pollen. It has typical short demicolpi on the proximal (Huynh, 1968) grain side, which makes grains distinctly heteropolar (compare fig. 15a with 15b). Erdtman (1952) noted: "one face provided with markings suggestive of a parasyncolpate (demicolpate) apertural status." Muller & Schuller (1989) described the proximal side as syncolpate with narrow apertural slits. A LM image indeed shows a syncolpate pattern (fig. 15c). However, closer inspection of this 'syncolpus', using LO-analysis, reveals such a structure to be solid instead of slit-like. SEM photographs show only small-meshed continuous tectum zones. Just a small triangular pit is left at the very pole (fig. 15a, 15c). It is hypothesised that the 'syncolpate' proximal structure in *Cardiospermum* pollen is a derivative of the syncolporate apertural system found in many other Sapindaceae (see Apertural system). The solid strips, which connect the tectum with the nexine, can be interpreted as coalesced mesocolpium margins. This also explains the small-meshed ornamentation over the strips: in Sapindaceae pollen margins of mesocolpia have a more closed

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[4] Short colpate ectoapertures were also observed in *Dimocarpus* (chapter 6.4, remark 1), but never in association with tubular/lamellate endoapertural structures.

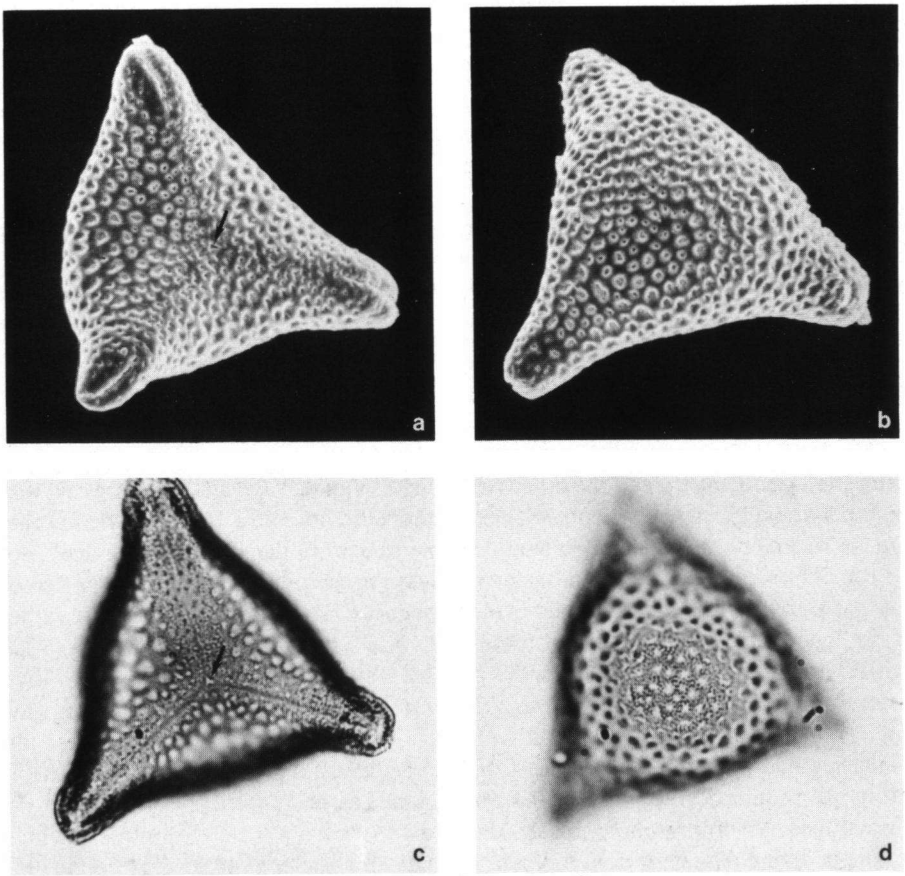

Fig. 15. *Cardiospermum halicacabum* L., tribe Paullinieae. a: proximal side of a grain showing demicolpi, fine-meshed 'syncolpate' pattern and small triangular pit at pole (arrow), × 1200; b: distal side showing homogeneous reticulate ornamentation, × 1200; c: proximal side showing triangular polar pit (arrow) and solid strips that underly the fine-meshed ornamentation shown in a, × 1000; d: distal side showing duplicolumellate muri, × 1000. Material: *Enriquez 24* (L), Philippines (not *Leandri 621* from Madagascar as mentioned in Muller & Schuller, 1989); prepared and photographed for Muller & Leenhouts (1976) and Muller & Schuller (1989).

tectum than the centres. The oldest fossil syncolporate Sapindaceae pollen is isopolar or subisopolar. It has to be assumed that the distal side of *Cardiospermum* pollen resulted from complete reduction of the distal ancestral syncolpus. The subisopolar *Cupanieidites acuminatus* from the Upper Cretaceous (Santonian to Maastrichtian) of Gabon (Boltenhagen, 1967, 1980) comes close to the hypothesised syncolporate ancestral type of *Cardiospermum* pollen. Both show the typical acuminate endoapertural areas, reticulate ornamentation, and the same size range. Boltenhagen (1967) already acknowledged this resemblance.

So much for *Cardiospermum*. What about *Pometia* pollen? Fine-meshed ornamentation is always present round the short colpi, but occasionally small lumina were also observed between the colpus ends and the poles (plate 31: 1, 2), though they are not as conspicuous as in *Cardiospermum* pollen and not supported by solid strips. As with *Cardiospermum* this feature may indicate that *Pometia* pollen was derived from a syncolporate pollen type. Such a type does not occur in extant Nephelieae, but it is common in the Cupanieae, with which the Nephelieae are probably sharing a common ancestor. Fine-meshed tectum zones are probably insignificant in the peristatic harmomegathy of *Pometia* pollen (chapter 7.1), and they have no obvious other function. Therefore they are looked upon as occasional remains, not as a novelty. The distal side of *Cardiospermum* pollen indicates that total absence of a syncolporate structure (the usual condition in *Pometia* pollen) may be the eventual result.

A syncolporate apertural system is usually associated with rugulate ornamentation. The reticulate tectum of *Pometia* pollen can be easily derived from such a pattern. Rugulate ornamentation may obtain a reticulate aspect by the presence of large lumina (compare fig. 16a with 16b). Then, possibly through paedomorphosis, the superficial pattern of muri may fail to appear, which results in a reticulate tectum (fig. 16c). Enlargement of the perforations may have happened also after reduction of the rugulate ornamentation (see fig. 14), since *Pometia* pollen occasionally shows a microreticulate tectum. Another possibility is to derive reticulate ornamentation from a striate pattern, which is usually present in colporate pollen (see Evolutionary status of some other features). However, this is a less probable option if the brevicolporate apertural system of *Pometia* pollen evolved from a syncolporate condition.

The opinion that *Pometia* pollen originated from a syncolporate pollen type contrasts with the view of Muller & Leenhouts (1976), who thought it was derived from the basic colporate Sapindaceae type.

It has been tried to find more clues in immature stages of *Pometia* pollen, but no additional evidence showed up: the youngest grains did not appear essentially different from mature ones (chapter 6.15). With respect to the apertural system this demonstrates, if the above hypothesis is true, the condensation principle of Gould (see Ornamentation: Rugulate—striate), the ancestral states being completely deleted (at least in the acetolysis-resistant stages).

Although the available literature of fossil *Pometia* pollen (referred to in chapter 1) does not mention or show differences between recent and fossil material, it may be worthwhile to reanalyse the fossil record. Features such as fine-meshed tectum zones might have been overlooked.

The *Pometia* pollen type did not appear until the Late Miocene, whereas the earliest records of syncolporate Sapindaceae pollen date from the Late Cretaceous. Because both types are well recognisable these data represent circumstantial evidence for the advanced status of the *Pometia* pollen features in comparison with the syncolporate condition. Unfortunately too little is known of fossil colporate Sapindaceae pollen (see Apertural system: Fossil evidence).

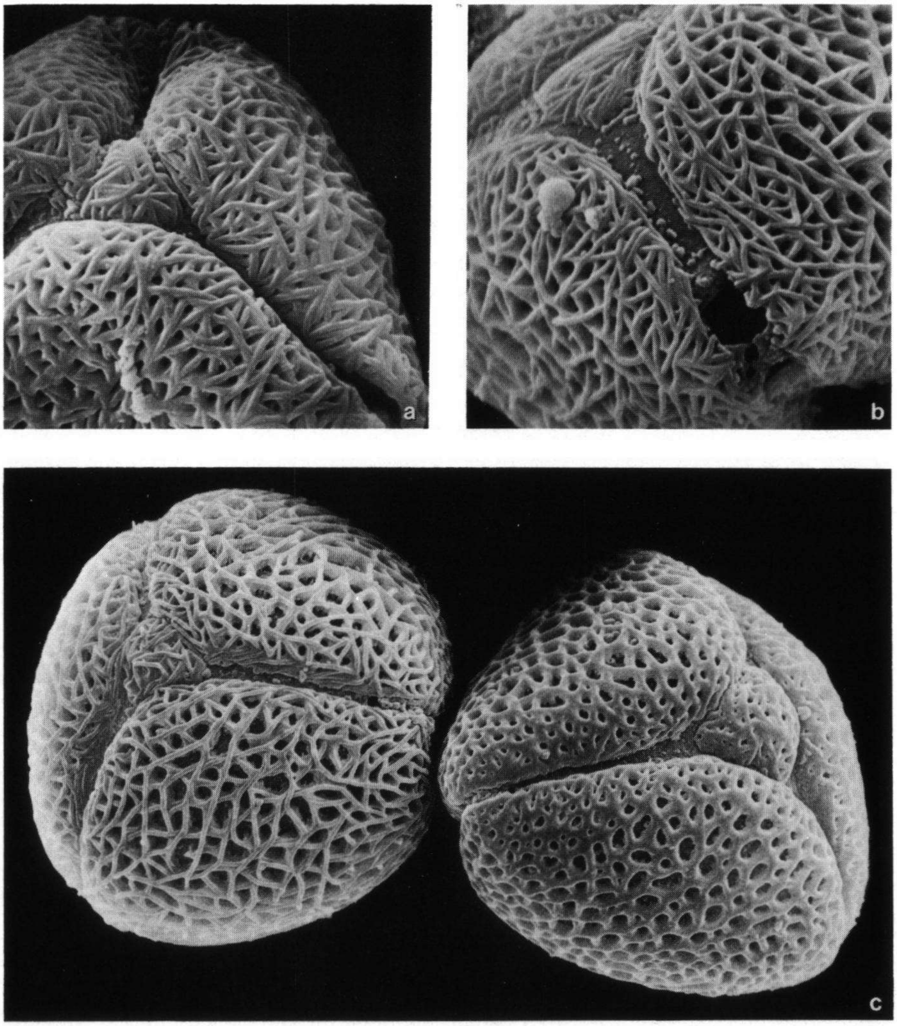

Fig. 16. *Arytera foveolata* F. Muell., tribe Cupanieae. a: rugulate ornamentation, × 3750; b: rugulate ornamentation with large lumina, × 3500; c: left-hand grain with rugulate ornamentation with large lumina, right-hand grain with reticulate ornamentation, × 3000. Material: a, b: *Lam 7631* (L), Australia (prepared and photographed for van der Ham, 1977a); c: *Williams s.n.* (BRI), Australia.

Whether derived from a colporate or from a syncolporate ancestral type, the rearrangement of the harmomegathic system probably involves a short and critical period of morphological reconstruction (see also Muller 1981b, 1984). This may account for the 'sudden' appearance of the fully elaborated *Pometia* pollen type in the fossil record. It would be an illustration of the punctuated equilibria model of Eldredge & Gould (1972): periods of stasis alternate with periods of rapid change.

9. POLLEN MORPHOLOGY AND THE TAXONOMY OF THE NEPHELIEAE

Pollen of most Nephelieae genera is hardly different from that of many genera belonging to other sapindaceous tribes. Only pollen of *Cubilia* and *Pometia* are sufficiently distinguishable, even from non-Sapindaceae. If SEM can be applied scabrate *Dimocarpus* pollen is identifiable too. If TEM data are available *Alectryon* and *Podonephelium* pollen can mostly be distinguished on account of the characteristic nexine and intine. Parasyncolporate grains may then be attributed to *Alectryon*. Obviously, composing an elaborate key to Nephelieae pollen is unfeasible.

A pollen-morphological subdivision of the Nephelieae

As will be clear, only a rough pollen-morphological subdivision of the Nephelieae is possible. Four pollen types are distinguished:

— the *Litchi* pollen type
— the *Alectryon* pollen type
— the *Cubilia* pollen type
— the *Pometia* pollen type

The *Litchi* type includes the pollen of *Dimocarpus, Litchi, Nephelium, Otonephelium, Pappea, Smelophyllum, Stadmania* and *Xerospermum*. Its apertural system is colporate. Generally, it has striate ornamentation, but psilate forms and striate/psilate intermediates occur commonly. Rugulate and scabrate forms are rarer. The nexine is relatively thick (usually ≥ tectum). The endexine is thin and regularly delimited. The mesocolpial intine is mostly homogeneous.

The *Alectryon* type includes the pollen of *Alectryon* and *Podonephelium*. Its apertural system is parasyncolporate or colporate, or it shows an intermediate condition. The ornamentation is striate to rugulate; psilate and scabrate forms do not occur. The nexine is relatively thin (nearly always < tectum). The endexine is thick and often irregularly delimited. The mesocolpial intine contains an outer sublayer with many electron-opaque inclusions.

The *Cubilia* type includes only the pollen of *Cubilia*. Its apertural system is colporate. The ornamentation is scabrate. The nexine is thin (< tectum). The mesocolpial endexine is hardly or not detectable. The intine was not studied. Grain size is the smallest in the Nephelieae.

The *Pometia* type includes only the pollen of *Pometia*. Its apertural system is brevicolporate and shows tubular/lamellate endoapertural areas. The ornamentation is (micro)reticulate. The nexine is thick (thicker to slightly thinner than the tectum). A mesocolpial endexine is hardly or not detectable. The mesocolpial intine is almost completely filled with electron-opaque inclusions. Grain size is the largest in the Nephelieae.

Van den Berg (1978), studying pollen of *Cubilia, Litchi, Otonephelium* and *Pometia,* distinguished three pollen types: the *Cubilia* type, the *Litchi* type and the *Pometia* type. Pollen of *Nephelium* and *Xerospermum* was provisionally examined and joined to the *Litchi* type. Van den Berg's types agree with those of the same name in the present study, though the *Litchi* type herein accommodates more genera.

The present pollen-morphological subdivision does not agree with the infratribal arrangement of the genera in the *Dimocarpus* and *Pappea* group (Radlkofer, 1931; Muller & Leenhouts, 1976). *Cubilia* and *Pometia* of the *Dimocarpus* group have considerably deviating pollen, and pollen of *Pappea, Smelophyllum* and *Stadmania* of the *Pappea* group differs distinctly from that of *Alectryon* and *Podonephelium*, but resembles that of *Dimocarpus, Litchi, Nephelium, Otonephelium* and *Xerospermum* much.

Further subdivision of the *Litchi* type seems possible considering the wide range of ornamentation forms. However, ornamentation often varies similarly within several genera, for example from striate to psilate in *Dimocarpus, Nephelium, Stadmania* and *Xerospermum*. Consequently a subtype based on striate or psilate ornamentation would be heterogeneous and unnatural from a taxonomic point of view. Moreover, the numerous transitional forms would greatly reduce the value of subdividing. Within the *Litchi* type only scabrate ornamentation may have taxonomic significance (see Pollen morphology and infrageneric taxonomy: *Dimocarpus*).

The present study does not yield pollen features that indicate special resemblances between certain genera of the *Litchi* type. Closer examination of the Cupanieae and Schleichereae pollen will probably reveal genera with similar pollen. Here, the difference between the macromorphological and pollen-morphological classification is evident: on the one hand pollen morphology is not or hardly able to exclude genera of other tribes, on the other it isolates genera such as *Cubilia* and *Pometia*. The main cause of this discrepancy is thought to be the 'simpleness' of Nephelieae pollen. Relatively few characters are available. Most of them are functionally integrated, and adapt as a unit to new environments. Such a functional integration means that pollen types can change considerably, almost without leaving behind indications of the ancestral state, neither in the ontogeny (condensation principle of Gould) nor in the mature form. Then it can be difficult to recognise parallel and convergent developments, especially if more general or simpler forms evolved, such as colporate from parasyncolporate and psilate from striate in the Nephelieae. In such cases macromorphological evidence is indispensable to unravel the nature of the similarity.

Alectryon and *Podonephelium* pollen form a coherent group. Species with a more or less regularly delimited endexine, which is usually associated with a parasyncolporate apertural system, resemble parasyncolporate Cupanieae. Muller & Leenhouts (1976) regarded *Alectryon* and *Podonephelium* closely allied, but an equally close relationship was found between *Alectryon* and *Stadmania*. Apertural features permit further subdivision of the *Alectryon* pollen type (see below).

Pollen morphology and infrageneric taxonomy

Alectryon

Two main aperture types occur in *Alectryon*: colporate (A) and parasyncolporate (B). In addition two intermediate types (A* and B*) are distinguished. A classification of *Alectryon* species according to the apertural system is provided in table 3.

The infrageneric taxonomy of *Alectryon* is still unsatisfactory. Radlkofer (1933) divided the genus into six sections: *Synalectryon, Plagialectryon, Platyalectryon, Spanoghea, Eualectryon* and *Mahoe*. P.W. Leenhouts (ms.) proposed two subgenera, *Alectryon* and *Synalectryon,* comprising seven informal groups (I to VII), six of which (I, II, IV, V, VI and VIII respectively) agree in the main with Radlkofer's sections. He considered the groups mostly well recognisable, but a clear demarcation between at least some of them would be impossible (particularly group V and VI were mentioned). G.K. Linney, working on fruit and seed anatomy in *Alectryon,* suggested a subdivision into three subgenera, with the acknowledgement that the genus *Podonephelium* may represent another one (written comm., 1987, 1988). Leenhouts (1988) formally described the subgenera *Alectryon* and *Synalectryon,* but expressed his preference for a final subdivision into three or four subgenera, alluding to Linney's work. Table 17 gives the infrageneric classification as outlined by Leenhouts (ms.). Later, Reynolds (1987) described *A. ramiflorus* and reduced the genus *Heterodendrum* to *Alectryon,* as *A. ramiflorus* proved to be transitional. However, she did not fit the new Alectryons into the infrageneric taxonomy. Because of the lack of petals, and the presence of a papillose sarcotesta on the seed basis they should be placed in the subgenus *Alectryon.* Whether they can be added to (one of) the existing groups or form a separate group is not clear. They are separately listed in table 17. *Alectryon coriaceus* and *A. semicinereus* were demonstrated to be distinct after all (Reynolds, 1982, 1987). Linney (1988) combined *A. macrococcus* and *A. mahoe.*

Table 17 shows that in most groups aperture morphology is fairly constant. In group I and III type B dominates, whereas in group IV, V and VI, and in the 'unplaced' species type A prevails. In group II and VII type A and type B are about equally important. Leenhouts (ms.) considered group II to represent a link between group I and the other five groups. Pollen-morphologically, group II takes an intermediate position between I plus III and the rest. Group VII is aberrant in subgenus *Alectryon,* being largely provided with type B. Pollen suggests a direct connection with subgenus *Synalectryon* plus group III. Linney (in prep.) reached the same conclusion on the basis of fruit and seed anatomy.

The reduction of *Heterodendrum* to *Alectryon* is pollen-morphologically fully justified. The inclusion of *Podonephelium* suggested by Linney is also supported by pollen features. Pollen of *Podonephelium* as well as the former *Heterodendrum* species can be easily connected with that of group IV, V or VI.

Ornamentation in *Alectryon* pollen corresponds more or less to the aperture type (table 3). Due to its greater variation it is less helpful in characterising taxa.

Cubilia

Variation is present in both the pollen morphology (chapter 6.3) and the macromorphology of the only species *C. cubili* (Leenhouts, 1978). The clinal variation of the prominence of the scabrate ornamentation from the Philippines, via Celebes to Borneo matches the clines described for the shape of the leaflet apex and the occur-

Table 17. Taxonomic distribution of aperture types in *Alectryon*.

taxonomy			pollen morphology			
			apertural system			
Leenhouts (1988)	Leenhouts (ms.) Linney (1988) Reynolds (1982, 1987)					
Subgenus *Synalectryon*	I	*affinis*				B
		connatus		[A*]	[B*]	B
		kangeanensis				B
	II	*coriaceus*	A	[A*]	[B*]	
		semicinereus	A	A*	B*	[B]
		subcinereus			[B*]	B
Subgenus *Alectryon*	III	*fuscus*			(B*)	B
		myrmecophilus				B
	IV	*forsythii*	A	[A*]		
		subdentatus	A	(A*)	(B*)	
	V	*cardiocarpus*	A			
		ferrugineus	A	(A*)		
		glaber	A			
		kimberleyanus	A			
		repandodentatus	A			
		tomentosus	A			
	VI	*carinatus*	A			
		excelsus	A	A*	B*	
		grandis	pollen not available			
		reticulatus	A			B
		unilobatus	A	A*	B*	
	VII	*grandifolius*	A	(A*)		
		macrococcus				B
		samoënsis			[B*]	B
	not placed	*diversifolius*	A			
		oleifolius	A	[A*]		
		pubescens	A	[A*]		
		ramiflorus	A			
		tropicus	pollen not available			

A = colporate; A* = intermediately colporate; B* = intermediately parasyncolporate; B = parasyncolporate; ( ) = uncommon; [ ] = rare. The 'unplaced' species *Alectryon diversifolius, A. oleifolius, A. pubescens,* and *A. tropicus* constitute the former genus *Heterodendrum*.

rence of glands on the lower side of the leaflets. The cline for leaflet number is from Celebes: 5–6(–7), via the Philippines: 3–5(–6) to Borneo: 3–5. Neither macromorphology nor pollen morphology permits infrageneric subdivision.

Dimocarpus

Ornamentation is the obvious character to use in a pollen-morphological classification of *Dimocarpus*. Three major types are distinguished (chapter 6.4): striate, psilate and scabrate. The macromorphological relationships are not very clear (Leenhouts, 1971, 1974). Depending on the character used several divisions are possible, but none seems natural. The main macromorphological criterion is provided by the development of the corolla, which is well developed in *D. australianus, D. dentatus, D. foveolatus, D. gardneri, D. leichhardtii, D. longan* subsp. *malesianus* and *Dimocarpus* spec., and slightly reduced to almost completely suppressed in *D. fumatus* and *D. longan* subsp. *longan* (Leenhouts, 1971). The group with well developed petals is pollen-morphologically heterogeneous (striate, psilate and scabrate occur). It contains all species with psilate pollen, but these species do not make up a distinct macromorphological group. Groups on the strength of vegetative characters do not coincide either with ornamentation types.

Reynolds (1982) stated *D. leichhardtii* to be close to *D. australianus* and *D. longan*. It might even be a variant of the latter, possibly a cultivated form. Pollen morphology supports this option, since both *D. leichhardtii* and cultivated *D. longan* yielded deviating pollen (chapter 6.4).

A notable case of variation in ornamentation is found in *D. longan* subsp. *malesianus*. It shows striate, psilate, scabrate and many intermediate forms within a single variety: var. *malesianus*. The other variety, var. *echinatus*, has only scabrate pollen. Macromorphologically, var. *malesianus* is variable too (Leenhouts, 1971). This mainly concerns the fruit and vegetative characters; the flowers are rather uniform. The greatest variation is found in Borneo, where 30 to 40 races might be distinguished. In contrast, the situation is fairly simple in continental Asia, the Malay Peninsula, Sumatra and the Philippines. Due to the lack of fruits the material from Celebes and the Moluccas remained unclassified. Leenhouts' data are summarised in table 18.

Table 18. Distribution of the races of *Dimocarpus longan* subsp. *malesianus* var. *malesianus* according to Leenhouts (1971). The numerous unnamed local races from Borneo are not included.

race	continental Asia	Malay Peninsula	Sumatra	Borneo	Philippines
'*gracilis*'	+	+		+	+
'*malaiensis*'		+	+	+	
"third form"		+	+		
'*cinerea*'				+	+

An attempt has been made to attribute the various ornamentation types in the pollen of var. *malesianus* to these races. Initially, Leenhouts (ms.) recognised many small homogeneous units in var. *malesianus*. It appeared that scabrate pollen, as far as the parent plants could be identified[5] is restricted to three of such units, one from Malaya, one from Sumatra, and one from Borneo. Together these units represent the race 'malaiensis', which largely agrees with the former *Euphoria malaiensis*.[6] Unfortunately pollen of the "third form" (Malay Peninsula, Sumatra) is unavailable. The material designated as *'malaiensis'* (ms., not on the sheets) embraces only one collection with nonscabrate ornamentation (*SF 23885*: a somewhat strange striate/perforate pattern with very short muri). Thus, taxonomically the specimens with scabrate pollen seem to make up a fairly distinct group within var. *malesianus*. The distribution of scabrate ornamentation is disjunct now (fig. 7), but it may have been continuous, since Malaya, Sumatra and Borneo were joined by the Sunda Shelf during the Pleistocene ice ages.

The fruits of *'malaiensis'* are nearly smooth or sparsely covered with low (< 1 mm) warts. Remarkably, var. *echinatus* has similar scabrate pollen, but its fruits possess a dense cover of long (7.5–10 mm) flattened spines. Leenhouts (1971) assigned a varietal rank to it because of the for *Dimocarpus* rather unusual fruit. Pollen morphology indicates var. *echinatus* to be clearly related to the race *'malaiensis'* of var. *malesianus*. Var. *echinatus* is the only scabrate *Dimocarpus* taxon in the Philippines. Besides, it occurs in northern Borneo.

None of the other two ornamentation types in var. *malesianus* (striate and psilate) corresponds with a particular race. Both types occur together at least in *'gracilis'*.

Litchi

Pollen morphology does not provide a clue for subdividing *L. chinensis* into the three subspecies recognised by Leenhouts (1978). The basically striate ornamentation is variable, but the range is continuous. Subsp. *philippinensis* shows only regularly striate pollen, whereas subsp. *chinensis* and subsp. *javensis* show also various irregularly striate patterns (chapter 6.5). This might be due to cultivation. Subsp. *philippinensis* represents a wild form, but subsp. *chinensis* has been grown and shaped by man for many centuries, and subsp. *javensis* is probably only known as a cultivated tree (Leenhouts, 1978). In *Dimocarpus longan* deviating ornamentation was mainly found in cultivated or naturalised trees (chapter 6.4).

Nephelium

Ornamentation and columella length are the main variables in *Nephelium* pollen (chapter 6.6). However, splitting according to these two characters yields dissimilar groups (table 8). Leenhouts (1986) experienced the same with macromorphology: –

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5) The races of var. *malesianus* are primarily based on fruit characters, which are seldom available in polliniferous material. Yet, Leenhouts (ms.) succeeded to fit in most flowering specimens, among which are about half of those with scabrate pollen.

6) Scabrate *malesianus* pollen indeed includes that of the type of *Euphoria malaiensis* (*Griffith KD 999* from Malaya).

the leaf and fruit characters, on which he based the delimitation of the species, seem to be not correlated, and consequently, it appeared impossible to arrange the majority of the species into more or less coherent groups. At most the commonest, widest distributed, most variable species (*N. cuspidatum, N. lappaceum, N. ramboutan-ake*) would form a central group in the genus, to which some more species (*N. hamulatum, N. juglandifolium, N. reticulatum*) might be connected. Pollen-morphologically, the central group is also a unit. However, of the species that can be joined (see table 8) only *N. juglandifolium* is found among Leenhouts' additions.

Nephelium havilandii and *N. hypoleucum,* which have very similar pollen, are not grouped together by Leenhouts. *Nephelium subfalcatum* and *N. uncinatum* also have resembling pollen. For example, the remarkable endoaperture fillings are very alike (chapter 6.1, remark 1). Macromorphologically, the species are considered related too (Leenhouts, 1986).

Otonephelium

Otonephelium is a monotypic genus with only minor macromorphological variation (Radlkofer, 1932). As opposed to Radlkofer (1932) and Leenhouts (1978), who mention a corolla to be absent and completely reduced respectively, Brandis (1906, addenda) records minute early caducuous petals. The limited material available does not permit conclusions as to the pollen-morphological variation within the genus.

Ellis (in Sharma et al., 1977) transferred *Otonephelium* to *Lepisanthes* of the tribe Lepisantheae, without any discussion. According to Leenhouts (personal comm., 1988) *O. stipulaceum* is certainly not a *Lepisanthes.* It clearly belongs to the Nephelieae. Pollen morphology supports this opinion. *Otonephelium* pollen does not resemble that of *Lepisanthes.* Tectum architecture and endoaperture structure especially are different (compare with Muller, 1970, fig. 1).

Pappea

Exell (1966) denoted *Pappea* to contain apparently one very variable species. According to Palmer & Pitman (1972) two well known forms occur: that from tropical Africa and the northern and eastern parts of southern Africa, and that of Namibia, Botswana and certain southern parts of South Africa. The latter grows in a harsher, more arid climate. All studied specimens from southern South Africa appeared to possess pollen with a thick tectum in comparison with those from the other regions (chapter 6.8). Material from Botswana and Namibia was not available. In view of the origin of the various specimens the difference in tectum thickness may very well agree with the distinction between the arid and less arid form. A relatively thick tectum might have a functional significance in arid regions (chapter 7.1: The colporate harmomegathic type).

Podonephelium

The genus *Podonephelium* awaits a critical taxonomic revision. Pollen is rather uniform. Only minor differences occur, which do not permit subdivision. As a whole *Podonephelium* pollen can be easily connected with colporate *Alectryon* pollen.

Pometia

Jacobs (1962) distinguished two species within *Pometia,* and eight formae within one of them. Pollen of the two species shows only minor differences, and that of the formae can hardly be told apart (see also van den Berg, 1978).

Smelophyllum

The monotypic genus *Smelophyllum* does not seem to show a wide range of variation or particular forms. The same holds true for its pollen.

Stadmania

Two characters vary considerably in *Stadmania* pollen: ornamentation and columella length (chapter 6.12). However, this variation does not reflect the subdivision by Capuron (1969) into the two sections *Stadmania* and *Tricoccodendron.* Similar ornamentation forms and columella lenghts occur in both of them. Yet, within *S. oppositifolia,* the only species of section *Stadmania,* pollen-morphological differences correspond with macromorphology.

Exell (1966) distinguished two subspecies in continental Africa: the northern *oppositifolia* and the southern *rhodesica.* They show a notable geographical gap. Subsp. *rhodesica* might represent a more arid form. The material of Madagascar and the Mascarene Islands belongs to subsp. *oppositifolia.* It appeared that pollen of subsp. *rhodesica* usually has distinctly longer columellae in the centre of a mesocolpium than that of subsp. *oppositifolia.* Besides, the samples belonging to subsp. *rhodesica* share the occasional presence of partly demarcated apocolpia.

Xerospermum

Much variation exists within *Xerospermum* pollen regarding ornamentation: from striate to psilate (chapter 6.13). However, this variation concerns both species, though the pure psilate forms are restricted to *X. laevigatum.* In contrast, the two subspecies recognised by Leenhouts (1983) in *X. laevigatum* are pollen-morphologically fairly distinct. Subsp. *laevigatum* has striate to shallowly striate pollen, whereas that of subsp. *acuminatum* is indistinctly striate to psilate.

The few samples that show grains with partly demarcated apocolpia (chapter 6.13, remark 2) all belong to *X. laevigatum* (both subspecies).

Summary

Pollen morphology does not appear to be very effective in characterising the Nephelieae. Both *Cubilia* and *Pometia* have distinct pollen (*Cubilia* type and *Pometia* type), but the other ten genera have pollen (*Litchi* type and *Alectryon* type) that is mutually similar and/or resembles pollen of non-Nephelieae.

Instead of the *Dimocarpus* group and *Pappea* group (Muller & Leenhouts, 1976) pollen morphology suggests a subdivision into four groups (the four pollen types mentioned above), whereby *Cubilia* and *Pometia* are separated from the *Dimocarpus* group, and *Pappea, Smelophyllum* and *Stadmania* are added to it (table 19).

Table 19. Macromorphological and pollen-morphological subdivision of the Nephelieae.

macromorphology	Nephelieae genera	pollen morphology
Dimocarpus group	*Cubilia*	*Cubilia* pollen type
	Pometia	*Pometia* pollen type
	Dimocarpus, Litchi, Nephelium *Otonephelium, Xerospermum*	*Litchi* pollen type
Pappea group	*Pappea, Smelophyllum, Stadmania*	
	Alectryon, Podonephelium	*Alectryon* pollen type

Pollen of *Cubilia, Otonephelium, Podonephelium, Pometia* and *Smelophyllum* shows only minor variability, not allowing infrageneric subdivision. Within *Alectryon, Dimocarpus, Litchi, Nephelium, Pappea, Stadmania* and *Xerospermum* more or less large variation was determined in several characters:

- aperture type: *Alectryon*
- ornamentation: *Dimocarpus, Litchi, Nephelium, Stadmania, Xerospermum*
- columella length: *Nephelium, Stadmania*
- tectum thickness: *Pappea*

Aperture types in *Alectryon* indicate groups of related species, though variation sometimes occurs within species, or even samples. The other characters also permit infrageneric subdivision, but generally, the resulting groups do not reflect the existing taxonomy. They are more useful at the infraspecific level, for example within *Dimocarpus longan* subsp. *malesianus* or *Xerospermum laevigatum* subsp. *laevigatum*.

10. POLLEN MORPHOLOGY AND THE PHYLOGENY OF THE NEPHELIEAE

Except for *Alectryon* the Nephelieae genera are fairly constant in their apertural features, whereas they show much variation with respect to other characters, especially ornamentation. Several of them display similar ornamentation ranges, sometimes within species, or even samples. This supports the opinion of Muller & Leenhouts (1976) that hypotheses concerning pollen evolution in the Sapindaceae must be primarily based on apertural features.

Evidence from apertural features

In chapter 8 it is defended that within the subfamily Sapindoïdeae (para)syncolporate pollen (type B) is plesiomorphic and colporate pollen (type A) apomorphic.

The recent distribution of type A and type B in the tribe Cupanieae, combined with palaeo-ecological data and the stratigraphical and geographical distribution of the fossil B type suggests that within the Cupanieae the B type frequently developed into the A type under the influence of climatic factors. The A type of the Nephelieae, which tribe is closely related to the Cupanieae, is considered derived too. Two independent lineages from type B to type A seem to be present here: one existing in the *Alectryon* pollen type, and another, leading to the *Litchi* pollen type.

The *Alectryon* pollen type is regarded as the most primitive on account of the presence of type B in *Alectryon*. According to Muller & Leenhouts (1976) the closely related genus *Pappea*, which has A type pollen belonging to the *Litchi* pollen type, is macromorphologically more primitive than *Alectryon*. *Pappea* would be the most primitive genus of their *Pappea* group (table 19). They did not compare *Pappea* with the genera of their *Dimocarpus* group, which, except for *Cubilia* and *Pometia*, are included in the *Litchi* type.

In the *Litchi* type genera *Dimocarpus*, *Nephelium*, *Stadmania* and *Xerospermum*, the intermediate aperture type A* was sometimes found. This type is considered to indicate an ancestral parasyncolporate condition. It designates the pertinent genera as relatively primitive within the *Litchi* type. Macromorphologically, *Dimocarpus*, *Nephelium* and *Xerospermum* are regarded by Muller & Leenhouts (1976) as the most primitive within the *Dimocarpus* group (table 19). The relative level of *Stadmania* as to macromorphology was not discussed.

The genera included in the *Litchi* type have similar pollen, which is thought to have originated from a single ancestral B type. However, it cannot be completely excluded on pollen-morphological evidence alone that, just as in the tribe Cupanieae, type A evolved more than once.

The *Cubilia* type is suggested to have developed from an ancestral A type, which it may share with a part of the *Litchi* type. Leenhouts (1978) included the genus in his phylogenetic scheme of the *Dimocarpus* group as "a basal offshoot before *Dimocarpus*". Herewith he asserted that it is more related to the alliance of *Dimocarpus*, *Litchi*, *Otonephelium* and *Pometia* than to that of *Nephelium* and *Xerospermum*. Pollen does not show this relationship.

The *Pometia* pollen type originated from a B type rather than from an A type. Leenhouts (1978) derived *Pometia* from an A type ancestor.

Thus, according to pollen data at least three different lineages that started from a B type ancestor would exist within the Nephelieae. Pollen morphology does not shed light on whether these lineages form a monophyletic group, since not a single synapomorphy could be demonstrated for Nephelieae pollen. Macromorphological data will be needed for that.

Alectryon and *Podonephelium*

Assuming that aperture type A evolved from type B implies particular relationships within *Alectryon*. A type taxa may be considered more advanced than B type taxa. As a working basis the subdivision of Leenhouts (ms.) into seven groups is adopted (see table 17). Group I and III would be the most primitive, whereas group IV, V and that formed by the 'unplaced' species would be the most advanced. Group II, VI and VII are in between. Leenhouts (ms.) arranged the groups I to VII in a more or less phylogenetic sequence, group I being the most primitive of all. Group II would link group I to the more advanced groups III to VII. Pollen-morphologically, group II is intermediate too, its species *A. subcinereus*, *A. semicinereus* and *A. coriaceus* displaying a perfect transition from B pollen to A pollen. However, group III is pollen-morphologically less advanced than group II, and group VII, which is macromorphologically the most advanced, stands on about the same level as group II. On the strength of fruit and seed anatomy Linney (in prep.) postulated group III and VII to form a separate lineage directly connected with subgenus *Synalectryon*. Group IV, V and VI, and the 'unplaced' species would form the other lineage. This confirms the pollen-morphological data.

Podonephelium pollen might be added to that of group IV, V, and the 'unplaced' species, thus occupying an advanced position. Macromorphologically, *Podonephelium* seems somewhat more specialised than *Alectryon* (ms. P.W. Leenhouts).

Evidence from ornamental features

Ornamental features do not contribute much to understanding the phylogenetic relationships of the tribe Nephelieae and its constituent genera. Yet, they may be useful within genera or infrageneric taxa.

Rugulate versus striate ornamentation

The presence of rugulate or striate ornamentation more or less depends on aperture type (type B or type A), which is a functional relation (chapter 7.1). Type A is assumed to have originated more than once (see above), and consequently, the same may be said with regard to the associated striate ornamentation. That of the *Alectryon* pollen type is considered a parallel of that in the other Nephelieae. In these Nephelieae it is thought to have originated from a single ancestral striate type, but, just as with aperture type, parallel development may not be excluded completely.

Occasional rugulate ornamentation in striate samples/taxa is looked upon as an ancestral feature (chapter 8: Ornamentation). It occurs in *Dimocarpus, Nephelium, Otonephelium, Stadmania* and *Xerospermum*. These genera are therefore denoted as relatively primitive with respect to ornamentation. Remarkably, four of these genera (*Otonephelium* excluded) occasionally show the allegedly ancestral aperture type A*, though both features do not coincide in individual grains. At most they were found in the same sample (*Brynard & Pienaar 4253* of *Stadmania oppositifolia*).

Psilate ornamentation

Psilate ornamentation in the Nephelieae is found only in the *Litchi* pollen type. It is regarded as a paedomorphic trait that developed independently in several genera (chapter 8: Ornamentation). Within *Dimocarpus, Nephelium, Stadmania* and *Xerospermum,* species with psilate pollen can be called more advanced that those with striate pollen.

Four *Dimocarpus* species have psilate pollen. Three of them, *D. foveolatus, D. gardneri* and *Dimocarpus* spec., are taxonomically isolated or have vague connections with other species (Leenhouts, 1971). They exclusively have psilate pollen, and show very restricted distributions (see Geographical aspects). The fourth, *D. longan,* is widespread and shows striate, psilate and several other ornamentation forms (chapter 6.4). The psilate pollen occurs in a part of the macromorphologically highly variable *D. longan* subsp. *malesianus,* which makes this subspecies more advanced than subsp. *longan,* which possesses only striate pollen. Probably, the diversity within subsp. *malesianus* has a relatively recent origin, and psilate ornamentation may have arisen not until diversification took place.

In *Nephelium* psilate ornamentation is more limited. It is only found, together with indistinctly striate forms, in *N. compressum* and *N. daedaleum* (chapter 6.6). In contrast, these species are indicated as belonging to the most primitive group and a fairly primitive group of species respectively according to macromorphology (Leenhouts, 1986). The same holds true for columella length: the most primitive species, *N. compressum* and *N. havilandii,* have long columellae in the centre of a mesocolpium (considered advanced), whereas the highest evolved *N. maingayi* has relatively low central columellae.

In *Stadmania* the two species with psilate pollen, *S. acuminata* and *S. leandrii,* belong to the dioecious section *Tricoccodendron* (Capuron, 1969). Dioecy would be more advanced than monoecy in Sapindaceae (van Welzen, 1989). However, the species of this section do have petals, which is primitive in comparison with the apetalous condition in section Stadmania. This section is monoecious, and usually shows striate pollen.

In *Xerospermum* psilate pollen is restricted to *X. laevigatum* subsp. *acuminatum.* This subspecies shows another derived feature not occurring in subsp. *laevigatum*: in male flowers the disc is nearly always interrupted, in female flowers sometimes (Leenhouts, 1983). So, macromorphologically subsp. *acuminatum* is advanced too.

Scabrate ornamentation

Scabrate pollen is found in *Cubilia* and in a part of *Dimocarpus* longan subsp. *malesianus.* It is considered derived relative to striate and psilate pollen. In chapter 8 (*Cubilia* pollen) it has been argued that the scabrate ornamentation developed independently in both genera.

In *Cubilia* it corresponds with several other apomorphies, in the pollen as well as in the flower. In *Dimocarpus* scabrate pollen seems to characterise the race *'malaiensis'* of var. *malesianus* (chapter 9: *Dimocarpus*). Besides, it is present in both samples of var. *echinatus.* Like psilate ornamentation, scabrate patterns probably arose during the relatively recent diversification process within subsp. *malesianus.* Scabrate pollen is considered as a synapomorphy of the race *'malaiensis'* and var. *echinatus.* It designates them as a monophyletic group. Accordingly, var. *malesianus* would be paraphyletic. Synapomorphies in the macromorphology are not known. The unusual dense cover of long flattened spines on the fruits of var. *echinatus* forms an autapomorphy.

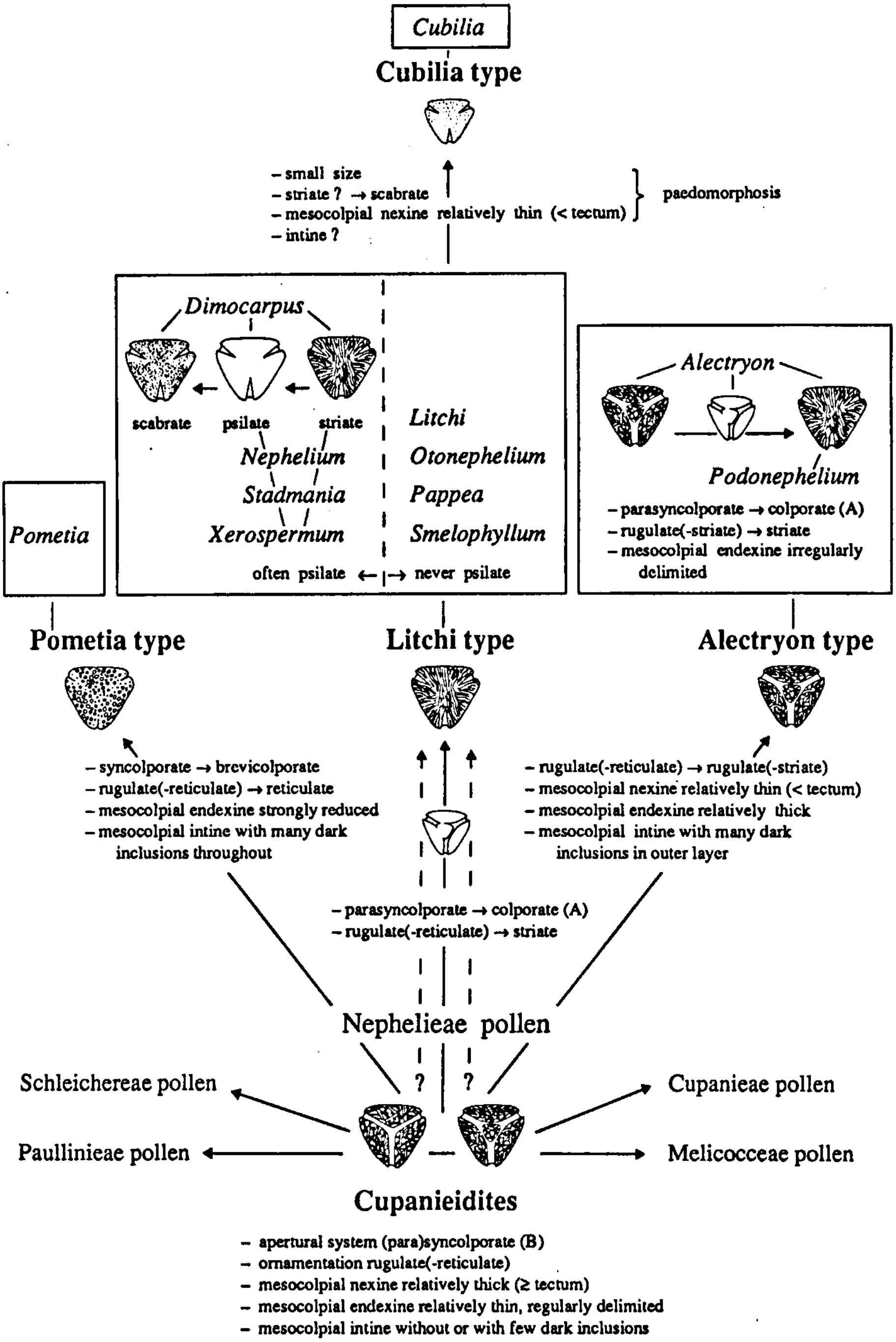


Fig. 17. Phylogenetic relationships of the pollen types in the Nephelieae.

Reticulate ornamentation

Reticulate ornamentation marks *Pometia* pollen. It is a derived feature, together with several other autapomorphies functionally integrated into the brevicolporate harmomegathic system (chapter 8: *Pometia* pollen). This makes the pollen of *Pometia* highly derived and isolated. Macromorphologically, the genus is regarded as the most derived within the Nephelieae, especially on the basis of the very juicy mesocarp of the fruit (Leenhouts, 1978). In contrast to pollen the macromorphology does not isolate *Pometia* from the other Nephelieae.

Phylogenetic relationships of the pollen types

Figure 17 depicts the phylogenetic relationships of the pollen types in the Nephelieae. It shows that at least three different lineages evolved from a B type ancestor. A few trends within pollen types are included too. The scheme summarises the foregoing sections in this chapter, and it incorporates various details from others, particularly chapter 8. Primarily aperture characteristics are used. Besides, features relating to ornamentation, intine structure, and relative thickness of the nexine and endexine are applied.

Nephelieae pollen is assumed to have originated from (a) fossil type(s) belonging to *Cupanieidites*. The apertural system of this form genus is generally (para)syncolporate. Additional information was derived from the comprehensive LM study of the genus by Chmura (1973) and the SEM study of *C. orthoteichus* by Taylor (1989). Many records of *Cupanieidites* mention reticulate ornamentation. However, one has to realise that LM observation often gives an incomplete picture. In modern Cupanieae pollen reticulate patterns determined with LM usually proved to be rugulate or rugulate-reticulate with SEM. For instance, the rugulate and rugulate-reticulate pattern shown by figures 16a and 16b respectively appear reticulate with LM.

Nothing is known of the endexine and intine of *Cupanieidites*. In view of the condition of these features in modern (para)syncolporate Cupanieae pollen, which comes closest to *Cupanieidites*, its mesocolpial endexine is thought to be relatively thin and regularly delimited, and its intine without or with few dark inclusions. TEM data are available of the pollen of *Guioa* (van der Ham & van Heuven, 1989), *Mischocarpus* (van der Ham, 1977b) and *Vouarana*. No intine data are known of the Nephelieae genera *Cubilia*, *Litchi* and *Otonephelium*.

In addition to the pollen of the tribes Cupanieae and Nephelieae, that of the Meliccoceae and Schleichereae can be connected with *Cupanieidites*. Paullinieae pollen can be derived from *Cupanieidites* through reduction of the distal (and proximal) syncolpate aperture(s) (see chapter 8: *Pometia* pollen).

Geographical aspects

Cupanieidites

In chapter 8 it is put forward that *Cupanieidites* originated in the Late Cretaceous in Gondwana. Muller & Leenhouts (1976) suggested *Cupanieidites* to have arisen in

America as well as Africa, whereas Muller (1981a) postulated a single African-Indian cradle. Taylor (1989) indicated a South American origin, since his fossil material, *Cupanieidites orthoteichus* from the Eocene of Tennessee, showed affinities with the pollen of extant South American Cupanieae. However, whatever its affinities, Eocene material is not relevant as to the origin of *Cupanieidites*. The oldest fossil evidence, Late Turonian *Cupanieidites reticularis* from Gabon (Boltenhagen, 1980), favours an origin in the Central African part of Gondwana.

The fossil record (see table 14) suggests subsequent dispersal of the parent plants from Africa into South America and India (perhaps via Madagascar), which were still relatively close to the African Plate (Smith & Briden, 1977; see also fig. 21). At the end of the Cretaceous also North America and Antarctica were reached, probably via South America. During the Palaeocene and Eocene *Cupanieidites* plants became abundant in North America. Europe was reached in the Eocene, possibly directly from Africa, since a connection between Africa and Spain seems to have existed in the Early Palaeocene (Raven & Axelrod, 1974).

The earliest records from Australia and New Zealand date from the Palaeocene. From the Eocene till the Miocene *Cupanieidites* plants seem to have been a common element in these regions. Australia and New Zealand did not separate from Antarctica until the Eocene. Because Africa as well as India were probably far remote already in the Late Cretaceous (Smith & Briden, 1977; see also fig. 21), Antarctica possibly provided the migration route for the *Cupanieidites* plants from South America to Australia and New Zealand (see also Askin, 1989). Late Cretaceous climatic conditions in Antarctica were probably moist, warm and equable (Askin, 1989). Antarctica may have played a crucial rôle in the history of many other Gondwanan plant groups. Southern South American-Australasian distributions form the dominant pattern of biogeographical relationship between extant austral angiosperms (Drinnan & Crane, 1989).

In Oligocene times *Cupanieidites* extended northwards in the Australasian region. Younger records suggest further migration into Malesia and continental SE Asia on the one hand and the Pacific on the other. The scarcity of Tertiary microfloras from Malesia, continental SE Asia and the Pacific must be born in mind, though *Cupanieidites* is conspicuously absent from the relatively rich Cretaceous and Tertiary deposits in Borneo (Muller, 1968; Anderson & Muller, 1975). The fossil record of *Cupanieidites* from India is poor and does not show any progression towards continental SE Asia and Malesia. Dispersal out of that direction is therefore less likely.

The distribution of Recent (para)syncolporate Sapindaceae pollen excludes most of the localities where *Cupanieidites* has been found (fig. 18). Probably due to cooling and aridification the *Cupanieidites* plants disappeared from many places in the course of the Tertiary. It is possible, however, that a part of them adapted to the new circumstances, as taxa with colporate pollen that are closely related to Sapindaceae with (para)syncolporate pollen still occur in continental Africa, W, C and S Australia, and New Zealand. The transformation of (para)syncolporate pollen (type B) to colporate pollen (type A) would have been a major element of the presumed adaptation (chapter 8).

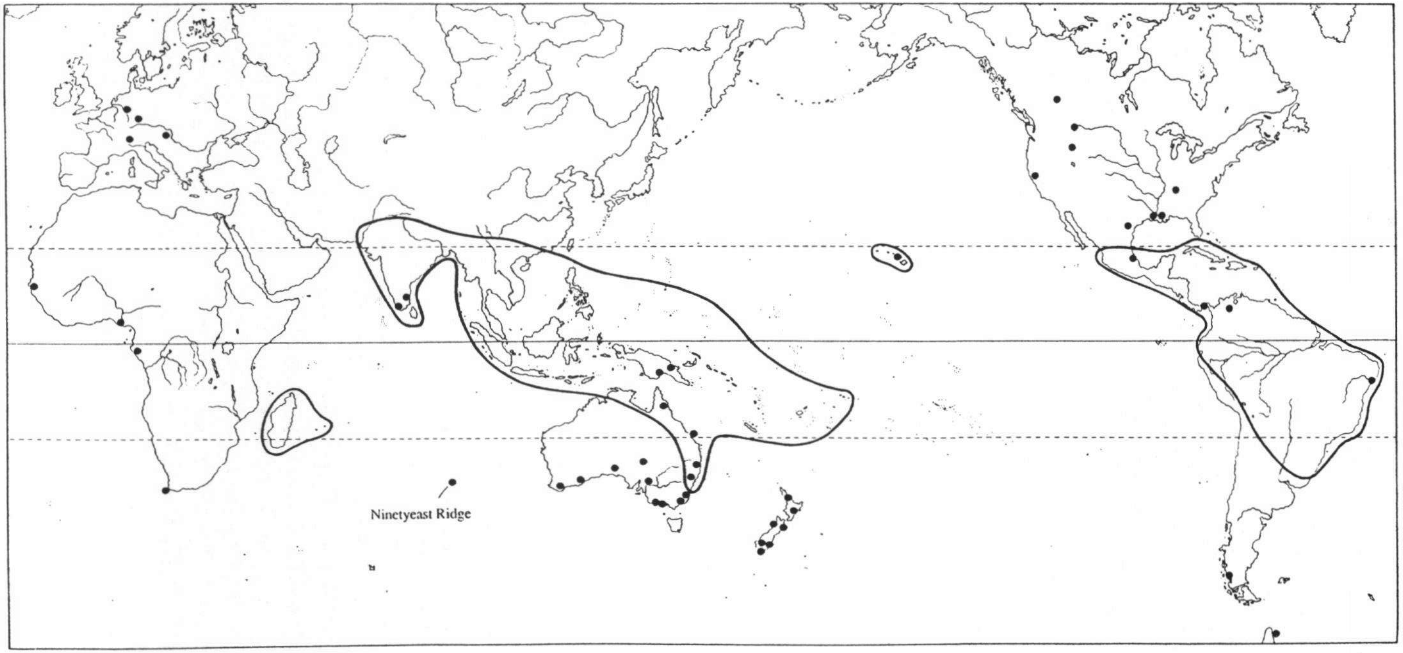


Fig. 18. Distribution of *Cupanieidites* (●) and Recent (para)syncolporate Sapindaceae pollen (———).

The *Alectryon* pollen type

Dispersal of *Cupanieidites* plants from South America to Australia, and from Australia to the Pacific, Malesia and continental SE Asia is supported by the distribution patterns of the Cupanieae in these regions. The Australian-Pacific-Malesian genus *Cupaniopsis* is regarded as closely related to and derived from the South American genus *Cupania* (Muller & Leenhouts, 1976; van Welzen, 1989). Great diversity exists in the Cupanieae from Australia and E Malesia, but relatively few taxa occur in W Malesia and continental SE Asia. Van Welzen (1989) concluded from a cladistic analysis that *Guioa* dispersed from Australia, New Guinea and New Caledonia to the Pacific and to W Malesia and continental SE Asia. The present distribution of *Alectryon* and *Podonephelium* fits this pattern well (fig. 19). Their ancestor might have been among the *Cupanieidites* plants that spread from Antarctica over the Australian region in the Early Tertiary. The most primitive subgenus *Synalectryon* (group I and II) is almost entirely restricted to Australia and New Guinea; one of its species occurs in Kangean (near E Java). The lineage formed by group III and VII, largely characterised by parasyncolporate pollen, reached the Philippines to the west and the Pacific (including the Solomon Islands, Fiji, Samoa and Hawaii) to the east. The lineage consisting of group IV, V and VI, and the 'unplaced' species, which mostly have the allegedly derived colporate pollen, reached E Java, Celebes and the Philippines, but it extends less far into the Pacific (New Guinea, the New Hebrides, New Caledonia and New Zealand form the eastern boundary). The area of the New Caledonian *Podonephelium* can be easily joined.

The *Litchi* pollen type

The genera belonging to the *Litchi* pollen type have quite different distributions than those of the Alectryon type. They occur in continental Africa, Madagascar, the Mascarene Islands, India, Ceylon, continental SE Asia and W Malesia (fig. 19). Wallacea, the archipelago between the Sunda Shelf and the Sahul Shelf, is crossed only by *Dimocarpus* (*D. australianus* and *D. leichhardtii* are found in NE Queensland). These data suggest a different migration history. The Malesian region seems to have been invaded from the northwest rather than from the southeast. Unfortunately fossil evidence is not available. On account of the occurrence of the *Litchi* pollen type in Africa as well as in Asia a connection between these continents is supposed. Assuming that the *Litchi* type originated in Africa from some *Cupanieidites*-like ancestral type a former migration route from Africa to Asia has to be searched for. During the Late Cretaceous and Early Tertiary the Tethys was probably still a major barrier for terrestrial plants, but from the Oligocene the African Plate (including Africa, Arabia and possibly parts of Iran, Pakistan and Afghanistan) closely approached Asia (Smith & Briden, 1977), after which dispersal may have occurred in easterly direction.

According to Audley-Charles (1987) parts of W Malesia and continental SE Asia separated from Australia in the Jurassic. These Gondwana fragments would have allowed the transfer/migration of an evolving angiosperm flora from Gondwana to Asia. However, the period indicated for the rifting process is considered too early to account for migration of the *Litchi* pollen type into Asia (see also Truswell et al.

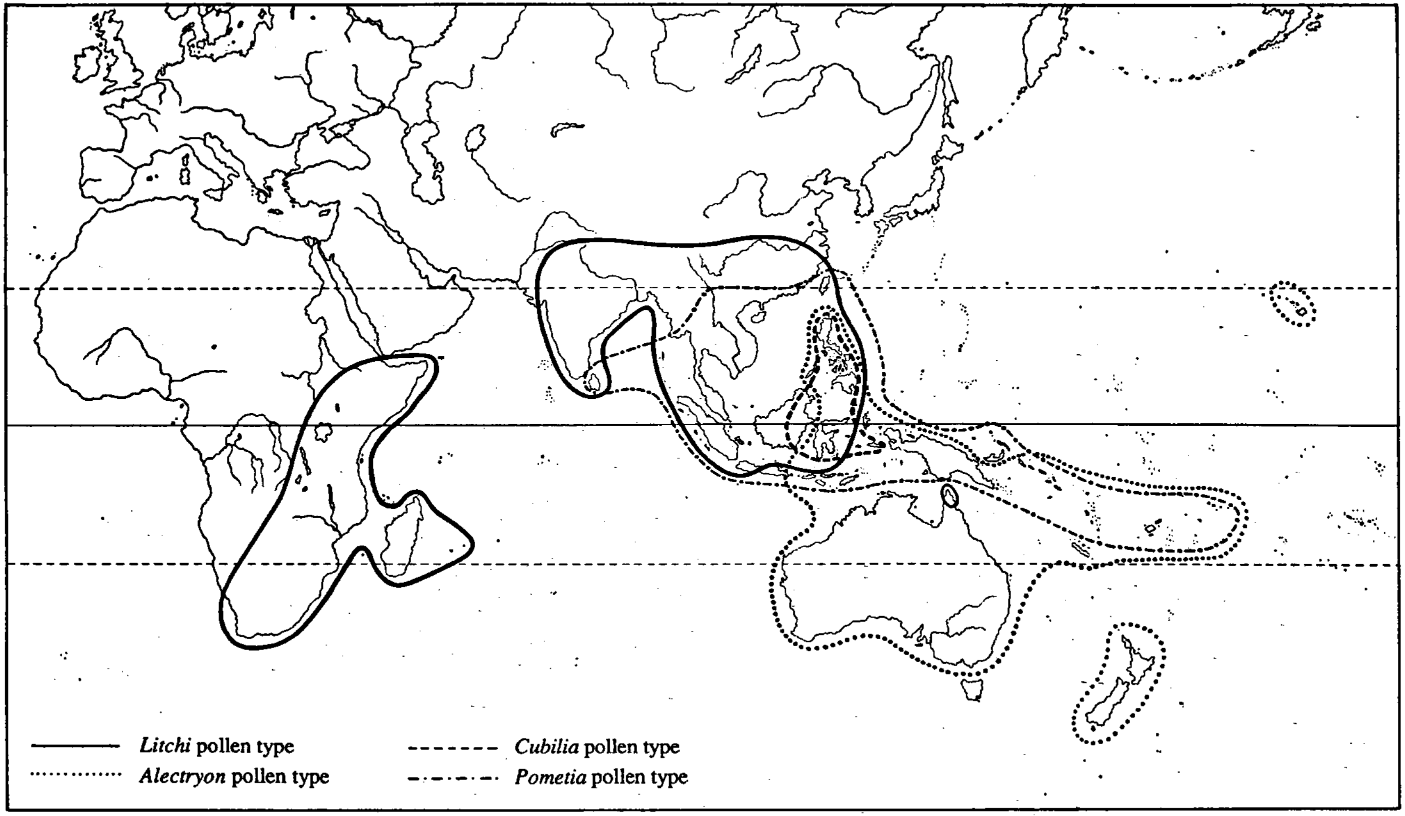


Fig. 19. Distribution of the four Nephelieae pollen types.

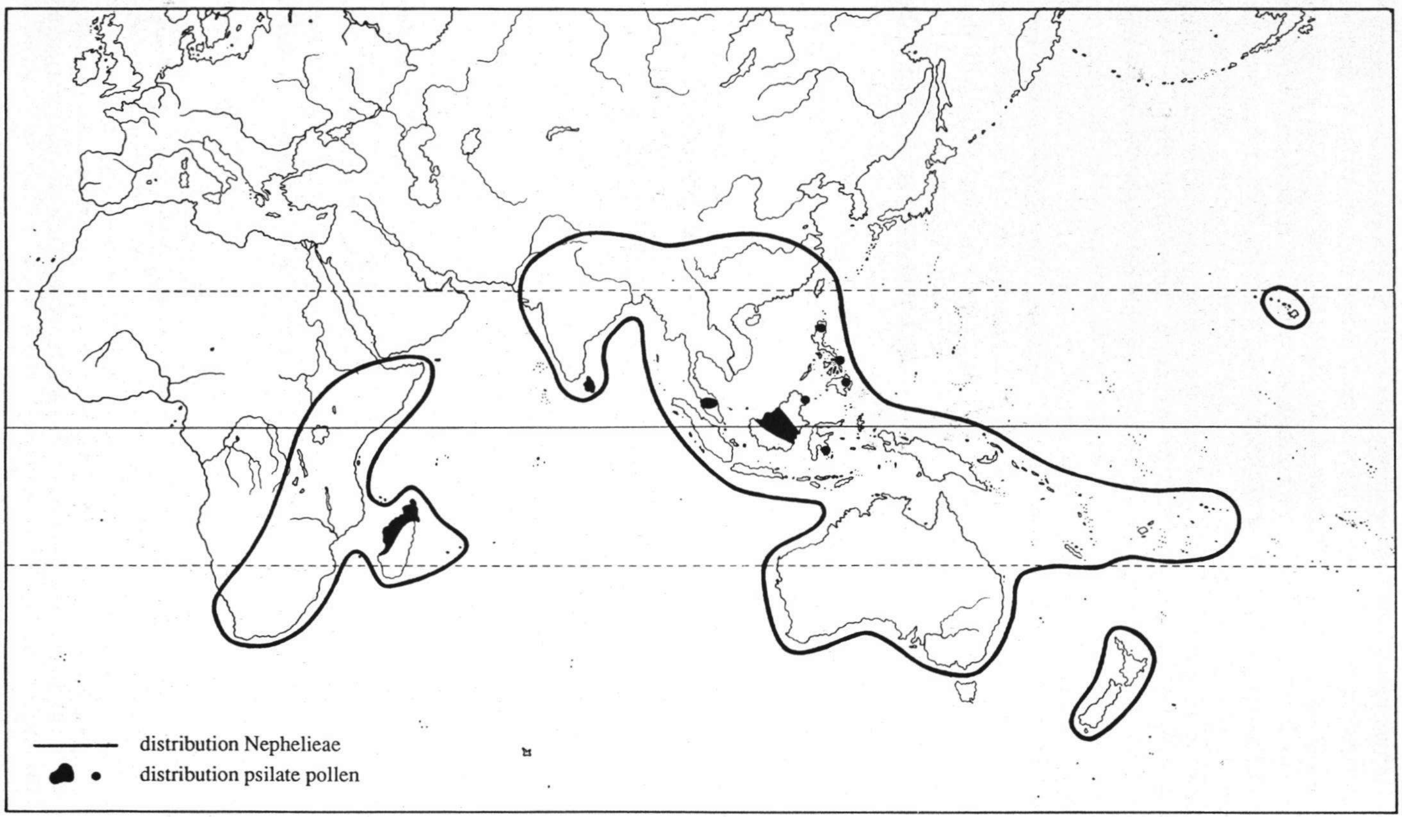


Fig. 20. Distribution of psilate Nephelieae pollen.

1987). India may have served as a stepping-stone and Noah's Ark in the route from Africa (perhaps via Madagascar) to Asia when it rafted east of Africa in the Late Cretaceous and Early Tertiary, or, more likely, after collision with Asia in the Late Eocene it may have been a link in a continuous migration route from Africa via Arabia, Iran, Pakistan to SE Asia. *Otonephelium* and the "old" *Dimocarpus gardneri* (Leenhouts, 1971), which occur in SE India and Ceylon respectively, might testify of the former involvement of India. Possibly, they became isolated in mid-Tertiary times due to competition or climatic change (Ashton & Gunnatilleke, 1987).

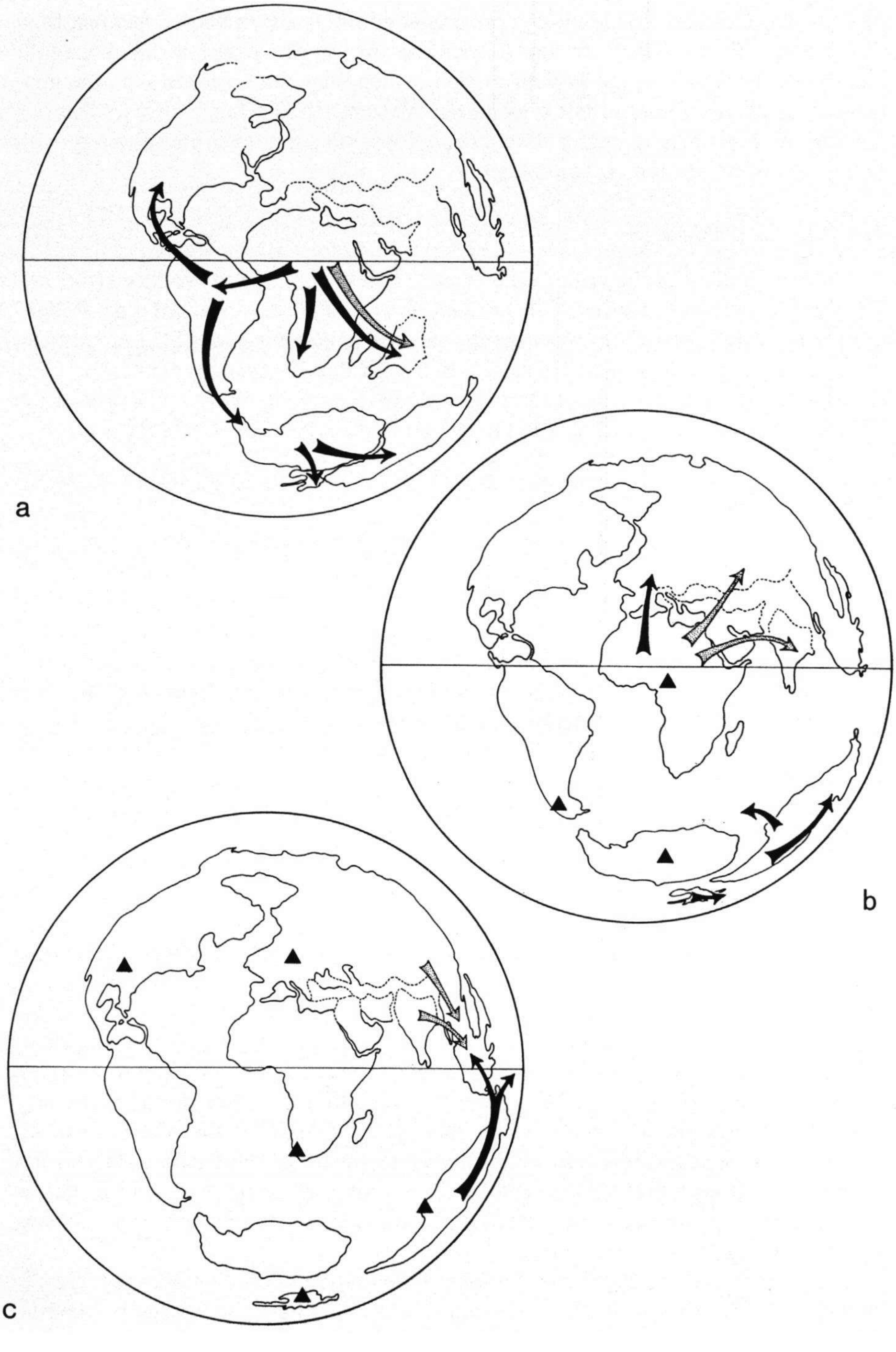
An Antarctic-Australian origin of the *Litchi* type would gain credibility if, by analogy with *Cupanieidites,* South America were involved. However, Nephelieae do not occur in South America. The same holds true for the tribe Schleichereae, which is nearly completely restricted to Africa and Madagascar. Only *Schleichera* is non-African. This genus occurs from India to Malesia, though it may be introduced into Malesia (ms. P.W. Leenhouts). Remarkably it is the sole Schleichereae with distinctly parasyncolporate (type B) pollen; all others have colporate pollen (type A), or sometimes type A* pollen. Ancestors of *Schleichera* might account for a part of the *Cupanieidites* records from India, for instance that of *C. decoratus* from the Oligocene/Miocene of the Cauvery Basin (Venkatachala & Rawat, 1973). Records of Quaternary parasyncolporate pollen from SW India (written comm. C. Tissot, 1988) pertain almost certainly to *Schleichera.*

A smaller scale geographical aspect concerns the character ornamentation. The striate type is by far the most common and widespread among the ornamentation forms in Nephelieae pollen. Rugulate ornamentation occurs in a number of *Alectryon* species and, occasionally, in a few other genera. It does not display a particular geographical pattern. However, the distribution of psilate and scabrate ornamentation is worth describing. Both types are considered more advanced than the striate type.

Psilate pollen is found in *Dimocarpus, Nephelium, Stadmania* and *Xerospermum,* which all belong to the *Litchi* pollen type. It appears that it is restricted to relatively small parts of the areas of these genera, in particular to (parts of) islands (fig. 20). Psilate *Dimocarpus* pollen occurs in Ceylon, Muna (near SE Celebes) and parts of Malaya, Borneo and the Philippines. In *Nephelium* and *Xerospermum* it is only known from Borneo. Psilate *Stadmania* pollen is restricted to a part of Madagascar.

Psilate pollen is commonest in Borneo. In addition, striate/psilate and psilate/scabrate intermediates are abundant, and scabrate ornamentation is the most diverse in Borneo. The typical form with oblong scabrae is endemic. This makes Borneo a

Fig. 21. Suggested migration routes of the plants that produced *Cupanieidites*) and the *Litchi* pollen type (➡). *Cupanieidites* may include fossil parasyncolporate *Alectryon* pollen. a: Late Cretaceous–Palaeocene (map: Santonian); b: Eocene–Oligocene (map: Late Eocene); c: Miocene–Quaternary (map: Late Miocene). The maps are redrawn (much simplified) from maps 45, 43 and 41 of Smith & Briden (1977). ▲ = extinction. Localities of *Cupanieidites* finds, as well as the distribution of Recent (para)syncolporate Sapindaceae pollen are shown in fig. 18, and the distribution of the *Alectryon* pollen type and the *Litchi* pollen type in fig. 19.


a
b
c

very heterogeneous region regarding ornamentation. It is a well known fact that Borneo contains much endemism and polymorphism (see for example Jacobs, 1962; Leenhouts, 1971, 1986; van Welzen, 1989), which may be correlated with the geomorphological instability of this region (van Welzen, 1989). Thus it appears that in a number of Nephelieae genera pollen morphology joins the macromorphology with respect to endemism and polymorphism.

The *Cubilia* pollen type

The area of the *Cubilia* pollen type is more or less confined to Wallacea (fig. 19). The *Cubilia* type is suggested to be derived from a colporate ancestral type. Pollen-morphologically, it cannot be connected with a particular member of the *Litchi* type, but from a geographical point of view a link with the SE Asian genera is the most obvious. This is supported by macromorphology (Leenhouts, 1978). The area of the *Cubilia* type overlaps with the easternmost part of the area of the *Litchi* type.

The *Pometia* pollen type

The *Pometia* pollen type is found from Ceylon to Samoa (fig. 19). Apparently, the centre of differentiation of *Pometia* is W Malesia (Jacobs, 1962). Indeed, the oldest (Late Miocene) fossils come from Borneo, which is a part of this region. From W Malesia it would have spread eastwards to New Guinea and the Pacific. The Pacific Pometias clearly represent an outlier of one of the New Guinean forms (Jacobs, 1962). Origin on the Australian Plate is considered unlikely, as fossils of the characteristic pollen are unknown in this area.

A syncolporate Miocene origin is hypothesised for the *Pometia* pollen type. However, this creates a geographical problem, since no syncolporate pollen is known from the Tertiary of W Malesia or continental SE Asia. The nearest finds come from the Tertiary of India.

Conclusion

Assuming that the Nephelieae indeed originated in Africa it is suggested that they reached Malesia by two routes (fig. 21). Plants with the *Litchi* pollen type, which would be derived from a *Cupanieidites*-like ancestral type, followed a northern route, either via Arabia or via Noah's Ark India. Plants with the *Alectryon* pollen type followed a southern route, via Australia and New Guinea. A similar twofold invasion was put forward by Muller (1985) for the tribe Harpullieae. Other examples are provided by the fern genus *Pyrrosia* (Hovenkamp, 1986) and the Palmae (Dransfield, 1987). The ancestors of the Recent Cupanieae in Australia, the Pacific, Malesia and continental SE Asia probably passed by the southern route only. According to the distribution of *Cupanieidites* they reached Australia via Antarctica in the Palaeocene, and Malesia not until the Miocene.

The pollen types of *Cubilia* and *Pometia* are unique in the Sapindaceae. Hence, they do not show geographical connections either. Both may have arisen in Malesia. *Pometia* is the only genus of the Nephelieae that clearly crosses Wallacea.

SUMMARY

A monograph of the pollen of the tribe Nephelieae (Sapindaceae) is presented. The body of this study consists of three chapters: Form (6), Function (7), and Evolution (8). Two further chapters (9 and 10) discuss the taxonomic and phylogenetic implications, and some geographical aspects of the pollen-morphological results.

Form — This chapter provides a general description of Nephelieae pollen as well as separate descriptions of the pollen of each of the 12 genera (chapter 6.1 to 6.13). Data of infrageneric taxa (and sometimes of individual samples) are accommodated in remarks, tables, and under headings such as Infrageneric variation and Geographical aspects. 75 out of the 78 species could be studied. The descriptions are based on LM and SEM data of all 454 samples. TEM data were derived from 44 samples.

The Nephelieae appeared to be a rather eurypalynous tribe of the Sapindaceae. Conspicuous characters such as aperture type and ornamentation display much variation. Three **aperture types** were found: colporate, parasyncolporate and brevicolporate. The genus *Alectryon* shows a continuous range from colporate to parasyncolporate. The brevicolporate *Pometia* pollen resembles the fossil *Atlantopollis* very much, but *Pometia* and the parent plants of *Atlantopollis* are considered unrelated.

Five main **ornamentation types** occur: rugulate, striate, psilate, scabrate and reticulate. Most of them are linked by intermediate forms. *Dimocarpus longan* subsp. *malesianus* var. *malesianus* exhibits a remarkably wide and continuous range: from striate, via psilate, to scabrate. Several genera show interesting geographical patterns as to ornamentation. The greatest diversity is found in Borneo.

Acetolysed pollen of all Nephelieae except *Pometia* may show membranaceous structures inside the exine. They are considered to be intine remains, and have been indicated as **intine ghosts**. The cause of their acetolysis-resistance is not understood.

Sapindaceae usually have unisexual flowers, which, however, may contain more or less conspicuous vestiges of the other sex. **Staminodial pollen** (pollen from female flowers) is often of inferior quality (chapter 6.14). It is excluded as much as possible from the present study. Although in the Nephelieae the anthers of staminodes do not dehisce, they may yield a small percentage of viable grains. Some literature data suggest that such viable staminodial pollen occasionally plays a role in pollination by means of an intraflower autogamous mechanism.

In order to get some insight in the development of the exine during microsporogenesis a SEM study of **immature pollen** was performed (chapter 6.15). Immature pollen is readily obtainable by acetolysing unripe buds. In several genera immature ornamentation differs essentially from mature ornamentation. In *Alectryon* a complete series from psilate to striate (-rugulate) was found. It is suggested that staminodial pollen is immature in comparison with pollen from male flowers. Hardly any ontogenetic differences were observed with respect to apertural system. Some data suggest that a parasyncolporate system may become colporate during exine growth.

Function — In this chapter the functional significance of the described structures is considered (chapter 7.1). Besides, the attractant function of pollen in the Sapindaceae is discussed (chapter 7.2).

A Nephelieae pollen grain is described as a multifunctional unit. Many structures and several functions can be related to harmomegathy. Therefore harmomegathy was choosen as the leading theme in treating function. On the basis of data derived from acetolysed pollen and simple experiments with unacetolysed pollen (from herbarium material) three **harmomegathic types** are described: the colporate, the parasyncolporate and the brevicolporate type. The first and the second type show folding, the third is peristatic. Each has a correlated type of ornamentation: striate, striate-rugulate to rugulate, and coarsely reticulate respectively, though 'less fitting' types such as psilate and scabrate occur as well.

The **Wodehouse effect** (Muller, 1979) is discussed. It is argued that it cannot explain deviating harmomegathic mechanisms in large grains, because its premise (large grains need additional harmomegathic mechanisms because of a lower surface / volume ratio in comparison with smaller grains) is invalid. A pollen grain that has to accommodate a given percent of volume reduction needs a fixed percent of surface and circumference decrease, whether it is small or large. If elasticity of the pollen wall is sufficient in the smaller grain, it will be so in the larger, as elasticity does not depend on the total amount of surface present.

A functional interpretation of the **intine morphology** is given. An increased harmomegathic role is assigned to the nonapertural intine in *Alectryon* and *Podonephelium* pollen. A functional relation is supposed to exist between intine thickness and nexine thickness.

A literature study was made of **pollination** in Sapindaceae, especially in the Nephelieae. Most Sapindaceae, among which all Nephelieae, are entomophilous. Social bees are the most frequent pollinators. The abundant pollen seems to have no role in attracting pollinators, but it may enhance the chance of successful cross-pollination, and it may indirectly benefit pollination by sustaining colonies of potential pollinators. An advertising function is attributed to the first male flower phase of (duo)dichogamous species. This phase would represent an economic means to announce the coming female phase, so that pollination proceeds most efficiently.

Evolution — This chapter deals with the evolutionary significance of the morphological series colporate—parasyncolporate and rugulate—scabrate. Besides, the evolutionary status of some minor features and of the isolated pollen types of *Cubilia* and *Pometia* are considered.

The variability of the apertural system in *Alectryon* pollen offered an excellent opportunity to study the relation between the **colporate** and the **parasyncolporate** condition (type A and type B respectively). Both are common in the Sapindaceae. On account of fossil evidence (distribution of *Cupanieidites*), palaeo-ecological and macromorphological data, and a functional interpretation it is hypothesised that within the subfamily Sapindoïdeae type B is plesiomorphic and type A apomorphic. *Alectryon* pollen provides some ontogenetic evidence for this hypothesis. Development of type A from type B would have taken place frequently, possibly under the influence of the worldwide aridification and cooling in the course of the Tertiary. As such, it must be considered a widespread reversal to the original colporate condition, which is believed to persist in the subfamily Dodonaeoïdeae.

The **brevicolporate** pollen of *Pometia* is certainly advanced: it may have originated from a syncolporate ancestral type. The derivation of both, colporate from parasyncolporate, and brevicolporate from syncolporate is opposed to the opinion of Muller & Leenhouts (1976) that colporate represents a basic condition throughout the Sapindaceae. The former trend also contrasts with the view that simple types are less advanced than more complex types.

With respect to ornamentation the series from rugulate, via striate and psilate, to scabrate is interpreted as an evolutionary trend. The transition of **rugulate** to **striate** is thought to be associated with the change from (para)syncolporate to colporate. **Psilate** ornamentation probably developed from striate ornamentation. It is interpreted as a paedomorphic (neotenous) feature that might have arisen by autogamy with staminodial pollen (progenesis). Obviously, the arguments of complexity (the more complex state is apomorphic) and ontogeny (the earlier ontogenetic state is plesiomorphic) do not hold here. The **scabrate** ornamentation of *Dimocarpus* pollen would have evolved from psilate ornamentation. It is speculated that it reflects the restoration of the sculptured tectum and optimal conditions for transfer by the usual pollinators.

The scabrate ornamentation of *Cubilia* pollen is not related to that of *Dimocarpus* pollen. Being associated with an aberrant flower structure, it might be connected with a different pollination mode, involving other pollinators than social bees. The aberrant character states of *Cubilia* pollen (scabrate tectum, thin mesocolpial nexine, small grain size) might be explained by assuming paedomorphosis.

The **reticulate** ornamentation of *Pometia* pollen is advanced; it represents an essential part of the derived peristatic harmomegathic mechanism.

Taxonomic implications — Pollen morphology does not appear to be very effective in characterising the Nephelieae. Both *Cubilia* and *Pometia* have distinct pollen, but the other ten genera have pollen that is mutually similar and/or resembles pollen of non-Nephelieae. Four **pollen types** are distinguished: the *Litchi* type, the *Alectryon* type, the *Cubilia* type and the *Pometia* type. This subdivision of the tribe does not coincide with that based on macromorphological data. The reduction of *Heterodendrum* to *Alectryon* is pollen-morphologicall fully justified, and inclusion of *Podonephelium* would be supported too.

Various pollen characters permit **infrageneric subdivision**. In some genera they indicate groups of related species (*Alectryon*), or they characterise infraspecific taxa, for instance: scabrate *Dimocarpus* pollen seems restricted to *D. longan* subsp. *malesianus* var. *echinatus* and the race '*malaiensis*' of var. *malesianus*.

Phylogenetic implications — According to pollen data the Nephelieae would consist of at least three different **lineages**. The extant taxa of these three lineages show the *Litchi* pollen type, the *Alectryon* pollen type, and the *Pometia* pollen type respectively. The *Cubilia* pollen type is tentatively connected with the *Litchi* lineage. Each lineage is supposed to have evolved from an ancestor with (para)syncolporate pollen (*Cupanieidites*). However, pollen morphology does not shed light on whether they form a monophyletic group, since not a single synapomorphy could be demonstrated for Nephelieae pollen.

The **colporate** apertural system would have developed independently in the *Litchi* lineage and the *Alectryon* lineage. In the latter the whole range from parasyncolporate to colporate is still present, but in the former only occasional intermediate forms remind of the ancestral state.

The **psilate** ornamentation occurring in several genera of the *Litchi* lineage developed parallely from striate ornamentation. It does not indicate close relationship of the parent taxa, and is restricted to relatively small parts of generic distributions, in particular to (parts of) islands.

The scabrate ornamentation in *Dimocarpus* is considered as a synapomorphy of *D. longan* subsp. *malesianus* var. *echinatus* and the race *'malaiensis'* of var. *malesianus*, which would mean that var. *malesianus* is paraphyletic.

The four pollen types show different geographical patterns. It is argued that the Nephelieae originated in Africa. Plants with the *Litchi* pollen type seem to have reached Malesia by a northern route, either via Arabia or via Noah's Ark India. Plants with the *Alectryon* pollen type would have followed a southern route, invading Malesia via Australia and New Guinea. *Cubilia* and *Pometia* may have originated in Malesia.

It appeared that in a number of genera ornamentation, just like the macromorphology, shows endemism and polymorphism in Borneo.

Cupanieidites — In view of the occurrence of parasyncolporate pollen in the genus *Alectryon*, and colporate/parasyncolporate intermediates in several other Nephelieae genera, a survey was made of the literature about the fossil pollen genus *Cupanieidites* (chapter 8). This form genus probably represents fossil (para)syncolporate Sapindaceae pollen. It is stated that it has wider affinities within the Sapindaceae than just the tribe Cupanieae. Certain Melicocceae, Nephelieae (*Alectryon*) and Schleichereae (*Schleichera*) must be considered too.

It is concluded that *Cupanieidites* has a Late Cretaceous origin in the African part of Gondwana (chapter 10). According to the fossil record *Cupanieidites* plants dispersed into America, India and Europe. Via South America and Antarctica they would have reached Australia and New Zealand, and subsequently invaded the Pacific and Malesia plus continental SE Asia.

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EXPLANATION OF PLATES

Plate 1. *Alectryon*, SEM photographs.
— 1–4: *A. affinis* (Fitzgerald 28). 1: polar view, × 2500; 2: polar view four-aperturate grain, × 2500; 3: endoapertural area, × 5000; 4: oblique section, × 2500.
— 5: *A. cardiocarpus*, approx. polar view, × 2500.
— 6: *A. carinatus* (Däniker 2320), approx. polar view, × 2500.

Plate 2. *Alectryon*, SEM photographs.
— 1, 2: *A. connatus*. 1: polar view, × 2500 (Leach s.n.); 2: apocolpial area, × 7500 (Dietrich 1371).
— 3: *A. coriaceus* (Simmonds s.n.), oblique and equatorial view, × 1800.
— 4–6: *A. diversifolius*. 4: polar view, × 2500 (Clemens s.n.); 5: approx. equatorial section, × 3000 (Mueller s.n.); 6: oblique section with endoaperture, × 7500 (Mueller s.n.).

Plate 3. *Alectryon*, SEM photographs.
— 1–6: *A. excelsus*. 1: oblique view, × 2500 (van Zanten 1301); 2: oblique view, × 2000 (Buchanan s.n.); 3: oblique view, × 2500 (Dallachy s.n.); 4: approx. polar and equatorial view, × 1400 (Gardner 2607); 5: approx. equatorial section, × 2500 (Buchanan s.n.); 6: part of approx. equatorial section including colpus membrane, × 7500 (Dallachy s.n.).

Plate 4. *Alectryon*, SEM photographs.
— 1, 2: *A. ferrugineus* (NGF 27583). 1: oblique view, × 2250; 2: oblique view four-aperturate grain, × 2000.
— 3, 4: *A. forsythii*. 3: oblique view, × 2500 (Rodd 2458); 4: polar part of mesocolpium, × 5000 (Gray 2513).
— 5: *A. fuscus*, polar view, × 2500.
— 6: *A. glaber* (Labillardière s.n.), polar and oblique view, × 1750.

Plate 5. *Alectryon*, SEM photographs.
— 1, 2: *A. grandifolius* (Parham 5835). 1: oblique view, × 2500; 2: oblique view, × 1400.
— 3, 4: *A. kangeanensis*. 3: oblique view, × 2500; 4: equatorial view, × 2500.
— 5: *A. kimberleyanus* (Kenneally 8578), oblique view, × 2500.
— 6: *A. macrococcus* (Degener 9536), polar view, × 2250.

Plate 6. *Alectryon*, SEM photographs.
— 1, 2: *A. myrmecophilus* (NGF 4077). 1: polar view, × 2250; 2: approx. equatorial section, × 2500.
— 3, 4: *A. oleifolius* subsp. *canescens* (Smith 6059). 3: oblique view, × 2500; 4: polar part of mesocolpium, × 7500.
— 5, 6: *A. oleifolius* subsp. *elongatus* (Smith 4520). 5: oblique view, × 2500; 6: approx. equatorial section, × 2500.

Plate 7. *Alectryon*, SEM photographs.
— 1, 2: *A. pubescens*. 1: oblique view, × 2500; 2: polar and oblique views, × 1500.
— 3: *A. ramiflorus* (Zillmann AQ 425108), oblique and equatorial views, × 1500.
— 4–6: *A. repandodentatus*. 4: oblique view with Ubisch bodies, × 2500 (Pullen 6908); 5: meridional section with endoaperture, × 3000 (Chalmers s.n.); 6: approx. equatorial section, × 4000 (Chalmers s.n.).

Plate 8. *Alectryon*, SEM photographs.
— 1–6: *A. reticulatus*. 1–5: staminodial grains from shrivelled anthers found at fruit bases (Anon. s.n.), 1–3: polar views, × 2500, 4: oblique view, × 2500, 5: approx. equatorial section, × 3500; 6: polar view, × 2250 (Hartmann sh. 1537050).

Plate 9. *Alectryon*, SEM photographs.
— 1–4: *A. semicinereus*. 1: polar view, × 2500 (Anon. sh. 908.269-1375); 2–4: apocolpial areas, × 5000 (Volck 1414).
— 5, 6: *A. subcinereus* (Floyd 775). 5: oblique view, × 2500; 6: oblique section with endoaperture, × 2500.

Plate 10. *Alectryon*, SEM photographs.
— 1, 2: *A. subcinereus* (Maiden 1664). 1: approx. polar view, × 1500; 2: grain devoid of meridional ectoapertures, × 2500.
— 3–6: *A. samoënsis*. 3, 4: polar views, × 2500 (Whistler 20); 5, 6: staminodial grains (Whistler 963), 5: polar view, × 4500, 6: oblique view, × 3000.

Plate 11. *Alectryon*, SEM photographs.
— 1: *A. subdentatus* forma *pseudostipularis* (Williams s.n.), polar and oblique view, × 1750.
— 2–4: *A. subdentatus* forma *subdentatus*. 2: polar view, × 2500 (Stuart s.n.); 3: apocolpial area, × 5000 (Stuart s.n.); 4: polar view, × 2500 (Longman s.n.).
— 5, 6: *A. tomentosus* (Blake 2337). 5: approx. polar view, × 2500; 6: oblique view, × 2500.

Plate 12. *Alectryon*, SEM photographs.
— 1–6: *A. unilobatus* (Morton 1238, except for 6). 1: approx. polar view, × 2500; 2: oblique views, × 1500; 3: polar view, × 2500; 4: equatorial view, × 2500; 5: approx. equatorial section, × 3000; 6: meridional section with endoaperture, × 2500 (Hegarty C 3).

Plate 13. *Cubilia*, SEM photographs.
— 1–6: *C. cubili*. 1: approx. polar view, × 5000 (PNH 22872); 2: oblique view, × 5000 (PNH 22872); 3: approx. equatorial view, × 5000 (NIFS Cel./V-236); 4: polar view, × 4500 (SAN 54920); 5: oblique section, × 5000 (NIFS Cel./V- 236); 6: part of oblique section including colpus membrane, × 6500 (SAN 54920).

Plate 14. *Dimocarpus*, SEM photographs.
— 1, 2: *D. australianus*. 1: oblique and equatorial view, × 1750 (Smith 11847); 2: oblique view, × 2500 (Hyland 2835).
— 3–5: *D. dentatus*. 3: approx. polar view, × 2000 (SAN 38200); 4: approx. polar view, × 2500 (SAN 54466); 5: part of approx. equatorial section, × 5000 (SAN 38200).
— 6: *D. foveolatus*, polar view, × 2500 .

Plate 15. *Dimocarpus*, SEM photographs.
— 1: *D. fumatus* subsp. *indochinensis*, oblique view, × 2500.
— 2–5: *D. fumatus* subsp. *fumatus*. 2: oblique view, × 2750 (Geesink & Hattink 6435); 3, 4: oblique views, × 2500 (SAN 44665); 5: meridional section with endoaperture, × 3500 (SAN 44665).
— 6: *D. fumatus* subsp. *philippinensis* (Elmer 15389), approx. polar view, × 2500.

Plate 16. *Dimocarpus*, SEM photographs.
— 1: *D. gardneri* (Meijer 345), approx. polar view, × 2500.
— 2: *D. leichhardtii*, oblique and polar view, × 1500.
— 3–7: *D. longan* subsp. *longan* var. *longan*. 3: approx. polar and equatorial view, × 1500 (Kostermans 25282): 4: polar view, × 2500 (van Beusekom & Santisuk 2852); 5: approx. equatorial section, × 3000 (Koelz 25001); 6, 7: aberrant ornamentation, × 5000 (RTH 26927).

Plate 17. *Dimocarpus*, SEM photographs.
— 1–4: *D. longan* subsp. *longan* var. *longan*. 1: approx. polar view, × 2500 (Popta 863/210); 2: polar view with aberrant ornamentation and attached sculptured body, × 2500 (Popta 863/210); 3: grains with different ornamentation, × 1500 (Anon. sh. 908.272-802); 4: grains with different ornamentation, × 1250 (Anon. sh. 908.272-822).
— 5, 6: *D. longan* subsp. *malesianus* var. *malesianus*. 5: polar view, × 2500 (Vidal 221): 6: oblique view, × 2500 (Pierre 4114).

Plate 18. *Dimocarpus*, SEM photographs.
— 1–6: *D. longan* subsp. *malesianus* var. *malesianus*. 1: oblique view, × 2500 (Parker 2717); 2: parts of oblique views, × 2500 (KEP 104556); 3: oblique and polar view, × 1750 (Elmer 13482); 4: approx. polar view, × 2500 (S 26148); 5: polar view, × 2500 (NIFS bb 13299); 6: approx. polar view, × 2250 (NIFS bb 21771).

Plate 19. *Dimocarpus*, SEM photographs.
— 1–6: *D. longan* subsp. *malesianus* var. *malesianus*. 1: polar view, × 2250 (SAN 38203); 2: approx. polar view, × 2250 (SAN 38203); 3: oblique view of grain with aberrant ectoaperture morphology, × 2250 (KL 2856); 4: detail of 3/4 tetrad with Ubisch bodies, × 2500 (SAN 66273); 5: endoapertural area, × 7500 (SAN 43034); 6: part of equatorial section, × 7500 (SAN 91011).

Plate 20. *Dimocarpus*, SEM photographs.
— 1–4: *D. longan* subsp. *malesianus* var. *malesianus* (S 23044, except for 4). 1: oblique view, × 2500; 2: part of polar view, × 3750; 3: part of equatorial view with endoapertural area, × 5000; 4: polar part of mesocolpium, × 7500 (S 23086).
— 5: *D. longan* subsp. *malesianus* var. *echinatus* (Santos 4124), oblique view, × 2000.
— 6: *Dimocarpus* spec., polar view, × 2500.

Plate 21. *Litchi*, SEM photographs.
— 1, 2: *L. chinensis* subsp. *chinensis* (Lei 465). 1: approx. polar view of almost syncolporate grain, × 3000; 2: approx. equatorial section with endoaperture, × 3000.
— 3, 4: *L. chinensis* subsp. *javensis* (Blume sh. 908.270-273). 3: grains with different ornamentation, × 2000; 4: part of approx. equatorial section, × 7500.
— 5, 6: *L. chinensis* subsp. *philippinensis* (BS 17429). 5: oblique view, × 3000; 6: equatorial section, × 3000.

Plate 22. *Nephelium*, SEM photographs.
— 1–3: *N. compressum*. 1: oblique view, × 3000 (Haviland 2270); 2: apocolpial area, × 7500 (Haviland 2270); 3: oblique section, × 3000 (Haviland 3175).
— 4: *N. costatum* (KEP 98852), approx. polar view, × 2500.
— 5: *N. cuspidatum* var. *bassacense* (Kerr 16434), oblique view, × 2500.
— 6: *N. cuspidatum* var. *eriopetalum* (SAN 89304), oblique view, × 3000.

Plate 23. *Nephelium*, SEM photographs.
— 1: *N. daedaleum* (SAN 60511), oblique view, x 3000.
— 2: *N. hamulatum*, oblique view, x 3000.
— 3–7: *N. havilandii*. 3: polar view with Ubisch bodies, x 3000; 4: oblique view rugulate grain, x 3000; 5: section with endoaperture, x 5000; 6: approx. equatorial section mesocolpium, x 6000; 7: approx. equatorial section, x 3750.

Plate 24. *Nephelium*, SEM photographs.
— 1, 2: *N. hypoleucum*. 1: oblique view, x 2500 (Poilane 2503); 2: polar view irregularly striate grain, x 2500 (Pierre 875).
— 3, 4: *N. juglandifolium* (Hort. Bogor. III-E-25a). 3: oblique view, x 2500; 4: endoapertural area, x 7500.
— 5: *N. lappaceum* var. *pallens* (Korthals sh. 908.269-1400), polar view, x 2500.
— 6, 7: *N. lappaceum* var. *lappaceum* (KEP 99135). 6: part of oblique section, x 6000 (detail of 7); 7: oblique section, x 2500.

Plate 25. *Nephelium*, SEM photographs.
— 1, 2: *N. laurinum* (Maxwell 80-126). 1: oblique view, x 3000; 2: oblique section, x 3000.
— 3, 4: *N. macrophyllum*. 3: approx. polar view, x 2750; 4: apocolpial area, x 7500.
— 5: *N. maingayi* (Rahmat si Boeea 8902), approx. polar view, x 3000.
— 6: *N. meduseum*, oblique view of grain from shrivelled anther found at fruit basis, x 2750.

Plate 26. *Nephelium*, SEM photographs.
— 1: *N. melanomiscum*, approx. polar view, x 2500.
— 2, 3: *N. melliferum*. 2: oblique view, x 2500 (d'Alleizette 1421); 3: section with endoaperture, x 7500 (Put 3570).
— 4: *N. papillatum*, approx. polar view, x 2500.
— 5, 6: *N. ramboutan-ake*. 5: oblique view, x 3000 (Meijer 5991) ; 6: approx. polar view, x 2500 (SAN 36302).

Plate 27. *Nephelium*, SEM photographs.
— 1, 2: *N. reticulatum*. 1: oblique view, x 2500; 2: approx. equatorial section, x 3000.
— 3, 4: *N. subfalcatum* (NIFS T 712). 3: oblique view, x 2500; 4: approx. polar view, x 2500.
— 5: *N. uncinatum* (Kostermans 6376), oblique view, x 3000.
— 6: *Nephelium* spec. nov. (KEP FRI 19144), oblique view, x 2500.

Plate 28. *Otonephelium*, SEM photographs.
— 1–6: *O. stipulaceum* (1, 2: Anon. s.n. in Herb. Hookerianum, 4–6: Pascal 1375). 1: polar view, x 3750; 2: part of approx. polar view, x 6000; 3: oblique view, x 3000; 4: approx. equatorial view, x 3000; 5: oblique section, x 3000; 6: section through and near colpus membranes, x 3750.

Plate 29. *Pappea*, SEM photographs.
— 1–6: *P. capensis*. 1: polar view, x 2500 (Dyer 1181a); 2: oblique and equatorial view, x 2000 (Dyer 1181a); 3: oblique view, x 3000 (Fanshawe 4497); 4: oblique section with endoapertures, x 3000 (Gillett 5058); 5: oblique section, x 3000 (Troupin 4935); 6: oblique section, x 3000 (Hardy & Bayliss 1204).

Plate 30. *Podonephelium*, SEM photographs.
— 1–3: *P. concolor* (Vieillard 2395). 1: oblique view, × 2500; 2: oblique section, × 2500; 3: approx. meridional section with endoaperture, × 2500.
— 4: *P. homei* forma *homei* (Vieillard 219), oblique view, × 2500.
— 5: *P. parvifolium*, equatorial view, × 2500.
— 6: *P. subaequilaterum*, tetrad, × 1500.

Plate 31. *Pometia*, SEM photographs (samples prepared and photographed for Muller & Leenhouts, 1976 and van den Berg, 1978).
— 1: *P. pinnata* forma *macrocarpa*, polar and oblique views, × 1000.
— 2: *P. pinnata* forma *tomentosa* (Winckel 1809β), approx. polar view, × 2000.
— 3: *P. pinnata* forma *alnifolia* (NIFS T 1 P 11), apertural area, × 5000.
— 4, 5: *P. pinnata* forma *glabra* (NIFS bb 29745). 4: apertural area, × 5000; 5: section through endoaperture, × 5000.
— 6: *P. ridleyi* (KEP FRI 9452), section with endoapertures, × 2500.

Plate 32. *Smelophyllum*, SEM photographs.
— 1–7: *S. capense* (Wells 3246, except for 7). 1, 2: polar views, × 2500; 3: approx. equatorial view, × 2500; 4: oblique views, × 2000; 5: approx. meridional section, × 2500; 6: approx. equatorial section, × 3000; 7: oblique views, × 1750 (Drège s.n.).

Plate 33. *Stadmania*, SEM photographs.
— 1, 2: *S. acuminata* var. *acuminata*. 1: oblique view, × 2500; 2: oblique section, × 2500.
— 3–6: *S. glauca*. 3: oblique view striate grain, × 3000; 4: striate and rugulate grain, × 1500; 5: rugulate grains, × 1500; 6: part of equatorial section of mesocolpium, × 7500.

Plate 34. *Stadmania*, SEM photographs.
— 1, 2: *S. excelsa*. 1: polar view, × 3000; 2: oblique section, × 3000.
— 3: *S. leandrii*. 3: polar view, × 3000 (prepared and photographed for Muller & Schuller, 1989).
— 4–6: *S. serratula*. 4: approx. polar view, × 3000; 5: oblique section with endoaperture showing endoaperture filling (compare with plate 55: 3), × 3750; 6: part of equatorial section of mesocolpium and endoaperture, × 7500.

Plate 35. *Stadmania*, SEM photographs.
— 1, 2: *S. oppositifolia* subsp. *oppositifolia* var. *grevei* (Grevé 243). 1: blique view, × 2500; 2: meridional section, × 3000.
— 3, 4: *S. oppositifolia* subsp. *oppositifolia* var. *oppositifolia* (Bradburne 102). 3: tetrad, × 2000; 4: approx. polar view, × 2500.
— 5, 6: *S. oppositifolia* subsp. *rhodesica* (Chase 4733). 5: oblique and polar view, × 1500; 6: oblique section, × 3750.

Plate 36. *Xerospermum*, SEM photographs.
— 1–7: *X. laevigatum* subsp. *laevigatum*. 1: oblique view, × 3000 (Kerr 17341); 2: different states of apo-/mesocolpium coherence, × 1500 (NIFS bb 2138); 3: polar view, × 3750 (S 15621); 4: oblique view, × 2500 (S 36947); 5: oblique section, × 3750 (Kerr 17341); 6: part of oblique section showing columellae attached to the tectum, × 12500 (Kerr 17341); 7: part of oblique section, × 12500 (Kerr 17341).

Plate 37. *Xerospermum*, SEM photographs.

— 1–6: *X. laevigatum* subsp. *acuminatum*. 1: approx. polar view, × 3000 (Haviland & Hose 2080); 2: approx. polar views, × 2000 (Haviland & Hose 2080); 3: approx. polar view, × 3000 (S 9801); 4: tetrad, × 2000 (S 8686); 5: 3/4 tetrad, × 2000 (S 8686); 6: equatorial view rugulate grain (S 12311), × 3000.

Plate 38. *Xerospermum*, SEM photographs.

— 1–6: *X. noronhianum*. 1: oblique view, × 2500 (van Steenis 738); 2: oblique view, × 3000 (Kerr 12105); 3: approx. polar view, × 2500 (SAN 25865); 4: oblique view, × 3000 (de Wilde & de Wilde-Duyfjes 14822); 5: approx. polar and equatorial view, × 1500 (Jacobs 5252); 6: section parallel to polar axis, with endoaperture, × 2500 (Jacobs 5252).

Plate 39. Immature pollen, SEM photographs.

— 1–6: *Alectryon excelsus* (van Zanten 1301), exine growth. 1: stage 1, × 2500 (bud size class: small); 2: stage 1/2, × 3750 (bud size class: small); 3: stage 2, × 3750 (bud size class: small); 4: stage 3, × 2500 (bud size class: small); 5: stage 4, × 2500 (bud size class: small); 6: stage 5, × 2500 (bud size class: large).

Plate 40. Immature pollen, SEM photographs.

— 1–4: *Alectryon subdentatus* forma *subdentatus* (Dunn s.n.), exine growth. 1: stage 1, with Ubisch bodies, × 3750; 2: stage 2, with Ubisch bodies, × 2500; 3: stage 3, × 3750; 4: stage 4 and 5, × 1750.

— 5, 6: *Alectryon connatus* (Dallachy s.n.). 5: immature grain, stage 2, × 3750; 6: immature and mature grain, stage 2 and 5, × 2000.

Plate 41. Immature pollen, SEM photographs.

— 1: *Cubilia cubili* (NIFS Cel./V-236, KOH method applied), oblique view immature grain, × 5000.

— 2: *Dimocarpus gardneri* (Meijer 345), oblique view immature grain, × 3000.

— 3–6: *Dimocarpus longan* subsp. *malesianus* var. *malesianus*. 3: approx. polar view, × 5000 (ANU 1602); 4: oblique view immature grain, × 3000 (S 26148); 5: immature and mature grain, × 3000 (SAN 31241, KOH method applied); 6: immature grain, × 5000 (detail of 5).

Plate 42. Immature pollen, SEM photographs.

— 1: *Litchi chinensis* subsp. *chinensis* (Poilane 11991, KOH method applied), immature grains, × 3500.

— 2: *Nephelium ramboutan-ake* (A 2733, KOH method applied), polar view immature grain, × 6000.

— 3: *Otonephelium stipulaceum* (Anon. s.n. in Herb. Hookerianum), oblique view immature grain, × 4000.

— 4: *Pappea capensis* (Dyer 1181a), oblique view immature grain, × 4000.

— 5, 6: *Podonephelium subaequilaterum*. 5: immature and mature grain, × 2000; 6: approx. polar view immature grain, × 3000 (detail of 5).

Plate 43. Immature pollen, SEM photographs.

— 1, 2: *Pometia pinnata* forma *acuminata* (S 19131), oblique views immature grains, x 3000 and x 2500 respectively (prepared and photographed for van den Berg, 1978).

— 3, 4: *Stadmania oppositifolia* subsp. *oppositifolia* var. *oppositifolia* (Person sh. 908.272-91, KOH method applied). 3: oblique view immature grain, x 4000; 4: oblique view immature grain, x 4000.

— 5: *Xerospermum laevigatum* subsp. *acuminatum* (S 8686), meridional view immature grain with Ubisch bodies, x 4000.

— 6: *Xerospermum noronhianum* (Suvarnakoses 2218, KOH method applied), approx. polar view immature grain, x 4000.

Plate 44. *Alectryon*, TEM photographs.

— 1, 2: *A. connatus*. 1: oblique section with one endoaperture, x 3100; 2: detail of 1 showing endoaperture and mesocolpial wall, x 14500.

— 3: *A. coriaceus*, cross section ectoapertural area showing interbedded electron-lucent lamellae (l) in outer part colpus membrane, and old (= juvenile) tectum surface (arrowheads), x 14500.

Other abbreviations explained on p. 192.

Plate 45. *Alectryon*, TEM photographs.

— 1, 2: *A. excelsus*. 1: oblique section endoapertural area showing interbedded electron-lucent lamellae (l) in outer endexine, x 14500; 2: cross section mesocolpial wall, x 14500.

— 3, 4: *A. ferrugineus*. 3: approx. equatorial section with one endoaperture, x 2400; 4: detail of 3 showing interbedded electron-lucent lamellae (l) in outer endexine, x 12600.

— 5: *A. forsythii*, cross section mesocolpial wall showing endexine protrusions that reach intercolumellar nexine surface, x 14500.

Other abbreviations explained on p. 192.

Plate 46. *Alectryon*, TEM photographs.

1: *A. grandifolius*, cross section marginal part mesocolpial wall (colpus membrane to the left), x 14500.

— 2: *A. macrococcus*, cross section of ectoapertural area and adjacent mesocolpial area showing electron-lucent lamellae (l) in outer part colpus membrane, x 14500.

— 3, 4: *A. myrmecophilus* (NGF 4077). 3 & 4: oblique section of ectoapertural area, adjacent mesocolpial areas, and inner part anther wall with several layers of Ubisch bodies (u), x 12200.

Other abbreviations explained on p. 192.

Plate 47. *Alectryon*, TEM photographs.

— 1–3: *A. oleifolius* subsp. *oleifolius*. 1: cross section showing endoaperture with endoaperture filling (ef) and adjacent mesocolpial area, x 7200; 2: approx. equatorial section with one endoaperture, x 2800; 3: detail of 2 showing endoaperture with endoaperture filling (ef), adjacent mesocolpial area, and Ubisch bodies (u), x 14500.

— 4, 5: *A. subdentatus* subsp. *pseudostipularis*, cross sections showing endoaperture with endoaperture filling (ef), x 11600 and x 14500 respectively.

Other abbreviations explained on p. 192.

Plate 48. *Cubilia* and *Dimocarpus*, TEM photographs.

— 1: *C. cubili*, ectoapertural and adjacent mesocolpia exine (acetolysis applied), × 15900 (prepared and photographed for van den Berg, 1978).

— 2: *D. australianus*, approx. equatorial section endoaperture; the inner oncus sublayer (ii) shows electron-opaque extensions (ext) from the middle sublayer (mi), × 4900.

— 3–5: *D. longan* subsp. *malesianus* var. *malesianus* (SAN 62963, which has striate pollen). 3: oblique section with two endoapertures, × 2800; 4 & 5: detail of 3 showing exine and intine stratification, × 14500.

Other abbreviations explained on p. 192.

Plate 49. *Dimocarpus* and *Litchi*, TEM photographs.

— 1, 2: *D. longan* subsp. *malesianus* var. *malesianus*. 1: oblique section showing endintinal evagination (ii) plus contents penetrating exintine (mi + oi) and reaching endoaperture (compare with plate 56: 7), × 4900 (SAN 62963, which has striate pollen); 2: cross section mesocolpial wall parts, × 14500 (S 23086, which has scabrate pollen).

— 3: *L. chinensis* subsp. *chinensis*, approx. equatorial section with one endoaperture, one colpus membrane, and interjacent mesocolpium (acetolysis applied), × 7400 (detail of plate IX: 3 in van den Berg, 1978).

Other abbreviations explained on p. 192.

Plate 50. *Nephelium*, TEM photographs.

— 1, 2: *N. cuspidatum* var. *eriopetalum*. 1: oblique section with inner part of anther wall, × 2800; 2: detail of 1 showing exine stratification, Ubisch bodies (u) and pollenkitt (p), × 14500.

— 3, 4: *N. havilandii*. 3: approx. equatorial section with two endoapertures and anther wall parts, × 3300; 4: detail of 3 showing two apertural areas and interjacent mesocolpium, × 14500.

Other abbreviations explained on p. 192.

Plate 51. *Nephelium*, TEM photographs.

— 1, 2: *N. lappaceum* var. *lappaceum*. 1: oblique section with one endoaperture, × 2800; 2: detail of 1 showing exine stratification, × 13500.

— 3: *N. subfalcatum*, cross section endoapertural area showing endoaperture filling (ef) and intine stratification, × 13500.

— 4, 5: *N. uncinatum*. 4: oblique section with one endoaperture, × 3300; 5: detail of 4 showing endoaperture with endoaperture filling (ef), × 13000.

Other abbreviations explained on p. 192.

Plate 52. *Otonephelium*, TEM photographs.

— 1–5: *O. stipulaceum*. 1: tetrad stage: enclosed daughter cells, × 3300; 2: detail of 1 (of largest cell on the right) showing mesocolpial primexine, × 14500; 3: detail of 1 (of largest cell on the right) showing apertural area (arrow) and adjacent mesocolpial primexine, × 14500 ; 4: free-grain stage: section with several apertural areas (arrows) showing absence of apertural nexine, × 4900; 5: free-grain stage: part of oblique section through two apertural areas (arrows) and interjacent mesocolpial wall showing intine (i) and discontinuous apertural nexine, × 14500.

Other abbreviations explained on p. 192.

Plate 53. *Pappea*, TEM photographs.

— 1–5: *P. capensis* (Dyer 1181a, except for 5). 1: oblique section with one endoaperture, × 2400; 2: detail of 1 showing endoaperture with endoaperture filling (ef), and exine and intine stratification, × 13800; 3: approx. equatorial section with one endoaperture showing endoaperture filling (ef), × 2600; 4: cross section central part mesocolpial area showing elaborate tectum architecture and oblique columellae (see also 2 and 5), × 12900; 5: cross section mesocolpial area showing relatively thin simple tectum (compare with 3 and 4) and several series of Ubisch bodies (u), × 7200 (Troupin 4935).

Other abbreviations explained on p. 192.

Plate 54. *Podonephelium* and *Pometia*, TEM photographs.

— 1–3: *Podonephelium homei* forma *homei*. 1: approx. equatorial section with one endoaperture, × 2500; 2: detail of 1 showing exine and intine stratification, × 12900; 3: cross section endoapertural area showing oncus stratification and endoaperture filling (ef), × 8100.

— 4: *Podonephelium concolor*, cross section mesocolpial exine showing irregular boundary between endexine (en) and foot layer (f), and Ubisch bodies (u), × 6600.

— 5–7: *Pometia pinnata* forma *glabra*. 5: approx. meridional section along one endoaperture showing exine and intine stratification, and apertural lamellae, × 3500; 6: part of oblique section with two apertural areas and interjacent mesocolpium showing exine stratification and sparse thin layer interpreted as endexine (en), × 5200; 7: part of oblique section (top right-hand corner near endoapertural area) showing exine stratification and sparse thin layer interpreted as endexine (en), × 2100. All sections prepared and photographed for van den Berg (1978).

Other abbreviations explained on p. 192.

Plate 55. *Smelophyllum* and *Stadmania*, TEM photographs.

— 1, 2: *Smelophyllum capense*. 1: cross section marginal part mesocolpial wall showing exine stratification, × 14500; 2: oblique section, × 3300.

— 3: *Stadmania serratula*, cross section endoapertural area showing intine stratification, endoaperture filling (ef; compare with plate 34: 5), and Ubisch bodies (u), × 8400.

— 4–7: *Stadmania oppositifolia* subsp. *rhodesica*. 4: approx. equatorial section with one (two) endoaperture(s), × 3300; 5: detail of 4 showing stratification mesocolpial wall, × 5500; 6: approx. equatorial section with one endoaperture, × 3300; 7: detail of 6 showing endoaperture with endoaperture filling (ef) and marginal part mesocolpial wall, × 8400.

Other abbreviations explained on p. 192.

Plate 56. *Xerospermum*, TEM photographs.

— 1–3: *X. laevigatum* subsp. *acuminatum*. 1: oblique sections and Ubisch bodies (u), × 3300; 2: cross section mesocolpial wall part with Ubisch bodies (u) and pollenkitt (p), × 12900; 3: detail of 1 showing exine and intine stratification, and tangential section through tectum (with perforations) and columellate layer in top left-hand corner, × 12900.

— 4, 5: *X. laevigatum* subsp. *laevigatum* (Kerr 17341). 4: approx. meridional section endoapertural area showing exine and intine stratification and electron-lucent lamellae (l) in outer endexine of adjacent grain, × 13500 (detail of 5); 5: parts of anther wall with Ubisch bodies (u), and approx. meridional section of grain showing endintinal folds (arrowheads), × 2900.

(Plate 56 continued)

— 6, 7: *X. noronhianum*. 6: equatorial section of grain showing endintinal folds (arrowheads), and parts of anther wall with Ubisch bodies (u), × 2500; 7: oblique section with one endoaperture showing endintinal evagination (ii) plus contents penetrating exintine (mi + oi) and reaching endoaperture (compare with plate 49: 1); adjacent grain (same grain, in approx. same position as in 6, but sectioned at different level) shows endintinal folds (arrowheads), × 2500.

Other abbreviations explained on p. 192.

Plate 57. *Alectryon* and *Cubilia*, LM photographs.

— 1–6: *A. diversifolius* (Mueller s.n. in Herb. Hookerianum). 1, 2: polar view; 3–6: equatorial view.

— 7, 8: *A. excelsus* (Travers s.n., M specimen). 7: mature and immature grain, × 700; 8: two immature grains.

— 9–12: *A. kangeanensis*. 9, 10: polar view; 11, 12: equatorial view.

— 13–16: *A. subcinereus* (NSW 106396). Unacetolysed grains from dehisced anther in oil. 13: polar view; 14–16: equatorial view.

— 17–26: *C. cubili* (PNH 22872). 17–20: polar view (20 showing intine ghost); 21, 22: equatorial view; 23–25: equatorial view; 26: three grains from dehisced anther in oil showing prolate grain shape.

× 1000, except 7. 17, 20 and 26 with 'interference contrast' (IC). Different foci mentioned together (for example '1, 2') pertain to the same grain. Upper foci precede lower foci.

Plate 58. *Dimocarpus*, *Litchi* and *Otonephelium*, LM photographs.

— 1–11: *D. longan* subsp. *malesianus* var. *malesianus* (1–6: SAN 62963, with striate ornamentation; 7–11: S 43524, with perforate ornamentation). 1, 2: polar view; 3–6: equatorial view (4 and 5 showing intine ghost); 7, 8: polar view (8 showing intine ghost); 9–11: equatorial view (10 and 11 showing intine ghost).

— 12–16: *D. longan* subsp. *malesianus* var. *echinatus* (SAN 26910, with scabrate ornamentation). 12, 16: polar view (16 showing intine ghost); 13–15: equatorial view.

— 17–20: *L. chinensis* subsp. *philippinensis* (BS 17429). 17, 18: polar view; 19, 20: equatorial view.

— 21–24: *O. stipulaceum* (Pascal 1375). 21, 22: polar view; 23, 24: equatorial view.

× 1000. Different foci mentioned together (for example '1, 2') pertain to the same grain. Upper foci precede lower foci.

Plate 59. *Nephelium*, *Pappea* and *Smelophyllum*, LM photographs.

— 1–6: *N. cuspidatum* var. *eriopetalum* (Endert 4867). 1, 2: polar view; 3–6: equatorial view.

— 7–12: *N. hypoleucum* (Bunchuai 1604). 7, 8: polar view; 9–12: equatorial view.

— 13–20: *P. capensis* (13–16: Gillett 5058; 17–20: Chase 7671). 13, 14: polar view (14 showing intine ghost); 15, 16: equatorial view; 17–19: polar view showing intine ghost, above, at and below equatorial plane respectively; 20: equatorial view showing intine ghost.

— 21–24: *S. capense* (Wells 3246). 21, 22: polar view (22 showing intine ghost); 23, 24: equatorial view.

× 1000. 17–20 and 22 with 'interference contrast' (IC). Different foci mentioned together (for example '1, 2') pertain to the same grain. Upper foci precede lower foci.

Plate 60. *Podonephelium* and *Pometia*, LM photographs.

— 1–8: *Podonephelium parvifolium*. 1, 2: polar view (2 showing intine ghost); 3, 4 equatorial view; 5–8: equatorial view (6 showing intine ghost).

— 9–14: *Pometia pinnata* forma *glabra* (NIFS bb 29745). 9–11: polar view; 12–14: equatorial view.

— 15–17: *Pometia pinnata* (NBFD 9087). Unacetolysed grains from dehisced anther in oil. 15: three grains of which two show air in and under endoapertures (the left-hand grain is a composition of an upper and a lower focus), × 600; 16: polar view; 17: equatorial view.

× 1000, except 15. Different foci mentioned together (for example '1, 2') pertain to the same grain. Upper foci precede lower foci.

Plate 61. *Stadmania* and *Xerospermum*, LM photographs.

— 1, 2: *S. oppositifolia* subsp. *oppositifolia* var. *oppositifolia* (Bradburne 102), tetrads showing grain arrangement according to Fischer's Law, × 800.

— 3–6: *S. serratula*. 3, 4: polar view; 5, 6: equatorial view.

— 7–14: *X. laevigatum* subsp. *laevigatum* (S 18096). 7, 8: polar view (8 showing intine ghost): 9, 10, 13, 14: equatorial view (13 showing intine ghost); 11, 12: polar view showing intine ghost.

— 15–17: *X. noronhianum* (Jacobs 5252). Unacetolysed grains from undehisced anther in glycerine jelly showing intine folds below apertures. 15, 16: polar view; 17: equatorial view.

— 18–20: *X. laevigatum* subsp. *laevigatum* (Kerr 17341). Unacetolysed grains from dehisced anther in oil. 18, 20: four grains showing prolate grain shape (top left-hand grain in polar view, the others in equatorial view); 19: five grains showing prolate grain shape.

× 1000, except 1 and 2. 11, 12, 14 and 18–20 with 'interference contrast' (IC). Different foci mentioned together (for example '3, 4') pertain to the same grain. Upper foci precede lower foci.

Explanation abbreviations

c = columellate layer, **cm** = colpus membrane, **en** = endexine, **endo** = endoaperture, **ef** = endoaperture filling, **ext** = electron-opaque extension of middle sublayer tract into inner oncus sublayer, **f** = foot layer, **i** = intine, **ii** = inner sublayer of oncus intine, **inc** = electron-opaque inclusion in outermost mesocolpial intine, **l** = electron-lucent lamella, **mi** = middle sublayer of oncus intine, **n** = nexine, **o** = oncus, **oi** = outer sublayer of oncus intine, **p** = pollenkitt, **t** = tectum, **tr** = parts of tubular/labyrinthic tract in middle sublayer of oncus intine, **u** = Ubisch body.

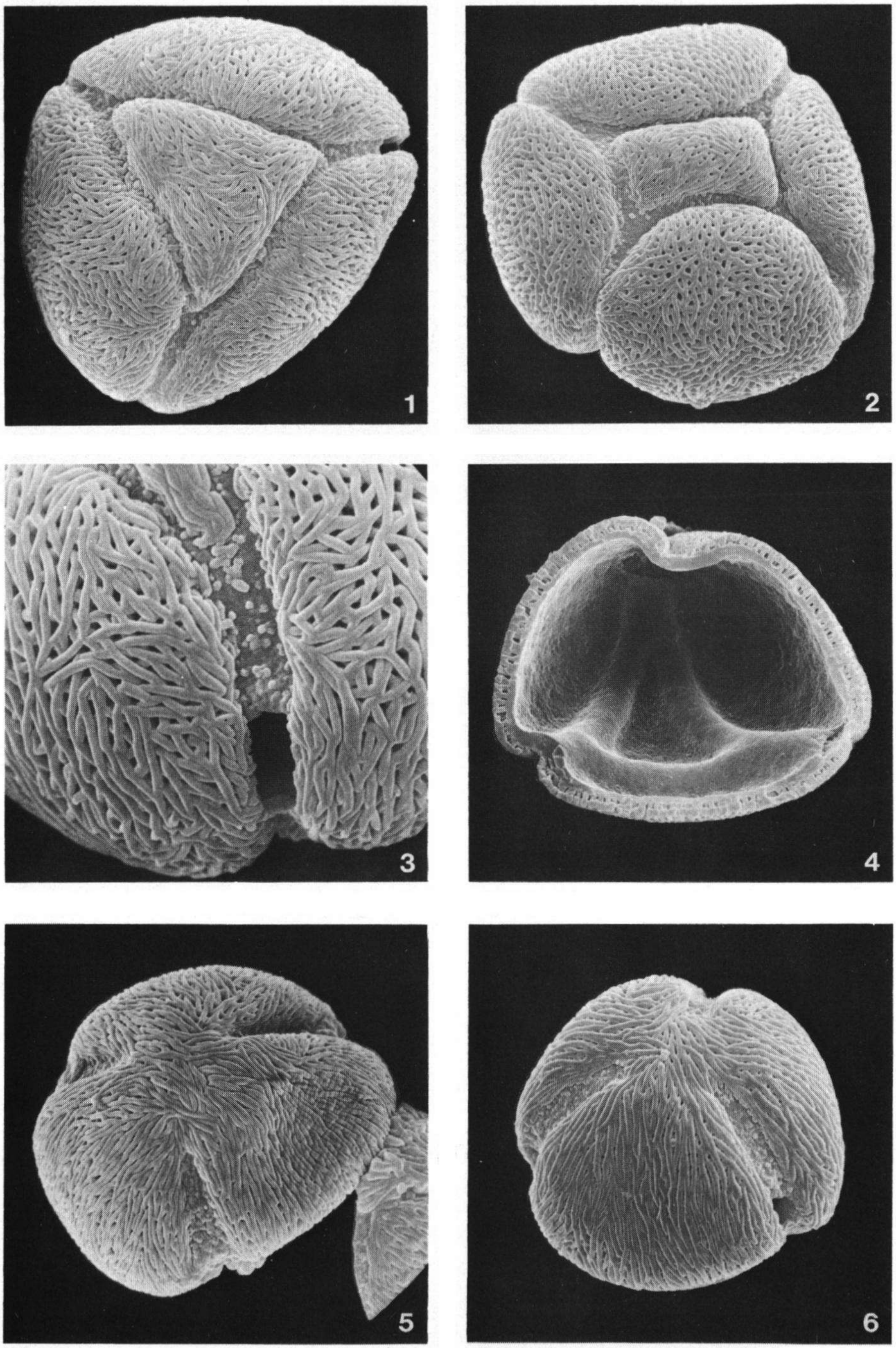


Plate 1: *Alectryon affinis* (1–4), *cardiocarpus* (5), *carinatus* (6).

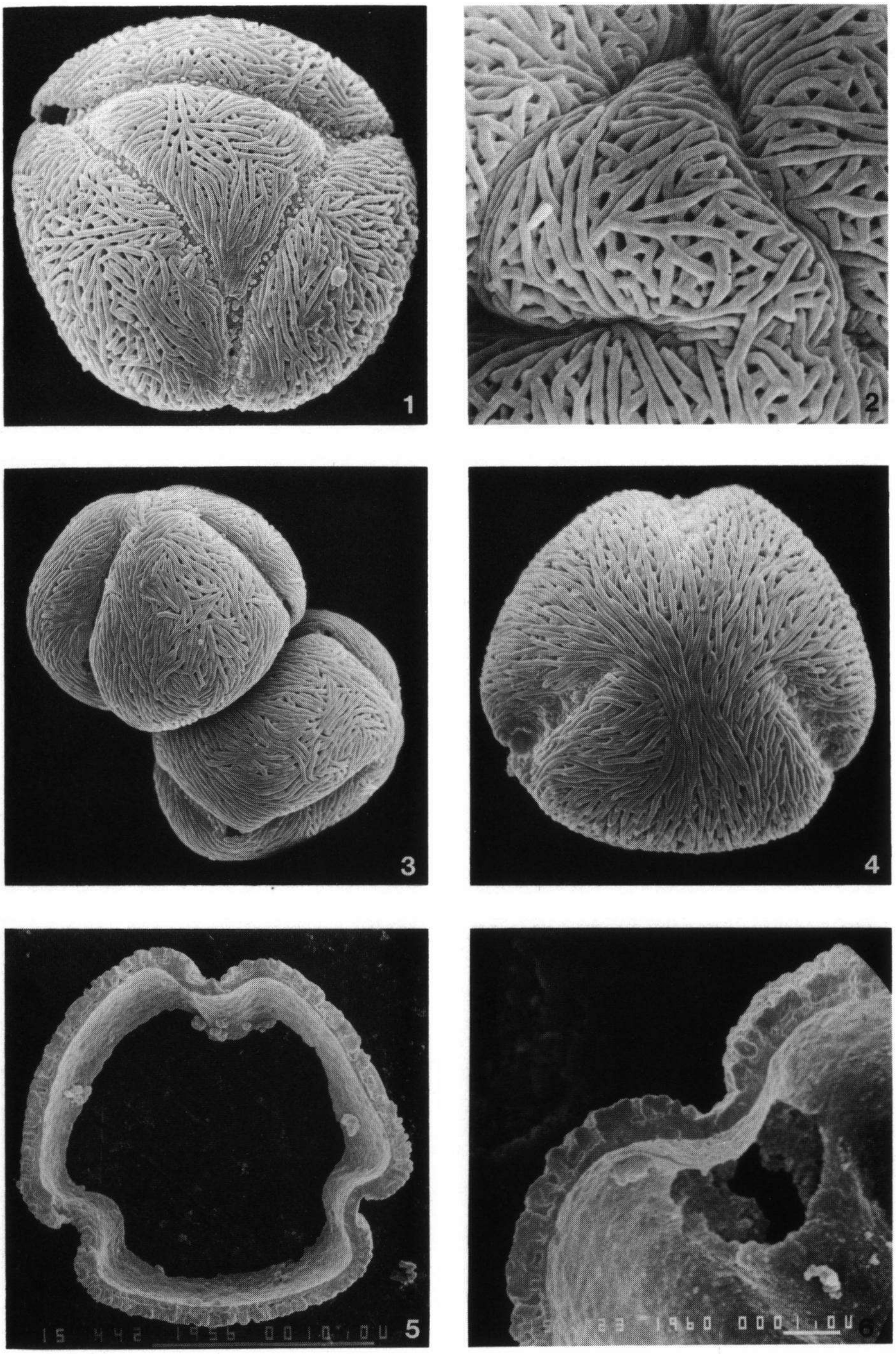


Plate 2: *Alectryon connatus* (1, 2), *coriaceus* (3), *diversifolius* (4–6).

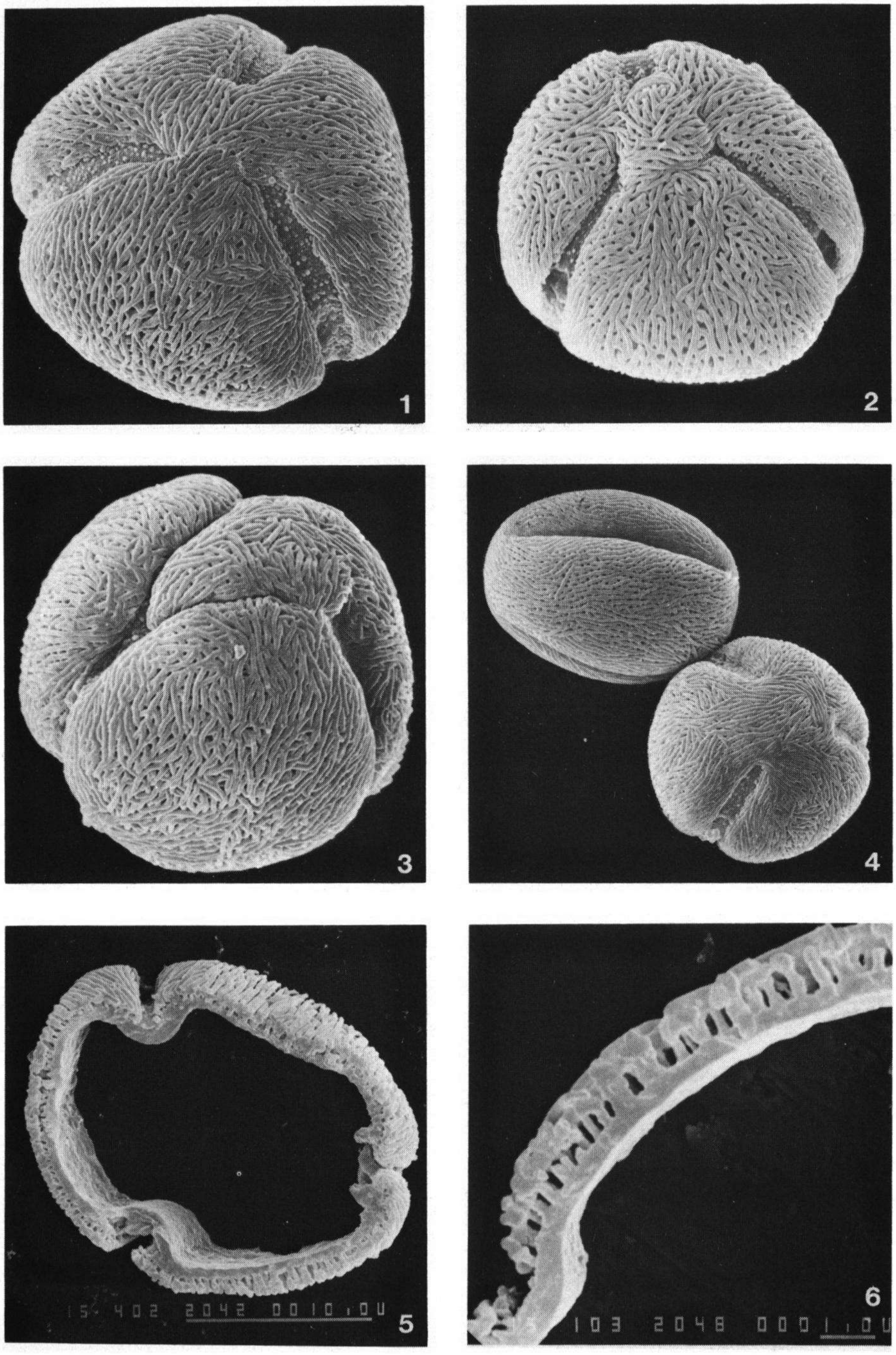


Plate 3: *Alectryon excelsus.*

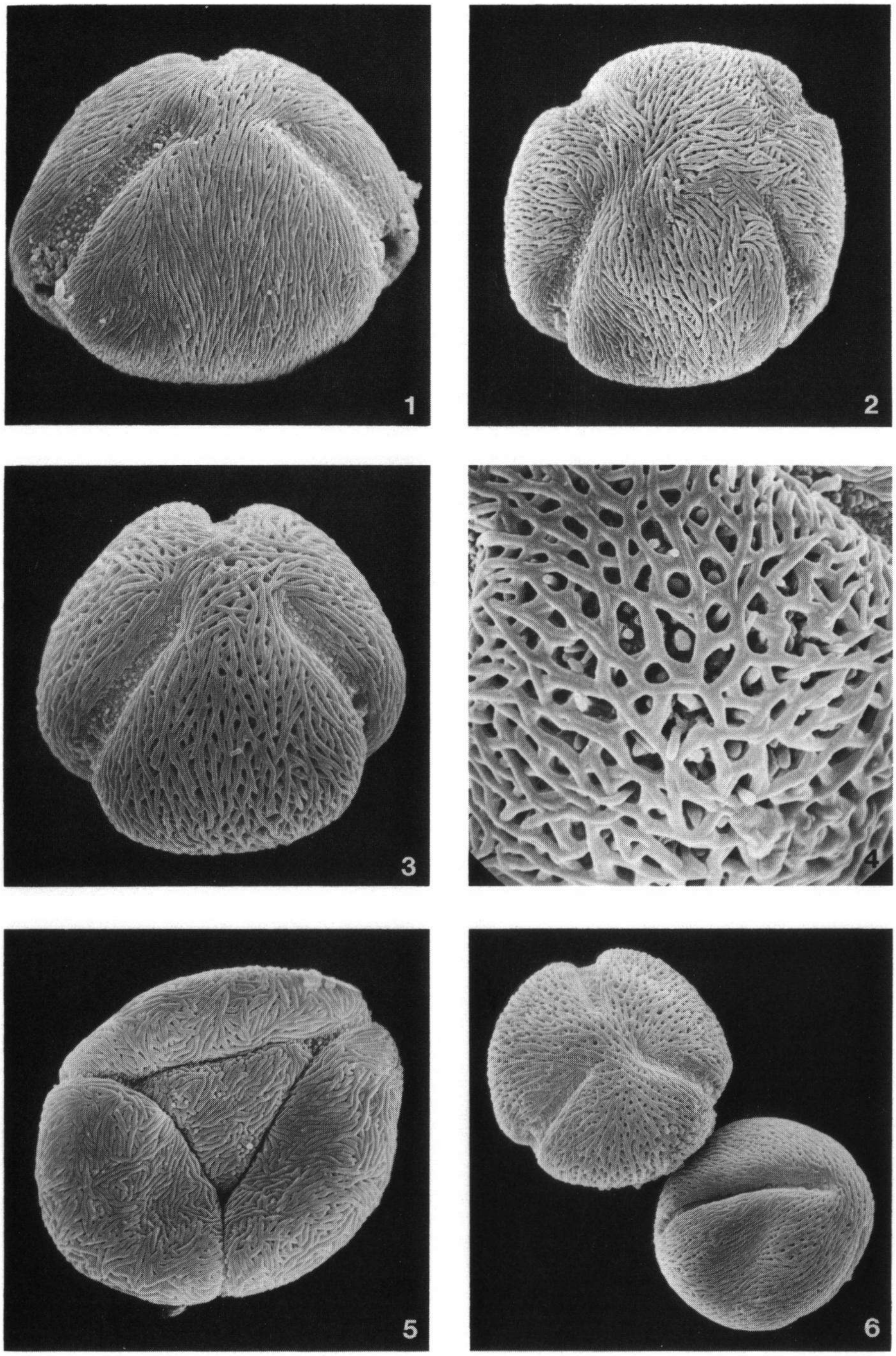


Plate 4: *Alectryon ferrugineus* (1, 2), *forsythii* (3, 4), *fuscus* (5), *glaber* (6).

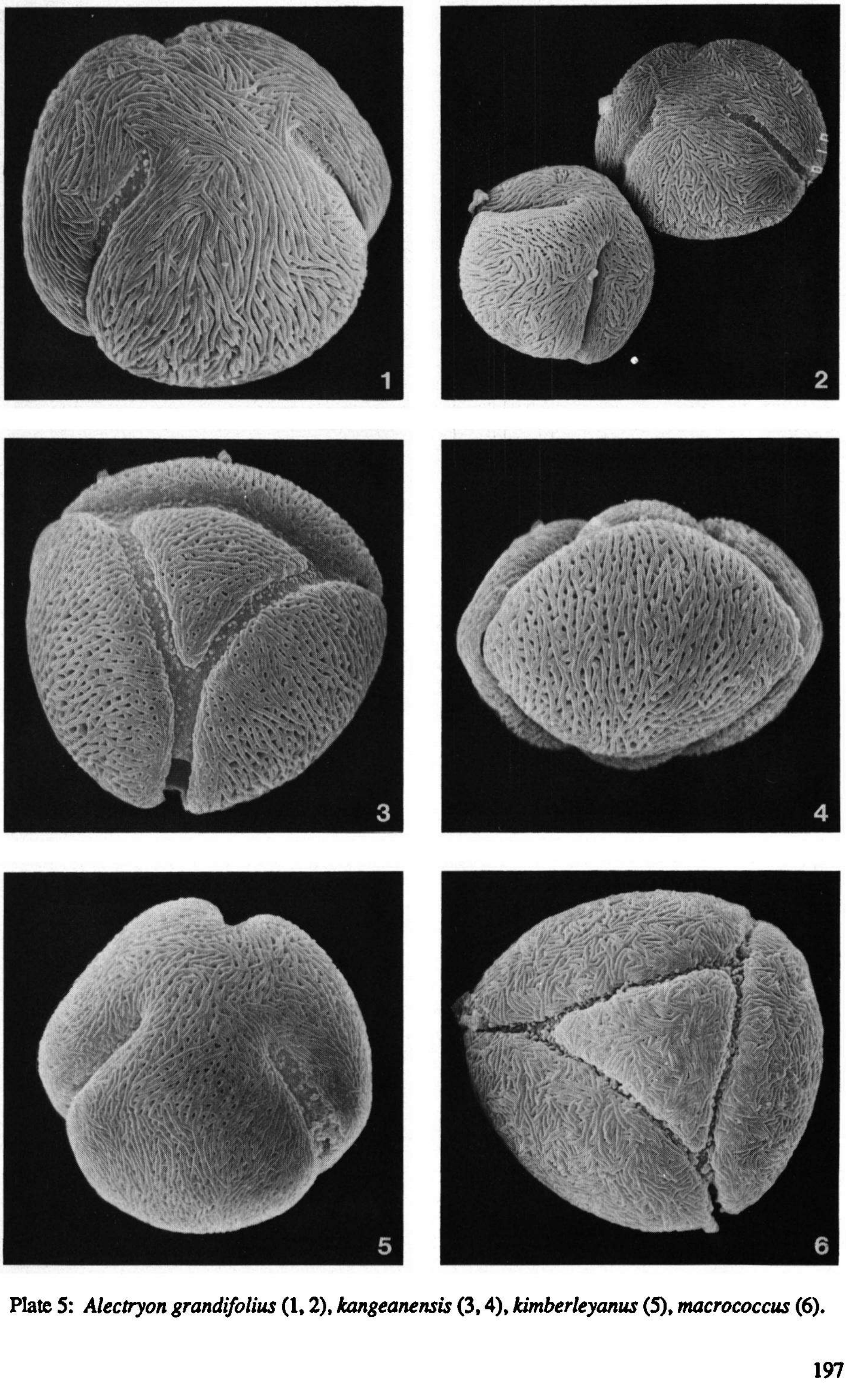


Plate 5: *Alectryon grandifolius* (1, 2), *kangeanensis* (3, 4), *kimberleyanus* (5), *macrococcus* (6).

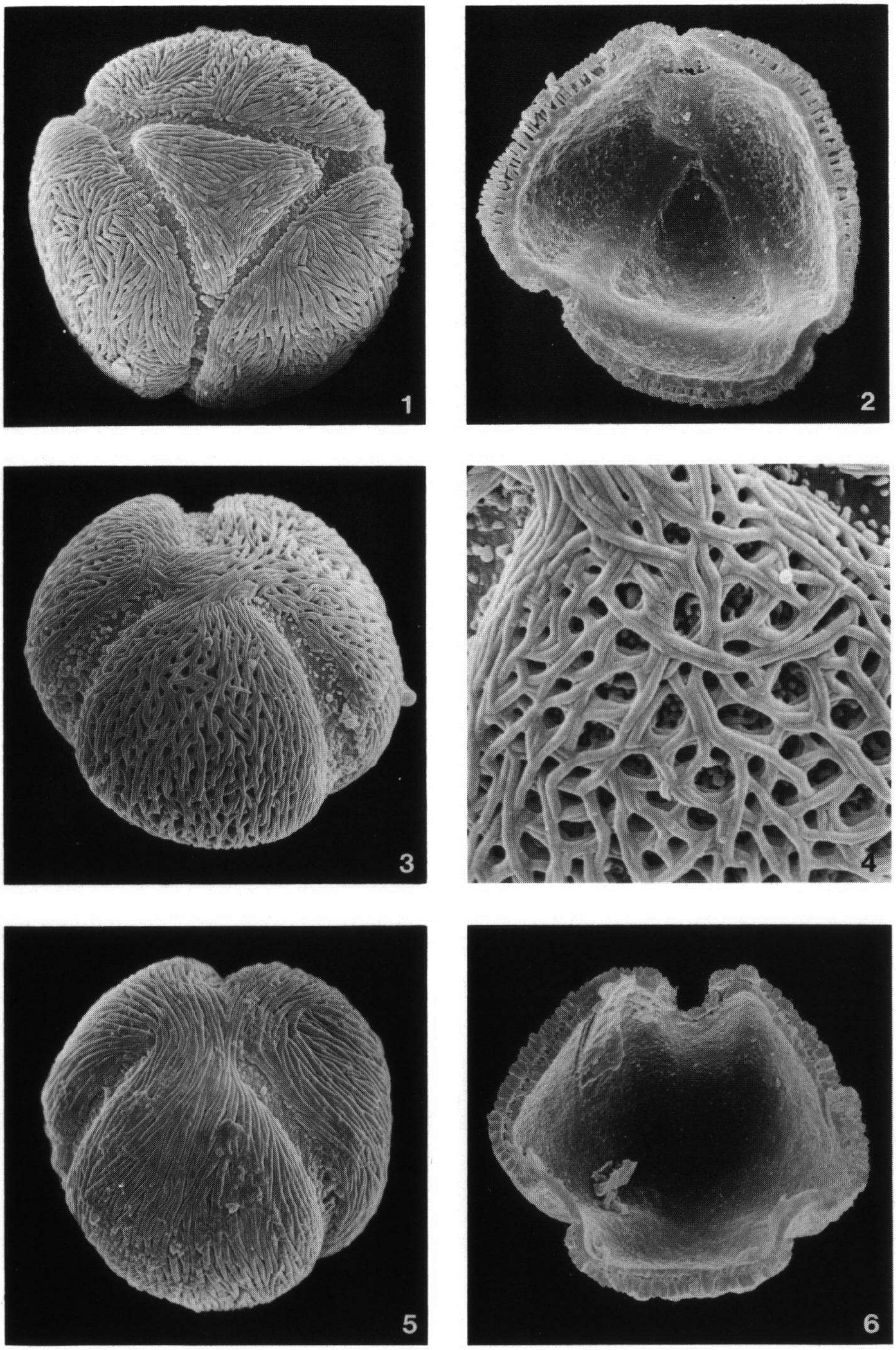


Plate 6: *Alectryon myrmecophilus* (1, 2), *oleifolius* (3–6).

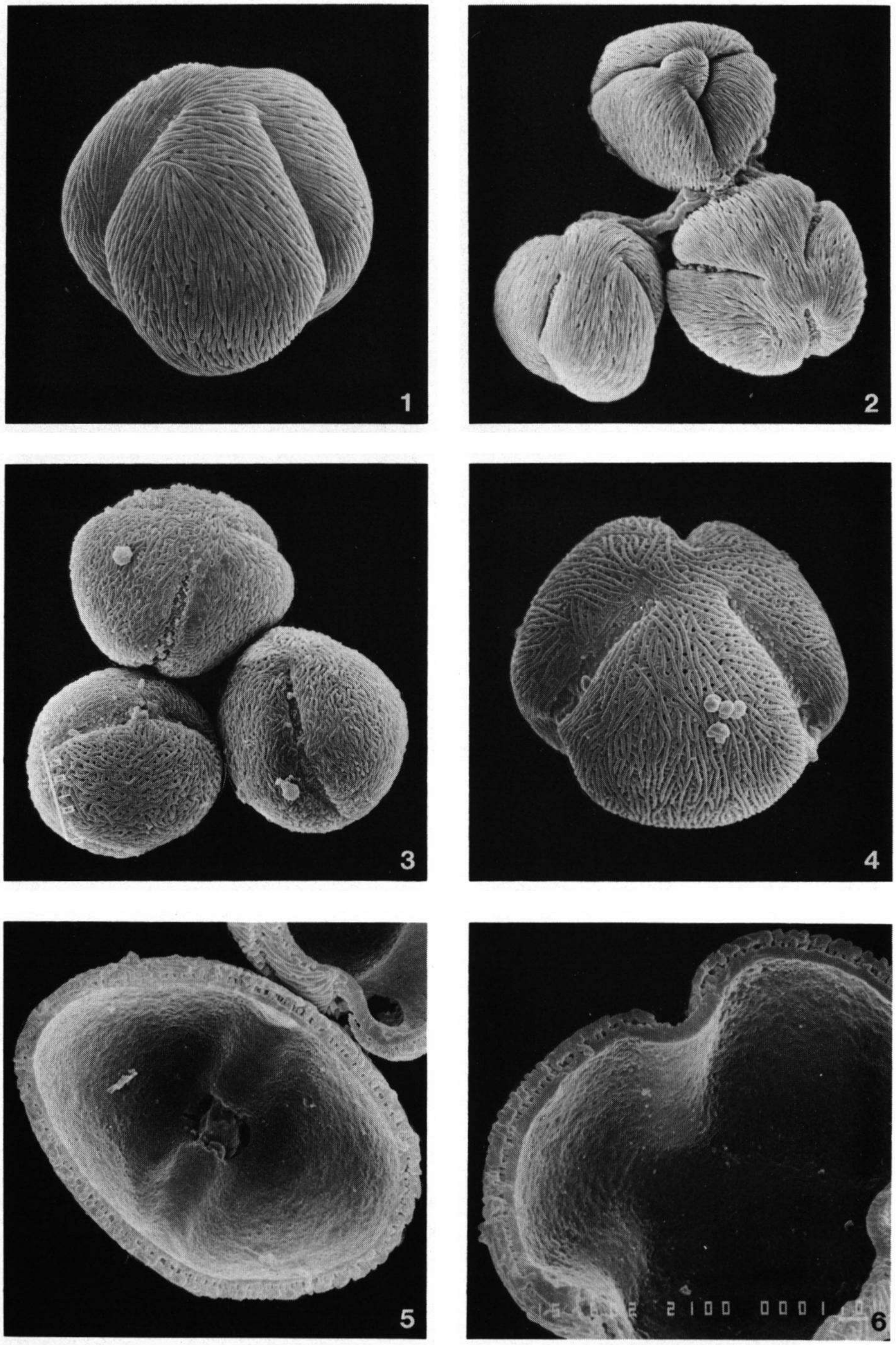


Plate 7: *Alectryon pubescens* (1, 2), *ramiflorus* (3), *repandodentatus* (4–6).

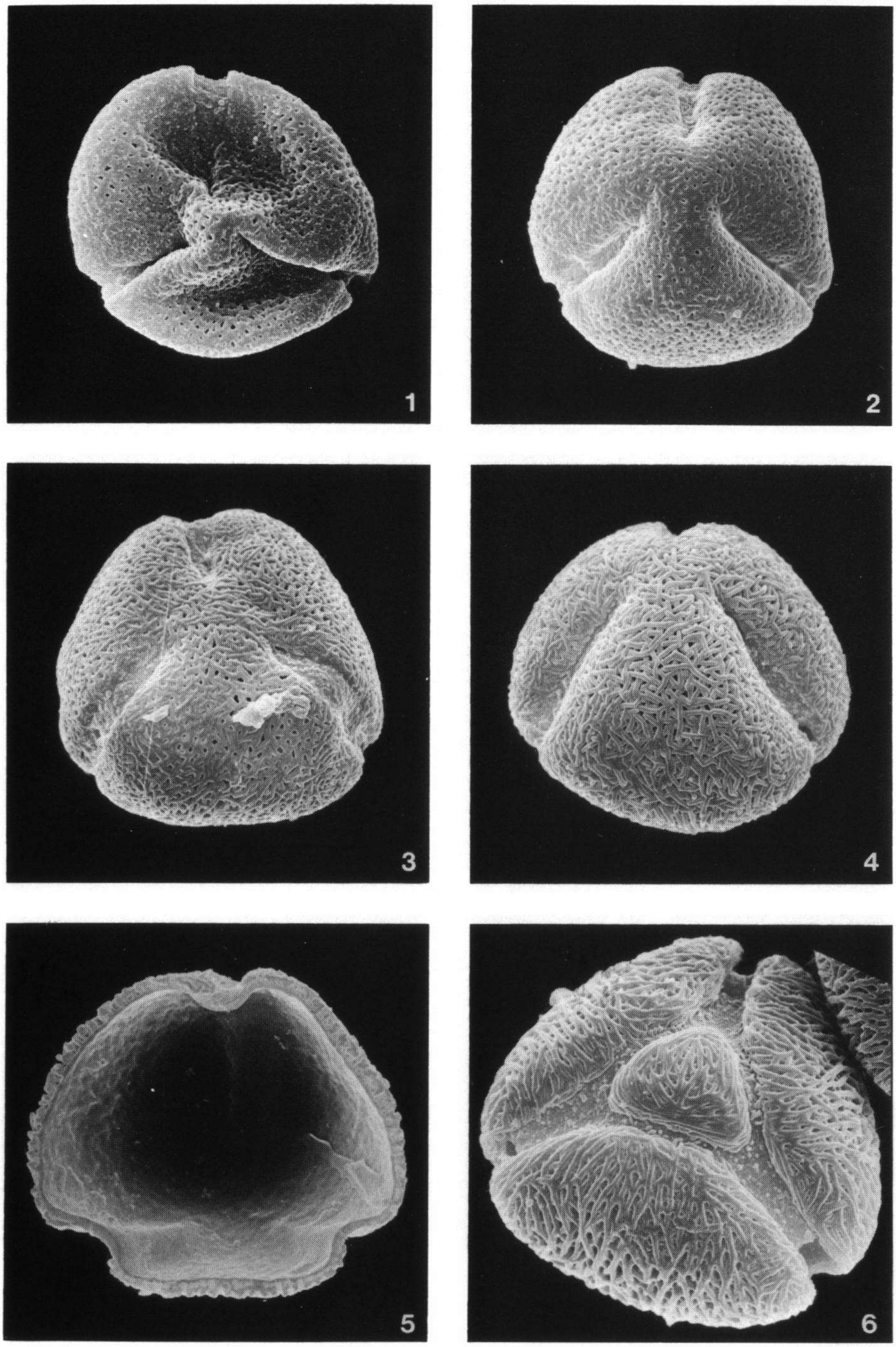


Plate 8: *Alectryon reticulatus.*

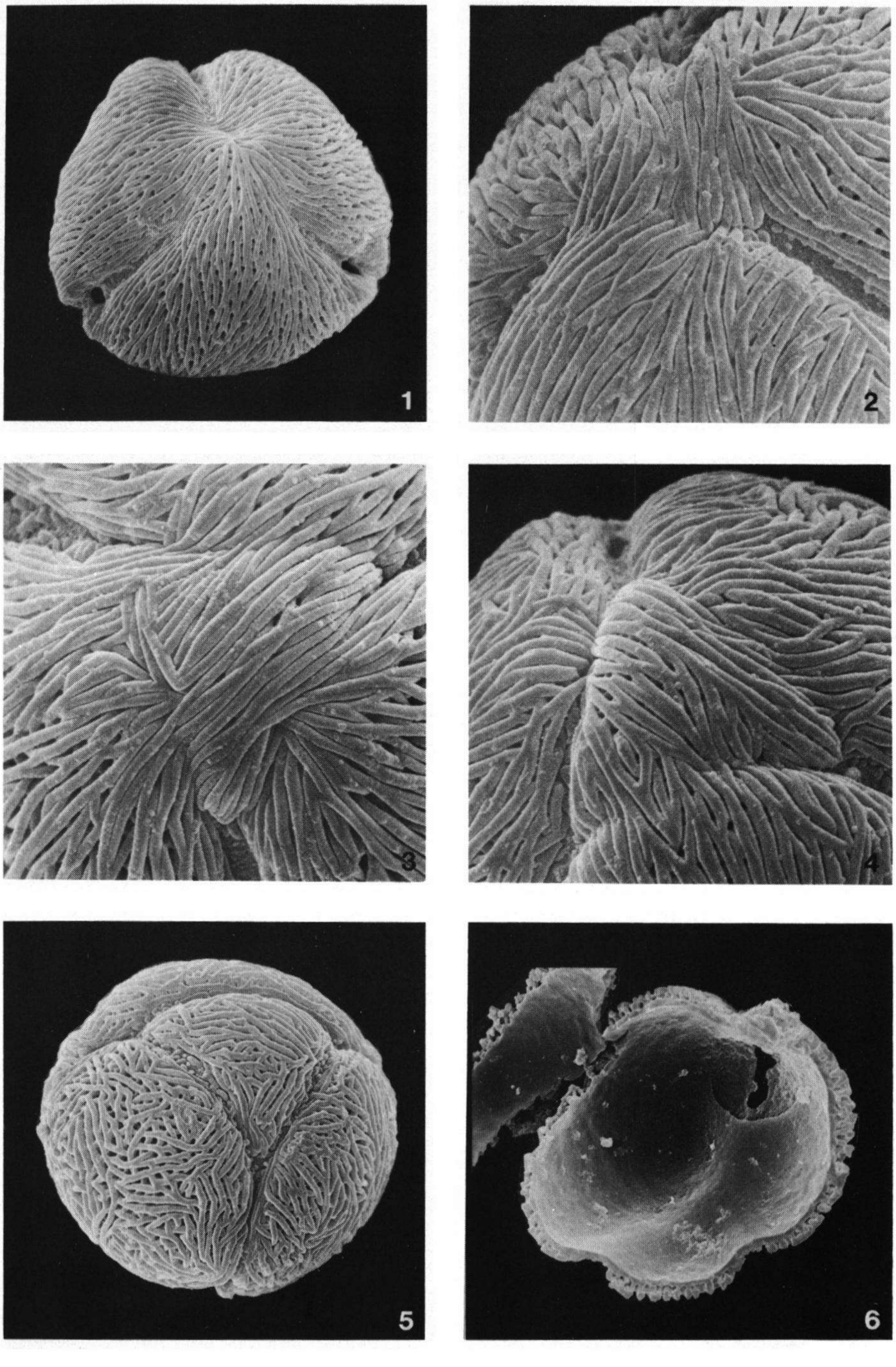


Plate 9: *Alectryon semicinereus* (1–4), *subcinereus* (5, 6).

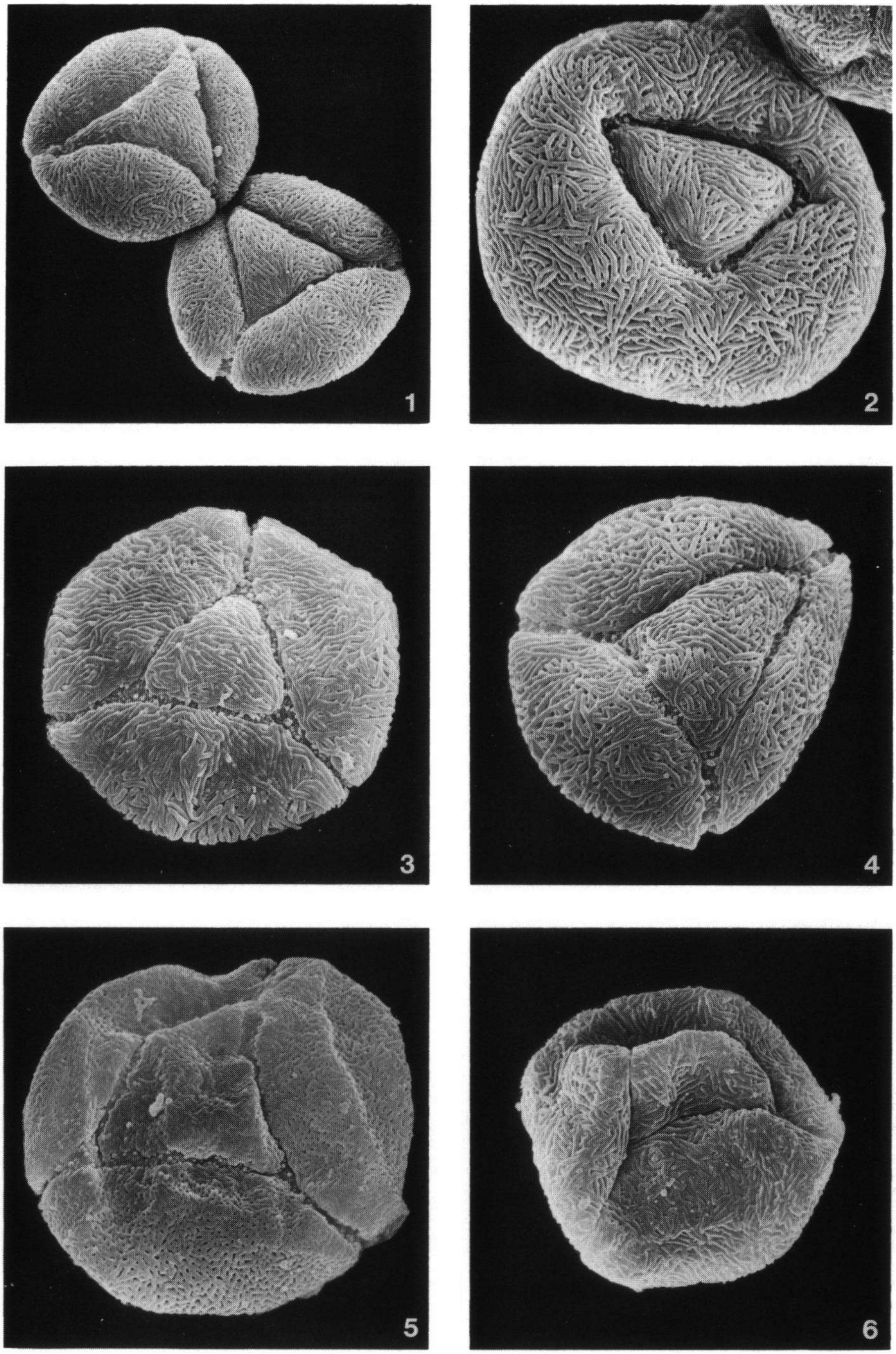


Plate 10: *Alectryon subcinereus* (1, 2), *samoënsis* (3–6).

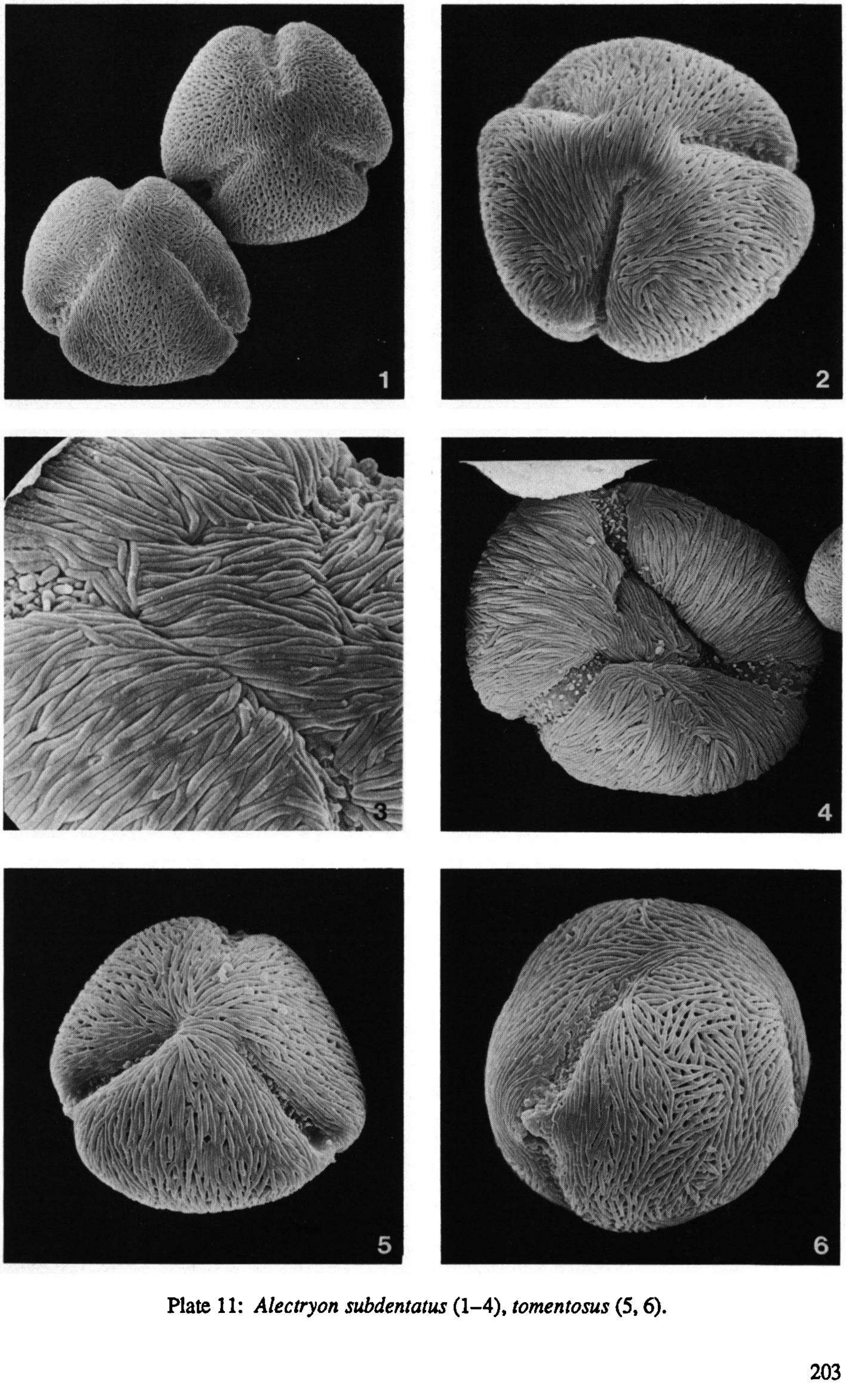
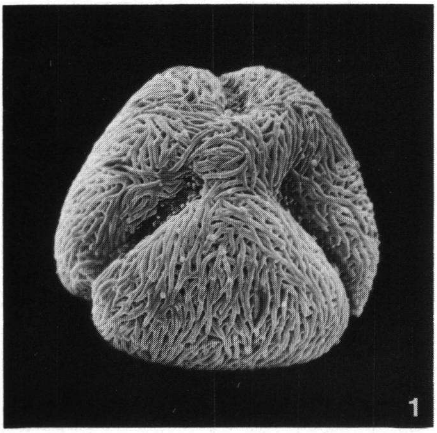
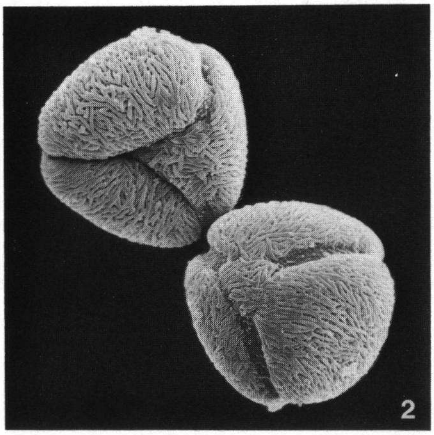
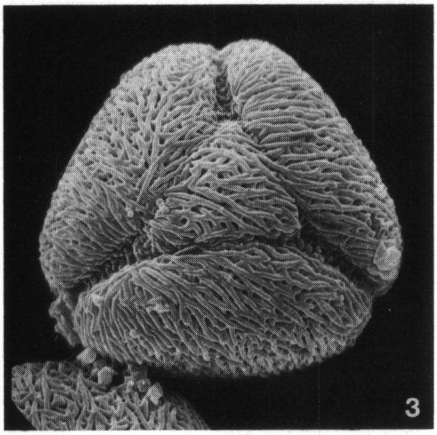
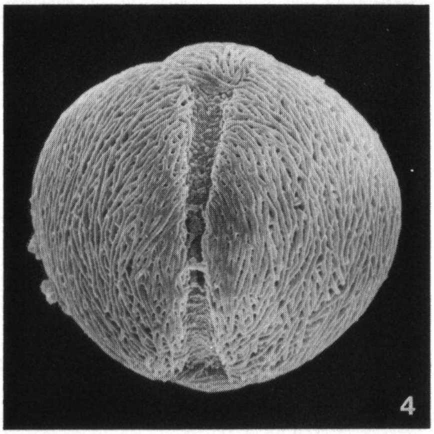


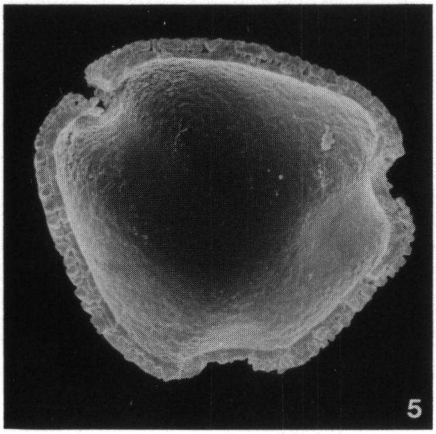
Plate 11: *Alectryon subdentatus* (1–4), *tomentosus* (5, 6).











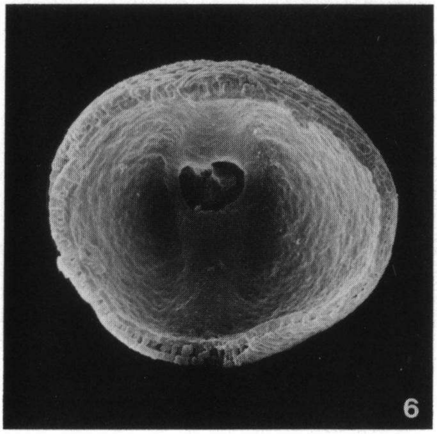


Plate 12: *Alectryon unilobatus.*

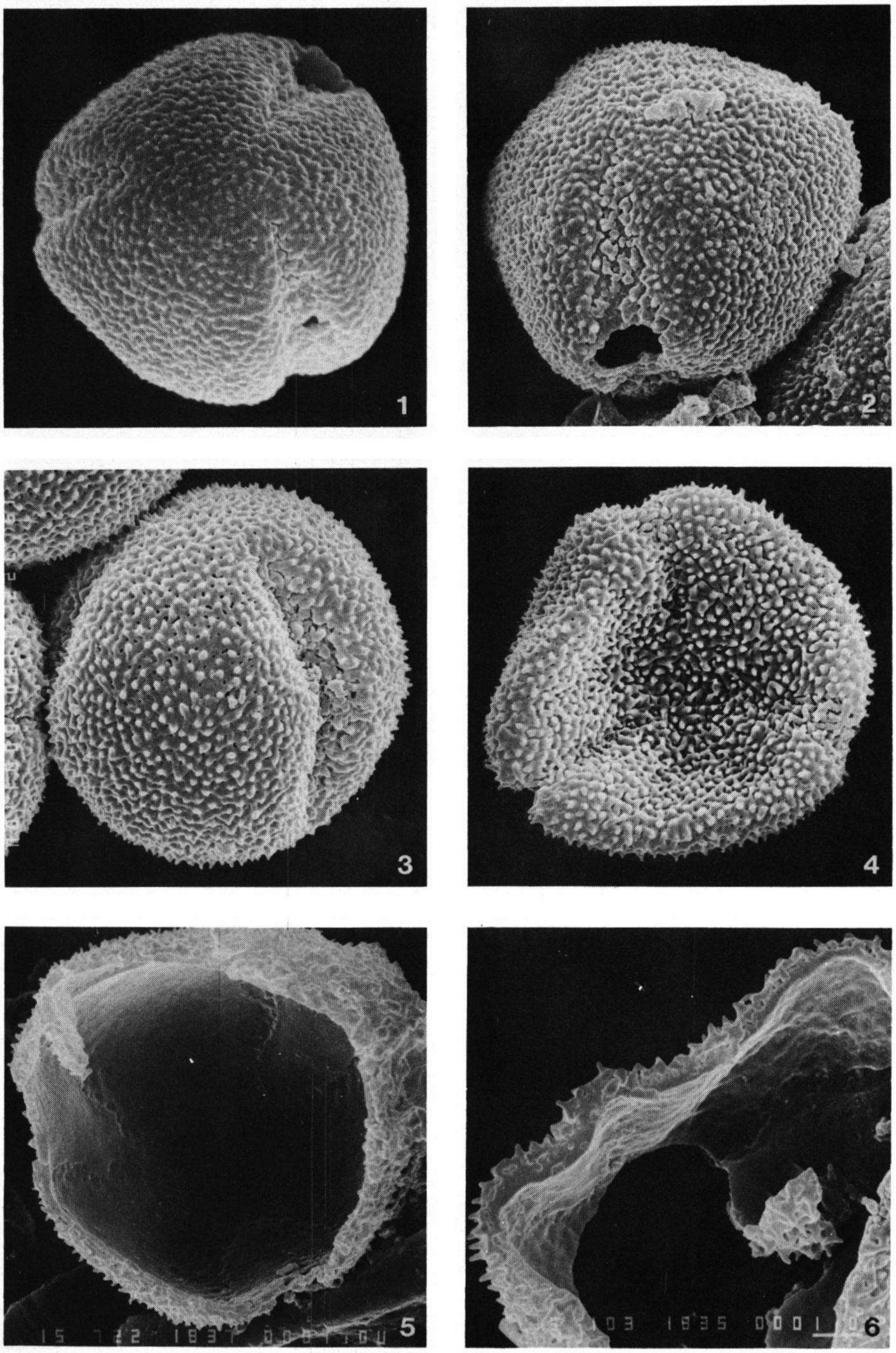


Plate 13: *Cubilia cubili.*

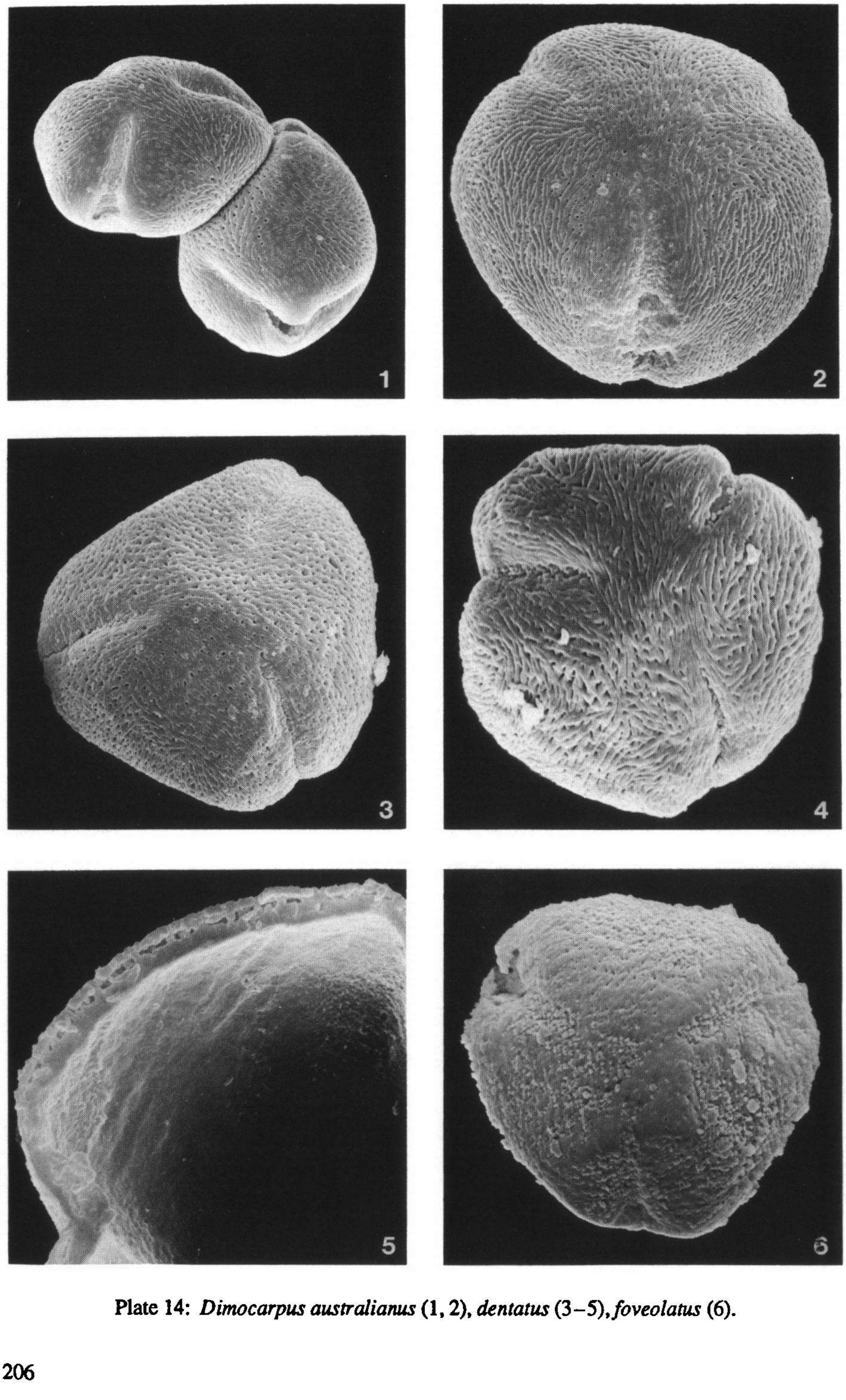


Plate 14: *Dimocarpus australianus* (1, 2), *dentatus* (3–5), *foveolatus* (6).

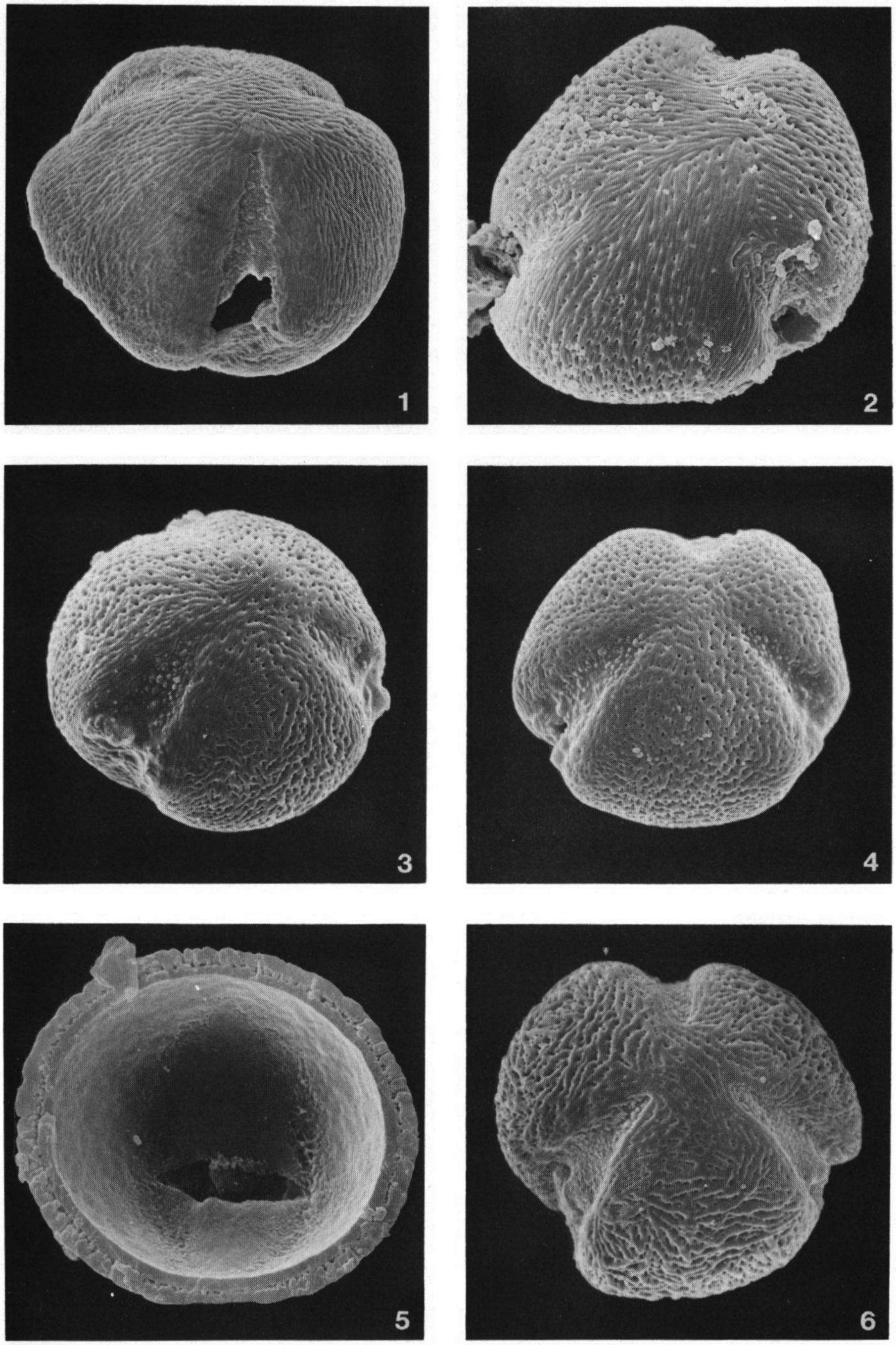


Plate 15: *Dimocarpus fumatus.*

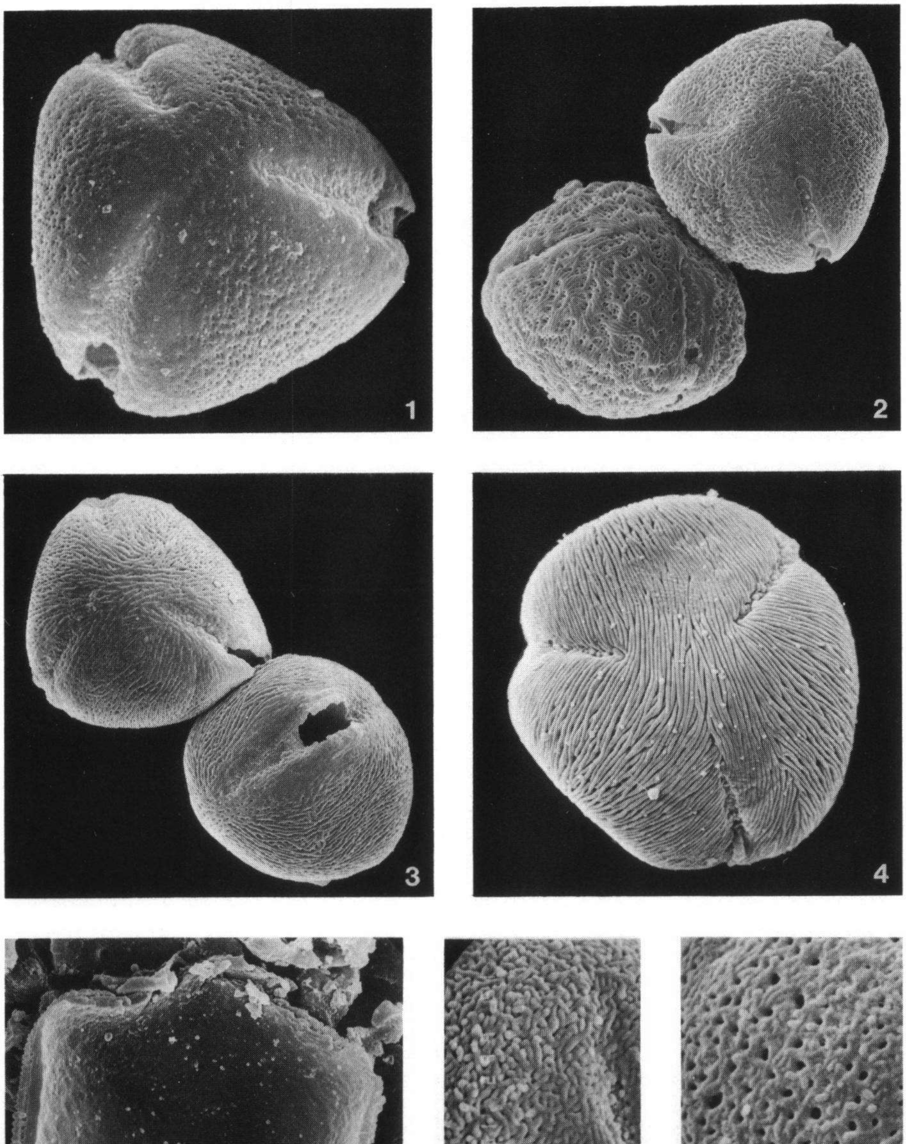


Plate 16: *Dimocarpus gardneri* (1), *leichhardtii* (2), *longan* (3–7).

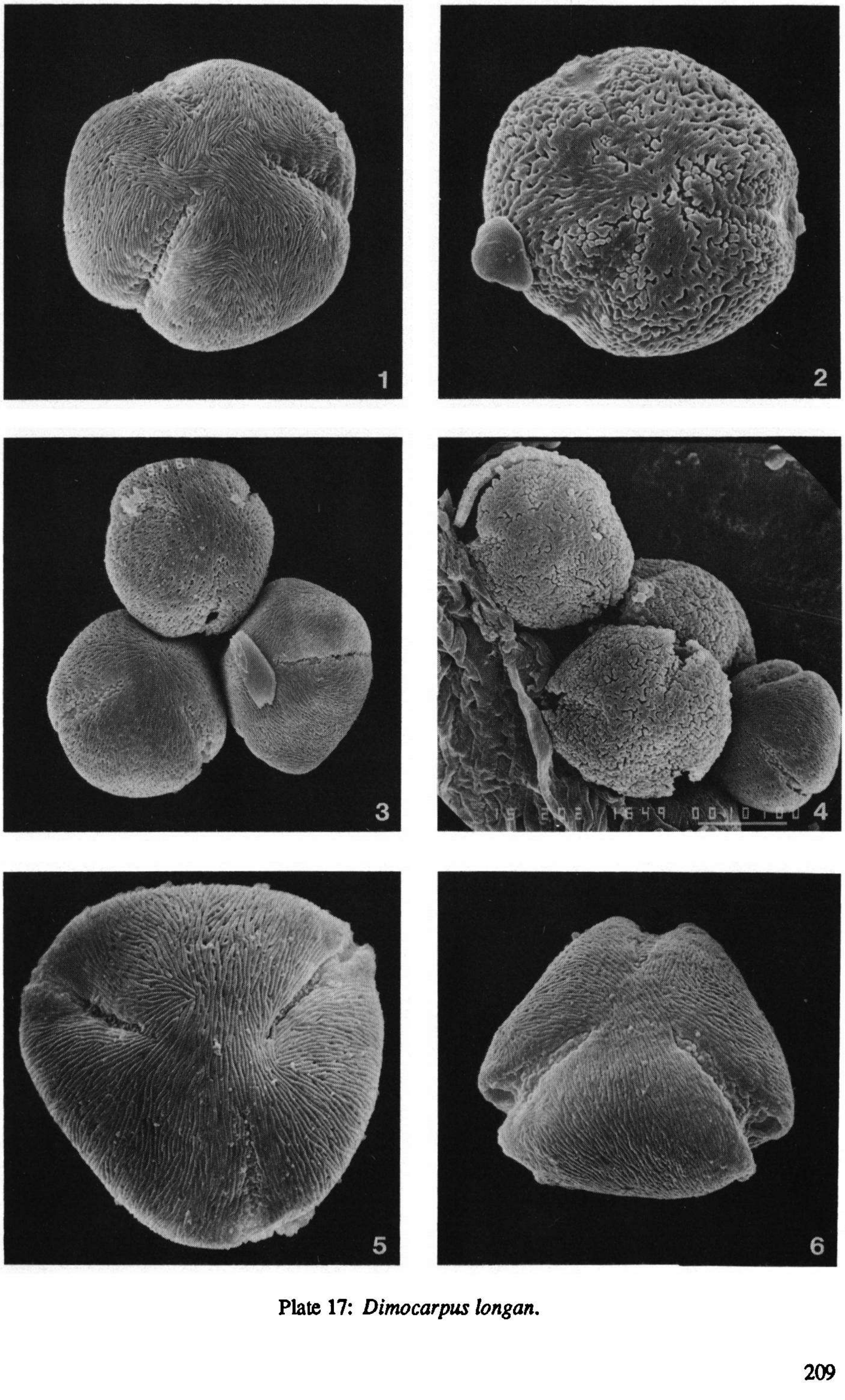


Plate 17: *Dimocarpus longan.*

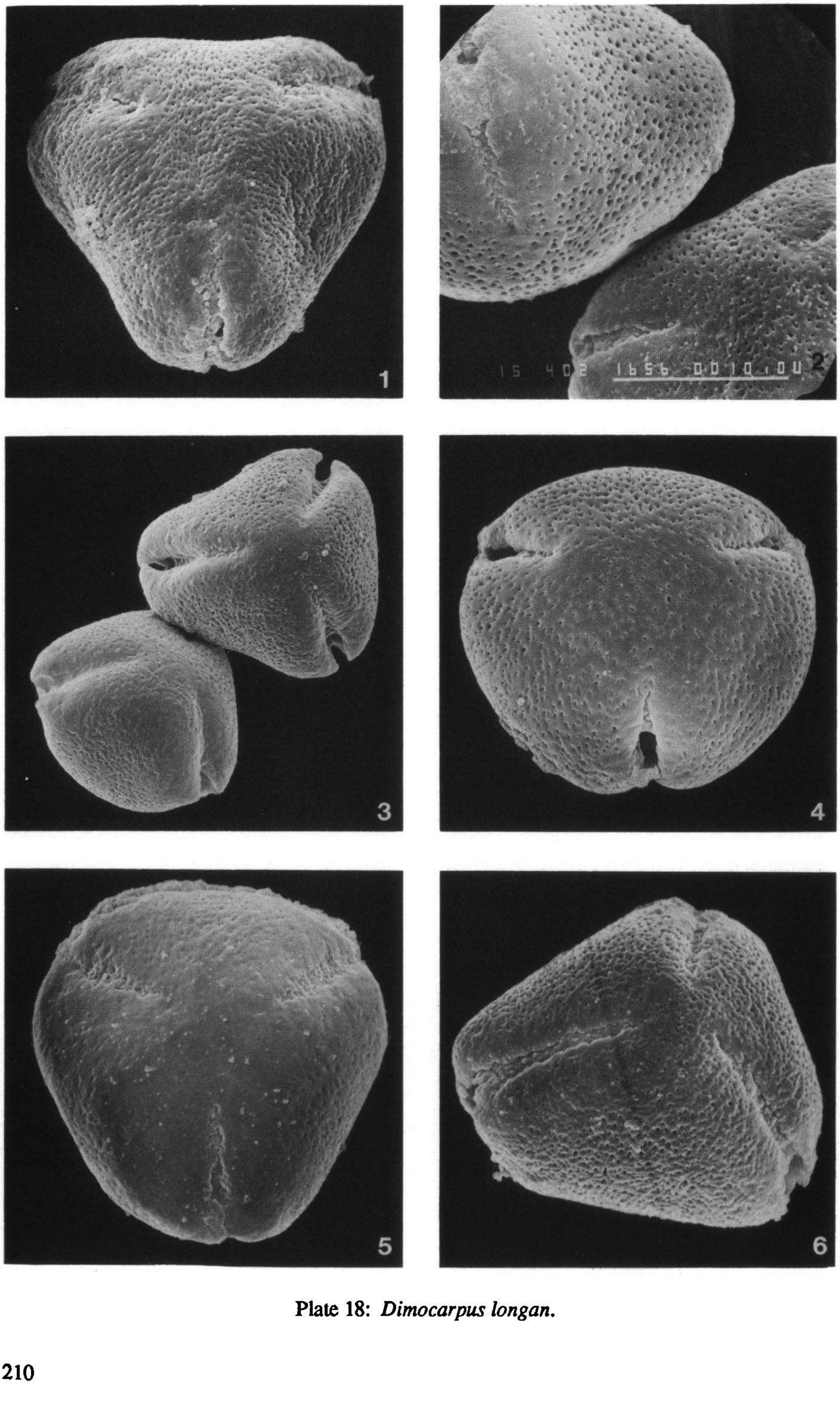


Plate 18: *Dimocarpus longan.*

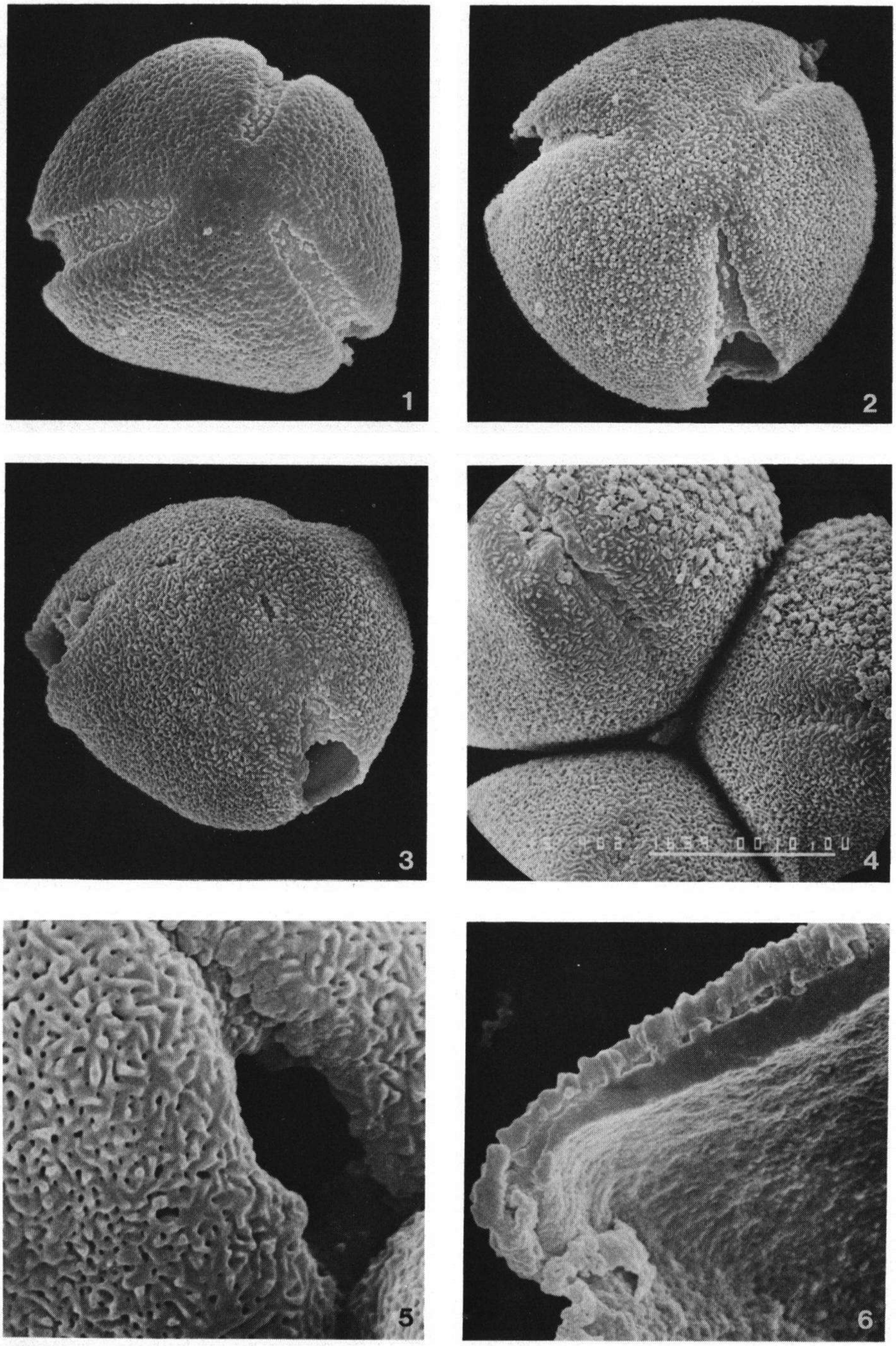


Plate 19: *Dimocarpus longan.*

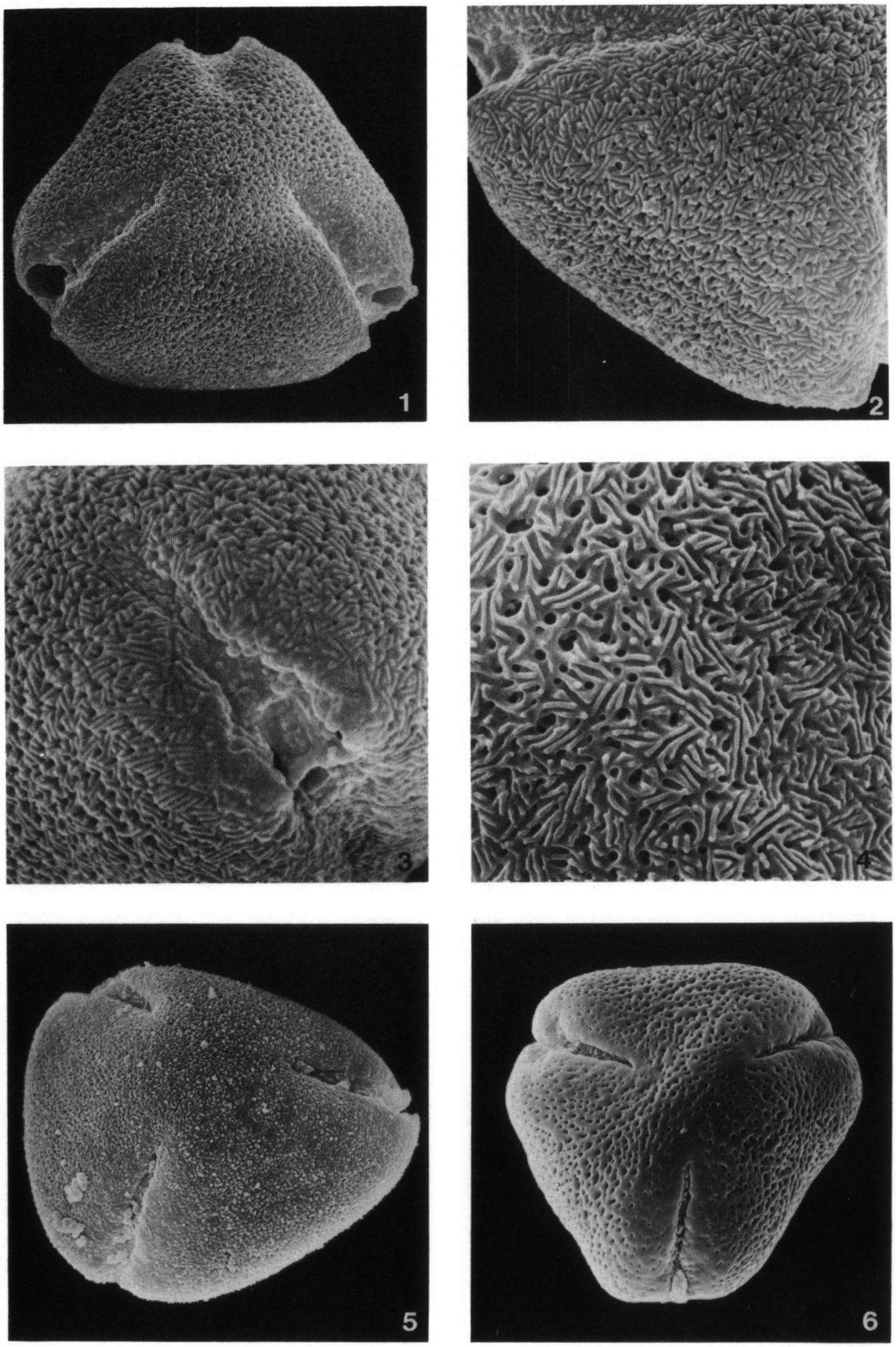


Plate 20: *Dimocarpus longan* (1–5), spec. (6).

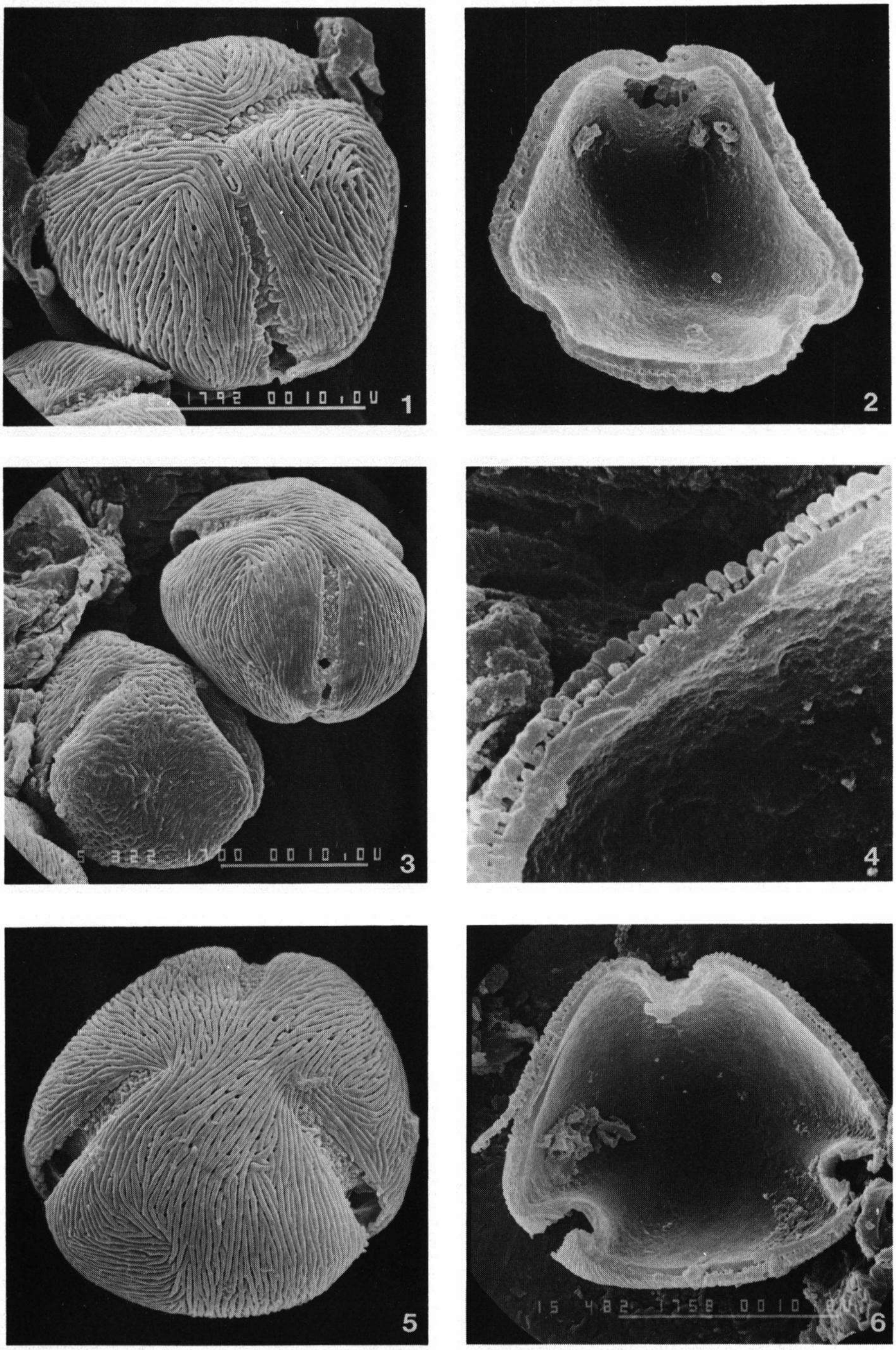
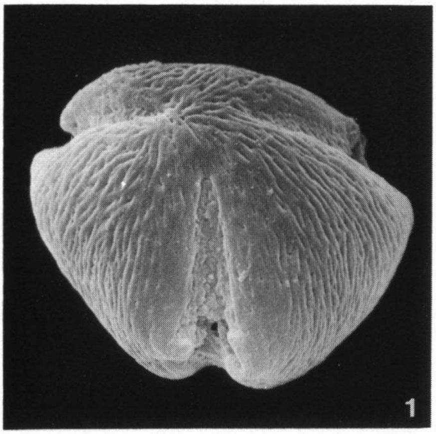
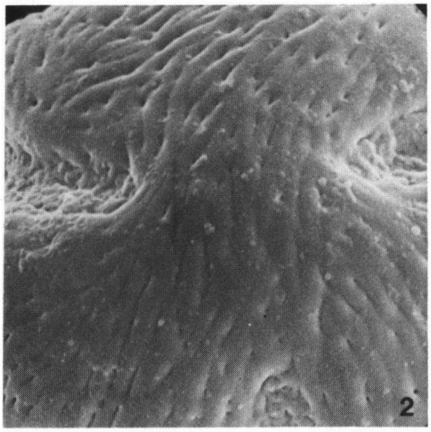
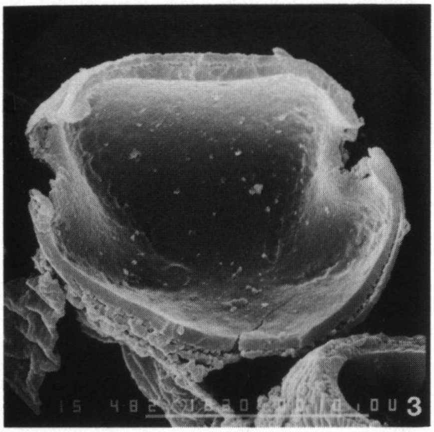
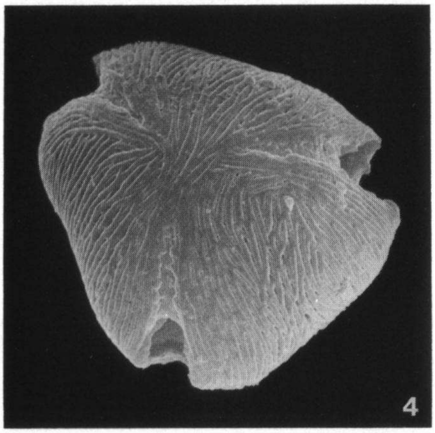


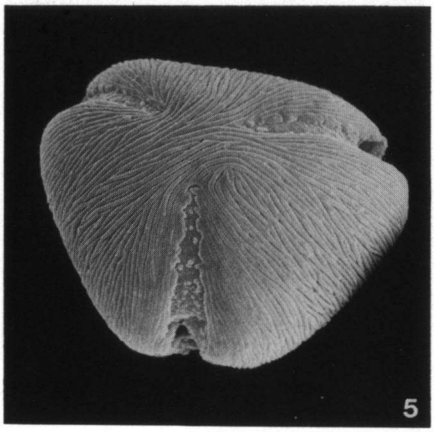
Plate 21: *Litchi chinensis.*











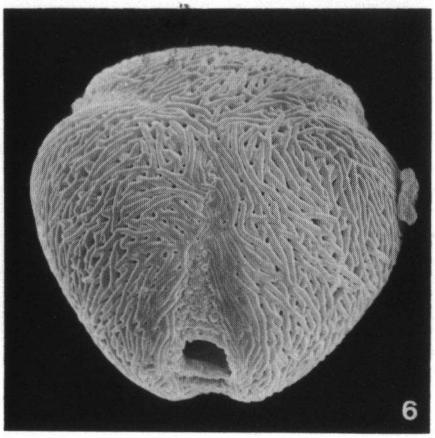


Plate 22: *Nephelium compressum* (1–3), *costatum* (4), *cuspidatum* (5, 6).

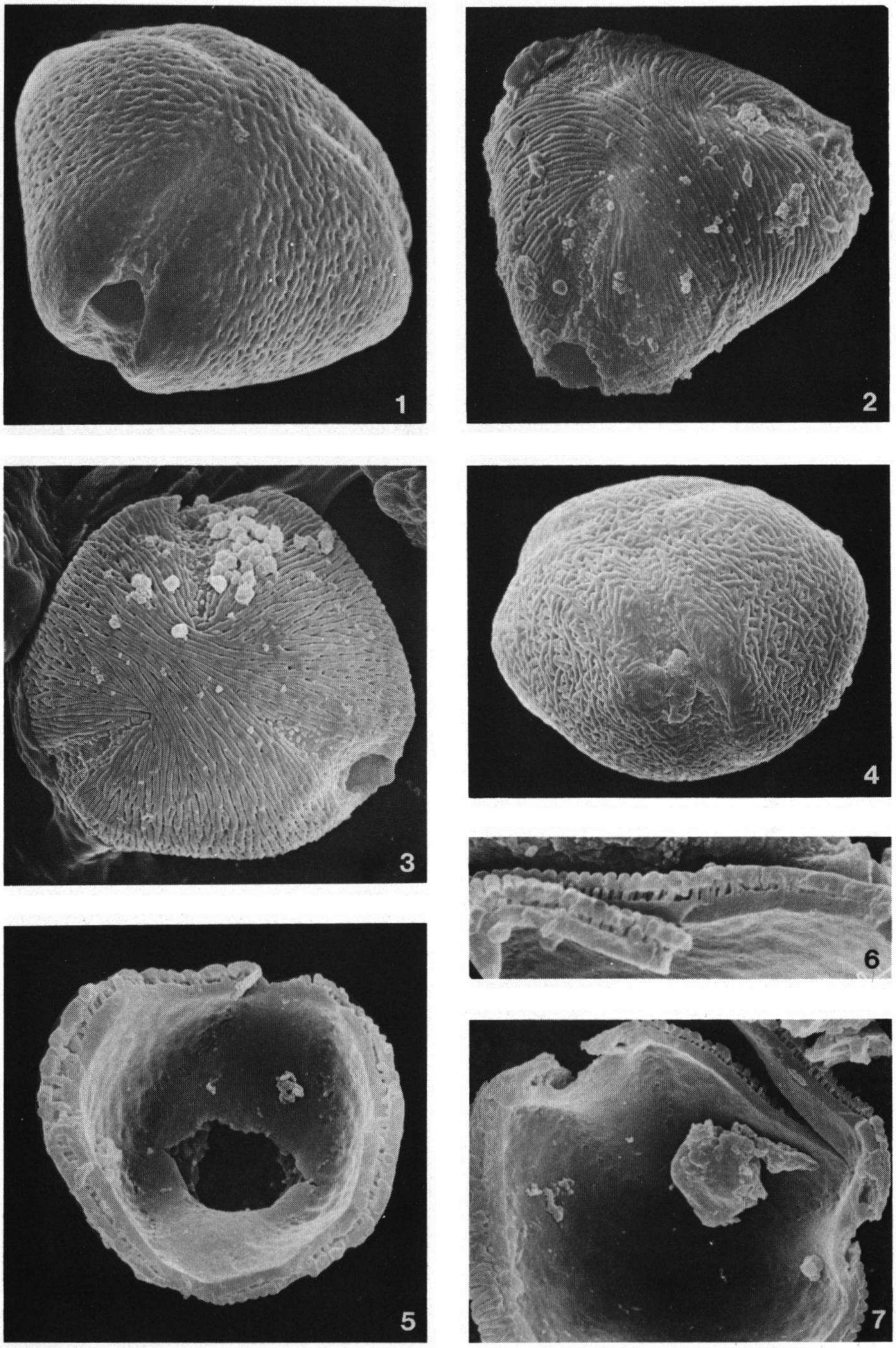


Plate 23: *Nephelium daedaleum* (1), *hamulatum* (2), *havilandii* (3–7).

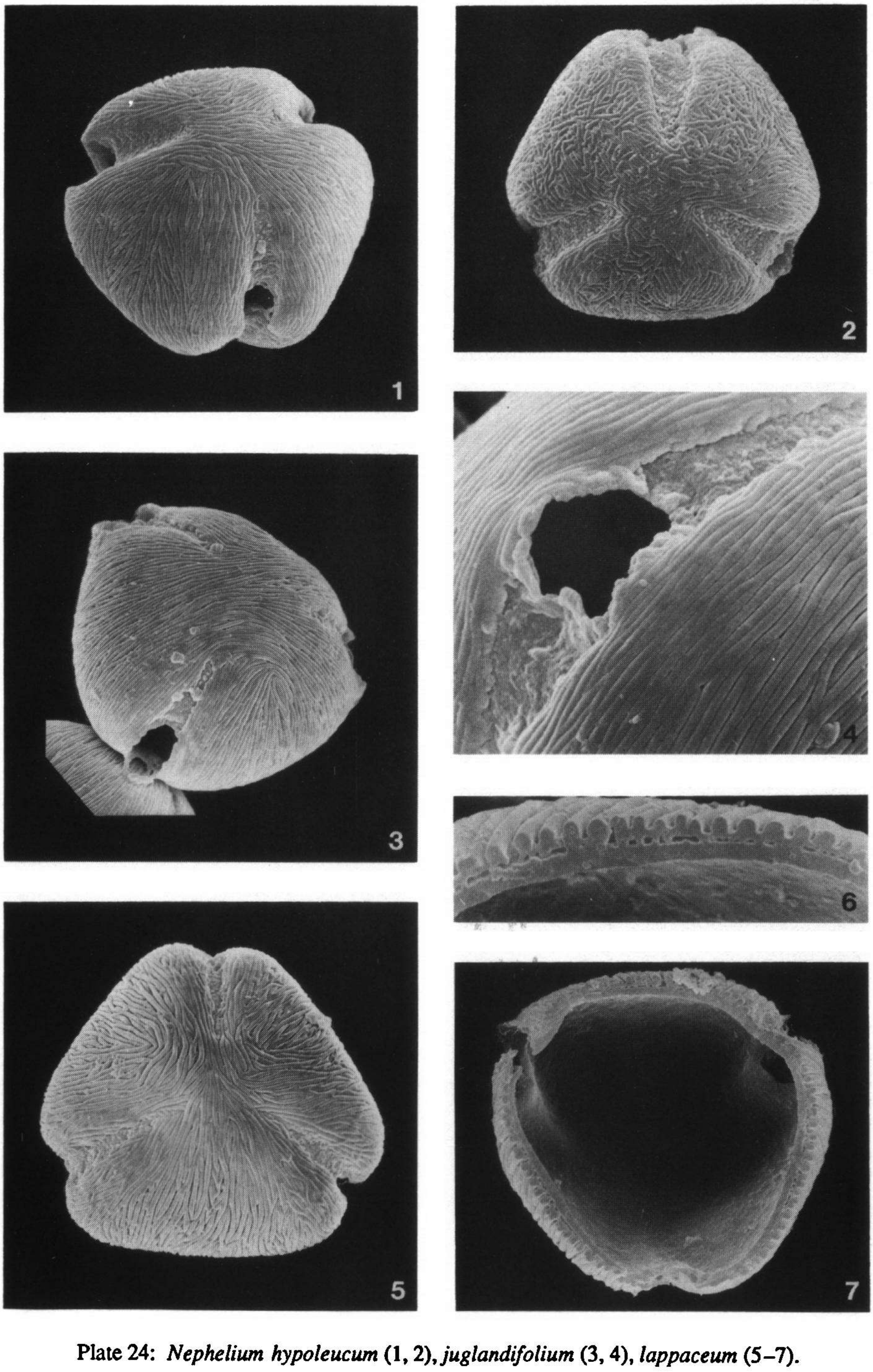


Plate 24: *Nephelium hypoleucum* (1, 2), *juglandifolium* (3, 4), *lappaceum* (5–7).

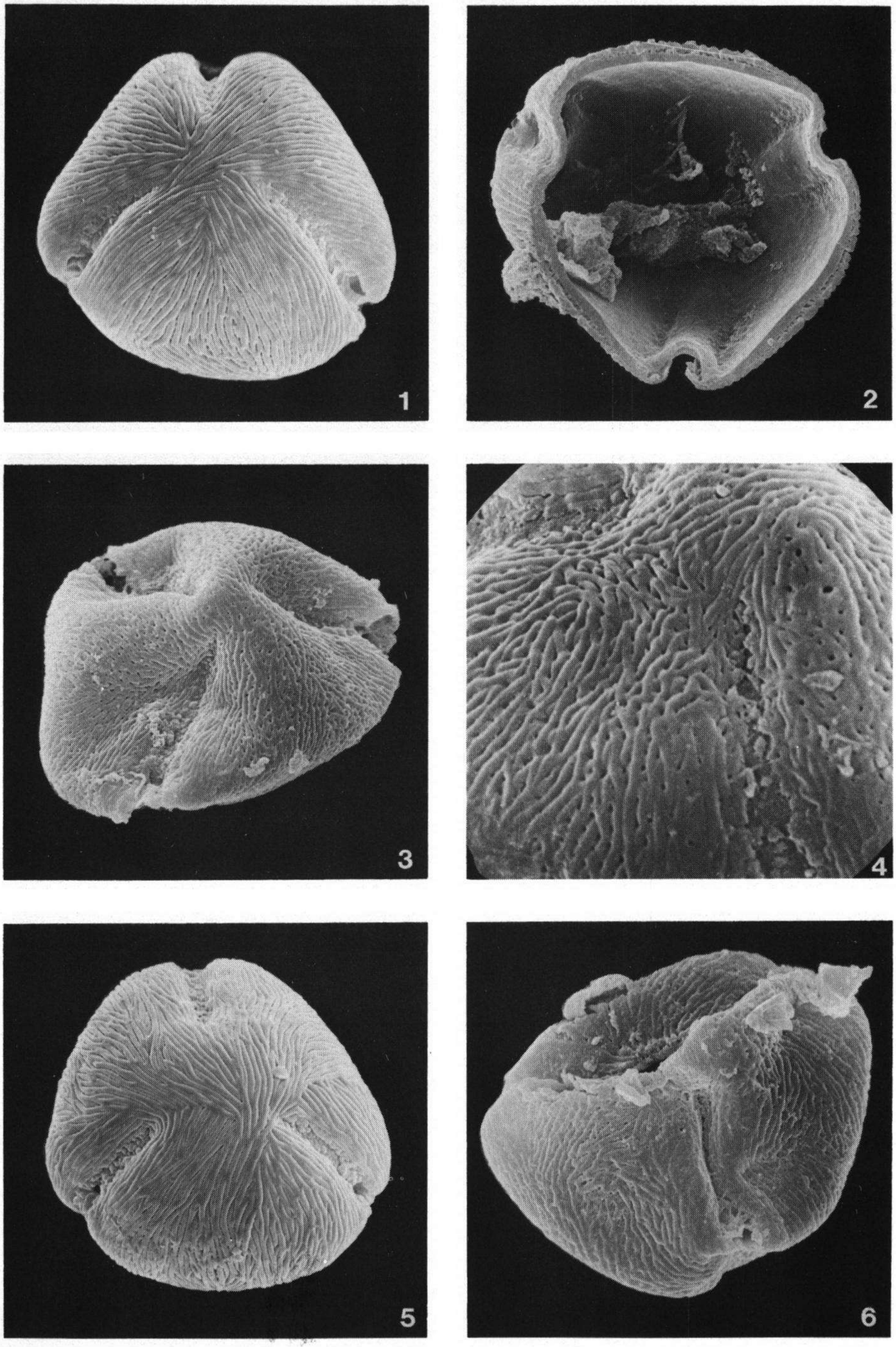


Plate 25: *Nephelium laurinum* (1, 2), *macrophyllum* (3, 4), *maingayi* (5), *meduseum* (6).

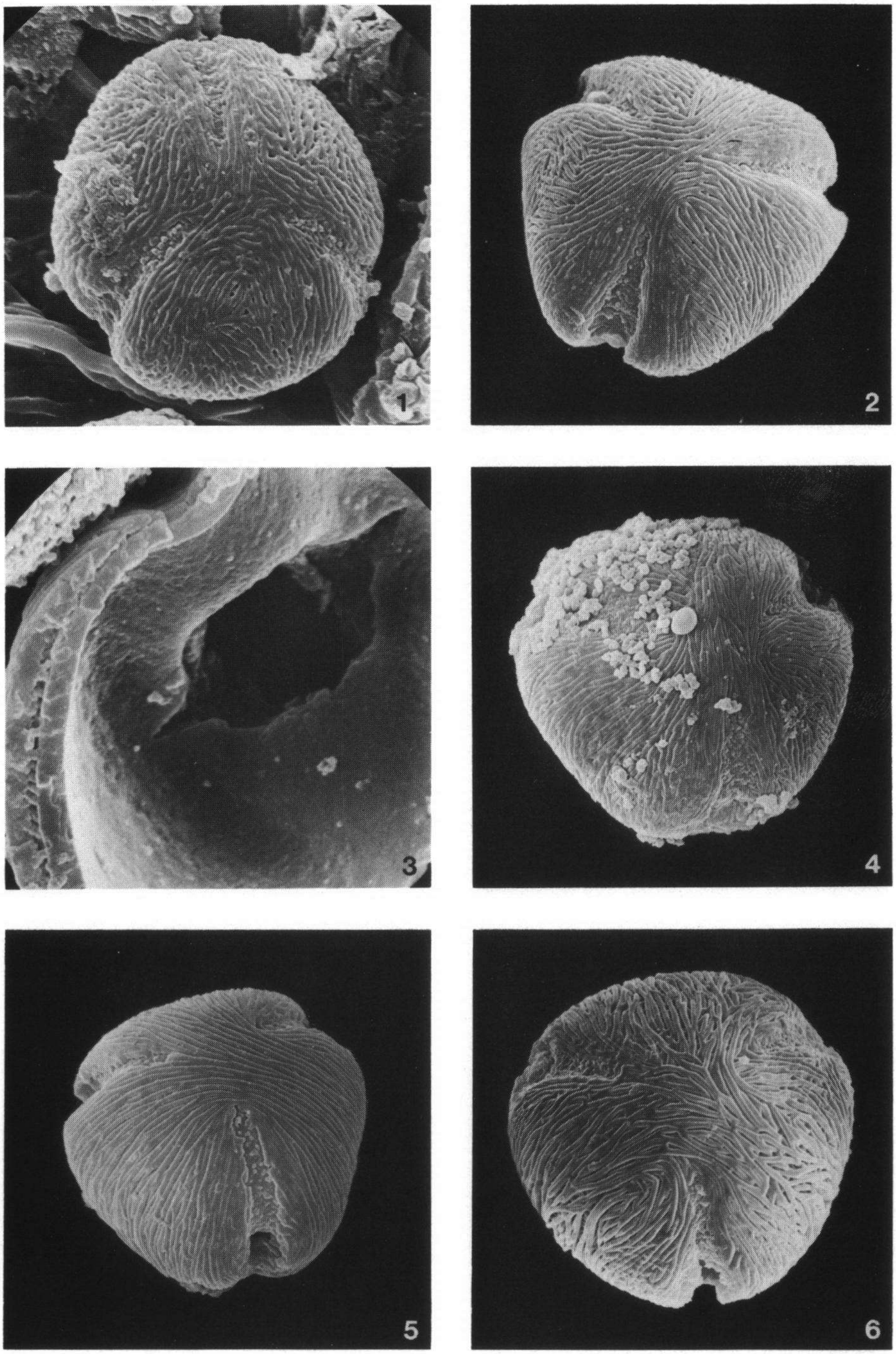


Plate 26: *Nephelium melanomiscum* (1), *melliferum* (2, 3), *papillatum* (4), *ramboutan-ake* (5, 6).

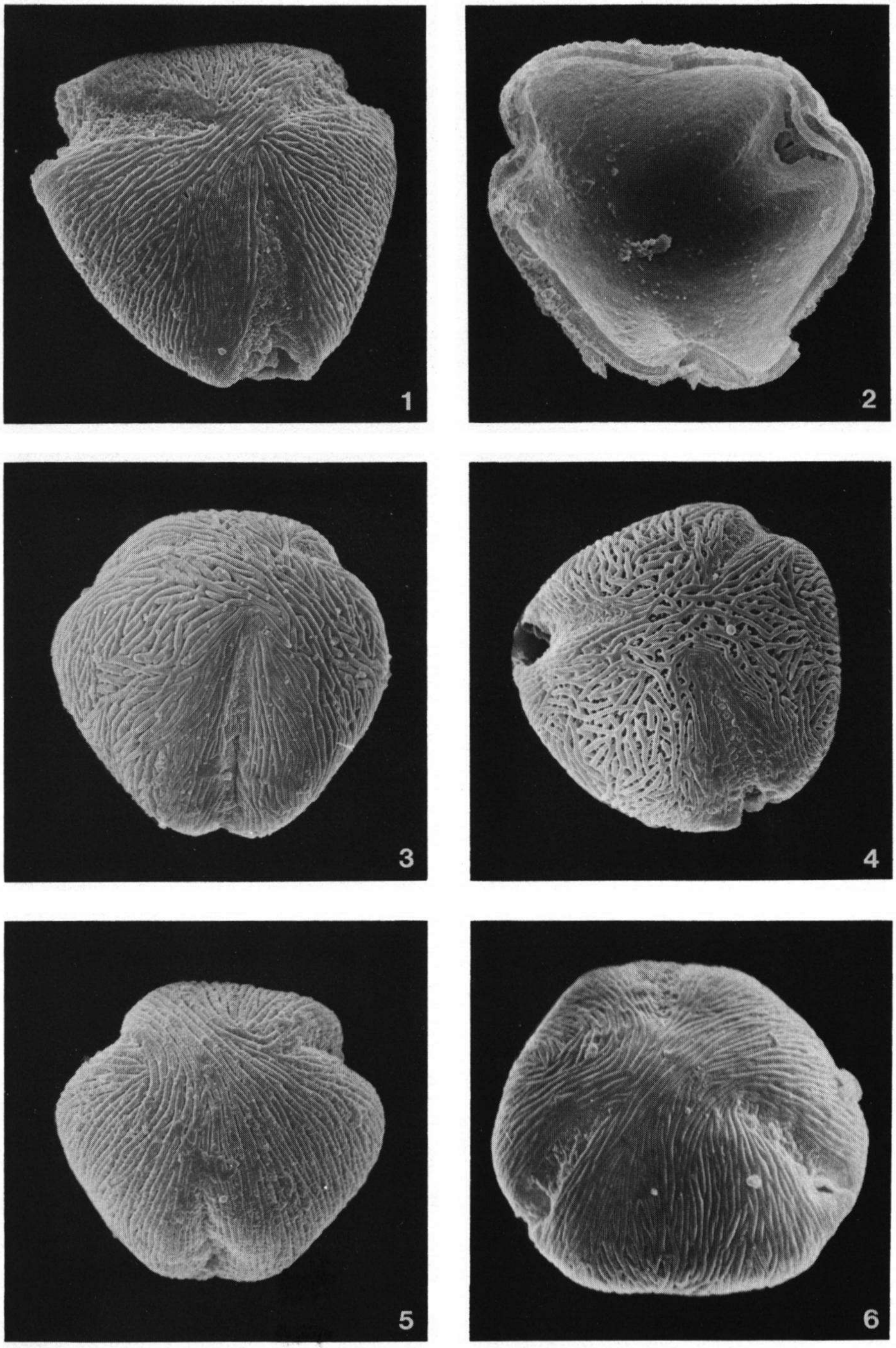


Plate 27: *Nephelium reticulatum* (1, 2), *subfalcatum* (3, 4), *uncinatum* (5), spec. nov. (6).

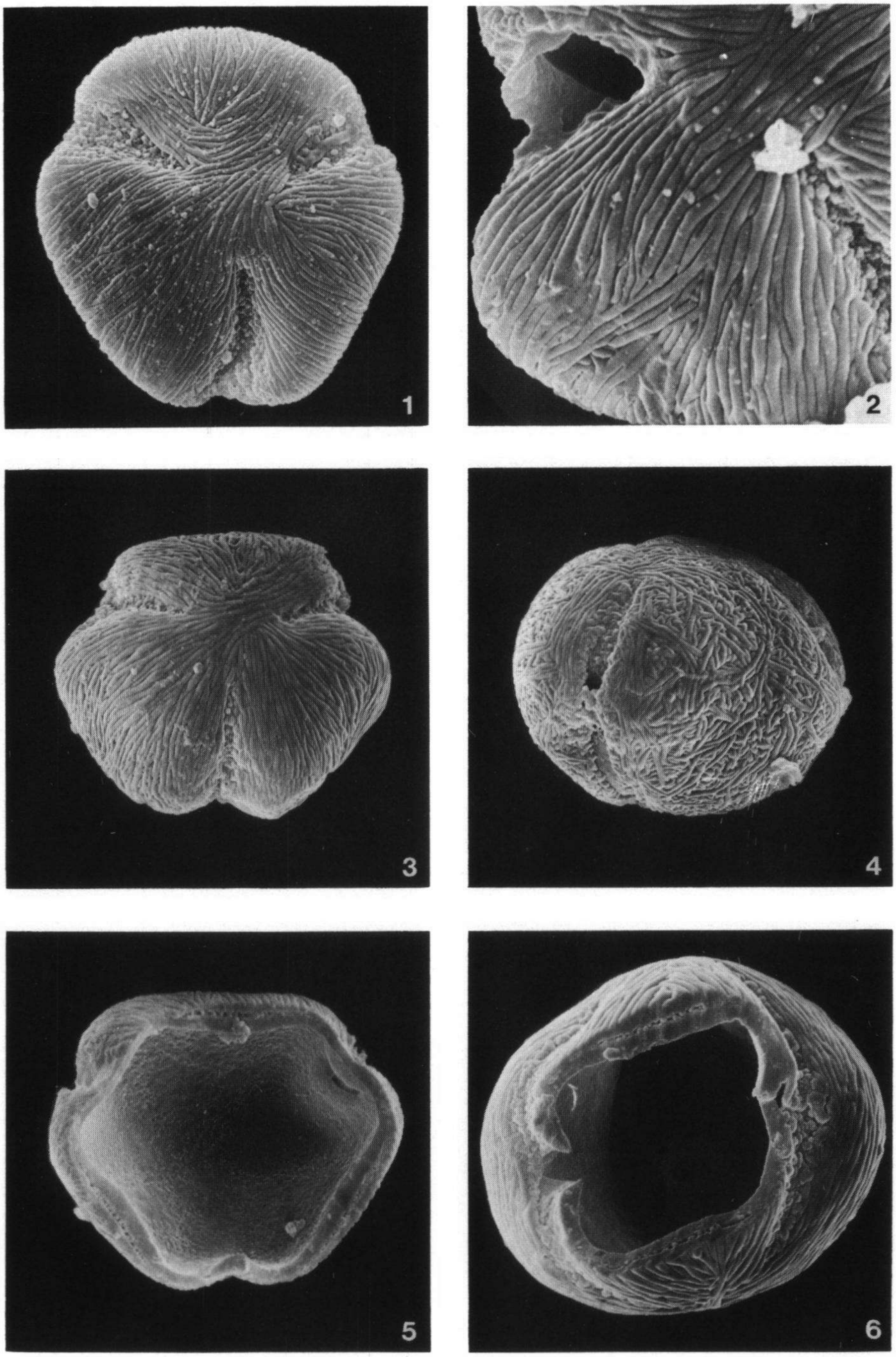


Plate 28: *Otonephelium stipulaceum.*

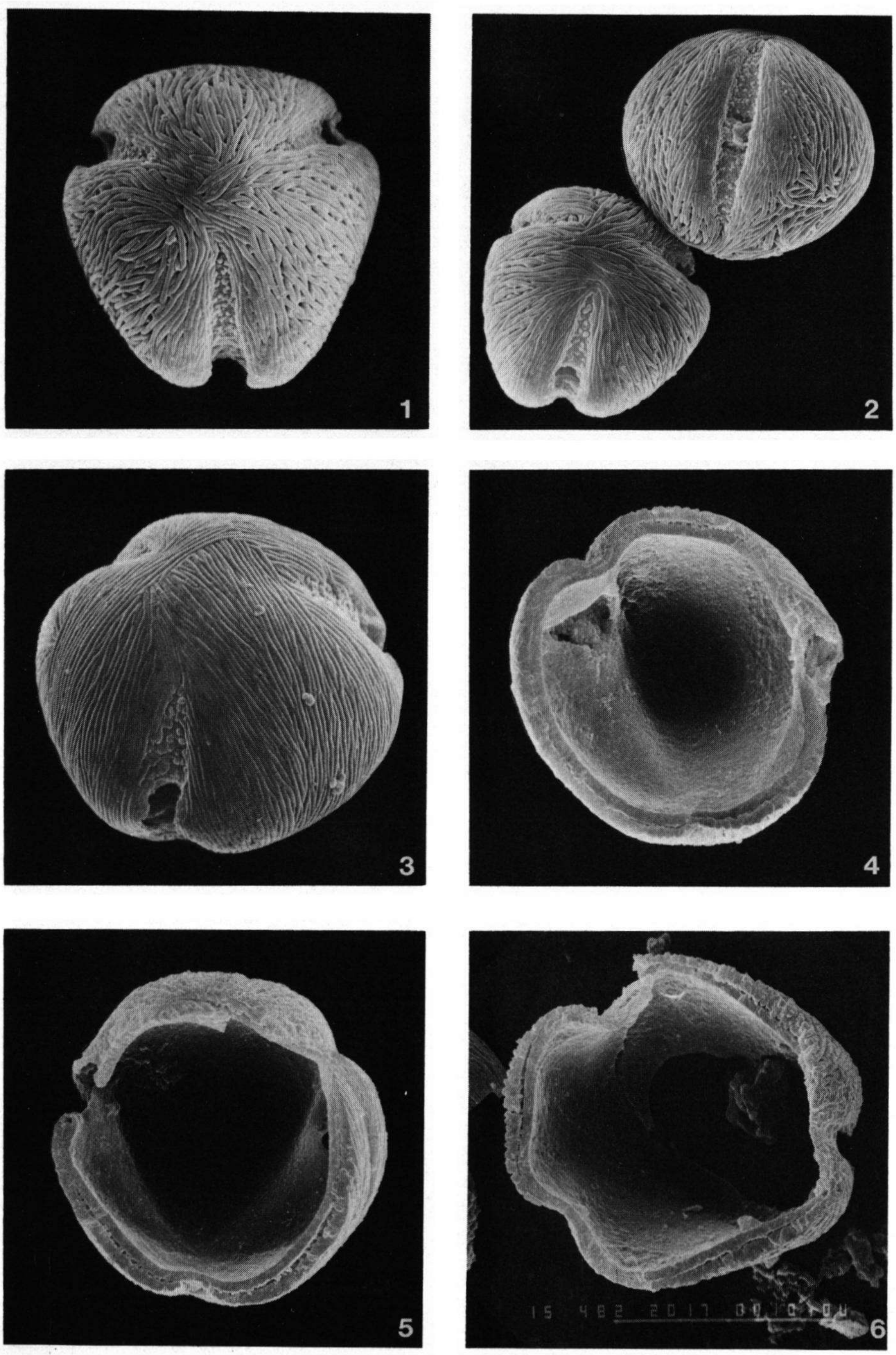


Plate 29: *Pappea capensis.*

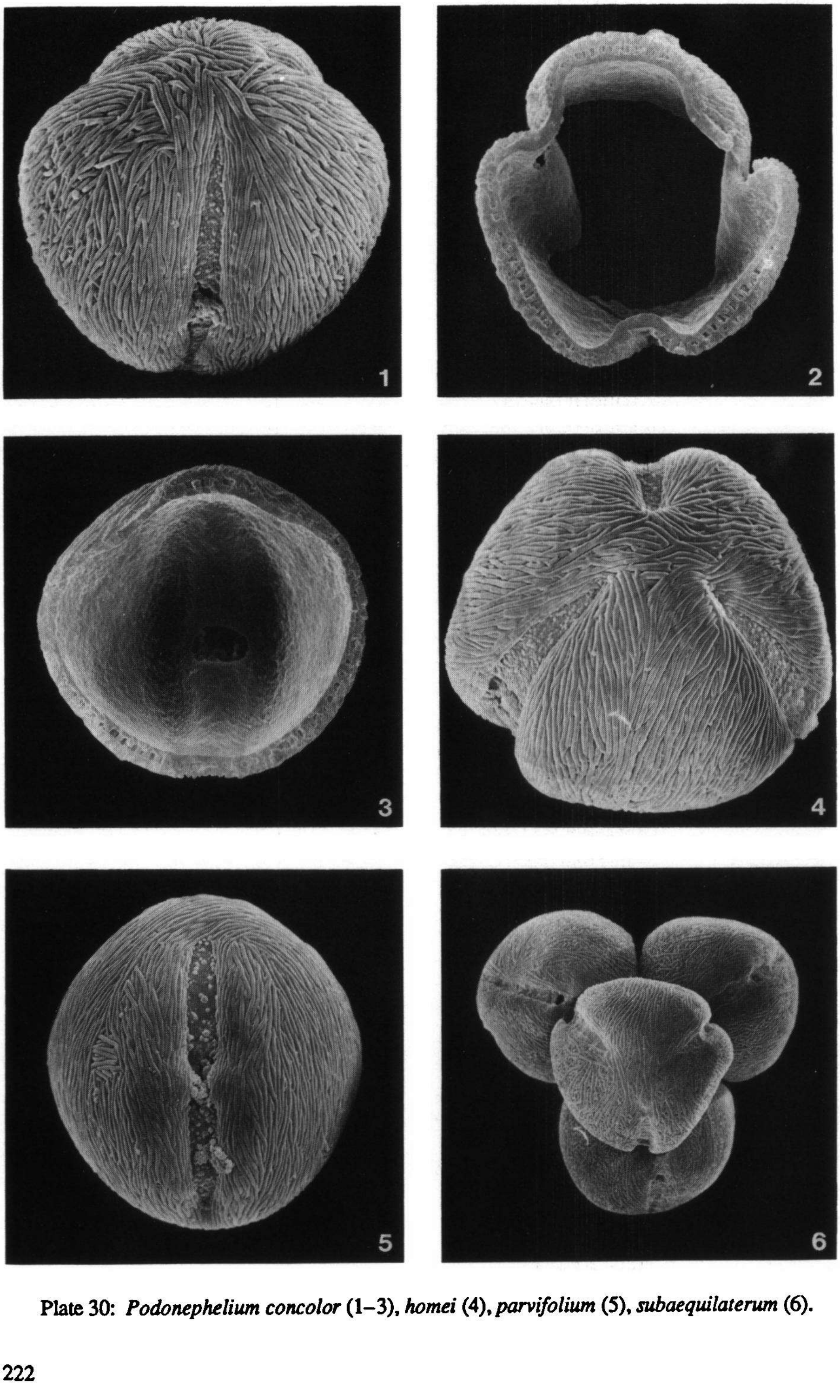


Plate 30: *Podonephelium concolor* (1–3), *homei* (4), *parvifolium* (5), *subaequilaterum* (6).

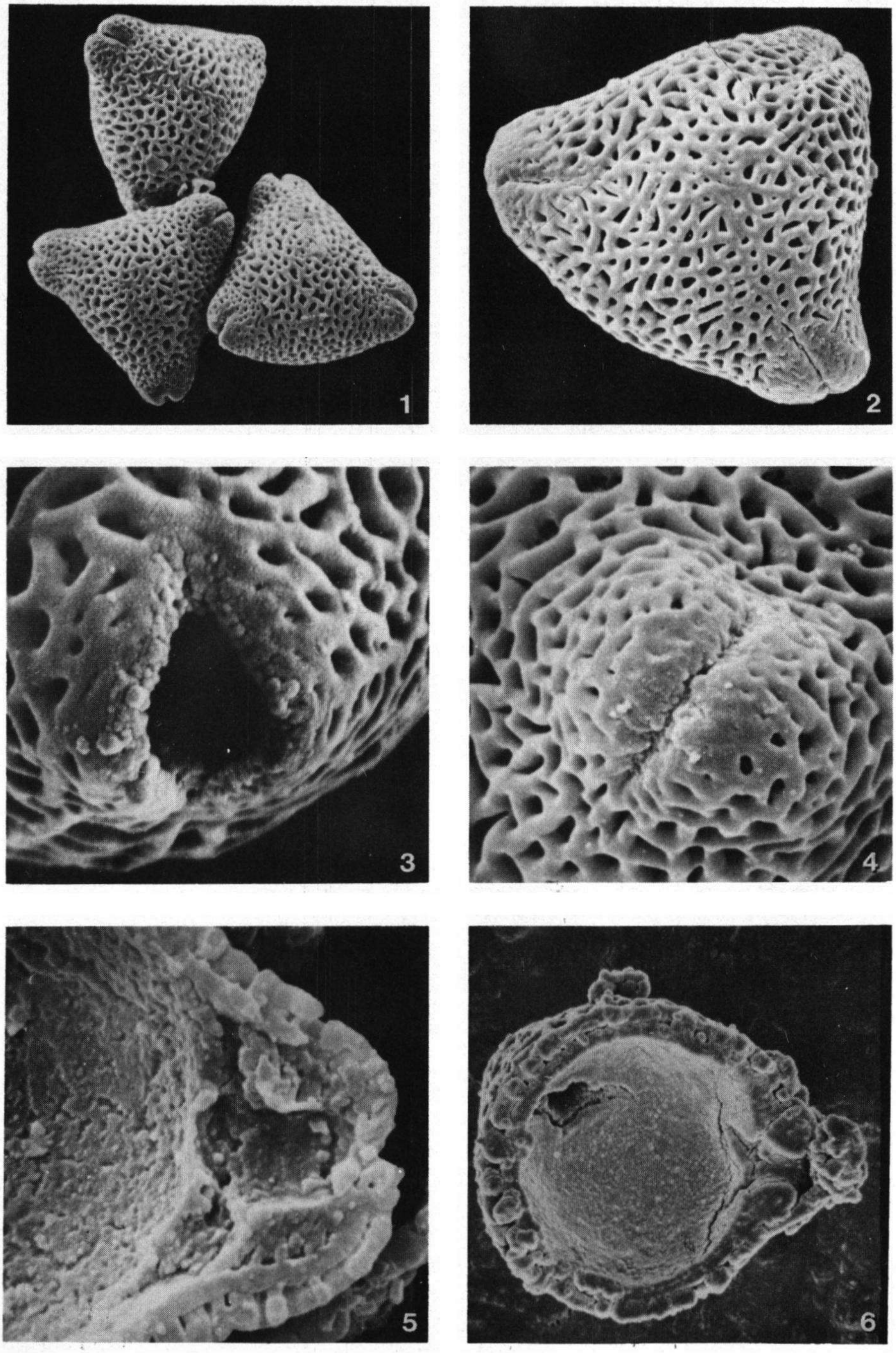
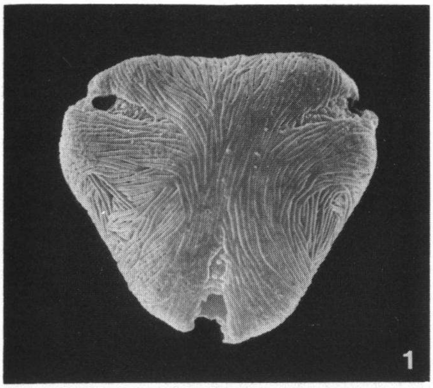
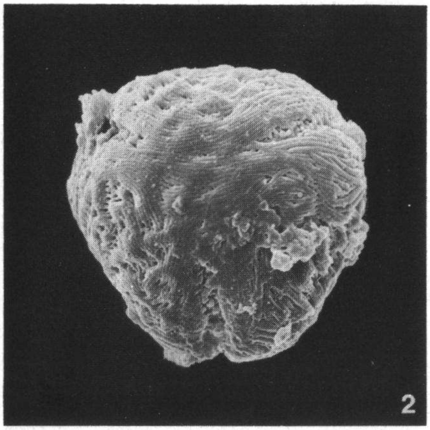
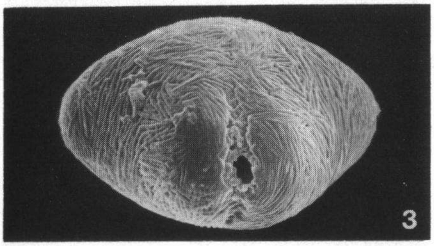
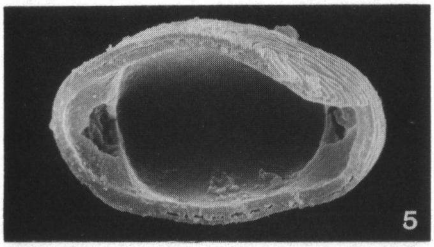


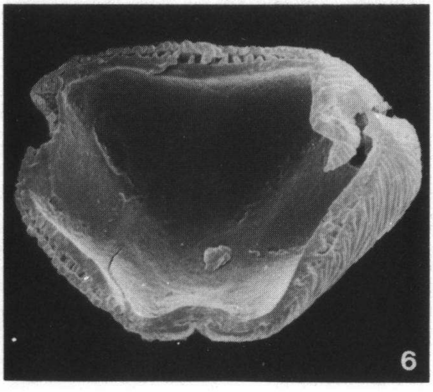
Plate 31: *Pometia pinnata* (1–5), *ridleyi* (6).











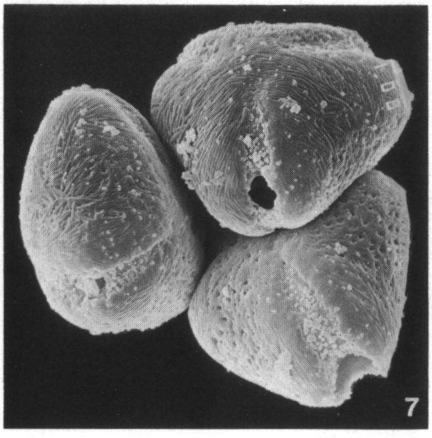


Plate 32: *Smelophyllum capense*.

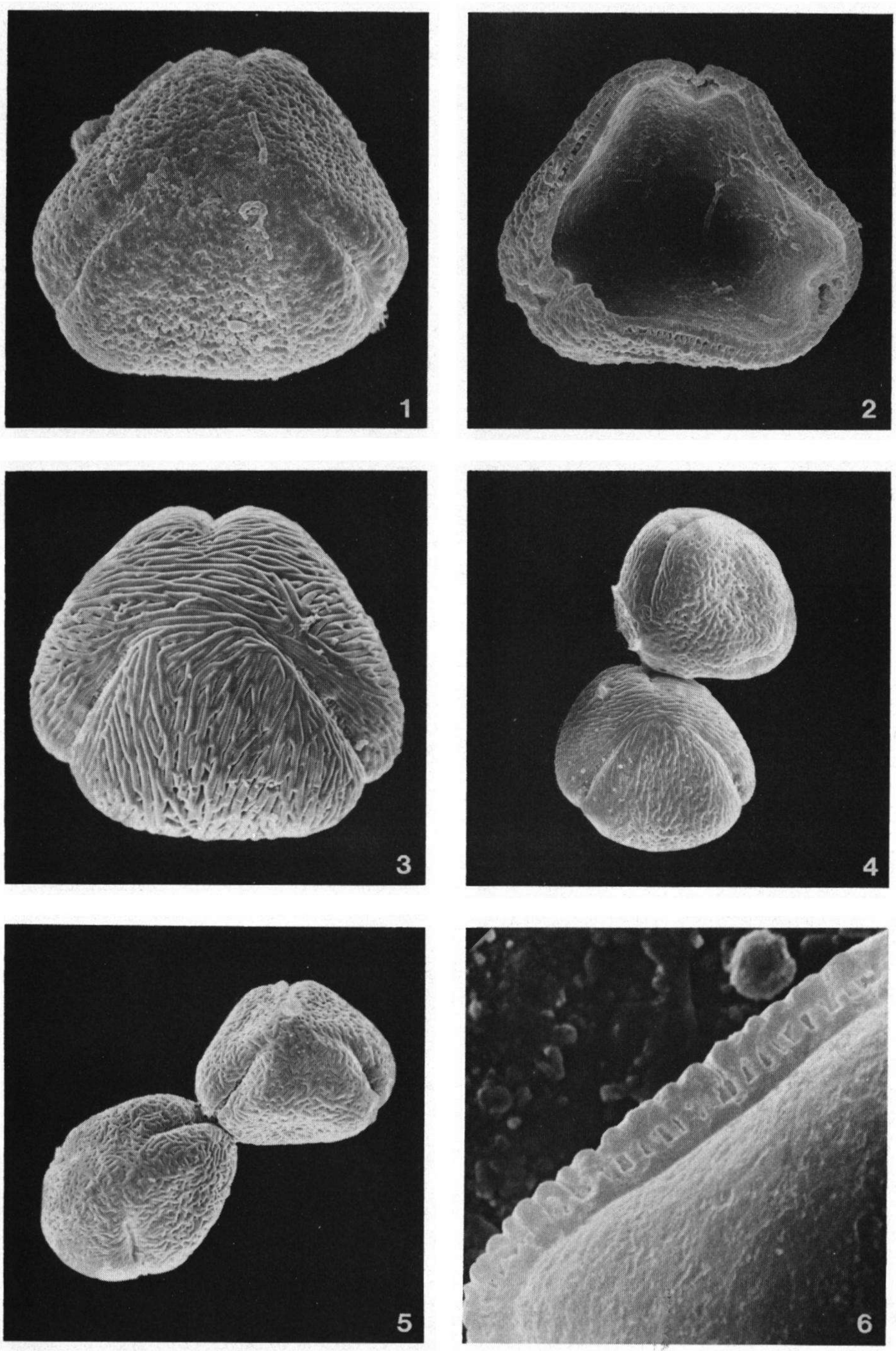


Plate 33: *Stadmania acuminata* (1, 2), *glauca* (3–6).

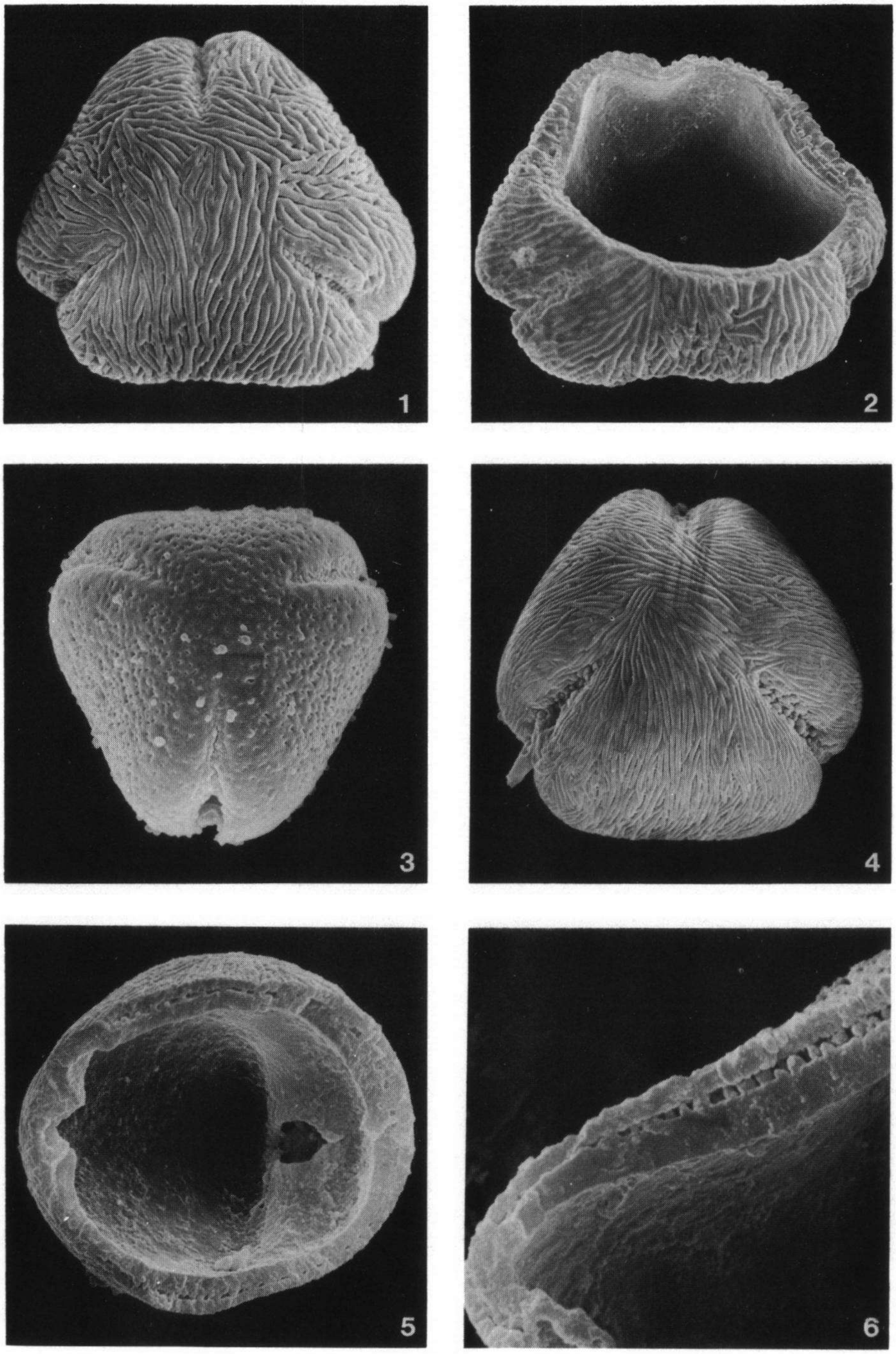


Plate 34: *Stadmania excelsa* (1, 2), *leandrii* (3), *serratula* (4–6).

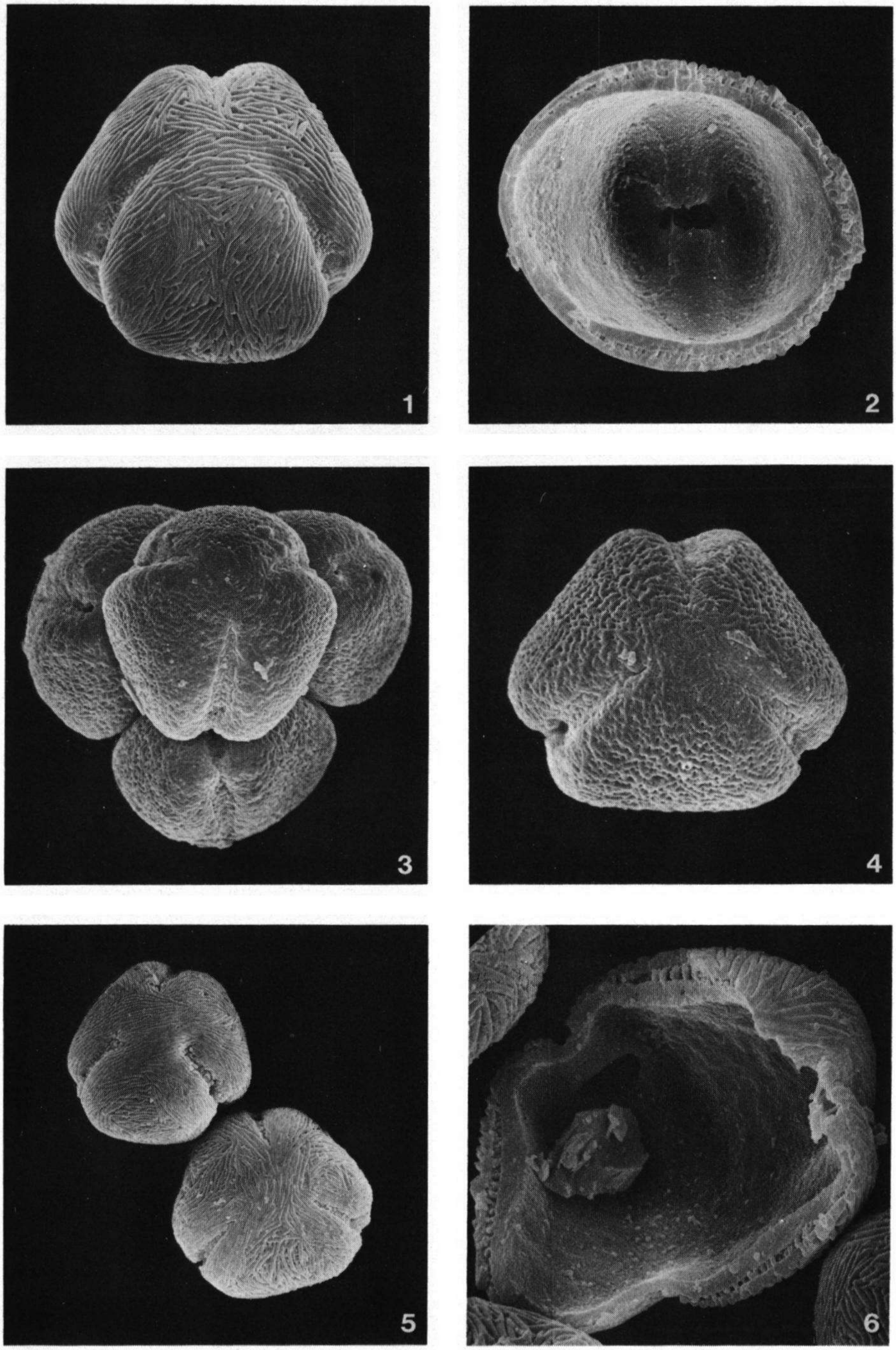


Plate 35: *Stadmania oppositifolia.*

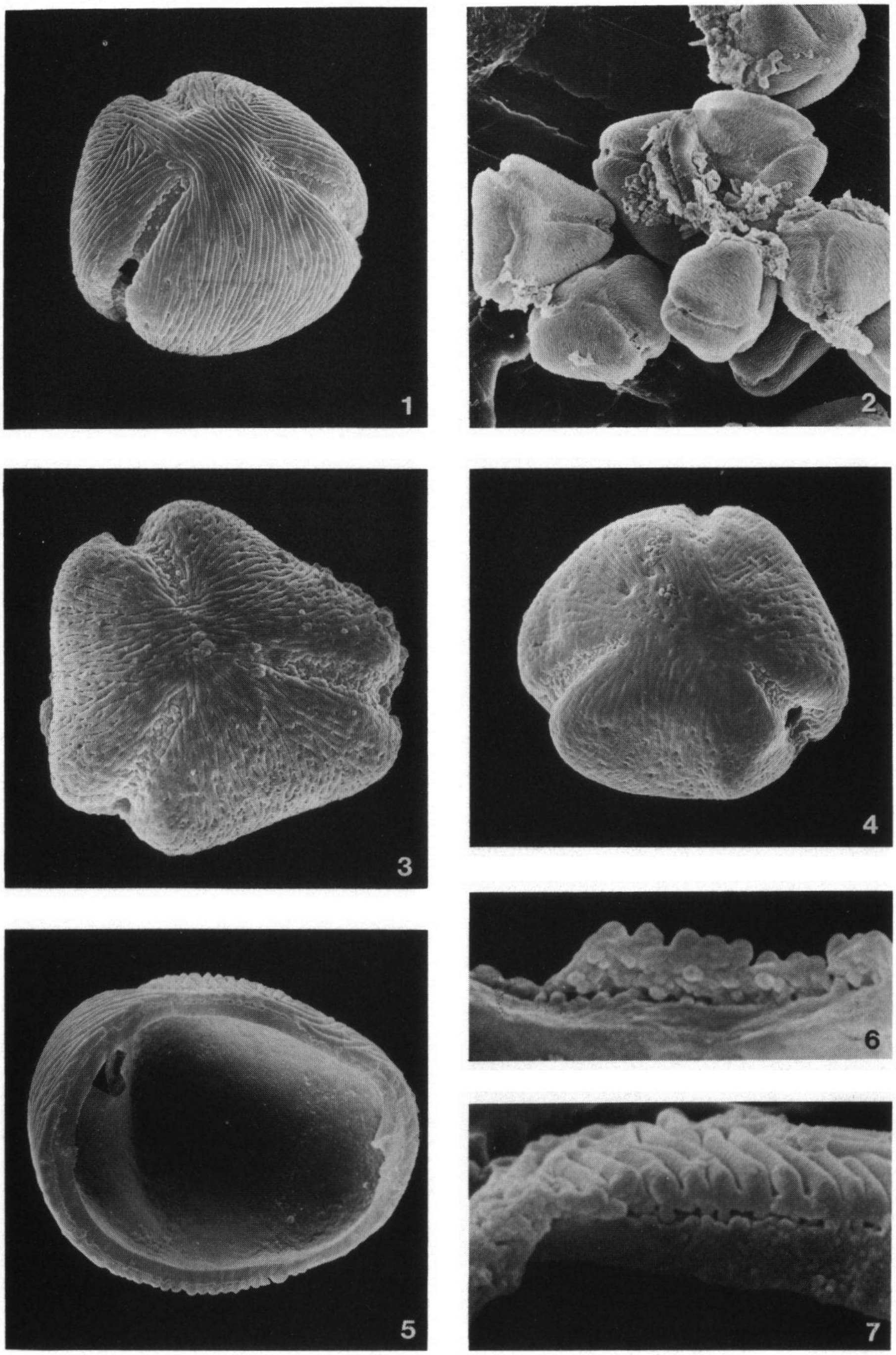
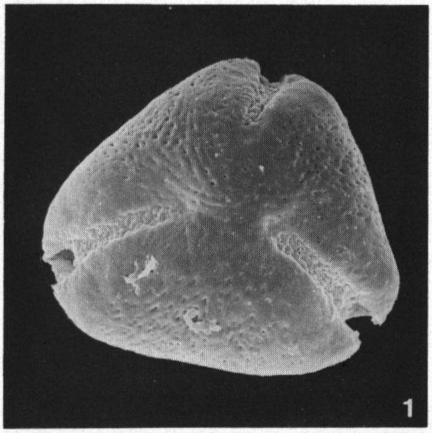


Plate 36: *Xerospermum laevigatum*.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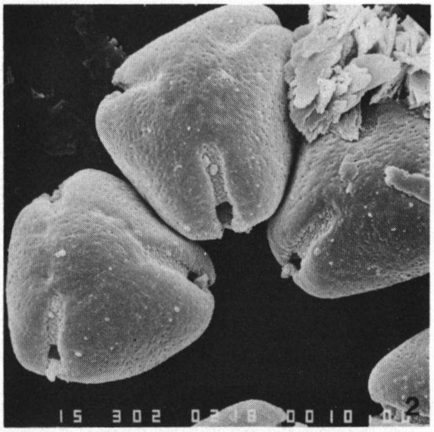

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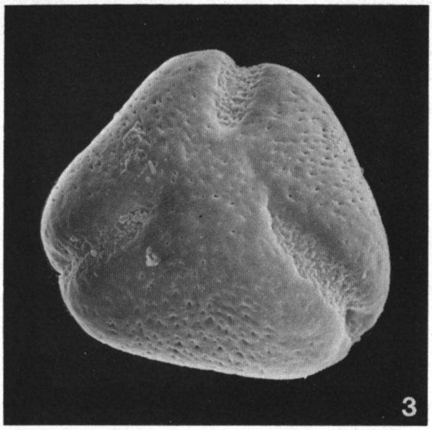
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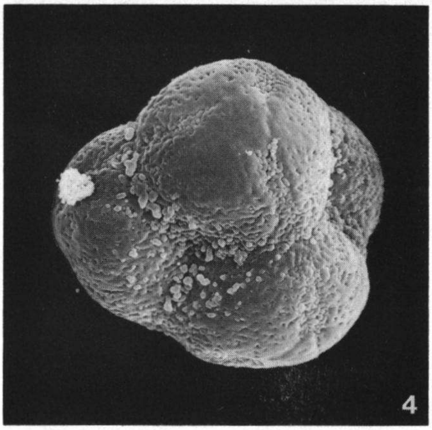
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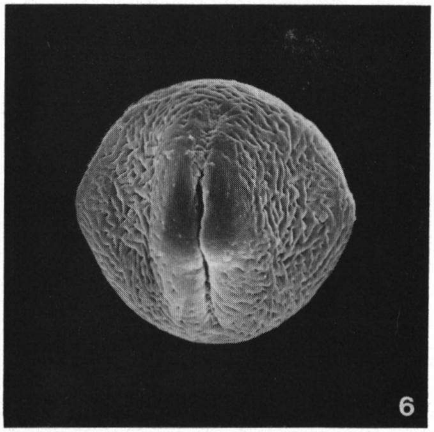
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Plate 37: *Xerospermum laevigatum.*

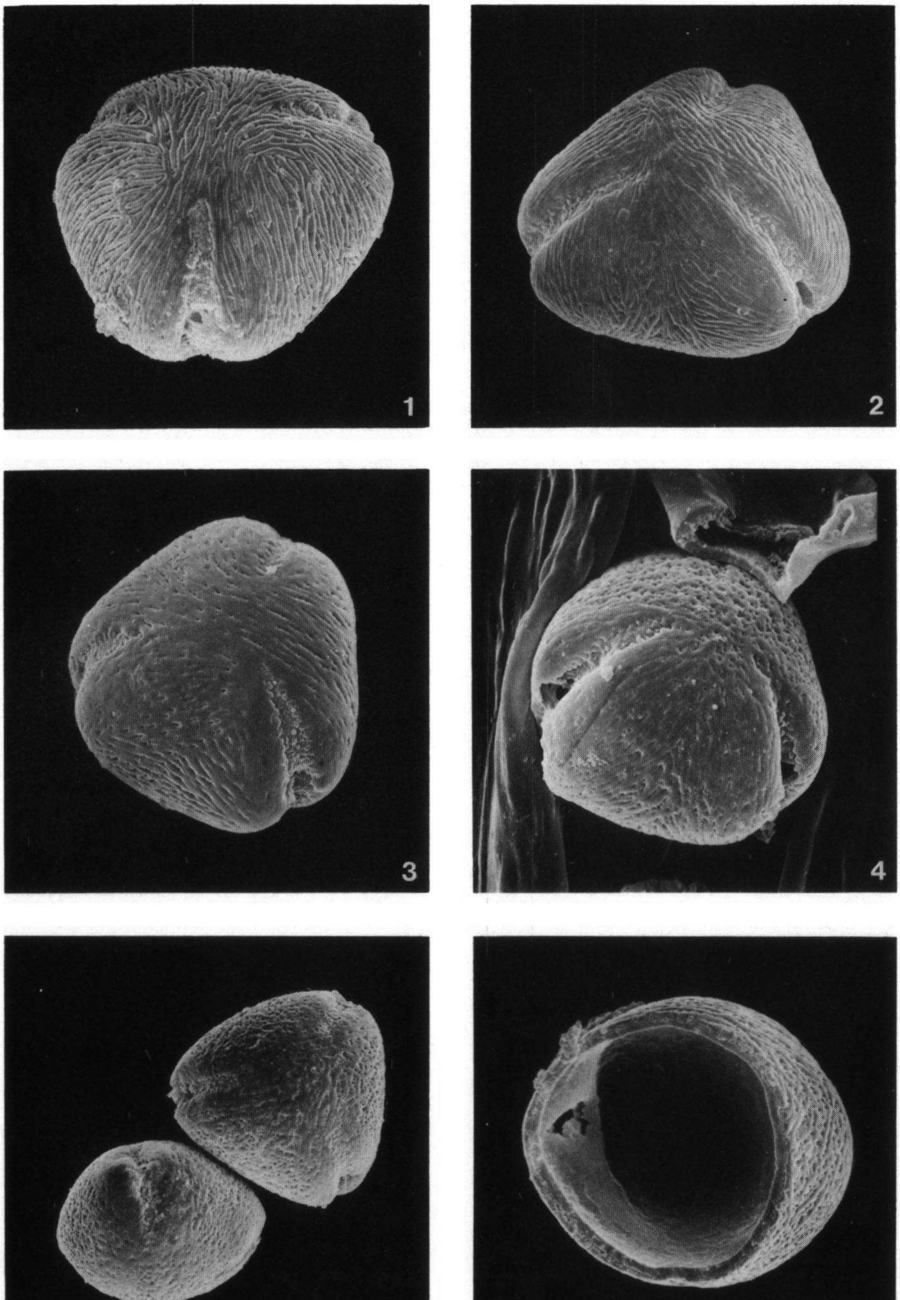


Plate 38: ***Xerospermum noronhianum.***

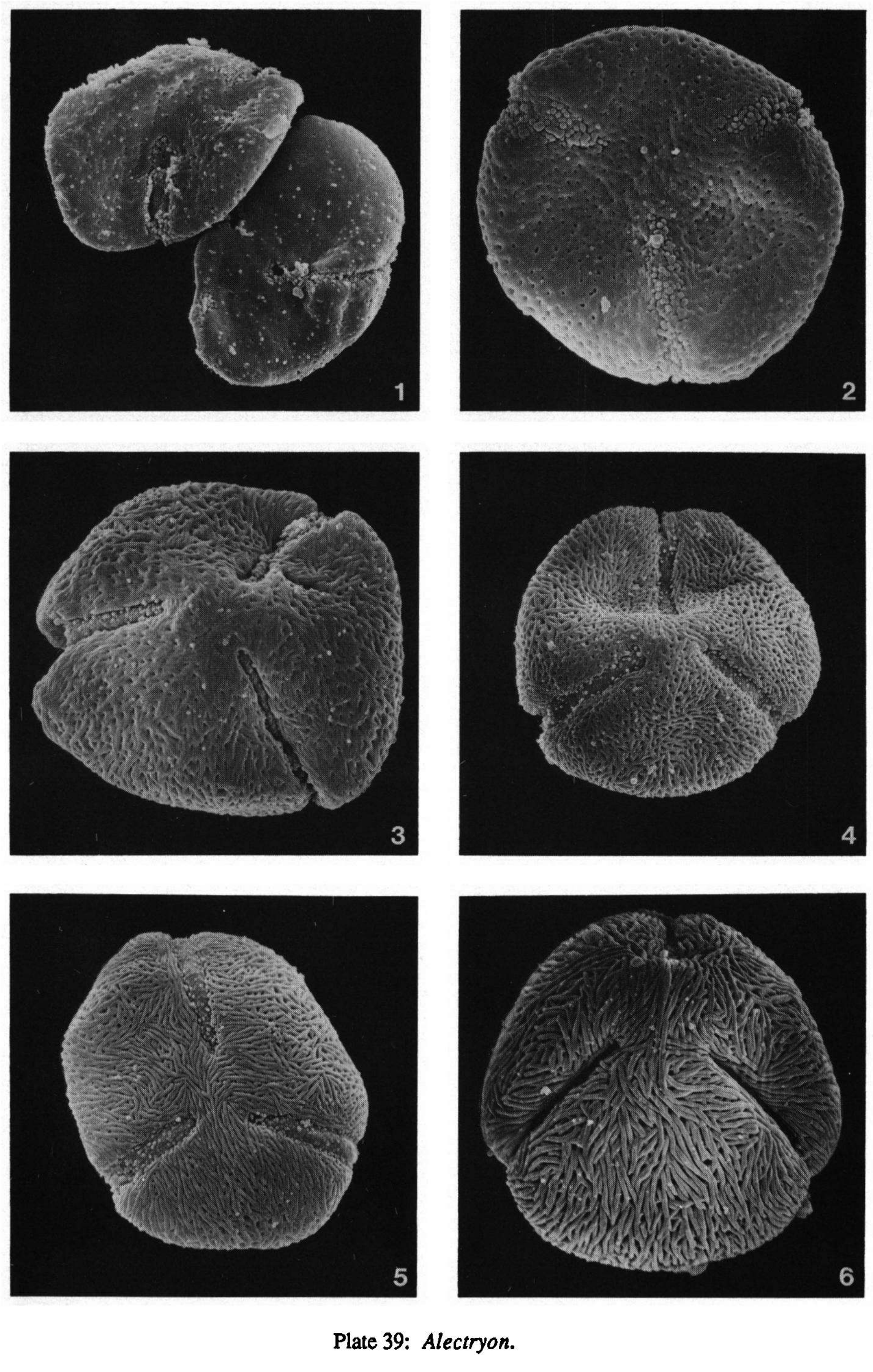
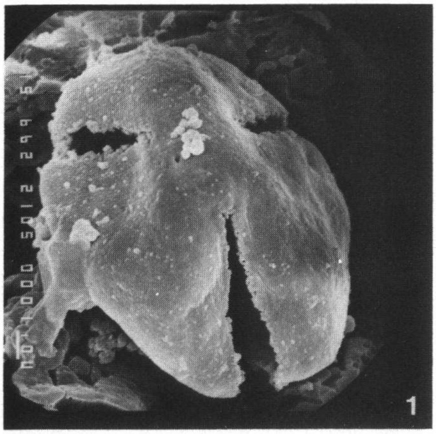
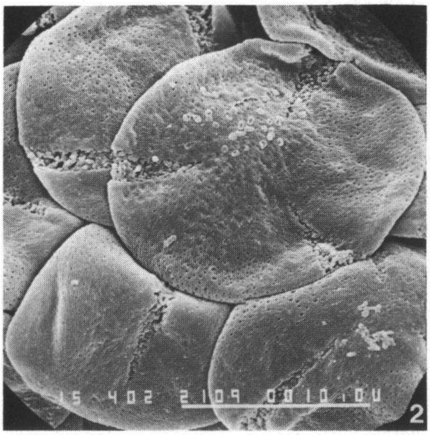
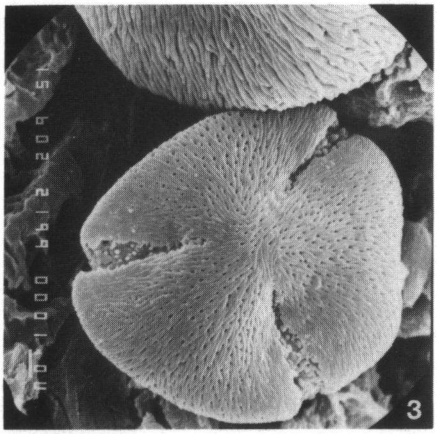
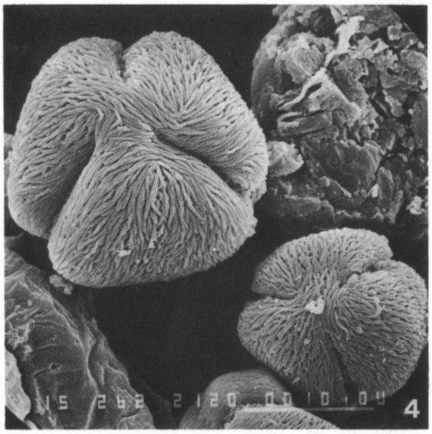


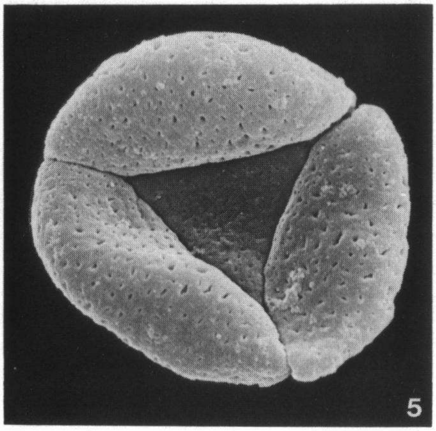
Plate 39: *Alectryon.*











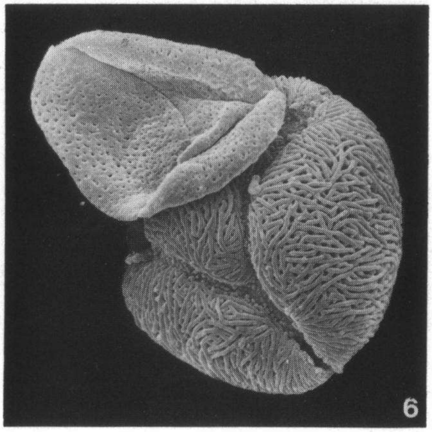


Plate 40: *Alectryon.*

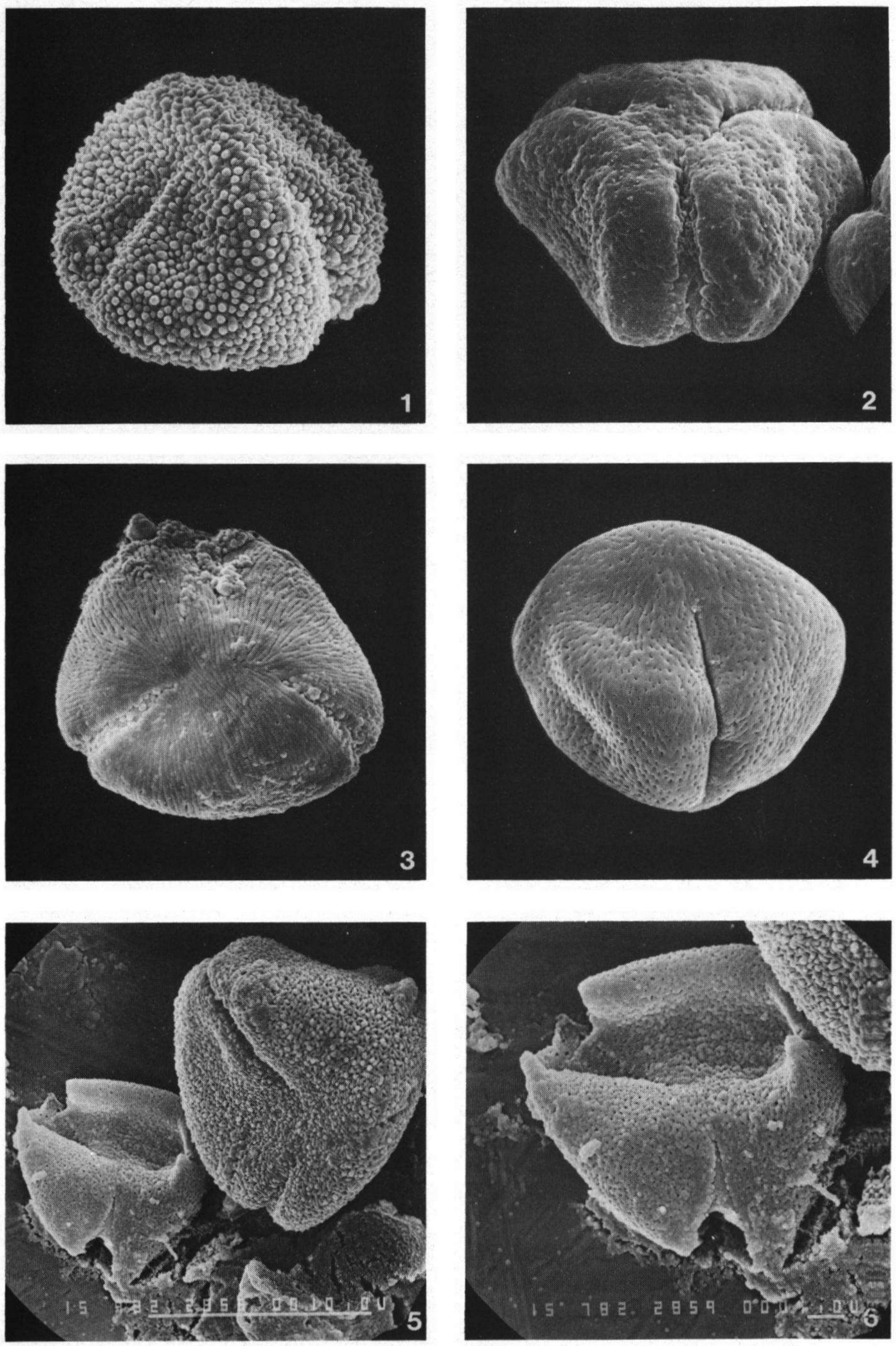


Plate 41: *Cubilia.*

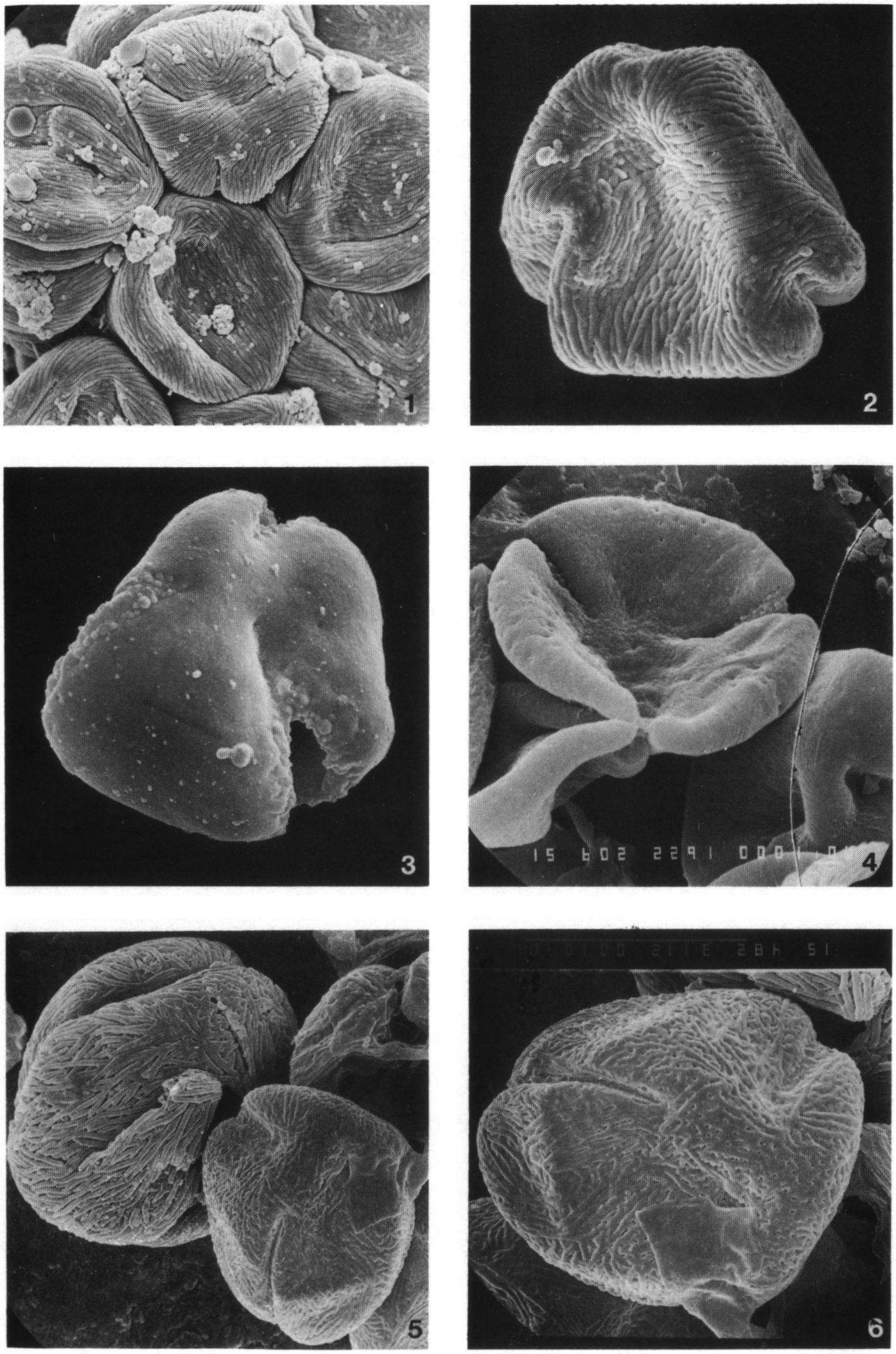
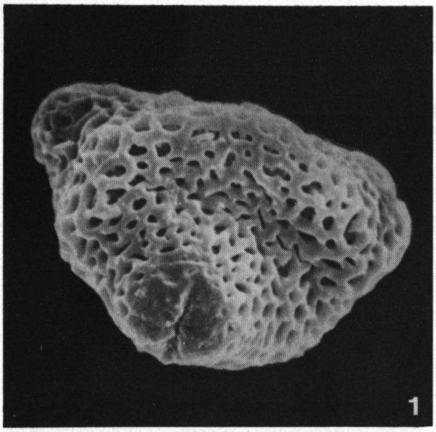
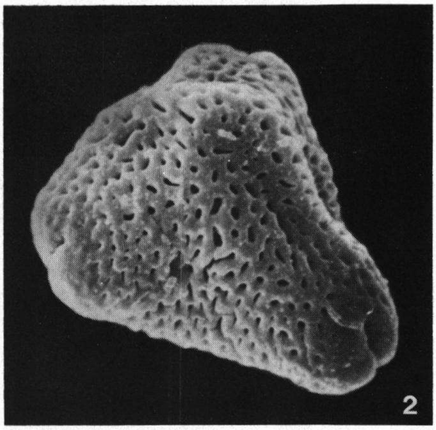
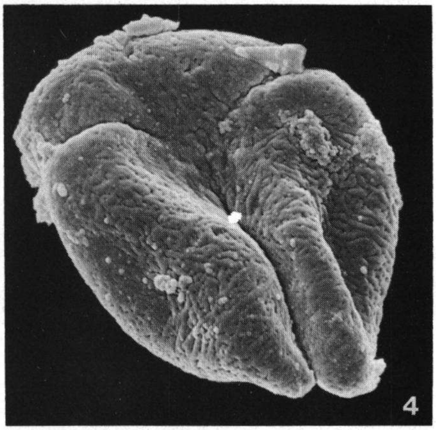
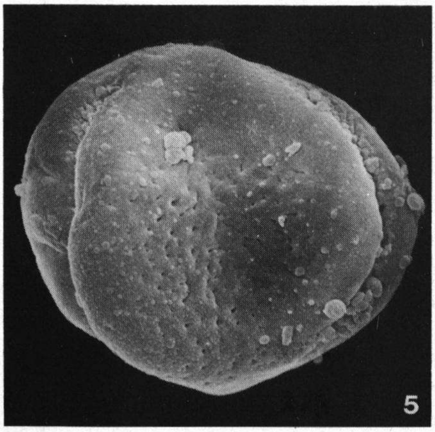


Plate 42: *Litchi* (1), *Nephelium* (2), *Otonephelium* (3), *Pappea* (4), *Podonephelium* (5, 6).









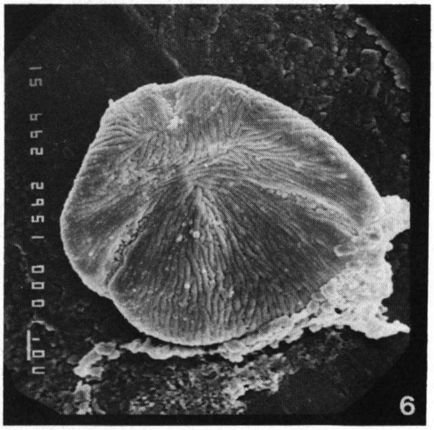


Plate 43: *Pometia* (1, 2), *Stadmania* (3, 4), *Xerospermum* (5, 6).

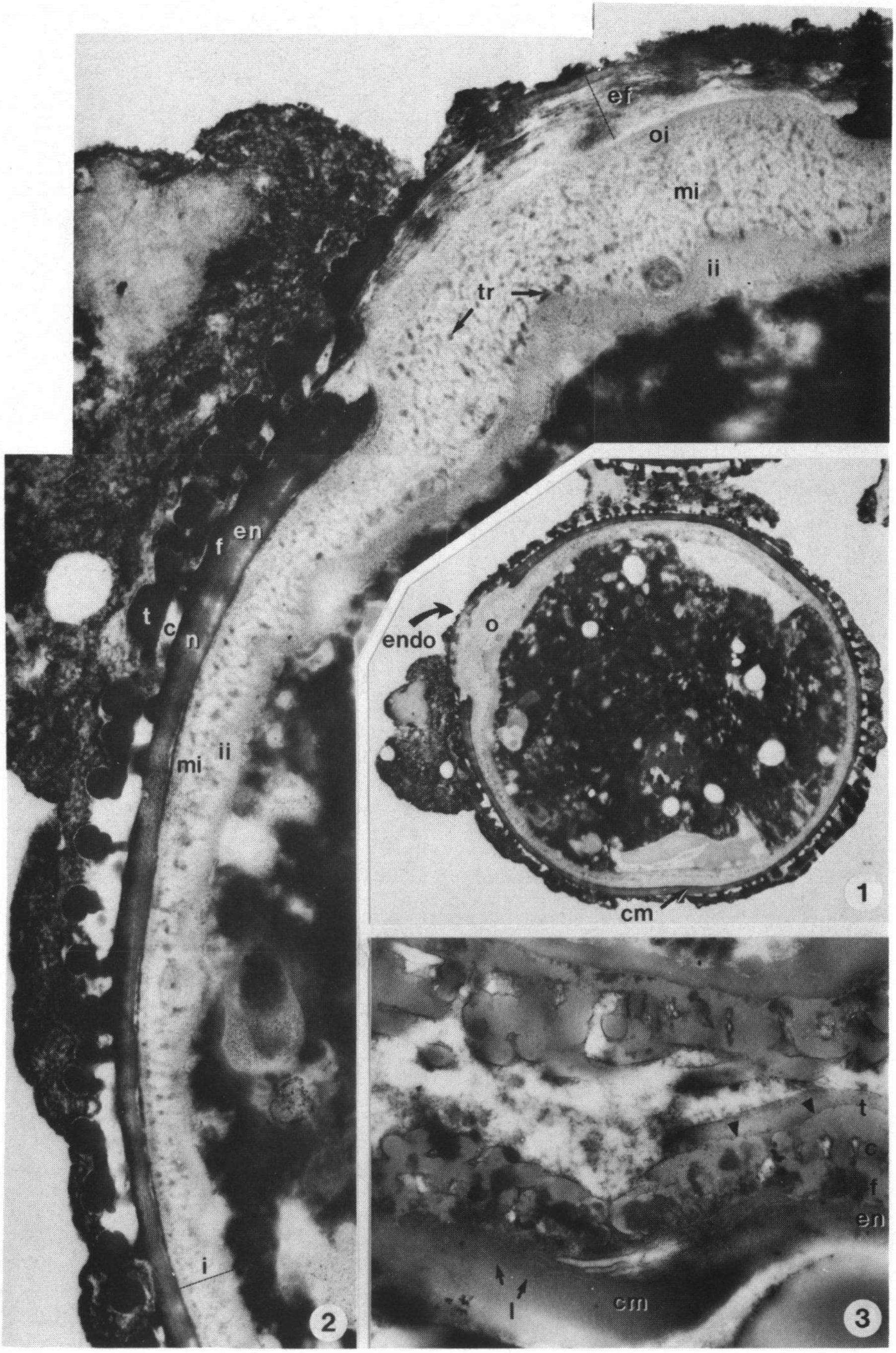


Plate 44: *Alectryon.*

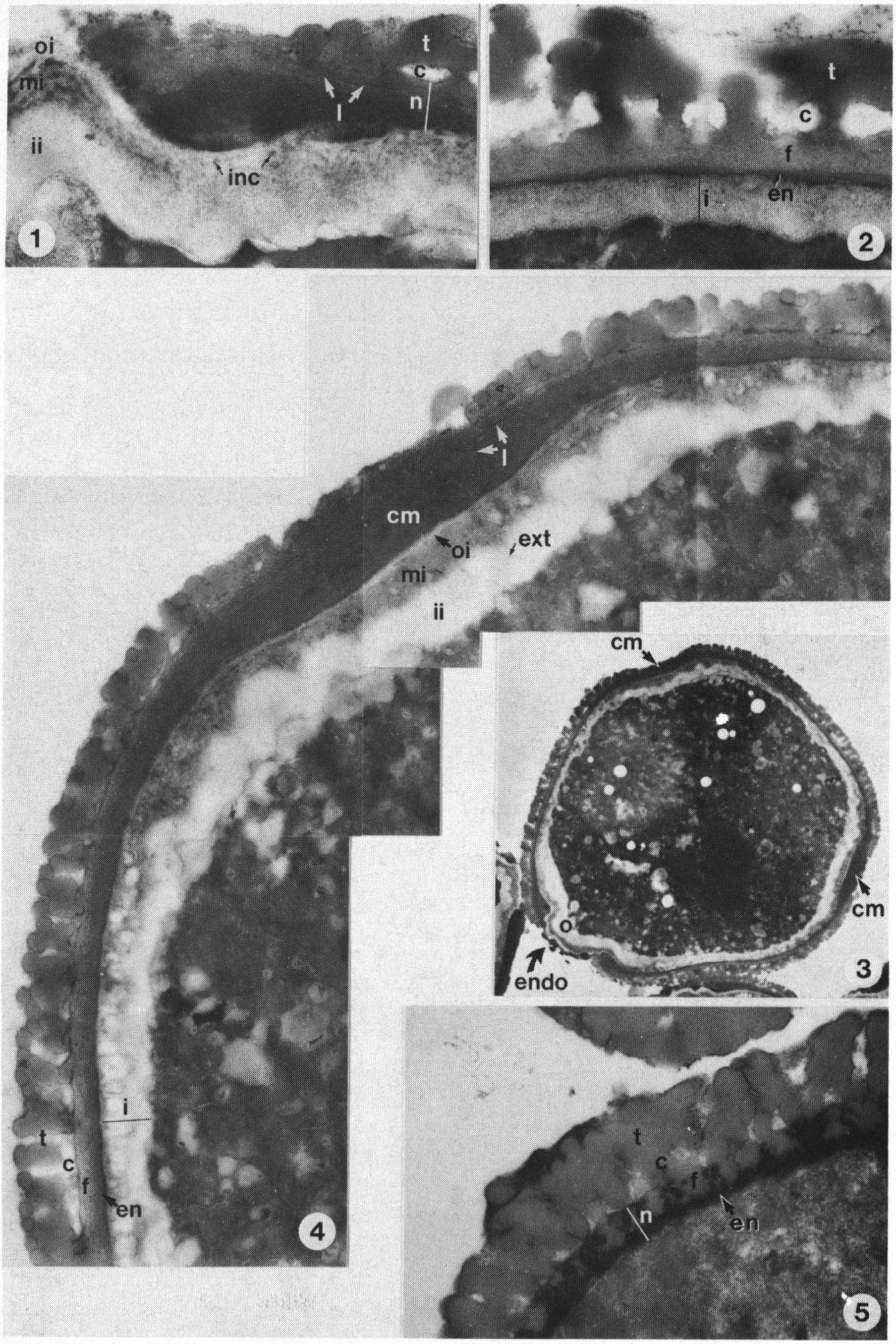


Plate 45: *Alectryon.*

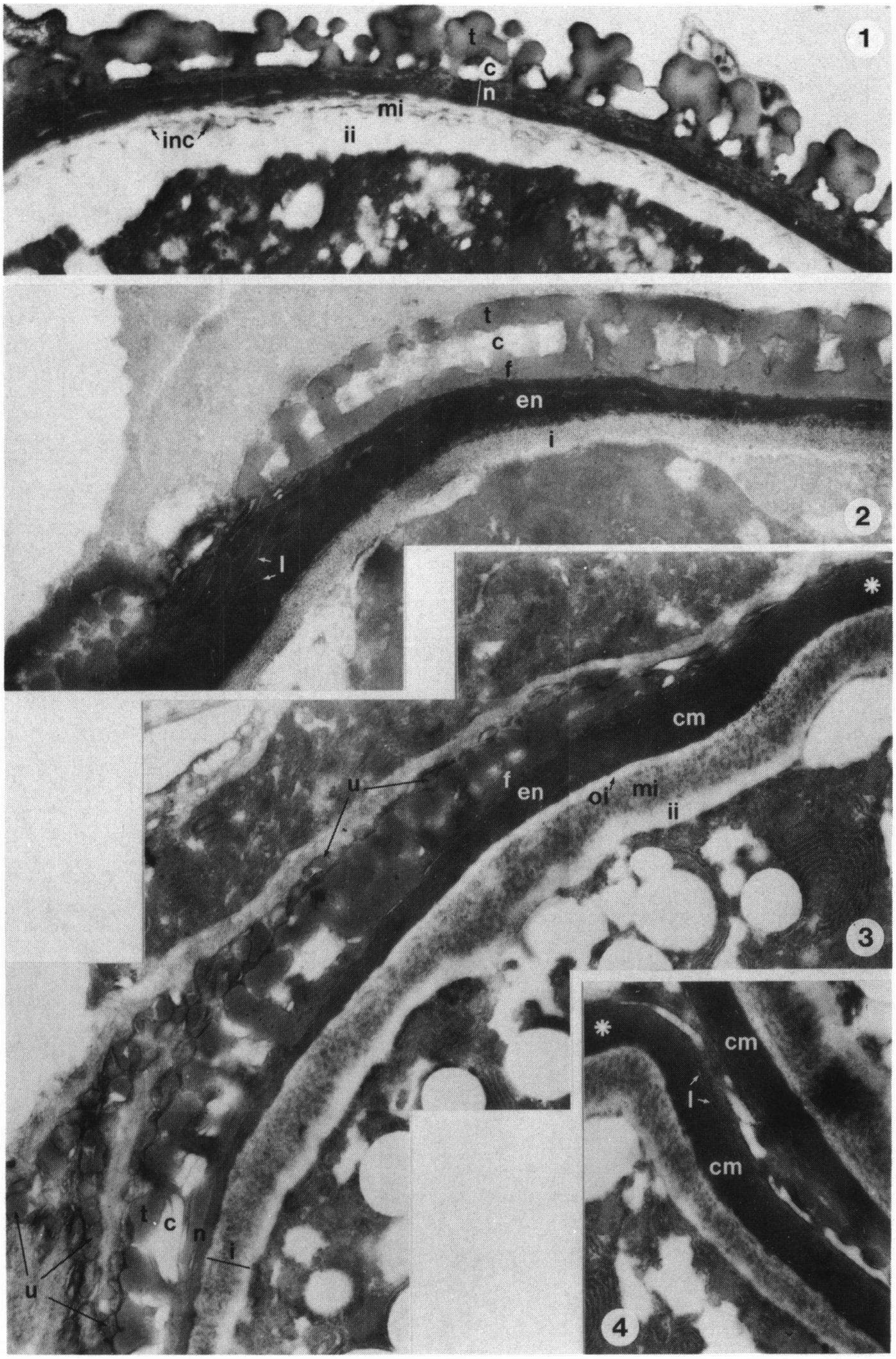
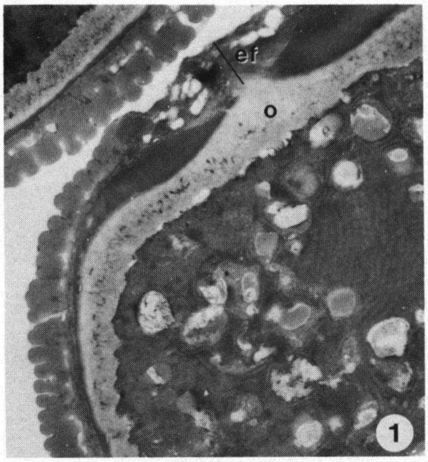
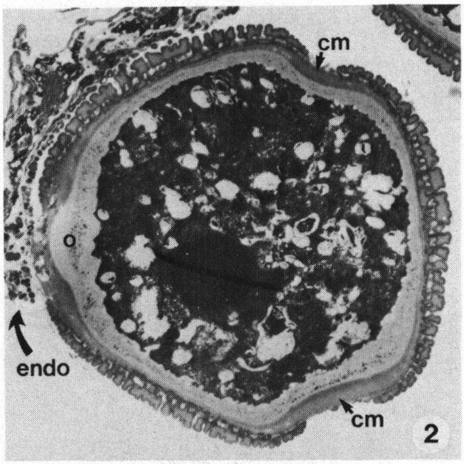
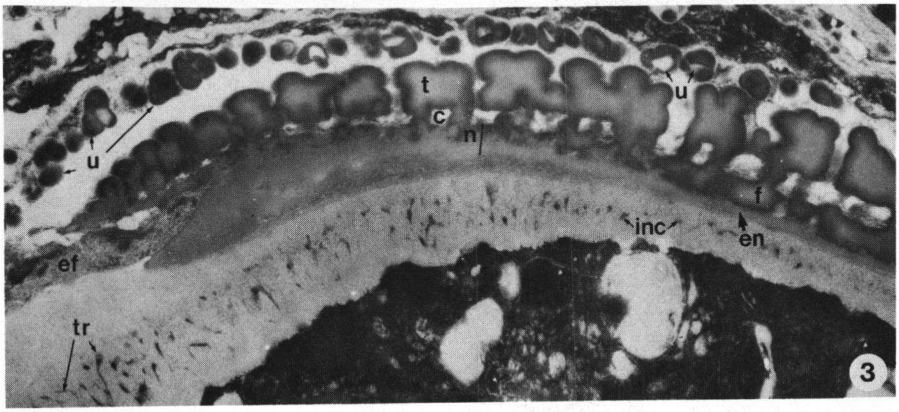
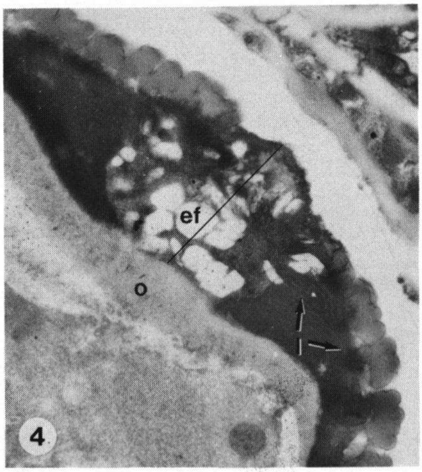


Plate 46: *Alectryon*.









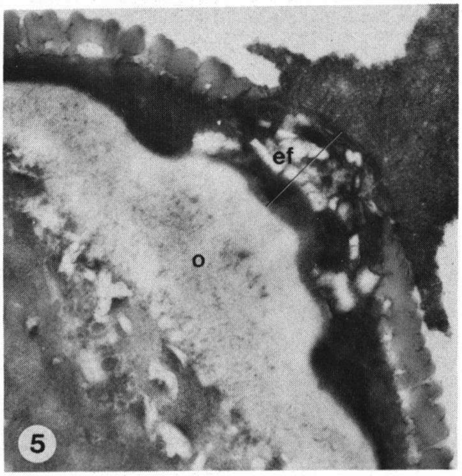


Plate 47: *Alectryon*.

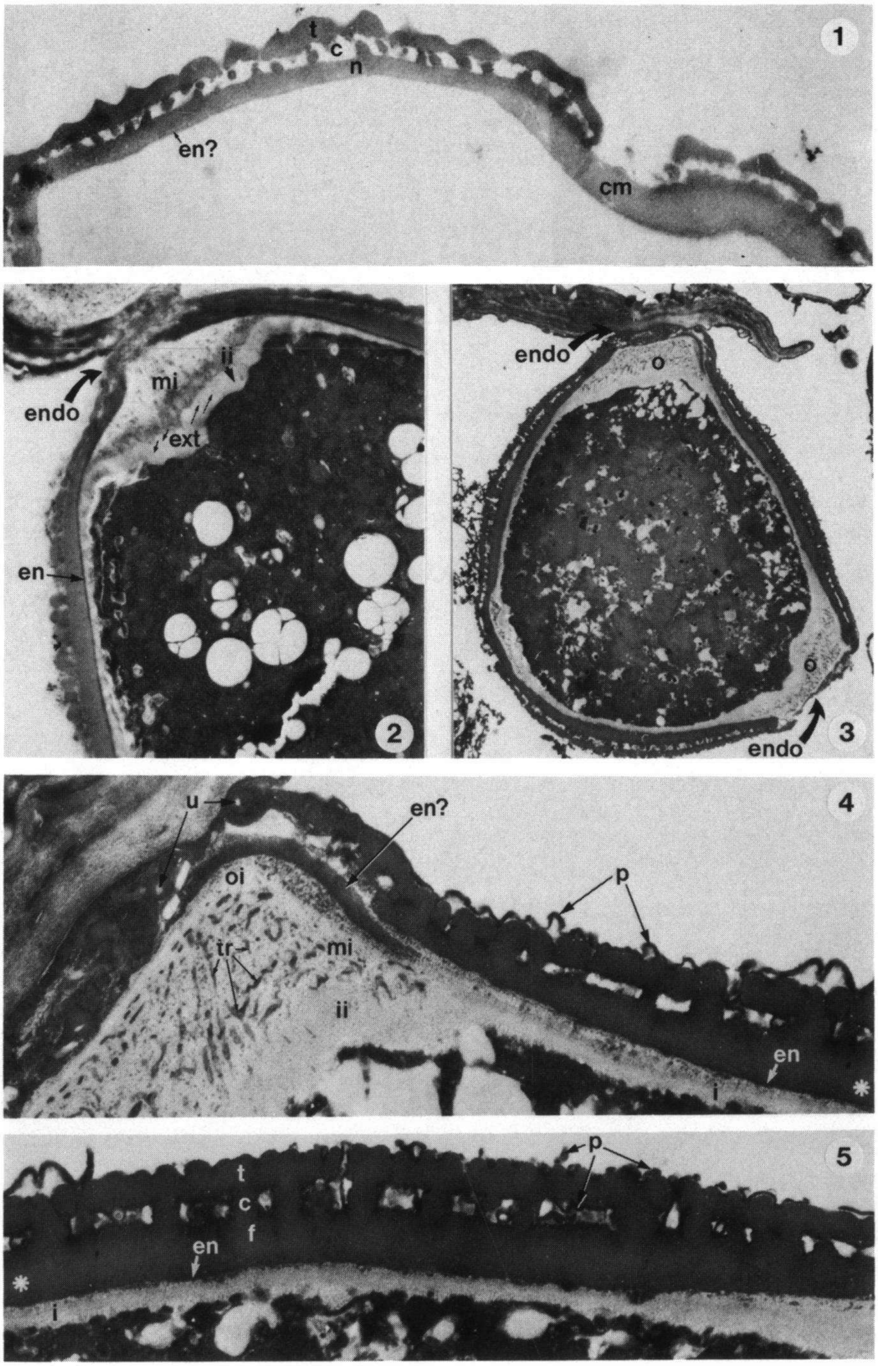


Plate 48: *Cubilia* (1), *Dimocarpus* (2–5).

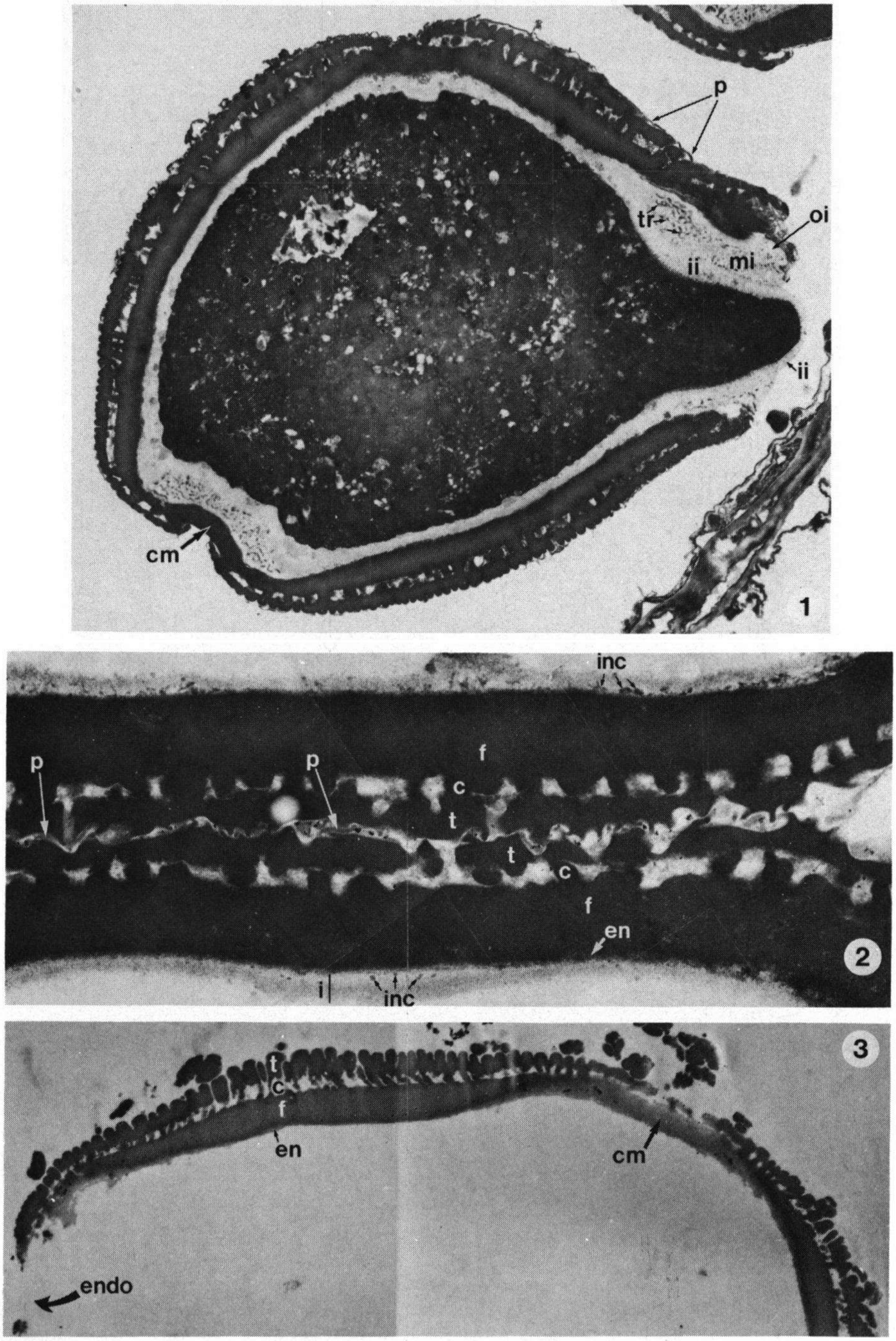


Plate 49: *Dimocarpus* (1, 2), *Litchi* (3).

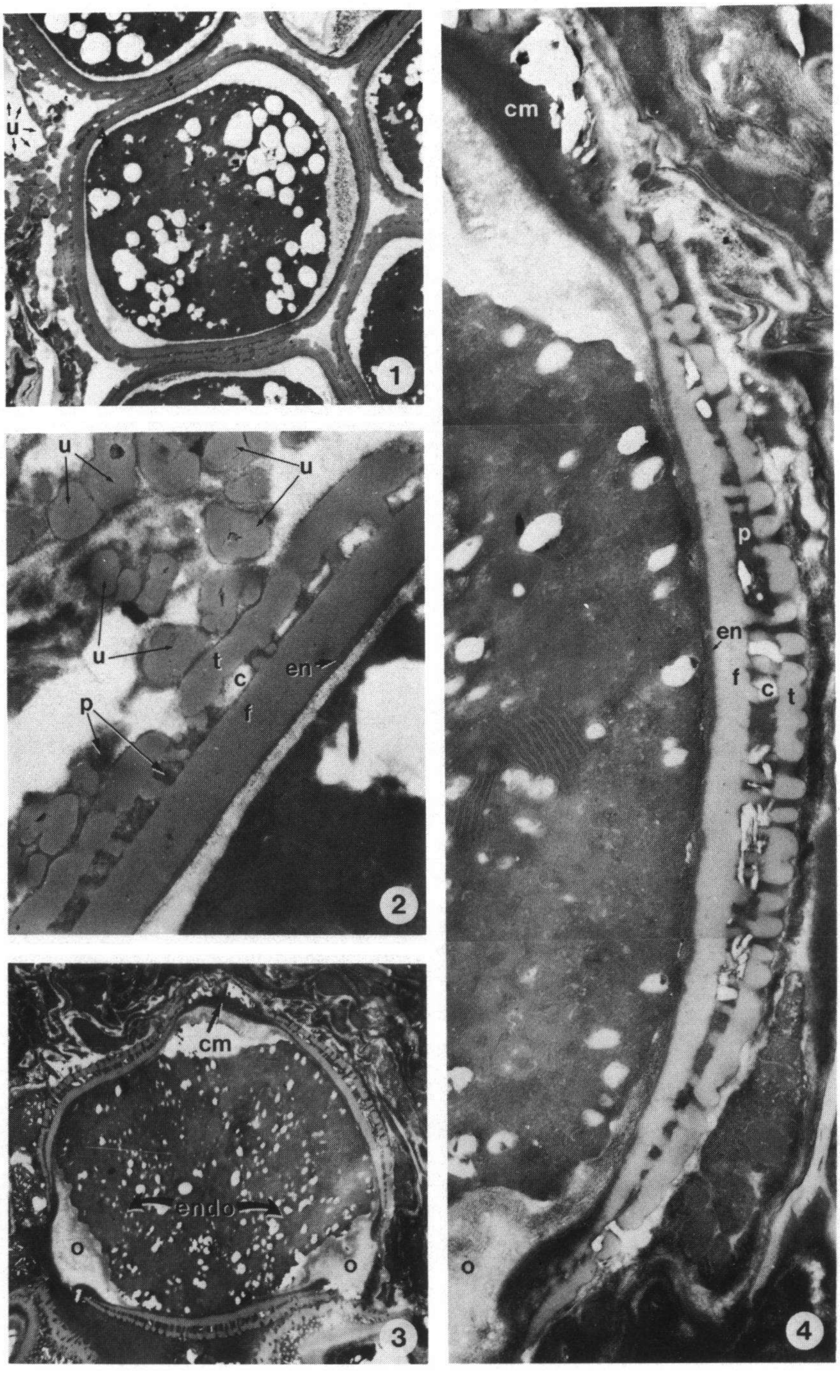


Plate 50: *Nephelium.*

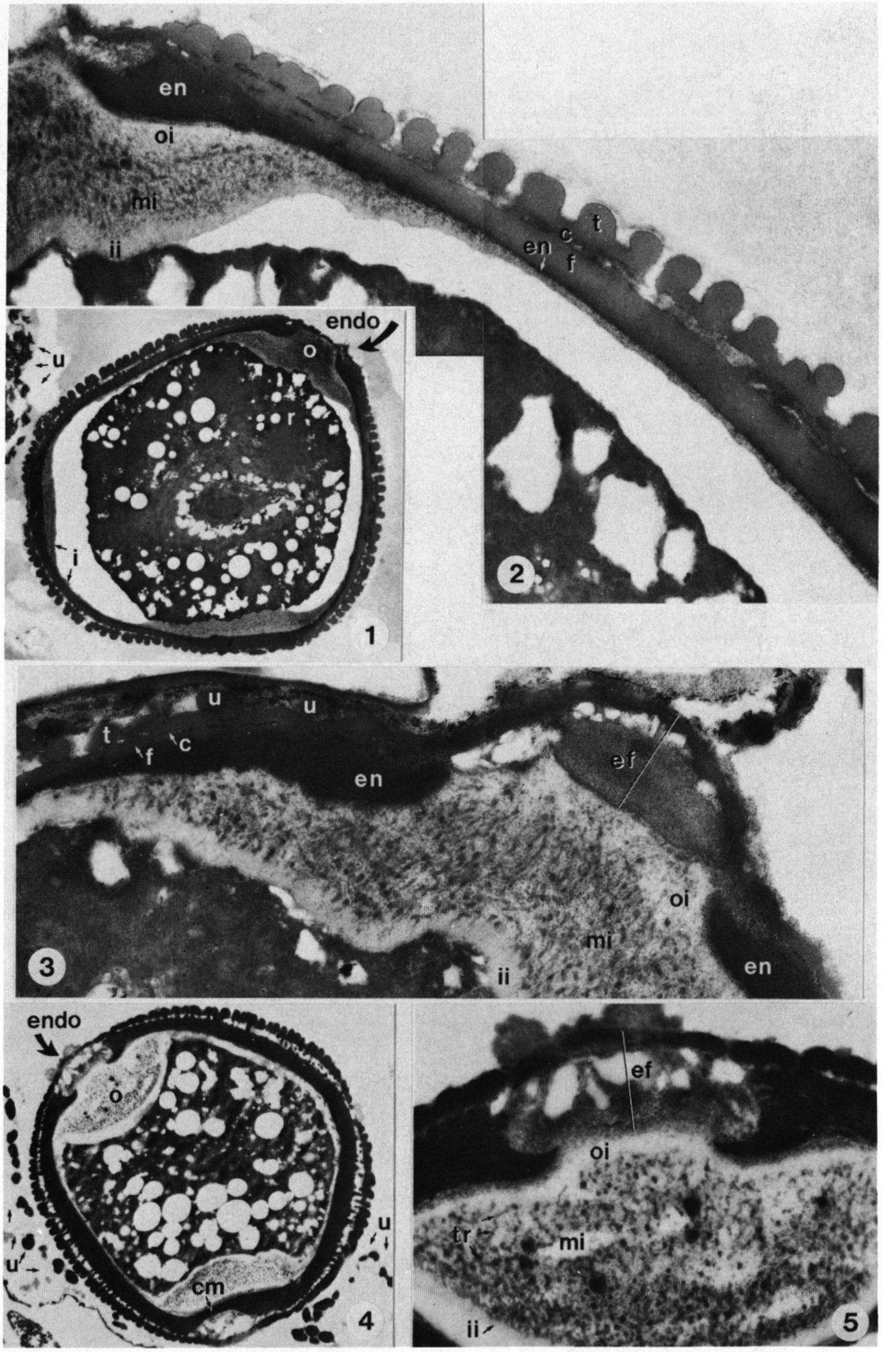


Plate 51: *Nephelium*.

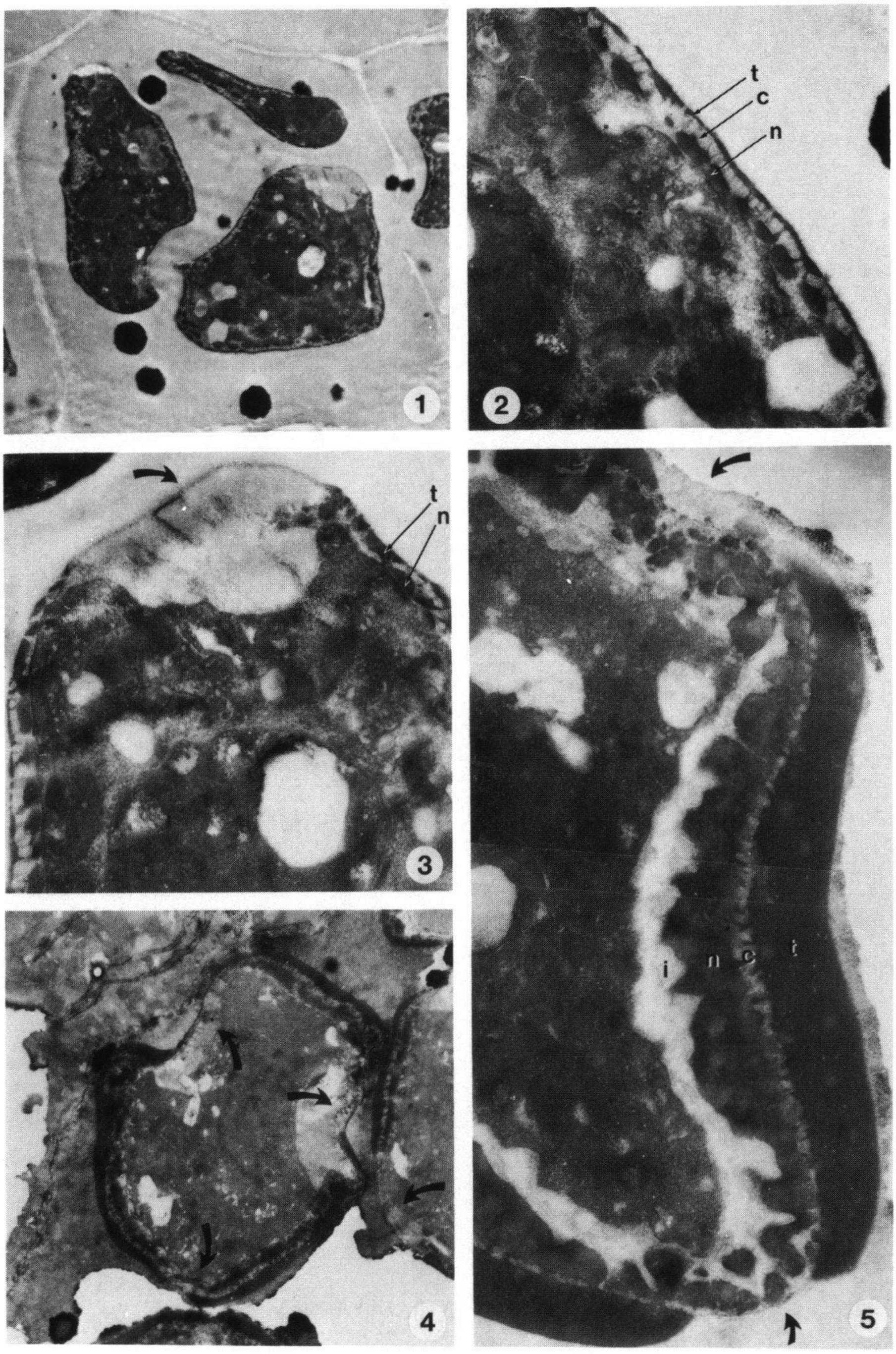


Plate 52: *Otonephelium.*

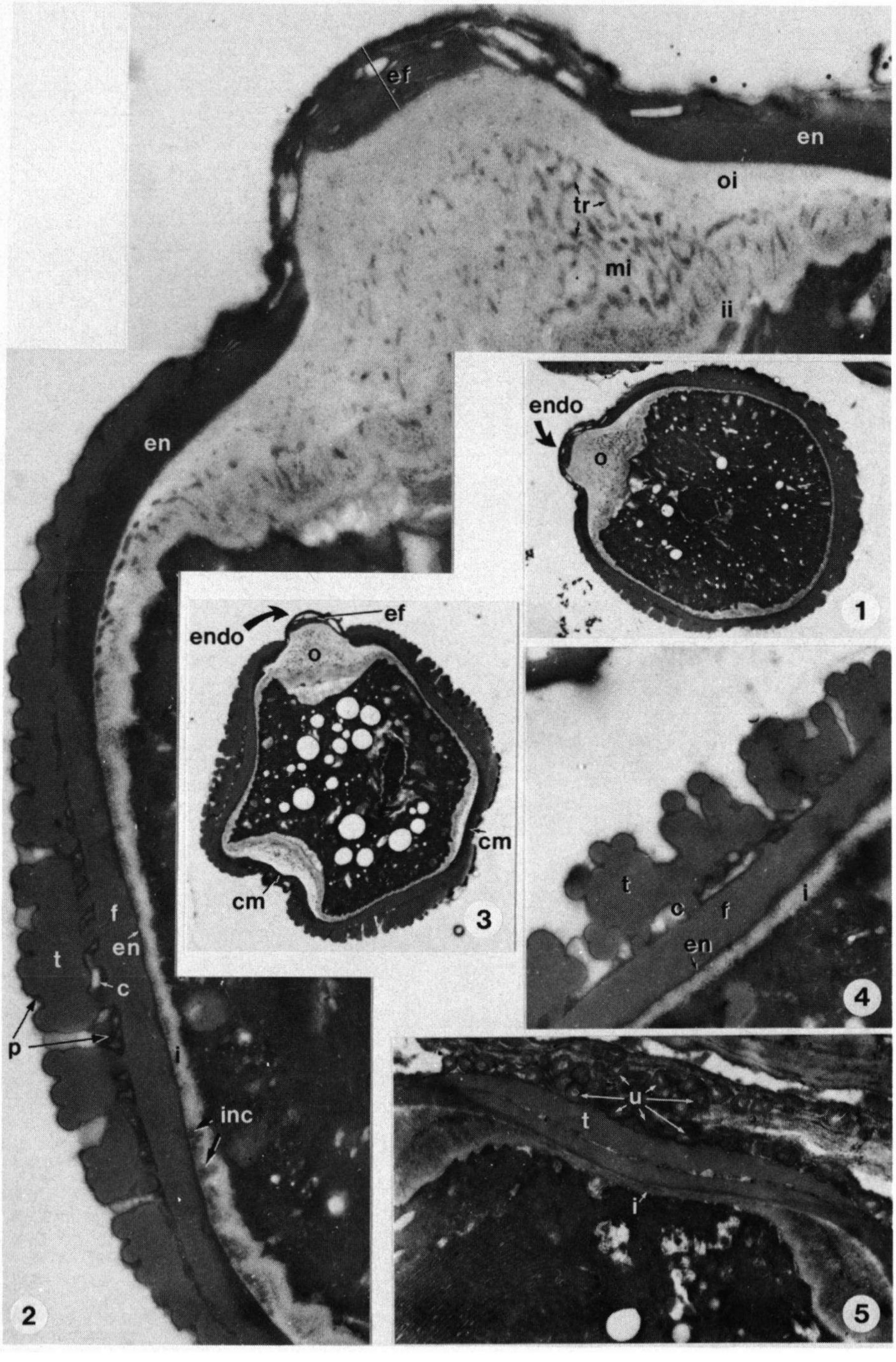
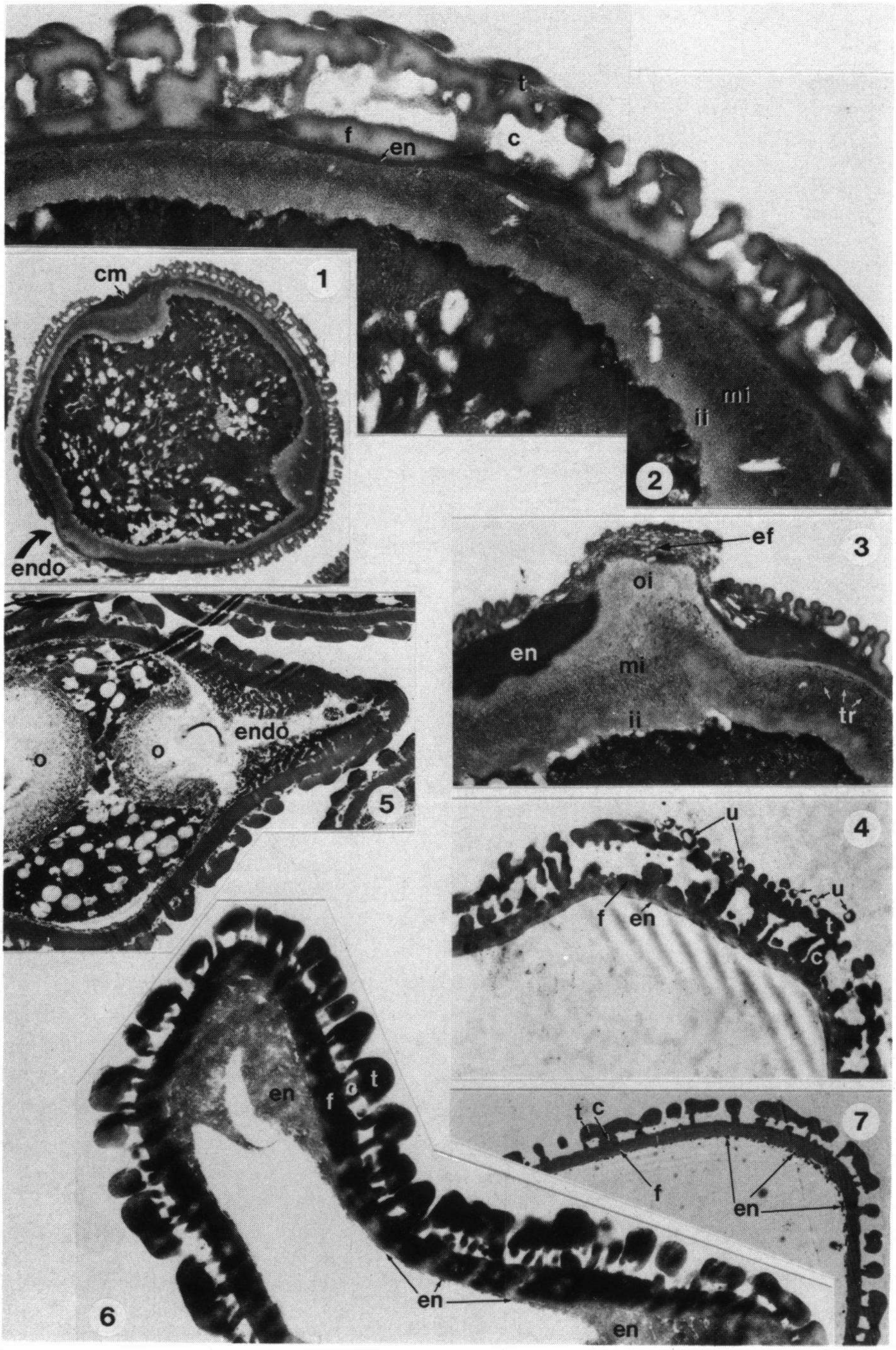


Plate 53: *Pappea*.



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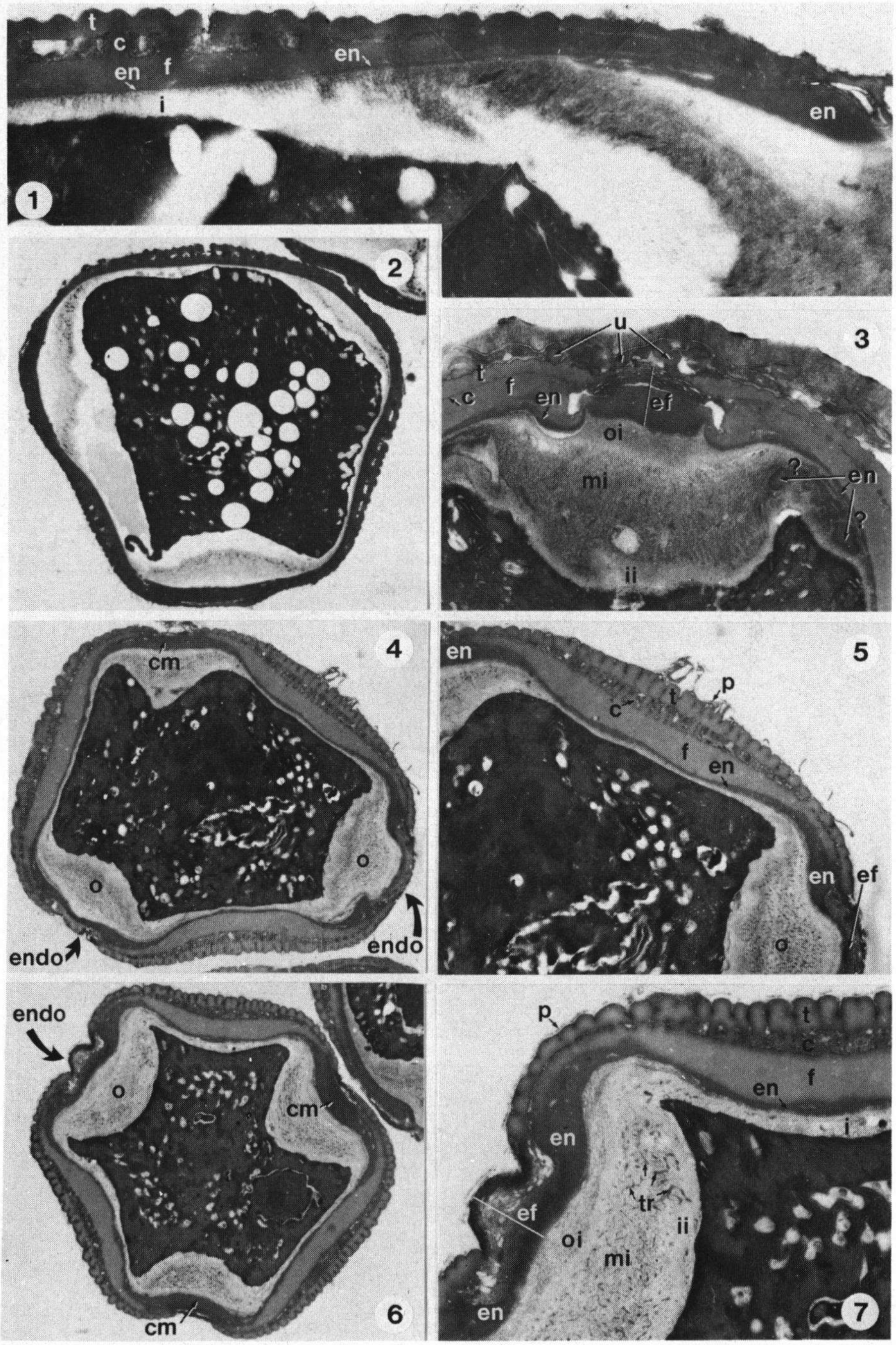

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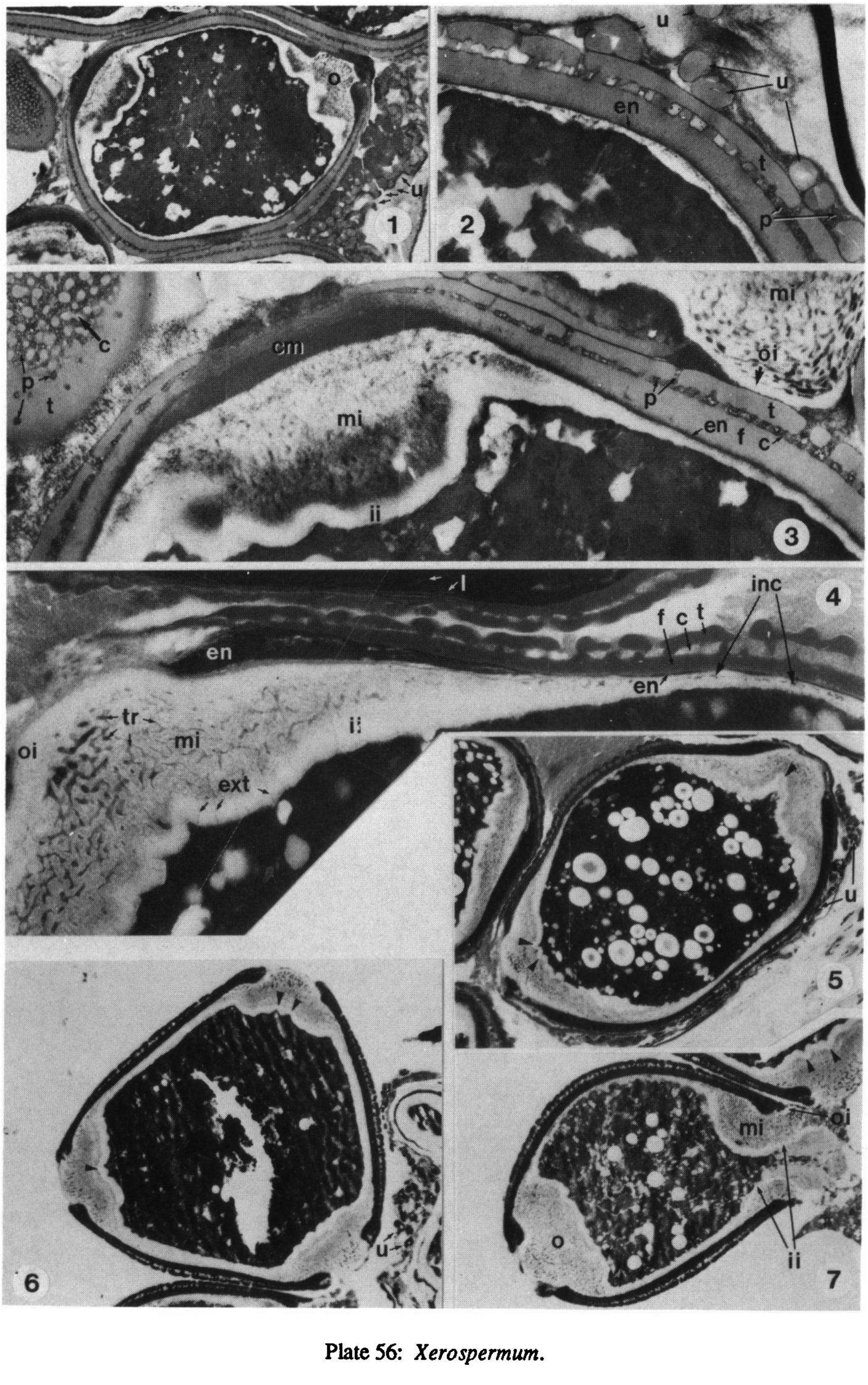

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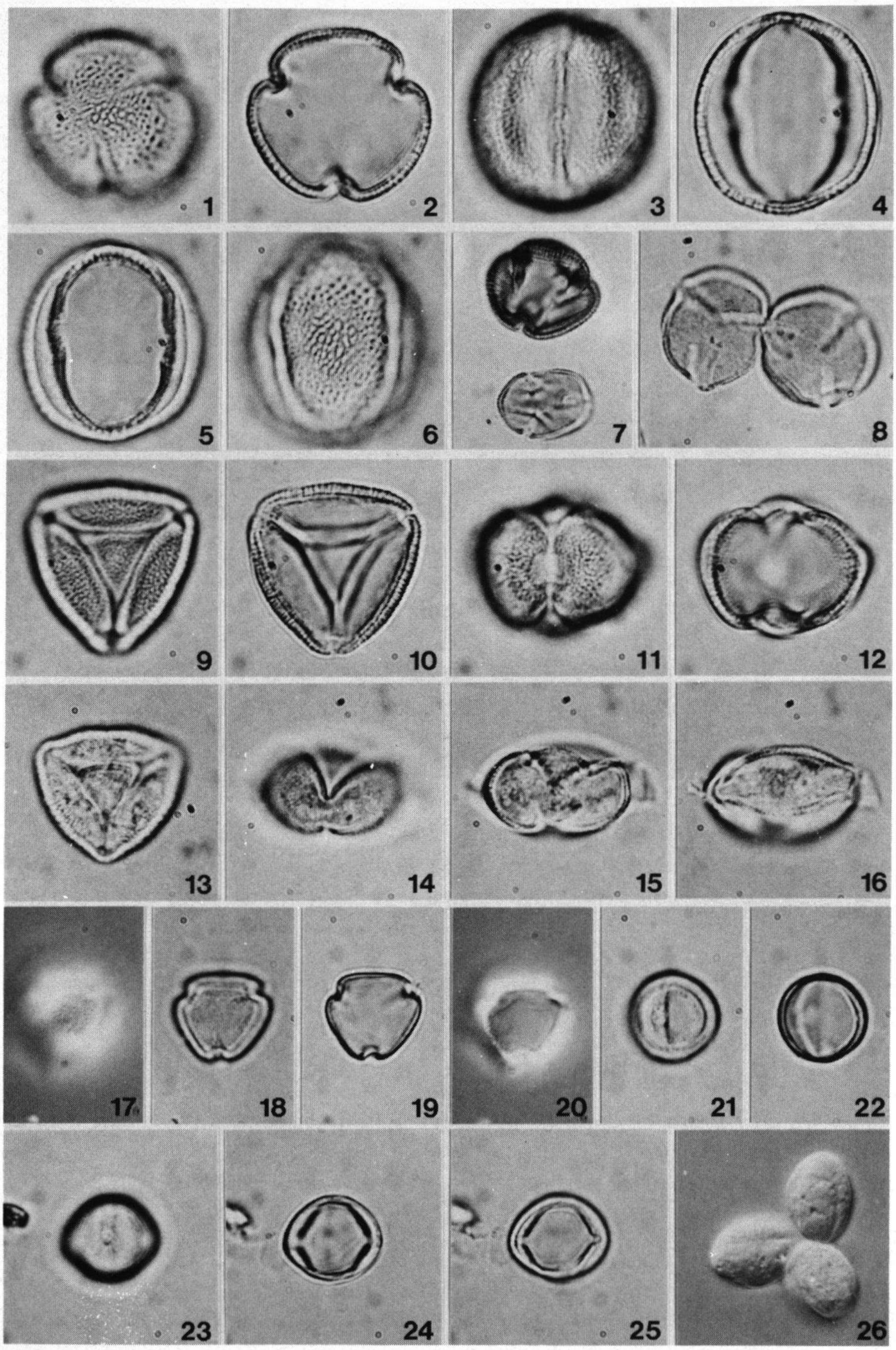

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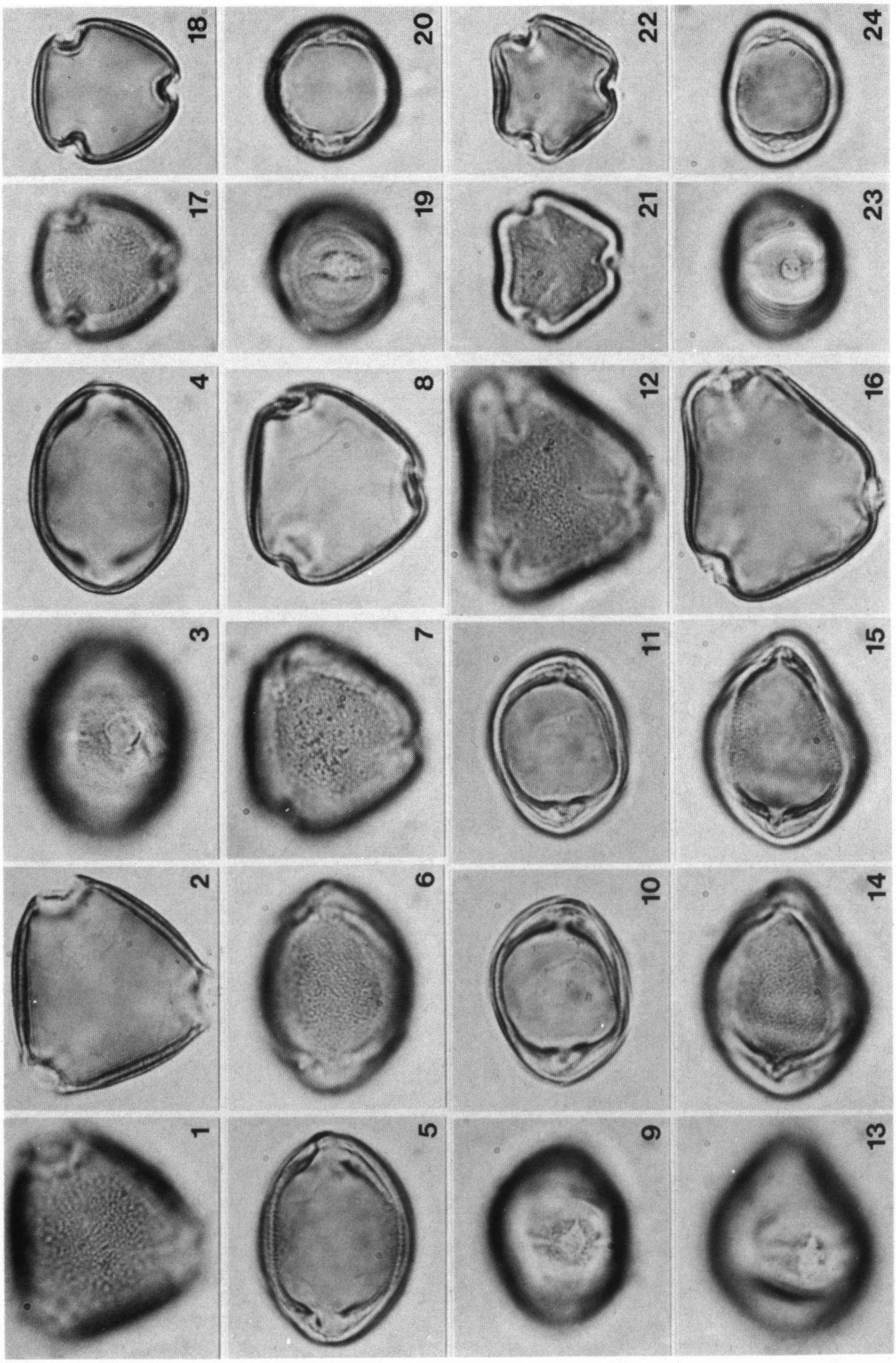

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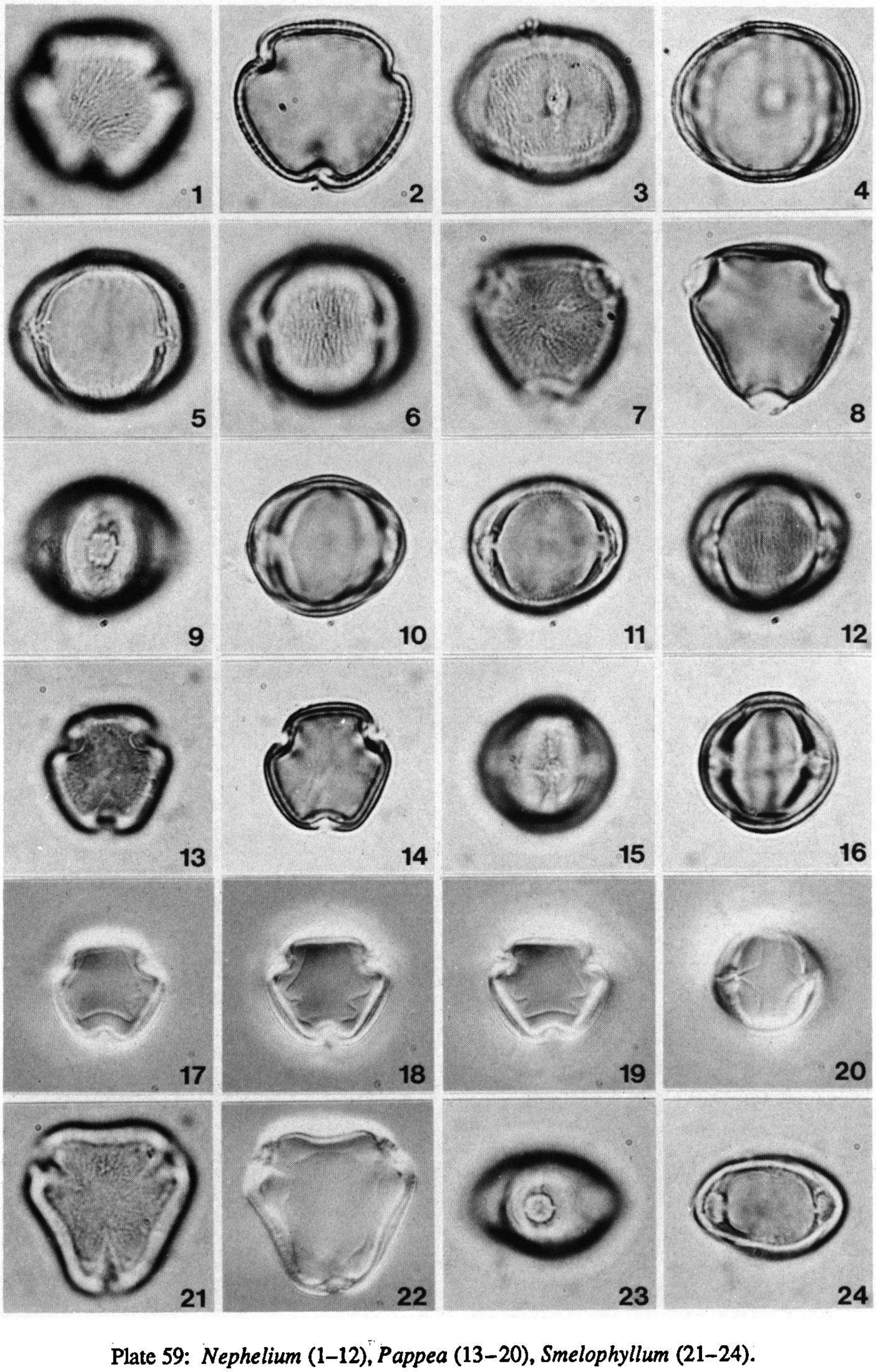

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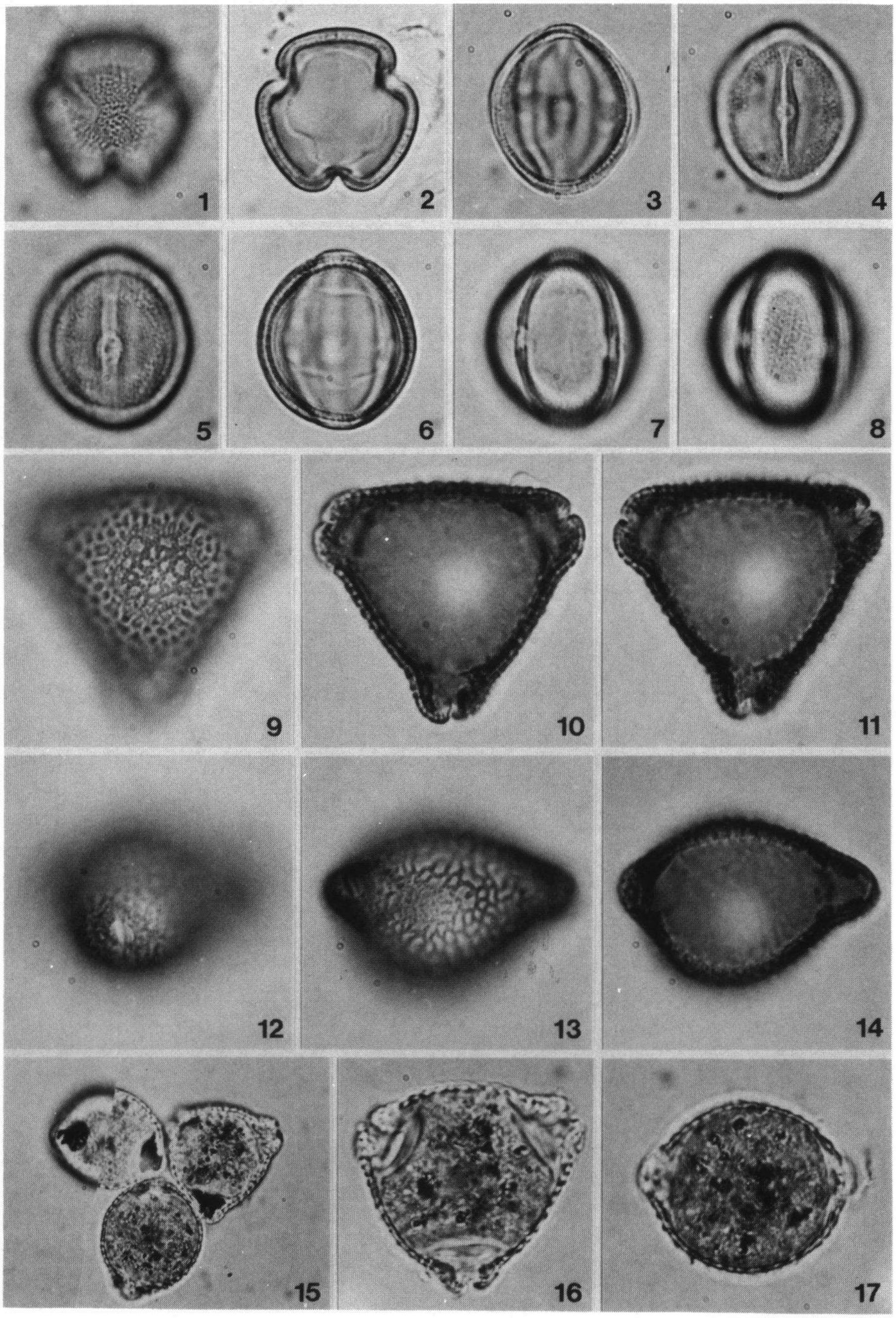

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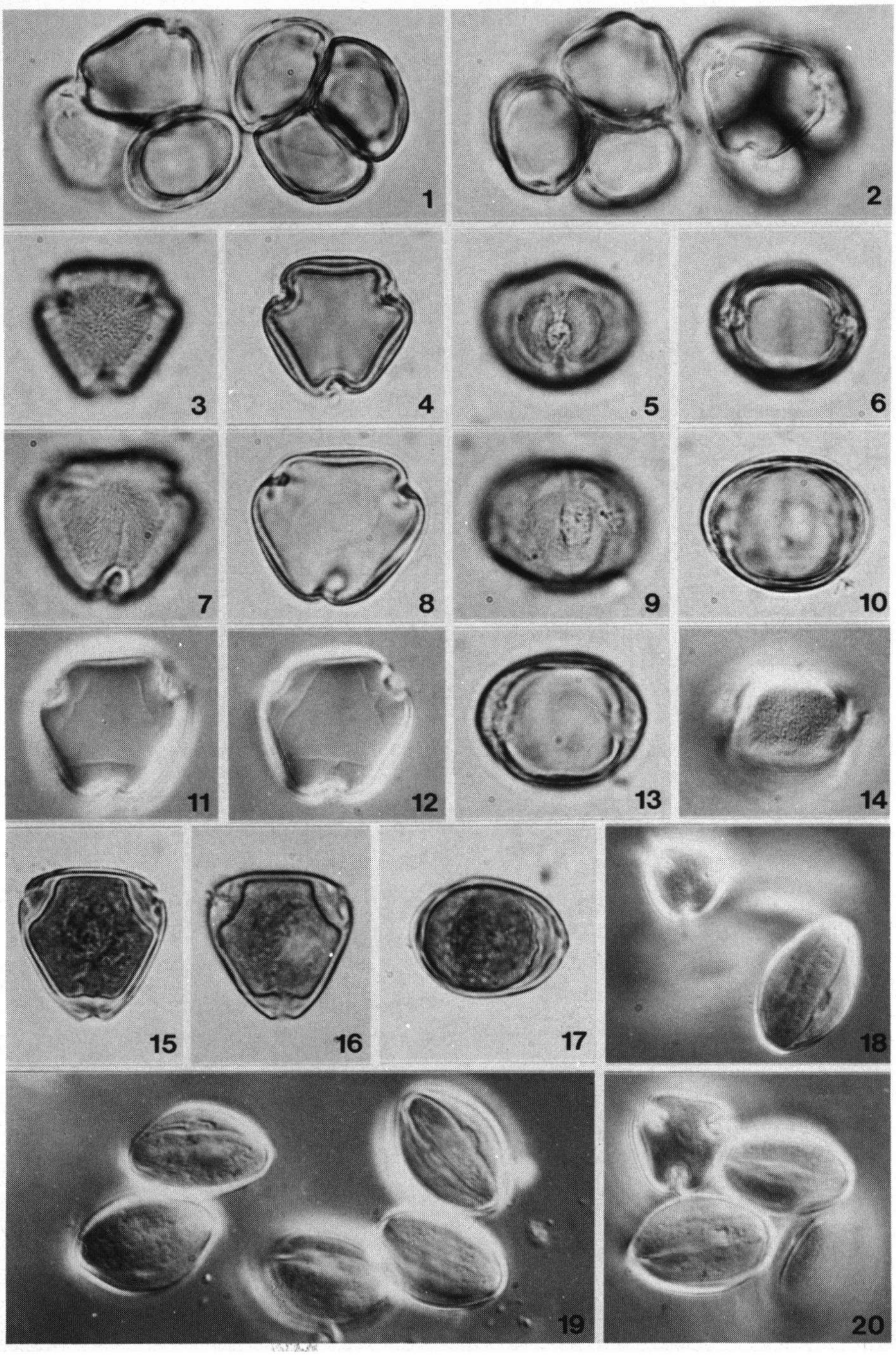

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