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EVOLUTIONARY TRENDS IN THE MORPHOLOGY AND HARMOMEGATHY OF THE POLLEN OF THE GENUS GUIOA (SAPINDACEAE-CUPANIEAE)

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SUMMARY

A pollen morphological survey of the genus *Guioa* is presented. Based on a study of the harmomegathy in relation to morphological series, evolutionary trends are postulated:

1. wide ectoapertures → narrow ectoapertures
2. grain parasyncolporate → grain colporate
3. grain parasyncolporate → grain syncolporate
4. ornamentation rugulate → ornamentation psilate-imperforate.

It is suggested that the most 'primitive' species of *Guioa* occur in the southeastern part of the distribution area of the genus. *Guioa* can be subdivided into four poorly delimited pollen morphological groups. Its affinities to other genera in the Cupanieae are briefly discussed. Pollen of the most 'primitive' group is similar to that of several 'primitive' genera (e.g. *Arytera, Matayba, Molinaea,* and *Tina*) in the tribe.

INTRODUCTION

This study deals with the pollen morphology of the genus *Guioa* (tribe Cupanieae) of the Sapindaceae. It was undertaken to provide additional taxonomic markers for a revision of the genus (Van Welzen, in prep.) and to increase our knowledge of pollen morphological diversity in the Cupanieae so that comparisons with the Nephelieae (Van der Ham, in prep.) can be more meaningful. Until now *Mischocarpus* was the only other genus in the large tribe of the Cupanieae (comprising 46 genera) of which pollen has been studied in detail (Van der Ham, 1977).

In a survey of sapindaceous pollen types Muller & Leenhouts (1976) assessed the pollen type of *Guioa* and considered its relations to other types within the family. They attributed a derived status to the type to which *Guioa* pollen belongs.

In the first part of the present study a general description of *Guioa* pollen will be given. Special attention will be paid to harmomegathy, variation in ectoaperture width, apocolpium morphology, and ornamentation. In the second part the evolutionary significance of the data will be evaluated. Finally, a pollen morphological subdivision of *Guioa* will be proposed and relations to other genera within the same tribe will be discussed.

MATERIAL AND METHODS

Of the 65 species recognised in *Guioa*, 53 could be studied. The following collections were included. The samples were obtained from material in the Rijksherbarium, Leiden (L), unless indicated otherwise (see Holmgren et al., 1981 for abbreviations).

G. acuminata Radlk., *FPRI 525*, Philippines
G. acutifolia Radlk., *Hyland 7225* (BRI), Australia
G. amabilis Kan. & Hat., *BW 14202*, New Guinea
G. aryterifolia Radlk., *NGF 19594*, New Guinea
G. asquamosa Welzen, *Metzner 226*, Timor
G. bicolor Merrill, *Ebalo 483* (A), Philippines
G. bijuga (Hiern) Radlk., *van Niel 4311*, Borneo
G. chrysea A.C. Smith, *Howard 124* (BSIP), Fiji
G. comesperma Radlk., *NGF 14031*, New Guinea
G. contracta Radlk., *Clemens 430*, New Guinea
G. coriacea (Radlk.) Radlk., *Cormish NSW 168626*, Australia
G. crenata Radlk., *MacPherson 5954*, New Caledonia
G. crenulata Radlk., *MacKee 19989*, New Caledonia
G. diplopetala (Hassk.) Radlk., *Poilane 21952* (A), Cambodia; *King's collector 3818*, Malaysia; *Korthals s.n.*, L sh. 908.268-95, *Reinwardt 776* (TEM sample only), Sumatra; *Beumée A765*, Hort. Bogor. III-K-23a (TEM sample only),*Wirawan 329*, Java; *Haviland 2137*, *Kostermans 6064*, Borneo; *NIFS bb 5461* (BO), Celebes
G. discolor Radlk., *Allen 259-81* (BSIP), Philippines
G. elliptica Welzen, *Corner RSS 2713* (BRI), Solomon Islands
G. fusca Radlk., *Franc 2272* (NY), New Caledonia
G. glauca (Labill.) Radlk. var. *glauca*, *Balansa 2843* (P), New Caledonia; var. *vulgaris* Welzen, *Compton 691* (BM), New Caledonia
G. gracilis (Panch. & Séb.) Radlk., *Baumann-Bodenheim 14787* (NY), New Caledonia

G. hirsuta Welzen, *Meijer 9706*, Celebes
G. koelreuteria (Blanco) Merrill, *Aranez 15*, Philippines
G. lasioneura Radlk., *Anon. s.n.*, 28-7-1868 (MEL), Australia
G. lentiscifolia Cav., *Yuncker 15503* (W), Tonga
G. megacarpa Welzen, *BSIP 1566*, Solomon Islands
G. membranifolia Radlk., *Kostermans 805*, Moluccas
G. microsepala Radlk., *Schodde 5233*, New Caledonia
G. montana C.T. White, *Kajewski 1286* (A), Australia
G. multijuga Welzen, *BW 4061*, New Guinea
G. myriadenia Radlk., *Clemens 16283* (NY), Philippines
G. normanbiensis Welzen, *NGF 24061* (BRI), New Guinea
G. novobritannica Welzen, *NGF 26918*, New Guinea
G. novoebudaensis Welzen, *Bernardi 13284*, New Hebrides
G. ovalis Radlk., *MacKee 14699*, New Caledonia
G. patentinervis Radlk., *Kornassi 863*, Moluccas
G. pectinata Radlk., *MacKee 23805*, New Caledonia
G. pleuropteris (Blume) Radlk., *Put 3686* (K), Thailand; *Maxwell 81-34*, Malaysia; *Voogd 552*, Sumatra; *SAN 20738* (TEM sample only), *66778*, *74533* (TEM sample only), Borneo; *Clemens s.n.*, 1906 (M), *PNH 36700*, Philippines
G. plurinervis Radlk., *MacGregor s.n.*, MEL sh. 31978, New Guinea
G. pseudoamabilis Welzen, *Clemens 9475*, New Guinea
G. pteropoda Radlk., *Brass 13082*, New Guinea
G. pterorhachis Welzen, *Kokawa & Hotta s.n.*, 1-11-1968, Borneo
G. pubescens (Zoll. & Mor.) Radlk., Sarawak Forestry Department *S 29279*, Borneo
G. punctata Welzen, *Greenwood 749* (K), Fiji
G. reticulata Radlk., *FB 22429*, Philippines
G. rhoifolia (A. Gray) Radlk., *Koroiveibau c.s. 14451*, Fiji
G. rigidiuscula Radlk., *Darbyshire 759*, New Guinea
G. scalariformis Welzen, *Hartley 12459*, New Guinea
G. semiglauca (F. Muell.) Radlk., *Brown s.n.*, NSW sh. 168600, Australia
G. subsericea Radlk., *Brass 29131*, New Guinea
G. sufusana Welzen, *BSIP 6994*, Solomon Islands
G. truncata Radlk., *PNH 10053*, Philippines
G. unguiculata Welzen, *Hoogland & Pullen 6193*, New Guinea
G. venusta Radlk., *Britton 54*, New Guinea
G. villosa Radlk., *MacKee 17677*, New Caledonia

For light microscopy (LM) and scanning electron microscopy (SEM) the material was acetolysed. LM examination was performed with grains imbedded in glycerine jelly using a Leitz Ortholux II microscope (PL Apo 100/1.32 oel). A Leitz Dialux 20 microscope (NPL Fluotar 100/1.32 oel ICT) was used for photography. For SEM the grains were coated with gold, using a Polaron E 5100 series II sputter-coater, and observed and photographed with the Jeol JSM 35 at the Rijksherbarium, Leiden. Sectioned grains for SEM (of *G. acuminata, G. bicolor, G. diplopetala,* and *G. pleuropteris*) were produced with a Leitz freezing microtome (see Muller, 1973).

Preparation for transmission electron microscopy (TEM) included fixing of non-acetolysed material (of *G. diplopetala* and *G. pleuropteris*) with 0.1% glutaraldehyde in 0.1 M sodium cacodylate buffer, pH 7.2 (15 days; a few drops of invadine were added for soaking followed by 1% OsO_4 (2 hours), prestaining with 1% uranyl-acetate during dehydration, embedding in Epon 3/7 by Luft, and poststaining with

5% uranylacetate (3 minutes) and Reynolds' lead citrate (3 minutes). Sectioning was performed with a diamond knife. Observations were made with the Philips EM 300 at the Botanical Laboratory, Leiden.

GENERAL MORPHOLOGY

Guioa pollen grains are isopolar or subisopolar monads. Sometimes anisopolar grains were found (see 'Apertures'). Young grains are arranged in tetrads according to Fischer's law (plate I: 5, 6), which is the rule in Sapindaceae.

Guioa pollen generally has three apertures; in some samples grains with two or four apertures occurred in small percentages.

The shape of the grains as determined by the ratio of the length of their polar axis (P) and equatorial diameter (E) is mostly peroblate or oblate (average P/E = 0.34–0.74). Extremely oblate grains were observed in *G. lasioneura* (P/E = 0.23–0.40). The highest P/E values occur in *G. rigidiuscula* (P/E = 0.65–0.82) and *G. membranifolia* (P/E = 0.61–0.94). Most samples show a wide P/E range.

The equatorial outline in three-aperturate grains is obtusely triangular, with concave to convex sides. Both P/E value and shape of the equatorial outline can be related to the harmomegathic state of a grain.

The grains are generally small-sized (average P = 7.6–16.7 μm, average E = 20.0–26.7 μm).

Apertures

Guioa pollen is usually syncolporate (plate IV: 5) or parasyncolporate* (plate II: 1–5); colporate grains occur rarely (plate VI: 6).

Apocolpia are isolated** or more or less extensively connected with one, two, or three of the adjacent mesocolpia (plate VI: 1–6).

Apocolpia measure from 1 μm up to 12.5 μm. The average apocolpium index A/E (apocolpium size/equatorial diameter) varies from 0.05 to 0.42. Grains with 'apocolpia' smaller than 1 μm are considered syncolporate (plate IV: 2). Apocolpia of up to 2 μm usually consist of several more or less connected granules (plate V: 3). Those from 2 to 4 μm are entire and usually psilate (plate III: 1). The larger ones are round-

* The term parasyncolporate was introduced by Van der Ham (1977) for pollen grains with isolated apocolpia (parasyn-) and compound apertures (-colporate). It is an addition to the terms parasyncolpate (Erdtman, 1952) and syncolporate (Reitsma, 1970).

** Punt et al. (1976) 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, 1977), introduced for parasyncolporate grains which show apocolpia connected with one or two mesocolpia, is considered superfluous.

ed triangular or triangular and usually bear the same type of ornamentation as shown at the borders of the mesocolpia (plate II: 1–5). Thus, syncolporate and parasyncolporate grains intergrade in *Guioa*. Many samples show both types. Often the two apocolpia of one grain are different in shape and size, or they are connected with the mesocolpia to a different extent, which causes such a grain to be more or less anisopolar. Grains with a syncolporate and a distinctly parasyncolporate side are found often in some species.

The ectoapertures are meridionally oriented and usually connected, either at (syncolporate) or near (parasyncolporate) the poles. The average width is up to 1.4 μm. They usually widen near the poles. Within a sample ectoaperture width is probably largely related to the harmomegathic state of a grain. The aperture membranes are smooth or more or less densely covered with granules. The latter are usually largest in the polar areas. In some species (e.g. *G. novobritannica*) grains were found which showed a tectal connection bridging an ectoaperture for some length in the region between the endoaperture and the polar area (plate III: 3).

The endoapertures are always pori. Their width ranges from 1.5 to 6.5 μm. They are mostly lalongate-elliptic or approximately isodiametric. Sometimes lolongate-elliptic or meridionally constricted pori were found. Again, much depends on the harmomegathic state of a grain. The polar sides of the pori are thick, whereas the lateral sides are usually thin (plate VII: 3, 4). Probably this facilitates the harmomegathic functioning of a (para)syncolporate grain, in which the whole equatorial belt acts as a hinge (Muller, 1979).

Exine architecture

Exine stratification is usually indistinct in LM. SEM (plate VII) and TEM (plates VIII, IX) images of wall sections yielded more detailed information. The total exine thickness* is 0.8 to 1.2 μm. Variation within a mesocolpium is mainly caused by differences in the thickness of the nexine.

The nexine measures* somewhat less than 1/2 up to 2/3 of the total thickness of the exine. It is thickest in the central part of a mesocolpium and thins gradually towards the ectoapertures (plate VII: 5, 6), until at a short distance from these it thickens again, thus providing a relatively thick and probably rigid layer underlying the ectoapertures and the borders of the adjacent mesocolpia (plate IX: 2). With TEM the nexine was shown to consist of two sublayers which are differently stained. The inner, electron-lucent one, is referred to as the endexine (en), the outer, electron-opaque one as the foot-layer (f). Foot-layer, columellate layer (c), and tectum (t), staining similarly, form the ectexinous part of the exine. The endexine is very thin throughout the whole central part of a mesocolpium, measuring approximately 1/10 of the total nexine thickness. Near the ectoapertures it thickens considerably, gradually replacing the fading foot-layer to constitute the whole of the aperture membrane (am) underlying the ectoapertures (plate VIII: 3; IX: 3).

The columellate layer measures* 0.1 to 0.2 μm, being thickest in the centre of a mesocolpium and gradually becoming thinner towards the ectoapertures (plate VII: 6;

* measured in the centre of a mesocolpium.

VIII; IX). Separate columellae are only rarely visible in LM. In SEM and TEM they proved to be 0.1 to 0.2 μm high* and approximately isodiametric.

The tectum is circa 0.3 μm thick. Its thickness is almost uniform throughout a mesocolpium or decreases slightly towards the ectoapertures. Perforations (up to 0.1 μm) are nearly always present. A totally imperforate tectum was only found in *G. pubescens*. Here, it also lacks any sculpture, thus displaying a psilate-imperforate tectum (plate V; 6). A few species (e.g. *G. myriadenia*, plate V: 3, 4) show pollen with a psilate-perforate tectum. All other species have pollen with a more or less densely rugulate ornamentation, which varies from prominently rugulate, with well-defined, high, often long muri (plate II), to shallowly rugulate with hardly discernible sculptural elements (plate IV: 5, 6; V: 5). The latter type merges into the psilate-perforate type. Usually the presence and size of the perforations, and the distinctiveness of the sculptural elements gradually decrease from the centre of a mesocolpium towards the ectoapertures, which results in a few species (e.g. *G. bicolor*, plate V: 1) in imperforate, more or less psilate borders. The edges of the mesocolpia and large apocolpia are mostly more or less entire; occasionally they are somewhat indented.

The maximal length of the muri is approximately 3 μm. Their width ranges from 0.2 to 0.7 μm. If they are well-pronounced, short grooves occur between them (plate II: 6; III: 4).

In TEM pollenkitt (p) was found covering the tectum and filling the (infra)tectal cavities (plates VIII, IX).

Intine

TEM (plates VIII, IX) also allows a description of the intine (i). This innermost layer of the pollen wall measures from 0.07 to 0.18 μm under the central part of a mesocolpium. Towards each endoaperture it gradually thickens, under the endoaperture yielding an oncus (o) up to circa 2.5 μm thick and 4 to 5 μm in diameter. The intine is irregularly bordered on its inside, especially under the endoapertures, where relatively large folds occur.

Under the mesocolpia the intine is more or less homogeneous. In an oncus three sublayers may be distinguished (plate VIII: 2, 4; IX: 1). The inner one (ii), about 0.4 μm thick, proceeds from the mesocolpial intine. It is usually homogeneous and often strongly folded. The middle sublayer (mi) forms the main part of the oncus. It is interlarded with a tubular and/or fibrous tract (tr), extensions (ext) of which sometimes seem to occur in the inner sublayer (plate IX: 1). Usually the middle sublayer rapidly thins out in all directions. However, in one collection of *G. pleuropteris* (*SAN 74533*) electron-opaque inclusions (inc) also occur in the outermost part of the mesocolpial intine (plate IX: 1), which suggests the extension of the middle oncus sublayer towards the centre of a mesocolpium. The outer sublayer (oi) is homogeneous and at most 0.1 μm thick in the centre of the oncus, thinning gradually around. It is not clear whether this sublayer is confined to the oncus or continues under the mesocolpia.

* measured in the centre of a mesocolpium.

Guioa intine morphology is similar to that of *Mischocarpus* (Van der Ham, 1977). The intines of *Pometia* (tribe Nephelieae; Van den Berg, 1978) and *Harpullia* (tribe Harpullieae; Muller, 1985) are less similar.

Table 1 lists the values of a number of the above mentioned characters for all *Guioa* species studied. The caption of this table contains some remarks concerning infraspecific variation. Further comments and more detailed information on several important characters are provided in the following chapters.

HARMOMEGATHY

Harmomegathy is, of course, performed only by living grains. However, much of the variation of the shape of a living pollen grain due to harmomegathy is reflected by the various degrees of folding shown in a sample of acetolysed grains. It is expected that by the lack of fully hydrated contents only the most inflated shapes of living grains will not be represented.

Apertural folding

Muller (1973, 1979) and Muller & Leenhouts (1976) mentioned that the narrow ectoapertures in the (para)syncolporate pollen types found in Myrtaceae and Sapindaceae appear to have little or no harmomegathic significance; volume changes would mainly take place by shortening and lengthening of the polar axis and by folding of the mesocolpia. Indeed, several *Guioa* species show pollen with narrow, superficial ectoapertures which are probably hardly involved in harmomegathy (plate V: 1, 6). However, pollen of many other *Guioa* species has wide ectoapertures which often show non-equatorial invagination (plate II: 3, 4). This indicates the involvement of the ectoapertures in harmomegathy.

Non-apertural folding

Observation of the shape and structure of the mesocolpia in *Guioa* pollen suggests that invagination of ectoapertures is not the only mechanism in accommodating the necessary volume reduction. The shape of the equatorial outline of a grain usually appeared variable within a single sample. Apparently the central part of a mesocolpium hinges along the thin exine zones (plates VII, VIII, IX) which border the relatively rigid (thickened nexine, dense tectum) apertural zones. A grain may get additional volume reduction by folding the relatively flexible central parts of its mesocolpia inwards. This is a widespread mechanism in oblate pollen. In *Guioa* it will especially benefit pollen with narrow ectoapertures or apo-/mesocolpium connections.

Elasticity of the exine

Apertural and non-apertural folding are the main harmomegathic mechanisms in *Guioa*. A similar combination was assessed by Blackmore & Barnes (1986) in comparing undehisced (hydrated) and dehisced (dehydrated) grains of the parasyncolporate *Eucalyptus cordata* (Myrtaceae). As noticed by them also the elasticity of

the exine usually contributes to harmomegathy. Contrary to harmomegathy in most colporate grains, in which the mesocolpia become prolate, harmomegathy in (para)-syncolporate *Guioa* pollen has no major direction. Folding as well as contracting and stretching of the exine is multi-directional, which matches very well the multi-directional (rugulate) arrangement of the sculpture elements. Colporate sapindaceous grains often have a predominantly meridionally oriented striate ornamentation, which forces the folding of the mesocolpia (and ectoapertures) to be also meridional (Muller, 1979).

Endoapertures

The thin lateral borders of the endoapertures (plate VII: 3, 4), which actually represent interruptions of the thickened nexine underlying the borders of the mesocolpia, may also be considered an adaptation to harmomegathy, as they facilitate the hinge action of the equatorial belt during shortening and lengthening of the polar axis.

(text continued on page 34)

Table 1. Values of a number of pollen morphological characters of the studied *Guioa* species.

(Part a — pages 30–31)

The length of the *polar axis* (P) and the corresponding *equatorial diameter* (E) were measured (in LM) in equatorial view in ten grains per sample. P/E is the ratio of the length of the polar axis and the equatorial diameter.

To denote the shape of the *equatorial outline* of a grain (in LM) the following symbols were used: **a** = concave; **sa** = slightly concave; **s** = straight; **se** = slightly convex; **e** = convex. Underlined symbols indicate predominance of the relevant shape. Symbols given between brackets indicate that the relevant shape was rarely observed.

A sample is considered *syncolporate* if 80% of the grains have no apocolpia (or 'apocolpia' < 1 μm), whereas a sample is *parasyncolporate* if more than 80% of the grains have apocolpia > 1 μm. If both syncolporate and parasyncolporate grains occur in considerable numbers (20–80%), an estimation of their ratio is given.

Apocolpium size (A), which is the maximal diameter of an apocolpium, was taken from five apocolpia in five grains per sample. The apocolpium index *A/E* gives the average relative apocolpium size. All apocolpium sizes refer to LM measurements.

(Part b — pages 32–33)

The occurrence of *apo-/mesocolpium connections* (in LM and SEM) is indicated by ± (observed in one or two grains), + (observed in a few grains, showing various degrees of apo-/mesocolpium coherence), ++ (in many grains, showing all degrees of coherence), and +++ (in at least 50% of the grains, showing all degrees of coherence). The (always limited) occurrence of *colporate* grains in a sample is denoted

by +, that of almost colporate grains (showing incomplete coalescence of the apocolpia and three mesocolpia) by ±.

Ectoaperture width was measured (in SEM) approximately halfway between an apocolpium and an endoaperture.

Endoaperture width and *shape* were observed in LM. **lo** = lolongate-elliptic shape; **is** = isodiametrical shape; **la** = lalongate-elliptic shape; **me** = lalongate-meridionally constricted.

On the basis of SEM photographs it has been tried to discern several ornamentation categories. **RR** indicates the prominently rugulate type, which has well-defined, high, often long (up to 3 μm) muri. Category **R** shows less prominent but still well-discernible, shorter (up to 2 μm) muri, whereas in category **r** sculpture elements are hardly discernible. Category **per** denotes the psilate-perforate type, which lacks sculpture elements, and **psi** the psilate-imperforate type, which has neither sculpture elements nor perforations. Underlined symbols indicate predominance of the pertinent category.

The column *remarks* provides information relating to various characters.

Finally the *pollen morphological group* to which a species belongs is mentioned (see 'A pollen morphological subdivision of Guioa').

All sizes are expressed in μm.

Guioa diplopetala — The given values are based on *Haviland 2137*. A SEM survey of additional collections showed that this widespread species is rather variable with respect to apocolpium morphology, ectoaperture width, and ornamentation:

	average apocolpium size	apo-/meso-colpium connections	colporate	average ectoaperture width	ornamentation
Poilane 21952 (Cambodja)	2.1			0.3	R
King's coll. 3818 (Malaysia)	2.1	++	±	0.1	R
Korthals s.n. L 908.268-95 (Sumatra)	4.0	++	±	0.15	r
Wirawan 329 (Java)	1.5	+		0.2	r–psi
Haviland 2137 (Borneo)	3.2	±		0.38	R
Kostermans 6064 (Borneo)	–			0.2	R–r
NIFS bb 5461 (Celebes)	1.2			0.25	R–RR

Guioa pleuropteris — The values are based on *SAN 66778*. Also this widespread species shows infraspecific pollen morphological variation, although to a less extent than *G. diplopetala:*

	average apocolpium size	apo-/meso-colpium connections	colporate	average ectoaperture width	ornamentation
Put 3686 (Thailand)	–			0.2	R
Maxwell 81-34 (Malaysia)	–			0.2	R
Voogd 552 (Sumatra)	1.5	±		0.25	r–per
SAN 66778 (Borneo)	2.2	+++	±	0.33	R–r
Clemens s.n. (Philippines)	–			0.3	R–r
PNH 36700 (Philippines)	–			0.15	R

(Table 1, part a)

Guioa	polar axis	equatorial diameter	P/E	equatorial outline	*	**	***	apocolpium size	A/E
acuminata	11.0 (12.3) 14.6	18.1 (21.8) 27.2	0.40 (0.56) 0.71	sa–s (se–e)		1:2		1.5	0.07
acutifolia	11.2 (12.8) 15.7	22.6 (24.5) 27.2	0.45 (0.52) 0.59	sa–s (se)			+	2.9	0.12
amabilis	8.9 (13.8) 15.9	16.3 (22.3) 25.8	0.33 (0.62) 0.81	sa–s (se)			+	2.8 (5.6) 9.2	0.24
aryterifolia	13.2 (14.3) 15.7	19.8 (23.4) 25.0	0.58 (0.61) 0.68	(a–sa) s (se–e)		1:3		1.2 (2.1) 2.5	0.09
asquamosa	8.7 (10.7) 12.4	20.1 (23.0) 25.8	0.39 (0.46) 0.54	(a) sa–s (se)			+	4.9 (6.3) 8.1	0.35
bicolor	13.7 (15.6) 17.4	20.0 (22.2) 24.4	0.59 (0.70) 0.83	(sa–s) se (e)			+	1.5 (3.0) 4.2	0.13
bijuga	10.5 (13.0) 15.0	23.3 (25.0) 27.4	0.43 (0.52) 0.64	sa (s–se)		3:1		1.4 (1.8) 2.4	0.07
chrysea	11.3 (11.7) 12.3	19.1 (20.0) 21.3	0.55 (0.59) 0.63	sa–s (se)		1:1		0.7 (2.3) 3.9	0.11
comesperma	12.5 (13.0) 13.7	19.4 (20.6) 22.1	0.57 (0.63) 0.67	sa–s (se)			+	1.7 (2.4) 3.6	0.12
contracta	11.9 (12.7) 13.7	20.3 (22.5) 24.6	0.52 (0.56) 0.64	(a) sa (s)	+			0.8 (1.0) 1.1	0.05
coriacea	10.1 (12.0) 13.8	22.5 (25.8) 28.0	0.39 (0.47) 0.57	sa–s			+	5.0 (6.4) 8.4	0.24
crenata	10.6 (12.3) 13.6	21.3 (23.3) 24.6	0.44 (0.52) 0.61	(sa) s (se)			+	5.6 (8.1)11.2	0.32
crenulata	12.3 (12.9) 13.7	19.2 (20.2) 22.4	0.58 (0.64) 0.68	(sa) s–se (e)			+	2.8 (3.8) 5.6	0.19
diplopetala	10.5 (11.5) 13.1	19.5 (20.8) 23.1	0.46 (0.55) 0.65	(a) sa (s)			+	1.7 (3.2) 5.8	0.13
discolor	11.2 (12.2) 13.4	19.4 (21.9) 23.6	0.49 (0.56) 0.60	(a) sa–s (se)	+			–	–
elliptica	9.9 (11.7) 12.7	22.6 (24.1) 26.7	0.43 (0.48) 0.56	(a) sa–s–se (e)			+	1.9 (3.6) 5.5	0.14
fusca	9.3 (10.7) 12.3	22.2 (24.2) 26.9	0.36 (0.44) 0.53	sa–s (se)			+	5.8 (8.5)11.2	0.35
glauca var. *glauca*	9.3 (11.6) 13.8	19.5 (24.0) 29.3	0.36 (0.48) 0.56	(a) sa–s (se)			+	4.5 (5.6) 6.4	0.22
glauca var. *vulgaris*	6.3 (10.0) 13.9	22.2 (24.0) 25.2	0.28 (0.42) 0.62	(sa) s–se	+			–	–
gracilis	9.9 (11.6) 12.7	20.7 (23.3) 26.4	0.39 (0.50) 0.59	sa–s (se)			+	6.7 (8.7)12.5	0.38
hirsuta	12.0 (13.6) 15.7	21.2 (23.4) 26.0	0.57 (0.58) 0.60	(sa) s–se (e)		1:1		0.9 (2.0) 2.8	0.09
koelreuteria	10.9 (11.7) 13.0	22.4 (24.1) 26.3	0.43 (0.48) 0.58	(a) sa–s (se–e)		2:1		1.5 (2.6) 3.1	0.11
lasioneura	4.5 (7.6) 9.0	19.3 (22.3) 23.7	0.23 (0.34) 0.40	(a–sa) s–se (e)		2:1		1.2 (2.0) 2.6	0.09
lentiscifolia	8.1 (11.0) 14.6	21.4 (24.4) 26.7	0.33 (0.45) 0.52	(sa) s (se)			+	8.2 (9.8)11.2	0.42
megacarpa	13.4 (14.8) 15.5	18.8 (23.2) 25.2	0.58 (0.64) 0.81	(sa) s–se (e)			+	1.3 (2.7) 3.9	0.12
membranifolia	14.9 (16.2) 19.0	20.2 (23.6) 25.6	0.61 (0.69) 0.94	(sa) s–se (e)		1:3		1.7 (2.4) 2.8	0.10

microsepala	7.3 (11.4) 13.6	19.7 (22.7) 25.4	0.29 (0.50) 0.63	(a) sa–s (se)			+	4.5 (5.9) 7.8	0.27
montana	13.8 (15.4) 17.1	23.4 (26.7) 29.1	0.51 (0.58) 0.69	(a) sa–s (se)		1:1		2.0 (3.8) 5.6	0.14
multijuga	10.3 (13.4) 15.7	21.2 (22.8) 24.5	0.44 (0.59) 0.71	(a–sa) s–se		1:1		2.3	0.09
myriadenia	11.3 (12.9) 14.8	22.2 (23.2) 24.9	0.51 (0.55) 0.65	(a) sa–s (se)			+	2.5 (3.3) 4.5	0.13
normanbiensis	10.6 (11.6) 12.7	20.2 (21.6) 23.7	0.45 (0.53) 0.62	(a) sa (s–se)			+	1.1 (2.0) 2.8	0.09
novobritannica	12.3 (13.0) 14.0	19.2 (20.4) 22.0	0.58 (0.63) 0.69	(sa) s–se (e)		1:1		2.2 (2.9) 3.9	0.13
novoebudaensis	7.3 (10.8) 13.2	19.0 (20.9) 23.4	0.38 (0.52) 0.68	(a) sa–s (se–e)	+			–	–
ovalis	12.4 (14.3) 18.7	19.6 (22.5) 24.4	0.54 (0.64) 0.80	(sa) s (se)		1:3		1.6 (2.4) 3.9	0.11
patentinervis	10.2 (11.9) 13.7	21.3 (22.4) 23.9	0.44 (0.53) 0.60	(a–sa) s (se–e)			+	2.5 (3.3) 4.5	0.14
pectinata	11.1 (11.8) 13.2	22.4 (23.7) 25.3	0.45 (0.50) 0.54	(a) sa–s (se)		3:1		1.6 (2.2) 3.1	0.09
pleuropteris	10.1 (13.2) 15.1	20.3 (22.5) 24.6	0.41 (0.58) 0.73	(a–sa) s–se (e)		1:2		0.9 (2.2) 2.9	0.09
plurinervis	11.4 (12.3) 13.6	23.0 (24.9) 27.2	0.45 (0.49) 0.52	(sa) s (se)			+	2.7 (3.6) 4.1	0.15
pseudoamabilis	10.5 (12.7) 17.0	20.2 (22.6) 25.0	0.42 (0.56) 0.78	(sa) s–se (e)			+	3.6 (4.9) 7.3	0.22
pteropoda	12.5 (14.0) 16.5	22.4 (24.0) 25.0	0.51 (0.58) 0.67	(sa) s–se (e)		1:2		0.9 (1.6) 2.8	0.06
pterorhachis	13.9 (15.2) 16.8	24.4 (26.1) 28.6	0.50 (0.58) 0.65	(sa) s–se (e)		1:3		1.9 (2.9) 3.6	0.11
pubescens	9.0 (13.6) 15.2	19.0 (22.2) 25.0	0.36 (0.61) 0.71	(sa) s–se (e)			+	1.7 (2.4) 3.9	0.11
punctata	10.2 (12.7) 14.2	18.0 (21.0) 23.2	0.57 (0.61) 0.67	(a) sa–s (se)			+	3.1 (5.0) 6.7	0.23
reticulata	8.4 (12.3) 15.7	21.4 (22.9) 24.6	0.37 (0.54) 0.65	(sa) s–se (e)		3:1		1.6 (2.3) 2.8	0.10
rhoifolia	10.1 (12.0) 14.1	22.0 (23.1) 24.6	0.42 (0.52) 0.64	(sa) s (se)			+	6.4 (7.5) 8.5	0.35
rigidiuscula	13.4 (15.0) 16.6	19.5 (20.3) 20.9	0.65 (0.74) 0.82	(s) se–e		1:1		2.8 (3.6) 4.5	0.17
scalariformis	13.6 (14.3) 16.7	23.0 (24.8) 27.1	0.53 (0.58) 0.64	(a–sa) s (se–e)		1:3		1.1 (2.5) 3.4	0.10
semiglauca	10.6 (12.6) 13.8	19.5 (21.9) 24.1	0.50 (0.58) 0.68	(a–sa) s–se (e)		2:1		1.3 (2.4) 3.6	0.10
subsericea	9.9 (11.6) 13.6	22.7 (24.2) 24.9	0.42 (0.48) 0.58	(a–sa) s–se (e)	+			–	–
sufusana	12.4 (14.5) 15.8	17.9 (20.8) 23.7	0.63 (0.70) 0.77	(a–sa) s–se (e)		1:2		1.7 (2.7) 3.4	0.13
truncata	15.7 (16.7) 17.8	23.5 (25.7) 28.2	0.60 (0.65) 0.71	(a–sa) s–se (e)			+	5.0 (6.6) 7.8	0.24
unguiculata	9.6 (11.4) 14.0	24.1 (26.1) 28.3	0.37 (0.44) 0.48	(a) sa–s (se)			+	2.2 (2.5) 2.8	0.09
venusta	9.0 (11.1) 12.5	16.2 (20.5) 23.7	0.39 (0.54) 0.77	(a) sa–s–se (e)	+			–	–
villosa	7.3 (12.4) 17.0	20.9 (23.9) 27.4	0.31 (0.52) 0.59	(sa) s–se (e)			+	2.5 (3.7) 5.5	0.14

* = syncolporate; ** = syncolporate/parasyncolporate; *** = parasyncolporate

(Table 1, part b)

Guioa	*	**	ectoaperture width	endoaperture width	endoaperture shape	ornamentation	remarks	illus. (LM, SEM) plate:	pollen morph. group
acuminata	+		0.1 (0.13) 0.15	2.5–3.5	me–la–is	r	mesocolpium borders ± psilate		IV
acutifolia	±		0.4 (0.58) 0.75	2.5	la–is	R			III
amabilis			0.45 (0.68) 0.9	2.5	la–is	RR	sometimes 2- or 4-aperturate	I: 1–4	I
aryterifolia	+		0.3 (0.60) 0.9	2.5	la–is–lo	R			II
asquamosa			0.5 (0.70) 0.9	2 –3	la	R	mesocolpium edges ± indented		I
bicolor	+++	+	0.05 (0.33) 0.6	4.5	me–la–is	r–per	mesocolpium borders ± psilate	V: 1; VII: 1–4	IV
bijuga	±		0.2 (0.35) 0.5	4	me–la	r			IV
chrysea	++		0.25 (0.45) 0.65	3	la–is	RR	sometimes 4-aperturate; mesocolpium edges ± indented		II
comesperma			0.1	3	me–la	r	mesocolpium borders ± psilate		IV
contracta			0.15 (0.23) 0.3	1.5–2.5	la–is	R		IV: 1, 2	III
coriacea			0.15 (0.43) 0.7	2.5–3.5	la	RR–R	sometimes 2-aperturate		I
crenata			0.25 (0.48) 0.7	3	me–la–is	RR	sometimes 4-aperturate	I: 7, 8	I
crenulata	±		0.65 (0.80) 0.95	2.5–4	la–is	R–r		I: 17–19	III
diplopetala	±		0.15 (0.38) 0.60	2.5–3.5	me–la–is	R	see caption; ectoapertures sometimes bridged	III: 1, 2, 4; V: 2	II–IV
discolor			0	3.5	la	per			IV
elliptica	±		0.3 (0.90) 1.5	3	la	R			II
fusca			0.25 (0.35) 0.45	3.5	me–la	RR		II: 1, 2	I
glauca var. *glauca*			0.6 (0.75) 0.9	3.5	la–is	R–r	mesocolpium edges ± indented		I
glauca var. *vulgaris*			0.05 (0.10) 0.15	3.5–4	me–la	r			IV
gracilis	±		0.8 (1.05) 1.3	3 –3.5	me–la–is	R			I
hirsuta			0.2 (0.43) 0.65	1.5–3	la–is–lo	r			IV
koelreuteria	+		0.1 (0.28) 0.45	2.5–3.5	la	r–per		V: 5	IV
lasioneura			0	4.5–6.5	la	RR			II
lentiscifolia			0.6 (0.80) 1.0	3.5–4.5	la	RR		I: 5, 6; II: 3, 4	I
megacarpa	+		0.1 (0.30) 0.8	4 –5	la–is	R			II

membranifolia	±		0.1	(0.40)	0.7	3 –4.5	me–la–is	R–r	ectoapertures sometimes bridged		III
microsepala			0.4	(0.70)	1.0	2 –3.5	is	R			I
montana			1.0	(1.40)	1.8	4.5–5	la–is	RR–R		I: 9–12	II
multijuga			0.4	(0.53)	0.65	2 –3.5	is–lo	RR			II
myriadenia	++	±	0.25	(0.38)	0.5	2.5–3.5	me–la–is	per		I: 20; V: 3, 4	IV
normanbiensis	±		0	(0.05)	0.1	2.5–3.5	me–la	RR			II
novobritannica			0.2	(0.23)	0.25	2 –3	la–is–lo	R	ectoapertures sometimes bridged	III: 3	II
novoebudaensis			0.2	(0.40)	0.6	2.5–3	la	R			III
ovalis			0.2	(0.35)	0.5	2.5–3.5	is	R–r		IV: 3, 4	III
patentinervis	+		0.3	(0.50)	0.8	2 –2.5	is	R		III: 5	II
pectinata	+		0.5	(0.75)	1.0	2.5–4	la	r		IV: 5	III
pleuropteris	+++	±	0.15	(0.33)	0.5	2.5–3.5	la	R–r	see caption	VII: 5, 6	III, IV
plurinervis	±		0.4	(0.50)	0.6	3 –3.5	la	R			III
pseudoamabilis	++	±	0.6	(0.90)	1.2	2 –3.5	la–is	RR	sometimes 4-aperturate		I
pteropoda	++	+		0		3 –4	is	r	mesocolpium borders ± psilate	I: 21–24	IV
pterorhachis	+		0.15	(0.23)	0.3	3 –3.5	is	r	mesocolpium borders ± psilate		IV
pubescens	+		0.1	(0.15)	0.2	3 –4	la–is	psi		V: 6	IV
punctata	+++	+	0.3	(0.50)	0.7	3 –3.5	la	RR		VI: 1–6	I
reticulata			0.25	(0.58)	0.9	3.5–4.5	me–la–is	per			IV
rhoifolia			0.2	(0.40)	0.6	3.5–4	me–la	RR		II: 5, 6	I
rigidiuscula	+		0.35	(0.50)	0.65	2.5–3	me–la–is	RR–R	sometimes 2-aperturate	III: 6	II
scalariformis	+++		0.6	(0.75)	0.9	3	me–la	R–r		I: 13–16; IV: 6	III
semiglauca			0.3	(0.45)	0.6	3 –5	me–la	RR	mesocolpium edges ± indented		II
subsericea			0.5	(0.63)	0.75	3.5	la–is	R			III
sufusana			0.8	(1.25)	1.7	2 –4	is–lo	RR			II
truncata			0.8	(1.15)	1.5	2 –3.5	la–is	R			I
unguiculata			0.3	(0.40)	0.5	3 –4.5	la	R–r			III
venusta				0		3.5	me–la	RR–R			II
villosa			0.3	(0.40)	0.5	2.5 3.5	la–is–lo	r			IV

* = apo-/mesocolpium connections; ** = colporate

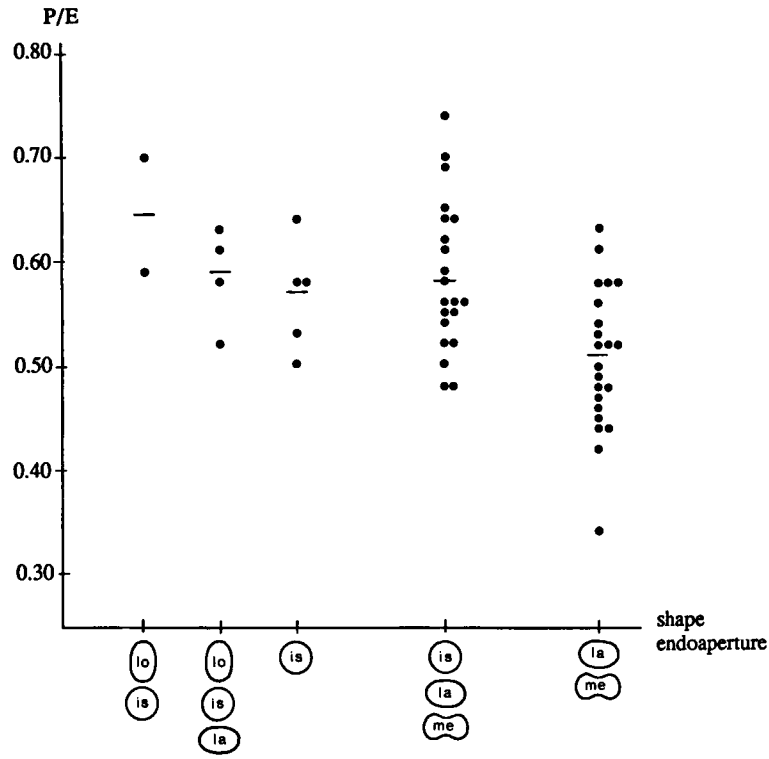


Fig. 1. Relation between endoaperture shape and P/E. Each dot represents one sample. **lo** = lolongate, **is** = isodiametric, **la** = lalongate, **me** = lalongate and meridionally constricted; the meridionally constricted shape occurs only in part of the samples shown in the two columns at the right hand side (see table 1).

The shape of the endoapertures proved to be related to harmomegathy. In LM the shape of an endoaperture is a projection of its three-dimensionally running edge. This projection is influenced by the shape of the grain, especially if defined by its P/E value. Lolongate pori occur in grains with the highest P/E values, whereas lalongate pori are mainly observed in those with the lower values (fig. 1). In strongly oblate and in peroblate grains they may even have a meridionally constricted shape, due to the projection of the invaginated aperture membrane above and below the pore.

Role of the apocolpia

The polar regions of syncolporate grains with wide, folding ectoapertures are the most susceptible places for rupture, as they are the major sites of invagination. This may account for the frequent presence of an apocolpium in the polar areas of a *Guioa* pollen grain. An apocolpium probably possesses stress-absorbing qualities (Muller, 1973), as it strengthens the polar area and transfers stress from a limited central area

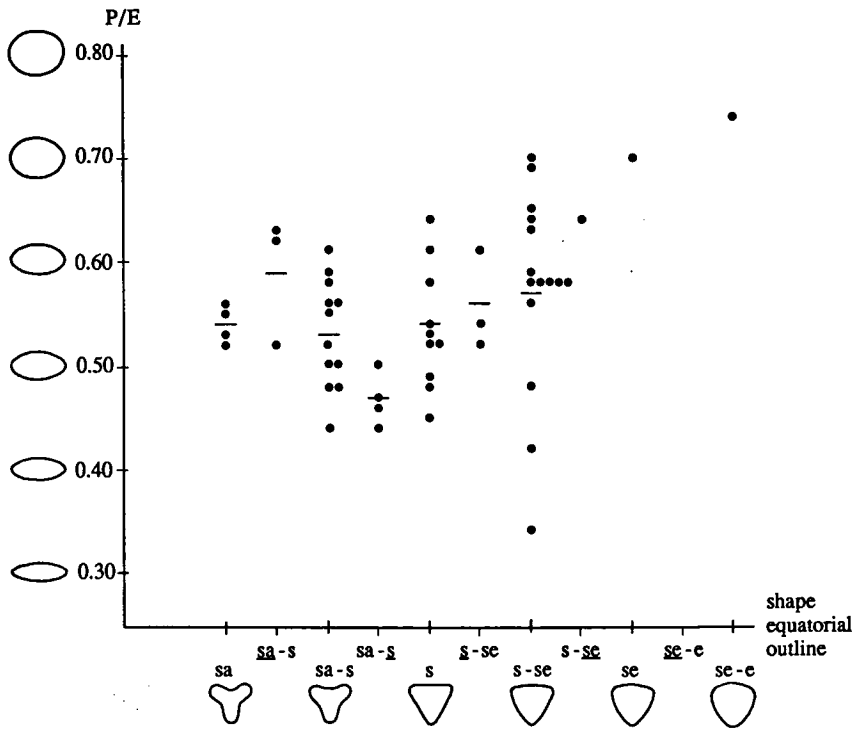


Fig. 2. Relation between shape of equatorial outline and P/E. Each dot represents one sample. sa = sides slightly concave, s = sides straight, se = sides slightly convex, e = sides convex. Underlined symbols indicate predominance of the relevant shape.

to the aperture membranes which surround the apocolpium. If a grain has relatively rigid apertural zones, preventing excessive invagination, the apocolpia may be small or absent.

Parasyncolporate *Guioa* pollen often shows tectal connections between an apocolpium and one, two, or all three of the adjacent mesocolpia, which not rarely yields colporate grains (plate V: 1; VI: 1–6). Such apo-/mesocolpium connections are expected to impede harmomegathic functioning, as they hamper the invagination of the polar parts of the ectoapertures. Pollen of several parasyncolporate *Alectryon* species (tribe Nephelieae) also shows much variation in occurrence of tectal bridges between apocolpia and mesocolpia (Van der Ham, 1988). It was noticed that *Alectryon* grains with such bridges can easily apply an alternative harmomegathic mechanism by invaginating the equatorial parts of their ectoapertures, thus folding their endoapertures inwards and producing prolate shapes. This was never observed in *Guioa* pollen. Apparently the ectoapertural zones with their thickened underlying nexine are too rigid to be folded inwards. Moreover, parasyncolporate *Alectryon* grains have much

higher P/E values (average 0.76, versus 0.55 in *Guioa*), which facilitates folding of the equatorial parts of their apertures. As *Guioa* grains can also follow the non-apertural way of volume reduction, apo-/mesocolpium connections are not necessarily lethal. This may explain their common occurrence in *Guioa*.

P/E value and equatorial outline

The P/E value and the shape of the equatorial outline, which often vary considerably within a sample, are closely interrelated in harmomegathic functioning. Much depends on the harmomegathic state of a grain. Figure 2 shows the relation between the shape of the equatorial outline and the P/E value of each studied sample. Although the values represent average shapes of treated exines, which may be largely specifically determined, they very well reflect the main harmomegathic mechanisms in *Guioa* pollen grains. Shortening of the polar axis, partly due to invagination of the non-equatorial parts of the ectoapertures, and straightening of the equatorial outline is demonstrated in the right part of the diagram. Non-apertural folding is demonstrated in the left part; the concomitant increase of the P/E value is probably due to mechanical constraints: strongly peroblate mesocolpia can not be concave at the same time. Species with very wide ectoapertures will probably rely predominantly on apertural folding and those with very narrow ectoapertures predominantly on non-apertural folding. Species with ectoapertures of intermediate width may use both mechanisms.

Summarising harmomegathy in *Guioa* pollen as inferred from acetolysed grains, shortening of the polar axis, partly due to invagination of the non-equatorial parts of the ectoapertures, and folding of the mesocolpia make the major contributions to harmomegathic volume reduction. The share of each mechanism probably depends on the width of the ectoapertures and the occurrence of apo-/mesocolpium connections. Equatorial invagination of apertures does not occur, not even in grains with apo-/mesocolpium connections, which is probably due to the rigidity of the apertural zones and the (per)oblate shape of the grains.

P/E value, equatorial outline, and endoaperture shape vary considerably in harmomegathy and are interrelated to a large extent.

APERTURAL SYSTEM

As in most other genera of the tribe Cupanieae, pollen in *Guioa* is syncolporate or parasyncolporate. It obviously belongs to pollen type B as distinguished by Muller & Leenhouts (1976). However, it is not possible to match *Guioa* pollen with one of the subtypes B1 and B2. Subtype B1 has a circular equatorial outline, whereas subtype B2 has reduced endoapertures. Actually, *Guioa* pollen resembles very much a third subtype B3 as distinguished by Van der Ham (1977) for all species of *Mischocarpus*, having a triangular outline and distinct endoapertures. Also the variation in its apocolpial region, encompassing syncolporate, parasyncolporate, and the various degrees of apo-/mesocolpium coherence, strongly resembles that in *Mischocarpus*. As in most *Guioa* species, the harmomegathic action of the ectoapertures in *Mischocarpus* pollen is absent only in the equatorial zone. Contrary to *Guioa* pollen,

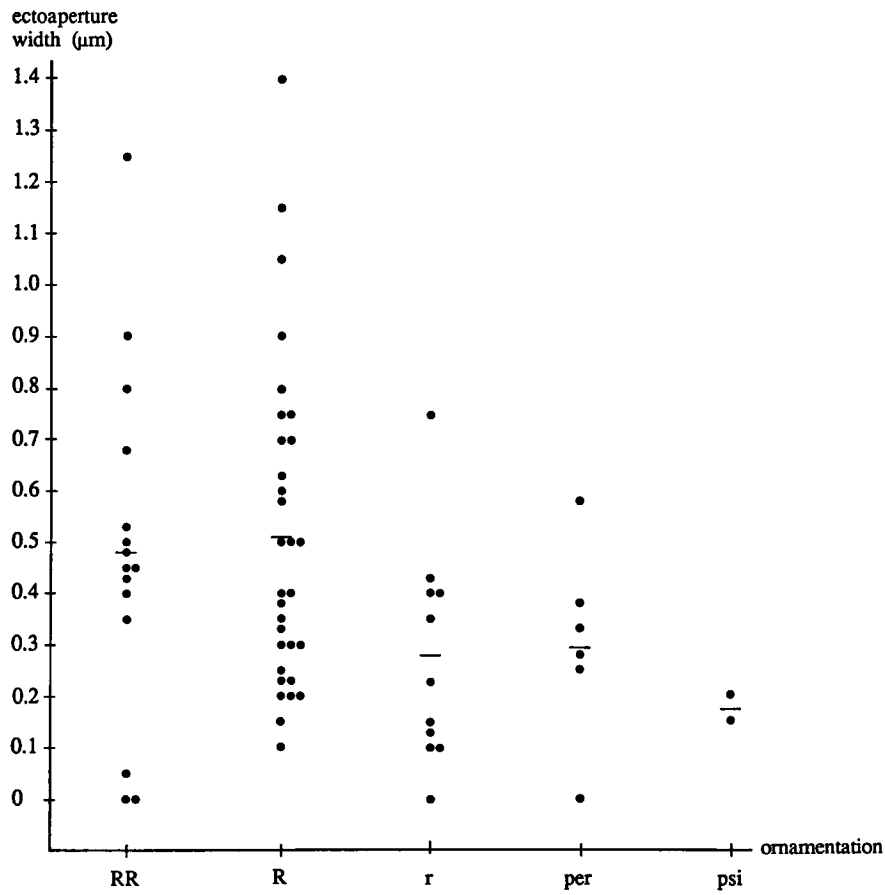


Fig. 3. Relation between ornamentation and ectoaperture width. Each dot represents one sample. **RR** = prominently rugulate, muri well-defined, high, up to 3 µm long, **R** = muri less prominent but still well-discernible, up to 2 µm long, **r** = sculpture elements hardly discernible, **per** = tectum psilate-perforate, **psi** = tectum psilate-imperforate; see also caption of table 1.

Mischocarpus pollen shows little variation in the shape of its equatorial outline: concave sides were observed only rarely. This may indicate that non-apertural folding is less important in *Mischocarpus*.

Ectoapertures

It was pointed out that within a sample ectoaperture width is largely related to the harmomegathic state of a grain. However, considerable interspecific differences also exist. Not all narrow ectoapertures represent invaginated wide ones; really narrow, relatively immobile ectoapertures also occur (plate V).

It appeared that ectoaperture width shows a relation to ornamentation in *Guioa* pollen (fig. 3). Wide ectoapertures (> 0.5 µm) mainly occur in the most prominently

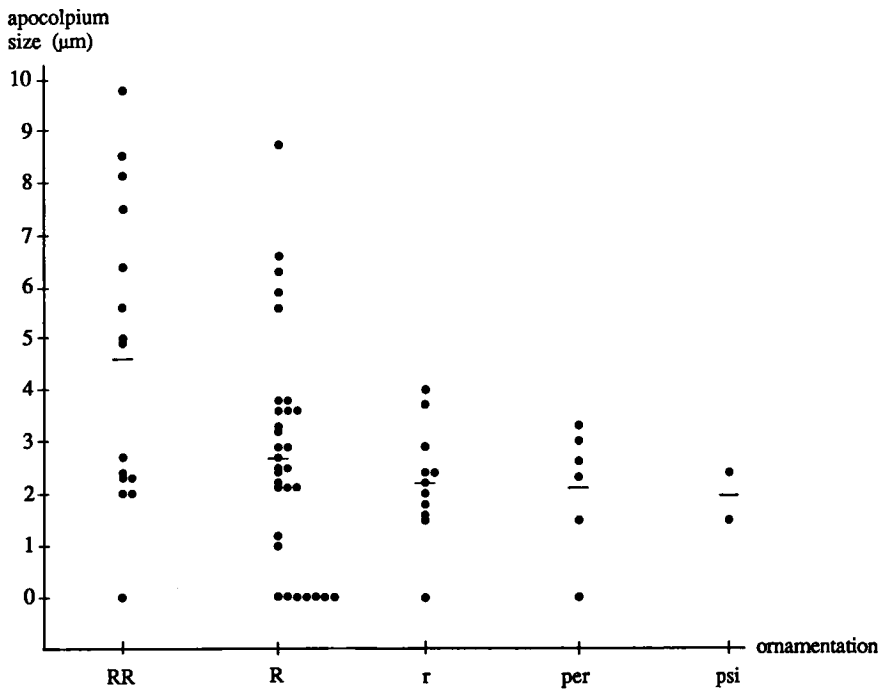


Fig. 4. Relation between ornamentation and apocolpium size. Each dot represents one sample. **RR** = prominently rugulate, muri well-defined, high, up to 3 µm long, **R** = muri less prominent but still well-discernible, up to 2 µm long, **r** = sculpture elements hardly discernible, **per** = tectum psilate-perforate, **psi** = tectum psilate-imperforate; see also caption of table 1.

sculptured categories RR and R. The other categories mostly have narrow ectoapertures. The very low values in category RR at least partly represent invaginated ectoapertures. Really narrow ectoapertures are remarkably common in the northwestern part of the area of *Guioa*.

Apocolpia

The presence of an apocolpium varies in *Guioa*. 13% of the species have predominantly (> 80%) or exclusively syncolporate grains, 50% have predominantly (> 80%) or exclusively parasyncolporate grains, whereas in 37% of the species considerable amounts of both syncolporate and parasyncolporate grains occur. Thus, many species (actually individuals, as most species are represented by one sample only) have both types. Sometimes even an individual grain shows both types, having a syncolporate pole and a distinctly parasyncolporate pole.

The size of the apocolpium is also variable. It relates to some extent to the ornamentation of the grain: large apocolpia (diameter > 4 µm) only occur in species with prominent sculptural elements (fig. 4). Apocolpium size correlates with the width of the ectoapertures (R = 0.52): large apocolpia mainly occur in species with wide

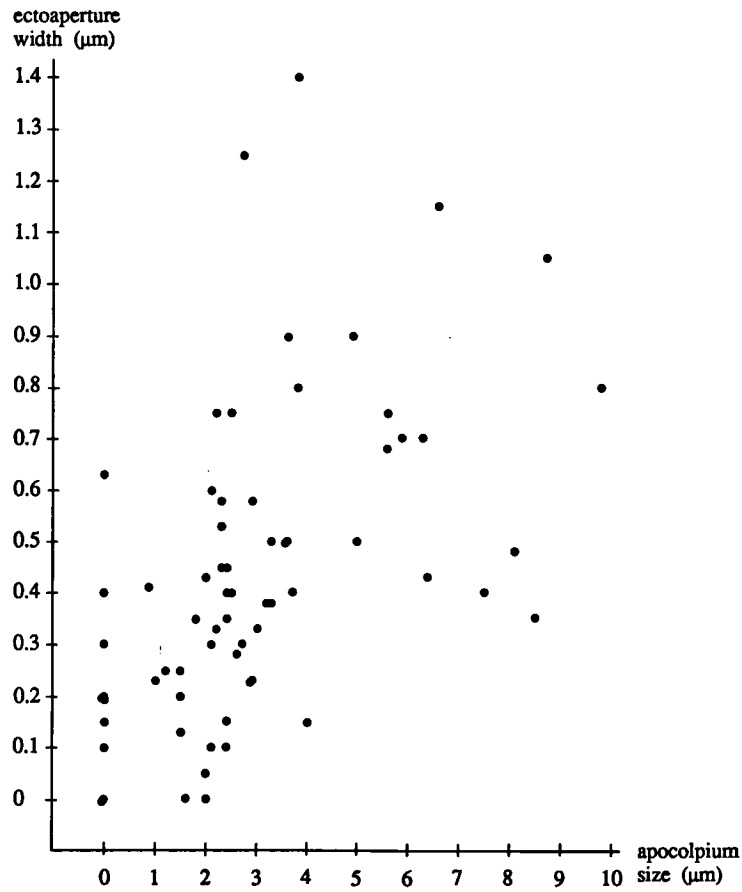


Fig. 5. Correlation between apocolpium size and ectoaperture width (R = 0.52). Each dot represents one sample.

ectoapertures (fig. 5). Moreover, there is a slight tendency for *Guioa* pollen to have larger apocolpia in species from the southeastern part of the area of the genus. A similar geographic trend with respect to apocolpium size was observed in *Mischocarpus* (Van der Ham, 1977).

Apo-/mesocolpium coherence

Approximately 60% of the samples containing parasyncolporate pollen show grains with various degrees of apo-/mesocolpium coherence in numbers up to 50%. Some samples (e.g. *G. punctata*) contain parasyncolporate and colporate grains, as well as all intermediates. Individual grains are mostly slightly anisopolar regarding the extent of cohesion. Large apocolpia (diameter > 4 µm) are only rarely affected (fig. 6) and prominently sculptured grains (categories RR and R) less often than

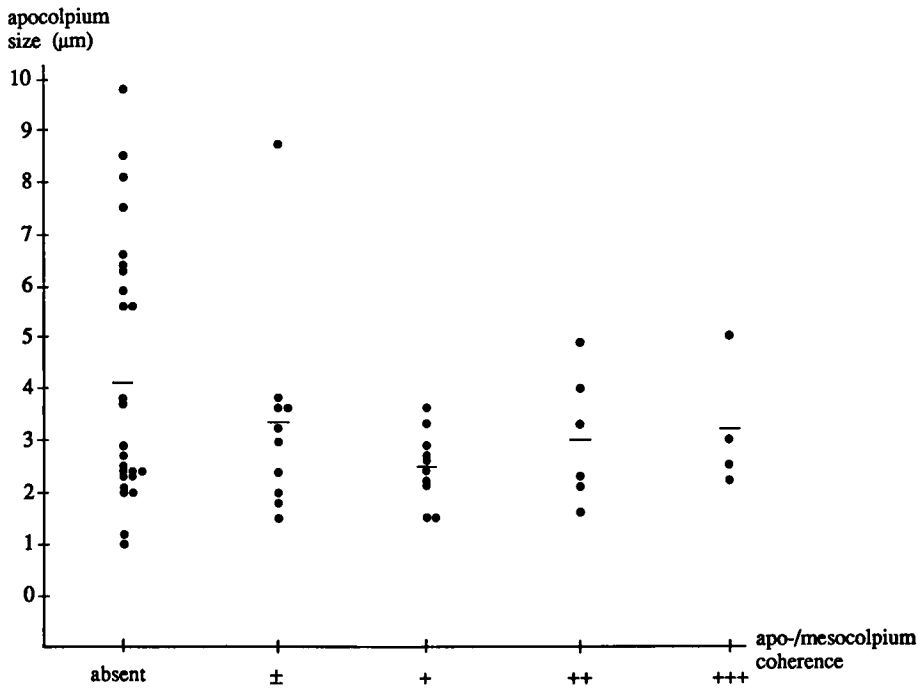


Fig. 6. Relation between apo-/mesocolpium coherence and apocolpium size. Each dot represents one sample. *absent* = apocolpium always isolated, ± = apo-/mesocolpium connections observed in 1 or 2 grains, + = connections observed in a few grains, ++ = connections in many grains, +++ = connections in at least 50% of the grains; see also caption of table 1.

shallowly sculptured grains (fig. 7). A slight relation exists with regard to ectoaperture width: pollen with wide ectoapertures (> 0.5 µm) less frequently show apo-/mesocolpium connections than pollen with narrow ectoapertures. Grains with apo-/mesocolpium connections are relatively well-represented in the northwestern part of the area of *Guioa*.

ORNAMENTATION

The various types of ornamentation which occur in *Guioa* can be arranged in a morphological series showing at one end the prominently rugulate type and at the other end the psilate-imperforate type. The shallowly rugulate and the psilate-perforate grains are in between. Although these types make up a continuous series, it has been tried to put them in categories (see caption table 1). Sometimes a large part of the total series is present in a single sample, which demonstrates the intra-individual variability of ornamentation. The widespread species *G. diplopetala* and *G. pleuropteris* show a wide infraspecific variability (see caption table 1).

ornamentation					
psi	0 %	100 %			
	–	1	1	–	–
per	20 %	80 %			
	1	1	1	1	1
r	25 %	75 %			
	3	4	3	2	–
R	55 %	45 %			
	12	2	5	1	2
RR	71 %	29 %			
	10	1	–	2	1
	absent	±	+	++	+++

apo-/mesocolpium coherence

Fig. 7. Relation between apo-/mesocolpium coherence and ornamentation. Within each ornamentation category the number of samples belonging to each coherence category is given. *absent* = apocolpium always isolated, ± = apo-/mesocolpium connections observed in one or two grains, + = connections observed in a few grains, ++ = connections in many grains, +++ = connections in at least 50% of the grains; see also the caption of table 1.

region	ornamentation				
	RR	R	r	per	psi
SE Asia		4			
Sumatra			1	1	
Java					1
Borneo		3	2		1
Philippines		3	1	5	
Celebes		1	1		
Timor		1			
Moluccas		1	1		
New Guinea	5	7	3		
NE Australia	2	3			
Solomon Islands	1	2			
New Hebrides			1		
New Caledonia	2	5	3		
Fiji	3				
Tonga	1				

Fig. 8. Geographical distribution of the ornamentation categories. The regions are listed from northwest (continental SE Asia) to southeast (Tonga). **RR** = prominently rugulate, muri well-defined, high, up to 3 μm long, **R** = muri less prominent but still well-discernible, up to 2 μm long, **r** = sculpture elements hardly discernible, **per** = tectum psilate-perforate, **psi** = tectum psilate-imperforate; see also caption of table 1.

Several more or less obvious relations were noticed with regard to ornamentation. As mentioned in the preceding chapter, ectoaperture width is related to ornamentation: wide ectoapertures occur mainly in the categories RR and R (fig. 1).

Also apocolpium size proved to some extent related to ornamentation: large apocolpia are only found in the categories RR and R. As there exists a slight tendency for *Guioa* pollen to have larger apocolpia in southeastern species than in northwestern species, and apocolpium size also relates to ornamentation, one may expect a relation between geography and ornamentation. Actually, listing the regions from

northwest to southeast (fig. 8) does show that the more or less prominently rugulate categories RR and R dominate in the southeastern part of the area of *Guioa*. RR is absent from the northwestern part. The categories per and psi only occur in the northwestern part. Remarkable is the presence of the psilate-perforate element in the Philippines. Category r is more or less evenly distributed. The boundary between the northwestern and the southeastern part might be drawn to the west of New Guinea and Australia.

EVOLUTIONARY TRENDS

In the previous chapters several morphological series were presented, either implicitly or explicitly:

1. wide ectoapertures – narrow ectoapertures
2. grain parasyncolporate – grain colporate
3. grain parasyncolporate – grain syncolporate
4. ornamentation rugulate – ornamentation psilate-imperforate.

In the following section it will be tried to recognise evolutionary trends (according to Punt, 1975) by attributing a direction to each of them.

1. *Wide ectoapertures – narrow ectoapertures*

A colporate, relatively unspecialised pollen type with long ectoapertures which lack marginal thickenings is considered to represent the basic pollen type in the Sapindaceae, whereas the (para)syncolporate type found so commonly in the tribe Cupanieae is probably derived (Muller & Leenhouts, 1976). Colporate grains with long ectoapertures almost invariably perform harmomegathy by invaginating especially the equatorial parts of their ectoapertures (thus including the endoapertures), meanwhile adopting a more prolate shape. This harmomegathic system is considered here the basic type in Sapindaceae. As noticed before it does not occur in *Guioa*: invagination of the apertures never includes the endoapertures. However, the non-equatorial parts of the ectoapertures can easily be invaginated in grains with wide ectoapertures. In grains with narrow ectoapertures non-equatorial folding is also hampered, which forces them to fold non-apertural region.

It is suggested here that in *Guioa* the former system, in which folding of the non-equatorial parts of the apertures takes place, is nearer to the basic harmomegathic system than the latter, in which predominantly folding of the mesocolpia occurs. *Alectryon* pollen may be considered intermediate between the basic type and the aperture folding type in *Guioa*, as, contrary to *Guioa* pollen, it can easily apply the basic type of apertural folding if a high degree of apo-/mesocolpium coherence impedes non-equatorial folding of the apertures. Apparently apertures in *Alectryon* pollen are less rigid than those in *Guioa* pollen.

Because in pollen of *Guioa* narrow ectoapertures represent an important component of the more advanced mesocolpium folding system, they are regarded as more derived than wide ectoapertures, which act in a more basic harmomegathic system (see also Muller & Leenhouts, 1976).

2. *Grain parasyncolporate – grain colporate*

According to Muller & Leenhouts (1976) the (para)syncolporate pollen type of the tribe Cupanieae is probably derived from a colporate type. One could wonder however, whether colporate *Guioa* pollen represents this primitive state. Van der Ham (1977) supposed a similar colporate type occurring rarely in *Mischocarpus* to be more primitive than the syncolporate type in that genus. However, colporate and almost colporate grains are more common in *Guioa,* which provided the opportunity to collect some circumstantial evidence regarding the direction of the morphological series parasyncolporate – colporate.

In general, colporate pollen grains with long ectoapertures perform harmomegathy by invaginating especially the equatorial parts of their ectoapertures (thus including the endoapertures). In Sapindaceae this mechanism is often accompanied by a striate ornamentation and distinctly bordered endoapertures. Colporate *Guioa* grains have none of these characteristics. Probably they are not capable of invaginating their endoapertures because of the rigidity of the apertural zones. The lateral sides of their endoapertures are thin and ornamentation is never striate. Their fundamental design is for the (para)syncolporate way of harmomegathic functioning, which provides a reason to regard the colporate condition in *Guioa* pollen not as primitive, but as relatively derived. The colporate condition in *Guioa* pollen is considered the result of complete coalescence of apocolpia and their adjacent mesocolpia. Some species also show local coalescence of adjacent mesocolpia (table 1; plate III: 3). Coalescences between apocolpia and mesocolpia, and between mesocolpia mutually may have served as handles for the selection processes which in several sapindaceous tribes have led to oblate grains with reduced (short) ectoapertures.

Pollen with some degree of apo-/mesocolpium coherence occurs in many genera throughout parasyncolporate Cupanieae. It is very well possible that it represents the same derived condition as in *Guioa* pollen. Instead of representing a primitive condition, as stated by Muller & Leenhouts (1976), colporate types may have originated in groups with a high degree of apo-/mesocolpium coherence. Moreover, in the most 'primitive'* genera of Cupanieae (*Cupania, Cupaniopsis, Rhysotoechia*) colporate grains have never been found up to now. The colporate genus *Diplokeleba,* which was recorded as still slightly more 'primitive' (Muller & Leenhouts, 1976), may prove to be misplaced in the Sapindaceae (private comm. Dr. P.W. Leenhouts). In conclusion, it can be doubted whether the basic colporate pollen type of the Sapindaceae really exists in the Cupanieae.

3. *Grain parasyncolporate – grain syncolporate*

The presence and size of an apocolpium are variable characters in *Guioa* pollen samples. However, as apocolpium size relates to some extent to ornamentation, to the occurrence of apo-/mesocolpium connections, and to geographic distribution, it does not seem inappropriate to establish a morphological series encompassing parasyncolporate (including the various apocolpium sizes) and syncolporate.

* 'primitive' = with relatively many primitive characters.

Large apocolpia especially occur in species having wide ectoapertures and/or lacking apo-/mesocolpium connections. As the latter characters are supposed to represent the more primitive conditions in *Guioa,* large apocolpia may be regarded as being more primitive than small apocolpia. In view of this, syncolporate pollen should be considered most derived. This is in contrast to the tendency recognised in *Mischocarpus.* On the basis of the predominance of syncolporate pollen in macromorphologically 'primitive' species, it was concluded that in this genus syncolporate is a more primitive state than parasyncolporate (Van der Ham, 1977).

4. *Ornamentation rugulate – ornamentation psilate-imperforate*

The prominently rugulate patterns of the categories RR and R prevail in grains which have wide ectoapertures and lack apo-/mesocolpium connections. As these latter characters are supposed to represent primitive conditions in *Guioa* pollen, prominent ornamentation is considered as a probably primitive state too. Consequently the less prominently sculptured types r, per, and psi may be regarded as derived.

This assertion implies the derivation of a simple structure from a more complex one (reduction), which is opposed to the often used argument of complexity (relatively complex characters are derived) and is therefore in need of further explanation.

Ornamentation appeared to be a variable character in many sapindaceous genera. Single species often show a wide range of ornamental types. For instance, Muller (1979) demonstrated six different types in *Allophylus cobbe* (tribe Thouinieae). In the genus *Dimocarpus* (tribe Nephelieae) several intergraded types occur even in a single variety: *Dimocarpus longan* subsp. *malesianus* var. *malesianus* (Van der Ham, in prep.). Beside striate and rugulate types, usually also more simple, psilate-perforate or finely reticulate patterns are involved. It has been put forward many times that perforate and finely reticulate exines represent relatively primitive conditions because of their simplicity and their predominance in the first angiosperm pollen types (Muller, 1970, 1971, 1973a, 1979, 1985). Thus, Muller considered such patterns primitive in several sapindaceous genera. However, Van der Ham (1988a) regarded perforate ornamentation in the tribe Nephelieae as a frequently occurring neotenous character (neoteny = retention of formerly juvenile characters by adult descendents), thus attributing a relatively primitive nature to the more prominently sculptured type and a derived status to the more simple type.

The variation in ornamentation, including prominently sculptured types, psilate-perforate types, and all intermediates, looks very much the same in pollen of Nephelieae and *Guioa.* For that reason neoteny is considered a good explanation for the relative simplicity of the derived ornamental types in *Guioa* pollen as well.

Concluding, four evolutionary trends have been postulated:

1. wide ectoapertures → narrow ectoapertures
2. grain parasyncolporate → grain colporate
3. grain parasyncolporate → grain syncolporate
4. ornamentation rugulate → ornamentation psilate-imperforate

Trends 1 and 2 were deduced independently from harmomegathic evidence. Trends 3 and 4 were inferred from 1 and 2.

A general picture of the pollen morphological evolution can be presented now. The most primitive pollen type is supposed to possess large, isolated apocolpia, wide ectoapertures, and a prominently rugulate ornamentation, the grains performing mainly apertural folding. The most derived pollen should be either colporate or syncolporate, and have narrow ectoapertures and a psilate-imperforate tectum, the grains showing mainly non-apertural folding.

The primitive states of the studied characters occur especially in the southeastern part of the area of *Guioa*, and the derived states predominate in the northwestern part. Therefore, the most 'primitive' *Guioa* species might be found in New Guinea, Australia, and/or in regions further eastwards.

A POLLEN MORPHOLOGICAL SUBDIVISION OF GUIOA

The range of variation in *Guioa* pollen is not wide. Moreover, the variation of all studied characters proved to be continuous. This hampers the delimitation of clear-cut groups, even if basing these on a single feature. Nevertheless, it has been attempted to discern pollen morphological groups in *Guioa*. On the basis of ornamentation and average apocolpium size four groups were distinguished, which will be described in the following section. The data between brackets after 'apo-/mesocolpium connections' and 'geographic distribution' in the descriptions of these groups refer to which degree the connections occur (see caption table 1) and to the number of species per region respectively.

GROUP I (plate I: 1–8; II)

ornamentation: mostly prominently rugulate (categories RR and R; rarely r: *G. glauca* var. *glauca*);
apocolpium size: 4.9 (6.8) 9.8 µm;
ectoaperture width: 0.35 (0.68) 1.15 µm;
apo-/mesocolpium connections: *G. gracilis* (±), *G. pseudoamabilis* (++), *G. punctata* (+++);
geographic distribution: Philippines (1), Timor (1), New Guinea (2), Australia (1), New Caledonia (5), Fiji (2), Tonga (1);
species: *G. amabilis, G. asquamosa, G. coriacea, G. crenata, G. fusca, G. glauca* var. *glauca. G. gracilis, G. lentiscifolia, G. microsepala, G. pseudoamabilis, G. punctata, G. rhoifolia, G. truncata;*
comments: *G. fusca* (New Caledonia) and *G. rhoifolia* (Fiji) have the longest and most prominent muri in *Guioa* (plate II: 1, 2, 5, 6). *G. glauca* var. *glauca* (New Caledonia) and *G. truncata* (Philippines) have the least prominently sculptured pollen in group I. A high degree of apo-/mesocolpium coherence (plate VI) is a remarkable feature of *G. punctata* (Fiji).

GROUP II (plate I: 9–12; III)

ornamentation: prominently rugulate (categories RR and R);
apocolpium size: 0 (2.4) 3.8 µm;
ectoaperture width: 0 (0.50) 1.40 µm;
apo-/mesocolpium connections: *G. diplopetala* (±), *G. elliptica* (±), *G. normanbiensis* (±), *G. aryterifolia* (+), *G. megacarpa* (+), *G. patentinervis* (+), *G. rigidiuscula* (+), *G. chrysea* (++);
geographic distribution: continental SE Asia (1), Borneo (1), Celebes (1), Moluccas (1), New Guinea (6), Australia (3), Solomon Islands (3), Fiji (1);
species: *G. aryterifolia, G. chrysea, G. diplopetala, G. elliptica, G. lasioneura, G. megacarpa, G. montana, G. multijuga, G. normanbiensis, G. novobritannica, G. patentinervis, G. rigidiuscula, G. semiglauca, G. sufusana, G. venusta*;
comments: the New Guinean species *G. multijuga, G. normanbiensis,* and *G. venusta* have the longest and most prominent muri in this group. *G. patentinervis* (Moluccas) has the least prominent ornamentation. The New Guinean *G. aryterifolia, G. multijuga* and *G. rigidiuscula,* and the Australian *G. semiglauca* share the rare occurrence of grains (one or a few observed per sample) with an abnormally large (9 to 15 µm) apocolpium at one pole.

GROUP III (plate I: 13–19; IV)

ornamentation: less than prominently rugulate or indistinctly rugulate (categories R and r);
apocolpium size: 0 (1.8) 3.8 µm;
ectoaperture width: 0.20 (0.48) 0.80 µm;
apo-/mesocolpium connections: *G. acutifolia* (±), *G. crenulata* (±), *G. membranifolia* (±), *G. pleuropteris* (±), *G. plurinervis* (±), *G. pectinata* (+), *G. diplopetala* (++), *G. pleuropteris* (+++), *G. scalariformis* (+++);
geographic distribution: continental SE Asia (3), Borneo (2), Philippines (1), Moluccas (1), New Guinea (5), Australia (1), New Caledonia (3), New Hebrides (1);
species: *G. acutifolia, G. contracta, G. crenulata, G. diplopetala, G. membranifolia, G. novoebudaensis, G. ovalis, G. pectinata, G. pleuropteris, G. plurinervis, G. scalariformis, G. subsericea, G. unguiculata*;
comments: *G. novoebudaensis* (New Hebrides) has the longest and most prominent muri in this group. *G. pectinata* (New Caledonia) and *G. scalariformis* (New Guinea) have the most indistinctly sculptured pollen (plate IV: 5, 6).

GROUP IV (plate I: 20–24; V)

ornamentation: indistinctly rugulate, psilate-perforate or psilate-imperforate (categories r, per, and psi);
apocolpium size: 0 (2.1) 4.0 µm;
ectoaperture width: 0 (0.25) 0.58 µm;

apo-/mesocolpium connections: *G. bijuga* (±), *G. acuminata* (+), *G. diplopetala* (+), *G. koelreuteria* (+), *G. pterorhachis* (+), *G. pubescens* (+), *G. diplopetala* (++), *G. myriadenia* (++), *G. pteropoda* (++), *G. bicolor* (+++);
geographic distribution: Sumatra (2), Java (1), Borneo (3), Philippines (6), Celebes (1), New Guinea (2), New Caledonia (2);
species: *G. acuminata, G. bicolor, G. bijuga, G. comesperma, G. diplopetala, G. discolor, G. glauca* var. *vulgaris, G. hirsuta, G. koelreuteria, G. myriadenia, G. pleuropteris, G. pteropoda, G. pterorhachis, G. pubescens, G. reticulata, G. villosa*;
comments: the six Philippine species in this group (*G. acuminata, G. bicolor, G. discolor, G. koelreuteria, G. myriadenia,* and *G. reticulata*) and the Bornean species *G. bijuga* are remarkably similar. The New Caledonian *G. glauca* var. *vulgaris* and *G. villosa* are somewhat aberrant in this group because of the indistinct, densely rugulate ornamentation and the relatively large, isolated apocolpia respectively. *G. pubescens* (Borneo) and the Javanese sample of *G. diplopetala* resemble each other in having a psilate-imperforate (or almost imperforate) tectum (compare plate V: 2 and 6). *G. pterorhachis* (Borneo) has the most prominent ornamentation in this group.

It must be stressed again that the groups are not clearly outlined and are not intended to be taxonomic groups. Not only are the group differences small, but also the borderlines between the groups are crossed by several variable species, for instance *G. diplopetala* which occurs in three groups.

The sequence of the four groups (from I to IV) roughly reflects evolution in *Guioa* as based on the evolutionary trends discerned in the previous chapter. Group I, which is considered the most primitive, accommodates relatively many species with primitive pollen characters and a southeastern distribution, whereas group IV, which is supposed to be the most derived, has many species with advanced pollen and a northwestern distribution.

Pollen of *G. pubescens* (Borneo) of group IV is regarded as most derived in *Guioa*. The most 'primitive' species is somewhat more difficult to indicate, as group I is rather homogeneous. Pollen of several New Caledonian species of this group, including *G. crenata, G. fusca, G. gracilis,* and *G. microsepala,* may represent the most primitive pollen type.

POLLEN MORPHOLOGICAL RELATIONS OF GUIOA

The ranges of variation of the studied characters in *Guioa* pollen occur either entirely or partially in many other genera of the Cupanieae. Muller & Leenhouts (1976) made a general survey of the sapindaceous pollen types, covering 78% of all genera and 74% of the 46 Cupanieae genera. This survey could be extended by the present authors, reaching a coverage of 94% of the Cupanieae, which provided the opportunity to compare *Guioa* pollen to that of nearly all other genera in the tribe.

Thus, pollen of group I of *Guioa* appeared similar to that of *Matayba* (tropical America), *Molinaea* and *Tina* (both Madagascar), *Arytera:* the *azarytera* group

(Pacific), the *chartacea* group (New Caledonia), and the *mischarytera* group (New Guinea, Australia) (see Van der Ham, 1977a), *Diploglottis* (New Guinea, Australia), *Euphorianthus* (E Malesia), *Gongrodiscus* (New Caledonia), and *Sarcotoechia* (New Guinea, Australia), all being (per)oblate, and with wide ectoapertures, large isolated apocolpia, and a more or less densely rugulate ornamentation. Except for *Diploglottis* and *Euphorianthus* these genera were reported to be macromorphologically more 'primitive' than *Guioa* (Muller & Leenhouts, 1976). *Diploglottis*, the most highly specialised genus of the Cupanieae, was tentatively derived from *Guioa*, which may be supported by pollen morphology. The allegedly related genus *Sisyrolepis* (= *Delpya*) however, is pollen morphologically quite different from all *Guioa* species in having a loosely striate ornamentation.

According to Muller & Leenhouts (1976) *Guioa* pollen can be directly derived from that of *Cupaniopsis* (E Malesia, Australia, Pacific). However, *Cupaniopsis* pollen proved to be different so far. Some species (*C. bilocularis, C. platycarpa*) may be accommodated in group II or III of *Guioa*. This also holds for most species of *Mischocarpus* (continental SE Asia, Malesia, Australia), *Pentascyphus* (tropical America), and several species of *Cupania* (tropical America).

Pollen with narrow ectoapertures, small apocolpia (often connected with the mesocolpia), and/or a more or less psilate, either perforate or imperforate ornamentation, like that of group IV in *Guioa*, was found in *Diploglottis, Euphorianthus, Jagera discolor* (New Guinea), and *Stortocalyx* (New Caledonia). Except for the latter these genera were recorded as macromorphologically more derived than *Guioa*.

On the basis of this comparison it is concluded that *Guioa* pollen resembles pollen of both less and more advanced genera within the tribe. The pollen type of group I in *Guioa* appears to occur in relatively 'primitive' genera, whereas the type of group IV shows up mainly in more derived genera. This may support the conclusion that *Guioa* group I is more 'primitive' than group IV.

In order to establish firmer evidence for the pollen morphological relations within the Cupanieae several large, macromorphologically 'primitive' genera (*Cupania, Cupaniopsis*, and *Matayba*) should be studied in more detail and data of wall sections, showing the architecture of the whole exine, must be included in the survey of the tribe.

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EXPLANATION OF PLATES

Plate I. Pollen morphological groups I–IV, LM photographs. First column (except 5): polar view, upper or lower focus; second column (except 6): polar view, optical section; third column: equatorial view, endoaperture in upper or lower focus; fourth column: equatorial view, endoaperture in optical section. All × 1000; 3, 12, 23, 26, and 29 with 'interference contrast'.

— 1–4: *Guioa amabilis*, group I. – 1 & 2: same grain; 3 & 4: same grain.
— 5, 6: *G. lentiscifolia*, group I. – 5: tetrad in upper focus; 6: the same tetrad in middle focus.
— 7, 8: *G. crenata*, group I. – 7 & 8: same grain.
— 9–12: *G. montana*, group II. – 9 & 10: same grain.
—13–16: *G. scalariformis*, group III. – 13 & 14: same grain; 15 & 16: same grain.
—17–19: *G. crenulata*, group III. – 17 & 18: same grain.
— 20: *G. myriadenia*, group IV.
—21–24: *G. pteropoda*, group IV. – 21 & 22 same grain; 23 & 24: same grain.

Plate II. Pollen morphological group I, SEM photographs.

— 1, 2: *Guioa fusca.* – 1: polar view, × 2500; 2: oblique equatorial view, × 2500.
— 3, 4: *G. lentiscifolia.* – 3: polar view, × 2500; 4: polar/equatorial view, × 2500.
— 5, 6: *G. rhoifolia.* – 5: polar view, × 2500 ; 6: detail of 5, × 7500.

Plate III. Pollen morphological group II, SEM photographs.

— 1, 2, 4: *Guioa diplopetala* (*Haviland 2137*). – 1: polar view, × 2500; 2: oblique equatorial view, × 2500; 4: detail of 2, × 7500.
— 3: *G. novobritannica,* oblique polar view, × 2500.
— 5: *G. patentinervis,* polar view, × 2500.
— 6: *G. rigidiuscula,* polar/equatorial view, × 2500.

Plate IV. Pollen morphological group III, SEM photographs.

— 1, 2: *Guioa contracta.* – 1: polar view, × 2500; 2: detail of 1, × 7500.
— 3, 4: *G. ovalis.* – 3: polar view, × 2500; 4: equatorial view, × 2500.
— 5: *G. pectinata,* polar view, × 2500.
— 6: *G. scalariformis,* polar view, × 2500.

Plate V. Pollen morphological group IV, SEM photographs.

— 1: *Guioa bicolor,* two grains in polar view, × 1750.
— 2: *G. diplopetala* (*Wirawan 329*), two grains in polar view, × 1750.
— 3, 4: *G. myriadenia.* – 3: polar view, × 2500; 4: oblique equatorial view, × 2500.
— 5: *G. koelreuteria,* two grains in polar view, × 1750.
— 6: *G. pubescens,* polar view, × 2500.

Plate VI. Apo-/mesocolpium coherence in *Guioa punctata,* SEM photographs.

— 1: polar view, apocolpium free, × 2500.
— 2: detail of 1, × 7500.
— 3: polar view, apocolpium slightly connected with two mesocolpia, × 2500.
— 4: detail of 3, × 7500.
— 5: polar/equatorial view, apocolpia connected with two mesocolpia, × 2500.
— 6: polar view, apocolpia connected with three mesocolpia, × 2500.

Plate VII. Exine stratification, SEM photographs.

— 1–4: *Guioa bicolor.* – 1: polar/equatorial view of grain with section through endoapertural region, × 2500; 2: detail of 1 showing nexine (thickened below ectoaperture), columellate layer, columellae, and tectum, × 7500; 3: grain with oblique section through two endoapertural regions showing thick polar sides and thin lateral sides of two endoapertures; 4: detail of 3, × 7500.
— 5, 6: *G. pleuropteris* (*Clemens s.n.*). – 5: approximately equatorial section showing moderately invaginated aperture membranes, × 2500; 6: detail of 5 showing nexine, columellate layer, columellae, and tectum, × 7500.

Plate VIII. Exine and intine stratification in *Guioa diplopetala* (Hort. Bogor. III-K-23a), TEM photographs.

— 1: approximately equatorial section showing two endoapertures, × 3450.
— 2–4: details of 1 showing exine and intine stratification, × 12080. 2 & 4 show an oncus; 3 gives a cross section of the ectoaperture membrane near the endoaperture; the very thin endexine in the mesocolpial regions is hardly visible.

t = tectum, **c** = columellate layer, **f** = foot-layer, **en** = endexine, **am** = aperture membrane, **o** = oncus, **i** = intine (appearing undifferentiated under the mesocolpia), **oi** = outer sublayer of oncus intine, **mi** = middle sublayer of the oncus intine, **ii** = inner sublayer of the oncus intine, **tr** = parts of the tubular/fibrous tract in the middle sublayer of the oncus, **p** = pollenkitt. Further explanation in General morphology: Exine architecture, Intine.

Plate IX. Exine and intine stratification in *Guioa pleuropteris* (1 & 2: *SAN 74533*; 3: *SAN 20738*), TEM photographs.

— 1: section through an endoaperture showing exine and intine stratification, × 12080. Note the presence of the electron-opaque extensions of the tubular/fibrous middle sublayer tract into the inner sublayer of the oncus. Electron-opaque inclusions occur in the outermost mesocolpial intine.
— 2: approx. equatorial section of a grain showing cross sections through three aperture membranes, × 3450.
— 3: cross section of an aperture membrane and adjacent areas showing the transition from the thick apertural endexine to the thin mesocolpial endexine, × 12080.

ext = electron-opaque extension of the middle sublayer tract into the inner sublayer of the oncus, **inc** = electron-opaque inclusion in the outermost mesocolpial intine. See caption of plate VIII for the other abbreviations. Further explanation in General morphology: Exine architecture, Intine.

(Plates I–IX, see pages 52–60)

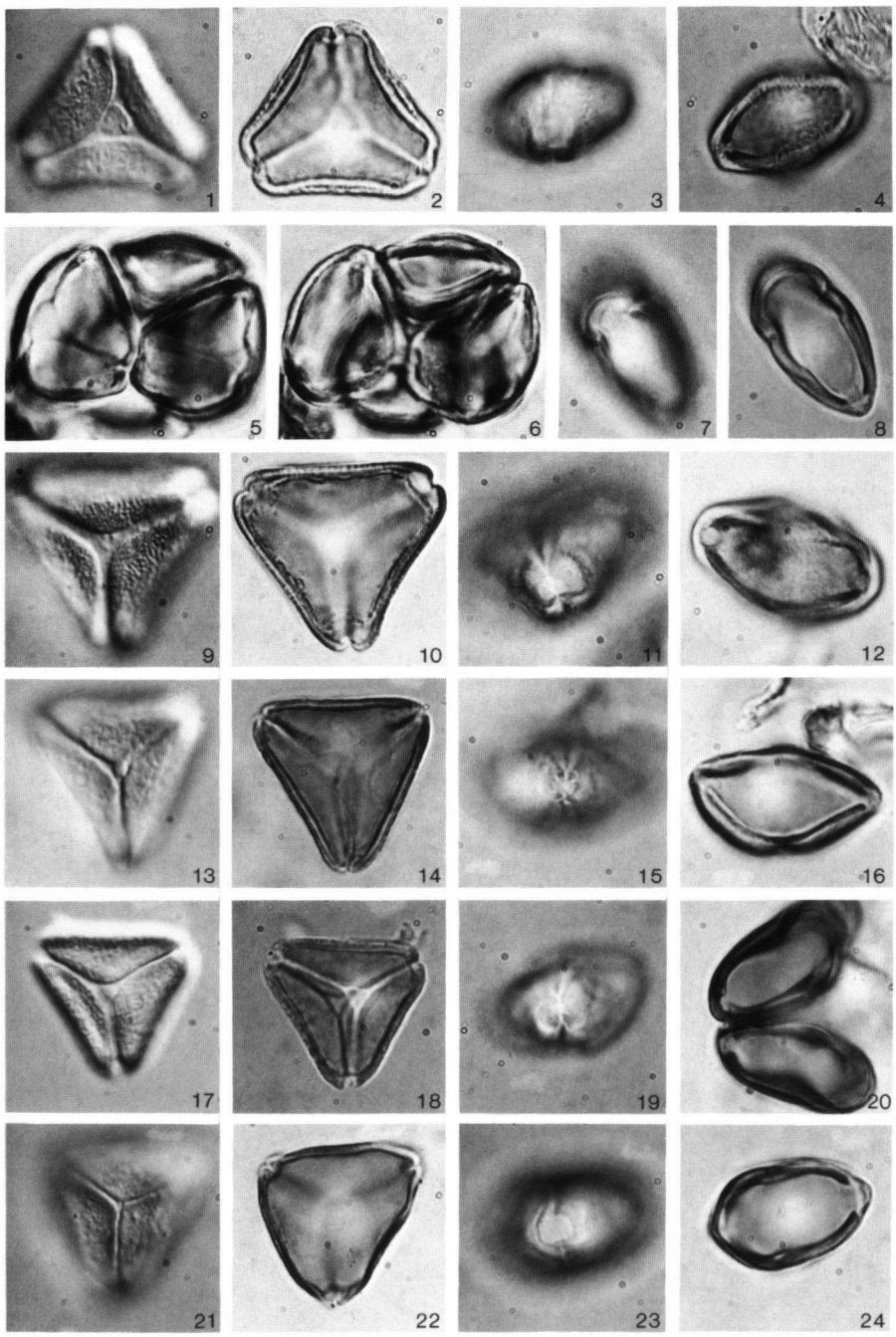
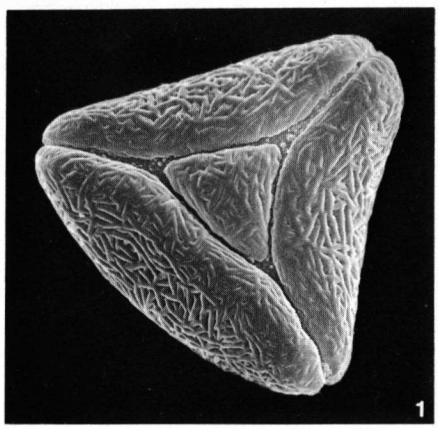
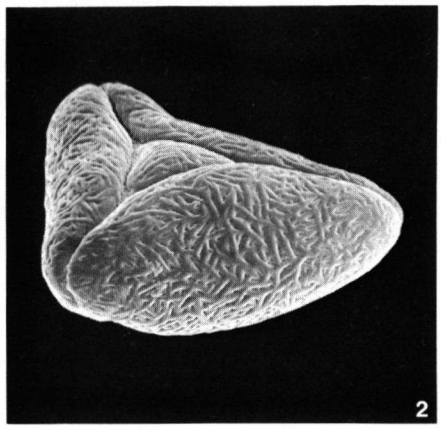
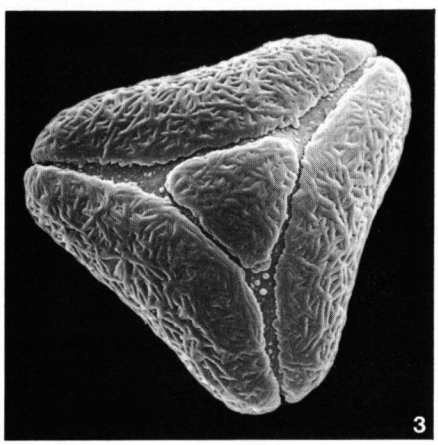
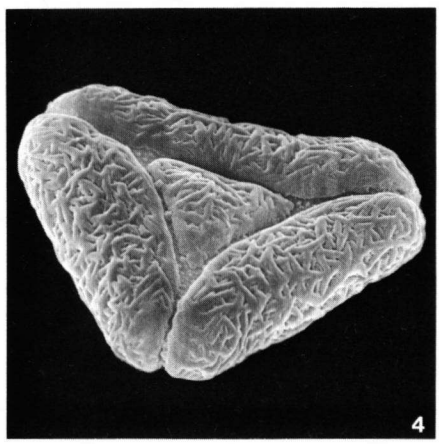


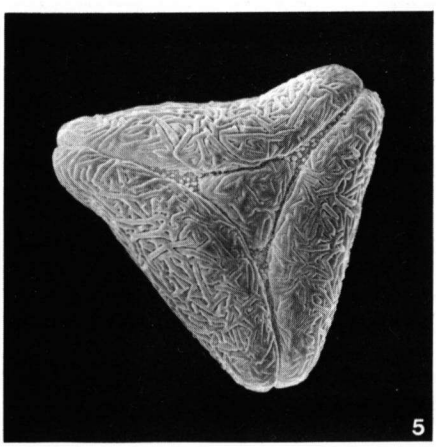
PLATE I











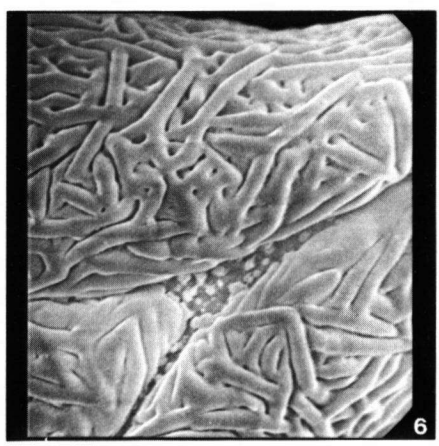
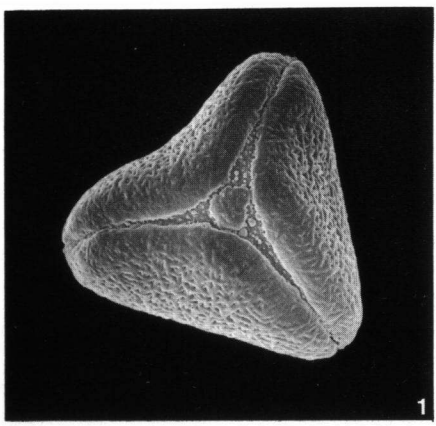
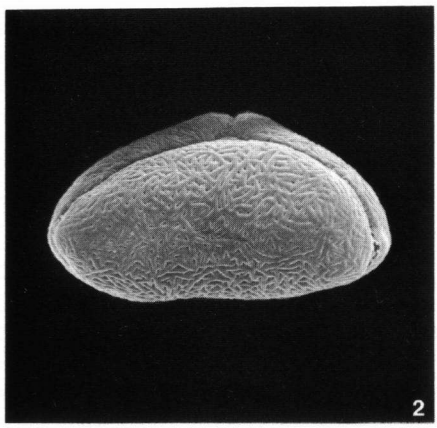
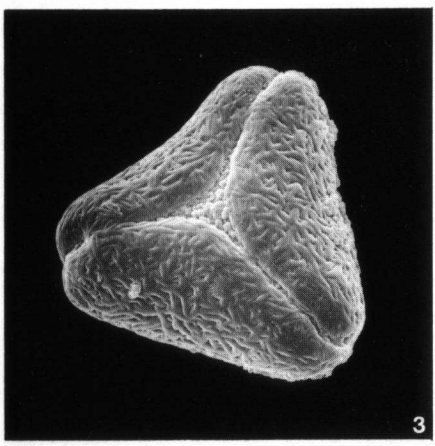
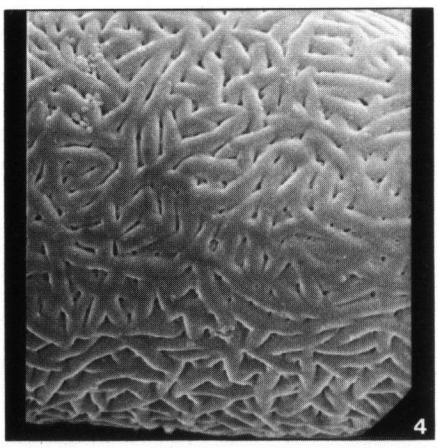


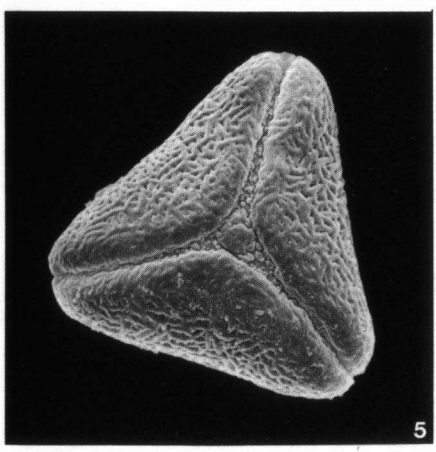
PLATE II











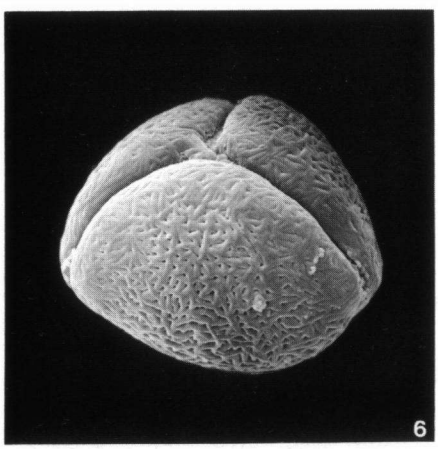
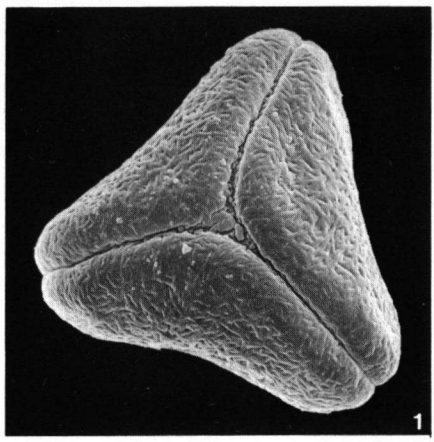
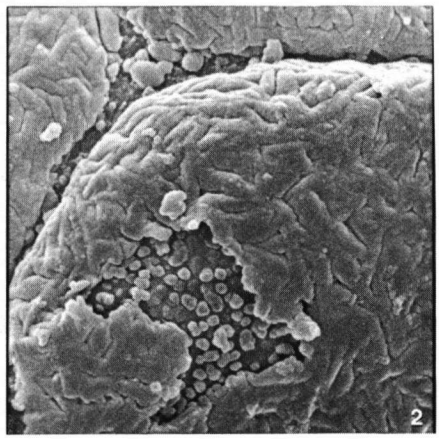
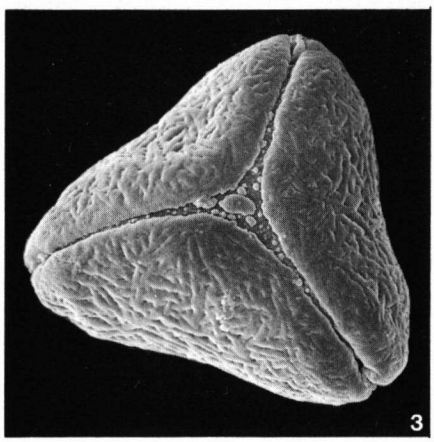
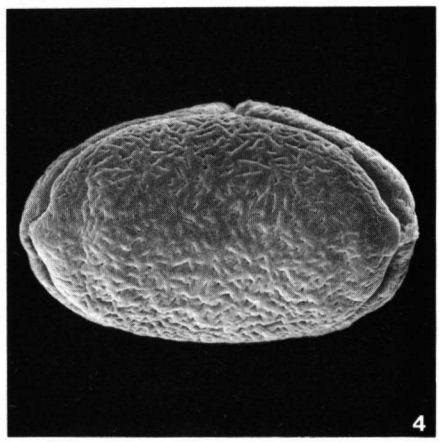


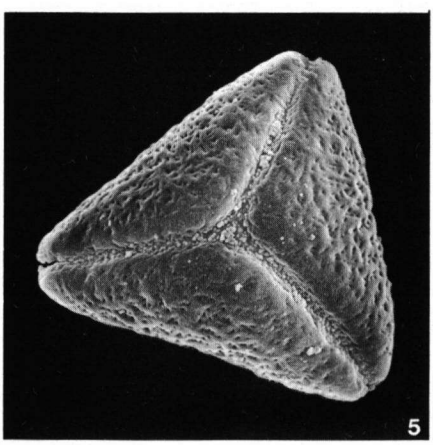
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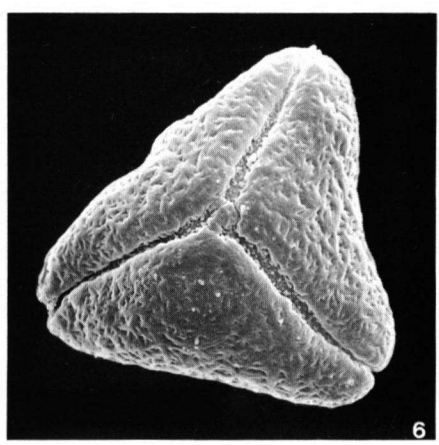


PLATE IV

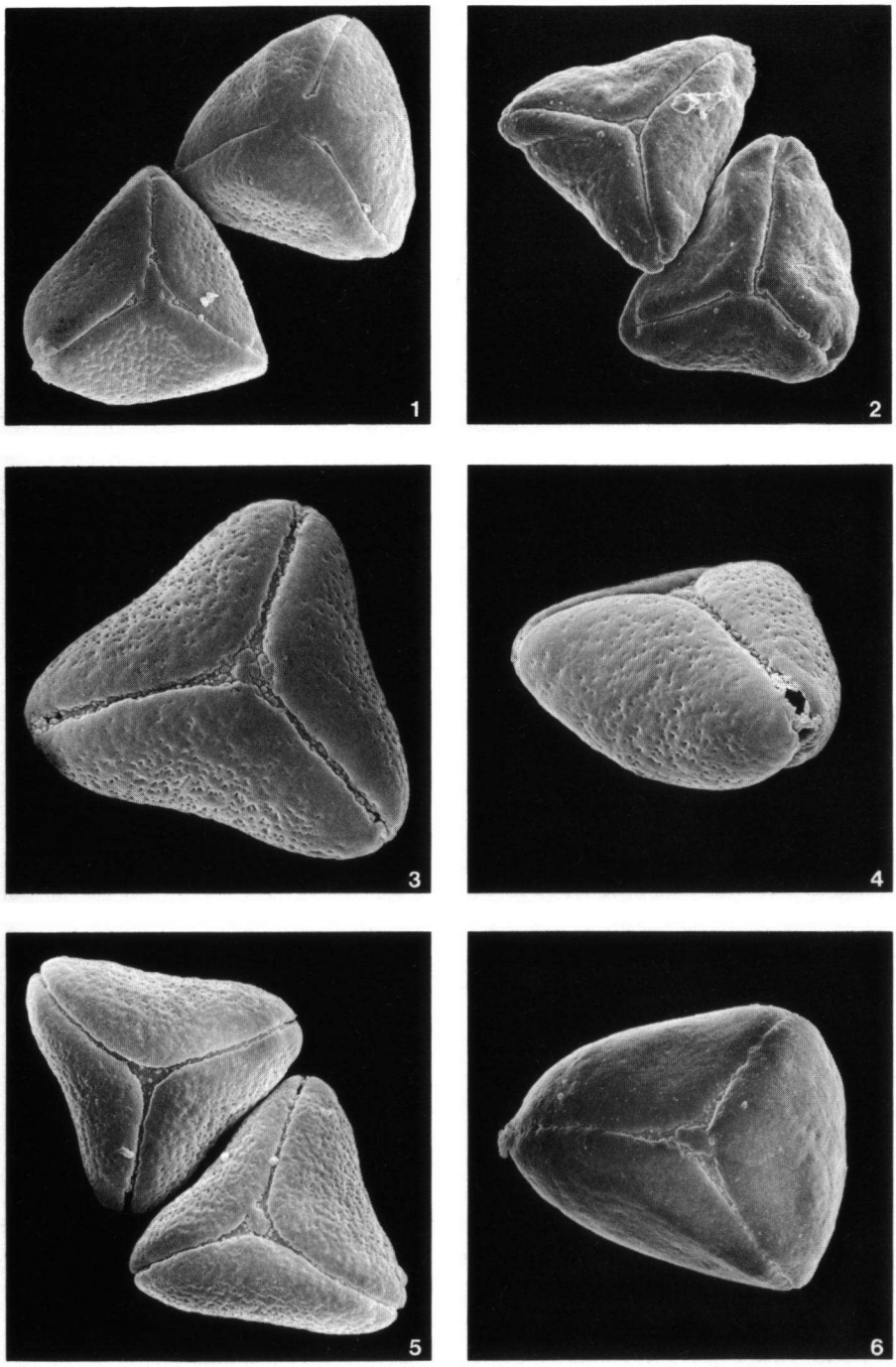
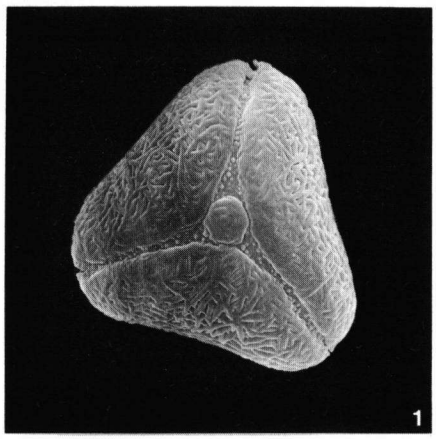
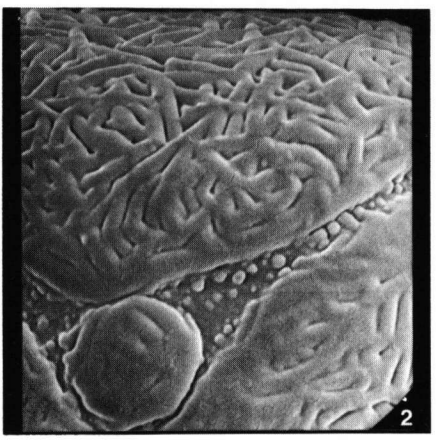
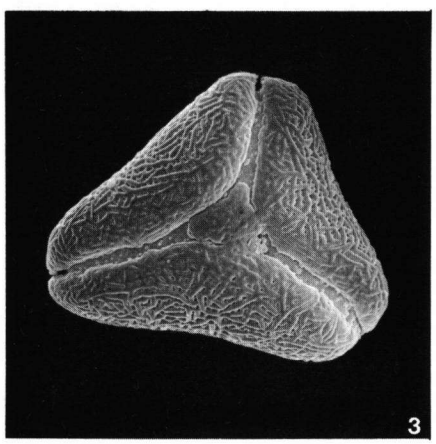
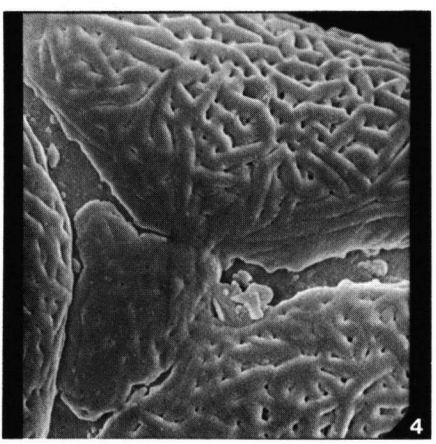


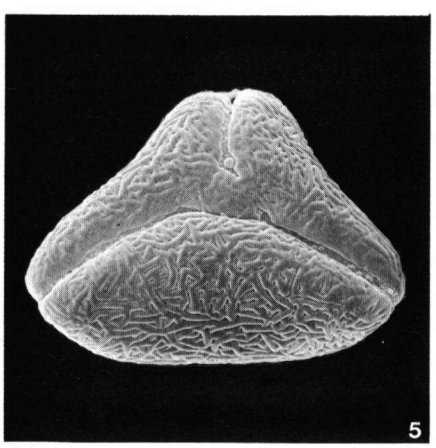
PLATE V











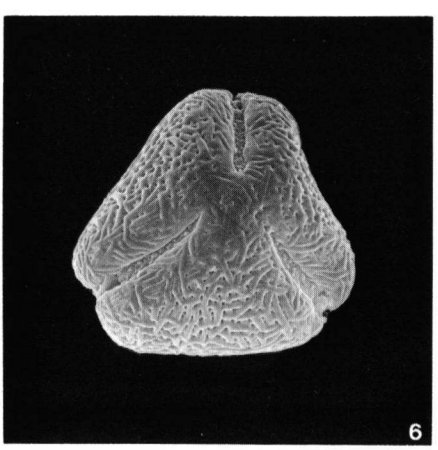


PLATE VI

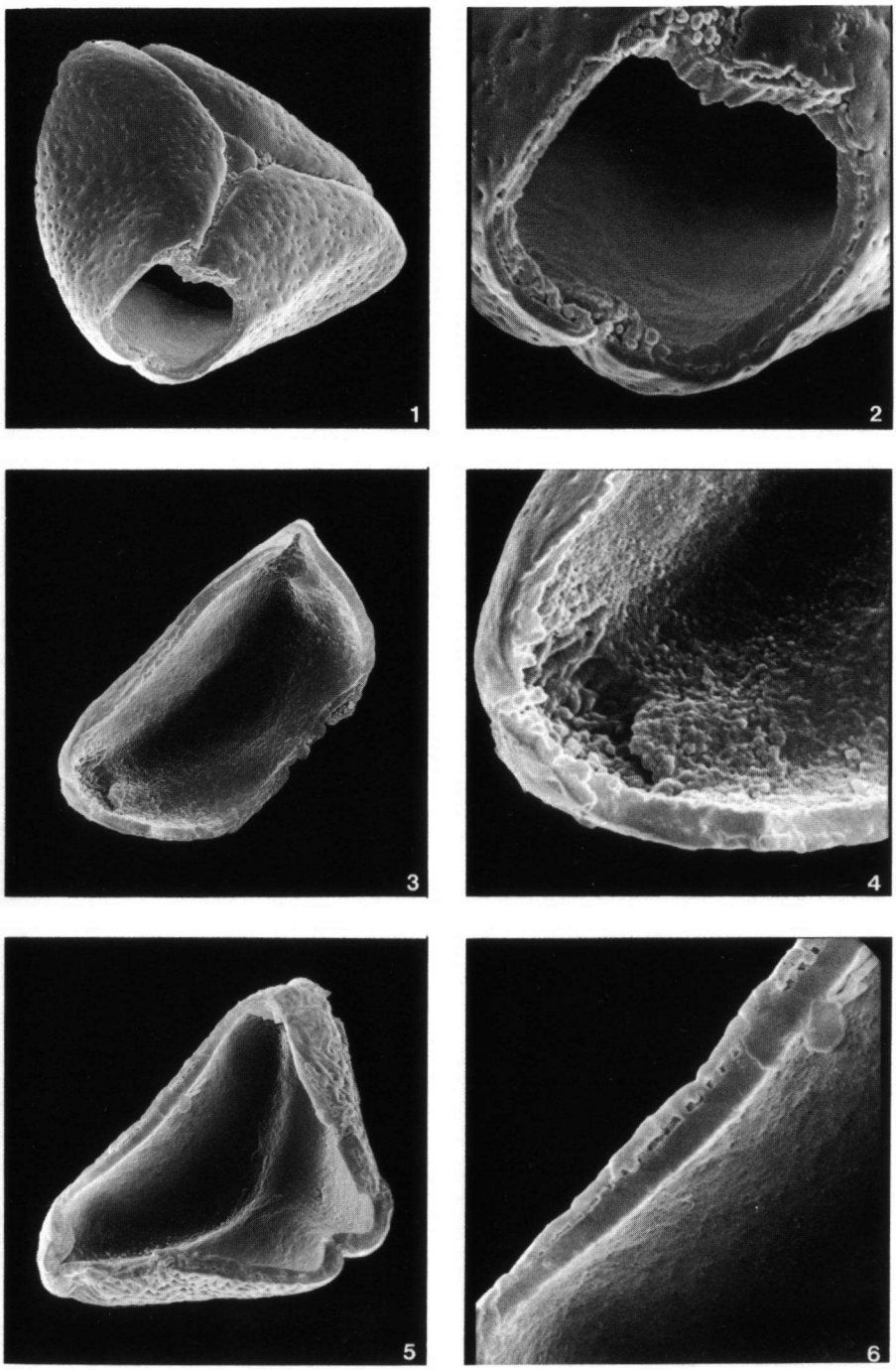


PLATE VII

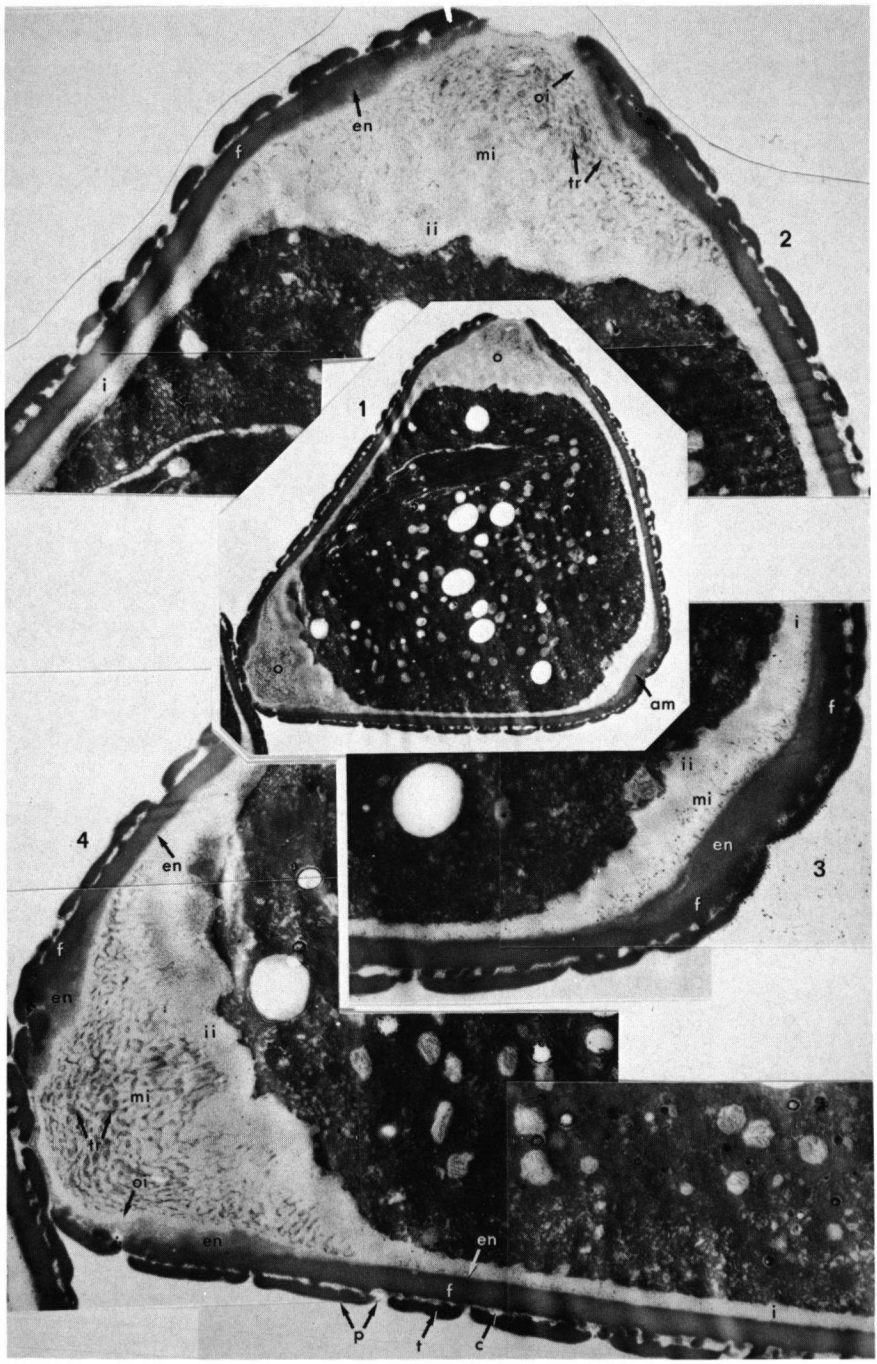

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PLATE VIII

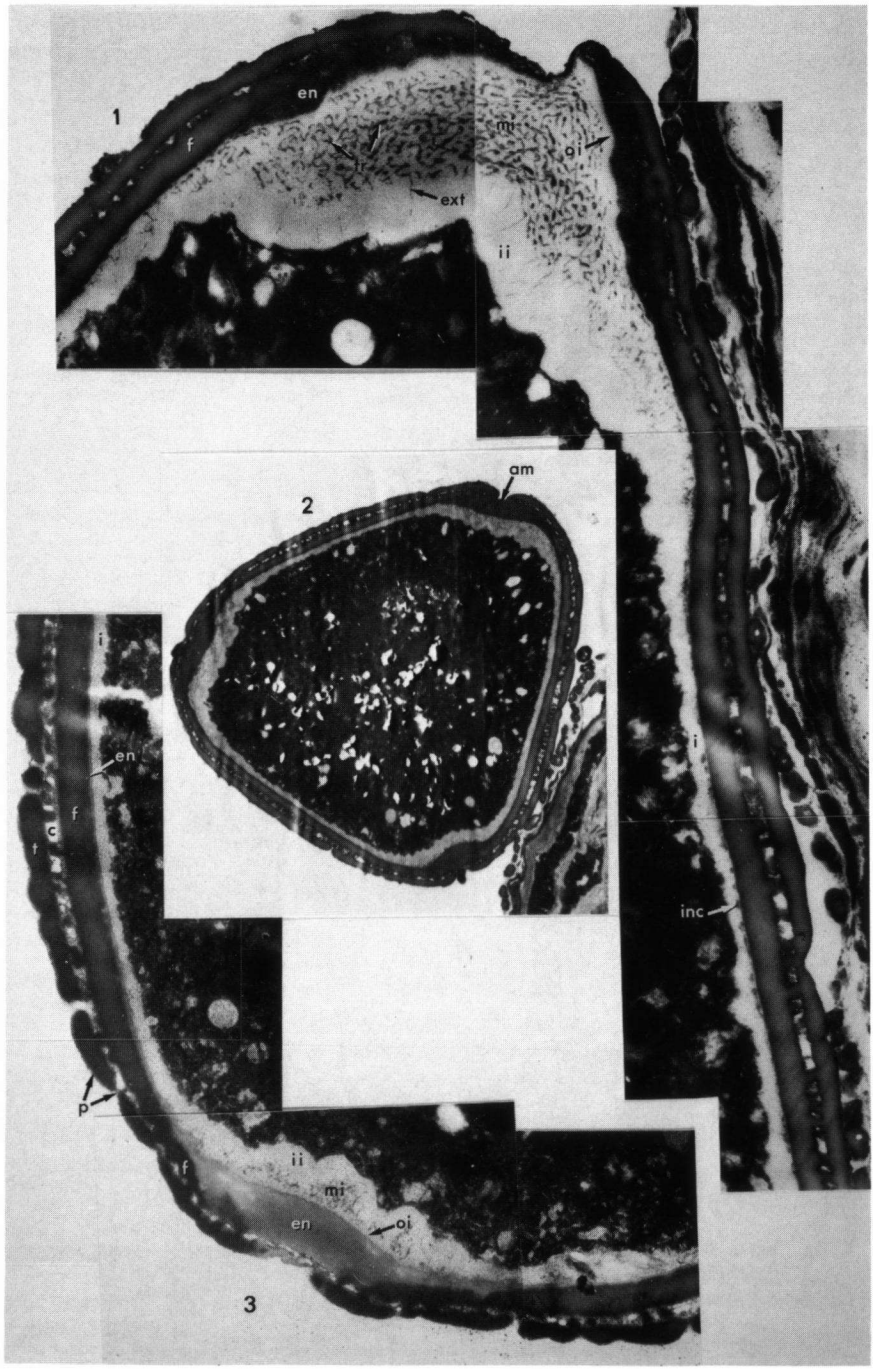


PLATE IX