POLLEN MORPHOLOGY AND TAXONOMY IN THE LOGANIACEAE

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Pollen Morphology
(W. Punt)

The Loganiaceae is a heterogeneous, eurypalynous family with colpate, colporate or porate pollen grains (Erdtman 1952). Some years ago Dr. Leeuwenberg, specialist in the taxonomy of African Loganiaceae, asked the senior author to undertake an investigation of the pollen grains of that family. Unfortunately that was impossible at the time because of other commitments. Later, however, a possibility presented itself for carrying out the investigation in connection with a sojourn at the Palynological Laboratory at Solna. I am much indebted to Professor Erdtman for the invitation to work at this Laboratory, for his approval of the subject, and for many discussions on pollen morphology. I am also much indebted to Dr.Leeuwenberg, Wageningen, and Dr. Leenhouts, Leiden for interesting, carefully determined plant material and for kind advice in taxonomic problems. I also want to express my thanks to all those in the Solna Laboratory, who kindly helped me in various ways during my visit. My work was supported by a grant from the U.S. Atomic Energy Commission to the Palynological Laboratory.

Materials and Methods

Herbarium material from the following botanical institutions was used: Botanisch Museum en Herbarium, Utrecht (U); Rijksherbarium, Leiden (L); Laboratorium voor Plantensystematiek en -geografie, Wageningen (WAG); Naturhistoriska Riksmuseet Stockholm (S). Some specimens from various herbaria were sent to Dr. Leeuwenberg at Wageningen. Besides, some slides from the sporotheke of the Palynological Laboratory Solna (SPL) were used.

The dry material was first boiled in water and then acetolysed (after washing with glacial acetic acid). Acetolysis was carried out in two ways: 1. "Macromethod" (Erdtman 1960). 2. "Micromethod" (Punt 1962). The latter method was used only when a very minute quantity of material was present. The specimens are marked "Mi" or "Ma" in Table 1 according to their treatment. The mounting medium was glycerine jelly. After mounting the slides were sealed off with paraffine wax.

Pollen grains of *Labordia tinifolia*, *Spigelia marilandica*, and *Anthocleista nobilis* were sectioned with a Spencer microtome (model 812) in the way described by Praglowski (in Erdtman 1957).

The pollen slides were examined with a Leitz Ortholux microscope (apochromatic objective 96 ×, A 1.32; eyepiece Periplan GF, 10 ×). The measurements were, as a rule, based on five grains only. The figures thus have no statistical significance. The photomicrographs were taken with a Leitz Ortholux microscope, objective C Pl Oel 160 ×, A 1.40. Ilford Chromatic, Panchromatic and sometimes Half Tone Chromatic plates were used. Yellow, orange or green filters were used. Original magnification usually 1500 ×.

The terminology used in this paper follows Erdtman (1943 and 1952) and Fægri and Iversen (1964). In some cases alternatives are given in brackets.

Pollen grains from all genera so far described were examined. In the following list the number of species examined is compared with the total number of species (according to Leenhouts, 1962):

	Number of species examined	Total number of spp.		Number of species examined	Total number of spp.
1. *Antonia*	1	1	10. *Fagraea*	26	ca. 31
2. *Adenoplea*	1	ca. 2	11. *Gardneria*	3	5
3. *Adenoplusia*	2	ca. 2	12. *Gelsemium*	2	3
4. *Androya*	1	1	13. *Geniostoma*	3	ca. 30
5. *Bonyunia*	4	ca. 4	14. *Gomphostigma*	1	2
6. *Buddleia*	13	ca. 110	15. *Labordia*	4	ca. 20
7. *Cynoctonum*	3	6	16. *Logania*	5	ca. 20
8. *Desfontainia*	1	1	17. *Mitrasacme*	6	ca. 40
9. *Emorya*	1	1	18. *Mostuea*	4	8

Number of species examined		Total number of spp.	Number of species examined		Total number of spp.
19. *Neuburiga*	4	ca. 10	25. *Retzia*	1	1
20. *Norrisia*	2	2	26. *Sanango*	1	1
21. *Nuxia*	6	ca. 20	27. *Spigelia*	3	ca. 50
22. *Peltanthera*	1	1	28. *Strychnos*	6	ca. 200
23. *Polypremum*	1	1	29. *Usteria*	1	1
24. *Potalia*	1	1	Gen. inc. sed.: *Plocosperma*	1	1

Pollen descriptions and comments

ANTONIEAE

ANTONIA-TYPE

Apertures. — Pollen grains 3-colporate. Colpi sunken. Colpus membrane smooth. Ora (endopori) circular to slightly lolongate, as wide as colpi. Margins of ora thickened (costae).

Shape. — Equatorial view: grains more or less spheroidal (subprolate in *Bonyunia superba*). Polar view: grains circular.

Exine. — Sexine thicker than nexine. Tectum smooth, usually perforate. In *Bonyunia aquatica* the bacules (columellae) form a regular pattern (infrastriate-infrareticulate). In the other species of *Bonyunia* the bacules are inordinate.

Antonia ovata —Pl. 1: 11–12	18 × 19 μ	OSph	
Bonyunia antoniifolia	30 × 33 μ	OSph	
B. aquatica—Pl. 1: 13	26 × 26 μ	Sph	exine infra-rugulose, muri straight
B. minor	26 × 24 μ	PSph	
B. superba	28 × 24 μ	SP	bacula distinct, longer at poles
Norrisia maior	13 × 14 μ	OSph or Sph	
N. malaccensis	17 × 17.5 μ	OSph or Sph	
Usteria guineensis	22 × 22 μ	Sph	

Antonia, Bonyunia, Norrisia and *Usteria* have pollen grains of the Antonia-type. Its most striking character is the circular ora accentuated by costae. The exine characters are very similar to those in the Logania-type and the Spigelia-type. Distinct ora are also found in the Gelsemium-type. A smooth perforated tectum is also present in the Logania-, Spigelia-, Potalia- and Geniostoma-types.

Pollen grains of the Antonia-type differ markedly from those in the genus *Peltanthera*, which undoubtely belong to the Buddleia type. This fits with the opinion of Leenhouts (1962) who included *Peltanthera* in the Buddleieae whereas Hutchinson (1959) placed it in the Antoniaceae. The pollen grains of Oleaceae are entirely different.

Antonia (S. America), *Usteria* (Africa) and *Norrisia* (Malesia) show a close resemblance in their pollen. It is remarkable that these small and geographically widely separated genera are so much alike in their pollen grains. The pollen grains of *Bonyunia* no doubt also belong to this type but they differ slightly in their exine structure. *Bonyunia aquatica* has short inordinate lirae (rugulate, Fægri & Iversen, 1964). The other species of *Bonyunia* differ more or less in their bacules characters. The differences are so small that no attempt for a further division of the genus is made here.

Neither illustrations nor chromosome numbers are published.

BUDDLEIEAE

Buddleia-type

Buddleia subtype

Apertures. — Pollen grains 3-colporate, sometimes 4-colporate. Colpi sunken, ends frequently blunt. Colpus membrane smooth. Ora lalongate (endocolpi), small and indistinct, ends diffuse. Margins not marked by costae.

Shape. — Equatorial view: grains usually subprolate to spheroidal, sometimes oblate-spheroidal. Polar view: grains circular, rarely goniotreme (semiangular or subangular). Grains rather small (longest axis not exceeding 25 μ).

Exine. — Sexine thicker than nexine. Tectum smooth. Bacules (columellae) frequently indistinct.

Adenoplea sinuata	18 × 18 μ	Sph	Finely reticulate (D'Alleizette s.n.)
—	17 × 15.5 μ	PSph	Not-reticulate (Afzelius s.n.)
Adenoplusia axillaris	ca. 15 μ		Bad material
A. uluguruensis	16 × 17.5 μ	OSph	
Androya decaryi	20 × 18.5 μ	PSph	Ora indistinct
Buddleia alpina	18.5 × 18 μ	Sph or PSph	Pollen grains sometimes 4-colporate
B. americana	17 × 18 μ	OSph	Usually 4-colporate
B. coriacea	21 × 17.5 μ	SP	
B. corrugata	19 × 15.5 μ	SP	
B. elegans	21 × 21 μ	Sph	Slightly angular in polar view

B. indica—Pl. 1: 1–2	20 × 17.5 μ	SP or PSph	
B. madagascariensis	16 × 15 μ	PSph	
B. marrubiifolia	17 × 15.5 μ	PSph	
B. salviifolia	16 × 13.5 μ	SP	
B. stachyoides	25 × 21 μ	SP	
Nuxia capitata	15 × 13 μ	SP	Ora indistinct and narrow
N. congesta	14 × 15.5 μ	OSph	
N. keniensis (syn. *N. congesta*)	17.5 × 15 μ	SP	
N. oppositifolia (syn. *N. autunesii*)	15.5 × 13 μ	SP	
Peltanthera floribunda	14 × 14 μ	Sph	
Sanango durum	15.5 × 16 μ	Sph or Osph	

Pollen grains of this subtype occur in most species of *Buddleia* (sect. Chilianthus excluded), most species of *Nuxia* and in some small. genera close to *Buddleia*, viz., *Adenoplea*, *Adenoplusia*, *Androya*, *Peltanthera*, and *Sanango*.

Chilianthus subtype

Apertures. — Pollen grains 3-colporate. Colpi sunken, Colpus membrane smooth. Ora lalongate (endocolpi), small and indistinct, their ends diffuse. Margins without costae.

Shape. — Equatorial view: grains spheroidal to subprolate. Polar view: grains circular or somewhat goniotreme (semiangular).

Exine. — Sexine thicker than nexine. Grains reticulate. Lumina irregular, small.

Buddleia dysophylla	17 × 15 μ	Psph or SP	
B. glomerata	17 × 13 μ	SP	
B. saligna — Pl. 1: 3–5	16 × 14 μ	Psph or SP	
Gomphostigma virgatum	21 × 21 μ	Sph	(Pont 1718)
	23 × 25.5 μ	Osph	(Norlindh & Weimarck 4499)
Nuxia floribunda (syn. *N. polyantha*)	13.5 × 13.5 μ	Sph	
N. verticillata	15 × 14 μ	PSph	reticulum fine, transition to a perforate tectum

This subtype is found in several species of *Buddleia* (sect. Chilianthus), some species of *Nuxia* and in the small genus *Gomphostigma*. The Chilianthus subtype closely resembles the Buddleia subtype. The only difference is found in the exine. The pollen grains in *Gomphostigma* differ from those in *Buddleia* and *Nuxia* in size only.

EMORYA-TYPE

Apertures. — Pollen grains 4-colporate (sometimes loxotreme). Colpi sunken. Colpus membrane smooth. Ora lalongate (endocolpi), small, indistinct, their ends diffuse. Margins without costae.

Shape. — Equatorial view: grains subprolate to prolate (sometimes depressed at the poles). Polar view: grains circular to slightly angular.

Exine. — Sexine thicker than nexine. Tectum smooth, perforate. Bacules (columellae) inordinate, comparatively long, sometimes placed in groups.

Emorya suaveolens — Pl. 1:6–10 $42 \times 32\ \mu$ SP–P

Only *Emorya* belongs to this type. It resembles the Buddleia-type in some characteristics (especially the ora). The number of colpi, however, is different and the bacules are always distinct.

The pollen grains of the Buddleia subtype show some slight variation in their morphological characters. There is some fluctuation in the shape, in the length of the colpi, and in the distinctness of the bacules.

The Chilianthus subtype differs from the Buddleia subtype only by the presence of a reticulum. In some species (e.g. *Nuxia verticillata*) the reticulum is so fine that it represents a transition to the non-reticulate Buddleia subtype. Therefore it seems better to unite these subtypes with the Buddleia-type.

The Emorya-type differs markedly from the Buddleia-type by its shape, by having four colpi, and by the distinctly visible bacules. Some species in the Buddleia-type also have four colpi (*B. alpina* and *B. americana*). The most important similarity between both types is in the ora which are small and indistinct. The notable difference in pollen grains between *Emorya* and *Buddleia* is in contrast with the overall resemblance between the two genera which made Leenhouts (1962) that they might be united.

The two types have little in common with other Loganiaceous types being considerably different in shape and apertures.

The pollen grains of *Peltanthera* and *Sanango* agree in all respects with the Buddleia subtype and do not share any character with the Antonia-type (Antonieae). The genera *Adenoplea, Adenoplusia, Androya,* and subgenus *Nicodemia* (*Buddleia*) also have pollen grains which clearly belong to the Buddleia subtype. The relationship of *Nuxia* with *Buddleia* is also confirmed by the pollen morphological results.

There is some pollen morphological support to place the Buddleieae near the Scrophulariaceae. The resemblance between their pollen grains and those of *Calceolaria* is so striking that the latter genus cannot be excluded from the Buddleia-type. The pollen grains of the genera *Antirrhinum, Halleria, Linaria, Scrophularia,* and *Verbascum* also have several characters in common with the Chilianthus subtype. The grains of the genera *Alonsia, Aplosium, Castilleja, Digitalis, Hebe, Hebenstreitia* (Selaginaceae), *Hydrotriche,* and *Paulownia* are completely different. This selection of genera is arbitrary and the list is far from complete.

According to Leenhouts (1962) the Buddleieae form a transition between the Loganiaceae and the Scrophulariaceae; they are, however, much easier to separate from the latter than from the former family.

Reduction of the genus *Chilianthus* to *Buddleia* is not supported by pollenmorphological evidence. *Chilianthus* Burch. was united with *Buddleia* Linn. by Phillips (1946) who was followed by Verdoorn (1963). The following three species belong to this taxon: *Buddleia saligna* Willd. [syn. *Chilianthus arboreus* (Linn. f.) A.DC.], *Buddleia dysophylla* (Benth.) Radlk. [syn. *Ch. dysophyllus* (Benth.) A.DC.], *Buddleia glomerata* Wendl. f. [syn. *Ch. lobulatus* (Benth.) A.DC.]. One species, *Buddleia corrugata* (Benth.) Phillips, forms a transition between "*Chilianthus*" and *Buddleia*. Pollen grains of this species undoubtedly belong to the Buddleia subtype. On the other hand, some *Nuxia* species (*N. polyantha* and *N. verticillata*) also have pollen grains of the Chilianthus subtype. This is an indication that *Nuxia* and *Chilianthus* may be closely related. In fact, all *Chilianthus* species have at one time or another been included in *Nuxia*.

Illustrations

Erdtman 1952, fig. 144B, *Buddleia japonica* Hemsl.
Wang 1960, Tab. LXII, *Buddleia lindleyana* Forst.

Chromosome numbers (Gadella 1962, 1963, Moore 1947, 1960)

Buddleia albiflora Hemsl.	$2n =$ ca. 114
B. alternifolia Maxim.	38
B. americana Linn.	76

B. asiatica Lour.	38
B. brasiliensis Jacq.	38
B. candida Dunn.	76
B. colvilei Hook. f. et Thoms.	ca. 300
B. crispa Benth.	38
B. davidii Franch.	76
B. delavayi Gagnep.	ca. 114
B. fallowiana Balf. f. et W. W. Smith	76
B. farreri Balf. f. et W. W. Smith	38
B. forestii Diels	ca. 114
B. globosa Hope	38
B. glandiflora Champ. et Schl.	38
B. hastata Prain ex Marq.	38
B. indica Lam.	76
B. japonica Hemsl.	38
B. limitanea Smith	ca. 114
B. lindleyana Fort.	38
B. madagascariensis Lam.	38
B. nappii Lorenz	38
B. nivea Duthie	ca. 114
B. paniculata Wall.	38
B. pterocaulis Jacks.	ca. 228
B. salviifolia (Linn.) Lam.	38
B. scordioides H. B. K.	38
B. stenostachya Reh. et Wils.	ca. 114
B. sterniana Cotton	38
Chilianthus arboreus (Linn. f.) DC.	38
Nuxia floribunda Benth.	38

SPIGELIEAE (p. p.)

SPIGELIA-TYPE

Apertures. — Pollen grains 3-colpate or 3-colporate. Colpi wide, not sunken, rather short, and their ends sharp. Colpus membrane absent or present only at the ends of the colpi. Ora congruent with the colpi in *Spigelia*, nearly congruent in *Desfontainia* and *Polypremum*.

Shape. — Equatorial view: grains suboblate or oblate. Polar view: grains goniotreme (semiangular or triangular).

Exine. — Sexine thicker than nexine. Tectum smooth, perforate. Bacules (columellae) short and different in shape and size.

Desfontainia spinosa — Pl. 2: 6–7	$39 \times 45\ \mu$	SO or O
Polypremum procumbens	$24.5 \times 29\ \mu$	SO
Spigelia anthelmia	$34 \times 62\ \mu$	O
S. leiocarpa — Pl. 2: 5	$45 \times 62\ \mu$	O
S. martiana	$29 \times 43\ \mu$	O

Spigelia, Desfontainia and *Polypremum* have pollen grains of this type. Colpus membranes are not present in the investigated species of *Spigelia*. In *Desfontainia* and *Polypremum*, however, a small part of the colpus membrane is present at the ends of the colpi. If there is no colpus membrane, we should speak of an endoaperture. In the genera *Desfontainia* and *Polypremum*, where a small part of the colpus membrane is left, it seems reasonable to speak of colporate grains. In *Spigelia*, where the colpus membrane is completely wanting, it seems better to speak of colpate grains, although, strictly theoretically, these grains are also colporate. The most remarkable character of the Spigelia-type is the absence or, indistinctness of the ora. This character separates the type from all other types in the Loganiaceae. There is, however, a similarity in shape and exine structure with the Logania-type.

The pollen grains of *Desfontainia* fit completely in the Spigelia-type and do not show any resemblance with the Potalia-type. Inclusion of *Desfontainia* in the Loganiaceae is supported by this result.

The pollen grains of *Polypremum*, although less oblate in shape than the grains of *Spigelia* and *Desfontainia*, are placed in the same type because of the indistinct lolongate ora.

The taxonomic position of *Desfontainia* is not clear. Solereder (1892), Klett (1924), and Leenhouts (1962) were doubtful with regard to its affinity. The two last named authors suggested a place near the Potalieae. Pollenmorphological characters are in favour of a place near *Spigelia* and *Polypremum*.

The pollen grains of the Rubiaceae-Hedyotideae, to which group Leenhouts (1962) believed *Polypremum* to be rather closely related, are different.

Pollen of *Mitrasacme elata* are similar in shape and apertures but differ in exine structure (reticulate).

Mitrasacme elata-type

Apertures. — Pollen grains 3-colporate. Colpi wide, not sunken, rather short, their ends sharp. Colpus membrane present only at the ends of the colpi. Ora lolongate, indistinct.

Shape. — Equatorial view: grains suboblate or oblate. Polar view: grains goniotreme (angular).

Exine. — Sexine thicker than nexine. Grains reticulate. Muri simplibaculate. Lumina 1–3 μ, smaller towards colpi and poles.

Mitrasacme elata var. *elata*	$31 \times 41\ \mu$	SO or O

To the Spigelieae sensu Leenhouts (1962) belong the genera *Spigelia*, *Cynoctonum*, *Polypremum*, and *Mitrasacme*. *Cynoctonum* has pollen grains which are characteristic for the Logania type. The species of *Mitrasacme* show different types of pollen grains. *Mitrasacme elata* pollen resemble to the Spigelia-type, *M. indica* and *M. erophila* pollen have several characters in common with the Logania-type, and *M. pygmaea* pollen seem to have some similarity with the Gelsemium-type.

Too few species of *Mitrasacme*—mainly Malesian ones—have been investigated, but as this largely Australian genus is in urgent need of a revision, it seems better to postpone further conclusions. It may be expected that pollen morphology will be of great help in a taxonomic revision.

Illustrations

Erdtman 1943. Pl. IX fig. 148, 149. *Desfontainia spinosa* Ruiz et Pavon.
Erdtman 1952. Fig. 145. D. *Spigelia anthelmia* Linn.

Chromosome numbers (Gadella 1962, Moore 1947)

Desfontainia spinosa Ruiz et Pavon	$2n = 14$
Polypremum procumbens Linn.	22
Spigelia anthelmia Linn.	32
S. marilandica (Linn.) Linn.	48
S. splendens Wendl. ex Hook.	26

STRYCHNEAE, CYNOCTONUM, LOGANIA AND MITRASACME (p. p.)

LOGANIA-TYPE

Apertures. — Pollen grains 3-colporate, rarely 4-colporate. Colpi sunken, their ends often blunt. Colpus membrane smooth. Ora circular to lalongate (endopori to endocolpi), their ends diffuse. Costae may be present.

Shape. — Equatorial view: grains usually suboblate to oblate-spheroidal, sometimes spheroidal or even prolate-spheroidal (*Cynoctonum* species, *Mitrasacme erophila*). Polar view: grains goniotreme (subangular, semi-angular or sexangular).

Exine. — Sexine mostly thicker than nexine. Tectum smooth, perforate. Some species in *Cynoctonum* have no perforations. Bacules (columellae) low, capita usually distinct.

Cynoctonum mitreola	$18 \times 18\ \mu$	Sph	perforations in tectum more crowded in the mesocolpia than in the apocolpia
Mitreola (= *Cynoctonum*) *petiolata*	$15 \times 15.5\ \mu$	OSph or Sph	tectum smooth, perforate

Cynoctonum sessilifolia	16 × 14 μ	SP or PSph	bacules indistinct, tectum not perforate
C. sphaerocarpum	15 × 19 μ	SO	colpi narrow, ora distinct, circular; rhomboic in equatorial view
Gardneria multiflora			pollen grains too young for measurements
G. nutans	23 × 26 μ	SO or OSph	
G. ovata	21 × 25 μ	SO	
Logania floribunda	20 × 24 μ	SO	costae faint; perforations in tectum rather wide
L. floribunda (syn. *L. angustifolia*)	25 × 25 μ	Sph	
L. hyssopoides	28 × 29 μ	OSph	no costae; grains semiangular
L. linifolia	23 × 26 μ	SO or OSph	
L. longifolia	25 × 25 μ	Sph	
L. ovata — Pl. 2: 1–4	25 × 25 μ	Sph	
Mitrasacme erophila	32 × 29 μ	PSph	ora indistinct
Neuburgia celebica	32 × 37 μ	SO	costae indistinct
Couthovia (= *Neuburgia*) *collina*	26 × 31 μ	SO	
Neuburgia corynocarpa	26 × 31 μ	SO	
Couthovia (= *Neuburgia*) *novocaledonica*	25 × 32 μ	SO	
Neuburgia tubiflora	34 × 41 μ	SO	
Strychnos angolensis	23 × 25 μ	OSph	ora circular or slightly lolongate
S. chrysophila	34 × 39 μ	SO or OSph	
S. mellodora	21 × 23 μ	OSph	
S. nux-vomica	37 × 42 μ	SO or OSph	Ora circular; no costae
S. parviflora	19 × 23 μ	SO	
S. variabilis	36 × 37 μ	OSph	

To this type belong the genera *Logania*, *Cynoctonum*, *Neuburgia*, *Gardneria* and *Strychnos*, and besides, the species *Mitrasacme erophila*.

The Logania-type has some characters in common with the Antonia-type as well as with the Spigelia-type. The differences separating it from the Antonia-type are in the ora, from the Spigelia-type in the apertures. The type is easily recognisable by its angular shape and smooth tectum. The grains are usually subangular but sometimes semiangular. All other characters are more or less variable. In equatorial view most grains have a polar axis shorter than the equatorial axis (exceptions in *Cynoctonum, Mitrasacme*). The ora are short and hardly or not longer than the colpus width.

The Geniostoma-type and the Spigelia-type have some pollenmorphological characters in common with the Logania-type.

To the tribe Strychneae belong the genera *Strychnos, Gardneria,* and *Neuburgia.* In this circumscription the group is accepted by Solereder (1892), Gandoger (1923), Klett (1924), and Leenhouts (1962). Pollenmorphologically related are the genera *Logania, Cynoctonum* and some species of *Mitrasacme,* but it seems that in most other characters they are divergent. No taxonomist has suggested this combination of genera before, though Leenhouts (1962) assumes a closer affinity between the Strychneae and the Loganieae via *Neuburgia.*

MITRASACME INDICA-TYPE

Apertures. — Pollen grains 3-colporate. Colpi rather wide and long, sunken, their ends blunt. Colpus membrane smooth. Ora circular, indistinct. No costae present.

Shape. — Equatorial view: grains subprolate. Polar view: grains circular.

Exine. — Sexine thicker than nexine. Tectum smooth, perforate. Bacules (columellae) inordinate to slightly rugulate.

Mitrasacme indica	27 × 25.5 μ	SP	Ora indistinct, no costae
M. neglecta	23 × 25 μ	OSph	Ora circular or slightly lolongate

The pollen grains of the Mitrasacme indica-type show a distinct morphological resemblance to those of *M. erophila.* The pollen of the latter species, however, undoubtedly belong to the Logania-type because of their angular shape, whereas those of the former species are circular in polar view.

MITRASACME PYGMAEA-TYPE

Apertures. — Pollen grains 3-colporate. Colpus ends sharp. Colpus membrane smooth. Ora slightly lalongate to circular (endopori), distinct. No costae present.

Shape. — Equatorial view: grains spheroidal or oblate-spheroidal. Polar view: grains circular.

Exine. — Sexine thicker than nexine. Grains reticulate. Lumina fine, smaller than 1 μ. Muri simplibaculate.

Mitrasacme pygmaea var. *malaccensis*	27.5 × 30 μ	OSph
M. polymorpha	31 × 31 μ	Sph

The pollen grains of *Mitrasacme polymorpha* and *M. pygmaea* resemble those of the Gelsemium-type in many characters. *Mitrasacme* grains have, however, a fine reticulum and the longest axis is shorter than in the Gelsemium-type.

The genus *Mitrasacme* is in urgent need of a revision. Further investigation of the pollen must be postponed until a new revision is available (see p. 478).

Perhaps the examined specimen of *M. polymorpha* also belongs to *M. pygmaea*, as nearly all specimens of *M. polymorpha* proved to be incorrectly determined.

Illustrations

Wang 1960. Tab. LXII *Gardneria multiflora* Makino, *Strychnos umbellata* (Lour.) Merr.

Chromosome numbers (Gadella 1962, 1963, Janaki-Ammal in Moore 1947) Mohrbutter 1936.

Strychnos aculeata Soler.	$2n = 44$
S. afzelii Gilg	44
S. angolensis Gilg	88
S. camptoneura Gilg	44
S. congolana Gilg	44
S. floribunda Gilg	44
S. icaja Baill.	44
S. laurina DC.	24
S. longicaudata Gilg	44
S. malacoclados C. H. Wright	88
S. nigritana Baker	44
S. nux-vomica Linn.	24
S. soubrensis Hutch. et Dalz.	44
S. spinosa Lam.	44
S. splendens Gilg	44

GELSEMIEAE

Gelsemium-type

Apertures. — Pollen grains 3-colporate. Colpi sunken. Colpus membrane smooth in *Mostuea* and with some scattered granules in *Gelsemium*. Ora slightly lalongate (endoporus slightly elongated). The margin of the os is distinctly thickened. Ora not much longer than the colpus width.

Shape. — Equatorial view: grains vary from spheroidal to subprolate. Polar view: grains circular to slightly semiangular, never subangular. Size of the grains is larger than in most other types in the Loganiaceae, usually ca. 40 μ.

Exine. — Sexine many times thicker than nexine. *Mostuea* species are striate on the tectum. *Gelsemium* species are striato-reticulate, simplibaculate. All *Mostuea* species studied have a tectum perforatum.

Gelsemium elegans	46 × 40 μ	PSph or SP	
G. rankinii	41 × 41 μ	Sph	
— Pl. 2: 8–10			
Mostuea batesii	60 × 51 μ	SP	
M. brunonis	52 × 50 μ	PSph	grains sometimes syncolpate
M. hirsuta	46 × 45 μ	Sph or PSph	
M. surinamensis	46 × 38 μ	SP	
— Pl. 2: 11–12			

Gelsemium and *Mostuea* have pollen grains of this type

The most remarkable characters of the type are the size of the grains, the distinct bacules (columellae), and the well marked margin of the ora. Distinct ora are also found in the Antonia-type, and, less pronouncedly, in the Logania-type. In the Logania-type, however, the ends of the ora are usually diffuse.

The two genera can be distinguished by their difference in exine structure.

A. Exine striato-reticulate . . . . *Gelsemium*
B. Striae on tectum, tectum perforatum, columellae inordinate . . . . *Mostuea*

Retzia, having indistinct ora, is placed in a type by itself. Several other characters distinguish it also from the Gelsemium-type (see p. 481).

Pollen grains of the Oleaceae, which are thought by some authors to be near the Gelsemieae are different from those of the Gelsemium-type. Although all genera examined had reticulate grains, the reticulation is quite different. The reticulum in *Forestieria*, *Forsythia*, *Schrebera*, and some other genera resembles the reticulum in the Fagraea ceilanica-type.

Taxonomic relationship between *Gelsemium* and *Mostuea* is accepted by most taxonomists, viz. Klett (1924), Leeuwenberg (1961), and Leenhouts (1962).

Illustrations

Erdtman 1943. Pl. XIV, fig. 237, *Gelsemium sempervirens* Ait.
Erdtman 1952, fig. 145. C, *Gelsemium sempervirens* Ait.
Wang 1960. Tab. LXII, p. 117, *Gelsemium elegans* (Gardn. et Champ.) Benth.

Chromosome numbers (Moore 1947, Gadella 1962, 1963)

Gelsemium sempervirens Ait.	$2n = 16$
Mostuea brunonis Dider.	20
M. hirsuta (T. Anders. ex Benth. et Hook.) Baill. ex Baker	20

RETZIEAE

Retzia-type

Apertures. — Pollen grains 3-colporate. Colpus ends sharp. Colpus membrane densely granulate. Ora indistinct, lalongate (endocolpus). No costae present.

Shape. — Equatorial view: grains oblate-spheroidal to spheroidal. Polar view: grains circular to semiangular.

Exine. — Sexine thicker than nexine. Grains reticulate. Lumina narrower than the muri, muri broad, duplibaculate.

Retzia capensis — Pl. 3: 1–4	$43 \times 45\ \mu$	OSph

To this type belongs *Retzia* only

The Retzia-type resembles the Gelsemium-type in several characters. The grains are rather large, 3-colporate, and have a coarse reticulum. There are, however, three important differences: 1. Ora indistinct. 2. Colpus membrane densely granulate. 3. Muri duplibaculate. Especially the indistinct ora separate the Retzia-type from the Gelsemium-type. Indistinct ora are also characteristic for both types of the Buddleieae, but in that tribe granulation of the colpus membrane is never found.

The affinities of *Retzia* are uncertain (Leenhouts, 1962). Leeuwenberg (1964) has the opinion that a relationship to the Solanaceae (*Metternichia* and *Sessea*) is less certain than to the Loganiaceae. Within the Loganiaceae *Retzia* should form a separate tribe near the tribes Antonieae and Buddleieae. Pollen grains of *Metternichia* and *Sessea* differ widely from *Retzia*; those of the Antonia type (Antonieae) are also quite different. The pollen grains of the Buddleieae, however, have some characters in common with the Retzia type.

Neither illustrations nor chromosome numbers published.

LOGANIEAE p. p. (EXCEPT LOGANIA)

GENIOSTOMA-TYPE

Apertures. — Pollen grains porate. Number of pores fluctuates from 3 to 5 and in some rare cases even 6 or 7 pores are present. Pores provided with costae, not protruding, not always in the same plane.

Shape. — Equatorial view: grains oblate to oblate-spheroidal. Polar view: grains distinctly goniotreme (semiangular or subangular).

Geniostoma subtype

Exine. — Sexine thinner than nexine. Tectum smooth, perforate.

Geniostoma balseanum	33 × 37 μ	SO	pollen grains 3-porate, pore diam. ca. 8 μ
G. pancheri	23 × 31 μ	O	pollen grains 3–7 porate, pore diam. ca. 4 μ
G. rupestre (syn. *G. australianum*) — Pl. 3: 5–7	22 × 28 μ	SO	pollen grains 3–5 porate, pore diam. ca. 5 μ
G. rupestre (syn. *G. ligustrifolium*)	20 × 25 μ	SO	pollen grains 3-porate, pore diam. 2–3 μ
Labordia hypoleuca	36 × 43 μ	SO	pollen grains 3–5 porate, pore diam. ca. 5 μ. Pores not always in the same plane; sometimes vestibulum present
L. hedyosmifolia	35 × 41 μ	SO	pollen grains 4–5 porate, pore diam. 3–4 μ. Pores not always in the same plane; sometimes a small vestibulum present

Darbolia subtype

Exine. — Sexine thicker than nexine. Grains reticulate. Reticulum very coarse, muri thick, lumina wide.

Labordia helleri According to Selling (1947): pollen grains 3–4-porate (rarely 5-porate), diam. pori ca. 3 μ, reticulum but slightly continuous, lumina about 5 (3–8) μ across.

L. tinifolia var. *tenuifolia* — Pl. 4: 1–5	32 × 40 μ	SO	pollen grains 3–4-porate, pore diam. ca. 6 μ.

Geniostoma and *Labordia* have pollen grains of this type.

The Geniostoma subtype differs from the Darbolia subtype in exine structure only. Superficially the Geniostoma-type resembles the Potalia-type. Both types are porate, but the Geniostoma-type is distinctly angular, whereas the Potalia-type is more or less spheroidal. The similarity is probably a matter of convergence. The exine structure of the Geniostoma-type and the Potalia-type is similar.

Although the Geniostoma-type and the Darbolia subtype differ considerably in surface pattern, their resemblances in shape and apertures are so striking that it seems better to place both as subtypes in one type.

Taxonomically the genera *Geniostoma* and *Labordia* are distinctly related. Klett (1924) placed *Geniostoma* and *Labordia* in the subtribe Geniostomae. Solereder (1892), Gandoger (1923), and Leenhouts (1962) added *Logania*, forming the tribe Loganieae. Although a certain similarity between the pollen grains of *Logania* and the Geniostoma-type is present, it seems better to place *Logania* next to the representatives of the Strychneae (*Strychnos, Gardneria*, and *Neuburgia*).

Illustrations

Erdtman 1948, fig. 6, *Geniostoma rupestre* Forst.
Erdtman 1952, fig. 145 B a–d *Labordia hedyosmifolia* Baill., e *Labordia tinifolia* A. Gray, f–g *Labordia helleri* Sherff.
Selling 1947, Pl. 41, fig. 641–643 *Labordia hedyosmifolia* Baill., 644–645 *Labordia molokaiana*, 646–649 *Labordia waialealae*, 650 *Labordia helleri* Sherff, 651–652 *Labordia tinifolia* A. Gray.

Chromosome numbers (Gadella 1963)

Geniostoma rupestre, Forst. (syn. *G. ligustrifolium*) $2n = 40$

POTALIEAE

Potalia-type

Apertures. — Pollen grains porate. Number of pores fluctuating between 3 and 5. When more than 3 pores are present the grains are usually stephanoporate. Sometimes the pori are not in the same plane. Pores protruding. Distinct annulus and costae present.

Shape. — Equatorial view: grains spheroidal or oblate spheroidal. Polar view: grains circular.

Exine. — Sexine thicker than nexine. Grains with a smooth usually perforated tectum.

Anthocleista amplexicaulis	$34 \times 34.5\ \mu$	OSph or Sph	pollen grains 3-(rarely 4-) porate, pore diam. ca. 5 μ

A. djalonensis	28 × 28 μ	Sph	pollen grains 3–5-porate, pore diam. ca. 4 μ, pores not always in the same plane. Tectum not perforate
A. grandiflora	30 × 35 μ	SO	pollen grains 3–5-porate, pore diam. ca. 5 μ. Perforations in tectum crowded, transition to reticulum
A. liebrechtsiana	43 × 46 μ	OSph	pollen grains 3–4-porate, pore diam. 6–7 μ. Perforations in tectum crowded, transition to reticulum
A. madagascariensis	33 × 35 μ	OSph	pollen grains 3–4-porate, pore diam. 6–7 μ
A. nobilis — Pl. 4: 9–10	33 × 34 μ	OSph or Sph	pollen grains 3–4 (rarely 5-)porate, pore diam. ca 4 μ. Perforations in tectum crowded, transition to reticulum
Fagraea gardenioides ssp. *borneensis*	32 μ (longest axis)		pollen grains 3–4-porate. Tectum not perforate
Potalia amara — Pl. 4: 6–8	39 × 40 μ	OSph or Sph	pollen grains 3-(rarely 4-) porate, pore diam. ca. 4 μ. Tectum not perforate

Potalia and *Anthocleista* and the species *Fagraea gardenioides* ssp. *borneensis* have pollen grains of this type

The Potalia-type shows a superficial resemblance to the Geniostoma type. Both types are porate, have a smooth tectum, and may have different numbers of pores. This similarity, however, is in my opinion only a convergence. In the Potalia-type the grains are spheroidal or oval in shape, in the Geniostoma-type angular.

It is uncertain which type of the Loganiaceae is morphologically closest to the Potalia-type. The exine structure and the pori of the Antonia-type have some similarity. If we consider reduction of colpi as a morphological evolution in Loganiaceae (see *Fagraea*), the Antonia-type with its circular ora (endopori) is probably closest to the Potalia-type.

Pollen grains of *Potalia* and *Anthocleista* are very much alike. The pori in *Potalia amara* are somewhat more protuberant than in the *Anthocleista* species, but this is a gradual difference only. Pollen grains of *Fagraea gardenioides* ssp. *borneensis* cannot be separated from *Anthocleista* pollen. They seem to be a perfect link between the Potalia- and the Fagraea-types.

Taxonomists regard *Potalia* and *Anthocleista* as distinctly related (Solereder 1892; Gandoger 1923; Klett 1924; Leeuwenberg 1961; Leenhouts 1962). They also suggest a close relationship with *Fagraea*. As pollen grains of *Fagraea gardenioides* ssp. *borneensis* belong to the Potalia-type and, on the other hand, are distinctly related to some pollen types in *Fagraea* (F. berteriana-type), this relationship seems justified.

Closer affinity of the Loganiaceae–Potalieae with the Apocynaceae–Tabernaemontanae has been suggested (Leenhouts, 1962); the pollen grains are, however, distinctly different.

Illustrations

Erdtman 1952, fig. 145 A. *Anthocleista parviflora* (*"parvifolia"*) (syn. = *A. nobilis* G. Don; Leeuwenberg, 1961).

Chromosome numbers (Gadella 1961, 1963)

Anthocleista djalonensis Cheval.	$2n = 60$
A. liebrechtsiana Wildem. et Durand	60

Fagraea fragrans-type

Fagraea fragrans subtype

Apertures. — Pollen grains 3-colporate. Colpi narrow, rather short. Ora circular (endopori). Costae present.

Shape. — Equatorial view: grains spheroidal to oblate-spheroidal. Polar view: grains circular.

Exine. — Sexine thicker than nexine. Grains reticulate, slightly striato-reticulate over the entire surface. Lumina small, not exceeding 2 μ in width, muri sharp-edged in the upper part, simplibaculate.

Fagraea fragrans — Pl. 6: 5–6	17.5 × 18 μ	OSph

Fagraea crenulata subtype

Apertures. — Pollen grains 3-colporate, nearly porate. Colpi very short and indistinct. Ora circular (endopori). Costae present.

Shape. — Equatorial view: grains oblate-spheroidal. Polar view: grains circular.

Exine. — Sexine thicker than nexine. Grains slightly striato-reticulate over the entire surface. Lumina angular, muri sharp-edged in the upper part, simplibaculate.

Fagraea crenulata — Pl. 6: 1–3	25 × 27 μ	OSph

Fagraea racemosa subtype

Apertures. — Pollen grains 3-colporate. Colpi narrow, rather short. Ora circular (endopori). Costae present.

Shape. — Equatorial view: grains oblate-spheroidal to spheroidal. Polar view: grains circular.

Exine. — Sexine thicker than nexine. Grains reticulate. In apocolpia the lumina of the reticulum smaller and distinctly striato-reticulate to striate, in mesocolpia distinctly reticulate. Lumina in mesocolpia rather coarse, muri sharp-edged in the upper part.

Fagraea elliptica	22 × 22 μ	Sph	
F. gracilipes — Pl. 6: 7–9	34 × 34 μ	Sph	
F. racemosa	31 × 33 μ	OSph	
F. umbelliflora			pollen grains immature

Fagraea ceilanica-type

Fagraea ceilanica subtype

Apertures. — Pollen grains 3-porate. Pori hidden in one lumen of the reticulum. Due to the thickness of the reticulum the costae of the pori are comparatively indistinct.

Shape. — Equatorial view: grains suboblate to spheroidal. Polar view: grains circular.

Exine. — Sexine much thicker than nexine. Grains coarsely reticulate. Lumina wide, irregular, may be ca. 9 μ across, muri simplibaculate or sometimes duplibaculate. In the lower part the bacules (columellae) are stout and not fused, thus forming a fragmentated reticulum. The upper parts (capita) are dilatated laterally and fused with the adjacent capita. These upper parts form a continuous reticulum. The solid muri of this continuous reticulum become thinner towards the top. At the top the muri are sharp-edged.

Fagraea acuminatissima	51 × 51 μ	Sph	pore diam. 5–6 μ
F. auriculata ssp. *borneensis*	38 × 40 μ	OSph	pore diam. ca. 4 μ
F. blumei var. *blumei*	36 × 38 μ	OSph	pore diam ca. 3 μ
F. ceilanica — Pl. 5: 5–8	52 × 52 μ	Sph	pore diam. 4–5 μ
F. fastigiata	44 × 47 μ	OSph	pore diam. ca. 4 μ
F. involucrata	37 × 41 μ	OSph	pore diam. ca. 4 μ

F. longiflora	34 × 37 μ	OSph	pore diam. ca. 4 μ
F. macroscypha	40 × 42 μ	OSph	pore diam. 2–3 μ, capita slightly rounded at the top
F. resinosa	38 × 43 μ	O or OSph	pore diam. 5–6 μ
F. tacapala var. *gracilis*	34 × 38.5 μ	SO or OSph	pore diam. ca. 5 μ
F. tubulosa	47 × 51 μ	OSph	pore diam. 5–6 μ.
F. woodiana	30.5 × 32.5 μ	OSph	pore diam. ca. 4 μ

Fagraea annulata subtype

Apertures. — Pollen grains 3-porate. Pori circular to oval. Costae pori present. Pori wider than one lumen of the reticulum (ca. 2–5 ×).

Shape. — Equatorial view: grains oblate-spheroidal. Polar view: grains circular.

Exine. — Sexine thicker than nexine. Grains coarsely reticulate. Lumina wide, can be ca. 6 μ across, muri simplibaculate or sometimes duplibaculate, lower part (columallae) slender, upper part more or less rounded.

Fagraea annulata — Pl. 5: 1	48 × 48 μ	Sph	pore diam. ca. 8 μ
F. carstensensis — Pl. 5: 2	41 × 44 μ	OSph	pore diam. 6–8 μ, elliptic
F. eymae — Pl. 6: 4	43 × 46 μ	OSph	pore diam. 5–7 μ

Fagraea berteriana-type

Apertures. — Pollen grains 3-(rarely 4-)porate or colporate. If colporate colpi very short, their ends a little blunt. Ora circular (endopori). Costae present.

Shape. — Equatorial view: grains suboblate to oblate-spheroidal. Polar view: grains circular.

Exine. — Sexine thicker than nexine. Grains finely reticulate. Lumina small (less than 1 μ) and irregular, but all of about the same size, muri simplibaculate, upper part rounded.

Fagraea berteriana	30 × 34 μ	SO or OSph	pore diam. 3–4 μ
F. berteriana (syn. *F. schlechteri*) — Pl. 5: 3–4	28 × 31 μ	SO	pollen grains colporate, colpi short
F. bodenii	39.5 × 42.5 μ	OSph	
F. carnosa	40 × 42 μ	OSph	pore diam. 5–6 μ
F. salticola — Pl. 6: 10–11	37 × 42 μ	OSph	pollen grains colporate, pore diam. 5–6 μ, colpi short

The types and subtypes in the genus *Fagraea* can be distinguished by their exine patterns. All *Fagraea* species except one (*F. gardenioides* ssp. *borneensis*) have a reticulate exine (the reticulum varies in the different types and subtypes). Points of similarity are found in the shape and the apertures. The colporate subtypes have circular ones. The porate ones are probably derived from the colporate subtypes by reduction of the colpi. In favour of this theory is the presence of colporate and porate grains, respectively, in two specimens of *F. berteriana*. Besides, the colpi in the colporate specimen are very short.

The F. fragrans subtype, F. crenulata subtype and F. racemosa subtype are related in their reticulum. In the F. fragrans subtype and F. crenulata subtype a striato-reticulate pattern is present in the apocolpia as well as in the mesocolpia. A distinct striato-reticulate pattern occurs in the F. racemosa subtype in the apocolpia only. The F. crenulata subtype differs from the F. fragrans subtype by very short, indistinct colpi. All subtypes have sharp-edged muri, a character also occurring in the F. ceilanica subtype.

The F. ceilanica subtype and the F. annulata subtype are placed together in one type because both have porate grains and a comparatively coarse reticulum. The typical sharp-edged muri, occurring in the F. ceilanica subtype and also present in the F. fragrans subtype, are, however, missing in the F. annulata subtype, where the muri are rounded in the upper part.

In the F. annulata subtype *F. carstensensis* represents a transition to the F. ceilanica subtype and *F. eymae* a transition to the F. berteriana-type. In *F. carstensensis* the columellae are thicker than in *F. annulata*, but thinner than in the F. ceilanica subtype. *F. eymae* grains have a reticulum with narrower lumina than in *F. annulata* but wider than in the F. berteriana-type.

The F. berteriana-type can be distinguished by its fine reticulum. As in the F. annulata subtype the upper part of the muri is rounded. In one specimen of *F. berteriana* the grains are not porate but colporate. The colpi, however, are very short. In *F. bodenii* sometimes pollen grains with four pores occur.

In pollen morphology there is a close similarity between *F. berteriana* and *F. gardenioides* ssp. *borneensis*. The pollen grains of the latter species are not reticulate, however, and belong to the Potalia-type (see page 485).

It is striking that in *Fagraea* the species show such a large variation in their pollen characters. This is in contrast with the relative uniformness of most genera in the Loganiaceae (another example is *Mitrasacme*).

In comparing the different types and subtypes with each other, it is possible to distinguish several "evolutionary" trends: 1. Reduction of the colpi. 2. Reduction of the lumina of the reticulum. 3. Enlargement of the lumina of the reticulum.

If tricolporate reticulate pollen grains are regarded as more primitive than porate tectate ones, it follows that the F. fragrans subtype is the most primitive one in *Fagraea*. This is in accordance with the taxonimic results of Leenhouts (1962). With this subtype as starting point it is possible to draft the following morphological series:

A. *F. fragrans*→*F. crenulata* { *F. ceilanica* / *F. annulata* }	Reduction of the colpi and enlarging of the lumina
B. *F. fragrans*→*F. berteriana*→*F. gardenioides*	Reduction of the colpi and lumina
C. *F. fragrans*→*F. racemosa*	Reduction of the lumina

Most *Fagraea* types are completely different from other Loganiaceous types with regard to exine structures. Shape and apertures are similar in the Potalia-type and Antonia-type and to those occurring in the porate pollen types of *Fagraea*.

Pollen grains in the Apocynaceae-Tabernaemontanae (*Tabernaemontana*, *Voacanga*, and *Hazunta*) are different from those in the Potalieae. This result does not support the suggestion that the Potalieae may be taxonomically related to that tribe of the Apocynaceae. On the other hand, some genera in the Oleaceae (viz. *Forestiera*, *Forsythia*, *Schrebera*, and some other genera) have an exine structure very similar to that met within the F. ceilanica-type. The apertures in the Oleaceous genera are, however, quite different.

Professor Rowley of the Department of Botany, University of Massachusetts, Amherst, kindly made some electron micrographs of *Fagraea blumei* and *Fagraea ceilanica*. Both species seemed to be identical in their morphological characters when examined with an ordinary light microscope. The replicas distinctly show that the muri of the reticula are different. Both species show a sharp-edged upper part of the muri, but the muri sides in *F. ceilanica* are smooth whereas those in *F. blumei* have small excrescences. Perhaps this character will prove to be of value in a further subdivision of the F. ceilanica type, but the making of replicas required much material and is very time-consuming. For these reasons a further investigation of the *Fagraea* species with the aid of an electron-microscope was not possible.

Illustrations

Wang 1960, pag. 117, tab. LXII, *Fagraea chinensis* (syn. *F. ceilanica* Thunb., Leenhouts, 1962).

Chromosome numbers (Gadella 1963, Mohrbutter 1963)

Fagraea ceilanica Thunb.	$2n = 66$
F. fragrans Roxb.	12
F. littoralis (= *F. ceilanica* Thunb.)	12

PLOCOSPERMA (Gen. inc. sed.)

PLOCOSPERMA-TYPE

Apertures. — Pollen grains 3-colporate. Colpi long.
Shape. — Equatorial view: grains probably subprolate or prolate; polar axis longer than equatorial axis. Polar view: grains circular.
Exine. — Sexine much thicker than nexine. Pollen grains reticulate. Lumina small, ca. 1 μ, simplibaculate, bacules high.

Plocosperma microphyllum: pollen grains immature

Morphologically the pollen grains of *Plocosperma* do not seem related to any pollen type in the Loganiaceae. The apertures differ greatly and the exine structure only shows similarity to that of the grains in the Gelsemium- and Retzia-types. These types, however, differ in too many other characters to suppose a pollen morphological relationship.

Key to pollen types

1	a	Pollen grains reticulate, striate or striato-reticulate	2
	b	Pollen grains smooth	15
2	a	Pollen grains porate or colpate	3
	b	Pollen grains colporate	7
3	a	Reticulum coarse (lumina >3 μ)	4
	b	Reticulum fine (lumina <3 μ)	6
4	a	Pollen grains angular in polar view; usually more than three pores	Darbolia subtype
	b	Pollen grains circular in polar view, triporate	5

5 a Upper part of muri sharp-edged . Fagraea ceilanica subtype
b Upper part of muri rounded . . Fagraea annulata subtype
6 a Pollen grains goniotreme with
apertures at the angles . . . . Mitrasacme elata-type
b Pollen grains circular in polar view Fagraea berteriana-type
7 a Colpi very short 8
b Length of colpi at least 3 × diameter of ora 9
8 a Reticulum fine (lumina $<2\ \mu$)
Upper part of muri rounded . . . Fagraea berteriana-type
b Reticulum coarse (lumina $\geq 2\ \mu$) .
Upper part of muri sharp-edged . . Fagraea crenulata subtype
9 a Apocolpia striate. Mesocolpia
reticulate . . . . Fagraea racemosa subtype
b Pollen grains not striate or if striate,
striation not in apocolpia only 10
10 a Colpus membrane densely granulate.
Ora indistinct . . . . Retzia-type
b Colpus membrane not granulate or
rarely with a few scattered granules (Gelsemium-type) . . 11
11 a Pollen grains with indistinct ora 12
b Pollen grains with distinct ora 13
12 a Pollen grains goniotreme with
apertures at the angles in polar view.
Ora lolongate . . . . Mitrasacme elata-type
b Pollen grains circular in polar view.
Ora lalongate . . . . Chilianthus subtype
13 a Ora circular. Grains small,
striato-reticulate . . . . Fagraea fragrans subtype
b Ora slightly lalongate 14
14 a Pollen grains finely reticulate
(lumina $<1\ \mu$) . . . . Mitrasacme pygmaea-type
b Pollen grains striate or striato-reticulate.
Longest axis $>25\ \mu$ . . . . Gelsemium-type
15 a Pollen grains porate 16
b Pollen grains colporate or colpate 17
16 a Pollen grains angular in polar view . . Geniostoma subtype
b Pollen grains circular in polar view.
Pores protruding . . . . Potalia-type
17 a Pollen grains colpate or, if colporate,
ora lolongate . . . . Spigelia-type

b Pollen grains colporate. Ora circular or lalongate 18
18 a Pollen grains angular in polar view . . . . . Logania-type
b Pollen grains circular in polar view 19
19 a Ora distinct, circular or slightly lolongate . . . Antonia-type
b Ora indistinct, circular or lalongate 20
20 a Ora circular . . . . Mitrasacme indica-type
b Ora lalongate 21
21 a Pollen grains small (longest axis not exceeding 25 μ) 3- or 4- colporate. Bacula short, sometimes indistinct. . . . . Buddleia subtype
b Pollen grains larger, 4-colporate. Bacula distinct . . . . Emorya-type

Table 1. Specimens investigated

Ma = Macromethod. Mi = Micromethod. NPC = number, position, character of apertures

Name		Method	NPC
Antonieae			
Antonia ovata Pohl	B. W. 4355; U	Ma	345
Bonyunia antoniifolia Progel	Ducke 12197; U	Mi	345
B. aquatica Ducke	Ducke 354; A	Mi	345
B. minor N. E. Brown	Lasser 1472; VEN	Mi	345
B. superba R. Schomb.	Schomburgk 614; P	Mi	345
Norrisia maior Soler.	Herb. Sandakan 25274; L	Mi	345
N. malaccensis Gardner	Griffith 3731; S	Ma	345
Usteria guineensis Willd.	Voorhoeve 106; WAG	Mi	345
Buddleieae			
Adenoplea sinuata Radlk.	D'Alleizette s.n.; L	Mi	345
	Afzelius s.n.; SPL	Ma	345
Adenoplusia axillaris Radlk.	Hildebrandt 3671; SPL	Ma	345
A. uluguruensis Melch.	Schlieben 2756 (isotype); P	Mi	345
Androya decaryi Perrier	Serv. Forest. 8488; P	Mi	343/345
Buddleia alpina Oerst.	P. H. Allen 3458; U	Ma	345/445
B. americana Linn.	Rutten & Rutten-Pekelharing 134; U	Ma	345/445
B. coriacea Remy	Brooke 6382; U	Ma	345
B. corrugata (Benth.) Phill.	Drège s.n. (3618?), anno 1837; S	Ma	345
B. dysophylla (Benth.) Radlk.	Verdcourt s.n., anno 1954; K (SPL)	Ma	345

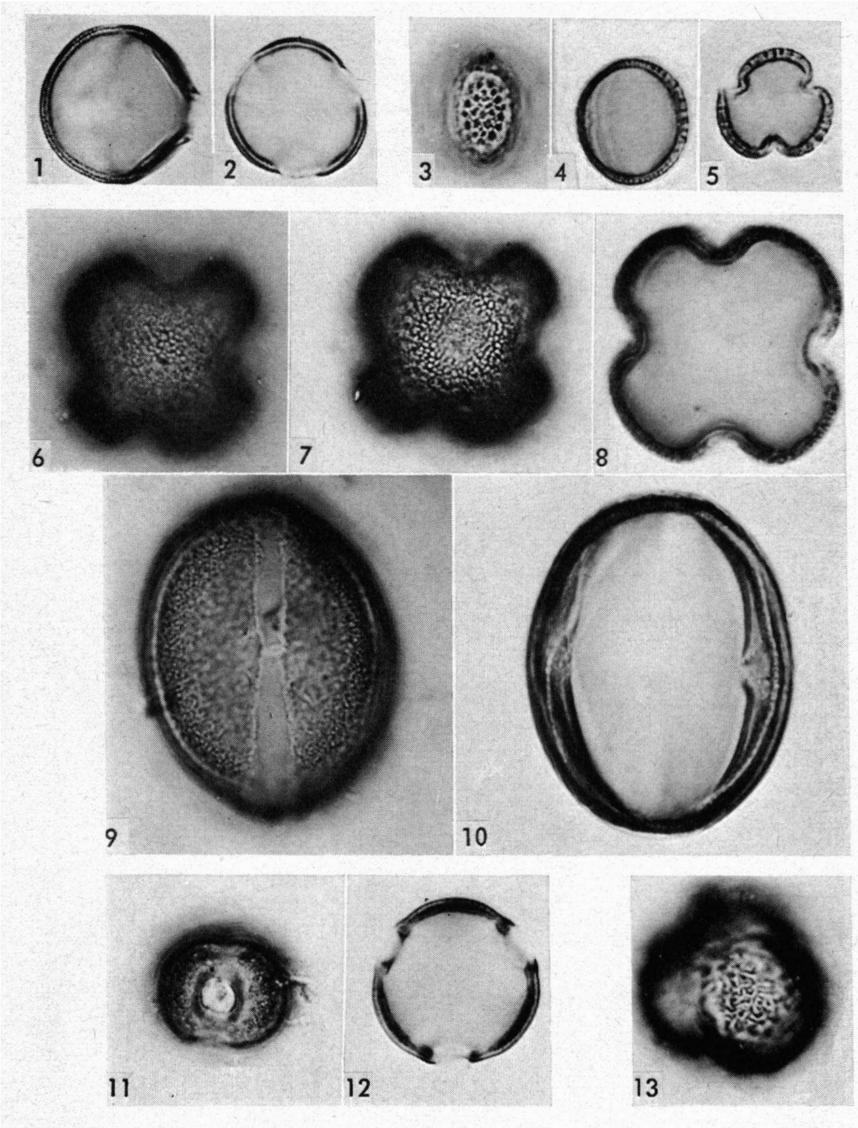
Name		Method	NPC
B. elegans Cham. et Schlecht.	Hatschbach 8298; U	Ma	345
B. glomerata Wendl. f.	Coll. ?, S. Africa, anno 1824; S	Ma	345
B. indica Lam.	Leeuwenberg 3511; WAG	Mi	345
B. madagascariensis Lam.	De Cary 10061; L	Mi	345
B. marubiifolia Benth.	Hinckley 3098; U	Ma	345
B. saligna Willd.	Scott Elliot 356; U	Mi	345
B. salviifolia (Linn.) Lam.	Stolz 2068; U	Mi	345
B. stachyoides Cham. et Schlecht.	R. Klein 560; U	Ma	345
Emorya suaveolens Torrey	Purpus 4748; BM	Mi	345/445
Gomphostigma virgatum (Linn.) Kuntze	Pont 1718; U	Ma	345
—	Norlindh & Weimarck 4499; LD	Mi	345
Nuxia capitata Baker	Bahon 3650 (isotype); P	Mi	345
N. congesta R. Brown ex Fresen	Breteler 2573; WAG	Ma	345
N. floribunda Benth. [syn. *N. polyantha*]	Stolz 2068; U	Ma	345
N. keniensis T. C. E. Fries [syn. *N. congesta*]	Fries & Fries 777 (type); UPS	Ma	345
N. oppositifolia (Hochst.) Benth. [syn. *N. antunessii*]	Baum 29 (type); S	Ma	345
N. verticillata Lam.	Johnston s.n., anno 1889; U	Mi	345
Peltanthera floribunda Benth.	A. E. Lawrence 432; A	Mi	345
Sanango durum Bunting et Duke	Wurdack 2018; US	Mi	345
Spigelieae (p.p.)			
Desfontainia spinosa Ruiz et Pavon	Leeuwenberg 3507; WAG	Mi	345 [344]
Mitrasacme elata R. Brown	Brass 27227; L	Mi	343
Polypremum procumbens Linn.	Kramer & Hekking 2547; U	Mi	345 [343]
Spigelia anthelmia Linn.	Jonker-Verhoef & Jonker 17; U	Mi	343
S. leiocarpa Benth.	Y. Mexia 6290; U	Mi	343
S. martiana Cham.	Hatschbach 8458; U	Mi	343
Strychneae, Loganieae (p.p.), Mitrasacme (p.p.)			
Cynoctonum mitreola (Linn.) Britt.	Smitinand 3565; L	Mi	345
Mitreola (= *Cynoctonum*) *petiolata* Torrey	E. Wall/Fischer s.n., anno 1933; S	Ma	345

Name		Method	NPC
Cynoclonum sessilifolia J. F. Gmelin	Vesterland s.n., anno 1889; S	Ma	345
C. sphaerocarpum Leenh.	J. & M. S. Clemens 29649 (type); L	Mi	345
Gardneria multiflora Makino	Ren Chang Ching 2955; S	Ma	345
G. nutans Sieb. et Zucc.	Coll. ? 459; L	Ma	345
G. ovata Wall.	Hohenacker 1445; U	Ma	345
Logania angustifolia R. Brown	Watson 23; U	Ma	345
L. floribunda R. Brown	Constable 7242; U	Ma	345
L. hyssopoides Nees	Mueller s.n.; U	Mi	345
L. linifolia Schlecht.	Kaspiew 6; U	Ma	345
L. longifolia R. Brown	Coll. ? S. Austr.; U	Ma	345
L. ovata R. Brown	Cunningham 252; U	Ma	345
Mitrasacme erophila Leenh.	Hook. f. & Thomson s.n., Mt. Khasia; L	Mi	345
M. indica Wight	Hook. f. & Thomson s.n., Malabar; L	Mi	345
M. neglecta Leenh.	Coert 917; L	Mi	345
M. polymorpha R. Brown	Constable 6239; U	Mi	345
M. pygmaea R. Brown var. *malaccensis* (Wight) Hara	Bünnemeyer 5770; U	Mi	345
Neuburgia celebica (Koord.) Leenh.	Kjellberg 2025; SPL	Ma	345
Couthovia (= *Neuburgia*) *collina* A. C. Smith	A. C. Smith 6157; S	Ma	345
Neuburgia corynocarpa (A. Gray) Leenh.	A. C. Smith 6330; S	Ma	345
Couthovia (= *Neuburgia*) *novo-caledonica* Gilg et Bened.	Däniker 1068; SPL	Ma	345
Neuburgia tubiflora Blume	Aet 143 (type); L	Mi	345
Strychnos angolensis Gilg	Welwitsch 4776 (type); LISU	Ma	345
S. chrysophylla Gilg	Le Testu 9377; P	Ma	345
S. mellodora S. Moore	Hack 4; FHO	Ma	345
S. nux-vomica Linn.	Cult. Hort. Bog. I. C. 6; U	Mi	345
S. parviflora Spruce ex Benth.	Ducke 1110; IAN	Ma	345
S. variabilis De Wildeman	A. Carlier 57; BR	Ma	345
Gelsemieae			
Gelsemium elegans (Gardn. et Champ.) Benth.	Balansa 1041; L	Ma	345
G. rankinii Small	Godfrey 56366; GB	Mi	345
Mostuea batesii Baker	Breteler 2750; WAG	Mi	345

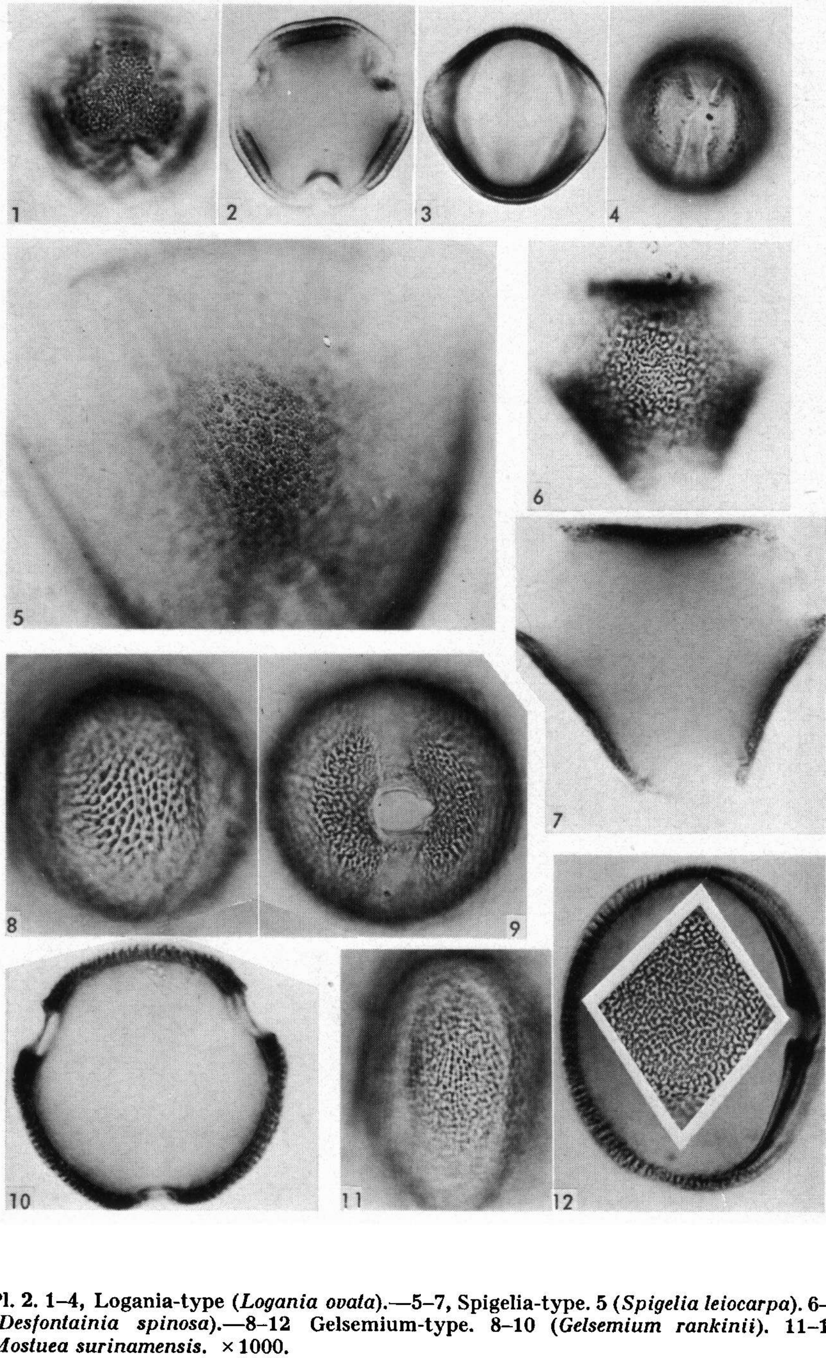
Name		Method	NPC
M. brunonis Dider.	Breteler 2331; WAG	Mi	245/345
M. hirsuta (T. Anders. ex Benth. et Hook.) Baill. ex Baker	Thomas 265; K (SPL)	Ma	345
M. surinamensis Benth.	Versteeg 878; U	Mi	345
Retzieae			
Retzia capensis Thunb.	Bos 674; WAG	Mi	345
Loganieae (p.p.)			
Geniostoma balseanum Baill.	Mackee 5429; L	Mi	344
G. pancheri Baill.	Däniker 3094; SPL	Ma	344/444–744
G. rupestre Forster (syn. *G. australianum*)	Mueller s.n. (Rockhampton Bay); U	Ma	344/544–744
G. rupestre Forster (syn. *G. ligustrifolium*)	H. Powell s.n., 2.IX.1947; U	Ma	344
Labordia hedyosmifolia Baill.	Selling s.n., Hawaii, 10.IX.1938; SPL	Ma	444/544
L. hypoleuca Degener	Degener 10,000; SPL	Ma	444/544
L. helleri Sherff	A. A. Heller 2579; BISH	Ma	344/444–644
L. tinifolia A. Gray var. *tenuifolia* Degener et Sherff ex Sherff	Degener 10272; SPL	Ma	344/444
Potalieae			
Anthocleista amplexicaulis Cheval.	Serv. Forest. 7388; P	Ma	344/444
A. djalonensis Cheval.	Leeuwenberg 3316; WAG	Mi	344/444–544
A. grandiflora Gilg	Stolz 497; S	Ma	344/444–544
A. liebrechtsiana De Wildeman et Dur.	Breteler 2806; WAG	Mi	344/444
A. madagascariensis Baker	Humbert 23018; P	Ma	344/444
A. nobilis G. Don	Leeuwenberg 2322; WAG	Mi	344/444
Fagraea acuminatissima Merr.	Jacobs 5633; L	Mi	344
F. annulata Hiern	Versteeg 1237 (type); U	Mi	344
F. auriculata Jack ssp. *borneensis* (Sheff.) Leenh.	Cult. Hort. Bog.; U	Mi	345
F. berteriana A. Gray ex Benth.	Brass 28140; L	Ma	344
F. berteriana A. Gray ex Benth. (syn. *F. Schlechteri*)	Däniker 648; SPL	Ma	345
F. blumei G. Don	Koorders 4321b; S	Ma	344
F. bodenii Wernh.	Pulle 894; U	Mi	345
F. carnosa Jack	Cult. Hort. Bog. X.G. 24; L	Mi	344

Name		Method	NPC
F. carstensensis Wernh.	P. v. Royen & Sleumer 7755; L	Mi	344
F. ceilanica Thunb.	Hulstijn 363; L	Mi	344
F. crenulata Clark	Hort. Bot. Singapore 1904; L	Mi	345
F. elliptica Roxb.	Hort. Bog. 592; L	Ma	345
F. eymae Backer	Eyma 4330 bis (type); L	Ma	344
F. fastigiata Blume	Coll. ? Herb. No 908.127–108; L	Ma	344
F. fragrans Roxb.	Kostermans 8955; L	Ma	345
F. gardenioides Ridl. ssp. *borneensis* Leenh.	Sarawak Museum 2508 (type); L	Mi	344
F. gracilipes A. Gray	Robins 570; L	Mi	345
F. involucrata Merr.	Sandakan Herb. 16380; L	Ma	344
F. aff. *longiflora* Merr.	Elmer 9159; L	Ma	344
F. macroscypha Baker	?; L	Ma	344
F. racemosa Jack ex Wall.	Santos 4256; L	Ma	345
F. resinosa Leenh.	Hallier 3162 (type); L	Ma	344
F. salticola Leenh.	Hoogland & Schodde 7425; L	Mi	344
F. tacapala Leenh. ssp. *gracilis* Leenh.	Kjellberg 1521a (type); S	Ma	344
F. tubulosa Blume	Coll. ? (type); L	Mi	344
F. umbelliflora Gilg et Bened.	Ledermann 9614 (type); L	Mi	345
F. woodiana F. v. Muell.	J. J. F. E. de Wilde 1202; L	Mi	344
Potalia amara Aubl.	Versteeg 323; U	Mi	344/444
Plocosperma (gen. inc.sed.)			
Plocosperma microphyllum Baill. ex Soler.	Galeotti (type); P [SPL]	Ma	343

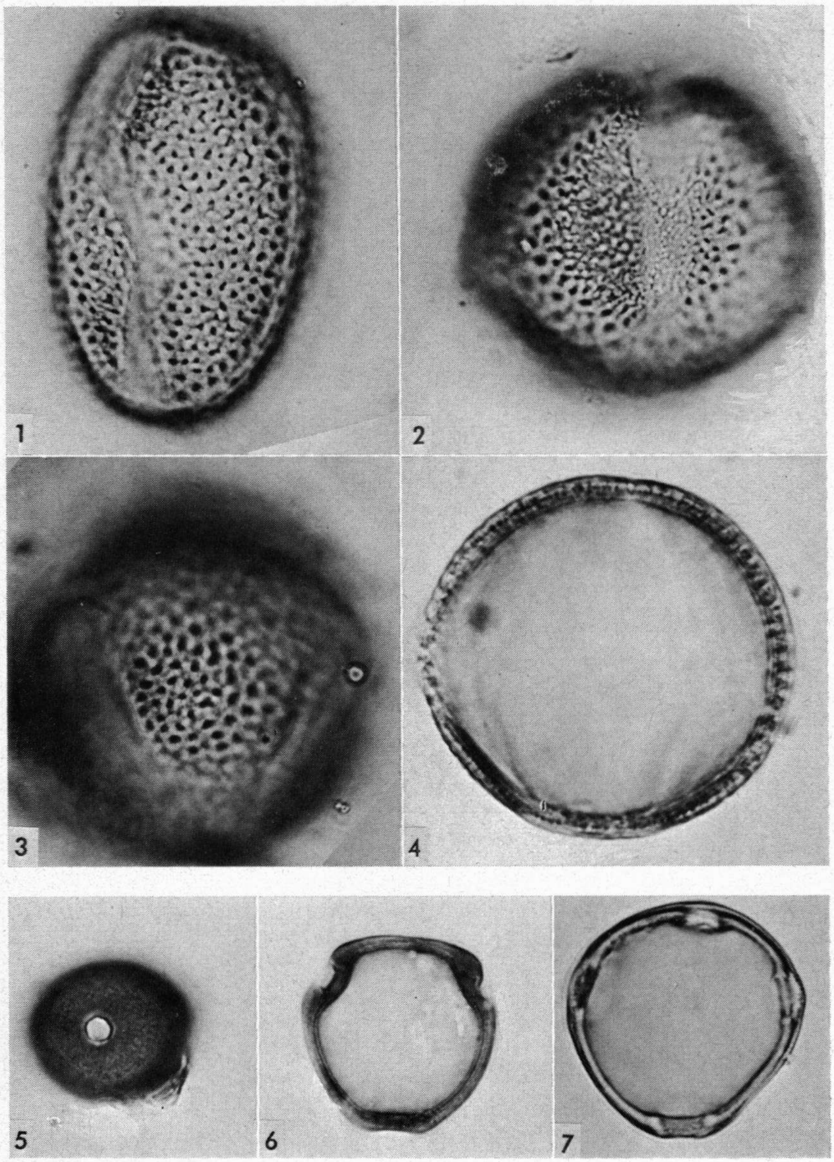
Botanisch Museum en Herbarium, Utrecht, Netherlands.



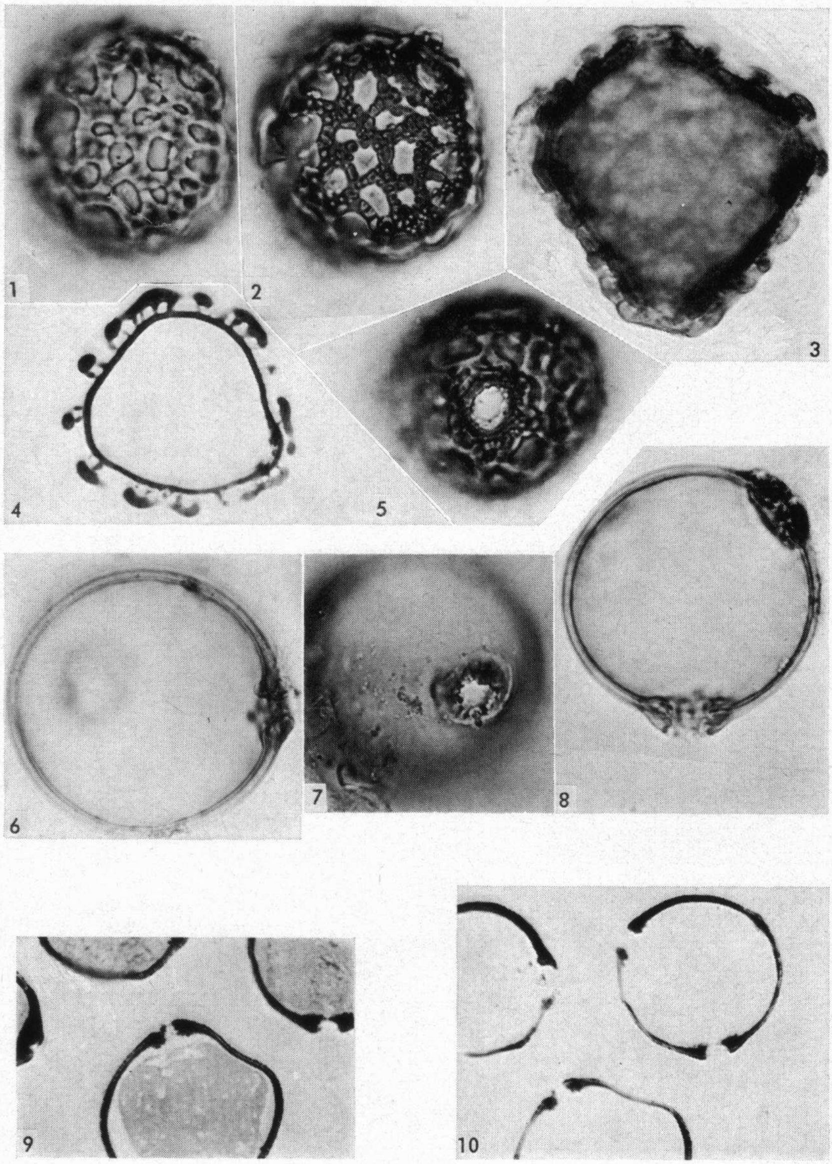
Pl. 1. 1–2, Buddleia-type, Buddleia subtype (*Buddleia indica*).—3–5, Buddleia-type, Chilianthus subtype (*Buddleia saligna*).—6–10, Emorya-type (*Emorya suaveolens*).—11–13, Antonia-type. 11–12 (*Antonia ovata*). 13 (*Bonyunia aquatica*). ×1200.



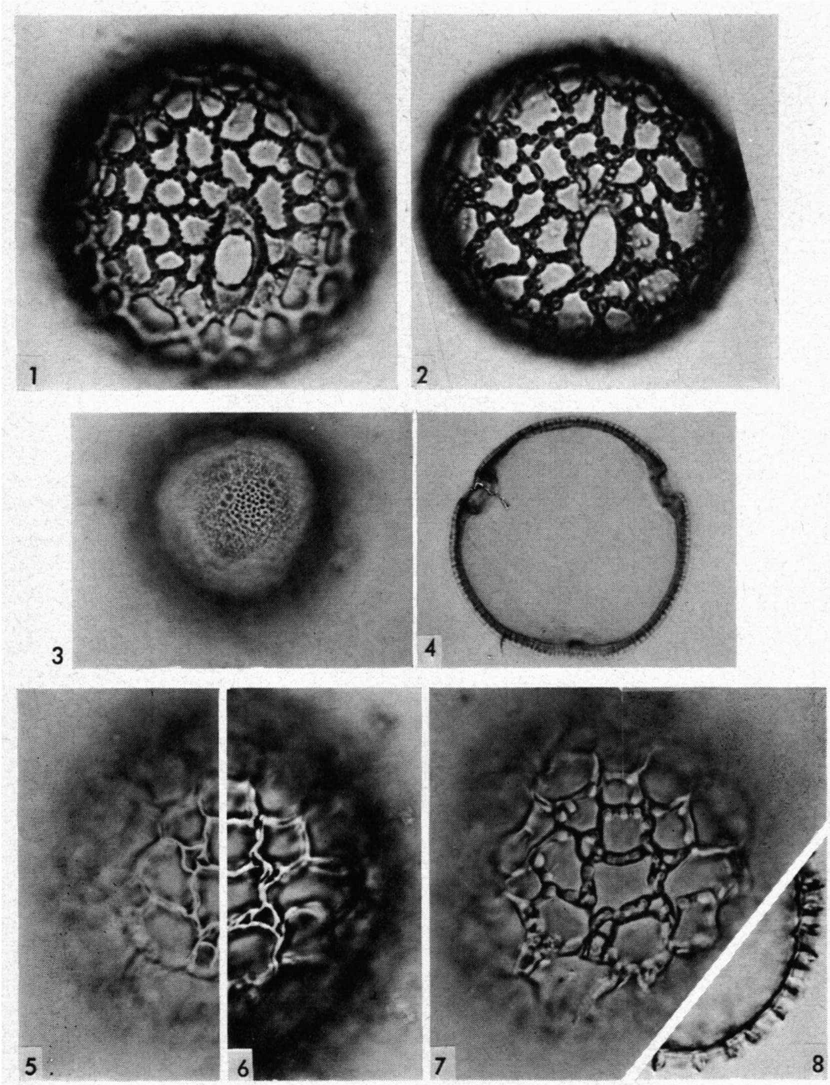
Pl. 2. 1–4, Logania-type (*Logania ovata*).—5–7, Spigelia-type. 5 (*Spigelia leiocarpa*). 6–7 (*Desfontainia spinosa*).—8–12 Gelsemium-type. 8–10 (*Gelsemium rankinii*). 11–12 *Mostuea surinamensis*. ×1000.



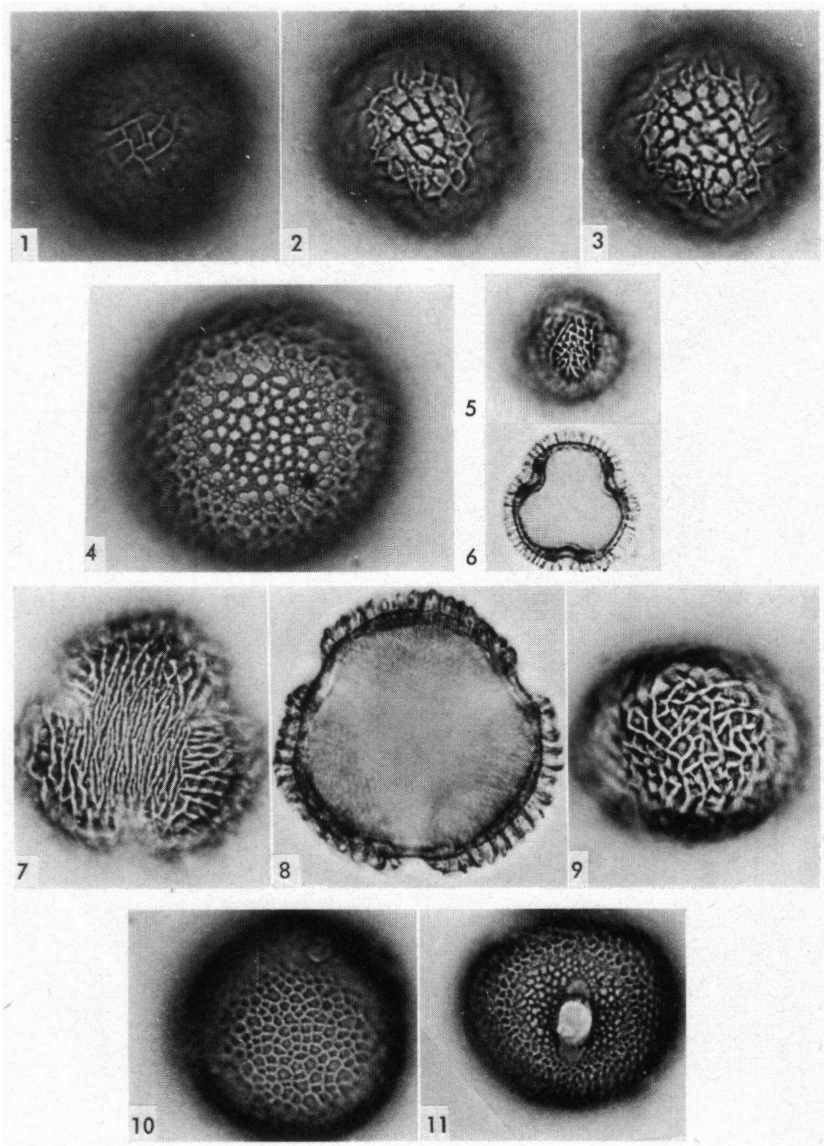
Pl. 3. 1–4, Retzia-type (*Retzia capensis*).—5–7, Geniostoma-type, Geniostoma subtype (*Geniostoma rupestre*). ×1200.



Pl. 4. 1–5, Geniostoma-type, Darbolia subtype (*Labordia tinifolia*).—6–10, Potalia-type. 6–8 (*Potalia amara*), 9–10 (*Anthocleista nobilis*), section about 0.5 μ thick. $\times 1000$.

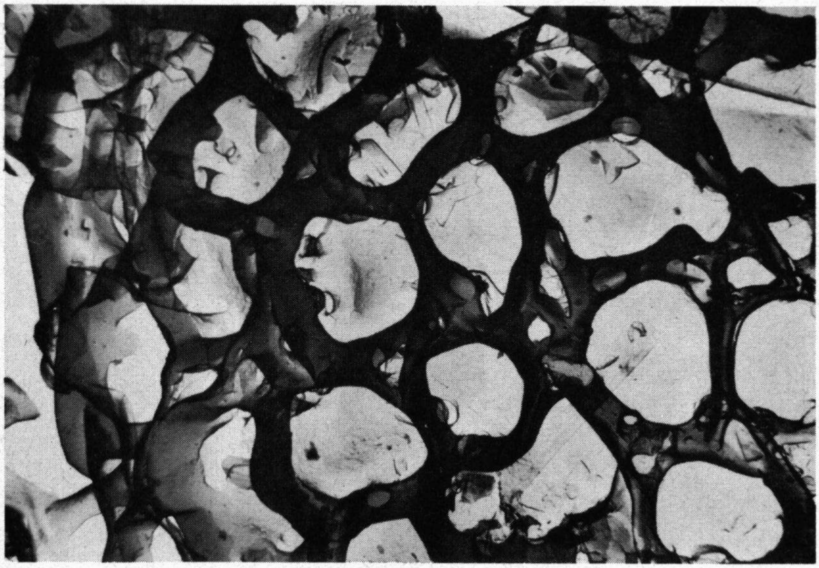


Pl. 5. 1–2, Fagraea ceilanica-type, Fagraea annulata subtype. 1, (*F. annulata*). 2, (*F. carstensensis*).—3, Fagraea berteriana-type (*F. berteriana*).—5–8, Fagraea ceilanica-type, Fagraea ceilanica subtype (*F. ceilanica*). ×1100.



Pl. 6. 1–3, Fagraea fragrans-type, Fagraea crenulata subtype (*F. crenulata*).—4, Fagraea ceilanica-type, Fagraea annulata subtype (*F. eymae*).—5–6, Fagraea fragrans-type, Fagraea fragrans subtype (*F. fragrans*).—7–9, Fagraea fragrans-type, Fagraea racemosa subtype (*F. gracilipes*).—10–11, Fagraea berteriana-type (*F. salticola*). ×1100.

1



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Pl. 7. Replicas. 1 (*Fagraea ceilanica*). ×2800.—2 (*Fagraea blumei*). ×5200.

A Systematic Commentary

(P. W. Leenhouts)

Dr. Punt intentionally chose for his systematic-palynological study a family on which in recent years much systematic work has been done or is still in progress. First of all this makes it possible to compare palynological results with the sytematics as based upon the data derived from other disciplines, mainly gross morphology, and to have this done by a systematist specialized in that family. Furthermore, this had three more advantages for him: 1) he could be guided in selecting the taxa which deserved to be studied in the first place, 2) revised material was available, and 3) he could discuss his results with specialized taxonomists.

Before discussing the different palynological types in more detail, we may compare a scheme of their relationships as they are given in the preceding paper (Scheme I) with a scheme of the supposed relationships of the tribes based upon gross morphology (Scheme III). To facilitate the comparison, in Scheme II the first scheme has been "translated" into tribes.

Scheme I. Relationships of palynological types.

```
Mitrasacme elata — Spigelia ⎫
                            ⎬ Logania
                Geniostoma  ⎭    |
                    ______________|
                   |                   ⎧ Mitrasacme pygmaea
Fagraea — Potalia — Antonia — Gelsemium ⎨
                                        ⎩ Retzia
                                            |
                                          Buddleia — Emorya
```

Scheme II. Relationships of tribes based upon palynology.

```
                  ⎧ Spigelieae
            ______⎨ Loganieae
           |      ⎩ Strychneae
           |
Potalieae — Antonieae — Gelsemieae — Retzieae — Buddleieae
```

Scheme III. Relationships of tribes based upon gross morphology.

(Scrophulariaceae)
|
Buddleieae
|
|—— Retzieae — (Solanaceae)
|
Antonieae — Potalieae — (Apocynaceae)
|
Gelsemieae — ? — (Oleaceae)
|
Strychneae — Loganieae — Spigelieae — (Rubiaceae)

When comparing the scheme of the relationships of the tribes as based upon gross morphology (Scheme III) with that based upon palynology (Scheme II) the overall similarity is striking. In both the basic group comprises the Antonieae and the Gelsemieae, the Potalieae are connected with the Antonieae, the series Strychneae—Loganieae—Spigelieae is connected more on the side of the Gelsemieae. The Retzieae connect in both schemes the Buddleieae more or less with the further Loganiaceae, though in Scheme II the Retzieae are placed more towards the Gelsemieae, in Scheme III more towards the Antonieae.

ANTONIA-TYPE

The mutual connexion of the four genera included in the tribe Antonieae—viz. *Bonyunia*, *Antonia*, *Norrisia*, and *Usteria*—is confirmed by palynological evidence. Whereas palynologically *Bonyunia* is slightly different, *Usteria* is gross morphologically more isolated, showing several specializations in the flower. The resemblance of this pollentype with several other types of the Loganiaceae is well in accordance with the central position of this tribe in the family.

BUDDLEIA-TYPE

The Buddleia-type of pollen characterizes the Buddleieae apart from the genus *Emorya*. This is the first point of systematic interest, a discussion of which will be given, however, under the Emorya-type. The second point which deserves more attention is the position of the Buddleieae in relationship to the Loganiaceae proper on the one side, to the Scrophulariaceae on the other. I have discussed this position at some length some years ago (Leenhouts 1962). The conclusion was that morphologically as well as anatomically the Buddleieae clearly take a position between Loganiaceae and Scrophulariaceae. However, the delimitation against the Loganiaceae is more vague, its inclusion in that family seems more natural, than is the case in relation to the Scrophulariaceae. The genus *Peltanthera*, on the one end, shows distinct relationships with the Antonieae, *Buddleia* on the other side comes nearest to the Scrophulariaceae. For the systematist it is disappointing that palynology—like phytochemistry—clearly reveals a close relationship to the Scrophulariaceae and hardly any to the Loganiaceae. See, however, also under the Retzia-type.

The two subtypes are systematically unimportant.

Emorya-type

As alluded to already under the Buddleia-type, the fact that the genus *Emorya* is apparently characterized among all Buddleieae by a different—though related—pollentype is interesting. *Emorya* is a monotypic genus from southwestern North America. It is at least closely related to *Buddleia*, should possibly even be included in that genus judging from gross morphology. There is one palynological fact that may point in the same direction, however. Out of the several *Buddleia* species, studied by Punt—about half of which American—two (*B. alpina* and *B. americana*), both American species, show sometimes, resp. usually 4-colporate pollen, thus partly breaking down the differences between the two types. It is possible that if more American species of *Buddleia* would be studied palynologically, more of these cases could be found, and hence the demarcation between these two types would turn out to be less sharp.

Spigelia-type

This type characterizes two out of four genera of the Spigelieae, viz. *Spigelia* and *Polypremum*, and the genus *Desfontainia* of uncertain position. According to Punt it is nearest related to the Logania type—to which among others belong *Cynoctonum* and part of *Mitrasacme*, the two other genera of the Spigelieae—and to the Mitrasacme elata type to which belongs another part of *Mitrasacme*. Palynological evidence hence distinctly supports the relationship between the Spigelieae and the Loganieae suggested in the third scheme though in detail there is a discrepancy between systematics and palynology.

Contrary to the great morphological resemblance between the

Spigelieae and the Rubiaceae-Hedyotideae, the pollen of these two tribes are completely different.

Palynological evidence now strengthens the argumentation for the inclusion of *Polypremum* in the Spigelieae instead of in the Buddleieae, as was usually done. Likewise, palynological evidence is in favour of the inclusion of *Desfontainia* in the Loganiaceae—though inclusion in the Spigelieae seems out of question.

MITRASACME-TYPES

From a palynological point of view, *Mitrasacme* is doubtless one of the most interesting genera among the Loganiaceae. Though only six out of a total of about 40 species have been studied, these represent already four distinct types. They are the M. elata-type (distinctly related to the Spigelia-type), the Logania-type, the M. indica type (close to the Logania-type), and the M. pygmaea-type (related to the Gelsemium-type). There is no doubt that *Mitrasacme* has to be included in the Spigelieae and that it represents an entity taxonomically. As the genus is in urgent need of revision, hardly anything can further be said. Only can be suggested that *M. elata* may belong to another subgenus or section than the other species studied.

LOGANIA-TYPE

The genera showing this type belong to three different, though doubtless mutually related, tribes: the Strychneae (complete), the Loganieae (*Logania*), and the Spigelieae (*Cynoctonum* and at least one species of *Mitrasacme*). The palynological resemblance with the Mitrasacme indica-type, the Spigelia-type, and the Geniostoma-type also reflect the closer connexion between these three tribes. Especially in this part of the family the palynological demarcations do not coincide with those based upon gross morphology.

GELSEMIUM-TYPE

Well in accordance with the conclusions derived from gross morphology, *Gelsemium* and *Mostuea* are also palynologically distincly closely related. The resemblance with the Antonia- and Logania-types is also in accordance with the supposed systematic relationships.

RETZIA-TYPE

This type characterizes the monotypic tribe Retzieae. The position of the genus *Retzia* has been uncertain for a long time. Recently, Leeuwenberg (1964) included it in the Loganiaceae as a tribe of its own, related to both the Antonieae and the Buddleieae. It is very satisfying that palynological evidence favours its inclusion in the Loganiaceae, and even to some degree its exact place in this family. For the Retzia-type comes nearest to the Gelsemium-type—the Gelsemieae being distinctly related to the Antonieae—, the Buddleia type following at the second place. Moreover, this strengthens the position of the Buddleieae within the Loganiaceae. On the other hand, the differences in pollen between *Retzia*, resp. *Metternichia* and *Sessea* are in contrast to a relationship with the Solanaceae as also often suggested.

GENIOSTOMA-TYPE

This type characterizes two out of the three genera of the Loganiaceae, *Logania*—which shows a certain similarity palynologically—being included under the Logania-type. These two genera are systematically intimately related; actually *Labordia* is hardly more than an isolated, in some characters more specialized offshoot of *Geniostoma*. The two subtypes are apparently hardly of any systematical importance.

POTALIA-TYPE

The Potalia-type and the Fagraea-types cover the genera *Fagraea*, *Potalia* and *Anthocleista* which together make up the tribe Potalieae. The Potalia-type is via *Fagraea gardenioides* and *F. berteriana* connected with the Fagraea berteriana-type which is the highest evolved one among the Fagraea-types. This position of the Potalia-type is in good accordance with the systematic affinities as *Fagraea* includes the doubtless most primitive members of the Potalieae, while *Potalia* and *Anthocleista* are clearly more specialized genera, especially as regards their flower characters.

The striking resemblance between Loganiaceae-Potalieae and Apocynaceae-Tabernaemontanae is not supported by palynology.

FAGRAEA-TYPES

Palynologically, *Mitrasacme* and *Fagraea* appear to be the most interesting genera of the Loganiaceae. Whereas *Mitrasacme* is systematically as well as palynologically too insufficiently known to draw any conclusions, our knowledge of the genus *Fagraea* seems to justify a closer consideration. Twenty-five out of thirty-one species have been studied palynologically, and a recent taxonomical revision is available (Leenhouts 1962).

Parallel with the grouping into palynological types and subtypes and the "evolutionary trends" given by Punt in the main part of this paper, a grouping of the species on morphological grounds and some more "evolutionary trends" derived from gross morphology may precede a closer study of the systematic relationships.

The species of *Fagraea* can be grouped as follows:

elliptica, fragrans and probably *umbelliflora,* together making up the section Cyrtophyllum; possibly, there is some relationship between *umbelliflora* and *gracilipes;*

racemosa, the only species of the section Racemosae;

ceilanica, annulata (which shows also relationship to the berteriana-group), *acuminatissima, tubulosa, ridleyi, blumei, fastigiata,* possibly *crenulata, truncata, tacapala, woodiana, longiflora,* and *carstensensis;* *auriculata, involucrata, macroscypha,* and *resinosa;* this group is doubtless related to the previous one;

carnosa;

gardenioides, curtisii, and *calcarea;* this group is possibly related with the berteriana-group;

gracilipes (relationships possibly with *umbelliflora* and *berteriana*);

eymae, salticola, bodenii, gitingensis, and *berteriana;* relationships possibly with *annulata,* the gardenioides-group, and *gracilipes.*

The "evolutionary trends" underlying the assumptions on primitive or advanced are:

1. tree → shrub or epiphyte; 2. leafbase without auricles → with auricles (wings are possibly a transitional stage phylogenetically); 3. inflorescences many-flowered → few-flowered → flowers solitary; 4. inflorescences dichasial → umbellate or glomerulous; 5. inflorescences dichasial → thyrsoid → racemose → spicate; 6. pedicels with one pair of bracteoles → without bracteoles; 7. pedicels with one pair of bracteoles → with two pairs of bracteoles; 8. bracteoles rather small and inserted halfway the pedicel → big, forming a kind

of involucre around the calyx. Other probable trends are: 9. inflorescences terminal → axillary; 10. stamens inserted directly on the corolla → inserted on a thickened ring; 11. anthers about oblong → linear; 12. stigma undivided → bilobed.

Now we may have a closer look at the different groups of species in the light of the "phylogenetical" series mentioned above and of palynological evidence.

Sect. Cyrtophyllum represents doubtless the most primitive group in *Fagraea*. *F. elliptica* is primitive according to 11 of the criteria mentioned above, only the bracteoles being occasionally absent. *F. fragrans* seems to be slightly more advanced (inflorescences axillary, sometimes few-flowered, bracteoles sometimes absent). *F. umbelliflora* is distinctly more advanced in several characters. Furthermore, these species fit better in with the whole of the Loganiaceae—especially with the Antonieae—than the other groups. *F. elliptica* and *fragrans* are both widespread—throughout Malesia, resp. also in continental Asia—which may also account for relative primitiveness; *F. umbelliflora* is a local endemic of New Guinea. All this is very well in accordance with palynological evidence: all three are characterised by F. fragrans-type pollen which is considered the most primitive type in the genus. This is especially satisfying as to *F. umbelliflora* as its inclusion in this section was provisional only. Moreover, its further relationship with *F. gracilipes* is also confirmed palynologically! The fragrans and gracilipes subtypes may be of less importance systematically.

F. racemosa, representing the monotypic section Racemosae, is, according to the trends cited above, relatively primitive. Only in its mostly shrublike habit and in the thyrsoid, racemose, spicate, or glomerulous inflorescences—in the last case rather few-flowered—is it more advanced. Its relatively wide geographical distribution—from SE. Asia to the Solomon Islands and northern Australia—also points to relative primitiveness. This is in accordance with palynology, as its pollen belong to the supposedly primitive F. fragrans-type.

The ceilanica group is the kernel of the section Fagraea. It seems too speculative and hardly of any use to try at a phylogenetic scheme within this group. Some of its species are about as primitive as *F. elliptica* and *fragrans* according to the above criteria, others show specializations mainly regarding shrublike or epiphytic habit, wings at the leafbase, few-flowered and glomerulous inflorescences, sometimes reductions or specializations in the bracteoles, in one case insertion of the stamens on a ring (*F. annulata*). First to be mentioned among the more primitive species are *F. crenulata* which will be discussed later, and *F. blumei* and, *F. tacapala* and *F. ceilanica*. *F. blumei* and *ceilanica*, both widespread, are doubtless closely related, and together constitute the base of the group. *F. ceilanica* is very variable, but can not be subdivided in well defined taxa; *F. blumei* is towards the east replaced by some taxa which show more advanced characters (ssp. *plumeriaeflora*, *F. fastigiata*, *truncata*, and *tacapala*). Palynologically, all species of this group have pollen of the F. ceilanica-type with the exception only of *F. crenulata* the pollen of which are included as crenulata subtype under the F. fragrans-type. *F. crenulata* is a rather primitive, relatively widespread species, which probably had better not be included in the ceilanica group. Furthermore, the subdivision of the ceilanica-type into two subtypes is of interest. Most of the species show the ceilanica subtype, *F. annulata* and *carstensensis* make up the annulata subtype. As a matter of fact, a palynological series can be made: *F. ceilanica–carstensensis–annulata–eymae–berteriana*. This series reflects surprisingly well the main systematic relationships. *F. carstensensis, annulata* and *eymae* are all rare local endemics of western New Guinea, where *F. ceilanica* has developed some related races. The position of *F. carstensensis* was morphologically not very clear; *F. annulata* is doubtless closely related to *F. ceilanica*, different, however, by the insertion of the stamens on a ring, a character pointing to the berteriana group; *F. eymae* and *berterinana* belong to the latter group and will be further discussed there. Here again the agreement between systematic conclusions derived from palynology, resp. gross morphology, is very satisfactory.

The auriculata group is a very coherent one. It consists of the widespread *F. auriculata*, and three Bornean endemics. The relationship seems to be with the ceilanica group, more especially with the alliance of *F. blumei*. The auriculata group is more advanced as a whole, however, by the tendency towards a solitary flower, towards two or three pairs of bracteoles, forming an involucre around the calyx, by the in principle epiphytic or shrublike habit, and by the auricles at the leafbase (missing in *F. resinosa*, possibly secondary?). Palynologically, all four species show the ceilanica subtype of pollen, thus stressing the relationship with the ceilanica group.

F. carnosa seems systematically rather isolated. Morphologically it is rather advanced in some characters (epiphyte, flowers solitary). It is relatively widespread (Lower Burma and West Malesia). Palynologically, it is included in the advanced berteriana type. There seems to be no reason, however, to look at the berteriana group—to which belong the other species with this type of pollen—for closer relationships.

The gardenioides group, distinctly cohering, shows no distinct closer relationships to any of the others. Only the presence of linear anthers and of a sometimes bilobed stigma may point to the berteriana group. This resemblance, up till now hardly taken serious—the gardenioides group being West Malesian till Borneo, the berteriana group East Malesian, though including the Philippines—is now strengthened by palynology. Only the pollen of *F. gardenioides* ssp. *borneensis* are known; they belong to the relatively advanced Potalia-type, show a distinct resemblance to *F. berteriana* pollen, however!

F. gracilipes is a rather isolated, in most characters relatively primitive species. Its area of distribution is fairly wide—from New Guinea and NE. Australia to Fiji; within this area about 5 local races are more or less distinguishable. This too speaks well for relative primitiveness. This is confirmed by its pollen which belong to the gracilipes subtype of the fragrans-type. Moreover, this strengthens the suggested relationship between *F. gracilipes* and *umbelliflora*.

The berteriana group is again very coherent. Apart from *F. eymae* —which seems to be related to *F. salticola*, however—they all show the probably advanced characters of a thickened ring on which the stamens are inserted (furthermore known only from *F. annulata*), linear anthers (furthermore in *F. gardenioides*), and a distinctly bilobed stigma (a tendency to which is also found in *F. woodiana*, *gardenioides*, and *gracilipes*). Furthermore, *F. berteriana* lacks bracteoles. Apart from *F. gitingensis* (Philippines and Moluccas) and *F. berteriana* (New Guinea, NE. Australia, and widely distributed in the SW. Pacific), it are endemics of New Guinea. *F. berteriana* shows the most advanced characters, and, though wide, its area of distribution makes also the impression of being young (for argumentation see Leenhouts 1962). These systematical reflections are fully supported by palynological evidence. All four species known (*F. gitingensis* is unknown) have F. berteriana-type pollen, and, as alluded to already under the ceilanica group, this type is connected with the F. ceilanica-type via a series *F. ceilanica–carstensensis–annulata–eymae–berteriana*. In how far the close similarity between *F. berteriana* pollen and *F. gardenioides* pollen—the latter representing the most advanced Potalia-type—reflects real close relationship can hardly be said; as *F. gardenioides* shows also the linear anthers and a tendency towards the bilobed stigma of the berteriana group, and as *F. gardenioides* reaches to Borneo, the berteriana group to the Philippines, this is far from impossible. Then, however, *F. gardenioides* may represent a rather early offshoot.

Summarizing, the agreement between palynology and hitherto accepted systematics based nearly exclusively upon gross morphology is surprisingly good. Of course, this is a great satisfaction for the students of both disciplines. The fact that (in *Fagraea*) even detail problems in systematics could partly be solved thanks to palynological evidence, may be exceptional, but it also shows the value of studying the pollen of as many species of a genus as possible. This will only be possible, however, if somebody is working systematically in the taxon concerned or if a recent revision of the taxon is available.

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