STUDIES OF INDIAN POLLEN GRAINS IN RELATION TO PLANT TAXONOMY—STERCULIACEAE

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The paper deals with pollen morphology of 103 species distributed over 22 genera. Based on the aperture as major and exine pattern as subsidiary characters, as many as 40 pollen types have been recognized. Out of the 22 genera studied here, about 13 genera show eurypalyny. *Hermannia* produces seven pollen types, *Sterculia* five types, *Rulingia*, *Dombeya* and *Heritiera* three types each, *Buettneria*, *Waltheria*, *Reevesia*, *Pterospermum*, *Melhania*, *Helicteres*, *Ayenia* and *Melochia* are segregated into two types each. The rest of the genera, viz. *Eriolaena*, *Pentapetes*, *Abroma*, *Guazuma*, *Commersonia*, *Fremontia* and *Leptonychia*, are stenopalynous. Further an attempt is made to see how far pollen morphology of Sterculiaceae helps in their taxonomy. Finally, on the basis of apertural and exine patterns of the pollen grains, an attempt is made to see how far palynological data throw light on evolutionary trends within the family. It is revealed that pollen study gives a mixed reaction. The taxa which are otherwise well advanced may have the so-called primitive type of pollen grains or vice versa. As a whole the applicability of pollen morphology in taxonomical, phylogenetical and evolutionary considerations is very limited.

INTRODUCTION

The palynological literature on Sterculiaceae is very meagre. A few workers like Lindley (1827), Fritzsche (1832, 1837), Mohl (1834), Schacht (1860), Berg and Schmidt (1853–63), Edgeworth (1877), Schumann (1886, 1890), Fischer (1890) and Zander (1935–51) have attempted work on pollen grains. Wodehouse (1935) made a reference in his master key. Selling (1947) dealt with the genus *Waltheria*. Rao (1950) described 11 species distributed over nine genera, presented a pollen key for the different taxa studied by him and incorporated pollen characters in the general description of the tribes. Erdtman (1952) dealt with this family in detail and put forward valuable suggestions. Ikuse (1956) described a few species of Sterculiaceae. Recently Chaudhuri and Mallik (1965) described pollen grains of three species of Sterculiaceae while dealing with the pollen morphological studies of the order Malvales.

Family Sterculiaceae is abundantly represented in tropics of both the hemispheres and also in subtropics of Africa and Australia. In India it is represented by approximately 88 species distributed over 18 genera (Hooker 1872).

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In the present study as many as 103 species distributed over 22 genera have been investigated.

Materials and Method

The polliniferous materials investigated comprise largely the herbarium materials collected from the Central National Herbarium, Calcutta. Quite a few foreign species, marked with an asterisk (Table I), have also been examined and the data tabulated along with the Indian species. The numbers below each species in Table I are the Central National Herbarium accession number and the Botanical Survey of India Sporotheca number respectively.

Pollen preparations were made by Erdtman's method of acetolysis and the permanent pollen slides examined have been deposited in the Sporotheca of the Botanical Survey of India, Calcutta.

Observations of the pollen material have been recorded with the help of light microscopy (Olympus FFETr—I model). The measurements are based on an average of 25 pollen grains. Photomicrographs are, as a rule, enlarged to $\times 1000$ unless otherwise mentioned. The descriptive terminology and the mode of description are the same as followed earlier (Vishnu-Mittre and Sharma 1962).

Description of Pollen Grains

The pollen grains are 3-(4) aperturate (brevissimicolpoid(or)ate), 3-zonobrevicolpate, 3-4 zonobrevicolp(oid)ate, 4-5 zonobrevicolpate, 3-zonobrevicolporate, 3-zonocolporoidate, 3-zonocolporate, (4)-5 zonocolporate, 3-(4-5) zonoporate, panporate and 3-4 zonopor(or)ate. Os, in most of the sterculaceous colporate pollen grains, is lalongate, varying greatly (rectangular, with rounded or acute lateral ends, constricted in the middle and sometimes merging with the general surface without distinct demarcation) in shape and other characters. Pore in the porate grains may be simple or with rim or annulus, formed by the thickening of the exine around the pore. Apertures are psilate or ornamented.

Exine pattern is greatly variable, faintly granulate, papillate, piloid or verrucoid, spinulate, ornate, retipilariate to reticulate. Meshes in some cases, e.g. *Sterculia villosa* Wall., are provided with fine papillae. Lumina psilate or ornamented. Muri simpli-dupli- or multi-baculate.

Nexine is invariably thinner than sexine. Taking aperture as major and exine pattern as subsidiary characters, the following major pollen types have been recognized:

3-4 aperturate grains (brevissimicolpoid(or)ate)

Genus *Buettneria* and *Ayenia* possess a peculiar type of aperture, the exact morphological nature of which is indistinct probably brevissimicolpoid-(or)ate. The aperture, which varies from circular to colpoid, is placed on the

TABLE I

Showing the morphological characters of the pollen grains

Name	Aperture					Shape	Size (μ)		Exine	
	Particular	Colpus size (μ) l.	Colpus size (μ) b.	Pore size (μ) l.	Pore size (μ) b.		P.	E.	Pattern	Thickness (μ)
1	2	3	4	5	6	7	8	9	10	11
Sterculia villosa Roxb. 27467/170	3-zonocolporate	23·2 21·9–24·0	3·8 2·5–4·0	3·9 3·6–4·0	8·1 8·0–10·9	Prolate spher.	32·4 32·0–34·0	30·0 28·0–32·0	ret.	2·4 1·8–3·0
**S. versicolor* Wall. 57455/532	,,	23·2 20·0–24·0	2·0 –	4·0 3·5–4·5	6·0 5–7	Subprolate	30·4 28·0–32·0	24·8 20·0–28·0	ret./pap.	1·7 1·5–2·0
S. kingii Prain 57675/523	3-zonocolporoidate occ. colporate	26·0 23·7–32·0	2·0 1·5–4·0	4·2 3·6–4·5	6·8 5·4–7·3	,,	37·6 36·0–40·0	30·0 28·0–32·0	ret.	2·9 1·8–3·5
S. roxburghii Wall. 57651/527	3-zonocolporate	23·7 21·9–25·5	3·6 –	3·5 –	7·3 –	,,	34·0 32·0–40·0	28·0 24·0–36·0	,,	2·3 1·8–2·5
S. coccinea Roxb. 26143/158	,,	21·8 20·0–23·7	1·6 1·5–1·8	3·2 2·5–3·6	6·6 5·4–7·3	Prolate spher.	28·8 28·0–32·0	26·6 24·0–28·0	,,	2·3 1·5–3·0
S. ornata Wall. ex Voigt 57574/433	,,	22·6 21·9–23·7	3·6 –	3·1 2·5–3·6	6·5 5·4–7·3	Subprolate	38·4 36·0–40·0	32·4 32·0–36·0	orn.	2·4 1·8–3·0

N.B.—Abbreviations: E., equatorial axis; fr., faintly reticulate; gr., granulate; psi., psilate; ret., reticulate; f. ret., finely reticulate; sp., spinose; spher., spheroidal; orn., ornate; pap., papillate; retipi., retipi., retipilate to retipilariate; f. gr., faintly granulate; pi., pilate; verr., verrucose; l., length; b., breadth; +, diameter of the aperture with rim; −, diameter of the aperture without rim. I.B.G., Indian Botanic Garden.

TABLE I—(*contd.*)

Name	Aperture					Shape	Size (μ)		Exine	
	Particular	Colpus size (μ) l.	Colpus size (μ) b.	Pore size (μ) l.	Pore size (μ) b.		P.	E.	Pattern	Thickness (μ)
1	2	3	4	5	6	7	8	9	10	11
**S. alata* Roxb. 58066/2502	3-zonocolporate	28·8 25·5–31·0	3·9 3·6–5·4	6·9 –	8·6 –	Subprolate	31·6 28·0–36·0	25·2 24·0–28·0	ret.	3·4 3·0–3·6
S. urens Roxb. 4529/166	,,	20·8 18·2–21·9	2·2 1·8–2·5	3·0 1·8–3·6	6·9 5·4–7·3	Prolate spher.	29·4 28·0–32·0	27·4 26·0–28·0	,,	2·0 1·8–2·5
S. foetida Linn. 57429/2504	,,	30·6 29·2–32·8	3·0 1·8–3·6	4·3 –	8·9 –	Subprolate	44·0 40·0–48·0	34·0 32·0–36·0	,,	2·8 2·5–3·0
S. guttata Roxb. 881/162	,,	21·5 18·2–25·5	2·3 1·8–3·0	2·4 1·8–3·0	6·4 5·4–7·5	Oblate spher.	29·0 28·0–31·0	30·2 28·0–32·8	pi. or verr. ,,	2·3 1·8–3·6
**Tarrietia simplicifolia* Mast. 58430/3074	,,	14·3 12·7–15·0	2·0 1·5–3·0	2·6 –	3·7 –	Subprolate	18·9 18·2–20·0	16·0 14·6–18·2	,,	1·5 1·2–1·8
Heritiera papilio Bedd. 5855/487	,,	17·6 16·4–20·0	1·5 1·5–1·8	3·1 2·5–3·6	6·7 5·4–7·3	Suboblate	26·0 24·0–28·0	27·9 24·0–30·0	fr.	2·0 1·8–2·0
**H. littoralis* Dryand. 58468/377	,,	20·0 16·4–21·9	2·1 1·5–3·5	3·1 2·5–3·6	5·2 3·6–7·3	Subprolate	24·8 21·9–27·3	20·3 18·2–21·9	ret.	1·6 1·5–1·8
H. minor Roxb. 58525/483	,,	15·7 14·5–19·5	1·5 –	1·7 1·5–2·0	4·5 4·0–5·4	,,	22·8 20·0–24·0	20·2 20·0–22·0	fr.	1·6 1·5–2·0

TABLE I—(*contd.*)

Name	Aperture					Shape	Size (μ)		Exine	
	Particular	Colpus size (μ) l.	b.	Pore size (μ) l.	b.		P.	E.	Pattern	Thickness (μ)
1	2	3	4	5	6	7	8	9	10	11
H. fomes Buch.-Ham. 58523/478	3-zonocolporoidate to colporate	18·8 18–20	1·5 –	3·7 3·6–4·0	5·1 4·5–5·4	Subprolate	25·3 24·0–26·0	23·3 22·0–24·0	orn. ret.	1–5
H. macrophylla Wall. 58499/482	3-zonocolporate	18·5 16·4–20·0	1·9 1·5–2·5	2·1 1·5–3·0	4·5 3·6–5·4	Prolate spher.	25·8 24·0–28·0	22·6 20·0–24·0	fr.	1·5 1·5–1·8
H. javanica (Bl.) Kostern. 58434/407	,,	13·4 12·7–14·6	1·5 –	2·0 1·5–2·5	3·5 3·0–4·0	Subprolate	19·4 18·0–20·0	17·4 16·0–20·0	,,	1·5 –
H. acuminata Wall. ex Voigt 58571/468	,,	19·6 18·2–20·0	1·7 1·5–1·8	3·0 2·5–3·6	5·6 4·5–7·3	Oblate spher.	23·7 22·0–24·0	23·7 22·0–26·0	,,	1·6 1·5–1·8
H. simplicifolia (Mast.) Kosterm. 58428/493	,,	14·9 14·6–14·9	1·7 1·5–2·5	3·0 2·5–3·6	4·4 4·0–5·4	Subprolate	20·0 20·0–22·0	16·6 16·0–20·0	,,	1·6 1·5–1·8
H. dubia Wall. ex Kurz 58577/469	,,	13·6 12·5–15·0	2·6 2·5–3·0	2·4 –	4·3 –	Oblate spher.	22·0	22·0	ret.	1·5 1·5–1·8

TABLE I—(*contd.*)

Name	Aperture					Shape	Size (μ)		Exine	
	Particular	Colpus size (μ) l.	Colpus size (μ) b.	Pore size (μ) l.	Pore size (μ) b.		P.	E.	Pattern	Thickness (μ)
1	2	3	4	5	6	7	8	9	10	11
Reevesia pubescens Mast. 58640/515	4-zonobrevicolpate	6·9 5·4–7·3	2·0 1·5–2·5	–	–	Rectangular (amb)	–	29·0 28·0–32·0	ret.	1·7 1·5–2·0
Reevesia pubescens Mast. 58640/515	5-zonobrevicolpate	6·9 5·4–7·3	2·0 1·5–2·5	–	–	Pentagonal (amb)	–	31·2 28·0–32·0	,,	1·7 1·5–2·0
Kleinhovia hospita (L.) Miq. 58672/2501	3-zonoporate				7·3 7·0–7·5	Oblate	16·4 14·6–18·2	27·7 23·7–31·0	,,	1·7 1·5–1·8
Helicteres hirsuta Lour. I.B.G./6389	3-zonoporate or brevissimicolpor-(oid)ate				+9·0 −7·0	,,	18·3 14·3–20·0	31·2 27·5–32·5	verr.	1·9 1·8–2·0
H. isora Linn. 20757/130	,,	–	–	–	+7·3 −4·5	,,	20·8 18·0–21·9	31·0 24·0–36·0	f. gr./pap.	1·4 1·2–1·5
Pterospermum lanceaefolium Roxb. 59118/390	3-zonoporate	–	–	–	+14·9 −5·8	Oblate–Oblate spher.	32·8	52·1 45·8–58·4	sp.	7·0 5·4–7·5

TABLE I—(*contd*).

Name	Aperture					Shape	Size (μ)		Exine	
	Particular	Colpus size (μ) l.	Colpus size (μ) b.	Pore size (μ) l.	Pore size (μ) b.		P.	E.	Pattern	Thickness (μ)
1	2	3	4	5	6	7	8	9	10	11
P. cinnamomeum Kurz 59185/385	3-zonoporate	–	–	–	+15·3 −6·2	Oblate– Oblate spher.	–	55·5 48·0–64·0	sp.	2·1 2·0–4·0
P. suberifolium Lamk. 58983/396	„	–	–	–	+15·3 −6·7	Oblate spher.	52·9 51·1–54·7	58·4 48·0–60·0	„	7·8 2·3–9·1
P. heyneanum Wall. 59140/420	„	–	–	–	+15·6 −6·5	„	–	52·9 51·1–54·7	„	2·2 1·5–3·6
P. aceroides Wall. 59083/506	„	–	–	–	+19·6 −11·6	„	–	84·0 72·0–100·0	„	6·3 5·4–7·3
P. semisagittatum Buch.-Ham. 59096/424	„	–	–	–	+15·6 −7·8	„	–	68·8 56·0–80·0	„	2·8 2·5–3·5
Eriolaena wallichii DC. 59363/369	panporate 12	–	–	–	+18·9 −11·8	Spher.	–	104·0 92·0–116	„	15·0 12·0–20·0
E. spectabilis Planch. ex Hk. f. 59358/460	„	–	–	–	+13·4 −4·7	„	–	77·0 72·0–80·0	„	13·0 10·0–18·0

TABLE I—*(contd.)*

Name	Aperture					Shape	Size (μ)		Exine	
	Particular	Colpus size (μ) l.	b.	Pore size (μ) l.	b.		P.	E.	Pattern	Thickness (μ)
1	2	3	4	5	6	7	8	9	10	11
E. hookeriana W. & A. 59375/455	panporate 12	–	–	–	+14·6 −8·2	Spher.	–	79·6 72·0–88·0	sp.	14·0 12·0–16·0
Pentapetes phoenicea Linn. 1149/150	3(4-5) porate				+18·5 −9·8	,,	–	78·6 72·0–84·0	,,	9·2 8·0–12·7
Melhania hamiltoniana Wall. 9642/138	,,				10·9 9·5–11·0	,,	–	86·4 80·0–92·0	sp. and pi.	11·8 12·0–20·0
M. indicana Heyne 9696/142	,,				+14·6 −8·7	,,	–	62·0 56·0–68·0	,,	11·3 8·0–12·0
M. futteyporensis Munro ex Mast. 63789/135	,,				11·6 10·9–12·7	,,	–	83·0 72·0–92·0	,,	17·4 16·0–20·0
**Dombeya palmata* Cav. 59480/2406	3-xonoporate				+15·6 −7·6	Suboblate	50·1 54·7–62·2	65·6 60·2–69·3	sp.	4·3 3·6–5·4
D. mastersii Hk. f. 59475/2390	,,				+11·1 −5·6	,,	40·1 38·3–43·8	47·2 43·8–51·1	,,	6·5 5·4–7·3

TABLE I—(*contd.*)

Name	Aperture					Shape	Size (μ)		Exine	
	Particular	Colpus size (μ) l.	b.	Pore size (μ) l.	b.		P.	E.	Pattern	Thickness (μ)
1	2	3	4	5	6	7	8	9	10	11
*_D. punctata_ Cav. 59520/2401	3-zonoporate				+9·4 −5·1	Suboblate	31·0 29·2–32·8	35·7 31·0–38·3	sp.	4·5 3·6–5·4
D. lancasteri Lanc. 59493/2432	,,				+13·1 −6·9	,,	46·7 36·5–51·1	56·2 47·4–62·0	,,	5·7 5·4–7·3
D. albomarginata Lanc. 59497/2438	,,				+12·4 −6·0	,,	42·8 40·1–44·6	51·8 47·4–54·7	,,	6·0 5·4–7·3
D. spectabilis Boj. 56492/2393	,,				+14·0 −6·4	Oblate spher.	53·5 51·1–54·7	57·1 54·7–58·4	,,	8·3 7·3–9·1
*_D. viburniflora_ Boj. 59525/2397	,,				+8·1 −4·0	,,	38·3 36·5–40·1	38·6 36·5–40·1	,,	3·6 3·5–4·0
D. gagiana Lanc. 59498/2426	,,				+14·9 −7·3	,,	61·2 60·2–62·0	64·5 62·0–65·7	,,	7·7 7·3–9·1
D. alipurensis Lanc. 59491/2435	,,				+13·8 −7·6	Suboblate	51·1 49·2–56·5	58·4 54·7–62·0	,,	7·8 7·3–9·1
D. clarkiana Lanc. 59499/2416	,,				+17·1 −8·3	Oblate spher.	64·2 62·0–56·7	72·2 69·3–73·0	,,	8·0 7·3–9·1

TABLE I—(*contd.*)

Name	Aperture					Shape	Size (μ)		Exine	
	Particular	Colpus size (μ) l.	b.	Pore size (μ) l.	b.		P.	E.	Pattern	Thickness (μ)
1	2	3	4	5	6	7	8	9	10	11
D. acutangula Cav. 59467/2445	3-zonoporate				+14·2 −7·0	Suboblate	49·6 47·4–51·1	57·6 56·5–60·2	sp.	6·0 5·4–7·3
**D. erythroleuca* K. Schum. 59510/2420	,,				+10·9 −6·7	Oblate spher.	55·8 54·7–58·4	59·4 –	,,	8·5 7·3–9·1
**D. leucorhoea* K. Schum. 59514/2429	,,				+14·2 −7·3	,,	52·2 47·4–60·2	58·4 54·7–65·7	,,	6·4 5·4–7·3
**D. wallichii* (Lindl.) K. Schum. 59485/2413	,,				+16·4 −8·6	,,	71·5 65·7–76·6	79·9 73·0–83·9	,,	9·4 9·1–10·9
**D. ovata* Cav. 59519/2423	,,				+10·9 −4·9	,,	33·7 32·8–34·6	37·5 36·5–38·3	,,	3·8 3·5–4·0
D. rosea Lanc. 59490/2442	,,				+12·7 −6·3	,,		53·6 51·1–56·5	,,	6·8 5·4–7·3
**D. natalensis* Sond. 59578/1441	,,				+14·2 −7·3	Spher.		64·6 62·2–67·6	,,	7·5 6·5–9·1

TABLE I—(*contd.*)

Name	Aperture					Shape	Size (μ)		Exine	
	Particular	Colpus size (μ) l.	b.	Pore size (μ) l.	b.		P.	E.	Pattern	Thickness (μ)
1	2	3	4	5	6	7	8	9	10	11
D. burgessiae Lanc. 59496/2410	3-zonoporate				+11·3 −4·6	Suboblate	45·6 43·8–47·4	52·9 47·4–58·4	sp.	4·5 3·6–5·4
Hermannia montana N. E. Brown 59689/6356	3-zonocolporate	9·7 8·1–11·2	1·25 –	2·1 1·9–2·5	5·0 4·3–5·0	Prolate spher.	15·4 15·16–2	13·7 12·5–13·8	f. ret.	1·6 1·5–1·8
H. cristata Bolus 59662/6371	,,	12·3 11·2–13·1	1·25 –	1·9 1·8–2·5	4·7 3·7–5·0	,,	17·0 15·6–18·1	15·0 15–16·2	ret.	1·5 1·4–1·7
H. exappendiculata Oliv. 59670/6331	,,	10·2 10–12·5	1·2	2·0 1·9–2·5	6·5 5·6–7·5	Subprolate	16·3 15·6–17·5	13·5 12·5–15·0	f. ret.	1·4 1·2–1·5
H. candicans Ait. 59653/6370	,,	18·5 –	2·0 1·9–2·5	2·6 2·5–3·1	7·5 6·2–8·1	Prolate spher. to subprolate	25·6 22·5–28·5	22·1 21·5–23·1	ret.	1·6 1·4–1·8
H. grandistipula (Buck.) Schinz. 59674/6374	,,	11·3 10–12·5	1·25 –	1·9 1·8–2·5	6·1 5·6–6·2	Prolate spher.	15·8 15–17·5	14·0 13·7–15·0	f. ret.	1·5 1·4–1·8
H. woodii Schinz. 59716/6345	,,	9·6 8·7–10	1·25 1·2–1·9	1·9 1·2–2·5	5·2 5–6·2	,,	15·4 15–16·4	13·6 13·1–14·4	ret.	1·5 1·4–1·8
H. gerardii Harv. 59672/6360	,,	10·0 –	1·25 –	1·8 1·2–1·9	5·3 5–5·6	,,	15·2 15–16·2	13·5 12·5–13·7	f. ret.	1·6 1·5–1·8

TABLE I—(*contd.*)

Name	Aperture					Shape	Size (μ)		Exine	
	Particular	Colpus size (μ) l.	Colpus size (μ) b.	Pore size (μ) l.	Pore size (μ) b.		P.	E.	Pattern	Thickness (μ)
1	2	3	4	5	6	7	8	9	10	11
H. schlechteriana Schinz. 59709/6339	3-zonocolporate	9·5 8·7–10·0	1·1 0·6–2·5	1·9 1·8–2·5	5·6 5–6·2	Subprolate	15·00 –	12·9 12·5–13·7	ret.	1·2 1·2–1·5
H. hyssopifolia Linn. 59681/6351	,,	19·3 18·7–20	2·7 2·5–5·0	3·2 3·1–3·7	12·5 10–13·7	Oblate spher.	32·2 30–33·7	31·9 30–33·7	–	1·7 1·5–1·8
H. holosericea Jacq. 59678/6347	,,	17·6 16·2–20	2·0 1·9–25	2·9 2·5–3·7	7·5 6·9–8·1	,,	24·2 22·5–30·0	22·8 20–27·5	f. ret.	1·7 1·5–1·8
H. conglomerata Eckl. & Zeyh. 59660/6375	,,	13·5 12·5–15·0	1·6 1·5–1·8	3·0 2·5–3·5	5·9 5·0–6·8	Subprolate	27·1 26·8–27·5	22·1 21·8–22·5	,,	1·7 1·5–2·0
H. oblongifolia Harv. 59691/6379	,,	9·6 9·3–10·0	1·3 1·2–1·5	2·0 1·8–2·5	4·8 5–5·6	,,	13·6 12·5–14·3	11·5 10·5–11·8	,,	1·4 1·2–1·5
H. velutina DC. 59714/6376	,,	17·6 17·5–18·1	1·9 1·5–2·5	2·5 –	8·6 7·5–10	Subprolate	26·7 25–27·5	23·4 22·5–24·4	ret.	1·8 1·7–2·0
H. alnifolia Linn. 59639/6326	,,	19 12·5–20	1·9 1·8–3·0	2·8 2·5–3·0	7·6 5–8	Subprolate to oblate spher.	29·7 28·7–30	24·3 22·5–30	,,	1·9 1·8–2·0
H. sandersoni Harv. 59705/6363	,,	18·4 15–20	1·7 1·2–2·5	2·3 1·9–2·5	9·8 7·5–11·2	Prolate spher.	29·6 27·5–30	27·1 25–27·5	,,	1·8 1·5–2·0

TABLE I—(*contd.*)

Name	Aperture					Shape	Size (μ)		Exine	
	Particular	Colpus size (μ) l.	Colpus size (μ) b.	Pore size (μ) l.	Pore size (μ) b.		P.	E.	Pattern	Thickness (μ)
1	2	3	4	5	6	7	8	9	10	11
H. diffusa Linn. 59669/6322	3-zonocolporate	10·5 10–11·2	1·2 –	2·5 –	4·1 3·7–5	Subprolate	15·4 13·1–16·2	13·0 12·5–13·7	ret.	1·6 1·5–1·8
H. candidissima Spreng. 59655/6354	„	13·7 12·5–15	1·5 1·2–1·9	2·5 –	7·5 6·2–8·7	„	20·8 19–22·5	17·6 17·5–18·7	obs. gr.	1·6 1·5–1·8
H. althaeifolia Linn. 59641/6365	„	18·9 17·5–20	1·7 1·2–1·9	2·6 2·5–3·1	10·0 8·7–10	„	29·6 27·5–30	25·0 23·1–26·2	f. ret.	1·8 1·5–2·0
H. inflata Link & Otto 59760/6373	„	18·8 17·5–20	1·5 1·2–1·9	2·6 2·5–3·1	8·6 7·5–10	Prolate spher. Subprolate	25·2 23·7–27·5	22·2 20–23·7	ret.	1·7 1·5–1·8
H. texana Gray 59761/6381	„	15·6 13·7–17·5	1·2 –	2·2 1·9–2·5	7·0 6·2–8·1	Subprolate	21·9 20–22·5	18·3 17·5–20	„	1·7 1·5–1·8
H. pallens Eckl. & Zeyh. 59692/6378	4-zonocolporate	17·6 15–20	2·4 1·9–3·1	3·0 1·9–4·4	8·7 6·2–11·2	Prolate spher.	29·5 27·5–32·5	27·6 27·5–30·0	„	1·6 1·5–1·8
H. cuneifolia Jacq. 59664/6335	„	15·3 12·5–17·5	3·9 3·1–5·0	2·5 –	7·8 7·5–10	Oblate spher.	27·0 25·0–28·7	27·6 25–30·0	„	1·6 1·5–1·8

TABLE I—(*contd.*)

Name	Aperture					Shape	Size (μ)		Exine	
	Particular	Colpus size (μ) l.	Colpus size (μ) b.	Pore size (μ) l.	Pore size (μ) b.		P.	E.	Pattern	Thickness (μ)
1	2	3	4	5	6	7	8	9	10	11
H. scabra E. et Z. 59708/6367	4-zonocolporate	19·8 18·7–21·2	2·5 1·9–31	3·2 3·1–3·7	9·5 8·7–10	Prolate spher.	31·4 28·7–33·7	27·8 25–32·5	f. ret.	1·6 1·5–1·8
H. prisimatocarpa E. Mey. 59703/6380	,,	20·3 19·3–22·5	1·8 1·2–2·5	4·1 3·0–4·5	7·4 6–8	,,	27·8 27·3–29·3	23·5 22·5–25·0	ret.	1·7 1·5–1·8
Melochia borbonica Cav. 59893/497	3-zonocolporate	29·5 29·2–31·0	1·9 1·5–3·0	6·5 5·4–7·3	15·3 14·6–18·2	,,	37·5 36·0–40·0	34·0 32·0–36·0	,,	1·8 1·5–2·5
M. guazumaefolia (Linn.) A. Ritch. 59899/403	,,	26·6 23·7–29·2	3·6 3·5–4·0	5·6 4·5–7·3	21·5 20–21·9	Oblate spher.	44·0 –	44·0 –	pap.	2·6 1·8–3·6
M. nodiflora Sw. 59946/415	,,	25·5 23·7–27·3	2·5 1·5–3·6	3·7 3·6–4·0	12·7 10·9–14·6	Prolate spher.	39·3 36·0–46·0	35·0 32·0–40·0	ret.	3·0 2·5–3·5
M. corchorifolia Linn. 59821/502	,,	24·6 10·0–27·3	2·4 1·5–3·6	3·6 3·0–4·0	14·6 13·5–15·0	Oblate spher.	40·0 –	40·0 –	,,	3·2 2·5–3·6
Waltheria indica Linn. 1974/174	5-(4)-zonocolporate	25·5 23·7–29·2	4·5 3·6–5·4	5·6 4·5–7·3	10·1 7·3–12·7	Subspher.	41·0 36·0–44·0	46·4 44·0–48·0	pi. to ret.	2·8 2·5–3·5

TABLE I—(*contd.*)

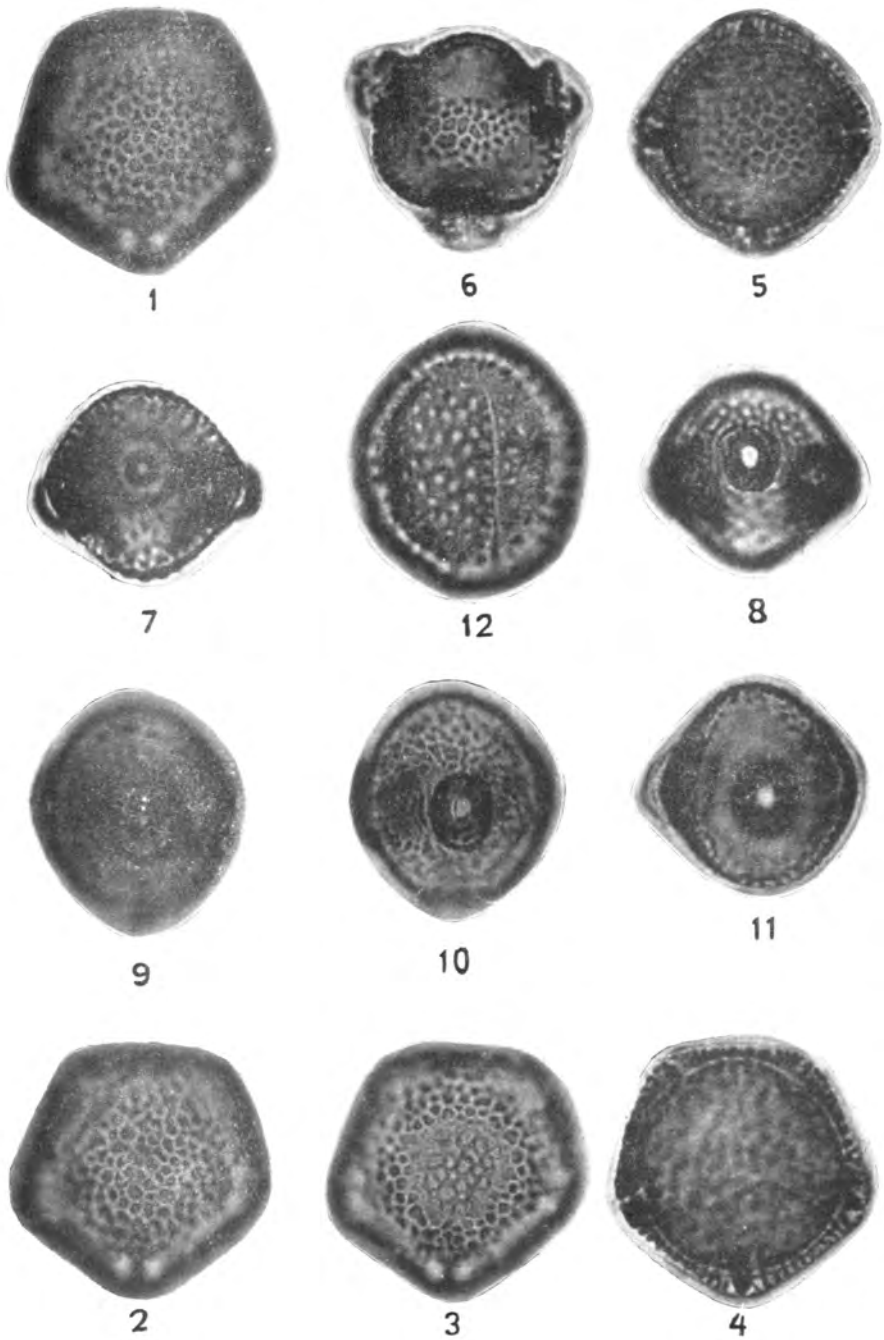
Name	Aperture					Shape	Size (μ)		Exine	
	Particular	Colpus size (μ) l.	b.	Pore size (μ) l.	b.		P.	E.	Pattern	Thickness (μ)
1	2	3	4	5	6	7	8	9	10	11
Abroma augusta Linn. 60125/438	3-(4)-zonobrevicolp(oid)ate	4·6 3·6–5·4	3·9 3·6–4·0			Oblate	21·0 18·2–22·0	29·0 28·0–32·0	ret.	1·7 1·5–1·8
Guazuma tomentosa H. B. & K. 998/126	3-zonocolporate	13·2 10·9–14·6	1·7 1·5–2·5	2·7 2·5–3·5	5·8 5·4–7·3	Prolate spher.	22·2 20·0–26·0	20·8 18·0–26·0	fr.	1·7 1·5–2·5
G. ulmifolia Wall. 60230/464	,,	10·9 9·1–12·7	1·5 –	2·7 2·5–3·6	6·3 5·4–7·3	,,	20·4 20·0–22·0	18·4 16·0–20·0	,,	1·6 1·5–1·8
Buettneria jackiana Wall. 60261/446	3-4-aperturate (brevissimicolpoid(or)ate)					Suboblate	25·6 23·7–25·5	30·3 28·0–32·0	ret.	1·6 1·5–1·8
**B. pilosa* Roxb. 21999/118	,,					Oblate spher.	24·6 23·7–25·5	26·2 24·0–29·2	,,	1·5 1·2–1·8
**B. maingayi* Mast. 60273/450	,,					,,	36·0 32·0–28·0	40·0 32·0–42·0	,,	1·4 1·2–1·5

TABLE I—(*contd.*)

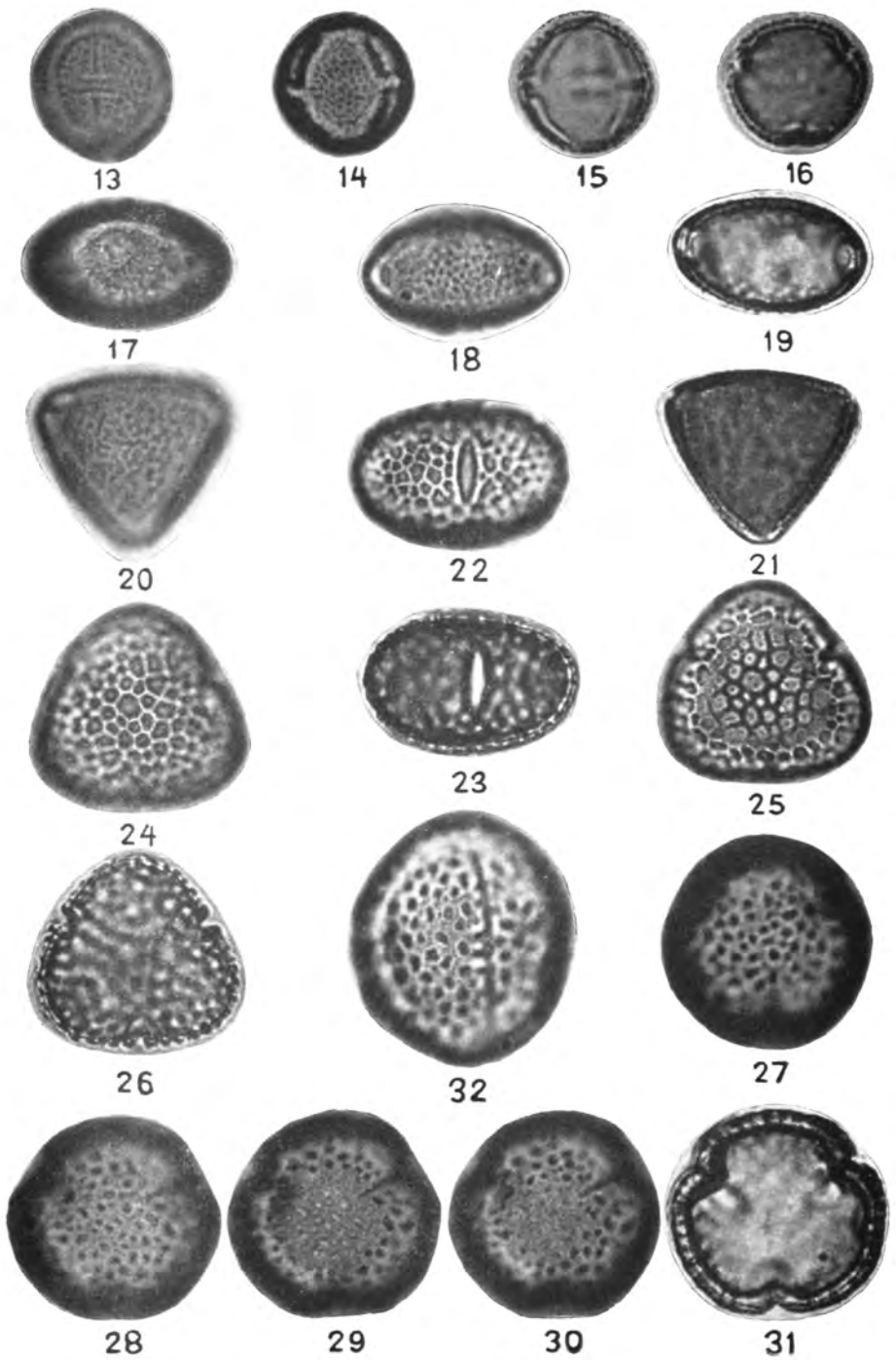
Name	Aperture					Shape	Size (μ)		Exine	
	Particular	Colpus size (μ) l.	Colpus size (μ) b.	Pore size (μ) l.	Pore size (μ) b.		P.	E.	Pattern	Thickness (μ)
1	2	3	4	5	6	7	8	9	10	11
B. aspera Colebr. 60283/441	3-4-aperturate (brevissimicolpoid(or)ate)					Suboblate	24·5 23·7–25·5	30·0 28·0–32	ret.	1·5 –
**Commersonia bartramia* (L.) Merr. 60458/2495	3-zonocolporate	11·9 10·9–12·7	1·9 1·5–2·5	2·6 1·8–3·5	6·0 5·4–7·3	Prolate spher. to oblate spher.	17·1 16·4–18·2	17·1 16·4–18·2	,,	1·8 1·6–2·0
**C. platyphylla* Andr. 60461/2490	,,	12·4 10·9–14·6	2·7 2·5–3·6	2·9 1·8–3·5	7·3 5·4–7·3	Prolate spher.	18·5 18·2–20·0	18·2	,,	1·8 1·6–2·0
Leptonychia moacurroides Bedd. 63499/2485	3-zonobrevicolpate	7·7 5·4–9·1	3·3 2·5–4·0			Oblate	18·6 16·4–20·0	27·4 25·5–29·2	,,	1·6 1·5–1·8
**L. glabra* Turcz. 63514/24	,,	5·6 5·4–6·5	3·4 2·5–4·0			,,	16·4 14·6–18·2	25·5 21·9–29·2	,,	1·8 1·6–2·0
**L. leiocarpa* K. Sch. 63532/2481	4-zonobrevicolpate	8·8 7·3–10·9	3·8 3·0–4·0			,,	19·7 18·2–21·9	29·5 29·2–31·0	,,	1·4 1·2–1·5
**Rulingia drummondii* F. Muell. 60439/2475	3-zonocolporate	19·3 18·2–20·2	1·8 1·2–2·5	3·6 3·4–5·0	7·3 7·2–7·5	Prolate	26·6 25·5–27·3	17·1 14·6–18·2	,,	2·3 1·8–2·5

TABLE 1—(*concld.*)

Name	Aperture					Shape	Size (μ)		Exine	
	Particular	Colpus size (μ) l.	Colpus size (μ) b.	Pore size (μ) l.	Pore size (μ) b.		P.	E.	Pattern	Thickness (μ)
1	2	3	4	5	6	7	8	9	10	11
**R. hermanniaefolia* Steetz. 60430/2463	3-zonocolporate	14·6 12·7–16·4	1·8 1·5–2·5	3·5 3–4	6·1 5·4–7·3	Subprolate	23·3 21·9–25·5	20·2 18·2–21·9	ret.	2·0 1·8–3·0
**R. corylifolia* Gray 60433/2478	,,	16·7 14·6–18·2	2·5 1·8–3·5	3·3 3–3·6	6·4 5·4–7·3	Prolate spher.	25·5 23·7–27·3	24·8 23·7–25·5	orn.-ret.	2·6 2·0–3·0
**R. pannosa* R. Br. 60444/2471	,,	16·4	2·2 2·0–2·5	3·6	5·9 5·4–6·5	Subprolate	21·9 –	19·1 18·2–20·0	ret.	1·6 1·6–1·8
**R. parviflora* Endl. 60438/2459	,,	13·1 10·9–14·6	2·0 1·8–2·5	3·6 3·5–4·5	6·2 5·4–7·5	Prolate spher.	21·9 20·0–23·7	20·1 18·2–21·9	,,	2·4 1·8–3·0
**R. densiflora* Benth. 60438/2459	,,	20·4 18·2–21·9	2·3 1·8–3·5	3·6 3–4	7·2 6·5–7·3	Prolate	26·2 23·7–29·2	19·6 18·2–21·9	,,	2·6 2·5–3·0
**Ayenia montana* Rose 60234/6388	3-4 aperturate (brevissimicolpoid(or)-ate)					Suboblate	23·3 21·6–26·6	30·1 29·4–31·2	sp.	2·7 2·5–3·5
**A. bertondieri* Watson 60231/6387	,,					,,	22·5 21·2–23·7	27·7 26·7–28·7	,,	2·5 2·0–3·0
**Fremontia californica* (Torr.) Coville.	3-zonobrevicolporate	11·2 10·0–12·5	3·2 2·5–5·5	6·1 4·5–7·5	3·5 2·5–5·0	Oblate	26·2 2·5–27·5	35·1 30·0–40·0	,,	2·1 2·0–2·5



FIGS. 1–12. 1–4, *Reevesia pubescens*, 5-colpate grains (polar view) under different foci; 5, *Reevesia pubescens*, 4-colpate grains in polar view; 6, *Buettneria pilosa*, in polar view; 7, 8 and 11, *Buettneria jackiana*, equatorial view under different foci; 9-10, *Buettneria jackiana*, equatorial view showing apertural character; 12, *Sterculia kingii*, equatorial view showing aperture.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sexinous protuberance. This sexinous protuberance is generally infundibuloid. On the basis of the nature of reticulation and luminal characters the four species of *Buettneria* examined here could be distinguished into two groups, whereas different species of *Ayenia* which are spinulate are grouped under one type.

Buettneria pilosa Roxb. type (Pl. XXV, fig. 6): Reticulations fine, simplibaculate, heterobrochate and lumina psilate, e.g. *Buettneria pilosa* Roxb. (oblate spheroidal) and *B. jackiana* Wall. (Pl. XXV, figs. 6–11; suboblate and lumina occ. ornamented). Reticulation in the latter species is very coarse and easily distinguishable from the rest of the species.

Buettneria aspera Colebr. type: This type is ± similar to the previous type except having ornamented lumina, e.g. *Buettneria aspera* Colebr.

Ayenia montana Rose type (Pl. XXXI, figs. 106–108): Apertural organization ± like that of *Buettneria* but ornamentation is spinulate, e.g. *Ayena montana* Rose (suboblate) and *A. bertandieri* Watson (suboblate).

3-(4) zonobrevicolp(oid)ate grains

Abroma augusta Linn. type (Pl. XXXI, figs. 100–103): Colpi psilate; oblate; reticulate, heterobrochate, duplibaculate, lumina psilate to ornamented, nexine thinner than sexine and surface undulating, e.g. *Abroma augusta* Linn.

3-zonobrevicolpate grains

Leptonychia moacurroides Bedd. type (Pl. XXVI, figs. 22–26): Pleurotreme with rounded corners, colpi membrane ornamented; oblate, amb triangular; reticulate, heterobrochate, simpli-duplibaculate and lumina ornamented. Nexine thinner than sexine. Surface undulating, e.g. *Leptonychia moacurroides* Bedd., *L. glabra* Turcz. and *L. leiocarpa* K. Sch. (occ. 4-zonobrevicolpate).

4-5 zonobrevicolpate grains

Reevesia pubescens Mast. type (Pl. XXV, figs. 1–5): Colpi margins occasionally fimbriate; amb rectangular or pentagonal depending upon the number of the colpi; reticulate, heterobrochate, simpli-duplibaculate, pilar heads occ. bifurcating and lumina psilate or ornamented. Nexine thinner than sexine but quite thick near apertures, e.g. *Reevesia pubescens* Mast.

FIGS. 13–32. 13–15, *Guazuma tomentosa*, equatorial view under different foci; 16, *Guazuma tomentosa*, polar view; 17–19, *Kleinhovia hospita*, equatorial view under different foci; 20-21, *Kleinhovia hospita*, polar view under different foci; 22-23, *Leptonychia moacurroides*, equatorial view under different foci; 24–26, *Leptonychia moacurroides*, polar view under different foci; 27–31, *Sterculia kingii*, polar view under different foci; 32, *Sterculia kingii*, equatorial view.

3-zonocolporoidate grains

Sterculia kingii Prain type (Pl. XXV, fig. 12; Pl. XXVI, figs. 27–32): Colpi long, occ. colporate, os lalongate with tapering lateral ends; exine pattern complicated—columellate, reticuloid, irregularly shaped and sized, psilate luminoid areas with slightly crassate margins, mural areas pitted, reticulate (meshes fine), multibaculate, mural pilar heads very thick and prominent. Sexine more than double of nexine. Amb subtriangular to circular, outline undulated, e.g. *Sterculia kingii* Prain.

Heritiera fomes Buch. type: Occasionally colporate, ora lalongate and psilate; subprolate; ornate to reticulate, heterobrochate, simplibaculate and lumina psilate. Nexine thinner than sexine, e.g. *Heritiera fomes* Buch.

3-zonobrevicolporate grains

Fremontia californica (Torr.) Coville type (Pl. XXXII, figs. 109–112): Pleurotreme, colpi short, apices tapering, ora lalongate, psilate?; reticulate, heterobrochate, coarser meshes in the polar region and finer in mesocolpium area, duplibaculate, lumina with or without excrescences; outline undulated and amb triangular with rounded corners. Nexine thinner than sexine, e.g. *Fremontia californica* (Torr.) Coville.

3-zonocolporate grains

Melochia guazumaefolia (Linn.) A. Ritch. type (Pl. XXVII, figs. 45–48): Colpi short, narrow and finely ornamented; ora lalongate, conspicuous and ornamented; oblate spheroidal; papillate, papillae dimorphic, i.e. bigger and smaller, with acute tips and interpapillar area negatively reticulate. Nexine and sexine ± equally thick, e.g. *Melochia guazumaefolia* (Linn.) A. Ritch.

Sterculia guttata Roxb. type (Pl. XXIX, figs. 69–73): Ora lalongate; columellate, grain beset with sparsely distributed piloid or verrucoid structures (shape variable). Nexine thinner than sexine, e.g. *Sterculia guttata* Roxb.

Rulingia corylifolia Grah. type (Pl. XXVII, figs. 40–44): Colpi narrow, ora lalongate and ornamented; prolate spheroidal; ornate to coarsely reticulate, curvimurate and duplibaculate. Nexine thinner than sexine. Occasionally the polar axis is shorter than equatorial axis. Surface undulating, e.g. *Rulingia corylifolia* Grah.

Heritiera macrophylla Wall. type: Colpi long, ora lalongate and psilate; finely reticulate, heterobrochate, simplibaculate, lumina psilate. Nexine thinner

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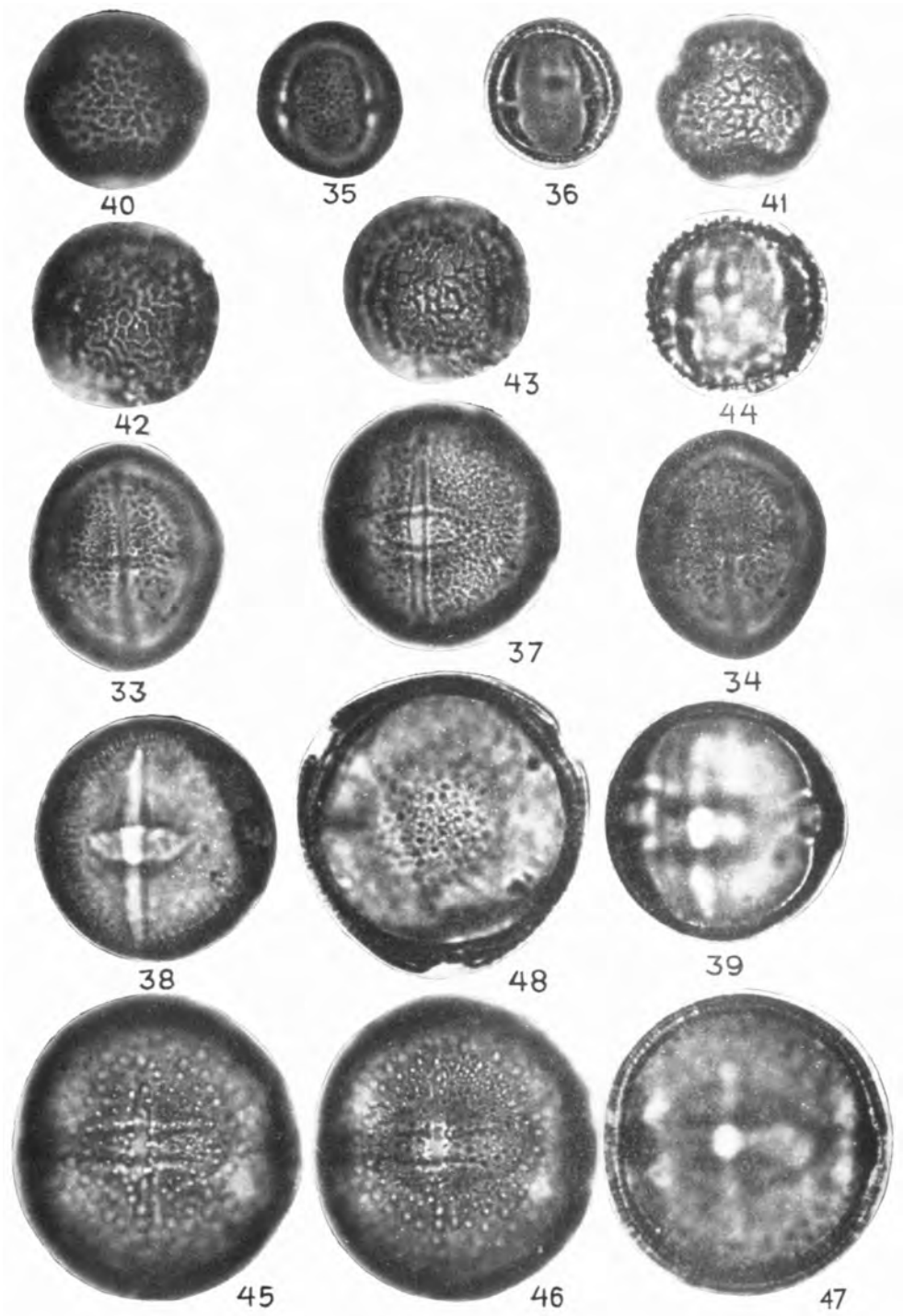
FIGS. 33-48. 33-34, *Sterculia versicolor*, equatorial view under different foci; 35-36, *Commersonia bartramia*, equatorial view under different foci; 37–39, *Melochia borbonica*, equatorial view under different foci; 40-41, *Rulingia corylifolia*, polar view under different foci; 42–44, *Rulingia corylifolia*, equatorial view under different foci; 45–47, *Melochia guazumaefolia*, equatorial view under different foci; 48, *Melochia guazumaefolia*, polar view.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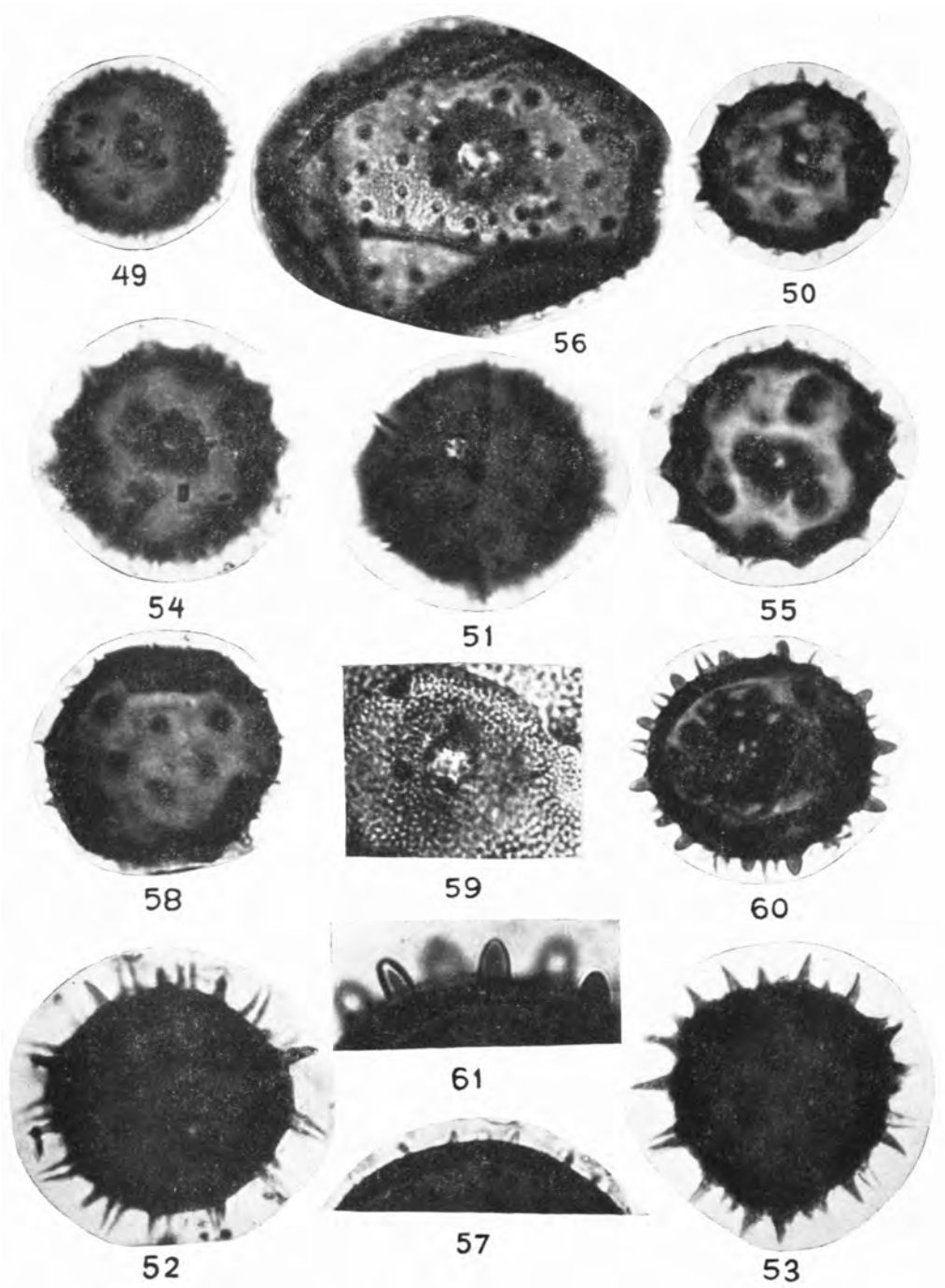
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than sexine, e.g. *Heritiera macrophylla* Wall. (prolate spheroidal), *H. simplicifolia* (Mast.) Kost. (subprolate), *H. dubia* Wall. ex Kurz (oblate spheroidal), *H. minor* Roxb. (suboblate), *Guazuma tomentosa* H. B. & K. (Pl. XXVI, figs. 13–16; prolate spheroidal) and *G. ulmifolia* Wall. (prolate spheroidal).

Heritiera papilio Bedd. type (Pl. XXX, figs. 82–86): This type is similar to *Heritiera macrophylla* Wall. type except having ornamented ora, e.g. *Heritiera papilio* Bedd. (suboblate), *H. javanica* (Bl.) Kost. (suboblate and occ. retipilariate), *H. acuminata* Wall. (oblate spheroidal), *H. elata* Ridley (subprolate and occ. ornate) and *Tarrietia simplicifolia* Mast. (subprolate).

Sterculia roxburghii Wall. type: Colpus long, ora psilate and lalongate; columellate, reticulate, simplibaculate, heterobrochate and lumina psilate. Nexine thinner than sexine. Surface undulating, e.g. *Sterculia roxburghii* Wall. (subprolate), *Commersonia bartramia* (Linn.) Merr. (Pl. XXVII, figs. 35-36), *C. platyphylla* Ander. and *Heritiera littoralis* Dryand. (subprolate). The last three species are quite distinguishable from the main type and could be designated as sub-type on the basis of size.

Sterculia villosa Roxb. type: Colpus long, ora lalongate and psilate; reticulate, heterobrochate, simpli-duplibaculate and lumina ornamented. Nexine thinner than sexine, e.g. *Sterculia villosa* Roxb. (prolate spheroidal), *S. coccinea* Roxb. (prolate spheroidal), *S. ornata* Wall. ex Voigt (colpus membrane ornamented; occ. ornate; subprolate), *S. alata* Roxb. (colpi ornamented; subprolate), *S. urens* Roxb. (Pl. XXIX, figs. 64–68; generally duplibaculate, prolate spheroidal) and *S. foetida* Linn. (subprolate).

Sterculia versicolor Wall. type (Pl. XXVII, figs. 33-34): Colpi long, ora circular to lalongate; subprolate; reticulate, heterobrochate, muri papillate and lumina ornamented. Nexine thinner than sexine, e.g. *Sterculia versicolor* Wall.

Melochia borbonica Cav. type (Pl. XXVII, figs. 37–39): Colpi long, ora lalongate and ornamented; prolate spheroidal; reticulate, meshes fine, simplibaculate and lumina psilate. Nexine thinner than sexine but quite thick at the margins of the pores, e.g. *Melochia borbonica* Cav.

Rulingia drummondii F. Muell. type: Colpus long, constricted in the middle, ora lalongate and finely ornamented; reticulate, heterobrochate, curvi-

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FIGS. 49–61. 49-50, *Dombeya mastersii*, equatorial view under different foci. ×500; 51-52, *Melhania indica*, equatorial view under different foci. ×500; 53, *Melhania indica*, polar view; 54-55, *Dombeya spectabilis*, equatorial view under different foci; 56, *Pterospermum cinnamomeum*, a part of the grain in equatorial view showing aperture; 57, *Pterospermum cinnamomeum*, a part of the grain in optical section showing spines; 58, *Dombeya palmata*, polar view. ×500; 59, *Dombeya palmata*, a part of the pollen showing pore. ×1000; 60, *Pterospermum suberifolium*, equatorial view. ×500; 61, *Pterospermum suberifolium*, a part of the grain in optical section showing spine character. ×1000.

murate, simpli-duplibaculate and lumina psilate. Nexine thinner than sexine. Surface undulating, e.g. *Rulingia drummondii* F. Muell. (prolate), *R. pannosa* R. Br. (subprolate) and *R. densiflora* Benth. (prolate).

Hermannia inflata Link & Otto type (Pl. XXXI, figs. 91-92): Colpus long, tapering, os lalongate, lateral ends gradually tapering or merging with the general surface without distinct demarcation, apertural thickening ± absent, os may be slightly thickened, apertural membranes with or without excrescences; distinctly reticulate, heterobrochate, simplibaculate and lumina psilate. Nexine thinner than sexine. Amb subtriangular to circular. Outline smooth or undulated, e.g. *H. inflata* Link & Otto (prolate sph.-subprolate), *H. texana* Gray (occ. 4-colporate; subprolate) and *H. velutina* DC. (subprolate).

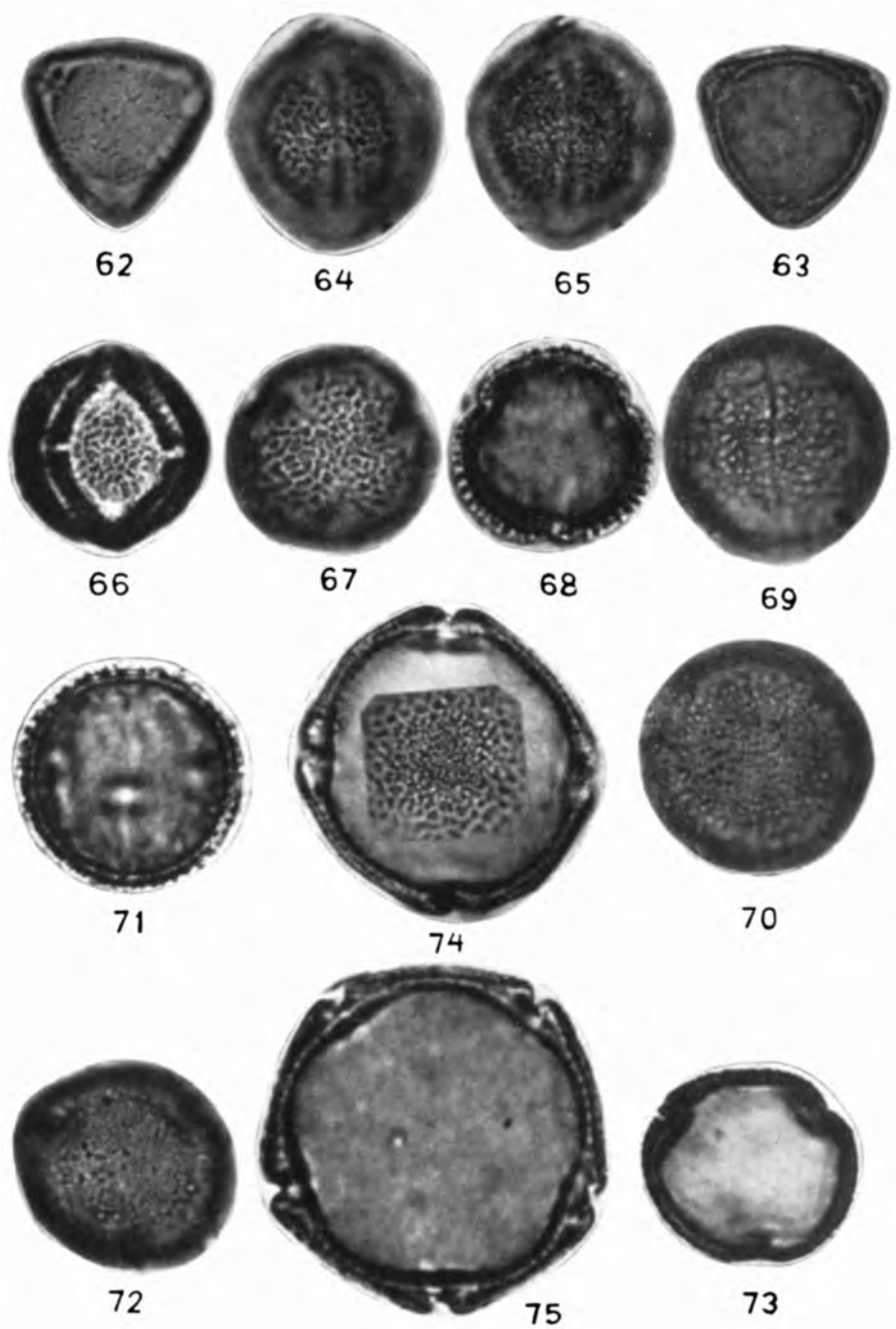
Hermannia candidissima Spreng. type: With thickened apertural margins giving spindle-shaped appearance; exine finely reticulate; rest of the characters like that of *H. inflata* Link & Otto type, e.g. *H. candidissima* Spreng. & Tent. (subprolate), *H. candicans* Ait. (prolate sph. to subprolate) and *H. althaeifolia* Linn. (subprolate).

Hermannia cristata Bolus type (Pl. XXXI, figs. 93-94): Grains small sized, colpus tapering, os lalongate, lateral ends tapering or merging with general surface without distinct demarcation, apertural membranes with or without excrescences; distinctly reticulate, heterobrochate, simplibaculate, lumina psilate; nexine thinner than sexine; outline undulated and amb subtriangular to circular, e.g. *H. cristata* Bolus (prolate sph.), *H. woodii* Schinz. (prolate sph.), *H. diffusa* Linn. (subprolate) and *H. schlechteriana* Schinz. (subprolate).

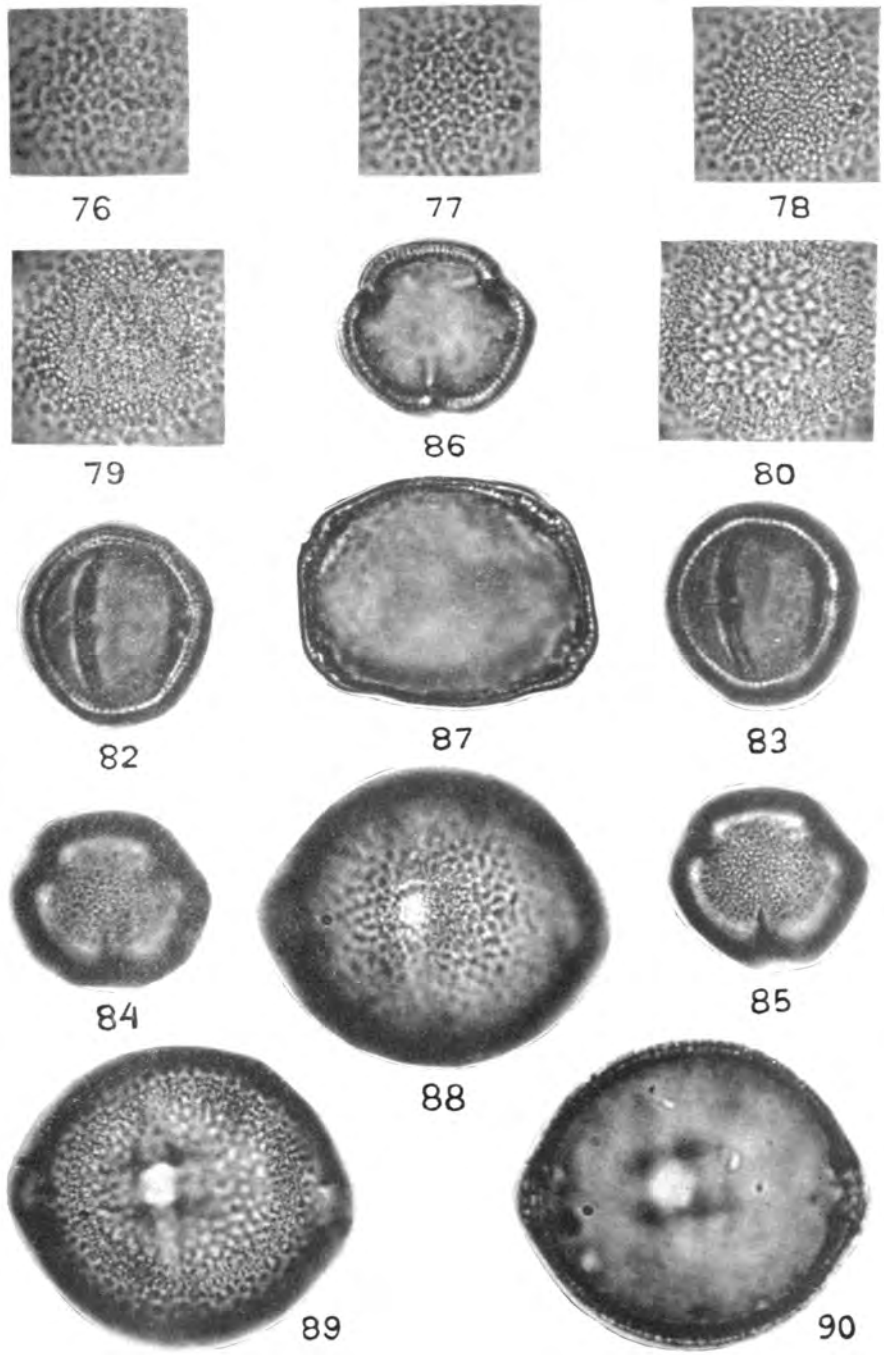
H. gerardii Harv. type: Grains small sized; colpus tapering; os lalongate, lateral ends tapering, rounded or merging with the general surface without distinct demarcation, apertural membranes psilate or ornamented; very finely reticulate, heterobrochate, simplibaculate and lumina psilate. Nexine thinner than sexine. Outline smooth or undulated. Amb subtriangular to circular, e.g. *H. gerardii* Harv. (prolate sph.), *H. oblongifolia* Harv. (prolate sph.), *H. montana* N. E. Brown (prolate sph.), *H. grandistipula* (Buck.) Schinz. (prolate sph.) and *H. exappendiculata* Oliv. (subprolate).

4-zonocolporate grains

Hermannia pallens Eckl. & Zeyh. type (Pl. XXXI, fig. 105): Colpi may be of equal or unequal sizes; os lalongate, lateral ends tapering or rounded, margins of both the apertures thickened, ± appearing like a spindle; apertural membranes with or without excrescences; distinctly reticulate, heterobrochate, meshes finer towards apertures, simplibaculate, lumina



FIGS. 62–75. 62-63, *Helicteres isora*, polar view under different foci; 64–66, *Sterculia urens*, equatorial view under different foci; 67-68, *Sterculia urens*, polar view under different foci; 69–71, *Sterculia guttata*, equatorial view under different foci; 72-73, *Sterculia guttata*, polar view under different foci; 74, *Waltheria indica*, 4-colporate grain in polar view; 75, *Waltheria indica*, 5-colporate grain in polar view.



FIGS. 76–90. 76–80, *Waltheria indica*, a part of the exine under different foci; 82–83, *Heritiera papilio*, equatorial view under different foci; 84–86, *Heritiera papilio*, polar view under different foci; 87, *Helicteres isora*, 4-aperturate grain; 88–90, *Waltheria indica*, equatorial view under different foci.

Note: Due to oversight no figure was given the number 81.—AUTHOR.

psilate; outline smooth to undulated; amb subtriangular to circular and nexine thinner than sexine, e.g. *H. pallens* Eckl. & Zeyh. (rarely 3-colporate; prolate spheroidal), *H. sandersoni* Harv. (prolate spheroidal) and *H. alnifolia* Linn. (subprolate-oblate sph.).

H. scabra Cav. type (Pl. XXXI, fig. 104): Grains with less distinct apertural thickening and ornamentation finely reticulate. Other characters ± like that of *H. pallens* Eckl. & Zeyh. type, e.g. *H. scabra* Cav. (prolate spheroidal), *H. conglomerata* Eckl. & Zeyh. (subprolate) and *H. cuneifolia* Jacq. (apertural thickening highly reduced and colpus membrane coarsely ornamented; oblate spheroidal).

H. prismatocarpa E. Mey. type: Apertural thickening very poorly developed or absent. Ornamentation very finely reticulate, e.g. *H. prismatocarpa* E. Mey. (subprolate) and *H. holosericea* Jacq. (rarely 3-colporate; prolate sph.).

Rulingia hermanniaefolia Steetz. type: This type is ± like that of *R. drummondii* F. Muell. type except having coarse meshes and ornamented lumina, e.g. *R. hermanniaefolia* Steetz. (subprolate) and *R. parviflora* Endl. (prolate spheroidal).

5-(4)-zonocolporate grains

Waltheria indica Linn. type (Pl. XXIX, figs. 74-75; Pl. XXX, figs. 76–80 and 88–90): Colpus long and ornamented; ora lalongate, margins thick and frequently bulging out; sub-spheroidal; reticulate, simpli-duplibaculate, pilar heads occasionally branched, lumina ornamented and nexine thinner than sexine, e.g. *Waltheria indica* Linn.

3-zonoporate grains

Kleinhovia hospita (L.) Miq. type (Pl. XXVI, figs. 17–21): Goniotreme, pores circular, ornamented, margins thin; oblate, amb triangular; reticulate, occ. pilate, heterobrochate, simplibaculate, lumina psilate and nexine thinner than sexine, e.g. *Kleinhovia hospita* (Linn.) Miq.

Dombeya palmata Cav. type (Pl. XXVIII, figs. 58-59): Pores circular, ornamented and rimmed; columellate, pilar heads distinct, spinulate, spine base slightly bulbous, spines sparsely distributed, interspinal area negatively reticulate and nexine thinner than sexine, e.g. *Dombeya palmata* Cav. (suboblate), *D. paniculata* Cav. (suboblate), *D. lancasteri* Lanc. (sub-oblate), *D. viburniflora* Boj. (oblate spheroidal) and *D. ovata* Cav. (oblate spheroidal).

Dombeya spectabilis Boj. type (Pl. XXVIII, figs. 54-55): This type is ± similar to that of *Dombeya palmata* Cav. type but differs in possessing very

prominent and high spinal mound (bulbous base), e.g. *Dombeya spectabilis* Boj. (oblate spheroidal), *D. albomarginata* Lanc. (suboblate), *D. gagiana* Lanc. (oblate spheroidal), *D. alipurensis* Lanc. (suboblate), *D. clarkiana* Lanc. (oblate spheroidal), *D. acutangula* Cav. (suboblate), *D. wallichii* (Lindl.) K. Schum. (oblate spheroidal), *D. rosea* Lanc. (oblate spheroidal) and *D. natalensis* Sond. (spheroidal).

Dombeya mastersii Hk. f. type (Pl. XXVIII, figs. 49-50): In general, this pollen type is ± similar to *Dombeya palmata* Cav. and *D. spectabilis* Boj. types but the height of the spinal mound is intermediate, e.g. *Dombeya mastersii* Hk. f. (suboblate), *D. erythroleuca* K. Schum. (oblate spheroidal), *D. leucorrhoea* K. Schum. (oblate spheroidal) and *D. burgessiae* Lanc. (suboblate).

Pterospermum cinnamomeum Kurz type (Pl. XXVIII, figs. 56-57): Pores circular, ornamented, rimmed; spinulate, spines short with blunt tips, without bulbous base or base very rudimentarily developed, interspinal area finely baculate and negatively reticulate. Nexine thinner than sexine but quite thick round the apertures, e.g. *Pterospermum cinnamomeum* Kurz (oblate to oblate spheroidal), *P. semisagittatum* Buch. (oblate), *P. heyneanum* Wall. (oblate spheroidal; spines comparatively thicker) and *P. aceroides* Wall. (oblate spheroidal).

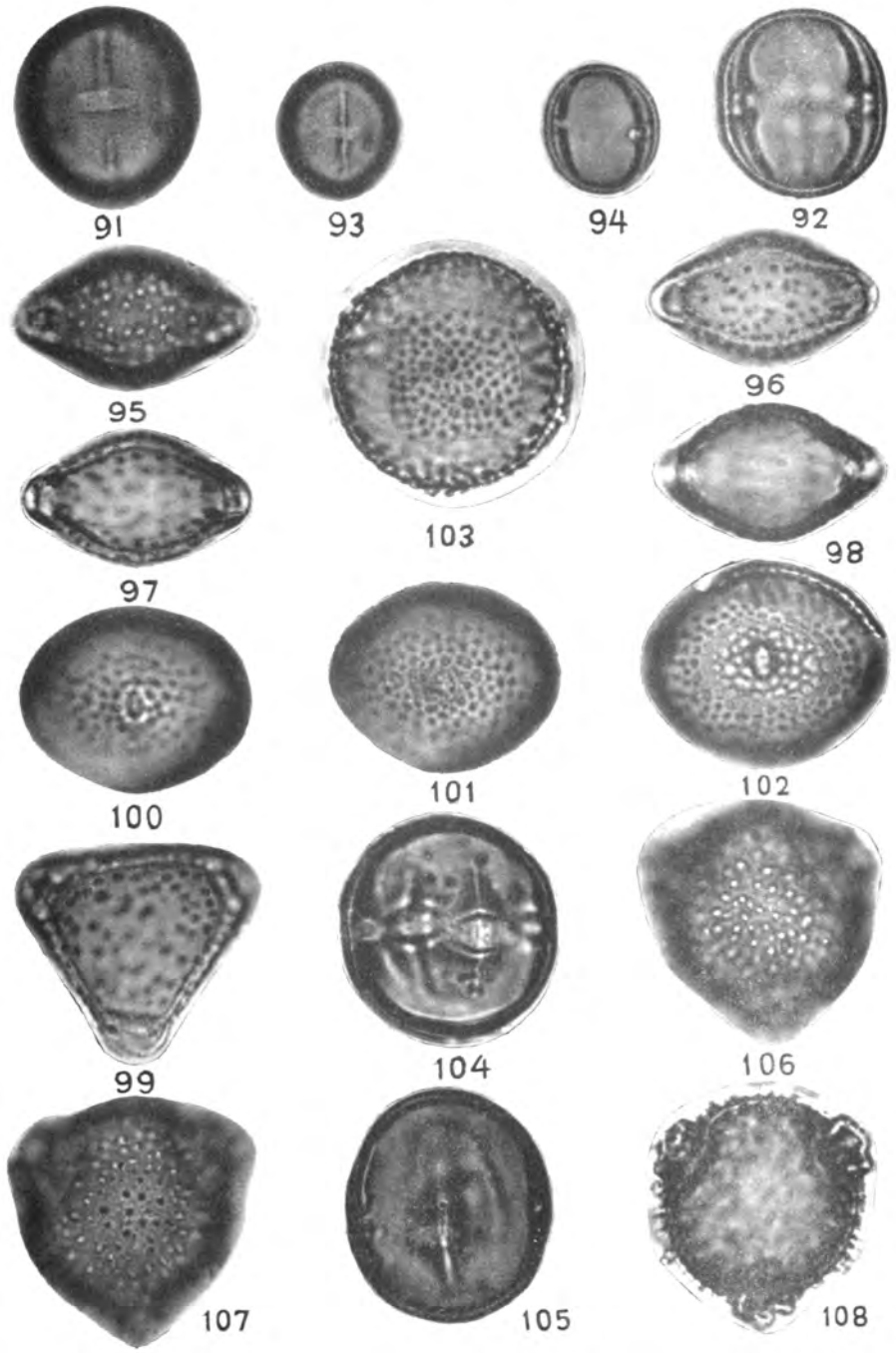
Pterospermum suberifolium Lamk. type (Pl. XXVIII, figs. 60-61): Most of the characters are like that of *Pterospermum cinnamomeum* Kurz type but differs in having large, acutely tipped spines and prominent bulbous base, e.g. *Pterospermum suberifolium* Lamk. (oblate spheroidal) and *P. lanceaefolium* Roxb. (oblate spheroidal).

3-(4-5) porate grains

Pentapetes phoenicea Linn. type: Pores circular and psilate; spheroidal; columellate, columella distinct and occasionally branched; spinulate, spines mounted on mounds, grains occ. non-tegillate and nexine thinner than sexine, e.g. *Pentapetes phoenicea* Linn.

Melhania hamiltoniana Wall. type: Pores circular, psilate, crassimarginate; spheroidal; non-tegillate to tegillate, columella and pila heads branched, spinulate, interspinal area negatively reticulate and nexine thinner than sexine, e.g. *Melhania hamiltoniana* Wall.

FIGS. 91–108. 91–92, *Hermannia inflata*, equatorial view under two foci; 93-94, *Hermannia cristata*, equatorial view under two different foci; 95–98, *Helicteres hirsuta*, equatorial view under different foci; 99, *Helicteres hirsuta*, polar view; 100–102, *Abroma augusta*, equatorial view under different foci; 103, *Abroma augusta*, polar view with exine pattern superimposed; 104, *Hermannia scabra*, equatorial view; 105, *Hermannia pallens*, equatorial view; 106–108, *Ayenia montana*, polar view under different foci.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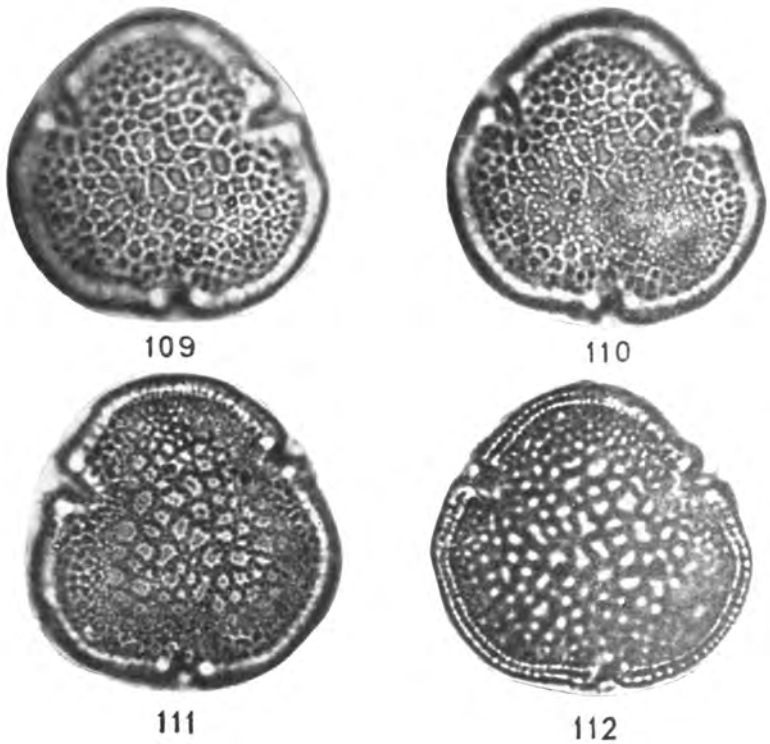
Melhania incana Heyne type (Pl. XXVIII, figs. 51–53): This species is ± that of *M. hamiltoniana* Wall. type except possessing ornamented pore membrane and conspicuous smaller size, e.g. *Melhania incana* Heyne (spheroidal) and *M. futteyporensis* Munro ex Mast. (spheroidal).



FIGS. 109–112, *Fremontia californica*, polar view under different foci.

Panporate grains, pores 12

Eriolaena wallichii DC. type: Pores circular, rimmed, pore membrane ornamented; spheroidal; spinulate, spine base bulbous, interspinal area pilate to pilariate and nexine thinner than sexine, e.g. *Eriolaena wallichii* DC., *E. spectabilis* Planch. ex Hook. and *E. hookeriana* W. & A.

3-(4)-zonopor(or)ate or brevissimicolpor(oid)ate grains

Helicteres isora Linn. type (Pl. XXIX, figs. 62-63; Pl. XXX, fig. 87): Goniotreme, pore circular, membrane ± ornamented; oblate, amb subtriangular; granulate, papillate, negatively reticulate, nexine thinner than sexine and dentate near the pores, e.g. *Helicteres isora* Linn.

Helicteres hirsuta Lour. type (Pl. XXX, figs. 95–99): Goniotreme, 3-zonobrevissimicolpor(oid)ate or por(or)ate; pores circular, crassimarginate, membrane ornamented; colpi (colpoids) very short, with or without excrescences; verrucose, verrucae variable in size, inter-verrucae space finely granulate and punctate ? Nexine and sexine ± equally thick, e.g. *Helicteres hirsuta* Lour. (oblate).

Discussion

As many as 40 pollen types, based on aperture and exine characters, have been recognized out of the 103 species examined here under light microscopy. The number of pollen types could be multiplied under electronic microscopy, etc. One of the objects of this study is to see how far pollen morphology of Sterculiaceae could help in its taxonomy. The classification of Bentham & Hooker is in vogue in India and for the taxonomical consideration the monograph on this family by Masters (in Hooker's Flora of British India) is strictly followed. Masters (1872) divided Sterculiaceae into six tribes, viz. Sterculieae, Helictereae, Eriolaeneae, Dombeyeae, Hermannieae and Buettnerieae.

Sterculieae (*Sterculia*, *Tarrietia* and *Heritiera*)

In this tribe the pollen grains, except that of *Heritiera fomes* Buch., where these are colporoidate, are all 3-zonocolporate. Os is exclusively lalongate. Exine pattern varies greatly. Out of the different species examined about eight pollen types have been recognized, five types in *Sterculia*, viz. *S. guttata* Roxb. type, *S. versicolor* Wall. type, *S. roxburghii* Wall. type, *S. villosa* Roxb. type and *S. kingii* Prain type, and three in the genus *Heritiera*, viz. *H. macrophylla* Wall. type, *H. papilio* Bedd. type and *H. fomes* Buch. type, are recognized. *Tarrietia* pollen grains are ± like that of *Heritiera papilio* Bedd. type.

Helictereae (*Reevesia*, *Kleinhovia*, *Helicteres* and *Pterospermum*)

The different genera included in this tribe show great diversity in pollen characters and each one stands out as a distinct type. Genus *Reevesia*, of which only one species is studied (*Reevesia pubescens* Mast. type), is characterized by 4-5-zonobrevicolpate grains. Erdtman (1952) reported 4-5-colporate grains in *Reevesia pubescens* Mast. *Kleinhovia* (*Kleinhovia hospita* Linn. type) pollen is 3-zonoporate and reticulate with triangular amb. Genus *Helicteres*, of which two representatives have been examined, produces two types of pollen grains, viz. *H. isora* Linn. type with 3-zonopor(or)ate or brevissimicolpor-(oid)ate and granulate, papillate, negatively reticulate pollen grains with

triangular amb and *H. hirsuta* Lour. type, characterized by 3-zonobrevissimicolpor(oid)ate or por(or)ate and verrucose pollen grains. *Pterospermum* grains are 3-zonoporate but on the basis of spine structure two pollen types, viz. *P. cinnamomeum* Kurz type and *P. suberifolium* Lamk. type, have been recognized.

Eriolaeneae (*Eriolaena*)

All the three species of genus *Eriolaena* have identical pollen grains and are grouped under *E. wallichii* DC. type which is characterized by panporate and spinulate grains.

Dombeyeae (*Pentapetes, Melhania* and *Dombeya*)

There is a close similarity in gross pollen morphological characters of these three genera, being 3-(4-5) zonoporate with spinulate exine pattern. But on closer examination six pollen types are recognized, viz. *Pentapetes phoenicea* Linn. type, *Melhania hamiltoniana* Wall. type, *Melhania incana* Heyne type, *Dombeya palmata* Cav. type, *Dombeya spectabilis* Boj. type and *Dombeya mastersii* Hk. f. type. The last three types are ± alike except the height and nature of mound and the psilate or ornamented ora.

Hermannieae (*Melochia, Waltheria* and *Hermannia*)

The different genera included in this tribe show various apertural and exine characters. In genus *Melochia* two pollen types, viz. *Melochia guazumaefolia* A. Ritch. type with 3-zonocolporate and papillate pollen grains and *M. borbonica* Cav. type which differs from the former type in having reticulate pattern. The rest of the species of this genus fit in the latter type.

Waltheria indica L. type produces (4)-5 zonocolporate grains with retipilariate to reticulate pattern. *Hermannia* represents a heterogeneous assemblage. Pollen grains may be 3-zonocolporate or 4-zonocolporate. All the 4-colporate grains and some of the 3-colporate ones are of bigger size while the rest of the members have small size. Taking all the different characters in view as many as seven pollen types are recognized, viz. *Hermannia pallens* E. & Z. type, *H. scabra* E. & Z. type, *H. prismatocarpa* E. & Mey. type, *H. inflata* Link. & Otto type, *H. candidissima* Spreng type, *H. cristata* Bolus type and *H. gerardii* Harv. type.

Buettnerieae (*Abroma, Guazuma, Buettneria, Commersonia, Leptonychia, Rulingia* and *Ayenia*)

Buettnerieae is an eurypalynous tribe. All the genera included here produce different types of pollen grains. Genus *Abroma* (*Abroma augusta* Linn. type) produces 3-(4-5)-colp(oid)ate and reticulate pollen grains. Both

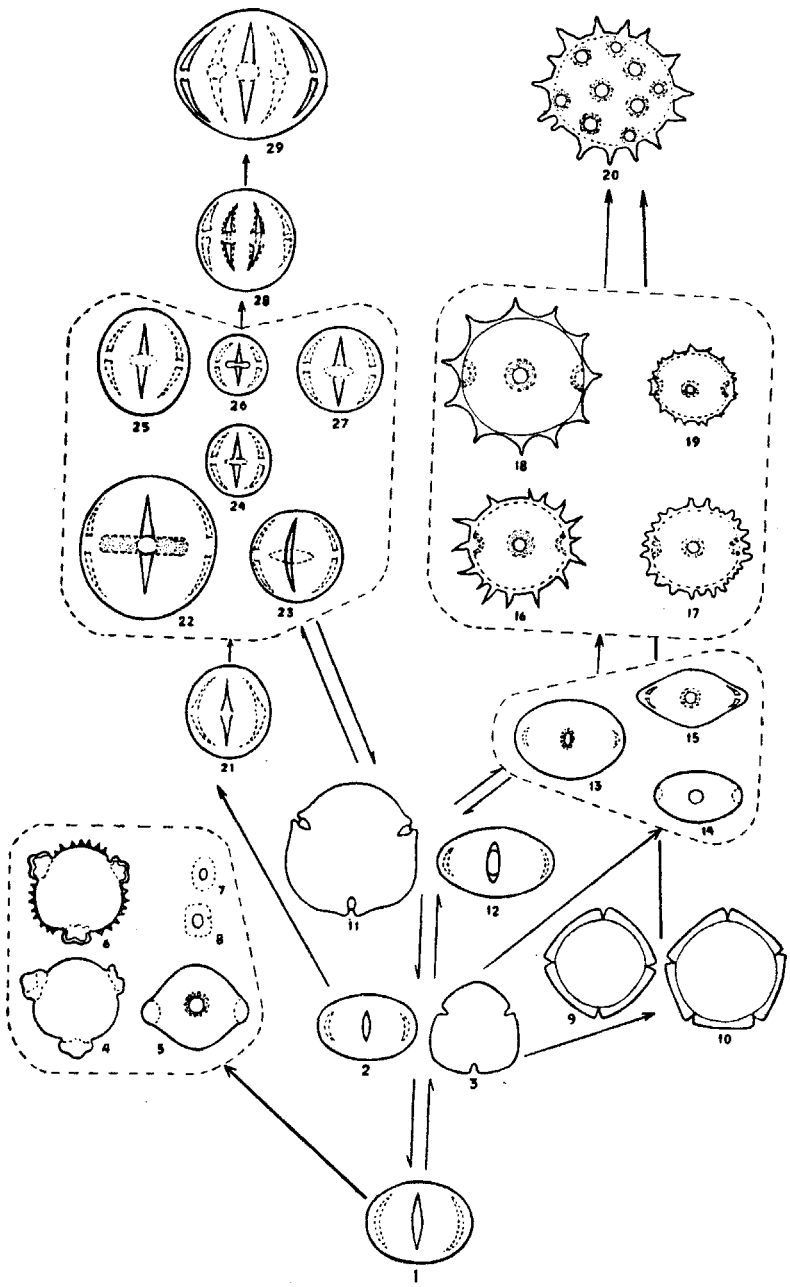


FIG. 113. Probable trends in the apertural evolution of Sterculiaceae pollen grains.

the species of genus *Guazuma*, viz. *G. tomentosa* H. B. & K. and *G. ulmifolia* Wall., have identical pollen grains (*Heritiera macrophylla* Wall. type).

Genus *Buettneria* possesses a peculiar type of aperture, as described earlier. The different species examined could be grouped under two types, viz. *B. pilosa* Roxb. type with psilate lumina and *B. aspera* Colebr. type with distinctly ornamented lumina.

Commersonia species produce *Heritiera macrophylla* Wall. type of pollen grains so far as aperture and nature of exine are concerned, but could be easily put under sub-type on the basis of size.

All the three species of *Leptonychia*, viz. *L. moacurroides* Bedd., *L. glabra* Turcz. and *L. leiocarpa* K. Sch., are grouped under *L. moacurroides* Bedd. type, which is characterized by 3-zonobrevicolpate, oblate, reticulate pollen grains with ornamented lumina.

The different species of genus *Rulingia*, examined here, are segregated into three distinct types, viz. *R. corylifolia* Grah. type, *R. drummondii* F. Muell type and *R. hermanniaefolia* Steetz. type.

The nature of aperture and general organization in *Ayenia* pollen is ± like that of *Buettneria* but differs in being spinulate. Both the species of *Ayenia* examined are put under *A. montana* Rose type.

Genus *Fremontia*, which is unrepresented in Indian flora, produces pollen grains of its own type (*Fremontia californica* (Torr.) Coville type). In general the pollen organization is ± that of *Leptonychia* but differs in apertural character.

Palynology in relation to Plant Taxonomy

The palynological survey reveals the eurypalynous nature of the family Sterculiaceae. Forty distinct pollen types, based on the aperture and ornamentation characters, have been recognized. Almost all the tribes, viz. Sterculieae, Helictereae, Dombeyeae, Hermannieae, Buettnerieae, are eurypalynous except Eriolaeneae. Coming to the generic level, it is seen that out of the 22 genera studied here only nine are stenopalynous. The genus *Hermannia* produces seven pollen types, *Sterculia* five types, *Rulingia*,

Fig. 113. 1, ancestral type of pollen grain; 2-3, *Leptonychia moacurroides* Bedd. type; 4-5, *Buettneria* type; 6, *Ayenia montana* Rose type; 7-8, different types of apertures met with in *Buettneria* and *Ayenia*; 9-10, *Reevesia pubescens* Mast. type; 11-12, *Fremontia californica* (Torr.) Coville type; 13, *Abroma augusta* Linn. type; 14, *Kleinhovia hospita* (L.) Miq. type; 15, *Helicteres isora* Linn. type; 16, *Melhania incana* Heyne type; 17, *Pterospermum suberifolium* Lamk. type; 18, *Pentapetes phoenicea* Linn. type; 19, *Dombeya mastersii* Hk. f. type; 20, *Eriolaena hookeriana* W. & A. type; 21, *Heritiera papilio* Bedd. type; 22, *Melochia guazumaefolia* (Linn.) A. Ritch. type; 23, *Melochia borbonica* Cav. type; 24, *Commersonia bartramia* (Linn.) Merr. type; 25, *Hermannia pollens* Eckl. & Zeyh. type; 26, *Guazuma tomentosa* H. B. & K. type; 27, *Rulingia corylifolia* Grah. type; 28, *Hermannia scabra* E. et Z. type; 29, *Waltheria indica* Linn. type.

Dombeya and *Heritiera* three types each. *Buettneria*, *Waltheria*, *Reevesia*, *Pterospermum*, *Melhania*, *Helicteres*, *Ayenia* and *Melochia* are segregated into two types each. The rest of the genera, viz. *Tarrietia*, *Kleinhovia*, *Eriolaena*, *Pentapetes*, *Abroma*, *Guazuma*, *Commersonia*, *Fremontia* and *Leptonychia*, are stenopalynous.

It is generally believed by the plant morphologists that the similarity in characters shows closeness whereas the diversity indicates distant relationships. If the same principle is applied to the palynological data, it becomes clear, as revealed by the present study, that the majority of the tribes do not constitute homogeneous assemblages. Further, in broader palynological sense, the eurypalyny is suggestive of further splitting or subgrouping of the genera as done by Bremekemp (1944) in the case of Acanthaceae and many others in different families. It would be rather improper to conclude this only on the basis of pollen characters; further support from cytology, embryology, anatomy and physiology must be sought. There appears to be no difference between Bentham & Hooker's and Engler & Prantl's classifications regarding the inclusion of different genera in different tribes, though their order of arrangement in different tribes within the family is altogether different. It is apparent that on the floral morphological grounds the different tribes are well established, but from purely palynological viewpoint the different tribes of both the classifications represent heterogeneous assemblages. This heterogeneity in pollen characters within tribes and different genera needs thorough consideration while giving taxonomical treatment. The eurypalyny suggests further splitting up of different genera so as to make the classification more natural.

An attempt is further made to evaluate applicability of the pollen character (aperture) to Hutchinson's (1964) classification, more particularly in respect of his evolutionary concept of fundamental differences between woody and herbaceous habit. It has been widely accepted by the palynologists that the composite and porate apertures are more recent and show an advancement over colpate condition. The palynological data show a mixed reaction to this concept, e.g. *Eriolaena*, *Kleinhovia* and *Guazuma*, which are fundamentally woody (trees), possess pollen grains with highly evolved apertures (3–12 porate and 3-colporate conditions). Some other genera with shrubby or arborescent habit, e.g. *Sterculia*, *Heritiera*, *Helicteres*, *Pterospermum*, *Abroma*, *Commersonia*, *Leptonychia* and *Reevesia*, produce colpate, colpoidate, colporate and porate grains. *Buettneria*, *Waltheria*, *Melochia*, *Pentapetes*, etc., which are under-shrubby, shrubby or herbaceous elements, produce pollen grains with variable apertures. From the foregoing account it is apparent that the recent and derived apertural pollen characters have no relation with woody or herbaceous nature of the family Sterculiaceae. But as a whole the high position assigned to Tiliales in the classification is supported by palynological studies. The higher position occupied by Malvales than that of

Tiliales is highly justified on palynological grounds as majority of the pollen grains of Malvales exhibit porate condition.

This phenomenon of eurypalyny and contemporary picture given by pollen studies could easily be explained on the simple principle of evolution, i.e. 'the evolution does not necessarily involve all organs of plant at the same time and one organ or the set of the organs may be advancing while the other set is stationary or retrograding'.

In general some genera, viz. *Pterospermum, Pentapetes, Melhania* and *Dombeya,* show Malvaceous pollen organization, being porate and spinulate. The palynological evidences, therefore, could suggest their reference to Malavaceae.

Similarly pollen organization of *Fremontia, Leptonychia* and to some extent that of *Abroma* is ± identical to that of Bombacaceae and could be referred to this family.

Some parts of Sterculiaceae show closeness to Tiliaceae. From the foregoing account it becomes quite clear that almost all the genera could easily be distinguished from each other on the basis of pollen morphology, though its application to specific level is very limited.

Evolutionary Significance

Though it is premature yet not out of place to say a few words regarding pollen structure and its evolutionary significance. In recent years, along with the improvement to the optical instruments to examine the microstructures, quite a big advancement is made in understanding the finer structures or details of the pollen grains. Electron microscopy is also one of the recent aids. Based on the modern techniques and palaeobotanical findings, many workers attempted to elucidate the importance of many pollen characters, e.g. aperture conditions, exine patterns and stratification. Recently interesting results of many layered nexine and occurrence of a third layer 'medine' have enhanced our knowledge. It has been pointed out that these characters may not be without evolutionary significance. It is generally accepted that colpate condition is primitive whereas porate condition is an advanced character (Wodehouse 1935).

Raj (1961) believes, along with other characters, that the apertural evolution in Acanthaceae starts from spiraperturate condition via colpate and colporate to porate nature. Saad (1961) in his studies of Linaceae pollen grains traced the origin of 3-colpate grain from triannuate one; from 3-colpate condition two major lines of evolution are apparent, one leading to the 3-colporate condition while the second one to pantoporate grains through pantocolpate condition.

Vishnu-Mittre (1964) presented an illustrated account of probable apertural evolution based on different schools of thought. It is pointed out that probably trichotomocolpate grains gave rise to non-aperturate sporomorph

from which various types of apertures evolved. Pollen grains with spiraperturate, alternate pores and colpi, diorate, pancolpate and panporate apertures are considered as highly evolved. Kuprianova (1964) presented a tentative code of ancient and derivative characters of pollen grains of angiosperms. In her opinion colpate condition, covered by membranes, porate, colporate, acolpate and aporate grains, are derived ones. Similarly faintly perceptible, scarcely seen or lacking nexine, considerably thicker sexine, reticulate or spinose, very conspicuous or minute with traces of reduction of sculpture are derived characters. She has further suggested that in considering the antiquity as many characters as possible should be taken into consideration. In Linaceae Saad (1961) found evolutionary trends from granulate via granulate striate and granulate baculate to tegillate and tegillate reticulate.

Vishnu-Mittre further commented that psilate, granulate, simply reticulate and spinate exine patterns are primitive though some may be derived, whereas complex reticulations, ornate, striate and tegillate conditions represent advanced characters.

Nair (1965) published an account of trends in morphological evolution of pollen and spores.

As mentioned earlier, under light microscopy only two layers of nexine are seen but electron microscope could help distinguishing three layers of nexine, i.e. N1, N2 and N3, in many cases. Raj (1961) comments that in advanced members of Acanthaceae N3 is absent, and that presence of N1 and N2 and absence of N3 is a highly advanced character.

From the palynological investigations it appears that Sterculaceous pollen grains probably originated from the 3-zonocolpate type with perhaps (?) shorter polar axis (Pl. IX). This ancestral type might have given rise to *Leptonychia* type (brevicolpate) by reduction and finally leading to the porate condition as in *Helicteres*, *Kleinhovia*, *Dombeya*, *Pentapetes*, *Pterospermum* and *Eriolaena*. *Eriolaena* with panporate condition might represent a climax in this line of apertural evolution. *Leptonychia* and *Kleinhovia-Helicteres* group might have given rise to *Fremontia* type or vice versa.

Colporate type of pollen grains might have originated from ancestral type in combination with porate type or the porate type might have evolved from colporate pollen grains (*Fremontia* type, brevicolporate) through reduction and obliteration of colpi. The 3-colporate grains might have given rise to 4-5 colporate grains as in *Waltheria indica* Linn. Erdtman (1952) reported 5–8 colporate grains in *Waltheria americana* L. which points out higher evolutionary trends in this genus. Another line of evolution from the ancestral type might have given rise to 5-aperturate type of grains. Similarly *Reevesia* type might have evolved from *Leptonychia* type by simple multiplication of the aperture number. Erdtman (1952) reported 4–8 colporate (brevicolpate) grains in the same species. This may indicate the continuation of the

evolutionary process within the species. The 3-zonocolporate grains as in *Commersonia, Rulingia, Melochia, Heritiera, Tarrietia, Hermannia, Guazuma,* etc., might have evolved from ancestral type via colporoidate grains or through *Fremontia* type. This complex might have given rise to 4-5 zonocolporate grains. *Buettneria* and *Ayenia,* where apertural nature is indistinct and complex, might represent some of the transitional stages in the evolutionary process. Some of the secondary or tertiary pollen morphological characters are also important from evolutionary point of view.

The presence of the shorter polar axis than the equatorial one is considered as the ancient character (Kuprianova 1964). The pollen grains of *Leptonychia, Abroma, Ayenia, Buettneria, Reevesia, Kleinhovia, Helicteres, Fremontia* possess shorter polar axis and are thus placed below the colporate grains with larger polar axis. On the contrary there are few members which are aperturally quite advanced, e.g. *Waltheria indica* Linn. and *Melochia guazumaefolia* (Linn.) Ritch., but they have shorter polar axis. Similarly among the porate and spinose grains, *Dombeya* and some species of *Pterospermum* have shorter polar axis.

It appears that the primitive and advanced apertural characters do not go side by side with primitive or advanced exine characters, e.g. *Abroma, Leptonychia* and *Reevesia,* etc., which possess primitive aperture, have reticulate, simpli-duplibaculate exine with psilate to ornamented lumina the characters which are quite advanced. *Waltheria indica* Linn. and some other members enjoy both advanced apertural and ornamentation characters, but the polar axis is shorter than the equatorial one. *Helicteres isora* Linn. though possesses an advanced aperture has primitive type of exine pattern. The nature, number and relative thickness of different layers of nexine also throw some light on the primitive and advance nature of pollen grains. In the present study it could not be possible to undertake finer detailed work of nexine except mentioning relative thickness of sexine and nexine.

The evolutionary tendencies as revealed by the present study are not words of finality and could be put to question if other morphological characters are taken into consideration. It is left to other plant morphologists and taxonomists to exploit the data as fully as possible so as to determine how far palynological data could help in assessing phylogenetic and evolutionary tendencies in the family as a whole.

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