Review of Palaeobotany and Palynology
Elsevier Publishing Company, Amsterdam–Printed in The Netherlands

POLLEN MORPHOLOGY OF THE PALMAE AND ITS BEARING ON TAXONOMY[1]

M. A. SOWUNMI

Institute of African Studies, University of Ibadan, Ibadan (Nigeria)

(Received December 3, 1969)
(Resubmitted May 4, 1971)

ABSTRACT

Sowunmi, M. A., 1972. Pollen morphology of the Palmae and its bearing on taxonomy. *Rev. Palaeobot. Palynol.*, 13: 1-80.

This paper presents a pollen-morphological study of the Palmae. A total number of 350 species out of 120 genera were investigated. Pollen-morphological groupings within the family are compared with the taxonomic groupings of several authors and tentative taxonomic suggestions are made on the basis of pollen-morphological characters.

INTRODUCTION

The Palmae is a eurypalynous family comprising about 2,640 species in about 230 genera, widely distributed in the tropics and subtropics, while a few occur in warm temperate regions. The family is considered to be in need of much systematic and morphological study (e.g. Lawrence, 1951; Hutchinson, 1959; and Moore, 1961). This study was therefore undertaken in order to ascertain what light, if any, palynology might shed on the taxonomic problems of this family. A total of 350 species in 120 genera were investigated. Pollen-morphological groupings within the subfamilies are compared with the taxonomic groupings of several authors and tentative taxonomic suggestions are made on the basis of pollen-morphological characters.

Only relatively few investigators had worked on the pollen-morphology of the Palmae. Their observations will be discussed later (pp. 30 ff.) in the light of results obtained from the present investigation.

In contrast to the relative paucity of published literature on the pollen morphology of the Palmae, there is a wealth of literature on their vegetative and gross floral characters,

---

[1] Being part of a doctorate thesis approved by the University of Ibadan. The study was financed by the same university.

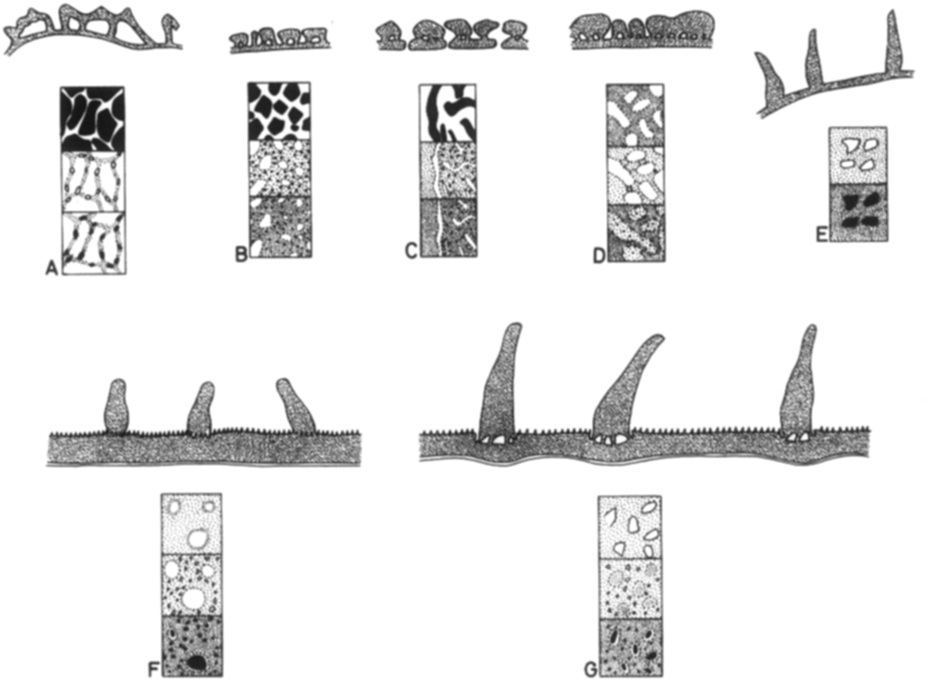
especially those of taxonomic significance (e.g. several monographs by Beccari, 1877-1890, 1908-1914). The schemes proposed by several taxonomists are outlined in Table I (pp. 5-8) which is an amplified modification of Tomlinson's (1961), and also includes subdivisions suggested on palynological evidence from the present investigation.

MATERIALS AND METHODS

The present investigation was based on pollen slides prepared from both herbarium and fresh materials. A list of the species investigated, together with author's name, place and date collected, collector's name and number, and herbarium where the material is kept, respectively, can be found on p. 67 (Appendix II). Both fresh and herbarium materials were acetolysed and a small portion chlorinated (Erdtman, 1960). The following procedures were adopted for some pollen grains (e.g. *Cocos nucifera, Lodoicea seychellarum*, and *Rhapidophyllum hystrix*) for which acetolysis appeared too drastic a treatment:

(*1*) The polliniferous material was boiled for two minutes in absolute alcohol to which some gentian violet had been added (Kumazawa, 1937, modified by present author).

(*2*) The material was stained with two drops of 1% safranine, acidified with 2% hydrochloric acid, and washed with distilled water until the supernatant liquid became colourless (Nair, 1960).



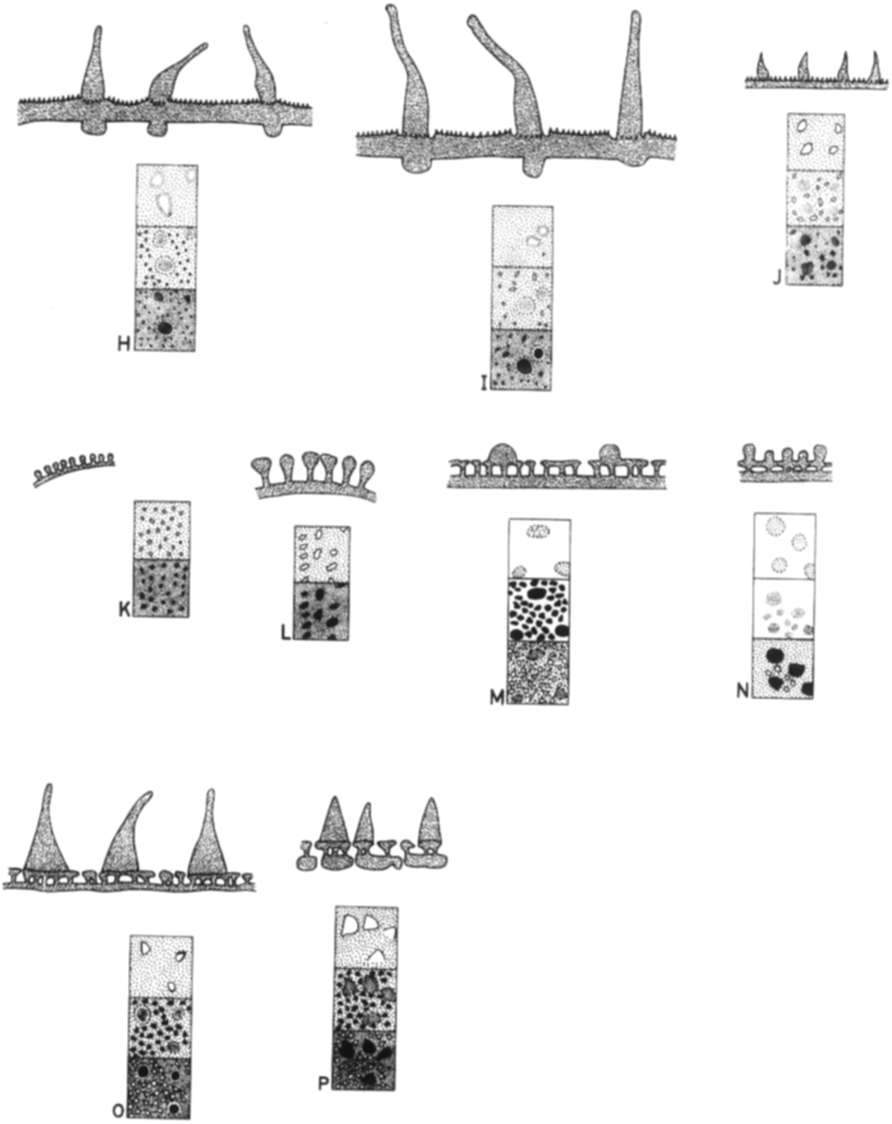


Fig.1. Schematical drawings of the main types of exine patterns in the Palmae.
The exine stratification (ca. X 300) was derived from unsectioned grains seen in optical cross section, with the exception of Text Fig.1M, derived from thin sections. The squares show LO-analysis in a sequence with the highest focus at the top (not drawn to scale).
A. Reticulate, muri curved. B. Reticulate, heterobrochate. C. Vermiculate. D. Negatively reticulate. E. Spinose, spines not deep-seated. F-G. Spinose, spines deep-seated and surrounded by very minute processes. H-I. Spinose, spines deep-seated and surrounded by very minute processes. J. Spinulose, spinules surrounded by very minute processes. K. Pilate. L. Clavate. M. Verrucae borne on a reticulate semitectum. N. Clavae borne on an apparently reticulate semitectum. O. Spines borne on a reticulate semitectum. P. Spinules borne on a reticulate semitectum.

(*3*) The material was chlorinated and stained with methylene blue (Nair, 1960, modified by present author).

The treated pollen grains were mounted in glycerin jelly, and sealed with paraffin wax.

Microscopic investigations were made with a binocular Leitz Laborlux microscope: apochromatic oil immersion objective 100X, n.a. 1.30, eyepiece periplane 10X (one division of a micrometer eyepiece inserted in this eyepiece tube = 1.14 μ), and eyepiece for measurements, Zeiss, 12.5X (here one division of same micrometer eyepiece = 0.75 μ). For finer measurements (e.g. thickness of exine layers), a Leitz "Screw micrometer eyepiece" was used (one division = 0.031 μ). For the investigation of thin sections Leitz phase contrast optics were used: apochromatic oil immersion objective 90X, n.a. 1.15. The figures recorded for the various pollen grain dimensions were generally the average of ten measurements. The thickness of the exine was measured midway along the distal face at the periphery. The dimensions of the processes were recorded separately and were not included in the figures for exine thickness except where otherwise stated. Frequencies of the various processes were calculated at the central part of the proximal face, within an area of about 10 μ^2. Photomicrographs were taken with an Aristophot camera on a Leitz Ortholux microscope and also on the same type of microscope fitted with an Orthomat 35 mm. camera. They illustrate pollen features at different foci, and were oriented in accordance with the principle for palynograms suggested by Erdtman (1952, p. 24).

TERMINOLOGY

The terminology adopted was derived from Erdtman (1952, 1969), Faegri and Iversen (1964), Harris (1955), and Jackson (1928) [latter two from Kremp, 1965], as well as an additional term introduced by the present author. (For definitions of some of the more important terms see Appendix III and Fig.1.)

DESCRIPTIONS OF POLLEN GRAIN TYPES

Twenty-five pollen-morphological types were recognised. In order to avoid repetitions only one or two representatives of each type were described. Details of the pollen morphological features of all the species studied as well as the constituents of each palynological type could be found in Appendix III. In this table, the subfamilies (sensu Moore, 1961) were arranged according to apparent palynological affinity.

The term "subgroup" used in the subsequent descriptions and in Appendix III was not meant to agree with any taxonomic unit recognised hitherto. It was used simply to denote the largest palynological grouping within each subfamily comprising species which had a combination of features in common. Similarly, the term "type" was used to denote a smaller palynological grouping within a "subgroup", comprising species which together had more features in common than with the rest of the "subgroup". A "subgroup" thus

TABLE I

Subdivisions of Palmae

Martius (1850)		Drude (1889)	
Families	Subgroups	Sub-families	Tribes
1. Arecinae	Caryotinae	4. Ceroxylinae	6. Arecinae (e) Areceae (b) Geonome (c) Iriarteae (*Ceroxylon* (d) Morenicea *Pseudoph* (a) Caryoteae (inc. *Oran*
5. Cocoinae	(i) Genera aculeata (ii) Genera inermia		7. Cocoinae (c) Bactridea (a) Elaeideae (b) Attaleae
2. Lepidocaryinae	*Pinnatifrondia* *Flabellifrondia* (*Mauritia,* *Lepidocaryum*)	3. Lepidocaryinae	5. Metroxyleae (a) Raphiae (b) Calamea 4. Mauritieae
3. Borassinae	*Veras heteroclitas*	2. Borassinae	3. Borasseae (i *Pholidocarp*
4. Coryphinae	Sabalinae Phoenicinae (*Phoenix*)	1. Coryphinae	2. Sabaleae 1. Phoeniceae
Genera heteroclita	*Nypa* *Phytelephas*	5. Phytelephantinae	*Nypa* *Phytelephas*

pp. 5-8

	Burret (1953), Burret and Potztal (1956)		Beccari and Pichi-Sermolli (1
	Tribes	Subtribes	Subfamilies
ie nc.) e (inc. *enix*) *ia*)	7. Arecoideae	(e) Kentieae (f) Ptychospermeae (inc. *Orania*) (h) (c)–Miscellaneous groups inc. e.g. *Phytelephas, Sclerosperma* (g) Geonomeae (b) Iriarteae (d) Chamaedoreae (a) Caryoteae (exc. *Orania*)	Arecoideae
e	1. Cocoideae	(b) Bactrideae (c) Cocoideae (d) Attaleae	Cocoideae
e	4. Lepidocaryoideae	1. *Eugeissona* 5. Metroxyleae 4. Raphieae 2. Calameae 3. Salacceae 6. Korthalsieae 7. Ancistrophylleae 8. Mauritiineae	Lepidocaryoideae
c. *s*)	3. Borassoideae		Borassoideae
	5. Coryphoideae 6. Phoenicoideae	1. inc. *Corypha,* *Corypha* *Nannorrhops* 2. inc. *Schipia*	Coryphoideae Phoenicoideae
	2. Nypoideae	*Nypa* (*Phytelephas* inc. in Arecoideae)	Nypoideae Phytelephantoideae

956)	Hutchinson (1959), based mainly on Bentham and Hooker (1883)		Tomlinson (1961)
Subgroups	Tribes	Subtribes	Subdivisions sugges by anatomical evide
1. Areceae 2. Kentieae 4. Ptychospermeae 3. Linospadiceae 5. Clinostigmeae 6. Iguanureae 7. Dypsideae 8. Cyrtostachyeae 9. Oncospermeae 11. Oranieae (inc. Sclerosperma) 10. Caryoteae (exc. *Orania*)	5. Areceae	1. Euareceae 2. Ptychospermeae 6. Linospadiceae 7. Malortieae 10. Iguanureae 8. Ceroxyleae 5. Oncospermeae 9. Geonomeae 4. Iriarteae 3. Wettenieae 11. Chamaedoreae 12. Caryotideae (inc. *Orania, Sclerosperma*)	Arecoid palms (exc several anomolous genera) Iriartoid palms Chamaedoroid paln Caryotoid palms (e *Orania, Sclerospern*
	6. Cocoineae		Bactroid palms Cocoid palms
Sub-tribes 1-8 as in Burret (q.v.) exc. Mauritiineae Mauritieae	4. Calameae 3. Lepidocaryeae	*Mauritia, Lepidocaryum*	Lepidocaryoid palr
	2. Borasseae		Borassoid palms
	1. Corypheae 7. Phoeniceae		Sabaloid palms Phoenicoid palms
	8. Phytelephantineae	*Nypa* *Phytelephas*	Nypoid palms Phytelephantoid pa Genera incertecedi (inc. *Ceroxylon, Leopoldinia, Orani Pseudophoenix, Sclerosperma*)

	Potztal (1964) in Engler's Syllabus der Pflanzenfamilien		Sowunmi (1967)
ted nce	Subfamilies	Tribes	Subdivisions suggested by Palynological evidence
	Arecoideae	1. Areceae	*Areca* type
		2. Kentieae	*Paralinospadix* type
		4. Ptychospermeae	*Gronophyllum* type
		3. Linospadiceae	*Pinanga* type
		5. Clinostigmeae	*Roystonea* type
		6. Iguanureae	*Socratea* type
ıs		7. Dypsideae	*Deckenia* type
ıc.		9. Cyrtostachyeae	*Cyrtostachys* type
ıa)		10. Oncospermeae	*Oncosperma* type
		11. Oranieae	*Phoenicophorium* type
		8. Ceroxyleae	*Ravenea* type
		12. Geonomeae	*Sclerosperma* type
		13. Iriarteae	*Arenga* type
		14. Chamaedoreae	
	Caryotoideae	Caryoteae	
	Cocosoideae	2. Bactrideae	*Elaeis* type
		3. Elaeideae	*Cocos* type
		4. Cocoseae	
		1. Attaleae	
ns	Lepidocaryoideae	Calameae	*Lepidocaryum* type
		Metroxyleae	*Mauritia armata* type
		(Raphieae	*Salacca* type
		inc. *Korthalsia*)	*Plecotocomia* type
		Lepidocaryeae	*Calamus microcarpa* type
		(Mauritieae)	*Plectocomiopsis* type
			Korthalsia type
			Daemonorops sparsiflorus type
	Borassoideae	Borasseae	*Borassus* type
	Coryphoideae	Corypheae	
	Phoenicoideae	(Sabaleae)	
		Trachycarpeae	
		Phoeniceae	
	Nypoideae	Nypeae	*Nypa* type
lms	Phytelephantoideae	Phytelephanteae	
;			
ı			

N.B. for the components of these subdivisions see Appendix III (pp. 68-80) consisted of a complex of "types". In a few instances where palynological and gross morphological groupings were in agreement, these palynological divisions agreed to some extent with certain recognised taxonomic units.

N.B. The figures given represent the mean and standard deviation.

P = Polar axis; E_1 = Longest axis of the grain, i.e. the longer equatorial diameter; E_2 = Shorter equatorial diameter which is perpendicular to E_1; it is also the largest breadth of the grains.

Subfamily Arecoideae

Twelve palynological types were recognized in this subfamily.

Areca subgroup

Diagnosis: Pollen grains monocolpate (a few species also had some trichotomocolpate grains). Amb elliptical to more or less circular, rounded-triangular in trichotomocolpate grains. Sexine tectate to semitectate; tectum reticulate, punctate, vermiculate, or negatively reticulate; without processes.

Five types, based on sexine pattern and aperture details, were recognized.

Areca type

Diagnosis: Amb elliptical. Sexine reticulate. Muri simplibaculate through to multibaculate.

Areca paniculata. Pollen grains monocolpate. P 17.5 ± 1.0 μ, E_1 34 ± 1.8 μ, E_2 25 ± 2.1 μ. Amb elliptical. Colpi practically as long as E_1; width 3.4 ± 0.5 μ, margins wavy.

Exine 1.3 ± 0.1 μ thick. Tectum 0.8 ± 0.2 μ thick, reticulate, heterobrochate, brochi more or less polygonal. Muri 0.6 ± 0.1 μ wide simpli- to duplibaculate. Lumina 1.0 ± 0.3 μ wide. Bacula 0.2 ± 0.1 μ high. Nexine 0.2 ± 0.1 μ thick.

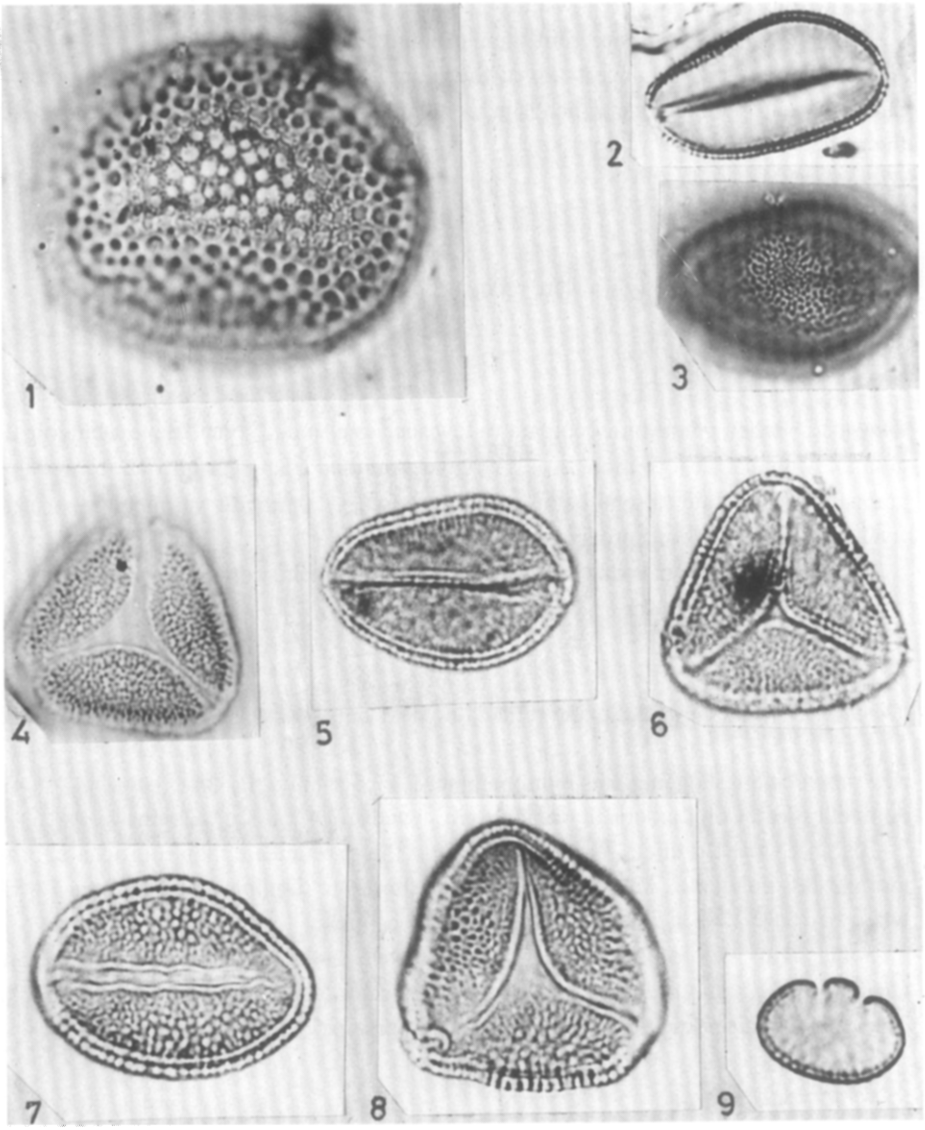
Some grains of *Roscheria melanochaetes* (Plate I, 2-4), *Kentia ramsayi* (Plate I, 5-6), *Gigliolia subacaulis* and *Pseudophoenix navassana* (Plate I, 7-8), were trichotomocolpate. The colpi in *Iriartella setigera* (Plate I, 9) were pontoperculate.

Paralinospadix type

Diagnosis: Amb mostly elliptical, sometimes more or less circular, or with one or two lateral bulges. Sexine tectate. Tectum punctate or minutely reticulate.

Basselinia sp. aff. *B. tomentosa.* Pollen grains monocolpate. P?, E_1 50 ± 3.5 μ, E_2 46 ± 3.1 μ. Amb mostly circular, sometimes circular–elliptical or elliptical. Colpi practically as long as E_1, their shape and width varying from grain to grain.

PLATE I



Arecoideae.

1. *Areca warburgiana.* (X 1,200)
2-4. *Roscheria melanochaetes.*
2-3. Monocolpate grains.
4. Trichomotocolpate grain. (X 1,200)
5-6. *Kentia ramsayi.*
5. Monocolpate grain.
6. Trichotomocolpate grain. (X 800)
7-8. *Pseudophoenix navassana.*
7. Monocolpate grain.
8. Trichotomocolpate grain. (X 800)
9. *Iriartella setigera.* (X 800)

Exine 1.8 ± 0.4 μ thick, gently undulating. Tectum minutely reticulate. Nexine 0.8 ± 0.3 μ thick.

Paralinospadix petrickiana. Pollen grains monocolpate. P 19.5 ± 2.0 μ, E_1 46 ± 3.3 μ, E_2 31 ± 1.8 μ. Amb more or less elliptical, sometimes with one or two lateral bulges which could be quite pronounced. Colpi practically as long as E_1, width 5.0 ± 0.5 μ, margins wavy.

Exine 1.0 ± 0.1 μ thick, undulating, with one or more inwardly directed infoldings; sometimes the infoldings were more pronounced forming tubercles in the exine. Tectum punctate to minutely reticulate. Nexine 0.3 ± 0.1 μ thick.

Gronophyllum type

Diagnosis: Amb elliptical. Tectum coarsely reticulate. Muri conspicuously winding, simplibaculate. Bacula usually quite distinct.

Gronophyllum luridium (Plate II, 4). Pollen grains monocolpate. P 23.5 ± 2.9 μ, E_1 38 ± 2.2 μ, E_2 31 ± 2.4 μ. Amb elliptical. Colpi 24 ± 2.3 μ long, 3.7 ± 0.9 μ wide, rounded at the ends.

Exine 3.8 ± 0.2 μ thick. Tectum coarsely reticulate, heterobrochate. Muri 0.7 ± 0.2 μ wide, winding, very distinctly simplibaculate. Lumina 4.8 ± 1.2 μ wide, a few bacula seemed to occur in some lumina (LO-analysis). Nexine 0.6 ± 0.1 μ thick, slightly undulating.

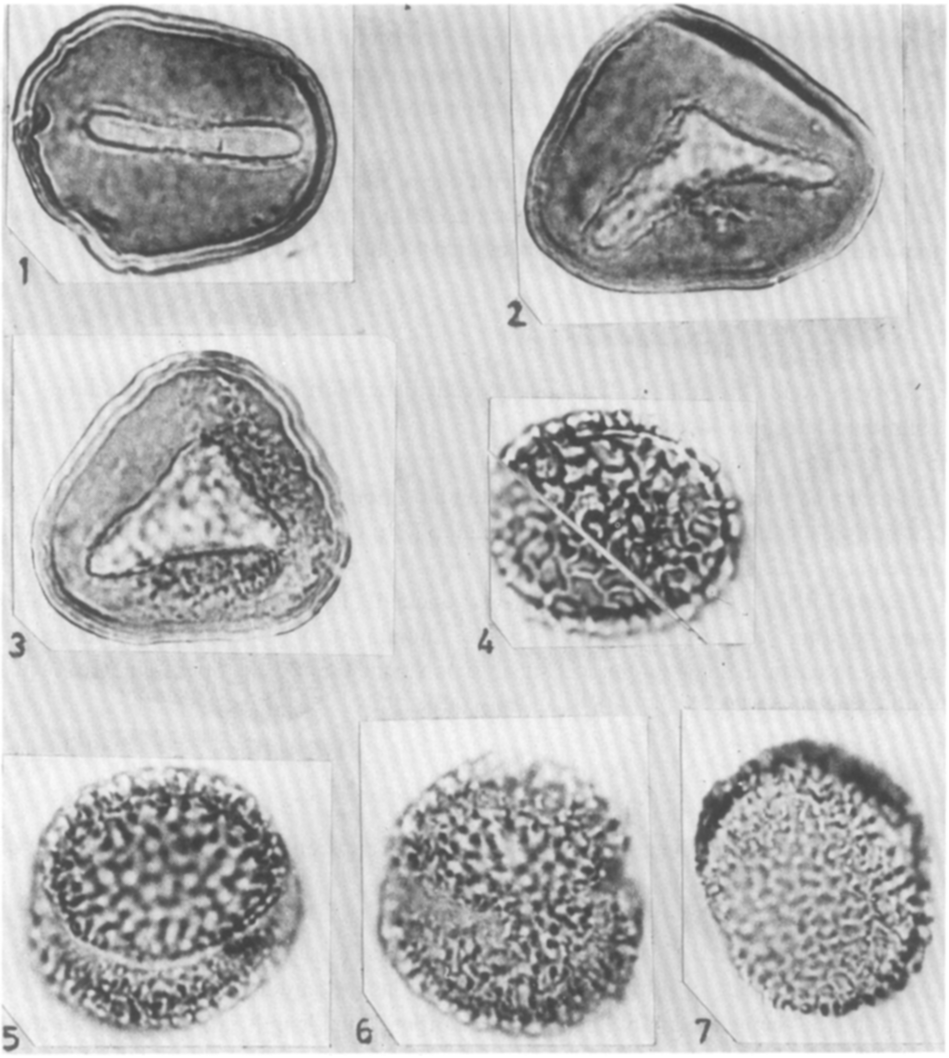
Pinanga type

Diagnosis: Pollen grains nearly annulocolpate, a few apparently dicolpate. Amb more or less circular.

Pinanga javana (Plate II, 5-7). Pollen grains nearly annulocolpate to dicolpate. P 39 ± 2.5 μ, E_1 45 ± 1.9 μ, E_2 37 ± 1.6 μ. Amb more or less subcircular; subisopolar, one "hemisphere" being distinctly larger than the other. Colpi length varied from grain to grain: In some grains the colpus formed an almost complete ring encircling the equator; in some others it completely encircled one half of the grain and a portion of the other half; in yet a few other grains it appeared "bridged" at two areas (presumably the polar areas) and therefore seemed to be two meridional apertures.

Exine 2.4 ± 0.2 μ thick. Tectum coarsely reticulate, markedly heterobrochate. Muri 0.6 ± 0.3 μ wide, winding, simplibaculate. Bacula very prominent. Lumina 3.0 ± 1.2 μ wide, mostly polygonal, a few of the smaller ones being narrow and elongated. Nexine 0.3 ± 0.1 μ thick, undulating.

PLATE II



Arecoideae (contd.). All photomicrographs are × 800.

1-3. *Paralinospadix caudiculata.*
1. Monocolpate grain.
2. Transitional grain.
3. Trichotomocolpate grain.
4. *Gronophyllum luridium.*
5-7. *Pinanga javana.*
5. Annulocolpate grain.
6. Nearly annulocolpate grain.
7. Half a grain detached from the other half during acetolysis.

P.S. If the grains in *Pinanga javana* and the other similar species *P. ternatensis* were definitely sometimes dicolpate, then these two would be the only species in the Arecoideae, so far, with dicolpate grains. Dicolpate grains were only otherwise found in the Lepidocaryoideae.

Roystonea type

Diagnosis: Amb more or less elliptical, with one or two lateral bulges, very rarely triangular or subtriangular. Tectum pattern rather irregular–finely reticulate or punctuate to vermiculate to negatively reticulate.

Deckenia subgroup

Diagnosis: Pollen grains monocolpate. Amb elliptical to more or less circular. Sexine apparently intectate, provided with processes–pila or spinules:

Two types, based on the nature of the processes, were recognised.

Socratea type

Diagnosis: Sexine spin(ul)ose.

Wettinia maynensis. Pollen grains monocolpate. P 27 ± 3.6 μ, E_1 42 ± 2.4 μ, E_2 37 ± 1.6 μ. Amb rounded elliptical to subcircular. Colpi length 42 ± 2.4 μ, width 6.0 ± 1.3 μ, sometimes slightly narrower towards the ends.

Sexine spin(ul)ose. Spin(ul)es 2.9 ± 0.4 μ long, sharply pointed at the tip, base "semilunar-shaped"; basal diameter 2.6 ± 0.3 μ; apparently deciduous (this might be an artifact due to acetolysis). Very minute processes (LO-analysis) were found between the spin(ul)es.

Nexine 1.3 ± 0.1 μ thick, slightly undulating especially at the inner part, slightly swollen below the spin(ul)es. There seemed to be a very thin inner layer below the nexine. This needs to be verified by the study of ultra-thin sections.

Deckenia type

Diagnosis: Pollen grains monocolpate. P 15.5 ± 1.5 μ, E_1 29 ± 0.7 μ, E_2 21.0 ± 1.1 μ. Amb elliptical. Colpi length 29 ± 0.7 μ, width 4.2 ± 0.9 μ at and near the distal pole, tapering towards the ends, 2.2 ± 0.3 μ wide.

Sexine pilate. Pila 0.8 ± 0.2 μ high, capita width 0.7 ± 0.1 μ, adjacent pila occasionally touched and apparently merged; frequency 57 per 10 μ^2. Nexine 1.2 ± 0.1 μ thick, outer part gently undulating.

Cyrtostachys subgroup

Diagnosis: Pollen grains monocolpate. Amb elliptical to more or less circular. Sexine tectate, with supratectal processes—verrucae, clavae, or spinules. Three types based on the nature of processes were recognised.

Cyrtostachys type

Diagnosis: Sexine provided with supratectal verrucae.

Cyrtostachys sp. Pollen grains monocolpate. P 18.0 ± 2.2 μ, E_1 31 ± 0.9 μ, E_2 23.5 ± 1.4 μ. Amb elliptical to more or less circular. Colpi 31 ± 0.9 μ long, 5.1 ± 0.6 μ wide (colpi were well seen in only very few grains).

Exine 1.3 ± 0.1 μ thick. Verrucae were borne on the tectum, height 0.6 ± 0.1 μ, diameter 1.0 ± 0.2 μ, frequency 16 per 10 μ^2. Tectum 0.3 ± 0.1 μ thick, minutely reticulate (OL-analysis); homobrochate. Bacula 0.3 ± 0.1 μ high. Nexine 0.6 ± 0.1 μ thick.

Oncosperma type

Diagnosis: Sexine provided with supratectal clavae.

Oncosperma tigillarium (Plate III, 5). Pollen grains monocolpate. P 19.0 ± 1.9 μ, E_1 31 ± 2.3 μ, E_2 25 ± 1.4 μ. Amb elliptical. Colpi practically as long as E_1, width 5.0 ± 0.8 μ at and near the distal pole, gradually tapering towards the ends.

Exine 1.5 ± 0.1 μ thick, gently undulating. Clavae apparently borne on the tectum, at least in part, height 1.5 ± 0.2 μ, capita diameter 0.8 ± 0.2 μ; frequency 44 per 10 μ^2. Tectum 0.3 ± 0.1 μ thick, apparently faintly and minutely OL-patterned, at least in some grains, supported by a baculate layer of the same thickness. Nexine 1.0 ± 0.2 μ thick, outer part more undulating than inner part.

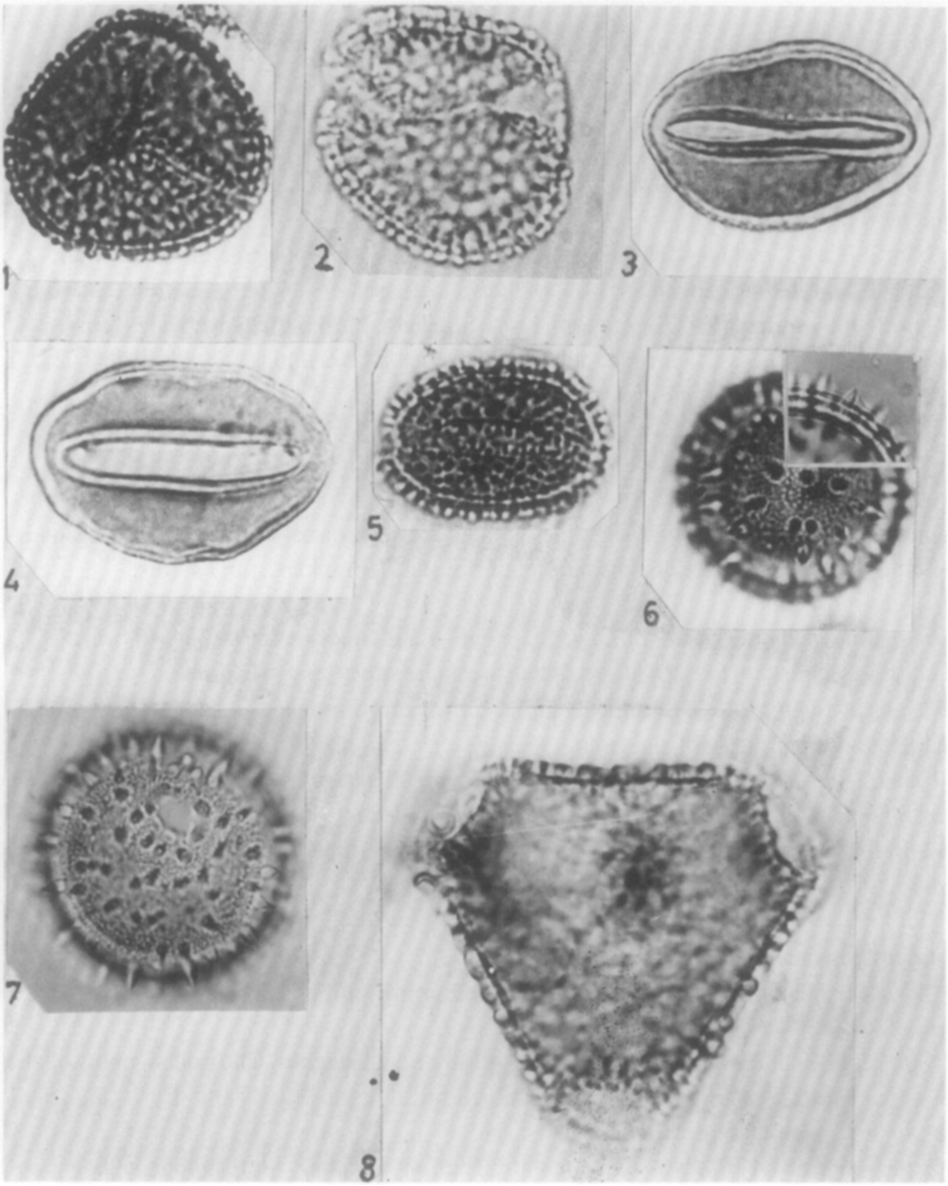
Phoenicophorium type

Diagnosis: Sexine provided with supratectal spinules.

Phoenicophorium borsigianum. Pollen grains monocolpate. P 14.0 ± 1.1 μ, E_1 23.0 ± 1.2 μ, E_2 18.5 ± 1.4 μ. Amb elliptical to more or less circular. Colpi length 23.0 ± 1.2 μ, width 2.7 ± 0.4 μ.

Exine 0.9 ± 0.1 μ thick, undulating. Spinules borne on the tectum, length 2.0 ± 0.1 μ, basal diameter 1.1 ± 0.1 μ; frequency 6 per 10 μ^2. Tectum 0.4 ± 0.1 μ thick, supported by a baculate layer 0.2 ± 0 μ thick. Nexine 0.3 ± 0.1 μ thick.

PLATE III



Arecoideae (contd.).

1. *Pinanga kuhlii.* (X 800)
2. *Pinanga ternatensis.* Annulocolpate grain. (X 800)
3-4. *Jessenia batana*, showing two different colpus shapes. (X 800)
5. *Oncosperma tigillarium.* (X 800)
6-7. *Ravenea hildebrandtii.* (X 1,200)
8. *Sclerosperma mannii.* (X 1,200)

Ravenea type

Diagnosis: Pollen grains monoporate. Amb circular. Pore more or less rounded. Sexine tectate, provided with supratectal spin(ul)es.

Ravenea hildebrandtii (Plate III, 6-7). Pollen grains monoporate, radiosymmetrical. P 20.0 ± 1.5 μ, E 26 ± 0.9 μ. Amb circular. Pore centric or, more often, slightly acentric, diameter 4.5 ± 0.4 μ.

Exine 1.7 ± 0.2 μ thick. Spin(ul)es sharply pointed at the tip; borne on the tectum; length 3.1 ± 0.9 μ, basal diameter 1.0 ± 0.2 μ; frequency 8 per 100 μ^2. Tectum 0.2 ± 0 μ thick, minutely reticulate (OL-analysis), homobrochate. Muri 0.2 ± 0.1 μ wide, simplibaculate. Lumina 0.5 ± 0.1 μ wide, polygonal. Bacula 0.4 ± 0 μ high. Nexine 1.1 ± 0.2 μ thick, apparently slightly undulating and perforated.

Sclerosperma type

Diagnosis: Pollen grains triporate. Sexine tectate. Tectum coarsely reticulate. A unigeneric type, unique among all other palms on account of its triporate apertural status.

Sclerosperma mannii (Plates III, 8; IV, 1). Pollen grains triporate, radiosymmetrical. P 11.5 ± 0.5 μ, E 45 ± 1.6 μ. Amb rounded triangular, sides straight. Pores (3.9 ± 0 X 8.5 ± 0.6) μ; when viewed from the distal face, the pores were seen to be situated on or just within the periphery of the grain.

Exine 2.3 ± 0.2 μ thick. Tectum coarsely reticulate, heterobrochate. Muri 0.8 ± 0.2 μ wide, simpli- to dupli- to triplibaculate. Bacula very distinct. Lumina 2.1 ± 0.8 μ wide, those in the central area larger than those towards the periphery. Nexine 0.4 ± 0.2 μ thick.

Subfamily Phoenicoideae

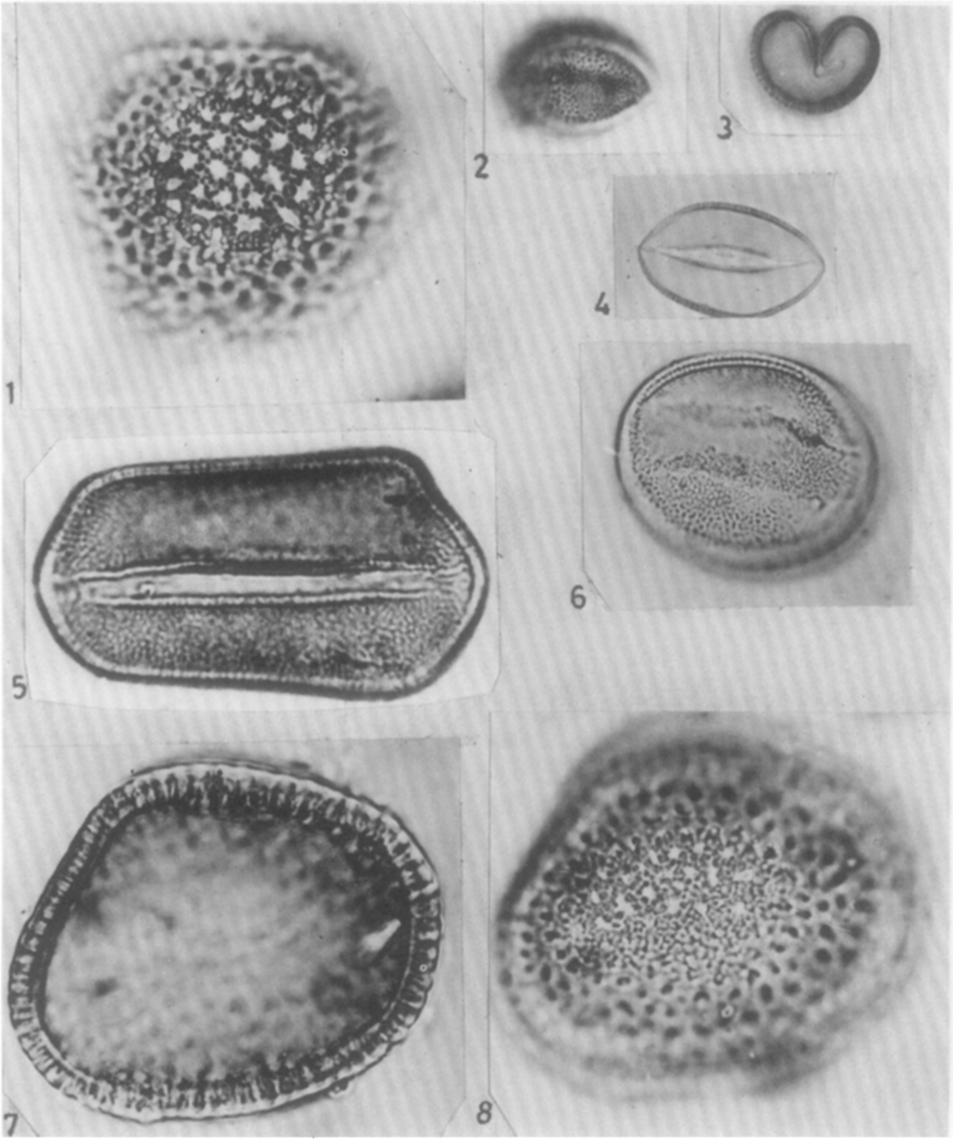
(No special palynological type was recognised in this subfamily).

A unigeneric subfamily which is palynologically homogeneous. The pollen grains of the sole genus, *Phoenix*, were monocolpate. Amb elliptical. P 9.5 μ to 17.0 μ, E_1 20.5 μ to 26 μ, E_2 13.5 μ to 20.5 μ.

Exine 0.6 μ to 1.1 μ thick. Sexine tectate. Tectum reticulate. Muri simplibaculate (Plate IV, 2-4).

There was no distinctive *Phoenix type*, because the grains were similar to those of *Areca type* (Arecoideae). The only probable distinction was the comparatively smaller size of *Phoenix* grains.

PLATE IV



Arecoideae (contd.).
1. *Sclerosperma mannii* (contd.). (X 1,000)

Phoenicoideae.
2-4. *Phoenix dactylifera.* (X 750)

Phytelephantoideae.
5. *Phytelephas poeppigii.* (X 750)

Coryphoideae.
6. *Chamaerops humilis*, note operculum. (X 1,000)
7-8. *Colpothrinax wrightii.* (X 1,000)

Subfamily Phytelephantoideae

(No special palynological type was recognised in this subfamily. Only pollen grains from the genus *Phytelephas* s.s. were available for study).

The pollen grains of *Phytelephas* were monocolpate. P 32 μ to 34 μ, E_1 70 μ to 75 μ, E_2 43 μ to 47 μ. Amb elliptical, very rarely rounded triangular.

Exine 1.9 μ to 2.0 μ thick. Sexine tectate. Tectum reticulate. Muri simpli- to duplibaculate (Plate IV, 5).

No distinctive *Phytelephas* type was recognised since the pollen grains were similar to those of *Areca* type (Arecoideae), the only probably notable distinction being the comparatively larger size of *Phytelephas* grains.

Subfamily Coryphoideae

(No special palynological type was recognised in this subfamily which was palynologically homogeneous).

Pollen grains monocolpate. P 11.5 μ to 32 μ, E_1 23.0 μ to 55 μ, E_2 17.0 μ to 45 μ. Amb elliptical, very rarely rounded triangular.

Exine 0.9 μ-2.3 μ thick. Sexine tectate. Tectum reticulate. Muri simpli–through to multibaculate.

Chamaerops humilis and *C. humilis* var. *elatior*, deviated from the general plan in having pontoperculate colpi (Plate IV, 6).

As with *Phoenix* and *Phytelephas*, no distinct *Corypha* type pollen grain was recognised, the grains in the subfamily Coryphoideae being practically indistinguishable from some of those in the *Areca* type (Arecoideae).

Subfamily Cocoideae

(Two palynological types were recognised in this subfamily).

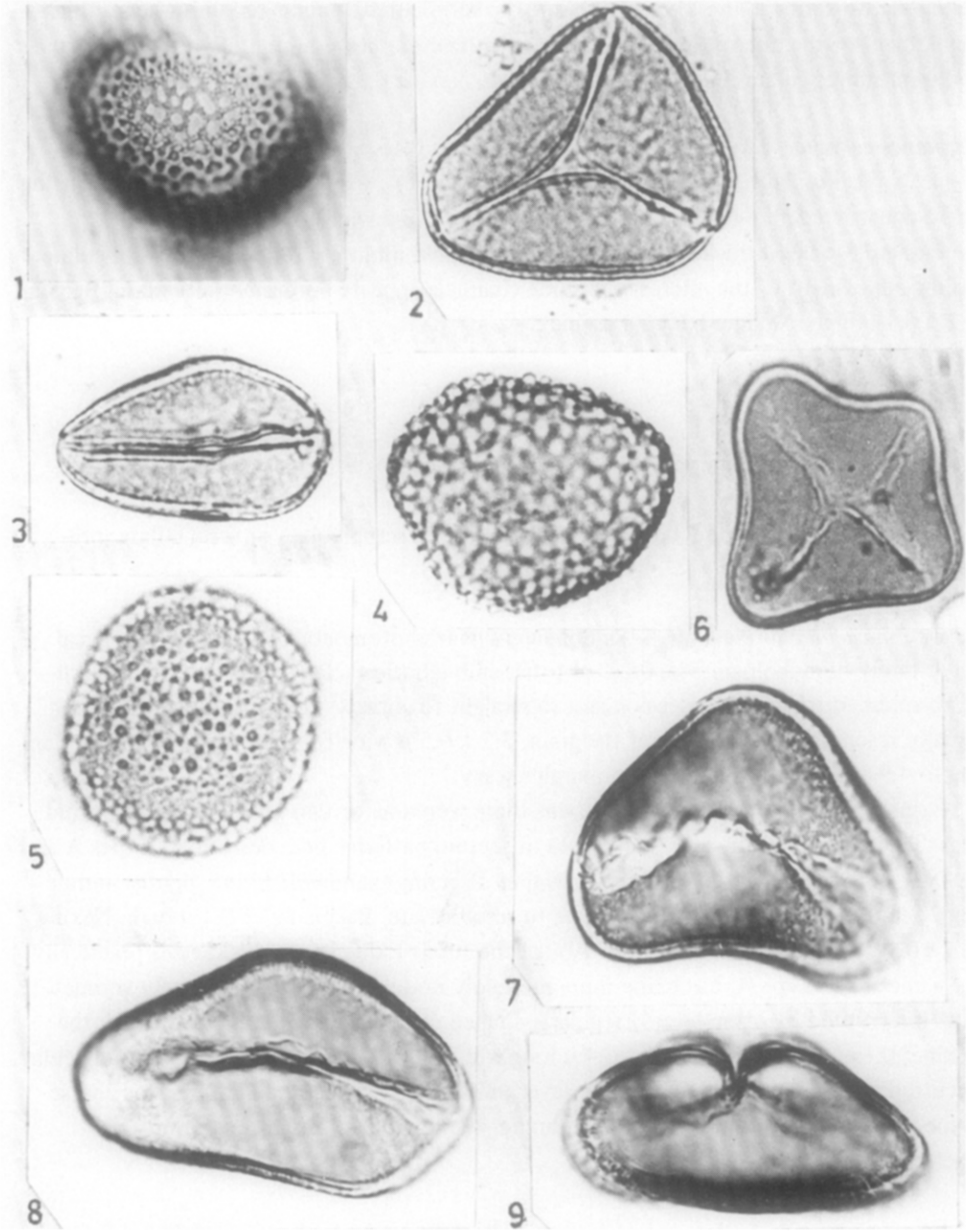
Elaeis type

Diagnosis: Pollen grains monocolpate or trichotomocolpate. Amb elliptical or rounded triangular.

Sexine semitectate. Tectum pattern more or less irregular–minutely reticulate or subreticulate to vermiculate to negatively reticulate; processes absent. (*Bactris gasipaes* with a verrucose sexine seemed to be the only exception so far, Plate V, 4-5).

Elaesis guineensis var. *tenera.* Pollen grains trichotomocolpate, radiosymmetrical. P 18.0 ± 1.9 μ, E 50 ± 2.6 μ. (Sometimes monocolpate, viz: about 6.0% of total. Amb elliptical, sometimes with one or two lateral bulges. Also very rarely tetrachotomocolpate, viz: 1% of total). Amb rounded triangular, sides concave. Colpi arm 18.0 ± 3.1 μ long, 1.9 ± 0.4 μ wide, not always reaching the periphery of the grain, margins wavy.

PLATE V



Coryphoideae (contd.).
1. *Corypha martiana.* (X 1,200)
2-3. *Pritchardia affinis.*
2. Trichtomocolpate grain.
3. Monocolpate grain. (X 800)

Cocoideae
4-5. *Bactris gasipaes.* (X 750)
6-9. *Elaeis guineensis* var. *dura.*
6. Tetrachotomocolpate grain. (X 750)
7. Transitional grain.
8. Monocolpate grain.
9. Trichotomocolpate grain, lateral view. (X 1,200)

Exine 1.1 ± 0.1 μ thick. Tectum 0.6 ± 0.1 μ thick, minutely subreticulate to negatively reticulate, to vermiculate. The channels of the vermiculation appeared unbroken at high adjustment of the microscope, but at low adjustment appeared minutely reticulate, hence the term subreticulate. Bacula 0.2 ± 0.1 μ high. Nexine 0.3 ± 0 μ thick.

Aiphanes caryotaefolia. Pollen grains monocolpate. P 15.5 ± 0.7 μ, E_1 31 ± 2.1 μ, E_2 19.5 ± 1.4 μ. Amb elliptical. Colpi length 31 ± 2.1 μ, width 4.8 ± 0.6 μ at and near the ends, constricted at and near the distal pole (3.2 ± 0.6 μ wide), margins wavy.

Exine 0.8 ± 0.2 μ thick. Tectum 0.4 ± 0.2 μ thick, minutely reticulate to vermiculate; at low adjustment of the microscope some channels appeared minutely reticulate. Bacula 0.2 ± 0.1 μ high. Nexine 0.2 ± 0.1 μ thick.

Cocos type

Diagnosis: Pollen grains monocolpate or trichotomocolpate. Amb elliptical or rounded triangular.

Sexine tectate or semitectate. Tectum punctate to scrobiculate or vermiculate; processes absent.

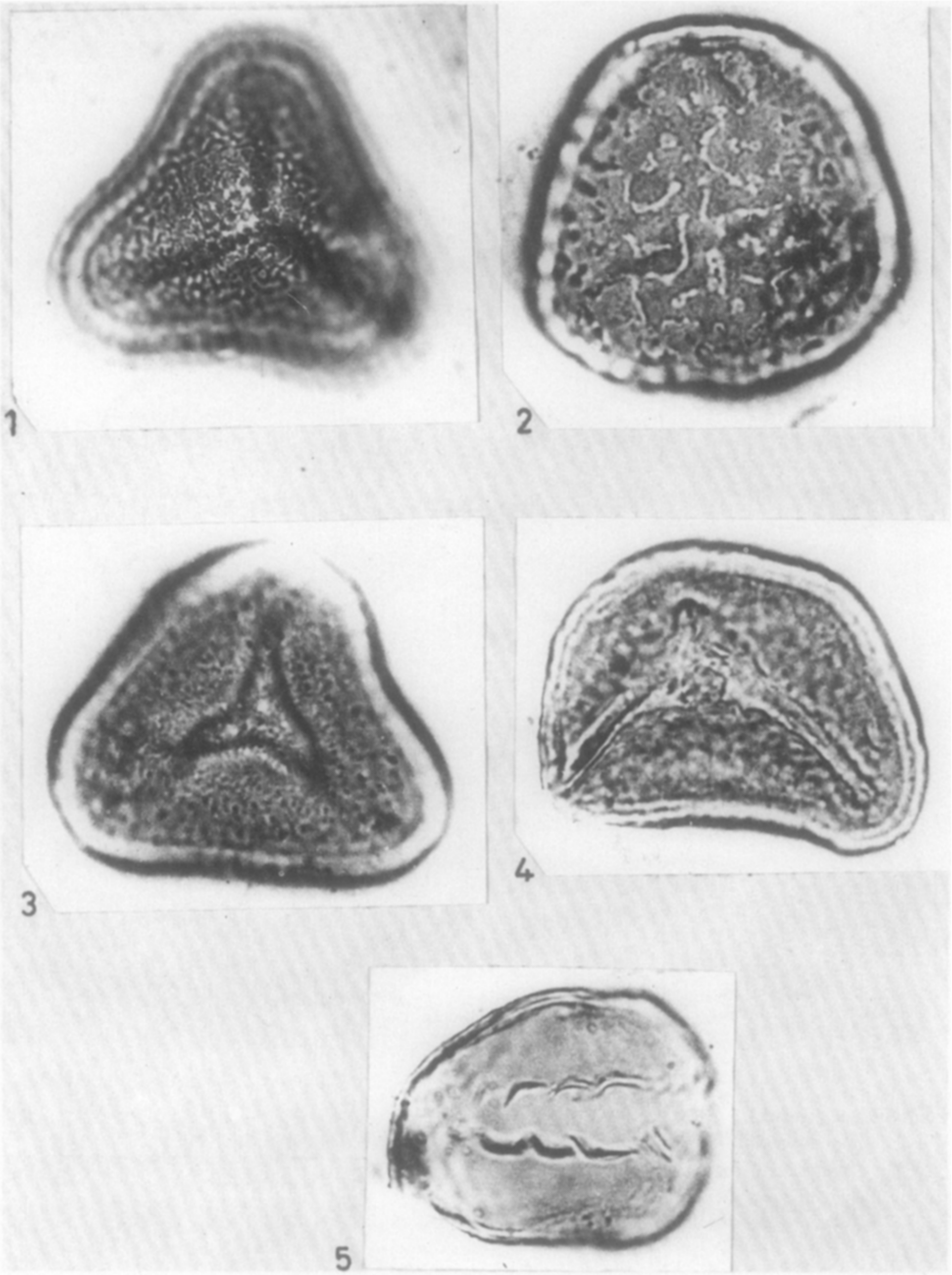
Acrocomia aculeata (Plate VI, 2-4). Pollen grains trichotomocolpate, radiosymmetrical (very rarely monocolpate, viz. 0.2% of total; amb elliptical). P 31 ± 1.7 μ, E 55 ± 3.2 μ. Amb rounded triangular, sides concave to straight to convex. Colpi arm 27 ± 4.1 μ long, usually reaching the periphery of the grain, 3.2 ± 0.5 μ wide for most of its length, widening to 4.9 ± 0.5 μ at the periphery, margins wavy.

Exine 2.3 ± 0.5 μ thick; in a few grains there were one or two marked exinous infoldings. There were broadly two main types of tectum patterns, here designated Types A and B. Type A–occurring in 81% of total number of grains examined: Exine slightly undulating. Tectum 1.2 ± 0.2 μ thick, punctate to scrobiculate. Bacula 0.3 ± 0.1 μ high. Nexine 0.8 ± 0.1 μ thick. Type B–found in 19% of the total: Exine strata thicknesses practically the same as for Type A, but exine more markedly undulating. Tectum coarsely vermiculate, interrupted by often large, irregularly-shaped channels which also cut through the nexine; these channels were 7.4 ± 6.4 μ long and 2.5 ± 1.0 μ wide. Densely spaced bacula occurred within them as well as in the layer immediately below the tectum. This coarse exine pattern was distinctly visible even under the low power magnification of the microscope.

P.S. Occasionally both types of tectum pattern occurred in the same grain.

Cocos nucifera (Plate VI, 5). Pollen grains monocolpate. (Very rarely trichotomocolpate, viz: 0.1% of total grains viewed; amb sharply rounded triangular, sides straight to convex). Amb elliptical to more or less circular. P 37 ± 2.2 μ, E_1 65 ± 1.8 μ, E_2 47 ± 3.4 μ. Colpi length 65 ± 1.8 μ, width 9.3 ± 0.7 μ, margins wavy.

PLATE VI



Cocoideae (contd.).

1. *Elaeis guineensis* var. *dura* (contd.). (X 1,200)

2-4. *Acrocomia aculeata.*

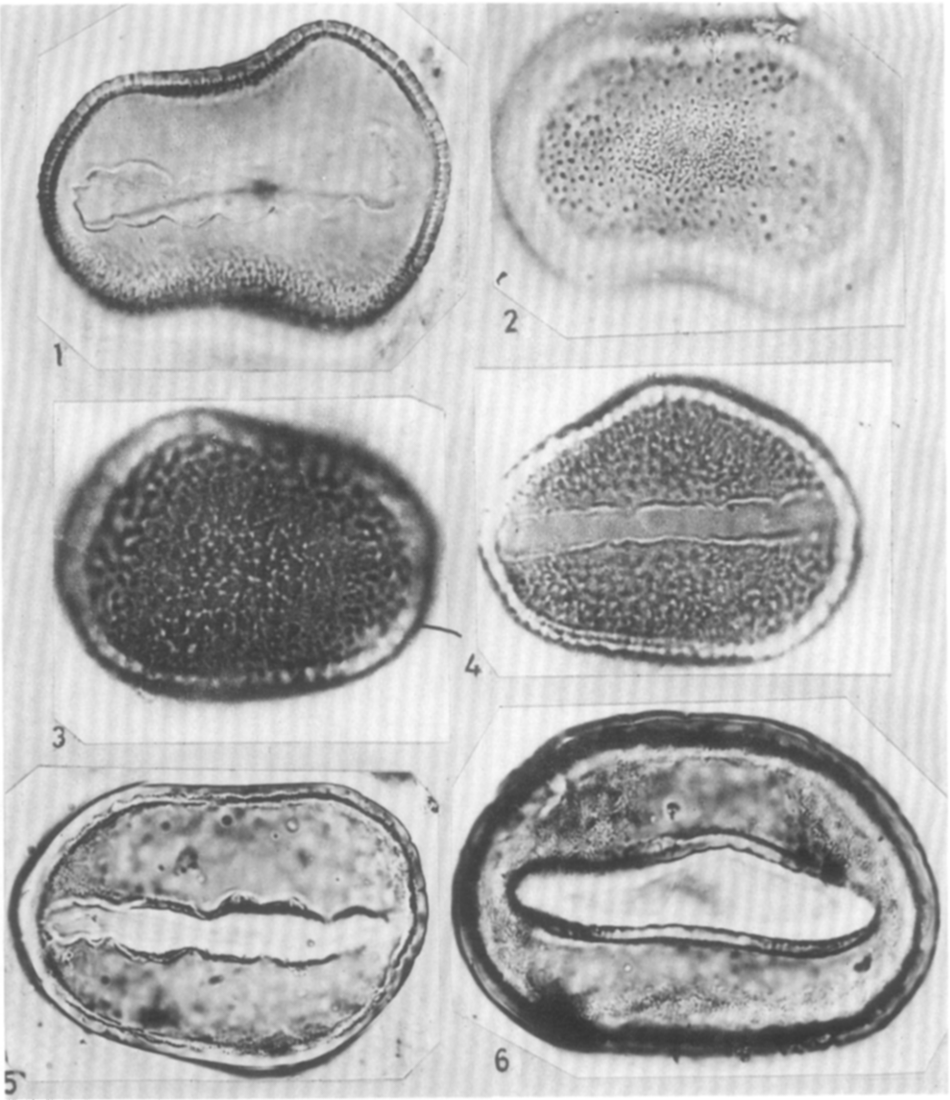
2. Type B grain.

3. Type A grain.

4. Transitional grain. (X 800)

5. *Cocos nucifera*, monocolpate grain. (X 800)

PLATE VII



Cocoideae (contd.).
1-2. *Maximiliana venatorum.* (X 950)
3-4. *Orbignya speciosa.* (X 800)
5. *Scheelea leandroana.* (X 950)
6. *Scheelea leandroana.* (X 1,200)

Exine 1.9 ± 0.2 μ thick, undulating, sometimes with exinous infoldings, and tubercles which were more prominent in some grains than in others. Tectum 0.6 ± 0.1 μ thick, punctate, supported by a finely but densely baculate layer 0.3 ± 0.1 μ thick. Nexine 1.0 ± 0.1 μ thick.

Arikuryroba and Lytocaryum. Pollen grains monocolpate. Sexine semitectate. Tectum reticulate.

The two genera *Arikuryroba* and *Lytocaryum* did not constitute a separate, distinct palynological type since the pollen grains in both were similar to some of those in *Areca* type (Arecoideae).

Subfamily Borassoideae

(Only one distinct palynological type was recognised in this subfamily).

Borassus type

Diagnosis: Pollen grains monocolpate. Amb elliptical. Sexine tectate. Tectum provided with supratectal verrucae.

Borassus flabellifer (Plate VIII, 2-3). Pollen grains monocolpate. P 34 ± 2.0 μ, E_1 65 ± 3.0 μ, E_2 45 ± 3.6 μ. Amb elliptical. Colpi 65 ± 3.0 μ long, 5.0 ± 1.2 μ wide, tapering to a point at each end.

Exine 1.8 ± 0.2 μ thick. Sexine tectate, provided with verrucae borne on the tectum. Verrucae 1.8 ± 0.2 μ high, basal diameter 2.7 ± 0.3 μ; frequency 5 per 10 μ^2. Tectum 0.4 ± 0.1 μ thick, minutely reticulate (OL-analysis). Muri simplibaculate. Lumina polygonal. Bacula 0.5 ± 0.1 μ high, distinctly visible. Nexine 1.0 ± 0.2 μ thick.

Bismarckia and related genera. Pollen grains monocolpate. P 21.0 μ to 31 μ, E_1 35 μ to 48 μ, E_2 29 μ to 55 μ. Amb elliptical to more or less circular.

Exine 1.4 μ to 2.6 μ thick. Sexine tectate to semitectate. Tectum punctate or reticulate to vermiculate to negatively reticulate.

The pollen grains in the genera in this subdivision were similar to those in *Roystonea* type (Arecoideae), and hence they were not considered a separate and distinct palynological type.

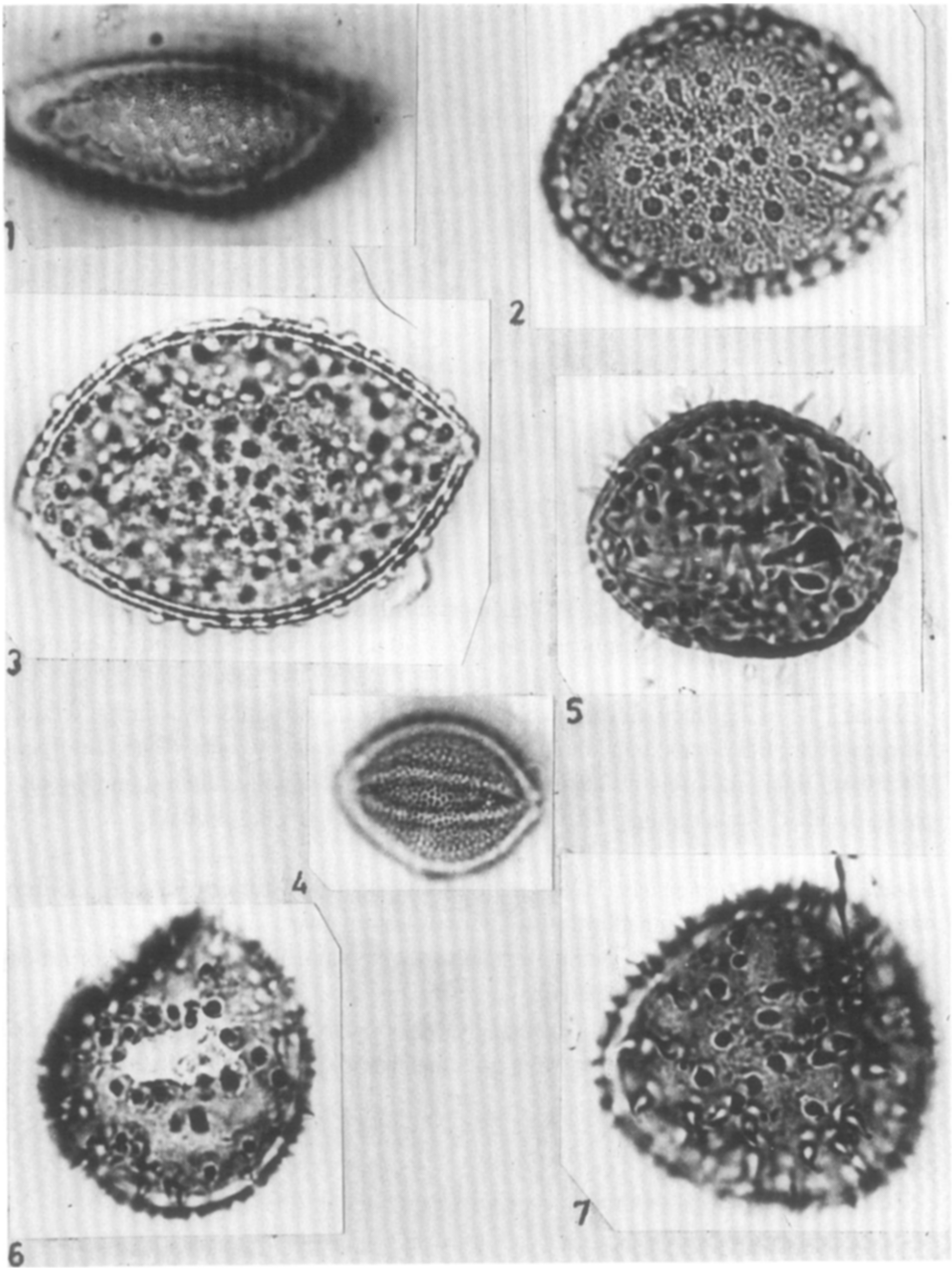
Subfamily Caryotoideae

(Only one distinct palynological type was recognised in this subfamily).

Arenga type

Diagnosis: Pollen grains monocolpate. Amb elliptical. Sexine intectate, spinulose, rarely spinose.

PLATE VIII



Cocoideae (contd.).
1. *Scheelea leandroana* (contd.). (X 950)

Borassoideae.
2-3. *Borassus flabellifer.* (X 800)

Caryotoideae.
4. *Caryota mitis.* (X 800)

Lepidocaryoideae.
5. *Lepidocaryum gracile.* (X 800)
6-7. *Mauritia flexuosa.* (X 800)

Arenga westerhouti. Pollen grains monocolpate. P 17.5 ± 1.4 μ, E_1 34 ± 0.9 μ, E_2 24.0 ± 1.0 μ. Amb elliptical. Colpi length 34 ± 0.9 μ, width mostly 2.3 ± 0 μ, slightly narrower at the ends.

Sexine intectate, spinulose. Spinules 2.6 ± 0.2 μ long, basal diameter 0.9 ± 0.2 μ, base swollen; not deeply seated, tip usually sharply-pointed; frequency 9 per 10 μ^2. Nexine 1.0 ± 0.2 μ thick, gently undulating, slightly swollen below spinules.

Caryota (Plate VIII, 4). Pollen grains monocolpate. Amb elliptical. Sexine intectate, pilate.

The pollen grains of this genus were similar to those of *Deckenia* type (Arecoideae), though the pila in the latter were slightly larger. The genus, *Caryota*, therefore did not constitute a separate, distinct palynological type.

Subfamily Lepidocaryoideae

(Eight palynological types were recognised in this subfamily).

Lepidocaryum type

Diagnosis: Pollen grains monocolpate. Amb elliptical to more or less circular.

Sexine intectate, consisting of deeply-seated, stout spines and spinules.

Lepidocaryum gracile (Plate VIII, 5). Pollen grains monocolpate. P 29 ± 2.2 μ, E_1 40 ± 1.8 μ, E_2 38 ± 1.8 μ. Amb elliptical to subcircular. Colpi 30.6 ± 1.8 μ long, 7.4 ± 2.9 μ wide for most of their length, gradually tapering to a point at the ends, margins wavy, not always distinct.

Sexine intectate, spinose and spinulose. Spines deeply seated in "pockets" within the nexine, length 6.2 ± 0.6 μ long, basal diameter 1.9 ± 0.2 μ. Apparently, at least in some cases, the spines were supported by slender bacula 0.7 ± 0.1 μ long. The upper part or neck of the spines was narrow, ending in a blunt tip which was sometimes club-shaped. The neck bent over to varying degrees, ranging from no bend at all (spine perpendicular to periphery of grain) to an inverted U-shaped loop. Frequency 3 per 10 μ^2. Occasionally few smaller spines (3.1 ± 0.4 μ long, basal diameter 1.1 ± 0.1 μ) occurred very close to some stout spines; these spinules had sharply pointed tips. Some nexinous "pockets" were seen to be empty, indicating that the spines might be deciduous; on the other hand this might be an artifact. In between and around the bases of the spines were very minute spinules. Nexine 1.1 ± 0.2 μ thick, undulating, bulging below spines (1.7 ± 0.2 μ thick). There appeared to be a thin inner layer below the nexine.

N.B. It is highly desirable that the exine pattern and stratification in *L. gracile* as described above be verified by the study of ultra-thin sections.

Mauritia flexuosa (Plate VIII, 6-7). Pollen grains monocolpate (or monoporate, viz. 33% of total). P 44 ± 2.9 μ, E_1 47 ± 1.6 μ. Amb circular to rounded elliptical. Colpi comparatively short, 16.5 ± 2.1 μ long, 8.1 ± 1.8 μ wide. Pores of porate grains were almost isodiametric, though they were elongated slightly, 12.0 ± 0.5 μ X 10.5 ± 1.4 μ.

Sexine intectate. Spines deeply seated in "pockets" within the nexine, length 5.3 ± 1.4 μ, basal diameter 1.7 ± 0.2 μ. The upper part or neck was either slender and straight or bent to varying extents, ending either in a sharply pointed tip or a very tiny knob. A few empty nexinous "pockets" were found as in *Lepidocaryum gracile*, indicating that the spines might be deciduous; on the other hand this might be an artifact. Densely spaced between and at the bases of the spines were very minute processes (spinules?). Nexine 1.3 ± 0.4 μ thick, undulating, bulging slightly below the spines.

Mauritia armata type

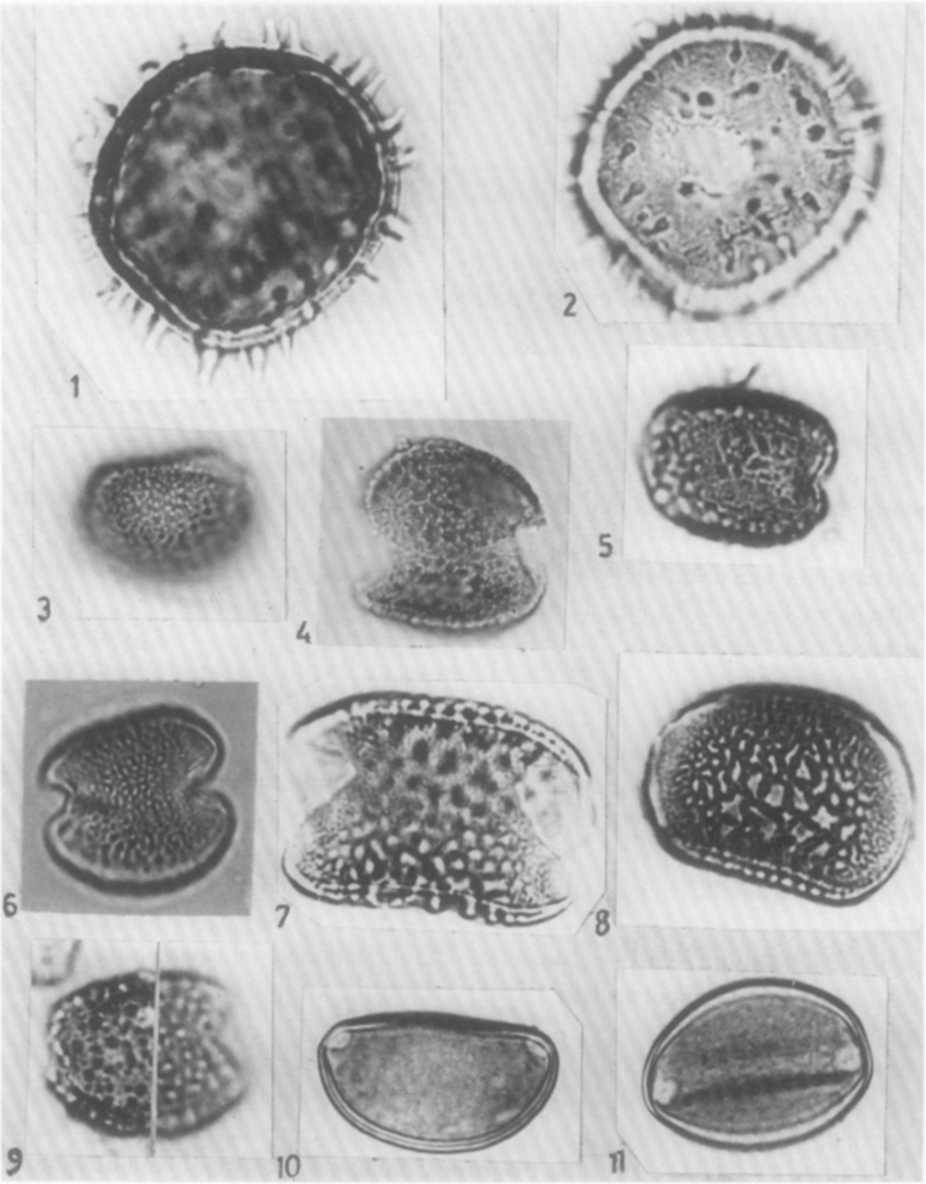
Diagnosis: Pollen grains monoporate. Amb circular. Sexine intectate, spinose and spinulose; spines generally stout.

Mauritia armata (Plate IX, 1-2). Pollen grains monoporate. P 41 ± 2.2 μ, E 47 ± 1.3 μ. Amb circular. Pores 12.5 ± 2.0 μ X 13.0 ± 3.3 μ almost isodiametric, but sometimes elongated (16.0 ± 2.5 μ X 10.5 ± 2.1 μ), usually acentrally situated.

Sexine intectate, spinose and spinulose. Spines seated in a small depression of the nexine, length 4.1 ± 0.5 μ, basal diameter 2.2 ± 0.4 μ, with a slight constriction at the point of origin. Spines usually perpendicular to the periphery of the grain or slightly inclined at an angle to it; tips blunt or club-shaped; frequency 2 per 10 μ^2. Occasionally very few spinules with pointed and curved tips also occurred. In between and around the bases of the spines were very minute spinules. Nexine 2.8 ± 0.2 μ thick, bulging slightly below the spines. There appeared to be a thin inner layer below the nexine; this was ragged and not well defined.

Mauritia vinifera. The apertural status of the grains in the specimen studied was very difficult to determine. There was a strong indication that it might be porate. The spines differed in detail from those in *M. armata:* Spines deeply seated in "pockets" within the nexine, length 10.5 ± 1.7 μ, basal diameter 1.7 ± 0.3 μ. Practically all the larger spines had long necks, which were usually as long as or slightly longer than half the total spinal length. They each ended in a distinct knob. The comparatively smaller spines either ended in a small knob or were simply blunt at the tip. The necks of the spines might be perpendicular to the periphery of the grain, or inclined to varying degrees. In a few grains, few still smaller spines occurred, length 4.7 ± 0 μ, basal diameter 1.0 ± 0 μ. These generally did not end in knobs; the tips were blunt or, apparently, pointed. Few empty "pockets" seen indicated that the spines might be deciduous, but this might also be an artifact. In between and around the bases of the spines were densely spaced and very minute processes which looked like minute pila or bacula.

PLATE IX



Lepidocaryoideae (contd.).
1- 2. *Mauritia armata.* (X 750)
3- 4. *Calamus guruba.* (X 1,000)
5. *Calamus rivalis.* (X 750)
6. *Daemonorops formicarius.* (X 750)
7- 8. *Metroxylon salomonense.* (X 750)
9. *Calamus microcarpa.* (X 750)
10-11. *Daemonorops sparsiflorus.* (X 750)

The spines in *Lepidocaryum* and *Mauritia* were unique to the Palmae in that they were usually stout and deeply seated. The only other stout spines encountered in this study—those in *Nypa fruticans*—were superficial, and were borne on the tectum.

Salacca type

Diagnosis: Pollen grains nearly annulocolpate. Sexine apparently intectate, spinulose or pilate.

The specimens of *S. affinis, S. borneensis,* and *S. edulis* available for study were too poor for any measurements to be made. The first two species were spinulose and the latter pilate.

Calamus subgroup

Diagnosis: Pollen grains of species in this subgroup differed from those of all other palms in being dicolpate.

Sexine semitectate or intectate. Tectum reticulate, verrucose reticulate, or baculate. Three palynological types, based on sexine details, were recognised.

Plectocomia type

Diagnosis: Pollen grains dicolpate.

Sexine semitectate. Tectum vermiculate to reticulate. Muri supported by one to several rows of bacula; rarely negatively reticulate.

Plectocomia elongata. Pollen grains dicolpate. P 27 ± 1.2 μ, E_1 27 ± 1.3 μ, E_2 21.5 ± 1.5 μ.

Exine 1.0 ± 0.1 μ thick. Sexine semitectate. Tectum minutely reticulate, homobrochate. Muri 0.2 ± 0.1 μ wide, simplibaculate. Lumina 0.4 ± 0.1 μ wide, polygonal. Nexine 0.3 ± 0.1 μ thick.

The sexine details in most of the other members deviated somewhat from this general pattern. *Calamus guruba* and *C. nobilis:* Muri simpli- to duplibaculate. Lumina mostly polygonal, but sometimes in the form of narrow elongated channels which usually anastomosed, resulting in a negative reticulum. *C. rivalis:* Tectum vermiculate to minutely subreticulate. Tectum isles separated by narrow channels which appeared unbroken at high adjustment of the microscope, but at low adjustment often became minutely reticulate (subreticulate). Muri simplibaculate.

The brochi in *Daemonorops formicarius* were sometimes discontinuous in parts. *Metroxylon salomonense* was very coarsely reticulate, heterobrochate, brochi becoming smaller and indistinct towards the colpi; in the immediate vicinity of the colpi only bacula could be seen. Muri 2.1 ± 0.9 μ wide, straight to slightly winding, sometimes discontinuous over small areas, supported by one to several rows of bacula. Lumina 4.3 ± 1.9 μ wide, very small bacula occurred in the very large lumina.

Calamus microcarpa type

Calamus microcarpa (Plate IX, 9). Pollen grains dicolpate. P 28 ± 2.7 μ, E_1 30 ± 1.7 μ, E_2 26 ± 2.6 μ.

Exine 0.8 ± 0.1 μ thick. Tectum reticulate, provided with verrucae. Verrucae 1.1 ± 0.2 μ high, basal diameter 1.6 ± 0.1 μ, occurring on top of the tectum; frequency 14 per 10 μ^2. Tectum 0.2 ± 0.1 μ thick, partly minutely reticulate (OL-analysis). Muri simplibaculate. Bacula not always distinctly seen. Nexine 0.3 ± 0.1 μ thick.

Plectocomiopsis type

Plectocomiopsis geminiflora var. borneensis. Pollen grains dicolpate. P 23.0 ± 1.2 μ, E_1 21.0 ± 1.0 μ, E_2 17.5 ± 1.1 μ.

Sexine baculate. Bacula 0.7 ± 0.1 μ long, 0.4 ± 0.1 μ wide, sometimes slightly swollen at the top; frequency 156 per 10 μ^2. There appeared to be no tectum. Nexine 0.3 ± 0.1 μ thick.

Korthalsia subgroup

Diagnosis: Pollen grains diporate. Amb more or less circular to elliptical.

Two palynological types were recognised on the basis of sexine and apertural details.

Korthalsia type

Korthalsia laciniosa. Pollen grains diporate. P 29 ± 1.3 μ, E_1 23.5 ± 2.6 μ, E_2 33 ± 2.1 μ. Amb subcircular to rounded elliptical. Pores subequatorial, their diameter 4.7 ± 1.0 μ. Sexine spinulose. Spinules not deeply seated, sharply-pointed; length 1.7 ± 0.2 μ long, basal diameter 0.6 ± 0.2 μ, frequency 8 per 10 μ^2; in between and apparently around the base of the spinules were very minute processes (minute spinules?)—these were seen more clearly in LO-analysis, Nexine 1.0 ± 0.2 μ thick.

Daemonorops sparsiflorus type

Daemonorops sparsiflorus (Plate IX, 10-11). Pollen grains diporate. P 21.5 ± 2.5 μ, E_1 37 ± 1.0 μ, E_2 26 ± 1.4 μ. Amb elliptical, slightly curved. Pores equatorial or slightly subequatorial, their diameter 3.7 ± 0.6 μ. In the presumably distal polar face there was a distinct, narrow, central area extending from one pore to the other and bordered by an upward infolding of the exine. This area probably represented a vestigial colpus.

Exine 1.9 ± 0.3 μ thick, slightly undulating. Tectum 0.7 ± 0.1 μ thick, punctate to very minutely reticulate. Bacula 0.2 ± 0 μ high. Nexine 1.0 ± 0.1 μ thick.

Subfamily Nypoideae

(One distinct palynological type was recognised in this subfamily).

Nypa—a monotypic genus—is represented by a single species, *Nypa fruticans*, with distinctive palynological features.

Nypa type

Nypa fruticans (Plates X, 4-5). Pollen grains annulocolpate. P ?, E_1 49 ± 2.3 μ, E_2 42 ± 2.4 μ. The colpus formed a complete ring encircling the polar axis; the two "hemispheres" composing a grain were easily separable. Colpus width was often impossible to ascertain.

Exine 1.8 ± 0.3 μ thick. Sexine semitectate. Tectum reticulate, provided with spines. Spines superficially borne on top of the tectum, and supported by bacula, length 7.4 ± 0.6 μ, basal diameter 3.1 ± 0.1 μ. Some spines appeared slightly curved near the tip which was sharply pointed or blunt. Bacula 1.0 ± 0.2 μ high, prominent. The tips of adjacent bacula often coalesced, forming a thin, minutely reticulate tectum (distinct OL-pattern). Nexine 0.7 ± 0.2 μ thick.

DISCUSSION OF POLLEN-MORPHOLOGICAL FEATURES

Size: Kuprianova (1948) gave the size range of palm pollen grains as 18-35 μ, rarely about 50 μ.

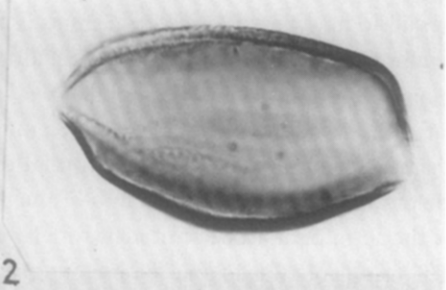
Erdtman (1952) gave the range of the longest axis as 20 μ or slightly more to about 80 μ. The range in the length of the longest axis obtained during the present investigation is from 20 μ in *Dypsis* sp. to about 75 μ in *Phytelephas poeppigii.* The author's results are much more in accordance with Erdtman's than with Kuprianova. The disparity is probably due to the fact that Kuprianova examined a fewer number of species.

Absolute pollen size is a relative parameter which is subject to a great deal of variation depending on at least three factors—method of preparation, and age of pollen slides, and the level of maturity of the pollen grains. It is, perhaps, the parameter of least specificity and hence of limited diagnostic significance.

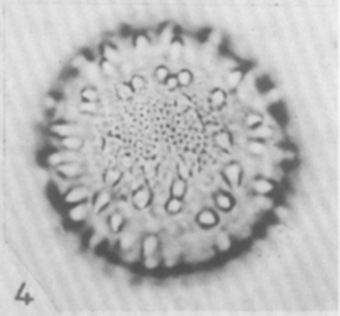
Shape: A few investigators had described the types of shapes found in this family. Gassner (1941) in a passing reference to the pollen-morphological features of 14 species whose development he studied described the shapes as oval or spherical. Cranwell (1953) in a summary of the pollen characters of the Palmae described the shape as ellipsoidal. Nair and Sharma (1963) recorded ellipsoidal and spheroidal shapes in eight varieties of *Cocos nucifera.* Punt and Wessels Boer (1966a) considered that the shape of the grain depended

PLATE X


1


2


3


4


5

Lepidocaryoideae (contd.).
1-3. *Ancistrophyllum secundiflorum.* (X 950)

Nypoideae.
4. *Nypa fruticans.* (X 1,200)
5. *Nypa fruticans,* ultra-thin section showing supratectal spines and exine stratification. (X 1,950)

upon the kind of aperture. Thus, trichotomocolpate grains were said to be regularly triangular, and monocolpate ones oblong or oval and usually asymmetric, but some species were said to have nearly symmetric grains (Punt and Wessels Boer, 1966b). The grains were also said to be kidney-shaped in equatorial view (transverse position). But Thanikaimoni (1966), in the most comprehensive palynological study of the Palmae published so far, considered the shape of the pollen mother cell and the type of tetrad formation (i.e. simultaneous or successive wall formation) to be important factors in deciding the shape of pollen grains. Thus the amb of the pollen grains could be equilaterally triangular, or in the form of an isoceles triangle, or else be spherical, or elliptic.

The results obtained from the present investigation regarding the types of shapes of palm pollen grains essentially agree with those of earlier investigators. In the majority of the grains (i.e. monocolpate ones) the shape was oval or oblong, the contour in polar view (amb) was elliptical–either regularly or irregularly. Many of them were slightly asymmetrical, the largest breadth not lying in the middle, but shifted to one side, but some were more or less bilaterally symmetrical.

Monocolpate grains were kidney-shaped in transverse equatorial view, and more or less boat-shaped in longitudinal equatorial view.

Monoporate grains had a more or less spherical amb. Trichotomocolpate and triporate grains had a rounded-triangular amb, the sides being straight, convex, or concave.

Observations of tetrad types and aperture forms in *Elaeis guineensis* showed that, as far as could be ascertained, all the grains from a tetrahedral tetrad (simultaneous wall formation) were rounded-triangular in shape, while those from decussate tetrads (successive wall formation) were either elliptical, rounded-triangular, or transitional (i.e. intermediate between elliptical and triangular; see Sowunmi, 1968). The author would therefore agree with Thanikaimoni (1966) rather than with Punt and Wessels Boer (1966a) regarding the factors that determine the shape of palm pollen grains.

Aperture: A few investigators had recorded the occurrence and prevalence of monocolpate grains in the Palmae (Wodehouse, 1935; Gassner, 1941; Kuprianova, 1948; Erdtman, 1952; Cranwell, 1953; Nair and Sharma, 1963; Punt and Wessels Boer, 1966a, b; and Thanikaimoni, 1966). In the present study too, the majority of the grains examined (81%) had monocolpate grains. Some of the investigators mentioned earlier (viz. Wodehouse, 1935; Kuprianova, 1948; and Thanikaimoni, 1966) pointed out the primitive nature of this single furrow.

Kuprianova (1948) recorded the presence of an operculum in the furrow of *Chamaerops humilis* grains. Erdtman (1952) described the colpus of this same species as being pontoperculate. Thanikaimoni (1966) described the pollen grains of *Caryota mitis* and *C. urens* as being "monosulcate-operculate", and those of *Chamaerops humilis* as "monosulcate-pontoperculate".

From the present investigation it was seen that the apical parts of the opercula in *Chamaerops humilis* were merged with the exine surrounding the colpus, as pointed out by the latter two investigators. The author did not observe opercula in *Caryota mitis* and

C. urens as observed by Thanikaimoni (ibid.). This was probably due to the fact that the specimens studied by the author were acetolysed, and the opercula must have become detached by then since, as pointed out by Thanikaimoni (ibid.), the opercula become detached after acetolysis.

The author wishes to point out, for the first time, the occurrence of pontoperculate grains in *Iriartella setigera.* It is of interest to note that *Chamaerops humilis* (Coryphoideae) and *Iriartella setigera* (Arecoideae) have very similar pollen grains, viz. monocolpate-pontoperculate, exine reticulate, but belong to different subfamilies, and are otherwise not very closely related. This is probably an instance of parallel evolution.

The colpi, as observed in the present investigation, were usually long. In most cases they extended from one end to another, and coincided with the longest axis of the grains. The shape of the colpi varied between the different species. They might be wide at the ends and constricted at or near the middle, as in *Jessenia batana* (Plate III, 3-4), or of a uniform width throughout as in *Phytelephas poeppigii* (Plate IV, 5); or they might be wide at and near the middle, tapering to a point at the ends as in *Phoenix dactylifera* (Plate IV, 2-4). Though only one form of colpus shape was generally found among the pollen grains of a species, there might also be variations in the same species (e.g. Plates III, 3-4; VII, 5-6).

It is known that with regard to fossil pollen grains, pollen genera had sometimes been recognised principally on the basis of their colpus characteristics, viz.: whether the colpus extended from end to end or not, and whether the maximum width was at and near the middle or at the ends (with a constriction in the middle). The variability of colpus shape and length within a species or genus, in the Palmae, raises some doubt as to the diagnostic value of these characters.

Annulocolpate grains occurred in *Nypa fruticans* (Nypoideae), and very probably in *Pinanga javana* and *P. ternatensis* (Arecoideae). In these three species, the two "hemispheres" had sometimes become separated, most probably during acetolysis. In the grains which were still entire, there was little doubt that the connection between the two "hemispheres" was very weak, the exine being thin in the colpus region. Most of the grains in *Pinanga javana, P. ternatensis, Salacca affinis,* and *S. edulis* were almost annulocolpate, the extension of the colpus varying somewhat from grain in each species. As pointed out by Thanikaimoni (1966) and, independently, by Sowunmi (1968) the aperture in *Nypa fruticans* is a meridional ring-like aperture perpendicular to the equatorial axis, and not a "zonisulculate", a ring parallel to the equator, as indicated by Erdtman (1952, p. 306).

Trichotomocolpate grains were found mainly in the Cocoideae where they formed the predominant type in certain species, e.g. *Bactris major, Elaeis guineensis* and *Acrocomia mexicana.* Such grains also occurred in the subfamilies Arecoideae, Coryphoideae, and Phytelephantoideae, where they constituted only a small proportion of the total number of grains viewed, varying from less than 0.1% to 5.3%. *Pinanga kuhlii* (Arecoideae) was an exception because its pollen grains were predominantly trichotomocolpate and only very rarely monocolpate. Trichotomocolpate grains were not encountered in the subfamilies Phoenicoideae, Caryotoideae, Borassoideae, Lepidocaryoideae, and Nypoideae. Several investigators had observed this type of aperture in palm pollen grains. Gassner (1941) observed that the grains of *Bactris speciosa* had a three-slit opening. It would seem that this appeared unexpected and unusual to him hence he tried to explain it away by referring to it as a "fixation artifact". Erdtman (1944) listed nine palm species whose pollen grains had a three-slit opening each. Four of these had a mixture of mono- and trichotomocolpate grains, while the other five had only the latter type of grains. He considered pollen with three-slit openings aberrant forms of the common monocolpate ones, and that a mechanical factor was probably involved in their formation. In this respect, Thanikaimoni's suggestion is relevant. He suggested that the shape of the mother cell and the type of tetrad formation seemed to be the important factors that determined the shape and the aperture of palm grains, if the differentiating aperture simulated the shape of the pollen grain amb.

Kuprianova (1948), Erdtman (1952), Cranwell (1953) and also Nair and Sharma (1963) referred to the occurrence of trichotomocolpate grains in the Palmae. Kuprianova (1948) furthermore pointed out the primitive nature of this trichotomocolpus. Punt and Wessels Boer (1966a) also recorded the occurrence of trichotomocolpate grains in the Cocoid palms studied by them. In several species they found a mixture of both mono- and trichotomocolpate grains, the monocolpate grains prevailing; but in one species, *Attalea oleifera* only trichotomocolpate grains were found.

Thanikaimoni (1966) also recorded the occurrence of trichotomocolpate grains in the subfamilies Arecoideae, Caryotoideae, Cocosoideae (Cocoideae), Coryphoideae, and Phytelephantoideae. According to him trichotomocolpate grains occurred, rarely, in *Caryota ochlandra*, but as the present author did not study this particular species, she could not record their occurrence in the subfamily Caryotoideae. The present author noted the occurrence of both trichotomocolpate and monocolpate pollen grains in some species which Thanikaimoni (1966) recorded as having only monocolpate ones. The species involved were *Pinanga kuhlii, Chrysalidocarpus madagascariensis* var. *lucubensis, Veitchia merrillii, Roscheria melanochaetes, Astrocaryum gynacanthum, Acrocomia aculeata,* and *Acrocomia mexicana.* Similarly Thanikaimoni (1966) observed that a few pollen grains of *Euterpe edulis* and *E. oleraceae* were trichotomocolpate, but the present author did not see any such grains in the specimen of *Euterpe oleraceae* which she studied. These disparities might be due to the fact that not enough grains were examined. It had indeed become apparent to the present author that the occurrence of trichotomocolpate grains in the Palmae had hitherto been underestimated. This might be mainly due to the fact that such grains were missed because the total number of grains examined in particular species was not sufficiently large. In the present study not less than 350 pollen grains were examined for each species, with one exception, *Acrocomia mexicana*, where only 210 grains could be counted. In spite of this, some trichotomocolpate grains were still, possibly, missed. The species with trichotomocolpate pollen grains are presented in Table II.

As could be seen from the figures quoted, practically all the species with trichotomocolpate grains also had grains with other types of apertures. This phenomenon of

TABLE II

Occurrence of trichotomocolpate pollen grains in the species of Palmae studied

Species	Percentage of trichotomocolpate	Number of grains counted
Arecoideae		
Chrysalidocarpus lucubensis	0.4	1,100
C. sp.	1.9	900
Gigliolia subacaulis	1.6	380
Kentia ramsayi	5.3	974
Neophloga tenuiseta	2.4	1,775
Paralinospadix caudiculata	0.5	858
Pinanga kuhlii	99.8	500
Pseudophoenix navassana	0.2	420
Roscheria melanochaetes	0.7	560
Veitchia merrillii	0.1	3,000
Cocoideae		
Acrocomia aculeata	99.8	500
A. mexicana	81.5	210
Bactris lindeliana	3.0	500
B. major	100.0	500
B. sp.	12.5	500
B. gasipaes	?	
Cocos nucifera	0.1	2,080
Corozo oleifera	2.0	500
Elaeis guineensis, var. *dura*	81.0	1,000
var. *pisifera*	99.3	581
var. *tenera*	94.0	914
Jubaeopsis caffra	1.0	500
Orbigniya speciosa	0.1	2,030
Coryphoideae		
Pritchardia affinis	0.2	2,000
Phytelephantoideae		
Phytelephas poeppigii	0.1	2,000

dimorphism had been noted by earlier investigators, but in fewer number of species. The other type of apertures were predominantly monocolpate and to a much smaller extent, "transitional forms". The latter occurred in three main varieties in *Elaeis guineensis:* the amb of the grain was triangular or subtriangular and the colpus incompletely slit, one arm being very diminutive or entirely missing (Plate V, 7); the amb of the grain was also triangular or subtriangular but the colpus was straight and un-slit; lastly, the amb of the grain was elliptical with a prominent lateral bulge and the colpus bent in the form of a wide, inverted V. For a discussion on the probable significance of the occurrence of trichotomocolpate, monocolpate and "transitional" pollen in some palm species see Sowunmi (1968). Thus, it could be seen that *Elaeis guineensis* was polymorphic and not dimorphic as recorded by Punt and Wessels Boer (1966a) and Thanikaimoni (1966).

In *Elaeis guineenis*, particularly var. *dura*, and in *Acrocomia aculeata*, a few pollen grains with a four-slit colpus each were occasionally found (Plate V, 6). Thanikaimoni (1966) who was the first to point out the occurrence of tetrachotomocolpate grains in the Palmae observed them only in *Acrocomia crispa*, and *A. totai*, and not in the other two species mentioned earlier. However, as Thanikaimoni (ibid.) pointed out such grains occur only very rarely in the Palmae, as far as is known.

Monoporate grains were found in *Dypsis* and *Ravenea* (Arecoideae) and *Mauritia* (Lepidocaryoideae). In the first two genera the pore was isodiametric or nearly so, while in the last-named genus it was nearly isodiametric or slightly elongated. In none of the three genera was the pore operculate or with a thickened margin. Kuprianova (1948) noted the occurrence of porate grains in *Mauritia martiana*, and she considered the pore a more advanced aperture type than the single furrow prevalent in the Palmae. Erdtman (1952) also described the pollen grains of *Mauritia martiana* as being "ulcerate", i.e. with a single pore-like aperture, and those of *M. flexuosa* as being "......brevisulcate (or provided with a ± ulceroid aperture)". Thanikaimoni (1966) recorded the presence of porate grains in some palm species, including *Mauritia* (three species were examined by him, viz. *M. carana, M. flexuosa*, and *M. vinifera*, but the species with porate grains were not specified), *Areca caliso, Louvelia albicans,* and *L. madagascariensis, Ravenea* (all the six species examined) and *Borassodendron machadonis.* It is curious to note that all the species of the genus *Dypsis* examined by him were said to have monocolpate grains, whereas the present author found only monoporate grains in *Dypsis* sp. aff. *D. procera.* The reason for this disparity is not known.

The occurrence of diaperturate grains in the subfamily Lepidocaryoideae only is remarkable (*Pinanga javana*, in the subfamily Arecoideae, with some apparently dicolpate grains being the only exception). This fact was also pointed out by Thânikaimoni (1966, p. 80). This feature clearly distinguishes the Lepidocaryoideae from all other subfamilies in the Palmae.

Only in one species, *Sclerosperma mannii*, were triaperturate pollen grains found. The uniqueness among the Palmae as well as the importance of this pollen type was pointed out by Erdtman and Singh (1957).

The subfamilies Arecoideae and Lepidocaryoideae were found to be the most heterogeneous with regard to aperture forms, being characterised by five and four different types, respectively. In the Arecoideae were found monocolpate, monoporate, annulocolpate, trichotomocolpate, and triporate grains, and in the Lepidocaryoideae monocolpate, monoporate, diporate, and dicolpate grains. It could be inferred that both the Lepidocaryoideae and Arecoideae were the subfamilies with the most highly evolved aperture forms within the Palmae. At the other end were three subfamilies, the Caryotoideae, Phoenicoideae, and Borassoideae, which had only monocolpate grains–an apertural status dating back to the Palaeozoic Cordaitales. With respect to aperture form therefore, these three subfamilies could be regarded as the most "conservative" within the Palmae. In between these two extremes were four subfamilies, the Nypoideae, Cocoideae, Phytelephantoideae, and Coryphoideae, which showed some advance over the monocolpate type grain, the first-named being characterised by annulocolpate grains, and the latter three by trichotomocolpate as well as monocolpate grains.

Exine pattern: There was a wide range of exine pattern. The grains in about 11.5% of the species studied were intectate, i.e. apparently without a tectum, but with sexinous processes: spinules (e.g. in *Arenga westerhouti*), pila (e.g. in *Deckenia nobilis*).

In most of the species studied–about 82.5%–the exine was semitectate, i.e. reticulate, vermiculate, or negatively reticulate. The reticulation varied greatly from minute (as in *Calyptrogne synanthera*, brochus diameter $<1.0\ \mu$) to coarse (as in *Nengella pterophylla*, brochus diameter $>6.0\ \mu$). The muri were supported by one to several rows of bacula. The vermiculate pattern could be fine (as in *Jubaea spectabilis*) or coarse (as in *Acrocomia aculeata*).

In some grains there was an imperceptible transition from a vermiculate to a reticulate pattern and vice versa. In *Orbignya speciosa*, for example, the exine pattern was mainly vermiculate, but in some areas the pattern became scrobiculate (Plate VII, 3). In *Calamus guruba*, on the other hand, the predominantly reticulate grains were vermiculate in some areas (Plate IX, 3). A reticulate pattern is formed by polygonal permeating channels, while a vermiculate one is due to the narrow, elongated, and sometimes bifurcated permeating channels. The occurrence of these two types of channels is one and the same grain gave the transition observed. Thus it might not always be easy to draw a sharp line of demarcation between pollen grains with a reticulate pattern and those with a vermiculate one; furthermore it afforded additional indication of how varied the exine pattern in some palm species could be.

In a few species, about 6% of the total studied, the exine was pertectate, i.e. finely perforated (as in *Butia capitata* var. *odorata*). Exine sculpturing; There were some species (about 19% of the total number studied) whose pollen grains were provided with various types of sexinous processes. There could be stout spines (as in *Lepidocaryum gracile*, Plate VIII, 5 and *Nypa fruticans* Plate X, 4-5) spinules (as in *Ravenea*, Plate III, 6-7) or pila (as in *Caryota*). Whereas only wart-like processes were found in the Borassoideae and only stout spines in the Nypoideae, the Arecoideae, Caryotoideae, and Lepidocaryoideae were heterogeneous, the first-named being the most heterogeneous. In the Arecoideae were found pollen with wart-like processes, pila, spinules borne on the nexine, a tectum being absent and clavae borne on the tectum (e.g. in *Oncosperma* Plate III, 5). Pollen grains in the Caryotoideae were pilate (e.g. in *Caryota* or spin(ul)ose e.g. in *Wallichia.* Those in the Lepidocaryoideae had wart-like processes (e.g. *Calamus microcarpa* Plate IX, 9) spines (e.g. *Lepidocaryum gracile* Plate VIII, 5), spinules e.g. in *Korthalsia* laciniosa, or pila e.g. in *Salacca edulis:*

Pollen grains in the Cocoideae (except *Bactris gasipaes*), Cotyphoideae, Phytelephantoideae, and Phoenicoideae did not possess any sexinous processes; the exine was reticulate in the latter three subfamilies, and punctate, vermiculate or negatively reticulate in the Cocoideae. Kuprianova (1948) mentioned only three types of exine pattern in the Palmae, viz. "tubercular, reticulate, and negatively-reticulate". Erdtman (1952) gave more types, viz. "sexine .... reticulate, tegillate, etc., sometimes provided with warts, spines or spinules". He also pointed out the uniqueness of the stout, deep-seated spines found in the Mauritieae. Cranwell (1953) gave only two types of exine pattern, viz. "reticulate or spiny". The main exine pattern given by Punt and Wessels Boer (1966a) were two, viz. perforated (punctate) tectum, and vermiculate tectum. Thanikaimoni (1966) referred very briefly to the exine pattern in the 608 species studied by him, the main patterns were: "reticulate, foveolate" (i.e. with more or less rounded lumina), "scabrate" (the exact meaning of this term in each case was not clear), "spinulose, and fossulate" (i.e. vermiculate). In most cases, the observations of the present author are in accordance with those of earlier investigators. The few disagreements that do occur are basically of degree rather than of kind, with some exceptions. The noteworthy exceptions relate to the present work and those of three earlier investigators, Punt and Wessels Boer (1966a) and Thanikaimoni (1966). The two first-named workers referred to the exine pattern in *Elaeis guineensis* as being "indistinct", while the last-named worker referred to it as "foveolate or fossulate". The author noted that the exine pattern of *E. guineensis* was not easy to decipher, and that it tended to vary somewhat in the same specimen. But with the aid of phase contrast optics and the use of stains she was able to observe that the pattern was vermiculate to subreticulate, to negatively reticulate in varieties *dura* and *tenera*, and punctate to negatively reticulate in var. *pisifera. Bactris gasipaes* was said by Thanikaimoni (1966) to have a finely reticulate exine, but the author found it to be verrucose. *Medemia argun* and *Bismarckia nobilis* were said by Thanikaimoni (1966) to have a verrucose to reticulate exine, but the author found that the exine was vermiculate to subreticulate and negatively reticulate, respectively. Some species of *Hyphaene*, according to Thanikaimoni (1966) had a verrucose exine, but the same species studied by the author were found to have not only a verrucose exine but also one that was finely reticulate between the verrucae. Also there were a few instances where Thanikaimoni (1966) described the exine of some species as finely reticulate, or foveolate, but which the author described as vermiculate, or punctate. The author is inclined to believe that these disagreements might be due to a difference in interpretation, or else result from the fact that one form of exine pattern may imperceptibly gradate to another form (e.g. reticulate to vermiculate); another possible explanation is that in some palm species the exine pattern within an individual species varies, and in order to comprehend the variations a large number of grains ought to be studied–a minimum of 500 pollen grains is here suggested.

Exine thickness and stratification: Exine thickness ranged from 0.8 ± 0.1 μ in *Calyptrogyne synanthera* to 6.3 ± 0.5 μ in *Nenga* sp.; a greater proportion of the values (64.2%) were between 1.0 μ and 3.0 μ. Generally, the exine, seen in profile in polar view, was thickest in the middle portion of the periphery of the grain, tapering towards the ends. The exine in tectate grains as seen in unsectioned grains under the light microscope appeared to consist of three layers: a tectum, a bacula layer below it, and a nexine below the bacula layer. This stratification agrees with that given by Punt and Wessels Boer (1966a), though the terminology is very different. In intectate grains, the exine seemed to consist of only two layers: the sexine (in form of various types of processes, e.g. bacules, spinules) and the nexine below it. In seven species, however, viz. *Deckenia nobilis* (Arecoideae), *Acrocomia mexicana, Maximiliana venatorum, Scheelea leandroana* (Cocoideae) *Lepidocaryum gracile, Mauritia armata,* and *Mauritia vinifera* (Lepidocaryoideae), there appeared to be a fourth layer below the nexine. Unfortunately, no thin sections of these species were available to verify this indication.

Intra-generic variations: In only 55 of the 120 genera examined could pollen grains from more than one species (usually two to five) in the same genus be studied. Certain tentative deductions could be made as to the pollen variation within these genera, pending a broader survey as more material become available. On the whole, the various species of a genus seemed to be alike in aperture type and general sexine pattern, sometimes even in the range of pollen dimensions. In 30 of these 55 genera, notably *Iriartea, Wettinia, Ravenea, Caryota, Arenga, Wallichia, Hyphaene, Borassus, Roystonea, Phytelephas, Corypha, Pinanga* (*javana* and *ternatensis*), *Plectocomia*, and *Phoenix*, it was hardly possible to tell one species apart from another.

In 20 genera, notably *Chamaedorea, Areca, Nenga, Mauritia, Linospadix*, and *Pritchardia*, the species within each genus differed somewhat in the range of pollen dimensions and details of sexine pattern, as indicated in Appendix III.

Only five genera, viz. *Calamus, Salacca, Bactris, Pinanga* and *Daemonorops*, showed marked pollen variations within a genus.

All the species of *Calamus* studied here had dicolpate grains, but the pollen grains of one species could be distinguished from those of another on the basis of sexine pattern or pollen size. The sexine pattern in both *Calamus guruba* and *C. nobilis* was reticulate to negatively reticulate, but the pollen grains in the latter were generally larger than those in *C. guruba.* The sexine in *C. microcarpa* and *C.* sp. was characterised by supratectal wart-like processes—a feature quite distinct from the reticulate pattern in *C. guruba* and *C. nobilis*, but the pollen grains in *C. microcarpa* were larger than those in *C.* sp. and had less warts per unit area. *Calamus rivalis* could be easily distinguished from the other four species because it had a predominantly vermiculate sexine.

Salacca affinis and *S. edulis* both had nearly annulocolpate grains, but the sexine in *S. affinis* was spinulose, while that in *S. edulis* was pilate. It is of interest to note that these two species also differ regarding some gross floral characteristics, and are separately classified by Beccari (quoted in Moore, personal communication, 1967). *S. edulis* is included under the typical section, *Salacca,* while *S. affinis* is placed in subgenus *Leiozalacca.* The ovary in *S. edulis* has "sharply pointed, erect, stiff scales" while that in *S. affinis* has "appressed scales not produced into a rasping point". Also female flowers borne on female spikes are accompanied by neuter flowers in *S. edulis*, but those of *S. affinis* are not. (ibid.) These two species afford an instance of some correlation between gross morphology and pollen morphology.

The wart-like processes in *Bactris gasipaes* distinguished it from the other three species of *Bactris* studies here, the latter had a vermiculate to negatively reticulate sexine. In this respect, *Bactris gasipaes* is unique in the subfamily Cocoideae. *Bactris major* differed from *B. lindeliana* and *B.* sp. in having only trichotomocolpate pollen grains. Both the latter two species had predominantly monocolpate grains, but the sexine pattern in *B.* sp. differed somewhat from that in *B. lindeliana* in that it was more distinctly vermiculate; also at high adjustment of the microscope (oil immersion objective), the sexine channels appeared minutely reticulate—a feature not found in *B. lindeliana.*

Both *Pinanga javana* and *P. ternatensis* had very similar pollen grains, which were nearly annulocolpate and coarsely reticulate. But the grains in *P. kuhlii* were different, being mainly trichotomocolpate and coarsely retipilate. This striking difference in aperture type within a genus is remarkable, and it seems to be another example of intrageneric heterogeneity.

A notable example of pollen variation within a genus was also found in *Daemonorops*, where the pollen grains of the two species studied were very different with regard to aperture form and sexine pattern details. The pollen grains in *D. formicarius* were dicolpate with a coarsely reticulate sexine while those in *D. sparsiflorus* were diporate and minutely reticulate.

TAXONOMIC CONSIDERATIONS

Since pollen grain characters in the Palmae were fairly diverse, it was thought that they might perhaps be useful in confirming previous taxonomic groupings or tentatively suggesting modifications.

In this section the pollen types in the major subgroups, recognised on gross morphology, within the subfamilies (sensu Moore) are analysed. Sub-divisions based on pollen-morphological similarities and named after representative species or genera are then outlined. Finally, in the light of palynological similarities or dissimilarities, suggestions are made as to the possible delimitations and compositions of subgroups already recognised by several taxonomists. It should be stressed that these suggestions are only tentative. A more emphatic proposition is impossible, partly because of the relative paucity of species available for study, partly because information from various other fields is required for satisfactory subdivisions. Moreover, similarity in pollen grain characters does not necessarily imply close relationship, neither does dissimilarity necessarily indicate a lack of it. It is therefore with the full consciousness of the limitations of pollen-morphological characters by themselves that the following taxonomic considerations are made.

Subfamily Arecoideae

This is the largest subfamily within the Palmae. It is very heterogeneous morphologically (Moore, 1961), and palynologically (Erdtman, 1952; and the present paper), but

TABLE III

Subgroups of Arecoideae suggested by Moore (personal communication, 1966) and by Beccari and Pichi-Sermolli (1955)

Moore	Beccari and Pichi-Sermolli
Areceae	Areceae
Areca	*Areca*
Gigliolia	*Gigliolia*
	Pinanga
	Howeia
Kentieae	Kentieae
Gronophyllum (*Kentia*)	*Gronophyllum*
Nenga	*Nenga*
Nengella	*Nengella*
Siphokentia	*Siphokentia*
Pinanga	*Pinanga*
Gulubia	*Gulubia*
Loxococcus (?)	*Hydriastele*
Hydriastele	*Kentia*
Linospadiceae	Linospadiceae
Paralinospadix	*Paralinospadix*
Howeia	*Linospadix*
Linospadix	
Ptychospermeae	Ptychospermeae
Normanbya	*Normanbya*
Veitchia	*Veitchia*
Balaka	*Balaka*
Ptychosperma	*Ptychosperma*
	Loxococcus
Dypsideae	Dypsideae
Chrysalidocarpus	*Chrysalidocarpus*
Dypsis	*Dypsis*
Vonitra	*Vonitra*
Neodypsis	*Neodypsis*
	Podococcus
? ? ? ?	Oncospermeae
Oncosperma	*Oncosperma*
Verschaffeltia	*Verschaffeltia*
Roscheria	*Roscheria*
Phoenicophorium	*Phoenicophorium*
Acanthophoenix	
Dackenia	
	Genera Oncospermeis ut videtur affinia:
	Acanthophoenix
	Deckenia

TABLE III continued on next page

TABLE III (continued)

Moore	Beccari and Pichi-Sermolli
	Oranieae
Orania	*Orania*
Sclerosperma	*Sclerosperma*
Ceroxylon	
Ravena	*Ravena*
	Cyrtostachyeae
Cyrtostachys	*Cyrtostachys*
Genomeae	
Aristeyera	
Calyptrogyne	
Geonoma	
Clinostigmeae	Clinostigmeae
Basselinea	*Basselinea*
Goniosperma	*Goniosperma*
Irarteae	
Irartea	
Socratea	
Iriartella	
Wettinia	

very uniform anatomically (Tomlinson, 1961). The subgroups, considered here (Table III), are some of those suggested by Moore (personal communication, 1966), and Beccari and Pichi-Sermolli (1955).

Areceae

According to Moore (personal communication, 1966) this subgroup comprises only *Areca* and *Gigliolia.* Both genera have similar pollen grains–monocolpate with a reticulate exine. Beccari and Pichi-Sermolli (1955) include *Pinanga* and *Howeia.* In *Pinanga* the grains are nearly annulocolpate and probably sometimes dicolpate, or trichotomocolpate, and the exine coarsely reticulate or coarsely retipilate, while *Howeia* has monocolpate and punctitectate grains. This subgroup (sensu Beccari and Pichi-Sermolli) is thus heterogeneous.

Kentieae (sensu Moore, 1961, but excluding *Loxococcus).*

This subgroup also has diverse pollen types. Those of *Gronophyllum, Nengella, Nenga,* and *Siphokentia* are monocolpate with a very coarsely reticulate exine. Those of *Pinanga javana* and *P. ternatensis* have the same type of exine pattern, but are nearly annulocolpate to apparently dicolpate; those of *P. kuhlii* are very different (trichotomocolpate; exine coarsely retipilate). The exine patterns in *Kentia* (a genus which Moore includes in *Gronophyllum*), *Hydriastele,* and *Gulubia* are somewhat similar to one another but different from that in *Gronophyllum* and related genera in that the reticulation is not as coarse as in the latter, neither are the muri winding. Moreover, *Kenti ramsavi* and probably *K. gibbsiana* also have some trichotomocolpate grains.

Linospadiceae

This tribe (including *Howeia*) is palynologically very uniform. The pollen grains in all the species studied are monocolpate; the exine is punctate or finely reticulate.

Ptychospermeae (including *Loxococcus*)

The grains in most of the genera studied here are similar to one another—monocolpate with a punctate or finely reticulate exine. Only those of *Normanbya* differ somewhat in having a vermiculate exine.

Dypsideae (including *Podococcus*)

Of the nine genera in this tribe six were studied, viz. *Vonitra, Neodypsis, Neophloga, Podococcus, Chrysalidocarpus,* and *Dypsis.* All except *Dypsis*, have monocolpate grains, with a punctate or finely reticulate exine. *Dypsis*, the type genus, has a remarkably different pollen type—monoporate with a spinulose-reticulate exine. There is thus a marked heterogeneity in this otherwise morphologically closed related group.

Oncospermeae (sensu Beccari and Pichi-Sermolli, including *Acanthophoenix* and *Deckenia*).

All the species in this tribe have monocolpate pollen, but there is a marked diversity with regard to exine pattern, indeed no two genera have similar patterns. The exine is clavate-reticulate in *Oncosperma,* punctate in *Verschaffeltia,* simply and finely reticulate in *Roscheria,* coarsely reticulate in *Acanthophoenix,* pilate in *Deckenia,* and spinulose-baculate in *Phoenicophorium.*

Oranieae (sensu Beccari and Pichi-Sermolli)

Three of the six genera in this tribe were studied, viz. *Orania, Sclerosperma*, and *Ravenea.* The grains in the three genera are very dissimilar. The grains are monocolpate and minutely reticulate in *Orania*, triporate and coarsely reticulate in *Sclerosperma*, while they are monoparate and spinulose-reticulate in *Ravenea.*

Cyrtostachyeae (sensu Beccari and Pichi-Sermolli)

This is a unigeneric tribe, comprising the genus *Cyrtostachys.* The pollen grains are monocolpate with a verrucose-reticulate sexine.

Geonomeae (sensu Moore)

Three of the six genera in this subgroup were studied, viz. *Aristeyera, Calyptrogyne,* and *Geonoma.* The pollen grains in all of them are monocolpate and reticulate.

Clinostigmeae

The pollen grains of the two genera studied, viz. *Basselinia* and *Goniosperma,* are monocolpate and minutely reticulate.

Iriarteae (sensu Moore)

The four genera studied, viz. *Iriartea, Iriartella, Socratea*, and *Wettinia*, have monocolpate grains, but the exine in *Iriartea* is pilate, that in *Iriartella* reticulate, while that in *Socratea* and *Wettinia* is spinulose.

Subgroups suggested on pollen-morphological evidence are presented in Table IV.

Suggested taxonomic modifications

The exine pattern in *Cyrtostachys* sp.–characterised by wart-like processes–is distinctly different from all the other patterns in the subfamily Arecoideae. Beccari and Pichi-Sermolli place the genus *Cyrtostachys* in its own tribe Cyrostachyeae, Burret and Potztal group it with *Areca* and some other genera under subgroup Kentia, while Hutchinson places it in subtribe Ptychospermeae. Its pollen features are in favour of its being placed in a separate tribe, as has been done by Beccari and Pichi-Sermolli.

Oncosperma, too, has a strikingly different exine pattern, characterised by a clavate sexine. Beccari and Pichi-Sermolli place it in the tribe Oncospermeae together with *Verschaffeltia, Roscheria, Phoenicophorium*, and *Nephrosperma* (*Acanthophoenix* and *Deckenia* being closely allied to them). It is similarly classified by Moore in his "Tentative grouping of palm genera by subfamilies" (personal communication, 1966). In none of these genera is the exine pattern of all similar to that of *Oncosperma* (*Nephrosperma* unfortunately was not available for study). Hutchinson places it in subtribe Oncospermeae, together with *Ptychandra, Clinostigma, Cyphokentia, Cyphosperma, Burretiokentia, Basselinia, Euterpe, Oenocarpus, Jessenia, Acanthophoenix, Hyospathe, Prestoea*, and *Oreodoxa*. In none of these genera is the pollen exine pattern like that in *Oncosperma* (*Ptychandra, Cyphokentia, Cyphosperma, Oenocarpus* and *Burretiokentia* were not available for study). Thus, palynologically, *Oncosperma* does not fit into any of the subgroups in which it has been placed by various taxonomists, but pollen morphology suggests that it may be closely related to *Cyrtostachys*.

That the triporate grains of *Sclerosperma mannii* are unique among the palms, as pointed out by Erdtman and Singh (1957), is confirmed by the present study. For various reasons–palynological (Erdtman and Singh, 1957), anatomical (Tomlinson, 1961), and morphological (Moore, personal communication, 1965)–the taxonomic position of *Sclerosperma* is considered to be uncertain. Hutchinson refers this genus to the subtribe Caryotideae, along with *Caryota, Arenga, Didymosperma, Wallichia, Orania*, and *Louvelia* (the first four genera constitute the tribe Caryoteae, sensu Beccari and Pichi-Sermolli). Beccari and Pichi-Sermolli group it with *Orania, Masoala, Sindroa, Louvelia* and *Ravenea* in the tribe Oranieae, while Burret and Potztal place it in the large subtribe Ptychospermeae. The palms included in the Caryotideae (sensu Hutchinson) differ from all the others in the rest of the family because the petals of their female flowers are generally valvate throughout their whole length, whereas those in the rest of the family are generally imbricate throughout their whole length. *Sclerosperma* shares this distinguishing feature with the other genera in the Caryotideae or Caryoteae and Oranieae. The present

TABLE IV

Subgroups of Arecoideae suggested on pollen-morphological evidence

Subgroups with subdivisions	Remarks
Areca subgroup	Pollen grains monocolpate. Sexine semitectate. Tectum reticulate, without processes. This is the largest subgroup, further subdivided into five sections on the basis of sexine pattern details.
(1) *Areca* type	Sexine reticulate. Muri simpli-through to multibaculate.
(a) *Areca* *Chamaedorea* *Aristeyera* *Ceroxylon* *Gulubia* *Neodypsis* *Opsiandra* *Chrysalidocarpus* *Calyptrogyne* *Euterpe* *Juania* *Linospadix* *Vonitra*	All grains monocolpate.
(b) *Roscheria* *Gigliolia* *Pseudophoenix* *Kentia*	Some grains trichotomocolpate.
(c) *Iriartella*	Colpus pontoperculate.
(d) *Acanthophoenix*	Sexine with coarse reticulation.
(2) *Paralinospadix* type	Sexine punctate or minutely reticulate.
(a) *Basselinia* *Goniosperma* *Ptychosperma* *Loxococcus* *Balaka* *Podococcus* *Howeia* *Verschaffeltia* *Chrysalidocarpus* (decipiens)	All grains monocolpate.
(b) *Paralinospadix* *Chrysalidocarpus* *Veitchia* *Neophloga*	Some grains trichotomocolpate.

TABLE IV continued on next page

TABLE IV (continued)

Subgroups with subdivisions	Remarks
(3) *Gronophyllum* type	Sexine reticulate, reticulation very coarse. Muri conspicuously winding.
Gronophyllum *Nenga* *Nengella* *Siphokentia*	
(4) *Pinanga* type	Sexine reticulate, reticulation very coarse. Muri conspicuously winding. Predominantly nearly annulocolpate, some apparently dicolpate.
Pinanga javana *P. ternantensis*	
(5) *Roystonea* type	Sexine pattern irregular. Tectum minutely reticulate or punctate to vermiculate to negative reticulate.
(a) *Cyphophoenix*	Minutely reticulate to vermiculate.
(b) *Normanbya*	Minutely reticulate to vermiculate.
Manicaria	Minutely reticulate to vermiculate.
Jessenia	Minutely reticulate to vermiculate.
(c) *Roystonea*	Punctate to vermiculate to negatively reticulate.
Irartea subgroup	Pollen grains monocolpate. Sexine intectate, provided with processes. This is a small subgroup, further subdivided according to the nature of processes.
(1) *Socratea* type *Socreatea* *Wettinia*	Grains with spinules.
(2) *Deckenia type* *Deckenia* *Iratea*	Grains with pila.
Cyrtostachys subgroup	Pollen grains monocolpate. Sexine provided with processes borne on the tectum. This is a very small subgroup, further subdivided on the nature of the processes.
(1) *Cyrtostachys* type *Cyrtostachys*	Grains with verrucae.

TABLE IV continued on next page

TABLE IV (continued)

Subgroups with subdivisions	Remarks
(2) *Oncosperma* type *Oncosperma*	Grains with clavae.
(3) *Phoenicophorium* type *Phoenicorium*	Grains with spinules.
(4) *Ravenea* type *Dypsis* *Ravenea*	Pollen monoporate. Sexine semitectate, provided with spinules borne on the tectum. This is a very small and homogenous subdivision.
(5) *Sclerosperma* type *Sclerosperma*	Pollen triporate. Sexine semitectate. Tectum coarsely reticulate. A unigeneric group whose pollen grains are unlike of any other palms studied.

author would therefore tentatively suggest that *Sclerosperma* be placed in a separate tribe near the Caryoteae and Oranieae with which it is otherwise closely related. The fact that its ovary is unilocular whereas that of all other genera in the Caryoteae and Oranieae is trilocular would seem to favour this proposal.

The pollen grains of *Dypsis* sp. and *Ravenea*—monoporate and spinulose, spinules borne on the tectum—are similar to one another and dissimilar to those in the rest of this subfamily, and indeed the whole family, so far. Palynologically, they seem to constitute a distinct group, here designated the *Ravenea* type (p. 16 of present paper). There is much disagreement as to the positions of these two genera in the Arecoideae. *Dypsis* is placed in the tribe Dypsideae by Beccari and Pichi-Sermolli, and in the subtribe Iguanureae by Hutchinson. *Ravenea*, on the other hand, is placed in the tribe Oranieae by Beccari and Pichi-Sermolli, and in subtribe Iriarteae by Hutchinson. It is therefore suggested that the position of these two genera need to be reconsidered in view of the lack of unanimity as to their exact relationships with other members of the Arecoideae subfamily, and in the light of the striking similarity of their pollen grains.

Palynologically, *Loxococcus*—exine minutely reticulate—is more closely similar to the other genera in the tribe Ptychospermeae in which it is placed by Beccari and Pichi-Sermolli than those in the subgroup Kentieae (Exine very coarsely reticulate) in which Moore (personal communication, 1966) tentatively places it.

Pollen morphology does not support Beccari and Pichi-Sermolli's inclusion of *Pinanga* in the Areceae, but rather indicates that *Pinanga*, with a very coarsely reticulate exine, be included in the Kentieae, as done by Burret, and by Moore (personal communication, 1966). The pollen grains of *Pinanga kuhlii* are predominantly trichotomocolpate and coarsely retipilate, whereas those of *P. javana* and *P. ternatensis* are nearly annulocolpate or apparently dicolpate and coarsely reticulate. This is likely to be an example of a palynologically heterogeneous genus.

Other taxonomic observations

Pollen morphologically, the genera *Gronophyllum, Nengella*, and *Nenga* are very similar—their exine is coarsely reticulate, the conspicuously winding muri are supported by distinct and relatively stout bacula. These three genera have been grouped together by various taxonomists, though along with other genera which do not have these distinct pollen-morphological features. For instance, Beccari and Pichi-Sermolli group them together along with *Kentia, Gulubia, Gulubiopsis, Siphokentia, Paragulubia, Adelonenga, Hydriastele*, and *Leptophoenix*, under subtribe Kentieae: while Moore (personal communication, 1966), similarly groups them under the same subtribe. Hutchinson, on the other hand, groups these three genera together in the Euareceae along with a set of genera different in some respects from those in the previous two systems, viz.: *Hydriastele, Adelonenga, Kentiopsis, Actinorhytis, Archontophoenix, Rhopalostylis, Dictyosperma, Veitchia, Hedyscepe, Loxococcus, Areca, Mischophlosus, Pinanga*, and *Kentia.* Though these three genera have not been separately grouped together on the basis of gross morphology, nevertheless their occurring jointly in the same subtribe in various systems of classification seems to indicate a basic similarity, which is also reflected by pollen-morphological features.

Socratea and *Wettenia* have distinctly similar pollen grains. The type of spinules on their exine—spinules with a semilunar-shaped base—has not been found in any other member of this family, so far. This indicates that the two genera are probably very closely related. The fact that they have both been grouped together (along with some other genera) by Burret and Potztal, as well as by Moore (personal communication, 1966) seems to support this.

The close relationship between *Iriartea* and *Iriartella* indicated in several taxonomic systems is not supported by pollen morphology. The pollen grains of *Iriartea* are monocolpate, non-operculate, with a clavate exine, whereas those of *Iriartella* are monocolpate, pontoperculate with a distinctly reticulate exine. The grains in *Chamaerops* (Coryphoideae), however, are very similar to those in *Iriartella.* Only in these two genera (*Chamaerops* and *Iriartella*) have pontoperculate grains been found, so far. It is known that the two genera are otherwise not very closely related. The remarkable similarity of their pollen grains may therefore suggest parallel evolution; it also indicates that pollen characteristics may vary independently of gross morphological and anatomical characteristics.

TABLE V

Subgroups of Borassoideae suggested on pollen-morphological evidence

Subgroups	Remarks
Borassus type	Pollen grains monocolpate. Sexine semitectate, with supra-tectal verrucae.
Borassus *Hyphaene*	
Bismarckia and other related genera	Pollen grains monocolpate. Semitectate, without processes. Tectum pattern irregular.
Latania *Lodoicea*	Tectum punctate or reticulate, to vermiculate.
Medemia *Bismarckia*	Tectum vermiculate to negatively reticulate.

Subfamily Borassoideae

This is a small subfamily comprising seven genera, six of which were studied (*Borassodendron* was not available for study). This subfamily has been classified into two subgroups by Burret, and by Moore (personal communication, 1966).

The first subgroup comprises *Bismarckia, Medemia*, and *Hyphaene*. The pollen grains in the three genera are monocolpate and elliptical in outline. Those in the first two genera have a vermiculate to negatively reticulate exine, while those in *Hyphaene* have a verrucose tectum.

The second subgroup comprises *Borassodendron, Borassus, Latania,* and *Lodoicea*. The pollen grains in the latter three genera are monocolpate and elliptical in outline. Those in *Borassus* have a verrucose tectum, those in *Latania* have a reticulate (scrobiculate) to vermiculate exine, while those in *Lodoicea* have a punctate to vermiculate exine.

Subgroups suggested on pollen-morphological evidence are presented in Table V.

This division into two pollen-morphological subgroups partially agrees only with Hutchinson's (albeit incomplete) classification of the Borassoideae, based on the characteristics of the male floral parts. Hutchinson groups together *Latania* and *Lodoicea* whose male flowers have numerous stamens, and *Porassus* and *Hyphaene* whose male flowers have only six stamens. Neither *Medemia* nor *Bismarckia* are included in this classification. Several taxonomists, e.g. Burret, Drude (in part), and Moore (personal communication, 1966), subdivide this taxon very differently. Their more detailed classification, based on inflorescence and fruit structures, appears more convincing than Hutchinson's. *Hyphaene, Medemia*, and *Bismarckia*, which have small, globose, pedicellate female flowers, and globose fruits, with basal stigmatic remains, are grouped together, while *Borassodendron, Borassus, Latania*, and *Lodoicea* with large, globose, sessile female flowers and symmetric fruits with apical stigmatic remains, are grouped together. *Hyphaene* and *Borassus*, separated on gross floral characters, are palynologically very similar. Similarly, the other four genera, separated on gross floral characters, have very similar pollen grains. This is another example of a lack of correlation between pollen morphology and gross morphology.

Subfamily Caryotoideae

Subgroups suggested by Moore:	Subgroups suggested by Burret:
Caryotoideae	Caryoteae
Arenga (including Didymosperma)	A. *Caryota*
Caryota	B. *Arenga*
Wallichia	*Didymosperma*
	Wallichia

The pollen grains of the three genera in this small subfamily (sensu Moore), viz.: Arenga, Caryota, and Wallichia, are elliptical in amb, and monocolpate. The exine is, apparently, without a tectum, but is provided with processes–spinules in *Arenga*, and *Wallichia*, and pila in *Caryota*.

Subgroups suggested on pollen-morphological evidence are presented in Table VI. Pollen morphologically, this subfamily is fairly homogeneous and distinct. *Caryota* has pila similar to those in *Deckenia* (Arecoideae) but the other two genera have persistent and superficial spinules with rounded bases, a feature not found in monocolpate grains in any subfamily.

Two subdivisions are recognised on the basis of differences in the types of processes (Table VI).

TABLE VI

Subdivision of Caryotoideae suggested on pollen-morphological evidence

Subdivision	Remarks
(1) *Arenga* type *Arenga* *Wallichia*	Exine spinulose.
(2) *Caryota*[1]	Exine pilate.

[1] *Caryota*, however, does not constitute a distinct palynological type.

These three genera together possess very distinctive morphological and anatomical features. Pollen morphology also indicates that they are very closely related, and supports their being separated from arecoid palms into their own subfamily, as done by Moore (1960). But *Caryota* differs from the other two genera in the type of processes on its pollen–pila, not spinules. It is also significant to note that this genus differs from the other two genera in two notable morphological respects: its first seedling leaflet is bifid, while those of the others are entire; and its mature leaves are bipinnate, while those of the others are simply pinnate (cf. Tomlinson 1961, and Moore 1960, 1961, respectively). Burret and Potztal do indeed separate it from the other genera in the Caryoteae tribe, a classification which seems to be borne out by the observation here.

Subfamily Cocoideae

The subdivisions considered here are some of those recognised by Burret, and by Moore (personal communication, 1966). They are represented in Table VII.

Attaleae (including *Parascheelea*)–this subgroup is included in Moore's Cocoeae.

Of the six genera in this subgroup, four were studied–*Orbignya, Maximiliana, Scheelea*, and *Parascheelea.* The pollen grains are monocolpate (except for occasional trichotomocolpate ones in *Orbignya speciosa*), with an elliptical outline, but usually with one or two lateral bulges, and are without any sexinous processes. The tectum is scrobiculate in *Maximiliana* and, to some extent, in *Orbignya;* vermiculate in *Scheelea, Parascheelea*, and *Orbignya;* and punctate in *Scheelea* and *Parascheelea.*

Bactrideae

Only *Aiphanes, Acrocomia, Astrocaryum*, and *Bactris* have been studied. The pollen grains are monocolpate in *Aiphanes, Astrocaryum*, in some species of *Bactris*, and, rarely, in *Acrocomia;* trichotomocolpate in *Acrocomia, Bactris major*, and sometimes in some other species of *Bactris.* There is more variation in exine pattern. The tectum is finely reticulate to vermiculate in *Aiphanes*, punctate to scrobiculate or vermiculate in *Acrocomia,* punctate in *Astrocaryum*, vermiculate to negatively reticulate in all *Bactris* species studied except *Bactris gasipaes* where it is tectate (tectum provided with verrucae).

Elaeideae (sensu Moore)

The pollen grains in *Elaeis* and *Corozo* are either monocolpate or trichotomocolpate–mostly the latter in *Elaeis.* The tectum pattern in both genera is subreticulate to vermiculate or negatively reticulate. This subgroup seems homogeneous palynologically. (*Barcella*, the third genus in this subgroup, was not available for study.)

TABLE VII

Subdivisions of Cocoideae suggested by Moore (personal communication, 1966) and by Burret

Moore	Burret
	Attaleae
	Orbignya
	Scheelea
	Maximiliana
Bactrideae	Bactrideae
Aiphanes	*Aiphanes*
Acrocomia	*Acrocomia*
Astrocaryum	*Astrocaryum*
Bactris	*Bactris*
Elaeideae	
Elaeis	
Corozo	
Cocoeae	Cocoideae
Maximiliana	
Barascheelea	
Scheelea	*Cocos*
Orbignya	*Butia*
Cocos	*Jubaea*
Butia	*Jubaeopsis*
Jubeaea	*Arikuryroba*
Jubaeopsis	*Elaeis*
Lytocaryum	*Corozo*

Cocoideae (sensu Burret, excluding *Elaeis* and *Corozo*)
Cocoeae (sensu Moore, excluding the genera in Burret's Attaleae)

The pollen grains in the six genera studied from this subgroup are monocolpate (except for the very rare trichotomocolpate grains in *Cocos nucifera* and *Jubaeopsis caffra*); the tectum is punctate in *Cocos nucifera* and *Butia*, vermiculate in *Jubaea, Jubaeopsis* and partly so in *Lytocaryum,* reticulate in *Arikyryroba*, and partly so in *Lytocaryum.*

Subgroups suggested on pollen-morphological evidence are presented in Table VIII. Three main subdivisions can be recognised on the basis of tectum pattern.

Suggested taxonomic modifications

Although pollen morphology seems to confirm the close relationship between *Elaeis* and *Corozo*, recognised by various taxonomists on morphological and anatomical grounds,

TABLE VIII

Subgroups of Cocoideae suggested on pollen-morphological evidence

Subgroups	Remarks
(1) *Elaeis* type	Tectum pattern more or less irregular (finely or subreticulate to vermiculate to negatively reticulate).
(a) *Aiphanes*	Pollen grains only monocolpate.
(b) *Bactria*[1] *Elaeis* *Corozo*	Pollen grains monocolpate or trichotomocolpate.
(2) *Cocos* type	Tectum punctate, scrobiculate, or vermiculate.
(a) *Acrocomia*	Tectum punctate to scrobiculate or vermiculate.
(b) *Maximiliana* *Orbignya*	Tectum scrobiculate or finely vermiculate.
(c) *Cocos*	Tectum punctate.
Butia	Tectum punctate.
Astrocaryum	Tectum punctate.
(d) *Jubaea*	Tectum punctate to vermiculate.
Jubaeopsis	Tectum punctate to vermiculate.
Scheelea	Tectum punctate to vermiculate.
Parascheelea	Tectum punctate to vermiculate.
(3) *Arikuryroba* and *Lytocaryum*	Tectum reticulate. These two genera do not contitute a distinct palynological type.

the two genera are not considered sufficiently palynologically distinct to constitute a separate subgroup. Evidence from the present study suggests that they be grouped along with *Bactris* and *Aiphanes* because of the great similarity in sexine pattern.

Pollen morphology also suggests that *Bactris* may be closely allied with *Aiphanes, Elaeis*, and *Corozo*, but not with *Acrocomia* and *Astrocaryum* with which it is grouped by several taxonomists.

That *Maximiliana* and *Orbignya* are similar in their gross morphology is clearly shown in various taxonomic systems. Pollen morphology confirms that similarity, and further indicates that the degree of affinity between them may probably be greater than hitherto recognised.

The close relationship between *Butia, Jubaea*, and *Jubaeopsis*, clearly manifested in several taxonomic systems, is supported by pollen-morphology. There is also pollen-morphological evidence to show that *Scheelea, Parascheelea* and *Astrocaryum* are probably also closely related to these three genera.

Pollen morphology indicates that *Arikuryroba* and *Lytocaryum* may be somewhat

---

[1] With exception of *B. gasipaes*, which has a verrucose exine.

related. They are the only genera in this subfamily, so far, with a clearly reticulate tectum. But more genera from the Cocoideae need to be studied before the relationship of these two genera with the others with which they have been grouped on gross morphological basis can be duly assessed.

Subfamily Coryphoideae

The subgroups considered here are those of Burret, and of Moore (personal communication, 1966) and are represented in Table IX.

TABLE IX

Subgroups of Coryphoideae suggested by Burret, and by Moore (personal communication, 1966)

Moore	Burret
Nannorrhops	*Nannorrhops*
Corypha	*Corypha*
	Sabal
Serenoa	*Serenoa*
Licuala	*Licuala*
Brahea	*Brahea*
Livistona	*Livistona*
Copernicia	*Copernicia*
Sabal	*Cryosophila*
	Rhapis
Cryosophila	*Trachycarpus*
	Rhapidophyllum
Rhapis	*Chamaerops*
Trachycarpus	*Washingtonia*
Rhapidophyllum	*Pritchardia*
Chamaerops	
Washingtonia	
Pritchardia	

All the species studied from this subfamily have remarkably similar and uniform pollen grains–monocolpate, exine reticulate. Trichotomocolpate grains occasionally occur in *Pritchardia affinis.*

This subfamily is, on the whole, homogenous palynologically, and therefore has not been subdivided. *Chamaerops*, with a pontoperculate colpus, and *Licuala* with coarse reticulation differ somewhat from the rest.

TABLE X

Subgroups of Lepidocaryoideae suggested by Moore and by Burret

Moore	Burret
	Mauritieae
Mauritia	*Mauritia*
Lepidocaryum	*Lepidocaryum*
	Calameae
Myrialepsis	*Myrialepsis*
Plectocomiopsis	*Plectocomiopsis*
Plectocomia	*Calamus*
	Daemonorops
Calamus	*Plectocomia*
Daemonorops	Ancistrophylleae
Ancistrophyllum	*Ancistrophyllum*
Oncocalamus	*Oncocalamus*
	Metroxyleae
Metroxylon	*Metroxylon*
	Korthalsieae
Korthalsia	*Korthalsia*
	Raphieae
Raphia	*Raphia*
	Salacceae
Salacca	*Salacca*

Subfamily Lepidocaryoideae

The subdivisions considered here are those recognised by Burret, and by Moore (personal communication, 1966) and are represented in Table X.

Mauritieae

This small subgroup, comprising three genera–*Mauritia, Lepidocaryum*, and *Mauritiella*–is characterised by a very distinctive pollen type. The grains are either monocolpate or monoporate, and have stout, mostly deep-rooted spines not found in any other member of the Palmae. (*Mauritiella* was not available for study.)

Calameae

The pollen grains in all the species studied are dicolpate (except *Daemonorops sparsiflorus* which has diporate grains). The tectum is reticulate and without processes, with the exception of *Calamus* sp. and *C. microcarpa* where it is verrucose, and *Plectocomiopsis geminiflorus* var. *borneensis* whose grains seem to be baculate and intectate.

Ancistrophylleae

Both *Ancistrophyllum* and *Oncocalamus* have monocolpate grains, with a reticulate exine. (*Eremospatha* was not available for study.)

Metroxyleae

Metroxylon has dicolpate, reticulate grains.

Korthalsieae

The grains in Korthalsia are diporate and spinulose.

Raphieae

The pollen grains in *Raphia* are monocolpate and reticulate.

Salacceae

The pollen grains in *Salacca* are monocolpate; those in *S. affinis* and *S. borneensis* are spinulose, while those in *S. edulis* are pilate.

Subdivisions suggested on pollen-morphological evidence are represented in Table XI. This subfamily can be divided into eight main types based on aperture number and type, and type of sexine pattern.

Taxonomic observations

The pollen grains of *Mauritia* and *Lepidocaryum* are, on the whole, very similar and distinctive. The present study confirms Erdtman's observation (1952), that the spines of these two genera are unlike those of any other palms so far studied. The close relation between these two genera seems clear since they have been grouped together (with *Mauritiella* also) in a major subgroup within the Palmae by practically all taxonomists, on gross morphological and anatomical criteria. In the systems of most taxonomists they constitute a section of the major taxon (tribe, or subfamily) Lepidocaryoideae. But in Hutchinson's system they constitute the Lepidocaryeae tribe, a taxon of the same rank as his other seven broadest taxa in the Palmae, equivalent to the subfamily status (sensu Beccari, and Moore). Pollen morphology seems to support Hutchinson's treatment of these two genera.

The *Calamus* type is distinct from all other palm species (with the possible exception of *Pinanga javana*) in having dicolpate grains. It is noteworthy that the genera in the tribe Calameae (sensu Hutchinson), of which all genera in the *Calamus* subgroup form a part, are distinguished from all other palms by the hard, shining and imbricate scales on their fruits; pollen-morphologically, too, they are distinct in having grains with two apertures. This constitutes a remarkable correlation between gross morphology and pollen morphology.

TABLE XI

Subdivisions of Lepidocaryoideae suggested on pollen-morphological evidence

Subdivisions	Remarks
(1) *Lepidocaryum* type	Pollen grains monocolpate. Sexine spinose, spines stout.
Lepidocaryum *Mauritia flexuosa*	
(2) *Mauritia armata* type	Pollen grains monoporate. Sexine spinose and spinulose; spines stout.
Mauritia armata *M. vinifera* (?) *M. flexuosa* (?)	
(3) *Salaca* type	Pollen grains nearly annulocopate. Sexine spinulose or pilate.
(a) *Salacca affinis*	Sexine spinulose.
S. borneensis	Sexine spinulose.
(b) *S. edulis*	Sexine pilate.
Calamus subgroup	Pollen grains dicolpate.
(4) *Plectocomia* type	
Calamus C. guruba	Tectum reticulate.
C. nobilis	Tectum reticulate.
C. rivalis	Tectum reticulate
Daemonorops formicarius	Tectum reticulate.
Metroxylon	Tectum reticulate.
Plectocomia	Tectum reticulate.
Myrialepis	Tectum reticulate.
(5) *Calamus microcarpa* type	
Calamus microcarpa	Tectum verrucose-reticulate.
C. sp.	Tectum verrucose-reticulate.
(6) *Plectocomiopsis* type	
Plectocomiopsis geminiflora var. *borneensis*	Sexine baculate.
Korthalsia subgroup	Pollen grains diporate. This very small subgroup is further subdivided on the basis of sexine pattern.
(7) *Korthalsia* type	Sexine spinulose.
Korthalsia laciniosa	
(8) *Daemonorops sparsiflorus* type	Tectum reticulate.
Daemonorops sparsiflorus	
Ancistrophyllum and related genera	Pollen grains monocolpate. Sexine reticulate. Subgroup further subdivided on sexine pattern details.
(a) *Ancistrophyllum*	Tectum punctate in parts.
(b) *Oncocalamus*	Tectum reticulate throughout.
Raphia	Tectum reticulate throughout.

The pollen grains in *Korthalsia* have a distinctive aperture form—two subequatorial pores. Although those in *Daemonorops sparsiflorus* have two peripheral pores, they also have a thin "colpod" streak extending from one pore to the other, hence these pores may not be exactly homologous with those in *Korthalsia*. So far, pollen-morphological evidence is in favour of separating *Korthalsia* into a subgroup of the Lepidocaryoideae as done by Burret, and by Moore (personal communication, 1966).

Subfamily Nypoideae

The pollen grains in *Nypa*—annulocolpate, spinose—are quite distinct from those in all other palms. The stout spines are not deep-rooted, but are supported by baculoid processes whose tips often coalesce.

This monotypic genus has been placed in a separate major group, the Nypoideae, by some taxonomists (e.g. Burret, Beccari and Pichi-Sermolli, and Moore), on gross morphological grounds. Some others, however (e.g. Rendle, Drude, and Hutchinson), group it together with *Phytelephas* in the tribe Phytelephantieae, or Phytelephantineae. Both *Nypa* and *Phytelephas* differ from all other palms in having a rudimentary perianth. There is also some evidence, yet to be confirmed, that they have a peculiar seedling morphology—it is the apex of the radicle, and not the cotyledon as in all other palms, that becomes enlarged and acts as a suctorial organ (Tomlinson, 1961). Although they both share these unique features, nevertheless they differ in some important morphological, anatomical, and pollen-morphological respects. For instance, *Phytelephas* is dioecious, *Nypa* monoecious. The guard cells in *Nypa* are sunken—a unique feature in palms—and the silica bodies in the stegmata (silica cells) are hat-shaped, while those in *Phytelephas* are spherical (Tomlinson, 1961). The pollen grains of *Phytelephas* are monocolpate and reticulate, in sharp contrast to the annulocolpate, spinose grains of *Nypa*. Pollen morphology therefore supports the separation of *Nypa* and *Phytelephas*, and the placing of the former in a major taxon of its own (next below family rank), as has been done by Moore and some other taxonomists.

Subfamily Phoenicoideae

This subfamily consists of only one genus, *Phoenix*, which comprises twelve species. The pollen grains of the four species investigated here are remarkably similar—monocolpate and minutely reticulate, the muri being simplibaculate. This therefore seems to be a very natural small group, already recognised by various taxonomists, e.g. Rendle (1959), Burret, and Moore, and by the anatomist, Tomlinson (1961). It should be noted that although this subfamily is known to possess distinctive morphological and anatomical features, its pollen-morphological features, though uniform, are not distinctive. Pollen grains similar to those in *Phoenix* are found in several genera in the subfamilies Arecoideae, Coryphoideae and Phytelephantoideae. Thus, this genus cannot be distinguished from others on the basis of pollen morphology.

Subfamily Phytelephantoideae

The pollen grains of *Phytelephas* are comparatively large, monocolpate, and reticulate (muri simpli-duplibaculate).

These grains can be distinguished from those of other palms, especially in the Arecoideae and Coryphoideae which have very similar exine pattern and aperture form, only by their comparatively large size. The pollen-morphological features of *Phytelephas* are therefore not distinctive. However, the gross morphological features that warrant its being placed in a subfamily of its own seem substantial. *Phytelephas* has been split into four distinct genera–*Ammandra, Palandra, Phytelephas* (sensu str.), and *Yarina*, comprising eight species. Since only two species of *Phytelephas* (s. l.) have been studied there is sufficient evidence to indicate whether pollen morphology supports this splitting.

GENERAL COMMENTS AND OBSERVATIONS

It is suggested that only mature pollen grains–preferably from dehisced anthers–be used in compiling descriptions of pollen types. This is essential in order to eliminate variability in pollen characteristics probably due to differences in the level of maturity attained. It is also desirable, wherever possible, that tetrads and immature pollen grains be examined for comparison, particularly if two or more different types of pollen occur in the same flower or anther.

The assumption that the single aperture in practically all monocotyledonoid pollen grains is distal needs to be substantiated by direct evidence from tetrads whose constituent grains already have a distinct aperture form. One investigator known to have observed the apertures at the tetrad stage of the pollen grains in a number of palm species is Thanikaimoni (1966). He was able to confirm that the single furrow in these species was distal in position.

The width of pollen grain apertures (especially furrows) may not be a reliable and diagnostic feature, at least in the Palmae. In this study there are several examples, some illustrated with photomicrographs, which clearly demonstrate the variability of colpus shape and width among the pollen grains of the same species. In certain cases, some colpi were unopened and the colpus membranes still intact, while other colpi were opened to various extents. It is very difficult to say which is the representative width. The value or indeed relevance of this character seems questionable; at least it appears to be of little diagnostic significance.

Increase in the size of pollen grains due to the different treatments to which they are subjected (e.g. moistening, acetolysis, prolonged mounting in glycerine jelly) has been reported by several authors. To minimise the variation in the pollen dimensions (i.e. polar and equatorial axes) of grains from the same species, and in order to compare measurements of grains from different samples or species, it is suggested that grains to be measured should not be treated drastically, but should only be stained (methylene blue or safranine may be used). For the measurements of finer details (e.g. exine layers, muri), acetolysed grains have to be used, but preferably within a few days of preparation.

SUMMARY AND CONCLUSION

A diversity of pollen form occurs in Palmae, particularly in the subfamilies Arecoideae and Lepidocaryoideae. The equatorial diameter ranges from 20 μ to 75 μ. The outline (amb) is frequently elliptical, sometimes rounded triangular, or circular. The aperture is usually a long furrow, but a few species have a single simple pore, a three-slit colpus, two colpi, and two or three pores. There is a great variety of exine pattern—punctate, reticulate, negatively reticulate, vermiculate, verrucose, pilate, clavate, baculate, spinulose, spinose, or a combination of some of these patterns—the most predominant being the reticulate one. Generally, the different species of a genus are very much alike with regard to aperture form and exine pattern, the main difference being in relative size; sometimes, however, the different species of a recognised genus may have very different pollen types. On the whole, pollen characteristics sometimes do not parallel morphological, anatomical, and cytological characteristics, the Borassoideae, Dypsideae, Oranieae, Kentieae, and Bactrideae being notable examples. There is however, a high degree of correlation between pollen morphological characteristics and gross morphological, anatomical and cytological characteristics within the subfamilies Caryotoideae, and Lepidocaryoideae. The unigeneric subfamilies Nypoideae, Phytelephantoideae, and Phoenicoideae each have uniform pollen types, but it is only in the Nypoideae that they are typical and very distinctive.

Although pollen morphology in the Palmae can be used in distinguishing some genera as well as the constituent species of some others, it does not clarify the delimitation of most major subgroups within the subfamilies.

ACKNOWLEDGEMENTS

I am greatly indebted to Professor G. Erdtman of Solna, Sweden, for suggesting this investigation, for the stimulating "induction period" I had in 1964 under his guidance at the Palynological Laboratory, Solna, Sweden, for his putting all necessary facilities at the Laboratory at my disposal, and for his continuous inspiration, valuable advice, and interest.

I am also grateful to all the staff at the Solna Laboratory for their ready help, encouragement, and interest; especially to Mrs. Molander for many pollen slide supplies, to Mrs. Wallmark and Mrs. Dunbar for ultra-thin sections, and to Dr. Praglowski for help with photomicrographs.

My thanks are also due to my colleagues Mrs. Williams and Mr. Osoba for the text figures reproduced from my original line drawings, and for help with photomicrographs, respectively.

I am particularly grateful to Dr. Moore, Director of the Bailey Hortorium, Ithaca, U.S.A., for polliniferous samples of a great number of palms, as well as for his most valuable help and comments on the taxonomical aspects of this work. I also want to thank Dr. Tomlinson, Research Scientist, Florida, U.S.A., who very kindly provided some palm pollen specimens too.

My thanks also go to Mr. Menendez, and Mr. Obasola, plant breeders at the Nigerian Institute for Oil. Palm Research, Benin, Nigeria, for supplying me with fresh pollen material of some indigenous Nigerian palms.

I am also grateful to the Directors of the Royal Botanic Gardens, Kew, England, and of the Botanical section, Riksmuseet, Stockholm, Sweden, for permitting me to collect polliniferous material from their herbaria.

REFERENCES

Beccari, O., 1877. Palms of New Guinea. *Malesia*, 1(1): 1-96; 1(2): 97-102, 171-175.

Beccari, O., 1884. Palms of New Guinea. *Malesia*, 2(1-2): 62-79.

Beccari, O., 1886. Asiatic Palms. *Malesia*, 3(1): 58-80; 3(2): 81-149.

Beccari, O., 1889. Asiatic Palms. *Malesia*, 3(4): 169-200.

Beccari, O., 1890a. The genus *Pritchardia. Malesia*, 3(5): 281-317.

Beccari, O., 1890b. The genus *Phoenix. Malesia*, 3(5): 345-416.

Beccari, O., 1902. Systematic enumeration of the species of Calamus and Daemonorops, with descriptions of the new ones. *Rec. Botan. Surv. India*, 2(3): 197-230.

Beccari, O., 1908. Asiatic Palms–Lepidocaryeae Part I. The species of *Calamus. Ann. Botan. Gard., Calcutta*, 11, 518 pp.

Beccari, O., 1911. Asiatic Palms–Lepidocaryeae Part II. The species of *Daemonorops. Ann. Botan. Gard., Calcutta*, 12(1): 237 pp.

Beccari, O., 1914. Asiatic Palms–Lepidocaryeae, Suppl. to Part I. The species of *Calamus. Ann. Botan. Gard., Calcutta*, 11(Appendix): 142 pp.

Beccari, O., 1918. Asiatic Palms–Lepidocaryeae Part III. The species of the genera *Ceratolobus, Calospatha, Plectocomia, Plectocomiopsis, Myrialepis, Zalacca, Pigafetta, Korthalsia, Metroxylon, Eugeissona. Ann. Botan. Gard., Calcutta*, 12(2): 213 pp.

Beccari, O. and Martelli, 1931. Asiatic Palms–Corypheae. *Ann. Botan. Gard., Calcutta*, 13: 356 pp.

Beccari, O. and Pichi-Sermolli, R. E. G., 1955. Subfamiliae Arecoidearum Palmae Gerontogeae. Tribuum et generum conspectus. *Webbia*, 11: 1-187.

Bentham, G. and Hooker, J. D., 1883. *Genera plantarum–Palmae.* (Mimeographed sheets), pp. 870-948.

Burret, M., 1953. Key of the family Palmae. *Willdenovia*, 1: 59-74 (In German).

Burret, M. and Potztal, E., 1956. Key of the family Palmae. *Willdenovia*, 1: 348-385 (In German).

Cranwell, L. M., 1953. New Zealand pollen studies. The monocotyledons. *Bull. Auckland Inst. and Museum*, 3: 91 pp.

Drude, O., 1889. *Die naturlichen Pflanzenfamilien. Palmae* (Mimeographed sheets), pp. 1-93.

Erdtman, G., 1944. Pollen morphology and plant taxonomy II–Notes on some monocotyledonous pollen types. *Svensk Botan. Tidskr.*, 38(2): 163-168.

Erdtman, G., 1952. *Pollen Morphology and Plant Taxonomy. Angiosperms.* Almqvist et Wiksell, Stockholm, 539 pp. (reprinted with corrections and an Addendum by Hafner, New York, 1966).

Erdtman, G., 1960. The acetolysis method. A revised description. *Svensk Botan. Tidskr.*, 54: 561-564.

Erdtman, G., 1963. Palynology. In: R. D. Preston (Editor), *Advances in Botanical Research.* Academic Press, London-New York, 1: 149-208.

Erdtman, G., 1969. *Handbook of Palynology.* (An Introduction to the Studies of Pollen Grains and Spores.) Munksgaard, Copenhagen, 486 pp.

Erdtman, G. and Praglowski, J. R., 1959. Six notes on pollen morphology and pollen-morphological techniques. *Botan. Notiser*, 112(2): 175-184.

Erdtman, G. and Singh, G., 1957. On the pollen morphology of *Sclerosperma mannii. Bull. Jardin Botan. Etat* (Belgique), 27(2): 217-220.

Faegri, K. and Iversen, J., 1964. *Textbook of Pollen Analysis.* Munksgaard, Copenhagen, 237 pp.
Gassner, G. G., 1941. Über Bau der männlichen Blüten und Pollenentwicklung einiger Palmen der Unterfamilie der Ceroxylinae. *Arb. Inst. Allg. Botan. Univ. Zürich,* III(I): 237-276.
Hutchinson, J., 1959. *The Families of Flowering Plants.* Vol. II *Monocotyledons.* Clarendon Press, Oxford, 792 pp.
Kremp, G. O. W., 1965. *Morphologic Encyclopedia of Palynology.* Univ. of Arizona Press, Tucson, 185 pp.
Kumazawa, M., 1937. Pollen grain morphology in Ranunkelaceae, Lardizabalaceae and Berberidaceae. *Japàn. J. Botan.*, 8: 19-51.
Kuprianova, L. A., 1948. Pollen morphology and the phylogeny of monocotyledons. *Comm. Komarov Inst. Acad. Sci.*, I(7): 163-262 (In Russian).
Lawrence, G. H. M., 1951. *Taxonomy of Vascular Plants.* McMillan, New York-London, 823 pp.
Moore Jr, H. E., 1960. A new subfamily of Palms–the Caryotoideae. *Princeps,* 4(3): 102-117.
Moore Jr, H. E., 1961. Botany and classification of Palms. *Am. Hort. Mag.*, 40(1): 17-26.
Moore Jr, H. E., 1963. An annotated checklist of cultivated palms. *Princeps,* 7(4): 119-184.
Nair, P. K. K., 1960. A modification in the method of pollen preparation. *J. Sci. Industr. Res.*, 19C: 26-27.
Nair, P. K. K. and Sharma, M., 1963. Pollen grains of *Cocos nucifera* L. *L. Grana Palynol.*, 4(3): 373-379.
Potztal, E., 1964. Family Palmae. In: H. Melchior (Editor), *A. Engler's Syllabus der Pflanzenfamilien. II. Angiosperms.* Borntraeger, Berlin, pp. 579-588.
Punt, W. and Wessels Boer, J. G., 1966a. A palynological study in cocoid Palms. *Acta Botan. Neerl.*, 15: 255-265.
Punt, W. and Wessels Boer, J. G., 1966b. A palynological study in Geonomoid Palms. *Acta Botan. Neerl.*, 15: 226-275.
Sharma, A. K. and Sarkar, S. K., 1956. Cytology of different species of palms and its bearing on the solution of the problems of phylogeny and speciation. *Genetica,* 28: 361-488.
Sowunmi, M. A., 1967. *On the pollen morphology of the Palmae and its bearing on taxonomy.* Ph.D. Thesis (University of Ibadan, Nigeria), 198 pp.
Sowunmi, M. A., 1968. Pollen morphology in the Palmae, with special reference to trends in aperture development. *Rev. Palaeobotan. Palynol.*, 7(1968): 45-53.
Thanikaimoni, G., 1966. Contribution à l'étude palynologique des Palmiers. *Inst. Francais de Pondichery travaux de la Section Scientifique et Technique,* 5(2): 91 pp. (Imprimerie de la Mission, Pondichery, India.)
Tomlinson, P. P., 1961. *Anatomy of the Monocotyledons, II. Palmae.* Clarendon Press, Oxford, 453 pp.
Von Martius, C. F. P., 1823-1850. *Historia Naturalis Palmarum.* Munich, 3 vols.
Wodehouse, R. P., (1935), 1959. *Pollen Grains. Their Structure, Identification and Significance in Science and Medicine.* McGraw-Hill, New York, 1st ed.; Hafner Publishing Company, New York, N.Y., 2nd ed., 574 pp.

APPENDIX I

Index of plants investigated

Altogether pollen grains from 350 palm species in 120 genera were investigated. Of these, 209 in 97 genera have been described–150 in detail. The latter are marked with asterisks in the list below. Subfamilies sensu Moore (1961).

Arecoideae

*Acanthophoenix crinita** H. Wendland (Mauritius 1934, R. E. Vaughn 852, BH).
Arecha catechu Linnaeus (Hainan May 1928, W. K. Tsang 16895, K.).

*A. paniculata** Scheffer (Glasenoin Botan. Gard. 1891, K.).
A. sp.* (New Guinea 1964, H. E. Moore and A. Millar 9260, BH).
*A. warburgiana** Beccari (New Guinea, Warborey s.n., Herb. Berlin).
Aristeyera spicata H. E. Moore (gen. nov. ined.) (Venezuela 1961, Steyermark 90010, BH).
Balaka cuneata Burret (Fiji, Smith 6674, S.).
Basselinia sp.* (aff. *B. tomentosa* Beccari) (New Caledonia 1964, Moore et al. 9234, BH).
*Calyptogyne synanthera** (Martius) Burret (Photo Field Mus. 18531).
Campecarpus fulcita Bronniar) Beccari (Calcutta 1912, Sarasin 724, FI.).
Ceroxylon sp.* (Colombia 1944, Cautrecass 19322, BH).
*Chamaedorea fragrans** (Ruiz et Pavon) Martius (Herb. Hort. Bot. Matritensis B.18, K.). N.B. (Unacetolysed grains measured).
C. gracilis Willdenow (Columbia, Moritz, K.).
*C. karwinskaya** H. Wendland (Cult. Hort. Bog. 1898, Beccari).
*C. stolonifera** H. Wendland (S. Mexico 1892, K.).
Chrysalidocarpus decipiens Beccari (Central Malagasy 1909, Beccari s.n., K.).
C. madagascariensis Beccari var. *lucubensis** Jumelle et Perrier (Malagasy 1963, H. E. Moore 9026, BH).
C. sp. (Zanzibar Cult. Williams anno 1957, K.).
*Cyphophoenix elegans** H. Wendland (New Caledonia 1964, Moore et al. 9323, BH).
Cyrtostachys sp.* (New Guinea 1964, Moore 9272, BH).
*Deckenia nobilis** Seeman (Mauritius 1933, Vaughn 806a, BH).
Dypsis sp.* (aff. *D. procera*) (Malagasy 1963, Moore 9017, BH).
Euterpe macrospadix Oersted (Costa Rica 1953, Moore 6553, BH).
*E. oleracea** Martius (New Caledonia 1911, Broadway 4004, K.).
E. precatoria Martius (Peru 1960, Moore et al. 8388, BH).
Geonoma intermedia Grisebach et H. Wendland (Island de Pinos, West Indies 1904, Curtis, K.).
*G. macrostachys** Martius (Upper Amazon 1875, Traill, K.).
*Gigliolia subacaulis** Beccari (Sarawak 1867, Beccari 3647).
Goniosperma vitiense Burret (Fiji 1933, Bishop Museum, Hawaii, Bernice, S.).
Gronophyllum chaunostachys Burret (New Guinea 1964, Moore et Millar 9258, BH).
*G. luridium** Beccari (New Guinea, Versteegh 1988).
*G. microcarpum** Scheffer (Amboina 1913, Robinson 1610, K.).
*Gulubia costata** (Beccari) Beccari (New Guinea 1964, Moore 9273, BH).
*G. mollucana** Beccari (Ternate 1874, Beccari).
*Iriartea cometes** Wendland (Brazil 1933, Krukoff 5739).
*I. ventricosa** Martius (Venezuela 1962, Steyermark 90777, BH).
*Iriartella setigera** H. Wendland (Colombia 1952, Carcia bariga 15172, BH).
*Jessenia batana** (Martius) Burret (Brazil 1933, Kenkopp 5758, K.).
J. sp.* (Peru 1960, Moore et al. 8398, BH).
*Juania australis** (Martius) Drude (Juan Fernandez 1917, 310, K.).
*Kentia gibbsiana** Beccari (New Guinea 1913, Gibbs 5951).
*K. ramsayi** Beccari (N. Australia 1910, Holtze s.n., FI.).
Leopoldinia piassaba Wallace (Brazil 1928, Luetzelburgh 22350, BH).
L. pulchra Martius (Guyana, Schomburg, K.).
Lepidorrachis mooreana O. F. Cook (Lord Howe Island, K.).
L. savaiiense E. Christopherson (Island of Hawaii 1931, Christopherson et Hime 2273, K.).
*Linospadix angustiseta** Beccari (New Guinea 1892, Lorio).
*L. monostachya** (Martius) H. Wendland (New South Wales 1957, Ford 17243, K.).
Loxococcus rupicola (Thwaites) H. Wendland et J. D. Hooker (Thwaites 2732).
Manicaria saccifera Gaertner (Guina, Parker, K.).
*Nenga pumila** (Martius) H. Wendland (Malay Peninsula 1883, Dr. King's, K.).
N. sp.* (Malaya 1963, Moore et Pennington 9061, BH).
*Nengella pterophylla** Beccari (Cult. Hort. Bog. 1915, x-D114).
*Neodypsis decaryi** Jumelle (Malagasy 1934, Humbert 14155).

Neophloga heterophylla Beccari (Malagasy 1881, Baron 486, K.).
N. tenuisecta Jumelle et Perrier (Ex Herb. Kew 15983, S.).
Nephrosperma vanhoutteanum (H. Wendland ex van Houtte) Balfour (Seychelles 1936, Vasey Fitzgerald 4964, BH).
*Normanbya normanbyi** (W. Hill) L. H. Bailey (Phillipines: Palawan Is. March 1911, Elmer 12708, K.).
*Oncosperma tigillarium** (Jack) Ridley (Sabah 1964, Moore et al. 9183, BH).
*Opsiandra maya** O. F. Cook (Cult. in U.S. 1952, Moore 6002, BH).
Orania lauterbachiana Beccari (New Guinea 1890, Lauterbach 970, S.).
O. palindan (Blanco) Merrill (Phillipines: Luzon 1893, Loher 1401).
*Paralinospadix caudiculata** Burret (New Guinea 1960, Sarkat 10).
P. hollrungii (Beccari) Burret (New Guinea 1964, Moore et Millar 9265, BH).
*P. petrickiana** (Cult. Hort. Bot. Reg. Kew 1906, K.).
*Phoenicophorium borsigianum** (C. Koch) Stuntz (Seychelles 1938, Vasey Fitzgerald 6169, BH).
*Pinanga javana** Blume (Cult. Hort. Bog. Beccari).
P. kuhlii Blume (Cult. Florida Jan. 1965, Read 825).
*P. ternatensis** Scheffer (Hort. Bog. 286).
Podococcus barteri Mann et Wendland (Herb. Mus. Paris 1909, 7690, K.).
*Pseudophoenix navassana** Ekman (Ex Mus. Botan. Stockholm 1928, 10802, Ekman, K.).
*P. vinifera** (Martius) Beccari (Ex Mus. Botan. Stockholm, 5496, Ekman, K.).
Ptychosperma macarthurii (Wendland) Nicholson (Cult. Manila, Luzon, Merrill, K.).
*Ravenea hildebrandtii** H. Wendland ex Bouche (Comoren, Humblot 1608a).
*R. madagascariensis** Beccari (Malagasy 1963, Moore 9010, BH).
*R. robustior** Jumelle et Perrier (Malagasy, Moore 9029, BH).
Rhopalostylis baueri H. Wendland et Drude (Norfolk Island, Cult. Kew 1956, K.).
R. sapida H. Wendland et Drude (Ex Herb. Hooker 1867, K.).
*Roscheria melanochaetes** (H. Wendland) H. Wendland (Seychelles Islands).
*Roystonea oleracea** O. F. Cook (Puerto Rico 1885, Sintenis 1525).
*R. regia** (Humboldt, Bonpland et Kunth) O. F. Cook (Isla de Pinos 1904, Curtis 432).
*Sclerosperma mannii** H. Wendland (Congo Kinshasa, Leonard 1614).
Siphokentia beguinii Burret (Cult. Florida Jan. 1965, Read 604).
Socratea oryniana H. Karsten (Peru 1960, Moore et al. 8541, BH).
Synecanthus fibrosus H. Wendland (Costa Rica 1903, Pittier 2191).
*Veitchia merrillii** (Beccari) H. E. Moore (Phillipines:Manila 1907, Merrill).
V. sessilifolia H. E. Moore (Fiji Islands 1964, Moore et Koroiveibau 9348, BH).
*Verschaffeltia splendida** H. Wendland (Seychelles 1962, Jeffrey et Zelia 1234, K.).
*Vonitra thouarsiana** (Baillon) Beccari (Cult. Ceylon 1963, Moore 9034, BH).
*V. utilis** Jumelle (Malagasy, Perrier 16067).
*Wettinia augusta** Poepp et Endl (Peru 1960, Moore et al. 8580, BH).
*W. maynensis** Spruce (Peru 1960, Moore et al. 8360, BH).

Borassoideae

*Bismarckia nobilis** Hildebrandt et H. Wendland (Malagasy, Jumelle).
*Borassus aethiopum** (Martius) Martius (West Africa:Kassai, Buchner, FI.).
*B. flabellifer** Linnaeus (India:Calcutta, Wallich).
*Hyphaene compressa** H. Wendland (Tanzania 1957, Drummond et Hemsley 1336, S.).
*H. crinita** Gaertner (S. Africa:Natal 1939, McClean 29223, K.).
*H. schatan** Bojer ex Dammer (Cult. in U.S. 1962, Read 720, BH).
H. sp.* (Kenya 1929, Graham 1591, K.).
*H. thebaica** Martius (Congo Kinshasa Sept. 1953, Wagemans 610, Br.).
*Latania lontaroides** (Gaertner) H. E. Moore (Guinea 1819, Poiteau).
*Lodoicea maldivicia** (Gmelin) Persoon (Cult. in Guyana 1922, Bailey 433, BH).
*L. verschaffeltii** Lemaire (Balfour, K.).
*Medemia argun** P. G. von Wurrt (Egypt, Talbot, K.).

Caryotoideae

*Arenga hookeriana** Beccari (Perak 1880, Dr. King's, K.).
*A. humile** Schum (New Guinea 1891, Ex Herb, Lanterbach, K.).
*A. pinnata** (Wurmb) Merrill (Cult. Florida, Read 772).
*A. westerhoutii** W. Griffith (Cult. Hort. Bog. VK.115).
*Caryota mitis** Loureiro (China, McClure 1921, 8035, K.).
*C. rumphiana** Martius (Solomon Is. 1964, Moore et al. 9313, BH).
*C. urens** Linnaeus (Belgium, Ritchie 753, K.).
*Wallichia caryotoides** Roxburgh (Siam 1911, Kerr, K.).
*W. densiflora** (Martius) Martius (Khasia, Hooker et Thomson).

Cocoideae

*Acrocomia aculeata** (Jacquin) Loddiges ex Martius (Glaziou 8057, K.).
*A. mexicana** Karwinski ex Martius (San Luis March 1889, Langlasse 938, K.).
Aiphaenes acanthophylla Burret (Hispaniola May 1930, Ekman, Mus. Bot. Stockholm H. 1445, K.).
*A. caryotaefolia** H. Wendland (Ex Herb. Hooker anno 1867, K.).
*A. erosa** Burret (Barbados, Eggers 7135).
*Arikuryroba schizophylla** L. H. Bailey (India:Cult. Calcutta 1913).
Astrocaryum gynacanthum Martius (Cult. Hort. Bog. 240, xII, E, 107).
Bactris lindmaniana Drude (Foster 2505).
*B. major** Jacquin (Cult. Hort. Bog. 12).
B. sp. (U.S.A.:Cult. Florida, Feb. 1964, Read 901).
B. gasipaes Humboldt, Bonpland et Kunth (Rio de Janeiro, 1876, Glaziou 8053, K.).
Butia capitata (Martius) Beccari var. *odorata** (Barbosa Rodrigues) Beccari (Kew 1960, Nilsson).
*Cocos nucifera** Linnaeus (Is. of Tau-Samoa 1922, Garger, K.; Cult. Bot. Nursery, Univ. of Ibadan Oct. 1954, Sowunmi anno 1965; Cult. NIFOR 1950, Menendez et Sowunmi anno 1965).
*Corozo oleifera** (Humboldt, Bonpland et Kunth) L. H. Bailey (Cult. NIFOR ex Panama, Menendez et Sowunmi anno 1965).
Elaeis guineesis Jacquin
var. *dura** (Ibadan 1962; NIFOR anno 1965, Menendez et al.).
var. *pisifera** (Ibadan 1962; NIFOR anno 1965, Menendez et al.).
var. *tenera** (Ibadan 1962; NIFOR anno 1965, Menendez et al.).
*Jubaea chilensis** (Molina) Baillon (Chile Feb. 1888, K.).
*Jubaeopsis caffra** Beccari (S. Africa 1915, Burtt-Davy 15302, K.).
*Lytocaryum hoehnei** (Burret) Toledo (Brazil 1943, Handro et Toledo 51606, BH).
*Maximiliana elegans** H; Karsten (Venezuela 1961, Steyermark 88912, BH).
*M. venatorum** H. Wendland (Peru 1924, Tessman 5492).
*Orbignya speciosa** (Martius) Barbosa Rodrigues (Brazil 1905, Glaziou 16488 FI.).
*Parascheelea anchistropetala** Dugand (Columbia 1952, Schultes et Cabrera 17518, BH).
*Scheelea leandroana** Barbosa Rodrigues (Brazil 1905, Glaziou 16485).
S. sp. (Cult. Miami Florida Feb. 1964, Read 900).

Coryphoideae

*Brahea dulcis** (Humboldt, Bonpland et Kunth) Martius (Royal Bot. Gardens, Kew 1027, K.).
*Chamaerops humilis** Linnaeus (Gibraltar, Ex Herb. Hooker 1854, K.; Gard. Bot. Paris 1949, Erdtman).
C. humilis Linnaeus var. *elatior** Gussone (Palermo 1847, S.).
*Cocothrinax argentea** (Loddiges ex J. A. et J. H. Schultes) Sargent ex Beccari (Miami Beach, Florida, Moldenke 286, S.).
C. jacunda Sargent (Florida 1929, O'Neill 5992, S.).
*Colpothrinax wrightii** Grisebach et H. Wendland ex Siebert et Voss (Isla de Pinos, Curtis 364).
*Copernicia prunifera** (Miller) H. E. Moore (Argentina 1875, Kerr, K.).

C. yarey Burret var. *robusta* León (Cult. in U.S.A. from Mexican seed 1961, Read 606, BH).
*Corypha martiana** Beccari (India: Cult. Calcutta 1898, Davies).
*C. talliera** Roxburgh (India: Cult. Calcutta 1893, 884, K.).
*Cryosophila warsewiczii** H. H. Barlett (Panama 1931, Bailey 558, BH).
Erythea edulis (H. Wendland ex S. Watson) S. Watson (Guadalupens 1893, Heine, K.).
Licuala modesta Beccari (Malay Peninsula: Perak-Maturelli Hill March 1924, Burkillet Haniff 12551, K.).
*L. peltata** Roxburgh (Cult. in Cuba 1952, Moore 6093, BH).
*Livistona chinensis** (Jacquin) R. Brown ex Martius (India: Dehra Dun 1891, Gamble, K.).
L..humilis R. Brown (N. Australia 1946, Blake 16347, K.).
L. rotundifolia (Lamarck) Martius (Phillipines, Loher 1391, K.).
*Nannorrhops ritchiana** (Griffith) J. E. T. Aitchison (H. Bot. Saharanpur 1887, Ritchie, K.).
*Pritchardia affinis** Beccari (Hawaii 1926, Skottsberg 2106, S.).
*P. gaudichaudii** H. Wendland (Ex Herb. Hooker 1867, K.).
P. pacifica Seeman et H. Wendland (Sierra Leone, Deighton, K.).
P. sp.* (Hawaii Dec. 1962, Hutchinson et al., BH).
*Rhapidophyllum hystrix** (Pursh) H. Wendland et Drude (U.S.A.:Florida 1962, Read 750, BH).
*Rhapis excelsa** (Thunberg) Henry (N.W. Yunnan, Forest 21168, K.).
Sabal mexicana Martius (Isla de Pinos, 1904, Curtis 484, K.).
*S. minor** (Jacquin) Persoon (Beccari anno 1907, S.).
*S. rosei** (O. F. Cook) Beccari (Mexico 1910, Rose 14350, K.).
Schippia concolor Burret (Cult. in Nassau from Honduras 1964, A.C. et M. Langlois, BH).
*Serenoa repens** (Bartram) Small (U.S.A. 1961, Read 608, BH).
Thrinax excelsa Grisebach (Cult. in U.S.A. 1962, Read 714, BH).
T. parviflora Swartz (Ex Herb. Hooker 1867, 1730, K.).
*Trachycarpus fortunei** (W. J. Hooker) H. Wendland (China, Law 522, K.).
Trithrinax acanthocoma Drude (Rio de Janeiro 1877, Glaziou 9014, K.).
T. braziliensis Martius (Ex.Herb. Hooker 1867, K.).
*Washigtonia filifera** (Linden) H. Wendland (San Diego 1880, Blasey 629, K.).
Wissmannia carinensis Burret (Somaliland 1953, Chedeville ex Herb. Dakar).

Lepidocaryoideae

*Ancistrophyllum secundiflorum** (Beauvois) Mann et H. Wendland (Mouth R. Niger 1860, Mann 453).
*Calamus guruba** Martius (India, Meebold 5530).
*C. microcarpa** Beccari (Phillipines, Elmer 15573).
*C. nobilis** Blanco (Phillipines 1906, Loher 7081, K.).
*C. rivalis** Thwaites (Ceylon, Thwaites 3914).
C. sp.* (New Guinea 1964, Moore et Womersley 9268, BH).
*Daemonorops formicarius** Beccari (Borneo 1963, Fuchs et Mueller 21157, KSEPL).
*D. sparsiflorus** Beccari (Sarawak 1894-5, Hose, K.).
*Korthalsia laciniosa** Martius (Luzon 1916, Elmer 16672 G.).
*Lepidocaryum gracile** Martius (Ex Herb. Berlin, Glaziou 14368a).
*Mauritia armata** Martius (Brazil, Martius 1720).
*M. flexuosa** Linnaeus f. (Guyana 1899, K.).
*M. vinifera** Martius (Brazil, Martius).
*Metroxylon amicarum** (H. Wendland) Beccari (Caroline Is. Fosberg 24522, BH).
M. sagu Roetboell (Solomon Is. 1964, Moore et al. 9315, BH).
*M. salomonense** (Warburgh) Beccari (Solomon Is. 1964, Moore et al. 9317, BH).
*M. warburgii** Heim (New Hebrides 1964, Moore 9319, BH).
*Myrialepis scortechinii** Beccari (Malaya 1963, Moore et al. 9075, BH).
*Oncocalamus mannii** H. Wendland (Paris 1893, Pierre).
*Plectocomia elongata** Martius ex Blume (Java, Ex Herb. Hook., Blume, K.).
*P. muelleri** Blume (Borneo; Sarawak 1963, Sarawak Forest Dept. S:17895, K.).
Plectocomiopsis geminiflora (W. Griffith) Beccari var. *borneensis** Beccari (Borneo:Sabah 1964, Moore et Meijer 9206, BH).

Raphia eximia Dammer (Kenya 1916, Polhill et Paulo 985, S.).
R. farinifera (Gaertner) Hylander (Digo, Kenya 1937, Dale, K.).
Salacca affinis W. Griffith (Ex Herb. Hooker 1837, K.).
S. borneensis Beccari (Borneo 1921, Elmer 20110 G).
S. edulis Reinwardt (Ex Herb. Hook. 1867, K.).

Nypoideae

*Nypa fruticans** Wurmb (Cult. Hort. Bog., ex Herb. Firenze, 52; Cult. Florida, Read 734).

Phoenicoideae

*Phoenix canariensis** Hortorum ex Chabaud (anno 1885, Smith, K.).
*P. dactylifera** Linnaeus (India: Bot. Lab. Calcutta 1957).
P. loureirii Kunth (Formosa 1912, Price, K.).
*P. reclinata** N. J. Jacquin (Natal, Stellenbosch 4271).

Phytelephantoideae

*Phytelephas macrocarpa** Ruiz et Pavon (Cult. Hort. Bog. anno 1878, Beccari).
*P. poeppigii** Gaudichaud (Cult. Hort. Bog.).

Index to the herbaria mentioned

BH = Bailey Hortorium, Ithaca, New York, U.S.A.
Br. = Jardin botanique de l'Etat, Bruxelles, Belgium.
FI. = Herbarium Universitatis Florentinae, Firenze, Italy.
K. = The Herbarium and Library, Royal Botanic Gardens, Kew, Great Britain.
S. = Botanical Department, Naturhistoriska Museum, Stockholm, Sweden.
G. = Conservatoire et Jardin botaniques, Genève, Switzerland.

APPENDIX II

Terminology

Annulocolpate	With a ring-like meridional (q.v.) aperture which encircles the polar axis (present author).
Bacules	"More or less perpendicular (radial) rods or more or less rod-like elements . . . Bacules are usually longer than broad" (Erdtman, 1969).
Meridional	". . . of a plane perpendicular to the equatorial plane . . ." (Faegri and Iversen, 1964).
Negative reticulum	Exine isles separated from one another by a network of grooves (Erdtman, 1952).
Nexine	". . . an inner, usually non-sculptured layer . . . ." of the exine (Erdtman, 1969).
Semitectate	Of a gradual transition between tectate and intectate, the tectum being "partially absent" (Faegri and Iversen, 1964).
Sexine	". . . an outer, usually sculptured layer . . ." of the exine (Erdtman, 1969).
Tectum	Roof: the outer of the two main subdivisions of the sexine, usually distinctly separated from the nexine by a baculate zone (Erdtman, 1969).
Tetrachotomocolpate	With a four-slit colpoid distal aperture (Erdtman, 1952).
Trichotomocolpate	With a three-slit colpoid distal aperture (Erdtman, 1952).
Tubercle	Knobby projection or process (Jackson in Kremp, 1965).
Vermiculate	With grooves like worm tracks (Harris in Kremp, 1965).

	Shape			Aperture									Sexine pattern																			Major dimensions			
APPENDIX III (1)*	amb elliptical	amb rounded triangular	amb circular	monocolpate	annulocolpate	nearly annulocolpate	monoporate	trichotomocolpate	tetrachotomocolpate	dicolpate	diporate	triporate	reticulate	scrobiculate	muri simpli-baculate	muri simpli-dupli-baculate	muri simpli-tripli-baculate	muri simpli-multi-baculate	verrucose-reticulate	spinulose-reticulate	spinose-reticulate	clavate-reticulate	negatively reticulate	spinulose-tectate	punctate	vermiculate	verrucose	spinulose	spinose	pilate	baculate	polar axis (P, in μ)	longer equatorial diameter (E_1, E, in μ)	shorter equatorial diameter (E_2, in μ)	exine thickness (in μ)
Coryphoideae																																			
Brahea dulcis	+			+									+		+																	15.5 ± 1.4	35 ± 2.0	18.5 ± 1.1	1.1 ± 0.1
Serenoa repens	+			+									+		+																	15.5 ± 1.8	37 ± 2.0	22.5 ± 1.7	1.2 ± 0.1
Copernicia prunifera	+			+									+		+																	13.5 ± 0	35 ± 2.3	20.0 ± 1.6	1.2 ± 0.1
Chamaerops humilis	+			+									+		+																	16.5 ± 0.9	28 ± 1.3	23.0 ± 1.3	1.0 ± 0.1
C. humilis var. *elatior*	+			+									+		+																	19.0 ± 1.1	29 ± 1.4	26 ± 0.9	1.3 ± 0.2
Corypha martiana	+			+									+			+																23.5 ± 1.4	34 ± 1.1	27 ± 1.7	1.3 ± 0.2
C. talliera	+			+									+			+																21.0 ± 1.7	34 ± 1.1	28 ± 2.1	1.5 ± 0.3
Nannorrhops ritchiana	+			+									+			+																20.5 ± 1.8	36 ± 4.7	26 ± 2.0	1.2 ± 0.2
Pritchardia sp.	+			+									+			+																19.0 ± 1.1	47 ± 1.9	30 ± 1.8	1.8 ± 0.2
Rhapis excelsa	+			+									+			+																–	–	–	–
Washingtonia filifera	+			+									+			+																18.0 ± 1.4	40 ± 2.0	27 ± 2.2	1.8 ± 0.2
Cryosophila warscewiczii	+			+									+				+															17.0 ± 1.6	29 ± 1.5	23.5 ± 1.5	1.1 ± 0.1
Rhapidophyllum hystrix	+			+									+				+															11.5 ± 0.7	23.0 ± 0.5	17.0 ± 0.7	1.2 ± 0.2
Livistona chinensis	+			+									+				+															14.0 ± 1.1	27 ± 2.6	18.5 ± 1.5	0.9 ± 0.2
Trachycarpus fortunei	+			+									+				+															15.5 ± 1.7	26 ± 1.7	20.0 ± 1.1	1.2 ± 0.3
Sabal mexicana	+			+									+					+														18.5 ± 1.6	33 ± 1.9	24.0 ± 1.3	1.1 ± 0.1
S. minor	+			+									+					+														?	42 ± 1.3	29 ± 1.4	1.3 ± 0
S. rosei	+			+									+					+														18.5 ± 1.2	35 ± 1.6	24.5 ± 1.7	1.1 ± 0.1
Cocothrinax argentea	+			+									+					+														16.5 ± 2.2	38 ± 1.9	24.0 ± 1.5	1.2 ± 0.2
Colpothrinax wrightii	+			+									+					+														32 ± 2.6	55 ± 2.9	45 ± 2.0	2.3 ± 0.2
Pritchardia gaudichaudii	+			+									+					+														24.0 ± 1.8	44 ± 2.5	26 ± 2.7	2.2 ± 0.2
P. affinis	++	(+)		++				(+)					+					+														19.0 ± 1.4	45 ± 2.0	29 ± 2.7	1.3 ± 0.1
Licuala peltata	++			+									+					+														30 ± 2.8	45 ± 2.3	36 ± 1.8	2.3 ± 0.1
Phoenicoideae																																			
Phoenix canariensis	+			+									+																			9.5 ± 0.9	20.5 ± 1.2	13.5 ± 1.2	0.6 ± 0.1
P. dactylifera	+			+									+		+																	12.0 ± 0.7	23.5 ± 1.6	14.5 ± 1.1	0.6 ± 0.1
P. loureirii	+			+									+		+																	11.5 ± 0.9	20.5 ± 1.1	15.0 ± 0.5	1.1 ± 0
P. reclinata	+			+									+		+																	17.0 ± 1.8	26 ± 1.0	20.5 ± 1.9	0.8 ± 0.1
Phytelephantoideae																																			
Phytelephas macrocarpa	+			+									+			+																32 ± 3.4	70 ± 3.0	43 ± 2.6	2.0 ± 0.3
P. poeppigii	++	(+)		++				(+)					+			+																34 ± 2.3	75 ± 4.3	47 ± 4.2	1.9 ± 0.1

In dimorphic species–++ represents a proportion 15% and above; + represents a proportion 15% or less; (+) represents a proportion less than 1%.

	Shape			Aperture								Sexine pattern		
APPENDIX III (2)*	amb elliptical	amb rounded triangular	amb circular	monocolpate	annulocolpate	nearly annulocolpate	monoporate	trichotomocolpate	tetrachotomocolpate	dicolpate	diporate triporate	reticulate	scrobiculate	muri simpli-baculate
Arecoideae														
Areca subgroup														
Gronophyllum type														
Gronophyllum luridium	+			+								+		+
G. microcarpum	+			+								+		+
Nenga pumila	+			+								+		+
N. sp.	+			+								+		+
Nengella pterophylla	+			+								+		+
Siphokentia beguinii	+			+								+		+
Pinanga type														
Pinanga javana			+			+			?+			+		+
P. ternatensis			+			+			?+			+		+
Paralinospadix type														
Balaka cuneata	+			+										
Verschaffeltia splendida	+			+										
Podococcus barteri	+			+								+		
Howeia belmoreana	+			+								+		
H. forsteriana	+			+								+		
Paralinospadix petrickiana	+			+								+		
Basselinia sp. (aff. *B. tomentosa*)	+		+	+								+		
Goniosperma vitiense	+			+								+		
Ptychosperma marcathurii	+			+								+		
Loxococcus rupicola	+			+								+		
Neophloga heterophylla	+			+								+		
Chrysalidocarpus madagascariensis var. *lucubensis*	++	(+)		++					(+)			+		
Paralinospadix caudiculata	++	(+)		++					(+)			+		
Veitchia merrillii	++	(+)		++					(+)					
Neophloga tenuiseta	++	+		++					+					
Areca type														
Neodypsis decaryi	+			+								+		+
Opsiandra maya	+			+								+		+
Chrysalidocarpus decipiens	+			+								+		+
Calyptrogyne synanthera	+			+								+		+

*In dimorphic species—++ represents a proportion 15% and above; + represents a proportion 15% or less and (+) represents a pro

pp. 69–70

																Major dimensions			
muri simpli-dupli-baculate	muri simpli-tripli-baculate	murisimpli-multi-baculate	verrucose-reticulate	spinulose-reticulate	spinose-reticulate	clavate-reticulate	negatively reticulate	spinulose-tectate	punctate	vermiculate	verrucose	spinulose	spinose	pilate	baculate	polar axis (P, in *μ*)	longer equatorial diameter (E$_1$, or E, in *μ*)	shorter equatorial diameter (E$_2$, in *μ*)	exine thickness (in *μ*)
																23.5 ± 2.9	37.5 ± 2.2	31.4 ± 2.4	3.8 ± 0.2
																19.0 ± 1.9	33 ± 1.3	25 ± 0.8	2.4 ± 0.2
																18.0 ± 0.7	30 ± 1.4	23.5 ± 0.7	1.4 ± 0.1
																37 ± 4.2	50 ± 2.1	43 ± 2.2	6.3 ± 0.5
																23.5 ± 2.6	35 ± 1.3	30 ± 1.9	3.6 ± 0.2
																–	–	–	–
																39 ± 2.5	45 ± 1.9	37 ± 1.6	2.4 ± 0.2
																36 ± 2.5	40 ± 2.5	34 ± 2.2	2.3 ± 0.4
									+							–	–	–	–
									+							17.0 ± 0.7	34 ± 1.4	20.5 ± 1.1	1.1 ± 0.1
									+							–	–	–	–
									+							–	–	–	–
																–	–	–	–
																19.5 ± 2.0	46 ± 3.3	31 ± 1.8	1.0 ± 0.1
																?	50 ± 3.5	46 ± 3.1	1.8 ± 0.4
																–	–	–	–
																–	–	–	–
																–	–	–	–
																–	–	–	–
																16.0 ± 0.7	36 ± 3.0	19.5 ± 1.4	0.9 ± 0.2
																?	47 ± 1.3	35 ± 2.2	2.0 ± 0.3
									+							23.5 ± 1.8	60 ± 2.0	34 ± 2.3	1.1 ± 0
									+							–	–	–	–
																20.0 ± 2.6	43 ± 2.8	22.5 ± 2.2	1.1 ± 0.1
																17.0 ± 1.0	26 ± 1.5	20.5 ± 0.4	1.3 ± 0.2
																–	–	–	–
																18.5 ± 1.5	42 ± 1.3	27 ± 1.2	0.8 ± 0.1

portion less than 1%.

	Shape			Aperture				Sexine pattern				
APPENDIX III (3)*	amb elliptical	amb rounded triangular	amb circular	monocolpate	annulocolpate nearly annulocolpate	trichotomocolpate	tetrachotomocolpate dicolpate diporate triporate	reticulate	scrobiculate	muri simpli-baculate	muri simpli-dupli-baculate	muri simpli-tripli-baculate
Arecoideae (contd.)												
Areca type (contd.)												
Euterpe oleracea	+			+				+		+		
Juania australis	+			+				+		+		
Linospadix angustiseta	+			+				+		+		
L. monostachya	+			+				+		+		
Geonoma macrostachys	+			+				+		+		
Vonitra thoursiana	+			+				+		+		
V. utilis	+			+				+		+		
Areca catechu	+			+				+		+		
Chamaedorea fragrans	+			+				+		+		
C. stolonifera	+			+				+		+		
Veitchia sessilifolia	+			+				+		+		
Aristeyera spicata	+			+				+		+	?+	
Roscheria melanochaetes	++	(+)		++		(+)		+		+		
Areca paniculata	+			+				+			+	
A. sp.	+			+				+			+	
A. warburgiana	+			+				+			+	
Ceroxylon sp.	+			+				+			+	
Gulubia costata	+			+				+			+	
G. mollucana	+			+				+			+	
Chamaedorea karwinskiana	+		+	+				+			+	
Pseudophoenix vinifera	+			+				+			+	
Kentia gibbsiana	++	(+)	(+)	++				+			+	
K. ramsayi	++	+		++		+		+			+	
Gigliolia subacaulis	++	+		++		+		+			+	
Pseudophoenix navassana	++	(+)		++		(+)		+			+	
Iriartella setigera	+			+				+			+	
Acanthophoenix crinita	++		+	+				+				
Roystonea type												
Cyphophoenix elegans	+			+								
Normanbya normanbyi	+			+								
Manicaria saccifera	+			+								
Jessenia batana	++	+	++	+								
J. sp.	++	(+)	++	++		?(+)						
Roystonea oleracea	+			+								
R. regia	+			+								

*In dimorphic species–++ represents a proportion 15% and above; + represents a proportion 15% or less and (+) represents

							Major dimensions			
muri simpli-multi-baculate	verrucose-reticulate spinulose-reticulate spinose-reticulate clavate-reticulate	negatively reticulate	spinulose-tectate	punctate	vermiculate	verrucose spinulose spinose pilate baculate	polar axis (P, in μ)	longer equatorial diameter (E_1, or E, in μ)	shorter equatorial diameter (E_2, in μ)	exine thickness (in μ)
							18.0 ± 1.6	39 ± 1.1	24.0 ± 1.1	1.2 ± 0.2
							16.0 ± 1.6	29 ± 1.2	22.5 ± 1.4	1.1 ± 0.1
							18.0 ± 0.1	38 ± 1.1	24.0 ± 3.3	1.0 ± 0.2
							13.5 ± 1.7	23.5 ± 0.5	20.5 ± 1.4	0.6 ± 0
							12.5 ± 0.7	31 ± 1.8	18.0 ± 1.8	0.7 ± 0.1
							13.5 ± 0	22.5 ± 0.6	18.0 ± 0.7	1.1 ± 0.2
							14.5 ± 1.7	24.0 ± 1.2	20.5 ± 1.6	1.0 ± 0.2
							–	–	–	–
							18.0 ± 0.1	27 ± 0.1	21.0 ± 1.3	1.1 ± 0.1
							18.0 ± 1.0	30 ± 1.4	26 ± 1.1	1.0 ± 0
							–	–	–	–
							–	–	–	–
							26 ± 0.4	31 ± 0.6	18.0 ± 1.2	0.9 ± 0.1
							17.5 ± 1.0	34 ± 1.8	25 ± 2.1	1.0 ± 0.1
							?	32 ± 1.6	28 ± 1.5	1.5 ± 0.2
							17.5 ± 0	43 ± 1.6	36 ± 1.5	2.0 ± 0.2
							18.5 ± 3.2	32 ± 1.4	25 ± 2.2	1.4 ± 0.2
							17.0 ± 1.8	34 ± 2.3	23.5 ± 0.8	1.2 ± 0.1
							19.5 ± 1.7	36 ± 1.7	28 ± 2.1	1.3 ± 0.1
							26 ± 1.9	41 ± 2.6	31 ± 1.4	1.3 ± 0.1
							24.5 ± 1.9	43 ± 3.5	31 ± 3.2	2.7 ± 0.5
							20.0 ± 1.4	31 ± 1.8	26 ± 1.4	0.9 ± 0.1
							21.0 ± 0	39 ± 2.8	26 ± 1.8	1.4 ± 0.2
							24.0 ± 1.3	48 ± 1.6	34 ± 1.2	1.4 ± 0.2
							21.5 ± 1.5	42 ± 2.0	30 ± 1.1	2.7 ± 0.3
							13.5 ± 1.1	22.5 ± 0.9	19.0 ± 1.1	1.0 ± 0.1
+							?	40 ± 3.5	37 ± 2.7	3.3 ± 0.5
					+		24.5 ± 2.0	47 ± 2.3	26 ± 1.8	1.2 ± 0.1
					+		?	47 ± 1.4	28 ± 1.4	1.7 ± 0.1
		++			++		–	–	–	–
		+					?	44 ± 1.5	31 ± 3.9	2.2 ± 0.1
		++			+		23.5 ± 2.0	43 ± 2.1	32 ± 3.2	1.5 ± 0.2
		++	(+)		++		26 ± 1.9	55 ± 1.4	33 ± 1.6	2.1 ± 0.2
			+		++		26 ± 2.1	55 ± 2.1	37 ± 1.9	1.9 ± 0.1

a proportion less than 1%.

	Shape			Aperture									Sexine pattern					
APPENDIX III (4)*	amb elliptical	amb rounded triangular	amb circular	monocolpate	annulocolpate	nearly annulocolpate	monoporate	trichotomocolpate	tetrachotomocolpate	dicolpate	diporate	triporate	reticulate	scrobiculate	muri simpli-baculate	muri simpli-dupli-baculate	muri simpli-tripli-baculate	muri simpli-multi-baculate
Arecoideae (contd.)																		
Deckenia subgroup																		
Socratea type																		
Socratea orbigniana	+			+														
Wettinia augusta	++		+	+														
W. maynensis	++		+	+														
Deckenia type																		
Deckenia nobilis	+			+														
Iriartea cometes	+			+														
I. ventricosa	+			+														
Cyrtostachys subgroup																		
Cyrtostachys type																		
Cyrtostachys sp.	++		+	+														
Oncosperma type																		
Oncosperma tigillarium	+			+														
Phoenicophorium type																		
Phoenicophorium borsigianum	++		+	+														
Ravenea type																		
Dypsis sp.			+				†											
Ravenea hildebrandtii			+				+											
R. madagascariensis			+				+											
R. robustior			+				+											
Sclerosperma type																		
Sclerosperma mannii		+										+	+				+	

*In dimorphic species—++ represents a proportion 15% and above; + represents a proportion 15% or less; (+) represents a proportion less th

pp. 73–74

											Major dimensions			
	spinulose-reticulate	spinose-reticulate	clavate-reticulate	negatively-reticulate	spinulose-tectate	punctate vermiculate verrucose	spinulose	spinose	pilate	baculate	polar axis (P, in µ)	longer equatorial diameter (E_1, E, in µ)	shorter equatorial diameter (E_2, in µ)	exine thickness (in µ)
							+				–	–	–	–
							+				?	42 ± 0.7	32 ± 1.4	1.2 ± 0
							+				27 ± 3.6	42 ± 2.4	37 ± 1.6	1.3 ± 0.1
									+		15.5 ± 1.5	29 ± 0.7	21.0 ± 1.1	1.2 ± 0.1
									+		20.5 ± 1.7	38 ± 1.7	29 ± 1.5	1.0 ± 0.2
									+		15.5 ± 0.8	33 ± 0.7	22.0 ± 2.0	1.0 ± 0.1
+											18.0 ± 2.2	31 ± 0.9	23.5 ± 1.4	1.3 ± 0.1
			+								19.0 ± 1.9	31 ± 2.3	25 ± 1.4	1.5 ± 0.1
					+						14.0 ± 1.1	23.0 ± 1.2	18.5 ± 1.4	0.9 ± 0.1
	+										15.5 ± 1.3	20.0 ± 0.5		0.7 ± 0.1
	+										20.0 ± 1.5	26 ± 0.9		1.8 ± 0.2
	+										16.5 ± 1.7	21.5 ± 1.1		0.8 ± 0.1
	+										18.5 ± 1.4	26 ± 0.9		0.7 ± 0
											11.5 ± 0.5	45 ± 1.6		2.3 ± 0.2

an 1%.

	Shape			Aperture									Sexine pattern					
APPENDIX III (5)*	amb elliptical	amb rounded triangular	amb circular	monocolpate	annulocolpate	nearly annulocolpate	monoporate	trichotomocolpate	tetrachotomocolpate	dicolpate	diporate	triporate	reticulate	scrobiculate	muri simpli-baculate	muri simpli-dupli-baculate	muri simpli-tripli-baculate	verrucose-reticulate
Caryotoideae																		
Arenga type																		
Arenga hookeriana	+			+														
A. humile	+			+														
A. pinnata	+			+														
A. westerhouti	+			+														
Wallichia caryotoides	+			+														
W. densiflora	+			+														
Caryota																		
Caryota mitis	+			+														
C. rumphiana	+			+														
C. urens	+			+														
Borassoideae																		
Borassus type																		
Borassus flabellifer	+			+									+		+			+
B. aethiopium	+			+									+					+
Hyphaene compressa	+			+									+					+
H. crinita	+			+									+					+
H. schatan	+			+									+					+
H. sp.	+			+									+					+
H. thebaica	+			+									+					+
Bismarckia and related gerera																		
Latania lontaroides	+		+	+									+	++			+	
L. verschaffeltii	+		+	+										++			+	
Lodoicea maldivica	+		+	+									++					
Medemia argun	+			+									+					
Bismarckia nobilis	+			+									+					
Nypoideae																		
Nypa type																		
Nypa fruticans			+	+	+								+					

*In dimorphic species–++ represents a proportion 15% and above; + represents a proportion 15% or less; (+) represents a proporti

pp. 75–76

												Major dimensions			
spinulose-reticulate	spinose-reticulate	clavate-reticulate	negatively-reticulate	spinulose-tectate	punctate	vermiculate	verrucose	spinulose	spinose	pilate	baculate	polar axis (P, in μ)	longer equatorial diameter (E_1, E, in μ)	shorter equatorial diameter (E_2, in μ)	exine thickness (in μ)
								+				15.0 ± 1.5	24.0 ± 1.5	18.5 ± 1.0	0.6 ± 0
								+				16.0 ± 0.9	23.0 ± 1.1	18.5 ± 1.1	0.5 ± 0.1
								+				17.5 ± 2.4	34 ± 1.0	26 ± 2.1	0.8 ± 0.1
									+			17.5 ± 1.4	34 ± 0.9	24 ± 1.0	0.9 ± 0.1
								+				14.5 ± 1.3	23.5 ± 2.1	18.5 ± 2.1	0.6 ± 0.1
								+				14.5 ± 1.7	26 ± 1.4	18.5 ± 1.1	0.5 ± 0.1
										+		15.0 ± 1.7	25 ± 1.9	19.5 ± 1.5	0.5 ± 0.1
										+		13.0 ± 0	24.5 ± 2.1	18.5 ± 1.5	0.6 ± 0.1
										+		12.5 ± 2.2	25 ± 1.3	19.0 ± 0.9	0.7 ± 0
												34 ± 2.0	65 ± 3.0	45 ± 3.6	1.8 ± 0.2
												–	–	–	–
												?	26 ± 2.0	37 ± 1.8	1.7 ± 0.1
												21.5 ± 2.4	41 ± 1.8	28 ± 1.7	1.1 ± 0.2
												21.0 ± 2.1	38 ± 2.6	25 ± 1.4	1.3 ± 0.1
												18.0 ± 1.8	35 ± 1.8	25 ± 2.6	1.2 ± 0.2
												31 ± 1.9	42 ± 2.3	31 ± 1.8	1.3 ± 0.2
												31 ± 2.2	48 ± 1.5	41 ± 1.7	2.6 ± 0.3
						+						29 ± 2.1	47 ± 2.4	40 ± 2.4	2.4 ± 0.2
					(+)	(++)						?	35 ± 1.5	55 ± 4.2	1.5 ± 0.2
						++						21.0 ± 2.0	41 ± 2.3	29 ± 2.0	1 ± 0.2
				+								28 ± 2.0	41 ± 1.4	31 ± 1.9	1.4 ± 0.2
	+											?	49 ± 2.3	42 ± 2.4	1.8 ± 0.3

n less than 1%.

	Shape			Aperture								Sexine pattern					
APPENDIX III (6)*	amb elliptical	amb rounded triangular	amb circular	monocolpate	monoporate	annulocolpate	nearly annulocolpate	trichotomocolpate tetrachotomocolpate	dicolpate	diporate	triporate	reticulate	scrobiculate	muri simpli-baculate	muri-simpli-dupli-baculate	muri simpli-tripli-baculate	muri simpli-multi- . .
Lepidocaryoideae																	
Lepidocaryum type																	
Lepidocaryum gracile	++		+	+													
Mauritia flexuosa	+		++	++	++												
Mauritia armata type																	
Mauritia armata			+		+												
M. vinifera			+		?+												
M. flexuosa	+		+	++	++												
Salacca type																	
Salacca affinis							++		?+								
S. borneensis							++		?+								
S. edulis							+										
Calamus subgroup																	
Plectocomia type																	
Calamus guruba									+			++			+		
C. nobilis									+			++			+		
C. rivalis									+			+		+			
Daemonorops formicarius									+			+			+		
Metroxylon amicarum									+			+					+
M. salomonense									+			+					+
M. warburgii									+			+				+	
Plectocomia elongata									+			+		+			
P. muelleri									+			+					
Myrialepis scortechinii									+			+		+			
Calamus microcarpa type																	
Calamus microcarpa									+			+		+			
C. sp.									+			+					
Plectocomiopsis type																	
Plectocomiopsis geminiflora var. *borneensis*									+								
Korthalsia subgroup																	
Korthalsia type																	
Korthalsia laciniosa	+	+								+							
Daemonorops sparsiflorus type																	
Daemonorops sparsiflorus	+									+		++		+			
Ancistrophyllum and related genera																	
Ancistrophyllum secundiflorum	+			+								++					+
Oncocalamus mannii	+			+								+					
Raphia eximia	+			+								+					
R. farinifera	+			+								+					

*In dimorphic species—++ represents a proportion 15% and above; + represents a proportion 15% or less and (+) represents a proportion less than

pp. 77–78

												Major dimensions			
baculate	verrucose-reticulate	spinulose-reticulate spinose-reticulate clavate-reticulate	negatively-reticulate	spinulose-tectate	punctate	vermiculate	verrucose	spinulose	spinose	pilate	baculate	polar axis (P, in μ)	longer equatorial diameter (E_1, E, in μ)	shorter equatorial diameter (E_2, in μ)	exine thickness (in μ)
								+	++			29 ± 2.2	40 ± 1.8	38 ± 1.8	1.1 ± 0.2
									+			44 ± 2.9	47 ± 1.6		1.3 ± 0.2
								(+)	++			41 ± 2.2	47 ± 1.3		3.1 ± 0.3
									+			36 ± 1.6	50 ± 2.5		2.0 ± 0.3
									+			44 ± 2.9	47 ± 1.6		1.3 ± 0.2
								+				–	–	–	–
								+				–	–	–	–
										+		–	–	–	–
			+									19.5 ± 1.5	23.5 ± 0.9	18.0 ± 2.2	1.3 ± 0.1
			+									27 ± 0.2	28 ± 2.6	25 ± 1.4	1.4 ± 0.3
						++						29 ± 1.6	33 ± 1.4	24.0 ± 1.9	1.4 ± 0.1
												30 ± 2.3	32 ± 1.3	28 ± 2.3	1.6 ± 0.2
												27 ± 1.9	42 ± 4.1	36 ± 2.1	3.1 ± 0.5
												32 ± 2.7	45 ± 2.3	32 ± 1.9	3.1 ± 0.6
												33 ± 0.6	42 ± 1.8	29 ± 1.8	2.2 ± 0.4
												27 ± 1.2	27 ± 1.3	2.1 ± 1.5	1.1 ± 0.1
												?	32 ± 1.7	23.0 ± 1.2	1.9 ± 0.1
												17.5 ± 1.6	27 ± 1.3	20.5 ± 1.2	1.2 ± 0.2
	+											28 ± 2.7	30 ± 1.7	26 ± 2.6	0.8 ± 0.1
	+											24.5 ± 1.5	27 ± 1.1	25 ± 1.4	1.1 ± 0.2
											+	23.0 ± 1.2	21.0 ± 1.0	17.5 ± 1.1	0.3 ± 0.1
								+				29 ± 2.3	23.5 ± 2.6	33 ± 2.1	
					+							21.5 ± 2.5	37 ± 1.0	26 ± 1.4	1.0 ± 0.1
					+							40 ± 1.0	55 ± 1.6	28 ± 1.6	1.2 ± 0.1
												16.5 ± 1.0	27 ± 1.9	19.5 ± 1.9	1.0 ± 0.1
												–	–	–	–
												–	–	–	–

1%.

	Shape			Aperture					Sexine pattern				
APPENDIX III (7)*	amb elliptical	amb rounded triangular	amb circular	monocolpate	monoporate annulocolpate nearly annulocolpate	trichotomocolpate	tetrachotomocolpate	dicolpate diporate triporate	reticulate	scrobiculate	muri simpli-baculate	muri simpli-dupli-baculate	muri simpli-tripli-
Cocoideae													
Elaeis type													
Aiphanes acanthophylla	+			+					+				
A. caryotaefolia	+			+					++				
A. erosa	+			+									
Bactris major	+	+				+			++				
B. lindeliana	++	+		++		+							
B. sp.	++	+		++		+							
Elaeis guineensis var. *dura*	++	++		++		++	+		+				
E. guineenis var. *tenera*	+	++		+		++			+				
E. guineensis var. *pisifera*	(+)	++		(+)		++	(+)						
Corozo oleifera	++	+		++		+			+				
Cocos type													
Acrocomia aculeata	(+)	++		(+)		++	(+)			+			
A. mexicana	(+)	++		(+)		++				+			
Maximiliana elegans	+			+					++	+			
M. venatorum	+			+						+			
Orbignya speciosa	++	(+)		++		(+)				+			
Cocos nucifera	++	(+)	++	+									
Butia capitata var. *odorata*	+			+									
Astrocaryum gynacanthum	++	+		++		+							
Jubaea chilensis	+			+									
Jubaeopsis caffra	++	+		++		+							
Scheelea leandroana	++		+	+									
Parascheelea anchistropetala	++		+	+									
Arikuryroba and *Lytocaryum*													
Arikuryroba schizophylla	+			+					+			+	
Lytocaryum hoehnei	+			+					+				+

*In dimorphic species–++ represents a proportion 15% and above; + represents a proportion 15% or less; (+) represents a propor

baculate	muri simpli-multi baculate	verrucose-reticulate spinulose-reticulate spinose-reticulate clavate-reticulate	negatively-reticulate	spinulose-tectate	punctate	vermiculate	verrucose spinulose spinose pilate baculate	Major dimensions			
								polar axis (P, in μ)	longer equatorial diameter (E_1, E, in μ)	shorter equatorial diameter (E_2, in μ)	exine thickness (in μ)
								–	–	–	–
						+		15.5 ± 0.7	31 ± 2.1	19.5 ± 1.4	0.8 ± 0.2
					++	+		16.0 ± 0.7	31 ± 1.9	22.0 ± 1.5	1.0 ± 0.2
			+			++		23.5 ± 1.6	38 ± 1.0		1.4 ± 0.3
			+			++					
			+			++					
			+			++		17.5 ± 1.1	43 ± 3.2		1.4 ± 0.2
			+			++		18.0 ± 1.9	50 ± 2.6		1.1 ± 0.1
			++		(+)			18.5 ± 1.9	40 ± 1.8		1.1 ± 0.1
						++		?	41 ± 1.8	26 ± 0.6	1.6 ± 0.3
					+	+		31 ± 1.7	55 ± 3.2		2.3 ± 0.5
					+			24.0 ± 1.6	55 ± 1.6		2.7 ± 0.3
	+							29 ± 3.4	50 ± 2.6	36 ± 1.3	
	+							26 ± 1.5	65 ± 1.4	46 ± 2.0	3.8 ± 0.7
	+					+		32 ± 3.4	60 ± 5.0	45 ± 4.7	2.0 ± 0.5
					+			37 ± 2.2	65 ± 1.8	47 ± 3.4	1.9 ± 0.2
					+			24.5 ± 2.4	48 ± 2.4	30 ± 3.3	2.0 ± 0.4
					+						
					++	+		27 ± 1.2	55 ± 2.5	37 ± 2.4	1.5 ± 0.4
					++	+		32 ± 2.7	65 ± 2.7	43 ± 2.5	2.5 ± 0.1
					+	++		46 ± 3.8	60 ± 5.6	44 ± 2.7	3.4 ± 0.7
					+	++		31 ± 1.5	55 ± 1.5	48 ± 2.8	3.6 ± 0.4
								25 ± 2.0	49 ± 4.2	32 ± 2.3	1.1 ± 0.1
								28 ± 2.0	39 ± 0.5	32 ± 2.3	1.4 ± 0.2

tion less than 1%.