POLLEN MORPHOLOGY AND THE BI-RETICULATE EXINE OF THE PHYLLANTHUS SPECIES (EUPHORBIACEAE) FROM MAURITIUS AND RÉUNION

J. BOR

Laboratory of Palaeobotany and Palynology, State University, Utrecht (The Netherlands) (Received March 10, 1978; revised version accepted May 22, 1978)

ABSTRACT

Bor, J., 1979. Pollen morphology and the bi-reticulate exine of the *Phyllanthus* species (Euphorbiaceae) from Mauritius and Réunion. Rev. Palaeobot. Palynol., 27: 149-172.

The pollen grains of the *Phyllanthus* species of Mauritius and Réunion have been divided into seven pollen types. The different species and varieties of the "phillyreifolius" group have close affinities and can be arranged in a continuous morphological series. All grains in this series are characterized by a two-layered or bi-reticulate ornamentation. They have a peripheral reticulum which consists of arch-like muri (in cross-section) and variform lumina and this covers an infra (micro-) reticulum, the structural units of which are connated with the muri of the suprareticulum.

Contrary to earlier observations the *Phyllanthus amarus* type also shows a bi-reticulate ornamentation; this suggests a relationship between this type and the "phillyreifolius" group. The *Phyllanthus maderaspatensis*, *P. casticum* and *P. tenellus* types, however, have eu-reticulate ornamentation. The *P. urinaria* type resembles the *P. amarus* type, but its ornamentation is not clearly bi-reticulate and is better termed tectate-perforate. In the *P. casticum* type the pollen grains show very characteristic ectoapertures and they are of special interest as many *Phyllanthus* spp. occurring in Africa and Asia belong to the same type.

INTRODUCTION

Various morphologists and taxonomists have pointed out the great diversity of pollen in the Euphorbiaceae. The Phyllanthoideae, and particularly the genus *Phyllanthus*, have received attention in recent times (Punt, 1962, 1967, 1972; Punt and Rentrop, 1974; Köhler, 1965, 1967; Webster, 1970; Bancilhon, 1971; Brunel, 1975). The descriptions of the pollen types in these papers, while often very detailed, were based mainly on light microscope (LM) investigations. But the observations presented here are also supported by scanning electron micrographs (SEM). It was to be expected, therefore, that some previous interpretations of the complex exine structure would be revised.

The main purpose of this investigation has been to discover how far the taxonomy of the *Phyllanthus* spp., native to Mauritius and Réunion, is

reflected by their pollen morphology. Introduced *Phyllanthus* spp. have also been studied as they represent a number of interesting pollen types which have not hitherto been described in detail. Investigations of the pollen morphology of the *Phyllanthus* spp. of Madagascar (c.f. Leandri, 1958) and East Africa are still at an early stage, so that it is too soon to draw conclusions about possible affinities with those species.

The material was mainly obtained from Mr. M.J.E. Coode (Kew, Great Britain) who is at present undertaking a revision of the Euphorbiaceae of Mauritius and Réunion. He recognizes nine native species (*P. casticum*, *P. consanguineus*, *P. dumetosus*, *P. lanceolatus*, *P. mauritianus*, *P. oppositifolius*, *P. phillyreifolius*, *P. pileostigma*, *P. revaughanii*) and five introduced weeds (*P. amarus*, *P. maderaspatensis*, *P. niruroides*, *P. tenellus*, *P. urinaria*). The endemic "phillyreifolius" group, represented by five species and seven varieties, is of special interest. Mueller (1866) described eleven varieties of *P. phillyreifolius* in Decandolle's Prodromus 15(2) (see also Baker, 1877). Taxonomic and morphological details will appear in Coode's forthcoming publication in which all species will be discussed and the new names validated.

MATERIAL AND METHODS

Specimens have been obtained from the following herbaria: Royal Botanic Garden, Edinburgh, Great Britain (E); Royal Botanic Gardens, Kew, Great Britain (K); Rijksherbarium, Leiden, The Netherlands (L); The Mauritius Herbarium, Mauritius (MAU); Botanical Museum and Herbarium, Utrecht, The Netherlands (U).

Pollen grains of the following taxa have been studied:

```
Phyllanthus amarus Schumacher et Thonning — Madagascar: D'Alleizette s.n. (L); Mauritius: Ayres s.n. (U).
```

Phyllanthus casticum P.R.F. Willemet — Mauritius: Herb. Splitgerberianum s.n. (L), Sieber s.n. (L).

Phyllanthus consanguineus Mueller-Arg. - Réunion: Balfour s.n. (K).

Phyllanthus dumetosus Poiret — Mauritius: Guého, Flora of Rodriguez 13973 (MAU), Rodrigues 1333 (K).

Phyllanthus lanceolatus Poiret — Mauritius: Barclay 2910 (K), Coode 4429 (K), Néraud s.n. (K).

Phyllanthus longifolius Poiret non Jacquin — see P. revaughanii Coode.

Phyllanthus maderaspatensis L. — Mauritius: Yerriah, Flora of Mauritius 17855 (MAU); Seychelles: Jeffrey 1198 (L); South Africa: Pont 1385 (U).

Phyllanthus mauritianus H.H. Johnston — Mauritius: H.H. Johnston s.n. (E), Vaughan 653 (MAU).

Phyllanthus niruroides Mueller-Arg. — Mauritius: Guého, Flora of Mauritius 17158 (K); Réunion: Cadet s.n. (K).

Phyllanthus nummalariifolius Poiret - Madagascar: Decary 11026 (L).

Phyllanthus oppositifolius Mueller-Arg. — Mauritius: Blackburn s.n. (K), Hooker s.n. (K). Phyllanthus phillyreifolius Poiret¹

var. commersonii Mueller-Arg. — Mauritius: Bojer s.n. (K), Barclay 2785 (K), Coll. Vaughan, Flora Mauritius 53 (K).

¹No male collections of the variety crassistigma were available.

```
var. gracilipes Coode — Mauritius: Ayres s.n. (K), Bouton 5 (K), Herb. Hooker s.n. (K).
var: phillyreifolius — Réunion: Cadet 2893B (K), Coode 4202 (K), Coode 4986 (K).
var. stylifer Coode — Mauritius: Coode 4346 (K).
var. telfairianus Mueller-Arg. — Mauritius: Coode 4695 (K), Coode 4433 (K), Graham s.n. (K).
var. triangularis Mueller-Arg. — Mauritius: Graham s.n. (K).
Phyllanthus pileostigma Coode — Mauritius: Coode 4759 (K).
Phyllanthus revaughanii Coode (syn. P. longifolius Poiret non Jacquin) — Mauritius:
Brown s.n. (K), Herb. Lugd. Bat. nr. 904.111.-368 (L).
Phyllanthus tenellus Roxburgh — Seychelles: Jeffrey 501 (L).
Phyllanthus urinaria Mueller-Arg. — Mauritius: Graham s.n. (K).
```

The pollen grains were prepared using the acetolysis method as described by Reitsma (1969). Descriptions were made based on observations with a Leitz light microscope, equipped with a 100 x plan apochromatic objective N.A. 1.32. The photomicrographs were taken with a Leitz Orthomat camera using an interference green filter. For scanning electron microscopy (SEM) acetolyzed pollen grains were coated with gold and micrographs were taken with a Cambridge S4 Stereoscan. A reconstruction of the exine was based on LO-analysis; pollen grains of various taxa were sectioned with a freezing microtome and examined in SEM.

The terminology used is based mainly on Reitsma (1970) and Praglowski and Punt (1973) but occasionally on Erdtman (1969).

DESCRIPTION OF THE POLLEN TYPES

Phyllanthus phillyreifolius var. phillyreifolius type (Plates II-V; VI, 1-4).

Pollen class: 3- Zonocolporate.

P/E ratio: Subprolate to prolate.

Apertures: Ectoaperture — colpus, long, narrow, slit-like, sunken; ends acute, margins distinct, regular or irregular; colpus membrane, if visible, beset with granules; costae colpi present, sometimes extending towards the middle of the colpus. Endoaperture — colpus, lalongate; ends diffuse or faint in the light microscope, but visible with SEM, costae distinct, often following the outline of the endoaperture, interrupted in the equatorial area.

Exine: Usually of constant thickness (P. pileostigma excepted). Nexine thinner than sexine. Sexine 2 about as thick as sexine 1; columellae (sexine 1) of two types: (a) distinct, supporting semitectal reticulum, and (b) shorter, forming an infrareticulum; sexine 2 of "arch"-like elements, distally massive, triangular in cross-section (see Fig.1A, Plate IV 3, 4).

Ornamentation: Bi-reticulate, outer reticulum coarse and infrareticulum fine. Outerreticulum with duplicolumellate muri, about as thick as lumina width or thinner, sometimes interrupted; coalescing with the minute muri of infrareticulum (indistinguishable in light microscope). Lumina irregular in outline, often elongated, sometimes smaller at apocolpia and colpus margins. Columellae circular in outline in LO-analysis, randomly arranged.

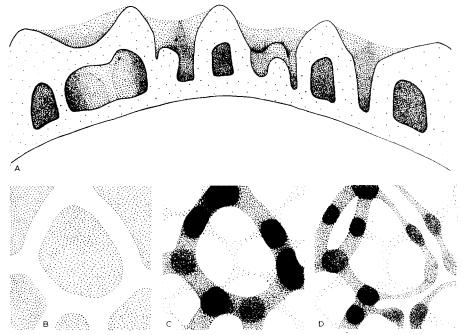


Fig.1. Bi-reticulate ornamentation. A. Schematic drawing of exine in longitudinal section. B—D. Reticulum and columellae in LO-analysis. B. High focus: suprareticulum light. C. Middle focus: suprareticulum greyish, "arches" dark and infrareticulum like bright islands. D. Low focus: separate columellae dark.

Outline: Equatorial view — elliptic, usually obtuse at poles. Polar view — circular to triangular with sunken colpi.

Measurements: P 20.0-32.0 μ m; E 16.0-24.0 μ m; P/E ratio 1.14-1.53. Exine ca. 1.8 μ m. Endoaperture: longest axis 4.5-7.5 μ m, shortest axis 0.5-3.0 μ m. Apocolpium index 0.25-0.55.*

Species and varieties: Phyllanthus consanguineus, P. lanceolatus, P. oppositifolius, P. phillyreifolius var. commersonii, var. phillyreifolius, var. stylifer, var. telfairianus, var. triangularis, P. pileostigma.

Comment

This type can be roughly divided into two groups which differ in the following characters:

- (a) Grains microreticulate, muri rarely interrupted and lumina more or less uniform in outline; margins of ectoaperture usually regular; costae of endoaperture conspicuous; apocolpium index ca. 0.25 (*P. phillyreifolius* var. *phillyreifolius*, var. *telfairianus*, var. *triangularis*; see Plates I, 1—3; II; III, 1—3, 6—8).
- (b) Grains reticulate, muri interrupted, lumina irregular in outline and elongated; margins of ectoaperture irregular; costae of endoaperture faint;

^{*}Apocolpium Index: syn. Polar Area Index (Faegri and Iversen, 1975).

apocolpium index 0.28—0.55 (P. consanguineus, P. lanceolatus, P. oppositifolius, P. phillyreifolius var. commersonii, var. stylifer, P. pileostigma; see Plates I, 4—8; III, 4, 5; IV; V; VI, 1—4).

Within these groups the pollen is variable in size. The range of sizes in different species overlaps, except in the case of *P. consanguineus* which has the smallest grains (P 20.0–24.0 μ m; E 16.0–19.5 μ m). The other taxa in group (b) are always larger than this size (P 24.0–28.5 μ m; E 19.0–23.0 μ m).

P. phillyreifolius var. *phillyreifolius* has the largest grains in group (b) (P 26.0–32.0 μ m; E 21.0–24.0 μ m) and *P.p.* var. *telfairianus* is smaller (P 22.5–26.5 μ m; E 16.0–19.5 μ m).

Two other species may also be distinguished using the following characters. In *P. pileostigma* the exine is thicker at the apocolpium than at the mesocolpium while *P. oppositifolius* is characterized by its shorter ectocolpi (apocolpium index 0.40–0.55) and obtuse poles.

A few grains of *P. phillyreifolius* var. *commersonii* and of *P. consanguineus* were 4-colporate.

Phyllanthus phillyreifolius var. gracilipes type (Plates VI, 5, 6; VII).

Pollen class: 3-Zonocolporate.

P/E ratio: Prolate spheroidal to subprolate.

Apertures: Ectoaperture — colpus, very long, extremely narrow, slit-like, hardly sunken; ends acute, but often indistinct; margins faint and very irregular; colpus membrane invisible; costae colpi extending to halfway along the colpus. Endoaperture — colpus, lalongate; margins not clear; ends diffuse; costae present but narrow.

Exine: Constant in thickness. Nexine thinner than sexine. Sexine 2 thicker than sexine 1; columellae (sexine 1) of two types: (a) distinct, supporting the high, steep semitectal reticulum, and (b) shorter, forming an infrareticulum; sexine 2 composed of "arch"-like elements, distally massive, elongated-triangular in cross-section (see Plate VII, 7, 8).

Ornamentation: Bi-reticulate, peripheral muri thin, erect, often interrupted, coalescing with muri of the infra-microreticulum; lumina very irregular in outline.

Outlines: Equatorial view — elliptic. Polar view — circular to slightly angular. Sides convex.

Measurements: P 25.0-27.0 μ m; E 22.0-25.0 μ m; P/E ratio 1.02-1.17. Exine ca. 2 μ m. Apocolpium index ca. 0.20. Endoaperture: longest axis 3.0-3.5 μ m; shortest axis 1.5-2.5 μ m.

Species and varieties: Pyllanthus phillyreifolius var. gracilipes.

Comment

The dissimilarity between the pollen of this variety and of the other taxa of the "phillyreifolius" group is so striking that I have placed it in a different pollen type. The grains are easily recognizable by their small size, indistinct endoaperture and very coarse reticulum with interrupted muri and elongated

lumina. On the basis of pollen morphology, a specimen in the Kew Herbarium (Herb. Hooker s.n.), incorrectly identified as var. gracilipes, could be renamed var. commersonii.

Phyllanthus casticum type (Plate VIII, 1-5).

Pollen class: Syncolpate, 3-zonocolporate. *P/E ratio*: Spheroidal to prolate spheroidal.

Apertures: Ectoaperture — colpus, narrow, sunken; margins distinct, irregular; colpus margins consisting of two distinct, parallel, simplicolumellate muri; almost completely separated from the reticulum; costae absent. Endoaperture — porus, circular or nearly so; margins distinct; costae present.

Exine: Of uniform thickness throughout. Nexine thinner than sexine. Sexine 1 about as thick as sexine 2; sexine 1 of columellae visible in LM; sexine 2 of circular capita in cross-section, forming a semi-tectum.

Ornamentation: Reticulate. Muri simplicolumellate; lumina irregular in size and outline; in LO-analysis columellae circular in outline.

Outlines: Equatorial view — circular to slightly elliptic. Polar view — circular with sunken colpi.

Measurements: P 12.5–15.0 μ m; E 12.5–14.0 μ m; P/E ratio 1.00–1.07. Exine ca. 1.5 μ m. Diam. endoaperture 2–2.5 μ m.

Species: Phyllanthus casticum.

Comment

This characteristic colpus structure occurs in many Asian and African *Phyllanthus* species (Punt, 1967; Bancilhon, 1971; Brunel, 1975). All these species may be related, but a more detailed comment on their interrelationships and of their pollen grains must await an investigation of all the species of the group.

Phyllanthus maderaspatensis type (Plate IX).

Pollen class: 3-Zonocolporate. P/E ratio: Subprolate to prolate.

Apertures: Ectoaperture — colpus, very long, rather narrow, sunken; ends acute; margins distinct, regular; colpus membrane granulate; costae faint. Endoaperture — porus, elliptic in outline, lalongate; ends distinct; margins distinct; costae completely surrounding the endoaperture.

Exine: Of uniform thickness. Nexine thinner than sexine; sexine 1 about as thick as sexine 2; sexine 1 of distinct columellae; sexine 2 of circular capita in cross-section, forming a semi-tectum.

Ornamentation: Reticulate in mesocolpium, lumina size decreasing towards colpi and apocolpia and here microreticulate or tectum perforate. Muri simplicolumellate; lumina variable in size, small circular lumina intermixed with larger ones; in LO-analysis columellae circular in outline.

Outlines: Equatorial view — elliptic to slightly rhombic. Polar view — circular to angular. Sides convex.

Measurements: P 22.5–26.5 μ m; E 19.0–20.0 μ m; P/E ratio 1.14–1.48. Exine 1.5–2.0 μ m thick. Endoaperture: longest axis ca. 3.5 μ m; shortest axis 2.0–3.5 μ m. Apocolpium index 0.15–0.25.

Species: Phyllanthus maderaspatensis, P. revaughanii (syn. P. longifolius).

Comment

The grains of *P. revaughanii* are usually prolate while those of *P. maderaspatensis* are subprolate. The outline of the endoapertures are also somewhat different; those in *P. revaughanii* are elliptic, whereas the endoapertures of *P. maderaspatensis* are almost circular. It would be difficult, however, to separate the grains on the basis of these characters alone. Leandri's (1958) statement: ".. cette espèce' (*P. longifolius*) n'est peut-être qu'une forme stationelle du *P. maderaspatensis* L.", is therefore, not contradicted by pollen morphology.

The following pollen types have previously been described by Punt and Rentrop (1974) (see also Brunel, 1975) but need additional comment as recent ultrastructural observations have led to a reinterpretation of the ornamentation and exine structure.

Phyllanthus amarus type (Plate X, 1-4; XI, 1-4)

Species: Phyllanthus amarus, P. dumetosus, P. mauritianus, P. niruroides.

The ornamentation is usually microreticulate (e.g. in P. niruroides) with a tendency to become almost suprareticulate (e.g. in P. amarus), but shows basically the same two-layered reticulum as described for the "phillyreifolius" group. The outer reticulum consists of duplicolumellate muri, usually thicker than the width of the lumina, coalescing with the smaller muri of the infrareticulum. The lumina are irregularly distributed and smaller (or absent) at the apocolpia and at the colpus margins.

The exine is usually constant in thickness; the capita not cup-shaped (as described by Punt and Rentrop, 1974), but composed of "arch"-like and rod-like elements.

The colpus membrane is granulate.

Phyllanthus tenellus type (Plate VIII, 6-8).

Species: Phyllanthus tenellus.

The SEM micrographs show a very irregular reticulum in which small lumina are intermixed with larger ones. A *Tilia* structure, as reported by Punt and Rentrop (1974), is doubtful.

Phyllanthus urinaria type (Plate XI, 5–6).

Species: Phyllanthus urinaria.

In LM micrographs the ornamentation resembles that of the P. amarus

type, but in SEM the presence of an outerreticulum is not clear, so its ornamentation is better classified as tectate perforate. The tectum has shallow depressions and the lumina are very small and irregularly distributed. This type is 4-zonocolporate.

DISCUSSION

The descriptions presented above provide strong evidence that the species and varieties of the endemic "phillyreifolius" group are closely related to one another. Only *P. phillyreifolius* var. gracilipes can definitely be separated from the other taxa as its pollen grains are smaller, usually prolate spheroidal, its reticulum is coarse with very irregular lumina and its ectocolpus indistinct (LM). The resemblance of the remaining pollen characters to those of the "phillyreifolius" group and especially of the bi-reticulate ornamentation, suggests a close affinity between this variety and the remaining variation of *P. phillyreifolius*.

The taxa of the "phillyreifolius" group may be arranged in a continuous series, based mainly on ornamentation features (see Table I; Plate I). At one extreme is P. phillyreifolius var. telfairianus which has microreticulate grains with small lumina and uninterrupted solid muri, distinct regular ectocolpus margins and conspicuous costae. At the other extreme P. phillyreifolius var. gracilipes has a reticulate ornamentation with wide, elongated or variform lumina interrupted, elevated muri, indistinct and irregular ectocolpus margins (LM) and faint costae. The group comprising P. oppositifolius and P. phillyreifolius var. commersonii has a transitional position, whereas P. lanceolatus tends towards the P. phillyreifolius var. gracilipes type.

The exine of all these taxa has an interesting architecture which has not previously been reported (cf. Praglowski, 1971). At high focus in LO-analyses (Fig.1B-D) (LM) the pattern could easily be mistaken for a normal reticulum with simplicolumellate muri, but careful observation reveals the presence of an infrareticulum (Fig.1C: outer reticulum dark; perforations of infrareticulum bright, and its muri greyish) which is confirmed by the lower foci and the scanning electron micrographs. Sectioned grains (SEM) and optical sections (LM) show typical "arch"-like structures which have a close resemblance to the optical sections of other previously described Phyllanthus spp. such as those of the P. amarus type or the P. urinaria type. The ornamentation of these pollen types has been wrongly interpreted as a Tilia structure, consisting of connate, cup-shaped capita (Bancilhon, 1971; Punt and Rentrop, 1974). The SEM micrographs show, however, that the "arches" form an (duplicolumellate) outer reticulum, whereas the infrareticulum consists of a delicate network of minute muri, which coalesce with the muri of the outer reticulum.

More research with the SEM may show that several pollen types of the complex genus *Phyllanthus* are related to one another, with regard to this type of ornamentation. Especially, in the *P. amarus* type there may be a similar range

TABLE I

Variations and morphological trends in pollen of P. phillyreifolius and related species

	P. phillyreifolius var. phillyreifolius var. telfairianus var. triangularis	P. phillyreifolius var. commersonii var. stylifer P. consanguineus P. lanceolatus P. oppositifolius P. pileostigma	P. phillyreifolius var. gracilipes
Ectoaperture colpus margin costae	distinct, regular conspicuous¹	distinct, irregular faint	indistinct, irregular faint
Ornamentation			
	microreticulate	microreticulate ² — reticulate	reticulate
lumina muri	small, rather uniform massive, not interrupted	elongated interrupted	large, multiform thin, erect, interrupted
Outlines			
P/E ratio	subprolate—prolate	subprolate—prolate	prolate spheroidal— subprolate
Measurements			
P	22.5-32.0 μm	22.5-28.5 μm ³	25.0-27.0 μm
E	16.0-24.0 μm	19.0—23.0 μm	22.0-25.0 μm
Apocolpium Index	ca. 0.25	ca. 0.30-0.40	ca. 0.20

¹In P. phillyreifolius var. triangularis the costae are faint.

of ornamentation to that described for the "phillyreifolius" group (Plate XI). The grains of P. tenellus are very similar to those of P. nummulariifolius, a related species occurring in Madagascar, but in the latter species the exine is twice as thick at the apocolpium as in the mesocolpium, whereas the reticulum of P. tenellus is characterized by the presence of very small lumina intermixed with larger ones (Plate VIII, 8). These observations support Webster (1957) who considered that P. tenellus should be kept distinct, while Leandri (1958) treated P. tenellus as synonym of P. nummulariifolius.

Finally, it should be mentioned that similar bi-reticulate pollen, in which the floor of the lumina is perforated, have recently been recorded in various species of the Labiatae (Nabli, 1972, 1976) and may well be found in other angiospermous families. Nabli found the columellae to be ramified in several species, while in others the columellae are simple.

²P. oppositifolius has microreticulate grains with shorter ectocopli (Apocolpium Index 0.50) and obtuse poles.

³P. consanguineus has smaller grains (P 20.0–24.0 μ m; E 16.0–19.5 μ m).

ACKNOWLEDGEMENTS

I would like to express my gratitude to Dr. W. Punt for introducing me into this branch of morphology. I am also grateful to Professor Dr. F.P. Jonker for his kind invitation to the Laboratory, to Mr. M.J.E. Coode for the loan of specimens and for valuable suggestions, to Dr. G.C.S. Clarke for his critical reading of the manuscript and to Mr. H.A. Elsendoorn for his technical assistance.

PLATE DESCRIPTIONS (all plates × 2000, except as otherwise stated)

PLATE I (p.159)

Ornamention, showing a trend from tectum perforatum to a coarse reticulum (cf. Table I) (magnification \times 5000)

- 1. Phyllanthus phillyreifolius var. telfairianus.
- 2. P.p. var, triangularis.
- 3. P.p. var. phillyreifolius.
- 4. Phyllanthus oppositifolius.
- 5. Phyllanthus phillyreifolius var. commersonii.
- 6. P.p. var. stylifer.
- 7. Phyllanthus consanguineus.
- 8. Phyllanthus lanceolatus.
- 9. Phyllanthus phillyreifolius var. gracilipes.

PLATE II (p.160)

Phyllanthus phillyreifolius var. phillyreifolius (Coode 4986: 1, 4, Cadet 2893B: 2, 3, 5)

- 1. SEM, equatorial view.
- 2. LM, ectocolpus.
- 3. LM, optical longitudinal section.
- 4. SEM, polar view.
- 5. LM, endoporus and distinct costae.

Phyllanthus phillyreifolius var. telfairianus (Coode 4695)

6. SEM, equatorial view; granulate colpus membrane.

PLATE III (p.161)

Phyllanthus phillyreifolius var. phillyreifolius (Coode 4986)

- 1. LM, suprareticulum at high focus.
- 2. LM, suprareticulum at middle focus.
- 3. LM, suprareticulum at low focus.

Phyllanthus oppositifolius (Hooker s.n.)

- 4. LM, optical longitudinal section, poles obtuse.
- 5. SEM, polar view, ectocolpi short.

Phyllanthus phillyreifolius var. triangularis (Graham s.n.)

- 6. LM, suprareticulum at high focus.
- 7. LM, suprareticulum at middle focus.
- 8. LM, suprareticulum at low focus.

PLATE I (Plate description on p.158)

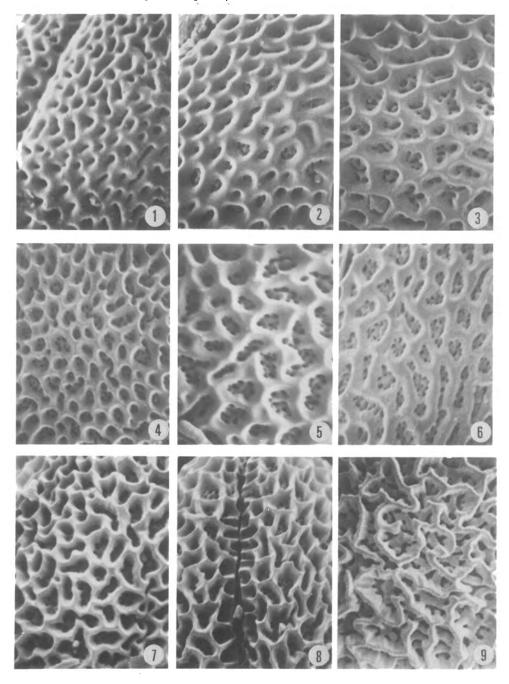


PLATE II (Plate description on p.158)

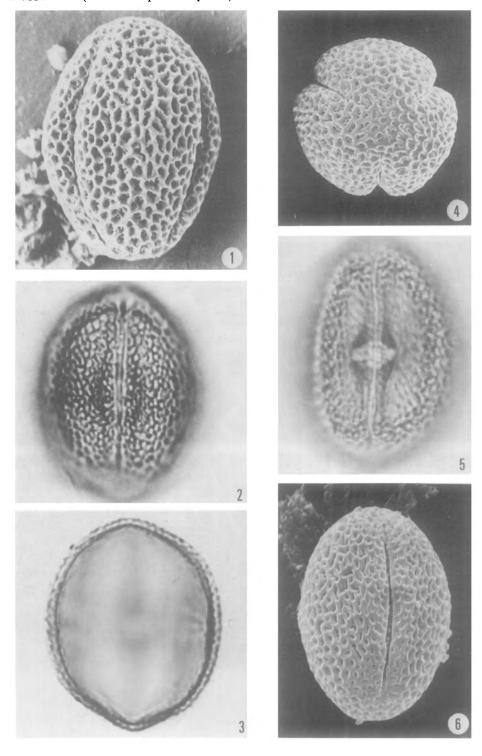


PLATE III (Plate description on p.158)

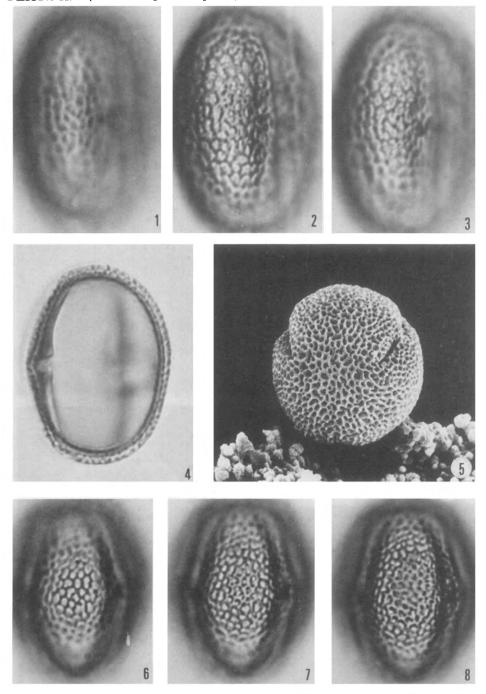


PLATE IV (Plate description on p. 170)

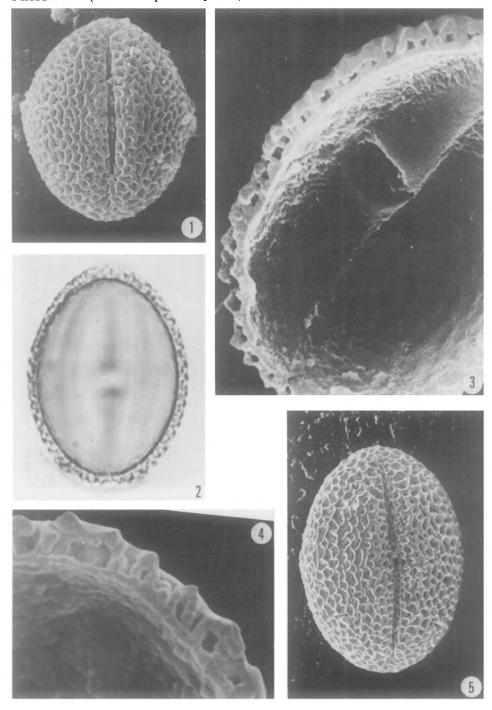


PLATE V (Plate description on p.170)

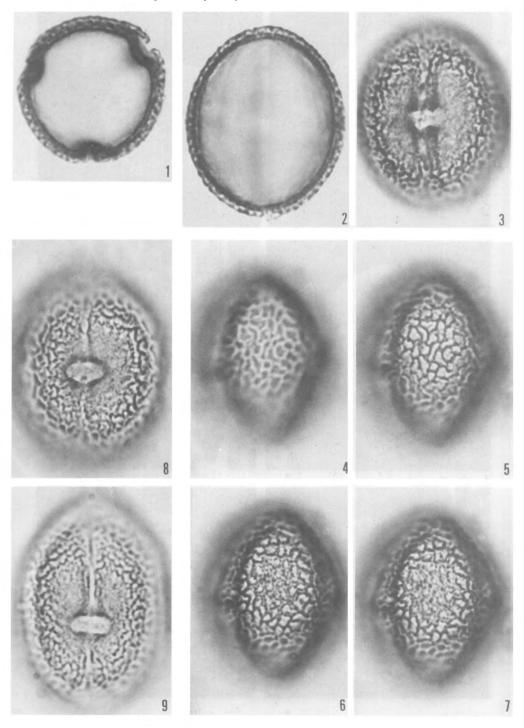


PLATE VI (Plate description on p.170)

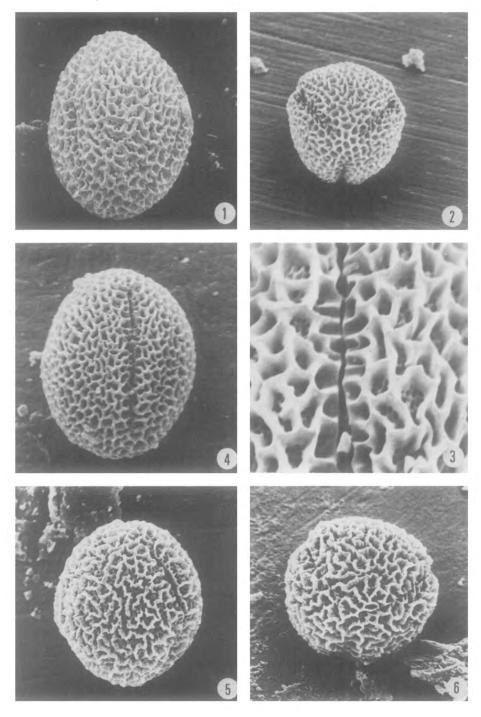


PLATE VII (Plate description on p.170)

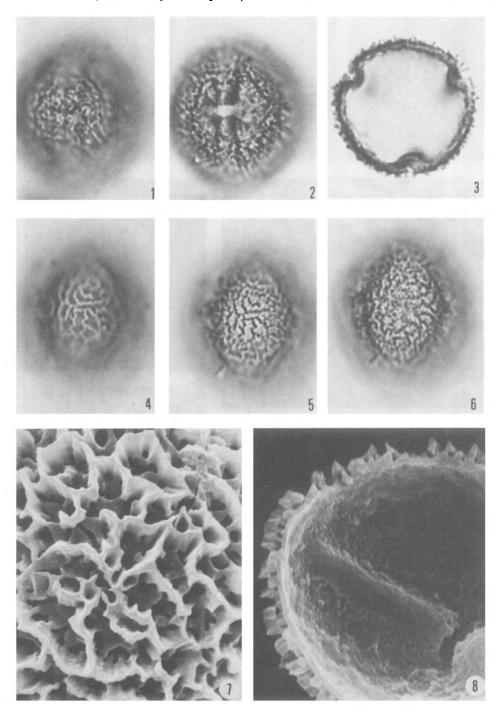


PLATE VIII (Plate description on pp.170-171)

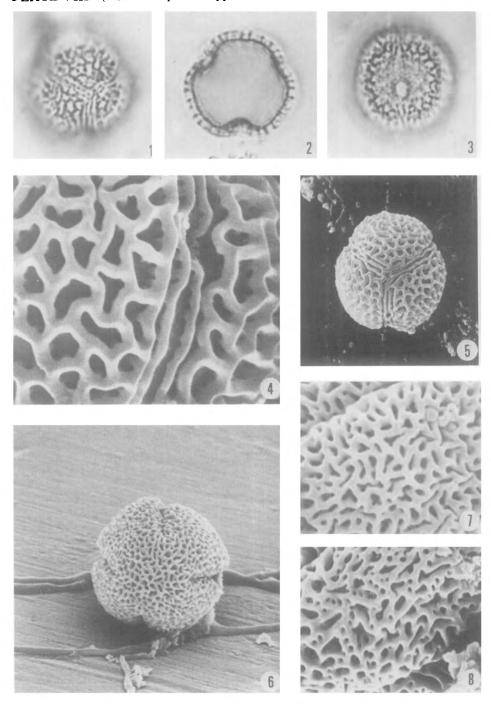


PLATE IX (Plate description on p.171)

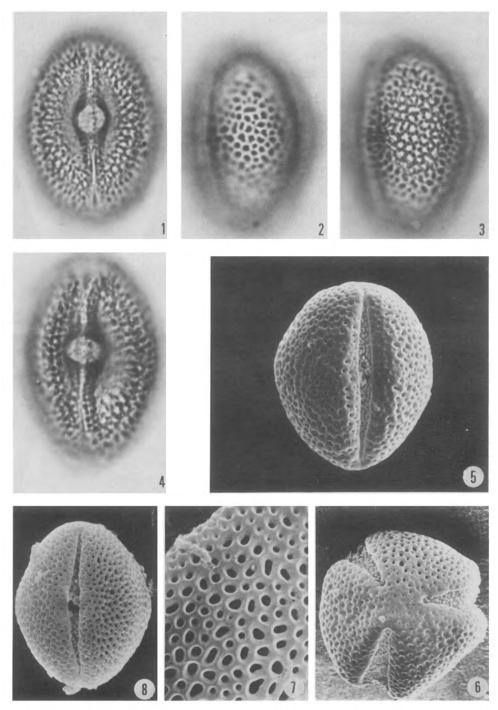


PLATE X (Plate description on p.171)

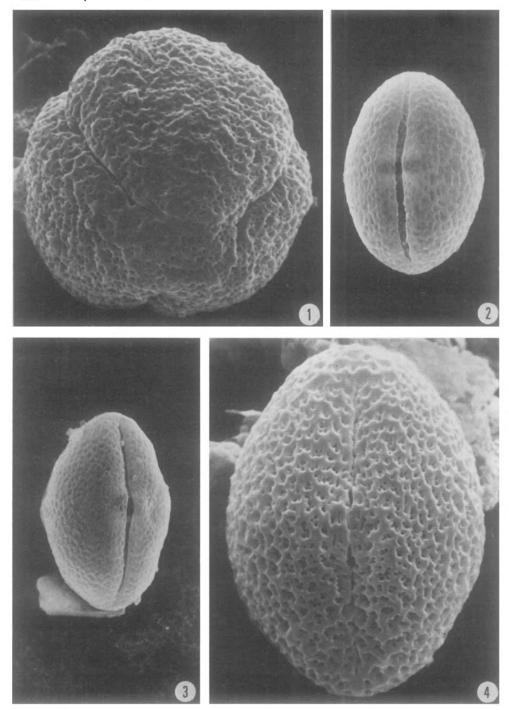


PLATE XI (Plate description on p.171)

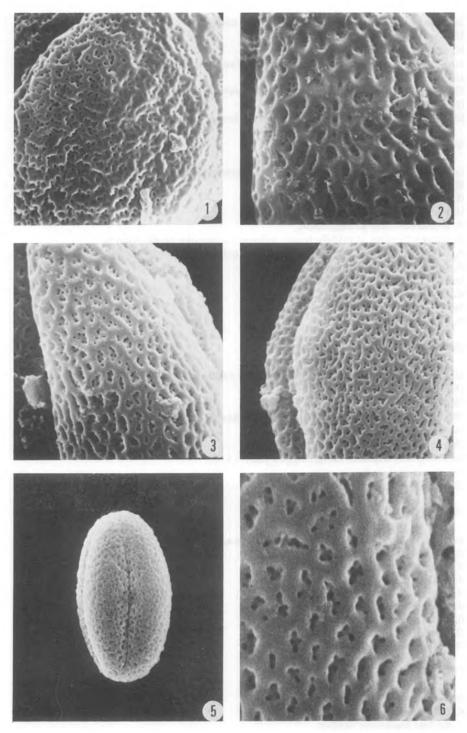


PLATE IV (p.162)

Phyllanthus phillyreifolius var. stylifer (Coode 4346)

- 1. SEM, equatorial view.
- 2. LM, optical longitudinal section.

Phyllanthus phillyreifolius var. commersonii (Vaughan, Flora of Mauritius 53:

- 5, Bojer s.n.: 4)
- 3. SEM, sectioned grain (× 5000), with endoaperture.
- 4. SEM, section of exine (\times 10,000).
- 5. SEM, equatorial view, granulate colpus membrane.

PLATE V (p.163)

Phyllanthus phillyreifolius var. commersonii (Barclay 2785)

- 1. LM, optical transverse section.
- 2. LM, optical longitudinal section.
- 3. LM, endocolpus with costae.
- 4. LM, suprareticulum at high focus.
- 5. LM, suprareticulum at middle focus, infrareticulum like bright islands.
- 6. LM, suprareticulum at low focus, muri duplicolumellate.
- 7. LM, suprareticulum at lowest focus.

Phyllanthus pileostigma (Coode 4759)

LM, endoaperture.

Phyllanthus lanceolatus (Coode 4429)

9. LM, endoaperture.

PLATE VI (p.164)

Phyllanthus lanceolatus (Néraud s.n.: 1, Coode 4429: 2, 3)

- 1. SEM, equatorial view.
- 2. SEM, polar view.
- 3. SEM, ectocolpus, narrow with irregular margins (x 10,000).

Phyllanthus consanguineus (Balfour s.n.)

4. SEM, equatorial view.

Phyllanthus phillyreifolius var. gracilipes (Ayres s.n.)

- 5. SEM, equatorial view.
- 6. SEM, polar view.

PLATE VII (p.165)

Phyllanthus phillyreifolius var. gracilipes (Ayres s.n.)

- 1. LM, ectocolpus, indistinct and very narrow.
- 2. LM, endocolpus with faint costae.
- 3. LM, optical transverse section.
- 4. LM, suprareticulum at high focus.
- 5. LM, suprareticulum at middle focus.
- 6. LM, suprareticulum at low focus.
- 7. SEM, ornamention (\times 10,000).
- 8. SEM, sectioned grain (\times 5000).

PLATE VIII (p.166)

Phyllanthus casticum (Sieber s.n.)

- 1. LM, polar view, colpi anastomosed.
- 2. LM, optical transverse section.

3. LM, equatorial view with circular endoporus. SEM, ornamentation with ectoaperture (× 10,000). 5. SEM, polar view. Phyllanthus nummulariifolius (Decary 11026) 6. SEM, polar view. 7. SEM, ornamention (× 5000). Phyllanthus tenellus (Jeffrey 501) 8. SEM, ornamentation (\times 5000). PLATE IX (p.167) Phyllanthus maderaspatensis (Jeffrey 1198) 1. LM, circular endoporus. 2. LM, reticulum at high focus. 3. LM, reticulum at low focus. Phyllanthus revaughanii (Brown s.n.: 4, Herb. Lugd Bat. s.c., s.n.: 5, 6) 4. LM, elliptic endoporus. 5. SEM, equatorial view, distinct granulate colpus membrane. 6. SEM, polar view. Phyllanthus maderaspatensis (Yerriah, Flora of Mauritius 17855) 7. SEM, ornamentation (× 5000). 8. SEM, equatorial view, colpus membrane with distinct granules. PLATE X (p.168) Phyllanthus amarus (Ayres s.n.) 1. SEM, polar view (× 5000). Phyllanthus niruroides (Guého, Flora of Mauritius 17185) 2. SEM, equatorial view. Phyllanthus dumetosus (Guého, Flora of Rodriguez 13973) 3. SEM, equatorial view. Phyllanthus mauritianus (Vaughan 653) 4. SEM, equatorial view (× 5000). PLATE XI (p.169) Phyllanthus amarus (Ayres s.n.) 1. SEM, ornamentation (× 5000). Phyllanthus niruroides (Guého, Flora of Mauritius 17158) 2. SEM, ornamentation (x 5000). Phyllanthus dumetosus (Guého, Flora of Rodriguez 13973) 3. SEM, ornamentation (x 5000). Phyllanthus mauritianus (Vaughan 653) 4. SEM, ornamentation (\times 5000). Phyllanthus urinaria (Graham s.n.) 5. SEM, equatorial view, narrow colpus. 6. SEM, ornamentation (\times 10,000). REFERENCES

Baker, J.G., 1877. Flora of Mauritius and the Seychelles. London, 357 pp. Bancilhon, L., 1971. Contributions à l'étude taxonomique du genre *Phyllanthus* (Euphorbiacées). Boissiera, 18: 1—81.

Brunel, J., 1975. Contribution à l'étude de quelques *Phyllanthus* africains et à la taxonomie du genre *Phyllanthus*. Thèse Biol. Vég., Univ. Strassbourg, 154 pp.

- Erdtman, G., 1969. Handbook of Palynology, Munksgaard, Copenhagen, 486 pp.
- Faegri, K. and Iversen, J., 1975. Textbook of Pollen Analysis. Munksgaard, Copenhagen, 3rd ed., 295 pp.
- Köhler, E., 1965. Die Pollenmorphologie der Biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomie, Grana Palynol., 6: 26-120.
- Köhler, E., 1967. Über Beziehungen zwischen Pollenmorphologie und Polyploidiestufen im Verwandschaftsbereich der Gattung Phyllanthus (Euphorbiaceae). Feddes Rep., 74: 159-165.
- Leandri, J., 1958. In: H. Humbert (Editor), Flore de Madagascar: 111e Famille Euphorbiacées. Tome 1. Paris, 209 pp.
- Mueller von Argau, J. and Boissier, E., 1866. In: A. Decandolle, Prodromus, 15(2): Euphorbiaceae. 1286 pp.
- Nabli, M.A., 1972. Le paroi d'Ajuga chamaepitys (L.) Schreb. (Labiées) en microscope électronique à transmission et à balayage. C.R. Acad. Sci. Paris, 274: 3210-3213.
- Nabli, M.A., 1976. Etude ultrastructurale comparée de l'exine chez quelques genres de Labiatées. In: I.K. Ferguson and J. Muller (Editors), the Evolutionary Significance of the Exine. Academic Press, London, 591 pp.
- Praglowski, J., 1971. Reticulate and allied exines. Grana, 11: 79-86.
- Praglowski, J. and Punt, W., 1973. An elucidation of the microreticulate structure of the exine. Grana, 13: 45-50.
- Punt, W., 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia, 7: 1-116.
- Punt, W., 1967. Pollen morphology of the genus *Phyllanthus* (Euphorbiaceae). Rev. Palaeobot. Palynol., 3: 141-150.
- Punt, W., 1972. Pollen morphology and taxomony of section *Ceramanthus* Baillon s.l. of the genus *Phyllanthus* (Eurphorbiaceae). Rev. Palaeobot. Palynol., 13: 213—228.
- Punt, W. and Rentrop, J., 1974. Pollen morphology of the *Phyllanthus* species occurring in the continental United States. Rev. Palaeobot. Palynol., 16: 243-261.
- Reitsma, Tj., 1969. Size modifications of recent pollen grains under different treatments. Rev. Palaeobot. Palynol., 9: 175-202.
- Reitsma, Tj., 1970. Suggestions towards unification of descriptive terminology of angiosperm pollen grains. Rev. Palaeobot. Palynol., 10: 39-60.
- Webster, G.L., 1957. A monographic study of the West Indian species of *Phyllanthus*. J. Arnold Arboretrum, 38: 51-80.
- Webster, G.L., 1970. A revision of *Phyllanthus* (Euphorbiaceae) in the continental United States. Brittonia, 22: 44-76.