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**The use of pollen morphology and wood anatomy in the study of
the phylogeny of Ebenaceae and Rutaceae subtribe Cuspariinae**

Morton, Cynthia Mareen, Ph.D.

City University of New York, 1994

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THE USE OF POLLEN MORPHOLOGY AND WOOD ANATOMY IN THE STUDY
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CUSPARIINAE.

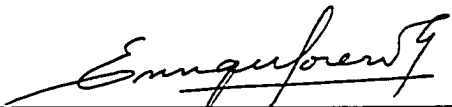
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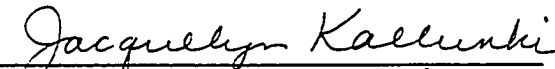
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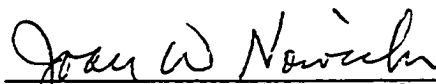
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Abstract

THE USE OF POLLEN MORPHOLOGY AND WOOD ANATOMY IN THE STUDY
OF THE PHYLOGENY OF EBENACEAE AND RUTACEAE SUBTRIBE
CUSPARIINAE.

by

CYNTHIA M. MORTON

Advisor: Dr. Enrique Forero

The following thesis is an anatomical study specializing in pollen morphology and wood anatomy. Chapter one examines the pollen morphology and wood anatomy of the Ebenaceae, chapter two the pollen morphology of the subtribe Cuspariinae of the Rutaceae, and chapter three provides a model for quantitative analysis of pollen morphology for use in phylogenetic studies.

The first chapter discusses the pollen morphology and wood anatomy of the family Ebenaceae and its usefulness to taxonomic classification. Pollen grains from 170 specimens representing four genera and 92 of the 450-500 species, of Ebenaceae were examined by light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM). The pollen of the Ebenaceae is relatively uniform; however, subtle variation is present, particularly in sculpturing patterns and size classes. Wood from 148 specimens representing 91 species were examined by LM and SEM. The wood anatomy of Ebenaceae as a whole is distinctive; however, much of the variation in anatomical

features occurs among the species of the large genus Diospyros. This diversity in the wood characters is similar to that of most other characters used to classify Diospyros. Until additional anatomical and morphological characters are fully understood and are subjected to a phylogenetic analysis, generic delimitation within the family will remain problematic.

The second chapter investigates the pollen morphology of the subtribe Cuspariinae and its usefulness to taxonomic classification. Pollen grains from 111 collections representing 71 species of the 125 species and 24 of the 26 genera were examined by LM, SEM, and TEM. The pollen morphology of this subtribe is very diverse particularly in sculpturing patterns and aperture types. Pollen data correlate well with macromorphological characters and are taxonomically useful.

The third chapter addresses the problem of pollen size class delimitation. Pollen size classes have been defined by Erdtman (1969) and Walker and Doyle (1975) as arbitrary groups which usually do not correspond to statistically significant differences among taxa. A model is proposed, using conventional statistical procedures coupled with data visualization, in an effort to address the problem of character state delimitation in pollen size classes. As a result the four genera of the Ebenaceae can be coded into three character states for size class.

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INTRODUCTION

This thesis is an anatomical study specializing in pollen morphology and wood anatomy. It is important to understand for anatomical studies such as this, that strict methodological standards must be followed. Anatomists strive to obtain random samples from the totality of the group(s) under investigation. This requires sufficient plant material and adequate sample sizes to assess the variability of characters within and among individuals.

The initial steps of a taxonomic anatomical study are fundamentally descriptive. These steps include the synthesis of comprehensive matrices that summarize data from the samples used, record sample sizes, list voucher specimens and localities, and circumscribe the known variability of quantitative and qualitative features. The second step of such a study is data analysis, where the practices of grouping characters can be purely intuitive or can be facilitated by statistical procedures. However, an anatomist must remain unbiased toward previous ideas about character trends and taxonomic relationships. To do this one must be familiar with various conditions concerning the features of his or her speciality so that groups can be established and so that descriptions will reflect differences between characters. It may take years of working with a wide spectrum of plant groups to feel confident of one's knowledge of the innate variability and of the circumscription of this variability into a

comprehensive working hypothesis. A complete anatomical study should question the traditional concepts of the characters and if appropriate reevaluate their usefulness.

This thesis adheres to the above guidelines in that it follows strict methodological standards, it works with different plant groups in order to gain a broad knowledge of the characters under examination, it questions traditional concepts, and it attempts to solve problems related to pollen morphology and wood anatomy of the groups under study. Chapter one examines the pollen morphology and wood anatomy of the Ebenaceae, chapter two the pollen morphology of the subtribe Cuspariinae of the Rutaceae, and chapter three provides a model for quantitative analysis of pollen morphology in reference to phylogeny.

Pollen grains from 170 specimens representing 92 of the 450-500 species, in four genera of Ebenaceae were examined by LM and SEM, and selected species were also observed with TEM. The pollen of the Ebenaceae is relatively uniform. Variation in sculpturing patterns occurs mainly within the large genus Diospyros. Pollen size, on the other hand, has proven to be a useful character in distinguishing genera within the Ebenaceae.

Wood from 148 specimens representing 91 species were examined by LM and SEM. The wood anatomy of Ebenaceae as a whole is distinctive, but significant differences for most wood characters within genera are low. Much of the variation in these characters occurs among the species of

the large genus Diospyros. Within the Ebenales, the Ebenaceae contains the greatest amount of variation in wood anatomy.

Pollen grains from 111 specimens representing 71 of the 125 species and 24 of the 26 genera of subtribe Cuspariinae (tribe Cusparieae, subfamily Rutoideae, Rutaceae) were examined by LM, SEM, and TEM. The pollen morphology of this subtribe is very diverse particularly in sculpturing patterns and aperture types. The pollen data correlates with macromorphological characters and is taxonomically useful.

Pollen size classes have been defined by Erdtman (1969) and Walker and Doyle (1975). Their groups, however, are arbitrary and usually do not correspond to statistically significant differences among taxa. A model is proposed using conventional statistical procedures coupled with data visualization to address the problem of delimitation of character states in pollen size classes. Realistic pollen data sets generated by a computer program written to perform Monte Carlo simulations are used to illustrate the model. This model is then applied to an original data set of 4,134 pollen grains from the Ebenaceae. As a result, pollen size class is divisible into three character states that can be used to code the specimens of the four genera of Ebenaceae.

No modern comprehensive morphological or anatomical study of the Ebenaceae has been published. Only limited studies have been carried out by Erdtman (1971) and Barth

(1983). Therefore, this thesis contributes to our knowledge of the wood anatomy and pollen morphology of these important tropical families.

This information will be useful not only for establishing phylogenetic classifications but also for various other studies such as ecological investigations and economical applications (e.g., wood product identification).

Chapter 1: Ebenaceae

Taxonomic Background

The Ebenaceae Gurke are a woody, dicotyledonous family containing two to five genera and 450 to 500 species (Hutchinson, 1973; Cronquist, 1981; Takhtajan, 1981, 1987; White, 1988). The family is distributed primarily in the tropical and subtropical regions of the Old and New Worlds, with a few species ranging into temperate zones. According to Goldberg (1986), the Ebenaceae are centered in the lowland rain forest of the East Indies and extend into India, Japan, Australia, Africa, and North and South America (Fig. 1).

The Ebenaceae have alternate or rarely opposite, simple, entire, exstipulate leaves, with anomocytic stomata. Flowers are usually unisexual, with a 3-7-lobed, persistent calyx; the corolla is 3-7-parted and the petals are united to form a tube at the base. The stamens are frequently attached to the base of the corolla tube, double the number of the corolla lobes, and paired. The syncarpous gynoecium is composed of a superior, 3-8- but most often 4-locular ovary and a deeply cleft 4-parted style with terminal stigmas. The locules are usually double the number of carpels due to median partitioning, with each locule containing one or two ovules on axile placentae. Fruits are usually drupaceous or rarely capsular, subtended by the persistent calyx, and contain one or two seeds per locule (Cronquist, 1981).

The Ebenaceae were first established in 1799 by Ventenat in his "Tableau du Regne Vegetal." The family name has been conserved (Greuter, 1988) as Ebenaceae Gurke (1897). A comparison of the intrafamilial classifications of the Ebenaceae is given in Table 1.

The most recent monograph on a world-wide basis is that of Hiern (1873) who recognized five genera in the family (Royena, Tetracelis, Euclea, Maba, and Diospyros) and separated the species of Diospyros into 15 sections. Gurke (1897) surveyed the family and recognized seven genera, raising doubt about the placement of the American genus Brachynema Benth. and the African genus Rhaphidanthe Hiern. Subsequently Bakhuizen (1936-1955) in his monograph of the Ebenaceae of Malaysia, recognized four genera (Tetracelis, Royena, Euclea, and Diospyros), united Maba with Diospyros, and divided Diospyros into 4 subgenera and 34 sections. In the treatment of the Ebenaceae for the Flora of Central Africa, White (1987) recognized only two genera (Diospyros and Euclea) and reduced Royena and Rhaphidanthe to two of eighteen sections within Diospyros. To date, the African and Pacific species of the Ebenaceae have not been critically compared with each other or with the Asiatic and South American species.

The family limits have been controversial. Brachynema Benth., included as a doubtful member of the Ebenaceae by Gurke (1897), is now generally regarded as belonging to the family Olacaceae (Sleumer, 1935). Maba is now commonly merged with Diospyros as first suggested by Bakhuizen (1936-1955). The African genera Rhaphidanthe and Royena either have been united with Diospyros and given sectional rank (White, 1980) or have been maintained at the generic level (Cronquist, 1981).

Within the Ebenales the Ebenaceae traditionally have been placed near the Styracaceae by Bentham and Hooker (1876), Perkins (1907), and Bessey (1915). Thorne (1968, 1976), Cronquist (1981),

and Takhtajan (1981, 1987) concur and share the opinion that the Ebenales --consisting of the families Sapotaceae, Ebenaceae, Symplocaceae, Styracaceae, and Lissocarpaceae-- have been derived from the thealean complex, an opinion generally supported by both anatomical and chemical characters. Wood and Channell (1960) in their treatment of the Ebenales for the southeastern United States, removed Lissocarpaceae from Ebenales and considered the four remaining families to be related to modern Theaceae. Wagenitz (1964), in Engler's *Syllabus der Pflanzenfamilien*, included Sapotaceae, Sarcospermataceae, Ebenaceae, Styracaceae, Lissocarpaceae, Symplocaceae, and Hoplestigmataceae in the Ebenales. Dahlgren (1980) assigned Ebenaceae, Sapotaceae, Styracaceae, and Lissocarpaceae to the Ebenales but considered Symplocaceae to be closer to the Theales. Nooteboom (1975) also believed, on the basis of morphological and anatomical differences in the pollen morphology, leaf and wood anatomy, gynoecium, and leaf margins, that the Symplocaceae were misplaced in the Ebenales and suggested that they may be better placed within the Cornaceae or possibly the Theaceae.

Hutchinson (1967, 1969, 1973) recognized the Ebenales as including Ebenaceae, Sapotaceae, and Sarcospermataceae. He believed the Ebenaceae provided a missing link between the Myrsinaceae (Myrsinales) and the Sapotaceae (Ebenales) and suggested that both orders probably were derived from thealean stock. Goldberg (1986), however, included only the Ebenaceae and Sapotaceae in the Ebenales, segregated the Styracaceae and Lissocarpaceae as the Styracales, and placed the Symplocaceae in the

Theales. Such arguments indicate that the Ebenales -- Lissocarpaceae, Styracaceae, Ebenaceae, Sapotaceae, and Symplocaceae-- do not represent a natural assemblage.

For the purpose of this study, Diospyros, Euclea, and Tetracelis, the three recognized genera, and Royena, which is found either at the sectional level (White, 1980) or at the generic level (Bakhuizen, 1936), will be investigated.

Pollen Morphology

Published Pollen Surveys of the Ebenaceae

An extensive literature search revealed that no modern comprehensive morphological or anatomical study of this family has been published. In the few published studies of the pollen morphology of Ebenaceae, the descriptions are either inadequate or based on few species. Studies at the light microscope level include those of Mohl (1835), Selling (1947), Erdtman (1971), Ikuse (1956), Guinet (1962), Straka et al. (1967), Huang (1968, 1972), Salgado-Labouriau et al. (1969), Bonnefille (1971), Salgado-Labouriau (1973), Sowunmi (1973), Sharma and Gupta (1979), Ybert (1979), and Gupta and Sharma (1986). Adams and Morton (1976) provided information from scanning electron microscopy on the equatorial and polar surfaces of D. virginiana. More recently, using both scanning electron (SEM) and light (LM) microscopy techniques, Bonnefille and Riollot (1980) examined Diospyros scabra from Africa; Lieux (1982) provided descriptions of the pollen of Diospyros virginiana; Ayala-Nieto and Ludlow-Wiechers (1983) described that of Diospyros verae-crucis, D. digyna, D. campechiana, and D. oaxacana from Veracruz, Mexico; and Cerceau-Larrival et al. (1984) presented information about the pollen of Diospyros sakalavarum, Euclea mayottensis, and Tetraclis ebenifera, three Old World species. In 1985, Nair and Kothari described the pollen of 11 species of Diospyros, ten species using LM and one species using SEM.

A majority of these palynological studies of Ebenaceae were restricted to light microscopy, thus the sculpturing and

ultrastructure of the exine have, so far, not been described. To date, no observations based on TEM have been published.

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Objectives of Pollen Research

The value of comparative morphology and anatomy in the clarification of problems of systematics of taxa above the species level is well documented (Metcalfe and Chalk, 1950, 1979, 1983; Bailey, 1951; Moseley, 1967; Eyde, 1971; Dickison, 1975; Stern, 1978). Anatomical methods frequently provide information that aids the formulation of hypotheses of evolution, the delimitation of taxonomic groups, and the realignment of families and genera.

The role of pollen morphology in providing taxonomic and phylogenetic information for angiosperm systematics has solidly been established. Walker and Doyle (1975), Nowicke and Skvarla (1979, 1984), Walker and Walker (1984), Ferguson (1986), and Johansson (1987), to name just a few, have demonstrated the valuable contributions of scanning electron and transmission electron microscope studies of pollen to assessments of the relationships of taxa.

Pollen morphological features within some of the families in the Ebenales have been taxonomically valuable. The detailed examination of apertures, exine sculpturing patterns, and interstitium-layering in the pollen of the Sapotaceae, a family closely related to Ebenaceae, have clarified taxonomic problems within this group (Harley, 1991). The genus Lissocarpa was segregated from the Ebenaceae because of triporate pollen and a tubular corolla ending in eight lobes (Gurke, 1897).

The main purpose of this study is to document the pollen morphology of the Ebenaceae based on light, scanning, and transmission electron microscopy and to discuss the systematic

implications of these data. In my analysis of pollen variation of the family I will attempt:

- (1) to provide a comprehensive palynological database for the Ebenaceae,
- (2) to employ pollen morphology to elucidate generic relationships,
- (3) to clarify relationships of the Ebenaceae with other families, and
- (4) to use the data to discern structural patterns and analyze their correlation with geographical or taxonomic parameters.

Materials and Methods for Pollen Morphology

Anatomical generalizations cannot be based on a single sample of an organ or tissue. Sufficient material must be examined to know the ranges of variability of anatomical characters within an individual and among individuals. Whenever possible, samples investigated should represent individuals from throughout the geographic range of a given taxon. In this study, pollen samples of 92 species (170 specimens), representing the four genera of the Ebenaceae accepted here were examined by light microscopy (LM) and scanning electron microscopy (SEM). Selected species of three genera were also observed with transmission electron microscopy (TEM).

Pollen was obtained from dried herbarium material housed in the following herbaria {herbarium abbreviations follow recommendations of Holmgren et al. (1990) Index Herbariorum}: the Royal Botanic Gardens, Kew (K), and the Missouri Botanical Garden (MO), The New York Botanical Gardens (NY), United States National Herbarium (US). The specimens studied and pertinent collection information are listed in Appendix 1.

Pollen was prepared using a modification of the method of acetolysis described by Erdtman (1960). Anthers were soaked for 15 minutes at room temperature in a 9:1 solution of acetic acid anhydride and sulfuric acid, placed in a boiling water bath for 3-5 min., allowed to cool, centrifuged and decanted. The sediment was neutralized with 95% ethanol, centrifuged and decanted and then washed twice with water.

The primary function of acetolysis is to clarify exine characteristics by removal of the cytoplasmic contents and, if present, any pollenkit.

Preparation for Light Microscopy

For light microscopy, acetolysed pollen was mounted in glycerine jelly on glass slides and sealed with paraffin. Slides were studied with a Nikon Optiphot microscope and measurements of 25 grains per sample were made using a computerized morphometric unit, programmed with Neurolucida software, under oil immersion (ca. X 1000). Photomicrographs were taken with a Nikon AFM automatic photomicrograph attachment.

Preparation for Scanning Electron Microscopy

For SEM studies, acetolysed pollen was washed several times in 95% ethanol and then mounted on stubs to which double-adhesive tape had been attached. A drop of ethanol containing pollen was applied to the stub, dried and vacuum-coated with gold/palladium for 80 seconds. Observations were made on a Jeol JSM-T300 scanning microscope, and photographs were taken using 656 P/N Polaroid film with 0 tilt and an accelerating voltage of 15 KV. To examine exine structure, acetolyzed grains were fractured with a glass rod before mounting on a standard stub.

Preparation for Transmission Electron Microscopy

For TEM, acetolysed pollen was washed in 95% ethanol and centrifuged, and the ethanol was carefully decanted. Hot, liquid 0.5%

agar was added to the pollen, centrifuged for 5 minutes at high speed, and allowed to cool and solidify. The solid agar was removed from the tubes, and the tips containing the grains were cut off with a razor blade and transferred to vials for subsequent processing.

Samples were then fixed with osmium tetroxide for two hours, stained with uranyl acetate for one hour, dehydrated in a graded ethyl alcohol series, and embedded in LR White at 60 C for several days. LR White was trimmed and preliminary sections (3-5 μm) were made with a glass knife. The sections were stained with toluidine blue in 1% aqueous sodium borate, and examined with a light microscope to locate pollen. Pollen was then thin-sectioned (80-90 nm) using a RMC MT6000 ultramicrotome with a Dupont diamond knife. Sections were stained with lead citrate and examined and photographed with a Jeol 1200EX TEM.

Measurements

The polar axis (P) and the corresponding equatorial diameter (E) were measured under LM. Pollen shape was determined from the ratio of the mean length of the polar axis to the mean length of the equatorial axis (Erdtman, 1969). Size classes are based on the measurement of the longest axis of the pollen grain (Erdtman, 1969). Size class dimensions and pollen shape terminology correspond to the definitions of Walker and Doyle (1975). The data set was stored, manipulated, and analyzed using Statview and JMP(SAS) on the Macintosh platform, and the statistical analysis basically followed Sokal and Rohlf (1981). Polar diameter, equatorial diameter, the ratio of polar diameter to equatorial diameter, sculpturing patterns,

geographical distributions, and genera were subjected to analyses of variance. Sculpturing patterns, geographical distributions, and genera were coded as grouping variables by integers. Following anova, the conservative Bonferroni method (Pagano and Gauvreau, 1993; Hoaglin et al., 1991) was used to make pairwise comparisons among genera of means of polar diameter, equatorial diameter, and the ratio of polar diameter to equatorial diameter. Logistic regression was used as a generic classification device with polar and equatorial diameters as independent variables. To measure the relationship between the polar diameter and equatorial diameter at the generic level, a bivariate analysis was completed using 95% confidence ellipses of the bivariate means in a graphical display.

In general, pollen terminology used for general morphological characters follows Walker and Doyle (1975), Erdtman (1971), and Harley (1991). Apertures present only in the endexine are described as "endoapertures" by Van Campo (1958). "Hemispherical" and "pointed" (Thomson and Pflug, 1953) are used to describe the shape of the polar region when seen from equatorial view. Most terms used to describe pollen morphology in this study are explained in Appendix 2 and illustrated in Figures 2 and 3.

Results for Pollen Morphology

The observations of the pollen samples presented in Tables 2, 3, 4 and in plates 1 through 14 were used as the basis of the following descriptions.

General Pollen Morphology of Ebenaceae

number of specimens examined: 170

number of species: 92

Pollen grains monads, radially symmetrical, isopolar, angulaperturate or rarely circulaperturate. Equatorial outline triangular, rarely circular in tricolporate or square in 4-colporate grains. Poles hemispherical, or hemispherical to pointed. Mean grain size 23.54 μm (P) X 20.49 μm (E) in Diospyros hoyleana to 53.87 μm (P) X 45.74 μm (E) in Diospyros crumenata. Grains predominantly subprolate, prolate-spheroidal, rarely perprolate, euprolate, spheroidal, or oblate-spheroidal, usually medium, infrequently small or large, 3- or rarely 4-aperturate. Ectoapertures meridionally aligned, long-colporate, or rarely short-colporate (Diospyros preussii), usually narrow or occasionally broad. Ectoapertures provided with a thick, usually granular membrane which does not rupture during acetolysis except in the endoapertural area. Endoapertures typically broadly lalongate (polar length more than half equatorial breadth), occasionally narrowly lalongate (polar length less than half equatorial breadth), or rarely circular. Exine sculpturing most commonly finely striate-foveolate or finely striate, occasionally finely anastomosed granular-striate, finely anastomosed granular-foveolate, or finely foveolate, or rarely finely

granular, finely striate-coarse foveolate, finely anastomosed granular, or coarsely striate-finely foveolate. Sculpturing pattern either uniform over the whole surface or different in the apocolpium and mesocolpium. Exine structure tectate-perforate, stratified into ektexine and endexine, with the ektexine frequently composed of a thick tectum, a narrow (28 percent of the exine thickness) or very narrow (15 percent of the exine thickness) infratectum, and a thick foot-layer. Nonapertural exine thickness from 0.53 μm in Euclea kellau to 1.35 μm in Royena whyteana. Tectum usually punctate or perforate, the perforations usually both shallow pits and deep fissures that penetrate into and through the tectum layer. Tectum sometimes clearly differentiated into solid apocolpium with perforations weakly to densely concentrated in the mesocolpium. Infratectum granular or mostly granular with scattered columellae. Foot-layer well developed. Ektexine reduced surrounding the colpi forming what is commonly defined as a margo. Endexine thickened under the colpus, especially surrounding the endoaperture, and either thin to absent, or rarely as thick as the tectum, in the mesocolpium.

Pollen Types

To facilitate comparison and discussion, the pollen was divided into three pollen types and seventeen subtypes based on mean polar length, type of sculpture pattern and similarity/difference of sculpture pattern on apocolpium and mesocolpium (see Table 4).

Boldfaced type in the following descriptions indicates species for which not all pollen samples fall into the specified type or subtype. For species for which samples exhibited more than one type

or subtype, the sample number corresponding to the voucher specimen in Appendix I precedes the specific epithet.

POLLEN TYPE A

Pollen grains angulaperturate or angulaperturate to circulaperturate, tricolporate, or rarely 4-aperturate (E. kellau and D. hoyleana). Equatorial outline triangular or triangular to circular, rarely square in 4-colporate grains. Poles hemispherical or hemispherical to pointed. Polar axis length 23.35 - 29.44 μm . Grains usually subprolate, or prolate-spheroidal, infrequently perprolate or spheroidal, usually medium or rarely small. Ectoapertures long-colporate. Endoapertures lalongate. Exine sculpturing usually finely striate-foveolate, finely anastomosed granular-foveolate, rarely finely anastomosed granular, finely striate, or finely striate-coarsely foveolate, that of the apocolpium and mesocolpium similar or dissimilar. Exine structure tectate-perforate, the nonapertural exine 0.53 - 1.29 μm thick, stratified into an ectexine and endexine. Ectexine composed of tectum, infratectum, and foot-layer. Tectum well developed, comprising ca. 39 percent of the total exine thickness. Infratectum reduced, mostly granular with scattered columellae, comprising ca. 17 percent of the total exine thickness. Foot-layer prominent, comprising ca. 45 percent of the total exine thickness. Endexine thin, or as thick as the tectum (E. acutifolia), under the mesocolpium, thicker under and along the margins of the colpi.

Taxa included: *Euclea*; *Diospyros bipindensis*, *D. diversilimba*-2, *D. hoyleana*, *D. sylvatica*.

Subtype A-1 (Plate 1)

Pollen grains tricolporate. Equatorial outline triangular to circular (*E. schimperi*). Poles hemispherical or hemispherical to pointed. Grains usually subprolate, or prolate-spheroidal, rarely spheroidal or perprolate, usually medium or rarely small. Exine sculpturing finely striate-foveolate, that of the apocolpium and mesocolpium similar.

Species included: *Euclea cripisa-1*, *E. dekindtii*, *E. divinorum*, *E. linearis*, *E. mayottensis*, *E. multiflora*, *E. racemosa*, *E. schimperi*, *E. undulata*, *Diospyros diversilimba-2*, *D. sylvatica*.

Subtype A-2 (Plate 2)

Pollen grains tricolporate. Equatorial outline triangular. Poles hemispherical or hemispherical to pointed. Grains subprolate, usually medium or rarely small. Exine sculpturing finely striate, that of the apocolpium and mesocolpium similar. Exine structure tectate-perforate, the nonapertural exine ca. 1.29 μm thick, stratified into an ectexine and endexine. Ectexine composed of tectum, infratectum, and foot-layer. Tectum well developed, comprising ca. 37 percent of the total exine thickness. Infratectum reduced, mostly granular with scattered columellae comprising ca. 19 percent of total exine thickness. Foot-layer prominent, comprising ca. 44 percent of the total exine thickness. Endexine thin under the mesocolpia, thicker under and along the margins of the colpi.

Species included: *Euclea natalensis-1-4*, *E. polyandra*, *E. pseudebenus*.

Subtype A-3 (Plate 3, 4)

Pollen grains usually tricolporate, rarely 4-colporate (E. kellau). Equatorial outline triangular or rarely square in 4-colporate grains. Poles hemispherical to pointed. Grains prolate-spheroidal, rarely perprolate and usually medium or infrequently small. Exine sculpturing finely anastomosed granular-foveolate, that of the apocolpium and mesocolpium similar. Exine structure tectate-perforate, the nonapertural exine 0.53 - 0.87 μm thick, stratified into an ectexine and endexine. Ectexine composed of tectum, infratectum, and foot-layer. Tectum well developed, comprising ca. 39 percent of the total exine thickness. Infratectum reduced, mostly granular with scattered columellae comprising ca. 16 percent of the total exine thickness. Foot-layer prominent, comprising ca. 46 percent of the total exine thickness. Endexine thin, or as thick as the tectum, under the mesocolpia, thicker under and along the margins of the colpi.

Species included: *Euclea acutifolia*, *E. kellau*, *E. lanceolata*.

Subtype A-4 (Plate 5, A-C)

Pollen grains tricolporate to circular. Equatorial outline triangular. Poles hemispherical to pointed. Grains prolate-spheroidal, medium. Exine sculpturing finely anastomosed granular, that of the apocolpium and mesocolpium similar.

Species included: *Diospyros bipindensis*.

Subtype A-5 (Plate 5, D-F)

Pollen grains usually tricolporate, or 4-colporate. Equatorial outline triangular or rarely square in 4-colporate grains. Poles hemispherical or hemispherical to pointed. Grains subprolate or prolate-spheroidal, small. Exine sculpturing finely striate-coarsely foveolate, that of the apocolpium striate and of the mesocolpium striate-coarsely foveolate.

Species included: *Diospyros hoyleana*.

POLLEN TYPE B

Pollen grains angulaperturate or rarely circulaperturate (*D. preussii*), usually tricolporate or rarely 4-aperturate. Equatorial outline triangular, rarely circular or square in 4-colporate grains. Poles hemispherical or hemispherical to pointed. Polar axis length 30.05 - 49.54 μm . Grains usually subprolate, rarely prolate-spheroidal, euprolate or oblate-spheroidal, usually medium or rarely large (*Diospyros malabarica*). Ectoapertures usually long-colporate or rarely short-colporate (*Diospyros preussii*). Endoapertures usually lalongate or rarely circular. Exine sculpturing usually finely striate, finely striate-foveolate, finely anastomosed granular-striate, foveolate, occasionally finely anastomosed granular-foveolate, finely granular, rarely finely striate-coarsely foveolate, finely anastomosed granular or coarsely striate-foveolate, that of the apocolpium and mesocolpium similar or dissimilar. Exine structure tectate-perforate, the nonapertural exine 0.72 - 1.35 μm thick, stratified into an ectexine and endexine. Ectexine composed of tectum, infratectum, and foot-layer. Tectum well developed,

comprising ca. 28-45 percent of the total exine thickness. Infratectum reduced, granular or mostly granular with scattered columellae, comprising ca. 21-28 percent of the total exine thickness. Foot-layer prominent, comprising ca. 28-50 percent of the total exine thickness. Endexine thin under the mesocolpia, thicker under and along the margins of the colpi.

Taxa included: *Royena austro-africana*, *R. cordata*, *R. dichrophylla*, *R. glabra*, *R. guerkei*, *R. hirsuta*, *R. lycioides*, *R. microphylla*, *R. pallens*, *R. sericea*, *R. usambarensis*, *R. villosa*, *R. whyteana*; *Diospyros abyssinica*, *D. armata*, *D. artanthaefolia*, *D. brideliaefolia*, *D. bullata*, *D. campechiana*, *D. candolleana*, *D. cauliflora*, *D. conocarpa*, *D. crassinervis*, *D. curranii*, *D. decandra*, *D. dendo*, *D. dichroa*, *D. discolor*, *D. ehretioides*, *D. filipendula*, *D. fischeri*, *D. gabunensis*, *D. gillettii*, *D. glandulosa*, *D. hispida*, *D. ierensis-1*, ***D. kaki-2***, *D. kamerunensis-1*, *D. kirkii-2*, *D. longibracteata*, *D. lotus*, *D. malabarica*, *D. maritima*, *D. mespiliformis*, *D. mollis*, *D. montana*, *D. morrisiana*, *D. multiflora*, *D. mweroensis*, *D. nicaraguensis*, *D. nummularia*, *D. ovalifolia*, *D. pendula*, *D. pentamera*, *D. philippinensis*, *D. pilosanthera*, *D. polystemon*, *D. preussii*, *D. pterocalyx*, *D. revoluta*, *D. samoensis*, ***D. scabrida***, *D. squarrosa*, *D. suaveolens*, *D. texana*, *D. vermoesenii*, *D. verrucosa*, *D. virgata*, *Tetracelis baronii*, *T. clusiaefolia*.

Subtype B-1 (Plate 6, A-C)

Pollen grains angulaperturate, and tricolporate. Equatorial outline triangular. Poles hemispherical. Grains subprolate or prolate-spheroidal, medium. Ectoapertures long-colporate.

Endoapertures lalongate. Exine sculpturing finely anastomosed granular-foveolate, that of the apocolpium and mesocolpium similar. Species included: *Royena dichrophylla*, *R. pallens*, *Diospyros artanthaefolia*, *D. squarrosa*.

Subtype B-2 (Plate 6, D-F)

Pollen grains angulaperturate, and tricolporate. Equatorial outline triangular. Poles hemispherical. Ectoapertures long-colporate. Endoapertures lalongate. Grains subprolate, or prolate-spheroidal, medium. Exine sculpturing finely striate-foveolate, that of the apocolpium and mesocolpium similar. Species included: *Diospyros lotus-1-2*.

Subtype B-3 (Plate 7, 8)

Pollen grains angulaperturate, and tricolporate. Equatorial outline triangular. Poles usually hemispherical, rarely hemispherical to pointed. Ectoaperture usually long-colporate, rarely short-colporate (*Diospyros preussii*). Endoapertures usually lalongate rarely circular. Grains usually subprolate, prolate-spheroidal, rarely oblate-spheroidal or euprolate, usually medium or infrequently large (*Diospyros malabrica-2*). Exine sculpturing finely striate, that of the apocolpium and mesocolpium similar. Species included: ***Royena austro-africana-2-3***, *R. hirsuta*, *R. sericea*, *R. usambarensis*, *R. villosa*, *Diospyros brideliaefolia*, *D. campechiana*, *D. cauliflora*, *D. curranii*, *D. dichroa*, *D. fischeri*, *D. glandulosa*, ***D. kaki-2***, *D. kamerunensis-1*, *D. malabarica*, *D. morrisiana*, *D. pentamera*, *D. preussii*, *D. pterocalyx*, *Tetracalis baronii*, *T. clusiaefolia*.

Subtype B-4 (Plate 9, A-C)

Pollen grains angulaperturate, and tricolporate. Equatorial outline triangular. Poles hemispherical. Ectoaperture long-colporate. Endoapertures lalongate. Grains usually subprolate, or prolate-spheroidal, medium. Exine sculpturing finely anastomosed granular, that of the apocolpium and mesocolpium similar.

Species included: *Royena austro-africana-1*, *R. guerkei*, *Diospyros scabrida-2*.

Subtype B-5 (Plate 9, D-K)

Pollen grains angulaperturate, and tricolporate, or rarely 4 aperturate (*D. whyteana*). Equatorial outline triangular, rarely square in 4-colporate grains. Poles hemispherical. Ectoaperture long-colporate. Endoapertures lalongate. Grains usually subprolate, or prolate-spheroidal, medium. Exine sculpturing finely granular, that of the apocolpium and mesocolpium similar. Exine structure tectate-perforate, the nonapertural exine 0.93-1.35 μm thick, stratified into an ectexine and endexine. Ektexine composed of tectum, infratectum, and foot-layer. Tectum well developed, comprising ca. 40 percent of the total exine thickness. Infratectum reduced, mostly granular with scattered columellae comprising ca. 24 percent of the total exine thickness. Foot-layer prominent, comprising ca. 37 percent of the total exine thickness. Endexine thin under the mesocolpia, thicker under and along the margins of the colpi.

Species included: *Royena cordata*, *R. whyteana*, *Diospyros montana*, *D. scabrida-1*.

Subtype B-6 (Plate 10)

Pollen grains angulaperturate, and triaperturate or rarely 4-aperturate (*D. microphylla* and *D. ehretioides*). Equatorial outline triangular, rarely square in 4-colporate grains. Poles usually hemispherical or rarely hemispherical to pointed. Ectoaperture long-colporate. Endoapertures usually lalongate or rarely circular. Grains usually subprolate, occasionally prolate-spheroidal, medium. Exine sculpturing finely anastomosed granular-striate that of the apocolpium and mesocolpium similar. Exine structure tectate-perforate, the nonapertural exine ca. 0.86 μm thick and stratified into an ectexine and endexine. Ectexine composed of tectum, infratectum, and foot-layer. Tectum well developed, comprising ca. 33 percent of the total exine thickness. Infratectum mostly granular with scattered columellae comprising ca. 23 percent of the total exine thickness. Foot-layer prominent, comprising ca. 44 percent of the total exine thickness. Endexine thin under the mesocolpia, thicker under and along the margins of the colpi.

Species included: *Royena glabra*, *R. lycioides*, *R. microphylla*, *Diospyros armata*, *D. bullata*, *D. ehretioides*, *D. gillettii*, *D. mollis*, *D. mweroensis*, *D. polystemon-2*, *D. texana*.

Subtype B-7 (Plate 11, A-E)

Pollen grains angulaperturate, and tricolporate. Equatorial outline triangular. Poles hemispherical. Ectoaperture long-colporate. Endoapertures lalongate. Grains subprolate, prolate-spheroidal, or euprolate, medium. Exine sculpturing foveolate, that of the apocolpium smooth and mesocolpium foveolate. Exine

structure tectate-perforate, the nonapertural exine 0.79-1.00 μm thick, stratified into an ectexine and endexine. Ektexine composed of tectum, infratectum, and foot-layer. Tectum well developed, comprising ca. 28 to 45 percent of the total exine thickness. Infratectum reduced, granular comprising ca. 23 percent of the total thickness. Foot-layer very prominent, comprising ca. 32 to 50 percent of the total exine thickness. Endexine thin under the mesocolpia, thicker under and along the margins of the colpi. Species included: *Diospyros ierensis-1*, *D. maritima*, *Diospyros mespiliformis*, *D. multiflora*, *D. philippinensis*, *D. pilosanthera*, *D. revoluta*, *D. suaveolens*, *D. virgata*.

Subtype B-8 (Plate 11, F-H)

Pollen grains angulaperturate, and tricolporate. Equatorial outline triangular. Poles hemispherical. Ectoaperture long-colporate. Endoapertures lalongate. Grains prolate-spheroidal, medium. Exine sculpturing coarsely striate-foveolate, that of the apocolpium and mesocolpium similar. Exine structure tectate-perforate.

Species included: *Diospyros dendo*.

Subtype B-9 (Plate 12, A-B)

Pollen grains angulaperturate, and tricolporate. Equatorial outline triangular. Poles hemispherical. Ectoaperture long-colporate. Endoapertures lalongate. Grains prolate-spheroidal, medium. Exine sculpturing finely anastomosed granular-foveolate,

that of the apocolpium anastomosed granular and of the mesocolpium anastomosed granular-foveolate. Exine structure tectate-perforate. Species included: *Diospyros abyssinica*.

Subtype B-10 (Plate 12 C-F, 13)

Pollen grains angulaperturate, and tricolporate. Equatorial outline triangular. Poles usually hemispherical or rarely hemispherical to pointed. Ectoaperture long-colporate. Endoapertures lalongate. Grains usually subprolate, occasionally prolate-spheroidal or euprolate, medium. Exine sculpturing finely striate-foveolate, that of the apocolpium striate and of the mesocolpium striate-foveolate. Exine structure tectate-perforate, the nonapertural exine 0.72-1.00 μm , stratified into an ectexine and endexine. Ectexine composed of tectum, infratectum, and foot-layer. Tectum well developed, comprising ca. 43 percent of the total exine thickness. Infratectum reduced, mostly granular with scattered columellae, comprising ca. 25 percent of the total thickness. Foot-layer prominent, comprising ca. 32 percent of the total exine thickness. Endexine thin under the mesocolpia, thicker under and along the margins of the colpi.

Species included: *Diospyros candolleana*, *D. conocarpa*, *D. crassinervis*, *D. decandra*, *D. kirkii*-2, *D. longibracteata*, *D. nicaraguensis*, *D. nummularia*, *D. ovalifolia*, *D. pendula*, *D. samoensis*, *D. vermoesenii*, *D. verrucosa*.

Subtype B-11 (Plate 14, A-D)

Pollen grains angulaperturate, and tricolporate. Equatorial outline triangular. Poles hemispherical. Ectoaperture long-colporate. Endoapertures lalongate. Grains subprolate or prolate-spheroidal, medium. Exine sculpturing finely striate-coarsely foveolate, that of the apocolpium striated and of the mesocolpium striate-coarsely foveolate. Exine structure tectate-perforate.

Species included: *Diospyros filipendula*, *D. hispida*.

POLLEN TYPE C

Pollen grains angulaperturate, tricolporate. Equatorial outline triangular. Poles hemispherical or hemispherical to pointed. Polar axis length 50.39 - 56.74 μm . Grains subprolate or prolate-spheroidal, large. Ectoaperture long-colporate. Endoapertures lalongate. Exine sculpturing finely striate or finely striate-foveolate, that of the apocolpium and mesocolpium similar or dissimilar.

Taxa included: *Diospyros virginiana*, *D. crumenata*, *D. kaki-1*.

Subtype C-1 (Plate 14, E-H)

Poles hemispherical. Grains prolate-spheroidal or subprolate. Exine sculpturing finely striate-foveolate that of the apocolpium striate and that of the mesocolpium finely striate-foveolate.

Species included: *Diospyros crumenata*, *D. virginiana-1-6*.

Subtype C-2 (Plate 14, I)

Poles hemispherical to pointed. Pollen grains subprolate. Exine sculpturing finely striate, that of the apocolpium and mesocolpium similar.

Species included: ***Diospyros kaki-1***.

Pollen samples lacking enough information to be placed into a type:

Euclea crista-2, *E. natalensis-5*, *Diospyros discolor*, *D. diversilimba-1*, *D. ierensis-2*, *D. gabunensis*, *D. kamerunensis-2*, *Diospyros kirkii-1*, *D. lotus-3*, *D. polystemon-1*, *D. verae-crucis*, and *D. virginiana-7-8*.

Statistical Results for Pollen

Descriptive statistics (mean, SD, and N) for polar diameter, equatorial diameter and P/E ratios are given in Table 5.

The primary method I have used for data analysis is analysis of variance (anova).

“In the broadest sense this tests whether samples belong to the same populations. The null hypothesis is that the means of the samples are equal. If there are only 2 groups involved, you are testing whether the means of the 2 samples are different. Anova also helps you understand the variability of your data including what levels of your study contain most of the variance (the so called “variance component”). Briefly, the key assumptions of anova are that within group i , the observations are assumed normally distributed about a particular mean with a particular variance. The means may indeed vary from group to group but the variance is assumed the same in all groups (homogeneity of variances)” (Kincaid, unpubl.).

A full explanation of the calculation and use of anova is found in Sokal and Rohlf (1981).

HETEROGENEITY OF POLAR DIAMETER, EQUATORIAL DIAMETER, AND P/E RATIO BETWEEN GENERA.

A single classification anova was completed for polar diameter, equatorial diameter, P/E ratio (shape) and genera (Table 6). Significant differences in mean polar diameter ($p=.0001$) and mean equatorial diameter ($p=.0001$) were found among Diospyros, Euclea, Royena, and Tetracelis.

Polar and equatorial diameters of the four genera were examined using the very conservative Bonferroni pairwise comparison ($\alpha' = .0083$ used to protect intended type 1 error of 0.01) (Hoaglin et al., 1991; Pagano and Gauvreau, 1993). Means of both polar and equatorial diameters of Euclea are significantly smaller than those of the remaining genera- Diospyros, Royena, and Tetracelis.

Although significant differences were found in the P/E ratio among genera ($p = .0001$), only 2 percent (.018 R-square) of the total variation (total sum of square) in the P/E ratio is accounted for by genera. In comparison, for polar diameter and equatorial diameter 40% and 36% (respectively) of total variation is accounted for by groups (genera). The P/E ratio is, therefore, less effective in accounting for the variation between genera of the Ebenaceae than are the measurements of polar diameter and equatorial diameter.

HETEROGENEITY OF POLAR DIAMETER AND EQUATORIAL DIAMETER BETWEEN GEOGRAPHICAL DISTRIBUTION PATTERNS IN THE GENUS DIOSPYROS.

A single classification anova was completed for polar diameter, equatorial diameter and geographical distribution patterns

(Table 7). Significant differences in mean polar diameter ($p=.0001$) and mean equatorial diameter ($p=.0001$) were found among the geographical patterns. For polar diameter and equatorial diameter the R-square is 31% and 38% (respectively), representing the total variation accounted for by the geographical patterns in Diospyros.

HETEROGENEITY OF SCULPTURING PATTERNS BETWEEN GENERA.

A single classification anova was completed for sculpturing patterns and genera (Table 8). Although significant differences were found among means of the sculpturing patterns of the four genera ($p = .0001$), only 2 % (0.2 R-square) of the total variation (total sum of square) in the sculpturing patterns is accounted for by the genera.

HETEROGENEITY OF POLAR DIAMETER, AND EQUATORIAL DIAMETER, BETWEEN SCULPTURING PATTERNS IN THE GENUS DIOSPYROS.

A single classification anova was completed for polar diameter, equatorial diameter and sculpturing patterns (Table 9). Although significant differences were found in the mean polar diameter ($p=.0001$) and mean equatorial diameter ($p=.0001$) among sculpturing patterns ($p = .0001$), only 12% and 9% (respectively), of the total variation (total sum of square) in the polar diameter and equatorial diameter is accounted for by sculpturing patterns in the genus Diospyros.

HETEROGENEITY OF SCULPTURING PATTERNS BETWEEN GEOGRAPHICAL DISTRIBUTION PATTERNS IN THE GENUS DIOSPYROS.

A single classification anova was completed for sculpturing patterns and geographical patterns (Table 10). Although significant differences were found in the sculpturing patterns among geographical patterns ($p = .0001$), only 10.5% of the total variation (total sum of square) in the sculpturing patterns is accounted for by geographical patterns in the genus Diospyros.

LOGISTIC REGRESSION.

Both polar diameter and equatorial diameter were used as independent, explanatory variables (X) in logistic regression, to estimate the probability "p" of generic membership (Figs. 4 & 5). According to the logistic regression model, the pollen grains of ca. $\leq 21 \mu\text{m}$ have a 100 percent probability of belonging to Euclea, while, for example, grains of ca. $29 \mu\text{m}$ have a very low probability of belonging to Euclea. As a pollen grain increases in size from ca. $37 \mu\text{m}$ to $70 \mu\text{m}$ the probability of the grain belonging to Euclea is 0 percent, while the likelihood of belonging to Diospyros, Royena, or Tetracelis adds up to 100 percent.

BIVARIATE ANALYSIS.

To display the central tendencies of polar diameter and equatorial diameter at the generic level 95% confidence ellipses of the bivariate means were completed and graphed in a composite coordinate system. A full treatment of the calculation and use of confidence ellipses for bivariate data is found in Sokal and Rohlf

(1981). Each ellipse can be described by two principal axes, the X or equatorial axis and the Y or polar axis. Both of these axes represent the bivariate means with their 95% confidence levels for the polar diameter and equatorial diameter of each genus (Fig. 6). Once the above parameters are plotted, we can then draw ellipses around the means. The shape of the outline of the ellipse is a function of the degree of correlation between the variables. If there is no relation (no correlation) between polar and equatorial diameters, the outlines would be circular; however, the outlines are elliptical, indicating varying degrees of correlation. The bivariate ellipses for Diospyros, Tetraclis, and Royena are nonoverlapping yet cluster near each other with an approximate polar diameter of 38 to 42 μm and equatorial diameter of 31 to 35 μm (Fig. 7). Euclea on the other hand is far removed and isolated from the rest of the genera with an approximate polar diameter of 26 to 28 μm and equatorial diameter of 23 to 25 μm (Fig. 7). Thus, pollen diameter is a useful character in distinguishing the genera within the Ebenaceae.

Discussion of Pollen Morphology

General characteristics of pollen of Ebenaceae

Pollen grains of all species are monads, radially symmetrical, with meridionally aligned ectoapertures, a mainly granular tectate-perforate exine, an ectexine with a well developed foot-layer, and an endexine that is thickened under the colpus. In addition, most grains are angulaperturate, triangular in polar view, subprolate or prolate-spheroidal, medium-sized, tricolporate, with long and narrow ectoapertures, lalongate endoapertures and finely striate-foveolate or finely striate sculpturing that is similar on the apocolpium and mesocolpium.

Observations of selected pollen characters from previously published studies of the Ebenaceae are presented in Table 11. Aside from minor discrepancies in grain size and sculpturing terminology, these generally agree with my observations. A few obvious differences include: Sharma and Gupta (1979) observed a circular (rather than lalongate) ora in D. crumenata and a longer polar axis in D. sylvatica; Gupta and Sharma (1986) a thicker exine (1.5 μm vs. 0.93 μm) in D. montana; and Nair and Kothari (1985) a longer polar axis (37.00 μm vs. 25.85 μm) in D. sylvatica. The present study and previously published studies agree that Euclea has grains with polar and equatorial axes of 29 μm or less, while most of the other genera have only grains with axes greater than 30 μm . Three studies (Selling, 1947; Erdtman, 1971; Huang, 1972) reported that pollen of D. ferrea (which was not examined in the present study) was consistently 29 μm or less in polar and equatorial lengths. Diospyros ferrea, D. hoyleana and D. bipindensis (examined in the present study),

are the only reported species of Diospyros that have pollen less than 29 μm in diameter.

The fundamental and distinguishing pollen character for all Ebenaceae examined in thin section is the presence of a granular infratectal layer instead of columellae. In addition, most species are characterized by a thick tectum. The occurrence of this loosely granular composition is the feature most useful in identifying Ebenaceae pollen.

The family is palynologically more variable than previous reports have indicated. In particular, sculpturing pattern can be finely anastomosed granular, finely striate, coarsely striate, or coarsely foveolate. Features not described previously include stratified exine, the ectexine consisting of a tectum, a thin and mostly granular infratectum, and a foot-layer, and the endexine thinner under the mesocolpium and thicker under the colpi. The increased range of morphological variation described here is mainly due to the greater numbers of species studied and the technique used in examination.

In comparison to other groups, such as the Cuspariinae (Rutaceae, Chapter 2), pollen morphology and exine structure of Ebenaceae are more uniform. Moreover, the level of pollen morphological variation is matched in wood anatomy and leaf architecture. Correlations of pollen morphology, wood and leaf anatomy with other morphological characters cannot be assessed because other features of Ebenaceae have not been thoroughly studied.

Correlation of pollen types with classification systems of Ebenaceae

The distribution of the pollen types among the genera recognized by White (1978, 1980, 1983, 1987, 1988), White and Cavencey (1980), and Bakhuizen (1936-1938) is summarized in Tables 12 and 13.

In his treatment of the African taxa, White recognized Euclea and 18 sections of Diospyros, including Royena and Rhaphidanthe; the genus Tetraclis, from Madagascar, was not treated. The present study examined pollen of approximately 12 of the 25 taxa that White included in Euclea and 29 of 108 taxa included in Diospyros. Approximately 54 species examined in this study were not treated by White (Table 12). Pollen type A is found throughout Euclea, and also in D. bipindensis (Diospyros sect. Latibulum) and in D. hoyleana, (Diospyros sect. Calvitiella). Small pollen was observed in more than one sample of D. hoyleana. The pollen and other morphological features of this species must be examined further to determine the taxonomic significance of this anomalously small pollen. Type A mostly occurs in Euclea. The subtypes for type A do not form patterns within the species or subspecies of Euclea. Type B is restricted to Diospyros, Royena, and Tetraclis, with the subtypes seemingly randomly dispersed among the sections, species and subspecies. The logistic regression (Figs. 4 & 5) is useful to represent visually this distribution of types A and B, which are based on size, among the genera of the Ebenaceae. Both figures 4 and 5 clearly shows that type A (grains less than 30 μm in diameter) is predominant in Euclea and also occurs to a limited extent in Diospyros.

Bakhuizen in his treatment of the Pacific taxa recognized only Diospyros and divided it into 36 sections (Table 13). The present study examined pollen of approximately 12 of the 171 species recognized by Bakhuizen. All samples of Diospyros exhibited pollen of type B, except for Diospyros kaki, which exhibited both type B (subtype B-3) and type C (subtype C-2). Once again the distribution of the subtypes seems to be randomly dispersed among the sections, species and subspecies. Because White's treatment of the African taxa and Bakhuizen's treatment of the Pacific taxa of the Ebenaceae have not been critically compared with each other or with the Asiatic or South American taxa, an assessment of the correlation of pollen characters with the taxonomy of the Ebenaceae on a world-wide basis is impossible at this time.

Pollen as a taxonomic character in Ebenaceae

With few exceptions the pollen morphology of the Ebenaceae as a whole is distinctive, but the usefulness at the generic level is limited.

Examination of the pollen of approximately 92 species from both the New World and the Old World, has demonstrated that patterns of variation in the pollen morphology for the family are more complex than previously thought and three pollen types are recognized here. Within these types, few characters show diversity, but sufficient variation exists for recognition of numerous subtypes.

Within the Ebenaceae, difference in pollen size is of some use as a taxonomic character. Small pollen (type A) distinguishes Euclea from Diospyros, Royena, and Tetraclis. Large pollen (type C) is

characteristic of D. virginiana and D. crumenata, the only two species of the genus native to north temperate areas. Most of the species of Diospyros from the New World, (North America and South America), have pollen grains significantly larger than those of the Old World species (Table 7). Exceptions to this included the several species of Diospyros with large pollen grains from China (Old World) and the one species from the Bahamas with small grains (New World).

The pollen subtypes, based on sculpturing pattern, appear to form a continuum; only the extremes of granular, foveolate, and striate patterns appear distinct. The observed intermediate states make sculpturing pattern of dubious taxonomic utility. Analyses of variance was completed using sculpturing patterns as a grouping variable (Tables 8, 9, 10) to test for significant differences between sculpturing patterns and generic relationships, polar and equatorial diameters, and geography used as a grouping variable, but observed variation was low. At present, predicting evolutionary trends in sculpturing pattern is impossible due to the lack of complete information about other characters in this family. In addition, a possible source of error in the analyses of variance (Tables 8, 9, 10) is the difficulty in coding sculpturing patterns.

For the most part, multiple samples of any given species exhibited a single pollen type or subtype. Exceptions to this are Royena austro-africana, D. kaki, and D. scabrida, which exhibited more than one type or subtype.

Pollen morphology of other families in the Ebenales

Pollen of the Symplocaceae is very distinctive, yet shows considerable variation in some characters. Grains are usually tricolporate, but sometimes triporate (less commonly 2- 4-colporate). The ectoapertures are distinctly brevicolpate. Endoapertures are broadly lalongate or circular. Endoapertures may or may not be associated with a deep radial groove on the equatorial circumference. Average pollen size is 30 μm , but varies between 20 and 70 μm . The pollen of Symplocos reveals a wide range of surface types, viz., smooth, finely reticulate, finely to coarsely verrucate, areolate, echinate, clavate, globulate, and pitted (perforate) (Erdtman, 1971; Meijden, 1971; Huang, 1972; Nooteboom, 1975; Barth, 1979, 1982a; Lieux, 1982). The rather specialized character of a micropapillate supratectal ornamentation is a feature shared with some Styracaceae. The exine structure appears to be columellate and tectate-perforate. Nonapertural exine thickness ranges from 1.30 μm to 2.60 μm . The exine is stratified into ectexine and endexine, with the ectexine composed of a distinct tectum, columellae, and a foot-layer. There is very little resemblance to the pollen of the Ebenaceae.

The Styracaceae are a fairly stenopalynous family that is, for the most part, palynologically quite distinct from the Ebenaceae and Sapotaceae. In general the pollen grains are solitary and range from 15.3 μm (P) X 21.4 μm to 43.3 μm (P) X 37.7 μm . Grains are most commonly tricolporate or less often tricolporoidate. Ectoapertures are meridionally aligned, sometimes nearly meeting at the poles. Endoapertures vary from ill-defined to typically distinctly lalongate

and are generally associated with a prominent equatorial bridge. Exine sculpturing is foveolate, foveolate-fossulate, fossulate-finely rugulate, reticuloid, intertwined rugulate-reticulate, and weakly crotonoid. Outer tectal surfaces are smooth, granulose, spinulose, beaded, and/or banded. All genera have an exine structure that is columellate and tectate-perforate. Nonapertural exine thickness ranges from 0.75 μm to 2.5 μm . The exine is stratified into ectexine and endexine, with the ectexine composed of a distinct tectum, columellae, and a foot-layer. The endexine is uniformly present and is often granular or characteristically internally fragmented and is conspicuously thickened under and along the margins of the colpi (Morton and Dickison, 1992).

Lissocarpa Benth. (Lissocarpaceae), a genus closely allied to the Ebenaceae and Styracaceae, has 3-porate pollen grains with rugulate sculpturing that are more similar to those of the Sapotaceae (Morton, unpublished data).

Pollen grains of the Sapotaceae are solitary and range between 16 μm and 92 μm in polar axis length. Grains are 3-5, (rarely 6)-colporate. Ectoapertures are usually narrow, occasionally broad. Endoapertures are narrowly lalongate or broadly lalongate, less frequently circular or very rarely lolongate. Exine sculpturing is psilate, subpsilate, scabrate, granular, anastomosed granular, striate-rugulate, striate, angular-rugulate, and coarsely rugulate. The tectum is essentially complete or perforate, with an outer surface that is smooth, finely granular, striate, or rugulate (Erdtman, 1971; Ayensu, 1972; Lieux, 1982; Harley, 1986, 1991). The ornamentation at the equator is sometimes different than that at the

poles. Throughout the family, with rare exceptions, the exine structure is tectate-perforate. Nonapertural exine thickness ranges from 1.0 μm to 8.0 μm . The exine is stratified into ectexine and endexine, with the ectexine composed of a thick tectum, a very narrow infratectum, and a foot-layer similar, equal or slightly thicker than the tectum. The infratectum is either granular or with very reduced columellae that may be interspersed with granules. The endexine is thickened, particularly in the area surrounding the endoapertures and underlying the colpi. In some species it is absent or very thin in the mesocolpium, while in others it may be slightly thinner than, or as thick as, that in the endoapertural area. This thickened endexine sometimes results in a continuous thickened band in the equatorial region. Harley (1986) commented that the pollen of the Sapotaceae cannot easily be confused with the Styracaceae or the Symplocaceae. The grains of Parastyrax (Styracaceae), however, are irregularly and sparsely pitted, occasionally 4-aperturate, and with thickened exines and appear to be similar to those of some Sapotaceae.

Of all families in the Ebenales, the Sapotaceae share the most pollen features with the Ebenaceae. The Sapotaceae are more variable in several ways. Firstly, aperture number varies from 3-5, and rarely 6. Pollen size ranges from slightly smaller to slightly larger than that of the Ebenaceae. The exine sculpturing patterns, although largely overlapping with those of the Ebenaceae, have various grades of psilate, subpsilate, scabrate, and angular-rugulate. Finally, the exine composition is very similar to that of the Ebenaceae because both families possess a mostly granular

infratectum. The pollen of Sapotaceae exhibits a greater range in features, and pollen of the Ebenaceae could easily be confused with that of the Sapotaceae.

Table 1. A Comparison of Intrafamilial Classifications of the Ebenaceae

Hiern (1873) World-wide	Gurke (1897) World-wide	Bakhuizen (1936) Malaysian	White (1980,1987) African
<u>Euclea</u>	<u>Euclea</u>	<u>Euclea</u>	<u>Euclea</u>
<u>Royena</u>	<u>Royena</u>	<u>Royena</u>	
<u>Tetracelis</u>	<u>Tetracelis</u>	<u>Tetracelis</u>	(<u>Tetracelis</u> not treated)
<u>Diospyros</u>	<u>Diospyros</u>	<u>Diospyros</u>	<u>Diospyros</u>
Sections	Sections	A. Subgenus Maba	Sections
1. Melonia	1. Melonia	Sections	1. Forsteria
2. Ebenus	2. Ebenus	1. Forsteria	2. Asteropetala
3. Noltia	3. Noltia	2. Miquelia	3. Katula
4. Gunisanthus	4. Gunisanthus	3. Hasselt	4. Entia
5. Guaiacana	5. Guaiacana	B. Subgenus Hiemiodendron	5. Dodonium
6. Cunalaria	6. Cunalaria	C. Subgenus Cargillia	6. Forbesia
7. Ermellinus	7. Ermellinus	D. Subgenus Eudiospyros	7. Brevituba
8. Patonia	8. Patonia	Sections	8. Myrmecophila
9. Leucoxylum	9. Leucoxylum	1. Brachycylix	9. Royena
10. Danzleria	10. Danzleria	2. Cavanilleastrum	10. Lagenaria
11. Paralea	11. Paralea	3. Stelechanta	11. Erikesi
12. Cargillia	12. Cargillia	4. Podophora	12. Latibulum
13. Rospidios	13. Rospidios	5. Ebenaster	13. Tabonaca
14. Cavanillea	14. Cavanillea	6. Basithrix	14. Noltia
15. Amuxis	15. Amuxia	7. Kurzella	15. Rhaphidanthe
		8. Phyllosepala	16. Calvitiella
		9. Eriantha	17. Brevistyla
	<u>Brachynema</u> (?)	10. Confertiflora	18. Marsupium
	<u>Rhaphidanthe</u> (?)	11. Acanthebenus	
		12. Lotus	
		13. Ebenus	
		14. Ebenopsis	
		15. Ptychocylix	
		16. Didymanthera	
		17. Nesindica	
		18. Liophylla	
		19. Eucarpon	
		20. Cladantha	
		21. Truncicalix	
		22. Saptanigra	
		23. Reflexocalix	
		24. Trisantha	
			25. Glutinosa
		26. Asterocalix	
		27. Verruculosa	
		28. Pachycylix	
		29. Saccocalix	
			30. Campanulata
		31. Rigidophylla	
<u>Maba</u>	<u>Maba</u>		
Sections	Sections		
1. Ferreola	1. Ferreola		
2. Macreightia	2. Macreightia		
3. Holochilus	3. Holochilus		
4. Rhipidostigma	4. Rhipidostigma		
5. Barberia	5. Barberia		
6. Trichanthera	6. Trichanthera		

Table 2. Morphological characters of pollen of the Ebenaceae as observed by LM and SEM. For species of which more than one sample was studied, the sample number corresponding to the voucher specimen in Appendix 1 precedes the name of the species. The number of grains upon which the measurements, if any, were made is given in parentheses following the specific epithet.

Taxon	Polar axis (µm)		Equatorial axis (µm)		P/E ¹	Shape ²	Size ³	Sculpture ⁴	Apo. vs 5
	Mean	SD	Mean	SD					
=====									
EUCIEA									
1-E. acutifolia (25)	27.27	1.288	25.62	1.303	1.07	pP	M	FAG-Fo	S
1-E. crispa (25)	25.20	1.718	22.11	1.224	1.14	PS	M	FS-Fo	S
2-E. crispa	-							FS-Fo	S
1-E. dekindtii (26)	26.81	1.398	23.66	0.802	1.13	PS	M	FS-Fo	S
1-E. divinatorum (25)	25.18	0.877	21.34	1.227	1.18	sP	M	FS-Fo	S
2-E. divinatorum (25)	29.77	1.620	26.62	1.767	1.12	PS	M	FS-Fo	S
3-E. divinatorum (25)	24.71	0.995	23.37	1.392	1.06	PS	S	FS-Fo	S
4-E. divinatorum (25)	24.04	1.418	21.30	1.152	1.13	PS	S	FS-Fo	S
1-E. kellaui (25)	27.68	1.496	24.86	1.456	1.12	PS	M	FAG-Fo	S
2-E. kellaui (25)	25.86	1.475	23.34	1.512	1.11	PS	M	FAG-Fo	S
3-E. kellaui (25)	24.76	1.444	22.06	1.204	1.13	PS	S	FAG-Fo	S
1-E. lanceolata (25)	26.52	1.879	25.05	1.562	1.07	PS	M	FAG-Fo	S
1-E. linearis (25)	27.95	2.734	22.50	1.413	1.25	sP	M	FS-Fo	S
1-E. mayottensis (25)	25.48	1.598	25.60	1.678	1.00	S	M	FS-Fo	S

class pattern Meso.

1-E. multiflora (25)	26.03	1.186	24.71	1.595	1.06	PS	M	FS-Fo	S
1-E. natalensis (25)	23.40	1.037	18.91	1.274	1.24	SP	S	FS	S
2-E. natalensis (25)	29.21	1.843	22.95	1.292	1.27	SP	M	FS	S
3-E. natalensis (25)	25.82	1.247	22.32	1.448	1.16	SP	M	FS	S
4-E. natalensis (25)	27.06	1.382	21.13	0.866	1.28	SP	M	FS	S
5-E. natalensis (25)	26.41	1.411	22.80	1.052	1.16	SP	M	-	-
1-E. polyandra (25)	25.85	1.089	22.27	0.788	1.16	SP	M	FS	S
2-E. polyandra (25)	26.37	1.578	22.77	2.264	1.16	SP	M	FS	S
1-E. pseudobenus (50)	26.91	1.539	22.47	1.595	1.20	SP	M	FS	S
2-E. pseudobenus (25)	27.85	1.523	23.48	1.336	1.19	SP	M	FS	S
1-E. racemosa (25)	25.88	1.117	24.43	1.127	1.06	PS	M	FS-Fo	S
2-E. racemosa (25)	28.66	2.185	23.54	1.327	1.22	SP	M	FS-Fo	S
3-E. racemosa (25)	27.51	1.155	22.71	0.928	1.21	SP	M	FS-Fo	S
4-E. racemosa (25)	28.06	1.578	24.18	1.433	1.16	SP	M	FS-Fo	S
1-E. schimperi (25)	25.60	0.906	24.01	1.063	1.07	PP	M	FS-Fo	S
2-E. schimperi (25)	25.69	1.159	22.05	1.152	1.17	SP	M	FS-Fo	S
3-E. schimperi (25)	25.73	1.077	24.86	1.241	1.04	PS	M	FS-Fo	S
4-E. schimperi (25)	27.02	1.596	23.40	2.008	1.16	SP	M	FS-Fo	S
5-E. schimperi								FS-Fo	S
1-E. undulata (25)	26.15	1.323	23.91	0.903	1.09	PS	M	FS-Fo	S
2-E. undulata (25)	27.43	2.792	21.69	2.469	1.27	SP	M	FS-Fo	S
ROYENA									
1-R. austro-africana (50)	37.37	2.524	34.52	1.871	1.08	PS	M	FAg	S

2-R. austro-africana (25)	35.53	1.310	27.95	2.015	1.28	SP	M	FS	S
3-R. austro-africana (25)	32.26	2.020	29.73	1.518	1.09	PS	M	FS	S
1-R. cordata (25)	41.55	2.266	38.49	2.227	1.08	PS	M	FG	S
1-R. dichrophylla (25)	46.10	1.821	38.49	1.864	1.20	SP	M	FAG-Fo	S
1-R. glabra (25)	40.62	2.182	32.05	2.379	1.27	SP	M	FAG-S	S
1-R. guerkei (25)	40.06	1.501	36.11	2.363	1.11	PS	M	FAG	S
1-R. hirsuta (25)	30.23	1.517	28.04	1.182	1.08	PS	M	FS	S
1-R. lycioides (25)	40.90	1.970	35.63	2.459	1.15	SP	M	FAG-S	S
2-R. lycioides (25)	42.74	1.767	36.34	1.892	1.18	SP	M	FAG-S	S
3-R. lycioides (25)	42.79	2.298	34.02	1.512	1.29	SP	M	FAG-S	S
4-R. lycioides (25)	42.66	1.664	37.34	1.988	1.14	PS	M	FAG-S	S
5-R. lycioides (25)	33.45	1.310	30.66	2.161	1.09	PS	M	FAG-S	S
1-R. microphylla (25)	42.52	1.661	36.84	1.775	1.16	SP	M	FAG-S	S
1-R. pallens (25)	38.35	2.074	31.68	1.583	1.21	SP	M	FAG-Fo	S
1-R. sericea (50)	43.87	1.998	36.56	2.490	1.21	SP	M	FS	S
2-R. sericea (25)	37.14	1.478	35.78	2.280	1.04	PS	M	FS	S
1-R. usambarensis (25)	33.45	1.310	33.90	1.577	0.99	OS	M	FS	S
1-R. villosa (25)	44.62	2.983	36.55	2.044	1.22	SP	M	FS	S
2-R. villosa (24)	42.85	2.652	38.10	1.208	1.13	PS	M	FS	S
1-R. whyteana (25)	37.01	1.384	33.70	1.792	1.10	PS	M	FG	S
2-R. whyteana (17)	38.40	1.780	36.24	2.414	1.06	PS	M	FG	S
3-R. whyteana (25)	42.21	1.784	34.48	1.879	1.23	SP	M	FG	S

DIOSPYROS

1-D. abyssinica (18)	30.61	1.830	29.14	2.005	1.05	PS	M	FAG-Fo	D
2-D. abyssinica (25)	30.89	1.423	27.07	1.333	1.14	PS	M	FAG-Fo	D
1-D. armata (33)	47.69	3.393	36.56	3.395	1.31	SP	M	FAG-S	S
1-D. artanthaeifolia (13)	37.26	1.245	34.60	2.537	1.08	PS	M	FAG-Fo	S
2-D. artanthaeifolia (6)	39.80	0.787	38.37	1.567	1.04	PS	M	FAG-Fo	S
3-D. artanthifolia (25)	39.87	2.441	37.04	2.363	1.08	PS	M	FAG-Fo	S
1-D. bipindensis (25)	29.44	1.854	26.91	1.696	1.10	PS	M	FAG	S
1-D. bridellaeifolia (14)	41.43	3.828	35.53	2.923	1.17	SP	M	FS	S
1-D. bullata (13)	43.42	2.710	39.41	2.007	1.10	PS	M	FAG-S	S
1-D. campechiana (25)	42.02	2.080	33.14	1.368	1.27	SP	M	FS	S
1-D. candolleana (50)	37.82	2.162	29.64	2.230	1.28	SP	M	FS-Fo	D
1-D. caulliflora (25)	33.28	1.885	32.87	1.754	1.02	PS	M	FS	S
1-D. conocarpa (25)	42.33	3.489	33.77	1.725	1.26	SP	M	FS-Fo	D
2-D. conocarpa (25)	43.22	2.730	33.29	1.739	1.30	SP	M	FS-Fo	D
1-D. crassinervis (25)	33.75	2.396	29.49	2.221	1.15	SP	M	FS-Fo	D
1-D. crumenata (25)	53.87	3.529	45.74	3.284	1.18	SP	L	FS-Fo	D
1-D. curranii (38)	40.32	3.554	32.98	3.293	1.22	SP	M	FS	S
1-D. decandra (25)	30.05	2.023	28.57	2.207	1.06	PS	M	FS-Fo	D
2-D. decandra (25)	33.57	2.284	25.60	2.074	1.32	SP	M	FS-Fo	D
1-D. dendo (3)	36.43	1.665	37.27	2.960	0.98	OS	M	CS-Fo	S
2-D. dendo (25)	31.03	1.693	29.69	1.257	1.05	PS	M	CS-Fo	S
1-D. dichroa (25)	41.08	2.607	36.87	2.679	1.12	PS	M	FS	S
1-D. discolor (25)	42.40	3.208	36.04	2.180	1.18	SP	M	-	-

2-D. discolor (18)	45.50	1.628	34.21	2.340	1.34	E	M	-	-
1-D. diversilimba	-							FS-Fo	S
2-D. diversilimba (25)	28.67	1.462	25.60	1.350	1.12	PS	M	FS-Fo	S
1-D. ehretioides (25)	34.48	2.389	29.30	1.979	1.18	SP	M	FAG-S	S
1-D. filipendula (25)	31.47	1.292	24.93	1.530	1.27	SP	M	FS-CFo	D
1-D. fischeri (9)	44.92	2.375	33.23	2.791	1.36	E	M	FS	S
2-D. fischeri (25)	33.04	1.869	33.76	1.707	0.98	OS	M	FS	S
1-D. gabunensis (25)	43.12	2.722	38.03	2.864	1.14	PS	M	-	-
2-D. gabunensis (25)	43.11	3.652	36.07	2.742	1.20	SP	M	-	-
1-D. gillettii (24)	39.70	2.702	30.13	2.337	1.31	SP	M	FAG-S	S
2-D. gillettii (25)	39.05	2.379	29.16	3.468	1.36	E	M	FAG-S	S
1-D. glandulosa (24)	46.36	1.874	34.77	2.174	1.34	E	M	FS	S
1-D. hispida (25)	38.51	2.504	36.08	3.132	1.07	PS	M	FS-CFo	D
2-D. hispida (26)	41.04	2.605	37.42	2.914	1.10	PS	M	FS-CFo	D
1-D. hoyleana (25)	23.70	1.216	19.62	1.073	1.21	SP	S	FS-CFo	D
2-D. hoyleana (24)	23.35	1.174	21.35	1.275	1.10	PS	S	FS-CFo	D
1-D. ierensis (25)	39.83	1.910	32.05	2.109	1.25	SP	M	FFo	D
2-D. ierensis	-							FFo	D
1-D. kaki (25)	50.39	3.719	41.67	4.220	1.22	SP	L	FS	S
2-D. kaki (25)	46.58	2.783	40.44	1.751	1.15	SP	M	FS	S
1-D. kamerunensis (25)	31.93	1.172	27.71	1.371	1.15	SP	M	FS	S
2-D. kamerunensis	-							FS	S
1-D. kiriki (25)	42.56	2.170	36.14	2.035	1.21	SP	M	-	-
2-D. kiriki (25)	42.38	2.170	32.92	2.587	1.29	SP	M	FS-Fo	D

1-D. longibracteata (26)	39.39	1.841	27.87	1.728	1.42	E	M	FS-Fo	D
1-D. lotus (25)	40.19	2.338	33.10	2.467	1.22	SP	M	FS-Fo	S
2-D. lotus (25)	36.73	1.803	32.72	2.097	1.14	PS	M	FS-Fo	S
3-D. lotus (25)	40.24	2.024	35.97	1.697	1.12	PS	M	-	-
1-D. malabarica (24)	39.92	2.737	33.91	3.842	1.19	SP	M	FS	S
2-D. malabarica (6)	49.54	7.028	38.23	4.695	1.30	SP	L	FS	S
1-D. maritima (21)	42.68	1.925	38.52	1.839	1.11	PS	M	FFo	D
2-D. maritima (24)	43.53	2.054	35.31	3.387	1.24	SP	M	FFo	D
1-D. mespiliformis '11)	39.03	3.480	28.49	2.049	1.37	E	M	FFo	D
2-D. mespiliformis (25)	35.70	1.651	35.13	1.971	1.02	PS	M	FFo	D
1-D. mollis (24)	30.83	1.333	25.47	2.670	1.22	SP	M	FAG-S	S
1-D. montana (25)	32.98	1.218	29.20	1.813	1.13	PS	M	FG	S
2-D. montana (25)	32.36	1.498	29.44	1.394	1.10	PS	M	FG	S
1-D. morisiana (24)	39.04	1.968	35.21	2.048	1.11	PS	M	FS	S
2-D. morisiana (25)	34.76	1.615	31.34	1.322	1.11	PS	M	FS	S
1-D. multiflora (24)	36.65	1.999	31.13	1.798	1.18	SP	M	FFo	D
1-D. mweroensis (25)	38.96	1.840	32.52	2.295	1.20	SP	M	FAG-S	S
2-D. mweroensis (25)	39.13	1.428	35.55	1.854	1.10	PS	M	FAG-S	S
1-D. nicaraguensis (24)	35.12	2.272	29.08	2.392	1.21	SP	M	FS-Fo	D
1-D. nummularia (25)	30.74	1.422	25.14	1.383	1.23	SP	M	FS-Fo	D
1-D. ovalifolia (25)	30.94	1.720	25.64	1.403	1.21	SP	M	FS-Fo	D
2-D. ovalifolia (25)	32.49	1.755	26.33	2.413	1.24	SP	M	FS-Fo	D
1-D. pendula (24)	37.01	2.092	32.66	1.994	1.13	PS	M	FS-Fo	D
1-D. pentamera (25)	34.22	1.853	31.31	1.994	1.10	PS	M	FS	S

2-D. pentamera (25)	37.06	1.920	31.17	2.023	1.19	SP	M	FS	S
1-D. philippinensis (25)	40.07	2.768	34.78	3.502	1.16	SP	M	FFo	D
1-D. pilosanthera (25)	31.77	1.150	26.02	1.393	1.22	SP	M	FFo	D
2-D. pilosanthera (25)	36.87	1.614	28.84	1.728	1.28	SP	M	FFo	D
3-D. pilosanthera (24)	36.53	2.444	30.80	1.760	1.19	SP	M	FFo	D
1-D. polystemon (25)	36.52	2.849	30.23	1.901	1.21	SP	M	-	-
2-D. polystemon (25)	34.93	1.977	31.89	1.872	1.10	PS	M	FAG-S	S
1-D. preussii (25)	43.49	1.899	43.80	1.441	0.99	OS	M	FS	S
2-D. preussii (17)	46.28	2.168	44.25	1.635	1.05	PS	M	FS	S
1-D. pterocalyx (24)	47.19	3.404	33.32	2.880	1.43	E	M	FS	S
1-D. revoluta (24)	36.09	1.116	32.97	1.454	1.09	PS	M	FFo	D
1-D. samoensis (50)	37.19	2.151	33.10	2.051	1.13	PS	M	FS-Fo	D
2-D. samoensis (25)	34.43	2.222	29.93	2.180	1.15	SP	M	FS-Fo	D
1-D. scabrida (25)	39.70	2.683	36.14	1.329	1.10	PS	M	FG	S
2-D. scabrida (25)	41.67	2.556	34.65	1.717	1.21	SP	M	FAG	S
1-D. squarrosa (25)	34.73	2.008	32.60	1.521	1.07	PS	M	FAG-Fo	S
2-D. squarrosa (25)	35.12	1.632	31.21	1.460	1.13	PS	M	FAG-Fo	S
3-D. squarrosa (25)	37.38	1.760	33.90	2.096	1.11	PS	M	FAG-Fo	S
1-D. suaveolens (25)	32.88	1.564	27.93	1.173	1.18	SP	M	FFo	D
2-D. suaveolens (25)	39.53	2.041	31.47	1.816	1.26	SP	M	FFo	D
3-D. suaveolens (25)	37.29	2.144	32.70	1.967	1.14	PS	M	FFo	D
1-D. sylvatica (26)	25.85	2.197	24.56	2.327	1.05	PS	M	FS-Fo	S
1-D. texana (25)	37.50	1.683	31.91	1.942	1.18	SP	M	FAG-S	S
2-D. texana (25)	40.22	2.214	32.76	1.588	1.23	SP	M	FAG-S	S

3-D. texana (25)	35.71	1.108	33.23	1.752	1.08	PS	M	FAG-S	S
1-D. verae-crucis (24)	38.20	2.945	30.32	2.077	1.26	SP	M	-	
1-D. vermoesenii (25)	31.17	1.765	25.41	1.752	1.23	SP	M	FS-Fo	D
2-D. vermoesenii (25)	31.08	1.557	26.06	1.576	1.20	SP	M	FS-Fo	D
1-D. verrucosa (26)	34.71	1.776	27.84	1.520	1.25	SP	M	FS-Fo	D
1-D. virgata (25)	30.61	1.371	24.18	2.005	1.27	SP	M	FFo	D
2-D. virgata (24)	39.08	2.262	31.17	1.632	1.26	SP	M	FFo	D
1-D. virginiana (26)	52.83	3.360	47.74	2.091	1.11	PS	L	FS-Fo	D
2-D. virginiana (25)	52.70	2.059	48.96	3.321	1.08	PS	L	FS-Fo	D
3-D. virginiana (25)	56.74	3.299	51.89	2.726	1.11	PS	L	FS-Fo	D
4-D. virginiana (25)	56.68	2.651	49.59	3.069	1.15	SP	L	FS-Fo	D
5-D. virginiana (25)	53.11	5.629	48.30	5.560	1.15	SP	L	FS-Fo	D
6-D. virginiana (25)	51.67	2.956	47.69	2.870	1.09	PS	L	FS-Fo	D
7-D. virginiana (25)	50.60	1.791	46.56	2.983	1.09	PS	L	-	-
8-D. virginiana (25)	52.33	3.262	48.06	2.929	1.09	PS	L	-	-

TETRACLIS

1-T. baronii (50)	38.18	1.813	31.07	2.014	1.23	SP	M	FS	S
2-T. clusiaefolia (25)	40.15	2.530	31.91	1.573	1.26	SP	M	FS	S

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¹ P/E = ratio of the length of the polar axis to that of the equatorial axis.

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2 pP = perprolate, E = euprolate, sP = subprolate, PS = prolate spheroidal, S = spheroidal, OS = oblate spheroidal. These terms are used in the sense of Walker and Doyle (1975).

3 S = small, M = medium, L = large. These terms are used in the sense of Walker and Doyle (1975).

4 Pattern of tectal surface in mesocolpium: FG = finely granular, FAG = finely anastomosed granular, FAG-S = finely anastomosed granular-striate, FAG-Fo = finely anastomosed granular-fossulate, FS = finely striate, FS-Fo = finely striate-fossulate, FFo = finely fossulate, FS-CFo = finely striate-coarsely fossulate, CS-Fo = coarsely striate-fossulate.

5 Similarity (S) or difference (D) in sculpture pattern of the Apo. = apocolpium and that of Meso. = mesocolpium.

Table 3. Morphological characters observed by TEM of genera of the Ebenaceae. For species of which more than one sample was studied, the sample number, preceding the specific epithet, corresponds to the voucher specimen in Appendix I. All measurements were made in the mesocolpium.

Taxon	Thickness of ectexine (μm)	% of thickness			Thickness of endexine (μm)
		Tectum	Intraectum	Foot-layer	
1-Euclea acutifolia	0.87	39	15	46	.11
3-Euclea kellau	0.53	39	16	45	.14
5-Euclea natalensis	1.29	37	19	44	.20
3-Royena whyteana	1.35	37	26	37	.14
1-Diospyros ehrenioides	0.86	33	23	44	.00-.05
1-Diospyros montana	0.93	42	22	36	.11
1-Diospyros pendula	0.72	43	21	36	.11
1-Diospyros philippinensis	1.00	45	23	32	.20
1-Diospyros samoensis	1.00	43	28	28	.14
3-Diospyros suaveolens	0.79	39	23	38	.09
1-Diospyros suaveolens	0.98	38	22	50	.08

Table 4. Types and subtypes of pollen of Ebenaceae.

Sculpture pattern	
Apocolpium	Mesocolpium
=====	
Type A-mean polar axis length $\leq 29.99 \mu\text{m}$	
A1	finely striate-foveolate
A2	finely striate
A3	finely anastomosed granular -foveolate
A4	finely anastomosed granular
Type B-mean polar axis length $\geq 30.00 \mu\text{m}$ & $\leq 49.99 \mu\text{m}$	
B1	finely anastomosed granular-foveolate
B2	finely striate-foveolate
B3	finely striate
B4	finely anastomosed granular
B5	finely granular
B6	finely anastomosed granular-striate
B7	smooth
B8	coarsely striate-foveolate
B9	finely anastomosed granular
B10	finely striate
B11	striate
Type C-mean polar axis length $\geq 50.00 \mu\text{m}$	
C1	striate
C2	finely striate

Table 5. The mean and standard deviation for polar and equatorial pollen diameters of the species of Ebenaceae, arranged from smallest to largest polar diameter.

Species	Polar (μm) Mean (SD)	Equatorial (μm) Mean (SD)	Sample size
Euclea			
<i>E. crispa</i>	25.20 (1.718)	22.11 (1.224)	25
<i>E. mayottensis</i>	25.48 (1.598)	25.60 (1.678)	25
<i>E. divinorum</i>	25.92 (2.586)	23.16 (2.580)	100
<i>E. schimperii</i>	26.01 (1.330)	23.58 (1.735)	100
<i>E. multiflora</i>	26.03 (1.186)	24.71 (1.595)	25
<i>E. kellau</i>	26.10 (1.893)	23.42 (1.796)	75
<i>E. polyandra</i>	26.11 (1.367)	22.52 (1.697)	50
<i>E. natalensis</i>	26.38 (2.342)	21.62 (1.915)	125
<i>E. lanceolata</i>	26.52 (1.879)	25.05 (1.562)	25
<i>E. undulata</i>	26.79 (2.256)	22.80 (2.154)	50
<i>E. dekindtii</i>	26.81 (1.398)	23.66 (0.802)	26
<i>E. pseudebenus</i>	27.23 (1.602)	22.81 (1.582)	75
<i>E. acutifolia</i>	27.27 (1.288)	25.62 (1.303)	25
<i>E. racemosa</i>	27.53 (1.862)	23.71 (1.375)	100
<i>E. linearis</i>	27.95 (2.734)	22.50 (1.413)	25
Royena			
<i>R. hirsuta</i>	30.23 (1.517)	28.04 (1.182)	25
<i>R. usambarensis</i>	33.45 (1.310)	33.90 (1.577)	25
<i>R. austro-africana</i>	35.63 (2.991)	31.68 (3.439)	100

<i>R. pallens</i>	38.35 (2.074)	31.68 (1.583)	25
<i>R. whyteana</i>	39.31 (2.832)	34.64 (2.205)	67
<i>R. guerkei</i>	40.06 (1.501)	36.11 (2.363)	25
<i>R. glabra</i>	40.62 (2.182)	32.05 (2.379)	25
<i>R. lycioides</i>	40.77 (4.076)	34.80 (3.077)	125
<i>R. cordata</i>	41.55 (2.266)	38.49 (2.227)	25
<i>R. sericea</i>	41.63 (3.814)	36.30 (2.445)	75
<i>R. microphylla</i>	42.52 (1.661)	36.84 (1.775)	25
<i>R. villosa</i>	42.75 (2.935)	37.31 (1.843)	49
<i>R. dichrophylla</i>	46.10 (1.821)	38.49 (1.864)	25
<i>Diospyros</i>			
<i>D. hoyleana</i>	23.54 (1.203)	20.49 (1.470)	49
<i>D. sylvatica</i>	25.85 (2.197)	24.56 (2.327)	26
<i>D. diversilimba</i>	28.67 (1.462)	25.60 (1.350)	25
<i>D. bipindensis</i>	29.44 (1.854)	26.91 (1.696)	25
<i>D. nummularia</i>	30.74 (1.422)	25.14 (1.383)	25
<i>D. abyssinica</i>	30.77 (1.591)	27.94 (1.926)	43
<i>D. mollis</i>	30.83 (1.333)	25.47 (2.670)	24
<i>D. vermoesenii</i>	31.12 (1.648)	25.74 (1.681)	50
<i>D. filipendula</i>	31.47 (1.292)	24.93 (1.530)	25
<i>D. dendo</i>	31.61 (2.375)	30.50 (2.784)	28
<i>D. ovalifolia</i>	31.71 (1.889)	25.98 (1.984)	50
<i>D. decandra</i>	31.81 (2.778)	27.09 (2.598)	50
<i>D. kamerunensis</i>	31.93 (1.172)	27.71 (1.371)	25
<i>D. montana</i>	32.67 (1.387)	29.32 (1.605)	50
<i>D. cauliflora</i>	33.28 (1.885)	32.87 (1.754)	25

<i>D. crassinervis</i>	33.75 (2.396)	29.49 (2.221)	2 5
<i>D. ehretioides</i>	34.48 (2.389)	29.30 (1.979)	2 5
<i>D. verrucosa</i>	34.71 (1.776)	27.84 (1.520)	2 6
<i>D. virgata</i>	34.76 (4.657)	27.61 (3.969)	4 9
<i>D. pilosanthera</i>	35.04 (2.952)	28.52 (2.544)	7 4
<i>D. nicaraguensis</i>	35.12 (2.272)	29.08 (2.392)	2 4
<i>D. pentamera</i>	35.64 (2.353)	31.24 (1.989)	5 0
<i>D. polystemon</i>	35.73 (2.556)	31.06 (2.048)	5 0
<i>D. squarrosa</i>	35.74 (2.134)	32.57 (2.022)	7 5
<i>D. revoluta</i>	36.09 (1.116)	32.97 (1.454)	2 4
<i>D. fischeri</i>	36.18 (5.677)	33.62 (2.016)	3 4
<i>D. samoensis</i>	36.27 (2.526)	32.04 (2.569)	7 5
<i>D. suaveolens</i>	36.57 (3.373)	30.70 (2.628)	7 5
<i>D. multiflora</i>	36.65 (1.999)	31.13 (1.798)	2 4
<i>D. mespiliformis</i>	36.72 (2.782)	33.10 (3.672)	3 6
<i>D. morrisiana</i>	36.86 (2.799)	33.24 (2.587)	4 9
<i>D. pendula</i>	37.01 (2.092)	32.66 (1.994)	2 4
<i>D. texana</i>	37.81 (2.527)	32.63 (1.827)	7 5
<i>D. candolleana</i>	37.82 (2.162)	29.64 (2.230)	5 0
<i>D. verae-crucis</i>	38.20 (2.945)	30.32 (2.077)	2 4
<i>D. lotus</i>	39.05 (2.626)	33.78 (2.624)	7 5
<i>D. mweroensis</i>	39.05 (1.632)	34.03 (2.569)	5 0
<i>D. gillettii</i>	39.08 (2.542)	29.70 (2.976)	4 9
<i>D. artanthaefolia</i>	39.09 (2.294)	36.50 (2.637)	4 4
<i>D. longibracteata</i>	39.39 (1.841)	27.87 (1.728)	2 6
<i>D. hispida</i>	39.44 (3.688)	36.42 (3.840)	5 1
<i>D. ierensis</i>	39.83 (1.910)	32.05 (2.109)	2 5

<i>D. philippinensis</i>	40.07 (2.768)	34.78 (3.502)	25
<i>D. curranii</i>	40.32 (3.554)	32.98 (3.293)	38
<i>D. scabrida</i>	40.69 (2.780)	35.39 (1.695)	50
<i>D. dichroa</i>	41.08 (2.607)	36.78 (2.679)	25
<i>D. brideliaefolia</i>	41.43 (3.828)	35.53 (2.923)	14
<i>D. malabarica</i>	41.84 (5.457)	34.87 (4.312)	30
<i>D. campechiana</i>	42.02 (2.080)	33.14 (1.368)	25
<i>D. conocarpa</i>	42.77 (3.133)	33.53 (1.731)	50
<i>D. kirkii</i>	42.97 (2.945)	34.53 (2.821)	50
<i>D. gabunensis</i>	43.02 (3.242)	36.83 (3.232)	50
<i>D. maritima</i>	43.13 (2.018)	36.81 (3.185)	45
<i>D. bullata</i>	43.42 (2.710)	37.41 (2.007)	13
<i>D. discolor</i>	43.70 (3.057)	35.27 (2.402)	43
<i>D. preussii</i>	44.62 (2.422)	43.98 (1.519)	42
<i>D. glandulosa</i>	46.36 (1.874)	34.77 (2.174)	24
<i>D. pterocalyx</i>	47.19 (3.404)	33.32 (2.880)	24
<i>D. armata</i>	47.69 (3.393)	36.56 (3.395)	33
<i>D. kaki</i>	48.49 (3.777)	41.06 (3.258)	50
<i>D. virginiana</i>	53.84 (3.932)	48.61 (3.596)	201
<i>D. crumenata</i>	53.87 (3.529)	45.74 (3.284)	25
Tetraclis			
<i>T. clusiaefolia</i>	38.18 (1.813)	31.07 (2.014)	25
<i>T. baronii</i>	40.15 (2.530)	31.91 (1.573)	50

Table 6. Analysis of variance of genera and polar diameter (μm) and equatorial diameter (μm) and p/e ratio (μm) within the Ebenaceae. For each of the variables genera are different in one-way anova ($P < 0.0001$). Superscripts a, b, c and d indicate significant differences between genera in Bonferroni pairwise comparisons ($\alpha = .0083$ used to protect intended type I error of 0.01). R-square is the proportion of the total sum of squares of each pollen variable that is accounted for by genera.

GENUS	POLAR (μm)			EQUATORIAL (μm)			P/E RATIO (μm)		
	Mean (SD)	F P (df)	R-square	Mean (SD)	F P (df)	R-square	Mean (SD)	F P (df)	R-square
Euclea ^a	6.55 (2.092) ^{b,c,d}	933.514 .0001 (3, 4137)	.40	23.20 (2.052) ^{b,c,d}	776.614 .0001 (3, 4137)	.36	1.15 (.107)	25.805 .0001 (3, 4137)	.018
Diospyros ^b	38.67 (7.257) ^{a,d}			33.19 (6.718) ^{a,d}			1.17 (.126)		
Tetraclis ^c	39.49 (2.487) ^a			31.63 (1.764) ^{a,d}			1.25 (.078)		
Royena ^d	39.58 (4.611) ^{a,b}			34.55 (3.563) ^{a,b,c}			1.15 (.108)		

Table 7. Analysis of variance of geographic distribution and polar diameter (μm) and equatorial diameter (μm) within *Diospyros*. For each of the variables geographical patterns are different in one-way anova ($P < 0.0001$). R-square is the proportion of the total sum of squares of each pollen variable that is accounted for by geographical patterns.

Geography	Polar (μm)		Equatorial (μm)			
	Mean (SD) P(df)	F	R-square	Mean (SD) P(df)	F	R-square
Bahamas	33.75 (2.396)	132.61 .0001 (8, 2355)	.31	29.49 (2.221)	176.538 .0001 (8, 2355)	.38
Australia	35.71 (2.388)			31.34 (2.093)		
Africa	35.81 (5.197)			30.75 (5.465)		
Sri Lanka & India	36.70 (8.115)			30.53 (6.351)		
Philippines	37.12 (4.780)			31.43 (4.382)		
Central America	38.67 (4.075)			31.15 (2.808)		
China	38.70 (7.088)			32.38 (5.624)		
South America	39.80 (2.555)			35.88 (3.224)		
North America	49.34 (7.919)			44.27 (7.809)		

Table 8. Analysis of variance of genera and sculpturing patterns within the Ebenaceae. Genera are different from sculpturing patterns in one-way anova ($p > .0001$). R-square is the proportion of the total sum of squares of the sculpturing pattern that is accounted for by genera.

Genus	Sculpturing patterns		
	Mean (SD)	F	R-square
		P (df)	
Tetracallis	3.000	27.768	.02
		.0001 (3, 3856)	
Euclea	3.344		
Diospyros	3.920		
Royena	4.031		

Table 9. Analysis of variance of sculpturing patterns and polar diameter (μm) and equatorial diameter (μm) within *Diospyros*. For each of the variables sculpturing patterns are different in one-way anova ($P < 0.0001$). R-square is the proportion of the total sum of squares of each pollen variable that is accounted for by sculpturing patterns.

Sculpturing ¹ Patterns	Polar (μm)		F	R-square P(df)	Equatorial (μm)		F	R-square P(df)
	Mean (SD)				Mean (SD)			
CS-Fo	.31.61 (2.375)	47.85 .0001 (7, 2355)	.1248	30.50 (2.784)	34.12 .0001 (7, 2355)	.092		
FS-CFo	31.61 (7.573)			27.89 (7.783)				
FG	32.67 (1.387)			29.32 (1.605)				
FFo	36.48 (4.743)			30.46 (4.490)				
FAG-S	37.47 (5.110)			31.36 (3.830)				
FAG-Fo	35.33 (3.694)			32.41 (3.826)				
FS	40.10 (5.941)			34.65 (5.391)				
FS-Fo	40.49 (9.474)			34.66 (9.229)				

¹ Tectum surface pattern in mesocolpium: FG = finely granular, FAG = finely anastomosed granular, FAG-S = finely anastomosed granular-striate, FAG-Fo = finely anastomosed granular-fossulate, FS = finely striate, FS-Fo = finely striate-fossulate, FFo = finely fossulate, FS-CFo = finely striate-coarse fossulate, CS-Fo = coarse striate-finely fossulate.

Table 10. Analysis of variance of geographic distribution and sculpturing patterns within *Diospyros*. Geographical patterns are different from sculpturing patterns in one-way anova ($P < 0.0001$). R-square is the proportion of the total sum of squares of the sculpturing patterns that is accounted for by geographical patterns.

Geography	Sculpturing patterns		F P (df)	R-square
	Mean	(SD)		
Australia	3.000	(0)	34.64 .0001 (8, 2355)	.105
China	3.302	(0.768)		
North America	3.457	(0.891)		
Central America	3.490	(0.505)		
Africa	3.763	(1.983)		
Bahama	4.000	(0)		
South America	4.125	(2.429)		
Sri Lanka	4.351	(1.815)		
India				
Philippines	5.207	(1.790)		

Table 11. Previously published examinations of Ebenaceae pollen morphology.

Author	Taxa	Polar (μm)	Equatorial ¹ (μm)	Sculpturing pattern	ora ²	Exine (μm)	Method ³
Mohl 1835	<i>Diospyros ebenum</i>						LM
	<i>Diospyros discolor</i>						LM
	<i>Diospyros virginiana</i>						LM
	<i>Embryopteris lanceolata</i>						LM
Selling 1947	<i>Diospyros hillebrandii</i>	no pollen					
	<i>Diospyros terrea</i>	28.00	26.00	smooth-minutely granular	LA	1.25	LM
Erdman 1971	<i>Diospyros bipindensis</i>	36.00	27.00	psilate-subreticulate			LM
	<i>Diospyros brideliaefolia</i>	45.00	34.00				LM
	<i>Diospyros terrea</i>	28.00	26.00		LA		LM
	<i>Diospyros virginiana</i>	59.00	46.00				LM
	<i>Euclea tomentosa</i>	29.00	23.00				LM
	<i>Maba warneckei</i>	33.00	24.50	scattered small pits			LM
Ikuse 1956	<i>Royena glabra</i>	36.00	27.00	psilate			LM
	<i>Diospyros kaki</i>			fine reticulate			LM

Guinet 1962	<i>Diospyros chloroxylon</i>	32.50	28.50	foveolate	LA, LO	1.00	LM
Straka et al. 1967	<i>Euclea mayottensis</i>	23.00	20.50		LA	1.50	LM
	<i>Tetracis ebenifera</i>	35.50	32.00	fossulate	LA	2.50	LM
	<i>Diospyros boivinii</i>	38.00	30.00		LA	2.00	LM
	<i>Diospyros pervillei</i>	35.00	28.00		LA	2.00	LM
Huang 1968	<i>Diospyros sakalavarum</i>	39.00	30.50	fossulate	LA	2.00	LM
	<i>Diospyros eriantha</i>	32.00	27.50	psilate-scabrate	LA	1.00	LM
	<i>Diospyros ferrea</i>	23.50	22.50	psilate-scabrate	LA	1.00	LM
	<i>Diospyros martinia</i>	38.00	41.50	psilate-scabrate	LA	1.00	LM
Salgado-Labouriau et al. 1969	<i>Diospyros morisiana</i>	44.00	40.00	psilate-scabrate	LA	1.00	LM
	<i>Diospyros oldhamii</i>	42.00	34.50	psilate-scabrate	LA	1.00	LM
	<i>Diospyros hispida</i>	45.75	32.95	smooth	LA-M	2.30	LM
	<i>Diospyros inconstans</i>	36.40	27.70	smooth	LA-M	2.20	LM
Bonnefille 1971	<i>Euclea kellaui</i>	28.00	21.00	fossulate	LA	1.50	LM
Huang 1972	<i>Diospyros eriantha</i>	32.00	27.50	psilate or scabrate	LA	1.00	LM
	<i>Diospyros ferrea</i>	23.50	22.50	psilate or scabrate	LA	1.00	LM
	<i>Diospyros martinia</i>	38.00	41.50	psilate or scabrate	LA	1.00	LM

	<i>Diospyros morrisiana</i>	44.00	40.00	psilate or scabrate	LA	1.00	LM
	<i>Diospyros oldhamii</i>	42.00	34.00	psilate or scabrate	LA	1.00	LM
Salgado-Labouriau 1973	<i>Diospyros hispida</i>	43.90	32.60	obscure	LA	2.30	LM
	<i>Diospyros inconstans</i>	36.30	28.20	obscure	LA	2.30	LM
Sowunmi 1973	<i>Diospyros crassiflora</i>	52.25	49.65	areolate	LA	1.20	LM
Adams and Morton 1976	<i>Diospyros virginiana</i>			psilate to scabrate			SEM
Sharma and Gupta 1979	<i>Diospyros bourdillonii</i>	37.20	32.30	obscure	LA	1.50	LM
	<i>Diospyros brandisiana</i>	46.00	32.50	obscure	LA	2.00	LM
	<i>Diospyros candolleana</i>	36.30	30.00	obscure	LA	1.50	LM
	<i>Diospyros chloroxylon</i>	32.50	25.00	granulate	LA	2.00	LM
	<i>Diospyros cordifolia</i>	40.50	28.50	obscure	LA	1.50	LM
	<i>Diospyros crumanata</i>	45.00	37.50	obscure	C	2.00	LM
	<i>Diospyros densiflora</i>	35.20	23.00	obscure	E	2.00	LM
	<i>Diospyros ebenum</i>	32.00	24.00	obscure	LA	2.00	LM
	<i>Diospyros ehretoides</i>	40.00	33.50	obscure	LA	2.00	LM
	<i>Diospyros excelsa</i>	43.10	35.80	obscure	LA	1.50	LM
	<i>Diospyros fasciculosa</i>	35.50	27.00	obscure	LA	2.00	LM
	<i>Diospyros foliolosa</i>	40.00	35.00	obscure	LA	2.00	LM

Ybert 1979	<i>Diospyros glandulosa</i>	40.00	30.20	obscure	LA	2.50	LM
	<i>Diospyros lotus</i>			obscure-granular	I	2.00	LM
	<i>Diospyros marmorata</i>	34.70	26.20	obscure	LA	2.00	LM
	<i>Diospyros melanoxylon</i>	43.70	34.90	obscure	LA	2.00	LM
	<i>Diospyros montana</i>	38.30	31.50	obscure	LA	2.00	LM
	<i>Diospyros nigrescens</i>	35.00	34.00	obscure	LA		LM
	<i>Diospyros nigricans</i>	31.50	27.50	psilate	LA	1.50	LM
	<i>Diospyros nilagrica</i>	35.00	28.00	psilate	LA	2.00	LM
	<i>Diospyros pyrhnocarpa</i>	45.00	38.70	obscure-psilate	LA	2.50	LM
	<i>Diospyros sylvatica</i>	30.50	28.50	obscure-psilate	LA	2.00	LM
	<i>Diospyros wallichii</i>	46.20	37.20	obscure-granular	LA	2.00	LM
	<i>Euclea undulata</i>	22.50	20.50	psilate	LA	2.00	LM
Bonneille and Riollot 1980	<i>Diospyros canaliculate</i>	40.00	30.00				LM
	<i>Diospyros gabunensis</i>	42.00	35.00				LM
	<i>Diospyros mespiliformis</i>	42.50	30.00				LM
	<i>Diospyros physocalycina</i>	37.00	32.00				LM
	<i>Diospyros soubreana</i>	37.00	30.00				LM
	<i>Diospyros scabra</i>	35.00	25.00	obscure	LA	1.50	SEM-LM

Lieux 1982	<i>Diospyros virginiana</i>	62.00	43.00	nanno-verrucae/nanno-gemmae	LA-DB	2.00	SEM-LM
Ayala-Nieto and Ludlow-Wiechers 1983 ⁴	<i>Diospyros verae-crucis</i>	32.60	40.50	scabrate-microperforations	M	2.40	SEM-LM
	<i>Diospyros digyna</i>	42.50	44.50	scabrate-microperforations	NM	1.50	SEM-LM
	<i>Diospyros campechiana</i>	36.00	41.60	psilate	NM	1.50	SEM-LM
	<i>Diospyros oaxacana</i>	35.30	35.40	psilate	NM	1.50	SEM-LM
Cerceau-Larival et al. 1984	<i>Diospyros sakalavarum</i>			microgranulose-microperforate			SEM-LM
	<i>Euclea mayottensis</i>			microgranulose-microperforate			SEM-LM
	<i>Tetraclis ebenifera</i>			microgranulose-microperforate			SEM-LM
Nair and Kothari 1985	<i>Diospyros cordata</i>	34.00	25.00	faintly reticulate	LA-M	2.50	LM
	<i>Diospyros cordifolia</i>	31.00	25.00		LA-DB		LM
	<i>Diospyros ebenum</i>	31.00	22.00	smooth	LA-DB		SEM-LM
	<i>Diospyros exsculpta</i>	31.00	25.50	psilate	C		LM
	<i>Diospyros melanoxylon</i>	36.50	26.00	faintly reticulate		1.00	LM
	<i>Diospyros microphylla</i>	34.00	26.00	psilate	LA		LM
	<i>Diospyros montana</i>	33.00	25.00	psilate			LM
	<i>Diospyros oocarpa</i>	32.00	24.00	psilate	LD		LM
	<i>Diospyros peregrina</i>	39.00	33.00	psilate	LA		LM
	<i>Diospyros sylvatica</i>	37.00	29.00	psilate	LA-DB		LM
	<i>Diospyros tupru</i>	45.00	33.00	faintly toveolate	LA		LM

Gupta and Sharma 1986	Diospyros montana	40.50	28.50	almost obscure	1	1.50 LM
	Diospyros lotus	37.00	22.50	obscure	1	2.00 LM

¹ ranges were averaged for polar and equatorial diameters.

² LA = lalongate, LO = lolongate, C= circular, E = elongate, I= indistinct, DB = dumb bell, M = margo, NM = no margo.

³ LM = light microscopy, SEM = scanning electron microscopy.

⁴ polar and equatorial diameters appear to be transposed.

Table 12. The types (and subtypes) of pollen of the species examined in this study that were treated by White (1978, 1980, 1983, 1987, 1988); and White and Caveney (1980)¹.

Species	Type and Subtype
Euclea	
<i>E. crispa</i> (Thunb.) Gurke	A - 1
subsp. <i>crispa</i> F. White	A - 1
subsp. <i>linearis</i> (Zeyher ex Hiern) F. White	A - 1
subsp. <i>linearis</i> sens. lat.	
subsp. <i>linearis</i> sens, strict.	
subsp. <i>ovata</i> (Burch.) F. White	
<i>E. divinorum</i> Hiern	A - 1
<i>E. natalensis</i> A. DC.	A - 2
subsp. <i>acutifolia</i> F. White	
subsp. <i>angolensis</i> F. White	
subsp. <i>angustifolia</i> F. White	
subsp. <i>capensis</i> F. White	
subsp. <i>magutensus</i> F. White	
subsp. <i>natalensis</i> F. White	A - 1
subsp. <i>obovata</i> F. White	
subsp. <i>rotundifolia</i> F. White	
<i>E. racemosa</i> Murr.	A - 1
subsp. <i>bernardii</i> F. White	
subsp. <i>daphnoides</i> (Hiern) F. White	
subsp. <i>macrophylla</i> (E. Mey. ex A. DC.) F. White	
subsp. <i>racemosa</i>	
subsp. <i>schimperii</i> (A. DC.) F. White	A - 3
	A - 1
subsp. <i>sinuata</i> F. White	
subsp. <i>zuluensis</i> F. White	
<i>E. undulata</i> Thunb.	A - 1
Tetraclis (not treated)	
Diospyros	
1. Section <i>Forsteria</i> Bakh.	
<i>D. ferrea</i> (Willd.) Bakh.	
<i>D. natalensis</i> (Harv.) Brenan.	B - 10
2. Section <i>Asteropetala</i> F. White	
<i>D. longiflora</i> Letouzey & F. White	
3. Section <i>Katula</i> F. White	
<i>D. mweroensis</i> F. White	B - 6
4. Section <i>Entia</i> F. White	
<i>D. chevalieri</i> De Wild.	
5. Section <i>Dodonium</i> F. White	
<i>D. mannii</i> Hiern	
<i>D. suaveolens</i> Gurke	B - 7

6. Section *Forbesia* F. White
 - D. consolatae* Chiov.
 - D. rotundifolia* Hiern
7. Section *Brevituba* F. White
 - D. abyssinica* (Hiern) F. White B - 9
 - subsp. *abyssinica*
 - subsp. *chapmaniorum* F. White
 - subsp. *attenuata* F. White
 - subsp. *reticulata* F. White -
 - D. deltoidea* F. White
 - D. dendo* Welw. ex Hiern B - 8
 - D. gillettii* De Wild. B - 6
 - D. inhacaensis* F. White
 - D. kanurii* F. White
 - D. platanoidea* Letouzey & F. White
 - D. piscatoria* Gurke
 - D. polystemon* Gurke B - 6
 - D. quiloensis* (Hiern) F. White
 - D. scabra* (Chior.) Cufodontis
 - D. soubreana* F. White
 - D. squarrosa* Klotzsch B - 1
 - D. viridicans* Hiern
 - D. wagemansii* F. White
 - D. wajirensis* F. White
8. Section *Myrmecophila* F. White
 - D. conocarpa* Gurke & K. Schum. B - 10
9. Section *Royena* (L.) F. White
 - D. acocksii* (de Winter) de Winter
 - D. anitae* F. White
 - D. austroafricana* de Winter B-4, B-3
 - D. dichrophylla* (Gand.) de Winter B - 1
 - D. fischeri* Gurke B - 3
 - D. galpinii* (Hiern) de Winter
 - D. glabra* (L.) de Winter B - 6
 - D. glandulifera* de Winter
 - D. heterotricha* (B.L. Burt) F. White
 - D. lycioides* Desf. B - 6
 - subsp. *guerkei* (Kuntze) de Winter B - 4
 - subsp. *lycioides* de Winter
 - subsp. *sericea* (Bernh.) DeWinter B - 3
 - D. pallens* (Thunb.) F. White B - 1
 - D. ramulosa* (E. Mey ex A. DC.) de Winter
 - D. simii* (Kuntze) de Winter
 - D. scabrida* (Harv. ex Hiern) de Winter B-4, B-5
 - D. truncatifolia* Caveny
 - D. usambarensis* F. White B - 3
 - subsp. *rufescens* A. N. Caveny
 - D. villosa* (L.) de Winter B - 3
 - D. whyteana* F. White B - 5

- D. zombensis* (B.L. Burtt) F. White
10. Section *Lagenaria* F. White
- D. crassiflora* Hiern
11. Section *Erikesi* F. White
- D. monbuttensis* Gurke
- D. senensis* Klotzsch
12. Section *Latibulum* F. White
- D. bipindensis* Gurke A-4
- D. canaliculata* De Wild.
- D. physocalycina* Gurke
- D. preussii* Gurke B-3
- D. shimbaensis* F. White
13. Section *Tabonaca* F. White
- D. amaniensis* Gurke
- D. batocana* Hiern
- D. boala* De Wild.
- D. chamaethamnus* Dinter ex Mildbr.
- D. fragrans* Gurke
- D. gabunensis* Gurke B-
- D. greenwayi* F. White
- D. grex* F. White
- D. kamerunensis* Gurke B-3
- D. pseudomespilus* Mildbr.
- subsp. *brevicalyx* F. White
- subsp. *undabunda* (Hiern ex Greves) F. White
- D. sanza-minika* A. Chev.
14. Section *Noltia* (Schumacher) Hiern
- D. barteri* Hiern
- D. chrysocarpa* F. White
- D. cinnabarina* (Gurke) F. White
- D. mafiensis* F. White
- D. simulans* F. White
- D. soyauxii* Gurke & Schum.
- D. tricolor* (Schumacher) Hiern
- D. vignei* F. White
15. Section *Rhaphidanth* (Hiern ex Gurke) F. White
- D. obliquifolia* (Hiern ex Gurke) F. White
16. Section *Calvitiella* F. White
- D. alboflavescens* (Gurke) F. White
- D. cooperi* (Hutch. & Dalz.) F. White
- D. elliotii* (Hiern) F. White
- D. feliciana* Letouzey & F. White
- D. hoyleana* F. White A-5
- subsp. *hoyleana* F. White
- subsp. *angustifolia* F. White
- D. iturensis* (Gurke) Letouzey & F. White
- D. magogoana* F. White
- D. melocarpa* F. White
- D. occulta* F. White

<i>D. troupinii</i> F. White	
<i>D. vermoesenii</i> De Wild.	B - 10
<i>D. zenkeri</i> (Gurke) F. White	
17. Section <i>Brevistyla</i> F. White	
<i>D. capricornuta</i> F. White	
<i>D. cornii</i> Chiov.	
<i>D. gracilescens</i> Gurke	
<i>D. heudelotii</i> Hiern	
<i>D. kabuyeana</i> F. White	
<i>D. kirkii</i> Hiern	B - 10
<i>D. liberiensis</i> Hutch. & Dalz.	
<i>D. mespiliformis</i> Hochst. ex A. DC.	B - 7
<i>D. thomasi</i> Hutch. & Dalz	
<i>D. verrucosa</i> Hiern	B - 10
18. Section <i>Marsupium</i> F. White	
<i>D. virgata</i> (Gurke) Brenan	B - 7

Except where indicated, samples are from Africa. Genera and species not treated by White included:

Euclea acutifolia E. Mey. ex A. DC.; *E. polyandra* E. Mey.; *E. pseudebenus* E. Mey. ex A. DC.; *Royena cordata* E. Mey.; *R. hirsuta* L.; *R. microphylla* (Burch.) F. White; *Diospyros anitae* F. White; *D. armata* Hemsl., China; *D. artanthifolia* Mart., S. America; *D. brideliaefolia* Elmer., Philippines; *D. bullata* A. C. Sm., S. America; *D. campechiana* Lundell, Mexico; *D. candolleana* Wight, India; *D. crassinervis* (Krug & Urb.) Standl., Bahama Islands; *D. crumenata* Thwaites, India; *D. curanii* Merr., Philippines; *D. decandra* Lour., China; *D. dichroa* Sandwith, Brazil; *D. discolor* Willd., Puerto Rico and Philippines; *D. diversilimba* Merr. & Chun, China; *D. ehretioides* Wall., China; *D. filipendula* Pierre ex Lecomte, China; *D. fischeri* Gurke; *D. glandulosa* Lace, India; *D. hispida* A. DC., S. America; *D. ierensis* Britton, S. America; *D. kaki* L., China; *D. longibracteata* Lecomte, China; *D. lotus* L., China; *D. malabarica* (Desr.) Kostel., Sri Lanka; *D. maritima* Blume, Indonesia and Philippines; *D. mollis* Wall., India; *D. montana* Roxb., India; *D. morrisiana* Hance, China; *D. multiflora* Blanco, Philippines; *D. nicaraguensis* (Standl.) Standl., Mexico; *D. nummularia* Brenan; *D. ovalifolia* Wight, Sri Lanka; *D. pendula* Hasselt. ex Hassk., Borneo; *D. pentamera* Woods & F. Muell. ex F. Muell., Australia; *D. philippinensis* A. DC., US; *D. pilosanthera* Blanco, Philippines and Borneo; *D. pterocalyx* Bojer (ex. A. DC.), Mauritius, Madagascar; *D. revoluta* Poir., West Indies; *D. samoensis* A. Gray, Fiji and Samoa; *D. scabrida* (Harv. ex Hiern) De Winter; *D. senensis* Klotzsch; *D. simulans* F. White; *D. sylvatica* Roxb., India; *D. texana* Scheele, US; *D. verae-crucis* (Standl.) Standl., Mexico; *D. virginiana* L., US; *Tetracelis baronii* H(US) Perrier, Madagascar; *T. cluciaefolia* Hiern, Madagascar.

1. Additional taxa treated in an other publication by White (1992) are not assigned to sections and, thus, are unusable in this comparison.

Table 13. The types (and subtypes) of pollen of the species examined in this study that were treated by Bakhuizen (1936-38).

Species	Type and Subtype
Euclea	
Royena	
Tetracelis	
Diospyros	
A. Subgenus Maba	
1. Section Forsteria Bakh.	
D. ferrea (Willd.) Bakh.	
D. ellipticifolia (Stokes) Bakh.	
2. Section Miquelia Bakh.	
D. tahanensis Bakh.	
D. Janowskyi Bakh.	
D. rostrata (Merr.) Bakh.	
D. carpinifolia (Ridl.) Bakh.	
D. malayana Bakh.	
3. Section Hasseltia Bakh.	
D. fasciculosa F. v. Muell.	
D. Holttumii Bakh.	
D. confertiflora (Hiern) Bakh.	
D. hermaphroditica (Zoll.) Bakh.	
B. Subgenus Hierniodendron Bakh.	
D. puncticulosa Bakh.	
D. evena Bakh.	
D. Maingayi (Hiern) Bakh.	
C. Subgenus Cargillia (R. Br.) Bakh.	
D. Subgenus Eudiospyros (L.) Bakh.	
1. Section Brachycylis Bakh.	
D. buxifolia (Bl.) Hiern	
D. subrhomboidea King et Gamble	
D. elegantissima Bakh.	
D. Clementium Bakh.	
D. Jaherii Bakh.	
D. plectosepala Hiern	
D. confusa Bakh.	
D. Baloen-idjoek Bakh.	
D. Paraoesi Bakh.	
D. kajangensis Bakh.	
D. singaporensis Bakh.	
D. poiensis Bakh.	
D. philippinensis A. DC.	B 7
D. Havilandi Bakh.	
D. glaucophylla Bakh.	
D. Scortechinii King et Gamble	
D. minutiflora Bakh.	

B 7

- D. oligantha Merr.
- D. setosa Bakh.
- D. graciliflora Hiern
- D. densa Bakh.
- D. nana Bakh.
- D. ellipsoidea King et Gamble
- D. penangiana King et Gamble
- D. penibukanensis Bakh.
- D. brevicalyx Boerl. et Kds. ex Kds. -
- D. sororia Bakh.
- D. Kingii Bakh.
- D. Gambleana Bakh.
- D. Hierniana (King et Gamble) Bakh.
- D. simaloerensis Bakh.
- D. malaccensis Bakh.
- D. bangkana Bakh.
- 2. Section Cavanilleastrum Bakh.
 - D. Poncei Merr.
 - D. durionoides Bakh.
 - D. Hackenbergii Diels
- 3. Section Stelechantha Bakh.
 - D. cauliflora Bl. B 3
- 4. Section Podophora Bakh.
 - D. daemona Bakh.
 - D. insidiosa Bakh.
 - D. Diepenhorstii Miq.
- 5. Section Ebenaster Bakh.
 - D. discolor Willd. B -
 - D. amboinensis Bakh.
 - D. Peekelii Lauterb.
 - D. Lolin Bakh.
 - D. celebica Bakh.
 - D. sogeriensis Bakh.
 - D. Rumphii Bakh.
 - D. argentea Griff.
- 6. Section Basithrix Bakh.
 - D. Forbesii Bakh.
 - D. ferox Bakh.
 - D. nutans King et Gamble
 - D. muricata Bakh.
 - D. pahangensis Bakh.
 - D. cordata Hiern
 - D. Everetti Merr.
 - D. euphlebia Merr.
 - D. selangorensis Bakh.
 - D. micromera Bakh.
 - D. apiculata Hiern
 - D. pulchra Bakh.
- 7. Section Kurzella Bakh.
 - D. Kurzii Hiern
 - D. Wrayi King et Gamble

- D. pubicarpa Ridl.
- D. nitida Merr.
- D. pubicalix Bakh.
- 8. Section *Phyllosepala* Bakh.
 - D. latisepala Ridl.
 - D. neurosepala Bakh.
- 9. Section *Eriantha* Bakh.
 - D. eriantha Champ. ex Benth.
 - D. sumatrana Miq.
 - D. vestita Bakh.
 - D. Hendersoni Ridl.
 - D. tuberculata Bakh.
- 10. Section *Confertiflora* Bakh.
 - D. frutescens Bl.
 - D. Curranii Merr. B 3
 - D. curraniopsis Bakh.
- 11. Section *Acanthebenus* Bakh.
 - D. montana Roxb. B 5
- 12. Section *Lotus* Bakh.
 - D. Kaki Linn. F. B 3, C 2
- 13. Section *Ebenus* Bakh.
 - D. Ebenum Koen.
 - D. hebecarpa Cunn. ex Benth.
 - D. samoensis A. Gray B 10
 - D. novoguineensis Bakh.
 - D. insularis Bakh.
- 14. Section *Ebenopsis* Bakh.
 - D. truncata Zoll. et Mor.
 - D. eucalyptifolia Bakh.
 - D. elliptifolia Merr.
 - D. aurea Teysm. et Binn.
 - D. Minahasae Bakh.
 - D. Beccarii Hiern
- 15. Section *Ptychocylix* Bakh.
 - D. polyalthioides Korth. ex Hiern
 - D. pilosanthera Blanco B 7
 - D. Elmeri Merr.
 - D. oblonga Wall. ex G. Don
 - D. cubica Bakh.
- 16. Section *Didymanthera* Bakh.
 - D. Hasseltii Zoll.
 - D. dictyoneura Hiern
 - D. piscicapa Ridl.
 - D. Siamang Bakh.
 - D. Wallichii King et Gamble ex King
- 17. Section *Nesindica* Bakh.
 - D. maritima Bl. B 7
 - D. multiflora Blanco B 7
 - D. lanceifolia Roxb.
 - D. undulata Wall. ex G. Don
 - D. javanica Bakh.

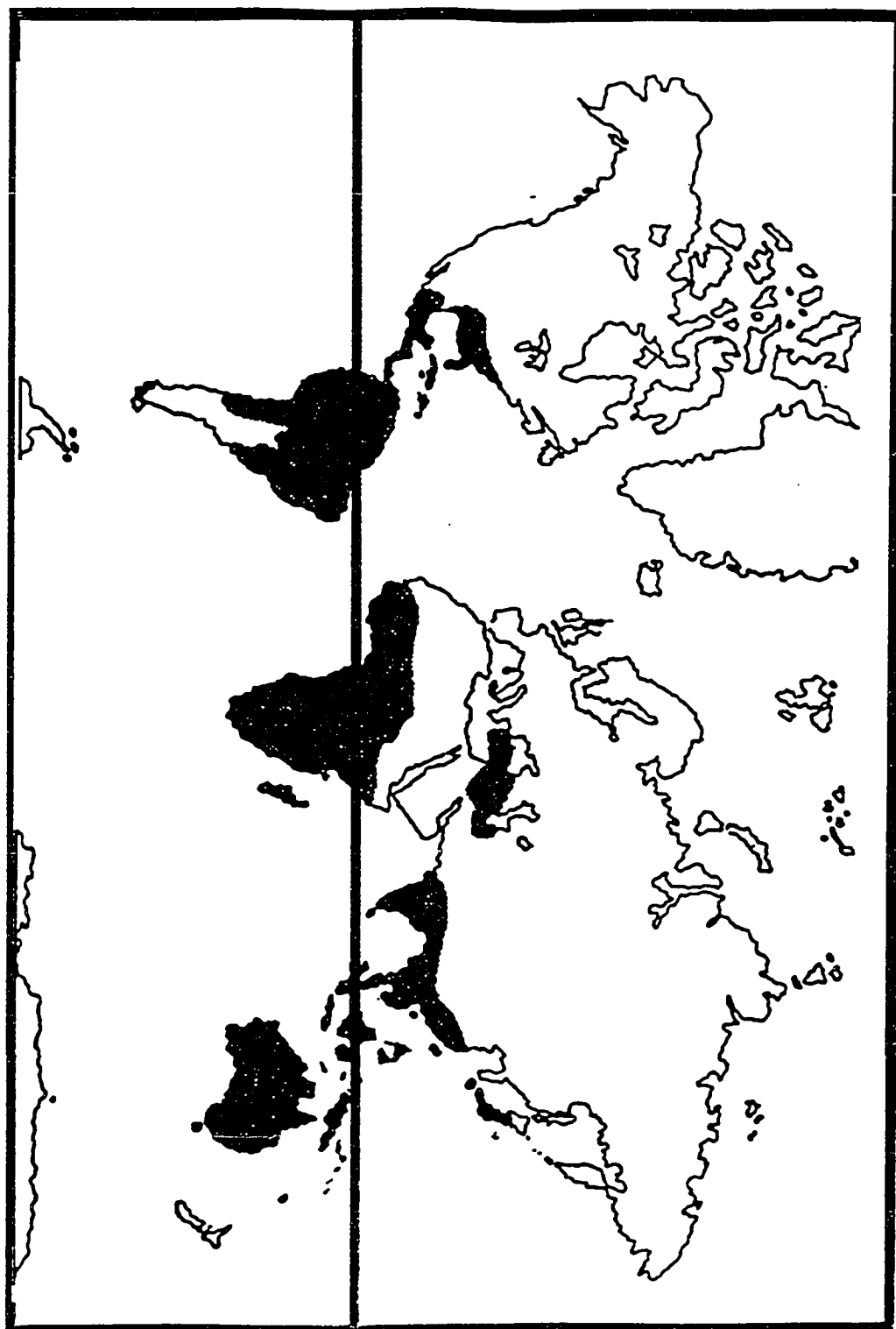
- D. venenosa Bakh.
- D. Greshoffiana Kds. ex Bakh.
- D. styraciformis King et Gamble
- D. sarawakana Bakh.
- D. clavipes Bakh.
- D. crassipes Bakh.
- 18. Section Liophylla Bakh.
 - D. Yeobi Bakh.
 - D. rufa King et Gamble
 - D. Foxworthyi Bakh.
 - D. levigata Bakh.
- 19. Section Eucarpon Bakh.
 - D. pendula Hasselt ex Hassk. B 10
 - D. adenophora Bakh.
 - D. Toposia Ham.
 - D. toposioides King et Gamble
 - D. pauciflora King et Gamble
 - D. palembanica Bakh.
 - D. nemorosa Bakh.
- 20. Section Cladantha Bakh.
 - D. pyrrhocarpa Miq.
 - D. papuana Val.
- 21. Section Truncicalix Bakh.
 - D. subtruncata Scheff. ex Hochr.
 - D. Ulo Merr.
 - D. borneensis Hiern
 - D. discocalyx Merr.
- 22. Section Sapotanigra Bakh.
 - D. nigra (J.F. Gmel.) Perrott.
- 23. Section Reflexocalix Bakh.
 - D. tritis King et Gamble
 - D. dajakensis Bakh.
- 24. Section Trisantha Bakh.
 - D. bantamensis Kds. et Val. ex Bakh.
 - D. Malam Bakh.
- 25. Section Glutinosa Bakh.
 - D. malabarica (Desr.) Kostel B 3
 - D. pseudo-malabarica Bakh.
 - D. koeboeensis Bakh.
 - D. britanno-borneensis Bakh.
 - D. eburnea Bakh.
 - D. siamensis Hochr.
- 26. Section Asterocalix Bakh.
 - D. Hallieri Bakh.
- 27. Section Verruculosa Bakh.
 - D. perfida Bakh.
 - D. bibracteata Bakh.
- 28. Section Pachycylix Bakh.
 - D. macrophylla Bl.
- 29. Section Saccocalix Bakh.
 - D. coriacea Hiern

- D. campanulata* Bakh.
- D. mindanaensis* Merr.
- D. soporifera* Bakh.
- 30. Section *Campanulata* Bakh.
 - D. lateralis* Hiern
 - D. sundaica* Bakh.
 - D. Ridleyi* Bakh.
 - D. Korthalsiana* Hiern
 - D. myrmecocalyx* (Hiern) Bakh.
 - D. transitoria* Bakh.
 - D. retrofracta* Bakh.
 - D. conformis* Bakh.
- 31. Section *Rigidophylla* Bakh.
 - D. perakensis* Bakh.
 - D. Enderti* Bakh.
 - D. areolata* King et Gamble
 - D. rigida* Hiern

Except where indicated, samples are from Africa. Genera and species not treated by Bakhuizen include:

Euclea acutifolia E. Mey. ex A. DC.; *E. crispa* (Thunb.) Gurke; *E. dekindtii* Gurke; *E. divinorum* Hiern; *E. kellau* Hochst.; *E. lanceolata* E. Mey.; *E. linearis* (Zeyh. ex Hiern) F. White; *E. mayottensis* H. Perrier, Comoro Islands, Madagascar; *E. multiflora* Hiern; *E. natalensis* A. DC.; *E. polyandra* E. Mey.; *E. pseudebenus* E. Mey. ex A. DC.; *E. racemosa* Murr; *E. schimperi* (A. DC.) Dandy; *E. undulata* Thunb.; *Royena austro-africana* De Winter; *R. cordata* E. Mey.; *R. dichrophylla* (Gand.) De Winter; *R. glabra* (L.) De Winter; *R. guerkei* (Kuntze) De Winter; *R. hirsuta* L.; *R. lycioides* Desf.; *R. microphylla* (Burch.) F. White; *R. pallens* (Thunb.) F. White; *R. sericea* (Bernh.) De Winter; *R. usambarensis* F. White; *R. villosa* (L.) De Winter; *R. whyteana* (Hiern) F. White; *Diospyros abyssinica* (Hiern) F. White; *D. armata* Hemsl., China; *D. artanthifolia* Mart., S. America; *D. bipindensis* Gurke; *D. brideliaefolia* Elmer, Philippines; *D. bullata* A. C. Sm., S. America; *D. campechiana* Lundell, Mexico; *D. candolleana* Wight, India; *D. conocarpa* Gurke et K. Schum.; *D. crassinervis* (Krug & Urb.) Standl., Bahama Islands; *D. crumenata* Thwaites, India; *D. decandra* Lour., China; *D. dendo* Welw. ex Hiern; *D. dichroa* Sandwith, S. America; *D. diversilimba* Merr. & Chun, China; *D. ehretioides* Wall., China; *D. filipendula* Pierre ex Lecomte, China; *D. fischeri* Gurke; *D. gabunensis* Gurke; *D. gillettii* De Wild.; *D. glandulosa* Lace, India; *D. hispida* A. DC., S. America; *D. hoyleana* F. White; *D. ierensis* Britton, S. America; *D. kamerunensis* Gurke; *D. kirkii* Hiern; *D. longibracteata* Lecomte, China; *D. lotus* L., China and British Columbia; *D. mespiliformis* Hochst. ex A. DC.; *D. mollis* Wall., India; *D. morrisiana* Hance, China; *D. mweroensis* F. White; *D. nicaraguensis* (Standl.) Standl., Mexico; *D. nummularia* Brenan; *D. ovalifolia* Wight, Sri Lanka; *D. pentamera* Woods & F. Muell. ex F. Muell., Australia; *D. polystemon* Gurke; *D. preussii* Gurke; *D. pterocalyx* Bojer (ex. A. DC.), Mauritius, Madagascar; *D. revoluta* Poir., West Indies; *D. scabrida* (Harv. ex Hiern) De Winter; *D. squarrosa* Klotzsch; *D. suaveolens* Gurke; *D. sylvatica* Roxb., India; *D. texana* Scheele, US; *D. verae-crucis* (Standl.) Standl., Mexico; *D. vermoesenii* De Wild; *D. verrucosa* Hiern; *D. virgata* (Gurke) Brenan; *D. virginiana* L., US; *Tetracelis baronii* H(US) Perrier, Madagascar; *T. cluciaefolia* Hiern, Madagascar.

Figure 1. Distribution of the Ebenaceae.



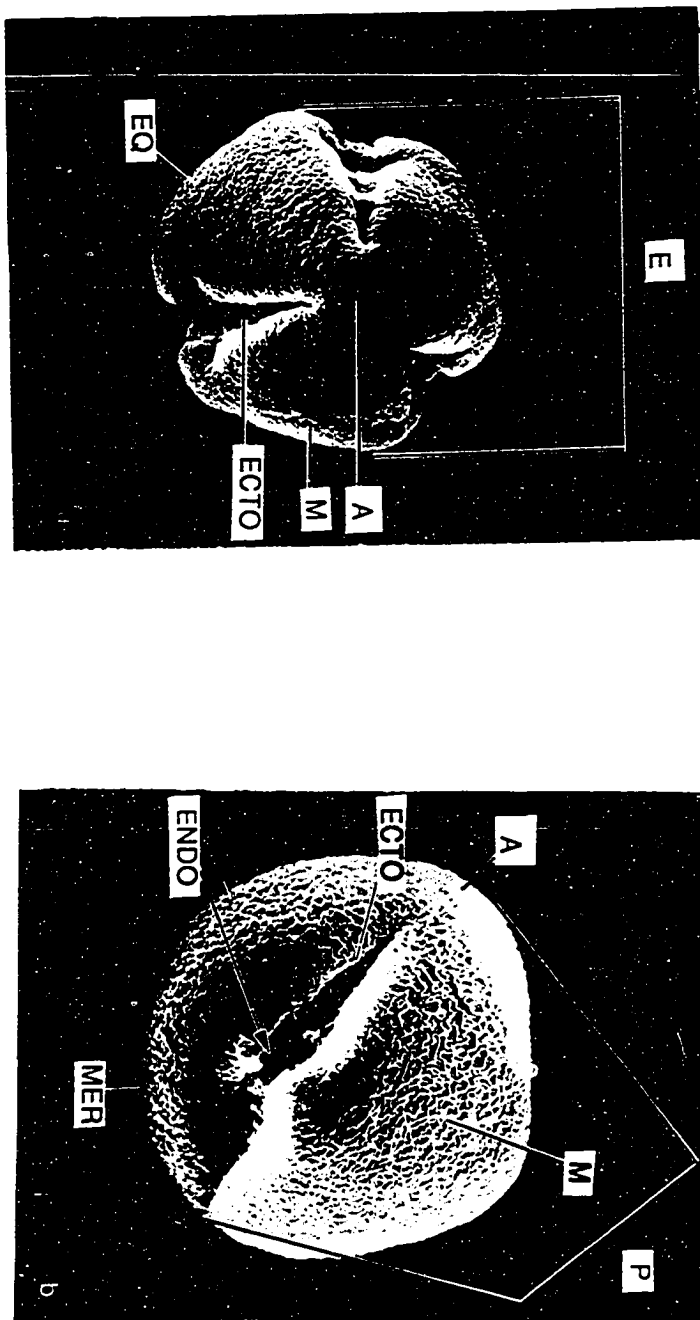


Fig 2. Colporate grain. a: polar view; b: slightly equatorial view. A = apocolpium, E = equatorial diameter, ECTO = ectopore, ENDO = endopore, EQ = equatorial outline; M = mesocolpium, MER = merocolpium, P = polar diameter.

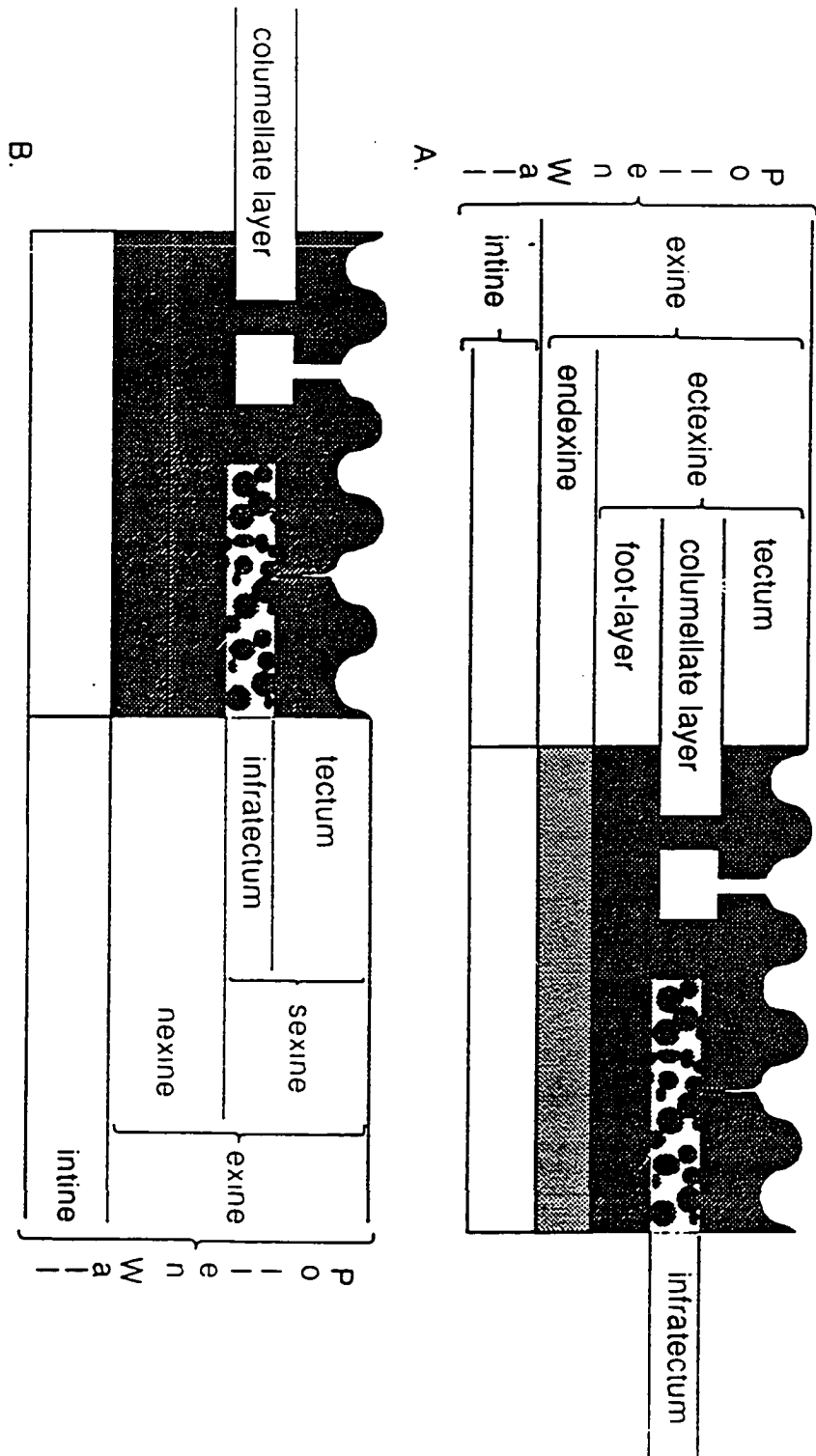


Fig. 3. Terms used to describe pollen wall stratification. A. terms used in TEM. B. terms used in LM and SEM.

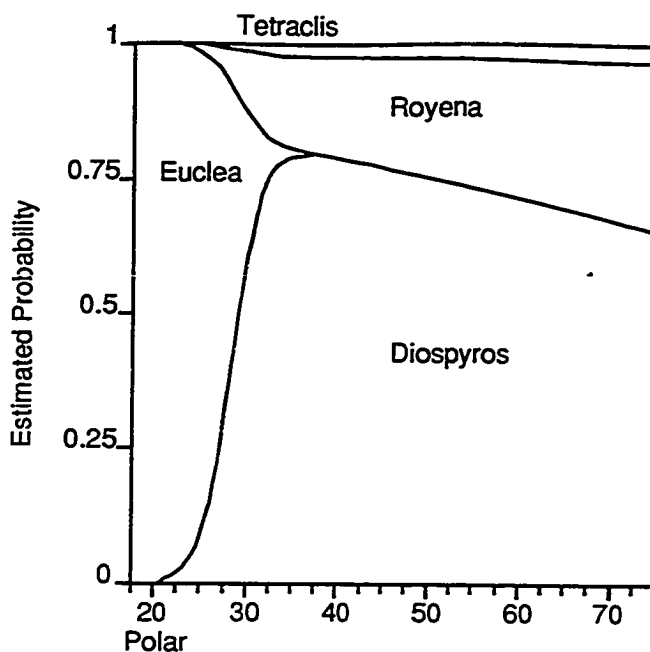


Fig 4. Logistic regression of genus membership regressed onto Polar diameter (Ebenaceae: Diospyros, Euclea, Royena and Tetraclis). ($P = .0000001$, Chi square = 2794.613 in analysis of loglikelihood; r -square = .3456, $N = 4138$ measured pollen grains). Output from JMP.

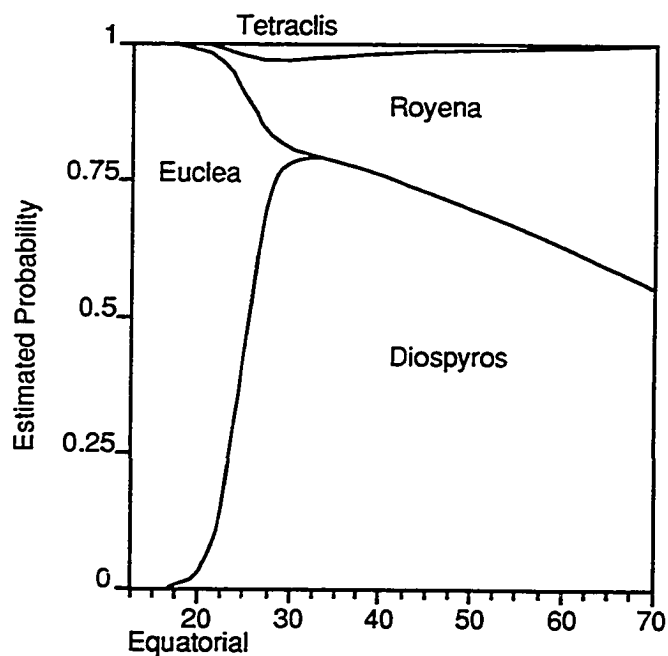


Fig 5. Logistic regression of genus membership regressed onto Equatorial diameter (Ebenaceae: Diospyros, Euclea, Royena and Tetraclis). ($P = .0000001$, Chi square = 2584.073 in analysis of loglikelihood; r -square = .3196, $N = 4138$ measured pollen grains). Output from JMP.

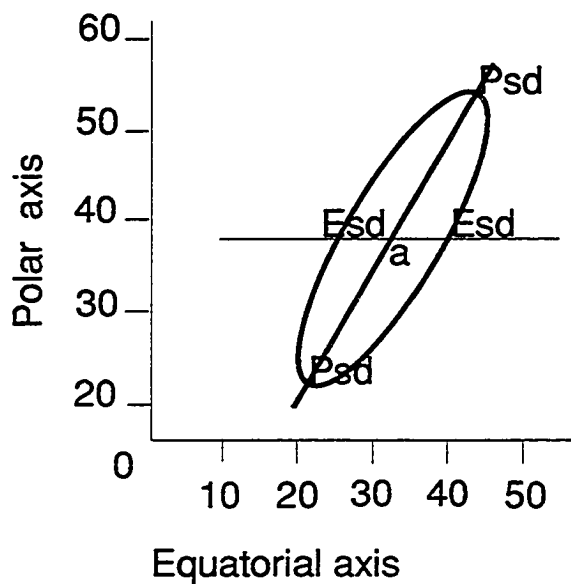


Fig. 6. 95% confidence region for the bivariate polar and equatorial mean of species X. a = polar and equatorial means, Psd = 95% confidence interval of the polar diameter. Esd = 95% confidence interval of the equatorial diameter.

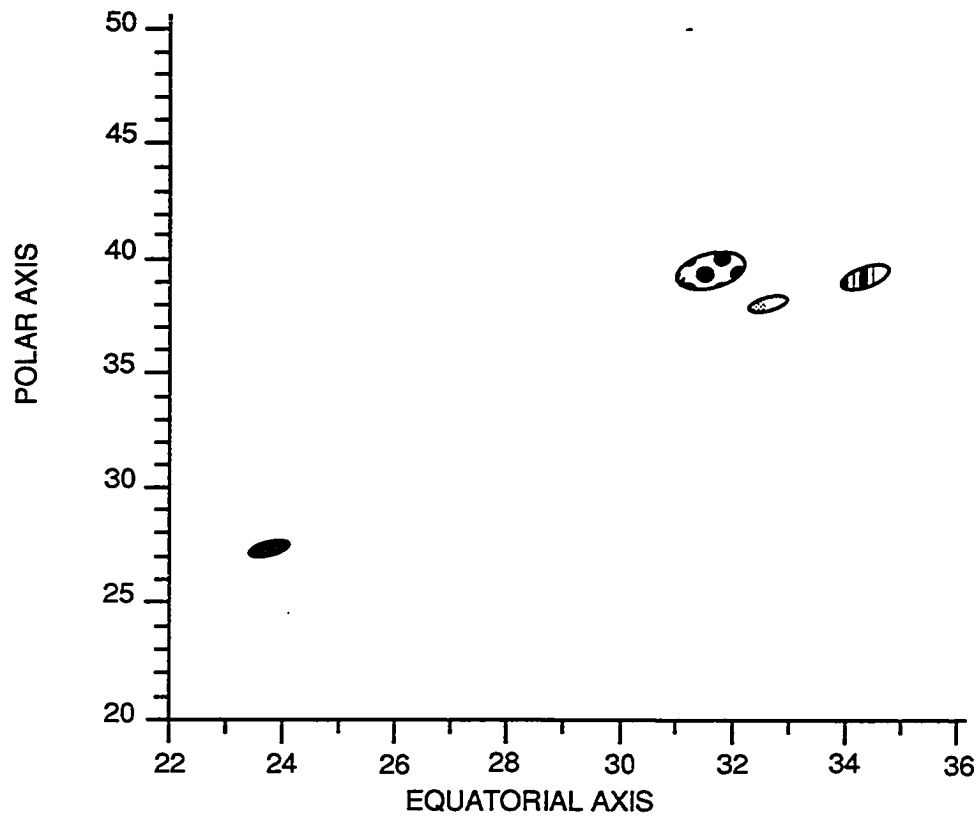


Fig. 7. The degree of interdependency between the polar diameter and equatorial diameter for each genus of the Ebenaceae displayed as 95% confidence ellipses for the bivariate means. *Diospyros* = [stippled], *Euclea* = [solid black], *Royena* = [horizontal stripes], and *Tetracis* = [vertical stripes].

Plate 1. Pollen of Ebenaceae. Subtype A-1. A-B. Euclea divinorum (Mooney 7292). A. Equatorial view (SEM). B. Equatorial view (LM). C-D. Euclea mayottensis (Lorence 2874). C. Equatorial view (LM). D. Polar view (SEM). E. Euclea multiflora (West 2924). Surface view of mesocolpus (SEM). F-G. Euclea racemosa (White 10422). F. Polar view (SEM). G. Equatorial view (SEM). H. Euclea schimperi (Burger 1750). Polar view (SEM). I. Euclea undulata (Bayliss 4124). Equatorial view (SEM). (Scale bars: A, D, F, G, H, I = 5 μm ; B, C = 20 μm ; E = 1 μm).

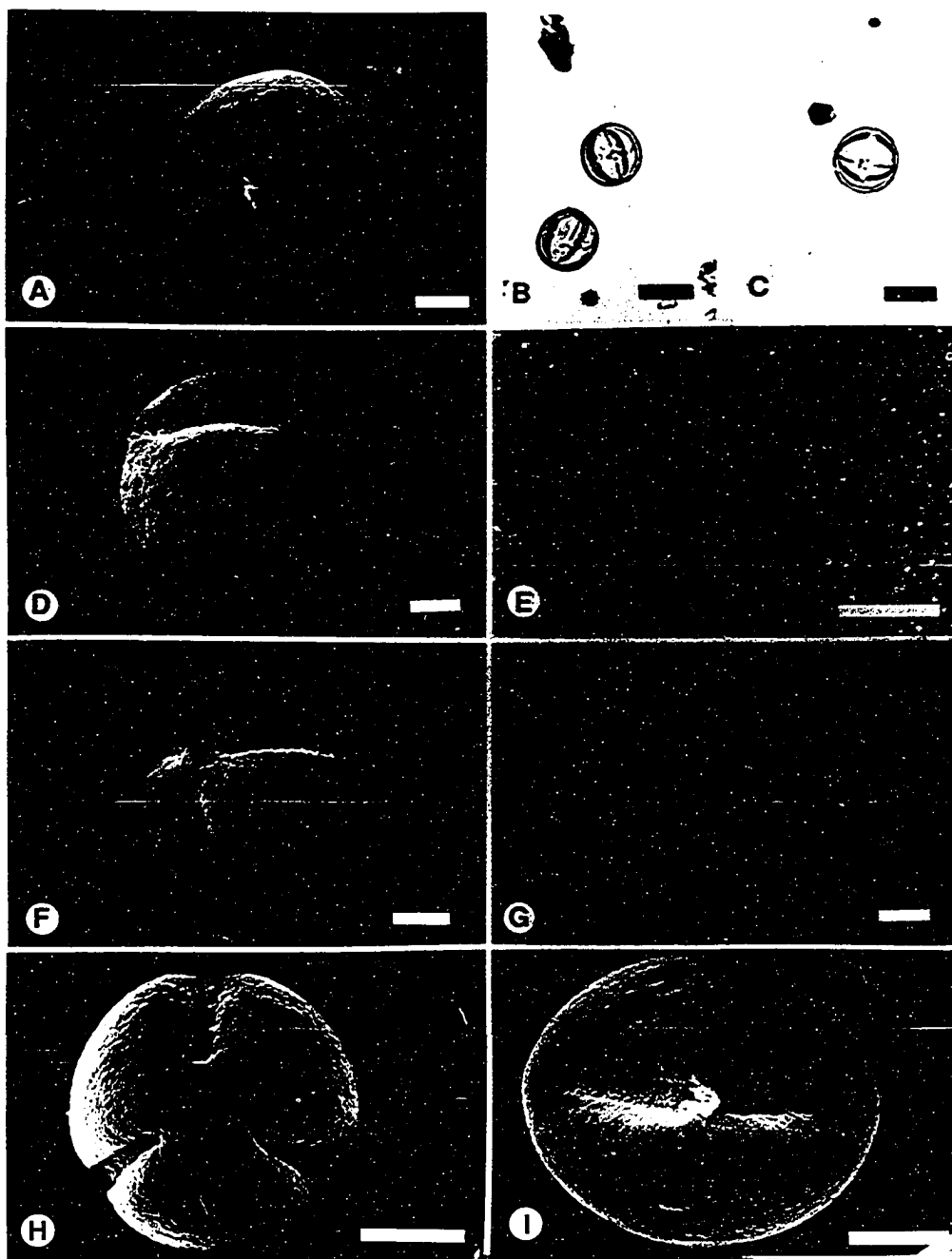


Plate 2. Pollen of Ebenaceae. Subtype A-2. A-D. Euclea natalensis (A, C, Frazier 1110; B, Bayliss 1533; D, Tanner 3025). A. Polar view (SEM). B. Equatorial view (SEM). C. Surface view of mesocolpus (SEM). D. Radial section (TEM). E. Euclea polyandra (Codd 2898). Surface view of mesocolpus (SEM). F. Euclea pseudebenus (Seydel 353). Equatorial view (SEM). (Scale bars: A, B, F = 5 μm ; C, E = 1 μm ; D = 2 μm).

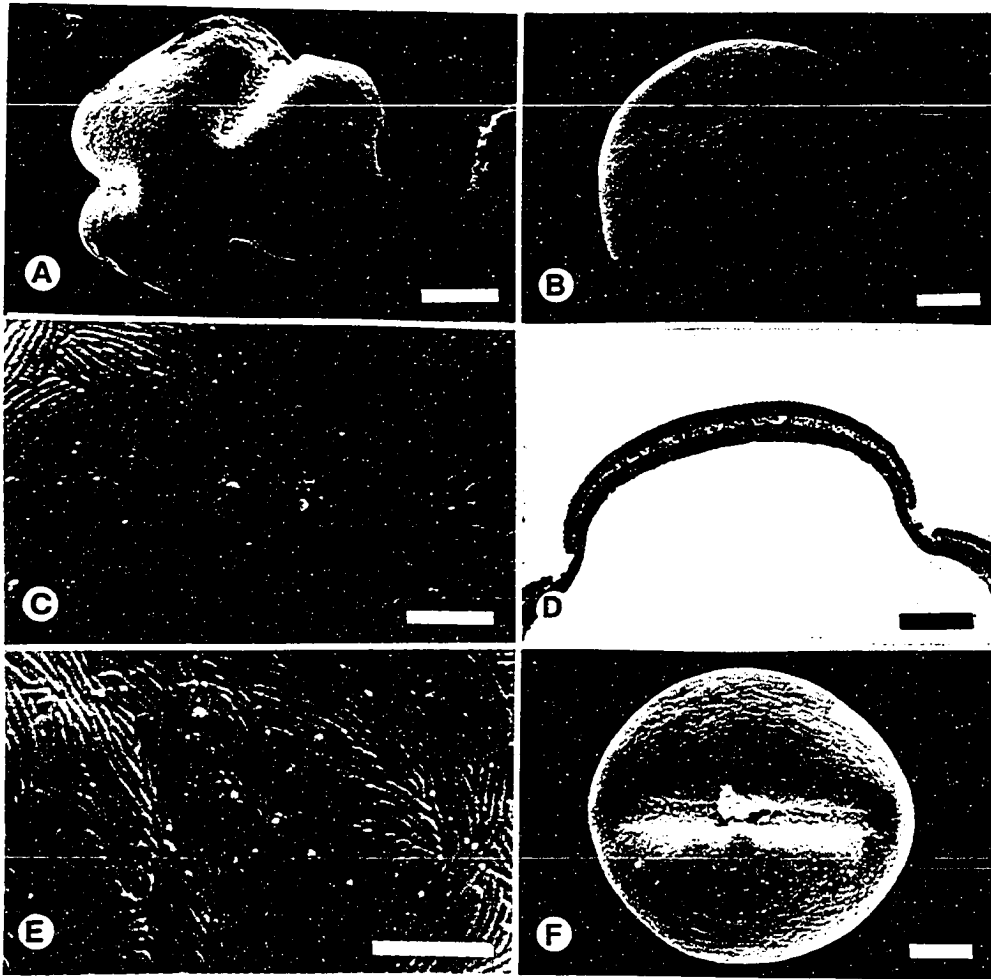


Plate 3. Pollen of Ebenaceae. Subtype A-3. A-B. Euclea acutifolia (van Jaarsveld 5725). A. Surface view of mesocolpus (SEM). B. Radial section (TEM). C-F. Euclea kellaui (C, D, Lebrun 4600; E, F, Linson 353). C. Polar view (SEM). D. Equatorial view (SEM). E. Radial section (TEM). F. Tangential section (TEM). (Scale bars: A= 1 μm ; B, F = 2 μm ; C, D = 5 μm ; E = 4 μm).

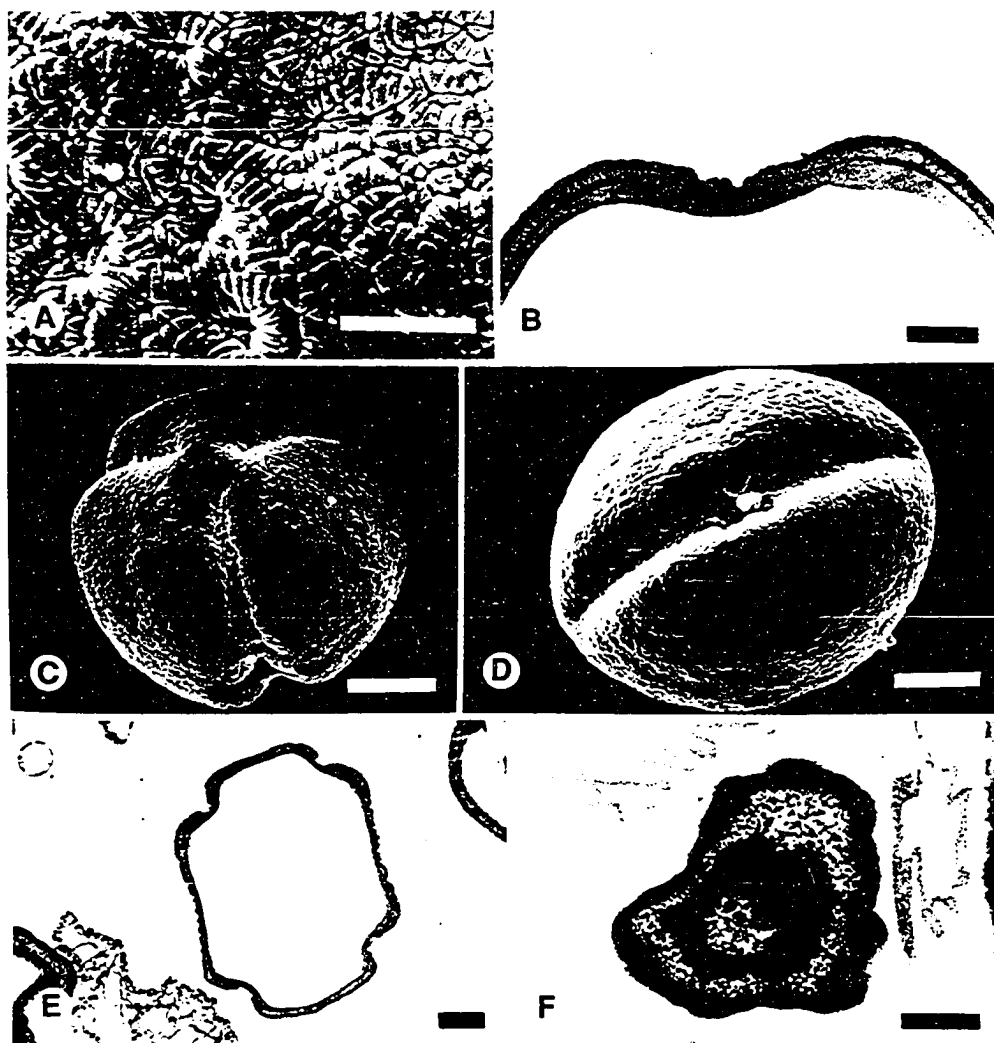


Plate 4. Pollen of Ebenaceae. Subtype A-3. A-C. Euclea kellaui (A, B, Linson 353; C, Lebrun 4600). A. Longitudinal section (TEM). B. Radial section (TEM). C. Equatorial view (LM). D-E. Euclea lanceolata (Chase 34513). D. Polar view (SEM). E. Equatorial view (SEM). (Scale bars: A, B = 2 μm ; C = 20 μm ; D, E = 5 μm).

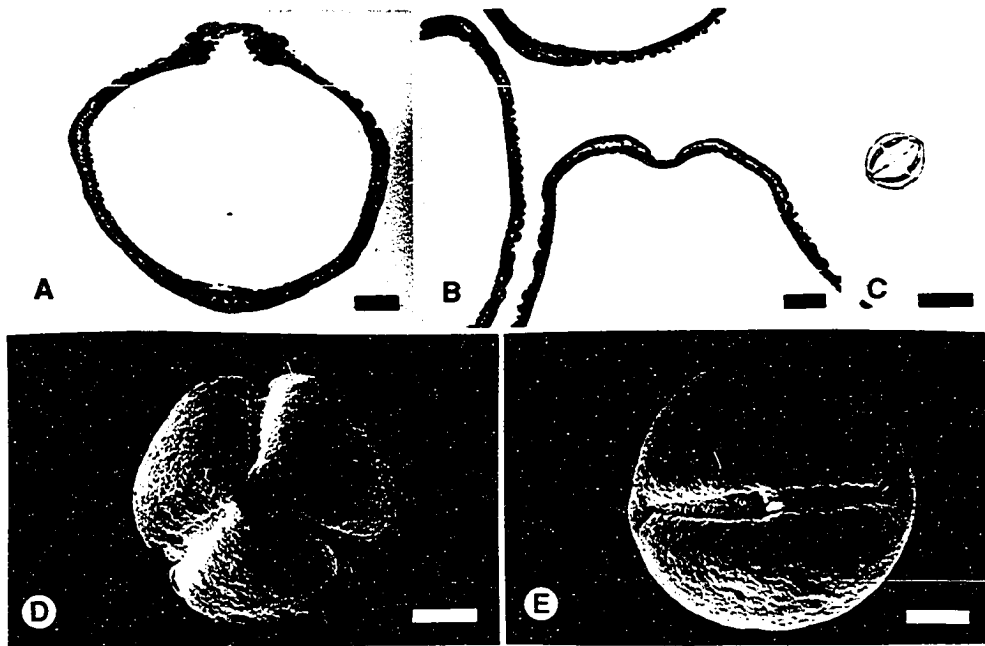


Plate 5. Pollen of Ebenaceae. Subtypes A-4 & A-5. A-C. Subtype A-4. Diospyros bipindensis (Zenker 4570). A. Polar view (SEM). B. Equatorial view (SEM). C. Surface view of mesocolpus (SEM). D-F. Subtypes A-5. Diospyros hoyleana (D, Bates 1794; E, F, Leeuwenberg & Berdd 9582). D. Polar view (SEM). E. Polar view (SEM). F. Surface view of mesocolpus (SEM). (Scale bars: A, B, D, E = 5 μm ; C, F = 1 μm).

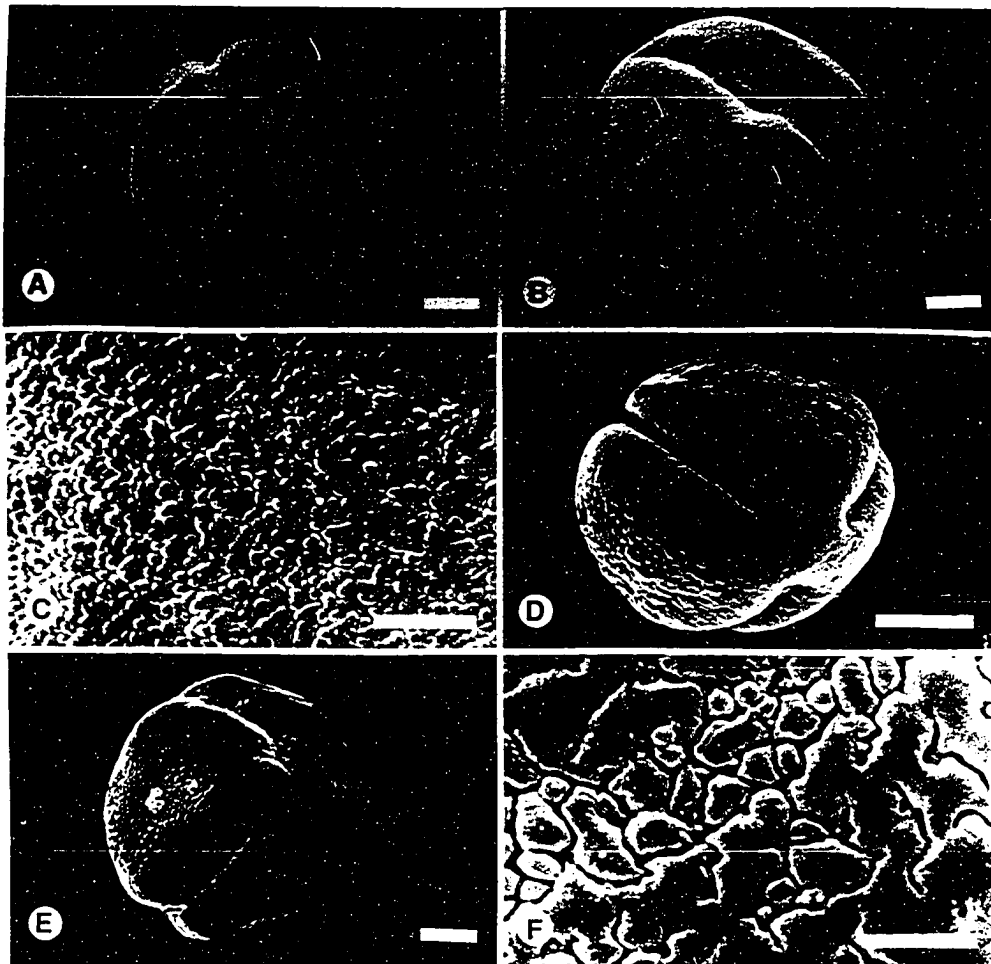


Plate 6. Pollen of Ebenaceae. Subtypes B-1 & B-2. A-C. Subtype B-1. A. Royena dichrophylla (Nicholas 1559). Equatorial view (SEM). B-C. Diospyros artanthaefolia (B, Prance, et al. 13486; C, Tessmann 3667). B. Polar view (SEM). C. Surface view of mesocolpus (SEM). D-F. Subtype B-2. Diospyros lotus (D, E, Stewart; F, Rock 8472). D. Polar view (SEM). E. Surface view of mesocolpus (SEM). F. Equatorial view (SEM). (Scale bars: A, B, D, F = 5 μm ; C, E = 1 μm).

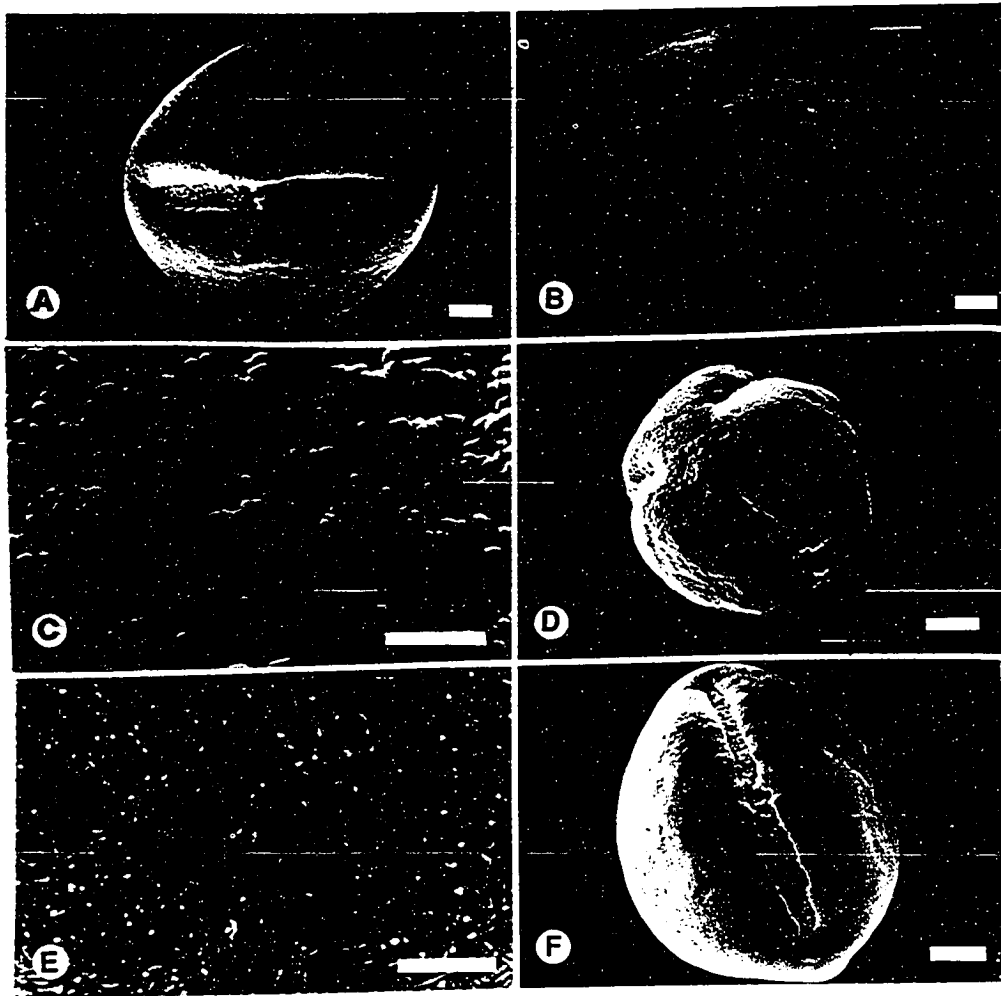


Plate 7. Pollen of Ebenaceae. Subtype B-3. A-B. Royena austro-africana (Sidey 3730). A. Polar view (SEM). B. Endoaperture view (SEM). C. Royena sericea (Brass 17882). Equatorial view (SEM). D-E. Diospyros curranii (Williams 2861). D. Polar view (SEM). E. Surface view of mesocolpus (SEM). F. Diospyros fischeri (Greenway & Kanuri 14000). Equatorial view (SEM). (Scale bars: A, C, D, F = 5 μm ; B = 2 μm ; E = 1 μm).

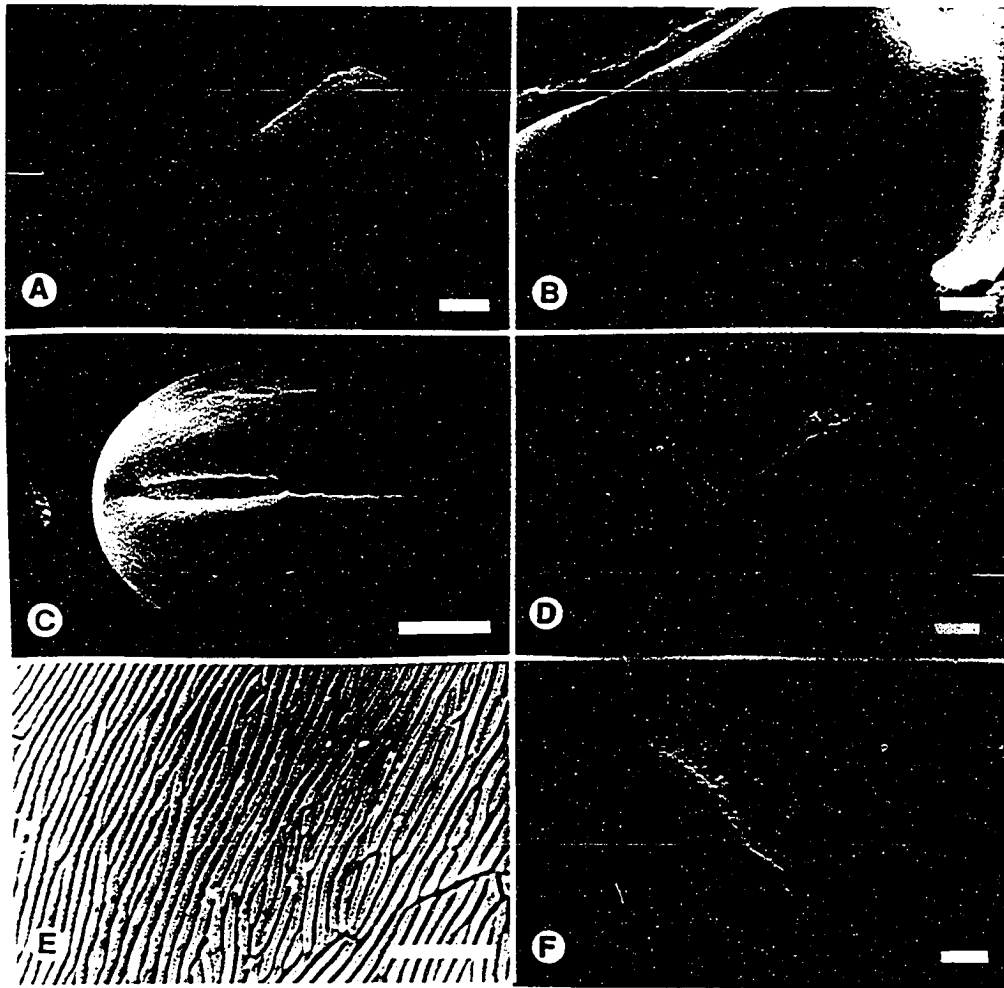


Plate 8. Pollen of Ebenaceae. Subtype B-3. A. Diospyros fischeri (Richards 13480). Surface view of mesocolpus (SEM). B. Diospyros morrisiana (Tsang 20616). Equatorial view (SEM). C-E. Diospyros preussii (C, E, Mambo & Namata 7566; D, Thomas 4770). C. Polar view (SEM). D. Equatorial view (SEM). E. Equatorial view (LM). F. Tetraclis baronii (Baron 2366). Surface view of mesocolpus (SEM). G. Tetraclis clusiaefolia (Baron 5044). Equatorial view (SEM). (Scale bars: A, F = 1 μm ; B, C, D, G = 5 μm ; E = 20 μm).

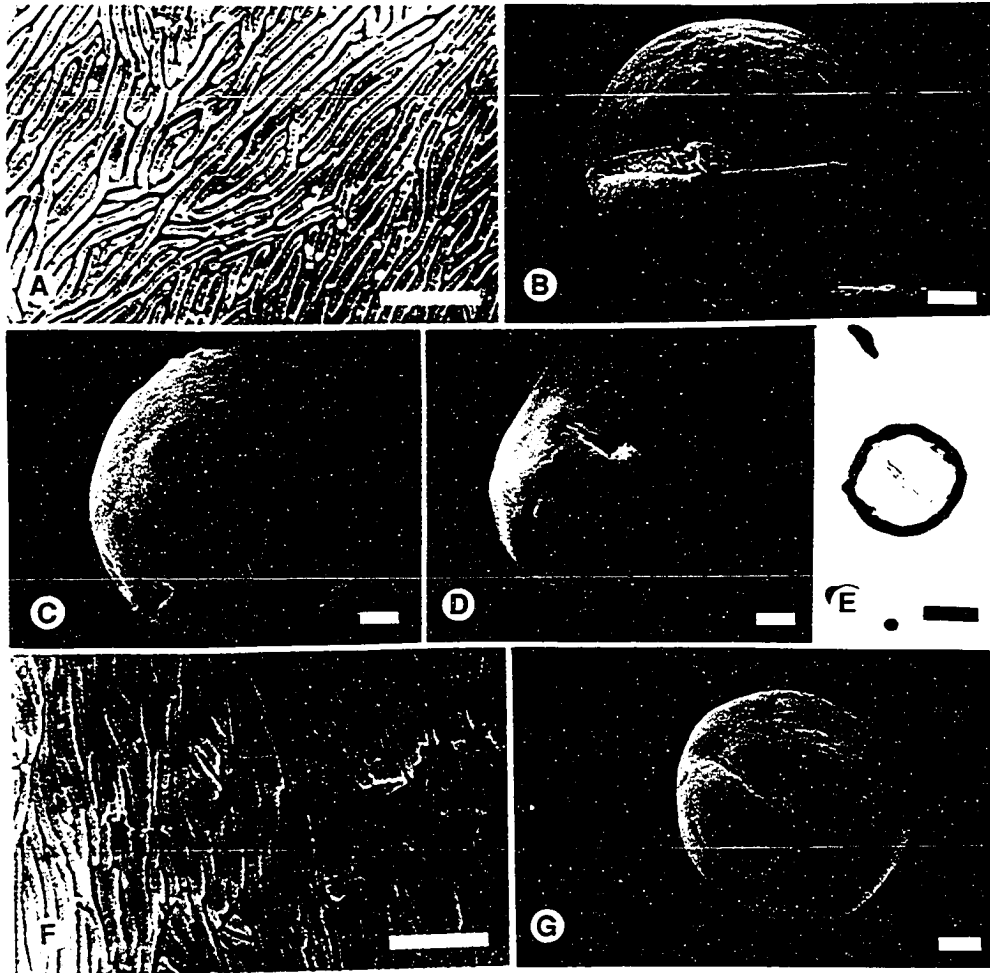


Plate 9. Pollen of Ebenaceae. Subtypes B-4 & B-5. A-C. Subtype B-4. A. Royena guerkei (Sidey 2484). Polar view (SEM). B-C. Diospyros scabrida (Sidey 3731). B. Equatorial view (LM). C. Surface view of mesocolpus (SEM). D-I. Subtype B-5. D-E. Royena cordata (Sidey 1907). D. Polar view (SEM). E. Equatorial view (SEM). F-I. Royena whyteana (F, G, Lovett, et al 932; H, I, Sidey 3769). F. Polar view (SEM). G. Equatorial view (LM). H. Radial section (TEM). I. Surface view of mesocolpus (SEM). J-K. Diospyros montana (Saldanha 12878). J. Polar view (SEM). K. Radial section (TEM). (Scale bars: A, D, E, F, J = 5 μm ; B, G = 20 μm ; C, I, K = 1; H = 4 μm).

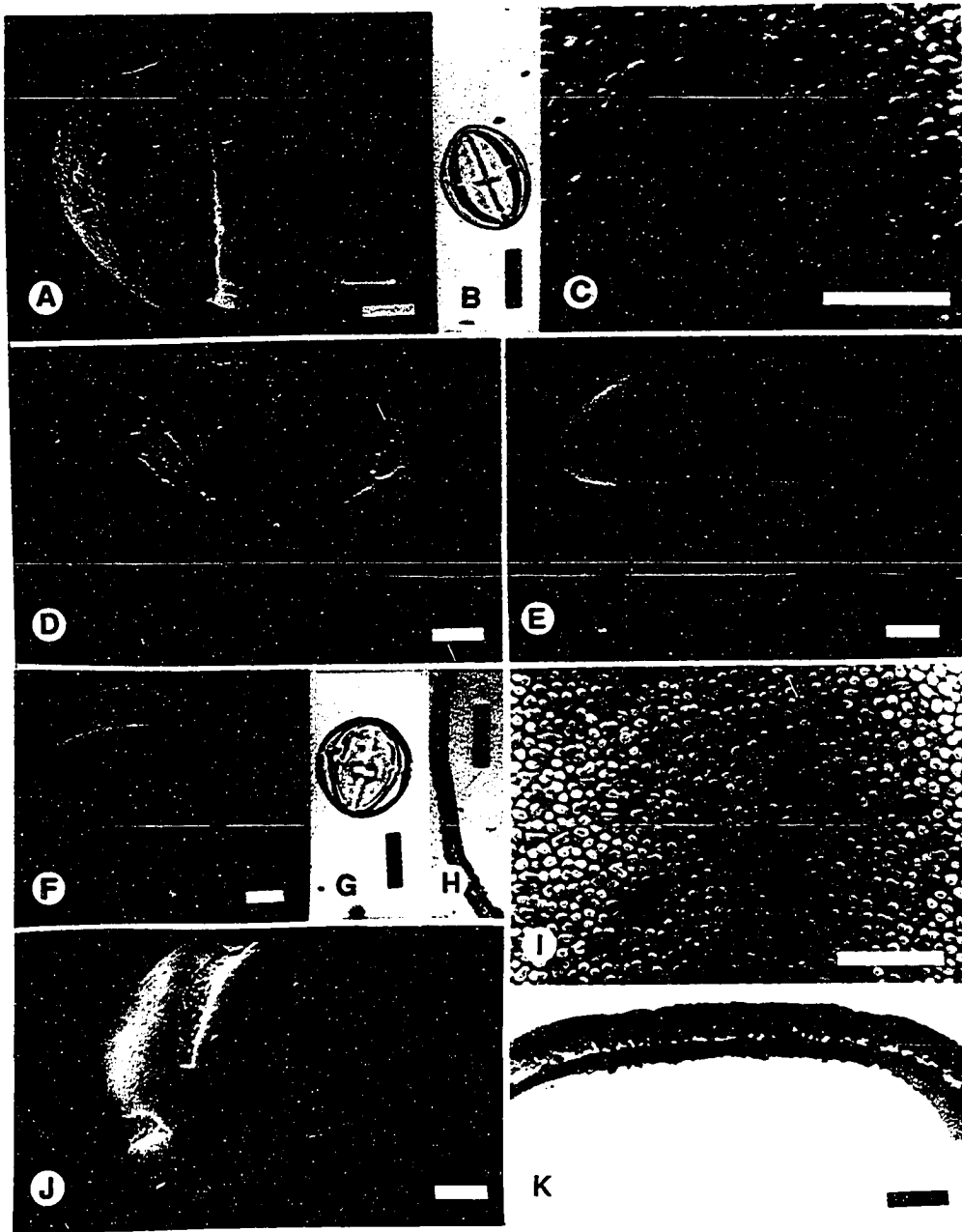


Plate 10. Pollen of Ebenaceae. Subtype B-6. A-B. Royena glabra (Salter 9106). A. Polar view (SEM). B. Surface view of mesocolpus (SEM). C-E. Royena lycioides (C, D, Giess & Wiss 3269; E, Lisowski 18). C. Equatorial view (SEM). D. Equatorial view (LM). E. Surface view of mesocolpus (SEM). F-G. Diospyros armata (Wilson 2912). F. Equatorial view (SEM). G. Surface view of mesocolpus (SEM). H-I. Diospyros ehretioides (Squires 928). H. Polar view (SEM). I. Radial section (TEM). (Scale bars: A, C, F, H = 5 μm ; B, E, G = 1 μm ; D = 20 μm ; I = 10 μm).

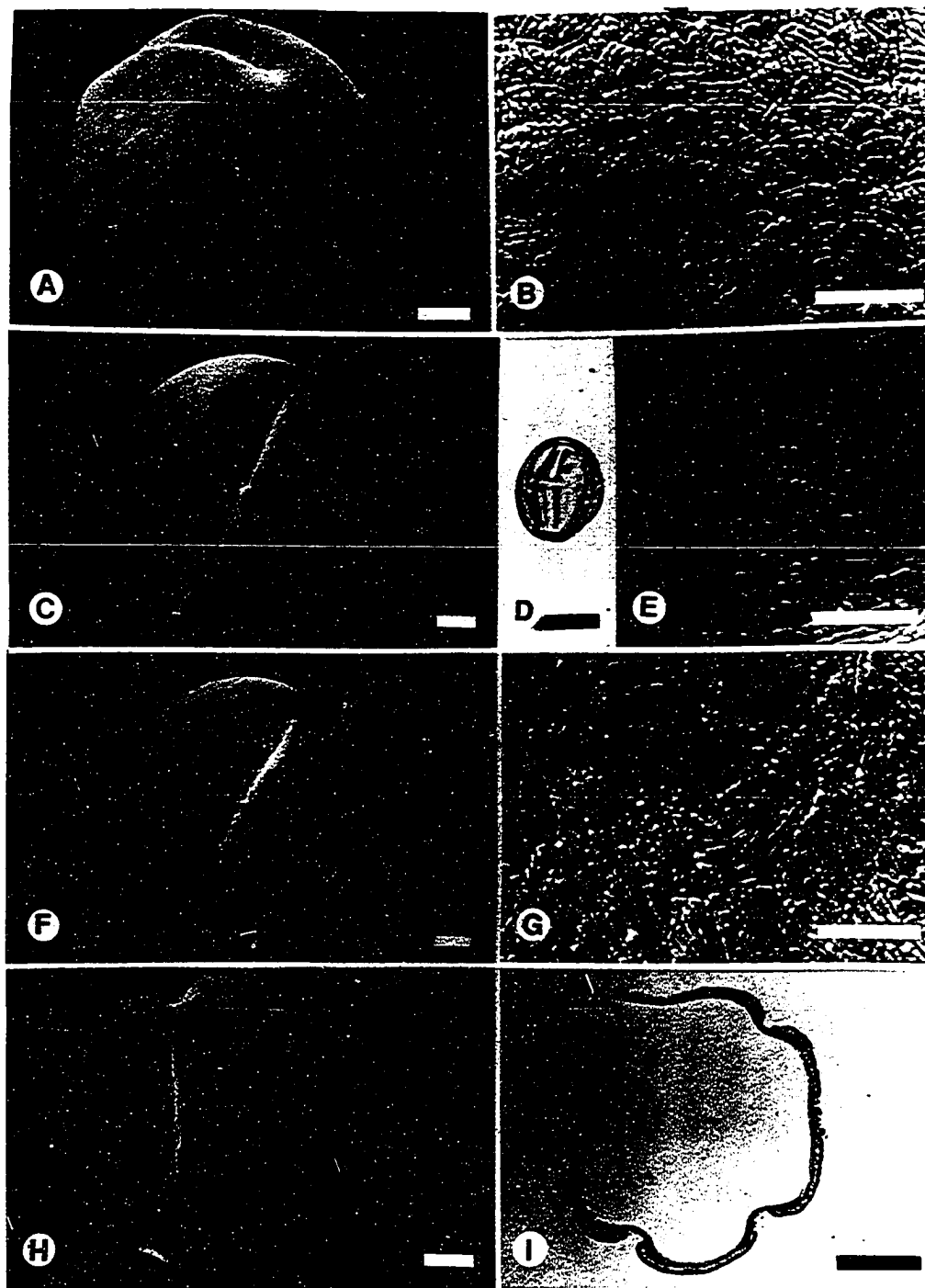


Plate 11. Pollen of Ebenaceae. Subtypes B-7 & B-8. A-E. Subtype B-7. A. Diospyros ierensis (Wurdack & Monachino 41396). Surface view of mesocolpus (SEM). B-C. Diospyros philippinensis (Pruski et al. 2736). Radial section (TEM). D-E. Diospyros pilosanthera (D, Van Niel 4256; E, Borden 2952). D. Equatorial view (SEM). E. Diospyros revoluta (Proctor 21068). Polar view (SEM). F-H. Subtype B-8. Diospyros dendo (McPherson 13804). F. Polar view (SEM). G. Equatorial view (SEM). H. Surface view of mesocolpus (SEM). (Scale bars: A, C, H = 1 μm ; D, E, F, G = 5 μm ; B = 4 μm).

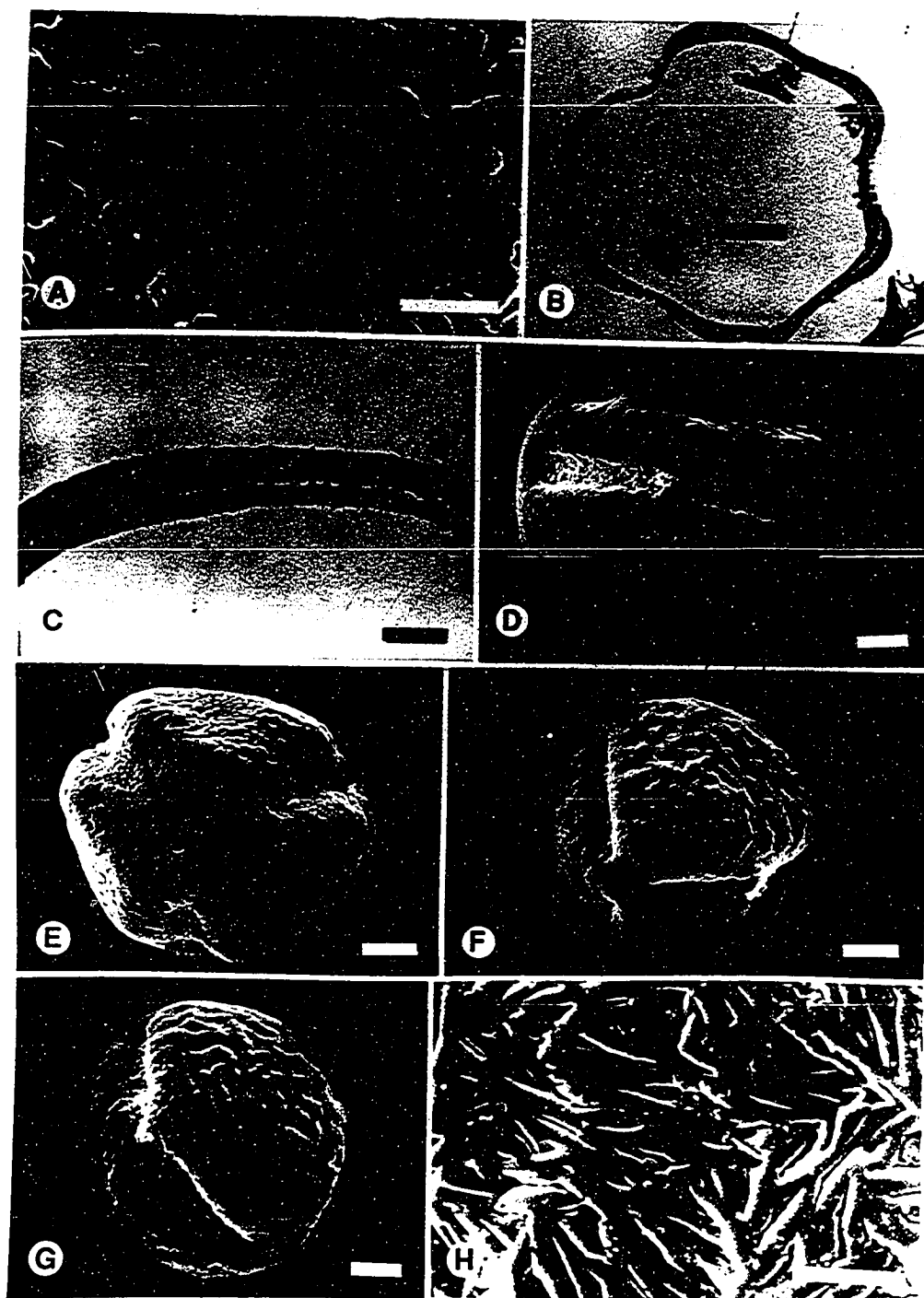


Plate 12. Pollen of Ebenaceae. Subtypes B-9 & B-10. A-B.

Subtype B-9. Diospyros abyssinica (A, Wimbush 103; B, Roberty 18-2-5). A. Equatorial view (SEM). B. Surface view of mesocolpus (SEM). C-F. Subtype B-10. C-D. Diospyros crassinervis (Correll & Proctor 48771). C. Polar view (SEM). D. Equatorial view (SEM). E-F. Diospyros decandra (Poilane 13409). E. Equatorial view (SEM). F. Surface view of mesocolpus (SEM). (Scale bars: A, C, D, E = 5 μm ; B, F = 1 μm).

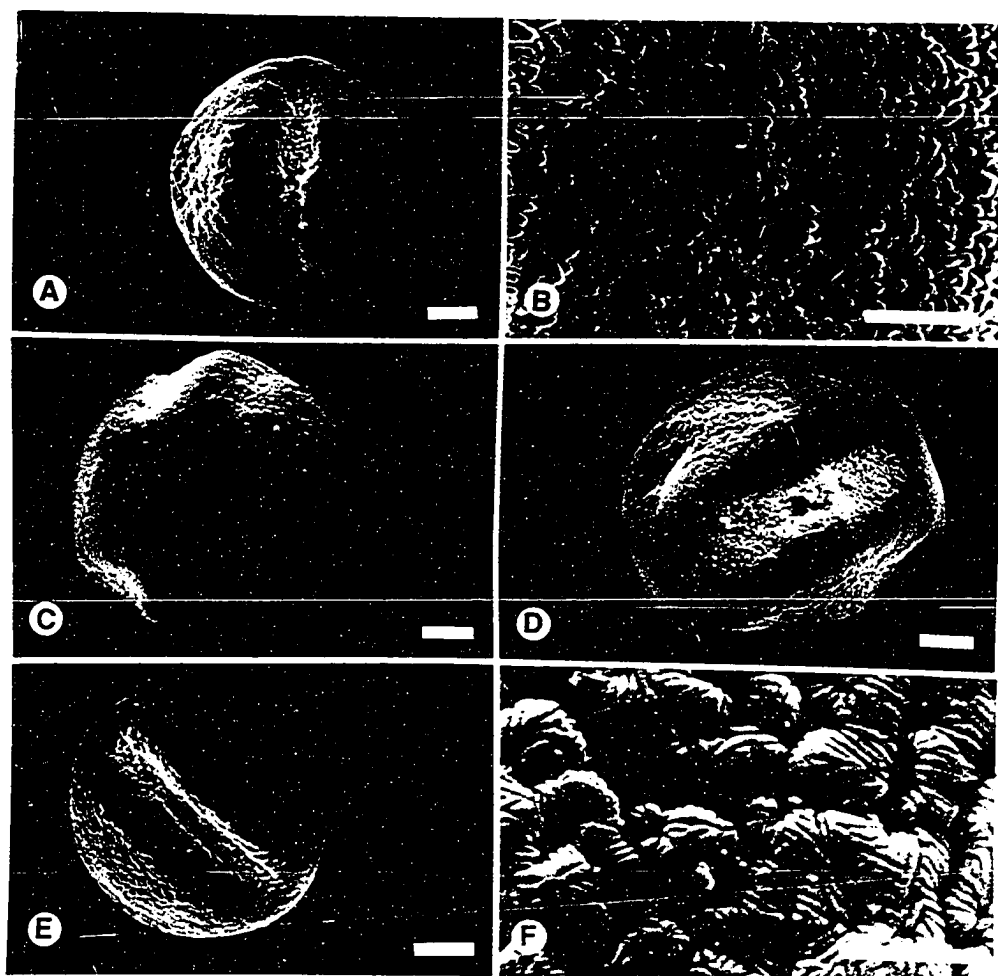


Plate 13. Pollen of Ebenaceae. Subtype B-10. A-C. Diospyros pendula (J. & M.S. Clemens). A. Polar view (SEM). B-C. Radial section (TEM). D-E. Diospyros samoensis (Smith 1451). D. Radial section (TEM). E. Equatorial view (SEM). (Scale bars: A, E = 5 μm ; B, C = 2 μm ; D = 1 μm).

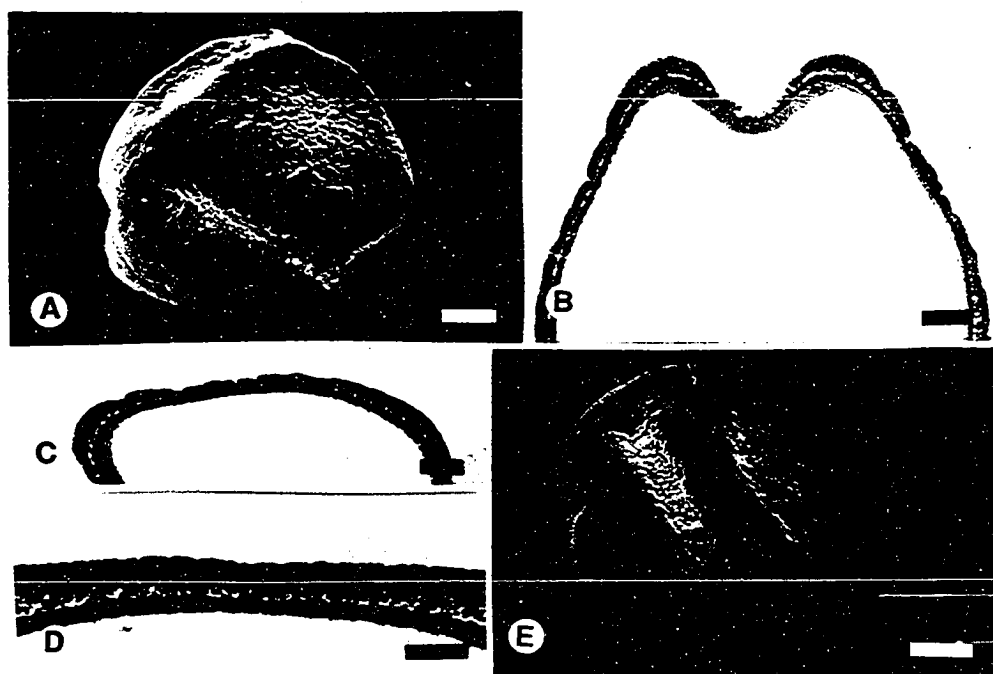
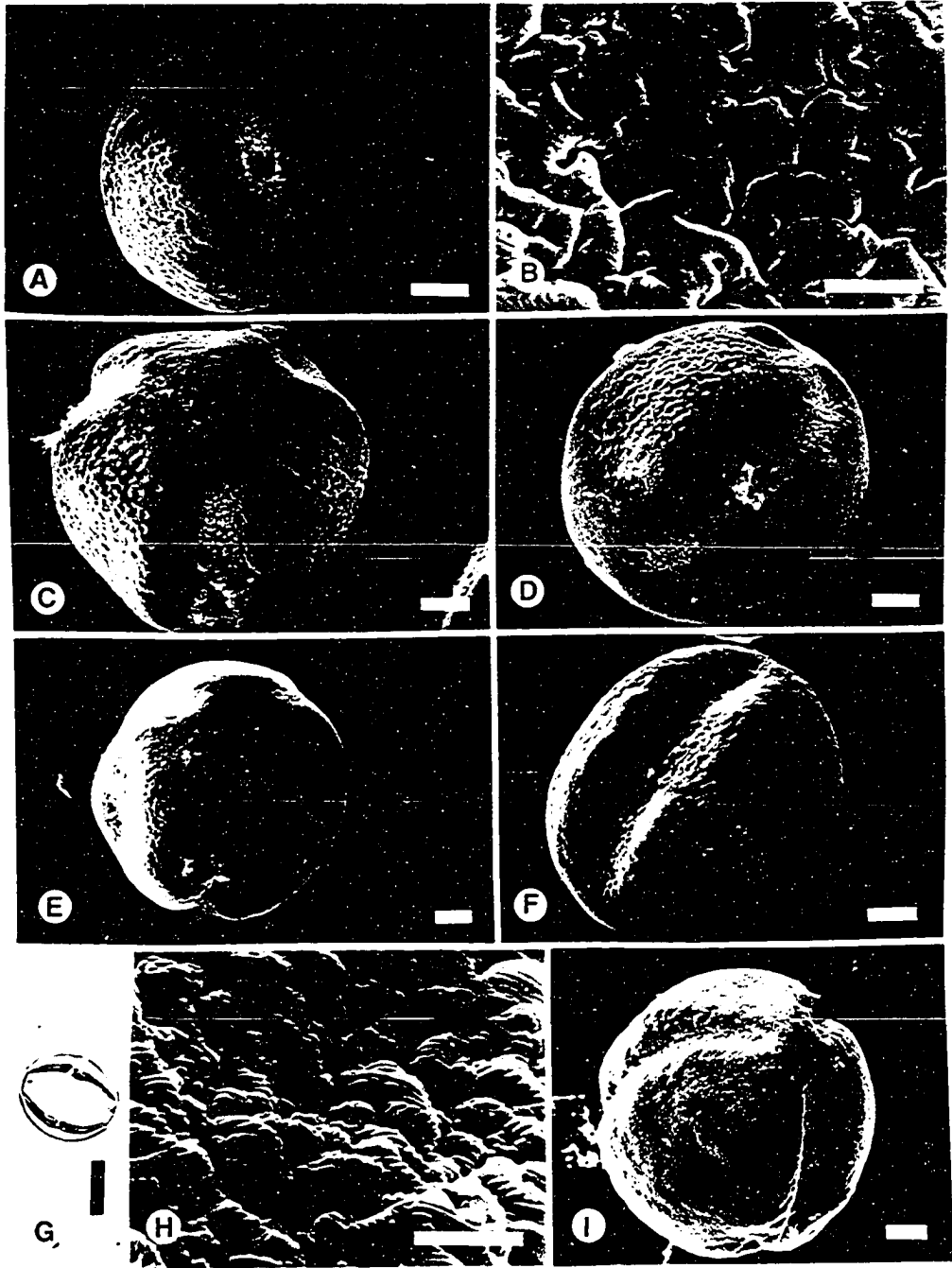


Plate 14. Pollen of Ebenaceae. Subtypes B-11, C-1 & C-2. A-D. Subtype B-12. A-B. Diospyros filipendula (Poilane 15.030). A. Equatorial view (SEM). B. Surface view of mesocolpus (SEM). C-D. Diospyros hispida (Christenson, et al. GMC 1152). C. Polar view (SEM). D. Equatorial view (SEM). E-H. Subtypes C-1. E-F. Diospyros crumenata (Saldanha 16025). E. Polar view (SEM). F. Equatorial view (SEM). G-H. Diospyros virginiana (G, Welch 6679; H, Bryson 8615). G. Equatorial view (LM). H. Surface view of mesocolpus (SEM). I. Subtype C-2. Diospyros kaki (Chow 220). Polar view (SEM). (Scale bars: A, C, D, E, F, I = 5 μm ; B, H = 1 μm ; G = 20 μm).



Appendix 1: Voucher specimens for pollen
samples of the Ebenaceae used in this study.

Voucher specimens for pollen samples of the Ebenaceae used in this study. All are dried specimens deposited at NY unless indicated otherwise. The sample number, used in Table 2, precedes the collector's name. Except where indicated, samples are from Africa.

Euclea acutifolia E. Mey. ex A. DC.

1) van Jaarsveld 5725 (K)

Euclea crispa (Thunb.) Gurke

1) Biegel 2338 (MO); 2) Kemp 543 (US)

Euclea dekindtii Gurke

1) Brenan & Greenway 8145

Euclea divinorum Hiern

1) Bainbridge 561; 2) J. & J. Lovett 701 (MO); 3) Mooney 7292;

4) Mr 23927

Euclea kellau Hochst.

1) Burt 3920 (K); 2) Lebrun 4600 (US); 3) Linson 353 (K)

Euclea lanceolata E. Mey.

1) Chase 34513 (MO)

Euclea linearis (Zeyh. ex Hiern) F. White

1) Schlieben 7534 (US)

Euclea mayottensis H. Perrier

1) Lorence 2874 (MO), Comoro Islands, Madagascar

Euclea multiflora Hiern

1) West 2924 (MO)

Euclea natalensis A. DC.

- 1) Bayliss 1533; 2) Frazier 1110 (US); 3) Norrgrann 168; 4) Tanner 3025 (K); 5) Tanner 3082 (K)

Euclea polyandra E. Mey.

- 1) Codd 2898 (K); 2) Gentry & Barclay 18957 (US)

Euclea pseudebenus E. Mey. ex A. DC.

- 1) Seydel 353; 2) Young 12 xi 1930 (K)

Euclea racemosa Murr.

- 1) Bayliss BRI 186; 2) Dahlstrand 1324 (MO); 3) White 10422 (MO); 4) Williams 632 (MO)

Euclea schimperi (A. DC.) Dandy

- 1) Gillett 12950 (K); 2) Richards & Arasululu 26792; 3) Rlower 37252 (MO); 4) De Wilde 10534; 5) Burger 1750

Euclea undulata Thunb.

- 1) Bayliss 4124 (US); 2) White 10724 (MO)

Royena austro-africana De Winter

- 1) Goldblatt 6270 (US); 2) Harrismith 2829 (MO); 3) Sidey 3730 (US)

Royena cordata E. Mey.

- 1) Sidey 1907 (MO)

Royena dichrophylla (Gand.) De Winter

- 1) Nicholas 1559 (MO)

Royena glabra (L.) De Winter

- 1) Salter 9106 (MO)

Royena guerkei (Kuntze) De Winter

- 1) Sidey 2484 (MO)

Royena hirsuta L.

- 1) De Winter

Royena lycioides Desf.

- 1) Gay 98855 (MO); 2) Giess & Wiss 3269; 3) Hanekom 1879 (MO); 4) La Croix 4128 (MO); 5) Lisowski 18 (K)

Royena microphylla (Burch.) F. White

- 1) Henvici 3169

Royena pallens (Thunb.) F. White

- 1) Becquaert 93 (US)

Royena sericea (Bernh.) De Winter

- 1) Brass 17882; 2) Davie 823 (MO)

Royena usambarensis F. White

- 1) Mrima & Dzomba 383 (K)

Royena villosa (L.) De Winter

- 1) Barbosa & De Lemos 8478 (K); 2) White 10205 (MO)

Royena whyteana (Hiern) F. White

- 1) Chase 5799 (K); 2) Lovett et al. 932 (K); 3) Sidey 3769 (US)

Diospyros abyssinica (Hiern) F. White

- 1) Roberty 18-2-5 (K); 2) Wimbush 103 (K)

Diospyros armata Hemsl.

- 1) Wilson 2912 (MO), China

Diospyros artanthaefolia Mart. ex Miq.

- 1) Maguire et al. 30406, Venezuela; 2) Prance et al. 13486, Brazil; 3) Tessmann 3667, Peru

Diospyros bipindensis Gurke

- 1) Zenker 4570 (MO)

Diospyros brideliaefolia Elmer

- 1) Sulit et al. 30436, Philippines

Diospyros bullata A. C. Sm.

- 1) Ducke 366 (K), Brazil

Diospyros campechiana Lundell

- 1) Barrios 1982 (MO), Mexico

Diospyros candolleana Wight

- 1) Saldanha 16859 (MO), India

Diospyros cauliflora Blume

- 1) De Vogel 3773 (MO), Indonesia

Diospyros conocarpa Gurke et K. Schum.

- 1) Ejiofor 29320 (MO); 2) Le Testu 8541

Diospyros crassinervis (Krug & Urb.) Standl.

- 1) Correll & Proctor 48771 (MO), Bahama Islands

Diospyros crumenata Thwaites

- 1) Saldanha 16025 (US), India

Diospyros curranii Merr.

- 1) Williams 2861, Philippines

Diospyros decandra Lour.

- 1) Poilane 10219, China; 2) Poilane 13409 (US), China

Diospyros dendo Welw. ex Hiern

- 1) Le Testu 8636; 2) McPherson 13804 (MO)

Diospyros dichroa Sandwith

- 1) Cowan 38358 (US), Brazil

Diospyros discolor Willd.

- 1) Liogier 35597, Puerto Rico; 2) Merrill 1393, Philippines

Diospyros diversilimba Merr. & Chun

- 1) Lau 1457, China; 2) Lau 1568, China

Diospyros ehretioides Wall.

- 1) Squires 928, China

Diospyros filipendula Pierre ex Lecomte

- 1) Poilane 15.030, China

Diospyros fischeri Gurke

- 1) Greenway & Kanuri 14000 (MO); 2) Richards 13480 (K)

Diospyros gabunensis Gurke

- 1) Le Testu 7683; 2) Thomas 4702 (US)

Diospyros gillettii De Wild.

- 1) Louis 8546 (MO); 2) De Wilde 2020 (MO)

Diospyros glandulosa Lace

- 1) Raizada 270, India

Diospyros hispida A. DC.

- 1) Christenson et al. GMC 1152 (US), Brazil; 2) Heringer et al. 5449 (US), Brazil

Diospyros hoyleana F. White

- 1) Bates 1794 (K); 2) Leeuwenberg & Berdd 9582 (K)

Diospyros ierensis Britton

- 1) Barabara 4520, Guyana; 2) Wurdack & Monachino 41396, Venezuela

Diospyros kaki L.

- 1) Chow 220 (MO), China; 2) Taam 549 (US), China

Diospyros kamerunensis Gurke

- 1) Enti (MO); 2) Zenken 1806 (K)

Diospyros kirkii Hiern

- 1) Carter 39877 (MO); 2) Fanshawe 2286 (MO)

Diospyros longibracteata Lecomte

- 1) How 71099, China

Diospyros lotus L.

- 1) Rock 8472 (US), China; 2) Stewart, China; 3) Straley 5533 (MO), British Columbia

Diospyros malabarica (Desr.) Kostel.

- 1) Koyama 13392, Sri Lanka; 2) Ripley 424 (US), Sri Lanka

Diospyros maritima Blume

- 1) Fosberg 44527 (US), Indonesia; 2) Merrill 9340 (US), Philippines

Diospyros mespiliformis Hochst. ex A. DC.

- 1) Arne Strid 2434 (MO); 2) Jacques-Georges 938 (MO)

Diospyros mollis Wall.

- 1) Maklva 111, India

Diospyros montana Roxb.

- 1) Saldanha 12878 (US), India; 2) Yeshoda 361, India

Diospyros morrisiana Hance

- 1) Shiu Ying Hu 11984 (US), China; 2) Tsang 20616 (US), China

Diospyros multiflora Blanco

- 1) Ramos 22378 (US), Philippines

Diospyros mweroensis F. White

- 1) Richards 12017 (K); 2) Richards 19664 (K)

Diospyros nicaraguensis (Standl.) Standl.

- 1) Alush Shilom Ton 2449, Mexico

Diospyros nummularia Brenan

- 1) Chase 7352 (MO)

Diospyros ovalifolia Wight

- 1) Hladik 932 (US), Sri Lanka; 2) Ribley 225 (US), Sri Lanka

Diospyros pendula Hasselt. ex Hassk.

- 1) J. & M. S. Clemens, Borneo

Diospyros pentamera Woods & F. Muell. ex F. Muell.

- 1) Clemens, Australia; 2) Clemens, Australia

Diospyros philippinensis A. DC.

- 1) Pruski et al. 2736, Florida

Diospyros pilosanthera Blanco

- 1) Borden 2952, Philippines; 2) Merrilt 4479, Philippines; 3) Van Niel 4256 (MO), Borneo

Diospyros polystemon Gurke

- 1) Letouzey & White 5202 (MO); 2) Luachima 13.862 (K)

Diospyros preussii Gurke

- 1) Mambo & Namata 7566 (MO); 2) Thomas 4770 (MO)

Diospyros pterocalyx Bojer (ex. A. DC.)

- 1) Lorence 2179 (MO), Mauritius, Madagascar

Diospyros revoluta Poir.

- 1) Proctor 21068 (US), West Indies

Diospyros samoensis A. Gray

- 1) Smith 1451, Fiji; 2) Whistler 3341 (US), Samoa

Diospyros scabrida (Harv. ex Hiern) De Winter

- 1) Bayliss 6664 (MO); 2) Sidey 3731 (US)

Diospyros squarrosa Klotzsch

- 1) Pawek 10606 (MO); 2) Robertson 5206A, (K); 3) Robertson 4144 (MO)

Diospyros suaveolens Gurke

- 1) Emwiogbon 47453 (MO); 2) Kennedy (MO); 3) Le Testu 1933

Diospyros sylvatica Roxb.

- 1) Saldanha 12839 (US), India

Diospyros texana Scheele

- 1) Correll 27018 (MO), Texas; 2) Jones 2922I (MO), Texas; 3) Palmer 11244 (MO), Texas

Diospyros verae-crucis (Standl.) Standl.

- 1) Solheim 1747, Mexico

Diospyros vermoesenii De Wild

- 1) Troupin 3988 (K); 2) Troupin 3980 (K)

Diospyros verrucosa Hiern

- 1) Le Testu 639

Diospyros virgata (Gurke) Brenan

- 1) Lisowski 1 (K); 2) Ren 120 (K)

Diospyros virginiana L.

- 1) Bryson 8615 (MO), Mississippi; 2) Clavsen 7748, Illinois; 3) D. S. & H. B. Correll 1557, Florida; 4) C. L. & A. A. Lundell (MO), Texas; 5) Monticello 17177 (MO), Arkansas; 6) Welch 6679, Indiana; 7) Witte, New Jersey; 8) Lomte 316 (MO), Missouri

Tetracalis baronii (US) H. Perrier

- 1) Baron 2366 (K), Madagascar

Tetracalis clusiaefolia Hiern

- 1) Baron 5044 (K), Madagascar

Appendix 2: Pollen Glossary

This glossary explains most pollen-morphological terms used in this study. The meanings of a few terms have been narrowed somewhat to apply more specifically to Ebenaceae pollen.

angulaperturate: said of a pollen grain with apertures situated at the angles of the equatorial outline.

apocolpium (pl.: apocolpia; Fig. 2): each of the two polar areas of a pollen grain. In colporate grains the apocolpia are delimited by imaginary lines running parallel to the equator between the ends of the colpi.

circulaperturate: said of a pollen grain with apertures located along a circular equatorial outline.

circular endoaperture: a endoaperture of circular outline. Compare lalongate endoaperture.

colporate (Fig. 2): said of a pollen grain with compound apertures (colpori; sing.: colporus), of which the ectoapertures are free colpi and the endoapertures are generally circular or elliptical.

columella (pl.: columellae; Fig. 3): a rod-like exine element occurring between the nexine and the tectum or the foot-layer and the tectum. As a whole the columella are usually designated as the columellate layer.

distal pole: the surface of the grain that faces away from the meiotic tetrad.

ectexine (Fig. 3): the outer part of the exine, which in TEM photographs contrasts with the inner part, the endexine. The kind of contrast, whether light/dark or dark/light, depends on the method used. Compare with endexine.

ectoaperture (Fig. 2): an aperture in the sexine. Compare with endoaperture.

endexine (Fig. 3): the inner part of the exine, which in TEM photographs contrasts with the outer part, the ectexine. Compare with ectexine.

endoaperture (Fig. 2): an aperture in the nexine. Compare with ectoaperture.

equatorial axis (Fig. 2): a line situated in the equatorial plane. Consequently, a single pollen grain has many equatorial axes.

equatorial diameter (Fig. 2): the length of the longest equatorial axis of a pollen grain.

equatorial outline: (Fig. 2): the outline of a pollen grain in polar view. Compare with meridional outline.

euprolate: said of a pollen grain with a P/E ratio between 1.34 and 1.99. See P/E.

exine (Fig. 3): the outer, acetolysis-resistant layer of the pollen wall. Compare with intine.

exine architecture: the morphology of the exine, including features relating to both structure and sculpture (Walker & Doyle, 1975).

foot-layer (Fig. 3): the innermost layer of the ectexine.

fossulate: said of the outer tectal wall of a grain with scattered elongated indentations or grooves over the surface, as observed by SEM.

granular: more or less beaded ornamentation as observed by SEM.

hemispherical: said of a pollen grain with a rounded polar cap.

intine (Fig. 3): the inner, acetolysis-nonresistant layer of the pollen wall. Compare with exine.

infratectum (Fig. 3): details or patterns that are confined to the spaces between the tectum and nexine or the tectum and foot-layer.

isopolar: said of a pollen grain with similar proximal and distal halves.

laongate endoaperture: a more or less elliptic endoaperture of which the longest axis is perpendicular to the longest axis of the corresponding ectoaperture. Compare with circular endoaperture.

margo, n., pl. margines: the area surrounding the colpi where the exine is reduced. Sculpturing patterns here may be different from the rest of the grain.

meridional outline (Fig. 2): the outline of a pollen grain in equatorial view. If the equatorial outline of the grain is not circular, the term used to describe the meridional outline reflects the position of the apertures. In this study meridional outline refers to the outline in a grain of which an equatorial axis through an endoaperture is directed towards the observer. Compare with equatorial outline.

mesocolpium (pl.: mesocolpia; Fig. 2): an area on a pollen grain delimited by two colpi and imaginary or actual connections between their ends. Compare with apocolpium.

nexine (Fig. 3): the inner layer of the exine. Under light microscopy this layer displays a more or less homogeneous structure. Compare with sexine.

oblate-spheroidal: said of a pollen grain with a P/E ratio between 0.88 and 0.99. See P/E.

ornamentation: the outer, visual aspect of a pollen grain.

P/E: the ratio of the length of the polar axis to the equatorial diameter of a pollen grain, which gives an indication of shape of the grain in equatorial view (Erdtman, 1952). See oblate-spheroidal, (eu)(per)(sub)prolate-spheroidal, and spheroidal.

perforate tectum: a tectum provided with perforations.

perprolate: said of a pollen grain with a P/E ratio greater than 2.00. See P/E.

pointed: said of a pollen grain with a pointed polar cap.

polar axis (Fig. 2): the line that connects the poles of a pollen grain and is perpendicular to the equatorial plane.

polar diameter (Fig. 2): length of the polar axis of a pollen grain.

prolate-spheroidal: said of a pollen grain with a P/E ratio between 1.01 and 1.14. See P/E.

proximal pole: the surface of the pollen grain that faces the center of the meiotic tetrad.

psilate: said of the outer tectal wall of a grain with little or no ornamentation (smooth).

radially symmetrical: said of a pollen grain that is divisible into equal symmetrical portions by planes of symmetry passing through the polar or equatorial axis.

sexine (Fig. 3): the outer part of the exine. Usually this layer is distinctly structured and/or sculptured, observable even with light microscopy. Compare with nexine.

size of a pollen grain: the maximum diameter of a pollen grain. A grain is small if its maximum diameter is between 10 and 24 μm , medium if between 25 and 49 μm , and large if between 50 and 99 μm . (Walker and Doyle, 1975).

spheroidal: said of a pollen grain with a P/E ratio of 1.00. See P/E.

striate: said of an ornamentation type with elongate (sub)parallel muri, as observed by SEM.

subprolate: said of a pollen grain with a P/E ratio between 1.15 and 1.14. See P/E.

tectate-perforate: said of a tectum with perforations, these lacking free-standing rods.

tectum (Fig. 3): the outer layer of the exine and hence the outermost layer of the pollen wall.

Wood Anatomy

Published Wood Surveys of the Ebenaceae

An extensive literature search revealed that no modern comprehensive morphological and anatomical study of this family has been published. There are no comparative evolutionary surveys of ebenaceous wood anatomy. Much of the anatomical literature treats selected species of economic importance and usually of restricted regions. The most notable of these are: Moll and Janssonius (1909), Burgerstein (1909), Kanehira (1921a, 1921b, 1924, 1926), Brown (1922), Record and Mell (1924), Lecomte (1926), Kribs (1928, 1959), Benoist (1931), Pearson and Brown (1932), Tang (1932), Brown and Panshin (1940), Record and Hess (1943), Metcalfe and Chalk (1950), Huber and Rouschal (1954), Sudo (1959), and Greguss (1959). Observation of only 11 species, using light microscopy, have been published since 1960. More recent papers containing information on the wood anatomy of Ebenaceae are: Normand (1960), Labacq and Dechamps (1964), Purkayastha et al. (1976), Dechamps (1979), Panshin and Zeeuw (1980), Prior and Gasson (1990), and Hayashi (1991). The wood anatomy of only about 12 percent of the species of this ecologically diverse subtropical and tropical family has been studied.

All of the above wood anatomical studies of Ebenaceae were done using only light microscopy, and thus, information is lacking about pits, crystals, and other structures that

require the higher resolution of SEM. To date, no studies employing scanning electron microscopy have been published.

Objectives of Wood Research

The value of wood anatomy to classification and phylogenetic studies has been clearly established. A few examples include Record (1933, 1934), Bailey and Howard (1941a, 1941b, 1941c), Dickison (1967, 1972, 1978, 1981), Carpenter and Dickison (1976), Dickison and Baas (1977), Zeeuw (1977), Carlquist (1988), and Baas et al. (1988).

The purpose of this study is to provide a comprehensive survey of the wood morphological features of the Ebenaceae using both light and scanning electron microscopy.

The main objective of this paper is to document the wood anatomy of the Ebenaceae as a whole and to discuss the systematic implications of these data. Specific objectives of this investigation are:

1. to provide a comprehensive wood anatomical database for the Ebenaceae,
2. to evaluate the usefulness of wood characters in elucidating generic relationships,
3. to compare the wood data of the Ebenaceae with those of other families in an attempt to clarify interfamilial relationships, and
4. to assess the correlation of wood anatomical variation with latitude and/or altitude.

Methods and Materials for Wood Anatomy

The assumption that a single plant sample provides reliable morphological or anatomical data upon which to base a taxonomic classification is invalid. This study has made every effort to examine sufficient material so that the range of variability within a species and between species, with respect to geographic range and environmental conditions, has been investigated. Furthermore, unlike most other recent studies (e.g. Zhang and Baas, 1992), this study has made every effort to examine samples from mostly vouchered material (Appendix 3).

In total, 148 wood samples representing 93 species were examined. Observations on most of the species were made on more than one individual to enhance the chances of spotting erroneous identifications. Wood samples were collected from dried material housed at the following xylaria {abbreviations follow recommendations of Stern's Index Xylariorum (1988)}: U.S. Forest Products Laboratory (MADw), Bundesforschungsanstalt für Forst-und Holzwirtschaft (RBHw), Smithsonian Institution (USw), and Rijksuniversiteit te Utrecht (Uw).

Preparation for Light Microscopy

Wood samples were prepared by boiling the dry specimens in water to remove excess air and then storing in 1:1 mixture of glycerine and 50% ethanol. Transverse, radial,

and tangential sections, usually between 15-20 mm thick (depending on wood behavior), were made with a sliding microtome, stained with safranin, dehydrated with an ethanol series, cleared in histoclear, and mounted in permount. In some instances radial sections were bleached to study crystal and silica grain structures (Welle, 1976). Maceration of all samples were made with Jeffrey's macerating fluid (Berlyn and Miksche, 1976) and stained with safranin.

Preparation for Scanning Electron Microscopy (SEM)

Unstained wood sections were placed between slides, dried, mounted on SEM stubs and observed for silica and crystal distribution. Other sections were bleached, placed between slides, dried, and mounted on SEM stubs for examination of unusual features such as type and distribution of pits.

Measurements

Wood anatomical characters that were analyzed include not only qualitative but also quantitative features: vessel frequency, ray frequency, vessel lumina diameter, vessel wall thickness, vessel element length, vessel pit diameter, vessel-ray pit diameter, fiber lumina diameter, fiber wall thickness, fiber length, fiber pit diameter, ray width, ray length, ray cell width, ray cell length, crystal type,

silica type, and number of cells per parenchyma strand.

Quantitative features for each sample were gathered as follows:

- 1) Frequency of vessel per square mm was determined in transverse section by counting all vessels individually (10 counts per sample) and the percentage of solitary vessels was determined as the proportion of solitary vessels in relation to the total number of vessels (Wheeler, 1986).
- 2) Lumina diameter and wall thickness of 25 tangential fibers and vessels were measured in cross sections at the widest point.
- 3) Length, including tails if present, of 25 fibers and vessel members were measured in macerations.
- 4) The diameter of the wall pits were measured at the broadest point of the horizontal diameter of the pit cavity for 25 intervascular pits, vessel-ray pits, and fiber pits.
- 5) Ray frequency was determined, in tangential sections, by counting the number of rays per square mm (10 counts per sample). Rays that were only partially in the field of count were included. The type of ray (uniseriate, biseriate, or triseriate) was also determined.
- 6) Ray size was expressed both by the number of cells and by the number of microns per length and width of the ray. Width was measured at the widest point.

Terminology, nomenclature, and characters used to describe these woods follow the recommendations of the

Committee on Nomenclature, International Association of Wood Anatomists (Wheeler et al., 1989). Rays were described according to Kribs (1935).

Statistical analyses

Statistical analyses were done to assess the relationships between anatomical characters and the latitude and altitude at which a sample was collected. Like many other studies of ecological wood anatomy, this study suffers from insufficient ecological data. For most samples with good locality information, exact latitude was determined. When specific locality information was not given, the latitude assigned represented the mid-point of the latitudinal range estimated from available collection data.

The data set was stored, manipulated, and analyzed using Statview and JMP(SAS) on the Macintosh platform, and the statistical analysis basically followed that of Sokal and Rohlf (1981). Descriptive statistics (mean, SD) for quantitative features were calculated.

Quantitative wood features, species, genera, sections, subgenera, and genera were subjected to analyses of variance. The above taxonomic ranks were coded in integers as grouping variables.

Skewness and kurtosis were assessed for each variable. All quantitative features were log-transformed to reduce skewness.

Dependencies on latitude and altitude were calculated using regression analysis. The results of these analyses were used to examine the relationship between latitude and/or altitude and the wood anatomical characters and patterns in the data matrix.

Results for Wood Anatomy

Description of the wood of Ebenaceae

Statistical data, i.e., the mean and standard deviation of the mean for each quantitative feature studied, of Ebenaceae wood anatomy are summarized in Table 14. Quantitative and qualitative features of 148 wood samples, listed in Appendix III and illustrated in Plates 1-9, were used as the basis for the following description.

GROWTH RINGS

Growth rings are mostly absent or sometimes indistinct (Plate 15 A-B). Indistinct growth rings were found in 21 percent of the samples examined in Royena, Euclea, and Diospyros. Indistinct growth rings usually occur as narrow zones of radially compressed and slightly thicker-walled imperforate tracheary elements of the latewood, or rarely as a decrease in frequency of parenchyma bands from earlywood to latewood or rarely as a reduction of pore diameter from earlywood to latewood (D. virginiana), or rarely as a decrease in the pore frequency (D. mwerensis) from earlywood to latewood. Rarely do growth rings differ among collections of the same species (only in D. vitiensis and D. inconstans).

VESSELS

Porosity: Vessels are usually diffuse-porous or rarely

semi-ring porous (D. virginiana).

Arrangement and grouping: Vessels are mostly solitary, frequently in pore multiples, or rarely in clusters (Plate 15 C-D). The percentage of solitary vessels ranges from 11% in E. natalensis to 87% in D. hoyleana (ave 53%). Pore multiples are mainly radial or rarely oblique in arrangement and range from 2 to 12 (ave. 2) cells in length. Clusters are usually of 3 to 8 (ave. 5) cells. Frequency and element size: Vessel frequency varies from 3.7/mm² in D. discocalyx to 99/mm² in D. cupilifera (ave. 18.6mm/2) (Plate 16 A-B). Taxa with vessel frequency over 70/mm² include the genus Tetraclis and several species of Diospyros and Royena. Mean vessel element length (tip to tip) ranges from 267.80 μ m in Euclea divinorum to 705.22 μ m in Diospyros thwaitesii (ave. 443.9 μ m). Occasionally ligule extensions occur on one or occasionally both ends and often are of unequal length (Plate 16 C). All samples examined (42%), inclusive of all samples of Diospyros, have vessel elements over 416 μ m in length (Fig. 8). The mean tangential diameter of the pores ranges from 31.98 μ m in Euclea divinorum to 194.70 μ m in Diospyros discocalyx (ave. 83.03 μ m). Many samples (62% of those examined) of Diospyros have vessel elements of over 86 μ m in diameter (Fig. 9). L/D ratios range from 4.27-9.94 in Royena and Euclea, 2.62-16.13 in Diospyros, and 6.42-14.40 in Tetraclis (Fig. 10). Mean thickness of the vessel wall ranges from 1.76 μ m- 8.98 μ m (ave. 4.39 μ m), with a

higher frequency of thin-walled vessels in Tetraclis. Perforation plates are simple and usually obliquely to rarely transversely oriented to the cell axis. Pores are circular or circular to angular in outline. Helical wall thickenings are absent except in Royena lycioides (Plate 16 D).

Wall pitting: Intervessel pits are usually alternate to transitional opposite, or rarely alternate, or very rarely opposite and crowded and usually polygonal to rarely elongate in outline (Plate 17). The mean tangential diameter of intervessel pits ranges from 1.58 μm in D. hoyleana to 8.78 μm in D. artantheaefolia (ave. 4.31 μm). Samples with intervessel pits of 4.5 μm and over in diameter (62% of all samples examined) occur only in species of Diospyros. Vessel-ray pits are similar in shape and size to intervessel pits (Plate 18 A-B).

CONTENTS AND TYLOSES

Gummy contents were observed often in vessels, ray parenchyma, and fibers and rarely in axial parenchyma (Plate 18 C). Tyloses were not seen but gummy contents, black or red, even after bleaching, restricted observations. Composition of chemical elements of selected gummy deposits include: carbon, aluminum, potassium, and calcium (Plate 18 D).

IMPERFORATE TRACHEARY ELEMENTS

Imperforate tracheary elements usually occur as libriform fibers or rarely (in 10% of the species of Diospyros) as libriform fibers and fiber-tracheids. Mean length of fibers (tip to tip) ranges from 713.40 μm in Tetraclis clusiaefolia to 1435.66 μm in Diospyros discocalyx (ave. 1034.93 μm). Mean tangential diameter of fibers ranges from 2.84 μm in D. natalensis to 12.14 μm in D. morrisiana (ave. 6.99 μm). Mean thickness of fiber wall ranges from 1.76 μm to 6.43 μm (ave. 3.17 μm). Pits vary from distinctly bordered and 3-3.9 μm in diameter (in some samples of Diospyros) to minutely bordered and 0.71-2 μm in diameter, both types with slit-like apertures, and usually with pits more numerous on radial walls than on tangential walls but sometimes distributed equally on both radial and tangential walls (Plate 19). Mean ratio of fiber length to vessel element length ranges from 1.51 to 3.44 in Diospyros, Royena, and Euclea and from 2.21 to 2.63 in Tetraclis (Fig. 11). Fibers are nonseptate.

RAYS

Rays are commonly both uniseriate and multiseriate or rarely (in D. amboinensis and D. castanea) uniseriate (Plate 20 A). Mean frequency of rays varies from 25/mm² in D. anisandra to 137/mm² in Royena dichrophylla (ave. 61.50/mm²). Uniseriate rays range in frequency from 9 to

154 /mm², in width from 4.65 μm (Tetraclis baroni) to 38.61 μm (D. batocana) (ave. 18.74 μm), and in height from 2 to 44 cells (ave. 9) and 87.49 μm (D. sylvatica) to 1964.77 μm (D. batocana) (ave. 396.54 μm). Multiseriate rays range in frequency from 1 to 58 /mm², in width from 2-4 cells and from 10.34 μm (D. abyssinica) to 57.36 μm (Euclea lanceolata) (ave. 26.17 μm) (Plate 20 B), and in height from 4 to 24 cells (ave. 13.63) and from 115.05 μm (D. bourdillonii) to 1780.71 μm (D. artanthaefolia) (ave. 439.34 μm). Within a sample, rays are usually both heterocellular and homocellular, or rarely homocellular; when heterocellular, the ray is often of 2 or more multiseriate parts (Plate 20 C). Rays are composed frequently of procumbent cells with 2 or more marginal rows of unevenly distributed square or erect cells or occasionally of a mixture of procumbent cells, square cells, and erect cells interspersed throughout the ray. Homogeneous rays are composed usually of erect cells or rarely of procumbent cells (Plate 20 C-F). Heterogeneous rays typically are of Krib's types II b and III, and homogeneous rays are of Krib's type I. Rays are storied in D. glandulosa, D. kaki, D. morrisiana, D. virginiana, and D. viridicans (Plate 21 A). Ray-to-ray pits are minute and simple.

AXIAL PARENCHYMA

Four types of parenchyma occur in the family: 1)

narrowly banded (usually 1 or 2 cells in width), 2) scanty paratracheal, 3) vasicentric, and 4) apotracheally diffuse (Plate 21 B-C). For arrangement and percentages of types among genera see Table 15. Axial parenchyma strands range from 2-12 cells in length (usually 4-8) and are mostly uniseriate (rarely biseriate) (Plate 21 D). Strands of apotracheal parenchyma are typically 4-celled, while strands of scanty paratracheal or vasicentric parenchyma are typically 8-celled.

CRYSTALS

Prismatic calcium oxalate crystals are both large and small and usually sharply angled, with one or more crystals per ray cell. Crystals are generally (in 37% of the samples examined) borne in chambered and nonchambered axial parenchyma cells, frequent (in 20% of the samples examined) in ray parenchyma, frequent (in 17% of the samples examined) in both chambered axial parenchyma and ray parenchyma cells, or absent (in 19% of the samples examined for Diospyros) (Plate 22 A-C). In most samples, crystals frequently do not occur in the same the cell types in all samples.

SILICA

Silica grains occur in ray cells of all samples of Royena and in three species of Diospyros (D. acuminata, D. montana, and D. sylvatica). There is one grain per body

cell, mostly globular in form, with a rough surface. Silica grains usually do not occur in combination with calcium oxalate crystals (Plates 22 D-E and Plate 23 A-B). All samples with silica grains, thus far examined, were collected from Africa.

PITH FLECKS

Pith flecks are sporadic in Diospyros and Royena and vary among different collections of the same samples. Pith flecks usually occur in tangential bands or are rarely diffuse (Plate 23 C-D).

Statistical results for wood

The relationships of seven of the quantitative wood anatomical characters to latitude and altitude of provenance are given in Tables 16-19. These relationships were analyzed by least squares univariate linear regression as well as in percentages of the total variation (R-sq) in each dependent variable (e.g. vessel diameter). With increasing latitude, vessel lumen diameter, vessel wall thickness, vessel member length, fiber lumen diameter, fiber wall thickness, and fiber length decrease, whilst vessel frequency increases (Table 16).

This pattern was also observed with increasing altitude, i.e., vessel lumen diameter, vessel wall thickness, vessel member length, fiber lumen diameter, fiber wall thickness, and fiber length decrease, whilst vessel frequency increases (Table 17).

An examination of the data set revealed that in the tropics the altitudinal range of Ebenaceae is greater than in temperate regions. To understand the effects of altitudinal dependencies for the Ebenaceae the data was split into two groups: one representing species from between 10° N and S (equatorial tropics) and another containing species from above 10° N and S (higher latitudes). The calculated regression formulas and percentages of the total variation explained by latitude and altitude are given in Tables 18 and 19. The results from this split dataset are

now different. In the equatorial belt, with increasing latitude, vessel lumen diameter, vessel member length, and fiber wall thickness decrease, whilst vessel frequency, fiber lumen diameter, and fiber member length increase. There are no significant regressions on latitude for vessel wall thickness.

In comparison, in the equatorial belt, with increasing altitude, vessel lumen diameter, vessel wall thickness, vessel member length, and fiber member length decrease, whilst vessel frequency and fiber wall thickness increase. There are no significant regressions on altitude for fiber lumen diameter.

In addition, with increasing latitudes, vessel frequency, and fiber lumen diameter decrease, whilst vessel lumen diameter, vessel member length, and fiber member length increase. There are no significant regressions on latitude for vessel wall thickness or fiber wall thickness.

With increasing altitudes, vessel lumen diameter, vessel wall thickness, vessel member length, and fiber lumen diameter decrease. There are no significant regressions on altitude for vessel frequency, fiber wall thickness, or fiber member length.

Discussion of Wood Anatomy

General characteristics of wood of Ebenaceae

Wood anatomical features present in all samples are: pores occurring as both solitaires and pore multiples; perforation plates simple; intervessel pits polygonal in outline; libriform fibers present; fibers non-septate; and ray-ray pits minute and simple.

In addition, most samples have no growth rings, diffuse porous vessels, perforation plates oblique to the cell axis, circular pores, intervessel pits arranged in an alternate to transitional opposite pattern, both uniseriate and multiseriate rays, both heterocellular and homocellular rays, each heterocellular ray often composed of 2 or more multiseriate parts, narrowly banded axial parenchyma, parenchyma strands 4-8 cells in length, and the occurrence of prismatic calcium oxalate crystals in axial and/or ray parenchyma cells.

Characters selected from previously published studies of the wood anatomy of the Ebenaceae are presented in Table 20. Aside from minor discrepancies in the size of various cell types and in the occurrence of prismatic calcium oxalate crystals in axial and/or ray parenchyma cells, the observations in these studies generally agree with mine, therefore helping to confirm the reliability of my results. A few obvious differences include: Burgerstein (1909) observed smaller vessel diameters (25 μm vs. 62 μm), longer

vessel elements (800 μm vs. 350-450 μm) and higher multiseriate rays (25 cells vs. 15 cells) in D. samoensis; Kanehira (1921) reported wider vessel diameters (20 μm vs. 11 μm), and wider rays of 1-3 (rather than 1-2) cells in D. morrisiana; Kanehira (1924) examined in D. philippinensis wider fiber diameters (6 μm vs. 14-17 μm) and narrower rays of 1 (rather than 1-2) cells; Kribs (1959) found in both D. mespiliformis and D. crassiflora broader rays of 1-3 (rather than 1-2) cells, and in D. crassiflora broader vessel-vessel and vessel-ray pits (4-6 μm vs. 3-4 μm) and storied (rather than non-storied) rays; Sudo (1959) recorded for D. morrisiana broader rays of 1-3 (rather than 1-2) cells; Labacq and Dechamps (1964) observed in both D. crassiflora and D. mespiliformis narrower rays of 1 (rather than 1-2) cells; Pearson and Brown (1932) examined in D. ebenum wider vessel diameters (135-150 μm vs. 66-69 μm) and wider fiber diameters (19-23 μm vs. 4-8 μm); Record and Hess (1943) found in D. virginiana narrower rays of 1-2 (rather than 1-3) cells; Metcalf and Chalk (1950) recorded for both D. glandulosa and D. virginiana broader rays of 1-4 (rather than 1-3) cells; Dechamps (1979) observed in D. guianensis shorter vessel elements (310 μm vs. 600 μm) and shorter parenchyma strands (2-4 cells vs. 4-7 cells); and Prior and Gasson (1990) recorded in both E. crispa and E. schimperi rays of 1-2 (rather than 1-3) cells and in D. natalensis broader rays of 1-3 (rather than 1-2) cells. The present

study and previously published studies agree that all samples, thus far examined, of Royena contain one silica grain per ray cell.

The increased range of morphological variation described here is mainly due to the greater number of samples studied from a wider geographical area. In addition, greater quantitative precision was acquired from using a computerized morphometric unit, programmed with Neurolucida software.

In comparison to other groups, such as the Dipterocarpaceae (Gottwald and Parameswaran, 1966; Zeeuw, 1977; Morton, in review), the variation in characters of wood anatomy within the Ebenaceae is rather low. Moreover, this subtle variation is matched by that in features of other organs and tissues, such as its pollen and leaves (personal observations). Correlation of other anatomical or morphological characters with generic limits or phylogenetic trends were not assessed because additional features of the family have not been thoroughly studied.

Correlation of wood features with taxa of Ebenaceae

To determine if the variation in wood characters bore any relationship into the existing classification systems of White (1978, 1980, 1983, 1987, 1988), White and Caveney (1980) and Bakhuizen (1936-1938) six independent single classification anovas were completed. Two single

classification anovas were completed for selected quantitative wood variables and the sections and genera of Ebenaceae as recognized by White. Three single classification anovas were completed for the same quantitative wood variables and the sections, subgenera, and genera of Ebenaceae as recognized by Bakhuizen. One single classification anova was completed for the total number of species examined in this study. Wood characters were used as variables and species, sections, subgenera, and genera were coded as integers. The species examined in the present study from taxa recognized by White, White and Caveney, and Bakhuizen are summarized in Tables 21 and 22.

White, in his treatments of African Ebenaceae, recognized the genus Euclea and 18 sections of Diospyros, including the genera Royena and Rhaphidanthe at the sectional level. The present study examined wood features of 5 of the 25 species that White included in Euclea and 28 of 108 species included in Diospyros. Approximately 60 species of Ebenaceae examined in this study, including those in the genus Tetraclis from Madagascar, were not treated by White (Table 21).

Results of the single classification anova for the quantitative wood variables, as grouped by the sections and the genera of Ebenaceae as recognized by White are given in Tables 23 and 24, respectively. Significant differences in the means of all wood variables ($p < .0001$ in overall anova)

were found to exist for the eleven sections of Diospyros recognized in Whites' classification but only five out of the thirteen wood variables had an R-square above 26 percent (Table 23). In comparison, significant differences ($p < .0001$) were found to exist in the means in 18 out of the 21 wood variables among the 3 genera, Diospyros, Euclea and Tetraclis, recognized by White but only 2 variables out of the 18 had a R-square above 10 percent (Table 24). Even though most of the wood variables were found to be significantly different among sections and genera, the low R-square values (the total variation accounted for by groups) revealed that in White's classification the sections are slightly more effective in accounting for variation in the wood variables than are the genera.

Bakhuizen in his treatment of the Pacific taxa recognized only Diospyros and divided it into 36 sections (Table 22). The present study examined wood variables of 13 of the 171 species, two of the four subgenera, and 11 of the 36 sections recognized by Bakhuizen. Approximately 80 species of Ebenaceae examined in this study, including those in the genera Euclea, Royena (from Africa), and Tetraclis (from Madagascar) were not treated by Bakhuizen (Table 22).

Results of the single-classification anova completed for the quantitative wood variables grouped by the sections, the subgenera, and the genera of Ebenaceae recognized by Bakhuizen are given in Tables 25-27, respectively.

Significant differences in the means of all wood variables ($p < .0001$) were found among the eleven examined sections of Bakhuizen's classification. Seven of the thirteen wood variables were not only significantly different among the sections but had an R-square above 50 percent (Table 25). Significant differences in the means were found in six of the thirteen wood variables among the two subgenera recognized by Bakhuizen but only one variable had a R-square above 10 percent (Table 26). In comparison, significant differences ($p < .0001$) were found in 19 of the 21 wood variables examined among the four genera, (Diospyros, Euclea, Royena, and Tetraclis) recognized by Bakhuizen but only four variables had a R-square above 10 percent (Table 27).

Both sections and genera were found to be significantly different among most of the wood variables, and the R-square values (the total variation accounted for by groups) revealed that in Bakhuizen's classification the sections are more effective in accounting for variation in the wood variables than are the subgenera or genera.

An analysis of variance was also completed for all quantitative wood variables among all samples examined in this study. Significant differences ($p < .0001$) in the means of all 21 wood variables were found among all of the 93 species examined, which includes the genera Diospyros, Euclea, Royena, and Tetraclis. The R-square values for nine

of the 21 wood variables among the samples were over 50 percent, representing a high proportion of the total variation accounted for by groups (Table 28). Therefore, the 91 species examined are highly effective in accounting for variation in at least nine of the wood variables.

In summary, the wood characters account for very little of the total variation at the sectional and generic levels in White's classification and at the subgeneric or generic level in Bakhuizen's classification. Wood characters appear to be useful at the sectional level of Bakhuizen's classification. Like most other taxonomic studies this study only examined a small subset of the total number of taxa in each of the above systems. However, increasing the sample size will most likely increase the variation of each character and therefore, diminish the total variation at each taxonomic rank.

Because White's treatment of the African taxa and Bakhuizen's treatment of the Pacific taxa of the Ebenaceae have not been critically compared with each other or with the Asiatic or South American taxa of Ebenaceae on a world-wide basis, it is impossible to compare these systems at this time.

Wood anatomy as a taxonomic character in Ebenaceae

The classification of the Ebenaceae has been a matter of continued debate. Based on this wood anatomical study

the family as a whole is distinctive, but differences for most wood characters among generic limits are low.

The main wood anatomical differences between the genera Diospyros, Euclea, Royena, and Tetraclis are summarized in Table 29.

Within the genera of the Ebenaceae, the wood anatomical characters are relatively homogeneous with only a few features having more diversity than indicated by earlier accounts. For example, Tetraclis has an exceptionally high degree of vessels per square millimeter. Royena possesses silica grains, one grain per ray body cell, a condition found in only three samples of Diospyros.

The largest genus Diospyros, containing 400 of the 500 species in the family, has features not present in the other three genera such as: semi-ring porosity, longer and wider vessel elements, larger intervessel pit diameters, fiber-tracheids, and storied rays. Furthermore, much of the variation in wood characters within the family occurs among the species of Diospyros. This variation is similar to that in most of the other macromorphological characters and pollen characters used in classifying Diospyros. Until additional anatomical and morphological characters are fully studied a phylogenetic analysis cannot be completed, and the generic delimitations will remain problematic.

Wood anatomy of other families in the Ebenales

Symplocaceae: The wood characters of the Symplocaceae are often used in systematic wood anatomy and in wood identification. The wood is diffuse-porous or rarely semi-ring-porous. Growth rings are absent to distinct. Vessel frequency varies from 12-271/mm². Vessels are typically solitary or in radial multiples of 2 or rarely in radial multiples of up to 4. Pores are angular to oval in outline. The mean tangential diameter of the pores range from 35 μm to 141 μm . Mean thickness of the vessel wall range from 1.0 μm -3.6 μm . The mean vessel element length ranges from 772 μm to 1836 μm . Inter-vessel pits are opposite or transitional between opposite and alternate and scalariform in outline. The tangential diameter of intervessel pits ranges from 4 μm to 15 μm , but the scalariform pits sometimes are wider. Intervessel-ray pits are opposite or transitional between opposite and alternate or tending to alternate and are half-bordered to almost simple or scalariform in outline. Perforations plates are scalariform with 9-59 bars. Spiral wall thickenings are absent, present in tails only, or well developed. Tyloses occur in only a few specimens. Warty cell wall layers occur in only a few specimens.

Imperforate tracheary elements are composed of fiber-tracheids. Mean length of fibers ranges from 1170 μm to 2920 μm . Mean thickness of fiber walls ranges from 2 μm to

10 μm . Pits are conspicuously bordered and 4-8 μm in diameter, with slit-like apertures and occur pits on both radial and tangential walls. Spiral or annular thickening are absent, restricted to fiber tips, or well developed.

Axial parenchyma is scanty paratracheal and apotracheally diffuse (very sparse to fairly abundant). Axial parenchyma strands range from 4-8 cells in length.

Heterogeneous rays are of Krib's type I and occasionally type II. Uniseriate rays range in frequency from 2 to 13 /mm. Multiseriate rays range in frequency from 2 to 11 /mm, in width from 2-11 cells, and in height up to 3.4 mm (usually much lower). Sheath cells are sometimes present.

Crystals are mostly absent, but if present they are either irregularly and rhomboidal or fragmented into crystalline masses. Crystals are generally borne in ordinary ray cells, rarely in chambered ray cells, or rarely in axial parenchyma cells. Silica bodies are absent. Pith flecks are rarely present (Oever et al., 1981)

Styracaceae: As compared with the other families of the Ebenales the wood anatomy of the Styracaceae contains a considerable amount of variation. Wood is usually diffuse-porous, infrequently semi-ring-porous or infrequently ring-porous. Growth rings are absent, indistinct, or distinct. Vessel frequency varies from 7-113/mm². Vessels are

typically solitary, or in radial multiples of 2-6, or rarely in radial multiples of up to 8. Pores are angular to circular in outline. The mean tangential diameter of the pores ranges from 43 μm to 158 μm . Mean thickness of the vessel wall ranges from 2 μm to 3 μm rarely 4 μm thick. The mean vessel element length ranges from 345 μm to 1520 μm . Inter-vessel pits are opposite or transitional to alternate and circular in outline. The tangential diameter of intervessel pits ranges from 4 μm to 10 μm . Intervessel-ray pits are similar to intervessel pits in outline and size except intervessel-ray pits are half-bordered. Perforations plates are predominately scalariform with 3-29 bars or rarely simple. Spiral wall thickenings have not been reported. Tyloses occur in only a few specimens. Warty cell wall layers occur in only a few specimens.

Imperforate tracheary elements are composed of fiber-tracheids. Mean length of fibers ranges from 1300 μm to 1800 μm . Mean thickness of fiber walls ranges from 3 μm to 7 μm . Pits are conspicuously bordered and 3-7 μm in diameter, with slit-like apertures and occur frequently on both radial and tangential walls but occasionally on radial walls only. Spiral wall thickenings have not been reported.

Axial parenchyma is scanty paratracheal, apotracheally diffuse in aggregates, or occasionally apotracheally diffuse approaching the banded condition. Axial parenchyma strands range from 2-7 cells in length.

Heterogeneous rays are of Krib's type I and II.

Uniseriate rays range in frequency from 8 to 32 /mm².

Multiseriate rays range in frequency from 6 to 28 /mm², in width from 2-7 cells, and in height up to 1.1 mm. Sheath cells are rarely present.

Crystals are usually present and are frequently borne in chambered axial parenchyma cells and infrequently in ray parenchyma cells. Silica bodies are usually present in combination with calcium oxalate crystals and restricted to the ray parenchyma cells. Pith flecks have not been reported (Dickison and Phend, 1985).

Lissocarpaceae: A comparable description of the wood of the Lissocarpaceae is lacking, but from the available observations a wood description has been formulated to facilitate comparison. Wood porosity is unknown. Growth rings are absent. Vessel frequency per square millimeter has not been reported. Vessel are typically in radial multiples and clusters of 2-9 cells or rarely solitary (24%). Pores are circular in outline. The mean tangential diameter of the pores range from 37 μm to 145 μm . The mean thickness of the vessel wall is unknown. The mean vessel element length ranges from 868 μm to 1464 μm . Inter-vessel pits are opposite or transitional between opposite and alternate and circular in outline. The tangential diameter of intervessel pits is approximately 4 μm . Intervessel-ray

pits are opposite and are half-bordered. Perforations are predominately simple or rarely scalariform with up to 25 bars. Some vessel elements have simple and scalariform perforations at opposite ends. Spiral wall thickenings, tyloses, or warty cell wall layers have not been reported.

Imperforate tracheary elements are composed of libriform fibers. Mean length of fibers ranges from 1434 μm to 2777 μm . Fiber are thick and sparsely pitted. There is no available information about pit size, pit appearance, pit location, or unusual thickenings.

Axial parenchyma is mostly scanty paratracheal and occasionally in biseriate bands. Information about the size of axial parenchyma strands is lacking.

Krib types are unknown. Uniseriate and multiseriate ray frequency is unknown. The height of biseriate rays is unknown. The biseriate condition is often restricted to localized regions along the ray body. Information about sheath cells information has not been reported.

Crystals and silica bodies are absent. Pith flecks have not been reported (Dickison and Phend, 1985).

Sapotaceae: The family Sapotaceae has been poorly studied and a complete description is lacking, but the available information indicates that the family appears to be quite variable. Wood porosity is unknown. Growth rings are absent, indistinct, or distinct. Vessel frequency varies

from 5-20/mm². Vessels are typically solitary or in radial pore multiples of 2-4 or sometimes more. Pores are circular to angular in outline (personal observation). The mean tangential diameter of the pores ranges from 100 μm to 200 μm . Mean thickness of vessel wall is unknown. The mean vessel element length ranges from 300 μm to 1600 μm . Intervessel pits are alternate or sometimes "subalternate" and of unknown outline. Mean tangential diameter of intervessel pits has not been reported. Intervessel-ray pits are large, simple, and round, elongated, or occasionally kidney-shaped. Perforations plates are frequently simple or rarely scalariform with 1-7 bars. Spiral thickenings are infrequent. Tyloses are common and often abundant. Warty layers have not been reported.

Vasicentric tracheids are frequent and occur with very small vessels.

Imperforate tracheary elements are composed of fiber-tracheids to libriform fibers. Mean length of fibers ranges from 800 μm to 2400 μm . Mean thickness of fiber walls is unknown. Pits are few and simple, occasionally small bordered or distinctly bordered, more numerous on the radial than on tangential walls. Spiral or annular thickening not reported.

Axial parenchyma is apotracheal narrowly banded or often apotracheal diffuse. Axial parenchyma strands are commonly 8 cells in length.

Heterogeneous rays are of Krib's type II and type III. Rays range in frequency from 9 to 15/mm. Uniseriate and multiseriate ray frequency is unknown. Multiseriate rays range in width from 2-3 cells and in height commonly to more than 1000 μm . Sheath cells unknown.

Crystals are commonly borne in axial parenchyma cells or infrequently in ray cells, in vessel elements, or in fibers. Silica bodies are common in ray cells, or scattered in axial parenchyma cells, in vessel elements, or in fibers. Pith flecks have not been reported (Kukachka, 1978, 1982).

According to our present knowledge of wood anatomy of the families of the Ebenales, the Ebenaceae contains the greatest amount of variation. Of all the families in the Ebenales, the Styracaceae share the most features with the Ebenaceae.

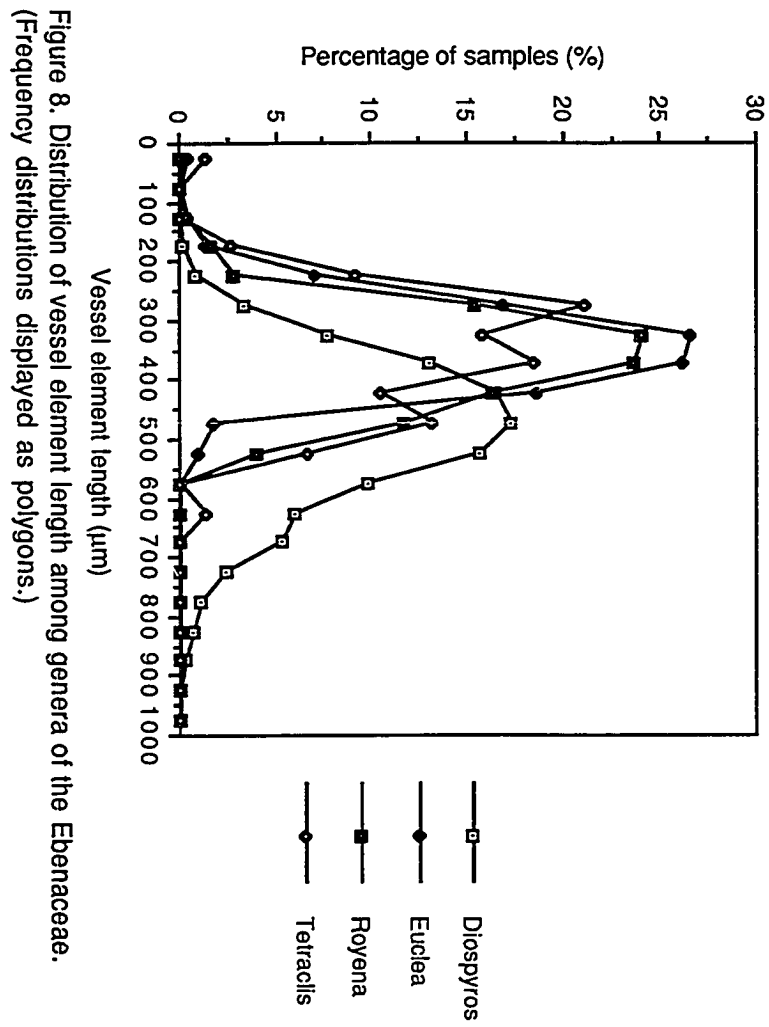
Biological implications of the provenance dependencies

Earlier studies have found in certain wood anatomical features ecological trends that are related to variation in latitude and altitude (Graaff and Baas, 1974; Oever et al., 1981; Zhang et al., 1988). The wood characters concerned are important parameters for two of the vital functions carried out by wood in the living plant: i.e., vessel element size and frequency for water conduction; and fiber diameter, wall thickness, and fiber length for mechanical support. The functional advantages of numerous, narrow, and

short vessels in temperate species have been reported by Zimmermann and Brown (1971) and Zimmermann (1978). Temperate species are subjected to fairly severe frosts in winter, and it is well known that gas bubbles abound in the water column upon thawing, and numerous narrow vessels reduce the risk of local embolism and facilitate faster resorption of gas bubbles. Additional safety provided by numerous short vessels in temperate areas lies in their capacity to prevent embolisms from spreading; embolisms will become trapped at vessel ends which localizes the damage so that it will not incapacitate a major part of the conductive system. Graaff and Baas (1974) found that variation in these wood characters with higher altitude generally follows the higher latitudinal trends. The corresponding advantages of numerous, narrower and short vessels at higher altitudes in the equatorial tropics can be explained because frosts, although sporadic, do occur in the tropical mountains and have effects on the water conducting system similar to those operating in temperate areas. The recent studies of Dickison (1977, 1979) and Dickison et al. (1978) found no relationship between these characters and altitude in the genera they studied. The present study, however, has found at higher latitudes and altitudes an increase in vessel frequency and a reduction in vessel diameter and length. Graaff and Baas (1974) and Oever et al. (1981) found lower vessel frequency and longer and wider vessels with

decreasing latitude. An increase in vessel diameter and length in the tropics is logical if one considers the high transpiration rates in tropical environments and the ample water supply (vs. temperate regions), allowing efficient water transport with a reduction in the need for embolism protection. Safety and efficiency are also related to vessel length. The advantage of longer vessel elements for efficiency is self-evident; conduction is more efficient in vessel strands with fewer endwalls to offer resistance. The present study confirms the observations of Graaff and Baas (1974) and Oever et al. (1981). Graaff and Baas (1974) and Oever et al. (1981) also reported shorter and sometimes narrower fibers in temperate species and longer and sometimes wider fibers in the tropical species. The study found longer fibers and wider fibers for both tropical and temperate species. Recent reports from other wood anatomists (T. Terrazas, pers. comm.) have also found variation in fiber characters to be unreliably associated with latitude and altitude.

Information from this study of wood anatomy will be useful for identification of ebony products, to help form the basis for establishing a stable phylogeny, and as a basis for future ecological investigations.



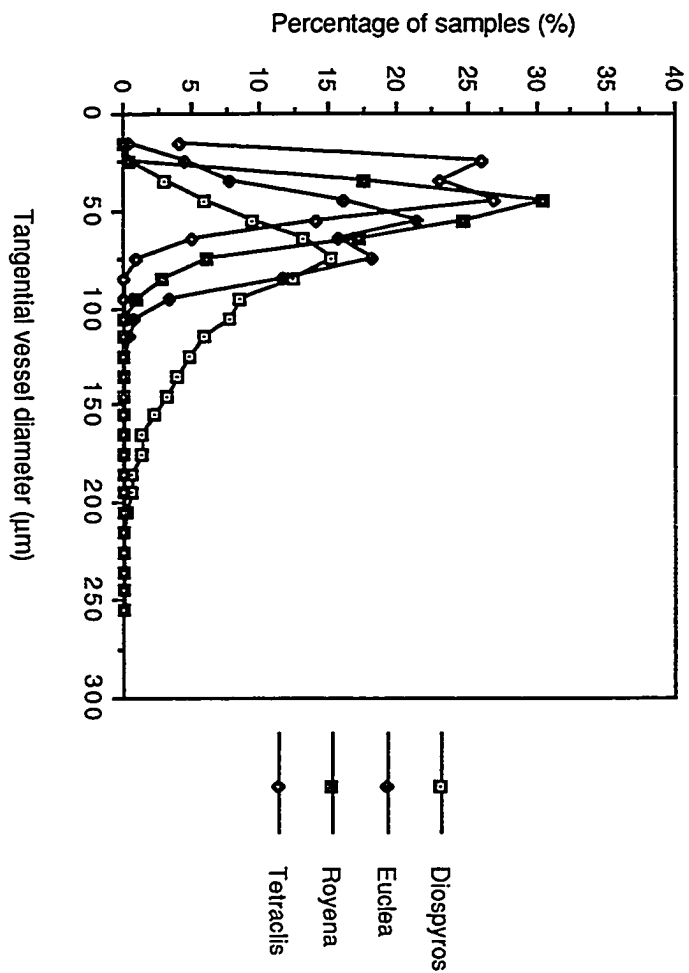
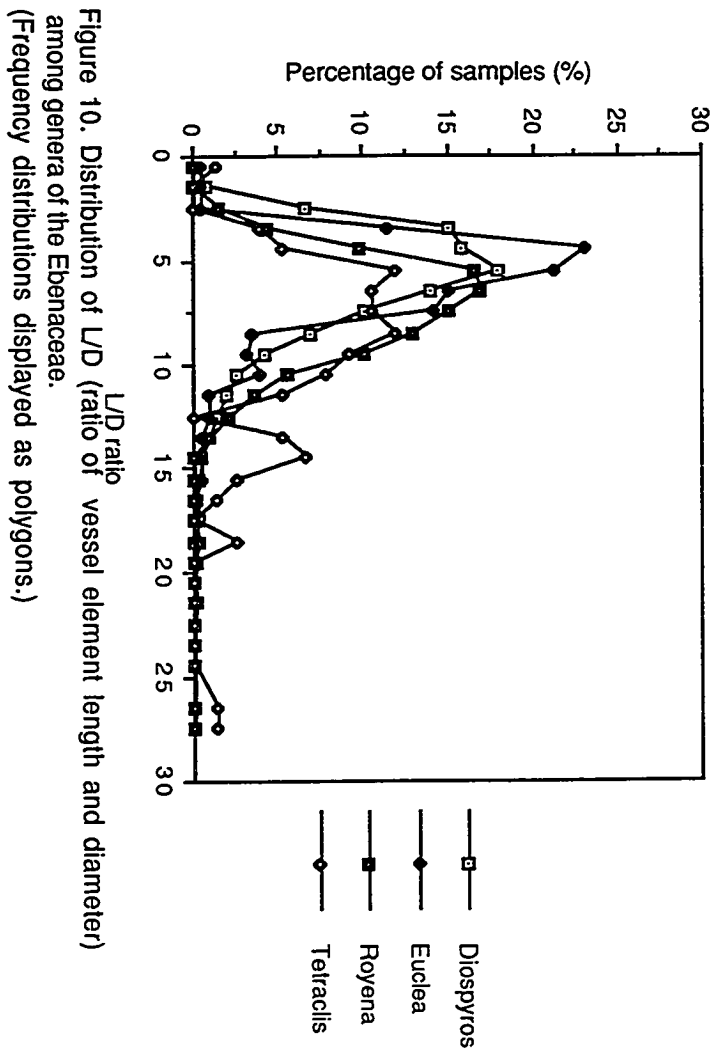


Figure 9. Distribution of tangential vessel diameter among genera of Ebenaceae.
(Frequency distributions displayed as polygons.)



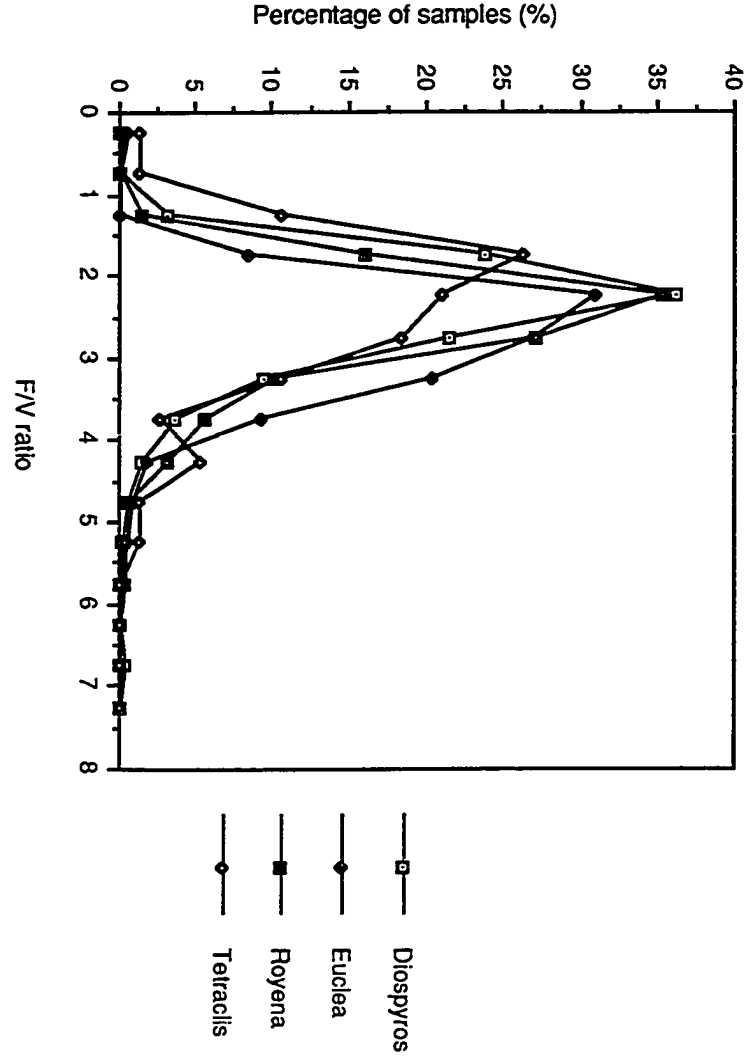


Figure 11. Distribution of F/V (ratio of fiber to vessel element length) ranges among the genera of Ebenaceae. (Frequency distributions displayed as polygons.)

Table 14. Statistically analysed quantitative wood anatomical characters of Ebenaceae.

	Taxa	G	SP	VFR	SD	VFR-SOL	SD1	VED	SD2	VWT	SD3	VEL	SD4	FD	SD5
1	<i>D. abyssinica</i> 3444	1	1	32.60	7.88	41.74	9.81	49.86	5.07	4.69	.73	341.47	64.43	4.37	1.32
2	<i>D. abyssinica</i> 13327	1	1	28.90	3.41	47.68	11.16	56.12	7.04	4.34	.91	347.01	59.58	4.81	1.68
3	<i>D. acuminata</i> 17872	1	2	9.10	3.04	44.03	17.87	86.32	8.12	4.50	.84	554.71	92.94	4.59	1.04
4	<i>D. acuta</i> 17871	1	3	8.80	2.10	46.72	22.83	58.94	12.95	4.11	1.14	596.40	90.80	5.42	1.77
5	<i>D. affinis</i> 17873	1	4	23.10	4.93	34.84	13.12	56.17	9.24	4.73	.93	473.60	69.69	4.81	1.57
6	<i>D. amazonica</i> 16817	1	5	15.70	4.17	32.62	8.61	101.49	12.21	5.53	.92	507.20	113.69	6.08	1.58
7	<i>D. amazonica</i> 13374	1	5	20.80	3.39	67.23	14.56	92.36	9.83	4.41	.91	444.22	107.81	9.81	2.62
8	<i>D. amboinensis</i> 13256	1	6	17.10	4.56	49.81	16.88	106.43	11.61	4.28	.79	575.93	108.77	5.38	1.21
9	<i>D. amboinensis</i> 13257	1	6	7.30	2.91	70.45	22.89	115.44	13.62	3.91	.88	494.40	107.59	6.30	1.39
10	<i>D. andersonii</i> 13385	1	7	4.90	2.13	39.00	27.78	70.22	8.33	4.10	1.02	402.60	105.03	5.68	1.24
11	<i>D. andersonii</i> 13388	1	7	14.00	4.97	65.96	14.91	71.22	9.84	3.91	.90	561.00	80.17	4.74	1.03
12	<i>D. anisandra</i> 13393	1	8	52.90	11.33	40.45	7.25	50.10	5.45	3.82	1.01	380.40	52.02	6.46	1.84
13	<i>D. apiculata</i> 13219	1	9	14.70	4.99	12.45	10.55	82.55	6.22	3.61	.70	561.60	127.20	6.86	1.47
14	<i>D. aranthaeolia</i> 13614	1	10	5.20	3.12	53.29	31.26	110.94	17.61	5.00	1.19	0	0	11.89	2.94
15	<i>D. aranthaeolia</i> 16816	1	10	9.20	2.86	70.63	21.07	94.87	9.67	4.70	.84	523.68	94.87	11.34	3.47
16	<i>D. batocana</i> 15110	1	11	10.50	5.50	19.48	16.74	76.14	8.84	5.21	1.08	417.40	58.53	6.34	2.22
17	<i>D. batocana</i> 13367	1	11	14.20	2.78	47.01	13.13	79.10	12.93	5.33	1.05	341.60	69.07	5.82	1.54
18	<i>D. bipindensis</i> 17978	1	12	13.60	5.06	35.90	19.57	72.16	8.96	4.77	1.16	376.00	58.72	5.49	2.31
19	<i>D. bipindensis</i> 13308	1	12	30.40	6.88	40.13	9.33	69.05	7.26	4.31	.72	379.40	58.37	5.87	1.36
20	<i>D. bourdillonii</i> 17360	1	13	39.50	5.44	43.83	11.94	64.84	11.21	4.48	.86	422.20	74.65	7.10	1.47
21	<i>D. bourdillonii</i> U32717	1	13	13.90	6.82	44.01	18.73	95.32	13.89	4.95	1.20	397.40	68.22	7.58	2.36
22	<i>D. canaliculata</i> 13317	1	14	14.00	3.02	57.13	21.10	69.32	9.80	3.55	.99	490.86	58.15	6.39	1.93
23	<i>D. canaliculata</i> 13898	1	14	12.50	3.03	46.08	13.54	73.52	9.34	4.56	.88	536.84	116.39	6.06	1.69
24	<i>D. carbaea</i> 13439	1	15	13.00	2.75	46.67	17.38	81.45	8.20	4.12	.96	474.82	80.92	6.35	1.76
25	<i>D. carbaea</i> 15811	1	15	10.90	1.91	50.15	10.18	84.97	8.82	4.54	1.19	462.60	68.76	7.24	1.55
26	<i>D. castanea</i> 17361	1	16	19.30	3.86	38.43	13.19	89.85	11.70	5.10	.92	450.25	83.17	5.71	1.40
27	<i>D. cauliflora</i> 13250	1	17	8.40	2.59	42.91	17.79	131.32	13.09	5.43	.84	485.20	65.25	9.89	2.27
28	<i>D. cauliflora</i> 13043	1	17	5.50	1.18	35.10	17.08	113.13	16.01	5.30	1.02	525.06	90.03	8.11	1.66
29	<i>D. christophersenii</i> 13410	1	18	9.90	2.47	45.32	26.37	73.18	11.61	4.37	1.04	610.27	83.43	7.82	1.75
30	<i>D. conzattii</i> 13394	1	19	11.80	3.68	76.43	15.48	57.78	5.71	4.19	.68	407.20	69.87	6.75	1.49
31	<i>D. cooperi</i> 1027	1	20	14.60	3.50	73.57	14.27	64.60	7.91	4.57	1.11	472.48	112.39	5.19	.71
32	<i>D. cooperi</i> 3430	1	20	13.40	3.60	51.63	27.12	64.00	8.21	3.96	.68	458.00	66.24	5.92	1.56
33	<i>D. crassiflora</i> 13897	1	21	0	0	0	0	78.57	7.47	3.53	1.06	478.40	78.18	8.27	1.23
34	<i>D. crassiflora</i> 13318	1	21	12.20	5.81	43.35	24.19	76.19	7.85	4.78	.94	462.80	43.21	10.91	2.49
35	<i>D. cuneata</i> 13386	1	22	27.40	3.89	43.92	11.06	56.69	7.12	5.31	1.12	434.00	79.92	6.63	1.81
36	<i>D. cupulifera</i> 17925	1	23	99.00	15.76	59.27	5.00	38.74	9.05	4.59	.88	459.40	56.63	4.58	1.11
37	<i>D. dasyphylla</i> 17362	1	24	26.40	3.89	39.56	11.43	68.11	10.23	4.09	.81	528.20	92.68	7.97	2.58

	FWT	SD6	FL	SD7	MRF	SD8	URF	SD9	MRW(c)	SD10	MRW(µm)	SD11	MRL(c)	SD12	MRL(µm)	SD13
1	3.66	.95	912.14	165.48	38.20	9.00	19.50	4.81	2.09	.29	19.11	4.31	17.65	7.76	344.51	173.09
2	2.55	.63	765.80	141.19	16.64	4.34	48.45	4.66	2.00	0	21.22	3.43	15.75	3.73	295.81	79.54
3	1.96	.36	1100.00	158.11	2.00	1.63	35.10	3.25	2.00	0	21.02	0	11.50	3.54	246.19	47.69
4	3.71	1.00	1116.40	288.31	.10	.32	37.80	6.09	0	0	0	0	0	0	0	0
5	3.21	.64	1009.00	146.82	13.40	3.56	34.70	6.58	2.00	0	24.69	4.78	14.13	3.80	383.20	122.69
6	3.97	.86	1422.00	196.50	15.20	2.74	60.70	8.96	2.14	.38	20.61	5.30	13.29	5.06	635.28	353.43
7	2.92	.80	1321.40	365.83	1.00	1.18	92.79	30.27	2.00	0	32.31	5.76	16.50	13.44	790.67	556.08
8	4.11	.71	1132.09	175.98	0	0	137.00	15.07	0	0	0	0	0	0	0	0
9	3.60	.90	1238.81	168.00	.69	.85	58.23	8.58	2.00	0	27.54	0	23.00	0	626.91	0
10	4.33	.98	1183.26	113.40	.57	.79	43.00	3.32	2.48	.60	26.15	5.12	15.24	5.51	403.19	137.69
11	5.74	.99	1433.20	222.03	2.20	1.55	38.40	5.97	2.00	0	21.68	2.06	12.86	3.53	475.41	150.79
12	3.11	1.08	899.87	198.70	6.00	1.73	19.00	9.16	2.00	0	32.68	4.75	9.20	1.30	312.68	142.95
13	3.70	.91	1230.11	138.52	2.00	1.94	45.30	5.56	2.00	0	22.84	5.31	15.00	3.61	647.99	201.62
14	2.09	.49	0	0	12.10	2.51	36.20	6.81	2.00	0	25.15	2.59	18.86	9.27	743.88	393.92
15	3.03	.65	1230.98	152.10	.20	.42	40.50	5.78	2.00	0	31.70	0	9.00	0	570.20	0
16	3.24	.69	1006.42	113.90	4.60	2.41	39.90	5.95	2.00	0	37.18	6.88	14.25	3.69	641.43	130.42
17	3.09	.73	924.47	129.52	11.50	3.63	36.30	4.52	2.00	0	25.43	5.59	19.40	7.06	596.51	216.97
18	4.02	.81	1034.12	126.41	7.00	3.16	51.10	3.67	2.00	0	19.89	4.75	6.00	0	214.42	29.38
19	3.54	.81	890.03	110.98	13.20	2.15	33.20	4.34	2.00	0	19.58	2.04	26.11	12.47	580.41	270.93
20	3.07	.65	929.39	102.97	5.20	2.10	35.90	6.69	2.00	0	23.26	3.73	16.25	7.41	548.16	249.48
21	2.77	.96	946.31	123.65	8.70	2.67	56.50	10.19	2.00	0	33.95	5.66	5.25	.96	177.41	46.64
22	3.76	.96	1263.95	142.31	4.70	2.11	47.10	4.82	2.00	0	22.28	0	6.00	0	227.97	0
23	3.95	.71	1274.77	110.01	.10	.32	50.60	4.93	0	0	0	0	0	0	0	0
24	3.41	.70	1189.53	112.97	21.50	5.60	25.10	5.02	2.12	.35	21.17	4.21	22.75	8.05	549.26	170.38
25	3.47	.79	1084.86	98.97	3.40	2.12	32.10	4.43	2.00	0	26.77	7.33	26.67	6.43	858.93	228.27
26	3.39	.78	1106.67	100.23	0	0	49.10	6.19	2.00	0	28.21	0	7.00	0	211.80	0
27	2.38	.56	1048.94	121.74	1.00	1.55	61.55	9.70	2.00	0	24.06	0	17.00	0	426.93	0
28	2.64	.53	1095.68	103.09	3.00	1.32	82.67	8.19	2.00	0	22.34	5.66	14.50	3.54	322.11	96.03
29	3.46	.81	1160.40	119.03	2.90	2.08	42.10	3.98	2.00	0	25.99	0	21.00	0	959.54	0
30	2.52	.41	1157.18	121.19	17.40	1.71	40.20	4.65	2.00	0	23.48	3.65	13.70	4.71	369.90	114.89
31	3.58	.63	1349.06	179.33	3.50	1.72	56.30	5.56	2.00	0	19.04	3.72	10.67	.58	428.57	42.24
32	3.86	.67	1117.49	118.40	.80	.92	55.30	4.88	2.00	0	17.48	2.35	7.50	.71	249.96	9.06
33	2.92	.81	1200.76	142.19	0	0	0	0	2.00	0	26.06	3.41	23.00	6.93	1041.70	388.10
34	2.90	.54	976.13	121.96	9.40	1.71	41.20	4.29	2.00	0	22.38	5.40	12.20	5.36	365.90	133.75
35	3.44	.47	989.90	105.59	20.70	4.30	39.30	6.88	2.00	0	29.07	3.70	13.33	3.71	413.11	138.01
36	4.01	.72	1035.66	144.50	8.60	1.84	55.70	6.39	2.00	0	23.20	3.70	12.25	2.92	340.96	114.29
37	2.39	.56	980.06	132.22	4.60	2.37	33.60	3.69	2.00	0	24.57	0	22.00	0	647.67	0

	UFW (um)	SD14	URL (c)	SD15	URL (um)	SD16	FPD	SD17	IVPD	SD18	IVRPD	SD19	L/D ratio	SD20	F/V ratio	SD21	C	S	LAT	ALT
1	17.11	2.07	11.00	0	229.96	36.81	2.02	.46	5.44	.86	3.94	.69	6.88	1.28	2.79	.86	2	0		0
2	15.50	2.76	13.29	5.41	255.63	100.35	2.27	.39	4.28	.42	3.18	.40	6.27	1.29	2.26	.51	2	0	6.20	75
3	13.75	2.75	8.74	4.20	254.56	91.66	2.20	.26	3.95	.49	3.79	.47	6.50	1.33	2.05	.51	3	0		0
4	20.02	2.96	7.52	3.64	495.39	185.68	2.18	.36	4.83	.77	4.24	.52	9.96	4.19	1.51	.78	2	*	7.09	21
5	19.18	2.93	10.12	4.69	312.00	131.62	2.11	.42	4.23	.50	4.82	.54	8.68	1.94	2.20	.59	2	0	7.09	240
6	16.83	3.56	8.39	5.92	486.75	241.88	2.31	.45	6.92	.64	6.87	.69	5.09	1.46	2.98	.96	2	0	1.16	50
7	24.57	4.01	11.30	8.37	610.89	357.03	1.98	.38	6.62	.68	7.06	1.45	4.89	1.43	3.14	1.17	*	0	5.14	350
8	15.37	2.02	8.96	3.30	440.89	149.90	2.57	.39	6.50	.47	6.41	1.41	5.49	1.34	2.03	.46	1	0	2.37	50
9	16.38	2.79	15.08	7.67	459.87	218.61	2.62	.41	7.22	.68	6.54	1.03	4.35	1.11	2.66	.82	1	0	2.37	50
10	14.29	2.42	5.50	1.00	249.07	42.20	1.66	.30	4.10	.36	5.12	1.84	5.79	1.56	3.14	.91	2	*	16.14	200
11	13.02	2.55	13.72	8.41	464.70	217.38	2.36	.52	4.35	.42	4.31	.68	7.96	1.19	2.58	.44	2	0		0
12	22.64	3.69	10.00	2.00	328.67	88.97	2.22	.32	5.08	.56	4.31	.49	7.68	1.35	2.39	.55	1	0	21.20	50
13	18.93	23.09	9.64	3.37	489.61	159.05	2.72	.40	3.02	.24	2.41	.43	6.83	1.61	2.31	.62	2	0	15.00	900
14	20.24	3.79	12.33	7.33	534.31	307.65	2.60	.29	6.68	.56	6.93	.61	0	0	0	0	*	*	3.24	50
15	21.57	2.93	8.96	4.22	496.04	207.92	2.85	.48	8.78	1.34	7.61	1.78	5.59	1.28	2.44	.58	2	0	7.16	100
16	29.40	3.44	12.33	7.61	631.91	413.22	1.94	.45	4.66	.49	4.62	.92	5.54	.87	2.46	.44	2	0	12.00	450
17	18.25	4.43	10.65	4.58	383.73	176.58	2.22	.43	5.42	.54	3.98	.64	4.42	1.13	2.80	.65	2	*	12.00	450
18	15.27	2.75	8.44	2.21	295.99	76.35	2.48	.36	3.26	.18	3.06	.31	5.30	1.13	2.83	.64	3	0	3.26	350
19	14.58	2.85	11.13	6.47	314.65	116.81	1.91	.39	3.80	.61	3.50	.40	5.56	1.07	2.39	.39	3	0	3.06	1250
20	20.92	3.96	7.81	3.98	461.81	198.09	1.69	.26	3.82	.24	4.35	.22	6.72	1.75	2.29	.57	1	0	8.00	500
21	25.10	5.09	6.71	1.93	242.62	61.90	1.35	.27	3.82	.53	3.93	.85	4.27	1.12	2.46	.59	1	0		0
22	20.78	3.58	9.46	4.50	381.30	134.72	2.12	.34	2.64	.50	3.09	.52	7.23	1.38	2.62	.48	3	0	1.13	350
23	16.16	2.34	12.76	6.78	489.62	229.87	2.08	.41	2.46	.33	2.08	.31	7.44	2.02	2.49	.61	3	*	1.12	350
24	14.45	3.22	8.35	3.10	306.01	83.09	2.13	.48	5.13	.33	5.19	1.27	5.88	1.17	2.59	.59	3	0		0
25	18.63	2.84	9.50	3.43	336.48	123.97	2.30	.39	3.04	.23	4.60	.53	5.48	.85	2.41	.49	3	0		750
26	18.17	3.86	6.20	3.32	266.87	85.59	2.01	.26	2.76	.49	3.09	.39	5.13	1.30	2.55	.57	2	0	20.00	350
27	13.75	2.39	12.08	3.65	377.53	100.06	2.72	.43	5.28	.44	2.51	.44	3.71	.55	2.20	.37	3	0	9.26	50
28	15.36	2.07	11.61	5.74	327.20	135.73	2.67	.41	6.20	.50	4.96	.44	4.72	1.04	2.15	.43	3	*	1.16	50
29	18.80	3.60	8.13	3.98	510.50	226.66	2.41	.35	4.93	.50	4.92	.58	8.50	1.61	1.94	.38	2	0	13.40	600
30	19.71	2.58	9.27	3.49	331.20	121.62	2.12	.38	4.56	.42	3.55	.48	7.08	1.21	2.94	.66	3	0	13.40	750
31	15.05	2.89	10.64	5.31	440.23	203.46	1.95	.25	2.64	.30	2.28	.32	7.48	2.21	3.01	.83	2	0	17.00	0
32	18.49	2.80	9.17	4.36	459.75	168.21	1.78	.25	2.17	.38	2.04	.34	7.29	1.56	2.50	.51	2	0		0
33	21.93	2.85	10.96	5.39	573.55	268.09	2.17	.29	4.46	.25	3.92	.41	6.12	1.05	2.58	.53	*	*		350
34	17.48	4.24	10.70	4.39	389.89	132.23	2.24	.43	3.13	.28	3.20	.41	6.13	.78	2.14	.40	2	0	1.12	350
35	24.02	3.79	9.00	3.46	310.99	67.76	1.77	.19	3.44	.34	4.11	.71	7.77	1.63	2.35	.48	3	0	1.38	0
36	17.46	3.00	8.53	3.38	278.85	89.91	2.29	.30	6.83	.63	4.22	.47	12.34	2.81	2.30	.50	*	*		0
37	20.45	2.67	11.46	6.89	424.45	217.26	1.78	.28	1.98	.26	1.88	.19	7.90	1.77	1.93	.54	3	0		600

	FWT	SD6	FL	SD7	MRF	SD8	URF	SD9	MRW (g)	SD10	MRW (µm)	SD11	MRL (g)	SD12	MRL (µm)	SD13
38	3.23	.87	866.18	167.41	18.00	5.23	51.20	7.70	2.00	0	22.66	3.15	11.86	3.58	304.54	137.94
39	3.20	.61	1130.62	101.67	14.30	2.26	41.80	3.39	2.00	0	19.80	4.39	12.20	6.18	385.35	181.26
40	3.68	.74	1247.88	158.26	9.50	2.72	34.40	4.27	2.00	0	33.74	6.88	20.40	6.35	640.26	262.96
41	3.02	.72	1201.77	154.79	4.00	1.70	45.40	5.60	2.00	0	23.89	5.54	15.60	6.58	488.88	182.52
42	4.39	.94	1209.46	162.81	31.80	3.39	15.00	3.05	2.00	0	22.45	3.90	17.13	6.92	589.04	237.05
43	4.02	1.00	1435.66	170.97	5.50	1.65	41.60	4.60	2.00	0	26.11	0	7.00	0	216.14	0
44	3.47	.92	1261.03	141.12	2.30	1.83	44.60	4.95	2.00	0	30.44	8.40	13.00	9.90	404.41	303.97
45	3.97	.94	1083.89	123.98	14.80	2.94	39.50	5.74	2.00	0	30.19	5.65	8.75	3.36	275.54	129.85
46	3.69	.86	803.93	107.87	0	0	0	0	2.00	0	32.59	5.95	11.50	5.42	329.35	195.46
47	4.02	.71	995.32	167.33	34.40	4.77	31.00	5.25	2.00	0	26.95	3.94	13.00	4.69	415.57	182.33
48	3.57	.75	800.98	89.14	26.30	8.87	41.70	12.13	2.00	0	29.27	5.64	14.67	7.84	477.12	249.07
49	2.94	.63	808.84	95.69	12.50	3.24	61.70	8.06	2.00	0	28.16	1.72	11.00	2.51	346.69	101.39
50	3.35	.69	925.45	89.00	16.20	4.10	47.30	6.60	2.06	.24	28.79	5.11	15.71	4.74	511.09	159.05
51	3.86	.86	1072.07	122.73	12.80	2.25	46.40	4.06	2.00	0	29.27	4.04	10.27	1.90	337.61	76.95
52	3.73	.79	1336.76	158.62	4.70	2.36	45.90	3.81	2.50	0	25.06	1.14	11.40	2.07	340.02	74.30
53	3.70	.70	1130.12	138.67	21.60	3.20	30.80	4.24	2.05	.22	25.72	4.14	11.45	2.70	376.49	112.96
54	3.53	.89	1139.97	130.35	1.30	.95	45.70	5.10	2.00	0	23.97	3.25	12.50	4.95	405.22	12.42
55	4.16	1.23	1198.51	146.06	7.20	2.62	47.60	6.43	2.00	0	26.83	2.54	11.13	3.23	658.79	203.13
56	3.13	.61	1255.59	94.47	30.40	3.31	29.90	5.11	2.06	.24	21.64	3.60	19.53	9.12	555.94	273.64
57	3.35	.54	778.71	95.46	4.80	1.93	74.10	4.04	2.00	0	18.17	3.95	7.71	1.11	224.95	35.67
58	2.65	.72	1184.24	104.46	.90	.88	63.00	7.75	2.00	0	29.34	3.19	17.50	9.19	572.55	323.43
59	3.44	.73	1050.95	113.91	6.30	1.89	34.40	6.50	2.00	0	34.39	6.44	12.71	3.35	573.06	235.20
60	3.52	.91	1063.21	105.22	6.30	2.58	46.40	6.87	2.00	0	21.70	0	18.00	0	532.15	0
61	3.40	.74	1063.21	110.76	1.30	1.16	58.00	3.43	2.00	0	20.80	6.19	10.50	.71	347.20	53.82
62	3.04	.81	1171.45	107.07	.10	.32	49.40	2.63	2.00	0	24.61	0	10.00	0	315.96	0
63	3.27	.95	1110.45	120.49	17.00	3.59	30.00	6.00	2.00	0	23.46	4.02	14.82	5.21	490.44	155.51
64	3.71	.65	0	0	4.80	2.66	47.20	4.87	2.00	0	31.80	5.38	10.50	4.04	481.16	196.74
65	2.67	.63	1175.41	93.79	.80	1.32	55.00	10.45	2.00	0	28.29	0	14.00	0	651.53	0
66	3.29	.78	1110.44	77.18	3.80	2.57	54.20	5.33	2.00	0	22.28	3.81	7.67	.58	367.59	70.01
67	2.33	.57	1072.56	140.60	29.00	4.22	26.80	4.42	2.12	.34	27.76	4.20	14.81	4.12	469.59	138.23
68	2.82	.73	968.75	99.38	1.90	1.45	73.80	5.51	2.00	0	18.85	0	13.00	0	498.99	0
69	2.87	1.22	1104.05	128.63	5.10	1.85	69.80	6.32	2.00	0	27.64	9.35	12.00	4.24	344.79	135.83
70	3.32	.83	1082.40	127.63	8.80	2.53	58.00	6.04	2.00	0	20.50	1.59	13.80	3.83	469.19	111.83
71	6.43	.96	1135.04	141.29	18.60	2.72	56.20	6.79	2.00	0	25.68	3.43	18.00	4.14	602.42	152.05
72	3.18	1.22	1184.24	128.10	34.50	5.04	31.50	4.62	2.44	.51	32.79	7.81	11.39	2.66	371.72	92.64
73	1.94	.50	1098.64	115.91	20.10	3.31	26.60	3.95	2.71	.59	38.16	8.05	10.12	1.65	398.34	41.07
74	3.79	.71	1294.45	110.89	.80	.70	55.60	3.69	2.00	0	25.03	0	19.00	0	717.75	0

	URW(μm)	SD14	URL(c)	SD15	URL(μm)	SD16	FPD	SD17	WPD	SD18	IVRPD	SD19	LD ratio	SD20	FN ratio	SD21	C	S	LAT	ALT
38	16.30	3.66	8.33	4.67	292.97	133.44	1.61	.23	4.65	.40	3.46	.45	10.19	2.31	2.06	.42	1	0	16.27	600
39	15.17	2.22	10.35	3.84	316.99	84.81	1.95	.24	4.63	.80	4.16	.57	7.77	1.32	2.34	.36	3	0	17.00	350
40	21.06	3.80	3.02	3.02	342.20	88.47	2.52	.26	6.30	.55	6.74	.76	3.48	.56	2.34	.43	2	0	1.38	50
41	19.18	3.64	12.30	5.73	391.04	172.08	1.66	.23	7.50	.65	4.83	.66	3.23	.81	2.29	.70	2	1	4.55	0
42	17.69	4.54	11.24	5.77	460.62	273.09	2.53	.44	7.26	.60	7.26	.70	3.30	.64	1.96	.42	1	0	2.50	0
43	24.28	3.40	9.08	4.11	496.51	243.57	2.40	.23	6.86	.77	7.82	.89	4.24	.66	2.31	.47	3	0	*	0
44	21.64	3.10	12.74	6.97	460.88	192.56	2.02	.29	6.02	.53	5.67	.86	4.30	.87	2.39	.44	2	0	*	0
45	19.09	3.93	8.23	2.56	254.12	98.71	2.23	.38	4.88	.45	5.13	1.13	3.66	1.16	2.51	.46	3	1	*	0
46	22.07	4.74	11.64	3.08	339.64	102.47	2.05	.26	3.86	.48	3.46	.52	5.88	1.04	2.08	.43	3	0	8.49	75
47	22.12	5.55	9.31	2.14	321.64	76.64	1.05	.16	4.23	.49	3.31	.50	5.58	1.01	2.70	.82	1	*	7.77	500
48	20.56	4.17	10.75	5.78	386.58	184.78	1.16	.19	4.59	.36	3.57	.88	5.97	1.19	2.10	.34	1	0	8.58	75
49	18.93	3.13	7.29	2.62	320.78	125.47	1.43	.19	3.28	.51	3.64	.49	9.36	2.46	2.28	.56	2	0	9.10	300
50	16.13	3.21	8.13	2.32	370.97	99.03	1.68	.32	3.86	.40	4.26	.88	6.99	1.83	1.82	.43	2	0	17.00	750
51	15.90	2.92	5.43	1.65	297.62	83.44	1.59	.25	3.94	.48	3.77	.62	8.93	3.41	2.17	.56	2	0	*	0
52	16.84	3.26	8.25	3.78	343.85	139.54	1.45	.27	3.68	.32	3.33	.54	16.13	3.58	2.21	.43	2	0	3.48	75
53	17.29	5.24	7.60	3.05	354.87	63.74	1.69	.22	5.73	.49	4.61	.45	3.02	.56	2.78	.51	0	0	*	300
54	18.55	3.77	10.00	5.99	497.97	228.69	1.87	.22	5.07	.45	5.08	.41	6.06	1.66	2.10	.41	0	0	7.50	50
55	21.43	3.34	7.71	3.20	592.04	241.40	1.95	.33	4.47	.31	3.62	.49	6.98	1.41	2.06	.49	0	0	3.08	50
56	13.90	3.44	6.50	2.27	306.32	129.58	1.26	.24	5.83	.41	3.57	.52	3.51	.65	2.38	.47	0	0	4.20	50
57	11.76	1.69	8.06	3.00	251.87	98.11	1.44	.41	3.01	.33	3.77	.61	6.51	2.14	2.68	.76	2	0	12.35	1500
58	20.21	4.39	8.04	3.48	391.43	153.05	1.36	.29	4.53	.39	4.06	.47	5.63	1.65	2.54	.91	2	0	6.04	350
59	25.76	3.38	8.56	4.64	469.85	181.40	1.56	.26	4.19	.48	3.91	.57	10.48	3.28	2.22	.49	2	0	21.38	450
60	17.27	2.91	8.25	3.15	429.23	135.54	1.49	.25	4.08	.50	3.86	.92	10.70	2.58	2.21	.44	2	0	21.38	450
61	17.84	3.25	7.65	4.79	494.84	202.43	1.77	.32	4.24	.36	3.94	.61	6.72	1.65	1.82	.53	0	0	6.44	75
62	21.35	3.42	7.33	3.68	517.33	212.01	1.71	.46	4.57	.60	3.99	.84	7.34	1.63	1.88	.38	1	0	8.46	200
63	19.16	3.83	10.79	4.66	412.99	147.52	1.62	.30	1.58	.22	2.48	.31	5.15	.95	2.45	.53	0	0	1.38	350
64	26.25	3.59	7.43	2.01	387.72	148.54	1.50	.33	4.18	.30	3.58	.64	0	0	0	0	0	0	*	0
65	18.57	3.89	9.25	3.63	427.51	143.88	1.60	.24	3.20	.34	3.56	.83	3.82	.88	2.30	.50	1	0	14.25	150
66	17.51	4.67	6.46	3.07	353.03	132.30	2.14	.27	4.39	.39	4.16	.75	11.74	3.88	2.65	.68	0	0	13.00	100
67	17.69	2.35	9.78	2.91	392.48	144.29	1.57	.23	4.38	.34	4.44	.65	5.66	1.44	2.85	.87	1	0	23.32	350
68	18.47	3.23	9.04	4.10	419.80	192.01	2.07	.31	6.24	.51	5.42	.58	4.84	1.38	1.98	.69	1	0	10.20	50
69	20.16	3.58	10.87	4.12	401.78	149.26	2.33	.23	5.25	.44	4.58	.61	4.23	1.24	2.06	.48	1	0	10.20	50
70	15.56	2.82	9.95	4.26	386.59	167.18	1.19	.28	2.06	.15	1.91	.23	6.64	1.32	1.95	.30	2	0	4.00	750
71	15.65	2.84	7.88	3.29	352.97	92.40	1.34	.27	2.26	.19	1.79	.23	6.90	1.39	2.49	.57	2	0	4.50	100
72	20.39	5.47	9.57	5.03	374.93	184.89	2.16	.44	4.70	.47	3.24	.31	3.03	.91	3.28	.57	3	0	22.00	100
73	21.54	4.28	6.38	1.51	401.58	55.21	2.22	.43	5.58	.41	4.10	.47	2.62	.64	2.98	.50	1	0	22.00	1500
74	19.37	3.11	8.21	3.02	467.68	123.66	1.57	.26	3.84	.23	3.51	.37	8.11	2.21	2.41	.68	2	0	24.00	100

	Taxa	G	SP	VFR	SD	VFR-SOL	SD1	VED	SD2	VWT	SD3	VEL	SD4	FD	SD5
75	D. kamerunensis 13307	1	47	13.50	7.06	51.88	14.55	82.37	11.49	3.29	.59	466.60	69.43	6.20	1.53
76	D. kirkii 15111	1	48	17.70	2.45	32.97	8.30	80.50	10.84	4.09	1.06	486.60	77.72	5.88	2.63
77	D. litosoides 13389	1	49	4.80	2.70	49.50	33.13	105.48	11.41	3.77	1.14	507.60	88.57	7.20	3.05
78	D. maitogrossensis 13438	1	50	11.80	1.55	50.19	4.16	87.27	11.63	3.83	1.09	406.20	76.98	6.35	1.87
79	D. mespiliformis 13370	1	51	11.30	3.53	18.51	11.46	92.03	14.10	4.65	.87	352.10	86.22	5.38	1.08
80	D. mespiliformis 13348	1	51	9.30	3.02	60.97	21.04	86.14	11.25	4.74	1.17	460.60	76.07	4.57	1.44
81	D. mweidensis 17378	1	52	23.50	6.15	63.65	14.29	74.72	9.72	3.82	1.02	310.60	69.47	6.40	2.80
82	D. mweidensis 17379	1	52	28.10	5.74	52.33	13.12	129.64	17.72	7.05	1.58	338.80	49.25	7.46	1.73
83	D. minhasae 17376	1	53	34.10	8.02	59.04	19.67	68.99	8.59	3.61	.77	642.34	111.27	6.01	1.24
84	D. monbutensis 17979	1	54	14.50	2.51	69.62	12.29	84.65	12.81	3.46	1.03	409.34	74.38	7.67	2.62
85	D. montana 17891	1	55	36.30	4.11	55.44	9.59	67.07	9.50	4.81	1.09	361.60	49.43	5.33	1.41
86	D. montana 17890	1	55	37.20	4.52	45.89	5.95	65.98	7.67	4.36	1.17	425.80	56.56	6.33	1.54
87	D. morrisiana Uw 27012	1	56	4.80	.63	37.17	17.45	120.42	18.25	5.11	1.28	482.60	32.15	12.14	3.79
88	D. morrisiana Uw 21645	1	56	4.10	.74	67.83	24.15	122.65	15.56	5.74	1.23	477.80	46.77	10.16	2.80
89	D. myrmecocarpa 17590	1	57	6.40	1.78	20.99	19.14	110.49	13.72	3.82	.68	453.20	71.63	10.62	2.29
90	D. natalensis 17930	1	58	40.90	4.68	76.32	8.99	34.42	4.86	2.57	.66	389.60	62.13	2.84	1.05
91	D. nummulialoia 17888	1	59	22.20	3.55	57.68	10.19	56.73	6.18	2.88	.59	472.40	82.93	3.78	1.13
92	D. paralela 13376	1	60	7.70	1.49	74.73	10.73	76.02	9.75	3.86	1.03	469.20	96.94	10.39	2.87
93	D. pentamera 13345	1	61	10.44	2.51	64.14	17.15	74.41	9.89	3.92	1.09	454.20	76.64	6.28	2.61
94	D. pentamera 13346	1	61	12.00	2.36	52.22	10.50	89.61	18.94	4.54	1.07	558.12	62.98	7.70	2.76
95	D. peruviana 13424	1	62	9.20	1.14	39.19	14.76	87.52	14.07	3.98	1.12	539.40	85.49	7.28	2.26
96	D. peruviana 13425	1	62	6.60	2.37	65.85	24.60	82.10	10.74	3.60	.73	608.20	107.74	9.99	4.38
97	D. philippinensis 13621	1	63	6.60	1.84	68.22	16.82	113.79	9.75	4.87	1.25	442.20	94.85	6.60	2.39
98	D. physocalycina 13305	1	64	19.30	5.56	64.92	14.75	51.94	6.29	2.67	.65	536.60	93.22	6.65	1.94
99	D. physocalycina 14355	1	64	19.80	4.29	48.10	7.53	82.95	9.75	3.84	.95	413.80	59.78	4.96	1.39
100	D. poeppigiana 13430	1	65	9.00	1.56	76.55	14.01	121.91	16.27	3.92	.95	403.82	97.14	9.91	2.42
101	D. poeppigiana 16802	1	65	6.80	1.48	84.92	12.94	91.89	10.78	4.69	.80	576.00	83.52	9.81	2.49
102	D. ponceli 13622	1	66	6.50	1.18	56.52	18.64	153.04	23.64	6.14	.86	509.24	71.99	4.04	1.59
103	D. pseudoxylloia 2872	1	67	4.60	.84	84.00	20.66	169.87	17.68	5.55	1.35	632.60	118.60	10.47	3.16
104	D. pseudoxylloia 13392	1	67	8.80	1.69	41.31	18.70	110.87	13.43	5.70	1.10	551.00	91.13	4.55	2.06
105	D. samoensis 13413	1	68	11.90	3.25	44.27	16.94	61.78	9.61	3.75	.61	395.20	59.55	3.74	1.46
106	D. suaveolens 13321	1	69	7.70	1.64	65.21	29.93	109.73	13.54	4.48	1.23	489.60	77.46	5.24	1.72
107	D. suaveolens 13306	1	69	18.40	4.70	54.67	20.89	127.09	17.25	4.72	1.04	384.80	56.91	6.48	1.66
108	D. sylvatica 17897	1	70	11.50	2.12	58.72	14.80	90.74	9.54	5.21	1.15	435.60	80.56	9.39	2.54
109	D. sylvatica 17388	1	70	7.80	1.87	49.58	19.91	113.36	13.30	5.62	1.45	457.00	67.03	6.46	2.05
110	D. tetrandria 13373	1	71	7.60	.84	53.12	12.01	72.56	8.79	3.63	1.02	667.80	84.42	10.31	2.10
111	D. tetrandria 16795	1	71	7.00	1.89	69.94	19.46	77.34	14.86	3.55	.62	500.00	112.27	7.84	2.04

	FWT	SD6	FL	SD7	MRF	SD8	URF	SD9	MRW (g)	SD10	MRW (µm)	SD11	MRL (g)	SD12	MRL (µm)	SD13
75	2.97	.61	1071.08	116.85	2.80	1.99	61.00	11.79	2.00	0	27.38	5.28	14.00	2.83	483.70	44.55
76	3.05	.61	894.95	96.54	8.80	3.01	66.20	9.61	2.00	0	30.86	2.81	9.30	6.51	369.43	200.10
77	2.40	.55	1128.91	130.47	14.30	1.95	57.40	7.32	2.00	0	23.10	3.50	12.25	3.85	453.47	131.30
78	3.31	.87	1161.12	117.38	17.00	3.30	51.60	6.02	2.08	.29	23.93	2.82	10.42	4.79	399.85	177.63
79	2.83	.66	813.28	115.13	3.10	1.29	69.80	12.46	2.00	0	28.91	6.64	13.50	2.08	444.98	65.33
80	3.31	.91	1023.38	94.42	6.70	2.21	74.30	8.97	2.00	0	32.55	0	12.00	0	442.44	0
81	3.87	.79	996.79	120.44	10.80	3.08	57.80	6.01	2.00	0	21.66	2.58	46.71	88.12	444.88	216.45
82	3.49	.85	815.24	98.94	29.80	5.69	48.90	5.09	2.00	0	31.59	7.74	13.11	6.51	361.09	183.19
83	2.97	.96	1312.14	117.14	5.57	2.82	45.00	7.72	2.00	0	36.13	0	7.00	0	371.86	0
84	2.89	.69	1101.59	136.74	17.20	2.15	44.00	5.12	2.00	0	21.39	2.81	11.57	3.50	444.89	162.36
85	3.67	.88	965.30	131.24	2.70	1.89	82.50	5.93	2.00	0	24.03	0	23.00	0	827.63	0
86	2.92	.76	933.82	118.67	2.30	1.42	81.60	8.96	2.00	0	23.28	2.90	10.75	5.12	361.48	128.00
87	3.08	.53	1243.26	115.00	27.70	3.06	22.80	3.19	2.00	0	22.84	5.33	13.18	2.67	402.51	131.90
88	3.23	1.12	1299.86	198.19	.33	.71	55.44	7.42	2.00	0	32.18	0	22.00	0	687.18	0
89	3.18	.66	1187.20	97.05	20.80	4.21	31.10	6.72	2.17	.38	31.36	5.33	16.33	5.68	664.52	275.09
90	3.25	.80	1029.26	83.70	35.50	3.27	55.80	8.16	2.00	0	17.66	2.92	9.78	2.92	319.09	105.67
91	3.21	.80	1190.64	100.37	8.30	2.31	59.10	4.04	2.00	0	24.90	3.52	9.64	3.23	413.40	149.82
92	2.06	.84	1137.99	136.79	23.40	3.17	45.30	6.22	2.00	0	31.88	4.75	12.67	8.12	506.21	352.21
93	3.66	1.00	1164.56	115.04	9.00	2.94	46.20	8.24	2.00	0	25.99	.52	10.00	0	469.93	14.75
94	2.82	.71	1241.81	79.11	19.10	3.87	38.80	6.23	2.00	0	23.43	3.74	12.78	3.93	463.80	132.36
95	3.03	.83	1152.26	117.64	13.20	1.62	48.50	7.37	2.00	0	29.90	3.23	14.00	7.07	522.58	278.93
96	2.57	.70	1281.66	118.67	1.10	.99	52.20	9.34	2.00	0	26.45	3.15	5.00	0	300.57	34.97
97	2.80	1.05	1093.72	114.17	4.40	2.17	80.40	7.04	2.00	0	29.46	2.20	16.00	1.41	584.69	59.55
98	3.43	1.10	1216.72	100.05	2.60	1.78	64.80	3.91	2.00	0	22.09	8.25	12.50	3.54	545.43	225.39
99	2.99	.80	933.32	99.88	2.80	1.99	62.20	7.55	2.40	.89	23.42	7.16	9.00	3.37	385.37	167.96
100	3.84	.83	1015.49	115.01	5.00	1.76	44.60	6.19	2.00	0	30.33	2.12	10.80	4.32	431.18	138.67
101	2.67	.70	1206.88	119.00	10.40	2.55	36.40	4.30	2.00	0	31.26	7.70	25.25	7.23	919.48	290.20
102	4.08	1.05	1261.98	146.91	7.60	2.76	78.30	6.25	2.00	0	27.45	4.56	8.00	2.65	349.78	101.84
103	4.31	1.10	1374.98	143.32	23.70	3.53	12.40	2.22	2.05	.22	21.18	5.17	19.00	9.44	657.03	299.89
104	3.92	.80	1076.00	107.06	5.90	2.69	39.40	7.23	2.00	0	19.20	3.30	28.75	14.89	908.87	420.85
105	2.68	.73	968.75	110.09	1.90	1.20	80.10	5.42	2.00	0	29.56	.93	15.00	0	341.77	26.14
106	4.21	.84	1206.38	145.44	14.00	4.47	49.40	5.97	2.00	0	19.28	3.00	13.43	5.53	425.32	165.59
107	3.05	.90	934.63	90.86	23.50	3.54	45.90	4.63	2.06	.24	24.01	5.12	13.60	5.74	366.79	154.25
108	3.13	.90	921.52	108.16	2.90	2.33	67.10	4.53	2.00	0	22.53	0	18.00	0	523.74	0
109	2.55	.78	979.08	109.56	27.20	5.87	46.40	7.18	2.07	.27	28.86	6.85	10.57	4.36	337.77	164.46
110	2.65	.60	1215.24	105.99	7.20	2.15	46.30	4.27	2.00	0	22.43	3.44	10.77	2.31	515.41	138.80
111	3.29	.88	1178.34	134.51	3.30	1.83	46.90	4.48	2.00	0	27.52	1.65	15.00	7.07	610.13	296.17

	URFW (um)	SD14	URL (c)	SD15	URL (um)	SD16	FPD	SD17	I/PD	SD18	I/V-RPD	SD19	L/D ratio	SD20	F/V ratio	SD21	C	S	LAT	ALT
75	17.91	3.13	9.00	4.77	436.76	193.69	1.30	.21	3.14	.29	2.97	.51	5.75	1.12	2.37	.61	2	0	5.00	75
76	23.10	3.70	10.23	4.44	372.40	164.30	1.82	.24	3.22	.33	3.40	.35	6.11	1.08	1.89	.37	3	0	3.06	1350
77	18.39	2.98	9.82	6.14	364.73	196.00	1.73	.18	3.95	.43	4.27	.34	4.87	1.07	2.30	.55	2	0	16.00	350
78	18.69	3.84	8.62	2.84	400.19	117.29	2.58	.30	4.98	.42	3.42	.61	4.75	1.15	2.97	.68	1	0	51.45	150
79	24.24	4.46	9.29	3.58	343.69	146.93	1.36	.21	3.01	.35	2.64	.36	3.97	1.39	2.45	.69	3	0	10.46	750
80	19.95	3.60	9.75	5.55	369.10	224.87	1.74	.22	3.77	.34	3.17	.46	5.42	1.12	2.31	.60	1	0	17.00	750
81	20.01	3.62	13.11	7.81	440.79	243.11	2.25	.26	5.71	.54	5.44	.74	4.22	1.12	3.38	.91	2	0	20.30	750
82	20.53	3.72	11.02	6.07	331.07	180.29	2.23	.43	6.53	.46	4.67	.58	2.68	.64	2.45	.46	3	0	7.00	750
83	24.58	5.15	8.88	7.12	521.88	444.38	1.67	.29	4.13	.32	4.41	.54	9.43	1.96	2.11	.47	2	0	7.00	750
84	21.88	3.19	7.56	4.09	458.20	18.00	1.76	.39	4.88	.49	3.52	.30	4.95	1.20	2.75	.46	3	0	5.50	750
85	20.12	3.17	9.46	4.87	334.82	173.06	1.71	.32	4.73	.33	3.71	.38	5.53	1.31	2.71	.50	1	0	8.45	100
86	16.78	2.73	11.29	3.54	341.70	116.30	1.57	.17	4.16	.45	3.42	.39	6.54	1.19	2.22	.36	1	0	8.45	100
87	13.97	2.05	6.33	2.08	289.88	84.46	2.01	.39	2.79	.36	3.59	.62	4.10	.67	2.59	.29	0	0	8.45	0
88	20.27	3.62	9.46	4.32	548.35	230.45	1.79	.33	2.60	.29	2.77	.50	3.96	.69	2.77	.62	1	0	29.06	100
89	22.26	2.92	7.43	1.72	401.35	72.90	2.37	.36	4.97	.53	4.27	.77	4.18	.92	2.69	.53	3	0	29.06	100
90	12.05	2.93	7.00	2.08	276.66	64.53	2.00	.43	3.79	.27	3.33	.30	11.55	2.54	2.71	.51	2	0	8.46	75
91	16.64	4.31	7.00	2.60	337.06	75.95	1.81	.26	4.14	.42	3.48	.56	8.43	1.73	2.60	.53	2	1	8.46	75
92	23.74	4.63	6.86	1.57	288.27	67.26	1.68	.33	4.14	.45	2.71	.33	6.32	1.84	2.52	.54	1	0	9.00	350
93	17.41	3.52	9.61	5.68	567.46	332.22	2.22	.33	4.14	.27	4.77	.96	7.41	1.23	2.17	.32	1	0	30.07	50
94	18.86	3.22	6.88	3.03	338.45	114.78	1.80	.30	4.35	.34	3.92	.48	6.53	1.68	2.25	.23	2	0	33.00	100
95	22.53	4.52	8.47	3.34	332.51	87.85	2.35	.34	4.90	.46	5.06	.73	6.30	1.34	2.18	.36	0	0	2.00	350
96	18.64	4.04	6.22	3.38	469.63	191.58	2.37	.37	5.83	.51	4.82	.81	7.60	1.98	2.18	.51	2	0	2.00	350
97	20.19	2.80	9.04	5.54	344.04	195.68	1.57	.35	5.92	.54	5.69	.37	3.91	.87	2.57	.57	1	0	12.00	50
98	17.26	2.76	7.35	3.98	438.65	221.99	1.37	.27	2.16	.22	1.58	.27	10.43	1.98	2.34	.48	3	0	6.00	75
99	19.42	2.68	6.90	2.73	330.47	117.10	1.40	.16	2.43	.24	2.27	.33	5.04	.86	2.30	.41	3	0	3.66	350
100	25.82	4.63	9.00	3.85	370.92	127.41	2.07	.34	5.61	.31	4.81	.60	3.37	.93	2.63	.57	0	0	3.08	50
101	25.32	3.96	12.71	7.66	526.72	273.60	2.09	.31	4.76	.35	4.17	.53	6.33	1.07	2.14	.37	2	0	5.00	750
102	22.08	3.99	8.24	3.65	351.66	118.28	2.54	.55	7.38	.57	5.28	.60	3.42	.80	2.54	.54	3	0	12.00	50
103	13.39	7.49	9.25	3.40	343.01	142.45	1.85	.31	4.83	.57	5.28	.31	3.76	.79	2.29	.71	2	0	31.00	50
104	14.04	3.46	14.90	7.32	487.46	229.79	1.43	.21	5.08	.60	5.03	.69	4.99	.79	2.00	.39	0	0	3.22	350
105	21.46	2.94	13.25	8.08	430.93	244.72	1.43	.23	3.66	.34	2.67	.38	6.58	1.51	2.50	.43	1	0	19.08	50
106	16.27	3.04	11.94	7.83	446.14	278.20	1.57	.30	5.33	.43	5.17	.87	4.51	.81	2.53	.56	2	0	3.51	750
107	16.32	3.99	8.40	4.34	283.41	124.33	1.29	.20	3.98	.31	3.36	.56	3.08	.61	2.50	.53	2	0	3.06	75
108	20.30	4.07	10.04	4.33	323.31	113.06	1.67	.21	5.69	.30	4.42	.43	4.86	1.06	2.19	.50	1	0	7.10	575
109	25.58	5.58	7.73	3.69	285.78	126.16	1.47	.18	5.35	.53	4.17	.44	4.07	.66	2.20	.47	1	0	7.28	75
110	14.63	4.05	8.50	2.84	470.11	96.58	1.79	.18	4.06	.26	3.58	.33	9.30	1.37	1.85	.29	1	0	3.00	1500
111	21.26	4.08	11.30	7.44	573.96	292.78	1.45	.16	3.92	.43	4.20	.38	6.71	2.06	2.50	.74	0	0	4.00	100

	Taxa	G	SP	VFR	SD	VFR-SOL	SD1	VED	SD2	VWT	SD3	VEL	SD4	FD	SD5
112	D. thwaitesii 17900	1	72	10.60	2.84	71.36	13.51	133.35	14.12	3.86	1.19	380.00	77.26	6.55	1.76
113	D. thwaitesii 17899	1	72	5.80	3.15	81.24	13.68	112.86	14.05	4.63	.92	705.22	81.95	6.36	1.13
114	D. virginiana 13433	1	73	10.30	2.63	71.05	23.06	125.77	20.83	6.19	1.38	436.80	50.06	9.28	2.62
115	D. virginiana 3440	1	73	8.10	1.66	44.56	15.95	140.73	19.41	8.98	2.06	472.40	47.15	9.12	2.88
116	D. viridicans 13315	1	74	9.20	1.81	43.65	17.18	125.38	11.65	5.49	1.44	429.20	46.11	6.25	1.54
117	D. viridicans 14357	1	74	11.10	3.04	63.44	19.23	78.81	7.70	3.12	.70	472.00	50.97	8.33	3.11
118	D. viliensis 13418	1	75	15.22	2.22	58.04	12.41	69.96	7.52	4.04	1.00	403.40	72.70	6.51	1.49
119	D. viliensis 13417	1	75	17.40	2.46	78.57	8.69	62.59	9.91	3.10	.49	483.00	94.09	7.05	1.67
120	D. zenkeri 13288	1	76	13.60	3.41	66.46	9.28	46.10	6.39	2.94	.78	487.20	106.40	7.99	2.46
121	D. zenkeri 17977	1	76	15.10	3.45	45.64	14.38	64.26	7.07	3.91	.73	414.00	84.39	4.80	1.20
122	Tetracis baroni 17983	4	92	72.75	13.23	70.74	9.47	49.40	10.92	2.35	.44	299.40	68.73	8.91	2.01
123	Tetracis baroni 17982	4	92	70.90	7.71	69.67	8.60	50.21	8.54	2.28	.40	416.00	80.98	8.24	2.26
124	Tetracis clusioides 17981	4	91	96.00	13.52	75.23	1.08	33.50	6.08	1.76	.47	351.00	97.28	6.87	1.96
125	Tetracis ebenifera 17984	4	93	0	0	0	0	33.50	5.83	2.23	.52	0	0	5.94	1.32
126	E. crispa 17816	2	77	38.30	8.25	45.45	8.26	67.07	11.72	3.29	.62	323.60	57.33	7.19	2.55
127	E. crispa 3433	2	77	14.40	1.43	42.40	17.62	71.57	11.07	4.34	1.14	372.20	56.77	6.96	1.97
128	E. divinum 15112	2	78	29.80	3.08	38.13	11.99	31.98	6.73	2.85	.57	267.80	45.05	5.84	2.03
129	E. divinum Mw37202	2	78	29.40	8.93	55.44	13.79	48.87	6.38	4.20	.90	273.80	55.08	4.61	1.68
130	E. lanceolata USw 18539	2	79	16.60	2.95	32.73	12.96	85.38	13.09	3.54	1.20	354.80	49.28	6.96	2.15
131	E. lanceolata 3801	2	79	12.70	5.01	29.59	17.91	72.10	9.82	5.19	1.65	0	0	4.99	1.27
132	E. mayottensis 17928	2	80	13.00	3.59	35.34	13.86	50.30	5.70	2.62	.74	382.40	54.34	4.83	1.25
133	E. natalensis 17817	2	81	21.20	8.46	44.15	14.38	52.05	13.27	2.59	.86	374.80	61.74	6.34	1.52
134	E. racemosa 3442	2	82	9.11	2.85	19.60	15.57	66.39	12.97	4.72	1.46	318.60	42.14	3.70	1.84
135	E. schimperi 955	2	83	20.60	6.13	22.83	11.93	68.68	11.96	5.21	.84	373.20	65.91	6.11	1.34
136	R. dichrophylla 17942	3	84	51.44	17.70	64.34	9.58	40.38	6.81	4.42	.84	330.60	54.13	6.19	1.94
137	R. dichrophylla U22016	3	84	8.70	3.59	26.85	26.39	65.58	10.05	4.84	1.29	393.00	63.02	7.77	2.99
138	R. glabra 17909	3	85	43.78	7.98	43.38	9.96	54.53	14.86	3.10	.84	335.80	61.18	7.37	2.98
139	R. heterotricha 16800	3	86	22.00	5.92	47.07	13.21	45.16	5.67	3.71	.72	356.40	62.89	4.92	2.44
140	R. heterotricha Uw 24539	3	86	18.80	3.65	45.90	9.07	68.98	13.07	3.50	.89	364.20	77.44	8.73	2.54
141	R. lucida USw 18570	3	87	43.60	15.46	45.12	12.91	51.56	9.22	4.37	4.37	378.00	57.12	8.18	2.47
142	R. lucida USw 21416	3	87	80.20	18.07	63.40	8.91	52.10	7.07	4.46	4.46	320.00	44.56	6.59	1.89
143	R. lycioides 17813	3	88	20.80	5.55	40.57	11.25	46.95	6.98	4.59	4.59	415.20	65.09	8.85	3.38
144	R. lycioides 17814	3	88	32.40	5.93	45.35	10.74	44.03	10.41	5.09	5.09	414.80	75.23	10.42	3.33
145	R. pallens USw20434	3	89	17.50	4.97	58.69	16.82	60.64	9.88	3.95	3.95	283.80	56.52	6.45	1.16
146	R. pallens 17907	3	89	33.56	9.17	61.19	10.75	64.77	9.38	4.12	.91	366.00	93.34	10.06	2.90
147	R. whyteana 3448	3	90	29.60	4.53	52.74	12.41	48.35	6.68	4.16	.76	415.60	69.84	7.68	2.29
148	R. whyteana 1325	3	90	27.50	4.12	55.59	10.79	41.45	5.79	3.27	.60	329.40	51.04	7.27	2.28

	FWT	SD6	FL	SD7	MRF	SD8	URF	SD9	MRW(c)	SD10	MRW(µm)	SD11	MRL(c)	SD12	MRL(µm)	SD13
112	2.91	.93	730.62	85.29	1.90	1.20	50.20	3.65	2.00	0	28.59	5.12	10.00	1.41	339.95	32.26
113	3.88	.66	1222.13	173.40	1.40	.97	51.80	5.71	2.00	0	23.13	6.69	11.00	2.83	336.69	129.66
114	3.64	1.06	1263.95	171.40	18.90	2.64	25.90	4.33	2.35	.49	32.76	6.21	12.71	1.90	421.98	61.56
115	3.58	1.12	1310.69	142.52	17.80	2.04	32.50	4.17	2.08	.28	32.49	6.73	10.77	2.20	376.87	61.13
116	3.17	.64	1066.16	151.43	18.00	4.29	29.80	6.65	2.00	0	28.98	4.80	11.73	1.42	401.63	44.83
117	3.17	.69	1174.90	126.14	15.80	2.86	35.80	2.25	2.00	0	32.43	6.43	11.60	3.13	442.45	129.98
118	2.64	.65	988.92	100.87	6.60	2.37	49.80	5.37	2.00	0	23.36	0	25.00	0	901.74	0
119	3.10	.59	1019.92	132.80	1.10	1.73	58.90	3.14	2.00	0	26.74	.57	11.50	.71	486.16	23.70
120	2.57	.61	1129.14	159.15	3.10	2.13	74.80	8.03	2.00	0	24.04	1.49	15.00	4.24	508.35	136.58
121	2.51	.79	990.40	83.20	30.50	4.55	52.50	7.62	2.00	0	23.49	5.48	16.61	10.71	465.00	316.52
122	2.26	.54	739.38	140.08	16.33	1.53	55.33	6.51	2.00	0	23.70	4.78	10.21	3.81	292.99	116.57
123	2.13	.49	972.21	350.58	4.50	3.31	60.80	4.73	2.00	0	20.93	0	7.00	0	329.15	0
124	2.03	.53	713.40	107.41	4.75	2.22	54.75	5.68	2.00	0	13.56	1.65	6.50	.71	348.98	24.01
125	2.31	.54	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	2.00	.71	767.52	49.71	24.70	2.06	38.90	5.13	2.17	.39	28.18	7.01	11.92	2.78	402.69	152.74
127	3.18	.97	925.94	132.83	19.40	4.70	37.40	4.40	2.33	.49	26.19	6.44	15.00	5.77	565.13	239.22
128	2.59	.73	883.14	135.86	18.30	2.71	73.20	5.73	2.00	0	24.08	5.75	11.75	3.10	411.85	123.03
129	3.21	.79	802.94	96.95	25.10	1.73	64.20	9.09	2.00	0	28.96	4.78	11.25	4.43	391.70	168.73
130	1.94	.48	1012.03	131.43	26.70	3.13	35.30	5.46	2.38	.51	30.63	10.51	10.54	4.39	342.68	149.50
131	3.61	.63	0	0	20.90	4.04	33.50	4.53	2.20	.42	28.82	5.70	11.70	7.04	458.26	264.91
132	1.99	.65	971.70	77.87	10.50	1.90	51.90	6.77	2.00	0	26.57	3.58	7.50	3.54	392.57	173.45
133	2.02	.52	824.10	71.90	24.90	2.77	39.90	7.09	2.10	.32	34.18	6.65	10.05	3.92	327.78	90.39
134	3.77	1.12	1068.62	110.55	48.40	4.55	27.60	4.65	2.22	.43	29.02	6.55	14.39	6.30	468.14	246.04
135	2.25	.57	875.27	96.05	30.90	6.56	31.30	5.56	2.05	.22	31.05	6.09	9.76	3.92	384.87	152.52
136	2.80	.39	739.97	73.60	22.50	5.72	73.50	12.06	2.00	0	17.20	0	16.00	0	501.04	0
137	2.72	.58	1225.57	157.35	3.20	3.91	75.50	6.85	2.00	0	18.71	.47	9.00	2.83	221.58	77.81
138	2.29	.79	850.17	134.57	19.00	4.24	37.00	5.66	2.00	0	27.13	4.62	19.83	15.39	654.23	527.13
139	3.14	.99	1016.96	82.64	0	0	0	0	2.00	0	15.66	1.00	7.67	.58	225.80	48.42
140	1.76	.42	982.03	132.46	1.50	1.18	82.70	9.78	2.00	0	20.82	4.21	8.50	3.54	262.29	184.96
141	2.53	.72	813.35	70.77	30.70	3.40	52.60	9.07	2.06	.25	25.42	4.30	17.12	7.56	477.00	208.36
142	2.46	.61	850.18	99.12	10.00	1.94	67.10	6.06	2.00	0	20.89	3.03	13.43	4.47	382.10	141.25
143	2.11	.48	983.00	119.63	3.80	1.93	60.60	6.06	2.00	0	30.55	.45	15.00	7.07	342.31	144.41
144	2.37	.76	846.24	89.26	10.60	4.33	49.70	8.89	2.00	0	29.04	0	13.00	0	551.60	0
145	2.89	.50	797.29	75.51	19.70	2.58	88.10	7.34	2.17	.41	23.82	3.84	11.67	1.75	296.20	47.93
146	2.55	.73	839.35	97.65	3.00	1.73	76.33	9.45	2.00	0	22.09	.45	29.00	0	766.75	6.67
147	2.68	.78	911.68	114.91	23.10	2.51	53.30	7.90	2.30	.47	23.03	4.49	13.40	6.32	360.04	156.08
148	3.08	.60	821.91	103.83	31.90	3.51	64.60	5.82	2.00	0	20.34	2.81	12.56	3.99	308.02	116.67

	URW (μm)	SD14	URL (c)	SD15	URL (μm)	SD16	FPD	SD17	IVPD	SD18	IV-RPD	SD19	L/D ratio	SD20
112	16.78	3.54	7.04	4.14	398.83	193.28	1.66	.34	3.70	.35	4.14	.54	2.90	.74
113	17.16	3.25	10.04	6.03	515.17	277.41	2.08	.35	4.35	.45	4.60	.75	6.34	1.06
114	21.95	2.73	8.50	3.38	347.00	87.83	1.66	.32	4.15	.41	3.36	.32	3.57	.72
115	19.90	2.82	7.42	2.27	328.89	90.39	1.76	.21	4.85	.40	3.57	.38	3.41	.57
116	19.21	3.68	11.07	3.12	382.67	61.47	2.56	.35	7.40	.45	5.49	.85	3.46	.53
117	25.55	5.93	6.80	1.87	343.86	66.29	1.99	.27	7.30	.68	4.85	.52	6.04	.87
118	24.60	2.55	10.42	6.37	423.25	191.45	1.50	.22	2.87	.33	3.37	.65	5.84	1.25
119	22.50	3.27	11.78	7.63	517.59	281.47	1.72	.17	3.16	.26	3.21	.26	7.86	1.84
120	17.12	2.84	6.26	2.54	382.54	153.37	1.79	.31	3.41	.26	3.32	.57	10.82	3.01
121	16.01	3.00	8.58	4.36	302.79	142.75	1.60	.23	2.27	.23	1.62	.21	6.50	1.37
122	12.56	2.08	5.73	3.00	262.05	189.17	1.59	.29	3.11	.44	2.63	.59	6.42	2.42
123	12.70	3.42	10.25	6.09	419.85	232.77	1.64	.22	2.96	.28	2.75	.46	8.47	2.07
124	10.92	2.35	10.56	5.60	616.33	273.24	1.35	.28	2.64	.34	2.86	.54	14.40	5.64
125	10.13	2.13	5.40	2.53	317.33	168.14	1.35	.23	2.01	.20	1.68	.20	0	0
126	16.33	2.41	8.92	5.71	328.73	204.50	1.98	.31	3.67	.28	3.26	.35	4.91	.96
127	15.94	3.61	7.85	3.41	409.15	182.96	1.64	.32	4.26	.43	3.75	.34	5.29	1.01
128	16.72	3.61	7.41	3.95	311.73	149.15	1.47	.24	2.58	.26	3.03	.55	8.77	2.55
129	16.78	3.12	8.62	5.39	343.76	218.78	1.75	.31	2.69	.33	3.29	.56	5.71	1.39
130	19.64	3.26	6.00	1.65	264.80	63.51	1.31	.22	3.94	.58	3.56	.60	4.27	.97
131	16.18	2.20	5.93	2.58	305.67	129.95	2.11	.42	3.98	.34	4.45	.73	0	0
132	16.03	4.16	5.65	1.70	338.75	88.98	1.48	.34	3.39	.28	3.05	.44	7.73	1.62
133	17.37	4.44	8.00	3.35	351.16	131.77	1.55	.23	3.77	.44	3.53	.47	7.73	2.68
134	17.59	3.04	7.57	2.23	270.54	71.41	1.51	.19	3.65	.48	3.25	.63	4.99	1.24
135	21.56	5.33	6.25	1.26	261.96	89.26	1.95	.46	3.81	.40	4.15	.61	5.65	1.41
136	12.75	3.18	5.29	2.23	209.35	113.99	1.53	.21	4.02	.48	4.16	.88	8.47	2.15
137	16.65	4.50	9.91	4.62	346.58	186.27	1.62	.23	4.25	.60	3.71	.41	6.14	1.41
138	19.28	4.46	7.63	2.97	304.08	153.95	1.39	.22	3.40	.31	3.22	.39	6.60	1.99
139	12.67	1.65	6.64	2.36	202.28	61.96	1.99	.31	4.37	.32	4.07	.45	8.01	1.65
140	20.35	2.83	7.52	3.34	307.20	119.02	1.17	.17	3.00	.32	2.26	.38	5.51	1.64
141	14.39	3.73	8.00	4.44	321.18	181.17	1.28	.22	3.23	.35	3.14	.36	7.66	2.17
142	14.08	3.29	6.50	2.71	233.55	88.83	1.12	.27	2.77	.27	2.62	.63	6.26	1.26
143	24.75	3.66	9.56	5.71	426.07	202.25	1.81	.37	4.42	.43	3.77	.63	9.05	2.01
144	19.67	5.24	11.29	8.18	447.10	251.96	1.62	.34	3.87	.42	3.21	.49	9.94	3.00
145	16.57	3.66	8.63	3.39	265.32	101.11	1.97	.36	3.11	.31	3.28	.54	4.79	1.26
146	13.77	3.28	9.04	4.78	457.08	202.39	1.46	.31	3.52	.41	3.26	.35	5.00	1.47
147	14.88	2.41	8.20	4.44	295.59	118.08	1.36	.30	3.40	.32	3.08	.46	8.76	1.96
148	11.58	.91	6.67	1.66	218.40	61.63	1.37	.23	3.07	.45	2.76	.36	8.05	1.44

Explanation of symbols: G=genera studied; SP=species studied; VFR= vessel frequency; VFR-SOL= solitary vessel (pore) frequency; VED= vessel element diameter; VWT= vessel wall thickness; VEL= vessel element length; FPD= fibre pit diameter; FWT= fibre wall thickness; FL= fibre length; MRF= multiple ray frequency; URF= uniseriate ray frequency; MRW(c)= multiple ray width in cells; MRW(μm)= multiple ray width in microns; MRL(c)= multiple ray length in cells; MRL(μm)= multiple ray length in microns; URW(μm)= uniseriate ray width in microns; URL(c)= uniseriate ray length in cells; URL(μm)= uniseriate ray length in microns; FPD= fibre pit diameter; IVPD= intervessel pit diameter; IV-RPD= intervessel to ray pit diameter ratio; VLR= vessel length to vessel diameter ratio; F/V ratio= fiber length to vessel length ratio; C= calcium oxalate crystals; S= silica bodies; LAT= latitude; ALT= altitude; S.D.= standard deviation of the mean.

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SD16	FPD	SD17	IVPD	SD18	IV-RPD	SD19	L/D ratio	SD20	F/V ratio	SD21	C	S	LAT	ALT
93.28	1.66	.34	3.70	.35	4.14	.54	2.90	.74	2.03	.62	3	0	6.20	50
77.41	2.08	.35	4.35	.45	4.60	.75	6.34	1.06	1.76	.32	1	0	6.20	50
87.83	1.66	.32	4.15	.41	3.36	.32	3.57	.72	2.94	.57	2	0	31.52	100
90.39	1.76	.21	4.85	.40	3.57	.38	3.41	.57	2.79	.37	0	0	25.50	19
61.47	2.56	.35	7.40	.45	5.49	.85	3.46	.53	2.51	.45	2	0	6.50	350
66.29	1.99	.27	7.30	.68	4.85	.52	6.04	.87	2.52	.40	3	0	2.60	350
91.45	1.50	.22	2.87	.33	3.37	.65	5.84	1.25	2.53	.54	1	0	16.50	350
81.47	1.72	.17	3.16	.26	3.21	.26	7.86	1.84	2.18	.48	3	0	19.00	150
53.37	1.79	.31	3.41	.26	3.32	.57	10.82	3.01	2.41	.54	2	0	3.26	75
42.75	1.60	.23	2.27	.23	1.62	.21	6.50	1.37	2.50	.59	2	0	3.06	750
89.17	1.59	.29	3.11	.44	2.63	.59	6.42	2.42	2.63	.87	1	0	17.44	400
32.77	1.64	.22	2.96	.28	2.75	.46	8.47	2.07	2.43	.97	2	0	17.10	800
273.24	1.35	.28	2.64	.34	2.86	.54	14.40	5.64	2.21	.78	2	0	20.54	150
68.14	1.35	.23	2.01	.20	1.68	.20	0	0	0	0	0	0	23.00	350
204.50	1.98	.31	3.67	.28	3.26	.35	4.91	.96	2.44	.45	2	-	-	0
182.96	1.64	.32	4.26	.43	3.75	.34	5.29	1.01	2.53	.45	0	0	-	0
149.15	1.47	.24	2.58	.26	3.03	.55	8.77	2.55	3.44	1.11	1	0	-	1420
218.78	1.75	.31	2.69	.33	3.29	.56	5.71	1.39	3.05	.70	0	0	12.00	0
63.51	1.31	.22	3.94	.58	3.56	.60	4.27	.97	2.90	.49	2	0	25.45	1250
129.95	2.11	.42	3.98	.34	4.45	.73	0	0	0	0	2	0	-	0
88.98	1.48	.34	3.39	.28	3.05	.44	7.73	1.62	2.61	.52	2	0	-	0
131.77	1.55	.23	3.77	.44	3.53	.47	7.73	2.68	2.26	.45	2	0	-	0
71.41	1.51	.19	3.65	.48	3.25	.63	4.99	1.24	3.39	.43	2	0	-	0
89.26	1.95	.46	3.81	.40	4.15	.61	5.65	1.41	2.37	.40	2	0	-	0
113.99	1.53	.21	4.02	.48	4.16	.88	8.47	2.15	2.29	.41	0	1	-	250
186.27	1.62	.23	4.25	.60	3.71	.41	6.14	1.41	3.20	.64	0	1	26.15	0
153.95	1.39	.22	3.40	.31	3.22	.39	6.60	1.99	2.60	.56	0	1	-	0
61.96	1.99	.31	4.37	.32	4.07	.45	8.01	1.65	2.94	.57	2	1	-	0
119.02	1.17	.17	3.00	.32	2.26	.38	5.51	1.64	2.86	.92	2	1	-	0
181.17	1.28	.22	3.23	.35	3.14	.36	7.66	2.17	2.21	.41	0	1	25.45	1250
88.83	1.12	.27	2.77	.27	2.62	.63	6.26	1.26	2.69	.39	0	1	-	0
202.25	1.81	.37	4.42	.43	3.77	.63	9.05	2.01	2.44	.56	-	-	-	0
251.96	1.62	.34	3.87	.42	3.21	.49	9.94	3.00	2.09	.37	0	1	-	0
101.11	1.97	.36	3.11	.31	3.28	.54	4.79	1.26	2.94	.73	0	1	25.45	1250
202.39	1.46	.31	3.52	.41	3.26	.35	5.00	1.47	2.48	.90	0	1	-	0
118.08	1.36	.30	3.40	.32	3.08	.46	8.76	1.96	2.28	.63	0	1	-	0
61.63	1.37	.23	3.07	.45	2.76	.36	8.05	1.44	2.55	.48	1	1	-	0

ls: G=genera studied; SP=species studied; VFR= vessel (pore)
 R-SOL= solitary vessel (pore) frequency; VED= vessel element
 length; FD= fibre
 length; VEL= vessel element length; FD= fibre
 length; FL= fibre length; MRF= multiple ray
 frequency; MRW(c)= multiple ray width in
 cells; MRL(c)= multiple ray length
 in microns; URL(c)= uniseriate ray length
 in microns; URW(μm)= uniseriate
 ray length in microns; URL(μm)= uniseriate
 ray length in microns; FPD= fibre pit diameter;
 IVPD= intervessel to ray pit diameter; L/D
 ratio; F/V ratio= fiber length to
 vessel diameter ratio; C= calcium oxalate crystals;
 S= silica bodies; LAT= altitude; S.D.= standard deviation of the mean.

Table 15. Occurrence in the four genera of Ebenaceae of four types of parenchyma (1 = narrowly banded, 2 = scanty paratracheal, 3 = vasicentric, 4 = apotracheally diffuse) in the wood and the percentage of the total number of samples examined that had each combination of parenchyma types.

<u>Genus</u>	<u>Types of Parenchyma</u>				
	1+2	1+2+3	1+3+4	1+2+3+4	2+4
<u>Diospyros</u>	X	X	X		X
<u>Royena</u>		X		X	X
<u>Tetracelis</u>				X	X
<u>Euclea</u>				X	
% of total	35%	30%	4%	9%	14%
					8%

Table 16. Regression analysis of wood variables in relation to the latitude as an independent variable.

Regression formula	Percentage explained by latitude
vessel frequency	
$=14.031 + 2.36 \text{ lat} - 0.055 \text{ lat}^2^{***}$	10.6
In vessel lumen diameter	
$=1.985 - 0.014 \text{ lat} + 0.0003 \text{ lat}^2^{***}$	7.6
In vessel wall thickness	
$=0.63 - 0.002 \text{ lat} + 0.00005 \text{ lat}^2^{***}$	0.2
In vessel member length	
$=2.713 - 0.009 \text{ lat} + 0.0002 \text{ lat}^2^{***}$	8.1
fiber lumen diameter	
$=7.46 - 0.073 \text{ lat} + 0.002 \text{ lat}^2^{***}$	0.9
In fiber wall thickness	
$=0.51 - 0.003 \text{ lat} + 0.00002 \text{ lat}^2^{***}$	2.4
In fiber member length	
$=3.066 - 0.007 \text{ lat} + 0.00016 \text{ lat}^2^{***}$	8.3

Latitude in N or S.

Significant levels: *** = significant at 0.5% probability level.

Table 17 Regression analysis of wood variables in relation to the altitude as an independent variable.

Regression formula	Percentage explained by altitude
In vessel frequency	
$=1.191 + 0.001 \text{ alt} - 0.0000002 \text{ alt}^2^{***}$	8.3
vessel lumen diameter	
$=98.39 - 0.059 \text{ alt} + 0.00003 \text{ alt}^2^{***}$	6.6
vessel wall thickness	
$=4.644 - 0.001 \text{ alt} + 0.0000007 \text{ alt}^2^{***}$	1.7
In vessel member length	
$=2.679 - 0.00007 \text{ alt}^{***}$	5.8
fiber lumen diameter	
$=7.16 - 0.0001 \text{ alt} + 0.0000005 \text{ alt}^2^{***}$	0.1
fiber wall thickness	
$=3.323 - 0.0003 \text{ alt}^{***}$	2.1
fiber member length	
$=1127.04 - 0.181 \text{ alt} + 0.0004 \text{ alt}^2^{***}$	5.6

Altitude in meters.

Significant levels: *** = significant at 0.5% probability level.

Table 18. Dependences on latitude or altitude in latitudes greater than 10° N and S on total research material, expressed in regression formulas and percentage of variation explained by latitude or altitude.

Regression formula		Percentage explained by latitude
In vessel frequency	$=1.417 + 0.009 \text{ lat} - 0 \text{ lat}^2$	8.3***
In vessel lumen diameter	$=2 - 0.015 \text{ lat} + 0 \text{ lat}^2$	4.8***
In vessel wall thickness	$=0.656 - 0.005 \text{ lat} + 0 \text{ lat}^2$	0.2-
In vessel member length	$=2.617 - 0.001 \text{ lat} + 0 \text{ lat}^2$	2.3***
fiber lumen diameter	$=0.053 \text{ lat} + 5.758$	3.1***
In fiber wall thickness	$=0.523 - 0.004 \text{ lat} + 0 \text{ lat}^2$	2.0***
fiber member length	$=965.474 + 1.193 \text{ lat} + 0.072 \text{ lat}^2$	3.6***
Latitude in N or S.		
Regression formula		
In vessel frequency	$=1.174 + 0.001 \text{ alt} - 0 \text{ alt}^2$	Percentage explained by altitude
vessel lumen diameter	$=101.267 - 0.086 \text{ alt} + 0 \text{ alt}^2$	12.8***
vessel wall thickness	$=4.885 - 0.002 \text{ alt} + 0 \text{ alt}^2$	10.3***
In vessel member length	$=2.647 - 0 \text{ alt} - 0 \text{ alt}^2$	3.2***
In fiber lumen diameter	$=0.765 + 0 \text{ alt} - 0 \text{ alt}^2$	9.1***
In fiber wall thickness	$=0.467 + 0 \text{ alt} - 0 \text{ alt}^2$	0.2-
fiber member length	$=126.429 - 0.308 \text{ alt} + 0 \text{ alt}^2$	2.3***
Latitude in N or S.		
Altitude in meters.		
Significant levels: *** = significant at 0.5% probability level		
		11.1***

Table 19. Dependences on latitude or altitude in latitudes between 10° N and S on total research material, expressed in regression formulas and percentage of variation explained by latitude or altitude.

Regression formula		Percentage explained by latitude
vessel frequency	$=25.444 - 4.581 \text{ lat} + 0.682 \text{ lat}^2$	3.9***
vessel lumen diameter	$=86.497 + 5.122 \text{ lat} - .17 \text{ lat}^2$	0.2-
vessel wall thickness	$=4.607 - 0.145 \text{ lat} + 0.017 \text{ lat}^2$	3.2***
In vessel member length	$=2.694 + 0.004 \text{ lat} - 0.001 \text{ lat}^2$	
In fiber lumen diameter	$=0.873 - 0.016 \text{ lat} + 0.001 \text{ lat}^2$	1.1-***
fiber wall thickness	$=2.999 + 0.175 \text{ lat} - 0.018 \text{ lat}^2$	0.002-
fiber member length	$=0.009 \text{ lat} + 3.08$	7.3***
Regression formula		Percentage explained by altitude
In vessel frequency	$=1.209 + .0003 - 0 \text{ alt}^2$	0.4
vessel lumen diameter	$=96.721 - 0.04 \text{ alt} + 0 \text{ alt}^2$	4.1***
vessel wall thickness	$=4.526 - 0.001 \text{ alt} + 0 \text{ alt}^2$	1.2***
vessel member length	$=516.303 - 0.181 \text{ alt} + 0 \text{ alt}^2$	3.4***
In fiber lumen diameter	$=0.849 - 0.0002 + 0 \text{ alt}^2$	1.5***
fiber wall thickness	$=3.42 - 0.001 \text{ alt} + 0 \text{ alt}^2$	0.9
fiber member length	$=1116.017 - 0.012 \text{ alt} - 0 \text{ alt}^2$	0.1-
Latitude in N or S. Altitude in meters.		
Significant levels: *** = significant at 0.5% probability level.		

Table 20. Previously published examinations of Ebenaceae wood anatomy.

	Taxa	VFR	VED	VEL	FD	FWT	FL	RW(c)	RW(um)	RL(c)	F
1	Moll & Janssonius (1909)										
2	<i>M. merguensis</i>	3-10	45-95	300-450	10-13		700-1100	1-2	8-20	12	15-20
3	<i>D. macrophylla</i>	3	80-180	150-325	15-20		700-1000	1-2	8-30	12	12-20
4	<i>M. buxifolia</i>	4		500				1-3	20		10-40
5	<i>D. horstii</i>	6						1-2		4-10	
6	<i>D. maritima</i>	12-15		500				1-4		45	
7	<i>D. maritima</i> var. <i>calycina</i>	8-12		500				1-2			
8	<i>D. truncata</i>	4						1-4		40	
9	<i>D. pendula</i>	10-15		500				1-2			
10	<i>D. pseudo-ebenum</i>	10-20		500	10-12			1-2		4-40	
11	<i>D. aurea</i>	8-12		500				1-4			
12	<i>D. embryopteris</i>	20		500				1-2		15-20	
13	<i>D. frutescens</i>	7		500				1-2			
14	<i>D. cauliflora</i>	6-8		500				1-2		40	
15	<i>D. enantha</i>	10		500				1-4			
16											
17	Burperstein (1909)										
18	<i>D. samoensis</i>		25	800					9	25	220
19											
20	Kanehira (1921)										
21	<i>D. lotus</i>	4-5	100-220	350-500	18-22	2-3	700-1600	1-3		1-15	
22	<i>D. kaku</i>	4-6	80-160		16-20	3	800-1400	1-3		4-16	
23											
24	Kanehira (1921)										
25	<i>D. discolor</i>	4-10	50-140	400-600	12-15	3	500-1600	1		3-20	
26	<i>D. kusanoi</i>	4-10	30-70		10-15	2-3	800-1400	1-2		3-25	
27	<i>D. enantha</i>	8-14	115	400-650	10-14	2-3	800-1800	1			
28	<i>D. momsana</i>	4-15	70-150	350-400	18-22	3-4	600-1300	1-3		3-15	
29	<i>D. sasaku</i>	8-10	80-180	300-500	14-18	2-3	700-1500	1-2		3-12	
30	<i>M. buxifolia</i>	8-15	55-90	250-500	12-15	3	500-1000	1-2			
31											
32	Kanehira (1924)										
33	<i>M. buxifolia</i>	9-13	60-100	250-450	10-14	2.5-3.5	950-1400	1-2			
34	<i>D. discolor</i>	6-10	90-180	350-650	15-18	2-3	600-1300	1			
35	<i>D. philippinensis</i>	17-25	60-130	300-550	14-17	3-4	650-1100	1			
36	<i>D. mindanaensis</i>	6-10	70-140	450-550	14-16	4	900-1600	1		2-15	
37	<i>D. piosanthra</i>	6-8	70-150	300-700	14-16	2.5-3	700-1500	1			
38											
39	Kanehira (1926)										
40	<i>Maba buxifolia</i>	8-15	55-120		12-15		500-1000	1-2			
41											
42	Brown (1922)		46				1000	1-2		1-30	50
43	<i>M. sandwicensis</i>		46				1000	1-2		1-30	50
44											
45	Record & Moll (1924)										
46		no	quantitative	information							
47											
48	Lecomte (1926a & b)										
49	<i>D. mun</i>	30-40	100	350	12-15			1-2			40
50	<i>D. rubra</i>	50	80					1			25
51	<i>D. nitidula</i>	4-5	200					1-2			25
52											
53	Knbs (1928)										
54	<i>D. guianensis</i>		66-100	380-580	19-27		1160-1540	1-2		1-30	60
55											
56	Knbs (1959)										
57	<i>D. discolor</i>		75-127-200					1-2			
58	<i>D. ebenum</i>		57-85-127					1-2			
59	<i>D. terre</i>		35-85-120					1-3			
60	<i>D. crassiflora</i>		50-86-128					1-3			
61	<i>D. mespiliformis</i>		57-86-128					2-3			
62											

Previously published examinations of Ebenaceae wood anatomy.

VFR	VED	VEL	FD	FWT	FL	RW(c)	RW(um)	RL(c)	RL(um)	FPD	IVPD	IV-RPD	C	S	C/P	STORIED
3-10	45-95	300-450	10-13		700-1100	1-2	8-20	12	15-70	3	4		P		4-6	
3	80-180	150-325	15-20		700-1000	1-2	8-30	12	12-90	2-4	3-8				4-6	
4		500				1-3	20	10-40		2	2		F,P			
6						1-2		4-10					F,P			
12-15		500				1-4		45								
8-12		500				1-2					2.5		R			
4						1-4		40			2.5		P,R		2-4	
10-15		500				1-2				2	2-3		P,R			
10-20		500	10-12			1-2		4-40		2-4			R		5-6	
8-12		500				1-4				2-3			R			
20		500				1-2		15-20					R			
7		500				1-2					2		R		4-6	
6-8		500				1-2		40			3-4		R			
10		500				1-4					3		R			
													P,R			
	25	800					9	25	220-580				P,R			
4-5	100-220	350-500	18-22	2-3	700-1600	1-3		1-15			6					
4-6	80-160		16-20	3	800-1400	1-3		4-16			4-6		P			
4-10	50-140	400-600	12-15	3	500-1600	1		3-20			10		R			
4-10	30-70		10-15	2-3	800-1400	1-2		3-25			5		R			
8-14	115	400-650	10-14	2-3	800-1800	1							R			
4-15	70-150	350-400	18-22	3-4	600-1300	1-3		3-15								
8-10	80-180	300-500	14-18	2-3	700-1500	1-2		3-12								
8-15	55-90	250-500	12-15	3	500-1000	1-2					5		P			
9-13	60-100	250-450	10-14	2.5-3.5	950-1400	1-2					5		P			
6-10	90-180	350-650	15-18	2-3	600-1300	1										
17-25	60-130	300-550	14-17	3-4	650-1100	1							P,R			
6-10	70-140	450-550	14-16	4	900-1600	1		2-15			3					
6-8	70-150	300-700	14-16	2.5-3	700-1500	1							R			
8-15	55-120		12-15		500-1000	1-2				3	5					
	46				1000	1-2		1-30	50				P,F			
	46				1000	1-2		1-30	50				P,F			
no	quantitative	information														
30-40	100	350	12-15			1-2			400-500							
50	80					1			250-700				R			
4-5	200					1-2			250-700				R			
	66-100	380-580	19-27		1160-1540	1-2		1-30	66-1390							
	75-127-200					1-2				F-T	4	4	R			
	57-65-127					1-2				F-T	3	3	R			
	35-85-120					1-3				F-T	4	4				
	50-86-128					1-3				L	4-6	4-6				S
	57-86-128					2-3				L	2-3	2-3	R			

	Taxa	VFR	VED	VEL	FD	FWT	FL	RW(c)	RW(um)	RL(c)	RL(um)	FPD	IVI
63	Benoit (1931)												
64	M. melinonii	1-7	240				800	1			200-1300		
65	D. carbonaria	1-5	160				600-800				400-1300		
66													
67	Pearson & Brown (1932)												
68	D. ebenum	4-12	135-150	66-850	19-23	4-6	500-1320	1-2	40-45	11	315	L	4-
69	D. melanoxylon	3-42	150-165	255-550	23-30	2-5	765-1575	1-2	40-45	12	350	L	4-
70	D. tomentosa	7-22	135-150	210-680	23-30	3-6	850-1400	1-2	38-40	12	400	L	4-
71	D. ehretoides	3-14	200-215	380-510	27-30	4-8	665-1700	1-3	50-60	13	470	SL	4-
72	D. burmanica	11-41	90-105	180-450	17-20	3-5	565-1150	1-2	33-38	11	330	L	4-
73	D. marmorata	9-32	110-120	900-1490	23-27	4-6	900-1490	1-2	30-35	12	400	SL	4-
74													
75	Tang (1932)												
76	D. lotus												
77	D. kaki												
78													
79	Brown & Panshin (1940)												
80	D. virginiana	5-20	120-200		12-30			1-3					2-
81													
82	Record & Hess (1943)												
83	D. virginiana							1-2		2-30			
84													
85	Mercalle & Chaik (1950)												
86	D. brachiata		100-200										
87	D. burmanica	15											
88	D. ebenum												
89	D. ehretoides		100-200					2					
90	D. embryopteris												
91	D. glandulosa							1-4					
92	D. kaki												
93	D. lotus												
94	D. malaccensis												
95	D. mangayi		100-200										
96	D. moonii												
97	D. morsiana												
98	D. polyanthoides												
99	D. qualesia												
100	R. lucida	15	25-50										
101	E. lanceolata							1-4					
102	D. virginiana							1-4					
103	M. verae-crucis							2					
104	D. sasaku												
105	D. truncata												
106	D. tristis												
107	D. sanz-minika												
108	D. undulata												
109	M. cooperi												
110	Mean total for family			200-500			750-1400				100		
111													
112	Huber & Rouschal (1954)												
113	D. lotus		60-70					1-3					
114													
115	Sudo (1959)												
116	D. morsiana	4-6	50-100					1-3	10-20		300-400 (800)		
117	D. lotus	3-5	50-170					1-3	10-30		200-400 (800)		
118	D. kaki	3-4	40-250					1-3	10-25(40)		350-500 (880)		
119													
120	Greguss (1959)												
121	D. ebenaster							1-2	12-22	1-32	65		
122	D. lotus		100-160		15-25		1000	1-3	8-21	10-16	8-35		
123													
124	Norman (1960)												

VFR	VED	VEL	FD	FWT	FL	RW(c)	RW(um)	RL(c)	RL(um)	FPD	IVPD	IV-RPD	C	S	C/P	STORIED
1-7	240				800	1			200-1300							
1-5	160				600-800				400-1300							
4-12	135-150	66-850	19-23	4-6	500-1320	1-2	40-45	11	315	L	4-5	3-4	R		3-5	
3-42	150-165	255-550	23-30	2-5	765-1575	1-2	40-45	12	350	L	4-5	3-4	R		3-5	
7-22	135-150	210-680	23-30	3-6	850-1400	1-2	38-40	12	400	L	4-5	3-4	R		3-5	
3-14	200-215	380-510	27-30	4-8	665-1700	1-3	50-60	13	470	SL	4-6	4-6	R		3-5	
11-41	90-105	180-450	17-20	3-5	565-1150	1-2	33-38	11	330	L	4-5	3-4	R			
9-32	110-120	900-1490	23-27	4-6	900-1490	1-2	30-35	12	400	SL	4-6	3-5	R		3-5	
																S
5-20	120-200		12-30			1-3					2-4					V.F.R
						1-2		2-30					P.R			S
	100-200															
15						2										S
	100-200					1-4									2	P.R
																P.R
																R
	100-200															R
15	25-50					1-4										
						1-4										P.R
						2										R
													F			
		200-500			750-1400				100							
	60-70					1-3							P.R		S	
4-6	50-100					1-3	10-20		300-400 (800)							
3-5	50-170					1-3	10-30		200-400 (800)							
3-4	40-250					1-3	10-25(40)		350-500 (880)							
						1-2	12-22	1-32	65							
	100-160		15-25		1000	1-3	8-21	10-16	8-35							

	Taxa	VFR	VED	VEL	FD	FWT	FL	RW(c)	RW(μm)	RL(c)	RL(μm)	FPD
125	<i>D. abyssinica</i>	20										
126	<i>D. canaliculata</i>											
127	<i>D. ganbunensis</i>											
128	<i>D. ivorensis</i>											
129	<i>D. kamerunensis</i>											
130	<i>D. kekemi</i>								35			
131	<i>D. mespiliformis</i>											
132	<i>D. monbutensis</i>											
133	<i>D. sanza-minika</i>	10										
134	Mean total for family	20	120				1000-1400	1-3				
135												
136	Labrecq & Dechamp (1964)											
137	<i>D. crassiflora</i>	5	31-100					1	30		300-500	
138	<i>D. kumba-kumba</i>	5-15	31-100					1	30		300-500	
139	<i>D. mespiliformis</i>	5-15	101-299					1	30		300-500	
140	<i>D. sanza-minika</i>	5	31-100					1	30		300-500	
141	<i>E. mildbraedii</i>	40	31-100					1	30		300-500	
142	<i>M. buxifolia</i>	5	31-100					1	30		300-500	
143												
144	Purkayastha et. al. (1976)											
145	<i>D. marmorata</i>	15-20	82	266-728	11	3	406-1428	1-2	28	25	588	
146												
147	Dechamp (1979)											
148	<i>D. guianensis</i>	many	78-98-130	91-310-611	18		910-1140-1235	1-2	8-12-15		156-311-780	
149												
150	Panshin & De Zeeuw (1980)											
151	<i>D. virginiana</i>							1-3				
152												
153	Phor & Gasson (1990)											
154	<i>E. crispa</i>											FT
155	<i>E. schimperi</i>											L
156	<i>D. mespiliformis</i>											FT
157	<i>D. natalensis</i>											FT
158	<i>D. whyteana</i>											FT
159												
160	Hayashi (1991)											
161	<i>D. japonica</i>		170					1-2	30		400	
162	<i>D. mormosana</i>		100					1-2	25		500	
163	<i>D. lotus</i>		280									
164	<i>D. kaku</i>		200									

Explanation of symbols: VFR= vessel frequency; VED= vessel element diameter; VEL= vessel element length; FD= fibre diameter; FWT= fibre wall thickness; FL= fibre length; RW(c)= ray width in cells; RW(μm)= ray width in microns; RL(c)= ray length in cells; RL(μm)= ray length in microns; FPD= fibre pit diameter; IVPD= intervessel pit diameter; IV-RPD= intervessel to ray pit diameter; C= calcium oxalate crystals; S= silica bodies; C/P= cell wall parenchyma strand; STORIED= the presence of storied rays.

VED	VEL	FD	FWT	FL	RW(c)	RW(μm)	RL(c)	RL(μm)	FPD	IVPD	IV-RPD	C	S	C/P	STORIED
						35						R			
												R			
120				1000-1400	1-3										
31-100					1	30		300-500							
31-100					1	30		300-500							
101-299					1	30		300-500							
31-100					1	30		300-500							
31-100					1	30		300-500							
31-100					1	30		300-500							
82	266-728	11	3	406-1428	1-2	28	25	588				P,R			
78-98-130	91-310-611	18		910-1140-1235	1-2	8-12-15		156-311-780						2,4	
					1-3						2,4	2,4			V,R,F
									FT			P			
									L			R			
									FT			P,R		2	
									FT			P			
									FT				R		
170					1-2	30		400							
100					1-2	25		500							
280															
200															

on of symbols: VFR= vessel frequency; VED= vessel element diameter; VEL= vessel element length; FD= fibre diameter; FWT= fibre wall thickness; FL= fibre length; RW(c)= ray width in cells; RW(μm)= ray width in microns; RL(c)= ray length in cells; RL(μm)= ray length in microns; FPD= fibre pit diameter; IVPD= intervessel pit diameter; IV-RPD= intervessel to ray pit diameter; C= calcium oxalate crystals; S= silica bodies; C/P= cells per enchyma strand; STORIED= the presence of storied rays.

Table 21. List of those species treated by White (1978, 1980, 1983, 1987, 1988); White and Caveney (1980) of which wood was examined in the present study¹.

Species	Species examined indicated by X and <u>Diospyros</u> coded at sectional level
Euclea	
<i>E. crispa</i> (Thunb.) Gurke	X
subsp. <i>crispa</i> F. White	
subsp. <i>linearis</i> (Zeyher ex Hiern) F. White	
subsp. <i>linearis</i> sens. lat.	
subsp. <i>linearis</i> sens. strict.	
subsp. <i>ovata</i> (Burch.) F. White	
<i>E. divinorum</i> Hiern	X
<i>E. natalensis</i> A. DC.	X
subsp. <i>acutifolia</i> F. White	
subsp. <i>angolensis</i> F. White	
subsp. <i>angustifolia</i> F. White	
subsp. <i>capensis</i> F. White	
subsp. <i>magutensus</i> F. White	
subsp. <i>natalensis</i> F. White	
subsp. <i>obovata</i> F. White	
subsp. <i>rotundifolia</i> F. White	
<i>E. racemosa</i> Murr.	
subsp. <i>bernardii</i> F. White	
subsp. <i>daphnoides</i> (Hiern) F. White	
subsp. <i>macrophylla</i> (E. Mey. ex A. DC.) F. White	
subsp. <i>racemosa</i>	X
subsp. <i>schimperi</i> (A. DC.) F. White	X
subsp. <i>sinuata</i> F. White	
subsp. <i>zuluensis</i> F. White	
<i>E. undulata</i> Thunb.	
Tetraclis (not treated)	
Diospyros	
1. Section <i>Forsteria</i> Bakh.	
<i>D. ferrea</i> (Willd.) Bakh.	X-1
<i>D. natalensis</i> (Harv.) Brenan.	X-1
2. Section <i>Asteropetala</i> F. White	
<i>D. longiflora</i> Letouzey & F. White	
3. Section <i>Katula</i> F. White	
<i>D. mweroensis</i> F. White	X-2
4. Section <i>Entia</i> F. White	
<i>D. chevalieri</i> De Wild.	
5. Section <i>Dodonium</i> F. White	
<i>D. mannii</i> Hiern	
<i>D. suaveolens</i> Gurke	X-3
6. Section <i>Forbesia</i> F. White	
<i>D. consolatae</i> Chiov.	
<i>D. rotundifolia</i> Hiern	

- D. consolatae* Chiov.
D. rotundifolia Hiern
 7. Section *Brevituba* F. White
 D. abyssinica (Hiern) F. White X-4
 subsp. *abyssinica*
 subsp. *chapmaniorum* F. White
 subsp. *attenuata* F. White
 subsp. *reticulata* F. White
 D. deltoidea F. White
 D. dendo Welw. ex Hiern X-4
 D. gillettii De Wild.
 D. inhacaensis F. White
 D. kanurii F. White
 D. platanoides Letouzey & F. White
 D. piscatoria Gurke
 D. polystemon Gurke
 D. quiloensis (Hiern) F. White
 D. scabra (Chior.) Cufodontis
 D. soubreana F. White
 D. squarrosa Klotzsch
 D. viridicans Hiern X-4
 D. wagemansii F. White
 D. wajirensis F. White
 8. Section *Myrmecophila* F. White
 D. conocarpa Gurke & K. Schum.
 9. Section *Royena* (L.) F. White
 D. acocksii (de Winter) de Winter
 D. anitae F. White
 D. austroafricana de Winter
 D. dichrophylla (Gand.) de Winter X-5
 D. fischeri Gurke
 D. galpinii (Hiern) de Winter
 D. glabra (L.) de Winter X-5
 D. glandulifera de Winter
 D. heterotricha (B.L. Burtt) F. White X-5
 D. lycioides Desf. X-5
 subsp. *guerkei* (Kuntze) de Winter
 subsp. *lycioides* de Winter
 subsp. *sericea* (Bernh.) DeWinter
 D. pallens (Thunb.) F. White X-5
 D. ramulosa (E. Mey ex A. DC.) de Winter
 D. simii (Kuntze) de Winter
 D. scabrida (Harv. ex Hiern) de Winter
 D. truncatifolia Caveny
 D. usambarensis F. White
 subsp. *rufescens* A. N. Caveny
 D. villosa (L.) de Winter
 D. whyteana F. White X-5
 D. zombensis (B.L. Burtt) F. White
 10. Section *Lagenaria* F. White
 D. crassiflora Hiern X-6
 11. Section *Erikesi* F. White

D. monbuttensis Gurke	X-7
D. senensis Klotzsch	
12. Section Latibulum F. White	
D. bipindensis Gurke	X-8
D. canaliculata De Wild.	X-8
D. physocalycina Gurke	X-8
D. preussii Gurke	
D. shimbaensis F. White	
13. Section Tabonaca F. White	
D. amaniensis Gurke	-
D. batocana Hiern	X-9
D. boala De Wild.	
D. chamaethamnus Dinter ex Mildbr.	
D. fragrans Gurke	X-9
D. gabunensis Gurke	
D. greenwayi F. White	
D. grex F. White	
D. kamerunensis Gurke	X-9
D. pseudomespilus Mildbr.	
subsp. brevicalyx F. White	
subsp. undabunda (Hiern ex Greves) F. White	
D. sanza-minika A. Chev.	
14. Section Noltia (Schumacher) Hiern	
D. barteri Hiern	
D. chrysocarpa F. White	
D. cinnabarina (Gurke) F. White	
D. mafiensis F. White	
D. simulans F. White	
D. soyauxii Gurke & Schum.	
D. tricolor (Schumacher) Hiern	
D. vignei F. White	
15. Section Rhabdanthus (Hiern ex Gurke) F. White	
D. obliquifolia (Hiern ex Gurke) F. White	
16. Section Calvitiella F. White	
D. alboflavescens (Gurke) F. White	
D. cooperi (Hutch. & Dalz.) F. White	X-10
D. elliotii (Hiern) F. White	
D. feliciana Letouzey & F. White	
D. hoyleana F. White	
subsp. hoyleana F. White	X-10
subsp. angustifolia F. White	
D. iturensis (Gurke) Letouzey & F. White	X-10
D. magogoana F. White	
D. melocarpa F. White	
D. occulta F. White	
D. troupinii F. White	
D. vermoesenii De Wild.	
D. zenkeri (Gurke) F. White	X-10
17. Section Brevistyla F. White	
D. capricornuta F. White	
D. cornii Chiov.	
D. gracilescens Gurke	

<i>D. heudelotii</i> Hiern	X-11
<i>D. kabuyeana</i> F. White	
<i>D. kirkii</i> Hiern	X-11
<i>D. liberiensis</i> Hutch. & Dalz.	
<i>D. mespiliformis</i> Hochst. ex A. DC.	X-11
<i>D. thomasii</i> Hutch. & Dalz	
<i>D. verrucosa</i> Hiern	
18. Section <i>Marsupium</i> F. White	
<i>D. virgata</i> (Gurke) Brenan	

Except where indicated, samples are from Africa. Genera and species not treated by White included: *E. lanceolata* E. Mey.; *E. mayottensis* H. Perrier; *D. lucida* L. (Royena); *Diospyros acuminata* (Hiern) F. White, Sri Lanka; *D. acuta* Thw., Sri Lanka; *D. affinis* Thw., Sri Lanka; *D. amazonica* Krause, Brazil; *D. amboinensis* Bakh., New Guinea; *D. andersonii* (Soland. ex Hiern) P. S. Green, Fiji; *D. anisandra* Blake, Mexico; *D. apiculata* Hiern, Thailand; *D. artanthesfolia* Mart. ex Miq., S. America; *D. bourdillonii* Brandis, India; *D. caribaea* (A. DC.) Staudl., Cuba; *D. castanea* (Craib) Fletcher, Thailand; *D. cauiflora* Bl., New Guinea; *D. christophersenii* Fosberg; *D. konzattii* Standl., Mexico; *D. cuneata* Standl., Belize; *D. cuplifera* Perr., Madagascar; *D. dasyphylla* Kurz, Thailand; *D. defectrix* Fletcher, Thailand; *D. dichroa* Sandwith, S. America; *D. discocalyx* Merr., Malaysia; *D. duckei* Sandw., Guyana; *D. ebum* Koenig ex Retzius, Sri Lanka; *D. elliptica* (J. R. & F. Forst.) P. S. Green, Fiji; *D. glandulosa* Lace, Thailand; *D. guatterioides* A. C. Smith, Brazil; *D. guianensis* (Aubl.) Gurke, Brasil; *D. hallierii* Bakh., Malaysia; *D. hillebrandii* (Seem.) Fosb., Hawaii; *D. hirsuta* L., Sri Lanka; *D. hillebrandii* (Seem.) Fosb., Hawaii; *D. inclusa* Merr., Philippines; *D. inconstans* Jacq., Brasil; *D. insularis* Bakh., Woodlark Island; *D. kaki* L., Burma; *D. liriosmoides* A. C. Smith, Brasil; *D. mattogrossensis* Hoehne, Brasil; *D. minihassae* Bakh., Indonesia; *D. montana* Roxb., Sri Lanka; *D. morrisiana* Hance, Japan; *D. myrmecocarpa* Mart., ex Miq., Brasil; *D. nummulariaefolia* Kosterm., Sri Lanka; *D. paraleia* Steud., Panama; *D. pentamera* Woods & F. Muell. ex F. Muell., Australia; *D. peruviana* Hiern, Peru; *D. philippinensis* A. DC., Philippines; *D. physocalycina* Gurke; *D. poeppigiana* A. DC. Peru; *D. poncei* Merr., Philippines; *D. pseudoxylopia* Mildbr., Peru; *D. samoensis* A. Gray, Fiji; *D. sylvatica* Roxb., Sri Lanka; *D. tetrandra* Hiern, S. America; *D. thwaitesii* Bedd., Sri Lanka; *D. virginiana* L., US; *D. vitiensis*, Gillespie; *Tetraclis baronii* H. Perrier, Madagascar; *T. clusiaefolia* Hiern, Madagascar; *T. ebenifera* H. Perrier, Madagascar.

1. Additional taxa treated in other publications by: White (1992) are not assigned to sections and, thus, are unusable in this comparison.

Table 22. List of those species treated by Bakhuizen (1936-38) of which wood was examined in the present study.

Species	Species studied coded by subgeneric and sectional levels
Euclea	
Royena	
Tetracelis	
Diospyros	
A. Subgenus Maba	
1. Section Forsteria Bakh.	
<i>D. ferrea</i> (Willd.) Bakh.	1 - 1
<i>D. ellipticifolia</i> (Stokes) Bakh.	
2. Section Miquelia Bakh.	
<i>D. tahanensis</i> Bakh.	
<i>D. Janowskyi</i> Bakh.	
<i>D. rostrata</i> (Merr.) Bakh.	
<i>D. carpinifolia</i> (Ridl.) Bakh.	
<i>D. malayana</i> Bakh.	
3. Section Hasseltia Bakh.	
<i>D. fasciculosa</i> F. v. Muell.	
<i>D. Holttumii</i> Bakh.	
<i>D. confertiflora</i> (Hiern) Bakh.	
<i>D. hermaphroditica</i> (Zoll.) Bakh.	
B. Subgenus Hierniodendron Bakh.	
<i>D. puncticulosa</i> Bakh.	
<i>D. evena</i> Bakh.	
<i>D. Maingayi</i> (Hiern) Bakh.	
C. Subgenus Cargillia (R. Br.) Bakh.	
D. Subgenus Eudiospyros (L.) Bakh.	
1. Section Brachycylix Bakh.	
<i>D. buxifolia</i> (Bl.) Hiern	
<i>D. subrhomboidea</i> King et Gamble	
<i>D. elegantissima</i> Bakh.	
<i>D. Clementium</i> Bakh.	
<i>D. Jaherii</i> Bakh.	
<i>D. plectosepala</i> Hiern	
<i>D. confusa</i> Bakh.	
<i>D. Baloen-idjoek</i> Bakh.	
<i>D. Paraoesi</i> Bakh.	
<i>D. kajangensis</i> Bakh.	
<i>D. singaporensis</i> Bakh.	
<i>D. poiensis</i> Bakh.	
<i>D. philippinensis</i> A. DC.	2 - 2
<i>D. Havilandi</i> Bakh.	
<i>D. glaucophylla</i> Bakh.	
<i>D. Scortechinii</i> King et Gamble	

- D. minutiflora Bakh.
- D. oligantha Merr.
- D. setosa Bakh.
- D. graciliflora Hiern
- D. densa Bakh.
- D. nana Bakh.
- D. ellipsoidea King et Gamble
- D. penangiana King et Gamble
- D. penibukanensis Bakh.
- D. brevicalyx Boerl. et Kds. ex Kds.
- D. sororia Bakh.
- D. Kingii Bakh.
- D. Gambleana Bakh.
- D. Hierniana (King et Gamble) Bakh.
- D. simaloerensis Bakh.
- D. malaccensis Bakh.
- D. bangkana Bakh.
- 2. Section Cavanilleastrum Bakh.
 - D. Poncei Merr. 2 - 3
 - D. durionoides Bakh.
 - D. Hackenbergii Diels
- 3. Section Stelechantha Bakh.
 - D. cauliflora Bl. 2 - 4
- 4. Section Podophora Bakh.
 - D. daemona Bakh.
 - D. insidiosa Bakh.
 - D. Diepenhorstii Miq.
- 5. Section Ebenaster Bakh.
 - D. discolor Willd.
 - D. amboinensis Bakh. 2 - 5
 - D. Peekelii Lauterb.
 - D. Lolin Bakh.
 - D. celebica Bakh.
 - D. sogeriensis Bakh.
 - D. Rumphii Bakh.
 - D. argentea Griff.
- 6. Section Basithrix Bakh.
 - D. Forbesii Bakh.
 - D. ferox Bakh.
 - D. nutans King et Gamble
 - D. muricata Bakh.
 - D. pahangensis Bakh.
 - D. cordata Hiern
 - D. Everetti Merr.
 - D. euphlebia Merr.
 - D. selangorensis Bakh.
 - D. micromera Bakh.
 - D. apiculata Hiern 2 - 6
 - D. pulchra Bakh.
- 7. Section Kurzella Bakh.
 - D. Kurzii Hiern
 - D. Wrayi King et Gamble
 - D. pubicarpa Ridl.
 - D. nitida Merr.

- D. pubicalix Bakh.
- 8. Section Phyllosepala Bakh.
 - D. latisepala Ridl.
 - D. neurosepala Bakh.
- 9. Section Eriantha Bakh.
 - D. eriantha Champ. ex Benth.
 - D. sumatrana Miq.
 - D. vestita Bakh.
 - D. Hendersoni Ridl.
 - D. tuberculata Bakh.
- 10. Section Confertiflora Bakh.
 - D. frutescens Bl.
 - D. Curranii Merr.
 - D. curraniopsis Bakh.
- 11. Section Acanthebenus Bakh.
 - D. montana Roxb. 2 - 7
- 12. Section Lotus Bakh.
 - D. Kaki Linn. F. 2 - 8
- 13. Section Ebenus Bakh.
 - D. Ebum Koen. 2 - 9
 - D. hebecarpa Cunn. ex Benth. 2 - 9
 - D. samoensis A. Gray 2 - 9
 - D. novoguineensis Bakh. 2 - 9
 - D. insularis Bakh.
- 14. Section Ebenopsis Bakh.
 - D. truncata Zoll. et Mor.
 - D. eucalyptifolia Bakh.
 - D. elliptifolia Merr.
 - D. aurea Teysm. et Binn.
 - D. Minahasae Bakh.
 - D. Beccarii Hiern
- 15. Section Ptychocylix Bakh.
 - D. polyalthioides Korth. ex Hiern
 - D. pilosanthera Blanco
 - D. Elmeri Merr.
 - D. oblonga Wall. ex G. Don
 - D. cubica Bakh.
- 16. Section Didymanthera Bakh.
 - D. Hasseltii Zoll.
 - D. dictyoneura Hiern
 - D. piscicapa Ridl.
 - D. Siamang Bakh.
 - D. Wallichii King et Gamble ex King
- 17. Section Nesindica Bakh.
 - D. maritima Bl.
 - D. multiflora Blanco
 - D. lanceifolia Roxb.
 - D. undulata Wall. ex G. Don
 - D. javanica Bakh.
 - D. venenosa Bakh.
 - D. Greshoffiana Kds. ex Bakh.
 - D. styraciformis King et Gamble
 - D. sarawakana Bakh.
 - D. clavipes Bakh.

- D. crassipes Bakh.
- 18. Section Liophylla Bakh.
 - D. Yeobi Bakh.
 - D. rufa King et Gamble
 - D. Foxworthyi Bakh.
 - D. levigata Bakh.
- 19. Section Eucarpon Bakh.
 - D. pendula Hasselt ex Hassk.
 - D. adenophora Bakh.
 - D. Toposia Ham.
 - D. toposioides King et Gamble
 - D. pauciflora King et Gamble
 - D. palembanica Bakh.
 - D. nemorosa Bakh.
- 20. Section Cladantha Bakh.
 - D. pyrrhocarpa Miq.
 - D. papuana Val.
- 21. Section Truncicalix Bakh.
 - D. subtruncata Scheff. ex Hochr.
 - D. Ulo Merr.
 - D. borneensis Hiern
 - D. discocalyx Merr.
- 22. Section Sapotanigra Bakh.
 - D. nigra (J.F. Gmel.) Perrott.
- 23. Section Reflexocalix Bakh.
 - D. tritis King et Gamble
 - D. dajakensis Bakh.
- 24. Section Trisantha Bakh.
 - D. bantamensis Kds. et Val. ex Bakh.
 - D. Malam Bakh.
- 25. Section Glutinosa Bakh.
 - D. malabarica (Desr.) Kostel
 - D. pseudo-malabarica Bakh.
 - D. koeboeensis Bakh.
 - D. britanno-borneensis Bakh.
 - D. eburnea Bakh.
 - D. siamensis Hochr.
- 26. Section Asterocalix Bakh.
 - D. Hallieri Bakh.
- 27. Section Verruculosa Bakh.
 - D. perfida Bakh.
 - D. bibracteata Bakh.
- 28. Section Pachycylix Bakh.
 - D. macrophylla Bl.
- 29. Section Saccocalix Bakh.
 - D. coriacea Hiern
 - D. campanulata Bakh.
 - D. mindanaensis Merr.
 - D. soporifera Bakh.
- 30. Section Campanulata Bakh.
 - D. lateralis Hiern
 - D. sundaica Bakh.
 - D. Ridleyi Bakh.
 - D. Korthalsiana Hiern

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- D. myrmecocalyx* (Hiern) Bakh.
- D. transitoria* Bakh.
- D. retrofracta* Bakh.
- D. conformis* Bakh.
- 31. Section *Rigidophylla* Bakh.
- D. perakensis* Bakh.
- D. Enderti* Bakh.
- D. areolata* King et Gamble
- D. rigida* Hiern

Except where indicated, samples are from Africa. Genera and species not treated by Bakhuizen include: *Euclea crispa* (Thunb.) Gurke; *E. divinorum* Hiern; *E. lanceolata* E. Mey.; *E. mayottensis* H. Perrier; *E. natalensis* A. DC.; *E. racemosa* Murr; *E. schimperi* (A. DC.) Dandy; *Diospyros dichrophylla* (Gand.) De Winter (=Royena); *D. glabra* (L.) De Winter; *D. heterotricha* (B. L. Burt) F. White; *D. lucida* L.; *D. lycioides* Desf.; *D. pallens* (Thunb.) F. White; *D. whyteana* (Hiern) F. White; *Diospyros abyssinica* (Hiern) F. White; *D. acuminata* (Hiern) Kosterm., Sri Lanka; *D. acuta* Thw., Sri Lanka; *D. affinis* Thw., Sri Lanka; *D. amazonica* Krause, Brazil; *D. andersonii* (Soland. ex Hiern) P. S. Green, Fiji; *D. anisandra* Blake, Mexico; *D. artanthaefolia* Mart. ex Miq., S. America; *D. batocana* Hiern; *D. bipindensis* Gurke; *D. bourdillonii* Brandis, India; *D. canaliculata* de Wild.; *D. caribaea* (A. DC.) Staudl., Cuba; *D. castanea* (Craib) Fletcher, Thailand; *D. christophersenii* Fosberg; *D. conzattii* Standl., Mexico; *D. cooperi* (Hutch. & Dalz.) F. White, Liberia; *D. crassiflora* Hiern; *D. cuneata* Standl., Belize; *D. cuplifera* Perr., Madagascar; *D. dasyphylla* Kurz, Thailand; *D. defectrix* Fletcher, Thailand; *D. dendo* Welw. ex Hiern; *D. dichroa* Sandwith, S. America; *D. duckei* Sandw., Guyana; *D. elliptica* (J. R. & F. Forst.) P. S. Green, Fiji; *D. fragrans* Gurke; *D. glandulosa* Lace, Thailand; *D. guatterioides* A. C. Smith, Brazil; *D. guianensis* (Aubl.) Gurke, Brasil; *D. heudelotii* Hiern; *D. hillebrandii* (Seem.) Fosb., Hawaii; *D. hirsuta* L., Sri Lanka; *D. hoyleana* F. White; *D. inclusa* Merr., Philippines; *D. inconstans* Jacq., Brasil; *D. iturensis* (Gurke) R. Letouzey & F. White; *D. kamerunensis* Gurke; *D. kirkii* Hiern; *D. liriosmoides* A. C. Smith, Brasil; *D. mattogrossensis* Hoehne, Brasil; *D. mespiliformis* Hochst. ex A. DC.; *D. minihassae* Bakh., Indonesia; *D. monbuttensis* Gurke; *D. morrisiana* Hance, Japan; *D. myrmecocarpa* Mart. ex Miq., Brasil; *D. mweroensis* F. White; *D. natalensis* (Harv.) Brenan, Madagascar; *D. nummulariaefolia* Kosterm., Sri Lanka; *D. paralea* Steud., Panama; *D. pentamera* Woods & F. Muell. ex F. Muell., Australia; *D. peruviana* Hiern, Peru; *D. physocalycina* Gurke; *D. poeppigiana* A. DC. Peru; *D. pseudoxylopia* Mildbr., Peru; *D. suaveolens* Gurke; *D. sylvatica* Roxb., Sri Lanka; *D. tetrandra* Hiern, S. America; *D. thwaitesii* Bedd., Sri Lanka; *D. virginiana* L., US; *D. viridicans* Hiern; *D. vitiensis*, Gillespie; *D. zenkeri* (Gurke) F. White; *Tetraclis baronii* H. Perrier, Madagascar; *T. clusiaefolia* Hiern, Madagascar; *T. ebenifera* H. Perrier, Madagascar.

Table 23. Results of analysis of variance of quantitative characters and the sections of Diospyros of White's classification of Ebenaceae.

Character	F-value	R-square	Degrees of freedom
Vessel lumina diameter	73.20**	.3622	(10, 1299)
Vessel wall thickness	10.72**	.0768	(10, 1299)
Vessel element length	30.47**	.1942	(10, 1274)
Vessel frequency/mm ²	11.27**	.1849	(10, 507)
Vessel pit diameter	196.53**	.6039	(10, 1299)
Vessel-ray pit diameter	97.93**	.4317	(10, 1299)
Fiber lumina diameter	21.89**	.1416	(10, 1299)
Fiber wall thickness	24.71**	.1608	(10, 1299)
Fiber element length	30.35**	.1936	(10, 1274)
Fiber pit diameter	46.56**	.2654	(10, 1299)
Ray frequency/mm ²	23.14**	.3285	(10, 483)
L/D ratio	25.38**	.1669	(10, 1276)
F/V ratio	6.276**	.0473	(10, 1275)

** difference highly significant at the p=.0001 level

Table 24. Results of analysis of variance of quantitative characters of the genera, Diospyros, Euclea and Tetracelis, as recognized by White.

Character	F-value	R-square	Degrees of freedom
Vessel lumina diameter	146.52**	.0735	(2, 3697)
Vessel wall thickness	154.14**	.0770	(2, 3697)
Vessel element length	159.48**	.0818	(2, 3584)
Vessel frequency/mm ²	126.18**	.1489	(2, 1444)
Vessel pit diameter	114.94**	.0585	(2, 3699)
Vessel-ray pit diameter	78.64**	.0408	(2, 3699)
Fiber lumina diameter	25.95**	.0139	(2, 3687)
Fiber wall thickness	82.91**	.0431	(2, 3687)
Fiber element length	140.31**	.0724	(2, 3599)
Fiber pit diameter	45.33**	.0239	(2, 3697)
Uni ray frequency/mm ²	7.44	.0105	(2, 1401)
Uni ray width (μm)	107.65**	.0756	(2, 2635)
Uni ray height (cells)	13.76**	.0136	(2, 2632)
Uni ray height (μm)	8.64**	.0065	(2, 2635)
Multi ray frequency/mm ²	93.73**	.1182	(2, 1401)
Multi ray width (cells)	8.43	.0160	(2, 1039)
Multi ray width (μm)	22.68**	.0419	(2, 1040)
Multi ray height (cells)	10.70**	.0202	(2, 1042)
Multi ray height (μm)	6.18	.0118	(2, 1039)
L/D ratio	52.30**	.0304	(2, 3590)
F/V ratio	28.88**	.0158	(2, 3589)

** difference highly significant at the p=.0001 level

Table 25. Results of analysis of variance of quantitative characters and the sections of Diospyros of Bakhuizen classification of Ebenaceae.

Character	F-value	R-square	Degrees of freedom
Vessel lumina diameter	115.320**	.6815	(10, 549)
Vessel wall thickness	27.318**	.3364	(10, 549)
Vessel element length	31.05**	.3655	(10, 549)
Vessel frequency/mm ²	56.912**	.7305	(10, 220)
Vessel pit diameter	154.202**	.7410	(10, 549)
Vessel-ray pit diameter	123.608**	.6964	(10, 549)
Fiber lumina diameter	24.786**	.3150	(10, 549)
Fiber wall thickness	17.669**	.2469	(10, 549)
Fiber element length	45.190**	.4561	(10, 549)
Fiber pit diameter	65.789**	.5497	(10, 549)
Ray frequency/mm ²	20.179**	.5022	(10, 210)
L/D ratio	53.723**	.4992	(10, 549)
F/V ratio	14.546**	.2125	(10, 549)

** difference highly significant at the p=.0001 level

Table 26. Results of analysis of variance of quantitative characters and the subgenera of Diospyros of Bakhuizen's classification of Ebenaceae.

Character	F-value	R-square	Degrees of freedom
Vessel lumina diameter	48.67**	.0783	(1, 549)
Vessel wall thickness	4.13	.0072	(1, 549)
Vessel element length	3.57	.0062	(1, 549)
Vessel frequency/mm ²	0.03	.0001	(1, 220)
Vessel pit diameter	57.46**	.0911	(1, 549)
Vessel-ray pit diameter	4.14	.0911	(1, 549)
Fiber lumina diameter	21.56**	.0363	(1, 549)
Fiber wall thickness	3.99	.0069	(1, 549)
Fiber element length	12.12	.0207	(1, 549)
Fiber pit diameter	20.40**	.0344	(1, 549)
Ray frequency/mm ²	3.57	.0162	(1, 210)
L/D ratio	101.21**	.1501	(1, 549)
F/V ratio	17.29**	.0293	(1, 549)

** difference highly significant at the p=.0001 level

Table 27. Results of analysis of variance of quantitative characters of the genera, Diospyros, Euclea, Royena and Tetracelis, as recognized by Bakhuizen.

Character	F-value	R-square	Degrees of freedom
Vessel lumina diameter	237.39**	.1616	(3, 3697)
Vessel wall thickness	111.92**	.0833	(3, 3697)
Vessel element length	224.08**	.1579	(3, 3588)
Vessel frequency/mm ²	110.71**	.1874	(3, 1443)
Vessel pit diameter	126.01**	.0928	(3, 3699)
Vessel-ray pit diameter	91.95**	.0694	(3, 3699)
Fiber lumina diameter	23.89**	.0191	(3, 3687)
Fiber wall thickness	112.26**	.0838	(3, 3687)
Fiber element length	204.28**	.1454	(3, 3604)
Fiber pit diameter	96.75**	.0728	(3, 3697)
Uni ray frequency/mm ²	32.87**	.0659	(3, 1401)
Uni ray width (μm)	89.77**	.0928	(3, 2635)
Uni ray height (cells)	12.92**	.0145	(3, 2632)
Uni ray height (μm)	17.84**	.0199	(3, 2635)
Multi ray frequency/mm ²	69.76**	.1302	(3, 1401)
Multi ray width (cells)	5.95	.0169	(3, 1039)
Multi ray width (μm)	21.15**	.0577	(3, 1040)
Multi ray height (cells)	7.36**	.0208	(3, 1042)
Multi ray height (μm)	6.10	.0174	(3, 1039)
L/D ratio	56.16**	.0449	(3, 3590)
F/V ratio	26.54**	.0217	(3, 3589)

** difference highly significant at the p=.0001 level

Table 28. Results of analysis of variance of quantitative features of the species of Ebenaceae.

Parameter	F-value	R-square	Degrees of freedom
Vessel lumina diameter	172.47**	.8149	(92, 3697)
Vessel wall thickness	31.92**	.4489	(92, 3697)
Vessel element length	33.83**	.4709	(92, 3588)
Vessel frequency/mm2	63.87**	.8131	(92, 1443)
Vessel pit diameter	202.03**	.8375	(92, 3699)
Vessel-ray pit diameter	103.91**	.7261	(92, 3699)
Fiber lumina diameter	24.13**	.3818	(92, 3687)
Fiber wall thickness	19.66**	.3347	(92, 3687)
Fiber element length	34.17**	.4723	(92, 3604)
Fiber pit diameter	44.32**	.5308	(92, 3697)
Uni ray frequency/mm2	31.82**	.6910	(92, 1401)
Uni ray width (um)	18.37**	.3993	(92, 2635)
Uni ray height (cells)	3.69**	.1179	(92, 2632)
Uni ray height (um)	5.12**	.1563	(92, 2635)
Multi ray frequency/mm2	31.75**	.6920	(92, 1392)
Multi ray width (cells)	4.69**	.3129	(92, 1039)
Multi ray width (um)	8.05**	.4385	(92, 1040)
Multi ray height (cells)	1.73**	.1437	(92, 1042)
Multi ray height (um)	3.56**	.2569	(92, 1039)
L/D ratio	53.70**	.5855	(92, 3590)
F/V ratio	10.55**	.2172	(92, 3589)

**+ difference highly significant at the $p=.0001$ level

Table 29. Presence, +, absence, -, or occasional presence, (+), of wood anatomical features in the genera of the Ebenaceae.

	Diospyros	Euclea	Royena	Tetracelis
Growth rings indistinct	-(+)	-(+)	-(+)	-
Semi-ring porous	-(+)	-	-	-
Vessels over 70/mm ²	-(+)	-	-(+)	+
Vessel length over 416 μ m	-(+)	-	-	-
Vessel diameter over 86 μ m	-(+)	-	-	-
Interessel pits over 4.5 μ m	-(+)	-	-	-
Fiber-tracheids	-(+)	-	-	-
Rays storied	-(+)	-	-	-
Axial parenchyma types 1&2	-(+)	-	-	-
Axial parenchyma types 1&2&3	-(+)	-	-(+)	-
Axial parenchyma types 1&2&4	-(+)	-	-(+)	-(+)
Axial parenchyma types 1&2&3&4	-	+	-(+)	-(+)
Axial parenchyma types 1&3	-(+)	-	-	-
Axial parenchyma types 1&3&4	-(+)	-	+	-
Silica	-(+)	-	+	-
Pith flecks	-(+)	-	-(+)	-

Plate 15. Wood of Ebenaceae.

A. Tetraclis baroni (RBHW 17982). Growth ring boundaries absent, wood diffuse porous. LM 4X. B. Royena lucida (USW 21416). Growth ring boundaries distinct, wood diffuse porous. LM 4X. C. Diospyros morrisiana (UW 27012). Vessel groupings solitary and in radial pore multiples of 2 or 3 cells. LM 4X. D. Euclea lanceolata (USW 18539). Vessel groupings in radial pore multiples of 3 or more cells and rarely solitary. LM 4X. (Scale bar: A, B, C, D = 20 μ m).

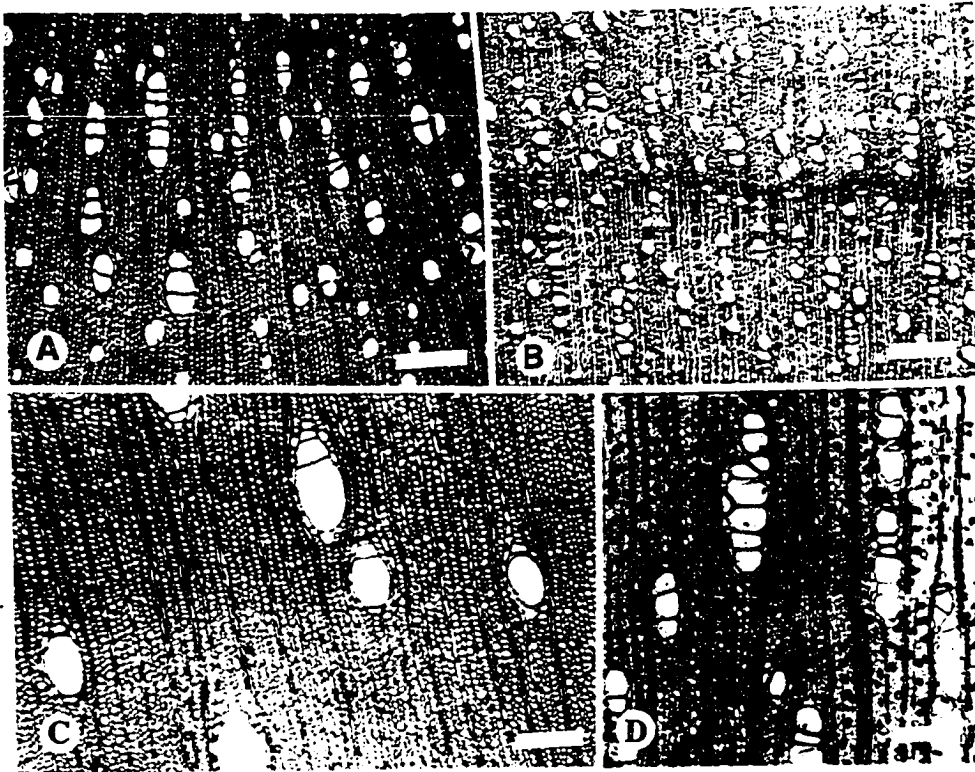


Plate 16. Wood of Ebenaceae.

A. Diospyros discocalyx (RBHw 13629). Vessel frequency low and tangential diameter large. LM 4X. B. Diospyros cupilifera (RBHw 17925). Vessel frequency high and tangential diameter small. LM 4X. C. Royena lucida (USw 18570). Vessel element with and without ligule extensions (arrows). SEM 350X. D. Royena lycioides (RBHw 17813). Vessel walls with helical thickenings. LM 20X. (Scale bar: A, B = 20 μm ; C = 40 μm ; D = 5 μm).

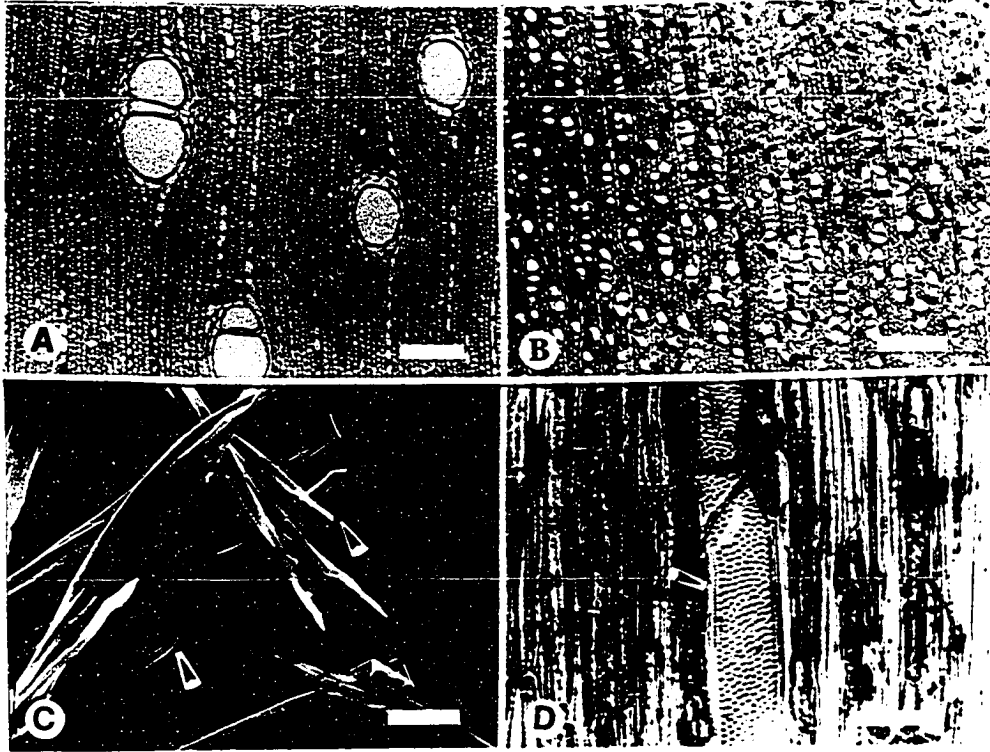


Plate 17. Wood of Ebenaceae.

- A. Diospyros artanthaefolia (RBHw 16816). Intervessel pitting alternate to transitional opposite, polygonal to elongate, and large. SEM 1000X. B. Diospyros hallierii (RBHw 13120). Intervessel pitting alternate to transitional opposite, polygonal, and small. SEM 1000X. C. Diospyros artanthaefolia (RBHw 16816). Intervessel pitting polygonal to elongate, and large. LM 100X. D. Diospyros hallierii (RBHw 13120). Intervessel pitting polygonal, and small. LM 100X. (Scale bar: A, B = 10 μm ; C, D = 1 μm).

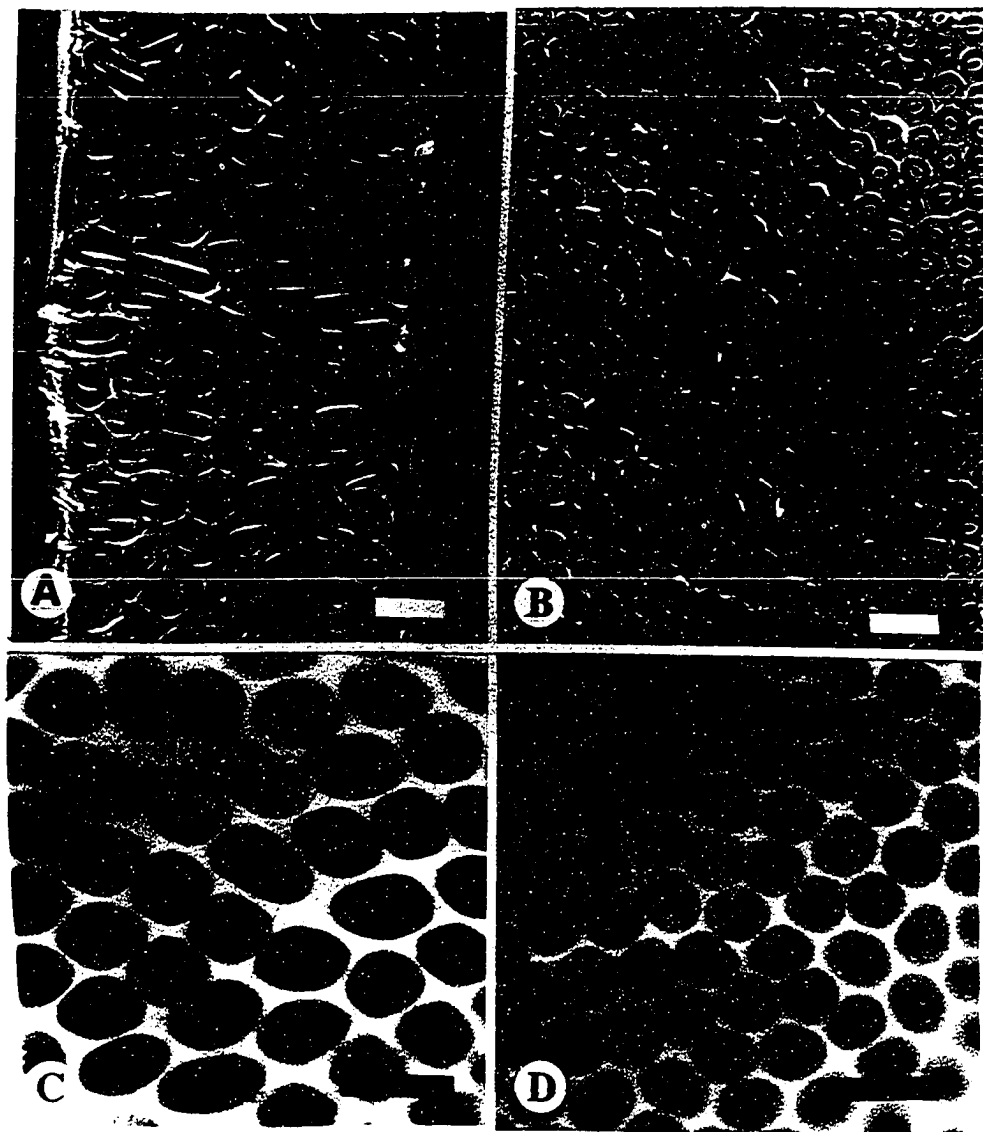


Plate 18. Wood of Ebenaceae.

A. Diospyros cauliflora (RBHw 13043). Vessel-to-ray pitting crowded and small. SEM 750X. B. Royena lucida (USw 18570). Vessel to ray pitting similar to intervessel pitting. LM 20X.

C. Diospyros anisandra (RBHw 13393). Gummy contents in vessels, ray parenchyma, fibers, and axial parenchyma. LM 4X. D. Diospyros crassiflora (RBHw 13897). SEM/EDXA point analysis on black gummy deposits, showing 4 elements identified as: C=carbon, Al=aluminum, K=potassium and Ca=calcium. (Scale bar: A = 20 μm ; B = 5 μm ; C = 10 μm).

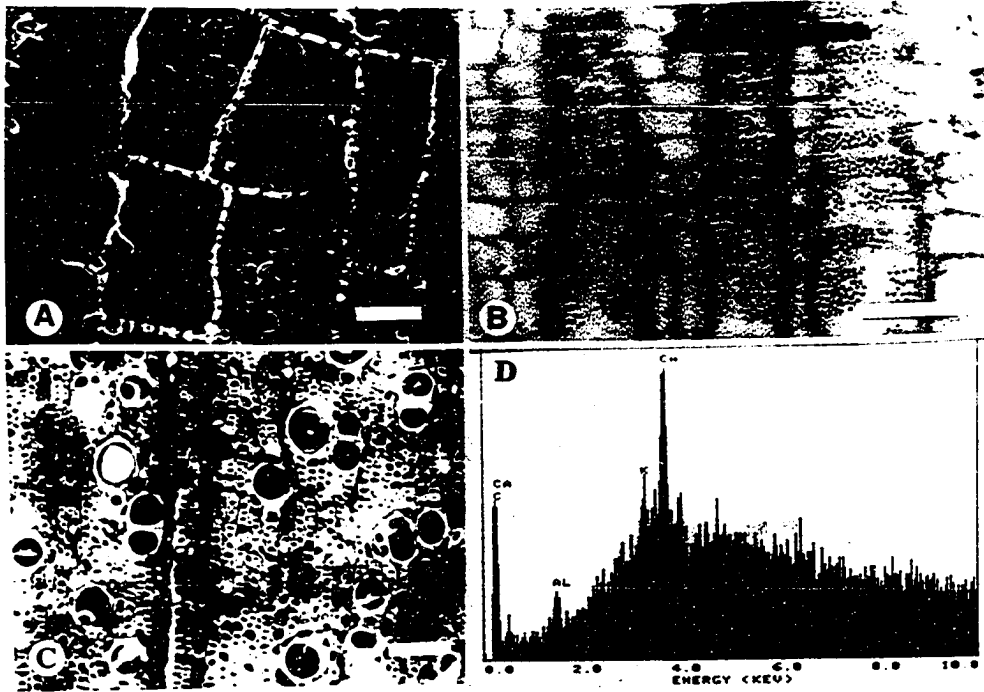


Plate 19. Wood of Ebenaceae.

A-B. Diospyros cauliflora (RBHw 13043). A. Libriform fiber with minute pits and slit-like apertures. SEM 1500X. B. Fiber-tracheids with distinctly bordered pits and slit-like apertures. SEM 1000X. C. Diospyros artanthaefolia (RBHw 16816). Intermediate imperforate tracheary elements. LM 100X. D. Diospyros crassiflora (RBHw 13897). Fiber-tracheids with distinctly bordered pits and slit-like apertures. LM 100X. (Scale bar: A, B = 10 μm ; C, D = 1 μm).

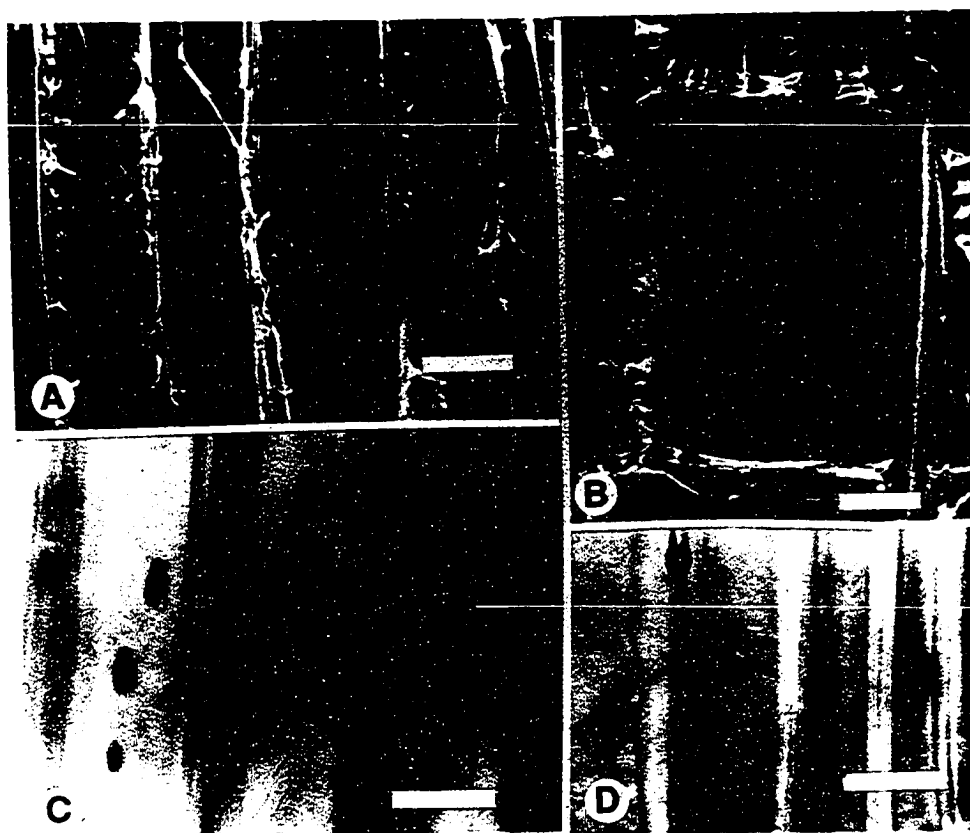


Plate 20. Wood of Ebenaceae.

A. Diospyros artanthaefolia (RBHw 13614). Uniseriate and biseriate rays. LM 4X. B. Euclea lanceolata (USw 18539). A four-celled mulitseriate ray (arrow). LM 10X. C. Diospyros cupilifera (RBHw 17925). Tangential section of a heterocellular ray, with 2 or more biseriate parts per ray cell (arrows). LM 4X. D. Diospyros quatterrioides (RBHw 13441). Mixed ray body cells composed of, from top to bottom, erect, procumbent, erect, square, and erect cells. LM 4X. E. Diospyros pseudoxylopia (RBHw 13392). Ray body cells, procumbent with one row of square marginal cells. LM 4X. F. Diospyros amazonica (RBHw 13374). Upper ray composed of body cells erect and square, lower ray composed of body cells erect. LM 4X. (Scale bar: A, C = 20 μ m; B, D, E, F = 5 μ m).

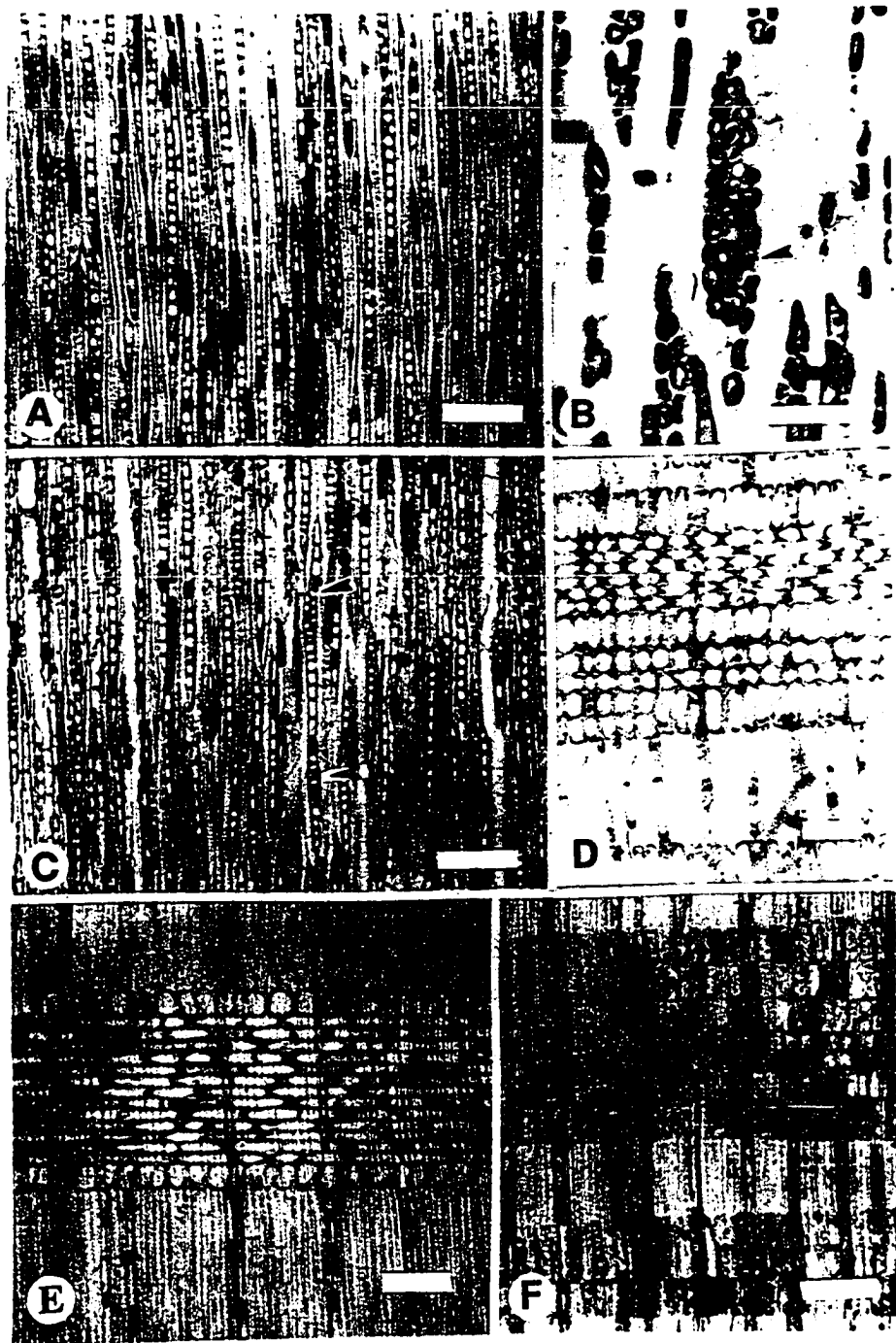


Plate 21. Wood of Ebenaceae.

A. Diospyros virginiana (RBHw 3440). Rays uniseriate and biseriate and storied. LM 4X. B. Diospyros glandulosa (RBHw 17368). Parenchyma banded, one cell in width, and vasicentric. LM 4X. C. Diospyros ebenum (RBHw 17877). Parenchyma banded, one cell in width, scanty paratracheal, and apotracheally diffuse. LM 10X. D. Diospyros artanthes (RBHw 13614). Parenchyma strand (arrow) 5 cells in length. LM 4X. (Scale bar: A, B, D = 20 μm ; C = 10 μm).

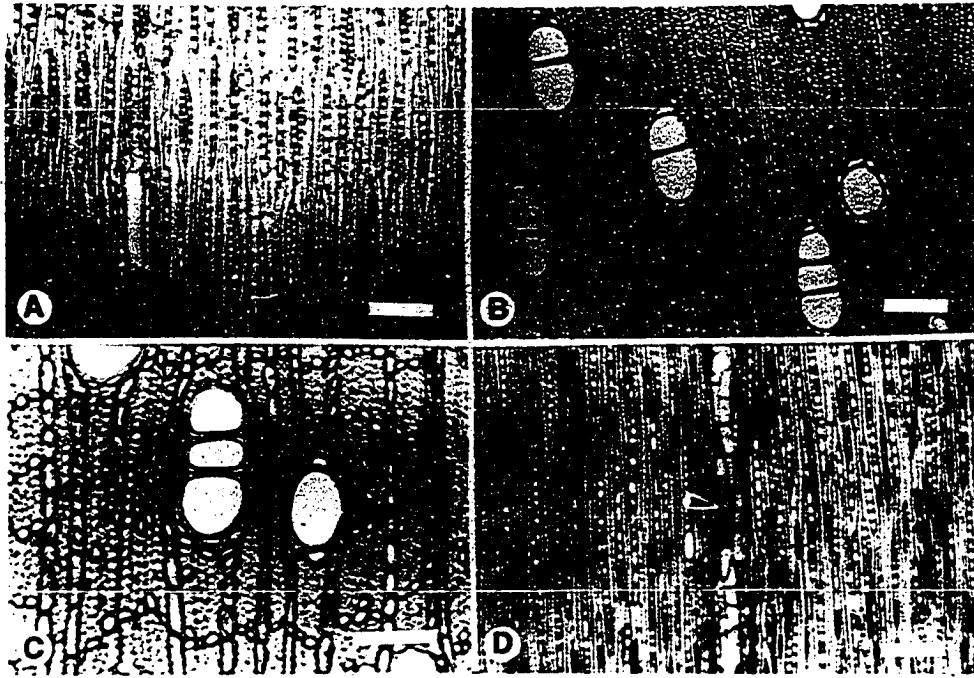


Plate 22. Wood of Ebenaceae.

A-B. Diospyros cauliflora (RBHw 13043). A. SEM/EDXA point analysis on crystal deposit, showing 4 elements identified as: C=carbon, Al=aluminum, Ca=calcium and Fe=iron. B. Prismatic crystals, large and small in size and shaply angled. SEM 350X. C. Diospyros ebenum (RBHw 17878). Prismatic crystals in ray cells (arrow), with one or more crystal per ray cell. LM 10X. D-E. D. Royena lucida (USw 21416). SEM/EDXA point analysis on silica body showing one element identified as silica. E. Silica bodies in ray cells. SEM 500X. (Scale bar: B = 40 μm ; C = 10 μm ; E = 20 μm).

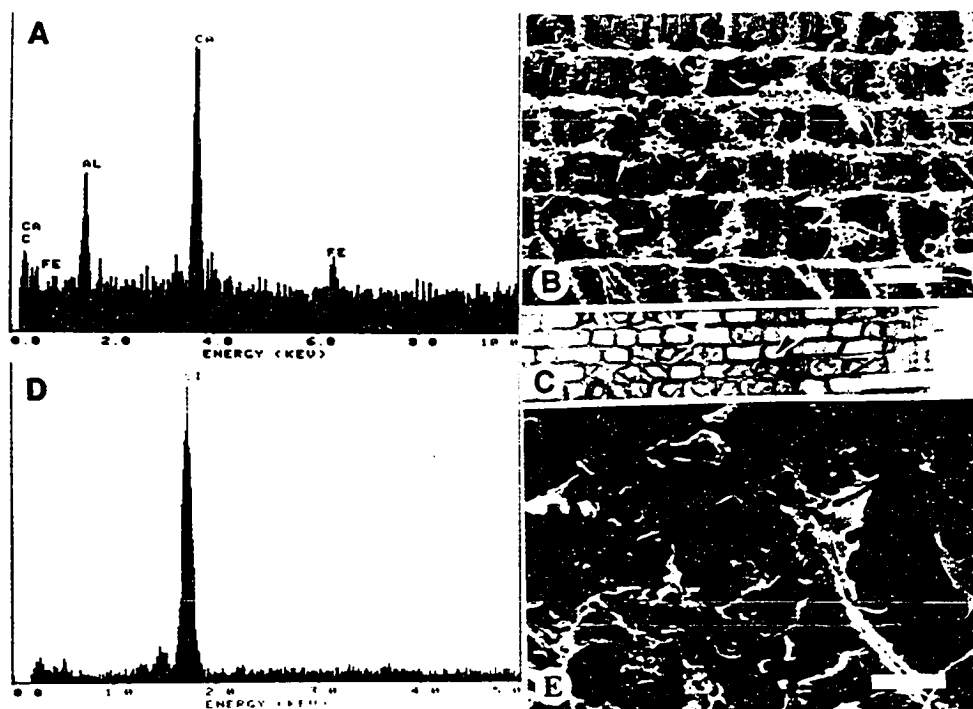
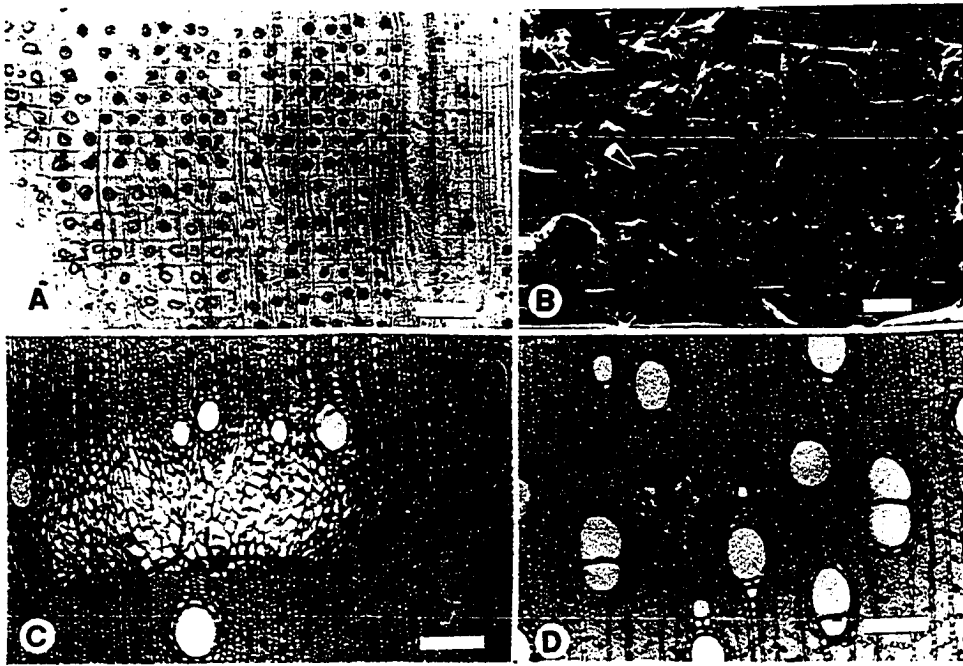


Plate 23. Wood of Ebenaceae.

A. Royena lucida (USw 21416). Silica bodies one per ray cell. LM 10X. B. Royena lucida (USw 18570). Silica bodies mostly globular in form with a rough surface (arrow). SEM 500X. C. Diospyros kaki (RBHw 13303). Pith fleck in a tangential band. LM 4X. D. Diospyros glandulosa (RBHw 17368). Pith fleck diffuse and nonbanded. LM 4X. (Scale bar: A = 5 μm ; B, C = 20 μm ; D = 10 μm).



Appendix 3: Voucher specimens for wood samples of the
Ebenaceae used in this study.

All are dried specimens deposited at RBHw unless indicated otherwise (Stern, 1988). The sample number, used in Table 14, precedes the collector's name.

Euclea crispa (Thunb.) Gurke

- 1) RBHw 17816, South Africa; 2) RBHw 3433, South Africa

Euclea divinorum Hiern

- 1) RBHw 15112, Africa; 2) Mw 37202, Africa

Euclea lanceolata E. Mey.

- 1) USw 18539, South Africa; 2) RBHw 3801, Africa

Euclea mayottensis H. Perrier

- 1) RBHw 17928, South Africa

Euclea natalensis A. DC.

- 1) RBHw 17817, South Africa

Euclea racemosa Murr.

- 1) RBHw 3442, South Africa

Euclea schimperi (A. DC.) Dandy

- 1) RBHw 955, Africa

Royena dichrophylla (Gand.) De Winter

- 1) RBHw 17942, Africa; 2) Uw 22016, Africa

Royena glabra (L.) De Winter

- 1) RBHw 17909, Africa

Royena heterotricha (B. L. Burtt) F. White

- 1) RBHw 16800, Africa; 2) Uw 24539, Africa

Royena lucida L.

- 1) USw 18570, South Africa; 2) USw 21416, South Africa

Royena lycioides Desf.

- 1) RBHw 17813, South Africa; 2) RBHw 17814, South Africa

Royena pallens (Thunb.) F. White

- 1) USw 20434, South Africa; 2) RBHw 17907, South Africa

Royena whyteana (Hiern) F. White

- 1) RBHw 3448, South Africa; 2) RBHw 1325, South Africa

Diospyros abyssinica (Hiern) F. White

- 1) RBHw 3444, Africa; 2) RBHw 13327, Africa

Diospyros acuminata (Hiern) Kosterm.

- 1) RBHw 17872, Sri Lanka

Diospyros acuta Thw.

- 1) RBHw 17871, Sri Lanka

Diospyros affinis Thw.

- 1) RBHw 17873, Sri Lanka

Diospyros amazonica Krause

- 1) RBHw 16817, Brazil; 2) RBHw 13374, Brazil

Diospyros amboinensis Bakh.

- 1) RBHw 13256, New Guinea; 2) RBHw 13257, New Guinea

Diospyros andersonii (Soland. ex Hiern) P. S. Green

- 1) RBHw 13385, Fiji; 2) RBHw 13388, Fiji

Diospyros anisandra Blake

- 1) RBHw 13393, Mexico

Diospyros apiculata Hiern

- 1) RBHw 13219, Thailand

Diospyros artanthaefolia Mart. ex Miq.

- 1) RBHw 13614, Brazil; 2) RBHw 16816, Brazil

Diospyros batocana Hiern

- 1) RBHw 15110, Africa; 2) RBHw 13367, Africa

Diospyros bipindensis Gurke

- 1) RBHw 17978, Africa; 2) RBHw 13308, Africa

Diospyros bourdillonii Brandis

- 1) RBHw 17360, India; 2) Uw 32717, India

Diospyros canaliculata de Wild.

- 1) RBHw 13317, Africa; 2) RBHw 13898, Africa

Diospyros caribaea (A. DC.) Standl.

- 1) RBHw 13439, Cuba; 2) RBHw 15811, Cuba

Diospyros castanea (Craib) Fletcher

- 1) RBHw 17361, Thailand

Diospyros cauliflora Bl.

- 1) RBHw 13250, New Guinea; 2) RBHw 13043, New Guinea

Diospyros christophersenii Fosberg

- 1) RBHw 13410, Africa

Diospyros konzattii Standl.

- 1) RBHw 13394, Mexico

Diospyros cooperi (Hutch. & Dalz.) F. White

- 1) RBHw 1027, Liberia; 2) RBHw 3430, Liberia

Diospyros crassiflora Hiern

- 1) RBHw 13897, Africa; 2) RBHw 13318, Africa

Diospyros cuneata Standl.

- 1) RBHw 13386, Belize

Diospyros cupilifera Perr.

- 1) RBHw 17925, Madagascar

Diospyros dasyphylla Kurz

- 1) RBHw 17362, Thailand

Diospyros defectrix Fletcher

- 1) RBHw 13218, Thailand

Diospyros dendo Welw. ex Hiern

- 1) RBHw 13314, Africa

Diospyros dichroa Sandw.

- 1) RBHw 16814, Brazil; 2) RBHw 13444, Brazil

Diospyros discocalyx Merr.

- 1) RBHw 13627, Malaysia; 2) RBHw 13629, Malaysia

Diospyros duckei Sandw.

- 1) RBHw 16812, Guyana; 2) Uw 31747, Guyana

Diospyros ebenum Koenig ex Retzius

- 1) RBHw 17363, Sri Lanka; 2) RBHw 17877, Sri Lanka;
3) RBHw 17878, Sri Lanka

Diospyros elliptica (J. R. & F. Forst.) P. S. Green

- 1) RBHw 13416, Fiji

Diospyros ferrea (Willd.) Bakh.

- 1) RBHw 13415, Fiji; 2) RBHw 13414, Fiji

Diospyros fragrans Gurke

- 1) RBHw 13316, Africa

Diospyros glandulosa Lace

- 1) RBHw 17368, Thailand

Diospyros guatterrioides A. C. Smith

- 1) RBHw 13441, Brazil

Diospyros guianensis (Aubl.) Gurke

- 1) RBHw 13618, Brazil

Diospyros hallierii Bakh.

- 1) RBHw 13120, Malaysia

Diospyros heudelotii Hiern

- 1) RBHw 13329, Africa; 2) RBHw 14356, Africa

Diospyros hillebrandii (Seem.) Fosb.

- 1) RBHw 13411, Hawaii; 2) RBHw 13435, Hawaii

Diospyros hirsuta L.

- 1) RBHw 17370, Sri Lanka; 2) RBHw 17881, Sri Lanka

Diospyros hoyleana F. White

- 1) RBHw 13328, Africa; 2) RBHw 169, Sri Lanka

Diospyros inclusa Merr.

- 1) RBHw 13620, Philippines

Diospyros inconstans Jacq.

- 1) RBHw 16810, Brazil; 2) RBHw 13366, Brazil

Diospyros insularis Bakh.

- 1) RBHw 17904, Woodlark Island; 2) RBHw 16013, Woodlark Island

Diospyros iturensis (Gurke) R. Letouzey & F. White

- 1) RBHw 13330, Africa; 2) RBHw 8047, Africa

Diospyros kaki L.

- 1) RBHw 13303, Burma; 2) RBHw 13144, Burma

Diospyros kamerunensis Gurke

- 1) RBHw 14353, Africa; 2) RBHw 13307, Africa

Diospyros kirkii Hiern

- 1) RBHw 15111, Africa

Diospyros liriosmoides A.C. Smith

- 1) RBHw 13389, Brazil

Diospyros mattogrossensis Hoehne

- 1) RBHw 13438, Brazil

Diospyros mespiliformis Hochst. ex A. DC.

- 1) RBHw 13370, Africa; 2) RBHw 13348, Africa

Diospyros mweroensis F. White

- 1) RBHw 17378, Africa; 2) RBHw 17379, Africa

Diospyros minihasae Bakh.

- 1) RBHw 17376, E. Indonesia

Diospyros monbuttensis Gurke

- 1) RBHw 17979, Africa

Diospyros montana Roxb.

- 1) RBHw 17891, Sri Lanka; 2) RBHw 17890, Sri Lanka

Diospyros morrisiana Hance

- 1) Uw 27012, Japan; 2) USw 21645, Taiwan

Diospyros myrmecocarpa Mart. ex Miq.

- 1) RBHw 17590, Brazil

Diospyros natalensis (Harv.) Brenan

- 1) RBHw 17930, Madagascar

Diospyros nummulariaefolia Kosterm.

- 1) RBHw 17888, Sri Lanka

Diospyros paralea Steud.

- 1) RBHw 13376, Panama

Diospyros pentamera F. Muell.

- 1) RBHw 13345, Australia; 2) RBHw 13346, Australia

Diospyros peruviana Hiern

- 1) RBHw 13424, Peru; 2) RBHw 13425, Peru

Diospyros philippinensis A. DC.

- 1) RBHw 13621, Philippines

Diospyros physocalycina Gurke

- 1) RBHw 13305, Africa; 2) RBHw 14355, Africa

Diospyros poeppigiana A. DC.

- 1) RBHw 13430, Peru; 2) RBHw 16802, Brazil

Diospyros poncei Merr.

- 1) RBHw 13622, Philippines

Diospyros pseudoxylopia Mildbr.

- 1) RBHw 2872, Peru; 2) RBHw 13392, Brazil

Diospyros samoensis A. Gray

- 1) RBHw 13413, Fiji

Diospyros suaveolens Gurke

- 1) RBHw 13321, Africa; 2) RBHw 13306, Africa

Diospyros sylvatica Roxb.

- 1) RBHw 17897, Sri Lanka; 2) RBHw 17388, Sri Lanka

Diospyros tetrandra Hiern

- 1) RBHw 13373, Guyana; 2) RBHw 16795, Brazil

Diospyros thwaitesii Bedd.

- 1) RBHw 17900, Sri Lanka; 2) RBHw 17899, Sri Lanka

Diospyros virginiana L.

- 1) RBHw 13433, USA; 2) RBHw 3440, USA

Diospyros viridicans Hiern

- 1) RBHw 13315, Africa; 2) RBHw 14357, Africa

Diospyros vitiensis Gillespie

- 1) RBHw 13418, Africa; 2) RBHw 13417, Fiji

Diospyros zenkeri (Gurke) F. White

- 1) RBHw 13288, Africa; 2) RBHw 17977, Africa

Tetraclis baroni H. Perrier

- 1) RBHw 17983, Madagascar; 2) RBHw 17982, Madagascar

Tetraclis clusiaefolia Hiern

- 1) RBHw 17981, Madagascar

Tetraclis ebenifera H. Perrier

- 1) RBHw 17984, Madagascar

Chapter 2: Pollen morphology of the Cuspariinae (Rutaceae)

(In cooperation with J. Kallunki)

Taxonomic Background

Cuspariinae Engl. and Pilocarpinae Engl. are the only two subtribes in the tribe Cusparieae DC. of the subfamily Rutoideae of the Rutaceae. The subtribe Cuspariinae is composed of about 28 neotropical genera with about 125 described species. Most genera are monotypic or represented by fewer than 10 species. The largest are Angostura with more than 35 species and Raveniopsis with 19 species. Most are small trees and shrubs with dehiscent fruit (as all Rutoideae), derived from either an apocarpous or syncarpous gynoecium. The Cuspariinae differ from the rest of the subfamily by several tendencies: zygomorphic flowers, union of petals into a tubular corolla, union of the filaments with the corolla, reduction in number of fertile stamens from five to two by sterilization, basally appendaged anthers, loss of endosperm, and plicate cotyledons.

The most recent treatment of the subtribe, that of Engler (1931) in which he recognized 16 genera, is outdated. Kallunki's (1990, 1992, unpubl.) study of the Cuspariinae has resulted in modifications of Engler's system. For purposes of the present study, Kallunki's system of 26 genera is recognized (Table 29), differing from Engler in the following cases. 1) Angostura includes A. trifoliata (the type of the genus), the apocarpous species of Galipea (e.g., G. longiflora), and some undescribed species. In addition to apocarpous ovaries, these share connate petals, anthers with free basal appendages, tuberculate seeds, and branched trichomes. 2) All

other species described in Angostura are here called "Angostura-1." This "genus" is a collection of species without a distinct combination of characters. Although all species have alternate leaves, the genus is polymorphic for all other characters examined so far. Most species have free carpels, free petals, free stamens, two fertile stamens, no anther appendages, and curved embryos, but others have various combinations of connate carpels (at least axially), coherent or connate petals, connate filaments, connate anthers, three or five fertile stamens, anther appendages, and straight embryos. Whether or not the species in "Angostura-1" form a coherent genus is not yet resolved. 3) Erythrochiton is recognized in a restricted sense by the segregation of Toxosiphon and Desmotes (Kallunki, 1992). 4) Galipea includes the syncarpous species, which share connate anthers with a gland-dotted dorsum, a sterilized base (above the point of attachment of the filament), and connate appendages; connate carpels (and consequently a capsular fruit); smooth seeds; and simple, if any, trichomes. 5) Raputia is recognized with the exclusion of Neoraputia, Raputiarana, and Sigmatanthus (Emmerich, 1978) and of Raputia heptaphylla Pittier (Kallunki, 1990) and with the inclusion of Ravenia amazonica Huber and Lubaria szczerbanii Steyerm. Raputia heptaphylla differs from the other species assigned to the genus by its alternate (vs. opposite) leaves, free (vs. connate) anthers, tuberculate (vs. smooth) seeds, and conduplicate and plicate (vs. merely conduplicate) cotyledons. It resembles Raputiarana in these characters and, therefore, is considered as a member of that genus. Ravenia amazonica differs from most species of Ravenia in its smooth (vs. tuberculate) seeds and leathery (vs. succulent)

cotyledons. Lubaria szczerbanii differs from the other species of Lubaria in its five connate (vs. four connate and one free) petals and no connate filaments (vs. the two fertile filaments connate). Both share with Raputia five connate petals, no connate filaments, smooth seeds, and leathery cotyledons and, therefore, are considered to belong in Raputia.

Because pollen morphology proved to be useful in distinguishing Toxosiphon from Erythrochiton (Kallunki, 1992), pollen of other Cuspariinae was examined to assess whether the pollen characters are taxonomically useful and whether they support the reorganization of the subtribe outlined above and in Table 30.

In this study, pollen was examined also of some possibly related genera: Rutaneblina Steyerm. & Luteyn, a genus of uncertain subtribal affinity, and Hortia, whose transfer from Engler's drupaceous-fruited subfamily Toddalioidae to the Cusparieae was suggested recently because of chemical similarities (Fernandes da Silva et al., 1988).

There are limited studies on the Cuspariinae pollen morphology. Erdtman (1971) described the pollen of six species representing six genera. Barth (1983) described using LM, SEM, and TEM, the pollen morphology of Hortia from Brazil. Within the Cuspariinae, there are limited number of observations employing SEM and no studies including TEM.

Pollen Morphology

Materials and Methods for Pollen Morphology

Pollen from 71 species (111 specimens), representing all but two of the 26 genera of the Cuspariinae were studied by light microscopy (LM) and scanning electron microscopy (SEM). Some species, chosen to represent the range of pollen types, were examined also with transmission electron microscopy (TEM). Pollen was obtained from the dried herbarium specimens and the few pickled specimens listed in Appendix 4.

For light microscopy, pollen was mounted in glycerine jelly on glass slides sealed with paraffin. Slides were studied with a Nikon Optiphot microscope, and measurements of pollen grains were made with a computerized morphometric unit and Neurolucida software. The size classes used in the descriptions are based on the measurement of the longest axis of the pollen grain, exclusive of any spines (Erdtman, 1969). Shape was determined by the ratio of the mean length of the polar axis and the mean length of the equatorial axis (Erdtman, 1969). Photomicrographs were taken with a Nikon AFM automatic photomicrograph attachment. Glass slides of all specimens examined are deposited at the New York Botanical Garden.

Pollen samples for SEM study were mounted on stubs to which double-adhesive tape had been attached and were coated with gold-palladium in a sputter-coater for approximately 90 seconds. Observations were made on an JSM-T300 scanning electron microscope. All SEM micrographs were taken using Polaroid Type 665 P/N film with 0 tilt and an accelerating voltage of 15 KV.

For TEM, acetolyzed pollen was washed in distilled water, suspended in agar, fixed with osmium tetroxide for 2 hours, stained with uranyl acetate for one hour, dehydrated in a graded ethyl alcohol series, and embedded in LR White at 60 C. Pollen was sectioned using a RMC MT6000 ultramicrotome with a DuPont diamond knife, and sections were stained with lead citrate and examined and photographed with a JEOL 1200EX TEM. Measurements of the exine thickness were obtained from only a single individual for all sampled taxa except from two each for Adiscanthus fusciflorus and Spiranthera odoratissima.

The terminology used here for morphological characters follows, with few exceptions, Walker and Doyle (1975). "Pantocolporate" and "mesocolpium" are used in the sense of Erdtman (1971) and "endoapertures" and "ectoapertures" in the sense of van der Ham (1990). The ratio of colpus length to polar axis length (CL/PL) is introduced in this paper to describe the length of the colpus. These ratios were arbitrarily divided into classes of: short (0.01-0.35), medium (0.36-0.65), long (0.66-0.9), and very long (0.91-1). When used to describe the frequency of infratectal rod-like structures, "dense" means that the surface of the foot-layer is obscured by the closely packed structures, "less dense" means that the surface can be seen between the structures, and "occasional" means that only a few structures are present.

Results for Pollen Morphology

The observations of the pollen samples in Table 31 and in Plates 24 through 35 were used as the basis of the following descriptions. To facilitate discussion and comparison, the pollen was divided into 12 types based on sculpture pattern and aperture type (Table 32).

Pollen of the subtribe Cuspariinae

Pollen grains are solitary, radially symmetrical, isopolar or rarely apolar (Almeidea), usually oblate-spheroidal, sometimes euprolate, subprolate, prolate-spheroidal, or spherical, rarely suboblate (Nycticalanthus) or perprolate (Leptothyrsa), usually large, sometimes medium, or infrequently very large (Erythrochiton brasiliensis, E. gymnanthus, and Ticorea longiflora). Mean grain size ranges from 32.9 μm (P) X 18.8 μm (E), in "Angostura-1" sp. 4, to 107.6 μm (P) X 114.1 μm (E), in Ticorea longiflora. Grains are 3-6-colporate or rarely 3-porate (Spiranthera) or pantocolporate (Almeidea). Ectoapertures are meridionally aligned or rarely evenly distributed (Almeidea). Colpi are short, medium, or long. Endoapertures are lalongate, circular, or inconspicuous. Exine sculpturing is most commonly reticulate, sometimes perforate, foveolate-perforate, foveolate, foveolate-reticulate, reticulate, striate-reticulate, echinate, clavate, or baculate. The exine structure is columellate and tectate-perforate, columellate and semitectate, or intectate, stratified into ectexine and endexine, with the ectexine composed either of a distinct tectum, columellae, and a foot-layer or of columellae and a foot-layer. Nonapertural exine thickness ranges from 1.29 μm (in "Angostura-1" ucayalina) to 9.4

μm (in Leptothyrsa sprucei). The endexine is thin to absent in the mesocolpium and thicker, or rarely equal (Angostura), along the margins of and/or under the colpi.

Pollen of the genera of the Cuspariinae

Adiscanthus Ducke (Plate 24 A-D)

Pollen grains 3-colporate, euprolate, large. Ectoapertures long (ave. CL/PL 0.8), narrow, with sparse small granules covering the surface. Endoapertures lalongate. Exine sculpturing reticulate, the lumina irregular in outline, small to medium, the reticulum forming a solid tectum along the colpi margins. Exine structure columellate, semitectate, with a nonapertural exine ca. $2.8 \mu\text{m}$ thick, stratified into a distinguishable ectexine and endexine. Ektexine composed of tectum, columellae, and foot-layer, the tectum well developed, ca. 37% of the total exine thickness, the columellae reduced, ca. 6.5% of the total exine thickness, the foot-layer very prominent, ca. 56.5% of the total exine thickness. Endexine thin in the mesocolpium and slightly thicker under and along the margins of the colpi.

Almeidea A. St.-Hil. (Plate 24 E)

Pollen grains pantocolporate, medium. Ectoapertures ca. $10 \mu\text{m}$ long, narrow to wide, with sparse polymorphic granules covering the surface. Endoapertures circular. Exine sculpturing foveolate-perforate, the lumina circular to irregular in outline and small. Exine structure columellate, tectate-perforate.

Angostura Roem. & Schult. (Plate 25 A-D)

Pollen grains 5-or 6-colporate, oblate-spheroidal, large. Ectoapertures short (ave. CL/PL 0.2), wide, with dense polymorphic granules covering the surface. Endoapertures inconspicuous. Exine sculpturing baculate, with small rod-like structures between bacula, the sculpturing elements more abundant surrounding the apertures. Exine structure intectate, with a nonapertural exine ca. 3.6 μm thick, stratified into a distinguishable ectexine and a reduced or absent endexine. Ectexine composed of columellae and foot-layer, the columellae distinct, ca. 67% of the total exine thickness, the foot-layer prominent, ca. 33% of the total exine thickness. Endexine thin to absent in the mesocolpium and thin under and along the margins of the colpi.

"Angostura-1" (Plates 25 E-G, 26)

Pollen grains 3-6-colporate, euprolate, subprolate, or oblate-spheroidal, medium or large. Ectoapertures of some grains medium (ave. CL/PL 0.38), of others long (ave. CL/PL 0.83), narrow to wide, with sparse or dense polymorphic granules covering the surface. Endoapertures lalongate. Exine sculpturing perforate, foveolate, reticulate, or rarely foveolate-reticulate (A. ucayalina), the lumina circular to irregular in outline, small to medium, either smooth or with occasional infratectal rod-like structures. Exine structure columellate, tectate-perforate or semitectate, with a nonapertural exine ca. 1.29 μm thick, stratified into a distinguishable ectexine and a reduced or absent endexine. Ectexine composed of tectum, columellae, and foot-layer, the tectum well developed, ca. 54% of the

total exine thickness, the columellae reduced or granular, ca. 2% of the total exine thickness, the foot-layer ca. 44% of the total exine thickness. Endexine thin to absent in the mesocolpium and thicker under and along the margins of the colpi.

Apocaulon R. S. Cowan (Plate 27 A-D)

Pollen grains 4-colporate, subprolate, large. Ectoapertures long (ave. CL/PL 0.85), narrow, with sparse small granules covering the surface. Endoapertures inconspicuous. Exine sculpturing striate-reticulate, the lumina irregular in outline, small to medium, with occasional infratectal rod-like structures. Exine structure columellate, semitectate, with a nonapertural exine ca. 2.0 μm thick, stratified into a distinguishable ectexine and endexine. Ectexine composed of tectum, columellae, and foot-layer, the tectum well developed, ca. 30% of the total exine thickness, the columellae distinct, ca. 36% of the total exine thickness, the foot-layer ca. 34% of the total exine thickness. Endexine thin in the mesocolpium and thicker under and along the margins of the colpi.

Decagonocarpus Engl. (Plate 27 E, F)

Pollen grains 3-colporate, subprolate, large. Ectoapertures very long (ave. CL/PL 0.91), narrow, with either sparse or no small granules covering the surface. Endoapertures short-lalongate. Exine sculpturing reticulate, the lumina irregular in outline, medium, with occasional infratectal rod-like structures. Exine structure columellate, semitectate.

Desmotes Kallunki

(One collapsed sample was observed.) Pollen solitary. Exine sculpturing echinate, with rod-like structures between the spines. Exine structure intectate.

Ertela Adans. (Plate 27 G)

Pollen grains 3-colporate, medium. Ectoapertures short, narrow, with sparse small granules covering the surface. Endoapertures inconspicuous. Exine sculpturing reticulate, the lumina irregular in outline, small to medium, either smooth or with occasional infratectal rod-like structures. Exine structure columellate, semitectate.

Erythrochiton Nees & Mart. (Plates 27 H, 28 A-D)

Pollen grains 3(4)-colporate, oblate-spheroidal, large or very large. Ectoapertures of some grains short (ave. CL/PL 0.35), of others medium (ave. CL/PL 0.45), wide, with dense polymorphic granules covering the surface. Endoapertures circular or inconspicuous. Exine sculpturing baculate, echinate, or clavate, with small rod-like structures between projections, the sculpturing elements more abundant around the apertures. Exine structure intectate, with a nonapertural exine ca. 6 μm thick, stratified into a distinguishable ectexine and endexine. Ektexine composed of columellae and foot-layer, the columellae distinct, ca. 64.5% of the total exine thickness, the foot-layer ca. 35.5% of the total exine thickness. Endexine thin in the mesocolpium and thicker under and along the margins of the colpi.

Euxylophora Huber (Plate 28 E)

Pollen grains 3-colporate, euprolate, large. Ectoapertures of medium length (ave. CL/PL 0.55), narrow, with sparse granules covering the surface. Endoapertures lalongate. Exine sculpturing perforate, the lumina circular in outline and small.

Galipea Aubl. (Plate 28 F-J)

Pollen grains 3- or 4-colporate, prolate-spheroidal or oblate-spheroidal, large. Ectoapertures inconspicuous, short (ave. CL/PL 0.28), narrow, with sparse small granules covering the surface. Endoapertures circular or inconspicuous. Exine sculpturing reticulate, the lumina irregular in outline, large, with less dense infratectal rod-like structures. Exine structure semi-tectate, with a nonapertural exine ca. 5.5 μm thick, stratified into a distinguishable ectexine and endexine. Ektexine composed of tectum, columellae, and foot-layer, the tectum well developed, ca. 36% of the total exine thickness, the columellae distinct, ca. 32% of the total exine thickness, the foot-layer prominent, ca. 32% of the total exine thickness. Endexine thin in the mesocolpium and thicker under and along the margins of the colpi.

Leptothyrsa Hook. f. (Plate 29)

Pollen grains 3-colporate, perprolate, large. Ectoapertures long (ave. CL/PL 0.86), narrow, with sparse polymorphic granules covering the surface. Endoapertures lalongate. Exine sculpturing striate-reticulate, the lumina irregular in outline, small to medium, with occasional infratectal rod-like structures, the reticulum

forming a solid tectum along the colpi margins. Exine structure columellate, semitectate, with a nonapertural exine 3.0-9.4 μm thick, stratified into a distinguishable ectexine and endexine.

Ectexine of the ridged mesocolpium, composed of tectum, columellae, and foot-layer, the tectum well-developed, 10-23% of the total exine thickness, the columellae distinct, 11-27% of the total exine thickness, the foot-layer very prominent, 50-79% of the total exine thickness. Endexine thin and granular in the mesocolpium and thicker under and along the margins of the colpi.

Lubaria Pittier (Plate 30 A, B)

Pollen grains 5-or 6-colporate. Ectoapertures inconspicuous, long (ave. CL/PL 0.73), narrow, with either sparse or no small granules covering the surface. Endoapertures inconspicuous. Exine sculpturing reticulate, the lumina irregular in outline, medium to large, with occasional infratectal rod-like structures. Exine structure columellate, semitectate.

Neoraputia Emmerich (Plate 30 C, D)

Pollen grains 3-colporate, oblate-spheroidal or spherical, large. Ectoapertures of medium length (ave. CL/PL 0.65), narrow, with sparse to dense polymorphic granules covering the surface. Endoapertures circular to short lalongate. Exine sculpturing reticulate, the lumina irregular in outline, medium, with less dense infratectal rod-like structures. Exine structure columellate, semitectate.

Nycticalanthus Ducke (Plate 30 E-G)

Pollen grains 4-short-colporate, suboblate, large. Ectoapertures short (ave. CL/PL 0.2), wide, with sparse to dense polymorphic granules covering the surface. Endoapertures inconspicuous. Exine structure columellate, tectate-perforate. Exine sculpturing baculate, with small rod-like structures (1.5 μm) between bacula, the sculpturing elements more abundant around the apertures. Exine structure intectate, with a nonapertural exine ca. 6.4 μm thick, stratified into a distinguishable ectexine and a reduced or absent endexine. Ectexine composed of columellae and foot-layer, the columellae distinct, ca. 70% of the total exine thickness, the foot-layer prominent, ca. 30% of the total exine thickness. Endexine absent in the mesocolpium and thin under and along the margins of the colpi.

Raputia Aubl. (Plate 31 A)

Pollen grains 5-or 6-colporate, spherical or prolate-spheroidal, large. Ectoapertures long (ave. CL/PL 0.88), narrow, with sparse small granules covering the surface. Endoapertures elongate. Exine sculpturing reticulate, the lumina irregular in outline, medium to large, with less dense infratectal rod-like structures. Exine structure columellate, semitectate.

Raputiarana Emmerich (Plate 31 B-D)

Pollen grains 3-colporate, prolate-spheroidal, large. Ectoapertures long (ave. CL/PL 0.8), narrow, with sparse to dense small granules covering the surface. Endoapertures inconspicuous.

Exine sculpturing reticulate, the lumina irregular in outline, medium to large, with less dense infratectal rod-like structures. Exine structure columellate, semitectate.

Rauia Nees & Mart. (Plate 31 E-G)

Pollen grains 3-colporate, euprolate, large. Ectoapertures long (ave. CL/PL 0.79), narrow, with sparse small granules covering the surface. Endoapertures lalongate. Exine sculpturing perforate, lumina circular or elongate in outline, small. Exine structure columellate, tectate-perforate, with a nonapertural exine ca. 1.75 μm thick, stratified into a distinguishable ectexine and endexine. Ectexine composed of tectum, columellae, and foot-layer, the tectum well-developed, ca. 39% of the total exine thickness, the columellae reduced, ca. 14% of the total exine thickness, the foot-layer prominent, ca. 47% of the total exine thickness. Endexine thin in the mesocolpium and thicker under and along the margins of the colpi.

Ravenia Vell. (Plate 32 A)

Pollen grains 5-or 6-colporate, oblate-spheroidal or prolate-spheroidal, large. Ectoapertures of medium length (ave. CL/PL 0.5), narrow, with sparse small granules covering the surface. Endoapertures circular. Exine sculpturing reticulate, lumina irregular in outline, medium to large, smooth or with occasional infratectal rod-like structures. Exine structure columellate, tectate-perforate or semitectate.

Raveniopsis Gleason (Plate 32 B-G)

Pollen grains 3-colporate or 5-or 6-colporate, euprolate, prolate-spheroidal, or subprolate, medium or large. Ectoapertures of some grains medium (ave. CL/PL 0.64), of others long (ave. CL/PL 0.84), narrow, with sparse small granules covering the surface. Endoapertures circular. Exine sculpturing reticulate, the lumina irregular in outline, medium, either smooth or with occasional infratectal rod-like structures. Exine structure columellate, tectate-perforate or semitectate, with a nonapertural exine ca. 2.75 μm thick, stratified into a distinguishable ectexine and endexine. Ektexine composed of tectum, columellae, and foot-layer, the tectum well-developed, ca. 23% of the total exine thickness, the columellae reduced, ca. 32% of the total exine thickness, the foot-layer prominent, ca. 45% of the total exine thickness. Endexine thin to absent in the mesocolpium and thicker under and along the margins of the colpi.

Sigmatanthus Emmerich (Plate 33 A)

Pollen grains 5-or 6-colporate, oblate-spheroidal, large. Ectoapertures inconspicuous, short (ave. CL/PL 0.31), narrow, with sparse to dense small granules covering the surface. Endoapertures inconspicuous. Exine sculpturing reticulate, the lumina very irregular in outline, medium to large, with less dense infratectal rod-like structures. Exine structure columellate, semitectate.

Spiranthera A. St.-Hil. (Plate 33 B-E)

Pollen grains 3-porate, oblate-spheroidal, large. Ectoapertures porate (ave. 4 μm in diam.). Endoapertures circular. Exine sculpturing echinate, with a dense infratectal rod-like structures between spines, the sculpturing elements more abundant around the apertures. Exine structure intectate, with a nonapertural exine ca. 3.9 μm thick. Exine stratified into a distinguishable ektexine and a reduced or absent endexine. Ektexine composed of columellae and foot-layer, the columellae distinct, ca. 53% of the total exine thickness, the foot-layer prominent, ca. 47% of the total exine thickness. Endexine absent in the mesocolpium and thin under and along the margins of the colpi.

Ticorea Aubl. (Plate 33 F-I)

Pollen grains 6-short-colporate, oblate-spheroidal, large or very large. Ectoapertures sometimes inconspicuous, short (ave. CL/PL 0.12), narrow, with either sparse or no small granules covering the surface. Endoapertures circular. Exine sculpturing reticulate, the lumina irregular in outline, medium to large, with dense, long to short infratectal rod-like structures. Exine structure columellate, semitectate, with a nonapertural exine ca. 4.6 μm thick, stratified into a distinguishable ektexine and a reduced or absent endexine. Ektexine composed of tectum, columellae, and foot-layer, the tectum well-developed, ca. 32% of the total exine thickness, the columellae distinct, ca. 37% of the total exine thickness, the foot-layer prominent, ca. 31% of the total exine thickness. Endexine

absent in the mesocolpium and thin under and along the margins of the colpi.

Toxosiphon Baill. (Plate 34)

Pollen grains 3-colporate, oblate-spheroidal, large. Ectoapertures of medium length (ave. CL/PL 0.5), narrow, with sparse small granules covering the surface. Endoapertures lalongate. Exine sculpturing reticulate, the lumina irregular in outline, medium to large, with occasional infratectal rod-like structures. Exine structure columellate, semitectate.

Pollen of possible relatives

Hortia Vand. (Plate 35)

Pollen grains solitary, radially symmetrical, isopolar, 3-colporate, subprolate, or euprolate, medium. Ectoapertures meridionally aligned, of medium length (ave. CL/PL 0.58), narrow, with either sparse or no polymorphic granules covering the surface. Endoapertures lalongate. Exine sculpturing psilate-perforate, the lumina infrequent, when present circular, small. Exine structure columellate, tectate-imperforate to infrequently perforate, with a nonapertural exine ca. 3.6 μm thick, stratified into a distinguishable ektexine and thin endexine. Ektexine composed of tectum, columellae and foot-layer, the tectum well-developed, ca. 25% of the total exine thickness, the columellae reduced, ca. 7% of the total exine thickness, the foot-layer very prominent, ca. 68% of the total exine thickness. Endexine thin in mesocolpium (at least in the few

instances in which it was stained sufficiently to be observed) and thick under and along the margins of the colpi.

Rutaneblina Steyerm. & Luteyn

Pollen grains solitary, radially symmetrical, isopolar, 3-colporate, subprolate, medium. Ectoapertures meridionally aligned, long (ave. CL/PL 0.72), narrow, with sparse to dense small granules covering the surface. Endoapertures inconspicuous. Exine sculpturing reticulate, the lumina irregular in outline, small to medium, with infratectal rod-like structures. Exine structure columellate, semitectate.

Discussion for Pollen Morphology

Pollen characters in the Rutaceae

No survey of the pollen of the family has been published. The published observations that do exist usually appear as a sampling of taxa found in geographically oriented pollen surveys (Barth, 1982b, 1983, 1985; Heusser, 1971; Selling, 1947; Ybert, 1979). Data are available for some representatives of all subfamilies but one (i.e., for Rutoideae, Toddalioideae, Citroideae, Dictyolomatoideae, and Flindersioideae but not for Spathelioideae). These data (Barth, 1982, 1983, 1985; Erdtman, 1971; Heusser, 1971; Selling, 1947; Ybert, 1979) indicate that pollen of the Rutaceae is (2) 3 (4--6) -colporate (rarely 3-porate), usually reticulate, rarely echinate, striate, foveolate, or psilate, prolate to suboblate (rarely perprolate), and 15--100 μm through the longest axis. That of the Rutoideae reflects this entire range of variation with the exception of the 2-colporate state.

The only previously published observations of pollen of Cuspariinae are those of Erdtman (1971) and Barth (1982b). Erdtman (1971) examined one species in each of six genera of the Cuspariinae. Except for minor differences in the reported measurements of the axes, our observations of the same genera correlate with his. Barth (1982b) reported observations of 12 genera and approximately 20 species. No voucher specimens are cited, specific epithets for some of the genera examined are lacking, photographs are present for only eight species, and full, comparable descriptions of the pollen of each genus are not given. Thus, an accurate comparison of our results is

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not possible, but, for the most part, our observations agree with hers.

Pollen characters and generic delimitation in the Cuspariinae.

Seven genera are uniquely characterized (Table 32) by a single pollen type--Almeidea (type 2), Leptothyrsa (type 7), Apocaulon (type 8), Spiranthera (type 9), Erythrochiton (type 10), Nycticalanthus (type 11) and Angostura (type 12).

The two largest genera, Raveniopsis and "Angostura-1", exhibit more than a single pollen type. The grains of Raveniopsis are reticulate, but are either 3-colporate (Plate 32 B) or type 5 or 5-or 6-colporate (Plate 32 E, G) and type 6. These two types correlate almost perfectly with two groups of species in Raveniopsis; the species with type 5 (Table 32) have simple trichomes, and, with one exception, the species with type 6 (Table 32) have branched trichomes. The exception is R. sericea, which has type 6 and simple trichomes. Raveniopsis fraterna, which has type 5, and R. sericea are quite similar in macromorphological features--so much so that they have been considered to be one species (Steyermark, 1984). That these two apparently closely related species have different pollen types argues against the usefulness of aperture number as a distinguishing character of the two groups within the genus.

Like the macromorphological characters, the pollen characters of "Angostura-1" are highly variable. Five pollen types occur in the genus. The sculpture pattern ranges from perforate (Plate 26E, F) to foveolate (Plate 26C) to foveolate-reticulate (Plate 26A) to reticulate (Plate 26D) to i.e., all patterns present in the subtribe

except the intectate pattern (types 9--12). Aperture class ranges from 3--6-colporate, i.e., all except pantocolporate (type 2) and porate (type 9). Because pollen of only 10 of the ca. 35 species has been examined, it is likely that additional variation in pollen characters will be found in other species. Sculpture pattern and aperture number are not useful in solving the generic problem in "Angostura-1."

Each of the fifteen other genera examined exhibits only one of three pollen types (1, 5, or 6), but these types are distributed among several genera (Table 32) and, therefore, are not unique identifiers of genera. The pollen characters are taxonomically useful, however, in supporting the separation of the apocarpous species described in Galipea (e.g., G. longiflora, here assigned to Angostura) from the syncarpous species of true Galipea. The former species have baculate, 5- or 6-colporate pollen (type 12; Plate 25A, B, D), and the latter have reticulate, 3- or 4-colporate pollen (type 5; Plate 28F, G). The presence in Angostura trifoliata of pollen type 12 (Table 32; Plate 25A, B) correlates with other macromorphological characters (discussed in the introduction to this paper) and supports its separation from all other species described in Angostura and its alliance with the apocarpous species of Galipea (Plate 25D).

Furthermore, as discussed by Kallunki (1992), the semitectate pollen of Toxosiphon (Plate 34), in combination with several macromorphological characters, supports its segregation from Desmotes and Erythrochiton, which have intectate pollen (Plates 27H, 28B, D).

Because Lubaria (Plate 30A, B), Raputia (Plate 31A), and Ravenia (Plate 32A) all have type 6 pollen, pollen data offer no additional support for, but do not negate, the alignment of Lubaria szczerbanii and Ravenia amazonica with Raputia.

Although morphological characters support the separation of Neoraputia, Raputiarana, and Sigmatanthus from Raputia, pollen data are equivocal with respect to the separation or union of these genera; Raputia and Sigmatanthus have pollen of type 6 and Neoraputia and Raputiarana of type 5.

A comparison of pollen and other characters in the Cuspariinae.

The taxa with perforate to foveolate (types 1--4) pollen grains, i.e., Almeidea, Rauia, Euxylophora, and some species of "Angostura-1", have free petals, stamens, and carpels and five rather than only two fertile anthers and may be more closely related to each other than to other genera in the subtribe. Almeidea is similar to many species of "Angostura-1" in its choripetalous flowers, five fertile stamens, and free carpels, but its anthers appear to be dorsifixed rather than basifixed as in most "Angostura-1", and its pollen is pantocolporate (Plate 24E), unique in the subtribe.

Rauia was distinguished from "Angostura-1" (as Cusparia) by Engler (1931) only by characters of dubious value: in Rauia the carpels initially united ventrally and ultimately becoming free in fruit and the petals valvate, and in "Angostura-1" the carpels free from the beginning and the petals imbricate. The species described in Rauia have linear petals, usually narrower than those in "Angostura-1", and some species have unequal cotyledons, a

character not found so far in "Angostura-1". Rauia is, however, similar to most species of "Angostura-1" in the free or only slightly coherent petals that are narrowly imbricate not valvate, free stamens, and two fertile stamens with unappendaged anthers. Given the variation in most characters in "Angostura-1", the addition to "Angostura-1" of Rauia with its characters of slightly connate carpels, narrower petals, and unequal cotyledons would not be discordant (cf. Gereau, 1990). Pollen characters do not negate this possibility.

Euxylophora resembles Rauia and some species of "Angostura-1" in its narrow, free petals and its free stamens bearing five fertile, unappendaged anthers, but differs from them by being a large tree rather than a shrub or treelet and by having connate carpels, and no cupular disc. That the pollen characters-- aperture number, aperture type, and sculpture pattern-- of "Angostura-1", Rauia, and Euxylophora are similar (Table 32; Plates 26E, 28E, 31E) may indicate that they are related.

The taxa with reticulate pollen form a variable group. Splitting these further into two groups (types 5 and 6) based on number of colpi results in variable groups as well. An examination of the genera in these groups will illustrate this point. "Angostura-1", as mentioned in the previous section, has a wide range of pollen types, of which types 5 and 6 are only two. Adiscanthus is quite unlike the other genera with type 5. It has actinomorphic 5-merous flowers with free petals, stamens, and carpels, and with dorsifixed, unappendaged anthers, and no cupular disc, while others have zygomorphic flowers with coherent or connate petals, basifixed,

basally appendaged anthers, and a cupular disc. Its relationships are not known. Decagonocarpus and the species of Raveniopsis with pollen of type 5 and Ertela, Lubaria, Raputia, Ravenia, and the species of Raveniopsis with pollen of type 6 form an apparently related group of genera characterized by opposite leaves, free, imbricate sepals, connate petals, and free carpels and usually by connate, appendaged anthers with a gland-dotted dorsum and by conduplicate, bilobed cotyledons. Galipea, Neoraputia, Toxosiphon (with type 5) and Ticorea (with type 6) form a group characterized by, among other features, connate carpels, and Raputiarana (with type 5) and Sigmatanthus (with type 6) form another characterized by free carpels. That the otherwise similar taxa within each of these two groups have different pollen types argues against the usefulness of aperture number as a generic character.

Striate-reticulate grains (type 7 and 8) occur in both Leptothyrsa and Apocaulon. In Leptothyrsa, the ectexine of the mesocolpium is longitudinally deeply ridged (Plate 29A, C--E), while in Apocaulon the ectexine is not ridged (Plate 27A). This difference in pollen structure correlates with differences in a multitude of macromorphological characters that distinguish these two genera, and despite their striate-reticulate pollen these two genera are probably not closely related. Leptothyrsa is a treelet with actinomorphic flowers ca. 2 cm long in which all anthers are fertile and unappendaged and the embryo is straight with planate cotyledons oriented sagittally to the floral axis. Apocaulon is a low, rhizomatous herb with zygomorphic flowers, ca. 7 mm long in which only two anthers are fertile and basally appendaged and the embryo

is curved with conduplicate cotyledons oriented proximally to the floral axis. Apocaulon despite its alternate leaves, shares many macromorphological characters with members of a group of genera with opposite leaves--including Decagonocarpus, Ertela, Lubaria, Raputia (sensu Kallunki, 1990), Ravenia, and Raveniopsis. Unlike Apocaulon, however, these latter six genera have reticulate pollen of type 5 or 6. In this case, Apocaulon may be closely related to this group of genera despite the difference in pollen characters.

Apart from this group of genera, opposite leaves occur only in Desmotes, which differs, however, in its echinate pollen, large, connate, valvate, rose-colored sepals, coherent petals, and free anthers without a gland-dotted dorsum. Although originally described, because of the large, colored calyx, as a species of Erythrochiton, D. incomparabilis, the only species of the genus, differs in several features from Erythrochiton (Kallunki, 1992). Its relationships are obscure, in part because it is known only by the flowering type collection, but its pollen is echinate like that of some Erythrochiton.

The four genera with intectate (echinate, clavate, or baculate) pollen (types 9--12) [Spiranthera (Plate 33B, D), Nycticalanthus (Plate 30F, G), Erythrochiton (Plates 27H, 28D), and Angostura (Plate 25A, D)] fall into two groups based on macromorphological characters. These two groups may not be related to each other, but within each, however, the taxa may indeed be closely related. Nycticalanthus (an endemic of the Brazilian Amazon) and Spiranthera (a genus of three or four species ranging from northern South America to Bolivia and southern Brazil) share rather large,

choripetalous flowers, five fertile stamens bearing unappendaged anthers, and a gynophore. Erythrochiton and Angostura share connate petals, tuberculate seeds, free anthers with free appendages and free carpels.

In Kallunki's (1992) revision, she mentioned that exceptional individuals of Erythrochiton from Iquitos, Peru, resembled E. brasiliensis in their actinomorphic flowers with red calyx and five fertile stamens, but differed from typical representatives of that species in, for example, their shorter and rather equally 3-dentate calyces and smaller anthers. Only one (Thomas 6782) of the specimens of E. brasiliensis examined for the present study had been collected in the Iquitos area. Its pollen grains were smaller than those of a typical representative (Mori et al. 9361) of the species (compare samples 2 and 5 in Table 31).

The pollen of Hortia, characterized by a psilate exine with rare perforations, a very thick foot-layer, and reduced columellae (Plate 35), is unlike that of any member of the Cuspariinae. Our observations differ from Barth's (1983) in that she reported the grains to be "punctate," i.e., possessing a perforate tectum, and somewhat larger, e.g., with a mean polar axis length of 50.5--51.0 μm vs. ours of 33.4--34.4 μm . In any case, data from pollen characters offer no support for the transfer of this genus from the Toddalioidae to the Cuspariinae, as was suggested based on chemical characters (Fernandes da Silva et al., 1988).

Rutaneblina was described by Steyermark and Luteyn (Steyermark, 1984) without reference to tribal affinity or possible relationships. Its 3-colporate, reticulate, subprolate, medium-sized

pollen is similar to the type 5 Cuspariinae pollen but also to that of the Pilocarpinae (Morton, unpubl.). Pollen characters offer equivocal evidence as to its placement within either subtribe.

Preliminary observations of the pollen of three genera (Pilocarpus, Metrodorea, and Esenbeckia) of the Pilocarpinae (Morton, unpubl.) show that the range of pollen characters in this subtribe fall within that of the Cuspariinae and support a close relationship between the two.

Conclusions

As discussed earlier, aperture number is not a useful generic character in Raveniopsis or in "Angostura-1." On this basis, types 5 and 6 may be better considered as a single type--reticulate and 3--6-colporate. The pollen characters that may be most useful at the generic level may be more broadly defined sculpture patterns and aperture classes defined without reference to aperture number, i.e., pantocolporate, colporate, and porate.

This survey of the pollen of the Cuspariinae has demonstrated the variety of pollen characters in the subtribe and has confirmed the taxonomic usefulness of such characters in delimiting some genera. The use of these characters in phylogenetic analyses will show whether or not such characters are also useful indicators of relationships among these genera. This study suggests that systematic examination of the pollen of other groups throughout the Rutaceae may provide information useful in assessing relationships within this diverse family.

Table 30. A comparison of the genera of Cuspariinae recognized for the present study with those recognized by Engler (1931)

Present study	Engler's circumscription
<u>Achuaria</u> Gereau a, b	.
<u>Adiscanthus</u> Ducke	same
<u>Almeidea</u> A. St.-Hil.	same
<u>Angostura</u> Roem. & Schult. [including <u>Angostura trifoliata</u> (Willd.) T. S. Elias and apocarpous <u>Galipea</u> , e.g., <u>G. longifolia</u> K. Krause] ^c	as <u>Cusparia</u> Humb., composed of <u>A. trifoliata</u> and "Angostura-1"
"Angostura-1" ^a (including all <u>Angostura</u> except <u>A. trifoliata</u>)	included in <u>Cusparia</u>
<u>Apocaulon</u> R. S. Cowan ^a	
<u>Decagonocarpus</u> Engl.	same
<u>Desmotes</u> Kallunki ^a	
<u>Ertela</u> Adans.	as <u>Monnieria</u> L.
<u>Erythrochiton</u> Nees & Mart. (excluding <u>Toxosiphon</u> and <u>Desmotes</u>)	including <u>Toxosiphon</u>
<u>Euxylophora</u> Huber	same
<u>Galipea</u> Aubl. (including only syncarpous species of <u>Galipea</u> and excluding the apocarpous species, e.g.,	including both syncarpous and apocarpous species

<u>G. longiflora</u>)	
<u>Leptothyrsa</u> Hook. f.	same
<u>Lubaria</u> Pittier	same
<u>Naudinia</u> Planch, & Linden ^b	same
<u>Neoraputia</u> Emmerich	included in <u>Raputia</u>
<u>Nycticalanthus</u> Ducke ^a	
<u>Raputia</u> Aubl. (including <u>Ravenia amazonica</u> Huber and <u>Lubaria szczerbanii</u> Steyerm. ^a) ^c	including <u>Neoraputia</u> , <u>Raputiarana</u> , <u>Sigmatanthus</u>
<u>Raputiarana</u> Emmerich (including <u>Raputia heptaphylla</u> Pittier) ^c	included in <u>Raputia</u>
<u>Rauia</u> Nees & Mart.	same
<u>Ravenia</u> Vell. (excluding <u>Ravenia amazonica</u>)	+same, but including <u>R.</u> <u>ruellioides</u> Oliv. (now included in <u>Raveniopsis</u>) and <u>R. amazonica</u>
<u>Raveniopsis</u> Gleason ^a	
<u>Sigmatanthus</u> Emmerich	included in <u>Raputia</u>
<u>Spiranthera</u> A. st.-Hil.	same
<u>Ticorea</u> Aubl.	same
<u>Toxosiphon</u> Baill.	included in <u>Erythrochiton</u>

^aThese taxa were described after 1931 (or not yet in the case of "Angostura-1") and were not treated by Engler.

^bPollen of these genera was not included in this study.

^cThe nomenclatural transfers will be published elsewhere (Kallunki, unpubl.).

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Table 31 Morphological characters observed by SEM and LM of genera of the Cuspariinae and also of Eulanebina and Hortia. The taxa are listed in the genera in which they are recognized in this study (cf. Table 1). Such listings are not nomenclatural transfers. For species of which more than one sample was studied, the sample number corresponding to the voucher specimen in Appendix 1 is given in parentheses following the specific epithet.

	na	Polar axis (µm) ^b	Equatorial axis (µm) ^b	P/E ^c	Aperture	Sculpture pattern ^d
ADISCANTHUS (1 sp.)						
<u>fuscllorus</u> (2)	3	53.0-(54.2)-56.7	24.3-(29.4)-33.0	1.84	3-colporate	R
<u>fuscllorus</u> (2)	25	45.3-(55.4)-59.7	29.5-(31.4)-34.5	1.76	3-colporate	R
ALMEIDEA (5 spp.)						
<u>limae</u>	25	42.6-(45.3)-47.2	38.0-(41.5)-45.0		pantocolporate	F-P
<u>rubra</u> (1)	25	42.3-(47.0)-52.0	37.9-(42.8)-47.1		pantocolporate	F-P
<u>rubra</u> (2)	20	45.0-(48.5)-52.0	39.7-(43.9)-50.0		pantocolporate	F-P

ANGOSTURA (ca. 6 spp.)						
<u>Gallipea longiflora</u>	25	77.1-(83.6)-94.5	79.2-(87.5)-100.1	0.96	5-6-short-colporate	B
sp. nov.	25	81.0-(91.2)-97.1	75.2-(94.4)-105.0	0.97	6-short-colporate	B
<u>trifoliata</u> (1)	24	66.1-(71.3)-78.5	70.1-(75.5)-83.1	0.94	5-6-short-colporate	B
"ANGOSTURA-1" (ca. 35 spp.)						
<u>Angostura larensis</u>					3-colporate	P
<u>A. macrophylla</u> (2)	25	34.9-(37.3)-39.6	33.8-(37.5)-40.0	0.99	4-colporate	P
<u>A. pentacyna</u> (1)	11	29.6-(36.1)-42.3	31.3-(39.2)-43.4	0.92	5-6-colporate	F
<u>A. ramiflora</u> (2)	14	56.9-(60.9)-64.8	58.4-(63.7)-68.3	0.96	6-colporate	R
<u>A. silvestris</u> (2)	25	38.9-(43.8)-47.3	41.6-(45.7)-51.7	0.96	4-5-colporate	F
sp. 1	25	34.2-(36.6)-39.4	25.0-(27.0)-29.1	1.36	4-colporate	F
sp. 2					4-colporate	R
sp. 3	25	37.5-(40.3)-43.0	27.6-(30.9)-34.9	1.30	3-colporate	R
sp. 4	25	30.8-(32.9)-34.4	17.6-(18.8)-20.9	1.75	4-colporate	F
<u>A. cf. transitionalis</u>	14	58.2-(63.8)-68.8	38.0-(40.9)-44.5	1.56	3-colporate	P
<u>A. ucayalina</u> (2)	25	42.4-(44.4)-47.7	28.4-(31.0)-33.1	1.43	3-colporate	F-R
APOCAULON (1 sp.)						
<u>carnosum</u>	17	49.7-(53.2)-55.6	39.7-(44.9)-52.0	1.18	4-colporate	S-R
DECAGONOCARPUS (2 spp.)						
<u>cornutus</u>					3-colporate	R
<u>oppositifolius</u> (1)	25	52.8-(70.1)-78.4	44.4-(53.0)-58.5	1.32	3-colporate	R

<i>oppositifolius</i> (2)	12	81.9-(85.0)-88.0	59.8-(66.7)-72.2	1.27	3-colporate	R
DESMOTES (1 sp.) <i>incomparabilis</i>						E
ERTELA (2 spp.) <i>trifolia</i>					3-colporate	R
ERYTHROCHITON (7 spp.)						
<i>brasiliensis</i> (2)	25	98.8-(103.3)-114.5	97.6-(106.0)-117.1	0.97	3-short-colporate	B
<i>brasiliensis</i> (5)	6	73.4-(75.6)-80.3	76.2-(80.8)-88.1	0.94	3-short-colporate	B
<i>fallax</i> (1)	25	72.2-(76.5)-79.9	71.5-(80.4)-83.9	0.95	3-short-colporate	E
<i>fallax</i> (2)	25	71.4-(77.9)-81.6	71.4-(79.6)-85.0	0.98	3-short-colporate	E
<i>fallax</i> (3)	25	66.6-(74.4)-86.4	71.1-(76.2)-85.1	0.98	3-short-colporate	E
<i>gymnanthus</i> (2)	25	82.5-(102.3)-112.5	82.5-(104.5)-117.5	0.98	3-4-short-colporate	C
EUXYLOPHORA (1 sp.) <i>paraensis</i> (2)	25	46.6-(50.2)-53.3	29.9-(33.1)-36.4	1.52	3-colporate	P
GALIPEA (ca. 12 spp.) <i>davisi</i>	25	70.2-(78.8)-85.4	66.0-(73.4)-80.3	1.07	3-short-colporate	R
<i>jasminiflora</i> (1)	10	53.3-(61.2)-68.2	67.2-(69.5)-72.8	0.88	3-4-short-colporate	R
<i>jasminiflora</i> (2)	25	58.5-(63.7)-67.6	66.3-(71.5)-75.4	0.89	3-4-short-colporate	R
<i>jasminiflora</i> (4)	11	60.7-(65.2)-71.4	67.7-(71.9)-75.1	0.91	3-4-short-colporate	R

sp. nov. 1 (1)	13	69.8-(73.4)-76.9	66.0-(69.7)-74.0	1.05	3-short-colporate	R
sp. nov. 1 (2)	25	63.9-(67.1)-70.9	69.7-(73.0)-76.4	0.92	3-4-short-colporate	R
LEPTOTHYRSA (1 sp.)						
<u>sprucei</u> (1)	25	72.7-(77.5)-83.5	30.6-(33.9)-37.2	2.29	3-colporate	S-R
<u>sprucei</u> (2)	25	72.8-(79.7)-83.6	29.4-(34.5)-39.9	2.31	3-colporate	S-R
LUBARIA (1 sp.)						
<u>arvensis</u> (2)					5-6-colporate	R
NEORAPUTIA (5 spp.)						
<u>alba</u>	25	72.3-(81.0)-88.2	80.9-(86.0)-93.8	0.94	3-colporate	R
<u>paraensis</u>	5	68.1-(68.9)-70.8	72.6-(76.6)-80.7	0.90	3-colporate	R
<u>trifoliata</u>	25	54.3-(59.5)-65.8	53.7-(59.7)-62.5	1.00	3-colporate	R
NYCTICALANTHUS (1 sp.)						
<u>speciosus</u>	4	66.6-(73.0)-76.8	84.2-(88.6)-90.8	0.82	4-short-colporate	B
RAPUTIA (ca. 9 spp.)						
<u>maroana</u>						R
sp. nov. 1					5-6-colporate	R
sp. nov. 2	22	68.6-(72.7)-77.5	67.2-(72.4)-78.4	1.00	5-6-colporate	R
<u>Lurata szcerbanii</u>	17	62.0-(65.8)-70.4	62.1-(64.9)-68.1	1.01	5-colporate	R
<u>uliei</u>					5-colporate	R

RAPUTIAFRANA (2 spp.)						
<u>subsigmoides</u> (1)	25	85.5-(92.5)-97.8	82.7-(87.7)-93.7	1.05	3-colporate	R
<u>subsigmoides</u> (2)	25	82.7-(88.7)-94.7	83.0-(86.7)-91.7	1.02	3-colporate	R
<u>Raputia heptaphylla</u>					3-colporate	R
RAUIA (ca. 10 spp.)						
<u>resinosa</u> (1)	25	46.8-(54.6)-58.5	31.2-(33.8)-36.4	1.62	3-colporate	P
sp. nov. 1					3-colporate	P
<u>spicata</u>	22	64.1-(68.4)-73.8	43.0-(48.1)-51.6	1.42	3-colporate	P
<u>subtruncata</u>					3-colporate	P
RAVENIA (11 spp.)						
<u>bitramosa</u>	25	85.9-(95.6)-105.4	74.3-(88.2)-97.6	1.08	5-6-colporate	R
<u>leonis</u>					6-colporate	R
<u>rosea</u>	8	67.7-(70.1)-74.7	72.4-(75.5)-80.0	0.93	5-colporate	R
<u>urbanii</u>	25	71.5-(74.6)-79.1	76.7-(79.7)-83.7	0.94	6-colporate	R
RAVENIOPSIS (19 spp.)						
<u>breweri</u>					6-colporate	R
<u>fraternia</u> (2)	25	27.2-(31.6)-37.3	19.1-(24.4)-28.0	1.30	3-colporate	R
<u>linearis</u>					3-colporate	R
<u>peduncularis</u> (2)	25	61.9-(66.8)-70.7	55.5-(59.3)-62.4	1.13	5-6-colporate	R
<u>ruellioides</u> (3)	25	74.9-(87.1)-94.6	56.1-(60.8)-64.8	1.43	3-colporate	R

<i>sericea</i>						5-colporate	R
<i>stelligera</i>						5-colporate	R
<i>steyermarkii</i>						5-colporate	R
SIGMATANTHUS (1 sp.)							
<i>trifoliatus</i> (1)	5	73.6-(79.4)-82.2	81.0-(83.4)-85.7	0.95	5-6-short-colporate		R
SPIRANTHERA (3 spp.)							
<i>odoratissima</i> (2)	25	54.0-(61.5)-65.6	59.4-(65.6)-70.7	0.94	3-porate		E
<i>parviflora</i>					3-porate		E
TICOREA (3 spp.)							
<i>foetida</i>	25	85.0-(89.5)-94.9	89.8-(95.4)-102.3	0.94	6-short-colporate		R
<i>longiflora</i>	21	97.0-(107.6)-120.4	105.6-(114.1)-124.4	0.94	6-short-colporate		R
<i>cf. longiflora</i>					6-short-colporate		R
TOXOSIPHON (4 spp.)							
<i>carinatus</i>					3-colporate		R
<i>lindenii</i>	25	79.3-(83.7)-89.7	80.9-(88.3)-94.4	0.95	3-colporate		R
<i>trifoliatus</i> (1)	25	73.7-(83.5)-88.7	77.3-(89.0)-97.3	0.94	3-colporate		R
<i>trifoliatus</i> (2)	25	53.9-(68.6)-77.4	59.2-(70.3)-76.3	0.98	3-colporate		R

HORTIA (ca. 9 spp.)

<u>arborea</u>	16	31.4-(34.4)-37.7	24.1-(26.6)-28.6	1.29	3-colporate	Ps-P
<u>brasiliana</u> (1)	25	29.3-(32.8)-34.8	23.3-(26.3)-28.4	1.25	3-colporate	Ps-P
<u>brasiliana</u> (2)	6	30.0-(34.1)-35.1	25.2-(26.9)-28.4	1.27	3-colporate	Ps-P
<u>excelsa</u>	25	36.7-(40.1)-42.8	23.9-(28.6)-31.7	1.40	3-colporate	Ps-P

RUTANEBLINA (1 sp.)

<u>pusilla</u> (2)	11	25.8-(28.1)-30.0	20.1-(21.6)-23.9	1.30	3-colporate	R

a The number of grains upon which the measurements, if any, of the axes were made.

b These measurements represent the range and, in parentheses, the mean.

c P/E = ratio of the length of the polar axis to that of the equatorial axis. Because the pantocolporate grains of Almeidaa, by definition, have no polar axis, the measurements in the "polar axis" column refer to another equatorial axis.

d B = baculate, C = clavate, E = echinate, F = foveolate, P = perforate, Ps = psilate, R = reticulate, S = striate (as use by Walker and Doyle, 1975).

Table 32. Pollen types of the Cuspariinae^a

Pollen type ^b	Taxon
1. Perforate, 3- or 4-colporate	"Angostura-1" <u>larensis</u> , "A.-1" <u>macrophylla</u> , "A.-1" cf. <u>transitionalis</u> <u>Euxylophora</u> <u>Rauia</u>
2. Foveolate-perforate, pantocolporate	<u>Almeidea</u>
3. Foveolate, 4-6-colporate	"Angostura-1" sp. 1, "A.-1" <u>pentagyna</u> , "A.-1" <u>silvestris</u> , "A.-1" sp. 4
4. Foveolate-reticulate, 3-colporate	"Angostura-1" <u>ucayalina</u>
5. Reticulate, 3- or 4-colporate	<u>Adiscanthus</u> "Angostura-1" sp. 2, "A.-1" sp. 3 <u>Decagonocarpus</u> <u>Ertela</u> <u>Galipea</u> <u>Neoraputia</u> <u>Raputiarana</u> <u>Raveniopsis fraterna</u> , <u>R. linearis</u> , <u>R. ruellioides</u> <u>Toxosiphon</u>
6. Reticulate, 5- or 6-colporate	"Angostura-1" <u>ramiflora</u> <u>Lubaria</u> <u>Raputia</u> <u>Ravenia</u> <u>Raveniopsis breweri</u> ,

	<u>R. peduncularis, R. sericea,</u> <u>R. stelligera, R. steyermarkii</u> <u>Sigmatanthus</u> <u>Ticorea</u>
7. Striate-reticulate, 3-colporate	<u>Leptothyrsa</u>
8. Striate-reticulate, 4-colporate	<u>Apocaulon</u>
9. Echinata, 3-porate	<u>Spiranthera</u>
10. Baculate, echinate, or clavate, 3(4)-colporate	<u>Erythrochiton</u>
11. Baculate, 4-colporate	<u>Nycticalanthus</u>
12. Baculate, 5- or 6-colporate	<u>Angostura</u>

^a not examined: Achuarina, Naudinia.

^b of uncertain type: Desmotes (echinate, but apertures unknown).

Fig. 24. Pollen of Cuspariinae. A-D. Adiscanthus fusciflorus (A, Daly et al. 5722; B-D, Ducke 234). A. Equatorial view showing long, narrow ectoaperture and reticulate sculpturing with the sculpturing forming a solid tectum along the colpus margin (arrow). B. Radial section of whole grain showing thicker endexine under and along the aperture (arrow). C. Equatorial view showing lalongate endoaperture. D. Radial section through mesocolpium showing reduced columellae and prominent foot-layer. E. Almeidea rubra (Farias 118). Pollen grains with foveolate-perforate sculpturing and pantocolporate apertures. (Scale bars: A, E = 10 μm ; B, D = 4 μm ; C = 30 μm .)

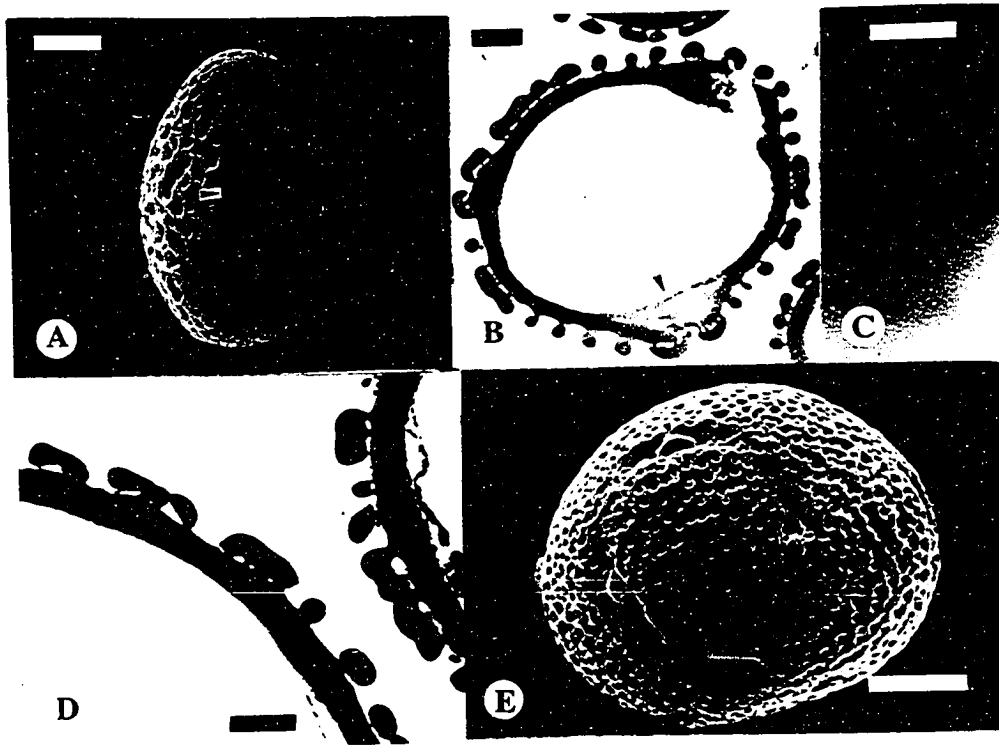


Fig. 25. Pollen of Cuspariinae. A-C. Angostura trifoliata (Stergios et al. 5909). A. Oblique equatorial view showing short-colporate apertures. B. Surface view showing baculate sculpturing with rod-like structures. C. Radial section through mesocolpium showing intectate exine. Note sizes of bacula and rod-like structures. D. Galipea longiflora (= Angostura) (Daly 6382). Oblique equatorial view showing baculate sculpturing with rod-like structures and short-colporate apertures. E, F. Angostura ucayalina (= "Angostura-1") (Schunke 5635). E. Radial section showing thickened endexine under and along the margin of the aperture. F. Radial section showing reduced and granular columellae. G. Angostura macrophylla (= "Angostura-1") (Thomas et al. 6817). Polar view showing 4 apertures. (Scale bars: A, B, D = 10 μm ; C, E, F = 4 μm ; G = 30 μm .)

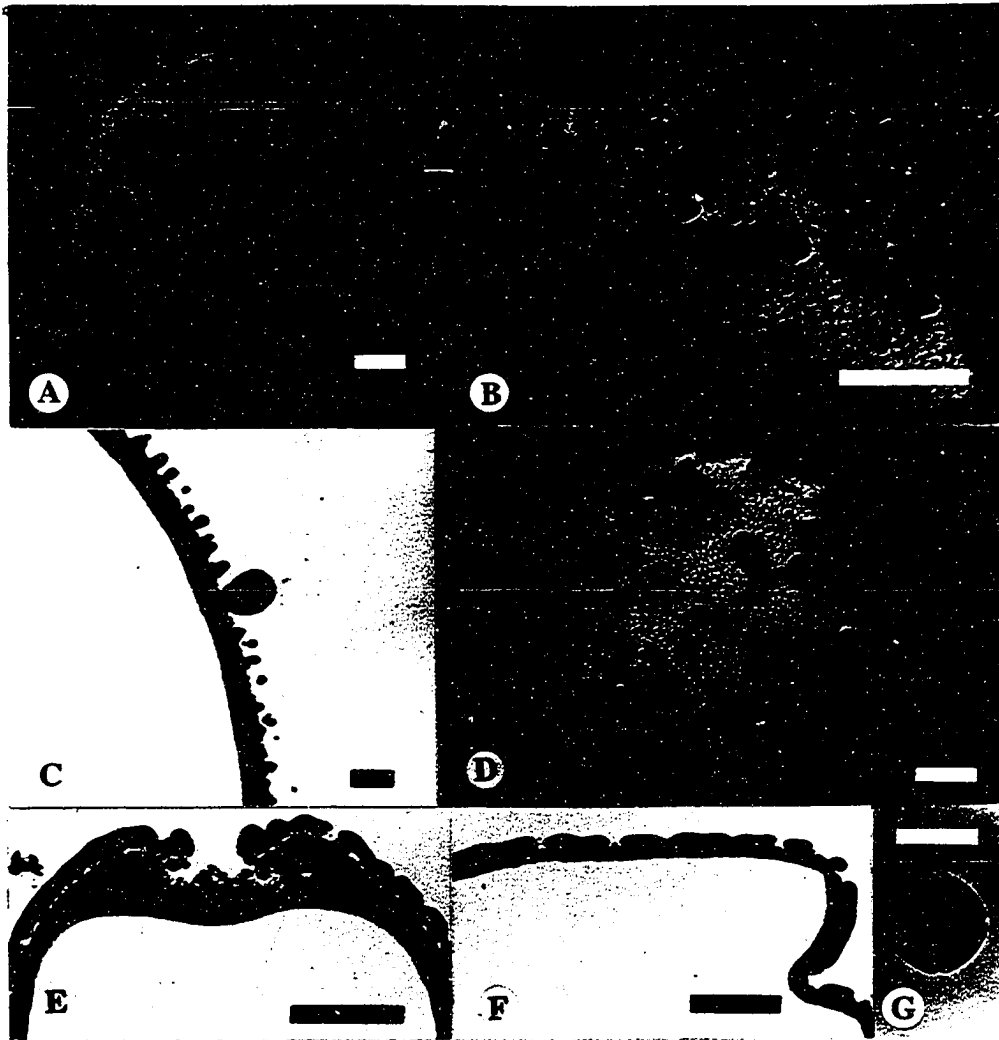


Fig. 26. Pollen of Cuspariinae. A, B. Angostura ucavalina (= "Angostura-1") (Schunke 5635). A. Oblique equatorial view showing foveolate-reticulate sculpturing. B. Surface view showing irregularly shaped lumina. C. Angostura pentagyna (= "Angostura-1") (Sousa 453). Polar view showing foveolate sculpturing. D. "Angostura-1" sp. 3 (Mattos Silva et al. 1822). Polar view showing reticulate sculpturing and 3 apertures. E. Angostura cf. transitionalis (= "Angostura-1") (Pinard 860). Equatorial view showing perforate sculpturing. F. Angostura macrophylla (= "Angostura-1") (Thomas 6817). Oblique polar view showing perforate sculpturing and 3 of the 4 apertures. (Scale bars: A, B, D, F = 10 μm ; C = 15 μm ; E = 11 μm .)

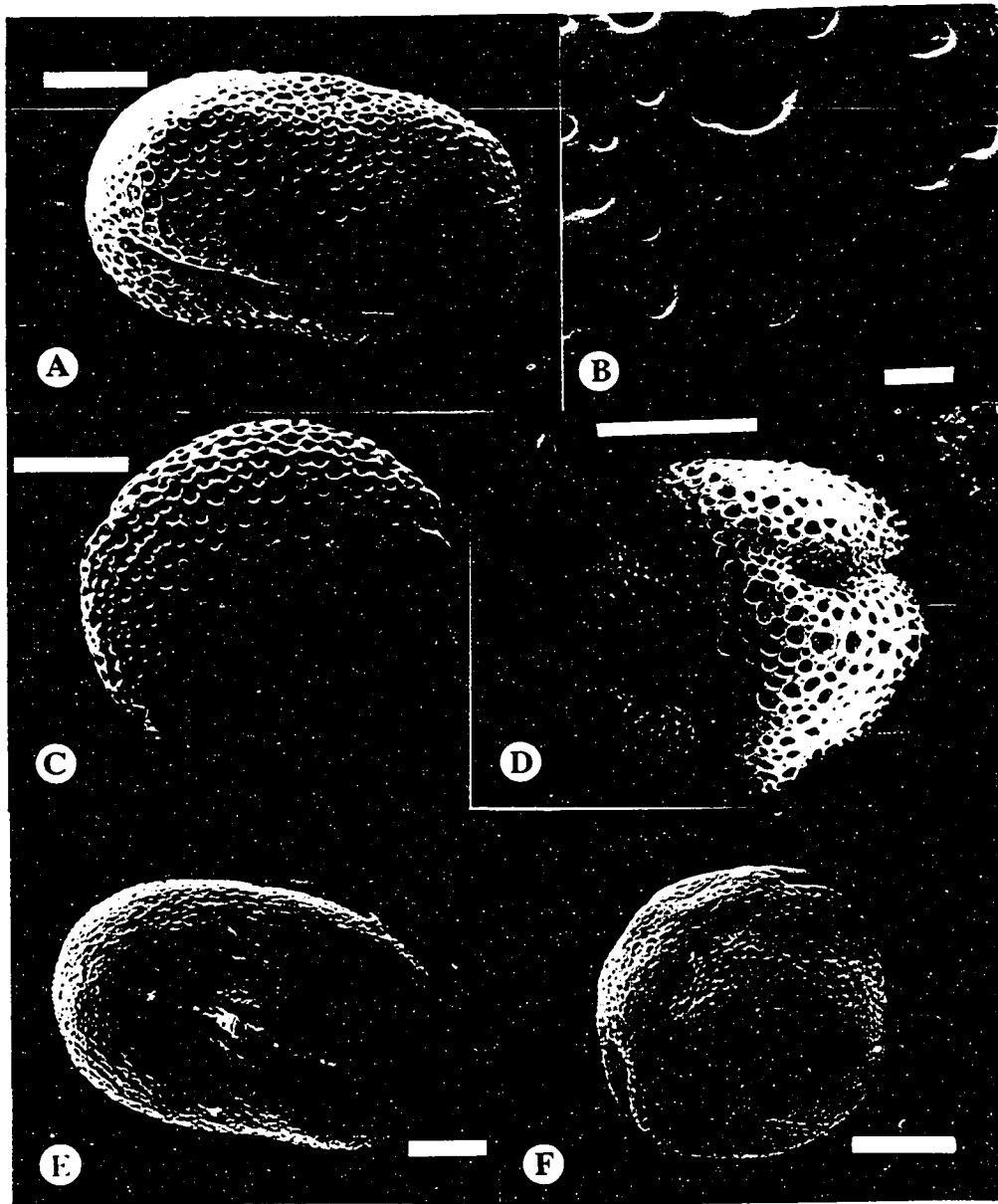


Fig. 27. Pollen of Cuspariinae. A-D. Apocaulon carnosum (Maguire & Maguire 29188). A. Equatorial view showing striate-reticulate sculpturing and long, narrow ectoaperture. B. Radial section of whole pollen grain. Note increased thickness of endexine under and along the aperture (arrow). C. Radial section through mesocolpium showing thin endexine. D. Surface view showing lumina with occasional infratectal rod-like structures. E, F. Decagnocarpus oppositifolius (E, Maguire et al. 37493; F, Maguire et al. 42618). E. Equatorial view showing reticulate sculpturing and ectoaperture. F. Surface view showing lumina with occasional infratectal rod-like structures. G. Ertela trifolia (H. T. Beck et al. 321). Surface view showing reticulate sculpturing. H. Erythrochiton gymnanthus (Kallunki 309). Equatorial view showing short-colporate apertures and clavate sculpturing. (Scale bars: A, B, E, F = 10 μm ; C = 4 μm ; D, G = 20 μm ; H = 15 μm .)

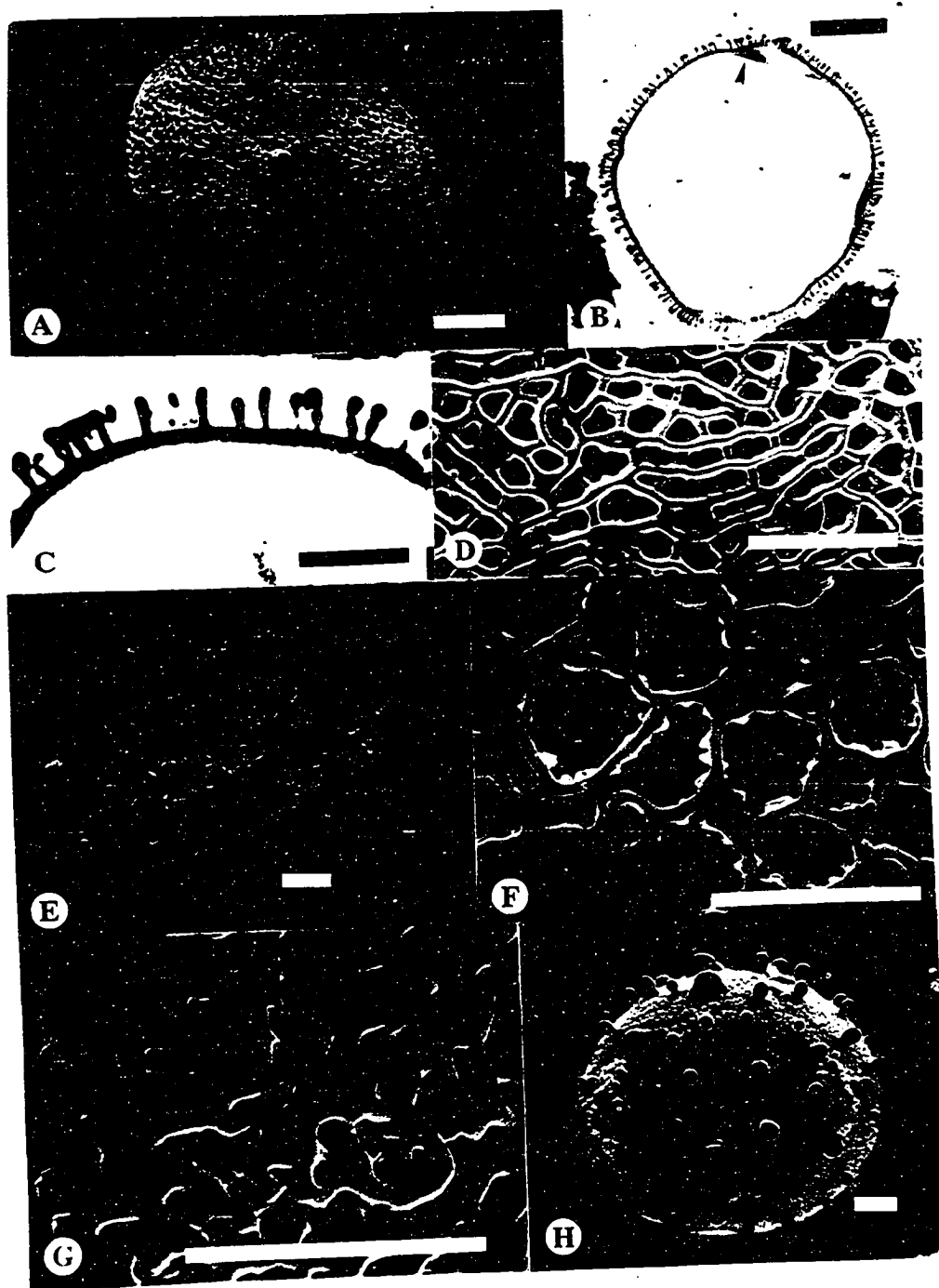


Fig. 28. Pollen of Cuspariinae. A-D. Erythrochiton fallax (A, B, Idrobo & Schultes 830; C, D, Daly et al. 6445). A. Radial section showing abundant spines near the aperture. B. Radial section through mesocolpium showing spines and reduced rod-like structures. Note thin endexine in the mesocolpium (arrow). C. Equatorial view. D. Oblique equatorial view showing short-colporate aperture and echinate sculpturing. E. Euxylophora paraensis (Rosa & Santos 2227). Equatorial view showing perforate sculpturing. F. Galipea sp. nov. 1 (Daly et al. 1891). Polar view showing reticulate sculpturing. G-I. Galipea jasminiflora (Anderson 12331). G. Surface view showing large lumina with rod-like structures. H. Radial section showing thickened endexine near the aperture (arrow). I. Radial section through mesocolpium showing semitectate exine with rod-like structures. J. Galipea davisii (Ducke RB-35598). Equatorial view. (Scale bars: A, B, H, I = 4 μm ; C, J = 30 μm ; D, F, G = 10 μm ; E = 13 μm .)

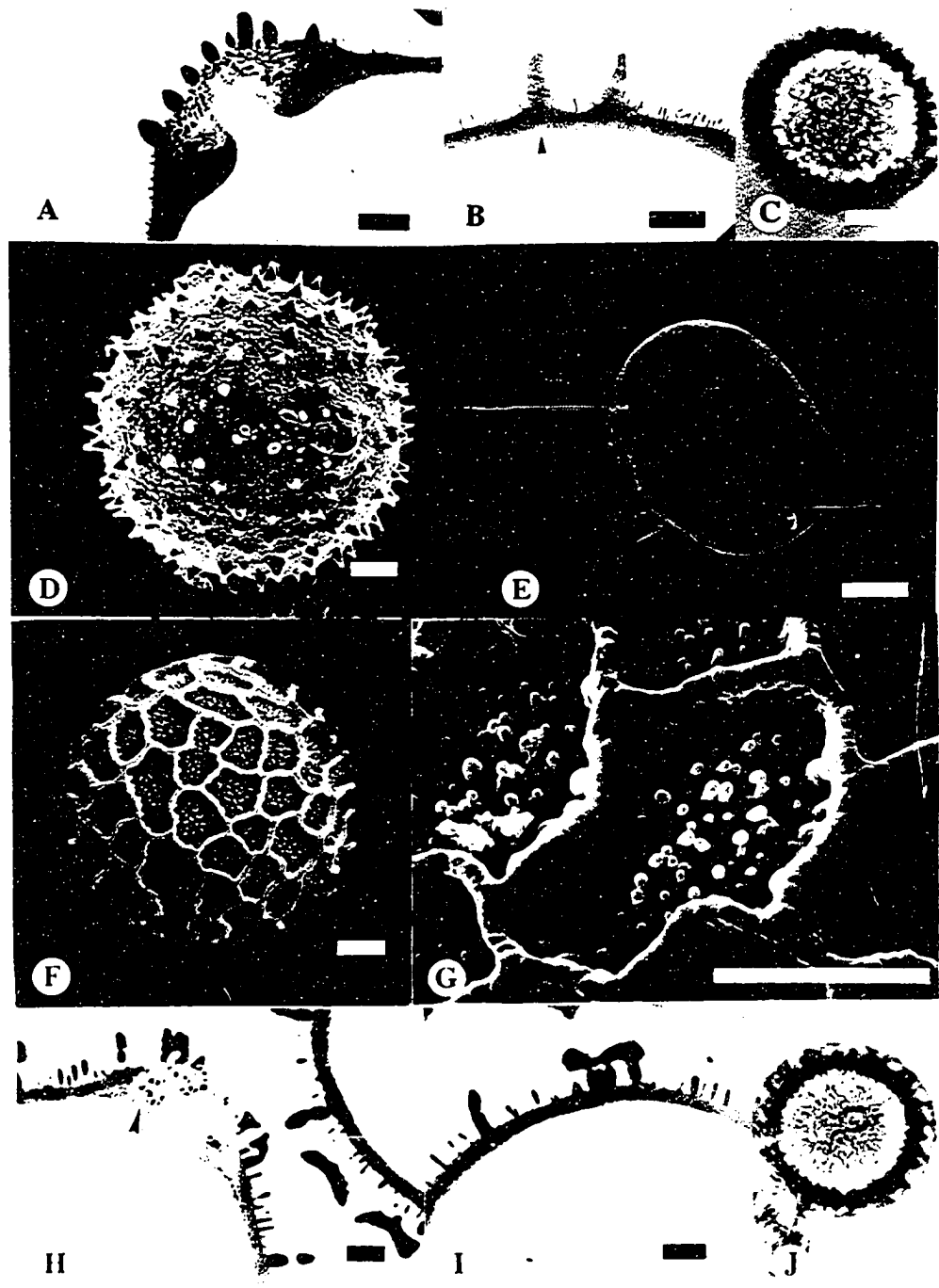


Fig. 29. Pollen of Cuspariinae. A-E. Leptothyrsa sprucei (A-C, Killip & Smith 29844; D, E, McDaniel & Rimachi Y. 29660). A. Equatorial view showing striate-reticulate sculpturing with ridged walls of the mesocolpium. B. Surface view showing striate-reticulate sculpturing with the sculpturing forming a solid tectum along the colpus margin. C. Equatorial view showing the ridged walls of the mesocolpium. D. Radial section showing the presence of endexine under and along the margins of the aperture. E. Radial section of whole grain showing ridged walls of the mesocolpium. (Scale bars: A, C = 12 μm ; B = 20 μm ; D = 4 μm ; E = 8 μm .)

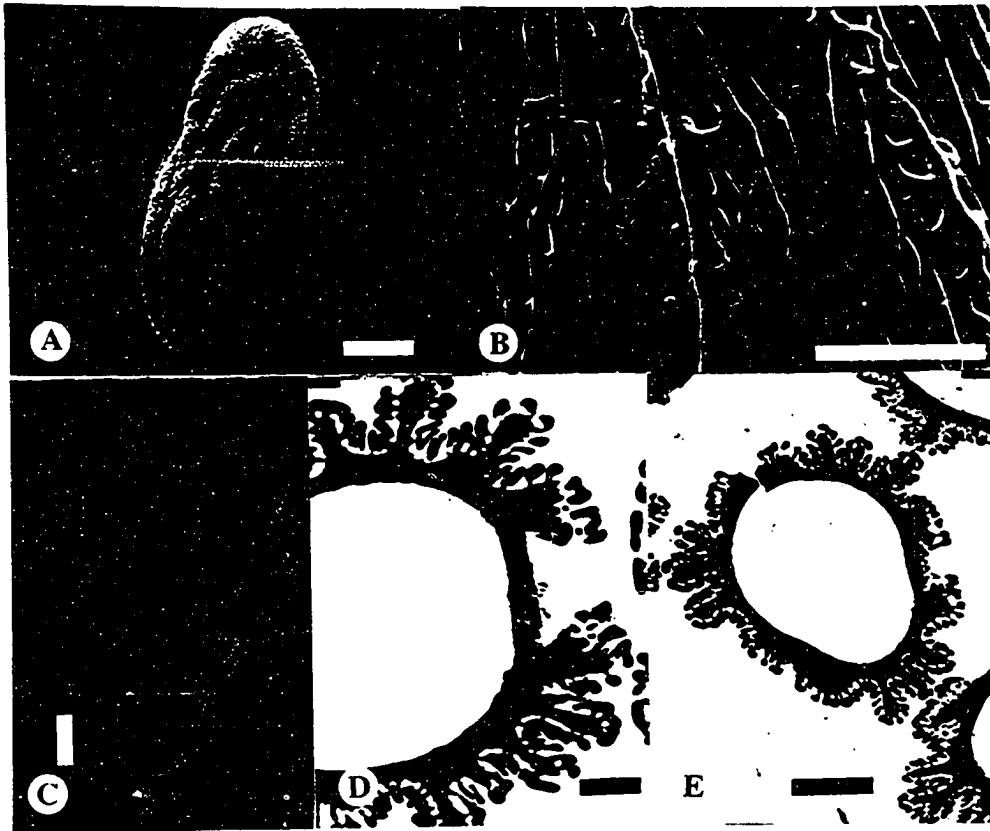


Fig. 30. Pollen of Cuspariinae. A, B. Lubaria aroensis (Bernardi 5824). A. Oblique polar view showing reticulate sculpturing and inconspicuous aperture. B. Surface view showing lumina with occasional rod-like structures. Note aperture (arrow). C, D. Neoraputia alba (Pirani et al. 2489). C. Polar view showing reticulate sculpturing, lumina with rod-like structures, and 3 apertures. D. Equatorial view showing colporate aperture. E-G. Nycticalanthus speciosus (Ducke 99). E. Radial view showing endexine (arrow) and ektexinous bacula near the aperture. F. Slightly oblique polar view showing baculate sculpturing and 4 apertures. G. Surface view showing rod-like structures between bacula. (Scale bars: A, B, F, G = 10 μm ; C = 14 μm ; D = 12 μm ; E = 4 μm .)

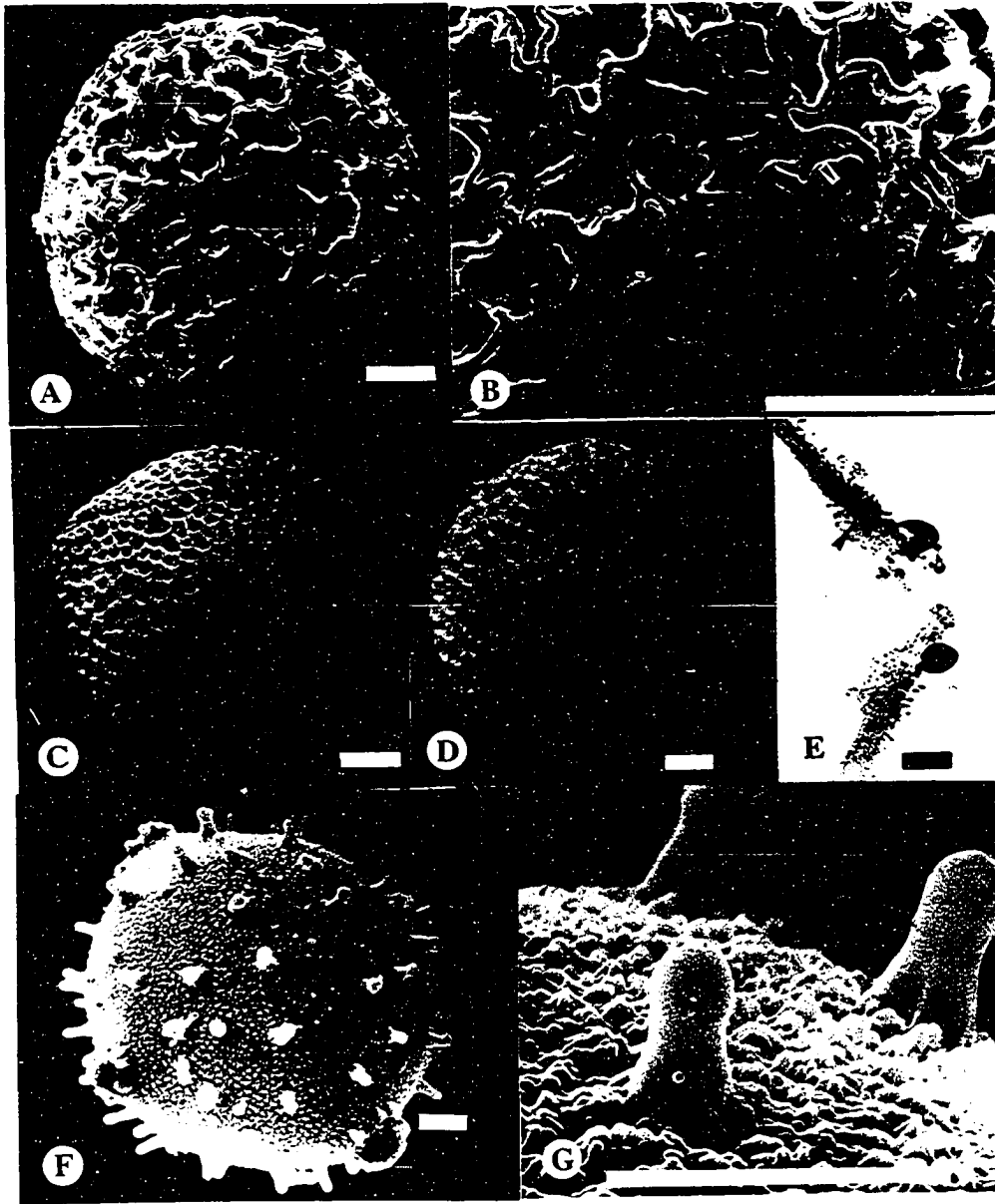


Fig. 31. Pollen of Cuspariinae. A. Raputia ulei (Maas & Maas 490). Oblique polar view showing reticulate sculpturing and lumina with occasional infratectal rod-like structures. B. Raputia heptaphylla (=Raputiarana) (Steiermark 91443). Oblique equatorial view showing meridionally aligned, long, narrow ectoapertures. C, D. Raputiarana subsigmoidea (C, Davidson 5209; D, Rimachi Y. 2728). C. Equatorial view showing reticulate sculpturing and irregular lumina with occasional infratectal rod-like structures. D. Polar view showing 3 apertures. E-G. Rauia resinosa (E, Mori et al. 11540; F, G, Duarte 6291). E. Equatorial view showing perforate sculpturing and 2 of 3 apertures. F. Radial view through mesocolpium showing tectate-perforate exine. G. Surface view showing elongate and circular perforations. (Scale bars: A, B, C = 10 μm ; D = 30 μm ; E = 13 μm ; F = 4 μm ; G = 20 μm .)

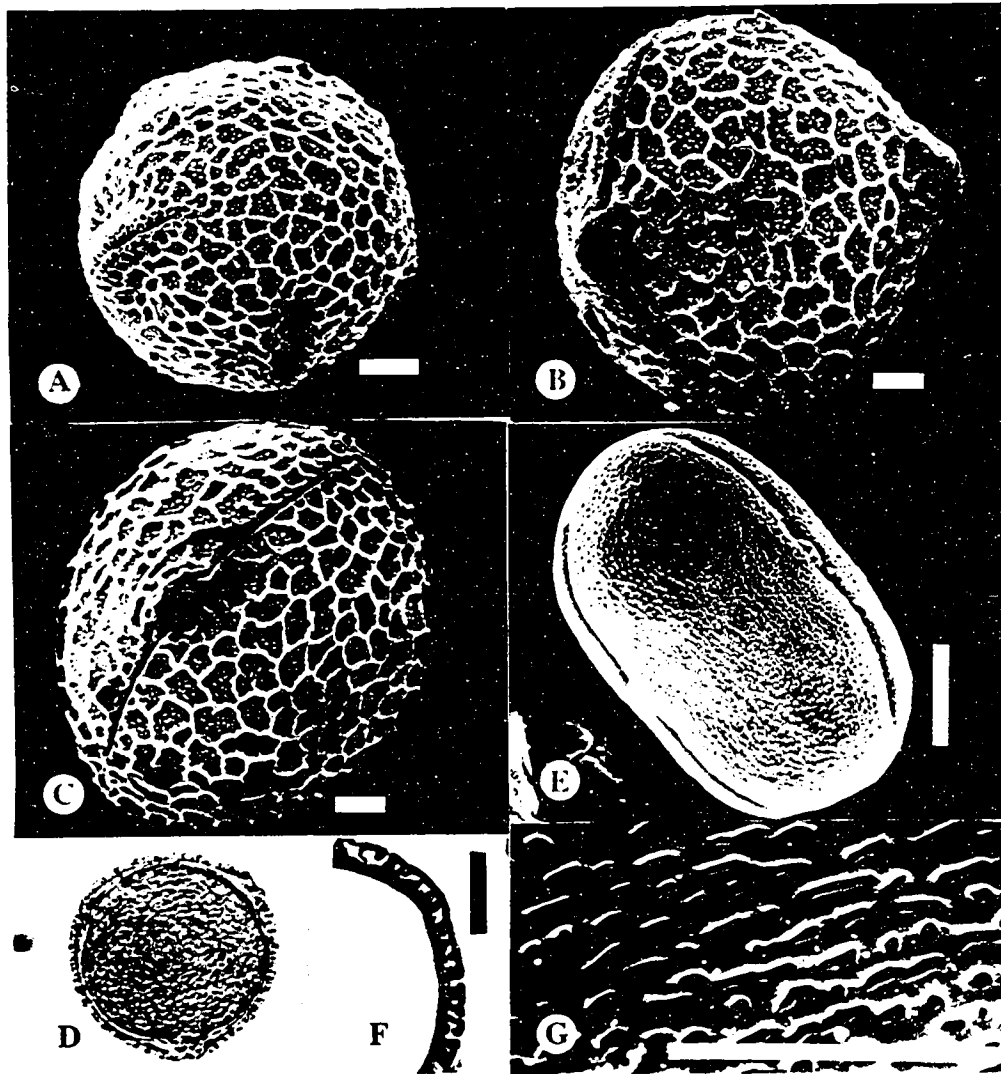


Fig. 32. Pollen of Cuspariinae. A. Ravenia leonis (Bro. Clemente 6240). Polar view showing reticulate sculpturing. B-D. Raveniopsis ruellioides (B, Huber et al. 8078; C, D, Maguire et al. 42447). B. Equatorial view showing reticulate sculpturing and long ectoaperture. C. Surface view showing lumina without infratectal rod-like structures. D. Radial section through mesocolpium showing semitectate exine. E. Raveniopsis stelligera (Maguire & Maguire 35262). Polar view showing 6 apertures. F, G. Raveniopsis peduncularis (F, Maguire 32815; G, Huber 10401). F. Equatorial view of prolate-spheroidal grain. G. Equatorial view showing reticulate sculpturing and lumina with occasional infratectal rod-like structures. (Scale bars: A, G = 10 μm ; B = 12 μm ; C = 20 μm ; D = 4 μm ; E, F = 30 μm .)

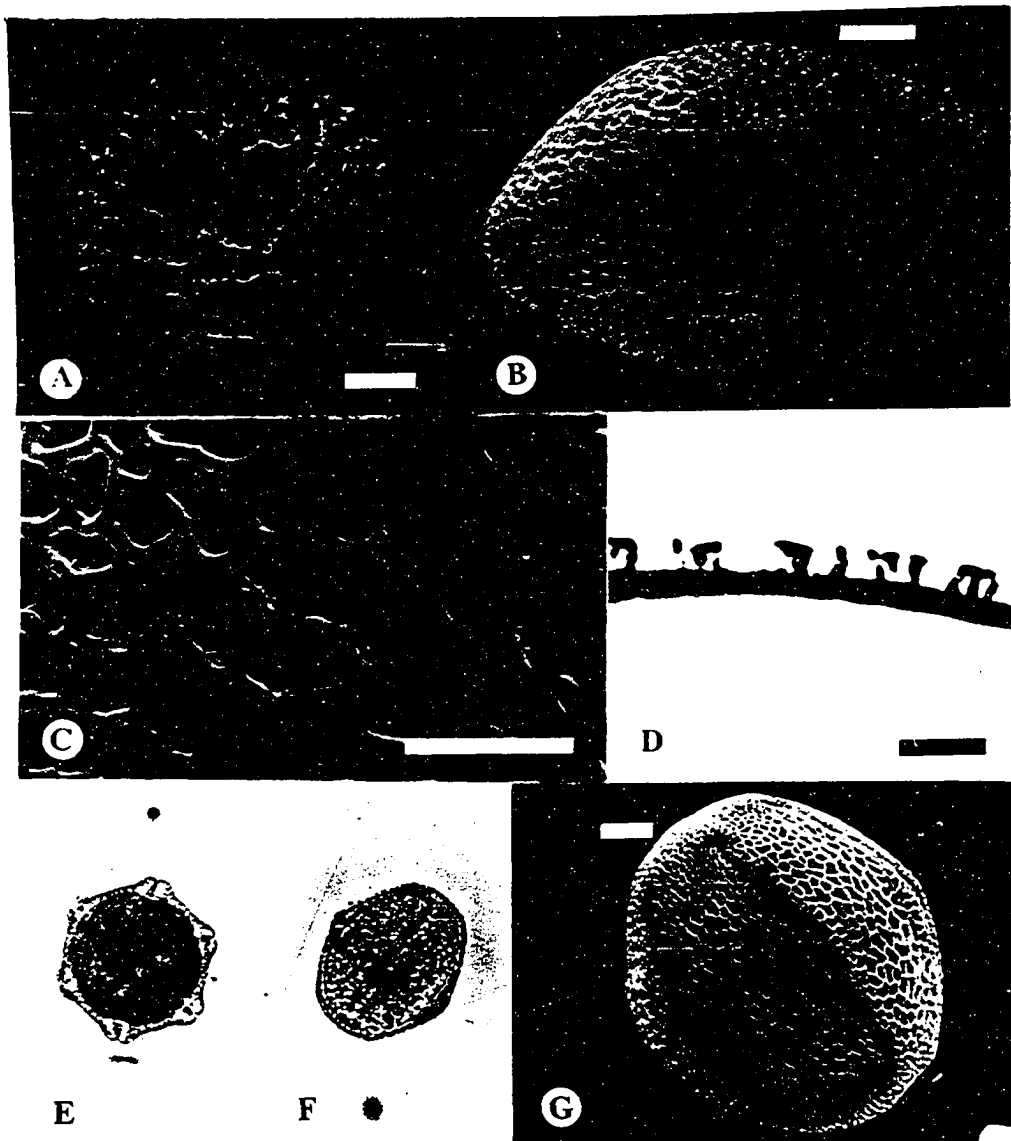


Fig. 33. Pollen of Cuspariinae. A. Sigmatanthus trifolius (Rosa et al. 4048). Equatorial view showing colporate apertures and reticulate sculpturing with dense infratectal rod-like structures. B-E. Spiranthera odoratissima (B, E, Harley et al. 18650; C, Irwin et al. 23085; D, Heringer 15954). B. Equatorial view showing porate aperture and echinate sculpturing. C. Radial section through mesocolpium showing spine (large arrow) and reduced rod-like structures (small arrow). D. Polar view showing 3 apertures. E. Radial section showing endexine (arrow) near the aperture. F-I. Ticorea cf. longiflora (Cid Ferreira et al. 6858). F. Surface view showing lumina with dense rod-like structures. Note short-colporate aperture (arrows at ends of aperture). G. Radial section through mesocolpium showing semitectate exine. H. Radial section showing endexine near aperture. I. Polar view showing reticulate sculpturing. (Scale bars: A = 8 μm ; B, F, H = 10 μm ; C = 2 μm ; D = 30 μm ; E, G = 4 μm ; I = 20 μm .)

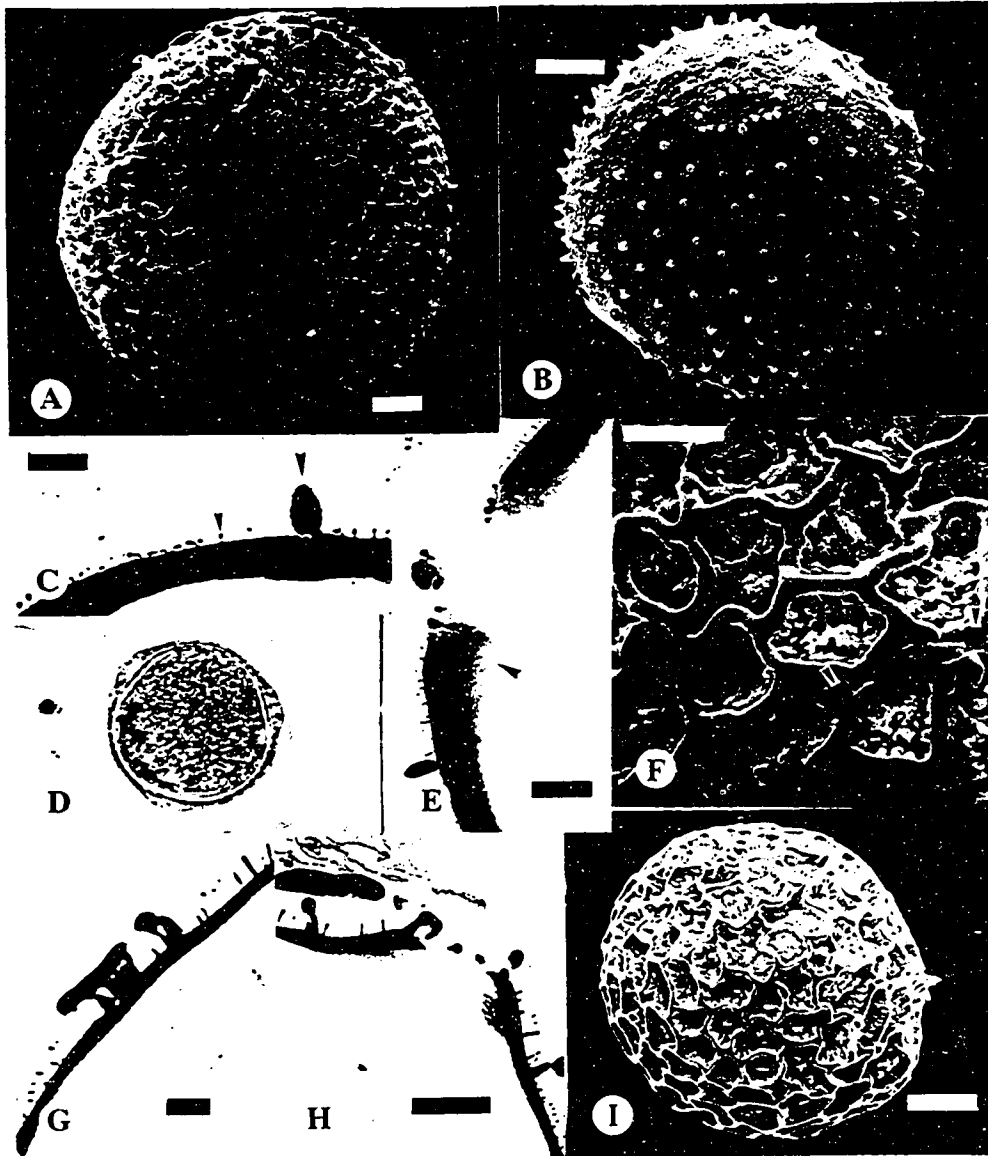
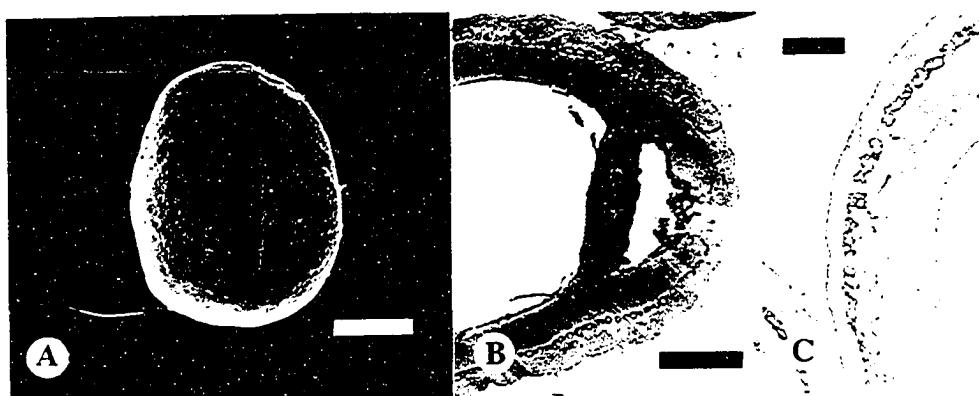
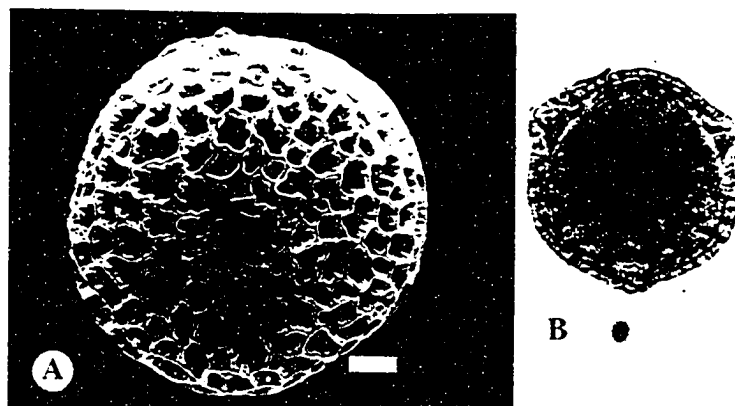


Fig. 34. Pollen of Cuspariinae. A. Toxosiphon trifolius (Klug 2729). Equatorial view showing reticulate sculpturing with occasional infratectal rod-like structures. B. Toxosiphon lindenii (Lent 2588). B. Polar view showing 3 apertures. (Scale bars: A = 10 μm ; B = 30 μm .)

Fig. 35. Pollen of Hortia. A-C. H. brasiliiana (Fonseca 843). A. Equatorial view showing psilate-perforate sculpturing with perforations infrequent and small. B. Radial section showing endexine under and along the margin of the aperture. C. Radial section through mesocolpium showing thick foot-layer, reduced columellae, and solid tectum. (Scale bars: A = 10 μm ; B = 4 μm ; C = 2 μm .)



Appendix 4: Voucher specimens for pollen samples of the
Cuspariinae (Rutaceae) used in this study.

Voucher specimens for pollen samples of the Cuspariinae (Rutaceae) used in this study. Specimens from which pollen samples were obtained for this study are from dried herbarium specimens deposited at NY unless indicated otherwise. The sample number (used in Table 30) is boldfaced. If a species is recognized in this study as belonging to a described genus to which it has not been transferred or to an undescribed genus, the name of that genus is indicated in parentheses, and in quotes if undescribed, after the species' name. Such indications are not nomenclatural transfers.

Adiscanthus fusciflorus Ducke

1) Daly et al. 5722, 2) Klug 723 (US), both Loreto, Peru; 3) Ducke 234, Amazonas, Brazil

Almeidea limae I. M. Silva

Martinelli 9904, Rio de Janeiro, Brazil

Almeidea ruba A. St.-Hil.

1) G. L. Farias 118, Espirito Santo, Brazil; 2) Octavio RB-96444, Rio de Janeiro, Brazil

Angostura larensis (Tamayo & Croizat) Albuq. (= "Angostura-1")

Dorr et al. 5641, Barinas, Venezuela

Angostura macrophylla (J. C. Mikan) Albuq. (= "Angostura-1")

1) Mori et al. 13072, 2) Thomas et al 6817, both Bahia, Brazil

Angostura pentagyna (A. St.-Hil.) Albuq. (= "Angostura-1")

1) Mori et al. 10692, 2) F. Sousa Santos 453, both Bahia, Brazil

Angosura ramiflora (Engl.) Albuquerque (= "Angostura-1")

1) Cid Ferreira 9327, Amazonas, Brazil; 2) Maguire et al. 36790,
Amazonas, Venezuela

Angosura silvestris (Nees & Mart.) Albuquerque (= "Angostura-1")

1) Maas & Tawjoeran LBB-10888, Surinam; 2) Schatz et al. 944,
Maranhao, Brazil

Angostura sp. nov.

Silva & Bahia 2883, Para, Brazil

Angostura cf. transitionalis Rizzini (= "Angostura-1")

Pinard 860, Acre, Brazil

Angostura trifoliata (Willd.) T. S. Elias

1) Colella et al. 1393, 2) Stergios et al. 5909 (MO), both Bolivar,
Venezuela

Angostura ucayalina (Huber) Albuquerque (= "Angostura-1")

1) Daly et al. 1835, Para, Brazil; 2) Schunke 5635, San Martin,
Peru

"Angostura-1" sp. 1

Mori et al. 9579, Bahia, Brazil

"Angostura-1" sp. 2

Schunke 4495, San Martin, Peru

"Angostura-1" sp. 3

Mattos Silva et al. 1822, Bahia, Brazil

"Angostura-1" sp. 4

Mattos Silva et al. 1488, Bahia, Brazil

Apocaulon carnosum R. S. Cowan

Maguire & Maguire 29188, Amazonas, Brazil

Decagonocarpus cornutus R. S. CowanHolst & Liesner 3352, Amazonas, VenezuelaDecagonocarpus oppositifolius Engl.Maguire et al. 1) 30457, 2) 37493, 3) 42618, all Amazonas, VenezuelaDesmotes incomparabilis (L. Riley) KallunkiCollenette in Riley 470 (MO), PanamaErtela trifolia (L.) KuntzeBeck et al. 321, Para, BrazilErythrochiton brasiliensis Nees & Mart.1) Harris 58 (herbarium ?), cult. in Jamaica; 2) Mori et al. 9361, 3) Pinheiro & dos Santos 2340 (CEPEC), both Bahia, Brazil; 4) Prance 9312, Roraima, Brazil; 5) Thomas 6782 (pickled), Loreto, Peru; 6) Oldeman 2047 (US), French GuianaErythrochiton fallax Kallunki1) Daly et al. 6445, Beni, Bolivia; 2) Idrobo & Schultes 830 (US), Colombia; 3) M. Saldias 78, Santa Cruz, BoliviaErythrochiton gymnanthus Kallunki1) Hammel et al. 13958 (MO), 2) Kallunki 294 (pickled), 3) Kallunki 309 (pickled), all Costa RicaEuxylophora paraensis Huber1) Ducke 27-9-23, 2) Rosa & Santos 2227, both Para, BrazilGalipea davisii SandwithDucke RB-35598 (US), Amazonas, Brazil

Galipea jasminiflora (A. St.-Hil.) Engl.

1) W. R. Anderson 6358, Goias, Brazil; 2) W. R. Anderson 12331 (US), Rondonia, Brazil; 3) W. Hoehne 15252, 4) E. Kuhn. 9 Mar 1967, both Sao Paulo, Brazil

Galipea longiflora K. Krause (= Angostura)

Daly 6382, La Paz, Bolivia

Galipea sp. nov. 1

Daly et al. 1) 1630, 2) 1891, both Para, Brazil

Hortia arborea Engl.

Mori et al. 12692, Bahia, Brazil

Hortia brasiliana Vand.

1) S. G. Fonseca 843, Distrito Federal, Brazil; 2) Hatschbach 43860 (US), Minas Gerais, Brazil

Hortia excelsa Ducke

Rabelo & Cardoso 2900, Amapa, Brazil

Leptothyrsa sprucei Hook. f.

1) Killip & Smith 29844, 2) McDaniel & Rimachi Y. 29660, both Loreto, Peru

Lubaria aroensis Pittier

1) A. L. Bernardi 5824, Miranda, Venezuela; 2) Ruiz & Rondon 3775, Falcon, Venezuela

Lubaria szczerbanii Steyerm. (=Raputia)

Boom 9491, Bolivar, Venezuela

Neoraputia alba (Nees & Mart.) Emmerich

Pirani et al 2489, Espirito Santo, Brazil

Neoraputia paraensis (Ducke) Emmerich

- Foster & Baldeon 12600, Madre de Dios, Peru
- Neoraputia trifoliata (Engl.) Emmerich
- D. A. Folli 764, Bahia, Brazil
- Nycticalanthus speciosus Ducke
- Ducke 99, Amazonas, Brazil
- Raputia heptaphylla Pittier (=Raputiarana)
- Steyermark 91443, Distrito Federal, Venezuela
- Raputia maroana (R. S. Cowan) Kallunki
- Guanchez & Melgueiro 3460 (MO), Amazonas, Venezuela
- Raputia sp. nov. 1
- Klug 544, Loreto, Peru
- Raputia sp. nov. 2
- Prance et al. 17015, Amazonas, Brazil
- Raputia ulei (K. Krause) Kallunki
- Maas & Maas 490, Amazonas, Brazil
- Raputiarana subsigmoidea (Ducke) Emmerich
- 1) Davidson 5209, 2) Rimachi Y. 2728, both Loreto, Peru
- Rauia resinosa Nees & Mart.
- 1) Duarte 6291 (US), Guanabara, Brazil; 2) Mori et al. 9379, 3) Mori et al. 11540, both Bahia, Brazil
- Rauia sp. nov. 1
- Thomas et al. 7674, Bahia, Brazil
- Rauia spicata Haye
- Steyermark 87821 (US), Bolivar, Venezuela
- Rauia subtruncata Steyerm.
- FDBG F1729, British Guiana
- Ravenia biramosa Ducke

Schunke 5711, San Martin, Peru

Ravenia leonis Vict.

Bro. Clemente 6240 (US), Cuba

Ravenia rosea Standl.

Kallunki 297 (pickled), Costa Rica

Ravenia urbanii Engl.

J. A. Duke 7515 (US), Puerto Rico

Raveniopsis breweri Steyerm.

1) Huber et al. 8092, Bolivar, Venezuela

Raveniopsis fraterna R. S. Cowan

1) Huber et al. 10215, 2) Pruski & Huber 3597, both Bolivar, Venezuela

Raveniopsis linearis (Gleason) R. S. Cowan

M. Farinas et al. 418, Amazonas, Venezuela

Raveniopsis peduncularia Pittier & Lasser

1) Huber 10401, 2) Maguire 32815 both Bolivar, Venezuela

Raveniopsis ruellioides (Oliv.) R. S. Cowan

1) Huber et al. 8078, 2) Wurdack 34166, both Bolivar, Venezuela; 3) Maguire et al. 42447, Amazonas, Venezuela

Raveniopsis sericea R. S. Cowan

Steyermark et al. 128764, Bolivar, Venezuela

Raveniopsis stelligera (R. S. Cowan) R. S. Cowan

Maguire & Maguire 35262, Amazonas, Venezuela

Raveniopsis steyermarkii R. S. Cowan

Luteyn & Steyermark 9575, Bolivar, Venezuela

Rutaneblina pusilla Steyerm. & Luteyn

1) Boom & Weitzman 5770, 2) Liesner 16030, both Amazonas,
Venezuela

Sigmatanthus trifolius Emmerich

1) Froes 11796, Maranhao, Brazil; 2) N. A. Rosa et al. 4048,
Para, Brazil

Spiranthera odoratissima A. St.-Hil.

1) Harley et al. 18650, Bahia, Brazil; 2) Heringer 15954,
Distrito Federal, Brazil; 3) Irwin et al. 23085 (US), Minas
Gerais, Brazil

Spiranthera parviflora Sandwith

N. A. Rosa 2417A, Para, Brazil

Ticorea foetida Aubl.

Granville 2795, French Guiana

Ticorea longiflora DC.

Cid. Ferreira et al. 6858, Amazonas, Brazil

Ticorea cf. longiflora DC.

Prance et al. 24022, Amazonas, Brazil

Toxosiphon carinatus (Little) Kallunki

Dodson & Gentry 9859, Ecuador (MO or SEL)

Toxosiphon lindenii Baill.

Lent 2588, Costa Rica

Toxosiphon trifolius (K. Krause) Kallunki

1) Camp 999, Ecuador; 2) Klug 2729, San Martin, Peru

Chapter 3: Strategies for Analysis of Quantitative Pollen Data with Reference to Phylogeny.

(In cooperation with D. Kincaid)

Introduction

Most genetically based features should be available for use in cladistic analysis. However, the analysis of continuous variables in plants (e.g., length of pollen polar axis) may not reveal discrete character states. These situations usually limit the type and the amount of information one can use in a cladistic analysis. In practice, researchers either exclude continuously varying characters from phylogenetic analyses or develop new methods for coding the data into discrete states (Almeida and Bisby, 1984; Chappill, 1989; Stevens, 1991).

Pollen morphologists routinely measure polar (P) and equatorial (E) axes and place pollen into the size classes defined by Erdtman (1971), Nilsson and Praglowski (1992), and Walker and Doyle (1975). Obviously, this grouping of pollen into globally arbitrary classes may not correspond to statistically significant differences among the taxa within a data set. Furthermore, the traditional definition of size class is based on the length of the longest axis, whether that axis is polar or equatorial, thus comparing nonequivalent biological variables (Figure 12).

Because of these problems we propose an alternative model based on bivariate analysis of these continuous measurement variables (P, E) using conventional statistical procedures coupled with data visualization and with Monte Carlo simulation. While

our model is not a final solution to the general problem of coding continuous characters into discrete states, it does address the specific problem of bivariate character state delimitation in pollen morphology using sound and rigorous statistical and Monte Carlo procedures. Our model is more heuristic than prescriptive. Although this type of data analysis is routine in many biological disciplines, it does not appear to have been utilized nor adequately mentioned in references to taxonomic pollen analysis. We suggest that the coding of continuous measurement variables into character states suitable for cladistic analysis should be done following a logical sequence of interactive data visualization and analysis of variance (anova).

We illustrate our approach using realistic pollen data sets simulated by a Monte Carlo method. Our model is then applied to the pollen variability found in an original data set of 4,134 measured grains from the Ebenaceae.

Methods

Simulated Pollen Data Sets--A computer program (POLSIM) was written to perform Monte Carlo sampling (Noreen, 1989) from normal distributions of polar (P) and equatorial (E) axes with these user specified inputs:

- number of pollen data sets to generate (replications)
- number of plant taxa and sample size of pollen for each taxon
- target parametric mean and standard deviation (SD) for P and for E for each taxon

Random sampling from normal distributions is warranted because it is reasonable to assume that P and E are normally distributed in plant taxa. Indeed, Kolmogorov-Smirnov goodness-of-fit tests (Sokal and Rohlf, 1981) were performed for each sample of Ebenaceae pollen and the null hypothesis of normality was accepted in most cases. The actions of multiple, independent factors, additive in influence, and with equal contributions to variability, are what "cause" a continuous measurement variable to be normally distributed (Sokal and Rohlf, 1981). This is why many variables in biology, especially those of the dimensions of whole structures such as pollen grains, are normally distributed.

In pollen research, investigators strive to obtain pollen that are random samples from the totality of pollen of the taxon. Sufficient floral material and adequate sample sizes of pollen are required to access the variability of characters within and among individual taxa across geographical ranges. Our program, POLSIM, mimics the investigator's sampling procedure and conveniently

automates the process. POLSIM not only generates simulations but also analyzes real pollen datasets. A researcher could enter into the program, sample means and sample standard deviations from a preliminary pollen study. The program would then allow the researcher to probe the influence of different sample sizes (including balanced versus unbalanced designs), of underlying distribution (normal, lognormal), and of various levels of pollen variability (SD) on the ability to recognize delimited character states that are suitable for phylogenetic analysis. This application of POLSIM is intended, however, as a probing device and is not meant to replace the original data gathering process.

Conceptually, the Monte Carlo method using POLSIM, withdraws random samples of pollen from normally distributed statistical populations (taxa) with user defined means and standard deviations (SD, measure of innate variability); P and E are "measured"; and the data are subjected to the series of steps outlined below.

We used POLSIM to generate realistically configured pollen data sets for three "taxa" of an hypothetical plant group in order to present our model as implemented on the Macintosh computer platform. We present one representative simulation from hundreds generated and studied. The model follows.

1. Pollen Measurement--Measure P and E for reasonably-sized samples of pollen from each taxon. Where appropriate, the polar axis (P) should be the pole-to-pole axis and the equatorial axis (E) should be the widest point perpendicular to

P (Figure 12); exceptions would include polyporate grains. A table of descriptive statistics, including means, standard deviations, and sample sizes, should be completed to provide not only preliminary insights but also the information needed for Monte Carlo simulations, should the investigator choose to probe the influence of unequal sample sizes in the raw data set by generating simulations based upon equal sample sizes.

2. Scatterplots--Observe scatterplots of P (y-axis) versus E (x-axis) for entire data set as well as for each taxon in isolation (Fig. 13). Examine the data for outliers, discontinuous ranges, and apparent clusterings of points.

3. Ellipses of points--For each subordinate taxon compute the 95% or 99% prediction ellipse of the points and graph in an x,y coordinate system (Sokal and Rohlf, 1981). Do these ellipses overlap? If so, note the amount of overlap of these ellipses. Based upon your sample of pollen, these ellipses express uncertainty in the circumscription of all individual pollen grains existing in the natural habitat for each taxon (Fig. 14). These ellipses do not provide reliable insights into statistically significant central tendencies and by themselves should not be used to code pollen into discrete states. Of course, nonoverlap of prediction ellipses is strong evidence for statistically significant differences among taxa. This step is provided for those investigators concerned about single pollen grains, and their positions in bivariate space

and desirous of quantification of predicted overlap amongst individual pollen measurements across different taxa.

4. Analysis of Variance--For P, and then separately for E and for P/E (a shape variable) perform an overall, single classification anova to determine if evidence exists for statistical heterogeneity among the means of the subordinate taxa. {Those familiar with, and able to interpret manova may use it here.} If overall anova is not significant, the investigator may not be able to produce a code for discrete character states. If anova is significant (e.g., probability of F less than, say, 0.05 or 0.01), then some means or groups of means for each variable are statistically significantly different. An evaluation of R-square should also be made as it is the proportion of the total variability in P, in E, and in P/E that is due to the grouping of pollen into taxa (Table 33).

5. 3D Topographic Plot--Study, in 3D perspective, topographic plots of P versus E for the entire data set. This provides a visualization of total variability devoid of taxonomic identification (Fig. 15). Various viewing angles maybe necessary to detect topographic features. The presence and location of these features, the gaps (regions of relative discontinuity) and peaks (major central tendencies), in combination with the anova results, may allow the formulation of coding schemes.

6. Confidence Ellipses--For each subordinate taxon, compute the 95% or 99% confidence ellipse of the bivariate mean (Fig. 16). Do these confidence regions overlap? This step is essential as it provides a visualization of central tendencies (the bivariate means) as they are statistically inferred to exist for each taxon. Separation of these confidence regions implies the existence of significant differences among bivariate central tendencies among the taxa (Sokal and Rohlf, 1981). Visual impressions of the separation/overlap of these confidence ellipses will generally correspond to results of anova.

7. Final coding--Personal observations, the knowledge of the pollen researcher, along with the information provided by 3D topography, confidence ellipses, and anova, remain essential for a wise coding scheme for pollen size classes. However, if further exploration is desired to probe additional questions resulting from steps 1-6, then Monto Carlo simulations may be used to investigate situations such as balanced versus unbalanced designs. These situations are easily studied in simulated data sets by iteratively using the steps above until the researcher produces a stable coding scheme.

Results

Pollen variability in the Ebenaceae--Pollen grains were obtained from dried herbarium material and prepared using a modification of the method of acetolysis described by Erdtman (1960). For light microscopy, grains were mounted in glycerine jelly on glass slides, sealed with paraffin, and studied with a Nikon Optiphot microscope. Measurements of polar and equatorial axes were made in a median plane using a computerized morphometric unit, programmed with Neurolucida software, under oil immersion (ca. X 1000). Measurements were installed in a commercial statistical analysis program (Statview) with P and E in separate columns and with genera and species coded as grouping variables in additional columns. A table of descriptive statistics, including means, standard deviations, and sample sizes, was completed. Scatterplots of P (y-axis) versus E (x-axis) were constructed for the Ebenaceae as well as for each of the four genera in isolation. An examination was made of the genera for outliers, discontinuous ranges, and apparent clusterings of points (Fig. 17). For each genus the 99% prediction ellipse of the points was graphed in order to statistically visualize patterns of overlap of pollen grains among genera (Fig. 18). Single classification anova was examined for polar diameter, equatorial diameter, and P/E ratio (Table 34). Significant differences in mean polar diameter ($p < .0001$) and mean equatorial diameter ($p < .0001$) were found to exist among Diospyros, Euclea, Royena, and Tetracelis. The Ebenaceae dataset, like most anatomical datasets, contained uneven sample sizes. A 3D topographic plot of P versus E was

completed for the entire pollen dataset (Fig. 19). Viewing from various angles, three peaks and two gaps were observed. In Figure 19, the first peak represents pollen from the genus Euclea, the second peak represents pollen from the genera Royena, Tetracilis, and Diospyros, and the small third peak contains the largest pollen grains. Examination of the descriptive statistics revealed that the third peak most likely represented pollen from Diospyros virginiana.

Monte Carlo simulations were pursued to investigate the effects of uneven sample sizes, 200 grains of Diospyros virginiana and 2384 grains of the genus Diospyros, on central tendencies in the 3D topography. The Ebenaceae data set was separated into five groups: Euclea, Royena, Tetracilis, Diospyros less D. virginiana, and D. virginiana. POLSIM was seeded with the means and SD from the five groups and pollen sample sizes were made equal. This investigation found the third peak to have a stable central tendency for the species Diospyros virginiana. Single classification anova was completed for polar diameter, equatorial diameter, and P/E ratio (Table 35). Significant differences in mean polar diameter ($p < .0001$) and mean equatorial diameter ($p < .0001$) were found to exist among Diospyros, Euclea, Royena, Tetracilis, and Diospyros virginiana. Although significant differences were found in the P/E ratio among genera ($p < .0001$), only 3-4 percent ($R\text{-square} = 0.035$) of the total variation (total sum of squares) in P/E ratio is accounted for by these five groups. In comparison, 59% of total variation in polar diameter and 62% of that in equatorial diameter, is accounted for by these five groups.

The P/E ratio is, therefore, less effective in accounting for the variation among genera of the Ebenaceae than are the measurements of polar diameter and equatorial diameter. In combination with the results from the 3D topographic plot, Euclea and D. virginiana remain isolated from Diospyros, Royena, and Tetracelis. To display the central tendencies for polar diameter and equatorial diameter at the generic level, 99% confidence ellipses of the bivariate means were computed by POLSIM, and graphed in a composite coordinate system; the visual impression of these confidence ellipses agreed with the results of anova (Fig. 20). Tetracelis, Royena, and Diospyros (all except D. virginiana), have central tendencies near each other with a mean polar diameter of 37 to 40 μm and a mean equatorial diameter of 31 to 35 μm . Euclea and D. virginiana on the other hand are far removed and isolated from the other genera, with a mean polar diameter of 26.55 μm and mean equatorial diameter of 23.20 μm in Euclea and a mean polar diameter of 53.54 μm and mean equatorial diameter of 48.50 μm in D. virginiana.

From the first author's personal observations and knowledge of the Ebenaceae, along with the information from the 3D topographic plot, anova, and simulations, the genera will be coded into three character states for size class and will not be coded into shape classes because of the low variability of this character (low R-sq. in anova for P/E). Tetracelis, Royena, and all of Diospyros (except D. virginiana) will be coded as one state, while Euclea will be coded as the second state and D. virginiana will be coded as the third state. This paper is part of a series dealing

with anatomical and morphological characters of the Ebenales. When additional features of this order have been rigorously examined and analyzed, these characters will be placed into a cladistic analysis to test generic limits and phylogenetic trends.

Discussion

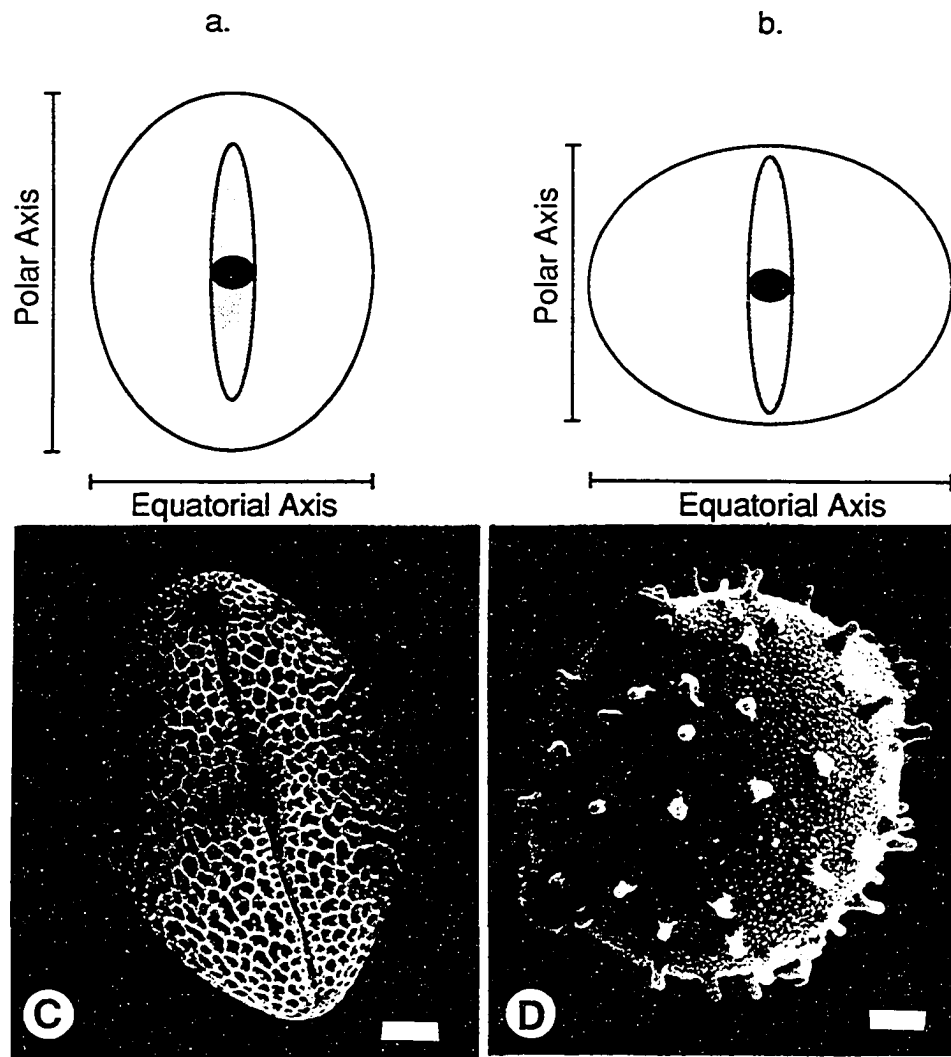
Character states formulated by our model are more useful than traditional size class delimitations based upon the size classes of (i.e., Erdtman, 1971, 1992) and Walker and Doyle (1975) because (1) this model uses statistical methods (e.g., anova) that are based on probability theory and that are accepted and commonly used across all scientific disciplines; (2) polar and equatorial axes are treated in bivariate fashion rather than the use of a single variable (length of longest grain axis); thus, we do not confuse non-equivalent biological variables; (3) rather than categorization into globally pre-defined and arbitrary pollen size classes, we recognize central tendencies in pollen size and code accordingly.

In addition, this model may be applied at various hierarchical taxonomic levels, and it is not restricted to binary coding but allows the recognition of as many character states as are represented in the data set by central tendencies that show themselves to be statistically reliable. As we have shown for the Ebenaceae, Monte Carlo simulation working in conjunction with more traditional statistical methods such as anova and confidence ellipses, provides a mechanism for exploring sample size effects upon the coding decisions made by the investigator. Simulation,

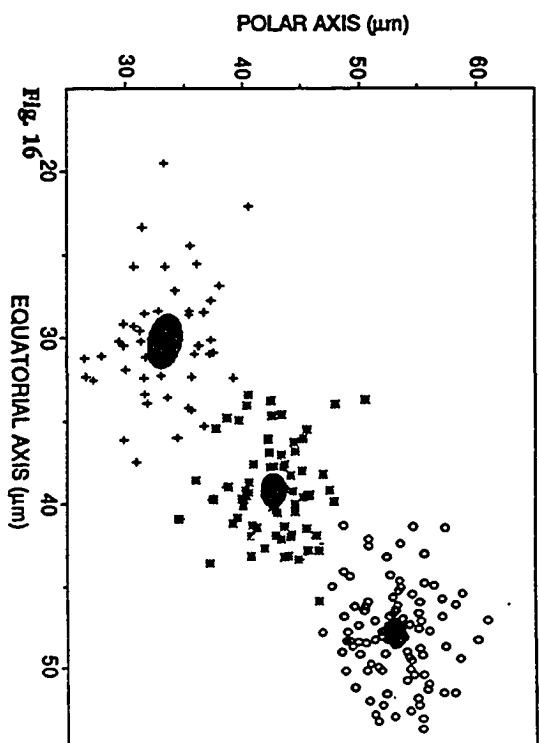
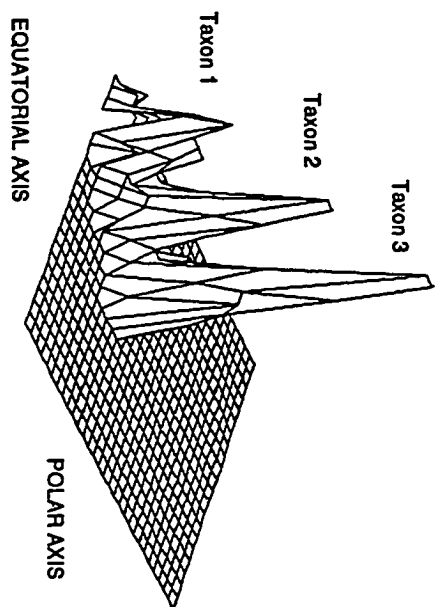
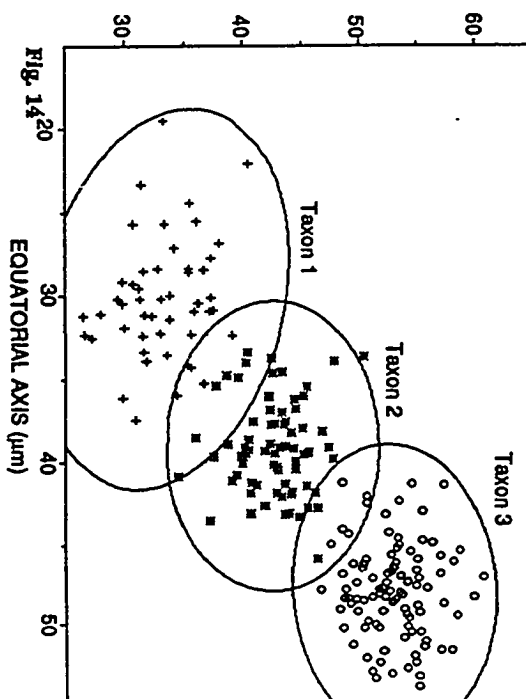
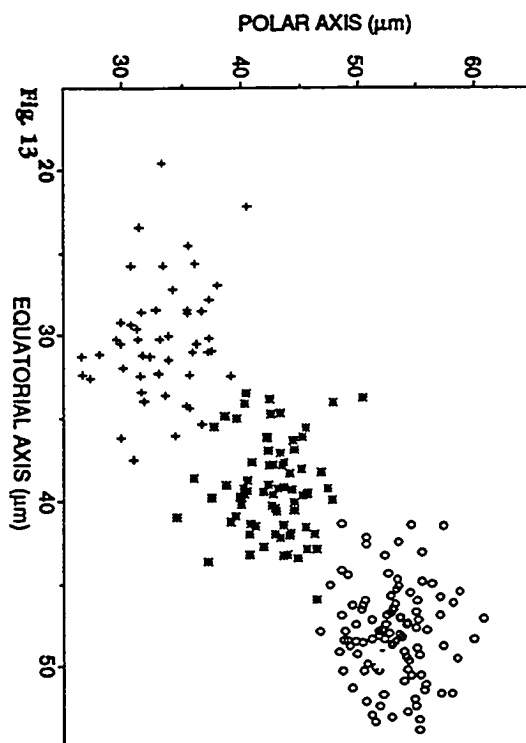
allowed us to determine that one peak represented pollen of Diospyros virginiana, rather than a collection of pollen "outliers" from other taxa. It was also by simulation that we were able to confirm that the statistically significant differences between the three peaks in the large unbalanced raw data set were stable even at low sample sizes (e.g., $N = 25$ pollen per group).

Current discussions in the literature (Almeida and Bisby, 1984; Archie, 1985; Chappill, 1989; Stevens, 1991) on proposed methods, and their relative merits, for coding continuously varying characters into discrete states focus more on the development of new methods than on the use of rigorous and well-accepted statistical tools and graphical visualization techniques that have long been available for determining statistically significant differences amongst the central tendencies displayed by a group of taxa. Although modest computer programming is required to produce a simulation/analysis program such as POLSIM, methods such as ours are easy to implement on small computers (e.g., with Statview and JMP(SAS) on Macintosh). While our model is not a final solution to the general problem of coding continuous characters into discrete states, it does address the specific problem of bivariate character state delimitation in pollen morphology using sound and rigorous statistical and Monte Carlo procedures.

Figure 12 a-d. Illustration of two pollen grains that, because of the length of their longest axes, would be placed in the same size class according to the definitions of Erdtman (1992) and Walker and Doyle (1975). Doing so, however, would equate nonequivalent biological variables because in a and c, the polar axis is the longest and in b and d, the equatorial axis is the longest. (Scale bars: C, D = 10 μm (1000X)).



Figures 13-16. Simulated pollen. 13. Scatterplot of P (y-axis) and E (x-axis) for the three taxa as simulated by POLSIM using sample sizes of N =50, 75, and 100, respectively, for the taxa labeled as 1, 2, and 3. A target SD of 3.0 was used for both variables for each taxon and means are in Table 1. 14. Scatterplot showing relationship between P and E with 99% prediction ellipses of the points for each taxon. 15. Topographic plot (3D) for P versus E for entire dataset. The two gaps and three peaks (central tendencies) allow for a provisional three character state delimitation. 16. The 99% confidence ellipses for the bivariate means are shaded black.



Figures 17-20. Ebenaceae pollen. 17. Scatterplot of P (y-axis) and E (x-axis) for the entire Ebenaceae (N = 4134) dataset. 18. The 99% prediction ellipses of the points for each of the four genera. 19. Topographic plot (3D) for P versus E for the entire dataset. There are two gaps and three peaks (central tendencies). 20. The 99% confidence ellipses for the bivariate means are displayed for five groups as labeled.

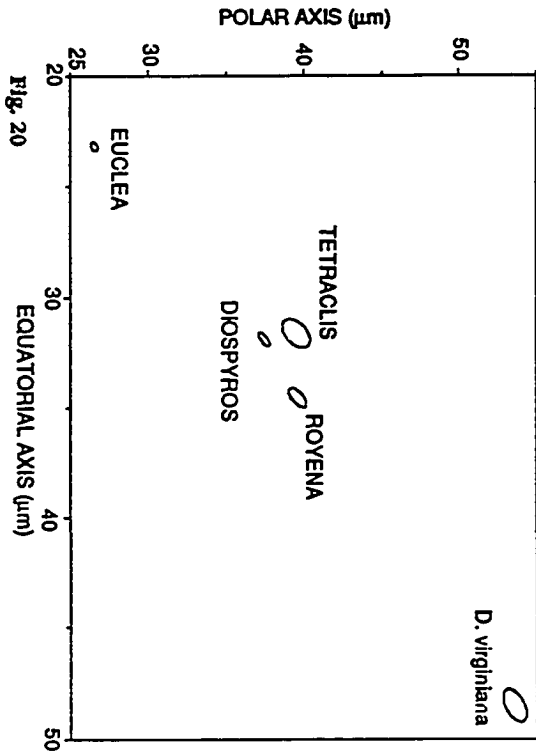
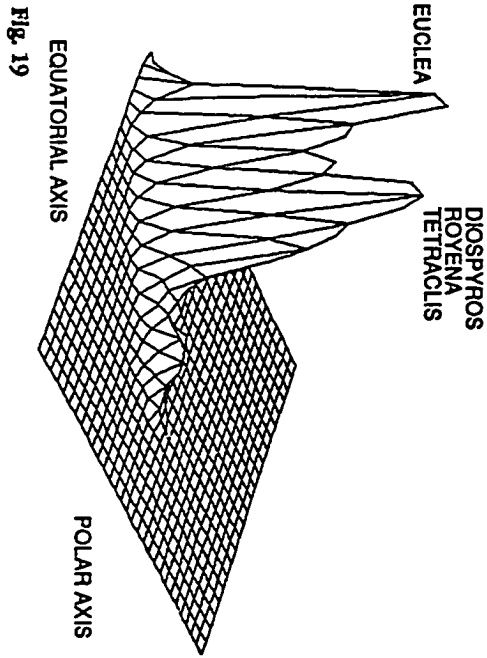
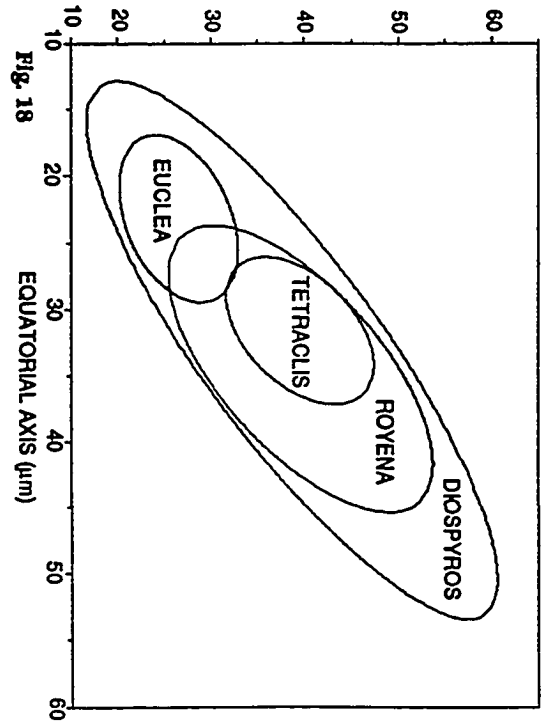
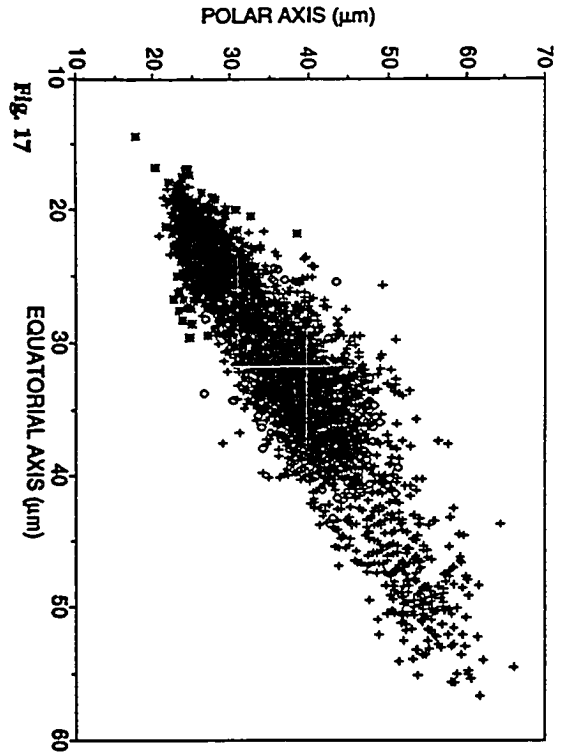


Table 33. Simulated pollen dataset. One-way analysis of variance performed for polar diameter, equatorial diameter, and polar/equatorial ratio for the three simulated taxa (2, 222 df). Means for P and E are significantly different among taxa ($P < 0.0001$) but mean P/E ratio is homogeneous. R-square is the proportion of the total sum of squares that is accounted for by heterogeneity among genera.

	Means for Simulated Taxa			One-Way Analysis of Variance			
	Taxon 1	Taxon 2	Taxon 3	F	df	P	R-square
Polar Diameter (μm)	33.40	42.72	53.14	778	2, 222	< 0.0001	0.875
Equatorial Diameter (μm)	30.25	39.18	47.97	603	2, 222	< 0.0001	0.845
Polar/Equatorial ratio	1.124	1.096	1.111	0.73	2, 222	0.4846	0.0065
Total N	50	75	100				

Table 34. Ebenaceae pollen dataset. One-way analysis of variance performed for polar diameter, equatorial diameter, and polar/equatorial ratio for the genera of Ebenaceae (3, 4133 df). Means for P, E, and P/E are significantly different among the genera of Ebenaceae ($P < 0.0001$). R-square is the proportion of the total sum of squares that is accounted for by heterogeneity among genera.

	Means for Genera of Ebenaceae				One-Way Analysis of Variance			
	Diospyros	Euclaea	Royena	Tetracilis	F	df	P	R-square
Polar Diameter (μm)	38.66	26.55	39.58	39.49	939	3, 4133	< 0.0001	0.405
Equatorial Diameter (μm)	33.18	23.20	34.55	31.63	783	3, 4133	< 0.0001	0.362
Polar/Equatorial ratio	1.174	1.150	1.149	1.250	25.8	3, 4133	< 0.0001	0.018
Total N	2584	862	616	75				

Table 35 Ebenaceae pollen dataset divided into five groups. One-way analysis of variance performed for polar diameter, equatorial diameter, and polar/equatorial ratio for five groups of Ebenaceae (4, 4132 df). Means for P, E, and P/E are significantly different among the five groups ($P < 0.0001$). R-square is the proportion of the total sum of squares that is accounted for by heterogeneity among the groups.

Means for 5 Groups of Ebenaceae						One-Way Analysis of Variance			
	Diospyros	Euclea	Royena	Tetraclis	D. virginiana	F	df	P	R-square
Polar Diameter (μm)	37.41	26.55	39.58	39.49	53.54	1504	4, 4132	< 0.0001	0.593
Equatorial Diameter (μm)	31.89	23.20	34.55	31.63	48.50	1672	4, 4132	< 0.0001	0.618
Polar/Equatorial ratio	1.180	1.150	1.149	1.250	1.106	37.7	4, 4132	< 0.0001	0.035
Total N	2384	862	616	75	200				

Literature Cited

- Adams, R. J. and J. K. Morton. 1976. An atlas of pollen of the trees and shrubs of Eastern Canada and the adjacent United States. Part III. Leguminosae to Cornaceae. Univ. Waterloo Bio. Ser. 11:1-27.
- Almeida, M. T. and F. A. Bisby. 1984. A simple method for establishing taxonomic characters from measurement data. *Taxon* 33:405-409.
- Archie, J. W. 1985. Methods for coding variable morphological features for numerical taxonomic analysis. *Syst. Zool.* 34:326-345.
- Ayala-Nieto, M. L. and B. Ludlow-Wiechers. 1983. Catálogo palinológico para la flora de Veracruz. No. 13. Familia Ebenaceae. *Biotica* 8(2):215-226.
- Ayensu, E. S. 1972. Morphology and anatomy of Synsepalum dulcificum (Sapotaceae). *Bot. J. Linn. Soc.* 65:179-187.
- Baas, P., P. M. Esser, M. E. T. van der Western and J. Zandee. 1988. Wood anatomy of the Oleaceae. *Int. Assoc. Wood Anat. News Bull.* 9(2):103-182.
- Bailey, I. W. 1951. The use and the abuse of anatomical data in the study of phylogeny and classification. *Phytomorphology* 1:67-69.
- Bailey, I. W. and R. A. Howard. 1941a. The comparative morphology of the Icacinaceae. II. Vessels. *J. Arnold Arbor.* 22:171-187.
- Bailey, I. W. and R. A. Howard. 1941b. The comparative morphology of the Icacinaceae. III. Imperforate tracheary elements and xylem parenchyma. *J. Arnold Arbor.* 22:432-442..
- Bailey, I. W. and R. A. Howard. 1941c. The comparative morphology of the Icacinaceae. IV. Rays of the secondary xylem. *J. Arnold Arbor.* 22:556-568.
- Bakhuizen van den Brink, R. C. (1936-55) *Revisio Ebenacearum Malayensium*. *Bull. Jard. Bot. Buitenz.*, ser. 3, 15:1-49 (1936); 50-368 (1938); 369-515 (1941); i-xx, pl. 1-92 (1955).

- Barth, O. M. 1979. Pollen morphology of Brazilian Symplocos species (Symplocaceae). Grana 18:99-107.
- Barth, O. M. 1982a. The sporoderm of Brazilian Symplocos pollen types (Symplocaceae). Grana 21:65-69.
- Barth, O. M. 1982b. Variações polínicas em espécies brasileiras da família Rutaceae. Bol. Inst. Geoci. Univ. São Paulo 13: 129-134.
- Barth, O. M. 1983. Pollen morphology of Brazilian Rutaceae: Dictyoloma and Hortia. Pollen et Spores 25: 409-419.
- Barth, O. M. 1985. Pollen morphology of Brazilian Rutaceae: Pilocarpus. Pollen et Spores 27: 145-154.
- Benoist, R. 1931. Les bois de la Guyane française. Arch. Bot. Caen, Mém. 5(1):1-292.
- Bentham, G. and J. D. Hooker. 1876. Genera Plantarum. Vol. II. L. Reeve and Company, London.
- Berlyn, G.P. and J.P. Miksche. 1976. Botanical Microtechnique and Cytochemistry. Iowa state Univ. Press. Ames.
- Bessey, C. E. 1915. The phylogenetic taxonomy of flowering plants. Ann. Missouri Bot. Gard. 2:109-164.
- Bonnefille, R. 1971. Atlas des pollens d'Ethiopie. Principales especes des forets de montagne. Pollen et Spores 13(1):61-65.
- Bonnefille, R. and G. Riollet. 1980. Pollens des savanes d'Afrique orientale. C.N.R.S. Paris.
- Brown, F. B. H. 1922. The secondary xylem of Hawaiian trees. Occas. Pap. Bernice Pauahi Bishop Mus. 8(6):217-371.
- Brown, F. B. H. and A. J. Panshin. 1940. Commercial Timbers of the United States. McGraw-Hill: New York.
- Burgerstein, A. 1909. Anatomische Untersuchungen samoanischer Holzer. Denkschr. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 84:495-514.

Carlquist, S. 1988. Wood anatomy and relationships of Duceodendraceae and Goetzeaceae. Int. Assoc. Wood Anat. News Bull. 9(1):3-12.

Carpenter, C. S. and W. C. Dickison. 1976. The morphology and relationships of Oncotheca balansae. Bot. Gaz. 137:141-153.

Cerceau-Larrival, M.-TH., H. Straka and B. Friedrich. 1984. Fam. 155-166. Microscopie électronique à balayage et addenda. In: H. Straka, (ed.), Palynologia Madagassica et Mascarenica. Addenda und REM. :73-116.

Chappill, J. A. 1989. Quantitative characters in phylogenetic analysis. Cladistics 5:217-234.

Cronquist, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

Dahlgren, R. 1980. A revised system of classification of the angiosperms. J. Linn. Soc., Bot. 80:91-124.

Dechamps, R. 1979. Étude anatomique du bois d'Amérique du Sud. I. Acanthaceae à Lecythdaceae. Ann. Mus. roy. Afr. cent., Tervuren, Belgium, ser. IN-8, Sci. econ., No. 10.

Dickison, W. C. 1967. Comparative morphological studies in Dilleniaceae, I. Wood Anatomy. J. Arnold Arbor. 48:1-29.

Dickison, W. C. 1972. Anatomical studies in the Connaraceae. II. Wood anatomy. Elisha Mitchell Sci. Soc. 88:120-136.

Dickison, W. C. 1975. The bases of angiosperm phylogeny: vegetative anatomy. Ann. Missouri Bot. Gard. 62:590-620.

Dickison, W. C. 1977. Wood anatomy of Weinmannia (Cunoniaceae). Bull. Torrey Bot. Club 104:12-23.

Dickison, W. C. 1978. Comparative anatomy of the Eucryphiaceae. Amer J. Bot. 65:722-735.

Dickison, W. C. 1979. A note on the wood anatomy of Dillenia (Dilleniaceae). Int. Assoc. Wood Anat. News Bull. 2-3:57-60.

- Dickison, W. C. 1981. The evolutionary relationships of the Leguminosae. In: R. M. Polhill and P. H. Raven (eds.), *Advances in Legume Systematics: Proceedings of the International Legume Conference, Kew 24-29 July 1978*. R. Bot. Gard, Kew, pp35-54.
- Dickison, W. C. and P. Baas. 1977. The morphology and relationships of Paracryphia (Paracryphiaceae). *Blumea* 23:417-438.
- Dickison, W. C., P. M. Rury and G. L. Stebbins. 1978. Xylem anatomy of Hibbertia (Dilleniaceae) in relation to ecology and evolution. *J. Arnold Arbor.* 59:32-49.
- Dickison, W. C. and K. D. Phend. 1985. Wood anatomy of the Styracaceae: evolutionary and ecological considerations. *Int. Assoc. Wood Anat. News Bull.* 6:3-22.
- Emmerich, M. 1978. Contribuição ao conhecimento da tribo Cusparineae [sic] (Rutaceae). Nova conceituação de Raputia e gêneros derivados. *Rodriguesia* 30 (45):223-307.
- Engler, A. 1931. Rutaceae. In: A. Engler and K. Prantl, (ed. 2), *Nat. Pflanzenfam.*, 19a.
- Erdtman, G. 1960. The acetolysis method. A revised description. *Sven. Bot. Tidskr.* 54:561-564.
- Erdtman, G. 1969. *Handbook of Palynology*. Munksgaard Co., Copenhagen.
- Erdtman, G. 1971. *Pollen morphology and plant taxonomy: angiosperms*. Hafner Publishing Co., New York.
- Eyde, R. H. 1971. Evolutionary morphology: Distinguishing ancestral structure from derived structure in flowering plants. *Taxon* 20:63-73.
- Feldman, D.S., Jr. and J. Gagnon. 1986. *Stat View*. Abacus. Inc.
- Ferguson, I. K. 1986. Observations on the variation in pollen morphology of Palmae and its significance. *Canad. J. Bot.* 64:3079-3090.

Fernandes da Silva, M. F. das G., O. R. Gottlieb and F. Ehrendorfer. 1988. Chemosystematics of the Rutaceae: suggestions for a more natural taxonomy and evolutionary interpretation of the family. *Plant Syst. Evol.* 161:97-134.

Gereau, R. 1990. Achuaria, nuevo género de Rutaceae, con una sinopsis de las Cuspariinae peruanas. *Contribución al estudio de la flora y de la vegetación de la Amazonía peruana.* XVIII. *Candollea* 45:363-372.

Goldberg, A. 1986. Classification, evolution and phylogeny of the families of dicotyledons. *Smithsonian Contr. Bot.* 58:122-124.

Gottwald, H. and N. Parameswaran. 1966. Das sekundäre Xylem der Familie Dipterocarpaceae. *Bot. Jahrb. Syst.* 85(3):410-508.

Graaff, N. A. van der and P. Baas. 1974. Wood structure in relation to latitudinal and altitudinal distribution. *Blumea* 22:101-121.

Greguss, P. 1959. *Holzanatomie der europäischen Laubhölzer und Sträucher.* Akadémiai Kiadó: Budapest.

Greuter, W. 1988. *International Code of Botanical Nomenclature.* Koeltz Scientific Books, Germany.

Guinet, Ph. 1962. Pollens d'Asie Tropicale. *Trav. Inst. Fr. Pondichery, Sect. Sci. tech., Ser. A*, 5:1-8, 52.

Gupta, H. P. and C. Sharma. 1986. Pollen flora of North-West Himalaya. *Indian Association of Palynostratigraphers*, Lucknow.

Gürke, M. 1897. Ebenaceae. In: A. Engler and K. Prantl, (eds.), *Die natürlichen Pflanzenfamilien.*, 4(1).

Harley, M. M. 1986. Distinguishing pollen characters for the Sapotaceae. *Can. J. Bot.* 64:3091-3100.

Harley, M. M. 1991. The pollen morphology of the Sapotaceae. *Kew Bull.* 46(3) 379-491.

Hayashi, S. 1991. *Micrographic Atlas of Japanese Woods.* Wood Res. Inst., Kyoto Univ., Kyoto.

- Heusser, C. J. 1971. Pollen and spores of Chile. University of Arizona Press, Tucson, Arizona.
- Hiern, W. P. 1873. A monograph of Ebenaceae. Trans. Camb. Philos. Soc. 12:1-300.
- Hoaglin, D. C., Mosteller, F., and Tukey, J. W. 1991. Fundamentals of exploratory analysis of variance. John Wiley & Sons, Inc. New York.
- Holmgren, P. K., N. H. Holmgren and L. C. Barnett. 1990. Index Herbariorum. Part I. Herbaria of the World. 8th edition. New York Botanical Garden, Bronx, New York.
- Huang, T. C. 1968. Pollen grains of Formosan plants (4). Taiwania 14: 133-270.
- Huang, T. C. 1972. Pollen Flora of Taiwan. National Taiwan Univ., Bot. Dept. Press, Taipei.
- Huber, B. and Rouschal, C. 1954. Mikrophotographischer Atlas mediterraner Holzer. Fritz Haller Verlag: Berlin-Grunewald.
- Hutchinson, J. 1967. The Genera of Flowering Plants. Dicotyledons. Vol. II. Clarendon Press, Oxford.
- Hutchinson, J. 1969. Evolution and Phylogeny of Flowering Plants. Dicotyledons: Facts and Theory. Academic Press, New York.
- Hutchinson, J. 1973. The Families of Flowering Plants. 3rd. ed. Vol. 1. Clarendon Press, Oxford.
- Ikuse, M. 1956. Pollens Grains of Japan. Hirokawa Pub. Co., Tokyo.
- JMP ver. 1.04. 1989. SAS Institute Inc., Cary, N.C. USA.
- Johansson, J. T. 1987. Pollen morphology of the tribe Morindeae (Rubiaceae). Grana 26:134-150.
- Kallunki, J. A. 1990. An emended description of and new combinations in Raputia Aublet (Cuspariinae, Rutaceae). Brittonia 42:175-177.

- Kallunki, J. A. 1992. A revision of Erythrochiton sensu lato (Cuspariinae, Rutaceae). *Brittonia* 44:107-139.
- Kanehira, R. 1921a. Identification of the important Japanese woods by anatomical characters. Govt. of Formosa: Taihoku.
- Kanehira, R. 1921b. Anatomical Characters and Identification of Formosan Woods. Govt. of Formosa: Taihoku.
- Kanehira, R. 1924. Identification of Philippine woods by anatomical characters. Govt. Res. Inst.; Taihoku, Formosa.
- Kanehira, R. 1926. Anatomical Characters and Identification of the Important Woods of the Japanese Empire. Dept. For., Govt. Res. Inst., Taihoku, Formosa.
- Kribs, D. A. 1928. The Persaud collection of British Guiana woods. *Trop. Woods* 13:7-46.
- Kribs, D. A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. *Bot. Gaz.* 96:574-557.
- Kribs, D. A. 1959. Commercial foreign woods on the American market. Pennsylvania State Univ., Pennsylvania.
- Kukachka, B. F. 1978. Wood anatomy of the neotropical Sapotaceae: VII. Chrysophyllum. USDA For. Serv. Res. Pap. FPL 331.
- Kukachka, B. F. 1982. Wood anatomy of the neotropical Sapotaceae: XXXI. Pouteria. USDA For. Serv. Res. Pap. FPL 419.
- Labacq, L. and R. Dechamps. 1964. Essai d'identification anatomique des bois d'Afrique centrale. *Ann. Mus. roy. Afr. cent.*, Tervuren, Belgium, ser. 8, Sci. econ., No. 3.
- Lecomte, H. 1926. Les bois de l'Indochine. Agence Economique de l'Indochine, Paris, Publ. No. 13.
- Lieux, M. H. 1982. An atlas of pollen of trees, shrubs and woody vines of Louisiana and other southeastern states, Part IV. Sapotaceae to Fabaceae. *Polien et Spores*, 24:331-368.

Meijden, R. van der 1971. A survey of the pollenmorphology of the indopacific species of Symplocos (Symplocaceae). Pollen et Spores 12:5134-527.

Metcalf, C. R. and L. Chalk. 1950. Anatomy of the Dicotyledons. Vol. II. Clarendon Press, Oxford.

Metcalf, C. R. and L. Chalk. 1979. Anatomy of the Dicotyledons. 2nd. ed. Vol I. Clarendon Press, Oxford.

Metcalf, C. R. and L. Chalk. 1983. Anatomy of the Dicotyledons. 2nd. ed. Vol II. Clarendon Press, Oxford.

Mohl, H. 1835. Sur la structure et les formes des graines de pollen. Ann. Sci. Nat. Ser. 2:318.

Moll, J. W. and H. H. Janssonius. 1909. Mikrographie des Holzes der auf Java vorkommenden Baumarten. E. J. Brill, Leiden.

Morton, C. M. 1994. Pseudomonotes, Dipterocarpaceae of the Western Hemisphere. (in review).

Morton, C. M. and J. A. Kallunki. 1993. Pollen morphology of the subtribe Cuspariinae (Rutaceae). Brittonia 45(4):286-314.

Morton, C. M. and W. C. Dickison. 1992. Comparative pollen morphology of the Styracaceae. Grana 31:1-15.

Moseley, M. F., Jr. 1967. The value of the vascular system in the study of the flower. Phytomorphology 17:159-164.

Nair, P. K. K. and S. Kothari. 1985. Studies in the pollen morphology of Indian Heteromerae. Advances in Pollen-spore Research 13:1-90.

Nilsson, S. and J. Praglowski, eds. 1992. Erdtman's handbook of palynology, 2nd revised ed. Munksgaard Co., Copenhagen.

Nooteboom, H.P. 1975. Revision of the Symplocaceae of the Old World, New Caledonia excepted. Leiden Bot. Ser. 1:1-335.

Noreen, E. W. 1989. Computer-intensive methods for testing hypotheses: an introduction. John Wiley, New York.

Normand, D. 1960. Atlas des bois de la Cote d'Ivoire. Centre Tech. For. Trop.: Nogent-sur-Marne. Vol III.

Nowicke, J. M. and J. J. Skvarla. 1979. Pollen morphology: The potential influence in higher order systematics. Ann. Missouri Bot. Gard. 66:633-700.

Nowicke, J. M. and J. J. Skvarla. 1984. Pollen morphology and the relationships of Simmondsia chinensis to the order Euphorbiales. Amer. J. Bot. 71:210-215.

Oever, L. van den, P. Baas, and M. Zandee. 1981. Comparative wood anatomy of Symplocos and latitude and altitude of provenance. Int. Assoc. Wood Anat. News Bull. 2:3-24.

Pagano, M. and K. Gauvreau. 1993. Principles of biostatistics. Duxbury Press, Belmont CA.

Panshin, A.J. and C. de Zeeuw. 1980. Textbook of wood technology. I. Structure, identification, uses, and properties of the commercial woods of the United States and Canada. McGraw Hill: New York. 4th. ed.

Pearson, R. S. and H. P. Brown. 1932. Commercial Timber of India. Central Publ. Branch, Govt. of India Central Publication Branch, Calcutta.

Perkins, J. 1907. Styracaceae. In: A. Engler, (ed.), Das Pflanzenreich. 4.241.

Prior, J.A.B. and P.E. Gasson. 1990. Comparative wood anatomy of Afromontane and Bushveld species from Swaziland, Southern Africa. Int. Assoc. Wood Anat. News Bull. 11:319-336.

Purkayastha, S. K., K. B. S. Juneja and S. M. H. Kazmi. 1976. Anatomy of the more important Andaman commercial timbers. Indian For. Rec. 2(1):1-48.

Record, S. J. 1933. The woods of Rhabdodendron and Duckeodendron. Trop. Woods 33:6-10.

Record, S. J. 1934. Notes on the classification of Geothalsia. Trop. Woods 40:18.

Record, S. J. and R. W. Hess. 1943. *Timbers of the New World*. Yale Univ. Press, New Haven.

Record, S.J. and C.D. Mell. 1924. *Timbers of tropical America*. Yale Univ. Press: New Haven.

Salgado-Labouriau, M. L. S. 1973. Contribuição a palinologia dos cerrados. Editado pela Academia Brasileira de Ciências. Rio de Janeiro.

Salgado-Labouriau, M. L., L. D. A. Freire De Carvalho and P. B. Cavalcante. 1969. Pollen grains of plants of the "Cerrado" XXI-Ebenaceae, Nyctaginaceae, Rhamnaceae and Solanaceae. *Botânica, Sao Paulo*. 32:1-14.

Selling, O. H. 1947. *Studies In Hawaiian Pollen Statistics. Part II. The pollens of the Hawaiian phanerograms*. Special Pub. Bernice Pauahi Bishop. Mus., 38.

Sharma, C. and H. P. Gupta. 1979. Pollen morphology and phylogeny of indian Ebenaceae. *Geophytology*. 8:209-214.

Sleumer, H. O. 1935. Olacaceae. In: A. Engler and K. Prantl, (ed. 2), *Nat. Pflanzenfam.*, 16b.

Sokal, R. R. and F. J. Rohlf. 1981. *Biometry*, 2nd. ed. W.H. Freeman and company, New York.

Sowunmi, M. A. 1973. Pollen grains of Nigerian plants. I. Woody species. *Grana* 13:145-186.

Stern, W. L. 1978. A retrospective view of comparative anatomy, phylogeny, and plant taxonomy. *Int. Assoc. Wood Anat. News Bull.* 2-3:33-39.

Stern, W. L. 1988. Index Xylariorum, institutional wood collections of the world. *Int. Assoc. Wood Anat. News Bull.* 9:203-252.

Stevens, P. F. 1991. Character states, morphological variation, and phylogenetic analysis: A review. *Systematic Botany* 16(3):553-583.

Steyermark, J. A. 1984. Flora of the Venezuelan Guayana-I. Ann. Missouri Bot. Gard. 71:297-340.

Straka, H., A. Simon, and M. Cerceau-Larival. 1967. Palynologia Madagassica et Mascarenica. Pollen et Spores 9(3):427-466.

Sudo, S. 1959. Identification of Japanese hardwoods. Bull. Gov. Forest Exp. Sta., Meguro 118:1-138.

Takhtajan, A. L. 1981. Flowering Plants: Origin and Dispersal. Repr. of 1969 ed. Lubrecht and Cramer, New York.

Takhtajan, A. L. 1987. Systema Magnoliophytorum. Officina Editorial Nauka, Leningradskoe.

Tang, Y. 1932. Timber studies of Chinese trees. I-IV. Bull. Fan Mem. Inst. Biol., Peking 3:157-210.

Thomson, P. W. and H. Pflug. 1953. Pollen und Sporen des mitteleuropaischen Tertiars. Palaeontographica 94: 1-138. Stuttgart.

Thorne, R. F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. Aliso 6:57-66.

Thorne, R. F. 1976. A Phylogenetic Classification of the Angiospermae. Evolutionary Biology 9:35-106.

Van Campo, M. 1958. Palynologie africaine, 2. Bull. I.F.A.N. 20:753-760.

Ventenat, E. P. 1799. Tableau du Regne Vegetal, Selon la Methode de Jussieu. II. Paris, (ed) J. Drisonnier.

Wagenitz, G. 1964. Ebenales. In: A. Engler, (12 ed.), Syllabus der Pflanzenfamilien. Angiospermen. Gebruder Borntraeger, Berlin.

Walker, J. W. and J. A. Doyle. 1975. The bases of angiosperm phylogeny: palynology. Ann. Missouri Bot. 62:664-723.

Walker, J. W. and A. G. Walker. 1984. Ultrastructure of lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants. Ann. Missouri Bot. Gard. 71:464-521.

Welle, B. J. H. ter. 1976. Silica grains in the woody plants of the Neotropics, especially Surinam. In: P. Baas, A. J. Bolton, and B. M. Catling, (eds), Wood Structure in biological and technological research. Leiden Bot. Ser. 3: pp.107-142. Leiden Univ. Press.

Wheeler, E. A. 1986. Vessel per square millimetre or vessel groups per square millimetre?. Int. Assoc. Wood Anat. News Bull. 7:73-74.

Wheeler, E. A., P. Baas and P. E. Gasson (eds.). 1989. IAWA list of microscopic features for hardwood identification. Int. Assoc. Wood Anat. News Bull. 10:219-332.

White, F. 1978. The taxonomy, ecology and chorology of African Ebenaceae. I. The Guineo-Congolian species. Bull. Jard. Bot. Nat. Belg. 48:245-358.

White, F. 1980. Notes on the Ebenaceae VIII. The African sections of Diospyros. Bull. Jard. Bot. Nat. Belg. 50:445-460.

White, F. 1983. Ebenaceae. In: Flora Zambesiaca. Vol 7. Clark Constable, Edinburgh.

White, F. 1987. Ebenaceae. Flore d'Afrique Centrale. Jardin botanique national de Belgique. Meise.

White, F. 1988. The taxonomy, ecology and chorology of African Ebenaceae II. The non-Guineo-Congolian species of Diospyros (excluding sect. Royena). Bull. Jard. Bot. Nat. Belg. 58:325-448.

White, F. 1992. Twenty-two new and little-known species of Diospyros (Ebenaceae) from New Caledonia with comments of section Maba. Bull. Mus. natl. Hist. nat., Paris, Section B, Adansonia, n 1. 4(14):179-222.

White, F. and A. N. Caveney. 1980. Notes on the Ebenaceae VII. Some new names and new taxa in Africa. Bull. Jard. Bot. Nat. Belg. 50:393-399.

Wood, C. E., and R. B. Channell. 1960. The genera of the Ebenales in the southeastern United States. J. Arnold Arbor. 41:1-35.

Ybert, J-P. 1979. Atlas de pollens de Cote D'Ivoire. O.R.S.T.O.M., Paris.

Zeeuw, C. de. 1977. Pakaraimoideae, Dipterocarpaceae of the Western Hemisphere. III. Stem anatomy. *Taxon* 26:368-380.

Zhang, X., D. Liang and P. Baas. 1988. The ecological wood anatomy of the lilacs (*Syringa oblata* var *giraldii*) on Mount Taibei in Northwest China. *Int. Assoc. Wood Anat. News Bull.* 9:24-30.

Zhang, Shu-Yin and P. Baas. 1992. Wood anatomy of trees and shrubs from China. III. Rosaceae. *Int. Assoc. Wood Anat. News Bull.* 13:21-91.

Zimmermann, M. H. 1978. Structural requirements for optimal water conduction in tree stems. In: P.B. Tomlinson and M.H. Zimmermann, (eds.), *Tropical trees as living systems*: 517-532. Cambridge University Press, Cambridge.

Zimmermann, M. H. and C. L. Brown. 1971. *Tree, structure and function*. Springer-Verlag, Berlin Heidelberg.