Order Number 9108183

# The embryology, reproductive morphology, and systematics of Lecythidaceae

Tsou, Chih-Hua, Ph.D.

City University of New York, 1990

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

A

# THE EMBRYOLOGY, REPRODUCTIVE MORPHOLOGY, AND SYSTEMATICS OF LECYTHIDACEAE

by

CHIH-HUA TSOU

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1990

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirements for the degree of Doctor of Philosophy.

Sept. 12, 1990
Date

Scott Mori
Chairman of Examining Committee
Dr. Scott A. Mori
The New York Botanical Garden

SEPT. 24, 1990
Date

Executive Officer

Arthur Cronquist
Dr. Arthur Cronquist
The New York Botanical Garden

James C French
Dr. James C. French
The Rutgers University

Thomas E. Jensen
Dr. Thomas E. Jensen
The City University of New York

Dennis W. Stevenson
Dr. Dennis W. Stevenson
The New York Botanical Garden

Dr. Hiroshi Tobe
Off-campus Reader
The Kyoto University

Supervisory Committee

The City University of New York

Abstract

THE EMBRYOLOGY, REPRODUCTIVE MORPHOLOGY, AND SYSTEMATICS OF LECYTHIDACEAE

by

Chih-Hua Tsou

Adviser: Dr. Scott A. Mori

Embryology prior to fertilization, palynology, and reproductive morphology are described at the generic level for the 20 genera of Lecythidaceae s.l.

These 20 genera are uniform in many embryological characters including: Basic-type anther wall formation, glandular tapetum of anther, bitegmic-tenuinucellate ovule, multi-cell-layered inner and outer integuments, Polygonum-type embryo sac formation, straight micropyle formed by inner integument only, and vasculatured outer integument. Embryological data suggest that the Lecythidaceae s.l. have greater similarities with the Theaceae, Ochnaceae, Scytopetalaceae, Ebenaceae, and Styracaceae than with other dicot families. However, good characters for resolving intrafamilial problems have not been discovered.

Palynology of the Lecythidaceae s.l. provides clearcut differences useful in separating the Planchonioideae as a monophyletic subfamily which is characterized by: syncolpate pollen with some specialized features, e.g., marginal ridges, marginal grooves, and polar cushions. The pollen of the other three subfamilies are of the common tricolpor(oid)at type without morphological autapomorphies and hence of no use in phylogenetic considerations.

The reproductive morphology of the 20 genera of Lecythidaceae s.l. exhibits a broad range of variation. The Lecythidaceae s.l. is considered as comprising a core group made up of the Planchonioideae and Lecythidoideae, and two problematic subfamilies, Foetidioideae and Napoleonaeoideae. The core-Lecythidaceae shares numerous characteristics in embryology, wood anatomy, and reproductive morphology with the Scytopetalaceae. On the other hand, the four genera of Foetidioideae and Napoleonaeoideae possess many specialized reproductive features, which suggests that they occupy positions more remote from the core-Lecythidaceae than the Scytopetalaceae does from the core-Lecythidaceae. Therefore, it is concluded that these four genera should not be included in a monophyletic Lecythidaceae consisting only of the Planchonioideae and Lecythidoideae.

# ACKNOWLEDGEMENTS

I am very grateful to Dr. Scott Mori, my advisor, for his constant guidance, encouragement, and support, and to the other members of my committee: Drs. Arthur Cronquist, James C. French, Thomas E. Jensen, Dennis W. Stevenson, and Hiroshi Tobe, for their valuable comments and suggestions. Special thanks are due to Arthur Cronquist, Carol Gracie, Scott Mori, and Chung-Fu Shen, who have carefully corrected different versions of my manuscript. The highly valuable guidance offered in discussions with Chung-Fu Shen, Dennis Stevenson, and Hiroshi Tobe, on various aspects, are specifically appreciated.

I also thank Donald Black and Mike Baxter, for teaching me morphological and SEM techniques, Dr. Tokushiro Takaso, for teaching me how to prepare floral materials for SEM observation; as well as Donald Black and Chung-Fu Shen, for helping with photographic techniques.

This work will not have been possible without help from the following people who either personally collected or made arrangements for collecting liquid preserved materials for this project: Hans Beck, Douglas Daly, Carol Gracie, Andrew Henderson, C. A. Herraez, Chang-Fu Hsieh, B. Jackes, A. H. M. Jayasuriya, Maria Lucia Kawasaki, Scott Mori, Michael Nee, Bruce Nelson, Juan Pancho, Timothy Plowman, Ghillean Prance, Peter Raven, George Schatz, Dennis Stevenson,

Duncan Thomas, and Kung-Ming Wang. The hospitality offered by Mr. Soo (FRIM), Ya-Kung Kuan, Drs. P. B. Tomlinson, and Tokushiro Takaso (of the Harvard Forest, Petersham), and Dr. Hiroshi Tobe (of Kyoto University) during my collecting trips or visits, are cordially acknowledged. In addition, I thank the curators of MO for loaning me specimens of Scytopetalaceae, as well as Dr. Hiroshi Tobe for sending me slides of floral sections of Asteranthos.

Financial support from the following institutions and fundations have enabled me to conduct my academic studies, laboratory work, and collecting trips: Lehman College of CUNY, The New York Botanical Garden, The Fund for Neotropical Plant Research of The New York Botanical Garden, CUNY Student Travel Fund, Lawrence & Conoco Foundation, and The National Museum of Natural Science of Republic of China.

At last, my sincere gratitude goes to my family members in Taiwan for their whole hearted support on various aspects for so many years.

This dissertation is dedicated to my mother, Ms. Chin-Hsia Hu.

TABLE OF CONTENTS

TABLE OF CONTENTS continued

TABLE OF CONTENTS continued

# LIST OF TABLES

# LIST OF FIGURES

# CHAPTER I INTRODUCTION

The Lecythidaceae is a pantropical family of 20 genera which have been segregated into four or five subfamilies in most contemporary systems of classification (Cronquist, 1988; Dahlgren, 1983; Prance & Mori, 1979; Takhtajan, 1987; Thorne, 1983). I refer to these 20 genera as Lecythidaceae s.l. (Table I). However, the fact that systematists have reached such a consensus concerning the classification of Lecythidaceae s.l. does not guarantee that the classification of this family is entirely satisfactory.

The Lecythidaceae s.l. are characterized by: alternate phyllotaxy, presence of cortical bundles, distinct petals (except in Foetidia, Asteranthos, Crateranthus, and Napoleonaea), numerous stamens (except twice as many as petals in Napoleonaea), tricolp(or)ate pollen, an inferior ovary (except in Asteranthos, Crateranthus, and some species of Eschweilera and Lecythis), axile placentation, and a bitegmic-tenuinucellate ovule. However, only alternate phyllotaxy, the presence of cortical bundles, axile placentation, and a bitegmic-tenuinucellate ovule are consistent throughout the species of Lecythidaceae s.l. that have been studied. Because alternate phyllotaxy and axile placentation are quite common in the dicots and because the nature of the ovule has heretofore been examined only in eight species of five genera (Mauritzon, 1939a;

Venkateswarlu, 1952a), it is evident that support for maintaining these 20 genera in a single family is weak.

On the other hand, the two world-wide monographers of Lecythidaceae s.l. (Miers, 1874, 1875a, 1875b; Knuth, 1939a, 1939b, 1939c) segregated each of the three or four subfamilies as separate families. Airy-Shaw (1973) treated the Lecythidaceae s.l. as five separate families.

In general, information about the comparative morphology and embryology of the Lecythidaceae s.l. is lacking. Studies of the Old World members (belonging to three subfamilies) are particularly incomplete. Consequently, simple questions such as what genera should be included in a natural Lecythidaceae have not been answered. One of the two major goals of my study is to provide a natural circumscription of the Lecythidaceae.

Another major problem with the Lecythidaceae s.l. is its phylogenetic position. Traditionally, the Myrtaceae have been considered the closest relatives of the Lecythidaceae s.l. Since 1957, when Cronquist removed the Lecythidaceae s.l. from the Myrtales, phylogenists have gradually come to agree that the closest kin of the Lecythidaceae is found in or around the Theales s.l. Cronquist (1981) suggested that "Lecythidales and Malvales have undergone partly parallel and partly divergent specialization from a common ancestry in the Theales." No other suggestions about the systematic position of the Lecythidaceae s.l. have been published since

Table I

Genera, number of species, and generic distributions of the subfamilies of Lecythidaceae s.l. (modified from Prance & Mori, 1979, Table III)

| Subfamily/Genus | No. sp. | Distribution |
|---|---|---|
| Planchonioideae | | |
| Abdulmajidia | 2 | Malay. Penn. |
| Barringtonia | 41 | E. Afr., Madag., Trop. Asia, Austr. & Pacif. |
| Careya | 4 | Trop. Asia |
| Chydenanthus | 2 | Java & Sumatra |
| Petersianthus | 2 | Trop. W. Afr. & Philipp. Is. |
| Planchonia | 8 | Andaman Is. to N. Austr. |
| Lecythidoideae | | |
| Allantoma | 1 | Venezuela & Brazil |
| Grias | 6 | Panama to Peru |
| Gustavia | 41 | Trop. Amer. |
| Cariniana | 15 | Trop. S. Amer. |
| Bertholletia | 1 | Trop. S. Amer. |
| Corythophora | 4 | Brazil |
| Couratari | 19 | Trop. S. Amer. |
| Couroupita | 3 | Trop. Amer. & W. I. |
| Eschweilera | 83 | Trop. Amer. |
| Lecythis | 26 | Trop. Amer. |

Table I continued

| | | |
|---|---|---|
| Foetidioideae | | |
| *Foetidia* | 17 | Madag., Mauritius & E. Afr. |
| Napoleonaeoideae | | |
| *Asteranthos* | 1 | N. Brazil |
| *Crateranthus* | 3 | Trop. W. Afr. |
| *Napoleonaea* | 8 | Trop. W. Afr. |

then. Consequently, the second major goal of my study is to establish the phylogenetic position of this family.

Because embryological features are among the most critical characters used to support the removal of the Lecythidaceae s.l. from the Myrtales and its placement near the Theales (Cronquist, 1981, 1988), and because reproductive features are important in establishing high-level classifications, I conducted a survey of embryological and reproductive features of the 20 genera of Lecythidaceae s.l. In this study, I intend to 1) establish a monophyletic circumscription of the Lecythidaceae, 2) establish the systematic position of this monophyletic Lecythidaceae, and 3) consider the systematic relationships of those genera removed from the Lecythidaceae s.l.

# Chapter II TAXONOMIC HISTORY

The taxonomic history of Lecythidaceae s.l. has been presented in detail by Prance and Mori (1979: 2-18) and summarized as follows:

"1. Period of discovery and description of new genera beginning with the work of Christovão, Marcgrave, and Linnaeus.

2. Alignment with the Myrtaceae, first proposed by Jussieu in 1789, followed by de Candolle (1828), Bentham and Hooker (1865), and many others.

3. Separation from the Myrtaceae into a separate family, first suggested by Poiteau (1825) and followed by Don (1832), Lindley (1846), Miers (1874), and all workers after Miers.

4. Continued accumulation of evidence for the segregation of the Lecythidaceae from the Myrtaceae.

5. Segregation of Asteranthaceae, Belvisiaceae, Napoleonaeaceae, and Barringtoniaceae from the Lecythidaceae, suggested in various combinations by Lindley (1846), Miers (1874), Knuth (1939a, b, c), Hutchinson (1969, 1973), and Raven (1975).

6. Lumping of the segregate families back into the Lecythidaceae by Hutchinson (1959), Payens (1967), Thorne (1968), Cronquist (1968), and Takhtajan (1969).

7. Placement in an order other than the Myrtales, the

Theales as suggested by Thorne (1968, 1976), the Lecythidales by Cronquist (1968) and Stebbins (1974).

8. Accumulation of information to determine the proper place for the Lecythidaceae among the angiosperms, and studies of the biology of Lecythidaceae, both steps in their initial phases."

Since 1979, there have been no novel opinions regarding the concept of Lecythidaceae s.l. as comprising 20 genera subordinated to four or five subfamilies as well as the systematic position of the family being within or nearby the Theales s.l. (Cronquist, 1981, 1988; Dahlgren, 1980, 1983; Thorne, 1983; Takhtajan, 1986, 1987).

The modern appearance of the classification of Lecythidaceae s.l. first took shape in Niedenzu (1892). Most later workers adopt his treatment to a great extent. However, before this, the taxonomic alignments of genera varied greatly from author to author, particularly those of Asteranthos and Napoleonaea. I would like to discuss more about the various arrangements of the lecythidaceous genera into the four subfamilies, by important authors, both historical and contemporary.

The six genera of Planchonioideae have always been grouped together after their respective publication. The only exception was made by de Candolle in 1828, who placed Barringtonia and Careya in different tribes of Myrtaceae to

which many other lecythidoid genera belonged.

This group (Planchonioideae) was always placed side by side with Grias and Gustavia (both of Lecythidoideae), and with Foetidia (the single genus of Foetidioideae) before 1874 (de Candolle, 1828; Lindley, 1846; Bentham & Hooker, 1865; Le Maout & Decaisne, 1873); because of the presence of the following common floral features: free petals (except in Foetidia), actinomorphic androecium, numerous and slender stamens, and inferior ovary -- all of which are characters used by most of the earlier authors to indicate membership in the Myrtaceae of these eight genera (de Candolle, 1828; Lindley, 1830, 1836; Don, 1832; Bentham & Hooker, 1865; Le Maout & Decaisne, 1873; Thompson, 1927).

The seven zygomorphic genera of Lecythidoideae have always been grouped together exclusively because of their peculiar and unique androecia. In the earlier days the zygomorphic group was either considered to be a family next to Myrtaceae (Poiteau, 1825; Don, 1832; Lindley, 1836, 1846), or assigned as a tribe or subtribe of Myrtaceae (de Candolle, 1828; Bentham & Hooker, 1865; Le Maout & Decaisne, 1873), despite the various treatments of the relationships between this group and members of other subfamilies of Lecythidaceae s.l.

Miers, noted as an acute observer, was the first to move Grias and Gustavia out of the "planchonioid group" to the zygomorphic lecythidoid group (Miers 1874, 1875a, 1875b).

His Lecythidaceae and Barringtoniaceae exactly correspond to the currently recognized Lecythidoideae and Planchonioideae.

Foetidia, the only genus of Foetidioideae, was considered as a subfamily of its own by Niedenzu (1892) who removed it from its association with the planchonioid genera as a member of Myrtaceae. Pichon (1945) is the only major author of this century who maintained Foetidia in the Planchonioideae.

The taxonomic history of Napoleonaeoideae is of great interest. Among the three constituent genera, Crateranthus has not been carefully studied since its publication in 1913, but has always been associated with Napoleonaea without due justification (Thompson, 1927; Knuth, 1939a; Pichon, 1945; Airy-Shaw, 1973). The taxonomic alignments of Asteranthos and Napoleonaea are much more complex. Prance (1979) has discussed specifically the taxonomic history and relationships which have been proposed for Asteranthos. Asteranthos and Napoleonaea are frequently associated together and are supposed to have relationships with Symplocaceae (Desfontaines, 1820), Styracaceae and Sapotaceae (Lindley, 1830), Campanulales (Lindley, 1836), Myrtaceae (Lindley, 1846; Le Maout & Decaisne, 1873), Vaccinieae and Columelliaceae (de Candolle, 1839), Passifloraceae and Loasaceae (Meisner, 1839), Mesembrianthemum or Cactaceae (Eichler, 1889), or Lecythidaceae (Bentham & Hooker, 1865; Niedenzu, 1892).

By the end of the 19th century, comparative data of some members of Lecythidaceae s.l. and Myrtaceae were provided by Constantin and Dufour (1885) and Lignier (1890) which favored the separation of Lecythidaceae s.l. from Myrtaceae. The former paper did not support the segregation of the Barringtonieae and Napoleonaeae from the Lecythideae. Niedenzu (1892) applied the anatomical information to his treatment of Lecythidaceae s.l. He removed all four subfamilies from the Myrtaceae into one family, i.e., Lecythidaceae s.l.

Diehl's (1935) wood anatomical work on all these four subfamilies also stressed the homogeneity of a Lecythidaceae composed of four subfamilies. Diehl's work is one of the few comparative studies published in the present century which covers all of the subfamilies of Lecythidaceae s.l. This fact could help to explain why Niedenzu's (1892) classification of Lecythidaceae as comprising all these subfamilies together is adopted by so many later workers (Hutchinson, 1959; Payens, 1967; Cronquist, 1957, 1968, 1981, 1988; Thorne, 1968, 1983; Stebbins, 1974; Prance & Mori, 1979; Takhtajan, 1959, 1981, 1987), Dahlgren (1983), although there are still some who support several segregated families with each made up of essentially one subfamily (Knuth, 1934, 1939c; Airy-Shaw, 1973).

# CHAPTER III PALYNOLOGY

## Introduction

Erdtman (1952), in his monumental work on the application of palynology to plant taxonomy, was the first to point out the existence of a clear difference in the pollen of different members of the Lecythidaceae s.l. The Planchonioideae are characterized by syntricolpate pollen, while the Lecythidoideae, Foetidioideae, and Napoleonaeoideae possess tricolp(or)ate pollen. His samples included four genera (seven species) of Planchonioideae, four genera (four species) of Lecythidoideae, one species of the monogeneric Foetidioideae, and three genera (three species) of Napoleonaeoideae.

Payens (1967), in his monograph of Barringtonia, mentioned Muller's work on the palynology of Barringtonia. After examining pollen grains of all species of this genus, Muller recognized two subtypes of syntricolpate pollen in Barringtonia, one with marginal grooves and one without. The first of Muller's own reports on the palynology of Lecythidaceae s.l. was published in 1972. Muller examined pollen grains of all known species of the other four planchonioid genera (Muller, 1972), Careya, Chydenanthus, Petersianthus and Planchonia (Abdulmajidia was not yet published), and some species of each of the genera of the

other subfamilies. Muller confirmed Erdtman's (1952) observation of the clearcut palynological distinction between the Planchonioideae and all other subfamilies (syntricolpate vs. tricolporate).

In addition, Muller (1973) further studied pollen ultrastructure and interpreted the functional significance of the syncolpate grains of Planchonicideae. He suggested an evolutionary pathway to explain the derivation of the various patterns found within the Planchonioideae and hypothesized a harmomegathical significance to the evolutionary processes.

Jacques (1965) first discovered pollen dimorphism in a zygomorphic species, Couroupita guianensis Aublet. Mori et al. (1980) further investigated the morphological differences between these two types of pollen with the SEM and the physiological differences with germination tests. Pollen differentiation has been shown to occur in several other zygomorphic-flowered species (Mori & Boeke, 1987). It is evident that the development of pollen dimorphism in the Lecythidoideae is associated with zygomorphic androecia and is probably related to specialized pollination strategies (Mori & Boeke, 1987).

In an attempt to understand more about the morphological variation of the pollen of Lecythidaceae s.l., I have examined the pollen of one or two species of all 20 genera of Lecythidaceae s.l.

## Materials and Method

Samples were obtained from herbarium specimens or pickled collections. Pollen grains were acetolysed and fixed with Carnoy's fluid (3 ethyl alcohol: 1 acetic acid) overnight. The sample fluid was directly dropped onto the stub without using sticky tape. After the grains were air-dried, they were coated with gold.

The samples used for this palynological study are listed in Table II. All collections are represented in the herbarium of The New York Botanical Garden (NY).

## Results and Discussion

My results support the palynological distinction first made by Erdtman (1952) and supported by Muller (1972) between the Planchonioideae and all other subfamilies. The two types have been described in detail by Muller (1972). According to him, the Planchonia type is characterized by larger grains, syntricolpate colpi, generally without clearly defined endoapertures, and a few specialized structures in the marginal zones of the ectoaperture, such as the marginal ridge and the marginal groove. The exine of the mesocolpia may possess a heavy tectum with funnel-like depressions supported by columellate structures. However, simpler exine structure also occurs in the Planchonia type.

Table II

Samples used for palynological study

| | |
|---|---|
| Planchonioideae | |
| *Abdulmajidia chaniana* | Tsou 160 |
| *Barringtonia asiatica* | A.C. Smith 1082 |
| *Careya arborea* | Moham Lal Pung 58, Tsou 163 |
| *Chydenanthus excelsus* | M. Rifai s.n. |
| *Petersianthus quadrialatus* | Herraez 4172 |
| *Planchonia spectabilis* | William 74 |
| *P. valida* | Cardoso-Timor 22 |
| Lecythidoideae | |
| *Allantoma lineata* | Ducke 1414 |
| *Grias cauliflora* | Nee & Mori 3663 |
| *G. peruviana* | Pennington 10733 |
| *Gustavia superba* | Nee & Mori 3679 |
| *G. hexapetala* | Mori 18676 |
| *Bertholletia excelsa* | Smith 2868 |
| *Cariniana domestica* | Hatschbach 37783 |
| *Corythophora amapaensis* | D.F.Austin et al. 7186 |
| *Couroupita guianensis* | Gentry et al. 11038 |
| *C. nicaraguariensis* | W.D. Stevens 6478 |
| *Eschweilera panamensis* | Mori & Crosby 6352 |
| *E. subglandulosa* | Prance et al. 15406 |
| *Lecythis corrugata* | |
| ssp. *corrugata* | Silva & Rosario 3949 |

Table II continued

| | |
|---|---|
| *Lecythis idatimon* | Mori & Boom 8528 |
| *L. pisonis* | Nee & Mori 4210 |
| Foetidioideae | |
| *Foetidia obliqua* | Schatz 1855 |
| Napoleonaeoideae | |
| *Asteranthos brasiliensis* | Ducke 39 |
| *Crateranthus* cf. *talbotii* | Mambo & Thomas 36 |
| *Napoleonaea gossweileri* | J.P.M. Brenan 7675 |

On the other hand, the Lecythis type is less specialized. The grains of this type are collectively characterized by Muller (1972) as smaller (the polar axis rarely exceeding 45 µm) and tricolporoidate or tricolporate. Moreover, the exine is generally simpler in structure, composed of a thin endexine, a layer of more or less distinct columellae, and a rather thin tectum which is smooth, finely reticulate, foveolate or scabrate-verrucate.

The pollen of Abdulmajidia is described for the first time in this study. The pollen morphology of Abdulmajidia is of the Planchonia type.

The syntricolpate pollen of the Planchonioideae is unique among the angiosperms in the combined presence of such specialized features as the extexinous ridge along the colpus margin (marginal ridge) (Figs. 1A-F,2A), the groove demarcating the mesocolpial region and the marginal ridge (marginal groove) (Figs. 1B, 1E, 2A), and the much thickened sexine at the polar region (polar cushion) (Figs. 1A, 1D, 2A). These palynological apomorphies offer strong evidence supporting the monophyly of the Planchonioideae.

Although the six genera of the Planchonioideae are characterized by syntricolpate pollen, the following features vary among the six genera: 1) shape of pollen from spheroidal to prolate; 2) tectum of the mesocolpial region which is either psilate or perforate; when perforate, the shape of the perforations differs; 3) presence or absence of

a marginal ridge; 4) presence or absence of marginal grooves; 5) presence or absence of a polar cushion; and 6) sculpturing on the colpus membrane which is either psilate or granulate; when granulate the shape and the arrangement of the granules differ.

The following brief descriptions of the pollen of the Planchonioideae are either based solely on my own (Abdulmajidia, Chydenanthus, and Petersianthus), on my own as well as Muller's (1972, 1973) (Barringtonia), or on my own as well as Erdtman's (1952) (Careya and Planchonia) observations.

Abdulmajidia (A. chaniana, Figs. 1A, 1B): Pollen subprolate (38 x 32 µm), tectum of mesocolpia foveolate in the central area and reticulate towards the circumference, marginal ridge, marginal groove, and polar cushion all well developed, the colpus membrane psilate.

Barringtonia (B. asiatica, Fig. 1C): The pollen of this genus is highly variable. Pollen spheroidal to prolate, tectum of mesocolpia fine-reticulate to foveolate to imperforate, marginal ridge present in most species, marginal groove and polar cushion present or absent, colpus membrane granulate, the granules gemmate.

Careya (C. arborea, Figs. 1E, 1F): Pollen spheroidal (40 x 40 µm), tectum of mesocolpia imperforate, with funnel-like depressions, marginal ridge forming an almost complete circle surround each mesocolpial region, marginal

groove very long and sometimes appearing as a deep trench well separating the ridge and the mesocolpial region, polar cushion not developed, the colpus membrane heavily granulate, granules clavate and sometimes aligned in about 4 regular rows towards the equatorial region and 2 rows towards the polar region.

Chydenanthus (C. excelsus, Fig. 1D): Pollen prolate (45 x 37 μm), tectum of mesocolpia foveolate in the central area and reticulate towards the margin, both marginal ridge and the polar cushion well developed, marginal groove not clear, the colpus membrane psilate.

Petersianthus (P. quadrialatus, Figs. 2A, 2B): Pollen subspheroidal (42 x 40 μm), tectum of mesocolpia evenly reticulate, marginal ridge well developed, marginal groove present but rather short, three polar cushions present and slightly fused, colpus short, the colpus membrane psilate.

Planchonia: Pollen prolate to spheroidal, tectum of mesocolpia imperforate and wavy, both marginal ridge and marginal groove well developed, polar cushion present or absent, colpus membrane heavily granulate, granules gemmate and irregularly arranged.

The pollen of some species of Planchonia resembles the pollen of Careya. The pollen of some other species of Planchonia resembles the most complicated forms of pollen found in Barringtonia, such as B. calyptrocalyx (Muller, 1973).

Because the results of my limited observations on the grains of the genera other than planchonioids are not significantly different from those made by Erdtman (1952) and Muller (1972, 1973, 1979), no detailed descriptions are here offered. Among the taxa with pollen of the Lecythis type, Asteranthos and Crateranthus are characterized by the granulate colpus membrane (Figs. 2C, 2D). Pollen grains of the Lecythidoideae are rather uniform in gross morphology, but, the variations of the size and shape of perforations on the tectum and that of the shape and relative length of the columellae in the exine are distinct and probably of taxonomic value on the generic and species levels.

Pollen morphological dimorphism in Lecythidaceae s.l., which was first recorded in Couroupita guianensis (Jacques, 1965), was also found in Couroupita nicaraguariensis in this study. The pollen grains are exclusively monads in all Lecythidaceae except C. guianensis, in which tetrads are present in the anthers of the androecial hood whereas normal monads are restricted to the anthers of the staminal ring. In C. nicaraguariensis, a mixture of monads and tetrads is found in anthers sampled from both ring stamens and hood stamens. There is a very low percentage of tetrads in samples from the ring anthers and a significantly higher percentage of tetrads in samples from the hood anthers. However, the contamination of grains between hood anthers and ring anthers is possible because my samples were

collected from pressed flowers from herbarium sheets. The morphology of the monad grains and the tetrad grains differs; the former are tricolporoidate, foveolate-punctate in surface sculpturing, and exhibit well marked colpus margin (Fig. 2E), while the latter are tricolpate, rugulate-verrucate in surface sculpturing, and show very blurred colpus margins (Fig. 2F).

# CHAPTER IV EMBRYOLOGY PRIOR TO FERTILIZATION

## Introduction

In the early nineteenth centry, Amici discovered the pollen tube and the biological relationships between the pollen tube, embryo sac, and embryo of angiosperms (Maheshwari, 1950). These discoveries of the cryptic portion of the reproductive process of plants stimulated numerous studies on both male and female sex organs (Maheshwari, 1950) and helped to establish plant embryology as a separate field of research. In the early part of the twentieth century, taxonomic papers applying embryological features as an aid to classification began to appear, and comparative embryology became established (Schnarf, 1931). However, at that time, embryology still played a rather insignificant role in providing information for making taxonomic decisions.

After World War II, Indian workers made significant contributions to the understanding of plant embryology (Maheshwari, 1950, 1962, 1963a), and also paid special attention to the value of embryology to taxonomy (Johri, 1963, 1967; Maheshwari, 1963b; Maheshwari & Kapil, 1966; Subramanyam, 1962). However, they primarily focused on taxonomic treatments of problematic genera or isolated families.

In 1966, G. Davis published her "Systematic Embryology of the Angiosperms." Her work represents the first compendium on systematic embryology, and is still the only book with this purpose written in English. This book is an excellent reference to embryological studies published up to 1965.

Subsequently, the theoretical study of the evolution of embryological features and their application in taxonomy provided new insights into taxonomic relationships. Bouman and his associates tried to explain the different mechanisms of the evolution of the single integument in terms of ontogeny (Bouman, 1974, 1984; Bouman & Calis, 1977), demonstrating the relationship between integumental structure and seed-coat structure and proposing the polarities of some important embryological features (Bouman, 1974; Boesewinkel, 1980). Philipson (1974, 1975) proposed that the four distribution patterns of the combinations of the number of integuments (2 vs. 1) and the nature of the nucellus (crass- vs. tenui-nucellate) in dicots show an overall correlation with the phylogeny of the dicots. Philipson was the first to show the value of these powerful and easy-to-use embryological features in resolving problems at higher taxonomic levels. Philipson (1977) also emphasized the close correlation among previously proposed groupings based principally on gross morphology, the distribution of iridoid compounds, and the distribution of

unitegmic and tenuinucellate ovules, with the latter two standing as independent characters respectively. Palser (1975) reviewed the application of embryological features in resolving phylogenetic problems of angiosperms at various levels, from class to genus. Herr and his pupils (Herr, 1984; George et al., 1979; Smith, 1975) developed new methods for detecting interspecific variations in embryological features, if any, by statistical analysis of growth of the developing female gametophyte.

Recently, Russian embryologists have published a four volume reference entitled "Comparative Embryology of Flowering Plants" (Yakovlev, 1981-1987). This book includes information based on previous embryological studies as well as numerous original observations. It stands as an important milestone in the study of plant embryology.

In recent years, Tobe has made numerous contributions on the taxonomic application of embryology (Tobe, 1989). Based on his comprehensive studies on Myrtales and some associated families, Tobe (1989) has established the levels of reliable application, based on the consistency of expression of 46 embryological characters.

Up to now, embryological features have been used in the Lecythidaceae s.l. mainly to establish the phylogenetic position of the family. The exclusion of Lecythidaceae s.l. from Myrtales and its placement in or around the Theales was based, to a large extent, on embryological characters.

Cronquist (1957) first used embryological discrepancies to support the segregation of Lecythidaceae s.l. from the typical myrtalean families. Additional embryological differences supporting the exclusion of Lecythidaceae s.l. from the Myrtales have been presented by Tobe & Raven (1983).

Until now, the embryology prior to fertilization of Lecythidaceae s.l. has been studied on five genera only (Mauritzon, 1939a; Venkateswarlu, 1952a, 1952b; Anisimova, 1985). Male embryological features before fertilization have only been studied in Barringtonia (3 sp.), Couroupita (1 sp.), and Napoleonaea (1 sp.), and female embryological features before fertilization have only been studied in Barringtonia (4 sp.), Careya (1 sp.), Couroupita (1 sp.), Gustavia (1 sp.), and Napoleonaea (1 sp.). I decided to work on the embryology of all 20 genera of Lecythidaceae s.l. in order to understand the features of each of them and to clarify intergeneric relationships. Fortunately, I have obtained at least some preserved collections of at least one species from each genus. The material studied is mostly vouchered by herbarium specimens deposited at NY (Table III).

My work is focused on male and female embryological features before fertilization because 1) the majority of my materials are confined to those of the pre-fertilization stages, and 2) the features before fertilization are more

numerous and generally more powerful for establishing phylogenetic relationships than are those that appear after fertilization (Davis, 1966; Tobe, 1989).

## Materials and Methods

The materials used in this embryological study are listed in Table III. All materials were fixed in F.A.A. immediately after being collected. For paraffin sectioning, materials were dehydrated through a butyol-alcohol series, embedded in paraplast, cut into sections of 6 to 9 $\mu$m thickness, then stained in the Safranin O-Fast Green series or the Hematoxylene-Safranin O-Fast Green series and prepared as permanent slides for LM observation.

## Characters Described and Terms

The characters enumerated in Table IV were recorded, when possible. The results of my observations are described at the generic level. Each description is presented in the following order: 1) early developmental stages, 2) meiosis, 3) late developmental stages, and 4) mature stages.

The definition of all embryological terms employed in this chapter follows Davis (1966) and Johri (1984).

Illustrations of some of the characters in Table IV are provided in Fig3. 3-I to 3-III.

Table III

Materials used for the current embryological study

| | |
|---|---|
| Planchonioideae | |
| *Abdulmajidia chaniana* | Tsou 160 |
| *Barringtonia racemosa* | Hsieh s.n. |
| *Careya arborea* | Jayasuriya 4334 |
| *Chydenanthus excelsus* | Rifai s.n. |
| *Petersianthus quadrialatus* | Herraez 4172 |
| *Planchonia careya* | Jackes s.n. |
| Lecythidoideae | |
| *Allantoma lineata* | Prance 17549 |
| *Grias cauliflora* | Nee & Mori 3663 |
| *Gustavia hexapetala* | Mori 18676 |
| *G. macarenensis* ssp. *paucisperma* | Nee & Mori 4159 |
| *Cariniana micrantha* | Mori 20191 |
| *Bertholletia excelsa* | Nelson s.n. |
| *Corythophora amapaensis* | Mori 18675 |
| *C. rimosa* | Mori 18547 |
| *Couratari oligantha* | Plowman 12546 |
| *Couroupita guianensis* | Hyge 1964 |
| *Eschweilera cyathiformis* | Mori 19385 |
| *E. sessilis* | Mori 7728 |
| *Lecythis corrugata* | Beck 293 |

Table III continued

| | |
|---|---|
| Foetidioideae | |
| *Foetidia obliqua* | Schatz 1855 |
| Napoleonaeoideae | |
| *Asteranthos brasiliensis* | Coradin 7 |
| *A. brasiliensis* | Kawasaki 62 |
| *Crateranthus* cf. *talbotii* | Mambo & Thomas 36 |
| *Napoleonaea* cf. *vogelii* | Reitsma 2946 |

Table IV

Embryological characters studied. The stage(s) examined and the alternative expressions of each character in the Lecythidaceae s.l. are indicated

---

Male Features before Fertilization:

| stage(s) | Character |
|---|---|
| 1 | Androecial initiation (centripetal, centrifugal) |
| 1 | Anther wall development pattern (Basic, Monocot) |
| 1 | Number of middle layers (1 to 4) |
| 2 | Number of nuclei in one tapetal cell (2 to 6) |
| 2 | Form of pollen tetrads (tetrahedral, isobilateral, decussate) |
| 3 | Tapetum type (glandular) |
| 2,3,4 | Distributions of starch and/or tannin inclusions (anther wall layers, connective, filaments) |
| 3,4 | Secondary thickenings of endothecium (rod-like, reticulate) |
| 4 | Anther wall composition at anthesis (epidermis & endothecium present, middle layers present or absent) |
| 4 | Anther cross section, configuration of sporangia and connective |
| 1-4 | Growth of the zygomorphic androecium |

Table IV continued

Female Features before Fertilization:

| stage(s) | Character |
|---|---|
| 1 | Zonation in ovule primordium (trizonate) |
| 1 | Inner integument initiation (dermal origin) |
| 1 | Outer integument initiation (dermal origin) |
| 1,2 | Number of archesporial cells (1, a few) |
| 1-3 | Position of ovule (anatropous, campylotropous) |
| 2 | Nature of nucellus (tenui- , crassi-nucellate) |
| 2 | Composition of basal nucellus in l.s. (scanty, 2 to 4 cell-rows) |
| 2 | Form of megaspore tetrads (linear) |
| 2-4 | Shape of nucellus (oblong, elliptic, rounded) |
| 2-4 | Formation of micropyle (i.i. only) |
| 2-4 | Widths of i.i. (2-8 cell-layered) |
| 2-4 | Widths of o.i. (2-24 cell-layered) |
| 2-4 | Differentiation of endothelium (with, without) |
| 3 | Embryo sac formation (Polygonum-type) |
| 3 | Morphology of egg apparatus (normal) |
| 3-4 | Behavior of antipodal cells (ephemeral, entering into basal nucellar tissue) |
| 4 | Fate of basal nucellus (destroyed, remained) |
| 4 | Number of vascular bundles in o.i. (1 to 14) |
| 4 | Junction between i.i. and o.i. (from the base of embryo sac to the middle part of micropyle) |
| 4 | Shape of ovule (oblong, elliptic, ovate, rounded) |

# Descriptions

## Planchonioideae

### Abdulmajidia chaniana Whitmore

Materials studied were medium-sized buds to mature flowers. The youngest stage observed was the end of meiosis in male gametogenesis and the megasporocyte stage in female gametogenesis.

1. Development and mature structure of anther.

When the microspores are just released from the callose wall, the tapetum is still intact and covered with a layer of Urbisch bodies (Fig. 5A). The middle layer(s) is (are) very compressed. The number of original middle layers is unknown. Soon after the endothecial cells expand to their full size, they first develop secondary thickenings on the inner tangential wall and then on all radial walls. In later stage most parenchymatous cells of the connective contain many starch granules (Fig. 5B). In the mature anther, the epidermis is persistent. Secondary thickenings of the endothecial cells form non-branching bands (Fig. 5B). The anthers are latrorse, with a medium-sized connective and a small vascular bundle in the center of the connective.

2. Development of ovule.

At the megasporocyte stage, the young ovule is oval and has already reached its typical anatropous position. The nucellus is oblong. Only one megasporocyte is found in each nucellus in the subdermal layer, with 3 rows of nucellar cells beneath it when viewed in longitudinal section (Fig. 5C). Neither living nor crushed parietal cells were present. The ovule is most likely tenuinucellate. The i.i. is 4 to 5 cell-layered and alone forms the micropyle. The o.i. is slightly wider but much shorter than the i.i. During meiosis, linear tetrads are formed. With further development, the three micropylar megaspores disintegrate and the chalazal megaspore undergoes embryo sac formation (Fig. 5D) via the Polygonum type development. The expanding embryo sac destroys all the nucellar tissue as well partially destroying the innermost layer of the i.i.

3. Mature structure of ovule.

Mature ovules are ovate. The embryo sac is elliptic but with irregular projections caused by the breakdown of the inner epidermis of the i.i. (Figs. 5E, 5F). Antipodal cells are not present. The i.i. is long, 7 to 8 cell layers thick and it alone forms a straight micropyle. The o.i. is much shorter. It consists of 12 to 14 cell layers around the embryo sac, but is constricted to 6 to 7 layers just above the embryo sac, where it curves outwards and slightly expands into a well defined rim. The junction between the i.i. and the o.i. is below the embryo sac (Fig. 5F).

Vasculature of the ovule is complicated. The raphe bundle branches pre- and post-chalazally. There are 7 to 10 bundles present in the o.i. (Fig. 5E).

## Barringtonia racemosa (L.) Sprenger

1. Androecial initiation.

In young floral buds numerous staminal primordia initiate in whorls centripetally. When the outermost ones have differentiated into filament and anther, the innermost ones just emerged (Fig. 4A).

2. Development and mature structure of anther.

The development of the anther wall conforms to the Basic-type. The two primary parietal layers periclinally divide to give rise the endothecium, two middle layers, and the tapetum (Figs. 6A, 6B), and sometimes the inner middle layer will periclinally divide again to make three middle layers in total. Before meiosis, the tapetal cells have undergone nuclear divisions to produce 2 to 4 nuclei per cell. The tetrads are generally tetrahedral. When the microspores are released, the tapetal cells are still intact. The tapetum is of glandular type. The secondary thickening of the endothecium develops after meiosis is completed. At anthesis, the epidermis persists, and the endothecial cell walls show non-branching, rod-like thickenings on all but the outer tangential walls. The

anthers are latrorse, and the relative area of connective in the anther is very broad (Fig. 6B). The vascular bundle is present in the center of the medium-sized connective.

3. Development of ovule.

Four carpels were observed. When the two ovule primodia are just initiated from the margins of each carpel, the four carpels are still widely opened on their ventral sides. The ovules are trizonate (Fig. 6C). Neither the initiation of the i.i. or the o.i. was observed.

There is only one archesporial cell present in each ovule. It develops from the subdermal layer and functions as a megasporocyte directly. The ovule is tenuinucellate. At the megasporocyte stage the ovule has already reached its typical anatropous position. The ovule is oblong, with an oblong and slender nucellus and a thick chalaza. Both the i.i. and o.i. are 4 to 5 cell layers thick. The i.i. has enclosed the nucellus and it alone forms the micropyle. Inside the nucellus, the expanding megasporocyte occupies the upper 1/3 of the nucellus. It has 3 rows of basal cells, when viewed in longitudinal section (Fig. 6D). Meiosis produces a linear tetrad. The process of embryo sac formation was not observed.

4. Mature structure of ovule.

Mature ovules are long-ovate. In the mature ovule, the embryo sac is elliptic and comparatively small. Antipodal cells are not present, and the nucellar tissue is totally

destroyed. The junction of the i.i. and the o.i. is much lower than the base of embryo sac. The i.i. and o.i. are 8 to 9 and 9 to 11 cell layers thick around the embryo sac, and 6 to 7 and 8 to 10 layers thick, respectively, around the micropyle. The micropyle is straight, rather long and formed by the i.i. only. The o.i. is about the same height as the i.i. (Fig. 6F). Vasculature in the mature ovule is elaborate. In the cross section through the embryo sac, there are usually 10 to 15 vascular bundles of various diameters, one in the raphe and the rest in the o.i. (Fig. 6E). The raphe bundle branches both before and after reaching the chalaza, and the secondary bundles continue to divide. No endothelial layer is formed.

## Careya arborea Roxburgh

1. Androecial initiation.

The individual staminal primordium emerges from a ring-like common androecial primordium. The earliest staminal primordia initiate from the central region of this structure with the later ones developing in both directions (Figs. 4B, 9B).

2. Development and mature structure of anther.

Anther wall formation follows the Basic-type to give rise to the endothecium, two middle layers, and the tapetum. Before meiosis, the tapetal cells are binucleate. Meiosis

and the late development of the anther were not observed. In the mature anther, the epidermis is persistent. The endothecial cell walls are ornamented with non-branching, rod-like secondary thickenings (Fig. 7A). The anthers are typically latrorse. The relative area of the connective to the anther in cross section is broad, and the vascular bundle is situated in the center of connective (Fig. 7A).

3. Development of ovule.

There are four carpels in the ovary. Four rows of ovule primordia simultaneously emerge along the placenta. The young ovules are trizonate. Both the i.i. and the o.i. initiate from dermal cells. The young ovules are rounded. In the archesporium there is usually one, rarely two, archesporial cells. However, only one megasporocyte differentiates (Fig. 7B). The ovule is tenuinucellate. At the megasporocyte stage, the nucellus is rounded and short, and the megasporocyte has 4 rows of nucellar cells beneath it in a longitudinal view. At this stage, the integuments have not yet enclosed the nucellus. The i.i. is 3 cell-layered and the o.i. is 4 cell-layered. Both are of the same height (Fig. 7B). During meiosis, a linear tetrad is formed. The upper three megaspores soon degenerate, and the chalazal one begins to divide to give rise to the embryo sac. The development of the embryo sac follows the Polygonum type. During the expansion of the embryo sac, an endothelium begins to differentiate, and the o.i. exhibits

preliminary curving.

4. Mature structure of ovule.

At maturity, the ovules are rounded or elliptic. The endothelium is persistent, and the embryo sac is confined in a spindle-like cavity. No basal nucellar tissue is present, and the antipodal cells are absent. The micropyle is straight to slightly curved and formed by the i.i. only. The i.i. is 6 to 7 cell-layered at the base and gradually reduced to 4 to 5 cell-layered upwards. The o.i. is 10 to 11 cell-layered at the base and gradually narrowed till the upper region of the micropyle where it forms an outfolded collar, the arilloid, covering the ovule (Fig. 7C). The same specialization of the o.i. is found in Pl. careya. The outgrowth is a complete circular layer, made up of the anterior part of the o.i. and the derivatives of the raphe. The junction between the i.i. and the o.i. is at the base of the embryo sac (Fig. 7C). There are 3 or 4 vascular bundles in the o.i. in addition to the raphe bundle.

## Chydenanthus excelsus (Blume) Miers

1. Development and mature structure of anther.

The formation of the anther wall follows the Basic-type. Two or three middle layers are formed in the beginning (Fig. 7D), but they soon disintegrate. During meiosis, the microspore tetrads are mostly tetrahedral.

When microspores are released from the tetrads, the tapetum is intact, and each tapetal cell contains 2 to 4 nuclei.

The mature anthers have a persistent epidermis and a radially elongated endothecium. The secondary thickenings are non-branching and rod-like on the endothecial walls (Fig. 7E). Starch granules are present in the parenchymatous cells of the connective. The anthers are latrorse. The vascular bundle in the rather broad connective is located in the center or slightly abaxially.

2. Development of ovule.

From early development, the space of the two locules of the ovary relative to the size of the ovules is very narrow in this species. Only one or two ovules are formed in each locule. The young ovule develops a very massive funiculus, and the ovules fill the whole locule. The initiation of the i.i. from dermal cells was observed in one ovule (Fig. 7G). One archesporial cell differentiates from the subdermal layer at the apex of nucellus (Fig. 7G). Whether or not the archesporial cell cuts off parietal cells before functioning as the megasporocyte was not investigated. The whole process of embryo sac formation was not observed. The inner epidermis of the i.i. expands during the early stages of embryo sac formation, but cells of this layer never show thick cytoplasm as typical endothelial cells do.

3. Mature structure of ovule.

No mature flowers were available. Some ovules extracted

from immature floral buds already possessed a mature egg apparatus. Although appearing mature, the thickness and length of the integuments seemed to have potential to increase further according to the observations made on the species of other genera. The ovule is long-elliptic, and the funiculus, raphe, and o.i. are very thick (Fig. 7H). In some ovules, the funiculus is bulged transversely into a triangular structure (Fig. 7F). The embryo sac is elliptic. Antipodal cells were not observed. The i.i. is 7 to 8 cell layers thick around the embryo sac, and 9 to 10 cell layers thick around the micropyle. The micropyle is straight and composed of the i.i. only. The o.i. is very thick, about 15 cell-layered around the embryo sac, and 18 to 21 cell-layered at the micropylar region (Fig. 7H). The junction between the i.i. and the o.i. is lower than the base of embryo sac at the antiraphe side, while the o.i. is completely fused with the raphe and highly fused with the i.i. on the raphe side (Fig. 7H). Vascular bundles are present in the o.i., however, the exact number of them is unknown.

## Petersianthus quadrialatus (Merrill) Merrill

1. Development and mature structure of anther.

Young anthers have an obvious protrusion from the connective. The filaments develop rapidly and are bent

inwards even when the sporogenous tissue is not differentiated. The fast growth of the filaments is not observed elsewhere in the Planchonioideae. Anther wall development follows the Basic-type (Fig. 8A). There are 2 or 3 middle layers formed. During meiosis, the two divisions proceed simultaneously (Fig. 8B) and the tetrads are mostly tetrahedral. The tapetal cells are binucleate and of the glandular type. At the free spore stage, all the parenchymatous cells of the connective contain many starch granules. At anthesis, only the epidermis and the endothecium are persistent, the latter shows non-branching, rod-like secondary thickenings (Fig. 8C). The anthers are introrse. The connective is rather broad and rhomboidal in cross section. A medium-sized vascular bundle is usually located at the abaxial side and sometimes at the center of the connective.

2. Development of ovule.

There are four carpels but only three locules in the ovary (Fig. 8F). The young ovules are trizonate. The funiculus grows so fast that when the i.i. has just initiated from 2 dermal cells viewed in l. s., the ovule has already curved 450°. The o.i. initiates later and is of dermal origin also. One archesporial cell develops from the subdermal layer in the nucellus and functions as the megasporocyte directly. The ovule is tenuinucellate. The i.i. has enclosed the nucellus at this stage to form a

straight micropyle of 5 or 6 cell layers. The o.i. has reached the same height as the i.i., but is comparatively thicker. The shape of the ovule varies from oval to elliptic, depending on the space available. The nucellus is oblong, with 3 rows of cells beneath the megasporocyte (Fig. 8D) During meiosis, the inner epidermal cells of i.i. enlarge in radial direction, but the cytoplasm is not especially dense. The tetrad is linear. The embryo sac formation is probably of the Polygonum type.

3. Mature structure of ovule.

At maturity, the ovules stay in the dorsal pleurotropous position (c.f. Radfford et al., 1974) (Fig. 8E). The raphe perpendicular to the funiculus is a unique feature of this species. The embryo sac is elliptic, with some nucellar tissue beneath it and the boundary. The inner epidermis of the i.i. is no longer especially elongated. The two integuments are fused at the level of the embryo sac where the thickness of the fused portion is about 13 to 15 cell layers (Fig. 8G). The thicknesses of the i.i. and the o.i. above the embryo sac are 5 to 7 and 11 to 12 cell-layered, respectively. The o.i. narrows down to 7 layers at its apex. The junction of the i.i. and the o.i. is at the middle part of the embryo sac. The straight micropyle is formed by the i.i. only (Fig. 8G). In the c.s. of the ovule through the embryo sac, there are one large vascular bundle in the raphe and 6 to 8 smaller bundles in the o.i.

## Planchonia careya (F.V.M.) Knuth

1. Androecial initiation.

The individual staminal primordium emerges from the ring-like common androecial primordium. The earliest staminal primordia initiate from the central portion of this structure with the later ones developing in both directions (Figs. 4B, 9B).

2. Development and mature structure of anther.

In young anthers both primary parietal layers will divide periclinally. Either of them may divide first. There are always 2 middle layers in the anther wall. At maturity, the anthers have rather large epidermal cells and endothecial cells, with the latter covered with non-branching, rod-like secondary thickenings. The anthers are in the typical latrorse position. The connective is of medium size as viewed in the anther cross section, and the vascular bundle is situated at its center (Fig. 9A).

3. Development of ovule.

There are four carpels in the ovary. Many ovule primordia emerge as two rows from the two margins of each septum. These primordia are trizonate. Before the initiation of the i.i. and the o.i., the young ovules have curved slightly towards the axis because of differential cell growth, especially the longer length of the cells on the abaxial side. Both the i.i. and the o.i. initiate from

the dermal cells at about the same time, or the i.i. appears somewhat earlier (Fig. 9C). The processes of meiosis and embryo sac formation were not observed.

4. Mature structure of ovule.

The ovules are rounded, mainly campylotropous, and rarely anatropous. They are covered by an outgrowth derived from the o.i. and the raphe (Figs. 9D, 9E). The embryo sac is spindle-like and surrounded by a typical endothelium (Fig. 9D). No nucellar tissue remains. Antipodal cells are absent. The i.i. is about 6 cell-layered around the embryo sac and 5 cell-layered around the micropyle. A well defined rim is formed at the apex of i.i. due to several regular periclinal divisions (Fig. 9D). The i.i. alone constitutes the straight or slightly curved micropyle. The o.i. is slightly thicker than the i.i. at the basal portion and becomes thinner upwards. It folds outward below the apex of the i.i. forming a very high collar, the arilloid, which curves down to the lower half of the ovule (Fig. 9D). The junction between the i.i. and the o.i. is a little above the base of embryo sac (Fig. 9D). There are 3 or 4 vascular bundles in the o.i. besides the one in the raphe.

## Lecythidoideae

### Allantoma lineata (Martius ex Berg) Miers

The androecium of this species is actinomorphic (Fig. 11 in Prance & Mori, 1979).

1. Development and mature structure of anther.

Anther wall development was not observed. The earliest stage available is that at which microspores have been released from the callose wall. At this time, the tapetum is broken down and a mixed medium is formed around the inside of the locule (Fig. 10B). The typical periplasmodium is not found, because no nuclei are present in the medium. I do not know at which stage the tapetal wall broke down. Because the floral material examined showed a severe pathological condition and the critical stage had not been obtained, the nature of the tapetum of this sample can not be determined. During the free spore stage, the endothecium is rather enlarged and there are secondary thickenings deposited on its cell walls. Starch granules are present in both the endothecium and the compressed middle layer(s). The staminal ring is a well developed cylinder with a complex vascular system (Fig. 10A). Two or more adjacent bundles fuse together at the base of each filament; the fused bundle enters the filament (Fig. 10C).

In mature anthers, the epidermis is persistent and the

endothecium is elongated with non-branching, rod-like thickenings on its cell walls. One middle layer is still present. The cells of the connective tissue contain scattered starch granules, and some crystals (Fig. 10B). Many more starch granules are present in the filaments. The filaments are fleshy and thick, and the anthers are versatile and latrorse (Fig. 10A).

2. Mature structure of ovule.

The stages before embryo sac formation were not observed. The ovules are long-elliptic and anatropous. The nucellus was much elongated before being crushed. The i.i. encloses the nucellus and forms a straight micropyle. The i.i. is 5 to 6 cell layers thick around the embryo sac, slightly thickened to 7 to 8 cell-layered around the upper portion of nucellus, and reduced to 5 cell-layered at the micropylar region. No endothelium is formed. The inner epidermis of the i.i. is damaged locally by the expansion of the embryo sac. The o.i. is slightly thicker, 8 to 10 cell-layered around the embryo sac and 7 to 8 cell-layered at the micropylar region. The junction of these two integuments is at the base of embryo sac. In mature ovules, no basal nucellar tissue or antipodal cells appear (Fig. 10D). There are 6 to 8 thin vascular bundles in the o.i., which are side branches from the thick bundle of the raphe.

## Grias cauliflora Linnaeus

The androecium of this species is actinomorphic (Fig. 11 F-G in Prance and Mori, 1979).

1. Development and mature structure of anther.

Anther wall formation follows the Basic-type. The inner primary parietal layer undergoes periclinal division earlier than the outer layer. Sporogenous cells begin meiosis early in development, but the development of the anthers is not synchronous among anthers of the same flower. When the buds are 0.5 cm in diameter, some anthers are initiating meiosis, some anthers are displaying simultaneous nuclear divisions, and some others have already entered the tetrad stage. During meiosis, the divisions are simultaneous and the tetrads are tetrahedral (Fig. 11A). At this stage, the tapetum is glandular. Its cells have 2 or 3 nuclei and very dense cytoplasm. From the beginning of the free spore stage, the endothecium becomes much more expanded and the secondary thickenings added later are non-branching bands. During this period, the connective has accumulated large quantities of starch granules.

Distinct features of this species are that the anthers are introrse and that the two pairs of sporangia are well separated. The vascular bundle of the filament bifurcates at the apex, one for each sporangial pair (Fig. 11B). In the mature stamens, the filaments are much thickened, and

each of the two sporangial pairs is connected with the filament by a narrow and short connective. Mature stamens have broad, but porous filaments. The epidermis and the endothecium of the anther wall are persistent. A layer of Urbisch bodies covers the inner surface of locule.

2. Development of ovule.

Both integuments initiate from dermal cells of the ovule primodium. The ovule starts to cuvre during the initiation of the nucellus and integuments. Only one archesporial cell is differentiated for each nucellus (Fig. 11C). The i.i. encloses the nucellus to form a short micropyle at a very early stage. The ovule is tenuinucellate. At the megasporocyte stage, the nucellus is oblong and much more narrow than those of other genera. There are 3 or 4 rows of cells beneath the megasporocyte when viewed in longitudinal section. The i.i. is 4 cell-layered around the nucellus and 5 cell-layered around the micropyle. The o.i. is 7 to 8 cell-layered at base and 6 cell-layered at the micropyle.

Embryo sac formation was not followed, but eight nuclei with a normal distribution were observed. During expansion of the embryo sac, the inner epidermis of the i.i. is damaged, but the basal nucellar tissue, which is about 5 cells high is persistent. The antipodal cells penetrate into the center of the basal nucellar tissue and connect with the central cells to form a channel which is probably a nutrient-conducting pathway (Fig. 11E). This is not common

in the Lecythidaceae s.l.

3. Mature structure of ovule.

Mature ovules are long ovate and anatropous. No endothelium is formed. The embryo sac is of irregular shape because of the irregular and partial breakdown of the inner epidermis of the i.i. (Figs. 11E, 11F). The basal nucellar tissue persists and the central cells are suberized. The antipodal cells are no longer distinguishable in this basal tissue. The i.i. is only 3 to 4 cell layers thick around the embryo sac and 6 to 7 cell layers thick around the micropyle. It alone forms the straight micropyle. The o.i. is 14 to 15 cell layers thick at the lower portion and 10 to 13 layered at the upper region. The o.i. is rather well developed and prominent on the raphe side (Fig. 11F), but not as completely fused with the raphe as it is in most other species of Lecythidaceae. The junction between the i.i. and the o.i. is at the base of the nucellus (Fig. 11F). There are 8 to 11 small to medium-sized vascular bundles in the o.i. and a thick bundle in the raphe as seen in the cross section of the ovule through its embryo sac (Fig. 11D). The bundle of the raphe branches before and after entering the chalaza.

## Gustavia hexapetala (Aublet) J. E. Smith

The androecium of this species is actinomorphic (Fig. 11 A-E in Prance & Mori, 1979).

1. Androecial initiation.

In young floral buds numerous staminal primordia appear in whorls centripetally (Fig. 4C).

2. Development and mature structure of anther.

The stamens of species of Gustavia are characterized by their relatively long, poricidally dehiscent anthers. In this species, The sporogenous tissue contains very numerous cells. Young anthers have an acute apex which is the protruded tip of the connective (Fig. 12A). Anther wall formation follows the Basic-type. After the original two middle layers are produced, cells in the inner middle layer often divide periclinally one more time, thus three middle layers are present in the anthers. The tapetal cells contain 2 nuclei before meiosis of the microsporocyte begins. The tetrads are mostly tetrahedral. The tapetum remains intact even after the microspores are released from the callose wall (Fig. 12B). Starting at the sporocyte stage, all endothecial cells are filled with tannin. Tannin also occurs in the cells of the cortex of the filament. During the free spore stage, starch granules accumulate in all wall layers of the anther as well as in the connective and the filament (Figs. 12B, 12C).

Before anthesis, the septum between the two adjacent sporangia dissolves, and two pores form at the apex of the anther, one on each side of the connective. The anthers are basifixed. Mature anthers are rounded to rectangular in cross section. The epidermis is persistent and is covered by a spiny, thick cuticle (Fig. 12D). The endothecium around the two adjacent sporangia forms a continuous arc (Fig. 12B). The secondary thickenings on the endothecial cells are reticulate (Fig. 12D). The outer middle layer is persistent, and contains starch granules and sometimes tannin also. The inner middle layer may or may not be present (Fig. 12D). The connective is rather broad and contains starch granules and/or tannin inside its cells. The filaments are thick but conspicuously collapsed in the cortical portion (Fig. 12C). The epidermal layer of the filament is also covered with a layer of spiny cuticle.

3. Development of ovule.

There are six carpels in this species. The placenta develops from both sides of the ventral slit of each carpel. The ovule primordia are arranged in 4 longitudinal rows on the placenta, 2 rows on each side of the ventral slit. In young ovules, both the i.i. and the o.i. initiate dermally with the i.i. always initiating development first Fig. 12E). The funiculus and the chalaza are massive. One archesporial cell is differented from the subdermal layer in each nucellus (Fig. 12E). At the megasporocyte stage, the

nucellus becomes much more slender. The archesporial cell functions directly as the megasporocyte without cutting off a parietal cell. The i.i. encloses the nucellus, and is about 3 cell-layered around the nucellus and 4 cell-layered around the micropyle. The o.i., which is 5 to 6 cell layers thick, is shorter but thicker than the i.i. There are 3 or 4 rows of nucellar cells below the megasporocyte when viewed in l.s. (Fig. 12F). At meiotic stage, the ovules have turned 360°, but in most of them, the axis connecting the chalaza, nucellus and micropyle is arc-like. The tetrads are linear. Both integuments have become much thickened. The i.i. and the o.i. are 6 to 7 and 15 cell-layered, respectively, at the nucellar region, and 5 to 6 and 7 to 9 cell-layered, respectively, at the micropylar region. The inner epidermal cells of the i.i. show radial elongation, but do not contain very dense cytoplasm as is typical of endothelial cells. After meiosis, the chalazal megaspore undergoes embryo sac formation following the Polygonum type development.

4. Mature structure of ovule.

The mature ovules are elliptic to ovate and anatropous to campylotropous. All nucellar tissue is gone. The size of the embryo sac relative to the entire ovule is very small. Inside the embryo sac, the antipodal cells have degenerated. The i.i. does not thicken further after meiosis stage. However, the o.i. has increased to 22 to 24

cell-layered at the base and 17 to 19 cell-layered at the apex (Fig. 12G). The cells of the i.i. around the micropyle contain many starch granules. The surrounding o.i., also at the level of the micropyle, contains particles of an unknown composition which stain blue. The junction between the i.i. and the o.i. is at the middle of the embryo sac. There are 6 to 8 small vascular bundles in the o.i. and a thick bundle in the raphe as viewed in cross section.

## Cariniana micrantha Ducke

This species has a zygomorphic androecium. Stamens extend from the staminal ring, through the ligule, and onto the hood. The flowers are among the smallest of all Lecythidaceae s.l. The ovary of a mature flower is only 3.5 mm in diameter. There are some unique features in the development of the anther and ovule of this species, which might be influenced by the small flower size.

1. Development and mature structure of anther.

The developmental pattern of the anther wall in this species is probably at the end of a transition from the Basic-type to the Monocot-type. In an early stage, when the archesporial cells have differentiated, there are only epidermis and two parietal layers in the anther wall. Male gametogenesis relative to female gametogenesis seems much slower in comparison with other species examined. Before

meiosis, the outer primary parietal layer usually enlarges and functions directly as endothecium (Fig. 13B). Later, the inner primary parietal layer undergoes periclinal division to give rise to the middle layer and the tapetum, which conforms to the Monocot-type. Occasionally, some outer primary parietal cells also divide periclinally, and Basic-type of anther wall formation appears.

During embryo sac formation, the microsporocytes are only in the meiosis stage. It's noteworthy that the anthers in the staminal ring develop more or less synchronously, which contrasts with the obvious heterochrony in the development of the anthers of the hood. When the former are simultaneously dividing to form four nuclei, the latter are either at the beginning of meiosis, in four nucleate stage, or in the tetrad stage. During meiosis, the tapetal cells contain two nuclei. The tapetum is of glandular type. Only after meiosis do the endothecial cells begin to deposit secondary thickenings on their walls and starch granules inside their cells. Crystals are randomly distributed within the connective. Both ring and hood anthers complete the normal developmental processes and both possess mature anthers with the same structure.

At anthesis, the epidermis and the endothecium are persistent. The secondary thickenings on the endothecial cells are non-branching bands. The anthers are basifixed. The connective is short. Anthers are narrow but laterally

expanded in the direction perpendicular to the axis of the connective (Fig. 13A). The anther is latrorse with a medium to wide connective (Fig. 13A).

2. Development of ovule.

The i.i. is of dermal origin and develops before the o.i. which also is of dermal origin. The further development of the ovule is rather restricted by the limited space in the small locule. One archesporial cell emerges from the subdermal layer and functions directly as the megasporocyte (Fig. 13D). At the megasporocyte stage, the nucellus is very poorly developed, with only 2 rows of cells beneath the megasporocyte when viewed in l.s. The i.i. is only 3 cell-layered and does not enclose the nucellus, while the o.i. is 4 cell-layered and only 2 to 3 cells high. During meiosis, the tetrads are linear and the chalazal cell enlarges to form the embryo sac (Fig. 13E). At this time, the i.i. encloses the nucellus to form the micropyle. Embryo sac formation is of the Polygonum type. As the embryo sac develops, the outer epidermis of the i.i. and the inner epidermis of the o.i. enlarge (Fig. 13F). The 2 polar nuclei stay unfused in the center of the embryo sac for a very long time. The antipodal cells extend into the center of the basal nucellar tissue. However, with the further expansion of the embryo sac, both the basal nucellar tissue and the antipodal cells are crushed, and the innermost layer of the i.i. is destroyed (Figs. 13F, 13G).

3. Mature structure of ovule.

The ovules are anatropous and triangular-like in cross section (Fig. 13G). Within the embryo sac the egg apparatus and one central cell with two fused nuclei are present (Fig. 13F). The i.i. alone forms the micropyle. The i.i. is only 3 cell-layered around the embryo sac and 4 to 5 cell-layered around the micropyle. The o.i. is 5 cell-layered with a rather enlarged inner epidermis and a tannin-containing outer epidermis. The junction between the i.i. and the o.i. is slightly below the base of the embryo sac (Fig. 13F). There are three vascular bundles in the cross section of the ovule, one in the raphe and two in the o.i. Each bundle occupies an angle of the triangle-like ovule (Fig. 13G).

## Bertholletia excelsa Humboldt & Bonpland

This species has a zygomorphic androecium (Fig. 45 in Mori & Prance, 1990). Stamens are present in the staminal ring only.

1. Development and mature structure of anther.

The young anthers have a protruded connective tip which is unusual in the zygomorphic-flowered genera of Lecythidoideae. The connective is rather wide at early stages of development. The anther wall consists of epidermis, endothecium, two middle layers, and tapetum. It follows the Basic-type formation. At the beginning of

meiosis, the connective has become reduced in size in relation to the rest of the anther, and the tapetal cells are binucleate (Fig. 14A). During meiosis, the development of the staminal ring anthers are not synchroneous. While most anthers of the anterior side (anti-ligule side) are still in the tetrad stage, the anthers of the posterior side (ligule side) have mostly advanced into the free spore stage. The tapetum is of the glandular type (Fig. 14B). The endothecium actively elongates and then develops rod-like secondary thickenings on its walls (Fig. 14C). The filaments are filled with starch granules. Mature anthers are latrorse, with a very narrow connective (Fig. 14C). Only epidermis and endothecium are present at maturity. The filaments contain no starch granules.

2. Development of ovule.

The i.i. initiates from dermal cells. The archesporial cell differentiates from the subdermal layer before the o.i. has initiated (Fig. 14D). The histological source of the latter is unknown. Meiosis of the megasporocyte proceeds earlier than that of microsporocyte. The ovule is tenuinucellate (Fig. 14F). During meiosis, linear tetrads are formed. The i.i. encloses the nucellus and forms a rather long micropyle. The i.i. is 4 to 5 cell-layered. The o.i. is shorter but thicker, being 6 to 8 cell-layered at the base and 5 cell-layered at the apex of the ovule. After meiosis, the three micropylar megaspores degenerate

and the chalazal one undergoes embryo sac formation following Polygonum-type development. The newly produced antipodal cells penetrate into the basal nucellar tissue. However, both antipodal and nucellar cells are totally destroyed by the expanding embryo sac (Fig. 14G).

3. Mature structure of ovule.

At maturity, the ovules are anatropous and elliptic to ovate in shape. The embryo sac contains the egg apparatus and the central cell only. The i.i. is 7 to 8 cell-layered around the embryo sac and 6 to 7 cell-layered around the micropyle. The i.i. alone forms the micropyle. The o.i. is especially thick, 20 to 24 cell-layered at the base and slightly thinner towards the apex. The inner epidermis of the o.i. becomes especially enlarged. The junction between the i.i. and the o.i. is much lower than the base of embryo sac (Fig. 14G). There are three vascular bundles in the cross section of the ovule, one in the raphe and two in the o.i. (Fig. 14E).

## Corythophora amapaensis Pires ex Mori & Prance and C. rimosa W. Rodrigues

Both species have zygomorphic androecia (Fig. 42 in Mori & Prance 1990 for C. amapaensis and Fig. 44 in Mori and Prance, 1990 for C. rimosa). C. amapaensis has relatively few anthers on the hood. In this species the anthers of

the ligular side of the staminal ring are yellow, in contrast to the white ones of the remainder of the ring. The appendages of the hood of C. rimosa bear numerous anthers which are yellow, whereas the anthers of the staminal ring are entirely white. The buds and flowers of these two species were difficult to section because of the abundance of fibers. Consequently, most prepared sections failed to provide good information, and the following description is very incomplete.

1. Androecial initiation in C. rimosa.

The ring anthers initiate centrifugally. The hood anthers initiate from the apical part of the young hood from the interior end outwards (centrifugally) (Fig. 15B). .

2. Mature structure of anther in C. amapaensis.

The anthers of the hood and the ring stamens have the same structure, but the ring stamens have longer filaments. The anther wall maintains an intact epidermis and an endothecium. The latter possesses rod-like secondary thickenings on its cell walls. Although the two middle layers are crushed, they are still discernable. The anthers are basifixed and latrorse, and the connective is very narrow (Fig. 15A).

3. Mature structure of ovule in C. amapaensis.

The ovule is long ovate. Antipodal cells are not present, and the nucellar tissue is totally destroyed. The micropyle is formed by the i.i. only, which is 5 cell-

layered around the embryo sac and 3 cell-layered around the micropyle. The o.i. is 8 to 10 cell-layered around the embryo sac and 6 to 7 cell-layered around the micropyle. The o.i. is slightly shorter than the i.i.. The junction between the o.i. and the i.i. is lower than the embryo sac.

4. Young ovule of C. rimosa.

Ovule primordia appear on the slope of the expanded axis (Fig. 15C). Ovule primordia are trizonate.

5. Mature structure of ovule in C. rimosa.

During late developmental stages, epidermal cells of placenta facing micropyles are specialized and develop derivatives called obturators (Fig. 15D). The ovules are long ovate, and the nucellus is totally absent. The i.i. alone forms the micropyle. The i.i. and the o.i. are 5 to 6 and 7 to 8 cell-layered, respectively, around the embryo sac portion and 6 and 5 to 6 cell-layered, respectively, around the micropylar portion (Fig. 15E). The o.i. is slightly shorter than the i.i. There are three vascular bundles present in cross section of the ovule at the embryo sac.

## Couratari oligantha A.C. Smith

Couratari oligantha has a zygomorphic androecium, but only the ring stamens are fertile. The hood stamens are modified glands.

1. Development and mature structure of anther.

The staminal ring around the style is a reversed triangular in l.s. (Fig. 16A). Anthers are basifixed. Early stages of anther wall development were not recorded. When the microsporocytes are enclosed in the callose wall, the anther wall consists of an epidermis, an endothecium, 2 or 3 middle layers, and binucleated tapetum (Fig. 16C). The stamens are distributed in the staminal ring and at the base of the ligule. All anthers have the same structure and are similar sized at this stage. However, at meiosis stage, there is obvious heterochrony in anther development. The ring anthers close to the ligule and furthest away from the style develop more slowly. A transitional sequence of developmental stages from the microsporocyte stage, to the tetrad stage, and then to the free spore stage is observed when one exams anthers sequentially from the ligule towards the style (Fig. 16B). However, on the anterior side (i.e., the side opposite the ligule of the same bud), all anthers are at tetrad stage. The tetrads are usually tetrahedral. All anthers complete the whole developmental process, and there are no significant differences among them at maturity. The tapetum is of the glandular type (Fig. 16D). After the free spore stage, when the endothecial cells enlarge to their full size, secondary thickenings begin to develop. Those connective cells adjacent to the locules are filled with many starch granules, but the granules gradually

disappear before anthesis.

The antherless appendages of the hood coil are morphologically reduced and modified stamens. In late stages of development, all the parenchymatous cells of the hood, staminal ring, and even the petals are filled with starch granules. As development progresses to maturity, the parenchymatous tissues of these floral organs, especially in the hood, begin to degenerate to form cavities. Although the epidermis and the subdermal layer of the hood remain intact, their starch granules gradually disappear. The development of the appendages at the apex of the hood is different. The cells of these appendages remain intact. They possess thick cytoplasm, a large nucleus, and abundant starch granules throughout.

Most of the mature anthers are latrorse. However, a few are introrse. The connective is rather wide as viewed in cross section. The epidermis is persistent and the endothecium possesses non-branching, rod-like secondary thickenings.

2.Development of ovule.

The ovules are tightly packed within the locules from very early development. Consequently, development of the ovules is restricted by the available space. The initiation of the i.i. and the o.i. was not observed. Only one archesporial cell develops in each nucellus from the subdermal layer. This archesporial cell functions directly

as the megasporocyte without cutting off a parietal cell. At the megasporocyte stage, the i.i. is about 3 cell-layered and has not enclosed the nucellus. The o.i. is 5 cell-layered and about the same height as the i.i. The nucellus is slender. There are 4 rows of cells beneath the megasporocyte when viewed in l.s. (Fig. 16E). During meiosis, linear tetrads are formed (Fig. 16F). Meiosis of the megasporocyte occurs earlier than that of the microsporocyte.

Embryo sac formation follows the Polygonum type. The entire process was observed. When the embryo sac expands rapidly, the nucellus and the inner epidermis of the i.i. are damaged. A hypostase is formed (Fig. 16G). The 2 polar nuclei of the central cell fuse with each other very late.

3. Mature structure of ovule.

The mature ovules are anatropous, with various shapes, ranging from very elongated to ovate. The thickness of the o.i. varies from 7 to 8 cell-layered in some ovules to 15 to 17 cell-layered in others. The thickness of the i.i. is much more constant. It is 5 to 6 cell-layered around the embryo sac, 8 cell-layered just above the nucellus, and 4 cell-layered at the micropylar region. The i.i. alone forms the straight micropyle. The junction between the i.i. and the o.i. is below the base of nucellus (Fig. 16H). In mature ovules, some basal nucellar tissue and the hypostase remain (Fig. 16H). Antipodal cells are not present in the

embryo sac. The raphe bundle enters through the chalaza into the o.i. without any branching, thus only two vascular bundles appear in cross section of the ovule.

## Couroupita guianensis Aublet

Couroupita guianensis has a zygomorphic androecium (Fig. 36 in Mori & Prance, 1990). Both ring and hood stamens have normal looking anthers and produce pollen. However, the pollen of the ring is in monads and has a relatively smooth exine surface, whereas that of the hood remains in tetrads and has a relatively rough exine surface (Jacques, 1965; Mori et al., 1980). My study of this species is very incomplete. Some information described by Thompson (1921) is referred to here.

1. Development and mature structure of anther.

According to Thompson (1921) the staminal primordia from the hood initiate later but appear much more massive than the staminal primordia of the ring. By the time all wall layers and the sporogeneous tissue have differentiated, both ring and hood anthers have reached the same level of maturity. Both types of anthers possess an epidermis, an endothecium, 3 middle layers, and a tapetum. The hood stamens have larger filaments and anthers than those of the ring.

Meiosis in both types of anthers was not observed by

Thompson (1921) or by me. After the microspores are released from the callose wall in the ring anthers, the tapetum is intact (Fig. 17A). It has very dense cytoplasm and its nuclei are not distinguishable. Two pressed middle layers in the ring anthers were found in my sample. At the early free spore stage, the endothecium is quite enlarged but without fibrous thickenings.

At anthesis, the ring anthers possess only the epidermis and the endothecium (Fig. 17B). The cells of the latter have become much elongated and possess non-branching bands on their cell walls. The ring anthers are basifixed, typically latrorse, and with a narrow connective (Fig. 17C). The anatomy of the hood anthers was not investigated in this study. Thompson (1921) has recorded that mature hood anthers produce more numerous and larger monad pollen grains than the ring anthers. Interestingly, he did not discover any tetrad pollen grains in the hood anthers of this species. Tetrad pollen is the most dominant type in the hood anthers of this species as examined by Mori et al. (1980) and myself (see chapter III).

2. Development and mature structure of ovule.

The stages before embryo sac formation were not observed. During embryo sac formation, the first and the third cell divisions proceed as in the Polygonum type. The ovule is oblong, and the embryo sac is small. The i.i. and the o.i. are 4 and 5 to 6 cell-layered respectively (Fig.

17E). At maturity, the embryo sac is rounded and has considerably expanded. Nucellar tissue is totally destroyed. The inner epidermis of the i.i. has slightly enlarged and contains dense cytoplasm (Fig. 17F). The raphe bundle enters the anti-raphe side of the o.i. without branching (Fig. 17D). The i.i. alone forms the micropyle. The junction between the i.i. and the o.i. is at the base of nucellus (Figs. 17E, 17F).

Eschweilera sessilis A.C. Smith & E. cyathiformis Mori

My material of E. sessilis was so seriously dehydrated that most prepared sections were unsatisfactory for observation. Both species have an expanded and completely coiled androecium. Anthers are absent from the hood.

1. Development and mature structure of the anther of E. sessilis.

In mature anthers, the epidermis and the endothecium are persistent. The latter possesses non-branching, rod-like secondary thickenings. Both middle layer(s) and tapetum are absent. The connective is very narrow. A small vascular bundle is located between the two pairs of sporangia. The anthers are latrorse.

2. Development and mature structure of the ovule of E. sessilis.

Only mature ovules were observed. The ovules of E.

sessilis are small and elliptic to somewhat oblong. The nucellus is totally destroyed. The embryo sac is of irregular shape because of the uneven and local breakdown of the inner epidermis of the i.i. Inside the embryo sac, only the egg apparatus and the central cell persist. The i.i. at this stage is only 2 or 3 cell-layered around the embryo sac but retains 5 to 6 cell layers around the micropyle. The straight micropyle is formed by the i.i. only. It's shorter than that of other Lecythidoideae. The o.i. is 7 cell-layered at the base and 9 cell-layered at the apex. The innermost layer of the o.i. is rather thickened. The junction of the i.i. and the o.i. is at the same level as the base of nucellus.

3. Development and mature structure of the anther of E. cyathiformis.

Very early development stages were not observed. Before meiosis, the anther wall consists of an epidermis, an endothecium, 2 middle layers, and a tapetum. During meiosis, the microspore tetrads are tetrahedral. After the microspores are released from the callose wall, the tapetum is still intact. The epidermis and the endothecium are about the same thickness. In mature anthers, the epidermis and the elongated endothecium persist. The latter possess rod-like secondary thickenings on its cell walls. The anthers are latrorse with a narrow connective as viewed in cross-section (Fig. 18C). The hood tissue became

disintegrated and porous (Fig. 18B), except that the apical finger-like appendages remained intact (Fig. 18A).

4. Development of the ovule in E. cyathiformis.

The ovules of E. cyathiformis are peculiar in their orientation. Their funiculus is usually short and stout. The funiculus is not always perpendicular to the placenta, nor the raphe to the funiculus (Fig. 18D). At the microsporocyte stage, the nucellus is slender and poorly developed. The single megasporocyte is subdermal at the apex of nucellus. No trace of any preexisting parietal cells is found superjacent to the megasporocyte, suggesting the normal tenuinucellate nature in the Lecythidoideae. Below the megasporocyte there are few nucellar cells when viewed in longitudinal section. The i.i. is 3 to 4 cell-layered thick, and the o.i. is 5 to 7 cell-layered. The i.i. alone encloses the nucellus, forming a short and straight micropyle. During meoisis, linear tetrads are formed. The three micropylar megaspores degenerate. Embryo sac formation follows the Polygonum type. At this stage, the i.i. has increased to 6 to 7 cell-layered, and the o.i. to 8 to 9 cell-layered (Fig. 18E).

## Lecythis corrugata Poiteau

Lecythis corrugata has a zygomorphic androecium. Stamens are limited to the staminal ring. Stamens nearest

to the ligule have yellow anthers, whereas those of the remainder of the staminal ring are white.

1. Androecial initiation of ring stamens.

Staminal primordia around the style initiate centrifugally (Figs. 4D-F). There are basically five whorls of stamens on the ring. When the innermost ones have differentiated anther and filament, the outermost ones have just emerged. Appendages of the hood initiate as early as the hood and the sequence of their appearance is also centrifugal.

2. Development and mature structure of anther.

Anther wall development follows the Basic-type, and only two middle layers are produced. From early development, the epidermal cells are enlarged and filled with tannin which is also present in the filaments and the staminal ring. The development of stamens on the anterior side is faster than that on the posterior side. In addition, those anthers closer to the style grow faster than those away from the style. On the anterior side, when the former are mostly in the free spore stage, the latter are still in meiosis or in the microsporocyte stage (Fig. 19C). At this time, the stamens near the ligule from the same flower are mostly in their meiotic or microsporocyte stages (Fig. 19B). The tetrads are tetradhedal. At this stage, the tapetal cells are binucleate, and both the epidermis and the endothecium are filled with tannin. After the microspores are released

from the callose wall, the tapetum is still intact. At this time, the tannin contents of the endothecial cells begin to degenerate, and secondary thickings first appear on their walls.

In late development, all anthers of a flower have no morphological or structural differences. At anthesis, the anther wall is covered with a thick and ornamented cuticle layer. Both epidermis and endothecium are present and may still contain scattered tannin deposits. The secondary thickenings on the endothecial walls are rod-like. The anthers are basifixed and latrorse. The connective is rather narrow as viewed in cross section. The hood is porous because of local breakdown of internal tissure. The sterile stamens are intact and contain abundant tannin.

3. Development of ovule.

The ovule primordia appear on the short slope of the thick but narrow axis (Fig. 19A). They begin to curve before the initiation of the nucellus and the integuments. The i.i. initiates from dermal cells. The o.i. emerges later, but its histological source was not observed. A single archesporial cell differentiates from the subdermal layer of a poorly developed nucellus. The i.i. is only 3 cell-layered. The i.i. alone encloses the nucellus. The o.i. is a little thicker but much shorter. The archesporial cell functions as the megasporocyte directly (Fig. 19D). During meiosis, the tetrads are linear. The i.i. is 5 to 6

cell-layered. The o.i. is 10 to 12 cell-layered around the nucellus and 8 to 9 cell-layered around the micropyle. The o.i. is the same height as the i.i. After meiosis, only the chalazal megaspore remains to undergo embryo sac formation via Polygonum type development.

4. Mature structure of ovule.

Mature ovules are mostly anatropous. Both the shape of the ovule and the thickness of the integuments are strongly influenced by available space in the locule. Most ovules are long ovate. The nucellus is totally destroyed. The embryo sac is basically elliptic, with an irregular margin because of localized damage on the inner epidermis of the i.i. Inside the embryo sac, only the egg apparatus and the central cell are present. The i.i is about 5 cell-layered, and the o.i. varies from 8 to 9 to 11 to 12 cell-layered. The micropyle is straight and rather long, and formed by the i.i. only. The junction between the i.i. and the o.i. is at the base of the embryo sac (Fig. 19E). Vasculature of the ovule is elaborate. The raphe bundle branches before or after entering the chalaza, into 6 to 8 smaller vascular bundles extending to the o.i. (Fig. 19F). At the apex of the micropyle, there is a kind of conducting fluid which fills the cavities between the placenta and ovules and the cavities in between those septa.

The two integuments show different colors when stained with Safranin O and Fast-Green. Cells in the i.i. are light

green while cells in the o.i. are red. The large nucleus and dense cytoplasm of the o.i. suggests that its cells are physiologically more active. In addition, the cells of the i.i. are smaller in size, have a large vacuole, and a small nucleus.

## Foetidioideae

### Foetidia oblique Blume

1. Development and mature structure of anther.

The formation of the anther follows the Basic-type. There are two middle layers in the anther wall (Fig. 20A). The sporogenous tissue occupies a rather broad area viewed in cross section of anther. Before meiosis, the epidermis and endothecium are filled with tannin (Fig. 20B). The parenchyma of the filaments also contains a large quantity of tannin. Meiosis stage was not observed. The tapetum is of the glandular type. The tannin deposits begin to decompose in both the epidermis and the endothecium when the microspores are released from the callose wall, but remain abundant in the connective (Fig. 20C).

At maturity, only epidermis and endothecium are present with or without some tannin. The endothecial cells are covered rod-like secondary thickenings. The anthers are dorsifixed and mainly introrse (Fig. 20B).

2. Development of ovule.

Young ovules are trizonate. At the time, when the nucellus and the i.i. begin initiation, the ovule has already curved into its typical anatropous position. The i.i. is initiated from several layers of dermal cells. Usually only one archesporial cell develops at the apex of the nucellus from the subdermal layer (Fig. 20D), but occasionally two cells develop. There are four rows of nucellar tissue below the archesporial cell as viewed in longitudinal section. From early development, the i.i. and the o.i. have already fused with each other for a short distance at their bases (Fig. 20D). Before meiosis, only one megasporocyte is differentiated in each nucellus. The ovule is tenuinucellate, rounded in shape. The nucellus is also rounded in contrast to the slender nucelli observed in most other species of Lecythidaceae s.l. Both integuments are thick and of the same length. Their basal parts are not distinguishable. The i.i. is 6 cell-layered and the o.i. is 5 cell-layered thick at the apex of the ovule (Fig. 20D). The tetrads are linear. Embryo sac formation was not observed. A well-developed endothelium is formed after meiosis. Its cells are radially elongated and contain very dense cytoplasm (Figs. 20E, 20F). Eight nuclei are present in the newly formed embryo sac. Some ovules are curved to somewhat campylotropous (Fig. 20F), while others are anatropous.

3. Mature structure of ovule.

The ovules are rounded to ovate at maturity, and a well-developed endothelium is present. Interior to the endothelium, a basal nucellus is still present (Fig. 20F). The three antipodal cells of the embryo sac degenerate. The i.i. and the o.i. are well fused along their lower halves, sometimes to such an extent that even the apical portions of the two integuments are indistinguishable from each other. The fused part is 15 to 17 cell-layered around the nucellus. The upper short segment of the i.i. is about 4 to 5 cell-layered and that of the o.i. is about 6 to 7 cell-layered (Fig. 20F). There are 4 to 5 vascular bundles present in the o.i. and one in the raphe (Fig. 20E). The epidermal layer of the ovule is filled with tannin.

## Napoleonaeoideae

### Asteranthos brasiliensis Desfontaines

1. Development of anther.

Young anthers have an acuminate tip caused by the protruded connective (Fig. 21A). Anther wall formation is of the Basic-type, and there are usually three middle layers (Fig. 21C). During meiosis, the tapetal cells are three or four nucleate, and the endothecium starts to enlarge. The tetrads are mainly tetrahedral. After the microspores are

released, the tapetum remains intact (Fig. 21B). The endothecial cells start to develop non-branching, rod-like secondary thickenings.

In the mature anthers, only the epidermis and the endothecium persist. The anthers are basifixed and introrse.

2. Development of ovule.

The ovule primordium is trizonate (Fig. 22A). Both the i.i. and the o.i. are of dermal origin (Fig. 22B). The i.i. initiates earlier than the o.i. Only one archesporial cell develops from the subdermal layer in each nucellus (Fig. 22C). It functions directly as the megasporocyte without cutting off a parietal cell (Fig. 22D). At the megasporocyte stage, the ovule has turned into the anatropous position. The nucellus is slender and with 3 to 4 rows of cells below the megasporocyte as viewed in longitudinal section. The i.i. encloses the nucellus and forms a straight micropyle. The i.i. is about 3 to 4 cell-layered and the o.i. is 4 cell-layered (Fig. 21D, 22D). Meiosis results in linear tetrads (Fig. 21E). The chalazal megaspore enlarges to begin the embryo sac formation. During meiosis, the inner epidermis of the i.i. differentiates into a typical endothelium, the cells of which elongate radially and contain dense cytoplasm (Fig. 21E). Embryo sac formation is of the normal Polygonum type.

3. Mature structure of ovule.

The mature ovules are elongated and anatropous. The nucellus is oblong but mostly destroyed except for its basal part. The embryo sac contains the egg apparatus and the central cell but no antipodal cells. The endothelium is persistent. The i.i. is 4 to 5 cell-layered around the embryo sac and 5 to 7 cell-layered around the micropyle. The elongated micropyle is formed by the i.i. only. The o.i. is usually 6 to 8 cell-layered (Fig. 21F). Vasculature in the ovule is elaborate. There are 6 to 8 bundles in the o.i. and one in the raphe as viewed in cross-section through the embryo sac. The junction of the i.i. and the o.i. is at the base of the nucellus.

## Crateranthus c.f. talbotii Baker

Early stages of development were not observed.

1. Development and mature structure of anther.

The anther is sagittate and very long. Four sporangia are embedded in the thick connective. The specialized endothecium forms a complete circle except for the two short discontinuities at the sites of stomia (Fig. 23A). This specialization of the subdermal layer also extends from the anther into the filament.

Before meiosis, there is usually an epidermis, endothecium, 3 middle layers, and a tapetum. When the

microspores are released from the callose wall, the tapetum is intact (Fig. 23A). An abnormal situation is that the cytoplasm of parts of the tapetal cells is ejected into the locule and the locule is filled with the cytoplasm (Fig. 23B). Sometimes the cytoplasm of the tapetum is dispersed in the locule, even though the cell wall is still intact and the nuclei are still included. At this stage, the wall layers (except the tapetum) and the connective are filled with large quantities of tannin. When the anthers are nearly mature, the endothecial cells have rod-like secondary thickenings on their walls (Fig. 23C). These bands stained deep red. Such a strong reaction between the secondary thickenings and Safranin-o is uncommon in Lecythidaceae s.l. The anther is basifixed, latrorse, usually rectangular in cross section, and with a rather broad connective in the cross-section. The vascular bundle is located in the center of the connective.

2. Development and mature structure of ovule.

The earliest stage observed was the end of meiosis. Linear tetrads are formed, and only the chalazal megaspore enlarges (Fig. 23D). Because the megasporocyte is situated in the subdermal layer at the apex of nucellus and no traces of parietal cells were found, the ovule is most likely tenuinucellate. At meiosis, the endothelium is well developed. Soon after embryo sac formation, the three antipodal cells degenerate, and the two polar nuclei fused.

When the ovules are mature, they are very long elliptic and flat. Nucellar tissue is totally absent, but the endothelium is still present. The micropyle is very long. It is longer than half the length of the ovule. Four or five rows of very slender cells of the i.i. form the micropyle (Fig. 23D). The i.i. is thicker (8 cell-layered) around the base of the embryo sac. The o.i. is slightly shorter than the i.i. and 16 to 18 cell-layered toward the base and 22 to 24 cell-layered toward the apex. Their junction is at the base of the nucellus (Fig. 23D). The raphe bundle enters the o.i. without branching (Fig. 23E).

## Napoleonaea cf. vogelii Hooker & Planchon

1. Development and mature structure of anther.

The anthers are bisporangiate and triangular in cross section (Fig. 24C). The connective is rather thick and penetrated by a single unbranched vascular strand. The two sporangia are extrorse at initiation. However, as the filament elongates, it turns 360° thereby placing the two sporangia toward the gynoecium while the connective faces outwards.

Young anthers possess an epidermis, an endothecium, two or three middle layers, and a tapetum (Fig. 24A). However, anther wall development was not observed. The sporangia are very large and elongated. In each sporangium there are very

numerous microsporocytes. Before meiosis, the tapetal cells have greatly enlarged and are binucleate (Fig. 24A). During meiosis, both tetrahedral and bilateral tetrads are present. When the microspores are separate from the tetrads, the tapetal cells are persistent, and each contains 3 to 6 nuclei of unequal size. No periplasmodium is formed. The tapetum is of glandular type (Fig. 24B).

After meiosis, the endothecium begins to elongate and then develops secondary thickenings. At anthesis, the connective between the two sporangia breaks down completely to produce a one-celled anther. The line of dehiscence is very long. The two inner surfaces of the anther wall nearly form a 180 degree angle and the smooth endothecium is clearly visible (Fig. 24D). Mature anthers possess an epidermis and an endothecium with rod-like, fibrous thickenings on the walls.

2. Development of ovule.

At the beginning of development, when nucellus and integuments are just discernible, the ovule has already turned into the anatropous position. Both integuments initiate simultaneously from dermal cells. The two integuments fuse with each other as they develop.

Only one archesporial cell differentiates from each nucellus. At the megasporocyte stage, the ovules are rounded to oblong. The i.i. encloses the nucellus and the o.i. is slightly shorter than the i.i. In some ovules, the

basal parts of the i.i. and the o.i. are histologically fused (by intercalary growth). The upper parts of both the i.i. and the o.i. are about 4 to 5 cell-layered. The i.i. is slightly higher than the o.i. (Fig. 24E).

The archesporial cell functions directly as the megasporocyte without cutting off a parietal cell (Fig. 24E). Meiosis of the megasporocyte and embryo sac formation were not observed. However, some ovules near maturity were studied. There was only one embryo sac in each of these ovules. Inside the embryo sac, the egg apparatus and the central cell were present in their normal positions. These nearly mature ovules are elliptic (Fig. 24F). The two integuments are not distinguishable in their lower parts. The i.i. is higher and alone forms the straight micropyle. The i.i. and o.i. are 9 to 10 cell-layered and 6 to 7 cell-layered, respectively, at their apical parts (Fig. 24F). The vascular bundle passes through the chalaza and enters into the o.i. without branching.

## Summary of Descriptions

Summaries of my embryological observations are presented in Table V for the Planchonioideae, Table VI for the Lecythidoideae, and Table VII for the Foetidioideae and Napoleonaeoideae. The 20 genera studied are rather similar to one other in both male and female embryological features. However, the relative configuration between sporangia and connective, as observed in cross section of the anther, the position of the vascular bundle in the connective, the presence or absence of tannin and/or starch granules in the anther (including the exact position and stages at which they are present), the thicknesses of and the degree of fusion of the two integuments, the fate of the antipodal cells, the vasculature of the ovule, and the further differentiation of the inner epidermis of the i.i. are features that vary. The following sections are summaries of the embryological features of Lecythidaceae s.l. before fertilization with an emphasis on intergeneric variations.

## Development of the anther

Differentiation of the anthers begins very early. Usually, before the ovule primordium initiates integuments and nucellus, four (two in Napoleonaea) microsporangia are

Table V

Embryological data of the genera of Planchonioideae.

| Features in anther \ Genus | Abdulmajidia | Barringtonia | Careya | Chydenanthus | Petersianthus | Planchonia |
|---|---|---|---|---|---|---|
| Tip of young anther | — | with | without | — | with | without |
| Anther wall formation | — | Basic | Basic | Basic | Basic | Basic |
| No.middle layers | — | 2-3 | 2 | 2-3 | 2-3 | 2 |
| Meiotic divisions | — | simultaneous | — | simultaneous | simultaneous | — |
| No. nuclei in tapetal cells | — | 2-4 | 2 | 2-4 | 2 | — |
| Tapetum type | glandular | glandular | — | glandular | glandular | — |
| Endothecial wall thickenings | rod-like | rod-like | rod-like | rod-like | rod-like | rod-like |
| Position of sporangia | latrorse | latrorse | latrorse | latrorse | introrse | latrorse |
| Features in ovule | | | | | | |
| No. carpels | 3 | 4 | 4 | 2 | 4 | 4 |
| Curvature in degree | 360° | 360° | 360° | 360° or 450° | 450° | 360° |
| Curvature pattern | anatropous (rare. campyl.) | anatropous | campylotropous (rare. anatr.) | anatropous | anatropous | campylotroup. (rare.anatr.) |
| Ovule primodium | — | trizonate | trizonate | — | trizonate | trizonate |
| i.i. initiation | — | — | dermal | dermal | dermal | dermal |
| o.i. initiation | — | — | dermal | — | dermal | dermal |

Table V continued

| Genus / Features in ovule | Abdulmajidia | Barringtonia | Careya | Chydenanthus | Petersianthus | Planchonia |
|---|---|---|---|---|---|---|
| Archesporium | 1-celled | 1-celled | 1-celled (occ. 2) | 1-celled | 1-celled | 1-celled |
| Nature of nucellus | tenuinucellate | tenui- | tenui- | — | tenui- | — |
| Magaspore tetrad | — | linear | linear | — | — | — |
| Embryo sac formation | Polygonum | — | Polygonum | — | Polygonum | — |
| Endothelium | not formed | not formed | formed | not formed | not formed | formed |
| Micropyle formation | i.i. | i.i. | i.i. | i.i. | i.i. | i.i. |
| Antipodal cells | ephemeral | ephemeral | ephemeral | ephemeral | ephemeral | ephemeral |
| Nucellar tissue in mature ovule | gone | gone | gone | gone | gone | gone |
| Thickness of i.i. | upper 7-8<br>lower 7-8 | 7<br>8-9 | 4<br>6 | 9-10<br>7-8 | 6<br>6-7 | 6<br>6-5 |
| Thickness of o.i. | upper 6-7<br>lower 12-14 | 9-10<br>11 | ariloid<br>10 | 18-21<br>15-16 | 7-8<br>9-10 | ariloid<br>8-9 |
| Vasculature in o.i. (in c.s.) | 7-10 v.b. | 9-14 | 3-4 | 2-4 | 6-8 | 2-4 |
| Junction of i.i. & o.i. | below the nucellus | below the nucellus | at the base of nucellus | at the base of nucellus | at midpoint of nucellus | at the base of nucellus |

Table VI--Part I

Embryological data of the genera of Lecythidoideae.--Part I. *Allantoma*, *Grias*, *Gustavia*, *Cariniana*, and *Bertholletia*.

| Genus / Features in anther | *Allantoma* | *Grias* | *Gustavia* | *Cariniana* | *Bertholletia* |
|---|---|---|---|---|---|
| Tip of young anther | — | without | with | without | with |
| Anther wall formation | — | Basic | Basic | Basic (Monocot) | Basic |
| No. middle layers | — | 2 | 2-3 | 2 (rare. 1) | 2 |
| Meiotic divisions | — | simultaneous | simultaneous | simultaneous | simultaneous |
| No. nuclei in tapetal cells | — | 2-3 | 2 | 2 | 2 |
| Tapetum type | — | glandular | glandular | glandular | glandular |
| Endothecial wall thickenings | rod-like | rod-like | reticulate | rod-like | rod-like |
| Position of sporangia | latrorse | introrse | poricidal dehiscing | latrorse | latrorse |
| Features in ovule | | | | | |
| No. of carpels | 4 | 4 | mostly 6 | 3 | 4 |
| Curvature pattern | anatropous | anatropous, | anatropous, campylotropous | anatropous | anatropous |
| i.i. initiation | — | dermal | dermal | dermal | dermal |
| o.i. initiation | — | dermal | dermal | dermal | — |

Table VI--Part I continued

| Features in ovule \ Genus | Allantoma | Grias | Gustavia | Cariniana | Bertholletia |
|---|---|---|---|---|---|
| Archesporium | — | 1-celled | 1-celled | 1-celled | 1-celled |
| Nature of nucellus | tenuinucellate | tenui- | tenui- | tenui- | tenui- |
| Megaspore tetrad | — | — | linear | linear | linear |
| Embryo sac formation | — | — | Polygonum | Polygonum | Polygonum |
| Endothelium | not formed | not formed | not formed | not formed | not formed |
| Micropyle formation | i.i. | i.i. | i.i. | i.i. | i.i. |
| Antipodal cells | ephemeral | persistent in chalaza | ephemeral | ephemeral | ephemeral |
| Nucellar tissue in mature ovule | gone | basal tissue remained | gone | gone | gone |
| Thickness of i.i. | upper 5<br>lower 5-7 | 6-7<br>3-4 | 5-6<br>6-8 | 4-5<br>3 | 6-7<br>7-8 |
| Thickness of o.i. | upper 7-8<br>lower 8-10 | 10-13<br>14-15 | 17-19<br>22-24 | 5 | 20-24 |
| Vasculature in o.i. (in c.s.) | 6-8 v.b. | 8-11 | 6-8 | 2 | 2 |
| Junction of i.i. & o.i. | at the base of nucellus | at the base of nucellus | at the base of nucellus | at the base of nucellus | below the nucellus |

Table VI--Part II

Embryological data of the genera of Lecythidoideae. --Part II. Corythophora, Couratari, Couroupita, Eschweilera, and Lecythis.

| Genus / Features in anther | Corythophora | Couratari | Couroupita | Eschweilera | Lecythis |
|---|---|---|---|---|---|
| Tip of young anther | without | without | — | without | without |
| Anther wall formation | — | — | — | — | Basic |
| No. middle layers | 2 | 2-3 | 3 | 2 | 2 |
| Meiotic divisions | — | simultaneous | — | simultaneous | simultaneous |
| No. nuclei in tapetal cells | — | 2 | — | — | 2 |
| Tapetum type | — | glandular | glandular | glandular | glandular |
| Endothecial wall thickenings | rod-like | rod-like | rod-like | rod-like | rod-like |
| Position of sporangia | latrorse | latrorse | latrorse | latrorse | latrorse |
| Features in ovule | | | | | |
| No. of carpels | 2 | 3 | 6 | 2 | 4 |
| Curvature pattern | anatropous | anatropous | anatropous (occ. campyl.) | anatropous (occ. hemitr.) | anatropous |
| i.i. initiation | — | — | — | — | dermal |
| o.i. initiation | — | — | — | — | — |

Table VI--Part II continued

| Genus / Features in ovule | Corythophora | Couratari | Couroupita | Eschweilera | Lecyhtis |
|---|---|---|---|---|---|
| Archesporium | 1-celled | 1-celled | 1-celled | 1-celled | 1-celled |
| Nature of nucellus | — | tenuinucellate | — | tenui- | tenui- |
| Megaspore tetrad | — | linear | — | linear | linear |
| Embryo sac formation | — | Polygonum | — | Polygonum | Polygonum |
| Endothelium | not formed | not formed | not typical | not formed | not formed |
| Micropyle formation | i.i. | i.i. | i.i. | i.i. | i.i. |
| Antipodal cells | ephemeral | ephemeral | ephemeral | ephemeral | ephemeral |
| Nucellar tissue in mature ovule | gone | basal tissue persistent | gone | gone | gone |
| Thickness of i.i. | upper 3<br>lower 5 | 4<br>5-8 | 4-5 | 3-7 | 5 |
| Thickness of o.i. | upper 10<br>lower 8 | 7-10 | 5-6 | 6-7 | 8-11 |
| Vasculature in o.i. (in c.s.) | 2-4 v.b. | 1 | 1 | 5-6 | 6-8 |
| Junction of i.i. & o.i. | below the nucellus | at the base of nucellus | at the base of nucellus | at the base of nucellus | at the base of nucellus |

Table VII
Embryological data of the genera of Foetidioideae and Napoleonaeoideae.

| Genus | Foetidia | Asteranthos | Crateranthus | Napoleonaea |
|---|---|---|---|---|
| Features in anther | | | | |
| Tip of young anther | without | with | with | without |
| Anther wall formation | Basic | Basic | — | — |
| No. middle layers | 2 | 3 | 3 | 2 |
| Meiotic divisions | — | simultaneous | — | simultaneous |
| No. nuclei in tapetal cells | — | 3-4 | 2 | 3-6 |
| Tapetum type | glandular | glandular | glandular | glandular |
| Endothecial wall thickenings | rod-like | rod-like | rod-like | rod-like |
| Position of sporangia | introrse | latrorse | latrorse | extrorse |
| Features in ovule | | | | |
| No. of carpels | 3-4 | 5-6 | 3 | 5-6 |
| Curvature pattern | campylotropous (occ. anatrop.) | anatropous | anatropous | anatropous, campylotrop. |
| i.i. initiation | dermal | dermal | — | dermal |
| o.i. initiation | — | dermal | — | dermal |

Table VII continued

| Genus / Features in ovule | Foetidia | Asteranthos | Crateranthus | Napoleonaea |
|---|---|---|---|---|
| Archesporium | 1-celled (occ. 2) | 1-celled | — | 1-celled |
| Nature of nucellus | tenuinucellate | tenui- | tenui- | tenui- |
| Megaspore tetrad | linear | linear | linear | linear |
| Embryo sac formation | — | Polygonum | Polygonum | Polygonum |
| Endothelium | formed | formed | formed | not formed |
| Micropyle formation | i.i. | i.i. | i.i. | i.i. |
| Antipodal cells | ephemeral | ephermal | ephermal | ephermal |
| Nucellar tissue in mature ovule | basal tissue remained | basal tissue remained | gone | gone |
| Thickness of i.i. | 4-5 | 5-7 | upper 4-5 lower 8-9 | 9-11 |
| Thickness of o.i. | 6-7 | 6-8 | upper 22-24 lower 16-18 | 6-7 |
| Vasculature in o.i. (in c.s.) | 4-5 v.b. | 6-8 | 1 | 1 |
| Junction of i.i. & o.i. | above the nucellus | at the base of nucellus | at the base of nucellus | above the nucellus |

already present. The primary parietal cells arranged in two layers situated between the sporogenous tissue and the epidermis will undergo two periclinal divisions to give rise to the endothecium, two middle layers, and the tapetum following the Basic-type of anther wall development (Fig. 3B). The only exception is Cariniana micrantha in which only one middle layer derived from the inner parietal layer is usually developed, which is confirmed to the Monocot-type anther wall development (Fig. 3B). In Cariniana micrantha this reduction of middle layers is probably caused by the extremely small flower size and concomitant reduced anthers. In one third of the genera (Barringtonia, Chydenanthus, Petersianthus, Gustavia, Couroupita, Asteranthos, Crateranthus), the inner middle layer may divide again into two middle layers which results in three middle layers. However, the two or three middle layers are soon crushed by the expanding sporogenous tissue. After the sporogenous cells have reached their full size, callose begins to accumulate in the immediate vicinity of the microsporocytes. At this time, meiosis begins.

Microsporogenesis is of relatively long duration in Lecythidaceae. Before or during meiosis, some Neotropical and African genera accumulate tannin in some sterile anther tissue, most commonly in the endothecium. The tapetal cells enlarge, before meiosis, but to a different extent in different genera. Without exception, the tapetal cells are

always smaller than the microsporocytes and normally undergo nuclear divisions. The number of nuclei normally present in the tapetal cells varies from two to six in different enera. The tapetal nuclei remain physiologically active during meiosis. Further divisions or fusions of nuclei occur. As a result, the size and number of nuclei in one tapetal cell is often inconsistent even in the same anther. Meiotic divisions of microsporocytes are of the simultaneous type. The tetrads formed are typically tetrahedral. However, small numbers of isobilateral and decussate tetrads are found (Fig. 3C). In the Planchonioideae, the successive developmental stages occur more or less synchronously in all anthers of a given flower. In contrast, in the zygomorphic genera of Lecythidoideae, as well as in the actinomorphic genus, Grias, the anthers of a single flower are more or less heterochronous in development. In the zygomorphic genera, the anthers of the ring stamens behave such that the ones situated closest to the style initiate and develop earliest (centrifugal development). When normal stamens are present on the hood, the ring anthers commonly develop faster than the hood anthers.

Subsequent to the disintegration of the callose walls and the release of microspores, the tapetum does not rupture immediately, except that in Allantoma lineata and Crateranthus cf. talbotii abnormal breakdown of tapetal cells may occur. This demonstrates that the tapetum of

Lecythidaceae s.l. is of the glandular type (Fig. 3D), which is conformable with Anisimova's study on Barringtonia and Couroupita (1985). Venkateswarlu (1952a) described the tapetum of Barrintonia acutangular and Napoleonaea imperialis as amoeboid. However, according to his description, the tapetal cells of these species maintain their cell walls intact, retain their nuclei, and simply release the cytoplasm, which is not typical for an amoeboid type tapetum (Fig. 3D). In Crateranthus, I observed many anthers with typical glandular tapetum as well as other anthers in the same flower in which the tapetal cells maintained their walls intact and retained the nuclei, but lost their cytoplasm into the locule. In other cases the tapetal cells broke down and released all their cytoplasm into the locule. The wall layers of these anthers displayed abnormal reaction to staining as well as many disrupted cells. Therefore, I suspect that these tapetal cells had plasmolyzed abnormally. Venkateswarlu's (1952a) observation of amoeboid tapetum may have been the result of similar abnormal lysis of the tapetal cells.

After meiosis, the initial development of the pollen grains, including the adding of sporopollenin on the primary pollen wall, cannot be observed with the LM. The developmental events observed in my study are mainly confined to the development of the endothecium and the appearance, distribution and disappearance of starch

granules in the anthers. In fact, the endothecia have already somewhat enlarged before the end of meiosis. But more prominent expansion, especially radially is often observed only after the end of meiosis. Those endothecial cells reach their full size very rapidly. In all 20 genera the endothecial cells undergo secondary thickenings. In the 19 genera with longitudinally dehiscent anthers, the secondary thickenings usually start to deposit on the inner tangential wall. In the sections of mature anther they appear as rod-like bands (Fig. 3E). However, reticulate-like thickenings on the endothecial walls (Figs. 3E, 12D) occur in the poricidally dehiscent and buzz-pollinated genus Gustavia. It is noteworthy that the chemical reactions of the endothecial secondary thickenings with safranin-o are uniformly weak, which perhaps indicates their cellulose rather than lignin composition (Bhandari, 1984), except that in Crateranthus the secondary thickenings stain red. With the exceptions of Gustavia and Crateranthus, the endothecia of the other 18 genera are derived from the primary parietal layer, and are confined to the abaxial side of each sporangium. In Gustavia (G. hexapetala), the endothecium is continous between the two adjacent sporangia. The endothecium of Crateranthus is of dual origin, partly derived from the primary parietal layer of the archesporium and partly from the subdermal layer of connective. This results in a specialized circular

subdermal layer which is disrupted only at the two stomia.

In development after meiosis, the appearance and disappearance of starch granules in the anthers is clearly due to the synthesis of the secondary thickenings of the endothecial walls. As a rule, the starch granules first appear in great amounts, either restricted to the connective such as in Abdulmajidia and Crateranthus, confined mostly to wall layers such as in Allantoma, Gustavia, and Cariniana, or widely distributed in both the anthers and hood as in Couratari and Eschweilera. The amount of starch granules is markedly reduced before anthesis. When the anthers mature and dehisce, only the epidermis and the endothecium are persistent. The only exception is in Gustavia which also possesses middle layers. Gustavia is also unusual in that the epidermis of its anthers is covered with a spiny cuticle layer at anthesis. In the Lecythidoideae, the connective and wall layers may still contain large amounts of tannin. The connectives of Allantoma and Cariniana contain scattered druce-like crystals.

Other features which exhibit a wide range of variation within each of the four subfamilies are the positions of sporangia in the anther, the relative cross sectional area of the connective compared with the cross sectional area of the entire anther. In the Planchonioideae, the cross section of the anther is 4-lobed. The anthers of Petersianthus quadrialatus are introrse, while the anthers

of the other five genera are latrorse. In Petersianthus and Chydenanthus, the relative area of the connective is wide and the vascular strand is usually located closer to the abaxial side of the connective. In the other four genera, the relative area of the connective is medium but never small, and the vascular strand penetrates the center of the connective. These two features display wider variation in the Lecythidoideae and even vary among the three actinomorphic genera. In Grias, the anthers are introrse and the two pairs of sporangia are widely separated. Gustavia has poricidally dehiscent anthers, with an anther somewhat rectangular in cross section, and a very broad connective. Allantoma has typically latrorse, 4-lobed, radially symmetrical anthers, and a wide connective. The seven zygomorphic genera are uniformly latrorse. Their anthers are slightly 4-lobed and radially symmetrical as viewed in cross section. The relative area of their connective in cross section varies from large (e.g., Cariniana), through medium (e.g., Couratari), to narrow (e.g., Bertholletia, Corythophora, Couroupita, Eschweilera and Lecythis).

## Development of the ovule

The embryological features of the gynoecium of Lecythidaceae s.l. are relatively homogeneous as compared to

other families of dicots. At the subfamiliar level, the 10 genera of Lecythidoideae are rather uniform. In contrast, the variation among the six genera of Planchonioideae and that among the three genera of Napoleonaeoideae is greater than that of the Lecythidoideae.

There are some unifying characteristics of the female embryology of Lecythidoideae s.l. at the familial level. The ovules are generally complex in structure and the nucelli are poorly developed. Ovule primordia are trizonate in those observed (Fig. 3F). The female archesporial cells usually differentiate later than the male ones of the same flower. In the ovule, it is the topmost one (rarely two) subdermal cell of the nucellus that develops as the archesporial cell. The differentiation of archesporial cells occurs at about the same time as the integuments begin to initiate. The archesporial cell enlarges rapidly and often destroys several cells adjacent to it.

For both the outer and inner integuments, the earliest indication of initiation is the periclinal division of a few dermal cells of the ovular primordium in the longitudinal section (Fig. 3G). Subsequently, subdermal cells may also join in the development of both integuments. Generally speaking, the i.i. initiates a little earlier than or simultaneously with the o.i. Considerable variation in the features of the female embryology of Lecythidaceae s.l. appear following the initiation of the integuments.

Venkateswarlu (1952a) reports a multicellular archesporium in Napoleonaea imperialis. However, my observations, with the exception of Careya, Foetidia, and Asteranthos which occassionally develop a two-celled archesporium in each nucellus, indicate that all other genera (based on one species each) are characterized by a single-celled archesporium. In any case, only one (even if two cells are present) archesporial cell will enlarge rapidly and occupy at least the upper one third of the nucellus and then function directly as the megasporocyte.

The nature of nucellus was not observed in four genera. In the other 16 genera the nucellus is characteristically tenuinucellate (Fig. 3I). In all genera, the nucelli are basically slender in the megasporocyte stage. The basal nucellar tissue consists of only three or four rows of cells situated below the megasporocyte as viewed in longitudinal section. In most other families characterized by tenuinucellar ovules, both the shape and the structure of the nucelli are different from those of Lecythidaceae s.l. For these taxa, the nucelli are extremely reduced at the megasporocyte stage, containing almost no extra nucellar tissue beneath the megasporocyte. This structure is what Mauritzon (1939a) considered as tenuinucellate. After a study of four genera of Lecythidaceae s.l., Mauritzon (1939a, p.80) concluded that, "The ovule is slightly crassinucellate," because the upper part of the nucellus

part of the nucellus is destroyed before fertilization while the basal part is retained. According to the current definitions of tenuinucellate and crassinucellate ovules (Davis, 1966; Johri, 1984), the ovules of Lecythidaceae s.l. in which the archesporial cell functions directly as the megasporocyte without cutting off a parietal cell should be considered "tenuinucellate."

In the material I studied, the meiosis of megasporocytes always results in linear tetrads (Fig. 3K). However, Venkateswarlu (1952a) reported both linear and T-shaped tetrads in Napoleonaea imperialis. The two dyads either divide synchroneously, or the upper divides first and is soon compressed. All cases of embryo sac formation observed follow the Polygonum type. The two polar nuclei either soon fuse with each other, or simply approach one another but remain unfused until the ovule nears maturity. The three antipodal cells are ephemeral in most genera of Lecythidaceae s.l. However, in Grias, Cariniana, Bertholletia, and Couratari, the three antipodal cells penetrate into the basal nucellar tissue. In Grias, the elongated antipodal cells connect with some central nucellar cells to form a pathway for conducting nutrients into the embryo sac (Fig. 11E). A hypostase is formed in Couratari oligantha (Fig. 16G). All the egg apparatuses observed were of normal structure. The egg cell and the two synergids are of about the same size. The egg cell is placed a little

closer to the central cell and possesses a distinct nucleus at its proximal end. The two synergids are positioned as a pair at the micropylar end. Each has a large vacuole at the proximal end, and a nucleus superjacent to the vacuole which is the same size as the nucleus of the egg cell. The filiform apparatus is always well developed thereby giving the micropylar end of the egg apparatus an acute apex.

During the early stages of embryo sac expansion, the nucellar tissure bordering the embryo sac is, without exception, totally destroyed. In the Planchonioideae, Foetidioideae, and Napoleonaeoideae, the endothelium evolves independently. One of the major functions of the endothelium, at least in this family, is to serve as a physical barrier to prevent possible damage to the inner integument caused by the expanding embryo sac. In those genera with a typical endothelium (Table V, VI, VII), the endothelium surround a well-defined, spindle-like or bell-like chamber (Figs. 9D, 20F, 21F, 23D). The expansion of the embryo sac seems to be confined within this chamber. In those genera in which the i.i. lacks a specialized endothelium, the inner epidermis is commonly damaged. In Petersianthus quadrialatus, Chydenanthus excelsus, and Gustavia hexapetala, a transitional stage is observed in which the inner epidermis of the i.i. expands, for the most part, in a radial direction, but the inner tangential wall does not possess a prominent cuticlar layer. The cytoplasm

of this epidermis is not especially dense, and the inner epidermal layer of the inner integument is usually destroyed before the ovule matures. I do not consider this as an endothelium. It surely represents a transitional stage in the evolution of a specialized endothelium. In some ovules of Couroupita guianensis, the inner epidermis of the i.i. not only increases in volume but the cytoplasm becomes more dense. Mauritzon (1939a) described this as a mantle-layer (endothelium). However, no thickened cuticle layer was noticed on the inner tangential wall. In some ovules with this specialized inner epidermis, the cells of this layer undergo periclinal divisions, a feature which does not take place in a typical endothelial cell. Thus, I do not consider this specialized inner epidermis of the i.i. of C. guianensis as a typical endothelium.

In Lecythidaceae s.l., the degree of complexity of the vasculature of the mature ovules varies greatly from genus to genus. A common feature is that the vascular bundle extends from the raphe, through the chalaza, to the anti-raphe side of the outer integument. With the exception of Couratari, Crateranthus, and Napoleonaea in which the trunk vascular bundle remains unbranched throughout its course, all genera have trunk ovular bundles which branch before entering the chalaza and/or after leaving the chalaza. When branching, the number of bundles in the outer integument varies slightly from ovule to ovule in the same

species, especially those species with tertiary branching.

The thicknesses and relationship of the two integuments also varies from genus to genus. The i.i. and o.i. are usually three to four cell-layered thick in the archesporial stage. In the early megasporocyte stage, or slightly later, the i.i. usually has completely enclosed the nucellus and forms the micropyle by itself. The o.i. is either slightly shorter than or as long as the i.i., but never longer than the i.i. However, a peculiar development is observed in Careya arborea and Planchonia careya in which the o.i. curves outwards around the micropylar region to form a long and reflexed collar at the stage of embryo sac formation (Figs. 3O, 7C, 9E). Mauritzon (1939a) described this structure in Careya arborea as an arilloid. However, the seeds of both Planchonia and Careya have never been described as arillate.

Both the i.i. and the o.i. increase their thicknesses throughout development. In mature ovules, the i.i. is mainly four to eight cell-layered, while the o.i. varies from six to seven to 22 to 24 cell-layered. In the same ovule, the thicknesses of both the i.i. and the o.i. are usually inconsistent from the lower to the upper portion (Table V, VI, VII). The i.i. and o.i. are closely appressed. In all genera studied but Petersianthus, Foetidia, and Napoleonaea, the i.i. and o.i. are histologically well separated throughout the entire

developmental stage of the ovule. The junction between them is usually situated near the base of the nucellus (or the embryo sac), or even lower as in Barringtonia and Bertholletia. In the species of Petersianthus, Foetidia and Napoleonaea examined, the i.i. and o.i. initiate individually. During the megasporocyte stage, the boundary between the two integuments (the two thick cuticle layers) begins to obscure in their lower portions, but with the border remains discernible. In late development, the boundary becomes hardly recognizable in the lower portion, or even disappears in the lower one half or two thirds of the ovule. However, at least the upper one third of the integuments of these three genera remains distinguishable until the very end of the existence of the integuments. Petersianthus, Foetidia ,and Napoleonaea are in transition from bitegmic to unitegmic ovules. In the species of these three genera examined the two integuments initiate at about the same time and are well developed individually. In Foetidia, the o.i. is always as long as the i.i. while in Napoleonaea the o.i. is always shorter.

The ovules of the genera of Lecythidaceae s.l. are mostly anatropous. All genera with apical-axile placentation have anatropous ovules (Fig. 3H). The more rounded ovules in the ovaries of genera with central-axile placentation are slightly curved into the micropylar region, resulting in campylotropous ovules, such as those of Careya,

Planchonia, Gustavia, Foetidia and Napoleonaea (Fig. 3H).

An unusual situation is found in Petersianthus in which some ovules have relatively long and curved funiculus. The entire ovule turns 450 degrees at maturity, thereby placing the micropyle perpendicular to, or directly facing, the funiculus. This specialized ovular orientation seems related to the restricted region of placenta on the central axis.

The ovules of all 20 genera of Lecythidaceae s.l. can be described as dorsally positioned, i.e., the funiculus is on the abaxial side, while the micropyle is on the adaxial side of the axis, regardless of the variation in placentation and ovular orientation relative to the placenta attachment.

## Discussion and Conclusion

The embryological features of Lecythidaceae s.l. demonstrate that those characters generally considered consistent at generic or higher ranks are rather homogeneously expressed in all genera. The family is characterized by the bitegmic-tenuinucellate ovule, the multicell-layered i.i. and o.i., the i.i. formed micropyle, one or more vascular bundles in the o.i., the Basic-type anther wall formation, and the glandular-type tapetum. Because none of these is autapomorphic for Lecythidaceae s.l., as in commonly the case in embryological features of

the angiosperms, embryology alone cannot be used to delimit the Lecythidaceae s.l.

My observations are in harmony with those of Mauritzon (1939a) and Anisimova (1985), with the exception that Mauritzon described the ovule of Lecythidaceae s.l. as "slightly crassinucellate." However, there are a few discrepancies between my observations and those of Venkateswarlu (1952a, 1952b). He observed both single-celled and multicelled archesporia in Napoleonaea imperialis, but I found only one archesporial cell in each ovule of N. cf. vogelii. In addition, he described the tapetum of both Napoleonaea and Barringtonia as amoeboid, with the tapetal cell walls and nuclei remaining intact but with the cytoplasm flowing out to form a periplasmodium. In my study, all the genera (each with at least one species represented), except Allantoma in which tapetal structure has not been determined, exhibit typical glandular-type tapeta.

A T-shaped megaspore tetrad and a reversed embryo sac which were recorded by Venkateswarlu (1952b) in Napoleonaea imperialis were not observed in this study.

## Interordinal relationships

Because of its peculiar combination of characters, Lecythidaceae s.l. was elevated as an order of its own by

Cronquist (1957) and a superorder of its own by Takhtajan (1986, 1987). The traditional placement of Lecythidaceae with the Myrtales and more recently near to the Malvales (Cronquist, 1981) is not supported by embryological features. The ten core myrtalean families are characterized by bitegmic, crassinucellate ovules, 2 cell-layered i.i., 2 or 3 cell-layered o.i., a micropyle formed from both integuments, and no vasculature in the integuments (Mauritzon, 1939a; Tobe & Raven, 1983; Yakovlev, 1985). All five core families of Malvales, Elaeocarpaceae (Mauritzon, 1935; Venkata Rao, 1953b), Tiliaceae (Sternar, 1925; Freiberg, 1983), Sterculiaceae (Venkata Rao, 1949-1953a), Bombacaceae (Venkata Rao, 1954a; Baker, 1960; Thirumalachan & Khan, 1941), and Malvaceae (Venkata Rao, 1954b; Chandra & Bhatnagar, 1976; Joshi et al., 1967) have bitegmic, crassinucellate ovules, a few cell-layered i.i. and o.i., a zig-zag micropyle formed by both integuments caused by the dominant growth of the o.i., and the vascular bundle ending at the chalaza. The differences between the embryological features of Lecythidaceae s.l. and those of the Myrtales negate close affinity between these two taxa. The same is applicable to the relationship between the Lecythidaceae s.l. and Malvales.

As far as I know, there are about 30 dicot families in which the B-T (bitegmic-tenuinucellate) ovule is either characteristic of the whole family or present at least in

some species (Davis, 1966; Yakovlev, 1981-1987). Philipson (1974) and Cronquist (1981) have noticed that this type of ovule is clearly more common in the Dilleniidae than elsewhere in the dicots. The distribution of B-T ovules within the Dilleniidae is as follows: Theales (Ochnaceae, Scytopetalaceae, Theaceae, Bonnetiaceae, Clusiaceae, Marcgraviaceae), Ebenales (Ebenaceae, Styracaceae), Primulales (Theophrastaceae, Primulaceae, Myrsinaceae), Violales (Frankeniaceae, Fouquieriaceae), Capparales (Resedaceae, Brassicaceae), and Nepanthales (Sarraceniaceae, Droseraceae, Byblidaceae). The B-T ovules found in other subclasses are in the following orders: Geraniales (Oxalidaceae, Tropaeolaceae, Limnanthaceae, Balsaminaceae), Linales (Linaceae), Celastrales (Celastraceae, Hippocrateaceae, Stackhousiaceae), Saxifragales s.s. (Parnassiaceae, Vahliaceae), Podostemales (Podostemaceae), Rafflesiales (Cytinaceae) and Piperales (Saururaceae).

Within the dicots, it is clear that the B-T ovule is derived from the B-C (bitegmic-crassinucellate) ovule, and that this evolution has occurred more than once in distinct lineages. Because the evolution of this feature (BC-BT) is conservative, usually unidirectional, and is found throughtout the dicots, beginning with supposedly more archaic and ending with supposedly more advanced dicot orders, it is extremely useful in helping to suggest the relationships between the Lecythidaceae with other families.

Among the orders mentioned above, the Violales, Capparales, Nepenthales, Geraniales, Linales, Celastrales, Saxifragales s.s., Podostemales, Rafflesiales and Piperales are collectively different from the Lecythidaceae s.l. in the following common embryological characters: a more reduced nucellus with no, or very little, basal nucellar tissue, both integuments usually two cell-layered; no vasculature in the integuments or vasculature is even absent in the funiculus; and the micropyle formed from either the o.i. or from both integuments in many species. In addition, the Lecythidaceae s.l. differ from those families in gross morphological characteristics as well. Many of them are chiefly or totally herbaceous groups. Some are extremely xerophytic or parasitic. It is propable that B-T ovules had evolved side by side with the unusual specialization or the reduction of reproductive structures in certain groups, or simply as a evolutionary product after a long enough period of evolution.

The Theales, Ebenales and Primulales are more similar to the Lecythidaceae s.l. in morphological and embryological features than are the previous orders. Approximately one-third of the families in the Theales, as broadly defined by Cronquist (1981), have not been surveyed embryologically. As expected from the heterogeneous morphology of the order, the embryology of the Theales is equally heterogeneous. Some thealean families are characterized by B-C (bitegmic-

crassinucellate) ovules, while some others are only known as U-T (unitegmic-tenuinucellate). The B-T ovules occur in all or some members examined from the following 6 families: Ochnaceae (Chiarugi & Francini 1929; Chikkanniah, 1954; Ghosh, 1964; Naumova, 1983), Scytopetalaceae (Vijayaraghavan & Dhar, 1976), Theaceae (Bala Bawa, 1970; Kapil & Sethi, 1963; Mathew, 1978; Wu, 1960), Bonnetiaceae (Davis, 1966; Kobuski, 1948; Prakash & Lau, 1976), Clusiaceae (Hoar & Haertl, 1932; Puri, 1939; Rao, 1957; Sokolovskaya, 1983), Marcgraviaceae (Mauritzon, 1939b; Swamy, 1948).

The Ebenales, as defined by Cronquist (1981), include five families, of which four have been examined embryologically. The Ebenaceae are characterized by B-T ovules (Nikiticheva, 1983; Woodburn, 1911; Yamazaki, 1972). Both B-T and U-T ovules are present in the Styracaceae (Mashard, 1936; Nikiticheva, 1983; Yamazaki, 1970a, 1972). The Symplocaceae (Gulati & Ravishankar, 1980; Nikiticheva, 1983; Yamazaki, 1970b) and Sapotaceae (Nikiticheva, 1983; Wood & Channel, 1960; Yamazaki, 1971) are characterized by U-T ovules.

In the Primulales, the Theophrastaceae are characterized by B-T Ovules (Dahlgren, 1916; Mauritzon, 1936). Both B-T and U-T are present in the Myrsinaceae (Carey & Fraser, 1932; Johansen, 1936; Mametyeva, 1983; Sankara Rao, 1972) and Primulaceae (Dahlgren, 1916; Mametyeva, 1983; Subramanyam & Narayana 1968). The naturalness of the

Primulales has never been questioned, and a close relationship to the Ebenales has been supported by many workers. These two orders are generally considered to have originated from somewhere within the broadly defined Theales, specifically around the Theaceae, as expressed in most contemporary dicot systems (Cronquist, 1981; Dahlgren, 1983; Takhtajan, 1987; Thorne, 1983).

It is probable that the B-T ovules of the Ebenales and Primulales are inherited from thealean-like ancestors. Unitegmic-tenuinucellate ovules probably then independently evolved within each order. Bouman (1984) suggested that there are four different mechanisms in the evolution of unitegmy in the dicots. Integumentary fusion has clearly played a role in the development of ovules with a single integument in at least the Ebenales and Primulales.

Among those 11 families with B-T ovules, the Lecythidaceae s.l. are embryologically most similar to the Ochnaceae, Scytopetalaceae, and Theaceae of the Theales s.l., as well as the Ebenaceae and Styracaceae of the Ebenales, especially in ovular structure. In addition to the common possession of B-T ovules, these families resemble each other in: the micropyle formed by the inner integument alone; the outer integument as long as inner integument; the nucellus slender with several rows of nucellar tissue beneath the megasporocyte; and both integuments multicell-layered (Table VIII). In the Bonnetiaceae and Clusiaceae of

Table VIII

A comparison of major embryological characters between Theaceae, Ochnaceae, Scytopetalaceae Lecythidaceae s.l., Ebenaceae, and Styracaceae.

| Family / Features in anther | Theaceae | Ochnaceae | Scytopetalaceae | Lecythidaceae s.l. | Ebenaceae | Styracaceae |
|---|---|---|---|---|---|---|
| No.middle layers | 1-3 | (1)-2 | 1-2 | (1)-2-(3) | 2 | 1 |
| Tapetum type | glandular | glandular | glandular | glandular | glandular | glandular |
| Mature pollen | 2-celled | 2-celled | 2-celled | 3-celled | 2-celled | 2-celled |
| Features in ovule | | | | | | |
| Archesporium | 1-celled | 1-celled (occ.2,3) | 1-celled | 1-celled (occ. 2) | 1-celled | 1-celled (occ. 2) |
| Embryo sac formation | Allium | Polygonum | Polygonum | Polygonum | Polygonum | Polygonum |
| Nature of nucellus | tenuinucellate | tenui- | tenui- | tenui- | tenui- | tenui- |
| No. integuments | 2 | 2 | 2 | 2 | 2 | 1, 2 |
| Micropyle formation | i.i. | i.i. | i.i. | i.i. | i.i. | i.i. |
| Thickness of i.i. | 4-5 | 3-5 | 4-6 | 4-8 | 9-11 | 5-7 |
| Thickness of o.i. | 5-6 | 3-6 | 8-12 | 6-24 | 10-20 | 10-20 |
| Endothelium | − | +, − | + | +, − | +, − | +, − |
| Antipodal cells | persistent | persistent | ephemeral | ephemeral | ephemeral | ephemeral |
| Vasculature | terminate in chalaza | terminate in chalaza | entering into o.i. | entering into o.i. | entering into o.i. | entering into o.i. |
| Curvature | anatropous | anatropous | anatropous | anatropous | anatropous | anatropous |

the Theales and the three families of the Primulales, the micropyle is formed by both integuments, the integuments are two or three cell-layered, and the nucellus is usually more reduced. Although the Marcgraviaceae is similar to Lecythidaceae s.l. in that the micropyle is formed by the i.i. alone, it differs from the Lecythidaceae s.l. in its very short outer integument, two to three cell-layered integuments, extremely reduced nucellus, and absence of vasculature in the ovule.

The degree of similarity among these six families, as can be appreciated in Table VIII, is striking. Before more embryological information on ebenalean and especially on thealean families is available, I can only suggest that, in terms of embryology, these six families are closely related. Their phenetic similarity implies a close phylogenetic relationship. Furthermore, the vast majority of the genera of Lecythidaceae s.l. are especially similar to Scytopetalaceae and Ebenaceae in embryology.

## Intrasubfamilial relationships of the Planchonioideae

Based on the palynological evidence presented in Chapter III, the Planchonioideae appears to be a monophyletic group within the Lecythidaceae s.l. The subfamily displays enough diversity in embryological features to permit a cladistic analysis. The polarities of some of the embryological

features, such as the number of middle layers in the anther, are well established. I established the polarity of some of the other characters by using the three actinomorphic genera (Allantoma, Grias and Gustavia) of the Lecythidoideae, as well as the Theaceae, Scytopetalaceae, Ebenaceae, and Styracaceae as out-groups. The embryological features used in the cladistic analysis are listed in Table IX.

In the cladogram (Fig. 25), Petersianthus and Chydenanthus represent the two primary clades within the Planchonioideae, each characterized by one of the following autapomorphies, the relative curvature of the end of funiculus to the placenta (Petersianthus and Chydenanthus), and the position of the vascular bundle in the connnective (the other fourgenera). Although the clades leading to Barringtonia and to Abdulmajidia possess no autapomorphies, the clade leading to Planchonia and Careya is supported by five autapomorphies. The cladogram suggests a linear progression in embryological features beginning with Barringtonia and ending with Planchonia and Careya. It also supports an extremely close phylogenetic interrelationship between Planchonia and Careya based on embryological features.

Table IX

Embryological features and their polarity used in a cladistic analysis of the Planchonioideae

| Character | Polarity | Reference |
|---|---|---|
| 1.No. middle layers | 3 --> 2 | Davis, 1966 |
| 2.Vascular bundle in connective | at side --> at center | cf. Grias, Ebenaceae |
| 3.Ovule curvature | antropous --> campylotropous | cf. Allantoma, Grias, Gustavia |
| 4.Degrees of ovule curvature | 360 --> 450 | cf. all outgroups |
| 5.Endothelium | absent --> present | cf. Allantoma, Grias, Gustavia |
| 6.Apex of o.i. | straight --> slightly curved --> as a collar | cf. all outgroups |
| 7.Vascular bundles in o.i. | >7 --> < or = 7 | cf. Allantoma, Grias, Gustavia |
| 8.Apex of young anther | with a connective tip --> without a tip | cf. Gustavia, Theaceae, Scytopetalaceae |

Table X

Character states of the genera of Planchonioideae based on the polarities in Table IX

| Genus\ Character | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| Abdulmajidia | - | 1 | 0 | 0 | 0 | 1 | 0 | - |
| Barringtonia | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Careya | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 |
| Chydenanthus | 0 | 0 | 0 | 0,1 | 0 | 0 | 1 | 1 |
| Petersianthus | 0 | 0 | 0 | 0,1 | 0 | 0 | 0 | 0 |
| Planchonia | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 |
| Outgroups | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

## Intrasubfamilial relationships of the Lecythidoideae

Although embryological information for some genera of this subfamily is not complete, the available data (as seen in Table VI), display little embryological variation, especially if the poricidal anthers of Gustavia are not considered. However, it cannot be claimed that these genera constitute a monophyletic group since no synapomorphies, based on embryology, are shared among them.

Gustavia possesses poricidally dehiscent anthers and two supposedly associated features. They are the reticulate secondary-thickenings on the endothecial walls and continuous endothecium from over the two adjacent microsporangia on the abaxial side of the anther. Because these three unique features form part of a syndrome related to poricidal anther dehiscence, they do not provide enough evidence to support the removal of Gustavia from the Lecythidoideae.

However, there are two features which differentiate the 10 genera to some degree. They are the vasculature in the o.i. and the mature morphology of the anther. All three actinomorphic genera have 6 to 11 vascular bundles in their o.i., whereas five of the seven zygomorphic genera (except Lecythis and Eschweilera) have reduced numbers of vascular bundles in the o.i. This reduction trend occurs in parallel in the Planchonioideae and the Lecythidoideae, and is not

correlated with the thickness of the o.i.

The second feature is the relative size of the cross sectional area of the connective of mature anthers. In general, this area is smaller in the zygomorphic genera than in the actinomorphic genera. The introrse anther of Grias has a very broad connective as does the poricidal anther of Gustavia. The anthers of all zygomorphic genera are latrorse. The connective of Cariniana is relatively broad, that of Couratari is of medium size, and that of the remaining five genera is very narrow. This reduction series may or may not have strong phylogenetic value. Nevertheless, the form of the anther seems to be a very stable character of the zygomorphic genera.

Because only a few of the embryological features exhibit appreciable variation within this subfamily, and they ordinarily vary slightly among zygomorphic genera, they cannot be used to produce a cladogram for this subfamily. However, it is worthwhile to indicate that the variation of these few features does serve to emphasize the relative primitiveness of the actinomorphic genera as compared to the zygomorphic ones. The consistency of all embryological features among most zygomorphic genera suggests that they are very closely related.

## Intra- and intersubfamilial relationships of the Napoleonaeoideae

Although there are only three genera within this subfamily, the number of embryological features which vary among them is comparable to that found among the genera of Planchonioideae (Table VII). Asteranthos resembles the Planchonioideae and Lecythidoideae in embryological features. It possesses plesiomorphic states of all but one feature, the presence of an endothelium.

Crateranthus exhibits the most plesiomorphies of the Lecythidaceae s.l. However, it has long-sagittate anthers which are nearly rectangular in cross-section (rather than 4-lobed in Asteranthos and triangular in Napoleonaea), and a completely closed endothecium that extends into the filament. These unique traits suggest that Crateranthus is distantly related to the rest of Lecythidaceae s.l. In addition, Crateranthus expresses two other distinct features in female embryology. It has an ovule with an extremely long micropyle caused primarily by the very slender cells of the inner integument which form it. Another uncommon feature is the non-branching ovular vasculature. The latter character is shared only by Napoleonaea and Couroupita.

The third genus, Napoleonaea, also possesses some peculiar traits including: bisporangiate, single celled, extrorse anthers, mainly campylotropous ovules with

non-branching vascular bundle, and partly fused integuments. It is noteworthy that although the integuments of Napoleonaea are fused for two-thirds of the entire length of the integuments, there is no indication of fusion in the ovules of Asteranthos and Crateranthus. Similar to Crateranthus, Napoleonaea also possesses some unique features in female embryology. If most embryological features of Asteranthos are considered as plesiomorphies of the Lecythidaceae s.l., then Crateranthus and Napoleonaea probably represent a distinct clade branching from the base of the group, in terms of embryology.

The occasionally multicelled archesporium, two integuments with integumentary fusion to two-thirds of the entire length, and the T-shaped tetrads of the ovule of Napoleonaea suggest a comparatively closer relationship, at least phenetically, between Napoleonaea and Styracaceae, a family in which the same characters and a similar type integumentary fusion have been described (Mashard, 1936).

## Intersubfamilial relationships of the Foetidioideae

The embryological features of Foetidia match quite well those of the Planchoioideae and Lecythidoideae, differing most prominently in its well-developed integumentary fusion. Foetidia, Petersianthus and Napoleonaea are the only genera of Lecythidaceae s.l. in which the two

integuments are fused to a large extent. The two integumentary primordia of Foetidia gradually fuse with each other as development proceeds. At maturity, the boundary between the two integuments along the lower one-half or more of their length disappears completely.

I can find no other uncommon embryological features shared by Foetidia and the Lecythidaceae s.l. Based on embryology, there is little basis for separating Foetidia from the genera of the other two subfamilies or from Asteranthos. More detailed information on thealean and ebenalean families is needed before phylogenetic relationships of Foetidia outside of the Lecythidaceae s.l. can be suggested.

# Chapter V OBSERVATIONS ON REPRODUCTIVE CHARACTERS

## Introduction

My study of Lecythidaceae has demonstrated that embryological features are taxonomically useful at the subclass, familial, and ordinal levels. On the other hand, they provide little insight into problems at lower taxonomic ranks, such as the subfamilial and generic levels. I have, therefore, studied reproductive morphology of Lecythidaceae s.l. in order to clarify intergeneric relationships.

The first comprehensive survey of the reproductive morphology of Lecythidaceae s.l. was contributed by Miers (1874, 1875a, 1875b). His original observations and detailed descriptions provide the foundation for my studies of Lecythidaceae s.l., especially the Old World taxa. More than a hundred years ago, Miers (1874, 1875a, 1875b) placed Barringtoniaceae (= Planchonioideae, excluding Abdulmajidia which was published in 1974) close to the Rhizophoraceae, associated Napoleonaea with the Sapotaceae, Asteranthos with Rhododendron (Ericaceae), Foetidia with the Lythraceae, and was the first to group Gustavia and Grias with the zygomorphic genera of Lecythidaceae (=Lecythidoideae). His phylogenetic considerations were not followed by subsequent students of plant phylogeny, who usually treated these taxa as belonging to the Lecythidaceae s.l.

The second monograph of the entire family was published by Knuth (1939a, 1939b, 1939c). His treatment included two new genera Crateranthus and Corythophora, many new species, and keys to genera and species. However, Knuth's work contains too many mistakes and his descriptions are not detailed enough to be very useful for phylogenetic analysis. Knuth combined the five genera of the Planchonioideae as well as Crateranthus, Napoleonaea and Foetidia into the single family Barringtoniaceae. He also recognized the Asteranthaceae (monotypic) and Lecythidaceae (=Lecythidoideae) as separate families.

Other than in the monographs of Miers and Knuth, extra-American taxa of Lecythidaceae s.l. have rarely been treated. Payens' (1967) monograph of Barringtonia, Kartawinata's (1965) study of Planchonia, and Liben's (1971) treatment of Napoleonaea provide useful data but do not address phylogenetic problems. Masters (1869) carefully studied the complex flowers of Napoleonaea, and concluded that its closest relative is Asteranthos. Among the nine extra-American genera, the published information of six of them is limited to Miers (1875b), Knuth (1939a, 1939c), and the protologues. Until more information on all genera of Lecythidaceae becomes available, phylogenetic hypotheses about the relationships of Old World taxa must be considered preliminary.

In contrast, knowledge of the tropical American taxa of

Lecythidaceae is more complete. Since about 1970, Scott Mori and Ghillean Prance have been studying New World Lecythidaceae. They have revised all New World genera of the family (Prance & Mori, 1979; Mori & Prance, 1990) and consequently, information for nearly all species on vegetative and reproductive features, phenology, ecology, etc., is available for use in further studies (Mori & collaborators, 1987; Mori and Prance, 1990; Prance and Mori, 1979). Besides, floral structures of all the ten genera of Lecythidoideae have been studied with a special focus on vascularization by Monteiro-Scanavacca (1974, 1975a, 1975b). In my study, floral characters were studied in an overall but preliminary way in an effort to elucidate intergeneric relationships.

## Materials and References

Information on floral structure was gathered from the literature and from detailed study of liquid preserved flowers (Table XI). I was fortunate to have access to the pickled floral materials accumulated by Dr. Mori and Dr. Prance during the last two decades. In this chapter, only features exhibiting variation and those first observed for a genus, are described. As a result, the characters described vary from subfamily to subfamily. Information about "infloresences" and "fruit and seeds" was obtained from the

literature.

Morphological terms referring to the structures of the zygomorphic androecium follow Prance and Mori (1979: 39-46).

The pickled materials and the major references for each genus are listed below. All the vouvhers are kept in NY.

Table XI

Pickled samples studied and major references

| species | | voucher |
|---|---|---|
| Planchonioideae | | |
| Abdulmajidia | chaniana | Tsou 160 |
| A. | maxwelliana | Tsou 165 |
| Ref.: Whitmore, 1974. | | |
| Barringtonia | racemosa | Hsieh s.n. |
| | | Tsou s.n. (FTG) |
| B. | asiatica | Prance 30096 |
| Ref.: Knuth, 1939a; Miers, 1875b; Payens, 1967. | | |
| Careya | arborea | Jayasuriya 4334 |
| | | Tsou 163 |
| Ref.: Knuth, 1939a; Miers, 1875b. | | |
| Chydenanthus | excelsus | M. Rifai s.n. |
| Ref.: Knuth, 1939a; Miers, 1875b. | | |
| Petersianthus | quadrialatus | Herraez 4172 |
| Ref.: Chevalier, 1909; Knuth, 1939a; Merrill, 1909, 1916; Miers, 1875b. | | |
| Planchonia | careya | Jacks, B. s.n. |
| Ref.: Kartawinata, 1965; Miers, 1875b. | | |
| Lecythidoideae | | |
| Ref. for all genera: Mori & Collaborators, 1987; Mori & Prance, 1990; Prance and Mori, 1979. | | |
| Allantoma | lineata | Prance 17549 |

Table XI continued

| | | |
|---|---|---|
| Grias | cauliflora | Nee & Mori 3574 |
| G. | neuberthii | Plowman & Davis 4365 |
| | | Luteyn 5827 |
| G. | peruviana | Peters s.n. 19 Nov 86 |
| Gustavia | hexapetala | Mori 18548, 18676 |
| G. | macarenensis subsp. paucisperma | Nee & Mori 4159 |
| Cariniana | decandra | Klug 979 |
| C. | integrifolia | Ducke 18 |
| C. | uaupensis | Spruce 2510 |
| C. | micrantha | Mori 20191 |
| C. | pauciramosa | Prance 17516 |
| Bertholletia | excelsa | Nelson s.n. |
| Corythophora | alata | Prance 10418 |
| C. | amapaensis | Mori 18675 |
| C. | rimosa | Mori 18547 |
| Couratari | oligantha | Plowman et al. 12546 |
| C. | stellata | Krukoff 8893 |
| Couroupita | guianensis | Hage 1964 |
| C. | nicaraguarensis | Mori 5420 |
| C. | subsessilis | Prance 16683 |
| Eschweilera | alata | Pruski 7526 |
| E. | cyathiformis | Mori 19358 |
| E. | decolorans | Mori & Bolten 8441 |
| E. | mexicana | Wendt 4468 |

Table XI continued

| | | |
|---|---|---|
| Eschweilera | odora | Mori 8564 |
| E. | ovata | Mori et al. 10937 |
| E. | parvifolia | Prance 26319 |
| E. | rabeliana | Daly et al. 3917 |
| E. | sessilis | Mori 6516 |
| E. | tenuifolia | Prance 24355 |
| Lecythis | chartacea | Lindeman 11171 |
| L. | holocogyne | Mori 8814 |
| L. | idatimon | Mori 14653 |
| L. | pneumatophora | Sabatier 1754 |
| L. | poiteaui | Mori 18533 |
| L. | prancei | Prance 23070 |
| L. | zabucaja | Prance 17769 |
| Foetidioideae | | |
| Foetidia | obliqua | Schatz 1855 |
| Ref.: Perrier de la Bathie, 1954; Knuth, 1939a. | | |
| Napoleonaeoideae | | |
| Asteranthos | brasiliensis | Kawasaki 62 |
| | | Stevenson 858 |
| Ref.: Miers, 1875a; Prance & MOri, 1979. | | |
| Crateranthus | cf. talbotii | Membo & Thomas 36 |
| Ref.: Baker, 1913; Knuth, 1939a. | | |
| Napoleonaea | cf. leonensis | Reitsma 2946 |
| N. | imperialis | Jayasuriya 4333 |
| Ref.: Liben, 1971; Masters, 1869; Miers, 1875a. | | |

# Descriptions

## Planchonioideae

The six genera of Planchonioideae are paleotropical in distribution. Five genera are very small, both in number of species and in geographical range. The sixth genus, Barringtonia, with 41 species is very widespread (Table I).

The gross floral morphology of these genera is very similar. They are well-defined as an easily recognizable group in the dicotyledons by the following common characters: flowers actinomorphic; ovary inferior throughout development; calyx 3-5 lobed except in Barringtonia Section Barringtonia in which it is unlobed; petals 3-5, free; aestivation imbricate; stamens numerous and monadelphous with a basal staminal ring; filaments filiform, incurved and twisted before anthesis; style slender (usually as long as the filaments and extending outside the mass of stamens before anthesis), and persistent in fruit; intrastaminal nectary disk annular except in Petersianthus in which the disk is poorly developed; stamens widely spreading at anthesis; and indehiscent fruit with persistent calyx at the distal end. This is a very homogeneous subfamily made up of well-defined, homogeneous genera. Although the genera possess very few characteristics common to all its species, most are easy to distinguish by their floral structures. An

exception is that Planchonia and Careya can only be separated by their embryo types.

## Abdulmajidia Whitmore

Only two species are published in this genus. The diagnostic generic characters are: flowers deep red, petals three, fruits large and containing few seeds, seeds large, and testa woody. Leaves are usually clustered at the ends of the twigs, but in A. maxwelliana the leaves are opposite as well as tufted.

Whitmore established Abdulmajidia as a new genus in 1974 based on two new species collected in the Malaya Peninsula. Since then, no further information has been published for this genus. Based on my collections from the type tree of A. maxwelliana and from a locality of A. chaniana, additional details are described here. Descriptions of staminodes, floral color, and the nectary disk are provided for the first time for these two species.

1. Inflorescences: According to Whitmore (1974), the inflorescence is terminal or axillary. My own collections show that the inflorescences of both species are terminal or axillary spikes. However, in A. chaniana, the spikes can be arranged in cauline fascicles from the old branches or pendulous from the leaf axils. Both species were collected at noon on a clear day, at which time there were no bloomimg

flowers on the inflorescences. Only post-anthesis flowers and flower buds were present. Androecia and petals found on the ground were still fresh, indicating that these two species are nocturnal-flowering and probably bat-pollinated, like some species of Barringtonia.

2. Calyx. In A. chaniana, the sepals are mostly 3, rarely 4 in number, more or less triangular, 2-3 mm high and 5-6 mm wide, and with ciliate margins. In A. maxwelliana the sepals are 4 in number, triangular, 4-5 mm high and 5-6 mm wide, and also with ciliate margins. The sepals of both species are deep red.

3. Corolla. In both species, the petals are 3 in number, imbricate, and with the apex ciliate. In A. chaniana, the petals are ovate, ca. 28 mm long and 18 mm wide. In A. maxwelliana, the petals are oblong, and ca. 28 mm long and 14 mm wide. The petals of both are the same deep red color as the sepals.

4. Androecium. In A. chaniana, the stamens are arranged in 7-8 whorls. The innermost whorl is composed of staminodes which are antherless and possess short filaments (Fig. 26A). The filaments, anthers, and the staminal ring of A. chaniana are 40 mm, 1.2-1.5 mm and 3.0-4.0 mm long respectively, and those of A. maxwelliana are 50 mm, 2.0 mm and 4.0-5.0 mm long, respectively. In A. chaniana, the degree of connation of filaments varies from low to high from the inner to the outer whorls of stamens (Fig. 26A).

5. Style. The style is persistent after anthesis in both species. It is ca. 30 mm long in A. chaniana and 45 mm in A. maxwelliana.

6. Ovary. In A. chaniana, the ovary is triangular in cross section, and has 3 carpels and 3 locules. In A. maxwelliana, the ovary is tetra-angular in cross section, and has 4 carpels and 3 locules. There are 8 carpellary bundles around the three locules separated by a T-shaped septum. This suggests a transition from the 4-carpelled state to the 3-carpelled one.

7. Placentation. There are about 20 ovules per locule in A. chaniana and 8-10 in A. maxwelliana. The placenta of both species is located around an O-shaped ventral slit. The ovules are aligned in one series on the placenta (Fig. 26A, 26B). Locules are elongated and triangular, with ovules situated in the upper half of the cavity (Fig. 26B).

8. Nectary disk. The nectary disk is well developed as an annulus in both species. That of A. chaniana is 2.0-2.5 mm in diameter and about 0.6 mm in height, and that of A. maxwelliana is 4.0 mm in diameter and 1 mm in height. The cross section of the disk is somewhat triangular. The summit of the ovary inside the disk is not sunken (Fig. 26B).

9. Fruit and seeds. According to Whitmore, the fruit of A. chaniana is rounded with about 5 seeds, while the fruit of A. maxwelliana is 2 to 4 seeded. Those seeds are 4 to 6 cm

long and morphologically resemble those of Brazil nuts (Bertholletia excelsa) except the seed coat of the former is pubescent (Fig. 1 in Whitmore, 1974).

The two species of Abdulmajidia form a natural group worthy of generic recognition.

## Barringtonia Foster

There are 41 species in this genus (Payens, 1967; Kiew & Wong, 1988). The diagnostic features of the genus are 1) unbranching and mainly pendulous inflorescences, 2) apical axile placentation, and 3) 1-seeded fruits.

1. Inflorescences. Axillary, less frequently cauline, and rarely terminal, racemes or spikes. The rachis is pendulous. It is usually 20-80 cm long and thickened when bearing mature fruits.

2. Calyx. Variation of the calyx is useful in separating species of Barringtonia. Payens (1967) recognized two sections of the genus based on features of the calyx. In section Barringtonia, the calyx is either completely fused (Fig. 26C) or with only an apical pore in early development. Whereas in section Stravadium, there are usually 4 distinct sepals from the beginning of development. My observations of B. racemosa (Section Barringtonia) indicate that the irregular lobing of the calyx taking place from mid development onwards is caused by

pressure exerted by the expanding petals. Usually, the unlobed calyx splits into 2 or 3 lobes. If two lobes develop, they may or may not split into 4 lobes. Infrequently, 4 lobes develop from the onset. No preexisting lines are present on the calyx.

3. Corolla. There are usually 4 distinct, oblong petals. However, variation from 3 to 4 or from 4 to 5 petals occurs in many species. The bases of the petals are usually adnate to the staminal tube and petals fall attached to the androecium.

4. Androecium. The stamens are arranged in 3 to 8 whorls. All species have a staminodial inner whorl and, in a few species, the second inner whorl is also sterile (Payens, 1967). My study of B. racemosa indicates that the stamens initiate from the annular androecial base freely and centripetally (Fig. 4A). This contrasts to the centrifugal androecial initiation of Barringtonia reported by Thompson (1927). The fertile stamens are about the same height, (1.5 to 4 cm long) and bear short and basifixed anthers. The innermost staminodial whorl is antherless and much shorter. The height of the staminal ring varies from 1 to 10 mm in different species.

5. Ovary. Most species usually have 4-celled ovaries, but 2-celled or 3-celled ovaries are dominant in a few species. The ovary is round or tetragonous in cross section. In the latter case, there are usually 4 ridges or even 4 narrow

wings at the angles.

6. Placentation. Barringtonia is characterized by apical axile placentation. An obscure ventral slit is located near the apex of the axis. The placenta develops from and is restricted to the cross zone (Fig. 26D, 26E). There are basically 4 elongate and pendulous ovules per cell. The locules are usually slender and ovules only occupy their upper portion.

7. Nectary disk. The disk is usually a well developed ring which may be minute or may reach 2 mm high. In all cases, the cross section of the ring is roughly semi-circular. Inside the disk, the ovary summit is not sunken (Fig. 26E).

8. Fruit and seeds: Fruits are 1-seeded and usually longer than broader. The shape of the fruit is somewhat correlated with the shape of the ovary. Fruits rounded in cross section are always developed from rounded ovaries, whereas tetra-angular, 4-ridged or 4-winged fruit in cross section develop from similarly shaped ovaries. Seeds are macropodial (i.e., without a differentiated embryo) (Fig. 2 in Payens, 1967).

## Careya Roxburgh

Considerable overlap in the floral features of Careya and Planchonia obscures the difference between these two genera. Miers' (1875b) and Knuth's (1939a) monographs of

the Barringtoniaceae and Kartawinata's (1965) monograph of Planchonia, provided only a single difference between these two genera, i.e., the embryo of Careya is undifferentiated, whereas that of Planchonia has two foliaceous, plicate cotyledons, and a coiled or curved radicle. However, only three out of eight species of Planchonia are known to have a differentiated embryo (P. crenata, Miers, 1875b, P. careya and P. valida, Kartawinata, 1965), and only C. arborea and C. sphaerica (Miers, 1875b) of the 4 species of Careya have been described as having macropodial embryo. Because of their similarity in floral morphology, as well as their similar embryological features (see Chapter IV), I question their treatment as distinct genera. However, until more species are examined for embryo morphology, I retain them as separate genera and describe them separetely.

There are four species of Careya. Their diagnostic characteristics are: 1) inflorescences erect, with few to about ten flowers crowded onto a short rachis, 2) large flowers, 3) many ovules in each locule which are longitudinally aligned along the axis, and 4) many seeds per fruit.

1. Inflorescences. Terminal (Miers, 1875b) or lateral (Knuth, 1939a) spikes.

2. Calyx. There are 4 distinct sepals in all species. The sepals are coriaceous and ciliate at the apex (Fig. 27A).

3. Corolla. There are four distinct petals which are

alternate with the sepals.

4. Androecium. The stamens and staminodes are numerous and arranged in 5-8 whorls. Stamens are basifixed and latrorse (Fig. 27B). The androecial initiation is neither centrifugal nor centripetal. The staminal primordia first appear in the central region of the zonal common primordium (Fig. 4B) and then gradually emerge away from the center on both sides. In C. arborea, the stamens from different whorls are of different heights and different colors. The filaments of the outermost whorl are 5-5.5 cm long, pink to red in color, and bear no anthers. The innermost series is composed of staminodes which are 1.2-1.4 cm long and white. In the intermediate whorl, the stamens are fertile, 2-3.5 cm long, and red in color. The staminal ring is about 1.2 cm high in C. arborea.

5. Ovary. This genus usually has a 4-celled, rarely, 5-celled ovary.

6. Placentation. Species of Careya have axile placentation with many ovules in each locule. In C. sphaerica, there are about 20 ovules in 2 rows on the placenta (Miers, 1875b). In C. arborea, each carpel has a elongated ventral slit which is almost as long as the axis. The placenta is O-shaped and developed along the margin of the slit. There are 35-40 ovules in 4 rows along the placenta. There are 2 rows on each side of the slit (Fig. 27D).

7. Nectary disk. The nectary disks are very well developed

rings which are triangular when viewed in longitudinal section. Inside the disk, the ovary summit is sunken, thereby forming a nectary reservoir (Fig. 27C). The nectary reservoir of C. arborea is about 7 mm in diameter and 5 mm in depth. The disk itself is about 1.5 mm high.

8. Fruit and seeds. The fruits are generally rounded and crowned by 4 persistent sepals. They are similar in appearance to those of guava (Psidium guayava, Myrtaceae). There are 4 locules per fruit, each with several seeds.

## Chydenanthus Miers

This genus of two species was established by Miers in 1875. It is characterized by 1) an articulate pedicel, 2) a cylindrical ovary which is 2-celled and as wide as the pedicel, and 3) paniculate inflorescences.

When Miers described this genus, he considered the paniculate inflorescence to be its most important characteristic because panicles were not found in other species of Barringtoniaceae. Although paniculate inflorescences also occur in Petersianthus quadriatalus (described in 1909), Chydenanthus still merits generic rank because of its unusual ovary structure and articulate pedicel.

1. Inflorescences. They are well-developed panicles. The rachis is 10 to 25 cm long.

2. Calyx. The calyx is cup-like. The upper, undulate margin possesses 4 minute tips. The calyx is about 3-4 mm high.

3. Corolla. There are 4 distinct, oblong petals.

4. Androecium. The stamens are arranged in 3 or 4 whorls in C. excelsa. The innermost whorl is staminodial and much shorter than the stamens of the other whorls. The filaments and the staminal ring of C. excelsa are 1.8-3.0 cm and 0.4 cm long respectively.

5. Ovary. An important feature of Chydenanthus is that the ovary is cylindrical and as thick as the pedicel. No clear-cut morphological distinction can be made between the ovary and the pedicel. The figure of C. excelsa published by Knuth (1939a), showing an ordinary, campanulate ovary is in conflict with my observations, and with Miers' description and figure (Miers, 1975b). The ovaries are 2-celled in C. excelsa (Miers, 1875b; my observations). Knuth's description as "4-loculare" is clearly a mistake. His figure of the cross section of the ovary of this species shows 2 locules.

6. Placentation. The cylindrical ovary has a rather narrow ovarian cavity. The basal, axile placenta is situated within a narrow range in the lower portion of the axis. One or two erect ovules are packed in each locule. A ventral slit was not observed.

7. Nectary disk. A well developed disk is present in C.

excelsa. It is a short ring quite similar to the disks of most species of Barringtonia.

8. Fruit and seeds. The fruits are long and elliptical. The number of seeds per fruit has not been reported for either species. However, based on Miers' statement that the fruit of C. excelsa is similar to the fruit of Barringtonia, it is most likely that there is only seed per fruit.

## Petersianthus Merrill

There are two species of Petersianthus. This genus is characterized by fruits with 4 broad, thin wings, similar to the winged fruits of many Combretaceae.

1. Inflorescences. Terminal panicles in P. macrocarpus and in P. quadrialatus (Merrill, 1916).

2. Calyx. There are 4 distinct sepals in both species.

3. Corolla. There are 4 distinct petals in both species. Petals of this genus are short compared with those of other genera of Planchonioideae. They are long-ovate and 6-10 mm long.

4. Androecium. The stamens are arranged in 4-5 series. The staminal ring is about 0.4 cm high in P. quadrialatus.

5. Ovary. Both species have ovaries in the shape of an upside down pyramid. The 4 angles of the ovary are narrowly winged (Fig. 28A). The 4 wings of the ovary develop into broad, submembraneous wings in the fruit. The ovary is

4-loculed in both P. macrocarpus (Miers, 1875b) and P. quadrialatus (Merrill, 1916; this study). However, Knuth (1939a) described the ovary of P. macrocarpus as 2-loculed.

6. Placentation. In both species the placentation is axile and central. In P. macrocarpus there are several ovules per locule. In P. quadrialatus the ovary is relatively shorter, and the placenta is restricted to the middle part of the central axis. Two ovules are erect and one or two are pendulous in each locule (Fig. 28B).

7. Nectary disk. The structure of the disk of Petersianthus is not mentioned in the literature. My study of P. quadrialatus shows that the disk is not as well defined as in other genera of the Planchonioideae. The disk itself is short, without a clear-cut inner margin and does not enclose a sunken nectar reservoir (Fig. 28B). The figures of P. macrocarpus published by Miers (1875b, P. africana in Plate 18) show a rather well developed ring-like disk similar to that in most species of Barringtonia.

8. Fruit and seeds. The fruits of both species are broadly winged. The wing is 1.0-1.3 cm wide in P. quadrialatus (Merrill, 1909) and 2.0-2.5 cm wide in P. macrocarpus (Miers, 1875b, Plate 18). The fruit itself is fusiform. There are 4 or 5 seeds per fruit. The embryo of P. macrocarpus (Niedenzu, 1892) has two plicate cotyledons and a long radicle.

## Planchonia Blume

There are 8 species of Planchonia. Planchonia has floral characteristics similar to those of Careya.

1. Inflorescences. Terminal racemes, spikes, or solitary flowers (Kartawinata, 1965).

2. Calyx. There are 4 distinct sepals with a ciliate apex.

3. Corolla. There are 4 free, obvate to oblong petals which are 3-5.5 cm in length.

4. Androecium. The stamens are multiseriate and the filaments are unequal in length. The innermost whorl is sterile and its filaments are shorter than those of the other whorls (Kartawinata, 1965). The staminal ring is 0.5 -1.5 cm long.

5. Ovary. The shape of the ovary of Planchonia varies from funnel-like to rounded. According to Kartawinata (1965), the ovary is 3- or 4-locular. However, he did not specify the exact number of ovarian locules for each species. In P. careya, I always found 4 locules per ovary.

6. Placentation. The placentation is central axile. The numerous ovules are horizontally aligned in 2 series along the placenta. The flowers that I examined of P. careya have about 20 ovules per locule. The placenta of this species is basically the same as that found in most species of Careya. The ventral slit of each carpel is an elongated opening (Figs. 27E, 27F). The placenta develops along the margin of

the slit. Ovules are covered with the arilloid extended from the outer integument (Fig. 27F).

7. Nectary disk. The morphology of the disk of Planchonia is similar to that of Careya. The disk is well-defined with a broadly-acute upper margin. Inside the disk, the ovary surface is concave forming a nectary reservoir. In P. careya the nectary reservoir is 4 mm deep and 5 mm in diameter. The disk itself is about 1.5 mm high (Fig. 27E). This highly specialized state has been noted only in Careya and Planchonia.

8. Fruit and seeds. The number of seeds per fruit ranges from one to many. The shape of the fruit varies from obovoid (similar to the fruits of Barringtonia), to ovoid or globular.

## Lecythidoideae

The Lecythidoideae includes ten genera of tropical American distribution. The floral features of this subfamily are very diverse in comparison with those of the Planchonioideae. Their common characters, though are few, 1) the presence of a staminal ring formed by the fusion the bases of the filaments, 2) free petals with imbricate aestivation, 3) axile or modified axile placentation, and 4) inferior or mostly inferior ovaries. All other reproductive features, such as those of inflorescences, calyx, corolla,

androecium, gynoecium, placentation, fruit, and seeds, vary greatly. Especially variable is the staminal ring of the androecium. A nearly continuous transformation series is found in the staminal ring, ranging from actinomorphic (e.g., Allantoma, Grias, Gustavia) to a diverse spectrum of zygomorphy (the remaining genera). No comparable variation in the androecium is found in any other group of angiosperms. The amazing androecial variation of Neotropical Lecythidaceae has been illustrated by Knuth (1939a, Fig. 1), Prance & Mori (1979, Fig. 9) and Mori and Prance (1990, Figs. 31, 34, 94).

Prior to the beginning of this century, two of the actinomorphic genera, Grias and Gustavia, were grouped with the planchonioid genera in Barringtoniaceae. Miers (1874) was the first to place these two genera with the zygomorphic genera in the Lecythidaceae and distinct from Barringtoniaceae.

## Allantoma Miers

Allantoma is a monotypic genus (Prance & Mori, 1979), characterized by actinomorphic flowers with a fleshy, short cylindrical staminal ring. The stamens are inserted on the inner wall of the ring (Fig. 11S-U in Prance & Mori, 1979).
1. Inflorescences. Terminal or subterminal racemes or once-branched panicles with very short pedicels.

2. Calyx. The calyx is unlobed with a 5-toothed upper margin. The teeth alternate with the petals and become more triangular in shape at maturity.

3. Corolla. The 5 (or 6) distinct petals are quincuncial, at least in early development. The petals are fleshy and oblong with an inwardly curved hook at their apex. In later stages, they tend to be valvate and connate at their bases.

4. Androecium. The cylindrical androecium is 1.3-1.6 cm long, and 0.5 cm in diameter at the base (Fig. 28C). About 30 stamens are arranged at more or less four different levels on the inner surface of the ring. The outermost and highest whorl curves downward from the upper margin of the ring. The filaments of this whorl are long and thick. The remaining three staminal whorls are inserted on the inner wall of the cylindrical portion of the ring. The filaments of these stamens are much shorter than those of the highest whorl (Fig. 28E).

5. Style. The style is short and rod-like. The stigma is capitate and exhibits 4 shallow lobes when viewed under the LM.

6. Ovary. The ovary is 4-loculed, cylindrical, and about 0.6 cm in length and 0.4-0.5 cm in diameter.

7. Placentation. There are about 20 ovules arranged in two long rows along the placenta in each elongate locule. The placenta is located along the lower 3/4 of the axis. The uppermost ovules are erect at later stages of development,

while the lowermost ones remain horizontally oriented (Fig. 28D).

8. Fruit and seeds. The pyxidium is tubular-cylindrical, and comparable in shape to that of the ovary. The columella of the operculum is very long and tetra-angular. There are many seeds per fruit. The seeds have a stipe-like funicle at their base (Fig. 16k in Prance & Mori, 1979).

## Grias Linnaeus

There are six species in Grias (Prance & Mori, 1979). Grias is similar to Barringtonia in its unlobed calyx, apical axile placentation with few ovules per locule, 1-seeded, indehiscent fruit, actinomorphic, 4-merous flower. However, Grias lacks the staminal disk and long, filiform filaments which radiate like a umbella at anthesis found in Barringtonia.

Species of Grias are characterized by 1) actinomorphic flowers (Fig. 11F-L in Prance & Mori, 1979), 2) 4 thick petals, 3) thick filaments, with the outer ones longer, 4) apical, axile placentation, 5) few ovules per locule, 6) 1 seed per fruit, and 6) macropodial embryos.

1. Inflorescences. Cauline fascicles or axillary racemes.

2. Calyx. The calyx is composed of 4 distinct sepals in G. neuberthii, but unlobed in all other species. When unlobed, the calyx envelops the floral bud to various degrees in

early to mid development. It may enclose the entire bud as in G. peruviana (Fig. 29A) or only cover the very base of the bud as in G. cauliflora (Fig. 29C).

3. Corolla. Four free petals are present in all species. Petals are thick or even massive reaching 4 mm thick in G. neuberthii. In G. peruviana, the petals are subimbricate when the bud is very small. However, when the bud becomes much larger, adjacent petals may be valvate and connate along their lower half.

4. Androecium. All stamens have fleshy, thick filaments. The outermost ones are the thickest and longest. No staminodes are present. The upper portion of the filaments bends inward and the anthers are hidden inside the staminal ring (Fig. 29B). The basal, connate part of the staminal ring is massive (Fig. 29E).

5. Style. The style is short, conical (Fig. 29E) or not well-differentiated. The stigma is relatively big, and usually divided into four parts.

6. Ovary. The ovaries are 4-loculed and inferior throughout development.

7. Placentation. Only apical, axile placentation occurs in the Grias. There are 2 to 4 pendulous ovules per locule. A very narrow ventral slit is located near the apex of the axis (Fig. 29D). The ovules develop from the region of the cross zone (Figs. 29D, 29E).

8. Fruit and seeds. The fruits are indehiscent, fusiform or

pyriform, and contain a single large seed. The seeds have macropodial embryos.

## Gustavia Linnaeus

This genus has about 40 species with considerable variation (Prance & Mori, 1979). Gustavia is characterized by 1) actinomorphic flowers (Fig. 11A-E in Prance & Mori, 1979), 2) very numerous and uniform stamens with long filaments, 3) poricidal anthers, 4) indehiscent fruit (Fig. 16 E-H in Prance & Mori, 1979) with usually more than one seed, and 5) embryos with thick, plano-convex cotyledons (Fig. 15 in Prance & Mori, 1979) .

1. Inflorescences. Suprafoliar, axillary or cauline racemes, or solitary in leaf axils.

2. Calyx. The calyx is unlobed in about half of the species and has 4 or 6 distinct sepals in the rest of the species. The calyx never completely encloses the bud.

3. Corolla. There are usually 6 or 8 distinct petals. An exception is Gustavia romeroi Mori & Barriga which has 12-18 petals.

4. Androecium. The stamens are very numerous (up to 1200) and inserted in 4 or more whorls in all species. A study of the early androecial development of G. hexapetala suggests that the androecial initiation is centripetal (Fig. 4C). The filaments are slender, somewhat dilated toward the apex,

and then abruptly constricted at the very apex. All filaments curve inwards, and the staminal ring is uniformly fused throughout the staminal whorls (Fig. 30A). All stamens are fertile. The anthers are relatively long, basifixed, and dehisce by 2 apical pores.

5. Ovary. The ovary is inferior throughout development in most species. In few species, the ovary is inferior at first, but the ovary summit is elevated during later development to make the mature ovary semi-inferior. Usually the ovary summit is broad and flat. The number of ovarian locules is usually 6, sometimes 4, and rarely more than 6.

6. Style. The style is conical or short and rod-like. It is less than 5 mm long.

7. Placentation. Based on the sample examined, the placenta develops from the two sides of the elongated ventral slit, and the ovules are arranged in either 2 rows or 4 rows on the placenta. The number of ovules per locule is always many (Fig. 30B). More ovules are found in locules with 4-rowed ovules than in locules with 2-rowed ovules.

8. Fruit and seeds. There are few to many seeds enclosed in an indehiscent berry-like fruit. The seeds are of two types, without well-developed funicles or with yellow, expanded funicles. An aril does not develop in Gustavia. The embryo has two large, fleshy, plano-convex cotyledons.

## Cariniana Casaretto

Flowers of some species of Cariniana are similar to that of Allantoma, but much smaller. Cariniana is characterized by 1) very small flowers, 2) actinomorphic to zygomorphic androecium, 3) 3-loculed ovary, and 4) a unilaterally winged seed. The reproductive differences between these two genera are the number of locules (4 in Allantoma and 3 in Cariniana), and the type of embryo (undifferentiated in Allantoma but with 2 foliaceous cotyledons and a well-developed radicle in Cariniana, Fig. 17A-D in Prance & Mori, 1979).

Cariniana has 15 species (Prance & Mori, 1979). A few species have a nearly actinomorphic androecium, but the majority of the species are zygomorphic (Fig. 11 M-Q in Prance & Mori, 1979).

1. Inflorescences. Terminal, rarely axillary racemes or panicles.

2. Calyx. The calyx is saucer- or cup-like, with 5 marginal teeth, or with 5 to 6 distinct sepals in most species.

3. Corolla. The 5 or 6 distinct petals are alternate with calyx teeth or sepals. They are fleshy to membraneous (Fig. 30E).

4. Androecium. The androecial structures vary greatly among species. In this genus, the androecium displays various degrees of zygomorphism. For example, in C. integrifolia,

the androecium is radially symmetrical, with a small, tubular staminal ring. Its filaments are thick and fleshy. The whole androecial structure is similar to, but smaller than, that of Allantoma. In C. uaupensis and in C. pauciramosa, the androecium is slightly asymmetrical, and both the height of stamens and that of the staminal ring are usually higher on the abaxial side, than on the other side. This represents the initial stage of evolution of the zygomorphic androecium in Cariniana.

In most other species of Cariniana, the abaxial side becomes highly developed, forming a ligule and even a hood above the summit of the ovary (Fig. 30E). In this species, both the staminal ring and the stamens are shortened on the adaxial side. The difference in appearance between the two sides is caused primarily by increased cell division on the ligule side. The increasing of cell size is noticable in the abaxial side of the ligule. The stamens are attached perpendicularly to the staminal ring, the ligule and the hood.

In zygomorphic-flowered species, the texture of both the staminal ring and the hood is thinner and more membraneous than that found in the actinomorphic-flowered species, displaying a parallel trend with the petals. The filaments of the species are mostly thin and thread like (Fig. 13A).

5. Style. The style is always short, but varies from short and rod-like to somewhat conical.

6. Ovary. The ovaries are very small and campanulate. The position of the ovary is inferior throughout development. The cross section of the ovary is rounded or triangular, and there are always 3 locules (Fig. 13C).

7. Placentation. The ovules are aligned biseriately on axile placentation (Fig. 30F). The placentation of Cariniana resembles that of Allantoma. However, the ovary is a much shorter ovary and the ovules are less numerous per locule. The upper 1/3 or 1/4 of the axis is not fertile, as in Allantoma, and the upper ovules are pushed erect into the upper space of the locule.

8. Fruit and seeds. The pyxidium is cylindrical, campanulate, or conical. It is always longer than broader. The columella is long and triangular. The seeds are many per fruit and each seed has a long, unilateral wing.

## Bertholletia Humboldt & Bonpland

Bertholletia is a monotypic genus which represents a side branch within the zygomorphic-flowered complex of genera (Mori & Prance, 1990).

Bertholletia is characterized by 1) a calyx which is unlobed in early to middle stages, but 2-lobed at maturity (Fig. 45 in Mori & Prance, 1990), 2) a dehiscent fruit with a tiny operculum which falls into the fruit cavity (Fig. 45 in Mori & Prance, 1990), 3) seeds triangular in cross

section, with a woody testa, and no aril, and 4) macropodial embryo (Fig. 45 in Mori & Prance, 1990).

1. Inflorescences. Terminal or axillary spikes or paniculate arrangements of spikes.

2. Calyx. In early development, the bud is enclosed by the cap-like calyx except for a slit at its apex. The calyx splits into 2 lobes in late developmental stages. The 3 tips at the apex of each lobe indicate that the 2-lobed calyx is probably derived from fusion of the six sepals.

3. Corolla. There are 6 distinct petals.

4. Androecium. The androecium is markedly zygomorphic. The hood apex curves inwards and expands into a ball-like structure formed by the expansion and fusion of the many staminodes into massive and fleshy appendages. The appendages of the hood are antherless and curved inwards, but they do not form a complete coil. There are numerous stamens on the staminal ring. The anthers are short and basifixed. The filaments are dilated at the apex (Fig. 7C).

5. Style. The style is up to 8 mm long and geniculate. It bends toward the anterior side of the flower (the side opposite the ligule) (Fig. 30C).

6. Ovary. The ovary is 4-loculed and inferior throughout development.

7. Placentation. The locule is tetragonal or pentagonal as viewed in longitudinal section (Fig. 30D), and the central axis is comparatively thick, with the very narrow ventral

slit near the midpoint. The placenta is developed from the surface slope of the axis below the ventral slit (Fig. 30D). There are about 8 to 10 ovules in each locule.
8. Fruit and seeds. The fruits are usually globose. Although each fruit develops an opening, it is smaller than the seeds, and therefore the seeds remain inside the fruit at maturity. There are 10 to 25 seeds per fruit. The seeds have a very hard woody testa and no aril.

## Corythophora Knuth

This is a small genus of four species (Mori & Prance, 1990) characterized by 1) a flat, dorsiventrally expanded hood, 2) usually 2-locular ovaries , 3) campanulate or cylindrical fruits, and 4) seeds with basal arils and macropodial embryos (Fig. 42-44 in Mori & Prance, 1990).
1. Inflorescences. Terminal or axillary racemes or panicles with 2-3 orders of branching.
2. Calyx. There are 6 distinct sepals.
3. Corolla. The 6 petals are alternate with the sepals.
4. Androecium. The hood is characterized by its flat, slightly or markedly dorsiventrally expanded shape. The hood appendages are fused or free and with or without anthers. Stamens on the staminal ring are very many and developed on the inner region of the ring instead of on the whole area of the ring.

5. Style. The style of this genus is short and conical.
6. Ovary. The ovary is usually 2-loculed. However, C. labriculata has 4 locules and the ovaries of some flowers of C. rimosa may have more than two locules. Although the summit of the mature ovary is slightly elevated, all ovaries observed are clearly inferior (Fig. 31A).
7. Placentation. The Corythophora have basal, axile placentation. The locule is very narrow (Fig. 31A).
8. Fruit and seeds. The pyxidium is campanulate or cylindric in shape and is always longer than its diameter. There are many seeds per fruit. The seeds have a basal aril and a macropodial embryo.

## Couratari Aublet

Couratari has 19 species (Mori & Prance, 1990). The androecium of this genus typically has an S-shaped hood, i.e., the hood apex folds inwards then curves outwards (Figs. 8B, 8C; Figs. 31, 46, 51, 62 in Mori & Prance, 1990). Staminodial glands are commonly present on the inside surface of the first coil. Couratari is characterized by 1) the unique androecium, 2) 3-locular ovaries, 3) campanulate fruit with an operculum having a long, triangular columella, and 4) bilaterally winged seeds with an embryo bearing two foliaceous cotyledons (Fig. 51 in Mori & Prance, 1990).

1. Inflorescences. Terminal or axillary racemes or panicles.

2. Calyx. There are always 6 sepals.

3. Corolla. The 6 petals are alternate with the sepals.

4. Androecium. The hood is curved inwards and then outwards to form an S-shaped pattern as viewed in medial section. There are gland-like staminodes on the inner surface of the inner coil (Fig. 31B, 31C). The staminal ring consists of 10- 75 fertile stamens arranged in several whorls surrounding the style. The short filaments are uniformly slender throughout.

5. Style. In most species, the style is short and straight (Fig. 31C). However, some species, e.g., C. asterotricha and C. stellata have a short and straight style with a ring-like expansion towards apex. In C. stellata (Krukoff 8893) the style is geniculate but bends towards the ligule.

6. Ovary. The ovary of this genus is always inferior and 3-loculed. The summit of the mature ovary is truncate to slightly convex.

7. Placentation. The placenta of this genus is only located below the ventral slit. When the locule is longer, central, axile placentation similar to that of Cariniana is present, however, when the locule is flatter and smaller, the placenta is placed very close to the base of the locule, but still remains on the axis (Fig. 31D).

8. Fruit and seeds. The pyxidium is cylindrical to

campanulate and is always longer than broader. The columella of the operculum is triangular and rather long, reaching the base of the pyxidium. The seeds are many per fruit with wings that surround the entire circumference. The embryo has 2 foliaceous cotyledons.

## Couroupita Aublet

Couroupita has only three species (Mori & Prance, 1990). This is the only zygomorphic genus of Lecythidoideae with 1) 6-loculed ovary, 2) numerous ovules per locule, 3) indehiscent fruit, and 4) small lenticular seeds with a hairy test and foliaceous cotyledons.

1. Inflorescences. The inflorescence of Couroupita is racemose from the trunk or old branches. It grows continuously from the apex and can reach as long as 3 m.

2. Calyx. There are 6 well-developed sepals.

3. Corolla. The 6 distinct petals alternate with the sepals.

4. Androecium. The staminal ring extends unilaterally into an uncurved hood (Fig. 31E; Fig. 34 in Mori & Prance, 1990). The stamens are very numerous, ranging from the staminal ring through the ligule to the hood (C. nicaraguariensis), or on the ring and the hood only (C. guianensis, and C. subsessilis). In C. guianensis, the anthers from the ring stamens are fertile and produce monad

pollen only, whereas the hood anthers are sterile and produce mainly tetrad pollen (Mori et al., 1980). The filaments of the ring stamens are dilated at the apex (Fig. 31E).

5. Style. The style is short and straight (Fig. 31E) with a 6-partite stigma.

6. Ovary. The ovary is 6-locular. The position of ovary is inferior in early development and changes into semi-inferior at maturity as a result of the elevation of the summit of gynoecium.

7. Placentation. There are very many small ovules arranged on elongated and expanded placentae (Fig. 31F). The ventral slit is short, and the placenta develops from the two sides of the slit and below the slit along the axis.

8. Fruit and seeds. The fruits are globose and indehiscent. The numerous lenticular-shaped seeds are embedded in a pulp which oxidizes bluish-green when exposed to the air. Each seed has a long funiculus. The embryo has 2 foliaceous cotyledons.

## Eschweilera Martius

Eschweilera is the largest genus of the Lecythidaceae s.l. with 83 described and many undescribed species (Mori & Prance, 1990). There is a single feature defining this genus, the complete spiral of the androecial hood. However,

the following characters aid in the recognition of this genus 1) bilocular ovaries, 2) placentation often basal axile or even on the floor of the locule, 3) seeds often with lateral arils (Fig. 32 D-E in Mori & Prance, 1990), and 4) macropodial embryos.

1. Inflorescences. The basic inflorescence is that of a raceme or a spike. They are terminal, axillary, or cauline. In most species, terminal and axillary inflorescences are found on the same plant. In rare cases, all three positions may occur in one plant. Only a few species are characterized by a cauline inflorescence.

2. Calyx. There are 6 distinct sepals.

3. Corolla. Six petals are present in most species except for five species which have only four petals.

4. Androecium. The zygomorphic androecium is characterized by a hood which curves inward to form at least one complete coil (lacking in only 4 species) (Fig. 18A). The appendages at the apex of this coil are staminodes which function as nectaries. In some species there may be a few vestigial anthers on the hood appendages. In some species the filaments of ring stamens are obviously clavate (Fig. 32A), whereas in others they are generally filiform.

5. Style. Styles are usually very short and stout at the apex of the umbonate surface of the ovary. The style is often not well-differentiated from the summit of the ovary (Fig. 32A).

6. Ovary. The ovary is 2-locular in most species (Fig. 32A). However, there are 4-locular ovaries in several species. The ovary is inferior at first; later when the ovary summit expands, it may become crown-shaped. This development elevates the relative level of the locule greatly producing a semi-inferior, or even "superior," ovary.

7. Placentation. All species have basal axile placentation. The locule is thin, flat, and packed with several to about ten ovules. The placenta is an expansion from the base of axis (Fig. 32B).

8. Fruit and seeds. Fruits are usually dehiscent and globose with many seeds. The seeds usually have a lateral aril in most species, but species without arils and species with arils completely covering the seed also occur.

## Lecythis Loefling

This zygomorphic genus, comprising 26 species (Mori & Prance, 1990) is the most variable genus of Lecythidaceae. Nearly all of the character-expressions that collectively define Lecythis can be found in at least one of the other zygomorphic genera. Consequently, Lecythis does not possess any autapomorphies. However, all species of Lecythis have a well-developed, but not completely coiled, hood (Fig. 94 in Mori & Prance, 1990) and a 4-locular ovary.

1. Inflorescences. Terminal or axillary racemes or spikes, or paniculate arrangements of racemes or spikes.
2. Calyx. There are always 6 distinct and equal sepals.
3. Corolla. There are always 6 subequal petals.
4. Androecium. The zygomorphic androecium has a flat hood, an expanded but not coiled hood, or a hood with inwardly oriented but not coiled appendages (Fig. 94 in Mori & Prance, 1990). The stamens of the hood are either antherless or fertile. The basal portion of the staminal ring where the erect and always fertile stamens are attached displays a wide range of variation among species of Lecythis, some are like a short and stout pilar, some are saucer-shaped with the saucer body thick, still others are thin, flattened and constricted into a narrow ring, especially on the adaxial side. Aside from the shape and size of the ring that vary greatly, the distribution of stamens on the ring also varies, from the case where dense stamens are found in a broad ring, to that where dense stamens are upright on very narrow ring in one direction, or that where only the inner 3/4-1/2 area -- in terms of diameter are covered by stamens with the outer portion naked on the other end. The small anthers are basifixed and the filaments are often constricted at the apex (Fig. 32C).
5. Style. There are four basic types of style, with some intermediate forms found between the types. The first type is straight, long, slender, to 5-6 mm long. It is found in

L. poiteaui. It is unique in the whole Lecythidoideae. The second type is geniculate, long, slender, and oriented to the anterior or open end of the flower. This type lacks a well-differentiated stigma. This type is found in L. corrugata, L. idatimon, L. prancei, and L. lurida. The style of Bertholletia excelsa belongs to this category also. The third type is conical and not clearly differentiated from the ovary summit nor is the stigma well-differentiated. This type occurs in L. zabucaja and L. tuyrana, and is the main type of stigma found in Eschweilera and Couratari. The fourth type is peculiar, with a well-differentiated but very short platform, on which another smaller platform extends upward. It is found in L. pisonis and some species of Couratari.

6. Ovary. The ovary is usually 4-locular but varies from 3 to 6-locular. The ovary is typically inferior in early development but, in some species, the ovary summit expands in later development to make the ovary semi-inferior at maturity. This transformation from an initial inferior position to a mature semi-inferior ovary is comparable to that in most species of Eschweilera. In some species of Lecythis, such as L. poiteaui (Fig. 32C), the ovary summit remains truncate at maturity, and the ovary is always inferior as found in most Couratari species.

7. Placentation. The placentation is central axile in species with relatively long locules, or basal axile in

species with short locules. In some species, a very narrow ventral slit is found along the upper 1/3 of the axis. The ovules only develop from the lower part of the ventral slit. In the case of basal placentation, the placenta is an expanded area around the base of the axis, but it is always associated with the axis (Fig. 32C).

8. Fruit and seeds. Most species have globose pyxidia. In a few species, the fruit is indehiscent (e.g., as L. lurida and L. parvifructa) and the fruit falls to the ground at maturity. The columellae of dehiscent fruits are short. There are usually many seeds per fruit. However, some species, such as L. lurida and L. parvifructa, may have only a single to several seeds per fruit. Seeds of most species have a basal aril, although some species have a partially lateral aril or lack an aril.

## Foetidioideae -- Foetidia

This subfamily consists of only Foetidia. The seventeen known species constitute a more or less homogeneous genus. Fifteen of them are confined to Madagascar, one to Mauritius, and one to East Africa (Bosser, 1988; Perrier de la Bathie, 1950). Foetidia is characterized by 1) apetaly, 2) numerous free stamens, and 3) valvate, woody sepals which enclose the bud until anthesis.

1. Inflorescences. The inflorescence is raceme or solitary.

The sample at hand, Foetidia obliqua, displays several to more than ten floral buds spirally crowded along the rachis. All of its young flowers are triangular in cross section.

2. Bracts. Each flower of F. obliqua is subtended by a bract at the base of pedicel which varies in shape and size and is caducous. They are sometimes small and leaf-like to several centimeters long. There are always 2 bracteoles, ca. 3 mm long, subopposite ly located along the lower portion of a pedicel (Fig. 32D).

3. Calyx. F. obliqua usually has 3, occasionally 4, sepals. There are usually 4, rarely 3 or 5, sepals in most other species. The calyx of Foetidia is unique in the Lecythidaceae s.l. The 3 or 4 sepals are valvate in aestivation and connate from their formation (Fig. 32D). At anthesis the splitting of the large and woody calyx releases the inner floral organs. The sepals are sharply acute at their apex, thick, hard, and filled with many fibers and unknown inclusions. They are deep purple in color on both surfaces.

4. Corolla. Species of Foetidia have no true petals. The origin of apetaly in Foetidia may have occurred because the calyx and androecium have taken over the normal functions of the corolla. Because of the thickened sepals, the calyx adequately protects the floral bud. The numerous showy, long-radiating stamens serve to attract pollinators.

Consequently, petals of Foetidia may no longer have been needed to ensure reproductive success. Since I have observed two parallel vascular strands entering the sepal of F. obliqua in the same radial plane, this suggests that the sepals of this species originated from the fusion of sepals and petals.

5. Androecium. There are numerous stamens which are free from each other (Fig. 32E). A staminal ring is not formed in Foetidia. All stamens are fertile. The filaments are long and upright, or slightly wavy in the bud, but always with the anther erect. The stamens of F. obliqua are entirely yellow. At anthesis, the filaments spread out to produce the characteristic ball-like appearance of the blooming flowers.

6. Style. The style is filiform, but slightly shorter than the sepals. In bud, it is erect and nearly reaches the very apex of the fused calyx. The stigma is bifid, trifid, or tetrafid. My study of F. obliqua, Niedenzu's illustration of F. retusa (1892: Fig. 11) and Perrier de la Bathie's illustration on the same species (1954) all show a slender style that branches distally into 3 or 4 linear ends. Knuth's figure of F. mauritiana (1939a, Fig. 14) showed the style apex slightly bulged, capitate, and 4-lobed, which is very different from the information from other sources mentioned above. The style of F. obliqua is deep purple in color, as are the ovary and sepals.

7. Disk. In F. obliqua (Schatz 1855), the surface of the ovary is slightly elevated adjacent to the androecium (Fig. 32E). This elevated region tapers down to the style. This structure is deep purple as is the color of the sepals and style, but different in color from the rest of the gynoecium. It does not take the shape of a well-defined ring-like area, nor does it have a complex vascular system entering it. It is thick, but not soft in texture, and does not appear to be a typical nectiferous disk. My observations support those of Niedenzu (1892, Fig. 11), but disagree with Knuth's illustration (1939a, Fig. 14) which depicts a well-defined, ring-like structure similar to the well-developed disks of species of Planchonioideae. Although I refer to this structure as a disk, its function is unknown.

8. Ovary. The ovary of Foetidia is inferior. Those species with 3 sepals have a triangular ovary in cross section, and 3 locules. Most species have 4 sepals and 4 ovarian locules.

9. Placentation. The species of Foetidia have central axile placentation. In F. obliqua, the placenta is located in the central portion of the axis. About 10-15 slightly flattened and erect ovules are aligned in two rows in each locule (Fig. 32E).

10. Fruit and seeds. The fruit is turbinate and 1- to 4-loculed. There are few seeds per fruit. The embryo is

slightly curved with a long radicle.

## Napoleonaeoideae

All three genera of this subfamily possess a showy, sympetalous corolla.

### Asteranthos Desfontaines

Asteranthos is monotypic and endemic to the upper Rio Negro region of Colombia, Venezuela, and Brazil. It is characterized by 1) a unique, rotate, synsepalous calyx, 2) a sympetalous corolla, 3) numerous free stamens, 4) a 1-seeded, indehiscent fruit, and 5) a J-shaped embryo embedded in ruminate endosperm.

1. Inflorescences. The flowers are solitary in both axillary and terminal positions, not only from the leaf axils as described by Miers (1875a), Knuth (1939c) and Prance (1979). The pedicel is 1.5-3.0 cm long and articulates at about 0.4 cm from the base.

2. Bracts. There are 3 or 4 small, leaf-like, alternately arranged bracts below the articulation. Each of the proximal two bracts usually encloses one minute bud, while the distal one or two are empty. Each bract is laterally flanked by a pair of tiny stipules.

3. Calyx. The synsepalous calyx is unlobed and rotate,

about 1.2 to 1.5 cm in diameter, chartaceous, and with 16 to 24 minute teeth on its margin (Fig. 33B). About 16 to 24 veins radiate from the receptacle, enter the calyx, and terminate in the marginal teeth.

4. Corolla. The corolla is sympetalous and composed of 27 to 31 pleated folds before anthesis. At anthesis, the corolla stretches and spreads as a circular fan (Fig. 33A). Each fold is supported by one midvein and a system of reticulate lateral veins. The margin is toothed. The entire corolla is fleshy in early development but becomes more and more membraneous as it matures.

5. Androecium. There are 200 to 300 free stamens densely arranged in 5 to 7 whorls (Fig. 33A). The stamens are uniform and entirely fertile. The filaments are slender, and the anthers are short and basifixed.

6. Style. The filiform style may be up to 1 cm long. The stigma is capitate and usually with 6 clefts.

7. Ovary. The ovary of this species is peculiar in that there are 4 to 6 prominent, buttress-like ridges on the surface of the mature ovary (Fig. 33B) which are outgrowths along the dorsal bundle of each carpel. In early developmental stages, the ovary is typically inferior, and the ovary summit is flat and narrow (Fig. 34A). Later, during the development of the buttress-like ridges, the ovary summit broadens and rises, and the base of the androecium is pressed outward and somewhat downward (Fig.

34B). In mature flower, the ovary becomes semi-inferior (Fig. 34C). There are 4 to 6 locules in the ovary.

8. Placentation. There are usually 4 ovules per locule. The placentation is apical axile. The ventral slit is located at the upper part but does not reach the very apex of the axis. The placenta is situated at the cross zone below the slit.

9. Fruit and seeds. The fruits are 1-seeded. The seed has prominent and ruminate endosperm, a straight or J-shaped embryo, and two small cotyledons.

## Crateranthus Baker

Published information about this genus is very scanty. Crateranthus is characterized by 1) large and imbricate sepals, 2) a sympetalous corolla, 3) numerous stamens which are aligned in many series, and 4) the basal parts of the androecium adnate to the corolla.

1. Inflorescences. They are solitary and axillary.

2. Bracts. In Crateranthus cf. talbotii there are 6 or 7 bracts subtending each flower. They are smooth, coriaceous, entire and alternate.

3. Calyx. There are 3 large, ovate, imbricate sepals. I observed a rare case in which there were only two sepals enclosing the bud. One of them was 2.5 cm wide at its base and probably resulted from the fusion of two sepals. The

sepals are coriaceous, have entire margins, and are glabrous on both surfaces. The calyx persists in the fruit.

4. Corolla. The sympetalous corolla has about 30 ribs. The petals are connate for nearly the entire length of the corolla (Fig. 33E). The thickness of the corolla varies from about 4 mm at the base to membranous toward the apex. Before anthesis, the upper portion of the corolla is curved inward to form a small column. However, the very tip of the corolla bends outward (upward) again and tightly surrounds the protruding long style, thereby separating the stamens and the upper portion of the style (Fig. 33E). At anthesis, the curved upper portion of the corolla straightens out to form a campanulate corolla with an outwardly curving apex. At this stage, the corolla is about 3 cm long.

5. Androecium. The stamens are numerous in Crateranthus. The base of the androecium is congenitally fused to the basal portion of corolla. In the sample of C. cf. talbotii that I examined, eight to ten whorls of stamens were extending out from the corolla. The filaments were not laterally fused with each other within a single whorl. This phenomenon is unique in the angiosperms. The stamens have filiform filaments. The sagittate, rather elongated, anthers dehisce longitudinally.

6. Style. The style is slender, possesses a pointed stigma (Fig. 33E), and is usually persistent.

7. Ovary. According to Baker (1913) and Knuth (1939a), the

ovary of Crateranthus is 3-4 locular and semi-inferior. In C. cf. talbotii, a transformation series, beginning with the ovary in an initial, inferior position and ending with it in a semi-inferior position at maturity, is observed. In two buds at about 1/2 of mature size, the summit of the ovary was truncate and the relative location of the locules was clearly inferior. In two mature flowers, the ovary summit was elevated, and the position of the locules relative to the androecium-corolla complex had risen, thereby producing a semi-inferior ovary (Fig. 33F). The same transformation is also observed in Eschweilera, Lecythis, and Asteranthos. In many species of Couratari, Couroupita, and Gustavia, the ovary summit also elevates, but the position of the ovary remains inferior.

The ovary of C. cf. talbotii is 5-locular. The size of each locule is relatively large and triangular in longitudinal view.

8. Placentation. The placentation is apical, axile placentation. There are about 15-18 pendulous ovules crowded in the upper portion of each locule (Fig. 33F), thus every ovule is very flat in cross section. The ovules only occupy the upper half of the locule (Fig. 33F).

9. Fruit and seeds. The fruits are indehiscent. In C. talbotii, the fruit is ovoid and about 2 cm in diameter (Baker, 1913). The persistent calyx is situated at the proximal end and the style at the distal end of the fruit.

The number of seeds in a fruit is not mentioned by either reference.

## Napoleonaea Beauvois

The floral structures of the eight species of Napoleonaea are similar to each other. Masters' (1869) very detailed and careful study is in harmony with my observations.

1. Inflorescences. The inflorescences are usually solitary and axillary. Occasionally, cauline fascicles on old branches and paniculate inflorescences in axillary positions are found.

2. Bracts. In those species with solitary or cauline inflorescences, there are usually 4-5 bracts inserted below the flowers and no bracteoles. Each bract has a pair of relatively large glands on the abaxial surface.

3. Calyx. There are usually 5, occasionally 6, distinct sepals with valvate aestivation. A pair of glands is present on each sepal. The glands are relatively small and located at the apex. The sepals completely enclose the bud until it reaches 0.5-0.6 cm in diameter.

4. Corolla. The sympetalous corolla is composed of about 35 plicate, incurved ribs (Figs. 33C, 33D). The bud is 5-(6-)angular with each angle subtended by a sepal and internally containing a folded corolla-segment consisting of

7 ribs. The ribs themselves are thickened at the base and taper toward the apex. The membranous corolla is so strongly concrescent that only the very apical parts of the segments are not connate. The margin of the corolla is wavy.

5. Androecium. The androecium of all species consists of three concentric whorls of stamens (Figs. 33C, 35C). Both the outer and the middle whorls are antherless. The outer whorl consists of 60-70 narrow straps which are completely free to slightly connate at their bases. The middle whorl is represented by 30-40 ribbon-like straps which are wider and longer than the outer straps. They are fused with each other laterally to more than two-thirds of their length. Not far from the bases of the outer and middle staminal whorls, there is a specialized folding structure in each whorl at the same level (Fig. 35C). These structures are so well positioned that the two whorls can match and hook up with each other. The significance of this extremely delicate device is not understood. No published report or field observations concerning the function of this structure is available.

The inner whorl consists of 20 stamens. The filaments of these antheriferous stamens have the same general morphology as the sterile ribbons of the middle whorl (Fig. 33C). All curve 360 degrees inwards and then insert their apex into the narrow space beneath the wide stigma, and

between the annular nectary-disk and the short style (Figs. 35A, 35D). Because the stigma is pentagonal, the 20 flattened stamens are grouped and aligned into five linear fascicles of four stamens. Of these four stamens, the outer two develop large, bisporangiate anthers and the inner two possess only a small vestigial anther at their tip (Fig. 35D). Although the anthers are morphologically extrorse, the longitudinal slit actually faces the style because of the 360 degree twisting of the filaments. The anthers remain hidden inside the flower even in anthesis.

The filaments of all three whorls are each supplied by a single, unbranched vascular bundle.

5. Style. The structure of the stigma of Napoleonaea is also unique in the dicots. The entire structure is table-like (Fig. 35A). The stigma is pentagonal (Fig. 35D), or hexagonal, with the number of sides corresponding to the number of sepals. The sides of the stigma alternate with the sepals. The stigma surface is broad, flat, and smooth, sometimes slightly depressed toward the center. The diameter of the stigma is about 4.5 mm. The very thin fusion lines of the 5 carpels are visible (Fig. 35B). A small, but clearly defined opening is situated at the distal end of each fusion slit, which is connected with an internal canal which is embedded within the stylar tissue. The five obliquely oriented lines of fusion meet at the center of the style.

6. Nectary disk. The nectary disk is a roughly ring-like structure which is differentiated from the receptacle on the inner side of the androecium. The disk is in the shape of a decagon surrounding the style (Fig. 35D). The disk is creamy white in color, soft, and penetrated by a very complex vascular system (Fig. 35A).

7. Ovary. The ovary of species of Napoleonaea is inferior. The 5 locules are short and very deeply seated (Fig. 35A).

8. Placentation. The placentation is central, axile. There are about 4 ovules in each locule (Fig. 35E).

9 Fruit and seeds. The fruits are indehiscent and subglobular. The seeds are solitary or two in each cell. The embryo consists of two plano-convex cotyledons and has a short radicle and a large plumule.

# Discussion and Conclusion

The present chapter is a discussion of the comparative morphology of reproductive features. The following discussion focuses on the phylogenetic relationships of the genera of Lecythidaceae s.l. based on the morphological characters described in this chapter only.

## Intergeneric Relationships of Planchonioideae

In Miers' monograph "On the Barringtoniaceae" (1875b), the first sentence is "The Barringtoniaceae form an extremely natural group, offering very distinct and uniform characters." I completely agree with his opinion. One century later, Abdulmajidia was described (Whitmore, 1974), and this new genus fits quite well into the Planchonioideae.

Traditionally, the Planchonioideae is placed in the Myrtales, which was based on the many phenetic similarities between them. But there is a basic difference in the gross floral morphology of the Planchonioideae and the Myrtaceae. In the Planchonioideae, the filaments are basally fused to form a wide tubular structure (the staminal ring), which is in turn adnate to the bases of the petals. This androecium-corolla complex falls as one piece after anthesis. In the core families of Myrtales (Dahlgren & Thorne, 1984), the stamens are entirely free and the petals

and androeium fall separately. Moreover, because of differences in embryology (Tobe & Raven, 1983) and wood anatomy (Van Vliet & Baas, 1984), a close relationship between the Planchonioideae and Myrtaceae is not supported. Therefore, I feel that most, if not all, similarities in floral features between the Planchonioideae and Myrtaceae are the result of convergent evolution.

The high homogeneity of the Planchonioideae supported by palynological features is also supported by floral features. This homogeneity extends to the generic level. Planchonia and Careya are so similar to each other that their generic status is questioned. The remaining four genera possess at least one unique character expression in terms of floral morphology.

The closest taxon to the Planchonioideae, based on reproductive features of those dicots possessing B-T ovules, is Grias of the Lecythidoideae. A description of the similarities between Barringtonia and Grias is given in Table XII.

The most prominent differences in floral features between these two genera are the slender filaments and style and the presence of an intrastaminal disk in Barringtonia (common to all Planchonioideae). This contrasts to the thick filaments, the thick and short style, and the absence of a disk in Grias.

In the cladistic analysis used to interpret the

Table XII

Reproductive morphological features shared by *Barringtonia* and *Grias*

---

Inflorescences: basically cauline or axillary racemes.

Calyx: unlobed in most species, or with 4 distinct sepals in the remaining species.

Corolla: four free, imbricate petals in all species.

Androecium: actinomorphic; numerous stamens arranged in 4 to 8 series, staminal ring formed by the basal fusion of filaments; anthers short and longitudinally dehiscent.

Ovary: inferior throughout development and 4-locular.

Placentation: apical, axile; each carpel with a narrow ventral slit on the upper part of the axis.

No. ovules/locule: basically 4.

Locule: elongated, with ovules occupying the upper half of the locule.

Fruit: indehiscent, fusiform, with 1 large seed.

Embryo: undifferentiated, macropodial.

inter-generic relationships among the Planchonioideae, I have chosen Grias as the outgroup because of its floral similarities with the Planchonioideae. Moreover, Grias is also considered to retain the most primitive character-states in comparison to other genera of Lecythidoideae. Allantoma and the seven zygomorphic genera are obviously more advanced, being far removed from the other two actinomorphic genera, Grias and Gustavia. Species of Gustavia differ from Grias and the Planchonioideae in their poricidally dehiscent anthers, large and more variable petal number (6, 8, 12), basically 6-carpelar gynoecium, and fleshy plano-convex cotylendons.

Twelve floral features that vary within Planchonioideae are polarized as shown in Table XIII. The character-states expressed by each genus are given in Table XIV and a cladogram is presented as Fig. 36.

This cladogram suggests that, in terms of floral features, Barringtonia is generally most primitive. Chydenanthus and Petersianthus possess a few synapomorphis, but no autapomorphies. Whereas Abdulmajidia, Planchonia and Careya, on the contrary, possess many more apomorphies. A clear evolutionary trend, beginning from an ancestor similar to Barringtonia and leading to Planchonia and Careya, is demonstrated by the fact that so many apomorphies are present on the main branch rather than along the lateral branches.

Table XIII

Polarities of 12 important reproductive characters in the Planchonioideae with Grias as the outgroup

| Character | Polarity |
|---|---|
| 1. Inflorescence | cauline or axillary --> cauline, axillary or terminal --> axillary or terminal |
| 2. Calyx | unlobed and lobed --> lobed only |
| 3. No. of petals | 4 --> 3 |
| 4. Nectary disk | not formed --> formed |
| 5. l.s. of disk | hemispheric --> more or less triangular |
| 6. Nectary cavity | not formed --> formed |
| 7. Filament | short --> slender |
| 8. Style | short --> slender |
| 9. Placentation | apical axile --> central axile |
| 10. No.locules/ovary | 4 --> 3 or 2 |
| 11. No.ovules/locule | about 4 --> 5-20 --> more than 20 |
| 12. No.seeds/fruit | 1 --> a few --> numerous |

Table XIV

The character-states of each genus of Planchonioideae based on the polarities shown in Table XIII

| Genus\ Character | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Abdulmajidia | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| Barringtonia | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| Careya | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1,2 | 1,2 |
| Chydenanthus | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| Petersianthus | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| Planchonia | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1,2 |
| Grias | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

An analysis of five features will help to explain evolution in the Planchonioideae. The first is the position of the inflorescence which changes from cauline, axillary, and pendulous in Barringtonia, through shortened and axillary in Abdulmajidia, to terminal, erect, with a short rachis in Planchonia and Careya. The second is a change in the nectary-disk from the primitive state in which the l.s. of the disk is semi-circular in Barringtonia to the advanced state in which the disk is slightly triangular with the upper margin angled, rather than rounded, in Abdulmajidia, and finally to a state in which the region surrounded by the disk is sunken to form a nectary-reservoir, as in Planchonia and Careya. The third and forth are expansion in the placenta with a concomitant increase in ovule number. In Barringtonia, the placenta is restricted to the cross zone at the apical part of the axis and each locule usually contains four pendulous ovules. In the more advanced state, the placenta is longer, along the slightly elongated ventral slit, and the number of ovules per locule rises to many (e.g., Abdulmajidia). A further step is represented by the presence of a very long ventral slit, sometimes as long as the axis, and an increase in the number of ovules per locule to 10-20 as in most species of Planchonia and Careya. The most extreme case is found in Careya arborea, in which the ovules are aligned in 4 rows, rather than in 2 rows as in most species in this subfamily, and the number of ovules per

locule increases to about 40. The fifth is an increase in the number of seeds per fruit from one in Barringtonia to 2-6 in Abdulmajidia, to many or numerous in Planchonia and Careya. Increase in seed number is positively correlated with increase in ovule number.

## Intergeneric Relationships of Lecythidoideae

Floral features are very variable within this subfamily. The ten genera of the Lecythidoideae are reticulately connected in terms of the similarities of their reproductive characters. I will divide my discussion of this subfamily into the actinomorphic genera and zygomorphic genera.

### Actinomorphic genera

Among the three strictly actinomorphic genera, Grias is small (6 species) and homogeneous in floral morphology. Allantoma is monotypic, and Gustavia is much larger with about 40 species. The flower of Allantoma is the most specialized of the actinomorphic genera. However, it shares floral features with Grias. Both Allantoma lineata and Grias cauliflora have a cup-like calyx, free, imbricate petals, a thick and fleshy staminal ring, and four whorls of stamens. A radially constricted and longitudinally

elongated G. cauliflora flower would produce a flower similar to that of A. lineata. In the evolution from a Grias-like flower to an Allantoma-like flower, two other floral features developed. Placentation changed from apical axile with few ovules per locule, as in Grias, to central axile with more than ten ovules per locule, as in Allantoma. The unlobed calyx, as found in most species of Grias, evolved into the 5-toothed calyx as currently expressed in Allantoma. Several significant changes also occurred in fruit and seed evolution. Single seeded, indehiscent fruits, as found in Grias, constant with the many-seeded pyxidium of Allantoma. In addition, the seeds of species of Grias are without an aril, whereas the seeds of Allantoma lineata have a well-developed aril.

The possible linear relationship between Grias and Allantoma has long been considered by Mori (pers. comm.). However, phylogenetic relationships of Gustavia were not clear. When concerning the reproductive features that express plesiomorphy represented by Barringtonia and Grias, the section Gustavia of Gustavia also maintain many of these plesiomorphies, such as cauline inflorescences, unlobed calyx, 4-merous floral parts, and indehiscent fruit.

In summary, the floral features common to Barringtonia and Grias, and to a lesser extent, Gustavia are: 1) the dominance of cauline inflorescences, 2) an entire calyx, 3) four free, imbricate petals, 4) numerous stamens, 5)

incurved filaments in bud, 6) the presence of a staminal ring, and 6) an inferior ovary throughout development. As far as I know, no other dicot families show this combination of floral syndromes. Based on this fact, I consider these common character-expressions as representing the symplesiomorphies of Lecythidaceae.

## Zygomorphic genera and the origin of the zygomorphic androecium in the Lecythidoideae

Many floral features, especially those associated with the zygomorphy of the androecium, vary greatly within this zygomorphic group. The distribution of this variation is such that some genera are similar to other genera in certain features, while closer to different genera in other features. These reticulate phenetic interrelationships inhibit an understanding of the phylogeny of the seven genera of zygomorphic-flowered Lecythidaceae.

Because zygomorphism, mostly of the androecium, is a common characteristic of these seven genera, I will first discuss the possible evolutionary origin of zygomorphy. In this connection, Cariniana occupies a key position because all stages of zygomorphy from actinomorphic, through slightly zygomorphic, to a strongly zygomorphic androecium are found in its 15 known species. One characteristic of the genus is its comparatively small flowers. There are

several species of Cariniana with flowers similar to those of Allantoma. Initial evolution of zygomorphy may have started with an ancestor with Grias-like flowers, through ancestors with Allantoma-like flowers into the zygomorphic flowers of Cariniana. Within such a small flower, in the earliest stage of androecial initiation, the degree of lateral fusion among staminal primordia may have been promoted because of the increased compactness of the primordia.

Later, or simultaneous with this process, another factor may have contributed to the establishment of zygomorphy in Cariniana. In a few species of Cariniana which have five fleshy petals, the androecium is only slightly zygomorphic. This suggests that the evolution of zygomorphism started with a five-petaled ancestor. The quincunically arranged petals of the hypothetical ancestor would have been thick from early stages of development, similar to the petals of Grias and Allantoma. When the staminal primordia of this type of flower initiate, the thick, young petals arch over the space immediately above the staminal primordia. It is possible that the availability of the space in these tiny flowers may have exerted some influence on the subsequent development of the androecium. In my observations of the materials of C. pauciramosa in early development, the fifth petal, i.e. the innermost one, although initiated last, is already thick enough to exsert pressure onto the adjacent

young stamens, which are shorter than the remaining stamens. This demonstrates the onset of the breakdown of radial symmetry. The perpetual suppression of the fifth petal on the adaxial part of the androecium throughout the developmental process would have caused a depression on this side, and the relatively larger space for the stamens next to the first petal would allow these stamens to extend their growth on the abaxial side of the flower.

The species of Cariniana have the same placentation type, 3-locular ovary, and fruit morphology as Allantoma. The androecia of Allantoma and some species of Cariniana are nearly identical. Consequently, I conclude that Cariniana must have a very intimate relationship with Allantoma. Consequently, Grias, Allantoma, and Cariniana demonstrate an evolutionary trend which is characterized by a transition from an actinomorphic to a zygomorphic androecium. Within the evolution of Cariniana, two features have been fixed. First, a calyx with six distinct sepals became established. Second, the number of locules, i.e., the number of carpels, was reduced from four (as in Grias and Allantoma) to three.

Couratari can be incorporated within this lineage without any serious question. The similarity in androecial structure is less between Cariniana and Couratari than between Couratari and some other zygomorphic genera. The hood of Cariniana is simple, being scarcely developed or represented by a flat surface. On the other hand, the hood

of Couratari is much more complex, being S-shaped as viewed in medial section, with nectary glands derived from sterile stamens. In structure, it is most comparable with the androecia of some species of Eschweilera. However, an analysis of three other reproductive characters reveals three important similarities between Cariniana and Couratari: 1) 3-locular ovary, 2) winged seeds, and 3) the operculum of the pyxidium which is attached by a long columella. These features are not found in any other genera of Lecythidaceae. Moreover, leaf-like cotyledons, are only present in these two genera and Couroupita. Another important similarity is found in the thin and unspecialized stamens of Couratari which are most similar to those of Cariniana. The other five zygomorphic genera are collectively characterized by specialized filaments which dilate toward the apex but constrict again at the apex.

A close phylogenetic relationship between Cariniana and Couratari is supported because of the following reasons. First, the number of phenetic similarities between these two genera is much higher than that between Couratari and the other zygomorphic genera. Second, three of these similarities (3-locular ovary, winged seeds, and long columella) are not found in other zygomorphic genera. This indicates a well-defined clade represented by them alone. Third, the similarities between these two genera are found in the flower, fruit, seed and embryo. The co-occurrence of

these characteristics, which are critical reproductive features, as the result of convergence is highly unlikely. On the contrary, it is more likely that the similar form of the hood of Couratari and Eschweilera is caused by convergence, since the modified hood structure is much more subject to change because of adaptation to similar pollinators. Finally, the poorly developed zygomorphism in the androecium of Cariniana, with further evolution, could lead to the highly zygomorphic androecium of Couratari.

Among the remaining zygomorphic genera, Bertholletia, Corythophora, Eschweilera, and Lecythis are grouped together by many similarities in reproductive features. Lecythis clearly occupies a central position in this group. Generally speaking, the main types of androecia found in the other genera are also found in Lecythis.

Bertholletia is monotypic, clearly separated from the other three genera by 1) the very large and unlobed calyx in bud, 2) the operculum of the fruit which is very small and falls inward rather than outwards, and 3) the bony seed testa. However, the unique, unlobed calyx does not support a remote position for Bertholletia, because the six teeth of the mature calyx indicate that it was derived from the fusion of six sepals, the only type of calyx found in the other zygomorphic genera. In addition, this genus is very similar to some species of Lecythis (e.g., L. lurida) in hood structure, style type, ovary structure, and

placentation. Particularly significant is the fact that the geniculate style, bending toward the anterior of the flower, is only found in Bertholletia and some species of Lecythis within the whole subfamily. As has been suggested elsewhere, Bertholletia, has probably evolved from ancestors similar to present-day species of Lecythis (Mori & Prance, 1990).

Corythophora is a small genus with four species. It is characterized by 1) usually 2-locular ovaries, 2) a flat, oblong, dorsi-ventrally expanded hood, 3) basal-axile placentation, 4) the operculum of the pyxidium with a short columella, and 5) arillate seeds. However, all these features are also found in Lecythis. It is apparent that this genus represents a minor clade that evolved from Lecythis-like ancestors (Mori, pers. comm.).

Eschweilera has a 1) 2-(4-)locular ovary, 2) basal-axile placenta, 3) gradually elevated ovary-summit during development, 4) globose fruit, 5) short columella, and 6) seeds usually with lateral arils. All these features can also be found individually or in combination in Lecythis. The unique, diagnostic hood of Eschweilera, which is expanded and completely coiled with highly modified sterile stamens located internally at the apex of the coil, is morphologically similar to the hoods of a few species of Lecythis, although these species of Lecythis never quite form the complete coil so characteristic of most species of

Eschweilera. The phylogeny of Eschweilera, similar to that of Bertholletia and that of Corythophora, can be explained as a clade which radiated from Lecythis-like ancestors.

Lecythis itself includes only 26 species. Some species of Lecythis are similar to Couroupita in hood structure, other species of Lecythis exhibit similarities with Couratari in style, and placentation features, and others resemble species of Bertholletia, Corythophora, and Eschweilera in the reproductive features mentioned above. Intrageneric relationships in Lecythis are extremely complicated. Although morphologically it is a genus which can be easily recognized, it may not represent a monophyletic group. Because Lecythis has no unique features, its phylogenetic relationships are still unclear.

The basic reproductive structures of nearly all species of Bertholletia, Corythophora, Eschweilera, and Lecythis are homogeneous; most of these reproductive features are apomorphic when compared with the actinomorphic genera. Finally, many of these features are not found in other genera of Lecythidaceae. Consequently, these four genera possess reproductive synapomorphies and represent a distinct group within the zygomorphic genera in terms of complexity and specialization of reproductive structures. The relatively large number of extant species in these genera (ca. 114 species, Mori & Prance, 1990) testifies to the evolutionary success of this clade.

The remaining zygomorphic genus of four species, Couroupita, is relatively isolated among the zygomorphic genera. In androecial morphology, however, it is comparable with some species of Lecythis (e.g. those species of Lecythis sect. Pisonis) in the erect staminal-ring and flat hood with non-fertile pollen in the anthers of the hood stamens. In Couroupita, the stamens are always densely compacted in the staminal ring, but relatively sparsely placed on the hood. The appendages may cover the entire ligule (e.g., Couroupita nicaraguarensis, Fig. 34 in Mori & Prance, 1990) or they may be completely lacking from the ligule (the remaining species, Fig. 34 in Mori & Prance, 1990). The gross morphology of the filaments of the ring stamens is comparable to that of Bertholletia, Corythophora, Eschweilera, and Lecythis in the clavate apex. However, Couroupita differs from all other zygomorphic genera in its 1) 6-locular ovary, 2) very long central axile placenta, 3) numerous ovules aligned on an elongated bilamellar placenta, 4) indehiscent woody fruit, 5) hairy, lenticular-shaped seeds, and 6) foliaceous cotyledons (also present in Cariniana and Couratari). In the ovaries of all other zygomorphic genera except Cariniana, the locules are more or less dorsiventrally flattened, the central axis is short, and the placenta is rather restricted. Moreover, the number of carpels per ovary is usually less than six. The only exception is the occasional occurrence of six locules in a

few species of Lecythis. Consequently, the position of Couroupita is rather isolated among the zygomorphic genera of Lecythidaceae.

The features of the androecium of Couroupita suggest that zygomorphism in Couroupita may represent an initial stage in the evolutionary trend from actinomorphism to zygomorphism. In the first place, the anterior side of the staminal ring is broader and more or less erect rather than flattened or much reduced in other zygomorphic genera (with the exception of Cariniana and few species of Lecythis). In this respect, the anterior side of the staminal ring of Couroupita resembles the staminal ring of Grias and Gustavia. In the second place, at least in Couroupita nicaraguarensis, the entire androecium is fertile. This situation is comparable to that found in species of Cariniana. All other zygomorphic genera have the ligule, and sometimes even the hood sterile. A comparision of the zygomorphism of Couroupita with that of Bertholletia, Corythophora, Couratari, Eschweilera and Lecythis reveals fundamental differences in structure. There are also fundamental differences between Couroupita and the lineage from Grias to Allantoma and Cariniana. Gustavia, however, exhibits many features similar to those of Couroupita. The number of stamens per flower is numerous in Gustavia and Couroupita, and the stamens are so densely distributed that separate whorls of stamens can not be distinguished. In

Grias-Allantoma-Cariniana, the number of stamens per flower ranges from 10-200 (85-210 in Grias, ca. 30 in Allantoma and 10-150 in Cariniana, Prance & Mori, 1979), and the stamens are usually arranged in several distinct whorls. The filaments of Gustavia and Couroupita are slender and clavate at the apex, but not so in Grias, Allantoma, and Cariniana. Besides the androecial similarities between Gustavia and Couroupita, these two genera also possess 6-locular ovaries, central axile placentation, numerous ovules aligned on the elongated placenta, and indehiscent fruit.

The character analysis presented above indicates Gustavia as the most probable candidate for the ascestor which has given rise to Couroupita. However, the species of Gustavia have poricidally dehiscent anthers, which negates a direct relationship between them. In summary, Couroupita seems rather isolated among the zygomorphic genera and probably has its closest relationship with Gustavia.

The zygomorphism of the seven zygomorphic genera must have evolved from lecythidoid actinomorphic ancestors. Although all of the evolutionary steps toward the most specialized androecia are not always represented by extant species, the evidence drawn from various reproductive features supports the existence of two distinct lineages in which zygomorphic androecia have occurred independently. The ancestors of these two lineages probably had reproductive features similar to those found in extant

species of Gustavia and Grias.

Gustavia and Grias have many common symplesiomorphic reproductive characteristics. These two genera retain many of the ancestral features of the subfamily Lecythidoideae. Allantoma and Cariniana show a direct relationship to Grias, and because all other zygomorphic genera of the subfamily have evolved from zygomorphic ancestors or from actinomorphic ancestors similar to either Gustavia or Grias, monophyly of Lecythidaceae subfamily Lecythidoideae is clearly supported.

## Inter-subfamilial Relationships of Foetidioideae

The Planchonioideae and Lecythidoideae form distinct groups in terms of floral features, as discussed in the previous paragraphs. Barringtonia, Grias, and Gustavia retain the most numerous primitive character states of these two subfamilies. The unifying features of this core group of Lecythidaceae include: free and imbricate petals, numerous stamens, a clear staminal-ring formed by the tangentially and radially fused basal portions of the filaments, and an inferior ovary.

Although Foetidia has an inferior ovary, it is without petals and has numerous completely free stamens. In addition, Foetidia possesses valvate and woody sepals enclosing the bud until anthesis, and a trifid (or tetrafid)

stigma, traits not found in any other genus of Lecythidaceae. In gross floral morphology, the resemblence between Foetidia and the core-Lecythidaceae is restricted to the inferior ovary and the numerous stamens. Based on the distribution of these two character expressions in the dicots, no arguments can be offered to support a close relationship between Foetidia and the core-Lecythidaceae.

## Inter-subfamilial Relationships of the Napoleonaeoideae

The difference among the three genera of Napoleonaeoideae in reproductive features is greater than the embryological divergences. Within the species of each genus, reproductive structures are rather homogeneous (Asteranthos is monotypic). However, the three genera possesses many unusual characteristics, some of which do not occur in the other subfamilies of Lecythidaceae s.l., or are even absent in other dicots. This points to very distinct relationships among the genera as well as a very isolated position of the subfamily. The differences in reproductive features among these genera and a comparison with Planchonioideae and Lecythidoideae are discussed below.

1. Calyx. Asteranthos has a plate-like, synsepalous calyx, with 16-24 radiating veins. Crateranthus has three very large, imbricate sepals, while the calyx of Napoleonaea is composed of five or six valvate sepals, each of which has

two large glands. In the Planchonioideae and Lecythidoideae, the calyx is unlobed in the more archaic genera and composed of distinct, imbricate sepals in the more advanced genera. Features of the calyx are rather uniform within the advanced genera.

2. Corolla. The three genera of the Napoleonaeoideae have highly derived, multi-veined, sympetalous, showy corollas. The origin of the corollas may be either petalar or staminodial. Only Masters (1869) has seriously argued that the corolla of Napoleonaea was of staminodial origin. No other solid work concerning this topic has been done. Taxonomists have grouped these three genera together because of their similar-looking and specialized corollas. However, to do so, without questioning their homology, is an obvious mistake. The difference between the sympetalous corolla in Napoleonaeoideae and the corolla of four to eight free petals in the Plachonioideae and Lecythidoideae is very significant phylogenetically because calyx and corolla aestivation is usually constant at the familial, or even the ordinal level. There are three possibilities for the common occurrence of a similar type of corolla in these three genera: homology, parallelism, and convergence. A SEM study on the early development of the corolla of these genera will offer the information needed to answer this question. Another way to approach this problem is through phylogenetic analysis of each genus. The nature of the corolla of each

genus may then become apparent by analyzing the homologous structure of their respective sister groups.

3. Androecium. Although all three genera of Napoleonaeoideae have many stamens, there are many differences in their androecia. The stamens of Asteranthos are uniform in morphology, free from each other, and bear tetrasporangiate, short anthers. The stamens of Crateranthus are also morphologically uniform, but their bases are congenitally fused with the base of the corolla, the anthers are rather elongated, tetrasporangiate, and sagittate. In Napoleonaea, there are two outer whorls of staminodes, and in the inner whorl only half of the stamens (ca. 10) are antheriferous. The anthers of Napoleonaea are bisporangiate, extrorse, and very large in comparison to most dicots. The clearly defined staminal ring, which is derived from fusion of the bases of the filaments, a major characteristic of both the Planchonioideae and Lecythidoideae, is absent in the genera of Napoleonaeoideae. In terms of the androecium, the genera of the Napoleonaeoideae and the Planchonioideae /Lecythidoideae have evolved distinctly different features.

4. Nectary disk. The Planchonioideae are characterized by a prominent nectary disk while the Lecythidoideae lack a nectary disk. Napoleonaea has a well-developed nectary disk. Because the disk of Napoleonaea and those of most species of Planchonioideae are morphologically primitive and

have a generalized annular shape, it is difficult to determine if their disks are of common origin or not.

5. Style and stigma. These three genera have very different styles and stigmas which are in turn, different from those in the Planchonioideae or Lecythidoideae. The unique style-stigma complex of Napoleonaea is somewhat similar to that of some species of Clusiaceae. However, the stigma of Napoleonaea is far more specialized.

6. Ovary position. In both Asteranthos and Crateranthus, the ovaries of the mature flowers are semi-inferior while those of young flowers are usually inferior. The same transformation of ovary position is also found in some species of Lecythidoideae. The ovaries of Napoleonaea, all species of Planchonioideae, and the remaining species of Lecythidoideae are inferior throughout development. The deeply embedded locules of the ovary of Napoleonaea represent an extreme modification.

7. Fruit. Both Asteranthos and Crateranthus possess a persistent calyx located at the proximal end of the mature fruit and a persistent style at the top. The position of the persistent calyx is comparable to that of fruits developed from superior ovaries in dicots. While in Napoleonaea and the other two subfamilies, the persistent calyx or scar of the calyx on the mature fruit, is located at the distal end as is typical for fruits developed from inferior ovaries.

Reproductive features vary so much within the Napoleonaeoideae, that it seems probable that these three genera should not be grouped together within the same subfamily and that they do not belong to a family of their own. In the Lecythidaceae s.l., the genera of the Napoleonaeoideae do not show direct relationships with either the Planchonioideae or Lecythidoideae.

## Conclusions

The six genera of Planchonioideae and the 10 genera of Lecythidoideae represent separate monophyletic groups. Furthermore, the genera retaining the most primitive character-states within these two subfamilies have enough plesiomorphies in common to support the idea that they are symplesiomorphies inherited from a common ancestor.

In terms of reproductive morphology, these two subfamilies constitute the core-group of Lecythidaceae s.l. However, the other two subfamilies do not appear to have close relationships with this core-group. Moreover, the Napoleonaeoideae is morphologically too heterogeneous to be accepted as a coherent taxon at the subfamilial rank.

# Chapter VI PHYLOGENY AND SYSTEMATIC TREATMENT

Many critical features have been investigated in the Lecythidaceae s.l., e.g., cytology mainly by Kowal (Kowal, 1989; Kowal et al 1977), Mangenot and Mangenot (1957, 1958, 1962), and Sarkar et al. (1976, 1978a, 1978b, 1982); palynology by Erdtman (1952) and Muller (1972, 1973, 1979); wood anatomy by Diehl (1935) and Zeeuw (1987, 1990); embryology by Mauritzon (1939a), Venkateswarlu (1952a), and in this work; general morphology by Miers (1874, 1875a, 1875b), Knuth (1939a, 1939b, 1939c), Prance & Mori (1979), Mori & Prance (1990), and in this work. Based on this information, I will first define the core-group of Lecythidaceae and then try to find its closest relative among the dicot families. Subsequently, I will evaluate the relationship of problematic taxa with the core-Lecythidaceae. After the problematic taxa have been removed from the Lecythidaceae s.l., a monophyletic Lecythidaceae will have been established. The systematic positions of the problematic taxa will also be briefly discussed.

## Are the Planchonioideae and Lecythidoideae Monophyletic Subfamilies?

Monophyly of the Planchonioideae has been supported in Chapter III and further reinforced in Chapter V. The six

genera of Planchonioideae form a monophyletic group defined by the common presence of a very specialized type of syn-tricolpate pollen (Figs. 1A-E, 2A-B) which is unique in the dicots. The basic chromosome number of x = 13 in five genera (Abdulmajidia is unknown) is different from the base numbers of x = 17 for the Lecythidoideae and x = 16 and 21 for the Napoleonaeoideae (Kowal, 1989). Chromosome numbers are unknown for the Foetidioideae. The cortical bundles of young stems are inverted (xylem outside, phloem inside) in all planchonioid genera investigated (Lignier, 1890), a characteristic shared only with Foetidia within the Lecythidaceae s.l. Wood features are expressed rather consistently within the Planchonioideae (Diehl, 1935).

Reproductive features as discussed in Chapter V are homogeneous among the six genera. Petersianthus and Chydenanthus represent an early offshoot, while the other four genera comprise the evolutionary mainstream of the subfamily, with Barringtonia perhaps representing the most archaic genus. Embryological features as discussed in Chapter IV, support these intrasubfamilial relationships.

Consequently, it is clear that the six genera of Planchonioideae constitute a very tightly knit group which merits subfamilial status within the Lecythidaceae s.l.

In contrast, the phylogeny of the Lecythidoideae is more complex and less clear. The pollen of the ten genera of Lecythidoideae is the most common type of the dicots, i.e.

tri-aperturated (3-colpate, 3-colporoidate, or 3-colporate). The surface sculpturing is generally foveolate to fine-reticulate (Muller, 1979). The androecial morphology of these ten genera, however, does support the monophyly of the Lecythidoideae.

In the analysis of reproductive features (Chapter V), I hypothesized that a Grias-like, actinomorphic-flowered ancestor probably gave rise to Allantoma, and subsequently to the zygomorphic-flowered genera Cariniana and Couratari. I also suggested that another evolutionary line, originating from a Gustavia-like ancestor, give rise to at least one zygomorphic-flowered genus, Couroupita.

The remaining zygomorphic-flowered genera of the subfamily ( Bertholletia, Corythophora, Eschweilera & Lecythis) include about three-fifths of the total number of species of the subfamily. These genera are more closely related to each other than they are to any other genus of the subfamily. At the same time they express similarities to other zygomorphic genera in most reproductive features and possess almost no unique or within-group characteristics. Although they can be viewed as representing a coherent group, the phylogenetic relationship of this group is not evident to me. The evolutionary history of these genera could represent an early branch diverging from the Gustavia-Couroupita line or from the Grias-Allantoma-Cariniana-Couratari line.

In considering the two most basic actinomorphic genera, Grias and Gustavia, the usually unlobed calyx and the unspecialized actinomorphic staminal ring which takes the shape of a short cylinder with rather long filaments around the apex, indicate the archaic evolutionary status of these genera. They also have numerous wood anatomical features in common which may represent plesiomorphies of the subfamily. The wood anatomy of Grias and Gustavia differs from the remaining eight genera, which have similar wood anatomy among themselves (Zeeuw, 1990).

Embryological features of the Lecythidoideae are homogeneous (Chapter IV). The basic chromosome number of the eight genera counted, including Grias and Gustavia is x = 17 (rarely 34, or 18) (Kowal, 1989). All genera investigated possess normally oriented cortical bundles (Lignier, 1890; Mori & Black, 1987). All ten genera have crystalliferous parenchymatous strands (Diehl, 1935; Zeeuw, 1990). All these studies support the hypothesis that the Lecythidoideae represent a monophyletic group.

## The core-group of Lecythidaceae

I have provided evidence which supports the monophyly of the Planchonioideae and Lecythidoideae. I now wish to establish the relationship between these two subfamilies. In terms of reproductive features, the two basic

actinomorphic genera of Lecythidoideae, Grias and Gustavia, and all genera of Planchonioideae are similar in the fusion and curvature of their filaments. In all genera, the filaments curve inwards from their inception until anthesis. This characteristic, as well as the presence of a differentiated staminal ring, are not common in dicots. Other reproductive features, such as floral merosity (basically 4 in the more primitive taxa), similarity in sepals (unlobed in the more primitive taxa), similarity in petals (free and imbricate), number of stamens (numerous), and position of ovary (inferior in more primitive taxa) further support the close relationship of the Planchonioideae and Lecythidoideae.

The remaining four genera of Lecythidaceae s.l., Foetidia, Asteranthos, Crateranthus, and Napoleonaea have been treated differently throughout their taxonomic history (Prance & Mori, 1979, p.13-16, 126). They have been placed in various families. None of these genera show clear affinities with the subfamilies Planchonioideae and Lecythidoideae. Hence, I consider the Planchonioideae and Lecythidoideae as the core-group of Lecythidaceae.

The principal characteristics within the core-Lecythidaceae are as follows:

1. Young stems with cortical bundles.
2. Some genera with inconspicuous stipules which are presumed vestigial.

3. Leaves simple and alternately arranged (except opposite and tufted in Abdulmajidia maxwelliana).
4. Calyx unlobed in early developmental stages in primitive state, evolved to distinct sepals in generally more advanced taxa, but secondarily unlobed in Bertholletia.
5. Petals always large, showy, free, and imbricate.
6. Stamens numerous and spiral in arrangement. The morphologically basal parts of the filaments are fused into a "staminal ring." In the Lecythidoideae, the unequal development of the two sides (abaxial and adaxial) of staminal ring causes the development of a zygomorphic androecium in seven of the ten genera.
7. Anthers tetrasporangiate and 2-locular at anthesis.
8. Ovary inferior (except secondarily semi-inferior in some advanced genera of the Lecythidoideae).
9. Placentation axile. In both subfamilies the evolution from apical to central axile placentation has occurred. In the Lecythidoideae there has also been a shift from central to basal axile placentation.
10. Ovules bitegmic and tenuinucellate.
11. Both integuments many cell layers thick.
12. The micropyle is formed by the inner integument only.
13. The raphe bundle enters the outer integument.

The differences between the two subfamilies making up the core-Lecythidaceae are presented in Table XV.

Table XV

A comparision of the differences between the two subfamilies of the core-Lecythidaceae

| | Planchonioideae | Lecythidoideae |
|---|---|---|
| 1.Basic chromosome no. | X= 13 (26) | x= 17 (34, 18) |
| 2.Cortical bundles orientation | reversed | normal |
| 3.Crystalliferous parenchyma strands | without | with |
| 4.Floral nectary disk | with | without |
| 5.Pollen type | syntricolpate | tri-colporoidate or tri-colporate |
| 6.Filament | linear, very elongated | short, except medium long in *Grias*, *Gustavia* |
| 7.Style | linear, very elongated | usually short, except long in *Bertholletia* and a few species of *Lecythis* |

## The closest relative of the core-Lecythidaceae

The systematic position of the Lecythidaceae has not been established with certainty. I have searched for the affinities of the core-Lecythidaceae through a literature survey of the dicot families and my own investigations of the Lecythidaceae s.l. As a result of this search, it is clear that the Scytopetalaceae share many phenetic similarities with the core-Lecythidaceae. Features of the young stem anatomy, wood anatomy, reproductive morphology, and embryology suggest a relatively close phylogenetic relationship between the Scytopetalaceae and the core-Lecythidaceae.

Both the Scytopetalaceae and the core-Lecythidaceae consistently have stratified phloem in the bark and cortical bundles in the young stem. The consistent presence of both these features is not common in dicot families (Cronquist, 1981; Metcalfe & Chalk, 1983). Metcalfe & Chalk (1983, p.54) pointed out that, "cortical bundles are diagnostically significant because of their taxonomically restricted occurrence."

Carlquist (1988), in his wood anatomical work on the Scytopetalaceae, has compared the expressions of 11 important wood features of Scytopetalaceae with those of four families with wood similar to that of the Scytopetalaceae. The Lecythidaceae share all 11 character-

states with the Scytopetalaceae. The Ochnaceae share 10, the Theaceae 9, and the Cunoniaceae 11 of these wood anatomical features with the Scytopetalaceae.

In terms of embryology, the core-Lecythidaceae resembles the Scytopetalaceae, Ochnaceae, Theaceae, Ebenaceae, and Styracaceae (Chapter IV).

In reproductive morphology, a feature found in the putatively primitive genera Barringtonia of the Planchonioideae and Grias and Gustavia of the Lecythidoideae is the unlobed calyx which is a uniform characteristic of the Scytopetalaceae. In addition, numerous stamens with the bases of filaments fused into a ring is characteristic of all the core-Lecythidaceae and also present in two of the five genera of Scytopetalaceae (Brazzeria and Pierrina) (Letouzey, 1978). In regard to reproductive morphology, Scytopetalaceae and the core-Lecythidaceae have only a few synapomorphies, mainly because the core-Lecythidaceae itself has very few reproductive apomorphies. The core-Lecythidaceae does not show a close affinity with any other thealean or ebenalean family in reproductive features.

In regard to palynology, the basic pollen type of the Lecythidoideae is tricolpor(oid)ate and the surface sculpturing is basically fine-reticulate to punctate. The colpus membrane is sometimes granulate. The pollen of all five genera of Scytopetalaceae is tricolp(or)ate (Erdtman, 1971). Both reticulate exine surface and granulate colpus

membranes are also commonly found in the pollen grains of the Scytopetalaceae. At a higher taxonomic level, the pollen of Lecythidoideae and Scytopetalaceae are similar to that of many other thealean families. Vijayaraghavar and Dhar (1976), in a study of the embryology of Scytopetalum tieghemii, described the pollen of this species as triporate. However, Erdtman's (1971) observation with the LM and my own study (Anschoff 2318, MO 2422449) with the SEM of the pollen of the same species show exclusively tricolpate pollen. Letouzey (1978) described the pollen type of the Scytopetalaceae as 3-porate which conflicts with Erdtman's survey of all the genera of Scytopetalaceae in which he shows the pollen as tricolpate. Unfortunately, Letouzey did not provide references to the source of his information.

Zeeuw (1990), in his extensive survey of the wood anatomy of Lecythidoideae, has pointed out that, "The Lecythidaceae are similar in gross appearance of the wood to the Chrysobalanaceae, Ebenaceae and Sapotaceae." Although his study did not emphasize the affinity between the core-Lecythidaceae and the Scytopetalaceae, a comparison of the wood features of the core-Lecythidaceae, Scytopetalaceae, Ochnaceae, Ebenaceae, and other supposedly related families is needed before we can conclude their relationships in terms of wood anatomy. The same degree of similarity in embryology is found between the core-Lecythidaceae and the

Scytopetalaceae and among the Scytopetalaceae, Ochnaceae, Ebenaceae, and Styracaceae. In contrast, the Theaceae have the Allium-type embryo sac formation.

The similarity between the core-Lecythidaceae and some ebenalean families, notably Ebenaceae, in wood anatomy and embryology is striking. However, their differences in young stem anatomy and reproductive morphology are almost equally striking. The ebenalean families do not have stratified phloem and cortical bundles. In their reproductive features, the Ebenales are characterized by a sympetalous corolla and more or less fixed number of stamens, which are usually 2 to 3 times as many as the corolla-lobes (excluding the Symplocaceae).

Cronquist (1988), in his discussion of the systematic position of the Lecythidaceae s.l., stated that, "the Lecythidales and Malvales have undergone partly parallel and partly divergent specializations from a common ancestry in the Theales." He implied that the ancestry of both the Lecythidaceae s.l. and Malvales lies in the Ochnales s.s. If we exclude the unique zygomorphic androecium of the Lecythidoideae from our consideration, it is possible to conceive a close relationship between the core-Lecythidaceae and the Scytopetalaceae.

## The systematic consideration of Foetididioideae

The following characteristics of Foetidia clearly separate it from the core-Lecythidaceae 1) large woody sepals, 2) lack of petals, 3) 3- or 4-fid stigma on a moderately long style, and 4) numerous free stamens. The first two features are autapomorphies of Foetidia. It is clear that Foetidia does not belong to the Lecythidaceae.

All other known characteristics of Foetidia are rather common in the broadly defined Theales. The possession of cortical bundles and B-T ovules with thick integuments in Foetidia suggests a greater affinity with the core-Lecythidaceae, Ochnaceae, and Scytopetalaceae than to other thealean (s.l.) families. The cortical bundles of Foetidia are reversed in orientation, as are those of the Planchonioideae. The inferior ovary is found in the Lecythidaceae, but not in the Ochnaceae and Scytopetalaceae. The very densely paralleled lateral veins of the leaves and the 3- or 4-fid stigma have precedent in the Ochnaceae. The numerous free stamens, without clustering into groups of fixed number, are similar to the stamens of many Scytopetalaceae. In conclusion, it seems best to segregate Foetidia as a distinct family, Foetidiaceae, as suggested by Airy-Shaw (1973), forming a satellite family around a core group including at least the Lecythidaceae, Ochnaceae, and Scytopetalaceae without showing any particular affinity to

any one of them.

## Systematic considerations of the Napoleonaeoideae (Asteranthos, Crateranthus and Napoleonaea)

The reproductive features of the genera of the Napoleonaeoideae are variable. The embryology of the genera of this subfamily is also not homogeneous. The basic chromosome number is x = 21 in Asteranthos and x = 16 in Napoleonaea (Kowal, 1989). Crystalliferous parenchymatous strands are present in Asteranthos, but absent in Napoleonaea (Diehl, 1935; Zeeuw, 1990). Because of the disparity in these taxonomic features, I will discuss the affinities of the members of this subfamily genus by genus.

### Asteranthos

In Asteranthos, the plate-like, multiveined, synsepalous calyx which is accrescent in the fruit; the umbel-like, multiveined, sympetalous corolla; the numerous free stamens; the semi-inferior ovary in mature flowers; and the abundant ruminate endosperm all negate a close relationship between this genus and other Lecythidaceae s.l. It is noteworthy that the features which segregate Asteranthos from the core-Lecythidaceae are compatible with the Scytopetalaceae. The characteristics of Scytopetalaceae are the plate-like, or

cup-like, synsepalous calyx; the valvate or even highly fused petals; the numerous stamens which are either free or slightly fused basally; the superior to semi-inferior ovary; and the abundant endosperm which is ruminate in at least two genera (Rhaptopetalum and Scytopetalum) (Letouzey, 1960). Other important characteristics of Scytopetalaceae, which also characterize Asteranthos, include the presence of cortical bundles, stratified phloem, simple petiole anatomy, crystalliferous parenchymatous strands, tricolpor(oid)ate pollen grains with fine-reticulate sculpturing and granulate colpus membranes (Fig. 2D), and similar embryological features. In addition, wood anatomical features are very similarly expressed in Asteranthos (Zeeuw, 1990) and the Scytopetalaceae (Carlquist, 1988).

The five genera of Scytopetalaceae are rather variable in reproductive morphology. The similarity in reproductive features between Asteranthos and Scytopetalum is greater than that between Scytopetalum and some other genera of Scytopetalaceae, such as Rhaptopetalum. Scytopetalum has stamens with long filaments and short anthers which dehisce longitudinally, a 6-lobed stigma, and a one-seeded fruit, all features shared with Asteranthos. On the other hand, the species of Rhaptopetalum have stamens with short filaments and long anthers which are obliquely poricidal, an unlobed stigma, and a many-seeded fruit.

The greatest differences between Asteranthos and the Scytopetalaceae are in the inflorescence, the structure of the corolla, and the cristarque cells (crystal-bearing cells with U-shaped wall-thickenings). All Scytopetalaceae have racemes or panicles while Asteranthos has simple inflorescences with only one or two flowers. In Asteranthos, the petals are highly fused into an obconic-like corolla which is plicate in the bud and does not split at all at anthesis. The corolla of Scytopetalaceae is usually composed of valvate, linear, and distinct petals, or sometimes sympetalous. When sympetalous, the corolla splits into few or many members, evenly or irregularly, or forms a calyptra at maturity. The cristarque cells are present in Scytopetalaceae, but absent in Asteranthos.

The basic chromosome number of Asteranthos brasiliensis is x = 21 (Kowal, 1989) which is different from the basic numbers in the Scytopetalaceae (X = 18 in Rhaptopetalum and x = 11 in Scytopetalum). Consequently, cytology does not support or negate a close relationship between Asteranthos and Scytopetalaceae because the chromosome numbers of the Scytopetalaceae are too variable to be of value in phylogenetic analysis.

I conclude that the closest group to Asteranthos is to be found in the Scytopetalaceae, especially with Scytopetalum. The Scytopetalaceae is also considered to be

the closest group to the core-Lecythidaceae. However, the degree of overall similarity between Asteranthos and the Scytopetalaceae is much higher than that between the core-Lecythidaceae and the Scytopetalaceae.

Apparently, Asteranthos separated from its African stock and independently evolved in South America after the two continents were separated in the mid-Cretaceous or later. Although Asteranthos has evolved a few autapomorphies in floral structure, it is still very similar in other aspects with the Scytopetalaceae. Whether Asteranthos should be treated as a separate subfamily of its own within the Scytopetalaceae or as a monotypic family, Asteranthaceae as proposed by Knuth (1934, 1939c), Hutchinson (1969), and Airy-Shaw (1973), next to the Scytopetalaceae is open to question. A more detailed study of the intergeneric relationships of the Scytopetalaceae is needed to resolve this question.

## Crateranthus

Crateranthus is one of the most poorly studied genera of Lecythidaceae s.l. Neither the wood anatomy, the young stem anatomy, nor the chromosome number is known. Consequently, my discussion is restricted to a phenetic comparison of reproductive and embryological features.

The three large sepals of Crateranthus are comparable in

morphology and shape to those of the Theaceae and Clusiaceae. The sympetalous corolla, however, is similar to those of the Scytopetalaceae, Napoleonaea and Ebenales. The androecium of Crateranthus which is composed of numerous, whorled stamens, is fused with the base of the corolla-tube, a syndrome which is rare in the Dilleniidae. The sagittate anther with a prolonged connective tip resembles the anthers of the Dipterocarpaceae and a few members of the Theaceae. The semi-inferior ovary with apical axile placentation and the indehiscent fruit with persistent calyx at the proximal end and persistent style at the distal end are not rare in the Theales s.l. and Ebenales, but are uncommon elsewhere. The embryological features of Crateranthus support a close affinity to the Lecythidaceae s.l., Ochnaceae, Scytopetalaceae, Theaceae, Ebenaceae, and Styracaceae. However, the endothecium of its anther, which forms a circle in a subdermal layer of dual origin, is not known in the Theales s.l. or the Ebenales. Its tricolporate pollen with granulate colpus membrane is very common in the Theales.

I conclude that Crateranthus should be removed from the Lecythidaceae and treated as a family within the broadly defined Theales.

## Napoleonaea

The numerous autapomorphies of the reproductive features

of Napoleonaea point to an isolated position of the genus far from other dicot families. The valvate calyx, sympetalous corolla, ribbon-like and incurved filaments, and extrose anthers have analogues in the Ebenaceae, Sapotaceae, and Styracaceae. The similarity in embryology between Napoleonaea, Ebenaceae, and especially Styracaceae is too striking to be ignored. Lindley (1830) and Miers (1874) have already considered an ebenalean affinity for Napoleonaea. Miers (1874) discussed the similarities and dissimilarities between Napoleonaea and Omphalocarpum (Sapotaceae) and suggested that Napoleonaea "must be placed in juxtaposition with the Sapotaceae." However, the affinity between these taxa may not be as close as Miers had claimed. The presence of cortical bundles, stratified phloem, and glands on sepals, floral bracts, and petioles in Napoleonaea separate it from the ebenalean families.

On the other hand, Napoleonaea is similar to the core-Lecythidaceae, Ochnaceae, and Scytopetalaceae in most embryological features as well as in having stratified phloem and cortical bundles. Napoleonaea seems to have affinities with both the broadly defined Theales and the Ebenales, but does not fit well into either of these groups.

Because of its highly specialized floral organization and structure, Napoleonaea occupies a rather remote and isolated position. I suggest that Napoleonaea be treated as a distinct family, Napoleonaeaceae,as proposed by

de Candolle (1839) and many others, and placed in an order of its own next to the Ebenales. It does, however, share an ancestral relationship with the group consisting of the Lecythidaceae, Ochnaceae, Scytopetalaceae, etc.

## The systematic treatment of Lecythidaceae

I have argued for a group of core-Lecythidaceae which has affinities with the Scytopetalaceae. Foetidia, Asteranthos, Crateranthus, and Napoleonaea are further removed from the core-Lecythidaceae. And therefore, this leaves a monophyletic Lecythidaceae composed of two subfamilies, the Planchonioideae and the Lecythidoideae. The constituents of these two subfamilies, as treated by Prance & Mori (1979), are supported in this study.

Fig. 1. Syntricolpate pollen grains of Abdulmajidia chaniana (A-B, Tsou 160), Barringtonia asiatica (C, Smith 1082), Chydenanthus excelsus (D, Rifai s.n.), and Careya arborea (E-F, Tsou 163). Note the polar cushion (pc), marginal ridge (mr), and marginal groove (mg).

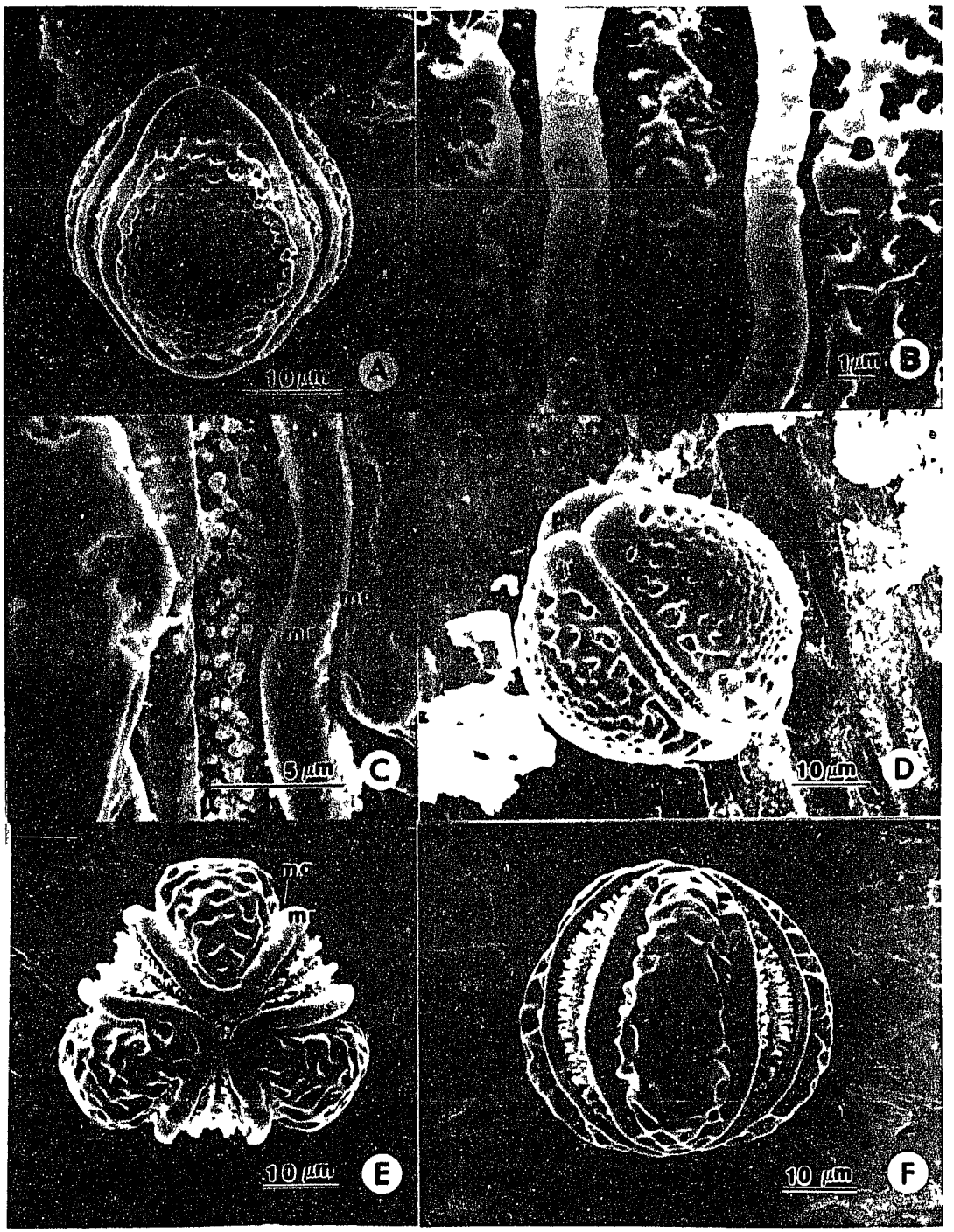

10 µm
A
1 µm
B
mc
mi
5 µm
C
10 µm
D
mc
mi
10 µm
E
10 µm
F

Fig. 2. Syntricolpate pollen grains of Petersianthus and tricolpate pollen grains of Asteranthos and Couroupita.
A-B. P. quadrialatus (Herraez 4172) showing the polar cushion, marginal ridge, and marginal groove.
C-D. Asteranthos brasiliensis (Duck 39) with wide colpi and granulate colpus membrane.
E-F. Couroupita nicaraguariensis (W. D. Stevens 6478) with dimorphic pollen. E. Monad pollen from ring anthers with foveolate tectum. F. One microspore of a tetrad grain from hood anthers showing vugulate tectum.

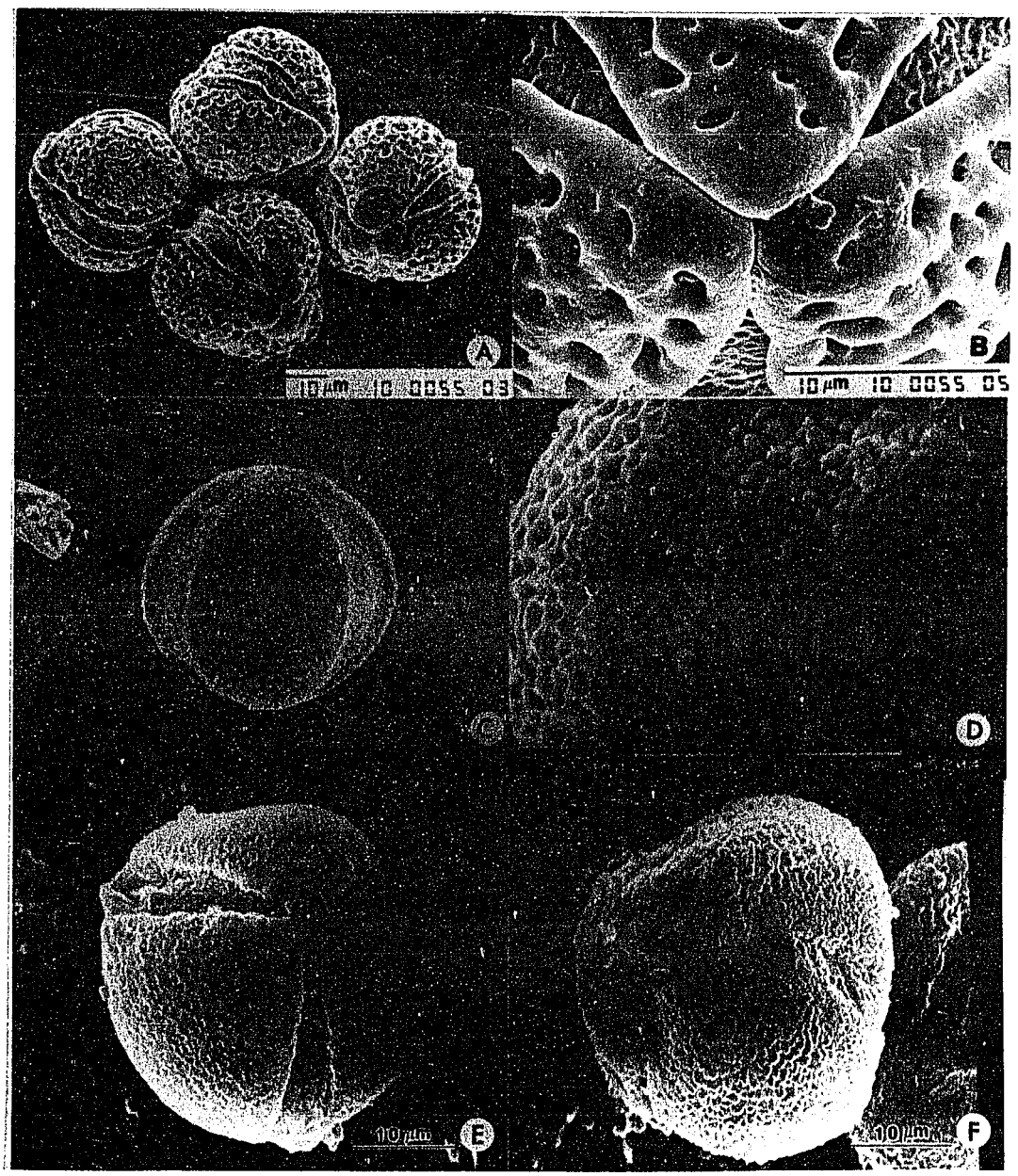

A
10 µm 10 0055 03
B
10 µm 10 0055 05
D
10 µm
E
10 µm
F

Fig. 3. Illustrations of some embryological characters.

Fig. 3-I.

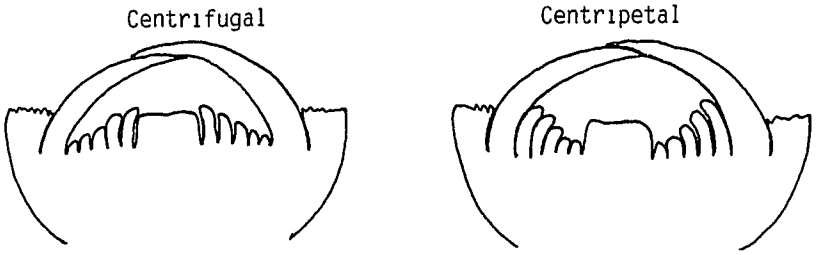
A. Androecial initiation.

B. Anther wall development pattern.

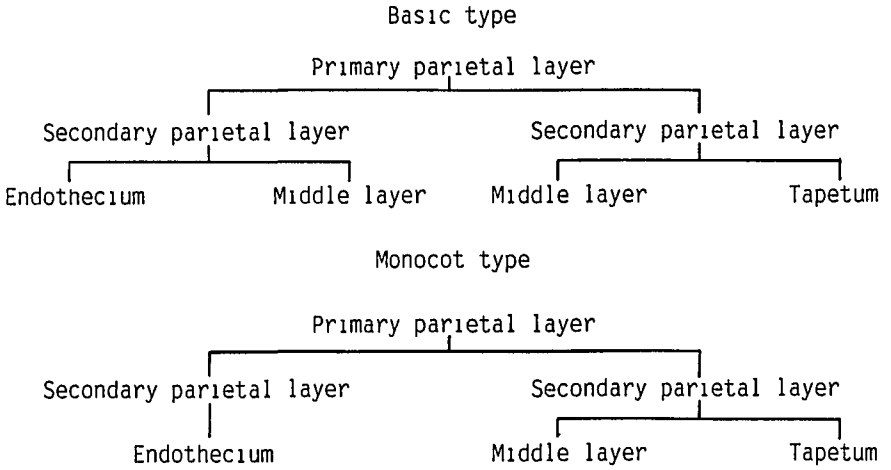
C. Pollen tetrads.

D. Tapetum type.

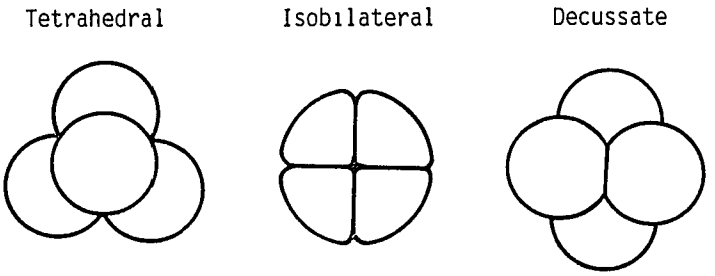
A. Androecial initiation




B. Anther wall development pattern




C. Pollen tetrads




D. Tapetum type

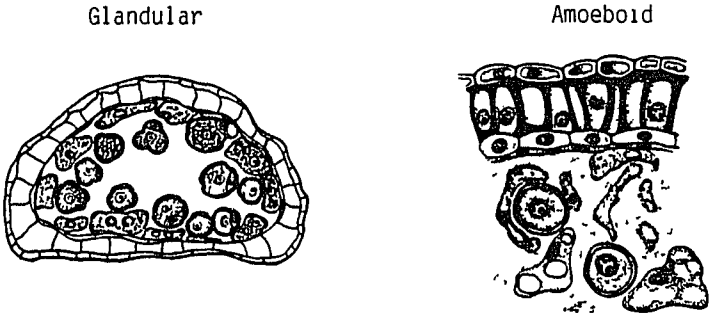


Fig. 3-II. Illustrations of some embryological characters.

E. Secondary wall thickenings of endothecial cells.

F. Zonation of ovule primordium.

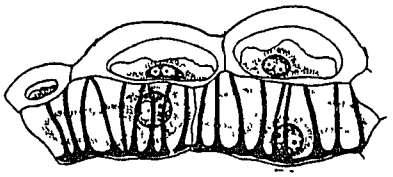
G. Initiation of inner integument and outer integument.

H. Position of ovule.

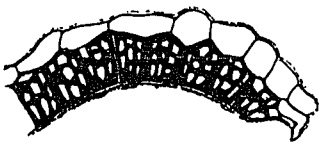
I. Nature of nucellus.

E. Secondary wall thickenings of endothecial cells (in transverse section)

Rod-like

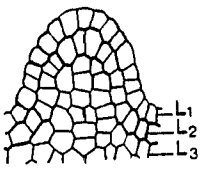


Reticulate

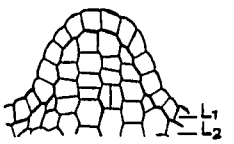


F. Zonation of ovule primodium

Trizonate

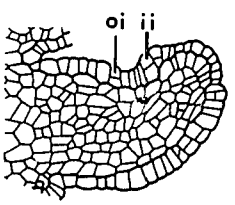



Bizonate

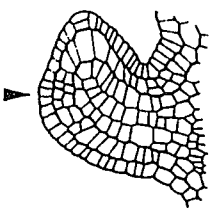



G. Initiation of inner integument, initiation of outer integument

Dermal

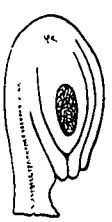



Subdermal

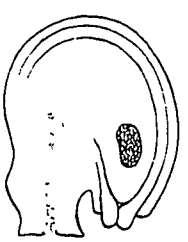


H. Position of ovule

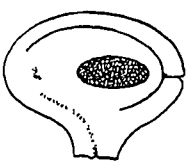
Anatropous



Campylotropous

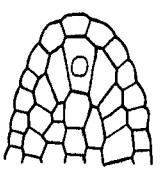


Hemitropous



I. Nature of nucellus

Tenuinucellate



Crassinucellate

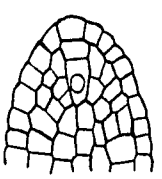


Fig. 3-III. Illustrations of some embryological characters.

J. Basal nucellar tissue in longitudinal section of ovule.

K. Form of megaspore tetrads.

L. Formation of micropyle.

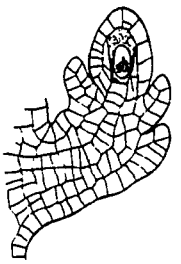
M. Embryo sac formation.

N. Behavior of antipodal cells.

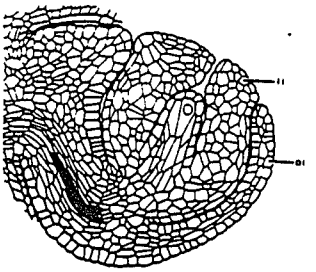
O. Structure of outer integument.

J. Basal nucellar tissue in longitudinal section of ovule

Scanty

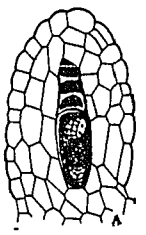


2-4 cell rows



K. Form of megaspore tetrads

Linear

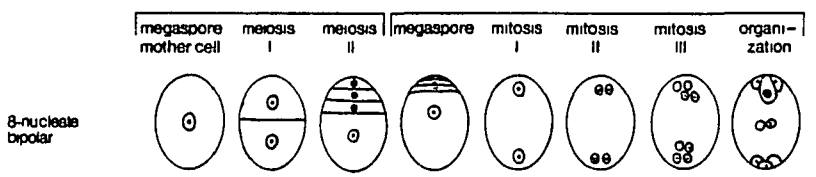


L. Formation of micropyle

Inner integument only

M. Embryo sac formation

Polygonum type



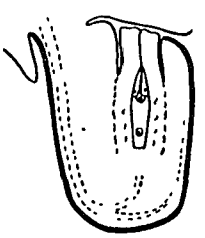

N. Behavior of antipodal cells

Ephermal

persistent

O. Structure of outer integument

Normal



with arilloid

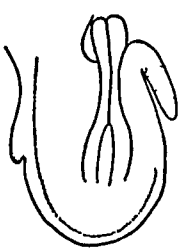


Fig. 4. Androecial initiation of Barringtonia, Careya, Gustavia, and Lecythis.

A. B. racemosa (Hsieh s.n.) showing centripetal initiation.

B. C. arborea (Jayasuriya 4334) with the earliest staminal primordia (arrows) initiating from the central region of the common androecial primordium. (g, gynoecium primodium)

C. G. hexapetala (Mori 18676) showing centripetal initiation.

D-F. L. corrugata (Beck 293) showing centrifugal initiation of ring stamens and the asymmetrical development of the staminal ring. D,E. The staminal ring starts to expand at the abaxial side. F. A stage slightly later than D & E. Note that the staminodial primordia of the hood initiate as soon as the hood begins to develop (arrows in D, F).

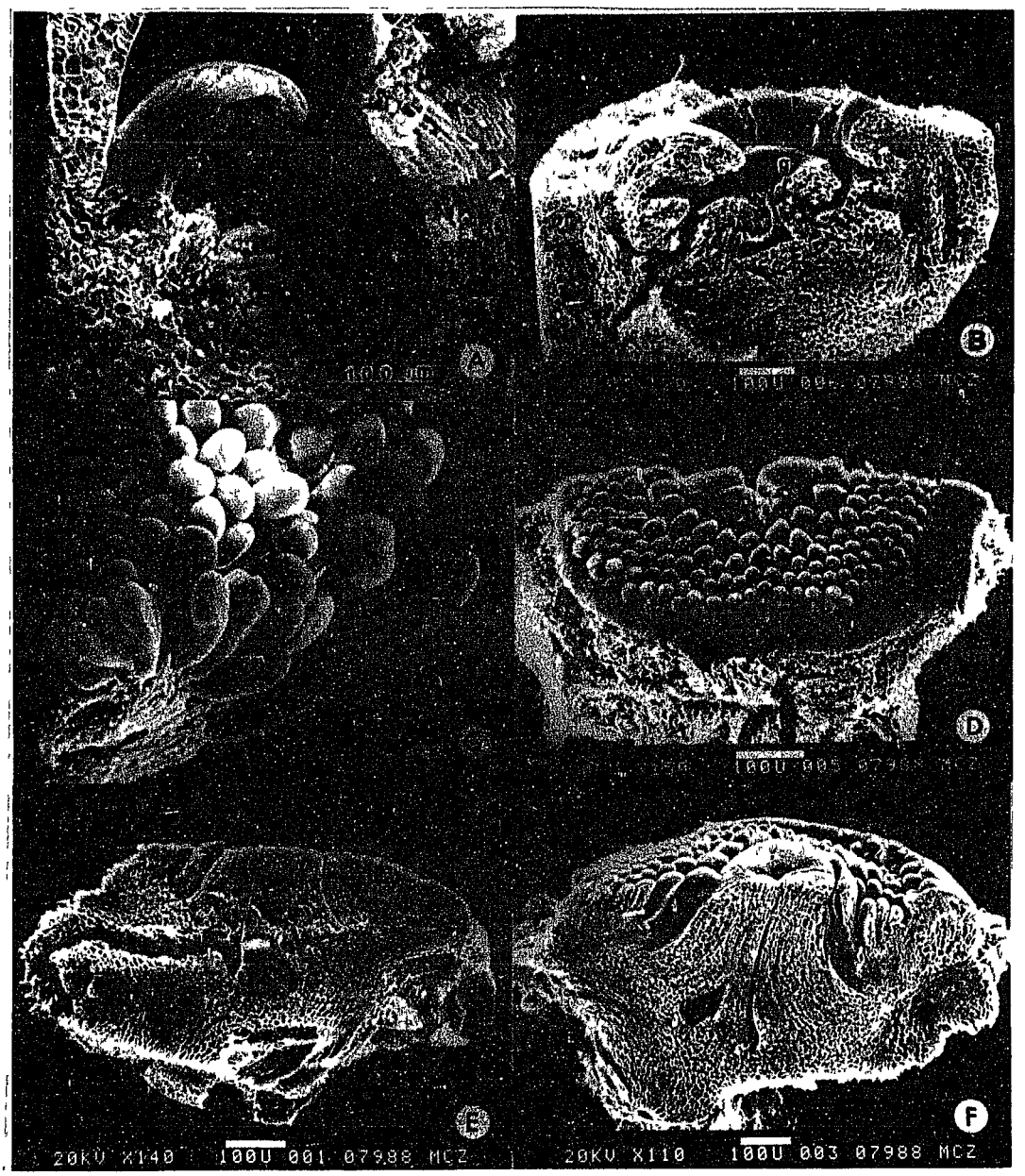

A
B
D
E
F
20kV X140 100U 001 07988 MCZ
20kV X110 100U 003 07988 MCZ

Fig. 5. A-F. Abdulmajidia chaniana (Tsou 160).

A. Longisection of an anther at free spore stage showing the glandular tapetum (ta) and the enlarged endothecium (ed).

B. Longisection of a mature anther. Note the Urbisch bodies (u) on the surface of locule and starch granules in the connective.

C. Longisection of a young ovule with single megasporocyte (mc) at subdermal layer.

D. Longisection of an ovule in early stage of embryo sac formation. Note the degenerated micropylar megaspores (arrows).

E. Cross section of a mature ovule with a thick raphe bundle (rb) and nine smaller vascular bundles in the outer integument (oi).

F. Longisection of a mature ovule.

Same scale bar for A-F, 0.05mm, 0.05mm, 0.05mm, 0.05mm, 0.1mm, 0.1mm, respectively.

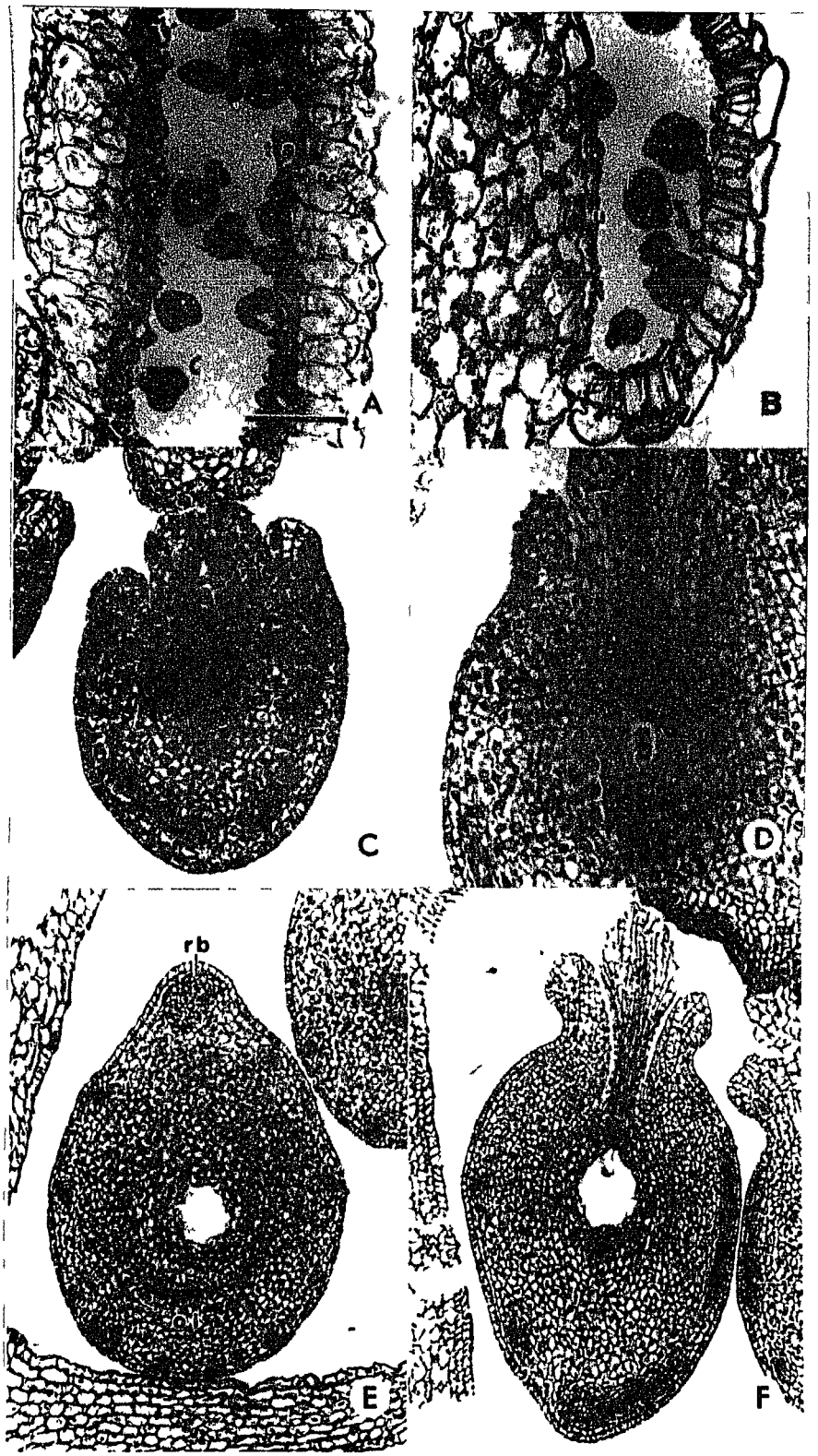

A
B
C
D
rb
E
F

Fig. 6. A-F. Barringtonia racemosa (Hsieh s.n.).
A. Longisection and cross section of young anthers. Note the two secondary parietal layers derived from the periclinal division of primary parietal layer (arrow).
B. Cross section of an anther right before meiosis with two compressed middle layers (arrow).
C. Two ovule primordia showing their trizonate structures.
D. Longisection of an ovule at the megasporocyte stage (mc).
E. Cross section of mature ovules. Note the upper section through the embryo sac with 15 vascular bundles in the outer integument (oi).
F. Longisection of a mature ovule.
Same scale bar for A-F, 0.05mm, 0.1mm, 0.05mm, 0.1mm, 0.2mm, 0.1mm, respectively.

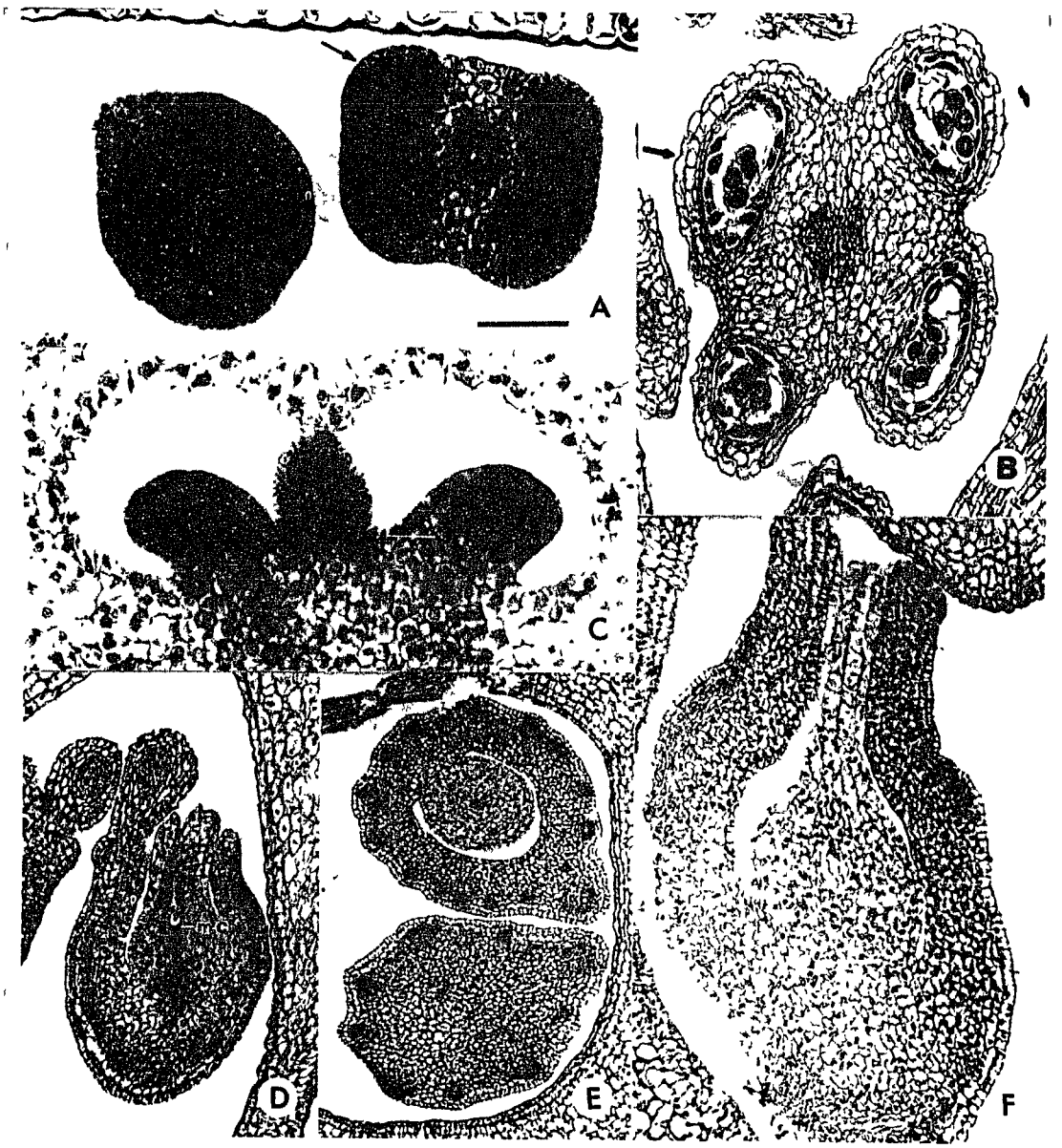

A
B
C
D
E
F

Fig. 7. A-C. Careya arborea (Jayasuriya 4334). D-H. Chydenanthus excelsus (Rifai s.n.).

A. Cross section of one-half of a mature anther.

B. Longisection of a young ovule with its single archesporial cell (arc).

C. Longisection of a mature ovule. Note the arilloid (ar) and the endothelium (et).

D. Longisection of an anther before meiosis showing the five wall layers: epidermis, endothecium, 2 middle layers (ml), and tapetum.

E. Section of a mature anther. Note the alignment of urbisch bodies (u) on the surface of locule.

F. Longisection of a nearly mature ovule. Note the much expanded funiculus (f).

G. Longisection of a young ovule showing a massive funiculus (f), single archesporial cell (arc), and the dermal initiation of inner integument (ii).

H. Higher magnification of F.

Same scale bar for A-H, 0.12mm, 0.06mm, 0.1mm, 0.05mm, 0.05mm, 0.4mm, 0.05mm,0.2mm, respectively.

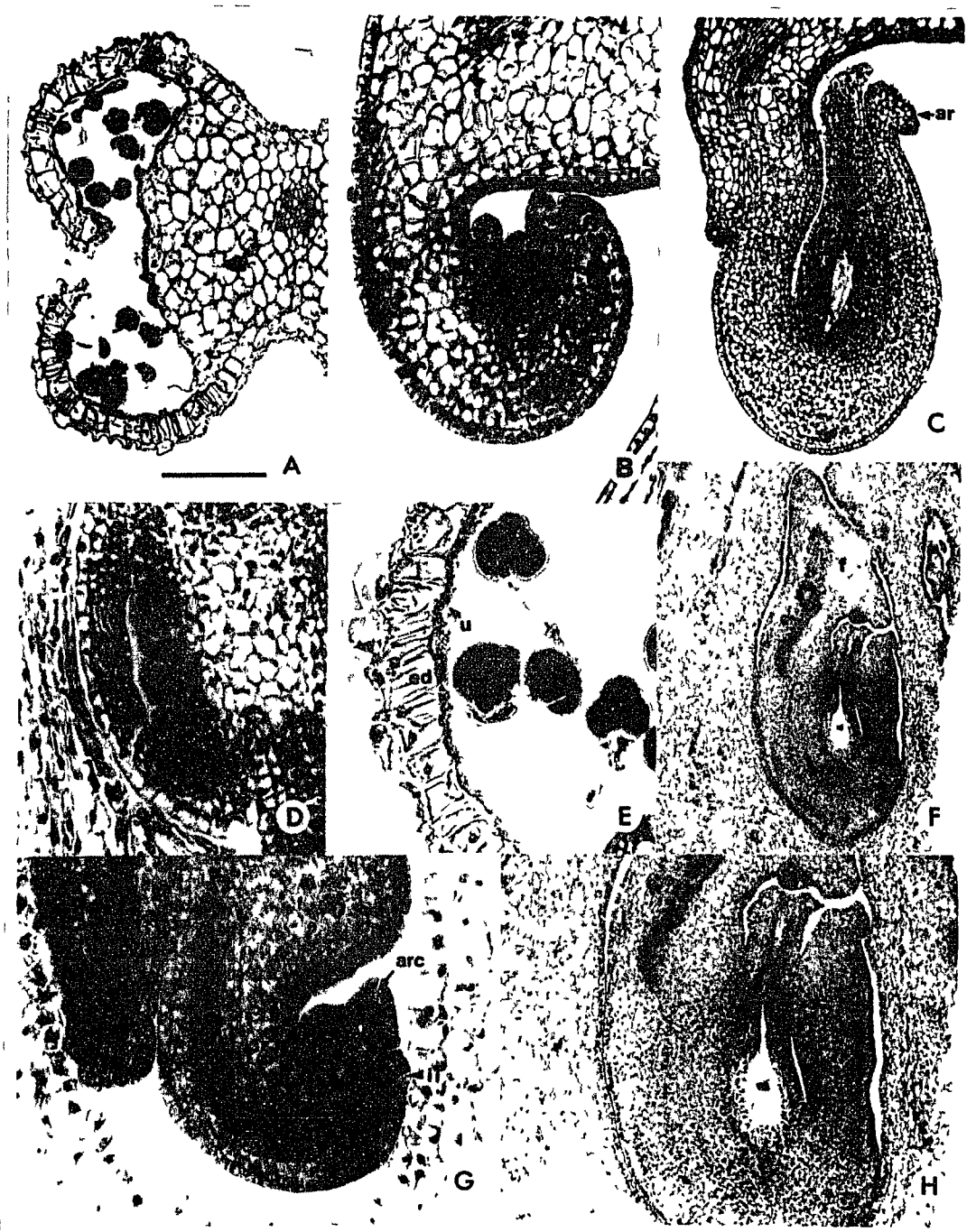

A
B
C
ar
D
E
u
ed
F
arc
lr
G
H

Fig. 8. A-G. Petersianthus quadrialatus (Herraez 4172).
A. Longisection of an anther before meiosis with five wall layers. The endothecium and the outer middle layer were derived from the same parietal layer (arrow).
B. Microspore mother cells undergoing simultaneous meiotic divisions (arrows).
C. Cross section of an anther before maturity.
D. Longisection of an ovule showing the first meiotic division of the megasporocyte (mc).
E. Cross section of an ovary. Note the arrangement of ovules.
F. Cross section of a young ovary. Note that there are 8 carpellary bundles but only 3 locules.
G. Longisection of a mature ovule with the egg apparatus (ea) near the micropyle.
Same scale bar for A-G, 0.05mm, 0.05mm, 0.1mm, 0.1mm, 0.25mm, 0.05mm, 0.12mm, respectively.

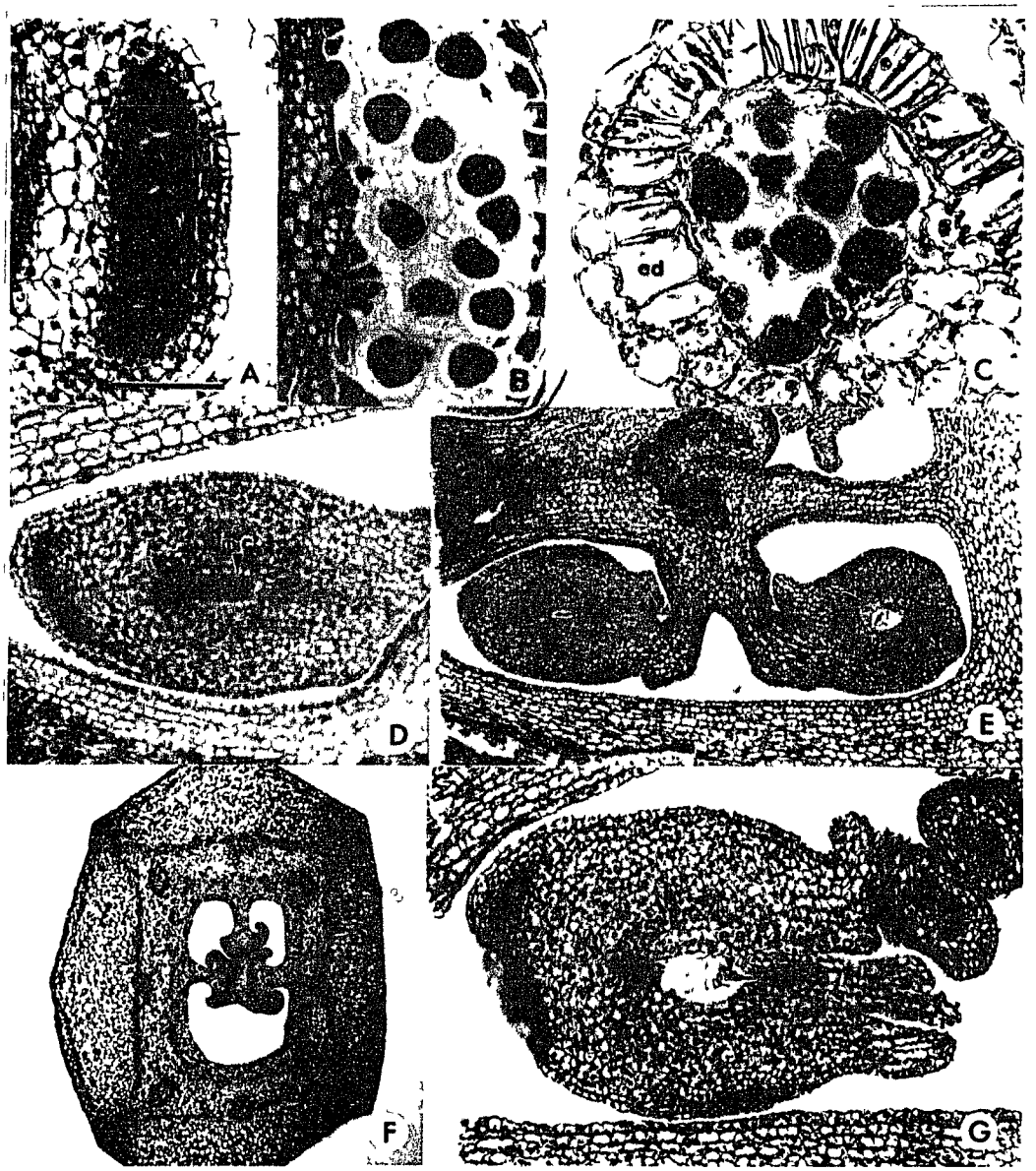

A
B
ad
C
D
E
F
G

Fig. 9. A-E. Planchonia careya (Jackes s.n.)

A. Cross section of a mature anther with rod-like secondary thickenings on the endothecium (ed).

B. Longisection of a young bud. The earliest staminal primordia appear on the central portion of the common androecial primordium, and the later ones initiate in both directions (arrows).

C. Longisection of a young ovule showing single archesporial cell (arc) and the dermal initiation of inner integument (ii).

D. Longisection of an ovule before maturity. Note the arilloid (ar) and the endothelium (et).

E. Longisection of a mature ovule.

Same scale bar for A-E, 0.1mm, 0.2mm, 0.05mm, 0.1mm, 0.15mm, respectively.

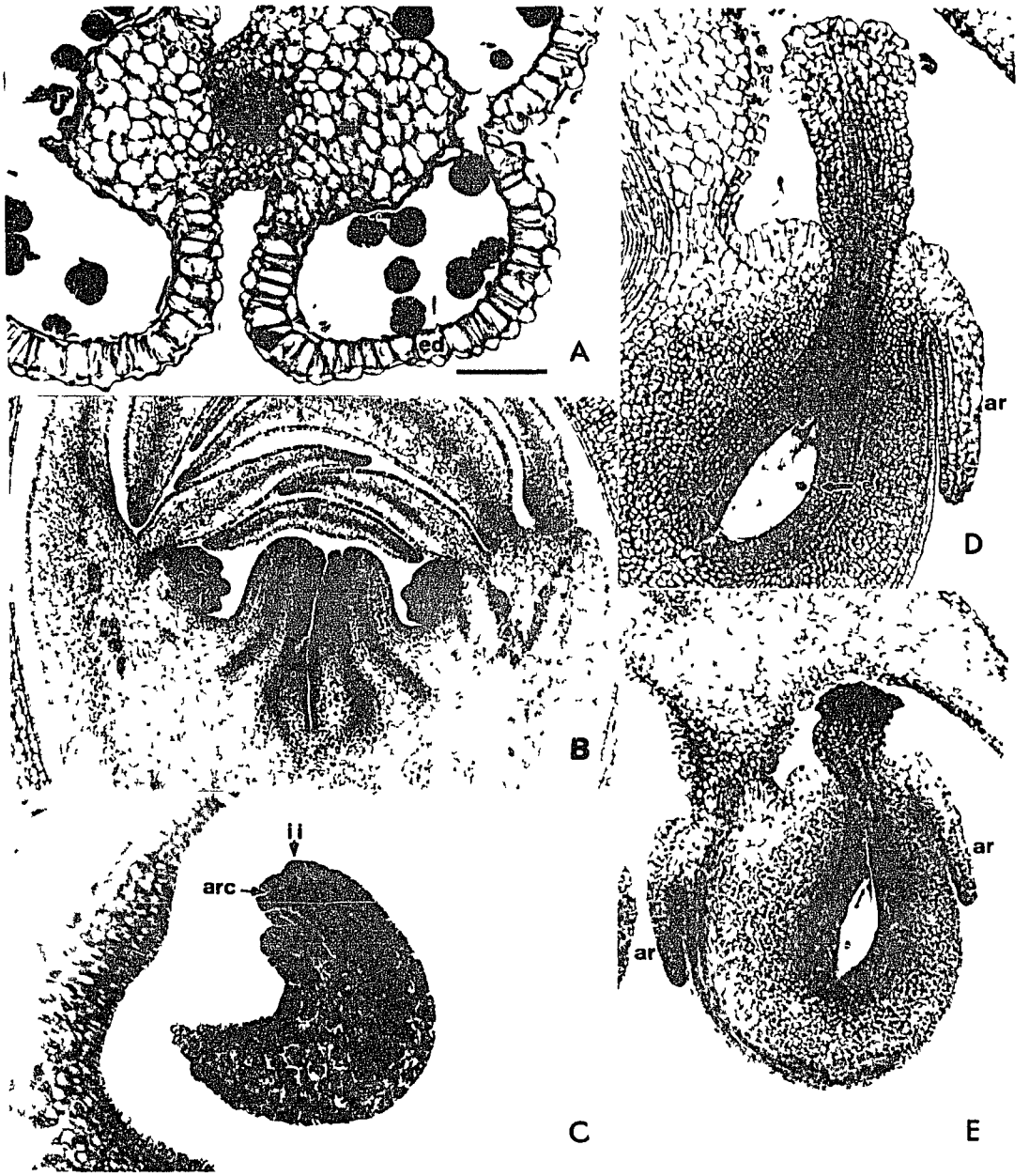

ed
A
B
II
arc
C
ar
D
ar
ar
E

Fig. 10. A-D. Allantoma lineata (Prance 17549).
A. Cross section of the androecium showing the ring-like staminal ring (sr). Note the vascular bundles are arranged in more or less four whorls in the staminal ring.
B. Longisection of an anther with disintegrated tapetum (ta). The endothecium (ed) has much elongated.
C. Cross section of androecium showing the fusion of two bundles in the base of a filament (arrow).
D. Longisection of a mature ovule with the egg apparatus (ea).
Same scale bar for A-D, 0.5mm, 0.1mm, 0.2mm, 0.1mm, respectively.

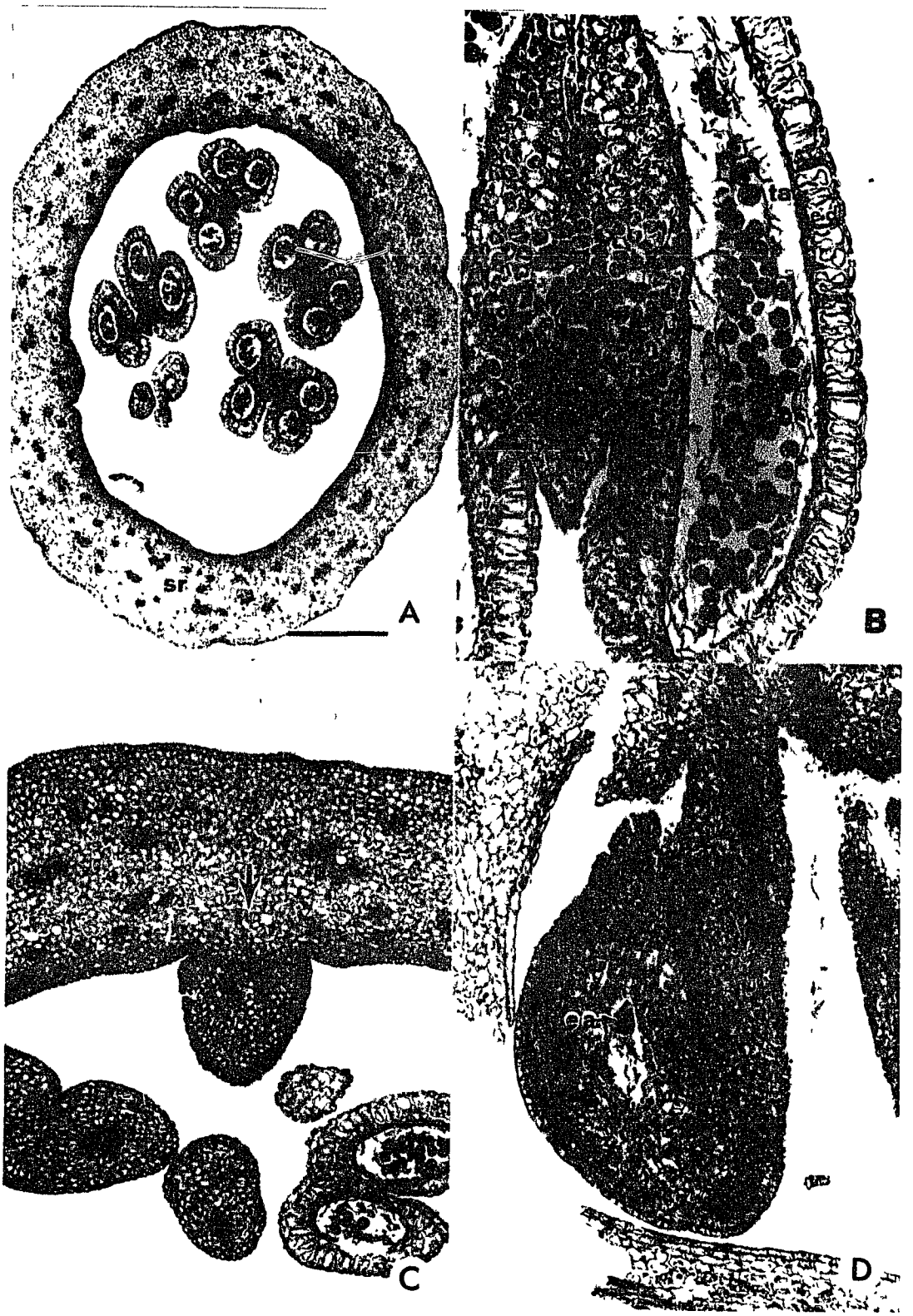

sf
A
ta
B
C
D

Fig. 11. A-F. Grias cauliflora (Nee & Mori 3663).
A. Anther in late meiotic stage. Microspore tetrads are mainly tetrahedral (arrows).
B. Cross section of an anther showing the widely separated sporangial pairs and the bifurcation of the vascular bundle.
C. Longisection of a young ovule with single megasporocyte (mc) at the subdermal layer.
D. Cross section of a mature ovule with 6 or 7 vascular bundles in the outer integument (oi).
E. Longisection of a mature ovule with a large central cell (cc). Note the breakdown of inner layers of the inner integument by the expanding embryo sac (upper arrow) and the conducting canal in the central region of basal nucellar tissue (lower arrow).
F. Longisection of a mature ovule.
Same scale bar for A-F, 0.05mm, 0.1mm, 0.05mm, 0.1mm, 0.05mm, 0.2mm, respectively.

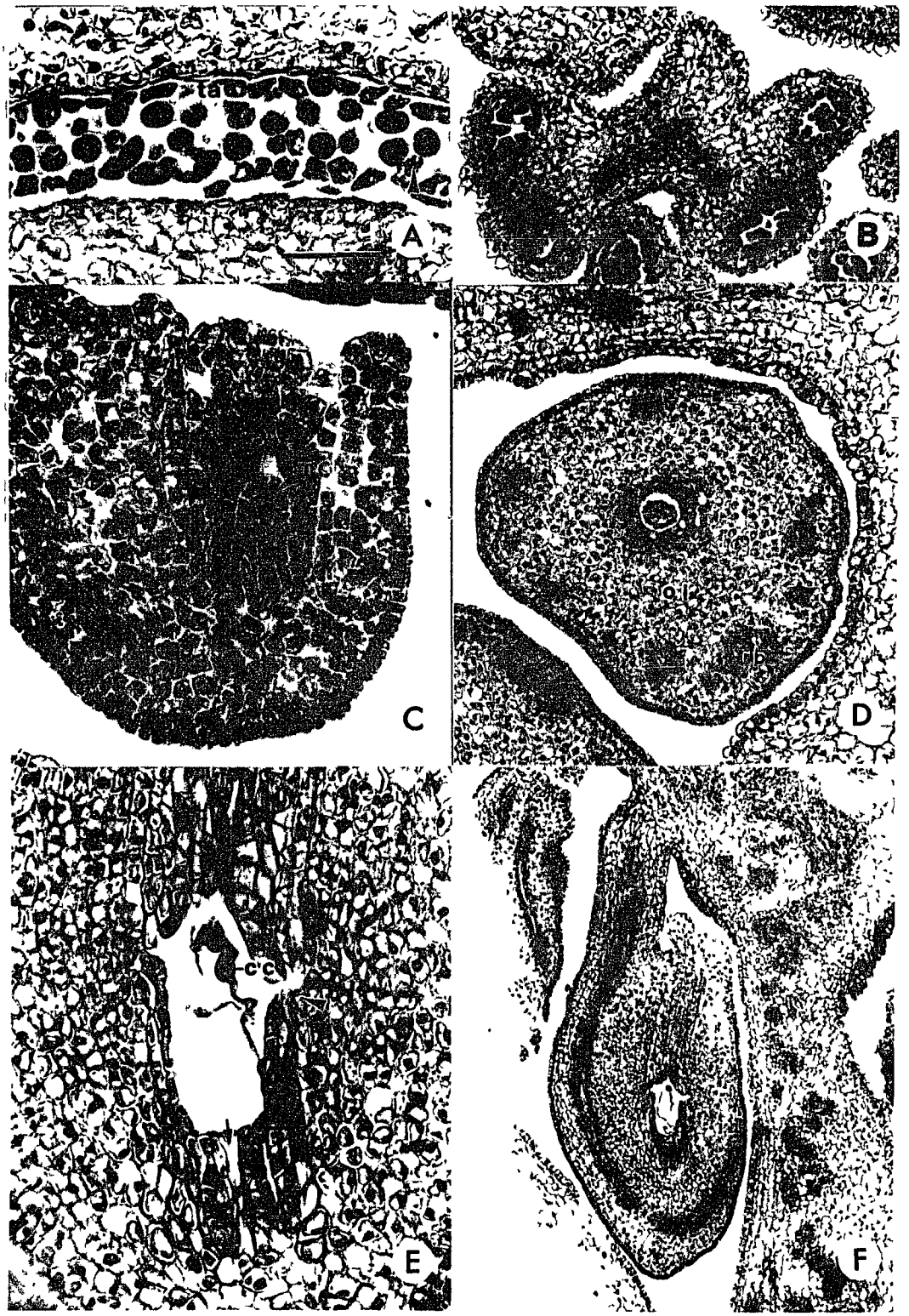

A
B
C
D
E
F

Fig. 12. A-G. Gustavia hexapetala (Mori 18676).

A. Longisection of young anthers showing the acute apex of anther and five wall layers (arrow).

B. Cross section of an anther showing the glandular tapetum (ta). Note the continuity of endothecial cells around the connective (arrows).

C. Longisection of part of a stamen. Note the constriction at the apex of filament (arrow).

D. Cross section of part of an anther showing reticulate pattern of secondary thickenings (arrow) of the endothecium (ed) and the tannin inclusions in wall layers.

E. Longisection of a young ovule. Note the two archesporial cells (arc) and the dermal initiation of outer integument (oi).

F. Longisection of a young ovule showing two archesporial cells (arc).

G. Longisection of a fertilized ovule at the stage of early embryogenesis.

Same scale bar for A-G, 0.1mm, 0.1mm, 0.1mm, 0.05mm, 0.04mm, 0.05mm, 0.2mm, respectively.

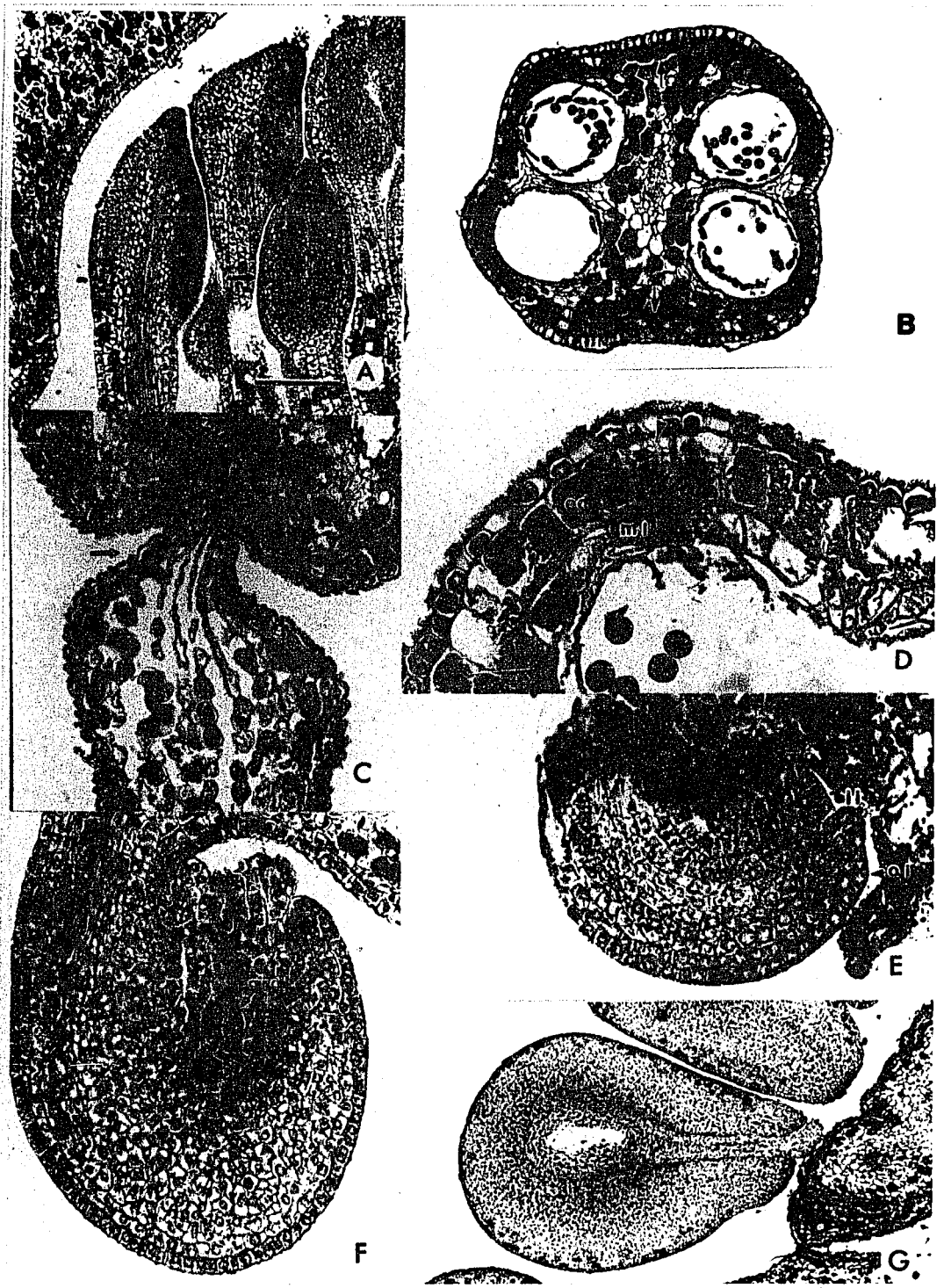

A
B
C
D
E
F
G

Fig. 13. A-G. Cariniana micrantha (Mori 20191)

A. Longisection of part of a flower. Note the triangular staminal ring (sr) and the stamens with very short connectives.

B. Longisection of some young anthers. The endothecium may differentiate from the outer secondary parietal layer directly (arrow).

C. Cross section of a young ovary.

D. Longisection of young ovules showing the dermal initiation of both integuments and the megasporocyte (mc).

E. Longisection of an ovule during meiosis. The tetrads are in linear sequence (arrow).

F. Longisection of a mature ovule showing its egg apparatus (ea) and central cell (cc).

G. Cross section of an ovule. There are two vascular bundles in the outer integument (oi).

Same scale bar for A-G, 0.2mm, 0.05mm, 0.2mm, 0.05mm, 0.05mm, 0.05mm, 0.05mm, respectively.

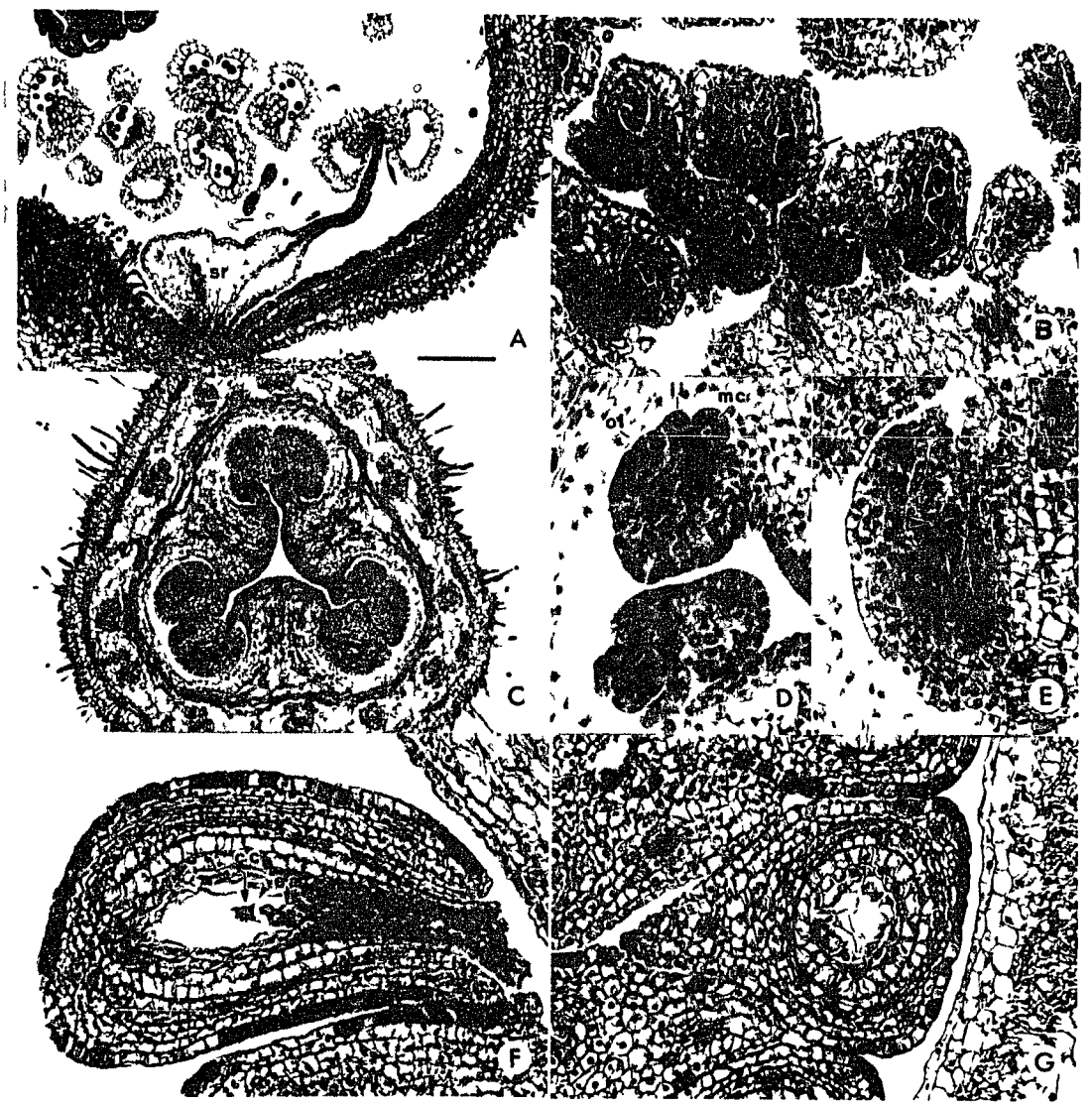

A
B
C
D
E
F
G
mc
of

Fig. 14. A-G. Bertholletia excelsa (Nelson s.n.).
A. Cross section of half of an anther. Before meiosis the tapetal cells may contain two big nuclei or four smaller ones (arrows).
B. Cross section of an anther showing the glandular tapetum.
C. Cross section of an anther before maturity. Note the very narrow connective and the rod-like secondary thickenings on the endothecial wall.
D. Longisection of a young ovule showing single archesporial cell and the dermal initiation of inner integument (ii).
E. Cross section of two mature ovules showing the thick raphe bundle (rb) and two or three smaller bundles in the outer integument (oi).
F. Longisection of an ovule at the stage of megasporocyte (mc).
G. Longisection of a mature ovule.
Same scale bar for A-G, 0.05mm, 0.1mm, 0.1mm, 0.04mm, 0.2mm, 0.05mm, 0.1mm, respectively.

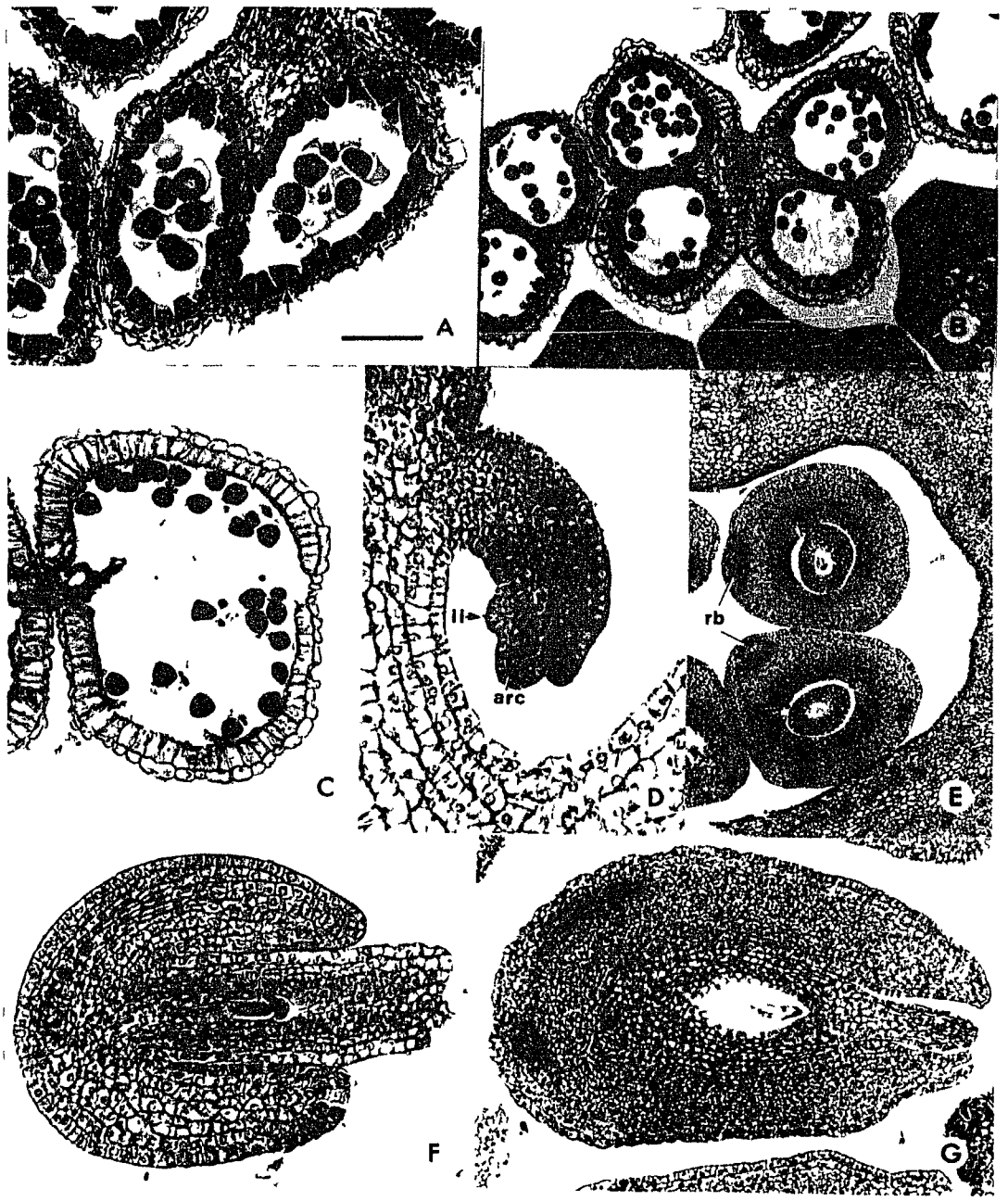

A
B
C
ll
arc
D
rb
E
F
G

Fig. 15. A. Corythophora amapaensis (Mori 18675). B-E. C. rimosa (Mori 18547).

A. Cross section of an anther in free spore stage.

B. Cross section of a young flower bud. Note the staminal primordia of the hood initiate outwards (arrow).

C. Longisection of an ovary. Ovule primordia emerge from the expanded axis.

D. The obturators (ob) developing from the placenta are against the micropyle.

E. Longisection of a mature ovule.

Same scale bar for A-E, 0.25mm, 0.25mm, 0.1mm, 0.1mm, 0.1mm, respectively.

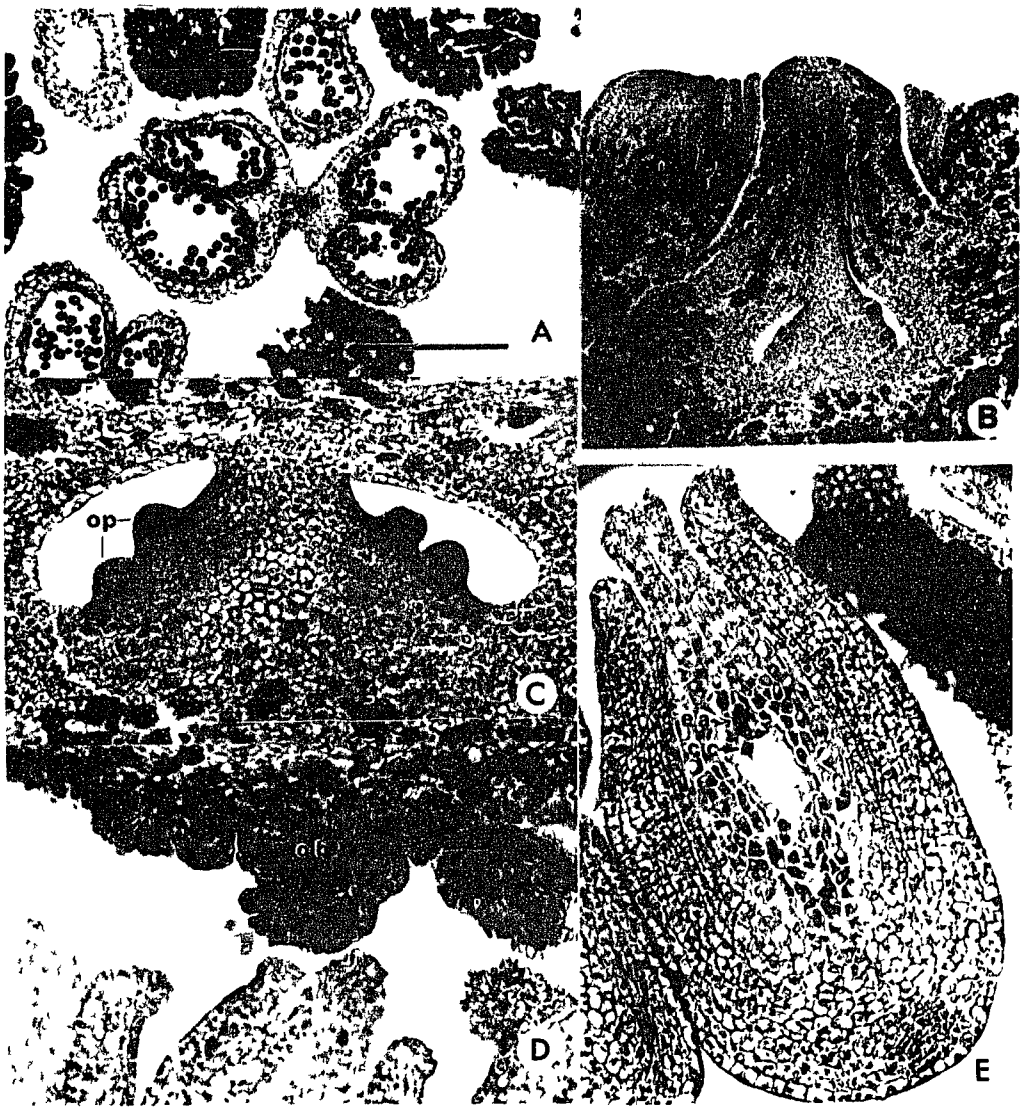

A
B
op
C
D
E

Fig. 16. A-H. Couratari oligantha (Plowman 12546).
A. Longisection of part of a bud showing the triangular staminal ring (sr).
B. Heterochrony of ring anthers, anther 1 before meiosis, anther 2 and anther 3 undergoing meiosis, and anther 4 after meiosis. Anther 4 is closest to the style.
C. Cross section of part of a young anther showing five or six wall layers: epidermis, endothecium (ed), two or three middle layers (ml) and tapetum (ta).
D. Longisection of an anther with glandular tapetum (ta).
E. Longisection of two young ovules showing their single megasporocyte (mc).
F. Longisection of an ovule during the second meiotic division. The upper two megaspores are degenerated (arrow).
G. Longisection of an ovule before maturity with the hypostase (hy).
H. Longisection of a mature ovule.
Same scale bar for A-H, 0.2mm, 0.2mm, 0.05mm, 0.1mm, 0.05mm, 0.05mm, 0.05mm, 0.1mm, respectively.

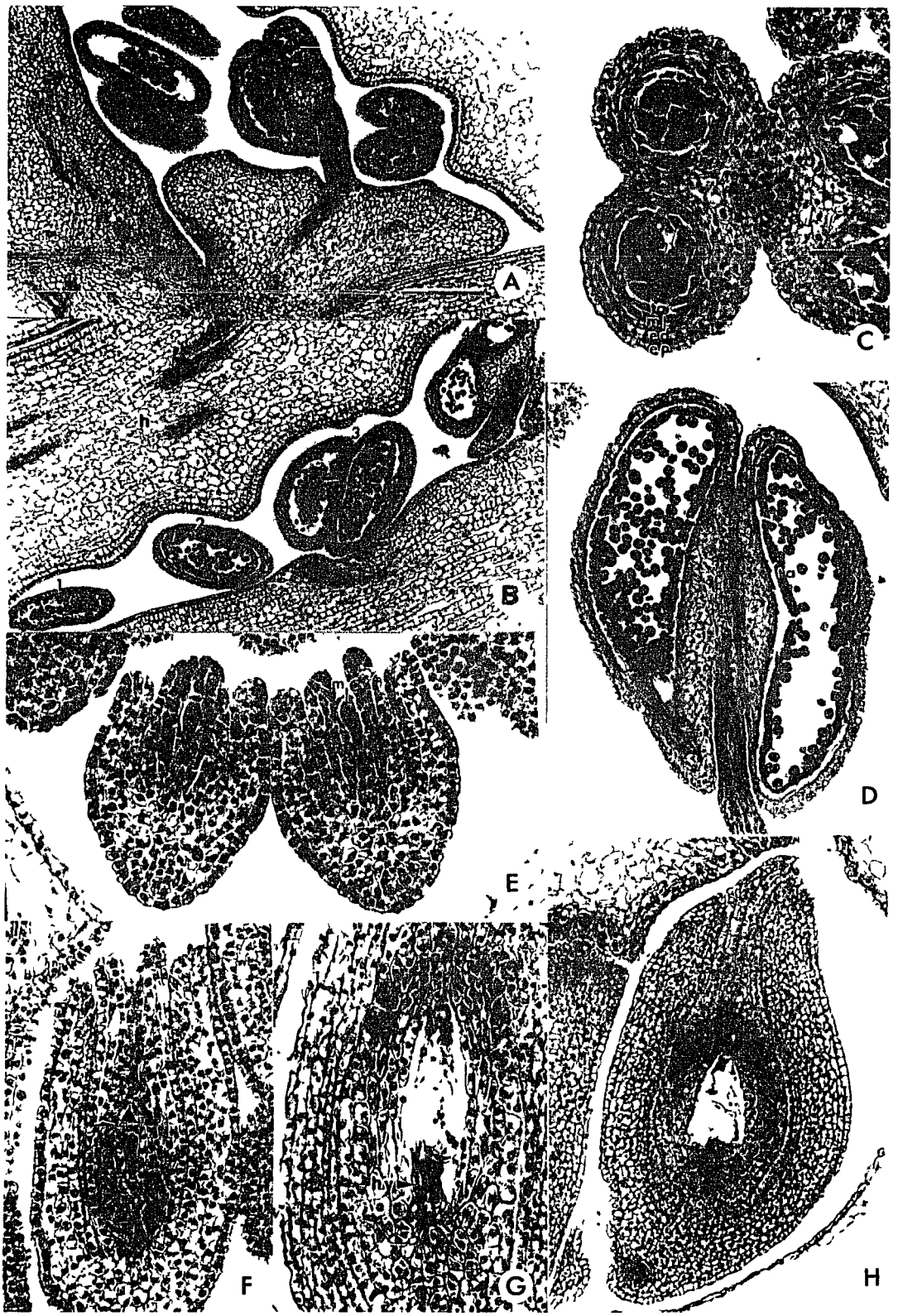

A
B
C
D
E
F
G
H

Fig. 17. A-F. Couroupita guianensis (Hyge 1964).

A. Longisection of an anther showing the glandular tapetum (ta) and the expanded endothecium (ed).

B. Longisection of a nearly mature stamen. Note the constriction at the apex of filament (arrow).

C. Cross section of an anther.

D. Cross section of a mature ovule showing the single vascular bundle in the outer integument (oi) besides the raphe bundle (rb).

E. Longisection of a mature ovule. Note the big embryo sac.

F. Longisection of a mature ovule showing the enlarged inner epidermis of inner integument (arrow).

Same scale bar for A-F, 0.1mm, 0.2mm, 0.2mm, 0.1mm, 0.1mm, 0.05mm, respectively.

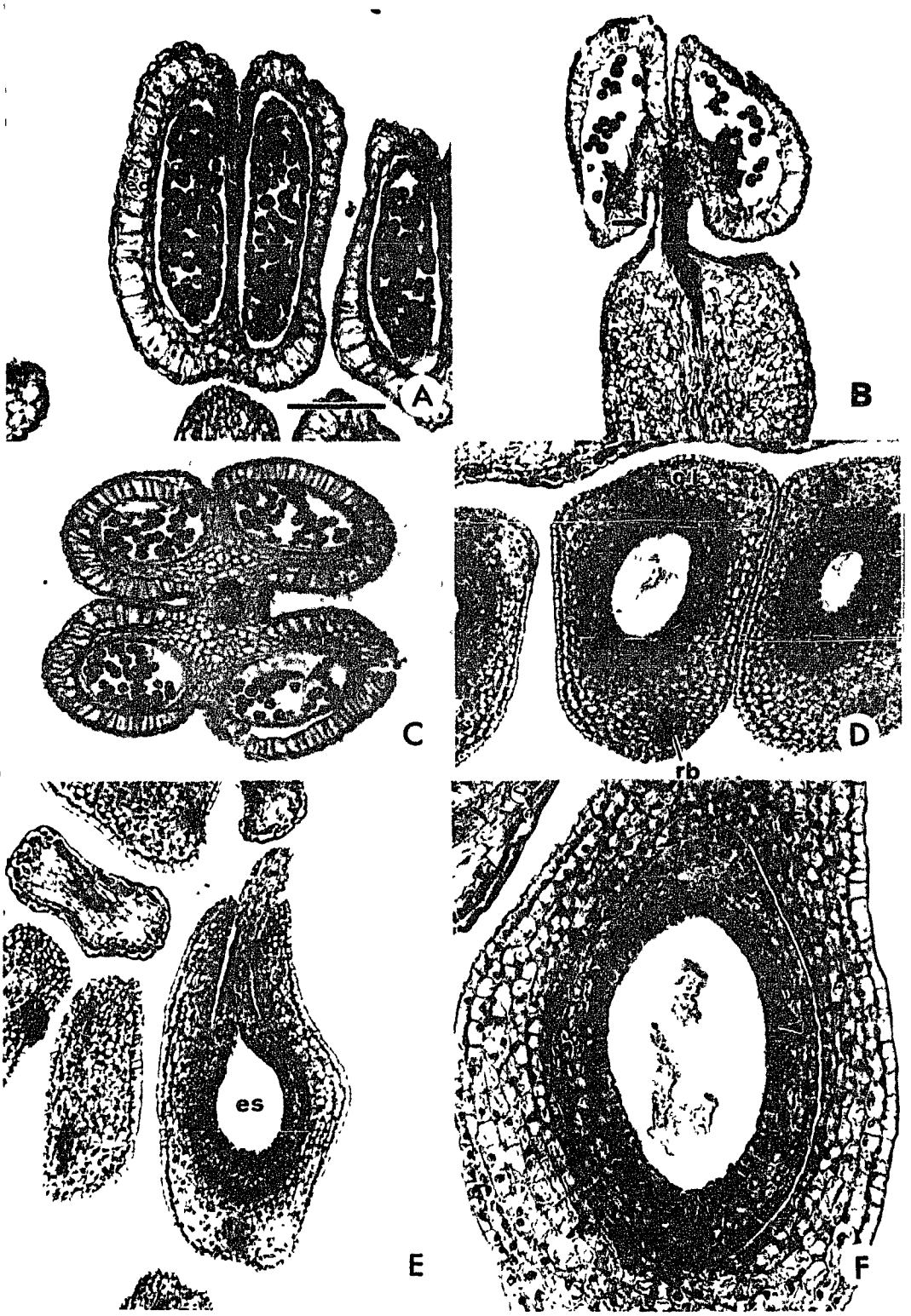

A
B
C
D
rb
es
E
F

Fig. 18. A-E. Eschweilera cyathiformis (Mori 19385).

A. Longisection of the ligule (l) and the hood (h) at early development.

B. Longisection of part of a mature hood showing the porous internal structure.

C. Cross section of a mature anther.

D. Longisection of a nearly mature gynoecium. The stylar canal (sc) is formed due to the degeneration of the tissue in the central region.

E. Longisection of a mature ovule.

Same scale bar for A-E, 0.5mm, 0.5mm, 0.1mm, 0.5mm, 0.1mm, respectively.

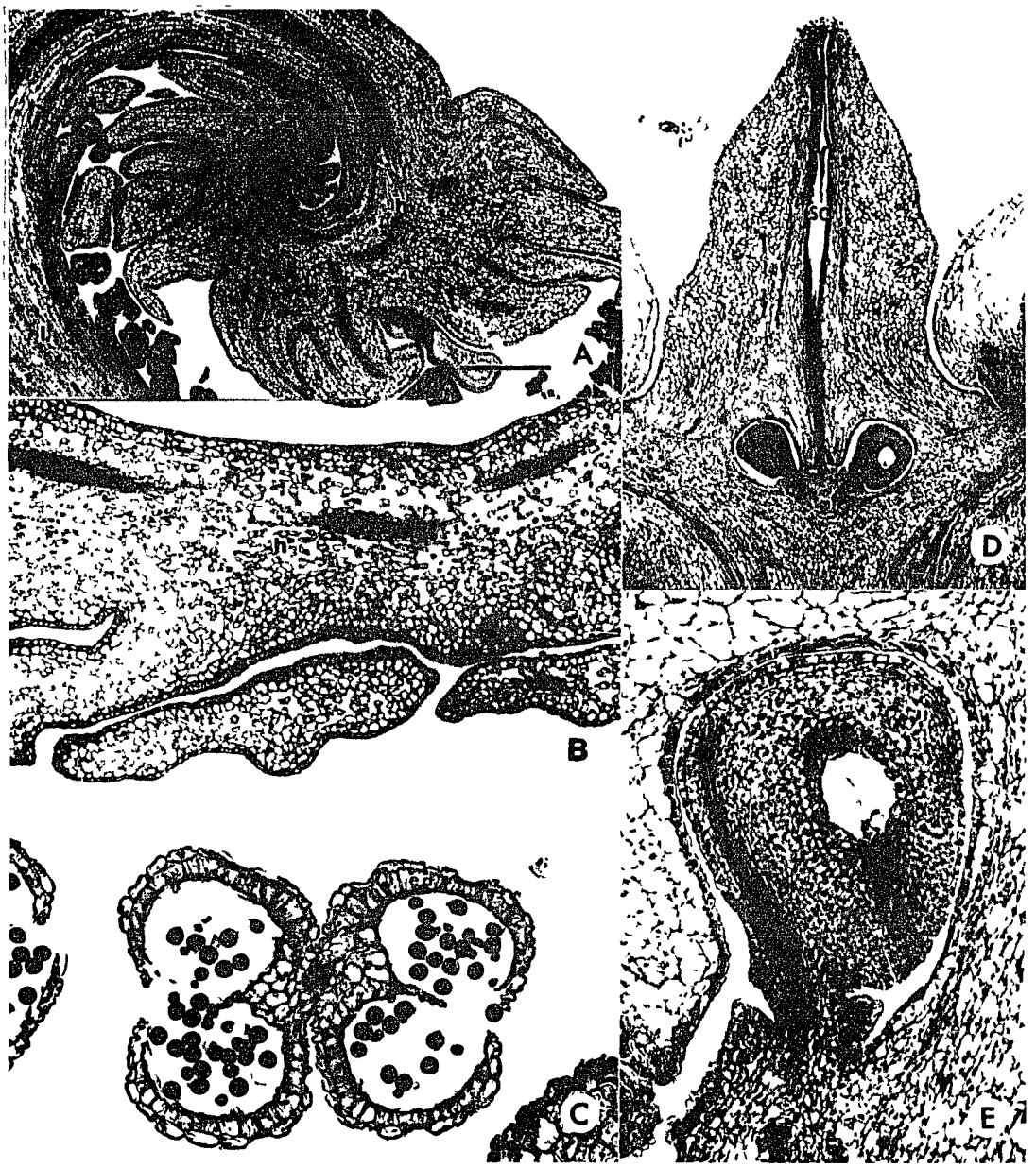

A
B
C
D
E

Fig. 19. A-F. Locythia corrugata (Beck 293).
A. Longisection of a young bud. Ovule primodia (op) initiate from the upper part of the expanded axis.
B. Stamens on the ligule. Anthers are in either the microsporocyte or the meiosis stage.
C. Stamens on the ring from the same androecium as B, anther 1 and anther 2 in the microsporocyte stage, anther 3 in the tetrad stage, and anther 4 in free spore stage.
D. Longisection of a young ovule showing the single megasporocyte (mc) at the subdermal layer.
E. Longisection of a mature ovule with its egg apparatus (ea). Note the pair of synergids and the egg cell.
F. Cross section of a mature ovule. There are more or less ten vascular bundles in the outer integument (oi).
Same scale bar for A-F, 0.2mm, 0.2mm, 0.2mm, 0.05mm, 0.1mm, 0.1mm, respectively.

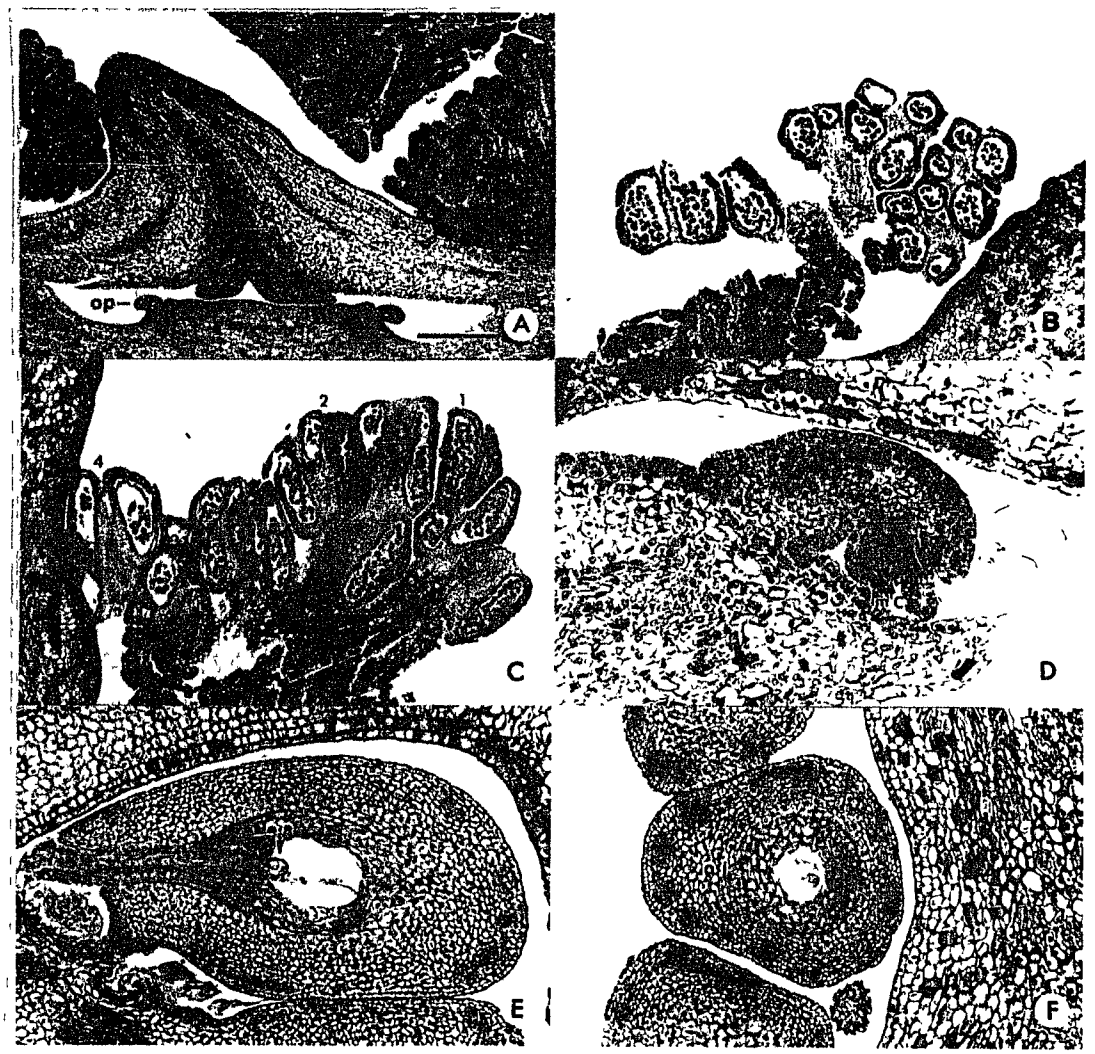

op
A
B
2
1
4
C
D
E
F

Fig. 20. A-F. Foetidia obliqua (Schatz 1855).
A. Longisection of a young anther showing five wall layers; epidermis, endothecium, two middle layers, and tapetum.
B. Cross section of a young anther. Note the introse arrangement of sporangia and the tannin inclusions in the epidermis, endothecium, and connective.
C. Longisection of a mature anther.
D. Longisection of young ovules showing the single archesporial cell (arc) at the subdermal layer. Note that the junction between inner and outer integuments is very high.
E. Cross section of a mature ovule showing a thick raphe bundle and five or six smaller vascular bundles in the integument.
F. Longisection of a mature ovule. Note the well developed endothelium, the presence of abundant basal nucellar tissue, and the fusion between the inner and outer integuments.
Same scale bar for A-F, 0.05mm, 0.05mm, 0.1mm, 0.05mm, 0.15mm, 0.1mm, respectively.


A
B
C
D
E
F
rb

Fig. 21. A-F. Asteranthos brasiliensis (A,D. Kawasaki 62; B,C,E,F. Coradin 7).

A. Longisection of young anthers. Note the acute apex.

B. An anther showing glandular tapetum (ta) and slightly enlarged endothecium (ed).

C. Longisection of part of a young anther showing five or six wall layers: epidermis, endothecium, two or three middle layers, and tapetum.

D. Longisection of a young ovule at the stage of megasporocyte.

E. Longisection of an ovule at meiosis. The lower two megaspores are just produced (arrow). The endothelium (et) is well developed.

F. Longisection of a mature ovule.

Same scale bar for A-F, 0.1mm, 0.05mm, 0.05mm, 0.05mm, 0.05mm, 0.1mm, respectively.

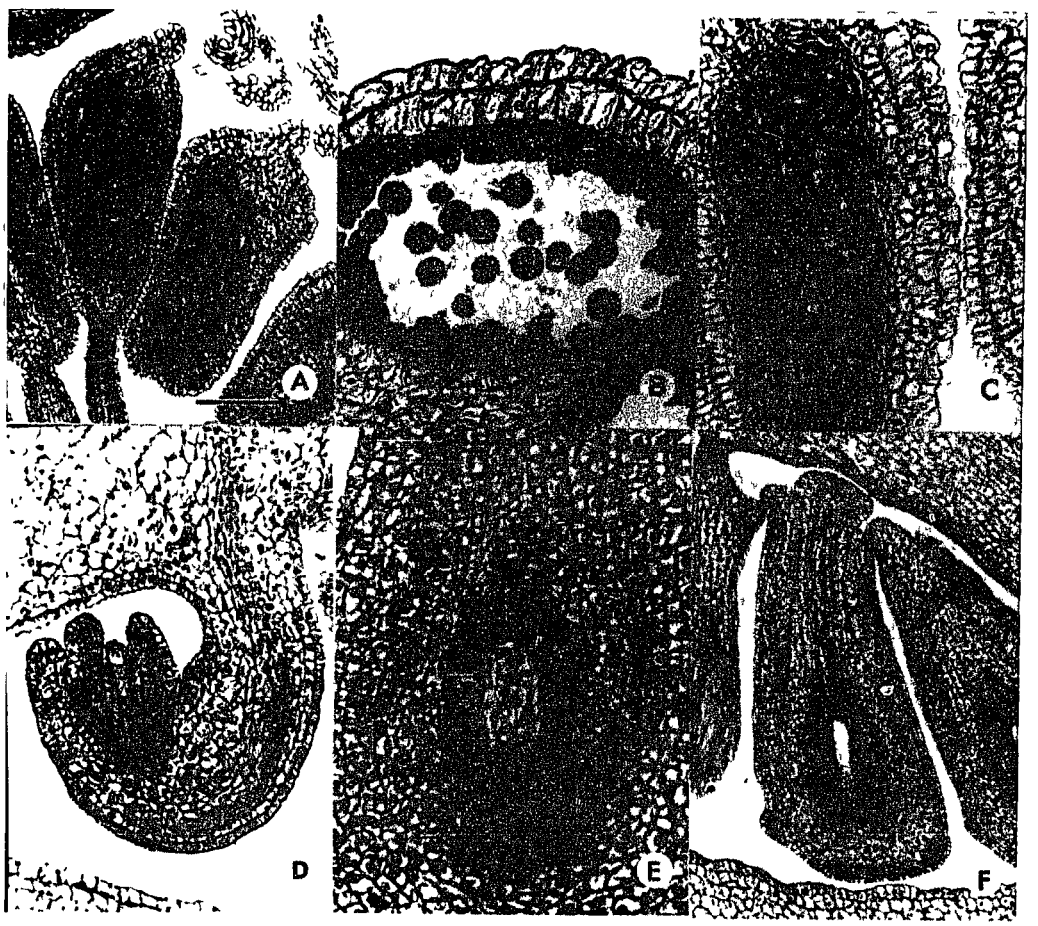

A
B
C
D
E
F

Fig. 22. A-D. Asteranthos brasiliensis (Kawasaki 62).
A. An ovule primordium with trizonate structure.
B-C, Dermal initiation of inner integument (ii) and outer integument (oi) with subdermal cells involved in later development. Only one archesporial cell (arc) is formed from the subdermal layer.
D. An ovule at the megasporocyte stage. The archesporial cell differentiates into the megesporocyte (mc) directly.

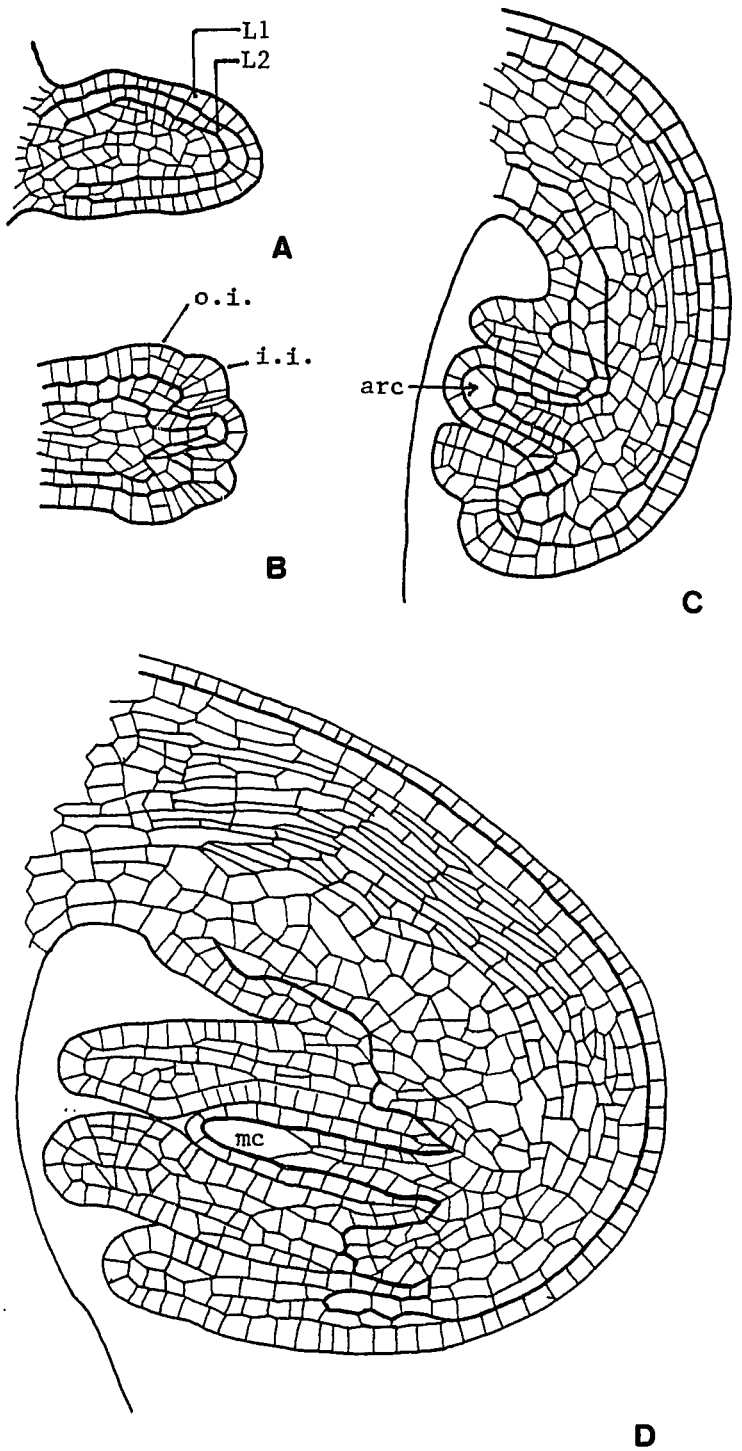

L1
L2
A
o.i.
i.i.
B
arc
C
mc
D

Fig. 23. A-E. Crateranthus cf. talbotii (Mambo & Thomas 36).
A. Cross section of an anther at free spore stage. Note the continuity of the endothecium around the connective (arrows). Part of the tapetal cells are empty.
B. Part of an anther showing the dense medium in the locule. The endothecium (ed) is filled with tannin.
C. Section of the wall of anther before maturity. The inner middle layer (ml) is still present. The rod-like secondary thickenings are thick and arranged uniformly.
D. Longisection of an ovule after meiosis.
E. Cross section of a mature ovule showing the raphe bundle (rb) entering the outer integument without branching (arrow below).
Same scale bar for A-E, 0.2mm, 0.08mm, 0.05mm, 0.2mm, 0.12mm, respectively.

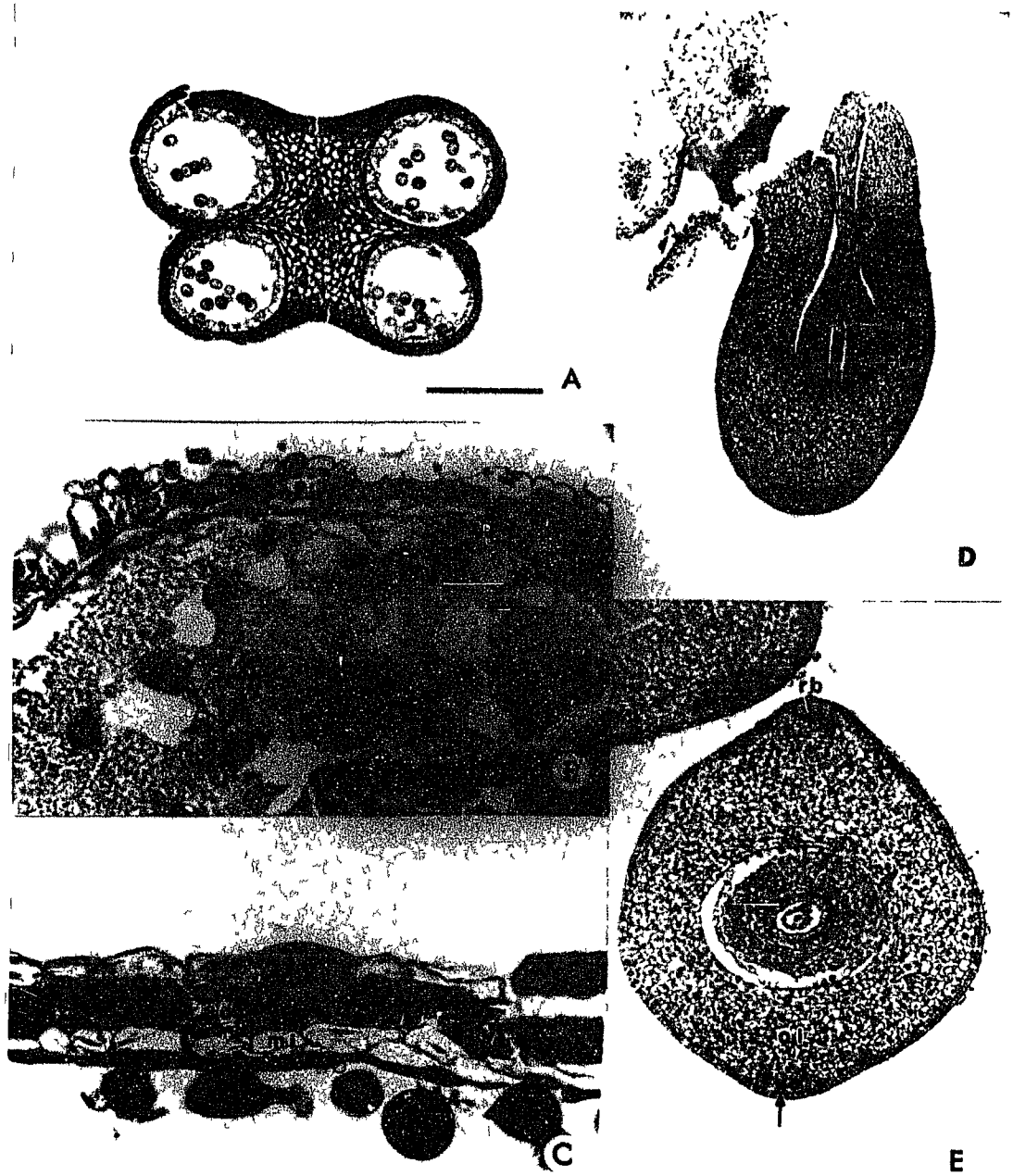
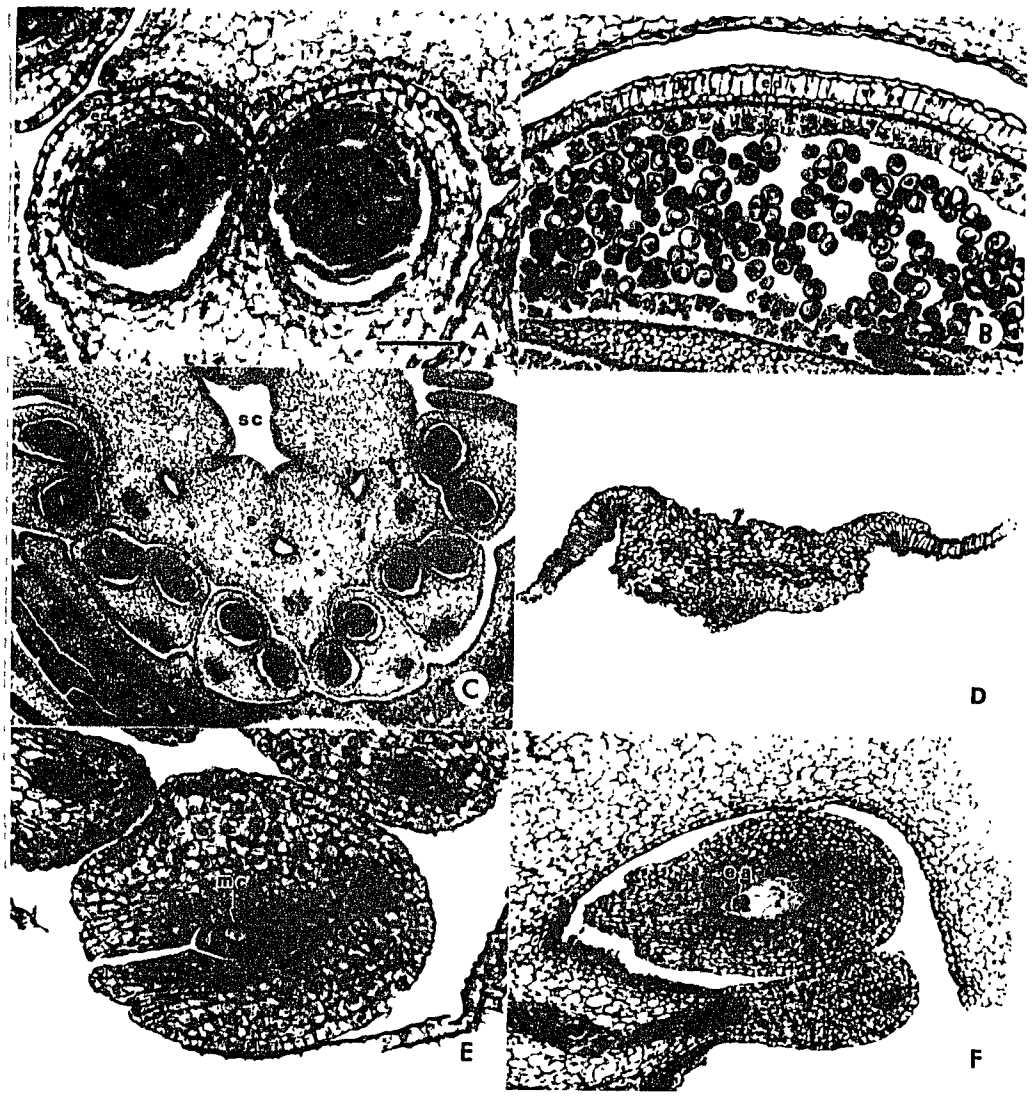

A
D
C
E
pb

Fig. 24. A-F. Napoleonaea cf. vogelii (Reitsma 2946).
A. Cross section of a young anther showing its two sporangia and the five or six wall layers: epidermis (ep), endothecium (ed), two or three middle layer (ml), and tapetum (ta).
B. Longisection of an anther with glandular tapetum (ta). The endothecium (ed) is elongated, and there is still one middle layer present.
C. Cross section of a young flower bud showing the relatively large style (s) and the arrangement of anthers.
D. A dehisced anther with only one cell.
E. Longisection of a young ovule showing the single megasporocyte (mc) at subdermal layer and the fusion between two integuments.
F. Longisection of a mature ovule with its rather large egg apparatus.
Same scale bar for A-F, 0.05mm, 0.1mm, 0.2mm, 0.2mm, 0.05mm, 0.1mm, respectively.


A
B
sc
C
D
mc
E
oq
F

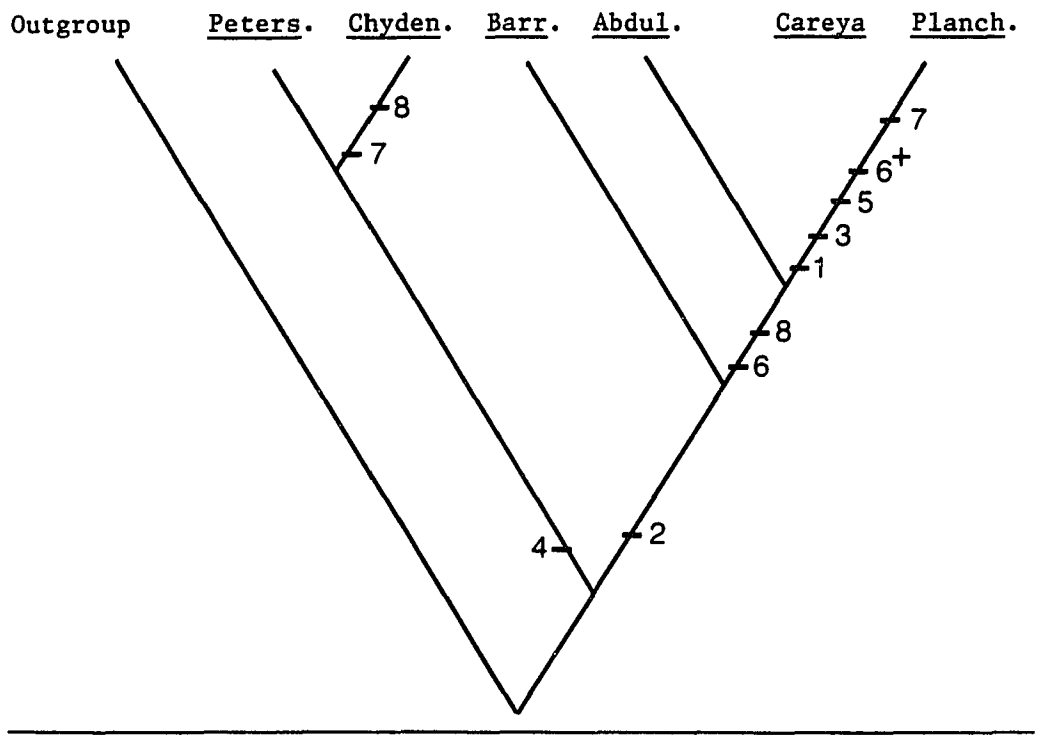



Fig. 25. Intergeneric relationship of the Planchonioideae based on the cladistic analysis of embryological characters.

Fig. 26. A-B. Abdulmajidia chaniana (Tsou 160). C-E. Barringtonia racemosa (Hsieh s.n.).
Note the structure of staminal ring (sr), the shapes of nectary disk (n) and ventral slit (vs), the position of placenta (pl), and the unlobed calyx of B. racemosa in C. All scale bars, 1mm.

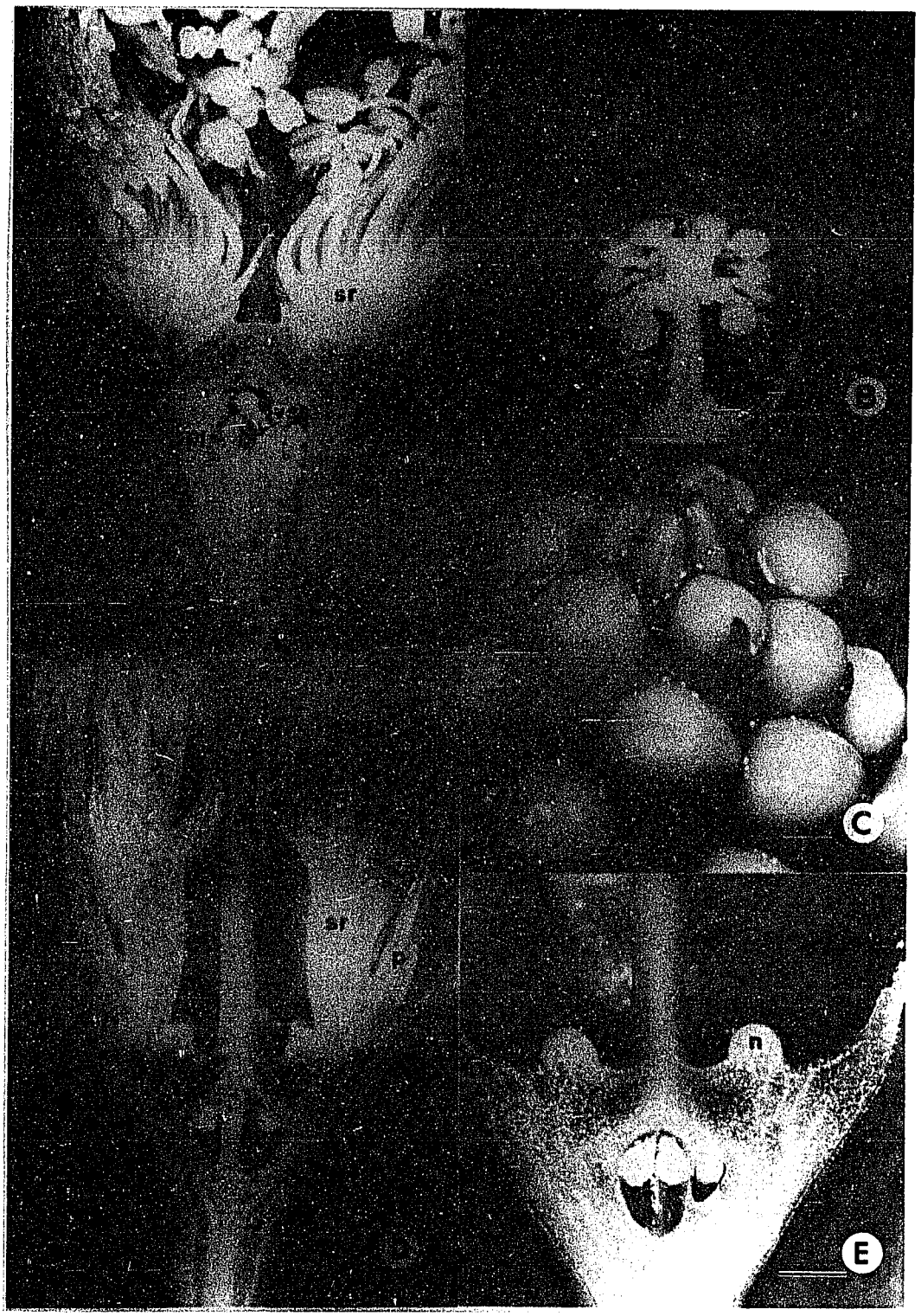

sr
B
C
sr
P
n
E

Fig. 27. A-D. Careya arborea (Jayasuriya 4334). E-F. Planchonia careya (Jackes s.n.).

A. The 4-lobed calyx.

B. Stamens showing general morphology of the stamens of most planchonioid genera.

C,E. Note the similar structures of nectary in these two species, i.e., the nectary disk (n) and the nectary reservior (nr).

D,F. Showing the placentation; D, from a medium bud; F, from a mature flower. In both species the placenta is spindle-like and completely surrunding the ventral slit (vs), and the ovule develops an arilloid (ar) structure. Scale bars, 2mm, 2mm, 1mm, 1mm, 1mm, 1mm, respectively.

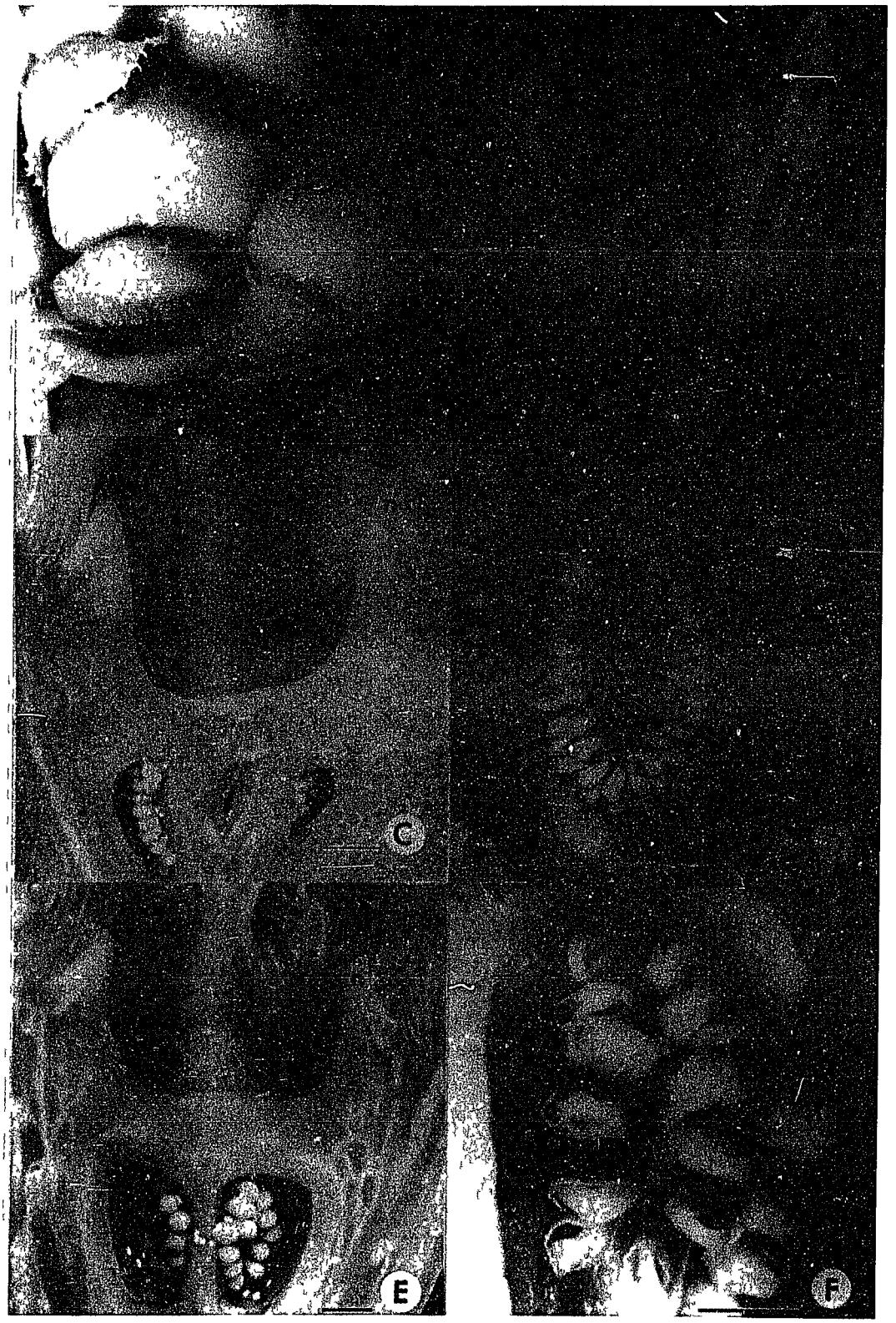

C
E
F

Fig. 28. A-B. Petersianthus quadrialatus (Herraze 4172).
C-E. Allantoma lineata (Prance 17549).
A. Inflorescences. There are four wings (w) on the surface of each ovary.
B. Note the arrangement of ovules and the nectary disk (n).
C, E. Note the tubular staminal ring (sr) and the arrangement of stamens in more or less four levels.
D. Axile placentation with ovules arranged in two rows in each locule..
Scale bars, 1cm, 1mm, 2mm, 1mm, 2mm, respectively.

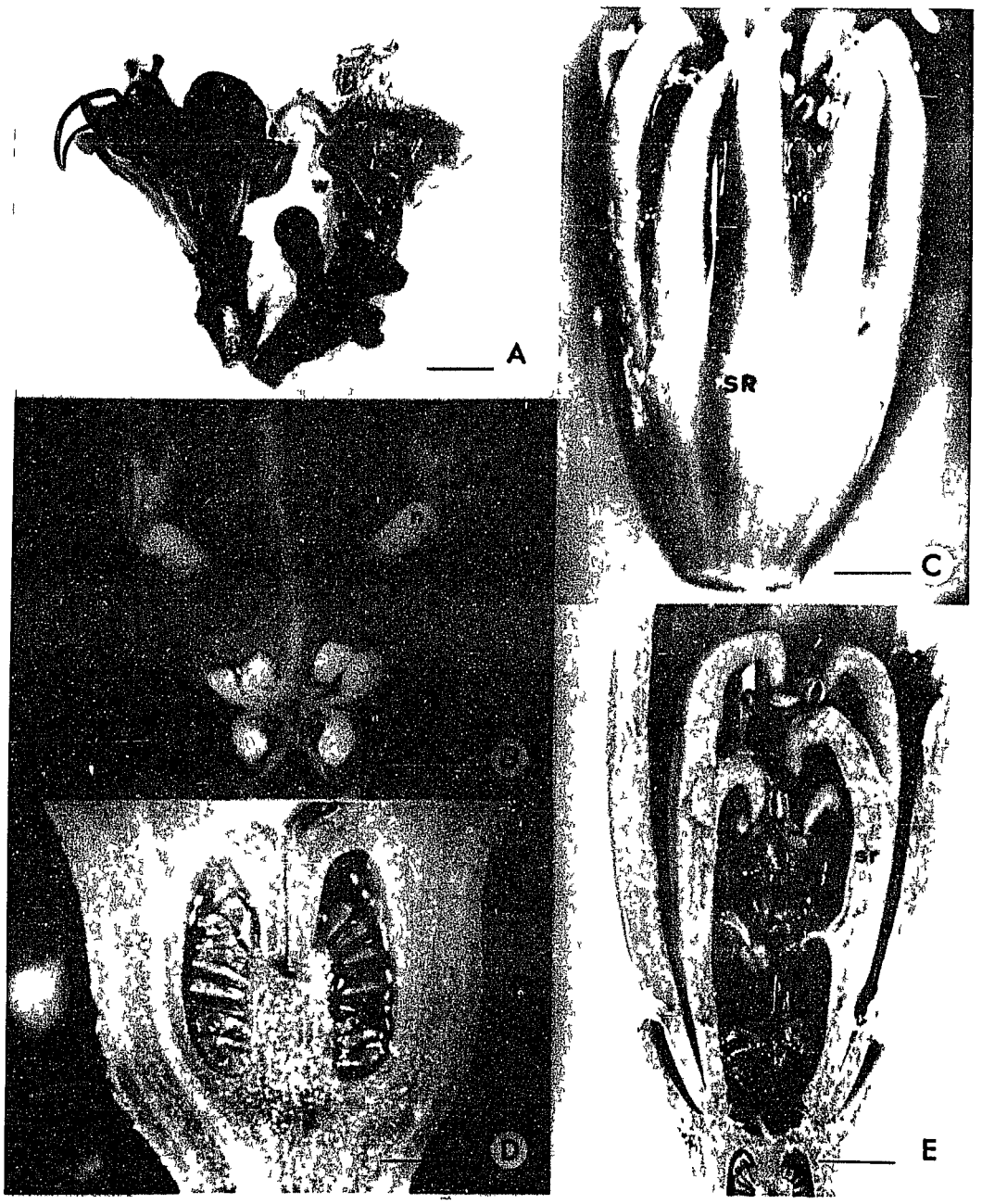

A
SR
C
D
E

Fig. 29. Grias species.

A-B. G. peruviana (Peters s.n.) showing the unlobed calyx and the young staminal ring (sr).

C-D. G. cauliflora (Nee & Mori 3574) showing the unlobed calyx with an apical pore and the placenta located right beneath the ventral slit (vs).

E. G. neuberthii (Plowman & Davis 4365). Note the massive staminal ring (sr) and the pendulous ovules.

Scale bars, 1mm, 2mm, 1mm, 0.5mm, 2mm, respectively.

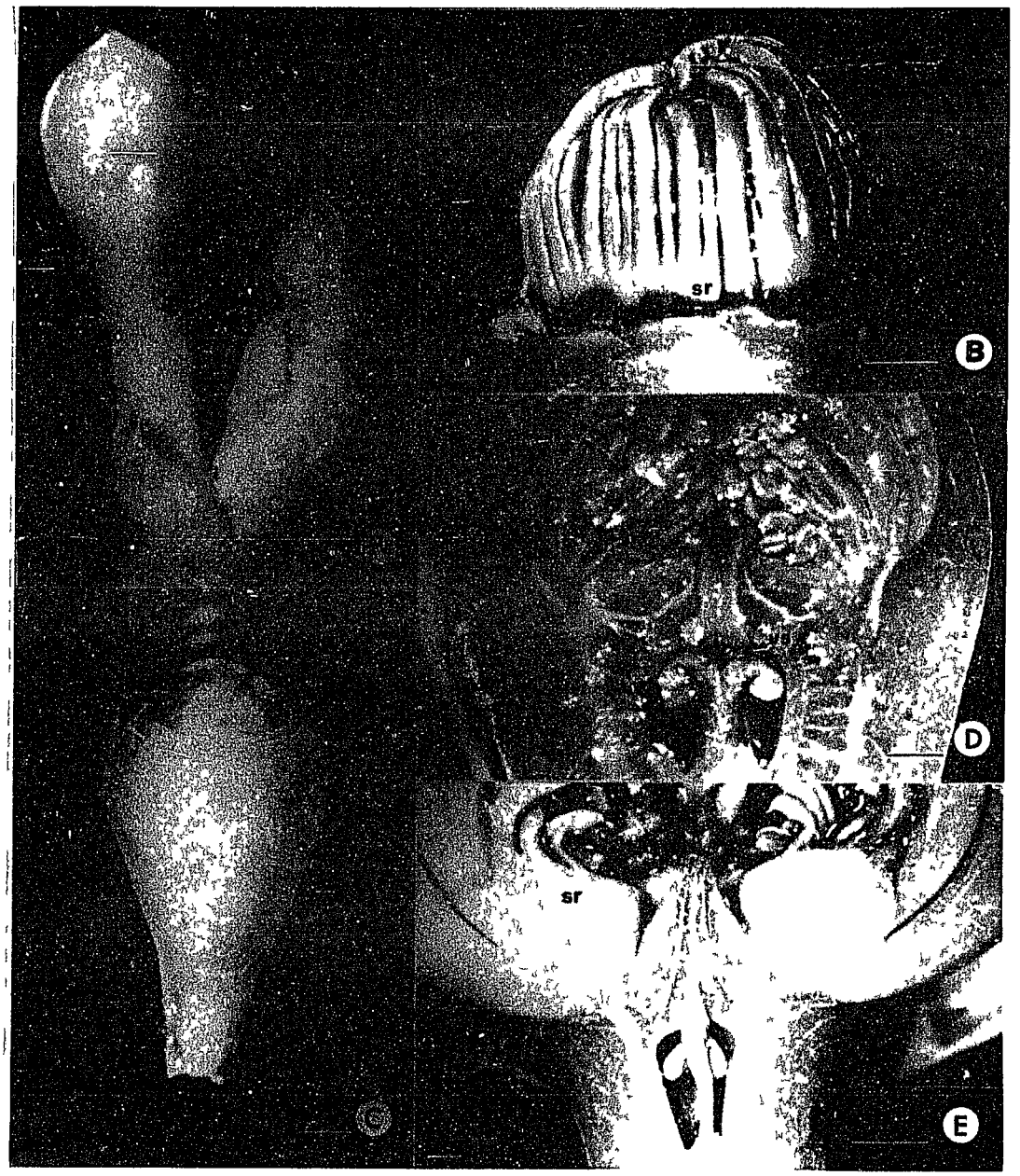

sr
B
D
sr
E

Fig. 30. Gustavia, Bertholletia, and Cariniana species.
A. G. macarenensis ssp. paucisperma (Nee & Mori 4159). Note the staminal ring (sr), the long anthers, and the dilated apex of the filament.
B. G. hexapetala (Mori 18676) showing the ventral slit (vs) and the placenta.
C-D. Bertholletia excelsa (Nelson s.n.) showing the zygomorphic androecium and placentation. Note the expanded hood (h) and the ligule (l).
E-F. C. micrantha (Mori 20191) showing a flat hood and the axile placentation.
Scale bars, 2mm, 0.5mm, 0.5cm, 1mm, 1mm, 2mm, respectively.

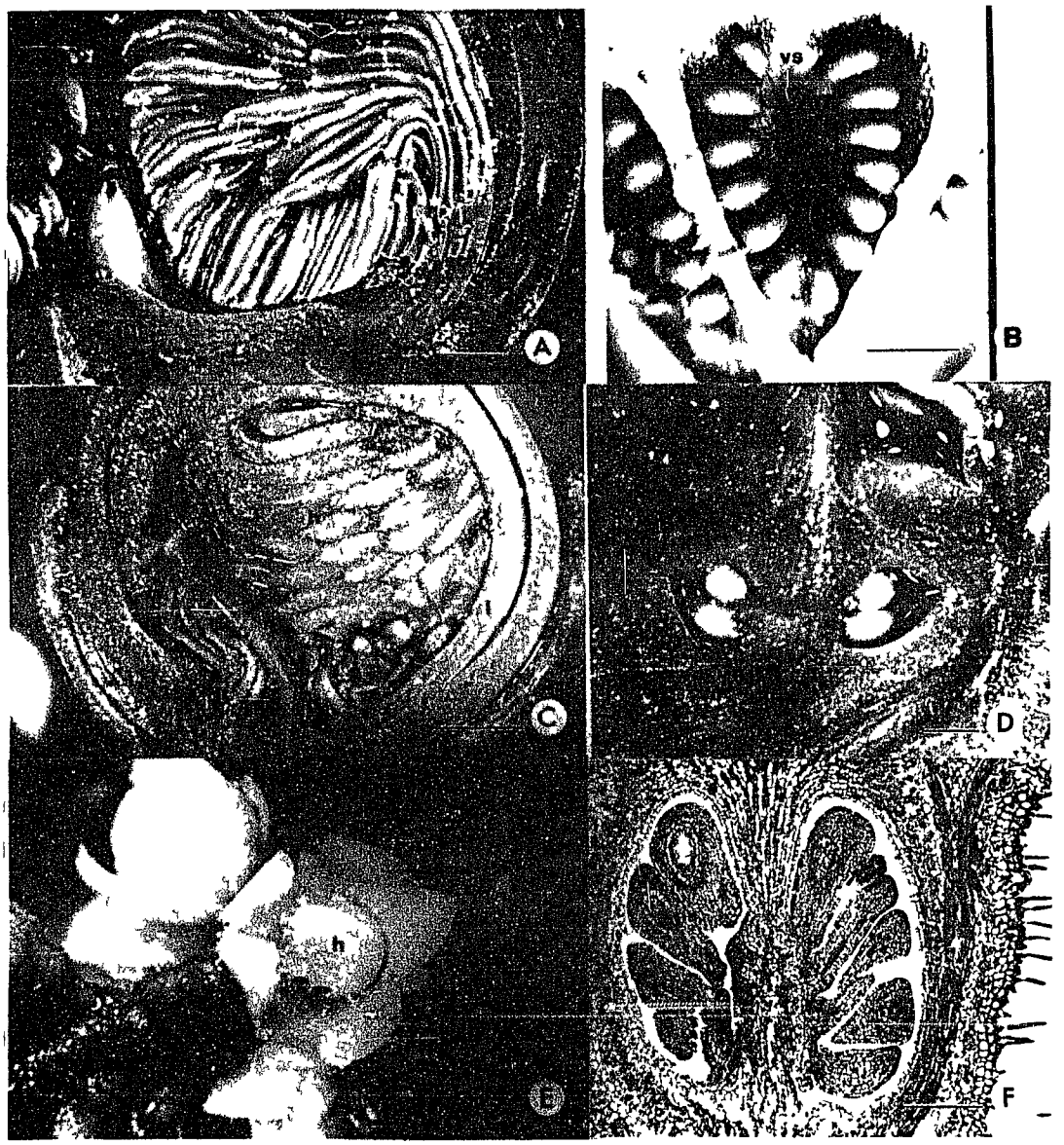

A
ys
B
C
h
D
E
F

Fig. 31. Corythophora, Couratari, and Couroupita species.
A. Corythophora amapaenensis (Mori 18675).
B-D. Couratari oligantha (Plowman et al. 12546). Note the ligule (l), the coiled hood (h), the appendages of the hood (arrows), and placentation.
E-F. Couroupita guianensis (Tsou 213) showing the expanded hood (h), the staminal ring (sr), and placentation. Note that the apex of the filament is dilated and then constricted.
Scale bars, 1mm, 0.5mm, 2mm, 0.5mm, 2mm, 2mm, respectively.

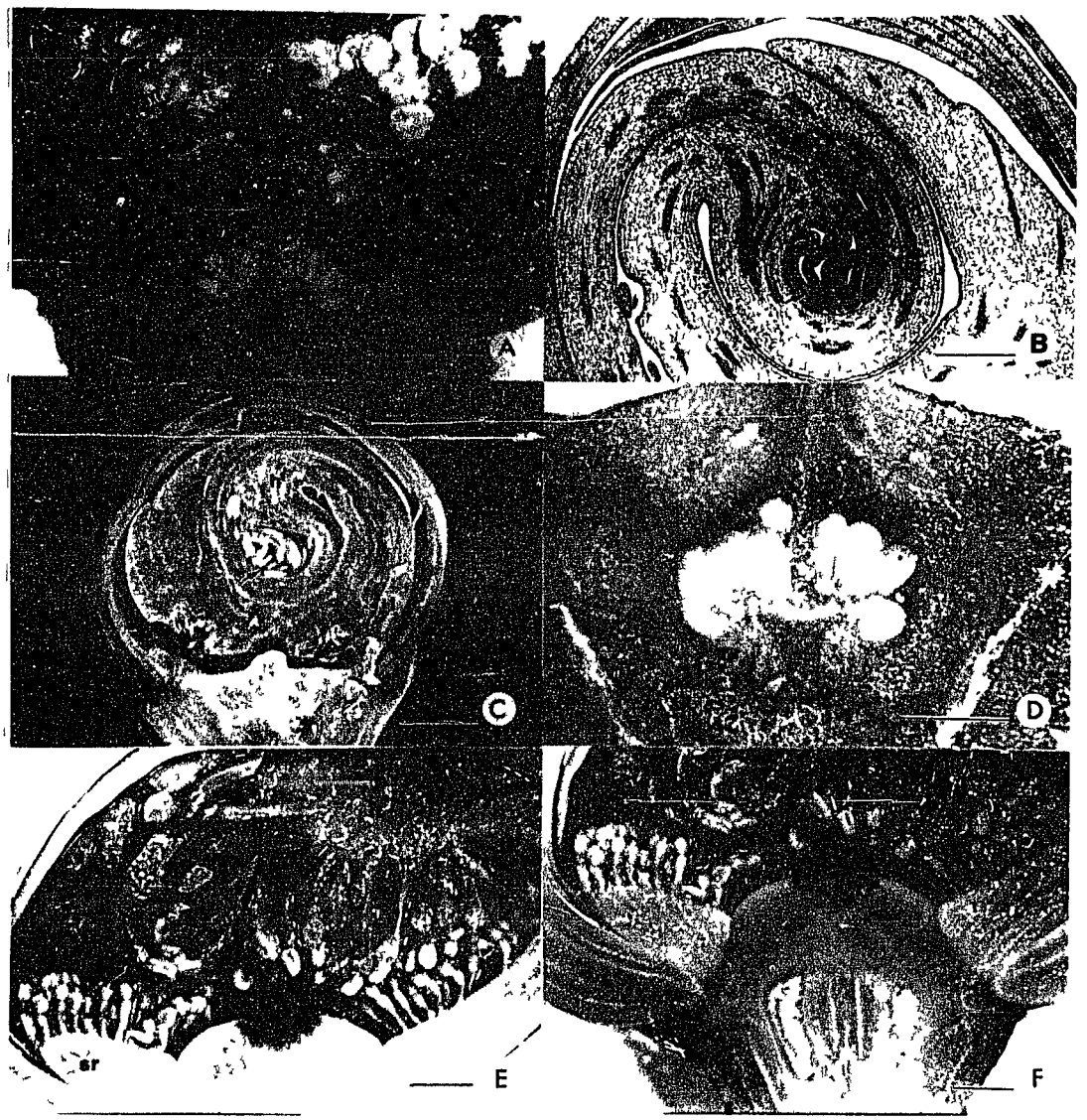

A
B
C
D
E
F
sr

Fig. 32. Eschweilera, Lecythis, and Foetidia species.
A-B. E. cyathiformis (Mori 19385) showing part of the zygomorphic androecium and the ovary. The placenta (pl) is much expanded.
C. L. poiteaui (Mori 18533) showing part of the hood (h), the ligule (l), the staminal ring (sr), and the constriction of filaments (arrows).
D-E. F. obliqua (Schatz 1855) showing the large calyx lobe (c), a pair of bracteoles (b), the absence of corolla, and placentation. The style in E is broken down.
Scale bars, 2mm, 0.5mm, 2mm, 1mm, 1mm, respectively.

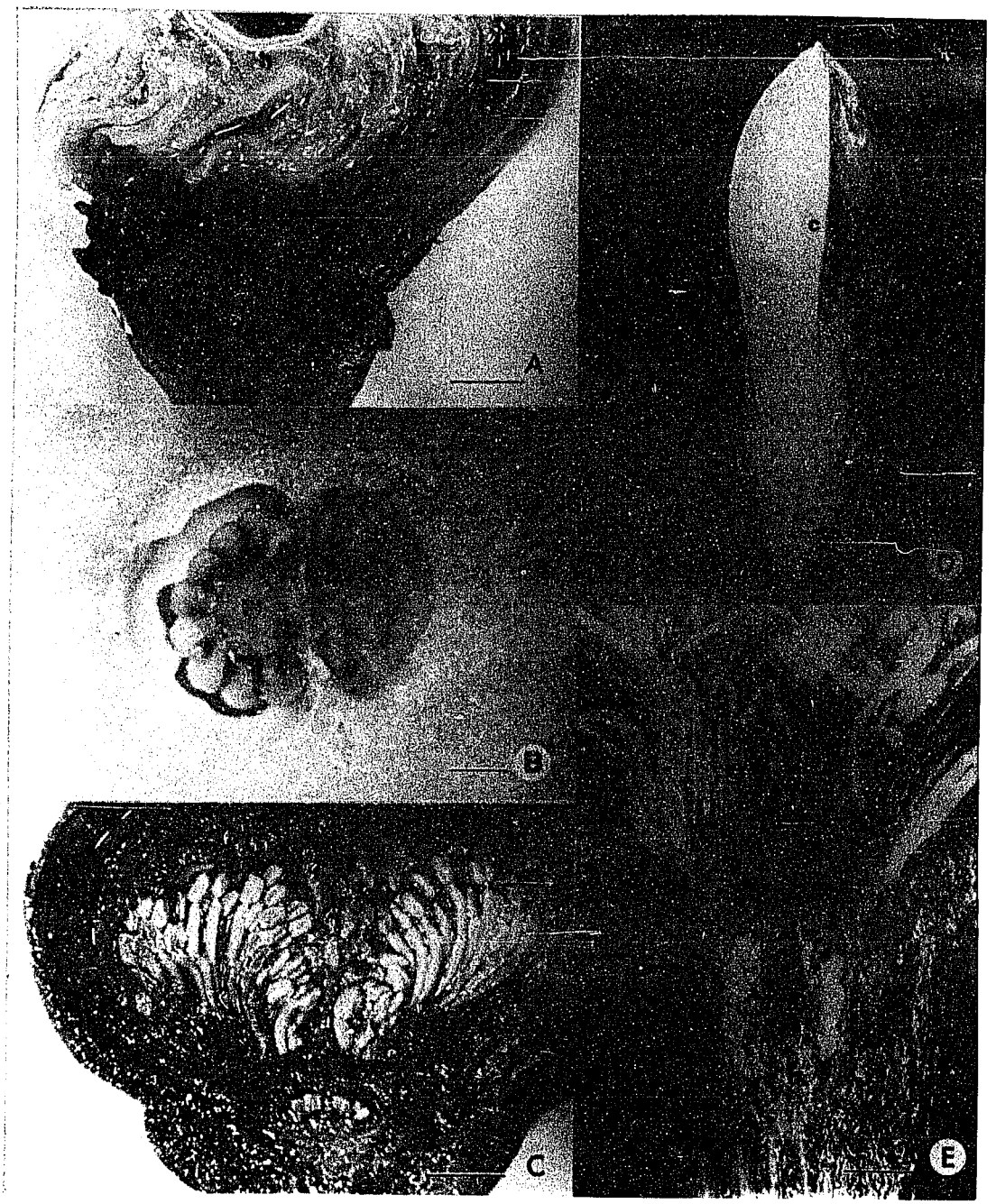
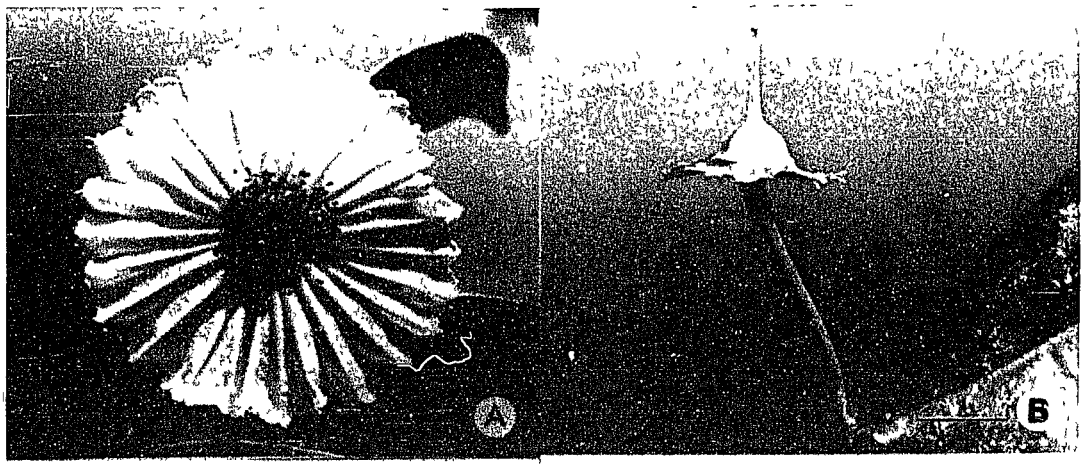
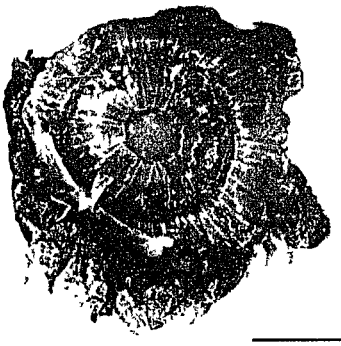
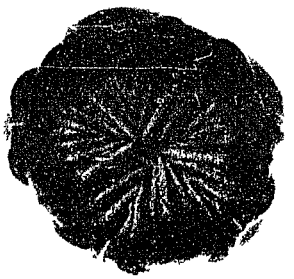

A
B
C
D
E

Fig. 33. Asteranthos, Napoleonaea, and Crateranthus species.
A-B. Asteranthos brasiliensis (Stevenson 858) showing the sympetalous corolla, the plate-like synsepalous calyx, and the buttress-like ridges on the ovary wall.
C-D. Napoleonaea cf. vogelii (Reitsma 2946). C. Open flower showing the sympetalous corolla, two whorls of staminodes, one whorl of stamens, and the large stigma. D. Medium bud showing the five valvate sepals and the plicated folds of corolla.
E-F. Crateranthus cf. talbotii (Mambo & Thomas 36). E. Medium bud showing the plicated folds of corolla and the extruded style. F. Mature flower with semi-inferior ovary and many pendulous ovules.
Scale bars, 1cm, 1cm, 1cm, 0.5cm, 0.5cm, 0.5cm, respectively.

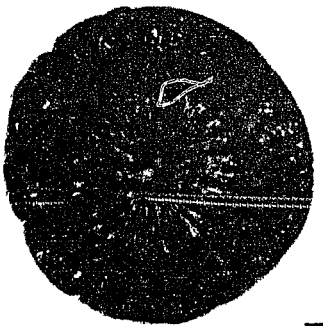


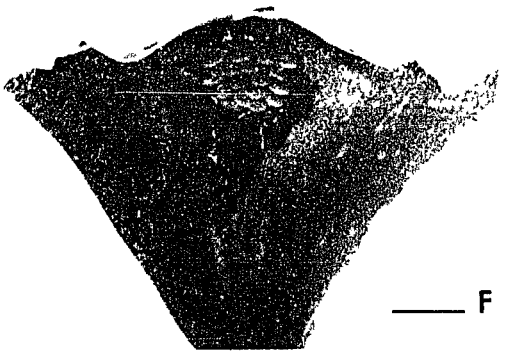
C



D



E



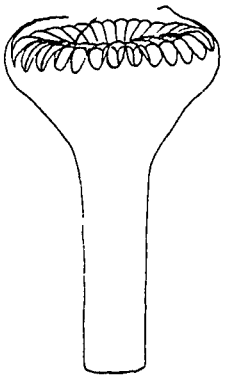
F

Fig. 34. Three developmental stages of Asteranthos brasiliensis (Kawasaki 62) showing the change of position of the ovary.

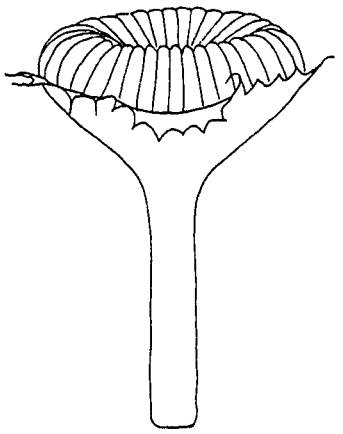
Aa, Ab. Tiny bud with an inferior ovary and relatively wide androecial base.

Ba, Bb. Small to medium bud with an inferior ovary and relatively slightly narrowed androecial base. The synsepalous calyx starts to open.

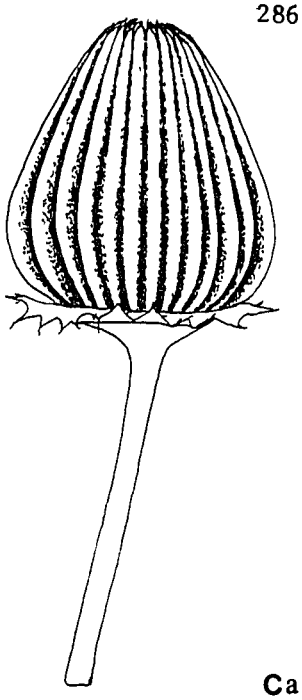
Ca, Cb. Large bud with a semi-inferior ovary and very narrowed androecial base. The calyx is plate-like.



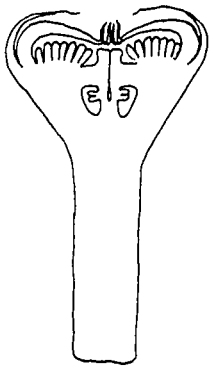
Aa



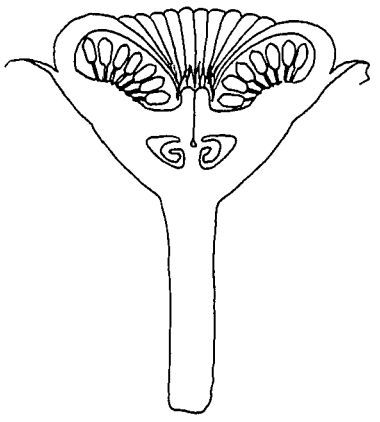
Ba



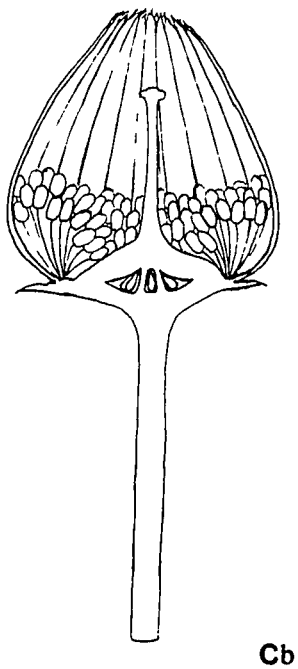
Ca



Ab

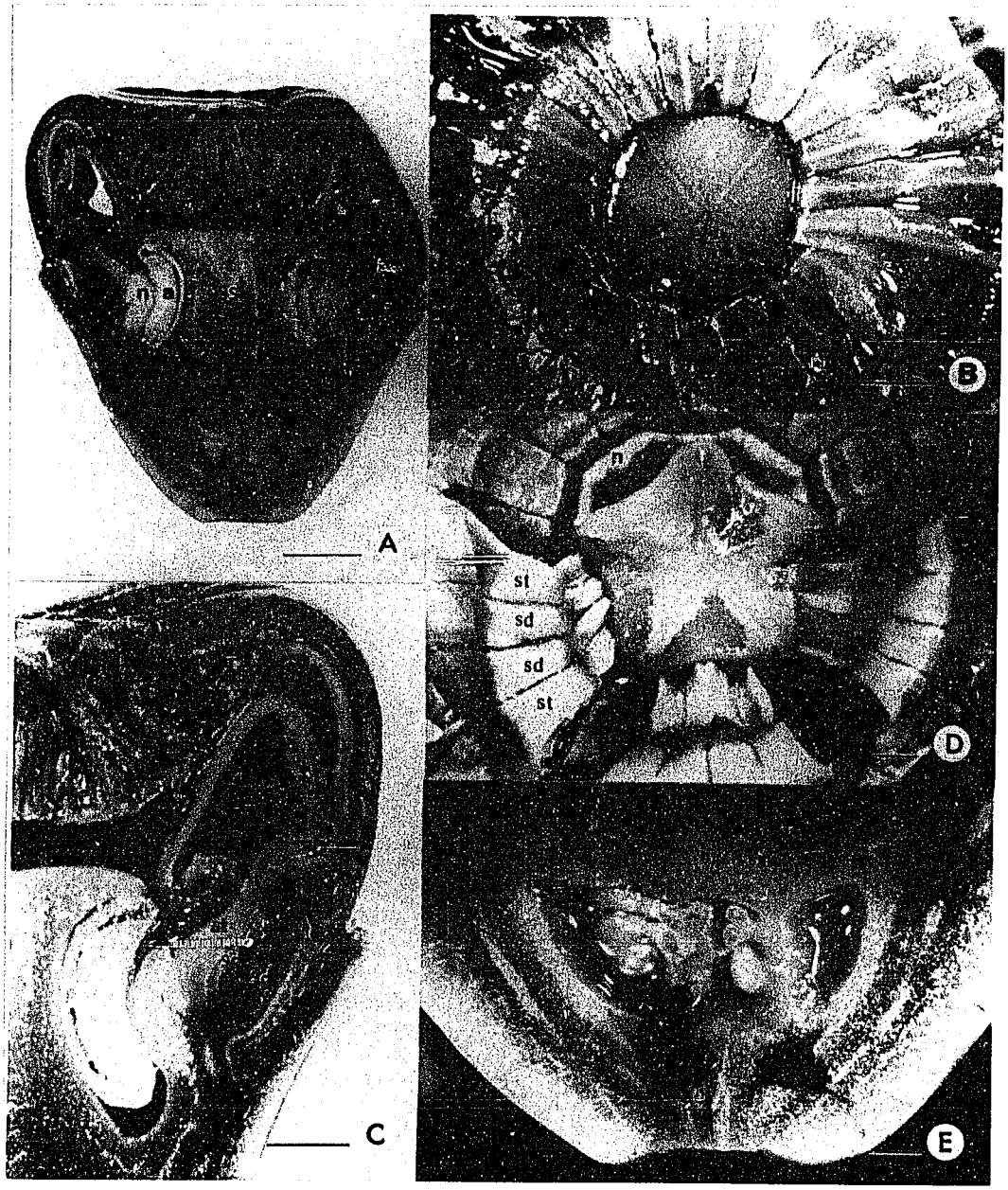


Bb



Cb

Fig. 35. A-E. Napoleonaea imperialis (Jayasuriya 4333).
A-C. Showing the thick style (s), the pentagonal stigma, the large anthers (a) beneath the stigma, the nectary disk (n), the curved stamen (st), the two whorls of staminodes (sd), and the hook between them (arrow).
D. Anthers are pulled out to show the arrangement of stamens (st) and staminodes (sd) in the same whorl.
E. Ovary showing the inferior position and few campylotropous ovules from the axis.
Scale bars, 2mm, 2mm, 1mm, 1mm, 0.05mm, respectively.


A
B
C
D
E
st
sd
sd
st

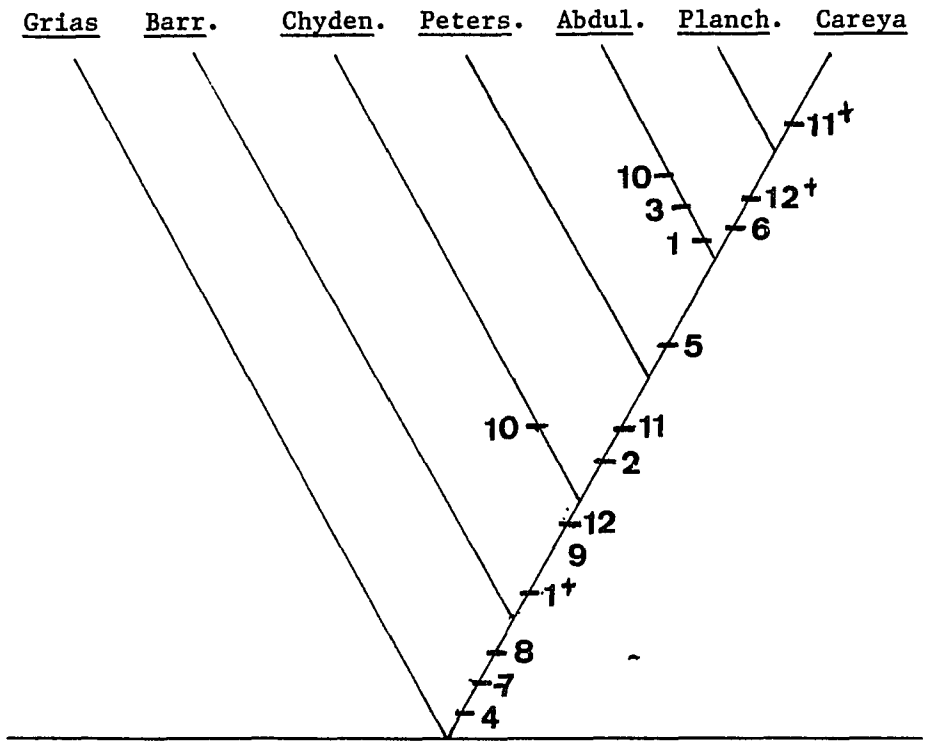



Fig. 36. Intergeneric relationships of the Planchonioideae based on the cladistic analysis of reproductive morphological characters.

## LITERATURE CITED

Airy-Shaw, H. K. 1973. A dictionary of the flowering plants and ferns of the late J. C. Willis; 8th edition. Cambridge University Press, Cambridge.

Anisimova, G. M. 1985. Lecythidaceae. In: M. S. Yakovlev (ed.) Comparative Embryology of Flowering Plants. Vol. III, pp.125-130. Nauka, Leningrad.

Baker, E. G. 1913. Crateranthus. In: Rendle, Catalogue of Talbot's Nigerian Plants. Brit. Mus. Nat. Hist. 35.

Baker, H. G. 1960. Apomixis and polyembryony in Pachira oleaginea (Bombacaceae). Amer. J. Bot. 47(4):296-302.

Bala Bawa, S. 1970. Theaceae. Bull. Indian Nat. Sci. Acad. 41:75-77.

Bentham, G. & W. J. Hooker. 1865. Myrtaceae: Tribus IV. Lecythideae. Genera planturum 1(2):720-725.

Bhandari, N. N. 1984. The microsporangium. In: B. M. Johri (ed.), Embryology of Angiosperms, pp. 53-121. Springer-Verlag, Berlin, Heidenberg.

Boesewinkel, F. D. 1980. Development of ovule and seed-coat in the Rutales-Geraniales assembly. Thesis. Amsterdam.

Bosser, J. 1988. Especes nouvelles du genre Foetidia (Lecythidaceae) de Madagascar. Bull. Mus. natn. Hist. nat., Paris, ser. 4, sect. B. Adansonia 2:105-119.

Bouman, F. 1974. Developmental studies of the ovule, integuments and seed in some angiosperms. Thesis. Amsterdam.

---------. 1984. The ovule. In: B. M. Johri (ed.), Embryology of Angiosperms, pp. 123-157. Springer-Verlag, Berlin, Heidenberg, New York, Tokyo.

---------- & J. I. M. Calis. 1977. Integumentary shifting--A third way to unitegmy. Ber. Deutsch. Bot. Ges. 90:15-28.

Candolle, A. P. de. 1828. Myrtaceae tribes Barringtonieae and Lecythideae. In: Prodomus systematis naturalis regni vegetabilis. 3:288-296.

----------. 1839. Napoleoneae. In: Prodromus systematis naturalis regni vegetablis, pp.550-551.

Carey, G. & L. Fraser. 1932. The embryology and seedling development of Aegiceras majus. Proc. Linn. Soc., N.S.W., 57(5-6):34-360.

Carlquist, S. 1988. Wood anatomy of Scytopetalaceae. Aliso 12(1):63-76.

Chandra, S. & S. P. Bhatnagar. 1976. Reproductive biology of Abelmoschus esculentus. IV. Ovule, fertilization, endosperm and embryo development. J. Indian Bot. Soc. 55 (1):1-13.

Chevalier, M. A. 1909. Petersia viridiflora. Veg. ut. Afr. trop. francaise. 5:301-302.

Chiarugi, A. & E. Francini. 1929. Apomissia in Ochna serrulata Walp. Atti soc. ital. progr. sci., 18 Riunione, Firenze.

Chikkanniah, D. S. 1954. The embryo sac of Ochna squarrosa Linn. Curr. Sci. 23(7):232.

Constantin, J. & L. Dufour. 1885. Contributions a l'etude de la tige de Lecythidees. Bull. Soc. Bot. France 32:115-119.

Cronquist, A. 1957. Outline of a new system of families and orders of dicotyledons. Bull. Jard. Bot. Etat Brux. 27(1):13-40.

----------. 1968. The Evolution and Classification of Flowering Plants. Houghton Mifflin, Boston.

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

----------. 1988. The Evolution and Classification of Flowering Plants, 2nd edition. The New York Botanical Garden, New York.

Dahlgren, K. O. V. 1916. Zytologische und embryologische studien uber die keichen Primulales und Plumbaginales. Handl. Kgl. Sven. Vetensk. 56(4):1-80.

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

----------. 1983. General aspects of angiosperm evolution and macrosystematics. Nord. J. Bot. 3(1):119-149.

---------- & R. Thorne. 1984. The order Myrtales: Circumscription, variation, and relationships. Ann.

Missouri Bot. Gard. 71(3):633-699.

Davis, G. L. 1966. Systematic Embryology of the Angiosperms. New York, Londen, Sydney.

Desfontaines, R. L. 1820. Description du quatre nouveaux genres. Mem. Mus. Hist. Nat. 6:9-11.

Diehl, G. A. 1935. A study of the Lecythidaceae. Trop. Woods 43:1-15.

Don, G. 1832. A general history of the Dichlamydeous plants. Vol. 2. Calyciflorae. London.

Eichler, A. W. 1889. Napoleonaceae. In: Martius, Flora Brasiliensis 12(1):497.

Erdtman, G. 1952. Pollen Morphology and Plant Taxonomy.-- Angiosperms. (An Introduction to Palynology. I.) Almqvist & Wiksell, Stockholm.

----------. 1971. Pollen Morphology and Plant Taxonomy.-- Angiosperms. (An introduction to Palynology. I.). 2nd edition. Hafner, New York.

Freiberg, T. E. 1983. Elaeocarpaceae, Tiliaceae. In: M. S. Yakovlev (ed.), Comparative Embryology of Flowering Plants. Vol. II, pp.244-246. Nauka, Leningrad.

George, G. P., R. A. George & J. M. Herr Jr. 1979. A comparative study of ovule and megagametophyte development in field-grown and greenhouse-grown plants of Glycine max and Phaseolus aureus (Papilionaceae). Amer. J. Bot. 66:1033-1043.

Ghosh, R. B. 1964. Supernumerary archesporial cell in Ochna atropurpurea. Curr. Sci. 33(4):116-117.

Gulati, M. & S. Ravishankar. 1980. Studies in Symplocaceae. I: Microsporangium, microsporogenesis and male gametophyte. Phytomorphology. 30:189-195.

Herr, J. M. 1984. Embryology and taxonomy. In: B. M. Johri (ed.), Embryology of Angiosperms, pp.647-696. Springer-Verlag, Berlin, Heidenberg.

Hoar, C. S. & E. J. Haertl. 1932. Meiosis in the genus Hypericum. Bot. Gaz. 93:197-204.

Hutchinson, J. 1959. The Families of Flowering Plants. Vol. I, 2nd edition. Dicotyledons. Clarendon Press, London.

----------. 1969. Barringtoniaceae, Lecythidaceae and Asteranthaceae. In: Evolution and Phylogeny of Flowering Plants, pp. 326-333.

----------. 1973. The Families of Flowwering Plants, 3rd edition. Clarendon Press, Oxford.

Jacques, F. 1965. Morphologie du pollen et des ovules de Couroupita guianensis Aubl. (Lecythidacees). Polle et Spores 7:175-180.

Johansen, D. A. 1936. Morphology and embryology of Fouquieria. Amer. J. Bot. 23:95-99.

Johri, B. M. 1963. Embryology and taxonomy. In: P. Maheshwari (ed.), Recent Advances in the Embryology of Angiosperms, pp. 395-444. Delhi.

----------. 1967. Angiosperm embryology and taxonomy. In: Symposium on newer trends in taxonomy. Bull. Natl. Inst. Sci. India 34:263-268.

---------- (ed.). 1984. Embryology of Angiosperms. Spring-Verlag, Berlin, Heidengerg, New York, Tokyo.

Joshi, P. C., A. M. Wadhwani & B. M. Johri. 1967. Morphological and embryological studies of Gossypium L. Proc. Nat. Inst. Sci. India B, 33:37-93.

Jussieu, A. L. de. 1789. Genera Plantarum, pp.326-328. Paris.

Kapil, R. N. & S. B. Sethi. 1963. Development of male and female gametophytes in Camellia sinensis (L.) Kuntze. Proc. Nat. Inst. Sci. India 29(5):567-574.

Kartawinata, E. K. 1965. The genus Planchonia Blume (Lecythidaceae). Bull Bot. Surv. India 7:162-187.

Kiew, R. & K. M. Wong. 1988. Barringtonia corneri (Lecythidaceae), a remarkable new litter -- trapping species from Johore, Malaysia. Malayan Nature Journal 41:457-459.

Knuth, R. 1934. Uber die Gattung Asteranthos. Notizbl. Bot. Gart. Berlin-Dahlem 11:1034-1036.

--------. 1939a. Barringtoniaceae. In: A. Engler, Pflanzenreich, IV. 219:1-82.

--------. 1939b. Lecythidaceae. In: A. Engler, Pflanzenreich, IV. 219a:1-146.

--------. 1939c. Asteranthaceae. In: A. Engler, Pflanzenreich, IV. 219b:1-3.

Kobuski, C. E. 1948. Studies in the Theaceae. XVII. A review of the genus Bonnetia. J. Arn. Arb. 29(4):393-413.

Kowal, R. R. 1989. Chromosome numbers of Asteranthos and the putatively related Lecythidaceae. Brittonia 41:131-135.

----------, S. A. Mori & J. A. Kallunki. 1977. Chromosome numbers of Panamanian Lecythidaceae and their use in subfamilial classification. Brittonia 29:399-410.

Le Maout, E. & J. Decaisne. 1873. General system of botany. Longmans Green, London.

Letouzey, R. 1960. Notes sur les Scytopetalacees (Revision des Scytopetalacees de L'herbier de Paris). Adansonia ser. 2, 1:106-142.

---------- 1978. Scytopetalaceae. In: A. Aubreville & J. F. Leroy (eds.), Flore du Gabon. 24:139-193.

Liben, L. 1971. Revision du genre africain Napoleonaea P. Beauv. (Lecythidaceae). Bull. Jard. Bot. Nat. Belg. 41: 363-382.

Lignier, O. 1890. Recherches sur l'anatomie des org. vegetatifs des Lecythidees, des Napoleonees et des Barringtoniees. Bull. Sci. France Belgique 21:291-420.

Lindley, J. 1830. Introduction to a natural system of botany. p.44, Lecythideae; p.177, Belvisiaceae.

----------. 1836. A Natural system of Botany. 2nd edition. P. 239.

----------. 1846. The Vegetable Kingdom, pp.716-730.

Maheshwari, P. 1950. An Introduction to the Embryology of Angiosperms. MacGill Co., New York.

----------. (ed.). 1962. Plant Embryology. A Symposium. CSIR, New Delhi.

----------. 1963a. Recent Advances in the Embryology of Angiosperms. Delhi.

----------. 1963b. Embryology in relation to taxonomy. In: W. B. Turrill (ed.), Vistas in Botany. IV. Recent Research in Plant Taxonomy. Pergamon, Oxford.

---------- & R. N. Kapil. 1966. Some Indian contributions to the embryology of angiosperms. Phytomorphology 16:239-291.

Mametyeva, T. B. 1983. Myrsinaceae, Theophrastaceae, Primulaceae. In: M. S. Yakovlev (ed.), Comparative Embryology of Flowering Plants. Vol. II, pp. 236-243. Nauka, Leningrad.

Mashard, E. 1936. Embryologische untersuchungen an Styrax obassia Sieb. et Zuss. Planta 25:364-383.

Mathew, C. J. 1978. Development of male and female gametophytes in Camellia sasanqua. Phytomorphology 28: 262-269.

Mangenot, S. & G. Mangenot. 1957. Nombres chromosomiques nouveaux xhez diverses Dicotyledones et Monocotyledones d'Afrique occidentale. Bull. Jard. Bot. Etat. 27:639-654.

---------- & ----------. 1958. Deuxieme liste de nombres chromosomiques nouveau chez diverses Dicotyledones et Monocotyledones d'Afrique occidentale. Bull. Jard. Bot. Etat. 28:315-329.

---------- & ----------. 1962. Enquete sur les nombres chromosomique dans une collection d'especes tropicales. Rev. Cytol. Biol. Veg. 25:411-447.

Masters, M. T. 1869. On the structure of the flower in the genus Napoleona. J. Linn. Soc. Bot. 10:492-504.

Mauritzon, J. 1935. Zur Embryologie der Elaeocarpaceae. Ark. bot. 26A(10):1-8.

----------. 1936. Embryologische Angaben uber Theophrastaceen. Ark. bot. 28B(1):1-4.

----------. 1939a. Contributions to the embryology of the Orders Rosales and Myrtales. Acta Univ. Lund. II. Sect. 2, 35:1-120.

----------. 1939b. Uber die Embryologie von Marcgravia. Bot. notis. 1:249-255.

Meisner, C. F. 1839. Belvisieae in Plantarum vascularium genera 125. Barringtonieae & Lecythideae 109.

Merrill, E. D. 1909. New or noteworthy Philippine plants, VII. Philippine J. Sci. (Bot.) 4(3):247-330.

----------. 1916. Lecythidaceae. In: New Plants from Samar. Philippine J. Sci. 11:200.

Metcalfe, C. R. & L. Chalk. 1957. Anatomy of the Dicotyledons. Oxford University Press. Cambridge.

---------- & --------. 1983. Anatomy of the Dicotyledons. Vol. II. Wood structure and conclusion of the general introduction. Oxford University Press. New York.

Miers, J. 1874. On the Lecythidaceae. Trans. Linn. Soc. London. 30:157-318.

--------. 1875a. On Napoleona, Omphalocarpum and Asteranthos. Trans. Linn. Soc. London, bot. 1:17-19.

--------. 1875b. On the Barringtoniaceae. Trans. Linn. Soc. II. 1:47-118

Monteiro-Scanavacca, W. R. 1974. Vascularizacao do gineceu em Lecythidaceae. Bol. Univ. Sao Paulo, Bot. 2:53-69.

----------. 1975a. Vascularizacao e natureza de estruturas do androceu em Lecythidaceae. Bol. Univ. Sao Paulo, Bot. 3:61-74.

----------. 1975b. Estudo da Placentacao em Lecythidaceae. Bol. Univ. Sao Paulo, Bot. 3:75-86.

Mori, S. A. & D. Black. 1987. Stem and Leaf. In: S. A. Mori & Collaborators, The Lecythidaceae of a Lowland Neotropical Forest: La Fumee Mountain, French Guiana, pp.72-85. Mem. New York Bot. Gard. 44.

---------- & J. D. Boeke. 1987. Pollination. In: S. A. Mori & Collaborators, The Lecythidaceae of a Lowland Neotropical Forest: La Fumee Mountain, French Guiana, pp.136-155. Mem. New York Bot. Gard. 44.

---------- & Collaborators. 1987. The Lecythidaceae of a Lowland Neotropical Forest: La Fumee Mountain, French Guiana. Mem. New York Bot. Gard. 44.

----------, J. E. Orchard & G. T. Prance. 1980. Intrafloral pollen differentiation in the New World Lecythidaceae, subfamily Lecythidoideae. Science 209:400-403.

---------- & G. T. Prance. 1990. Lecythidaceae -- Part II. the Zygomorphic-flowered New World Genera (Couroupita, Corythophora, Bertholletia, Couratari, Eschweilera & Lecythis). Fl. Neotrop. Monogr. 21(II).

Muller, J. 1972. Pollen morphological evidence for subdivision and affinities of Lecythidaceae. Blumea 20:351-355.

---------. 1973. Pollen morphology of Barringtonia calyptrocalyx K. Sch. (Lecythidaceae). Grana Palynol. 13:29-44.

---------. 1979. Pollen. In: G. T. Prance & S. A. Mori, Lecythidaceae --Part I. The actinomorphic-flowered New World Lecythidaceae (Asteranthos, Gustavia, Grias, Allantoma, & Cariniana), pp.72-76. Fl. Neotrop. Monogr. 21.

Naumova, T. N. 1983. Ochnaceae. In: M. S. Yakovlev (ed.), Comparative Embryology of Flowering Plants. Vol. II, pp.78-82. Nauka, Leningrad.

Niedenzu, F. 1892. Lecythidaceae. In: Engler & Prantl, Nat. Pflanzenfam. 3(7):26-41.

Nikiticheva, Z. I. 1983. Styracaceae, Symplocaceae, Lissocarpaceae, Ebenaceae, Sapotaceae. In: M. S. Yakovlev (ed.), Comparative Embryology of Flowering Plants. Vol. II, pp.221-235. Nauka, Leningrad.

Palser, B. F. 1975. The bases of angiosperm phylogeny: Embryology. Ann. Missouri Bot. Gard. 62(3):621-646.

Payens, J. P. D. W. 1967. A monograph of the genus Barringtonia (Lecythidaceae). Blumea 15:157-263.

Perrier de la Bathie, H. 1950. Lecythidaceae. In: H. Humbert, Flore de Magagascar. Fam. 149.

Philipson, W. R. 1974. Ovular morphology and the major classification of the dicotyledon. J. Linn. Soc. Bot. 68:89-108.

----------. 1975. Evolutionary lines within the dicotyledons. New Zeal. J. Bot. 13:73-91.

----------. 1977. Ovular morphology and the classification of dicotyledons. Pl. Syst. Evol., Suppl. 1:123-140.

Pichon, M. 1945. Le genre Combretodendron et les Lecythidacees. Not. Syst. Paris 12:192-197.

Poiteau, M. A. 1825. Memoire sur les Lecythidees. Mem. Mus. Hist. Nat. 13:141-165.

Prakash, N. & Y. Y. Lau. 1976. Morphology of Ploiarium alternifolium and the taxonomic position of Ploiarium. Bot. notis. 129(3):279-285.

Prance, G. T. 1979. Asteranthos. In: G. T. Prance & S. A. Mori, Lecyhtidaceae -- Part I. The actinomorphic-flowered New World Lecythidaceae (Asteranthos, Gustavia, Grias, Allantoma, & Cariniana), pp.122-128. Fl. Neotrop. Monogr. 21.

---------- & S. A. Mori. 1979. Lecythidaceae -- Part I. The actinomorphic-flowered New World Lecythidaceae (Asteranthos, Gustavia, Grias, Allantoma, & Cariniana). Fl. Neotrop. Monogr. 21.

Puri, V. 1939. Studies in the order Parietales. II. A contribution to the morphology of Garcinia livingstonii T. Andero. Proc. Indian Acad. Sci., B, 9(2):74-86.

Radfford, A. E., W. C. Dickison, J. R. Massey & C. R. Bell. 1974. Vascular Plant Systematics. Harper & Row, Publishers, New York.

Rao, A. N. 1957. The embryology of Hypericum patulum and H. mysorence. Phytomorphology 7:36-45.

Raven, P. H. 1975. The bases of angiosperm phylogeny: Cytology. Ann. Missouri Bot. Gard. 62:724-784.

Sankara Rao, K. 1972. Studies in Myrsinaceae. I. A contribution to the embryology of Maesa dubia Wall. Proc. Indian Acad. Sci. B, 75(4):160-166.

Sarkar, A. K., N. Datta, R. Mallick & U. Chatterjee. 1976. Lecythidaceae: Planchonia vallida Blume. 649. In: A. Love (ed.), IOPB chromosome number reports LIV. Taxon 25:631-649.

----------, --------, ---------- & ----------. 1978a. Lecythidaceae: Careya arborea roxb. and Gustavia augusta L. 54. In: A. Love (ed.), IOPB chromosome number reports LIX. Taxon 27:53-61.

----------, -------- & U. Chatterjee. 1978b. Lecythidaceae: Chydenanthus excelsa (Blume) Miers. 520. In: A. Love (ed.), IOPB chromosome number reports LXII. Taxon 27:519-535.

----------, ---------, ---------- & D. Hazra. 1982. Myrtaceae: Barringtonia acutangula (L.) Gaertn., 578. In: A. Love (ed.), IOPB chromosome number reports LXXVI. Taxon 31:574-598.

Schnarf, K. 1931. Vergleichende Embryologie der Angiospermen. Berlin, 354pp.

Smith, B. B. 1975. A quantitative analysis of the megagametophyte of five species of Cornus L. Amer. J. Bot. 62:387-394.

Sokolovskaya, T. B. 1983. Bombacaceae. In: M.S. Yakovlev (ed.), Comparative Embryology of Flowering Plants, Vol. II, pp.256-259. Nauka, Leningrad.

Stebbins, G. L. 1974. Flowering Plants: Evolution Above the Species Level. Belknap Press of Harvard University, Cambridge.

Sternar, H. 1925. Embryologische Studien, 1. Zur Embryologie einiger Columniferen. 2. Die Embryologie der Amaryllidaceen. Diss. Uppsala, 197pp.

Subramanyam, K. 1962. Embryology in relation to systematic botany, with particular reference to the Crassulaceae. In: Plant Embryology. A Symposium, CSIR, pp.94-112, New Delhi.

---------- & L. L. Narayana. 1968. Floral anatomy and embryology of Primula floribunda Wall. Phytomorphology 18: 105-113.

Swamy, B. G. L. 1948. A contribution to the embryology of the Marcgraviaceae. Amer. J. Bot. 35:628-633.

Takhtajan, A. 1959. Die Evolution der Angiospermen. Transl. to German by W. Hoppner. Gustav Fischer Verlag. Jena.

----------. 1969. Flowering Plants, Origin and Dispersal. Edinburg. PP.224.

----------. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. 46:225-359.

----------. 1986. Floristic Regions of the World. Univ. California Press.

----------. 1987. Systema Magnoliophytorum. Nauka, Leningrad.

Thirumalachan, M. J. & B. A. Khan. 1941. Megesporangenesis and endosperm formation in Eriodendron anfractuosum. Proc. Indian Acad. Sci., B, 14:461-465.

Thompson, J. M. 1921. Studies in floral morphology II. The staminal zygomorphy of Couroupita guianensis Aubl.

Trans. Roy. Soc. Edinburgh 53:1-15.

----------. 1927. A study in advance gigantism. Publ. Hartley Bot. Lab. Liverpool 4:5-44.

Thorne, R. F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. Aliso 6:57-66.

----------. 1976. A phylogenetic classification of the Angiospermae. Evol. Biology 9:35-106.

----------. 1983. Proposed new realignments in the angiosperms. Nord. J. Bot. 3:85-117.

Tobe, H. 1989. The embryology of angiosperms: its broad application to the systematic and evolutionary study. Bot. Mag. Tokyo 102:131-147.

-------- & P. H. Raven. 1983. An embryological analysis of Myrtales: its definition and characteristics. Ann. Missouri Bot. Gard. 70:71-94.

Van Vliet, G. J. C. M. & P. Baas. 1984. Wood anatomy and classification of the Myrtales. Ann. Missouri Bot. Gard. 71:783-800.

Venkata Rao, C. 1949-1953a. Contributions to the embryology of Steculiaceae. I-IV. J. Indian Bot. Soc. 28:180-197, 1949. 29:163-176, 1950. 30:122-131, 1951. 31:251-260, 1953.

----------. 1953b. Floral anatomy and embryology of two species of Elaeocarpus. J. Indian Bot. Soc. 32:21-33.

----------. 1954a. Contribution to the embryology of Bombacaceae. Proc. Indian Acad. Sci., B, 39:51-75.

----------. 1954b. Embryological studies in Malvaceae. I. Development of gametophytes. Proc. Nat. Inst. Sci. Indian, B, 20:127-150.

Venkateswarlu, J. 1952a. Embryological studies in Lecythidaceae-I. J. Indian Bot. Soc. 32:103-116.

----------. 1952b. Reversed polarity of the embryo-sac of Napoleonaea imperialis Pal. B. Curr. Sci. 21:167.

Vijayaraghavan, M. R. & U. Dhar. 1976. Scytopetalum tieghemii--Embryologically unexplored taxon and affinities of the family Scytopetalaceae. Phytomorphology 26:16-22.

Whitmore, T. C. 1974. Abdulmajidia a new genus of Lecythidaceae from Malaysia. Kew Bull. 29:207-211.

Wood, C. E. J. & R. B. Channell. 1960. The genera of the Ebenales in the Southeastern United States. J. Arnold Arboretum 41:1-35.

Woodburn, W. L. 1911. Development of the embryo sac and endosperm in some seedless perimmons. Bull. Torrey Bot. Club 38:379-384.

Wu, H. K. 1960. Embryogenesis in the tea plant. Bot. Bull. Acad. Sin. Taipei, 1:165-168.

Yakovlev, M. S. (ed.). 1981-1987. Comparative Embryology of Flowering Plants. Vol. I, Winteraceae-Juglandaceae, 1981. Vol. II, Phytolaccaceae-Thymelaeaceae, 1983. Vol. III, Brunelliaceae-Tremandraceae, 1985. Vol. IV, Davidiaceae-Asteraceae, 1987. Nauka, Leningrad.

Yamazaki, T. 1970a. Embryological studies in Ebenales. (1). Styracaceae. J. Jap. Bot. 45:267-273.

Yamazaki, T. 1970b. Embryological studies in Ebenales. (2). Symplocaceae. J. Jap. Bot. 45:353-358.

----------. 1971. Embryological studies in Ebenales. (3). Sapotaceae. J. Jap. Bot. 46:161-166.

----------. 1972. Embryological studies in Ebenales. (4). Ebenaceae. J. Jap. Bot. 47:20-28.

Zeeuw, C. H. de. 1990. Chapter II. Secondary xylem of Neotropical Lecythidaceae. In: S. A. Mori & G. T. Prance, Lecythidaceae--Part II. The zygomorphic-flowered New World Genera (Couroupita, Corythophora, Bertholletia, Couratari, Eschweilera, & Lecythis), pp. 4-59. Fl. Neotrop. Monogr. 21(II).

---------- & S. A. Mori. 1987. Chapter IX. Wood anatomy. In: S. A. Mori & Collaborators, The Lecythidaceae of a lowland Neotropical forest: La Fumee Mountain. French Guiana. Mem. New York Bot. Gard. 44: 100-112.