POLLEN MORPHOLOGY AND RELATIONSHIPS OF THE FLACOURTIACEAE

Richard C. Keating

Abstract

Light microscopic studies of the pollen of 51 genera and 151 species of Flacourtiaceae were made from KOH-acetolyzed specimens. The pollen is always found as single grains and is usually triaperturate with compound apertures, isopolar, and psilate to reticulate. Within the triaperturate type, the pollen of the family ranges from unspecialized to moderately specialized. Differences in pollen morphology do not often serve to delineate the taxonomic tribes. The Berberidopsideae and Oncobaeae show a considerable range of size and sculpturing patterns. Scopelieae, Banareae, Homalieae, and Flacourtieae have pollen which can scarcely be distinguished. Pollen of Casearieae is similar to that of the preceding group of tribes but adds more specialized trends. Both Pangieae and Paropsieae are isolated in the family, and the Paropsieae should be assigned to the Passifloraceae. Comparisons with families of putatively related orders indicate that the relationships of the Flacourtiaceae based on pollen morphology accord well with Takhtajan's system.

By one recent estimate (Hutchinson, 1967), the Flacourtiaceae include about 90 genera and 1284 species. This large, tropical family has received little attention by taxonomists and morphologists in proportion to its size and evolutionary importance. Such neglect seems to be due to the complex taxonomic history of the family and its reputation as a taxon in which to place many genera of uncertain status (cf. Williams, 1965). As understood by Warburg (1893) and Gilg (1925) the family is quite heterogeneous and indeterminate. The concept of the family has been greatly improved by the generic treatment of Hutchinson (1967).

The Flacourtiaceae include some very primitive genera in the tribes Berberidopsideae and Oncobaeae (Hutchinson, 1967), and the family usually occupies a basal position in the Violales (Cronquist, 1968; Takhtajan, 1969), Cistales (Gundersen, 1950; Thorne, 1968) or Bixales (Hutchinson, 1959). In most of these schemes the Violales are considered close to the Theales, but their relationship to Ranalian lineage is still controversial (Takhtajan, 1969; Meeuse, 1970). A brief resumé of suggested affinities has been presented by Angely (1966). As many as nine orders have been suggested to be derived from flacourtiaceous stock (Takhtajan, 1969), and many of these suggestions will probably prove correct. However, in spite of the potential importance of microscopic characters in interpreting evolutionary trends, such observations are so scarce in many families as to make many statements of taxonomic affinity with Flacourtiaceae fall within the realm of speculation. Recognizing that pollen provides only one line of evidence in phylogenetic studies (Thorne, 1963), I have begun with a survey of the light microscopic features of the pollen in order to provide an

---

1I am grateful to the curators of the U. S. National Herbarium and of the Missouri Botanical Garden for permission to use the collections and for their assistance. The SEM photomicrographs (Figs. 171–172) were made possible through the courtesy of Walter H. Lewis, to whom thanks are extended.

2Department of Biological Sciences, Southern Illinois University, Edwardsville, Illinois 62025.

overview of the family. The value of this feature for comparative investigations has been attested to by many (cf. Canright, 1963). More intensive studies of the tribes will include studies of the wall morphology by scanning and transmission electron microscopy of which the present study will provide a basic reference. More detailed studies will definitely be needed to determine the trends of specialization of the wall structure and to better document relationships to other families.

Erdtman (1952, 1969) has called the Flacourtiaceae a eurypalynous family. When considered as understood by Hutchinson (1967) there is diverse pollen morphology, although several of the tribes show a monotonous uniformity. There is less diversity than in the more specialized families of the Malvales and Theales.

In his pollen study of the Alangiaeae, Reitsma (1970b) states that the work would not have been possible without reference to the recent monograph of the family. One of the formidable problems in my study was the need to sample herbarium specimens which were not well annotated. Large gaps in the monographic work on the family made the choice of specimens difficult. In order to prevent future confusion, vouchers from each specimen examined are listed by genus.

Previous treatments of flacourtiaceous pollen grains are not common. Erdtman’s (1952) study of 25 genera and 35 species included genera which are not presently assigned to the family. Spirlet (1965) and Presting (1965) treated the tribe Paropsieae which has been placed in either the Flacourtiaceae or the Passifloraceae. Rethoré (1963) described pollen of Tissonia, Sabourea, and Casearia of Madagascar. Van Campo et al. (1965) and Bronckers (1967) have described pollen of six genera of Flacourtiaceae in their series on African palynology.

**Materials and Methods**

In the present study, 51 genera and 151 species of flacourtiaceous pollen have been examined. Due to their rarity, the three genera included in the tribes Alzateae and Benhiciæae are not represented. A number of pollen slides of putatively related genera, especially of Passifloraceae and Tiliaceae, were also prepared or were available for comparison. It has been noted that although the whole ecological amplitude of collections is needed to give a complete picture of pollen morphology, a good picture of a family can also be gained by an extensive rather than an intensive view (Whitehead, 1963).

The material was prepared by KOH-acetolysis (Faegri & Iversen, 1964). This gave clean preparations, and no damage to the exines was observed when compared to acetolysis alone. Expansion is negligible after this treatment (Reitsma, 1969). Pollen was mounted in glycerine-jelly with or without saframin-O added. Several authors have commented on the efficacy of measurements made from treated grains (Dickson, 1967). However, there appears to be no reason why the size and shape of KOH-acetylated, glycerine-jelly mounted grains cannot be considered characters in their own right. These methods are widely enough used to preserve the comparative value of such measurements. Whitehead (1965) calculated the conversion factor for pollen mounted in glycerine jelly when compared to silicone oil mounts. Measurements from glycerine-jelly mounts should be divided by 1.06 when compared to silicone-oil preparations.

Measurements of polar (P) and equatorial (E) dimensions were made of at least 20 grains per specimen.

**Descriptions and Terminology**

Descriptive terminology, already overproduced, is further confused by the addition of terminology from electron microscopy. It is important to avoid
confusing appearance with structure. Since most of the recent progress in recognition of wall layers has originated with electron microscopy, one should not use EM inspired terms for optical microscope observations where the structures cannot be clearly seen.

The terminology used here is based on Faegri and Iversen (1964) with some modifications as suggested by Erdtman (1952), Reitsma (1970a), Van Campo (1958), and Wittman and Walker (1965).

Grains of Flacourtiaceae observed in this study were always single and never in tetrads or larger units. Grains are isopolar in almost all instances. In some cases, e.g. *Hecatostemon* (Figs. 171-172), sculpturing elements consistently on one side of the endoaperture produced anisopolar grains, but it was not possible to distinguish the proximal from the distal end.

Shape of the grains is prolate in most genera, but spheroidal grains are also found. Oblate grains are uncommon in the family.

Wall structure and sculpture pattern were occasionally difficult to determine. In optical cross section, most flacourtiaceous grains appeared to have an outer sculptured portion of the exine about equal in thickness to the non-sculptured exine. This observation is not further repeated and, in terms of phylogenetic studies, is not very meaningful. The thickness of the foot layer and other chemically defined layers are not visible with the light microscope. The terms ektexine and endexine are used when referring to wall layers, since they have been demonstrated to be preferable to other terms (Faegri & Iversen, 1966). Wall thickness usually varies little between the polar and equatorial regions. The total exine thickness in the equatorial region is given in the descriptions.

The patterns of sculpture occasionally caused problems of terminology. Sculpture has been described as “external geometrical features without reference to their internal construction” (Reitsma, 1970a: 46), but in the case of reticulate grains it is difficult to separate the two. Most flacourtiaceous grains have a perforated tectum or reticulate pattern in gradual transitions up to per-reticulate. The smallest muri and lumina are near the limits of resolution at 1000×. When these patterns were smaller than 1 μ, L-O patterns were often helpful in determining the structure. The terms simpli- or duplibaculate are used to describe muri supported by single or double rows of baculae (Columellae), when either condition is visible.

Apertures in the Flacourtiaceae are always meridionally and zonally arranged, the edges being more or less level with the exine. The apertures are almost always compound, consisting of a wide or narrow colpus (ectoaperture) which is lens shaped with pointed ends converging on the polar areas. A distinct aperture-free polar area is always present at both ends. Edges of the colpus are distinct and straight unless noted as being ragged or obscure. An inner aperture (endoaperture, Van Campo, 1958) is usually present and found in the endexine (Figs. 171-172). The equatorially placed endoaperture is usually equatorially elongate beyond the edges of the colpus, often with truncate or indeterminate ends. Distinctness of these apertures is noted in the descriptions and is highly variable. This kind of aperture has been called a “colpus transversales” (Faegri & Iversen, 1964), if it has a length-breadth ratio of greater than 2 (Reitsma, 1970b). Endo-
apertures with less than this ratio have been called porae or ora. It has been stated that "a porus is supposed to be nothing more than a short colpus" (Reitsma, 1970b: 284), but it has not been demonstrated that the elongate endoaperture described here is homologous with all other types of pores occupying the centers of colpi. Therefore, I will retain the more purely descriptive term "endoaperture" which at least accurately reflects placement in the endexine layer.

Thickenings in the endexine layer bordering the apertures, the costae, occur in most species observed. Costae may outline only the ectoaperture, the endoaperture, both, or may be restricted to the four corners of the intersection of the two apertures. The colpi "membranes" are usually free of sculpturing elements.

A number of genera have colpi with endoapertures being either obscure or absent. Grains are called colporoidate, if the equatorial area of the colpus has lighter optical density or shows a constriction.

The distribution of grain sizes is mostly limited to Erdtman's (1952) categories of small (10-25 μ) and medium-sized (25-50 μ).

**Observations**

**Berberidopsideae**


Pollen grains spheroidal to prolate spheroidal. Structure obscure but probably tectate, no baculae seen. Psilate. Exine thickness 1.5 μ. Tricolpate, colpi delimitation distinct, not costate. Average size: P = 25-30 μ; E = 30-33 μ.

Specimen examined: *B. corallina* J. D. Hook.—Chile, *Philippi s. n.* (US).

*Erythrospermum* Lam. Figs. 3-4.

Pollen grains prolate-spheroidal. Structure obscure but probably tectate. Finely verrucate. Exine thickness 1.5 μ. Tricolpate-tricolporoidate. Colpi may be constricted at equator. Faintly costate. Average size: P = 19 μ; E = 18 μ.

Specimen examined: *E. acuminatissimum* (A. Gray) A. C. Sm.—Fiji, *Smith 1254* (US).

*Ahernia* Merrill Figs. 5-6.

Pollen grains spheroidal to prolate-spheroidal, semitectate, reticulate, lumen less than 1 μ. Exine thickness 1.5 μ. Tricolporoidate. Colpi constricted at the equator. Faintly costate. Average size: P = 18-20 μ; E = 18 μ.


---

Dasylepis Oliv. Figs. 7-8.

Pollen grains spheroidal, semitectate, reticulate to verrucate, lumen 0.3-0.5μ. Exine thickness 1.5–2μ. Tricolporate, endoapertures rectangular, equatorially elongate. Colpi costate. Average size: \( P = 25\mu; \ E = 23-25\mu. \)

Specimens examined: \( D. \ lereti \) DeWild.—West Africa, \( De \) Giorgi 1738 (US). \( D. \) integra Warb.—West Africa, \( Holst \) 1220 (US).

Scottellia Oliv. Figs. 9-12.

Pollen grains spheroidal, semitectate, reticulate. Baculae not visible, lumen less than 1μ. Exine thickness 1.5μ. Tricolporate, endoapertures rectangular, costate, equatorially elongate. Average size: \( P = 18-20\mu; \ E = 18-20\mu. \)

Specimens examined: \( S. \) coriacea A. Chev.—Nigeria, \( Kennedy \) 1674 (US). \( S. \) klaineana Poire—Gabon, Klaine 3438 (US).

ONCOBEAE


Pollen grains spheroidal, semitectate, finely reticulate to duplibaculate and per-reticulate, lumen 0.1–4μ. Exine thickness 1.5–4μ. Tricolpor(-oid-)ate, endoapertures may be costate but faintly delimited. Average size: \( P = 37-40\mu; \ E = 37-40\mu. \)

Specimens examined: \( C. \) platyptera Pittier—Honduras, Kuylen 69x (US). \( C. \) sp.—Brazil, Fröes 21101 (US).

Mayna Aubl. Figs. 16-19.

Pollen grains spheroidal, semitectate, reticulate or per-reticulate, simpli- or duplibaculate. Lumen 1–4.5μ. Exine thickness 1.5–2.5μ. Tricolpor(-oid-)ate. Colpi costate near endoapertures, delimitation of endoapertures diffuse. Average size: \( P = 33–50\mu; \ E = 33–46\mu. \)

Specimens examined: \( M. \) echinata Spruce—Peru, Klug 3808 (US). \( M. \) longifolia P. & E. var heliocarpa R. E. Schult.—Brazil, Schultes 6593 (US). \( M. \) odorata Aubl.—Brazil, Ducke 15136 (US).

Oncoba Forsk. Figs. 20-21.

Pollen grains prolate-spheroidal, semitectate, reticulate to per-recticulate, simpibaculate. Lumen 0.5–1.5μ. Exine thickness 1–2μ. Tricolporoidate, costate, endoaperture delimitation diffuse. Average size: \( P = 20–30\mu; \ E = 20–30\mu. \)

**Caloncoba** Gilg Figs. 22–23.

Pollen grains prolate-spheroidal, tectate, reticulate to finely reticulate, simplibaculate, lumen 0.1–0.5 μ. Exine thickness 1–2 μ. Tricolporate, colpi divided transversely by a bridge in the exine. Average size: P = 20–38 μ; E = 23–35 μ.


**Lindackeria** Presl Figs. 24–25.

Pollen grains prolate-spheroidal to prolate, semitectate or tectate, reticulate to finely reticulate, lumen 0.2–1 μ. Exine thickness 1.5–2 μ. Tricolporate, costate in some specimens, delimitation of endoapertures may be diffuse. Average size: P = 18–30 μ; E = 18–30 μ.


**Poggea** Gürke Figs. 26–27.


Specimen examined: P. kameronumensis Gilg—Cameroons, Zenker 239 (US).

**Buchnerodendron** Gürke Figs. 28–29.

Pollen grains spheroidal, tectate, finely reticulate, lumen 0.2–0.5 μ. Exine thickness 1 μ. Tricolpate, tricolporate. Apertures diffuse and difficult to orient. Average size: P = 18–20 μ; E = 18–20 μ.

Specimen examined: B. speciosum Gürke—Congo, Robyns 1336 (US).

**SCOLOPIACEAE**

**Scolopia** Schreb. Figs. 30–34.

Pollen grains prolate-spheroidal to prolate, tectate, reticulate, lumen 0.3–1 μ. Exine thickness 1–2 μ. Tricolporate, colpi costate, endoapertures diffuse at edges. Average size: P = 23–25 μ; E = 18–23 μ.


**BANAREAE**

**Banara** Aubl. Figs. 35–37.

Pollen grains prolate-spheroidal, tectate, reticulate. Lumen 0.5–1 μ. Exine thickness 1 μ. tricolpor-(oid)-ate, costate, endoapertures diffuse, equatorially
elongate. Average size: \( P = 15-28 \mu; \ E = 13-23 \mu \).—This description does not apply to \( B. \) costaricensis Figs. 44-45.

Specimens examined: \( B. \) guinensis Aubl.—Venezuela, Pittier 11606 (US). \( B. \) mollis Tul.—Peru, Klug 3301 (US). \( B. \) costaricensis (Standl.) Sleumer.—Costa Rica, Holm & Hillis 787 (US).

**Pineda Ruiz & Pav. Figs. 40-41.**

Pollen grains prolate-spheroidal, tectate, simplibaculate, reticulate; lumen 0.5 \( \mu \). Exine thickness 2 \( \mu \). Tricolporoidate, colpi costate; equatorial bridge in the ektexine may replace diffuse endoaperture. Average size: \( P = 23-25 \mu; \ E = 18-20 \mu \).

Specimen examined: \( P. \) incana R. & P.—Peru, Vargas 7596 (US).

**Trimeria Harv. Figs. 42-43.**

Pollen grains prolate, tectate, reticulate. Lumen 1–1.5 \( \mu \). Exine thickness 1.3–2 \( \mu \). Tricolporate to tricolporoidate, costate, endoapertures equatorially elongate or replaced by an equatorial bridge in the ektexine. Average size: \( P = 18-20 \mu; \ E = 13-15 \mu \).

Specimen examined: \( T. \) abnifolia Planch.—Praetoria, Ratray 313 (US).

**Pleuranthodendron L. O. Wms. Figs. 38-39.**

Pollen grains prolate-spheroidal, tectate, reticulate, lumen 0.5–1 \( \mu \). Exine thickness 1 \( \mu \). Tricolpor(-oid-)ate, costate, endoapertures diffuse. Average size: \( P = 15-18 \mu; \ E = 13-15 \mu \).

Specimen examined: \( P. \) mexicana (A. Gray) L. O. Wms.—Mexico, Mexia 9284 (US).

**HOMALIEAE**

**Dissomeria Benth. Figs. 46-47.**

Pollen grains prolate, tectate, reticulate, lumen 0.3 \( \mu \). Exine thickness 2 \( \mu \). Apertures tricolporate, costate, endoapertures equatorially elongate. Average size: \( P = 25-30 \mu; \ E = 20-25 \mu \).

Specimen examined: \( D. \) crenata Benth.—Ghana, Vigue 1550 (US).

**Calantica Jaub. ex. Tul. Figs. 48-49.**

Pollen grains prolate, tectate, finely reticulate, lumen 0.7–1 \( \mu \). Exine thickness 2 \( \mu \). Tricolporate, costate, endoapertures equatorially elongate, edges diffuse. Average size: \( P = 28-30 \mu; \ E = 20-23 \mu \).

Specimen examined: \( C. \) ceratifolia Endl.—Madagascar, Hildebrandt 3817 (US).

**Homalium Jacq. Figs. 52-59.**

Pollen grains prolate, tectate, finely reticulate to obscure, lumen 0.3–1 \( \mu \). Exine thickness 1.5–2 \( \mu \). Tricolporate, costate, endoapertures equatorially elongate with constricted, or branched, indeterminate ends. Occasional ektexine elements on the colpi membrane above or below endoapertures. Average size: \( P = 15-35 \mu; \ E = 13-25 \mu \).

**Gerrardina** Oliv. Figs. 50–51.

Pollen grains spheroidal, subangulaperturate, tectate, finely reticulate, lumen 0.5–1.2 μ. Exine thickness 1 μ. Tricolpor- (oid-) ate, costate, endoapertures diffuse, equatorially elongate. Average size: P = 13–15 μ; E = 13–15 μ.


**PANGIEAE**

**Hydnocarpus** Gaertn. Figs. 62–63.

Pollen grains spheroidal, semitectate, per-reticulate, simplibaculate, lumen 2–6 μ. Exine thickness 4.5 μ. Tricolporate, costae not visible, endoapertures probably equatorially elongate but obscured by heavy reticulum. Average size: P = 33–43 μ; E = 33–35 μ.


**Pangium** Reinw. Figs. 67–68.


Trichadenia Thw. Figs. 60-61.

Pollen oblate-spheroidal, intectate, baculate and verrucate in a mixed, random pattern. Bacules to 3μ high, verrucate to 4μ wide and high. Exine thickness 5-6μ. Tricolporate, costate, endoapertures distinct and variable. Colpi diffuse. Average size: P = 33-38μ; E = 40-45μ.

Specimen examined: T. philippensis Merr.—Philippines, Ahern 2982 (US).

Ryparosa Bl. Figs. 64-66.

Pollen grains prolate-spheroidal, tectate, finely reticulate, lumen 0.2-0.5μ. Exine thickness 1.5-2μ. Tri (bi-)colpate or tricolporate, endoapertures distinct, the margins with small processes extending over the opening. Colpi diffuse. Average size: P = 20-27μ; E = 18-23μ.


Kiggelaria L. Figs. 69-71.

Pollen grains prolate to prolate-spheroidal, tectate with a finely granular pattern. Exine thickness 2-2.5μ. Tricolpor(-oid-)ate, endoapertures constricted or equatorially elongate. Costae prominent. Average size: P = 30-45μ; E = 33 = 45μ.


FLACOURTIEAE

Bennettiodendron Merrill Figs. 72-73.

Pollen grains subprolate, semitectate, reticulate, lumen 0.5-1.5μ. Exine thickness 1.5μ. Tricolpor(-oid-)ate, costate, endoapertures equatorially elongate with diffuse ends. Ends of colpi occasionally connect over poles. Average size: P = 18-20μ; E = 18-20μ.

Specimen examined: B. leprosipes (Clos) Merr.—Sumatra, Toroos 3329 (US).

Flacourtia L’Herit. Figs. 74-76.

Pollen grains prolate-spheroidal, tectate, reticulate, lumen 0.8-1.5μ. Exine thickness 1-1.5μ. Tricolpor(-oid-)ate, costate, endoapertures equatorially elongate with diffuse ends. Average size: P = 15-25μ; E = 13-20μ.


←

Dovegali E. Mey. ex Arn. Figs. 77-78.

Pollen grains spheroidal, tectate, reticulate, lumen 0.8-2.0μ. Exine thickness 1.2μ. Tricolporate, weakly costate, endoapertures equatorially elongate. Average size: P = 25-28μ; E = 23-25μ.


Aphloia Benn. Figs. 79-80.

Pollen grains spheroidal, interhexagonal to spherical in polar view, intetcate, striate, lumen 0.8μ. Exine thickness 1.5-2μ. Tricolporate(-oid-)ate, costate, endoapertures equatorially elongate with diffuse ends. Scattered costal thickenings in the vicinity of the endoapertures in some specimens. Average size: P = 18-25μ; E = 15-20μ.

Specimens examined: A. theaformis subsp. madagascariensis var. minima (Bak.) H. Perr.—Madagascar, Humbert 6175 (US).

Azara Ruiz & Pav. Figs. 81-82.

Pollen grains prolate, tectate, reticulate, lumen 0.8-1.5μ. Exine thickness 1.5-2μ. Tricolpor(-oid-)ate, costate, endoapertures equatorially elongate with diffuse ends. Scattered costal thickenings in the vicinity of the endoapertures in some specimens. Average size: P = 25-28μ; E = 23-25μ.


Pollen grains prolate to prolate-spheroidal, tectate, reticulate, lumen 0.5-1.5μ. Exine thickness 1-2μ. Tricolpor(-oid-)ate, costate, endoapertures equatorially elongate with diffuse ends. Scattered costal thickenings in the vicinity of the endoapertures in some specimens. Average size: P = 25-28μ; E = 23-25μ.


elongate, distinct, with diffuse ends. Colpi and endoapertures may be constricted. Sculpturing elements occasionally found on colpi membranes when endoapertures absent. Average size: \( P = 18-25\mu; E = 15-25\mu \).


**Poliothrys** Oliv. Figs 89-90.

Pollen grains prolate, tectate, reticulate, lumen 0.5-1.0. Exine thickness 2.5\( \mu \). Tricolporate, costate, endoapertures equatorially elongate. Average size: \( P = 18-20\mu; E = 15-18\mu \).

Specimen examined: \( P. \) sinensis Oliv.—China, Wilson 500 (US).

**Carrierea** Franch. Figs. 91-92.

Pollen grains prolate, tectate, finely reticulate, lumen 0.5\( \mu \). Exine thickness 1.3\( \mu \). Tricolpor(-oid-)ate, costate, endoapertures equatorially elongate, irregular. Average size: \( P = 23-25\mu; E = 18-20\mu \).

Specimen examined: \( C. \) calycina Franch.—China, Wilson 1104 (US).

**Itoa** Hemsl. Figs. 93-95.

Pollen grains prolate-spheroidal, tectate, reticulate, lumen 0.5-1.0. Exine thickness 1-1.5\( \mu \). Tricolporate, costate, endoapertures equatorially elongate with diffuse ends. Average size: \( P = 18-43\mu; E = 15-30\mu \).

Specimens examined: \( I. \) orientalis Hemsl.—China, Henry 10703 (US). \( I. \) stapfii (Koord.) Sleum.—New Guinea, Hoogland 5079 (US).

---

Figures 116–130. Pollen of Flacourtiaceae, tribe Casearieae, × 1000.—116–118. Gossypiospermum eriophorum (Jack 4970).—116. Equatorial view with indeterminate colpus.—117. Equatorial view showing grain with verrucate-rugulate surface.—118. Polar view, optical cross section and polar surface of pentaperturate grain.—119. Lactia procera (Ekman 12380), polar view, optical cross section and reticulate polar surface.—120–121. L. apetala (Hassler 7515).—120. Equatorial view with colpus and pore.—121. Polar view, optical cross section
**Idesia Maxim.** Figs. 96-97.

Pollen grains prolate-spheroidal, semitectate, reticulate, lumen 1-2μ. Exine thickness 1.5μ. Tricolporidate, costate, endoapertures often absent due to constrained colpi at equator. Average size: P = 23-28μ; E = 20-25μ.

Specimen examined: *I. polycarpa* Maxim.—China, Forrest 17558 (US).

**CASEARIEAE**

**Casearia Jacq.** Figs. 98-115.

Pollen grains spheroidal to prolate, polar view circular to semiarithmetic, semitectate to tectate, psilate to mostly reticulate or per-reticulate, lumen 0.3-4μ. Exine thickness 1-3μ. Tri(-4-)colporate, endoapertures equatorially elongate with pointed ends, costate. Average size: P = 18-58μ; E = 18-45μ.


**Gossypiospermum Urb.** Figs. 116-118.

Pollen grains prolate to prolate-spheroidal, semitectate, rugulate-reticulate, lumen 0.3μ. Exine thickness 1.3μ. Apertures 3, 4, 5-colporate in equal quantities, costate, colpi may be branched often with ragged edges and indeterminate ends; often very diffuse. Average size: P = 28-33μ; E = 23-28μ.

Specimen examined: *G. criophorum* (C. Wr.) Urb.—Cuba, Jack 4970 (US).

**Laetia Loefl. ex L.** Figs. 119-123.

1-4\(\mu\). Exine thickness 1.3–2.3\(\mu\). Apertures 3, 4-colporate, costate, ends of colpi often indeterminate, ends diffuse. Average size: \(P = 25–40\mu\); \(E = 25–35\mu\).


**Hecatostemon** Blake Figs. 124–125, 171–172.

Pollen grains prolate-spheroidal, semitectate, reticulate, duplibaculate, lumen 1–3\(\mu\). Exine thickness 2\(\mu\). Tricolporate, costate, endoapertures equatorially elongate, ends diffuse. Grains often appearing anisopolar due to proliferations of ektexine over colpi membranes on one side of ora. Average size: \(P = 35–42\mu\); \(E = 30–38\mu\).


**Ryania** Vahl Figs. 126–128.

Pollen grains prolate, tectate, reticulate, simplicibaculate, lumen 0.3–1\(\mu\). Exine thickness 2\(\mu\). Tricolporate, costate, endoapertures equatorially elongate. Average size: \(P = 35–48\mu\); \(E = 23–33\mu\).


Pollen grains prolate, tectate, finely reticulate or psilate, lumen 0.3\(\mu\) or absent. Exine thickness 1.5–2\(\mu\). Apertures 3, 4-colporate, costate, endoapertures equatorially elongate. Average size: \(P = 28–38\mu\); \(E = 28–35\mu\).

Specimens examined: *Z. guidonia* (Sw.) Britton & Millsp.—Mexico, Purpus 10703 (US), Enriquez 567 (US).

**Osmelia** Thwaites Figs. 133–134.

Pollen grains prolate, tectate, finely reticulate, lumen 0.5\(\mu\). Exine thickness 1–1.5\(\mu\). Tricolporate, costate, endoapertures equatorially elongate with pointed ends. Average size: \(P = 20–33\mu\); \(E = 13–23\mu\).
Ophiobothrys Gilg. Figs. 135–136.

Pollen grains prolate, tectate, finely reticulate, lumen 0.5μ. Exine thickness 1.5–2μ. Tricolporate, costate, endoapertures equatorially elongate, often with pointed ends. Occasional ekteixine elements above endoapertures on colpi membranes. Average size: P = 28–30μ; E = 18–20μ.

Specimen examined: O. zenkeri Gilg.—Ghana, Vique 1753 (US).


Pollen grains prolate, tectate, reticulate, lumen 1–3μ. Exine thickness 1.5μ. Tricolporate, costate, endoapertures equatorially elongate with blunt or usually pointed ends. Average size: P = 18–25μ; E = 13–18μ.


Euceraea Mart. Figs. 139–140.

Pollen grains are prolate, tectate, reticulate, simplibaculate, lumen 1μ. Exine thickness 1μ. Tricolporate, costate, endoapertures equatorially elongate, oval. Average size: P = 30–33μ; E = 23–25μ.

Specimen examined: E. nitida Mart.—Colombia, Fernandez s. n. (US).

Tetrathyllum Poepp & Endl. Figs. 141–142.

Pollen grains spheroidal, semitectate, reticulate to verrucate, lumen 0.5μ. Exine thickness 1–2.5μ. Tricolporate, costate, colpi short, narrow, endoapertures equatorially elongate with blunt, indeterminate ends. Average size: P = 20–28μ; E = 20–25μ.


Samyda Jacq. Figs. 143–145, 149–150.

Pollen grains prolate-spheroidal, tectate, reticulate to rugulate, lumen 0.3–0.7μ. Exine thickness 1.5–2μ. Apertures 4, 5-colporate, costate, placement of apertures often irregular, off the equator and diagonal to the meridian. Colpi often reduced or fragmented. Endoapertures elliptical meridionally with constricted pointed ends, equatorially elongate extensions give a cross shape to the endoaperture. Some ekteixine elements on colpi membranes. Average size: P = 30–40μ; E = 30–40μ.


Neoptychocarpus Buchheim Figs. 146–148.

Pollen grains spheroidal or prolate spheroidal, semianthopaperturate in polar view, semitectate, per-reticulate, simplibaculate, lumen 4–5μ. Exine thickness 2.5μ. Tricolporate, costate, endoapertures equatorially elongate and elliptical. Average size: P = 28–30μ; E = 28–30μ.
Specimen examined: *N. apodanthus* (Kuhl.) Buchheim—Brazil, *Ducke 1633* (US).

_Abatia_ Ruiz & Pavon Figs. 151–156.

Pollen grains prolate to prolate-spheroidal, tectate, finely reticulate, lumen 0.5μ. Exine thickness 1.5–2μ. Tricolporate, endoapertures equatorially elongate, costate, ekctexine elements occasionally on the colpi membranes above and below endoapertures. Average size: P = 18–30μ; E = 15–30μ.


_Aphaerema_ Miers Figs. 157–158.

Pollen grains prolate, tectate, finely reticulate, lumen 0.3μ. Exine thickness 1.5μ. Tricolporate, costate, endoapertures equatorially elongate with pointed ends. Average size: P = 18–20μ; E = 15–18μ.


**LEVEL OF ADVANCEMENT**

Traditionally, comparative morphologists state that the only trend of specialization anchored in the fossil record is that of tracheary tissue. Recent pollen analysis from carefully dated Mesozoic and Cenozoic strata, however, have added another order of precision to our knowledge of evolutionary specialization of the angiosperms (Brenner, 1967; Doyle, 1969; Muller, 1970).

In schemes depicting the earliest evolution of dicotyledonous pollen, trizoniaperturate pollen is considered relatively specialized (Muller, 1970; Kuprianova, 1967, 1969; Nair, 1965). However, in surveys of the complete range of modern dicotyledonous pollen types, the small, reticulate, tricolpate and tricolporate types form the basis for considerable further specialization and elaboration. This kind of pollen is represented in Cenomanian strata (Brenner, 1967).

In his study of the Cretaceous pollen record of the Atlantic coast, Doyle (1969) found a statistical trend in the triaperturate type which included tricolpate, tricolporoidate, tricolporate and triporate pollen in successively higher levels. The earliest grains were prolate or subspheroidal, retipilate or reticulate, occurred as single grains, and were small in size. In the evolution of the triaperturate type, many genera of Flacourtiaceae are primitive in all criteria.

While the affinities of these early pollen types are uncertain, it has been suggested that grains of Polycarpaceae, Amentiferae and Cistiflorae are represented (Muller, 1970). Specialized trends as found in the Theales make the identification of those pollen types from early strata less tentative. Many early Cretaceous pollen grains have been assigned to Dilleniaceae, Ochnaceae, Salicaceae, and Columniferae. Despite the fact that pollen of many extant genera of Flacourtiaceae are indistinguishable from pollen occurring in the above mentioned families, the earliest pollen assigned to the Flacourtiaceae is from the upper Miocene (Muller, 1970). It seems probable that earlier pollen of Flacourtiaceae has been misidentified due to lack of knowledge of the family. Previous statistical correlations between vegetative and floral features have placed the Flacourtiaceae among the most primitive of angiosperm families (Sporne, 1954).
Many genera of Flacourtiaceae have pollen that conform to the criteria of wind pollination as defined by Whitehead (1969). These include production and release of numerous grains, exposed anthers and stigmas, grain diameter 20–40μ, thin exines and a smooth surface. Considerably more observations are needed in this family before the relation between pollen morphology and mechanisms of pollination can be adequately discussed. Detailed studies of the records of several families indicate that pollen evolution is concurrent with taxonomic diversification (Muller, 1970). This should prove to be the case in the Flacourtiaceae.

**SUMMARY OF INTRAFAMILIAL RELATIONSHIPS**

The tribes Berberidopsideae and Oncobeae do not appear sharply defined from each other. While the grains of the Berberidopsideae are small to medium-sized, some of the largest grains in the family are found in *Mayna* and *Carpetroche* of the Oncobeae. Both tribes have a tendency toward high, equatorially elongate, rectangular endoapertures. The tricolpate pollen of *Berberidopsis* is the most primitive of the family.

Sculpturing varies in these tribes from psilate to coarsely reticulate. Some treatments of the family (Bamps, 1968; Gilg, 1925) do not separate the two tribes, leaving all genera in the Oncobeae. The limited pollen sample of this study, while diverse, does not clearly show a separation along tribal lines as suggested by Hutchinson (1967).

The tribes Scolopieae, Banareae, Homalieae, and Flacourtieae have pollen which can scarcely be distinguished. The tribe Prockieae, assigned by Hutchinson to the Tiliaceae, could easily be added to this group. All have costate colpi, a wide or narrow endoaperture, and a reticulate or finely reticulate exine. Costae in the Homalieae tend to be abbreviated. In *Homalium* and *Dissomera*, the costae are concentrated at the four corners of the intersection formed by the endo- and ecto-apertures. In some *Homalium* specimens, the costae only define the margins of the endoapertures. It is doubtful if keys to the pollen of most of these genera could be made without electron microscope preparations of the wall. One specimen labelled *Banara costaricensis* (Standl.) Sleumer (Figs. 44–45) is about twice as large as any other known *Banara* specimen. In aperture morphology and sculpturing, it most closely resembles pollen of the genus *Casearia*.
Some of the genera of Casearieae resemble the previous group of four tribes but add more specialized trends. These include greater size, more frequent 4–5 aperturate grains, and wide elongate endoapertures with pointed ends (Casearia). Some per-reticulate grains (Neoptychocarpus) and breviaperturate grains (Samyda) are also found. Thicker, unsculptured and unstructured exines are found in Casearia.

The Pangieae are isolated and have a number of different specialized features in different genera. Among these are brevicolpate to porate apertures (Pangium, Ryparosa), large grains with per-reticulate sculpturing (Hydnocarpus), rugulate sculpturing (Trichadenia), thick, conspicuously costate exines (Kiggelaria), and medium to large size in all specimens examined.

The Paropsieae are as isolated from the other tribes in their pollen morphology as are the Pangieae. Their sculpturing pattern is per-reticulate of the simplibaculate type and is separable from the other tribes on this appearance. This sculpturing pattern most closely resembles the per-reticulate type of the Passifloraceae rather than the perforated tectum, duplibaculate type found in the Oncobeae (Mayna). The hexacolporate, paired apertures especially separate this tribe from other Flacourtiaceae.

**Interfamilial Relationships**

Although pollen provides but one set of characters which must be correlated with observations on other structures before intrageneric and familial relationships will be resolved, it remains useful to comment on the degree of resemblance of pollen of various families to that of the Flacourtiaceae. Families from eleven orders are thought to be related to a flacourtiaceous stock (Takhtajan, 1969). In the following comparison, Takhtajan’s (1969) organization will be followed. Unless otherwise acknowledged, comparative pollen data is from Erdtman (1952).

**Violales.**—The Lacistemaceae and Stachyuraceae have been considered quite close to the Flacourtiaceae. The pollen morphology is quite supportive of this arrangement, the grains being small to medium-sized, finely reticulate, tricolporate and with equatorially elongate endoapertures.

The Violaceae are considered by Takhtajan (1969) to be linked to the Flacourtiaceae through the primitive tribe Rinoreae. Some pollen of this family is well within the range of the Flacourtiaceae, but other tribes show increased specialization. This includes large size, up to five apertures, and protruding aperture margins.

The Bixaceae and Cochlospermaceae, considered related in most schemes, have pollen which allows separation of the two families and separation from the Flacourtiaceae (Keating, 1972; Nair, 1962a). Their pollen fits the range of the Flacourtiaceae, especially resembling the tribe Oncobeae. However, cochlolspermaceous and bixaceous pollen is distinct enough to make any tribal alliance uncertain. The Cistaceae have pollen quite similar to that of the Flacourtiaceae. The endoapertures are oval or circular. More specialized tendencies include larger size, striate grains, and a more complex reticulum (Heydacker, 1963; Jean & Pons, 1963).
On the basis of pollen the Violales seem to be a related group of families with the Flacourtiaceae as basic for this assemblage.

Passiflorales.—The Passifloraceae have long been considered closely allied to the Flacourtiaceae through the tribe Paropsiaceae (see review by DeWilde, 1971). Gilg (1925) considered the Paropsiaceae to be Tribe III of the Flacourtiaceae, but on the basis of pollen it forms an isolated group in the family. Pollen morphology of the tribe has been described by Spirlet (1965) and Presting (1965) with the finding that the genera agree quite closely with other Passifloraceae. Pollen of the Passifloraceae can be tricolporate, but many genera are distinctly six and twelve zonicolporate. Paropsiopsis (Figs. 167–168) and Sneathmannia (Figs. 165–166) illustrate another characteristic feature of some Passifloraceae, especially of Passiflora, the tendency for multiple apertures to be grouped in pairs. This highly distinctive pattern seems unquestionably to belong in the Passifloraceae. Pollen of the genera Ancistrothyrsis (Figs. 169–170) and Soyauxia (Figs. 163–164) are only tricolporate and closer to the Flacourtiaceae.

When included in the Flacourtiaceae, the tribe is distinguished by the presence of a corona; in the Passifloraceae, the tribe is distinguished by its arboreous habit (DeWilde, 1971). The evidence from pollen supports the consensus of intermediacy of the tribe, but its best placement seems to be with the Passifloraceae (Sleumer, 1970; DeWilde, 1971).

The remaining families of the Passiflorales (Turneraceae, Malesherbiaceae, Achariaceae, and Caricaceae) seem derived from the Passifloraceae on the basis of pollen and more distantly related to the Flacourtiaceae. Their pollen grains are tricolporate, tend to be of large size, and often have more complex sculpturing patterns.

Cucurbitales.—The Cucurbitaceae, considered derived from the Passifloraceae (Takhtajan, 1969), show more highly evolved pollen than the Passifloraceae (Jeffrey, 1964; Awasthi, 1962a, b; Saad, 1964; Marticorena, 1963). Pollen of several tribes in the subfamily Cucurbitoideae (Jeffrey, 1964) are similar to flacourtiaceous pollen. Pollen of the tribes Joliffieae, Melothrieae, Schizopheneae and of the subfamily Zanonioideae are tricolporate, small, prolate, and finely reticulate. An equatorially elongate endoaperture is often present. More highly evolved types are found in the remaining tribes which include 4–10 apertures, pantoporate, and spinose grains. Clearly, pollen provides data compatible with the systematic position of the family.

Salicales.—Persistant suggestions have related the Salicaceae to the Flacourtiaceae, especially to Flacourtiaceae (Hutchinson, 1967) or Idesiinae (Gilg, 1925). Pollen of Salix is tricolporoidate or tricolporate with a reticulate sculpture and size (Risch, 1960) that is quite similar to that found in Idesia or Itoa. Pollen of Populus is inaperturate and derived. The data of Nair (1967) on pollen of Monochlamydeae, while not explicit on this relationship, is compatible with this scheme. Rowley and Erdtmann (1967) have provided structural data by electron microscopy which will be of value for comparisons of similar studies of Idesiineae.

Begoniaceae.—The Begoniaceae and Datiscaceae produce pollen grains with some features similar to pollen of Flacourtiaceae. They are small, spheroidal to
perprolate and have an obscure sculpture. They differ in the presence of a striate pattern, having endoapertures with granulate membranes and occasionally being shed as tetrads. This group may be derived from Violales but is more distantly related.

**Capparales.**—Pollen of Capparaceae, while similar in some ways to the Flacourtiaceae, has evolved a thicker and more complicated reticulate exine with small spines.

**Tamaricales.**—The Tamaricaeae and Frankeniacaeae have pollen which does not resemble that of the Flacourtiaceae. The grains are 2, 3, 4-colpate and may have granulate colpi membranes.

**Malvales.**—The Elaeocarpaeae have small, tricolporoid, prolate pollen quite similar to the Homalieae type within the Flacourtiaceae. With their finely reticulate pattern, these grains would not be readily distinguishable.

While pollen of the Tiliaceae is quite variable, that of the *Grewia* type is quite similar to flacourtiaceous pollen. It is not very different from the genus *Kiggelaria* (Chaudhuri & Mallik, 1965; Erdtman, 1952). Pollen of *Heritiera* is also quite similar to the Flacourtiaceae. The morphology of the compound apertures and of the exine is similar to that found in the Flacourtiaceae (Tarnavski & Ţerbănescu-Jitariu, 1968).

Pollen of the Sterculiaeae even more closely resembles that of the Flacourtiaceae. The tribe Sterculieae shows the closest pattern, especially the equatorially elongate endoapertures and the finely reticulate exine (Litchfield, 1966; Rao, 1950; Erdtman, 1964). (E.g. *Brachychiton* and *Argyrodendron* would fit easily among flacourtiaceous pollen.) Of the other tribes, pollen of the Buttnerieae is also not very different.

The tribe Prockieae, including the genera *Hasseltia* (Figs. 159-160), *Prockia* (Figs. 161-162), and *Neosprucia*, was removed from the Flacourtiaceae by Hutchinson (1959) and placed in the Tiliaceae. On the basis of pollen morphology, there is no support for the removal of these genera. They fit perfectly well among the Banarieae.

Among the Tiliaceae and Sterculiaeae are many genera showing highly evolved pollen including spininess, triangular shape, and elaborate porate apertures. Nevertheless, among the less specialized members of these families, a definite affinity can be found with the Flacourtiaceae. The pollen of these two families can be considered as a type distinct from malvaceous or bombacaceous pollen (Chaudhuri & Mallik, 1965).

Pollen grains of the Rhopalocarpaeae are medium to large, 3-6-colpate, colporate, and oblate. The exine is echinate or subechinate. In the past this group has been placed in the Violales (with the Cochlospermaceae), the Theales or Malvales, but recent studies by Huard (1965a, b) confirm their placement in the Malvales. They are not close to the Flacourtiaceae.

The Bombacaceae have pollen which are quite different from the Flacourtiaceae. Advanced trends include highly spinose, per-reticulate rugulate or verrucate exines, fossaperturate shape, or elaborate aperture patterns. (Tsukada, 1964; Fuchs, 1967; Robyns, 1963; Nair, 1962b).

Malvaceae have mostly large, spinose pollen with thick walls and large
apertures. Many are panporate. Pollen of this family has the least similarity to the Flacourtiaceae of all of the malvalian families (Prasad, 1963; Sharma & Rastogi, 1965; Bronckers & Horvat, 1963; Saad, 1960; Nair, 1962b; Chaudhuri & Mallik, 1965).

**Euphorbiaceae.**—The Euphorbiaceae have features in common with both primitive Violales and Malvales and may have arisen from an ancestral group between them (Takhtajan, 1969). Pollen of the subfamily Phyllanthoideae (Punt, 1967), especially that of the *Antidesma* and *Richeria* types (Punt, 1962), is quite similar to flacourtiaceous pollen. The grains tend to be prolate, costate, small-to medium-sized, have equatorially elongate apertures with diffuse ends, and are reticulate or psilate-TECTate. Other genera are more specialized in being verrucate, per-reticulate, fissaperturate, spinose or suprabaculate, and have to 4–5 apertures. Some genera are stephanocolpate, -porate, or inaperturate. The subfamily Crotonoideae is considerably more specialized.

This large, diverse family may well have had its origins in the Violales. On the other hand, Chaudhuri and Mallik (1965) have pointed out an apparent affinity between the Sterculiaceae and Phyllanthoideae, because of resemblances in the tricolporate, spheroidal-oblate pollen of some genera.

**Dilleniaceae.**—Studies by Dickison (1967), have shown the Dilleniaceae to have a variety of morphological types but, as with the Flacourtiaceae, the tribes cannot be delineated easily by pollen morphology. Dickison concluded that the Dilleniaceae show more resemblance to the Theales than to the Ranalian families. Violales were not considered closely related.

Direct comparisons in the present study show that the pollen of the Flacourtiaceae is quite compatible with that of the Dilleniaceae. Agreement includes the prolate to spheroidal shape, circular polar outline, small to medium size, tectate or semi-tectate structure, and finely reticulate to reticulate sculpture. Costae seem to be present but are not mentioned in Dickison's study. The compound apertures are somewhat different. The furrows are said to be provided with an operculum and often a margo. Trends toward four apertures and porate grains are paralleled in the Flacourtiaceae. It seems quite feasible to consider the Dilleniaceae a primitive connecting link between the Violales and Theales as stated by Takhtajan (1969).

**Theales.**—The Ochnaceae, a basal group in the Theales, have pollen which bears a strong resemblance to the Flacourtiaceae. The tricolporate, prolate, costate grains have an equatorially elongate endoaperture which is quite similar to the Flacourtiaceae. The ekxine is smooth, subverrucate, to finely reticulate (Muller, 1969). There is also an unmistakable resemblance to several higher families of Violales (Cochlospermaceae, Bixaceae, and Cistaceae).

Pollen of the Theaceae shows some similarities to flacourtiaceous pollen in size, shape, reticulate exine, equatorially elongate endoapertures, smooth colpi membranes, and costate margins. Some genera differ in having densely spaced pila, a spinuliferous exkxine, and granulate aperture membranes. The overall resemblance here is not as close as with the Ochnaceae.

The Clusiaceae (Guttiferae) and Hypericaceae have pollen with tendencies toward greater size, 4–5 apertures in an angulaperturate condition, and more
Figures 171–172. Pollen of Flacourtiaceae, tribe Casearieae, *Hecatostemon guazumifolius* (Smith 174). Scanning electron photomicrographs of acetolyzed grains.—171. Oblique polar view and equatorial view of collapsed grain. ×2400. Note reticulate surface.—172. View of aperture. ×5900. Note equatorially elongate endoaperture disappearing from view beyond the edge of the colpus. An ektesine proliferation is visible extending along one side of endoaperture. It appears to originate on one side of the colpus margin. This ektesinal proliferation is also visible in both grains of Fig. 171.
highly specialized sculpture. A few species are tricolporate and finely reticulate. The equatorially elongate endoaperture is similar to the Flacourtiaceae.

Of the Theales, flacourtiaceous pollen most clearly resembles that of the Ochnaceae with the Theaceae, Clusiaceae, and Hypericaceae showing generally more highly evolved pollen.

It must be kept in mind that comparisons of the Flacourtiaceae with only the more highly evolved or “average” condition of other families could create a picture of the Flacourtiaceae as being a large isolated family. I have deliberately attempted to find genera and tribes which most resemble the Flacourtiaceae, thus pointing out possible phyletic bridges. This is a long way from demonstrating phylogeny, and I would hope that these suggestions might stimulate further investigation.

Comments on miscellaneous groups occasionally placed near the Flacourtiaceae.—The Canellaceae, at one time placed in the Parietales have been demonstrated (Wilson, 1964) to belong with the monosulcate Ranales closest to the Myristicaceae.

The Hoplestigmataceae have 6–9-angular, tricolporate, finely reticulate grains with a compound aperture not found in the above orders.

The Droseraceae have very specialized 7–8 porate, spinuliferous pollen. The family has possible affinities with the Centrospermae.

Sabouraea was described by Leandri (1962) and placed by him and by Hutchinson (1967) in the Flacourtiaceae. Its pollen, studied by Rethore (1963), is pantocolpate and altogether novel for the Flacourtiaceae. Its best home is still uncertain.

Barteria J. D. Hook., a myrmecophyte of west tropical Africa, has been treated as a member of the Flacourtiaceae (Wheeler, 1922). Pollen of Barteria fistulosa Masters is illustrated and described as being flacourtiaceous by Van Campo, Bronckers and Guinet (1965). Its pollen is spiny, polyporate, and has a diameter of about 165μ. It is not flacourtiaceous; it has been included with the Passifloraceae by Spirlet (1965).

Literature Cited


