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A SYNOPSIS OF FLACOURTIACEAE

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ABSTRACT

Flacourtiaceae are a large, mostly tropical, family containing more than 800 species. As circumscribed by Warburg and Gilg the family is rather heterogeneous and indeterminate. The most recent generic treatment, that of Hutchinson, represents a considerable improvement in our understanding of the family, yet Hutchinson's Flacourtiaceae still contain a number of disparate elements. This preliminary generic treatment, based upon studies of gross morphology, wood anatomy, palynology, and phytochemistry, attempts to provide a revised framework for future studies of this diverse family. Ten tribes (Berberidopsidae, Erythrospermeae, Oncobeeae, Pangieae, Homalieae, Scolopieae, Prockieae, Flacourtiaceae, Casearieae, Bembicieae) comprising 79 genera are recognized. The tribes Abatieae, Alzateae, Lacistemeae, Paropsieae, and Trichostephaneae are excluded from the family, as are the genera *Aphloia*, *Asteropeia*, *Lethedon* (= *Microsemma*), and *Plagiopteron*. Hutchinson's tribe Banareae is not recognized as a distinct taxon.

Key words: Flacourtiaceae, systematics, classification, wood anatomy, pollen morphology, cyclopentenyl fatty acids, cyanogenic glycosides.

INTRODUCTION

Flacourtiaceae are a pantropical family, comprising 79 genera and approximately 880 species, which remains relatively poorly known taxonomically. The family is placed at the base of the order Violales by Takhtajan (1980), Cronquist (1981), and Thorne (1981) and is widely recognized as being of major phylogenetic importance. Nonetheless, Flacourtiaceae have received scant attention in proportion to their size and systematic importance (Keating 1973).

In their present circumscription, Flacourtiaceae are a highly polythetic taxon. As Sleumer (1954) noted, "no single character exists wherewith to distinguish Flacourtiaceae from other families or to recognize them in the field." Consequently, the family has developed a reputation as a taxon in which to place many genera of uncertain affinities. Even the respected tropical botanist Pittier was a believer in the usefulness of Flacourtiaceae as a receptacle for all those things not recognized. "When in doubt, put it in the Flacourtiaceae!" he is reported to have said (Williams 1965).

The early taxonomic history of Flacourtiaceae has been adequately summarized by Sleumer (1980). The first modern approach to the classification of the family was taken by Warburg (1894), who treated Flacourtiaceae as comprising 61 genera arranged in 11 tribes. Gilg (1925) expanded upon Warburg's system and presented a classification with 84 genera in 12 tribes. The most recent treatment of the family is that of Hutchinson (1967), who recognized 10 tribes and 90 genera.

As circumscribed by Warburg (1894) and Gilg (1925), Flacourtiaceae were rather heterogeneous and indeterminate. The generic treatment of Hutchinson (1967) represented a considerable improvement in our understanding of the family, but Hutchinson's Flacourtiaceae still contained a number of disparate elements.

The ultimate goal of this author is to prepare a revised generic treatment of the family based upon evidence from as many lines of investigation as possible. The preliminary work presented here is based primarily upon published morphological studies, particularly the treatments by H. Sleumer (e.g., Sleumer 1954, 1980), wood anatomy (Miller 1975), pollen morphology (Erdtmann 1971; Schaeffer 1972; Keating 1973, 1975), and the distribution of selected chemical constituents (Hegnauer 1966; Gibbs 1974; Spencer and Seigler 1985b), as well as on unpublished personal observations. It is hoped that this treatment will provide an improved framework for future studies of this diverse family.

TAXONOMIC TREATMENT

FLACOURTIACEAE DC., Prodr. 1:255. 1824.

Trees or shrubs or rarely climbers, sometimes armed with axillary spines, often producing cyclopentenoid cyanogenic glycosides and/or cyclopentenyl fatty acids ("chaulmoogra oils"), sometimes producing alkaloids. Wood diffuse porous with poorly defined growth rings; pores generally rounded in cross section but angular in some genera, average diameter 50–100 μm , 50–80% (rarely to 100%) solitary, the remainder in short radial multiples; vessel elements ligulate with oblique endwalls, spiral thickenings occurring in some genera; perforation plates scalariform or simple or a combination of the two in different taxa; intervacular and vessel-ray pitting almost always alternate, the vessel-ray pits larger than or similar in size to the intervacular pits; fiber-tracheids and libriform fibers present, with gelatinous fibers in a few genera, the fibrous elements septate, rarely nonseptate; axial parenchyma absent; rays of two types present, uniseriate homocellular rays composed of upright cells and multiseriate heterocellular rays with long uniseriate extensions; prismatic crystals present in the rays cells of virtually all genera. Leaves alternate (opposite in one genus), simple, entire or gland-toothed, often 2-ranked. Stipules usually present, often caducous, rarely absent. Flowers in terminal or axillary inflorescences, occasionally solitary, perfect or imperfect. Sepals 3–6, rarely more, distinct or connate towards the base. Petals 3–8, rarely more, distinct, alternating with the sepals or sometimes spirally arranged and poorly differentiated from the sepals, occasionally provided with an adaxial scale, sometimes absent. Stamens numerous or occasionally equal in number to the petals, the filaments distinct or grouped into clusters opposite the petals. Pollen grains always single, never in tetrads or larger units, prolate to spheroidal, tectate, reticulate, tricolpate to tricolporoidate or tricolporate, the apertures usually compound, consisting of a wide or narrow colpus and equatorially elongate endoapertures, binucleate. Disk often present, intrastaminal or extrastaminal or occasionally composed of separate glands. Ovary superior, half-inferior, or inferior, of 2–10 united carpels. Placentation usually parietal (sometimes appearing almost basal) or occasionally axile, the ovules 1–many per placenta. Styles free or united. Fruits various, dry or fleshy, dehiscent or indehiscent. Seeds occasionally arillate or with a tuft of silky hairs, containing a straight embryo surrounded by an abundant oily endosperm.

SYNOPTICAL KEY TO TRIBES OF FLACOURTIACEAE

1. Plants often producing cyanogenic glycosides and/or cyclopentenyl fatty acids; sepals and petals spirally-arranged or, if in separate whorls, the petals more numerous than the sepals and not regularly-arranged in relation to them.

- 2. Scandent shrubs; wood with exclusively solitary pores, tracheids present, septate fibers absent, rays >1 cm in height; pollen tricolpate 1. Berberidopsideae
- 2. Shrubs or trees, never scandent; wood with 50–80% solitary pores, tracheids absent, septate fibers present, rays <1 cm in height; pollen tricolporoidate to tricolporate.
 - 3. Cyclopentenyl fatty acids absent; vessel elements mostly with exclusively scalariform perforation plates, perianth parts poorly differentiated into sepals and petals 2. Erythrospermeae
 - 3. Cyclopentenyl fatty acids often present; vessel elements with simple or a combination of simple and scalariform perforation plates; perianth clearly differentiated into sepals and petals.
 - 4. Flowers mostly perfect; petals lacking an adaxial scale 3. Oncobeeae
 - 4. Flowers mostly imperfect; petals bearing an adaxial scale 4. Pangieae
- 1. Plants rarely (1 genus) producing cyanogenic glycosides, occasionally producing cyclopentenyl fatty acids; sepals and petals in separate whorls, the petals equal in number to the sepals or, if more numerous than the sepals, then regularly-arranged in relation to them, or petals absent.
 - 5. Petals present, at least in staminate flowers.
 - 6. Stamens antepetalous or in antepetalous clusters; disk present 5. Homalieae
 - 6. Stamens not regularly-arranged in relation to the petals; disk present or absent.
 - 7. Leaves pinnately nerved, lacking petiolar glands; distribution in Old World tropics 6. Scolopieae
 - 7. Leaves 3–5-nerved from the base, usually with a pair of petiolar glands; distribution in New World tropics 7. Prockieae
 - 5. Petals absent.
 - 8. Vessels with spiral thickenings and a combination of scalariform and simple perforation plates; flowers mostly imperfect; pollen strictly triaperturate; ovary superior 8. Flacourtieae
 - 8. Vessels without spiral thickenings and with mostly simple perforation plates (wood structure unknown in Bembicieae); flowers mostly perfect; pollen 3-, 4-, or 5-aperturate; ovary half- to completely inferior.
 - 9. Floral bracts small or obsolete; ovary half-inferior 9. Casearieae
 - 9. Floral bracts large, enclosing each flower; ovary inferior 10. Bembicieae

1. BERBERIDOPSIDEAE Veldk., Blumea 30:24. 1984.

Scandent shrubs, often producing cyanogenic glycosides. Vessels almost exclusively solitary, the vessel elements very long to extremely long with exclusively scalariform perforation plates, intervascular pitting almost absent, vessel-ray pits large; fibrous elements consisting of nonseptate tracheids with distinctly bordered pits. Leaves alternate, exstipulate. Flowers perfect, the petals well developed and distinct from the sepals or the outer tepals sepaloid and gradually changing into the inner petaloid ones. Stamens in a single whorl of 6–13 or numerous and without an apparent arrangement. Pollen tricolpate. Ovary unilocular, the ovules 2–many on each of 3–5 parietal placentae. Fruit berrylike. Distribution in Australia and South America (Chile).

Genera: *Berberidopsis* Hook. f., *Streptothamnus* F. Muell.

2. ERYTHROSPERMEAE DC., Prodr. 1:257. 1824.

Trees or shrubs, occasionally producing cyanogenic glycosides. Vessel elements very long, usually with exclusively scalariform or occasionally a combination of scalariform and simple perforation plates; intervascular pitting frequently opposite, vessel-ray pits large; fibrous elements consisting exclusively of fiber-tracheids or (in *Camptostylus*) of a combination of fiber-tracheids and libriform fibers. Leaves alternate, petiolate, stipulate, the stipules small and deciduous or more often absent. Flowers in terminal or axillary inflorescences, perfect or occasionally polygamous. Sepals and petals usually spirally arranged and often in-

distinguishable from one another, the petals in some genera with an adaxial scale. Stamens numerous, rarely as few as 5. Pollen tricolporate, the endoapertures rectangular in a few genera. Ovary superior, unilocular, of 3–5 united carpels, bearing many ovules on parietal placentae. Fruit a berry or capsule or woody and indehiscent. Distribution in the Old World tropics and Oceania.

Genera: *Ahernia* Merrill, *Camptostylus* Gilg, *Dasylepis* Oliv. (= *Pyramidocarpus* Oliv.), *Erythrospermum* Lam., *Rawsonia* Harv. & Sond., *Scottellia* Oliv.

3. ONCOBEAE Benth., J. Proc. Linn. Soc. Bot. 5(Suppl. 2):77. 1861.

Trees or shrubs, often producing cyanogenic glycosides and/or cyclopentenyl fatty acids. Vessel elements medium-sized to moderately long, usually with simple perforation plates and alternate intervascular pitting, a few genera having exclusively scalariform or both scalariform and simple perforation plates and opposite intervascular pitting, vessel-ray pits large. Leaves alternate, stipulate, the stipules often caducous. Flowers perfect or imperfect, borne in terminal or axillary inflorescences or sometimes solitary. Sepals and petals in separate whorls distinguishable from one another, the petals more numerous than the sepals and not regularly arranged in relation to them. Stamens numerous. Pollen tricolporoidate to tricolporate, the endoapertures often not well defined at the edges. Ovary superior, unilocular, bearing many ovules on 2–10 parietal placentae. Fruits capsular, berrylike, or woody and indehiscent. Distribution in tropical Africa and South America.

Genera: *Buchnerodendron* Gurke, *Caloncoba* Gilg (= *Paraphyadanthé* Mildbr.), *Carpotroche* Endl., *Grandidiera* Jaub., *Lindackeria* Presl, *Mayna* Aubl. (= *Dendrostigma* Gleason), *Oncoba* Forssk., *Peterodendron* Sleumer, *Poggea* Gurke, *Prockiopsis* Baill., *Xylothea* Hochst.

4. PANGIEAE Clos, Ann. Sci. Nat. Bot. IV 8:267. 1857.

Trees and shrubs, often producing cyanogenic glycosides and/or cyclopentenyl fatty acids. Vessel elements in most genera moderately long with exclusively simple perforation plates and alternate intervascular pitting (*Hydnocarpus* differs in having exclusively scalariform perforation plates and opposite intervascular pitting); vessel-ray pits large. Leaves alternate, usually stipulate. Flowers small, imperfect, in axillary or cauline inflorescences, rarely solitary. Sepals and petals in separate whorls distinct from one another, each petal bearing a scale on its adaxial surface. Stamens 5–many, free or slightly connate at the base. Pollen tricolporoidate to tricolporate, the endoapertures often equatorially elongate. Ovary superior, unilocular, of 2–6 united carpels, bearing 1–many ovules on each parietal placenta. Fruits various. *Kiggelaria* occurs in east Africa, the remaining genera in Asia and Oceania.

Genera: *Baileyoxylon* C. T. White, *Chlorocarpa* Alston, *Eleutherandra* van Slooten, *Gynocardia* R. Br., *Hydnocarpus* Gaertn. (= *Taraktogenos* Hassk.), *Kiggelaria* L., *Pangium* Reinw., *Ryparosa* Bl., *Scaphocalyx* Ridl., *Trichadenia* Thw.

5. HOMALIEAE Benth., J. Proc. Linn. Soc. Bot. 5(Suppl. 2):88. 1861.

Trees or shrubs, not producing cyanogenic glycosides. Vessel elements medium-sized to very long, ligulate, with exclusively simple perforation plates; intervas-

cular pitting alternate, vessel-ray pits small; fiber-tracheids, libriform fibers, and gelatinous fibers commonly present. Leaves alternate, stipulate, the stipules often caducous. Flowers small, perfect or imperfect, in terminal or axillary inflorescences. Sepals and petals in separate whorls, the petals equal in number to or twice as many as the sepals or absent in pistillate flowers. Stamens equal in number to the petals and opposite them or in fascicles of 2—many opposite the petals and alternating with glands. Pollen tricolporate, the endoapertures equatorially elongate. Disk present, often divided into glands. Ovary superior, of 2–5 united carpels, unilocular, with 1—many ovules borne on each parietal placenta. Fruits various. Most genera are confined to the tropics of Africa and the New World, *Homalium* is pantropical.

Genera: *Bartholomaea* Standl. & Steyerl., *Byrsanthus* Guillem., *Calantica* Jaub. ex Tul., *Dissomeria* Benth., *Gerrardina* Oliv., *Homalium* Jacq. (= *Nisa* Nor.), *Neopringlea* Wats., *Trimeria* Harv.

6. SCOLOPIEAE Warb., Nat. Pfl. 3(6):28. 1894.

Trees or shrubs, never producing cyanogenic glycosides. Vessel elements medium-sized, ligulate, with almost exclusively simple perforation plates and alternate intervascular pitting, vessel-ray pitting small. Leaves alternate (opposite in *Pseudoscopia*); stipules usually present, persistent or caducous. Flowers perfect or imperfect, solitary or borne in terminal or axillary inflorescences, these sometimes adnate to the midrib of a large subtending bract. Sepals and petals in separate whorls, distinguishable from one another, petals the same in number as the sepals or, if more numerous, then regularly arranged in relation to them. Stamens usually numerous. Pollen tricolporoidate, the endoapertures not well defined at the edges. Disk present or absent. Ovary superior, unilocular, bearing 1—many ovules on each of 2–5 parietal placentae. Fruits berrylike or capsular. Distribution in the Old World tropics.

Genera: *Hemiscolopia* van Slooten, *Mocquerysia* Hua, *Phyllobotryon* Muell. Arg., *Phylloclinium* Baill., *Pseudoscopia* Gilg, *Scolopia* Schreb.

7. PROCKIEAE Endl., Gen. 918, 1839.

Trees or shrubs, rarely producing cyanogenic glycosides (several species of *Banara*). Wood anatomy of *Prockia* and *Banara* very similar to that of members of Scolopieae and Homalieae, the other genera with vessel elements clustered, having spiral thickenings and a combination of scalariform and simple perforation plates, the intervascular pitting alternate, the pits medium-sized. Leaves alternate, stipulate, the stipules often caducous. Flowers small, perfect or imperfect, in terminal or axillary inflorescences. Sepals and petals in distinct whorls, the petals unlike the sepals and equal in number to them (absent in *Macrohasseltia*). Stamens numerous, not fascicled. Pollen tricolporoidate, the endoapertures diffuse. Disk glands, when present, small and inserted among the bases of the filaments. Ovary superior, of 2–5 united carpels, unilocular or semiplurilocular by intrusion of the parietal placentae, plurilocular in *Prockia* and *Hasseltia*. Ovules usually many on each placenta. Fruits baccate or capsular. Distribution in the New World tropics.

Genera: *Banara* Aubl., *Hasseltia* H.B.K., *Hasseltiopsis* Sleumer, *Macrohasseltia* L. O. Williams, *Neosprucea* Sleumer, *Pineda* Ruiz & Pavon, *Pleuranthodendron* L. O. Williams, *Prockia* Browne ex L.

8. FLACOURTIEAE DC., Prodr. 1:256. 1824.

Trees or shrubs, never producing cyanogenic glycosides, occasionally producing cyclopentenyl fatty acids. Vessel elements moderately short to very long with scalariform and simple perforation plates, the intervascular pitting alternate or opposite in different genera, vessel-ray pitting variable. Leaves alternate, stipulate or exstipulate. Flowers small, usually imperfect, occasionally perfect, borne in terminal or axillary inflorescences (the pistillate flowers solitary in *Dovyalis*). Petals absent. Stamens numerous. Pollen tricolporoidate to tricolporate, the endoapertures usually equatorially elongate. Ovary superior, of 2–8 united carpels, unilocular in most genera (plurilocular in *Flacourtia*). Fruits various. Distribution of the tribe is pantropical.

Genera: *Azara* Ruiz & Pavon (= *Arechavaleteia* Spegazzini), *Bennettiodendron* Merrill (= *Bennettia* Miq.), *Carrierea* Franch., *Dovyalis* E. Mey. ex Arn., *Flacourtia* L'Herit., *Guya* Frapp., *Idesia* Maxim., *Itoa* Hemsl., *Ludia* Comm. ex Juss., *Olmiediella* Baill., *Poliothyrsis* Oliv., *Priamosia* Urb., *Tisonia* Baill., *Xylosma* Forst. (= *Eichlerodendron* Briq., *Myroxylon* Forst.).

9. CASEARIEAE Benth., J. Proc. Linn. Soc. Bot. 5(Suppl. 2):87. 1861.

Trees or shrubs, never producing cyanogenic glycosides. Vessel elements medium-sized to moderately long with exclusively simple perforation plates, the intervascular pitting alternate, the vessel-ray pits small. Leaves alternate, stipulate or exstipulate. Flowers perfect or imperfect, borne in terminal or axillary inflorescences, rarely solitary. Petals absent. Stamens usually 4–12, rarely numerous, often inserted on or between the lobes of a disk. Pollen tricolporate or occasionally 4- or 5-porate, the endoapertures usually equatorially elongate. Ovary more or less half-inferior, unilocular, with many ovules borne on 3–4 parietal placentae. Fruits various. Distribution pantropical.

Genera: *Bivinia* Jaub. ex Tul., *Casearia* Jacq. (= *Gossypiospermum* (Griseb.) Urb., *Synandrina* Standl. & Steyerl.), *Euceraea* Mart., *Hecatostemon* Blake, *Laetia* Loefl. ex L., *Lunania* Hook., *Neoptychocarpus* Buchheim, *Ophiobotrys* Gilg, *Osmelia* Twaites, *Pseudosmelia* Sleumer, *Ryania* Vahl, *Samyda* N. J. Jacquin, *Tetrathylacium* Poepp. & Endl., *Zuelania* A. Rich.

10. BEMBICIEAE Warb., Nat. Pfl. 3(6):52. 1894.

Tree, not producing cyanogenic compounds. Wood structure unknown. Leaves alternate, stipulate. Flowers perfect, borne in short, axillary, conelike inflorescences composed of imbricate leathery bracts. Petals absent. Stamens many, inserted on an annular disk. Pollen tricolporate, poorly known. Ovary inferior, unilocular, bearing few ovules on two parietal placentae. Fruit 1-seeded. Known only from Madagascar.

Genus: *Bembicia* Oliv.

DISCUSSION

As circumscribed here, Flacourtiaceae consist of 79 genera and approximately 880 species arranged in 10 well-delimited tribes. Most of these genera are small. *Homalium*, *Casearia*, and *Xylosma* collectively account for over half of the species in the family, while 70 genera contain fewer than 15 species each; of these, 28

are monotypic. The classification presented in this treatment, as well as the schemes of Warburg (1894), Gilg (1925), and Hutchinson (1967), is summarized in Table 1.

Flacourtiaceae are a polythetic group, consisting of a rather heterogeneous assortment of more or less homogeneous tribes. The question of whether or not the family is polyphyletic as well cannot, in my opinion, be answered at the present time. Our knowledge of members of the family is insufficient to enable us to accurately circumscribe two or more monophyletic groups, and much remains to be learned about the comparative morphology, anatomy, and chemistry of the family. Nonetheless, several distinct groupings of tribes, not here recognized as formal taxonomic units, can be seen within the family.

When data from comparative morphology, wood anatomy, palynology, and the distribution of selected classes of chemical constituents are combined it becomes apparent that the tribes of Flacourtiaceae form three distinct groups. The first, comprising Berberidopsidae, Erythrospermeae, Oncobae, and Pangieae, contains the least specialized genera within the family. These genera were distributed among three tribes (Erythrospermeae, Oncobae, and Pangieae) by Warburg (1894) and between only two tribes (Oncobae and Pangieae) by Gilg (1925). On morphological grounds, Gilg considered the genera of his Oncobae to be the most primitive members of the family. Hutchinson (1967) divided these genera into two groups, Berberidopsidae, comprising those genera with (in his view) spirally arranged perianth parts, and Oncobae, containing the genera with sepals and petals in separate cycles. Recent studies, however, do not fully support this alignment. Data from studies of wood (Miller 1975) and leaf (Baas 1984) anatomy and pollen morphology (Keating 1973; van Heel 1984) support a close alliance between *Berberidopsis* and *Streptothamnus*. Both genera are characterized by wood with 100% solitary vessels, the presence of tracheids and absence of septate fibers, rays greater than 1 cm in height, and tricolpate pollen. These characteristics are not shared with any other members of Flacourtiaceae and serve to isolate the two genera within the family. Takhtajan (1986) has segregated *Berberidopsis* and *Streptothamnus* as the family Berberidopsidaceae, but following Veldkamp (1984) I choose to retain them in Flacourtiaceae as the tribe Berberidopsidae, the remaining genera of Hutchinson's Berberidopsidae constituting the tribe Erythrospermeae. *Goethalsia* Pitt., included in Pangieae by Hutchinson (1967), is here transferred to Tiliaceae on the basis of wood structure (Kukachka and Rees 1943; Miller 1975).

Spencer and Seigler (1985b) surveyed Flacourtiaceae to ascertain the distribution of cyanogenic glycosides and found that, with one exception (*Banara* in tribe Prockieae), only members of Berberidopsidae, Erythrospermeae, Oncobae, and Pangieae were cyanogenic. The relationships among these taxa and the other known cyanogenic families of Violales such as Caricaceae (Spencer and Seigler 1984), Malesherbiaceae (Spencer and Seigler 1985a), Passifloraceae (Hegnauer 1966), and Turneraceae (Spencer and Seigler 1985c) should be examined more carefully.

A second group of tribes within Flacourtiaceae comprises Homalieae, Scolopieae, and Prockieae. The genera constituting these tribes form a very natural group, being scarcely distinguishable in terms of wood anatomy (Miller 1975) or pollen morphology (Keating 1973) and therefore delimited here strictly on morphological grounds. The concept of these tribes adopted in the present study is similar to that of Gilg (1925), with the exceptions noted below.

Table 1. Comparison of the classifications of Warburg (1894), Gilg (1925), and Hutchinson (1967) with that proposed in the present study. Within each tribe the genera are listed alphabetically to facilitate comparisons. Numbers in parentheses represent the number of species in each genus. Synonyms are listed in the text.

| Lemke (1988) | Warburg (1894) | Gilg (1925) | Hutchinson (1967) |
|-------------------------------|---------------------------|----------------------------|---------------------------|
| Tribe Berberidopsidae | Tribe Erythrospermeae | Tribe Oncobeeae | Tribe Berberidopsidae |
| 1. <i>Berberidopsis</i> (2) | 1. <i>Berberidopsis</i> | 1. <i>Ahernia</i> | 1. <i>Ahernia</i> |
| 2. <i>Streptothamnus</i> (1) | 2. <i>Dasylepis</i> | 2. <i>Berberidopsis</i> | 2. <i>Berberidopsis</i> |
| Tribe Erythrospermeae | 3. <i>Erythrospermum</i> | 3. <i>Buchnerodendron</i> | 3. <i>Camptostylus</i> |
| 3. <i>Ahernia</i> (1) | 4. <i>Pyramidocarpus</i> | 4. <i>Caloncoba</i> | 4. <i>Dasylepis</i> |
| 4. <i>Camptostylus</i> (4) | 5. <i>Rawsonia</i> | 5. <i>Camptostylus</i> | 5. <i>Erythrospermum</i> |
| 5. <i>Dasylepis</i> (6) | Tribe Oncobeeae | 6. <i>Carpotroche</i> | 6. <i>Rawsonia</i> |
| 6. <i>Erythrospermum</i> (5) | 6. <i>Buchnerodendron</i> | 7. <i>Dasylepis</i> | 7. <i>Scottellia</i> |
| 7. <i>Rawsonia</i> (2) | 7. <i>Carpotroche</i> | 8. <i>Erythrospermum</i> | 8. <i>Streptothamnus</i> |
| 8. <i>Scottellia</i> (3) | 8. <i>Grandidiera</i> | 9. <i>Grandidiera</i> | Tribe Oncobeeae |
| Tribe Oncobeeae | 9. <i>Mayna</i> | 10. <i>Lindackeria</i> | 9. <i>Buchnerodendron</i> |
| 9. <i>Buchnerodendron</i> (2) | 10. <i>Oncoba</i> | 11. <i>Mayna</i> | 10. <i>Caloncoba</i> |
| 10. <i>Caloncoba</i> (10) | 11. <i>Poggea</i> | 12. <i>Oncoba</i> | 11. <i>Carpotroche</i> |
| 11. <i>Carpotroche</i> (1) | 12. <i>Prockiopsis</i> | 13. <i>Paraphyadanthé</i> | 12. <i>Dendrostigma</i> |
| 12. <i>Grandidiera</i> (1) | Tribe Pangieae | 14. <i>Poggea</i> | 13. <i>Grandidiera</i> |
| 13. <i>Lindackeria</i> (13) | 13. <i>Gynocardia</i> | 15. <i>Prockiopsis</i> | 14. <i>Lindackeria</i> |
| 14. <i>Mayna</i> (6) | 14. <i>Hydnocarpus</i> | 16. <i>Pyramidocarpus</i> | 15. <i>Mayna</i> |
| 15. <i>Oncoba</i> (4) | 15. <i>Kiggelaria</i> | 17. <i>Rawsonia</i> | 16. <i>Oncoba</i> |
| 16. <i>Peterodendron</i> (1) | 16. <i>Pangium</i> | 18. <i>Scottellia</i> | 17. <i>Peterodendron</i> |
| 17. <i>Poggea</i> (5) | 17. <i>Ryparosa</i> | 19. <i>Xylothea</i> | 18. <i>Poggea</i> |
| 18. <i>Prockiopsis</i> (1) | 18. <i>Trichadenia</i> | Tribe Pangieae | 19. <i>Prockiopsis</i> |
| 19. <i>Xylothea</i> (2) | Tribe Paropsieae | 20. <i>Gynocardia</i> | 20. <i>Xylothea</i> |
| Tribe Pangieae | 19. <i>Barteria</i> | 21. <i>Hydnocarpus</i> | Tribe Scolopieae |
| 20. <i>Baileyoxydon</i> (1) | 20. <i>Hounea</i> | 22. <i>Kiggelaria</i> | 21. <i>Bartholomaea</i> |
| 21. <i>Chlorocarpa</i> (1) | 21. <i>Paropsia</i> | 23. <i>Pangium</i> | 22. <i>Dioncophyllum</i> |
| 22. <i>Eleutherandra</i> (1) | 22. <i>Paropsiopsis</i> | 24. <i>Ryparosa</i> | 23. <i>Hemiscolopia</i> |
| 23. <i>Gynocardia</i> (1) | 23. <i>Soyauxia</i> | 25. <i>Scaphocalyx</i> | 24. <i>Mocquersia</i> |
| 24. <i>Hydnocarpus</i> (40) | Tribe Abatieae | 26. <i>Trichadenia</i> | 25. <i>Phyllobotryon</i> |
| 25. <i>Kiggelaria</i> (1) | 24. <i>Abatia</i> | Tribe Paropsieae | 26. <i>Phylloclinium</i> |
| 26. <i>Pangium</i> (1) | 25. <i>Aphaerema</i> | 27. <i>Barteria</i> | 27. <i>Pseudoscolopia</i> |
| 27. <i>Ryparosa</i> (18) | Tribe Scolopieae | 28. <i>Hounea</i> | 28. <i>Sabournaea</i> |
| 28. <i>Scaphocalyx</i> (2) | 26. <i>Banara</i> | 29. <i>Paropsia</i> | 29. <i>Scolopia</i> |
| 29. <i>Trichadenia</i> (2) | 27. <i>Dioncophyllum</i> | 30. <i>Paropsiopsis</i> | Tribe Banareae |
| Tribe Homalieae | 28. <i>Hasseltia</i> | 31. <i>Smeathmannia</i> | 30. <i>Asteropeia</i> |
| 30. <i>Bartholomaea</i> (2) | 29. <i>Pineda</i> | Tribe Abatieae | 31. <i>Banara</i> |
| 31. <i>Byrsanthus</i> (1) | 30. <i>Prockia</i> | 33. <i>Abatia</i> | 32. <i>Pineda</i> |
| 32. <i>Calantica</i> (9) | 31. <i>Scolopia</i> | 34. <i>Aphaerema</i> | 33. <i>Trimeria</i> |
| 33. <i>Dissomeria</i> (2) | 32. <i>Streptothamnus</i> | Tribe Trichostephaneeae | Tribe Homalieae |
| 34. <i>Gerrardina</i> (2) | Tribe Homalieae | 35. <i>Trichostephanus</i> | 34. <i>Byrsanthus</i> |
| 35. <i>Homalium</i> (ca. 200) | 33. <i>Byrsanthus</i> | Tribe Scolopieae | 35. <i>Calantica</i> |
| 36. <i>Neopringlea</i> (3) | 34. <i>Calantica</i> | 36. <i>Banara</i> | 36. <i>Dissomeria</i> |
| 37. <i>Trimeria</i> (2) | 35. <i>Dissomeria</i> | 37. <i>Dioncophyllum</i> | 37. <i>Gerrardina</i> |
| Tribe Scolopieae | 36. <i>Gerrardina</i> | 38. <i>Hasseltia</i> | 38. <i>Homaliopsis</i> |
| 38. <i>Hemiscolopia</i> (1) | 37. <i>Homalium</i> | 39. <i>Pineda</i> | 39. <i>Homalium</i> |
| 39. <i>Mocquersia</i> (2) | 38. <i>Trimeria</i> | 40. <i>Pseudoscolopia</i> | 40. <i>Nisa</i> |
| 40. <i>Phyllobotryon</i> (4) | Tribe Phyllobotryae | 41. <i>Prockia</i> | Tribe Pangieae |
| 41. <i>Phylloclinium</i> (4) | 39. <i>Mocquersia</i> | 42. <i>Scolopia</i> | 41. <i>Baileyoxydon</i> |
| 42. <i>Scolopia</i> (37) | 40. <i>Phyllobotryon</i> | | 42. <i>Chlorocarpa</i> |

Table 1. Continued.

| Lemke (1988) | Warburg (1894) | Gilg (1925) | Hutchinson (1967) |
|--|---------------------------|----------------------------|---|
| Tribe Prockieae | 41. <i>Phylloclinium</i> | 43. <i>Streptothamnus</i> | 43. <i>Eleutherandra</i> |
| 43. <i>Banara</i> (31) | Tribe Flacourtieae | Tribe Homalieae | 44. <i>Goethalsia</i> |
| 44. <i>Hasseltia</i> (3) | 42. <i>Azara</i> | 44. <i>Byrsanthus</i> | 45. <i>Gynocardia</i> |
| 45. <i>Hasseltiopsis</i> (1) | 43. <i>Bennettia</i> | 45. <i>Calantica</i> | 46. <i>Hydnocarpus</i> |
| 46. <i>Macrohasseltia</i> (1) | 44. <i>Dovyalis</i> | 46. <i>Dissomeria</i> | 47. <i>Kiggelaria</i> |
| 47. <i>Neosprucea</i> (5) | 45. <i>Flacourtia</i> | 47. <i>Gerrardina</i> | 48. <i>Pangium</i> |
| 48. <i>Pineda</i> (1) | 46. <i>Idesia</i> | 48. <i>Homaliopsis</i> | 49. <i>Ryparosa</i> |
| 49. <i>Pleuranthoden-</i> <i>dron</i> (1) | 47. <i>Ludia</i> | 49. <i>Homalium</i> | 50. <i>Scaphocalyx</i> |
| 50. <i>Prockia</i> (2) | 48. <i>Myroxylon</i> | 50. <i>Trimeria</i> | 51. <i>Taraktogenos</i> |
| Tribe Flacourtieae | 49. <i>Neumannia</i> | Tribe Phyllobotryae | 52. <i>Trichadenia</i> |
| 51. <i>Azara</i> (10) | 50. <i>Poliothyrsis</i> | 51. <i>Mocquersysia</i> | Tribe Flacourtieae |
| 52. <i>Bennettiodendron</i> (2) | 51. <i>Tisonia</i> | 52. <i>Phyllobotryon</i> | 53. <i>Aphloia</i> |
| 53. <i>Carrierea</i> (3) | Tribe Caseariae | 53. <i>Phylloclinium</i> | 54. <i>Azara</i> |
| 54. <i>Dovyalis</i> (15) | 52. <i>Casearia</i> | Tribe Flacourtieae | 55. <i>Bennettioden-</i> <i>dron</i> |
| 55. <i>Flacourtia</i> (10) | 53. <i>Euceraea</i> | 54. <i>Azara</i> | 56. <i>Carrierea</i> |
| 56. <i>Guya</i> (2) | 54. <i>Laetia</i> | 55. <i>Bennettia</i> | 57. <i>Dovyalis</i> |
| 57. <i>Idesia</i> (1) | 55. <i>Lunania</i> | 56. <i>Carrierea</i> | 58. <i>Eichlerodendron</i> |
| 58. <i>Itoa</i> (2) | 56. <i>Osmelia</i> | 57. <i>Dovyalis</i> | 59. <i>Flacourtia</i> |
| 59. <i>Ludia</i> (23) | 57. <i>Patrisia</i> | 58. <i>Eichlerodendron</i> | 60. <i>Guya</i> |
| 60. <i>Olmediella</i> (1) | 58. <i>Samyda</i> | 59. <i>Flacourtia</i> | 61. <i>Idesia</i> |
| 61. <i>Poliothyrsis</i> (1) | 59. <i>Tetrathylacium</i> | 60. <i>Guya</i> | 62. <i>Itoa</i> |
| 62. <i>Priamosia</i> (1) | 60. <i>Zuelania</i> | 61. <i>Idesia</i> | 63. <i>Ludia</i> |
| 63. <i>Tisonia</i> (15) | Tribe Bembicieae | 62. <i>Itoa</i> | 64. <i>Neopringlea</i> |
| 64. <i>Xylosma</i> (ca. 100) | 61. <i>Bembicia</i> | 63. <i>Ludia</i> | 65. <i>Olmediella</i> |
| Tribe Caseariae | | 64. <i>Neumannia</i> | 66. <i>Poliothyrsis</i> |
| 65. <i>Bivinia</i> (1) | | 65. <i>Olmediella</i> | 67. <i>Priamosia</i> |
| 66. <i>Casearia</i> (ca. 180) | | 66. <i>Poliothyrsis</i> | 68. <i>Synandrina</i> |
| 67. <i>Euceraea</i> (2) | | 67. <i>Priamosia</i> | 69. <i>Tisonia</i> |
| 68. <i>Hecatostemon</i> (1) | | 68. <i>Quadrasia</i> | 70. <i>Xylosma</i> |
| 69. <i>Laetia</i> (10) | | 69. <i>Tisonia</i> | Tribe Caseariae |
| 70. <i>Lunania</i> (14) | | 70. <i>Xylosma</i> | 71. <i>Abatia</i> |
| 71. <i>Neoptychocarpus</i> (2) | | Tribe Caseariae | 72. <i>Aphaerema</i> |
| 72. <i>Ophiobotrys</i> (1) | | 71. <i>Arechavaleteia</i> | 73. <i>Bivinia</i> |
| 73. <i>Osmelia</i> (4) | | 72. <i>Casearia</i> | 74. <i>Casearia</i> |
| 74. <i>Pseudosmelia</i> (1) | | 73. <i>Euceraea</i> | 75. <i>Euceraea</i> |
| 75. <i>Ryania</i> (8) | | 74. <i>Hecatostemon</i> | 76. <i>Gossypiosper-</i> <i>mum</i> |
| 76. <i>Samyda</i> (9) | | 75. <i>Laetia</i> | 77. <i>Hecatostemon</i> |
| 77. <i>Tetrathylacium</i> (2) | | 76. <i>Lunania</i> | 78. <i>Laetia</i> |
| 78. <i>Zuelania</i> (1) | | 77. <i>Ophiobotrys</i> | 79. <i>Lunania</i> |
| Tribe Bembicieae | | 78. <i>Osmelia</i> | 80. <i>Neoptychocarpus</i> |
| 79. <i>Bembicia</i> (1) | | 79. <i>Patrisia</i> | 81. <i>Ophiobotrys</i> |
| | | 80. <i>Samyda</i> | 82. <i>Osmelia</i> |
| | | 81. <i>Stapfiella</i> | 83. <i>Pseudosmelia</i> |
| | | 82. <i>Tetrathylacium</i> | 84. <i>Ryania</i> |
| | | 83. <i>Zuelania</i> | 85. <i>Samyda</i> |
| | | Tribe Bembicieae | 86. <i>Tetrathylacium</i> |
| | | 84. <i>Bembicia</i> | 87. <i>Zuelania</i> |
| | | | Tribe Alzateae |
| | | | 88. <i>Alzatea</i> |
| | | | Tribe Bembicieae |
| | | | 89. <i>Bembicia</i> |
| | | | 90. <i>Bembiciopsis</i> |

Homalieae include those genera in which the sepals and petals are equal in number (petals twice as many as the sepals in *Dissomeria*) and which have stamens, either equal in number to the petals and opposite them or arranged in antepetalous fascicles of 2–many, alternating with small, pilose nectar-glands. *Neopringlea*, long considered to be of uncertain familial relationship, was placed in Flacourtiaceae by Lemke (1983, 1987a) and is here allied with Homalieae, as is *Bartholomaea*, a neotropical genus of two species which was placed in Scolopieae by Hutchinson (1967) and in Caseariae by Sleumer (1980). Careful examination of the small staminate flowers of *Bartholomaea* (Lemke 1987b) revealed that they have the antepetalous fascicles of stamens alternating with disk glands characteristic of many other members of the tribe. The monotypic genus *Homaliopsis* S. Moore, included in Homalieae by Gilg (1925) and Hutchinson (1967), has been shown by Sleumer (1969) to be conspecific with *Tristania suaveolens* Sm. (Myrtaceae) and is here removed from the tribe.

Two groups of genera can be recognized within Homalieae. One, comprising *Byrsanthus*, *Calantica*, *Dissomeria*, *Gerrardina*, and *Homalium*, is characterized by pinnately veined leaves and relatively large, perfect flowers. The second, consisting of *Bartholomaea*, *Neopringlea*, and *Trimeria*, is characterized by leaves 3–5-nerved from the base and small, imperfect flowers. Further study may show these groups to deserve subtribal rank, but they are not so recognized here.

Scolopieae include those genera with perianth parts arranged in separate whorls and distinguishable from one another, the petals equal in number to the sepals or, if more numerous, then regularly arranged in relation to them, the stamens usually numerous and never fascicled. A relationship to Homalieae can be seen through *Mocquerysia*, an African genus with flowers that have five sepals, five petals, and five antepetalous stamens, but which has an inflorescence that is adnate to the midrib of a large subtending bract as in several other members of Scolopieae, and which lacks the antesealous disk glands.

Warburg (1894) and Gilg (1925) placed *Streptothamnus* in Scolopieae, but the genus is here excluded on the basis of wood anatomy and pollen morphology, as noted above, and placed in Berberidopsidae. Both Gilg (1925) and Hutchinson (1967) included *Dioncophyllum* Baill. *sensu lato* in Scolopieae, but this genus too is excluded on morphological and anatomical grounds (Metcalf 1952) and referred to Dioncophyllaceae following Cronquist (1981). *Sabournaea* J. Leandri, placed in Scolopieae by Hutchinson (1967), is synonymous with *Talinella* Baill. and referred to Portulacaceae (Willis 1966). The transfer of *Bartholomaea*, included in Scolopieae by Hutchinson (1967), to Homalieae makes the tribe a morphologically and geographically homogeneous group, restricted in distribution to the Old World tropics.

Prockieae are an enigmatic group of genera whose relationships are not fully understood. While *Hasseltiopsis*, *Macrohasseltia*, *Pineda*, and *Pleuranthodendron* have a unilocular ovary with parietal placentation, the ovary of *Prockia* and *Hasseltia* is characterized by axile placentation. This feature led Hutchinson (1967) to remove the entire tribe from Flacourtiaceae and transfer it to Tiliaceae. Sleumer (1938, 1980) treated Prockieae as a tribe of Flacourtiaceae, questioning whether the septa are primary (ovules borne on a true axile placenta) or secondary (ovules borne on parietal placentae, these protruding into the locule and fused, forming a central pseudoaxis). Support for the latter position comes from an examination

of *Banara* and *Neosprucea*, in which the ovary is incompletely 2–9-loculed by intrusion of the parietal placentae and from an ontogenetic study by Lemke and Vodicka-Asbury (unpubl.) which demonstrated that in *Hasseltia floribunda* H.B.K. the intruding parietal placentae eventually meet in the center of the locule, giving rise to a 2-chambered ovary in the mature flower.

The similarity of the secondary xylem of *Prockia* and *Banara* to that of Homalieae and Scolopieae has already been noted. Miller (1975) reported, however, that the wood structure of Prockieae could also support its placement in Elaeocarpaceae. A comparison of the xylem anatomy of Tiliaceae and Elaeocarpaceae (Kukachka and Rees 1943) with that of Prockieae suggests a close alliance between Prockieae and Elaeocarpaceae. Keating (1973) noted that Scolopieae, Homalieae, Prockieae, and Flacourtiaceae have very similar pollen morphology. He also pointed out that the pollen of Homalieae (and presumably, therefore, of Prockieae as well) is very similar to that of Elaeocarpaceae. Evidence from xylem anatomy and pollen morphology thus seems to suggest that Prockieae are allied to both Flacourtiaceae and Elaeocarpaceae. As Cronquist (1981) noted, "all these genera remain in the indefinite boundary-land between the highly diversified family Flacourtiaceae and the more narrowly limited family Elaeocarpaceae." The present author chooses to retain Prockieae in Flacourtiaceae at this time.

The monotypic Asian genus *Plagiopteron* Griff., a climbing shrub with opposite leaves, was placed in Prockieae by Hutchinson (1967) but seems anomalous in this tribe on account of its habit, morphology, and distribution. A recent morphological, anatomical, and palynological study of the genus (Baas, Geesink, van Heel, and Muller 1979) found some similarities to Flacourtiaceae, but concluded that the placement of *Plagiopteron* as a monotypic family in the Malvales, with a position close to Elaeocarpaceae, was supported by a preponderance of the evidence. The genus is here excluded from Flacourtiaceae and referred instead to Plagiopteraceae (Airy Shaw 1965). With the removal of *Plagiopteron*, Prockieae become a morphologically better-defined group, limited in distribution to the New World tropics.

Hutchinson's (1967) classification established a new tribe, Banareae, comprising *Asteropeia* Thouars, *Banara*, *Pineda*, and *Trimeria*, which had not been recognized by either Warburg or Gilg, but which has been treated as a distinct taxon in recent studies of the family (Keating 1973; Miller 1975; Spencer and Seigler 1985b). Banareae are a highly artificial group and are not recognized in the present treatment. *Banara* and *Pineda* are neotropical genera with perfect flowers, sepals and petals in distinct whorls, and numerous stamens; they are here referred to Prockieae. *Trimeria* is an African genus with small, imperfect flowers and stamens in antepetalous fascicles of 2–3 alternating with pilose nectar-glands; the genus is here placed in Homalieae. *Asteropeia*, a genus of ca. five species endemic to Madagascar, is referred to Theaceae, following Cronquist (1981). Studies of xylem anatomy (Miller 1975) and pollen morphology (Erdtmann 1971; Keating 1973) support these placements.

The third group of tribes within Flacourtiaceae comprises Flacourtiaceae, Casarieae, and Bembicieae. All members of these tribes have small, apetalous flowers, relatively specialized wood (Miller 1975) and pollen (Keating 1973) features, and presumably represent the most highly derived genera within the family. The tribes are distinguished primarily on the basis of ovary position (superior in

Flacourtiaceae, more or less half-inferior in Caseariae, completely inferior in Bembiciaceae), although wood and pollen characteristics support this arrangement.

Flacourtiaceae are an interesting group, which, although clearly differentiated morphologically from the other tribes of Flacourtiaceae, may occupy a somewhat transitional place among them. Sleumer (1972) noted a strong morphological resemblance between *Ludia* (Flacourtiaceae) and *Scolopia* (Scolopiaceae) while Miller (1975) felt the xylem structure of Flacourtiaceae to be transitional between the generalized structure of such putatively primitive tribes as Oncobeeae and the more highly specialized xylem of Caseariae. Evidence from chemotaxonomy also supports a transitional position for Flacourtiaceae. Cyclopentenyl fatty acids ("chaulmoogra oils") have long been known from Oncobeeae and Pangieae and were thought to be restricted to those tribes. Recently, however, they have been isolated from species of *Azara*, *Dovyalis*, and *Flacourtia* (Rehfeldt, Schulte, and Spener 1980).

Warburg (1894), Gilg (1925), Hutchinson (1967), Takhtajan (1980), and Cronquist (1981) included the monotypic African genus *Aphloia* (DC.) Benn. (= *Neumannia* A. Rich.) in Flacourtiaceae. Miller (1975) reported that in terms of wood anatomy the genus has many unspecialized features and is most similar to *Berberidopsis* and *Streptothamnus*, yet the floral morphology is specialized. *Aphloia* is characterized by apetalous flowers with the stamens reduced to a single whorl, an apparently unilocular gynoecium, and seeds containing a horseshoe-shaped embryo and scanty endosperm. The genus probably arose from the same ancestral stock as did Flacourtiaceae and retained the generalized wood structure found in certain members of that family while developing a specialized floral morphology. The combination of morphological and anatomical features found in *Aphloia* makes the genus anomalous in Flacourtiaceae, and I concur with Miller (1975) in referring the genus instead to the monotypic Neumanniaceae Van Tiegh. *Quadraria* Elmer, included in Flacourtiaceae by Gilg (1925), is synonymous with *Claoxylon* Juss. and is referred to Euphorbiaceae (Willis 1966).

Caseariae consist of the large, taxonomically difficult genus *Casearia*, with ca. 180 species and a number of much smaller genera. *Stapfiella* Gilg was included in the tribe by Gilg (1925), but is now placed in Turneraceae (Willis 1966). With the transfer of *Bartholomaea*, included in Caseariae by Sleumer (1980), to Homalieae as noted above, the tribe becomes a very natural group characterized by a homogeneous set of morphological and wood anatomical features.

Bembiciaceae contain a single species, *Bembicia axillaris* Oliver, a small tree native to Madagascar, which has a conelike inflorescence composed of many imbricate, coriaceous bracts, each subtending a single apetalous flower with a completely inferior ovary. Although the wood structure of this poorly collected genus is unknown and the pollen morphology has been treated only cursorily (Erdtmann 1971), it is here retained provisionally in Flacourtiaceae. *Bembiciopsis* H. Perrier, included in Flacourtiaceae by Hutchinson (1967) and Cronquist (1981), is referred instead to Theales.

Several taxa, placed in Flacourtiaceae by previous authors, are here excluded from the family. These include the tribes Alzateae, Paropsieae, Abatieae, Trichostephaneae, and Lacistemeae, and the genus *Lethedon* Spreng.

Alzatea Ruiz & Pavon has long been of uncertain systematic position, having been placed in as many as eight different families in five orders (Lourteig 1965).

Hutchinson (1967) recognized the genus as constituting a new tribe of Flacourtiaceae however, recent studies of its morphology, anatomy, pollen morphology, and embryology have led to its placement in the monotypic family Alzateaceae, with a somewhat isolated position in the Myrtales (Graham 1984). This disposition is followed here.

Paropsieae were included as a tribe of Flacourtiaceae by Warburg (1894) and Gilg (1925), but treated as belonging to Passifloraceae by Hutchinson (1967), while Abatieae were included in Flacourtiaceae by all of these authors. With respect to growth habit (shrubs or small trees) the members of both tribes are admittedly anomalous in Passifloraceae, yet the presence of an extrastaminal corona militates against their inclusion in Flacourtiaceae. Evidence from studies of gross morphology (De Wilde 1971), wood anatomy (Ayensu and Stern 1964), and pollen morphology (Erdtmann 1971; Keating 1973) indicates that many of the genera included in these tribes are transitional between the two families and that they perhaps form a connecting link. I concur with Cronquist's (1981) statement that it seems more useful to draw the arbitrary distinction between Flacourtiaceae and Passifloraceae on the basis of the presence or absence of a corona rather than on growth habit, and I favor the inclusion of these two tribes in the latter family.

The poorly known, monotypic African genus *Trichostephanus* Gilg (Trichostephaneae), described and illustrated by Gilg (1925), seems anomalous in Flacourtiaceae. The solitary, imperfect flowers have four unequal, decussate sepals, no petals, and numerous stamens which are connate among themselves and adnate to the lobes of the intrastaminal corona to form an annulus. The genus does not fit comfortably into Flacourtiaceae as the family is here circumscribed, and until further studies of its wood anatomy, pollen morphology, and chemical constituents have been completed I prefer to treat *Trichostephanus* as a *genus incertae sedis* with affinities in the Violales.

The taxonomic position of *Lacistema* Swartz and *Lozania* S. Mutis has been much disputed, although recent authors (Takhtajan 1980; Cronquist 1981; Thorne 1981) are in agreement that their affinities lie with the Violales. Krause (1925) believed these genera to be related to Flacourtiaceae through *Prockia*, and Sleumer (1980) included them in the family as the tribe Lacistemeae. In terms of xylem structure (Metcalf and Chalk 1950), most of the features of Lacistemeae, such as radial multiples of very long vessel elements with small to moderately small diameters, scalariform perforation plates, opposite intervacular pitting with small pits, septate fibers, and heterogeneous rays, can be found in Flacourtiaceae (but not in that combination), although their apotracheal parenchyma is anomalous. Morphologically, however, *Lacistema* and *Lozania* are quite specialized. The small, perfect flowers have 1–6 sepals, no petals, a single stamen borne on the inner side of a concave to cup-shaped disk, the thecae often widely separated by an enlarged connective, and a unilocular, superior ovary of 2–3 united carpels. They seem to represent another evolutionary line which had its origin in the same ancestral stock as Flacourtiaceae but which developed a highly specialized floral morphology. I prefer to segregate these genera as the family Lacistemaceae Martius, following Cronquist (1981), while recognizing their affinities to Flacourtiaceae.

Warburg (1894), with some degree of uncertainty, placed *Lethedon* Spreng.

(=*Microsemma* Labill.) in Flacourtiaceae, but later authors have generally followed Gilg (1925) in excluding the genus from that family and referring it instead to Thymeleaceae or the closely related Aquilariaceae. Recently, however, Spencer and Seigler (1985b) found *Lethedon* to be cyanogenic and advocated its transfer back to Flacourtiaceae. This disposition, based upon a single character, is not supported by the preponderance of available evidence. The wood anatomy and pollen morphology of *Lethedon*, examined by Miller (1975) and Erdtmann (1971), respectively, are definitely not flacourtiaceous, while the floral morphology (Hutchinson 1967) is not incompatible with a placement in Thymeleaceae. In the present treatment the genus is therefore excluded from Flacourtiaceae.

With the exclusion of Alzateae, Paropsieae, Abatieae, Trichostephanaceae, and Lacistemeae, Flacourtiaceae become a better-defined family comprising 10 well-delimited tribes. Although the family, as circumscribed herein, is admittedly polythetic, and perhaps polyphyletic as well, I believe that the present treatment more accurately reflects the current state of our understanding than do the schemes of Warburg, Gilg, or Hutchinson. As our knowledge of the family increases, future studies will doubtlessly suggest realignments of various genera and the inclusion or exclusion of certain taxa. I hope that the present study will stimulate more interest in this diverse, yet poorly known family, and will provide a foundation for such studies.

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