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SYNOPSIS OF THE GENERA AND SUPRAGENERIC TAXA OF EUPHORBIACEAE¹

Grady L. Webster²

ABSTRACT

This revised synopsis of the taxa of Euphorbiaceae recognizes, and provides keys to, 5 subfamilies, 49 tribes, and 317 genera. Two new tribes, Crozatieae and Podocalyceae, are proposed, as well as four new subtribes, Leptopinae, Podocalycinae, Pycnocominae, and Tetracoccinae; five taxa are reduced to subtribal status. One genus (*Ophellantha*) is reduced to a section; 14 new binomial combinations are proposed. Lectotypifications are provided for almost all taxa not previously typified.

The synoptic classification given here provides keys to and descriptions of the taxa of Euphorbiaceae at the subfamilial, tribal, and subtribal levels. It represents an extension and, in places, a considerable revision of the synoptic classification in which the five subfamilies were first recognized (Webster, 1975). Within the tribes and subtribes, keys are provided to the genera, and these are enumerated with citation of important synonyms. Keys are intended to provide the salient diagnostic characters of taxa, but do not necessarily allow for exceptions; in some instances, they may be of limited use in identifying unknown specimens to genus. Citations of synonyms and relevant works have been deliberately kept brief and are not intended to be all-inclusive; by and large, only strictly systematic papers are cited. Some obscure synonyms, including most of the names proposed by Rafinesque and Otto Kuntze, have been omitted. Typifications follow *Index Nominum Genericorum* (Farr et al., 1979); new typifications or alterations of entries in *ING* are explicitly noted. Generic concepts are relatively conservative; i.e., traditional usage is followed where possible. In borderline cases, genera are enumerated as distinct even though their claim to generic status may be questionable; listing of taxa here is therefore not intended to be canonical. A list of new taxa and an index to the genera and higher taxa are given in the appendices to this article.

Euphorbiaceae A. L. de Jussieu, Gen. Pl. 384.
1789. TYPE: *Euphorbia* L.

Monoecious or dioecious trees, shrubs, or herbs (some climbing or twining); stems sometimes succulent and/or with latex. Leaves alternate or opposite (rarely whorled); stipules free (less commonly connate or absent), deciduous or persistent; leaf blades pinnately or palmately veined, entire to dentate or palmately lobed or compound; indumentum simple to stellate or lepidote (sometimes absent). Inflorescences terminal or axillary, basically cymose; flowers solitary or in glomerules, these often grouped into spiciform or capitate thyrses or pseudanthia; bracts often glandular. Flowers unisexual, actinomorphic (but pseudanthia often zygomorphic); perianth segments free or connate, valvate or imbricate, sometimes reduced or absent; sepals and petals (1-)3-6(-8), sometimes distinctly colored; disk present or absent, intrastaminal or extrastaminal, entire to dissected; stamens (1-)3-50(-400) [always 1 in *Euphorbia*], hypogynous; filaments free or connate; anthers mostly 2-locular and dehiscing longitudinally, introrse or extrorse; pollen grains tectate or semi-TECTATE, mostly 3-colporate (inaperturate to polytrema); gynoecium syncarpous, ovary (1-)2-5(-20)-locular; placentation axile; ovules 1 or 2 per locule, anatropous or hemitropous (orthotropous in *Panda*), inserted beneath an obturator, crassinucellate with 2 integ-

¹ I express my gratitude to John Hayden and Geoffrey Levin for reviewing the treatment of the Oldfieldioideae, Lynn Gillespie for tribe Plukenetieae, and Daryl Koutnik for tribe Euphorbieae. Their suggestions have led to some important modifications in circumscriptions and interpretations of taxa. I am also particularly indebted to Michael Huft and Geoffrey Levin for their critical reviews of the manuscript, to Geoffrey Levin for compiling the index, and to Robert Rhode for help in formatting the text.

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uments, nucellus often beaked, embryo sac mostly 8-nucleate; styles free or connate, entire to lobed or multifid. Fruit typically a capsular schizocarp with mericarps elastically dehiscent from a persistent columella, but sometimes baccate or drupaceous; seeds 1 or 2 per locule (rarely 1 per fruit); seed coat thin to indurate, sometimes with a sarcotesta; endosperm present or absent; embryo straight to curved or folded; cotyledons usually broader than radicle.

The family Euphorbiaceae is here construed as having 317 genera associated into 49 tribes in 5 subfamilies. A reflection of the diversity of the family is that over 20 segregate families have been proposed (Webster, 1987). Hurusawa (1954) was the first modern author to propose a major dismantling of the family, with his recognition of Antidesmataceae, Euphorbiaceae (sensu stricto), Porantheraceae, and Ricinocarpaceae. This system, based on inflation of the subfamilies of Pax & Hoffmann (1931), has met with little acceptance.

More influential have been the efforts of Airy Shaw, who recognized seven segregate families: Androstachydeae, Bischofiaceae, Hymenocardiaceae, Peraceae, Picrodendraceae, Stilaginaceae, and Uapacaceae (Airy Shaw, 1965, 1966). Among modern authors, the most extreme splitter is Meeuse (1990), who recognizes nine segregate families, plus the Pandaceae. Radcliffe-Smith in Carter & Radcliffe-Smith (1988) partially followed Airy Shaw in recognizing the Hymenocardiaceae and Pandaceae, but treats *Antidesma*, *Bischofia*, and *Uapaca* as anomalous genera of Euphorbiaceae. Of all these segregate taxa, only the family Pandaceae is recognized as distinct by Cronquist (1981) and Takhtajan (1980).

KEY TO THE SUBFAMILIES OF EUPHORBIACEAE

- 1a. Locules of ovary each with 2 ovules (except in *Scagea*); milky latex, intraxylary phloem, and stinging hairs absent; indumentum simple or rarely lepidote or dendritic; embedded foliar glands rare; pollen grains binucleate.
- 2a. Leaves alternate (very rarely opposite), stipulate, blade simple and unlobed (trifoliate in *Bischofia*); petals present or absent; pollen grains tricolporate to porate, sexine not with conspicuous spines (irregularly spiny in *Amanoa*); seeds ecarunculate I. PHYLLANTHOIDEAE
- 2b. Leaves alternate, opposite, or whorled, stipulate or exstipulate, blade simple or trifoliate; petals absent (except in *Croizatia*); pollen grains colpoidorate to porate, sexine spiny; seeds carunculate or ecarunculate, endosperm copious (except in *Hyaenanche* and *Picrodendron*) II. OLDFIELDIOIDEAE

- 1b. Locules of ovary each with 1 ovule (except in *Dicoelia*); latex present or absent; indumentum various; pollen grains binucleate or trinucleate.
- 3a. Milky latex absent; laticifers (if present) inarticulate; leaves unlobed or lobed; indumentum simple or stellate; petals present or absent; pollen grains binucleate, mostly tricolporate or triporate III. ACALYPHOIDEAE

- 3b. Latex milky or colored (rarely absent); laticifers articulate or inarticulate; leaves unlobed to compound; pollen grains binucleate or trinucleate.
- 4a. Latex reddish or yellowish to milky (sometimes scanty or absent); laticifers articulate or inarticulate; leaves unlobed to lobed or compound; indumentum simple, stellate, dendritic, or lepidote; bracts usually not biglandular at base; sepals imbricate to valvate, usually completely covering anthers in bud; petals mostly present (at least in staminate flower); pollen grains tricolporate or more often porate or inaperturate, with "crotonoid" pattern of exinous processes IV. CROTONOIDEAE

- 4b. Latex whitish, often caustic or toxic; laticifers inarticulate; leaves usually unlobed; indumentum simple or absent, never stellate or lepidote (dendritic in *Mabea*); bracts often biglandular at base; sepals imbricate or reduced, anthers mostly not covered in bud; petals absent; pollen grains tricolporate, sexine mostly perforate-reticulate, never with "crotonoid" pattern V. EUPHORBIOIDEAE

Subfamily I. PHYLLANTHOIDEAE Ascherson, Fl. Prov. Brandenburg 1: 59. 1864.
TYPE: *Phyllanthus* L.

Euphorbiaceae subordo Dispermae Zoll., Natur-Geenesk. Arch. Ned.-Indië 2: 17. 1845.

Phyllanthaceae J. G. Agardh, Theor. Syst. Pl. 249. 1858 (as Phyllanthae); Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Berlin 1859: 246. 1859.

Trees, shrubs, or herbs; indumentum simple (rarely branched; lepidote in *Hyeronima* and *Uapaca*); leaves alternate (very rarely opposite), spiral to distichous, usually stipulate; leaf blade simple, entire (except in *Drypetes* and *Bischofia*), without embedded foliar glands. Inflorescences axillary (rarely terminal), mostly racemiform or spiciform, or reduced to glomerules or solitary flowers; bracts eglandular, mostly inconspicuous. Sepals mostly 4–6, imbricate, sometimes connate; petals and disk present or absent; stamens (2–)4–8(–50), filaments free or united; pollen grains mostly 3–4-colporate (rarely porate; periporate in *Phyllanthus*), exine semitectate, rarely echinate; male ga-

metophyte binucleate; pistillode present or absent; carpels (1-)2-5(-20); styles mostly free except at base, usually bifid; ovules 2 in each locule, anatropous or hemitropous, nucellar beak sometimes prominent. Fruit capsular or less commonly baccate or drupaceous; seeds ecarunculate or with rudimentary caruncle; endosperm present or absent; cotyledons plane or folded. Base chromosome numbers mostly 12 or 13.

This large "basal" subfamily of Euphorbiaceae is so diverse that Meeuse (1990) proposed dividing it into six separate families. The 60 genera included are grouped into 10 tribes, a reduction from Webster (1975), where 13 tribes were recognized. The work of Levin (1986a, b, c) has shown that some proposed tribes need to be incorporated as subtribes within the Antidesmeae.

KEY TO THE TRIBES AND SUBTRIBES OF SUBFAMILY PHYLLANTHOIDEAE

- 1a. Leaves simple, mostly entire; styles usually bifid.
 - 2a. Flowers in axillary clusters (inflorescence axes less than 1 cm long except in some Phyllanthaeae); seeds with or without endosperm; leaves mostly with paracytic stomata, lacking tanniferous epidermal cells.
 - 3a. Staminate disk extrastaminal or absent; leaves entire; ovary 2-3(-6)-locular; fruit mostly capsular or baccate, less commonly drupaceous.
 - 4a. Petals present, at least in staminate flowers; sepals imbricate; wood parenchyma conspicuous, fibers mostly thick-walled; vessel element perforations scalariform or simple; ovules anatropous; endosperm present or absent.
 - 5a. Pollen exine finely reticulate, not coarsely spinose; stipules deciduous 1. WIELANDIEAE
 - 5b. Pollen exine coarsely and deeply reticulate or spinose; stipules persistent 2. AMANOEAE
 - 4b. Petals absent, or if present then sepals valvate, or wood and ovule characters otherwise; endosperm usually present.
 - 6a. Sepals valvate; petals present, usually shorter than sepals 3. BRIEDELIEAE
 - 6b. Sepals imbricate; petals absent, or if present then often as long as sepals 4. PHYLLANTHEAE
 - 3b. Staminate disk intrastaminal; leaves often dentate; wood fibers thick-walled, not septate; fruit drupaceous; ovary 1-2-locular 5. DRYPETEAE
 - 2b. Flowers in axillary or terminal spicate or racemose inflorescences (axis usually over 1 cm long; capitata in *Uapaca*); petals absent (or if present, inflorescence terminal); leaves with stomata paracytic or anomocytic; seeds with endosperm.
 - 7a. Fruits not winged; leaves with tanniferous epidermal cells, not granulose-glandular; floral disk present or absent; pollen 3-colporate; styles usually bifid 6. ANTIDESMEAE
 - 7b. Fruits winged, samaroid; leaves granulose-glandular, without tanniferous epidermal cells; inflorescences amentlike; floral disk absent; pollen zonoporate; styles unlobed 7. HYMENOCARDIEAE
- 1b. Leaves trifoliolate; inflorescence paniculate; flowers apetalous, floral disk absent; styles entire; fruits baccate 8. BISCHOFIEAE

Tribe 1. WIELANDIEAE Baillon ex Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 339. 1954. Wielandiidae Baillon, Etude Gén. Euphorb. 568. 1858. Phyllanthaeae subtribe Wielandiinae Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 180. 1922. TYPE: *Wielandia* Baillon.

Monoecious or dioecious trees or shrubs; indumentum simple; leaves alternate, entire, penninerved, eglandular; stipules deciduous. Inflorescences axillary; flowers in glomerules or the pistillate solitary; bracts inconspicuous. Sepals mostly 4-6, imbricate; petals usually 5; disk usually annular; stamens 5-10, free or filaments connate at base; anthers dehiscing longitudinally, connective not enlarged; pollen grains 3-colporate, semitectate, reticulate; pistillode present; carpels 3-5; styles bifid;

ovules anatropous, usually with a single obturator. Fruit capsular; seeds 1 or 2 per locule; endosperm present or absent; embryo with cotyledons plane or folded, much longer than the radicle.

The taxa with the greatest numbers of unspecialized morphological features are gathered together in this tribe, which is unified on the basis of pollen morphology (Köhler, 1965) and leaf venation (Levin, 1986a, b, c). It is probably paraphyletic in cladistic terms, which is essentially inevitable for the basal tribe in a large family such as the Euphorbiaceae. Relationships among the nine genera appear reticulate, and it does not seem feasible to group them into subtribes. It is notable that all of the genera occur in South America, Africa, and the Indian Ocean islands, and only *Savia* extends into the Northern Hemisphere.

KEY TO THE GENERA OF TRIBE WIELANDIEAE

- 1a. Seeds with endosperm.
 - 2a. Stamens 8-10; sepals and petals mostly 4, very similar; ovary 4-5-locular 1. *Heywoodia*

- 2b. Stamens mostly 5; sepals and petals mostly 5; ovary mostly 3-locular.
 3a. Pistillate disk entire, not glandular 2. *Savia*
 3b. Pistillate disk glandular-lobed 3. *Gonatogyne*
- 1b. Seeds with little or no endosperm.
 4a. Staminate disk dissected 4. *Petalodiscus*
 4b. Staminate disk annular, sometimes lobed
 5a. Ovary 3- or 4-locular.
 6a. Monoecious.
 7a. Leaves coriaceous; petals longer than sepals; stamens free except at base 5. *Blotia*
 7b. Leaves chartaceous; petals shorter than sepals; stamens connate into a column 6. *Actephila*
 6b. Dioecious; leaves coriaceous.
 8a. Petals present; staminate flowers pedicellate.
 9a. Styles dilated; staminate disk glabrous; stamens free from pistillode 7. *Discocarpus*
 9b. Styles slender; staminate disk pubescent; stamens adnate to pistillode 8. *Lachnostylis*
 8b. Petals absent; staminate flowers subsessile 9. *Chonocentrum*
 5b. Ovary 5-locular 10. *Wielandia*

1. **Heywoodia** Sim, For. Fl. Cape Col. 326, pl. 140. 1907; Pax & Hoffm., Pflanzenr. 147. XV. (Heft 81): 280. 1922; Hutchinson, Kew Bull. 1922: 114. 1922; Milne-Redhead, Bull. Jard. Bot. Brux. 27: 327, pl. X. 1957; Radcliffe-Smith, Fl. Trop. E. Afr., Euphorb. 1: 85, fig. 12. 1987. TYPE: *Heywoodia lucens* Sim.

Monotypic; Uganda and Kenya south to Natal and Transkei. On the basis of foliar venation characters, Levin (1986b) suggested a relationship between *Heywoodia* and *Astrocasia*, and regarded both genera as closer to the tribe Phyllanthaeae. There are indeed some resemblances between *Heywoodia* and *Astrocasia*, but the former genus seems the more primitive, and appears to me as perhaps nearest in morphological characters to the hypothetical ancestor of the family. This would not preclude an affinity with *Astrocasia*, which may connect the tribes Wielandiaeae and Phyllanthaeae.

2. **Savia** Willdenow, Sp. Pl. 4: 771. 1805; Muell. Arg. in DC. Prodr. 15(2): 228. 1866; Bentham, Gen. Pl. 3: 270. 1880; Fawc. & Rend., Fl. Jam. 4: 271. 1920; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 181. 1922; Urban, Repert. Sp. Nov. 28: 209. 1928; Alain, Fl. Cuba 3: 41. 1953; Webster, J. Arnold Arbor. 48: 325. 1967; Taxon 31: 535. 1982; Radcliffe-Smith, Kew Bull. 27: 508. 1972; Fl. Trop. E. Afr., Euphorb. 1: 83, fig. 11. 1987. TYPE: *Savia sessiliflora* (Sw.) Willd.

Kleinodendron Smith & Downs, Sellowia 16: 177. 1964. TYPE: *Kleinodendron riosulense* Smith & Downs [= *Savia dictyocarpa* Muell. Arg.].

About 25 species of America, Africa, and Madagascar. Three sections have been recognized: sect. *Savia*, 2 spp., the type and *S. dictyocarpa* of Brazil; sect. *Heterosavia* Urb., ca. 20 spp. of the

West Indies and Madagascar; and the recently described sect. *Afrosavia* Radcl.-Sm. of Kenya (which as noted below actually belongs to *Petalodiscus*). A number of other genera of tribe Wielandiaeae have been included in *Savia* by Mueller and other workers.

3. **Gonatogyne** Muell. Arg., Fl. Bras. 11(2): 13. 1873; Pax & Hoffm., Repert. Sp. Nov. 31: 190. 1933. *Savia* sect. *Gonatogyne* ("Klotzsch") Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 187. 1922. TYPE: *Gonatogyne brasiliensis* (Baillon) Muell. Arg. [*Amanoa*? *brasiliensis* Baillon].

Monotypic; Brazil.

4. **Petalodiscus** (Baillon) Pax, Natürl. Pflanzenfam. I. 3(5): 15. 1890. *Savia* sect. *Petalodiscus* Baillon, Etude Gén. Euphorb. 571. 1858. TYPE: *Petalodiscus platyrhachis* (Baillon) Pax (lectotype, selected here; this was the species illustrated by Pax, loc. cit.).

A genus of five or six species endemic to Madagascar; combined with *Savia* by Pax & Hoffmann (1922, 1931) and Leandri (1958), but differing from *Savia* in being monoecious and having exalbuminous seeds.

5. **Blotia** Leandri, Mém. Inst. Sci. Madag. 88: 240. 1957; Fl. Madag. 111: 126. 1958. *Savia* sect. *Charidia* Baillon, Etude Gén. Euphorb. 572. 1858; Muell. Arg., DC. Prodr. 15(2): 229. 1866. *Petalodiscus* sect. *Charidia* (Baillon) Pax, Natürl. Pflanzenfam. I. 3(5): 15. 1890. TYPE: *Blotia oblongifolia* (Baillon) Leandri [*Savia oblongifolia* Baill.].

This genus of five or six Madagascan species is closely related to *Petalodiscus* and may not be distinct.

6. **Actephila** Blume, Bijdr. Fl. Ned. Ind. 581. 1825; Muell. Arg., DC. Prodr. 15(2): 221. 1866; Baillon, Adansonia I. 6: 231. 1866; Bentham, Gen. Pl. 3: 269. 1880; J. J. Smith, Add. Cogn. Fl. Arb. Jav. 12: 45. 1910; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 191. 1922; Airy Shaw, Kew Bull. 25: 496. 1971; Kew Bull. Add. Ser. 8: 21. 1980. TYPE: *Actephila javanica* Miq.

Anomospermum Dalzell, Hook. J. Bot. Kew Gard. Misc. 3: 228. 1851 (non Miers, 1851). TYPE: *Anomospermum excelsum* Dalz. [= *Actephila excelsa* (Dalz.) Muell. Arg.].

An Asian/Australasian genus of ca. 20 described species, still poorly understood taxonomically. The position of the genus has been variously interpreted. Pax & Hoffmann (1922) associated it with *Amanoa*, which has similar flowers but very different pollen. Köhler (1965) pointed out a palynological similarity to *Andrachne*, and Levin (1986 a, b, c) found a resemblance in leaf venation to that genus. However, the exalbuminous seeds with plicate embryo of *Actephila* would appear to rule out a close association with *Andrachne*. It is worth noting that Mennega (1987) recommended assignment of *Actephila* to the *Wielandieae*. For the present, it seems best to retain *Actephila* in the tribe *Wielandieae*.

7. **Discocarpus** Klotzsch, Arch. Naturgesch. 7: 201. 1841; Muell. Arg., DC. Prodr. 15(2): 223. 1866; Fl. Bras. 11(1): 11, t. 2. 1873; Benth., Gen. Pl. 3: 269. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 202. 1922; Jablonski, Mem. New York Bot. Gard. 17(1): 84. 1967. TYPE: *Discocarpus essequiboensis* Klotzsch.

According to the recent treatment of Jablonski, the five species of *Discocarpus* are restricted to the Amazonian/Guianan region of South America. The phylogenetic position of *Discocarpus* is somewhat uncertain. Pax & Hoffmann (1922) assigned it to a separate subtribe (including *Lachnostylis*); Köhler (1965) suggested it was close to *Amanoeae* and *Brideliaceae*; and Mennega (1987) regarded it as out of place in the *Wielandieae*.

8. **Lachnostylis** Turczaninow, Bull. Soc. Imp. Naturalistes Moscou 19: 503. 1846; Muell. Arg., DC. Prodr. 15(2): 224. 1866; Bentham, Hook. Ic. Pl. 13: 61, t. 1279. 1879; Gen. Pl. 3: Dyer, Gen. S. Afr. Fl. Pl. 1: 309. 1975. TYPE: *Lachnostylis capensis* Turcz. [= *Lachnostylis hirta* (L.) Muell. Arg.].

This genus, endemic to South Africa, includes a single variable species or, according to some workers (e.g., Dyer), two species. Although combined with *Discocarpus* by Pax & Hoffmann (1922), it differs in a number of characters.

9. **Chonocentrum** Pierre ex Pax & Hoffmann, Pflanzenr. 147. XV (Heft 81): 205. 1922; Jablonski, Mem. New York Bot. Gard. 17: 121. 1967. TYPE: *Chonocentrum cyathophorum* (Muell. Arg.) Pax & Hoffm. [*Drypetes cyathophora* Muell. Arg.].

A monotypic genus of Amazonian South America, regarded by Pax & Hoffmann as related to *Discocarpus*; however, the pollen is still unstudied, and its relationships must be regarded as uncertain.

10. **Wielandia** Baillon, Etude Gén. Euphorb. 568. 1858; Bentham, Gen. Pl. 3: 270. 1880; Hemsley, Hook. Ic. Pl. 29: t. 2813. 1906; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 181. 1922; Leandri, Notul. Syst. (Paris) 7: 190. 1939; Fl. Madag. 111(1): 135. 1958. TYPE: *Wielandia elegans* Baillon.

Monotypic; restricted to Madagascar and the Seychelles. Although combined with *Savia* by Mueller, *Wielandia* appears closer to *Petalodiscus* by virtue of its exalbuminous seeds and monoecious flower production.

- Tribe 2. AMANOEAEE** (Pax & Hoffmann) Webster, Taxon 24: 594. 1975. Phyllanthaceae subtribe *Amanoinae* Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 190. 1922. TYPE: *Amanoa* Aublet.

Monoecious trees; indumentum simple (extremely scarce to absent); leaves alternate, simple, entire, penninerved, eglandular; stipules persistent, sometimes adnate to petiole. Flowers in glomerules, these sometimes forming spikes; bracts conspicuous or inconspicuous. Sepals and petals 5, imbricate; staminate disk annular or dissected; stamens 5, free; anthers introrse; pollen grains tricolporate, very coarsely reticulate or irregularly spinose; pistillode prominent; pistillate disk cupular; ovary 3-locular; ovules anatropous; styles twice bifid or dilated, emarginate; fruit a tardily dehiscent capsule; seeds 1 per locule; endosperm present, scanty or absent; cotyledons massive but not plicate, much longer than radicle.

As here interpreted, the tribe *Amanoeae* includes the genera *Amanoa* and *Pentabrachion*. In the original circumscription of the tribe (Webster,

1975), *Actephila* was also included. However, evidence from pollen morphology (Köhler, 1965), leaf venation (Levin, 1986a, b, c), and wood anatomy (Mennega, 1987) argues against a close association of *Amanoa* and *Actephila*.

KEY TO THE GENERA OF TRIBE AMANOEAE

- 1a. Stipules not intrapetiolar; floral bracts inconspicuous, not indurate; styles slender, twice bifid; fruit thin-walled, seeds 2 per locule, endosperm present 11. *Pentabrachion*
- 1b. Stipules \pm intrapetiolar; floral bracts conspicuous, indurate; styles dilated, emarginate; fruit thick-walled, seeds 1 per locule; endosperm absent 12. *Amanoa*

11. *Pentabrachion* Muell. Arg., *Flora* 47: 532. 1864; DC. *Prodr.* 15(2): 223. 1866 (as *Pentabrachium*); Pax & Hoffm., *Pflanzenr.* 147. XV (Heft 81): 188. 1922. TYPE: *Pentabrachion reticulatum* Muell. Arg.

Monotypic; West Africa (Cameroon, Gabon). Levin (1986a, b, c) suggested a possible relationship to *Dicoelia* on the basis of foliar venation characters, but this is not supported by pollen characters (Köhler, 1965). Indeed, Köhler associated *Pentabrachion* with the Amanoeae and Brideliaceae because of its coarsely reticulate pollen grains. It appears that this palynological similarity may be a better guide to affinity, so *Pentabrachion* is here placed in the same tribe with *Amanoa*, despite the obvious differences between the genera.

12. *Amanoa* Aublet, *Fl. Guiane Fr.* 256, pl. 101. 1775; Muell. Arg., DC. *Prodr.* 15(2): 219. 1866; Bentham, *Gen. Pl.* 3: 268. 1880; Baillon, in Grandidier, *Atlas Hist. Madag. Pl. tt.* 210, 211. 1892; Pax & Hoffm., *Pflanzenr.* 147. XV (Heft 81): 195. 1922; Jablonski, *Mem. New York Bot. Gard.* 17: 82. 1967; Webster, *Ann. Missouri Bot.* 54: 1968; Hayden, *Brittonia* 4: 260. 1990. TYPE: *Amanoa guianensis* Aublet.

A mainly neotropical genus of 16 species; the three African species have been referred to an endemic section.

Tribe 3. BRIEDELIEAE Muell. Arg., *Bot. Zeit.* 22: 324. 1864 (as Brideliaceae). Tribe Biovulatae sect. Brideliaceae Thwaites, *Enum. Pl. Zeyl.* 279. 1861. Antidesmataceae subfam. Bridelioideae Hurusawa, *J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot.* 6: 321. 1954. TYPE: *Briedelia* Willd.

Monoecious (rarely dioecious) trees or shrubs;

leaves alternate, entire, pinnately veined, without laminar glands; stipules usually deciduous. Flowers in bracteate glomerules, these axillary or in spikes. Sepals mostly 5, valvate; petals 5, imbricate or valvate, usually smaller than the sepals, sometimes dentate or reduced; disk annular or dissected; stamens mostly 5, filaments connate into a column; anthers introrse; pollen grains tricolporate, reticulate or striate; pistillode present; pistillate sepals 5, imbricate or valvate, deciduous; disk annular or cupular; ovary 2- or 3- (rarely 4-)locular; ovules anatropous; styles 2- or 4-fid; fruit capsular or drupaceous, 1-3-celled; seeds with endosperm; cotyledons much longer and broader than the radicle.

The tribe has traditionally been considered to comprise two closely related genera, *Cleistanthus* and *Briedelia*. However, the diagnostic characters are not entirely satisfactory (as indicated, for example, in the complicated distinctions in the key of Léonard, 1962a) and generic delimitation requires further study. Baillon (1858) regarded *Briedelia* as being close to *Amanoa*, and Köhler (1965) saw resemblances between pollen of *Amanoa* and the African species of *Cleistanthus*; following the latter's suggestion, it would be possible to associate the Amanoeae and Brideliaceae as subtribes of a single tribe. Nevertheless, neither the floral nor pollen characters of the Brideliaceae appear sufficiently close to *Amanoa* to associate them in the same tribe.

KEY TO THE GENERA OF TRIBE BRIEDELIEAE

- 1a. Ovary mainly of 3 carpels (rarely 2 or 4); fruits capsular, lobed, mainly 3-locular with 2 seeds per locule; leaf venation mainly reticulate 13. *Cleistanthus*
- 1b. Ovary mainly of 2 carpels (rarely 3); fruits drupaceous or rarely capsular, unlobed, 1- or 2-locular with 1 seed per locule; leaf venation mainly percurrent 14. *Briedelia*

13. *Cleistanthus* Hooker f. ex Planchon, *Hook. Ic. Pl.* 8: t. 779. 1848; Muell. Arg., DC. *Prodr.* 15(2): 503. 1866; Bentham, *Gen. Pl.* 3(1): 268. 1880; Jablonski, *Pflanzenr.* 147. VIII (Heft 65): 8. 1915; Gagnepain, *Fl. Indochine* 5: 482. 1926; Croizat, *J. Arnold Arbor.* 23: 38. 1942; Leandri, *Fl. Madag.* 111: 181. 1958; Léonard, *Bull. Jard. Bot. Brux.* 30: 421. 1960; *Fl. Congo* 8(1): 5. 1962; Radcliffe-Smith, *Fl. Trop. E. Afr.*, *Euphorb.* 130. 1987. TYPE: *Cleistanthus polystachyus* Hook. f.

Nanopetalum Hassk., *Versl. Meded. Afd. Natuurk. Kon.*

- Akad. Wetensch. Amsterdam 4: 140. 1856. TYPE: *Nanopetalum myrianthum* Hassk. [= *Cleistanthus myrianthum* (Hassk.) Kurz].
- Leiopyxis* Miquel, Fl. Ned. Ind., Erste Bijv. 445. 1861. TYPE: *Leiopyxis sumatrana* Miq. [= *Cleistanthus sumatranus* (Miq.) Muell. Arg.].
- Lebidieropsis* Muell. Arg., Linnaea 32: 80. 1863. TYPE: *Lebidieropsis collina* (Roxb.) Muell. Arg. [= *Cleistanthus collinus* (Roxb.) Benth.].
- Schistostigma* Lauterbach, Fl. Deutsches Schutzgeb. Nachtr. 299. 1905. TYPE: *Schistostigma papuanum* Laut. [= *Cleistanthus papuanus* (Laut.) Jabl.].
- Paracleistus* Gagnepain, Bull. Soc. Bot. France 70: 499. 1923. TYPE: *Paracleistus subgracilis* Gagnep. [= *Cleistanthus saichikii* Merr. & Chun; lectotype, designated by Wheeler, 1975.].
- Godefroya* Gagnepain, Bull. Soc. Bot. France 70: 435. 1923. TYPE: *Godefroya rotundata* (Jabl.) Gagnep. [= *Cleistanthus rotundatus* Jabl.].

A large and rather diverse genus of over 100 species, of which about 30 occur in Africa/Madagascar and the rest in tropical Asia, from India to northern Australia and Melanesia. Both Köhler (1965) and Levin (1986a) found *Cleistanthus* to be heterogeneous on the basis of pollen and leaf characters, respectively; clearly, generic limits in the tribe need to be critically reevaluated.

- 14. *Briedelia*** Willdenow, Sp. Pl. 4(2): 978. 1805; Sprengel, Anleit. Kenntn. Gew. 2(2): 887. 1818 (as *Bridelia*); Muell. Arg., DC. Prodr. 15(2): 493. 1866; Pfeiffer, Nomencl. Bot. 1(1): 467. 1874; Bentham, Gen. Pl. 3(1): 267. 1880; Gehrmann, Bot. Jahrb. 41(Beibl. 95): 1. 1908; Hutchinson, Fl. Trop. Afr. 6(1): 611. 1912; Jablonski, Pflanzenr. 147. VIII (Heft 65): 54. 1915; Leandri, Fl. Madag. 111: 192. 1958; Léonard, Fl. Congo 8(1): 27. 1962; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 120. 1987; Chapman, Austral. Pl. Name Index 476. 1991. TYPE: *Briedelia scandens* (Roxb.) Willd. [*Clutya scandens* Roxb.; lectotype, selected here; of the 3 species included in the original description of Willdenow, it is the only one placed in subg. *Briedelia* by Gehrmann (1908) and of which Willdenow saw herbarium material].

- Candelabria* Hochstetter, Flora 26: 79. 1843. TYPE: *Candelabria micrantha* Hochst. [= *Briedelia micrantha* (Hochst.) Baillon].
- Neogoetzea* Pax, Bot. Jahrb. 28: 419. 1900. TYPE: *Neogoetzea brideliifolia* Pax [= *Briedelia brideliifolia* (Pax) Fedde].
- Gentilia* Beille, Comptes Rend. Acad. Sci. Paris 114: 1294. 1907. TYPE: *Gentilia hygrophila* Beille [= *Briedelia ndellensis* Beille].
- Tzellemtinia* Chiovenda, Ann. Bot. Roma 9: 55. 1911. TYPE: *Tzellemtinia nervosa* Chiov. [= *Briedelia scleroneura* Muell. Arg.].

An Old World genus of more than 60 species, the majority Asian. I agree with Pfeiffer (1874) and Chapman (1991) in adopting Willdenow's original spelling for the genus; Sprengel's correction to match the name of the botanist honored (S. E. Bridel) is contrary to the current rules of nomenclature.

- Tribe 4. PHYLLANTHEAE** Dumortier, Anal. Fam. Pl. 45. 1829. Euphorbiaceae sect. Phyllanthae Blume, Bijdr. 578. 1826 (nom. illeg.). Ordnung Phyllanthaceae Kl. & Gcke., Monatsber. Königl. Akad. Wiss. Berlin 1859: 246. 1859. TYPE: *Phyllanthus* L.

Monoecious or dioecious trees, shrubs, or herbs; leaves alternate, entire, pinnately veined, without laminar glands; stipules persistent or deciduous. Flowers in axillary racemes or glomerules, bracts inconspicuous. Staminate sepals 4–6, free or connate, imbricate; petals present or absent; disk extrastaminal, dissected or entire (rarely absent); stamens (2–)3–5(–10), filaments free or connate; anthers mostly extrorse; pollen grains prolate to oblate, mostly 3-colporate (sometimes stephanocolporate or porate); pistillode present or absent; pistillate sepals mostly 5, imbricate, persistent or deciduous; disk cupular to lobed (less commonly dissected or absent); ovary mostly 3–5-locular; ovules anatropous or hemitropous; styles bifid or entire (rarely multifid). Fruit usually capsular (rarely baccate or drupaceous); seeds 1 or 2 per locule; endosperm present; embryo with cotyledons broader than and at least equal in length with the radicle.

As here interpreted, tribe Phyllanthae is considerably narrower in scope than the circumscription of Pax & Hoffmann (1922), but broader than that of Webster (1975). The relationships of some of the taxa (e.g., *Astrocasia*, *Leptopus*) point toward the Wielandieae, but Phyllanthae are anatomically more advanced in such characters as septate fibers and scarcity of scalariform perforations. The inclusion of petaliferous and apetalous genera together seems justified by similarities in pollen (Punt, 1962; Köhler, 1965) and some of the leaf venation characters pointed out by Levin (1986a).

Subdivision of this heterogeneous tribe into subtribes is still controversial; the present classification with six subtribes must be considered provisional. The distinction between anatropous and hemitropous ovules, pointed out by Baillon (1858), appears systematically significant even though not all genera have yet been carefully studied, and there may prove to be transitional stages.

KEY TO THE SUBTRIBES OF TRIBE PHYLLANTHEAE

- 1a. Petals present; ovules anatropous; seeds smooth.
 2a. Pistillate sepals deciduous; staminal column adnate to peltate pistillode 4a. *Astrocasiinae*
 2b. Pistillate sepals persistent; stamens free or connate below 4b. *Leptopinae*
- 1b. Petals absent (except in some *Andrachninae*); ovules anatropous or hemitropous; seeds smooth or sculptured.
 3a. Ovules anatropous; pistillode present.
 4a. Staminate disk annular; pollen grains reticulate; seed coat dull or sculptured 4c. *Pseudolachnostylidinae*
 4b. Staminate disk dissected; pollen grains verruculose; seed coat blackish, smooth 4d. *Securineginae*
- 3b. Ovules hemitropous; staminate disk annular or dissected; pistillode present or absent.
 5a. Petals present; stamens 5, free; staminate disk dissected 4e. *Andrachninae*
 5b. Petals absent; stamens 2–10 or more, free or connate; staminate disk annular or dissected 4f. *Flueggeinae*

Subtribe 4a. ASTROCASIINAE Webster, Syst. Bot. 17: 315. 1992. TYPE: *Astrocasia* Rob. & Greenm.

Dioecious (or subdioecious) trees or shrubs; stipules deciduous; flowers in axillary glomerules; staminate sepals 5; disk annular; stamens 5, filaments connate into a column; pollen grains 3-colporate, reticulate; pistillode peltate; pistillate sepals 5, deciduous; disk annular; ovary 3-locular; ovules anatropous; styles bifid; fruits capsular; seeds 1 or 2 per locule, smooth; cotyledons much longer than radicle.

This monogeneric tribe includes only the type genus *Astrocasia*, which was included in tribe Wielandieae by Webster (1975), following Pax & Hoffmann (1922). However, Pax & Hoffmann referred *Astrocasia* to the Wielandieae on the basis of a mistaken interpretation of the floral morphology. Pollen studies of Köhler (1965) and leaf venation studies of Levin (1986a, b, c) suggest, on the contrary, that *Astrocasia* shows more similarities to the tribe Phyllanthae, particularly to genera of subtribes Leptopinae and Pseudolachnostylidinae.

15. *Astrocasia* Robinson & Greenman, Bot. Jahrb. 36 (Beibl. 80): 19. 1905; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 189. 1922; Webster, Syst. Bot. 17: 311. 1992. TYPE: *Astrocasia phyllanthoides* Rob. & Greenm. [= *Astrocasia tremula* (Griseb.) Webster].

A neotropical genus of five species distributed

from Mexico and Cuba south to Bolivia and eastern Brazil.

Subtribe 4b. LEPTOPINAE Webster, subtribe nov. TYPE: *Leptopus* Dcne.

Stipulae persistentae; petala conspicua; stamina 5, filamenta libera vel connata; pistillodio trifidum; sepala pistillata persistentia; ovarium 3-loculare, ovulis anatropis; fructus capsularis; semina laevia.

Dioecious shrubs or herbs; stipules persistent; flowers in axillary glomerules; staminate sepals 5; disk annular or dissected; stamens 5, filaments free or connate below; pollen grains 3-colporate, reticulate; pistillode 3-fid; pistillate sepals 5, persistent; disk annular or dissected; ovary 3-locular; ovules anatropous; styles bifid; fruit capsular; seeds 2 per locule, testa smooth; cotyledons much longer than radicle.

This subtribe includes only the single genus *Leptopus*, which was submerged in *Andrachne* by Mueller (1866), Bentham (1880), and Pax & Hoffmann (1922). However, *Leptopus* differs from *Andrachne* (sensu stricto) in its anatropous ovules, and appears to represent a connecting link between *Astrocasia* and *Andrachne*. It therefore appears best to assign it to a separate subtribe.

16. *Leptopus* Decaisne, in Jacquemont, Voy. Inde Bot. 4: 155. 1836; Pojarkova, Not. Syst. Herb. Inst. Bot. Acad. Sci. USSR 20: 269. 1960; Li Ping-T'ao, Notes Roy. Bot. Gard. Edinburgh 40: 467. 1983. TYPE: *Leptopus cordifolius* Dcne.

Lepidanthus Nuttall, Trans. Amer. Phil. Soc. 5: 175. 1837 (non *Lepidanthus* Nees, 1830). TYPE: *Lepidanthus phyllanthoides* Nutt. (loc. cit.) [= **Leptopus phyllanthoides** (Nutt.) Webster, comb. nov.].

Thelypetalum Gagnepain, Bull. Soc. Bot. France 71: 876. 1924. TYPE: *Thelypetalum pierrei* Gagnep. [= *Leptopus australis* (Zoll.) Pojark.].

Chorisandrachne Airy Shaw, Kew Bull. 23: 40. 1969. TYPE: *Chorisandrachne diplosperma* Airy Shaw [= **Leptopus diplospermus** (Airy Shaw) Webster, comb. nov.].

A genus of ca. 10 species of widely scattered distribution in the Old World (India to China, Indonesia, and tropical Australia) and North America (Mexico, southern U.S., and Greater Antilles).

Subtribe 4c. PSEUDOLACHNOSTYLIDINAE Pax & Hoffmann, Pflanzenr. 147. XV (Heft 81): 206. 1922. TYPE: *Pseudolachnostylis* Pax.

Monoecious or dioecious trees, shrubs, or undershrubs; stipules persistent or deciduous; flowers in axillary glomerules or cymes, bracts inconspicuous; staminate sepals 5, petals absent; disk annular; stamens usually 5, filaments free or connate; pollen grains 3-colporate, reticulate; pistillode present; pistillate sepals 5, persistent or deciduous; petals absent; disk annular; ovary 3-locular; ovules

anatropous; styles bifid; fruit capsular; seeds 1 or 2 per locule, testa smooth or sculptured; cotyledons much longer than radicle.

This subtribe of six genera is heterogeneous and possibly unnatural, as it is quite possible that *Pseudolachnostylis* and *Keayodendron* may not be closely related to the other genera.

KEY TO THE GENERA OF SUBTRIBE PSEUDOLACHNOSTYLIDINAE

- 1a. Fruit capsular, 3-locular, with 3–6 seeds; staminate disk annular.
 - 2a. Capsule thin-walled; cymes (glomerules) not pedunculate; seeds with sculptured testa; pistillate sepals persistent.
 - 3a. Chalaza dorsal on seed; staminate flowers subsessile 17. *Chascotheca*
 - 3b. Chalaza ventral; staminate flowers pedicellate.
 - 4a. Filaments free from pistillode.
 - 5a. Stipules foliaceous, persistent; sepals broad and imbricate 18. *Zimmermannia*
 - 5b. Stipules narrow, deciduous; sepals linear-lanceolate, not imbricate 19. *Zimmermanniopsis*
 - 4b. Filaments connate to pistillode; stipules narrow 20. *Meineckia*
 - 2b. Capsule thick-walled; pistillate cymes pedunculate; seeds with smooth testa; pistillate sepals deciduous; filaments connate 21. *Pseudolachnostylis*
 - 1b. Fruit drupaceous, 2-locular, with one seed; staminate disk dissected 22. *Keayodendron*

17. *Chascotheca* Urban, Symb. Ant. 5: 14. 1904; Alain, Fl. Cuba 3: 44. 1953. *Chaenotheca* Urban, Symb. Ant. 3: 284. 1902 (non T. M. Fries, 1860). TYPE: *Chascotheca neopeltandra* (Griseb.) Urb.

Three species have been described in this Greater Antillean genus (Cuba and Hispaniola), but *Chascotheca domingensis* (Urb.) Urb. is probably a synonym of the type species.

18. *Zimmermannia* Pax, Bot. Jahrb. 45: 235. 1910; Hutchinson, Fl. Trop. Afr. 6(1): 739. 1912; Verdcourt, Kew Bull. 9: 38. 1954; Poole, Kew Bull. 36: 129. 1981; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 71. 1987. TYPE: *Zimmermannia capillipes* Pax.

As interpreted by Radcliffe-Smith (1987), *Zimmermannia* includes six east African species, plus a dubious Madagascan species transitional to *Meineckia*.

19. *Zimmermanniopsis* Radcliffe-Smith, Kew Bull. 45: 152. 1990. TYPE: *Zimmermanniopsis uzungwaensis* Radcl.-Sm.

A monotypic genus from Tanzania (Iringa Distr.), very close to *Zimmermannia*, and questionably distinct.

20. *Meineckia* Baillon, Etude Gén. Euphorb. 586. 1858; Webster, Acta Bot. Neerl. 14: 323. 1965; Radcliffe-Smith, Hook. Ic. Pl. 37:

t. 3698. 1971; Brunel & Roux, Bull. Mus. Hist. Nat. Paris, IV. 4: 79. 1982; Radcliffe-Smith, Fl. Trop. E. Afr. Euphorb. 76. 1987. TYPE: *Meineckia phyllanthoides* Baillon.

Cluytiandra Muell. Arg., J. Bot. 2: 328. 1864. TYPE: *Cluytiandra trichopoda* Muell. Arg. [= *Meineckia trichopoda* (Muell. Arg.) Webster].
Peltandra Wight, Icon. Pl. Ind. Or. 5(2): 24. 1852 (non *Peltandra* Raf., 1819). *Neopeltandra* Gamble, Fl. Madras 1285. 1925. TYPE: *Peltandra parvifolia* Wight [= *Meineckia parvifolia* (Wight) Webster; lectotype].

A genus of 20 species with a disjunct distribution in the New World and Old World, from Mexico to Colombia and Brazil, and from central Africa to Madagascar, southern India, Sri Lanka, and Assam.

21. *Pseudolachnostylis* Pax, Bot. Jahrb. 23: 19. 1899; Hutchinson, Hook. Ic. Pl. 31: t. 3011. 1915; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 206. 1922; Phillips, Gen. S. Afr. Pl. ed. 2, 457. 1951; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 80. 1987. TYPE: *Pseudolachnostylis dekindtii* Pax.

An African genus of six described species, reduced by Radcliffe-Smith (1987) to four varieties of *P. maprouneifolia* Pax. The phylogenetic position of *Pseudolachnostylis* remains uncertain, although the disposition of Pax & Hoffmann (1922) in locating it adjacent to *Meineckia* is followed here. However, the pedunculate inflorescence and

massive fruits of *Pseudolachnostylis* are quite different from the preceding genera, and it is not clear that it really belongs in the same subtribe. Köhler (1965) has proposed that *Pseudolachnostylis* be classified with *Amanoa* because of its coarsely reticulate pollen grains and large fruits. However, the flowers differ from those of *Amanoa* in lacking petals or conspicuous bracts, and in having bifid styles; furthermore, the plants are dioecious, and the stipules are deciduous. Because of all these differences, it seems possible that the similarity in pollen ornamentation represents convergence rather than close affinity.

22. Keayodendron Leandri, Soc. Bot. France 105: 517. 1959. TYPE: *Keayodendron briodelioides* (Mildbr. ex Hutch. & Dalz.) Leandri.

A monotypic genus from tropical west Africa, still poorly known. As the specific epithet suggests, the fruits and aspect suggest *Briedelia*, but the flowers are apetalous, with imbricate sepals. *Keayodendron* is diffidently referred to this subtribe for lack of a better alternative.

Subtribe 4d. SECURINEGINAE Muell. Arg., DC. Prodr. 15(2): 446. 1866. TYPE: *Securinega* Comm. ex Juss.

Dioecious shrubs or small trees; stipules deciduous; flowers in axillary glomerules, bracts inconspicuous; staminate sepals 5; petals absent; disk dissected; stamens 5(-10), free; pollen grains 3-colporate, sexine verruculose; pistillode present; pistillate sepals 5, persistent; disk angled or absent; ovary 3-locular; ovules anatropous; styles bifid; fruit capsular; seeds 1 or 2 per locule, testa dark and smooth; cotyledons about equaling the radicle.

Although Mueller's name is applied to this subtribe, its present circumscription is very different, since Mueller (1866) included *Hymenocardia* and genera of subtribe Scepinae. The distinctive pollen and seeds of *Securinega* set it apart from other taxa in tribe Phyllanthae and suggest a possible affinity with subfamily Oldfieldioideae.

23. Securinega Commerson ex Jussieu, Gen. Pl. 388. 1789 (nom. cons.); Leandri, Fl. Madag. 111: 107. 1958. TYPE: *Securinega durissima* J. F. Gmel. (typ. cons.).

A Malagasian genus of five closely related species, the type from Reunion and Mauritius, the others from Madagascar. The majority of workers have confounded the genus with *Flueggea*, and

only Leandri among modern writers has presented the genus as accepted here.

Subtribe 4e. ANDRACHNINAE Muell. Arg., Linnaea 34: 64. 1865 (as *Andrachneae*); Pax, Nat. Pflanzenfam. ed. 1, 3(5): 15. 1890; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 169. 1922. TYPE: *Andrachne* L.

Monoecious herbs or subshrubs; stipules persistent; flowers in axillary glomerules, bracts inconspicuous; staminate sepals and petals 5; disk dissected; stamens 5, filaments free or connate; pollen grains 3-colporate, sexine reticulate or striate; pistillode present; pistillate sepals 5, persistent; petals 5; disk annular or dissected; ovary 3-locular; ovules hemitropous; styles bifid; fruit capsular; seeds 2 per locule, testa sculptured; cotyledons much longer than radicle.

The subtribe includes only the genus *Andrachne* (sensu stricto); Mueller (1866) and most later workers included *Leptopus* within *Andrachne*. Except for the presence of petals, species of *Andrachne* resemble herbaceous species of *Phyllanthus*; however, it is not clear whether this indicates close affinity. Earlier (Webster, 1975), I associated the Australian genus *Poranthera* with *Andrachne* because of similarity in the pollen pointed out by Köhler (1965). However, other characters of *Poranthera* now seem to me to point toward affinity with tribe Antidesmeae.

24. Andrachne L., Spec. Pl. 1014. 1753; Gen. Pl. ed. 5, 444. 1754; Muell. Arg., DC. Prodr. 15(2): 232. 1866; Bentham, Gen. Pl. 3: 270. 1880; Kossinki, Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 2: 77. 1921; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 169. 1922; Croizat, J. Wash. Acad. Sci. 33: 11. 1942; Vindt, Trav. Inst. Sci. Chérifien 6: 4. 1953; Pojarkova, Not. Syst. Herb. Inst. Bot. Acad. Sci. USSR 20: 256. 1960; Webster, J. Arnold Arbor. 48: 327. 1967; Radcliffe-Smith, Fl. Trop. E. Afr., Euphorb. 7. 1987; Gilbert & Thulin, Nordic J. Bot. 8: 159. 1988. TYPE: *Andrachne telephioides* L. [lectotype, designated by Small in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 453. 1913].

Eraclissa Forsskål, Fl. Aegypt.-Arab. 208. 1775. TYPE: *Eraclissa hexagyna* Forssk. [= *Andrachne telephioides* L.].
Telephioides Gomez Ortega, Tabulae Bot. 15. 1773. TYPE: *Telephioides procumbens* Moench [= *Andrachne telephioides* L.].

Phyllanthidea Didrichsen, Vidensk. Medd. Naturh. Foren. Kjøbenhavn 1857: 450. 1857. TYPE: *Phyllanthidea microphylla* (Lam.) Dir. [= *Andrachne microphylla* (Lam.) Baillon].

In the restricted circumscription adopted here, *Andrachne* includes about 15 species with a primarily Tethyan distribution from Persia through the Mediterranean to the West Indies, with one species (*A. microphylla*) disjunct from Baja California to Pacific South America. The majority of species listed under *Andrachne* by most authors are better classified in a separate genus *Leptopus*.

Subtribe 4f. FLUEGGEINAE Muell. Arg., Linnaea 34: 64. 1865 (as Flüggæe). TYPE: *Flueggea* Willd.

Tribe Phyllanthae subtribe Euphyllanthae Muell. Arg., Linnaea 34: 64. 1865 (nom. illeg.). TYPE: *Phyllanthus* L.

Tribe Phyllanthae subtribe Sauropodeae Muell. Arg., Linnaea 34: 64. 1865. TYPE: *Sauropus* Bl.

Tribe Phyllanthae subtribe Phyllanthinae Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 17. 1890. TYPE: *Phyllanthus* L.

Monoecious or dioecious trees, shrubs, or herbs;

branchlets deciduous in some taxa; flowers in axillary glomerules (except *Richeriella*); sepals mostly 4–6, free or connate; stamens 2–15, free or connate; disk extrastaminal and usually dissected (less commonly cupular or absent); anthers introrse or extrorse; pistillode present or absent; pistillate sepals mostly 5 or 6, persistent in fruit; disk usually cupular, often lobed (sometimes dissected); carpels mostly 3 (rarely 2 or 4–10); styles free or connate, bifid or entire; ovules hemitropous; fruit usually capsular (sometimes baccate or drupaceous); seeds usually 2 per locule; testa smooth or sculptured; endosperm copious; cotyledons broader than and 1–2 times longer than the radicle.

A variable subtribe of nine genera with over 1000 species, evidently monophyletic (possibly excluding *Aerisilvaea*, however). The vast majority of the species in genera lacking pistillodes (except for *Margaritaria* and some species of *Phyllanthus*) share a distinctive vegetative specialization: leaves are reduced to scales on main axes and are developed only on lateral deciduous floriferous axes. This has been designated as “phyllanthoid branching” (Webster, 1956).

KEY TO THE GENERA OF SUBTRIBE FLUEGGEINAE

- 1a. Pistillode present in staminate flower (sometimes minute).
 - 2a. Dioecious; stamens 3–7; pistillate calyx not accrescent.
 - 3a. Flowers in axillary clusters; staminate flowers distinctly pedicellate; seeds mostly 2 per locule 25. *Flueggea*
 - 3b. Flowers in axillary or cauliflorous racemes or panicles; staminate flowers subsessile; seeds mostly 1 per locule 26. *Richeriella*
 - 2b. Monoecious; stamens 17–21; pistillate calyx accrescent 27. *Aerisilvaea*
- 1b. Pistillode absent; monoecious or dioecious.
 - 4a. Seed coat with bony endotesta (not ventrally invaginated) and fleshy exotesta; fruits dry, irregularly dehiscent; disk annular in both staminate and pistillate flowers; dioecious shrubs or trees 28. *Margaritaria*
 - 4b. Seed coat lacking bony endotesta and fleshy exotesta (or else endotesta usually ventrally invaginated); fruits, when capsular, usually regularly septicial; disk usually dissected or absent in staminate flower; monoecious or dioecious trees, shrubs, or herbs.
 - 5a. Floral disk usually present; seeds dry, not ventrally invaginated.
 - 6a. Staminate disk extrastaminal; stamens various, but rarely 2 and introrse; cotyledons much broader than radicle 29. *Phyllanthus*
 - 6b. Staminate disk lobed, intrastaminal; stamens 2, anthers introrse; cotyledons scarcely broader than radicle 30. *Reverchonia*
 - 5b. Floral disk absent or completely adnate to calyx; pollen grains stephanocolporate; styles bifid or entire; seeds with thickened dry or fleshy exotesta, and usually ventrally invaginated.
 - 7a. Styles bifid or emarginate; anthers not apiculate; ovary 3-locular.
 - 8a. Seed-coat dry; staminate calyx ± discoid, not turbinate 31. *Sauropus*
 - 8b. Seed-coat fleshy; staminate calyx turbinate 32. *Breynia*
 - 7b. Styles usually entire; anthers apiculate; seed-coat usually fleshy; ovary 3–8-locular 33. *Glochidion*

25. *Flueggea* Willdenow, Sp. Pl. 4: 637. 1806; Bentham, Gen. Pl. 3: 276. 1880; Webster, Allertonia 3: 273. 1984; Hayden, Brittonia 39: 268. 1987. TYPE: *Flueggea leucopyrus* Willd.

Acidoton P. Browne, Civ. Nat. Hist. Jamaica 335. 1756 (nom. rej.; non *Acidoton* Sw., 1788). TYPE: *Adelia acidoton* L. [= *Flueggea acidoton* (L.) Webster].
Bessera Sprengel, Pl. Minus Cogn. Pugillus 2: 90. 1815. TYPE: *Bessera inermis* Sprengel [prob. = *Flueggea virosa* (Roxb. ex Willd.) Voigt].

- Geblera* Fischer & Meyer, Index Sem. Hort. Petropol. 1: 28. 1835. TYPE: *Geblera suffruticosa* (Pallas) Fischer & Meyer [= *Flueggea suffruticosa* (Pallas) Baillon].
- Colmeiroa* Reuter, Bibliot. Univers. Genève 38: 215. 1842. TYPE: *Colmeiroa buxifolia* Reuter [= *Flueggea tinctoria* (L. in Loeff.) Webster].
- Pleioctemon* Sonder, Linnaea 23: 135. 1850. TYPE: *Pleioctemon verrucosum* (Thunb.) Sonder [= *Flueggea verrucosa* (Thunb.) Webster].
- Neowawraea* Rock, Indig. Trees Haw. I. 243. 1913. TYPE: *Neowawraea phyllanthoides* Rock [= *Flueggea neowawraea* Hayden].

A genus of 14 species, widespread in the tropics and temperate eastern Asia, but with a disjunct relict distribution. The genus was merged with *Securinega* by Mueller (1866), who was followed by many subsequent workers. However, Baillon (1858), Bentham (1880), and J. D. Hooker (1887) maintained *Flueggea* as distinct, and indeed it is not closely related to *Securinega*, as indicated by both pollen and seed characters.

- 26. Richeriella** Pax & Hoffmann, Pflanzenr. 147. XV (Heft 81): 26. 1922; Natürl. Pflanzenfam. ed. 2, 19c: 48. 1931; Henderson, Garden Bull. Str. Settle. 7: 122, t. 32. 1933; Airy Shaw, Kew Bull. 25: 489. 1971. TYPE: *Richeriella gracilis* (Merr.) Pax & Hoffm. [*Baccaurea gracilis* Merr.].

A genus of two species native to southern China, the Philippines, Malaya, and Borneo. It is very close to *Flueggea*.

- 27. Aerialvaea** Radcliffe-Smith, Kew Bull. 45: 149. 1990; 47: 677. 1992. TYPE: *Aerialvaea sylvestris* Radcliffe-Smith.

A genus of two species, one from Tanzania and the other from Malawi. It is anomalous within this subtribe because of its high stamen number, and its placement must be regarded as provisional until the pollen can be examined. Levin (pers. comm.) suggested that it may be referable to the Drypeteae.

- 28. Margaritaria** L. f., Suppl. Pl. 66. 1781; Airy Shaw, Kew Bull. 20: 386. 1966; Fosberg, Kew Bull. 33: 185. 1978; Webster, J. Arnold Arbor. 60: 407. 1979; Airy Shaw, Kew Bull. 35: 657. 1980; Radcliffe-Smith, Kew Bull. 36: 219. 1981; Fl. Trop. E. Afr. Euphorb. 63. 1987. TYPE: *Margaritaria nobilis* L. f.

- Prosorus* Dalz., J. Bot. Kew Misc. 4: 345. 1852. TYPE: *Prosorus indicus* Dalz. [= *Margaritaria indica* (Dalz.) Airy Shaw].
- Zygosperrum* Thw. ex Baillon, Etude Gén. Euphorb. 620. 1858. TYPE: *Zygosperrum zeylanicum* Thw. ex Baillon [= *Margaritaria cyanosperma* (Gaertner) Airy Shaw].
- Wurtzia* Baillon, Adansonia I. 1: 186. 1861. TYPE: *Wurtzia tetracocca* Baillon [= *Margaritaria tetracocca* (Baillon) Webster].
- Calococcus* Kurz ex Teijsm. & Binn., Nat. Tijdschr. Ned. Ind. 27: 48. 1864. TYPE: *Calococcus sundaicus* Kurz ex Teijsm. & Binn. [= *Margaritaria indica* (Dalz.) Airy Shaw].

A genus of 14 species occurring in tropical America, Africa, Asia, and Australia.

- 29. Phyllanthus** L., Sp. Pl. 981. 1753; Gen. Pl. ed. 5, 422. 1754; Baillon, Adansonia I. 1: 24. 1860; Muell. Arg., DC. Prodr. 15(2): 274. 1866; Bentham, Gen. Pl. 3(1): 272. 1880; Hutchinson, Fl. Trop. Afr. 6(1): 692. 1912; Beille, Fl. Indochine 5: 571. 1927; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 60. 1931; Webster, J. Arnold Arbor. 48: 332. 1967; Brittonia 22: 44. 1970; Webster & Airy Shaw, Kew Bull. 26: 85. 1971; Brunel & Roux, Willdenowia 11: 69. 1981; Bull. Mus. Hist. Nat. IV. 3B: 185. 1981; Nordic J. Bot. 4: 469. 1984; Radcliffe-Smith, Fl. Trop. E. Afr. Euphorb. 9. 1987; Rossignol et al., Amer. J. Bot. 74: 1853. 1987; Santiago, Bradea 5(2): 44. 1988; Lebrun & Stork, Enum. Pl. Afr. Trop. 1: 232. 1991; Schmid, Fl. Nouv.-Caléd. 14(2): 31. 1991. TYPE: *Phyllanthus niruri* L. [lectotype, designated by Small in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 453. 1913].

Niruri Adanson, Fam. Pl. 2: 356. 1763. TYPE: *Phyllanthus niruri* L. [lectotype, selected here].

Cicca L., Syst. Nat. ed. 12, 2: 621. 1767. TYPE: *Cicca disticha* L. [= *Phyllanthus acidus* (L.) Skeels].

Xylophylla L., Mant. Alt. 147, 221. 1771. TYPE: *Xylophylla latifolia* L. [= *Phyllanthus epiphyllanthus* L.; lectotype].

Conami Aublet, Hist. Pl. Guiane Fr. 926. 1775. TYPE: *Conami brasiliensis* Aubl. [= *Phyllanthus brasiliensis* (Aubl.) Muell. Arg.].

Genesiphylla L'Herit., Sert. Angl. 29. 1778. TYPE: *Genesiphylla asplenifolia* L'Herit. [= *Phyllanthus latifolius* Sw.].

Cathetus Loureiro, Fl. Cochinch. 607. 1790. TYPE: *Cathetus fasciculata* Lour. [= *Phyllanthus cochinchinensis* Spreng.].

Nymphanthus Loureiro, Fl. Cochinch. 543. 1790. TYPE: *Nymphanthus ruber* Lour. [= *Phyllanthus ruber* (Lour.) Spreng.].

- Emblia* Gaertner, Fruct. Sem. Pl. 2: 122. 1790. TYPE: *Emblia officinalis* Gaertner [= *Phyllanthus emblica* L.].
- Kirganelia* Juss., Gen. Pl. 387. 1789. TYPE: *Kirganelia virginea* J. F. Gmelin [= *Phyllanthus virgineus* (Gmel.) Pers.].
- Tricarum* Loureiro, Fl. Cochinch. 557. 1790. TYPE: *Tricarum cochinchinense* Lour. [= *Phyllanthus acidus* (L.) Skeels].
- Epistylum* Swartz, Fl. Ind. Occ. 2: 1095. 1800. TYPE: *Epistylum axillare* (Sw.) Sw. [= *Phyllanthus axillaris* (Sw.) Muell. Arg.; lectotype].
- Geminaria* Rafinesque, Western Minerva 42. 1821. TYPE: *Geminaria obovata* Raf. [= *Phyllanthus carolinensis* Walt.].
- Menarda* Commerson ex A. Jussieu, Euphorb. Tent. 23, 109. 1824. TYPE: *Menarda cryptophila* Comm. ex A. Juss. [= *Phyllanthus cryptophilus* (Comm. ex A. Juss.) Muell. Arg.].
- Anisonema* A. Jussieu, Euphorb. Tent. 19. 1824 (nom. rej.). TYPE: *Anisonema reticulatum* (Poir.) A. Juss. [= *Phyllanthus reticulatus* Poir.].
- Scepasma* Blume, Bijdr. Fl. Jav. 582. 1825. TYPE: *Scepasma buxifolia* Bl. [= *Phyllanthus buxifolius* (Bl.) Muell. Arg.].
- Synexemia* Rafinesque, Neogenyton 2. 1825. TYPE: *Synexemia caroliniana* Raf. [= *Phyllanthus carolinensis* Walt.; lectotype].
- Hexadena* Rafinesque, Sylva Tell. 92. 1838. TYPE: *Hexadena angustifolia* (Sw.) Raf. [= *Phyllanthus angustifolius* (Sw.) Sw.].
- Moeroris* Rafinesque, Sylva Tell. 91. 1838. TYPE: *Moeroris stipulata* Raf. [= *Phyllanthus stipulatus* (Raf.) Webster].
- Nellica* Rafinesque, Sylva Tell. 92. 1838. TYPE: *Nellica maderaspatensis* (L.) Raf. ["*maderaspatana*" = *Phyllanthus maderaspatensis* L.].
- Asterandra* Klotzsch, Arch. Naturgesch. 7(1): 200. 1841. TYPE: *Asterandra cornifolia* (HBK) Kl. [= *Phyllanthus cornifolius* HBK].
- Eriococcus* Hasskarl, Tijdschr. Natuurl. Gesch. Physiol. 10: 143. 1843. TYPE: *Eriococcus gracilis* Hassk. [= *Phyllanthus gracilipes* Muell. Arg.].
- Ceramanthus* Hasskarl, Cat. Pl. Hort. Bogor. Alt. 240. 1844. TYPE: *Ceramanthus gracilis* Hassk. [= *Phyllanthus albidiscus* (Ridley) Airy Shaw].
- Macraea* Wight, Icon. Pl. Ind. Or. 5(2): 27, t. 1901, 1902. 1852 (non *Macraea* Lindley, 1828). TYPE: *Macraea oblongifolia* Wight [= *Phyllanthus simplex* Retz.; lectotype].
- Reidia* Wight, Icon. Pl. Ind. Or. 5(2): 27, t. 1903, 1904. 1852. TYPE: *Reidia floribunda* Wight [= *Phyllanthus wightianus* Muell. Arg.; lectotype chosen here].
- Chorisandra* Wight, Icon. Pl. Ind. Or. 6: 13, t. 1994. 1853. TYPE: *Chorisandra pinnata* Wight [= *Phyllanthus pinnatus* (Wight) Webster].
- Dichelactina* Hance, Walp. Ann. Bot. Syst. 3: 375. 1852. TYPE: *Dichelactina nodicaulis* Hance [= *Phyllanthus acidus* (L.) Skeels].
- Staurothyra* Griffith, Notul. Pl. Asiat. 4: 476. 1854. TYPE: not designated [ex descr., = *Phyllanthus acidus* (L.) Skeels].
- Hemicicca* Baillon, Etude Gén. Euphorb. 645. 1858. TYPE: *Hemicicca japonica* Baillon [= *Phyllanthus flexuosus* (Sieb. & Zucc.) Muell. Arg.].
- Williamia* Baillon, Etude Gén. Euphorb. 559. 1858. TYPE: *Williamia pruinosa* Baill. [= *Phyllanthus discolor* Poepp. ex Spr.].
- Orbicularia* Baillon, Etude Gén. Euphorb. 616. 1858. TYPE: *Orbicularia phyllanthoides* Baillon [nom. illeg., = *Phyllanthus orbicularis* HBK].
- Phyllanthodendron* Hemsley, Hook. Ic. Pl. 26: t. 2563, 2564. 1898. TYPE: *Phyllanthodendron mirabilis* (Muell. Arg.) Hems. [= *Phyllanthus mirabilis* Muell. Arg.].
- Aporosella* Chodat, Bull. Herb. Boiss. II. 5: 488. 1905. TYPE: *Aporosella hassleriana* Chod. [= *Phyllanthus chacoensis* Morong].
- Flueggeopsis* (Muell. Arg.) K. Schumann, Fl. Deutsche Schutzgeb. Nachtr. 289. 1905. TYPE: *Phyllanthus glaucus* Muell. Arg.
- Nymanina* K. Schumann, Fl. Deutsche Schutzgeb. Nachtr. 291. 1905. TYPE: *Nymanina insignis* K. Schum. [= *Phyllanthus schumannianus* L. S. Smith].
- Uranthera* Pax & Hoffm., Pflanzenz. 147. III (Heft 47): 95. 1911. TYPE: *Uranthera siamensis* Pax & Hoffm. [= *Phyllanthus roseus* (Craib & Hutch.) Beille].
- Dimorphocladium* Britton, Mem. Torrey Bot. Club 16: 74. 1920. TYPE: *Dimorphocladium formosum* (Urb.) Britton [= *Phyllanthus formosus* Urb.].
- Ramsdenia* Britton, Mem. Torrey Bot. Club 16: 72. 1920. TYPE: *Ramsdenia incrustata* (Urb.) Britton [= *Phyllanthus incrustatus* Urb.].
- Roigia* Britton, Mem. Torrey Bot. Club 16: 73. 1920. TYPE: *Roigia comosa* (Urb.) Britton [= *Phyllanthus comosus* Urb.].
- Dendrophyllanthus* Spencer Moore, J. Linn. Soc. Bot. 45: 395. 1921. TYPE: *Dendrophyllanthus comp-tonii* Sp. Moore [= *Phyllanthus moorei* Schmid].
- Pseudoglochidion* Gamble, Kew Bull. 1925: 329. 1925. TYPE: *Pseudoglochidion anamalayanum* Gamble [= **Phyllanthus anamalayanus** (Gamble) Webster, comb. nov.].
- Hexaspermum* Domin, Bibl. Bot. 89: 315. 1927. TYPE: *Hexaspermum paniculatum* Domin [= *Phyllanthus clamboides* (F. Muell.) Diels].
- Arachnodes* Gagnepain, Notul. Syst. (Paris) 14: 32. 1950; Airy Shaw, Kew Bull. 14: 469. 1960. TYPE: *Arachnodes chevalieri* Gagnep., loc. cit. [= **Phyllanthus chevalieri** (Gagnep.) Webster, comb. nov.].

A large and very diverse genus of 750–800 species, about 200 of which are American, 100 African, 70 Madagascan, and the remainder Asian and Australasian. Many attempts have been made to subdivide the genus, which very possibly is unnatural. Here, the broad concept of Mueller (1866) has been modified by the recognition of *Glochidion* and *Margaritaria* as distinct.

30. Reverchonina A. Gray, Proc. Amer. Acad. Arts Sci. 16: 107. 1880; Webster & Miller, Rhodora 65: 200. 1963. TYPE: *Reverchonina arenaria* A. Gray.

A monotypic genus confined to sand dunes in the southwestern United States and adjacent Mex-

ico. Although it is very close to *Phyllanthus*, it would appear excessively foreign if placed in that genus.

31. *Sauropus* Blume, Bijdr. 595. 1826; Muell. Agr., DC. Prodr. 15(2): 239. 1866; Bentham, Gen. Pl. 3: 271. 1880; Pax & Hoffm., Pflanzenz. 147. XV (Heft 81): 215. 1922; Airy Shaw, Kew Bull. 23: 42. 1969; Kew Bull. 35: 669. 1980. TYPE: *Sauropus albicans* (L.) Blume [= *Sauropus androgynus* (L.) Merr.; lectotype, selected here].

Ceratogynum Wight, Icon. Pl. Or. 5(2): 26. 1852. TYPE: *Ceratogynum rhamnoides* Wight [= *Sauropus quadrangularis* (Willd.) Muell. Arg.].

Diplomorpha Griffith, Notul. Pl. Asiat. 4: 479. 1854. TYPE: *Diplomorpha herbacea* Griffith [= *Sauropus bacciformis* (L.) Airy Shaw].

Synostemon F. Muell., Fragm. Phyt. Austral. 1: 32. 1858. TYPE: *Synostemon ramosissimus* F. Muell. [= *Sauropus ramosissimus* (F. Muell.) Airy Shaw; lectotype, designated by Wheeler, 1975].

Breyniopsis Beille, Bull. Soc. Bot. France 72: 157. 1925. TYPE: *Breyniopsis pierrei* Beille [= ***Sauropus pierrei*** (Beille) Webster, comb. nov.].

Heterocalymnantha Domin, Bibl. Bot. 89: 313. 1927. TYPE: *Heterocalymnantha minutifolia* Domin [= *Sauropus rigens* (F. Muell.) Airy Shaw].

A genus of about 50 species distributed from India and Sri Lanka to southern China, the Philippines, Borneo, and Australia. Airy Shaw (1980) has transferred a large number of Australian species of *Synostemon* to *Sauropus*, and it appears he may have good reason to do so, although the demarcation of *Sauropus* from *Breynia* is almost as problematical as its separation from *Synostemon*.

32. *Breynia* J. R. & G. Forster, Char. Gen. Pl. 145. 1776 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 438. 1866; Bentham, Gen. Pl. 3: 277. 1880; Hook f., Fl. Brit. Ind. 5: 329. 1887; Beille, Fl. Indochine 5: 631. 1927; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 59. 1931. *Foersteria* Scopoli, Intr. Hist. Nat. 98. 1777. TYPE: *Breynia disticha* J. R. & G. Forster.

Melanthesa Blume, Bijdr. 590. 1826. TYPE: *Melanthesa racemosa* Blume [lectotype, selected here; = *Breynia racemosa* (Blume) Muell. Arg.].

Melanthesopsis Muell. Arg., Linnaea 32: 74. 1863. TYPE: *Melanthesopsis lucens* (Poir.) Muell. Arg. [= *Breynia fruticosa* (L.) Hook. f.; lectotype, designated by Wheeler, 1975].

A difficult genus of 10–15 highly variable spe-

cies, found in tropical eastern Asia, Indonesia, tropical Asia, and the Pacific islands. The genus is barely separable from *Sauropus* on the one hand, and *Glochidion* on the other.

33. *Glochidion* J. R. & G. Forster, Char. Gen. Pl. 113, t. 57. 1776 (nom. cons.); Muell. Arg., Flora 1865: 369. 1865; Hook. f., Fl. Brit. Ind. 5: 305. 1887; Beille, Fl. Indochine 5: 608. 1927; Alston, Ann. Roy. Bot. Gard. Peradeniya 11: 1. 1928; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 56. 1931; Airy Shaw, Kew Bull. Add. Ser. 4: 115. 1975; Kew Bull. Add. Ser. 8: 92. 1980; Kew Bull. 35: 633. 1980; 36: 298. 1981; A. C. Smith, Fl. Vitiensis Nova 2: 467. 1981. TYPE: *Glochidion ramiflorum* J. R. & G. Forster.

Agyneia L., Mantissa Pl. 2: 161. 1771. TYPE: *Agyneia pubera* L. [= *Glochidion puberum* (L.) Muell. Arg.; lectotype, selected here].

Bradleja Banks ex Gaertner, Fruct. Sem. Pl. 2: 127. 1790. TYPE: *Bradleja sinica* Gaertner [= *Glochidion sinicum* (Gaertner) H. & A.].

Gynoon A. Juss., Mém. Mus. Hist. Nat. Paris 10: 335. 1823. TYPE: *Gynoon rigidum* A. Juss. [= *Glochidion rigidum* (A. Juss.) Muell. Arg.].

Glochidionopsis Blume, Bijdr. 588. 1826. TYPE: *Glochidionopsis sericea* Blume [= *Glochidion sericeum* (Blume) Hook. f.].

Glochisandra Wight, Icon. Pl. Ind. Or. 5: 26. 1852. TYPE: *Glochisandra acuminata* Wight [= *Glochidion lanceolarium* (Roxb.) Dalz.].

Zarcoa Llanos, Bot. Zeit. 15: 423. 1857. TYPE: *Zarcoa philippica* Llanos [= *Glochidion album* (Blanco) Boerl.].

Coccoglochidion K. Schum., Nachtr. Fl. Schutzgeb. 292. 1905. TYPE: *Coccoglochidion ethryococcus* [= *Glochidion philippicum* (Cav.) C. B. Robinson].

Hemiglochidion (Muell. Arg.) K. Schum., Nachtr. Fl. Schutzgeb. 289. 1905. TYPE: *Glochidion ramiflorum* Forst. [lectotype, designated by Wheeler, 1975; the choice of *Hemiglochidion hylo dendron* K. Schum. as lectotype by Farr et al. (1979) appears invalid, as the species was not included in *Glochidion* sect. *Hemiglochidion* by Mueller].

Tetraglochidion K. Schum., Nachtr. Fl. Schutzgeb. 291. 1905. TYPE: *Tetraglochidion gimi* K. Schum. [= *Glochidion gimi* (K. Schum.) Pax & Hoffm.].

An Asian and Australasian genus of more than 200 species, a few extending to Polynesia. The genus was combined with *Phyllanthus* by Mueller (1866) and Bentham (1880), but most subsequent workers have treated it as distinct, even though it represents a specialized offshoot from ancestral taxa within *Phyllanthus*.

Tribe 5. DRYPETEAE (Grisebach) Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 334. 1954 (as tribe in Antidesmataceae). Phyllan-

theae subtribe Drypeteae Griseb., Fl. Br. W. Ind. 31. 1859. TYPE: *Drypetes* Vahl.

Antidesmeae * Putranjiveae Endl., Gen. Pl. 287. 1837. Ordo Putranjiveae Endlicher, Gen. Pl. Ord. Nat. 287. 1837. Putranjivaceae Endl. ex Meeuse, Euphorbiaceae Auct. Plur. 30. 1990. TYPE: *Putranjiva* Wallich.

Cyclostemonées Baillon, Etude Gén. Euphorb. 561. 1858. Phyllanthaeae subtribe Cyclostemonae Baillon ex Muell. Arg., Linnaea 34: 64. 1865. TYPE: *Cyclostemon* Blume [= *Drypetes* Vahl].

Dioecious trees or shrubs; leaves entire or dentate, stipulate; flowers in axillary clusters, or cauliflorous; sepals mostly 4 or 5, imbricate; petals absent; staminate disk intrastaminal; stamens (2–) 3–20(–50), free, anthers introrse or extrorse; pollen grains 3-colporate, reticulate; pistillode small or obsolete; pistillate sepals deciduous (persistent in *Sibangea*); disk annular or lacking; ovary usually 1- or 2-locular; styles mostly entire and dilated; ovules anatropous, with massive obturator; fruit capsular or drupaceous; seeds 1 per locule or fruit; endosperm copious; cotyledons plane, broader and somewhat longer than radicle.

As circumscribed here, tribe Drypeteae includes four genera, with the vast majority of species in the large and variable genus *Drypetes*. The recent study by Hayden has demonstrated that *Neowarrea*, included in the Drypeteae by Webster (1975), is really a species of *Flueggea*.

KEY TO THE GENERA OF TRIBE DRYPETEAE

- 1a. Ovary 3-locular; fruit capsular; styles bifid, style-branches slender 34. *Lingelsheimia*
- 1b. Ovary mostly 1- or 2-locular; fruit drupaceous; styles not bifid.
 - 2a. Disk present; stamens mostly 4 or more; styles stigmatiform.
 - 3a. Pistillate sepals imbricate in bud, deciduous in fruit 35. *Drypetes*
 - 3b. Pistillate sepals open in bud, persistent in fruit 36. *Sibangea*
 - 2b. Disk absent; stamens mostly 2 or 3; styles petaloid-dilated 37. *Putranjiva*

34. *Lingelsheimia* Pax, Bot. Jahrb. 43: 317. 1909; Mildbraed, Deutsche Zentral-Afr. Exped. 2: t. 54, 55. 1912; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 279. 1922; Léonard, Bull. Soc. Roy. Bot. Belg. 84: 49. 1951; Brenan, Kew Bull. 1952: 445. 1953; Léonard, Bull. Jard. Bot. Brux. 32: 513. 1962. TYPE: *Lingelsheimia frutescens* Pax.

Danguyodrypetes Leandri, Bull. Soc. Bot. France 85: 524. 1938. TYPE: *Danguyodrypetes manongari-*

vensis Leandri [= *Lingelsheimia manongari-vensis* (Leandri) Webster, comb. nov.].

As interpreted by Léonard (1951, 1962b), *Lingelsheimia* is an African genus of two species. However, the four Madagascan species referred to *Danguyodrypetes* by Leandri clearly appear congeneric. The genus appears anomalous in the Drypeteae, and it is possible that its correct place is in tribe Phyllanthaeae. Levin (pers. comm.) suggests a possible affinity to *Aerisilvaea*.

35. *Drypetes* Vahl, Eclog. Amer. 3: 49. 1810; Muell. Arg., DC. Prodr. 15(2): 453. 1866; Bentham, Gen. Pl. 3: 278. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 229. 1922; Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 337. 1954; Leandri, Fl. Madag. 111(1): 144. 1958; van Steenis, Blumea 10: 140. 1960; Léonard, Bull. Jard. Bot. Brux. 32: 513. 1962; Smith & Ayensu, Brittonia 16: 220. 1964; Airy Shaw, Kew Bull. 18: 272. 1965; 27: 309. 1972; Add. Ser. 4: 97. 1975; Kew Bull. 36: 286. 1981; A. C. Smith, Fl. Vitiensis Nova 2: 455. 1981. TYPE: *Drypetes glauca* Vahl.

Koelera Willd., Sp. Pl. ed. 4, 750. 1806, nom. illeg. (non *Koelera* Pers., 1805). *Limacia* Dietr., Nachr. Vollst. Lex. Gartn. 4: 383. 1818, nom. illeg. (non *Limacia* Lour., 1790). TYPE: *Koelera laurifolia* Willd. [= *Drypetes lateriflora* (Sw.) Kr. & Urb.].

Liparena Poit. ex Leman, Dict. Sci. Nat. 27: 6. 1823. TYPE: not designated.

Cyclostemon Blume, Bijdr. 597. 1826. TYPE: *Cyclostemon macrophyllum* Blume [lectotype, selected here; = *Drypetes macrophylla* (Blume) Pax & Hoffm.]. *Hemicyclia* Wight & Arn., Edinb. New Phil. J. 14: 297. 1833 (as *Hemicyclia*). TYPE: *Hemicyclia sepiaria* Wight & Arn. [= *Drypetes sepiaria* (Wight & Arn.) Pax & Hoffm.].

Astylis Wight, Icon. Pl. Ind. Orient. 6: t. 1992. 1853. TYPE: *Astylis venusta* Wight [= *Drypetes venusta* (Wight) Pax & Hoffm.].

Sphragidia Thwaites, Hook. J. Bot. Kew Misc. 7: 269. 1855. TYPE: *Sphragidia zeylanica* Thwaites [= *Drypetes longifolia* (Blume) Pax & Hoffm.].

Dodecastemon Hasskarl, Versl. Meded. Afd. Natuurk. Kon. Akad. Wet. 4: 141. 1856. TYPE: *Dodecastemon teysmanii* Hassk. [= *Drypetes teysmanii* (Hassk.) Bakh. f. & van Steenis].

Pycnosandra Blume, Mus. Bot. Lugd.-Bat. 2: 191. 1856. TYPE: *Pycnosandra serrata* (Blume) Blume [= *Drypetes serrata* (Blume) Pax & Hoffm., nom. illeg. (non *D. serrata* (Krug & Urb.) = *Drypetes teysmanii* (Hassk.) Bakh. f. & van Steenis].

Cometia Du Petit Thouars ex Baillon, Etude Gén. Euphorb. 642. 1858. TYPE: *Cometia thouarsii* Baillon [= *Drypetes thouarsii* (Baillon) Leandri].

Anaua Miquel, Fl. Ned. Ind., Eerste Bijv. 410. 1861. TYPE: *Anaua sumatrana* Miq. [= *Drypetes sumatrana* (Miq.) Pax & Hoffm.].

- Laneasagum* Beddome, Madras J. Lit. Sci., ser. 2, 22: 71. 1861. TYPE: *Laneasagum oblongifolia* Bedd. [= *Drypetes longifolia* (Bl.) Pax & Hoffm.].
- Stelechanteria* Thouars ex Baillon, Adansonia I. 4: 147. 1864. TYPE: *Stelechanteria thouarsiana* Baillon [= *Drypetes thouarsiana* (Baillon) Capuron].
- Freireodendron* Muell. Arg., DC. Prodr. 15(2): 245. 1866. TYPE: *Freireodendron sessiliflorum* (Fr. Allem.) Muell. Arg. [= *Drypetes sessiliflora* Fr. Allem.].
- Humblotia* Baillon, Bull. Mens. Soc. Linn. Paris 1: 593. 1886. TYPE: *Humblotia comorensis* Baillon [= *Drypetes comorensis* (Baillon) Pax & Hoffm.].
- Guya* Frappier ex Cordemoy, Fl. Ile Réunion 350. 1895. TYPE: *Guya caustica* Frapp. ex Cordemoy. [= *Drypetes caustica* (Frapp. ex Cordemoy) Airy Shaw].
- Riseleya* Hemsley, J. Bot. 55: 286. 1917. TYPE: *Riseleya griffithii* (Hook. f.) Hemsl. [= *Drypetes indica* (Muell. Arg.) Pax & Hoffm.].
- Calyptosepalum* Spencer Moore, J. Bot. 63 (suppl.): 91. 1925. TYPE: *Calyptosepalum sumatranum* Sp. Moore [= *Drypetes calyptosepala* Airy Shaw].
- Brexiopsis* H. Perrier, Notul. Syst. (Paris) 10: 192. 1942. TYPE: *Brexiopsis aquifolia* H. Perr. [= *Drypetes bathiei* Capuron & Leandri].

A large and variable genus of ca. 200 species; poorly represented in the New World, with ca. 10 species; ca. 60 species in Africa and Madagascar; the remainder in Asia and Australasia. Mueller (1866) and Bentham (1880) recognized *Cyclostemon* and *Hemicyclia* as distinct from *Drypetes*, but most 20th century students have followed Pax & Hoffman (1922) in combining them. There is considerable anatomical and palynological variation within *Drypetes* sensu lato, however, and the generic limits require further study. I am indebted to Geoffrey Levin (pers. comm.) for critical suggestions on the generic synonymy.

- 36. *Sibangea*** Oliver, Hook. Ic. Pl. 15: 9, t. 1411. 1883; Radcliffe-Smith, Kew Bull. 32: 480. 1978; Fl. Trop. E. Afr., Euphorb. 101. 1987. TYPE: *Sibangea arborescens* Oliver.

As interpreted by Radcliffe-Smith, *Sibangea* includes three African species. The genus is very close to *Drypetes*, and it remains to be seen whether it can be maintained as distinct.

- 37. *Putranjiva*** Wallich, Tent. Fl. Nepal 61. 1826; Muell. Arg., DC. Prodr. 15(2): 443. 1866; Bentham, Gen. Pl. 3: 277. 1880; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 59. 1931. TYPE: *Putranjiva roxburghii* Wallich [= *Nageia putranjiva* Roxburgh].

- Palenga* Thwaites, Hook. J. Bot. Kew Gard. Misc. 8: 270. 1856. TYPE: *Palenga zeylanica* Thwaites [= *Putranjiva zeylanica* (Thwaites) Muell. Arg.].
- Li dendron* Keng, J. Washington Acad. Sci. 41: 201. 1951. TYPE: *Li dendron matsumurae* (Koidzumi) Keng [= *Putranjiva matsumurae* Koidz.].

A small genus of three or four Asian species (India, Sri Lanka, Taiwan, and the Ryukyu Islands), questionably separable from *Drypetes*.

- Tribe 6. ANTIDESMEAE** (Sweet) Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 322. 1954 [as tribe of Antidesmataceae]. Ordo Stilagineae Agardh, Aphor. 199, Class. Pl. 9. 1825. Ordo Antidesmeae Sweet, Hort. Brit. ed. 2, 460. 1830. Tribe Biovulatae sect. Antidesmeae Thw., Enum. Pl. Zeyl. 289. 1861. TYPE: *Antidesma* L.

Dioecious (rarely monoecious) trees or shrubs (rarely herbs); leaves alternate, entire, penninerved, glandular or eglandular, stipulate; inflorescences usually axillary, amentlike; sepals 3–6, free or connate, imbricate; petals reduced or absent (except *Spondianthus*); disk annular, lobed, or dissected; stamens 2–8, free or nearly so; anthers extrorse or introrse; pollen grains mostly prolate, 3-colporate, reticulate; pistillode present or absent; carpels (1) 2 or 3 (–5); ovules anatropous; styles bifid to bipartite (rarely entire, sometimes dilated); fruit capsular or drupaceous; seeds mostly 1 per locule (or 1 per fruit); seed-coat dry or fleshy; endosperm thin to copious; cotyledons mostly broader than radicle.

This mainly paleotropical tribe of 18 genera in 5 subtribes is well characterized by its leaves with tanniferous epidermis (Levin, 1986a) and prolate pollen grains with 3 narrow colpi (Köhler, 1965). The tribe is here given a broader circumscription than that of Hurusawa (1954), who did not include the Spondianthinae, Uapacinae, or Porantherinae.

KEY TO THE SUBTRIBES OF TRIBE ANTIDESMEAE

- 1a. Stems with resinous secretion; inflorescence paniculate, or capitulate.
- 2a. Petals present; inflorescence terminal, paniculate, bracts small; pollen sexine not spinulose; fruit capsular; stomata paracytic 6a. Spondianthinae
- 2b. Petals absent; inflorescences axillary, capitate, bracts large and involucrate; pollen sexine spinulose; fruit drupaceous; stomata anisocytic 6b. Uapacinae
- 1b. Stems lacking resin; inflorescence not paniculate or capitulate; petals mostly absent.
- 3a. Inflorescences axillary, amentlike; trees or shrubs (except *Cyathogyne*).
- 4a. Pollen grains globose or slightly prolate; anther locules not pendulous; leaves sometimes glandular; stomata anisocytic 6c. Scepinae
- 4b. Pollen grains distinctly prolate; anther locules ± pendulous; leaves not glandular; stomata paracytic 6d. Antidesminae

- 3b. Inflorescences terminal, corymbiform; herbs
..... 6e. Porantherinae

Subtribe 6a. SPONDIANTHINAE (Webster)

Webster, stat. nov. Tribe Spondiantheae Webster, Taxon 24: 594. 1975. TYPE: *Spondianthus* Engler.

Diocious trees; leaves entire, penninerved, stipules caducous; inflorescences terminal (at least in part), paniculate, bracts small; flowers (at least the staminate) with petals; staminate disk dissected; stamens 5, filaments free, anthers introrse; pistillode present; pistillate disk lobed; styles free; fruit loculicidally dehiscent; columella persistent; seeds 1 per locule, testa dry; endosperm scanty; embryo with cotyledons much broader than radicle.

A monotypic tribe, including only the African genus *Spondianthus*. Pax & Hoffmann (1922) placed it adjacent to *Thecacoris*, a genus of subtribe Antidesminae. Levin (1986c), on the basis of foliar characters, suggested that it is the primitive sister group of the other woody tribes of Antidesmeae. The observations of Köhler (1965) on pollen suggest a similar position.

- 38. *Spondianthus*** Engler, Bot. Jahrb. 36: 215. 1905; Hutch., Hook. Icon. Pl. 30: t. 2986. 1911; Fl. Trop. Afr. 6(1): 1044. 1913; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 13. 1922; Keay, Fl. W. Trop. Afr. ed. 2, 1: 372. 1958; Aubreville, Fl. Forest. Côte d'Ivoire, ed. 2, 2: 62. 1959; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 104. 1987; Léonard & Nkounkou, Bull. Jard. Bot. Nat. Belg. 59: 133. 1989. TYPE: *Spondianthus preussii* Engler.

Megabaria De Wild., Etud. Fl. Bas & Moy. Congo 2: 284. 1908. TYPE: *Megabaria trillesii* De Wild. [= *Spondianthus preussii* Engler].

A monotypic genus of a single variable species, widespread in tropical Africa from Liberia to Angola and Tanzania.

- Subtribe 6b. UAPACINAE** Muell. Arg., Linnaea 34: 64. 1865 (as Phyllanthae subtr. Uapaceae). Tribe Uapaceae (Muell. Arg.) Hutch., Amer. J. Bot. 56: 747. 1969. Family Uapaceae (Muell. Arg.) Airy Shaw, Kew Bull. 18: 270. 1965. TYPE: *Uapaca* Baillon.

Diocious trees or shrubs; leaves entire, pinnately veined, stipules caducous; inflorescences axillary, capitate, involucrate, pedunculate; flowers apetalous and without floral disk; calyx gamo-

phyllous; stamens 5, filaments free, anthers introrse; pistillode apically dilated; pistillate calyx gamophyllous; ovary mostly 3-locular; styles free, multifid; fruit drupaceous; seeds 1 per locule, albuminous; cotyledons much longer than radicle.

This subtribe includes only the single genus *Uapaca*, which has always appeared isolated because of its remarkable involucrate inflorescences: Airy Shaw (1965) and Meeuse (1990) have assigned it to a separate family, Uapacaceae. However, Bentham (1880) juxtaposed it with *Aporusa*, and Pax (1890) referred it to his subtribe Antidesminae. Those intuitions appear confirmed by the foliar anatomical studies of Levin (1986a, b, c), who has found that the tanniferous epidermal cells and anisocytic stomata indicate an affinity with subtribe Scepiniae. On the other hand, the distinctive pollen and resiniferous stems of *Uapaca* are divergent characters, and it appears best referred to a separate subtribe.

- 39. *Uapaca*** Baillon, Etude Gén. Euphorb. 595. 1858; Muell. Arg., DC. Prodr. 15(2): 489. 1866; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 298. 1922; Leandri, Fl. Madag. 111(1): 163. 1958; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 567. 1988. TYPE: *Uapaca thouarsii* Baillon [lectotype, selected by Airy-Shaw, Kew Bull. 18: 271. 1965].

A genus of ca. 60 species in Africa and Madagascar.

- Subtribe 6c. SCEPINAE** (Lindley) Webster, stat. nov. Ordo Scepaceae Lindl., Nat. Syst. Bot. ed. 2, 171. 1836. TYPE: *Scepa* Lindl. [= *Aporusa* Bl.].

Ordo Aporuseae Lindl. ex Miq., Fl. Ind. Bat. 1(2): 430. 1858. Tribe Aporuseae (Lindl. ex Miq.) Airy Shaw, Hook. Icon. Pl. 38: t. 3701. 1974; Webster, Taxon 24: 594. 1975. TYPE: *Aporusa* Bl.

Diocious or monoecious trees or shrubs, stems without resinous secretion; leaves often with laminar glands, stomata mostly anisocytic (paracytic in *Jablonskia*), stipules deciduous or persistent; staminate bracts mostly each with 3 or more flowers; sepals 4–8, free; petals absent; disk lobed, dissected, or absent; stamens 4–8, free; anthers dehiscent longitudinally, connective not enlarged; pollen grains subglobose to subprolate, 3-colporate, reticulate or tectate; pistillode present; ovary 2–5-locular; styles bifid or unlobed; fruit capsular or tardily dehiscent and subdrupaceous; seeds 1–6 per fruit, seed-coat dry or fleshy; endosperm thin

to copious, cotyledons mostly distinctly broader and longer than radicle.

This taxon, although early designated by Lindley (1836) as an "ordo," was confounded by Muelller (1866) and later authors with the Antidesminae, and was first recognized in the 20th century by

Airy Shaw (1974) at the tribal rank. Since Lindley published the Scepaeae over 20 years before the ordo Aporuseae was proposed, it seems preferable to preserve his name. The seven genera of Scepinae are scattered through the tropics in America, Africa, and Asia, with only *Baccaurea* attaining the Pacific islands.

KEY TO THE GENERA OF SUBTRIBE SCEPINAE

- 1a. Pistillate disk dissected; styles dilated, entire to slightly lobed 40. *Protomegabaria*
 1b. Pistillate disk cupular or absent.
 2a. Staminate disk present.
 3a. Pistillate disk present; pistillate sepals persistent in fruit.
 4a. Dioecious; flowers racemose; stipules deciduous.
 5a. Capsule loculicidal; staminate flowers mostly one per bract 41. *Maesobotrya*
 5b. Capsule septicidal; staminate flowers several per bract 42. *Richeria*
 4b. Monoecious; flowers in axillary glomerules; stipules persistent; capsule septicidal 43. *Jablonskia*
 3b. Pistillate disk absent; pistillate sepals deciduous.
 6a. Dioecious; styles bifid 44. *Baccaurea*
 6b. Monoecious; styles unlobed 45. *Apodiscus*
 2b. Staminate disk absent.
 7a. Pistillode massive, peltate; stamens 5 or 6; carpels mostly 3 or 4; styles stigmatiform 46. *Ashtonina*
 7b. Pistillode small; stamens mostly 2 (rarely 3-5); carpels mostly 2 (rarely 3 or 4); styles bifid
 47. *Aporusa*

40. *Protomegabaria* Hutchinson, Hook. Icon. Pl. 30: t. 2929. 1911; Fl. Trop. Afr. 6(1): 656. 1912; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 43. 1922; Keay, Fl. W. Trop. Afr. ed. 2, 1: 373. 1958; Aubreville, Fl. For. Côte, d'Ivoire 2: 68, t. 147. 1959. TYPE: *Protomegabaria stapfiana* (Beille) Hutch. (lectotype, selected here).

Two species of West Africa.

41. *Maesobotrya* Bentham, Hook. Icon. Pl. 13: 75, t. 1296. 1879; Gen. Pl. 3: 284. 1880; Hutchinson, Fl. Trop. Afr. 6(1): 663. 1912; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 17. 1922; Léonard, Bull. Jard. Bot. Brux. 17: 256. 1945; Keay, Fl. W. Trop. Afr. ed. 2, 1: 373. 1958; Radcliffe-Smith, Fl. Trop. E. Afr. Euphorb. 112. 1987. TYPE: *Maesobotrya floribunda* Bentham.

Staphysora Pierre, Bull. Soc. Linn. Paris 1233. 1896; Pax, Bot. Jahrb. 23: 521. 1897. TYPE: *Staphysora dusenii* Pax [= *Maesobotrya dusenii* (Pax) Hutch.].

An African genus of ca. 20 species, all in West Africa and only 1 species extending east to Uganda. The genus is extremely close to the neotropical *Richeria*.

42. *Richeria* Vahl, Eclog. Amer. 1: 30, t. 4. 1797; Muell. Arg., DC. Prodr. 15(2): 466.

1866; Fl. Bras. 11(2): 13. 1873; Bentham, Genera Plantarum 3: 286. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 26. 1922; Jablonski, Mem. New York Bot. Gard. 17: 124. 1967; Philcox, Fl. Trin. Tob. 2(9): 638. 1979; Webster, Ann. Missouri Bot. Gard. 75: 1093. 1989; Secco & Webster, Bol. Mus. Para. Emilio Goeldi, Bot. 6: 141-158. 1990. TYPE: *Richeria grandis* Vahl.

Guarania Weddell ex Baillon, Etude Gén. Euphorb. 598. 1858. TYPE: *Guarania gardneriana* Baillon [= *Richeria gardneriana* (Baillon) Baillon; lectotype].

A genus of several poorly defined taxa, treated as two species by Secco & Webster (1990); extending in lowland and montane tropical rainforest from Costa Rica and the Lesser Antilles to Peru and Brazil.

43. *Jablonskia* Webster, Syst. Bot. 9: 232. 1984. TYPE: *Jablonskia congesta* (Benth. ex Muell. Arg.) Webster [*Securinega congesta* Benth. ex Muell. Arg.].

Monotypic, the single species confined to Amazonian South America. The genus is isolated in subtribe Scepinae by its distinctive pollen type and paracytic stomata and shows some similarities to *Celianella* Jabl. in subtribe Antidesminae. Its placement requires further evaluation.

44. *Baccaurea* Loureiro, Fl. Cochinch. 661. 1790; Muell. Arg., Prodr. 15(2): 456. 1866; Bentham, Gen. Pl. 3: 283. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 45. 1922; Airy Shaw, Kew Bull. 14: 353. 1960; Backer & Bakh., Fl. Java 1: 453. 1963; Whitmore, Tree Fl. Malaya 2: 63. 1973; A. C. Smith, Fl. Vit. Nov. 2: 450. 1981; Thin, Công Trình Nghiên Cứu Khoa Học 10: 78. 1986. TYPE: *Baccaurea ramiflora* Lour. [lectotype, selected by Merrill, 1935].

Pierardia Roxb. ex Jack, Trans. Linn. Soc. London 14: 119. 1823. TYPE: *Pierardia dulcis* Jack [= *Baccaurea dulcis* (Jack) Muell. Arg.].

Adenocrepis Blume, Bijdr. 579. 1825. TYPE: *Adenocrepis javanica* Bl. [= *Baccaurea javanica* (Bl.) Muell. Arg.].

Calyptroon Miquel, Fl. Ned. Ind., Erste Bijv. 471. 1861. TYPE: *Calyptroon sumatranum* Miq. [= *Baccaurea sumatrana* (Miq.) Muell. Arg.].

Microsepala Miquel, Fl. Ned. Ind., Erste Bijv. 444. 1861. TYPE: *Microsepala acuminata* Miq. [= *Baccaurea javanica* (Bl.) Muell. Arg.].

Everettiodendron Merrill, Phil. J. Sci. Bot. 4: 279. 1909. TYPE: *Everettiodendron philippinense* Merr. [= *Baccaurea philippinensis* (Merr.) Merr.].

Gatnaia Gagnepain, Bull. Soc. Bot. France 71: 870. 1924. TYPE: *Gatnaia annamica* Gagnep. [= *Baccaurea oxycarpa* Gagnep.].

A diversified genus of ca. 75 paleotropical species, extending from India to the Philippines, New Guinea, and the Pacific islands.

45. *Apodiscus* Hutchinson, Bull. Soc. Bot. France 58, Mem. 8: 205. 1912; Fl. Trop. Afr. 6(1): 1045. 1913; Hook. Icon. Pl. 31: t. 3032. 1915; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 45. 1922. TYPE: *Apodiscus chevalieri* Hutch.

A poorly understood monotypic genus from the Guinea region of west Africa; said by Pax and Hoffmann to be related to *Maesobotrya*.

46. *Ashtonia* Airy Shaw, Kew Bull. 357. 1968; Hook. Icon. Pl. 38: t. 3702. 1974; Whitmore, Tree Fl. Malaya 2: 62. 1972; Airy Shaw, Kew Bull. Add. Ser. 4: 42. 1975. TYPE: *Ashtonia excelsa* Airy Shaw.

An Old World genus of two species in Borneo and the Malay peninsula.

47. *Aporusa* Blume, Bijdr. 514. 1826 (as *Aporosa*); Fl. Jav. 1: viii. 1828; Muell. Arg., DC. Prodr. 15(2): 469. 1866; Bentham, Gen. Pl.

3: 282. 1880; Hook. f., Hook. Icon. Pl. 16: 5. 1583. 1887; Fl. Brit. Ind. 5: 345. 1887; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 80. 1922; Backer & Bakh., Fl. Java 1: 455. 1963; Airy Shaw, Kew Bull. 30: 380. 1966; 23: 2. 1969; 25: 474. 1971; Thin, Công Trình Nghiên Cứu Khoa Học 10: 82. 1986. TYPE: *Aporusa frutescens* Blume.

Leiocarpus Blume, Bijdr. 581. 1826. TYPE: *Leiocarpus fruticosus* Blume [= *Aporusa fruticosa* (Blume) Muell. Arg.; lectotype, designated by Wheeler, 1975].

Lepidostachys Wallich ex Lindley, Nat. Syst. ed. 2, 441. 1836. TYPE: *Lepidostachys roxburghii* Wallich ex Lindley [nom. illeg.; = *Aporusa dioica* (Roxb.) Muell. Arg.].

Scepa Lindley, Nat. Syst. ed. 2, 441. 1836. TYPE: *Scepa stipulacea* Lindley [= *Aporusa dioica* (Roxb.) Muell. Arg.].

A genus of 80 Old World species, from India and Sri Lanka to Indonesia and Melanesia (Solomon Islands).

Subtribe 6d. ANTIDESMINAE Muell. Arg., Linnaea 34: 64. 1865 (as *Antidesmeae*); Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 26. 1890; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 3. 1922. TYPE: *Antidesma* L.

Ordo Stilagineae C. A. Agardh, Aphor. Bot. 14: 199. 1824. TYPE: *Stilago* L. [= *Antidesma* L.].

Subtribe Hieronymaeae Muell. Arg., Linnaea 34: 64. 1865. TYPE: *Hyeronima* Fr. Allem.

Dioecious (rarely monoecious) trees or shrubs (rarely herbs); leaves eglandular, stomata paracytic, stipules caducous; inflorescences axillary, \pm amentlike; staminate bracts mostly 1-flowered; sepals 3–6, free or connate; petals mostly absent or reduced; disk lobed or dissected; stamens 3–6, free or nearly so, anthers with \pm enlarged glandular connectives, anther-sacs usually pendulous; pollen grains prolate, 3-colporate, reticulate; pistillode present; carpels 1–3(–5), ovules anatropous; styles bifid (rarely entire); fruit capsular or drupaceous; seeds mostly 1 per locule or fruit; seed-coat dry; endosperm thin to copious, cotyledons broader than but scarcely exceeding radicle.

Subtribe Antidesminae corresponds to the family Stilaginaceae as recognized by Airy Shaw (1965, and many subsequent publications). However, pollen and foliar anatomical evidence clearly supports membership of *Antidesma* in the Euphorbiaceae. Two of the six genera (*Phyllanoea* and *Leptonema*) are not well understood, and their inclusion here must be regarded as provisional.

KEY TO THE GENERA OF SUBTRIBE ANTIDESMINAE

- 1a. Indumentum absent or of simple or stellate hairs.
 2a. Carpels 3-5; fruit dehiscent.
 3a. Disk present; ovary 3-locular.
 4a. Pistillode present; pistillate sepals not accrescent in fruit; pistillate flower sometimes with petals and staminodes.
 5a. Leaves entire; pistillate flowers not bracteolate; fruits pedicellate 48. *Thecacoris*
 5b. Leaves dentate; pistillate flowers bracteolate; fruits sessile 49. *Phyllanoa*
 4b. Pistillode absent; pistillate sepals accrescent; pistillate flowers lacking petals or staminodes
 50. *Celianella*
 3b. Disk absent; ovary 4-5-locular 51. *Leptonema*
 2b. Carpel solitary; fruit indehiscent 52. *Antidesma*
 1b. Indumentum lepidote; fruit indehiscent 53. *Hyeronima*

48. *Thecacoris* A. Jussieu, Euphorb. Tent. 12. 1824; Baillon, Etude Gén. Euphorb. 605. 1858; Bentham, Gen. Pl. 3: 286. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 8. 1922; Keay, Fl. W. Trop. Afr. ed. 2, 1: 371. 1958; Leandri, Fl. Madag. 1: 4. 1958; Radcliffe-Smith, Fl. Trop. E. Afr. Euphorb. 107. 1987. TYPE: *Thecacoris madagascariensis* A. Juss.

Cometia Du Petit Thouars ex Baillon, Etude, Gén. Euphorb. 642. 1858. TYPE: *Cometia thouarsii* Baillon [= *Thecacoris cometia* Leandri].

Cyathogyne Muell. Arg., Flora 47: 536. 1864. TYPE: *Cyathogyne viridis* Muell. Arg. [= *Thecacoris viridis* (Muell. Arg.) Leandri].

Baccaureopsis Pax, Bot. Jahrb. 43: 319. 1909. TYPE: *Baccaureopsis lucida* Pax [= *Thecacoris ludica* (Pax) Hutch.].

As here delimited, *Thecacoris* includes about 20 species from Africa and Madagascar. The herbaceous species have been segregated as a separate genus *Cyathogyne* by Mueller (1866) and Pax & Hoffmann (1922, 1931), but as noted by Radcliffe-Smith (1987), *Thecacoris usambarensis* Verdc. bridges the gap between the two generic concepts.

49. *Phyllanoa* Croizat, Caldasia 2: 123. 1943. TYPE: *Phyllanoa colombiana* Croizat.

A monotypic genus from the Colombian Andes, known only from the imperfect type specimen. The floral details of the pistillate flower, especially the staminodes, suggest a possible affinity with *Thecacoris*, although there is also a general resemblance to *Richeria*, in subtribe Scepinae.

50. *Celianella* Jablonski, Mem. New York Bot. Gard. 12: 176. 1965. TYPE: *Celianella montana* Jabl.

A monotypic genus of the Venezuelan Guayana highlands. The plant is distinctive in the semisucculent leaves and accrescent pistillate sepals. Levin (1986c) allied it with *Hyeronima* on the basis of foliar characters.

51. *Leptonema* A. Jussieu, Euphorb. Tent. 19. 1824; Bentham, Gen. Pl. 3: 275. 1880; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 59. 1931; Leandri, Notul. Syst. (Paris) 6: 22. 1937; Mém. Inst. Sci. Madag. 8B: 212. 1957; Fl. Madag. 111(1): 12. 1958. TYPE: *Leptonema venosum* (Poir.) A. Juss.

A poorly known genus of two species endemic to Madagascar.

52. *Antidesma* Burman ex L., Sp. Pl. 1027. 1753; Gen. Pl. 451. 1754; Muell. Arg., DC. Prodr. 15(2): 247. 1866; Bentham, Gen. Pl. 3: 284. 1880; Hooker, Fl. Brit. Ind. 5: 354. 1887; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 107. 1922; Airy Shaw, Kew Bull. 23: 277. 1969; 26: 457. 1972; 28: 269. 1973; 33: 15, 423. 1979; 36: 358, 635. 1981; Léonard, Bull. Jard. Bot. Nat. Belg. 58: 4. 1988. *Bestram* Adanson, Fam. Pl. 354. 1763. TYPE: *Antidesma alexiteria* L.

Stilago L., Mant. Pl. 16. 1767. TYPE: *Stilago bunius* L. [= *Antidesma bunius* (L.) Spreng.].

Rhytis Lour., Fl. Cochinchin. 660. 1790. TYPE: *Rhytis fruticosa* Lour. [= *Antidesma fruticosum* (Lour.) Muell. Arg.].

A large Old World genus of ca. 200 species, only 10 of which occur in Africa and Madagascar. The remainder of the species are Asian except for a few species in Australia and the Pacific islands.

53. *Hyeronima* Allemão, Pl. Novas Bras. 1. 1848; Muell. Arg., DC. Prodr. 15(2): 268. 1866 (as *Hieronyma*); Bentham, Gen. Pl. 3: 284. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 31. 1922; Jablonski, Mem. New York Bot. Gard. 17: 122. 1967; Webster, Ann. Missouri Bot. Gard. 75: 1094. 1988; Franco, Bot. Jahrb. Syst. 111: 297. 1990. TYPE: *Hyeronima alchorneoides* Allemão.

Stilaginella Tul., Ann. Sci. Nat. III. 15: 240. 1851. TYPE: *Stilaginella laxiflora* Tul. [= *Hyeronima laxiflora* (Tul.) Muell. Arg.].

A neotropical genus of more than 20 described species, many of these difficult to distinguish. Franco (1990) recognized 10 species for South America, and there are a few additional species in the West Indies.

Subtribe 6e. PORANTHERINAE (Muell. Arg.)

Köhler, Grana Palynologica 6: 99. 1965. Tribe Poranthereae Muell. Arg., Bot. Zeitung 22: 324. 1864. TYPE: *Poranthera* Rudge.

Monoecious or dioecious herbs or shrubs; leaves \pm ericoid; flowers in terminal corymbose racemes; sepals 5; petals present or absent; stamens 5; disk present; anthers pendulous; pistillode small or absent; pistillate disk annular; ovary 3-locular; ovules anatropous; styles bifid; fruits capsular; seeds 2 per locule; endosperm copious; cotyledons about as broad as radicle.

Two closely related Australasian genera. Their systematic position remains controversial. Pax & Hoffmann (1931) followed Mueller (1866) in placing tribe Porantheae in the division "Stenolobae," because of the narrow cotyledons. In 1975, I associated *Poranthera* with *Andrachne*, partly because of the pollen data of Punt (1962). However, Köhler (1965) showed that the pollen of *Poranthera* was more compatible with an affinity to the *Antidesma* complex, and he demoted Porantheae to a subtribe of Antidesminae. Because he did not cite the basionym, his combination was not validly published, and it presumably is validated here.

KEY TO THE GENERA OF SUBTRIBE PORANTHERINAE

- 1a. Monoecious; petals and pistillode present
..... 54. *Poranthera*
1b. Dioecious; petals and pistillode absent
..... 55. *Oreoporanthera*

54. *Poranthera* Rudge, Trans. Linn. Soc. London 10: 302. 1811; Bentham, Fl. Austral. 6: 54. 1873; Gen. Pl. 3: 262. 1880; Grüning, Pflanzenr. 147. (Heft 58): 13. 1913. TYPE: *Poranthera* Rudge.

Ten species from Australia.

55. *Oreoporanthera* Hutchinson, Amer. J. Bot. 56: 747. 1969. *Poranthera* sect. *Oreoporanthera* Grüning, Pflanzenr. 147. (Heft 58): 21. 1913. TYPE: *Oreoporanthera alpina* (Cheeseman) Hutchinson.

A monotypic genus endemic to New Zealand. As pointed out by Huft (pers. comm.) Hutchinson described *Oreoporanthera* as a new genus (with

Latin description), even though he was obviously basing it on Grüning's section.

Tribe 7. HYMENOCARDIEAE (Muell. Arg.)

Hutchinson, Amer. J. Bot. 56: 746. 1969. Phyllantheae subtribe Hymenocardieae Muell. Arg., Linnaea 34: 64. 1865. Hymenocardieae Airy Shaw, Kew Bull. 18: 261. 1965; Léonard & Mosango, Fl. Afr. Centrale, Hymenocarpaceae 1. 1985. TYPE: *Hymenocardia* Wall. ex Lindley.

Dioecious trees or shrubs; indumentum of simple hairs and sessile glands; leaves alternate, entire, penninerved, stipulate; inflorescences axillary, spicate, racemose, or paniculate; staminate sepals 4–8, connate; petals absent; stamens 4–8, filaments free or basally connate; anthers longitudinally dehiscent; pollen porate; pistillode present; pistillate flowers pedicellate; sepals 4–9, free, caducous; ovary 2-locular; styles 2, elongated, entire or lacerate, free; ovules anatropous, 2 per locule; fruit capsular or winged, samaroid; seeds 1 per locule; endosperm scanty; cotyledons broader and longer than radicle.

A distinctive group originally including a single Old World genus, considered to be a distinct family by a number of modern workers (e.g., Léonard & Mosango, 1985; Meeuse, 1990). However, most floral and anatomical details (e.g., in Levin, 1986a, b, c) indicate that it is better retained within the Euphorbiaceae. A second genus, *Didymocistus*, is provisionally included here, although it is very distinct from *Hymenocardia* in many ways, and could perhaps be placed in a separate tribe or subtribe.

KEY TO THE GENERA OF TRIBE HYMENOCARDIEAE

- 1a. Fruit capsular; inflorescence paniculate; styles lacerate 56. *Didymocistus*
1b. Fruit samaroid; inflorescence racemose; styles papillose 57. *Hymenocardia*

56. *Didymocistus* Kuhlmann, An. Prim. Reun. Sud-Amer. Bot. 3: 82. 1940. TYPE: *Didymocistus chrysadenius* Kuhlmann.

A monotypic genus of Amazonian Brazil. Kuhlmann related it to *Aporosa*, but the anatomical studies of Levin (1986a, b, c) suggest that it is possibly closer to *Hymenocardia*. It does appear that *Didymocistus* may possibly represent a link between tribes Antidesmeae and Hymenocardieae.

57. *Hymenocardia* Wallich ex Lindley, Nat. Syst. ed. 2, 441. 1836; Muell. Arg., DC. Prodr. 15(2): 476. 1866; Oliver, Hook. Ic. Pl. 12: 29, t. 1131. 1873; Bentham, Gen.

Pl. 3: 284. 1880; Pax & Hoffm., Pflanzentr. 147. XV (Heft 81): 72. 1922; Léonard & Mosango, Fl. Afr. Centrale, Hymenocardiaceae 2. 1985; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorbiaceae 577. 1988. TYPE: *Hymenocardia punctata* Wallich ex Lindl.

Samaropyxis Miquel, Fl. Ned. Ind., Erste Bijv. 464. 1861. TYPE: *Samaropyxis elliptica* Miq. [= *Hymenocardia wallichii* Tul.].

An Old World genus of eight species, of which seven are African and one southeast Asian; absent from Madagascar.

Tribe 8. BISCHOFIEAE (Muell. Arg.) Huru-sawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 339. 1954. Phyllanthaceae subtribe Bischoffieae Muell. Arg., Linnaea 34: 64. 1865. Family Bischofiaceae (Muell. Arg.) Airy Shaw, Kew Bull. 18: 252. 1965. TYPE: *Bischofia* Blume.

A monotypic tribe of a single Asian species, very distinct from other Phyllanthoideae by virtue of its trifoliolate leaves. Although Airy Shaw (1965) suggested a relationship with the Staphyleaceae, evidence from embryology (Bhatnagar & Kapil, 1974) and leaf anatomy (Levin, 1986a, b, c) supports retention in the Euphorbiaceae.

58. *Bischofia* Blume, Bijdr. 1168. 1826; Muell. Arg., DC. Prodr. 15(2): 478. 1866; Bentham, Gen. Pl. 3: 280. 1880; Pax & Hoffm., Pflanzentr. 147. XV (Heft 81): 312. 1922; Airy Shaw, Kew Bull. 18: 253. 1965; 21: 327. 1967; A. C. Smith, Fl. Vitiensis Nova 2: 494. 1981. TYPE: *Bischofia javanica* Blume.

Microelus Wight & Arnott, Edinb. New Philos. J. 14: 298. 1833. TYPE: *Microelus roeperianus* Wight & Arnott [= *Bischofia javanica* Blume].

Stylodiscus Bennett, Pl. Jav. Rar. 133. 1840. TYPE: *Stylodiscus trifoliatus* (Roxb.) Bennett [*Andrachne trifoliata* Roxb. = *Bischofia javanica* Blume].

A genus of a single species distributed from India and Sri Lanka to China, Indonesia, and the Pacific islands.

INCERTAE SEDIS

59. *Centroplacus* Pierre, Bull. Mens. Soc. Linn. Paris II. 1: 114. 1899; Gilg, Bot. Jahrb. 40: 516. 1908; Hutchinson, Fl. Trop. Afr. 6(1): 629. 1912; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 46. 1931. TYPE: *Centroplacus glaucinus* Pierre.

This genus is based on a single poorly known

species from Gabon that was referred to a flacourtiaceous affinity by Pierre, but to the Euphorbiaceae by Gilg (1908) and Hutchinson (1912). Pax & Hoffmann (1931) placed it in the Antidesminae next to *Spondianthus*, but its place within the Euphorbiaceae still appears uncertain.

60. *Meborea* Aublet, Hist. Pl. Guiane 825. 1775; Lanjouw, Euphorb. Suriname 9, t. 1. 1931. TYPE: *Meborea guianensis* Aublet.

This monotypic genus from French Guiana was referred by Mueller (1866) to *Phyllanthus*. Lanjouw was unable to place the genus, but regarded it as not synonymous with *Phyllanthus*, a view with which I agree. Judging from Aublet's description and illustration, it seems probable that *Meborea* belongs to tribe Phyllanthaceae, but it cannot be identified with certainty.

Subfamily II. OLDFIELDIOIDEAE Köhler & Webster, J. Arnold Arbor. 48: 308. 1967; Webster, Taxon 24: 595. 1975. TYPE: *Oldfieldia* Benth.

Paivaeusaceae Meeuse, Euphorbiaceae Auct. Plur. 30. 1990. TYPE: *Paivaeusa* Welw. ex Benth. [= *Oldfieldia* Benth. & Hook.].

Monoecious or dioecious trees, shrubs, or subshrubs; leaves alternate or more commonly opposite or verticillate, simple or palmately compound, entire or dentate; stipules small and caducous or absent; inflorescences axillary, glomerulate, racemose, capitulate, or paniculate; flowers apetalous (except in *Croizatia*); staminate sepals (3-)4-8(-12), imbricate, usually free; disk intrastaminal or absent (extrastaminal in *Croizatia*); stamens (2)3-30, filaments free or connate; pollen grains spheroidal, tectate, exine mostly with conspicuous spines, brevicolporate or porate; pistillode present or absent; pistillate sepals (3-)4-8(-13), free; disk annular to lobed or dissected, or absent; ovary 2-4(-5)-locular; ovules 2 per locule (except in *Scagea*); styles entire or stigmatoid (rarely bifid); fruit capsular (rarely drupaceous); seeds 1 or 2 per locule, often carunculate, testa usually smooth and shiny; endosperm usually copious (rarely obsolete).

This most recently recognized subfamily includes 28 genera with only ca. 100 species, overwhelmingly found in the Southern Hemisphere.

KEY TO THE TRIBES OF SUBFAMILY OLDFIELDIOIDEAE

- 1a. Petals present; staminate disk extrastaminal, annular; styles twice bifid; ovules hemitropous
..... 9. CROIZATIEAE

- 1b. Petals absent; staminate disk dissected, intrastaminal or absent; styles entire or rarely once bifid; ovules anatropous.
- 2a. Pollen apertures four; vessel elements at least in part with scalariform perforation plates (except in *Tetracoccus*); staminate disk extrastaminal or absent; leaves simple 10. PODOCALYCEAE
- 2b. Pollen with more than 4 apertures (rarely inaperturate); vessel elements with simple perforation plates; staminate disk intrastaminal or absent; leaves simple, unifoliate, or palmately compound.
- 3a. Leaves simple; monoecious or dioecious trees, shrubs, or herbs; seeds mostly carunculate 11. CALETIEAE
- 3b. Leaves compound, or if simple then lamina stipellate or stipules adnate to petiole; dioecious trees or shrubs; seeds carunculate or ecarunculate 12. PICRODENDREAE

Tribe 9. CROIZATIEAE Webster, trib. nov.
TYPE: *Croizatia* Steyermark.

Folia alterna integra; discus annularis; petalae 5, imbricatae; stamina 5, antheris extrorsis; pollinis grana 3-colporata spinulosa; ovarium 3-loculare, stylis bis bifidis, ovulis hemitropis; semina ecarunculata, exalbuminata.

Dioecious trees or shrubs; leaves alternate, entire; stipules deciduous or persistent; flowers in axillary clusters; staminate sepals and petals 5, imbricate; disk annular; stamens 5, free, anthers introrse; pollen grains globose, 3-colporate, exinuous spines conspicuous; pistillode present; pistillate sepals and petals 5, imbricate; disk annular, glabrous; ovary pubescent, 3-locular; styles free, twice bifid; ovules hemitropous; fruit capsular; columella persistent, dilated; seeds 1–2 per locule, ecarunculate; endosperm absent; cotyledons broader than and about equaling radicle.

The tribe is represented by the single genus *Croizatia*. This taxon shows clear affinities with the tribe Amanoeae in subfamily Phyllanthoideae, and it is more or less arbitrary where it is placed.

61. *Croizatia* Steyermark, Fieldiana 28: 308, fig. 57. 1952; Webster, Gillespie & Steyermark, Syst. Bot. 12: 6. 1987. TYPE: *Croizatia neotropica* Steyermark.

A neotropical genus of four species, distributed from Panama to Venezuela and Ecuador.

Tribe 10. PODOCALYCEAE Webster, trib. nov. TYPE: *Podocalyx* Klotzsch.

Folia alterna vel opposita, integra vel serrata; stipulae deciduae; discus ♂ nullus; petalae nullae; stamina 5–13, antheris extrorsis vel introrsis; pollinis grana

4-brevicolporata, echinata; ovarium 3-loculare, stylis integris, ovulis anatropis; semina albuminata.

Dioecious trees; leaves alternate or opposite, entire or serrate; stipules caducous. Inflorescences in thyrses or ebracteate cymes. Flowers apetalous, disk absent; staminate sepals (3)4 or 5, free or connate, imbricate; stamens 5–13, free; anthers extrorse or introrse; pollen grains 4-brevicolporate, echinate, tectum smooth; pistillode present or absent; pistillate sepals 4 or 5, imbricate, persistent; disk present or absent; ovary 3-locular; styles dilated, stigmatiform; ovules anatropous. Fruit capsular or drupaceous; seeds carunculate or ecarunculate; endosperm present; cotyledons plane or plicate, much broader than radicle.

This tribe includes three American genera that are different in many respects and are classified together on the basis of pollen characters (pollen grains with four shortened colpi). The differences between the genera are so striking that it seems necessary to assign them to different subtribes.

KEY TO THE SUBTRIBES OF TRIBE PODOCALYCEAE

- 1a. Peduncle free from petiole; fruit capsular.
- 2a. Staminate sepals connate; pistillode present; staminate and pistillate flowers in elongated spikes; seeds ecarunculate; leaves alternate, entire 10a. Podocalycinae
- 2b. Staminate sepals discrete; pistillode absent; pistillate flowers solitary or clustered; seeds carunculate; leaves alternate, opposite, or whorled, entire or dentate 10b. Tetracoccinae
- 1b. Peduncle adnate to the petiole; staminate sepals discrete; pistillode absent; fruit drupaceous 10c. Paradrypeatinae

Subtribe 10a. PODOCALYCINAE Webster, subtr. nov. TYPE: *Podocalyx* Kl.

Folia alterna, integra; flores spicatis; antheris extrorsis; flos ♂ pistillodio; discus ♀ sericeus; fructus capsularis; cotyledones planis.

Trees with alternate leaves; stipules caducous; flowers in axillary spikes; staminate sepals 5, connate below; disk obsolete; stamens 5 or 6, anthers extrorse; pollen grains 4-colporate, echinate; pistillode present; pistillate flowers pedicellate; sepals 5, imbricate, persistent; disk cupular, sericeous; ovary sericeous; fruit capsular; columella slender, persistent; cotyledons plane.

This subtribe includes only the single genus *Podocalyx*.

62. *Podocalyx* Klotzsch, Arch. Naturgesch. 7: 202. 1841. *Richeria* sect. *Podocalyx* (Kl.)

Muell. Arg., DC. Prodr. 15(2): 469. 1866.
TYPE: *Podocalyx loranthoides* Kl.

A monotypic genus restricted to Amazonian South America. Although Pax & Hoffmann (1922, 1931) and recent workers (e.g., Jablonski, 1967) have followed Mueller in treating *Podocalyx* as a section of *Richeria*, its pollen is completely different and characteristic of the subfamily Oldfieldioideae.

Subtribe 10b. TETRACOCINAE G. Levin,
subtr. nov. TYPE: *Tetracoccus* Engelm. ex Parry.

Frutices dioicae; folia simplicia, alterna, opposita, vel verticillata, dentata vel integra; stipulae 0; discus ♂ intrastaminalis, lobatus; stamina 4–10, antheris extrorsis; pollinis grana 4-porata, echinata; pistillodio 0; discus ♀ glabrus, lobatus; styli elongati; fructus capsularis; semina carunculata, albuminata, cotyledonibus plicatis.

Shrubs; leaves alternate, opposite, or whorled, margins toothed or entire; stipules absent; staminate flowers in axillary racemes or panicles, or fasciculate; pistillate flowers solitary or fasciculate, axillary; staminate sepals 4–10, discrete; disk intrastaminal, lobed; stamens 4–10, anthers extrorse; pollen grains 4-porate, tectum verruculose between spines; pistillode absent; pistillate sepals 5–13; disk lobed; ovary (2–)3–4(–5)-locular; styles elongated; fruit capsular; seeds carunculate; endosperm abundant; cotyledons plicate.

This monogeneric subtribe is very difficult to place and perhaps should constitute a distinct tribe. Vegetatively, *Tetracoccus* is intermediate between *Podocalyx* and *Paradrypetes* in phyllotaxy and leaf margins. In some characters, such as the intrastaminal staminate disk and verruculose pollen sexine, there is a closer resemblance between *Tetracoccus* and other tribes of Oldfieldioideae. Levin & Simpson (1994) would refer the Tetracoccinae to the tribe Picrodendreae.

63. Tetracoccus Engelmann ex Parry, W. Amer. Scientist 1: 13. 1885; Croizat, Bull. Torrey Bot. Club 69: 456. 1942; Dressler, Rhodora 56: 49. 1954. TYPE: *Tetracoccus dioicus* Parry.

Halliophytum I. M. Johnston, Contr. Gray Herb. 68: 88. 1923. TYPE: *Halliophytum fasciculatum* (S. Wats.) I. M. Johnston [= *Tetracoccus fasciculatus* (S. Wats.) Croizat; lectotype].

As interpreted by Dressler (1954), a genus of four species endemic to southwestern North America (southern California and adjacent Arizona, southern Baja California, and northern Mexico).

Subtribe 10c. PARADRYPETINAE G. Levin,
Syst. Bot. 17: 78. 1992. TYPE: *Paradrypetes* Kuhlmann.

Leaves opposite, margin ± spinose; stipules enclosing apical bud; staminate flowers in ebracteate cymes, pistillate solitary, the peduncle in both sexes adnate to the subtending petiole; staminate sepals 3 or 4, free; disk obsolete; stamens 9–13, anthers extrorse; pistillode absent; pistillate sepals 4; ovary 3-locular; fruit drupaceous, 1-seeded; embryo with plicate cotyledons.

A monogeneric subtribe, considered by Levin to be closest to subtribe Podocalycinae.

64. Paradrypetes Kuhlmann, Arq. Inst. Biol. Veg. Rio Jan. 2: 84. 1935; Levin, Syst. Bot. 17: 74. 1992. TYPE: *Paradrypetes ilicifolia* Kuhlmann.

A genus of two South American species, one in the Amazonian rainforests, the other in the Brazilian Atlantic rainforest.

Tribe 11. CALETIEAE Muell. Arg., Bot. Zeit. 22: 34. 1865; DC. Prodr. 15(2): 190. 1866; Grüning, Pflanzenr. 147 (Heft 58): 21. 1913. TYPE: *Caletia* Baillon [= *Micranthemum* Desf.].

Diocious or monoecious trees or shrubs; leaves alternate, opposite, or verticillate, simple, entire or dentate, stipules obscure or absent; flowers apetalous, in axillary clusters or panicles; staminal sepals 4–8(–12), free; disk present or absent; stamens 4–30, filaments usually free; anthers extrorse or latrorse; pollen grains spheroidal, with exinous spines, colpate or zonoporate; pistillode present or absent; pistillate sepals 3–8(–13), free; disk present or absent; ovary 2–5-locular; styles unlobed, ± elongated, often dilated; fruit capsular; seeds usually 1 per cocculus, carunculate or ecarunculate; endosperm usually copious; cotyledons much broader or scarcely broader than the radicle.

This variable tribe of 4 subtribes with 15 genera is entirely paleotropical, and indeed except for *Hyaenanche*, the genera are nearly confined to Australasia (with a few species of *Austrobuxus* in Indonesia).

KEY TO THE SUBTRIBES OF TRIBE CALETIEAE

- 1a. Leaves whorled (at least in part); filaments shorter than anthers; pollen tectum granulose, exinous spines long 11a. *Hyaenanchinae*
- 1b. Leaves alternate or opposite; filaments longer than anthers; pollen tectum smooth.
 - 2a. Pollen grains zonoaperturate; stipules de-

ciduous or reduced; leaves opposite or if alternate then capsule fleshy.

3a. Leaves opposite; stamens free; anthers not apiculate; capsule dry; pistillate sepals persistent 11b. Dissiliariinae

3b. Leaves alternate; stamens connate; anthers apiculate; capsule fleshy; pistillate sepals deciduous 11c. Petalostigmatinae

2b. Pollen grains pantoporate; stipules deciduous or persistent; leaves alternate; capsule dry 11d. Pseudanthinae

Subtribe 11a. HYAENANCHINAE Baillon ex Muell. Arg., *Linnaea* 34: 64. 1865 (as *Hyaenancheae*); DC. *Prodr.* 15(2): 479. 1866. Tribe *Hyaenancheae* (Baillon ex Muell. Arg.) Hutch., *Amer. J. Bot.* 56: 746. 1969. TYPE: *Hyaenanche* Lambert.

Toxicodendrinae Pax, *Natürl. Pflanzenfam.* ed. 1, 3(5): 31. 1890; Pax & Hoffm., *Pflanzenr.* 147. XV (Heft 81): 284. 1922. TYPE: *Toxicodendrum* Thunb. (non P. Miller) [= *Hyaenanche* Lambert].

Dioecious trees or shrubs; leaves opposite or verticillate, simple, coriaceous, stipules obscure or absent; flowers in axillary clusters or panicles; staminate sepals 4–8(–12), ± connate; disk absent; stamens 8–30, filaments free, much shorter than anthers; anthers introrse or extrorse; pollen grains 6- or 7-zonoporate, spinose, tectum granulose; pistillode absent; pistillate sepals 3–8, free, deciduous in fruit; disk absent; ovary 3–4-locular, sericeous; styles elongated, ± dilated; fruit capsular; seeds carunculate; endosperm sparse.

This subtribe is here circumscribed to include only the type genus *Hyaenanche*, as treated by Mueller and Pax & Hoffmann. Clearly *Hyaenanche* is a very isolated genus whose relationships are still uncertain. It is isolated in the tribe Caletieae because of the verruculose microsculpturing of the pollen sexine, which recalls genera of tribe Picrodendreae. There is some resemblance to the Sri Lankan genus *Mischodon* in habit and pollen morphology, but it still is not clear whether the two genera should be grouped together.

65. *Hyaenanche* Lambert, *Descr. Cinchona* 52, t. 10. 1797; Muell. Arg., DC. *Prodr.* 15(2): 479. 1866; Dyer, *Gen. S. Afr. Fl. Pl.* 1: 311. 1975. TYPE: *Hyaenanche globosa* (Gaertner) Lambert.

Toxicodendrum Thunberg, *Kongl. Vetensk. Acad. Handl.* 17: 188. 1796 (non *Toxicodendron* P. Miller, 1754); Bentham, *Gen. Pl.* 3: 280. 1880; Pax & Hoffm., *Pflanzenr.* 147. XV (Heft 81): 284. 1922. TYPE:

Toxicodendrum capense Thunb. [= *Hyaenanche globosa* (Gaertner) Lambert].

A monotypic genus of the Cape region of South Africa. The seeds of *Hyaenanche* are unusual within the Oldfieldioideae in the scanty endosperm, green cotyledons, and production of a unique toxin (*Hyaenanchin*).

Subtribe 11b. DISSILIARIINAE Pax & Hoffmann, *Pflanzenr.* 147. XV (Heft 81): 288. 1922. TYPE: *Dissiliaria* F. Muell.

Monoecious or dioecious trees or shrubs; leaves opposite, simple, entire; stipules reduced or absent; flowers in axillary panicles or clusters; staminate sepals 4–6, imbricate, free; disk absent; stamens 8–50, free; pollen grains with long to short spines, tectum smooth; pistillode absent; pistillate sepals 4–6, free; disk cupulate or absent; ovary 2- or 3-(rarely 4-)locular, glabrous; styles short; fruit capsular; seeds carunculate or ecarunculate.

This Australasian subtribe includes 6 genera with ca. 25 species. Generic limits require further critical study.

KEY TO THE GENERA OF SUBTRIBE DISSILIARIINAE

- 1a. Pollen exine with elongated spines; pistillode mostly absent.
 - 2a. Dioecious; stamens 8–25; pistillate disk cupular or absent.
 - 3a. Seeds with fimbriate caruncle; ovary 3(–4)-locular; styles ovate, erect 66. *Austrobuxus*
 - 3b. Seeds ecarunculate.
 - 4a. Styles elongated, recurved; ovary 3(–4)-locular 67. *Dissiliaria*
 - 4b. Styles ovate, erect; ovary 2-locular 68. *Canaca*
 - 2b. Monoecious; stamens ca. 50; pistillate disk of subulate segments 69. *Whyanbeelia*
- 1b. Pollen exine with reduced spines; pistillode present.
 - 5a. Stamens 4–6; styles separated at base, recurved; seeds ecarunculate 70. *Choriceras*
 - 5b. Stamens 8–17; styles proximate, not recurved; seeds carunculate 71. *Longetia*

66. *Austrobuxus* Miquel, *Fl. Ned. Ind. Suppl.* 444. 1861; Steenis, *Blumea* 12: 362. 1964; Airy Shaw, *Kew Bull.* 25: 506. 1971; *Kew Bull.* 29: 303. 1974; *Kew Bull.* 35: 597. 1980; A. C. Smith, *Fl. Vitiensis Nova* 2: 495. 1981; McPherson & Tirel, *Fl. Nouv.-Caléd.* 14(1): 193. 1987. TYPE: *Austrobuxus nitidus* Miquel.

Bureavia Baillon, *Adansonia* 11: 83. 1873. TYPE: *Bureavia carunculata* (Baillon) Baillon [= *Austrobuxus carunculatus* (Baillon) Airy Shaw]. *Choriophyllum* Bentham, *Hook. Icon. Pl.* 13: 62, t.

1280. 1879. TYPE: *Choriophyllum malayanum* Benth. [= *Austrobuxus nitidus* Miq.].

In the circumscription of Airy Shaw (1974) and McPherson & Tirel (1987), *Austrobuxus* is the largest genus of subfamily Oldfieldioideae, with ca. 20 species. The distribution is disjunct, with areas in Malaya and western Indonesia, Queensland, New Caledonia, and Fiji, but absent from New Guinea.

- 67. Dissiliaria** F. Mueller ex Baillon, *Adansonia* I. 7: 366. 1867; Benth., *Fl. Austral.* 6: 90. 1873; Pax & Hoffm., *Pflanzenr.* 147. XV (Heft 81): 291. 1922; Airy Shaw, *Muelleria* 4: 220. 1980; *Kew Bull.* 35: 625. 1980. TYPE: *Dissiliaria baloghoides* F. Muell. ex Baillon [lectotype, selected here; the generic name was associated with that species in Baillon's original description].

According to Airy Shaw (1980), *Dissiliaria* includes three species endemic to Australia (Queensland).

- 68. Canaca** Guillaumin, *Arch. Bot. Caen* 1: 74. 1927; Airy Shaw, *Kew Bull.* 25: 508. 1971. TYPE: *Canaca vieillardii* Guill.

As noted by Airy Shaw (1971), *Canaca* was originally misplaced in the Monimiaceae by Guillaumin but recognized as related to *Austrobuxus* by McKee. McPherson & Tirel (1987) followed Airy Shaw in relegating *Canaca* to synonymy of *Austrobuxus*. However, if *Dissiliaria* is maintained as distinct from *Austrobuxus*, it appears that *Canaca* is equally deserving of recognition. It is possible that all three genera should be combined under the name *Austrobuxus*.

- 69. Whyanbeelia** Airy Shaw & Hyland, *Kew Bull.* 31: 375, fig. 2. 1976; *Kew Bull.* 35: 691. 1980. TYPE: *Whyanbeelia terra-reginae* Airy Shaw & Hyland.

A monotypic genus of tropical Australia (Queensland).

- 70. Choriceras** Baillon, *Adansonia* I. 11: 119. 1873; Airy Shaw, *Kew Bull.* 14: 356. 1961; *Muelleria* 4: 220. 1980; *Kew Bull.* 35: 604. 1980. TYPE: *Choriceras australiana* Baillon [= *Choriceras tricorne* (Benth.) Airy Shaw].

A genus of two species restricted to tropical Australia and Papua. Although Pax & Hoffmann (1922) reduced *Choriceras* to a synonym of *Dissiliaria*, Airy Shaw (1961) pointed out its distinguishing characters.

- 71. Longetia** Baillon ex Muell. Arg., DC. *Prodr.* 15(2): 244. Aug. 1866; Baillon, *Adansonia* I. 6: 352, t. 9. Oct. 1866; Benth., *Gen. Pl.* 3: 279. 1880; Pax & Hoffm., *Pflanzenr.* 147. XV (Heft 81): 289. 1922; McPherson & Tirel, *Fl. Nouv.-Caléd.* 14(1): 188. 1987. TYPE: *Longetia buxoides* Baillon ex Muell. Arg.

As interpreted by McPherson & Tirel, *Longetia* is a monotypic genus endemic to New Caledonia. Pax & Hoffmann (1922) construed *Longetia* in a broad sense, including species now placed in *Austrobuxus*. Airy Shaw (1971, 1974) held a similar broad view, except that *Longetia* species were now transferred to *Austrobuxus*. In view of the distinct difference in pollen, McPherson's return to the classical concept of Baillon and Mueller seems fully justified.

- Subtribe 11c. PETALOSTIGMATINAE** Pax & Hoffmann, *Pflanzenr.* 147. XV (Heft 81): 281. 1922. Tribe Petalostigmateae (Pax & Hoffm.) Webster, *Taxon* 24: 595. 1975. TYPE: *Petalostigma* F. Muell.

Dioecious trees or shrubs; leaves alternate, simple, entire; stipules caducous; flowers in axillary clusters; staminate sepals 4–6, imbricate; disk absent; stamens 20–40, filaments connate below into a column; anther connective typically pilose; pollen grains with short spines; pistillode obscure or absent; pistillate sepals 4–8, imbricate; disk absent; ovary 3–4-locular, pubescent; styles dilated; fruit a fleshy capsule; seeds carunculate.

A monogeneric subtribe restricted to Australia and New Guinea (Papua).

- 72. Petalostigma** F. Mueller, *Hook. J. Bot. Kew Gard. Misc.* 9: 16. 1857; Muell. Arg., DC. *Prodr.* 15(2): 273. 1866; Baillon, *Adansonia* I. 7: 352. 1867; Benth., *Fl. Austral.* 6: 92. 1873; *Gen. Pl.* 3: 277. 1880; Pax & Hoffm., *Pflanzenr.* 147. XV (Heft 81): 281. 1922; Airy Shaw, *Kew Bull.* 31: 366. 1976; *Kew Bull.* 35: 661. 1980. TYPE: *Petalostigma quadriloculare* F. Muell.

As treated by Airy Shaw (1980), *Petalostigma* is a genus of six variable Australian species, one of which extends to New Guinea (Papua).

- Subtribe 11d. PSEUDANTHINAE** Muell. Arg., *Linnaea* 34: 55. 1865; DC. *Prodr.* 15(2): 195. 1866. TYPE: *Pseudanthus* Sprengel.

Monoecious (rarely dioecious) trees, shrubs, or herbs; leaves mostly alternate, entire; stipules de-

ciduous or persistent; flowers in axillary clusters; staminate sepals 3–6, imbricate, free; disk intrastaminal or absent; stamens 3–20 (rarely more), filaments free or connate; pollen grains with long or short spines, tectum smooth; pistillode present or absent; pistillate sepals 4–6, free, usually persistent; disk present or absent; ovary 2–3-locular; styles unlobed, dilated or elongated; fruit capsular; seeds carunculate.

The subtribe Pseudanthinae is here circumscribed in concurrence with suggestions by Levin (pers. comm.) to include six Australasian genera. The referral of *Kairothamnus* and *Scagea* to the Pseudanthinae needs confirmation, but appears compatible with the anatomical and palynological evidence.

KEY TO THE GENERA OF SUBTRIBE PSEUDANTHINAE

- 1a. Cotyledons broader than radicle; trees or shrubs.
 - 2a. Staminate sepals 4; stamens 10–12 73. *Kairothamnus*
 - 2b. Staminate sepals (5)6; stamens 4–6.
 - 3a. Ovules 1 per locule; pistillode present; staminate inflorescence racemose or umbellate; stipules conspicuous but deciduous 74. *Scagea*
 - 3b. Ovules 2 per locule; pistillode absent; staminate flowers in axillary glomerules; stipules minute or obsolete 75. *Neoroepera*
- 1b. Cotyledons scarcely broader than radicle; herbs or undershrubs.
 - 4a. Stipules foliose; fruits 3-seeded; pollen grains with long exinuous spines 76. *Micranthemum*
 - 4b. Stipules not foliose; fruits 1-seeded; pollen grains with reduced spines.
 - 5a. Stamens free; pistillode present 77. *Pseudanthus*
 - 5b. Stamens connate; pistillode absent 78. *Stachystemon*

73. *Kairothamnus* Airy Shaw, Kew Bull. 34: 596. 1980; Kew Bull. Add. Ser. 8: 121, t. 1 fig. 1. 1980. TYPE: *Kairothamnus phyllanthoides* (Airy Shaw) Airy Shaw.

A monotypic genus of eastern New Guinea (Morobe District). The alternate caudate-acuminate leaves of this plant indeed give it an aspect suggestive of *Phyllanthus*, as noted by Airy Shaw, but its pollen is typical of the Oldfieldioideae, and the genus appears very close to *Austrobuxus*.

74. *Scagea* McPherson, Bull. Mus. Nat. Hist. Nat. Paris, IVB. 7: 247. 1985; Fl. Nouv.-Caléd. 14(1): 90. 1987. TYPE: *Scagea depauperata* (Baillon) McPherson.

A genus of two species endemic to New Caledonia. The genus was originally referred to sub-

family Crotonoideae by McPherson because of the uniovulate carpels, but the pollen clearly suggests placement in the Oldfieldioideae. The genus appears very similar to *Choriceras*, but differs in ovule number and pollen morphology.

75. *Neoroepera* Muell. Arg. & F. Mueller, DC. Prodr. 15(2): 488. 1866; Bentham, Fl. Austral. 6: 116. 1873; Gen. Pl. 3: 276. 1880; Airy Shaw, Kew Bull. 35: 658. 1980. TYPE: *Neoroepera buxifolia* Muell. Arg. & F. Muell.

A genus to two species endemic to Australia (Queensland).

76. *Micranthemum* Desf., Mém. Mus. Hist. Nat. Paris 4: 253, t. 14. 1818; Muell. Arg., DC. Prodr. 15(2): 195. 1866; Bentham, Fl. Austral. 6: 58. 1873; Gen. Pl. 3: 262. 1880; Grüning, Pflanzenr. 147. (Heft 58): 23. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 224. 1931. TYPE: *Micranthemum ericoides* Desf.

Caletia Baillon, Etude Gén. Euphorb. 553. 1858. TYPE: *Caletia micrantheoides* Baillon, nom. illeg. [= *Micranthemum hexandrum* Hook. f.].

Allenia Ewart, Proc. Roy. Soc. Vict. II. 22: 7. 1909. TYPE: *Allenia blackiana* Ewart, nom. illeg. [= *Micranthemum demissum* F. Muell.].

A genus of three Australian species.

77. *Pseudanthus* Sieber ex Sprengel, Syst. Veg. 4(2): 22, 25. 1827; Muell. Arg., DC. Prodr. 15(2): 196. 1866; Bentham, Fl. Austral. 6: 58. 1873; Gen. Pl. 3: 262. 1880; Grüning, Pflanzenr. 147. (Heft 58): 26. 1913. TYPE: *Pseudanthus pimeleoides* Sieber ex Sprengel.

Chrysostemon Klotzsch, Pl. Preiss. 2: 232. 1848. TYPE: *Chrysostemon virgatus* Kl. [= *Pseudanthus virgatus* (Kl.) Muell. Arg.].

Chortizotheca Muell. Arg., Linnaea 32: 76. 1863. TYPE: *Chortizotheca micrantheoides* Muell. Arg. [= *Pseudanthus virgatus* (Kl.) Muell. Arg.].

An Australian genus of seven or eight species.

78. *Stachystemon* Planchon, Hook. London J. Bot. 4: 471, t. 15. 1845; Muell. Arg., DC. Prodr. 15(2): 198. 1866; Bentham, Fl. Austral. 6: 61. 1873; Gen. Pl. 3: 263. 1880; Grüning, Pflanzenr. 147 (Heft 58): 32. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 226. 1931. TYPE: *Stachystemon vermiculare* Planch.

A genus of three species in western Australia.

Tribe 12. PICRODENDREAE (Small) Webster, Taxon 24: 595. 1975. Family Picrodendraceae Small, J. New York Bot. Gard. 18: 184. 1917. TYPE: *Picrodendron* Planchon.

Monoecious or dioecious trees or shrubs; leaves alternate or opposite, 3–9-parted (rarely unifoliate), entire; stipules caducous, fused to petiole, or absent; flowers in axillary cymes, racemes, or glomerules; staminate sepals 4–8 (or obsolete), free; disk intrastaminal or absent; stamens 4–50, free; anthers extrorse or introrse; pollen grains spheroidal, brevicolporate or porate, with exinous spines, tectum granulose; pistillode minute or absent; pistillate sepals 4–8, persistent or deciduous; disk present or absent; ovary 2–3-locular; styles elongated or stigmatiform; fruit capsular or drupaceous; seeds carunculate or ecarunculate; endosperm usually copious; cotyledons broader and longer than radicle.

This tribe of ten genera in three subtribes contrasts markedly with the Caletieae in its distribution: all the genera are either American or African/Madagascan, with one genus (*Mischodon*) in Sri Lanka. The tribe is generally well characterized by its compound leaves, although the leaf blade appears unifoliate in *Mischodon*, some species of *Androstachys*, and *Parodiodendron*.

KEY TO THE SUBTRIBES OF TRIBE PICRODENDREAE

- 1a. Stipules caducous or obsolete, free from petiole.
 2a. Staminate sepals free; capsule septicial 12a. Picrodendrinae
 2b. Staminate sepals connate; capsule loculicidal 12b. Paivaeusinae
 1b. Stipules persistent, ± adnate to petiole; seeds ecarunculate 12c. Mischodontinae

Subtribe 12a. PICRODENDRINAE (Small) Webster, stat. nov. Family Picrodendraceae Small, J. New York Bot. Gard. 18: 184. 1917. TYPE: *Picrodendron* Planchon.

Dioecious trees or shrubs; leaves alternate; leaves 3-foliolate or 1-foliolate, margins entire; stipules small and caducous or absent; inflorescences axillary, cymose, sometimes reduced to catkins or glomerules; staminate sepals 4–8, free or obsolete; disk intrastaminal or absent; stamens 5–15, free; pollen grains 5–8-porate or brevicolporate, sexine with long spines and verruculose tectum; pistillode minute or absent; pistillate sepals 4–8, deciduous; disk cupular or absent; ovary 2- or 3-locular; styles elongated or stigmatiform; fruit capsular or drupaceous; seeds 1 or 2 per locule, carunculate or ecarunculate.

The four American genera of tribe Picrodendreae are all referable to this subtribe.

KEY TO THE GENERA OF SUBTRIBE PICRODENDRINAE

- 1a. Leaves mostly 3–5-foliolate.
 2a. Fruits dehiscent; staminate sepals not reduced.
 3a. Stamens 6; pistillate flowers solitary 79. *Celaenodendron*
 3b. Stamens 8–15; pistillate flowers racemose 80. *Piranhea*
 2b. Fruits indehiscent, drupaceous; staminate sepals reduced 81. *Picrodendron*
 1b. Leaves simple (unifoliate), stipellate; pistillate sepals foliose, persistent 82. *Parodiodendron*

79. Celaenodendron Standley, Contr. Dudley Herb. 1: 76. 1927. TYPE: *Celaenodendron mexicanum* Standley.

A monotypic genus of western Mexico (Tres Marias Islands, Jalisco).

80. Piranhea Baillon, Adansonia I. 6: 235. 1866; Muell. Arg., Fl. Brasil. 11(2): 79. 1873; Benth., Gen. Pl. 3: 281. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 295. 1922; Jablonski, Mem. New York Bot. Gard. 17: 121. 1967. TYPE: *Piranhea trifoliolata* Baillon.

A genus of two species endemic to South America.

81. Picrodendron Planchon, Hook. London J. Bot. 5: 579. 1846; nom. cons. prop.; Krug & Urban, Bot. Jahrb. 15: 308. 1893; Fawc. & Rend., J. Bot. 55: 268. 1917; Hayden et al., J. Arnold Arbor. 65: 110. 1984. TYPE (typ. cons.): *Picrodendron baccatum* (L.) Krug & Urban.

A monotypic genus endemic to the West Indies (Greater Antilles, Bahamas, Cayman Islands, Swan Islands).

82. Parodiodendron Hunziker, Kurtziana 5: 331, fig. 1. 1969. TYPE: *Parodiodendron marginivillosum* (Speg.) Hunziker.

A monotypic genus of northern Argentina.

Subtribe 12b. PAIVAEUSINAE Pax & Hoffmann, Pflanzenr. 147. XV (Heft 81): 294. 1922. TYPE: *Paivaea* Welw. ex Benth. [= *Oldfieldia* Benth. & Hook. f.].

Dioecious trees; leaves alternate or opposite, 5–8-foliolate; stipules obsolete; staminate inflorescences in pedunculate ± congested cymes, the pistillate usually reduced to 1–3 flowers; staminate sepals 5–8, basally connate; disk intrastaminal, lobed; stamens

4–12, free, anthers extrorse; pistillode minute or absent; pistillate sepals 5–8, persistent; disk annular; ovary 2–3-locular; styles dilated, lobed; capsule tardily loculicidally dehiscent; seeds carunculate.

As circumscribed here, in agreement with the studies of Levin, subtribe Paivaeusinae includes only the single African genus *Oldfieldia*. Pax & Hoffmann (1922) also included in the Paivaeusinae *Piranhea*, which is here referred to Picrodendrinae, and *Aristogeitonia*, which appears better placed in Mischodontinae.

83. *Oldfieldia* Bentham & Hooker f., Hook. J. Bot. Kew Gard. Misc. 2: 184. 1850; Bentham, Gen. Pl. 3: 281. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 297. 1922; Milne-Redhead, Kew Bull. 1948: 456. 1948; Léonard, Bull. Jard. Bot. Brux. 26: 338. 1956; Radcliffe-Smith, Fl. Trop. E. Afr., Euphorb. 114. 1987. TYPE: *Oldfieldia africana* Benth. & Hook.

Paivaeusa Welw. ex Benth., Gen. Pl. 1: 993. 1867. TYPE: *Paivaeusa dactylophylla* Welw. ex Oliver [= *Oldfieldia dactylophylla* (Welw. ex Oliver) Léonard]. *Cecchia* Chiovenda, Fl. Somala 2: 397, fig. 227. 1932. TYPE: *Cecchia somalensis* Chiovenda [= *Oldfieldia somalensis* (Chiovenda) Milne-Redhead].

As delimited by Léonard (1956) and Radcliffe-Smith (1987), *Oldfieldia* includes four African species. The distinction in phyllotaxy (alternate vs. opposite leaves) used by Pax & Hoffmann to distinguish *Paivaeusa* is clearly unworkable, because alternate and opposite leaves occur in both *Paivaeusa* and *Oldfieldia*.

Subtribe 12c. MISCHODONTINAE Muell. Arg., Linnaea 34: 202. 1865; DC. Prodr. 15(2): 1124. 1866; Webster, Taxon 24: 595. 1975. TYPE: *Mischodon* Thwaites.

Androstachydeaceae Airy Shaw, Kew Bull. 18: 250. 1965. TYPE: *Androstachys* Prain.

Monococious or dioecious trees or shrubs; leaves alternate or opposite, simple or 3-foliolate, entire; stipules persistent, adnate to petiole; flowers in axillary cymes or clusters; staminate sepals (2–)5–8, free; disk intrastaminal or absent; stamens 5–50, free; pistillode present or absent; pistillate sepals 5 or 6, deciduous; disk annular or absent; ovary 3–4(–5)-locular, glabrous or pubescent; styles slightly to distinctly connate below; fruit capsular; seeds ecarunculate.

KEY TO THE GENERA OF SUBTRIBE MISCHODONTINAE

1a. Leaves alternate; pistillode present 84. *Aristogeitonia*

1b. Leaves opposite; staminate disk or pistillode (or both) absent.

2a. Stamens with filaments elongated, free; leaves simple.

3a. Staminate disk absent; pistillode present; pistillate sepals deciduous 85. *Mischodon*

3b. Staminate disk present; pistillode absent; pistillate sepals accrescent in fruit 86. *Voatomalo*

2b. Stamens with filaments united into a long column, anthers subsessile; leaves 1–7-foliolate.

4a. Leaves unifoliolate; fruit apically depressed 87. *Androstachys*

4b. Leaves 3–7-foliolate; fruit beaked 88. *Stachyandra*

84. *Aristogeitonia* Prain, Kew Bull. Misc. Inf. 1908: 439. 1908; Hook. Icon. Pl. 30: t. 2926. 1911; Fl. Trop. Afr. 6(1): 625. 1912; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 296. 1922; Airy Shaw, Kew Bull. 26: 495. 1972; Radcliffe-Smith, Fl. E. Trop. Euphorb. 1: 118. 1987; Radcliffe-Smith, Kew Bull. 43: 627. 1988. TYPE: *Aristogeitonia limoniifolia* Prain.

Paragelonium Leandri, Bull. Soc. Bot. France 85: 231. 1939. TYPE: *Paragelonium perrieri* Leandri [= *Aristogeitonia perrieri* (Leandri) Radcl.-Sm.].

An African genus of three species (Angola, Kenya, Tanzania, and Madagascar). Radcliffe-Smith (1988) has recently demonstrated that *Paragelonium* from Madagascar cannot be separated from the mainland African *Aristogeitonia*.

85. *Mischodon* Thwaites, Hook. J. Bot. Kew Gard. Misc. 6: 299. 1854; Muell. Arg., DC. Prodr. 15(2): 1124. 1866; Bentham, Gen. Pl. 3: 280. 1880; Hook. f., Fl. Br. Ind. 5: 344. 1887; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 292. 1922; Raju, J. Econ. Tax. Bot. 5: 165. 1984. TYPE: *Mischodon zeylanicus* Thwaites.

A monotypic genus of Sri Lanka; perhaps native (but very rare) in southern India.

86. *Voatomalo* Capuron ex Bosser, Adansonia II. 15: 333. 1976. TYPE: *Voatomalo eugenioides* Capuron ex Bosser.

This genus of two species from Madagascar was mentioned by Leandri (1958) but not formally published until 1976.

87. *Androstachys* Prain, Kew Bull. Misc. Inf. 1908: 438. 1908; Fl. Trop. Afr. 6(1): 740. 1912; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 287. 1922; Leandri, Fl. Madag. 111: 197. 1958; Airy Shaw, Kew Bull. 18: 251. 1965; Adansonia II. 10: 519. 1970; Dyer, Gen. S.

Afr. Fl. Pl. ed. 3, 312. 1975; Leroy, C. R. Acad. Sci. Paris 283D: 147. 1976; Alvin, Ann. Bot. 59: 579. 1987. TYPE: *Androstachys johnsonii* Prain [= *Androstachys subpeltata* (Sim) Phillips].

If *Stachyandra* is recognized as a distinct genus, *Androstachys* becomes a monotypic genus confined to eastern Africa.

88. *Stachyandra* Leroy ex Radcliffe-Smith, Kew Bull. 45: 562. 1990. TYPE: *Stachyandra merana* (Airy Shaw) Leroy ex Radcl.-Sm.

This genus of four Madagascan species has recently been segregated from *Androstachys*. The two taxa are closely related, and it might be more appropriate to treat *Stachyandra* as a subgenus of *Androstachys*.

Subfamily III. ACALYPHOIDEAE Ascherson, Fl. Prov. Brandenb. 1: 58. 1864. Family Acalyphaceae Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 246. 1859. TYPE: *Acalypha* L.

Trees, shrubs, or herbs; milky latex absent (rarely present, or represented by colored exudate); indumentum simple or hairs often branched or lepidote;

leaves alternate (rarely opposite), usually stipulate; blade simple or palmately lobed (rarely compound), often with foliar glands. Inflorescences axillary or terminal, racemose or spicate, or reduced to glomerules or solitary flowers; bracts sometimes glandular. Staminate flower: sepals imbricate or often valvate (and then often connate and rupturing at anthesis); petals and disk present or absent; stamens 2–100+, free or connate; pollen grains mostly 3–4-colporate, exine semitectate (very rarely echinate); male gametophyte binucleate; pistillode present or absent. Pistillate flower: sepals (2–)3–6(–12), imbricate or open at anthesis, sometimes connate; petals and disk present or absent; ovary mostly 2–4-locular; styles entire to bifid or multifid; ovules solitary in each locule (except in *Dicoelia*), anatropous. Fruit capsular or rarely baccate or drupaceous; seeds carunculate or ecarunculate, testa sometimes fleshy; endosperm usually copious; cotyledons longer and broader than radicle. Base chromosome numbers mostly 9, 10, or 11.

With 116 genera in 20 tribes, subfamily Acalyphoideae is the largest and most complex of the subfamilies of Euphorbiaceae. Through *Clutia* it approaches the Phyllanthoideae, and through *Omphalea* both the Crotonoideae and Euphorbioideae. These multiple connections suggest that the Acalyphoideae may not be a monophyletic group.

KEY TO THE TRIBES OF SUBFAMILY ACALYPHOIDEAE

- 1a. Staminate flowers with 5 imbricate sepals and petals, 5 stamens, and perforate-tectate pollen grains; indumentum simple or malpighiaceous; dioecious; fruit capsular.
 - 2a. Petals not adaxially barbate; filaments connate; disk segments glandular-lobed; seeds carunculate; leaves usually pellucid-punctate, indumentum simple 13. CLUTIEAE
 - 2b. Petals adaxially barbate; filaments free; disk segments not glandular-lobed; seeds ecarunculate; leaves not pellucid-punctate 14. POGONOPHOREAE
- 1b. Staminate flowers not with 5 imbricate sepals and petals and 5 stamens (or if so, then pollen not perforate-tectate or fruit not capsular).
 - 3a. Staminate sepals distinctly imbricate, or else flowers enclosed in bibracteolate involucre; flowers apetalous; dioecious trees or shrubs.
 - 4a. Leaves alternate; pollen exine rugulose or micropunctate.
 - 5a. Filaments connate; pistillode conspicuous; pollen tectum not spinulose; seeds carunculate, testa dry.
 - 6a. Flowers in axillary glomerules, not involucre; stamens 8–15; styles elongated, bifid; capsule echinate; leaves stipulate 15. CHAETOCARPEAE
 - 6b. Flowers enclosed in bibracteolate involucres; stamens 2–6; styles abbreviated, dilated; capsule not echinate; leaves exstipulate 16. PEREAE
 - 5b. Filaments free; pistillode small or absent; pollen tectum spinulose; seeds ecarunculate, testa fleshy 17. CHEILOSEAE
- 4b. Leaves opposite; pollen exine reticulate; seeds ecarunculate, testa dry 18. ERISMANTHEAE
- 3b. Staminate sepals valvate or slightly imbricate; flowers not in bibracteolate involucres; petals present or absent; pollen grains various, not micropunctate; indumentum various.
 - 7a. Staminate petals with depressions opposite anthers, or else fruit drupaceous with channeled endocarp.
 - 8a. Ovules 2 per locule; fruit capsular; plants monoecious; styles unlobed 19. DICOELIEAE
 - 8b. Ovules 1 per locule; fruit drupaceous; plants dioecious; styles bifid 20. GALEARIEAE
 - 7b. Staminate petals lacking depressions opposite anthers; fruit not drupaceous with channeled endocarp.
 - 9a. Cotyledons scarcely broader than radicle; monoecious (rarely dioecious) herbs or subshrubs with ericoid foliage; indumentum simple; pollen grains perforate-tectate, colpi distinctly marginate; seeds carunculate 21. AMPEREAE
 - 9b. Cotyledons distinctly broader than radicle; habit otherwise.

- 10a. Petals present, at least in staminate flowers.
- 11a. Dioecious; indumentum simple; anther connective enlarged, anther sacs pendulous; pollen sexine coarsely reticulate, not heterobrochate 22. AGROSTISTACHYAE
 - 11b. Monoecious (rarely dioecious); indumentum (at least in part) malpighiaceus, stellate, or lepidote; anthers not with enlarged connective and pendulous anther-sacs; pollen sexine often distinctly heterobrochate 23. CHROZOPHOREAE
- 10b. Petals absent.
- 12a. Styles free or basally connate (if long-connate, then styles bifid or indumentum stellate); plants rarely scandent; stinging hairs absent.
 - 13a. Staminate disk present; pollen exine coarsely reticulate, colpi mostly inoperculate.
 - 14a. Leaves usually with laminar glands; indumentum simple or stellate; inflorescence axillary or terminal.
 - 15a. Pollen colpi not marginate; staminate disk massive, pubescent; anther connective enlarged 24. CARYODENDREAE
 - 15b. Pollen colpi marginate; staminate disk tenuous, glabrous; anther connective not enlarged 25. BERNARDIEAE
 - 14b. Leaves eglandular; indumentum simple; stamens many; inflorescence axillary 26. PYCNOCOMEAE
 - 13b. Staminate disk absent (or if present, then pollen colpi operculate).
 - 16a. Pollen grains coarsely reticulate or perforate-tectate; indumentum stellate; stamens inflexed in bud (except in *Koilolepas*); monoecious; pistillate calyx often accrescent; seeds ecarunculate 27. EPIPRINEAE
 - 16b. Pollen grains finely perforate-tectate to rugulose; indumentum simple or stellate; stamens not inflexed in bud.
 - 17a. Pollen grains with operculate colpi; staminate disk present or absent; seeds mostly ecarunculate, testa not fleshy; stipules deciduous or obsolete.
 - 18a. Leaves eglandular; styles subentire to multifid; staminate disk (if present) extrastaminal or interstaminal; pollen sexine finely perforate-tectate (nanospines regularly arranged) 28. ADELIEAE
 - 18b. Leaves usually with embedded laminar glands; styles entire or if divided then inflorescences terminal; staminate disk (if present) intrastaminal; pollen sexine rugulose to striate (nanospines not regularly arranged) 29. ALCHORNEAE
 - 17b. Pollen colpi inoperculate, often reduced; seeds carunculate or ecarunculate, testa dry or fleshy 30. ACALYPHEAE
 - 12b. Styles unlobed, mostly connate into a distinct column; often scandent or twining, sometimes with stinging hairs; inflorescences mostly terminal or pseudoaxillary, bisexual; seeds ecarunculate, testa dry.
 - 19a. Staminate sepals valvate, splitting apart at anthesis; latex absent; inflorescence not paniculate; bracts eglandular; filaments free or connate 31. PLUKENETIEAE
 - 19b. Staminate sepals imbricate; latex clear or reddish; inflorescence paniculate; bracts foliose and biglandular; stamens 2 or 3, filaments connate; pollen grains colporate, exine rugulose 32. OMPHALEAE

Tribe 13. CLUTIEAE (Muell. Arg.) Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 81. 1890 (as Cluytieae). Hippomaneae subtribe Cluytieae Muell. Arg., Linnaea 34: 202. 1865. Cluytieae subtribe Cluytiinae Pax, Pflanzenr. 147. III (Heft 47): 49. 1911. TYPE: *Clutia* L.

Dioecious (rarely monoecious) perennial herbs or shrubs; indumentum simple or absent; leaves alternate, simple, entire, penninerved, often pellucid-punctate, eglandular; stipules small or obsolete; flowers in axillary glomerules (pistillate often solitary); sepals 5,

imbricate; petals 5, free; disk dissected, segments 5, \pm palmately lobed or glandular; stamens 5, filaments connate; anthers mucous, introrse; pollen grains prolate, 3-colporate, colpi inoperculate and slightly to distinctly marginate, exine perforate-tectate; pistillode present; ovary 3-(rarely 4)-locular, glabrous or pubescent; styles free or nearly so, bifid; fruit capsular; seeds carunculate, smooth (or rarely punctate), testa dry; endosperm copious; cotyledons broader and somewhat longer than the radicle.

As here interpreted, the tribe Clutieae is restricted

to the type genus *Clutia*, in accordance with the original concept of Mueller. None of the genera associated in subtribe Clutiinae by Pax (1911) are at all closely related to *Clutia*. Jussieu (1824) had placed *Clutia* in the tribe Phyllanthae, presumably because of its striking similarity in habit. Baillon (1858), who clearly demonstrated that *Clutia* has uniovulate carpels, considered the resemblance to *Briedelia* and *Phyllanthus* to be superficial, and suggested an affinity with *Chiropetalum*. However, the pollen structure does not support Baillon's view, and in fact is more compatible with Jussieu's original suggestion of a relationship with the Phyllanthoideae.

- 89. *Clutia* L.**, Sp. Pl. 1042. 1753; Gen. Pl. ed. 5, 464. 1754; Muell. Arg., DC. Prodr. 15(2): 1043. 1866; Benth. Gen. Pl. 3: 302. 1880; Pax, Pflanzenr. 147. III (Heft 47): 50. 1911; Hutchinson, Fl. Trop. Afr. 6(1): 801. 1912; Prain, Fl. Cap. 5(2): 427. 1920; Dyer, Gen. S. Afr. Fl. Pl. 1: 321. 1975; Léonard, Fl. Congo Belge 8(1): 93. 1962; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 331. 1987. TYPE: *Clutia pulchella* L.

A large African genus of ca. 75 species, with two extending to tropical Arabia; the greatest diversity is in South Africa.

- 14. Tribe POGONOPHOREAE** (Muell. Arg.) Webster, Taxon 24: 595. 1975. Hippomaneae subtribe Pogonophoreae Muell. Arg., Linnaea 34: 202. 1865; DC. Prodr. 15(2): 1040. 1866. TYPE: *Pogonophora* Miers.

Diocious trees; indumentum simple or (in inflorescence) malpighiaceae; leaves alternate, simple, entire, penninerved, eglandular; stipules very small or obsolete; inflorescences axillary, of thyrses or glomerules; staminate sepals 5, coriaceous, broadly imbricate (\pm biseriata); petals 5, imbricate, adaxially barbate; disk intrastaminal, urceolate, 5-lobed; stamens 5, filaments free; anthers basifixed, elongated; pollen grains prolate, 3-colporate, colpi inoperculate, not marginate, sexine perforate-tectate; pistillode present; pistillate perianth as in staminate; disk cupulate, tenuous; ovary 3-locular; styles bilobed; fruit capsular, seeds ecarunculate, smooth, shining, hilum large; endosperm copious; cotyledons much longer and broader than radicle.

The tribe Pogonophoreae is unigeneric, with the same circumscription as that of Mueller (1866). The relationships of the genus *Pogonophora* have remained problematical; affinities have been suggested with *Micrandra*, *Microdesmis*, and it has even been

claimed that the membership of the taxon in the Euphorbiaceae is suspect. Airy Shaw (1966) suggested that it may be more closely allied to the Icacinaceae. However, the pollen of *Pogonophora* is similar to that of *Clutia*, and the floral resemblances to the Icacinaceae are probably superficial.

- 90. *Pogonophora* Miers ex Benth.**, Hook. J. Bot. Kew Gard. Misc. 6: 372. 1854; Muell. Arg., DC. Prodr. 15(2): 1040. 1866; Fl. Bras. 11(2): 435. 1874; Benth. Gen. Pl. 3: 288. 1880; Pax, Pflanzenr. 147. III (Heft 47): 108. 1911; Letouzey, Adansonia II. 9: 275. 1969; Secco, Rev. Gen. *Anomalocalyx* . . . Amer. Sul. 88. 1990. TYPE: *Pogonophora schomburgkiana* Miers ex Benth.

A genus of two species, one neotropical (Amazonian and coastal Brazil), the other west African.

- Tribe 15. CHAETOCARPEAE** (Muell. Arg.) Webster, Taxon 24: 595. 1975. Hippomaneae subtribe Chaetocarpeae Muell. Arg., Linnaea 34: 202. 1865. TYPE: *Chaetocarpus* Thwaites.

Diocious trees or shrubs; indumentum simple or absent; leaves alternate, simple, entire, penninerved, eglandular; stipules deciduous; flowers in axillary bracteate glomerules; staminate sepals 4 or 5, imbricate, free or connate; petals present or absent; disk dissected; stamens 5–15, filaments hirsute, connate below; anthers dehiscent longitudinally; pollen grains globose, 3-colporate (colpi with irregular margins), exine rugulose and micropunctate; pistillode prominent, hirsute; pistillate sepals 4–8, imbricate; disk urceolate; ovary 3-locular; styles bipartite, papillose; fruit capsular; seeds smooth, blackish, carunculate; endosperm copious; cotyledons broader and longer than radicle.

This taxon, originally including only the type genus, was enlarged by Webster (1975) through the inclusion of *Trigonopleura*. The close similarity of the pollen in the two genera seems decisive as an indication of affinity. The blackish carunculate seeds are reminiscent of those of *Clutia*. There may also be a more distant relationship with *Cheilosa*, as suggested by Pax & Hoffmann (1912). Airy Shaw (1975) independently suggested a tribe Chaetocarpeae (not formally published) including *Chaetocarpus* and *Trigonopleura*, and saw a resemblance to *Casearia* in the Flacourtiaceae.

KEY TO THE GENERA OF TRIBE CHAETOCARPEAE

- 1a. Petals present; anthers nearly sessile on staminal column; ovary smooth 91. *Trigonopleura*

1b. Petals absent; filaments well developed; ovary echinate 92. *Chaetocarpus*

91. *Trigonopleura* Hook. f., Fl. Brit. Ind. 5: 399. 1887; Hook. Icon. Pl. 18: t. 1753. 1888; Pax & Hoffm., Pflanzenr. 147. III (Heft 47: 95). 1911; Merrill, Phil. J. Sci. 11C: 76. 1916; Ridley, Fl. Malay Pen. 3: 263. 1924; Whitmore, Tree Flora Malaya 2: 134. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 201. 1975; Kew Bull. 36: 350. 1981. TYPE: *Trigonopleura malayana* Hook. f.

A monotypic genus of southeast Asia (Malaya to the Philippines and Borneo).

92. *Chaetocarpus* Thwaites, Hook. J. Bot. Kew Gard. Misc. 6: 300, t. 10a. 1854 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 1121. 1866; Benth. Gen. Pl. 3: 323. 1880; Pax & Hoffm., Pflanzenr. 147. IV (Heft 52): 7. 1912; Fawc. & Rend., Fl. Jam. 4: 318. 1920; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 179. 1931; Léonard, Fl. Congo 8(1): 127. 1962; Capuron, Adansonia II. 12: 209. 1972; Whitmore, Tree Fl. Malaya 2: 76. 1973. TYPE: *Chaetocarpus pungens* Thwaites [= *Chaetocarpus castanicarpus* (Roxb.) Thw.].

Mettenia Griseb., Fl. Brit. W. Ind. 43. 1859. TYPE: *Mettenia globosa* Griseb. [= *Chaetocarpus globosus* (Griseb.) Fawc. & Rend.].

Regnaldia Baillon, Adansonia I. 1: 87. 1861. TYPE: *Regnaldia chuytioides* Baillon [= *Chaetocarpus castanicarpus* (Roxb.) Thw.].

Neochevaliera Beille, Compt. Rend. Hebd. Acad. Sci. Paris 145: 1295. 1907. TYPE: *Neochevaliera brazzavillensis* Beille [= *Chaetocarpus africanus* Pax].

A genus of 12 species with a disjunct distribution: West Indies, South America, west Africa, Madagascar, and tropical Asia.

Tribe 16. PEREAE (Kl. & Gcke.) Pax & Hoffmann, Pflanzenr. 147. XIII (Heft 68): 1. 1919. Peraceae Kl. & Gcke., Monatsber. Konigl. Preuss. Akad. Wiss. Berlin 1859: 246. 1859. Acalyphaeae subtribe Perinae (Kl. & Gcke.) Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 69. 1890. TYPE: *Pera* Mutis.

Prosopidoclineae Klotzsch, Arch. Naturgesch. 7: 176. 1841. TYPE: *Pera* Mutis.

Dioecious trees or shrubs; indumentum simple, stellate, or lepidote; leaves alternate (rarely opposite), entire, pinnately veined, exstipulate. Flowers in axillary involucrate glomerules; involucre usually of 2 valvate bracts entirely enclosing flowers in bud. Flow-

ers apetalous, disk absent; staminate calyx 2–4-fid or rudimentary; stamens 2–8, filaments connate; pollen grains 3-colporate, rugulose; pistillodes (representing reduced pistillate flowers) surrounding staminate flower. Pistillate flower without perianth; ovary 3-locular; styles stigmatiform. Fruit capsular, valves woody; seeds smooth, dark, carunculate; endosperm copious; cotyledons much longer and broader than radicle.

This tribe, by the unanimous consensus of workers since Baillon, includes only the single genus *Pera*. The relationships of *Pera* have been in doubt, however, because of the reduced nature of the flowers and the peculiar inflorescences that have no counterpart elsewhere in the family. Mueller (1866) placed *Pera* at the end of the Acalyphaeae (Acalyphoideae), Benth. (1880) at the end of the Hippomaneae, and Pax & Hoffmann (1922) following Dalechampiaeae. Airy Shaw (Dict. Fl. Pl. ed. 7, xxii. 1966) recognized Peraceae as a distinct family, but without discussion of its affinities. I believe that the closest relationship of *Pera* may be with tribe Chaetocarpeae, as indicated by similarity in the pollen and also the woody capsules with smooth carunculate seeds.

93. *Pera* Mutis, Kongl. Vetensk. Akad. Nya Handl. 5: 299. 1784; Muell. Arg., DC. Prodr. 15(2): 1025. 1866; Fl. Bras. 11(2): 421. 1874; Benth. Gen. Pl. 3: 340. 1880; Pax & Hoffm., Pflanzenr. 147. XIII (Heft 68): 2. 1919; Jablonski, Mem. New York Bot. Gard. 17: 147. 1967. *Perula* Schreber, Gen. Pl. 703. 1791. TYPE: *Pera arborea* Mutis.

Spixia Leandro de Sacramento, Denkschr. Königl. Akad. Wiss. München, Math. Phys. 7: 231. 1821 (non Schrank, 1821). TYPE: *Spixia heteranthera* Schrank [= *Pera heteranthera* (Schrank) I. M. Johnston].

Schismatopera Klotzsch, Arch. Naturgesch. 7: 178. 1841. TYPE: *Schismatopera martiana* Kl. [= *Pera distichophylla* (Mart.) Baillon].

A neotropical genus of ca. 30 species, extending from Cuba and Central America south to Brazil, with the greatest concentration of taxa in the Amazon basin.

Tribe 17. CHEILOSEAE (Muell. Arg.) Airy Shaw & Webster, Taxon 24: 595. 1975. Hippomaneae subtribe Cheiloseae Muell. Arg., Linnaea 34: 202. 1865. Gelonieae subtribe Chaetocarpiinae series Cheilosiformes Pax & Hoffm., Pflanzenr. 147. XIV (Heft 68): 50. 1919. TYPE: *Cheilosa* Blume.

Dioecious trees; indumentum simple, stellate, or

nearly absent; leaves alternate, simple, entire or crenulate, penninerved, glandular or eglandular; stipules caducous; inflorescences axillary or sometimes terminal, paniculate, bracts eglandular; flowers apetalous; sepals 4 or 5, imbricate; staminate disk dissected, intrastaminal or extrastaminal; stamens 4–10, free; anthers muticous, introrse; pollen grains globose, 3-colporate, colpi inoperculate, exine echinate; pistillode present; pistillate disk annular or absent; ovary 2–3-locular; styles bifid; fruit capsular; seeds ecarunculate, testa fleshy; cotyledons longer and broader than radicle.

This tribe includes two genera, but has a different circumscription from the "series" Cheilosiformes of Pax & Hoffmann (1919, 1931), since *Elateriospermum* is assigned to the subfamily Crotonoideae, and *Neoscortechinia* is added. Airy Shaw (1972) appears to have been the first to suggest that *Neoscortechinia* should be placed in the same tribe as *Cheilosa*.

KEY TO THE GENERA OF TRIBE CHEILOSEAE

- 1a. Fruit thick-walled, capsular, with 3 seeds; indumentum simple; stamens 8–10 94. *Cheilosa*
- 1b. Fruit thin-walled, with 1 seed; indumentum stellate; stamens 5 or 6 95. *Neoscortechinia*

94. *Cheilosa* Blume, Bijdr. 613. 1826; Muell. Arg., DC. Prodr. 15(2): 1122. 1866; Bentham, Gen. Pl. 3: 322. 1880; J. J. Sm., Add. Cogn. Fl. Arb. Jav. 12: 604. 1910; Pax & Hoffm., Pflanzenz. 147. IV (Heft 52): 12. 1912; Airy Shaw, Kew Bull. 16: 364. 1963; Whitmore, Tree Fl. Malaya 2: 77. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 68. 1975; Kew Bull. 36: 276. 1981. TYPE: *Cheilosa montana* Blume.

A genus of two species (perhaps conspecific) in southeast Asia (Malaya to the Philippines and Borneo).

95. *Neoscortechinia* Pax, Natürl. Pflanzenfam. Nachtr. 1: 213. 1897; Pax & Hoffm., Pflanzenz. 147. XIV (Heft 68): 52. 1919; Airy Shaw, Kew Bull. 16: 368. 1963; Whitmore, Tree Fl. Malaya 2: 119. 1973; Airy Shaw, Kew Bull. 36: 333. 1981. *Scortechinia* Hook. f., Hook. Ic. Pl. 18: t. 1706. 1887 (non *Scortechinia* Saccardo, 1885). TYPE: *Scortechinia kingii* Hook. f. [= *Neoscortechinia kingii* (Hook. f.) Pax & Hoffm.].

Alcinaeanthus Merrill, Phil. J. Sci. Bot. 7: 379. 1912. TYPE: *Alcinaeanthus philippinensis* Merr. [= *Neoscortechinia forbesii* Hook. f.) Pax ex S. Moore].

A tropical Asian genus of four species, distributed from Burma to the Philippines and Solomon Islands.

Tribe 18. ERISMANTHEAE Webster, Taxon 24: 595. 1975. TYPE: *Erismanthus* Wall. ex Muell. Arg.

Monococious trees or shrubs; indumentum simple; leaves opposite, subsessile, simple, entire or obscurely dentate, basally oblique, penninerved, stipulate; inflorescences axillary, racemose or spicate; staminate sepals 4 or 5, imbricate or nearly valvate; petals 5; disk absent; stamens 5–15, filaments free; anthers muticous, introrse; pollen grains 3-colporate, angulaperturate, colpi inoperculate, not marginate, sexine reticulate; pistillode present; pistillate sepals 5–6, imbricate; petals present or absent; disk absent; ovary 3-locular; ovules anatropous; styles free to connate, entire or bifid; fruit capsular; seeds smooth, ecarunculate, testa dry.

This tribe includes three tropical Asian genera that share some common features with tribe Epiprineeae. *Erismanthus* and *Moultonianthus* have a distinctive habit due to the opposite phyllotaxy and oblique leaf bases; this is present, but less pronounced, in *Syndyophyllum*.

KEY TO THE GENERA OF TRIBE ERISMANTHEAE

- 1a. Pistillode in staminate flower greatly elongated, clavate; young staminate inflorescence covered with closely imbricate bracts; pistillate flowers apetalous; staminate petals shorter than calyx; stamens 12–15 96. *Erismanthus*
- 1b. Pistillode not greatly elongated; young staminate inflorescences not covered with densely imbricate bracts; stamens 5–10.
 - 2a. Styles distinctly bifid; staminate petals longer than calyx; pistillate flowers petaliferous; stipules persistent, foliaceous, and clasping 97. *Moultonianthus*
 - 2b. Styles entire or nearly so; staminate petals shorter than sepals; pistillate flowers apetalous; stipules small, deciduous 98. *Syndyophyllum*

96. *Erismanthus* Wallich ex Muell. Arg., DC. Prodr. 15(2): 1138. 1866; Bentham, Gen. Pl. 3: 325. 1880; Hook. f., Fl. Brit. Ind. 5: 405. 1887; Pax & Hoffm., Pflanzenz. 147. III (Heft 47): 33. 1911; Gagnep., Fl. Indochine 5: 464. 1926; Airy Shaw, Kew Bull. 26: 260. 1972; Whitmore, Tree Fl. Malaya 2: 95. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 110. 1975; Kew Bull. 36: 294. 1981. TYPE: *Erismanthus obliquus* Muell. Arg.

An Asian genus of two species, the type species

occurring from Thailand to Sumatra and Borneo, the other species (*E. sinensis* Oliver) in Indochina and Hainan.

- 97. Moultonianthus** Merrill, *Phil. J. Sci. Bot.* 11: 70. 1916; Pax & Hoffm., *Pflanzenr.* 147. XIV (Heft 68): 41. 1919; *Natürl. Pflanzenfam.* ed. 2, 19c: 170. 1931; Steenis, *Bull. Bot. Gard. Buitenz.* III. 17: 404. 1948; Airy Shaw, *Kew Bull. Add. Ser.* 4: 176. 1975; *Kew Bull.* 36: 332. 1981. TYPE: *Moultonianthus borneensis* Merr. [= *Moultonianthus leembruggianus* (Boerl. & Koord.) Steenis].

A monotypic genus known only from Sumatra and Borneo.

- 98. Syndyophyllum** Lauterbach & K. Schumann, *Fl. Deutsche Schutzg.* 403. 1901; Pax & Hoffm., *Pflanzenr.* 147. III (Heft 47): 104. 1911; Airy Shaw, *Kew Bull.* 14: 392. 1960; *Hook Ic. Pl.* 38: t. 3722. 1974; *Kew Bull. Add. Ser.* 4: 199. 1975; 8: 204. 1980. TYPE: *Syndyophyllum excelsum* Lauterb. & K. Sch. [lectotype].

A monotypic genus, the single variable species found in Sumatra, Borneo, and New Guinea.

- Tribe 19. DICOELIEAE** Hurusawa, *J. Fac. Sci. Univ. Tokyo Sect. 3, Bot.* 6: 322. 1954; Webster, *Bot. J. Linn. Soc.* 94: 6. 1987. TYPE: *Dicoelia* L.

Monoecious trees or shrubs; indumentum simple; leaves simple, entire, pinnately veined, eglandular; stipules caducous. Inflorescences bisexual, racemose. Staminate sepals 5, valvate or nearly so; petals 5, valvate, with 2 concavities opposite anthers; disk absent; stamens 5; filaments slightly connate to base of 3-5-fid pistillode; pollen grains 3-colporate, tectate. Pistillate sepals 5, valvate; petals 5, slightly imbricate; disk absent; ovary 3-locular; ovules 2 per locule, anatropous; styles free or nearly so, unlobed, slender. Fruit capsular; seeds ecarunculate.

A monogeneric tribe, referred to subfamily Phyllanthoideae by Pax & Hoffmann (1922) because of the biovulate carpels. Although Airy Shaw (1981) suggested an affinity to *Trigonostemon* in the Crotonoideae, Bentham's original suggestion of a relationship to the Galearieae seems perceptive and best supported by the available data.

In my last review of the placement of *Dicoelia* (Webster, 1987), the tribe Dicoelieae was referred to the family Pandaceae as one of its two tribes, the other being the Galearieae. If the Euphorbiaceae were

to be subdivided into segregate families, this arrangement still seems logical. However, in the present synopsis, where a broad concept of the family is taken, it appears necessary to include the Dicoelieae in the Acalyphoideae adjacent to the Galearieae. It might be possible to recognize a separate subfamily for the tribes Dicoelieae and Galearieae, but this seems premature until phylogenetic relationships within the subfamily Acalyphoideae are much better understood.

- 99. Dicoelia** Bentham, *Hook. Ic. Pl.* 13: 70, t. 1289. 1879; *Gen. Pl.* 3: 286. 1880; J. J. Smith, *Bull. Jard. Bot. Buitenz.* III. 1: 392. 1920; Pax & Hoffm., *Pflanzenr.* 147. XII (Heft 81): 15. 1922; Croizat, *J. Arnold Arbor.* 23: 38. 1942; Airy Shaw, *Kew Bull.* 27: 3. 1972; 36: 285. 1981. TYPE: *Dicoelia beccariana* Benth.

A monotypic genus of Malaya, Sumatra, and Borneo according to Airy Shaw (1981), who does not accept *D. affinis* J. J. Sm. as distinct.

- Tribe 20. GALEARIEAE** Bentham, *Gen. Pl.* 3: 247, 287. 1880. Cluytieae subtribe Galeariinae Pax, *Natürl. Pflanzenfam.* ed. 1, 3(5): 81. 1890. TYPE: *Galearia* Zoll. & Mor.

Bennettieae R. Brown, *Pl. Jav. Rar.* 250. 1850 (nom. prov.). Bennettieae R. Brown ex Schnizlein, *Iconogr. Fam. Nat. Regni Vegetab.* 3: 172. 1860. TYPE: *Bennettia* R. Brown [non *Bennettia* S. F. Gray, 1821; = *Galearia* Zoll. & Mor.].

Pandaceae Pierre, *Bull. Soc. Linn. Paris* 1255. 1896; Engler & Gilg, *Syll. Pflanzenfam.* ed. 7, 223. 1913; Forman, *Kew Bull.* 20: 309. 1966; Webster, *Bot. J. Linn. Soc.* 94: 6. 1987. TYPE: *Panda* Pierre.

Dioecious trees or shrubs; indumentum simple; leaves alternate, simple, entire or dentate, pinnately veined, eglandular, stipulate. Inflorescences terminal thyrses or axillary glomerules; bracts sometimes persistent. Staminate sepals free or connate, slightly imbricate or valvate; petals valvate or somewhat imbricate, with ventral paired depressions opposite anthers; disk absent; stamens 5-15, free; anthers introrse; pistillode unlobed, sometimes peltate; pollen grains subglobose, angulaperturate, 3-colporate, sexine finely reticulate. Pistillate sepals free or connate; petals valvate; ovary mainly 3-(2-5)-locular; ovules 1 per locule, anatropous or orthotropous; styles bifid or multifid. Fruit drupaceous; exocarp fleshy or woody; endocarp bony and corrugated or channeled; seeds ecarunculate, endosperm copious.

The tribe Galearieae as treated here corresponds exactly, except for rank, with the family Pandaceae

as circumscribed by Forman (1966). The group has had a rather complicated taxonomic history, which Forman has discussed thoroughly as far as *Panda* is concerned. Bentham (1878, 1880) perceptively noted the resemblance of *Dicoelia* with *Galearia*, even though he retained *Dicoelia* in the Phyllanthaceae (no doubt because of its biovulate carpels). His tribe Galearieae, proposed rather apologetically as a transitional group between Phyllanthaceae and Crotonaceae, included *Galearia* and *Microdesmis* juxtaposed.

The Pandaceae have generally been accepted in the 20th century as a distinct family, usually with a position next to the Euphorbiaceae (e.g., Cronquist, 1981; Radcliffe-Smith, 1987). In my previous review of the group (Webster, 1987), Pandaceae was expanded to include the tribe Dicoelieae (previously situated in subfamily Phyllanthoideae). Whatever their eventual disposition, it appears that Dicoelieae and Galearieae (as here defined) form a coherent and apparently monophyletic group.

The key to the three genera follows that of Forman.

KEY TO THE GENERA OF TRIBE GALEARIEAE

- 1a. Inflorescences axillary, flowers solitary or in glomerules; staminate petals imbricate; leaves usually pellucid-punctate 100. *Microdesmis*
 1b. Inflorescences terminal or cauliflorous, thyrsoid; staminate petals valvate or nearly so; leaves not pellucid-punctate.
 2a. Endocarp thin-walled; ovules usually anatropous; petals valvate; inflorescences mostly terminal 101. *Galearia*
 2b. Endocarp thick-walled; ovules orthotropous; petals \pm imbricate; inflorescences cauliflorous 102. *Panda*

100. *Microdesmis* Planchon, Hook. Ic. Pl. 8: t. 758. 1848; Muell. Arg., DC. Prodr. 15(2): 1041. 1866; Bentham, Gen. Pl. 3: 287. 1880; Pax & Hoffm., Pflanzenr. 147. III (Heft 47): 105. 1911; Gagnepain, Fl. Indochine 5: 458. 1926; Léonard, Bull. Jard. Bot. Brux. 31: 159. 1961; Fl. Congo 8(1): 102. 1962; Whitmore, Tree Fl. Malaya 2: 118. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 222. 1975. TYPE: *Microdesmis puberula* Hook. f. ex Planch.

A paleotropical genus of ten species, eight African and two Asian.

101. *Galearia* Zollinger & Moritz, Syst. Verz. 19. 1846 (nom. cons. prop.); Muell. Arg., DC. Prodr. 15(2): 1036. 1866; Bentham, Gen. Pl.

3: 287. 1880; Hook. f., Fl. Brit. Ind. 5: 377. 1887; Pax & Hoffm., Pflanzenr. 147. III (Heft 47): 97. 1911; Gagnepain, Fl. Indochine 5: 456. 1926; Forman, Kew Bull. 26: 155. 1971; Whitmore, Tree Fl. Malaya 2: 97. 1973. TYPE: *Galearia sessilis* Zoll. & Mor. [= *Galearia filiformis* (Bl.) Boerl.; lectotype selected here because the other species of Zollinger & Moritz, *G. pedicellata*, could be confused with *Bennettia pedicellata* R. Br.].

Cremostachys Tulasne, Ann. Sci. Nat. III. 15: 259. 1851. TYPE: *Cremostachys filiformis* (Bl.) Tul. [= *Galearia filiformis* (Bl.) Boerl.; lectotype].

Bennettia R. Brown, Pl. Jav. Rar. 249. 1852 (non S. F. Gray, 1821). TYPE: *Bennettia javanica* R. Br. [= *Galearia filiformis* (Bl.) Boerl.].

As treated by Forman (1971), *Galearia* includes six species of tropical southeast Asia (Burma to Solomon Islands).

102. *Panda* Pierre, Bull. Mens. Soc. Linn. Paris 1255. 1896; Aubréville, For. Fl. Côte Iv. 1: 300. 1959; Keay, Fl. W. Trop. Afr., ed. 2, 1: 634. 1958; Forman, Kew Bull. 20: 309. 1966. TYPE: *Panda oleosa* Pierre.

Porphyranthus Engler, Bot. Jahrb. Syst. 26: 367. 1899. TYPE: *Porphyranthus zenkeri* Engler [= *Panda oleosa* Pierre].

A monotypic genus of west tropical Africa. Although *Panda* diverges from nearly all other Euphorbiaceae in its distinctive characters (e.g., orthotropous ovules), Forman appears correct in seeing it as the terminus of a sequence of morphological changes within the Galearieae.

Tribe 21. AMPEREAE Muell. Arg., Bot. Zeit. 22: 324. 1864; DC. Prodr. 15(2): 211. 1866. TYPE: *Amperea* A. Juss.

Ampereae subtribe Monotaxideae Muell. Arg., Linnaea 34: 63. 1865. TYPE: *Monotaxis* Brongn.

Monoecious (rarely dioecious) herbs or shrubs; indumentum simple; leaves alternate, ericoid, stipulate; flowers in terminal or axillary glomerules; staminate calyx 3–5-lobed, lobes valvate or slightly imbricate; petals present or absent; disk entire or dissected; stamens 6–10, biseriate, filaments free, anthers with disjunct or pendulous locules; pollen grains 3-colporate, colpi inoperculate, distinctly marginate, sexine perforate-tectate; pistillode present or absent; pistillate sepals 4 or 5, imbricate or valvate; petals small or absent; disk annular, dissected, or absent; ovary 3-locular; styles bifid to multifid; fruit capsular; seeds smooth, ca-

runculate; endosperm copious; embryo cylindrical, cotyledons scarcely broader than radicle.

In the circumscription of Pax (1890) and Grüning (1913), which is followed here, tribe Ampereae includes two genera confined to Australia. Although the pollen grains are similar in exine sculpturing and marginate colpi, the genera are dissimilar in many ways, and it is not certain that they should be associated in the same tribe.

KEY TO THE GENERA OF TRIBE AMPERAE

- 1a. Staminate petals present; sepals imbricate; anther locules disjunct; pollen grains 3-angled, sexine reticulate; style-branches fimbriate; cymes terminal 103. *Monotaxis*
- 1b. Staminate petals absent; sepals valvate; anther locules pendulous from glandular connective; pollen grains 3-lobed, sexine perforate-foveolate; style-branches entire; flowers axillary 104. *Amperea*

103. *Monotaxis* Brongniart, Voy. Coquille Bot. 223. 1829; Muell. Arg., DC. Prodr. 15(2): 212. 1866; Bentham, Fl. Austral. 6: 78. 1873; Gen. Pl. 3: 264. 1880; Grüning, Pflanzenr. 147. (Heft 58): 75. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 227. 1931; Airy Shaw, Muelleria 4: 239. 1980. TYPE: *Monotaxis linifolia* Brongn. [lectotype].

Hippocrepantha Muell. Arg., Linnaea 34: 61. 1865. TYPE: *Hippocrepantha gracilis* Muell. Arg. [= *Monotaxis lurida* (Muell. Arg.) Benth.; lectotype, designated by Wheeler, 1975].

An Australian genus of about ten species. Brongniart, in his original description, suggested an affinity to *Chiropetalum* and *Ditaxis* in tribe Chrozophoreae. Punt (1962) related pollen of *Monotaxis* to his "Sumbavia type," which includes genera of tribe Chrozophoreae. Perhaps further study will demonstrate that *Monotaxis* is indeed an aberrant genus of Chrozophoreae.

104. *Amperea* A. Jussieu, Euphorb. Tent. 35. 1824; Muell. Arg., DC. Prodr. 15(2): 213. 1866; Bentham, Fl. Austral. 6: 81. 1873; Gen. Pl. 3: 265. 1880; Grüning, Pflanzenr. 147 (Heft 58): 86. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 228. 1931; Henderson, Austral. Syst. Bot. 10 (in press). 1993. TYPE: *Amperea ericoides* A. Juss.

According to Henderson (1993), *Amperea* is a genus of eight Australian species, all except two confined to Western Australia. On the basis of pollen characters, Punt (1962) related *Amperea*

to genera in tribe Epiprineae; this suggestion merits further inquiry.

Tribe 22. AGROSTISTACHYDEAE (Muell. Arg.) Webster, Taxon 24: 596. 1975. Acalypheae subtribe Agrostistachydeae Muell. Arg., Linnaea 34: 143. 1865. TYPE: *Agrostistachys* Dalz.

Dioecious (rarely monoecious) trees or shrubs; indumentum simple or absent; leaves alternate, simple, entire or denticulate, lamina glandular or eglandular; stipules persistent or deciduous; inflorescences axillary, racemose or spicate, sometimes with scarious imbricate bracts; staminate calyx closed in bud, splitting into 2–5 valvate lobes; petals 3–8; disk receptacular or extrastaminal and dissected; stamens 10–50, filaments free (at least in part), anthers introrse, with \pm enlarged connective, anther-sacs often pendulous; pollen grains subglobose, 3-colporate, colpi inoperculate, not distinctly marginate, sexine coarsely reticulate; pistillode present or absent; pistillate sepals 4 or 5, open or valvate; petals 5, small and deciduous, or absent; disk lobed, pitted, or dissected; ovary 3-locular, often tomentose; styles bifid; fruit capsular; seeds smooth or granulate, ecarunculate, testa sometimes fleshy.

This tribe is here considered to include four genera, two African and two Asiatic.

KEY TO THE GENERA OF TRIBE AGROSTISTACHYDEAE

- 1a. Petals present; flowers in spikes or racemes.
 - 2a. Dioecious; staminate petals imbricate in bud; petals present in pistillate flower.
 - 3a. Staminate disk dissected; stamens 8–10; stipules free; leaves eglandular 105. *Agrostistachys*
 - 3b. Staminate disk receptacular; stamens 20–55; stipules connate, leaving an annular scar; leaves glandular at base 106. *Pseudagrostistachys*
 - 2b. Monoecious; staminate petals not imbricate in bud; pistillate flowers apetalous; leaves glandular at base 107. *Cyttaranthus*
- 1b. Petals absent; flowers in panicles; monoecious, leaves glandular at base 108. *Chondrostylis*

105. *Agrostistachys* Dalzell, Hook. J. Bot. Kew Gard. Misc. 2: 41. 1850; Muell. Arg., DC. Prodr. 15(2): 725. 1866; Bentham, Gen. Pl. 3: 302. 1880; Hook. f., Fl. Brit. Ind. 5: 405. 1887; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 98. 1912; Gagnep., Fl. Indochine 5: 463. 1926; Airy Shaw, Kew Bull. 14: 472. 1960; 26: 210. 1972; Whitmore, Tree Fl. Malaya 2: 52. 1973; Airy Shaw, Kew Bull. Add. Ser.

4: 26. 1975; Kew Bull. 36: 248. 1981. TYPE: *Agrostistachys indica* Dalz.

Heterocalyx Gagnepain, Notul. Syst. (Paris) 14: 33. 1950. TYPE: *Heterocalyx laoticus* Gagnep. [= *Agrostistachys indica* Dalz.].

An Asiatic genus of ten species, some difficult to distinguish, distributed from India and Sri Lanka to New Guinea.

106. Pseudagrostistachys Pax & Hoffmann, Pflanzenr. 147. VI (Heft 57): 96. 1912; Lebrun, Bull. Soc. Roy. Belge 67: 97. 1934; Léonard, Fl. Congo 8(1): 183. 1962; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 166. 1987. TYPE: *Pseudagrostistachys africana* (Muell. Arg.) Pax & Hoffm.

An African genus of two species distributed from São Tome and Nigeria to Zaire and Uganda.

107. Cyttaranthus Léonard, Bull. Jard. Bot. Brux. 25: 286. 1955; Fl. Congo 8(1): 180. 1962. TYPE: *Cyttaranthus congolensis* Léonard.

A monotypic genus confined to west Africa (Congo and Cabinda); extremely close to *Chondrostylis* and perhaps not separable.

108. Chondrostylis Boerlage, Ic. Bogor. 1: t. 23. 1897; Koorders, Ann. Jard. Bot. Buitenz. 19: 45. 1904; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 15. 1914; Airy Shaw, Kew Bull. 14: 358. 1960; Whitmore, Tree Fl. Malaya 2: 77. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 69. 1975; Kew Bull. 36: 276. 1981. TYPE: *Chondrostylis bancana* Boerl.

Kunstlerodendron Ridley, Fl. Malay Penin. 3: 283. 1924. TYPE: *Kunstlerodendron sub lanceolata* Ridl., nom. illeg. [= *Chondrostylis kunstleri* (King ex Hook. f.) Airy Shaw].

A monotypic genus of southeast Asia (Thailand to Sumatra and Borneo).

Tribe 23. CHROZOPHOREAE (Muell. Arg.) Pax & Hoffmann, Pflanzenr. 147. XIV (Heft 68): 5. 1919. Chrozophoreae subtribe Regulares (Pax & Hoffm.) Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 89. 1931. TYPE: *Chrozophora* Necker ex A. Juss.

Trees, shrubs, or herbs, monoecious or dioecious; indumentum usually stellate, lepidote, or malpighiaceus (at least in part; rarely entirely simple); leaves alternate, unlobed or lobed, entire

or dentate, pinnately or palmately veined, sometimes with laminar glands; stipules persistent or deciduous, sometimes obsolete; inflorescences axillary or terminal, mostly racemose or spicate. Staminate flower: sepals 3–5, valvate; petals 4 or 5 (rarely 10 or absent); disk dissected or absent; stamens 5–many, filaments free or connate; anthers introrse, mucicous, locules not pendulous; pollen grains subglobose to oblate, mostly 3–6-colporate, colpi sometimes operculate, not distinctly marginate, sexine reticulate, often distinctly heterobrochate; pistillode present or absent. Pistillate flower: sepals 5 or 6, imbricate or valvate; petals 5 (sometimes reduced or absent); disk annular or dissected (rarely absent); ovary (2-)3-locular, smooth or muricate; styles unlobed to bifid or twice-bifid, sometimes lacerate. Fruit capsular; seeds dry or fleshy, endotesta smooth or roughened to pitted, ecarunculate.

As delimited by Webster (1975) and here, tribe Chrozophoreae corresponds almost exactly to the subtribe Regulares as treated by Pax & Hoffmann (1931); their other subtribe Irregulares includes genera belonging to tribe Agrostistachydeae and subfamily Crotonoideae. Pollen characters in genera such as *Doryxylon* suggest a possible relationship between Chrozophoreae and tribe Epipirineae.

KEY TO THE SUBTRIBES OF TRIBE CHROZOPHOREAE

- 1a. Pollen grains not distinctly heterobrochate; indumentum simple or malpighiaceus; leaves not with basal laminar glands.
 - 2a. Inflorescences terminal; indumentum entirely simple; stamens 10–15, free; pistillate disk annular; ovary muricate 23a. Speranskiinae
 - 2b. Inflorescences axillary; indumentum malpighiaceus or stellate (at least in part); stamens, if more than 6, connate; pistillate disk dissected or obsolete 23b. Ditaxinae
- 1b. Pollen grains distinctly heterobrochate; indumentum stellate; leaves with basal laminar glands.
 - 3a. Shrubs or trees; pollen grains 3-colporate; stamens free; seeds fleshy 23c. Doryxylineae
 - 3b. Herbs; pollen grains stephanocolporate; stamens connate; seeds not fleshy 23d. Chrozophorinae

Subtribe 23a. SPERANSKIINAE Webster, Taxon 24: 596. 1975. TYPE: *Speranskia* Bailon.

Monoecious herbs; indumentum simple; leaves alternate, coarsely dentate or lobulate, with glandular teeth, stipulate; inflorescences terminal, spicate, bisexual, pistillate flowers proximal; staminate sepals and petals 5; disk dissected; stamens 10(–15),

filaments free; pollen grains 3-colporate, evenly reticulate; pistillode absent; pistillate sepals 5; petals 5, small or absent; disk annular; ovary 3-locular, verrucose; styles free, bifid, branches lacerate; fruit capsular; seeds dry, ecarunculate, testa foveolate-asperate.

This monogeneric subtribe is morphologically similar to subtribe Ditaxinae, and indeed Mueller (1866) included *Speranskia* as a section of *Argythamnia*. However, the Speranskiinae diverge from the Ditaxinae in a number of characters, particularly the androecium of free stamens and the terminal inflorescence.

109. *Speranskia* Baillon, Etude Gén. Euphorb. 388. 1858; Bentham, Gen. Pl. 3: 305. 1880; Pax & Hoffm., Pflanzenz. 147. VI (Heft 57): 14. 1912; Hurusawa, J. Fac. Sci. Univ. Tokyo III. Bot. 6: 310. 1954. TYPE: *Speranskia tuberculata* (Bunge) Baillon.

A genus restricted to China; there are three species according to Pax & Hoffmann (1912) or two according to Hurusawa (1954).

Subtribe 23b. DITAXINAE Grisebach, Fl. Brit. W. Ind. 43. 1859; Abh. Gesell. Wiss. Goettingen 9: 15. 1861. TYPE: *Ditaxis* Vahl ex A. Juss.

Acalyphaeae subtribe Caperoneiae Muell. Arg., Linnaea 34: 143. 1865. TYPE: *Caperonia* St. Hil.

Monoecious (rarely dioecious) trees, shrubs, or herbs; indumentum predominantly malpighiaceae, sometimes also stellate, simple, or glandular; leaves alternate, entire or serrate, without laminar glands; inflorescences axillary, racemose or glomerulate, usually bisexual; staminate sepals mostly 4 or 5; petals 4 or 5; disk dissected or absent; stamens 4–15, filaments connate (rarely almost free); anthers introrse; pollen grains subglobose to oblate, 3-colporate to stephanocolporate, sexine reticulate, not distinctly heterobrochate; pistillode present or absent; pistillate sepals 5 or more, imbricate to valvate; petals 5(6), sometimes obsolete; disk dissected or absent; ovary sometimes muriccate; styles bifid to laciniate; fruit capsular; seeds dry, smooth or ornamented (foveolate, asperate, or reticulate), ecarunculate.

In the circumscription of Webster (1975), which is continued here, subtribe Ditaxinae includes five genera that are confined to the New World except for a few species of *Caperonia*. The subtribe approaches subtribe Speranskiinae via *Caperonia*,

which resembles the Chinese genus in its muriccate ovary and laciniate style-branches, but differs in its axillary racemes and stephanocolporate pollen. Generic delimitation within the subtribe is still controversial, but pollen characters such as pointed out by Punt (1962) support the narrow circumscription of Pax & Hoffmann rather than the broad delimitation of Mueller (1866) and Ingram (1979).

KEY TO THE GENERA OF SUBTRIBE DITAXINAE

- 1a. Pistillode present; styles dissected; indumentum simple or glandular (not malpighiaceae); leaves finely serrate with straight parallel lateral veins; pollen grains 6-colporate 110. *Caperonia*
- 1b. Pistillode absent; styles bifid to dissected; indumentum (at least in part) malpighiaceae; leaves otherwise; pollen grains 3- or 4-colporate.
 - 2a. Dioecious; tepals scarious; shrubs or trees, branches often spiny 111. *Philyra*
 - 2b. Monoecious; tepals not scarious; undershrubs or herbs, not spiny.
 - 3a. Petals entire; styles twice bifid to multifid; stellate hairs absent.
 - 4a. Stamens 8–10, anthers in 2 whorls; pollen grains 3- or 4-colporate, bilaterally symmetrical 112. *Ditaxis*
 - 4b. Stamens 4 or 5, anthers in 1 whorl; pollen grains stephanocolporate 113. *Argythamnia*
 - 3b. Petals toothed or lacerate; styles once bifid; stellate hairs sometimes present; pollen grains 3-colporate 114. *Chiropetalum*

110. *Caperonia* St. Hilaire, Pl. Remarq. Bresil 244. 1826; Muell. Arg., DC. Prodr. 15(2): 751. 1866; Fl. Bras. 11(2): 315. 1874; Bentham, Gen. Pl. 3: 304. 1880; Pax & Hoffm., Pflanzenz. 147. VI (Heft 57): 27. 1912; Léonard, Bull. Jard. Bot. Brux. 26: 313. 1956; Fl. Congo 8(1): 166. 1962; Webster, J. Arnold Arbor. 48: 363. 1967; Dyer, Gen. S. Afr. Fl. Pl. 1: 314. 1975; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 163. 1987. TYPE: *Caperonia castaneifolia* (L.) St. Hil. [lectotype, designated by Britton & Wilson, Bot. Porto Rico 6: 486. 1925].

A genus of ca. 40 species, mostly American, less than 10 species in Africa. *Caperonia* is quite sharply distinct from the other genera in subtribe Ditaxinae, and Mueller referred it to a separate subtribe Caperoneiae. On the basis of present reports (Hans, 1973), *Caperonia* appears to have a different chromosome number ($x = 11$) from the other genera ($x = 13$).

111. *Philyra* Klotzsch, Arch. Naturgesch. 7(1): 199. 1841; Baillon, Etude Gén. Euphorb. 297.

1858; Pax & Hoffmann, *Pflanzenr.* 147. VI (Heft 57): 49. 1912; *Natürl. Pflanzenfam.* ed. 2, 19c: 92. 1931; O'Donell & Lourteig, *Lilloa* 8: 60. 1942. TYPE: *Philyra brasiliensis* Kl.

A monotypic genus of Paraguay and southern Brazil.

112. *Ditaxis* Vahl ex A. Jussieu, *Euphorb. Tent.* 27. 1824; Pax, *Natürl. Pflanzenfam.* ed. 1, 3(5): 44. 1890; Pax & Hoffm., *Pflanzenr.* 147. VI (Heft 57): 51. 1912; *Natürl. Pflanzenfam.* ed. 2, 19c: 93. 1931. TYPE: *Ditaxis fasciculata* Vahl ex A. Juss.

Aphora Nuttall, *Trans. Amer. Phil. Soc.* II. 5: 174. 1837. TYPE: *Aphora mercurialina* Nutt. [= *Ditaxis mercurialina* (Nutt.) Coulter].

Serophyton Benth., *Bot. Voy. Sulphur* 52. 1844. TYPE: *Serophyton lanceolatum* Benth. [= *Ditaxis lanceolata* (Benth.) Pax & Hoffm.].

Stenonia Didrichsen, *Vidensk. Medd. Dansk Naturhist. Foren. Kjøbenhavn* 1857f: 146. 1857 (non Endlicher, 1947). TYPE: *Stenonia montevidensis* Didr. [= *Ditaxis montevidensis* (Didr.) Pax].

Paxiuscula Herter, *Rev. Sudamer. Bot.* 6: 92. 1941. TYPE: *Paxiuscula acaulis* (Herter ex Arech.) Herter [= *Ditaxis acaulis* Herter].

An American genus of 40–50 species distributed in drier areas from the United States south to Argentina. *Ditaxis* is very close to *Argythamnia*, and it remains to be demonstrated whether it should be combined with that genus, as many workers, including Mueller (1866), Bentham (1880), and Ingram (1979), have proposed. However, evidence from pollen morphology (Punt, 1962; Webster, ined.) tends to support its status as a distinct genus.

113. *Argythamnia* P. Brown, *Civ. Nat. Hist. Jamaica* 338. 1756; Swartz, *Fl. Ind. Occid.* 1: 335. 1797; Muell. Arg., *DC. Prodr.* 15(2): 732. 1866; Benth., *Gen. Pl.* 3: 303. 1880; Pax & Hoffm., *Pflanzenr.* 147. VI (Heft 57): 78. 1912; Johnston & Warnock, *Southw. Nat.* 7: 154. 1962; Ingram, *Brittonia* 16: 271. 1964; Gentes *Herb.* 10(1): 1–46. 1967; 11(7): 426. 1979; Correll & Correll, *Fl. Bahama Arch.* 777. 1982; Snee & De Roon, *Fl. Neth. Ant.* 3: 250. 1984. TYPE: *Argythamnia candidans* Swartz.

In the revisional study by Ingram (1967), 18 species of *Argythamnia* (sensu stricto) are recognized. It is a Caribbean genus with over half the species in the West Indies, but a number also occurring in Mexico and Central America.

114. *Chiropetalum* A. Jussieu, *Ann. Sci. Nat.* I. 25: 21. 1832; Pax & Hoffm., *Pflanzenr.*

147. VI (Heft 57): 86. 1912; Ingram, *Gentes Herb.* 11(7): 437. 1979; L. Smith et al., *Fl. Illustr. Catar. EUFO* 154. 1988. TYPE: *Chiropetalum tricuspdatum* (Lam.) A. Juss.

Desfontaena Vellozo, *Fl. Flum.* 95. 1825. TYPE: *Desfontaena tricocca* Vell. [= *Chiropetalum tricoccum* (Vell.) Chod. & Hassl.].

Chlorocaulon Kl. ex Endl., *Gen. Pl. Suppl.* 4(3): 89. 1850. TYPE: *Chiropetalum schiedeana* (Muell. Arg.) Pax & Hoffm.

Aonikena Spegazzini, *Anal. Mus. Nac. Hist. Nat. Buenos Aires* II. 7: 162. 1902. TYPE: *Aonikena patagonica* Speg. [= *Chiropetalum patagonicum* (Speg.) O'Don. & Lourt.].

A genus of ca. 20 species, almost entirely in temperate South America except for a single Mexican species. Although reduced to a section of *Argythamnia* by Ingram, *Chiropetalum* is distinctive in its lobed petals and different pollen type (Punt, 1962).

Subtribe 23c. DORYXYLINAE Webster, *Taxon* 24: 596. 1975. TYPE: *Doryxylon* Zoll.

Monoecious shrubs or trees; indumentum stellate; leaves alternate, entire or dentate, with laminar glands; stipules small; inflorescences terminal or axillary, usually bisexual; staminate sepals 3–5; petals 5–10 or absent; disk reduced or absent; stamens many (ca. 30–250), free or partially connate; pollen grains 3-colporate, angulaperturate, coarsely reticulate, slightly heterobrochate along colpi; pistillode present or absent; pistillate sepals 5 or 6, imbricate or valvate; petals rudimentary or absent; disk annular (or obsolete); ovary 2- or 3-locular, stellate-pubescent; styles unlobed or bifid; seeds with fleshy exotesta, foveolate endotesta.

This subtribe of four Asian genera stands out from other Chrozophoreae by the combination of woody habit and stellate pubescence.

KEY TO THE GENERA OF SUBTRIBE DORYXYLINAE

- 1a. Petals present; ovary 3-locular; stamens ca. 30–100.
 - 2a. Inflorescences axillary; styles unlobed, basally connate; stamens free ... 115. *Doryxylon*
 - 2b. Inflorescences terminal; styles bifid, ± free.
 - 3a. Stamens free; staminate disk absent; pistillate sepals imbricate 116. *Sumbaviopsis*
 - 3b. Stamens connate; staminate disk present; pistillate sepals valvate 117. *Thyrsanthera*
- 1b. Petals absent; ovary usually 2-locular; stamens 200 or more; inflorescences terminal; styles entire 118. *Melanolepis*

115. *Doryxylon* Zollinger, *Tijdschr. Ned.-Indië* 14: 172. 1857; *Linnaea* 29: 469. 1859; Ba-

lakrishnan, Bull. Bot. Surv. India 9: 56. 1967.
TYPE: *Doryxylon spinosum* Zoll.

Sumbavia Baillon, Etude Gén. Euphorb. 390. 1858; Muell. Arg., DC. Prodr. 15(2): 727. 1866; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 11. 1912. TYPE: *Sumbavia rottleroides* Baillon [= *Doryxylon spinosum* Zoll.].

This Asian genus, according to Balakrishnan, includes two species, but he treated *Sumbaviopsis* as a synonym of *Doryxylon*. He may be correct in this, but until the relationships can be further investigated, also taking *Thyrsanthera* into account, it seems best to provisionally keep the genera distinct. Earlier workers, from Mueller (1866) to Pax & Hoffmann (1912, 1931), used *Sumbavia* as the name for this genus because they thought *Doryxylon* was first published in *Linnaea* in 1859, and hence did not have priority.

116. *Sumbaviopsis* J. J. Smith, Add. Fl. Arb. Jav. 12 (Med. Dept. Landbouw 10): 356. 1910; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 13. 1912; Gagnep., Fl. Indochine 5: 418. 1926; Airy Shaw, Kew Bull. 14: 357. 1960; Whitmore, Tree Fl. Malaya 2: 132. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 197. 1975. TYPE: *Sumbaviopsis albicans* (Bl.) J. J. Sm.

A monotypic tropical Asian genus (Assam to Borneo and Palawan).

117. *Thyrsanthera* Pierre ex Gagnepain, Bull. Soc. Bot. France 71: 878. 1925; Gagnepain, Fl. Indochine 5: 299. 1925; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 90. 1931; Backer & Backh., Fl. Jav. 1: 477. 1963; Airy Shaw, Kew Bull. 19: 308. 1965; 26: 343. 1972. TYPE: *Thyrsanthera suborbicularis* Pierre ex Gagnep.

A monotypic genus known from Thailand and Cambodia. Airy Shaw (1972, in clavi) suggested that it may be more closely related to *Chrozophora* than to *Sumbaviopsis*.

118. *Melanolepis* Reichb. f. & Zoll., Verh. Naturk. Ver. Ned. Ind. 1: 22. 1856; *Linnaea* 28: 324. 1856; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 142. 1914; Gagnepain, Fl. Indochine 5: 347. 1925; Kanehira, Fl. Micronesica 180. 1933; Airy Shaw, Kew Bull. Add. Ser. 8: 174. 1980. TYPE: *Melanolepis multiglandulosa* (Reinw.) Reichb. f. & Zoll.

An Asian genus of two species extending from Thailand and Cambodia to Taiwan, Marianas, and Bismarck Archipelago.

Subtribe 23d. CHROZOPHORINAE Muell. Arg., *Linnaea* 34: 143. 1865; DC. Prodr. 15(2): 726. 1866; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 1. 1912. TYPE: *Chrozophora tinctoria* (L.) A. Juss.

Monoeocious herbs or subshrubs; indumentum stellate; leaves alternate, entire or lobed, biglandular at base, stipulate; inflorescences axillary, racemose, bisexual; staminate sepals and petals 5; disk inconspicuous, adnate to staminal column; stamens 4–15, filaments connate into a column; anthers introrse; pollen grains oblate, stephanocolporate, colpi short and broad, sexine distinctly heterobrochate; pistillode absent; pistillate sepals 5; petals 5, small or absent; disk lobed or dissected; ovary 3-locular, stellate or lepidote, sometimes muciculate; styles bifid; fruit capsular; seeds carunculate, somewhat fleshy, endotesta smooth or tuberculate.

In the present circumscription, subtribe Chrozophorinae is monogeneric. It is very close to subtribe Doryxylineae, as noted by Airy Shaw (1972, 1975), and further study may show that *Thyrsanthera* bridges the apparent gap between the two taxa.

119. *Chrozophora* Necker ex A. Jussieu, Euphorb. Tent. 27. 1824 (as *Crozophora*), nom. & orth. cons.; Muell. Arg., DC. Prodr. 15(2): 746. 1866; Bentham, Gen. Pl. 3: 305. 1880; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 17. 1912; Prain, Kew Bull. Misc. Inf. 1918: 49. 1918; Pojarkova, Fl. URSS 14: 288. 1949; Rech. f. & Schiman-Czeika, Fl. Iranica 6: 5. 1964; Berhaut, Fl. Ill. Sénégal 3: 397. 1975; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 160. 1987. TYPE: *Chrozophora tinctoria* (L.) A. Juss.

An Old World genus of ca. ten species distributed from southern Europe to east Africa, central and southern Asia.

Tribe 24. CARYODENDREAE Webster, Taxon 24: 596. 1975. TYPE: *Caryodendron* Karsten.

Dioecious trees or shrubs; indumentum simple; leaves alternate, penninerved or triplinerved, with basal glands; stipules persistent, reduced, or absent; inflorescences terminal or axillary, spicate. Flowers apetalous; staminate sepals 3–5, valvate; disk intrastaminal, pubescent; stamens 4–15, filaments free; anthers introrse, connective enlarged or glandular; pollen grains oblate, 3-colporate, colpi not marginate, sexine coarsely reticulate; pistillode

present or absent. Pistillate sepals 4–6, imbricate or valvate, deciduous; disk annular or dissected, pubescent; ovary 3-(rarely 2- or 4-)locular; styles free, unlobed. Fruit capsular; seeds ecarunculate, testa dry or fleshy.

This tribe of three genera is represented by two genera in the New World and one genus in Africa. The pollen grains are very similar to those in tribe Agrostistachydeae, which may be the most closely related taxon; however, they clearly differ from Caryodendreae in having petaliferous flowers, more stamens, a glabrous floral disk, and bifid styles.

KEY TO THE GENERA OF TRIBE CARYODENDREAE

- 1a. Pistillode absent; inflorescence terminal.
 2a. Staminate disk massive, pulviniform; capsule thick-walled, seed coat dry; leaves penninerved, stipules deciduous 120. *Caryodendron*
 2b. Staminate disk dissected; capsule thin-walled, seed coat fleshy; leaves triplinerved, exstipulate 121. *Discoglypremna*
- 1b. Pistillode present; inflorescences axillary; staminate disk massive, annular; capsule thin-walled; seed coat fleshy; leaves triplinerved, exstipulate 122. *Alchorneopsis*

120. *Caryodendron* Karsten, Fl. Colombiae 1: 91, t. 45. 1860; Muell. Arg., Fl. Bras. 11(2): 706. 1874; Bentham, Gen. Pl. 3: 314. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 263. 1914; Ducke, Trop. Woods 76: 18. 1943; Webster, Ann. Missouri Bot. Gard. 54: 287. 1968; Huft, Ann. Missouri Bot. Gard. 76: 1077. 1989. TYPE: *Caryodendron orinocense* Karst.

A neotropical genus of three species recorded from Panama to Colombia and Brazil. Huft (1989) has recently shown that *Centrodiscus* Muell. Arg., cited by Pax & Hoffmann and others as a synonym of *Caryodendron*, was not validly published; hence it is not listed as a synonym.

121. *Discoglypremna* Prain, Kew Bull. 1911: 317. 1911; Fl. Trop. Afr. 6(1): 931. 1912; Hook. Ic. Pl. 30: t. 2988. 1913; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 18. 1914; Keay, Fl. W. Trop. Afr., ed. 2, 1: 403. 1958; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 222. 1987. TYPE: *Discoglypremna caloneura* (Pax) Prain.

A monotypic African genus, distributed from Guinea and São Tome to Cabinda and Uganda. *Discoglypremna* is clearly the African vicariant

of *Alchorneopsis*; the two taxa could as easily be regarded as subgenera of a single genus.

122. *Alchorneopsis* Muell. Arg., Linnaea 34: 156. 1865; DC. Prodr. 15(2): 764. 1866; Fl. Bras. 11(2): 327. 1874; Bentham, Gen. Pl. 3: 315. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 267. 1914; Webster, Ann. Missouri Bot. Gard. 54: 284. 1968. TYPE: *Alchorneopsis floribunda* (Benth.) Muell. Arg.

A neotropical genus of three described species that are probably conspecific, recorded from the West Indies (Puerto Rico), Panama, Brazil, and the Guianas.

Tribe 25. BERNARDIEAE Webster, Taxon 24: 596. 1975. Acalyphaeae subtribe Mercurialinae series Bernardiiformes Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 13. 1914. TYPE: *Bernardia* Houstoun ex Miller.

Monoecious or dioecious shrubs or herbs; indumentum simple or stellate; leaves alternate, simple, penninerved, often with laminar glands, stipulate; inflorescences terminal, pseudoterminal, or axillary, racemose or spicate; flowers apetalous. Staminate calyx splitting into 3 or 4 valvate segments; disk intrastaminal, pulviniform, dissected, or obsolete; stamens 3–60, filaments free; anthers mucicous or apiculate; pollen grains 3-lobed, 3-colporate, colpi inoperculate, conspicuously marginate, sexine perforate-tectate; pistillode rudimentary or absent. Pistillate sepals 4–6, imbricate; disk annular or dissected; ovary 3-locular; styles bifid, branches sometimes lacerate. Fruit capsular; seeds ecarunculate, smooth, roundish, sometimes carinate.

This tribe includes only part of the genera assigned to the series Bernardiiformes by Pax & Hoffmann (1914). The type genus, *Bernardia*, has often been associated with *Adelia*, and indeed Bailon (1858) treated *Bernardia* as a synonym of *Adelia*. However, the pollen of *Adelia* differs markedly in having operculate colpi and a finely punctate-tectate sexine; tribes Bernardieae and Adeliae do not appear to be closely related. Hutchinson (1969) referred *Bernardia* to tribe Macaranga, but its pollen is very different from *Macaranga*.

KEY TO THE GENERA OF TRIBE BERNARDIEAE

- 1a. Styles bifid; stamens 4–50, anther connective not greatly enlarged.
 2a. Leaf blades not stipellate.

- 3a. Stamens 30 or fewer, anthers emarginate; seeds carinate 123. *Bernardia*
3b. Stamens more than 30, anthers apiculate; seeds not carinate 124. *Necepsia*
2b. Leaf blades stipellate.
4a. Leaves penninerved, short-petioled; anthers apiculate 125. *Paranecepsia*
4b. Leaves palmatinerved, long-petioled; anthers muticous 126. *Discocleidion*
1b. Styles unlobed, dilated, forming a cap over the top of the ovary; stamens 2 or 3, anther connective greatly dilated 127. *Adenophaedra*

123. *Bernardia* *Houstoun* ex Miller, Gard. Dict. abr. ed. 1754; *Houstoun* ex P. Browne, Civ. Nat. Hist. Jamaica 361. 1756; Muell. Arg., Prodr. 15(2): 915. 1866; Fl. Bras. 11(2): 389. 1874; Bentham, Gen. Pl. 3: 308. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 21. 1914; Fawc. & Rend., Fl. Jam. 4: 290. 1920; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 105. 1931; Standley & Steyerl., Fieldiana Bot. 24(6): 52. 1949; Buchheim, Willdenowia 2: 291. 1960; 3: 217. 1962; Allem, Rev. Brasil. Biol. 39: 529. 1979; Liogier, Fl. Española 4: 85. 1986. TYPE: *Bernardia carpinifolia* Griseb.

Bivonia Spreng., Neue Entd. Pflanzenk. 2: 116. 1820. TYPE: *Bivonia axillaris* Spreng. [= *Bernardia axillaris* (Spreng.) Muell. Arg.].

Traganthus Klotzsch, Arch. Naturgesch. 7(1): 188. 1841. TYPE: *Traganthus sidoides* Kl. [= *Bernardia sidoides* (Kl.) Muell. Arg.].

Phaedra Klotzsch ex Endlicher, Gen. Pl. Suppl. 4(3): 88. 1850. TYPE: *Bernardia jacquiniana* Muell. Arg. [lectotype, selected here].

Polyboea Klotzsch ex Endlicher, Gen. Pl. Suppl. 4(3): 88. 1850. TYPE: *Acalypha corensis* Jacq. [= *Bernardia corensis* (Jacq.) Muell. Arg.].

Tyria Klotzsch ex Endlicher, Gen. Pl. Suppl. 4(3): 88. 1850. TYPE: *Bernardia mexicana* (Hook. & Arn.) Muell. Arg. [lectotype, selected here].

Alevia Baillon, Etude Gén. Euphorb. 508. 1858. TYPE: *Alevia leptotashia* Baillon, sphalm. [= *Bernardia interrupta* (Schlecht.) Muell. Arg.].

Passaea Baillon, Etude Gén. Euphorb. 507. 1858. TYPE: *Passaea spartioides* Baillon [= *Bernardia spartioides* (Baill.) Muell. Arg.].

A diverse American genus of ca. 50 species, divided into seven sections by Pax & Hoffmann (1914, 1931); some of these, especially section *Traganthus*, may deserve generic status on further study.

124. *Necepsia* Prain, Kew Bull. Misc. Inf. 1910: 343. 1910; Hook. Ic. Pl. 30: t. 2987. 1913; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 16. 1914; Bouchat & Léonard, Bull. Jard. Bot. Brux. 56: 179. 1986; Radcliffe-Smith,

Fl. E. Trop. Afr. Euphorb. 1: 218. 1987. TYPE: *Necepsia afzelii* Prain.

Neopalissya Pax, in Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 16. 1914. *Palissya* Baillon, Etude Gén. Euphorb. 502. 1858 (non *Palissya* Endlicher, 1847). TYPE: *Neopalissya castaneifolia* (Baillon) Pax [= *Necepsia castaneifolia* (Baillon) Bouch. & Léon.].

As interpreted by Bouchat & Léonard (1986), *Necepsia* is an African genus of three species.

125. *Paranecepsia* Radcliffe-Smith, Kew Bull. 30: 684. 1976; Fl. E. Trop. Afr. Euphorb. 1: 220. 1987. TYPE: *Paranecepsia alchorneifolia* Radcl.-Sm.

A monotypic east African genus (Tanzania and Mozambique).

126. *Discocleidion* (Muell. Arg.) Pax & Hoffmann, Pflanzenr. 147. VII (Heft 63): 45. 1914. TYPE: *Discocleidion ulmifolium* (Muell. Arg.) Pax & Hoffm.

A genus of two species found in southeast China and the Ryukyus; reduced to *Alchornea* by Hurusawa (1954).

127. *Adenophaedra* (Muell. Arg.) Muell. Arg., Fl. Bras. 11(2): 385. 1874; Bentham, Gen. Pl. 3: 314. 1880; Pax & Hoffmann, Pflanzenr. 147. VII (Heft 63): 261. 1914; Croizat, Trop. Woods 88: 30. 1946; Jablonski, Mem. New York Bot. Gard. 17: 140. 1967; Huft, Ann. Missouri Bot. Gard. 75: 1099. 1988. TYPE: *Adenophaedra grandifolia* (Kl.) Muell. Arg. [lectotype, designated by Jablonski, 1967].

A neotropical genus of three species extending from Costa Rica south to Brazil. The relationships of the genus require further study, as it is somewhat aberrant in the tribe Bernardieae. Although Mueller (1866) originally treated *Adenophaedra* as a section of *Bernardia*, Bentham (1880) placed it next to *Caryodendron*, as did Pax & Hoffmann (1914). There is indeed some resemblance, but the pollen studies of Punt (1962) appear to confirm the intuition of Mueller that the closer relationship of *Adenophaedra* is with *Bernardia*.

Tribe 26. PYCNOCOMEAE Hutchinson, Amer. J. Bot. 56: 753. 1969; Webster, Taxon 24: 596. 1975. TYPE: *Pycnocomia* Bentham.

Dioecious trees; indumentum simple, often glandular, or absent; leaves alternate, opposite, or ver-

ticillate, simple, penninerved, eglandular, sometimes resinous; stipules caducous or absent; inflorescences axillary, racemose or paniculate, or contracted into capitula; flowers apetalous. Staminate calyx closed in bud, splitting into 3 or 4 valvate segments; disk glabrous and receptacular, or absent; stamens 15-many, free, anthers sometimes with enlarged connective; pollen grains oblate or subglobose, 3-colporate, colpi short and narrow, inoperculate, sexine tectate-perforate, gemmate or spinulose; pistillode absent. Pistillate sepals 3-7, imbricate; disk glabrous or absent; ovary (2-)3-locular; styles bifid or unlobed. Fruit capsular, often thick-walled and subdrupaceous; seeds ecarunculate, testa dry or fleshy.

As defined by Webster (1975) and here, only the type genus *Pycnocomma*, of the genera included by Hutchinson, is retained in the tribe Pycnocomaeae; the other genera are relegated to tribes Epiprineae and Plukenetiae. However, the membership of the taxa here included in the Pycnocomaeae is still a matter of doubt. The two subtribes recognized here are divergent both morphologically and in geographical distribution, so that they may have to be separated on further study. However, there is some resemblance in pollen characters between *Pycnocomma* and *Blumeodendron*, so the two subtribes are kept together provisionally.

KEY TO THE SUBTRIBES OF TRIBE PYCNOCOMEAE

- 1a. Monoecious; seed-coat not fleshy; pollen sexine gemmate 26a. Pycnocominae
 1b. Dioecious; seed-coat fleshy; pollen sexine punctate-tectate or coarsely reticulate
 26b. Blumeodendrinae

Subtribe 26a. PYCNOCOMINAE Webster, subtr. nov. TYPE: *Pycnocomma* Benth.

Monoicae; stamina numerosa; antherarum connectivum incrassatum; pollinis grana 3-colpoidorata, sexino gemmato; semina non carnosia.

Monoecious shrubs or small trees; leaves alternate or pseudo-verticillate; stamens 50 or more; pistillate flowers sessile; pistillate disk absent; styles elongated, connate below, barely lobed at tip; fruit thin-walled, horned or not; seeds with dry testa.

This subtribe includes three genera, two African and one Malagasian.

KEY TO THE GENERA OF SUBTRIBE PYCNOCOMINAE

- 1a. Pistillate flower terminating the inflorescence; pistillate disk absent.
 2a. Ovary 6-horned, pubescent; staminate

- flowers distinctly pedicellate; filaments inflexed in bud 128. *Pycnocomma*
 2b. Ovary unappendaged, glabrous; staminate flowers subsessile, filaments not inflexed in bud 129. *Droceloncia*
 1b. Pistillate flower not terminating inflorescence; pistillate disk annular 130. *Argomuelleria*

128. *Pycnocomma* Benth., Niger Fl. 508. 1849; Muell. Arg., DC. Prodr. 15(2): 951. 1866; Benth., Gen. Pl. 3: 326. 1880; Prain, Fl. Trop. Afr. 6(1): 955. 1913; Pax & Hoffm., Pflanzenz. 147. VII (Heft 63): 52. 1914; Leandri, Notul. Syst. (Paris) 9: 161. 1941; Keay, Fl. W. Trop. Afr. ed. 2, 1: 405. 1958; Léonard, Bull. Soc. Roy. Bot. Belge 91: 273. 1959; Racliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 228. 1987. TYPE: *Pycnocomma macrophylla* Benth.

A tropical African genus of ca. 15 species.

129. *Droceloncia* Léonard, Bull. Soc. Roy. Bot. Belge 91: 279. 1959. TYPE: *Droceloncia rigidifolia* (Baillon) Léonard.

A monotypic genus of the Comores and Madagascar.

130. *Argomuelleria* Pax, Bot. Jahrb. 19: 90. 1894; Prain, Fl. Trop. Afr. 6(1): 925. 1912; Leandri, Notul. Syst. (Paris) 9: 161. 1941; Léonard, Bull. Soc. Roy. Bot. Belge 91: 274. 1959; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 225. 1987. *Pycnocomma* sect. *Wettriaria* Muell. Arg., DC. Prodr. 15(2): 952. 1866. *Wettriaria* (Muell. Arg.) Pax, Pflanzenz. 147. VII (Heft 63): 49. 1914. TYPE: *Argomuelleria macrophylla* Pax.

An Afro-Malagasian genus of ca. ten species, as delimited by Léonard (1959).

Subtribe 26b. BLUMEODENDRINAE Webster, Taxon 24: 596. 1975. TYPE: *Blumeodendron* (Muell. Arg.) Kurz.

Dioecious trees; leaves long-petiolate, entire, with scalariform veinlets; inflorescences racemose or paniculate; stamens 15-many; anther connective enlarged; pollen grains perforate-tectate or coarsely reticulate; ovary (2-)3-locular; styles unlobed; fruit large, thick-walled; seeds with fleshy testa.

This subtribe includes three Asian genera that differ in aspect from the Pycnocominae by the long-petiolate leaves and more or less paniculate inflorescence.

KEY TO THE GENERA OF SUBTRIBE BLUMEODENDRINAE

- 1a. Anther connective no more than moderately enlarged, not umbraculiform; pistillate disk tenous or absent; styles elongated.
2a. Anther-cells 2; fruit lacking spines or ridges.
3a. Anther-cells adnate to connective; pistillate disk annular; flowers without glandular hairs 131. *Blumeodendron*
3b. Anther-cells pendulous; pistillate disk absent; flowers with stalked glandular hairs 132. *Podadenia*
2b. Anther-cells 4; fruit with spines or ridges 133. *Ptychopyxis*
1b. Anther connective umbraculiform, with 4 pendent locules; pistillate disk massive, pulviniform; styles stigmatiform 134. *Botryophora*

131. *Blumeodendron* (Muell. Arg.) Kurz, J. Asiatic Soc. Bengal 42: 245. 1873; J. J. Smith, Meded. Depart. Landbouw 10: 458. 1910; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 47. 1914; Airy Shaw, Kew Bull. 16: 348. 1963; Whitmore, Tree Fl. Malaya 2: 68. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 57. 1975; Kew Bull. Add. Ser. 8: 37. 1980; Kew Bull. 36: 267. 1981. TYPE: *Blumeodendron tokbrai* (Bl.) Kurz [lectotype, designated by Wheeler, 1975].

An Asian genus of six species distributed from the Andaman Islands and Burma through Indonesia to the Bismarck Archipelago.

132. *Podadenia* Thwaites, Enum. Pl. Zey 4: 273. 1861; Muell. Arg., DC. Prodr. 15(2): 791. 1866; Bentham, Gen. Pl. 3: 318. 1880; Hook. f., Fl. Brit. Ind. 5: 422. 1887; Trimen, Handb. Fl. Ceylon 4: 62. 1898; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 19. 1914. TYPE: *Podadenia sapida* Thwaites.

A monotypic genus endemic to Sri Lanka. Although combined by Croizat (1942) with *Ptychopyxis*, it is a very distinctive group, as noted by Airy Shaw (1963). Until its status can be critically evaluated, it seems best to retain it as a distinct genus.

133. *Ptychopyxis* Miquel, Fl. Ned. Ind. Suppl. 402. 1861; Hooker f., Hook. Ic. Pl. 18: t. 1703. 1887; Croizat, J. Arnold Arbor. 23: 47. 1942; Airy Shaw, Kew Bull. 14: 363. 1960; 16: 347. 1963; Whitmore, Tree Fl. Malaya 2: 126. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 188. 1975; Add. Ser. 8: 197. 1980; Kew Bull. 36: 340. 1981. TYPE: *Ptychopyxis costata* Miq.

Clarorivinia Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 17. 1914. TYPE: *Clarorivinia chrysantha* (K. Schum.) Pax & Hoffm. [= *Ptychopyxis chrysantha* (K. Schum.) Airy Shaw].

A tropical Asian genus of 10–12 species distributed from Thailand through Indonesia to the Philippines and New Guinea.

134. *Botryophora* Hooker f., Fl. Brit. Ind. 5: 476. 1888 (nom. cons.); Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 228. 1931; Airy Shaw, Kew Bull. 3: 484. 1949; 14: 374. 1960; Hook. Ic. Pl. 36: t. 3576. 1962; Kew Bull. Add. Ser. 4: 61. 1975; Kew Bull. 36: 267. 1981. TYPE: *Botryophora kingii* Hook. f. [= *Botryophora geniculata* (Miq.) Beumée ex Airy Shaw].

A monotypic genus of tropical Asia (Burma to Sumatra and Borneo).

Tribe 27. EPIPRINEAE (Muell. Arg.) Huru-sawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 309. 1954. Acalypheae subtribe Epi-prineae Muell. Arg., Linnaea 34: 144. 1865; DC. Prodr. 15(2): 1024. 1866. TYPE: *Epi-prinus* Griffith.

Monoecious trees or shrubs; indumentum stellate; leaves alternate, simple, pinnately veined, eglandular or with petiolar glands, stipulate; inflorescences terminal or axillary, paniculate, racemose, or spicate (or staminate capitate); flowers apetalous. Staminate calyx closed in bud, splitting into 2–6 valvate segments; disk absent; stamens 5–15, filaments free or connate, usually inflexed in bud (except in *Koilocedrus*); pollen grains subglobose to subprolate, 3-colporate, angulaperturate, colpi inoperculate, scarcely marginate, sexine perforate-tectate or rather coarsely reticulate. Pistillate sepals 4–8, imbricate, sometimes foliaceous or toothed; disk absent or rudimentary; ovary 3-(4-) locular; styles free or connate, bifid or multifid. Fruit capsular (rarely drupaceous); seeds subglobose, smooth, dry, ecarunculate.

This tribe includes nine paleotropical genera that have never all been associated in previous treatments, although a number were brought together under subtribe Cephalocrotoninae by Mueller (1866), and by Pax & Hoffmann (1914, 1931) in their series Cladogyniformes. There is considerable resemblance between the Epi-prineae and the Agrostistachydeae, and in some respects with the Erismanthaeae.

KEY TO THE SUBTRIBES OF TRIBE EPIPRINEAE

- 1a. Staminate calyx splitting into distinct segments; pollen sexine not spinulose; pistillate sepals often persistent, accrescent 27a. *Epiprininae*
 1b. Staminate calyx turbinate, 2-5-lobed, lobes verrucose; pollen sexine spinulose; pistillate sepals caducous 27b. *Cephalomappinae*

Subtribe 27a. EPIPRININAE Muell. Arg., *Linnaea* 34: 144. 1865. TYPE: *Epiprinus* Griffith.

- Acalyphaeae subtribe *Cephalocrotonae* Muell. Arg., *Linnaea* 34: 143. 1865. TYPE: *Cephalocroton* Hochst.
 Acalyphaeae subtribe *Mercurialinae* series *Cladogyniformes* Pax & Hoffm., *Pflanzenr.* 147. VII (Heft 63): 264. 1914. TYPE: *Cladogynos* Zipp. ex Span.
 Epiprineae subtribe *Cleidocarpinae* Thin, *Tap Chi Sinh Hoc* 10(2): 32. 1988. TYPE: *Cleidocarpum* Airy Shaw.

KEY TO THE GENERA OF SUBTRIBE EPIPRINAE

- 1a. Staminate flowers in racemes or spikes; stipules (if present) glandular.
 2a. Pistillate calyx foliose, accrescent, involucrate with deciduous biglandular bracts; styles connate into a column, distally bifid or multifid; stamens 5-15; leaves with petiolar glands 135. *Epiprinus*
 2b. Pistillate calyx neither accrescent nor involucrate; styles \pm free, distally multifid; stamens 3-6.
 3a. Filaments inflexed in bud.
 4a. Fruits capsular; leaves eglandular.
 5a. Pistillate sepals entire; staminate flowers not in heads 136. *Symphyllia*
 5b. Pistillate sepals glandular-dissected; staminate flowers in heads 137. *Adenochlaena*
 4b. Fruit indehiscent; petiole biglandular 138. *Cleidocarpum*
 3b. Filaments not inflexed in bud 139. *Koilolepas*
 1b. Staminate flowers in pedunculate capitula; stipules not glandular.
 5a. Inflorescences axillary, inconspicuous; stamens 3-5; pistillate sepals accrescent, unlobed; leaves white-tomentose beneath 140. *Cladogynos*
 5b. Inflorescences terminal; leaves not white-tomentose beneath.
 6a. Pistillate sepals entire, connate; styles free; leaves coriaceous 141. *Cephalocrotonopsis*
 6b. Pistillate sepals pinnatifid; styles connate; leaves thinner 142. *Cephalocroton*

135. *Epiprinus* Griffith, *Notul. Pl. Asiat.* 4: 487. 1854; Muell. Arg., *DC. Prodr.* 15(2): 1024. 1866; Bentham, *Gen. Pl.* 3: 325. 1880; Hook. f., *Fl. Brit. Ind.* 5: 463. 1887; Pax & Hoffmann, *Pflanzenr.* 147. X (Heft 68): 109. 1919; Gagnepain, *Bull. Soc. Bot. France* 72: 465. 1925; *Fl. Indochine* 5: 474. 1926; Croizat, *J. Arnold Arbor.* 23: 52. 1942; Airy Shaw, *Kew Bull.* 16: 356. 1963; *Kew Bull.* 26: 259. 1972; Whitmore, *Tree Fl. Malaya* 2: 95. 1973; Thin, *Tap Chi Sinh Hoc* 10(2): 30. 1988. TYPE: *Epiprinus malayanus* Griff.

A rather variable genus of ca. six species in tropical Asia, from Assam to Malaya. Mueller (1866), followed by Pax & Hoffmann (1919), placed *Epiprinus* by itself in subtribe *Epiprininae*, on the basis that the pistillate flower is involucrate.

136. *Symphyllia* Baillon, *Etude Gén. Euphorb.* 473. 1858; Muell. Arg., *DC. Prodr.* 15(2):

Leaves entire or dentate, pinnately or palmately veined; staminate flowers in clusters on spicate or racemose axes, or in capitula; pistillate flowers at same nodes as staminate, or proximal; stamens 4-10, filaments free; pollen grains globose, with relatively large colpi, sexine not spinulose; pistillate sepals 4-6, \pm persistent; capsule smooth.

The eight genera of this subtribe occur in Africa, Madagascar, and tropical Asia. Although Pax & Hoffmann (1919, 1931) and Hurusawa (1954) maintained *Epiprinus* in a monotypic tribe or subtribe, its relationship to the other genera of *Epiprineae* enumerated below seems clear from resemblances in pollen and floral structures (e.g., staminate flowers with filaments inflexed in the bud).

763. 1866; Gagnepain, *Fl. Indochine* 5: 477. 1926. TYPE: *Symphyllia siletiana* Baillon.

A genus of three species distributed from India to Hainan and Malaya. Croizat (1942) combined *Symphyllia* with *Epiprinus* on the basis that *Epiprinus balansae* (Pax & Hoffm.) Gagnep. represents a transitional link between the two taxa. Airy Shaw (1963, 1972) and Thin (1988) followed him in this, but neither discussed the morphology of the pistillate flower or demonstrated that the "involucre" described by Mueller is without systematic significance. It is possible that Croizat was correct, but until the problem is given further study, it seems preferable to maintain *Symphyllia* as distinct.

137. *Adenochlaena* Baillon, *Etude Gén. Euphorb.* 472. 1858; Pax, *Pflanzenr.* 147. II (Heft 44): 12. 1910; Pax & Hoffm., *Natürl.*

Pflanzenfam. ed. 2, 19c: 124. 1931. TYPE: *Adenochlaena leucocephala* Baillon.

Centrostylis Baillon, Etude Gén. Euphorb. 469. 1858. TYPE: *Centrostylis zeylanica* Baillon [= *Adenochlaena zeylanica* (Baillon) Thw.].

Niendezua Pax, Bot. Jahrb. 19: 106. 1894. TYPE: *Niendezua cordata* Pax [= *Adenochlaena leucocephala* Baillon].

A genus of two disjunct species (Madagascar/Comores; Sri Lanka); treated by Mueller (1866) as a section of *Cephalocroton*.

138. Cleidiocarpon Airy Shaw, Kew Bull. 19: 313. 1965; Kew Bull. 32: 410. 1978; Thin, Tap Chi Sinh Hoc 10(2): 32. 1988. TYPE: *Cleidiocarpon laurinum* Airy Shaw.

Sinopimelodendron Tsiang, Acta Bot. Sinica 15: 132. 1973. TYPE: *Sinopimelodendron kwangsiense* Tsiang [= *Cleidiocarpon cavaleriei* (Levl.) Airy Shaw].

A genus of two closely related species of Burma and China; Thin (1988) placed it in a separate subtribe, Cleidiocarpaceae.

139. Koilodepas Hasskarl, Versl. Med. Afd. Natuurk. Kon. Akad. Wetensch. 4: 139. 1856; Flora 40: 531. 1857 (as *Coelodepas*); Muell. Arg., DC. Prodr. 15(2): 759. 1866; Bentham, Hook. Ic. Pl. 13: t. 1288. 1879; Gen. Pl. 3: 313. 1880; Hook. f., Fl. Brit. Ind. 5: 419. 1887; Pax, Pflanzenr. 147. VII (Heft 63): 268. 1914; Croizat, J. Arnold Arbor. 23: 50. 1942; Airy Shaw, Kew Bull. 14: 382. 1960; 16: 354. 1963; 26: 284. 1972; Whitmore, Tree Fl. Malaya 2: 103. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 137. 1975; Airy Shaw, Kew Bull. 36: 310. 1981. TYPE: *Koilodepas bantamense* Hassk.

Calpigyne Blume, Ann. Mus. Bot. Lugd.-Batav. 2: 193. 1857. TYPE: *Calpigyne frutescens* Bl. [= *Koilodepas frutescens* (Bl.) Airy Shaw].

Nephostylus Gagnepain, Bull. Soc. Bot. France 72: 467. 1925. TYPE: *Nephostylus poilanei* Gagnep. [= *Koilodepas longifolium* Hook. f.].

A genus of ten species of India and southeastern Asia as far as Hainan and Borneo.

140. Cladogynos Zippelius ex Spanoghe, Linnaea 15: 349. 1841; Muell. Arg., DC. Prodr. 15(2): 895. 1866; Bentham, Gen. Pl. 3: 323. 1880; J. J. Smith, Meded. Dept. Landb. 10: 383. 1910; Pax, Pflanzenr. 147. VII (Heft 63): 264. 1914; Gagnepain, Fl. Indochine 5: 478. 1926; Backer & Bakhuizen, Fl. Java 1: 485. 1963; Airy Shaw, Kew Bull. 26: 232.

1972. TYPE: *Cladogynos orientalis* Zipp. ex Span.

Adenogynum Reichenbach & Zollinger, Acta Soc. Regiae Sci. Indo-Neerl. 1: 23. 1856. TYPE: *Adenogynum discolor* Reich. & Zoll. [= *Cladogynos orientalis* Zipp. ex Span.].

A monotypic genus of tropical southeast Asia, Thailand to the Philippines, Java, and Timor.

141. Cephalocrotonopsis Pax, Pflanzenr. 147. II (Heft 44): 15. 1910; Radcliffe-Smith, Kew Bull. 28: 131. 1973. TYPE: *Cephalocrotonopsis socotrana* (Balf. f.) Pax.

A monotypic genus of Socotra; reduced by Radcliffe-Smith (1973) to a section of *Cephalocroton*.

142. Cephalocroton Hochstetter, Flora 24: 370. 1841; Muell. Arg., DC. Prodr. 15(2): 760. 1866; Bentham, Gen. Pl. 3: 307. 1880; Pax, Pflanzenr. 147. II (Heft 44): 7. 1910; Prain, Fl. Trop. Afr. 6(1): 843. 1912; Radcliffe-Smith, Kew Bull. 28: 123. 1973; Fl. E. Trop. Afr. Euphorb. 1: 282. 1987. TYPE: *Cephalocroton cordofanus* Hochst.

An Old World genus of five species recorded from east Africa, Madagascar and the Comores, and Sri Lanka.

Subtribe 27b. CEPHALOMAPPINAE Webster, Taxon 24: 597. 1975. TYPE: *Cephalomappa* Baillon.

Leaves entire, pinnately veined; staminate flowers in capitula on racemose axes, pistillate flowers at proximal nodes of inflorescence; stamens 2-4, filaments connate; pollen grains globose, coarsely reticulate, reticulum spinulose; pistillate sepals 4-6, deciduous; capsule verrucose.

This subtribe includes only the type genus.

143. Cephalomappa Baillon, Adansonia I. 11: 130. 1874; Bentham, Gen. Pl. 3: 323. 1880; Pax, Pflanzenr. 147. II (Heft 44): 16. 1910; Airy Shaw, Kew Bull. 14: 378. 1960; Kostermans, Reinwardtia 5: 413. 1961; Airy Shaw, Kew Bull. Add. Ser. 4: 66. 1975; Kew Bull. 36: 274. 1981. TYPE: *Cephalomappa beccariana* Baillon.

Muricococcum Chun & How, Acta Phytotax. Sin. 5: 14. 1956. TYPE: *Muricococcum sinense* Chun & How [= *Cephalomappa sinensis* (Chun & How) Kosterm.].

A genus of five species in southeast Asia (Malaya to Sumatra and Borneo, southern China).

Tribe 28. ADELIEAE Webster, Taxon 24: 597. 1975. Acalypheae subtribe Mercurialinae series Adeliiformes Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 59. 1919. TYPE: *Adelia* L.

Dioecious (rarely monoecious) trees or shrubs; indumentum simple or stellate; leaves alternate, simple, entire or dentate, eglandular; stipules small; inflorescences axillary, flowers apetalous, in glomerules or racemes. Staminate calyx splitting into 4 or 5 valvate segments; disk extrastaminal, annular or obsolete; stamens 8–18, \pm connate at base; anthers versatile; pollen grains 3-(4-)colporate, colpi operculate, exine tectate-perforate with polygonally arranged nanospines; pistillode present or absent. Pistillate sepals 5 or 6, valvate or open at anthesis, often reflexed; disk annular, glabrous or pubescent; seeds roundish, smooth, ecarunculate (rarely carunculate).

An American tribe of five genera.

KEY TO THE GENERA OF TRIBE ADELIEAE

- 1a. Indumentum simple; stipules deciduous; pollen grains with finely perforate tectum; styles lacinate.
 2a. Ovary 3-locular; staminate disk present; stamens 8–20; seeds ecarunculate.
 3a. Pistillode present; staminate disk annular or segmented; flowers in axillary clusters 144. *Adelia*
 3b. Pistillode absent; staminate disk of interstaminal processes; flowers in racemes 145. *Crotonogynopsis*
 2b. Ovary 2-locular; staminate disk absent; stamens more than 20; seeds carunculate 146. *Enriquebeltrania*
 1b. Indumentum stellate or stellate-lepidote; stipules absent; pollen grains with coarsely perforate tectum.
 4a. Pistillate disk entire; styles bifid or subentire; filaments free; pollen 3-colporate; leaves triplinerved, indumentum stellate 147. *Lasiocroton*
 4b. Pistillate disk lobed; styles lacerate; filaments \pm connate; pollen 4-colporate; leaves penninerved, indumentum stellate-lepidote 148. *Leucocroton*

144. *Adelia* L., Syst. Nat. ed. 10, 2: 1298. 1759 (nom. cons.); Bentham, Gen. Pl. 3: 312. 1880; Pax, Pflanzenr. 147. VII (Heft 63): 64. 1914; Fawc. & Rend., Fl. Jam. 4: 291. 1920; Webster, Ann. Missouri Bot. Gard. 54: 272. 1968; Sneep & De Roon, Fl. Neth. Ant. 3: 254. 1984. TYPE: *Adelia ricinella* L. (typ. cons.).

Ricinella Muell. Arg., Linnaea 34: 153. 1865. TYPE: *Ricinella pedunculosa* (A. Rich.) Muell. Arg. [= *Adelia ricinella* L.].

A neotropical genus of ca. 10–12 species, Mexico to Paraguay and Brazil but best represented in the West Indies.

145. *Crotonogynopsis* Pax, Bot. Jahrb. 26: 328. 1899; Prain, Fl. Trop. Afr. 6(1): 924. 1912; Pax & Hoffmann, Pflanzenr. 14. XII (Heft 63): 14. 1914; Keay, Fl. W. Trop. Afr. ed. 2, 1: 404. 1958; Radcliffe-Smith, Fl. Trop. E. Afr. Euphorb. 1: 213. 1987. TYPE: *Crotonogynopsis usambarica* Pax.

A monotypic African genus (Zaire to Uganda and Tanzania).

146. *Enriquebeltrania* Rzedowski, Bol. Soc. Bot. México 38: 75. 1979. *Beltrania* Miranda, Bol. Soc. Bot. México 21: 4. 1957 (non *Beltrania* Penzig, 1882). TYPE: *Enriquebeltrania crenatifolia* (Miranda) Rzedowski [*Beltrania crenatifolia* Miranda].

A monotypic genus of the Yucatan peninsula, very similar to *Adelia* and questionably distinct.

147. *Lasiocroton* Griseb., Fl. Brit. W. Ind. 46. 1859; Abh. Königl. Ges. Wiss. Göttingen 9: 20. 1861; Bentham, Gen. Pl. 3: 317. 1880; Pax, Pflanzenr. 147. VII (Heft 63): 60. 1914; Fawc. & Rend., Fl. Jam. 4: 293. 1920; Alain, Fl. Cuba 3: 87. 1953. TYPE: *Lasiocroton macrophyllus* (Sw.) Griseb.

A West Indian genus of five species (Bahamas, Cuba, Jamaica, and Hispaniola).

148. *Leucocroton* Griseb., Abh. Königl. Ges. Wiss. Göttingen 9: 20. 1861; Muell. Arg., DC. Prodr. 15(2): 757. 1866; Bentham, Gen. Pl. 3: 312. 1880; Pax, Pflanzenr. 147. VII (Heft 63): 62. 1914; Urban, Ber. Deutsch. Bot. Ges. 36: 504. 1918; Alain, Fl. Cuba 3: 89. 1953; Borhidi, Acta Bot. Acad. Sci. Hungar. 21: 222. 1975. TYPE: *Leucocroton wrightii* Griseb.

A genus of 20 species of Cuba and Hispaniola.

Tribe 29. ALCHORNEAE (Hurusawa) Hutchinson, Amer. J. Bot. 56: 752. 1969. Acalypheae subtribe Alchorneinae Hurus., J. Fac. Sci. Univ. Tokyo III. 6: 302. 1954. TYPE: *Alchornea* Sw.

Dioecious trees or shrubs; indumentum simple or stellate; leaves alternate, entire or dentate, pinnately or palmately veined, sometimes stipellate or with laminar glands; stipules mostly deciduous,

sometimes obsolete; inflorescences terminal or axillary, spicate or paniculate (compounded spikes); bracts glandular or eglandular; flowers apetalous. Staminate calyx splitting into 2–5 valvate segments; disk intrastaminal or absent; stamens (2–) 4–60, free; anthers introrse, mucous or apiculate; pollen grains 3-colporate, colpi operculate, sexine rugulose to vermiculate; pistillode rudimentary or absent. Pistillate sepals 3–8, imbricate, usually persistent, sometimes glandular; disk mostly rudimentary or absent; ovary 2- or 3- (rarely 4-)locular; styles entire to bifid or multifid. Fruit capsular; seeds smooth or tuberculate, testa not fleshy.

As delimited earlier (Webster, 1975) and here, tribe Alchorneae is somewhat more comprehensive than the circumscription of Hutchinson (1969), since *Conceveiba* and its allies—referred to the Malloteae by Hutchinson—are included. The distinctive pollen grains that characterize this tribe indicate an affinity to *Mallotus* and related genera, but are distinctive in the operculate colpi.

KEY TO THE SUBTRIBES OF TRIBE ALCHORNEAE

- 1a. Styles entire or if distinctly bifid, then indumentum simple; stamens 4–9; staminate inflorescences axillary 29a. ALCHORNEINAE
- 1b. Styles bifid; indumentum stellate; stamens 15–60; staminate inflorescences terminal or axillary 29b. CONCEVEIBINAE

Subtribe 29a. ALCHORNEINAE Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 302. 1954. Acalyphaeae subtribe Mercurialinae series Alchorneiformes Pax & Hoffm., Pflanzenz. 147. VII (Heft 63): 220. 1914. TYPE: *Alchornea* Sw.

Indumentum simple or stellate; staminate inflorescences axillary; stamens 2–9; pistillate sepals glandular; styles mostly entire, often stigmatiform or dilated; ovary 2- or 3-(rarely 4-)locular.

This subtribe of six genera with ca. 70 species is well represented in both the Neotropics and Palearctic. Most of the genera are only weakly separated from *Alchornea*, and the number may be reduced on further study.

KEY TO THE GENERA OF SUBTRIBE ALCHORNEINAE

- 1a. Styles bifid; indumentum simple.
 - 2a. Dioecious; ovary smooth; pistillode absent; seeds ecarunculate 149. *Orfilea*
 - 2b. Monoecious; ovary cristate; pistillode present; seeds carunculate 150. *Bossera*
- 1b. Styles unlobed or bifid only at tip.
 - 3a. Styles elongated and slender; indumentum simple or stellate; ovary 2- or 3-locular 151. *Alchornea*

- 3b. Styles stigmatiform or dilated; indumentum simple; ovary 3-locular.
 - 4a. Stamens usually 8, free; stigmas smooth; pistillate sepals glandular at base 152. *Coelebogyne*
 - 4b. Stamens 2–4, basally connate.
 - 5a. Stamens 4; styles elongated, dilated; seeds ecarunculate 153. *Aparisthium*
 - 5b. Stamens 2 or 3; styles stigmatiform; seeds minutely carunculate 154. *Bocquillonia*

149. Orfilea Baillon, Etude Gén. Euphorb. 452. 1858. TYPE: *Orfilea coriacea* Baillon.

Diderotia Baillon, Adansonia I. 1: 274. 1861. *Laurembergia* Baillon, Etude Gén. Euphorb. 451. 1858 (sphalm. *Lautembergia*; non *Laurembergia* Bergius, 1767). TYPE: *Diderotia multispicata* (Baillon) Baillon [= *Orfilea multispicata* (Baillon) Webster, comb. nov.].

A Malagasian genus of four species, closely related to *Alchornea* but differing in the distinctly bifid styles. A species from Mauritius discussed by Coode (Kew Bull. 33: 111. 1978) also appears to belong to this genus: *Orfilea neraudiana* (Baillon) Webster (comb. nov.; based on *Claoxylon neraudianum* Baillon, Adansonia I. 1: 280. 1861).

150. Bossera Leandri, Adansonia II. 2: 216. 1962. TYPE: *Bossera cristatocarpa* Leandri.

This monotypic genus described from Madagascar is very close to *Alchornea* and is weakly distinguished by its androecium of ten stamens and the distinctively cristate ovary.

151. Alchornea Swartz, Prodr. 6, 98. 1788; Fl. Ind. Occ. 2: 1153. 1800; Muell. Arg., DC. Prodr. 15(2): 899. 1866; Fl. Bras. 11(2): 374. 1874; Bentham, Gen. Pl. 3: 314. 1880; Pax, Pflanzenz. 147. VII (Heft 63): 220. 1914; Webster, Ann. Missouri Bot. Gard. 54: 279. 1968; 75: 1100. 1989; Whitmore, Tree Fl. Malaya 2: 53. 1973; Dyer, Gen. S. Afr. Fl. Pl. ed. 3, 317. 1975; Airy Shaw, Kew Bull. Add. Ser. 4: 28. 1975; Thin, Tap Chi Sinh Hoc 6(3): 26. 1984. TYPE: *Alchornea latifolia* Sw.

Cladodes Loureiro, Fl. Cochinch. 574. 1790. TYPE: *Cladodes rugosa* Lour. [= *Alchornea rugosa* (Lour.) Muell. Arg.].

Hermesia Humb. & Bonpl. ex Willd., Sp. Pl. 4: 809. 1805. TYPE: *Hermesia castanifolia* Humb. & Bonpl. ex Willd. [= *Alchornea castanifolia* (Humb. & Bonpl. ex Willd.) A. Juss.].

Schousboea Schumacher, Beskr. Guin. Pl. 449. 1827 (non Willd., 1799). TYPE: *Schousboea cordifolia* Schum. [= *Alchornea cordifolia* (Schum.) Muell. Arg.].

Stipellaria Benth. J. Bot. Kew Gard. Misc. 6: 2. 1854.

TYPE: *Stipellaria trewioides* Benth. [= *Alchornea trewioides* (Benth.) Muell. Arg.; lectotype, designated by Thin, 1984].

Lepidoturus Bojer ex Baillon, Etude Gén. Euphorb. 448. 1858. TYPE: *Lepidoturus alnifolius* Boj. ex Baillon

[= *Alchornea alnifolia* (Baillon) Pax & Hoffm.].

Bleekeria Miquel, Fl. Ind. Bat. 1(2): 407. 1859 (non Hassk., 1855). TYPE: *Bleekeria zollingeri* (Hassk.) Miq. [= *Alchornea villosa* (Benth.) Muell. Arg.].

A variable genus of ca. 50 species distributed in the tropics of both the New World and Old World. Pax (1914) drew the generic boundaries more narrowly than Mueller (1866) by recognizing such segregates as *Aparisthmium* and *Coelebogyne*. However, the Paxian genus still includes three sections, and the relationships between these and the segregate taxa badly need clarification.

152. *Coelebogyne* J. Smith, Proc. Linn. Soc. London 1: 41. 1839; Baillon, Etude Gén. Euphorb. 416. 1858; Pax, Pflanzenr. 147. VII (Heft 63): 255. 1914. TYPE: *Coelebogyne ilicifolia* J. Smith.

A monotypic genus from tropical Australia, very weakly distinguished from *Alchornea* and perhaps better treated as a section of that genus.

153. *Aparisthmium* Endlicher, Gen. Pl. 1112. 1840; nom. cons. prop.; Pax, Pflanzenr. 147. VII (Heft 63): 257. 1914; Jablonski, Mem. New York Bot. Gard. 17: 135. 1967. *Conceveibum* A. Rich. ex A. Jussieu, Euphorb. Tent. 42. 1824. TYPE: *Conceveibum cordatum* A. Juss. [= *Aparisthmium cordatum* (A. Juss.) Baillon].

In the concept of Pax (1914), accepted by Jablonski and other neotropical floristic authors, *Aparisthmium* is a monotypic neotropical genus widely distributed from Colombia to Bolivia and southern Brazil. Unfortunately, the genus is technically a synonym of *Conceveiba*, because Endlicher cited A. Jussieu's figure 42B, which in the legend is clearly indicated as Aublet's *Conceveiba guianensis*. Endlicher's description, on the other hand, clearly seems to fit the plant that Baillon and later writers have accepted as *Aparisthmium*. If Endlicher's citation is regarded as a misprint, then *Aparisthmium* becomes a synonym of *Conceveibum* Rich. ex A. Juss., unless *Conceveibum* can be regarded as an intentional orthographic variant of *Conceveiba*. The easiest course out of this tangle would be to propose the generic name *Aparisthmium* for conservation, which seems warranted in view of the abundance of the plant in neotropical vegetation.

154. *Bocquillonia* Baillon, Adansonia I. 2: 225. 1861; Muell. Arg., DC. Prodr. 15(2): 894. 1866; Benth. Gen. Pl. 3: 313. 1880; Pax, Pflanzenr. 147. VII (Heft 63): 260. 1914; Airy Shaw, Kew Bull. 29: 321. 1974; McPherson & Tirel, Fl. Nouv.-Calédonie 14(1): 114. 1987. TYPE: *Bocquillonia sessiliflora* Baillon [designated by McPherson & Tirel, 1987].

Ramelia Baillon, Adansonia I. 11: 132. 1874. TYPE: *Ramelia codonostylis* Baillon [= *Bocquillonia codonostylis* (Baillon) Airy Shaw].

As treated by McPherson & Tirel (1987), *Bocquillonia* is a genus of 14 species endemic to New Caledonia.

Subtribe 29b. CONCEVEIBINAE Webster, Taxon 24: 597. 1975. TYPE: *Conceveiba* Aubl.

Leaves long-petiolate, entire or subentire, not stipellate; indumentum stellate (at least in part); floral disk absent; stamens 15–60; pistillate sepals often glandular; ovary 2–3-locular; styles bifid.

This subtribe of three genera and about ten species was thought to be entirely American until the recent discovery of *Conceveiba* in west Africa. Pax & Hoffmann (1914) included *Conceveiba* and *Gavarretia* in their series *Trewiiformes* (Mallo- teae), an entirely paleotropical group.

KEY TO THE GENERA OF SUBTRIBE CONCEVEIBINAE

- 1a. Inflorescences terminal.
 - 2a. Pistillate sepals separate, often glandular; anthers muticous; ovary 3-locular; style-branches blunt 155. *Conceveiba*
 - 2b. Pistillate sepals eglandular, connate, lobes scarcely evident; anthers apiculate; ovary 2-locular; style-branches acute 156. *Gavarretia*
- 1b. Inflorescences axillary; anthers muticous 157. *Polyandra*

155. *Conceveiba* Aublet, Hist. Pl. Guiane Fr. 923. 1775; Muell. Arg., DC. Prodr. 15(2): 895. 1866; Benth. Gen. Pl. 3: 316. 1880; Pax, Pflanzenr. 147. VII (Heft 63): 214. 1914; Jablonski, Mem. New York Bot. Gard. 17: 131. 1967; Thomas, Ann. Missouri Bot. Gard. 77: 856. 1990. TYPE: *Conceveiba guianensis* Aubl.

Conceveibastrum (Muell. Arg.) Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 217. 1914. TYPE: *Conceveibastrum martianum* (Baillon) Pax & Hoffm. [= *Conceveiba martiana* Baillon].

Veconcibea (Muell. Arg.) Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 218. 1914. TYPE: *Veconcibea lati-*

folia (Benth.) Pax & Hoffm. [= *Conceveiba latifolia* Benth.].

A genus of seven or eight neotropical species extending from Costa Rica to Amazonian Peru and Brazil, and one recently discovered African species from Gabon (Thomas, 1990).

156. Gavarretia Baillon, *Adansonia* I. 1: 185, t. 7. 1861; Bentham, *Gen. Pl.* 3: 316. 1880; Pax, *Pflanzenr.* 147. VII (Heft 63): 213. 1914; Jablonski, *Mem. New York Bot. Gard.* 17: 130. 1967. TYPE: *Gavarretia terminalis* Baillon.

A monotypic South American genus; the single species occurs in Amazonian Venezuela, Guiana, and Brazil. Mueller (1874) treated *Gavarretia* as a section of *Conceveiba*, and this may yet prove to be the best systematic disposition.

157. Polyandra Leal, *Arch. Jard. Bot. Rio de Janeiro* 11: 63. 1951. TYPE: *Polyandra bracteosa* Leal.

A poorly understood genus known only from the type species in the Brazilian Amazon; pistillate flowers and fruits are still unknown.

Tribe 30. ACALYPHEAE Dumortier, *Anal. Fam. Pl.* 45. 1829. TYPE: *Acalypha* L.

Monoecious or dioecious trees, shrub, or herbs; indumentum simple or stellate; leaves alternate or opposite, simple, entire or dentate, pinnately or palmately nerved, often punctate or with laminar glands, stipulate; inflorescences terminal or axillary, unisexual or bisexual, bracts sometimes glandular; flowers apetalous. Staminate calyx closed in bud, valvately splitting into 2–5 segments; disk receptacular (intrastaminal), of interstaminal processes, or absent; stamens 4–many, usually free; anthers sometimes apiculate, anther-sacs sometimes pendulous; pollen grains globose, brevicolporate or porate, apertures not or scarcely operculate; sexine coarsely foveolate to striate or rugulose; pistillode usually absent. Pistillate sepals mostly 3–6, free; disk cupular or absent; ovary 2–4-locular; styles free or basally connate, unlobed to lacerate. Fruit capsular or drupaceous; seeds carunculate or ecarunculate, testa dry or fleshy.

The largest tribe of Acalyphoideae, here divided into 11 subtribes with 30 genera and over 1000 species.

KEY TO THE SUBTRIBES OF TRIBE ACALYPHEAE

- 1a. Seeds carunculate; inflorescences terminal; indumentum stellate or absent; styles bifid.
 - 2a. Monoecious; filaments connate into fascicles; pistillate sepals deciduous; stipules connate 30a. Riciniinae
 - 2b. Dioecious; filaments free; pistillate sepals persistent; stipules free 30b. Adrianinae
- 1b. Seeds ecarunculate, or if carunculate then inflorescences axillary, or styles unlobed.
 - 3a. Stamens not connate into fascicles.
 - 4a. Anther-sacs not vermiform and pendulous; pollen colporate; seeds usually ecarunculate.
 - 5a. Indumentum usually simple (except Lobaniliinae); leaves alternate, eglandular or with embedded laminar glands, not granulose-glandular.
 - 6a. Herbs, often with opposite leaves; indumentum simple; styles undivided.
 - 7a. Staminate sepals free; stamens free; ovary 2-locular; pollen grains 3-colporate; anthers not apiculate; cotyledons broader than radicle 30c. Mercurialinae
 - 7b. Staminate sepals connate; filaments connate; ovary 3-locular; pollen grains inaperturate; anthers apiculate; cotyledons scarcely broader than radicle 30d. Dysopsidinae
 - 6b. Shrubs or trees (or herbs with bifid styles).
 - 8a. Anther-sacs not parted to the connective; staminate disk absent; leaves mostly with laminar glands.
 - 9a. Styles bifid; anthers 2-locular; pollen grains vermiculate-rugulose; seed-coat dry or fleshy 30e. Cleidiinae
 - 9b. Styles unlobed; anthers 3–4-locular; pollen grains spinulose-rugulose; seed-coat usually fleshy 30f. Macaranginae
 - 8b. Anther-sacs parted to the connective, erect or pendulous; interstaminal disk present; styles unlobed.
 - 10a. Indumentum simple 30g. Claoxylinae
 - 10b. Indumentum stellate 30h. Lobaniliinae
 - 5b. Indumentum usually stellate; leaves often opposite, often with embedded laminar glands and usually glandular-granulose as well; usually dioecious; inflorescences often terminal; staminate disk present or absent; pollen grains \pm spinulose-rugulose 30i. Rottlerinae
 - 4b. Anthers vermiform and pendulous; staminate disk absent; pollen porate; styles lacerate; seeds \pm carunculate; pistillate bracts usually large and foliaceous 30j. Acalyphinae
 - 3b. Stamens many, connate into fascicles; shrubs or trees with alternate eglandular leaves, indumentum simple or lepidote 30k. Lasiococcinae

Subtribe 30a. RICININAE Grisebach, Fl. Brit. W. Ind. 37. 1859; Abh. Königl. Ges. Wiss. Göttingen 9: 15. 1860; Muell. Arg., DC. Prodr. 15(2): 143. 1866; Pax & Hoffm., Pflanzenr. 147. XI (Heft 68): 112. 1919; Natürl. Pflanzenfam. ed. 2, 19c: 149. 1931; Webster, Taxon 24: 597. 1975. TYPE: *Ricinus* L.

Monoecious trees or shrubs (herbs in temperate climates); indumentum absent; leaves alternate, long-petiolate, palmately lobed; stipules connate into a sheath, deciduous; inflorescences terminal, paniculate, proximal cymules staminate, distal pistillate; bracts glandular; stamens many, filaments united into branching fascicles; pollen grains 3-colporate, colpi narrow and inoperculate; pistillate flowers pedicellate; ovary muricate; styles bifid; capsule echinate; seeds carunculate.

As here defined, subtribe Ricininae is restricted to the single genus *Ricinus*. Pax & Hoffmann (1919) also included *Homonoia* and *Lasiococca* in the Ricininae, mainly because of their rather similar androecium of stamens united into fascicles. However, *Ricinus* differs from those genera (here referred to subtribe Lasiococcinae) in its terminal inflorescence, distinctly carunculate seeds, palmately lobed leaves with glandular petiole, and bifid styles. I am inclined to agree with Airy Shaw (1974) that the character of fasciculate stamens is homoplasious, and the Ricininae do not appear closely related to the Lasiococcinae. On the other hand, *Adriana* is much more similar to *Ricinus* and appears to be the most closely related genus.

158. *Ricinus* L., Sp. Pl. 1007. 1753; Gen. Pl. ed. 5, 437. 1754; Muell. Arg., DC. Prodr. 15(2): 1016. 1866; Bentham, Gen. Pl. 3: 321. 1880; Pax & Hoffm., Pflanzenr. 147. XI (Heft 68): 119. 1919; Webster, J. Arnold Arbor. 48: 379. 1967; Correll & Correll, Fl. Bahama Arch. 840. 1982; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 322. 1987. TYPE: *Ricinus communis* L.

A monotypic genus native to northeast Africa (according to Radcliffe-Smith), now widely cultivated and ruderal in tropical and subtropical regions worldwide.

Subtribe 30b. ADRIANINAE Bentham, Gen. Pl. 3: 250. 1880; Webster, Taxon 24: 597. 1975. Tribe Adrianeae (Benth.) Pax, Pflanzenr. 147. II (Heft 44): 1. 1910. TYPE: *Adriana* Gaud.

Dioecious; indumentum stellate or absent; leaves alternate or opposite, unlobed or palmately lobed,

stipules glandular; inflorescences spicate, terminal or opposite the leaves, bracts glandular; stamens numerous, free; anthers apiculate, sacs adnate to linear connective; ovary 3-locular, smooth; styles bifid; fruit capsular; seeds carunculate.

In contrast to the concepts of Bentham (1880) and Pax (1910), subtribe Adrianinae is here restricted to the type genus *Adriana*. Pax (1910) rather slavishly followed Bentham in including within his Adrianinae such unrelated genera as *Manihot* and *Pachystroma*. In his later work (Pax & Hoffmann, 1931), he abandoned the tribe Adrianeae and included *Adriana* in his subtribe Mercurialinae adjacent to *Conceveiba* and *Gavarretia*, which is a better and not implausible suggestion of affinity.

159. *Adriana* Gaudichaud, Ann. Sci. Nat. Paris 5: 223. 1825; Muell. Arg., DC. Prodr. 15(2): 889. 1866; Bentham, Fl. Austral. 6: 133. 1873; Gen. Pl. 3: 306. 1880; Pax, Pflanzenr. 147. II (Heft 44): 17. 1910; Airy Shaw, Kew Bull. 35: 589. 1980. TYPE: *Adriana tomentosa* Gaud. [lectotype].

A genus endemic to Australia; treated by Airy Shaw (1980) as having five species and several varieties. The resemblances between *Ricinus* and *Adriana* appear too significant to be explained away as due to convergence, despite the great geographical disjunction. However, *Adriana* also has a number of characters in common with genera such as *Cephalocroton* and *Cephalomappa* that were included in the Adrianeae by Pax (1919) but are referred to the Epiptineae here. It is possible, therefore, that *Adriana* provides the phylogenetic link between the tribe Epiptineae and subtribe Ricininae. It may be necessary to remove the Adrianinae and Ricininae from the Acalypheae as we accumulate further knowledge.

Subtribe 30c. MERCURIALINAE Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 46. 1890. Acalypheae subtribe Mercurialinae series Mercurialiiformes Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 270. 1914. TYPE: *Mercurialis* L.

Monoecious or dioecious herbs; indumentum simple; leaves alternate or opposite, pinnately veined, eglandular; inflorescences axillary, spicate or in glomerules; stamens 4–20 (rarely fewer), free; anthers extrorse, mucous; pollen grains 3-colporate, colpi operculate; ovary 2-locular, smooth; styles unlobed; fruit capsular, smooth or muricate; seeds carunculate; cotyledons much broader than radicle.

This subtribe includes three genera, one Eurasian and the other two South African.

KEY TO THE GENERA OF SUBTRIBE MERCURIALINAE

- 1a. Dioecious; stamens 8–20; pistillate flower with 2 subulate staminodia (or disk-segments); seeds carunculate 160. *Mercurialis*
1b. Monoecious; stamens 2–7; pistillate staminodia absent or very small; seeds ecarunculate.
2a. Capsule smooth; pistillate sepals 3; leaves entire or denticulate 161. *Seidelia*
2b. Capsule setose-muricate; pistillate sepals nearly obsolete; leaves crenulate
..... 162. *Leidesia*

160. *Mercurialis* L., Sp. Pl. 2: 1035. 1753; Gen. Pl. ed. 5, 437. 1754; Muell. Arg., DC. Prodr. 15(2): 794. 1866; Bentham, Gen. Pl. 3: 309. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 271. 1914; Zimmermann et al., in Hegi, Ill. Fl. Mitteleur. 5(1): 126. 1925; Webster, J. Arnold Arbor. 48: 366. 1967; Tutin, Fl. Europaea 2: 212. 1968. TYPE: *Mercurialis perennis* L. [lectotype, designated by Small, in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 460. 1913].

A Eurasian genus of eight species, seven in Europe and Mediterranean Africa, and one in east temperate Asia.

161. *Seidelia* Baillon, Etude Gén. Euphorb. 465. 1858; Bentham, Gen. Pl. 3: 310. 1880; Prain, Ann. Bot. 27: 398. 1913; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 282. 1914; Prain, Fl. Capensis 5(2): 464. 1920; Dyer, Gen. S. Afr. Fl. Pl., ed. 3, 316. 1975. TYPE: *Seidelia mercurialis* Baillon (nom. illeg.) [= *Seidelia triandra* (E. Mey.) Pax; lectotype, designated by Pfeiffer, Nomencl. Bot. 2: 1128. 1874].

A South African genus of two species.

162. *Leidesia* Muell. Arg., DC. Prodr. 15(2): 792. 1866; Bentham, Hook. Ic. Pl. 13: 66, t. 1284. 1879; Gen. Pl. 3: 310. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 284. 1914; Prain, Ann. Bot. 27: 399. 1913; Fl. Capensis 5(2): 462. 1920; Dyer, Gen. S. Afr. Fl. Pl., ed. 3, 316. 1975. TYPE: *Leidesia obtusa* (Thunb.) Muell. Arg. [loc. cit. 793; lectotype, chosen here].

A South African genus of two or three species, very closely related to *Seidelia*; the two genera could certainly be combined without obscuring phylogeny. Although Pax & Hoffmann (1914) used

the name *Leidesia procumbens* (L.) Prain for the two species of Mueller combined, this epithet belongs to the same taxon as *Leidesia capensis* Muell. Arg., which unfortunately is based on a confusion with *Urtica capensis* L. f. (a name referable to a species of *Acalypha*). It therefore seems better to choose Mueller's other species as lectotype.

Subtribe 30d. DYSOPSIDINAE Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 302. 1954. TYPE: *Dysopsis* Baillon.

Monoecious herbs; leaves alternate, simple, crenate, eglandular; stipules caducous; flowers axillary, mostly solitary; staminate calyx gamophyllous; stamens 3–6, interior connate; anthers apiculate, sacs adnate to connective; pollen grains globose, porate; pistillate sepals 3; ovary 3-locular, pubescent; styles unlobed, lacerate; fruit capsular; seeds with obsolete caruncle.

A monogeneric tribe of South America; closely related to the Mercurialinae, and further study may indicate that the two subtribes should be combined.

163. *Dysopsis* Baillon, Etude Gén. Euphorb. 435. 1858; Muell. Arg., DC. Prodr. 15(2): 949. 1866; Bentham, Gen. Pl. 3: 264. 1880; Grüning, Pflanzenr. 147. (Heft 58): 10. 1913; Pax & Hoffmann, Pflanzenr. 147. VII (Heft 63): 286. 1914. *Molina* Gay, Hist. Chile Bot. 5: 345. 1851 (non *Molina* Cav., 1790). TYPE: *Molina chilensis* Gay = *Dysopsis gayana* Baillon, nom. illeg. [= *Dysopsis glechomoides* (A. Rich.) Muell. Arg.].

A monotypic genus of the South American Andes (Ecuador to Chile), Juan Fernandez, and Costa Rica.

Subtribe 30e. CLEIDIINAE Webster, Taxon 24: 598. 1975. TYPE: *Cleidion* Blume.

Monoecious or dioecious trees or shrubs; indumentum simple; leaves alternate, simple, pinnately veined, with laminar glands, stipulate; inflorescences axillary, spicate or racemose; bracts eglandular; flowers apetalous, without disk; staminate sepals 3 or 4; stamens 25–80, free or basally connate; anthers mucous or apiculate; pollen grains 3-colporate, colpi not operculate; sexine rugulose-vermiculate, spinules vestigial; pistillode absent; pistillate sepals 3–6, imbricate; ovary (2-)3-locular; styles bifid, branches elongate; fruit capsular; seeds with dry or fleshy testa.

As here construed, subtribe Cleidiinae includes three genera, of which two are paleotropical and

the third pantropical. The characteristic globose pollen grains with vermiculate sexine ornamentation indicate an affinity between *Wetria* and *Cleidion* not clearly expressed in previous classifications. Pax & Hoffmann (1914) assigned *Wetria* to the series Trewiiformes adjacent to Alchorneae subtr. Conceveibinae; however, in those genera the indumentum is stellate and the pollen grains operculate.

KEY TO THE GENERA OF SUBTRIBE CLEIDIINAE

- 1a. Staminate flowers pedicellate, usually 2 or more per bract; stamens 25–80.
 2a. Anthers muticous, connective scarcely enlarged; stamens 25–30; pistillate pedicel less than 1 cm long 164. *Wetria*
 2b. Anthers apiculate, connective enlarged; stamens mostly 30–80 or more; pistillate pedicel over 1 cm long 165. *Cleidion*
 1b. Staminate flowers sessile, 1 per bract; stamens 15–25, anthers apiculate, connective not enlarged 166. *Sampantaea*

164. *Wetria* Baillon, Etude Gén. Euphorb. 409. 1858; J. J. Smith, Med. Dept. Landb. 10: 470. 1910; Pax & Hoffm., Pflanzenr. VII (Heft 63): 219. 1914; Backer & Bakhuizen, Fl. Java 1: 485. 1963; Airy Shaw, Kew Bull. 26: 350. 1972; Whitmore, Tree Fl. Malaya 2: 136. 1973; Airy Shaw, Kew Bull. 36: 358. 1981. TYPE: *Wetria trewioides* Baillon, nom. illeg. [= *Wetria insignis* (Steud.) Airy Shaw].

A monotypic genus, the single species occurring from Burma to Indonesia and New Guinea. Airy Shaw has suggested that the genus is closely related to *Alchornea*, but it differs in its simple indumentum, bifid styles, and larger stamen number.

165. *Cleidion* Blume, Bijdr. Fl. Ned. Ind. 612. 1826; Muell. Arg., DC. Prodr. 15(2): 983. 1866; Benth., Gen. Pl. 3: 320. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 288. 1914; Croizat, J. Arnold Arbor. 24: 166. 1943; Léonard, Bull. Jard. Bot. Nat. Belge 42: 297. 1972; Leandri, Adansonia II. 12: 193. 1972; A. C. Smith, Fl. Vitiensis Nova 2: 514. 1981; McPherson & Trel, Fl. Nouv.-Caléd. 14: 143. 1987; Huft, Ann. Missouri Bot. Gard. 75: 1103. 1989. TYPE: *Cleidion javanicum* Blume.

Redia Casaretto, Nov. Stirp. Bras. 51. 1843. TYPE: *Redia tricocca* Casar. [= *Cleidion tricoccum* (Casar.) Baillon].

Psilostachys Turcz., Bull. Soc. Imp. Naturalistes Moscou 16: 58. 1843. TYPE: *Psilostachys axillaris* Turcz. [= *Cleidion tricoccum* (Casar.) Baillon].

Lasiostyles Presl, Abh. Königl. Böhm. Ges. Wiss. V. 3: 579. 1845. TYPE: *Lasiostyles salicifolia* Presl [= *Cleidion javanicum* Blume].

Traglossa Beddome, Madras J. Lit. Sci. II. 22: 70. 1861. TYPE: *Traglossa indica* Beddome [= *Cleidion javanicum* Blume].

A well-marked genus of ca. 25 species, of which 5 are neotropical, 1 west African, 12 New Caledonian, and the remainder tropical Asian.

166. *Sampantaea* Airy Shaw, Kew Bull. 26: 328. 1972; Hook. Ic. Pl. 38: t. 3717. 1974. TYPE: *Sampantaea amentiflora* (Airy Shaw) Airy Shaw.

A monotypic genus restricted to Thailand and Cambodia. It appears closely related to *Wetria* and may prove congeneric.

Subtribe 30f. MACARANGINAE (Hutchinson) Webster, Taxon 24: 598. 1975. Tribe Macarangeae Hutchinson, Amer. J. Bot. 56: 755. 1969. TYPE: *Macaranga* Du Petit Thouars.

Dioecious trees or shrubs; indumentum simple; leaves alternate, unlobed or palmately lobed, pinnately to palmately veined, glandular or eglandular; stipules minute to enlarged; inflorescences axillary, racemose or panicle; bracts ± glandular; flowers apetalous and lacking disk; staminate calyx of 2–5 segments; stamens (1)2–50, free; anthers muticous, 2–4-valved; pollen grains 3- or 4-colporate, sexine finely to coarsely rugulose-spinulose; pistillate sepals 3–5, free or connate; ovary (1-)2- or 3-(–)locular; styles unlobed; fruit capsular; seeds ecarunculate, testa fleshy.

As defined by Webster (1975) and here, subtribe Macaranginae is much more narrowly defined than Hutchinson's tribe Macarangeae, which included seven other genera from various tribes of subfamilies Acalyphoideae and Crotonoideae; only the genus *Macaranga* is included here.

167. *Macaranga* Du Petit Thouars, Gen. Nova Madag. 26. 1806; Muell. Arg., DC. Prodr. 15(2): 987. 1866; Benth., Gen. Pl. 3: 320. 1880; Hook. f., Fl. Brit. Ind. 5: 445. 1887; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 298. 1914; Gagnepain, Fl. Indochine 5: 434. 1926; Perry, J. Arnold Arbor. 34: 191. 1953; Whitmore, Tree Fl. Malaya 2: 105. 1973; Kew Bull. Add. Ser. 4: 140. 1975; Kew Bull. Add. Ser. 8: 123. 1980; A. C. Smith, Fl. Vitiensis Nova 2: 500. 1981; Coode, Taxon

25: 184. 1976; McPherson & Tirel, Fl. Nouv.-Caléd. 14: 172. 1987; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 239. 1987. TYPE: *Macaranga mauritiana* Bojer ex Muell. Arg. [lectotype, selected by Coode, 1976, who rejected the proposed selection of *M. roxburgii* Wight by Wheeler, 1975].

Mapa A. Jussieu, Euphorb. Tent. 44. 1824. TYPE: *Mapa glabra* A. Juss. [= *Macaranga glabra* (A. Juss.) Pax & Hoffm.].

Pachystemon Blume, Bijdr. Fl. Ned. Ind. 626. 1826. TYPE: *Pachystemon trilobum* (Reinw. ex Bl.) Bl. [= *Macaranga triloba* (Reinw. ex Bl.) Muell. Arg.].

Mecostylis Kurz ex Teysmann & Binnendijk, Natuurk. Tijdschr. Ned.-Indië 27: 44. 1864. TYPE: *Mecostylis acalyphoides* Kurz ex Teysm. & Binn. [= *Macaranga involucreta* (Roxb.) Baillon].

Phoecea Seemann, J. Bot. 8: 69. 1870. TYPE: *Phoecea andersonii* Seem. [= *Macaranga* sp.; not identified by Pax & Hoffm., 1931, or McPherson & Tirel, 1987].

A very large and diverse paleotropical genus of ca. 300 species; there are about 50 species in Africa/Madagascar, over 200 in tropical Asia from India to New Guinea, and a few in Fiji and other Pacific islands. The genus has acquired several generic synonyms, but no plausible system of segregate genera has ever been proposed.

Subtribe 30g. CLAOXYLINAE Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 301. 1954. Tribe Acalyphaeae subtribe Mercurialinae series Claoxyloformes Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 75. 1914. Tribe Claoxyleae Hutchinson, Amer. J. Bot. 56: 752. 1969. TYPE: *Claoxylon* A. Juss.

Tribe Mareyeae Hutchinson, Amer. J. Bot. 56: 751. 1969. TYPE: *Mareya* Baillon.

Monoecious or dioecious trees, shrubs, or herbs; indumentum simple; leaves alternate, unlobed, mostly dentate, pinnately veined, without laminar glands; stipules small, persistent or deciduous; inflorescences axillary, racemose or paniculate; bracts eglandular; flowers apetalous; staminate sepals 2–5; disk mostly of interstaminal processes or annular (rarely absent); stamens 5–40(–200), free; anther sacs separated to the connective, ± erect; pollen grains rugulose-spinulose; pistillate sepals 2–4, open or imbricate; disk annular or dissected; ovary mostly 2- or 3-locular; styles ± elongated, unlobed but lacerate; fruit capsular; seeds ecarunculate, testa usually fleshy.

A paleotropical subtribe of nine genera, some hardly distinct, and others not certainly belonging here.

KEY TO THE GENERA OF SUBTRIBE CLAOXYLINAE

- 1a. Styles undivided; pistillate disk unlobed to 5-lobed.
 - 2a. Buds perulate; stipules mostly persistent 168. *Erythrococca*
 - 2b. Buds not perulate; stipules mostly deciduous.
 - 3a. Racemes uniformly floriferous; capsules coriaceous; leaves not stipellate.
 - 4a. Staminate disk of interstaminal segments.
 - 5a. Anther sacs erect; mostly dioecious.
 - 6a. Stamens mostly 20 or more; styles recurved, papillose but hardly lacerate 169. *Claoxylon*
 - 6b. Stamens up to 15; styles erect, lacerate 170. *Claoxylopsis*
 - 5b. Anther sacs pendent; styles lacerate; stamens 10–40; monoecious 171. *Mareya*
 - 4b. Staminate disk urceolate; stamens 6–12; styles recurved, lacerate 172. *Discoclaoxylon*
 - 3b. Racemes interrupted; capsules crustaceous; leaves stipellate 173. *Micrococca*
- 1b. Styles bifid; pistillate disk 8–10-lobed; staminate disk of interstaminal segments; stamens up to 25; seed-coat not fleshy 174. *Amyrea*

168. *Erythrococca* Bentham, Niger Fl. 506. 1849; Muell. Arg., DC. Prodr. 15(2): 790. 1866; Bentham, Gen. Pl. 3: 308. 1880; Prain, Ann. Bot. 25: 606. 1911; Fl. Trop. Afr. 6(1): 847. 1912; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 86. 1914; Keay, Fl. W. Trop. Afr. ed. 2, 1: 400. 1954; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 265. 1987. TYPE: *Erythrococca aculeata* Benth., nom. illeg. [= *Erythrococca anomala* (Juss. ex Poir.) Prain].

Poggeophyton Pax, Bot. Jahrb. 19: 88. 1894. TYPE:

Poggeophyton aculeatum Pax [= *Erythrococca poggeophyton* Prain].

Chloropatane Engler, Bot. Jahrb. 26: 383. 1899. TYPE: *Chloropatane africana* (Baillon) Engler [= *Erythrococca africana* (Baillon) Prain].

Athroandra (Hook. f.) Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 76. 1914. TYPE: *Claoxylon mannii* Hook. f. [= *Erythrococca mannii* (Hook. f.) Prain].

A diverse African genus of ca. 50 species, whose delimitation apparently requires further analysis. Although Prain, Keay, and Radcliffe-Smith treat *Athroandra* as part of *Erythrococca*, Airy Shaw

(1966) suggested that *Erythrococca* is close to *Claoxylon*.

- 169. Claoxylon** A. Jussieu, Euphorb. Tent. 43. 1824; Muell. Arg., DC. Prodr. 15(2): 775. 1866; Bentham, Gen. Pl. 3: 309. 1880; Pax & Hoffm., Pflanzenz. 147. VII (Heft 63): 100. 1914; Merrill, Enum. Phil. Pl. 2: 429. 1923; Whitmore, Tree Fl. Malaya 2: 78. 1973; A. C. Smith, Fl. Vit. Nova 2: 516. 1981. TYPE: *Claoxylon parviflorum* A. Juss.

Erythrochilus Reinw. ex Blume, Bijdr. Fl. Ned.-Ind. 614. 1826. TYPE: *Erythrochilus indicus* Reinw. ex Bl. [= *Claoxylon indicum* (Reinw. ex Bl.) Hassk.; designated by Wheeler, 1975].

Quadrasia Elmer, Leaf. Phil. Bot. 7: 2656. 1915. TYPE: *Quadrasia euphorbioides* Elmer [= *Claoxylon euphorbioides* (Elmer) Merr.].

A paleotropical genus of ca. 75 species, absent from Africa but extending from Madagascar to Melanesia and Hawaii.

- 170. Claoxyloopsis** Leandri, Bull. Soc. Bot. France 85: 526. 1938; Radcliffe-Smith, Kew Bull. 43: 642. 1988. TYPE: *Claoxyloopsis perrieri* Leandri.

A genus of three species endemic to Madagascar. Although apparently very close to *Claoxylon*, it is still poorly known and its position and status must be regarded as tentative.

- 171. Mareya** Baillon, Adansonia I. 1: 73. 1860; Muell. Arg., DC. Prodr. 15(2): 792. 1866; Bentham, Hook. Ic. Pl. 13: 63, t. 128. 1879; Gen. Pl. 3: 312. 1880; Prain, Fl. Trop. Afr. 6(1): 910. 1912; Pax & Hoffm., Pflanzenz. 147. XIV (Heft 68): 11. 1919; Léonard, Bull. Jard. Bot. Brux. 25: 291. 1945; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 216. 1987. TYPE: *Mareya spicata* Baillon.

Mareyopsis Pax & Hoffm., Pflanzenz. 147. XIV (Heft 68): 13. 1919. TYPE: *Mareyopsis longifolia* (Pax) Pax & Hoffm. [= *Mareya longifolia* Pax].

An African genus of three species.

- 172. Discoclaoxylon** (Muell. Arg.) Pax & Hoffmann, Wiss. Ergebn. Deutsche Zentral-Afr. Exped. 2: 452. 1912; Pflanzenz. 147. VII (Heft 63): 137. 1914; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 279. 1987. *Claoxylon* sect. *Discoclaoxylon* Muell. Arg., Flora 47: 137. 1864. TYPE: *Discoclaoxylon hexandrum* (Muell. Arg.) Pax & Hoffm. [lectotype, chosen here; the larger staminate disk

in the lectotype species appropriately reflects the taxon name].

A mainly west African genus of three species, extending from Sierra Leone and Fernando Póo to Uganda.

- 173. Micrococca** Bentham, Niger Fl. 503. 1849; Gen. Pl. 3: 309. 1880; Prain, Ann. Bot. 25: 628. 1911; Fl. Trop. Afr. 6(1): 876. 1912; Airy Shaw, Kew Bull. 25: 524. 1971; Dyer, Gen. S. Afr. Fl. Pl., ed. 3, 1: 315. 1975; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 260. 1987. TYPE: *Micrococca mercurialis* (L.) Benth.

A paleotropical genus of 12 species, reported from tropical Africa and Madagascar to Malaya.

- 174. Amyrea** Leandri, Notul. Syst. (Paris) 9: 168. 1940. TYPE: *Amyrea sambiranensis* Leandri [lectotype, selected here].

A genus of two species endemic to Madagascar. *Amyrea* diverges from all of the other genera of subtribe Claoxylinae in its bifid styles, and its position requires evaluation.

- Subtribe 30h. LOBANILIINAE** Radcliffe-Smith, Kew Bull. 44: 339. 1989. TYPE: *Lobanilia* Radcl.-Sm.

Dioecious trees or shrubs; indumentum stellate (sometimes simple as well); leaves alternate, unlobed, mostly pinnately veined, without embedded or granular laminar glands; stipules minute and deciduous; inflorescences axillary, racemose; flowers apetalous; staminate sepals 3; disk of interstaminal segments; stamens 17–30, free; anthers free to base; pistillate sepals 3; disk annular or ± dissected; ovary 3–4-locular; styles unlobed, papillose or plumose; fruit capsular; seeds ecarunculate.

This monotypic subtribe, recently proposed by Radcliffe-Smith, appears very similar to subtribe Claoxylinae except for the stellate indumentum. It is provisionally recognized here until detailed comparisons with taxa of Claoxylinae can be made to determine whether *Lobanilia* should be kept in a separate subtribe.

- 175. Lobanilia** Radcliffe-Smith, Kew Bull. 44: 334. 1989. TYPE: *Lobanilia luteobrunnea* (Baker) Radcl.-Sm.

A genus of seven species confined to Madagascar. Originally these were treated as a section of

Claoxylon, but Radcliffe-Smith presented persuasive arguments for recognition of a separate genus.

Subtribe 30i. ROTTLERINAE Meisner, Pl. Vasc. Gen. 1: 339. 1841; Webster, Taxon 24: 598. 1975. TYPE: *Rottlera* Roxb. [= *Mallotus* L.].

Family Trewiaceae Lindley, Intr. Nat. Syst. ed. 2, 174. 1835. Acalypheae subtribe Mercurialinae series Trewiiformes Pax & Hoffm., Pflanzenz. 147. VII (Heft 63): 139. 1914. TYPE: *Trewia* L.

Tribe Acalypheae subtribe Coelodisceae Muell. Arg., Linnaea 34: 143. 1865. TYPE: *Coelodiscus* Baillon [= *Mallotus* Lour.].

Tribe Malloteae Hutchinson, Amer. J. Bot. 56: 752. 1969. TYPE: *Mallotus* Lour.

Diococious (rarely monoecious) trees or shrubs; indumentum stellate (rarely simple); leaves alter-

nate or opposite, unlobed or lobed, pinnately or palmately veined, sometimes with embedded laminar glands; stipules present or obsolete; inflorescences terminal or axillary, racemose or paniculate; flowers apetalous; staminate sepals 3–5; disk intrastaminal, of interstaminal segments, or absent; stamens 15–300, free; anthers mucicous, anthersacs not pendulous; pollen grains 3(–4) colpiate, finely to coarsely tectate-perforate and spinulose; pistillate sepals 3–6(–10), free or connate; disk absent; ovary 2–4(–8)-locular, sometimes echinate; styles unlobed, \pm plumose or lacinate; fruit capsular or baccate; seeds ecarunculate (rarely carunculate), testa often fleshy.

This Old World subtribe of eight closely related genera is most strongly represented in tropical Asia.

KEY TO THE GENERA OF SUBTRIBE ROTTLERINAE

- 1a. Carpels 2–4 (rarely 5); fruit capsular or drupaceous.
 - 2a. Styles unlobed; leaves usually glandular.
 - 3a. Fruit capsular, dehiscent; pistillate sepals free or connate.
 - 4a. Ovary smooth to echinate, not winged; inflorescences terminal or opposite leaves (sometimes axillary as well); bracts small; stamens 20–200; pollen sexine tectate-perforate to rugulose.
 - 5a. Styles elongate; leaves usually granulose-glandular 176. *Mallotus*
 - 5b. Styles contracted; leaves eglandular 177. *Deuteromallotus*
 - 4b. Ovary \pm winged; inflorescences axillary.
 - 6a. Stamens many (over 200); seeds ecarunculate 178. *Cordemoya*
 - 6b. Stamens 15–20; seeds carunculate 179. *Coccoceras*
 - 3b. Fruit indehiscent; pistillate calyx gamophyllous.
 - 7a. Staminate disk absent; ovary 2–4-locular 180. *Trewia*
 - 7b. Staminate disk present; ovary 1(2)-locular 181. *Neotrewia*
 - 2b. Styles bifid; leaves eglandular 182. *Rockinghamia*
 - 1b. Ovary 8-locular; fruit baccate; leaves alternate, glandular; stamens 15–20 183. *Octospermum*

176. *Mallotus* Loureiro, Fl. Cochinch. 635. 1790; Muell. Arg., DC. Prodr. 15(2): 956. 1866; Bentham, Fl. Austral. 6: 138. 1873; Gen. Pl. 3: 319. 1880; Forbes & Hemsley, J. Linn. Soc. Bot. 26: 439. 1894; Schum. & Lauterb., Fl. Deutsche Schutzgeb. 394. 1901; J. J. Smith, Meded. Dept. Landb. 10: 394. 1910; Prain, Fl. Trop. Afr. 6(1): 927. 1912; Pax & Hoffm., Pflanzenz. 147. VII (Heft 63): 145. 1914; Natürl. Pflanzenfam. ed. 2, 19c: 113. 1931; Merrill & van Steenis, Webbia 8: 405. 1951; Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 304. 1954; Airy Shaw, Kew Bull. 20: 41. 1866; 21: 379. 1968; 25: 526. 1971; Whitmore, Tree Fl. Malaya 2: 113. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 160. 1975; 8: 162. 1980; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 235. 1987. TYPE: *Mallotus cochinchensis* Lour.

Echinus Loureiro, Fl. Cochinch. 633. 1790. TYPE: *Echi-*

nus trisulcus Lour. [= *Mallotus cochinchensis* Lour.].
Rottlera Roxburgh, Pl. Coromandel 2: 36. 1798 (non Willd., 1797). TYPE: *Rottlera tinctoria* Roxb. [= *Mallotus philippensis* (Lam.) Muell. Arg.].
Adisca Blume, Bijdr. Fl. Ned. Ind. 609. 1826. TYPE: *Adisca floribunda* Bl. [= *Mallotus floribundus* (Bl.) Muell. Arg.; lectotype, chosen here].
Plagianthera Reichb. f. & Zollinger, Verh. Naturk. Ver. Ned. Ind. 1(4): 19. 1856. TYPE: *Plagianthera oppositifolia* (Bl.) Reichb. f. & Zoll. [= *Mallotus blumeanus* Muell. Arg.].
Hancea Seemann, Bot. Voy. Herald 409. 1857. TYPE: *Hancea hookeriana* Seem. [= *Mallotus hookerianus* (Seem.) Muell. Arg.].
Axenfeldia Baillon, Etude Gén. Euphorb. 419. 1858. TYPE: *Axenfeldia intermedia* Baillon [= *Mallotus muricatus* (Wight) Muell. Arg.].
Coelodiscus Baillon, Etude Gén. Euphorb. 293. 1858. TYPE: *Ricinus dioicus* Wall. ex Baill. [= *Mallotus eriocarpus* (Thw.) Muell. Arg.].
Aconceveibum Miquel, Fl. Ind. Bat. 1(2): 389. 1859. TYPE: *Aconceveibum trinerve* Miq. [= *Mallotus philippensis* (Lam.) Muell. Arg.].
Echinocroton F. Mueller, Fragm. Phytogeogr. Austral.

- 1: 31. 1859. TYPE: *Echinocroton claoxyloides* F. Muell. [= *Mallotus claoxyloides* (F. Muell.) Muell. Arg.].
Diplochlamys Muell. Arg., Flora 47: 539. 1864. TYPE: *Diplochlamys griffithianus* Muell. Arg. [= *Mallotus griffithianus* (Muell. Arg.) Hook. f.].

This large and complex paleotropical genus includes ca. 150 species, of which there are only two in Africa and Madagascar, the rest in Asia and Australasia (to Fiji).

- 177. Deuteromallotus** Pax & Hoffmann, Pflanzenz. 147. VII (Heft 63): 212. 1914; Leandri, Bull. Soc. Bot. France 103: 605. 1956. TYPE: *Deuteromallotus acuminatus* (Baillon) Pax & Hoffm.

A genus of two species endemic to Madagascar.

- 178. Cordemoya** Baillon, Adansonia I. 1: 255. 1861; Pax & Hoffm., Pflanzenz. 147. VII (Heft 63): 208. 1914. TYPE: *Cordemoya integrifolia* Willd. ex Baill. [lectotype].

A monotypic genus endemic to Malagasia.

- 179. Coccoceras** Miquel, Fl. Ind. Batav. Suppl. 455. 1860; Muell. Arg., DC. Prodr. 15(2): 949. 1866; Bentham, Gen. Pl. 3: 308. 1880; Pax & Hoffm., Pflanzenz. 147. VII (Heft 63): 209. 1914; Airy Shaw, Kew Bull. 16: 349. 1963. TYPE: *Coccoceras sumatranus* Miq.

A tropical Asian genus of three or four species, distributed from Burma to Borneo. Airy Shaw (1963) reduced *Coccoceras* to a section of *Mallotus*, perhaps correctly so.

- 180. Trewia** L., Sp. Pl. 1193. 1753; Klotzsch, Arch. Naturgesch. 7: 255. 1841; Muell. Arg., DC. Prodr. 15(2): 953. 1866; Bentham, Gen. Pl. 3: 318. 1880; J. J. Smith, Meded. Dept. Landb. 10: 389. 1910; Pax & Hoffm., Pflanzenz. 147. VII (Heft 63): 140. 1914; Airy Shaw, Kew Bull. 20: 406. 1966; Kew Bull. Add. Ser. 4: 200. 1975. TYPE: *Trewia nudiflora* L.

A monotypic genus, the single species widely distributed from India to southern China and Indonesia.

- 181. Neotrewia** Pax & Hoffmann, Pflanzenz. 147. VII (Heft 63): 211. 1914; Merrill, Enum. Phil. Pl. 2: 437. 1923. TYPE: *Neotrewia cumingii* (Muell. Arg.) Pax & Hoffm.

A monotypic genus of the Philippines and Celebes, dubiously separable from *Trewia*.

- 182. Rockinghamia** Airy Shaw, Kew Bull. 20: 29. 1966; 35: 667. 1980. TYPE: *Rockinghamia angustifolia* (Benth.) Airy Shaw.

A genus of two species endemic to tropical Australia (Queensland).

- 183. Octospermum** Airy Shaw, Kew Bull. 19: 311. 1965; Hook. Ic. Pl. 38: t. 3716. 1974; Kew Bull. Add. Ser. 8: 176. 1980. TYPE: *Octospermum pleiogynum* (Pax & Hoffm.) Airy Shaw.

A single species of New Guinea.

- Subtribe 30j. ACALYPHINAE** Grisebach, Fl. Br. W. Ind. 45. 1859; Pax & Hoffm., Pflanzenz. 147. XVI (Heft 85): 1. 1924. TYPE: *Acalypha* L.

Monoecious or dioecious trees, shrubs, or herbs; indumentum simple or stellate, often glandular; leaves alternate, unlobed, pinnately or palmately veined, stipulate; inflorescences spicate or the pistillate (in a few species) paniculate, terminal or axillary, unisexual or bisexual; pistillate bracts usually enlarged in fruit; staminate sepals 4; disk absent; stamens usually 8, filaments free, anther sacs pendulous and vermiform; pollen grains porate, rugulose; pistillate sepals 3–5, imbricate; disk absent; ovary (2-)3-locular; styles mostly free, lacinate (rarely entire); fruit capsular; seeds with caruncle minute or absent.

As here defined, subtribe Acalypinae includes only the genus *Acalypha*; it appears closely related to subtribe Claoxylinae, but differs in its unique anthers, enlarged pistillate bracts, distinctive porate pollen, and dissected styles.

- 184. Acalypha** L., Sp. Pl. 1003. 1753; Gen. Pl. ed. 5, 436. 1754; Muell. Arg., DC. Prodr. 15(2): 799. 1866; Bentham, Gen. Pl. 3: 311. 1880; Hutchinson, Fl. Trop. Afr. 6(1): 880. 1912; Pax & Hoffm., Pflanzenz. 147. XVI (Heft 85): 12. 1924; Natürl. Pflanzenfam. ed. 2, 19c: 134. 1931; Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 295. 1954; Webster, J. Arnold Arbor. 48: 370. 1967; A. C. Smith, Fl. Vit. Nova 2: 522. 1981; Seberg, Nordic J. Bot. 4: 159. 1984; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 185. 1987. TYPE: *Acalypha virginica* L. [lectotype, designated by Small, in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 457. 1913].

Caturus L., Syst. Nat. ed. 12, 2: 650. 1767; Mant. Pl. 19, 127. 1767. TYPE: *Caturus spiciflora* L. [= *Acalypha hispida* Burm. f.].

Linostachys Klotzsch ex Schlecht., *Linnaea* 19: 235. 1846.
TYPE: *Linostachys padifolia* Schlecht. [= *Acalypha schlechtendaliana* Muell. Arg.].

Odonteilema Turczaninow, *Bull. Soc. Imp. Natur. Moscou* 21: 587. 1848. TYPE: *Odonteilema clausenii* Turcz. [= *Acalypha clausenii* (Turcz.) Muell. Arg.].

Gymnalypha Grisebach, *Bonplandia* 6: 2. 1858. TYPE: *Gymnalypha jacquinii* Griseb., nom. illeg. [= *Acalypha villosa* Jacq.].

Corythea S. Watson, *Proc. Amer. Acad. Sci.* 22: 451. 1887. TYPE: *Corythea filipes* S. Wats. [= *Acalypha filipes* (S. Watson) McVaugh].

Acalyphopsis Pax & Hoffm., *Pflanzenr.* 147. XVI (Heft 85): 178. 1924. TYPE: *Acalyphopsis celebica* Pax & Hoffm. [= *Acalypha hoffmanniana* Hurus.].

With ca. 450 species, *Acalypha* is the fourth largest genus of Euphorbiaceae; in addition to the small number of temperate species, species are widespread throughout the tropics except in Hawaii and a few Pacific archipelagos.

Subtribe 30k. LASIOCOCINAE Webster, *Taxon* 24: 597. 1975. TYPE: *Lasiococca* Hook. f.

Monoecious or dioecious trees or shrubs; indumentum simple or lepidote; leaves alternate, unlobed, pinnately veined; eglandular, stipulate; inflorescences axillary, unisexual, racemose or the pistillate flowers solitary, bracts eglandular; staminate sepals usually 3; disk absent; stamens many, filaments connate, anthers on filaments of branching fascicles; pollen grains 3-colporate; not operculate; pistillate sepals 5–8, imbricate; disk absent; ovary 3-locular; styles unlobed, smooth to papillose or plumose; fruit capsular; seeds ecarunculate, testa usually fleshy.

This subtribe includes three genera that were treated by Pax & Hoffmann (1919) as part of subtribe Ricininae, doubtlessly because of the androecium of many stamens with anthers borne on branches of a dendritic column. However, this character almost surely represents a convergence, since the Lasiococcinae diverge from *Ricinus* in many important characters, including ecarunculate seeds, pinnately veined unlobed leaves, and axillary inflorescences. Airy Shaw (1974) has suggested a close relationship of subtribe Lasiococcinae to *Malotus*.

KEY TO THE GENERA OF SUBTRIBE LASIOCOCINAE

- 1a. Monoecious; pistillate sepals persistent; indumentum simple; ovary muricate 185. *Lasiococca*
- 1b. Dioecious; pistillate sepals deciduous; indumentum simple or lepidote.
 - 2a. Lepidote scales absent; ovary tuberculate; pollen sexine not striate 186. *Spathiostemon*
 - 2b. Lepidote scales present; ovary smooth; pollen sexine striate 187. *Homonioia*

185. Lasiococca Hooker f., *Hook. Ic. Pl.* 16: t. 1587. 1887; *Fl. Brit. Ind.* 5: 456. 1887; Haines, *Kew Bull. Misc. Inf.* 1920; 70. 1920; Airy Shaw, *Kew Bull.* 16: 358. 1963; 21: 406. 1968; Whitmore, *Tree Fl. Malaya* 2: 104. 1973; Thin, *J. Biol. Sinh Hoc* 8(3): 36. 1986. TYPE: *Lasiococca symphyllifolia* (Kurz) Hook. f.

A tropical Asian genus of three species, with a disjunct distribution in India, Malaya and Indochina, and Hainan.

186. Spathiostemon Blume, *Bijdr. Fl. Ned. Ind.* 621. 1826; Airy Shaw, *Kew Bull.* 16: 357. 1963; 20: 408. 1966; 26: 341. 1972; *Hook. Ic. Pl.* 38: t. 3720. 1974; *Kew Bull. Add. Ser.* 4: 196. 1975; 8: 202. 1980. TYPE: *Spathiostemon javense* Bl.

Polydragma Hook. f., *Hook. Ic. Pl.* 18: t. 1701. 1887; *Fl. Brit. Ind.* 5: 456. 1887. TYPE: *Polydragma mallotiforme* Hook. f. [= *Spathiostemon javense* Bl.].

Clonostylis Sp. Moore, *J. Bot.* 63 (suppl.): 101. 1925. TYPE: *Clonostylis forbesii* Sp. Moore [= *Spathiostemon forbesii* (Sp. Moore) Airy Shaw].

A genus of two species distributed from Thailand to the Philippines and New Guinea. Although united with *Homonioia* by Mueller (1866), Benthams (1880), and Pax & Hoffmann (1919), it may be distinct, as indicated by Airy Shaw.

187. Homonioia Loureiro, *Fl. Cochinch.* 636. 1790; Muell. Arg., *DC. Prodr.* 15(2): 1022. 1866; Benthams, *Gen. Pl.* 3: 322. 1880; J. J. Smith, *Med. Dept. Landb.* 10: 542. 1910; Pax & Hoffm., *Pflanzenr.* 147. XI (Heft 68): 114. 1919; Gagnepain, *Fl. Indochine* 5: 330. 1925; Airy Shaw, *Kew Bull. Add. Ser.* 4: 136. 1975; *Kew Bull.* 36: 310. 1981. TYPE: *Homonioia riparia* Lour.

Lumanaja Blanco, *Fl. Filip.* 821. 1837. TYPE: *Lumanaja fluviatilis* Blanco [= *Homonioia riparia* Lour.].

A genus of two Asian species (India to Taiwan, the Philippines, and New Guinea).

Tribe 31. PLUKENETIEAE (Benthams) Hutchinson, *Amer. J. Bot.* 56: 753. 1969. Crotonae subtribe Plukenetiae Benthams, *Gen. Pl.* 3: 252. 1880. TYPE: *Plukenetia* L.

Monoecious (rarely dioecious) trees, shrubs, or herbs, sometimes climbing or twining; indumentum simple, often glandular, sometimes urticant; leaves alternate, unlobed to palmately parted, pinnately to palmately veined, sometimes glandular or sti-

pellate at base; stipules present. Inflorescences terminal or axillary, usually bisexual, mostly racemose or spicate; bracts eglandular; flowers apetalous. Staminate calyx splitting into 3–5 valvate segments; disk interstaminal, extrastaminal, or absent; stamens (2)3–100, usually free; anthers introrse or extrorse, mucous or apiculate; pollen grains 3-colporate, porate, or inaperturate, sexine varying from tectate to intectate; pistillode absent. Pistillate sepals 3–6, imbricate; disk absent; ovary 3- or 4-locular; styles unlobed, slender or dilated, sometimes papillose or lacerate, usually connate into a distinct column. Fruit capsular; columella persistent; seeds ecarunculate, testa usually dry; endosperm copious; cotyledons much longer and broader than radicle.

This distinctive tribe includes 16 genera with more than 250 species in the tropics of both the Old World and New World; the majority are neotropical.

KEY TO THE SUBTRIBES OF TRIBE PLUKENETIINAE

- 1a. Flowers in racemes or spikes, not bibracteate pseudanthia; pollen grains subglobose.
 - 2a. Stinging hairs absent; fruit winged, crested, carinate, or indehiscent; pollen grains 3-colpate 31a. Plukenetiinae
 - 2b. Stinging hairs present; fruit usually unapended; pollen grains 3-colpate, 3-porate, or inaperturate, rugulose 31b. Tragiinae
- 1b. Flowers in bibracteate pseudanthia; pollen grains prolate, coarsely reticulate; stinging hairs present 31c. Dalechampiinae

Subtribe 31a. PLUKENETIINAE Benth., Gen. Pl. 3: 253. 1880; Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 62. 1890; Pax & Hoffm., Pflanzenz. 147. IX (Heft 68): 1. 1919; Natürl. Pflanzenfam. ed. 2, 19c: 141. 1931; Webster, Taxon 24: 598. 1975. TYPE: *Plukenetia* L.

Trees, shrubs, lianas, or twining vines; indumentum entirely of simple hairs; leaf blades simple and unlobed, entire or dentate, often with embedded laminar glands, sometimes stipellate; inflorescence axillary or terminal and appearing leaf-opposed; stamens 4–50, filaments free or anthers subsessile; pollen grains suboblate to subglobose, tricolpate, tectate-perforate to semitectate-reticulate; ovary 3- or 4-locular, often winged; styles massive, partly to entirely connate; fruit capsular or rarely indehiscent.

As delimited by Webster (1975), subtribe Plukenetiinae is here treated in a narrower sense than the concepts of Bentham (1880) or Pax & Hoff-

mann (1919, 1931). In contrast to subtribe Tragiinae, the distribution of the Plukenetiinae is almost entirely neotropical (a few species of *Plukenetia* occur in Africa).

KEY TO THE GENERA OF SUBTRIBE PLUKENETIINAE

- 1a. Ovary 3-locular; pistillate sepals 5 or 6; trees, shrubs or vines.
 - 2a. Stamens 4; staminate disk segments 4 (or if absent replaced by 4-lobed pseudodisk); leaves pinnately veined; trees or shrubs.
 - 3a. Disk absent; base of stamens dilated, forming an intrastaminal pseudodisk; style urceolate 188. *Haematostemon*
 - 3b. Disk extrastaminal; style ovoid 189. *Astrococcus*
- 2b. Stamens 10 or more; staminate disk segments absent or minute, numerous.
 - 4a. Stamens ca. 20; style urceolate; flowers fasciculate in leaf axils; leaves pinnately veined; tree or shrub 190. *Angostyles*
 - 4b. Stamens 10; style cylindrical, clavate, apically 3-lobed; flowers in axillary racemes; leaves palmately veined; twining vine 191. *Romanoa*
- 1b. Ovary 4-locular; pistillate sepals 4; twining vines or lianas.
 - 5a. Styles mostly free, connate for less than one-half their length, tips bifid; stamens 40–50 192. *Eleutherostigma*
 - 5b. Styles entirely connate into a massive column; stamens 8–30(–40).
 - 6a. Fruit dehiscent (rarely indehiscent, but then staminate receptacle not globose) 193. *Plukenetia*
 - 6b. Fruit indehiscent; staminate receptacle globose 194. *Vigia*

188. Haematostemon (Muell. Arg.) Pax & Hoffmann, Pflanzenz. 147. IX (Heft 68): 31. 1919; Sandwith, Kew Bull. 1950: 133. 1951; Jablonski, Mem. New York Bot. Gard. 17: 143. 1967. *Astrococcus* sect. *Haematostemon* Muell. Arg., Linnaea 34: 157. 1865. TYPE: *Haematostemon coriaceus* (Baill.) Pax & Hoffm.

A genus of two species from rainforests in southern Venezuela and Guiana. The gynoecium is very similar to that of *Angostyles*, but the staminate flowers are quite different.

189. Astrococcus Bentham, Hook. J. Bot. Kew Gard. Misc. 6: 327. 1854; Muell. Arg., DC. Prodr. 15(2): 766. 1866; Fl. Bras. 11(2): 330. 1874; Bentham, Gen. Pl. 3: 326. 1880; Pax & Hoffm., Pflanzenz. 147. IX (Heft 68): 30. 1919. TYPE: *Astrococcus cornutus* Benth.

A monotypic genus from Amazonian Brazil and Venezuela.

190. Angostyles Bentham, Hook. J. Bot. Kew Gard. Misc. 6: 328. 1854; Muell. Arg., DC. Prodr. 15(2): 767. 1866; Fl. Bras. 11(2): 331, t. 50. 1874; Bentham, Gen. Pl. 3: 327. 1880; Pax & Hoffm., Pflanzenz. 147. IX (Heft 68): 29. 1919. TYPE: *Angostyles longifolia* Benth.

A monotypic genus from the Brazilian Amazon.

191. Romanoa Trevisan, Saggio Monogr. Alghe Cocc. 99. 1848 (nom. cons.); Radcliffe-Smith, Kew Bull. 34: 589. 1980. *Anabaena* A. Juss., Euphorb. Tent. 46. 1824. *Anabaenella* Pax & Hoffm., Pflanzenz. 147. IX (Heft 68): 27. 1919. TYPE: *Anabaena tamnoides* A. Juss. [= *Romanoa tamnoides* (A. Juss.) Radcl.-Sm.].

A monotypic genus of Brazil, also very close to *Plukenetia* and questionably distinct.

192. Eleutherostigma Pax & Hoffmann, Pflanzenz. 147. IX (Heft 68): 11. 1919. TYPE: *Eleutherostigma lehmannianum* Pax & Hoffm.

A poorly known monotypic genus of Colombia and Ecuador, apparently closely related to *Plukenetia*, and combined with it by Gillespie (1993).

193. Plukenetia L., Sp. Pl. 1192. 1753; Gen. Pl. ed. 5, 438. 1754; Muell. Arg., DC. Prodr. 15(2): 768. 1866; Bentham, Gen. Pl. 3: 327. 1880; Pax & Hoffm., Pflanzenz. 147. IX (Heft 68): 12. 1919; Jablonski, Mem. New York Bot. Gard. 17: 142. 1967; Webster, Ann. Missouri Bot. Gard. 54: 293. 1968; Huft, Ann. Missouri Bot. Gard. 75: 1105. 1989; Gillespie, Syst. Bot. 18: 575. 1993. TYPE: *Plukenetia volubilis* L.

Pterococcus Hasskarl, Flora 25(2), Beibl. 41. 1842 (nom. cons.); Croizat, J. Arnold Arbor. 22: 423. 1941; Airy Shaw, Kew Bull. Add. Ser. 4: 187. 1975. *Ceratococcus* Meissner, Pl. Vasc. Gen. 2: 369. 1843. *Sajorium* Endl., Gen. Pl. Suppl. 3: 98. 1843. TYPE: *Pterococcus glaberrimus* Hassk., nom. illeg. [= *Plukenetia corniculata* J. E. Smith].

Hedraiostylus Hasskarl, Tijdschr. Natuurl. Gesch. Physiol. 10: 141. 1843. TYPE: *Hedraiostylus glaberrimus* (Hassk.) Hassk. [= *Plukenetia corniculata* J. E. Smith].

Tetracarpidium Pax, Bot. Jahrb. 26: 329. 1899. TYPE: *Tetracarpidium staudtii* Pax [= *Plukenetia conophora* Muell. Arg.].

Pseudotragia Pax, Bull. Herb. Boiss. II. 8: 635. 1908. TYPE: *Pseudotragia scandens* Pax [= *Plukenetia corniculata* J. E. Sm.].

Angostylidium Pax & Hoffm., Pflanzenz. 147. IX (Heft 68): 17. 1919. TYPE: *Angostylidium conophorum*

(Muell. Arg.) Pax & Hoffm. [= *Plukenetia conophora* Muell. Arg.].

Apodandra Pax & Hoffm., Pflanzenz. 147. IX (Heft 68): 20. 1919. TYPE: *Apodandra lorentensis* (Ule) Pax & Hoffm. [= *Plukenetia lorentensis* Ule].

Elaeophora Ducke, Ann. Jard. Bot. Rio Jan. 4: 112. 1925. TYPE: *Elaeophora abutaefolia* Ducke [= *Plukenetia abutifolia* (Ducke) Pax & Hoffm.].

A genus of about 15 species, mostly neotropical, but with three species in Africa, one in Madagascar, and one in southeast Asia. The genus is rather variable, and a number of workers have accepted either *Pterococcus* or *Tetracarpidium* as distinct genera. However, the present conservative concept may not be broad enough, since some of the other genera of subtribe Plukenetiinae listed here (e.g., *Vigia* and *Romanoa*) are only questionably distinct from *Plukenetia*.

194. Vigia Vellozo, Fl. Flum. 9: t. 127. 1832. TYPE: *Vigia serrata* Vell.

Fragariopsis St. Hilaire, Leçons Morph. Veg. 426. 1840. TYPE: *Fragariopsis scandens* St. Hil. [= *Vigia serrata* Vell.].

Accia St. Hilaire, Leçons Morph. Veg. 499. 1840. TYPE: *Accia scandens* St. Hil. [= *Vigia serrata* Vell.].

Botryanthe Klotzsch, Arch. Naturgesch. 7(1): 190. 1841. TYPE: *Botryanthe discolor* K. [= *Vigia serrata* Vell.].

A South American genus, probably monotypic, although Pax & Hoffmann (1931) recognized a second species, *Fragariopsis paxii* Pitt. Even though the name *Fragariopsis* has been universally used for this segregate from *Plukenetia* since the treatment of Baillon (1858), the name *Vigia* of Vellozo clearly has priority. Although the plate of Vellozo is crude, it represents publication as valid as the casual mention of *Fragariopsis* by St. Hilaire in his textbook. There seems no good reason to propose the name *Fragariopsis* for conservation, especially since it is only dubiously distinct from *Plukenetia*.

Subtribe 31b. TRAGIINAE Webster, Taxon 24: 598. 1975. TYPE: *Tragia* L.

Shrubs or herbs, often twining; indumentum of simple and stinging hairs; leaves simple to distinctly lobed, entire or dentate, without embedded laminar glands, not stipellate; inflorescences axillary or terminal and opposite leaves; stamens (2)3–50, filaments free or connate; pollen grains subglobose to suboblate, 3-colpate, 3-porate, or inaperturate, sexine intectate-baculate, semitectate-reticulate, or tectate-perforate; ovary 3-locular; styles nearly free to distinctly connate; fruit capsular.

As here delimited, the subtribe includes 8 genera with ca. 150 species; besides the widespread *Tragia*, there are 5 Old World and only 2 neotropical genera.

KEY TO THE GENERA OF SUBTRIBE TRAGIINAE

- 1a. Staminate sepals adaxially inflexed to form a pseudodisk; stamens 3 or 4, anthers introrse; styles massive.
- 2a. Pistillate sepals entire or toothed; pistillode absent in staminate flower.
- 3a. Pistillate sepals entire; anther connective enlarged, triangular, sometimes caudate; stamens free.
- 4a. Styles free or nearly so, long-papillose on adaxial surface; inflorescence terminal and leaf-opposed; leaves with stinging hairs 195. *Cnesmone*
- 4b. Styles connate into a massive globose or clavate column, not papillose; inflorescence axillary; leaves subglabrous 196. *Megistostigma*
- 3b. Pistillate sepals toothed; anther connective not enlarged or caudate; stamens connate at base; styles connate, column globose; inflorescence terminal and leaf-opposed; leaves subglabrous 197. *Sphaerostylis*
- 2b. Pistillate sepals distinctly pinnatifid; pistillode present in staminate flower; leaves with stinging hairs 198. *Tragiella*
- 1b. Staminate sepals not adaxially inflexed; stamens 2 to many, anthers introrse or extrorse; styles usually slender.
- 5a. Anthers 3 or more, if 2 then not subsessile; staminate calyx concave; styles free to partly connate.
- 6a. Anther connective without tuft of stinging hairs; stamens (2)3-many; subshrubs, herbs, or twining vines, usually monoecious.
- 7a. Styles thick, papillose; staminal receptacle convex; stamens 4-18 199. *Platygyne*
- 7b. Styles slender, not papillose; staminal receptacle plane; stamens 2-8(-50) 200. *Tragia*
- 6b. Anther connective ending in tuft of stinging hairs; erect shrubs, leaves glabrescent, dioecious 201. *Acidoton*
- 5b. Anthers 2, subsessile; staminate calyx flat with lobes reflexed; styles connate into a thick column 202. *Pachystylidium*
- 195. *Cnesmone*** Blume, Bijdr. Fl. Ned. Ind. 630. 1826 (as *Cnesmosa*); Fl. Javae vi. 1828; Muell. Arg., DC. Prodr. 15(2): 926. 1866; Bentham, Gen. Pl. 3: 330. 1880; Hook. f., Fl. Brit. Ind. 5: 466. 1888; J. J. Smith, Med. Dept. Landbouw 10: 513. 1910; Pax & Hoffm., Pflanzenr. 147. IX (Heft 68): 102. 1919; Croizat, J. Arnold Arbor. 22: 427. 1941; Airy Shaw, Kew Bull. 26: 240. 1972; Balakrisnan &

Nair, Gardener's Bull. 31: 49. 1978. TYPE: *Cnesmone javanica* Bl.

Cnesmon Gagnep., Bull. Soc. Bot. France 71: 866. 1924; Fl. Gen. Indochine 5: 386. 1926. TYPE: *Cnesmon tonkinense* Gagnep. [= *Cnesmone tonkinense* (Gagnep.) Croizat; lectotype, designated by Wheeler, Taxon 24: 534. 1975].

This Asian genus of ca. ten species is here delimited following Croizat (1941).

196. *Megistostigma* Hooker f., Hook. Ic. Pl. 16: t. 1592. 1887; Fl. Brit. Ind. 5: 466. 1888; Merrill, Phil. J. Sci. 16C: 563. 1920; Croizat, J. Arnold Arbor. 22: 425. 1941; Airy Shaw, Kew Bull. 23: 119. 1969. TYPE: *Megistostigma malaccense* Hook. f.

Clavistylus J. J. Smith, Med. Dept. Landb. 10: 517. 1910. TYPE: *Clavistylus peltatus* J. J. Sm. [= *Megistostigma peltatum* (J. J. Sm.) Croizat].

A tropical southeast Asian genus of five species distributed from Burma to China, the Philippines, and Borneo; combined with *Sphaerostylis* by Pax & Hoffmann (1919) but maintained as distinct by Croizat (1941).

197. *Sphaerostylis* Baillon, Etude Gén. Euphorb. 466. 1858; Muell. Arg., DC. Prodr. 15(2): 768. 1866; Bentham, Gen. Pl. 3: 327. 1880; Baillon, Hist. Phys. Nat. Madag. 4(29): t. 196. 1891; Pax & Hoffm., Pflanzenr. 147. IX (Heft 68): 106. 1919; Croizat, J. Arnold Arbor. 22: 430. 1941. TYPE: *Sphaerostylis tulasneana* Baill.

A genus of two species endemic to Madagascar.

198. *Tragiella* Pax & Hoffmann, Pflanzenr. 147. IX (Heft 68): 104. 1919; Radcliffe-Smith, Kew Bull. 35: 777. 1981; Fl. E. Trop. Afr. Euphorb. 1: 318. 1987. TYPE: *Tragiella natalensis* (Sond.) Pax & Hoffm. [lectotype, chosen here].

An African genus of five species, extremely close to *Sphaerostylis* and doubtfully separable.

199. *Platygyne* Mercier, Bull. Bot. (Seringe) 1: 168. 1830; Muell. Arg., DC. Prodr. 15(2): 913. 1866 (as *Platygyne*); Bentham, Gen. Pl. 3: 328. 1880; Pax & Hoffm., Pflanzenr. 147. IX (Heft 68): 26. 1919; Alain, Fl. Cuba 3: 100. 1953; Mem. New York Bot. Gard. 21: 132. 1971; Borhidi, Ann. Hist.-Nat. Mus. Nat. Hung. 64: 89. 1972. TYPE: *Platygyne urens* Merc. [= *Platygyne hexandra* (Jacq.) Muell. Arg.].

Acanthocaulon Klotzsch ex Endl., Gen. Pl. Suppl. 4(3): 88. 1850. TYPE: *Acanthocaulon pruriens* Kl. ex Endl. [= *Platygyne hexandra* (Jacq.) Muell. Arg.].

In the most recent revision of Borhidi (1972), *Platygyne* is a genus of seven species endemic to Cuba. Alain (1971) reduced *Platygyne* to a synonym of *Tragia*, a disposition that merits further study.

200. *Tragia* Plumier ex L., Sp. Pl. 980. 1753; Gen. Pl. ed. 5, 421. 1754; Muell. Arg., DC. Prodr. 15(2): 927. 1866; Bentham, Gen. Pl. 3: 329. 1880; Prain, Fl. Trop. Afr. 6(1): 964. 1913; Pax & Hoffm., Pflanzenz. 147. IX (Heft 68): 32. 1919; Prain, Fl. Capensis 5(2): 502. 1920; Lourteig & O'Donnell, Lilloa 6: 347. 1941; Johnston, Rhodora 64: 137. 1962; Miller & Webster, Rhodora 69: 241. 1967; Webster, J. Arnold Arbor. 48: 376. 1967; Leandri, Adansonia II. 11: 437. 1971; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 291. 1987; Webster & Huft, Ann. Missouri Bot. Gard. 75: 1106. 1989. TYPE: *Tragia volubilis* L. [lectotype, designated by Small, in Britton & Brown, Ill. Fl. N. U.S., ed. 2, 2: 458. 1913].

Bia Klotzsch, Arch. Naturgesch. 7(1): 189. 1841. TYPE: *Bia alienata* Didr. [= *Tragia alienata* (Didr.) Múlg. & M. Gutiérrez, Candollea 46: 523. 1991; this name unfortunately must replace *Tragia sellowiana* Muell. Arg., 1866; lectotype].

Leptorhachis Klotzsch, Arch. Naturgesch. 7(1): 189. 1841. TYPE: *Leptorhachis hastata* Kl. [= *Tragia hastata* (Kl.) Muell. Arg.].

Leucandra Klotzsch, Arch. Naturgesch. 7(1): 188. 1841. TYPE: *Leucandra betonicaefolia* Kl. [= *Tragia leucandra* Pax & Hoffm.].

Ctenomeria Harvey, Hook. London J. Bot. 1: 29. 1842. TYPE: *Ctenomeria cordata* Harv. [= *Tragia capensis* Thunb.].

Lassia Baillon, Etude Gén. Euphorb. 464. 1858. TYPE: *Lassia scandens* Baill. [= *Tragia scandens* (Baill.) Muell. Arg.].

Zuckertia Baillon, Etude Gén. Euphorb. 495. 1858. TYPE: *Zuckertia cordata* Baill. [= *Tragia bailloniana* Muell. Arg.].

A large and diverse genus of ca. 125 species, mainly in Africa and America. The genus is palynologically heterogeneous, and some taxa such as *Zuckertia* may prove to merit segregation on further study.

201. *Acidoton* Swartz, Prodr. 6, 83. 1788 (nom. cons.); Fl. Ind. Occ. 2: 952, t. 18. 1800; Muell. Arg., DC. Prodr. 15(2): 914. 1866; Bentham, Gen. Pl. 3: 328. 1880; Urban, Symb. Ant. 7: 513. 1913; Pax & Hoffm.,

Pflanzenz. 147. IX (Heft 68): 24. 1919; Fawc. & Rend., Fl. Jam. 4: 303. 1920; Webster, Ann. Missouri Bot. Gard. 54: 191. 1967; 54: 289. 1968; Liogier, Fl. Española 4: 71. 1986. TYPE: *Acidoton urens* Sw.

Gitara Pax & Hoffm., Pflanzenz. 147. XVII (Heft 85): 187. 1924. TYPE: *Gitara venezolana* Pax & Hoffm. [= *Acidoton nicaraguensis* (Hemsl.) Webster].

A neotropical genus of six or seven species, in the Greater Antilles (Jamaica and Hispaniola), southern Central America, and northern South America.

202. *Pachystylidium* Pax & Hoffmann, Pflanzenz. 147. IX (Heft 68): 108. 1919; Backer & Bakh., Fl. Java 1: 491. 1963; Airy Shaw, Kew Bull. 23: 115. 1969. TYPE: *Pachystylidium hirsutum* (Bl.) Pax & Hoffm. [*Tragia hirsuta* Bl.].

A monotypic genus of tropical Asia (India to Indochina, Java, and the Philippines; not reported from Sumatra or Borneo).

Subtribe 31c. DALECHAMPIINAE (Muell. Arg.) Webster, stat. nov. Tribe Dalechampiae Muell. Arg., Bot. Zeit. 22: 324. 1864; DC. Prodr. 15(2): 1232. 1866. TYPE: *Dalechampia* Plum. ex L.

Monoecious undershrubs or more often clambering or twining; indumentum of simple and stinging hairs (sometimes almost absent); leaves alternate, blades simple, lobed or partite, usually stipellate; stipules persistent; inflorescences pseudanthial, subtended by a pair of usually showy involucre bracts; pistillate flowers 3 per pseudanthium, in a basal cymule; staminate pleiochasium terminal, with mostly 8–12 flowers; staminate bractlets mostly resiniferous; stamens 8–100 or more, filaments connate; pollen grains prolate, 3-colporate, sexine with prominent raised reticulum; pistillode absent; pistillate sepals entire to pinatifid; ovary 3-locular; stylar column elongated, stigmatic surface extending down upper $\frac{1}{3}$ to $\frac{3}{4}$; fruit capsular.

This subtribe contains only the single genus *Dalechampia*. Although it has been treated at tribal rank by almost all workers since Mueller (1866), *Dalechampia* has links to both the Tragiinae (stinging hairs) and Plukenetiinae (elongate stylar column).

203. *Dalechampia* Plumier ex L., Sp. Pl. 1054. 1753; Gen. Pl. ed. 5, 473. 1754; Muell. Arg.,

DC. Prodr. 15(2): 1232. 1866; Fl. Bras. 11(2): 633. 1874; Bentham, Gen. Pl. 3: 330. 1880; Pax & Hoffm., Pflanzenr. 147. XII (Heft 68): 3. 1919; Léonard, Fl. Congo Rwanda-Burundi 8(1): 194. 1962; Jablonski, Mem. New York Bot. Gard. 17: 145. 1967; Webster, Ann. Missouri Bot. Gard. 54: 308. 1968; Webster & Armbruster, Brittonia 31: 352. 1979; Syst. Bot. 7: 484. 1982; Armbruster, Syst. Bot. 9: 272. 1984; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 285. 1987; Armbruster, Syst. Bot. 13: 303. 1988; Webster, Ann. Missouri Bot. Gard. 75: 1108. 1988; Armbruster, Brittonia 41: 44. 1989; Webster, Brittonia 41: 1. 1989; Webster & Armbruster, Bot. J. Linn. Soc. 105: 137. 1991. TYPE: *Dalechampia scandens* L.

Cremophyllum Scheidweiler, Bull. Acad. Roy. Sci. Brux. 9(1): 23. 1842. TYPE: *Cremophyllum spathulatum* Scheidw. [= *Dalechampia spathulata* (Scheidw.) Baillon].

Megalostylis Spencer Moore, J. Bot. 54: 208. 1916. TYPE: *Megalostylis poeppigii* Sp. Moore [= *Dalechampia micrantha* Poepp.].

A genus of slightly over 100 species, about 90 of which are American, with a few in Africa, Madagascar, and India, and a single species reaching southern China and Java. The genus is diverse, and Webster & Armbruster (1991) have recognized 6 sections for the 90-odd neotropical species.

Tribe 32. OMPHALEAE (Pax & Hoffmann) Webster, Taxon 24: 598. 1975. Hippomaneae subtribe Omphaleinae Pax & Hoffm., Pflanzenr. 147. IV (Heft 52): 14. 1912. TYPE: *Omphalea* L.

Monoecious trees, shrubs, or lianas; stems with reddish latex; indumentum simple; leaves alternate, simple or lobed, pinnately or palmately veined, usually with 2 sessile basal glands; stipules deciduous. Inflorescences terminal or axillary, paniculate, bracts \pm foliose and biglandular; flowers apetalous. Staminate sepals 4 or 5, decussate or imbricate; disk annular or lobed, often massive; stamens 2 or 3, filaments connate, anther connectives free or fused; pollen grains oblate, 3-colporate, sexine finely punctate-spinulose; pistillode absent. Pistillate sepals 4 or 5, imbricate; disk tenuous or obsolete; ovary 3-locular; styles connate into a stout column, stigmas undivided. Fruit thick-walled, capsular or indehiscent; seeds large, globose, ecarunculate, testa dry; endosperm copious.

This tribe contains the single genus *Omphalea*,

whose affinities have been controversial for many years. Early workers, such as A. Jussieu (1824) and Baillon (1858), associated it with the Hippomaneae. Mueller (1866) kept it in the tribe Hippomaneae, in subtribe Gelonieae. Pax & Hoffmann (1912) created a special subtribe of Hippomaneae for *Omphalea*, but later (1931) abandoned their subtribe and inserted the genus in the Gelonieae. Croizat (1942), in contrast, pointed out affinities with the tribe Plukenetieae, and Punt (1962) noted that pollen morphology supports Croizat's opinion.

Although *Omphalea* shows striking resemblances to the Plukenetieae in a number of characters, it also approaches the tribe Stomatocalyceae, and thus provides a link between subfamilies Acalyphoideae and Euphorbioideae. Clarification of its affinities appears to be critical in establishing the phylogeny of the uniovulate Euphorbiaceae.

204. *Omphalea* L., Syst. Nat. ed. 10, 1264. 1759 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 1134. 1866; Bentham, Gen. Pl. 3: 332. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 14. 1912; Fawc. & Rend., Fl. Jam. 4: 319. 1920; Croizat, Bull. Jard. Bot. Buit. III. 17: 204. 1941; Alain, Fl. Cuba 3: 109. 1953; Webster, Ann. Missouri Bot. Gard. 54: 295. 1968; Airy Shaw, Kew Bull. 23: 130. 1969; Alain, Mem. New York Bot. Gard. 21(2): 124. 1971; Airy Shaw, Kew Bull. Add. Ser. 8: 177. 1980; Liogier, Fl. Española 4: 178. 1986; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 371. 1987; Gillespie, Rev. Phyl. Anal. *Omphalea* 144 (dissert.). 1988. *Omphalandra* P. Browne, Civ. Nat. Hist. Jamaica 334. 1756 (nom. rej.). *Duchola* Adanson, Fam. Pl. 2: 357. 1763 (nom. superfl.). TYPE: *Omphalea triandra* L. (typ. cons.).

Ronnowia Buchoz, Pl. Nouv. Decouv. 6, t. 4. 1779. TYPE: *Ronnowia domingensis* Buchoz (nom. illeg.) [= *Omphalea triandra* L.].

Hecatea Thouars, Hist. Pl. Iles Afrique Austr. 27, t. 5. 1804. TYPE: *Hecatea oppositifolia* Willd. [= *Omphalea oppositifolia* (Willd.) Gillespie; lectotype, designated by Gillespie].

Hebecocca Beurling, Kongl. Vetensk. Akad. Handl. 1854: 146. 1856. TYPE: *Hebecocca panamensis* Beurl. [= *Omphalea diandra* L.].

Neomphalea Pax & Hoffm., Pflanzenr. 147. XIV (Heft 68): 54. 1919. TYPE: *Neomphalea papuana* (Pax & Hoffm.) Pax & Hoffm. [= *Omphalea papuana* Pax & Hoffm.].

A genus of ca. 15 species in both the Old World and New World, but with the greatest species concentrations in the Greater Antilles and Madagascar.

Subfamily IV. CROTONOIDEAE Pax, Bot.

Jahrb. 5: 413. 1884; Natürl. Pflanzenfam. ed. 1, 3(5): 14. 1890. TYPE: *Croton* L.

Trees, shrubs, or herbs; latex colored or absent; indumentum simple, stellate, or lepidote; leaves alternate, opposite, or rarely whorled, stipulate or exstipulate; blade simple or palmately lobed or compound, often with foliar glands. Inflorescences axillary or terminal, dichasial to racemose or spicate. Staminate flower: sepals imbricate or valvate; petals and disk present or absent; stamens (3–)5–many, filaments free or connate; pollen grains binucleate or trinucleate, tricolporate to more commonly porate or inaperturate, sexine mostly with ornamentation of knobs in hexagonal pattern; pistillode present or absent. Pistillate flower: sepals (2)3–6, imbricate or valvate, often connate; petals and disk present or absent; ovary mostly 2–4-locular; styles bifid to multifid (rarely entire); ovules solitary in each locule, anatropous. Fruit capsular (rarely indehiscent); seeds carunculate or ecarunculate, testa sometimes fleshy; endosperm usually copious, often oily.

As defined here, following Webster (1975), subfamily Crotonoideae includes 12 tribes. This is a

much narrower circumscription than that of Pax (1890), which took in nearly all of the uniovulate taxa of Euphorbiaceae. It is considerably broader than the subfamily Crotonoideae of Hurusawa (1954), which included only the tribe Crotoneae.

In the classic system of Mueller (1866), genera of the presently accepted Crotonoideae were dispersed between tribes Crotoneae, Acalyphaeae, and Hippomaneae. Bentham (1880) placed many of the Crotonoideae in the first two subtribes of his tribe Crotoneae, but in other subtribes had a mixture of Acalyphoideae and Crotonoideae. Hutchinson (1969) placed many Crotonoideae in his tribes 13–20, 38, and 39; but 5 of those tribes also included genera of either Acalyphoideae or Euphorbioideae.

As predicted by Erdtman (1952), pollen morphology has provided decisive evidence in establishing lines of phylogenetic affinity within the Crotonoideae. Punt (1962), following Erdtman's lead, grouped most of the genera of Crotonoideae under his "*Croton* configuration." However, "crotonoid" pollen is useful mainly for establishing membership in the subfamily, and except in the more primitive tribes does not help to clarify problems of tribal delimitation.

KEY TO THE TRIBES OF SUBFAMILY CROTONOIDEAE

- 1a. Pollen grains colporate or porate, sexine reticulate to clavate; petals absent; indumentum mostly simple.
 - 2a. Laticifers articulated; pollen grains 3-nucleate; plants mostly monoecious; basic chromosome number $x = 9$.
 - 3a. Pollen grains colporate; styles bifid; seeds carunculate or ecarunculate; endosperm oily 33. MICRANDREAE
 - 3b. Pollen grains periporate; styles mostly multifid; seeds carunculate; endosperm starchy 34. MANIHOTEAE
 - 2b. Laticifers nonarticulated; pollen grains 2-nucleate; plants mostly dioecious; basic chromosome number $x = 11$.
 - 4a. Pollen grains colporate; leaves non-pellucid-punctate, stipules free; inflorescences axillary, mostly spicate or paniculate 35. ADENOCLINEAE
 - 4b. Pollen grains periporate; leaves pellucid-punctate, stipules connate; flowers in clusters opposite the leaves 36. GELONIEAE
- 1b. Pollen grains inaperturate, sexine with "crotonoid" pattern; petals usually present; indumentum simple, malpighiaceus, or stellate; laticifers nonarticulate (except in some Jatropheae).
 - 5a. Seeds without endosperm, cotyledons massive; inflorescences dichasial; petals absent; styles undivided, dilated; latex milky 37. ELATERIOSPERMEAE
 - 5b. Seeds with copious endosperm, cotyledons thin; petals present at least in staminate flowers (except in Neoboutoniae); inflorescences various; styles bifid to multifid, less commonly unlobed.
 - 6a. Staminate sepals imbricate, free or if connate then not completely covering petals in the bud; seeds carunculate or ecarunculate.
 - 7a. Indumentum simple.
 - 8a. Stamens mostly more than 5, free or connate; pollen sexine coarsely clavate.
 - 9a. Inflorescences terminal, mostly dichasial; leaves mostly palmately lobed or compound; fruits capsular or drupaceous, seeds carunculate or ecarunculate 38. JATROPHEAE
 - 9b. Inflorescences terminal or axillary, racemose or spicate to paniculate; leaves unlobed, usually without basal glands; fruit capsular 39. CODIAEAE
 - 8b. Stamens 3–5, filaments connate; pollen sexine finely clavate; monoecious; inflorescences terminal or axillary, racemose or thyrsoïd; seeds ecarunculate 40. TRIGONOSTEMONEAE

7b. Indumentum (at least in part) of stellate or lepidote hairs.

- 10a. Fruit capsular, seeds ecarunculate; petals free or absent.
 11a. Pollen sexine with spinose or reduced processes; leaves exstipulate; filaments often connate, at least in part; cotyledons broad or narrow 41. RICINOCARPEAE
 11b. Pollen sexinose, processes not spinose or reduced; leaves usually stipulate; filaments free; cotyledons broad 42. CROTONEAE
 10b. Fruit drupaceous, seeds ecarunculate; petals \pm coherent 43. RICINODENDREAE
 6b. Staminate sepals fused in the bud, splitting valvately or irregularly into segments; fruit capsular or drupaceous; seeds ecarunculate 44. ALEURITIDEAE

Tribe 33. MICRANDREAE (Muell. Arg.) Webster, Taxon 24: 598. 1975. Crotonae subtribe Micrandreae Muell. Arg., DC. Prodr. 15(2): 709. 1866. Gelonieae subtribe Chaetocarpinae series Micrandriformes Pax & Hoffm., Pflanzenr. 147. XIV (Heft 68): 49. 1919. TYPE: *Micrandra* Benth.

Monoecious or dioecious trees; stems with articulate laticifers and usually whitish latex; indumentum simple or stellate; leaves alternate, unlobed, entire, pinnately veined or triplinerved, with laminar glands at apex of petiole; stipules often caducous. Inflorescences terminal or axillary, dichasial-paniculate, bracts small or large; flowers apetalous. Staminate sepals 5, imbricate, free or connate; disk dissected, lobed, or absent; stamens 5–10, free or connate; pollen grains 3-nucleate, 3-colporate, colpi operculate, sexine reticulate; pistillode present or absent. Pistillate sepals 5, imbricate, free, deciduous in fruit; disk 5-lobed; ovary 3-locular; styles free, bifid. Fruit capsular; columella persistent; seeds large, carunculate or ecarunculate, endosperm oily.

As treated by Webster (1975), the tribe includes three or four genera distributed into two subtribes. The Micrandreae clearly form a link between subfamilies Acalyphoideae and Crotonoideae.

KEY TO THE SUBTRIBES OF TRIBE MICRANDREAE

- 1a. Leaves simple; stamens free, sometimes inflexed in bud; sepals discrete, imbricate or valvate 33a. Micrandrinae
 1b. Leaves palmately compound; stamens connate; sepals connate, valvate 33b. Heveinae

Subtribe 33a. MICRANDRINAE Muell. Arg., DC. Prodr. 15(2): 709. 1866. TYPE: *Micrandra* Benth.

Leaves simple, unlobed. Panicles with bracts conspicuous or inconspicuous. Staminate sepals imbricate, free or nearly so; disk dissected; stamens 5–7, filaments free, \pm inflexed in bud; pistillode present; pistillate disk annular.

A subtribe of three South American genera.

KEY TO THE GENERA OF SUBTRIBE MICRANDRINAE

- 1a. Sepals free; staminate disk present; stamens 5–8; floral bracts small.
 2a. Anthers elliptical; indumentum simple 205. *Micrandra*
 2b. Anthers linear; indumentum stellate 206. *Micrandropsis*
 1b. Sepals connate; staminate disk absent; stamens 8–10; floral bracts large 207. *Cunuria*

205. *Micrandra* Bentham, Hook. Kew J. Bot. 6: 371. 1854 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 709. 1866; Fl. Bras. 11(2): 289. 1873; Bentham, Gen. Pl. 3: 289. 1880; Pax, Pflanzenr. 147. I (Heft 42): 18. 1910; Schultes, Bot. Mus. Leaf. 15: 201. 1952. TYPE: *Micrandra siphonioides* Benth. (typ. cons.).

Pogonophyllum Didr., Vidensk. Medd. Dansk Naturh. Foren. Kjøbenhavn 1857: 144. 1857. TYPE: *Pogonophyllum elatum* Didr. [= *Micrandra elata* (Dir.) Muell. Arg.].

A poorly understood genus of about seven Amazonian species.

206. *Micrandropsis* Rodrigues, Acta Amazonica 3(2): 5. 1973. TYPE: *Micrandropsis scleroxylon* (W. Rodr.) W. Rodr.

A monotypic genus of Amazonian Brazil.

207. *Cunuria* Baillon, Adansonia I. 4: 287. Aug. 1864; Muell. Arg., DC. Prodr. 15(2): 1123. 1866; Bentham, Gen. Pl. 3: 289. 1880; Pax, Pflanzenr. 147. I (Heft 42): 16. 1910; Baldwin & Schultes, Bot. Mus. Leaf. Harvard Univ. 12: 325. 1947. TYPE: *Cunuria spruceana* Baillon.

Clusiophyllum Muell. Arg., Flora 47: 518. 25 Oct. 1864. TYPE: *Clusiophyllum sprucei* Muell. Arg. [= *Cunuria crassipes* Muell. Arg.].

Baldwin & Schultes (1947) recognized five species of *Cunuria*, all from Amazonian South America. Schultes (1952) on reconsideration reduced *Cunuria* to a synonym of *Micrandra*, and because of his intimate knowledge of these South American

trees his opinion must be weighted heavily. The listing of *Cunuria* as a separate genus is done here mainly to call attention to the problem, not to affirm its generic distinctness.

Subtribe 33b. HEVEINAE Muell. Arg., *Linnaea* 34: 202. 1865; DC. *Prodr.* 15(2): 716. 1866. TYPE: *Hevea* Aubl.

Leaves palmately compound. Panicles with inconspicuous bracts. Staminate sepals connate into a cup, lobes valvate; disk lobed or dissected; stamens 5–10, filaments connate into a column, anthers sessile; pistillode present; pistillate disk dissected or obsolete; seeds ecarunculate.

As originally delimited by Mueller (1865, 1866), subtribe Heveinae is here interpreted to include the single genus *Hevea*. Pax (1910) placed *Hevea* in subtribe Jatrophinae, a disposition that is contradicted by pollen morphology, chromosome number, and other characters.

208. *Hevea* Aublet, *Hist. Pl. Guiane Fr.* 2: 871, t. 335. 1775; Muell. Arg., DC. *Prodr.* 15(2): 716. 1866; *Fl. Brasil.* 11(2): 297. 1874; Pax, *Pflanzenr.* 147. I. (Heft 42): 117. 1910; Ducke, *Arch. Inst. Biol. Veg. Rio Janeiro* 2: 217. 1935; Schultes, *Bot. Mus. Leaflet. Harvard Univ.* 12: 1. 1945; 13: 1. 1947; 14: 79. 1950; 15: 111, 247, 255. 1952; 16: 21. 1953; 25: 243. 1977; *Bot. Review* 36: 197. 1970; *Econ. Bot.* 41: 125. 1987; *Malaysian Rubber Res. Dev. Board Mon.* 14: 5. 1990. TYPE: *Hevea guianensis* Aubl.

Siphonia L. C. Richard, in Schreber, *Gen. Pl.* 2: 656. 1791. TYPE: *Siphonia elastica* Pers. [= *Hevea guianensis* Aubl.; lectotype].

Caoutchoua J. F. Gmelin, *Syst. Nat.* 2: 677. 1791. TYPE: *Caoutchoua elastica* Gmel. [= *Hevea guianensis* Aubl.].

According to Schultes (1990), *Hevea* includes ten species with several varieties, all found within Amazonian South America. Because of the economic importance of the genus, there is extensive literature on its systematics; references may be found in Schultes (1970, 1990).

Tribe 34. MANIHOTEAE (Muell. Arg.) Pax, *Natürl. Pflanzenfam.* ed. 1, 3(5): 77. 1890. Hippomaneae subtribe Manihoteae Muell. Arg., DC. *Prodr.* 15(2): 1056. 1866. TYPE: *Manihot* Miller.

Monoecious (rarely dioecious) trees, shrubs, or herbs; laticifers articulated, latex white; indumen-

tum simple (stinging hairs sometimes present); leaves alternate, mostly palmately lobed or dissected; petioles glandular or stipellate at apex; stipules usually present. Inflorescences terminal or pseudoaxillary, most racemose-paniculate or dichasial-paniculate, usually bisexual; flowers apetalous. Staminate flower: calyx synsepalous, sepals 5, imbricate, \pm petaloid; disk intrastaminal or extrastaminal; stamens 8–10(–25), filaments free or connate; pollen grains globose, 3-nucleate, periporate, sexine with Croton-pattern; pistillode present or absent. Pistillate flower: sepals 5, free or connate, sometimes deciduous; disk annular, sometimes with staminodia; ovary 3-locular (rarely 5-locular); styles free, mostly multifid or lacerate (rarely bifid). Fruit capsular; columella often persistent; seeds carunculate, testa dry.

As delimited here, tribe Manihoteae includes two genera, both confined to the New World. The close affinity between *Manihot* and *Cnidocolus* was independently confirmed on palynological grounds by Punt (1962) and Miller & Webster (1962).

KEY TO THE GENERA OF TRIBE MANIHOTEAE

- 1a. Stinging hairs absent; stamens free, staminate disk intrastaminal; staminate perianth usually yellowish or greenish; leaf blades stipellate (not glandular) at base; inflorescence racemose or racemose-paniculate 209. *Manihot*
- 1b. Stinging hairs present; stamens connate (very rarely free); staminate disk extrastaminal, annular; staminate perianth whitish; leaf blades glandular (not stipellate) at base; inflorescence dichasial-paniculate 210. *Cnidocolus*

209. *Manihot* Miller, *Gard. Dict.* ed. 4. 1754; Pohl, *Pl. Bras. Ic.* 1: 17. 1827; Muell. Arg., DC. *Prodr.* 15(2): 1057. 1866; Bentham, *Gen. Pl.* 3: 306. 1880; Pax, *Pflanzenr.* 147. II (Heft 44): 21. 1910; Croizat, *J. Arnold Arbor.* 23: 216. 1942; Rogers & Appan, *Fl. Neotrop.* 13: 1. 1973; Rogers & Fleming, *Econ. Bot.* 27: 1. 1973; Allem, *Rev. Brasil. Biol.* 49: 1–26. 1989. *Mandioca* Link, *Handb.* 2: 436. 1831. TYPE: *Manihot esculenta* Crantz [*Jatropha manihot* L.].

Janipha HBK, *Nov. Gen. Sp.* 2: 106, t. 109. 1817. TYPE: *Janipha aesculifolia* HBK [= *Manihot aesculifolia* (HBK) Pohl].

Manihotoides Rogers & Appan, *Fl. Neotrop.* 13: 247. 1973. TYPE: *Manihotoides pauciflora* (Bdge.) Rogers & Appan [= *Manihot pauciflora* Bdge.].

A neotropical genus of ca. 60 species, mostly native to Brazil. Rogers & Appan (1973) created a new genus, *Manihotoides*, for an aberrant spe-

cies in Mexico characterized by reduced inflorescences, and trifoliolate leaves clustered on short shoots. However, the recent discovery of another Mexican species (ined.) with unlobed leaves on short shoots largely erases the supposed distinction.

210. *Cnidocolus* Pohl, Pl. Bras. 1: 56. 1827; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 1964. 1931; Lourteig & O'Donell, Lilloa 9: 105. 1943; McVaugh, Bull. Torrey Bot. Club 71: 457. 1944; Lundell, Bull. Torrey Bot. Club 72: 319. 1945; Webster, J. Arnold Arbor. 48: 349. 1967; Breckon, Brittonia 31: 125. 1979. TYPE: *Cnidocolus hamosus* Pohl [lectotype, designated by Small, in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 462. 1913].

Jussiaea Houstoun, Reliq. Houst. 6. 1781 (non *Jussiaea* L., 1753). TYPE: *Jatropha herbacea* L. [= *Cnidocolus herbaceus* (L.) I. M. Johnston].

Bivonea Raf., Specchio 1: 156. 1814 (nom. rej.). TYPE: *Bivonea stimulosus* (Michx.) Raf. [= *Cnidocolus stimulosus* (Michx.) Engelm. & Gray].

Victorinia León, Mem. Soc. Cub. Hist. Nat. Felipe Poey 15: 242. 1941. TYPE: *Victorinia regina* (León) León [*Jatropha regina* León; = *Cnidocolus regina* (León) McVaugh].

A neotropical genus of ca. 50 species, with the greatest concentration in Mexico. The genus was reviewed by McVaugh (1944), and his reduction of *Victorinia* to synonymy appears justified.

Tribe 35. ADENOCLINEAE (Muell. Arg.) Webster, Taxon 24: 598. 1975. Hippomaneae subtribe Adenoclineae Muell. Arg., Linnaea 34: 203. 1865; DC. Prodr. 15(2): 1139. 1866. TYPE: *Adenocline* Turcz.

Monoecious or dioecious trees, shrubs, or herbs; latex clear (\pm colored); indumentum simple, malpighiaceus, or stellate; leaves alternate (rarely opposite), simple, penninerved or triplinerved, with or without laminar or petiolar glands; stipules persistent or deciduous. Inflorescences terminal, axillary, or opposite the leaves, spicate to paniculate or glomerular; flowers apetalous. Staminate sepals 3–5, imbricate, free or connate; disk dissected or absent; stamens 3–30, filaments free or connate; pollen grains 2-nucleate, 3-colporate, colpi operculate or inoperculate, sexine with Croton-pattern; pistillode present or absent. Pistillate sepals 3–5, imbricate, free or connate; disk dissected or annular, sometimes staminodial; ovary 2–6-locular; styles bifid or stigmatiform. Fruit capsular or drupaceous; seeds ecarunculate, seed-coat dry or fleshy; endosperm present.

Most of the genera of this tribe were referred to the Gelonieae by Pax & Hoffmann (1931), but were scattered in different subtribes and associated with genera belonging to three different subfamilies. Following the arrangement of Webster (1975), the six genera are grouped into two subtribes.

KEY TO THE SUBTRIBES OF TRIBE ADENOCLINEAE

- 1a. Indumentum simple; stamens free; fruit dehiscent or indehiscent, 2–3-locular 35a. Adenoclineae
1b. Indumentum stellate; stamens connate; fruit baccate, 1–7-locular 35. Endosperminae

Subtribe 35a. ADENOCLININAE Muell. Arg., Linnaea 34: 203. 1865; DC. Prodr. 15(2): 1139. 1866. TYPE: *Adenocline* Turcz.

Gelonieae subtribe Tetrorchidiinae Pax, Pflanzenz. 147. IV (Heft 52): 29. 1912. TYPE: *Tetrorchidium* Poepp.

Trees, shrubs, or herbs; indumentum simple or malpighiaceus; inflorescence diverse; stamens 3–30, free; ovary 2- or 3-locular; stigmas distinct; fruit capsular or drupaceous.

This subtribe includes 5 genera with ca. 30 species of the Neotropics and Africa.

KEY TO THE GENERA OF SUBTRIBE ADENOCLININAE

- 1a. Pistillate disk present, at least as staminodia.
2a. Stamens 25–30; fruits drupaceous; ovary 2-locular; leaves entire, with laminar glands 211. *Glycydendron*
2b. Stamens less than 20; fruits capsular; ovary 2–3-locular; leaves \pm dentate, with or without laminar glands.
3a. Trees or shrubs; seed-coat fleshy; staminate disk not of interstaminal processes.
4a. Stamens 8–10; anthers 2-locular, not peltate; staminate disk present; leaves eglandular, stipules caducous; indumentum simple; endotesta smooth 212. *Klaineanthus*
4b. Stamens 3; anthers 4-locular, peltate; staminate disk absent; leaves usually with laminar glands, stipules persistent; indumentum malpighiaceus (at least in part); endotesta foveolate or echinulate 213. *Tetrorchidium*
3b. Herbs; seed-coat dry; staminate disk of interstaminal processes 214. *Adenocline*
1b. Pistillate disk absent; leaves glandular-dentate, without laminar glands 215. *Ditta*

211. *Glycydendron* Ducke, Arq. Jard. Bot. Rio Janeiro 3: 199. 1922; 4: 107, pl. 10 figs. a–

i. 1925. TYPE: *Glycydendron amazonicum* Ducke.

A monotypic genus of Amazonian Brazil. Pax & Hoffmann (1931) mistakenly reduced it to a synonym of *Nealchornea* because they misread the plate (Ducke, 1925), which contains both genera.

212. Klaineanthus Pierre ex Prain, Kew Bull. 1912: 105; Fl. Trop. Afr. 6(1): 963. 1913; Hook. Ic. Pl. 30: t. 2985. 1913; Pax & Hoffm., Pflanzenz. 147. VII (Heft 63): 408. 1914; Léonard, Fl. Congo 8(1): 130. 1962. TYPE: *Klaineanthus gaboniae* Pierre ex Prain.

A monotypic genus of West Africa (Nigeria to Gabon).

213. Tetrochidium Poeppig in Poeppig & Endlicher, Nov. Gen. Sp. 3: 23, t. 227. 1842; Muell. Arg., DC. Prodr. 15(2): 1132. 1866; Bentham, Gen. Pl. 3: 288. 1880; Pax & Hoffm., Pflanzenz. 147. IV (Heft 52): 1912; Natürl. Pflanzenfam. ed. 2, 19c: 184. 1931; Cuatrecasas, Brittonia 9: 76. 1957; Léonard, Fl. Congo 8(1): 133. 1962; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 373. 1987; Huft, Ann. Missouri Bot. Gard. 75: 1110. 1989. TYPE: *Tetrochidium rubrivenium* Poepp.

Hasskarlia Baillon, Adansonia I. 1: 51. 1860 (non Meisner, 1843). *Tetrochidiopsis* Rauschert, Taxon 31: 559. 1982. TYPE: *Hasskarlia didymostemon* Baill. [= *Tetrochidium didymostemon* (Baillon) Pax & Hoffm.].

A genus of ca. 20 species, mostly in tropical America but ca. 5 species in Africa. The African species were referred to a separate genus *Hasskarlia* by Pax & Hoffmann (1912), but they later (Pax & Hoffmann, 1931) reduced it to a section of *Tetrochidium*.

214. Adenocline Turczaninov, Bull. Soc. Imp. Nat. Moscou 16: 59. 1843; Muell. Arg., DC. Prodr. 15(2): 1139. 1866; Bentham, Gen. Pl. 3: 310. 1880; Prain, Ann. Bot. 27: 404. 1913; Pax & Hoffm., Pflanzenz. 147. VII (Heft 63): 409. 1914; Prain, Fl. Cap. 5(2): 488. 1920; Milne-Redhead, Kew Bull. 5: 349. 1951; Dyer, Gen. S. Afr. Fl. Pl. ed. 3, 1: 315. 1975. *Mercurialis* sect. *Adenocline* (Turcz.) Baillon, Adansonia I. 3: 159. 1864. TYPE: not designated [lectotypification not de-

sirable at this time due to confusion in Turczaninov's application of names to specimens].

Diplostylis Sonder, Linnaea 23: 113. 1850. TYPE: not designated.

Paradenocline Muell. Arg., DC. Prodr. 15(2): 1141. TYPE: *Paradenocline procumbens* Muell. Arg. [= *Adenocline violifolia* (Kunze) Prain].

As treated by Prain (1920), *Adenocline* includes eight species of the Cape region of South Africa.

215. Ditta Grisebach, Mem. Amer. Acad. Arts. Sci. II. 8: 160. 1861; Muell. Arg., DC. Prodr. 15(2): 1138. 1866; Pax & Hoffm., 147. V (Heft 52): 270. 1912; Urban, Symb. Ant. 7: 261. 1912; Alain, Fl. Cuba 3: 112. 1953; Borhidi et al., Acta Agron. Acad. Sci. Hungar. 27: 432. 1978; Liogier, Fl. Española 4: 135, 348. 1986; Descr. Fl. Puerto Rico 2: 383. 1988. TYPE: *Ditta myricoides* Griseb.

A genus of one or two species of the Greater Antilles (Cuba, Hispaniola, Puerto Rico).

Subtribe 35b. ENDOSPERMINAE Pax & Hoffmann, Pflanzenz. 147. XIV (Heft 68): 53. 1919 (nomen); Natürl. Pflanzenfam. ed. 2, 19c: 42. 1931 (in clavi). TYPE: *Endospermum* Bentham.

Diocious trees or shrubs, indumentum stellate; inflorescences axillary; staminate calyx gamophyllous; stamens 6–10, filaments connate; pistillode small or absent; ovary 2–6-locular; styles stigmatiform, confluent into a cap; fruit capsular.

The subtribe includes only the type genus *Endospermum*.

216. Endospermum Bentham, Fl. Hongkong. 304. 1861 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 1131. 1866; Bentham, Gen. Pl. 3: 322. 1880; Beccari, Malesia 2: 45, t. 2. 1884; Pax & Hoffmann, Pflanzenz. 147. IV (Heft 52): 33. 1912; Docters van Leeuwen, Treubia 10: 431, tt. 12, 13. 1919; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 184. 1931; Schodde, Blumea 15: 397. 1967; Schaeffer, Blumea 19: 171. 1971; Airy Shaw, Kew Bull. Add. Ser. 8: 78. 1980. TYPE: *Endospermum chinense* Benth.

Capellenia Teijsmann & Binnendijk, Natuurk. Tijdschr. Ned.-Ind. 29: 238. 1867. TYPE: *Capellenia moluccana* Teijsm. & Binn. [= *Endospermum moluccanum* (Teijsm. & Binn.) Kurz].

A paleotropical genus of ten species, occurring

from China to Malaya, New Guinea, and tropical Australia (Queensland).

Tribe 36. GELONIEAE (Muell. Arg.) Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 88. 1890. Hippomaneae subtribe Gelonieae Muell. Arg., Linnaea 34: 202. 1865; DC. Prodr. 15(2): 1124. 1866. TYPE: *Gelonium* Roxb. ex Willd. [= *Suregada* Roxb. ex Rottl.].

Dioecious (very rarely monoecious?) trees or shrubs; latex not evident; indument simple, usually very scant or absent; leaves alternate, simple, penninerved, lamina usually pellucid-punctate; stipules caducous. Inflorescences opposite the leaves; flowers apetalous, in glomerules. Staminate sepals usually 5 or 6, imbricate, free, sometimes glandular abaxially; disk extrastaminal or intrastaminal, annular or dissected; stamens (6-)10-25(-60), filaments free; anthers dehiscent longitudinally; pollen grains 2-nucleate, subglobose, 3-6-porate, exine with Croton-pattern; pistillode absent. Pistillate sepals mostly 5(4-8), imbricate, sometimes glandular abaxially; disk annular, sometimes with staminodes; ovary 3-(rarely 2- or 4-)locular; styles bifid (rarely multifid). Fruit capsular or sometimes indehiscent and drupaceous; seeds ecarunculate, seed-coat ± fleshy; endosperm present.

A monogeneric paleotropical tribe, as treated here. Pax & Hoffmann (1931), in their final treatment, construed Gelonieae as a large tribe with 18 genera in 7 subtribes; a considerable number of those genera are here included in the Adenoclineae.

217. Suregada Roxburgh ex Rottler, Ges. Naturf. Freunde Berlin, Neue Schriften 4: 206. 1803; Baillon, Etude Gén., Euphorb. 395. 1858; Croizat, Bull. Bot. Gard. Buitenzorg III. 17: 212. 1942; Merrill, J. Arnold Arbor. 37: 79. 1951; Léonard, Bull. Jard. Bot. Brux. 28: 443. 1958; Fl. Congo 8(1): 124. 1962; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 376. 1987. TYPE: *Suregada roxburghii* Rottler.

Gelonium Roxb. ex Willd., Sp. Pl. 4: 831. 1806 (non Gaertn., 1791). TYPE: *Gelonium lanceolatum* Willd. [= *Suregada lanceolata* (Willd.) Croiz.].

Erythrocarpus Blume, Bijdr. Fl. Jav. 604. 1825. TYPE: *Erythrocarpus glomerulatus* Bl. [= *Suregada glomerulata* (Bl.) Baillon; lectotype].

Ceratophorus Sonder, Linnaea 23: 120. 1850. TYPE: *Ceratophorus africanus* Sond. [= *Suregada africana* (Sond.) Croiz.].

A paleotropical genus of ca. 40 species, the majority in tropical Asia.

Tribe 37. ELATERIOSPERMEAE Webster, Taxon 24: 599. 1975. TYPE: *Elateriospermum* Blume.

Monoecious trees; stems with whitish latex; indumentum simple; leaves alternate, pinnately veined, entire, petiole biglandular at apex; stipules caducous. Inflorescences terminal or axillary, cymose, bisexual; flowers apetalous. Staminate sepals 5, free, imbricate; disk lobed, pubescent; stamens 10-18, filaments free; anthers apiculate; pollen grains globose, inaperturate, with Croton-pattern; pistillode rudimentary or absent. Pistillate sepals 5, imbricate, caducous; disk cupular, pubescent; ovary 2-4-locular; styles unlobed, stigmas dilated. Fruit capsular but exocarp fleshy; seeds ecarunculate endosperm scanty, cotyledons massive.

A monotypic tribe including only *Elateriospermum*. The genus was placed between *Suregada* and *Endospermum* by Mueller (1866), while Bentham (1880) and Pax (1910) positioned it with *Cunuria* and *Micrandra*. The inaperturate pollen grains contradict both these positions, however. Airy Shaw (1975) included it in his subtribe Jatrophiae along with *Aleurites*, *Annesijoa*, *Tapoides*, and *Loerzingia*. The genus appears to be a relict, without any close affinities, but perhaps it is a distant relative of *Micrandra* and *Manihot*.

218. Elateriospermum Blume, Bijdr. Fl. Jav. 620. 1826; Muell. Arg., DC. Prodr. 15(2): 1130. 1866; Bentham, Hook. Ic. Pl. 13: t. 1294. 1879; Gen. Pl. 3: 288. 1880; Pax, Pflanzenz. 147. I (Heft 42): 17. 1910; J. J. Smith, Med. Dept. Landb. 10: 571. 1910; Backer & Bakh. f., Fl. Java 1: 497. 1963; Whitmore, Tree Fl. Malaya 2: 91. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 108. 1975; Kew Bull. 36: 292. 1981. TYPE: *Elateriospermum tapos* Bl. [lectotype; the other species of Blume, *E. tokbrai*, was transferred to *Blumeodendron*].

A monotypic genus of tropical southeast Asia: Thailand to Java and Borneo.

Tribe 38. JATROPHEAE (Meisner) Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 72. 1890; Pflanzenz. 147. I (Heft 42): 1. 1910. Crotonaceae subtribe Jatrophae Meisn., Pl. Vasc. Gen. 1: 341. 1841. Jatrophae subtribe Jatrophiae Pax, Pflanzenz. 147. I (Heft 42): 21. 1910. TYPE: *Jatropha* L.

Joannesiae (Muell. Arg.) Pax, Bot. Jahrb. 59: 142. 1924. Acalyphae subtribe Joannesiae ('Johanneseae') Muell. Arg., Linnaea 34: 201. 1865. TYPE: *Joannesia* Vell.

Monoecious (less commonly dioecious) trees, shrubs, or herbs; stems with articulated and/or nonarticulated laticifers, latex clear, white, or reddish; indumentum simple, sometimes glandular; leaves unlobed or palmately lobed or parted, usually with glands at apex of petiole; stipules persistent or deciduous. Inflorescences terminal and sometimes axillary as well, dichasial-paniculate but sometimes reduced. Staminate sepals usually 5, distinct, imbricate; petals 5, free or sometimes coherent or connate; disk entire or dissected; stamens (6)8–30, filaments at least partly connate; pollen grains globose, binucleate, inaperturate, sexine with Croton-pattern; pistillode present or absent. Pistillate sepals 5(6), free, imbricate, \pm persistent in fruit; disk annular, lobed, or dissected, sometimes with staminodia; ovary mostly 2–3-locular; styles unlobed or bifid, sometimes dilated. Fruit capsular or drupaceous; seeds carunculate or ecarunculate, endosperm present.

As circumscribed here, tribe Jatropheae includes only two of the genera (*Jatropha* and *Joannesia*) assigned by Pax (1910). None of the genera enumerated for the Jatropheae by Hutchinson (1969) appear to belong in the same tribe with *Jatropha*. My previous circumscription (Webster, 1975) of the Joannesieae (a name mistakenly adopted for the Jatropheae) was broader than the present Jatropheae, since it included two genera, *Givotia* and *Ricinodendron*, that are now referred elsewhere. It might be possible to maintain two subtribes within the Jatropheae, based on *Jatropha* and *Joannesia* respectively; but *Deutzianthus* and *Oligoceras* are intermediate in many respects, and it now seems better not to recognize any subtribes within the Jatropheae.

KEY TO THE GENERA OF TRIBE JATROPHEAE

- 1a. Leaves simple (lobed or unlobed); monoecious or dioecious; staminate sepals free or connate; latex usually reddish.
- 2a. Styles bifid or unlobed; sepals distinct; monoecious (rarely dioecious).
- 3a. Fruit capsular; sepals not horned on back.
 - 4a. Seeds carunculate; leaves often lobed or dentate, without distinct paired glands at apex of petiole; stipules usually persistent, not infra-axillary 219. *Jatropha*
 - 4b. Seeds ecarunculate; leaves unlobed, entire, with paired glands at apex of petiole; stipules infra-axillary, caducous 220. *Vaupesia*
- 3b. Fruit drupaceous; sepals horned on back 221. *Oligoceras*
- 2b. Styles twice bifid; staminate sepals connate below; dioecious 222. *Deutzianthus*

- 1b. Leaves palmately compound; monoecious; seeds ecarunculate.
- 5a. Styles dilated, subentire to lacinate; ovary 2-locular; anthers apiculate; foliage with malpighiaceus hairs.
- 6a. Staminate calyx cupular, not covering the petals in bud; stamens 7–10, inner filaments connate; staminate disk dissected; fruit drupaceous. 223. *Joannesia*
- 6b. Staminate calyx fused in bud, completely covering the petals; stamens 18–33, inner filaments connate; staminate disk annular and intrastaminal; fruit unknown 224. *Leeuwenbergia*
- 5b. Styles slender, bifid; ovary 3-locular; anthers muticous; foliage glabrous; staminate calyx 5-lobed; stamens 15–25, inner filaments connate; staminate disk dissected; fruit capsular 225. *Annesijoa*

219. *Jatropha* L., Sp. Pl. 1006. 1753; Gen. Pl. ed. 5, 437. 1754; Muell. Arg., DC. Prodr. 15(2): 1076. 1866; Bentham, Gen. Pl. 3: 290. 1880; Pax, Pflanzenz. 147. I (Heft 42): 21. 1910; Hutchinson, Fl. Trop. Afr. 6(1): 775. 1912; Fawc. & Rend., Fl. Jam. 4: 310. 1920; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 160. 1931; McVaugh, Bull. Torrey Bot. Club 72: 271. 1944; Webster, J. Arnold Arbor. 48: 340. 1967; Dehgan & Webster, Univ. California Publ. Bot. 74: 1. 1979; Radcliffe-Smith, Fl. Trop. E. Afr., Euphorb. 1: 343. 1987. *Adenoropium* Pohl, Pl. Bras. Ic. Descr. 1: 12. 1827. TYPE: *Jatropha gossypifolia* L. [lectotype].

- Curcas* Adanson, Fam. Pl. 2: 356. 1763. TYPE: *Jatropha curcas* L.
- Castiglionia* Ruiz & Pavón, Fl. Peruv. 139. 1794. TYPE: *Castiglionia lobata* Ruiz & Pavón, nom. illeg. [= *Jatropha curcas* L.].
- Loureira* Cavanilles, Icon. Descr. Pl. 5: 17. 1799. TYPE: *Loureira glandulifera* Cav. [= *Jatropha cordata* (Ort.) Muell. Arg.].
- Mozinna* Ortega, Nov. Rar. Pl. Hort. Bot. Matr. 8: 104. 1798. TYPE: *Mozinna spathulata* Ort. [= *Jatropha dioica* Sesse].
- Zimapania* Engler & Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 119. 1891. TYPE: *Zimapania schiedeana* Engler & Pax [= *Jatropha dioica* Sesse].
- Collenucia* Chiovenda, Fl. Somalia 1: 177. 1929. TYPE: *Collenucia paradoxa* Chiov. [= *Jatropha paradoxa* (Chiov.) Chiov.].

A diverse genus of ca. 175 species of tropics and subtropics in the Old World and New World; native species absent from Australia and the Pacific islands. The assignment of species into subgenera and sections is given by Dehgan & Webster (1979).

220. *Vaupesia* Schultes, Bot. Mus. Leaflet. Harvard Univ. 17: 27. 1955. TYPE: *Vaupesia cataractarum* Schultes.

A monotypic genus of the Rio Negro region, Amazonian Colombia. *Vaupesia* is a remarkable genus with latex and foliage of tribe Micrandreae but inaperturate pollen very similar to that of *Jatropha*. It may therefore represent a connecting link between tribes Micrandreae and Jatropheae; Schultes (pers. comm.) regards it as better placed in the Micrandreae.

- 221. *Oligoceras*** Gagnepain, Bull. Soc. Bot. France 71: 872. 1925; Fl. Indochine 5: 467. 1926; Airy Shaw, Kew Bull. 14: 392. 1960. TYPE: *Oligoceras eberhardtii* Gagnep.

A monotypic genus of Indochina; closely related to *Deutzianthus* but distinguished by its monoecious flower production and curious horned sepals.

- 222. *Deutzianthus*** Gagnepain, Bull. Soc. Bot. France 71: 139. 1924; Fl. Indochine 5: 297. 1925; Wu, Acta Phytotax. Sin. 6: 245. 1957; Airy Shaw, Kew Bull. 14: 362. 1960; 16: 346. 1963. TYPE: *Deutzianthus tonkinensis* Gagnep.

Loerzingia Airy Shaw, Kew Bull. 16: 365. 1963; 25: 543. 1972; 36: 312. 1980, syn. nov. TYPE: *Loerzingia thyrsoiflora* Airy Shaw [= *Deutzianthus thyrsoiflorus* (Airy Shaw) Webster, comb. nov.].

A genus of two species, in Indochina and Sumatra. Airy Shaw compared his *Loerzingia* with *Tapoides* Airy Shaw from Borneo; however, the staminate calyx, with distinct imbricate lobes, suggests a closer affinity to tribe Jatropheae. Comparison of the illustrations of Gagnepain (1926) and Airy Shaw (1981) indicates that in fact the Sumatran *Loerzingia* is extremely similar to the Indochinese *Deutzianthus*, and their differences seem of specific rather than generic value.

- 223. *Joannesia*** Vellozo, Alogr. Alkalis 199. 1798; Muell. Arg., DC. Prodr. 15(2): 715. 1866; Bentham, Gen. Pl. 3: 290. 1880; Pax, Pflanzenr. 147. I (Heft 42): 116. 1910; Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 198. 1922; Schultes, Bot. Mus. Leaf. Harvard Univ. 17: 25. 1955; Smith et al., Fl. Illustr. Catar., EUFO 165. 1988. TYPE: *Joannesia princeps* Vell.

Anda A. Juss., Tent. Euphorb. 3. 1824. TYPE: *Anda gomesii* A. Juss., nom. illeg. [= *Joannesia princeps* Vell.].

Andicus Vellozo, Fl. Flum. 80, t. 86. 1825. TYPE: *Andicus pentaphyllus* Vell. [= *Joannesia princeps* Vell.].

A neotropical genus of two South American species.

- 224. *Leeuwenbergia*** Letouzey & Hallé, Adansonia II. 14: 379. 1974. TYPE: *Leeuwenbergia letestui* Letouzey & Hallé.

A tropical west African genus of two species in Cameroon, Congo, and Gabon. The genus is in many ways intermediate between *Joannesia* and *Annesijoa*, but the type species (*L. letestui*) differs strikingly from both in having a completely gamophyllous calyx that splits open on anthesis as in genera of Aleuritideae. Unfortunately, the staminate flowers of the second species, *Leeuwenbergia africana* Let. & Hallé, are still unknown.

- 225. *Annesijoa*** Pax & Hoffmann, Pflanzenr. 147. XIV (Heft 68): 9. 1919; Airy Shaw, Kew Bull. 16: 345. 1963; Hook. Ic. Pl. 38: t. 3713. 1974; Kew Bull. Add. Ser. 8: 27. 1980. TYPE: *Annesijoa novoguineensis* Pax & Hoffm.

A monotypic genus endemic to New Guinea.

- Tribe 39. CODIAEAE** (Pax) Hutchinson, Amer. J. Bot. 56: 747. 1969. Clutieae subtribe Codiaceinae Pax, Pflanzenr. 147. III (Heft 47): 10. 1911. TYPE: *Codiaeum* Rumph. ex A. Juss.

Monoecious or dioecious trees or shrubs; stems with nonarticulated laticifers, latex clear (sometimes reddish) and nontoxic; indumentum simple or stellate; leaves penninerved or triplinerved, unlobed, usually eglandular; stipules often caducous, sometimes obsolete. Inflorescences terminal or axillary, racemose or paniculate. Staminate sepals 4–6, free or connate, imbricate or valvate; petals mostly 5, free, usually imbricate; disk dissected or lobed; stamens (5–)10–100 or more, free or basally connate; pollen grains binucleate, globose, inaperturate, sexine with Croton-pattern; pistillode absent. Pistillate sepals 4, usually imbricate, sometimes accrescent; petals usually 5, sometimes absent; disk annular (rarely dissected or absent); ovary mostly 3-locular; styles unlobed to bipartite. Fruit capsular; columella usually persistent; seeds carunculate or ecarunculate, testa sometimes fleshy; endosperm present.

This tribe of 15 genera with over 100 species has the greatest generic diversity in the Crotonoideae, and relationships between the genera are not clear; it seems premature to attempt to recognize formal subtribes at this time.

KEY TO THE GENERA OF TRIBE CODIAEAE

- 1a. Petals present, at least in staminate flowers.
 2a. Petals present in pistillate flowers.
 3a. Staminate calyx lobed; fruit capsular.
 4a. Leaves without beadlike glands beneath; anthers and petals not gland-tipped; inflorescences terminal or axillary, not opposite the leaves.
 5a. Inflorescences terminal; seeds carunculate; staminate disk and receptacle glabrous.
 6a. Ovary 3-locular; petals glabrous outside 226. *Baloghia*
 6b. Ovary 2-locular; petals golden-sericeous outside 227. *Hylandia*
 5b. Inflorescences axillary; staminate disk or receptacle pilose.
 7a. Indumentum simple; styles bifid 228. *Ostodes*
 7b. Indumentum (in inflorescence) malpighiaceous; staminate disk cupular.
 8a. Styles bifid; staminate disk glabrous; stamens mostly 5-7; petals pubescent adaxially; seeds carunculate 229. *Pausandra*
 8b. Styles multifid; staminate disk pubescent; stamens 14-16; petals not pubescent adaxially; seeds ecarunculate 230. *Dodecastigma*
 4b. Leaves with beadlike glands beneath; anthers and petals with apical glands; inflorescences opposite the leaves 231. *Pantadenia*
 3b. Staminate calyx almost truncate.
 9a. Pistillate calyx accrescent; petals glabrous; fruit capsular 232. *Dimorphocalyx*
 9b. Pistillate calyx not accrescent; petals tomentose; fruit drupaceous 233. *Fontainea*
 2b. Petals absent in pistillate flowers.
 10a. Inflorescences axillary.
 11a. Flowers in racemes; stipules caducous or absent; anthers muticous.
 12a. Styles entire, slender 234. *Codiaeum*
 12b. Styles twice bifid 235. *Sphyrantha*
 11b. Flowers in axillary clusters; stipules persistent, \pm spinose; anthers apiculate; styles bifid or dilated 236. *Acidocroton*
 10b. Inflorescences terminal.
 13a. Pistillate sepals accrescent, not recurved; floral disk present.
 14a. Pistillate sepals eglandular; seeds mostly ecarunculate 237. *Blachia*
 14b. Pistillate sepals glandular; seeds carunculate 238. *Strophoblachia*
 13b. Pistillate sepals recurved, not accrescent; floral disk absent 239. *Sagotia*
 1b. Petals absent; styles bifid; seeds carunculate; leaves glandular 240. *Baliospermum*

226. *Baloghia* Endlicher, Prodr. Fl. Norf. 84. 1833; Bentham, Gen. Pl. 3: 300. 1880; Pax, Pflanzenr. 147. III (Heft 47): 12. 1911; Maiden, For. Fl. N. S. W. 1: 165, t. 28. 1904; White, Proc. Roy. Soc. Queensl. 53: 226. 1942; Airy Shaw, Kew Bull. 35: 598. 1980; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 43. 1987; James & Harden, Fl. N. S. W. 1: 410, 1990. TYPE: *Baloghia lucida* Endl.

Steigeria Muell. Arg., Linnaea 34: 215. 1865; DC. Prodr. 15(2): 1121. 1866. TYPE: *Steigeria montana* Muell. Arg. [= *Baloghia montana* (Muell. Arg.) Pax].

An Australasian genus of 15 species, 12 in New Caledonia and the others in Norfolk Island, Lord Howe Island, and Australia.

227. *Hylandia* Airy Shaw, Kew Bull. 29: 329. 1974; 35: 643, fig. 4. 1980. TYPE: *Hylandia dockrillii* Airy Shaw.

A monotypic genus of tropical Australia (Queensland). Airy Shaw (1974) suggested a relationship with *Dimorphocalyx*, *Ostodes*, and

Loerzingia (*Deutzianthus*), especially the latter. These suggestions are generally compatible with the present treatment, but it appears that *Baloghia* may prove to be the closest genus.

228. *Ostodes* Blume, Bijdr. Fl. Ned. Ind. 619. 1825; Muell. Arg. 15(2): 1114. 1866; Bentham, Gen. Pl. 3: 299. 1880; Hook. f., Fl. Brit. Ind. 5: 400. 1887; Pax & Hoffm., Pflanzenr. 147. III (Heft 47): 17. 1911; Gagnepain, Fl. Indochine 5: 322. 1925; Airy Shaw, Kew Bull. 20: 409. 1966; 26: 311. 1971; 35: 334. 1981. TYPE: *Ostodes paniculata* Bl.

As circumscribed by Airy Shaw (1966), *Ostodes* is a genus of four species of tropical Asia, from the eastern Himalayas to northern Borneo. A number of species included by Pax & Hoffmann (1911) were removed by Airy Shaw (1966) to *Fahrenheitia*, a disposition that is accepted here pending further study.

229. *Pausandra* Radlkofer, Flora 53: 92, t. 2. 1870; Baillon, Adansonia I. 11: 92. 1873; Muell. Arg., Fl. Brasil. 11(2): 503, t. 99.

1874; Pax & Hoffm., Pflanzenr. 147. III (Heft 47): 41. 1911; Lanjouw, Rec. Trav. Bot. Neerl. 33: 758. 1936; Jablonski, Mem. New York Bot. Gard. 17: 153. 1967; Secco, Bol. Mus. Par. Emilio Goeldi, Bot. 3: 59. 1987; Huft, Ann. Missouri Bot. Gard. 75: 1115. 1989; Secco, Rev. Gen. *Anomalocalyx* . . . Amer. Sul 58. 1990. TYPE: *Pausandra morisoniana* (Casar.) Radlk.

As revised by Secco (1990), *Pausandra* is a neotropical genus of ca. eight species, extending from Honduras to Brazil. The genus is very distinctive and isolated from other genera of the tribe except for *Dodecastigma*, which is similar in indumentum and staminate disk, but very different in a number of other characters.

230. Dodecastigma Ducke, Notizbl. Bot. Gart. Berlin 11: 343. 1932; Arq. Jard. Bot. Rio Janeiro 6: 58, t. 5. 1933; Sandwith, Kew Bull. 1950: 134. 1951; Jablonski, Mem. New York Bot. Gard. 17: 154. 1967; Secco, Rev. Gen. *Anomalocalyx* . . . Amer. Sul 42. 1990. TYPE: *Dodecastigma amazonicum* Ducke.

A genus of two species of the Brazilian Amazon and the Guianas.

231. Pantadenia Gagnepain, Bull. Soc. Bot. France 71: 873. 1925; Fl. Indochine 5: 470. 1926; Airy Shaw, Kew Bull. 28: 122. 1969; 26: 312. 1972. TYPE: *Pantadenia adenantha* Gagn.

Parapantadenia Capuron, Adansonia II. 12: 206. 1972. TYPE: *Parapantadenia chauvetiae* Leandri [= **Pantadenia chauvetiae** (Leandri) Webster, comb. nov.].

A paleotropical genus of two widely disjunct species, one endemic to Madagascar, the other found in Thailand and Indochina. The genus *Parapantadenia* was distinguished by the 2-locular ovary that develops into a 1-seeded, indehiscent fruit. However, the species are otherwise so similar in the peculiar indumentum and inflorescence that it seems best to regard them as congeneric.

232. Dimorphocalyx Thwaites, Enum. Pl. Zeyl. 278. 1861; Bentham, Gen. Pl. 3: 301. 1880; Hook. f., Fl. Brit. Ind. 5: 403. 1887; Trimen, Handb. Fl. Ceylon 4: 54, pl. 84. 1898; Pax, Pflanzenr. 147. III (Heft 47): 31. 1911; Airy Shaw, Kew Bull. 23: 123. 1969; 26: 251. 1972; Whitmore, Tree Fl. Malaya 2: 86. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 95.

1975; Kew Bull. 35: 624. 1980. TYPE: *Dimorphocalyx glabellus* Thw.

A genus of ca. 15 species, mainly in tropical Asia (India and Sri Lanka to Hainan and Borneo) but extending to Australia.

233. Fontainea Heckel, Etudes sur *Fontainea pancheri*. 1870; Baillon, Hist. Pl. 5: 194. 1874; Pax, Pflanzenr. 147. III (Heft 47): 30. 1911; Airy Shaw, Kew Bull. 35: 632. 1980; Jessup & Guymmer, Austrobaileya 2: 112. 1985; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 74. 1987. TYPE: *Fontainea pancheri* (Baillon) Heckel.

An Australasian genus of six species, extending from Australia to New Guinea, New Caledonia, and Vanuatu.

234. Codiaeum Rumphius ex A. Jussieu, Euphorb. Tent. 33. 1824 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 1116. 1866; Bentham, Gen. Pl. 3: 299. 1880; Pax, Pflanzenr. 147. III (Heft 47): 23. 1911; Airy Shaw, Kew Bull. Add. Ser. 4: 88. 1975; 8: 62. 1980; A. C. Smith, Fl. Vitiensis Nova 2: 549. 1981; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 95. 1987. TYPE: *Codiaeum variegatum* (L.) A. Juss.

Phyllaurea Loureiro, Fl. Cochinch. 575. 1790. TYPE: *Phyllaurea codiaeum* Lour. [nom. illeg., = *Codiaeum variegatum* (L.) A. Juss.].

Synapisma Endlicher, Gen. Pl. 1110. 1840. TYPE: *Crozophora peltata* Labill. [= *Codiaeum peltatum* (Labill.) P. Green].

Junghuhnia Miquel, Fl. Ind. Batav. 1(2): 412. 1859 (non Corda, 1842). TYPE: *Junghuhnia glabra* Miq. [= *Codiaeum variegatum* (L.) A. Juss.].

An Australasian genus of ca. 15 species, from Borneo and the Philippines to New Guinea, tropical Australia, New Caledonia, and the Pacific islands. Mueller (1866) adopted an extremely broad concept of *Codiaeum*, including *Baloghia* and *Blachia* as sections; however, recent workers concur in the narrower definition.

235. Sphyranthera Hooker f., Hook. Ic. Pl. 18: t. 1702. 1887; Chakrabarty & Vasudeva Rao, J. Econ. Tax. Bot. 5: 959. 1984; 6: 429. 1985. TYPE: *Sphyranthera capitellata* Hook. f., nom. illeg. [= *Sphyranthera lutescens* (Kurz) Pax & Hoffm.].

An endemic genus of the Andaman/Nicobar archipelago; there are two species, the type and the recently described *S. airyshawii* Chakrab. &

Vasud. The relationships of the genus are still uncertain; Hooker suggested that *Sphyranthera* might belong to the Acalyphaeae.

236. *Acidocroton* Grisebach, Fl. Br. W. Ind. 42. 1859 (nom. cons. prop.; proposed here); Muell. Arg., DC. Prodr. 15(2): 1042. 1866; Bentham, Gen. Pl. 3: 291. 1880; Pax, Pflanzenz. 147. I (Heft 42): 13. 1910; Urban, Symb. Ant. 7: 513. 1913; Fawc. & Rend., Fl. Jam. 4: 316. 1920; Urban, Symb. Ant. 9: 208. 1924; Ark. Bot. 20A(15): 62. 1926; Alain, Fl. Cuba 3: 73. 1953; Fl. Española 4: 69. 1986. TYPE: *Acidocroton adelioides* Griseb.

Ophellantha Standley, J. Wash. Acad. Sci. 14: 97. 1924; syn. nov. TYPE: *Ophellantha spinosa* Standl., op. cit. 98 [= *Acidocroton spinosus* (Standl.) Webster, comb. nov.].

A mainly Caribbean genus of 12 species, 2 from Central America (Chiapas/Guatemala) and the remainder from the Greater Antilles, with the majority in Cuba (an undescribed species is reported from Colombia by Huft; pers. comm.). The genus has been subject to both nomenclatural and taxonomic problems since its description. Grisebach cited *Acidoton* P. Brown and *Adelia acidoton* L. as the basis for his genus and type species; unfortunately, the Jamaican plant of Browne and Linnaeus represents *Flueggea acidoton* (L.) Webster (Allertonia 3: 299. 1984). Although Grisebach's description is indeed based on material of the genus accepted by later authors as *Acidocroton*, by typification his genus is a synonym of *Flueggea*. Conservation of this genus that is common and widespread in the Greater Antilles would seem to be the best solution.

Although *Ophellantha*, described from Central America, has been accepted as a distinct genus (e.g., by Standley & Steyermark, Fieldiana Bot. 24(6): 139. 1949), it has never been compared with *Acidocroton*. While the two taxa appear different in aspect because of the reduced leaves and greater spinosity of the West Indian plants, they are very similar in floral characters except for the more accrescent calyx in the Central American plants. It therefore appears that *Ophellantha* is best treated as *Acidocroton* sect. *Ophellantha* (Standl.) Webster, comb. nov. The only other species in the section besides the type is *Acidocroton steyermarkii* (Standl.) Webster, comb. nov. [*Ophellantha steyermarkii* Standley, Field Mus. Bot. 23: 123. 1944].

The affinities of *Acidocroton* have been vari-

ously interpreted. Mueller (1866) created for it a subtribe placed between *Pogonophora* and *Clutia*. Bentham (1880) suggested an affinity with *Jatropha*; and Pax (1910), apparently following Bentham's lead, referred *Acidocroton* to tribe Jatrophaeae, but located it in subtribe Micrandrinae adjacent to *Garcia*. Although the matter still needs more study, the totality of floral characters support a placement in tribe Codiaeae.

237. *Blachia* Baillon, Etude Gén. Euphorb. 385. 1858; Bentham, Gen. Pl. 3: 301. 1880; Hook. f., Fl. Brit. Ind. 5: 402. 1887; Pax, Pflanzenz. 147. III (Heft 47): 36. 1911; Gagnepain, Fl. Indochine 5: 410. 1926; Airy Shaw, Kew Bull. 23: 121. 1969; 26: 223. 1972; Kew Bull. Add. Ser. 4: 57. 1975; Thin, Tap Chi Sinh Hoc 11(3): 16. 1989. TYPE: *Blachia umbellata* (Willd.) Baill. [*Croton umbellatus* Willd.].

A genus of ca. ten species, in tropical Asia from southern India to Hainan, the Philippines, and perhaps Borneo. The genus appears related to *Acidocroton* of the New World, especially the section *Ophellantha*.

238. *Strophoblachia* Boerlage, Handl. Fl. Ned. Ind. 3(1): 235. 1900; Pax, Pflanzenz. 147. III (Heft 47): 35. 1911; Merrill, Univ. California Publ. Bot. 10: 425. 1925; Gagnepain, Fl. Indochine 5: 408. 1926; Airy Shaw, Kew Bull. 25: 544. 1971; Thin, Tap Chi Sinh Hoc 11(3): 15. 1989. TYPE: *Strophoblachia fimbriicalyx* Boerl.

A genus of two species in southeast Asia: Indochina to Hainan, the Philippines, and Celebes.

239. *Sagotia* Baillon, Adansonia I. 1: 53. 1860 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 1113. 1866; Fl. Bras. 11(2): 504. 1874; Bentham, Gen. Pl. 3: 302. 1880; Pax, Pflanzenz. 147. III (Heft 47): 39. 1911; Jablonski, Mem. New York Bot. Gard. 17: 151. 1967; Secco, Acta Amazonica 15(1-2, suppl.): 81. 1985; Rev. Gen. *Anomalocalyx* . . . Amer. Sul 99. 1990. TYPE: *Sagotia racemosa* Baillon.

According to Secco (1985), *Sagotia* includes two species of Amazonian South America; Levin (pers. comm.) also reports the genus from Costa Rica and Panama. The systematic position of the genus is rather doubtful; it shows some resemblances to *Ostodes* but also to *Croton* and related genera.

240. *Baliospermum* Blume, Bijdr. Fl. Ned. Ind. 603. 1826; Decaisne in Jacquemont, Voy. Inde Atlas 2: t. 155. 1844; Muell. Arg., DC. Prodr. 15(2): 1125. 1866; Hook. f., Fl. Brit. Ind. 5: 461. 1887; J. J. Smith, Meded. Dept. Landb. 10: 599. 1910; Pax & Hoffm., Pflanzenz. 147. IV (Heft 52): 24. 1912; Gagnepain, Fl. Indochine 5: 429. 1926; Airy Shaw, Kew Bull. 26: 222. 1972; 36: 267. 1981; Thin, Tap Chi Sinh Hoc 11(3): 16. 1989. TYPE: *Baliospermum axillare* Bl.

An Asian genus of ca. 12 species, distributed from India to China (Yunnan) and Java. Mueller (1866) associated *Baliospermum* with *Gelonium*, which it somewhat resembles in habit, and has been followed in this by Pax & Hoffmann (1912) and other later workers. However, the nonaperturate pollen is quite different from that of *Suregada*, and Airy Shaw (1975) seems closer to the mark in referring it to his "subtribe Codiaeinae" along with *Codiaeum*, *Blachia*, and *Strophoblachia*. Thin (1989) has described a new section, *Dioicea*, based on *Baliospermum balansae* Gagnep.

Tribe 40. TRIGONOSTEMONEAE Webster, Taxon 24: 599. 1975. TYPE: *Trigonostemon* Bl.

Monoecious trees or shrubs; indumentum simple; leaves alternate, unlobed, pinnately veined, sometimes stipellate at base but lacking paired glands at apex of petiole; stipules persistent or deciduous, often small. Inflorescences terminal or axillary, racemose or thyrsoid. Staminate sepals 5, free, imbricate; petals 5, exceeding the calyx; disk cupular or dissected; stamens 3(–5), filaments connate, anther connective enlarged, often elongated; pollen grains globose, inaperturate, with Croton-pattern, sexinous processes small; pistillode absent. Pistillate sepals 5, free, imbricate; disk cupular; ovary 3-locular; styles free or nearly so, unlobed or bifid. Fruit capsular; seeds ecarunculate, testa dry; endosperm present.

The tribe contains the single paleotropical genus *Trigonostemon*.

241. *Trigonostemon* Blume, Bijdr. Fl. Ned. Ind. 600. 1825 (as *Trigostemon*); Fl. Javae Praef. viii. 1828 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 1105. 1866; Bentham, Gen. Pl. 3: 298. 1880; Hook. f., Fl. Brit. Ind. 5: 395. 1887; Pax & Hoffm., Pflanzenz. 147. III (Heft 47): 85. 1911; Gagnepain, Fl. Indochine 5: 309. 1925; Quisumbing, Phil. J.

Sci. 41: 329. 1930; Jablonski, Brittonia 15: 151. 1963; Airy Shaw, Kew Bull. 23: 126. 1969; 25: 545. 1971; Whitmore, Tree Fl. Malaya 2: 134. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 201. 1975; Kew Bull. 35: 352. 1981. TYPE: *Trigonostemon serratus* Bl.

Enchidium Jack, Malayan Misc. 2(7): 89. 1822 (nom. rej.). TYPE: *Enchidium verticillatum* Jack [= *Trigonostemon verticillatus* (Jack) Pax].

Silvaea Hook. & Arn., Bot. Beechey's Voy. 211. 1837. TYPE: *Silvaea semperflorens* (Roxb.) Hook. & Arn. [= *Trigonostemon semperflorens* (Roxb.) Muell. Arg.].

Athroisma Griffith, Not. Pl. As. 4: 477. 1854 (non A. P. DeCandolle, 1833. TYPE: not designated (Griffith cited two species, neither positively identified by Pax & Hoffmann [1911])).

Telogyne Baillon, Etude Gén. Euphorb. 327. 1858. TYPE: *Telogyne indica* Baill. [= *Trigonostemon verticillatus* (Jack) Pax].

Tritaxis Baillon, Etude Gén. Euphorb. 342. 1858. TYPE: *Tritaxis gaudichaudii* Baillon [= *Trigonostemon gaudichaudii* (Baill.) Muell. Arg.].

Tylosepalum Kurz ex Teysm. & Binn., Natuurk. Tijdschr. Ned.-Indië 27: 50. 1864. TYPE: *Tylosepalum aurantiacum* Kurz ex Teysm. & Binn. [= *Trigonostemon aurantiacum* (Kurz ex Teysm. & Binn.) Boerl.].

Nepenthandra Sp. Moore, J. Bot. 43: 149. 1905. TYPE: *Nepenthandra lanceolata* Sp. Moore [= *Trigonostemon lanceolatus* (Sp. Moore) Pax].

Prosartema Gagnepain, Bull. Soc. Bot. France 71: 875. 1925. TYPE: *Prosartema stellaris* Gagnep. [= *Trigonostemon stellaris* (Gagnep.) Airy Shaw].

Poilaniella Gagnepain, Bull. Soc. Bot. France 72: 467. 1925. TYPE: *Poilaniella fragilis* Gagnep. [= *Trigonostemon fragilis* (Gagnep.) Airy Shaw].

Neotrigonostemon Pax & Hoffm., Notizbl. Bot. Gart. Berlin 10: 385. 1928. TYPE: *Neotrigonostemon diversifolius* Pax & Hoffm. [= *Trigonostemon viridissimus* (Kurz) Airy Shaw].

Kurziodendron Balakrishnan, Bull. Bot. Surv. India 8: 68. 1966. TYPE: *Kurziodendron viridissimum* (Kurz) Balakr. [= *Trigonostemon viridissimus* (Kurz) Airy Shaw].

A rather diverse genus of tropical Asia, extending from India and Sri Lanka to New Guinea. The diversity of the genus is clearly indicated by the remarkably extensive generic synonymy. The relationships of the genus have been differently understood. Mueller (1866), who accepted a broad circumscription (including *Dimorphocalyx*), referred *Trigonostemon* to the Jatrophaeae. Pax & Hoffmann (1911) included it in tribe Clutieae subtribe Clutiinae, where it is clearly out of place. Airy Shaw (1975) placed it in his informal "subtribe" Ostodinae along with *Fahrenheitia* and *Dimorphocalyx*. This placement has much to recommend it, and it is possible that the tribe Trigonostemoneae cannot be maintained as distinct from the Codiaeae.

Tribe 41. RICINOCARPEAE Muell. Arg., Bot. Zeit. 22: 324. 1864; DC. Prodr. 15(2): 199. 1866. Subfam. Ricinocarpoideae Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 113. 1890. Family Ricinocarpaceae (Muell. Arg.) Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 224. 1954. TYPE: *Ricinocarpos* Desf.

Monoecious (rarely dioecious) shrubs or herbs; latex scanty or apparently absent; indumentum stellate, glandular hairs often present; leaves alternate, entire, often ericoid, eglandular, exstipulate. Inflorescences terminal or axillary, racemose or reduced to clusters or solitary flowers. Staminate sepals 4–6, free, imbricate, often petaloid; petals usually 5, or absent; disk dissected or absent; stamens mostly 15 or more, filaments connate into a column or short and apparently free; anthers exserted; pollen grains globose, inaperturate, sexine with modified Croton-pattern (processes spinose, or reduced); pistillode absent. Pistillate sepals (4)5, imbricate; petals 5, sometimes reduced or absent; disk dissected or absent; ovary 3-locular; styles unlobed, bifid, or multifid. Fruit capsular, 1–3-locular; seeds carunculate; endosperm present; embryo cylindrical, with narrow cotyledons.

As indicated by pollen characters, tribe Ricinocarpeae definitely belongs in subfamily Crotonoideae and not in a separate group of “Stenolobae” as treated by Mueller (1866), Benthams (1880), and Pax & Hoffmann (1931). The tribe appears rather closely related to the Crotonaeae, and further work may show that the two groups should be combined.

KEY TO THE SUBTRIBES OF TRIBE RICINOCARPEAE

- 1a. Pollen grains with large clavate sexinous processes; petals and disk usually present; ovary 3-locular; leaves alternate 41a. Ricinocarpinae
- 1b. Pollen grains with reduced sexinous processes; petals and disk absent; ovary 1–3-locular; leaves alternate, opposite, or whorled 41b. Bertyinae

Subtribe 41a. RICINOCARPINAE Webster, Taxon 24: 599. 1975. TYPE: *Ricinocarpos* Desf.

Trees, shrubs, or undershrubs; leaves alternate, sometimes resinous; flowers in terminal or axillary racemes or clusters (or solitary); sepals distinct or connate; petals usually present, longer or shorter than sepals; stamens 20 or more, filaments free (or inner connate at base); pollen grains with large clavate processes; ovary 3-locular; styles bifid or unlobed; fruit capsular, with 3 seeds.

An Australasian group of three genera, two endemic to Australia.

KEY TO THE GENERA OF SUBTRIBE RICINOCARPINAE

- 1a. Styles bifid to multifid; stamens at least partially connate.
 - 2a. Staminate calyx lobed halfway or more; filaments all connate; petioles short 242. *Ricinocarpos*
 - 2b. Staminate calyx lobed less than halfway; outer filaments free; petioles long 243. *Alphandia*
- 1b. Styles unlobed, dilated, forming a cap over the ovary; stamens all free 244. *Beyeria*

242. Ricinocarpos Desfontaines, Mém. Mus. Hist. Nat. Paris 3: 459, t. 22. 1817; Muell. Arg., DC. Prodr. 15(2): 203. 1866 (as *Ricinocarpos*); Benthams & Mueller, Fl. Austral. 6: 68. 1873; Benthams, Gen. Pl. 3: 263. 1880; Maiden, Ill. N. S. W. Pl., t. 16. 1908; Grüning, Pflanzenz. 147 (Heft 58): 37. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 226. 1931; Stanley, Fl. S.-E. Queensland 1: 432. 1983. TYPE: *Ricinocarpos pinifolius* Desf.

Roeperia Sprengel, Syst. Veg. 3: 147. 1826. TYPE: *Roeperia pinifolia* (Desf.) Spreng. [= *Ricinocarpos pinifolius* Spreng.].

An Australian genus of ca. 15 species grouped into 4 sections by Grüning. Although reported from New Caledonia, it does not occur there; the supposed New Caledonian species has been transferred to *Baloghia* by McPherson & Tirel (1987).

243. Alphandia Baillon, Adansonia I. 11: 85. 1873; Pax & Hoffmann, Pflanzenz. 147. III (Heft 47): 22. 1911; Airy Shaw, Kew Bull. Add. Ser. 8: 27. 1980; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 86. 1987. TYPE: *Alphandia furfuracea* Baillon.

A Melanesian genus of three species in New Guinea, New Caledonia, and Vanuatu.

244. Beyeria Miquel, Ann. Sci. Nat. III. 1: 350, t. 15. 1844; Muell. Arg., DC. Prodr. 15(2): 201. 1866; Benthams & Mueller, Fl. Austral. 6: 63. 1873; Benthams, Gen. Pl. 3: 263. 1880; Grüning, Pflanzenz. 147. (Heft 58): 63. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 227. 1931; James & Harden, Fl. N. S. W. 1: 412. 1990. TYPE: *Beyeria viscosa* (Labill.) Miq.

Calyptrostigma Klotzsch in Lehm., Pl. Preiss. 1: 175. 1845. TYPE: *Calyptrostigma viscosum* (Labill.) Kl. [= *Beyeria viscosa* (Labill.) Miq.].

Beyeriopsis Muell. Arg., Linnaea 34: 56. 1865. TYPE: *Beyeriopsis brevifolia* Muell. Arg. [= *Beyeria brevifolia* (Muell. Arg.) Benth.; lectotype, designated by Wheeler, 1975].

A genus of ca. 15 species endemic to Australia.

Subtribe 41b. BERTYINAE Muell. Arg., Linnaea 34: 56. 1865; DC. Prodr. 15(2): 208. 1866. TYPE: *Bertya* Planchon.

Trees or shrubs; leaves alternate, opposite, or verticillate; flowers in axillary racemes or clusters (or solitary); sepals distinct or absent; petals present or absent; stamens numerous, filaments connate into a column, anthers often pubescent; pollen grains with sexinous processes reduced; ovary 2–3 locular; styles bifid to multifid; fruit 1–3-seeded.

This Australasian subtribe includes one genus from Australia, two from New Caledonia, and one from Borneo.

KEY TO THE GENERA OF SUBTRIBE BERTYINAE

- 1a. Staminate sepals present; petals present or absent; ovary 3-locular.
 2a. Leaves alternate; anthers glabrous; fruit usually 1-seeded 245. *Bertya*
 2b. Leaves opposite or whorled; anthers pubescent; fruit 3-seeded.
 3a. Leaves opposite; inflorescences racemose, terminal; styles multifid 246. *Myricanthe*
 3b. Leaves whorled; inflorescences 1-flowered, axillary; styles 2–4-fid 247. *Cocconerion*
 1b. Staminate sepals absent; petals absent; ovary 2-locular; staminate flowers in terminal bracteate catkins, pistillate solitary, axillary; anthers pubescent; styles bifid 248. *Borneodendron*

245. *Bertya* Planchon, Hook. Lond. J. Bot. 4: 472. 1845; Muell. Arg., DC. Prodr. 15(2): 208. 1866; Bentham & Mueller, Fl. Austral. 6: 74. 1873; Bentham, Gen. Pl. 3: 264. 1880; Grüning, Pflanzenz. 147. (Heft 58): 49. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 226. 1931; Guymer, Austrobaileya 2: 427. 1988; James & Harden, Fl. N. S. W. 1: 414. 1990. TYPE: *Bertya rosmarinifolia* Planchon [lectotype, chosen here].

A genus of ca. 20 species endemic to Australia.

246. *Myricanthe* Airy Shaw, Kew Bull. 35: 390. 1980; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 72. 1987. TYPE: *Myricanthe discolor* Airy Shaw.

A monotypic genus restricted to northwestern New Caledonia.

247. *Cocconerion* Baillon, Adansonia 11: 87. 1873; Guillaumin, Fl. Syn. Nouv.-Caléd. 189. 1948; Airy Shaw, Kew Bull. 25: 503. 1971; 32: 382. 1978; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 38. 1987. TYPE: *Cocconerion balansae* Baillon.

A genus of two species endemic to New Caledonia.

248. *Borneodendron* Airy Shaw, Kew Bull. 16: 359. 1963; Hook. Ic. Pl. 7(2): t. 3633. 1967; Kew Bull. Add. Ser. 4: 60. 1975. TYPE: *Borneodendron aenigmaticum* Airy Shaw.

A monotypic genus endemic to Borneo. In the original description, Airy Shaw (1963) compared *Borneodendron* to *Baloghia*, a genus that it somewhat resembles in foliar characters. Later (Airy Shaw, 1975), he regarded it as most closely allied with *Cocconerion*, a disposition that is followed here.

Tribe 42. CROTONEAE Dumort., Anal. Fam. Pl. 45. 1829 (“Crotonieae”). TYPE: *Croton* L.

Monoecious or dioecious trees, shrubs, or herbs; stems with nonarticulated laticifers; latex clear or reddish, often scanty or apparently absent; indumentum stellate or lepidote; leaves alternate, simple to palmately lobed, sometimes pellucid-punctate; petiole with or without apical paired glands; stipules present or absent. Inflorescences terminal or axillary, racemose or spicate. Staminate sepals mostly 5, imbricate to valvate, free; petals 5, imbricate, sometimes absent; disk annular or dissected, receptacle often villose; stamens 3–400, filaments free, often inflexed in bud; anthers muticous; pollen grains globose, inaperturate, with sexinous Croton-pattern; pistillode absent. Pistillate sepals 4–7(–10), ± free, sometimes accrescent, imbricate to reduplicate-valvate; petals 5, mostly reduced or obsolete; ovary mostly 3-locular; styles free or nearly so, once to several times bifid. Fruit capsular; seeds carunculate, testa dry; endosperm copious.

The circumscription of tribe Crotonae is expanded from my previous treatment (Webster, 1975), in which only *Croton* and the two satellite genera *Crotonopsis* and *Eremocarpus* were included. The suggested inclusion of *Mildbraedia*, *Fahrenheitia*, and *Moacroton* in the tribe is still rather shakily supported and requires further evaluation, but at least has the merit of not leaving

Croton in a taxonomic "black box" without any apparent relatives.

KEY TO THE GENERA OF TRIBE CROTONEAE

- 1a. Filaments not distinctly inflexed in bud; pistillate flowers petaliferous.
2a. Stamens 10–30; staminate petals thinner in texture than sepals; pistillate flowers petaliferous; styles bifid.
3a. Stamens free; staminate petals free; inflorescences axillary; seed coat dry 249. *Mildbraedia*
3b. Stamens with filaments connate; staminate petals coherent; inflorescences terminal; seed coat fleshy 250. *Fahrenheitia*
2b. Stamens 3–6; staminate petals similar in texture to sepals; pistillate flowers apetalous; styles unlobed or emarginate 251. *Moacroton*
1b. Filaments \pm distinctly inflexed in bud; pistillate petals mostly reduced to absent 252. *Croton*

249. *Mildbraedia* Pax, Bot. Jahrb. 43: 319. 1909; Pflanzenr. 147. III (Heft 47): 11. 1911; Hutchinson, Fl. Trop. Afr. 6(1): 798. 1912; Léonard, Fl. Congo Belge 8(1): 85. 1962; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 340. 1987. TYPE: *Mildbraedia paniculata* Pax.

Neojatropha Pax, Pflanzenr. 147. I (Heft 42): 114. 1910. TYPE: *Neojatropha carpinifolia* (Pax) Pax [= *Mildbraedia carpinifolia* (Pax) Hutch.].

A tropical African genus of four species.

250. *Fahrenheitia* Reichb. f. & Zoll., Linnaea 28: 599. 1856; Muell. Arg., DC. Prodr. 15(2): 1256. 1866; Airy Shaw, Kew Bull. 20: 409. 1966; 26: 270. 1972; Whitmore, Tree Fl. Malaya 2: 97. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 114. 1975; Kew Bull. 36: 298. 1981. TYPE: *Fahrenheitia collina* Reichb. f. & Zoll. [= *Fahrenheitia pendula* (Hassk.) Airy Shaw].

A tropical Asian genus of four species, found from southern India and Sri Lanka to the Philippines and Borneo. Pax & Hoffmann (1911) included the then-known species within *Ostodes*, but Airy Shaw (1966) showed that *Fahrenheitia* was quite distinct, although he later (Airy Shaw, 1975) referred it to the same informal "subtribe" as *Ostodes*.

251. *Moacroton* Croizat, J. Arnold Arbor. 26: 189. 1945; Alain, Fl. Cuba 3: 85. 1953. TYPE: *Moacroton leonis* Croiz.

As defined by Croizat and Alain, *Moacroton* is a genus of six species endemic to Cuba. It appears closely related to *Croton*, and its status requires evaluation (Webster, 1992).

252. *Croton* L., Sp. Pl. 2: 1004. 1753; Gen. Pl., ed. 5, 436. 1754; Klotzsch, Hook. London J. Bot. 2: 48. 1843; Muell. Arg., DC. Prodr. 15(2): 512. 1866; Fl. Bras. 11(1): 81. 1873; Bentham, Gen. Pl. 3: 293. 1880; Hook. f., Fl. Brit. Ind. 5: 385. 1887; Ferguson, Rep. Missouri Bot. Gard. 12: 33. 1901; Hutchinson, Fl. Trop. Afr. 6(1): 746. 1912; Gagnepain, Fl. Indochine 5: 256. 1925; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 83. 1931; Leandri, Ann. Inst. Bot.-Geol. Colon. Marseille, V. 7(1): 1. 1939; Carabia, Carib. For. 3: 114. 1942; Croizat, Darwiniana 5: 417. 1941; 6: 442. 1944; Johnston & War-nock, Southw. Nat. 7: 1. 1962; Webster, J. Arnold Arbor. 48: 353. 1967; Leandri, Adansoniana II. 10: 191. 1970; Liogier, Fl. Española 4: 108. 1986; Thin, Tap Chi Sinh Hoc 8(2): 28. 1986; Webster, Ann. Missouri Bot. Gard. 75: 1116. 1989; Novon 2: 270. 1992; Taxon 42: 793. 1993. TYPE: *Croton aromaticus* L. [lectotype, designated by Webster, J. Arnold Arbor. 48: 354. 1967; this replaced the earlier but incorrect selection of *Croton tiglium* L. by Small, in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 254. 1913].

Cieca Adanson, Fam. Pl. 2: 355. 1763 (nom. rej.). TYPE: *Croton argenteus* L.

Crotonopsis Michaux, Fl. Bor.-Amer. 2: 185. 1803. *Lep-temon* Raf., Med. Repos. II. 5: 353. 1808 (nom. superfl.). TYPE: *Crotonopsis linearis* Michaux [= *Croton michauxii* Webster].

Friesia Sprengel, Anleit. Kenntn. Gewächse, ed. 2, 2(2): 885. 1818. TYPE: *Friesia argentea* Sprengel [= *Croton michauxii* Webster].

Decarinium Raf., Neogenyton 1. 1825. TYPE: *Decar-inium glandulosum* (L.) Raf. [= *Croton glandulosus* L.].

Drepadenium Raf., Neogenyton 2. 1825. TYPE: *Dre-padenium maritimum* (Walt.) Raf. [= *Croton mar-itimum* Walt.].

Heptallon Raf., Neogenyton 1. 1825. TYPE: *Heptallon graveolens* Raf. [= *Croton capitatus* Michx.; lectotype, chosen here].

Julocroton Martius, Flora 20(2) Beibl.: 119. 1837. TYPE: *Julocroton phagedaenicus* Mart. [= *Croton tri-queter* Lam.].

Astrogynne Bentham, Pl. Hartweg. 14. 1839. TYPE: *Astrogynne crotonoides* Benth. [= *Croton diocus* Cav.].

Astraea Klotzsch, Arch. Naturgesch. 7: 194. 1841. TYPE: *Astraea lobata* (L.) Kl. [= *Croton lobatus* L.].

Cleodora Klotzsch, Arch. Naturgesch. 7: 196. 1841. TYPE: *Cleodora sellowiana* Kl. [= *Croton sphaerogynus* Baill.].

Eutropia Klotzsch, Arch. Naturgesch. 7: 196. 1841.

- TYPE: *Eutropia brasiliensis* Kl., nom. illeg. [= *Croton polyandrus* Spreng.].
- Medea* Klotzsch, Arch. Naturgesch. 7: 193. 1841. TYPE: *Medea hirta* Klotzsch [= *Croton timandroides* (Didr.) Muell. Arg.].
- Ocalia* Klotzsch, Arch. Naturgesch. 7: 195. 1841. TYPE: *Croton perdicipes* St. Hil. [= *Croton antisiphiliticus* Mart., lectotype, designated by Wheeler, 1975].
- Pilinophytum* Klotzsch, Arch. Naturgesch. 7: 255. 1841. TYPE: *Pilinophytum capitatum* (Michx.) Kl. [= *Croton capitatus* Michx.].
- Podostachys* Klotzsch, Arch. Naturgesch. 7: 193. 1841. TYPE: *Podostachys subfloccosa* Didr. [= *Croton lundianus* (Didr.) Muell. Arg. var. *subfloccosa* (Didr.) Muell. Arg.; lectotype, designated by Wheeler (1975)].
- Timandra* Klotzsch, Arch. Naturgesch. 7: 197. 1841. TYPE: *Croton serratus* Muell. Arg. [lectotype, designated by Wheeler (1975)].
- Heterochlamys* Turcz., Bull. Soc. Imp. Nat. Moscou 16: 61. 1843. TYPE: *Heterochlamys quinquervia* Turcz. [= *Croton argenteus* L.].
- Lasiogyne* Klotzsch, Nov. Act. Acad. Caes. Leop.-Carol. Nat. Cur. 19(suppl.): 418. 1843. TYPE: *Lasiogyne brasiliensis* Kl. [= *Croton compressus* Lam.].
- Tiglitum* Klotzsch, Nov. Act. Acad. Caes. Leop.-Carol. Nat. Cur. 19(suppl.): 418. 1843. TYPE: *Tiglitum officinale* Kl. (nom. illeg.) [= *Croton tiglitum* L.].
- Eremocarpus* Benth., Bot. Voy. Sulphur 53. 1844. *Piscaria* Piper, Contr. U.S. Nat. Herb. 11: 382. 1906 (nom. superfl.). TYPE: *Eremocarpus setigerus* (Hook.) Benth. [= *Croton setigerus* Hook.].
- Angelandra* Endlicher, Gen. Pl. Suppl. 5: 91. 1850. TYPE: *Croton ellipticus* Nutt., non *C. ellipticus* Geiseler [= *Croton lindheimerianus* Scheele].
- Barhamia* Klotzsch, in Seem., Bot. Voy. Herald 104. 1853. TYPE: *Barhamia panamensis* Kl. [= *Croton hircinus* Vent.; lectotype, designated by Wheeler (1975)].
- Cyclostigma* Klotzsch, in Seem., Bot. Voy. Herald 104. 1853. TYPE: *Cyclostigma panamensis* Kl. [= *Croton draco* Schlecht. ssp. *panamensis* (Kl.) Webster; designated by Wheeler (1975)].
- Gynamblosis* Torrey, Rep. Marcy Exped. 295. 1853. TYPE: *Gynamblosis monanthogyna* (Michx.) Torr. [= *Croton monanthogynus* Michx.].
- Centrandra* Karsten, Linnaea 28: 440. 1857. TYPE: *Centrandra hondensis* (Karst.) Webster.
- Myriogomphos* Didrichsen, Vidensk. Medd. Dansk Naturh. Foren. Kjoebenhavn 1857: 142. 1857. TYPE: *Myriogomphos fuscus* Didr. [= *Croton fuscus* (Didr.) Muell. Arg.].
- Heterocroton* Spencer Moore, Trans. Linn. Soc. II. 4: 461. 1895. TYPE: *Heterocroton mentiensi* Sp. Moore [= *Croton mentiensi* (Sp. Moore) Pax].

A large and highly diverse but definitely monophyletic genus of at least 800 species, the majority American but also with more than 200 paleotropical species. Only a selection of the more important references has been given here. The complexity of the genus is indicated by the 40 sections recently discriminated (Webster, 1993).

The relationships of *Croton* within the family have been obscured by the fact that it has generally been referred to a separate tribe associated only with the satellite genera *Crotonopsis*, *Eremocarpus*, and *Julocroton*. However, these commonly accepted segregate genera cannot be maintained under a phylogenetic circumscription of *Croton* (Webster, 1992). The African genus *Mildbraedia* seems to be a likely candidate for the sister group, since it has in common characters of indumentum, flowers, and seeds, but it diverges in its axillary, unisexual, more or less cymose inflorescences. The 3-nucleate pollen grains of *Croton* suggest a possible relationship with the tribe Ricinocarpeae.

Tribe 43. RICINODENDREAE (Pax) Hutchinson, Amer. J. Bot. 56: 749. 1969. Cluytieae subtribe Ricinodendrinae Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 87. 1890. TYPE: *Ricinodendron* Muell. Arg.

Diocious trees or shrubs; indumentum stellate; leaves alternate, unlobed to lobed or palmatisect; stipules entire to lobed, or absent. Inflorescences axillary or the pistillate terminal, paniculate or reduced to clusters or solitary flowers. Staminate sepals 4 or 5, imbricate; petals 5, \pm coherent into a tube; disk dissected or lobed; stamens (3)5–20, filaments united below; pistillode absent. Pistillate sepals 4 or 5, imbricate; petals 5, coherent; disk lobed; ovary 1–3-locular; styles bifid. Fruit drupaceous, 1–3-seeded; seeds ecarunculate; endosperm copious, oily.

This paleotropical tribe of two genera is entirely African or Madagascan except for one species in India. Relationships of the tribe are uncertain. *Givotia* suggests *Jatropha* in its habit, but diverges in its stellate indumentum and different inflorescence; nevertheless, Ricinodendreae may be related to Jatrophaeae.

KEY TO THE GENERA OF TRIBE RICINODENDREAE

- 1a. Leaves unlobed to 5-lobed; stipules small, unlobed 253. *Givotia*
- 1b. Leaves palmately parted.
 - 2a. Stipules flabellate-lobed, persistent; ovary mostly 2–3-locular; endocarp smooth, thin-walled 254. *Ricinodendron*
 - 2b. Stipules small, unlobed, deciduous; ovary mostly 1-locular; endocarp pitted, thick-walled 255. *Schinziophyton*

253. *Givotia* Griffith, Calcutta J. Nat. Hist. 4: 88. 1843; Muell. Arg., DC. Prodr. 15(2): 1112. 1866; Benth., Gen. Pl. 3: 297. 1880;

Pax & Hoffm., Pflanz. 147. III (Heft 47): 44. 1911; Radcliffe-Smith, Kew Bull. 22: 493. 1968; Fl. Trop. E. Afr. Euphorb. 1: 329. 1987. TYPE: *Givotia rottleriformis* Griffith ex Wight.

A genus of four species, one from Africa, two from Madagascar, and one from India.

254. Ricinodendron Muell. Arg., Flora 47: 533. 1864; DC. Prodr. 15(2): 1111. 1866; Bentham, Hook. Ic. Pl. 13: t. 1300. 1879; Gen. Pl. 3: 297. 1880; Pax, Pflanz. 147. III (Heft 47): 45. 1911; Mildbraed, Notizbl. Bot. Gart. Berlin 12: 516. 1935; Léonard, Fl. Congo 8(1): 116. 1962; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 325. 1987. TYPE: *Ricinodendron africanus* Muell. Arg.

A genus of two African species, closely related to *Givotia* and apparently differing only in vegetative characters.

255. Schinziohyton Hutchinson ex Radcliffe-Smith, Kew Bull. 45: 157. 1990. TYPE: *Schinziohyton rautanenii* (Schinz) Radcl.-Sm.

A monotypic African genus, discriminated by Hutchinson in an unpublished manuscript and characterized by Radcliffe-Smith as distinct from *Ricinodendron* in a number of characters, including its truly compound leaves, small stipules, and large fruits with deeply pitted endocarp.

Tribe 44. ALEURITIDEAE Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 309. 1954. TYPE: *Aleurites* G. Forster.

Monoecious trees or shrubs; stems with nonarticulated laticifers, latex scanty or absent; indumentum simple or stellate; leaves alternate, pinnately to palmately veined or lobed, eglandular or with laminar glands; stipules present or absent. Inflorescences terminal or axillary, dichasial-paniculate or reduced to cymose clusters. Staminate calyx closed in bud, splitting into valvate segments; petals mostly 5(6–13), free, imbricate; disk dissected or of intrastaminal segments; stamens 8–20(–100), filaments free; pollen grains globose, inaperturate, with Croton-pattern; pistillode absent. Pistillate sepals and petals as in staminate; disk lobed, dissected, or obsolete; ovary 2–5-locular; styles bifid. Fruit drupaceous or capsular and tardily dehiscent; seeds ecarunculate, testa dry; endosperm copious, oily.

Tribe Aleuritideae is circumscribed as previously (Webster, 1975) to include 5 subtribes with a total of 15 genera and 45–50 species. It is overwhelmingly paleotropical, with only two American genera. The tribe as presently constituted is still not satisfactorily defined. Bentham (1880) included *Aleurites* and other genera of Aleuritideae within the Jatrophaeae. There are indeed many points of similarity between *Aleurites* and *Jatropha*, and Bentham's disposition is much better than that of Pax & Hoffmann (1931), who included *Aleurites* in a very artificial subtribe along with *Agrostistachys*. *Joannesia* has characters that suggest both the Jatrophaeae and Aleuritideae, and it may prove desirable to resurrect tribe Joannesieae (Pax, 1924) in order to arrive at a more natural classification.

KEY TO THE SUBTRIBES OF TRIBE ALEURITIDEAE

- 1a. Monoecious.
 - 2a. Petals 5, glabrous; stamens 8–20, filaments connate; inflorescence paniculate; leaves palmately veined or lobed 44a. Aleuritinae
 - 2b. Petals 6–13, sericeous; stamens 30–100, filaments free; inflorescence a cymose cluster; leaves pinnately veined 44b. Garciniinae
- 1b. Dioecious.
 - 3a. Petals present, at least in staminate flower.
 - 4a. Indumentum simple or absent; petals free; inflorescence mostly terminal 44c. Grosserinae
 - 4b. Indumentum stellate or lepidote; petals often coherent or connate; inflorescence terminal or axillary 44d. Crotonogyninae
 - 3b. Petals absent; indumentum stellate; leaves with beadlike glands 44e. Neoboutoninae

Subtribe 44a. ALEURITINAE (Hurusawa) Webster, Taxon 24: 599. 1975. TYPE: *Aleurites* J. R. & G. Forster.

Monoecious trees or shrubs; indumentum simple or stellate; leaf blades palmately veined or lobed, with glands at apex of petiole; inflorescence ± paniculate; staminate calyx segments 2 or 3; petals 5, free, glabrous; disk-segments 5; stamens 8–20, inner filaments connate; ovary 2- or 3-locular; fruit drupaceous or capsular; seeds ecarunculate.

The subtribe Aleuritinae is here equivalent to the tribe Aleuritideae of Hurusawa (1954), except that the genus *Aleurites* is treated as subdivided into three genera, following Airy Shaw (1967). There is considerable doubt whether these segregates need to be recognized, as I indicated earlier

(Webster, 1967); however, they are provisionally accepted here, pending further critical study.

KEY TO THE GENERA OF SUBTRIBE ALEURITINAE

- 1a. Ovary 2-locular; fruit drupaceous; stamens 15–20, anthers introrse; indumentum distinctly stellate 256. *Aleurites*
 1b. Ovary 3–5-locular; fruit dehiscent; stamens 7–12.
 2a. Indumentum stellate; anthers extrorse; inflorescence densely pubescent, bracts conspicuous 257. *Reutealis*
 2b. Indumentum of bifid or simple hairs; anthers introrse; inflorescence not densely pubescent, bracts inconspicuous 258. *Vernicia*

256. *Aleurites* J. R. & G. Forster, Charact. Gen. Pl. 111, t. 56. 1776; Muell. Arg., DC. Prodr. 15(2): 722. 1866; Bentham, Gen. Pl. 3: 292. 1880; Hemsley, Hook. Ic. Pl. 29: t. 2801, 2802. 1909; Pax, Pflanzenr. 147. I (Heft 42): 128. 1910; Gagnepain, Fl. Indochine 5: 290. 1925; Airy Shaw, Kew Bull. 20: 393. 1967; Webster, J. Arnold Arbor. 48: 342. 1967; Walker, Fl. Okinawa 644. 1976; Smith, Fl. Vitiensis Nova 2: 547. 1981; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 176. 1987. TYPE: *Aleurites triloba* J. R. & G. Forster [= *Aleurites moluccana* (L.) Willd.].

In the restricted sense adopted by Airy Shaw (1967), *Aleurites* is a genus of two species extending from India to the Pacific islands.

257. *Reutealis* Airy Shaw, Kew Bull. 20: 394. 1967. TYPE: *Reutealis trisperma* (Blanco) Airy Shaw.

A monotypic genus endemic to the Philippines; more or less intermediate between *Aleurites* (sensu stricto) and *Vernicia*.

258. *Vernicia* Loureiro, Fl. Cochinch. 586. 1790; Hemsley, Hook. Ic. Pl. 29: t. 2801, 2802. 1906 (under *Aleurites*); Airy Shaw, Kew Bull. 20: 394. 1967; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 178. 1987. TYPE: *Vernicia montana* Lour.

An Asian genus of three species distributed from Burma to Indochina, China, and Japan; found in more temperate latitudes or elevations than *Aleurites* and *Reutealis*.

Subtribe 44b. GARCHINAE Muell. Arg., Linnaea 34: 143. 1865; DC. Prodr. 15(2): 719.

1866; Pax & Hoffm., Pflanzenr. 147. XIV (Heft 68): 9. 1919. TYPE: *Garcia* Vahl in Rohr.

Monoecious trees or shrubs; indumentum simple; leaves entire, pinnately veined, without glands at apex of petiole, exstipulate; inflorescences terminal, reduced to cymose clusters; petals 6–13, sericeous; staminate disk dissected, intrastaminal; stamens 30–100, filaments free; ovary 3-locular; styles bifid; fruit capsular; seeds ecarunculate.

Although Mueller (1866) included three other genera (*Aleurites*, *Crotonogyne*, and *Manniophyton*) in his subtribe Garchinae, Pax & Hoffmann (1919) removed them. In the treatment of Webster (1975), this monogeneric delimitation was followed, and it is still accepted here.

259. *Garcia* Vahl in Rohr, Skriv. Naturh.-Selsk. Kjobenh. 2: 217, t. 9. 1792; Muell. Arg., DC. Prodr. 15(2): 721; Lundell, Wrightia 1: 1. 1945; Webster, Ann. Missouri Bot. Gard. 54: 238. 1968. TYPE: *Garcia nutans* Vahl ex Rohr.

A neotropical genus of two species distributed from Mexico to Colombia.

Subtribe 44c. GROSSERINAE Webster, Taxon 24: 600. 1975. TYPE: *Grossera* Pax.

Diocious trees or shrubs; indumentum simple or absent; leaves pinnately veined or triplinerved, glandular or eglandular; stipules deciduous or absent; inflorescences terminal, racemose or paniculate; staminate petals 4 or 5, free; stamens 6–40, filaments free or connate; pistillate petals 4 or 5, free; ovary 3–5-locular; styles bifid; fruit capsular; seeds ecarunculate.

The seven genera of this subtribe are American/African in distribution, except for *Tapoides* from Indonesia.

KEY TO THE GENERA OF SUBTRIBE GROSSERINAE

- 1a. Sexinuous processes of pollen rounded to obtuse; leaves pinnately veined.
 2a. Staminate petals glabrous; leaves pellucid-punctate.
 3a. Bracts large, imbricate, caducous, forming a cone before anthesis; leaves entire; stipular scars subannular, conspicuous; pistillate sepals unthickened 260. *Cavacoa*
 3b. Bracts small, persistent, not forming a cone before anthesis; leaves denticulate; stipule scars very small; pistillate sepals medially thickened 261. *Grossera*

- 2b. Staminate petals pubescent; leaves not pelucid-punctate.
- 4a. Inflorescences axillary; seeds ecarunculate; staminate disk annular.
- 5a. Stamens 6–8; capsule tomentose 262. *Tapoides*
- 5b. Stamens over 20; capsule glabrous 263. *Anomalocalyx*
- 4b. Inflorescences terminal; seeds carunculate; staminate disk dissected; stamens over 20; capsule tomentose 264. *Sandwithia*
- 1b. Sexinuous processes of pollen echinate; leaves triplinerved; staminate disk dissected.
- 6a. Pistillate sepals 4 or 5, imbricate; staminate receptacle glabrous 265. *Tannodia*
- 6b. Pistillate sepals 2 or 3; staminate receptacle pilose 266. *Domohinea*

260. Cavacoa Léonard, Bull. Jard. Bot. Brux. 25: 320. 1955; Fl. Congo Belge 8(1): 191. 1962; Elffers & Taylor, Hook. Ic. Pl. 36: t. 3561. 1956; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 174. 1987. *Grossera* sect. *Racemiformes* Pax & Hoffm., Pflanzenz. 147. VI (Heft 57): 105. 1912. TYPE: *Cavacoa quintasii* (Pax & Hoffm.) Léonard [*Grossera quintasii* Pax & Hoffm.].

A genus of three species of central and east Africa.

261. Grossera Pax, Bot. Jahrb. 33: 281. 1903; Pax & Hoffm., Pflanzenz. 147. VI (Heft 57): 105. 1912; Cavaco, Bull. Mus. Hist. Nat. Paris 21: 272. 1949; Léonard, Bull. Jard. Bot. Brux. 25: 316. 1955; Bull. Jard. Bot. Brux. 28: 118. 1958; Fl. Congo 8(1): 188. 1962. TYPE: *Grossera paniculata* Pax [lectotype, designated by Léonard, 1955].

An African genus of seven species.

262. Tapoides Airy Shaw, Kew Bull. 14: 473. 1960; 20: 412. 1966; Hook. Ic. Pl. 37: t. 3632. 1967; Kew Bull. Add. Ser. 4: 200. 1975. TYPE: *Tapoides villamilii* (Merr.) Airy Shaw [*Ostodes villamilii* Merr.].

A monotypic genus of Borneo.

263. Anomalocalyx Ducke, Notizbl. Bot. Gart. Berlin 11: 344. 1932; Arq. Jard. Bot. Rio Janeiro 6: 60. 1933; Secco, Rev. Gen. *Anomalocalyx* . . . Amer. Sul 39. 1990. TYPE: *Anomalocalyx uleanus* (Pax) Ducke.

A monotypic genus of Amazonian Brazil. The phylogenetic position of *Anomalocalyx* is dubious,

and it possibly belongs close to *Dodecastigma* and *Sagotia*.

264. Sandwithia Lanjouw, Kew Bull. 1932: 184. 1933; Secco, Bull. Mus. Par. Emilio Goeldi Bot. 3: 157. 1987; 4: 177. 1988. TYPE: *Sandwithia guyanensis* Lanj.

A genus of two species of the Guyana region and Amazonian Brazil and Venezuela. Secco (1988) regarded *Sagotia* as the most closely related genus, an opinion that needs careful consideration. *Sandwithia* is here provisionally retained in subtribe *Grosserinae* because of its resemblance to *Anomalocalyx*, but it is quite possible that all three genera may prove to belong to the same tribe or subtribe.

265. Tannodia Baillon, Adansonia I. 1: 251. 1861; Muell. Arg., DC. Prodr. 15(2): 728. 1866; Bentham, Gen. Pl. 3: 304. 1880; Pax & Hoffm., Pflanzenz. 147. VI (Heft 57): 110. 1912; Prain, J. Bot. 50: 125. 1912; Léonard, Bull. Jard. Bot. Brux. 25: 300. 1955; Fl. Congo 8(1): 186. 1962; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 172. 1987. *Tandonia* Baillon, Adansonia I. 1: 184. 1861 (non *Tandonia* Moq.-Tand., 1849). TYPE: *Tannodia cordifolia* (Baill.) Baill. [*Tandonia cordifolia* Baill.].

Holstia Pax, Bot. Jahrb. 43: 220. 1909. *Tannodia* sect. *Holstia* (Pax) Prain, J. Bot. 50: 127. 1912. *Neoholstia* Rauschert, Taxon 31: 559. 1982 (nom. superfl.). TYPE: *Holstia tenuifolia* Pax [= *Tannodia tenuifolia* (Pax) Prain; lectotype].

A genus of three or four species in east Africa and the Comoro Islands. Although Radcliffe-Smith (1987a) maintained *Holstia* (as *Neoholstia*) as a distinct genus, it differs only in a relatively trivial perianth character, and Prain's reduction of it to a section of *Tannodia* appears justified.

266. Domohinea Leandri, Bull. Soc. Bot. France 87: 285. 1940. TYPE: *Domohinea perrieri* Leandri.

A monotypic genus from Madagascar. In describing it, Leandri noted its affinity to *Grossera* and *Tannodia*, and this disposition appears correct.

Subtribe 44d. CROTONOGYNINAE Webster, Taxon 24: 600. 1975. TYPE: *Crotonogyne* Muell. Arg.

Trees or shrubs, sometimes scandent; indumentum stellate or lepidote; leaves pinnately or pal-

mately veined, biglandular at juncture with petiole, stipulate; inflorescences axillary, spicate or racemose to paniculate; staminate petals coherent or connate; staminate disk dissected; stamens 7–40, filaments free or connate; anthers often apiculate; pistillate sepals 4 or 5, imbricate or valvate; disk cupular; ovary 3-locular; styles bifid or multifid; fruit capsular; seeds ecarunculate.

An African tribe of three genera. *Crotonogyne* and *Manniophyton* were originally referred to subtribe *Garciae* by Mueller (1866); however, they differ from *Garcia* in having stellate indumentum, dioecious inflorescences, and fewer petals that are more or less coherent. The *Crotonogyninae* seem most closely related to the *Grosserinae*.

KEY TO THE GENERA OF SUBTRIBE CROTONOGYNINAE

- 1a. Trees or shrubs; leaves pinnately veined; petioles lacking inflated trichomes.
 2a. Styles bifid; inflorescences terminal, paniculate; staminate petals free; staminate disk receptacular and extrastaminal, of more than 10 segments 267. *Cyrtogonone*
 2b. Styles multifid; inflorescences axillary, racemose or spicate; staminate petals mostly coherent or connate; staminate disk extrastaminal, of 5–8 segments 268. *Crotonogyne*
 1b. Lianas; leaves palmately veined; petioles with inflated trichomes; styles bifid; staminate petals connate 269. *Manniophyton*

267. *Cyrtogonone* Prain, Kew Bull. 1911: 231. 1911; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 111. 1912; Prain, Hook. Ic. Pl. 31: t. 3008. 1915; Keay, Fl. W. Trop. Afr., ed. 2, 1: 399. 1958. TYPE: *Cyrtogonone argentea* (Pax) Prain [*Crotonogyne argentea* Pax].

A monotypic genus of west Africa (Nigeria to Cameroon).

268. *Crotonogyne* Muell. Arg., Flora 47: 535. 1864; DC. Prodr. 15(2): 720. 1866; Bentham, Gen. Pl. 3: 305. 1880; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 111. 1912; Prain, Hook. Ic. Pl. 31: t. 3019. 1915; Léonard, Fl. Congo 8(1): 174. 1962; Adam, Fl. Mt. Nimba 468, t. 165. 1971. TYPE: *Crotonogyne manniana* Muell. Arg.

Neomanniophyton Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 115. 1912. TYPE: *Neomanniophyton impeditum* (Prain) Pax [= *Crotonogyne impedita* Prain; lectotype, chosen here].

A genus of 15 species in west Africa (Sierra Leone to Congo and Angola).

269. *Manniophyton* Muell. Arg., Flora 47: 530. 1864; DC. Prodr. 15(2): 719. 1866; Bentham, Hook. Ic. Pl. 13: t. 1267. 1878; Gen. Pl. 3: 297. 1880; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 120. 1912; Keay, Fl. W. Trop. Afr., ed. 2, 1: 400. 1954; Léonard, Bull. Jard. Bot. Brux. 25: 290. 1955; Fl. Congo 8(1): 171. 1962; Adam, Mém. Mus. Hist. Nat. Paris 20: 495, t. 183. 1971. TYPE: *Manniophyton africanum* Muell. Arg.

A monotypic genus of west Africa (Sierra Leone to Angola and Príncipe).

Subtribe 44e. NEOBOUTONINAE (Hutchinson) Webster, Taxon 24: 600. 1975. Acalypheae subtribe *Mercurialinae* ser. *Neoboutoniiformes* Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 71. 1914. Tribe *Neoboutoniae* Hutch., Amer. J. Bot. 56: 752. 1969. TYPE: *Neoboutonia* Muell. Arg.

Tribe *Benoistieae* Radcliffe-Smith, Kew Bull. 43: 632. 1988. TYPE: *Benoistia* Perrier & Leandri.

Dioecious trees or shrubs; indumentum stellate or lepidote; leaves unlobed, pinnately or palmately veined, glandular-dotted, stipulate; inflorescences terminal or axillary, racemose to paniculate; calyx-segments 2 or 3; disk dissected or absent; stamens 15–40, filaments free, shorter than anthers; anthers with glandular connective; ovary 3-locular; styles bifid; fruit capsular; seeds carunculate or ecarunculate.

A subtribe of two genera, one African and one Madagascan. The two genera are quite distinct, and Radcliffe-Smith (1988) has proposed to place *Benoistia* in a separate tribe. However, *Neoboutonia* and *Benoistia* still seem more closely related to one another than to other taxa, so they are provisionally kept in the same subtribe.

KEY TO THE GENERA OF SUBTRIBE NEOBOUTONINAE

- 1a. Leaves palmately veined; stipules persistent; seeds carunculate 270. *Neoboutonia*
 1b. Leaves pinnately veined; stipules deciduous; seeds ecarunculate 271. *Benoistia*

270. *Neoboutonia* Muell. Arg., J. Bot. 2: 336. 1864; DC. Prodr. 15(2): 892. 1866; Bentham, Hook. Ic. Pl. 13: t. 1298, 1299. 1879; Gen. Pl. 3: 317. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 71. 1914; Robyns, Fl. Sperm. Parc Nat. Albert 1: 451, t. 44. 1948; Radcliffe-Smith, Fl. E. Trop. Afr., Eu-

phorb. 1: 231. 1987. TYPE: *Neoboutonia africana* Muell. Arg.

A genus of three African species.

271. *Benoistia* Perrier & Leandri, Bull. Soc. Bot. France 85: 528. 1938; Radcliffe-Smith, Kew Bull. 43: 632. 1988. TYPE: *Benoistia perrieri* Leandri [lectotype, chosen here].

A Madagascan genus of three species.

Subfamily V. EUPHORBIOIDEAE. TYPE: *Euphorbia* L.

Subfamily Sapioidae Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 310. 1954. TYPE: *Sapium* P. Browne.

Monoecious or less commonly dioecious trees, shrubs, or herbs (rarely scandent); laticifers non-articulated, latex usually whitish, sometimes scanty or apparently absent; indumentum simple or absent (dendritic in *Mabea*); leaves alternate or opposite, simple and unlobed, entire or dentate, usually pinnately veined, often with glands at base of blade; stipules usually small, often reduced or absent. Inflorescences terminal or axillary, spicate to racemose, paniculate, or pseudanthial (cyathium); bracts often biglandular at base; flowers apetalous. Staminate sepals 3–6, imbricate to valvate, mostly open in bud, commonly reduced or obsolete; disk absent; stamens 1–20(–70), filaments free or connate; pollen grains oblate to prolate, 3-colporate, colpi usually marginate, sexine usually tectate-perforate; pistillode absent. Pistillate sepals 3–6, free or connate, imbricate or open in bud, sometimes reduced or obsolete; disk absent; ovary 2–3(–20)-locular; styles nearly always unlobed, free or commonly connate into a column. Fruit capsular (rarely drupaceous); seeds carunculate or ecarunculate, testa dry or fleshy; endosperm copious.

The circumscription of subfamily Euphorbioideae and its five tribes is essentially the same as that adopted earlier (Webster, 1975). It corresponds roughly to the tribes Hippomaneae and Euphorbieae in the sense of Pax & Hoffmann (1931), except that the tribe Stomatocalyceae (included in the Gelonieae by Pax & Hoffmann) is added.

KEY TO THE TRIBES OF SUBFAMILY EUPHORBIOIDEAE

1a. Pollen sexine reticulate; inflorescences racemose or paniculate, bracts eglandular; stamens 10–30, free; staminate calyx 3–8-lobed; styles undivided; seeds ecarunculate; dioecious trees or lianas 45. STOMATOCALYCEAE

1b. Pollen sexine perforate-ectate; inflorescences mostly racemose, spicate, or pseudanthial; bracts mostly glandular or adnate to rachis; stamens 1–many, free or connate; monoecious (rarely dioecious) trees, shrubs or herbs, not scandent.

2a. Inflorescences mostly racemose or spicate (if capitate, then not pseudanthial); styles mostly undivided; staminate calyx usually developed.

3a. Floral bracts usually biglandular at base, not peltate nor adnate to the rachis; stamens free or connate.

4a. Staminate calyx open in bud; leaves mostly not spinulose-dentate; stamens free or filaments connate; seeds carunculate or ecarunculate 46. HIPPOMANEAE

4b. Staminate calyx closed in bud, valvately dehiscent into 2 segments; leaves spinose-dentate; filaments and anthers connate; seeds ecarunculate 47. PACHYSTROMATEAE

3b. Floral bracts eglandular, peltate or adnate to the rachis and covering flowers; seeds ecarunculate 48. HUREAE

2b. Inflorescences pseudanthial (cyathial), usually with a single terminal pistillate flower and 4 or 5 lateral staminate monochasia or dichasia; perianth reduced or absent; styles mostly bifid; seeds carunculate or ecarunculate 49. EUPHORBIEAE

Tribe 45. STOMATOCALYCEAE (Muell. Arg.) Webster, Taxon 24: 600. 1975. Hippomaneae subtribe Stomatocalyceae Muell. Arg., Linnaea 34: 202. 1865. TYPE: *Stomatocalyx* Muell. Arg. [= *Pimelodendron* Hassk.].

Dioecious trees, shrubs, or lianas; latex yellowish, often scanty; indumentum usually absent; leaves alternate, unlobed, pinnately veined, without glands at base of blade; stipules small and caducous or absent. Inflorescences axillary, racemose, bracts eglandular. Staminate sepals 4–8, free and imbricate or connate and calyx 2-lipped; stamens 10–30, free, filaments short; pollen grains coarsely reticulate or reticulate-perforate. Pistillate sepals 5 or 6, free or connate and 2-lipped; ovary 2–10-locular; styles unlobed, sometimes dilated or stigmatiform. Fruit capsular or indehiscent, 1–3-seeded; seeds ecarunculate; endosperm copious, oily.

This tribe includes one neotropical and three paleotropical genera, distributed into two subtribes. Some characteristics within the Stomatocalyceae, such as the liana habit, colored latex, and oily endosperm, suggest possible affinity with *Omphalea*, in the Acalyphoideae.

KEY TO THE SUBTRIBES OF TRIBE STOMATOCALYCEAE

- 1a. Pollen grains finely reticulate-perforate; fruits indehiscent; styles abbreviated; ovary 2-10-locular 45a. Stomatocalycinae
 1b. Pollen grains coarsely reticulate; fruits capsular; styles \pm elongated; ovary 2-3-locular 45b. Hamilcoinae

45a. Subtribe STOMATOCALYCINAE Muell. Arg., *Linnaea* 34: 202. 1865; DC. Prodr. 15(2): 1142. 1866. TYPE: *Stomatocalyx* Muell. Arg. [= *Pimelodendron* Hassk.].

Trees or shrubs; leaves entire or dentate; racemes simple or slightly branched; sepals distinct or connate; stamens 10-20; pollen grains finely reticulate; ovary 1-10-locular; styles stigmatiform; fruit indehiscent, 1-seeded.

This subtribe includes two genera, one of Indonesia, the other of Africa.

KEY TO THE GENERA OF SUBTRIBE STOMATOCALYCINAE

- 1a. Sepals 6-8, free; ovary 1-locular 272. *Plagiostyles*
 1b. Sepals connate, staminate calyx 2-lipped; ovary 2-10-locular 273. *Pimelodendron*

272. *Plagiostyles* Pierre, Bull. Mens. Soc. Linn. Paris 2: 1326. 1897; Prain, Kew Bull. 1912: 107. 1912; Fl. Trop. Afr. 6(1): 1001. 1913; Pax & Hoffm., Pflanz. 147. VII (Heft 63): 420. 1914; Stapf, Hook. Ic. Pl. 31: t. 3010. 1915; Léonard, Fl. Congo 8(1): 131. 1962. TYPE: *Plagiostyles klaineana* Pierre [= *Plagiostyles africana* (Muell. Arg.) Prain].

A monotypic genus of west Africa (southern Nigeria to Gabon and Congo).

273. *Pimelodendron* Hasskarl, Versl. Med. Afd. Natuurk. Kon. Akad. Wetensch. 4: 140. 1856; Benth., Gen. Pl. 3: 331. 1880; Pax & Hoffm., Pflanz. 147. V (Heft 52): 54. 1912; J. J. Smith, Bull. Jard. Bot. Buit. III. 6: 100. 1924; Whitmore, Tree Fl. Malaya 2: 124. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 186. 1975; 8: 196. 1980; Kew Bull. 36: 339. 1981. TYPE: *Pimelodendron amboinicum* Hassk.

Stomatocalyx Muell. Arg., DC. Prodr. 15(2): 1142. 1866. TYPE: *Stomatocalyx griffithianus* Muell. Arg. [= *Pimelodendron griffithianum* (Muell. Arg.) Benth. ex Hook. f.].

An Australasian genus of six to eight species distributed from Malaya to New Guinea, tropical Australia (Queensland), and the Solomon Islands.

45b. Subtribe HAMILCOINAE Pax & Hoffmann, Pflanz. 147. VII (Heft 63): 419. 1914. TYPE: *Hamilcoa* Prain.

Trees or lianas; leaves long-petiolate, entire or crenate; racemes simple or branched; staminate sepals 4 or 5, distinct, imbricate; stamens 10-20, free, filaments very short; pollen grains coarsely reticulate; pistillate sepals 4-6, \pm distinct; ovary 2- or 3-locular; styles connate below, erect or spreading; fruit capsular.

A group of two genera, one American and one African. Although included in two different subtribes of the Gelonieae by Pax & Hoffmann (1931), *Hamilcoa* and *Nealchornea* share similar distinctively coarse-reticulate pollen grains that are curiously similar in ornamentation to those of *Daléchampia*.

KEY TO THE GENERA OF SUBTRIBE HAMILCOINAE

- 1a. Ovary 3-locular; styles erect; stamens 18-20; pistillate sepals not glandular; stems \pm scandent 274. *Hamilcoa*
 1b. Ovary 2-locular; styles spreading; stamens 10; pistillate sepals with large basal glands; stems not scandent 275. *Nealchornea*

274. *Hamilcoa* Prain, Kew Bull. 1912: 107. 1912; Fl. Trop. Afr. 6(1): 1000. 1913; Pax & Hoffm., Pflanz. 147. VII (Heft 63): 419. 1914; Stapf, Hook. Ic. Pl. 31: t. 3009. 1915; Keay, Fl. W. Trop. Afr., ed. 2, 1: 413. 1958. TYPE: *Hamilcoa zenkeri* (Pax) Prain [*Plukenetia zenkeri* Pax].

A monotypic genus of west African rainforests (Cameroon).

275. *Nealchornea* Huber, Bol. Mus. Goeldi 7: 297. 1913; Pax & Hoffm., Pflanz. 147. XIV (Heft 68): 51. 1919; Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 107. 1925; Macbride, Field Mus. Nat. Hist., Bot. 13(III A, 1): 180. 1951. TYPE: *Nealchornea yapurensis* Huber.

A monotypic genus of the Amazonian rainforests (eastern Colombia and Peru to Brazil).

Tribe 46. HIPPOMANEAE A. Jussieu ex Spach, Hist. Nat. Veg. 2: 522. 1834. TYPE: *Hippomane* L.

Monocious (less commonly dioecious) trees, shrubs, or herbs; latex usually milky, commonly acrid or toxic; indumentum simple or absent (dendritic in *Mabea*); leaves alternate (rarely opposite),

simple and unlobed, pinnately veined (rarely palmately veined), commonly with laminar or petiolar glands; stipules conspicuous to reduced or absent. Inflorescences terminal or axillary, racemose or spicate (sometimes paniculate), usually bisexual with one or a few pistillate flowers at base; bracts mostly glandular. Staminate calyx open in bud (exposing anthers), sepals distinct or connate, imbricate to valvate, sometimes vestigial or absent; stamens 1–70, free or filaments connate below; anthers discrete, exorse; pollen grains 3-colporate, colpi usually marginate, sexine perforate-tectate. Pistillate sepals 3–6, imbricate, sometimes reduced or absent; ovary 2–3-locular (rarely 4–10); styles free or connate, unlobed. Fruit capsular or drupaceous; seeds carunculate or ecarunculate, testa dry or fleshy; endosperm copious, not markedly oily.

This diverse complex of 400–500 species was divided by Pax & Hoffmann (1912) into four subtribes, but these are so poorly defined that it seems impossible to maintain them. Generic delimitations are uncertain and controversial, and may change drastically when a monographic revision is completed.

KEY TO THE SUBTRIBES OF TRIBE HIPPOMANEAE

- 1a. Staminate receptacle convex or conical; staminate sepals 3–6, imbricate; stamens mostly 6–70, free; seeds carunculate; inflorescences terminal, paniculate; leaves stipulate, without petiolar glands 46a. Mabeinae
- 1b. Staminate receptacle plane; staminate sepals mostly 2 or 3, sometimes only 1 or absent; stamens 1–6(–20), filaments free or united; inflorescences terminal or axillary, racemose or spicate (axes not compound); leaves often with petiolar glands.
 - 2a. Staminate calyx laterally compressed; stamens 5–20, free; leaves with petiolar glands, stipules large and deciduous; latex watery; seeds carunculate 46b. Carumbiinae
 - 2b. Staminate calyx not laterally compressed; stamens 1–20, filaments free or connate; leaves with or without petiolar glands, stipules small or absent; latex usually milky; seeds carunculate or ecarunculate 46c. Hippomaninae

Subtribe 46a. MABEINAE Pax & Hoffmann, *Pflanzenr.* 147. V (Heft 52): 22. 1912. TYPE: *Mabea* Aubl.

Monoecious trees or shrubs; latex milky, innocuous; indumentum of dendritic hairs, or absent; leaves alternate, pinnately veined, without laminar or petiolar glands, stipulate; inflorescences terminal, bisexual, racemose or paniculate, bracts biglan-

dular; staminate sepals 3–6, imbricate; stamens 2–70, free from an expanded receptacle or connate into a column; pistillate sepals 3–6, sometimes glandular; ovary 3-locular, exappendiculate; styles connate into a column, tips slender and unlobed; fruit capsular; seeds carunculate.

This neotropical subtribe includes three genera as conventionally defined.

KEY TO THE GENERA OF SUBTRIBE MABEINAE

- 1a. Styler column elongate; style tips slender, unlobed; inflorescence rachis \pm flexuous; staminate flowers long-pedicellate; stamens (3–)10–70; leaves and stems with dendritic hairs 276. *Mabea*
- 1b. Styler column short, style tips rather thick; inflorescence rachis rigid; stamens 3–12.
 - 2a. Latex very scanty or absent; indumentum absent; stamens 5–12; leaves chartaceous 277. *Senefeldera*
 - 2b. Latex copious, milky; indumentum of dendritic hairs present on inflorescence axes; stamens 2 or 3; leaves rigid 278. *Senefelderopsis*

276. *Mabea* Aublet, *Hist. Pl. Guyane Fr.* 2: 867, t. 334. 1775; Muell. Arg., DC. *Prodr.* 15(2): 1148. 1866; *Fl. Bras.* 11(2): 515. 1874; Bentham, *Gen. Pl.* 3: 363. 1880; Pax & Hoffm., *Pflanzenr.* 147. V (Heft 52): 26. 1912; Jablonski, *Mem. New York Bot.* 17: 164. 1967; den Hollander & Berg, *Proc. Kon. Ned. Akad. Wet.* 89C: 147. 1986; Huft, *Phytologia* 62: 339. 1987; Ann. *Missouri Bot. Gard.* 75: 1125. 1989. TYPE: *Mabea piri* Aubl. [lectotype, designated by Pfeiffer, *Nomencl. Bot.* 2(1): 191. 1874].

A diverse and difficult genus of ca. 50 neotropical species.

277. *Senefeldera* Martius, *Flora* 24 (Beibl. 2): 29. 1841; Muell. Arg., DC. *Prodr.* 15(2): 1153. 1866; *Fl. Bras.* 11(2): 529. 1874; Bentham, *Gen. Pl.* 3: 332. 1880; Pax & Hoffm., *Pflanzenr.* 147. V (Heft 52): 23. 1914; Jablonski, *Mem. New York Bot. Gard.* 12: 171. 1965; Webster, *Ann. Missouri Bot. Gard.* 75: 1127. 1989. TYPE: *Senefeldera multiflora* Mart.

A neotropical genus of 8–10 species, mainly in Amazonian South America but reaching north to Panama.

278. *Senefelderopsis* Steyermark, *Bot. Mus. Leaflet.* Harvard Univ. 15: 45. 1951; Jablonski,

Mem. New York Bot. Gard. 12: 174. 1965; Gillespie, Brittonia 45: 92. 1993. TYPE: *Senefelderopsis croizatii* Steyerl.

A genus of four species endemic to South America (tepui areas of Colombia, Venezuela, northern Brazil).

Subtribe 46b. CARUMBIINAE Muell. Arg., Linnaea 34: 203. 1865; DC. Prodr. 15(2): 1142. 1866. TYPE: *Carumbium* Reinw. [= *Omalanthus* A. Juss.].

Hippomaneae subtribe Homalanthinae Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 42. 1912. TYPE: *Omalanthus* A. Juss.

Monoecious or dioecious trees or shrubs; latex watery, innocuous; leaves entire, pinnately to palmately veined, petiolate, glandular at apex of petiole, stipulate; inflorescence terminal, racemose, usually bisexual, bracts biglandular; staminate calyx compressed and 2-lipped, or of only 1 lobe; stamens 5–50, filaments free; pistillate calyx 2- or 3-lobed; ovary 2-locular (rarely 3-locular), exapp pendiculate; styles free or nearly so, unlobed to bifid, usually glandular near tip; fruit dehiscent or indehiscent; seeds with large caruncle.

As interpreted earlier (Webster, 1975), subtribe Carumbiinae is here treated as including only the type genus *Omalanthus*. Pax & Hoffmann (1912) also included *Pimelodendron* in the subtribe, probably because of the similar staminate calyx. However, *Pimelodendron* differs in its pollen sexine ornamentation, eglandular bracts, and ecarunculate seeds.

279. *Omalanthus* A. Jussieu, Tent. Euphorb. 50. 1824; Bentham, Gen. Pl. 3: 331. 1880 (as *Homalanthus*); Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 42. 1912; J. J. Smith, Nova Guinea 8: t. 140, 141. 1912; 12: t. 228, 229. 1917; Airy Shaw, Kew Bull. 21: 409. 1968; Kew Bull. Add. Ser. 8: 115. 1980; Sykes, New Zeal. J. Bot. 7: 302. 1969; A. C. Smith, Fl. Vit. Nova 2: 558. 1981; St. John, Nordic J. Bot. 4: 53. 1984. TYPE: *Omalanthus leschenaultianus* A. Juss. [= *Omalanthus populneus* (Geisel.) Pax].

Carumbium Reinwardt, Syll. Pl. Nov. 2(1): 6. 1826. TYPE: *Carumbium populifolium* Reinw. [= *Omalanthus populneus* (Geisel.) Pax].

Wartmannia Muell. Arg., Linnaea 34: 218. 1865. TYPE: *Wartmannia stillingiifolia* (F. Muell.) Muell. Arg. [= *Omalanthus stillingiifolius* F. Muell.].

Dibrachion Regel, Index Sem. Hort. Bot. Petropol. 1865: 51. 1866. TYPE: *Dibrachion peltatum* Regel [= *Omalanthus fastuosus* (Linden) Villar].

An Old World genus of ca. 30 species, extending from Malaya through Indonesia to the Pacific islands (as far as Tahiti and the Austral Islands).

Subtribe 46c. HIPPOMANINAE Grisebach, Fl. Brit. W. Ind. 49. 1859; Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 91. 1890. TYPE: *Hippomane* L.

Hippomaneae subtribe Adenopeltinae Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 57. 1912. TYPE: *Adenopeltis* Bert.

Hippomaneae subtribe Excoecariinae Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 153. 1912. TYPE: *Excoecaria* L.

Hippomaneae subtribe Gymnanthinae Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 57. 1912. TYPE: *Gymnanthes* Sw.

Hippomaneae subtribe Stillingiinae Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 174. 1912. TYPE: *Stillingia* Garden ex L.

Monoecious or dioecious trees, shrubs, or herbs; latex milky, often caustic; indumentum simple or absent; leaves alternate (rarely opposite), usually unlobed, pinnately veined, often with laminar or petiolar glands; stipules mostly small, sometimes obsolete or absent; inflorescences terminal or axillary, mostly spicate (sometimes racemose), bracts usually biglandular; staminate calyx open in bud, sepals 0–3; stamens 1–20, free or connate; pistillate sepals mostly 2 or 3, sometimes obsolete or absent; ovary 2–4-locular (6–10-locular in *Hippomane*), often carinate or horned; styles \pm connate, unlobed; fruit capsular or drupaceous; seeds carunculate or ecarunculate.

This subtribe is the major taxon within the subfamily other than the tribe Euphorbieae. The 500-odd species are distributed among about 15 genera, many of which are notoriously poorly delimited. Pax & Hoffmann (1912) proposed an unworkable system in which the genera were assigned to five subtribes; these cannot be satisfactorily distinguished. Future monographic work may provide some clues that will make it possible to subdivide subtribe Hippomaninae, but at present, a subdivision seems premature.

KEY TO THE GENERA OF SUBTRIBE HIPPOMANINAE

- 1a. Ovary 2–3-locular; fruits capsular or drupaceous.
 - 2a. Staminate spikes not capitular (or if so, seeds not foveolate).

- 3a. Staminate spikes conspicuously bracteate; staminate sepals mostly 3–5; stamens 3; seeds ecarunculate 280. *Spirostachys*
- 3b. Staminate spikes usually not conspicuously bracteate; staminate sepals 2 or 3 (or obsolete).
 - 4a. Seeds generally carunculate, testa dry.
 - 5a. Spikes usually terminal or opposite leaves; staminate calyx 2–3-lobed; pistillate flowers sessile or short-pedicellate (fruiting pedicels less than 1 cm long).
 - 6a. Columella not 3-horned at base; pistillate flowers often pedicellate 281. *Sebastiania*
 - 6b. Columella 3-horned at base; pistillate flowers sessile 282. *Stillingia*
 - 5b. Spikes axillary; staminate sepals 1 or 2, often reduced or obsolete; pistillate flowers distinctly pedicellate (1 cm long or more in fruit) 283. *Gymnanthes*
 - 4b. Seeds generally ecarunculate, testa dry or fleshy.
 - 7a. Fruit capsular (or if drupaceous then bracts glandular).
 - 8a. Dioecious (rarely monoecious); petioles usually eglandular; inflorescences axillary; staminate sepals distinct; ovary not appendiculate; caruncle deciduous from seed and persistent on columella 284. *Excoecaria*
 - 8b. Monoecious; petioles often glandular; inflorescences terminal or axillary.
 - 9a. Bracts glandular; leaves mostly with petiolar glands.
 - 10a. Seed coat dry; calyx suppressed.
 - 11a. Columella not 3-horned.
 - 12a. Stamens 2–4; leaves pinnately veined, unlobed 285. *Colliguaja*
 - 12b. Stamen 1; leaves palmately veined, ± lobed 286. *Dalembertia*
 - 11b. Columella 3-horned; leaves pinnately veined 287. *Adenopeltis*
 - 10b. Seed coat fleshy; staminate calyx present 288. *Sapium*
 - 9b. Bracts eglandular.
 - 13a. Spikes capitular, pseudoaxillary; stamens 3, filaments exerted beyond gamophyllous calyx; styles connate 289. *Glyphostylus*
 - 13b. Spikes elongated.
 - 14a. Spikes terminal; filaments connate; leaves with glands at apex of petiole 290. *Grimmeodendron*
 - 14b. Spikes axillary; filaments free; leaves eglandular 291. *Bonania*
 - 7b. Fruit drupaceous; inflorescences axillary; bracts eglandular 292. *Duvigneaudia*
 - 2b. Staminate spikes capitular, terminal; bracts glandular; seeds foveolate, with large caruncle 293. *Maprounea*
 - 1b. Ovary 6–10-locular; fruits drupaceous; spikes terminal; bracts glandular 294. *Hippomane*

280. *Spirostachys* Sonder, *Linnaea* 23: 106. 1850; Pax & Hoffm., *Pflanzenr.* 147. V (Heft 52): 153. 1912; Prain, *Fl. Trop. Afr.* 6(1): 1005. 1913; Alfaro Cardoso, *Serv. Agric. Moçamb.*, Publ. A18: 1. 1964; Dyer, *Gen. S. Afr. Fl. Pl.* ed. 3, 322. 1975; Radcliffe-Smith, *Fl. E. Trop. Afr.*, *Euphorb.* 1: 385. 1987. TYPE: *Spirostachys africana* Sond.

An African genus of one species (or two, if *Excoecaria venenifera* Pax is included).

281. *Sebastiania* Sprengel, *Neue Entdeck. Pflanzenk.* 2: 118, t. 3. 1820; Muell. Arg., *DC. Prodr.* 15(2): 1164. 1866; *Fl. Bras.* 11(2): 544. 1874; Bentham, *Gen. Pl.* 3: 336. 1880; Pax & Hoffm., *Pflanzenr.* 147. V (Heft 52): 88. 1914; *Natürl. Pflanzenfam.* ed. 2, 19c: 192. 1931; Smith, Downs & Klein, *Fl. Illustr. Catar.* EUFO 242. 1988; Webster & Huft, *Ann. Missouri Bot. Gard.* 75: 1127. 1989. TYPE: *Sebastiania brasiliensis* Spreng.

Gussonia Sprengel, *Neue Entdeck. Pflanzenk.* 2: 119. 1820. TYPE: *Gussonia discolor* Spreng. [= *Sebastiania discolor* (Spreng.) Muell. Arg.].

Microstachys A. Jussieu, *Euphorb. Tent.* 48. 1824. TYPE: *Microstachys bicornis* (Vahl) A. Juss. [= *Sebastiania corniculata* (Vahl) Muell. Arg.; lectotype].
Cnemidostachys Martius & Zuccarini, *Nova Gen. Sp.* 1: 66. 1824. TYPE: not designated (Martius described a large number of taxa of *Cnemidostachys*, and the choice of lectotype is best left to a future monographer of this group).

Ditrysinia Raf., *Neogenyton* 2. 1825. TYPE: *Ditrysinia ligustrina* (Mx.) Raf. [= *Sebastiania ligustrina* Mx.].
Adenogyne Klotzsch, *Arch. Naturgesch.* 7: 183. 1841. TYPE: *Adenogyne pachystachya* Kl. [= *Sebastiania pachystachys* (Kl.) Muell. Arg.].

Sarothrostachys Klotzsch, *Arch. Naturgesch.* 7: 185. 1841. TYPE: *Gymnanthes multiramea* Baillon [= *Sebastiania multiramea* (Baillon) Muell. Arg.].

Elachocroton F. Mueller, *Hook. J. Bot. Kew Gard. Misc.* 9: 17. 1857. TYPE: *Elachocroton asperococcum* F. Muell. [= *Sebastiania chamaelea* (L.) Muell. Arg.].

Tragiopsis Karsten, *Wochenschr. Gaertneri Pflanzenk.* 2: 5. 1859. TYPE: *Tragiopsis fruticulosa* Karst. [= *Sebastiania corniculata* (Vahl) Muell. Arg.].

Dendrocousinsia Millspaugh, *Field Mus. Publ. Bot.* 2: 374. 1913. TYPE: *Dendrocousinsia spicata* Millsp. [= *Sebastiania spicata* (Millsp.) Pax & Hoffm.].

A genus of ca. 100 species, mainly neotropical, but with outliers in temperate North America, Asia, and Australasia. The herbaceous species of section

Microstachys appear very different from the woody ones and may possibly represent a distinct genus. However, there are connecting links such as *Sebastiania panamensis* Webster (Webster & Huft, 1988), so that it seems preferable at present to maintain the broad (and probably unnatural) generic circumscription of Pax & Hoffmann (1931).

282. *Stillingia* Garden ex L., Syst. Nat. ed. 12, 2: 637. 1767; Mant. Pl. 19, 126. 1767; Muell. Arg., DC. Prodr. 15(2): 1155. 1866; Fl. Bras. 11(2): 537. 1874; Bentham, Gen. Pl. 3: 334. 1880; Pax & Hoffm., Pflanzenr. 146. V (Heft 52): 180. 1912; Rogers, Ann. Missouri Bot. Gard. 38: 207. 1951; van Steenis, Blumea Suppl. 5: 302. 1966; Webster, J. Arnold Arbor. 48: 388. 1967; A. C. Smith, Fl. Vit. Nov. 2: 565. 1981. TYPE: *Stillingia sylvatica* L.

Gymnostillingia Muell. Arg., Linnaea 32: 89. 1863. TYPE: *Gymnostillingia acutifolia* (Benth.) Muell. Arg. [= *Stillingia acutifolia* (Benth.) Hemsl.; lectotype, designated by Wheeler, 1975].

A mainly American genus of ca. 25 species, with a few disjunct taxa in the Mascarene Islands, eastern Malaysia, and Fiji.

283. *Gymnanthes* Swartz, Prodr. Veg. Ind. Occ. 6, 95. 1788; Grisebach, Fl. Brit. W. Ind. 50. 1859; Bentham, Gen. Pl. 3: 337. 1880; Sargent, Silva N. Amer. 7: t. 309. 1895; Pax & Hoffm., Pflanzenr. 147. V. (Heft 52): 81. 1912; Fawc. & Rend., Fl. Jam. 4: 329. 1920; Webster, J. Arnold Arbor. 48: 387. 1967; Taxon 32: 304. 1983; Ann. Missouri Bot. Gard. 75: 1129. 1989. TYPE: *Gymnanthes lucida* Sw. [lectotype, chosen by Grisebach, 1859].

Actinostemon Martius ex Klotzsch, Arch. Naturgesch. 7: 184. 1841; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 57. 1912; Jablonski, Phytologia 18: 213. 1969. TYPE: *Actinostemon concolor* (Spreng.) Muell. Arg. [*Gussonia concolor* Spreng. = *Gymnanthes concolor* (Spreng.) Muell. Arg.; lectotype, designated by Jablonski, Mem. New York Bot. Gard. 17: 177. 1967; Farr et al. (1979) incorrectly cited *Actinostemon grandifolius* Kl., an invalid name].

Dactylostemon Klotzsch, Arch. Naturgesch. 7: 181. 1841. TYPE: *Dactylostemon schomburgkii* Kl., Hook. London J. Bot. 2: 44. 1843 [= *Gymnanthes schomburgkii* (Kl.) Webster, comb. nov.; lectotype, chosen here].

As circumscribed here following Webster (1989), *Gymnanthes* is an American genus of ca. 40 species. Although most 20th-century workers have followed Pax & Hoffmann (1912) in recognizing

Actinostemon as a distinct genus, there appear to be no satisfactory distinguishing characters. In the previous century, Baillon (1858) upheld *Actinostemon* as distinct, while Mueller (1866) maintained *Actinostemon* and *Dactylostemon* as separate genera but combined *Gymnanthes* with *Sebastiania*. Generic delimitation clearly remains a major problem in this complex of neotropical Hippomaninae with reduced staminate flowers.

Following Rothmaler (1944), a number of American botanists have adopted the name *Ateramnus* P. Browne in place of *Gymnanthes*. However, this is based on a very questionable identification of Browne's plant from Jamaica with *Gymnanthes lucida* Sw.; it appears more likely that Browne had a species of *Sapium* (Webster, 1983).

284. *Excoecaria* L., Syst. Nat. ed. 10, 1288. 1759; Bentham, Gen. Pl. 3: 337. 1880; Hook. f., Fl. Brit. Ind. 5: 472. 1888; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 157. 1912; Gagnepain, Fl. Indochine 5: 402. 1926; Airy Shaw, Kew Bull. 26: 268. 1971; Whitmore, Tree Fl. Malaya 2: 96. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 112. 1975; 8: 88. 1980; Kew Bull. 35: 630. 1980; 36: 296. 1981; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 382. 1987. TYPE: *Excoecaria agallocha* L.

Commia Loureiro, Fl. Cochinchin. 605. 1790. TYPE: *Commia cochinchinensis* Lour. [= *Excoecaria agallocha* L. ?].

Anomostachys (Baillon) Hurusawa, J. Fac. Sci. Univ. Tokyo Bot. 6: 311. 1954. TYPE: *Stillingia lastellii* Baillon [= *Excoecaria lastellii* (Baillon) Muell. Arg.].

A paleotropical genus of ca. 40 species, mostly in tropical Asia but a few taxa in Africa, Madagascar, and tropical Australia. Mueller (1866, 1974) gave *Excoecaria* a very broad circumscription including *Sapium*, but this has not been followed by recent authors.

285. *Colliguaja* Molina, Saggio Chile 158. 1781; Hooker, Bot. Misc. 1: 138. 1830; Muell. Arg., DC. Prodr. 15(2): 1226. 1866; Fl. Bras. 11(2): 630, t. 85. 1874; Bentham, Gen. Pl. 3: 338. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 265. 1912; L. Smith et al., Fl. Illustr. Catar. EUFO 326. 1988. TYPE: *Colliguaja odorifera* Mol.

A South American genus of five species.

286. *Dalembertia* Baillon, Etude Gén. Euphorb. 545. 1858; Muell. Arg., DC. Prodr. 15(2): 1225. 1866; Bentham, Gen. Pl. 3:

339. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 268. 1912; Standley & Steyererm., Fieldiana Bot. 24(6): 86. 1949. TYPE: *Dalembertia populifolia* Baillon.

Alcoceria Fernald, Proc. Amer. Acad. Arts Sci. 36: 493. 1901. TYPE: *Alcoceria pringlei* Fern. [= *Dalembertia populifolia* Baillon].

A well-marked genus of five species in Mexico and Guatemala, distinguished by its compact inflorescence and highly reduced staminate flowers.

287. *Adenopeltis* Bertero ex A. Jussieu, Ann. Sci. Nat. I. 25: 24. 1832; Muell. Arg., DC. Prodr. 15(2): 1164. 1866; Bentham, Gen. Pl. 3: 338. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 264. 1912. TYPE: *Adenopeltis colliguaya* Bert. ex A. Juss. (nom. illeg.) [= *Excoecaria serrata* Ait., Hort. Kew. ed. 2, 5: 418. 1813; = *Adenopeltis serrata* (Ait.) Webster, comb. nov.].

A monotypic genus of Chile.

288. *Sapium* P. Browne, Civ. Nat. Hist. Jam. 338. 1756; Jacquin, Select. Stirp. Amer. Hist. 249. 1763; Bentham, Gen. Pl. 3: 334. 1880; Hemsley, Hook. Ic. Pl. 27: t. 2647–2650, 2677–2684. 1901–1902; 29: t. 2878–2900. 1909; Pittier, Contr. U.S. Natl. Herb. 12: 159. 1906; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 199. 1912; Fawc. & Rend., Fl. Jam. 4: 324. 1920; Gagnepain, Fl. Indochine 5: 394. 1926; Léonard, Bull. Jard. Bot. Brux. 29: 133. 1959; Fl. Congo 8(1): 151. 1962; Webster, J. Arnold Arbor. 48: 391. 1967; Jablonski, Phytologia 14: 441. 1967; 16: 393. 1968; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 389. 1987; Huft, Ann. Missouri Bot. Gard. 75: 1132. 1989; Kruijt & Zijlstra, Taxon 38: 320. 1989. TYPE: *Sapium jamaicense* Sw.

Triadica Loureiro, Fl. Cochinchin. 610. 1790. TYPE: *Triadica sinensis* Lour. [= *Sapium sebiferum* (L.) Roxb.; lectotype, chosen here].

Falconeria Royle, Ill. Bot. Himal. 354. 1839. TYPE: *Falconeria insignis* Royle [= *Sapium insigne* (Royle) Benth.; lectotype, designated by Wheeler, Taxon 24: 535].

Conosapium Muell. Arg., Linnaea 32: 87. 1863. TYPE: *Conosapium madagascariense* Muell. Arg. [= *Sapium madagascariense* (Muell. Arg.) Pax].

Taeniosapium Muell. Arg., DC. Prodr. 15(2): 1200. 1866. TYPE: *Taeniosapium goudotianum* (Muell. Arg.) Muell. Arg. [= *Sapium goudotianum* (Muell. Arg.) Pax].

Shirakia Hurusawa, J. Fac. Sci. Univ. Tokyo, Bot. 6:

317. 1954. TYPE: *Shirakia japonica* (Sieb. & Zucc.) Hurus. [= *Sapium japonicum* (Sieb. & Zucc.) Pax].

As here delimited, *Sapium* is a large and diverse genus of ca. 90–100 species, the majority neotropical, a minority Asian. *Triadica*, accepted by some Asian workers, is distinctively different from the neotropical species in such features as its non-arillate seeds; further investigation may show that it should be generically separate from *Sapium*.

289. *Glyphostylus* Gagnepain, Bull. Soc. Bot. France 71: 871. 1925; Fl. Indochine 5: 402. 1926; Airy Shaw, Kew Bull. 16: 372. 1963; 26: 281. 1972. TYPE: *Glyphostylus laoticus* Gagnep.

A monotypic genus of southeast Asia (Thailand to Vietnam).

290. *Grimmeodendron* Urban, Symb. Ant. 5: 397. 1908; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 258. 1912; Fawc. & Rend., Fl. Jam. 4: 326. 1920; Alain, Fl. Cuba 3: 119. 1953; Correll & Correll, Fl. Bahama Arch. 818. 1982; Liogier, Fl. Española 4: 153. 1986. TYPE: *Grimmeodendron jamaicense* Urban [lectotype, designated by Wheeler, 1975].

A West Indian genus of two species.

291. *Bonania* A. Richard, Hist. Fis. Cuba, 2, 11: 201. 1853; Bentham, Gen. Pl. 3: 335. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 259. 1912; Alain, Fl. Cuba 3: 115. 1953; Borhidi, Acta Bot. Acad. Sci. Hungar. 22: 305. 1976; Correll & Correll, Fl. Bahama Arch. 784. 1982. TYPE: *Bonania cubana* A. Rich.

Hypocoton Urban, Symb. Ant. 7: 263. 1912. TYPE: *Hypocoton domingensis* Urb. [= *Bonania domingensis* (Urb.) Urb.].

A genus of ca. eight species, mostly in Cuba but with one each in the Bahamas and Hispaniola.

292. *Duvigneaudia* Léonard, Bull. Jard. Bot. Brux. 29: 15. 1959; Fl. Congo 8(1): 139. 1962. TYPE: *Duvigneaudia inopinata* (Prain) Léonard.

A monotypic genus of west Africa (Cameroon to Congo and Gabon).

293. *Maprounea* Aublet, Hist. Pl. Guiane Fr. 895. 1775; Muell. Arg., DC. Prodr. 15(2):

1190. 1866; Fl. Bras. 11(2): 542. 1874; Bentham, Gen. Pl. 3: 333. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 175. 1912; Léonard, Fl. Congo 8(1): 142. 1962; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 395. 1987; Webster, Ann. Missouri Bot. Gard. 75: 1131. 1988; L. Smith et al., Fl. Illustr. Catar. EUFO 316. 1988. TYPE: *Maprounea guianensis* Aubl.

Aegopricum L., Pl. Surinam. 15. 1775. TYPE: *Aegopricum betulinum* L. [= *Maprounea guianensis* Aubl.].

A genus with a disjunct distribution, one or two species in South America and Panama, and two in west Africa.

294. Hippomane L., Sp. Pl. 1191. 1753; Gen. Pl. 499. 1754; Muell. Arg., DC. Prodr. 15(2): 1199. 1866; Bentham, Gen. Pl. 3: 333. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 261. 1912; Fawc. & Rend., Fl. Jam. 4: 327. 1920; Webster, J. Arnold Arbor. 48: 393. 1967; Correll & Correll, Fl. Bahama Arch. 818. 1982; Liogier, Fl. Española 4: 158. 1986; Webster, Ann. Missouri Bot. Gard. 75: 1131. 1988; Howard, Fl. Lesser Ant. 5: 54. 1989. *Mancanilla* Miller, Gard. Dict. Abr. Ed. 4. 1754. TYPE: *Hippomane mancinella* L. [lectotype, designated by M. L. Green, Prop. Brit. Bot. 195. 1929].

A neotropical genus of three species, one widespread in the Caribbean and Galápagos, the other two endemic to Hispaniola.

Tribe 47. PACHYSTROMATEAE (Pax & Hoffmann) Pax, Bot. Jahrb. 59: 145. 1924. Acalypheae subtribe Pachystromatinae Pax & Hoffm., Pflanzenr. 147. XIV (Heft 68): 3. 1919. TYPE: *Pachystroma* Muell. Arg.

Monoecious trees or shrubs; stems with milky latex; indumentum absent; leaves alternate, unlobed, pinnately veined, margins entire to mostly spinose-dentate, stipulate. Inflorescence spicate, terminal, pistillate flowers proximal on spikes or in upper axils; staminate bracts biglandular. Staminate flowers subsessile; sepals 5 or 6, valvate; disk absent; stamens 3, filaments connate into a column, anthers extrorse; pollen grains 3-colporate, perforate-tectate; pistillode absent. Pistillate flowers subsessile; sepals 3, persistent; disk absent; ovary 3-locular; styles basally connate, unlobed. Fruit capsular; columella 3-horned at base; seeds ecarunculate, endosperm present.

This tribe includes only the type genus *Pachystroma*. The position of this tribe has been poorly understood owing to its initial misplacement by Mueller (1866) in the Acalypheae because of the valvate staminate calyx. Bentham, apparently misled by Mueller, referred *Pachystroma* to his subtribe Adrianeae. Pax & Hoffmann (1919) followed Mueller's example by creating a subtribe Pachystrominae in the Acalypheae, and finally (Pax, 1924; Pax & Hoffmann, 1931) placed the genus in a separate tribe following the Acalypheae. Curiously, no one seems to have paid attention to the opinion of Baillon (1865, 1866), who placed his synonymous genus *Acantholoma* in the Hippomaneae in the vicinity of *Stillingia*. In support of Baillon's disposition, characters such as the laticiferous stems, spicate inflorescence with glandular bracts, and perforate-tectate pollen grains of *Pachystroma* clearly rule out a placement in the Acalypheae and indicate a position in the Euphorbioideae. In fact, it is rather doubtful that *Pachystroma* should be kept in a distinct tribe; further study will probably show that it should be referred to a subtribe of the Hippomaneae.

295. Pachystroma Muell. Arg., Linnaea 34: 177. 1865; DC. Prodr. 15(2): 893. 1866; Fl. Bras. 11(2): 387, t. 54. 1874; Bentham, Gen. Pl. 3: 307. 1880; Pax, Pflanzenr. 147. II (Heft 44): 99. 1910; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 151. 1931; Smith et al., Fl. Illustr. Catar. EUFO 225. 1988. TYPE: *Pachystroma ilicifolium* Muell. Arg. [= *Pachystroma longifolium* (Nees) I. M. Jhnt.].

Acantholoma Gaudichaud ex Baillon, Adansonia I. 6: 231. 1866. TYPE: *Acantholoma spinosum* Gaud. ex Baillon [= *Pachystroma longifolium* (Nees) I. M. Jhnt.].

This monotypic Brazilian genus includes a single variable species found from Minas Gerais to Rio Grande do Sul.

Tribe 48. HUREAE Dumortier, Anal. Fam. Pl. 45. 1829 (as Huraceae); Webster, Taxon 24: 600. 1975. Hippomaneae subtribe Hureae Muell. Arg., Linnaea 34: 203. 1865. TYPE: *Hura* L.

Monoecious trees or shrubs; latex \pm toxic; indumentum absent; leaves alternate, unlobed, pinnately veined, biglandular at base of blade, stipulate. Inflorescences terminal or axillary, spicate; bracts \pm adnate to rachis of inflorescence, eglandular. Staminal calyx 2–3-lobed; disk absent; sta-

mens 1–20, free or filaments connate; pollen grains 3-colporate, colpi somewhat marginate, sexine very finely perforate-tectate. Pistillate sepals 5 or 6, free or connate; ovary 3–20-locular, exappendiculate; styles unlobed, connate. Fruit capsular; seeds ecarunculate, testa dry.

This strictly American tribe of four genera, with its center of diversity in eastern Brazil, closely approaches the tribe Hippomaneae via *Dalembertia*.

KEY TO THE GENERA OF TRIBE HUREAE

- 1a. Sepals 3–5, imbricate; styles united halfway or less.
 - 2a. Filaments of stamens connate; styles connate less than halfway; petioles mostly 1 cm or longer 296. *Tetraplandra*
 - 2b. Filaments free; styles connate halfway or more; petioles mostly 1 cm or shorter 297. *Algernonia*
- 1b. Sepals not imbricate; styles completely connate into a long column.
 - 3a. Ovary 3-locular; stylar column apically 3-lobed; stamen 1; staminate calyx rupturing into 2 or 3 segments; inflorescences axillary; leaves oblanceolate, cuneate at base 298. *Ophthalmoblapton*
 - 3b. Ovary 5–20-locular; stylar column apically dilated into a lobed disk; stamens 10–80, filaments connate; staminate calyx cupulate, truncate; inflorescences terminal (or pistillate flowers axillary); leaves ovate, rounded to cordate at base 299. *Hura*

296. *Tetraplandra* Baillon, Ann. Sci. Nat. IV. 9: 200. 1858; Etude Gén. Euphorb. 549. 1858; Muell. Arg., DC. Prodr. 15(2): 1230. 1866; Fl. Bras. 11(2): 533. 1874; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 275. 1912; Emmerich, Arq. Mus. Nac. Rio de Janeiro 56: 94. 1981. TYPE: *Tetraplandra leandri* Baill.

A neotropical genus of seven species, mostly in eastern Brazil, but also recorded from the Amazonian region as far west as Peru (Huft, pers. comm.).

297. *Algernonia* Baillon, Ann. Sci. Nat. IV. 9: 198. 1858; Etude Gén. Euphorb. 546. 1858; Muell. Arg. 15(2): 1230. 1866; Bentham, Gen. Pl. 3: 339. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 276. 1912; Emmerich, Arq. Mus. Nac. Rio de Janeiro 56: 92. 1981; Bradea 3: 148. 1981. TYPE: *Algernonia brasiliensis* Baill.

A neotropical genus of five species, endemic to eastern Brazil. The genera *Algernonia* and *Tetraplandra* appear very closely related, and it might be preferable to treat them as subgenera of a single genus.

298. *Ophthalmoblapton* Fr. Allemão, Pl. Novas Brasil, 1849; Ann. Sci. Nat. Bot. III. 13: 119. 1849; Muell. Arg. 15(2): 1155. 1866; Fl. Bras. 11(2): 531. 1874; Bentham, Gen. Pl. 3: 333. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 278. 1912; Emmerich, Bol. Mus. Nac. Rio de Janeiro, Bot. 62: 1. 1981; L. Smith et al., Fl. Illustr. Catar. EUFO 325. 1988; Howard, Fl. Lesser Ant. 5: 57. 1989. TYPE: *Ophthalmoblapton* Fr. Allem.

A neotropical genus of four species endemic to eastern Brazil.

299. *Hura* L., Sp. Pl. 1008. 1753; Gen. Pl. ed. 5, 439. 1754; Muell. Arg., DC. Prodr. 15(2): 1228. 1866; Bentham, Gen. Pl. 3: 339. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 271. 1912; Fawc. & Rend., Fl. Jam. 4: 333. 1920; Standley & Steyerl., Fieldiana Bot. 24(6): 124. 1949; Burch, Ann. Missouri Bot. Gard. 54: 330. 1968; Correll & Correll, Fl. Bahama Arch. 821. 1982. TYPE: *Hura crepitans* L.

A neotropical genus of two species, the type widespread from Cuba and Mexico south to Brazil, the other (*H. polyandra* Baill.) recorded from Mexico to Costa Rica; widely introduced throughout the tropics.

Tribe 49. EUPHORBIEAE [Blume, Bijdr. 631. 1825]; Pax & Hoffmann, Natürl. Pflanzenfam. ed. 2, 19c: 207. 1931; Wheeler, Amer. Midl. Nat. 30: 477. 1943. TYPE: *Euphorbia* L.

Monoecious (or less commonly dioecious) trees, shrubs, or herbs; latex milky, innocuous or toxic; indumentum simple or absent; leaves alternate, opposite, or whorled, mostly unlobed and pinnately veined, without laminar or petiolar glands; stipules present or absent. Inflorescences pseudanthial, the connate bracts forming a cyathium enclosing a single terminal pistillate flower and 4 or 5 lateral staminate monochasia; bracts eglandular. Staminate flower with calyx reduced or absent; stamen 1; pollen grains 3-colporate, colpi marginate, sexine perforate-tectate. Pistillate flower with calyx

3–6-lobed or absent; ovary (2-)3-(4-)locular; styles free or basally connate, bifid (rarely entire). Fruit capsular (rarely drupaceous); seeds carunculate or ecarunculate; testa dry, smooth or ornamented.

A large tribe of more than 1500 species, here divided (following Webster, 1975) into 3 subtribes with 11 genera. A catalogue of the more than 2000 species names in tribe Euphorbieae has recently been published by Oudejans (1990).

KEY TO THE SUBTRIBES OF TRIBE EUPHORBIEAE

- 1a. Staminate calyx present; involucre of 4 bracts, partially fused; cyathial glands commissural, not on rim of cyathial tube 49a. Anthosteminae
- 1b. Staminate calyx absent; involucre bracts usually 5, connate into a tube.
 - 2a. Petaloid appendages bracteal (dilated involucre lobes), opposite the staminate monochasia; cyathial glands commissural; bracts of staminate monochasia large, imbricate, enclosing staminate flowers; pistillate sepals 5 or 6, large, imbricate 49b. Neoguillauminiinae
 - 2b. Petaloid appendages interbracteal (i.e., opposite cyathial glands), alternate with staminate monochasia (sometimes absent); cyathial glands on rim of cyathium; bracts of staminate monochasia small or obsolete 49c. Euphorbiinae

Subtribe 49a. ANTHOSTEMINAE (Baillon) Webster, *Taxon* 24: 600. 1975. Anthostemideae Baillon, *Ann. Sci. Nat.* IV. 9: 192. 1858. Anthostemeae Kl. & Gcke., *Monatsber. Königl. Preuss. Akad. Wiss. Berlin* 1859: 247. 1859. TYPE: *Anthostema* A. Juss.

Monoecious or dioecious trees; leaves alternate, pinnately veined, stipules inconspicuous; cyathia in terminal or axillary dichasia; cyathial involucre of 4 outer bracts subtending or enclosing 4 subflorescences; pistillate flower solitary, central and terminal (or apparently lateral); staminate flowers in dichasia \pm enclosed by 4 secondary (inner) bracts; cyathial glands projecting inward from infolded margins of outer bracts; staminate flowers and pistillate flowers with gamophyllous calyx; ovary 3–4-locular; styles emarginate to bifid; fruit capsular; seeds carunculate or ecarunculate.

This paleotropical subtribe includes two genera of Africa and Madagascar. The cyathia in the Anthosteminae are apparently tetramerous and somewhat bilaterally symmetrical; the tetramery carries over to some extent in the Neoguillauminiinae, suggesting that the pentamerous condition in the Euphorbiinae may be a derived condition.

KEY TO THE GENERA OF SUBTRIBE ANTHOSTEMINAE

- 1a. Cyathia bisexual; involucre bracts laterally connate into an open 4-lobed involucre; cyathial glands at margins of internal bracts; inflorescences axillary; ovary 3-locular. 300. *Anthostema*
- 1b. Cyathia mostly unisexual; outer involucre bracts connate into a closed tube; cyathial glands fused by pairs into 4 lobes alternating with involucre lobes; inflorescences terminal; ovary 4-locular 301. *Dichostemma*

300. *Anthostema* A. Jussieu, *Euphorb. Tent.* 56. 1824; Baillon, *Ann. Sc. Nat.* 9: 193. 1858; Boissier, *DC. Prodr.* 15(2): 188. 1862; Bentham, *Gen. Pl.* 3: 261. 1880; Hutchinson, *Fl. Trop. Afr.* 6(1): 607. 1912; Pax & Hoffm., *Natürl. Pflanzenfam.* ed. 2, 19c: 207. 1931; Keay, *Fl. W. Trop. Afr.* ed. 2, 1: 416. 1958; Berhaut, *Fl. Ill. Sénégal* 3: 379. 1975. TYPE: *Anthostema senegalense* A. Juss.

A paleotropical genus of three species, two in west Africa and one in Madagascar.

301. *Dichostemma* Pierre, *Bull. Mens. Soc. Linn. Paris* 1 (159): 1259. 1896; Hutchinson, *Fl. Trop. Afr.* 6(1): 605. 1912; Pax & Hoffm., *Natürl. Pflanzenfam.* ed. 2, 19c: 207. 1931; Keay, *Fl. W. Trop. Afr.* ed. 2, 1: 416. 1958. TYPE: *Dichostemma glaucescens* Pierre.

A genus of three species in tropical west Africa.

Subtribe 49b. NEOGUILLAUMINIINAE Croizat, *Phil. J. Sci.* 64: 408. 1938; Webster, *Taxon* 24: 601. 1975. TYPE: *Neoguillauminiina* Croiz.

Trees or shrubs; indumentum absent; leaves alternate or opposite, entire; stipules obsolete; cyathia in axillary pedunculate cymes; involucre bracts 4(5), dilated or petaloid, connate near base; glands 4, 8, or 10, in 4 or 5 pairs, partitioning the staminate inflorescences; pistillate flower central, staminate flowers in bracteate monochasia; staminate calyx absent; pistillate sepals 5 or 6, imbricate; ovary 3-locular; styles connate at base, unlobed, dilated; fruit capsular; seeds smooth, carunculate.

As defined by Webster (1975), this subtribe includes two Australasian genera. In their pseudopetals developed from the involucre bracts, the cyathia of the Neoguillauminiinae are distinctively different from those in *Euphorbia*, with appendages developed from the interbracteal glands.

KEY TO THE GENERA OF SUBTRIBE
NEOGUILLAUMINIAE

- 1a. Cyathial glands 8 or 10, massive; petaloid involucre bracts large (ca. 1 cm long); leaves spiral 302. *Neoguillauminia*
1b. Cyathial glands 4, small; involucre bracts, if petaloid, less than 1 cm long; leaves opposite 303. *Calycopeplus*

302. Neoguillauminia Croizat, Phil. J. Sci. 64: 398. 1938; Bull. Jard. Bot. Buit. III. 17: 206. 1941; Guillaumin, Fl. Anal. Synopt. Nouv.-Caléd. 182. 1948; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 22, t. 3. 1987. TYPE: *Neoguillauminia cleopatra* (Baill.) Croiz. [*Euphorbia cleopatra* Baill.].

A monotypic New Caledonian genus, very different in habit from its Australian sister genus.

303. Calycopeplus Planchon, Bull. Soc. Bot. France 8: 30. 1861; Boissier, Ic. Euphorb. t. 120. 1866; Bentham, Fl. Austral. 6: 52. 1873; Gen. Pl. 3: 261. 1880; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 221. 1931; Airy Shaw, Kew Bull. 35: 603. 1980. TYPE: *Calycopeplus ephedroides* Planch.

A genus of three species endemic to Australia; although xeromorphic in vegetative morphology, they have cyathia that approach those of the Anhosteminae in structure.

Subtribe 49c. EUPHORBIINAE. TYPE: *Euphorbia* L.

Family Pedilanthaceae Kl. & Gcke., Monatsber. Preuss. Akad. Wiss. Berlin 1859: 247, 253. 1859. Eu-

phorbieae subtribe Pedilanthinae (Kl. & Gcke.) Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 226. 1954. TYPE: *Pedilanthus* Poit.

Euphorbieae subtribe Anisophyllae Kl. & Gcke., Monatsber. Preuss. Akad. Wiss. Berlin 1859: 247. 1859. TYPE: *Anisophyllum* Haw. [= *Chamaesyce* S. F. Gray].

Euphorbieae subtribe Tithymalinae Kl. & Gcke., Monatsber. Preuss. Akad. Wiss. Berlin 1859: 247. 1859. TYPE: *Tithymalus* Scopoli [= *Euphorbia* L.].

Monoecious (rarely dioecious) trees, shrubs, or herbs; latex milky, innocuous or toxic; indumentum simple or absent; leaves alternate, opposite, or whorled, unlobed (rarely lobed), usually pinnately veined, stipulate or exstipulate; inflorescences terminal or axillary, cyathia often subtended by paired bracts; cyathium distinctly cupulate with 4 or 5 interbracteal glands on the rim (rarely glands only 1 or 2); glands usually discrete, with or without petaloid appendages; pistillate flower central, staminate flowers in 4 or 5 monochasia, monochasial bracts reduced; staminate calyx absent; pistillate calyx 3-6-lobed, or often vestigial or absent; ovary 3-locular; styles distinct or connate, bifid (rarely entire); fruit capsular (rarely drupaceous); seeds carunculate or ecarunculate.

The subtribe is here considered to include seven genera, although some authors have subdivided *Euphorbia* into many segregates. There appears to be no necessity for further subdivision into subtribes such as the Pedilanthinae. Typification of the taxa is reviewed by Wheeler (1943).

KEY TO THE GENERA OF SUBTRIBE EUPHORBIINAE

- 1a. Cyathia (\pm) radially symmetrical, the glands not hidden within a nectar spur; styles mostly free or nearly so.
2a. Involucre glands (1-4) or 5, free, alternating with the lobes of the cyathium along the rim.
3a. Leaves alternate, opposite, or whorled, but if opposite then not inaequilateral at base; veins of leaf not chlorenchyma-sheathed; stipules present or absent; main (embryonic) axis not aborting; seeds carunculate or ecarunculate 304. *Euphorbia*
3b. Leaves opposite, stipulate, inaequilateral at base, veins with chlorenchyma sheaths; main axis ceasing growth above the cotyledons; seeds usually ecarunculate 305. *Chamaesyce*
2b. Involucre glands not 4 or 5 alternating with lobes; bracts subtending cyathium connate into a cup.
4a. Pistillate flower calyculate; involucre lobes fused and the 2 glands fused into a shield; seeds ecarunculate; stems not succulent 306. *Cubanthus*
4b. Pistillate flower naked; involucre and glands connate into an annular ring; seeds mostly carunculate; stems succulent.
5a. Cyathium somewhat bilaterally symmetrical, the gland with a gap on the lower side 307. *Monadenium*
5b. Cyathium radially symmetrical, without a gap on one side.
6a. Involucre glands conspicuous, ovary without angular crests 308. *Synadenium*
6b. Involucre glands distinct, located below the crenulate rim; ovary with prominent double crests at the angles 309. *Endadenium*

- 1b. Cyathium distinctly bilaterally symmetrical, the glands hidden within the nectar spur; styles connate into a long column 310. *Pedilanthus*

- 304. Euphorbia** L., Sp. Pl. 450. 1753; Gen. Pl. ed. 5, 208. 1754; Roeper, Enum. Euphorb. Germ. 9. 1824; Boissier, DC. Prodr. 15(2): 7. 1862; Icones Euphorbiarum, 1. 1866; Muell. Arg., Fl. Bras. 11(2): 666. 1874; Bentham, Gen. Pl. 3: 258. 1880; Norton, Ann. Rep. Missouri Bot. Gard. 11: 85. 1899; Pax, Bot. Jahrb. 34: 61. 1905; Berger, Sukkulente Euphorbien 1. 1907; N. E. Brown, Fl. Trop. Afr. 6(1): 470. 1911; Fl. Capensis 5(2): 222. 1925; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 208. 1931; Prokhanov, Consp. Syst. Tithymal. Asiae Mediae. 1933; Croizat, Bull. Jard. Bot. Buitenzorg III. 16: 351. 1940; Hurusawa, J. Jap. Bot. 16: 330. 1940; White, A., R. A. Dyer & B. L. Sloane, Succul. Euphorbieae. 1941; Wheeler, Amer. Midl. Nat. 30: 478. 1943; Leandri, Not. Syst. Paris 12: 64. 1946; Vindt, Trav. Inst. Sci. Chérifien 6: 23. 1953; Ursch & Leandri, Mém. Inst. Sci. Madag. 5B: 109. 1954; Dyer, Bull. Jard. Bot. Etat 27: 487. 1957; Dressler, Ann. Missouri Bot. Gard. 48: 329. 1961; Croizat, Webbia 20: 573. 1965; Webster, J. Arnold Arbor. 49: 395. 1967; Radcliffe-Smith & Tutin, Fl. Europaea 2: 213. 1968; Allem & Irgang, Fl. Illustr. Rio Grande do Sul 11: 15. 1975; M. C. Johnston, Wrightia 5: 120. 1975; Leach, Dinteria 12: 1. 1976; Hassall, Austral. J. Bot. 25: 430. 1977; Subils, Kurtziana 10: 83. 1977; Carter, Hook. Ic. Pl. 39: 5. 1982; Huft, Ann. Missouri Bot. Gard. 71: 1021. 1984; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 10. 1987; Gilbert, Kew Bull. 42: 231. 1987; Carter, Kew Bull. 42: 673. 1987; Fl. E. Trop. Afr., Euphorb. 2: 409. 1988; Deil & Müller-Hohenstein, Euphorbia J. 5: 109. 1988; Lebrun & Stork, Enum. Pl. Afr. Trop. 1: 213. 1991; Mayfield, Sida 14: 573. 1991; Lewton, Euphorbia J. 8: 113. 1992. TYPE: *Euphorbia antiquorum* L. (lectotype, designated by Millspaugh, Publ. Field Columbian Mus., Bot. 2: 306. 1909).
- Tithymalus* Gaertner, Fruct. 2: 115. 1790, nom. cons. TYPE: *Tithymalus peplus* (L.) Gaertner (= *Euphorbia peplus* L.).
- Dactylanthes anacantha* (Ait.) Haw. [= *Euphorbia anacantha* Ait.; lectotype].
- Esula* (Persoon) Hayworth, Syn. Pl. Succul. 153. 1812 (non Morandi, 1761). TYPE: *Esula dalechampii* Haw. [= *Euphorbia esula* L.].
- Galarhoeus* Haworth, Syn. Pl. Succul. 143. 1812. TYPE: *Galarhoeus helioscopius* (L.) Haw. [= *Euphorbia helioscopia* L.].
- Medusea* Haworth, Syn. Pl. Succul. 133. 1812. TYPE: *Medusea major* (Ait.) Haw. [= *Euphorbia capit-medusae* L. var. *major* Ait.; lectotype].
- Treisia* Haworth, Syn. Pl. Succul. 131. 1812. TYPE: *Treisia clava* (Jacq.) Haw. [= *Euphorbia clava* Jacq.].
- Poinsettia* Graham, Edinb. New Phil. J. 20: 412. 1836. TYPE: *Poinsettia pulcherrima* (Willd.) Graham [= *Euphorbia pulcherrima* Willd.].
- Lacanthis* Rafinesque, Fl. Tell. 2: 94. 1837. TYPE: *Lacanthis splendens* (Boj.) Raf. [= *Euphorbia splendens* Boj. = *E. milii* Desm.].
- Agaloma* Rafinesque, Fl. Tell. 4: 116. 1838. TYPE: *Euphorbia corollata* L. [lectotype].
- Alectoroctonum* Schlecht., Linnaea 19: 252. 1847. TYPE: *Alectoroctonum scotatum* Schlecht. [= *Euphorbia scotana* Schlecht.].
- Anthacantha* Lemaire, Ill. Hort. 4: Misc. 73. 1857. TYPE: *Euphorbia heptagona* L. [lectotype].
- Adenopetalum* Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 250. 1859 (non Turcz., 1858). TYPE: *Euphorbia graminea* Jacq. [lectotype].
- Arthrothamnus* Kl. & Gecke., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 251. 1859 (non Ruprecht, 1848). TYPE: *Arthrothamnus tirucalli* (L.) Kl. & Gecke. [= *Euphorbia tirucalli* L.].
- Dichrophyllum* Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 249. 1859. TYPE: *Dichrophyllum marginatum* (HBK) Kl. & Gecke. [= *Euphorbia marginata* HBK.].
- Euphorbiastrum* Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 252. 1859. TYPE: *Euphorbiastrum hoffmannianum* Kl. & Gecke. [= *Euphorbia hoffmanniana* (Kl. & Gecke.) Boiss.; lectotype].
- Sterigmanthe* Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 252. 1859. TYPE: *Euphorbia splendens* Boj. [= *Euphorbia milii* Desm.; lectotype].
- Tithymalopsis* Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 249. 1859. TYPE: *Euphorbia corollata* L. [lectotype].
- Trichosterigma* Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 248. 1859. TYPE: *Euphorbia fulgens* Karw. [lectotype].
- Lyciopsis* (Boissier) Schweinfurth, Beitr. Fl. Aethiop. 1: 37. 1867 (non Spach, 1835). TYPE: *Euphorbia cuneata* Vahl.
- Elaeophorbia* Stapf, in Johnston, Liberia 2: 646. 1906. TYPE: *Elaeophorbia drupacea* (Schum.) Stapf [= *Euphorbia drupacea* Schum.].
- Diplocyathium* H. Schmidt, Beih. Bot. Centralbl. 22(1): 40. 1907. TYPE: *Diplocyathium capitulatum* (Rchb.) Schmidt [= *Euphorbia capitulata* Rchb.].
- Euphorbiodendron* Millspaugh, Publ. Field Columbian Mus. Bot. 2: 305. 1909. TYPE: *Euphorbiodendron latazii* (HBK) Millsp. [= *Euphorbia latazii* HBK.; lectotype, chosen here; perhaps = *Euphorbia laurifolia* Lam.].
- Ctenadena* Prokhanov, Consp. Syst. Tithymal. Asiae Me-

diae 28. 1933. TYPE: *Ctenadena lanata* (Sieb.) Prokh. [= *Euphorbia lanata* Sieb.].

Cystidospermum Prokhanov, Consp. Syst. Tithymal. Asiae Mediae 25. 1933. TYPE: *Cystidospermum cheirolepis* (Fisch. & Mey.) Prokh. [= *Euphorbia cheirolepis* Fisch. & Mey.].

Sclerocyathium Prokhanov, Consp. Syst. Tithymal. Asiae Mediae 30. 1933. TYPE: *Sclerocyathium popovii* Prokh. [= *Euphorbia sclerocyathium* Korov. & Pop.].

A vast genus of over 1000 species, subdivided into many subgenera and sections, a number of which have been treated as distinct genera. The large number of synonyms cited here (lectotypifications by Wheeler, 1943) represents only a fraction of the published names that are referable to *Euphorbia*; they have been chosen because in the literature they have been treated as distinct at the generic or subgeneric level. The literature on *Euphorbia*, especially the succulent taxa, is vast, and it is not possible to cite here even a fraction of the relevant papers, including many important papers on succulent taxa by Leach and Rauh. Many references are provided by Wheeler (1943), Vindt (1960), Webster (1967), Carter & Radcliffe-Smith (1988), and Lebrun & Stork (1991); and numbers of taxa are discussed and illustrated in the eight volumes of the *Euphorbia Journal*. Nevertheless, there is great need for a comprehensive bibliographic guide to the taxonomic work on *Euphorbia* that would complement the list of species of Oudejans (1990). Some segregates, especially *Poinsettia*, have been adopted by a number of workers, and it remains to be seen if future work will confirm the conservative generic circumscription adopted by Boissier and his followers.

305. *Chamaesyce* S. F. Gray, Nat. Arrang. Brit. Pl. 2: 260. 1821; Croizat & Degener, Fl. Haw. 1936; Wheeler, Rhodora 43: 97. 1941; Burch, Ann. Missouri Bot. Gard. 53: 90. 1966; Webster, J. Arnold Arbor. 48: 420. 1967; Hassall, Austral. J. Bot. 24: 633. 1976; Mulligan & Lindsay, Naturaliste Canad. 105: 37–40. 1978; Koutnik, S. Afr. J. Bot. 3: 262. 1984; Allertonia 4(6): 331. 1987. TYPE: *Chamaesyce maritima* S. F. Gray [= *Chamaesyce pepelis* (L.) Prokh.].

Anisophyllum Haworth, Syn. Pl. Succ. 159. 1812 (non Jacquin, 1763). TYPE: *Anisophyllum pepelis* (L.) Haw. [= *Chamaesyce pepelis* (L.) Prokh.].

A widely distributed genus of ca. 250 species, most of them in tropical America and Africa; often treated as a subgenus of *Euphorbia*. Koutnik (1987) presented the most detailed analysis of the char-

acters that support generic status for *Chamaesyce*. However, it must be admitted that *Euphorbia* subsect. *Acutae* is in many ways intermediate between *Chamaesyce* and *Euphorbia* subg. *Agaloma*. By strictly phylogenetic criteria, conservative workers are correct in retaining *Chamaesyce* as a subgenus of *Euphorbia*, because its recognition makes the latter a paraphyletic group. An obvious solution to this is to further dismantle *Euphorbia* into segregate genera, in the tradition of Klotzsch and Garcke. However, this would not get workers using cladistic methodology off the hook, because a monophyletic *Chamaesyce* would probably have to include both *Euphorbia* subg. *Agaloma* as well as *Pedilanthus* and possibly *Cubanthus*. Until a detailed phylogenetic analysis of the Euphorbieae is completed, we have no practical alternative to continuing the use of the present artificial (but reasonably usable) system.

306. *Cubanthus* (Boissier) Millspaugh, Field Mus. Nat. Hist. Bot. 2: 371. 1913; Alain, Fl. Cuba 3: 127. 1953. TYPE: *Cubanthus linearifolius* (Griseb.) Millsp. [*Pedilanthus linearifolius* Griseb.].

A genus of three species endemic to the West Indies (Cuba and Hispaniola); very similar to species of *Euphorbia* sect. *Adenorima*, and perhaps to be included in that group.

307. *Monadenium* Pax, Bot. Jahrb. 19: 126. 1894; N. E. Brown, Fl. Trop. Afr. 6(1): 450. 1911; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 222. 1931; Bally, Genus *Monadenium*, 14. 1961; Carter, Kew Bull. 42: 903. 1987; Fl. E. Trop. Afr., Euphorb. 2: 540. 1988. TYPE: *Monadenium coccineum* Pax.

Stenadenium Pax, Bot. Jahrb. 30: 343. 1901. TYPE: *Stenadenium spinescens* Pax [= *Monadenium spinescens* (Pax) Bally].

An African genus of ca. 50 species, distributed from Somalia to the Transvaal.

308. *Synadenium* Boissier, DC. Prodr. 15(2): 187. 187. 1862; N. E. Brown, Fl. Trop. Afr. 6(1): 462. 1911; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 221. 1931; White, Dyer, & Sloane, Succ. Euphorbieae 951. 1941; Carter, Kew Bull. 42: 667. 1987; Fl. E. Trop. Afr., Euphorb. 2: 534. 1988. TYPE: *Synadenium arborescens* Boissier [= *Synadenium cupulare* (Boiss.) L. C. Wheeler].

A genus of 10–15 species of eastern and southern Africa, closely related to *Monadenium*.

- 309. Endadenium** Leach, Garcia de Orta 1: 31. 1973. TYPE: *Endadenium gossweileri* (N. E. Brown) Leach.

A monotypic genus of Angola; perhaps not distinct from the genus *Monadenium*.

- 310. Pedilanthus** Necker ex Poiteau, Ann. Mus. Nat. Hist. Nat. 19: 388. 1812; Boissier, DC. Prodr. 15(2): 4. 1862; Millspaugh, Field Mus. Publ. Bot. 2: 353. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 223. 1931; Wheeler, Contr. Gray Herb. 124: 43. 1939; Dressler, Contr. Gray Herb. 182: 1. 1957; Webster, J. Arnold Arbor. 48: 427. 1967; Koutnik, Euphorbia J. 3: 38. 1985. TYPE: *Pedilanthus tithymaloides* (L.) Poit.

Tithymalus Miller, Gard. Dict. Abr. Ed. 4. 1754. *Tithymaloides* Gomez Ortega, Tabl. Bot. 9. 1773 (nom. rej.). *Crepidaria* Haworth, Syn. Pl. Succ. 136. 1812. TYPE: *Tithymalus myrtifolius* Miller [= *Pedilanthus tithymaloides* (L.) Poit.].

Ventenatia Trattinick, Gen. Pl. 86. 1802 (non Cavanilles, 1798). TYPE: *Ventenatia bracteata* (Jacq.) Trat. [= *Pedilanthus bracteatus* (Jacq.) Boiss.].

Diadenaria Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 254. 1859. TYPE: *Diadenaria pavonis* Kl. & Gcke. [= *Pedilanthus bracteatus* (Jacq.) Boiss.].

Hexadenia Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 253. 1859. TYPE: *Hexadenia macrocarpa* (Benth.) Kl. & Gcke. [= *Pedilanthus macrocarpus* Benth.].

A neotropical genus of ca. 15 species, all except one confined to Mexico and adjacent Central America.

INCERTAE SEDIS

- 311. Chlamydojatropha** Pax & Hoffmann, Pflanzenr. 147. VI (Heft 57): 125. 1912; Natürl. Pflanzenfam., ed. 2, 19c: 167. 1931. TYPE: *Chlamydojatropha kamerunica* Pax & Hoffm.

This mysterious plant, known only from pistillate specimens from Cameroon, was placed next to *Mildbraedia* by Pax & Hoffmann (1931). Until the staminate flowers are described, it cannot be definitely placed.

- 312. Martretia** Beille, Compt. Rend. Hebd. Séances Acad. Sci. (Paris) 145: 1294. 1907; Bull. Soc. Bot. France 55 (Mém. 2) 8: 64. 1908; Pax & Hoffmann, Natürl. Pflanzenfam.

ed. 2, 19c: 52. 1931; Léonard, Bull. Jard. Bot. Nat. Belg. 59: 319. 1989. TYPE: *Martretia quadricornis* Beille.

This west African genus of two species was placed next to *Aporusa* by Pax & Hoffmann (1931), but J. Léonard (1989) proposed that it be placed in a new tribe Martretieae Köhler ex Léonard, within subfamily Phyllanthoideae. Meeuse (1990) regarded *Martretia* as more appropriately included in the Acalyphoideae (Chrozophoreae).

- 313. Tacarcuna** Huft, Ann. Missouri Bot. Gard. 76: 1080. 1989. TYPE: *Tacarcuna gentryi* Huft.

This recently described genus of three species from Panama and South America was proposed by the author without any indication of affinity, although the description of uniovulate locules of the ovary, together with the general aspect, would suggest subfamily Acalyphoideae. However, examination of material of an isotype of the type species (*Gentry 16869*, DAV) shows that the ovary has biovulate locules. Although floral structure suggests that *Tacarcuna* belongs to subfamily Phyllanthoideae, and perhaps to tribe Wielandieae (where it may be close to *Savia*), scanning micrographs of pollen (courtesy of Joan Nowicke; Webster, ined.) show a striate exine suggestive of pollen in other tribes such as Antidesmeae or Briedelieae.

- 314. Avellanita** R. A. Philippi, Linnaea 33: 27. 1864. TYPE: *Avellanita bustillosii* R. A. Philippi.

The systematic position of this genus has remained questionable up to the present. In his original description, Philippi assigned *Avellanita* to the "Crotoneae," and Bentham (1880), on the basis of that description alone, placed it in tribe Crotoneae between *Micrandra* and *Hevea*. Pax (1910), following these earlier dispositions, located *Avellanita* within tribe Jatropheae following *Garcia*; however, he noted that its habit was aberrant and its leaves suggestive of *Argythamnia*. Pax & Hoffmann (1931), in an abrupt shift of opinion, assigned *Avellanita* to tribe Acalyphaeae, in juxtaposition with the Old World genera *Trewia* and *Melanolepis*. Croizat, in manuscript notes (1960) on a specimen in the Chilean Museo Nacional de Historia Natural (SGO), remarked on the vegetative similarity of *Avellanita* to genera of Chrozophoreae; however, the apetalous flowers and polyandrous androecium of the Chilean plant would be quite discordant with that tribe.

Examination of scanning micrographs from a specimen in the Museo Nacional (SGO 051523) clearly contradicts an assignment of *Avellanita* to subfamily Crotonoideae, as the exine does not show a Croton-pattern. The 3-colporate grains with rather coarse muri topped by nanospinules are somewhat similar to those in tribe Adelleae subfam. Acalyphoideae, but they are also not dissimilar to the grains found in tribe Acalypheae, e.g., *Trewia*. Although the precise affinity of *Avellanita* remains ambiguous, the evidence from pollen and floral characters clearly points to its placement within subfamily Acalyphoideae.

315. Cubacroton Alain, Candollea 17: 116. 1960. TYPE: *Cubacroton maestrense* Alain.

I have not been able to examine material of this enigmatic genus, which is known only from the type collection in the Sierra de Maestra, Cuba. Judging from the description, the plant probably belongs in tribe Crotonaeae; it appears similar to the Cuban endemic genus *Moacroton*, and possibly may prove to be an aberrant species of that genus.

ADDENDUM

316. Dendrothrix Esser, Novon 3: 245. 1993. TYPE: *Dendrothrix yutajensis* (Jabl.) Esser.

This genus, referred by its author to subtribe Mabeinae, was published too late to be accommodated in the main sequence of this synopsis. It is related to *Senefelderopsis*, and therefore should be inserted in subtribe Mabeinae following that genus. Esser provides several keys to distinguish *Dendrothrix* from the other genera of Mabeinae.

317. Cladogelonium Leandri, Bull. Soc. Bot. France 85: 530. 1939. TYPE: *Cladogelonium madagascariense* Leandri.

This monotypic genus from Madagascar remains poorly known. Judging from the description and illustration, it does appear to be similar to the widespread paleotropical genus *Suregada*, so it may prove to belong to tribe Gelonieae.

EXCLUDED TAXA

1. Burseranthe Rizzini, Leandra 4/5: 5. 1974. TYPE: *Burseranthe pinnata* Rizz.

This monotypic genus, based on a single species from eastern Brazil (Alagoas), was referred to subfamily Phyllanthoideae by Rizzini. The plant, however, has pinnate leaves, which are otherwise unknown in the family (except for the dubious case

of *Bischofia*). Examination of authentic material (kindly furnished by Rizzini) shows that the plant belongs to the Meliaceae and, following the treatment of Pennington (1981), clearly represents *Trichilia lepidota* Mart. subsp. *lepidota*.

2. Casabitoa Alain, Phytologia 47: 175. 1980; Fl. Española 4: 92. 1986. TYPE: *Casabitoa perfae* Alain.

This inadequately characterized genus, based on pistillate specimens of a single species from Hispaniola, is not euphorbiaceous. According to Tom Zanoni (in press), who visited the type locality, the plant is a species of Simarubaceae (*Picramnia dityoneura* (Urb.) Urb.).

3. Polygonanthus Ducke, Notizbl. Bot. Gart. Berlin 11: 345. 1932. TYPE: *Polygonanthus amazonicus* Ducke.

The genus is not euphorbiaceous, although its systematic position has been controversial. Although Baehni & Dansereau (1939) referred *Polygonanthus* to the Saxifragaceae (sensu lato), placement in the Anisophylleaceae by Pires and Rodrigues (1971) probably has the most support (e.g., in Cronquist, 1981).

4. Pseudocroton Muell. Arg., Flora 55: 24. 1872; Huft, Ann. Missouri Bot. Gard. 69: 429. 1982. TYPE: *Pseudocroton tinctorius* [= *Capparis indica* (L.) Fawc. & Rend.].

5. Skutchia Pax & Hoffmann, J. Wash. Acad. Sci. 27: 306. 1937; Burger, Fieldiana Bot. 40: 212. 1977. TYPE: *Skutchia caudata* Pax & Hoffm. [= *Trophis mexicana* (Liebm.) Bur.].

6. Trisyngyne Baillon, Adansonia 11: 136. 1874; Bauman-Bodenheim, Bull. Mus. Hist. Nat. Paris II. 25: 420. 1953; Steenis, Adansonia II. 11: 615. 1971. TYPE: not designated (Baillon published 2 species: *Trisyngyne balansae* and *T. codonandra*; but neither Bauman-Bodenheim nor van Steenis designated a type).

The New Caledonian genus *Trisyngyne* was reduced by van Steenis (1971) to *Nothofagus* subsect. *Bipartitae*.

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APPENDIX 1. Outline of taxa as treated in the text.

I. Subfamily PHYLLANTHOIDEAE

1. Tribe WIELANDIEAE

1. Heywoodia
2. Savia
3. Gonatogyne
4. Petalodiscus
5. Blotia
6. Actephila
7. Discocarpus
8. Lachnostylis
9. Chonocentrum
10. Wielandia

2. Tribe AMANOEAEE

11. Pentabrachion
12. Amanoa

3. Tribe BRIEDELIEAE

13. Cleistanthus
14. Briedelia

4. Tribe PHYLLANTHEAE

4a. Subtribe ASTROCASIINAE

15. Astrocasia

4b. Subtribe LEPTOPINAE

16. Leptopus

4c. Subtribe PSEUDOLACHNOSTYLIDINAE

17. Chascotheca
18. Zimmermannia
19. Zimmermanniopsis
20. Meinekia
21. Pseudolachnostylis
22. Keayodendron

4d. Subtribe SECURINEGINAE

23. Securinea

4e. Subtribe ANDRACHNINAE

24. Andrachne

4f. Subtribe FLUEGGEINAE

25. Flueggea
26. Richeriella
27. Aerialsilvaea
28. Margaritaria
29. Phyllanthus
30. Reverchonnia
31. Sauropus
32. Breynia
33. Glochidion

5. Tribe DRYPETEAE

34. Lingelsheimia
35. Drypetes
36. Sibangea
37. Putranjiva

6. Tribe ANTIDESMEAE

6a. Subtribe SPONDIANTHINAE

38. Spondianthus

6b. Subtribe UAPACINAE

39. Uapaca

6c. Subtribe SCEPINAE

40. Protomegabaria
41. Maesobotrya
42. Richeria
43. Jablonskia
44. Baccaurea

- 45. Apodiscus
- 46. Ashtonia
- 47. Aporusa
- 6d. Subtribe ANTIDESMINAE
 - 48. Thecacoris
 - 49. Phyllanoa
 - 50. Celianella
 - 51. Leptonema
 - 52. Antidesma
 - 53. Hyeronima
- 6e. Subtribe PORANTHERINAE
 - 54. Poranthera
 - 55. Oreoporanthera
- 7. Tribe HYMENOCARDIEAE
 - 56. Didymocistus
 - 57. Hymenocardia
- 8. Tribe BISCHOFIEAE
 - 58. Bischofia
- Incertae Sedis (within Phyllanthoideae)
 - 59. Centroplocus
 - 60. Meborea
- II. Subfamily OLDFIELDIOIDEAE
 - 9. Tribe CROIZATIEAE
 - 61. Croizatia
 - 10. Tribe PODOCALYCEAE
 - 10a. Subtribe PODOCALYCINAE
 - 62. Podocalyx
 - 10b. Subtribe TETRACOCINAE
 - 63. Tetracoccus
 - 10c. Subtribe PARADRYPETINAE
 - 64. Paradrypetes
 - 11. Tribe CALETIEAE
 - 11a. Subtribe HYAENANCHINAE
 - 65. Hyaenanche
 - 11b. Subtribe DISSILARIINAE
 - 66. Austrobuxus
 - 67. Dissiliaria
 - 68. Canaca
 - 69. Whyanbeelia
 - 70. Choriceras
 - 71. Longetia
 - 11c. Subtribe PETALOSTIGMATINAE
 - 72. Petalostigma
 - 11d. Subtribe PSEUDANTHINAE
 - 73. Kairothamnus
 - 74. Scagea
 - 75. Neoroepera
 - 76. Micrantheum
 - 77. Pseudanthus
 - 78. Stachystemon
 - 12. Tribe PICRODENDREAE
 - 12a. Subtribe PICRODENDRINAE
 - 79. Celaenodendron
 - 80. Piranhea
 - 81. Picrodendron
 - 82. Parodiodendron
 - 12b. Subtribe PAIVAEUSINAE
 - 83. Oldfieldia
 - 12c. Subtribe MISCHODONTINAE
 - 84. Aristogeitonia
 - 85. Mischodon
 - 86. Voatomalo
 - 87. Androstachys
 - 88. Stachyandra
- III. Subfamily ACALYPHOIDEAE
 - 13. Tribe CLUTIEAE
 - 89. Clutia
 - 14. Tribe POGONOPHOREAE
 - 90. Pogonophora
 - 15. Tribe CHAETOCARPEAE
 - 91. Trigonopleura
 - 92. Chaetocarpus
 - 16. Tribe PEREAE
 - 93. Pera
 - 17. Tribe CHEILOSEAE
 - 94. Cheilosa
 - 95. Neoscortechinia
 - 18. Tribe ERISMANTHEAE
 - 96. Erismanthus
 - 97. Moultonianthus
 - 98. Syndyophyllum
 - 19. Tribe DICOELIEAE
 - 99. Dicoelia
 - 20. Tribe GALEARIEAE
 - 100. Microdesmis
 - 101. Galearia
 - 102. Panda
 - 21. Tribe AMPEREAE
 - 103. Monotaxis
 - 104. Amperea
 - 22. Tribe AGROSTISTACHYDEAE
 - 105. Agrostistachys
 - 106. Pseudagrostistachys
 - 107. Cyttaranthus
 - 108. Chondrostylis
 - 23. Tribe CHROZOPHOREAE
 - 23a. Subtribe SPERANSKIINAE
 - 109. Speranskia
 - 23b. Subtribe DITAXINAE
 - 110. Caperonia
 - 111. Philyra
 - 112. Ditaxis
 - 113. Argythamnia
 - 114. Chiropetalum
 - 23c. Subtribe DORYXYLINAE
 - 115. Doryxylon
 - 116. Sumbaviopsis
 - 117. Thyrsanthera
 - 118. Melanolepis
 - 23d. Subtribe CHROZOPHORINAE
 - 119. Chrozophora
 - 24. Tribe CARYODENDREAE
 - 120. Caryodendron
 - 121. Discoglypsemna
 - 122. Alchorneopsis
 - 25. Tribe BERNARDIEAE
 - 123. Bernardia
 - 124. Necepsia
 - 125. Paranecepsia
 - 126. Discocleidion
 - 127. Adenophaedra
 - 26. Tribe PYCNOCOMEAE
 - 26a. Subtribe PYCNOCOMINAE
 - 128. Pycnoma
 - 129. Drocelonia
 - 130. Argomuellera
 - 26b. Subtribe BLUMEODENDRINAE
 - 131. Blumeodendron
 - 132. Podadenia
 - 133. Ptychopyxis
 - 134. Botryophora
 - 27. Tribe EPIPRINEAE
 - 27a. Subtribe EPIPRININAE
 - 135. Epiprinus
 - 136. Symphyllia

137. Adenochlaena
138. Cleidiocarpum
139. Koilodepas
140. Cladogynos
141. Cephalocrotonopsis
142. Cephalocroton
27b. Subtribe CEPHALOMAPPINAE
143. Cephalomappa
28. Tribe ADELIEAE
144. Adelia
145. Crotonogynopsis
146. Enriquebeltrania
147. Lasiocroton
148. Leucocroton
29. Tribe ALCHORNEAE
29a. Subtribe ALCHORNEINAE
149. Orfilea
150. Bossera
151. Alchornea
152. Coelebogyne
153. Aparisthium
154. Bocquillonina
29b. Subtribe CONCEVEIBINAE
155. Conceveiba
156. Gavarretia
157. Polyandra
30. Tribe ACALYPHEAE
30a. Subtribe RICININAE
158. Ricinus
30b. Subtribe ADRIANINAE
159. Adriana
30c. Subtribe MERCURIALINAE
160. Mercurialis
161. Seidelia
162. Leidesia
30d. Subtribe DYSOPSISINAE
163. Dysopsis
30e. Subtribe CLEIDIINAE
164. Wertia
165. Cleidion
166. Sampantaea
30f. Subtribe MACARANGINAE
167. Macaranga
30g. Subtribe CLAOXYLINAE
168. Erythrococca
169. Claoxylon
170. Claoxylopsis
171. Mareya
172. Discoclaoxylon
173. Micrococca
174. Amyrea
30h. Subtribe LOBANILIINAE
175. Lobanilia
30i. Subtribe ROTTLERINAE
176. Mallotus
177. Deuteromallotus
178. Cordemoya
179. Coccoceras
180. Trewia
181. Neotrewia
182. Rockinghamia
183. Octospermum
30j. Subtribe ACALYPHINAE
184. Acalypha
30k. Subtribe LASIOCOCGINAE
185. Lasiococca
186. Spathiostemon
187. Homonoia
31. Tribe PLUKENETIEAE
31a. Subtribe PLUKENETIINAE
188. Haematostemon
189. Astrococcus
190. Angostyles
191. Romanoa
192. Eleutherostigma
193. Plukenetia
194. Vigia
31b. Subtribe TRAGIINAE
195. Cnesmone
196. Megistostigma
197. Sphaerostylis
198. Tragiella
199. Platygyne
200. Tragia
201. Acidoton
202. Pachystylidium
31c. Subtribe DALECHAMPIINAE
203. Dalechampia
32. Tribe OMPHALEAE
204. Omphalea
- IV. Subfamily CROTONOIDEAE
33. Tribe MICRANDREAE
33a. Subtribe MICRANDRINAE
205. Micrandra
206. Micrandropsis
207. Cunuria
33b. Subtribe HEVEINAE
208. Hevea
34. Tribe MANIHOTEAE
209. Manihot
210. Cnidoscolus
35. Tribe ADENOCLINEAE
35a. Subtribe ADENOCLININAE
211. Glycydendron
212. Klaineanthus
213. Tetrochidium
214. Adenocline
215. Ditta
35b. Subtribe ENDOSPERMINAE
216. Endospermum
36. Tribe GELONIEAE
217. Suregada
37. Tribe ELATERIOSPERMEAE
218. Elateriospermum
38. Tribe JATROPHEAE
219. Jatropa
220. Vaupesia
221. Oligoceras
222. Deutzianthus
223. Joannesia
224. Leeuwenbergia
225. Annesijoa
39. Tribe CODIAEAE
226. Baloghia
227. Hylandia
228. Ostodes
229. Pausandra
230. Dodecastigma
231. Pantadenia
232. Dimorphocalyx
233. Fontainea
234. Codiaeum
235. Sphyranthera
236. Acidocroton
237. Blachia
238. Strophoblachia

239. *Sagotia*
240. *Baliospermum*
40. Tribe TRIGONOSTEMONEAE
241. *Trigonostemon*
41. Tribe RICINOCARPEAE
41a. Subtribe RICINOCARPINAE
242. *Ricinocarpos*
243. *Alphandia*
244. *Beyeria*
41b. Subtribe BERTYINAE
245. *Bertya*
246. *Myricanthe*
247. *Cocconerion*
248. *Borneodendron*
42. Tribe CROTONEAE
249. *Mildbraedia*
250. *Fahrenheitia*
251. *Moacrotion*
252. *Croton*
43. Tribe RICINODENDREAE
253. *Givotia*
254. *Ricinodendron*
255. *Schinziophyton*
44. Tribe ALEURITIDEAE
44a. Subtribe ALEURITINAE
256. *Aleurites*
257. *Reutealis*
258. *Vernicia*
44b. Subtribe GARCIIINAE
259. *Garcia*
44c. Subtribe GROSSERINAE
260. *Cavacoa*
261. *Grossera*
262. *Tapoides*
263. *Anomalocalyx*
264. *Sandwithia*
265. *Tannodia*
266. *Domohinea*
44d. Subtribe CROTONOGYNINAE
267. *Cyrtogonone*
268. *Crotonogyne*
269. *Manniophyton*
44e. Subtribe NEOBOUTONINAE
270. *Neoboutonia*
271. *Benoistia*
V. Subfamily EUPHORBIOIDEAE
45. Tribe STOMATOCALYCEAE
45a. Subtribe STOMATOCALYCINAE
272. *Plagiostyles*
273. *Pimelodendron*
45b. Subtribe HAMILCOINAE
274. *Hamilcoa*
275. *Nealchornea*
46. Tribe HIPPOMANEAE
46a. Subtribe MABEINAE
276. *Mabea*
277. *Senefeldera*
278. *Senefelderopsis*
46b. Subtribe CARUMBIINAE
279. *Omalanthus*
46c. Subtribe HIPPOMANINAE
280. *Spirostachys*
281. *Sebastiania*
282. *Stillingia*
283. *Gymnanthes*
284. *Excoecaria*
285. *Colliguaja*
286. *Dalembertia*
287. *Adenopeltis*
288. *Sapium*
289. *Glyphostylus*
290. *Grimmeodendron*
291. *Bonania*
292. *Duvigneaudia*
293. *Maprounea*
294. *Hippomane*
47. Tribe PACHYSTROMATEAE
295. *Pachystroma*
48. Tribe HUREAE
296. *Tetrapandra*
297. *Algernonia*
298. *Ophthalmoblapton*
299. *Hura*
49. Tribe EUPHORBIEAE
49a. Subtribe ANTHOSTEMINAE
300. *Anthostema*
301. *Dichostemma*
49b. Subtribe NEOGUILLAUMINIINAE
302. *Neoguillauminia*
303. *Calycoeplus*
49c. Subtribe EUPHORBIINAE
304. *Euphorbia*
305. *Chamaesyce*
306. *Cubanthus*
307. *Monadenium*
308. *Synadenium*
309. *Endadenium*
310. *Pedilanthus*
- Incertae Sedis (within Euphorbiaceae)
311. *Chlamydojatropa*
312. *Martretia*
313. *Tacarcuna*
314. *Avellanita*
315. *Cubacroton*
316. *Dendrothrix*
317. *Cladogelonium*
- APPENDIX 2. List of new taxa.
- CROIZATIEAE Webster, trib. nov.
LEPTOPINAE Webster, subtr. nov.
PODOCALYCEAE Webster, trib. nov.
PODOCALYCINAE Webster, subtr. nov.
PYCNOCOMINAE Webster, subtr. nov.
TETRACOCINAE Levin, subtr. nov.
DALECHAMPIINAE (Muell. Arg.) Webster, stat. nov.
PICRODENDRINAE (Small) Webster, stat. nov.
PORANTHERINAE (Muell. Arg.) Webster, stat. nov.
SCEPINAE (Lindl.) Webster, stat. nov.
SPONDIANTHINAE (Webster) Webster, stat. nov.
Acidocroton sect. *Ophellantha* (Standl.) Webster, comb. nov.
Acidocroton spinosus (Standl.) Webster, comb. nov.
Acidocroton steyermarkii (Standl.) Webster, comb. nov.
Adenopeltis serrata (Ait.) Webster, comb. nov.
Deutzianthus thyrsoflorus (Airy Shaw) Webster, comb. nov.
Gymnanthes schomburgkii (Kl.) Webster, comb. nov.
Leptopus diplopermus (Airy Shaw) Webster, comb. nov.
Leptopus phyllanthoides (Nutt.) Webster, comb. nov.
Lingelsheimia manongarivensis (Leandri) Webster, comb. nov.
Orfilea multispicata (Baillon) Webster, comb. nov.
Orfilea neraudiana (Baillon) Webster, comb. nov.
Pantadenia chauvetiae (Leandri) Webster, comb. nov.

Phyllanthus anamalayanus (Gamble) Webster, comb. nov.
Phyllanthus chevalieri (Gagnep.) Webster, comb. nov.
Sauropus pierrei (Beille) Webster, comb. nov.

APPENDIX 3. *Index to genera and higher taxa.* This index includes all the genera and higher taxa mentioned in this paper. Accepted taxa are shown in bold, with suprageneric taxa all capitalized. Synonymized taxa are italicized, and those merely mentioned are shown in regular text. Taxa are numbered as they appear in the text, with those in Roman numerals referring to subfamilies, those preceded by "T" referring to tribes or subtribes, those preceded by "E" referring to excluded taxa, and others referring to genera.

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		<i>Barhamia</i>	252
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<i>Conami</i>	29	Dissiliaria	67
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<i>Corythea</i>	184	Dodecastigma	230
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<i>Ctenomeria</i>	200	<i>Elaeophora</i>	193
Cubacroton	315	<i>Elaeophorbia</i>	304
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<i>Cyathogyne</i>	48	<i>Emblica</i>	29
<i>Cyclostemon</i>	35	<i>Enchidium</i>	241
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<i>Dactylostemon</i>	283	<i>Epistylum</i>	29
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