Euphorbiaceae

Euphorbiaceae Juss. (1789), nom. cons.
Phyllanthaceae Martinov (1833).
Peraceae Klotzsch (1859).
Picrodendraceae Small (1917), nom. cons.

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Monoecious or dioecious trees, shrubs, or herbs, sometimes succulent or scandent; stems with or without laticifers; indumentum simple, malphighiaceous, stellate, or lepidote, sometimes glandular or 0. Leaves alternate, spiral or distichous, less commonly opposite or whorled; leaf blades simple to palmately lobed or compound, pinnately to palmately nerved, sometimes with basal, laminar, or marginal glands; stipules persistent or deciduous, sometimes reduced or 0. Inflorescences axillary or terminal, sometimes cauliflorous, thyrsoid, paniculate dichasial, glomerulate or synanthial, or flowers solitary; bracts sometimes colored, glandular, or hypertrophied. Flowers unisexual, usually actinomorphic; perianth segments distinct or connate, imbricate to valvate, rarely obsolete or suppressed; sepals (–)3–6(−10), entire or lobed, sometimes glandular, the pistillate persistent or deciduous in fruit; petals + or 0, greenish to white, yellow, pink, or red; disk + or 0, extrastaminal or less commonly interstaminal, entire to toothed, lobed, or dissected; stamens (1–)3–50 (−400), filaments distinct or connate; anthers mostly 2-locular, dehiscing longitudinally or laterally, extrorse or less commonly introrse; gynoecium syncarpous, ovary (1)2–5(−20)-locular; placentation axile (basal); ovules 1 or 2 per locule, anatropous or hemitropous, epitropous, usually inserted beneath an obturator. Fruits mostly schizocarpic, splitting from the columella, commonly explosively dehiscent, mesocarp often separating from endocarp, sometimes baccate or drupaceous. Seeds often carunculate; seed coat mostly exotegmic; endosperm copious, often fleshy, or 0, sometimes oily; embryo straight, curved or plicate.

[1] By the end of 2004 Dr. Grady L. Webster sent me a far advanced version of his treatment of the Euphorbiaceae for this book series and, in June 2005 a few months before his death (Oct. 27, 2005), I received an additional document from him dealing with a review of suprageneric and generic taxa in the family. That year, I could not immediately take care of these documents because I was busy with other volumes of this series. In 2008, through the courtesy of Drs. K.J. Wurdack and P.E. Berry, I received what I thought to be further updated documents left by Grady at the time of his death in his laboratory; contrary to my expectation, however, these did not differ from those supplied earlier by Grady himself. Although the author had made perusal of many taxonomic revisions and publications on pollen morphology and seed anatomy, it was evident that the manuscript needed substantial revision in the light of more recent publications in molecular systematics accrued before and after Grady's death. Regrettably, Dr. Wurdack, the born heir of Grady, did not wish to revise the manuscript so that this task fell onto me, in an effort to not loose Grady's work spanning several years. The paper thus contains many changes introduced by me without being able to secure the author's formal approval, but these were essential for this paper to reflect the high standard that distinguished Dr. Webster's scientific production. Whereas the molecular-cladistic papers on the euphorbs in the widest sense, mainly those by Wurdack and Berry and their co-authors, were of greatest value for me in this task, I must emphasise that the main objective of this series is to give baseline information, whereas further elaboration of a cladistic classification of the family would have been beyond my desire and capacity.

My thanks go to Drs. K.J. Wurdack and P.E. Berry for showing me the manuscripts left by the late Dr. Webster. Prof. W.S. Armbruster is warmly thanked for going through parts of the manuscript lying within his interest and for updating the section on reproductive biology. I am also most grateful to Dr. R. Secco for his comments on Amazonian euphorbs, and to Dr. V.W. Steinmann for advice on subtribe Euphorbiinae.

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The family is here construed to include 299 genera with 8,000 species; these are grouped into 47 tribes in seven subfamilies, the biovulate Phyllanthoideae and Oldfieldioideae, and the uniovulate Peroideae, Cheilosoideae, Acalyphoideae, Crotonoideae, and Euphorbioideae (see below under CIRCUMSCRIPTION AND SUBDIVISION OF THE FAMILY). Although the family is nominally cosmopolitan (except for the polar regions), it is poorly represented in cool temperate zones and best developed in subtropical and tropical regions.

VEGETATIVE MORPHOLOGY. Euphorbiaceae are highly variable in vegetative structure, with a great range of life forms, including trees, shrubs, and perennial and annual herbs. Sympodial growth related to inflorescence production is common, especially in subfamilies Crotonoideae and Euphorbioideae (Hallé 1971). Scandent life forms are rare in Euphorbioideae (tribe Stomatocalyceae), unknown in Oldfieldioideae and Crotonoideae (except *Omphalea*), but common in Acalyphoideae tribe Plukenetieae. In subfam. Phyllanthoideae the branching pattern tends to be monopodial and inflorescences axillary, and there is a striking tendency toward monopodial plagiotropic branching as in *Flueggea* and *Phyllanthus*. A further specialization of this pattern yields the deciduous, floriferous, phyllomorphic branchlets found in several genera of the Phyllanthinae, including *Breynia*, *Glochidion*, *Phyllanthus*, and *Sauropus*. This highly specialized growth from, first documented by Dingler (1885) and designated as "phyllanthoid branching" by Webster (1956), includes some unique patterns such as the relegation of photosynthetic leaves and flowers to specialized deciduous branchlets in *Phyllanthus* and related genera (Dingler 1885; Webster 1956; Roux 1968; Bancilhon 1971; Rossignol and Rossignol 1985). Subfam. Oldfieldioideae resembles the Phyllanthoideae in having relatively unspecialized monopodial branching patterns. The most divergent life form in the Euphorbiaceae is found in a single neotropical section (*Salviniopsis*) of *Phyllanthus*. Mature plants float unrooted on the surface of white-water streams and lakes in the Amazonian region.

Phyllotaxis in Euphorbiaceae is predominantly alternate (spiral or distichous), but opposite or whorled leaves are common in the Oldfieldioideae and Euphorbioideae. Leaves in the Euphorbiaceae vary in size from scale leaves less than 1 mm long in succulent Euphorbias to the umbracular leaves of *Macaranga gigantea* with blades exceeding 50 cm in diameter. Leaves are usually stipulate, although stipules have been lost in various taxa, notably in *Croton* and *Euphorbia* (Uhlarz 1978). Leaf blades are prevailingly simple or lobed, but palmate/pinnately dissected laminae occur in Oldfieldioideae (*Piranhea*), and Crotonoideae (*Hevea*, *Joannesia*, *Leeuwenbergia*, and species of *Manihot*). There is some variation in ptyxis (leaf blade folding in bud): the study of Cullen (1978), although based on a limited sample, indicates that most of the subfamilies have conduplicate ptyxis, but Euphorbioideae are mainly supervolute. Leaves are persistent in tropical rainforest taxa, but usually deciduous in genera adapted to monsoonal or arid climates. Leaf blade venation is mostly brochidodromous; margins may be entire or toothed with "theoid" or "violoid" teeth (Hickey and Wolfe 1975). An atlas of leaf venation has been published by Klucking (1997, 2003).

The widespread adaptation of Euphorbiaceae to arid habitats has led to characteristic morphological and physiological traits. The succulent life form is well represented in Euphorbiaceae, especially in subfamilies Crotonoideae and Euphorbioideae. Succulent species, mostly caudiciform or geophytic, also occur in African and American *Jatropha*. The immense diversity of the genus *Euphorbia*, which comprises over 2,000 recognized species, is paralleled by enormous structural, ecological and physiological variation; it is the only land plant genus in which the three major photosynthetic pathways are expressed. In a phylogenetic analysis Horn et al. (2012) identify a woody, non-succulent growth form with C_3 photosynthetic pathway as ancestral. Cactiform succulents with CAM photosynthesis amount to nearly 650 species and have arisen in two clades within *Euphorbia*; most of them are concentrated in eastern and southern Africa. An independent evolution of herbs has taken place in the *Esula* Clade and *Chamaesyce* Clade of *Euphorbia*, in the latter accompanied by the acquisition of all three photosynthetic pathways.

VEGETATIVE ANATOMY. Wood anatomy in the Euphorbiaceae was reviewed by Pax (1884) in his first study of the family, and treated in greater detail by students of Radlkofer (Rittershausen 1892; Froembling 1896; Rothdauscher 1896; Herbert 1897), and by Solereder (1908). Metcalfe and Chalk

(1950) synthesized much of these data in their classic work on the anatomy of the dicots. From the studies of Mennega (1987) on Phyllanthoideae and Hayden (1994) on Oldfieldioideae, it appears that the apparently least specialized wood structure is present in Phyllanthoideae tribes Wielandieae and Antidesmateae, evidenced by thick-walled, non-septate fibers, abundant axial parenchyma, and vessel elements with scalariform perforations. In other tribes of Phyllanthoideae, there are trends toward wood with septate, thin to moderately thick-walled fibers, scanty parenchyma, and porous vessel element perforations. In Oldfieldioideae, fibers are non-septate, the rays narrow and heterocellular, axial parenchyma is abundant and diffuse or in wide bands, and vessel perforations are simple with exception of *Podocalyx* (and *Paradrypetes*), which have multiple perforation plates in very long vessel elements. With some exceptions (*Acalypha*, *Clutia*, *Pogonophora*), the basic pattern of wood structure is similar in Acalyphoideae, Crotonoideae and Euphorbieae. Scalariforn vessel perforation plates are lacking; intervascular and vessel/ray pitting is medium to very large; axial parenchyma is apotracheal diffuse or banded; rays are numerous, narrow, heterocellular, and often vertically fused; fibers are non-septate, often wide and thin-walled (Mennega 1987).

Laticifers appear to be completely absent in Phyllanthoideae and Oldfieldioideae but are well-developed in subfamilies Crotonoideae and Euphorbioideae (Rudall 1987). Most laticifers are unicellular (non-articulated) and produce whitish latex, but colored (yellow or red) latex occurs in some Crotonoideae. In the two basal tribes of Crotonoideae (Micrandreae and Manihoteae), the laticifers are mostly multicellular (articulated), with mainly whitish latex. According to Rudall (1994), the multicellular laticifers of *Hevea* and *Manihot* may have evolved from the non-articulated type, and the articulated laticifers reported in *Jatropha* (Dehgan and Craig 1978) may have evolved independently. The latex in tribe Euphorbieae is unusual in containing distinctively shaped (rod- or dumbbell-like) starch grains; the distribution of these starch grain types is considered to be of taxonomic significance (Mahlberg 1975). Latex of Euphorbieae is often toxic, due to triterpenes and diterpenes. Foliar sclereids have been detected in various Acalyphoideae. Rudall (1994) suggests that sclereids (in at least some instances) may be homologous with laticifers.

The indumentum of leaves and stems is highly diverse in the Euphorbiaceae (Metcalfe and Chalk 1950), and has often been used as a diagnostic character. In the biovulate subfamilies it consists usually of simple unicellular or uniseriate trichomes; bifurcate trichomes are known from *Austrobuxus*. Both glandular and branched hairs are common in the uniovulate subfamilies. In *Croton*, there is great diversity in the size, color, and number of rays of branched trichomes (Webster 1993). Dibrachiate (malpighiaceous) trichomes are characteristic of various genera in the Acalyphoideae and Crotonoideae. Particularly notable are the stinging hairs found in Acalyphoideae (Plukenetieae) and Crotonoideae (*Cnidoscolus*). The urticant hairs have clearly evolved independently in the two subfamilies and are basically different in morphology: *Cnidoscolus* stinging hairs are of the *Urtica* type—hollow, with thin walls and deciduous tip (Thurston and Lersten 1969); those of the Plukenetieae represent a unique type, with a central crystalliferous cells forming a kind of hypodermic syringe (Thurston 1976).

Detailed analyses of foliar vention patterns and leaf structure in Phyllanthoideae and Oldfieldioideae have been presented by Levin (1986a, b) and Hayden (1994). Accordingly, stomata are paracytic, brachyparacytic, or anisocytic in Phyllanthoideae, and brachyparacytic (derived) in Oldfieldioideae, with exception of the anomocytic *Podocalyx* (and paracytic *Paradrypetes*). The occurrence of tanniniferous cells in the adaxial leaf epidermis has been confirmed for supertribe Antidesmodae. An atlas of leaf venation in all the subfamilies has been published by Klucking (1997, 2003).

Foliar glands are rare in the Phyllanthaceae, but common in the uniovulate subfamilies. Laminar (embedded) glands appear to be usually derived independently of those at the leaf base or apex of petiole (Bernhard 1966). Inflorescence bracts in the Crotonoideae and especially the Euphorbioideae often have glands that appear homologous to foliar glands, although morphologically divergent. The glands of the cyathium of *Euphorbia* are anatomically similar to and appear to be homologous with those of the thyrses of the Hippomaneae. Although the function of foliar

glands may be to attract ants that can deter herbivores, bracteal glands of genera such as *Mabea* appear to be a major source of nectar to attract pollinators (Steiner 1981, 1983).

Inflorescence Structure. The basic inflorescence pattern in Euphorbiaceae is cymose, as in many angiosperm families. The prevailingly cymose nature of the Euphorbiaceous inflorescence is most explicit in the dichasial inflorescences of genera such as *Cnidoscolus* (Bawa et al. 1982) and *Jatropha* (Dehgan and Webster 1979), where a terminal pistillate flower is subtended by lateral staminate axes. These inflorescences are usually protogynous; the spatial and temporal separation of the staminate and pistillate flowers have the effect of limiting the degree of geitonogamy in pollination. In many genera, the dichasia are reduced to axillary glomerules, and separation of the sexes is commonly achieved by dioecy or by spatial separation. A common modification is a spicate arrangement of cymules (the thyrse). Paniculate and thyrsopaniculate inflorescences, arising from elaboration of dichasia or aggregation of thyrses, appear to represent an end-point in elaboration. Primitively, each flower in an inflorescence is bracteate. Bracts may be deciduous or persistent, and are sometimes distinctively colored, especially in aggregations of flowers into pseudanthia.

Pseudanthia have arisen in all of the subfamilies except for the Cheilosoideae and Crotonoideae. In *Uapaca* (Phyllanthoideae), the pedunculate pseudanthia with 5–10 imbricate colored bracts resemble single flowers (the pistillate flowers are solitary). In Peroideae, the flowers of *Pera* form involucrate capitula enclosed in involucres of 1–2 smaller outer and two larger inner valvate bracts. Most species of *Dalechampia* (Acalyphoideae) have spectacular bisexual, bilaterally symmetrical pseudanthia in which the paired bracts may vary greatly in size, color, and lobing; the pistillate dichasium of three flowers is ventral to a staminate dichasium of mostly 4–21 flowers associated with a resiniferous gland derived from modified bractlets (Webster and Armbruster 1991). Finally, in the Euphorbioideae an entire tribe, the Euphorbieae, is characterized by the pseudanthial cyathium, which closely resembles a bisexual flower and traditionally is interpreted as an inflorescence with a single terminal pistillate flower surrounded by clusters of highly reduced staminate flowers. Hoppe and Uhlarz (1982) and Hoppe (1985) studied the morphogenesis of several species of *Euphorbia* and interpreted their findings within the classical morphological framework. Prenner and Rudall (2007) and Prenner et al. (2008), who included in their study a broader sampling of genera of the Euphorbieae such as *Anthostema*, *Dichostemma*, *Neoguillauminia*, *Calycopeplus*, and *Euphorbia*, suggested several scenarios for a derivation of the cyathium; their findings imply that the nectariferous appendages may not all be of stipulate derivation, as previously believed.

Floral Structure. Since the classic essays on floral structure by Baillon (1858) and Eichler (1875), there have been few comprehensive surveys besides that of Michaelis (1924). Hermaphroditic flowers are rare and sporadic (e.g., in *Jatropha*, and less commonly in *Croton* and *Phyllanthus*), and are not consistently present in any single species. The basic floral pattern is pentamerous, as found in the Phyllanthoideae tribe Wielandieae (e.g., in *Heywoodia*, *Wielandia*). The presumably plesiomorphic and apomorphic states of some of the salient floral characters have been tabulated by Webster (1994a). In virtually all genera, the flowers are hypogynous. Whereas more than half of the genera of the Phyllanthoideae have well-developed petals in at least one of the sexes, nearly all members of the Oldfieldioideae are apetalous. The sepals in some apetalous genera may be distinctly petaloid (e.g., in *Cnidoscolus*, *Manihot*, and *Phyllanthus*). Aestivation of the floral parts, especially the sepals, has been used as a diagnostic character; sepals are imbricate in most of the Pyllanthoideae, whereas in the majority of genera of Acalyphoideae the staminate sepals, at least, are valvate. In pistillate flowers petals are present in some genera of all the subfamilies except the Euphorbioideae; they are usually inconspicuous but can be distinctly showy in some Crotonoideae (e.g., *Aleurites*, *Jatropha*). Except for the Euphorbioideae, a floral disk is generally present although sometimes reduced in pistillate flowers. In the majority of genera, the androecium includes 2–20 stamens, but the stamen number is reduced to 1 in *Dalembertia* and the Euphorbieae, and in some Acalyphoideae and Crotonoideae it has proliferated to 50–100 stamens or more. In many instances, the filaments of the stamens are united into a column,

and sometimes (e.g., in *Phyllanthus* and *Omphalea*) the anthers are connate as well. This may also apply to *Androstachys* and *Stachyandra* (Oldfieldioideae), the stamens of which have been interpreted as *spirally* inserted; for details, see under the generic treatment (p. 93). Müller (1866) used anther dehiscence (introrse or extrorse) as a diagnostic character, and it is still a useful indicator of affinity in many cases. Sometimes, there is a rudimentary gynoecium (pistillode) in the center of the staminate flower. The perianth of pistillate flowers is often meristically the same as in staminate flowers, but the sepals often become modified during fruit development to enlargement (accrescence) in some cases, but in other cases the sepals are deciduous in fruit.

The Euphorbiaceous gynoecium is generally described as hypogynous and 3-carpellate. However, carpel number may vary from 2 (sporadically) to 5 or 10, and occasionally the gynoecium may be unilocular or 20-locular (*Hura*). Stylodia vary greatly in configuration, but most commonly are bifid, and often are connate at least at the base; in various taxa they are unbranched (e.g., *Alchornea*, Hippomaneae) or may be repeatedly bifurcate (e.g., in *Croton*). Placentation is axile; Berg (1975) is of the opinion that the Euphorbiaceae show a variation of the axile structure that is linked to the explosive capsular fruit. Each locule contains one or two ovules, which are anatropous and epitropous (i.e., with raphe adaxial) and crassinucellate; the nucellus is extended and may protrude as a nucellar beak far out of the micropyle. There is usually an obturator projecting from the placenta over the micropylar region of the ovule. Epitropous ovules are common among the Malpighiales, and obturators are not restricted to the Euphorbiaceae, but nucellar beaks appear to be very rare elsewhere (only in Malpighiaceae, Polygonaceae). However, the combination of epitropous ovules, obturators and extended nucellar beaks has not been reported for any other angiosperm family, and therefore provides a strong morphological argument for the monophyly of the Euphorbiaceae s.l. (Sutter and Endress 1995; Merino Sutter et al. 2006).

Pollen Morphology. The taxonomic significance of pollen morphology in the Euphorbiaceae, first demonstrated by Erdtman (1952), has stimulated investigations by a number of later workers. Punt (1962), using light microscopy, produced a survey of pollen in the family and established many palynological "types" that were more or less well correlated with phylogenetic position. Köhler (1965), also using LM, proposed a number of taxonomic realignments, notably a new subfamily, the Oldfieldioideae. Detailed palynological surveys using SEM and TEM have been made for the Oldfieldioideae (Levin and Simpson 1994), the Crotonoideae (Nowicke 1994), the Peroideae, the Cheilosoideae, and the Acalyphoideae (Nowicke et al. 1998, 1999, Takahashi et al. 2000; Nowicke and Takahashi 2002). Although no complete atlas of pollen in Phyllanthoideae and Euphorbioideae has been published, there have been a number of studies of infrasubfamilial scope. A detailed survey of pollen morphology in the tribe Plukenetieae has been provided by Gillespie (1994). The genus *Phyllanthus* and its satellites display the most extensive variation of exine sculpturing as well as aperture structure and number, which has led to elevated numbers of colpi (often diploporate) and even to pantoporate grains (Meewis and Punt 1983; Punt 1987; Webster and Carpenter 2002; Sagun and van der Ham 2003).

Pollen features have been used as diagnostic characters to distinguish the seven subfamilies recognized here. The putatively plesiomorphic states are found in the Phyllanthoideae (tribes Wielandieae, Phyllantheae): prolate 3-colporate grains with reticulate (semitectate) exine; transmission electron microscopy has revealed a perforate or discontinuous ektexine with distinct columellae and a continuous homogeneous endexine (Levin and Simpson 1994). In subfam. Oldfieldioideae the grains are mostly oblate-globose and the apertures are contracted, grading from brevicolpate to porate and from zonoporate to pantoporate; basal taxa have at least four apertures, but in the pantoporate condition their number can reach 40; the exine is modified to radially elongate, tapering spines that are continuous with the tectum. The Peroideae are quite diversified palynologically and it is not easy to recognize a common pattern, whereas the Cheilosoideae are characterized by their echinate tectum. In Acalyphoideae the pollen is invariably tricolporate but exhibits a great diversity in structure and sculpture. Although in Crotonoideae colporate, colpate and porate pollen is present, most members of the group have inaperturate

grains with an exine sculpture of triangular (−rounded) structures in continuous arrays—now widely known as "Croton pattern". Euphorbioideae have 3-colporate pollen; among them, tribe Euphorbieae appears to have strange conspicuous intine bands bordering the colpi (Suárez-Cervera et al. 2001).

KARYOLOGY. It is apparent from the excellent survey of Hans (1973), and later additions by Urbatsch et al. (1975) and others, that the Euphorbiaceae are quite diversified in chromosome number. There is no single base number from which the chromosomal variation can be derived, although Hans (1973) thought $x = 11$ to be the base number both in the Acalyphoideae and Crotonoideae. However, as 9 and 10 are nearly equally frequent base numbers, the question remains whether these numbers have an aneuploid connection and in which direction this took place. In *Euphorbia* s. l., where very many counts are available, $x = 11$ is rare. It seems that here descending aneuploidy has led to secondary base numbers 10, 9, 8, 7, 6, which were the starting points for effective polyploid speciation. The *Synadenium* clade ($x = 18$) and the *Monadenium* clade ($x = 19$, 18, 17, 16, and 12) apparently represent a mostly decreasing aneuploid series from an ancestral base number of $x = 9$ (Jones and Smith 1969). A similar descending aneuploid series can be found elsewhere in *Euphorbia*, beginning with a base number of $x = 10$ (Hans 1973). The few chromosome numbers known from Hippomaneae are based on 11, 9, and 7. According to the survey of Hans (1973) polyploidy is more frequent in the family than in other woody plant families. *Bischofia javanica* ($2n = 198$, 28-ploid if based on $x = 7$), systematically and geographically isolated, seems to represent the final stage of development in a polyploid complex, i.e., a "relictual polyploid".

REPRODUCTIVE SYSTEMS. In Euphorbiaceae, with open-pollinated strictly unisexual flowers, self-incompatibility is rare, and earlier reports of it appear to be incorrect. Self-incompatibility has been shown to be absent or incomplete in *Chamaesyce* (herbaceous species, Ehrenfeld 1976), *Hevea* (Bouharmont 1962), and *Manihot* (Jennings 1963; George and Shifriss 1967). A documented instance of self-incompatibility is that recorded for some woody Hawaiian species of *Chamaesyce* by Koutnik (1987). The absence of self-incompatibility is also well documented in *Mercurilis annua*. Both hermaphroditic and androdioecious populations are reported, and both exhibit mixed mating (i.e., a mix of self-fertilization and outcrossing; Korbecka et al. 2011). Self-compatibility is also the rule in *Dalechampia* (e.g., Sazima et al. 1985).

It seems likely that primitive Euphorbiaceae were dioecious with binucleate pollen (Webster and Rupert 1973); it is possible that the near-absence of self-incompatibility in the family is a consequence of the evolution of monoecious taxa from dioecious ancestors. Only 19 of the 300 genera of Euphorbiaceae include both monoecious and dioecious species, and the number of monoecious (131) and dioecious (142) genera is nearly equal (Webster 1994a). The Oldfieldioideae are mostly dioecious and the Euphorbioideae are mostly monoecious, but both types are well represented in the other subfamilies. As predicted by Bawa (1980) and others, taxa with ornithochorous dispersal are mainly dioecious, and myrmecochorous taxa are somewhat more likely to be monoecious. Taxa with binucleate pollen grains may be monoecious or dioecious, but it appears that trinucleate grains are produced only in monoecious species.

Prevention of autogamy in the self-compatible monoecious taxa is generally facilitated by spatial separation of the sexes, often in separate inflorescences (e.g., in *Acalypha*), and/or by dichogamy (usually protogyny). In the inflorescences of a number of genera (notably *Cnidoscolus*, *Jatropha*, and *Euphorbia*), the pistillate flowers terminate the main axis or lower dichotomies, and open before the staminate flowers (Bawa et al. 1982). In *Euphorbia*, which has bisexual pseudanthia, monoecious species are self-compatible, but in some species there is functional andromonoecy, with some early-produced cyathia lacking functional pistillate flowers (Narbona et al. 2002). The staminate cyathia are proximal in the inflorescence and open earlier than the cyathia with pistillate flowers, so there is effective protandry, in contrast to the usual protogyny and proximal position of pistillate flowers. As noted by Narbona et al. (2002), andromonoecy appears to be more frequent in perennial species, which are known to have a higher percentage of outcrossing. In *Bridelia tomentosa*, a rarely

documented (but possibly frequent, see Sapindaceae in Vol. X of this book series) temporal mating system has been analyzed (Luo et al. 2007), in which each individual produces subsequently staminate, then pistillate, and then staminate flowers, with the resting periods between the flowering phases precluding selfing, and asynchrony among individuals ensuring mating partners (duodichogamy).

Although polyploidy is common in large genera such as *Croton*, *Euphorbia*, and *Phyllanthus*, published records of interspecific hybridization are rare (Webster 1967). Polyploidy is associated with apomixis in some species of *Euphorbia* (Cesca 1961).

Pollination. Consistent with their floral and inflorescence diversity, Euphorbiaceae show a great diversity of pollination systems and pollinator species. Pollination occurs abiotically via wind in *Acalypha*, some *Macaranga* and *Mallotus* species, *Mercurialis* (Daumann 1972; Korbecka et al. 2011), *Ricinus* (Alex 1957), and probably many other Acalypheae. Wind pollination has also been reported in *Bernardia* (Bernardieae; Bullock 1994), *Bertya* (Ricinocarpeae; Fatemi and Gross 2009), "*Celaenodendron*" (= *Piranhea*, Oldfieldioideae; Bullock 1994), some *Croton* species (Crotoneae; Bullock 1994) and possibly in two or more species of *Phyllanthus* (Subba-Reddi and Reddi 1984). Anemophilous taxa characteristically have a reduced or lacking perianth and nectary disk combined with a multiplication of stamens, catkin-like inflorescences, and smaller pollen grains than their zoophilous relatives; *Mallotus* may be transitional in this respect (Lock and Hall 1982). The extraordinarily elaborate androecium of *Ricinus*, with branching filaments and hundreds of anthers, doubtlessly reflects adaptation to anemophilous pollination, and is not a primitive character, as claimed by Venkata Rao and Ramalakshmi (1968).

Species with biotic pollination can be divided into two groups: those in which unisexual flowers are visited individually and those in which the flowers operate pseudanthially, i.e., the unisexual flowers are united into generally bisexual blossoms and pollinators visit several flowers (usually of both sexes) simultaneously (with simultaneous or sequential receptivity). Most euphorbs in the former category (visitation of individual flowers) probably have ecologically generalized pollination by a variety of pollinator species seeking nectar, particularly those belonging to the insect orders Hymenoptera and Diptera. These plants include *Croton* (Crotoneae), *Jatropha* (Jatropheae), and *Tragia* (Plukenetieae; see review in Webster 1994). Specialized pollination (by few pollinator species or functional groups) is seen in some species of *Macaranga* (Acalypheae; by thrips, Moog et al. 2002), *Breynia*, *Glochidion*, and some *Phyllanthus* (Phyllantheae; by moths, Kawakita 2010). These four cases represent the recent discovery of the brood-reward systems in the Euphorbiaceae. Here the pollinators lay eggs on or near the flowers and the larvae feed on floral tissues, much as do fig wasps on figs and yucca moths on yuccas. Moderately specialized lepidopteran pollination has been reported in *Cnidoscolus* (Manihoteae; by sphingid moths, butterflies, and even hummingbirds, depending on species). Moderately specialized pollination by mammals has been reported in Central American *Mabea occidentalis* (Hippomaneae; by bats, marsupials, and the woolly opossum, Steiner 1983) and in Central American *Hura* (Hureae; by bats, Steiner 1982). These last two cases are somewhat intermediate between individual-flower and pseudanthial functioning in that mammal pollinators respond to clusters of staminate flowers, although only one or a few pistillate flowers are involved; the less important insect pollinators of *Mabea* presumably respond to individual flowers (Steiner 1983). Incidentally, the primarily bat-pollinated *Mabea fistulifera* in disturbed semi-deciduous forest and woodland of southeastern Brazil has become the meeting point of many forest animals, including more than 30 bird species many of which are frugiverous, two ceboid primates, four frugivorous bat species, the common opossum, and the coati (*Nasua nasua*), the majority of which probably can act as pollinators (Torres de Assumpção 1981; Vieira and Carvalho-Okano 1996; Olmos and Boulhosa 2000). The unspecialized reproductive system of this tree allows its continued existence in biotically impoverished habitats, and at the same time maintains a significant part of the pollinator and frugivore community during a period when fruits are scarce or not available.

Euphorbs with fully pseudanthial inflorescences have either "normal" unisexual flowers (*Dalechampia*, *Pera*) or highly reduced unisexual

flowers united in a cyathium (*Euphorbia* and relatives in Euphorbieae). In the latter case the staminate flowers are reduced to a single stamen and the pistillate flowers to a single pistil, with perianth absent in both cases. In both situations, pollinators visit the clusters of flowers as if they were a single flower—hence, application of the term pseudanthium (false flower) or blossom. Pollination of euphorbs with pseudanthial inflorescences is often highly generalized. Pollination by several to many types of insects occurs in some species of Malagasy *Dalechampia* (Plukenetieae; Armbruster and Baldwin 1998), in South American *Pera* (Pereae; Freitas et al. 2011), and many or possibly most species of *Euphorbia*. Other pseudanthiate euphorbs exhibit highly specialized pollination. Most neotropical *Dalechampia* are pollinated by females of one or a few species of resin-collecting bees (Armbruster 1984, 1988). The rewards are oxygenated triterpene resins secreted by modified bractlets borne by the staminate subinflorescence (Armbruster et al. 1997). Specialized pollination by fragrance-collecting, male euglossine bees has evolved independently from resin-reward ancestors at least three times (Armbruster 1993; Armbruster et al. 2009). The fragrance rewards are secreted by the stigmatic surface in two of these clades, and by a modified "resin gland" in one clade (Armbruster 1993). Specialized pollination by hummingbirds is seen in the *Pedilanthus* clade of *Euphorbia*; Cacho et al. 2010).

Fruit and Seed. The typical Euphorbiaceous fruit is a 3-locular capsule (schizocarp) that dehisces, often explosively, into three 1- or 2-seeded units (cocci or mericarps). The seeds are released when the cocci separate septicidally and sometimes loculicidally as well; in some genera the cocci remain more or less closed. The axis of the fruit, including the three placentae, persists as a columella, which may be massive or appendaged (e.g., in *Stillingia*), but is sometimes deciduous. However, in a sizeable number of genera scattered through all the subfamilies, the fruit remains indehiscent and the carpellar walls become fleshy, sometimes with a sclerified endocarp. One-seeded fruits are almost always indehiscent. Somewhat counter-intuitively, Stuppy (1996) recorded in biovulate genera only 19 (28%) with 2 seeds per locule in fruit.

The seed coat in Euphorbiaceaous seeds, investigated by Netolitzky (1926), Wunderlich (1968), Corner (1976), Stuppy (1996), and Tokuoka and Tobe (1995, 1998, 2001, 2002, 2003), usually consists of two primary layers: the testa, derived from the outer integument of the ovule, and the tegmen, derived from the outer layer(s) of the inner integument. The testa usually has few cell layers, except in seeds with a sarcotesta, which may have 10 cell layers or more (Stuppy 1996). In indehiscent fruits, however, the testa may be thin or even rudimentary. Corner (1976) recognized that the variable structure of the sclerified cells derived from the outer layer of the inner integument (exotegmen) furnished important clues to relationships between genera. In biovulate euphorbs, the exotegmen is often fibrous, but the studies of Stuppy (1996) and Tokuoka and Tobe (2001) have revealed such a great variation in its structure that these authors even considered the exclusion of the aberrant genera *Oldfieldia*, *Picrodendron*, *Hymenocardia* and *Didymocistus* from the family. Among the uniovulate subfamilies, Peroideae (except for the problematic *Pogonophora*) have a peculiar seed coat consisting of only two persistent cell layers, the well-developed exotesta of radially elongated cells and the more weakly developed tracheoidal exotegmen. All remaining uniovulate Euphorbiaceae have the palisadal exotegmen composed of radially elongated cells. Carunculate seeds are lacking in the Phyllanthoideae but occur, though not consistently, in all other subfamilies. The caruncle can function as an elaiosome and, after the ballistic or barochorous ejection of the seeds, attracts ants that are implicated in a further dispersal event (Berg 1975). Bianchini and Pacini (1996) and Lisci et al. (1996) point out that the caruncle may also have functions other than mymecochory, such as facilitation or inhibition of germination.

In Euphorbiaceous seeds, starch as a storage product is replaced by protein and fat oil.

Dispersal. The typical Euphorbiaceous fruit (upon drying) dehisces explosively into three 1- or 2-seeded merocarps (cocci). This kind of autochorous dispersal can be quite effective in genera such as *Hevea* or *Hura*, whose seeds may be dispersed as far as 43 m (Swain and Beer 1976). However, in many genera the seed may produce appendages or a sarcotesta, and the primary

autochorous dispersal is followed or superseded by animal dispersal. Seeds with fleshy integumental elaiosomes (caruncles) are dispersed by ants. In Australia, myrmecochory is especially prominent, perhaps reflecting the widespread open and xeromorphic vegetation (Berg 1975). As reported by Clifford and Monteith (1989), seed dispersal of Australian *Petalostigma pubescens* implies three distinct phases, beginning with the ingestion and transport of the drupes by migrating emus. Voided endocarps, freed from the fleshy epicarp, upon exposure to the sun dehisce explosively and project the seeds up to 2.5 m from the point of origin, and the seeds can be carried off by ants feeding on the conspicuous elaiosomes. In *Croton*, where myrmecochory is a very widespread mode of dispersal, the typical caruncles have been lost in sect. *Cuneati* with riverine species such as *C. cuneatus* and *C. yavitensis* showing an arillate structure possibly adapted to attract fish (Riina et al. 2010). Dispersal of diaspores by fish during their upstream-directed spawning migrations is a frequent phenomenon in the periodically overflooded river plains of Amazonia, where large fish such as tambaqui (*Colossoma macropomum*) and jatuarana (*Brycon* sp.) show strong preferences for the fruits of *Hevea spruceana* and *H. brasiliensis* (Goulding 1980) but have also been found to disperse the propagules of *Piranhea trifoliata* and *Mabea* sp.

Ornithochory seems to be confined to the tropics, especially in Africa and Asia, but is less common in the Oldfieldioideae and Euphorbioideae (Webster 1994a). Seeds with fleshy coats (sarcotesta), found in all five subfamilies, are generally dispersed by birds. In *Baccaurea*, for example, which has non-explosive fruits, some species have orange arils and are dispersed by birds, whereas other species have berries with sweet pulp and are dispersed by rats, fruit bats, or squirrels (Ridley 1930: 427). The fruits of the shade-intolerant riverine tree *Trewia nudiflora* (= *Mallotus*) are large, hard, and dull-colored upon ripening, unattractive to the usual seed dispersers such as monkeys, bats, and birds, but regularly eaten by the greater one-horned Asian rhinoceros (*Rh. unicormis*). Seeds deposited into the animals' dung on open grassland develop into robust, fast-growing seedlings, providing an interesting example of megafaunal dispersal (Dinerstein and Wemmer 1988).

PHYTOCHEMISTRY. Euphorbiaceae are one of the chemically most diverse angiosperm families (Hegnauer 1966, 1989; Seigler 1994). Many taxa produce toxic or medicinally important compounds (e.g., ricinin in the seed coat and castor oil in the endosperm of *Ricinus* seeds); in the tropics, they have acquired a wide use for many purposes such as for arrow poisons (*Sapium*) or as fish poisons (*Phyllanthus*). A number of genera (*Cnidoscolus*, *Dalechampia*, *Tragia*) are implicated in dermatitis. The sap of several Euphorbioideae (*Euphorbia* subg. *Euphorbia*, *Hippomane*, *Ophthalmoblapton*, *Synadenium*, *Excoecaria agallocha* = "blind-your-eye") is dangerously toxic.

Among the more significant secondary metabolites produced by Euphorbiaceae are tannins, alkaloids, cyanogenic glycosides, diterpenes, glucosinolated lipids, and triterpenes. Both condensed and hydrolysable tannins are present in the family, mostly in woody species. The ellagitannin geraniin has been found in all subfamilies, and in the uniovulate ones it is often accompanied by the similar mallotusinic acid. Alkaloids are particularly diverse in Phyllanthoideae, Crotonoideae (especially *Aleurites*, *Croton*, *Jatropha*) and in some Acalyphoideae (*Alchornea*, *Mallotus*, *Ricinus*), but there is no structural type of alkaloids characteristic for the family. Cyanogenic glycosides are widespread in Phyllanthoideae (*Andrachne*, *Bridelia*, *Flueggea*, *Phyllanthus*) and Crotonoideae (*Aleurites*, *Croton*, *Elateiospermum*, *Hevea*, *Manihot*), but have also been reported from Acalyphoideae (*Acalypha*, *Mercurialis*, *Ricinus*) and several Euphorbioideae. A considerable variety of diterpenes occur in Euphorbiaceae. Cyclic diterpenes are especially prominent in Crotonoideae (*Bertya*, *Croton*, *Jatropha*). Tetracyclic diterpenes isolated from species of *Croton* have been implicated as cocarcinogens. Triterpenes are common in many Euphorbiaceae, especially the Euphorbioideae. In *Euphorbia*, investigations of triterpene composition have produced suggestive evidence for delimiting subgenera and sections (Ponsinet and Ourisson 1965). Terpene-rich latex in many Euphorbiaceae is also accompanied by rubber (polyisoprenes). Although *Hevea* is the best known source of rubber, it is also produced by other Crotonoideae such as *Cnidoscolus*, *Manihot*, and *Micrandra*, as well as *Chamaesyce* and *Euphorbia* (Rizk 1987).

PALEOBOTANY. The Euphorbiaceae, despite their contemporary prominence and broad distribution, do not have an impressive fossil record. Fossil woods, such as the much-cited *Paraphyllanthoxylon* from the Cretaceous of North America (Bailey 1924; Cahoon 1972), cannot be convincingly verified as Euphorbiaceous. Mädel (1962), in a study of Cretaceous fossils from South Africa, plausibly suggested that *Paraphyllanthoxylon capense* is similar to *Margaritaria discoidea*. Mädel's *Securinegoxylon biseriatum* can perhaps be compared with *Heywoodia lucens*, which grows in South Africa today.

There is greater certainty in the relationships of the Eocene fossils of fruits from America and Europe that have been referred to the Hippomaneae by Mazer and Tiffney (1982) and Dilcher and Manchester (1988). Both *Wetherellia* and *Palaeowetherellia*, in fruit morphology and in the depositional facies in which they occur, can be associated with the living genus *Hippomane*; Dilcher and Manchester consider *Crepetocarpon* to be unquestionably close to *Hippomane*.

Fossil flowers of Euphorbiaceae are little known, but the Eocene *Hippomaneoidea* of Crepet and Daglian (1982) is well-preserved, and the pollen suggests a relationship to *Senefeldera*, a neotropical genus considerably less specialized than *Hippomane*.

Dispersed fossil pollen can be hazardous to identify but, according to Muller (1984), genera resembling the Oldfieldioideae, Acalyphoideae, and Crotonoideae are known from the early Tertiary. A notable record of Euphorbiaceous pollen from the Eocene in France (Gruas-Cavagnetto and Köhler 1992) includes a wide range of taxa: *Actephila*, *Antidesma*, *Bischofia*, *Leptopus*, and *Phyllanthus* (Phyllanthoideae); *Austrobuxus* and *Dissiliaria* (Oldfieldioideae); *Alchornea* and *Ricinus* (Acalyphoideae). In Australia, Oldfieldioideae appear in the Paleocene and, in the early Eocene, in greater diversity (Martin 1974, 1978). Because the pollen of most Phyllanthoideae is morphologically unspecialized, it may be difficult to follow the record of fossil pollen of the Euphorbiaceae back into the Cretaceous. Taking the available evidence into account, however, it seems reasonable to surmise that the Phyllanthoideae and Oldfieldioideae, at least, had differentiated by the upper Cretaceous and that the radiation of the subfamilies had occurred by the Paleocene.

DISTRIBUTION AND HABITATS. Although Euphorbiaceae are a pantropical family, they also extend into subtropical and warm temperate regions, and some herbaceous species of *Euphorbia* occur in subpolar and alpine areas. Generic diversity for Phyllanthoideae is greatest in Africa, for Oldfieldioideae in Australasia, and for Acalyphoideae and Euphorbioideae in Asia; diversity is approximately equal in American and Asiatic Crotonoideae (Webster 1994a). In total generic diversity, American leads with 111 genera, followed by Asia with 107, Africa with 102, and Australasia with 77. Madagascar, with 51 genera (17 endemic), is the most distinctive subregion.

Among the Phyllanthoideae there are genera—mostly smaller ones—that are restricted to Africa/Madagascar, such as *Wielandia*, *Lachnostylis*/*Securinega*, and *Uapaca*. Some large genera such as the *Meineckia*, *Flueggea*, and *Margaritaria* have a pantropical distribution that includes the African/Malagasy region. There are remarkable disjunctions between closely related genera, such as between the African *Heywoodia* and the neotropical *Chascotheca* + *Astrocasia*. The closest relatives of the strictly African/Malagasy *Wielandia* are the east Asian *Dicoelia* + *Chorisandrachne*, and African *Hymenocardia* is close to neotropical *Didymocistus*. This highly disjunct distribution of the tribes and genera is most likely the result of long-distance dispersal, as has been suggested for *Bridelia*, which very likely dispersed from tropical Africa to Asia and Australia once or twice from 10 million years ago onward (Li et al. 2009).

In the Oldfieldioideae, which are best developed in Australasia, much more compact distribution patterns of the (sub)tribes can be recognized. The whole group is highly disjunct, with the tribally isolated neotropical *Podocalyx* and tribe Picrodendreae disjunct between the New World and Africa/Madagascar. The genera of Mischodontinae, with exception of the Ceylonese *Mischanthus*, all are Madagascan. Tribe Caletieae is a group of 14 genera centered in Australia with a paleontological record dating back there into the Paleocene (Martin 1974, 1978).

Peroideae are utterly disjunct, and Cheilosoideae restricted to the Oriental region. Acalyphoideae are widely distributed in the neo- and paleotropical region including Australia, and only few and smaller tribes are restricted to a single continent, such as neotropical Adelieae, Asian Erismantheae, and Australian Ampereeae;

the large tribes Acalypheae and Plukenetieae are pantropical. Crotonoideae are well represented in the New World, with Crotoneae, Micrandreae, etc., or in the Old World with inclusion of the Australasian region (Codieae, Ricinocarpeae), but have a weak representation in Africa. In Euphorbiodeae the four genera of Stomatocalyceae, two of them monotypes, present a highly disjunct picture, with one genus in the New World, two in Africa, and one in Australasia. A similar trend is evident in the equally relictual basal subtribes of the Euphorbieae, the Anthostematinae and Neoguillauminiinae. Subtribe Euphorbiinae, i.e., *Euphorbia* s. l., is subcosmopolitan, with the *Rhizanthium* clade including mostly southern African xerophytes, the *Esula* clade with predominantly northern hemisphere herbaceous species, the *Euphorbia* clade representing the greatest diversity within the genus formed mainly by African/Madagascan xerophytes, and the mainly New World *Chamaesyce* clade.

Despite their diversity, Euphorbiaceae are predominantly shrubs or short-lived trees adapted to secondary succession in dry to mesic seasonal habitats. In savannas, tropical deciduous forests, and deserts, genera such as *Chamaesyce*, *Cnidoscolus*, *Croton*, *Euphorbia*, *Hymenocardia*, and *Jatropha* are well represented. However, there are also a significant number of genera in lowland tropical rainforest: in America, *Alchornea*, *Amanoa*, *Hevea*, *Hieronyma*, *Micrandra*, and *Richeria*; in Africa, *Maesobotrya*, *Spondianthus*, and other Phyllanthoideae; in Asia and Australasia, *Antidesma*, *Aporosa*, *Baccaurea*, *Glochidion*, *Macaranga*, and *Mallotus*. Adaptation to diverse habitats can be seen even within single genera. For example, while most *Dalechampia* are twining vines or lianas adapted to secondary environments with very high light levels, one clade of 3–4 species, sect. *Cremophyllum*, is a small monopodial shrub largely restricted to the dark understorey of primary rainforests. In tropical regions, some Euphorbiaceae have adopted specialist roles. Along rivers, there are a number of rheophytes adapted to surviving strong currents and submergence, including species of *Phyllanthus* and *Homonoia*. Rooted aquatics are found in *Caperonia* and *Phyllanthus*; the only floating aquatic in the family is the Amazonian *Phyllanthus fluitans*.

Ericoid life forms are common in Australia, especially in *Bertya*, *Beyeria*, *Micrantheum*, and *Pseudanthus*. Ultramafic (serpentinic) outcrops, especially in Cuba and New Caledonia, have housed a spectacular radiation of sclerophyll species of *Phyllanthus*. Sand dunes in subtropical arid regions support psammophile species of *Chamaesyce*, *Chrozophora*, and *Croton*.

Circumscription and Subdivision of the Family. The circumscription of the Euphorbiaceae had remained surprisingly stable over a long period of time (Webster 1987), whereas its infrafamilial classification remained contentious (reviewed in Webster 1987, 1994a). Delimitation of infrafamilial taxa was long obfuscated by Müller's unnatural binary division of the family into Platylobeae and Stenolobeae (Müller 1866), which—despite its rejection by Bentham (1880)—was adopted by Pax (1890) and Pax and Hoffmann (1931). Bentham (1880) and later Hutchinson (1969) recognized only the tribal level as the major infrafamilial rank, whereas Pax (1884, 1890) recognized two main subfamilies, Phyllanthoideae and Crotonoideae, for the biovulate and uniovulate taxa, a critical distinction not grasped by Müller and Bentham but accepted since then by most systematists. Nevertheless, the heterogeneity within these two major infrafamilial groups prompted Webster (1975, 1994b) to propose a system of five subfamilies: Phyllanthoideae, Oldfieldioideae, Acalyphoideae, Crotonoideae, and Euphorbioideae. This was generally adopted, notwithstanding the claims by various authors to elevate superficially anomalous genera such as *Hymenocardia*, *Uapaca*, *Bischofia*, etc. to family rank—after closer inspection, these were found to be untenable. In the system of Webster (1994b), the number of tribes was increased from 14 to 49, a number again slightly increased by Radcliffe-Smith (2001).

Corner's (1976) studies in seed coat structure of the dicotyledons led him to question the homogeneity of the family, an opinion that received support from upcoming DNA sequence studies. Molecular systematics, beginning with the work of Wurdack (2002), led to a radical dismemberment of the family into three families, the Phyllanthaceae and Picrodendraceae (= Oldfieldioideae), both biovulate, and the uniovulate

Euphorbiaceae, apart from the hardly disputed expulsion of some extraneous genera relegated to the Putranjivaceae, Centroplacaceae, and Pandaceae. More recently, and not unexpectedly, increased molecular resolution of the deeper nodes of the Malpighiales tree has resolved Phyllanthaceae and Picrodendraceae (Oldfieldioideae) as strongly supported sisters (Tokuoka and Tobe 2006; Wurdack and Davis 2009; Korotkova et al. 2009; Soltis et al. 2011); this means that, for those who want to maintain different families for biovulate and uniovulate euphorbs, there is no longer any compelling necessity for distinguishing between Phyllanthaceae s. str. and Picrodendraceae.

Broad-based molecular phylogenetic analyses of representatives of the traditional uniovulate subfamilies Acalyphoideae, Crotonoideae, and Euphorbioideae have recovered the uniovulate euphorbs as monophyletic (Wurdack et al. 2005; Tokuoka 2007; Xi et al. 2012), and have brought to light novel groupings that largely correlate with the distribution of traditional characters such as latex and laticifers, pollen morphology, and ovular and seed coat characters. Two strongly supported basal clades have been proposed as additional subfamilies (Peroideae and Cheilosoideae), whereas the rest of the family is divided into seven major lineages. Among them, the core Acalyphoids and the Euphorbioideae are monophyletic groups, whereas the Crotonoideae are resolved as several distinct and partly not well-supported clades.

Strong molecular evidence supports the monophyly both of the biovulate and uniovulate Euphorbiaceae, whereas molecular proof for the monophyly of the Euphorbiaceae s. l. is still lacking. The most recent analysis (Xi et al. 2012) places the biovulate and uniovulate euphorbs, the latter together with Linaceae and Ixonanthaceae, in a weakly supported clade. There are, however, important similarities in embryological, gynoecial and fruit structures between Phyllanthaceae s. l. and Euphorbiaceae s.str. First, the combination of nucellar beaks, epitropous ovules, and obturators within the angiosperms is restricted to Euphorbiaceae s. l. (Sutter and Endress 1995; Merino Sutter et al. 2006; see above under FLORAL STRUCTURE). Second, the fruit morphology of the Euphorbiaceae s. l., which has attracted the interest of botanists since the time of Baillon (1858; see also Berg 1975), is highly significant; the formation of cocci, separating from a central column, is a characteristic of the family and has been the basis of the earlier ordinal name, Tricoccae. The cocci and their xerochastic sclerenchymatic endocarp tissue instrumental in the explosive dehiscence are the basic elements of the explosive seed release characteristic for the family.

These structural traits support the close relationship between the uni- and biovulate euphorbs, and have led us to retain the broad family concept of the family. Further molecular inquiry into the deeper nodes of the phylogeny of the Malpighiales beyond the interesting findings of Xi et al. (2012) is impatiently expected for a clarification of this issue.

ECONOMIC IMPORTANCE. As a consequence of their chemical diversity, the Euphorbiaceae include a considerable number of economically important species (Schultes 1987). The currently most valuable commodity is probably the starchy tubers of cassava (*Manihot*), widely cultivated in America and Africa. The Pará rubber tree (*Hevea*), the most important Euphorbiaceous crop in the 19th century, is still the major source of non-synthetic commercial rubber. Seed oils of tung (*Aleurites*) and castor bean (*Ricinus*) continue to be widely used, but in South America there is now considerable interest in the seed oil of inchi (*Caryodendron*), which is considered superior to the oil of the African oil palm, *Elais* (Schultes 1987). Waxes from neotropical species of *Sapium* and *Euphorbia* (especially *E. antisyphilitica*) are still a minor source of commercial waxes. Use of the latex of *Euphorbia tirucalli* plants as "gasoline trees", once vigorously advocated by Calvin (1987), appeared not competitive with sugar cane.

As pointed out by Schultes (1987), many Euphorbiaceae have been cultivated in tropical areas for thousands of years. Schultes observed Amerinidians in the Amazon basin exploiting Euphorbiaceae in a variety of ways, including food, medicines, and piscicides. For example, the reddish latex of some neotropical species of *Croton* ("Sangre de Drago") is widely used in South America as a salve applied to cuts and sores. The alkaloids in Sangre de Drago latex appear to be non-toxic to humans, but other species of *Croton* produce phorbol esters that

have been implicated in human cancer (Kinghorn 1979). Herbaceous species of *Phyllanthus* have long been used in folk medicine in the tropics to treat kidney and urinary problems and jaundice (Webster 2002), and pharmaceutical research has revealed many useful applications of the antiviral compounds of *Ph. amarus*, which are of potential value in treating the hepatitis B virus.

Because of their generally small inconspicuous flowers, the Euphorbiaceae include relatively few ornamental plants, but species of a few genera are commonly cultivated in tropical gardens or greenhouses for their colorful inflorescences or foliage: *Acalypha*, *Codiaeum*, *Jatropha*, *Euphorbia*. Succulent taxa of *Euphorbia* subgenus *Euphorbia*—e.g., sects. *Monadenium*, *Pedilanthus*, *Synadenium*—are popular in tropical and subtropical gardens. *Dalechampia aristolochiifolia* Kunth is a recently marketed horticultural vine increasingly cultivated in warm temperate regions for its colorful bracts (generally advertised on the internet incorrectly as *D. dioscoreifolia*).

Some Euphorbiaceae have a distinctly negative economic value; the family includes many taxa adapted for secondary succession, and hence there are a number of aggressive weeds. In temperate regions, the most damaging invaders of cultivated fields, especially in North America, are species of *Euphorbia* section *Esula*, especially *E. esula* and related species. Some weedy taxa—species of *Euphorbia*, *Mercurialis*, *Phyllanthus*—are particularly obnoxious because of their toxicity to livestock (Burrows and Tyrl 2001). Recently exotic woody Euphorbiaceae, including species of *Glochidion*, have invaded the southern United States. The most aggressive species is the Chinese tallow tree, *Triadica sebifera* (*Sapium sebiferum*), which has invaded forests and even grasslands from Florida to Texas and has become established in California.

SUBFAMILIES, TRIBES AND GENERA OF EUPHORBIACEAE

In all generic descriptions given below,

- for the sake of briefness it is generally assumed—*if not stated otherwise*—that the plants have alternate simple leaves with entire margins, distinct stipules, lack foliar glands and domatia, have anthers dehiscing longitudinally, and that their petioles are not pulvinate;
- rarely occurring character states are given in parentheses ( ), whereas square brackets [ ] are used in taxonomic descriptions for comments and explanations.

Users of this treatment who want to make determinations of genera of Euphorbiaceae may use this **multichoice key:**

Hoffmann, P., Kirkup, D., Galster, A.M., Challen, G., Radcliffe-Smith, A. 2005. Key to the genera of Euphorbiaceae *sensu lato*. Available at www.kew.org/herbarium/keys/euphorbs

Conspectus of the Subfamilies of Euphorbiaceae

1. Locules of ovary each with 2 ovules; milky latex, intraxylary phloem, and stinging hairs 0; indumentum simple (lepidote or dendritic); embedded foliar glands rare; pollen grains binucleate **2**
– Locules of ovary each with 1 ovule; latex + or 0; indumentum various; pollen grains binucleate or trinucleate 3
2. Leaves alternate (opposite), stipulate, simple and unlobed [except in *Bischofia*]; petals + or 0; pollen grains tricolporate to -porate, sexine lacking spines [except in *Amanoa and Croizatia*]; seeds ecarunculate
I. Subfam. Phyllanthoideae (p. 64)
– Leaves alternate, opposite, or whorled, stipulate or estipulate, simple to trifoliolate; petals 0; pollen grains colporoidate to porate, sexine spiny; seeds carunculate or ecarunculate
II. Subfam. Oldfieldioideae (p. 90)
3. Ovules with thin integuments [inner integument < 6 cells thick]; seeds arillate; seed coat with tracheoidal exotegmen
III. Subfam. Peroideae (p. 102)
– Ovules usually [Adenoclineae excepted] with thick integuments [inner integument > 8 cells thick]; seeds arillate or not; seed coat with palisadal exotegmen **4**
4. Pollen exine echinate; flowers apetalous; seeds exarillate **IV. Subfam. Cheilosoideae** (p. 105)
– Pollen exine not echinate; flowers petaliferous or apetalous; seeds arillate or exarillate 5
5. Milky latex 0; laticifers, if present, non-articulate; pollen grains binucleate
V. Subfam. Acalyphoideae (p. 106)
– Latex + (scanty or 0), milky or colored; laticifers articulate or non-articulate; pollen grains binucleate or trinucleate **6**
6. Latex reddish or yellowish to milky; laticifers articulate or non-articulate; 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 + [at least in

pistillate flowers]; pollen grains tricolporate or more often porate or inaperturate, with hexagonal sexinous processes

VI. Subfam. Crotonoideae (p.156)

– Latex whitish (yellow), often caustic or toxic; laticifers non-articulate; leaves usually unlobed; indumentum simple or lepidote (dendritic in some Hippomaneae); bracts often biglandular at base; sepals imbricate to reduced or 0, anthers mostly not covered in bud; petals 0; pollen grains tricolporate, exine mostly perforate-reticulate

VII. Subfam. Euphorbioideae (p. 190)

I. Subfam. Phyllanthoideae Beilschm. (1833).

Phyllanthaceae Martinov (1820).

Monoecious or dioecious trees, shrubs, or herbs; vessel elements with simple to scalariform perforations; indumentum mostly simple. Leaves alternate (opposite), spiral to distichous, usually stipulate, simple and entire, trifoliolate and dentate in *Bischofia*, without embedded glands, stomata mostly paracytic or anisocytic; petiole eglandular. Inflorescences axillary (terminal), of racemoid or spikelike thyrses or reduced to glomerules or flowers solitary; bracts eglandular. Sepals mostly 4–6, imbricate (valvate), usually ± basally connate; petals and disk + or 0; stamens (2)3–8(−60), filaments distinct or connate; anthers dehiscing horizontally to vertically; pollen grains mostly 3–4(−7)-colporate (−porate), exine mostly semitectate (echinate); male gametophyte binucleate; pistillode + or 0; ovary (1)2–5(−20)-locular, ovules 2 in each locule, anatropous or hemitropous, nucellar beak sometimes prominent; stylodia mostly distinct, usually bifid, sometimes unlobed. Fruit mostly capsular, less commonly baccate or drupaceous; columella often persistent. Seeds ecarunculate [except for *Celianella*]; endosperm + or 0; cotyledons plane, incrassate, or folded. $x = 12$ or 13 (8, 10 or 11).

A diverse subfamily comprising about 59 genera, sometimes recognized as a separate family Phyllanthaceae or Antidesmataceae. Airy Shaw (1965) split off from it four families—Bischofiaceae, Hymenocardiaceae, Stilaginaceae, and Uapacaceae; Meeuse (1990) added one more segregate, Putranjivaceae. Except for *Bischofia*, none of Airy Shaw's proposed segregates is sufficiently aberrant to make its membership in the Phyllanthoideae questionable, and all structural and molecular evidence accrued since 1990 confirms *Bischofia* as a member of Phyllanthoideae. On the other hand, Putranjivaceae have now been excluded definitely from the Euphorbiaceae on the basis of chemical and molecular studies (e.g., Chase et al. 1993; Wurdack 2002), corroborated by Tokuoka and Tobe (1999) in the demonstration of an impressive number of embryological differences between the reinstated Putranjivaceae and Euphorbiaceae and the findings by Xi et al. (2012), which place *Putranjiva* in a clade with *Lophopyxis*.

In the classification of Phyllanthoideae, which largely follows the one given by Hoffmann and Wurdack (2006), the group is subdivided into 10 tribes and 12 subtribes, which correspond with strongly supported clades of the multigene analysis of Kathriarachchi et al. (2005). In spite of this, morphologically they are often utterly disparate and, in extreme cases, determination of species and genera is said to depend on molecular analyses.

Key to the Tribes of Subfam. Phyllanthoideae

1. Leaves simple; inflorescence mainly of glomerules or thyrses; flowers with or without petals; stylodia entire to multifid; fruits capsular, baccate, or drupaceous **2**
– Leaves palmately 3–5-foliolate; inflorescence paniculate or racemose; flowers lacking petals and disk; stylodia entire; fruits drupaceous **10. Bischofieae**
2. Fruits winged or lobed; petals and disk 0; ovary locules 2; pollen zonoporate **5. Antidesmateae-Hymenocardiinae**
– Fruits not winged; inflorescences mostly not ament-like [except in Antidesmeae]; stylodia entire to bifid (multifid); floral disk + or 0; pollen rarely zonoporate **3**
3. Stems with resinous exudate; inflorescences paniculate or capitulate **4**
– Stems lacking resin; inflorescences not paniculate or capitate 5
4. Petals +; inflorescence terminal, paniculate; pollen not spinulose; fruit capsular **8. Spondiantheae**
– Petals 0; inflorescence axillary, capitate; pollen spinulose; fruit drupaceous **9. Uapaceae**
5. Leaves with tanniniferous cells in upper epidermis; flowers in axillary or terminal spike-like or raceme-like inflorescences, with discernible axes **6**
– Leaves without tanniniferous cells in upper epidermis; flowers in axillary glomerules, usually without discernible axes [except in *Flueggea gracilis* and some *Phyllanthus*] **7**

6. Thecae usually separate and connective enlarged, anther locules ± pendulous; leaves not glandular **5. Antidesmateae**
– Thecae not separate and connective not enlarged (enlarged in some *Aporosa*), anther locules not pendulous; leaves sometimes glandular **6. Scepeae**
7. Indumentum 0; pistillate sepals persistent; inflorescence sometimes [*Celianella*] pedunculate **7. Jablonskieae**
– Indumentum + or 0; pistillate sepals usually not persistent; inflorescences not pedunculate **8**
8. Foliar glands rarely +; sepals distinct or nearly completely connate; petals 0 [+ in *Heterosavia*]; disk + or 0; pistillode + or 0; ovules hemitropous or rarely [*Heterosavia*] anatropous; seeds exarillate or rarely with colored sarcotesta **4. Phyllantheae**
– Foliar glands 0; sepals ± distinct; petals + or 0; disk +; pistillode +; ovules anatropous [hemitropous in *Andrachne*]; seeds exarillate **9**
9. Petals + in staminate flowers, 0 in *Chascotheca*, usually equaling the sepals **3. Wielandieae**
– Petals + or 0 in staminate flowers 10
10. Sepals 4–6(7), imbricate (valvate in *Bridelia*, *Cleistanthus*); stamens 4–10(−19); fruit dehiscent or indehiscent **2. Bridelieae**
– Sepals (3)5–6, imbricate; stamens 3–6; anthers rarely poricidal [*Poranthera*]; fruit explosively dehiscent **1. Poranthereae**

IA. Supertribe Phyllanthodae G.L. Webster, **supertrib. nov.**[1]

Subfam. Phyllanthoideae Kostel. (1836).

1. Tribe Poranthereae Grüning (1913),

recircumscribed by Hoffmann et al., Kew Bull. 61: 41 (2006), Vorontsova et al., Amer. J. Bot. 94: 2026–2040 (2007), mol. syst.; Vorontsova & Hoffmann, Kew Bull. 63: 41–59 (2008), classif.

Staminate disk in distinct parts or extrastaminal-annular, pistillate disk simple; stamens 3–6; filaments distinct or variously connate; anthers longitudinally dehiscing or poricidal; thecae not separate and connective not enlarged; pistillode usually +; ovary 3-locular; stylodia distinct or completely connate; fruits explosively dehiscent; seeds exarillate.

Eight genera, (sub)tropical regions, worldwide. The circumscription of this group of genera was first suggested by Wurdack et al. (2004) and later confirmed by, among others, Vorontsova et al. (2007). The clade comprises genera that formerly belonged to three different tribes, and the group (and even some of its genera!) cannot be recognized on the basis of morphological characters alone. $x = 11, 12$.

Key to the Genera of Poranthereae (from Voronts. & Hoffm. 2008).

1. Anther dehiscence poricidal; flowers appearing to be in terminal umbels or racemes (in fact in dense aggregations of axillary flowers); fruit deeply 6-lobed; no secondary leaf venation visible with the naked eye. Australia and New Zealand **4. *Poranthera***
– Anther dehiscence longitudinal; flowers clearly axillary, staminate flowers sometimes on short densely bracteate inflorescences; fruit 3(−5)-lobed or globose; secondary leaf venation visible with the naked eye, usually prominent **2**
2. Petals in staminate flowers 0 or, if present, less than half the sepal length, if petals longer, then of unequal size or filiform [5(6) perianth segments clearly visible]; petals in pistillate flowers, if present, very similar to those in staminate ones; disk annular, entire or shallowly undulate; stipules usually deciduous **3**
– Petals in staminate flowers 5(6), nearly as long as sepals, all equal in size, white [10(12) perianth segments clearly visible]; petals in pistillate flowers, if present, less than half the sepal length, often hidden by the disk; staminate disk glands distinct or fused at the base, bilobed, or almost 10-crenate (*Notoleptopus*) or irregularly crenate (*Pseudophyllanthus*); pistillate disk glands distinct or disk annular, more or less crenate; stipules persistent **4**
3. Seeds smooth; endosperm scanty or 0; disk convex, thick and fleshy, becoming thinner toward edge; filaments distinct or connate at base only; petals in staminate flowers 0 or, if present, unequal or filiform; stipules deciduous **2. *Actephila***
– Seeds rugose to fenestrate; endosperm copious; disk concave, slightly cupular, usually thin and chartaceous; filaments connate for 1/4 to 9/10 of their length, rarely (former *Zimmermannia* and *Zimmermanniopsis*) distinct; petals in staminate flowers 0 or rarely (subg. *Petaliferae*) 5, equal, less than half of the sepal length; stipules deciduous or persistent **7. *Meineckia***
4. Plant including branches, leaves, sepals, ovaries and fruit densely covered with hairs about 1 mm long, visible to the naked eye; seed intensely black, rugose **6. *Notoleptopus***
– Plant glabrous, with sparse covering of simple hairs, or rough with gland-tipped hairs not visible to the naked eye; seed whitish to dark brown, smooth to rugose **5**
5. Procumbent herbs to subshrubs up to 0.5 m tall (erect in *Andrachne fruticulosa*); ovule adnation hemitropous; seed rough, with star-shaped sculpture visible at high magnification when dry **8. *Andrachne***

[1] Supertribe **Phyllanthodae** G.L. Webster, **supertrib. nov.**, floribus cymulis axillaribus, cellulis epidermalibus foliorum non tanniniferis, embryonibus plerumque non chlorophyllosis, fructibus saepe capsularibus. Typus: *Phyllanthus* L.

– Erect shrubs to trees 0.2–6 m tall (*Leptopus clarkei* procumbent); ovules anatropous; seed smooth, rugose or pitted, without star-shaped sculpture **6**

6. Staminate disk irregularly crenate to almost lacerate; pistillate disk annular, finely crenulate; filaments usually connate for about one half of their length, rarely distinct. Seed undulate to shallowly rugose; endosperm invaginate independently of seed coat sculpture **5. *Pseudophyllanthus***

– Staminate disk regularly divided into 5 rounded bilobed segments; pistillate disk regularly divided into 5 emarginate segments; filaments distinct; seeds smooth, rugose or pitted; endosperm entire in cross section or with undulations following seed coat curvature **7**

7. Stylodia bifid for half their length or less; stigmas acute to dilated; seed smooth **3. *Phyllanthopsis***

– Stylodia bifid to base or almost so; stigmas capitate to dilated; seed smooth, rugose or pitted **1. *Leptopus***

1. *Leptopus* Decne.

Leptopus Decne., Voy. Inde 4 (Bot.): 155 (1836); Voronts. & Petra Hoffm., Kew Bull. 63: 46 (2008) and 64: 627–644 (2009), rev.
Archileptopus P. T. Li (1991).

Monoecious (dioecious) herbs or shrubs; indumentum simple or 0. Leaves entire; stipules persistent. Inflorescences axillary, fasciculate but mostly flowers solitary; staminate flowers sometimes on short bracteate inflorescences. Staminate flowers with pedicels articulate above base; sepals 5(6), petals 5(6), shorter than or as long as sepals; disk of 5(6) contiguous, bilobed segments; stamens 5, filaments distinct; anthers longitudinally dehiscent; pollen prolate to subprolate, exine tectate to microperforate; pistillode of 3 distinct segments or 3-lobed. Pistillate flowers with pedicels apically dilated; perianth as in staminate flowers but petals often minute; disk annular, regularly divided into 5 emarginate segments; ovary 3–4(5)-locular; ovules anatropous; stylodia distinct, bifid to base or nearly so; stigmas apically dilated to capitate. Fruit 3(−5)-lobate to subglobose; columella 4–5 times longer than its narrowest width. Seeds 2 per locule, ecarunculate; endosperm copious, in cross section entire to deeply invaginate; embryo curved to almost straight; cotyledons as long as radicle or longer, wider than radicle. $2n =$ 22, 24.

Nine spp., deciduous forests, Caucasus to Malesia.

2. *Actephila* Blume

Actephila Blume, Fl. Ned. Ind.: 581 (1825); Forster, Austrobaileya 7: 57–98 (2005), Austral. spp.; Vorontsova & Petra Hoffm., Kew Bull. 63: 46–47 (2008).

Monoecious trees to subshrubs; indumentum simple or 0. Leaves subverticillate or subopposite, entire or rarely toothed; stipules deciduous. Inflorescences axillary, fasciculate, or flowers solitary; pedicels usually elongated, not articulate. Staminated flowers: sepals 4–6; petals 4–6(0), shorter than sepals; disk annular, entire or shallowly undulate; stamens (3–)5(6), filaments distinct or connate basally with pistillode; anthers introrse; pollen prolate to subprolate, exine reticulate-striate; pistillode apically 3(5)-fid. Pistillate flowers: pedicels longer than staminate ones; sepals and petals as in staminate; disk annular; ovary 3-locular, ovules 2 per locule, anatropous; stylodia short, distinct or nearly so, entire to bifid to base at apex. Fruit capsular, loculicidally 3-valved or separating into 2-valved cocci; columella apically 3-pronged, basally dilated. Seeds 2(1) per locule, sometimes ecarunculate, ovoid, carinate; testa smooth and dry; endosperm scanty or 0; embryo folded, cotyledons thick, fleshy, sometimes plicate.

About 35 spp., Asia, Australia and Melanesia, in rainforest understorey.

3. *Phyllanthopsis* (Scheele) Voronts. & Petra Hoffm.

Phyllanthopsis (Scheele) Voronts. & Petra Hoffm., Kew Bull. 63: 47 (2008).
Phyllanthus subg. *Phyllanthopsis* Scheele (1853).
Andrachne sect. *Phyllantopsis* (Scheele) Müll. Arg. (1866); Petra Hoffm., Bot. Jahrb. 116: 321–331 (1994).

Monoecious or dioecious shrubs; indumentum simple or 0. Leaves entire; stipules persistent. Inflorescences axillary, fasciculate or flowers solitary. Staminate flowers pedicellate; sepals 5; petals 5, slightly shorter than sepals; disk annular, divided into 5 bilobed segments; stamens 5; filaments distinct; anthers longitudinally dehiscent; pistillode of 3 distinct segments. Pistillate flowers pedicellate, sepals 5; petals 5, much shorter than sepals; disk annular, divided into 5 emarginate segments; ovary 3-locular; ovules anatropous; stylodia distinct, bifid for up to half their length; stigmas acute to apically dilated. Fruit rounded to 3-lobed; columella 6 times longer than its narrowest width. Seeds 2 per locule, ecarunculate, smooth; endosperm copious, entire in cross section; embryo

curved; cotyledons broad, thin, longer and wider than radicles.

Two spp., Mexico, USA, in dry scrub.

4. *Poranthera* Rudge Fig. 11

Poranthera Rudge, Trans. Linn. Soc. London 10: 302 (1811); Halford & Henderson, Austrobaileya 7: l–27 (2005); Voronts. & Petra Hoffm., Kew Bull. 63: 50 (2008).
Oreoporanthera (Grüning) Hutch. (1969).

Monoecious (dioecious) annual or perennial herbs, sometimes suffruticose; indumentum 0. Leaves alternate (opposite), sessile or petiolate, entire, 2–20 times longer than wide; stipules pale, scarious. Inflorescences axillary but appearing to be in terminal umbels or racemes, fasciculate or flowers solitary. Staminate flowers: sepals (3)5, not accrescent; petals (3)5 or 0, smaller than sepals; disk of (3)5 distinct globular entire glands, stamens (3)5; filaments distinct; anthers dehiscing by terminal pores; pollen prolate(−spheroidal), exine tectate-perforate to reticulate; pistillode 3-fid. Pistillate flowers: sepals and petals as in staminate; disk annular and divided into (3)5 erose to undular segments; ovary 3-locular, 6-angled; stylodia bifid to base; stigmas rounded to capitate. Fruit deeply 6-lobed; columella 8 times longer than its narrowest width, persistent. Seeds 2 per locule, ecarunculate, smooth, reticulate, rugose or fenestrate; endosperm copious; embryo curved or straight; cotyledons shorter than radicle.

Fifteen spp., Australia, Tasmania, and New Zealand, in temperate grassland and woodland. This is the morphologically most aberrant genus of the tribe.

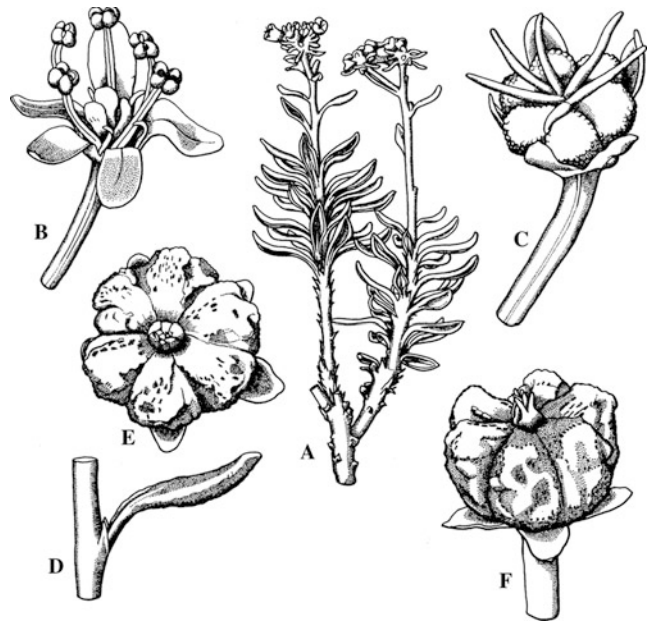

Fig. 11. Euphorbiaceae-Phyllanthoideae. *Poranthera obovata*. **A** Flowering branchlet. **B** Staminate flower. **C** Pistillate flower. **D** Branchlet with stipulate leaf. **E** Fruit seen from above. **F** Same from side. (Halford & Henderson 2005, drawn by W. Smith)

5. *Pseudophyllanthus* (Müll. Arg.) Voronts. & Petra Hoffm.

Pseudophyllanthus (Müll. Arg.) Voronts. & Petra Hoffm., Kew Bull. 63: 50 (2008).
Andrachne sect. *Pseudophyllanthus* Müll. Arg. (1866), Petra Hoffm., Bot. Jahrb. 116: 321–331 (1994).

Dioecious (monoecious) pubescent shrubs to small trees. Leaves entire; stipules membranaceous. Inflorescences axillary, fasciculate or flowers solitary or in twos, staminate flowers on short densely bracteate inflorescences leaving pedicel stumps ("podia"); pedicels articulate. Staminate flowers: sepals 5; petals 5; disk annular, irregularly crenate to almost lacerate; stamens 5; filaments distinct to connate for about half their length; pollen subprolate, exine tectate-perforate to micro-reticulate; pistillode 3-lobed. Pistillate flowers: sepals and petals as in staminate; disk annular, finely crenulate; ovary 3-locular; stylodia distinct, bifid to base; stigmas capitate. Fruit 3-lobed; columella 2.5–5 times longer than its narrowest width. Seeds ecarunculate; endosperm copious, deeply invaginate independently of outer seed coat sculpture; embryo almost straight; cotyledons longer and wider than radicle.

One sp., *P. ovalis* (E. Mey. ex Sond.) Voronts. & Petra Hoffm., southern Africa, deciduous forests.

6. *Notoleptopus* Voronts. & Petra Hoffm.

Notoleptopus Voronts. & Petra Hoffm., Kew Bull. 63: 50 (2008).

Monoecious, densely pubescent shrubs. Leaves entire; stipules persistent. Inflorescences axillary, fasciculate or flowers solitary; pedicels articulate. Staminate flowers: sepals 5; petals 5; disk annular, regularly divided into 5 bilobed segments; stamens 5; filaments distinct; anthers longitudinally dehiscent; pollen prolate, exine tectate-perforate to microreticulate; pistillode of 3 distinct segments.

Pistillate flowers: sepals 5; petals 5, much shorter than sepals; disk annular, regularly and deeply divided into 5 emarginate or erose segments; ovary 3-locular, densely pilose; stylodia distinct, bifid to base; stigmas rounded to apically dilated. Fruit 3-lobed; columella 6 times longer than its narrowest width. Seeds ecarunculate, rounded triquetrous, rugose; endosperm copious, deeply invaginate; cotyledons broad, thin, as long as radicle, wider than radicle.

One sp., *N. decaisnei* (Benth.)Voronts. & P. Hoffm., from Java to New Guinea, Australia, in open forest and savannah. Although habitually very similar to *Leptopus* (see Vorontseva et al. 2007), molecular evidence placed this taxon close to the Southern Hemisphere *Pseudophyllanthus* and *Poranthera*.

7. *Meineckia* Baill.

Meineckia Baill., Étude Gén. Euphorb.: 587 (1858); Webster, Acta Bot. Neerl. 14: 323–365 (1965), rev.; Vorontsova & Petra Hoffm., Kew Bull. 63: 53–55 (2008).
Zimmermannia Pax (1910).
Zimmermanniopsis Radcl.-Sm. (1990).

Monoecious or dioecious shrubs or subshrubs; indumentum simple or 0. Leaves distichous, epeltate or rarely (*M. peltata*) peltate; stipules persistent or deciduous. Inflorescences axillary, fasciculate or flowers solitary; staminate flowers sometimes on short densely bracteate inflorescences, on which the pedicels leave "podia"; pedicels articulate. Staminate flowers: sepals 5 (6); petals 0 (5 small ones in subg. *Petaliferae*); disk annular, entire or shallowly undulate; stamens 5, filaments distinct to connate up to 9/10 of their length; pollen prolate to speroidal, exine reticulate to verrucate; pistillode subentire to 3-lobed. Pistillate flowers: sepals 5, imbricate, persistent in fruit; petals 0; disk annular; ovary 3-locular, glabrous or densely pilose; stylodia distinct or connate at base, entire to bifid to base, stigmas apically dilated to capitate. Fruit 3-lobed; columella slender, persistent. Seeds 1 or 2 per locule, ecarunculate; endosperm copious, deeply invaginate; cotyledons much broader than radicle.

Thirty spp., mostly in deciduous forests of Meso-America and South America, Africa, Madagascar and South Asia. Two of them represent ***M.* subg. *Petaliferae*** Voronts. & Petra Hoffm.; these have minute petals and in the molecular analysis of Vorontsova et al. (2007) were found to be basal to the otherwise apetalous species of ***M.* subg. *Meineckia***; morphologically, they are also very close to *Pseudophyllanthus* (see Hoffmann, Adansonia III, 22: 123–133. 2000).

8. *Andrachne* L.

Andrachne L., Sp. Pl.: 1014 (1753); Petra Hoffm., Bot. Jahrb. 116: 321, figs. 1, 2 (1994), Adansonia III, 22: 123 (2000).

Monoecious annual to perennial herbs or subshrubs; indumentum simple, glandular, or 0. Leaves with persistent stipules. Inflorescences axillary, fasciculate, or flowers solitary, the staminate in glomerules, the pistillate solitary; pedicels articulate. Staminate flowers: sepals 5(6), distinct; petals 5, slightly shorter than sepals in staminate flowers; disk in staminate flowers of 5 contiguous bilobed segments or distinct globular glands; stamens 5; filaments distinct to connate up to half of their length; pollen (spheroidal-)prolate, exine striate to micro-reticulate; pistillode of 3 distinct segments or 3-lobed. Pistillate flowers: sepals 5(6), distinct; petals much shorter than sepals to minute or 0; disk either divided into 5 emarginate segments or 5 distinct globular glands; ovary 3-locular; ovules hemitropous; stylodia $\pm$ distinct, bifid, stigmas capitate. Fruit rounded to 3-lobed; columella 5–6 times longer than its narrowest width. Seeds ecarunculate, rounded-triquetrous, rough, with star-shaped sculpture visible at high magnification (see illustration in Stuppy 1996: 283); endosperm copious, entire in cross section; embryo curved; cotyledons broader than and about equaling radicle in length. $2n = 24$.

Twenty-two spp., in semi-deserts of South Asia, northern Africa, southern Europe and the Americas; two subgenera, ***A.* subg. *Andrachne***, 16 spp., Old World, and ***A.* subg. *Phyllanthidea*** (Didr.) Voronts. & Petra Hoffm., 6 spp., also in the New World.

2. Tribe Bridelieae Müll. Arg. (1864), recircumscribed by Hoffmann et al., Kew Bull. 61: 37–53 (2006).

Armature 0 or rarely +; leaves entire or slightly crenate; stipules distinct or rarely intrapetiolar; pedicels sometimes articulated; sepals 4–6 (7), imbricate (valvate); petals (3)4–6 or 0; staminate disk extrastaminal-annular or in distinct parts or 0; pistillate disk simple or double; stamens 4–10 (−19), distinct or variously fused; thecae not

separate and connective not enlarged; ovary locules 2–4; stylodia distinct or completely connate; fruit explosively or tardily dehiscent or indehiscent; seeds exarillate.

Twelve genera in five subtribes.

2a. Subtribe Amanoinae Pax & K. Hoffm. (1922).

A monotypic subtribe.

9. *Amanoa* Aubl. (1775).

Amanoa Aubl., Fl. Gui. Fr.: 256 (1775); Hayden, Brittonia 42: 260–290 (1990), Neotrop. spp.

Monoecious (dioecious) glabrous trees or shrubs. Leaves entire; stipules persistent, distinct or intrapetiolar. Inflorescences terminal or axillary, spiciform-thyrsoid; pedicels not articulated. Staminate flowers: sepals 5, imbricate, persistent; petals 5, scale-like; disk extrastaminal-annular; stamens 5, distinct; anthers introrse; pollen oblate, 3-colporate, intectate or tectum widely perforate; pistillode columnar. Pistillate flowers: sepals 5, deciduous in fruit; petals much shorter than sepals or sometimes 0; disk patelliform; staminodes 0; ovary subglobose, 3-locular; ovules anatropous; stylodia connate into a massive column, tips dilated, stigmatiform. Fruit 3-angled, tardily dehiscent; columella massive, dilated toward base and at apex. Seeds usually 1 per locule; endosperm scanty or 0; cotyledons fleshy.

Sixteen spp., 13 in tropical South America, mostly northern, and 3 in west and west-central tropical Africa. This is the only genus of Bridelieae that occurs in both the New World and the Old.

2b. Subtribe Saviinae Müll. Arg. (1865), as 'Savieae'.

Croizatieae G.L. Webster (1994).

Dioecious; pedicels sometimes articulated; sepals imbricate, persistent; staminate disk extrastaminal-annular; pistillate disk simple; staminodes rarely +; stylodia 2-fid or 4-fid; fruit dehiscent.

Five genera, neotropical.

10. *Savia* Willd.

Savia Willd., Sp. Pl. 4: 771 (1805); P. Hoffmann & McPherson, Ann. Miss. Bot. Gard. 94: 519–55 (2007); P. Hoffmann, Brittonia 60: 136–166 (2008), rev.
Kleinodendron L.B. Sm. & Downs (1964).

Dioecious shrubs or trees. Leaves deciduous; stipules deciduous. Inflorescences axillary glomerules, the staminate dense glomerules, the pistillate few- to 1-flowered; bracts obscure; pedicels articulated. Staminate flowers subsessile; sepals 3–5, imbricate; disk annular; petals 5, imbricate, shorter than sepals, or 0; stamens 5, filaments distinct; anthers basifixed, introrse; pistillode 3-fid. Pistillate flowers: sepals 5, distinct, imbricate; petals 5 or 0; ovary 3-locular, sometimes pubescent; stylodia distinct, bifid, branches slender. Fruit capsular; columella 3-angled distally, persistent. Seeds mostly 1 per locule, smooth; endosperm copious, embryo straight; cotyledons much longer than radicle.

Two or three spp., neotropical. Other species formerly included in this genus have been transferred to *Heterosavia* (Tribe Phyllantheae) or *Wielandia* (Tribe Wielandieae) (Hoffmann and McPherson 2007; Hoffmann 2008).

11. *Gonatogyne* Müll. Arg.

Gonatogyne Müll. Arg., Fl. Bras. 11(2): 13 (1873).
Savia sect. *Gonatogyne* (Müll. Arg.) Pax & K. Hoffm. (1922).

Dioecious evergreen trees; indumentum simple. Leaves entire; stipules deciduous. Inflorescences axillary bracteate glomerules; sepals 5, imbricate, the pistillate deciduous in fruit; petals 5, imbricate, as long as sepals; staminate disk fleshy, corrugated; stamens 5, filaments connate into a column; anthers stipitate, erect, introrse; pollen grains 3-colporate, reticulate; pistillode atop column; pistillate flowers pedicellate; staminodes 0; disk multiglandular; ovary 3(4)-locular, sericeous; stylodia twice bifid. Fruit capsular, persistent; seeds smooth; endosperm copious; cotyledons flat, greenish.

One sp., *G. brasiliensis* (Baill.) Müll. Arg., Brazil (São Paulo).

12. *Croizatia* Steyerm.

Croizatia Steyerm., Fieldiana 28: 308 (1952); Webster et al., Syst. Bot. 12: 1–8, figs. 1–8 (1987); Dorr, Sida 18: 831–836 (1999).
Pseudosagotia Secco (1985).

Dioecious trees or shrubs. Leaves alternate to subopposite; stipules deciduous or persistent. Inflorescences axillary, glomerular; bracts inconspicuous. Staminate flowers pedicellate; sepals 5, distinct, imbricate; petals 5, very small; disk

annular, glabrous; stamens 5, filaments distinct; anthers introrse; pollen grains spheroidal, 3-brevicolporate, sexine tectate-perforate and spinose; pistillode 3–4-lobed. Pistillate flowers pedicellate; sepals 5, distinct, persistent in fruit; petals 5, much shorter than sepals; disk annular, glabrous; ovary 3-locular, pubescent; ovules hemitropous; stylodia distinct, slender, twice 2-fid. Fruits capsular, 3-lobed, cocci reticulate; columella distally expanded in papery wings. Seeds 1 or 2 per locule, ecarunculate; testa smooth; endosperm 0; embryo large, cotyledons thin, contorted.

Four spp., Panama to Venezuela and Ecuador and possibly Peru. Because of its spinose pollen, *Croizatia* was placed in the Oldfieldioideae (Webster 1994; Radcliffe-Smith 2001), but there is now strong molecular support for its inclusion in this subtribe.

13. *Discocarpus* Klotzsch

Discocarpus Klotzsch, Archiv. Naturg. 7: 201 (1841); Hayden & Hayden, Ann. Missouri Bot. Gard. 83: 153–167 (1996).

Dioecious trees or shrubs. Stipules deciduous. Flowers in axillary glomerules, the staminate ± compounded. Staminate flowers sessile; sepals 5, basally connate; petals 5, often reduced; disk cupular, lobed or toothed, stamens (4)5; filaments basally connate, exserted from perianth; anthers longitudinally introrsely dehiscent; pollen grains ± oblate, 4- or 5-colporate, exine finely reticulate; pistillode divided into 2 or 3 narrow segments; pistillate flowers subsessile or pedicellate; sepals and petals ± as in staminate; disk slightly lobed, glabrous; ovary 3-locular, densely hirtellous; ovules anatropous; stylodia dilated, bifid or irregularly incised. Fruits capsular, dehiscent into 1- or 2-seeded mericarps; columella massive, 3-winged distally. Seeds subglobose, testa smooth and shiny; endosperm scanty or 0; embryo large, cotyledons thin, contorted.

Four spp., northern South America: Amazon and Orinoco basins, Guayana region, E Brazil.

14. *Tacarcuna* Huft

Tacarcuna Huft, Ann. Missouri Bot. Gard. 76: 1080 (1989); Webster, Ann. Missouri Bot. Gard. 81: 130 (1994); Wurdack in Wurdack et al., Amer. J. Bot. 91: 1892 (2004).

Dioecious trees. Stipules deciduous. Inflorescences axillary, glomerular, sessile or subsessile. Staminate flowers pedicellate; sepals 5, imbricate; petals 5, equaling or exceeding sepals; disk obscure; stamens 5 or [*T. amanoifolia* Huft] 14–19, filaments distinct; pollen grains 3-colporate, exine striate- reticulate; pistillode columnar; pistillate flowers pedicellate; sepals 3 and "petals" 3, persistent in fruit, or sepals 5 and petals 0; disk annular (?); ovary 3-locular, sericeous; stylodia bifid. Fruit capsular; columella scarcely winged. Seeds apparently 1 per coccus, angled in cross section, testa smooth; endosperm scant; embryo large; cotyledons thin, contorted.

Three spp., Panama and South America, still unsatisfactorily known.

2c. Subtribe Keayodendrinae P. Hoffm. (2006).

A monotypic subtribe, distinguished by the combination of apetalous flowers, indehiscent, 1-locular and 1-seeded fruits.

15. *Keayodendron* Leandri

Keayodendron Leandri, Bull. Soc. Bot. France 105: 517 (1959); Breteler, Bull. Jard. Bot. Nat. Belg. 62: 187–190 (1993).

Dioecious trees; indumentum simple. Stipules deciduous. Flowers in axillary glomerules. Pedicels nor articulated. Staminate flowers subsessile or pedicellate; sepals 5–7, imbricate; petals 0; disk extrastaminal-annular; stamens 5–6; filaments connate; anthers introrse, dehiscing longitudinally; pistillode dilated and subpeltate. Pistillate flowers subsessile or pedicellate; perianth similar to staminate, sepals 5 or 6, persistent in fruit; disk double, minutely pubescent; ovary 2-locular; stylodia 2-fid. Fruit drupaceous, 1-locular. Seed 1 per fruit, linear-compressed, deeply invaginate ventrally; endosperm scanty, embryo curved, cotyledons much longer than radicle.

One sp., *K. bridelioides* Leandri, semi-deciduous forests of west tropical Africa (Ivory Coast to Cameroun).

2d. Subtribe Pseudolachnostylidinae Pax & K. Hoffm. (1922).

Armature rarely +; leaves entire, rarely slightly crenate; pedicels sometimes articulated; sepals imbricate or valvate; staminate disk

extrastaminal-annular; pistillate disk usually double; stamens 4–7; fruit dehiscent or indehiscent.

Four Old World genera.

16. *Bridelia* Willdenow (1806).

Bridelia Willd., Sp. Pl. 4(2): (1806; as *Briedelia*); Webster, Ann. Missouri Bot. Gard. 81: 39 (1994); Dressler, Blumea 41: 263–331 (1996); Radcl.-Sm., Gen. Euphorb.: 19 (2001).

Monoecious (dioecious) trees or shrubs, branches sometimes thorny; indumentum simple. Leaves entire or subentire; stipules persistent or deciduous. Flowers in axillary glomerules, flowering branches sometimes appearing racemose due to reduction of leaves; bracts persistent. Staminate flowers pedicellate or subsessile; sepals 5, valvate; petals 5, erect or inflexed, smaller than sepals; disk annular or somewhat cupular, glabrous or pubescent; stamens 5, filaments basally connate; pollen grains slightly oblate, 3-colporate, exine reticulate with ± striate pattern; pistillode 2–4-lobed or -divided. Pistillate flowers sessile or subsessile; sepals 5, basally connate into a hypanthium, valvate, persistent in fruit; petals as in staminate; disk duplex, outer part annular and adnate to hypanthium, inner part inflexed as cupule surrounding the ovary; ovary 1- or 2-locular; stylodia distinct or basally connate, bifid to subentire. Fruits pseudobaccate with fleshy exocarp but sometimes dehiscent or drupaceous, 1- or 2-locular; columella not persistent. Seeds usually 1 per locule, plano-convex, adaxially grooved [in 2-locular fruits] or ventrally invaginate [in 1-locular fruits]; endosperm copious, excavated adaxially; embryo chlorophyllous, curved, cotyledons broad, not fleshy. $2n = 26$.

About 50 spp. extending from Africa and Madagascar to Australia and the Pacific islands.

17. *Cleistanthus* Hook. f. ex Planch. (1848).

Cleistanthus Hook. f. ex Planch. in Hook. Ic. Pl. 8: t. 779 (1848); Kathriarachchi et al., Molec. Phylogenet. Evol. 36: 112–134 (2005); Li et al., Syst. Bot. 34: 529 (2009).

Monoecious (dioecious) shrubs or trees; indumentum simple. Leaves entire; stipules persistent or deciduous. Flowers in axillary, rarely terminal glomerules or axillary thyrses; bracts deciduous. Staminate flowers usually sessile; sepals (4)5(6), valvate; petals (4)5(6), scale-like and shorter than sepals; disk annular or cupulate, entire or lobed; stamens (4)5(6); filaments connate at base; pollen grains subglobose, 3-colporate, exine striate; pistillode at apex of column, 3-lobed. Pistillate flowers sessile or pedicellate; sepals mostly 5, valvate, connate basally, usually persistent in fruit; petals 5, scale-like, adnate to sepalar cup; disk annular or cupular; ovary (2)3(4)-locular; ovules anatropous, rarely hemianatropous; stylodia 1–4-lobate or -fid. Fruit capsular, septicidal or tardily dehiscent to nearly indehiscent [sect. *Chartacei* Jabl.], with subtending podium; columella usually persistent. Seeds 1 or 2 per coccus; testa smooth and shiny; endosperm copious; embryo straight; cotyledons longer and broader than radicle. $2n = 22$.

About 140 spp. distributed from Africa and Madagascar to Malesia, Australia, and Polynesia. The genus is highly variable in various characters including foliar venation, pollen morphology and seed anatomy (Stuppy 1996; Tokuoka and Tobe 2001), is polyphyletic and needs profound taxonomic readjustment.

18. *Pentabrachion* Müll. Arg.

Pentabrachion Müll. Arg., Flora 47: 532 (1864); Pax & K. Hoffm., Pflanzenr. 147: XV: 188, fig. 15 (1922); Radcl.-Sm., Gen. Euphorb.: 15 (2001).

Monoecious or dioecious subglabrous shrubs or trees. Leaves entire; stipules persistent. Inflorescences axillary glomerules. Staminate flowers pedicellate; sepals (4)5(6), imbricate; petals 4–6, smaller than sepals; disk annular, unlobed; stamens 5(−7), filaments basally connate; pollen grains oblate sphaeroidal, 3-colporate, colpi c. 2/3 length of grain, exine coarsely heterobrochate; pistillode 3-fid, segments laminar. Pistillate flowers long-pedicellate; sepals 5, imbricate; disk annular; ovary glabrous; stylodia twice bifid. Fruits capsular, 3-lobed. Seeds smooth, endosperm copious, embryo with cotyledons longer than radicle.

One sp., *P. reticulatum* Müll. Arg., western equatorial Africa.

19. *Pseudolachnostylis* Pax

Pseudolachnostylis Pax, Bot. Jahrb. 28: 19 (1899); Radcl.-Sm., Fl. Trop. E. Afr., Euphorb. 1: 80, fig. 10 (1987), Gen. Euphorb.: 28 (2001).

Dioecious shrubs or trees; buds perulate; indumentum simple. Leaves entire; stipules deciduous. Inflorescences axillary or arising below the

leaves, staminate flowers in few-flowered pedunculate or subsessile cymes, pistillate flowers (sub) solitary. Staminate flowers sessile; sepals 5(6), imbricate; petals 0; disk annular-lobed; stamens (4)5–7; filaments adnate to pistillode; pollen grains ± oblate, 3-colporate, coarsely reticulate; pistillode 3-fid. Pistillate flowers: pedicels 2-bracteolate; sepals 5(6), imbricate, deciduous in fruit; petals 0; disk dentate or lobed; ovary 3-locular; ovules hemitropous; stylodia bifid. Fruit a tardily dehiscent woody capsule with fleshy exocarp; columella not persistent. Seeds 1 per locule, ellipsoid, hilum submedian; endosperm copious; cotyledons much longer than radicle. $2n = 26$.

Apparently only one variable sp., *P. maprouneifolia* Pax, distributed from Zaire and Tanzania to South Africa.

2e. Subtribe Securineginae Müll. Arg. (1866).

Two Afro-Madagascan genera without evident similarities, but strongly supported in a subclade that is sister to the remaining four subtribes.

20. *Securinega* Comm. ex Juss. (1789).

Securinega Comm. ex Juss., Gen. Pl.: 388 (1789), nom. cons.; Leandri, Fl. Madag. 111(1): 107–116 (1958); Radcl.-Sm., Gen. Euphorb.: 31 (2001); Schatz, Generic Tree Fl. Madagascar: 164, fig. 171 (2001).

Dioecious shrubs. Leaves entire; stipules deciduous. Flowers in axillary glomerules, the pistillate flowers solitary or few; pedicels not articulated. Staminate flowers pedicellate; sepals 5–7, imbricate, deciduous; petals 0; disk in 5 distinct segments; stamens (4)5(−10), filaments distinct, exserted from calyx; pollen grains subglobose, 3-colporate, colpi long, exine spiny or finely reticulate; pistillode mostly 2–3-fid. Pistillate flowers pedicellate; sepals 5, imbricate, persistent in fruit; petals 0; disk annular; ovary 3(4)-locular; stylodia 3 (4), sessile, recurved, 2-fid. Fruit capsular; columella deciduous. Seeds ovoid, testa dark, smooth; hilum submedial, narrowly elliptic; endosperm copious; embryo straight, cotyledons longer and broader than the radicle.

Five spp., Madagascar, Réunion and Mauritius. This genus had been circumscribed to include *Flueggea* by Müller (1866), in which he was followed by Pax and Hoffmann (1931) who added *Meineckia*. This broad circumscription was reduced by the removal of the latter two genera and of *S. congesta* Müll. Arg. (=*Jablonskia*) by Webster (1965–1984), resulting in a core Malagasy group characterized by distinctive spiny pollen and smooth seeds (Wurdack et al. 2004). *Lachnostylis* has a strongly supported relationship with *Securinega capuronii* Leandri, despite the lack of morphological resemblance (Wurdack et al. 2004).

21. *Lachnostylis* Turcz. (1846).

Lachnostylis Turcz., Bull. Soc. Imp. Naturalistes Moscou 19: 503 (1846); Dyer, Gen. S. Afr. Pl. 1: 309 (1975); Radcl.-Sm., Gen. Euphorb.: 12 (2001).

Dioecious shrubs; indumentum simple. Leaves small; stipules deciduous. Inflorescences axillary glomerules; bracts scarious; female flowers often solitary. Staminate flowers pedicellate; perianth abaxially sericeous; sepals 5, distinct, imbricate, persistent; petals 5, equaling the sepals; disk extrastaminal, annular, massive, unlobed, hirtellous; stamens 5, filaments connate below, villous; anthers dehiscing longitudinally; pollen grains subprolate, 3-colporate, exine reticulate; pistillode 3–4-fid, villous, adnate to staminal column. Pistillate flowers pedicellate; perianth similar to the staminate; disk massive, unlobed, villous; ovary 2- or 3-locular, tomentose, ovules hemitropous; stylodia bifid. Fruits capsular, valves tomentose; each coccus with 1(2) seeds. Seeds subglobose, testa smooth, endosperm scanty; cotyledons plicate, longer than the radicle.

One variable or perhaps 2 spp., *T. capensis* Turcz., South Africa.

3. Tribe Wielandieae Baill. ex Hurus. (1954), recircumscribed by Hoffmann et al., Kew Bull. 61: 37–53 (2006).

Monoecious or dioecious; leaf base sometimes peltate; petioles sometimes pulvinate; sepals 4–6 (−8), imbricate, ± distinct; petals 4–6, sometimes reduced or 0; disk + or rarely 0; staminate disk annular or in distinct parts, pistillate disk simple; stamens (3)4–6(−12); filaments distinct or variously connate; ovary 3–6-locular; fruits explosively dehiscent.

Six genera, New and Old World, except Australia.

3a. Subtribe Astrocasiinae G.L. Webster (1992).

Three genera, two New World, one African.

22. *Heywoodia* Sim

Heywoodia Sim, For. Fl. Cape Col.: 326, t. 140/1 (1907); Hutchinson, Bull. Misc. Inf. Kew 1922: 115 (1922); G. L. Webster, Ann. Missouri Bot. Gard. 81: 36 (1994); Radcl.-Sm, Fl. Zamb. 9(4): 6, t. 1 (1996), Gen. Euphorb.: 6 (2001).

Dioecious glabrous trees. Leaves of seedlings and sucker-shoots peltate; stipules persistent. Inflorescences axillary bracteate glomerules, staminate flowers many, pistillate 3 or 4. Staminate flowers sessile or nearly so; perianth poorly differentiated, sepals 3(4), distinct, imbricate, unequal; petals (4)5, distinct, longer than sepals, imbricate; disk extrastaminal, lobed, projecting between filaments; stamens 8–12, ± in 2 whorls, filaments distinct, anthers dorsifixed, introrse, muticous, dehiscing longitudinally; pollen 3-colporate-spheroidal; pistillode minute, trifid. Pistillate flowers pedicellate; sepals and petals as in staminate; staminodes 6–8, filiform; ovary 4–5-locular; stylodia 4 or 5, stigmatiform, bilobed. Fruit capsular, 4–5-locular, separating into 4–5 2-valved cocci; columella not persistent. Seeds 1(2) per locule, smooth (minutely striate); endosperm papyraceous, embryo small, cotyledons chlorophyllous, inflexed, much longer than the radicle.

One sp., *H. lucens* Sim, eastern and southern Africa, disjunct along mountain ranges from Tanzania to South Africa (Transkei and Natal). Levin (1986b) suggested a close relationship between *Heywoodia* and *Astrocasia*, which is confirmed by the molecular evidence. Webster (1994) considered *Heywoodia* as an ancient relict genus because he interpreted traits such as dioecy, the poorly differentiated perianth, the variability of stamen and carpel number, and the small embryo as plesiomorphic.

23. *Chascotheca* Urb.

Chascotheca Urb., Symb. Ant. 5: 14 (1904); Alain, Fl. Cuba 3: 44, fig. 8 (1953); Radcl.-Sm., Gen. Euphorb.: 26, fig. 3 (2001).
Chaenotheca Urb. (1902; nom. illeg.).

Dioecious shrubs; indumentum simple. Leaves narrowly peltate at base; stipules persistent. Staminate flowers in axillary glomerules, the pistillate solitary and axillary. Staminate flower subsessile; sepals 5, imbricate, somewhat unequal; petals 0; disk annular; stamens 5, filaments connate at base; anthers dorsifixed, dehiscing longitudinally; pollen grains prolate, 3-colporate, exine coarsely reticulate; pistillode 3-fid, adnate to staminal column. Pistillate flower long-pedicellate, sepals and disk as in staminate, persistent, petals 0; ovary 3-locular, ovules anatropous; stylodia short, 2-fid. Fruit capsular, venose; columella slender, persistent. Seeds 1 per locule; testa dry, smooth; reticulate; chalaza appearing dorsal, hilum in depression beneath terminal beak; endosperm copious; embryo deflexed, cotyledons about equaling radicle.

One sp., *Ch. neopeltandra* (Griseb.) Urb., Greater Antilles (Cuba and Hispaniola).

24. *Astrocasia* B. L. Rob. & Millsp.

Astrocasia B. L. Rob. & Millsp., Bot. Jahrb. 36, Beibl. 80: 19 (1905); G.L. Webster, Syst. Bot. 17: 311–323 (1992); Jiménez R. & Gordillo, Acta Bot. Mex. 55: 1, fig. 1 (2001).

Dioecious or subdioecious evergreen or deciduous trees or shrubs; indumentum 0. Leaves sometimes peltate or stipellate; stipules ribbed, deciduous. Inflorescences axillary glomerules, pistillate flowers sometimes solitary. Staminate flowers pedicellate; sepals 5, usually unequal; petals 5, longer than sepals, prominently veined; stamens 3–5, filaments connate into a column; anthers extrorse in bud, dehiscing horizontally or deflexed; pollen grains subglobose, 3-colporate, colpi elongated, exine reticulate; pistillode discoid, sessile or stipitate atop the staminal column. Pistillate flowers long-pedicellate [1.5 cm or more in fruit]; sepals and petals similar to staminate, deciduous; disk annular to cupular; ovary 3(4)-locular; stylodia distinct, 2-fid. Fruit capsular, thin-walled; cocci veiny; columella slender, persistent. Seeds 1 or 2 per locule; testa dry, smooth or roughened, raphe conspicuous; endosperm copious; cotyledons much longer and broader than radicle.

Six spp., Cuba and from Mexico south to Bolivia and eastern Brazil.

3b. Subtribe Wielandiinae Pax & K. Hoffm. (1922).

Three genera, western Indian Ocean, East Africa and SE Asia.

25. *Dicoelia* Benth.

Dicoelia Benth., Hook. Icon. Pl. 13, 70: t. 1289 (1879); Pax & K. Hoffmann, Pflanzenr. 147 XV: 15, fig. 3 (1922); Airy Shaw, Kew Bull. 36: 285 (1981).

Monoecious trees or shrubs; indumentum simple. Stipules deciduous. Inflorescences axillary,

thyrsoid, pedunculate; glomerules often bisexual, staminate flowers several, pistillate 1/node. Staminate flowers pedicellate; sepals 5, valvate, shorter than petals; petals 5, valvate, convex, apically thickened, with 2 paired cavities; disk 0; stamens 5, filaments distinct, basally adnate to pistillode, exserted from perianth; anthers introrse, thecae fitted into paired cavities in the petals in bud; pollen large, prolate, the exine with nearly continuous tectum; pistillode massive, apically 3–5-fid. Pistillate flowers pedicellate; sepals 5, valvate, shorter than petals; disk 0; ovary 3-locular, pubescent; ovules anatropous; stylodia unlobed, elongated, erect. Fruits spheroidal, capsular, thin-walled. Seeds with smooth testa; endosperm copious; cotyledons orbicular.

One sp., *D. beccariana* Benth., Malaya, Sumatra, Borneo. Kathriarachchi et al. (2005) provided molecular support for the relationship of *Dicoelia* to *Chorisandrachne*, and gave a detailed discussion of its peculiar, strongly autapomorphic appearance that, up to very recently, has camouflaged its true relationship.

26. *Chorisandrachne* Airy Shaw

Chorisandrachne Airy Shaw, Kew Bull. 23: 40 (1969), 26: 323 (1972), Hooker's Icon. Pl. 38: t. 3707 (1974).

Apparently dioecious trees or shrubs; indumentum simple. Leaves at the base asymmetric, shortly petiolate; stipules subulate, deciduous. Inflorescences axillary, flowers pedicellate, the staminate ones in upper axils of branches solitary or in twos, the pistillate solitary in lower axils. Staminate flowers: sepals 5, broadly obovate, surmounted by the obtuse, unguiculate petals; disk large, flat, subentire; stamens 5, filaments at the base connate, distally distinct, divaricate; anthers small, subglobose; pistillode narrowly cylindric. Pistillate flowers [incompletely known]: sepals 5; petals 5, exceeding the sepals, persistent; disk broadly cupulate, sinuous-pentagonous. Fruits capsular, subtended by persistent disk and calyx; columella persistent. Seeds 2 per locule, orbicular, plano-convex, much flattened.

A single sp., *Ch. diplosperma* Airy Shaw, southwest Thailand. Both Webster (1994) and Radcliffe-Smith (2001) included *Chorisandrachne* in *Leptopus*, but the molecular data (Kathriarachchi et al. 2005: 129) placed it as sister to *Dicoelia beccariana*. Morphologically, *Chorisandrachne* and *Dicoelia* have little in common, and the seed coat of *Chorisandrachne* shows some similarity with that of *Chascotheca* (Stuppy 1996).

27. *Wielandia* Baill.

Wielandia Baill., Étude Gén. Euphorb.: 568 (1858); P. Hoffmann, Adansonia III, 20: 333–340 (1998); P. Hoffmann & McPherson, Ann. Missouri Bot. Gard. 94: 519–553 (2007), rev.
Savia Willd. sect. *Wielandia* (Baill.) Müll. Arg. (1863).
Petalodiscus Baill. (1858).
Savia sect. *Petalodiscus* Baill. (1858).
Blotia Leandri (1957).

Monoecious trees or shrubs; indumentum simple and scanty or 0. Petioles channeled or terete; stipules sometimes peltate, persistent or deciduous. Inflorescences axillary or cauline thyrses, or flowers solitary; staminate and pistillate flowers in the same or separate fascicles. Staminate flowers pedicellate; pedicels inarticulate; sepals (4)5(6); petals (4)5(6), half as long to 3 x as long as sepals; disk extrastaminal, glabrous (pubescent), of antesepalous lobes, crenate, annular, or lacerated, sometimes of different structure in staminate and pistillate flowers; stamens 5(6), filaments distinct or partly connate; anthers introrse; pistillode 3(5)-fid. Pistillate flowers pedicellate, perianth and disk as in staminate, ovary 3(−5)-locular; stylodia 3(−5), distinct, 2-fid to base, stigmas acute to slightly capitate. Fruits solitary 3(−5)-lobed schizocarps with irregular dehiscence; columellae 3(−5)-angled, base and apex thickened; disk and perianth usually persistent in fruiting stage. Seeds 1 or 2 per locule, usually with ± distinct perichalazal annulus; endosperm very sparse; embryo either with hemispherical to hemi-ovoid cotyledons and short radicle, or with thin and folded cotyledons and prominent radicle.

Thirteen spp., Madagascar (10 endemic), Seychelles, Comoro Islands, and SE Kenya, most in humid forest.

4. Tribe Phyllantheae Dumort. (1829).

Monoecious or dioecious trees, shrubs, or herbs; leaves simple, alternate, entire, petioles not pulvinate; inflorescences axillary or rarely on branches; pedicels not articulated; sepals 4–6(7); petals 0 or very rarely +; disk + or 0; stamens 2–15; anthers usually with thecae not separate

and connective not enlarged; ovary 2–6(−15)-locular; ovules hemitropous or rarely (*Heterosavia*) anatropous; fruits dehiscent or indehiscent; seeds exarillate.

A tribe of worldwide distribution comprising 10 genera.

Key to the Genera of Phyllantheae

1. Phyllotaxy spiral or distichous on lateral axes but deciduous branchlets not developed; pistillode mostly + in staminate flowers; seeds ventrally invaginated. **4a. Flueggeinae** **2**
– Phyllotaxy spiral on penultimate axes, distichous on deciduous branchlets; pistillode 0; seeds with or without ventral invaginations. **4b. Phyllanthinae** **7**
2. Petals +; petioles 2-winged to channeled adaxially **31. *Heterosavia***
– Petals 0; petioles terete **3**
3. Monoecious; stamens 15–21, inserted on disk; pistillate calyx accrescent **30. *Lingelsheimia***
– Dioecious or monoecious; stamens 2–7, not exserted on disk; pistillate calyx not accrescent **4**
4. Monoecious; terminal branches distinctly flattened; stamens **2** **28. *Plagiocladus***
– Dioecious; terminal branches not distinctly flattened (sometime slightly so in *Margaritaria*); stamens more than 2 **5**
5. Capsule with 1 seed per locule; staminate flowers subsessile; flowers in racemoid paniculate thyrses; seed exotegmen vittate **32. *Richeriella***
– Capsule usually with 2 seeds per locule; staminate flowers pedicellate; flowers in axillary glomerules; seed exotegmen palisadal **6**
6. Pistillode + in staminate flowers; seed testa 2-layered, exotegmen 3- or 4-layered, not woody; leaves spiral **33. *Flueggea***
– Pistillode 0; seed testa 6–11-layered, distinctly fleshy; exotegmen 6–14-layered, + bony; leaves distichous **29. *Margaritaria***
7. Floral disk usually +, not completely adnate to calyx; pollen grains 3–4(6)-colporate/monoporate; seeds with dry testa, not ventrally invaginated **34. *Phyllanthus***
– Floral disk 0 or completely adnate to calyx; pollen grains 3–6(−16)-colporate/monoporate or diporate; seeds mostly not ventrally invaginated, with dry or fleshy testa **8**
8. Stylodia unlobed; anthers apiculate; pollen grains 3–6-colporate-monoporate; ovary 3–8-locular; seed coat usually fleshy **35. *Glochidion***
– Stylodia bifid or emarginate; pollen grains up to 16-colporate/diploporate; anthers not apiculate; ovary 3-locular **9**
9. Seed coat dry; staminate calyx ± discoid, not turbinate; pollen grains 6–16-colporate **36. *Sauropus***
– Seed coat fleshy; staminate calyx turbinate-truncate; pollen grains 4–12-colporate **37. *Breynia***

4a. Subtribe Flueggeinae Müll. Arg. (1865).

Dioecious; branches persistent; flowers in axillary glomerules or thyrses; sepals 4–7, imbricate, the pistillate ± persistent in fruit; petals 0; disk annular; stamens 4–7, filaments distinct, anthers extrorse; pollen grains prolate, 3-colporate, ora circular, exine finely reticulate; pistillode +; ovary 2–6-locular, ovules hemitropous; stylodia bifid; fruits capsular or baccate; seeds ventrally invaginated, testa dry or fleshy; endosperm copious, embryo, curved.

This subtribe of four genera appears closely related to the Phyllanthinae, and earlier (Webster 1994) was more broadly circumscribed to include that group.

28. *Plagiocladus* Brunel ex Petra Hoffm. Fig. 12

Plagiocladus Brunel ex Petra Hoffm., Kew Bull. 61: 45 (2006).

Phyllanthus diandrus Pax (1904); Breteler Bull. Mus. Hist. nat. Paris IV, 12 B Adansonia: 293–295, fig. 1 (1991).

Phyllanthus sect. *Diandri* Pax & K. Hoffm. in Engler & Drude, Veget. der Erde 9 (Pflw. Afr. III, 2): 29 (1921).

Monoecious, glabrous shrub; terminal branches distinctly flattened. Leaves shortly petiolate, entire; stipules unequally subcordate, deciduous. Inflorescences axillary; staminate flowers axillary glomerules; pistillate long-pedicellate, solitary. Staminate flowers: sepals 6; disk flat, annular; stamens 2, filaments distinct; anthers dehiscing longitudinally. Pistillate flower sepals and disk as in staminate; ovary glabrous, 3-locular; stylodia deeply 2-fid. Fruit a 3-carpellate schizocarp; endocarp hard; dehiscence explosive loculicidal, septicidal and septifrague. Seeds deeply invaginated (?).

One sp., *P. diandrus* (Pax) Brunel ex Petra Hoffm., western C Africa, most common in Gabon. *Plagiocladus* is strongly supported as sister to *Margaritaria*, but is easily distinguished from it by the difference in sepal and stamen number and the distinctly flattened terminal branches.

29. *Margaritaria* L. f.

Margaritaria L. f., Suppl. Pl.: 66 (1781); Webster, Ann. Missouri Bot. Gard. 54: 217, fig. 2 (1968), J. Arnold Arb. 60: 403–444, figs. 11–13 (1979), rev.

Dioecious (monoecious) trees or shrubs; indumentum simple. Leaves evergreen or deciduous,

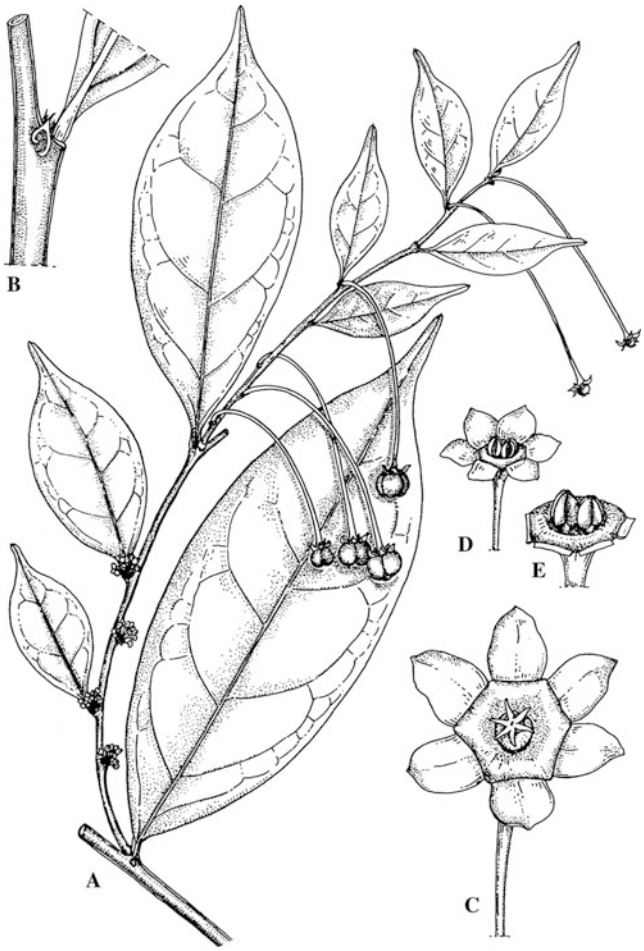

Fig. 12. Euphorbiaceae-Phyllanthoideae. *Plagiocladus diandrus*. **A** Branchlet with glomerules of staminate and single pistillate flowers. **B** Leaf axil with stipule. **C** Pistillate flower. **D** Staminate flower. **E** Same, only disk and stamens. (Breteler 1990; drawn by W. Wessel-Brand)

distichous; stipules deciduous or somewhat persistent. Inflorescences axillary glomerules, the pistillate ones sometimes of solitary flowers. Staminate flowers pedicellate; sepals 4, distinct, biseriate; petals 0; disk annular, sometimes slightly lobed; stamens 4, filaments usually distinct; anthers extrorse; pollen subglobose, 3-colporate, semitectate; pistillode 0. Pistillate flowers pedicellate; sepals 4, persistent in fruit; disk annular; ovary (2)3–4(−6)-locular, ovules hemitropous; stylodia distinct or basally connate, 2-fid, often dilated. Fruit capsular, ± irregularly dehiscent, endocarp papery. Seeds 2(1) per locule, ventrally invaginated; testa fleshy, bluish or greenish; tegmen bony; endosperm copious; embryo straight or curved, cotyledons longer than the radicle. $2n = 26$.

Fourteen spp., extending through most tropical regions from America and the Caribbean through Africa and Madagascar to tropical Asia and N Australia.

30. *Lingelsheimia* Pax

Lingelsheimia Pax, Bot. Jahrb. Syst. 43: 317 (1909); Mildbr., Wiss. Erg. Deut. Zentr.-Afr. Exped., Bot. 2: t. 54, 55 (1912); Pax & K. Hoffmann, Pflanzenr. 147. XV: 279 (1922); Léonard, Bull. Soc. Roy. Bot. Belg. 84: 49 (1951), Bull. Jard. Bot. État. 32: 513 (1962); Radcl.-Sm., Gen. Euphorb.: 49 (2001).
Danguyodrypetes Leandri (1939).
Aerisilvaea Radcl.-Sm. (1990).

Monoecious shrubs; indumentum 0. Stipules ± persistent. Inflorescences axillary glomerules. Staminate flowers pedicellate; sepals (4–)6–7, imbricate; petals 0; disk glandular-lobed and ± intrusive between filaments; stamens 15–35, filaments distinct; anthers basifixed; pollen grains somewhat prolate, 3-colporate, ora circular, exine reticulate; pistillode rudimentary or 0. Pistillate flowers pedicellate; sepals 6, imbricate, persistent and accrescent in fruit; petals 0; disk massive, angled; ovary 3-locular, ovules anatropous [?]; stylodia distinct, 2-fid or -partite. Fruits capsular, dehiscing into three 2-valved cocci or 6 valves. Seeds 1 per locule, ventrally invaginated, testa smooth, dry.

Seven spp., tropical Africa (Zaire, Tanzania), and Madagascar. This genus was placed with *Drypetes* and later with genera like *Meineckia*, but in the molecular analyses of Kathriarachchi et al. (2005, 2006) it has been recovered among the basal genera of Phyllantheae. This placement is also compatible with pollen morphology (Köhler 1965), leaf morphology (Levin 1986b), and seed coat structure (Tokuoka and Tobe 2001).

31. *Heterosavia* (Urb.) Petra Hoffm.

Heterosavia (Urb.) Petra Hoffm., Brittonia 60: 152 (rev.: 136–166) (2008).
Savia sect. *Heterosavia* Urb. (1902).

Dioecious trees or shrubs; indumentum simple. Petioles 2-winged to channeled adaxially; stipules persistent. Inflorescences axillary glomerules; staminate flowers 10–25 per inflorescence, subsessile; pistillate flowers solitary, rarely in twos or threes. Pedicels not articulated; staminate flowers: sepals and petals (4)5(6)-merous, sepals imbricate, petals

shorter than sepals; disk extrastaminal, annular, crenate to entire, narrow, thick; stamens (4)5(6); filaments distinct or connate for up to half of their length; anthers introrse; pollen 3(long)-colporate, tectate-perforate vermiculate; pistillode 3-fid to base or nearly so, the branches erect; pistillate flowers sepals, petals and disk as in staminate flowers but petals as long as or hardly shorter than sepals; staminodes sometimes +; ovary 3(4) locular; stylodia 3(4), 2-fid to about half of their length; stigmas acute to obtuse. Fruits explosive schizocarps, solitary, rarely in twos, subglobose, 3 (4)-lobed, glabrous to pilose, dehiscence septicidal, loculicidal and septifragous; columella 1.5–2 times as long as wide; perianth persistent in fruit. Seeds 2 per locule, smooth; endosperm copious; cotyledons straight, 3–4 times as long as radicle; radicle 3–4 times as long as wide.

Four spp., Caribbean, from Florida to Swan Islands (Honduras). Recognized as distinct from *Savia* mainly on molecular evidence; distinguishing morphological characters are subtle, and species identification may be problematic unless pistillate material is available.

32. *Richeriella* Pax & K. Hoffm.

Richeriella Pax & K. Hoffm., Pflanzenreich 147, XV: 30 (1922); Airy Shaw, Hook. Icon. Pl. 38: t. 3703 (1974), Kew Bull. Add. Ser. 4: 190 (1975).

Dioecious trees; indumentum 0. Stipules deciduous. Inflorescences axillary spiciform thyrses. Staminate flowers sessile or subsessile; sepals 5, imbricate; petals 0; disk-segments 5; stamens 5, filaments distinct, long-exserted; anthers dorsifixed, extrorse; pollen grains subprolate, 3-colporate, coarsely reticulate; pistillode 2–3-fid. Pistillate flowers subsessile in flower but pedicellate in fruit; sepals 5, imbricate; petals 0; disk annular; ovary 3-locular; ovules anatropous?; stylodia distinct, 2-fid. Fruits capsular. Seeds mostly 1 per locule, ventrally invaginated, testa dry, smooth; endosperm scanty; embryo curved, cotyledons thin, longer than the radicle.

One sp., *R. gracilis* (Merr.) Pax & K. Hoffm. [= *Flueggea gracilis* (Merr.) Petra Hoffm.], S and SE Asia from India to Borneo. *Richeriella* and *Flueggea* are similar in leaf anatomy (Levin 1986a) and pollen morphology (various studies), and the molecular results (Kathriarachchi et al. 2005: 127) confirm the close relationship between them but fail to prove that the one is nested in the other. They differ significantly in inflorescence structure and seed anatomy (Stuppy 1996; Tokuoka and Tobe 2001).

33. *Flueggea* Willd.

Flueggea Willd., Sp. Pl. 4: 637 (*Flüggea*), 757 (*Fluggea*) (1806); Webster, Allertonia 3: 259–312 (1984), rev.; Hayden, Brittonia 39: 268, fig. 1 (1987).

Dioecious (monoecious) shrubs or trees; branches sometimes spiny; indumentum mostly 0. Stipules persistent or deciduous. Inflorescences axillary glomerules. Staminate flowers pedicellate; sepals 4–7, imbricate; petals 0; disk dissected, or segments ± confluent; stamens 4–7, filaments distinct; anthers extrorse, dehiscing longitudinally; pollen grains tricolporate, colpi short; pistillode 2–3-fid, rarely rudimentary or 0. Pistillate flowers pedicellate; sepals 4–7, imbricate, persistent in fruit; petals 0; disk annular or lobed; ovary (2)3 (4)-locular; ovules hemitropous; stylodia distinct, 2-fid, sometimes dilated. Fruits capsular or baccate; columella persistent. Seeds usually 2 per locule, ± ventrally invaginated; testa smooth to verruculose; endosperm copious; embryo straight to curved; cotyledons longer than radicle. $2n = 26$.

About fifteen spp. from the West Indies through South America, tropical Africa and southeast Asia to the Pacific islands.

4b. Subtribe Phyllanthinae Pax (1890).

Monoecious or dioecious trees, shrubs, or herbs; branching mostly "phyllanthoid" with main axis distally bearing scale-like leaves that subtend leafy flowering deciduous branchlets; indumentum simple or 0; leaves spiral on main axes, distichous on deciduous branchlets; stipules usually persistent; flowers in axillary glomerules on branchlets, sometimes cauliflorous; staminate sepals (4)5(6), imbricate, entire or dentate; petals 0; disk annular or segmented; stamens (1)2–4 (−10), filaments free or connate; anthers extrorse, dehiscing horizontally to longitudinally; pollen grains prolate to oblate, 3–6-colpate, porate, or panporate, exine reticulate; pistillode 0; pistillate flowers pedicellate; sepals mostly 4–6; disk annular or segmented; ovary 3-locular, ovules anatropous to hemitropous; stylodia bifid or entire; fruits mostly capsular (baccate or drupaceous); columella persistent; seeds usually 2/locule, smooth to striate or ribbed.

This subtribe, with 5 genera and nearly 1,000 species, is the most species-rich taxon in the Phyllanthoideae, due to the large size of *Phyllanthus*. Most of the species, except in some sections of *Phyllanthus*, are characterized by the unique phyllanthoid branching pattern (Webster 1956). The Phyllanthinae appear to have evolved from the Flueggeinae, as suggested by the close relationship between some species of *Flueggea* and *Phyllanthus* subg. *Isocladus*.

34. *Phyllanthus* L. Fig. 13

Phyllanthus L., Sp. Pl. 981 (1753); Müll. Arg. in DC., Prodr. 15(2): 274 (1866), Fl. Bras. 11(2):23, t. 4–10 (1873); Hutch., Fl. Trop. Afr. 6(1): 692 (1912); Fawc. & Rend., Fl. Jam. 4: 251, fig. 85 (1920); Pax & K. Hoffm., Nat. Pflanzenfam. ed. 2, 19c: 60, figs. 28–30 (1931); Alain, Fl. Cuba 3: 44, fig. 9 (1953); Leandri, Fl. Madag. 111(1): 30, t. 7–14 (1958); G.L. Webster, J. Arnold Arb. 37: 91–122, 217–256, 340–357 (1956); 38: 51–79, 170–198, 295–373 (1957); 49–100, 111–212, t. XIII–XXXII (1958), J. Arnold Arb. 48: 332 (1967), Jablonski, Mem. N. Y. Bot. Gard. 17: 85, figs. 17–22 (1967); Webster, Ann. Missouri Bot. Gard.54: 220; fig. 3 (1968); Bancilhon, Boissiera 18: 1–81 (1971); Radcl.-Sm., Fl. E. Trop. Afr., Euphorb. 1: 9, figs. 2–5 (1987); Santiago, Bradea 5(2): 44 (1988); Howard, Fl. Less. Ant. 5: 70, fig. 34 (1989); Schmid, Fl. Nouv. Caléd. 17: 31, figs. 7–68 (1991); J.R. Wheeler, Fl. Kimberley Reg.: 619, fig. 190 (1992); Webster, Ann. Missouri Bot. Gard. 81: 44 (1994); Friedmann, Fl. Seychelles, Dicot.: 362, figs. 100–103 (1994); Murillo & Franco, Euf. Reg. Araracuara 129, figs. 35–38 (1995); Hunter & Bruhl, Fl. Victoria 3: 74 (2000); Radcl.-Sm., Gen. Euphorb.: 38 (2001); Schatz, Generic Tree Fl. Madag.: 63 (2001); Webster, Contr. Univ. Michigan Herb. 23: 376, fig. 2 (2001), Novon 12: 290, figs. 1, 2 (2002); Li Bingtao & M.G. Gilbert, Fl. China 11: 180–190 (2008).

Niruri Adans. (1763).
Cicca L. (1767).
Kirganelia Juss. (1789).
Cathetus Lour. (1790).
Emblica Gaertn. (1790).
Nymphanthus Lour. (1790).
Epistylium Sw. (1800).
Eriococcus Hassk. (1843).
Macraea Wight (1852).
Hemicicca Baill. (1858).
Reverchonia A. Gray (1880).
Diasperus L. ex Kuntze (1891).
Phyllanthodendron Hemsl. (1898).

Monoecious or dioecious trees, shrubs, or herbs; branching phyllanthoid or unspecialized; indumentum simple, unicellular or multicellular. Leaves on penultimate axes alternate, spiral, those on ultimate axes spiral or distichous on floriferous deciduous branchlets; lamina pinnately veined, often inaequilateral at base; petioles mostly much shorter than blade; stipules persistent or deciduous. Flowers in axillary glomerules

Fig. 13. Euphorbiaceae-Phyllanthoideae. *Phyllanthus zornioides*. **A** Flowering branch system. **B** Staminate flower. **C** Stamens with glands. **D** Pistillate flower. **E** Distal (left) and lower leaf. (Radcliffe-Smith 1996; drawn by J.M. Fothergill)

on persistent or deciduous branchlets, sometimes cauliflorous. Staminate flowers pedicellate; sepals (4) 5–6, imbricate, entire or dentate; petals 0; disk usually dissected, sometimes annular; stamens (1) 2–4(−10), filaments distinct or connate, anthers dehiscing horizontally to longitudinally, muticous or apiculate; pollen grains prolate to oblate, 3–4 (6)-colporate, rarely diploporate, porate, or panporate, exine patterns various; pistillode 0. Pistillate flowers pedicellate; sepals (4)5–6, imbricate, usually entire, persistent in fruit; petals 0; disk annular or dissected; ovary 3-locular, ovules hemitropous, inner integument thin, 3–5 cell layers; stylodia bifid or entire, sometimes dilated. Fruits capsular, baccate, or drupaceous; columella usually persistent in dehiscent fruits. Seeds usually 2 per locule, trigonous, mostly not ventrally invaginated; testa smooth, striate, ribbed, foveolate, or verruculose; endosperm copious; embryo straight or curved, cotyledons broader than and equal to or longer than the radicle. $2n = 16, 24, 26, 28, 52$.

Over 800 spp., pantropical, and also entering warm temperate regions. Molecular systematic studies (Kathriarachchi et al. 2005, 2006) found three of the eight subgenera of *Phyllanthus* to be polyphyletic, and the genus in its traditional circumscription to be paraphyletic. *Sauropus*, *Breynia* and *Glochidion* are deeply embedded within *Phyllanthus* s. str., and ultimately may be included into an expanded generic concept that would comprise over 1,250 species. At present, however, the nomenclatural changes conforming to the molecular results hardly have been initiated, and the non-monophyletic subtaxa of *Phyllanthus* s. str. and the genera deeply embedded in it will require careful taxonomic revision of the different elements before being amalgamated in the expanded generic concept, as has already been initiated for *Sauropus* by the work of van Welzen (2003), Sagun and van der Ham (2003), and Pruesapan et al. (2008). At present, merging *Phyllanthus* with its embedded genera would displace the lack of a workable taxonomic structure for the expanded genus only to the infrageneric level.

35. *Glochidion* J.R. & G. Forst.

Glochidion J.R. & G. Forst., Char. Gen. Pl.: 57 (1775), nom. cons.; A.C. Sm., Fl. Vit. Nova 2: 467 (1981); McPherson & Tirel, Fl. Nouv. Caléd. 17: 18, t. 4 (1991); Webster, Ann. Missouri Bot. Gard. 81: 46 (1994); Florence, Fl. Polynésie Française 1: 66, figs. 9–16 (1997).

Monoecious (dioecious) trees or shrubs; branching phyllanthoid. Leaves alternate, those on penultimate axes spiral and reduced to cataphylls; leaves on deciduous branchlets distichous, often inaequilateral at base, entire; stipules ± persistent. Flowers in axillary glomerules, bracts persistent. Staminate flowers pedicellate; sepals 5–9, imbicate; petals 0; disk 0; stamens 3–8, filaments connate; anthers apiculate, extrorse, dehiscing longitudinally; pollen grains slightly prolate, 3–6-colporate-monoporate, reticulate; pistillode 0. Pistillate flowers pedicellate; sepals usually 6, imbricate, persistent in fruit; petals and disk 0; ovary 3–15-locular, ovules hemitropous; stylodia unlobed, rarely emarginate or bifid, often connivent or connate. Fruit capsular; columella persistent. Seeds usually 2 per locule, ventrally invaginated, testa fleshy; endosperm copius; embryo curved, cotyledons much longer and broader than the radicle. $2n = 26, 52$.

Over 300 spp., Asia and Australasia; the spp. described from Madagascar appear of dubious affinity.

36. *Sauropus* Blume

Sauropus Blume, Bijdr. Fl. Ned. Ind.: 595 (1826); Airy Shaw, Hook. Icon. Pl. 38: t. 3708, 3709 (1974); Webster, Ann. Missouri Bot. Gard. 81: 46 (1994); J.T. Hunter & Bruhl, Austrobaileya 4: 661 (1997); Philcox, Fl. Ceylon 13: 99 (1999); Radcl.-Sm., Gen. Euphorb.: 46 (2001); van Welzen, Blumea 48: 319–391 (2003), Males. & Thai spp.; Pruesepan et al., Ann. Bot. 102: 1007–1018 (2008), mol. syst.
Aalius Rumph. ex Lam. (1793).
Ceratogynum Wight (1852).
Diplomorpha Griff. (1854) not Meissn. (1841).
Synostemon F. Muell. (1858).
Breyniopsis Beille (1925).
Heterocalymnantha Domin (1927).

Monoecious shrubs, subshrubs, or herbs; branching phyllanthoid or phyllotaxy entirely spiral; leaves on deciduous branchlets alternate, distichous; lamina pinnately veined, margins entire; stipules persistent. Flowers in axillary glomerules. Staminate flowers pedicellate; sepals 6, connate, the calyx sometimes flattened and discoid; petals and disk 0 but sometime inflexed sepal tips mimicking a disk; stamens 3, filaments connate into a column; anthers sessile, extrorse, dehiscing longitudinally; pollen grains ± oblate, 6–16-colporate-diploporate, reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 6, connate, persistent

and sometimes accrescent in fruit; petals and disk 0; ovary 3-locular, ovules hemitropous; stylodia bifid. Fruit capsular but pericarp often fleshy; columella persistent. Seeds 2 in each locule, trigonous, hilum linear, within a large ventral invagination, testa dry; endosperm copious; embryo straight or curved, cotyledons broader and longer than radicle. $2n = 24$.

Traditionally comprising about 80 spp. in tropical Asia, Malesia, and Australia except for the widespread *Sauropus bacciformis*. The molecular data of Pruesapan et al. (2008) suggest the splitting of *Sauropus* into two clades, the mainly southeast Asian *Sauropus* s. str., which should be united with *Breynia* under the latter name, and the mainly Australian *Sauropus*, for which the former name *Synostemon* should be reinstated.

37. *Breynia* J.R. & G. Forster

Breynia J.R. & G. Forst., Char. Gen. Pl.: 73 (1775; nom. cons.); Airy Shaw, Kew Bull. Add. Ser. 4: 61 (1975), 8: 38 (1980); McPherson & Tirel, Fl. Nouv.-Caléd. 17: 14, fig. 3, 6–10 (1991); Webster, Ann. Missouri Bot. Gard. 81: 46 (1994); Philcox, Fl. Ceylon 11: 238 (1997); Radcl.-Sm., Gen. Euphorb.: 46 (2001).
Foersteria Scop. (1777).
Melanthesa Blume (1826).
Melanthesopsis Müll. Arg. (1863).

Monoecious shrubs; branching phyllanthoid; indumentum 0. Leaves on penultimate axes spiral, reduced to scales, those on deciduous branchlets alternate, distichous; lamina entire; stipules persistent. Flowers in axillary glomerules, the pistillate solitary. Staminate flowers pedicellate; sepals 6, connate into a turbinate cup, sepal tips inflexed; petals and disk 0; stamens 3, filaments connate; anthers basifixed, muticous, dehiscing longitudinally; pollen grains 4–12-colporate-diploporate; pistillode 0. Pistillate flowers pedicellate; sepals 6, nearly distinct to connate, imbricate, persistent and sometimes accrescent in fruit; petals and disk 0; ovary 3-locular, rounded to turbinate, ovules hemitropous; stylodia distinct or basally connate, emarginate to bifid. Fruits somewhat fleshy, capsular; columella usually not persistent. Seeds 2 in each locule, trigonous, ventrally invaginated, testa fleshy; endosperm copious; embryo curved, cotyledons equaling or longer than radicle. $2n = 26, 52$.

Traditionally comprising about 35 spp., many difficult to distinguish, east Asia and Australasia. Molecular data suggest a reclassification as indicated under the previous genus.

IB. Supertribe Antidesmodae G.L. Webster, *supertrib. nov.*[1]

Subfam. Antidesmatoideae Hurus. (1954).
Antidesmatinae Pax (1890), "Antidesminae".

Dioecious or rarely monoecious; leaves simple (compound: *Bischofia*), entire (subentire or toothed); leaf epidermis usually with tanniniferous cells; inflorescences usually thyrsoid with distinct axes; flowers usually apetalous; ovary locules 1–5; ovules anatropous; fruits indehiscent or tardily dehiscent (explosively dehiscent). Tropics and subtropics.

This supertribe corresponds to the tanniniferous clade of Wurdack et al. (2004); in molecular analyses (Kathriarachchi et al. 2005; Samuel et al. 2005), it is placed sister to Phyllanthodae.

5. Tribe Antidesmateae Benth. (1873).

Dioecious (monoecious); exudate 0; indumentum simple (lepidote); petioles sometimes pulvinate; foliar glands and domatia 0 or +; sepals (3)4–6 (−8), imbricate to nearly completely connate; petals 0 or [*Thecacoris*] +, small; disk + or 0; stamens 2–8(−13); thecae usually separate and connective enlarged; pistillode + (0); ovary locules (1)2–4(5); ovules anatropous; stylodia + or 0; fruits indehiscent or dehiscent; seeds exarillate, usually albuminous.

Eight genera, pantropical, in five apparently isolated mono- or digeneric subclades (Kathriarachchi et al. 2005; Samuel et al. 2005).

Key to the Genera of Antidesmateae

1. Ovary 2-locular above, appearing 4-locular below; fruits 4-gonous; pollen with atria **42. *Martretia***
– Ovary locules not as above; fruits commonly 1–3-gonous; pollen grains exatriate 2
2. Fruit winged; floral disk 0; tanninferous cells in leaf epidermis 0 3

[1] Supertribe **Antidesmodae** G.L. Webster, **supertrib. nov.**, floribus inflorescentiis paniculatis spicatisve, cellulis epidermalibus foliorum saepe tanniniferis, embryonibus plerumque chlorophyllosis, radicula quam cotyledonibus breviore, fructibus plerumque baccatis vel drupaceis. Type: *Antidesma* L.

– Fruit not winged; floral disk + or 0; tanniferous cells in leaf epidermis + 4
3. Fruit capsular; inflorescence paniculate; stylodia lacerate **40. *Didymocistus***
– Fruit samaroid; inflorescence racemoid; stylodia papillose **41. *Hymenocardia***
4. Indumentum lepidote; fruit indehiscent **44. *Hieronyma***
– Indumentum 0 or of simple or stellate hairs 5
5. Ovary 1-locular; fruit indehiscent **38. *Antidesma***
– Ovary 2–5-locular; fruit dehiscent 6
6. Disk 0; pistillode 0; ovary 4–5-locular **45. *Leptonema***
– Disk +; pistillode +; ovary 3–4-locular 7
7. Dioecious; ovary 3-locular; stylodia 2-fid; endosperm copious **39. *Thecacoris***
– Monoecious; ovary 4-locular; stylodia entire; seeds exalbuminous; embryo massive **43. *Apodiscus***

5a. Subtribe Antidesmatinae Müll. Arg. (1865).

Two genera, Old World.

38. *Antidesma* Burm. ex L.

Antidesma Burm. ex L., Sp. Pl.: 1027 (1753); Airy Shaw, Kew Bull. Add. Ser. 4: 207 (1975), 8: 208 (1980); Léonard, Fl. Afr. Centr. Euph. (2): 16–40 (1995); Chakrabarty & Gangopadkyay, J. Econ. Tax. Bot. 24: 1 (2000).
Stilago L. (1767).

Dioecious trees and shrubs; indumentum simple. Leaves sometimes domatiiferous; marginal glands rarely + (*A. vaccinioides*); stipules mostly entire. Inflorescences axillary or terminal, sometimes fasciculate. Flowers in catkin-like, sometimes branched thyrses; bracts 1-flowered. Staminate flowers sessile to pedicellate; calyx cupular or 3–5(8)-lobed, sepals imbricate; petals 0; disk segments distinct or connate; stamens mostly (2)3–5(6); filaments distinct; anthers 2-lobate, thecae distinct, divergent; connective enlarged; pollen grains perprolate, 3-colporate, pores conspicuously lalongate, exine tectate-punctate, scabrate; pistillode small or 0. Pistillate flowers pedicellate; calyx usually cupular-lobed, persistent in fruit; disk annular or cupular; ovary 1(2)-locular; stylodia usually 2, bifid. Fruit drupaceous, asymmetric and flattened, endocarp reticulate or foveolate. Seeds 1(2) per fruit; endosperm fleshy, not copious; embryo flat, cotyledons much longer and broader than radicle. $2n = 26$.

At least 150 spp., mostly from India to Malesia, southern Japan, Australia, and the Pacific islands, only 10 in Africa/Madagascar.

39. *Thecacoris* A. Juss. Fig. 14

Thecacoris A. Juss., Euphorb. Tent.: 12 (1824); Léonard, Bull. Jard. Bot. Nat. Belg. 64: 13–52 (1995).
Cyathogyne Müll. Arg., Flora 47: 536 (1864).

Dioecious or rarely monoecious trees, shrubs, subshrubs or perennial herbs; indumentum simple. Leaves entire or repand; stipules deciduous or persistent. Inflorescences axillary, sometimes fasciculate, racemoid or spiciform; bracts persistent, 1-flowered. Staminate flowers sessile or pedicellate; sepals 5(6), imbricate; petals 5, small or 0; disk segments 5, distinct; stamens 5, filaments distinct; anthers pendent; anther thecae discrete, parallel and pendulous at first, later divaricate and erect; connective enlarged; pollen grains perprolate, 3-colporate, pores lalongate, exine finely reticulate; pistillode massive, dilated. Pistillate flowers pedicellate, pedicel geniculate in fruit; sepals 5, imbricate, persistent in fruit; petals variable in number, sometimes 0; disk annular; ovary 3(4)-locular; stylodia distinct or connate at base, bifid. Fruits capsular, septicidal; columella persistent. Seeds usually 1 per locule; testa dry and shiny; endosperm copious; embryo greenish, cotyledons flat, much longer and broader than radicle.

About 25 spp., four in Madagascar and the rest in tropical Africa from Sierra Leone to Angola and Tanzania. In the concept of Léonard, *Cyathogyne* includes five herbaceous species of Africa and Madagascar. Webster (1994) and Radcliffe-Smith (2001) followed Leandri (in Fl. Madag., 1958) in reducing *Cyathogyne* to a section of *Thecacoris*, with *Th. usambarensis* bridging the gap between the two genera. Léonard's case (1995) for maintaining *Cyathogyne* distinct may find support in the pollen and seed coat structure (Köhler 1965; Stuppy 1996).

5b. Subtribe Hymenocardiinae P. Hoffm. (2006).

Two genera, one neotropical, the other African.

40. *Didymocistus* Kuhlm.

Didymocistus Kuhlm., An. Prim. Reun. Sud-Amer. Bot. 3: 82 (1940); Radcl.-Sm., Gen. Euphorb.: 76, fig. 7 (2001).

Dioecious trees or shrubs; indumentum simple. Leaves with sessile abaxial glands; stipules deciduous. Inflorescences terminal, paniculate; bracts deciduous. Staminate flowers subsessile; sepals 5,

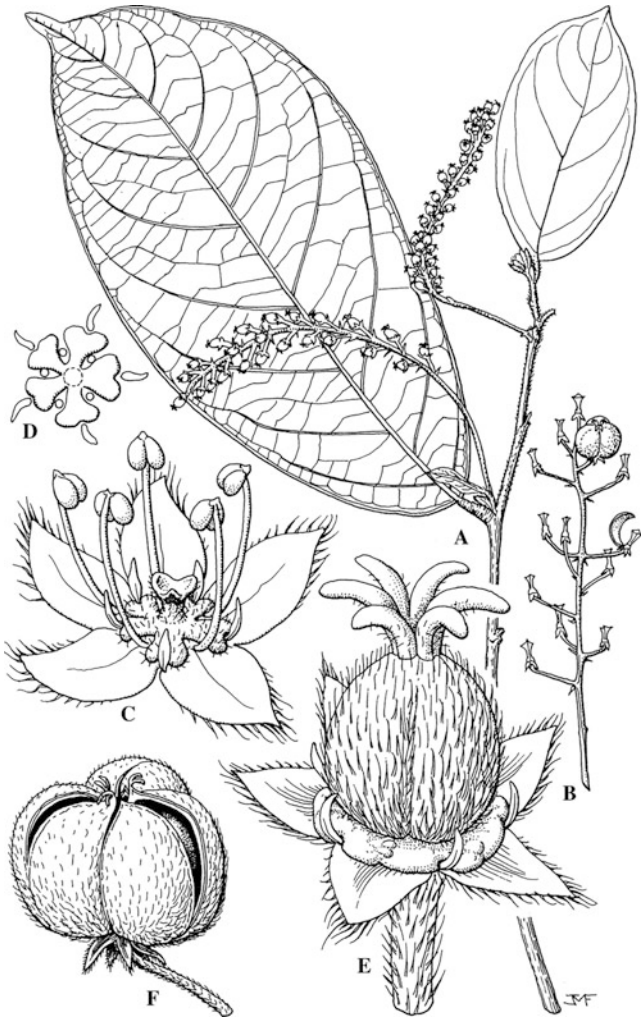

Fig. 14. Euphorbiaceae-Phyllanthoideae. *Thecacoris trichogyne*. **A** Branch tip with pistillate flowers. **B** Infructescence. **C** Staminate flower. **D** Staminate disk glands and petals. **E** Pistillate flower. **F** Fruit. (Radcliffe-Smith 1996; drawn by J.M. Fothergill)

imbricate, distinct; petals 0; disk 0; stamens 5, filaments distinct, exserted, anthers introrse, dorsifixed; pollen grains globose, 3-colporate, exine scabrate, tectum rugulose; pistillode 2–3-lobed; pistillate flowers sessile or subsessile; calyx 5-lobed, petals 0; disk 0; ovary 2-locular, stylodia unlobed, plumose. Fruits capsular, valves thin, inflated, deciduous; columella persistent. Seeds hemitropous, endosperm copious; embryo straight, cotyledons much longer and broader than radicle.

One sp., *D. chrysadenius* Kuhlm., in floodplain forests of Amazonian Brazil, Colombia and Peru; seed dispersal probably hydrochorous (Wurdack et al. 2004).

41. *Hymenocardia* Wall. ex Lindl. Fig. 15

Hymenocardia Wall. ex Lindl., Nat. Syst. ed. 2, 441 (1836); J.G. Adam, Mém. Mus. natl. Hist. Nat., N.S. Bot. 20: 481, t. 174 (1971); Léonard & Mosango, Fl. Afr. Centr., Hymenocardiaceae: 2 (1985); Radcl.-Sm., Fl. Zamb. 9: (4): 113, fig. 18 (1996).

Dioecious trees or shrubs; indumentum simple. Leaves abaxially with domatia and laminar glands; stipules deciduous. Staminate inflorescences axillary, spicate or catkin-like; pistillate flowers solitary or in axillary or terminal, racemoid inflorescences. Staminate flowers subsessile; sepals (4)5(−8), slightly imbricate, connate into a dentate or lobed cup; petals 0; disk 0; stamens usually 5, filaments distinct; anthers introrse in bud, anther sacs discrete, dehiscing longitudinally; pollen grains suboblate, 3-porate or brevicolporate, pores marginate, exine scabrate, tectum rugulose; pistillode cylindric or 2-lobed. Pistillate flowers pedicellate; sepals 5 (4–9), distinct, deciduous; petals 0; disk 0; ovary 2-locular, flattened perpendicular to septum; stylodia 2, unlobed. Fruits samaroid, dehiscing into two 1-seeded winged indehiscent mericarps; columella persistent. Seeds compressed, testa striate, shiny; endosperm copious; embryo flattened, cotyledons longer and broader than radicle. $2n = 26, 28$.

Six or seven spp., all African except one in southeast Asia. A very distinctive genus that has been accepted as a separate tribe or even family by Airy Shaw (1965), Léonard and Mosango (1985), and Meeuse (1990). The ament-like inflorescences and unique samaroid fruits make it one of the more aberrant genera of Phyllanthoideae. However, the pollen evidence weighted so heavily by Léonard must be seen in connection with the complete anemophily found in the genus. In contrast to the pollen data, the wood anatomy of *Hymenocardia*, according to Mennega (1987), is compatible with genera of Antidesmeae, and the foliar venation studies of Levin (1986a, b) show no incompatibility with Phyllanthoideae. The placement of *Didymocistus* with *Hymenocardia* appears strongly supported by the similarities of pollen structure demonstrated by Simpson and Levin (1994), the possession of multicellular

Fig. 15. Euphorbiaceae-Phyllanthoideae. *Hymenocardia ulmoides*. **A** Branchlet with staminate flowers. **B** Staminate flower. **C** Stamen, rear view, showing gland. **D** Branchlet with pistillate flowers. **E** Pistillate flower. **F** Fruiting branch. **G** Fruit. (Radcliffe-Smith 1996; drawn by Pat Halliday).

secretory leaf glands in the absence of tanniniferous leaf epidermal cells, the tanniniferous endotegmic seed coat (Tokuoka and Tobe 2001), and the molecular data of Wurdack et al. (2004) and Kathriarachchi et al. (2005).

5c. Subtribe Martretieae P. Hoffm. (2006).

Two genera held together by strong molecular support; they had been of dubious affinity and have little in common morphologically.

42. *Martretia* Beille

Martretia Beille, C. R. Séances Acad. Sci. Paris 145: 1294 (1907), Bull. Soc. Bot. France 55 (Mém. 8b): 64 (1908); Léonard, Bull. Jard. Bot. Nat. Belg. 59: 319 (1989); Radcl.-Sm., Gen. Euphorb.: 80 (2001).

Dioecious; indumentum 0 on stems and leaves. Tanniniferous epidermal cells 0. Stipules entire, deciduous. Inflorescences axillary, spiciform to racemoid, sometimes compound. Staminate flowers pedicellate; sepals 4 or 5, distinct; petals 0; disk 0; stamens 4–8, filaments distinct; anthers latrorse, dehiscing longitudinally, connective glandular at the apex and pubescent; pollen subspheroidal, 3-colporate, angulaperturate, colpi narrow, unbordered, exine semitectate, vermiculate-rugulose; pistillode 2-fid, pubescent apically. Pistillate flowers pedicellate; sepals 4–6, not persistent in fruit; petals 0; disk of 5 or 6 minute segments; ovary 2-locular, appearing 4-locular below due to intercalary partitions, glabrous or puberulent; stylodia 2, basally connate, unlobed, subulate, elongated. Fruits capsular, 4-gonous, dehiscing into four 1-seeded segments. Seeds albuminous, ellipsoid; testa smooth, fleshy; cotyledons suborbicular.

One sp., *M. quadricornis* Beille, from W and C Africa (Sierra Leone to C.A.R., Congo and Gabon), in swamp and riverine forests. Unique in Phyllanthoideae for its pollen apertures and false-partitioned fruit. Beille (1908) suggested a placement in Antidesmeae, and it was placed in Antidesminae by Pax and K. Hoffmann (1922, 1931).

43. *Apodiscus* Hutch.

Apodiscus Hutch., Bull. Soc. Bot. France 58, Mém. 8: 205 (1912), and in Hook. Ic. Pl. 31: t. 3032 (1915); Keay, Fl. W. Trop. Afr. ed. 2, 1: 373 (1958); Radcl.-Sm., Gen. Euphorb.: 63 (2001).

Monoecious trees; indumentum simple, confined to the inflorescence. Leaves deciduous; stipules deciduous. Inflorescences axillary, spiciform, fasciculate; bracts uniflorous; pistillate flowers 1 or 2 at base of inflorescence. Staminate flowers sessile; sepals 5, imbricate; petals 0; disk segments 5, pubescent; stamens 5, filaments distinct; anthers introrse, thecae subglobose, longitudinally dehiscent, connective slightly produced; pollen prolate, tricolporate, colpus transversalis elongate; pistillode depressed-globose, pubescent. Pistillate flowers pedicellate; sepals 5, imbricate; petals 0; disk 0;

ovary (3)4(5)-locular; stylodia unlobed, recurved. Fruits capsular, septicidally dehiscent into 3 cocci. Seeds exalbuminous; embryo massive, cotyledons much longer and broader than radicle.

One imperfectly known sp., *A. chevalieri* Hutch., from W Africa (Guinea, Liberia and Sierra Leone); it appears aberrant in the Antidesmateae because of its monoecy and exalbuminous seeds.

5d. Subtribe Hieronyminae Müll. Arg. (1865).

Monotypic.

44. *Hieronyma* Allemão

Hieronyma Allemão, Pl. Nov. Bras.: 22 (1848); Pax & K. Hoffm., Pflanzenreich 147, XV: 31, fig. 8 (1922); Jablonski, Mem. N. Y. Bot. Gard. 17: 122 (1967); Webster, Ann. Missouri Bot. Gard. 75: 1094 (1988) and ibid. 81: 52 (1994); Franco, Bot. Jahrb. Syst. 111: 297, figs. 1–16 (1990).
Hyeronima Allemão (orth. var.)

Dioecious trees or shrubs; indumentum lepidote or rarely simple. Stipules usually small, cochleate, often soon deciduous. Inflorescences axillary, ± compound racemoid to subspicate thyrses; bracts inconspicuous. Staminate flowers subsessile; calyx 4- or 5-lobed; petals 0; disk pulvinular or cupular; stamens 3–6, filaments distinct; anthers introrse; thecae divergent; anther sacs pendent, dehiscing longitudinally; pollen perprolate, 3-colporate, pores elliptic, exine tectate-perforate or microreticulate; pistillode columnar. Pistillate flowers pedicellate; calyx 4- or 5-lobed, ± persistent in fruit; petals 0; disk cupular; ovary 2(3)-locular, glabrous or lepidote; inner integument thin [2–4 layers]; stylodia very short, stigmatoid. Fruits drupaceous, 1–2-locular by suppression; exocarp fleshy, endocarp hard and bony or fibrous. Seeds usually 1 per fruit by abortion; endosperm fleshy; embryo green, cotyledons much longer and broader than radicle.

Approximately 15(−40?) spp., from S Mexico and Cuba south to Bolivia and S Brazil.

5e. Subtribe Leptonematinae Müll. Arg. (1865).

Monotypic.

45. *Leptonema* A. Juss.

Leptonema A. Juss., Euphorb. Tent.: 19 (1824); Leandri, Fl. Madag. 111 (1): 12, fig. IV, 1–6 (1958); Schatz, Generic Tree Fl. Madag.: 157 (2001).

Dioecious (monoecious) shrubs; indumentum simple. Leaves circular to heart-shaped; stipules persistent. Inflorescences axillary, staminate racemoid or corymbiform, pistillate brachyblastic; bracts subulate; flowers 1 per bract. Staminate flowers pedicellate; sepals 5, connate at base, imbricate; petals 0; disk 0; stamens 5, filaments distinct, capillary, exserted; anther connective globose, glandular; thecae separate; pollen sacs pendulous; pollen grains 3-colporate, pores transversely elongate; exine very finely reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 5, persistent in fruit; petals 0; disk 0; ovary 4–5-locular; stylodia bifid. Fruits capsular, splitting into 4–5 2-valved cocci; columella persistent. Seeds 2 per locule, testa verruculose.

Two spp. endemic to Madagascar, still poorly known.

6. Tribe Scepeae Horan. (1847).

Aporuseae (Lindl. ex Miq.) Airy Shaw (1974).

Dioecious; exudate 0; leaves often with laminar glands; inflorescences axillary or terminal, sometimes cauliflorous; sepals 4–5(−7), distinct; petals 0; disk lobed to dissected or 0; pollen grains 3-colporate, reticulate or tectate; pistillode +; ovary 2–5-locular; stylodia bifid or unlobed; fruit capsular or baccate; seed coat dry or fleshy.

This subtribe of eight genera, all paleotropical except for *Richeria*, was subsumed within the Antidesminae by Pax (1924) and Pax and K. Hoffmann (1922, 1931). Airy Shaw (1974) was the first to formally recognize it, as tribe Aporuseae, which was accepted by Webster (1975) and more recently by Thin (1995).

Key to the Genera of Scepeae

1. Pistillate disk dissected; stylodia 2-lobate or 2-fid **46. *Protomegabaria***
– Pistillate disk cupular or 0; stylodia 2-fid or unlobed 2
2. Staminate disk +; pistillate disk + or 0 3
– Staminate and pistillate disk 0 6
3. Pistillate disk +; sepals persistent in fruit 4
– Pistillate disk 0; sepals deciduous 5
4. Capsule loculicidal; staminate flowers mostly 1 per bract **51. *Maesobotrya***
– Capsule septicidal; staminate flowers several per bract **47. *Richeria***
5. Staminate sepals distinct, shorter than stamens; staminodes usually 0; stipules narrow **52. *Baccaurea***

– Staminate sepals basally connate, longer than stamens; staminodes + in pistillate flower; stipules broad
53. *Nothobaccaurea*

6. Leaves spiral; stamens 5 or 6; pistillode massive, peltate
50. *Ashtonia*

– Leaves spiral or distichous; stamens mostly 2 [unknown in *Distichirrhops*]; pistillode small or 0
7

7. Leaves spiral; pistillate flowers subtended by 1 bract; pistillate disk + but obscure; pedicels not articulated
48. *Aporosa*

– Leaves distichous; pistillate flowers subtended by 3 bracts; pistillate disk 0; pedicels articulated
49. *Distichirrhops*

46. *Protomegabaria* Hutch.

Protomegabaria Hutch., Hook. Icon. Pl. 30: t. 2929 (1911); Léonard, Bull. Jard. Bot. Nat. Belg. 64: 53–63 (1995), Fl. Afr. Cent., Euph. 2: 79, t. 13 (1995).

Dioecious, semipachycaul trees; trunk buttressed and stilt-rooted; indumentum simple or 0. Stipules fugacious. Inflorescences racemose to subspicate, axillary, sometimes cauliflorous, solitary or clustered; pedicels articulate; staminate flowers in clusters partly enclosed by cupular central bractlet; pistillate flowers 1 per bract. Staminate flowers: sepals 5(4), imbricate; petals 0; disk segments usually 5, fleshy; stamens usually 5, distinct; anthers introrse; pollen grains prolate, 3-colporate, pores laterally elongated, exine finely reticulate; pistillode columnar, small. Pistillate flowers: sepals 5, imbricate, persistent in fruit; petals 0; disk annular; ovary 3(4)-locular; stylodia 2-lobate or 2-fid. Fruit capsular, somewhat lignified; columella persistent, dilated at base and clavate distally. Seeds ellipsoid, testa smooth and shiny; endosperm copious; embryo straight. $2n = 26$.

Three African spp. (Guinea to Gabon and Congo), in lowland tropical rainforest.

47. *Richeria* Vahl

Richeria Vahl, Eclog. Amer. 1: 30, t. 4 (1797); Secco & Webster, Bol. Mus. Para. Emilio Goeldi, N.S., Bot. 6: 141–158 (1990), rev.

Dioecious trees or shrubs; indumentum simple or 0. Leaves entire or crenulate, sometimes glandular near the base; stipules deciduous. Inflorescences racemoid or spicate, axillary; staminate flowers in dense glomerules; pistillate flowers 1 per bract. Staminate flowers sessile; calyx 3–5-lobed, tips of lobes imbricate; petals 0; disk-segments 3–5; stamens 3–6, filaments distinct and exserted from calyx; anthers introrse, versatile; pollen grains prolate, 3-colporate, semitectate-reticulate; pistillode cylindric, hirtellous. Pistillate flowers pedicellate; calyx 3–5-lobed, sepals imbricate; petals 0; disk cupular; ovary 2–3-locular, sericeous; stylodia 2- or 3-fid. Fruit capsular, tardily dehiscent septicidally; columella flattened, winged, persistent. Seeds 1 per locule, ovoid; testa fleshy, exotegmen vittate; endosperm copious; cotyledons flat, much longer than radicle, both cotyledons and radicle chlorophyllous.

Two or three spp., distributed from the Lesser Antilles and Panama to Bolivia and Brazil.

48. *Aporosa* Blume

Aporosa Blume, Bijdr.: 514 (1826; orth. cons.); Airy Shaw, Hook. Icon. Pl. 38: pl. 3701 (1974), Kew Bull. Add. Ser. 4: 30 (1975), ibid. 8: 28 (1980); Schot, Blumea 40: 449 (1995). *Scepa* Lindl. (1836).

Dioecious trees and shrubs [flowers bisexual in four spp.]; indumentum simple. Leaves often with laminar glands, petioles long, often geniculate and distally glandular; stipules mostly persistent, sometimes foliaceous or falcate. Inflorescences usually axillary, often fasciculate, the staminate spiciform and catkin-like, the pistillate racemoid. Staminate flowers sessile or subsessile; sepals 3–6, imbricate; petals 0; disk 0; stamens 2(−5), filaments distinct; anthers subglobose, basifixed; pollen grains subprolate, 3-colporate, pores lalongate, exine semitectate-reticulate; pistillode minute or 0. Pistillate flowers pedicellate; sepals 4 or 5, imbricate, persistent in fruit; petals 0; disk small; ovary 2(−4)-locular; stylodia usually bipartite, often papillose or laciniate. Fruit capsular; pericarp ± leathery, dehiscing into valves or irregularly; columella persistent. Seeds 1 or 2 per fruit, with colored sarcotesta; endosperm copious; embryo chlorophyllous, straight, cotyledons much longer and broader than radicle. $2n = 26, 52$.

About 75 spp., distributed from India and Sri Lanka to the Philippines and New Guinea.

49. *Distichirrhops* Haegens

Distichirrhops ('*Distichirhops*') Haegens, Blumea Suppl. 12: 193, figs. 3.28, 3.29 (2000).

Dioecious trees; indumentum simple. Leaves distichous, entire, with marginal glands; petioles

apically pulvinate; stipules deciduous. Inflorescences axillary or ramiflorous, thyrsoid [only pistillate plants known], unbranched, 10–15-flowered. Pistillate flowers in triads, each subtended by 3 bracts, with articulated pedicels; sepals 4 or 5, deciduous to persistent; petals, staminodes and disk 0; ovary 2–4-locular; ovules 2 per locule; stylodia unlobed to 2-fid. Fruits 0–4-seeded, baccate or capsular and tardily dehiscent, often glandular, 0–4-seeded. Seeds albuminous, with fleshy testa.

Three incompletely known spp., Borneo and New Guinea. According to Haegens, the genus seems to be related to *Aporosa*.

50. *Ashtonia* Airy Shaw

Ashtonia Airy Shaw, Kew Bull. 21: 357 (1968), Hook. Icon. Pl. 38: t. 3702 (1974), Kew Bull. Add. Ser. 4: 42 (1975).

Dioecious trees; indumentum 0. Leaves biglandular at base; stipules deciduous. Inflorescences spiciform [staminate] and racemoid [pistillate], solitary; staminate flowers in glomerules, pistillate solitary. Staminate flowers subsessile; sepals 3 or 4, imbricate; petals 0; disk obscure or 0; stamens 5 or 6, filaments distinct, shorter than sepals, anthers latrorse, dehiscing longitudinally; pollen subglobose, 3-colporate, colpi margins broad, exine coarsely reticulate; pistillode massive. Pistillate flowers pedicellate; sepals 3 or 4, deciduous; petals 0; disk 0; ovary 3 or 4(5)-locular; stylodia 2-lobed, stigmatiform. Fruits capsular with fleshy pericarp; columella persistent. Seeds with thin fleshy testa; endosperm layer thin, exotegmen vittate; embryo massive, cotyledons flat, chlorophyllous.

Two spp. from SE Asia: Thailand to Malaya and Borneo.

51. *Maesobotrya* Benth.

Maesobotrya Benth., Hook. Icon. Pl. 13, 75: t. 1296 (1879); Léonard, Fl. Afr. Centr., Euph. 2: 46–79, t. 7–12 (1995).

Dioecious trees or shrubs; indumentum simple. Leaves entire or dentate; stipules ± subulate (foliaceous), deciduous or persistent. Inflorescences terminal or axillary, sometimes ramiflorous; staminate flowers in racemoid thyrses, sometimes fasciculate or paniculate; pistillate flowers solitary in axils of bracts on spiciform thyrses; pedicels shortly articulated. Staminate flowers: sepals 4–6, imbricate, distinct or basally connate; petals small, 1–3, or more often 0; disk intrastaminal, segments ± confluent, usually pubescent; stamens 4–6(7), filaments distinct, usually exserted from calyx, anthers introrse, connective not enlarged; pollen grains subprolate, 3-colporate, pores ± elliptic, exine semitectate, finely reticulate; pistillode cylindric or clavate, pubescent. Pistillate flowers: sepals and petals as in staminate; disk cupular, sometimes lobed, rim usually ciliate; ovary 2–3(4)-locular, glabrous or slightly pubescent; stylodia bifid. Fruits capsular, dehiscing loculicidally; pericarp thin; columella not persistent. Seeds 1 or 2 per locule; testa fleshy and often blue; endosperm copious; embryo chlorophyllous, cotyledons flat, much longer than radicle. $2n = 26$.

Some 20 spp., mostly in the West Africa/Congo lowland rainforest area, one in Uganda and another in Zambia.

52. *Baccaurea* Lour.

Baccaurea Lour., Fl. Cochinch.: 661 (1790); Haegens, Blumea Suppl. 12: 80–129, figs. 3.1–3.27 (2000).

Dioecious trees; indumentum simple or stellate. Leaves entire to undulate or obscurely crenate, often with laminar and marginal glands; petiole apically and rarely basally pulvinate; stipules deciduous or subpersistent. Inflorescences axillary or ramiflorous, often fasciculate, racemoid to paniculate; staminate flowers mostly in bracteate triads, pistillate 1 per bract. Flowers pedicellate; staminate flowers sepals (3)4 or 5(−8), connate, imbricate; petals 0; disk segments mostly small or obsolete, sometimes confluent; stamens 3–10, filaments distinct; anthers basifixed to dorsifixed, introrse; pollen grains subprolate, 3-colporate, pores lalongate, exine semitectate-reticulate; pistillode massive, sometimes peltate. Pistillate flowers sepals 4–6(−9), deciduous or persistent; petals 0; disk 0; staminodes very rarely +; ovary 2–4-locular; ovules 2 per locule; stylodia unlobed to bifid, often minutely dentate or laciniate. Fruits baccate or capsular, dehiscent or indehiscent; persistent columella lacking. Seeds 0–2 per locule [or capsule]; testa ± fleshy; endosperm copious; embryo straight, cotyledons much longer and broader than radicle. $2n = 26$.

About 45 spp., mainly in southeast Asia and New Guinea, with one sp. in India and two in the Pacific, mostly in rainforest and freshwater swamp forest. Studies of Levin (1986a, b) and

Haegens (2000) indicated that *Baccaurea* is probably most closely related to African *Maesobotrya*, which was confirmed by the molecular data (Kathriarachchi et al. 2005).

53. *Nothobaccaurea* Haegens

Nothobaccaurea Haegens, Blumea Suppl. 12: 198, figs. 3.30, 3.31 (2000).

Dioecious trees or shrubs; indumentum simple. Leaves alternate or opposite, often with marginal and laminar glands; petioles apically pulvinate; stipules deciduous. Inflorescences axillary or ramiflorous, solitary or fasciculate, racemoid or spiciform; pedicels articulate or not. Staminate flowers sepals 3–7, fused at base; petals and disk 0; stamens 5–7, longer than sepals, filaments distinct; anthers dehiscing longitudinally or with apical slit; pistillode cylindrical, glabrous. Pistillate flowers: sepals 5 or 6, slightly imbricate, persistent in fruit; petals and disk 0; staminodes +; ovary 2-locular; stylodia bifid. Fruits baccate or tardily dehiscent; pericarp fleshy and glandular. Seed coat fleshy; embryo with cotyledons much longer and broader than radicle.

Two spp., Melanesia: Solomons and Fiji. Appears quite similar to *Baccaurea* and the African *Maesobotrya*.

7. Tribe Jablonskieae Petra Hoffm. (2006).

Monoecious or dioecious; indumentum and exudate 0; inflorescences racemoid or glomerular; sepals 5, imbricate, petals 0; disk +; stamens 5, distinct.

Two neotropical genera, which differ in several traits such as the reproductive system and the structure of the anthers, fruits, and seeds (but see Tokuoka and Tobe 2002), but share similarities in pollen (Webster 1984) and wood structure (Mennega 1987), and appear in a strongly supported sister position (Kathriarachchi et al. 2005).

Key to the Genera of Jablonskieae

1. Monoecious; leaves distichous; flowers in axillary glomerules; fruit dehiscing irregularly **54. *Jablonskia***
– Dioecious; leaves spiral; staminate flowers in pedunculate pseudo-racemes, pistillate ones in few-flowered brachyblasts; fruit septicidal **55. *Celianella***

54. *Jablonskia* G.L. Webster

Jablonskia G.L. Webster, Syst. Bot. 9: 232 (1984); Radcl.-Sm., Gen. Euph.: 62 (2001).

Monoecious glabrous shrubs or trees. Leaves distichous, shortly petiolate, with minute pigment streaks and basal laminar glands; tanniniferous cells 0; stipules deciduous. Inflorescences axillary, glomerules bracteate. Flowers sessile or subsessile; staminate flowers sepals 5, imbricate; petals 0; disk segments 5; stamens 5, filaments distinct; anthers introrse, versatile, dehiscing longitudinally; pollen grains prolate, 3-colporate, pores lalongate, exine tectate-perforate; pistillode much shorter than calyx. Pistillate sepals persistent in fruit, petals 0; disk patelliform; ovary 3-locular; stylodia distinct, bifid, erect. Fruit a baccate thin-walled capsule, dehiscing irregularly; columella subpersistent. Seeds 2 per locule; testa thin and fleshy; endosperm copious; cotyledons broader than and about equaling radicle.

One sp., *J. congesta* (Benth. ex Müll. Arg.) G.L. Webster, rainforests of Amazonian South America.

55. *Celianella* Jabl.

Celianella Jabl., Mem. New York Bot. Garden 12(3): 176, fig. 28 (1965); Radcl.-Sm., Gen. Euph.: 68 (2001).

Dioecious shrubs; indumentum 0. Leaves subsessile, semisucculent, minutely puncticulate abaxially; stipules deciduous, leaving conspicuous scars. Inflorescences pedunculate, axillary or subterminal, staminate racemoid, pistillate 3–1-flowered brachyblasts; bracts uniflorous, entire, deciduous. Staminate flowers pedicellate; sepals 5, imbricate; petals 0; stamens 5, filaments distinct; anthers introrse, pendulous; pollen grains prolate, 3-colporate, exine finely tectate-perforate; disk central, 5-lobate; pistillode 0. Pistillate flowers pedicellate; sepals 5, imbricate, entire, strongly veined, persistent and accrescent in fruit; petals 0; disk annular; ovary 3-locular; ovules 2 per locule, pendulous beneath an obturator; stylodia connate in lower half, 2-fid. Fruits capsular, septicidal; columella persistent. Seeds fusiform, testa reticulate, micropyle with minute caruncle; endosperm copious; embryo straight, cotyledons flat, much longer and broader than radicle.

One sp., *C. montana* Jabl., on sandstone tepuis of southern Venezuela above 1,000 m.

8. Tribe Spondiantheae G.L. Webster (1975).

Dioecious; exudate reddish; inflorescences mostly terminal, paniculate, bracts small; flowers,

at least the staminate, petaliferous, subsessile; staminate disk dissected; stamens 5, filaments distinct; pistillode +; pistillate disk lobed; stylodia distinct, bilobed; fruit loculicidally dehiscent; seed testa dry; endosperm scanty; cotyledons much broader than the radicle.

A single, monotypic African genus.

56. *Spondianthus* Engler

Spondianthus Engler, Bot. Jahrb. 36: 215 (1905); Hutchinson, Hook. Icon. Pl. 30: t. 2986 (1911); Léonard & Nkounkou, Bull. Jard. Bot. Nat. Belg. 59: 133–149 (1989).

Dioecious trees; stems with reddish exudate; indumentum simple or 0. Petioles with paired minute glands; stipules deciduous. Inflorescences terminal or subterminal, paniculate; flowers bracteate, staminate in glomerules, pistillate solitary. Staminate flowers subsessile; sepals (4)5, imbricate; petals (4)5, smaller than sepals; disk segments 5; stamens 5, filaments distinct; anthers introrse, connective glandular; pollen subprolate, 3-colporate, pores dumbbell-shaped, exine tectate-perforate; pistillode massive, apically flattened. Pistillate flowers pedicellate; sepals and petals as in the staminate, or petals 0; disk cupular, fleshy; ovary 3(5)-locular; ovules 2 per locule; stylodia 3, distinct, shortly 2-lobate, reflexed; stigmas papillose. Fruit capsular, dehiscing loculicidally; columella persistent. Seeds usually 1 per locule, compressed, testa reddish; endosperm scanty; embryo straight, cotyledons broad, flat.

A single sp., *S. preussii* Engl., widespread in tropical Africa: Guinea to Angola, Uganda and Tanzania. Due to the presence of fluoroacetic acid (Hegnauer 1989; Neuwinger 2000), *Spondianthus* is strongly toxic, and shares with *Uapaca* the unique presence of resinous exudate in the Phyllanthoideae. The molecular data place these genera in a sister position but with low support. The available seed anatomical data are inconclusive.

9. Tribe Uapaceae Hutch. (1969).

Uapacaceae (Müll. Arg.) Airy Shaw (1965).

Dioecious; exudate reddish; inflorescences axillary, capitular, conspicuously bracteate; flowers apetalous, disk 0; sepals 5, connate; stamens 4–6; pistillode large; ovary mostly 3-locular; stylodia laciniate; fruits drupaceous.

A monotypic Afro-Malagasian tribe.

57. *Uapaca* Baill. Fig. 16

Uapaca Baill., Étude Gén. Euph.: 595 (1858); Benth., Hook. Icon. Pl. 13: t. 1287 (1879); Pax & K. Hoffm., Pflanzenr. 147, XV: 298–311 (1922); Leandri, Fl. Madag. 111(1): 163 (1958); Radcl.-Sm., Fl. Zamb. 9(4): 93 (1996).

Dioecious pachycaul trees or shrubs with reddish resinous exudate; trunks often stilt-rooted; indumentum simple or microlepidote. Leaves petiolate or subsessile, entire; stipules deciduous or 0. Inflorescences axillary, pedunculate, globose-capitular, solitary or clustered, bracts 5–12, conspicuous, becoming reflexed, each with 5–10 staminate or solitary pistillate flowers. Staminate flowers sessile; calyx small, truncate to 4–6-lobate, lobes imbricate; petals and disk 0; stamens 4–6, filaments distinct; anthers introrse, erect; pollen grains oblate spheroidal, 3-colporate, angulaperturate, colpi narrow, pore large and rectangular, exine semitectate-reticulate; pistillode clavate to pileiform, sometimes lobate. Pistillate flowers sessile, perianth similar to staminate; disk 0; ovary mostly (2)3(5)-locular; stylodia distinct, dilated, recurving, distally laciniate. Fruit drupaceous with mostly 3 dorsally carinate pyrenes, tardily loculicidal into 2 valves each; columella persistent. Seeds usually 1 per pyrene, compressed; endosperm copious; embryo straight, cotyledons green, flat or slightly plicate, longer and broader than the radicle. $2n = 26$.

About 50 spp. in Madagascar and Africa; growing from humid evergreen to semi-deciduous and sclerophyllous forest and from sea level up to over 2,000 m elevation. The largest number of species are known from the Congo basin and are in need of reevaluation, 12 are endemic to Madagascar. The involucrate heads of disk-less flowers have always set *Uapaca* apart from other Euphorbiaceae, so that Airy Shaw (1965) and similarly Meeuse (1990) removed it to the separate family Uapacaceae. However, the basic floral and fruit structure is clearly euphorbiaceous.

10. Tribe Bischofieae (Müll. Arg.) Hurus. (1954).

Bischofiaceae (Müll. Arg.) Airy Shaw (1965).

Dioecious; exudate 0; indumentum simple, sparse. Leaves palmately 3(5)-foliolate; stipules caducous. Inflorescences axillary, paniculate; flowers apetalous. Sepals 5, imbricate, margins induplicate; disk 0; stamens 5; pollen grains

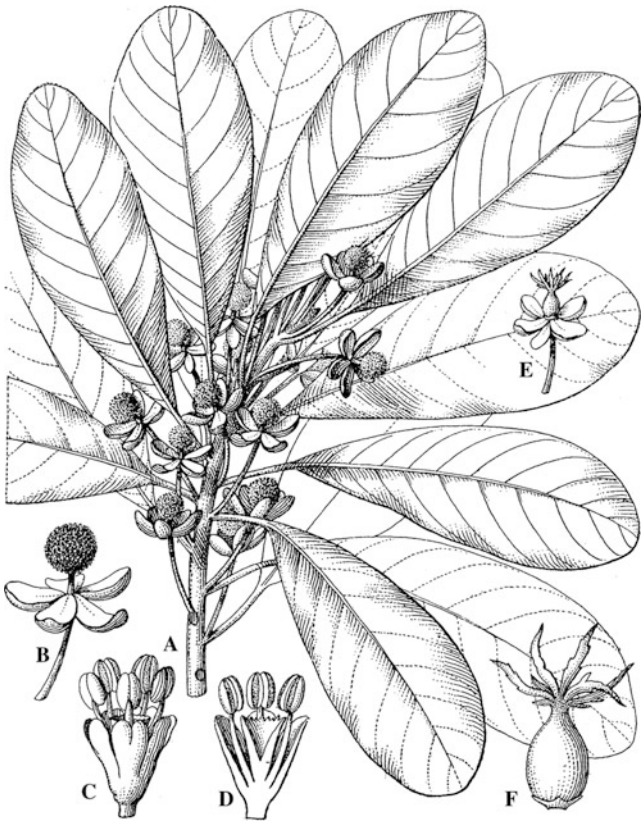

Fig. 16. Euphorbiaceae-Phyllanthoideae. *Uapaca heudelotii*. **A** Flowering branch. **B** Staminate inflorescence. **C, D** Staminate flowers. **E** Pistillate flower. **F** Pistil. (Pax & Hoffmann 1922)

subglobose, 3-colporate; pistillode +; ovary 3(4)-locular; stylodia simple, entire; fruits baccate.

A monotypic paleotropical tribe.

58. *Bischofia* Blume

Bischofia Blume, Bijdr.: 1168 (1826); Hook., Icon. Pl. 9: t. 844 (1852); Pax & K. Hoffm., Pflanzenr. 147, XV: 312, fig. 26 (1922); Li Bingtao & Gilbert, Fl. China 11: 217 (2008).

Dioecious (monoecious) trees; vessel element perforations simple and scalariform; wood fibers septate; indumentum simple, very sparse. Leaves palmately 3(5)-foliolate; leaflets petiolulate, crenate-serrate, abaxially with marsupiform domatia and with paired glands on the petiole and the petiolule of the terminal leaflet [interpreted by Wurdack et al. 2004 as stipels]; stipules deciduous. Inflorescences axillary, paniculate, bracts 1-flowered, deciduous; pedicels not articulated. Staminate flowers pedicellate; sepals 5, imbricate, cucullate-concave and enclosing anthers; petals and disk 0; stamens 5, filaments distinct, much shorter than sepals; anthers extrorse, muticous; pollen grains subglobose, 3-colporate, nearly syncolpate, exine tectate-perforate; pistillode peltate. Pistillate flowers pedicellate; sepals 5, imbricate, deciduous; petals and disk 0; staminodes minute or 0; ovary 3(4)-locular; stylodia 3(4), partially connate, subulate, unlobed; stigmas terete, smooth. Fruits oblate, baccate, epicarp thin, mesocarp fleshy, endocarp corneo-pergamaceous; locules 1–2-seeded; columella not persistent. Seeds smooth; endosperm copious; embryo green, curved, cotyledons much broader and longer than radicle. $2n = 196$.

Two spp., *B. javanica* Blume being widespread from India to eastern Asia, Melanesia, and Polynesia (to Samoa and Niue); *B. polycarpa* (Lévl.) Airy Shaw is endemic to China.

The distinctive characters of *Bischofia*, especially the trifoliolate leaves, the marsupiform domatia, and the sepals partly enclosing the anthers led Airy Shaw (1965) to move it to the segregate family Bischofiaceae, but the evidence provided by Bhatnagar and Kapil (1974), Levin (1986a), Mennega (1987), and Tokuoka and Tobe (2001) indicates that *Bischofia* belongs to Phyllanthoideae without showing a clear affinity with any other genus. In the molecular analyses it appears always in basal position within the Tanniniferous Clade.

Incertae sedis:

59. *Chonocentrum* Pierre ex Pax & K. Hoffmann

Chonocentrum Pierre ex Pax & K. Hoffmann, Pflanzenr. 147, XV: 205 (1922); Webster, Ann. Missouri Bot. Gard. 81: 37 (1994); Hayden & Hayden, Ann. Missouri Bot. Gard. 83: 165 (1996); Radcl.-Sm., Gen. Euphorb.: 12, fig. 2 (2001).

Dioecious trees or shrubs; indumentum simple. Leaves alternate, entire; stipules persistent. Flowers in axillary glomerules. Staminate flowers subsessile; sepals 4–5, connate, apically pubescent; petals 0; disk cupular; stamens 4–6, filaments distinct; anthers erect, basifixed, longer than filaments, introrse, pubescent, connective not enlarged; pollen grains prolate, 3-colporate, exine apparently tectate; pistillode large, cyathiform, 4- or 5-lobed, glabrous. Pistillate flowers and fruits unknown.

One sp., *Ch. cyanophorum* (Müll. Arg.) Pax & K. Hoffm., Amazonian Brazil, only once collected (Spruce 3781, K, P). Originally described by Müller (1873) as *Drypetes cyatophora*, it was regarded to be related to *Discocarpus* by Pax and Hoffmann (1922). S.M. and W.J. Hayden (1996) have shown that it is not closely related to *Discocarpus* and instead suggested placing it in the Antidesmeae, but there it would be anomalous in its cupular staminate disk and non-versatile anthers.

II. Subfam. Oldfieldioideae Eg. Köhler & G.L. Webster (1967)[1].

Hyaenanchoideae Baillon ex Hassk. (1859) ('Hyaenachneae' [sic!]).
Picrodendraceae Small (1917), nom. cons.

Monoecious or dioecious trees, shrubs or subshrubs; vessel elements (excepting Podocalyceae) mainly with simple perforations; wood fibers not septate except in *Parodiodendron*; indumentum simple [trichomes unicellular or uniseriate]. Leaves alternate, opposite or whorled; leaf blades simple or palmately compound, venation mostly brochidodromous, margins entire or dentate; stomata mostly brachyparacytic; stipules mostly deciduous or 0. Inflorescences axillary, glomerulate, racemoid, capitulate, or paniculate; bracts eglandular. Flowers mostly apetalous; staminate sepals (3)4–8(−12), imbricate, usually distinct; disk mostly intrastaminal or 0; stamens (2)3–30, filaments distinct or connate; anthers mostly extorse; pollen spheroidal to oblate, 3–7-zono-brevicolporoidate or -porate or 10–40-pantoporate, microperforatetectate, mostly with conspicuous spines; male gametophyte binucleate; pistillode + or 0. Pistillate sepals (3)4–8(−13), distinct, imbricate; disk annular to lobed, dissected or 0; ovary 2–4(5)-locular; ovules 2 per locule; stylodia entire, often dilated (2-fid). Fruit capsular (drupaceous). Seeds 1 or 2 per locule, often carunculate, testa usually smooth and shiny; endosperm usually copious; cotyledons plane or plicate, usually much longer and broader than the radicle. $x = 12$ or 13.

A predominantly Southern Hemisphere group of three tribes with 26 genera and c. 95 species. Relationships within Oldfieldioideae have been greatly clarified by the anatomical and morphological studies of Hayden (1994) and Levin and Simpson (1994), by the analysis of seed structure by Stuppy (1996), and by the molecular analyses of Wurdack (2002) and Wurdack et al. (2004). The latter work suggests the maintenance of three tribes, of which the monotypic Podocalyceae are basal to Picrodendreae and Caletieae, the latter being sister to each other. In Picrodendreae, *Tetracoccus* is first-branching, followed by a subclade in which *Picrodendron* is followed by *Parodiodendron* and then by *Piranhea*. *Hyaenanche* (formerly included in Caletieae) appears sister to *Oldfieldia* and both are sister to Miscodontinae, with which they agree in the whorled leaves and also in seed and general anatomy, but differ from them in the lack of stipules and among themselves in floral traits. Therefore, for these two genera Subtribe Paveusinae is upheld. In Caletieae, from which *Securinega* and *Hyaenanche* have been removed, *Petalostigma* occupies a basal position, whereas the morphologically clearly recognizable Dissilariinae and Pseudanthinae are also supported by the molecular analyses.

Key to the Tribes of Subfam. Oldfieldioideae

1. Pollen grains with 4 apertures; vessel elements at least in part with scalariform perforation plates; staminate disk extrastaminal or 0; leaves simple
1. Podocalyceae
– Pollen grains [except in *Tetracoccus*] usually with more than 4 apertures, rarely inaperturate; vessel elements with simple perforation plates; staminal disk intrastaminal or 0; leaves simple, unifoliolatae, or palmately compound 2
2. Leaf blades compound [if simple, then lamina stipellate or stipules adnate to petiole]; pollen grains zonoporate [except *Androstachys*]; dioecious trees or shrubs
2. Picrodendreae

[1] Reveal in his Website (since 1995) indicates that the subfamily name Hyaenanchoideae Baill. & Hassk. should have priority over Oldfieldioideae Eg. Köhler & G.L. Webster. Because the latter name has been in use in very many publications during the last four and a half decades, it is exasperating to have to replace it with an obscure, completely unfamiliar and originally misspelled name that obviously never has been used since its proposal by Hasskarl (1859) by taxonomists working on the Euphorbiaceae. For the sake of better communication, we are continuing to use the younger, well-introduced name. This is also so because there is so much still unearthed but nomenclaturally relevant botanical literature especially from the 19th century—e.g., in seed lists and annual reports from botanic gardens or colleges and grammar schools—that there is no end in sight for discoveries of even older botanical names and/or authorships.

– Leaf blades undivided [pseudo-trifoliolate in *Micrantheum*]; pollen grains zonoporate or pantoporate; monoecious or dioecious trees, shrubs, or subshrubs **3. Caletieae**

1. Tribe Podocalyceae G.L. Webster (1994).

After the exclusion of *Tetracoccus* (to Picrodendreae) and *Paradrypetes* (to Rhizophoraceae), the tribe is monotypic. It is remarkable for its vessel elements, 4-aperturtate pollen and ecarunculate seeds; in the molecular analysis of Wurdack (2002), *Podocalyx* is sister to all other Oldfieldioideae.

60. *Podocalyx* Klotzsch

Podocalyx Klotzsch, Arch. Naturgesch. 7: 202 (1841); Radcl.-Sm., Gen. Euphorb.: 84 (2001).
Richeria sect. *Podocalyx* (Klotzsch) Müll. Arg. (1866).

Dioecious trees; indumentum simple; vessel elements with simple, scalariform, and reticulate perforations. Leaves simple; petioles thickened at both ends, stomata anomocytic; stipules appearing obsolete [precociously deciduous?]. Inflorescences axillary or pseudo-terminal, staminate spiciform with dense pubescent capitular glomerules, pistillate racemoid, often fasciculate. Flowers apetalous; staminate flowers pedicellate, sepals usually 4, scarcely imbricate, basally connate; stamens usually 4, filaments distinct, far exserted above the calyx; anthers extrorse; pollen oblate, 4-zoniporate, echinate; pistillode represented by massive lobed intrastaminal disk. Pistillate flowers pedicellate, sepals 4, entire, distinct, persistent but not accrescent in fruit; disk cupular, 5-lobed; ovary 3-locular, ovules anatropous; stylodia stigmatoid, dilated. Fruiting pedicels massive, lenticellate; fruits capsular, loculicidally and septicidally dehiscent; columella persistent. Seeds 1/locule, hypostase basal, hilum subterminal; testa smooth, blackish, exotegmen cells elongated; endosperm copious; embryo straight, flat, cotyledons much longer and broader than radicle.

A single sp., *P. loranthoides* Klotzsch, widespread and common in Amazonian riparian and inundated forests of Colombia, Venezuela, and Brazil. Treated by Müller (1873) as a section of *Richeria* (Phyllanthoideae-Antidesmateae), *Podocalyx* has spinose pollen grains typical of Oldfieldioideae, but is an isolated genus in the subfamily.

Doubtful genus (for its formal treatment, see under Rhizophoraceae):

60a. *Paradrypetes* Kuhlm.

Formerly included in Oldfieldioideae but, on the basis of molecular findings by Wurdack (2002) and Wurdack and Davis (2009), this genus has been shifted (close) to the Rhizophoraceae. Although there is a general resemblance in habit between *Paradrypetes* and genera such as *Cassipourea*, none of the Rhizophoraceae has echinate pollen, such strongly pronounced unisexual and apetalous flowers, thin, distinct and imbricate sepals, and sessile stigmas (see Levin 1992; Matthews and Endress 2011). Therefore, doubts on the implications of the molecular data persist, and a clarification of the issue would be highly desirable.

2. Tribe Picrodendreae (Small) G.L. Webster (1975).

Picrodendraceae Small (1917).

Monoecious or dioecious; leaves alternate or opposite, simple, unifoliolate or 3–9-parted; stipules fused to petiole or 0; flowers in axillary cymes, racemes, or glomerules; sepals 4–8 or obsolete; disk intrastaminal or 0; stamens 4–50, distinct; pollen [sub]oblate, 4–7-zoniporate, rarely [*Picrodendron*] 5–8-brevicolporate or [*Androstachys*] 5–7-pantoporate, echinate; ovary 2- or 3-locular; fruit capsular or drupaceous; seeds carunculate or ecarunculate; endosperm usually copious.

This heterogeneous tribe includes 9 genera in 4 subtribes: 2 neotropical and 2 paleotropical.

The West Indian genus *Picrodendron* has been placed by some authors in a separate family Picrodendraceae because of its unusual foliage, flowers, and fruits, but the pollen indicates its membership in the Oldfieldioideae. *Androstachys*, placed in family Androstachydaceae by Airy Shaw (1965) because of its highly specialized flowers, also has pollen typical of the Oldfieldioideae. The tribal position of *Tetracoccus* would merit further inquiry; see the discussion by Stuppy (1996: 172).

Key to the Subtribes of Picrodendreae

1. Pollen grains with 4 apertures, interspinal tectum verrucate ; pistillate sepals persistent in fruit; ovary 2–5-locular; seeds carunculate **2a. Tetracoccinae**
– Pollen grains [at least in part] with 5 apertures or more; pistillate sepals persistent or deciduous; ovary 2–3-locular; seeds carunculate or ecarunculate 2
2. Stipules adnate to petiole and persistent, or intrapetiolar-connate and deciduous; pollen grains with

interspinal tectum psilate; seeds ecarunculate **2b. Mischodontinae**

– Stipules distinct, deciduous or 0; interspinal tectum baculate or verrucate; seeds carunculate or ecarunculate 3

3. Leaves alternate; staminate sepals distinct; capsule septicidal or indehiscent **2e. Picrodendrinae**

– Leaves alternate or more often opposite or whorled; staminate sepals connate; capsule loculicidal 4

4. Leaves digitately foliolate; stamen filaments as long as or longer than anthers **2c. Paivaeusiinae**

– Leaves simple, whorled [at least in part]; filaments shorter than anthers **2d. Hyaenanchinae**

2a. Subtribe Tetracoccinae G. Levin (1994).

Dioecious; inflorescences racemoid or paniculate; stamens 5–10, distinct; pollen grains 4-zoniporate; ovary 2–5-locular; fruit capsular.

A monogeneric North American subtribe.

61. *Tetracoccus* Engelm. ex Parry

Tetracoccus Engelm. ex Parry, W. Amer. Sci. 1: 13 (1885); Croizat, Bull. Torrey Bot. Club 69: 456 (1942); Dressler, Rhodora 56: 49 (1954), rev.
Halliophytum I.M. Johnston (1923).

Dioecious shrubs; indumentum simple. Leaves alternate, opposite or whorled, 1-veined or pinnately veined, entire or dentate; stipules 0. Staminate inflorescences axillary, racemoid or paniculate, sometimes fasciculate; pistillate flowers axillary, solitary or clustered. Staminate flowers pedicellate; petals 0; sepals 4–10, filaments distinct, exserted; anthers extrorse, dehiscing longitudinally; pollen grains spheroidal, zono-4-porate, echinate; disk [pistillode?] intrastaminal, ± lobed. Pistillate flowers pedicellate; petals 0; sepals 5–13, imbricate, persistent in fruit; disk lobed; ovary (2)3–4(5)-locular, ovules anatropous; stylodia distinct, unlobed. Fruits capsular; columella persistent. Seeds carunculate; testa smooth, shiny, blackish, exotegmen tracheoidal; endosperm copious; embryo straight, green; cotyledons flat, much longer and broader than radicle.

Five spp., North America, in deserts of California, Arizona, and northern Mexico.

2b. Subtribe Mischodontinae Müll. Arg. (1865).

Androstachydaceae Airy Shaw (1965).

Monoecious or dioecious; leaves simple or 3–7-foliolate; stipules persistent and adnate to petiole or intrapetiolar-connate; pollen 5–8-zonoporate [*Androstachys* pantoporate]; stylodia ± connate.

This subtribe of 5 genera is African/Madagascan in distribution, except for *Mischodon* in Ceylon.

Key to the Genera of Mischodontinae

1. Staminate "flowers" of 30–50 solitary stamens allegedly spirally arranged on an elongated column; stylodia connate into a common style with distal style branches 2

– Staminate flowers compact, with 6–25 stamens and the filaments in 1 or 2 whorls; stylodia distinct or basally connate 3

2. Stipules discrete, adnate to petiole; leaves 3–7-foliolate, leaflets pinnately veined; pollen grains zonoporate **66. *Stachyandra***

– Stipules connate, free from petiole; leaf blade simple, palmately veined; pollen grains pantoporate **65. *Androstachys***

3. Leaves alternate, 1–3-foliolate; staminate disk 0; pistillode + **62. *Aristogeitonia***

– Leaves opposite or whorled, simple; staminate disk and/or pistillode 0 4

4. Staminate disk 0, pistillode +; pistillate sepals deciduous **63. *Mischodon***

– Staminate disk +; pistillode 0; pistillate sepals accrescent in fruit **64. *Voatamalo***

62. *Aristogeitonia* Prain

Aristogeitonia Prain, Kew Bull. Misc. Inf. 1908: 338 (1908); Hook. Icon. Pl. 30: t. 2926 (1911); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 118 (1987).
Paragelonium Leandri (1939).

Dioecious or monoecious trees or shrubs; indumentum simple. Leaves long-petiolate, 1–3-foliolate, leaflets entire; stipules subulate, adnate to petiole. Inflorescences axillary, ± ramiflorous, in glomerules. Staminate flowers pedicellate; sepals 6, distinct, biseriate, imbricate; petals and disk 0; stamens 11–15, filaments distinct; anthers extrorse, dehiscing longitudinally; pollen grains oblate spheroidal, 5–7-zono-brevicolporate, exine echinate, microperforate; pistillode lobed. Pistillate flowers pedicellate, sepals 6, distinct, biseriate, imbricate, deciduous; petals 0; disk annular, somewhat lobed; ovary 3-locular, slightly pubescent; stylodia short, flat, ± stigmatiform. Fruits capsular, septicidal; columella not persistent. Seeds 1 or 2 per locule; testa shiny, 3–5 cell layers thick, ecarunculate; endosperm copious; embryo straight, cotyledons much longer and broader than radicle.

Seven spp., disjunct in Angola, Kenya/Tanzania, one of them in Madagascar.

63. *Mischodon* Thwaites

Mischodon Thwaites, Hook. J. Bot. Kew Gard. Misc. 6: 299 (1854); Raju, J. Econ. Tax. Bot. 5: 165 (1984); Philcox, Rev. Handb. Fl. Ceylon 11: 267 (1997).

Dioecious trees; indumentum simple. Leaves whorled, simple, entire; stipules minute, adnate to petiole, deciduous [sometimes obsolete]. Inflorescences axillary, paniculate [pistillate ± reduced to glomerules]. Staminate flowers pedicellate; sepals 5–8, distinct, imbricate; petals 0; disk 0; stamens usually 6(5–10), filaments distinct, exserted; anthers extrorse, dehiscing longitudinally; pollen grains spheroidal, 5–7-brachycolporate, echinate; pistillode 3-lobed. Pistillate flowers subsessile but pedicels elongating and thickened in fruit; sepals 6, distinct, imbricate, deciduous in fruit; petals 0; disk annular; ovary 3- or 4-locular, glabrous; stylodia stigmatiform. Fruits capsular, thin-walled; columella persistent. Seeds with smooth shiny testa; exotegmen 1-layered; endosperm copious; embryo straight, cotyledons much longer and broader than radicle. $n = 24$.

A single sp., *M. zeylanicus* Thwaites, restricted to Ceylon and southern India.

64. *Voatamalo* Capuron ex Bosser

Voatamalo Capuron ex Bosser, Adansonia II, 15: 333 (1976); Radcl.-Sm., Gen. Euphorb.: 108 (2001).

Dioecious trees; indumentum 0 or very sparse. Leaves opposite, simple; stipules intrapetiolar, connate, deciduous. Inflorescences axillary, cymose. Staminate flowers pedicellate; sepals 6 (7), biseriate, distinct, imbricate; petals 0; disk irregularly lobed, partly intrastaminal; stamens 9–14, filaments distinct, exserted; anthers extrorse; dehiscing longitudinally; pollen grains spheroidal, 5- or 6-zonoporate; sexine echinate, microperforate; pistillode 0. Pistillate flowers pedicellate; sepals 6, biseriate, distinct, imbricate, persistent in fruit; petals 0; disk annular; ovary 3–5-locular; stylodia connate in lower half, unlobed, distally dilated. Fruits capsular; columella persistent. Seeds carunculate.

Two spp., endemic to Madagascar, said by Bosser to be related to *Austrobuxus*; however, he also compared *Voatamalo* with *Androstachys*. The distinctive intrapetiolar stipules strongly support a relationship with *Androstachys* and *Stachyandra*.

65. *Androstachys* Prain Fig. 17

Androstachys Prain, Kew Bull. Misc. Inf. 1908: 438 (1908); Airy Shaw, Adansonia II, 10: 519 (1970); J.-F. Leroy, C.R. Acad. Sci. D 283: 147 (1976); Radcl.-Sm., Fl. Zambesiaca 9 (4): 120, t. 20 (1996).

Dioecious trees; indumentum simple. Leaves opposite, simple or 3–7-foliolate; stipules intrapetiolar, connate, sheathing, deciduous. Inflorescences axillary; the staminate ones in triad of elongate spikes; pistillate flowers solitary. Staminate flowers subtended by 3–5 distinct, narrow sepals; petals and disk 0; stamens 30–50, allegedly spirally but probably not so inserted on an elongate "receptacle" probably formed by connation of the filaments; anthers extrorse, elongated, connective setose, dehisicing longitudinally; anther connective hispidulous; pollen grains spheroidal, pantoporate; exine echinate; pollen grains spheroidal, 5–7-pantoporate, echinate; pistillode 0. Pistillate flowers pedicellate; sepals 5 or 6, lanceolate, distinct, imbricate, deciduous or persistent in fruit; petals 0; disk 0; ovary 3(−5)-locular; stylodia connate into a long columnar style; stylar branches unlobed. Fruits capsular, depressed-globose; endocarp thin and crustaceous; columella persistent. Seeds 2 per locule, carunculate or not; testa smooth and shiny, 4 or 5 cell layers thick, exotegmen uniseriate; endosperm copious; embryo green, cotyledons much longer and broader than radicle.

One sp., *A. johnsonii* Prain, Madagascar and southeast Africa.

In *Androstachys* and *Stachyandra*, the male flowers are usually interpreted as possessing numerous stamens spirally inserted on an elongated column (Radcliffe-Smith 2001), but from the morphological point of view this is unlikely in the extreme, because flowers with numerous spirally arranged stamens on elongate floral axes are unknown in the higher eudicots. It is likely that the androecia of these probably anemophilous plants simply have strongly developed androecia but are not catkin-like pseudanthia, as probably erroneously assumed by Airy Shaw (1965) and Leroy (1976). In all other characters, including the characteristic stipules, fruits and seeds, the two genera agree perfectly with the rest of the subtribe, and there is no need for an elevated taxonomic status.

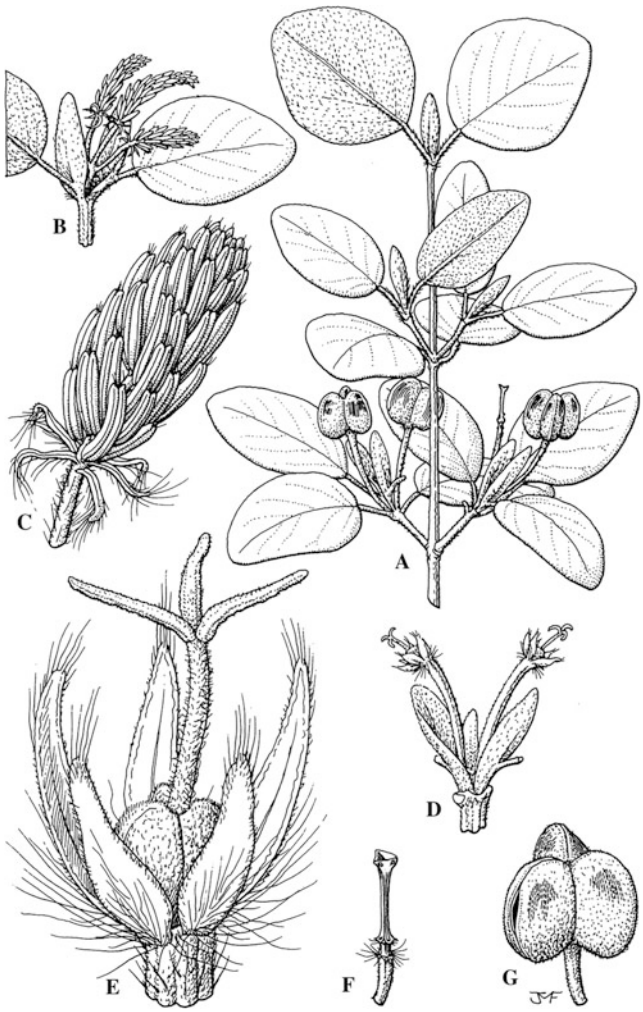

Fig. 17. Euphorbiaceae-Oldfieldioideae. *Androstachys johnsonii*. **A** Distal portion of fruiting branch. **B** Staminate inflorescence. **C** Staminate flower. **D** Pistillate inflorescence. **E** Pistillate flower. **F** Columella. **G** Fruit. (Radcliffe-Smith 1996; drawn by J.M. Fothergill)

66. *Stachyandra* Leroy ex Radcl.-Sm.

Stachyandra Leroy ex Radcl.-Sm., Kew Bull. 45: 562 (1990).

Dioecious trees; indumentum simple. Leaves opposite, 3–7-foliolate; leaflets pinnately veined, entire; stipules intrapetiolar, laterally connate, sheathing, caducous. Inflorescences and staminate floral structures as in *Androstachys*; pollen grains spheroidal, 4–7-zonoporate; exine echinate. Pistillate flowers pedicellate; sepals 6, verticillate, persistent in fruit; disk 0; ovary 3-locular; stylodia connate into a columnar style; tips unlobed. Fruits capsular; apiculate; columella persistent. Seeds 2 per locule, carunculate, testa smooth.

Four spp., endemic to Madagascar. Closely related to *Androstachys* and combined with it by Schatz (2001) on the basis of the close resemblance in floral morphology.

2c. Subtribe Paivaeusinae Pax & K. Hoffm. (1922).

Dioecious; leaves alternate, opposite, or in whorls, long-petiolate, digitately 3–8-foliate, entire; stipules 0; exotegmen 1 or 4–5 cell layers thick.

A single African genus.

67. *Oldfieldia* Benth. & Hook. f. Fig. 18

Oldfieldia Benth. & Hook. f., Hook. J. Bot. Kew Gard. Misc. 2: 184, t. 6 (1850); Pax & K. Hoffm., Pflanzenr. IV, 147: 297 (1922); Léonard, Bull. Jard. Bot. État 26: 338 (1956); Radcl.-Sm., Fl.Trop. E. Afr., Euphorb. 1: 114, t. 21 (1987), Fl. Zambesiaca 9(4): 117, t. 19 (1996).
Paivaeusa Welw. ex Benth. (1867).

Dioecious trees or shrubs; indumentum simple. Leaves alternate, opposite or in whorls of 3, long-petiolate, digitately 3–8-foliolate; leaflets entire; stipules 0. Inflorescences axillary, staminate cymose, ± densely congested, pistillate 1–3-flowered. Staminate flowers pedicellate or subsessile; sepals 5–8, basally connate, imbricate; petals 0; disk intrastaminal; stamens 4–12, filaments distinct, exserted, inserted between lobes of disk; anthers extrorse, dehiscing longitudinally; pollen spheroidal, 5–8-zoniporate or brachycolporate, echinate; pistillode small or 0. Pistillate flowers pedicellate in fruit; sepals 5–8, imbricate, persistent in fruit; petals 0; disk annular; ovary 2- or 3-locular; stylodia unlobed, apically dilated. Fruits capsular, tardily loculicidally dehiscent; columella persistent. Seeds 1 or 2/locule, carunculate, testa fleshy; exotegmen 4 or 5 cell layers thick; endosperm copious; embryo green, cotyledons flat, much longer and broader than radicle.

Four spp., tropical Africa. Stuppy (1996) has questioned the position of *Oldfieldia* in the Oldfieldioideae—and indeed in the Euphorbiaceae—because of its aberrant fruits and seeds. However, the spinose pollen as well as the anatomical and molecular data do not provide any reason to remove *Oldfieldia* from the Euphorbiaceae.

2d. Subtribe Hyaenanchinae Baill. ex Müll. Arg. (1865).

Dioecious; disk 0; pollen grains 6- or 7-zonoporate; stylodia elongated, dilated; seeds carunculate.

A single genus endemic to the Cape region.

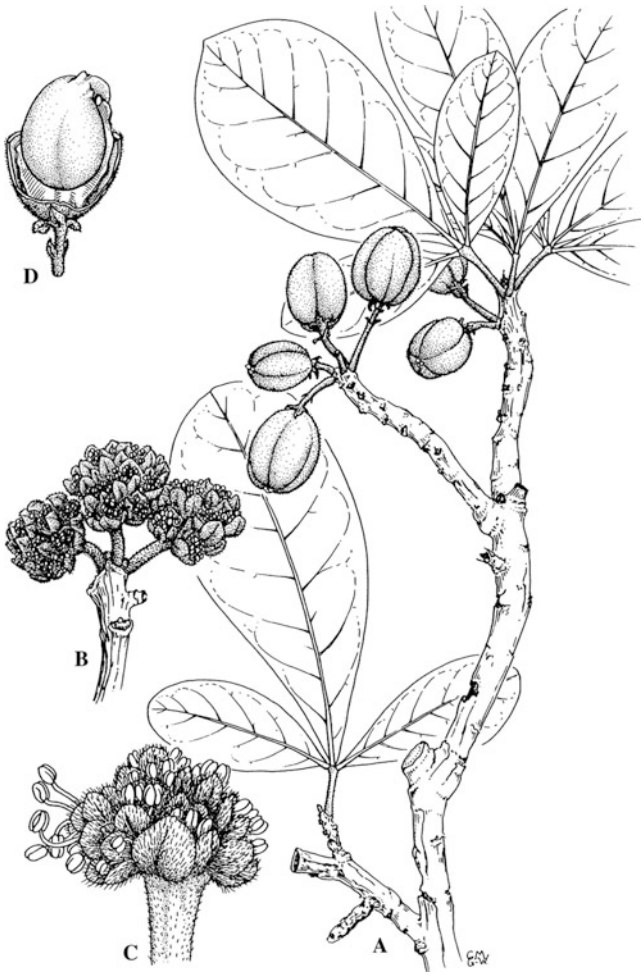

Fig. 18. Euphorbiaceae-Oldfieldioideae. *Oldfieldia dactylophylla*. **A** Fruiting branch. **B** Staminate inflorescence. **C** Staminate flowers. **D** Fruit, partly cut away to show attachment of seed. (Radcliffe-Smith 1987; drawn by Christine Grey-Wilson)

68. *Hyaenanche* Lamb.

Hyaenanche Lamb., Descr. *Cinchona*: 52, t. 10 (1797); Müll. Arg. in DC., Prodr. 15(2): 479 (1866); Connell, Fl., Pl. S. Afr. 21: t. 837 (1941); Dyer, Gen. S. Afr. Pl. 1: 311 (1975); Radcl.-Sm., Gen. Euphorb.: 89 (2001).
Toxicodendrum Thunb. (1796); non *Toxicodendron* P. Miller (1754).

Dioecious shrubs; indumentum simple [inflorescences only]. Leaves opposite or in whorls of 4, simple, entire; stipules 0. Inflorescences axillary, in glomerules or panicles. Staminate flowers pedicellate; sepals 4–8(−12), basally connate; petals 0; disk 0; stamens 8–30, filaments distinct, shorter than anthers, inserted on a convex receptacle; anthers introrse to extrorse, dehiscing longitudinally; pollen oblate, 6–8-zoniporate, echinate; pistillode 0. Pistillate flowers pedicellate; sepals 3–8, distinct, deciduous in fruit; petals 0; ovary 3–4-locular, sericeous; stylodia elongated, ± dilated. Fruit capsular; columella persistent. Seeds carunculate, caruncule subterminal, hypostase subbasal; testa black, shiny, exotegmen 1 cell layer thick; endosperm copious, embryo green, somewhat bent, cotyledons much longer and broader than radicle.

A single sp., *H. globosa* (Gaertn.) Lamb. & Vahl, Cape region of South Africa. The molecular data (Wurdack et al. 2004) show *Hyaenanche* out of place among the Old World genera of Caletieae, where it had been accommodated, and suggest a place close to *Oldfieldia*, from which it differs in, among other things, its entire, whorled leaves.

2e. Subtribe Picrodendrinae (Small) G.L. Webster (1994).

Dioecious; leaves simple [unifoliolate] or digitately 3-foliolate; pollen 5–8-porate or brevicolporate, echinate; fruit capsular or drupaceous.

This subtribe of three neotropical genera represents the Picrodendraceae of Small (s. str.).

Key to the Genera of Picrodendrinae

1. Leaves simple [unifoliolate], subsessile; pistillate disk 6-lobed **70. *Parodiodendron***
– Leaves mostly 3–5-foliolate, long-petiolate 2
2. Fruits capsular; ovary 3-locular; staminate flowers pedicellate, in spiciform thyrses; disk intrastaminal **71. *Piranhea***
– Fruits indehiscent; ovary 2-locular; staminate flowers sessile or subsessile, in catkins; disk 0 **69. *Picrodendron***

69. *Picrodendron* Planch.

Picrodendron Planch., Hook. London J. Bot. 5: 579 (1846; nom. cons.); Fawcett & Rendle, J. Bot. 55: 268 (1917); Correll, Fl. Bahama Arch. 410, t. 165 (1982); Hayden et al., J. Arnold Arb. 65: 109, t. 1, 2 (1984); M.I. Hakki, Bot. Jahrb. 107: 379 (1985); Radcl.-Sm., Gen. Euphorb.: 103 (2001).

Dioecious (monoecious) trees; indumentum simple. Leaves long petiolate, 3-foliolate, leaflets entire; stipules rudimentary, deciduous. Staminate inflorescences axillary, spicate, catkin-like, flowers 1 per bract; pistillate flowers solitary. Staminate flowers sessile or subsessile; perianth apparently 0; stamens subtended by (1–)3(−7) bracts; disk 0;

stamens (3–)10–15(−55), filaments inserted on convex receptacle, shorter than anthers; anthers slightly extrorse, basifixed, apically puberulent, dehiscing longitudinally; pollen oblate, 5–8-zonibrevicolporate, echinate; pistillode 0. Pistillate flowers long-pedicellate; sepals [bracts?] 4 or 5, valvate, mostly persistent in fruit; petals 0; disk 0; ovary 2-locular, ovules anatropous; stylodia connate c. halfway, distal branches lanceolate, revolute. Fruits drupaceous; exocarp with vesicles. Seeds usually 1 per fruit, labyrinthic, with invaginations of the tegmen into the endosperm that coats the plications of the cotyledons.

One sp., *P. baccatum* (L.) Krug & Urb., endemic to the Greater Antilles, Bahamas, Cayman Islands, and Swan Islands. Stuppy (1996) provided the first correct analysis of the labyrinthic seed of *Picrodendron* and pleaded for its exclusion from Euphorbiaceae, but the anatomical data summarized by Hayden et al. (1984), the typically Oldfieldioid pollen grains, and the molecular data (Wurdack 2002) argue strongly for a position of *Picrodendron* in Oldfieldioideae.

70. *Parodiodendron* Hunz.

Parodiodendron Hunz., Kurtziana 5: 331, t. 1–3 (1969); Radcl.-Sm., Gen. Euphorb.: 102 (2001).

Dioecious trees; wood with septate fibers; indumentum simple. Leaves unifoliolate, subsessile, entire; stipules deciduous; apex of petiole with a pair of minute stipels. Inflorescences axillary, staminate flowers in glomerules, the pistillate solitary. Staminate flowers pedicellate; sepals (5)6(−9), distinct, imbricate; petals 0; disk intrastaminal; stamens 13–19, filaments distinct, inserted in glandular disk, exserted beyond calyx; anthers extrorse, dehiscing longitudinally; pollen grains spheroidal, 6–8-zonoporate, echinate, tectum smooth; pistillode 0. Pistillate flowers pedicellate; sepals 6, biseriate, imbricate, foliose, deciduous; petals 0; disk annular, 6-lobed; ovary 3-locular; stylodia basally connate, short, unlobed, recurved. Fruits capsular, spheroidal; columella persistent. Seeds 1 or 2/locule; hilum subterminal; testa smooth, 5 or 6 cell layers thick, exotegmen 1-layered; endosperm copious; embryo straight, cotyledons flat, much longer and broader than radicle.

One sp., *P. marginivillosum* (Speg.) Hunz., Bolivia and northern Argentina. The minute acropetiolar stipels and the often disarticulated petioles (Hayden 1994: 183) suggest that the leaves are unifoliolate.

71. *Piranhea* Baill.

Piranhea Baill., Adansonia 6: 235 (1866); Jablonski, Mem. New York Bot. Gard. 17: 121 (1967); Radcl.-Sm. & Ratter, Kew Bull. 51: 543 (1996), rev.
Celaenodendron Standl. (1927).

Dioecious trees or shrubs; indumentum simple. Leaves 3-foliolate, long-petiolate; leaflets entire; stipules deciduous. Inflorescences axillary, staminate flowers in spiciform thyrses, pistillate flowers solitary or in racemoid thyrses. Staminate flowers pedicellate; sepals 4–6, distinct, imbricate; petals 0; disk intrastaminal, lobed; stamens (3–)6–15, filaments distinct; anthers introrse, dehiscing longitudinally; pollen grains ± spheroidal, 6-zonoporate, echinate; pistillode 0. Pistillate flowers subsessile to long-pedicellate; sepals 4–6, biseriate, imbricate, persistent or deciduous in fruit; petals 0; disk divided into subulate lobes; ovary 3-locular; stylodia unlobed, recurved. Fruits capsular, 3-angled; columella persistent. Seeds 1 per locule, ecarunculate, testa smooth; endosperm copious; embryo straight, cotyledons flat, much longer and broader than radicle.

Four neotropical spp., 3 from Brazil, 1 from western Mexico.

3. Tribe Caletieae Müll. Arg. (1865).

Dioecious or monoecious; staminate sepals 4–8(−13); stamens 4–30; pollen grains spheroidal, zonoporate or pantoporate, exine echinate; pistillate sepals 3–8(−13); seeds carunculate or ecarunculate; endosperm usually copious.

This is the largest tribe of Oldfieldioideae, with 14 genera in 4 subtribes. It is entirely Old World in distribution, confined to Australia and neighboring Melanesia.

Key to the Subtribes of Caletieae

1. Pollen grains pantoporate; capsule dry; cotyledons as broad as or broader than radicle **3b. Pseudanthinae**
– Pollen grains zonoaperturate; capsule dry or fleshy; cotyledons broader than radicle; trees or shrubs 2
2. Leaves opposite; stamens distinct; anthers not apiculate; pistillate sepals persistent in fruit; capsule dry **3c. Dissilariinae**
– Leaves alternate; stamens connate; anthers apiculate; pistillate sepals deciduous; capsule fleshy **3a. Petalostigmatinae**

3a. Subtribe Petalostigmatinae Pax & K. Hoffm. (1922).

Dioecious; stamens 18–40 or more, filaments connate; pollen oblate, 5- or 6- zonoporate, breviechinate; stylodia petaloid-dilated; fruits capsular; seeds carunculate.

A monogeneric Australasian subtribe.

72. *Petalostigma* F. Muell.

Petalostigma F. Muell., Hook. J. Bot. Kew Gard. Misc. 9: 16 (1857); Airy Shaw, Kew Bull. 35: 661 (1980); Forster & van Welzen, Blumea 44: 104–107 (1999).

Dioecious trees or shrubs; indumentum simple. Leaves simple, entire; stipules deciduous. Inflorescences axillary, glomerular. Staminate flowers pedicellate; sepals 4, distinct, imbricate; petals 0; disk 0; stamens 18–85, filaments basally connate into a column; anthers extrorse, dehiscing longitudinally; pollen grains globose, 5- or 6-porate, breviechinate; exine psilate-striate; pistillode usually 0. Pistillate flowers pedicellate, sepals 4–6, imbricate, deciduous; disk 0; ovary (3)4-locular, ovules anatropous; stylodia entire, dilated, petaloid. Fruits capsular, exocarp ± fleshy; columella slender, persistent. Seeds somewhat compressed, carunculate; testa smooth, mostly 4 cell layers thick; endosperm copious; embryo straight, cotyledons flat, much longer and broader than radicle.

Five spp., Australia, one of these reaching eastern New Guinea (Papua). The pollen of *Petalostigma* was found to be close to that of *Hyaenanche* (Köhler 1965), while Stuppy (1996) regards the seed structure as suggesting an affinity with subtribe Pseudanthinae. In the analyses of Levin and Simpson (1994), *Petalostigma* appears as the sister group to subtribe Pseudanthinae and in the analyses of Wurdack et al. (2004) as sister to the rest of tribe Caletieae.

3b. Subtribe Pseudanthinae Müll. Arg. (1865).

Monoecious (dioecious) trees, shrubs, or herbs; stamens 3–20; pollen pantoporate. $x = 12$.

An Australasian subtribe of six genera.

Key to the Genera of Pseudanthinae

1. Fruit 1-locular and 1-seeded by abortion 2
– Fruit (2)3-locular with all locules fertile 3
2. Stamens 3–6, ± distinct; staminate flowers with central disk **77. *Pseudanthus***
– Stamens (7–)10–50, variously connate; staminate flowers without central disk **78. *Stachystemon***
3. Stipules foliaceous, appearing as if 2 further leaves per node **76. *Micrantheum***
– Stipules not foliose 4
4. Leaves caudate-acuminate; staminate sepals 4; stamens 10–12 **73. *Kairothamnus***
– Leaves not caudate-acuminate; staminate sepals 4–7; stamens 4–6 5
5. Ovules 1/locule; pistillode columnar; pistillate sepals deciduous in fruit **75. *Scagea***
– Ovules 2/locule; pistillode replaced by intrastaminal disk; pistillate sepals persistent **74. *Neoroepera***

73. *Kairothamnus* Airy Shaw

Kairothamnus Airy Shaw, Kew Bull. 34: 596 (1980), Kew Bull. Add. Ser. 8: 121 (1980); Radcl.-Sm., Gen. Euphorb.: 97 (2001).

Dioecious trees or shrubs; indumentum simple. Leaves alternate; stipules deciduous. Inflorescences axillary, thyrsoid. Staminate flowers pedicellate; sepals 4, distinct, imbricate; petals 0; disk annular; stamens 10–12, filaments distinct, inserted in convex receptacle; anthers extrorse, dehiscing longitudinally; pollen grains 10–12-pantoporate, echinate, tectum granular; pistillode 0. Pistillate flowers pedicellate; sepals 6 , biseriate, distinct, dorsally carinate, deciduous; petals 0; disk 0; ovary 3-locular, strigose; stylodia stigmatoid, ovate. Fruit capsular, stigmas persistent at apex. Seeds ecarunculate, testa dark and smooth, with 2- or 3-cell layers; endosperm copious; embryo straight, cotyledons flat, much longer and broader than radicle.

One sp., *K. phyllanthoides* (Airy Shaw) Airy Shaw, eastern New Guinea.

74. *Neoroepera* Müll. Arg. & F. Muell.

Neoroepera Müll. Arg. & F. Muell. in DC., Prodr. 15(2): 488 (1866); Airy Shaw, Kew Bull. 35: 658, t. 5, A1–4 (1980); Henderson, Austrobaileya 3: 618, figs. 1–3 (1992); 81: 59 (1994).

Monoecious arborescent shrubs; indumentum simple. Leaves short-petiolate; stipules minute or obsolete. Inflorescences of axillary glomerules, the pistillate flowers often solitary. Staminate flowers pedicellate; sepals (4–)6(−8), biseriate, distinct, imbricate; petals 0; stamens mostly 5 or 6, filaments distinct; anthers extrorse, dehiscing longitudinally; pollen grains spheroidal, 16–25-pantoporate, sexine echinate, tectum granular or psilate; pistillode replaced by central

intrastaminal disk. Pistillate flowers pedicellate, sepals usually 6, biseriate, distinct, persistent in fruit; petals 0; disk annular, lobed; ovary 3-locular; ovules 2/locule; stylodia proximally connate, spreading. Fruits capsular. Seeds carunculate, testa smooth and shiny or minutely pitted, 2 cell layers thick; endosperm copious; embryo straight, cotyledons much broader and longer than radicle.

Two spp., Australia (Queensland).

75. *Scagea* McPherson

Scagea McPherson, Bull. Mus. Nat. Hist. Nat. Paris, IV B Adansonia 7: 247 (1985); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 90, t. 18 (1987); Radcl.-Sm., Gen. Euphorb.: 97 (2001).

Monoecious trees or shrubs; indumentum simple. Leaves short-petiolate; stipules deciduous. Inflorescences axillary, racemoid, unisexual or bisexual. Staminate flowers pedicellate; sepals (5)6(−7), distinct, imbricate; petals 0; disk 0; stamens 4–6, filaments distinct, shorter than anthers; anthers extrorse, dehiscing longitudinally; pollen grains spheroidal, 16–20-pantoporate, echinate, tectum rugulose, granular; pistillode usually present. Pistillate flowers pedicellate; sepals 6, distinct, imbricate, deciduous; petals 0; disk segments 3; ovary 3-locular, pubescent; ovules anatropus, 1/locule; stylodia short, erect, thick. Fruit capsular; columella persistent, distally enlarged. Seeds carunculate, testa smooth, 3 or 4 cell layers thick, exotegmen uniseriate; endosperm copious; embryo green, cotyledons flat, much longer and broader than radicle.

Two spp. endemic to New Caledonia, originally described in the Crotonoideae because of the (secondarily) uniovulate carpels. However, the pollen is typical for Oldfieldioideae.

76. *Micrantheum* Desf.

Micrantheum Desf., Mém. Mus. Hist. Nat. Paris 4: 253, t. 14 (1818); Grüning, Pflanzenr. 147, XV: 21 (1913); Jeanes, Fl. Victoria 4: 70 (1999); Radcl.-Sm., Gen. Euphorb.: 98 (2001).

Monoecious ericoid shrubs or subshrubs; indumentum simple. Leaves pseudo-3-foliate [the stipules as large as the lamina], 1-veined. Inflorescences of axillary glomerules, pistillate flowers often solitary. Staminate flowers pedicellate; sepals 4 or 6, biseriate, distinct, imbricate; petals 0; disk 0; stamens 3–6(−9), filaments distinct; anthers extrorse, dehiscing longitudinally; pollen grains prolate-spheroidal, panto[30–40]-porate, pores prominently marginate, exine echinate, tectum granular; pistillode glandular, lobed. Pistillate flowers pedicellate or subsessile; sepals 4–6, distinct, imbricate, persistent in fruit; petals 0; disk + or 0; ovary 2- or 3-locular; ovules anatropous, 2/locule; stylodia connate at the base, unlobed. Fruits capsular; columella persistent. Seeds 1/locule, carunculate, testa smooth, 2 cell layers thick, exotegmen uniseriate; endosperm copious; embryo green, straight, cylindric, cotyledons longer than radicle.

Three spp., endemic to Australia. The leaves interpreted by Grüning and Jeanes as ternate clusters seem more plausibly interpreted as spirally arranged leaves with foliose stipules.

77. *Pseudanthus* Sieber ex Spreng. Fig. 19

Pseudanthus Sieber ex Spreng., Syst. Veg. 4(2): 22, 25 (1827); Halford & Henderson, Austrobaileya 6: 497–532 (2003), rev.

Pseudanthus Sieber ex Spreng. sect. *Pseudanthus*

Monoecious ericoid shrubs; branchlets longitudinally ridged by decurrent margins of stipules along internodes; indumentum simple, sparse or 0. Leaves alternate or opposite, margins entire and thickened; petioles short; stipules persistent. Flowers in upper leaf axils solitary or 2 or 3; distal branchlet internodes often contracted to produce terminal flower clusters. Staminate flowers pedicellate; sepals (5)6, distinct; petals 0; disk 0; stamens (3–)6, filaments distinct; anthers dehiscing longitudinally; pollen grains spheroidal, panto(6–)10–14(−25)-porate, brevi-echinate, exine granular; disk generally 3-lobed, fleshy. Pistillate flowers sessile or subsessile; sepals (4–)6, distinct, persistent in fruit; petals 0; disk 0; ovary (2)3-locular; ovules (1)2/locule, anatropous; stylodia connate at the base or to about halfway into a style, the stigmatic branches undivided. Fruits capsular, unilocular by suppression, 1-seeded; splitting at maturity into 3 bivalved segments. Seed solitary, carunculate, testa smooth, 2 cell layers thick, exotegmen uniseriate; endosperm copious; embryo cylindric, cotyledons a little broader than radicle.

Nine spp., eastern Australia.

78. *Stachystemon* Planch.

Stachystemon Planch., Hooker's Lond. J. Bot. 4: 471, t. 15 (1845); Halford & Henderson, Austrobaileya 6: 497–532 (2003), rev.

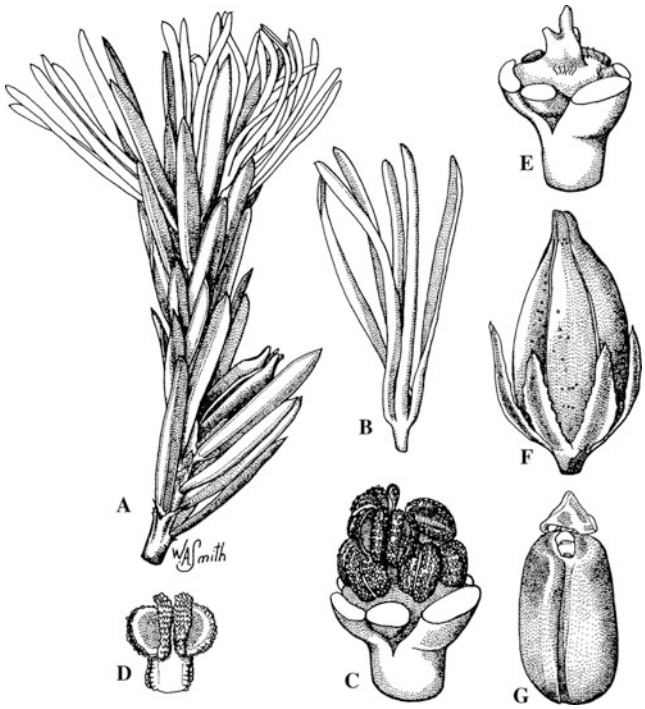

Fig. 19. Euphorbiaceae-Oldfieldioideae. *Pseudanthus ligulatus* subsp. *ligulatus*. **A** Branchlet with flowers and fruit. **B** Staminate flower from side. **C** Staminate flower with sepals removed. **D** Stamen. **E** Pistillate flower with sepals and stamens removed showing central disk. **F** Fruit with persistent sepals. **G** Carunculate seed. (Halford & Henderson 2003; drawn by W. Smith)

Monoecious shrubs; branchlets ridged by decurrent stipular margins; indumentum sparse or 0. Leaves alternate or opposite, thickened along margins; stipules persistent. Flowers few or solitary in upper leaf axils; distal branchlet internodes often contracted to produce terminal flower clusters. Staminate flowers pedicellate or rarely sessile; sepals (3)4–6(−10); receptacle hemispherical to elongated; stamens 7 to numerous; filaments variously connate or distinct, mostly bifid distally; anthers of 2 separate contiguous cells, each transverse on the apex of the filament, dehiscing longitudinally; disk 0. Pistillate flowers sessile or shortly pedicellate, sepals 4 or 6, persistent; disk 0; ovary 2(3)-locular; ovules 2/locule; stylodia 2(3), at the base shortly connate or distinct, entire. Fruit capsular, unilocular by suppression, 1-seeded, splitting at maturity into 2 (3) bivalved segments. Seeds solitary, carunculate, endosperm copious; cotyledons several times broader than radicle.

Nine spp., endemic to southwestern Western Australia.

3c. Subtribe Dissilariinae Pax & K. Hoffm. (1922).

Monoecious or dioecious; stamens 8–50, filaments distinct; pollen grains 5–7-zonoporate, echinate.

Seven Australasian genera with c. 25 species. The subtribe seems clearly monophyletic, but generic boundaries are subject to revision.

Key to the Genera of Dissilariinae

1. Dioecious 2
– Monoecious 5
2. Staminate flowers without pistillodes; seeds semielliptic in outline, laterally compressed **80. *Dissilaria***
– Staminate flowers with pistillodes; seeds globose or ovoid, not laterally compressed 3
3. Stylodia linear in outline; fruit subglobose, strongly tricoccous with remnants of stylodia widely separated **84. *Choriceras***
– Stylodia cordate-ovate in outline; fruit globose, remnants of stylodia in close proximity 4
4. Ovary 3–4-locular; seeds with arilloid caruncle **79. *Austrobuxus***
– Ovary 2-locular; seeds ecarunculate **81. *Canaca***
5. Stipules very large, conspicuous, > 8 mm long; pistillate flowers with 3 sepals; receptacle of staminate flowers glabrous **83. *Sankowskya***
– Stipules small, inconspicuous, > 8 mm long, or 0; pistillate flowers with 2+2 or 2+3 sepals; receptacle of staminate flower hairy 6
6. All flowers with glandular disk; stylodia linear in outline; stamens > 45; pollen spiny **82. *Whyanbeelia***
– All flowers without glandular disk, stylodia cordate-ovate in outline; stamens < 45; pollen smooth **85. *Longetia***

79. *Austrobuxus* Miq.

Austrobuxus Miq., Fl. Ned. Ind. Suppl.: 444 (1861); Airy Shaw, Kew Bull. 29: 303 (1974); A.C. Smith, Fl. Vitiensis Nova 2: 495 (1981); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 193, figs. 40–43 (1987); Forster, Austrobaileya 4: 619–626 (1997).
Bureavia Baill. (1873).
Choriophyllum Benth. (1879).

Dioecious (monoecious) trees or shrubs; indumentum simple. Leaves opposite, mostly entire; stipules 0. Inflorescences axillary, cymose, sometimes paniculate. Staminate flowers pedicellate; sepals 4–6, distinct, imbricate; petals 0; disk 0 or represented by convex receptacle; stamens 8–27, filaments distinct, inserted in the raised

receptacle; anthers extrorse, dehiscing longitudinally; pollen grains 6–7-zonoporate, echinate, exine between spines rugulose; pistillode 0. Pistillate flowers subsessile or pedicellate; sepals 4–6, distinct, imbricate, persistent in fruit; petals 0; disk cupular or 0; ovary 3(4)-locular; stylodia very short, dilated, stigmatiform. Fruits capsular; columella persistent. Seeds smooth, caruncle laciniate; testa smooth, 3 or 4 cell layers thick, exotegmen uniseriate; endosperm copious; embryo green, straight or curved, cotyledons much longer and broader than radicle.

A genus of c. 20 species, from Malaysia and Australia to New Caledonia and Fiji.

80. *Dissiliaria* F. Muell. ex Baill.

Dissiliaria F. Muell. ex Baill., Adansonia I, 7: 366 (1867); Forster, Austrobaileya 5: 9–27 (1997), rev.; Radcl.-Sm., Gen. Euphorb.: 91, fig. 10 (2001).

Monoecious or dioecious trees or shrubs; indumentum simple. Leaves opposite, entire or crenulate; stipules interpetiolar, deciduous. Inflorescences axillary, glomerular. Staminate flowers pedicellate; sepals 3+3, imbricate; petals 0; extrastaminal disk 0; stamens 8–26, filaments distinct, shorter than sepals, inserted on slightly convex receptacle; anthers dehiscing longitudinally; pollen grains 5–7-zonoporate, pores bordered; exine echinate, tectum baculate; pistillode 0. Pistillate flowers pedicellate; sepals 3+3, persistent in fruit; petals 0; disk annular; ovary 2 or 3-locular; stylodia unlobed, shortly connate at the base. Fruits capsular, dehiscing septicidally into 2 or 3 bivalved cocci. Seeds laterally compressed, carunculate; endosperm copious; cotyledons broad, flat.

Six spp., Australia (Queensland).

81. *Canaca* Guillaumin

Canaca Guillaumin, Arch. Bot. Caen 1: 74 (1927); Airy Shaw, Kew Bull. 25: 508 (1971); Radcl.-Sm., Gen. Euphorb.: 91 (2001).

Dioecious trees or shrubs; indumentum of abaxial leaf blades appressed, crystalloid, dark, partly malpighiaceous. Leaves opposite; stipules 0. Inflorescences axillary, dichasial. Staminate flowers pedicellate, sepals 4, imbricate; petals 0; disk 0; stamens (8–)15–26, filaments distinct, inserted on convex receptacle; anthers dehiscing longitudinally; pistillode 0. Pistillate flowers distinctly pedicellate; sepals 4, imbricate, persistent in fruit; petals 0; disk annular; ovary 2-locular; stylodia very short, stigmatoid. Fruits capsular, endocarp thin; columella persistent or deciduous. Seeds suborbicular, compressed tangentially, rugose, pale, ecarunculate; endosperm copious; cotyledons flat, much longer and broader than the radicle.

Seven spp., all endemic to New Caledonia. This genus was combined with *Austrobuxus* by McPherson and Tirel (1987); however, Airy Shaw (1971), who first reduced *Canaca* to synonymy, said that it "almost merits generic recognition" because of the very distinctive seeds. The distinctive indumentum and 2-locular thin-walled capsule with deciduous columella also support the generic distinctiveness of *Canaca*.

82. *Whyanbeelia* Airy Shaw & Hyland

Whyanbeelia Airy Shaw & Hyland, Kew Bull. 31: 375 (1976) and ibid. 35: 691 (1980); Hyland & Whiffin, Austral. Trop. Rain For. Trees 2: 152 (1993).

Dioecious (?) trees; indumentum simple. Leaves opposite, short-petiolate; stipules obsolete. Inflorescences axillary, cymosely paniculate. Staminate flowers pedicellate; sepals 6, biseriate, imbricate; petals 0; disk 0; stamens 50–55, inserted on the pubescent central receptacle; filaments distinct, exserted; anthers subspheroidal; pollen grains oblate, 5–6-zonoporate, echinate, interspinal tectum verrucate; pistillode 0. Pistillate flowers pedicellate; sepals 6; petals 0; disk dissected into subulate segments, glabrous; ovary 3-locular, pubescent; stylodia unlobed, recurved. Fruit capsular. Seeds carunculate, testa 4 or 5 cell layers thick, exotegmen uniseriate; cotyledons green.

A single sp., *W. terra-reginae* Airy Shaw & B. Hyland from Australia (Queensland), with the habit of *Dissiliaria*. Although the genus was first described as monoecious, Airy Shaw (1971) characterized it as dioecious.

83. *Sankowskya* P.I. Forster Fig. 20

Sankowskya P.I. Forst., Austrobaileya 4: 329, fig. 1 (1995); Radcl.-Sm., Gen. Euphorb.: 93 (2001).

Monoecious trees; indumentum simple. Leaves opposite, petiolate; stipules interpetiolar, deciduous. Inflorescences axillary, cymose, bracteate. Staminate flowers pedicellate; sepals 4, biseriate, imbricate; petals 0; disk 0; stamens 12–15, filaments distinct, inserted on convex receptacle; anthers

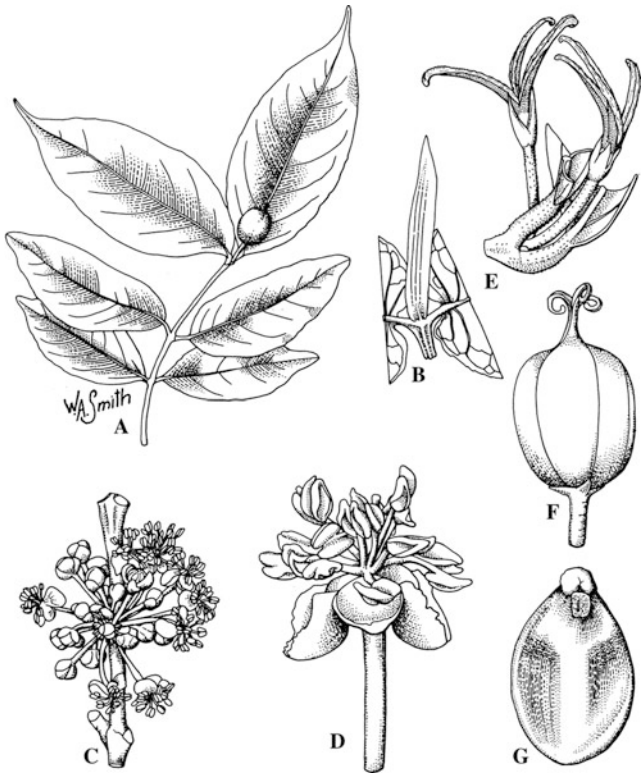

Fig. 20. Euphorbiaceae-Oldfieldioideae. *Sankowskya stipularis*. **A** Fruiting branchlet. **B** Base of leaf pair with interfoliar stipule. **C** Staminate inflorescence. **D** Staminate flower. **E** Pistillate inflorescence. **F** Fruit. **G** Carunculate seed, adaxial view. (P.I. Forster 1995; drawn by W. Smith)

extrorse, longitudinally dehiscent; pistillode 0. Pistillate flowers pedicellate; sepals 3, imbricate; petals 0; disk 0; ovary 3-locular; stylodia distinct, unlobed, papillose, recurving. Fruit capsular; endocarp thin. Seeds carunculate, testa smooth.

A single sp., *S. stipularis* P.I. Forst. from Australia, NE Queensland. Forster (1995) suggests that *Sankowskya* may be closest to *Longetia*, with which it shares smooth pollen.

84. *Choriceras* Baill.

Choriceras Baill., Adansonia I, 11: 119 (1873); Airy Shaw, Kew Bull. 35: 604 (1961), Muelleria 4: 220 (1980); Hyland & Whiffin, Austral. Rain For. Trees: 310 (1993); Forster & van Welzen, Blumea: 44: 99–101 (1999).

Monoecious trees; indumentum simple. Leaves opposite, subentire or crenulate, short-petiolate; stipules deciduous. Inflorescences axillary, cymose, unisexual or bisexual. Staminate flowers pedicellate; sepals 4–6, biseriate, imbricate; petals 0; disk 0; stamens 4–6, distinct, inserted on the pubescent central receptacle; anthers extrorse, dehiscing longitudinally; pollen grains oblate, 6-zonoporate, exine pilate-wrinkled, scabrate; pistillode small, pubescent. Pistillate flowers pedicellate; sepals 6, biseriate, imbricate; petals 0; disk of 3 segments; ovary 3(4)-locular, sericeous; stylodia distinct, undivided, recurved. Fruits capsular, apex trifid due to persistent stylodia bases; columella persistent [?], slender. Seeds 1 or 2 per locule, ecarunculate; testa smooth, 2 or 3 cell layers thick, tegmen uniseriate; endosperm copious; embryo straight, cotyledons flat, much longer and broader than radicle.

One or two spp., tropical Australia and New Guinea. Forster and van Welzen (1999) reduced *C. australiana* Benth. to synonymy. Pollen morphology indicates that the genus is closely related to *Longetia*.

85. *Longetia* Baill.

Longetia Baill., Adansonia I, 6: 352 (1866); Pax & K. Hoffmann, Pflanzenr. 147, XV: 289 (1922); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 188 (1987).

Monoecious shrubs; indumentum simple, very sparse. Leaves opposite, glabrous, simple, entire; stipules 0. Inflorescences terminal or axillary, cymose-paniculate, unisexual or bisexual. Staminate flowers pedicellate; sepals 6, imbricate; petals 0; disk 0; stamens 9–17, filaments distinct; anthers extrorse, dehiscing longitudinally; pollen grains zono(5–)6–7-brevicolporate, apertures bordered; exine rugulose, microspinulose; pistillode present. Pistillate flowers pedicellate; sepals 6, biseriate, imbricate; petals 0; disk dissected; ovary 3-locular; ovules anatropous; stylodia short, stigmatoid, stigmas emarginate. Fruit capsular, columella persistent. Seeds 1/locule, tangentially compressed, carunculate; testa smooth; endosperm copious; embryo green, straight, cotyledons flat, much longer and broader than radicle.

A single sp., *L. buxoides* Baillon, endemic to New Caledonia. Pax & Hoffmann (1922) had included several species now placed in *Austrobuxus* within *Longetia*, but the pollen is so different in the two genera that they cannot be very closely related.

III. Subfam. Peroideae Baill. & Hassk. (1859), taken up by K. Wurdack & P. Hoffmann in Amer. J. Bot. 92: 1413 (2005).

Dioecious (monoecious) trees, shrubs, or herbs; latex 0; indumentum simple, malpighiaceous, stellate, or lepidote. Leaves alternate (opposite), simple, entire; stipules + or 0. Inflorescences axillary, mostly strongly condensed, rarely [*Pera*] surrounded by involucral bracts; sepals 2–6 [in *Pera* 0 in pistillate flowers and sometimes rudimentary in staminate flowers]; petals + or 0; disk +, 0 in *Pera*; stamens 2–20; pollen prolate to oblate spheroidal, 3(4)-colporate, mostly tectate-perforate; pistillode + [0 in *Pera* but reduced pistillate flowers surrounding staminate flowers in some spp.]; ovary 3(4)-locular; stylodia bifid to bipartite; ovule 1 per locule. Fruit dehiscent (indehiscent); septa membranous, fragile, without visible vascularization. Seeds black, shiny, smooth, carunculate; seed coat with tracheoidal exotegmen [*Pogonophora* excepted]; endosperm usually copious; cotyledons longer and wider than radicle.

Four genera with about 125 spp., pantropical.

Peroideae are characterized by fruits with membranous, fragile septa without visible vascularization, and very peculiar seed coats which in *Clutia*, *Chaetocarpus* and *Pera* have a large tanniniferous exotesta and a tracheoidal exotegmen, whereas *Pogonophora*, like the cheilosoids, acalyphoids, crotonoids, and euphorbioids, has a palisadal exotegmen (Tokuoka and Tobe 2003). Therefore, the inclusion of *Pogonophora* in the Peroideae remained uncertain (Tokuoka 2007), but its inclusion in a strongly supported clade with *Pera* and *Clutia* (Xi et al. 2012) now leaves little doubt of this.

Key to the Tribes of Subfam. Peroideae

1. Staminate flowers with 5 imbricate sepals and petals; stamens 5; pollen exine tectate-perforate; indumentum simple or malpighiaceous; seeds carunculate; dioecious 2
– Staminate flowers not with 5 imbricate sepals and petals (or if so, cotyledons not broader than radicle); stamen number variable; pollen grains various 3
2. Petals adaxially barbate; filaments distinct; disk segments not glandular-lobed; seeds ecarunculate; leaves not pellucid-punctate **4. Pogonophoreae**
– Petals not adaxially barbate; filaments connate; disk segments glandular-lobed; seeds carunculate; leaves usually pellucid-punctate **1. Clutieae**
3. Flowers in axillary glomerules, not involucrate; stamens 5–15; stylodia bifid, elongated; capsule echinate; leaves stipulate **2. Chaetocarpeae**
– Flowers enclosed in involucres of bibracteolate bracts; stamens 2–6; stylodia very short, stigmatoid; capsule not echinate; leaves exstipulate **3. Pereae**

1. Tribe Clutieae (Müll. Arg.) Pax (1890).

A monogeneric tribe, containing only the African genus *Clutia*.

86. *Clutia* L.

Clutia L., Sp. Pl.: 1042 (1753); Léonard, Fl. Congo Rwa.-Bur. 8(1): 93, t. 7 (1962); Radcl.-Sm., Fl. E. Trop. Afr., Euphorb. 1: 331, fig. 63 (1987), Kew Bull. 47: 111, figs. 1–3 (1992), Fl. Zambesiaca 9(4): 123, t. 21, 22 (1996).

Dioecious (monoecious) shrubs or perennial herbs; indumentum simple or 0. Leaves alternate, entire, often pellucid-punctate; stipules small or obsolete. Flowers in axillary glomerules, the pistillate often solitary. Staminate flowers pedicellate; sepals and petals 5, distinct, imbricate; disk segments 5 or more, lobed or glandular; disk of numerous glands in 1–3 series at the base of the perianth and staminal column; stamens 5, filaments connate into a column; anthers introrse; muticous; pollen grains prolate, 3-colporate, colpi inoperculate, exine tectate-perforate/reticulate; pistillode inserted on top of staminal column. Pistillate flowers pedicellate; sepals 5, imbricate, entire, persistent in fruit; petals 5, usually persistent in fruit; disk segments 5; ovary 3 (4)-locular, glabrous or pubescent; ovules anatropous, inner and outer integuments thin, mostly 3 or 4 cell layers; stylodia distinct, bifid. Fruits capsular; columella persistent, with deciduous wings in distal half. Seeds carunculate, testa dry, mostly smooth, exotegmen tracheoidal; endosperm copious, cotyledons broader and somewhat longer than radicle.

About 75 African spp., most in South Africa, two in Arabia.

2. Tribe Chaetocarpeae (Müll. Arg.) G.L. Webster (1975).

Dioecious; indumentum simple or 0; leaves entire; flowers in axillary bracteate glomerules; sepals 4 or 5, imbricate; petals + or 0; stamens 5–15; fruits capsular; seeds carunculate, exotegmen tracheoidal.

Two genera; their close relationship is confirmed by Tokuoka (2007).

Key to the Genera of Chaetocarpeae

1. Petals +; anthers extrorse, subsessile on staminal column; ovary smooth; endosperm 0
87. *Trigonopleura*
– Petals 0; anthers introrse or latrorse, filaments well developed; ovary tuberculate or echinate; endosperm +
88. *Chaetocarpus*

87. *Trigonopleura* Hook. f.

Trigonopleura Hook. f., Fl. Brit. Ind. 5: 399 (1887), Icon. Pl. 18: t. 1753 (1888); Pax & K. Hoffm., Pflanzenr. 147, III: 95, fig. 30 (1911); van Welzen et al., Blumea 40: 363–374, fig. 2 (1995).

Dioecious trees; indumentum simple, scale-like on young growth. Leaves simple, petiolate [petiole adaxially sulcate], entire; stipules deciduous. Flowers in axillary glomerules, the staminate multiflowered, the pistillate 1–3-flowered; bracts minute. Staminate flowers pedicellate, articulate at or above the middle; sepals 5, coriaceous, imbricate, distinct; petals (4) 5, distinct, valvate, pubescent; disk segments 5, erect; stamens (5–) 8–15, biseriate, filaments connate into a column; 5 anthers of lower whorl subsessile on column, 3 upper anthers ± equaling filaments; anthers extrorse; apiculate; pollen grains subprolate, 3-colporate, colpi inoperculate, exine tectate-punctate, tectum psilate; pistillode adnate to staminal column, apically trifid. Pistillate flowers pedicellate, pedicels mid-articulate; sepals 5, imbricate, entire, deciduous in fruit; disk-segments 5; ovary 3-locular, tomentose; stylodia distinct, erect, bipartite, adaxially papillose. Fruits capsular, subglobose, tomentose, carinate-angled, ± reticulate-venose; columella persistent, translucent-winged. Seeds carunculate, the fleshy caruncle partially covering testa; exotegmen tracheoidal, mesotesta vascularized; hilum lobed; endosperm 0.

Three spp., Malay Peninsula and Sumatra to the Philippines and Borneo. According to Nowicke et al. (1998), the pollen of *Trigonopleura* is different from that of *Chaetocarpus*. Although the seeds of *Trigonopleura* are exalbuminous, the genus is resolved as sister to *Chaetocarpus* (Tokuoka 2007).

88. *Chaetocarpus* Thwaites Fig. 21

Chaetocarpus Thwaites, Hook. J. Bot. Kew Gard. Misc. 6: 300, t. 10a (1854); Léonard, Fl. Congo Rwa.-Bur. 8(1): 127, fig. 8 (1962); Capuron, Adansonia II, 12: 209–211, t. 2 (1972); Alves, An. Jard. Bot. Madrid 51: 302 (1994); van Welzen, Rheedea 4: 93, fig. 1 (1994); Philcox, Fl. Ceylon 11: 177 (1997); Radcl.-Sm., Fl. Zambesiaca 9(4): 135, t. 23 (1996).

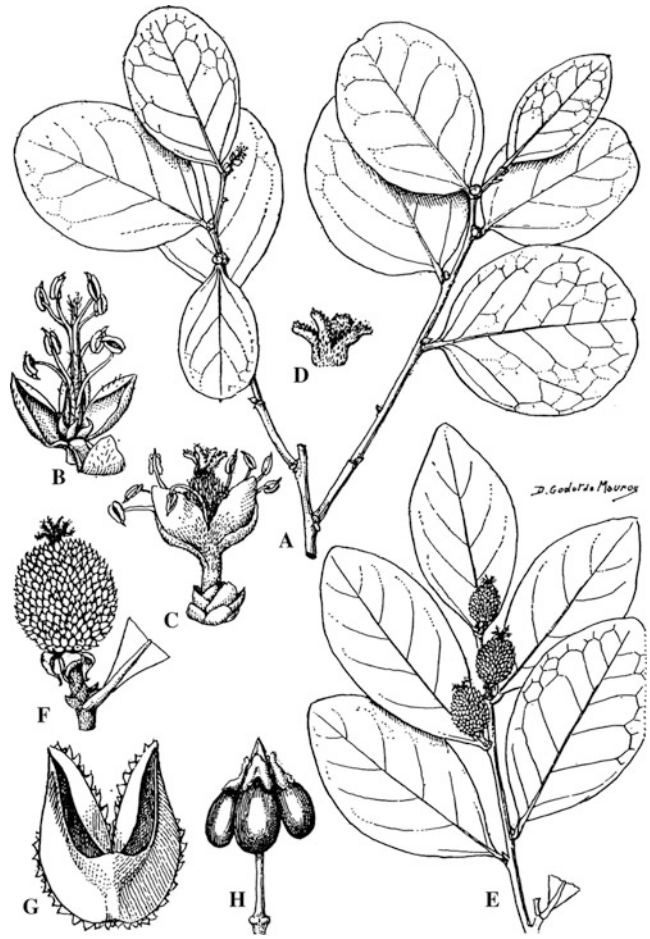

Fig. 21. Euphorbiaceae-Peroideae. *Chaetocarpus rabaraba*. **A** Flowering branchlet. **B** Staminate flower. **C** (Pseudo?)hermaphrodite flower. **D** Stylodia. **E** Fruiting branchlet. **F** Young fruit. **G** Two-valved coccus. **H** Columella with seeds. (Capuron 1972; drawn by D. Godot de Mauroy)

Dioecious trees or shrubs; indumentum simple. Leaves distichous; stipules persistent, sometimes foliose (deciduous). Flowers in axillary glomerules. Staminate flowers pedicellate, pedicels mid-articulate; sepals 3–5, imbricate, distinct or connate; petals 0; disk segments 5; stamens 5–15, filaments proximally connate; anthers introrse or latrorse, basifixed; pollen grains subprolate, 3-colporate, exine tectate-perforate, tectum microrugulose; pistillode distinct from stamens, trifid, villose. Pistillate flowers pedicellate; sepals 3–8, imbricate, distinct, deciduous in fruit; petals 0; disk cupular, lobed; ovary 3(4)-locular, hirsute;

ovules anatropous, inner and outer integuments thin, 3–6 cell layers; stylodia bifid, tips ± laciniate. Fruits capsular, muricate to echinate; columella persistent. Seeds ovoid, compressed, carunculate; testa dry, smooth and shiny; exotegmen tracheoidal; endosperm copious; cotyledons longer and broader than radicle.

Fivteen spp. scattered from the West Indies and South America to Africa, Madagascar, India, and Malesia. The seeds of *Chaetocarpus*, with shiny blackish testa, are strikingly similar to those of *Pera*, and suggest a close relationship between the two genera.

3. Tribe Pereae (Klotzsch & Garcke) Pax & K. Hoffm. (1919).

Monogeneric; represented only by the New World genus *Pera*.

89. *Pera* Mutis Fig. 22

Pera Mutis, Kongl. Vetensk. Acad. Nya Handl. 5: 299 (1784); Pax & K. Hoffm., Pflanzenr. 147, XIII: 2, figs. 1, 2 (1919); Correll, Fl. Bahama Arch.: 834, fig. 347 (1982); L. Gillespie & Armbruster, Smiths. Contr. Bot. 86: 8, figs. 2, 3 (1997); Bigio & Secco, Rodriguésia 63: 163–207 (2012), spp. of Braz. Amazonia.

Dioecious (monoecious) trees or shrubs; indumentum lepidote or stellate (simple). Leaves alternate (opposite), simple, entire, exstipulate. Inflorescences pseudanthial, axillary, fascicled; each pseudanthium usually unisexual, of 3 or 4 flowers subtended by a laterally dehiscing compound involucrate bract [of 2 connate bracts]; petals and disk 0. Staminate flowers sessile, surrounded by "pistillodes" [reduced pistillate flowers]; calyx irregularly lobed; stamens (2)3–4(−8), filaments distinct or connate; anthers introrse to extrorse; pollen grains suboblate to subprolate, 3-colporate, exine intectate or tectate, reticulate to microrugulate. Pistillate flowers sessile or subsessile; perianth and disk 0; ovary 3-locular; ovules anatropous, inner and outer integuments thin, 3–5 cell layers; stylodia very short and connate into a thick peltate stigmatic structure. Fruits capsular, valves woody; columella slender, usually not persistent. Seeds carunculate, testa dry, smooth, dark, shiny, exotegmen tracheoidal.

About 30–35 neotropical spp. In its floral morphology the genus is very distinct from all other Euphorbiaceae, but the seed morphology (Tokuoka and Tobe 2003) suggests a relationship with *Chaetocarpus*.

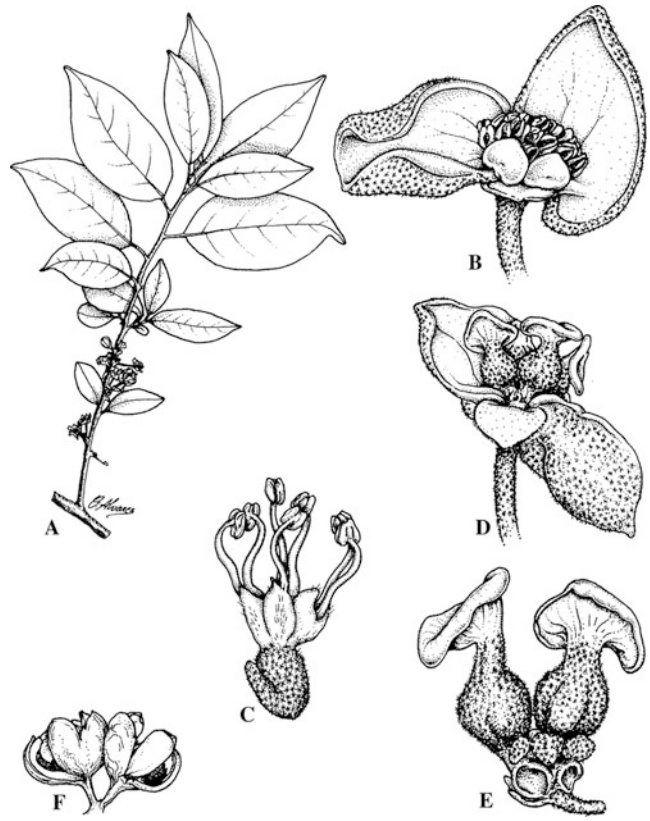

Fig. 22. Euphorbiaceae-Peroideae. *Pera anisotricha*. **A** Flowering branchlet. **B** Staminate inflorescence with involucre. **C** Three staminate flowers. **D** Four pistillate flowers subtended by the opened involucre. **E** Two of these flowers with basal staminodes. **F** Part of infructescence with two septifragal capsules. (Bigio & Secco 2012; drawn by B. Alvarez)

4. Tribe Pogonophoreae (Müll. Arg.) G.L. Webster (1975).

A single genus with a disjunct African/South American distribution.

90. *Pogonophora* Miers ex Benth.

Pogonophora Miers ex Benth., Hook., J. Bot. Kew Gard. Misc. 6: 372 (1854); Letouzey, Adansonia II, 9: 275, fig. 1 (1969); Secco, Revisão dos gêneros *Anomalocalyx* Ducke, *Dodecastigma* Ducke, *Pausandra* Radlk., *Pogonophora* Miers ex Bent. e *Sagotia* Baill.: 88, figs. 26, 27 (1990).

Dioecious trees or shrubs; indumentum simple, alpighiaceous in inflorescence. Leaves alternate; stipules small or obsolete. Inflorescenes of axillary thyrses or spikes; bracts persistent, eglandular. Staminate flowers sessile; sepals 5, distinct, scarious, imbricate, unequal, outer bract-like; petals 5,

distinct, imbricate, longer than sepals, barbate adaxially; stamens 5, filaments distinct; anthers introrse, basifixed; pollen grains subprolate, 3-colporate, exine tectate-perforate, tectum psilate; disk intrastaminal, urceolate, enclosing the 2–3-fid pistillode. Pistillate flowers pedicellate; sepals and petals similar to staminate, the calyx persistent in fruit; disk cupular; ovary 3-locular; inner and outer integuments thin, 5 or 6 cell layers; stylodia basally connate, bifid, branches fimbriate-papillate. Fruits capsular, columella slender, persistent. Seeds carunculate; testa smooth or slightly rugulose; exotegmen palisadal.

Three spp., widely disjunct, *P. schomburgkiana* Miers ex Benth. neotropical, the recently described *P. africana* Letouzey and *P. letouzeyi* Feuillet from West Africa (Gabon).

IV. Subfam. Cheilosoideae (Müll. Arg.) K. Wurdack & P. Hoffm. (2005).

Dioecious trees; latex 0; indumentum simple and/or stellate. Leaves alternate, simple, entire or toothed. Inflorescences pseudo-terminal or axillary, thyrsopaniculate. Flowers apetalous; staminate flowers: sepals 4–6, distinct, imbricate; disk with 4 or 5 segments; stamens 5–10, distinct; pollen grains suboblate, 3-colporate, colpi inoperculate, exine echinate; pistillode pubescent; pistillate flowers: sepals 5 or 6, distinct, imbricate, persistent in fruit; disk annular or 0; ovary 2–3-locular; ovules with thick integuments, the outer vascularized; stylodia bifid. Fruits capsular; columella persistent. Seeds with sarcotesta; mesotesta vascularized; exotegmen palisadal; endosperm copious.

Only one tribe:

1. Tribe Cheiloseae (Müll. Arg.) Airy Shaw & G.L. Webster (1975).

Two closely related genera of southeast Asia and Malesia. Cheiloseae are remarkable for their echinate exine sculpture; the seed structure with the fleshy exotesta and vascularized mesotesta (Tokuoka and Tobe 2003) is similar to that of *Trigonopleura*.

Two genera, 7 spp., SE Asia to Melanesia.

Key to the Genera of Cheiloseae

1. Ovary 3-locular; stamens 8–10, anthers apiculate; leaves without laminar glands; bracts eglandular **91. *Cheilosa***
– Ovary 2-locular; stamens 5–8 (9), anthers muticous; leaves with laminar glands (except *N. kingii*); bracts glandular **92. *Neoscortechinia***

91. *Cheilosa* Blume

Cheilosa Blume, Bijdr.: 613 (1826); Müll. Arg. in DC., Prodr. 15(2): 1123 (1866); J. J. Sm., Meded. Dept. Landb. Ned.-Ind. 10: 604 (1910); Pax & K. Hoffmann, Pflanzenr. 147, XV: 12, fig. 3 (1912); Whitmore, Tree Fl. Malaya 2: 77 (1973); van Welzen et al., Blumea 38: 162, fig. 1 (1993).

Dioecious trees; indumentum simple or fascicled. Leaves dentate to crenate, teeth with abaxial discoid glands; petiole apically pulvinate; stipules deciduous or subpersistent. Inflorescences axillary or terminal, the staminate thyrsoid-paniculate, the pistillate thyrsoid-racemoid; bracts eglandular, persistent, sometimes foliose. Staminate flowers pedicellate; sepals 5 (6), distinct, imbricate; petals 0; disk annular, ± 5-lobed, pubescent; stamens 9 or 10, ± biseriate, filaments distinct; anthers basifixed, introrse, apiculate; pollen grains suboblate, 3-colporate, colpi inoperculate, tectum echinate and rugulose; pistillode mainly 3-lobed, hirsutulous. Pistillate flowers pedicellate; sepals (4) 5 (6), distinct or nearly so, imbricate, entire, ± persistent in fruit; petals 0; disk annular, pubescent; ovary 3-locular, pubescent; ovules anatropous, inner and outer integuments moderately thick, the outer vascularized; stylodia basally connate, unlobed, recurving. Fruits capsular, rugulose; mesocarp woody; columella cylindrical, persistent. Seeds 1–3 per fruit, ovoid, ecarunculate, exotesta fleshy.

A single sp., *Ch. montana* Blume, widespread in western Malesia: Malay Peninsula and Sumatra to Borneo and the Philippines.

92. *Neoscortechinia* Pax

Neoscortechinia Pax, Natürl. Pflanzenfam. Nachtr. 1: 213 (1897); Pax & K. Hoffm., Pflanzenr. 147, XIV: 52 (1919); Whitmore, Tree Fl. Malaya 2: 119 (1973); van Welzen, Blumea 39: 301–320, fig. 3 (1994).

Dioecious trees; indumentum of simple and fasciculate hairs. Leaves usually with 2 raised adaxial basal glands, subentire to glandular-dentate, petioles ± pulvinate; stipules deciduous. Inflorescences axillary or pseudo-terminal, thyrsoid, staminate ± compounded; bracts entire, sometimes glandular; flowers subsessile. Staminate sepals 4–5(6), imbricate; petals 0;

disk dissected; stamens (4)5–9, filaments distinct; anthers basifixed, introrse to latrorse, muticous; pollen grains subglobose, 3-colporate, colpi inoperculate, exine echinate, tectum microrugulose; pistillode 2–3-fid. Pistillate flowers pedicellate, sepals 4 or 5, imbricate, persistent or deciduous in fruit; petals and disk 0; ovary 2-locular, hirsute; ovules anatropous, inner and outer integuments thick, the outer vascularized; stylodia stigmatoid. Fruits capsular, oblong, ribbed; columella persistent or deciduous. Seeds 1 (2) per fruit, exotesta fleshy, endotesta smooth.

Six spp., mainly western Malesian, extending to Burma in the West and Borneo, New Guinea and the Solomons in the East.

V. Subfam. Acalyphoideae Beilschm. (1833).

Subfam. Ricinoideae Baillon ex Hassk. (1859).

Subfam. Dysopsidoideae Baillon ex Hassk. (1859).

Trees, shrubs, or herbs; milky latex 0 [colored exudate in some genera]; indumentum simple, malpighiaceous, or lepidote. Leaves alternate (opposite); lamina simple and pinnately veined, or palmately veined or lobed , often with foliar or petiolar glands. Inflorescences axillary or terminal, racemose, spicate, or paniculate, or reduced to axillary glomerules or solitary flowers; bracts sometimes glandular. Staminate flower: sepals imbricate or valvate [sometimes connate in bud and rupturing at anthesis]; petals and disk + or 0; stamens 2–100+, filaments distinct or connate; pollen grains binucleate, mostly 3- or 4-colporate (3-colpate in some Plukenetieae), exine mostly semitectate-reticulate (echinate); pistillode + or 0. Pistillate flower: sepals mostly 3–6 (2–12), imbricate or open at anthesis; petals and disk + or 0; ovary mostly 2–4-locular, ovules solitary in each locule, anatropous, inner integument nonvascularized; stylodia entire to multifid. Fruit capsular (baccate or drupaceous). Seeds carunculate or ecarunculate; seed coat with palisadal exotegmen; endosperm usually copious; cotyledons longer and broader than radicle [except in Ampereeae]. x mostly = 9, 10, 11.

The Acalyphoideae, with 99 genera in 14 tribes and a total of over 3,000 species, are the largest and most complex of the seven subfamilies. They are resolved as monophyletic with exception of the isolated Erismantheae, which may occupy a sister position to the rest of the subfamily.

Key to the Tribes of Subfam. Acalyphoideae

1. Leaves opposite; pollen exine reticulate; seeds ecarunculate **1. Erismantheae**
– Leaves alternate; pollen exine rugulose or micropunctate; seeds carunculate or not 2
2. Cotyledons scarcely broader than radicle; monoecious (dioecious) subshrubs with ericoid foliage; seeds carunculate **9. Ampereeae**
– Cotyledons distinctly broader than radicle; foliage generally not ericoid; seeds carunculate or ecarunculate 3
3. Petals +, at least in staminate flowers 4
– Petals 0 6
4. Monoecious (dioecious); indumentum malpighiaceous, stellate, or lepidote [simple in Speranskiinae and *Philyra*]; anther connective not enlarged, sacs not pendulous; pollen sexine often distinctly heterobrochate **11. Chrozophoreae**
– Dioecious; indumentum simple; anther connective enlarged, sacs pendulous; pollen sexine coarsely reticulate, not heterobrochate 5
5. Stylodia bifid; pistillate petals usually present; inflorescences paniculate, racemose, or spiciform; pollen spheroidal; leaves stipulate **3. Agrostistachydeae**
– Stylodia multifid; pistillate petals 0; inflorescences capitellate; pollen prolate; leaves exstipulate **4. Sphyranthereae**
6. Stylodia connate, unlobed; plants often scandent; stinging hairs sometimes present; pollen tectum microverrucate **14. Plukenetieae**
– Stylodia distinct or basally connate; plants rarely scandent; stinging hairs 0; pollen tectum psilate to microverrucate 7
7. Pollen tectum perforate, psilate to scabrate 8
– Pollen tectum usually rugulose, microverrucate 11
8. Staminate disk 0; indumentum stellate **10. Epiprineae**
– Staminate disk + [except in *Adenophaedra*]; indumentum simple 9
9. Pistillate sepals deciduous; staminate disk massive, intrastaminal; stamens 4–15; pistillode + or 0 **2. Caryodendreae**
– Pistillate sepals usually persistent; staminate disk not massive and extrastaminal; stamens (2–)8–100 or more; pistillode usually 0 10
10. Pollen colpi distinctly marginate; indumentum simple or stellate; anthers sometimes 4-locellate **13. Bernardieae**
– Pollen colpi emarginate; indumentum simple; anthers 2-locellate **8. Pycnocomeae**
11. Pollen grains with operculate colpi; seeds mostly ecarunculate, testa not fleshy; stipules deciduous or obsolete 12

– Pollen grains with inoperculate colpi; seeds carunculate or ecarunculate; testa dry or fleshy; stipules deciduous or persistent 13

12. Leaves without laminar glands; stylodia subentire to multifid; inflorescences axillary; pollen sexine finely perforate-tectate **12. Adelieae**
– Leaves usually with embedded laminar glands; stylodia mostly entire, if divided, then inflorescences terminal; pollen exine rugulose to striate **5. Alchorneeae**

13. Seeds carunculate; inflorescences terminal; indumentum stellate or 0 **6. Ricineae**
– Seeds mostly ecarunculate; inflorescences axillary or terminal; indumentum simple or stellate **7. Acalypheae**

1. Tribe Erismantheae G.L. Webster (1975).

Monoecious trees or shrubs; indumentum simple; leaves opposite, entire or obscurely dentate; stipules interpetiolar; inflorescences axillary, racemoid or spicate; staminate sepals 4 or 5, imbricate (valvate); petals 5 or 0, disk minute or 0; stamens 5–15, filaments distinct; pollen grains 3-colporate, angulaperturate, colpi emarginate, inoperculate, sexine tectate-reticulate; pistillode +; pistillate sepals 5 or 6, imbricate; petals + or 0; disk 0; stylodia distinct or connate, bifid; fruit capsular; seeds ecarunculate, testa smooth and dry.

Three tropical Asian genera with a total of 5 spp. Nowicke et al. (1998) note the anomalous nature of the pollen grains of *Syndyophyllum*, which are operculate and resemble the pollen of *Alchornea*, but in the *rbc*L analysis of Wurdack et al. (2005), *Moultonianthus* and *Syndyophyllum* form a monophyletic group. Later (Wurdack and Davis 2009), *Moultonianthus* has been resolved in a position sister to the rest of subfamily Acalyphoideae s.str., thus confirming the placement of Erismantheae by Webster (1994).

The apetalous flowers of *Erismanthus* (and possibly of *Syndyophyllum* as well) and their elongate stylodia and catkin-like staminate inflorescences are indicative of wind pollination. The opposite leaves are thought to be due to strong shortening of each second internode beginning in the seedling stage (see Radcliffe-Smith 2001: 121).

Key to the Genera of Erismantheae

1. Pistillode elongated, clavate; staminate inflorescence covered with closely imbricate bracts; staminate pedicel > 1.5 cm long; stamens 12–15; pistillate flowers apetalous **93. *Erismanthus***
– Pistillode deeply trifid into slender branches; staminate inflorescence not closely bracteate; staminate pedicel < 1.5 cm long; stamens 4–11 2

2. Stipules persistent, foliaceous and cordate at the base; staminate pedicels > 2 mm long; cymules unisexual; pistillate flowers petaliferous **94. *Moultonianthus***
– Stipules deciduous, triangular, not cordate; staminate pedicels < 1 mm long; cymules bisexual; pistillate flowers apetalous **95. *Syndyophyllum***

93. *Erismanthus* Wall. ex Müll. Arg.

Erismanthus Wall. ex Müll. Arg. in DC., Prodr. 15(2): 1138 (1866); Pax & K. Hoffm., Pflanzenr. 147. III: 33, fig. 9 (1911); Airy Shaw, Kew Bull. 36: 294 (1981); van Welzen, Blumea 40: 379, fig. 2 (1995).

Monoecious trees or shrubs, branching sympodially; indumentum simple, often inconspicuous. Leaves opposite, minutely glandular-serrulate, petiole not pulvinate; stipules interpetiolar, subpersistent or deciduous. Inflorescences unisexual or bisexual, staminate flowers in bracteate catkins or capitula, pistillate flowers solitary. Staminate flowers pedicellate; sepals (4) 5, imbricate; petals 5, shorter than sepals; disk 0; stamens 12–15, filaments distinct; anthers biseriate, basifixed, dehiscing latrorsely; pollen grains subprolate, 3-colporate, exine tectate-punctate/reticulate, reticulum slightly vermiculate; pistillode long-exserted, slender, trifid at apex. Pistillate flowers pedicellate; sepals 5, imbricate, subentire, ± foliose, persistent and reflexed in fruit; petals and disk 0; ovary 3-locular, hirsute; stylodia proximally connate, distally bifid, slender, papillose. Fruit oblate, capsular; columella persistent, apically dilated. Seeds 1–3 per fruit, subglobose, ecarunculate, testa smooth.

Two spp., southeast Asia: Vietnam to Sumatra and Borneo.

94. *Moultonianthus* Merr. Fig. 23

Moultonianthus Merr., Phil. J. Sci. Bot. 11: 70 (1916); Pax & K. Hoffm., Pflanzenr. 147, XIV: 41 (1919); van Steenis, Bull. Bot. Gard. Buitenz. III, 17: 404 (1948); van Welzen, Blumea 40: 384, fig. 3 (1995).

Monoecious trees or shrubs; indumentum simple but axes early glabrescent. Leaves opposite, shallowly crenate; stipules interpetiolar, foliose, cordate, persistent. Inflorescences axillary, unisexual, racemiform; bracts small, eglandular. Staminate pedicel articulate; sepals 5, imbricate, biseriate; petals 5 (7), longer than sepals, white, entire; disk rudimentary, 5-lobed; stamens 8–11,

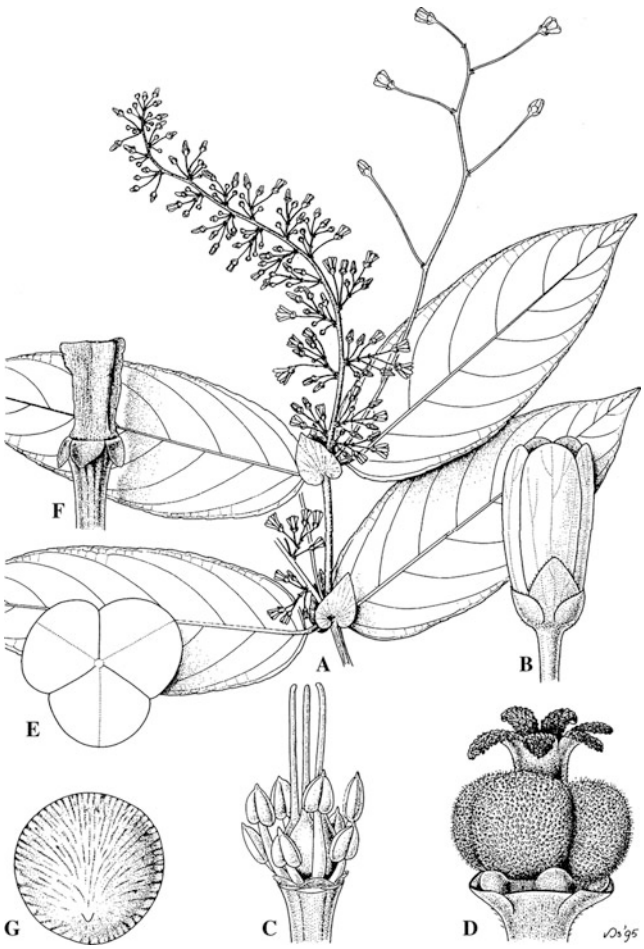

Fig. 23. Euphorbiaceae-Acalyphoideae. *Moultonianthus leembruggianus*. **A** Branchlet with separate staminate and pistillate flowers. **B** Staminate flower. **C** Staminate flower with disk lobes, androecium and pistillode. **D** Pistillate flower with perianth lobes removed, showing disk lobes and pistil. **E** Outline of young fruit. **F** Fruit column after dehiscence. **G** Seed. (van Welzen 1995; drawn by J. van Os)

biseriate, filaments distinct; anthers basifixed, latrorse to introrse, apiculate; pollen grains subprolate, 3-colporate; pistillode deeply trifid, branches slender. Pistillate pedicel articulate; sepals 5, imbricate, entire or glandular-denticulate, persistent in fruit; petals similar to staminate; disk 5-lobed; ovary 3-locular, tomentose; ovules anatropous, inner and outer integuments very thick, the outer vascularized; stylodia basally connate, bifid, branches dilated and papillate. Fruit capsular, spheroidal; columella winged. Seeds 1–3 per fruit, subglobose, ecarunculate; testa smooth.

One sp., *M. borneensis* Merr., Sumatra and Borneo.

95. *Syndyophyllum* Lauterb. & K. Schum.

Syndyophyllum Lauterb. & K. Schum., Fl. Schutzgeb. Südsee: 403 (1901); Pax & K. Hoffm., Pflanzenr. IV. 147: 104 (1911); Airy Shaw, Hook. Ic. Pl. 38(1): t. 3722 (1974); van Welzen, Blumea 40: 388, fig. 4 (1995).

Monoecious trees; indumentum simple, glabrescent. Leaves opposite, distichous, simple, minutely puncticulate, sometimes with abaxial domatia, obscurely crenulate; stipules interpetiolar, deciduous. Inflorescences axillary, bisexual or staminate thyrses, pistillate flowers solitary; bracts minute. Staminate flowers subsessile; sepals 5, imbricate, basally connate; petals shorter than sepals or 0; disk 0; stamens 4–10, filaments distinct, in 1 or 2 series, much longer than anthers; anthers basifixed, apiculate, introrse; pollen grains subspheroidal, 3-colporate, colpi operculate, pistillode deeply trifid, shorter than filaments. Pistillate flowers subsessile; sepals 4 or 5, imbricate, basally connate, entire, persistent and reflexed in fruit; petals and disk 0; ovary 3-locular, hirsute; stylodia connate halfway, tips apically bifid and adaxially papillose. Fruits capsular; columella ± persistent, trigonous and apically dilated. Seeds subglobose, ecarunculate, testa smooth.

Two spp. from Sumatra, Borneo, and New Guinea.

2. Tribe Caryodendreae G.L. Webster (1975).

Dioecious; indumentum simple; leaves with basal laminar glands; inflorescences terminal or axillary, spiciform; staminate sepals 3–5, valvate; petals 0; disk massive, pubescent; stamens 4–15; pollen grains oblate, 3-colporate, colpi not marginate, inoperculate; pistillode + or 0; pistillate flowers sessile, sepals 4–6; disk pubescent; ovary mostly 3-locular; stylodia distinct, unlobed; fruit capsular; seeds ecarunculate, testa dry or fleshy.

As treated here, Caryodendreae comprise three genera, two from the New World, and one African. The group will need a critical revision: in the molecular analysis (Wurdack et al. 2005), *Caryodendron* is resolved in a clade with two bernardioid genera (*Bernardia* and *Adenophaedra*), which is sister to the Plukenetieae, whereas *Alchorneopsis* and, farther away, *Discoglypremna* appear at the base of the "Alchorneoid" grade together with agrostistachyoid genera and *Mareyopsis*.

Key to the Genera of Caryodendreae

1. Leaves pinnately veined, stipulate; pistillode massive; seed coat dry **96. *Caryodendron***
– Leaves triplinerved, exstipulate; pistillode slender or 0; seed coat fleshy 2
2. Staminate disk dissected; anthers apiculate; pistillode 0; seeds trigonous, testa foveolate **97. *Discoglypremna***
– Staminate disk entire, receptacular; anthers muticous; pistillode +; seeds lenticular, testa reticulate **98. *Alchorneopsis***

96. *Caryodendron* Karsten

Caryodendron Karsten, Fl. Colombiae 1: 91, t. 45 (1860); Müll. Arg., Fl. Brasil. 11(2): 706 (1874); Pax & K. Hoffm., Pflanzenr. 147, VII: 263 (1914); Ducke, Trop. Woods 76: 18 (1943); Webster, Ann. Missouri Bot. Gard. 54: 287 (1968); Huft, Ann. Missouri Bot. Gard. 76: 1077 (1989); Radcl.-Sm., Gen. Euphorb.: 153, fig. 15 (2001).

Dioecious trees, glabrous except for inflorescences; indumentum simple. Leaves biglandular adaxially near base and with small dispersed glands; stipules lanceolate, entire, deciduous. Inflorescences mostly terminal or subterminal, spiciform, the staminate sometimes compound; bracts eglandular, scarious, rounded to truncate with ciliate margins, multiflorous. Staminate flowers pedicellate; calyx closed in bud, sepals 3 or 4, valvate; petals 0; disk massive, pulviniform, instrastaminal, pubescent; stamens 4–7, filaments distinct; anthers introrse, locules ± pendulous, connective apiculate; pollen grains suboblate, 3-colporate, colpi narrow and emarginate, inoperculate; endoaperture ovate to lalongate, sexine tectate-perforate; pistillode 0. Pistillate flowers with stout pedicels articulated at base; sepals 5 or 6, imbricate, persistent and accrescent in fruit; petals 0; disk annular, sometimes angled; ovary 3-locular, glabrous, ovules with inner integument moderately thick, outer integument thin; stylodia basally connate, unlobed. Fruits thick-walled, (2)3(4)-locular, loculicidally and septicidally dehiscent; columella ± persistent. Seeds ovoid; testa smooth, dry, thin-walled, hilum elliptic.

Three or four closely related neotropical spp., from Costa Rica to Amazonian Brazil. *Caryodendron orinocense* H. Karst., the "inchi", is cultivated for the seed oil in Colombia.

97. *Discoglypremna* Prain

Discoglypremna Prain, Kew Bull. 1911: 317 (1911); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 222, fig. 44 (1987); Léonard, Fl. Afr. Centr. Euphorb. 3: 11, t. 1 (1996).

Dioecious trees; indumentum simple. Leaves often crowded near apices, pinnately veined and triplinerved, subentire, with abaxial embedded glands and biglandular at junction with petiole; stipules deciduous. Inflorescences terminal, paniculate, bracts minute, eglandular; flowers subsessile, the staminate several per axil, the pistillate solitary. Staminate flowers pedicellate, calyx closed in bud, sepals 3–4(5), valvate; disk pubescent, dissected, segments extra- and intrastaminal; petals 0; stamens (5–)8–12(−15), filaments distinct; anthers basifixed, introrse, locules pendulous, connective apiculate; pollen grains subprolate to prolate spheroidal, 3-colporate, colpi narrow, inoperculate and emarginate, endoaperture ± circular, sexine tectate; pistillode 0. Pistillate flowers pedicellate, articulate near base; sepals mostly 5, valvate, acute, persistent in fruit; petals 0; disk dissected into 6–8 distally pubescent segments; ovary 3(4)-locular, glabrous or sericeous; inner and outer ovular integuments thick, the outer vascularized; stylodia distinct, unlobed, adaxially fimbriate. Fruit 3-lobed, capsular but exocarp somewhat fleshy; cocci reticulate; columella slender, persistent. Seeds: exotesta fleshy, reddish, endotesta blackish, foveolate, mesotesta vascularized. $n = 11$.

A single sp., *D. caloneura* (Pax) Prain, rainforests of West Africa (including São Tomé) to Uganda.

98. *Alchorneopsis* Müll. Arg.

Alchorneopsis Müll. Arg., Linnaea 34: 156 (1865), and in DC., Prodr. 15(2): 764 (1866); Pax & K. Hoffm., Pflanzenr. 147: 267 (1914); Liogier, Descr. Fl. Puerto Rico 2: 352, fig. 59–4 (1988); Burger & Huft, Fieldiana Bot. n.s. 36: 62 (1995); Radcl.-Sm., Gen. Euphorb.: 156, fig. 16 (2001).

Dioecious trees; indumentum scanty, simple. Leaves triplinerved, biglandular abaxially at base, entire or remotely crenulate; stipules 0. Inflorescences axillary, the staminate often fascicled, spiciform [flowers subsessile or shortly pedicellate]; bracts minute, eglandular; staminate flowers in glomerules, pistillate solitary. Staminate flowers pedicellate, calyx closed in bud; lobes 3 or 4, valvate; petals 0; disk massive, hirsutulous; stamens (5)6(−8), filaments distinct; anthers introrse, locules unequal; pollen grains subspheroidal, 3-colporate, colpi inoperculate, emarginate, endoaperture lalongate; sexine tectate, granulate; pistillode ± 3-lobed, strigose-hirtellous.

Pistillate flowers pedicellate, articulate; sepals 4 or 5, slightly imbricate, acute, persistent in fruit; petals 0; disk annular, pulviniform, hirsutulous; ovary 3-locular; pubescent; inner and outer ovular integuments thin; stylodia unlobed or emarginate. Fruit capsular; columella persistent, broadly 3-winged. Seeds flattened, ecarunculate; exotesta fleshy, endotesta reticulate-striate.

A single sp., *A. floribunda* (Benth.) Müll. Arg., ranging from the Greater Antilles to Costa Rica and Brazil.

3. Tribe Agrostistachydeae (Müll. Arg.) G.L. Webster (1975).

Dioecious (monoecious) trees or shrubs; indumentum simple or 0; inflorescences racemoid or spicate; the calyx closed in bud, splitting into 2–5 valvate lobes; petals 3–8, imbricate in bud [except *Cyttaranthus*]; disk receptacular or extrastaminal and dissected; stamens 10–120; anthers introrse, connective ± enlarged or apiculate, thecae often pendulous; ovary 3-locular, often tomentose; stylodia distinct, bifid, sometimes lacerate; fruit capsular; seeds carunculate, not fleshy.

Four genera, two African and two Asian. Nowicke et al. (1999) stated that *Cyttaranthus* and *Chondrostylis* differ in pollen structure from *Agrostistachys* and *Pseudagrostistachys*, implying that the Agrostistachydeae may not be monophyletic. This is confirmed by the molecular data of Wurdack et al. (2005).

Key to the Genera of Agrostistachydeae

1. Petals +; anther connective narrow; flowers in spiciform or racemoid thyrses; anthers extrorse; pistillate disk annular 2
– Petals 0; anther connective flattened, broader than high; flowers in thyrses or panicles; pistillate disk 5-lobed **102. *Chondrostylis***
2. Dioecious; staminate petals imbricate in bud; petals present in pistillate flower 3
– Monoecious; staminate petals not imbricate in bud; pistillate flowers apetalous; leaves with laminar glands **101. *Cyttaranthus***
3. Staminate disk dissected; stamens 8–10; stipules distinct, leaves lacking laminar glands **99. *Agrostistachys***
– Staminate disk receptacular; stamens 20–55; stipules connate, leaving an annular scar; leaves with laminar glands **100. *Pseudagrostistachys***

99. *Agrostistachys* Dalzell

Agrostistachys Dalzell, Hook. J. Bot. Kew Gard. Misc. 2: 41 (1850); Pax & Hoffm., Pflanzenr. 147, VI: 98, figs. 19, 20 (1912); Gagnep., Fl. Indochine 5: 465, t. 57 (7–11), 58 (1–2) (1926); Airy Shaw, Kew Bull. Add. Ser. 4: 25 (1975); Sevilla & van Welzen, Blumea 46: 76–89, figs. 1–3 (2001).

Dioecious (monoecious) trees or shrubs; branches ± resinous; indumentum simple. Leaves alternate, lamina decurrent on the petiole, entire or dentate; stipules deciduous. Inflorescences axillary, racemoid or spicate; bracts glumaceous, indurate, sometimes glandular, persistent, each subtending 1–10 staminate flowers or solitary pistillate flowers. Staminate flowers subsessile or short-pedicellate; calyx closed in bud, dehiscent into 2–5 valvate segments; petals (0)5–8, imbricate; disk segments (4)5(−7); stamens (8)10 (−13), biseriate, filaments distinct or basally connate; anthers basifixed, introrse, minutely apiculate; pollen grains subspheroidal, angulaperturate, 3-colporate, colpi inoperculate with narrow to broad margo, endoaperture lalongate, sexine tectate, intrareticulate; pistillode 2–3-fid or entire (0). Pistillate flowers articulate-pedicellate; sepals (4) 5, imbricate, entire or denticulate, persistent in fruit; petals 5, longer than sepals; disk annular to 5-lobed, sometimes with staminodes; ovary (2)3-locular, glabrous or pubescent; ovules pachychalazal, inner integument thick, outer integument thin; stylodia distinct or basally connate, bifid, papillate. Fruits capsular, thin-valved; columella persistent, narrowly 3-winged. Seeds subglobose, ecarunculate; testa smooth; hilum deltoid-reniform, large.

Ten spp., from India and Sri Lanka to New Guinea, five in Malesia.

100. *Pseudagrostistachys* Pax & K. Hoffm.

Pseudagrostistachys Pax & K. Hoffm., Pflanzenr. 147, VI: 96, fig. 18 (1912); Léonard, Fl. Congo 8(1): 183, fig. 15 (1962); Airy Shaw, Kew Bull. 36: 248, t. 1 A-G (1981); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 166, fig. 30 (1987), Fl. Zambesiaca 9(4): 136 (1996).

Dioecious shrubs or trees; indumentum simple, sparse except in inflorescences. Leaves subentire or somewhat dentate, with dispersed laminar glands and 2–4 glands near junction with petiole; stipules connate, sheathing, deciduous, leaving a circular scar. Inflorescences axillary or ramiflorous, sessile to short-pedunculate, flowers usually 1 per bract; bracts glumaceous, ciliate, persistent, eglandular. Staminate flowers pedicellate, articulate near base; calyx closed in bud, splitting into 2–5 valvate lobes; petals 5–8, distinct, imbricate, longer than sepals; disk receptacular, pubescent;

stamens 20–55, filaments distinct, erect in bud; anthers extrorse, connective thickened and glandular, thecae pendulous; pollen grains subprolate, 3-colporate, colpi inoperculate, emarginate, endoaperture obscure; sexine tectate-reticulate; pistillode small or 0. Pistillate flowers pedicellate; sepals mostly 4 or 5, scarcely imbricate, entire, persistent in fruit; petals 4 or 5; disk thick, annular, pitted; ovary 3-locular, tomentose; stylodia distinct, bipartite, branches papillose. Fruit capsular, 3-lobed, valves crustaceous; columella persistent. Seeds subglobose, ecarunculate, hilum elliptic; testa smooth, shiny.

Two spp., West Africa, one of these reaching Uganda and Zambia.

101. *Cyttaranthus* Léonard

Cyttaranthus Léonard, Bull. Jard. Bot. Brux. 25: 286 (1955); Fl. Congo Rwa.-Bur. 8(1): 180, t. 12 (1962).

Monoecious shrubs; indumentum simple. Leaves subentire to crenate or dentate, trinerved at base and pinnately veined, with scattered discoid glands abaxially, stipellate at junction with petiole; stipules minute, deciduous. Inflorescences axillary, usually unisexual, spiciform; bracts concave, glumaceous, persistent. Staminate flower pedicellate, articulate at base; calyx splitting into 2 or 3 valvate lobes; petals 3(6–8), not imbricate, shorter than calyx lobes; disk segments glabrous, intrastaminal, on the convex receptacle; stamens 25–40, filaments distinct; anthers extrorse, connective apiculate, thecae pendulous; pollen grains prolate spheroidal, 3-colporate, colpi inoperculate, scarcely marginate; sexine irregularly tectate-perforate; pistillode 0. Pistillate flowers pedicellate, pedicel distally dilated and articulate at base; sepals 3, connate into a cup, persistent in fruit; petals 0; disk swollen, appearing as a gynophore; ovary 3-locular, ± pubescent; stylodia slightly connate basally, deeply bifid. Fruit capsular, invaginated between cocci; columella persistent. Seeds oblong to subglobose, ecarunculate, testa smooth.

A single sp., *C. congolensis* Léonard, rainforests and semi-deciduous forests in the Congo.

102. *Chondrostylis* Boerl.

Chondrostylis Boerl., Ic. Bogor. 1: t. 23 (1897); Pax & K. Hoffm., Pflanzenr. 147, VII: 15 (1914); Airy Shaw, Kew Bull. 14: 358 (1960), Kew Bull. Add. Ser. 4: 69 (1975), Kew Bull. 36: 276, fig. 3C (1981); Sevilla & van Welzen, Blumea 46: 89–93, fig. 4 (2001).

Monoecious shrubs; indumentum simple to nearly 0. Leaves subsessile, serrate, usually minutely punctate with dispersed embedded glands and biglandular at base; stipules deciduous. Inflorescences axillary (ramiflorous), paniculate, unisexual; bracts glumaceous, entire, eglandular. Staminate flowers short-pedicellate; calyx splitting into 3 or 4 valvate segments; petals 0; disk of discrete interstaminal segments; stamens 50 +; anthers basifixed, introrse, connective enlarged, thecae divergent; pollen grains spheroidal, angulaperturate, 3-colporate, colpi inoperculate, emarginate, endoaperture lalongate, sexine tectate-perforate and microverrucate; pistillode 0. Pistillate flowers subsessile; sepals 5, imbricate, connate into a cup; petals 0; disk annular, tomentose; ovary 3-locular, pubescent; stylodia distinct, bifid, branches adaxially fimbriate. Fruit capsular, valves thin; columella persistent, slender, trigonous. Seeds spheroidal, ecarunculate, testa smooth.

Two spp., distributed from Thailand to Sumatra and Borneo.

4. Tribe Sphyranthereae Radcl.-Sm. (2001).

A monotypic tribe containing only the genus *Sphyranthera*.

103. *Sphyranthera* Hook. f.

Sphyranthera Hook. f., Hook. Ic. Pl. 18: t. 1702 (1887); Chakrabarty & Vasudeva Rao, J. Econ. Tax. Bot. 5: 959 (1984); 6: 429 (1985); Radcl.-Sm., Gen. Euphorb.: 135, fig. 12 (2001).

Dioecious shrubs; indumentum simple, scanty. Leaves glandular; stipules 0. Inflorescences axillary or extraaxillary, sometimes fasciculate, pedunculate and subumbellately capitulate, the staminate many-flowered capitula, the pistillate 1–4-flowered; bracts crowded at apex of peduncle. Staminate flowers pedicellate, basally articulated; sepals (3)4(5), valvate; petals 4, entire to bifid; disk segments 4, apically bilobed; stamens (8–)12–20, filaments distinct; connectives enlarged and minutely bifid, anthers subglobose; pollen prolate, 3-colporate, sexine reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 3 or 4 (5), valvate or open in bud, entire, deciduous in fruit; petals 0; disk segments 3 or 4; ovary 3-locular, pubescent; stylodia distinct, bifid, somewhat lacerate. Fruits capsular; columella persistent, emarginate. Seeds globose, ecarunculate, testa smooth.

Two spp., endemic to the Andaman/Nicobar archipelago. The curious malleiform anthers suggest a possible relationship with *Chondrostylis*.

5. Tribe Alchorneeae (Hurus.) Hutch. (1969).

Dioecious (monoecious) trees or shrubs; wood rays with lysigenous canals; indumentum simple or stellate; leaves entire or dentate, sometimes stipellate or with laminar glands; stipules mostly deciduous or obsolete; inflorescences terminal or axillary; staminate flowers subsessile; calyx closed in bud, splitting into 2–5 valvate segments; petals 0; disk + or 0; stamens (2–)4–60; pollen grains 3-colporate, colpi operculate; pistillode rudimentary or 0; pistillate flowers subsessile; sepals 3–8, imbricate; petals 0; disk mostly rudimentary or 0; ovary 2–3(4)-locular; stylodia entire to multifid; fruits capsular; columella persistent; seeds carunculate or ecarunculate, testa smooth or tuberculate, not fleshy.

The Alchorneae include 10 genera grouped into 3 subtribes; the monogeneric subtribe Mareyopsinae is added provisionally because *Mareyopsis* is resolved in the Alchorneoid clade of Wurdack et al. (2005).

Key to the Genera of Alchorneeae

1. Stylodia bifid; indumentum stellate; stamens 15–60 **109. *Conceveiba***
– Stylodia unlobed (or if bifid then indumentum simple); stamens 2–12; seeds ecarunculate or caruncle, minute 2
2. Indumentum stellate; ovary 2-locular; stylodia unlobed, elongated, slender; pollen exine coarsely rugulose **105. *Alchornea***
– Indumentum simple; ovary 3-locular; pollen exine finely tectate-punctate 3
3. Dioecious or monoecious; stamens 7–12 4
– Monoecious; stamens up to 8 5
4. Dioecious; staminate disk of 8 segments in 4 pairs; stamens 8; fruit indehiscent **111. *Mareyopsis***
– Monoecious; staminate disk 0; stamens 7–12; fruit dehiscent **110. *Aubletiana***
5. Stylodia distinctly bifid; leaf blades pinnately veined, not stipellate; stamens 8 **104. *Orfilea***
– Stylodia entire to emarginate; stamens 2–8; leaf blades pinnately to palmately veined 6
6. Stamens usually 8, distinct; stigmas smooth; pistillate sepals glandular at base; leaf blades spinose-dentate **106. *Coelebogyne***
– Stamens 2–4, filaments basally connate; leaf blades not spinose-dentate 7
7. Stamens 4; stylodia elongated, apically dilated; seeds ecarunculate; leaf blade stipellate; inflorescences terminal **107. *Aparisthmium***
– Stamens 2 or 3; stylodia stigmatiform; seeds minutely carunculate; leaf blade not stipellate; inflorescences axillary or ramiflorous **108. *Bocquillonia***

5a. Subtribe Alchorneinae Hurus. (1954).

Indumentum simple or stellate; staminate inflorescences axillary; stamens 2–10; pollen exine with complex infratectum of columellae; pistillate sepals eglandular; stylodia mostly unlobed, often dilated or stigmatiform; ovary 2–3(4)-locular.

Six genera with c. 70 spp. in both the Neotropics and Paleotropics. Generic limits within the Alchorneae are still controversial; *Orfilea*, *Coelebogyne*, and *Aparisthmium* possibly might be included within *Alchornea* s. lat.

104. *Orfilea* Baill.

Orfilea Baill., Étude Gén. Euphorb.: 452 (1858); Pax & K. Hoffmann, Pflanzenr. 147. VII: 253 (1914, under *Lautembergia*); Coode, Fl. Mascar. 160: 55, fig. t. 11 (1982, under *Lautembergia*); Radcl.-Sm., Gen. Euphorb.: 192 (2001); Schatz, Generic Tree Fl. Madag.: 162, fig. 166 (2001).

Dioecious (monoecious) trees or shrubs; indumentum simple. Leaves entire or crenulate, biglandular at base or eglandular; stipules subulate, subpersistent. Inflorescences terminal and axillary, spiciform or paniculate; pistillate bracts trifid. Staminate flowers subsessile; calyx closed in bud, splitting into 2–4 valvate segments; petals and disk 0; stamens (4)5–10, filaments basally connate; anthers 2-celled; pollen grains prolate spheroidal, angulaperturate, 3-colporate, operculate, emarginate; endoapertures lalongate; tectum microrugulose, microverrucate; pistillode 0. Pistillate flowers sessile or subsessile; sepals 5 (6), entire, persistent in fruit; disk of 5 segments or 0; ovary 3-locular, glabrous; stylodia connate basally, bifid. Fruits capsular; columella persistent. Seeds rounded, ecarunculate, testa smooth.

Four spp. from Madagascar and Mauritius.

105. *Alchornea* Sw. Fig. 24

Alchornea Sw., Prodr.: 98 (1788), Fl. Ind. Occ. 2: 1153, t. 24 (1800); Thin, Tâp Chi Sinh Hoc 6 (3): 26 (1984); Burger & Huft, Fieldiana Bot. II. 36: 59 (1995); Radcl.-Sm., Fl. Zambesiaca 9 (4): 151, t. 31 (1996), Gen. Euphorb.: 192 (2001); Secco, Fl. Neotrop. 93: 55–134 (2004); van Welzen & Bulalacao, Syst. Bot. 32: 803–818 (2007), Males. spp.
Bossera Leandri (1962).

Dioecious (monoecious) trees and shrubs; indumentum simple or stellate. Leaves entire to

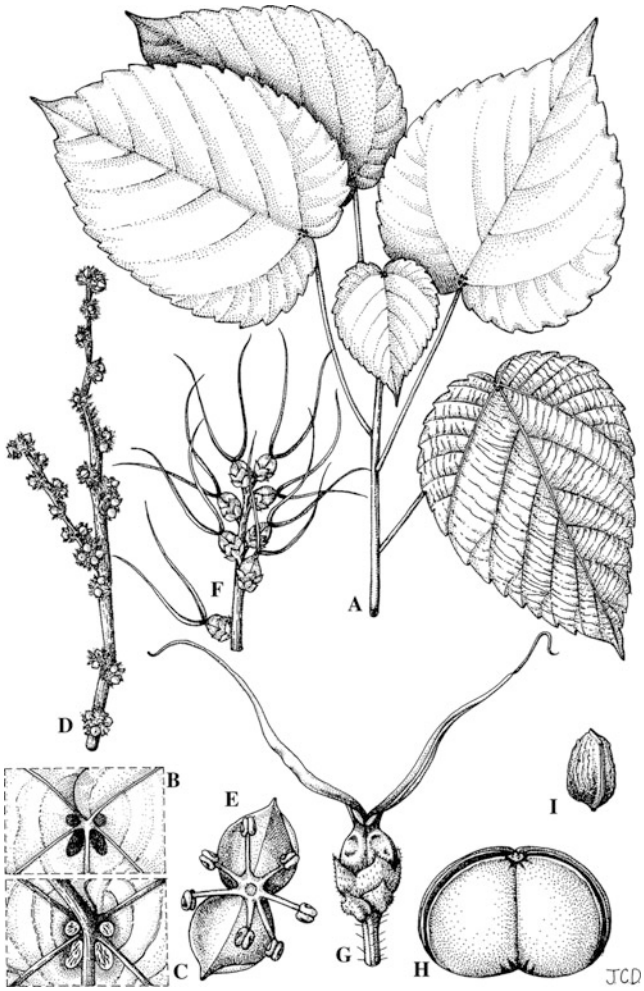

Fig. 24. Euphorbiaceae-Acalyphoideae. *Alchornea cordifolia*. **A** Branchlet. **B**, **C** Base of upper resp. lower leaf surface with extrafloral nectaries. **D** Part of staminate inflorescence, flowers in bud stage. **E** Staminate flower. **F** Tip of pistillate inflorescence, with anthetic flowers. **G** Pistillate flower. **H** Fruit. I Seed. (Radcliffe-Smith 1987; drawn by Judy Dunkley)

dentate, with laminar glands abaxially, sometimes stipellate; stipules persistent to deciduous, sometimes rudimentary. Inflorescences axillary, spiciform, often compound; bracts eglandular. Staminate flowers subsessile, in glomerules; calyx closed in bud, splitting into 2–5 valvate segments; petals 0; disk receptacular, confluent with base of filaments; stamens (3–)6–8(10), filaments basally slightly connate; anthers introrse or extrorse, muticous; pollen grains ± spheroidal, angulaperturate, 3-colporate, colpi operculate, endoapertures small and obscure, sexine tectate-rugulose, microverrucate; pistillode 0 or rudimentary. Pistillate flowers sessile or pedicellate; sepals usually (3)4(−6), imbricate, entire or denticulate, ± persistent in fruit; petals 0; disk obsolete; ovary 2(−5)-locular, usually pubescent (cristate); ovules with outer integument vascularized; stylodia nearly distinct, unlobed (emarginate). Fruits capsular, smooth or tuberculate; columella persistent. Seeds subglobose or elliptic, ecarunculate (with rudimentary caruncle), testa smooth or tuberculate; mesotesta vascularized. $n = 9, 18$.

About 42 spp., distributed in the Neotropics (23 spp.), Africa and Madagascar, and in Asia and Malesia. The American taxa differ from the Old World taxa in a number of characters such as indumentum and carpel number, and the palynological studies of Takahashi et al. (2000) indicate that the pollen grains of neotropical species have a prominently vermiculate-rugose exine, in distinct contrast with the punctate-spinulose tectum of the paleotropical species. *Bossera* was distinguished by the elevated number of stamens (10) and the cristately ornamented ovary, which is also present in *A. alnifolia*.

106. *Coelebogyne* Js. Sm.

Coelebogyne Js. Sm., Proc. Linn. Soc. London 1: 41 (1839); Baill., Étude Gén. Euphorb.: 416 (1858); Pax & K. Hoffm., Pflanzenr. 147, VII: 255, fig. 38 (1914); Radcl.-Sm., Gen. Euphorb.: 194 (2001).

Dioecious shrubs; indumentum simple. Leaves dentate, with basal and scattered laminar glands; stipules persistent. Inflorescences axillary, spiciform; bracts eglandular. Staminate flowers subsessile; calyx closed in bud, splitting into usually 4 valvate segments; petals and disk 0; stamens 8, filaments distinct; anthers muticous; pollen grains spheroidal, 3-colporate, colpi operculate, sexine tectate-perforate, microverrucate; pistillode 0. Pistillate flowers subsessile; sepals 5 or 6, imbricate, entire, basally glandular; petals and disk 0; ovary (2)3-locular; glabrous; stylodia stigmatiform. Fruits capsular; columella persistent. Seeds ecarunculate; testa smooth.

One or two spp., Australia (Queensland, NSW), very similar to the paleotropical spp. of *Alchornea* (*Cladodes*) and often merged with that genus.

107. *Aparisthmium* Endl.

Aparisthmium Endl., Gen. Pl.: 1112 (1840); Webster, Fl. Venez. Guayana 5: 99, fig. 97 (1999); Radcl.-Sm., Gen. Euphorb.: 194 (2000); Secco, Fl. Neotrop. 93: 134–143, fig. 56 (2005).

Dioecious trees or shrubs; indumentum simple. Leaves glandular-crenate, with basal laminar glands, stipellate at junction with petiole; stipules deciduous. Inflorescences terminal; staminate spicate-paniculate, pistillate racemose; bracts biglandular. Staminate flowers glomerulate, subsessile; calyx closed in bud, splitting into 3(4) valvate segments; petals and disk 0; stamens 3–5 (−10), filaments basally connate; anthers latrorse, muticous; pollen grains subspheroidal, 3-colporate, colpi operculate; sexine finely tectate-perforate, microverrucate; pistillode 0. Pistillate flowers pedicellate, with 2 basal glands; sepals 4, valvate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, ovules anatropous, smooth, pubescent; inner integuments thick, outer integuments thinner; stylodia thick, dilated, shallowly bifid at tip, papillose. Fruits capsular; columella persistent. Seeds ellipsoid, ecarunculate, testa smooth.

A single sp., *A. cordatum* (A. Juss.) Baill., widespread in tropical South America.

108. *Bocquillonia* Baill.

Bocquillonia Baill., Adansonia I, 2: 225 (1862); Airy Shaw, Kew Bull. 29: 321 (1974); McPherson & Tirel, Fl. Nouv. Calédonie 14(1): 114–143, t. 23–29 (1987).

Dioecious (monoecious) trees or shrubs; indumentum simple, but usually very sparse or 0. Leaves dentate, with dispersed laminar glands; stipules persistent but often minute. Inflorescences axillary, spiciform, sometimes reduced to glomerules; bracts ± persistent. Staminate flowers subsessile; calyx closed in bud, splitting into 2 or 3 valvate segments; petals and disk 0; stamens 2–4, filaments basally connate; anthers latrorse or extrorse, muticous; pollen grains suboblate to prolate spheroidal, 3-colporate, colpi operculate, sexine finely tectate-perforate, microverrucate; pistillode vestigial or 0. Pistillate flowers subsessile; sepals 4 or 5, imbricate, entire, ± persistent in fruit but inconspicuous; petals and disk 0; ovary 3-locular, pubescent; ovules anatropous, inner integuments moderately thick, outer thin; stylodia unlobed, ± ovate, dilated. Fruits capsular; columella persistent. Seeds oblong, ecarunculate (?), testa smooth.

Fourteen spp., all endemic to New Caledonia.

5b. Subtribe Conceveibinae G.L. Webster (1975).

Leaf blades not stipellate; indumentum stellate; floral disk 0; stamens 15–60; pistillate sepals often glandular; ovary 2–3-locular, inner integuments equaling or thicker than outer integuments; stylodia bifid; seeds carunculate.

Two genera, one neotropical, the other African.

109. *Conceveiba* Aubl.

Conceveiba Aubl., Hist. Pl. Gui.: 923, t. 353 (1775); Müll. Arg. in DC., Prodr. 15(2): 895 (1866), Fl. Brasil. 11(2): 370, t. 55 (1874); Pax & K. Hoffm., Pflanzenr. 147, VII: 214, fig. 32 (1914); Macbride, Field Mus. Nat. Hist., Bot. 13 (3A, 1): 152 (1951); Jablonski, Mem. N. Y. Bot. Gard. 17: 131 (1967); Secco, Fl. Neotrop. 93: 143–177 (2005).
Gavarretia Baill. (1860).
Conceveibastrum (Müll. Arg.) Pax & K. Hoffm. (1914).
Veconcibea (Müll.Arg.) Pax & K. Hoffm. (1914).

Dioecious (monoecious) trees or shrubs; indumentum stellate and sometimes simple as well. Leaves glandular-crenate or entire; stipules persistent or deciduous, or 0. Inflorescences terminal or axillary, the staminate paniculate or racemose, the pistillate racemose or spicate; bracts often biglandular. Staminate flowers subsessile or pedicellate; calyx closed in bud, splitting into 3 or 4 valvate segments or lobes; petals and disk 0; outer staminodes sometimes +; stamens 7–60, filaments distinct or slightly connate at base; up to 35 inner stamens sometimes infertile; anthers extrorse or introrse, connective sometimes enlarged; pollen grains oblate to prolate spheroidal, 3-colporate, colpi operculate, endoapertures lalongate, sexine finely tectate-perforate, microverrucate; pistillode 0 (+). Pistillate flowers pedicellate; sepals 3–8, distinct or connate, glandular at base, deciduous in fruit; petals and disk 0; ovary 2–3-locular, pubescent; ovules anatropous, inner and outer integuments moderately thick; stylodia usually completely distinct and distally to deeply bipartite. Fruits capsular, smooth to rugose; columella not persistent. Seeds oblong, carunculate, hilum triangular, testa smooth.

About 12 spp., tropical Central and South America.

110. *Aubletiana* J. Murillo-A. Fig. 25

Aubletiana J. Murillo-A., Rev. Colomb. Cienc. 24: 360 (2000).
Conceveiba Aubl. quoad Thomas, Ann. Missouri Bot. Gard. 77: 856, fig. 1 (1990) et Breteler & Mennega, Bull. Jard. Bot. Belg. 63: 209–217, t. 1 (1994).

Monoecious trees; indumentum simple. Leaves dentate with often gland-tipped teeth; the blade with two glands at the junction of the petiole;

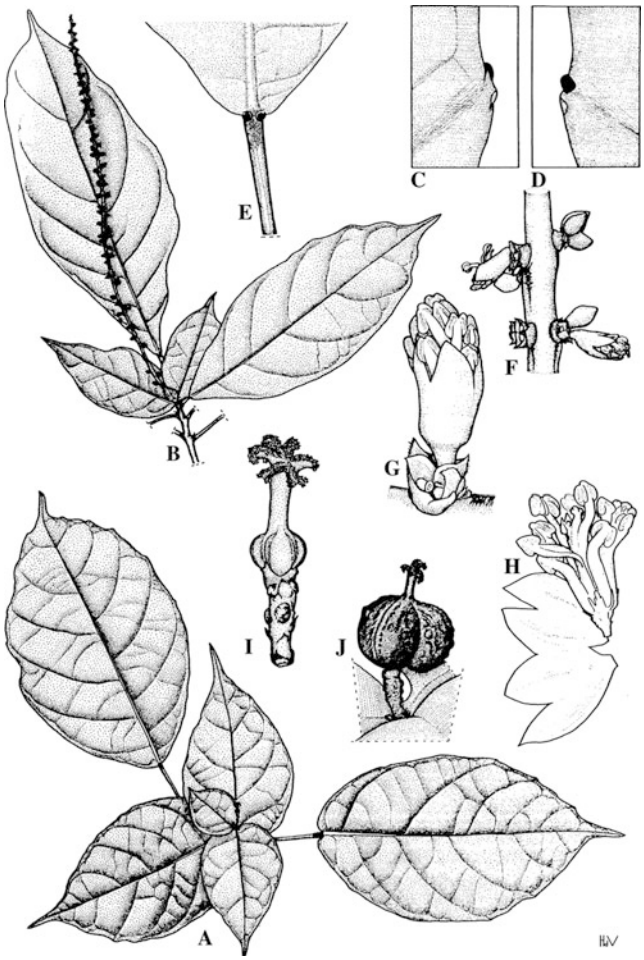

Fig. 25. Euphorbiaceae-Acalyphoideae. *Aubletiana leptostachys*. **A** Branchlet. **B** Same, with staminate inflorescence. **C** Leaf margin with gland seen from above. **D** Same, from beneath. **E** Base of leaf blade with glands. **F** Detail of inflorescence. **G** Staminate flower. **H** Androecium and perianth of staminate flower. **I** Pistillate flower. **J** Fruit. (Breteler 1994; drawn by H. de Vries)

stipules lateral. Staminate inflorescences axillary panicles with contracted 3–4-flowered cymes; pistillate inflorescences terminal spikes or flowers solitary. Staminate flowers: sepals 4 or 5, for lower half connate, valvate; petals and disk 0; stamens 7–12, sometimes with a few staminodes; pollen tricolporate-operculate [Murillo fide Punt]; pistillode +, glabrous or pubescent. Pistillate flowers solitary, sepals sometimes basally glandular; petals and disk 0; ovary 3-carpellate; ovule 1 per locule; stylodia at the base connate into a style provided with 3 undivided or divided style branches. Fruit papillose, 3-lobed, dehiscent, splitting into 3 1-seeded cocci, leaving no column. Seeds ellipsoid, with a triangular hilum, ecarunculate, exarillate.

Two West African spp., Cameroun, Gabon.

5c. Subtribe Mareyopsinae G.L. Webster (2004).

Dioecious; indumentum simple; leaves alternate, lamina puncticulate; inflorescences axillary; flowers subsessile; staminate disk segments and stamens 8; fruits indehiscent, seeds ecarunculate.

A monogeneric African tribe.

111. *Mareyopsis* Pax & K. Hoffm.

Mareyopsis Pax & K. Hoffm., Pflanzenr. 147, XIV: 13 (1919); Léonard, Bull. Jard. Bot. Nat. Belg. 65: 15, fig. 3 (1996), Fl. Afr. Centr. Euphorb. 3: 16, t. 2 (1996); Breteler, Bull. Jard. Bot. Belg. 66: 133, figs. 1, 3 (1997); Radcl.-Sm., Gen. Euphorb.: 223 (2001).

Dioecious trees or shrubs; indumentum simple. Leaves translucent-punctate with scattered embedded glands, ± glandular-dentate; stipules deciduous. Inflorescences axillary, often ramiflorous, generally fasciculate, spiciform; bracts entire, persistent. Staminate flowers subsessile; calyx closed in bud, splitting into 3–5 valvate segments; petals 0; disk-segments 8, in 4 pairs, extrastaminal; stamens 8, biseriate, filaments distinct, flattened and ligulate; anthers muticous or apiculate, connective somewhat enlarged, thecae pendulous; pollen grains 3-angled, 3-colporate, colpi granulose, neither marginate nor operculate; sexine tectate-perforate and ± rugulose, microverrucate; pistillode prominent, 2- or 3-lobed. Pistillate flowers subsessile; sepals 3–4(5), basally connate, open in bud; petals 0; disk 3- or 4-lobed; ovary 2–3(4)-locular, pubescent; stylodia nearly distinct, unlobed, papillate. Fruits indehiscent, exocarp coriaceous. Seeds ecarunculate, testa smooth.

Two spp. of tropical West Africa. *Mareyopsis* was incorrectly treated by Webster (1994) as a synonym of *Mareya*, but Léonard (1996) conclusively demonstrated that the two genera are not closely related.

6. Tribe Ricineae Bartl. (1830).

Monoecious or dioecious trees or shrubs; indumentum stellate or 0; leaves simple to deeply lobed, dentate; inflorescences terminal or opposite leaves; spiciform or paniculate; staminate calyx closed in bud, splitting into valvate

segments; petals and disk 0; stamens 30–1,000, filaments distinct or connate; anthers biloculate; pollen grains spheroidal, 3–5-colpate, colpi inoperculate, emarginate; pistillate sepals 3–5, imbricate; petals and disk 0; ovary 3-locular; stylodia bifid; fruits capsular; seeds carunculate.

The genera comprised in this tribe earlier had been included in two different subtribes of the Acalypheae (Webster 1994), from which they differ in many respects such as the carunculate seeds and terminal inflorescences. The exine structure, which is very similar in both genera (Takahashi et al. 2000), led Webster to unite them in a tribe. The molecular data of Wurdack et al. (2005) place both genera in the alcalyphoid clade A4, but *Ricinus* as sister to *Speranskia*, and *Adriana* as sister to *Monotaxis*, though both with low support. Available data are insufficient for improving this unsatisfactory placement.

Key to the Genera of Ricineae

1. Dioecious; filaments distinct; pistillate sepals persistent in fruit; stipules distinct, glandular **112. *Adriana***
– Monoecious; filaments connate into fascicles; pistillate sepals deciduous; stipules connate, deciduous **113. *Ricinus***

112. *Adriana* Gaud.

Adriana Gaud., Ann. Sci. Nat. Paris 5: 223 (1825); Pax, Pflanzenr. 147, II: 17 (1910); Airy Shaw, Kew Bull. 35: 589 (1980); C.L. Gross & M.A. Whalen, Austral. Syst. Bot. 9: 757, figs. 1–4 (1996); Radcl.-Sm., Gen. Euphorb.: 202, fig. 25 (2001).

Dioecious shrubs; indumentum stellate or 0. Leaves alternate or opposite, petiolate or sessile, pinnately or palmately veined, coarsely dentate; stipules persistent, ± glandular. Inflorescences terminal or opposite the leaves, spiciform, the pistillate shorter and more condensed than the staminate; bracts glandular. Staminate flowers subsessile; calyx splitting into 4–5 valvate segments; petals and disk 0; stamens numerous, filaments distinct; anthers extrorse, linear, much longer than filaments, connective conspicuously apiculate; pollen grains spheroidal, 3–5-colporate, colpi inoperculate, sexine finely tectate-perforate and microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 6–8, imbricate, persistent in fruit; petals and disk 0; ovary 3-locular, stellate-tomentose, sometimes muricate; ovules with outer integuments vascularized, equaling inner integuments in thickness; stylodia bipartite, coarsely papillate. Fruits capsular; columella persistent. Seeds oblong, carunculate, testa pale, rugulose.

Two variable spp., Australia.

113. *Ricinus* L.

Ricinus L., Sp. Pl.: 1007 (1753), Gen. Pl. ed. 5: 437 (1754); Müll. Arg. in DC., Prodr. 15(2): 1016 (1866); Pax & K. Hoffm., Pflanzenr. 147, XI: 119 (1919); Webster, J. Arnold Arb. 48: 379, fig. 4 (1967); Purseglove, Trop. Crops, Dicot. 1: 180, fig. 27 (1968); van Welzen, Blumea 43: 151 (1998).

Monoecious shrub or tree, herbaceous in temperate regions; indumentum simple or 0. Leaves palmately lobed, peltate, denticulate to serrulate; petiole elongated, glandular basally and at junction with blade; stipules connate into a deciduous sheath, leaving a circumaxial scar. Inflorescences terminal, sometimes pseudo-axillary, paniculate; staminate cymules proximal, distal cymules bisexual or pistillate; bracts papery, glandular at base. Staminate flowers pedicellate, articulate in the middle; calyx closed in bud, splitting into 3–5 valvate segments; petals and disk 0; stamens very numerous, to 1,000, filaments partially connate and irregularly branched; anthers introrse, locules distinct and subglobose; pollen grains subspheroidal, angulaperturate, 3-colporate, colpi not operculate, sexine finely tectate-perforate/reticulate and microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 3–5, entire, deciduous; petals and disk 0; ovary 3-locular, prominently echinate, glabrous; ovules pachychalazal, with inner integuments thick, outer integuments thin; stylodia basally connate, bifid, conspicuously papillate. Fruits capsular; columella persistent, distally winged. Seeds ellipsoid-compressed, carunculate, testa smooth. $2n = 20$.

The single sp., *R. communis* L., is probably native originally to east Africa but early dispersed by man to India. It is highly variable due to its cultivation for the oil from the seeds ("castor beans"). The combination of a thick inner integument, a pachychalazal ovule, and an arillate seed makes *Ricinus* unique among Acalyphoids (Tokuoka and Tobe 2003).

7. Tribe Acalypheae Dumort. (1829).

Monoecious or dioecious trees, shrubs, or herbs; indumentum simple or stellate; leaves simple or lobed, pinnately or palmately veined, glandular or eglandular; inflorescences terminal or axillary, spiciform or racemose to paniculate, unisexual or

bisexual; staminate calyx closed in bud, splitting into 2–5 valvate segments; disk intrastaminal, interstaminal, or 0; stamens 4–many; anthers sometimes apiculate, anther sacs sometimes pendulous; pollen grains ± spheroidal, 3–4-colporate, colpi inoperculate; sexine tectate-perforate or rugulose, usually microverrucate; pistillode usually 0; pistillate sepals mostly 3–6, distinct; petals 0; disk cupular or 0; ovary 2–4-locular; stylodia unlobed to multifid or lacerate; fruits capsular or drupaceous; seeds carunculate or ecarunculate; testa dry or fleshy.

This is the largest tribe in the Acalyphoideae, with 9 subtribes including a total of 28 genera, and over 1,000 species. With the removal of subtribes Adrianinae and Ricininae, tribe Acalypheae is somewhat more homogeneous but still remarkably diverse, and further revision of its boundaries will be necessary.

Key to the Subtribes of Acalypheae

1. Filaments connate, distally ramified; stylodia unlobed **7i. Lasiococcinae**
– Filaments distinct or basally connate, not ramified; stylodia bifid or unlobed 2
2. Indumentum stellate and abaxial leaf surfaces with minute beadlike glands [0.1 mm in diam.]; stylodia unlobed, often plumose or laciniate; seed testa often fleshy **7h. Rottlerinae**
– Indumentum mostly simple; abaxial leaf surfaces lacking minute beadlike glands; stylodia lobed or unlobed; seed testa dry or fleshy 3
3. Pollen exine finely reticulate; syles unlobed; seeds carunculate; mostly herbaceous 4
– Pollen exine tectate-perforate to rugulose; stylodia lobed or unlobed; seeds carunculate or ecarunculate; mostly woody 5
4. Staminate sepals discrete; anthers muticous; pollen grains distinctly colporate; cotyledons broader than radicle **7c. Mercurialinae**
– Staminate sepals connate; anthers apiculate; pollen grains with rudimentary colpi; cotyledons scarcely broader than radicle **7d. Dysopsidinae**
5. Anthers apicifixed, thecae divergent from filament; stylodia unlobed, sometimes plumose or laciniate 6
– Anthers basifixed or dorsifixed, thecae adnate to connective, not divergent from filament; stylodia bifid to multifid 7
6. Anthers not vermiform; pollen grains colporate; staminate disk present **7b. Claoxylinae**
– Anthers vermiform; pollen grains pseudo-porate; staminate disk 0 **7f. Acalyphinae**
7. Staminate disk of interstaminal segments, pistillate disk 0; seed testa fleshy **7g. Blumeodendrinae**
– Staminate and pistillate disk 0; seed testa dry 8
8. Stylodia bifid; inflorescences axillary, racemoid or spiciform; staminate flowers pedicellate **7a. Cleidiinae**
– Stylodia unlobed; inflorescences terminal, dichasial; staminate flowers subsessile **7e. Avellanitinae**

7a. Subtribe Cleidiinae G.L. Webster (1975).

Monoecious or dioecious; indumentum simple; leaves with laminar glands, stipulate; inflorescences axillary, spiciform or racemose; staminate flowers without petals or disk, sepals 3 or 4, stamens 25–80, anthers 2(4)-celled, usually apiculate; pollen grains 3-colporate, colpi not operculate, sexine tectate-perforate or rugulose-vermiculate, microverrucate; pistillode 0; pistillate sepals 3–6, imbricate; ovary (2)3-locular; stylodia bifid, branches elongate; fruit capsular; seeds ecarunculate, testa not fleshy.

Three genera, two restricted to southeast Asia and Australia, *Cleidion* widespread. The very graceful, elongate stylodia of *Cleidion* and *Wetria* and their distantly placed pistillate flowers (see our Figs 26 and 27 and Fig. 27 in Radcliffe-Smith 2001) are strongly indicative of anemophily.

Key to the Genera of Subtribe Cleidiinae

1. Staminate flowers subsessile, 1 per bract; stamens 15–25; pollen exine tectate-perforate **115. *Sampantaea***
– Staminate flowers pedicellate, usually 2 or more per bract; stamens 25–80; pollen exine tectate-rugulose 2
2. Pistillate sepals valvate; anthers muticous, 2-celled, dehiscing longitudinally; stamens 25–30 **114. *Wetria***
– Pistillate sepals imbricate; anthers apiculate, 4-celled, dehiscing cruciately; stamens mostly 30–80 **116. *Cleidion***

114. *Wetria* Baill. Fig. 26

Wetria Baill., Étude Gén. Euphorb.: 409 (1858); J. J. Smith, Med. Dept. Landb. 10: 470 (1910); Pax & Hoffm., Pflanzenr. 147,VII: 219 (1914); Forster, Austrobaileya 4: 139–143, fig. 1 (1994); Webster, Ann. Missouri Bot. Gard. 81: 86 (1994); van Welzen, Blumea 43: 156, fig. 5 (1998); Radcl.-Sm., Gen. Euphorb.: 209, fig. 27 (2001).

Dioecious trees; indumentum simple, scanty. Leaves subentire, with several glands near base; stipules deciduous. Inflorescences axillary, slender, the staminate spiciform, nodes with solitary flowers or glomerules, the pistillate racemoid, with solitary flowers; bracts entire, acute, persistent. Staminate flowers pedicellate; calyx closed in bud, splitting into 3 or 4 valvate segments;

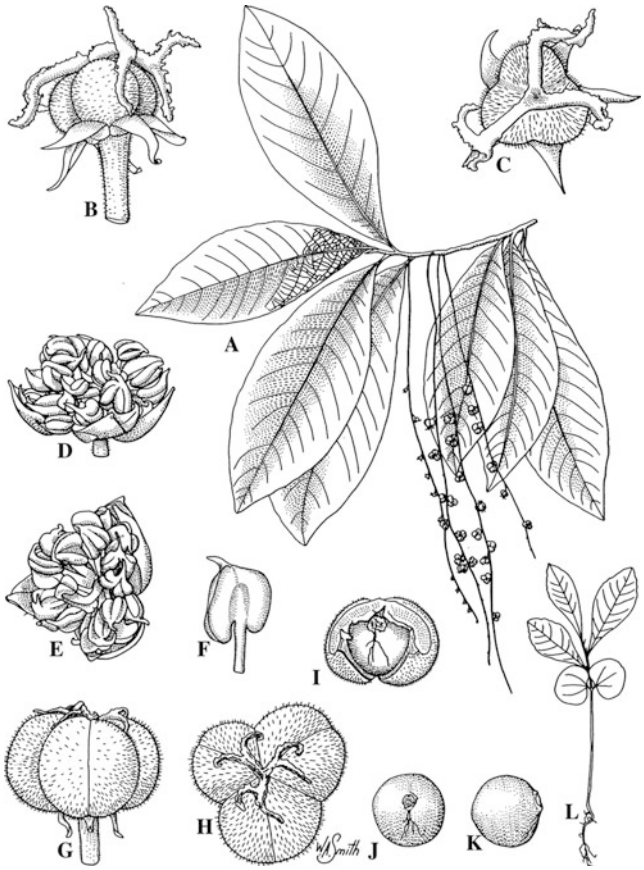

Fig. 26. Euphorbiaceae-Acalyphoideae. *Wetria australiensis*. **A** Branchlet with flowers and fruits. **B**, **C** Pistillate flower in side and face view. **D**, **E** Staminate flower in side and face view. **F** Stamen. **G**, **H** Fruit in side and face view. **I** Capsule with seed. **J**, **K** Seed in ventral and lateral view. **L** Seedling. (P.I. Forster 1994; drawn by W. Smith)

petals and disk 0; receptacle pubescent; stamens 25–30, filaments distinct; anthers latrorse, muticous or apiculate, 2-celled; pollen grains prolate spheroidal, (3)4-colporate, colpi emarginate, sexine tectate-vermiculate, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 5, imbricate, persistent in fruit; petals and disk 0; ovary 3-locular, pubescent; ovules anatropous, inner integument thick, outer integument thin; stylodia bifid, branches thin, elongate. Fruits capsular, 3-lobed; columella persistent, angled and apically dilated. Seeds spheroidal, testa smooth.

Two spp., one in southeast Asia and Malesia, the other in Queensland and New Guinea. In Webster (1994) *Wetria* was placed in subtribe Cleidiinae, a disposition supported by the more recent studies of Fernández-González and Lobreau-Callen (1996) and van Welzen (1998). In the molecular analysis of Wurdack et al. (2005), *Wetria* is resolved in a clade with the African/Malagasy genera *Argomuellera* and *Pycnocoma* (in the combined analysis) and in a clade with the Thai genus *Sampantaea* (see note under following genus).

115. *Sampantaea* Airy Shaw

Sampantaea Airy Shaw, Kew Bull. 26: 328 (1972), Hook. Ic. Pl. 38: t. 3717 (1974); Radcl.-Sm., Gen. Euphorb.: 212 (2001).

Dioecious trees; indumentum simple. Leaves subsessile or short-petiolate, entire, with 1–3 small glands near base; stipules deciduous. Inflorescences axillary, solitary or fascicled, spiciform, flexuous; bracts persistent, eglandular. Staminate flowers sessile; calyx closed in bud, splitting into 2 (3) valvate segments; petals and disk 0; stamens 15–25, filaments nearly suppressed; anthers subsessile, oblong, minutely apiculate; pollen grains subprolate, 3-colpate or rarely 3-colporate, endoaperture minute; sexine tectate-perforate and microverrucate; pistillode 0. Pistillate flowers subsessile; sepals 5, imbricate, entire; petals and disk 0; ovary 3-loculare, pubescent; stylodia basally connate, erect, thin, elongate. Fruits not seen.

A single sp., *S. amentiflora* (Airy Shaw) Airy Shaw, known from Thailand and Cambodia. In spite of the pollen morphological difference between *Sampantaea* and *Cleidion*/*Wetria* (Fernández-González and Lobreau-Callen 1996), the genus is strongly resolved as sister to *Wetria* in the *trn*L-F analysis of Wurdack et al. (2005).

116. *Cleidion* Blume Fig. 27

Cleidion Blume, Bijdr. Fl. Ned. Ind.: 612 (1826); Leandri, Adansonia II, 12: 193 (1972); A.C. Smith, Fl. Vitiensis Nova 2: 514, fig. 136 (1981); McPherson & Tirel, Fl. Nouv.-Caled. 14: 143–169, t. 30–34 (1987); Webster, Ann. Missouri Bot. Gard. 81: 86 (1994); Philcox, Fl. Ceylon 9: 166 (1997); Kulju & van Welzen, Blumea 50: 197–219, figs. 1–6 (2005); Qiu Huaxing & Gilbert, Fl. China 11: 244 (2008).
? *Polyandra* Leal, Arch. Jard. Bot. Rio de Janeiro 11: 63, fig. 1 (1961); Webster & Huft, Ann. Missouri Bot. Gard. 75: 1087–1144 (1988); Secco, Fl. Neotrop. 93: 13, 178 (2004).

Monoecious or dioecious trees or shrubs; indumentum simple or 0. Leaves often dentate, abaxially with laminar glands; stipules persistent or deciduous. Inflorescences axillary, usually unisexual; staminate spiciform, sometimes compound,

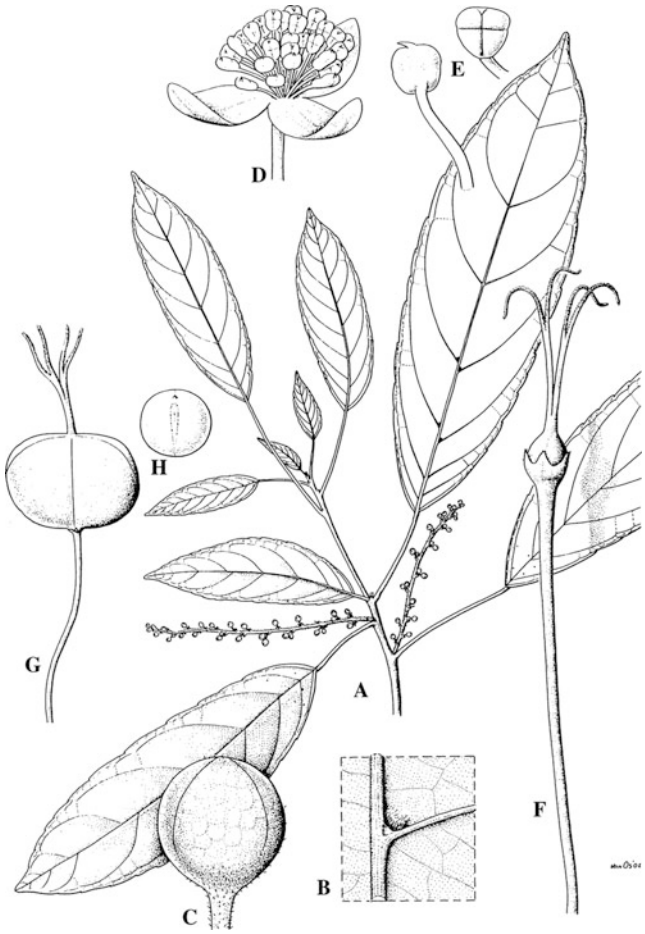

Fig. 27. Euphorbiaceae-Acalyphoideae. *Cleidion javanicum*. **A** Branch of staminate plant. **B** Domatium on lower leaf surface. **C** Staminate bud. **D** Staminate flower. **E** Anthers with cruciate cells. **F** Pistillate flower. **G** Fruit. **H** Seed. (Kulju and van Welzen 2005; drawn by J. van Os)

flowers in glomerules, pistillate racemose, sometimes reduced to 1 or 2 flowers; bracts eglandular, inconspicuous. Staminate flowers subsessile or pedicellate; calyx closed in bud, splitting into 3 or 4 valvate segments; petals and disk 0; receptacle convex, stamens 20–100, filaments distinct, straight in bud; anthers with enlarged connective, apiculate, 4-celled, on both sides 2 cells above each other, dehiscing introrsely and cruciately; pollen grains oblate to prolate spheroidal, 3-colporate, colpi inoperculate, sexine tectate-punctate, tectum rugulate or microverrucate; pistillode 0. Pistillate flowers long-pedicellate; sepals 3–5, imbricate, entire, persistent in fruit; petals and disk 0; ovary (2)3-locular, pubescent; ovules anatropous, inner integument thick, outer integument thin; stylodia basally connate, erect, deeply bifid, branches elongate, thin. Fruits capsular; columella persistent. Seeds subglobose, testa smooth.

About 25 spp., 5 neotropical [except the West Indies], 2 in west Africa and Madagascar, the remainder from India and China to islands in the southwest Pacific, 12 endemic in New Caledonia. In the molecular analysis (Wurdack et al. 2005), *Cleidion* is resolved as basal to *Blumeodendron*, *Macaranga* and *Mallotus*, but lacks the vascular bundles in the outer integuments of those genera.

Polyandra, which is only known from a single staminate specimen collected in central Amazonia, possesses 4-locellate stamens, which led Webster and Huft (1988) to propose a relationship to *Cleidion*. Murillo-A. (2000) synonymised *Cleidion prealtum* Croizat with *Polyandra* and transferred it into *Conceveiba*. The identity of *Polyandra* with *C. prealtum* is still uncertain because the type of the latter species has only solitary pistillate flowers, which would exclude it from *Conceveiba* (Secco 2004). Although both *Polyandra* and the type collection of *C. prealtum* come from the same region of Central Amazonia near Borba, a clarification of the status of *Polyandra* and confirmation of its place in subtribe Cleidiinae would require pistillate material of *Polyandra*.

7b. Subtribe Claoxylinae Hurus. (1954).

Monoecious or dioecious trees, shrubs, or herbs; indumentum simple; inflorescences axillary, racemose or paniculate; staminate sepals 2–5; disk annular and extrastaminal or segmented and interstaminal; stamens 5–40(−200); filaments distinct; anthers extrorse, thecae discrete, ± erect from enlarged connective; pollen grains 3-colporate, colpi inoperculate, emarginate; pistillate sepals 2–4, open or imbricate; disk annular or dissected; ovary mostly 2- or 3-locular; stylodia unlobed, lacerate; fruits capsular, columella ± deciduous; seeds ecarunculate, testa usually fleshy.

Subtribe Claoxylinae is a paleotropical group of 6 genera, best represented in Africa. *Amyrea*, included here in Webster (1994), is now placed in the Pycnocomeae. The systematic position of *Mareya* is still controversial. Baillon (1860) originally noted similarities to *Claoxylon* and *Pycnocoma*, while Müller (1866) saw an affinity with *Alchornea*.

Pax and Hoffman (1919) inserted *Mareya* in their Bernardiiformes [= Bernardieae], but it clearly does not belong in the same taxon as *Bernardia*. Webster (1994) assigned *Mareya* to Acalypheae subtribe Claoxylinae, but Radcliffe-Smith (2001) created a new subtribe Mareyinae to include both *Mareya* and *Mareyopsis*. Pollen evidence (Fernández-González and Lobreau-Callen 1996) indicates that *Mareya*, but not *Mareyopsis*, has pollen characteristic of the Claoxylinae. In the molecular analysis of Wurdack et al. (2005), *Mareyopsis* goes with *Alchorneopsis* and *Alchornea*, and the Old World *Mareya* is in a clade with New and Old World *Acalypha*. Morphological similarities between the two genera include traits such as the laciniate stylodia, the pendulous anther locules, and seed and pollen morphology. It is remarkable that in the molecular analysis *Mercurialis* is basal to the Claoxylinae clade.

Key to the Genera of Subtribe Claoxylinae

1. Leaf blades stipellate; seed coat not fleshy **117. *Mareya***
– Leaf blades not stipellate or, if so, then seed coat fleshy 2
2. Indumentum stellate **119. *Lobanilia***
– Indumentum simple 3
3. Stipules usually persistent; buds perulate **122. *Erythrococca***
– Stipules usually deciduous; buds not perulate 4
4. Racemes interrupted; capsules crustaceous; leaf blades stipellate **121. *Micrococca***
– Racemes uniformly floriferous; capsules coriaceous; leaf blades not stipellate 5
5. Staminate disk of interstaminal segments; stamens 10–200 **118. *Claoxylon***
– Staminate disk urceolate, extrastaminal; stamens 6–12 **120. *Discoclaoxylon***

117. *Mareya* Baillon

Mareya Baillon, Adansonia 1: 73 (1860); Adam, Mém. Mus. Nat. Hist. Nat. Bot. 20: 495, fig. 184 (1971); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb.:1: 216 (1987); J. Léonard, Fl. Afr. Centr. Euphorb. 3: 18, t. 3 (1996).

Monoecious trees or shrubs; indumentum simple. Leaves abaxially glandular-puncticulate, entire to denticulate, adaxially with 2 or more embedded glands near base; petiole sometimes adaxially stipellate at junction with blade, the stipels deciduous; stipules deciduous. Inflorescences axillary and sometimes terminal as well, spiciform, slender; bisexual; with proximal staminate and distal bisexual glomerules; bracts eglandular, persistent. Staminate flowers subsessile or pedicellate; calyx closed in bud, splitting into (2) 3 or 4 valvate segments; petals 0; disk of numerous interstaminal segments; stamens (9) 10–40, filaments distinct; anther connective bifurcate, locules pendent; pollen grains subspheroidal, angulaperturate, 3-colp(or)ate, inoperculate, emarginate, endoapertures very narrow; sexine tectate-perforate, microverrucate; pistillode usually 0. Pistillate flowers subsessile or pedicellate; sepals 3–5, imbricate or open in aestivation, entire, persistent in fruit; petals 0; disk annular-lobed; ovary 3-locular, pubescent; ovules with inner integument thick, outer integument thin; stylodia distinct, unlobed, ± plumose or laciniate. Fruits capsular; columella persistent. Seeds subglobose, testa smooth, not fleshy.

Three spp., tropical West and Central Africa.

118. *Claoxylon* A. Juss.

Claoxylon A. Juss., Euphorb. Tent.: 43, t. 14 (1824); A.C. Sm., Fl. Vit. Nova 2: 516 (1981); Coode, Fl. Mascar. 160: 58, t. 12, 13 (1982); N. Rani & N.P. Balakr., Rheedea 5: 113, figs. 1–8 (1995); Florence, Fl. Polynésie Française 1: 54, figs. 6–8 (1997); Forster, Austrobaileya 7: 451–472 (2007), Austral. spp.; Qiu Huaxing & Gilbert, Fl. China 11: 245–246 (2008).
Claoxylopsis Leandri (1938); Radcl.-Sm., Kew Bull. 43: 625–647 (1988).

Dioecious (monoecious) trees and shrubs; indumentum simple or 0. Leaves entire or dentate, often purplish when young, abaxially minutely punticulate and eglandular; stipules minute, deciduous. Inflorescences axillary, racemoid; staminate bracts with 1–several flowers, pistillate bracts with 1 flower; bracts eglandular. Staminate flowers pedicellate; calyx closed in bud, splitting into 2–4 valvate segments; petals 0; disk of interstaminal segments; stamens (10–)20–30(−200), filaments distinct; anthers extrorse, muticous, connective not enlarged, anther sacs distinct from connective and erect; pollen grains spheroidal, 3–5-colporate, colpi granulose, sexine finely tectate-perforate, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals (2)3(4), distinct, imbricate, entire, persistent in fruit; petals 0; disk cupular or deeply lobed; ovary 2–3(4)-locular, glabrous or pubescent; ovules anatropous, inner and outer integuments thin [4–6 cell layers]; stylodia nearly distinct, unlobed, papillose. Fruits capsular or indehiscent, 3-lobed, cocci reticulate; columella sometimes persistent. Seeds globose, exotesta fleshy, endotesta hard and rugose or foveolate. $n = 18, 31, 54$.

About 75 spp., all Asiatic and Australasian except for 10 species in Madagascar. *Claoxylopsis* was accepted as distinct by Webster (1994) and Radcliffe-Smith (1988, 2001), but it does not appear to have any convincing differences. It might be included in *Claoxylon* sect. *Parviflora*.

119. *Lobanilia* Radcl.-Sm.

Lobanilia Radcl.-Sm., Kew Bull. 44: 334, t. 1 (1989); Schatz, Generic Tree Fl. Madagascar: 157 (2001).
Claoxylon sect. *Luteobrunnea* Pax & K. Hoffm. (1914).

Dioecious trees; indumentum stellate, sometimes simple as well. Leaves glandular-serrate to entire, densely stellate-pubescent abaxially; stipules deciduous. Inflorescences axillary, racemiform, the staminate elongate, pistillate contracted. Staminate flowers pedicellate; calyx closed in bud, splitting into 3 valvate segments; petals 0; disk segments interstaminal; stamens 15–30, filaments distinct; anthers extrorse, basifixed, 2-celled, thecae erect; pollen grains subspheroidal, 3-colporate, colpi inoperculate, sexine finely tectate-perforate and microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 3, open in bud, reflexed; petals 0; disk annular or of 3 segments; ovary 3–4-locular; stylodia nearly distinct, unlobed, reflexed, papillate-plumose. Fruit capsular, loculicidally dehiscent. Seeds subglobose, extotesta fleshy.

Eight spp., endemic to Madagascar.

120. *Discoclaoxylon* (Müll. Arg.) Pax & K. Hoffm.

Discoclaoxylon (Müll. Arg.) Pax & K. Hoffm., Wiss. Ergebn. Deutsche Zentral-Afr. Exped. 2: 452 (1912), Pflanzenr. 147, VII: 137, fig. 19 (1914); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 279, fig. 54 (1987).
Claoxylon sect. *Discoclaoxylon* Müll. Arg. (1864).

Dioecious trees and shrubs; indumentum simple. Leaves abaxially minutely puncticulate, margins glandular-dentate, without laminar glands; stipules deciduous. Inflorescences axillary, staminate racemose, flowers several per glomerule, pistillate spiciform, flowers 1 per node; bracts small, persistent, eglandular or obscurely glandular. Staminate flowers pedicellate; calyx closed in bud, splitting into 3 or 4 valvate segments; petals 0; disk urceolate or dissected; stamens 6–12, filaments distinct, shorter than anthers; anthers muticous; pollen grains subprolate, 3-colporate, exine tectate-perforate, microverrucate; pistillode 0. Pistillate flowers subsessile; sepals 4, entire, persistent in fruit; disk 2-lipped, segments petaloid; ovary 2-locular, pubescent; stylodia abbreviated, dilated, lacerate. Fruits capsular, deeply 2-lobed, loculicidal; columella not persistent. Seeds globose, exotesta fleshy, endotesta smooth or reticulate.

Four spp., W African, three of them endemic to the São Tomé Islands.

121. *Micrococca* Benth.

Micrococca Benth., Niger Fl.: 503 (1849), Gen. Pl.: 309 (1880); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 260, fig. 52 (1987), Fl. Zambesiaca 9(4): 176, t. 37 (1996); Sagun & van Welzen, Blumea 47: 149, fig. 1 (2002).
Claoxylon sect. *Micrococca* (Benth.) Müll. Arg. (1865).

Monoecious or dioecious shrubs or herbs; buds not perulate; indumentum simple. Leaves minutely puncticulate adaxially, entire or dentate; stipules persistent. Inflorescences axillary, sometimes fasciculate, unisexual or sometimes bisexual, ± spiciform; bracts eglandular, ± glumaceous. Staminate flowers pedicellate; calyx closed in bud, splitting into 3 valvate segments; petals 0; disk of interstaminal segments, or 0; stamens 5–50, filaments distinct; anthers extrorse, basifixed, muticous, pollen grains spheroidal, 3–4-colporate, colpi inoperculate, sexine finely tectate-reticulate, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 3 or 4, imbricate, persistent in fruit, petals 0; disk segments 3, linear; ovary 3-locular, pubescent; ovules anatropous, inner integument thin, outer integument thinner; stylodia distinct, unlobed, plumose-laciniate. Fruits capsular, 3-lobed, scabridulous, sometimes purplish; columella persistent. Seeds subglobose, exotesta thin and fleshy, endotesta rugulose.

Twelve spp., distributed from South Africa and tropical Africa to Madagascar, Arabia, southern Asia, and Malesia.

122. *Erythrococca* Benth.

Erythrococca Benth., Niger Fl.: 506 (1849); Gilbert, Kew Bull. 42: 363, fig. 5 (1987); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 265, fig. 53 (1987), Fl. Zambesiaca 9(4): 165, figs. 35, 36 (1996).

Dioecious shrubs; buds perulate; indumentum simple. Leaves short-petiolate, without laminar glands, margins glandular-dentate to subtentire; stipules entire, persistent, sometimes spinose. Inflorescences axillary, glomerular or racemoid, glomerules sessile or capitellate-pedunculate; bracts minute. Staminate flowers pedicellate,

pedicels basally or mid-articulate; calyx closed in bud, splitting into 3–5 valvate segments; petals 0; disk segmented, sometimes segments interstaminal; stamens (2)10–60, filaments distinct; anthers extrorse, 2-celled, locules discrete, erect; pollen grains spheroidal, 3–5-colporate, narrowly operculate, sexine tectate-reticulate, obscurely verrucate; pistillode 0. Pistillate flowers articulate-pedicellate; sepals 2(−4), valvate, entire, persistent in fruit; disk segments 2 or 3, rarely entire; ovary 2(3)-locular, glabrous or pubescent; ovules anatropous; stylodia distinct or basally connate, unlobed, smooth to laciniate. Fruits capsular, deeply lobed, without a persistent columella. Seeds subglobose, exotesta fleshy, endotesta foveolate to nearly smooth.

Forty spp., from southern Africa to Ethiopia, 1 sp. extending into Arabia.

7c. Subtribe Mercurialinae Pax (1890).

Monoecious or dioecious herbs; indumentum simple; leaves alternate or opposite, without embedded laminar glands; inflorescences axillary, mostly unisexual, spiciform, glomerular, or of solitary flowers; stamens (2–)4–20, filaments distinct; anthers extrorse, muticous; pollen grains 3-colpor(oid)ate, sexine tectate-perforate and finely reticulate; ovary 2-locular, smooth or muricate; stylodia unlobed; fruit capsular; seeds ecarunculate.

A problematic alliance of three Old World genera: *Mercurialis* shows a number of characters in common with taxa in the Claoxylinae and is resolved in the same molecular clade (A2), but *Seidelia* and *Leidesia* appear in a different lineage (A5). The pollen grains of the three genera of Mercurialinae are very similar among themselves and to those of *Dysopsis* (Takahashi et al. 2000).

Key to the Genera of Subtribe Mercurialinae

1. Dioecious; stamens 8–20; pistillate disk segments (staminodia) 2; seeds carunculate **123. *Mercurialis***
– Monoecious; stamens 2–7; pistillate disk 0 or rudimentary; seeds ecarunculate 2
2. Capsule smooth; pistillate sepals 3; leaf blades entire or denticulate **124. *Seidelia***
– Capsule setose; pistillate sepals obsolete; leaf blades crenate-dentate **125. *Leidesia***

123. *Mercurialis* (Tournefort) L.

Mercurialis (Tournefort) L., Sp. Pl. 2: 1035 (1753), Gen. Pl. ed. 5: 437 (1754); Zimmermann et al. in Hegi, Ill. Fl. Mitteleur. 5(1): 126, figs. 1746–1750 (1925); Pojarkova, Fl. URSS 14: 295, t. 17.5 (1949); Vindt, Trav. Inst. Sci. Chérifien 6:13, fig. 7 (1953); Webster, J. Arnold Arb. 48: 366 (1967); Tutin, Fl. Europaea 2: 212 (1968); Radcl.-Sm., Fl. Iraq 4(1): 222, fig. 60 (1980); Correll, Fl. Bahama Arch.: 831, fig. 345 (1982); Güemes, Fl. Iberica 8: 201, t. 49, 50 (1997).

Dioecious (monoecious) perennial or annual herbs; rootstocks with purplish pigment; indumentum simple. Leaves opposite, dentate, with minute paired basal glands at junction with petiole; stipules scarious, sometimes glandular, persistent. Inflorescences axillary, unisexual, the staminate spiciform with flowers in glomerules, the pistillate glomerular or on brachyblasts; bracts scarious, persistent. Staminate flowers sessile or subsessile; petals and disk 0; calyx closed in bud, splitting into 3 valvate segments; petals and disk 0; stamens 8–15 (−20), filaments distinct; anthers extrorse, locules distinct, diverging from connective; pollen grains subprolate, 3-colporate; pistillode 0. Pistillate flowers pedicellate; sepals 3, imbricate, scarious, entire, ± persistent, sexine finely tectate-perforate and densely microverrucate; petals 0; disk segments [staminodia] 2, elongated; ovary 2-locular, glabrous or pubescent, sometimes appendiculate; ovules anatropous, inner integument thin, outer integument thick; stylodia distinct, unlobed, papillose. Fruits capsular; columella membranous-winged, persistent. Seeds ovoid or globose; testa smooth or papillate. $x = 8$.

Eight spp. of temperate Eurasia (Macaronesia to eastern Asia). The genus has been intensely studied in Europe since the 17th century, and biosystematics studies of the European taxa have been made by Durand (1963) and Krähenbühl et al. (2002). *Mercurialis* resembles genera of Claoxylinae in its leaves and flowers with bluish pigment, but its pollen grains are different, and more suggestive of the Ricininae.

124. *Seidelia* Baill.

Seidelia Baill., Étude Gén. Euphorb.: 465 (1858); Prain, Ann. Bot. 27: 398 (1913), Fl. Capensis 5(2): 464 (1920); Dyer, Gen. S. Afr. Fl. Pl., ed. 3: 316 (1975); Radcl.-Sm., Gen. Euphorb.: 206 (2001).

Monoecious (dioecious) annual herbs; indumentum simple. Leaves alternate or opposite below, subentire or denticulate, ± purplish, colliculose, eglandular; stipules minute, deciduous. Inflorescences axillary, glomerular, unisexual or bisexual, with the pistillate at proximal axils, the staminate distal. Staminate flowers pedicellate, pedicels

mid-articulate; calyx splitting into 3 valvate segments; petals and disk 0; stamens (1) 2–5, filaments nearly distinct; anthers extrorse, muticous, 2-locular, with locules distinct, opening 4-valved; pollen grains prolate spheroidal, 3-lobed, sexine finely tectate-perforate, microverrucate, muri crested; pistillode 0. Pistillate flowers pedicellate, articulate above the middle; sepals 3 (4), imbricate, entire, persistent; petals and disk 0; ovary 2-locular, glabrous or pubescent, smooth; ovules anatropous, inner and outer integuments thin; stylodia distinct, unlobed. Fruits capsular, 2-lobed; columella slender, persistent. Seeds ovoid; testa smooth or reticulate.

Two spp., South Africa.

125. *Leidesia* Müll. Arg.

Leidesia Müll. Arg., DC. in Prodr. 15(2): 792 (1866); Benth., Hook. Ic. Pl. 13: 66, t. 1284 (1879); Dyer, Gen. S. Afr. Fl. Pl., ed. 3: 316 (1975); Radcl.-Sm., Fl. Zambesiaca 9(4): 159, t. 33 (1996).

Monoecious annual herbs; indumentum simple, very sparse. Leaves alternate or subopposite, pinnately veined or triplinerved, crenate-dentate, minutely puncticulate, eglandular; stipules minute, subulate. Inflorescences terminal, bisexual, racemoid-spiciform, pistillate flower solitary and basal, staminate glomerules distal; occasional axillary pistillate flowers produced as well; bracts entire, gland-tipped. Staminate flowers subsessile or pedicellate; calyx closed in bud, splitting into 3 valvate segments; petals and disk 0; stamens 4–7, filaments distinct; anthers introrse, muticous, subglobose, discrete and ± pendulous; pollen grains oblate spheroidal, 3-colporoidate, sexine tectate-perforate; pistillode 0. Pistillate flower subsessile; calyx obsolete; disk 0; ovary 2-locular, hispid-muricate; ovules anatropous, inner and outer integuments thin; stylodia nearly distinct, unlobed. Fruits capsular, setose; columella membranous-winged, subpersistent. Seeds subglobose; testa smooth.

A single sp., *L. procumbens* (L.) Prain, in southern Africa, in habit somewhat resembling *Dysopsis*.

7d. Subtribe Dysopsidinae Hurus. (1954).

Monoecious herbs; indumentum simple; leaves alternate, crenate; flowers axillary, mostly solitary; staminate calyx gamophyllous; stamens 3–6; pollen grains globose, colpate, finely reticulate; ovary 3-locular, stylodia unlobed, lacerate; fruit capsular; seeds with obsolete caruncle.

Monogeneric, the single genus *Dysopsis* restricted to Central and South America. It shows clear resemblances with the Mercurialinae in both habit and flowers, but these appear to be superficial, because in the molecular analysis it is resolved as sister to *Caperonia*.

126. *Dysopsis* Baill.

Dysopsis Baill., Étude Gén. Euphorb.: 435 (1858); Pax & K. Hoffm., Pflanzenr. 147, VII (Heft 63): 286, fig. 45 (1914); Burger & Huft, Fieldiana Bot. n.s. 36: 113 (1995); Radcl.-Sm., Gen. Euphorb.: 207, fig. 26 (2001).
Molina Gay (1851; nom. illeg.).

Monoecious herbs; indumentum simple. Leaves ± palmately veined, eglandular; stipules deciduous. Flowers axillary, mostly solitary; bracts minute. Staminate flowers pedicellate; sepals 3 (4), connate; petals and disk 0; stamens 3, or 6 in 2 whorls, the inner filaments connate; anthers introrse, thecae adnate to slender connective; pollen grains subprolate, 3-colpate, colpi narrow, sexine tectate-reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 3, subvalvate, entire, persistent; petals and disk 0; ovary 3-locular, pubescent; ovules anatropous, inner and outer integuments thin; stylodia unlobed, ± laciniate. Fruits capsular. Seeds subglobose, minutely carunculate, testa smooth; embryo linear.

A single polymorphic sp., *D. glechomoides* (A. Rich.) Muell. Arg., Costa Rica to Chile and Juan Fernandez.

7e. subtribe avellanitinae G.L. Webster, subtr. nov.[1]

A monotypic subtribe endemic to Chile.

127. *Avellanita* Phil.

Avellanita Phil., Linnaea 33: 237 (1864); Benth., Gen. Pl. 3: 289 (1880); Radcl.-Sm., Gen. Euphorb.: 229, fig. 29 (2001); Barrera et al., Bol. Mus. Nac. Hist. Nat. Chile 30: 7 (2001).

[1] Subtribe **Avellanitinae** G.L. Webster, **subtr. nov.**, arbusculae monoicae; indumentum simplex; folia alterna, integra, purpurea; dichasia terminales; flores ♂ subsessiles, stamina > 50; flores ♀ sepalis 6, valvatis, stylodiis integris; fructus capsularis; semina earunculata. Typus: *Avellanita* Philippi.

Monoecious shrubs; indumentum simple. Leaves alternate or distally pseudo-verticillate, entire, eglandular, purplish-tinged; stipules persistent. Inflorescences terminal, pedunculate, dichasial, with 1 central pistillate flower and 2 or 3 lateral staminate flowers. Staminate flowers subsessile; sepals 5, valvate; petals and disk 0; stamens > 50, filaments distinct; anthers small, subglobose, dehiscing horizontally, together forming a globose mass; pollen grains subspheroidal, 3-colporate, sexine tectate-rugulose, microverrucate; pistillode 0. Pistillate flowers subsessile or pedicellate; sepals 6, valvate, entire, persistent in fruit; ovary 3-locular, hirtellous; stylodia distinct, erect, elongated, unlobed, papillose. Fruits capsular; columella persistent. Seeds spheroidal, ecarunculate; testa smooth, dry.

A single sp., *A. bustillosii* Philippi, endemic to central Chile. It seems to be correctly placed in tribe Acalypheae (Radcliffe-Smith 2001), but its exact position within this tribe remains to be determined. It shares characters such as the purplish foliar pigment with subtribe Mercurialinae, but differs from that group in its high stamen number, 3-locular ovary, and ecarunculate seeds. It also shares purplish foliar pigments with the Claoxylinae, but differs in stamen morphology and seeds with a non-fleshy testa. Barrera et al. (2001), on the basis of epidermal characters, suggest an affinity with *Chiropetalum* (Chrozophoreae), but this is contradicted by the palynological evidence.

7f. Subtribe Acalyphinae Griseb. (1859).

A monogeneric subtribe, distinctive for its unusual anthers and accrescent fruiting calyx. It appears in some respects most similar to the Claoxylinae, but differs in its very distinctive pollen grains (Nowicke and Takahashi 2002), inflorescence structure, remarkably modified stamens, and flowers lacking a disk.

128. *Acalypha* L.

Acalypha L., Sp. Pl.: 1003 (1753); Pax & K. Hoffm., Pflanzenr. 147, XVI: 12, figs. 1–3 (1924); Wilson, Hook. Ic. Pl. 36: t. 3588 (1962); P.I. Forster, Austrobaileya 4:209–226 (1994); Cardiel, Fl. Colombia, Mon. 15: 23, figs. 1–25 (1995); Qiu Huaxing & Gilbert, Fl. China 11: 251–255 (2008); Sagun et al., Blumea 55: 21–60 (2010), rev. Malesian spp.

Monoecious (dioecious) trees, shrubs, or herbs; indumentum simple or glandular (stellate). Leaves alternate, pinnately or palmately veined, entire or dentate, sometimes gland-dotted but not with embedded laminar glands, rarely stipellate at base; stipules usually persistent. Inflorescences terminal or axillary, unisexual or bisexual, the staminate spiciform with flowers in glomerules, the pistillate spiciform, sometimes racemose or paniculate, the bisexual with proximal pistillate and distal staminate glomerules; staminate bracts minute, subtending several flowers, pistillate bracts ± foliose, entire or dentate, subtending 1–3 flowers, usually accrescent in fruit. Staminate flowers subsessile; calyx closed in bud, splitting into 4 valvate segments; petals and disk 0; stamens 4–8(−16), filaments distinct or basally connate; anthers 2-celled, theca discrete, ± elongated, twisted, vermiform; pollen grains about 10–14 x 12–15 μm, oblate-spheroidal, 3–5-porate, sexine rugulose-tectate, verrucate; pistillode 0. Pistillate flowers sessile or subsessile (pedicellate); sepals 3–4(5), basally connate, imbricate, entire, persistent in fruit; petals and disk 0; ovary (1)2–3-locular, smooth or muricate, often pubescent or papillose; ovules anatropous, inner and outer integuments thin; stylodia nearly distinct, laciniate (bifid or entire). Fruits capsular; columella persistent. Seeds ovoid or ellipsoid, carunculate or not, testa smooth or foveolate. $n = 7, 10, 14, 20$.

Over 450 spp., pantropical, with a few extratropical spp. in the Americas and E Asia, relatively stereotyped morphologically but one section, *Linostachys*, differing in its pedicellate pistillate flowers.

7g. Subtribe Blumeodendrinae G.L. Webster (1975).

Dioecious trees; indumentum simple or minutely stellate; leaves alternate, opposite, or verticillate, long-petiolate; stipules minute or 0; inflorescences axillary, spiciform to racemose or paniculate; staminate flowers pedicellate; calyx splitting into 3–5 valvate segments; disk of interstaminal segments; stamens 15–70, anther connectives enlarged; pollen grains 3-colporate, colpi short, sexine tectate-perforate or coarsely reticulate, tectum thick, with crotonoid sculpture; pistillode

0; pistillate flowers sessile or pedicellate; sepals 3–5, distinct or basally connate; disk annular or pulviniform; ovary 2- or 3-locular; ovules with thick integuments, the outer vascularized; stylodia unlobed; fruits large, thick-walled, indehiscent or tardily dehiscent; seeds ecarunculate, with fleshy testa.

This group of four Asiatic genera was earlier (Webster 1994) included as a subtribe of the Pycnocomeae. Radcliffe-Smith (2001) suggested that they might represent a separate tribe, and this is supported by the pollen evidence of Nowicke et al. (1999). Here they are shifted from the Pycnocomeae, from which they differ in the long petiolate leaves, paniculate inflorescences and large indehiscent fruits, to the Acalypheae, which is also supported by the thick vascularized outer integuments shared by *Blumeodendron*, *Mallotus* and *Macaranga* and by the molecular data (Wurdack et al. 2005).

KEY TO THE GENERA OF SUBTRIBE BLUMEODENDRINAE

1. Anther connective moderately enlarged, not umbraculiform; pistillate disk tenuous or 0; stylodia elongated 2
– Anther connective greatly enlarged, umbraculiform; pistillate disk massive; stylodia stigmatiform **132. *Botryophora***
2. Anther locules adnate to connective; fruits not glandular 3
– Anther locules pendent; fruits glandular **131. *Podadenia***
3. Anther locules 2; fruits smooth, sometimes carinate, not beaked **129. *Blumeodendron***
– Anther locules 4; fruits ± ribbed or spinose, beaked **130. *Ptychopyxis***

129. *Blumeodendron* (Müll. Arg.) Kurz

Blumeodendron (Müll. Arg.) Kurz, J. Asiatic Soc. Bengal, Nat. Hist. 42: 245 (1873); J.J. Smith, Meded. Dept. Landbouw 10: 458 (1910); Whitmore, Tree Fl. Malaya 2: 68, figs. 2, 3 (1973); Airy Shaw, Kew Bull. Add. Ser. 4: 57 (1975), Kew Bull. 36: 267, fig. 3A (1981).
Mallotus sect. *Blumeodendron* Müll. Arg. (1866).

Dioecious; indumentum scanty, simple and stellate on new growth. Leaves alternate or more often opposite or verticillate, long-petiolate, pinnately veined or triplinerved, entire, eglandular (obscurely punctate); stipules minute or 0. Inflorescences axillary, the staminate glomerular or racemoid, pistillate spiciform; staminate flowers pedicellate, calyx closed in bud, splitting into 3 or 4 valvate segments, microlepidote abaxially, petals 0; disk receptacular, convex, segments interstaminal; stamens 15–50, filaments distinct, flexed in bud; anthers introrse or latrorse, locules adnate to the enlarged connective, pollen grains oblate spheroidal, 3-colporate, colpi short and narrow, costate, inoperculate; sexine thick, tectate-perforate, microverrucate; pistillode 0. Pistillate flowers pedicellate, articulate; sepals 3–5, imbricate, entire, deciduous in fruit; disk annular; ovary 2- or 3-locular, smooth, glabrous; inner integuments very thick, outer integuments thinner, vascularized; stylodia unlobed, papillate. Fruits capsular, dehiscing tardily; columella not persistent. Seeds large, compressed, testa fleshy.

Five spp., ranging from Burma and the Andamans through Indonesia to the Bismarck Archipelago, several spp. in Borneo.

130. *Ptychopyxis* Miq.

Ptychopyxis Miq., Fl. Ned. Ind., Suppl.: 402 (1861); Hook. f., Hook. Ic. Pl. 18: t. 1703 (1887); Croizat, J. Arnold Arb. 23: 47 (1942); Airy Shaw, Kew Bull. 14: 363 (1960), Kew Bull. Add. Ser. 4: 188 (1975), Kew Bull. 36: 340 (1981).

Dioecious trees; indumentum simple or 0. Leaves sometimes clustered at branch tips, entire; petioles pulvinulate at both ends; stipules minute or 0. Inflorescences axillary, racemoid or paniculate; bracts persistent, eglandular. Staminate flowers pedicellate, pedicel articulate above the base; calyx closed in bud, splitting into 3–5 valvate segments; petals 0; disk of many small interstaminal segments; stamens 35–65, filaments distinct; anthers introrse, connective apiculate; pollen grains oblate spheroidal, 3-colporate, colpi short, narrow, inoperculate; sexine tectate-reticulate; pistillode 0. Pistillate flowers subsessile; sepals 4 or 5, basally connate, entire, ± persistent in fruit; disk annular, glabrous or pubescent; ovary 2–3-locular, pubescent; ovules anatropous, inner integuments very thick, outer integuments thinner and vascularized; stylodia connate, unlobed. Fruits capsular but tardily dehiscent; beaked, smooth to distinctly ribbed. Seeds oblong, exotesta fleshy, endotesta bony.

Thirteen spp., ranging from Thailand through Malesia to New Guinea.

131. *Podadenia* Thwaites

Podadenia Thwaites, Enum. Pl. Zeyl. 4: 273 (1861); Trimen, Handb. Fl. Ceylon 4: 62 (1898); Philcox, Fl. Ceylon 11: 144 (1997); Radcl.-Sm., Gen. Euphorb.: 170, fig. 19 (2001).

Dioecious trees; indumentum simple, glandular on inflorescences. Stipules 0. Inflorescences axillary, paniculate (compound thyrsoid), glandular-pubescent; bracts persistent. Staminate flower pedicellate; calyx closed in bud, splitting into 3 or 4 glandular-pubescent reflexed segments; petals 0; disk of numerous interstaminal segments; stamens 20–30, filaments distinct; anthers latrorse, with enlarged apiculate connective; locules pendent; pollen grains 3-colporate, colpi short and narrow; sexine tectate-punctate, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 4–7, imbricate, entire, glandular-pubescent, persistent or deciduous in fruit; disk 0; ovary 3-locular, glandular-pubescent; ovules anatropous, inner integuments moderately thick, outer integuments thinner, vascularized; stylodia nearly distinct, unlobed, papillate. Fruit indehiscent, beaked, covered with gland-tipped setae. Seeds 1 or 2 per fruit, ± compressed; exotesta fleshy, endotesta bony.

A single sp., *P. thwaitesii* (Baill.) Müll. Arg., from Ceylon. Although Philcox (1997) treated it as a species of *Ptychopyxis*, the Ceylonese species appears sufficiently different from the other known taxa of *Ptychopyxis* that its placement in a separate genus is justifiable.

132. *Botryophora* Hook. f.

Botryophora Hook. f., Fl. Brit. Ind. 5: 476 (1888; nom. cons.); Airy Shaw, Kew Bull. 14: 374 (1960), Hook. Ic. Pl. 36: t. 3576 (1962), Kew Bull. 36: 269, fig. 4 (1981).

Dioecious trees; indumentum simple. Leaves sometimes clustered, entire, eglandular; petioles long, pulvinate at both ends; stipules obsolete. Inflorescences axillary, the staminate paniculate (compound spiciform or contracted), the pistillate spiciform; bracts minute. Staminate flowers subsessile; calyx closed in bud, glabrous, splitting into 2 spathaceous segments; petals 0; disk glands receptacular, numerous, several surrounding each stamen; stamens c. 30–60, filaments distinct; anther connective pileiform-peltate, anthers 4-locellate; pollen grains spheroidal, 3-colporate, inoperculate and emarginate, sexine tectate-punctae, microverrucate; pistillode 0. Pistillate flowers sessile or subsessile; sepals 3 or 4, minute, hidden under the massive pulviniform ± segmented disk; petals 0; ovary 3- or 4-locular, smooth and glabrous; stylodia unlobed, thick, shorter than ovary, papillate. Fruit capsular but tardily dehiscent. Seeds somewhat angular, plano-convex, testa smooth and dry.

A single sp., *B. kingii* Hook. f., ranging from Burma to Sumatra, Java and Borneo. Airy Shaw (1960) provided a taxonomic revision of this genus, and was the first investigator to clearly relate it to *Blumeodendron*.

7h. Subtribe Rottlerinae Meisner (1841).

Dioecious (monoecious) trees or shrubs; indumentum stellate (simple); leaves alternate or opposite; blade unlobed or lobed, pinnately or palmately veined; sometimes with embedded laminar glands; stipules deciduous or obsolete; inflorescences terminal or axillary, racemose or paniculate; staminate calyx splitting into valvate segments; petals 0; disk of interstaminal segments or 0; stamens 15–300, filaments distinct; anthers muticous, anther sacs not pendulous; pollen grains 3(4)-colporate, finely to coarsely tectate-perforate and microverrucate; pistillate sepals 3–6(−10), distinct or connate; disk 0; ovary 2–4(−8)-locular, sometimes echinate; stylodia unlobed, ± plumose or lacerate; fruit capsular, baccate, or drupaceous; seeds ecarunculate (carunculate), testa often fleshy.

After the drastic reductions of the satellite genera around *Mallotus*, which were found to be embedded in this genus, subtribe Rottlerinae comprises only three genera, although two very large ones.

Key to the Genera of Subtribe Rottlerinae

1. Anthers 3- or 4-celled; indumentum simple; leaves alternate **134. *Macaranga***
– Anthers 2-celled; indumentum simple or stellate; leaves alternate or opposite with one member of the pair smaller 2
2. Indumentum of simple and stellate hairs; leaf blades usually granulose-glandular beneath; pollen grains with tectae-microperforate exine; stylodia not particularly elongate **133. *Mallotus***
– Indumentum not stellate but of simple hairs or gland-tipped hairs or sessile peltate-stellate hairs with central cells; leaf blades eglandular; pollen grains with areolate exine sculpture; stylodia often very long [> 20 mm] **135. *Hancea***

133. *Mallotus* Lour. Fig. 28

Mallotus Lour., Fl. Cochinch.: 635 (1790), nom. cons.; Pax & K. Hoffm., Pflanzenr. 147, VII: 145, figs. 23–29 (1914); Airy Shaw, Kew Bull. 21: 379 (1968), Hook. Ic. Pl 38: t. 3715 (1974), Kew Bull. Add. Ser. 4: 160 (1975), 8: 162 (1980);

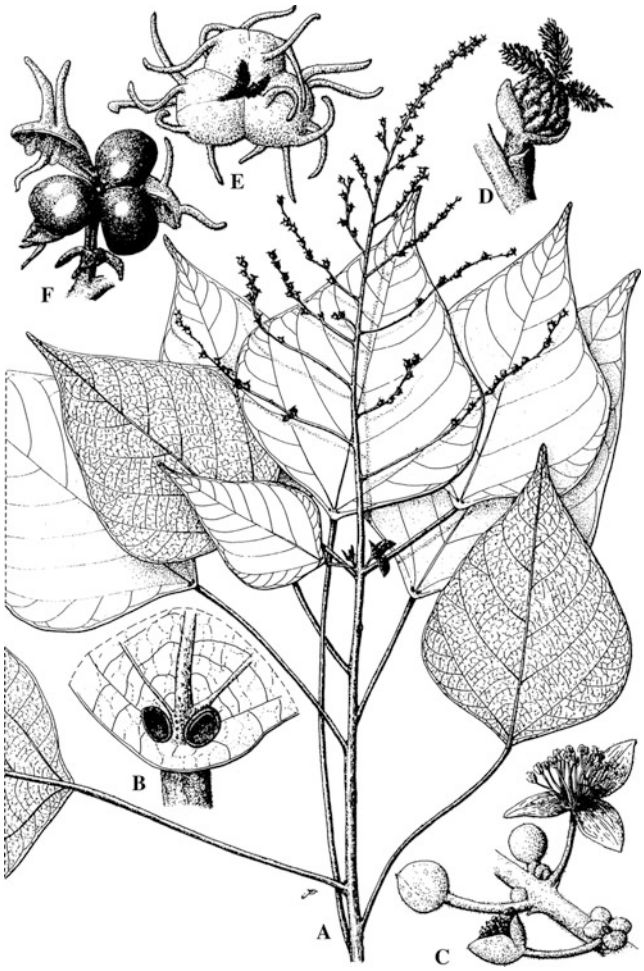

Fig. 28. Euphorbiaceae-Acalyphoideae. *Mallotus paniculatus*. **A** Flowering branch. **B** Base of upper leaf surface with extrafloral nectaries. **C** Staminate flowers and buds. **D** Pistillate flower. **E** Fruit. **F** Dehisced fruit with seeds and apex of column. (Sierra & van Welzen 2005)

McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 104, t. 35, 6–9 (1987); Radcl.-Sm., Fl. E. Trop. Afr. Euph. 1: 235 (1987); McPherson, Adansonia III, 17: 169 (1995); Bollendorf et al., Blumea 45: 319, figs. 1–10 (2000); Slik & van Welzen, Blumea 46: 3, figs. 1–22 (2001); Sierra & van Welzen, Blumea 50: 249–274 (2005), tax. sect. *Mallotus*; Kulju et al., Amer. J. Bot. 94: 1726–1743 (2007), mol. syst.; Kulju et al., Blumea 52: 115–136 (2007), *Neotrewia*, *Octospermum* and *Trevia* reduced; Qiu Huaxing & Gilbert, Fl. China 11: 225–237 (2008); Sierra, Kulju, Fiser, Aparicio & van Welzen, Taxon 59: 101–116 (2010), mol. syst.; van Welzen et al., Blumea 55: 285–290 (2011), key to Males. spp.

Trevia L. (1753) (= *Trewia*).

Echinus Lour. (1790).

Rottlera Roxb. (1802).

Coelodiscus Baill. (1858).

Neotrewia Pax & K. Hoffm. (1914).

Octospermum Airy Shaw (1965).

Dioecious (monoecious) trees, shrubs or climbers; indumentum simple and stellate or tufted and glandular. Leaves alternate or opposite, unlobed or palmately lobed, entire to dentate, sometimes peltate, usually with extrafloral nectaries adaxially; stipules persistent, deciduous, or obsolete. Inflorescences terminal or axillary, spiciform to racemoid or paniculate, glomerulate or umbel-like, usually unisexual; bracts eglandular, persistent or deciduous; staminate flowers 1–15 per bract; pistillate flowers 1 per bract, several when umbel-like. Staminate flowers pedicellate; calyx closed in bud, sepals (2)3–5, valvate; petals 0; interstaminal disk glands sometimes +; stamens 15–130, filaments distinct or connate; anthers basifixed, 2-locellate; connective sometimes broadened or apiculate; pollen grains spheroidal, 3(4)-colporate, colpi vestigially operculate, sexine tectate/microperforate; pistillode 0 (+). Pistillate flowers pedicellate; sepals (2)3–6, valvate, ± connate at least at base, sometimes calyx cupular or spathaceous; petals and disk 0; ovary (1)2–3(−9)-locular; ovules anatropous, inner integuments thick, outer integuments thinner, sometimes vascularized; style + or 0; stylodia distinct or basally connate into a common style, stylodia or their distal tips unlobed, papillose to plumose. Fruits capsular (drupaceous), 3(2–5)-locular, very rarely 1-locular [*Neotrewia*] or 7–9-locular [*Octospermum*], smooth or softly spiny; columella persistent. Seeds globose to ovoid, ecarunculate, exotesta sometimes fleshy, endotesta hard, smooth to rugose. $n = 11, 12, 18$.

According to Sierra et al. (2010), *Mallotus* includes about 110 spp. distributed mainly in (sub)tropical Asia, Malesia, Australia, and the southwestern Pacific islands, and only two spp. in Africa/Madagascar, growing in various habitats ranging from the understorey to swamp forest and montane forest, and often in disturbed and secondary vegetation.

134. *Macaranga* Thouars

Macaranga Thouars, Gen. Nov. Madag.: 26 (1806); Gagnep., Fl. Indochine 5: 434, figs. 52–54 (1926); Perrry, J. Arnold Arb. 34: 191 (1953); Whitmore, Tree Fl. Malaya 2: 105, figs. 8, 9 (1973); A.C. Smith, Fl. Vitiensis Nova 2: 500, figs.131–135 (1981); Coode, Taxon 25: 184 (1976), Fl. Mascar. 160: 53, t. 10 (1982); McPherson & Tirel, Fl. Nouv.-Caléd. 14: 172–185, t. 37 (1987); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 239, fig. 49 (1987), Fl. Zambesiaca 9(4): 161, t. 34 (1996); McPherson, Adansonia III, 18: 275 (1996); Florence, Fl. Polynésie Française 1: 104, figs. 17–19 (1997); Slik et al., Gard. Bull. Singapore 52: 12,

figs. 1–24 (2000); Qiu Huaxing & Gilbert, Fl. China 11: 237–240 (2008).
Mappa Juss. (1824).
Pachystemon Blume (1826).

Dioecious trees and shrubs; indumentum of simple (fasciculate) and conspicuous, usually colourful glandular hairs; twigs sometimes hollow, often with reddish exudate. Leaves long-petiolate, unlobed to palmately lobed, pinnately to palmately veined, often peltate, abaxially granulose-glandular; stipules minute to large, persistent or deciduous. Inflorescences axillary, the staminate spiciform or capitulate, the pistillate racemoid, sometimes compound; bracts often conspicuous and glandular. Staminate flowers subsessile or pedicellate; calyx closed in bud, splitting into 2–4 valvate segments; petals and disk 0; stamens (1–)3–20(−30), filaments distinct or basally connate; anthers muticous, 3- or 4-locellate; pollen grains spheroidal, 3-colporate, colpi ± granulate, sexine tectate-microperforate; pistillode 0. Pistillate flower pedicellate; calyx cupular, subentire to 4–6-lobed or -partite, persistent in fruit; petals and disk 0; ovary 1–6-locular, glandular-granulose and sometimes echinate; ovules anatropous, inner integument thick, outer integument thicker, vascularized; stylodia distinct (shortly connate), unlobed. Fruits capsular, (1)2–3(−6)-locular; smooth or spiny, loculicidal; columella not persistent. Seeds globose, ecarunculate; exotesta fleshy, endotesta indurate, often rugose. $n = 11$.

About 260 spp., 26 in Africa, 10 in Madagascar, the rest distributed from India and Ceylon east to Malesia and New Caledonia and the Pacific islands as far east as Polynesia but not Hawaii, usually as forest plants and often as members of secondary vegetation.

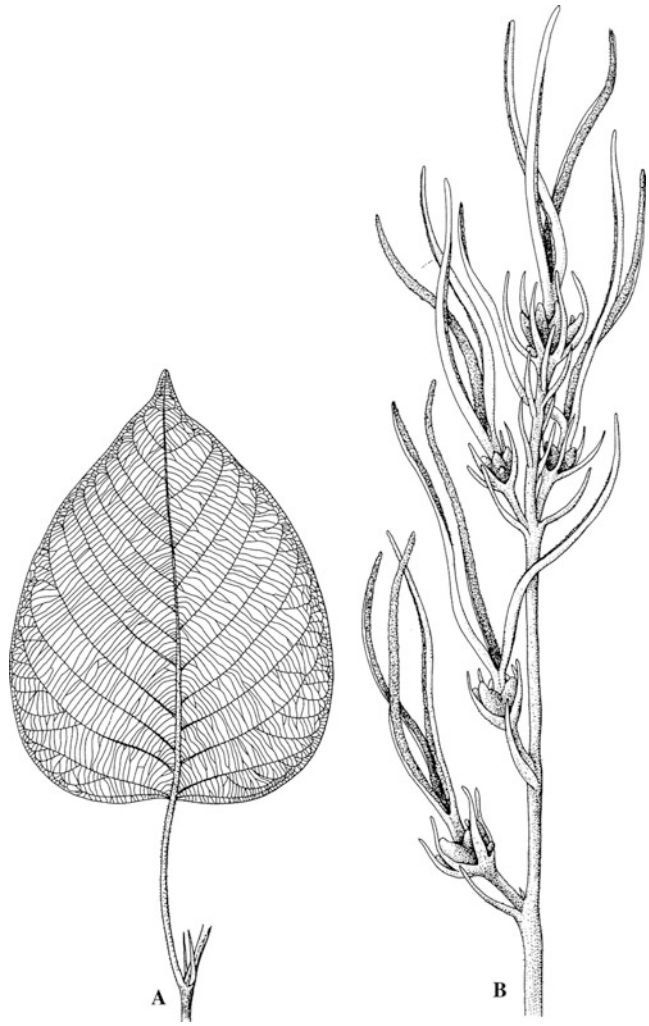

Fig. 29. Euphorbiaceae-Acalyphoideae. *Hancea integrifolia* . **A** Stipulate leaf. **B** Part of inflorescence with pistillate flowers. (Sierra et al. 2006; drawn by A. Walsmit Sachs)

135. *Hancea* Seem. Fig. 29

Hancea Seem., Bot. Voy. Herald : 409 (1857); Slik & van Welzen, Blumea 46: 3–66 (2001), as *Mallotus* sect. *Hancea*; Sierra et al., Blumea 51: 524–537 (2006), sub *Cordemoya*; Sierra et al., Blumea 52: 361–366 (2007), new comb. under *Hancea*.
Mallotus Lour. sect. *Hancea* (Seem.) Pax & K. Hoffm. (1914).
Boutonia Bojer ex Bouton (1846).
Cordemoya Baill. (1861), Radcl.-Sm., Gen. Euph.: 228 (2001).
Mallotus sect. *Cordemoya* Müll. Arg. (1865).
Deuteromallotus Pax & K. Hoffm. (1914).

Monoecious or dioecious shrubs or trees; indumentum of simple hairs and gland-tipped hairs or sessile peltate-stellate hairs with central cells; resin sometimes +. Leaves opposite [alternate in *H. subpeltata*], entire, pinnately or palmately 3-veined, with one of each leaf of a pair either slightly smaller than the other [subg. *Cordemoya*] or strongly reduced to appear like a stipule [sect. *Diplochlamys*)]; stipules axillary or intrapetiolar, persistent. Inflorescences axillary, terminal, or ramiflorous, uni- or bisexual, racemes or less often panicles; staminate flowers 1–3 per

bract, pistillate flowers 1 per bract. Staminate flowers pedicellate; sepals 2–4, valvate, distinct to basally connate; petals and disk 0; stamens 40–250; filaments distinct; anthers extrorse; pollen grains oblate spheroidal, 3-colporate, sexine areolate, scabrate; pistillode 0. Pistillate flowers pedicellate; sepals (3)4–6(7), valvate or imbricate, distinct; petals and disk 0; ovary 2–3-locular; ovules anatropous, inner integuments very thick, outer integuments thinner, vascularized; stylodia 2–3, unbranched, erect, 5–25 mm long, only basally shortly connate. Fruits capsular, spiny, spines 4–6 or up to 170, sometimes gland-tipped. Seeds subglobose, ecarunculate, testa not fleshy.

A genus of 17 spp., as enumerated by Sierra et al. (2007), four of them in Madagascar and the Mascarenes (subg. *Cordemoya*), the rest (subg. *Hancea*, with 2 sections) distributed from Hong Kong throughout SE Asia to New Guinea. The whole floral structure and particularly the numerous stamens and extremely elongate stylodia are strongly indicative of wind pollination.

7i. Subtribe Lasiococcinae G.L. Webster (1975).

Monoecious or dioecious trees or shrubs; indumentum simple or lepidote; leaves alternate, stipulate; inflorescences axillary, unisexual, racemose or solitary, bracts eglandular; staminate sepals usually 3; disk 0; stamens many, filaments connate and ramified; pollen grains 3-colporate, not operculate, sexine tectate-microperforate or striate-verruculose; pistillode 0; pistillate sepals 5–8, imbricate, persistent or deciduous; disk 0; ovary 3-locular; stylodia unlobed, smooth to papillose or plumose; fruit capsular; seeds ecarunculate, testa usually fleshy.

Three Asiatic genera, originally placed in the subtribe Ricininae by Pax and Hoffmann (1919) because of the ramified filaments, but the totality of characters suggests that the androecial resemblance to *Ricinus* may be due to convergence. Airy Shaw (1974) and van Welzen et al. (1998) thought that the Lasiococcinae may be related to the Malloteae, whereas the molecular signals (Wurdack et al. 2005) place *Homonoia* and *Spathiostemon* with low support close to Acalypheae and Pycnocomeae.

Key to the Genera of Subtribe Lasioccinae

1. Monoecious; pistillate sepals persistent; indumentum simple; ovary muricate **136. *Lasiococca***
– Dioecious; pistillate sepals deciduous; indumentum simple or lepidote 2
2. Lepidote scales 0; ovary tuberculate; pollen sexine not striate **137. *Spathiostemon***
– Lepidote scales present; ovary smooth; pollen sexine striate **138. *Homonoia***

136. *Lasiococca* Hook. f.

Lasiococca Hook. 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); van Welzen, Thin & Hoai Duc, Blumea 43: 141–144, fig. 3 (1998).

Monoecious trees or shrubs; indumentum simple or glandular. Leaves alternate or subopposite, sometimes pseudo-verticillate, entire, glandular on margins; stipules deciduous. Inflorescences axillary, unisexual; staminate flowers in racemes, bracts uniflorous; pistillate flowers solitary, axillary, bracts deciduous. Staminate flowers pedicellate; calyx closed in bud, splitting into 3 valvate segments; petals and disk 0; stamens $>$ 100, filaments connate and paniculately branching; anthers introrse, muticous, thecae globose; pollen grains spheroidal, 3-colporate, sexine tectate-perforate, slightly rugulose, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 5 (−7), foliose, imbricate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, tuberculate; stylodia basally connate, unlobed. Fruits capsular, echinate; columella persitent. Seeds ± ovoid, ecarunculate, testa smooth.

Three spp., distributed from India to SE Asia and Malesia.

137. *Spathiostemon* Blume

Spathiostemon Blume, Bijdr.: 621 (1816); Airy Shaw, Kew Bull. 16: 357 (1963), Hook. Ic. Pl. 38: t. 3720 (1974), Kew Bull. 36: 345, fig. 9 (1981); van Welzen et al., Blumea 43: 145–150, fig. 4 (1998).
Polydragma Hook. f. (1887).
Clonostylis S. Moore (1925); still incompletely known; van Welzen (Blumea 43: 150. 1988) argues for its independent generic status.

Monoecious trees or shrubs; indumentum simple. Leaves glandular at base; petioles pulvinate; stipules deciduous. Inflorescences axillary (pseudo-terminal), racemose, not fasciculate, unisexual; bracts entire, eglandular, persistent. Staminate flowers sessile to shortly pedicellate, articulate above the middle; calyx closed in bud, splitting into 3 valvate segments; petals and disk 0; stamens > 100, filaments connate into 4–7 ramified phalanges; anthers introrse or latrorse, muticous, 2-celled; pollen grains spheroidal, 3-colporate, sexine coarsely rugulose-tectate and verrucate; pistillode 0. Pistillate flowers pedicellate; sepals 5 or 6, entire, imbricate, persistent in fruit; petals and disk 0; ovary 3-locular, smooth or papillate; ovules anatropous, inner integument thick, outer integument thin; stylodia distinct, unlobed, acuminate, adaxially papillate. Fruits capsular, smooth or echinate, septicidal and loculicidal; columella sometimes persistent, apically dilated. Seeds obovoid, ecarunculate, hilum triangular, testa smooth.

Two spp., distributed from peninsular Thailand and Indonesia to New Guinea. Pax and Hoffmann (1919) combined *Spathiostemon* with *Homonoia*, and both genera are strongly supported as sisters (*rbc*L only) in the analysis of Wurdack et al. (2005), but their pollen exine ornamentation is very different (Nowicke and Takahashi 2002).

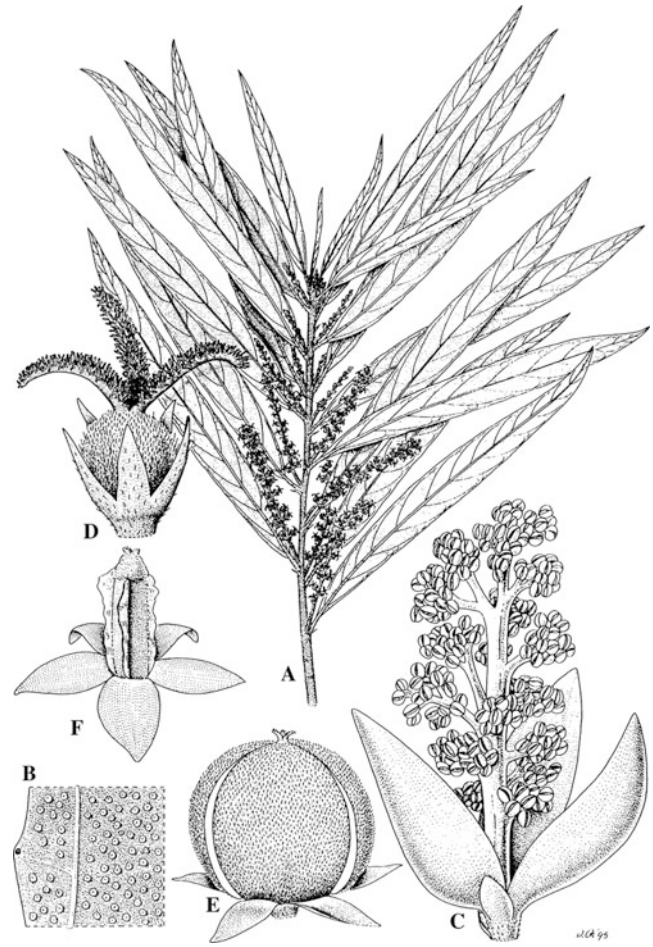

Fig. 30. Euphorbiaceae-Acalyphoideae. *Homonoia riparia*. **A** Flowering branch. **B** Lower leaf surface showing marginal gland and scale hairs. **C** Staminate flower. **D** Pistillate flower. **E** Fruit. **F** Fruit column after dehiscence. (van Welzen et al. 1998; drawn by J. van Os)

138. *Homonoia* Lour. Fig. 30

Homonoia Lour., Fl. Cochinch.: 636 (1790); Airy Shaw, Kew Bull. 36: 310 (1981); Philcox, Fl. Ceylon 11: 173 (1997); van Welzen, Blumea 43: 136–141, fig. 2 (1998).

Dioecious (monoecious) arborescent shrubs; indumentum simple and lepidote. Leaves eglandular; stipules deciduous. Inflorescences axillary, solitary, spiciform, usually unisexual; glomerules uniflorous. Staminate flowers sessile; petals and disk absent; calyx splitting into 3 valvate segments; stamens > 100, filaments connate into a paniculate androecium; anthers introrse, muticous; pollen grains spheroidal, 3-colporate, colpi narrow and operculate, sexine tectate, striate-beaded; pistillode 0. Pistillate flowers sessile; sepals 5, basally connate, imbricate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, pubescent; ovules anatropous, inner and outer integuments thin; stylodia unlobed, linear, plumose-laciniate. Fruits capsular, loculicidal; columella sometimes persistent, 3-angled. Seeds ovoid, carinate, ecarunculate, exotesta fleshy, endotesta smooth.

Two spp., distributed from India to China and throughout Malesia to New Guinea, growing as rheophytes mainly in and along rivers at low altitudes. The absence of petals and a disk, the numerous stamens united into a "staminate tree", and the plumose, stigmatic stylodia suggest wind pollination.

8. Tribe Pycnocomeae Hutch. (1969).

Monoecious or dioecious trees or shrubs; indumentum simple or 0; leaves alternate, sometimes stipellate or with laminar glands; stipules deciduous or rudimentary; inflorescences axillary, racemoid or spiciform (compounded); staminate

calyx splitting into 3–5 valvate segments; petals 0; disk of intrastaminal segments or 0; stamens 8–120, filaments distinct; anthers mostly introrse, sometimes with enlarged connective; pollen grains subspheroidal, 3-colporate, colpi inoperculate and lacking costae; sexine tectate-perforate, or with granules arranged in areoles; pistillode 0; pistillate sepals 3–7, imbricate, persistent in fruit; disk annular, glabrous or 0; ovary 3-locular; ovules usually with inner integuments thicker than the outer; stylodia bifid to unlobed, sometimes laciniate; fruits dehiscent or indehiscent; columella usually persistent; seeds roundish, ecarunculate, testa smooth and dry.

The tribe Pycnocomeae is here redefined from the treatments of Webster (1994) and Radcliffe-Smith (2001) by the expulsion of the Blumeodendrinae and the addition of the Necepsinae, but remains heterogeneous: both *Paranecepsia* and *Necepsia* are resolved as sister taxa to *Pseudagrostis* (Wurdack et al. 2005; Kulju et al. 2008), whereas *Amyrea* is resolved in a clade with *Cyttaranthus* and *Discoglypremna*.

Key to the Subtribes of Pycnocomeae

1. Stylodia bifid; inflorescences mostly unisexual; leaf blades with or without discoid glands **8a. Necepsinae**
– Stylodia unlobed; inflorescences usually bisexual; leaf blades eglandular or minutely punctuate **8b. Pycnocominae**

8a. Subtribe Necepsinae G.L. Webster (2004).

Monoecious or dioecious; leaves alternate, venation mostly eucamptodromous, with scattered laminar glands [except in *Paranecepsia*]; bisexual inflorescences lacking terminal pistillate flower; stamens 10–120; connective sometimes enlarged or apiculate; pistillate disk annular or lobed; stylodia bifid, sometimes lacerate.

Five genera, all African, one extending to Madagascar.

Key to the Genera of Necepsinae

1. Pistillate disk 8–10-lobed; anthers muticous; pollen sexine tectate-striate **141. *Amyrea***
– Pistillate disk annular to crenulate; anthers apiculate; pollen sexine tectate-perforate 2
2. Ovary verruculose; leaf lamina not stipellate at base **139. *Necepsia***
– Ovary smooth; leaf lamina stipellate at base **140. *Paranecepsia***

139. *Necepsia* Prain

Necepsia Prain, Kew Bull. 1910: 343 (1910); Léonard, Fl. Afr. Centr. Euphorb. 3: 32 (1996); Radcl.-Sm., Fl. Zambesiaca 9(4): 23, t. 27 (1996).
Palissya Baill. (1858; nom. illeg.).
Neopalissya Pax (1914).

Monoecious (dioecious) trees or shrubs; indumentum simple. Leaves denticulate, abaxially with embedded scattered glands; stipules persistent or deciduous. Inflorescences axillary, unisexual or bisexual, spiciform, the staminate elongated, the pistillate abbreviated; bracts scarious, persistent. Staminate flowers pedicellate, pedicel articulate at base; calyx closed in bud, splitting into (3)4(5) valvate segments; petals 0; receptacle convex; disk of numerous pubescent interstaminal segments; stamens numerous, mostly $>$ 50, filaments distinct; anthers with enlarged $\pm$ glandular apiculate connective, locules pendent; pollen grains subprolate, 3-colporate, scarcely marginate, angulaperturate, colpar membrane granulose; sexine tectate-perforate; pistillode 0. Pistillate flowers subsessile; sepals (4)5(6), imbricate, persistent in fruit; petals 0; disk annular; ovary 3-locular, verruculose and pubescent; ovules anatropous, inner integument thick, outer integument thin; stylodia bifid to twice bifid. Fruits capsular, 3-lobed, verruculose; columella winged, persistent. Seeds subglobose, ecarunculate, testa smooth, hilum lunate, conspicuous.

Three spp., tropical Africa. In Webster (1994) and Radcliffe-Smith (2001), *Necepsia* was included in Bernardieae but here has been transferred to Pycnocomeae because of the palynological similarities with that tribe. See also the comments under the tribe.

140. *Paranecepsia* Radcl.-Sm.

Paranecepsia Radcl.-Sm., Kew Bull. 30: 684 (1976), Fl. E. Trop. Afr. Euphorb. 1: 220, fig. 43 (1987); Fl. Zambesiaca 9 (4): 145, t. 28 (1996).

Dioecious trees; indumentum simple. Leaves $\pm$ clustered at branch tips, serrate, eglandular, stipellate at base; stipules entire, pubescent. Inflorescences axillary, solitary, lax, racemoid, often aggregated paniculately; staminate glomerules 1–5-flowered, pistillate flowers solitary at each bract. Staminate flowers pedicellate, pedicels articulate; calyx closed in bud, splitting into 3–5 valvate

segments; petals 0; disk segments numerous, intrastaminal; stamens 25–40, filaments distinct; anthers dorsifixed, introrse, connective apiculate but not enlarged, thecae pendulous; pollen grains spheroidal, 3-colporate, scarcely marginate, sexine tectate-perforate; pistillode 0. Pistillate flowers pedicellate; sepals 5–7, distinct, unequal, imbricate, accrescent and persistent in fruit; petals 0; disk annular; ovary 3-locular, pubescent; stylodia basally connate, bifid, papillose. Fruits 3-lobed, septicidally and loculicidally dehiscent; columella persistent. Seeds globose, ecarunculate, testa smooth.

A single sp., *P. alcheornifolia* Radcl.-Sm., East Africa: Tanzania and Mozambique. The stipellate leaf blades suggest a relationship with the Alchorneae, but the inoperculate pollen grains rule out assignment to that tribe. For its possible relationship with *Necepsia*, see above under the tribal description.

141. *Amyrea* Leandri

Amyrea Leandri, Notul. Syst. 9: 168, t. 1, figs. 16–19 (1941); Radcl.-Sm., Kew Bull. 53: 438, t. 1–6 (1998), Gen. Euphorb.: 161 (2001); Schatz, Generic Tree Flora Madag.: 143, fig. 131 (2001).

Dioecious shrubs or trees; indumentum simple or 0. Leaves entire or dentate, eglandular; stipules deciduous. Inflorescences axillary, subterminal, or terminal, spiciform or racemoid, bracts convex, glumiform, subtending solitary flowers. Staminate flowers subsessile to pedicellate; calyx closed in bud, splitting into 3–5 valvate segments; petals 0; disk segments interstaminal, pubescent; stamens 20–30, filaments distinct; anthers muticous, latrorse, subpendulous; pollen grains 3-angled, 3-colporate, colpi narrow and not bordered; sexine tectate-striate; pistillode 0. Pistillate flowers pedicellate; sepals 5, imbricate, entire, usually persistent; disk fleshy, 8–10-lobed; ovary 3-locular, smooth and glabrous; stylodia bifid, papillose. Fruit capsular; columella persistent. Seeds ovoid, ecarunculate; testa smooth, blackish.

Eleven spp. endemic to Madagascar. In describing the genus, Leandri noted resemblance to *Neopalissya* (*Necepsia*) and to *Mareya*, which furnished the basis of the anagrammatic generic name. See also above under the tribe.

8b. Subtribe Pycnocominae G.L. Webster (1994).

Monoecious; leaves alternate, lacking dispersed laminar glands, venation brochidodromous; pistillate flowers solitary, terminating inflorescences, rarely so in *Argomuellera*, the staminate glomerules proximal; stamens 15–80, anther connective not enlarged; pollen sexine tectate-perforate or gemmate; pistillate disk + or 0; stylodia distinct or connate, unlobed, apically dilated.

Three genera of Africa and Madagascar.

Key to the Genera of Pycnocominae

1. Pistillate disk +; pistillate flowers usually not terminal in inflorescence **142. *Argomuellera***
– Pistillate disk 0; pistillate flowers terminating inflorescences 2
2. Terminal bud not perulate; pistillate flower solitary and terminal at apex of inflorescence; filaments arcuate in bud; ovary 6-horned, pubescent **143. *Pycnocoma***
– Terminal bud perulate; pistillate flowers not solitary and terminal at apex of inflorescence; filaments straight in bud; ovary unappendaged, glabrous **144. *Droceloncia***

142. *Argomuellera* Pax

Argomuellera Pax, Bot. Jahrb. 19: 90 (1894); Prain, Fl. Trop. Afr. 6(1): 925 (1912); Léonard, Bull. Soc. Roy. Belg. 91: 274 (1959), Fl. Afr. Centr. Euphorb. 3: 56, t. 10, 11 (1996); Radcl.-Sm., Fl. Zambes. 9(4): 147, t. 29 (1996).
Pycnocoma sect. *Wetriaria* Müll. Arg. (1866).
Neopycnocoma Pax (1909).

Monoecious trees or shrubs; indumentum simple. Leaves sometimes apically clustered, simple, subsessile or short-petiolate, entire or denticulate, sometimes with abaxial glands; stipules deciduous. Inflorescences axillary, spiciform (compound); cymules usually bisexual; bracts persistent. Staminate flowers pedicellate, pedicel articulated near base; calyx closed in bud, splitting into 2–5 valvate segments; petals 0; disk segments interstaminal, pilose; stamens (15–) 25–120, filaments distinct, erect in bud; anthers with enlarged connective, muticous, locules pendent; pollen grains spheroidal, angulaperturate, 3-colporate, emarginate, colpar membrane granulose, sexine tectate-reticulate; pistillode usually 0. Pistillate flowers pedicellate; sepals usually (3–) 5–6(−9), imbricate, entire, persistent in fruit; disk annular; ovary 3(4)-locular, pubescent; ovules pachychazal, inner integument thick, outer thinner; stylodia basally connate, unlobed, tips recurved. Fruits capsular, 3-lobed; columella persistent, apically dilated. Seeds globose, ecarunculate, smooth.

Eleven spp., Africa and Madagascar. The group was first treated by Müller (1866) as a section of *Pycnocoma*. Pax originally regarded *Argomuellera* as related to *Mallotus*, but noted a

resemblance in habit to *Pycnocoma*, and Radcliffe-Smith (2001) has included *Argomuellera* in the subtribe Pycnocominae.

143. *Pycnocoma* Benth.

Pycnocoma Benth., Niger Fl.: 508 (1849); Léonard, Bull. Jard. Bot. Nat. Belg. 65: 38 (1996), Fl. Afr. Centr. Euphorb. 3: 36, fig. 2, t. 6–9 (1996); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 228; fig. 46 (1987).
Wetriaria (Müll. Arg.) Kuntze (1903).

Monoecious trees or shrubs; indumentum simple. Leaves sometimes pseudo-verticillate, subsessile, entire or dentate, rarely lobed, eglandular but minutely punctate abaxially; stipules deciduous or 0. Inflorescences axillary, bisexual, racemiform or spiciform, staminate flowers in glomerules at proximal nodes, pistillate solitary and terminal; staminate bracts concave. Staminate flowers pedicellate, pedicel articulate at base; calyx closed in bud, splitting into 2–5 valvate segments; petals 0; disk receptacular, usually glabrous; stamens > 50, filaments distinct, flexuous in bud, long-exserted; anthers introrse, muticous, connective not enlarged; pollen grains 3-angled, 3-colporate, emarginate, inoperculate but colpar membrane granulose; sexine minutely tectate-punctate, slightly rugulose, with coarse reticulum of granular projections; pistillode 0. Pistillate flowers pedicellate; sepals (4)5–8, imbricate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, 6-horned or -winged, pubescent; ovules anatropous, inner and outer integuments moderately thick; stylodia connate into a column, unlobed, apically dilated. Fruits capsular, 3-lobed; columella persistent. Seeds globose, ecarunculate, testa minutely puberulent.

Eighteen spp., tropical Africa. The pollen of *Pycnocoma* is unique in its areolate tectum, which somewhat simulates the pattern in *Croton*.

144. *Droceloncia* Léonard

Droceloncia Léonard, Bull. Soc. Roy. Bot. Belge 91: 279 (1959); Webster, Ann. Missouri Bot. Gard. 81: 76 (1994); Radcl.-Sm., Gen. Euphorb.: 167, fig. 18 (2001).

Monoecious shrubs; indumentum simple; terminal buds perulate. Leaves subentire or dentate, eglandular; stipules deciduous. Inflorescences axillary, spiciform, bisexual, staminate flowers in glomerules, pistillate solitary and apical; bracts large, persistent. Staminate flowers pedicellate; calyx closed in bud, splitting into several valvate segments; petals 0; disk receptacular, convex, glabrous; stamens c. 40, filaments distinct and straight in bud; anther connective not enlarged; pollen grains subprolate, 3-colporate, inoperculate and emarginate, sexine tectate-perforate; pistillode 0. Pistillate flowers pedicellate; sepals 5 or 6 (?), imbricate; petals and disk 0; ovary 3-locular, smooth and glabrous; stylodia distinct, unlobed, apically dilated. Fruit capsular.

A single sp., *D. rigidifolia* (Baill.) Léonard, Madagascar and Comoro I. Although originally included in *Pycnocoma*, its pollen is very different from that genus (Nowicke et al. 1999).

9. Tribe Ampereeae Müll. Arg. (1864).

Monoecious (dioecious) herbs or subshrubs; indumentum simple; leaves alternate, narrow, ericoid, stipulate. Inflorescences glomerular, axillary or terminal; staminate flowers pedicellate; sepals 3–5, basally connate, valvate; petals + or 0; disk dissected or obsolete; stamens 3–10, filaments distinct; anthers biseriate, locules pendulous; pollen grains subprolate to suboblate, 3-colporate, colpi inoperculate; exine reticulate, tectum psilate; pistillode present or 0; pistillate flowers subsessile on a 1(3)-flowered peduncle; sepals (4) 5, imbricate, entire to fimbriate; disk cupular, crenulate; ovary 3-locular, integuments thin; stylodia distinct or nearly so, spreading, bifid; fruits capsular, septicidal; seeds carunculate.

The two Australian genera of Ampereeae have been associated in the taxonomic literature since the treatment of Müller (1866), who placed them in separate subtribes of the tribe Ampereeae. Henderson (1992), on the basis of supposedly intermediate characters in *Amperea spicata* Airy Shaw, has suggested that *Monotaxis* should probably be combined with *Amperea*. However, although Tokuoka and Tobe (2003) did not find any significant differences in ovule and seed anatomy, Nowicke et al. (1998), on the basis of pollen characters, have indicated that there are clear palynological distinctions between the genera. Furthermore, since there are distinct differences in stipules, inflorescences, anthers, and stylodia, amalgamation of the two genera seems premature. The finding of Wurdack et al. (2005) that *Adriana* appears in a clade with the two Ampereeae genera needs attention; also Nowicke et al. (1998) had observed a palynological resemblance between *Amperea* and *Adriana*.

KEY TO THE GENERA OF AMPEREEAE

1. Staminate petals +; sepals imbricate; anther connective not glandular, locules disjunct; pollen grains 3-angled, sexine reticulate; stylodia fimbriate; cymes terminal **145. *Monotaxis***
– Staminate petals 0; sepals ± valvate; anther locules pendulous from a glandular connective; pollen grains 3-lobed, sexine perforate-foveolate; stylodia usually entire; flowers axillary **146. *Amperea***

145. *Monotaxis* Brongn. Fig. 31

Monotaxis Brongn., Voy. Coq. Bot.: 223 (1829); Airy Shaw, Muelleria 4: 239 (1980); Halford & Henderson, Austrobaileya 6: 273–292 (2002), rev.

Monoecious (dioecious) perennial or annual herbs, sometimes suffruticose; indumentum 0. Leaves alternate (subopposite or verticillate), entire (dentate), one-veined, lateral veins obscure; stipules entire or lobed, persistent. Inflorescences glomerular, terminal, each usually with 1–3 pistillate and several staminate flowers subtended by small scarious bracts. Staminate flowers pedicellate; sepals 4 or 5, often petaloid; petals 4 or 5, clawed, basally auriculate; disk segments 4–5; stamens 8–10(11), filaments distinct; anthers 2-celled; anther cells distinct, divergent to pendent on transverse connective; pollen grains subprolate, angulaperturate, 3-colporate, colpi marginate, exine very thick, sexine reticulate, transitional to tectate-perforate; pistillode trifid to subulate or 0. Pistillate flowers pedicellate; sepals 4 or 5, imbricate, persistent in fruit; petals + or 0; disk segments 3–10, truncate or bifid; ovary 3-locular; ovules anatropous, inner and outer integuments thin; stylodia shortly connate at base, distally distinct, deeply bifid, branches fimbriate. Fruit capsular; columella slender, persistent. Seeds oblong, smooth, carunculate; endosperm copious; embryo cylindrical, straight or curved; cotyledons much longer than radicle.

Eleven spp., endemic to tropical and temperate Australia.

146. *Amperea* A. Juss.

Amperea A. Juss., Euphorb. Tent.: 35 (1824); Henderson, Austral. Syst. Bot. 5: 1, figs. 1–4 (1992); Radcl.-Sm., Gen. Euphorb.: 130 (2001).

Monoecious or dioecious perennial herbs; indumentum scanty or 0. Leaves sessile or petiolate, one-veined, laterals obscure, entire or dentate, often revolute; sometimes scale-like; stipules entire to fimbriate, persistent to deciduous.

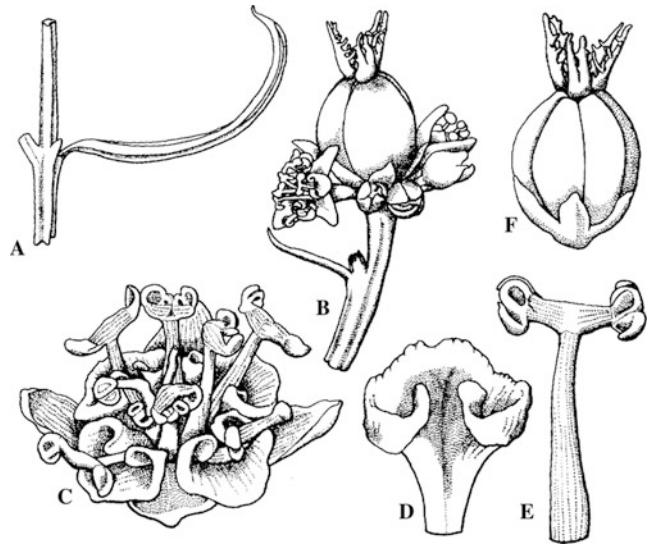

Fig. 31. Euphorbiaceae-Acalyphoideae. *Monotaxis linifolia*. **A** Section of twig with stipulate leaf. **B** Inflorescence. **C** Staminate flower. **D** Auriculate petal. **E** Antepetalous stamen, abaxial view. **F** Fruit. (Halford & Henderson 2002; drawn by W. Smith)

Inflorescences [except in *A. spicata*] axillary, flowers in dense unisexual or bisexual glomerules, subtended by ± dissected persistent bracts. Staminate flowers pedicellate; sepals 3–5(6), basally connate, entire, ± petaloid; petals 0; disk rudimentary or 0; stamens 3–10, filaments distinct, exserted; anthers with enlarged minutely glandular connective, thecae pendulous; pollen grains oblate spheroidal, 3-colporate and 3-lobed in polar view, colpi inoperculate, with broad margo, sexine tectate-perforate and ± verrucate; pistillode 0. Pistillate flowers subsessile; sepals 4 or 5, nearly distinct, imbricate, entire, persistent in fruit; petals 0; disk annular, tenuous; ovary 3-locular; ovules anatropous, inner and outer integuments thin; stylodia basally connate, bifid. Fruits capsular, valves sometimes with distal appendages; columella ± persistent. Seeds ellipsoidal, somewhat compressed, carunculate; testa smooth (minutely foveolate-striate); embryo cylindrical, cotyledons narrow and longer than radicle.

Eight spp., all Australian, 6 of these confined to Western Australia. The 3-lobed pollen with broad margo and verrucate exine of *Amperea* resembles that of *Bernardia*. However, that genus differs in its larger number of pistillate sepals and ecarunculate seeds; the pollen similarity may be homoplasious.

10. Tribe Epiprineae (Müll. Arg.) Hurus. (1954).

Monoecious; indumentum stellate; leaves alternate (opposite), petiole sometimes with apical paired glands; stipules sometimes glandular; inflorescences terminal or axillary, paniculate, racemoid, or the staminate capitulate; staminate flowers sessile or subsessile; calyx splitting into 2–6 valvate segments; petals and disk 0; stamens 4–15(−50); pollen grains 3-colporate, colpi inoperculate and scarcely marginate, endoaperture large, sexine tectate-perforate or coarsely reticulate; pistillode +; pistillate flowers sessile or pedicellate; sepals (4)5–8, imbricate, entire to lacerate, usually persistent in fruit; petals and disk 0; ovary 3(4)-locular, stellate-tomentose; stylodia distinct or connate, bifid to multifid (unlobed); fruits capsular (indehiscent); columella winged, usually persistent; seeds subglobose, ecarunculate; testa smooth (rugose).

Seven genera, all Asiatic except *Cephalocroton*. Except for the enigmatic *Rockinghamia*, which is added only tentatively, the Epiprineae appear to be a monophyletic group, also in the light of the molecular analysis (Wurdack et al. 2005), although the sampling (4 genera) is limited. *Rockinghamia* has a habit suggestive of *Mallotus*, but the studies of Nowicke et al. (1999) show that its pollen differs from that of all Acalypheae in the lack of microverrucae, whereas it shares with Epiprineae the deeply puntate-microreticulate exine sculpture. In the *rbc*L tree of Wurdack et al. (2005), it is resolved (without support) as basal to the genera of the Epiprineae.

Key to the Subtribes and Genera of Epiprineae

1. Anthers 4-celled; leaves opposite; staminate disk as interstaminate pubescent disk glands; pistillate disk annular. Subtribe **10c. Rockinghamiinae** **154. *Rockinghamia***
– Anthers 2-celled; leaves alternate; staminate and pistillate disk 0 2
2. Pistillate sepals persistent in fruit; staminate calyx of distinct segments; pollen sexine not spinulose. Subtribe **10a. Epiprininae** 3
– Pistillate sepals deciduous; staminate sepals connate; pollen sexine spinulose. Subtribe **10b. Cephalomappinae** **153. *Cephalomappa***
3. Staminate flowers in racemoid or spiciform inflorescences 4
– Staminate flowers in pedunculate capitula 7
4. Pistillate flower sessile, calyx involucrate, accrescent in fruit; stylodia connate into a distinct column; stamens mostly 8–15; leaf blades with paired basal glands at junction with petiole **147. *Epiprinus***
– Pistillate flowers pedicellate, calyx not involucrate; stylodia scarcely connate; stamens (3) 4 or 5; leaf blades eglandular [except *Cleidiocarpon*] 5
5. Filaments straight in bud; staminate sepals connate; stipules persistent **150. *Koilodepas***
– Filaments ± inflexed in bud; staminate calyx of distinct segments; stipules deciduous or obsolete 6
6. Monoecious; fruits capsular; leaves without laminar or petiolar glands **148. *Symphyllia***
– Dioecious; fruits indehiscent; petiole with paired distal glands **149. *Cleidiocarpon***
7. Inflorescences axillary; stamens (2–)4(5); pistillate flowers subsessile, sepals unlobed, accrescent; leaf blades white-tomentose beneath **151. *Cladogynos***
– Inflorescences terminal; stamens 6–10; pistillate flowers pedicellate, sepals pinnately or bipinnately lobed (entire); leaf blades not white-tomentose beneath **152. *Cephalocroton***

10a. Subtribe Epiprininae Müll. Arg. (1865).

Leaves pinnately or palmately veined; staminate sepals distinct; stamens mostly 6–8 or more, filaments distinct; pollen sexine not spinulose; pistillate sepals mostly persistent; capsules smooth.

Six paleotropical genera.

147. *Epiprinus* Griffith

Epiprinus Griffith, Notul. Pl. Asiat. 4: 487 (1854); Croizat, J. Arnold Arb. 23: 52 (1942); Thin, Tâp Chi Sinh Vât Hoc 10(2): 30 (1988); Radcl.-Sm., Gen. Euphorb.: 176 (2001).

Monoecious shrubs or trees; indumentum stellate. Leaves alternate or subopposite, clustered at ends of branches, subsessile, subentire, with sparse glands; petiole biglandular at apex; stipules entire, glandular at base, deciduous. Inflorescences terminal, spiciform, bisexual, with 1 or 2 proximal pistillate flowers and distal glomerules or spikelets of staminate flowers. Staminate flowers sessile; calyx splitting into mostly 3 or 4 valvate segments; petals and disk 0; stamens (5–)8–15, filaments distinct, inflexed in bud; anthers introse, minutely apiculate; pollen grains oblate spheroidal, 3-colporate, colpi narrow, inoperculate and emarginate; sexine tectate-perforate transitional to reticulate, with microverrucae at angles of lumina; pistillode clavate, pubescent. Pistillate flowers pedicellate; calyx involucrate, bracts glandular at base, deciduous; sepals 5 or 6, imbricate, entire, accrescent and persistent in fruit; ovary

3-locular, stellate-tomentose; ovules with inner integument thin, outer thick; stylodia bifid or unlobed, papillose-lacerate. Fruits capsular, valves thick and woody; columella ± persistent. Seeds roundish, ecarunculate, testa smooth.

Four spp., southeast Asia and Indonesia.

148. *Symphyllia* Baill.

Symphyllia Baill., Étude Gén. Euphorb.: 473 (1858); Gagnep., Fl. Indochine 5: 477, fig. 60, 10–12 (1926); Webster, Ann. Missouri Bot. Gard. 81: 78 (1994); Radcl.-Sm., Gen. Euphorb.: 177, fig. 21 (2001).

Monoecious trees or shrubs; indumentum stellate. Leaves eglandular; stipules glandular, deciduous. Inflorescences terminal or axillary, spiciform or paniculate, usually bisexual; bracts inconspicuous. Staminate flowers subsessile; calyx closed in bud, splitting into 3–6 valvate segments; petals and disk 0; stamens 3–6, mostly 4 or 5, filaments distinct, inflexed in bud; anthers muticous, 2-locellate; pollen grains prolate spheroidal, 3-colporaate, colpi inoperculate and emarginate, sexine tectate-peroratae, heterobrachate; pistillode +. Pistillate flowers subsessile, not involucrate; sepals 5–7, entire, valvate, persistent in fruit; petals and disk 0; ovary 3-locular, stellate-tomentose; stylodia connate into a column longer than the ovary, bifid or twice bifid. Fruits capsular. Seeds smooth.

Three spp., eastern Asia: India to Hainan and Malaya. Croizat (1942) combined *Symphyllia* with *Epiprinus*, which was followed by Govaerts et al. (2000); however, it differs from that genus in its eglandular leaves and lack of a pistillate involucre. *Symphyllia* is therefore provisionally retained as a distinct genus.

149. *Cleidiocarpon* Airy Shaw

Cleidiocarpon Airy Shaw, Kew Bull. 19: 313 (1965), 32: 410 (1978); Thin, Tâp Chi Sinh Vât Hoc 10(2): 32 (1988); Webster, Ann. Missouri Bot. Gard. 81: 79 (1994); Radcliffe-Smith, Gen. Euphorb.: 179 (2001); Qiu Huaxing & Gilbert, Fl. China 11: 250 (2008).
Sinopimelodendron Tsiang (1973).

Monoecious trees; indumentum stellate. Leaves apically clustered on branches, eglandular; petiole stipellate at apex; stipules deciduous. Inflorescences terminal, spiciform-paniculate, bisexual or sometimes unisexual; bracts and prophylls conspicuous. Staminate flowers subsessile; sepals 4 or 5, valvate; petals and disk 0; stamens 4 or 5, filaments distinct, inflexed in bud; anthers introrse, 4-locellate; pollen grains prolate spheroidal, 3-colporate, colpi inoperculate and emarginate, sexine tectate-punctate; pistillode +. Pistillate flowers subsessile; sepals 4–8, valvate, entire, persistent in fruit; petals and disk 0; ovary 2-locular, stellate-tomentose; stylodia basally connate, distally distinct, multifid. Fruits indehiscent, drupaceous, rugose, beaked. Seed solitary, rugose.

Two spp. from northern Burma, China, western Thailand and Vietnam. Thin (1988) has proposed a new subtribe Cleidiocarpinae for it, and the genus is indeed unusual in the drupaceous fruit.

150. *Koilodepas* Hassk.

Koilodepas Hassk., Versl. Med. Afd. Natuurk. Kon. Akad. Wetensch. 4: 139 (1856), Flora 40: 531 (1857, *Coelodepas*); Croizat, J. Arnold Arb. 23: 50 (1942); Airy Shaw, Kew Bull. 14: 382 (1960), Kew Bull. 36: 310 (1981); Radcl.-Sm., Gen. Euphorb.: 180, fig. 22 (2001).

Monoecious trees; indumentum stellate. Leaves entire or crenate-dentate, abaxially biglandular or with scattered glands; stipules ± dentate, persistent. Inflorescences axillary, spiciform, usually bisexual, with 1 or few proximal pistillate flowers and distal staminate or bisexual glomerules; bracts ovate, ± dentate apically, eglandular. Staminate flowers sessile; calyx closed in bud, splitting into 3 or 4 valvate segments; petals and disk 0; stamens 4–5(−8), filaments basally connate, dilated above the middle, anthers introrse, connective not enlarged, 2-locellate, locules divergent; pollen grains subspheroidal, 3-colporate, colpi narrow, inoperculate and emarginate; sexine tectate-punctate, psilate; pistillode +. Pistillate flowers sessile; sepals 4–10, basally connate, entire; persistent in fruit; petals and disk 0; ovary (2)3-locular, stellate-tomentose; ovules with thick integuments; stylodia bifid to multifid, ± laciniate. Fruits capsular; columella persistent, broadly winged. Seeds subglobose, testa smooth.

Eleven spp., distributed from India to Borneo and New Guinea. Airy Shaw (1960) proposed 2 sections, one (sect. *Hyalodepas* Airy Shaw) including 2 spp. with accrescent fruiting calyx suggestive of *Epiprinus*, and referring the other 9 spp. to sect. *Koilodepas*, with non-accrescent calyx.

151. *Cladogynos* Zipp. ex Span.

Cladogynos Zipp. ex Span., Linnaea 15: 349 (1841); Pax & K. Hoffm., Pflanzenr. 147, VII: 264, fig. 41 (1914); Gagnep., Fl. Indochine 5: 478, fig. 61 (1926); Airy Shaw, Kew Bull. 26: 232 (1972); Radcl.-Sm., Gen. Euphorb.: 182 (2001).

Monoecious shrubs; indumentum stellate. Leaves pinnately veined or triplinerved, double-dentate, peltate or subpeltate at base, eglandular; stipules minute, deciduous. Inflorescences axillary, bisexual, of 1 proximal pedicellate pistillate flower and a distal capitulum of staminate flowers. Staminate flowers sessile; petals and disk 0; stamens (3)4(5), filaments distinct, inflexed in bud; anthers introrse, muticous, locules; pollen grains 3-colporate, colpi narrow, sexine tectate-perforate; pistillode +. Pistillate flowers pedicellate; sepals 5–7, subfoliaceous, basally contracted, subentire, persistent in fruit; petals and disk 0; ovary 3(4)-locular, pubescent; ovules with inner integument thick, outer thin; stylodia basally connate, twice bifid or more, papillose. Fruits capsular, columella persistent, apically dilated. Seeds spheroidal, testa smooth.

A single sp., *C. orientalis* Zipp. ex Span., widespread in southeast Asia and Malesia.

152. *Cephalocroton* Hochst.

Cephalocroton Hochst., Flora 24: 370 (1841); Müll. Arg. in DC., Prodr. 15(2): 760 (1866); Pax, Pflanzenr. 147, II: 7, figs. 3, 4 (1910); Prain, Fl. Trop. Afr. 6(1): 843 (1912); Radcl.-Sm., Kew Bull. 28: 123 (1973); Fl. E. Trop. Afr. Euphorb. 1: 282, fig. 55 (1987); Gilbert, Kew Bull. 42: 365, fig. 6 (1987); Webster, Ann. Missouri Bot. Gard. 81: 79 (1994); Radcl.-Sm., Gen. Euphorb.: 183 (2001).
Adenochlaena Baill. (1858).
Cephalocrotonopsis Pax (1910).

Monoecious shrubs; indumentum stellate and glandular-setose. Leaves palmately veined or triplinerved, usually dentate, eglandular; stipules persistent, sometimes minute or obsolete. Inflorescences terminal (axillary), the staminate flowers in distal capitula, the pistillate flowers proximal, separated by a long internode. Staminate flowers pedicellate (sessile), articulate at base of calyx; sepals closed in bud, splitting into 3–6 valvate lobes; petals and disk 0; stamens (4–)6–8(−10), filaments distinct, inflexed in bud; anthers dorsifixed, introrse, muticous, 2-locellate; pollen grains prolate spheroidal, 3-colporate, colpi narrow, inoperculate and emarginate, sexine tectate-perforate, muri microverrucate; pistillode 2- or 3-lobed. Pistillate flowers pedicellate, the pedicel usually greatly elongating in fruit; sepals 4–6, pinnately or bipinnately lobed (entire), persistent and accrescent in fruit; petals and disk 0; ovary 3-locular, stellate-tomentose; ovules with inner integuments thicker than outer integuments; stylodia multifid. Fruits capsular, 3-lobed, glandular-verrucate; columella persistent, broadly winged. Seeds roundish, smooth or sparsely pubescent.

About seven spp. in tropical Africa, Madagascar, Socotra and Ceylon.

In Webster (1994), *Adenochlaena* and *Cephalocrotonopsis* were accepted as distinct genera. Radcliffe-Smith (2001) also accepts both genera, even though he earlier sank *Cephalocrotonopsis* into *Cephalocroton*. However, the pollen grains of these taxa are identical (Takahashi et al. 2000), and it now seems preferable to treat both *Adenochlaena* and *Cephalocrotonopsis* as sections of an enlarged genus *Cephalocroton*, distinguished by its unique inflorescence type.

10b. Subtribe Cephalomappinae G.L. Webster (1975).

A monotypic subtribe.

153. *Cephalomappa* Baill.

Cephalomappa Baill., Adansonia 11: 130 (1874); Pax, Pflanzenr. 147, II: 16. 1910; Airy Shaw, Kew Bull. 14: 378 (1960); Kosterm., Reinwardtia 5: 413 (1961); Backer & Backh., Fl. Java 1: 486 (1963); Whitmore, Tree Fl. Malaya 2: 75, fig. 4 (1973); Airy Shaw, Kew Bull. 36: 274 (1981); Widuri & van Welzen, Reinwardtia 11: 153, figs. 1–16 (1998); Radcl.-Sm., Gen. Euphorb.: 186, fig. 23 (2001).

Monoecious trees or shrubs; indumentum simple, stellate, and lepidote. Leaves entire to dentate, eglandular or sometimes with abaxial glands; petioles pulvinate; stipules deciduous. Inflorescences terminal or axillary, racemiform, sometimes compounded and corymbose; staminate flowers in pedunculate capitula, pistillate flowers 1–3 at proximal axils; bracts deciduous. Staminate flowers sessile; calyx turbinate, truncate, 2–5-lobed, lobes valvate; petals and disk 0; stamens (2)3–4, filaments connate into a column, tips inflexed in bud; anthers latrorse, connective glandular, muticous, 2-celled; pollen grains oblate spheroidal, 3-brevicolporate, sexine coarsely reticulate and muri spinulose; pistillode clavate, sometimes apically lobed. Pistillate flowers pedicellate; sepals 4–6(−8), imbricate, connate at base, deciduous; petals and disk 0; ovary 3-locular, stellate-tomentose or lepidote; ovules anatropous, inner integuments very thick, outer integuments thick; stylodia connate, tips bifid or palmately incised. Fruits capsular, verrucose, 3-lobed, lepidote. Seeds spheroidal, hilum ovate, testa smooth.

Five spp., southern China, Malay Peninsula, Sumatra and Borneo. The pollen of *Cephalomappa* is so distinctive that Takahashi et al. (2000) suggest the genus should be placed in a separate tribe. However, in other features it appears similar to genera of Epriprineae, and in the molecular analysis of Wurdack et al. (2005) it is resolved in a clade with *Koilodepas* and *Cephalocroton*.

10c. Subtribe Rockinghamiinae G.L. Webster (2004).

A monogeneric Australasian subtribe.

154. *Rockinghamia* Airy Shaw

Rockinghamia Airy Shaw, Kew Bull. 20: 29 (1966), 35: 667, fig. 6 (1980); Hyland & Whiffin, Austral. Trop. Rain For. Trees: 150 (1993); Radcl.-Sm., Gen. Euphorb.: 232 (2001).

Monoecious trees; indumentum simple, sparse. Leaves mostly opposite, often pseudo-verticillate at end of branches, entire or crenate, eglandular; petioles pulvinate; stipules deciduous. Inflorescences terminal (axillary), racemoid or paniculate, bisexual; bracts glandular, entire, persistent. Staminate flowers pedicellate; calyx closed in bud, splitting into 4 valvate segments; petals 0; disk segments numerous, interstaminal, pubescent; stamens 25–50, filaments distinct; anthers 4-celled, muticous; pollen grains prolate spheroidal, 3-colpor(oid)ate, inoperculate and emarginate, endoapertures indistinct; sexine perforate-tectate to reticulate with narrow muri and deep lumina, sometimes heterobrochate; pistillode + or 0. Pistillate flowers pedicellate; sepals 5, imbricate, subentire, persistent in fruit; petals 0; disk annular; ovary 3-locular, pubescent; ovules anatropous, inner integument thick, outer thin; stylodia distinct or basally connate, bifid or unlobed. Fruits capsular, 3-lobed, muricate; columella persistent, winged-dilated. Seeds roundish or oblong, hilum deltoid, testa smooth.

Two spp., tropical Australia (Queensland).

11. Tribe Chrozophoreae (Müll. Arg.) Pax & K. Hoffm. (1919).

Monoecious or dioecious trees, shrubs, or herbs; indumentum stellate, lepidote, malpighiaceous, or simple; leaves alternate, unlobed or lobed, entire or dentate, sometimes with laminar glands; stipules persistent or deciduous; inflorescences axillary or terminal, mostly racemoid or spicate; staminate flowers subsessile or pedicellate; calyx splitting into 3–5 valvate sepals; petals (0)4–5(10); disk dissected or 0; stamens 5–many, filaments distinct or connate; connectives generally not enlarged and thecae not pendulous; pollen grains mostly 3–6-colporate, colpi inoperculate, sexine reticulate and often distinctly heterobrochate; pistillode + or 0; pistillate flowers usually pedicellate; sepals 5 or 6, imbricate or valvate, usually entire, persistent in fruit; petals 5 (reduced or 0); disk annular or dissected (0); ovary (2)3-locular; stylodia unlobed to bifid or twice bifid, sometimes lacerate; fruit capsular; columella usually persistent; seeds ecarunculate.

With 11 genera and 125 species or more, tribe Chrozophoreae is widespread and diverse in warm temperate to tropical areas. As the tribal description indicates, the morphological diversity is extreme, and the molecular data of Wurdack et al. (2005) (still with incomplete sampling) point to placements in different clades of the acalyphoids: Ditaxinae as sister to Adelieae, and Speranskiinae and Chrozophorinae into a clade together with Epiprineae. Available data permit, however, the transfer of *Caperonia* from Speranskiinae to Ditaxinae, and to merge Doryxylinae with monotypic Chrozophorinae.

Key to the Subtribes of Chrozophoreae

1. Indumentum stellate; leaves with basal laminar glands **11c. Chrozophorinae**
– Indumentum simple or malpighiaceous, or if stellate then leaves without basal laminar glands 2
2. Inflorescence terminal; indumentum simple; stems not spinose; ovary muricate **11a. Speranskiinae**
– Inflorescence axillary; indumentum malpighiaceous or stellate (entirely simple and stems spinose in *Philyra*) **11b. Ditaxinae**

11a. Subtribe Speranskiinae G.L. Webster (1975).

Monoecious herbs; indumentum simple; leaves glandular-dentate; inflorescences terminal, spiciform; sepals and petals usually 5 in both sexes; stamens 10–15, filaments distinct; pollen grains 3-colporate; pistillate flowers pedicellate or subsessile; disk cupular or 0; ovary usually muricate; inner and outer ovular integuments thin; stylodia distinct, branches lacerate; seed coat dry.

A monogeneric Asian subtribe.

155. *Speranskia* Baill.

Speranskia Baill., Étude Gén. Euphorb.: 388 (1858); Pax & K. Hoffmann, Pflanzenr. 147,VI: 14, fig. 3 (1912); Hwang Shu-mei, Bull. Bot. Res. Harbin 9 (4): 37–40 (1989); Radcl.-Sm., Gen. Euphorb.: 138 (2001); Qiu Huaxing & Gilbert, Fl. China 11: 223 (2008).

Monoecious perennial herbs; indumentum simple. Leaves petiolate or sessile, glandular-dentate, without laminar glands, stipellate at base; stipules deciduous or persistent. Inflorescences terminal, spiciform; proximal cymules bisexual or pistillate, distal staminate; bracts eglandular, persistent. Staminate flowers pedicellate; calyx splitting into 5 valvate sepals; petals 5; disk segments 5; stamens 10–15, filaments distinct; anthers in 2 (3) whorls, dorsifixed, extrorse; pollen grains subprolate, 3-colporate, colpi operculate, endoaperture lalongate, exine tectate-punctate to tectate-reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 5, distinct, lanceolate, entire, deciduous or persistent; petals 5 or 0; disk cupular; ovary 3-locular, verruculose or tuberculate; inner and outer integuments thin; stylodia distinct, bifid, branches lacerate. Fruits capsular, 3-lobed; columella deciduous or persistent. Seeds globose, testa smooth or foveolate to rugulose.

Two spp., endemic to China.

11b. Subtribe Ditaxinae Griseb. (1859).

Monoecious (dioecious) trees, shrubs, or herbs; indumentum simple, glandular, stellate or malpighiaceous; leaves entire or serrate, stipulate; inflorescences axillary, racemoid or glomerulate; staminate sepals mostly 4 or 5; petals 5, distinct or adnate to staminal column; disk dissected, reduced, or 0; stamens 4–15, filaments connate (almost distinct); anthers introrse, pollen grains 3–4-colporate; pistillode + or 0; pistillate flowers sessile or pedicellate; sepals 5 (6), distinct, imbricate; petals 5 or 0; disk dissected or 0; ovary 3-locular, smooth or muricate; stylodia bifid to laciniate; seeds with dry testa, smooth or ornamented.

As here delimited, subtribe Ditaxinae includes 5 mostly neotropical genera with 110–115 species.

Key to the Genera of Ditaxinae

1. Leaves finely serrate with straight parallel lateral nerves; disk 0; pollen 3–6-colporate; pistillode +; stylodia dissected **160. *Caperonia***
– Leaves not as above; disk +, at least in staminate flowers; pollen 3–4-colporate; pistillode 0 or scarcely developed; stylodia bifid to dissected 2
2. Dioecious; tepals scarious; shrubs or trees, branches often spiny **156. *Philyra***
– Monoecious; tepals not scarious; undershrubs or herbs, not spiny 3
3. Petals 3–7-lobed or -partite; stylodia once bifid; stellate hairs sometimes present; pollen grains 3-colporate **159. *Chiropetalum***
– Petals entire; stylodia twice bifid to multifid; stellate hairs 0 4
4. Stamens 8–10, anthers in 2 whorls; pollen grains mainly 3-colporate, bilaterally symmetrical **158. *Ditaxis***
– Stamens 4 or 5, anthers in 1 whorl; pollen grains stephanocolporate, not bilaterally symmetrical **157. *Argythamnia***

156. *Philyra* Klotzsch

Philyra Klotzsch, Arch. Naturgesch. 7(1): 199 (1841); Pax & K. Hoffm., Pflanzenr. 147,VI: 49, fig. 10 (1912); O'Donell & Lourteig, Lilloa 8: 60 (1942); Radcl.-Sm., Gen. Euphorb.: 141 (2001).
Argythamnia sect. *Philyra* (Klotzsch) Müll. Arg. (1865).

Dioecious trees or shrubs; indumentum 0 except for simple hairs on inflorescences. Leaves alternate; stipules persistent, indurate, often associated with long infrastipular spines. Inflorescences axillary, brachyblastic, or the pistillate flowers on expanded tenuous racemes; bracts indurate, persistent. Staminate flowers pedicellate; sepals 3–5, fused in bud, splitting into valvate segments; petals 5, distinct; disk segments 5, adnate to staminal column; stamens (8) 10, filaments connate below into a column; anthers in 2 superposed whorls, extrorse; pollen grains prolate spheroidal to subprolate, 3-colporate, colpi exoperculate and emarginate, endoaperture circular; sexine tectate-punctate; pistillode trifid, at apex of staminal column. Pistillate flowers long-pedicellate; sepals 5, linear-lanceolate, entire, persistent in fruit; petals 5, longer than sepals; disk thickened as gynophore; ovary 3-locular; ovules with inner integument moderately thick, outer thin; stylodia bifid, branches multifid or lobed. Fruits capsular; columella persistent, trifid at apex. Seeds globose; testa smooth.

A single sp., *P. brasiliensis* Klotzsch, from Argentina and Paraguay to northeastern Brazil (Bahia), in deciduous or semi-deciduous tropical woodlands. Although appearing in a clade with three adelioid genera (Wurdack et al. 2005), this petaloid genus differs significantly from them, and the pollen is very distinct.

157. *Argythamnia* P. Browne

Argythamnia P. Browne, Civ. Nat. Hist. Jamaica: 338 (1756); Ingram, Gentes Herb. 10(1): 1, figs. 3–19 (1967); Correll, Fl. Bahama Arch. 777, fig. 325 (1982); Howard, Fl. Lesser Ant. 5: 14, fig. 5 (1989); Webster, Ann. Missouri Bot. Gard. 81: 72 (1994); L.J. Gillespie, Fl. St. John 203 (1996); Radcl.-Sm., Gen. Euphorb.: 143 (2001).

Monoecious (dioecious) shrubs or subshrubs; indumentum malpighiaceous. Leaves entire or denticulate, pinnately veined (triplinerved), with steeply ascending laterals; stipules entire, ± persistent. Inflorescences axillary, glomerular or racemiform, pistillate flowers proximal and staminate distal in bisexual inflorescences; bracts 1-flowered, persistent. Staminate flowers subsessile; sepals connate in bud, dehiscing into 4(5) valvate segments; petals 4(5), shorter than sepals, imbricate, entire; disk segments 4(5), adnate to base of staminal column; stamens 4–6, filaments connate at the base, sometimes forming a short column; anthers introrse; pollen grains 4-colporate, colpi inoperculate, sexine tectate-perforate; pistillode rudimentary. Pistillate flowers subsessile; sepals 5(6), distinct, valvate, entire, persistent in fruit; petals 5, distinct, entire, often reduced or rudimentary; disk divided into 5 segments; ovary 3-locular; ovules with inner and outer integuments thin; stylodia bifid or twice bifid. Fruits capsular; columella persistent. Seeds round, testa dry, roughened (alveolate).

About 18 spp., most of which occur in the West Indies, and 8 from S Mexico to Honduras.

158. *Ditaxis* Vahl ex A. Juss.

Ditaxis Vahl ex A. Juss., Euphorb. Tent.: 27 (1824); O'Donell & Lourteig, Lilloa 8: 62, figs. 5–10, t. I, III–VII (1942); Wiggins, Fl. Sonoran Desert: 784 (1964); Webster, Jepson Man. Pl. Calif.: 572 (1993); Diggs et al., Fl. North Central Texas: 600 (1999); Radcl.-Sm., Gen. Euphorb.: 142 (2001).
Argythamnia sect. *Ditaxis* (P. Browne) Müll. Arg. (1865).

Monoecious (dioecious) shrubs, perennial herbs, and annual herbs; indumentum malpighiaceous. Leaves entire or dentate, pinnately veined (triplinerved), often with steeply ascending laterals; stipules entire, persistent. Inflorescences axillary, glomerular or racemiform, typically bisexual. Staminate flowers pedicellate; sepals connate, separating into usually 5 segments at anthesis; petals 5, imbricate, distinct but each petal unguiculate and adnate to base of staminal column; stamens (7–)10, filaments connate into a column; anthers biseriate, introrse, dehiscing vertically; pollen grains ± oblate, asymmetrically 3-colporate; colpi inoperculate; sexine tectate-punctate (superreticulate); pistillode at apex of staminal column, divided (0). Pistillate flowers pedicellate; sepals 5, distinct, imbricate, entire or denticulate, persistent in fruit; petals 5, imbricate, entire, often persistent in fruit; disk segments 5, often confluent; ovary 3-locular; glabrous or pubescent; ovules with inner integument moderately thick, outer thin; stylodia bifid, branches sometimes emarginate or shortly bifid. Fruits capsular; columella persistent, 3-pronged. Seeds smooth to rugose or foveolate.

About 40–50 spp. ranging from the USA south to Argentina, primarily in subarid regions. The distinct pollen grains furnish the best diagnostic character (Takahashi et al. 1995; Nowicke et al. 1999).

159. *Chiropetalum* A. Juss.

Chiropetalum A. Juss., Ann. Sci. Nat. (Paris) 25: 21 (1832); O'Donell & Lourteig, Lilloa 8: 38, figs. 1–3, t. II (1942); Ingram, Gentes Herb. 11(7): 437, figs. 4–9 (1980); L.B. Smith et al., Fl. Ilustr. Catar. EUFO: 154 (1988); Radcl.-Sm., Gen. Euphorb.: 144 (2001).
Argythamnia subg. *Chiropetalum* (A. Juss.) Ingram (1980).

Monoecious shrubs or subshrubs; indumentum malpighiaceous, sometimes also simple or stellate. Leaves alternate, serrate (entire), 3–5-veined from base; stipules entire, persistent. Inflorescences axillary, racemiform, pistillate flowers proximal, staminate flowers distal; bracts 1-flowered, persistent. Staminate flower pedicellate; sepals connate in bud, dehiscing into 5 valvate segments; petals 5, distinct, imbricate, unguiculate, 3–7-lobed or -partite; disk segments 5; stamens 5 (6), filaments connate into a column; anthers stipitate atop column; pollen grains spheroidal to prolate spheroidal, 3-colpate, colpi operculate, emarginate; exine finely tectate; pistillode rudimentary. Pistillate flower pedicellate; sepals 5, valvate, entire, persistent in fruit; petals 5, shorter than sepals, entire (lobed), sometimes obsolete; disk segmented into 5 lobes; ovary 3-locular; ovules with inner and outer integuments thin; stylodia distinct or basally connate, bifid. Fruits capsular; columella persistent. Seeds spheroidal; testa rugose.

About 22 spp., 2 in Mexico and 20 in South America: Peru and Chile to S Brazil. Nowicke

et al. (1999) point out that the 3-colpate operculate pollen grains of *Chiropetalum* are very different from the 4-colporate inoperculate grains of *Argythamnia*, contradicting the merging of the two genera by Ingram (1967).

160. *Caperonia* St. Hil.

Caperonia St. Hil., Pl. Remarq. Brésil: 244 (1826); Fawc. & Rendle, Fl. Jam. 4: 288, fig. 93 (1920); O'Donell & Lourteig, Lilloa 8: 54, fig. 4 (1942); Léonard, Fl. Congo 8(1): 166, t. 11 (1962); Webster, J. Arnold Arb. 48: 363 (1967), Ann. Missouri Bot. Gard. 54: 265, fig. 10 (1968); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 163, fig. 29 (1987); Webster, Fl. Venez. Guayana 5: 102, fig. 100 (1999), Fl. Nicaragua: 856 (2001); Radcl.-Sm., Gen. Euphorb.: 140 (2001).

Monoecious annual or perennial herbs, sometimes rhizomatous or fruticose, stems often hollow; indumentum simple, sometimes prickly or glandular. Leaves alternate, serrate, pinnately and strikingly parallel-veined; stipules scarious, persistent. Inflorescences axillary, spiciform, usually bisexual, with 1–5 basal pistillate flowers; bracts entire, persistent, subtending solitary flowers. Staminate flowers with articulate pedicels; calyx of 5 valvate lobes fused in bud; petals 5, often unequal, basally adnate to the staminal column; disk 0; stamens 10, filaments partly connate into a column, anthers in 2 superposed whorls; pollen grains subspheroidal, 3- or 6-colporate, colpi operculate, emarginate, endoapertures obscure, germ pores large, sexine tectate-punctate to -reticulate; pistillode at apex of staminal column. Pistillate flowers subsessile; calyx deeply 5-lobed, with 0–5 smaller supernumerary lobes, persistent in fruit; petals 5, often unequal or reduced; disk 0; ovary 3-locular, usually muricate; ovules anatropous, inner and outer integuments thin; stylodia distinct, laciniate. Fruit capsular, valves thin, usually verrucose; columella persistent, apically dilated. Seeds globose; testa minutely foveolate. $n = 11$.

About 35 spp., mostly American, but a few spp. in Africa and Madagascar, widely spread in marshy habitats.

11c. Subtribe Chrozophorinae Müll. Arg. (1865).

Doryxylinae G.L. Webster (1975).

Monoecious trees, shrubs or herbs; indumentum stellate or lepidote; leaves with laminar glands; inflorescences terminal or axillary, usually bisexual; staminate sepals 3–5; petals 5–10 or 0; disk reduced or 0; stamens (4–)30–250, distinct or partially connate; pollen grains 3(6–9)-colporate, angulaperturate, sexine reticulate; pistillate sepals 5–6, imbricate or valvate, petals rudimentary or 0; disk annular or obsolete; ovary 2–3-locular; stylodia bifid or unlobed; seeds with fleshy exotesta, foveolate endotesta.

An Old World, mainly Asiatic, subtribe of 5 genera.

Key to the Genera of Chrozophorinae

1. Petals 0; ovary usually 2-locular; stamens 200 or more **164. *Melanolepis***
– Petals +; ovary 3-locular; stamens 4–100 2
2. Stamens connate; pollen grains stephanocolporate; herbs or subshrubs **165. *Chrozophora***
– Stamens distinct [except in *Thyrsanthera*]; pollen grains 3-colporate; shrubs or trees 3
3. Inflorescences axillary; stylodia unlobed, basally connate; stamens distinct **161. *Doryxylon***
– Inflorescences terminal; stylodia bifid, ± distinct 4
4. Stamens distinct; staminate disk 0; pistillate sepals imbricate **162. *Sumbaviopsis***
– Stamens connate; staminate disk +; pistillate sepals valvate **163. *Thyrsanthera***

161. *Doryxylon* Zoll.

Doryxylon Zoll., Tijdschr. Ned.-Indië 14: 172 (1857); N.P. Balakr., Bull. Bot. Surv. India 9: 56, figs. 1–7 (1967); Webster, Ann. Missouri Bot. Gard. 81: 72 (1994); van Welzen, Blumea 44: 422, fig. 3 (1999).

Monoecious trees or shrubs; twigs often with axillary spines; indumentum simple and stellate. Leaves palmately veined, dentate, whitish-tomentose abaxially; stipules minute, deciduous. Inflorescences terminal, racemoid, often unisexual; bracts uniflorous. Staminate flowers pedicellate or subsessile; sepals 5, valvate; petals 5, shorter than sepals; disk 0; stamens 30–130, filaments distinct, inserted on hairy receptacle; anthers dorsifixed, latrorse; pollen grains oblate spheroidal, angulaperturate, 3-colporate, colpi inoperculate and emarginate, sexine reticulate, heterobrochate; pistillode 0. Pistillate flowers pedicellate; sepals 5 or 6, imbricate, entire; petals 0; disk annular, glabrous; ovary 3(4)-locular, tomentose; stylodia unlobed, connate below. Fruits capsular; columella persistent. Seeds with fleshy exotesta, foveolate endotesta.

A single Malesian sp., *D. spinescens* Zoll., from the Philippines and Lesser Sunda Islands.

162. *Sumbaviopsis* J.J. Sm.

Sumbaviopsis J.J. Sm., Meded. Dept. Landb. Ned.-Indië 10: 356 (1910); Airy Shaw, Kew Bull. Add. Ser. 4: 197 (1975); van Welzen, Blumea 44: 426, fig. 4 (1999); Radcl.-Sm., Gen. Euphorb.: 148, fig. 13 (2001).

Monoecious trees or shrubs; indumentum mainly stellate. Leaves peltate, palmately veined or triplinerved, subentire or dentate, densely stellate-tomentose abaxially, with small embedded glands; stipules deciduous. Inflorescences terminal (pseudo-axillary), unisexual, staminate thyrsoid, pistillate racemoid; bracts subtending 1–3 staminate flowers or solitary pistillate flowers. Staminate flowers pedicellate; calyx closed in bud, splitting into 3–5 valvate segments; petals 4 or 5, shorter than sepals; disk represented by a convex pubescent torus; stamens 35–45(−75?), inserted on torus, filaments distinct; anthers basifixed, introrse; pollen grains suboblate, 3-colporate, colpi inoperculate, emarginate; sexine coarsely reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 5(6), imbricate, entire, persistent in fruit; petals 0; ovary 2- or 3-locular, tomentose; ovules anatropous; stylodia distinct or nearly so, bifid. Fruits capsular, valves laterally corrugated; columella persistent, apically dilated. Seeds spheroidal, exotesta fleshy, endotesta smooth.

A single sp., *S. albicans* (Blume) J.J. Sm., distributed from Thailand and Laos to Java, Borneo, and Palawan.

163. *Thyrsanthera* Pierre ex Gagnep.

Thyrsanthera Pierre ex Gagnep., Bull. Soc. Bot. France 71: 878 (1924); Gagnep., Fl. Indochine 5: 299, figs. 32, 33 (1925); Backer & Backh., Fl. Java 1: 477 (1963); van Welzen, Blumea 44: 431, fig. 5 (1999); Radcl.-Sm., Gen. Euphorb.: 148, fig. 14 (2001).

Monoecious shrubs; indumentum stellate. Leaves palmately veined, entire, at margin with reddish indumentum, stipellar abaxially at junction with petiole; stipules deciduous. Inflorescences terminal, racemoid, bisexual, pistillate flowers proximal; bracts pubescent, 1-flowered (?). Staminate flowers pedicellate; sepals 5, valvate, tomentose abaxially; petals 5, imbricate; disk 0; stamens 40–60, filaments connate into a column; anthers stipitate, basifixed, latrorse; pollen grains suboblate, 3-colporate, exine reticulate; pistillode 0. Pistillate flowers sessile or subsessile; sepals 5, narrow, entire, valvate; disk annular; ovary 3-locular, tomentose; stylodia distinct, unlobed, papillose. Fruits capsular, thin-walled; columella slender, persistent, apically 3-angled. Seeds obovoid, angular, with thin fleshy exotesta, mesotesta vascularized.

A single sp., *Th. suborbicularis* Pierre ex Gagnep., recorded only from Thailand and Cambodia.

164. *Melanolepis* Rchb. f. & Zoll.

Melanolepis Rchb. f. & Zoll., Verh. Natuurk. Ver. Ned. Ind. 1: 22 (1856); Gagnep., Fl. Indochine 5: 347 (1925); Airy Shaw, Kew Bull. Add. Ser. 8: 174, t. 5 fig. 3 (1980); van Welzen, Blumea 44: 438, fig. 1 (1999).

Dioecious trees or shrubs; indumentum mainly stellate or dendritic. Leaves long-petiolate, deltoid, palmately veined, coarsely dentate, often 3-lobed, with raised glandular area at junction with petiole; stipules inconspicuous, deciduous. Inflorescences terminal, paniculate with 2 or 3 elongated racemoid or spiciform axes, usually unisexual; bracts entire, subtending several staminate flowers or 1(2) pistillate flower. Staminate flowers pedicellate; sepals (4)5, valvate; petals 0; disk 0; stamens 200–250, filaments distinct, inserted on convex receptacle; anthers introrse, with glandular connective; pollen grains suboblate, angulaperturate, 3-colporate, colpi inoperculate but with granular membranes, emarginate, endoaperture ovate to lalongate, exine tectate-punctate to reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 5, basally connate, valvate, entire, persistent in fruit; petals 0; disk annular; ovary 2–3-locular, tomentose; ovules anatropous; stylodia unlobed or emarginate. Fruits capsular; leathery, valves and columella ± persistent. Seeds roundish, with thin sarcotesta, foveolate endotesta.

Two Asiatic spp., one endemic to Cambodia, the other distributed from Thailand to Malesia and the Pacific islands (Ryukyus, Micronesia).

165. *Chrozophora* Necker ex A. Juss. Fig. 32

Chrozophora Necker ex A. Juss., Euphorb. Tent.: 27 (1824, nom. cons.); Prain, Kew Bull. Misc. Inf. 1918: 49 (1918); Pojark., Fl. SSSR 14: 288, t. 17, 1–4 (1949); Vindt, Monogr. Euphorb. Maroc. 10, t. 6 (1953); Rech. f. & Schiman-Czeika, Fl. Iranica 6: 5 (1964); Zohary, Fl. Palaestina 2: 266, t. 384–387 (1972); Radcl.-Sm., Fl. Iraq 4(1): 318, t. 59 (1980), Fl. Zambesiaca 9(4): 141, t. 26 (1996); van Welzen, Blumea 44: 418, fig. 2 (1999).

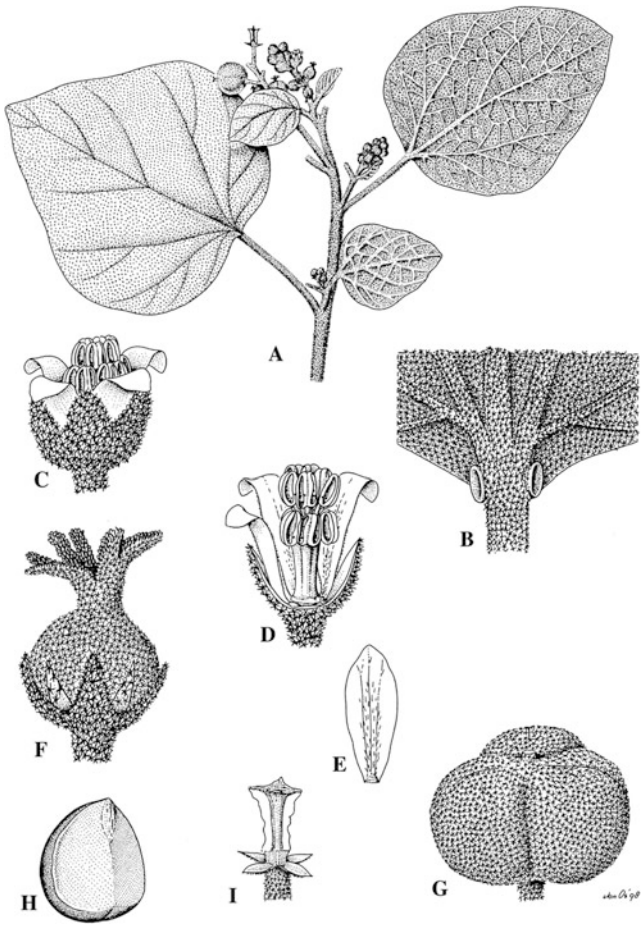

Fig. 32. Euphorbiaceae-Acalyphoideae. *Chrozophora rottleri*. **A** Flowering/fruiting branchlet. **B** Abaxial side of leaf base with extrafloral nectaries. **C**, **D** Staminate flower. **E** Staminate petal. **F** Pistillate flower. **G** Fruit. **H** Seed. **I** Fruit column after dehiscence. (van Welzen 1999; drawn by J. van Os)

Monoecious herbs or subshrubs; indumentum stellate or lepidote. Leaves subentire or crenate, ± palmately veined, with paired sessile patelliform glands near junction with petiole; stipules deciduous or persistent. Inflorescences terminal or pseudo-lateral, bisexual, racemiform; pistillate flowers proximal, staminate flowers distal; bracts subtending solitary flowers. Staminate flowers subsessile; calyx dehiscing into 5 valvate lobes; petals 5; disk segments 5; stamens 4–16, filaments connate into a column; anthers in 1–3 superposed series, extrorse; pollen grains oblate, 6–9-colporate, colpi short, inoperculate and emarginate, sexine coarsely reticulate, sometimes heterobrochate; pistillode 0. Pistillate flowers pedicellate; sepals and petals 5, narrow, entire, persistent in fruit; disk annular; ovary 3-locular, smooth or muricate, with stellate or lepidote hairs; ovules anatropous; stylodia distinct except at base, bifid. Fruits capsular, valves thin; columella persistent. Seeds ovoid to subglobose, ecarunculate, with thin fleshy sarcotesta, mesotesta vascularized. $n = 11, 22$.

About 10 spp., central and southern Asia, southern Europe to East Africa. The genus appears very different in habit from the other genera of the subtribe, but resembles them by characters of indumentum and seeds, and in the molecular analysis of Wurdack et al. (2005) is resolved in the same clade. The ovules of *Chrozophora* have thin inner and outer integuments, as opposed to the much thicker inner and outer integuments of the remaining genera of the subtribe (Tokuoka and Tobe 2003).

12. Tribe Adelieae G.L. Webster (1975).

Dioecious (monoecious) trees or shrubs; indumentum simple or stellate; leaves alternate, simple; lamina pinnately or palmately veined, entire or dentate, eglandular; stipules small; flowers in axillary glomerules or racemes; staminate flowers pedicellate; calyx closed in bud, splitting into 4 or 5 valvate segments; petals 0; disk annular or obsolete; stamens 8–18(−30), filaments distinct or connate at base; anthers introrse, muticous, versatile; pollen grains 3(4)-colporate, ± spheroidal, colpi emarginate, operculate, opercula stratified; sexine tectate-perforate or reticulate, microverrucate, the sculpture crotonoid; pistillode usually +; pistillate flowers pedicellate; sepals 5 or 6, valvate or open at anthesis, persistent in fruit; petals 0; disk annular; ovary 3-locular, pubescent; ovules with inner integuments thick, outer thin to thick; stylodia bifid to multifid; fruits capsular; columella persistent, apically 3-pronged; seeds roundish, ecarunculate, exotegmic, testa smooth.

This American tribe is here expanded to include *Garciadelia*. *Crotonogynopsis* and *Enriquebeltrania*, which were added by Webster (1994) and Radcliffe-Smith (2001), are excluded and treated as unplaced core acalyphoid genera.

Key to the Genera of Adelieae

1. Indumentum simple; stipules deciduous; stylodia lacerate **166. *Adelia***
– Indumentum stellate or stellate-lepidote; stipules 0; stylodia bifid to lacerate 2

2. Pistillate disk 0; stylodia aplanate, undivided, apically incised **169. *Garciadelia***
– Pistillate disk conspicuous; stylodia usually not aplanate, bifid or lacerate 3
3. Pistillate disk entire; stylodia bifid or subentire; filaments distinct; pollen 3-colporate; leaves triplinerved, indumentum stellate **167. *Lasiocroton***
– Pistillate disk lobed; stylodia lacerate; filaments ± connate; pollen grains 4-colporate; leaves pinnately veined, indumentum stellate-lepidote **168. *Leucocroton***

166. *Adelia* L.

Adelia L., Syst. Nat. ed. 10, 2: 1298 (1759, nom. cons.); Lourteig & O'Donell, Lilloa 8: 285, fig. 3 (1942); Webster, Ann. Missouri Bot. Gard. 54: 272, fig. 11 (1968); De-Nova, Sosa & Steinmann, Syst. Bot. 32: 583–595 (2007), rev.

Dioecious trees or shrubs; indumentum simple; twigs often spinescent. Leaves often clustered on short shoots, entire or sometimes crenate, beneath domatiiferous; stipules minute, deciduous. Inflorescences axillary, glomerulate; bracts persistent. Staminate flowers pedicellate; sepals 4 or 5, valvate; petals 0; disk annular or 5-lobed, fleshy; stamens 6–30, filaments basally connate; anthers versatile, muticous; pollen grains ± spheroidal, angulaperturate, 3–4-colp(oroid)ate, colpi operculate, operculum fusiform, sexine tectate-perforate, microverrucate; pistillode minute, trifid. Pistillate flowers long-pedicellate; sepals 5–7, narrow, persistent and ± reflexed in fruit; petals 0; disk annular, pubescent; ovary (2)3(4)-locular, pubescent; stylodia 3, multifid-lacerate. Fruits capsular; columella persistent, apically 3-pronged. Seeds spheroidal to oblate, testa smooth.

Nine spp., ranging from North America (N Texas) through Mexico and the Greater and Lesser Antilles to South America (Bolivia/Argentina).

167. *Lasiocroton* Griseb.

Lasiocroton Griseb., Fl. Brit. W. Ind.: 46 (1859), Abh. Königl. Ges. Wiss. Göttingen 9: 20 (1861); Fawc. & Rend., Fl. Jamaica 4: 293, fig. 96 (1920); Alain, Fl. Cuba 3: 87 (1953); Correll & Correll, Fl. Bah. Arch.: 825, fig. 342 (1982); Radcl.-Sm., Gen. Euphorb.: 189 (2001).

Dioecious shrubs; indumentum simple and stellate. Leaves triplinerved or palmately veined, entire; stipules 0. Inflorescences axillary, racemose; staminate flowers in glomerules, pistillate flowers 1 per bract. Staminate flowers pedicellate; calyx closed in bud, splitting into 5 valvate segments; petals 0; disk annular; stamens 7–18, filaments distinct, purplish, pubescent; anthers introrse, versatile, muticous; pollen grains oblate spheroidal, 3-colpate, colpi operculate; sexine tectate-perforate, microverrucate; pistillode minute or 0. Pistillate flowers pedicellate, mid-articulate; sepals 5, aestivation open, persistent in fruit; disk annular-pulvinate, tomentose; ovary 3(4)-locular, pubescent; stylodia bifid or unlobed, tips ± laciniate. Fruits capsular; columella persistent, slender, apically trifid. Seeds roundish, testa smooth.

Six spp., Greater Antilles and Bahamas.

168. *Leucocroton* Griseb.

Leucocroton Griseb., Mem. Amer. Acad. Sci. 8: 160 (1860), Abh. Ges. Wiss. Göttingen 9: 20 (1861); Borhidi, Acta Bot. Acad. Hungar. 36: 13, figs. 1–16 (1990); Jestrow et al., Taxon 59: 1801–1814 (2010).

Dioecious (monoecious) shrubs; indumentum stellate or stellate-lepidote. Leaves pinnately veined or triplinerved, eglandular; stipules 0. Inflorescences axillary, pedunculate, staminate flowers in glomerules on spiciform thyrses, pistillate flowers solitary or paired on shorter bracteate axes; bracts prominent. Staminate flowers subsessile or pedicellate; calyx closed in bud, splitting into 3–5 valvate segments; petals 0; disk annular or lobed; stamens (5–)7–15(−28), filaments distinct or basally connate; anthers introrse, muticous; pollen grains prolate-spheroidal, 3-colpate, colpi operculate, sexine tectate-perforate, microverrucate; pistillode pubescent. Pistillate flowers pedicellate; sepals 5 or 6, persistent in fruit; disk massive, annular or lobed, pubescent; ovary 2–3-locular, stellate-pubescent; ovules with inner integuments thick, outer thin; stylodia plicate, multifid. Fruits capsular, columella slender, 3-pronged, persistent. Seeds roundish, testa smooth.

About twenty-six spp., all endemic to Cuba where it grows exclusively in serpentine-rich areas. The genus is unique insofar that all spp. have the ability for hyperaccumulation of nickel, having radiated along the fragmented patches of serpentine soils across the island (Jestrow et al. 2010).

169. *Garciadelia* Jestrow & Jiménez Rodr.

Garciadelia Jestrow & Jiménez Rodr., Taxon 59: 1809 (2010).

Dioecious treelets or shrubs; indumentum stellate. Leaves cordate, eglandular; stipules 0. Inflorescences axillary, the staminate subpaniculate, the pistillate racemes. Staminate flowers 5-merous, sepals triangular, valvate; petals 0; stamens twice the number of sepals; anthers dorsifixed; disk weakly lobed; pistillate flowers with perianth as in males; disk 0; ovary 3-locular; stylodia 3, aplanate, undivided but apically incised. Fruit a 3-lobed schizocarp, covered with stellate trichomes. Seeds orbicular.

Four spp., endemic to Hispaniola.

13. Tribe Bernardieae G.L. Webster (1975).

Monoecious or dioecious shrubs or herbs; indumentum simple or stellate; leaves alternate, entire, often with laminar glands; stipules deciduous; inflorescences terminal to axillary, racemiform or spiciform; flowers pedicellate, the staminate several per bract, the pistillate solitary; staminate calyx closed in bud, splitting into 3–4 valvate segments; petals 0; disk intrastaminal, pulviniform, dissected or obsolete; stamens 3–60, filaments distinct; anthers sometimes appearing 4-locellate; connective sometimes apiculate; pollen grains subspheroidal, 3-lobed, 3-colporate, colpi inoperculate, sexine perforate-tectate; pistillode rudimentary or 0; pistillate sepals 4–6, imbricate; disk annular or dissected; ovary 3-locular, ovules with thick inner and thin outer integuments; stylodia bifid, the branches sometimes lacerate; fruit capsular; seeds roundish, carunculate or ecarunculate, exotegmic, testa smooth.

The circumscription of this tribe is still problematic: in the molecular analysis (Wurdack et al. 2005) *Bernardia* and *Adenophaedra* are resolved with *Caryodendron* in a sister position to Plukenetieae, whereas *Discocleidion*, differing, i.a., in a vascularized outer integument, appears (without support) in a clade with *Ricinus* and *Speranskia*.

Key to the Genera of Bernardieae

1. Leaf blades stipellate, palmately veined; seeds carunculate, testa rugose **172. *Discocleidion***
– Leaf blades not stipellate, pinnately veined; seeds ecarunculate, testa smooth 2
2. Stylodia bifid or trifid; staminate disk of interstaminal segments; seeds carinate; stamens (3)4–25; leaf blades usually with abaxial embedded glands **170. *Bernardia***
– Stylodia unlobed and dilated; staminate disk 0; seeds not carinate; stamens 2(3); leaf blades lacking abaxial glands **171. *Adenophaedra***

170. *Bernardia* Houston ex Mill.

Bernardia Houston ex Mill., Gard. Dict. abr. edn (1754); Fawc. & Rend., Fl. Jam. 4: 290, fig. 94 (1920); Lourteig & O'Donell, Lilloa 8: 275, figs. 1, 2 (1942); Allem, Rev. Brasil. Biol. 39: 529, figs. 1–9 (1979); Correll, Fl. Bahama Arch. 781, fig. 327 (1982); Liogier, Fl. Española 4: 85, t. 116–7 (1986); Webster, Fl. Venez. Guayana 5: 101, fig. 99 (1999). *Traganthus* Klotzsch (1841).

Monoecious or dioecious shrubs or subshrubs (herbs); indumentum of simple or fasciculate hairs. Leaves often with basal embedded glands, usually dentate; stipules small, persistent. Inflorescences axillary, [pistillate ones sometimes pseudo-terminal], spiciform or racemose; bracts eglandular. Staminate flowers sessile or pedicellate; calyx splitting into 3 or 4 valvate lobes; petals 0; disk of many interstaminal pubescent segments; stamens (2–)5–20(−45), filaments distinct; anthers 4-locellate, introrse to latrorse, connective emarginate to enlarged; pollen grains 3-lobed, 3-colporate, colpi marginate and inoperculate; endoaperture lalongate, sexine tectate-perforate; pistillode rudimentary or 0. Pistillate flowers sessile or subsessile; sepals 4–6, imbricate, entire, ± persistent in fruit; petals 0; disk annular or dissected; ovary 3-locular, pubescent; ovules pachychalazal, inner integument thick, outer thin; stylodia bifid to flabellate. Fruits capsular (indehiscent), 3-angled or -lobed; columella slender, persistent. Seeds roundish, distinctly carinate, ecarunculate, testa smooth or rugulose; endosperm copious; cotyledons longer and broader than receptacle. $n = 26$.

A genus of over 50 spp., mostly neotropical, one sp. in southwestern USA. Govaerts et al. (2000) list 68 species, some of which may be synonyms. The genus is variable in both vegetative and floral characteristics; Pax & Hoffmann (1914) recognized 7 sections. Section *Traganthus* is distinctive in its herbaceous habit, but has the pollen and seed morphology of other sections; its recognition as a genus would clearly make *Bernardia* excessively paraphyletic.

171. *Adenophaedra* (Müll. Arg.) Müll. Arg.

Adenophaedra (Müll. Arg.) Müll. Arg., Fl. Brasil. 11(2): 385, t. 101 (1874); Pax & K. Hoffm., Pflanzenr. 147, VII: 261 (1914); Webster & Huft, Ann. Missouri Bot. Gard. 75: 1099 (1988).
Bernardia sect. *Adenophaedra* Müll. Arg. (1865).

Dioecious trees or shrubs; indumentum simple. Leaves dentate, abaxial laminar glands + or 0;

stipules deciduous. Inflorescences axillary or the pistillate sometimes appearing terminal, spiciform, the staminate sometimes fasciculate or paniculate-clustered; bracts eglandular. Staminate flowers pedicellate; calyx splitting into 3 valvate lobes; petals and disk 0; stamens 2 (3); anthers longer than filaments, introrse, connective enlarged; pollen grains prolate spheroidal, 3-lobed, 3-colporate, colpi marginate and inoperculate, endoaperture lalongate; sexine tectate-perforate; pistillode 0. Pistillate flowers pedicellate; sepals 6, biseriate, imbricate, ± persistent in fruit; petals 0; disk 3-lobed; ovary 3-locular; ovules anatropous, inner integument very thick, outer integument thin; stylodia contracted into dilated sessile stigmas. Fruits capsular, 3-lobed; columella apically dilated, 3-winged, persistent. Seeds roundish, ecarunculate, testa smooth.

Three neotropical spp., occurring from Costa Rica to Brazil. Although *Adenophaedra* has highly reduced flowers and differs from *Bernardia* in a number of other characters, the similarity in pollen noted by Punt (1962) and Nowicke et al. (1999) supports its inclusion in the Bernardieae.

172. *Discocleidion* (Müll. Arg.) Pax & K. Hoffm.

Discocleidion Pax & K. Hoffm., Pflanzenr. 147, VII: 45, fig. 6 (1914); Webster, Ann. Missouri Bot. Gard. 81: 75 (1994); Qiu Huaxing & Gilbert, Fl. China 11: 241 (2008).

Dioecious trees or shrubs; indumentum simple. Leaves glandular-serrulate, 2–4-glandular abaxially above the stipellate base; stipules persistent. Inflorescences mostly terminal, the staminate paniculate, pistillate spiciform or racemoid (branched); staminate bracts lobed, persistent, eglandular. Staminate flowers pedicellate; calyx splitting into 3–5 valvate segments; petals 0; disk segments interstaminal, on the convex receptacle; stamens 35–60, filaments distinct, longer than anthers; anthers apicifixed, supertrorse to latrorse, muticous, thecae discrete and ± pendulous; pollen grains spheroidal, 3-colporate, colpi with broad margins, inoperculate, sexine tectate-perforate, sometimes with prominent excrescences; pistillode 0. Pistillate flowers pedicellate; sepals 5, entire, imbricate, ± persistent in fruit; petals 0; disk annular, crenulatae, pubescent; ovary 3(4)-locular, sericeous; ovules with inner integument thick, outer thinner and vascularized; stylodia bifid, densely papillose. Fruit capsular; columella slender, persistent. Seeds ovoid, carunculate, caruncle deciduous; exotesta rugulose, purplish-tinged; mesotesta vascularized.

Two spp, China, Ryukyu islands.

14. Tribe Plukenetieae (Benth.) Hutch. (1969).

Monoecious (dioecious), woody or herbaceous; leaves alternate, unlobed to palmately lobed or parted, pinnately to palmately veined, sometimes glandular or stipellate at base; stipules usually persistent; inflorescences terminal or axillary, usually bisexual, mostly racemoid or spiciform; bracts eglandular; staminate calyx closed in bud, splitting into 3–5 valvate segments; petals 0; disk + or 0; stamens (2)3–100, filaments usually distinct; pollen grains mostly 3-colpate with irregular colpar margins, sometimes 3-porate or inaperturate but 3-colporate in *Dalechampia*, sexine intectate to tectate, microverrucate; pistillode 0; pistillate sepals 3–6, imbricate; petals and disk 0; ovary 3- or 4-locular; stylodia unlobed, usually connate into an elongated column, tips smooth to lacerate; fruit capsular; columella persistent; seeds ecarunculate, testa usually smooth and dry.

Sixteen genera in three subtribes, both in the New World and the Old, but the majority of taxa neotropical. Although the tribe appears to be monophyletic (nine genera included in the molecular analysis of Wurdack et al. 2005), palynologically it is the most diverse tribe in subfamily Acalyphoideae (Gillespie 1994). For the position of *Dalechampia* within the tribe, see under Subtribe Dalechampiinae.

Key to the Subtribes of Plukenetieae

1. Inflorescence pseudanthial, bibracteate; pollen grains prolate, coarsely reticulate, with pronounced costae equatoriales **14c. Dalechampiinae**
– Inflorescence racemoid or spiciform; pollen grains subglobose, 3-colpate, not coarsely reticulate, lacking costae equatoriales 2
2. Stinging hairs 0; fruit winged, crested, carinate, or indehiscent; pollen grains 3-colporate **14a. Plukenetiinae**
– Stinging hair +; fruit usually appendaged; pollen grains 3-colporate or -porate (inaperturate), sexine tectate-perforate to rugulose **14b. Tragiinae**

14a. Subtribe Plukenetiinae Benth. (1880).

Trees, shrubs, lianas, or herbaceous vines; indumentum simple, sometimes glandular, never urticant. Leaves alternate, often with embedded laminar glands, sometimes stipellate; inflorescences axillary or terminal; stamens 4–50, filaments distinct; pollen grains tectate-perforate to semitectate-reticulate; ovary 3–4-locular, often appendaged; stylodia partly to entirely connate into a common style; fruit capsular (indehiscent).

Five genera, all neotropical except for a few species of *Plukenetia* in Africa.

Key to the Genera of Plukenetiinae

1. Ovary 3-locular; pistillate sepals 5 or 6; trees, shrubs, or vines 2
– Ovary 4-locular; pistillate sepals 4; twining vines or lianas **177. *Plukenetia***
2. Stamens 4; staminate disk segments 4 or filament bases forming a pseudo-disk; leaves pinnately veined; trees or shrubs 3
– Stamens 10 or more; staminate disk 0 or of numerous minute segments 4
3. Disk exstrastaminal; ovary horned **173. *Astrococcus***
– Disk 0, the filament bases forming a pseudo-disk; ovary verrucate **174. *Haematostemon***
4. Trees or shrubs; flowers in axillary glomerules; leaves pinnately veined; stamens c. 20; style urceolate **175. *Angostyles***
– Twining vines; flowers in axillary racemes; leaves palmately veined; stamens 10; style apically 3-lobed **176. *Romanoa***

173. *Astrococcus* Benth.

Astrococcus Benth., Hook. J. Bot. Kew Gard. Misc. 6: 327 (1854); Müll. Arg. in DC., Prodr. 15(2): 766 (1866), Fl. Brasil. 11(2): 330, t. 49 (1874); Benth., Gen. Pl. 3: 326 (1880); L.J. Gillespie, Fl. Venez. Guayana 5: 100, fig. 98 (1999).

Monoecious trees or shrubs, branches rib-angled distally; indumentum simple. Leaves subentire (minutely glandular-serrulate), eglandular; stipules minute, deciduous. Inflorescences axillary, spiciform, bisexual; pistillate flowers solitary at the 4 or 5 proximal nodes, staminate in 1- or 2-flowered glomerules at distal nodes, terminal flower pistillate; bracts entire, eglandular, recurved. Staminate flowers short-pedicellate; calyx closed in bud, splitting into 4 valvate segments; petals 0; disk extrastaminal, 4-lobed, lobes enclosing anthers; stamens 4, filaments basally confluent; anthers basifixed, introrse, muticous; pollen grains oblate spheroidal, 3-colpate with very irregular margins; sexine tectate-rugulose, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals usually 4, imbricate, narrowly lanceolate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, glabrous, 3-horned; stylodia connate into a clavate hollow column with lobulate rim. Fruits capsular, cocci horned; columella massive, 3-angled, persistent. Seeds turbinate-truncate, testa smooth.

A single sp., *A. cornutus* Benth., Amazonian Brazil and Venezuela.

174. *Haematostemon* (Müll. Arg.) Pax & K. Hoffm. Fig. 33

Haematostemon (Müll. Arg.) Pax & K. Hoffm., Pflanzenr. 147, IX: 31, fig. 11 C, D (1919); Sandwith, Kew Bull. 1950: 133 (1951); Jablonski, Mem. N. Y. Bot. Gard. 17: 143 (1967); L.J. Gillespie & Armbruster, Smiths. Contr. Bot. 86: 28, fig. 9 (1997); Radcl.-Sm., Gen. Euphorb.: 241, fig. 31 (2001).
Astrococcus sect. *Haematostemon* Müll. Arg. (1865).

Monoecious trees or shrubs; indumentum simple. Leaves crenulate or serrulate, eglandular or obscurely glandular adaxially; stipules minute. Inflorescences axillary, bisexual, spiciform; lower nodes with solitary pistillate flowers or bisexual cymules, distal with glomerules of staminate flowers, terminal flower pistillate; bracts eglandular. Staminate flowers pedicellate; calyx splitting into 4 valvate segments; petals 0; stamens 4, filaments basally dilated and connate into a pseudo-disk; anthers basifixed, introrse, muticous; pollen grains suboblate, 3-colpate, colpi sometimes occluded by sexine, tectum foveolate-rugulose, microverrucate; pistillode 0 or incorporated into pseudo-disk. Pistillate flowers pedicellate; sepals 4–6, imbricate, entire; disk 0; ovary 3-locular, tuberculate; stylodia connate into a cup-shaped hollow column with multidentate rim. Fruits capsular.

Two spp. in northern South America: Venezuela (Guayana Highland) and Guyana.

175. *Angostylis* Benth.

Angostylis Benth., Hook. J. Bot. Kew Gard. Misc. 6: 328 (1854, as *Angostyles*); Müll. Arg. in DC., Prodr. 15(2): 767 (1866), Fl. Brasil. 11(2): 331, t. 50 (1874); Radcl.-Sm., Gen. Euphorb.: 244 (2001).

Monoecious trees or shrubs; indumentum simple, non-urticant. Leaves subsessile, clustered at branch-tips, denticulate, pluriglandular; stipules

Fig. 33. Euphorbiaceae-Acalyphoideae. *Haematostemon guianensis*. **A** Flowering branch. **B** Base of leaf blade, adaxial surface. **C** Pistillate flower, with verrucate ovary lobes and massive truncate style. **D** Staminate flower. (Gillespie & Armbruster 1997; drawn by Cathy Pasquale)

subulate. Inflorescences axillary, glomerular, the staminate 2 or 3 per cymule, the pistillate solitary. Staminate flowers pedicellate; calyx closed in bud, splitting into 3 (4) valvate segments; petals 0; stamens c. 20, filaments distinct; anthers dorsifixed, extrorse, muticous; pollen grains suboblate, angulaperturate, 3-brevicolpate, colpar margins irregular, tectum foveolate-rugulose, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 5, imbricate, entire, adaxially glandular; petals and disk 0; ovary 3-locular, muricate; stylodia connate into a hollow infundibiliform column with 6-dentate rim. Fruits capsular, muricate. Seeds subglobose, testa smooth.

A single sp., *A. longifolia* Benth., Brazilian Amazon.

176. *Romanoa* Trevis.

Romanoa Trevis., Saggio Algh. Coccot.: 99 (1848, nom. cons.); Pax & K. Hoffm., Pflanzenr. 147, IX: 28, fig. 9 (1919, under *Anabaenella*); Radcl.-Sm., Kew Bull. 34: 589 (1980); Radcl.-Sm., Gen. Euphorb.: 244 (2001).
Anabaena A. Juss. (1824, nom. illeg.).
Anabaenella Pax & K. Hoffm. (1919).

Monoecious vines; indumentum simple. Leaves palmately veined, biglandular on margins at base; stipules deciduous. Inflorescences axillary, usually bisexual with 1 or 2 basal pistillate flowers and several glomerules of staminate flowers; bracts entire, eglandular. Staminate flowers susbsessile or short-pedicellate, pedicel medially articulate; calyx closed in bud, splitting into 5 segments; petals 0; receptacle ± glandular; stamens 10, filaments distinct; anthers extrorse or introrse, 2-celled but opening into 4 valves; pollen grains oblate spheroidal, angulaperturate, 3-colpate, colpi broad with uneven margins, sexine tectate-perforate, microverrucate; pistillode subulate. Pistillate flowers pedicellate; sepals 5 or 6, narrow, entire, ± persistent in fruit but not accrescent; petals and disk 0; ovary 3-locular, glabrous; stylodia connate into a clavate, apically 3-lobed column. Fruits capsular, valves not veiny; columella persistent, slender, 3-pronged. Seeds carinate-angled, testa smooth.

A single sp., *R. tamnoides* (A. Juss.) Radcl.-Sm., eastern and southern Brazil, Paraguay. Although *Romanoa* appears similar to *Plukenetia* in many respects, the pollen is distinctive (Gillespie 1994).

177. *Plukenetia* L.

Plukenetia L., Sp. Pl.: 1192 (1753), Gen. Pl. ed. 5: 438 (1754); Müll. Arg. in DC., Prodr. 15(2): 768 (1866), Fl. Brasil. 11(2): 232 (1874); Pax & K. Hoffm., Pflanzenr. 147. IX: 12 (1919); Webster, Ann. Missouri Bot. Gard. 54: 293, fig. 15 (1968), ibid. 81: 93 (1994); Huft, Ann. Missouri Bot. Gard. 75: 1105 (1989); Gillespie, Syst. Bot. 18: 575 (1993), Fl. Venez. Guayana 5: 207, figs. 196, 197 (1999); L.J. Gillespie & Armbruster, Smiths. Contr. Bot. 86: 30, figs. 10–12 (1997).
Vigia Vell. (1832).
Apodandra Pax & K. Hoffm. (1919).
Eleutherostigma Pax & K. Hoffm. (1919).
Elaeophora Ducke (1925).

Monoecious (dioecious) lianas or twining vines; indumentum simple. Leaves pinnately or palmately veined, subentire to serrulate, adaxially with embedded laminar basal glands and often stipellate at base; stipules deciduous. Inflorescences axillary

or terminal on short shoots, bisexual, racemose; pistillate flowers at proximal nodes, staminate glomerules distally; bracts minute, eglandular. Staminate flowers pedicellate; calyx splitting into 4 or 5 valvate segments; petals 0; disk interstaminal or extrastaminal, sometimes 0; stamens 15–40, filaments distinct, sometimes shorter than anthers, inserted on convex or conical receptacle; anthers extrorse or introrse, muticous, thecae divergent; pollen grains suboblate, angulaperturate, 3-colpate, colpi broad with uneven margins, sexine tectate-perforate to semitectate-reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 4 (5), imbricate, entire, ± persistent in fruit but not accrescent; petals and disk 0; ovary 4-locular, angled or lobed, glabrous; ovules anatropous, inner integument moderately thick, outer thin; stylodia connate into a column, the stigmatic tips entire to bilobed. Fruits capsular or baccate; columella persistent, apically dilated. Seeds lenticular to subglobose, testa smooth.

In the concept of Gillespie (1993), *Plukenetia* includes 13 spp. scattered from tropical America to Africa, Madagascar, and southeast Asia. The genus is very heterogeneous in vegetative, floral, and palynological characters, and it is not surprising that Pax and Hoffmann (1919) recognized a number of segregate genera. Gillespie has in effect included all Plukenetiinae with 4-locular ovaries within *Plukenetia*; although *Eleutherostigma* was maintained as distinct by Webster (1994) and Radcliffe-Smith (2001), it was merged with *Plukenetia* by Gillespie (1993, 1994). The reduction of *Eleutherostigma* and *Vigia*, accepted as generically distinct by Webster (1994), is followed here, but it still appears possible that further analysis will result in redefinition of the generic boundaries of *Plukenetia* and other Plukenetiinae.

14b. Subtribe Tragiinae G.L. Webster (1975).

Monoecious shrubs or herbs, often scandent; indumentum of simple and urticant hairs; leaves simple (lobed), without embedded laminar glands, not stipellate; stipules persistent or deciduous; inflorescences axillary or terminal and opposite leaves; stamens (2) 3–50, filaments distinct or connate; pollen grains 3-colpate, 3-porate, or inaperturate, sexine mostly tectate-perforate and microverrucate; ovary 3-locular; stylodia nearly distinct to completely connate; fruit capsular.

Ten genera with c. 150 species. *Tragia* is pantropical, *Acidoton* and *Platygyna* are neotropical, and the other genera paleotropical.

Key to the Genera of Tragiinae

1. Stylodia usually slender; sepals not adaxially inflexed; anthers extrorse or introrse; stamens 2–many; pollen grains tectate-perforate 2
– Stylodia massive; staminate sepals uually inflexed to form a pseudo-disk; stamens 3 or 4, anthers introrse 7
2. Anthers 2, subsessile; staminate calyx flat with lobes reflexed; stylodia distally recurved and proximally connate into a broad conic-cylindrical base **183. *Pachystylidium***
– Anthers 3 or more, rarely 2, but then not subsessile; staminate calyx concave; stylodia distinct to partly connate into a columnar style 3
3. Anther connective with tuft of stinging hairs; stamens 25–60; dioecious shrubs **182. *Acidoton***
– Anther connective lacking tuft of stinging hairs; stamens (2)3–50; monoecious subshrubs, herbs, or vines 4
4. Stylodia thickened, apically bifid; inflorescences unisexual, contracted [< 1 cm]; pollen grains inaperturate **181. *Platygyna***
– Stylodia slender, entire; inflorescences bisexual, elongated [> 1 cm]; pollen grains 3-colporate 5
5. Stamens 8–40; inflorescences bifurcate, staminate and pistillate flowers on separate axes; pollen sexine coarsely tectate-perforate **178. *Bia***
– Stamens 2–4 (or else pistillate sepals pinnatifid); inflorescences not bifurcate, usually bisexual; pollen sexine finely tectate-perforate-rugulose 6
6. Stamens 2–4, anthers not linear, often shorter than filaments; pistillate calyx entire or pinnatifid **179. *Tragia***
– Stamens 30–50, anthers linear and much longer than filaments; pistillate calyx pinnatifid **180. *Ctenomeria***
7. Pistillate sepals entire or dentate; pistillode 0 8
– Pistillate sepals pinnatifid; pistillode present in staminate flower; stylodia connate into a conical or infundibular column **187. *Tragiella***
8. Pistillate sepals entire; anther connective enlarged, sometimes caudate 9
– Pistillate sepals toothed; inflorescences terminal and leaf-opposed; leaves subglabrous **185. *Sphaerostylis***
9. Stylodia distinct or nearly so, adaxially papillose; inflorescences terminal and leaf-opposed; leaves with stinging hairs **184. *Cnesmone***
– Stylodia connate into a clavate or globose column, not adaxially papillose; inflorescences axillary; leaves subglabrous, not urticant **186. *Megistostigma***

178. *Bia* Klotzsch

Bia Klotzsch, Arch. Naturgesch. 7(1): 189 (1841).
Zuckertia Baillon (1858).
Tragia sect. *Bia* (Klotzsch) Müll. Arg. (1865).

Monoecious vines; indumentum simple (unicellular) and urticant. Leaves palmately veined and usually cordate at base, dentate, eglandular; stipules persistent. Inflorescences axillary, bisexual, eglandular, bifurcate, pistillate branch spiciform, with 5–20 subsessile flowers, staminate branch racemoid, with c. 20–30 glomerules of 1–3 pedicellate flowers; bracts entire, eglandular. Staminate flowers pedicellate; calyx splitting into 3–6 valvate segments; petals 0; disk of interstaminal segments or 0; stamens (5–)8–40, filaments distinct; anthers introrse, muticous, sagittate; pollen grains suboblate or spheroidal, 3-colpate or inaperturate, tectate-perforate to semitectate-reticulate; pistillode 0. Pistillate flowers subsessile; sepals 6, imbricate, entire, persistent in fruit; disk 0; ovary 3-locular, pubescent with simple and urticant hairs; stylodia unlobed, adaxially papillose with complex papillae, basally connate. Fruits capsular; columella persistent. Seeds spheroidal, testa smooth, without distinct microsculpturing.

Five neotropical spp. The genus *Bia* is here reinstated from the synonymy of *Tragia* and construed to include two sections[1]. The work of Nowicke and Takahashi shows great palynological heterogeneity in *Tragia*, and *Bia* appears morphologically distinct from *Tragia* (s. str.) not only in its coarsely tectate-perforate exine, but also in other traits such as the larger stamen number (see key and description above). With the recognition of *Bia* and *Ctenomeria* as distinct genera, *Tragia* becomes less heterogeneous and easier to define, although much more study needs to be given to identifying monophyletic groups.

[1] A. ***Bia* sect. *Bia***. Type: *Bia sellowiana* Klotzsch ex Baillon (= *B. alienata* Didrichsen).
Staminate flowers with dissected disk; stamens introrse, 8–20, anthers muticous; style column slender. Four spp.:

1. *B. alienata* Didrichsen (1857) (= *B. sellowiana* Klotzsch ex Baill. 1858).
2. ***Bia fallax*** (Müll. Arg.) G.L. Webster, **comb. nov.** Basionym: *Tragia fallax* Müll. Arg., Linnaea 34: 179 (1865). Type: Peru, *Pavon* (holotype G-Less., photograph F7155). – *Tragia japurensis* Müll. Arg.
3. ***Bia fendleri*** (Müll. Arg.) G.L. Webster, **comb. nov.** Basionym: *Tragia fendleri* Müll. Arg., Linnaea 34: 179 (1865). Type: Venezuela, Biscaina, 3,000 feet, *Fendler* 1208 (holotype G; photograph F7156).
4. *Bia lessertiana* Baillon (1858) [*lesseriana*]. – *Tragia lessertiana* (Baill.) Müll. Arg.

B. ***Bia* sect. *Zuckertia*** (Baill.) Müll. Arg., Linnaea 34: 178 (1865) (as *Tragia* sect. *Zuckertia*).
Zuckertia Baill., Étude Gén. Euphorb.: 495 (1858). Type: *Zuckertia cordata* Baill.

1. ***Bia cordata*** (Baill.) G.L. Webster, **comb. nov.** Basionym: *Zuckertia cordata* Baill, Étude Gén. Euphorb.: 496, t. 10, figs. 10–13 (1858). Type: Mexico, Tabasco: Teapa, *Linden* (holotype P).

179. *Tragia* (Plumier) L. Fig. 34

Tragia (Plumier) L., Sp. Pl.: 980 (1753), Gen. Pl. ed. 5: 421 (1754); Müll. Arg. in DC., Prodr. 15(2): 927 (1866); Pax & Hoffm., Pflanzenr. 147, IX: 32, figs. 12–22 (1919); Fawc. & Rendle, Fl. Jam. 4: 304, fig. 100 (1920); Lourteig & O'Donell, Lilloa 6: 347 (1941); Miller & Webster, Rhodora 69: 241, figs. 17–29 (1967); Webster, J. Arnold Arb. 48: 376 (1967), Ann. Missouri Bot. Gard. 54: 291, fig. 14 (1968); Leandri, Adansonia II, 11: 437 (1971); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 291, figs. 57–59 (1987); Radcl.-Sm., Fl. Zambesiaca 9(4): 216, figs. 46–48 (1996), Gen. Euphorb.: 253 (2001).

Monoecious (dioecious) shrubs or herbs, often twining; indumentum simple and urticant, sometimes glandular. Leaves usually petiolate, mostly palmately veined or triplinerved, entire to dentate (lobed or divided), often cordate; stipules usually persistent. Inflorescences usually terminal or opposite leaves, bisexual, spiciform or racemoid, with 1–3 basal pistillate flowers and distal staminate flowers; bracts subfoliose, eglandular, mostly uniflorous. Staminate flowers pedicellate; pedicel articulated just above base to mid-length; calyx closed in bud, splitting into 3–6 valvate segments; petals and disk 0; stamens (2)3–4(−40), filaments distinct or ± basally connate; anthers extrorse or introrse, muticous; pollen grains suboblate to spheroidal, 3-colpate or inaperturate, colpi narrow to broad, sometimes circular; sexine reticulate to tectate-rugulose, sometimes microverrucate; pistillode laminar to globose. Pistillate flowers pedicellate; sepals mostly 6–8, imbricate, entire to pinnatifid, persistent and sometimes accrescent in fruit; petals and disk 0; ovary 3-locular, glabrous or urticant-pubescent; ovules pachychalazal, inner integument thick, outer thin; stylodia unlobed, smooth or papillose, basally connate. Fruits capsular; columella persistent, apically 3-fid. Seeds globose, testa smooth.

About 170 spp., most in America and Africa but extending to Asia and Australia (Govaerts et al. 2000). The genus is quite variable in all

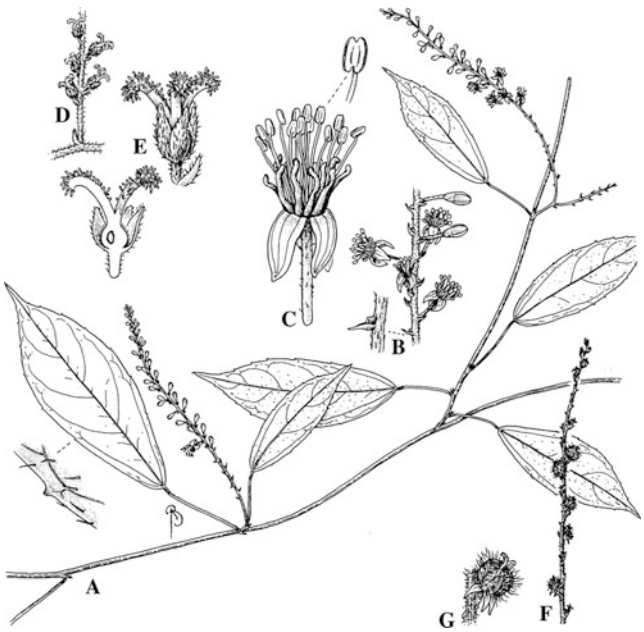

Fig. 34. Euphorbiaceae-Acalyphoideae. *Tragia lessertiana*. **A** Part of stem with leaves and staminate flowers. **B** Part of staminate inflorescence with detail of bract on left. **C** Staminate flower. **D** Part of pistillate inflorescence. **E** Lateral view and medial section of pistillate flower. **F** Part of infructescence. **G** Capsule. (Reproduced with kind permission of the artist Bobbi Angell)

characters and has presented a continuing challenge to systematists. Pax and Hoffmann (1919) recognized 9 sections, and 9 subsections in the African sect. *Tagira*; Gillespie (1994) recognized 5 sections for the Americas. Pollen evidence presented by Gillespie (1994) indicates great heterogeneity within the genus, and suggests that *Tragia* may be an unnatural taxon.

180. *Ctenomeria* Harv.

Ctenomeria Harv., Hook. London J. Bot. 1: 29 (1842); Baill., Étude Gén. Euphorb.: 494 (1858); Prain, Fl. Capensis 5(2): 500 (1920); Dyer, Gen. S. Afr. Fl. Pl. 1: 318 (1975).
Tragia sect. *Ctenomeria* (Harv.) Benth. (1880).

Monoecious twining herbs; indumentum simple and scantily urticant. Leaves palmately veined, sometimes palmately lobed or subpeltate, dentate, eglandular; stipules reflexed, persistent. Inflorescences terminal or leaf-opposed, mostly bisexual, with 1 or 2 proximal pistillate flowers and distal glomerules of staminate flowers; bracts 1-flowered, eglandular. Staminate flowers pedicellate, pedicel articulate and bracteate at or above the base; calyx closed in bud, splitting into 5 valvate segments; petals and disk 0; receptacle convex; stamens 30–60, filaments distinct; anthers longer than filaments, apiculate; pollen grains oblate spheroidal, 3-aperturate, apertures elliptic, occluded by thin exine layer, sexine tectate-perforate, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 6, pinnatifid, imbricate, persistent and ± accrescent in fruit; ovary 3-locular, pubescent; stylodia unlobed, densely papillate-laciniate. Fruits capsular. Seeds globose, testa smooth.

Two spp., southern Africa. Although treated as a synonym of *Tragia* by most recent authors, including Webster (1994) and Radcliffe-Smith (2001), the palynological studies of Gillespie (1994) support the concepts of Prain and Dyer in recognizing *Ctenomeria* as generically distinct.

181. *Platygyna* P. Mercier

Platygyna P. Mercier, Bull. Bot. 1: 168 (1830); Müll. Arg. in DC., Prodr. 15(2): 913 (1866, as *Platygyne*); Pax & K. Hoffm., Pflanzenr. 147, IX: 26 (1919); Alain, Fl. Cuba 3: 100, fig. 28 (1953), Mem. N. Y. Bot. Gard. 21: 132 (1971); Borhidi, Ann. Hist.-Nat. Mus. Nat. Hung. 64: 89 (1972); Radcl.-Sm., Gen. Euphorb.: 255, fig. 33 (2001).
Acanthocaulon Klotzsch (1850).

Monoecious woody vines; indumentum simple and urticant. Leaves dentate, eglandular; stipules ± persistent. Inflorescences terminal, axillary or leaf-opposed, glomerular or contracted-spiciform (< 1 cm long). Staminate flowers pedicellate; calyx closed in bud, splitting into 4 or 5 valvate segments; petals 0; disk pulviniform, strigose-hispid; stamens 5 (4–14), filaments distinct; anthers extrorse, muticous; pollen grains spheroidal, inaperturate, sexine tectate-perforate, sometimes vermiculate, not verrucate; pistillode 0. Pistillate flowers subsessile or pedicellate; sepals 6 (5–9), imbricate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, tomentose; ovules pachycaulous, inner integument thick, outer integument thin; stylodia 3 (4), bifid or emarginate, contiguous in a thick, infundibuliform stylar column. Fruits capsular; columella 3-pronged, persistent. Seeds globose, testa smooth.

According to the revision of Borhidi (1972) seven spp., endemic to Cuba. Alain (1971) reduced *Platygyna* to a synonym of *Tragia*, but the pollen evidence of Gillespie (1994) does not support this.

182. *Acidoton* Sw.

Acidoton Sw., Prodr. 6: 83 (1788; nom. cons.), Fl. Ind.. Occid. 2: 952, t. 18 (1800); Müll. Arg. in DC., Prodr. 15(2): 914 (1866); Urb., Symb. Ant. 7: 513 (1913); Pax & K. Hoffm., Pflanzenr. 147, IX: 24, fig. 8 (1919); Fawc. & Rendle, Fl. Jam. 4: 303, fig. 99 (1920); Webster, Ann. Missouri Bot. Gard. 54: 191 (1967), 289, fig. 13 (1968); Liogier, Fl. Española 4: 71 (1986); Webster, Ann. Missouri Bot. Gard. 81: 95 (1994); Burger & Huft, Fieldiana Bot. 36: 56 (1995); Govaerts et al., World Checkl. Bibl. Euporb. 1: 111 (2000); Radcl.-Sm., Gen. Euphorb.: 257, fig. 34 (2001); Webster, Fl. Nicaragua 1: 852 (2001).
Gitara Pax & Hoffm. (1924).

Monoecious or dioecious shrubs, sometimes arborescent; indumentum simple and urticant. Leaves petiolate or subsessile, entire or dentate, eglandular; stipules aristate, persistent. Inflorescences axillary, glomerular or racemoid; unisexual, the pistillate much longer than the staminate; bracts eglandular, persistent, subtending solitary flowers. Staminate flowers pedicellate; calyx closed in bud, splitting into 3–5 valvate segments; petals 0; disk 0 or obscure; stamens 20–60, filaments distinct; anthers extorse, much shorter than filaments, connective with apical tuft of urticant hairs; pollen grains spheroidal or subprolate, 3-colpate or inaperturate, colpi with uneven margins and sexinous islands, sexine tectate-perforate and microverrucate or rugulose and smooth; pistillode 0. Pistillate flowers pedicellate; sepals 5 or 6, imbricate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, urticant-pubescent; ovules pachycaulous, inner integument moderately thick, outer integument thin; stylodia distally recurved, papillose, and basally connate into acommon style. Fruits capsular, covered with urticant hairs; columella persistent, 3-pronged apically. Seeds spheroidal, testa smooth.

Six spp., 5 in the Greater Antilles, 1 on mainland (Nicaragua to Venezuela). Radcliffe-Smith (2001) has accepted the segregate genus *Gitara* as distinct, based largely on the palynological evidence of Gillespie (1994). It is true that the coarsely dentate leaves and colpate pollen of the mainland *Acidoton* (*Gitara*) *nicaraguensis* considerably differ from the entire leaves and inaperturate pollen of the West Indian species. However, the inflorescences, flowers, and fruits are very similar overall. It seems preferable, therefore, in accordance with the opinion of Govaerts et al. (2000), to maintain *Acidoton* in the broader sense, but retaining *Gitara* at the sectional level.

183. *Pachystylidium* Pax & K. Hoffm.

Pachystylidium Pax & K. Hoffm., Pflanzenr. 147, IX: 108 (1919); Backer & Bakh., Fl. Java 1: 491 (1963); Airy Shaw, Kew Bull. 23: 115 (1969), 26: 310 (1971); Webster, Ann. Missouri Bot. Gard. 81: 95 (1994); Radcl.-Sm., Gen. Euphorb.: 260, fig. 36 (2001).

Monoecious vines; indumentum simple and urticant. Leaves cordate, palmately veined, dentate, eglandular; stipules persistent. Inflorescences terminal or leaf-opposed, pedunculate, bisexual, with proximal pistillate flowers and distal glomerules of staminate flowers; bracts concave, ovate, eglandular. Staminate flowers pedicellate; calyx closed in bud, splitting into 4 or 5 valvate segments; petals 0; disk or pseudo-disk with 2 cavities; stamens 2, filaments distinct; anthers extrorse, longer than filaments, muticous; pollen grains oblate spheroidal, 3-porate, apertures ill-defined with sexinous islands; sexine tectate-punctate, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 6, narrow, entire, imbricate; ovary 3-locular, pubescent; stylodia distally recurved, proximally connate into a broad conic-cylindrical base. Fruits capsular; columella persistent, 3-pronged. Seeds globose, testa smooth.

A single sp., *P. hirsutum* (Blume) Pax & K. Hoffm., widespread from India east as far as Sulawesi. *Pachystylidium* is similar in habit to *Cnesmone*, and a close relationship is supported by Gillespie's palynological evidence.

184. *Cnesmone* Blume

Cnesmone Blume, Bijdr.: 630 (1826, as *Cnesmosa*); Croizat, J. Arnold Arb. 22: 427 (1941); Airy Shaw, Kew Bull. 26: 240 (1972); Balakr. & Nair, Gardener's Bull. Singapore 31: 49 (1978); Radcl.-Sm., Gen. Euphorb.: 250 (2001).
Cenesmon Gagnep. (1924).

Monoecious shrubs or lianas; indumentum simple and urticant. Leaves pinnately or palmately veined, often cordate, entire or serrate, eglandular; stipules entire, reflexed, subpersistent. Inflorescences terminal or pseudo-axillary leaf-opposed, spiciform, bisexual, proximal nodes with solitary pistillate flowers, distal with glomerules of staminate flowers; bracts persistent, appearing trifid due to prominent bracteoles, eglandular. Staminate flowers pedicellate, pedicel articulate at base; calyx closed in bud, splitting into 3 valvate segments; petals and disk 0; stamens 3, filaments basally connate; anthers basifixed, ± introrse, connective enlarged and apiculate, thecae discrete; pollen grains

± spheroidal, weakly 3-colpate, colpi broad and covered with sexinous granules; sexine tectate-perforate and microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 3–6, imbricate, entire, foliose, persistent in fruit; petals and disk 0; ovary 3-locular, not angled, pubescent with simple and urticant hairs; ovules with very thick integuments; stylodia distally spreading, unlobed, papillate, basally connate. Fruits capsular, endocarp thick and woody; columella persistent. Seeds globose, testa smooth.

Eleven spp., Assam and Andaman Is. to China and Malesia.

185. *Sphaerostylis* Baill.

Sphaerostylis Baill., Étude Gén. Euphorb.: 466 (1858), in Grandidier, Hist. Phys. Nat. Madag. 4 (29): t. 4 (1891); Leandri, Bull. Soc. Bot. France 85: 527 (1939); Croizat, J. Arnold Arb. 22: 430 (1941); Radcl.-Sm., Gen. Euphorb.: 252 (2001); Schatz, Gen. Tree Fl. of Madagascar: 165 (2001).

Monoecious shrubs to vines; indumentum simple and urticant, scanty. Leaves 3-palmatinerved at the base and penninerved above, cordate or peltate at base, entire or dentate; stipules entire, auriculiform, deciduous. Inflorescences terminal or leaf-opposed, unisexual or bisexual, racemoid; bracts uniflorous, eglandular. Staminate flowers pedicellate, pedicel articulate at base; calyx closed in bud, splitting into 3 valvate segments; calyx segments inflexed into a pseudo-disk; petals and disk 0; stamens 2 or 3, filaments distinct, much shorter than anthers, connate; anthers introrse, connective enlarged and apiculate, 2-celled, locules divergent, dehiscing longitudinally/horizontally; pollen grains oblate spheroidal, 3-colpate, exine tectate-perforate, microverrucate; pistillode 0. Pistillate flowers subsessile; sepals 5 or 6, valvate or slightly imbricate, dentate; petals and disk 0; ovary 3-locular, pubescent; stylodia connate into a globose column, tips emarginate. Fruit capsular. Seeds globose, testa smooth.

Two spp., Madagascar, in humid forest.

186. *Megistostigma* Hook. f.

Megistostigma Hook. f., Hook. Ic. Pl. 16: t. 1592 (1887), Fl. Brit. Ind. 5: 466 (1888); Merr., Phil. J. Sci. 16C: 563 (1920): Croizat, J. Arnold Arb. 22: 425 (1941); Backer & Bakh. f., Fl. Java 1: 491 (1963); Airy Shaw, Kew Bull. 23: 119 (1969), 36: 330 (1981); Radcl.-Sm., Gen. Euphorb.: 251 (2001). *Clavistylus* J.J. Sm. (1910).

Monoecious shrubs or lianas; indumentum simple and urticant. Leaves palmately veined, often peltate or cordate; stipules persistent or deciduous. Inflorescences axillary, racemoid, unisexual or bisexual, bracts eglandular, persistent, with prominent bracteoles. Staminate flowers subsessile or pedicellate; calyx closed in bud, splitting distally into 3 valvate lobes, proximally connate into a cup; petals 0; receptacular disk 0, pseudodisk at rim of calycine cup; stamens 3, filaments distinct; anthers muticous, introrse, ovate, obtuse, connective enlarged, apiculate; pollen grains spheroidal, irregularly aperturate or inaperturate; sexine tectate-perforate, fissured, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 3–5, imbricate, lanceolate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, pubescent; stylar column globose or clavate, broadly 3-lobed distally. Fruits capsular; columella persistent, 3-pronged. Seeds globose, exotesta ± fleshy, endotesta hard, smooth.

Five spp., distributed from Burma to Malesia.

187. *Tragiella* Pax & K. Hoffm.

Tragiella Pax & K. Hoffm., Pflanzenr. 147, IX: 104, fig. 24 (1919); Radcl.-Sm., Kew Bull. 35: 777 (1981), Fl. E. Trop. Afr. Euphorb. 1: 318, fig. 60 (1987), Fl. Zambesiaca 9(4): 212, t. 45 (1996), Gen. Euphorb.: 252 (2001); Webster, Ann. Missouri Bot. Gard. 81: 94 (1994).

Monoecious herbs to twining vines; indumentum of simple and urticant hairs. Leaves palmately veined, denticulate, eglandular; stipules persistent. Inflorescences terminal or leaf-opposed, racemose, bisexual, with 1 or 2 basal pistillate flowers, distal nodes with glomerules of staminate flowers; bracts 1-flowered. Staminate flowers pedicellate; calyx closed in bud, distally splitting into 3 valvate lobes introrsely projecting at top of calyx tube; petals and disk 0; stamens 3 (4), filaments distinct or basally connate; anthers dorsifixed, introrse, muticous, connective enlarged, thecae discrete; pollen grains oblate spheroidal, 3-colpate, colpi narrow with uneven margins; sexine semi-tectate-reticulate, microverrucate; pistillode +. Pistillate flowers pedicellate; sepals 6, imbricate, pinnatifid, persistent in fruit; petals and disk 0; ovary 3-locular, pubescent and sometimes urticant-setose; ovules pachycaulous, inner integument thick, outer integument thin; stylodia united into a conical or infundibuliform column

or spherical mass. Fruits capsular, endocarp woody; columella 3-pronged, not persistent. Seeds globose; testa smooth.

Five spp. from east Africa. The genus appears to be linked to *Tragia* by its urticant hairs and pollen morphology, but resembles *Cnesmone* and *Sphaerostylis* in its distinctive staminate flowers and enlarged stylodia. There is also a resemblance to *Ctenomeria* in the pinnatifid pistillate sepals, but the pollen of the two genera is very different.

14c. Subtribe Dalechampiinae (Müll. Arg.) G.L. Webster (1994).

Includes only the genus *Dalechampia*, whose relationships to the Plukenetiinae and Tragiinae remain unclear. The inflorescence of *Dalechampia* has no counterpart in other Plukenetieae, and Gillespie (1994) and Nowicke and Takahasi (2002) have emphasized that its distinctive pollen is strikingly different from that of either Plukenetiinae or Tragiinae. The primitive *Dalechampia* species in sect. *Rhopalostylis* (Armbruster 1996) have the stylar apparatus of Plukenetiinae (especially *Romanoa*) but the persistent stipules and bipartite inflorescence of Tragiinae (*Bia*). Urticant trichomes, which are present in the Tragiinae, from *Dalechampia* are recorded in the more derived sect. *Dioscoreifoliae* (on both vegetative and reproductive parts) but not in the basal sect. *Rhopalostylis*. Obviously, the subtribal classification of the Plukenetieae needs a profound revision. The molecular data available (Wurdack et al. 2005) indicate that *Dalechampia* might be embedded in the Plukenetieae (sister to *Astrococcus*).

188. *Dalechampia* [Plumier] L. Fig. 35

Dalechampia [Plumier] L., Sp. Pl.: 1054 (1753), Gen. Pl. ed. 5: 473 (1754); Müll. Arg. in DC., Prodr. 15(2): 1232 (1866), Fl. Brasil. 11(2): 633, t. 88–91 (1874); Pax & K. Hoffm., Pflanzenr. 147, XII: 3, figs. 1–9 (1919); Gagnep., Fl. Indochine 5: 342, t. 39, 40 (1926); Léonard, Fl. Congo 8 (1): 194 (1962); Webster & Armbruster, Brittonia 31: 352 (1979); Armbruster, Syst. Bot. 9: 272 (1984), 13: 303 (1988); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 285, fig. 56 (1987); Webster, Brittonia 41: 1, figs. 1–3 (1989); Webster & Armbruster, Bot. J. Linn. Soc. 105: 137, figs. 1–5 (1991); Armbruster, Syst. Bot. 21: 209, figs. 5–14 (1996), Smiths. Contr. Bot. 86: 14, figs. 4–8 (1997); Radcl.-Sm., Gen. Euphorb.: 262 (2001).
Cremophyllum Scheidw. (1842).
Rhopalostylis Klotzsch ex Baill. (1858).
Megalostylis S. Moore (1916).

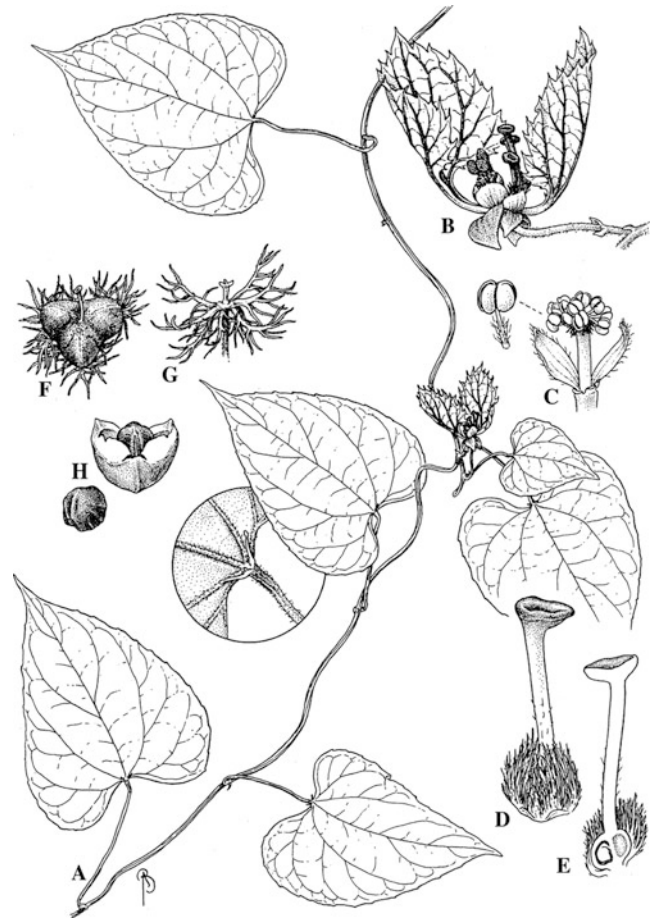

Fig. 35. Euphorbiaceae-Acalyphoideae. *Dalechampia dioscoreifolia*. **A** Part of stem with leaves and inflorescence; note detail of adaxial leaf blade base with stipels. **B** Inflorescence subtended by bracts. **C** Staminate flower; three sepals removed. **D** Pistillate flower. **E** Same, medial section. **F** Fruit. **G** Sepals and column after fruit dehiscence. **H** Fruit segment with seed and isolated seed. (Reproduced with kind permission of the artist Bobbi Angell)

Monoecious undershrubs or vines; indumentum simple and urticant, sometimes scanty. Leaves entire or dentate, unlobed and pinnately veined to lobed and palmately veined, sometimes palmatisect, often stipellate at base; stipules persistent. Inflorescences pseudanthial, pedunculate, axillary or terminating short shoots, mostly bilaterally symmetrical with a pair of subopposite involucral bracts, bisexual; pistillate cymule proximal, 3-flowered, bracteolate; staminate cymule terminal, involucellate, mostly of 8–12 flowers, bractlets subtending staminate flowers resiniferous or odoriferous. Staminate flowers

pedicellate, pedicels articulate; calyx closed in bud, splitting into mostly 3–6 valvate segments; petals and disk 0; stamens 5–90; filaments connate into a thick column; anthers latrorse, 2-celled, muticous; pollen grains prolate, 3-colporate, with costae equatoriales of two thickened bands, sexine coarsely reticulate with very large lumina and high muri; pistillode 0. Pistillate flowers subsessile or pedicellate; sepals 5–12, imbricate, basally connate, entire or pinnatifid; disk 0; ovary 3-locular, glabrous or pubescent; ovules anatropous, inner integument thick, outer integument thinner, vascularized; stylodia completely connate into an elongate, sometimes clavate or peltate column, stigmatic surface extending down much of the stylar surface. Fruits capsular, usually enclosed by the accrescent urticant calyx, dehiscing explosively by elastic twisting of the dry cocci; columella persistent. Seeds globose, smooth or rugose. $2n = 44, 46, 72, 138$.

About 120 spp., mainly in tropical regions of the Americas, also in tropical Africa/Madagascar and S and SE Asia. The genus was divided into 6 sections by Webster & Armbruster (1991), and Armbruster (1996) has added an additional section. *Dalechampia* had been placed in a separate tribe since Müller (1866) until treated by Webster (1994), who demoted the Dalechampieae to a subtribe of the Plukenetieae.

Three unplaced acalyphoid genera:

189. *Afrotrewia* Pax & K. Hoffm.

Afrotrewia Pax & K. Hoffm. in Engl., Pflanzenreich 147. VII: 14 (1914); Radcliffe-Smith, Gen. Euphorb.: 420 (2001); Kulju, van der Ham & Breteler, Taxon 57: 137–143 (2008).

Shrubs to small trees, presumably dioecious; indumentum minute, stellate to simple. Leaves subentire to shallowly serrate, with extrafloral nectaries on both sides, petiole apically pulvinate; stipules deciduous to somewhat persistent. Inflorescences unisexual, with prophylls at the bases of the inflorescence branches and pedicels; staminate inflorescences axillary to terminal panicles, pistillate inflorescences 2–3-flowered racemes. Staminate flowers: sepals 2 or 3, valvate; petals 0; receptacle conical; disk interstaminal, of hairy glands; stamens 30–40, distinct; anthers basifixed, thecae 2, pendulous, unequally bilobed, latrorse or introrse; connective horizontally enlarged, partly covering the thecae, papillose; pollen grains spheroidal, tricolporate-lalongate, tectate-microreticulate; pistillode 0. Pistillate flowers: sepals 5–6, imbricate?; petals 0; disk annular, thick; ovary 3-locular; stylodia 2. Fruits lobed capsules, dehiscing septicidally, septifragally and loculicidally; column 0?. Seeds subglobose; hilum ± triangular to heart-shaped; testa not fleshy; cotyledons broad, flat.

One sp., *A. kamerunica* Pax & K. Hoffm., Cameroon and Gabon.

In the molecular analysis of Kulju et al. (2008), *Afrotrewia* falls into the core acalyphoid clade basal to clades A2 and A3 of Wurdack et al. (2005).

190. *Crotonogynopsis* Pax

Crotonogynopsis Pax, Bot. Jahrb. 26: 328 (1899); Prain, Fl. Trop. Afr. 6(1): 924 (1912); Pax & K. Hoffm., Planzenr. 147, VII: 14 (1914); Radcl.-Sm., Fl. Trop. E. Afr. Euphorb. 1: 213, fig. 40 (1987); Webster, Ann. Missouri Bot. Gard. 81: 80 (1994); Léonard, Fl. Afr. Centr. Euph. 3: 28, t. 4 (1996); Radcl.-Sm., Gen. Euphorb.: 188 (2001).

Monoecious or dioecious trees or shrubs; indumentum simple. Leaves sessile or subsessile, denticulate, with scattered glands abaxially; stipules deciduous. Inflorescences axillary (ramiflorous), unisexual, racemoid, the pistillate shorter and few-flowered; bracts persistent. Staminate flowers pedicellate; calyx closed in bud, splitting into 2–5 valvate segments; petals 0; disk of many interstaminal glabrous segments; stamens 10–15, filaments distinct; anthers dorsifixed, introrse or extrorse, connective apiculate, not enlarged; pollen grains 3-angled, 3-colporate, colpi granulate, sexine tectate-perforate; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, ± imbricate, persistent in fruit; petals 0; disk annular-lobed; ovary 3(4)-locular, smooth and glabrous; ovules anatropous, inner integument thick, outer integument thin; stylodia nearly distinct, bifid, branches laciniate. Fruit capsular; columella persistent. Seeds subglobose, ecarunculate, testa smooth.

Two spp., tropical Africa. Radcliffe-Smith (2001) referred the genus to the Adelieae, from which it differs in its 3-colporate pollen grains with non-operculate colpi and a complex infratectum with double-layered columellae, otherwise known only from Alchorneinae (*Alchornea*, *Orfila*) (Takahashi et al. 2000). The molecular data (Wurdack et al. 2005) resolve it in the Acalypheae, close to *Mareya* and *Acalypha*.

191. *Enriquebeltrania* Rzedowski

Enriquebeltrania Rzedowski, Bol. Soc. Bot. México 38: 75 (1979); Webster, Ann. Missouri Bot. Gard. 81: 80 (1994); Radcl.-Sm., Gen. Euphorb.: 189 (2001); De-Nova et al., Syst. Bot. 31: 533–546 (2006).
Beltrania Miranda (1957; nom. illeg.).

Dioecious shrubs; branches often spinescent; indumentum simple. Leaves fasciculate, distally crenate to dentate, pellucid-punctate; stipules persistent. Flowers in axillary glomerules. Staminate flowers pedicellate; sepals 3 or 4, valvate; petals and disk 0; stamens 20–30, filaments distinct; anthers extrorse, apiculate; pollen grains oblate spheroidal, 3-colporoidate, colpi inoperculate, with obscure margins, sexine tectate-puncate, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, entire, persistent in fruit; disk 0; ovary 2-locular; inner integuments very thick, outer integuments thin; stylodia distinct, unbranched. Fruits capsular, glabrous. Seeds subglobose, carunculate, testa minutely rugulose.

Two spp., Mexico, Yucatan and Pacific coast. Formerly this genus was included in Adelieae, but Takahashi et al. (2000) found the inoperculate pollen grains of *Enriquebeltrania* very different from the operculate grains of *Adelia*. By molecular studies (Wurdack et al. 2005; De-Nova et al. 2006), no precise placement within the New World acalyphoids could be indicated either.

VI. Subfam. Crotonoideae Beilschm. (1833).

Monoecious or dioecious trees, shrubs, or herbs; laticifers articulated or non-articulated, latex colored or 0; indumentum simple, stellate, or lepidote; leaves alternate or opposite (whorled), stipulate or estipulate, lamina simple to palmately lobed or compound, often with basal laminar glands. Inflorescences axillary or terminal, dichasial to thyrsoid or spiciform. Staminate flowers with imbricate or valvate sepals; petals and disk + or 0; stamens (3–)5–many, filaments distinct or connate; pollen grains binucleate or trinucleate, tricolpate, porate or inaperturate, sexine reticulate to more commonly tectate with triangular or rounded-triangular processes [pillars] frequently forming continuous [triangular] arrays; pistillode + or 0. Pistillate flowers with (2) 3–6 imbricate or valvate sepals; petals and disk + or 0; ovary mostly 3-locular; outer integuments of ovules sometimes vascularized; stylodia bifid to multifid, less often unlobed; ovules solitary in each locule, anatropous. Fruit usually capsular or rarely indehiscent. Seeds carunculate or ecarunculate; exotegmen palisadal, testa sometimes fleshy; endosperm usually copious, often oily.

This subfamily, subfam. Crotonoideae s.l., which comprises 68 genera in twelve tribes, contains lactiferous taxa with crotonoid pollen sculpture and has been resolved to consist of four clades (definition and topology of clades after Wurdack et al. 2005): (I) the Adenoclineae s.l. (tribe 1), (II) the Gelonieae (tribe 2), (III) the articulated crotonoids (tribes 3–6), and (IV) the inaperturate crotonoids (= Crotonoideae s. str.), comprising the remaining tribes 7–12. Members of clades I–III share apetalous flowers, mostly thin integuments (thick in I), and aperturate pollen, whereas clade IV has apetalous flowers, inaperturate pollen, and thick inner integuments that contain vascular bundles. These clades form a grade, in which (I), (II) and (III) subsequently are unsupported sister clades to (IV), the latter comprising two subclades, C1, with tribes 7 and 8, and subclade C2, with tribes 9–12. Subclade C1 is from the New World and the Old, whereas C2 is (nearly) confined to the Old World. Molecular support for subclade C2 is strengthened by a large *trn*L-F spacer deletion.

Key to the Tribes of Subfam. Crotonoideae

1. Pollen grains aperturate; petals 0; laticifers articulated or inarticulated 2
– Pollen grains inaperturate; petals usually present, at least in staminate flowers; laticifers inarticulated (articulated) 5
2. Laticifers articulated; staminate calyx gamophyllous; pollen grains 3-nucleate; plants monoecious or dioecious; chromosome base number $x = 9$ 3
– Laticifers non-articulated; staminate calyx mostly not gamophyllous; pollen grains 2-nucleate; chromosome base number $x = 11$ 4
3. Leaves palmately compound; inflorescences cymose-paniculate, pistillate flowers terminal on lateral axes; calyces gamophyllous; pollen grains colpate; stylodia stigmatiform; seeds ecarunculate, endosperm oily **6. Heveeae**

– Leaves simple to deeply lobed but not compound; inflorescences without terminal pistillate flowers on lateral branches; calyces of distinct sepals; pollen grains pantoporate; stylodia mostly multifid; stylodia mostly multifid; seeds carunculate; endosperm starchy **4. Manihoteae**

4. Pollen grains pantoporate; leaves pellucid-punctate, stipules connate; inflorescences of leaf-opposed glomerules **2. Gelonieae**

– Pollen grains colp(or)ate; leaves not pellucid-punctate, stipules distinct; inflorescences terminal or axillary 6

5. Pollen exine lacking distinct Croton pattern, colpi operculate; monoecious (dioecious); pistillate flowers subsessile **5. Micrandreae**

– Pollen exine with distinct Croton pattern, colpi inoperculate; mostly dioecious; pistillate flowers subsessile to pedicellate **1. Adenoclineae**

6. Leaves simple, unlobed to palmately lobed; inflorescences terminal or axillary; seeds carunculate or ecarunculate 7

– Leaves palmatisect [except *Givotia*]; inflorescences axillary; seeds ecarunculate **11. Ricinodendreae**

7. Staminate sepals distinct or connate but not fused and enclosing petals in bud [except in *Anomalocalyx*]; seeds carunculate or ecarunculate; stipules persistent or deciduous 8

– Staminate sepals joined in bud, splitting into segments valvately or irregularly; seeds ecarunculate **12. Aleuritideae**

8. Indumentum simple or malpighiaceous; pollen grains binucleate; seeds carunculate or ecarunculate 9

– Indumentum stellate or lepidote; pollen grains binucleate or trinucleate; seeds mostly carunculate [except in *Paracroton*] 11

9. Seeds nearly exalbuminous; petals 0; stylodia unlobed; fruits indehiscent **3. Elateriospermeae**

– Seeds albuminous; petals usually present; stylodia mostly bifid; fruits usually dehiscent 10

10. Inflorescences mostly dichasial, terminal, at least in part; usually monoecious; indumentum often glandular; leaf blades often palmately lobed or parted; stamens 5–12, filaments distinct or connate; seeds carunculate **7. Jatropheae**

– Inflorescences racemoid or spiciform to paniculate, terminal or axillary; monoecious or dioecious; indumentum rarely glandular; leaf blades rarely palmately lobed; stamens 7–35, filaments mostly distinct or nearly so; seeds carunculate or ecarunculate **9. Codiaeae**

11. Branches and leaves with resinous glands, or else leaves opposite or verticillate; filaments erect in bud; cotyledons as narrow as radicle or much broader **10. Ricinocarpeae**

– Branches and leaves lacking resinous glands; leaves alternate; filaments erect or inflexed in bud; cotyledons much broader than radicle **8. Crotoneae**

1. Tribe Adenoclineae (Müll. Arg.) G.L. Webster (1975).

Monoecious or dioecious; laticifers non-articulated, latex clear, often colored; indumentum simple, malpighiaceous, or stellate; leaves alternate (opposite), simple; inner integument usually lacking vascular bundles and < 6 cells thick [thick and vascularized in *Klaineanthus*]; stylodia bifid or stigmatiform, rarely completely connate into a column; fruits capsular or drupaceous; seeds ecarunculate.

Unlike the Micrandreae and Manihoteae, tribe Adenoclineae is represented in both the Neotropics and Paleotropics. Subtribe Endosperminae differs markedly in its stellate indumentum, connate stamens, and multilocular ovary, but is linked with *Omphalea* and *Suregada* by the possession of alkaloidal glycosidase inhibitors and/or by being host plants for diurnal uraniine moths (Kite et al. 1991; Wurdack et al. 2005).

Key to the Subtribes and Genera of Adenoclineae

1. Indumentum stellate; stamens connate; fruits baccate, 1–7-locular. **Subtribe 1b. Endosperminae** **197. *Endospermum***

– Indumentum simple or malpighiaceous; stamens distinct, rarely connate; fruits dehiscent or indehiscent; 2- or 3-locular. **Subtribe 1a. Adenoclininae** 2

2. Stylodia completely connate into an obtuse or shortly 2–3-lobate stylar column; stamens 2–3, connate into a short, slender column **195. *Omphalea***

– Stylodia distinct or largely so; stamens > 3, filaments distinct 3

3. Pistillate disk 0; leaves glandular-dentate, without laminar glands **193. *Ditta***

– Pistillate disk +, at least as staminodia; leaves sometimes with laminar glands 4

4. Herbs; seed coat not fleshy; staminate disk segments interstaminal **192. *Adenocline***

– Trees or shrubs; seed-coat fleshy; staminate disk extrastaminal or 0 5

5. Stamens 8–10; anthers 2-locular, not peltate; pollen grains tricolporate; staminate disk of 4 or 5 segments; leaves eglandular, stipules deciduous; indumentum simple; endotesta smooth **196. *Klaineanthus***

– Stamens 3; anthers 4-locular, peltate; pollen grains tricolpate; staminate disk 0; leaves usually with laminar glands, stipules persistent; indumentum [at least in part] malpighiaceous; endotesta foveolate or echinulate **194. *Tetrorchidium***

1a. Subtribe Adenoclininae Arg. (1865).

Trees, shrubs, or herbs; indumentum simple or malpighiaceous; stamens 3–30, filaments distinct; ovary 2- or 3-locular; stigmas distinct; fruit capsular or drupaceous.

This subtribe comprises five genera, which are found in the Neotropics and in tropical and temperate Africa.

192. *Adenocline* Turcz.

Adenocline Turcz., Bull.Soc. Imp. Nat. Moscou 16: 59 (1843); Prain, Ann. Bot. 27: 404 (1913), Fl. Cap. 5(2): 488 (1920); Dyer, Gen. S. Afr. Fl. Pl., ed. 3, 1: 315 (1975); Radcl.-Sm., Gen. Euphorb. 279 (2001).

Dioecious (monoecious) annual or perennial herbs, sometimes scrambling; laticifers non-articulated, latex not apparent; indumentum 0. Leaves alternate or opposite, petiolate or sessile, entire or dentate, triplinerved to 1-veined, eglandular or stipellate at apex of petiole; stipules persistent, lanceolate or subulate, ± dentate or lacerate, sometimes foliaceous. Flowers axillary, the staminate in ± umbellate cymes or glomerules at upper axils, sometimes aggregated into terminal panicles; pistillate flowers solitary, leaf-opposed; bracts dissected, persistent, eglandular. Staminate flowers pedicellate; sepals 5, imbricate; petals 0; disk segments interstaminal, sometimes stipitate; stamens mostly (6–)10(−12), biseriate; filaments distinct; anthers basifixed, thecae discrete, globose, dehiscing vertically; pollen grains oblate spheroidal, 3-colpate, colpus margins irregular; sexine tectate, finely clavate; pistillode 0. Pistillate flowers pedicellate; sepals 5, entire, persistent in fruit; petals 0; disk of 3 ± petaloid segments; ovary 3-locular; ovules anatropous; stylodia nearly distinct, bipartite. Fruits capsular. Seeds ecarunculate, testa smooth, rugulose, or foveolate.

Eight spp. in temperate and subtropical South Africa (Dyer 1975; Radcliffe-Smith 2001), but only three in the enumeration of Govaerts et al. (2000).

193. *Ditta* Griseb.

Ditta Griseb., Mem. Amer. Acad. Arts Sci. II. 8: 160 (1861); Urban, Symb. Ant. 7: 261 (1912); Alain, Fl. Cuba 3: 112, fig. 36 (1953); Little et al., Trees Puerto Rico & Virgin I. 2: 400, t. 436 (1974); Liogier, Fl. Española 4: 135, 348, fig. 116–13 (1986), Descr. Fl. Puerto Rico 2: 383, fig. 59–13 (1988); Radcl.-Sm., Gen. Euphorb.: 280 (2001).

Dioecious shrubs; stems with resinous exudate; indumentum simple, scanty. Leaves rigid, subentire or obscurely crenate with embedded marginal glands, ± revolute; stipules persistent, incrassate, dark, resiniferous. Flowers axillary, staminate in few-flowered glomerules, pistillate solitary. Staminate flowers sessile; sepals 3, distinct; petals and disk 0; stamens 3, filaments suppressed; anthers sessile, dorsifixed; pollen grains spheroidal, 3-colpate, sexine tectate with apiculate pillars; pistillode 0. Pistillate flowers sessile; sepals suppressed; petals and disk 0; ovary 2- or 3-locular; ovules anatropous; stylodia distinct, unlobed, incrassate, stigmatiform. Fruits capsular, reddish. Seeds ecarunculate. $n = 11$.

Two spp. described from the Greater Antilles (Cuba, Hispaniola, and Puerto Rico), but Liogier (1986) doubts that *D. maestrensis* Borhidi is distinct from *D. myricoides* Griseb. *Ditta* is morphologically distant from the other genera of Adenoclineae in its resinous axes and highly reduced flowers. However, the pollen is consistent with the Adenoclineae (Nowicke 1994), and in the molecular analysis *Ditta* is sister to *Tetrorchidium*.

194. *Tetrorchidium* Poepp.

Tetrorchidium Poepp., in Poepp. & Endl., Nov. Gen. Sp. 3: 23, t. 227 (1842); Müll. Arg. in DC., Prodr. 15(2): 1132 (1866); Pax & K. Hoffm., Pflanzenr. 147, IV: 29, figs. 8, 9 (1912); Cuatrecasas, Brittonia 9: 76, figs. 1–4 (1957); Léonard, Fl. Congo 8(1): 133, t. 9 (1962); Radcl.-Sm., Fl. E. Trop. Afr., Euphorb. 1: 373, fig. 70 (1987); Breteler, Adansonia III, 21: 97 (1999).
Hasskarlia Baill. (1860).
Tetrorchiopsis Rauschert (1982).

Dioecious trees or shrubs; latex whitish, often scanty or 0; indumentum simple or malpighiaceous. Leaves entire to dentate, eglandular [African spp.] or with raised or stipitate glands at base or laterally on petiole; stipules ± glandular, persistent. Inflorescences axillary or leaf-opposed; staminate spiciform, pistillate racemoid or paniculate; bracts persistent, entire, sometimes glandular. Staminate flowers subsessile, several per bract; sepals 3, distinct, imbricate, adaxially ribbed; petals and disk 0; stamens 3, distinct, filaments shorter than anthers; anthers extrorse, peltate, 4-locular; pollen grains ± spheroidal, 3-colpate, sexine tectate with rounded or angular pillars; pistillode small or obsolete. Pistillate

flowers subsessile or pedicellate; sepals 3, distinct, imbricate, entire, persistent in fruit; petals 0; disk cupular or 3-lobed; ovary 2- or 3-locular; ovules anatropous; stylodia distinct, bifid, style branches sometimes dilated. Fruits capsular, thin-walled. Seeds rounded, ecarunculate, exotesta fleshy, endotesta hard, foveolate.

Nineteen spp. in the Neotropics, and four in Africa (Govaerts et al. 2000). In agreement with Radcliffe-Smith (2001), the African *Hasskarlia* is treated as a section of *Tetrorchidium*.

195. *Omphalea* L. Fig. 36

Omphalea L., Syst. Nat. ed. 10: 1264 (1759; nom. cons.); Müll. Arg. in DC., Prodr. 15(2): 1134 (1866), Fl. Brasil. 11 (2): 513, t. 72 (1874); Hemsl., Hook. Ic. Pl. 26: t. 2537 (1897); Croizat, Bull. Jard. Bot. Buit. III, 17: 204 (1941); Alain, Fl. Cuba 3: 109 (1953); P.I. Forst., Austrobaileya 4: 381, t. 1 (1995); Gillespie, Novon 7: 127, t. 1 (1997), Smiths. Contr. Bot. 86: 6, t. 1 (1997).

Monoecious trees, shrubs, or lianas; sap red or pinkish; indumentum simple; foliage evergreen or deciduous. Leaves pinnately or palmately veined or lobed, with paired glands at base or apex of petiole; stipules mostly entire, ± deciduous. Inflorescences terminal, racemoid or paniculate, bisexual or distal nodes staminate; bracts foliose, generally glandular, stipulate. Staminate flowers pedicellate; sepals (3)4–5, discrete, imbricate; petals 0; disk extrastaminal, annular or segmented; stamens 2 or 3, filaments connate into a ± apically dilated column; anthers latrorse; pollen grains oblate spheroidal to oblate, 3-colpate, sexine tectate-foveolate, microverrucate; pistillode 0. Pistillate flowers subsessile or pedicellate; sepals 4 or 5, discrete, imbricate, deciduous; disk 0; ovary 3(4)-locular, glabrous; ovules pachycaulous, inner and outer integuments moderately thick; stylodia completely connate into a stylar column, distally obtuse or very shortly 2–3-lobate. Fruits capsular or baccate; columella not persistent. Seeds subglobose, sometimes compressed or angular, ecarunculate; exotesta fleshy to papery, endotesta hard, smooth.

Seventeen spp. (Gillespie 1997; 22 according to Govaerts et al. 2000), scattered through neotropical and paleotropical regions, except the Pacific islands. In terms of systematics, *Omphalea* is one of the most problematic genera of the family. Müller (1866) assigned it to his subtribe Gelonieae, associated with *Endospermum*, *Elaterospermum*, and other genera now assigned to the Crotonoideae. Pax and Hoffmann first (1919) placed *Omphalea* into the Hippomaneae, and later in a subtribe of the Gelonieae. Croizat (1941) suggested an affinity with the Plukenetieae. The molecular data (Wurdack et al. 2005) place *Omphalea* in the Adenoclineae. Interestingly, *Omphalea*, *Endospermum*, *Tetrochidium* and *Suregada* (Gelonieae) accumulate alkaloidal protease inhibitors, and are host plants for specialist diurnal uraniine moths (Kite et al. 1991; Wurdack et al. 2005).

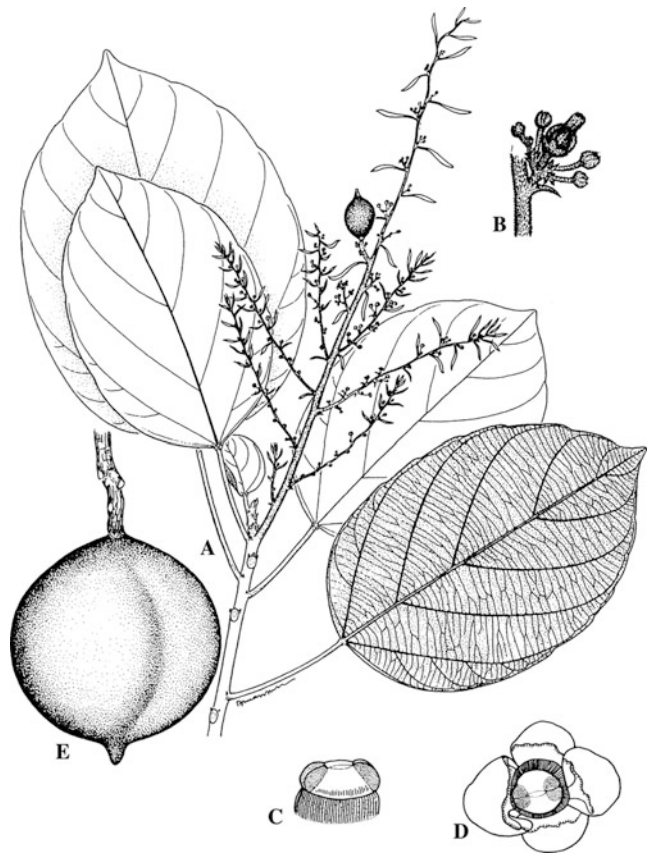

Fig. 36. Euphorbiaceae-Crotonoideae. *Omphalea diandra*. **A** Flowering branch. **B** Partial inflorescence with central pistillate flower and outer staminate flower buds. **C** Androecium above annular nectary. **D** Staminate flower at anthesis. **E** Fruit. (Gillespie 1997)

196. *Klaineanthus* Pierre ex Prain

Klaineanthus Pierre ex Prain, Kew Bull. Misc. Inf. 1912: 105 (1912), Fl. Trop. Afr. 6(1): 963 (1913), Hook. Ic. Pl. 30: t. 2985 (1913); Keay, Fl. W. Trop. Afr., ed. 2, 1: 413 (1958); Léonard, Fl. Congo 8(1): 130 (1962).

Dioecious trees; latex not recorded; indumentum simple. Leaves long-petiolate, eglandular; stipules minute, deciduous. Inflorescences terminal and axillary, the staminate paniculate, the pistillate racemose; bracts deciduous. Staminate flowers pedicellate; sepals (3) 4 or 5, basally connate, imbricate; petals 0; disk segments 4 or 5; stamens 8–10, biseriate, filaments distinct; anthers basifixed, introrse; pollen grains suboblate, 3-colporate, sexine tectate, with clavate pillars; pistillode 2–3-lobed. Pistillate flowers pedicellate; sepals 5 (4), distinct, imbricate, entire, deciduous in fruit; petals 0; disk annular, with 4 or 5 staminodes; ovary 3-locular, glabrous; ovules anatropous, inner integuments with 9–11 cell layers, vascularized; stylodia almost distinct, bipartite, the arms 2-lobulate at their apices. Fruits capsular, with thin papery walls; columella persistent, slender; seeds with fleshy exotesta, endotesta smooth.

A single sp., *K. gaboniae* Pierre ex Prain from West Africa (Nigeria to Gabon). It is anomalous in the Adenoclineae in having a thick, vascularized integument.

1b. Subtribe Endosperminae Pax & K. Hoffm. (1931).

Dioecious trees or shrubs, indumentum stellate; staminate calyx gamophyllous; stamens 6–10, filaments connate; ovary 2–6-locular; inner integuments thin, not vascularized; stylodia stigmatiform, confluent; fruit capsular.

Monotypic, including only the paleotropical genus *Endospermum*.

197. *Endospermum* Benth.

Endospermum Benth., Fl. Hongkong.: 304 (1861; nom. cons.); Beccari, Malesia 2: 45, t. 2 (1884); Pax & K. Hoffm., Pflanzenr.147, IV: 33 (1912); Radcl.-Sm., Gen. Euphorb.: 281 (2001); Guerrero & van Welzen, Edinb. J. Bot. 68:443–482 (2011), rev.

Dioecious trees; latex white, often not evident; indumentum stellate-fasciculate, sometimes scanty. Leaves long-petiolate, sometimes peltate, palmately veined or triplinerved, with abaxial paired sessile patelliform or conical glands at junction with petiole; stipules entire, deciduous. Inflorescences axillary, staminate paniculate, pistillate spicate or racemose, sometimes narrowly paniculate; bracts entire or unidentate, persistent or deciduous, eglandular. Staminate flowers subsessile, basally articulate; calyx 2–4-lobed, often open in bud; petals 0; disk extrastaminal, 4–5-angled; stamens (3–)6–10, filaments connate, anthers nearly sessile on staminal column, didymous and 4-locellate; pollen grains suboblate, 3-colpate, sexine tectate with clavate pillars; pistillode minute or 0. Pistillate flowers subsessile or pedicellate; calyx 5-angled or -lobed; ± persistent in fruit; petals 0; disk patelliform or cupular; ovary 2–6-locular, pubescent; ovules anatropous; stylodia stigmatiform, coalescing into a disk. Fruits separting into indehiscent, sometimes fleshy, cocci; columella not persistent. Seeds spheroidal, ecarunculate, testa rugose or verrucose. $n = 24$.

About 10 spp., distributed from China to northern Australia, Melanesia and Fiji. All Malesian *Endospermum* have extrafloral nectaries on the lower leaf surface, and two New Guinean species are myrmecophilous, of which one, *E. moluccanum* (Teijsm. & Binn.) Kurz, produces food bodies on which the ants feed (Guerrero and van Welzen 2011).

2. Tribe Gelonieae (Müll. Arg.) Pax (1890).

Dioecious trees or shrubs, without evident latex; indumentum simple, usually scanty or 0; leaves alternate, simple; inflorescences leaf-opposed; flowers in glomerules; disk receptacular or extrastaminal; stamens 6–60; pollen grains spheroidal, pantoporate, sexine with Croton pattern; ovules with inner integuments thin, not vascularized.

Two genera, Africa, Madagascar, and tropical Asia.

Key to the Genera of Gelonieae

1. Inflorescences leaf-opposed; pistillode 0; stylodia bifid or multifid, branches terete, not dilated; leaves petiolate, lamina pellucid-punctate, stipules deciduous **198. *Suregada***
– Inflorescences terminal; pistillode present; stylodia dilated, stigmatiform; branches flattened, dilated; lamina not pellucid-punctate; stipules foliaceous, persistent **199. *Cladogelonium***

198. *Suregada* Roxb. ex Rottl.

Suregada Roxb. ex Rottler, Ges. Naturf. Freunde Berlin, Neue Schriften 4: 206 (1803); Baillon, Étude Gén. Euphorb.: 395 (1858); Croizat, Bull. Bot. Gard. Buitenzorg III, 17: 212 (1942); Léonard, Bull. Jard. Bot. Brux. 28: 79 (1958), Fl. Congo 8(1): 124 (1962); Radcl.-Sm., Fl. E. Trop. Afr., Euphorb. 1: 376, fig. 71 (1987), Fl. Zambes. 9(4): 249, t. 53 (1996); Radcl.-Sm. et al., Kew Bull. 58: 965–970 (2003), key Malagasy spp.; Li-Bingtao & Esser, Fl. China 11: 276 (2008). *Gelonium* Roxb. ex Willd. (1806; nom. illeg.).

Dioecious trees or shrubs, without evident latex; indumentum simple, usually scanty or 0. Leaves usually pellucid-punctate, without excavated glands; stipules deciduous. Inflorescences leaf-opposed, glomerular, sessile or subsessile. Staminate flowers subsessile or pedicellate; sepals 5(6), distinct, broadly imbricate; petals 0; disk receptacular or extrastaminal, annular or dissected; stamens (6)10–30(−60), filaments distinct; anthers dorsifixed, introrse, muticous; pollen grains spheroidal, 2-nucleate, 3–6-porate; sexine tectate with clavate pillars in Croton pattern; pistillode 0. Pistillate flowers subsessile or pedicellate; sepals (4)5(−8), distinct, imbricate, entire, persistent in fruit; petals 0; disk annular, tenuous, sometimes with staminodes; ovary (2)3(4)-locular; ovules pachychalazal, inner integuments thin; stylodia bifid or multifid, branches slender. Fruits capsular or sometimes indehiscent; columella persistent. Seeds ellipsoid, ecarunculate, testa smooth. $2n = 22$.

About 30 spp., Africa/Madagascar and tropical Asia.

199. *Cladogelonium* Leandri

Cladogelonium Leandri, Bull. Soc. Bot. France 85: 530, t. 1.15–19bis (1938); Webster, Ann. Missouri Bot. Gard. 81: 131 (1994); Radcl.-Sm., Gen. Euphorb.: 284, fig. 38 (2001).

Monoecious shrubs; branches sympodial, flattened into platyclades similar in texture to the leaves; latex not recorded; indumentum 0. Leaves not pellucid-punctate, obscurely dentate and with abaxial excavated marginal glands; stipules foliaceous, persistent. Inflorescences terminating sympodial axes, glomerulate, unisexual, sessile. Staminate flowers pedicellate; sepals 5, imbricate, distinct, each with an abaxial gland; petals 0; stamens 10, filaments distinct; anthers dorsifixed, extrorse; pistillode 3-fid. Pistillate flowers solitary, pedicellate; sepals 5, distinct, imbricate, each with an abaxial gland; petals 0; disk tripartite [staminodial?]; ovary 3-locular; stylodia stigmatiform. Fruit capsular. Seeds ellipsoid, with minute caruncle, testa foveolate.

A single very rare sp., *C. madagacariense* Leandri, in dry deciduous forest of Madagascar. It appears to be a satellite genus of *Suregada*, from which it differs in details of inflorescence and floral structure. Lobreau-Callen and Suarez Cervera (1997) report 3- or 6-colpate pollen from *Cladogelonium* and a nexine structure similar to *Tetrorchidium*; they suggest the transfer of the genus to Adenoclineae.

3. Tribe Elateriospermeae G.L. Webster (1975).

Monoecious laticiferous trees; leaves biglandular at base; pollen inaperturate; fruits capsular; seeds ecarunculate.

A monotypic paleotropical tribe. Although articulated laticifers are not yet documented for this genus (and not for *Glycydendron* either), the lack of petals, the presence of a vascularized inner integument, and the molecular data safely place them into the articulated crotonoids. For the problematic "inaperturate" pollen grains, see Nowicke (1994).

200. *Elateriospermum* Blume Fig. 37

Elateriospermum Blume, Bijdr.: 620 (1826); Whitmore, Tree Fl. Malaya 2: 91, fig. 6 (1973); Hoang Van Sam & van Welzen, Blumea 49: 427–436 (2004).

Monoecious trees; stems with white latex; indumentum simple or 0. Leaves long-petiolate, biglandular at junction with petiole; stipules deciduous. Inflorescences axillary, dichasial, bisexual, pistillate flower central; bracts minute. Staminate flowers pedicellate; sepals 4–5, distinct, imbricate; petals 0; disk massive, lobed, pubescent; stamens 10–20 or more, filaments distinct; anthers introrse, connective apiculate; pollen grains spheroidal, exine with Croton pattern, muri broad, pillars angular; pistillode minute or 0. Pistillate flowers pedicellate; sepals (4)5(−7), distinct, entire, deciduous (?); disk annular, with subulate staminodia; ovary 2–4-locular, villose; ovules with inner integuments thin, vascularized; stylodia 2–4, massive, stigmas thick, dilated. Fruits capsular, endocarp thick and woody; columella not persistent. Seeds over 3 cm long, testa smooth; endosperm scanty, cotyledons massive.

A single sp., *E. tapos* Blume, distributed in lowland rainforests from peninsular Thailand through Malaya to Sumatra, Java and Borneo.

4. Tribe Manihoteae (Müll. Arg.) Pax (1890).

Monoecious (dioecious); laticifers articulated, latex white; indumentum simple (urticant); leaves mostly palmately lobed or dissected, sometimes unlobed; staminate calyx synsepalous; disk intrastaminal or extrastaminal; stamens 8–10

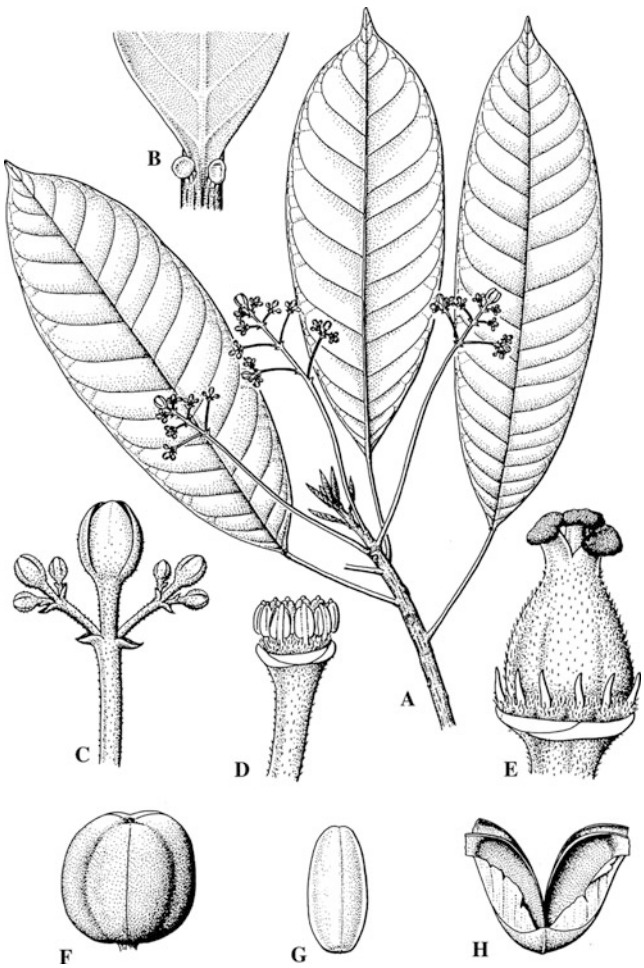

Fig. 37. Euphorbiaceae-Crotonoideae. *Elateriospermum tapos*. **A** Flowering branch. **B** Basal leaf glands. **C** Part of inflorescence with one pistillate and six staminate flower buds. **D** Staminate flower with sepals removed. **E** Pistillate flower with sepals removed, showing pistil and disk lobes. **F** Fruit. **G** Seed. **H** Fruit valves with complete septicidal dehiscence and partly loculicidal dehiscence. (Hoang Van Sam & van Welzen 2004; drawn by J. van Os)

(−25); pollen grains 3-nucleate, pantoporate; inner integuments thick, vascularized.

A small neotropical tribe of only two genera but with over 100 spp., mostly found in deciduous or thorn forests in arid regions of both North and South America.

Key to the Genera of Manihoteae

1. Stinging hairs 0; stamens distinct, staminate disk intrastaminal, perianth usually yellowish or greenish; leaf blades stipellate at base; inflorescence racemoid or racemose-paniculate **201. *Manihot***

– Stinging hairs +, very rarely 0; stamens connate, very rarely distinct; staminate disk extrastaminal, perianth whitish; leaf blades glandular at base; inflorescence dichasial-paniculate **202. *Cnidoscolus***

201. *Manihot* Miller

Manihot Miller, Gard. Dict. ed. 4 (1754); Pohl, Pl. Bras. Ic. 1: 17 (1827); Croizat, J. Arnold Arb. 23: 216 (1942); Webster, J. Arnold Arb. 48: 345 (1967); Rogers & Appan, Fl. Neotrop. 13: 1, figs. 9–124 (1973); Allem, Rev. Brasil. Biol. 49: 1 (1989), Genet. Res. Crop Evol. 41: 133 (1994).
Manihotoides C.J. Rogers & Appan (1973).

Monoecious trees or shrubs, sometimes scandent or nearly herbaceous, often with tuberous roots; latex white; indumentum simple or 0. Leaves mostly long-petiolate, simple, mostly palmately lobed, entire (serrulate), stipellate at junction with petiole; stipules mostly deciduous. Inflorescences terminal or pseudo-axillary, racemoid or paniculate, pistillate flowers generally basal, staminate in distal glomerules; bracts entire to laciniatae, mostly deciduous. Staminate flowers subsessile to pedicellate; sepals 5, imbricate, ± connate basally; petals 0; disk central, intrastaminal, entire or 5-lobed, lobes ± bifid; stamens 10, biseriate, filaments distinct; anthers introrse; pollen spheroidal, pantoporatae; pistillode rudimentary or 0. Pistillate flowers distinctly pedicellate; sepals 5, imbricate, deciduous in fruit; disk annular, fleshy, scarcely lobed; ovary 3-locular, glabrous; ovules anatropous, thick, vascularized; stylodia basally connate, branches dilated to lacerate. Fruits capsular, sometimes ribbed or winged; columella often persistent. Seeds carunculate, testa smooth. $2n = 36$.

About 100 spp. in the Neotropics, divided by Rogers and Appan (1973) into 19 sections, plus the proposed segregate genus *Manihotoides*, which could easily be accommodated in *Manihot* adjacent to sect. *Parvibracteatae*.

202. *Cnidoscolus* Pohl

Cnidoscolus Pohl, Pl. Bras. Icon. Descr. 1: 56 (1827); León, Mem. Soc. Cubana Hist. Nat. 15: 235, t. 23, 24 (1941); Lourteig & O'Donell, Lilloa 9: 105, figs. 5–9 (1943); McVaugh, Bull. Torrey Bot. Club 71: 457 (1944); Breckon, Brittonia 31: 125, figs. 3–6 (1979); Fernández Casas, Fontqueria 55: 69 (2002).
Victorinia León (1941).

Monoecious trees, shrubs, or perennial herbs; stems with septate pith; latex white; indumentum

simple and urticant. Leaves palmately (pinnately) veined or lobed or sometimes dissected, glandular at junction with petiole; stipules entire to laciniate, ± glandular, mostly persistent. Inflorescences terminal or sometimes pseudo-axillary, pedunculate, dichasial, pistillate flowers at proximal nodes, staminate in clusters at distal nodes; bracts entire to laciniate, sometimes foliaceous, eglandular. Staminate flowers subsessile or short-pedicellate; sepals imbricate, connate, the calyx ± salverform; disk annular, extrastaminal; stamens 8–10(−25), filaments connate into a column or those in the outer whorl distinct [all filaments distinct in *C. urnigerus*]; anthers in 2–3 (4–5) whorls, basifixed to dorsifixed, introrse; pollen grains spheroidal, 3-nucleate, pantoporate, sexine with angular pillars; pistillode of 3 filiform processes atop the column. Pistillate flowers subsessile or pedicellate; sepals 5, distinct or connate, entire, deciduous in fruit; petals 0; disk annular, sometimes with staminodia; ovary 3-locular, often with urticant hairs; ovules anatropous, inner integuments thick, vascularized; stylodia distinct or nearly so, multifid (bifid). Fruits capsular or less often fleshy and tardily dehiscent; columella slender, persistent. Seeds carunculate, testa smooth. $2n = 36$.

About 70 spp. in the Neotropics. McVaugh (1944) recognized 5 sections that have not yet been evaluated by a phylogenetic analysis. Speciation has been most pronounced in Mexico; Breckon (1975) revised sect. *Calyptosolen* and recognized 20 species in Mexico and Central America.

5. Tribe Micrandreae (Müll. Arg.) G.L. Webster (1975).

Monoecious or dioecious; stems with inarticulated laticifers and usually whitish latex; indumentum simple or stellate; leaves unlobed, entire; disk dissected, lobed, or 0; pollen grains 3-nucleate, 3-colpate, colpi operculate; inner integument thick, vascularized.

This tribe resembles various taxa of subfam. Acalyphoideae; *Micrandra* in particular shows many acalyphoid characters, resembling Cheiloseae in its androecium and Alchorneae in its operculate pollen grains.

Key to the Genera of Micrandreae

1. Sepals connate; staminate disk 0; stamens 8–10; floral bracts large **204. *Cunuria***
– Sepals distinct; staminate disk +; stamens 5–8; floral bracts small 2
2. Indumentum simple; anthers elliptical; pollen muri smooth **203. *Micrandra***
– Indumentum stellate; anthers linear; pollen muri irregularly appendaged **205. *Micrandropsis***

203. *Micrandra* Benth.

Micrandra Benth., Hook. Kew J. Bot. 6: 371 (1854; nom. cons.); Schultes, Bot. Mus. Leafl. 15: 201, t. 66–73 (1952); Webster, Ann.. Missouri Bot. Gard. 81: 98 (1994); Radcl.-Smith, Gen. Euphorb.: 268 (2001); Berry & Wiedenhoeft, Syst. Bot. 29: 125–133 (2004).

Monoecious trees, often buttressed or with stilt roots at base; laticifers non-articulated; latex copious, white; indumentum simple. Leaves eglandular at base [except *M. elata*]; stipules mostly deciduous. Inflorescences terminal on principal and lateral shoots, pedunculate; staminate flowers in glomerules, pistillate solitary at tips of lateral axes; bracts entire, eglandular, deciduous. Staminate flowers subsessile or pedicellate; sepals 5, valvate or slightly imbricate; petals 0; disk-segments 5; stamens usually 4 or 5, filaments distinct, apically inflexed in bud; anthers subglobose, dehiscing laterally; pollen grains spheroidal, 3-colpate, colpi operculate, sexine [except in *M. elata*] tectate-reticulate, with smooth muri; pistillode much shorter than filaments or obsolete. Pistillate flowers subsessile; sepals 5, entire, distinct, deciduous; petals 0; disk annular; ovary 3-locular, sericeous, ± beaked; ovules anatropous, inner integument thick, vascularized; stylodia distinct, bifid. Fruits capsular; columella slender, subpersistent. Seeds large, > 1 cm long, ecarunculate or with rudimentary caruncle, testa smooth.

Five or six neotropical spp. from lowland Amazonian forests; following Webster (1994) and in contrast to Govaerts et al. (2000) and Berry and Wiedenhoeft (2004), *Micrandra* is here delimited to exclude *Cunuria*. Even in this limited sense, it is heterogeneous: *M. siphonioides* Benth. and *M. minor* Benth. have 3-colpate operculate pollen grains with tectate-reticulate exine very suggestive of pollen grains in the

Acalyphoideae, but *M. elata* has pollen grains with Crotonoid ornamentation distinct from all other Micrandrinae. *M. inundata* P.E. Berry & A.C. Wiedenhoeft is known from the banks of seasonally flooded blackwater rivers in southwestern Venezuela; its trunks consist of very lightweight wood.

204. *Cunuria* Baill.

Cunuria Baill., Adansonia I, 4: 287 (1864); Baldwin & Schultes, Bot. Mus. Harvard Univ. 12: 325, t. 42–46 (1947); Webster, Ann. Missouri Bot. Gard. 81: 98 (1994); Radcl.-Sm., Gen. Euphorb.: 270 (2001).

Monoecious or dioecious trees; laticifers non-articulated, latex white or yellow; indumentum simple. Leaves biglandular at basal juncture with petiole; stipules deciduous. Inflorescences terminal or axillary, pedunculate, dichasially paniculate; staminate flowers in glomerules, pistillate solitary, terminal on axes; bracts entire, eglandular, deciduous. Staminate flowers sessile or subsessile; sepals 5, distinct, imbricate; petals and disk 0; stamens 7–10, distinct; anthers dorsifixed, muticous; pollen grains spheroidal, 3-colpate, colpi operculate, sexine with raised muri and usually regular or irregular processes; pistillode trifid. Pistillate flowers subsessile; sepals 5, imbricate, entire, deciduous; disk cupular or annular, sometimes lobed; ovary 3-locular, glabrous or pubescent; stylodia bifid, branches thickened. Fruits capsular. Seeds ecarunculate; testa smooth and shiny.

Six neotropical spp. This genus was generally accepted by botanists until Schultes (1952) decided to combine it with *Micrandra*, in which he is followed by Berry and Wiedenhoeft (2004). However, if *Micrandra elata* is transferred to *Cunuria*, the remainder of the *Micrandra* species differ from *Cunuria* in having leaf blades without basal glands and very different pollen ornamentation.

205. *Micrandropsis* W.A. Rodrigues

Micrandropsis W.A. Rodrigues, Acta Amazonica 3(2): 5 (1973); Webster, Ann. Missouri Bot. Gard. 81: 98 (1994); Murillo & Franco, Euphorb. Reg. Araracuara 117, fig. 119 (1995); Radcl.-Sm., Gen. Euphorb.: 270, fig. 37 (2001).

Monoecious trees; latex scanty; indumentum minute, stellate. Leaves with 1 or 2 sessile glands at juncture with petiole. Inflorescences terminal on principal and lateral axes, pedunculate, staminate flowers in few-flowered dichasia, pistillate flowers solitary; bracts glandular or eglandular. Staminate flowers subsessile; sepals 5, distinct, imbricate; disk 5-lobed; stamens 5(−7), filaments distinct; anthers linear; pollen grains spheroidal, 3-colpate, tectate-reticulate with irregularly spinose muri; pistillode 0. Pistillate flowers subsessile; sepals 5, distinct, entire, deciduous in fruit; disk annular, tenuous; ovary 3-locular, sericeous. Fruits capsular, valves rugose; seeds carunculate.

A single sp., *M. scleroxylon* (W.A. Rodrigues) W.A. Rodrigues from the lowland rainforest in the vicinity of Manaus, Amazonas, Brazil, but later reported from Amazonian Colombia by Murillo & Franco (1995). The pollen grains of *Micrandropsis* are quite distinct from both *Micrandra* and *Cunuria* in their unique irregularly ornamented muri.

6. Tribe Heveeae (Müll. Arg.) G.L. Webster, stat. nov.[1]

Monoecious; leaves palmately compound; inflorescence with terminal pistillate flower; staminate sepals connate, valvate; stamen filaments connate into a column; pollen grains 3-colpate, colpi operculate, sexine tectate-baculate.

In Webster (1994), *Hevea* was assigned to subtribe Heveinae in the Micrandreae. However, *Hevea* differs from the Micrandreae in a number of characters, such as its articulated laticifers, gamophyllous calyx, connate stamens, very fine pollen exine ornamentation, and palmately compound leaves. It appears that *Hevea* has more in common with the Manihoteae, despite differences in pollen apertures.

206. *Hevea* Aubl. Fig. 38

Hevea Aubl., Hist. Pl. Guiane Fr. 2: 871, t. 335 (1775); Ducke, Arch. Inst. Biol. Veg. Rio Janeiro 2: 217 (1935); Schultes, Bot. Mus. Leafl. Harvard Univ. 25: 243, t. 51, 52 (1977); Bot. Review 36: 197 (1970); Malaysian Rubber Res. Dev. Board Mon. 14: 5 (1990); Murillo & Franco, Euforb. Reg. Araracuara 78, figs. 17, 18 (1995); Hoang Van Sam & van Welzen, Blumea 49: 427–435 (2004).

Monoecious trees; laticifers articulated, latex whitish; indumentum simple. Leaves palmately compound, with 1–3 raised glands at apex of petiole, leaflets entire; stipules entire, deciduous.

[1] Tribus **Heveeae** (Müll. Arg.) G.L. Webster, **stat. nov.** Basionym: Subtribus Heveinae Müller Argoviensis, Linnaea 34: 202 (1865). Type: *Hevea* Aubl.

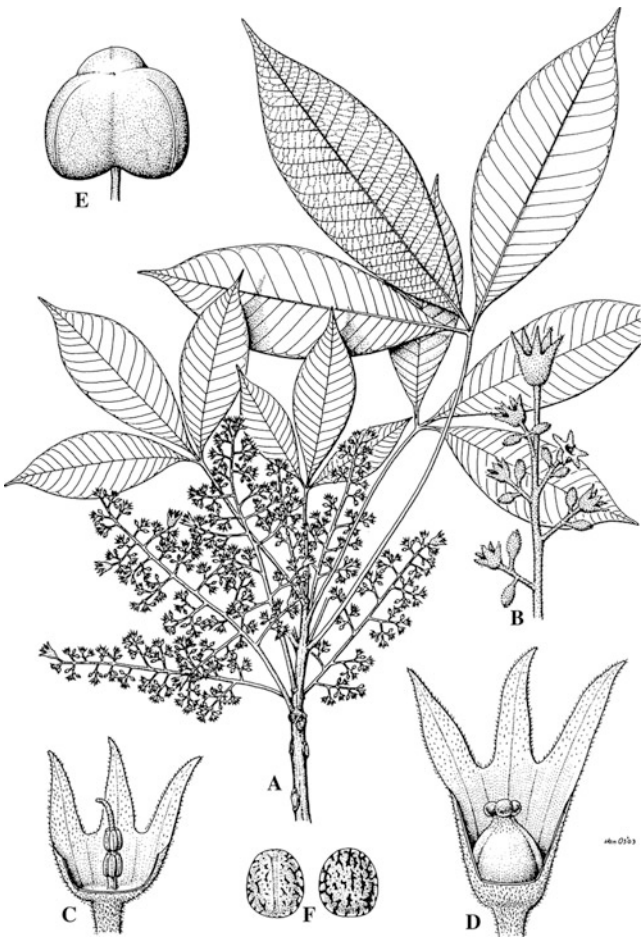

Fig. 38. Euphorbiaceae-Crotonoideae. *Hevea brasiliensis*. **A** Flowering branchlet. **B** Part of inflorescence with a large terminal pistillate flower and smaller staminate flowers. **C** Staminate flower, part of calyx removed. **D** Pistillate flower, part of calyx removed. **E** Fruit. **F** Seed, ventral and dorsal view. (Hoang Van Sam and van Welzen 2004; drawn by J. van Os)

Inflorescences axillary, paniculate with dichasial subunits, the pistillate flowers solitary and terminal on lateral axes; bracts small, entire, deciduous. Staminate flowers pedicellate; sepals connate with valvate lobed; disk segments distinct or connate; stamens 6–9 (10) in 2 irregular whorls; anthers sessile; pollen grains 3-colpate, colpi inoperculate, sexine tectate-reticulate, muri hexagonal or pentagonal, with rounded or angular projections; pistillode represented by terminal appendage of staminal column. Pistillate flowers pedicellate, sepals 5, connate, deciduous in fruit; disk rudimentary or 0; ovary 3-locular; ovules anatropous, inner integuments thick, vascularized; stylodia basally connate, stigmatiform. Fruits capsular; columella fragile, semipersistent. Seeds ellipsoid, smooth, ecarunculate; endosperm oily. $n = 18$.

According to Schultes (1970), *Hevea* includes nine spp. with a total of five varieties that are essentially confined to the Amazon basin, although *Hevea brasiliensis* (A. Juss.) Müll. Arg. is widely cultivated circumtropically. In its compound leaves and connate sepals and stamens, *Hevea* is distinct from the taxa of tribe Micrandreae; however, the pollen grains show some similarities to species such as *Micrandra lopezii*.

Unplaced genus with a strong affinity to the articulated crotonoids:

207. *Glycydendron* Ducke

Glycydendron Ducke, Arq. Jard. Bot. Rio Janeiro 3: 199 (1922), 4: 107, t. 10 figs. a–i (1925); Pax & K. Hoffm., Nat. Pflanzenfam. ed. 2, 19c: 181 (1931, as *Glycynodendron*); Webster, Ann. Missouri Bot. Gard. 81: 100 (1994); Vásquez Martínez, Fl. Res. Biol. Iquitos, Peru: 287, t. 35A (1997); Radcl.-Sm., Gen. Euphorb.: 277 (2001).

Dioecious trees; latex whitish, translucent; indumentum simple. Leaves long-petiolate, deciduous before flowering, simple, entire, triplinerved, with paired adaxial excavated basal glands; stipules minute, deciduous. Inflorescences axillary, staminate also subterminal, sometimes fasciculate, the staminate cymose-paniculate, pistillate racemose; bracts minute, eglandular. Staminate flowers pedicellate; sepals 4, distinct, imbricate; petals 0; disk glands intrastaminal on the pilose receptacle; stamens 25–30, filaments distinct; anthers introrse, basifixed, muticous; pollen grains oblate, 3-colpate, sexine tectate with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 4, imbricate, distinct, entire, deciduous; petals 0; disk annular with staminodia; ovary 2-locular, sericeous; ovules anatropous, inner integuments 8–10 cells thick, vascularized; stylodia distinct, bipartite. Fruits drupaceous, 1-seeded, endocarp woody. Seeds ecarunculate.

Probably monotypic, *G. amazonicum* Ducke appears to be common and widespread from Pará in eastern Brazil west to Ecuador, Peru, and Bolivia, with an outlying population in the mata atlántica of eastern Brazil (Espírito Santo). In the molecular analyses (Wurdack et al. 2005; Tokuoka 2007), it is resolved in the articulated crotonoids; in its larger stamen number and drupaceous fruit, it comes close to paleotropical *Elateriospermum*.

7. Tribe Jatropheae (Meisn.) Pax (1890).

Monoecious (dioecious); stems with articulated and/or non-articulated laticifers, the latex white or reddish; indumentum simple, sometimes glandular; leaves simple to deeply palmately lobed or compound; pollen grains spheroidal, binucleate, inaperturate, sexine with Croton pattern; inner integuments thick, vascularized.

Three genera, two of which are neotropical whereas one, *Jatropha*, is well developed in America and Africa and extends to Madagascar and Asia. Among the genera previously placed in this tribe, *Leeuwenbergia* safely belongs to the inaperturate crotonoid clade C2 with the large deletion in the *trn*L-F spacer (Wurdack et al. 2005), whereas molecular data for the Old World *Deutzianthus* and *Oligoceras* are lacking (provisionally placed in Aleuritideae-Grosserinae).

Key to the Genera of Jatropheae

1. Leaves simple, entire, elobate; stipules infra-axillary, deciduous; seeds ecarunculate **210. *Vaupesia***
– Leaves palmately lobed or palmately compound; stipules not infra-axillary or 0 2
2. Leaves 3- to more palmatilobed or -partite; sepals distinct, covering the petals in bud; fruit capsular; seeds carunculate **208. *Jatropha***
– Leaves compound; staminate calyx open in bud, not covering the petals; fruit drupaceous; seeds ecarunculate **209. *Joannesia***

208. *Jatropha* L.

Jatropha L., Sp. Pl.: 1006 (1753); Müll. Arg. in DC., Prodr. 15(2): 1076 (1866); Pax, Pflanzenr. 147, I: 21 (1910); McVaugh, Bull. Torrey Bot. Club 72: 271, figs. 1–24 (1944); Webster, J. Arnold Arb. 48: 340 (1967); Dehgan & Webster, Univ. California Publ. Bot. 74: 35, t. 1–33 (1979); Radcliffe-Smith, Fl. Trop. E. Afr., Euphorb. 1: 343, figs. 65–67 (1987).

Monoecious (dioecious or gynodioecious) trees, shrubs, or herbs often with thickened caudices or rhizomes; stems with articulate, inarticulate, or idioblastic laticifers producing yellowish to red latex; indumentum simple, sometimes glandular. Leaves petiolate to subsessile, simple to palmately 3–7-lobed or divided, entire to serrate, lacking paired basal glands; stipules entire to dissected, sometimes glandular or spinose (obsolete). Inflorescences axillary to terminal, often long-pedunculate, of simple to paniculate cymes, sometimes solitary and axillary; pistillate flowers central in bisexual cymules. Staminate flowers pedicellate; sepals 5, imbricate, distinct to basally connate, entire to dentate, sometimes foliaceous; petals 5, distinct to coherent or connate; disk entire to lobed or dissected; stamens (6–)8–10 (−12), filaments distinct or connate; anthers mostly biseriate, dorsifixed; pollen grains spheroidal, binucleate, inaperturate, exine with Croton pattern, pillars rounded or angular, smooth or sulcate; pistillode 0. Pistillate flowers pedicellate; sepals 5, nearly distinct, imbricate, entire or dentate, persistent in fruit; petals 5, distinct to coherent or connate, imbricate; disk annular or deeply lobed; ovary (1–)3-locular, glabrous or pubescent; ovules anatropous, inner integuments thick, vascularized; stylodia bifid, sometimes dilated (multifid). Fruits capsular, sometimes with fleshy exocarp and tardily dehiscent, (1–)3-seeded; columella generally not persistent. Seeds ellipsoidal to spherical, carunculate; testa thin and smooth; endosperm oily; cotyledons much longer and broader than radicle. $2n = 22$.

Over 180 spp., widely distributed in the tropics and subtropics of America and Africa, rare in Madagascar and Asia. The circumscription of *Jatropha* in the 19th and early 20th century was confused due to the mistaken inclusion of *Cnidoscolus* by Müller (1866) and Pax (1910), but McVaugh (1944) demonstrated that the two genera are not closely related.

209. *Joannesia* Vell.

Joannesia Vell., Alogr. Alkalis: 199 (1798); Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 198, t. 21 (1922); Schultes, Bot. Mus. Leafl. Harvard Univ. 17: 25 (1955); Radcl.-Sm., Gen. Euphorb.: 292 (2001).

Monoecious trees; laticifers non-articulate, branches sometimes with viscid reddish latex; indumentum simple. Leaves palmately compound; leaflets entire; petioles with 2 apical glands; stipules gland-tipped or obsolete. Inflorescences terminal or subterminal, bisexual, cymose-paniculate; bracts entire, deciduous. Staminate flowers pedicellate; calyx cupular-truncate, the 5 sepals represented by minute teeth; petals 5, distinct, imbricate, much longer than calyx, pubescent on both faces; disk segments 5; stamens 7–10, filaments biseriate, the inner longer; anthers basifixed-cordate, introrse or latrorse; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode usually 0. Pistillate flowers subsessile, calyx and petals as

in the staminate; disk dissected into 5 segments; ovary 2-locular, pubescent; ovules anatropous, inner integuments thick, vascularized; stylodia short, stigmas lobate. Fruits drupaceous or subdehiscent, verrucose, exocarp 1 cm thick. Seeds ecarunculate, endosperm oleaginous.

Three neotropical spp., from Venezuela and Amazonian and coastal Brazil.

210. *Vaupesia* R.E. Schultes

Vaupesia R.E. Schultes, Bot. Mus. Leafl. Harvard Univ. 17: 27, t. 12 (1955); Murillo & Franco, Euforb. Reg. Araracuara 158, fig. 48 (1995); Radcliffe-Smith, Gen. Euphorb.: 290 (2001).

Monoecious trees; latex of trunk whitish, scanty, of branches reddish. Leaves with conspicuous basal glands; stipules deciduous. Inflorescences terminal, bisexual, paniculate; bracts entire, persistent. Staminate flowers pedicellate; sepals 5, imbricate, entire; petals 5, entire; disk segments 5, at base of staminal column; stamens 8, filaments connate into a column; anthers biseriate; pollen grains spheroidal, inaperturate, exine with hexagonal pillars; pistillode 0. Pistillate flowers pedicellate; sepals 5, distinct, imbricate, margins fimbriate; petals 5, entire; disk 5-lobed, reddish; ovary 3-locular; stylodia proximally connate, bifid. Fruits capsular, thick-walled; columella not persistent. Seeds ecarunculate, subprolate, compressed, dorsally carinate, with conspicuous hilum.

One sp., *V. cataractarum* R.E. Schultes, from the upper Rio Negro region in SE Colombia and adjacent Brazil.

8. Tribe Crotoneae Dumort. (1829).

Monoecious (dioecious) trees, shrubs, or herbs; laticifers non-articulated, latex clear to yellowish or reddish, sometimes 0; indumentum simple, lepidote, or stellate; leaves simple to palmately lobed with or without basal paired glands; stamens 3–400; anthers extrorse; pollen grains trinucleate, spheroidal, inaperturate, with Croton pattern; ovules with thick vascularized inner integuments; stylodia distinct or basally connate, bifid to multifid; seeds mostly carunculate; cotyledons mostly broader than radicle.

Following the molecular work of Berry et al. (2005) and Wurdack et al. (2005), tribe Crotoneae is here construed to comprise several genera that formerly were included in tribe Codiaeae (*Sagotia*, *Acidocroton* with *Ophellanthe*) and tribe Aleuritideae (*Sandwithia*). The close relationship between *Sagotia* and *Sandwithia* had first been recognized by Secco (1988).

Key to the Genera of Crotoneae

1. Indumentum simple 2
– Indumentum stellate and/or lepidote 4
2. Inflorescences axillary; stipules transformed into spines **213. *Acidocroton***
– Inflorescences mostly terminal; stipules not transformed into spines 3
3. Staminate sepals 2–3, completely connate in bud; disk +; stylodia connate into a common style with distal bifid or entire style branches **211. *Sandwithia***
– Staminate sepals 5(6), distinct; disk 0; stylodia distinct or nearly so, bifid **212. *Sagotia***
4. Stamen filaments not inflexed in bud; stylodia deeply bifid **215. *Brasiliocroton***
– Stamen filaments distinctly inflexed in bud; stylodia bifid to multifid 5
5. Stamens (3)8–20(−400); receptacle usually pilose; seeds terete to compressed; stylodia various **216. *Croton***
– Stamens 8–15; receptacle usually glabrous; seeds quadrangular; stylodia multifid **214. *Astraea***

211. *Sandwithia* Lanj.

Sandwithia Lanj., Kew Bull. 1932: 184 (1933); Jablonski, Mem. N. Y. Bot. Gard. 17: 152 (1967); Secco, Bull. Mus. Par. Emilio Goeldi Bot. 3: 157 (1987), 4: 177 (1988); Fl. Venez. Guayana 5: 217, fig. 203 (1999).

Monoecious or dioecious trees; latex reddish; indumentum simple. Leaves alternate, petiolate (slightly pulvinate at apex), entire, eglandular; stipules deciduous. Inflorescences terminal, flowers in cymose racemes or clusters; bracts deciduous. Staminate flowers pedicellate; sepals 2 or 3, completely connate in bud; petals 3 or 4, distinct, imbricate, s.t. reduced; disk segments 2–4, receptacle pilose; stamens 15–25, filaments distinct; pollen grains spheroidal, inaperturate, exine granular, with Croton pattern, pillars smooth; pistillode 0. Pistillate flowers pedicellate; sepals 4, ± connate, tips imbricate in bud, erect; petals 4, minute, deciduous; disk annular; ovary 3-locular, pilose; stylodia connate into a common style with bifid or entire style branches. Fruits capsular; columella not persistent? Seeds carunculate, testa smooth.

Two spp., Amazonian South America.

212. *Sagotia* Baill.

Sagotia Baill., Adansonia I, 1: 53 (1860; nom. cons.); Jablonski, Mem. N. Y. Bot. Gard. 17: 151 (1967); Secco, Acta Amazonica 15 (1–2, suppl.): 81 (1985); Rev. Gen. *Anomalocalyx*, etc.: 99, figs. 29–34 (1990); Webster, Ann. Missouri Bot. Gard. 81: 107 (1994).

Monoecious trees or shrubs; latex clear, yellowish, or reddish; indumentum simple. Leaves petiolate (pulvinate), entire, eglandular; stipules deciduous, leaving annular scars. Inflorescences terminal, racemoid or thyrsoid-paniculate, unisexual or bisexual; pistillate flowers proximal; bracts deciduous. Staminate flowers pedicellate; sepals 5 (6), distinct, imbricate; petals 5 (7), distinct, imbricate, longer than the sepals; disk not evident; stamens 20–30, filaments distinct; anthers subsessile, basifixed, latrorse, connective broad; pollen grains spheroidal, inaperturate, exine granular, with Croton pattern, pillars acute or spinose; pistillode 0. Pistillate flowers pedicellate; sepals 5 (6), distinct, recurved, persistent and accrescent in fruit; petals and disk 0; ovary 3-locular, pilose; ovules pachychalazal, inner integuments thick, vascularized; stylodia distinct or early so, bifid. Fruits capsular; columella not persistent. Seeds ellipsoidal, carunculate, testa smooth.

Two spp., Central America and northern South America, in lowland rainforest.

213. *Acidocroton* Griseb.

Acidocroton Griseb., Fl. Br. W. Ind.: 42 (1859; nom. cons.); Müll. Arg. in DC., Prodr. 15(2): 1042 (1866); Pax, Pflanzenr. 147, I: 13 (1910); Urban, Symb. Ant. 7: 513 (1913); Fawc. & Rend., Fl. Jam. 4: 315, fig. 104 (1920); Alain, Fl. Cuba 3: 73 (1953), Fl. Española 4: 69 (1986); Webster, Ann. Missouri Bot. Gard. 81: 107 (1994); Fernández-Alonso & Jaramillo-Mejía, Caldasia 17: 389 (1995); Radcl.-Sm., Gen. Euphorb.: 303 (2001).
Ophellantha Standl. (1924).

Monoecious shrubs; latex not recorded; indumentum simple. Leaves petiolate to subsessile, entire, eglandular; stipules transformed into spines. Inflorescences unisexual, axillary and glomerular or pistillate flowers solitary and subterminal. Staminate flowers pedicellate; sepals 5–6, imbricate; petals 5–7, distinct, imbricate, glabrous, longer than the sepals; disk annular, pubescent; stamens 20–50(−100), filaments distinct; anthers introrse, with enlarged apiculate connective; pollen grains spheroidal, inaperturate, with Croton pattern; pistillode obsolete. Pistillate flowers pedicellate; sepals 5 or 6, ± imbricate, persistent in fruit and sometimes accrescent; petals rudimentary; ovary 3-locular, glabrous or pubescent; ovules anatropous, inner integuments thick, vascularized; stylodia unlobed or bifid, ± dilated and petaloid. Fruits capsular; sepals 5 or 6, distinct, imbricate, entire, persistent in fruit; columella persistent in fruit. Seeds trigonous, carunculate, testa smooth.

Thirteen spp., of which ten in sect. *Acidocroton* are confined to the West Indies, whereas the three of sect. *Ophellantha* occur from Mexico to Colombia. Radcliffe-Smith (2001) rejects the combining of *Ophellantha* with *Acidocroton* by Webster (1994). However, Radcliffe-Smith's characters based on higher stamen number and lower carpel number in *Ophellantha* do not hold, and the only remaining distinction is in the bifid stylodia and somewhat more accrescent pistillate sepals of *Ophellantha*. *Acidocroton* and *Ophellantha* form a monophyletic group (Berry et al. 2005), and there is little to gain in generic subdivision.

214. *Astraea* Klotzsch

Astraea Klotzsch, Arch. Naturgesch. 7: 194 (1841); Baill., Étude Gén. Euphorb.: 363 (1858, as section); Caruzo & Cordeiro, Hoehnea 34: 572 (2007); Cavalari De-Paula et al., Pl. Syst. Evol. 292: 1–14 (2011), floral morph.

Monoecious subshrubs or herbs; indumentum stellate; laticifers non-articulated, latex scanty or apparently 0. Leaves deeply palmately lobed (simple); stipules entire or dissected, sometimes glandular, persistent. Inflorescences terminal, bisexual, racemoid; pistillate flowers solitary at proximal nodes; bracts entire, persistent, eglandular. Staminate flowers pedicellate; sepals 5, imbricate; petals 5, imbricate, densely pilose at the basis; receptacle glabrous; disk 5-lobate; stamens 8–15, distinct; filaments glabrous, inflexed in bud; anthers basifixed, muticous; pollen grains spheroidal, with Croton pattern; pistillode 0. Pistillate flowers subsessile, elongating in fruit; sepals 5, valvate, ± glandular-dentate; disk segments 5; ovary glabrous or hispidulous with stellate or simple hairs; stylodia distinct, multifid. Fruits capsular; columella persistent. Seeds quadrangular, rugose, carunculate, caruncle reniform-peltate, testa rugulose-costate. $2n = 18$.

About 10 spp. in the Neotropics. This genus has been treated as a section of *Croton* by

nearly all 20th century authors. Webster (1967) remarked that *Astraea* had the best claim of any *Croton* section to generic status, and molecular studies (Berry et al. 2005) have resoled *Astraea* as the sister group of *Acidocroton* in the grade leading from *Jatropha* to *Croton* s.str.

215. *Brasiliocroton* P.E. Berry & I. Cordeiro

Brasiliocroton P.E. Berry & I. Cordeiro, Syst. Bot. 30: 357, fig. 2 (2005).

Monoecious tree; indumentum stellate. Leaves with two stipitate glands at the junction with the petiole; stipules filiform, deciduous. Inflorescences terminal bisexual panicles, the distal flowers pistillate and opening earliest. Staminate flowers: sepals 5(6), valvate, slightly connate at base; petals 5(6); disk of 5 distinct antesepalous lobes; stamens (20–)25(−30); filaments erect in bud; anthers bilobed, latrorse; pollen inaperturate with Croton pattern, the subunits striate. Pistillate flowers: sepals 5(6), valvate, basally connate for 1/2 to 2/3 their length; petals 0; disk 5-lobate; ovary 3(4)-locular; ovule 1 per locule; stylodia 3, deeply bifid and basally connate into a short column. Fruits schizocarpic, the exocarp separating from the woody cocci; columella 8–12 mm long. Seeds ellipsoid, dorsally angled, with a small caruncle.

A single sp., *B. mamoninha* P.E. Berrry & I. Cordeiro, lowland forests in N and E Brazil.

216. *Croton* L. Fig. 39

Croton L., Sp. Pl. 2: 1004 (1753); Müll. Arg. in DC., Prodr. 15(2): 512 (1866); Ferguson, Rep. Missouri Bot. Gard. 12: 33, t. 4–31 (1901); Hutchinson, Fl. Trop. Afr. 6(1): 746 (1912); Gagnepain, Fl. Indochine 5: 256, figs. 28, 29 (1925); Leandri, Ann. Inst. Bot.-Geol. Colon. Marseille V, 7(1): 1 (1939); Webster, J. Arnold Arb. 48: 358, fig. 2 (1967); Leandri, Adansonia II, 10: 191 (1970); Liogier, Fl. Española 4: 108 (1986); Chakrabarty & Balakrishnan, Bull. Bot. Survey India 34: 1–88, figs. 1–16 (1992); Webster, Novon 2: 270 (1992), Taxon 42: 793 (1993); Ann. Missouri Bot. Gard. 81: 111 (1994), Fl. Nicaragua 1: 864–875 (2001), Contr. Univ. Michigan Herb. 23: 353, fig. 1 (2001); Martínez Gordillo, Contr. Herb. UNAM 2: 9 (1995); Berry, Fl. Venez. Guayana 5: 111, figs. 108–125 (1999); Radcl.-Sm., Gen. Euphorb.: 319 (2001); Berry et al., Amer. J. Bot. 92: 1520–1534 (2005) (mol. systematics); Forster, van Ee & Berry, Syst. Bot. 35: 151–167 (2010), mol. syst. sect. *Heptallon*; Riina et al., Syst. Bot. 34: 360–374 (2009), mol. syst. sect. *Cyclostigma*; Riina et al., Taxon 59: 1147–1160 (2010), mol. syst. sect. *Luntia*; van Ee et al., Taxon 60: 791–823 (2011), rev. class. of New World taxa.
Tridesmis Lour. (1790).

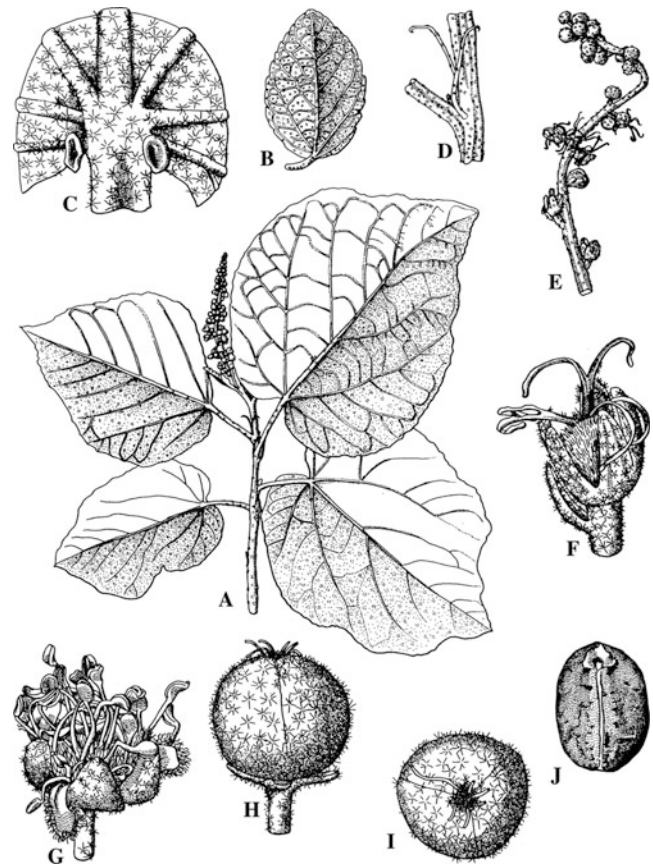

Fig. 39. Euphorbiaceae-Crotonoideae. *Croton arnhemicus*. **A** Flowering branchlet. **B** Undersurface of leaf. **C** Base of leaf lamina showing extrafloral nectaries. **D** Node with stipules. **E** Inflorescence with pistillate flowers in lower half and staminate flowers in upper. **F** Pistillate flower. **G** Staminate flower. **H, I** Fruits. **J** Seed. (P.I. Forster 2003; drawn by W. Smith)

Crotonopsis Michx. (1803).
Julocroton Mart. (1837, nom. cons.).
Eremocarpus Benth. (1844).
Colobocarpos Esser & van Welzen (2001).

Monoecious (dioecious) trees, shrubs, or herbs; laticifers non-articulated (0), latex clear to red or yellow, sometimes resinous; indumentum stellate or lepidote; sessile or stipitate glands sometimes present. Leaves alternate (opposite), simple or lobate, petiolate (sessile), entire, dentate or serrate, usually 2-glandular at the junction of the petiole with the blade; stipules entire or dentate to dissected, persistent or deciduous, sometimes 0. Inflorescences terminal (axillary), usually bisexual, mostly racemoid with solitary pistillate flowers at proximal nodes and

glomerules of staminate flowers distally, staminate flowers sometimes 1 per bract; bracts entire to dissected, sometimes glandular. Staminate flowers pedicellate; sepals (4) 5 (6), essentially distinct to connate, imbricate to valvate; petals usually 5(0), distinct, imbricate, glabrous or pubescent; disk entire or dissected; receptacle usually pilose (glabrous); stamens (3–)8–20 (−400), distinct, filaments usually inflexed in bud, glabrous or pubescent; anthers extrorse in bud; pollen grains spheroidal, inaperturate, exine with Croton pattern, pillars rounded or angular, mostly sulcate; pistillode 0. Pistillate flowers sessile to pedicellate; sepals (4)5–7 (−10), distinct to connate, imbricate, entire to dentate, usually persistent in fruit and often accrescent; petals 0 (+); disk annular (dissected), sometimes with staminodia [reduced petals?]; ovary 3(−1)-locular; ovules anatropous, inner integuments thick, vascularized; stylodia distinct or basally connate, bifid to multifid. Fruits capsular (indehiscent); columella persistent, usually slender. Seeds terete to compressed, carunculate (arillate), testa smooth. $2n = 20, 28, 64$.

Over 1,200 spp., circumglobal in warm-temperate to tropical regions, 712 spp. recognized for the New World. *Croton* is the second largest genus of Euphorbiaceae and is highly diverse morphologically and cytologically. Not surprisingly, many generic segregates had been proposed in the past but have been brought back to *Croton* again, and those upheld until recently (*Crotonopsis*, *Eremocarpus*, *Julocroton*, *Moacroton*) have been reduced on the basis of extensive molecular studies. There is also evidence pointing to a New World origin of *Croton*, with a subsequent divergence in the Old World, followed, back in the New World, by the principal morphological diversification of the genus (Berry et al. 2005).

Two subgenera:

216a. *Croton* subg. *Croton*

Indumentum mostly stellate; stylodia usually multifid; sepals of pistillate flowers usually valvate.

Contains the bulk of the *Croton* species, which generally show a preference for xeric habitats.

216b. *Croton* subg. *Moacroton* (Croizat) van Ee & P.E. Berry, Bot. Rev. 74: 158 (2008).

Moacroton Croizat (1945); Borhidi, Acta Bot. Acad. Sci. Hung. 36: 7 (1990), rev.
Cubacroton Alain (1960).
Croton sect. *Corylocroton* G.L. Webster (1993).

Indumentum usually lepidote; stylodia bifid or simple; sepals of pistillate flowers usually connate at the base but not valvate.

About 28 or more spp., distributed in North America, Mesoamerica, the Caribbean, and South America, where they generally show a preference for mesic habitats. In addition to the taxa synonymized above, the group comprises a number of South American species of *Croton* hitherto not assigned to a section; they have been revealed as a basal clade of *Croton* by van Ee et al. (2008). The six spp. formerly included in *Moacroton* are endemic to Cuba, where they grow on serpentine outcrops.

9. Tribe Codiaeae (Pax) Hutch. (1969).

Monoecious or dioecious trees or shrubs; laticifers non-articulated, latex clear or sometimes reddish; indumentum simple or malpighiaceous; leaves alternate, pinnately veined or triplinerved, usually without laminar glands; stipules deciduous or obsolete; inflorescences terminal or axillary, racemoid-thyrsoid or paniculate; staminate sepals 4–6, distinct or connate, imbricate or valvate; petals 5, distinct, usually imbricate; disk dissected or lobed; stamens (5–)10–100 or more, distinct or basally connate; pollen grains binucleate, spheroidal, inaperturate, exine with Croton pattern; pistillode 0; pistillate sepals 4 or 5, usually imbricate, sometimes accrescent; disk mostly annular; ovary mostly 3-locular; ovules anatropous, inner integuments thick, vascularized; stylodia unlobed to bipartite; fruits capsular; columella usually persistent; seeds carunculate or ecarunculate, testa sometimes fleshy; endosperm present.

This pantropical but predominantly Asiatic tribe shows the greatest generic diversity in the Crotonoideae. Further study since the treatment of Webster (1994) has led to the recognition of four subtribes. The geographic distribution of the Codiaeae is distinctive in its primarily South American/Asian concentration (10 genera), with a

secondary concentration in Australasia (4 genera), and a single genus (*Pantadenia*) disjunct from southeast Asia to Madagascar; continental Africa is entirely excluded. The treatment of the neotropical taxa adopted here is indebted to the careful work of Secco (1990) on the Amazonian taxa of Codiaeae.

Key to the Subtribes of Codiaeae

1. Petals 0 or rudimentary in pistillate flowers **9d. Codiaeinae**
– Petals well-developed in pistillate flowers 2
2. Stamens 3 (5), filaments all connate into a column **9a. Trigonostemoninae**
– Stamens 7 or more, filaments not all connate into a column 3
3. Inflorescences mostly terminal; monoecious (except *Hylandia*); anthers extrorse; seeds carunculate or fruit drupaceous **9b. Baloghiinae**
– Inflorescences mostly axillary; anthers mostly introrse; seeds ecarunculate, fruits capsular **9c. Ostodeinae**

9a. Subtribe Trigonostemoninae (G.L. Webster) G.L. Webster[1]

Monoecious; latex reddish; indumentum simple; anthers with enlarged connective; stylodia bifid or twice bifid; fruits capsular. Seeds ecarunculate.

A monogeneric paleotropical subtribe with nearly 100 species. In the molecular analysis (Wurdack et al. 2005), *Trigonostemon* is resolved as the sister group to the rest of the genera forming clade C2.

217. *Trigonostemon* Blume

Trigonostemon Blume, Bijdr. Fl. Ned. Ind. 600 (1825; nom. cons.); Müll. Arg. in DC. Prodr. 15(2): 1105 (1866); Pax & K. Hoffm., Pflanzenr. 147, III: 85 (1911); Gagnepain, Fl. Indochine 5: 309, fig. 35, 3–10 (1925); Airy Shaw, Kew Bull. Add. Ser. 4: 201 (1975), Kew Bull. 35: 352 (1981); Webster, Ann. Missouri Bot. Gard. 81: 108 (1994); Milne, Kew Bull. 50: 23, figs. 1–3 (1995); Radcl.-Sm., Gen. Euphorb.: 307 (2001).
Kurziodendron Balakr. (1966).

Monoecious shrubs or trees; reddish latex sometimes present; indumentum simple. Leaves alternate or opposite, entire, without paired basal glands; stipules entire, ± persistent, sometimes minute. Inflorescences terminal or axillary, usually bisexual, racemoid; bracts entire, eglandular, usually persistent. Staminate flowers pedicellate; sepals 5, distinct, imbricate; petals 5, yellow to orange or red, distinct, imbricate, usually longer than calyx; disk dissected or urceolate; stamens 3 (5), filaments connate into a column; anthers extrorse, basifixed, connective enlarged and often apiculate or bifid; pollen grains spheroidal, inaperturate, exine with Croton pattern, pillars spinulose; pistillode 0. Pistillate flowers pedicellate; sepals 5, imbricate, entire, persistent in fruit, sometimes accrescent; petals 5, yellow to orange or red, distinct, imbricate, mostly glabrous; disk annular or 5-lobed; ovary 3-locular, glabrous or pubescent; stylodia distinct or nearly so, unlobed to bifid or bipartite. Fruits capsular, cocci thin-walled; columella not persistent. Seeds ecarunculate, testa smooth.

Nearly 100 spp., distributed from India and China south and east to the Philippines, northern Australia (Queensland), New Guinea, and Fiji.

9b. Subtribe Baloghiinae G.L. Webster[1]

Dioecious (monoecious); basal laminar glands present or 0; inflorescences terminal or subterminal; pistillate flowers petaliferous; petals longer than sepals; ovary often pubescent; columella usually persistent.

Four Australasian genera. The subtribe is possibly related to subtribe Cocconerioninae in the Ricinocarpeae.

Key to the Genera of Baloghiinae

1. Indumentum stellate; inflorescences covered with resin **221. *Alphandia***
– Indumentum mainly simple; inflorescences not resinous 2
2. Staminate calyx truncate; fruits drupaceous **220. *Fontainea***
– Staminate calyx distinctly lobed; fruits capsular 3
3. Ovary 3-locular; petals glabrous adaxially **218. *Baloghia***

[1] Subtr. **Trigonostemoninae** (G.L. Webster) G.L. Webster, **stat. nov.**, based on Tribe Trigonostemoneae G.L. Webster, Taxon 24: 599 (1975). Type: *Trigonostemon* Blume.

[1] Subtr. **Baloghiinae** G.L. Webster, **subtr. nov.**: plantae dioicae inflorescentiis terminalibus, staminibus 10–100, liberis, antheris extrorsis, seminibus carunculatis vel ecarunculatis. Type: *Baloghia* Endlicher.

– Ovary 2-locular; petals sericeous abaxially
219. *Hylandia*

218. *Baloghia* Endl.

Baloghia Endl., Prodr. Fl. Norf.: 84 (1833); Airy Shaw, Kew Bull. 35: 598 (1980); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 43–72, t. 8–13 (1987); Hyland & Whiffin, Austral. Trop. Rain For. Trees 2: 119 (1993).

Monoecious or dioecious trees or shrubs; laticifers non-articulated, latex yellowish to reddish; indumentum simple or 0. Leaves alternate (opposite), pinnately veined, brochidodromous, basal laminar glands mostly 0 [+ on margins near base]; stipules 0. Inflorescences terminal, thyrsoid, unisexual; bracts entire, persistent, uniflorous. Staminate flowers pedicellate; sepals (4)5(6), slightly connate at base, imbricate; petals (4)5(6), white, distinct, usually longer than sepals; disk annular or dissected (0); stamens (10–)40–50(−100), distinct or connate on a ± convex receptacle; anthers dorsifixed, extrorse; pollen grains spheroidal, inaperturate, sexine with Croton pattern, pillars obtuse and slightly sulcate; pistillode 0. Pistillate flowers pedicellate; sepals (4)5(6), imbricate, entire, persistent in fruit; petals (4)5(6), pubescent adaxially; disk annular, sometimes lobed; ovary 3(4)-locular, sericeous; ovules anatropous, inner integuments very thick, vascularized; stylodia bifid to multifid. Fruits capsular; columella persistent. Seeds spheroidal or ellipsoidal, mostly carunculate, testa smooth, exotesta parenchymatous.

Fifteen spp., Australasia, 12 of them endemic to New Caledonia.

219. *Hylandia* Airy Shaw

Hylandia Airy Shaw, Kew Bull. 29: 329 (1974); ibid. 35: 643, fig. 4 (1980); Hyland & Whiffin, Austral. Rain For. Trees 2: 140 (1993).

Dioecious trees; latex viscid, pith reddish; indumentum simple. Leaves with or without raised glands at junction with petiole; stipules 0. Inflorescences terminal, thyrsoid-paniculate; bracts not evident. Staminate flowers pedicellate; sepals 5, distinct, imbricate, unequal; petals 5, white, distinct, imbricate, obovate to spathulate, pubescent adaxially, appressed-sericeous abaxially; disk segments 5, massive, glabrous; stamens 10–16, filaments basally connate; anthers extrorse; pollen grains inaperturate, with Croton pattern; pistillode 0. Pistillate flowers with pedicel articulate near base; sepals 5, distinct, imbricate, entire; petals 5, distinct, whitish, pubescent adaxially and abaxially; disk of 5 lobes or segments; ovary 2-locular, densely hispid-sericeous; stylodia bifid, branches somewhat dilated. Fruits indehiscent, ribbed, exocarp somewhat fleshy. Seeds spheroidal, apparently ecarunculate, testa hard, smooth.

A single sp., *H. dockrillii* Airy Shaw, tropical rainforests of Queensland. *Hylandia* appears to be closely related to the more widely distributed genus *Baloghia*.

220. *Fontainea* Heckel

Fontainea Heckel, Études sur *Fontainea pancheri* (1870); Baillon, Adansonia I, 11: 80 (1873); Airy Shaw, Kew Bull. 35: 632 (1980); Jessup & Guymer, Austrobaileya 2: 112–125, figs. 1–6 (1985); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 74–78 (1987); Forster, Austrobaileya 5: 29–37, figs. 1–3 (1997); Forster & van Welzen, Blumea 44: 101, fig. 2 (1999).

Dioecious (monoecious) trees or shrubs; latex reddish to brown; indumentum simple, scanty. Leaves alternate (opposite), usually with basal or subbasal marginal glands; stipules 0. Inflorescences terminal, sometimes axillary, compound cymose; bracts entire, inconspicuous. Staminate flowers pedicellate; sepals pubescent, connate into a shallowly 3–6-toothed or angled cup; petals 5, white, distinct, densely pubescent, exserted well beyond the calyx; disk obscure; receptacle densely woolly; stamens 18–32 (40), filaments distinct or basally connate; anthers dorsifixed, extrorse, connective sometimes apiculate; pollen grains spheroidal, inaperturate, exine with Croton pattern, pillars acute, sulcate; pistillode 0. Pistillate flowers pedicellate; sepals connate, dehiscing irregularly, deciduous in fruit; petals 5, white, distinct, exserted from calyx; disk annular, glabrous; ovary (2)3(−6)-locular, pubescent; ovules anatropous, inner integuments thick, vascularized; stylodia bifid. Fruits drupaceous; endocarp bony, angled, sometimes beaked, smooth or rugose. Seeds ecarunculate.

Nine or more spp., distributed from Australia to New Guinea, New Caledonia, and Vanuatu.

221. *Alphandia* Baill.

Alphandia Baill., Adansonia I, 11: 86 (1873); Pax, Pflanzenr. 147, III: 22 (1911); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 86–90, fig. 17 (1987); Airy Shaw, Kew Bull. Add. Ser. 8: 27 (1980).

Monoecious trees or shrubs; stems with yellowish or reddish resinous latex, branches and leaves with resinous exudate; indumentum stellate. Leaves with paired glands at base; stipules 0.

Inflorescences terminal or subterminal, unisexual or bisexual, thyrsoid-paniculate; bracts entire, eglandular. Staminate flowers pedicellate; sepals 5, connate, not closed in bud; petals 5, yellowish, distinct, imbricate, pubescent abaxially; disk segments 5, distinct or confluent; stamens 20–35, inner filaments connate at base, outer distinct, apically deflexed; anthers extrorse; pollen grains spheroidal, inaperturate, with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5, connate at base, not imbricate; petals 5, distinct, imbricate, deciduous; disk annular; ovary 3-locular, pubescent and resinous; ovules anatropous, inner integuments thick; stylodia bifid. Fruits capsular, thin-walled; columella persistent. Seeds oblong, apiculate, carunculate or ecarunculate; cotyledons much broader than radicle.

Three spp., Melanesia, 1 in New Guinea and 2 in New Caledonia/Vanuatu. Pax (1911) referred *Alphandia* to the Codiaeinae, where it could be placed except for the stellate indumentum. Although the stellate indumentum of *Alphandia* suggests a relationship with Ricinocarpeae subtribe Cocconeriinae, the pollen exine (Lobreau-Callen in McPherson and Tirel 1987) shows the typical Crotonoid sculpturing of the Baloghiinae and other Codieae, which is very different from the reduced sculpturing of the Cocconeriinae. It seems possible that *Alphandia* may provide a connecting link between the Baloghiinae and Cocconeriinae, and that these Australasian taxa may belong to a single clade.

9c. Subtribe Ostodeinae G.L. Webster[1]

Dioecious; leaves with or without basal paired glands or dispersed laminar glands; stamens 5–35, filaments distinct; anthers mostly introrse; stylodia bifid or multifid; seeds ecarunculate (except in *Pausandra*).

A heterogeneous subtribe of six genera, three paleotropical and three neotropical. *Pausandra* in particular appears aberrant and may prove not to belong to this subtribe.

Key to the Genera of Ostodeinae

1. Staminate calyx cupular, barely lobed; fruiting calyx accrescent **223. *Dimorphocalyx***
– Staminate calyx distinctly lobed; fruiting calyx not accrescent 2
2. Indumentum partly malpighiaceous; flowers subsessile, monoecious **227. *Pausandra***
– Indumentum simple; pistillate flowers distinctly pedicellate; seeds ecarunculate 3
3. Leaf blades dentate, with basal paired glands; anthers not glandular **222. *Ostodes***
– Leaf blades mostly entire, lacking basal paired glands 4
4. Anthers glandular; leaf blades with dispersed laminar glands, inflorescences leaf-opposed **226. *Pantadenia***
– Anthers not glandular; leaf blades with or without dispersed laminar glands; inflorescences terminal or axillary 5
5. Staminate and pistillate flowers externally glabrous; stamens 20+, inserted on convex receptacle; staminate disk and ovary glabrous; stylodia 6-branched **224. *Anomalocalyx***
– Staminate and pistillate flowers externally pilose; stamens 7–16, inserted on an almost plane receptacle; staminate disk pilose, ovary densely pilose; stylodia 10–12-branched **225. *Dodecastigma***

222. *Ostodes* Blume

Ostodes Blume, Bijdr.: 619 (1825); Müll. Arg. in DC. Prodr. 15(2): 1114 (1866); Gagnepain, Fl. Indochine 5: 322, fig. 33, 7–9 (1925); Airy Shaw, Kew Bull. 20: 409 (1967), 35: 334 (1981); Grierson & Long, Fl. Bhutan 1(3): 795, fig. 49 p–r (1987); Chakrabarty & Balakr., Bull. Bot. Surv. India 27: 259 (1987).

Dioecious trees; latex not recorded; indumentum simple. Leaves crenate-serrate, with 2 or more adaxial basal glands at junction with petiole; stipules gland-tipped, entire, deciduous. Inflorescences axillary, unisexual, the staminate thyrsoid, pistillate paniculate; bracts entire, eglandular, persistent. Staminate flowers pedicellate; sepals 5, connate, imbricate, glabrous; petals 5 or 6, white or pinkish, imbricate, concave, glabrous, longer than sepals; disk segments 8–12, massive, puberulent; stamens 30–35, filaments distinct, pilose; anthers dorsifixed, introrse; pollen grains spheroidal, inaperturate, with Croton pattern, pillars rounded; pistillode 0. Pistillate flowers pedicellate, articulate near base; sepals 5, connate, imbricate, entire, deciduous in fruit; petals 5, distinct, imbricate, longer than sepals; disk annular-cupulate, puberulent; ovary 3-locular, sericeous; ovules anatropous, inner integuments thick, vascularized; stylodia bifid. Fruits capsular, exocarp fleshy, verrucose, endocarp bony; columella persistent. Seeds angular, ecarunculate, exotesta fleshy, tenuous, endotesta bony; cotyledons much longer and broader than radicle. $2n = 20$.

[1] Subtr. **Ostodeinae** G.L. Webster, **subtr. nov.**: plantae dioicae inflorescentiis terminalibus, staminibus 5–35, liberis, antheris plerumque introrsis, seminibus plerumque ecarunculatis. Typus: *Ostodes* Blume.

A single polytypic sp., *O. paniculata* Blume, extending from Assam through southeast Asia to Malaya and Java. Partly because of the jumbled treatment of Pax and Hoffmann (1911), the genus has been confused with *Paracroton*, which now is referred to the Aleuritideae.

223. *Dimorphocalyx* Thwaites

Dimorphocalyx Thwaites, Enum. Pl. Zeyl.: 278 (1861); Pax & K. Hoffm., Pflanzenr. 147, III: 31, fig. 8 (1911); Airy Shaw, Kew Bull. 23: 123 (1969); Chakrabarty & Balakrishnan, Proc. Indian Acad. Sci. 100: 286, figs. 1–4 (1990); Philcox, Fl. Ceylon 11: 107 (1997); Naithani et al., Forest Fl. Goa 552, t. 118 (1997).

Dioecious trees or shrubs; latex not evident; indumentum simple, scanty or 0. Leaves entire or denticulate, without basal glands; stipules entire, persistent or deciduous. Inflorescences terminal or subterminal, sometimes axillary, pedunculate, cymose or racemoid, pistillate sometimes reduced to solitary flowers; bracts entire, persistent, eglandular. Staminate flowers pedicellate; sepals 5, connate into a dentate or lobed cup; petals 5, white, distinct, glabrous, equaling or longer than the calyx; disk segments 5, glabrous; stamens (5)8–20(−100), the inner 3–10 filaments connate; anthers basifixed or dorsifixed, introrse; pollen spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5, distinct, imbricate, entire, ± persistent and accrescent in fruit; petals 5, distinct, imbricate, shorter than sepals; disk annular or cupular; ovary pubescent, sometimes rugose; ovules anatropous, inner integuments thick, vascularized; stylodia connate at base (distinct), bifid, branches slender. Fruits capsular; columella persistent. Seeds ellipsoidal, ecarunculate, testa smooth.

Seventeen spp., distributed from India and Ceylon to the Philippines, New Guinea, and northern Australia.

224. *Anomalocalyx* Ducke

Anomalocalyx Ducke, Notizbl. Bot. Gart. Berlin 11: 344 (1932), Arq. Jard. Bot. Rio Jan. 6: 60, figs. 7–9 (1933); Secco, Rev. Gen. *Anomalocalyx* et al.: 39, figs. 7, 8 (1990); Webster, Ann. Missouri Bot. Gard. 81: 115 (1994); Radcl.-Sm., Gen. Euphorb.: 338, fig. 43 (2001).

Dioecious trees; latex white; indumentum malpighiaceous but flowers glabrous. Leaves petiolate (pulvinate), adaxially with paired basal glands, abaxially with embedded glands; stipules entire, deciduous. Inflorescences terminal; staminate flowers thyrsoid-paniculate, pistillate flowers solitary; bracts entire, eglandular, deciduous. Staminate flowers pedicellate; sepals 3 or 4, glabrous, connate in the bud, opening in 2 lobes at anthesis; petals 5, distinct, imbricate, adaxially pubescent at base; disk annular, glabrous; stamens 23–30, filaments distinct from the convex receptacle; anthers introrse; pollen spheroidal, inaperturate, sexine with Croton pattern, pillars rounded, sulcate; pistillode 0. Pistillate flowers pedicellate; sepals 3–5, glabrous, connate in bud, splitting into (2) 3 lobes at anthesis, persistent in fruit; petals 5, scantily pilose adaxially at base; disk annular, glabrous; ovary 3-locular, glabrous; stylodia bifid. Fruit capsular, endocarp woody; columella stout, persistent. Seeds rounded, carinate, ecarunculate, testa slightly rugose.

A single sp., *A. uleanus* (Pax) Ducke, Amazonian Brazil, from near Manaus to Amapá. Although it closely resembles *Dodecastigma* in habit, Secco notes that it is immediately distinguishable by its glabrous inflorescences.

225. *Dodecastigma* Ducke

Dodecastigma Ducke, Notizbl. Bot. Gart. Berlin 11: 343 (1932); Arq. Jard. Bot. Rio Jan. 6: 58, t. 5 (1933); Sandw., Kew Bull. 1950: 134 (1951); Jablonski, Mem. N. Y. Bot. Gard. 17: 154 (1967); Secco, Rev. Gen. *Anomalocalyx* et al.: 42, figs. 10–12 (1990); Webster, Ann. Missouri Bot. Gard. 81: 106 (1994).

Dioecious trees or shrubs; latex turning reddish; indumentum simple and malpighiaceous, flowers pilose. Leaves petiolate (pulvinate), ± cuspidate, entire with cartilaginous border, abaxially with small dispersed embedded discoid glands but lacking paired basal glands, stipules minute, deciduous. Staminate inflorescences axillary, thyrsoid-paniculate; pistillate inflorescences racemoid, terminal and axillary; bracts entire, inconspicuous, persistent, subtending glomerules of staminate flowers or solitary pistillate flowers. Staminate flowers pedicellate; calyx 3- or 4-lobed, lobes imbricate; petals 3 or 4, green or yellow-green, distinct, imbricate, pilose abaxially; disk annular-crenulate, pilose; stamens 7–16, filaments distinct; anthers introrse; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers long-pedicellate; sepals (2) 3–4, imbricate, entire, abaxially pubescent, deciduous in fruit; petals mostly 3 or

4, green or yellow-green, imbricate, pilose abaxially, subpersistent in fruit; disk annular, pilose; ovary 3-locular; densely sericeous; ovules anatropous, inner integuments thick, vascularized; stylodia multifid. Fruits capsular, endocarp wood; columella massive, persistent. Seeds elliptic, ecaruncule, testa smooth and mottled.

Three spp. in Amazonian Brazil and the Guianas. The genus appears to be closely related to *Anomalocalyx*.

226. *Pantadenia* Gagnep.

Pantadenia Gagnep., Bull. Soc. Bot. France 71: 873 (1925); Airy Shaw, Kew Bull. 23: 122 (1969), 26: 312 (1972); Webster, Ann. Missouri Bot. Gard. 81: 106 (1994); Radcl.-Sm., Gen. Euphorb.: 298 (2001).
Parapantadenia Capuron (1972).

Dioecious trees; latex not recorded; indumentum simple. Leaves petiolate or subsessile, abaxially with dispersed scutelliform glands; stipules subulate, ± deciduous. Inflorescences leaf-opposed, the staminate thyrsoid-racemose, pistillate flowers mostly solitary; bracts entire, eglandular. Staminate flowers pedicellate; sepals 5, distinct, imbricate; petals 5, distinct, imbricate, with 3 apical marginal glands; disk cupular, undulate; stamens 13–15, filaments distinct; anthers introrse, dorsifixed, connective glandular at apex; pollen grains spheroidal, inaperturate, exine with Croton pattern, lumina large, pillars rounded; pistillode rudimentary. Pistillate flowers pedicellate; sepals 5 or 6, distinct, imbricate, entire, persistent in fruit; petals 2 or 3, apically glandular; disk annular; ovary 2- or 3-locular, hispidulous; stylodia bifid. Fruits capsular or indehiscent and 1-seeded; columella 3-pronged, persistent. Seeds spheroidal, ecaruncular, testa smooth.

Two spp., widely disjunct: Madagascar and Vietnam. Govaerts et al. (2000) and Radcliffe-Smith (2001) uphold *Parapantadenia* as a distinct genus, based on its 2-locular ovary and indehiscent 1-seeded fruit. The question of generic status is problematic, but there is no doubt of a close relationship between the two species despite the considerable geographical disjunction.

227. *Pausandra* Radlk.

Pausandra Radlk., Flora 53: 92, t. 2 (1870); Jablonski, Mem. N. Y. 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. *Anomalocalyx*, etc.: 58, figs. 14–25 (1990); Webster, Ann. Missouri Bot. Gard. 81: 105 (1994); Murillo & Franco, Euforb. Reg. Araracuara: 124, fig. 34 (1995); Radcl.-Sm., Gen. Euphorb.: 296 (2001).

Dioecious trees or shrubs; laticifers non-articulated, latex reddish; indumentum malpighiaceous. Leaves with paired basal glands at junction with petiole; stipules entire, eglandular, subpersistent or deciduous. Inflorescences axillary, spiciform-thyrsoid, staminate flowers in glomerules, pistillate solitary at nodes; bracts inconspicuous, eglandular. Staminate flowers subsessile; sepals 5, distinct, imbricate; petals 5 (6), imbricate, basally connate, adaxially villous; disk extrastaminal, urceolate-lobate, glabrous; stamens (3–)5–7, filaments distinct; anthers introrse; pollen grains spheroidal, inaperturate, exine with Croton pattern, pillars distinctly sulcate; pistillode 0. Pistillate flowers subsessile; sepals 5, imbricate, entire, persistent in fruit; petals 5, distinct, imbricate, adaxially villous; disk urceolate, sometimes lobate, glabrous; ovary 3-locular, pubescent; ovules anatropous, inner integuments thick, vascularized; stylodia distinct, bifid. Fruits capsular; columella persistent. Seeds carunculate, testa smooth.

Six neotropical spp., extending from Nicaragua to Bolivia and southern Brazil (Secco 1990). The status of some species awaits verification. *Pausandra* is isolated within neotropical Codiaeae by a number of features such as the massive petiolar glands or stipels, the subsessile flowers, and the malpighiaceous indumentum; its placement needs reevaluation.

9d. Subtribe Codiaeinae Pax (1911).

Monoecious (dioecious); leaf blades without basal laminar glands; inflorescences terminal or axillary; bracts eglandular; pistillate flowers apetalous or petals rudimentary; seeds mostly carunculate; columella persistent.

Four genera, all paleotropical.

Key to the Genera of Codiaeinae

1. Inflorescences axillary; ovary glabrous 2
– Inflorescences terminal; ovary pubescent 3
2. Staminate flowers apetalous; leaf blades with basal laminar glands; inflorescences bisexual, long thyrsopaniculate **231. *Baliospermum***
– Staminate flowers petaliferous; leaf blades without basal laminar glands; inflorescences unisexual, racemoid **228. *Codiaeum***

3. Pistillate sepals glandular-fimbriate; stipules ± persistent; seeds carunculate **230. *Strophioblachia***
– Pistillate sepals not glandular-fimbriate; stipules deciduous; seeds ecarunculate **229. *Blachia***

228. *Codiaeum* Rumph. ex A. Juss.

Codiaeum Rumph. ex A. Juss., Euphorb. Tent.: 33 (1824; nom. cons.); 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): 95–101, t. 19 (1987); Howard, Fl. Lesser Antilles 5: 32, fig. 13 (1989); Radcl.-Sm., Gen. Euphorb.: 301 (2001).

Monoecious trees or shrubs; laticifers non-articulated, latex clear; indumentum simple. Leaves alternate (opposite); stipules 0. Inflorescences axillary, unisexual, racemoid; bracts entire, persistent, eglandular. Staminate flowers pedicellate; sepals mostly (3–)5(6), distinct, imbricate; petals 4–6, minute, distinct, imbricate; disk segments 4–6; stamens 10–35, filaments distinct; anthers basifixed, ± latrorse, muticous; pollen grains spheroidal, inaperturate, exine with Croton pattern, pillars smooth and rounded; pistillode 0. Pistillate flowers pedicellate; sepals mostly 5, distinct, imbricate, entire, usually deciduous in fruit; petals 0; disk cupular; ovary 3-locular, glabrous; ovules anatropous, inner integuments thick, vascularized; stylodia slender, unlobed. Fruits capsular; columella mostly persistent. Seeds carunculate, testa smooth. $2n = 48, 72, 96, 120$.

Seventeen spp., distributed from Java and Borneo to the Philippines, New Guinea, tropical Australia and New Caledonia. Müller (1866) construed *Codiaeum* in a very broad sense, to include species of *Austrobuxus*, *Baloghia*, *Blachia*, *Fontainea*, and *Trigonostemon*, but Bentham (1880) reconstituted it in the circumscription that is accepted at present.

229. *Blachia* Baill.

Blachia Baill., Étude Gén. Euphorb.: 385 (1858); Pax, Pflanzenr. 147, III: 36 (1911); Gagnep., Fl. Indochine 5: 410, fig. 48, 5–13 (1926); Airy Shaw, Kew Bull. 23: 121 (1969), 26: 223 (1972); Balakrishnan & Chakrabarty, Proc. Indian Acad. Sci. 99 568, figs. 1–4 (1989); Thin, Tap Chi Sinh Hoc 11(3): 16 (1989); Webster, Ann. Missouri Bot. Gard. 81: 107 (1994); Philcox, Fl. Ceylon 11: 105 (1997).
Bruxanellia Dennst. ex Kostel. (1830; nom. rej.).

Monoecious shrubs or trees; latex not recorded; indumentum simple, often 0 or nearly so. Leaves alternate (subopposite), eglandular; stipules deciduous or persistent. Inflorescences terminal [or pistillate terminal and axillary], racemoid, sometimes ± umbellate; bracts inconspicuous or 0 above basal nodes. Staminate flowers pedicellate; sepals 4 or 5, distinct, concave, membranous; petals 4 or 5, distinct, imbricate, shorter than sepals; disk a convex receptacle; disk segments 5; stamens 10–20(−40), filaments distinct; anthers basifixed, extrorse, connective broad, muticous; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, imbricate, entire, usually accrescent and persistent in fruit; petals rudimentary or 0; disk annular; ovary 3–5-locular, glabrous or pubescent; ovules anatropous, inner integuments thick (18–20 cell layers), vascularized; stylodia bifid, branches slender. Fruits capsular; columella persistent or not. Seeds subspheroidal, ecarunculate; testa smooth. $2n = 36$.

Eleven spp., from India to China and Malesia, south to the Andaman Islands. Balakrishnan and Chakrabarty (1989) regard *Pantadenia* as the closest relative of *Blachia*.

230. *Strophioblachia* Boerl.

Strophioblachia Boerl., Handl. Fl. Ned. Ind. 3(1): 235 (1900); Pax, Pflanzenr. 147, III: 35, fig. 10 (1911); Gagnepain, Fl. Indochine 5: 408, figs. 47, 8–14, 48, 1–4 (1926); Airy Shaw, Kew Bull. 25: 544 (1971); Thin et al., Blumea 43: 484, t. 1–4 (1998).

Monoecious shrubs; latex not recorded; indumentum simple. Leaves eglandular; stipules entire, pilose, deciduous or persistent. Inflorescences terminal, unisexual, racemoid, few-flowered. Staminate flowers pedicellate; sepals 4 or 5, distinct, imbricate; petals 5, white, dentate; disk segments 5; stamens 15–30, filaments distinct; anthers extrorse, rounded, muticous; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5, distinct, imbricate, persistent and with glandular-fimbriate margins in fruit; petals 0; disk annular; ovary 3-locular, glabrous; ovules anatropous, inner integuments thick, vascularized; stylodia connate at base, bifid. Fruits capsular, thin-walled; columella persistent. Seeds subspheroidal, carunculate, testa smooth.

Two spp., southern China to Vietnam, the Philippines and Sulawesi.

231. *Baliospermum* Blume

Baliospermum Blume, Bijdr.: 603 (1826); Decaisne in Jacquemont, Voy. Inde Atlas 2: 155 (1844); Müll. Arg. in DC. Prodr. 15(2): 1125 (1866); J.J. Sm., Meded. Dept. Landb. 10: 599 (1910); Pax & K. Hoffm., Pflanzenr. 147, IV: 24, figs. 6, 7 (1912); Gagnepain, Fl. Indochine 5: 429, figs. 51, 6–19, 52, 1–6 (1926); Airy Shaw, Kew Bull. 36: 267 (1981); Long, Fl. Bhutan 1(3): 809, fig. 50 m–o (1987); Chakrabarty & Balakrishnan, Bull. Bot. Survey India 32: 3, figs. 1–8 (1992); Webster, Ann. Missouri Bot. Gard. 81:108 (1994).

Monoecious or dioecious shrubs, sometimes scandent; latex not recorded; indumentum simple. Leaves pellucid-punctate, glandular-dentate or serrate, ± biglandular at base or subbasal on margins; stipules minute, glandular, persistent. Inflorescences mostly axillary, long-pedunculate, thyrsoid-paniculate; bracts entire, eglandular. Staminate flowers pedicellate; sepals 4–5(6), distinct, imbricate, orbicular; petals 0; disk annular, lobed, or segmented; stamens 10–25, filaments distinct; anthers extrorse, muticous, connective narow; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5 or 6, distinct, imbricate, entire or denticulate, persistent in fruit and often accrescent; petals 0; disk annular; ovary 3 (4)-locular, glabrous or pubescent, ovules pachychalazal, inner integuments thick, vascularized; stylodia bifid. Fruits capsular; columella persistent, distally alate. Seeds carunculate, caruncle apical, discoidal; testa smooth. $2n = 44$.

Five spp., distributed from the Himalayas and Yunnan south to Sumatra and Java. Pax (1912) followed Müller (1866) in placing *Baliospermum* next to *Suregada*; however, the pollen study of Punt (1962) demonstrated that *Baliospermum* has pollen much more similar to genera of Codiaeae than to *Suregada*.

10. Tribe Ricinocarpeae Müll. Arg. (1864).

Monoecious (dioecious); latex reddish, often scanty or 0; indumentum stellate, sometimes glandular; sepals 4–6, distinct, imbricate, often petaloid; petals 5 (0); disk dissected or 0; stamens 15–100, filaments mostly connate; pollen grains inaperturate, exine with Croton pattern; stylodia unlobed to multifid; seeds carunculatae.

This strictly Australasian tribe includes seven genera. It has certain characters in common with *Alphandia*, a possible sister group, which is here referred to the Codiaeae.

Key to the Subtribes and Genera of Ricinocarpeae

1. Embryo with cotyledons much broader than the radicle; pollen exine with reduced pillars; leaves alternate, not ericoid. **10a. Cocconeriinae** 2
– Embryo with narrow cotyledons no broader than radicle; pollen exine with massive pillars (except *Bertya*); leaves opposite or verticillate; shrubs or trees, often with reddish latex. **10b. Bertyinae** 4
2. Leaves opposite; inflorescences terminal, racemoid; stylodia multifid **232. *Myricanthe***
– Leaves verticillate; staminate inflorescences subcapitate or flowers axillary; stylodia bifid or twice bifid 3
3. Sepals 4–7; ovary (2)3-locular; stylodia bifid or twice bifid; flowers axillary, solitary **233. *Cocconerion***
– Staminate sepals 0, pistillate sepals 3; ovary 2-locular; stylodia bifid; staminate inflorescences terminal, subcapitate **234. *Borneodendron***
4. Stylodia dilated, connivent into a pseudo-stigma over the top of the ovary, discoid or rarely with 2 appressed entire limbs or shallowly 3-lobulate **236. *Beyeria***
– Stylodia 3 spreading and divergent limbs, entire or 2–5-lobed 5
5. Stylodia entire; flowers in racemes **237. *Shonia***
– Stylodia deeply 2(−5)-lobed; flowers usually not in racemes 6
6. Petals 0 or rudimentary; calyx strongly recurved at anthesis; disk 0 **238. *Bertya***
– Petals conspicuous, or if 0 then calyx spreading at anthesis; disk + **235. *Ricinocarpos***

10a. Subtribe Cocconeriinae G.L. Webster, subtrib. nov.[1]

Subtribe Bertyinae sensu Webster (1994), excluding the genus *Bertya*.

Monoecious trees or shrubs; latex reddish or 0; leaves opposite or verticillate; stipules deciduous or 0; inflorescences terminal or axillary, racemoid or flowers solitary; petals and disk 0; stamens 30–100, filaments connate into a column, anthers extrorse, pubescent; pollen grains with minute clavae instead of pillars; ovary 2- or 3-locular; fruits capsular, columella persistent; seeds carunculate, cotyledons broader than radicle.

Three Melanesian genera; these appear to be related to *Alphandia*, and also to the Bertyinae,

[1] Subtrib. **Cocconeriinae** G.L. Webster, **subtrib. nov.**, plantae monoicae foliis oppositis vel verticillatis, antheris pilosis, filamentis connatis, pollinis grana exinio microclavato, cotyledonibus quam radicula latioribus. Typus: *Cocconerion* Baillon

although the phylogenetic connections are not yet very clear. In Webster (1994), these genera were included in subtribe Bertyinae.

232. *Myricanthe* Airy Shaw

Myricanthe Airy Shaw, Kew Bull. 35: 390 (1980); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 72–73, t. 14, figs. 1–5 (1987).

Monoecious shrubs; latex not recorded; indumentum stellate. Leaves opposite; stipules 0. Inflorescences terminal, unisexual or bisexual, racemoid; bracts deciduous. Staminate flowers pedicellate; sepals 3, distinct, imbricate; petals and disk 0; stamens 60–80, filaments connate into an elongated column; anthers subsessile on column, minutely pilose; pollen grains spheroidal, inaperturate, with Croton pattern, clavae minute and spinulose; pistillode 0. Pistillate flowers pedicellate; sepals 6, distinct, entire, subpersistent in fruit; petals and disk 0; ovary 3-locular, stellate-tomentellous; ovules anatropous, inner integuments very thick, vascularized; stylodia multifid (palmatifid). Fruits capsular; columella persistent. Seeds ± cylindrical, carunculate.

A single sp., *M. discolor* Airy Shaw, confined to ultrabasic substrates in northern New Caledonia.

233. *Cocconerion* Baill.

Cocconerion Baill., Adansonia I, 11: 87 (1873); Airy Shaw, Kew Bull. 25: 503 (1971); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 38–43, t. 7 (1987); Webster, Ann. Missouri Bot. Gard. 81: 110 (1994).

Monoecious trees or shrubs; latex translucent, yellowish to reddish; indumentum stellate-lepidote. Leaves verticillate, 6–10 per node, tapering gradually to an ill-defined petiole, abaxially densely brownish appressed-stellate; stipules 0. Flowers solitary, axillary. Staminate flowers pedicellate; sepals 4–7, imbricate, pubescent on both faces; petals and disk 0; stamens 30–100, filaments connate into a column; anthers pubescent; pollen grains spheroidal, inaperturate, reticulate with micro-clavae; pistillode 0. Pistillate flowers pedicellate; sepals 5–7, imbricate, entire, pubescent on both faces, persistent in fruit; petals and disk 0, staminodes sometimes present; ovary (2)3-locular; ovule anatropous, inner integuments thick, vascularized; stylodia bifid or twice bifid, branches slender. Fruits capsular; columella persistent. Seeds ellipsoidal, carunculate, testa smooth.

Two spp. endemic to New Caledonia.

234. *Borneodendron* Airy Shaw

Borneodendron Airy Shaw, Kew Bull. 16: 359 (1963), Hook. Icon. Pl. 7(2): t. 3633 (1967), Kew Bull. Add. Ser. 4: 60 (1975); Webster, Ann. Missouri Bot. Gard. 81: 110 (1994); Radcl.-Sm., Gen. Euphorb.: 315 (2001).

Monoecious tree; latex reddish; indumentum stellate. Leaves verticillate (ternate), petiolate, without basal paired glands; stipules deciduous. Staminate inflorescences terminal, subcapitate, pedunculate, bracts verticillate; pistillate flowers solitary, axillary. Staminate flowers without perianth or disk; stamens 25–30, filaments connate into a column, anthers basifixed, anther sacs pubescent; pistillode 0. Pistillate calyx 4–5-lobed; petals and disk 0; ovary 2-locular; stylodia bifid. Fruits capsular, endocarp woody; columella persistent. Seeds ellipsoid, carunculate, hilum smooth; cotyledons much broader than radicle.

A single sp., *B. aenigmaticum* Airy Shaw, endemic to northeastern Borneo, in hill forest or *Casuarina* forest on ultrabasic substrate. Radcliffe-Smith (2001) refers to several traits in which it resembles Oldfieldioid genera such as *Aristogeitonia* and *Mischodon*; hence, knowledge of its pollen structure would be highly desirable. The strongly reduced flowers suggest a shift to wind pollination. Unpublished sequence data on *Borneodendron* mentioned by Hoffmann and Wurdack (2007) have not been accessible to us.

10b. Subtribe Bertyinae Müll. Arg. (1865).

Subtribe Ricinocarpinae G.L. Webster (1975).

Monoecious or dioecious; stems and foliage often resinous or with reddish latex; flowers petaliferous; pollen grains with large pillars [except in *Bertya*]; embryo with cotyledons as narrow as radicle.

An entirely Australian subtribe of four genera.

235. *Ricinocarpos* Desf.

Ricinocarpos Desf., Mém. Mus. Hist. Nat. Paris 3: 459, t. 22 (1817); Müll. Arg. in DC., Prodr. 15(2): 203 (1866); Halford & Henderson, Austrobaileya 7: 387–449 (2007), rev.

Monoecious (dioecious) shrubs or small trees; laticifers non-articulated; latex 0 but stems and foliage sometimes resinous; indumentum stellate and simple. Leaves linear, 1-veined, entire, often revolute; stipules 0. Inflorescences terminal or pseudo-axillary, glomerulate or of solitary flowers in upper axils; bracts persistent.

Staminate flowers pedicellate; sepals (4)5(6), nearly distinct; petals (4)5(−7) or 0; disk of distinct alternipetalous segments or forming a continuous ring; stamens numerous, > 15, filaments connate into a column; anthers dorsifixed, extrorse; pollen grains spheroidal, inaperturate, with Croton pattern, pillars massive and spinulose; pistillode 0. Pistillate flowers pedicellate; sepals persistent or deciduous in fruit; petals often marcescent, deciduous or sometimes 0; disk annular or urceolate; ovary 3-locular; ovule 1/locule, inner integument very thick, vascularized; stylodia basally very shortly connate, the distinct branches spreading, deeply 2(3–5)-fid. Fruits capsular, smooth or echinate; columella persistent. Seeds ellipsoidal, carunculate, testa smooth; endosperm copious; cotyledons longer than radicle.

According to the revision of Halford and Henderson, 28 spp., all endemic to Australia.

236. *Beyeria* Miq.

Beyeria Miq., Ann. Sci. Nat. III, 1: 350, t. 15 (1844); Müll. Arg. in DC., Prodr. 15(2): 201 (1866); Halford & Henderson, Austrobaileya 7: 577–635 (2008), rev.

Monoecious (dioecious) shrubs or small trees; stems and foliage resinous; laticifers non-articulated, latex not recorded; indumentum stellate. Leaves petiolate or subsessile, 1-veined, often revolute; stipules 0. Inflorescences axillary, glomerular (racemoid) or the pistillate flowers solitary. Staminate flowers pedicellate; sepals (4) 5 (6), distinct, imbricate, often petaloid; petals (4) 5, sometimes or 0; disk segments mostly 5 or disk 0; stamens 15–40, filaments distinct, shorter than anthers; anthers glabrous, extrorse; pollen grains spheroidal, inaperturate, exine with Croton pattern, pillars massive; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, persistent and sometimes accrescent in fruit; petals 4 or 5; disk obsolete; ovary 2–3-locular; ovules anatropous, inner integuments very thick; stylodia connivent into a conical pseudo-stigma. Fruits capsular; columella persistent. Seeds oblong, carunculate, testa smooth; embryo cylindrical, cotyledons as narrow as radicle.

Twenty-four spp. endemic to Australia recorded by Halford and Henderson (2008).

237. *Shonia* R. Henderson & Halford Fig. 40

Shonia R. Henderson & Halford, Austrobaileya 7: 218 (2005).

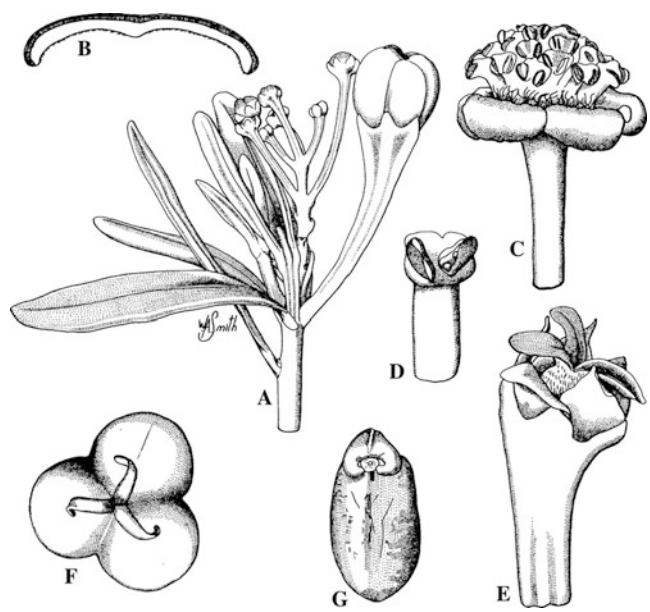

Fig. 40. Euphorbiaceae-Crotonoideae. *Shonia tristigma* subsp. *borealis*. **A** Flowering branchlet. **B** Transverse section of leaf. **C** Side view of staminate flower. **D** Stamen. **E** Side view of pistillate flower. **F** Face view of fruit. **G** Ventral view of seed. (Henderson & Halford 2005; drawn by W. Smith)

Monoecious (dioecious) shrubs or small trees; latex and resin not recorded; indumentum stellate. Leaves shortly petiolate, abaxially pubescent; stipules 0. Inflorescences racemose (paniculate), terminal or apparently axillary, proximally with 1–2 pistillate flowers and few to several staminate flowers distal to them. Staminate flowers with calyx 5(4)-lobed; petals +; disk of distinct alternipetalous glands or a continuous ring; stamens 10–30, erect; filaments distinct; anthers extrorse; pistillode 0. Pistillate flowers with calyx lobes persistent and appressed to ovary; petals +; disk circular; ovary 3-locular; stylodia distinct, entire. Fruit trilobate, capsular, separating into three 2-valved cocci; columellla persistent. Seeds carunculate; endosperm copious; cotyledons narrower than radicle.

Four spp., endemic to Australia (Northern Territory, Queensland).

238. *Bertya* Planch.

Bertya Planch., Hook. London J. Bot. 4: 472 (1845); Müll. Arg. in DC., Prodr. 15(2): 208 (1866); Halford & Henderson, Austrobaileya 6: 187–245 (2002), rev.

Monoecious or dioecious shrubs (trees); laticifers non-articulated, latex not recorded; stems often resinous; indumentum stellate. Leaves alternate (opposite), abaxially densely tomentose, margins revolute; stipules 0. Inflorescences axillary, flowers solitary or in glomerules; bracts forming an involucre at base of calyx. Staminate flowers pedicellate; sepals 5 (4), basally connate, imbricate, sometimes petaloid; petals and disk 0; stamens 15–70; filaments connate into a column, shorter than anthers; anthers dorsifixed, extrorse; pollen grains spheroidal, inaperturate, exine with Croton pattern, clavae reduced; pistillode 0. Pistillate flowers pedicellate or subsessile; sepals 5, distinct, imbricate, entire, persistent and sometimes accrescent in fruit; petals 0 or rudimentary; disk 0; ovary (2)3(−5)-locular, glabrous or stellate-pubescent; ovules anatropous, inner integument very thick, vascularized; stylodia 3(4), proximally shortly connate, distally 2- to several-lobed. Fruits capsular, usually 1-seeded; columella not persistent. Seeds oblong or rounded, carunculate, testa smooth; embryo cylindrical, cotyledons as broad as radicle.

Twenty-eight spp. distinguished by Halford & Henderson (2002), widely distributed in Australia except for the Northern Territory.

11. Tribe Ricinodendreae (Pax) Hutch. (1969).

Dioecious or monoecious trees or shrubs; laticifers non-articulated; reddish latex + or not; indumentum stellate, malpighiaceous, or 0; leaves alternate or opposite, simple to lobed or palmatisect, petiole usually glandular at apex; stipules entire, lobed, or 0; inflorescences axillary or the pistillate terminal, cymose-paniculate, glomerular, or reduced to solitary flowers; sepals 4 or 5, distinct or connate; petals 5; disk dissected or lobed; stamens (3–)5–35; pollen inaperturate, with Croton pattern; pistillode 0; ovary 1–3-locular; stylodia bifid; fruits drupaceous or capsular; seeds ecarunculate.

Four paleotropical genera, entirely African/Madagascan except for the New Guinean *Annesijoa* and one Indian species of *Givotia*. In Webster (1994) and Radcliffe-Smith (2001), *Leeuwenbergia* and *Annesijoa* were part of the broadly circumscribed Jatropheae, but in the molecular analysis of Wurdack et al. (2005), *Leeuwenbergia* is resolved (*rbc*L only) in clade C2 together with *Ricinodendron*, *Schinziophyton* and *Givotia*.

Key to the Genera of Ricinodendreae

1. Leaves simple, unlobed to 5-lobed; stipules minute or 0 **239. *Givotia***
– Leaves palmatisect 2
2. Stipules flabelliform; indumentum stellate **240. *Ricinodendron***
– Stipules not flabelliform; indumentum malpighiaceous or 0 3
3. Stylodia slender, bifid; ovary 3-locular; stamens 15–25, anthers muticous; staminate disk dissected; fruit capsular; foliage glabrous **242. *Annesijoa***
– Stylodia dilated, subentire to lacerate; ovary 2-locular; stamens 18–33; anthers apiculate; staminate disk annular and intrastaminal; fruit drupaceous; indumentum malpighiaceous **241. *Leeuwenbergia***

239. *Givotia* Griff.

Givotia Griff., Calcutta J. Nat. Hist. 4: 88 (1843); Müll. Arg. in DC., Prodr. 15(2): 1112 (1866); Pax & K. Hoffm., Pflanzenr. 147, III: 44, fig. 15 (1911); Radcl.-Sm., Kew Bull. 22: 493, fig. 2, t. 5 (1968), Fl. Trop. E. Afr. Euphorb. 1: 329, fig. 62 (1987).

Dioecious trees or shrubs; latex clear; indumentum stellate. Leaves simple to 3–5-lobed, entire to coarsely dentate with sessile discoid glands, base of lamina with or without paired glands; stipules coarsely glandular-toothed or 0. Staminate inflorescences axillary, racemoid, with scattered glomerules; pistillate inflorescences terminal, of solitary or clustered flowers; bracts subulate, entire, deciduous. Staminate flowers pedicellate; sepals 5, distinct, imbricate; petals 5, greenish-yellow, distinct at first, later becoming partially adnate; disk segments 5, sometimes confluent; stamens (3–)8–20, filaments connate at base into a column shorter than the filaments; anthers dorsifixed, extrorse, muticous; pollen grains spheroidal, inaperturate, with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals (4) 5, distinct, imbricate, entire, deciduous in fruit; petals (4) 5, greenish-yellow, distinct, imbricate; disk annular; ovary 1–3-locular, pubescent; ovules anatropous, inner integuments thick, vascularized; stylodia bifid, compressed. Fruits drupaceous, 1-seeded; endocarp thin. Seeds ecarunculate, smooth.

Four spp., one in Africa, two in Madagascar, and one in India and Ceylon.

240. *Ricinodendron* Müll. Arg.

Ricinodendron Müll. Arg., Flora 47: 533 (1864), in DC., Prodr. 15(2): 1111 (1866); Benth., Hook. Icon. Pl. 13: t. 1300 (1879); Léonard, Fl. Congo Belge 8(1): 116 (1962); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 325, fig. 61

(1987), Fl. Zambesiaca 9(4): 294, t. 59, 60 (1996); Webster, Ann. Missouri Bot. Gard. 81: 113 (1994); Radcl.-Sm., Gen. Euphorb.: 328 (2001).
Schinziophyton Hutch. ex Radcl.-Sm. (1990).

Dioecious trees; laticifers non-articulated, latex clear; indumentum stellate. Leaves palmatisect, 3–7-foliolate, pellucid-punctate, denticulate; petiole glandular at apex; stipules flabellately dentate, persistent or deciduous. Inflorescences axillary or subterminal, the staminate cymose-paniculate, the pistillate contracted; bracts entire, deciduous, the pistillate foliaceous. Staminate flowers pedicellate; sepals 4 or 5, distinct, imbricate; petals 5, greenish or whitish, imbricate, coherent to form a tube; disk segments 4–6, glabrous; stamens (7–) 10–20, filaments connate basally into a short column, exserted beyond calyx; anthers dorsifixed, versatile, introrse; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals (4) 5, distinct, imbricate, deciduous in fruit; petals 5, greenish or whitish, imbricate, coherent; disk annular, crenulate, glabrous; ovary 1–3-locular, pubescent, ovules anatropous, inner integuments very thick, vascularized; stylodia bifid. Fruits drupaceous, exocarp fleshy, endocarp woody. Seeds ecarunculate, subspheroidal, testa irregularly ridged. $2n = 22$.

Two spp. widely distributed in tropical Africa. Originally, six African spp. had been described in *Ricinodendron*, of which only a single polymorphic species, *R. heudelotii*, with 3 subspecies was recognized by Govaerts et al. (2000); an additional species was transferred to the segregate genus *Schinziophyton*. However, the key to the Congo spp. of *Ricinodendron* by Léonard contrasts two species that are very distinct, but which in my opinion can easily be accommodated in a single genus; *Schinziophyton* is therefore here relegated to synonymy, and *Ricinodendron* is considered to include at least 2 species.

241. *Leeuwenbergia* Letouzey & Hallé Fig. 41

Leeuwenbergia Letouzey & Hallé, Adansonia II, 14: 379, figs. 2, 3 (1974); Webster, Ann. Missouri Bot. Gard. 81: 104 (1994).

Dioecious trees; latex reddish; indumentum malpighiaceous. Leaves palmatisect, petiolate with 1 or 2 large apical glands; leaflets entire; stipules deciduous. Inflorescences axillary or subterminal, unisexual, racemoid-thyrsoid or paniculate; bracts deciduous. Staminate flowers pedicellate; sepals connate, irregularly dehiscent into 2 or 3 lobes, closed in bud; petals 5, white, orbiculate, distinct; disk interstaminal, receptacular; stamens 18–33, distinct, inserted in cavities of the disk; filaments distinct; anthers introrse, apiculate; pollen grains inaperturate, with Croton pattern; pistillode 0. Pistillate flowers pedicellate; calyx and petals as in staminate; disk annular-cupular, hirsute; ovary 2–3-locular, hirsute; ovules anatropous, inner integuments thick, vascularized; stylodia foliose-stigmatiform, crenulate. Fruits and seeds unknown.

Two spp. of west African rainforests: Gabon to Cameroon and Zaire.

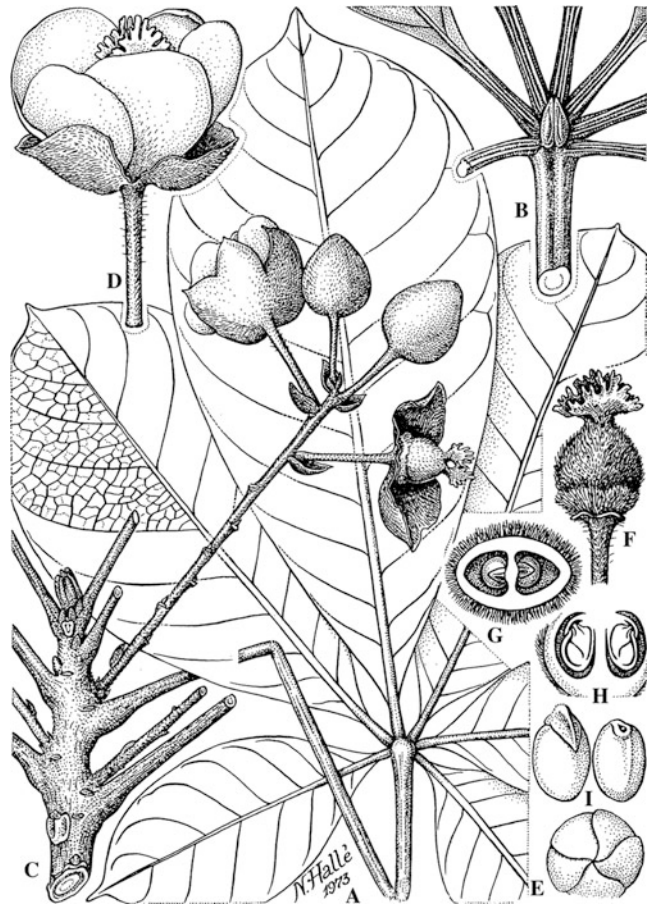

Fig. 41. Euphorbiaceae-Crotonoideae. *Leeuwenbergia africana*. **A** Leaf, seen from below. **B** Glands on petiole apex. **C** Flowering branch. **D** Pistillate flower. **E** Corolla aestivation. **F** Ovary, side view. **G** Same, transversal section. **H** Same, longitudinal section. **I** Ovule with and without obturator. (Letouzey & N. Hallé 1974; drawn by N. Hallé)

242. *Annesijoa* Pax & K. Hoffm.

Annesijoa Pax & K. Hoffm., Pflanzenr. 147, XIV: 9 (1919); Airy Shaw, Kew Bull. 16: 345 (1963), Hook. Icon. Pl. 38: t. 3713 (1974), Kew Bull. Add. Ser. 8: 27, t. 7 (1980); Hoang Van Nam & van Welzen, Blumea 49: 427–437 (2004).

Monoecious trees; latex not recorded; indumentum 0. Leaves palmatisect, petiolate with apical paired stipelliform deciduous glands; leaflets entire; stipules rudimentary. Staminate inflorescences axillary, dichasial-paniculate, pistillate flowers few and subterminal; bracts inconspicuous. Staminate flower pedicellate; calyx cupular, shallowly lobed, of 5 connate sepals, open in bud; petals 5, white, distinct; disk segments 5; stamens 15–25, filaments distinct or coherent in part; anthers ellipsoidal; pollen grains spheroidal, inaperturate, with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5, distinct or nearly so, entire; petals 5, distinct, imbricate; disk segments 5; ovary 2-locular, glabrous; ovules anatropous, inner integuments moderately thick, vascularized; stylodia bipartite. Fruits capsular; endocarp woody; columella not persistent. Seeds spheroidal or angled, ecarunculate (?), testa smooth.

One sp., *A. novoguineensis* Pax & K. Hoffm., of rainforests in New Guinea.

12. Tribe Aleuritideae Hurus. (1954).

Monoecious trees or shrubs; laticifers non-articulated, latex white or reddish; indumentum simple or stellate; leaves alternate, simple, entire (dentate), pinnately to palmately veined or palmately lobed, eglandular or with basal laminar glands; stipules present or 0; inflorescences terminal or axillary, cymose-paniculate or reduced to glomerules; staminate calyx closed in bud, splitting into valvate segments; petals 5(6–13), distinct, imbricate; disk dissected or interstaminal; stamens 7–20(−100); pollen grains spheroidal, inaperturate, with Croton pattern; sepals and petals as in staminate; disk lobed, dissected, or obsolete; ovary 2–5-locular; ovules anatropous, inner integuments thick, vascularized; stylodia bifid; fruit drupaceous or capsular; seeds ecarunculate (carunculate).

As here circumscribed, the Aleuritideae are an exclusively paleotropical group, except for *Garcia*, the affinities of which are dubious. The five subtribes contain a total of 13 genera and 45 species. van Welzen and Stuppy (1999) have shown in a cladistic analysis of the tribe that subtribe Grosserinae as delimited by Webster (1994) is unnatural. *Paracroton*, formerly doubtfully included in the Codiaeae, in the combined and the partial molecular analyses (Wurdack et al. 2005) always goes together with genera of the Aleuritideae and here is shifted to this tribe.

Key to the Subtribes of Aleuritideae

1. Petals 0; leaves gland-dotted **12e. Neoboutoninae**
– Petals +, at least in staminate flowers; leaves not gland-dotted 2
2. Petals 6–13; stamens 30–100, filaments distinct; inflorescences terminal, glomerular; leaf blades pinnately veined **12b. Garciinae**
– Petals 4 or 5; stamens 6–40, filaments distinct or connate 3
3. Stamens 7–20, filaments connate; monoecious; inflorescences terminal; leaf blades palmately lobed or veined; monoecious; stems with latex **12a. Aleuritinae**
– Stamens 6–40, filaments distinct or connate; dioecious (monoecious); inflorescences terminal or axillary; leaf blades pinnately or palmately veined; stems mostly without latex 4
4. Indumentum simple or 0; inflorescences mostly terminal [axillary in *Tapoides*] **12c. Grosserinae**
– Indumentum stellate or lepidote; inflorescences terminal or axillary 5
5. Staminate petals usually coherent or connate; leaves entire; caruncle 0; dioecious **12d. Crotonogyninae**
– Staminate petals distinct; leaves serr(ul)ate; caruncle + or 0; dioecious or monoecious **12f. Paracrotoninae**

12a. Subtribe Aleuritinae (Hurus.) G.L. Webster (1975).

Monoecious trees or shrubs; indumentum simple or stellate; leaves palmately veined or lobed, with glands at apex of petiole; inflorescences ± paniculate; bracts eglandular, deciduous; staminate calyx segments 2 or 3; petals 5, distinct, glabrous; disk-segments 5; stamens 7–20, inner filaments connate; ovary 2–3-locular; fruit drupaceous or capsular.

This small paleotropical subtribe includes all of the species traditionally referred to *Aleurites*. The fractionation into 3 genera proposed by Airy Shaw has been widely accepted, but despite the critical study of the Aleuritinae by Stuppy et al. (1999), it seems preferable to combine *Reutealis* with *Vernicia*.

Key to the Genera of Aleuritinae

1. Fruits drupaceous; indumentum stellate; stamens 17–32, anthers in 2 or 4 whorls; leaf blades triplinerved, brochidodromous **243. *Aleurites***
– Fruits capsular; indumentum simple or stellate; stamens 8–12(−14), mostly in 2 whorls; leaf blades palmately veined, eucamptodromous **244. *Vernicia***

243. *Aleurites* J.R. & G. Forst.

Aleurites J.R. & G. Forst., Charact. Gen. Pl.: 111, t. 56 (1776); Müll. Arg. in DC., Prodr. 15(2): 722 (1866); Airy Shaw, Kew Bull. 20: 393 (1967); Webster, J. Arnold Arb. 48: 342 (1967); Walker, Fl. Okinawa: 644, figs. 96–98 (1976); A.C. Sm., Fl. Vitiensis Nova 2: 547 (1981); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 176, fig. 34 (1987); P.I. Forster, Muelleria 9: 6, figs. 1, 2 (1996); Stuppy et al., Blumea 44: 79, fig. 1 (1999).

Monoecious trees; latex not obvious; indumentum simple and stellate. Leaves shallowly 3–5-palmately lobed or unlobed, triplinerved, entire, with paired basal glands at junction with petiole; stipules deciduous. Inflorescences terminal, cymose-paniculate, uni- or bisexual; bracts deciduous. Staminate flowers pedicellate; calyx splitting valvately or irregularly into 2 or 3 lobes; petals 5(6), distinct, imbricate, exserted from calyx; disk segments 5; stamens 17–32, 4-seriate, the filaments of the outer ones distinct, of the inner connate into a column; anthers dorsifixed, introrse, muticous, with dilated connective; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; perianth as in staminate flowers; disk annular, 5-lobed; ovary 2–3(4)-locular, tomentose; stylodia 2 or 3, connate at the base, bilobed. Fruits drupaceous; exocarp fleshy, endocarp thin-walled; seeds massive, subspheroidal, ecarunculate; endosperm copious. $2n = 22$.

Three spp., distributed from Ceylon to SE Asia, Australia, Melanesia and Polynesia, where it is commonly introduced.

244. *Vernicia* Lour.

Vernicia Lour., Fl. Cochinch.: 586 (1790); Hemsley, Hook. Icon. Pl. 29: t. 2801, 2802 (1906, under *Aleurites*); Airy Shaw, Kew Bull. 20: 394 (1967); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 178, fig. 35 (1987); Webster, Ann. Missouri Bot. Gard. 81: 114 (1994); Stuppy et al., Blumea 44: 88, fig. 3 (1999); Radcl.-Sm., Gen. Euphorb.: 331 (2001).
Reutealis Airy Shaw (1967).

Monoecious trees; laticifers non-articulated, latex whitish or reddish, often not apparent; indumentum simple, bifid, or stellate. Leaves unlobed to 3(−5)-lobed, palmately veined, entire, basally with paired glands at junction with petiole; stipules deciduous. Inflorescences terminal, usually bisexual, thyrsoid-paniculate, bracts persistent or deciduous. Staminate flowers pedicellate; calyx splitting into 2 or 3 valvate lobes; petals 5, distinct, contorted-imbricate, adaxially pubescent; disk segments 5, glabrous; stamens 7–12(−15), biseriate, those of the outer stamens distinct to basally connate, of the inner connate halfway or more; anthers basifixed, extrorse or introrse; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; perianth and disk as in staminate flowers; ovary 3(−5)-locular, pubescent; ovules anatropous, inner integuments moderately thick; stylodia bifid. Fruits capsular. Seeds trigonous, ecarunculate, testa thick and woody.

Four spp., SE Asia, Malesia, and extending to Japan.

12b. Subtribe Garciinae Müll. Arg. (1865).

Monoecious; indumentum simple; leaves entire, without glands at apex of petiole, estipulate; inflorescences terminal, glomerular; petals 6–13; staminate disk intrastaminal; stamens 30–100, filaments distinct; ovary 3-locular, pubescent; ovules anatropous, inner integuments thick; stylodia bifid; fruits capsular; seeds ecarunculate.

In accord with Webster (1975, 1994), subtribe Garciinae is restricted to *Garcia*, which is very isolated within the Aleuritideae. There are striking resemblances between *Garcia* and *Sagotia* and *Sandwithia*, so that *Garcia* might belong to the Crotoneae.

245. *Garcia* Vahl

Garcia Vahl, Skriv. Naturh. Selsk. Kjöbenh. 2: 217, t. 9 (1792); Müll. Arg. in DC. Prodr. 15 (2): 721 (1866); Pax, Pflanzenr. 147, I: 14 (1910); Lundell, Wrightia 1: 1 (1945); Webster, Ann. Missouri Bot. Gard. 54: 238, fig. 6 (1968); Burger & Huft, Fieldiana Bot. n. s. 36: 122, fig. 21 (1995).

Monoecious shrubs or trees; laticifers non-articulated; latex not recorded; indumentum simple. Leaves petiolate (pulvinate), cartilaginous, without paired basal glands; stipules 0. Inflorescences terminal, glomerular, bisexual, each with 1 or 2 pistillate and several staminate flowers; bracts entire, inconspicuous. Staminate

flowers pedicellate; calyx splitting into 2 or 3 valvate segments; petals 6–13, reddish, distinct, narrow, sericeous on both faces, exserted from calyx; disk ill-defined, mainly represented on the convex pilose and glandular receptacle; stamens 30–100, filaments distinct; anthers basifixed, minutely apiculate; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; calyx splitting into 2 or 3 valvate segments, deciduous; petals as in the staminate flowers; disk deeply lobed; ovary 3-locular, sericeous; ovules anatropous, inner integuments thick, vascularized; stylodia thick, reflexed, bifid. Fruits capsular; columella persistent. Seeds subspheroidal, ecarunculate; testa smooth. $2n = 66$.

Two spp., Mexico south to Colombia.

12c. Subtribe Grosserinae G.L. Webster (1975).

Dioecious (monoecious) trees or shrubs; latex usually not recorded; indumentum simple or 0; leaves pinnately veined or triplinerved, with or without basal laminar glands; stipules deciduous or 0; inflorescences terminal, racemoid, or paniculate; staminate petals 4 or 5, distinct or basally connate; staminate disk dissected; stamens 6–40, filaments distinct or connate; pistillate petals 4 or 5, distinct; ovary 3–5-locular; stylodia (twice) bifid; fruit capsular; seeds ecarunculate (carunculate).

Six paleotropical genera, three African/Madagascan and three SE Asian/Malesian. *Deutzianthus* and *Oligoceras*, included by Webster (1994) and Radcliffe-Smith (2001) in the Jatropheae, are here brought to tribe Aleuritidae, in consonance with Thin (1995), and provisionally included in subtribe Grosserinae. Molecular data for this placement are still lacking.

Key to the Genera of Grosserinae

1. Pollen grains with echinate exinous pillars; leaf blades triplinerved; bracts glandular **249. *Tannodia***
– Pollen grains with rounded exinous pillars; leaves pinnately veined; bracts eglandular 2
2. Leaf blades not pellucid-punctate 3
– Leaf blades pellucid-punctate 5
3. Staminate petals adaxially pubescent **248. *Tapoides***
– Staminate petals glabrous 4
4. Monoecious; glabrous; stylodia 3, connate at the base, bifid **250. *Oligoceras***
– Dioecious; indumentum simple, largely confined to inflorescences and fruits; stylodia 3, ± distinct, twice bifid, or deeply branched and distally bifid, hence appearing as 6 stylodia **251. *Deutzianthus***
5. Bracts small, persistent; inflorescence paniculate; leaf blades denticulate; stipular scars minute; pistillate sepals medianly thickened **247. *Grossera***
– Bracts large, imbricate, deciduous; inflorescence cone-like; leaf blades entire; stipular scars subannular, conspicuous; pistillate sepals not thickened **246. *Cavacoa***

246. *Cavacoa* Léonard

Cavacoa Léonard, Bull. Jard. Bot. Brux. 25: 320, fig. 54 (1955), Fl. Congo Belge 8(1): 191, fig. 16 (1962); Elffers & Taylor, Hook. Icon. Pl. 36: t. 3561 (1956); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 174, fig. 33 (1987); Radcl.-Sm., Fl. Zambesiaca 9(4): 304, t. 63 (1996).

Dioecious trees or shrubs; branches terminating in perulate buds; latex not recorded; indumentum simple. Leaves pellucid-punctate, entire, usually with basal paired glands and scattered embedded glands; stipules deciduous. Inflorescences terminal, racemoid; bracts large, covering flowers in bud, deciduous. Staminate flowers pedicellate; calyx splitting into 2 segments; petals 4 or 5, distinct, imbricate, glabrous; disk segments 4 or 5, glabrous; stamens 15–30, filaments connate into a column [outer filaments ± distinct]; anthers with enlarged connective; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, distinct, imbricate, entire, deciduous in fruit; petals 4 or 5, distinct, imbricate, glabrous; disk annular, glabrous; ovary 3-locular, glabrous; ovules anatropous, inner integuments thick, vascularized; stylodia bifid. Fruits capsular; columella persistent. Seeds ecarunculate, testa smooth.

Three spp. of tropical Africa south to Natal.

247. *Grossera* Pax

Grossera Pax, Bot. Jahrb. 33: 281 (1903); Pax & K. Hoffm., Pflanzenr. 147, VI: 105, fig. 21 (1912); Leandri, Bull. Soc. Bot. France 85: 524 (1939); Cavaco, Bull. Mus. Hist. Nat. Paris 21: 272 (1949); Léonard, Bull. Jard. Bot. Brux. 25: 316 (1955), 28: 118 (1958), Fl. Congo Belge 8(1): 188 (1962); Keay, Fl. W. Trop. Afr. ed. 2, 1: 398 (1958); Radcl.-Sm., Gen. Euphorb.: 337, fig. 42 (2001).

Dioecious shrubs; latex not recorded; indumentum simple. Leaves entire or denticulate, pellucid-punctate, usually with paired basal glands at junction with petiole; stipules deciduous. Inflorescences terminal, cymose-paniculate; bracts entire, eglandular, the pistillate deciduous. Staminate flowers pedicellate; calyx closed in bud, splitting into 2 or 3 valvate segments; petals 5, white, distinct, imbricate, glabrous; disk segments 5, glabrous; stamens 13–40, filaments

irregularly connate at the base; anthers with enlarged connective; pollen spheroidal, grains inaperturate, exine with Croton pattern, pillars acute, smooth; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, distinct, imbricate, entire, persistent in fruit; petals 4 or 5, distinct, imbricate; disk cupular, lobed, glabrous; ovary 3-locular, glabrous; ovules anatropous, inner integuments thick, vascularized; stylodia bifid. Fruits capsular; columella triquetrous, persistent. Seeds ecarunculate, testa smooth.

Eight spp., C and W Africa and (1) Madagascar.

248. *Tapoides* Airy Shaw

Tapoides Airy Shaw, Kew Bull. 14: 473 (1960), 20: 412 (1966), Hook. Icon. Pl. 37: t. 3632 (1967), Kew Bull. Add. Ser. 4: 200 (1975); Radcl.-Sm., Gen. Euphorb.: 337 (2001).

Dioecious trees; latex reddish; indumentum simple, scanty. Leaves petiolate (pulvinate), crowded at ends of branches, entire, lacking basal glands; stipules subulate, minute. Inflorescences axillary or subterminal, the staminate thyrsoid-paniculate, the pistillate glomerular; bracts entire. Staminate flowers pedicellate; calyx closed in bud, splitting into 3 valvate segments; petals 5, distinct, imbricate, adaxially pubescent; disk segments 5; stamens 6–8, filaments distinct, pubescent; pistillode 0. Pistillate flowers pedicellate; calyx splitting into 3 valvate segments, persistent in fruit; petals and disk unknown; ovary 3-locular, pubescent. Fruits capsular. Mature seeds not recorded.

A single sp., *T. vilamilii* (Merr.) Airy Shaw, endemic to Borneo (Sabah). Airy Shaw (1967) suggested that it is most closely related to *Aleurites* and *Elateriospermum* but also pointed out possible affinities with *Omphalea*. However, the reddish latex, mainly axillary inflorescences, and distinct stamens of *Tapoides* set it apart from the other Grosserinae; this suggests that it may be misplaced.

249. *Tannodia* Baill.

Tannodia Baill., Adansonia I, 1: 251 (1861); Müll. Arg. in DC., Prodr. 15(2): 728 (1866); Pax & K. Hoffm., Pflanzenr. 147, VI: 110 (1912); Léonard, Bull. Jard. Bot. Brux. 25: 300 (1955), Fl. Congo Belge 8(1): 186 (1962); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 172, fig. 32 (1987); Webster, Ann. Missouri Bot. Gard. 81: 115 (1994); Radcl.-Sm., Fl. Zambesiaca 9(4): 306, t. 64 (1996), Kew Bull. 53: 173 (1998), Gen. Euphorb.: 338 (2001).
Tandonia Baillon (1861).
Holstia Pax (1909; nom. illeg.).
Domohinea Leandri (1941).
Neoholstia Rauschert (1982).

Monoecious or dioecious trees; latex not recorded; indumentum simple, scanty [inflorescences only]. Leaves eglandular; stipules persistent or deciduous. Inflorescences terminal, racemoid or spiciform, or the staminate in contracted glomerules, unisexual or bisexual; bracts entire to glandular-lacerate. Staminate flowers pedicellate; calyx closed in bud, splitting into 2–5 valvate segments; petals 4 or 5, white, distinct, imbricate, longer than calyx; disk segments 4 or 5, glabrous; stamens 7–12, filaments connate below, biseriate; anthers dorsifixed, the outer extrorse, inner introrse, connective broad; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, basally connate, imbricate, entire, persistent in fruit; petals 4 or 5, distinct, imbricate, exserted beyond sepals; disk annular; ovary 3-locular, pubescent; ovules anatropous, inner integuments thick, vascularized; stylodia basally connate, erect, bifid. Fruits capsular. Seeds ellipsoidal, ecarunculate, testa smooth.

Nine spp., three in Africa and six in Madagascar (including the Comoros).

250. *Oligoceras* Gagnep.

Oligoceras Gagnep., Bull. Soc. Bot. France 71: 872 (1925); Fl. Indochine 5: 467, fig. 58, 3–9 (1926); Airy Shaw, Kew Bull. 14: 392 (1960).

Monoecious trees; latex not recorded; foliage glabrous. Leaves long-petiolate, lamina $\pm$ deltoid, with 2 discoid glands at apex of petiole; stipules 0. Inflorescences terminal, paniculate, bisexual; bracts scale-like, apically fimbriate. Staminate flowers pedicellate; calyx campanulate, sepals 5, connate, each with a cylindric-cornute truncate appendage; petals 5, distinct, imbricate, unguiculate; disk segments 5, connate around the base of the staminal column; stamens and staminodes connate in 2 whorls into a cylindrical column, outer whorl of 5 stamens, inner of 3 staminodes; anthers introrse; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; calycine appendages obtuse, otherwise perianth as in staminate flowers; disk annular; ovary 3-locular, stylodia nearly distinct,

bifid, stigmatic portion coiled. Fruits drupaceous. Seeds unknown.

A single sp., *O. eberhardtii* Gagnep., known only from Annam, Vietnam.

251. *Deutzianthus* Gagnep.

Deutzianthus Gagnep., Bull. Soc. Bot. France 71: 139 (1924), Fl. Indochine 5: 296, figs. 31, 3–9, 32, 1 (1925); Airy Shaw, Kew Bull. 14: 362 (1960), 16: 346 (1963); Webster, Ann. Missouri Bot. Gard. 81: 104 (1994); Radcl.-Sm., Gen. Euphorb.: 291 (2001).
Loerzingia Airy Shaw (1963).

Dioecious trees; latex yellowish-orange; indumentum simple. Leaves long-petiolate, with 2 adaxial disciform glands at junction with petiole; stipules deciduous. Inflorescences long-pedunculate, terminal or subterminal, of compound unisexual dichasia, bracts linear, eglandular, persistent. Staminate flowers pedicellate; sepals 5, ± connate, the calyx 5-dentate, valvate or subimbricate; petals 5, distinct, entire, adaxially pilose; disk glands 5; stamens 7 or 8, biseriate, 5 outer distinct, 2 or 3 inner connate to halfway; anthers cordulate or sagittate at the base; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0 or rudimentary. Pistillate flowers pedicellate; perianth as in staminate; disk annular or 5-lobed; ovary 3-locular, sericeous; stylodia 3, distally twice bifid, or deeply branched and apically bifid, hence appearing as 6 stylodia. Fruits ± indehiscent or tardily dehiscent. Seeds unknown.

Two species, disjunct in Vietnam and Sumatra. Radcliffe-Smith (2001) maintains *Loerzingia* as a distinct genus on the basis of its deciduous foliar glands, imbricate sepals, and presence of pistillode in the staminate flower. The type species, *D. tonkinensis* Gagnep., does indeed differ in these characters, but the similarities seem more important than the differences.

12d. Subtribe Crotonogyninae G.L. Webster (1975).

Trees or shrubs, sometimes scandent; latex apparently not produced; indumentum stellate or lepidote; leaves pinnately or palmately veined, biglandular at junction with petiole, stipulate; inflorescences axillary, spiciform or racemoid to paniculate; staminate sepals connate in bud, valvately dehiscent; petals coherent or connate; disk dissected; stamens 7–40, distinct or connate; anthers often apiculate; pistillate sepals 4 or 5, imbricate or valvate; ovary 3-locular; stylodia bifid or multifid; fruits capsular; seeds ecarunculate.

A subtribe of three African genera.

Key to the Genera of Crotonogyninae

1. Leaf blades palmately veined; petioles with inflated hairs; stylodia bifid; lianas **254. *Manniophyton***
– Leaf blades pinnately veined; petioles lacking inflated hairs; stylodia bifid or multifid; trees or shrubs 2
2. Stylodia bifid; inflorescences terminal, paniculate; staminate petals distinct; staminate disk receptacular and extrastaminal, of > 10 segments **252. *Cyrtogonone***
– Stylodia multifid; inflorescences axillary, racemoid or spiciform; staminate petals usually coherent or connate; staminal disk extrastraminal, of 5–8 segments **253. *Crotonogyne***

252. *Cyrtogonone* Prain

Cyrtogonone Prain, Kew Bull. 1911: 231 (1911), Hook. Icon. Pl. 31: t. 3009 (1915); Pax & K. Hoffm., Pflanzenr. 147, VI: 111, fig. 23 (1912); Keay, Fl. W. Trop. Afr., ed. 2, 1: 399 (1958); Webster, Ann. Missouri Bot. Gard. 81: 116 (1994); Radcl.-Sm., Gen. Euphorb.: 342 (2001).

Dioecious trees; latex not recorded; indumentum lepidote. Leaves entire or dentate, silvery-lepidote abaxially, with paired basal glands at junction with petiole; stipules minute. Inflorescences terminal, cymose-paniculate; bracts inconspicuous. Staminate flowers pedicellate; calyx closed in bud, splitting into 2–4 valvate segments; petals 5 (6), distinct, contorted, glabrous; disk segments c. 10, receptacle glandular; stamens 12–30, filaments distinct, glabrous; anthers dorsifixed, introrse; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, imbricate, entire; petals 5, distinct, imbricate; disk annular; ovary 3-locular, pubescent; stylodia bifid. Fruits capsular, cocci dorsally verrucate. Seeds subspheroidal, ecarunculate.

A single sp., *C. argentea* (Pax) Prain, W Africa.

253. *Crotonogyne* Müll. Arg.

Crotonogyne Müll. Arg., Flora 47: 535 (1864), in DC., Prodr. 15(2): 720 (1866); Pax & K. Hoffm., Pflanzenr. 147, VI: 111, fig. 24 (1912); Prain, Hook. Icon. Pl. 31: t. 3019 (1915); Keay, Fl. W. Trop. Afr., ed. 2, 1: 399 (1958); Léonard, Fl. Congo Belge 8(1): 174, fig. 14 (1962); Webster, Ann. Missouri Bot. Gard. 81: 116 (1994); Radcl.-Sm., Gen. Euphorb.: 342 (2001).
Neomanniophyton Pax (1912).

Dioecious (monoecious); latex not recorded; indumentum simple and stellate or lepidote. Leaves with basal laminar glands at junction with petiole; stipules entire, ± persistent. Inflorescences axillary, racemoid or spiciform, sometimes branched; bracts biglandular at base. Staminate flowers pedicellate; calyx closed in bud, splitting into 2–4 valvate segments; petals 5, mostly ± connate; disk segments 5–8, glabrous; receptacle glabrous; stamens (7–)10–28, filaments distinct; anthers apiculate; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals (4)5, slightly connate basally, imbricate, abaxially lepidote, persistent in fruit; petals (4)5(6), distinct, imbricate, glabrous; disk annular-lobed, glabrous; ovary 3-locular, stellate-pubescent or lepidote; ovules anatropous, inner integuments thick, vascularized; stylodia multifid. Fruits capsular; columella persistent, slender, apically dilated. Seeds somewhat compressed, ecarunculate, testa smooth.

Sixteen spp., W Africa, from Sierra Leone to Angola. Pax (1912) separated *Neomanniophyton* from *Manniophyton* on the basis of leaf venation and division of the stylodia. However, further study has shown that *Neomanniophyton* is closer to *Crotonogyne* in its leaf venation and stylar branching. Although generic boundaries in the Crotogyninae need further study, it appears best to follow Webster (1994) and Radcliffe-Smith (2001) in combining *Crotonogyne* and *Neomanniophyton*.

254. *Manniophyton* Müll. Arg.

Manniophyton Müll. Arg., Flora 47: 530 (1864), in DC., Prodr. 15(2): 719 (1866); Benth., Hook. Icon. Pl. 13: t. 1267 (1878); Pax & Hoffm., Pflanzenr. 147, VI: 120, fig. 25 (1912); Keay, Fl. W. Trop. Afr. et. 2, 1: 400 (1958); Léonard, Fl. Congo Belge 8(1): 171, fig.13 (1962); Radcl.-Sm., Gen. Euphorb.: 343 (2001).

Dioecious lianas; latex reddish; indumentum simple to stellate. Leaves simple, sometimes 3–5-lobed, palmately veined, with paired stipels and bottle-shaped glands abaxially near junction with petiole; stipules deciduous. Inflorescences terminal and axillary, often in pairs, ± thyrsoid-paniculate; bracts biglandular at base. Staminate flowers pedicellate; calyx closed in bud, splitting into 2 or 3 valvate segments; petals 5, glabrous, connate into an urceolate corolla [lobes much shorter than tube]; disk segments 5 or 6, pubescent; receptacle pilose; stamens 10–20, filaments distinct; anthers basifixed, apiculate, connective enlarged; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5, slightly connate at base, imbricate, entire, persistent and somewhat accrescent in fruit, petals 5, yellowish-green, distinct, imbricate, adaxially pubescent; disk annular, pubescent; ovary 3-locular, sericeous-hispid; ovules anatropous, inner integuments moderately thick, vascularized; stylodia bipartite. Fruits capsular, cocci thick and woody; columella persistent. Seeds compressed, ecarunculate, thin and shiny.

A single sp., *M. africanum* Müll. Arg., West Africa, Liberia to Angola.

12e. Subtribe Neoboutoninae (Hutch.) G.L. Webster (1975).

Dioecious trees or shrubs; indumentum stellate or lepidote; leaves unlobed, pinnately or palmately veined, glandular-dotted, stipulate; inflorescences terminal or axillary, racemoid to paniculate; calyx segments 2 or 3; disk dissected or 0; stamens 15–40, filaments distinct, shorter than anthers; anthers with glandular connective; ovary 3-locular; stylodia bifid; fruit capsular; seeds carunculatae or ecarunculate.

Two genera, African and Malagasy.

Key to the Genera of Neoboutoninae

1. Leaf blades palmately veined; stipules persistent; seeds carunculate; indumentum stellate **255. *Neoboutonia***
– Leaf blades pinnately veined; stipules deciduous; seeds ecarunculate; indumentum lepidote **256. *Benoistia***

255. *Neoboutonia* Müll. Arg.

Neoboutonia Müll. Arg., J. Bot. 2: 336 (1864), in DC., Prodr. 15(2): 892 (1866); Benth., Hook. Icon. Pl. 13: t. 1298, 1299 (1879); Pax & K. Hoffm., Pflanzenr. 147, VII: 71 (1914); Radcl.-Sm., Fl. Zambesiaca 9(4): 310, t. 66 (1996).

Dioecious trees and shrubs; latex not recorded; indumentum tufted-stellate and simple. Leaves palmately veined, cordate, with basal laminar stipellate glands and minute dispersed discoid glands; stipules ± foliaceous, entire, persistent. Inflorescences terminal and axillary, cymose-paniculate; staminate bracts entire, eglandular, persistent. Staminate flowers pedicellate; calyx closed in bud, splitting into 2 or 3 segments; petals 0; disk segments 8–10, minute; stamens 15–40, filaments distinct; anthers basifixed,

introrse, glandular-apiculate; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5, distinct, imbricate, entire, persistent, sometimes accrescent; petals 0; disk annular; ovary 3-locular, stellate-pubescent or lepidote; ovules anatropous, inner integuments very thick, vascularized; stylodia bipartite, branches slender. Fruits capsular; columella persistent. Seeds subspheroidal, caruncle small, adpressed; testa smooth.

Three spp., widespread in tropical Africa. Pax and Hoffmann (1914) spectacularly misplaced *Neoboutonia* into the Acalypheae-Mercurialinae, assigning it to series Neoboutoniiformes. This was negated by Punt (1962), who showed that the pollen of *Neoboutonia* has the typical Crotonoid pattern of exine ornamentation.

256. *Benoistia* H. Perrier & Leandri

Benoistia H. Perrier & Leandri, Bull. Soc. Bot. France 85: 528 (1938); Radcl.-Sm., Kew Bull. 43: 632 (1988).

Dioecious trees; latex not recorded; indumentum simple and glandular-lepidote. Leaves pellucid-punctate, lacking basal glands at junction with petiole; stipules minute, deciduous. Inflorescences axillary, racemoid or paniculate; pistillate bracts foliose. Staminate flowers pedicellate; calyx closed in bud, splitting into 2 or 3 valvate lobes; petals 0; disk segments interstaminal or 0; stamens 28–30, filaments distinct, shorter than anthers; anthers basifixed, introrse, connective apically glandular; pollen grains spheroidal, inaperturate, with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5–7, imbricate, persistent and ± accrescent in fruit; petals 0; disk annular, pubescent; ovary mainly (2)3(4)-locular, stellate-tomentose; ovules anatropous, inner integuments very thick, vascularized; stylodia bifid. Fruits smooth to tuberculate, dehiscing septicidally; columella trigonous, persistent. Seeds ellipsoidal, ecarunculate, testa smooth; endosperm oily.

Three spp., endemic to Madagascar.

12f. Subtribe Paracrotoninae G.L. Webster[1]

Monoecious trees or shrubs; leaves ± dentate; sepals and petals 5(6), distinct; staminate disk of distinct glands, pistillate disk annular; stamens 10–32, outer filaments distinct, the inner connate into a column; inflorescences terminal or axillary; seeds carunculate or ecarunculate.

Mildbraedia and *Paracroton* appear to represent sister genera united by a distinctive synapomorphy of the androecium with the outer filaments distinct and the inner connate.

Key to the Genera of Paracrotoninae

1. Dioecious; inflorescences axillary; leaf blades without paired basal glands; seed coat dry **257. *Mildbraedia***
– Monoecious; inflorescences terminal; leaf blades with paired basal glands; seed coat fleshy **258. *Paracroton***

257. *Mildbraedia* Pax Fig. 42

Mildbraedia Pax, Bot. Jahrb. 43: 319 (1909); Pflanzenr. 147, III: 11 (1911), 147, VII: 403 (1914); Léonard, Fl. Congo Belge 8(1): 85 (1962); Radcliffe-Sm., Fl. E. Trop. Afr., Euphorb. 1: 340, fig. 64 (1987), Fl. Zambesiaca 9(4): 273, t. 56 (1996).
Neojatropha Pax (1910).

Dioecious trees or shrubs; latex not recorded; indumentum stellate. Leaves simple, sometimes lobed, triplinerved or pinnately veined, dentate, eglandular; stipules subulate, deciduous. Inflorescences axillary or slightly supraaxillary, pedunculate, dichasial, the pistillate flowers central; bracts minute, deciduous. Staminate flowers pedicellate; sepals 5 (6), distinct, imbricate; petals 5 (6), distinct, imbricate, pubescent abaxially; disk segments 5; stamens 10–25, outer filaments distinct but inner connate into a column, not inflexed in bud; anthers dorsifixed, introrse, muticous; pollen grains spheroidal, inaperturate, eine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5 (6), distinct, imbricate, persistent in fruit; petals 5 (6), distinct, imbricate; disk annular, slightly lobed, glabrous; ovary 3-locular, pubescent; ovules pachychalazal, inner integuments thick, vascularized; stylodia nearly distinct, deeply bifid, branches slender. Fruits capsular, cocci thin-walled; columella persistent. Seeds subspheroidal, caruncle subspherical, appressed; testa crustaceous, smooth.

Three or four spp., tropical Africa, from Liberia and Gabon to Kenya and Mozambique.

258. *Paracroton* Miq.

Paracroton Miq., Fl. Ind. Batav. 1(2): 382 (1859); Müll. Arg. in DC., Prodr. 15(2): 1112 (1866); J.J. Sm., Meded. Dept. Landb. 12: 585 (1910); Pax, Pflanzenr. 147, III: 12

[1] Subtr. **Paracrotoninae** G.L. Webster, **subtrib. nov.**, monoici; inflorescentiis axillaribus; fructibus capsularis; sepalis foemineis persistentibus; petalis connatis vel liberis. Typus: *Paracroton* Miquel.

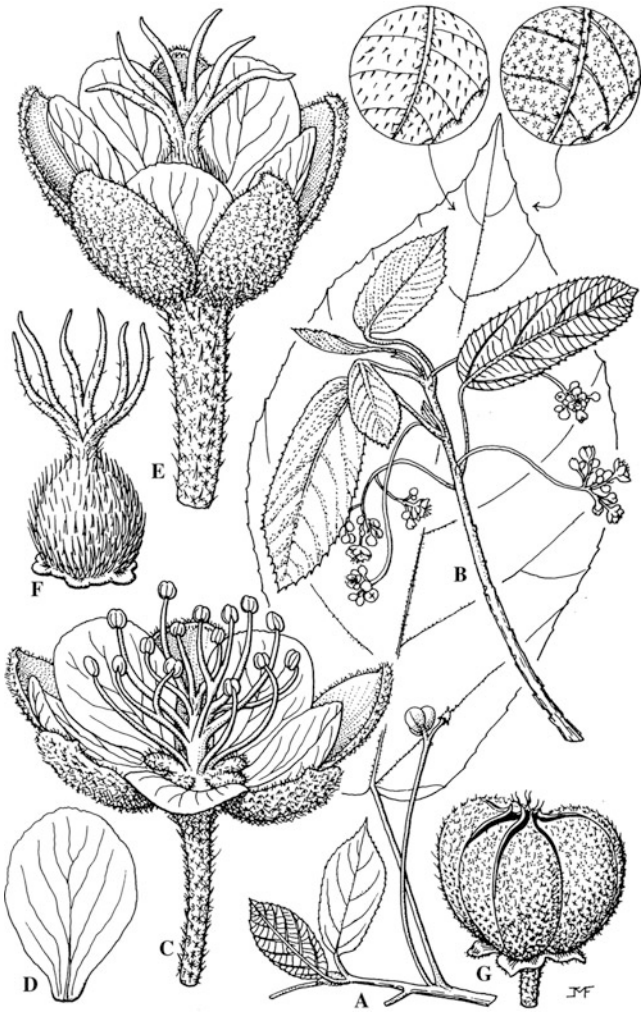

Fig. 42. Euphorbiaceae-Crotonoideae. *Mildbraedia carpinifolia* var. *strigosa*. **A** Distal portion of fruiting branch. **B** Distal portion of branch with staminate flowers. **C** Staminate flower. **D** Petal. **E** Pistillate flower. **F** Pistil. **G** Fruit. (Radcliffe-Smith 1996; drawn by J.M. Fothergill)

(1911); N.P. Balakr. & Chakrab., Kew Bull. 48: 716, figs. 1–3 (1993); Radcl.-Sm., Gen. Euphorb.; 318 (2001).

Fahrenheitia Rchb. f. & Zoll. (1857).

Desmostemon Thwaites (1861).

Monoecious trees; latex not recorded; indumentum stellate or lepidote. Leaves petiolate (pulvinate), glandular-dentate or serrate, biglandular at junction with petiole; stipules represented by sessile glands. Inflorescences terminal, unisexual; staminate inflorescences terminal and axillary, narrowly thyrsoid; pistillate inflorescences terminal, thyrsoid, sparsely branched, flowers 1–3 per node; bracts deciduous. Staminate flowers subsessile; sepals 5, slightly connate, imbricate, dorsally often with knob- or horn-like appendage; petals 5, distinct; disk segments 5, 7 or 10; stamens 12–32, outer filaments distinct, inner ones connate into a column; anthers dorsifixed, extrorse, muticous; pollen grains spheroidal, inaperturate, with Croton pattern. Pistillate flowers pedicellate; calyx as in staminate, persistent in fruit, petals 5, coherent, glabrous, deciduous; disk annular, lobed, pilose; ovary 3-locular, pubescent; stylodia bifid. Fruits capsular. Seeds spheroidal, ecarunculate, testa smooth or striate, slightly fleshy.

Four spp., tropical Asia from Sri Lanka to W Malesia, the Philippines, and New Guinea. Balakrishnan and Chakrabarty (1993) believe that the closest allies of *Paracroton* are *Ostodes* and *Dimorphocalyx*.

Unplaced genus of inaperturate crotonoids:

259. *Radcliffea* P. Hoffm. & K. Wurdack

Radcliffea P. Hoffm. & K. Wurdack, Kew Bull. 61: 194 (2006).

Dioecious shrub or tree, probably latescent; indumentum stellate. Leaves long-petiolate, domatiiferous, at base palminerved, at junction with petiole provided on both sides with minute glands; stipules apparently sometimes replaced by minute glands. Inflorescences terminal, paniculate, with 3–5 orders of branching. Staminate flowers pedicellate, sepals 5, distinct, imbricate, outermost bearing a small abaxial gland; petals 5, distinct, imbricate; disk glands 5, distinct; stamens 5, with the filaments connate for more than half their length into a column; pollen grains spheroidal, inaperturate, with Croton pattern; pistillode +. Pistillate flowers pedicellate, sepals 5, distinct, imbricate, all with abaxial gland; petals 4–7, distinct, imbricate; disk-glands 5, distinct or irregularly connate; ovary 1-locular, asymmetrical; ovule 1, anatropous, inserted subapically; stylodia 3, inserted excentrically, simple, unequal. Fruits and seeds unknown.

A single sp., *R. smithii* P. Hoffm. & K. Wurdack, from deciduous forests on limestone in W Madagascar.

VII. Subfam. Euphorbioideae

Monoecious (dioecious) trees, shrubs, or herbs (scandent); laticifers non-articulate, latex mostly whitish; indumentum simple or 0, dendritic in *Mabea* and *Senenefelderopsis*. Leaves alternate or opposite, simple, unlobed, entire or dentate, usually pinnately veined, often with basal glands at junction with petiole; stipules often reduced or 0. Inflorescences terminal or axillary, spiciform to racemoid or paniculate or condensed into the pseudanthial cyathium; bracts often biglandular at base. Flowers apetalous, erect or inclinate in bud; staminate sepals (1)3–6, imbricate to valvate, mostly open in bud, commonly minute or 0; disk 0; stamens 1–20(−80), filaments distinct or connate; pollen grains binucleate or trinucleate, 3-colporate, colpi usually marginate, exine usually tectate-perforate; pistillode 0; pistillate sepals 3–6, distinct or connate, imbricate or open in bud, sometimes reduced to obsolete; disk 0; ovary 2–3(−20)-locular; stylodia distinct or connate, nearly always unlobed. Fruits capsular (drupaceous). Seeds carunculate or ecarunculate; testa dry or fleshy, exotegmen palisadal; endosperm copious.

Molecular analyses (Wurdack et al. 2005; Tokuoka 2007) confirm the broad lines of the classification of this subfamily and the inclusion of the Stomatocalyceae, which had been suggested by Webster (1975) and accepted by Radcliffe-Smith (2001); the Stomatocalyceae are resolved as sister to the rest of the subfamily. This is divisible into two subclades, which contain the Hippomaneae and the Euphorbieae, the latter broadened by inclusion of the Hureae and Pachystromateae.

Key to the Tribes of Subfam. Euphorbioideae

1. Pollen exine tectate-reticulate; bracts eglandular, distinct from rachis; stylodia unlobed; seeds ecarunculate; dioecious trees or lianas **1. Stomatocalyceae**
– Pollen exine tectate-perforate; bracts glandular, often adnate to rachis; stylodia bifid or unlobed; seeds carunculate or ecarunculate; monoecious (dioecious) trees, shrubs, or herbs, rarely scandent 2
2. Inflorescences mostly racemoid or spiciform, sometimes capitate but never cyathial; flower buds usually inclinate; staminate calyx usually well developed; stylodia mostly unlobed; intine thickenings along the colpi 0 **2. Hippomaneae** s. l.
– Inflorescences pseudanthial, i.e., cyathial, usually with a single terminal pistillate flower, and 4 or 5 lateral staminate monochasia or dichasia; perianth reduced or 0; stylodia mostly bifid; colpi bordered by two conspicuous intine thickenings **3. Euphorbieae**

1. Tribe Stomatocalyceae (Müll. Arg.) G.L. Webster (1975).

Dioecious trees, shrubs, or lianas; latex yellowish, often scanty; indumentum simple or 0; leaves alternate, unlobed, pinnately veined, without glands at base of blade; stipules small and caducous or 0; inflorescences axillary, racemoid, bracts eglandular; staminate sepals 4–8, distinct and imbricate or connate; stamens 10–30, distinct, filaments shorter than anthers; pollen grains coarsely reticulate or reticulate-perforate; pistillate sepals 5 or 6, distinct or connate; ovary 2–10-locular; stylodia unlobed, sometimes dilated or stigmatiform; fruit capsular or indehiscent, 1–3-seeded; seeds ecarunculate; endosperm copious, oily.

Four genera and about 12 spp., pantropical.

Key to the Genera of Stomatocalyceae

1. Fruits indehiscent; stylodia abbreviated; ovary 1–10-locular; pollen grains finely reticulate-perforate 2
– Fruits capsular; stylodia elongated; ovary 2–3-locular; pollen grains coarsely reticulate 3
2. Sepals 6–8, distinct; ovary 1-locular **262. *Plagiostyles***
– Sepals connate, calyx 2-lipped; ovary 2–10-locular **263. *Pimelodendron***
3. Ovary 3-locular; stylodia erect; stamens 18–20; pistillate sepals not glandular; stems ± scandent **261. *Hamilcoa***
– Ovary 2-locular; stylodia spreading; stamens 10; pistillate sepals with large basal glands; stems not scandent **260. *Nealchornea***

260. *Nealchornea* Huber

Nealchornea Huber, Bol. Mus. Goeldi 7: 297 (1913); Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 201, t. 10 (1922); Wallnöfer, Linzer Biol. Beitr. 23(2): 777 (1991); Radcl.-Sm., Gen. Euphorb.: 352 (2001).

Dioecious trees; latex whitish or yellowish; indumentum simple, scanty. Leaves remotely glandular-crenate, with small abaxial basal or submarginal glands; stipules obsolete. Inflorescences axillary and subterminal, the staminate paniculate, the pistillate racemose; bracts eglandular. Staminate flowers pedicellate; sepals 4, biseriate, slightly imbricate, open in bud; stamens 8–15 (−18), distinct; anthers sessile, erect, dehiscing

longitudinally; connective enlarged, conspicuously appendiculate terminally; pollen grains oblate spheroidal, 3-colporate, sexine coarsely reticulate. Pistillate flowers pedicellate; sepals 4, basally connate, slightly imbricate, glandular, persistent in fruit; ovary 2-locular; ovules anatropous, inner integuments moderately thick, outer integuments vascularized; stylodia unlobed, thickened, slightly connate at base. Fruits ± baccate, not regularly dehiscent, thin-walled. Seeds ecarunculate.

Two spp., lowland Amazonian forests of Brazil and adjacent Peru and Colombia.

261. *Hamilcoa* Prain

Hamilcoa Prain, Kew Bull. 1912: 107 (1912), Fl. Trop. Afr. 6(1): 1000 (1913); Stapf, Hook. Icon. Pl. 31: t. 3990 (1915); Keay, Fl. W. Trop. Afr., ed. 2, 1: 413 (1958).

Dioecious lianas; latex white; indumentum 0. Leaves simple or occasionally lobed, entire or subentire, eglandular; stipules minute, caducous. Inflorescences racemoid, staminate axillary, pistillate terminal; bracts eglandular, 1-flowered. Staminate flowers pedicellate; sepals 5, distinct, imbricate; stamens 18–30, distinct, filaments much shorter than anthers; anthers basifixed, the exterior extrorse, dehiscing longitudinally; pollen grains coarsely reticulate. Pistillate flowers with thick reflexed pedicels; sepals 6, biseriate, imbricate, subentire; ovary 3-locular; stylodia connate at base, erect, dilated, unlobed. Fruits capsular. Seeds with spongy testa.

Only one sp., *H. zenkeri* Prain, from lowland forests in Nigeria and Cameroon.

262. *Plagiostyles* Pierre

Plagiostyles Pierre, Bull. Mens. Soc. Linn. Paris 2: 1326 (1897); Prain, Fl. Trop. Afr. 6(1): 1001 (1913); Stapf, Hook. Icon. Pl. 31: t. 3010 (1915); Léonard, Fl. Congo 8 (1): 131 (1962); Radcl.-Sm., Gen. Euphorb.: 348, fig. 44 (2001).

Dioecious trees or shrubs; latex white, scanty; indumentum simple. Leaves eglandular or with small paired adaxial glands; stipules entire, deciduous. Inflorescences axillary, paniculate or racemoid; bracts eglandular, 1-flowered. Staminate flowers pedicellate; sepals 5–8, unequal, imbricate but not covering the stamens in bud; stamens 15–32, distinct, aggregated-capitulate, filaments much shorter than anthers; anthers extrorse, reddish, dehiscing longitudinally; pistillode 0. Pistillate flowers pedicellate; sepals 5, unequal, imbricate, entire, persistent in fruit; ovary 1(2)-locular; ovules anatropous, inner integuments moderately thick; stylodia lateral with discoid stigma. Fruit drupaceous; endocarp membranaceous, adherent to seed. Seeds ecarunculate, transversally veined; endosperm yellowish, oily; cotyledons reniform.

Only one sp., *P. klaineana* Pierre, from the rainforests in Nigeria, Gabon, and Congo.

263. *Pimelodendron* Hassk.

Pimelodendron Hassk., Versl. Med. Afd. Natuurk. Kon. Akad. Wetensch. 4: 140 (1856); J.J. Sm., Bull. Jard. Bot. Buit. III, 6: 100 (1924); Airy Shaw, Kew Bull. 36: 339 (1981).

Dioecious trees; latex whitish or yellowish; indumentum 0 on twigs. Leaves subentire or crenate, eglandular; stipules minute, deciduous. Inflorescences axillary, sometimes cauliflorous, racemoid; bracts eglandular. Staminate flowers pedicellate; sepals connate into a 2-lipped calyx; stamens 10–16, distinct or coherent, shorter than anthers; anthers basifixed, extrorse, dehiscing longitudinally; pistillode 0. Pistillate flowers pedicellate; calyx cupular, 2–3-lobed, persistent in fruit; ovary 2–10-locular; ovules anatropous, inner integuments thick; outer integuments vascularized; stylodia coalescent into a stigmatoid apex. Fruit indehiscent, fleshy. Seed solitary, carunculate, subspheroidal, testa striate-reticulate.

Six to eight spp. from tropical Asia and Australia.

2. Tribe Hippomaneae A. Juss. ex Spach (1834).

Hureae Dumort. (1829).
Pachystromateae (Pax & Hoffm.) Pax (1924).

Monoecious, less commonly dioecious trees, shrubs, or herbs; latex usually milky, sometimes toxic; indumentum simple or 0, dendritic in *Mabea*; leaves alternate (opposite), simple and unlobed; lamina pinnately (palmately) veined, commonly with laminar or petiolar glands; stipules sometimes reduced or 0; inflorescences terminal or axillary, racemoid or spiciform (paniculate), usually bisexual with 1 or 2 pistillate flowers at proximal nodes; bracts mostly glandular; flowers usually inclinate in bud; staminate calyx usually open in bud, sepals 0–3, distinct or connate, imbricate to valvate; stamens 1–70,

filaments distinct or connate proximally; anthers extrorse; pollen grains 3-colporate, colpi usually marginate, exine tectate-perforate: pistillate sepals 3–6, imbricate, sometimes reduced or 0; ovary 2–3(−10)-locular; stylodia distinct or connate, unlobed, in one genus the stigmas connate into an umbrella-shaped disk; fruits capsular or drupaceous; seeds carunculate or ecarunculate, testa dry or fleshy; endosperm copious, not oily.

A mainly neotropical tribe of about 30 genera, broadened here to include tribes Pachystromateae and Hureae. In the analysis of Wurdack et al. (2005), the monotypic Pachystromateae are embedded in the Hureae, and the Hureae form part of one of the two strongly supported subclades representing the Hippomaneae. This confirms earlier expectations by Webster (1994b), who doubted the justification of tribal distinctness of *Pachystroma* and pointed to the closeness of the Hureae to the Hippomaneae (which had been included in that tribe as subtribe Hurinae by previous authors). The subtribal division of the Hippomaneae by Webster (1994) and Esser (2001) is not confirmed by the molecular data and their subtribes are not maintained here, but in the molecular analysis two subclades (H1 and H2) are recognized that cannot be characterized morphologically. The classification of the Hippomaneae presents some of the most intractable problems in the family, and both the delimitation of some larger genera such as *Excoecaria*, *Gymnanthes*, *Sapium*, and *Sebastiana* and the justification of several recently described small genera remain controversial. Overall, the preponderance of small genera (five monotypic, five others with only two or three species) is striking and appears as the work of excessive splitting.

Key to the Genera of Tribe Hippomaneae

1. Leaves present only on young branchlets, plants later leafless, succulent, thorny shrubs, flowering when leafless **288. *Spegazziniophytum***
– Leaves present on older branches; flowering with leaves or, if flowering when leafless, then not a succulent thorny shrub 2
2. Floral bracts eglandular, peltate or adnate to the rachis and covering the flowers; seeds ecarunculate 3
– Floral bracts 2-glandular at the base or eglandular, not peltate nor adnate to the rachis 5
3. Ovary 5–20-locular; stamens 10–80, connate; tips of stylodia radiating from apical disk of column; seeds strongly compressed **279. *Hura***
– Ovary 3-locular; stamens 1–3, distinct or connate; stylodia connate but tips not radiating from a disk 4
4. Stylodia connate 1/3 to 2/3 their length, not distally clavate; tips of staminal sepals distinct, imbricate; staminate spikes mostly terminal **280. *Algernonia***
– Stylodia connate their entire length, distally clavate with deltoid apices; staminal sepals completely connate into a cup; staminate spikes axillary **281. *Ophthalmoblapton***
5. Flowers erect in bud; staminate calyx closed in bud, splitting valvately into 2 segments; filaments and anthers connate; seeds ecarunculate; leaves spinose-dentate **282. *Pachystroma***
– Flowers inclinate in bud; staminate calyx open in bud; stamens distinct or filaments connate; seeds carunculate or ecarunculate; leaves mostly not spinose-dentate [Hippomaneae s. str.] 6
6. Staminate calyx laterally compressed or zygomorphic inclinate, with 1 or 2 distinct lobes; stylodia apically glandular and often bifid **271. *Homalanthus***
– Staminate calyx radially symmetric or rarely zygomorphic-inclinate, with 2 or more lobes or completely connate; stylodia apically undivided and eglandular 7
7. Staminate flowers with 5(6) sepals; stylodia usually connate into a long common style with slender branches; leaves and stems with dendritic hairs **275. *Mabea***
– Staminate flowers with 0–3(4) sepals, calyx with more or less connate lobes, or without distinct lobes, or calyx lacking at all 8
8. Ovary 6–10-locular; bracts glandular **283. *Hippomane***
– Ovary 2- or 3-locular; bracts glandular or eglandular 9
9. Seed testa dry [at most with thin fleshy layer] 10
– Seed testa fleshy [arillate] 28
10. Columella 3-horned at base 11
– Columella not 3-horned at base 12
11. Staminate calyx 2-lobed; petiole glandular near apex **289. *Stillingia***
– Staminate calyx 0; petiole eglandular **287. *Adenopeltis***
12. Leaf blades palmately 3–11-lobed; staminate flower with 1 stamen **270. *Dalembertia***
– Leaf blades simple; staminate flower at least with 2 stamens 13
13. Staminate flowers in a glomerulate head; upper part of seed covered by an enlarged caruncle; leaves long-pedicellate **264. *Maprounea***
– Staminate flowers in an elongated inflorescence; caruncle 0 or small on top of seeds 14
14. Pistillate flowers sessile or subsessile, pedicel usually < 5 mm long in fruit; inflorescences mostly terminal, sometimes axillary as well 15

– Pistillate flowers pedicellate, pedicel usually > 5 mm long in fruit, or else ovary appendiculate; inflorescences mostly axillary 27
15. Inflorescences axillary; leaves alternate or opposite; calyx lobes of staminate flowers distinct or nearly so; mostly dioecious **293. *Excoecaria***
– Inflorescences terminal or axillary; leaves mostly alternate, opposite in *Microstachys* and *Colliguaja*, calyx lobes connate; mostly monoecious 16
16. Inflorescences mostly opposite leaves and with staminate flowers distichous; ovary with 2 vertical rows of appendages on each locule; seeds cylindric, truncate, with a stipitate caruncle **272. *Microstachys***
– Inflorescences terminal; staminate flowers spiral on inflorescence axis; ovary not with 2 rows of appendages on each locule; seeds neither cylindric nor truncate, mostly ecarunculate 17
17. Floral bracts with basal glands, or else stipules caducous; fruits capsular or indehiscent 18
– Floral bracts without basal glands; stipules persistent, ovate, ciliate; fruits capsular 23
18. Staminate calyx completely connate without distinct lobes; stamens 4–17 **267. *Senefeldera***
– Staminate calyx of 3 basally connate calyx lobes; stamens 2–3 19
19. Staminate flowers 5–9 per bract 20
– Staminate flowers 1–3 per bract 22
20. Sepals and stamens 2 per flower; ovary 2-locular, not appendaged; fruit drupaceous **278. *Balakata***
– Sepals 3, stamens 2–3 per flower; fruit capsular 21
21. Leaves eglandular above; ovary and fruit with 3 pairs of appendages **274. *Sclerocroton***
– Leaves above often with a pair of petiolar glands at the junction with the blade; ovary and fruit not appendaged **284. *Pleradenophora***
22. Stylodia distinct or nearly so; staminate flowers sessile to subsessile; leaves serrate **276. *Sebastiana***
– Stylodia proximally connate into a style, style branches undivided; staminate flowers shortly but distinctly pedicellate; leaves entire **273. *Ditrysina***
23. Lobes of staminate calyx 2–3, evident though basally connate 24
– Lobes of staminate calyx 1 or 2 and minute or completely reduced 26
24. Inflorescence axillary; ovary 2–3-locular and with 4 or 6 appendages **277. *Anomostachys***
– Inflorescence terminal; ovary 3-locular, unappendaged 25
25. Staminate flowers 6–20 per bract; stamens 2–5, filaments distinct; indumentum simple, often colored **266. *Senefelderopsis***
– Staminate flowers 2–4 per bract; stamens 3, filaments connate into a column; plants glabrous **286. *Grimmeodendron***
26. Inflorescences axillary; leaves (sub)opposite **292. *Colliguaja***
– Inflorescences on lateral short shoots; leaves alternate **285. *Bonania***
27. Inflorescence buds covered by caducous bud-scales; floral bracts irregular and weak, often nearly 0; stamens 4–16 **265. *Actinostemon***
– Inflorescence buds sheathed by the stiff, scaly floral bracts, not by sterile scales; stamens 2–6 **269. *Gymnanthes***
28. Inflorescences unisexual; fruits irregularly dehiscent; seeds whitish arillate **290. *Falconeria***
– Inflorescences bisexual 29
29. Seed aril reddish; flowers sessile or subsessile; leaf blades pinnately veined **291. *Sapium***
– Seed aril whitish; flowers pedicellate; leaf blades triplinerved **268. *Triadica***

264. *Maprounea* Aubl.

Maprounea Aubl., Hist. Pl. Guiane: 895, t. 342 (1775); Pax & K. Hoffm., Pflanzenr. 147, V: 175, fig. 32, 33 (1912); Léonard, Fl. Congo 8(1): 142, fig. 9 (1962); Radcl.-Sm., Fl. Trop. E. Africa, Euphorb. 1: 395, fig. 75 (1987); Webster & Huft, Ann. Missouri Bot. Gard. 75: 1131 (1988); Esser, Novon 9: 32, fig. 1 (1999).

Monoecious (dioecious) trees or shrubs; latex whitish; indumentum 0. Leaves usually with prominent subbasal laminar glands abaxially; petiole eglandular; stipules entire, eglandular, persistent. Inflorescences terminal, usually bisexual, with 1–5 proximal pistillate flowers separated from an ament-like staminate subflorescence; bracts biglandular at base, the staminate subtending 1–3(−5) flowers. Staminate flowers sessile to subsessile; sepals 2–3, connate into a cupular calyx; stamens (1)2–3, filaments connate into a column exserted beyond the calyx; anthers extrorse, dehiscing longitudinally. Pistillate flowers pedicellate, spreading or recurving; sepals 3, discrete, persistent in fruit; ovary 3-locular, smooth; ovules anatropous, inner and outer integuments thin (5 or 6 cell layers); stylodia connate into a common style [except in *M. amazonica*], style branches unlobed. Fruits capsular; columella slender, not persistent. Seeds ellipsoid, with a cap-like caruncle covering the upper half, testa smooth or foveolate.

Five spp., three in South America and two in Africa.

265. *Actinostemon* Mart. ex Klotzsch

Actinostemon Mart. ex Klotzsch, Arch. Naturg. 7: 184 (1841); Pax & K. Hoffm., Pflanzenr. 147, V: 57, figs. 10–14 (1912); Jablonski, Phytologia 18: 213–240 (1969); Burger & Huft, Fieldiana Bot. II, 36: 57 (1995); Berry & Esser, Fl. Venez. Guayana 5: 87, fig. 84 (1999).

Monoecious trees or shrubs; latex scanty; indumentum simple, often scanty. Leaves alternate or pseudo-verticillate, with dispersed glands abaxially; stipules deciduous. Inflorescences terminal and sometimes axillary, racemoid, and in bud

ament-like, enclosed by imbricate bud scales, axis glabrous or hirtellous; pistillate flowers proximal, 1–3 per bract; staminate flowers distal, 2 or 3 per bract; bracts biglandular (eglandular) at base, lamina minute or obsolete. Staminate flowers pedicellate; calyx rudimentary or 0; stamens 4–15 or more, filaments distinct; anthers basifixed, extrorse, dehiscing longitudinally; pollen grains 3-lobed, 3-colpate, exine tectate-perforate; pistillode 0. Pistillate flowers pedicellate, pedicel elongating in fruit; sepals minute or 0; ovary 3-locular, sometimes appendaged; stylodia unlobed, connate basally. Fruits capsular; columella persistent. Seeds spheroidal, subapically carunculate, testa smooth.

About 15 spp. ranging from the Caribbean to South American. The genus was combined by Webster (1994) with the superficially similar *Gymnanthes* but this is not supported by the molecular evidence.

266. *Senefelderopsis* Steyerm.

Senefelderopsis Steyerm., Bot. Mus. Leafl. Harvard Univ. 15: 45, t. 16 (1951); Jablonski, Mem. N. Y. Bot. Gard. 12: 174 (1965); Gillespie, Brittonia 45: 92 (1993); Murillo & Franco, Euforb. Reg. Araracuara 153, fig. 46 (1995); Esser in Radcl.-Sm., Gen. Euphorb.: 376 (2001).
Dendrothrix Esser (1993).

Monoecious trees or shrubs; latex white; indumentum simple, on inflorescence axes sometimes dendritic. Leaves with paired adaxial or abaxial glands; stipules caducous. Inflorescences bisexual, terminal, compound, axes thyrsoid; floral bracts eglandular, subtending proximal solitary pistillate flowers and distal cymules of 6–20 staminate flowers on each axis. Staminate flowers subsessile to pedicellate; sepals 2 or 3, basally ± connate; stamens 2–5, filaments distinct or connate, as long as anthers. Pistillate flowers short-pedicellate; sepals 3(−6), basally connate; ovary 3-locular, pubescent; ovules anatropous, inner integuments moderately thick, outer integuments thick, non-vascularized; stylodia undivided, basally connate into a short common style. Fruits capsular, sometimes partly fleshy; columella persistent, distally alate; seeds carunculate or ecarunculate.

Five spp., centered on the Guayana highlands and extending to its southern and eastern foreland. Except for the number of staminate sepals and the dendritic indumentum, *Dendrothrix* does not appear to be strongly different from *Senefelderopsis* s. str., and there seems to be no reason why it cannot be accommodated as a section of that genus.

267. *Senefeldera* Mart.

Senefeldera Mart., Flora 24 (Beibl. 2): 29 (1841); Jablonski, Mem. N. Y. Bot. Gard. 12: 171 (1965); Webster, Ann. Missouri Bot. Gard. 75: 1127 (1989); Murillo & Franco, Euforb. Reg. Araracuara 149, fig. 45 (1995); Esser in Radcl.-Sm., Gen. Euphorb.: 389 (2001).
Rhodothyrsus Esser (1999).
Pseudosenefeldera Esser (2001).

Monoecious trees; latex white; indumentum simple, dibrachiate or 0. Leaves sometimes pseudoverticillate, abaxially with scattered (sometimes marginal) glands; stipules caducous. Inflorescences axillary, pedunculate, usually bisexual, compound thyrsoid, floral bracts with a pair of elliptic glands; pistillate flowers solitary at 1–4 proximal nodes, glomerules of 1–3 staminate flowers at distal nodes. Staminate flowers pedicellate to sessile or subsessile; calyx completely connate without distinct lobes, sometimes zygomorphic; stamens (2) 4–17, filaments distinct; anthers dehiscing longitudinally. Pistillate flowers pedicellate to subsessile; sepals 3, distinct or basally connate; ovary 3-locular, smooth, glabrous; ovules anatropous, inner integuments moderately thick (8–10 cell layers), outer integuments thin (3–5 cell layers), non-vascularized; stylodia proximally usually connate into a short style with 3 distal stigmatic branches. Fruits spheroidal, capsular; columella triquetrous, distinctly alate, persistent. Seeds subspheroidal, ecarunculate, testa smooth or sculptured.

Six spp., tropical South America from Panama south to Peru. The two segregate genera proposed by Esser have some distinctive characters, but they share a very similar Gestalt and it does not seem necessary to dismember a genus as small as *Senefeldera*. With some modification, the segregate taxa could be fitted into the sectional arrangement of Pax and Hoffmann (1912).

268. *Triadica* Lour.

Triadica Lour., Fl. Cochin. 2: 598, 610 (1790); Small, Man. Southeastern Flora 789 (1933); Hurus., J. Fac. Sci. Univ. Tokyo, III. 6: 315 (1954); Kruijt, Bibl. Bot. 146: 7 (1996); Esser, Harvard Papers Bot. 7: 17–21 (2002).

Monoecious trees; latex white; indumentum 0. Leaves entire with submarginal glands and adaxial

paired glands at junction with petiole; stipules entire, persistent. Inflorescences terminal, bisexual, spiciform; bracts biglandular at base, subtending solitary pistillate flowers and distal cymules of 3–8 staminate flowers. Staminate flowers pedicellate; sepals 3, basally connate; stamens 2 or 3, filaments distinct; anthers basifixed, extrorse, dehiscing longitudinally; pollen grains 3-nucleate. Pistillate flowers pedicellate; sepals 3, basally connate, deciduous in fruit; ovary 3-locular; ovules anatropous, inner integuments moderately thick, outer integuments thick; stylodia connate at base, unlobed. Fruits capsular, dehiscing into 6 valves; columella persistent, alate. Seeds ecarunculate, adherent to columella, sarcotesta whitish. $2n = 44$.

Three spp., India, China, and Malesia. The genus has usually been included in *Sapium*, but differs in its pedicellate flowers and the whitish (not reddish) sarcotesta.

269. *Gymnanthes* Sw.

Gymnanthes Sw., Prodr. Veg. Ind. Occ.: 95 (1788); Grisebach, Fl. Brit. W. Ind.: 50 (1859); Bentham, Gen. Pl. 3: 337 (1880); Sargent, Silva N. Amer. 7: t. 309 (1995); Pax & K. Hoffm., Pflanzenr. 147, V: 81 (1912); Fawc. & Rend., Fl. Jam. 4: 329, fig. 111 (1920); Webster, J. Arnold Arb. 48: 387 (1967), Taxon 32: 304 (1983), Ann. Missouri Bot. Gard. 75: 1129 (1989), 81: 122 (1994); Howard, Fl. Lesser Ant. 5: 52, figs. 16, 18 (1989); Esser in Radcl.-Sm., Gen. Euphorb.: 382 (2001); Burger & Huft, Fieldiana n.s. 36: 123 (1995); Berry & Esser, Fl. Ven. Guayana 5: 149 (1999); Webster, Fl. Nicaragua 1: 884 (2001).
Shirakia Hurus. (1954), nom. illeg.
Neoshirakia Esser (1998).
Shirakiopsis Esser (1999).

Monoecious or dioecious trees or shrubs, branches sometimes spinose; latex whitish, sometimes not evident; indumentum simple or 0. Leaves entire or serrate, egandular adaxially, abaxially with marginal (scattered) glands; stipules entire, sometimes glandular. Inflorescences usually bisexual, racemoid, terminal and axillary, solitary, sometimes with minor proximal branches; bracts sometime pedunculate, usually biglandular at base; pistillate flowers solitary at proximal 1–3 nodes, staminate flowers in (1)3–5-flowered cymules. Staminate flowers pedicellate; sepals 1–2, often reduced or obsolete; stamens (2) 3–6, filaments often longer than anthers; anthers basifixed, extrorse, longitudinally dehiscent; pollen grains 3-nucleate. Pistillate flowers pedicellate, often expanding in fruit; sepals 3, distinct or connate; ovary 3-locular, smooth or appendiculate; ovules anatropous, inner integuments moderately thick (8–10 cell layers), outer integuments thin (4–6 cell layers); stylodia distinct or basally connate, simple. Fruits capsular (indehiscent); columella triquetrous, alate, persistent. Seeds elliptic, smooth, caruncle small or 0.

About 45 spp., most in the New World from the southern USA through the Antilles to South America, few spp. in Africa, S and SE Asia, Malesia, and extending to Micronesia, Melanesia and Japan.

Apart from the exclusion of *Actinostemon*, Esser (2001) has modified the circumscription of *Gymnanthes* by including *Sarothrostachys*, *Duvigneaudia*, and *Adenogyne*. In the treatment presented here, *Gymnanthes* is only enlarged by the inclusion of his segregate genera *Neoshirakia* and *Shirakiopsis* (see Esser, Blumea 44: 165–172. 1999). The boundaries of *Gymnanthes* have not yet been established satisfactorily, and it remains to be seen whether they will be decreased to exclude *Neoshirakia*.

270. *Dalembertia* Baill.

Dalembertia Baill., Étude Gén. Euphorb.: 545 (1858); Müll. Arg. in DC., Prodr. 15(2): 1225 (1866); Standley, Contr. U. S. Nat. Herb. 23: 646 (1923); Standley & Steyerm., Fieldiana Bot. 24 (6): 86 (1949); Webster, Ann. Missouri Bot. Gard. 81: 122 (1994); Esser in Radcl.-Sm., Gen. Euphorb.: 391 (2001).

Monoecious herbs or subshrubs, often with tuberous roots; latex white; indumentum simple, multiseriate. Leaves usually palmately 3–11-lobed, entire or distantly serrate; petioles eglandular; stipules persistent. Inflorescences terminal, bisexual, with pedicellate proximal pistillate flowers and a spiciform ament of staminate flowers; bracts biglandular, subtending solitary pistillate flowers and cymules of 1–3 staminate flowers. Staminate flowers pedicellate; calyx completely connate without distinct lobes, zygomorphic; stamen solitary, filament long-exserted; anthers longitudinally dehiscent; pistillode 0. Pistillate flowers with elongated ± recurved pedicels; sepals 3, distinct, entire, deciduous in fruit; ovary 3-locular, smooth; ovules anatropous, inner integuments moderately thick, outer integuments thin; stylodia connate into a common style with 3 apical unlobed, recurved tips. Fruits capsular; columella 3-angled, persistent. Seeds smooth, ecarunculate.

Four or five spp. native to Mexico and Guatemala, where they grow in deciduous woodland. Their inflorescences, with basal recurved long-pedicellate pistillate flowers subtending an ament of staminate flowers, are strikingly similar to those of *Maprounea*. However, no relationship between the two genera is discernible in the molecular analysis of Wurdack et al. (2005).

271. *Homalanthus* A. Juss.

Homalanthus A. Juss., Tent. Euphorb.: 50 (1824) (*Omalanthus*, orth. rej.); Airy Shaw, Kew Bull. 21: 409 (1968), Kew Bull. Add. Ser. 8: 115 (1980); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 25, t. 4 (1987); Forster, Telopea 6: 169 (1994); Florence, Fl. Polynes. Franc. 1: 115, fig. 20 (1997).

Monoecious or dioecious trees or shrubs; exudate watery, innocuous; indumentum simple or 0. Leaves often peltate, without laminar glands; petioles with paired glands at junction with lamina; stipules caducous. Inflorescences terminal and sometimes axillary as well, bisexual or unisexual, spiciform with pistillate flowers at base or at separate axils; bracts uniflorous, biglandular at base. Staminate flowers pedicellate; calyx laterally compressed, sepals 2, cordate, rarely 1, subimbricate; stamens (5–)10–50, filaments distinct; anthers extrorse, dehiscing longitudinally; pollen grains 2-nucleate; pistillode 0. Pistillate flowers long-pedicellate; sepals 2 or 3, deciduous in fruit; ovary 2(3)-locular; ovules anatropous, the inner integuments thin, the outer thick and non-vascularized; stylodia distinct or basally connate, unlobed, often glandular at apex. Fruits capsular or indehiscent; columella persistent. Seeds with hypertrophied arilloid caruncle. $2n = 36, 44$.

About 23 spp., distributed from SE Asia to Australia, New Caledonia, New Zealand, and Polynesia. The resemblance of this genus with the Stomatocalyceae has been noted since the time of Müller (1866), who included *Homalanthus* in *Pimelodendron* (as *Carumbium* sect. *Pimelodendron*), but in the light of the molecular findings (Wurdack et al. 2005), this similarity appears homoplasious.

272. *Microstachys* A. Juss. Fig. 43

Microstachys A. Juss., Euphorb. Tent.: 48 (1824); Griseb., Fl. Brit. W. Ind. 1: 49 (1859); Esser, Blumea 44: 173–179 (1999), Gen. Euphorb.: 365 (2001).
Cnemidostachys Mart. & Zucc. (1824).
Sebastiania sect. *Microstachys* (A. Juss.) Müll. Arg. (1866).

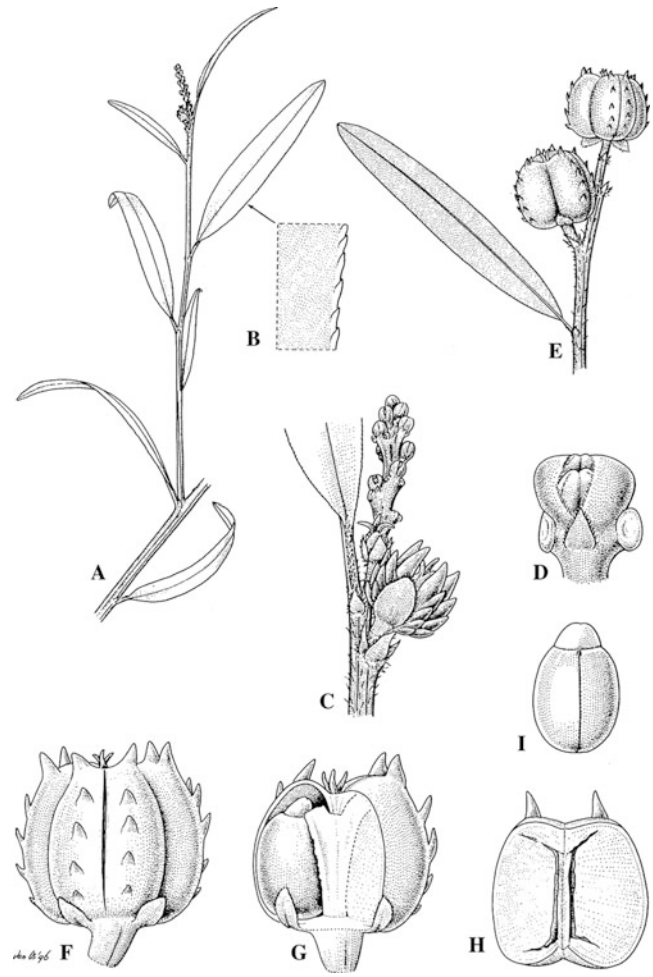

Fig. 43. Euphorbiaceae-Euphorbioideae. *Microstachys chamaelea*. **A** Flowering branchlet. **B** Detail of leaf margin with densely packed glandular teeth. **C** Stipulate node with young fruit and inflorescence. **D** Subsessile staminate flower with large bract glands and distinct sepals. **E** Infructescence. **F** Fruit with excrescences. **G** Partly opened fruit with alate columella. **H** Mericarp with the large septa. **I** Carunculate seed. (Esser 1999; drawn by J. van Os)

Monoecious herbs or subshrubs; latex not evident; indumentum simple or dendritic. Leaves entire or serrulate; stipules scarious, usually obscure. Inflorescences spiciform, mostly opposite the leaves, sometimes terminal or axillary; pistillate flowers proximal, solitary at 1 (2) basal nodes; staminate flowers distichous (spiral), 1–3 per node; staminate bracts biglandular (eglandular) at base. Staminate flowers sessile or subsessile; sepals 3, distinct or basally connate; stamens 3, filaments distinct; anthers basifixed, extrorse, dehiscing longitudinally; pistillode 0. Pistillate flowers sessile or

subsessile; sepals 3, distinct, eglandular or basally minutely glandular; ovary 3-locular, usually with 6 vertical rows of appendages; ovules anatropous, inner and outer integuments thin; stylodia distinct, unlobed. Fruits capsular; columella persistent, alate. Seeds elliptic to cylindrical, often truncate, caruncle discoid, testa smooth.

Approximately 15 spp., mainly neotropical, 3–4 disjunct in Africa and 1 in southwest Asia and Australia. *Microstachys* has previously been classified as part of *Sebastiania* (Webster 1994), but Esser (1994) insisted on generic status for *Microstachys*. In the molecular analysis it is resolved as sister to *Ditrysinia*.

273. *Ditrysinia* Raf.

Ditrysinia Raf., Neogenyton: 2 (1825); Esser in Radcl.-Sm., Gen. Euph.: 385 (2001).
Gymnanthes sect. *Ditrysina* Müll. Arg. (1865).
Sebastiana sect. *Stillingiopsis* (Müll. Arg.) G.L. Webster (1967).

Monoecious shrubs; indumentum simple or 0. Leaves entire; stipules undivided. Inflorescences terminal, solitary; bracts with paired elongate kidney-shaped glands, 2–6 proximal ones with 1 female flower, numerous distal ones with 1 male flower; prophylls 0. Staminate flowers shortly pedicellate; calyx 3-lobed, lobes partly connate; stamens 3, filaments short, distinct, anthers basifixed, extrorse, longitudinally dehiscent; pistillode 0. Pistillate flowers shortly to moderately pedicellate; calyx 3-lobed, lobes nearly distinct; ovary glabrous, 3-locular; stylodia connate into a short common style with 3 undivided branches. Fruits spheroidal, capsular, columella triquetrous, alate, persistent. Seeds elliptic, smooth, with small caruncle.

A single sp., *D. fruticosa* (Bartram) Govaerts & Frodin (= *D. ligustrina* (Michx.) Raf.), eastern USA. Formerly subsumed under *Gymnanthes* and *Sebastiana*, this genus is resolved as sister to *Microstachys* (Wurdack et al. 2005).

274. *Sclerocroton* Hochst.

Sclerocroton Hochst. in C. Krauss, Flora 28: 85 (1845); Kruijt & Roebers, Bibl. Bot. 146: 16–27 (1996); Esser in Radcl.-Sm., Gen. Euphorb.: 378 (2001).
Excoecaria sect. *Sclerocroton* Müll. Arg. (1866).
Sapium subg. *Sclerocroton* Pax in Pflanzenr. IV, 147, V: 213–249 (1912).

Monoecious shrubs or trees; latex not evident; indumentum 0. Leaves abaxially with basal or submarginal glands; stipules deciduous. Inflorescences mostly terminal, unbranched, bisexual, 1 or 2 proximal nodes with pistillate flowers, distally with cymules of 5–9 staminate flowers; bracts rounded to acuminate, biglandular at base. Staminate flowers pedicellate; sepals 3, basally connate; stamens 2–3, filaments distinct; anthers dehiscing longitudinally; pollen grains 3-colporate, exine tectate-reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 3, distinct, often with basal glands; ovary 3(4)-locular, each locule with 2 appendages; stylodia basally connate into a short common style with 3 short undivided style branches. Fruits capsular, sometimes with fleshy exocarp, endocarp woody; columella persistent, alate. Seeds ellipsoid to spheroidal, mostly ecarunculate or with small apical caruncle.

Six spp., Africa and Madagascar.

275. *Mabea* Aubl. Fig. 44

Mabea Aubl., Hist. Pl. Guiane 2: 867, t. 334 (1775); Müll. Arg. in DC., Prodr. 15(2): 1148 (1866), Fl. Bras. 11(2): 515, t. 73, 74 (1874); Pax & K. Hoffm., Pflanzenr. 147, V: 26, figs. 4–6 (1912); Jablonski, Mem. N. Y. Bot. Gard. 17: 164 (1967); Huft, Phytologia 62: 339 (1987), Ann. Missouri Bot. Gard. 75: 1125 (1989); Esser, Syst. Hippom.: 118–221, figs. 7–10 (1994).

Monoecious trees or shrubs; latex whitish; indumentum mostly dendritic. Leaves eglandular [except marginally], entire or denticulate; petiole eglandular; stipules subpersistent or deciduous. Inflorescences terminal or axillary, mostly bisexual racemoid thyrses, sometimes distinctly branched; bracts mostly biglandular, subtending pedunculate glomerules of mostly 3 staminate flowers or solitary pistillate flowers. Staminate flowers long-pedicellate; sepals 5(6), partly connate; stamens (3–)10–80, inserted on the ± convex receptacle; filaments 0 to as long as the extrorsely dehiscent anthers; pollen grains 2-nucleate; pistillode 0. Pistillate flowers distinctly pedicellate; sepals 5(6); ovary 3-locular, finely and densely tomentose; inner integuments moderately thick, outer integuments thick, non-vascularized; stylodia connate into a short to long common style, the distal tips simple, recurved. Fruits capsular; columella alate, persistent. Seeds carunculate.

About 40 spp., restricted to the (sub)humid neotropical lowlands from Mexico to São Paulo, Brazil. Esser (1994) recognized 2 sections: sect.

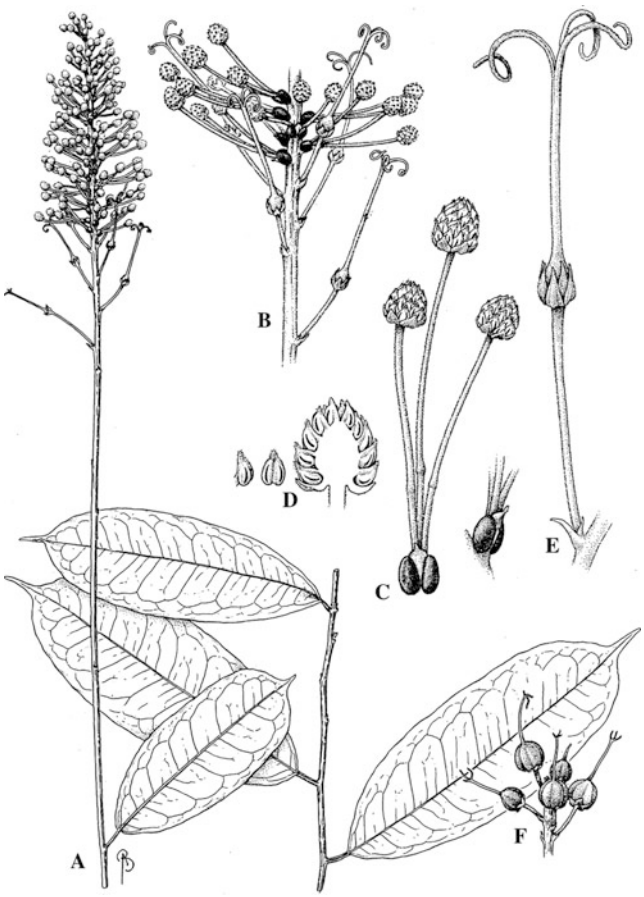

Fig. 44. Euphorbiaceae-Euphorbioideae. *Mabea speciosa*. **A** Inflorescence and part of stem with leaves (right); note that inflorescence is pendent on plant. **B** Proximal portion of inflorescence with pistillate flowers at base and staminate ones above; note glands on bracts subtending staminate flowers. **C** Cluster of staminate flowers subtended by biglandular bract. **D** Medial section of staminate flowers (right) and two views of anthers (left). **E** Pistillate flower. **F** Immature capsules. (Reproduced with kind permission of the artist Bobbi Angell)

Spiculigerae Pax & K. Hoffm., with 2 spp. (one of them the widespread Brazilian *M. fistulifera* Mart.); and sect. *Mabea*, which includes the other sections of Pax and Hoffmann (1912).

276. *Sebastiania* Sprengel

Sebastiania Spreng., Neue Entd. Pflanzenk. 2: 118, t. 3 (1820); Müll. Arg. in DC., Prodr. 15(2): 1164 (1866), Fl. Bras. 11(2): 544 (1866); Pax & K. Hoffm., Pflanzenr. 147, V: 88 (1914); figs. 19–22, 26–28 (1912), Natürl. Pflanzenfam. ed. 2, 19c: 192, fig. 103 (1931); L.B. Sm. et al., Fl. Illustr. Catar. EUFO 295, fig. 40 (1988); Webster, Ann. Missouri Bot. Gard. 81: 121 (1994); Burger & Huft, Fieldiana n.s. 36: 155 (1995); Esser, Syst. Hippom.: 55 (1994), in Radcl.-Sm., Gen. Euphorb.: 363 (2001).

? *Adenogyne* Klotzsch (1841).
Dendrocousinsia Millsp. (1913).

Monoecious (dioecious) trees, shrubs, or herbs; latex whitish, often not evident; indumentum simple or 0. Leaves eglandular except sometimes for marginal glands; margins entire to serrulate or dentate; stipules minute and often dissected. Inflorescences terminal or leaf-opposed, solitary, bisexual; bracts biglandular at base, glands usually flat and elongated or sometimes divided or rugulose; pistillate flowers solitary at proximal nodes, often separated from the distal staminal cymules of mostly 1–3 flowers. Staminate flowers sessile or subsessile; sepals 3, slightly connate at base, sometimes unequal; stamens 3, distinct, filaments longer than anthers; anthers basifixed, extrorse, dehiscing longitudinally; pollen grains 3-nucleate. Pistillate flowers sessile to short-pedicellate; sepals 3, discrete, denticulate, ± persistent in fruit; ovary 3-locular, sometimes appendiculate; ovules anatropous, inner and outer integuments thin; stylodia distinct or nearly so, undivided. Fruits capsular; columella persistent, alate, often with adherent caruncles. Seed smooth, carunculate, caruncles ± stipitate and deciduous.

About 25 spp., distributed from Mexico south into tropical South America. The circumscription of this genus has been one of the most contentious issues in the taxonomic history of tribe Hippomaneae. Pax and Hoffmann (1912) followed Müller (1866) in adopting a very broad and patently unnatural circumscription of *Sebastiania*. Esser (1994) has provided a radical solution to the problems of circumscribing *Sebastiania* by transferring sections *Sarothrostachys* and *Adenogyne* from *Sebastiania* to *Gymnanthes*. However, the species of *Adenogyne* assigned to *Sebastiania* by Müller (1866) have terminal inflorescences and pedicellate pistillate flowers, and the species of *Sarothrostachys* have axillary inflorescences and sessile or subsessile pistillate flowers. Both species groups have character combinations that conflict with the characters of *Gymnanthes* and *Sebastiania*, and it is obvious that the current generic boundaries are unsatisfactory. *Sarothrostachys* has axillary branched inflorescences, and its transfer to *Anomostachys* should be considered. *Dendrocousinsia* is treated by Esser as a highly distinct genus, but in fact the diagnostic character—adaxial ciliae or glands in the staminate and pistillate calyx—was described

by Müller for a considerable number of species of *Sebastiania*, including the type (*S. brasiliensis* Spreng.). The molecular data of Wurdack et al. (2005) fail to indicate the position of this genus within the Hippomaneae, because the signals of the two species included in the analysis representing the core of *Sebastiana* (S. *klotzschiana* Müll. Arg. and S. *pavoniana* Müll. Arg.) point to different subclades of the Hippomaneae.

277. *Anomostachys* (Baill) Hurus.

Anomostachys (Baill.) Hurus., J. Fac. Sci. Univ. Tokyo, III. Bot. 6: 311 (1954); Kruijt, Biblioth. Bot. 146: 8–12, fig. 2 (1996); Esser in Radcl.-Sm., Gen. Euphorb.: 385 (2001).
? *Sarothrostachys* Klotzsch (1841).
Duvigneauia Léonard (1959); Kruijt & Roebers, Biblioth. Bot. 146: 12–15 (1996), rev.

Monoecious trees and shrubs; latex whitish; indumentum 0. Leaves below with marginal glands, otherwise eglandular; stipules caducous. Inflorescences axillary, solitary, ramified, branches racemoid; bracts eglandular, the proximal 2–5 subtending single pistillate flowers and the distal ones subtending cymules of 2–8 staminate flowers. Staminate flowers sessile; sepals 3, basally connate; stamens 3; anthers dehiscing longitudinally; pistillode 0. Pistillate flowers pedicellate; sepals 3, distinct, often bifid; ovary 2- or 3-locular, appendiculate when young but smooth at maturation; ovules anatropous, inner integuments thick [10–20 cell layers], outer integuments thin [3 or 4 cell layers], non-vascularized; a common style short but evident, with 3 undivided distal branches. Fruits indehiscent. Seeds carunculate or not.

Three (or more?) spp., tropical Africa, Madagascar.

278. *Balakata* Esser

Balakata Esser, Blumea 44: 154 (1999), in Radcl.-Sm., Gen. Euphorb.: 378 (2001).
Sapium sect. *Pleurostachya* Pax & K. Hoffm. (1912).

Monoecious trees or shrubs; latex white; indumentum 0. Leaves abaxially with marginal or submarginal glands; stipules entire, eglandular. Inflorescences terminal and axillary, compound, bisexual; bracts biglandular at base, at proximal nodes subtending solitary pistillate flowers, at distal nodes cymules with 5–9 staminate flowers. Staminate flowers pedicellate; sepals 2, connate; stamens 2, filaments distinct; anthers basifixed, extrorse, dehiscing longitudinally. Pistillate flowers pedicellate; sepals 2, connate; ovary 2-locular; stylodia 2, basally connate, unlobed. Fruits drupaceous. Seeds oblate-spheroidal, ecarunculate, with thin sarcotesta. $2n = 44$.

Two spp., India to China and New Guinea. *Balakata* appears to be closely related to *Anomostachys*, and the two genera should perhaps be united.

279. *Hura* L. Fig. 45

Hura L., Sp. Pl.: 1008 (1753); Müll. Arg. in DC., Prodr. 15 (2): 1228 (1866), Fl. Brasil. 11(2): 632, t. 86 (1874); Pax & K. Hoffm., Pflanzenr. 147, V: 271 (1912); Standl. & Steyermark, Fieldiana Bot. 24(6): 124 (1949); Burch, Ann. Missouri Bot. Gard. 54: 330, fig. 24 (1968); Burger & Huft, Fieldiana n.s. 36: 126, fig. 32 (1995); Esser in Radcl.-Sm., Gen. Euphorb.: 397 (2001).

Monoecious trees, trunk spiny; latex white; indumentum simple. Leaves deciduous, dentate, with paired sessile glands at the junction with petiole; stipules caducous. Inflorescences unisexual, the staminate terminal, pedunculate, compound-spicate, bracts numerous, united into a membranaceous, tunica-like sheath; pistillate flowers solitary, at base of staminate spike or axillary. Staminate flowers pedicellate; sepals connate into a crenulate cup; stamens 10–80, in 2 or more whorls of 12–15 sessile anthers on a stout column formed by the stamen filaments; pistillode 0. Pistillate flowers pedicellate; sepals 5, completely connate into a truncate calyx; ovary 5–20-locular; stylodia connate into a long columnar style with a distal 5–20-lobed discoid stigma. Fruits capsular, dehiscing explosively; columella not persistent. Seeds laterally compressed, suborbicular, ecarunculate. $2n = 44$.

Two neotropical spp., common in lowland deciduous forests. *Hura polyandra* Baill. of Mexico and Central America is replaced in Nicaragua by *H. crepitans* L., which is widely distributed from Nicaragua to the West Indies, Peru, and Brazil. *Hura crepitans* is cultivated throughout most of the Neotropics, and has been introduced into paleotropical regions with monsoonal climates. The unusual floral structure, at first glance very different from that in *Algernonia* and *Ophthalmoblapton*, evidently reflects adaptation for bat pollination (Steiner 1982).

280. *Algernonia* Baill.

Algernonia Baill., Ann. Sci. Nat. IV, 9: 198 (1858), Étude Gén. Euphorb.: 546 (1858); Müll. Arg. in DC., Prodr. 15 (2): 1230 (1866); Fl. Bras. 11(2): 533, t. 87 (1874); Benth., Gen. Pl. 3: 339 (1880); Pax & Hoffm., Pflanzenr. 147, V:

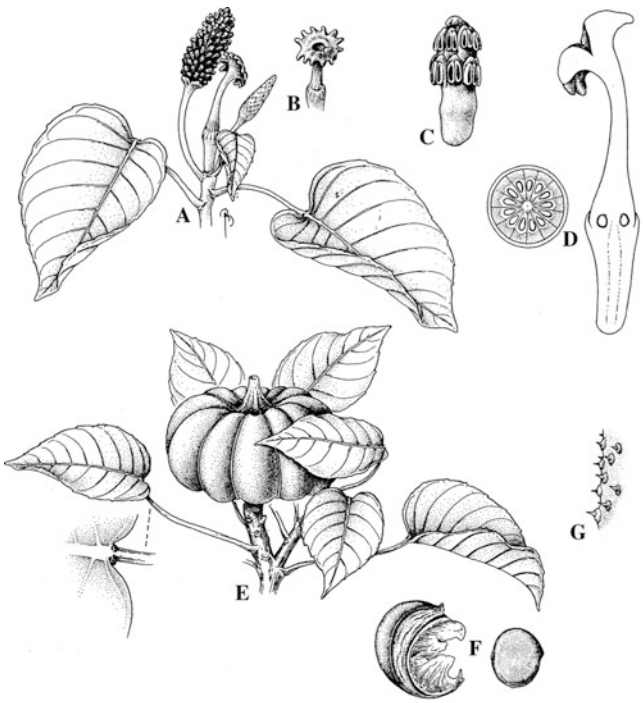

Fig. 45. Euphorbiaceae-Euphorbioideae. *Hura crepitans*. **A** Stem with leaves and staminate inflorescences (left) and pistillate flower (right). **B** Pistillate flower. **C** Androecium with staminal column bearing two rows of anthers. **D** Ovary in transverse section (left) and medial section of pistillate flower (right). **E** Stem with capsule. **F** Segment of capsule and seed. **G** Prickles on trunk. (Reproduced with kind permission of the artist Bobbi Angell)

276, fig. 56 (1912); Emmerich, Arq. Mus. Nac. Rio Janeiro 56: 91–110, t. 1–11 (1981).
Tetraplandra Baill. (1858); Emmerich, l.c.

Monoecious trees or shrubs; latex white; indumentum 0. Leaves entire or obscurely crenulate and occasionally with small abaxial glands, biglandular at base; stipules caducous. Inflorescences terminal, the staminate ones occasionally axillary, bisexual, spiciform; bracts adnate to rachis, eglandular; pistillate flowers solitary at distal nodes, staminate cymules with mostly 3 flowers. Staminate flowers subsessile; sepals 3–5, distinct or connate; stamens 1–3, filaments mostly connate; anthers basifixed, extrorse, dehiscing longitudinally. Pistillate flowers sessile or subsessile; sepals distinct or connate, persistent in fruit; ovary 3-locular, exappendiculate; stylodia connate c. 1/3 to 2/3 of length into a columnar common style, tips terete, papillose. Fruits capsular; trigonous base of columella persistent. Seeds subspheroidal, smooth, ecarunculate.

About 10 spp., ranging from E Brazil to Peru. Baillon (1858) described both *Algernonia* and *Tetraplandra* simultaneously, and Bentham (1880) selected the former on joining the two genera, in which he is followed here. Pax and Hoffmann (1912) distinguished the genera by the more gamophyllous staminate calyx in *Algernonia*, but in both floral and vegetative structures the two taxa appear similar overall. Emmerich (1981) provided detailed descriptions and excellent illustrations of both genera, and the entire reliance on vegetative characters in her generic key is revealing.

281. *Ophthalmoblapton* Allem.

Ophthalmoblapton Allem., Pl. Novas Brasil: 4 (1849), Ann. Sci. Nat. Bot. III, 13: 119 (1849); Müll. Arg. in DC., Prodr. 15(2): 1155 (1866), Fl. Bras. 11(2): 531 (1874); Benth., Gen. Pl. 3: 333 (1880); Pax & K. Hoffm., Pflanzenr. 147, V: 278, fig. 58 (1912); Emmerich, Bol. Mus. Nac. Rio de Janeiro, Bot. 62: 1, t. 1 (1981); L.B. Sm. et al., Fl. Illustr. Catar. EUFO 325, t. 41 figs. h–m (1988); Howard, Fl. Lesser Ant. 5: 57 (1989).

Monoecious trees; latex white, highly toxic; indumentum 0. Leaves entire or dentate, adaxially with basal glands at junction with petiole; stipules caducous. Inflorescences axillary, bisexual or staminate, spiciform; pistillate flowers basal and solitary, ± separated from crowded staminate flowers; bracts eglandular, staminate bracts subtending 3–12 flowers. Staminate flowers sessile, sometimes laterally confluent; calyx closed in bud, splitting into 2 or 3 lobes or segments; stamen solitary, exserted from calyx; anther dehiscing longitudinally. Pistillate flowers sessile or subsessile, becoming somewhat pedunculate in fruit; sepals 5 or 6, discrete, imbricate, persistent in fruit; ovary 3-locular; stylodia basally connate into a columnar style with distal stigmatic style branches. Fruits capsular; endocarp woody; columella deciduous. Seeds ovoid, ecarunculate, testa smooth.

Four spp. of the mata atlântica region in eastern Brazil (Bahia to Santa Catarina).

282. *Pachystroma* Müll. Arg. Fig. 46

Pachystroma Müll. Arg., Linnaea 34: 177 (1865), in DC., Prodr. 15(2): 893 (1866), Fl. Bras. 11(2): 387, t. 54 (1874); Pax, Pflanzenr. 147, II: 99 (1910); Senna, Bradea 3 (48): 421 (1983).

Monoecious trees or shrubs; latex white; indumentum 0. Leaves eglandular, usually spinose-

Fig. 46. Euphorbiaceae-Euphorbioideae. *Pachystroma longifolium*. **A** Flowering branchlet. **B** Staminate flower. **C** Same, longitudinally sectioned. **D** Transversal section of androecium. **E** Pistillate flower. **F** Ovary medially sectioned. **G** Fruit locule. **H** Columella after seed dehiscence. (Pax 1910)

dentate; petioles eglandular; stipules caducous. Inflorescences terminal, spiciform, bisexual; bracts biglandular, basally up to 2 with 1 pistillate flower, apically numerous ones with cymules of 1–3 staminate flowers. Staminate flowers sessile; calyx cupular, 2-lobed; stamens 3, filaments connate into a column; anthers basifixed, extrorse, dehiscing vertically, exserted from calyx. Pistillate flowers subsessile; sepals 3, distinct, imbricate, persistent in fruit; ovary 3-locular; stylodia connate into a columnar style, style branchlets unlobed, compressed. Fruits capsular, valves woody and thick-walled; trigonous base of columella persistent. Seeds ovoid, somewhat compressed, ± cordate at base, ecarunculate.

A single sp., *P. longifolium* (Nees) I.M. Johnston of SE Brazil, Bolivia and Peru. Müller (1866) misplaced the genus among the Acalyphoideae, and Pax (1910) placed it in the Adrianeae, although noting its resemblance in habit to Hippomaneae. Pax and Hoffmann (1931) created a tribe for it, but still placed it between the Acalypheae and Dalechampieae. In the molecular analysis of Wurdack et al. (2005), *Pachystroma* is embedded within the Hureae, which are part of one of the hippomanoid subclades, as foreseen by Webster (1994a).

283. *Hippomane* L.

Hippomane L., Sp. Pl.: 1191 (1753); Müll. Arg. in DC., Prodr. 15(2): 1199 (1866); Pax & K. Hoffm., Pflanzenr. 147, V: 261, fig. 51 (1912); Fawc. & Rend., Fl. Jam. 4: 327, fig. 110 (1920); Webster, J. Arnold Arbor. 48: 393 (1967); Webster, Ann. Missouri Bot. Gard. 81: 124 (1994).
Mancanilla Miller (1754).

Monoecious trees or shrubs; latex white, toxic; indumentum 0. Leaves ± cordate at base, entire or obscurely crenulate to spinose-dentate, with a single adaxial gland at junction with petiole; stipules lanceolate, caducous. Inflorescences terminal, bisexual, spiciform, bisexual; bracts biglandular at base, subtending 1 or 2 proximal solitary pistillate flowers and distal cymules of 8–15 staminate flowers. Staminate flowers subsessile; sepals 2 or 3, connate; stamens 2, filaments connate into a column; anthers basifixed, extrorse, dehiscing longitudinally. Pistillate flowers sessile or subsessile; sepals 3, distinct, persistent in fruit; ovary 5–10-locular; stylodia basally connate into a short style, branches unlobed, densely papillate adaxially. Fruits drupaceous with bony endocarp. Seeds smooth, ecarunculate. $2n = 22$.

Three Caribbean spp., two of which are endemic to Hispaniola, while *H. mancinella* L., the noted highly toxic "manchineel", is widely distributed along littoral zones from Florida to northern South America and the Galapagos. In the molecular analysis of Wurdack et al. (2005), Hippomane is resolved in a clade with *Pleradenophora*, *Bonania*, and *Grimmeodendron*.

284. *Pleradenophora* Esser

Pleradenophora Esser in Radcl.-Sm., Gen. Euph.: 377 (2001).

Monoecious shrubs or trees; indumentum 0; latex white. Leaves serrate, below sometimes with marginal glands, often with a pair of disk-shaped petiolar glands on the junction of the petiole with the blade; stipules small. Inflorescences

terminal or laterally displaced, solitary; floral bracts with several pairs of disk- or cup-shaped glands, 1–3 basal ones with 1 pistillate flower, numerous apical ones with 5–10 staminate flowers. Staminate flowers shortly pedicellate; calyx 3-lobed, partly connate; stamens 2–3(5), filaments distinct, anthers basifixed, extrorse, longitudinally dehiscent; pistillode 0. Pistillate flowers (sub)sessile; calyx 3-lobed, lobes distinct; ovary smooth, 3-locular; stylodia undivided, basally connate or not into a short common style. Fruit subglobose, smooth, dehiscing septicidally into 3 mericarps, columella 3-quetrous, alate, persistent. Seeds ovoid-globose, smooth, often maculate, ecarunculate.

Three spp., Mexico, Guatemala, Belize; formerly treated as part of *Sebastiana* (*S. longicuspis* Standl.).

285. *Bonania* A. Rich.

Bonania A. Rich., Hist. Fis. Cuba 2, 11: 201, t. 68 (1853); Benth., Gen. Pl. 3: 335 (1880); Pax & K. Hoffm., Pflanzenr. 147, V: 259 (1912); Borhidi, Acta Bot. Acad. Sci. Hungar. 22: 305 (1976); Webster, Ann. Missouri Bot. Gard. 81: 123 (1994); Esser in Radcl.-Sm., Gen. Euphorb.: 369 (2001).

Monoecious shrubs; latex not recorded; indumentum 0. Leaves distichous, subsessile, eglandular, margins glandular-crenate; stipules persistent. Inflorescences terminal on axillary branches, unbranched, bisexual, pistillate flower solitary at base, staminate flowers in numerous distal 1–3-flowered cymules; bracts eglandular. Staminate flowers subsessile; calyx nearly completely connate, without distinct lobes; stamens 2 or 3, filaments about as long as anthers, distinct or basally connate; anthers basifixed, extrorse, dehiscing longitudinally. Pistillate flowers sessile, calyx urceolate, 2–3-lobed or toothed; ovary 3-locular, smooth; ovules anatropous, inner integuments moderately thick [8–10 cell layers], outer integuments thin [3–5 cell layers]; stylodia incrassate, recurved, papillate adaxially. Fruits capsular; columella persistent, alate. Seeds spheroidal, ecarunculate, testa smooth.

Seven spp., endemic to the Greater Antilles and Bahamas but not in Jamaica.

286. *Grimmeodendron* Urb.

Grimmeodendron Urb., Symb. Ant. 5: 397 (1908); Pax & K. Hoffm., Pflanzenr. 147, V: 258, fig. 50 (1912); Borhidi, Acta Bot. Acad. Sci. Hungar. 22: 305 (1976); Esser in Radcl.-Sm., Gen. Euphorb.: 368 (2001).

Monoecious trees or shrubs; latex white; indumentum 0. Leaves serrulate, adaxially biglandular at base at junction with petiole; stipules deltoid or lunate, the fimbriate scarious tip deciduous, the lunate base persistent. Inflorescences terminal, bisexual; bracts eglandular, subtending 1 or 2 solitary proximal pistillate flowers and several distal staminate cymules with 2 or 3 flowers. Staminate flowers subsessile; sepals 3, valvate, distinct or basally connate, entire; stamens 3, filaments connate into a column ± exserted from the calyx; anthers extrorse, dehiscing longitudinally. Pistillate flowers sessile; sepals 3, deltoid, entire, persistent in fruit; ovary 3-locular; stylodia united at base into a short style, tips unlobed, recurving. Fruits capsular; columella alate distally, persistent. Seeds ovoid-subspheroidal, smooth, ecarunculate.

Two spp., Greater Antilles except Puerto Rico and Bahamas.

287. *Adenopeltis* Bert. ex A. Juss.

Adenopeltis Bert. ex A. Juss., Ann. Sci. Nat. I, 25: 24 (1832); Müll. Arg. in DC., Prodr. 15(2): 1164 (1866); Pax & K. Hoffm., Pflanzenr. 147, V: 264, fig. 52 (1912); Esser in Radcl.-Sm., Gen. Euphorb.: 369 (2001).

Monoecious shrubs; latex not recorded; scabrid emergences on stems and inflorescence axes. Leaves short-petiolate or subsessile, eglandular, glabrous, margins prominently glandular-denticulate; stipules small, divided into several ciliae, eglandular. Inflorescences terminal and axillary, solitary, bisexual, spiciform; bracts ovate, entire, with a pair of stipitate, disk-shaped glands, the 0–2 basal ones subtending solitary pistillate flowers, and numerous apical ones with 1–3 staminate flowers. Staminate flowers subsessile; calyx 0; stamens 2 or 3, connate at base; anthers basifixed, dehiscing longitudinally; pistillode 0. Pistillate flowers pedicellate; sepals 0; ovary 3-locular; stylodia distinct or basally connate, slender. Fruits capsular, 3-lobed; columella not persistent, base of cocci persistent as three lobes. Seeds subspheroidal, ecarunculate, testa smooth.

A single sp., *A. serrata* (Ait.) G.L. Webster, Chile and Peru.

288. *Spegazziniophytum* Esser

Spegazziniophytum Esser in Radcl.-Sm., Gen. Euporb.: 371 (2001).

Monoecious, succulent shrubs, branches transformed into thorns. Leaves present only on

young branches, subsessile. Inflorescences axillary, solitary, catkin-like; bracts with a pair of cup- to disk-shaped glands; pistillate flowers 1 per bract, staminate flowers 2 or 3 per bract. Staminate flowers sessile; calyx 2-lobed, connate; stamens 2, filaments distinct; pistillode 0. Pistillate flowers subsessile; calyx 3-lobed, lobes nearly distinct; ovary smooth; stylodia entire. Fruit 2-locular, dehiscent; columella alate but lacking a carpidiophore. Seeds 2 per fruit, subglobose, with minute apical caruncle.

A single sp., *S. patagonicum* (Speg.) Esser, Argentinian Patagonia. Formerly included in *Colliguaja*, but in the molecular analysis (Wurdack et al. 2005) resolved in a clade with *Stillingia* and *Adenopeltis*, from which it differs by the lack of a carpidiophore.

289. *Stillingia* Garden ex L.

Stillingia Garden ex L., Syst. Nat. ed. 12, 2: 637 (1767); Müll. Arg. in DC., Prodr. 15(2): 1155 (1866); Fl. Bras. 11 (2): 537 (1874); Pax & K. Hoffm., Pflanzenr. 147, V: 180 (1912); Rogers, Ann. Missouri Bot. Gard. 38: 207, figs. 1–3, 6–16 (1951); van Steenis, Blumea Suppl. 5: 302 (1966); Webster, J. Arnold Arb. 48: 388, fig. 5 (1967); A.C. Sm., Fl. Vit. Nov. 2: 565, fig. 161 (1981); Esser in Radcl.-Sm., Gen. Euphorb.: 370 (2001).
Gymnostillingia Müll. Arg. (1863).

Monoecious arborescent shrubs, subshrubs, or herbs, sometimes with succulent stems; latex white; indumentum 0. Leaves alternate or opposite, entire to glandular-serrulate, with paired basal glands at junction with petiole; stipules ± laciniate-dissected. Inflorescences terminal, unbranched, spiciform, bisexual; bracts biglandular at base; with distal cymules of 1–3 staminate flowers. Staminate flowers subsessile; sepals 2, connate; stamens 2 (3), filaments distinct, exserted from calyx; anthers basifixed, extrorse, dehiscing longitudinally; pollen grains 2-nucleate. Pistillate flowers subsessile; sepals 3, sometimes reduced or 0; ovary 2- or 3-locular; ovules anatropous, inner integuments moderately thick, outer integuments thin, vascularized; stylodia connate basally, unlobed. Fruits capsular; columella alate, usually persistent, with 3 horn-like projections from base; seeds subspheroidal, carunculate (caruncle reduced). $2n = 22, 30, 36$.

About 30 spp., most of them in the New World (North, Central and South America), a few spp. with scattered distribution in the Old World (2 in Madagascar, 1 in Malesia, and 1 or 2 on Pacific islands extending to Fiji). The Old World species ascribed to *Stillingia* would merit critical revision. Also the inclusion of *Adenopeltis* and *Spegazziniophytum* in *Stillingia* should seriously be considered; it is not formally proposed here only because not all new combinations are available.

290. *Falconeria* Royle

Falconeria Royle, Ill. Bot. Himal.: 354 (1839); Wight, Ic. Pl. Ind. Or. 5(2): 20, t. 1866 (1853); Esser, Blumea 44: 160–165 (1999), rev.
Sapium sect. *Falconeria* (Royle) Hook. f. (1888); Pax & K. Hoffm., Pflanzenr. IV: 147, V: 241, fig. 45 (1912).

Monoecious trees; latex white; indumentum 0. Leaves deciduous, sometimes apically clustered, serrate, abaxially with paired basal glands at junction with petiole; stipules dissected. Inflorescences terminal, unisexual, spiciform; bracts biglandular at base with discoid glands, subtending solitary pistillate flowers or cymules of 10–15 staminate flowers. Staminate flowers subsessile; sepals 2, connate; stamens 2, filaments distinct; anthers basifixed, extrorse, dehiscing longitudinally. Pistillate flowers subsessile [short-pedicellate in fruit]; sepals 2 or 3, connate below, eglandular; ovary 2- or 3-locular, smooth; stylodia distinct or basally connate, unlobed. Fruits spheroidal, dehiscing irregularly, pericarp fleshy becoming papery; columella 2- or 3-angled, alate, caducous. Seeds spheroidal, ecarunculate, testa pale, arillate. $2n = 32$.

A single sp., *F. insignis* Royle, E Asia from India to SW China and peninsular Malaysia. *Falconeria* is distinctive due to its unisexual spikes and irregularly dehiscing fruits enclosing seeds with whitish aril. It seems to be closer morphologically to *Sapium* (s. str.) than to other Asiatic Hippomaneae.

291. *Sapium* Jacq.

Sapium Jacq., Enum. Syst.: 9 (1760), nom. cons.; Pax & K. Hoffm., Pflanzenr. 147, V: 199 (1912); Webster, J. Arnold Arb. 48: 391 (1967), pro parte; Kruijt & Zijlstra, Taxon 38: 320 (1989); Kruijt, Bibl. Bot. 146: 27–91, figs. 10–31, 33–35 (1996), rev.; Esser in Radcl.-Sm., Gen. Euphorb.: 373 (2001).

Monoecious or dioecious trees or shrubs; latex white, often viscous; indumentum 0. Leaves entire to serrulate; petioles usually biglandular; stipules ovate, persistent. Inflorescences terminal and axillary, solitary or clustered, spiciform; bracts biglandular, discoid to oblong, subtending solitary proximal pistillate flowers and distal cymules of (2–)5–10(−15) staminate flowers.

Staminate flowers mostly subsessile; sepals 2, connate; stamens 2, distinct or basally connate; anthers basifixed, extrorse, dehiscing longitudinally. Pistillate flowers sessile or subsessile; sepals 2 or 3, basally connate; ovary (1)2–3-locular, unappendaged; ovules anatropous, inner and outer integuments moderately thick; stylodia distinct to basally connate into a common style, distally unlobed. Fruits capsular; columella persistent. Seeds spheroidal, ecarunculate, testa covered with red aril. $2n = 22, 44$.

About 25 spp. from the Neotropics. The classical circumscription of the genus of Pax and Hoffmann (1912), which has been followed in most floristic works until recently, was much more inclusive, but Kruijt (1996) has excluded all taxa lacking an aril, so that *Sapium* appears restricted to the New World.

292. *Colliguaja* Molina

Colliguaja Molina, Saggio Chile: 158 (1781); Müll. Arg. in DC., Prodr.15(2): 1226 (1866), Fl. Bras. 11(2): 630, t. 85 (1874); Pax & K. Hoffm., Pflanzenr. 147, V: 265, fig. 53 (1912); L.B. Smith et al., Fl. Illustr. Catar. EUFO: 326 (1988).

Monoecious shrubs, sometimes arborescent; latex not recorded; indumentum 0. Leaves mostly opposite or subopposite, short-petiolate, glandular-denticulate or entire; stipules entire, minute, deciduous. Inflorescences terminal, bisexual, spiciform, bracts ovate, eglandular, subtending 1 or 2 proximal solitary pistillate flowers and several cymules of 3 staminate flowers. Staminate flowers subsessile; sepals 1 or 2 and minute or 0; stamens 2–4 (12–18 in *C. brasiliensis*), filaments distinct or connate; anthers basifixed, extrorse, longitudinally dehiscent. Pistillate flowers subsessile; sepals 3, minute; ovary 2–3(4)-locular; ovules anatropous, inner integuments moderately thick, outer integuments thin; stylodia basally connate into a short style, the distinct branches recurved, adaxially papillate. Fruits capsular, trigonous; columella triquetrous, alate apically, persistent. Seeds subspheroidal, ecarunculate, testa smooth. $2n = 36$.

Four spp., three in C Chile and one in S Brazil and adjacent Paraguay and Uruguay; *C. brasiliensis* is rheophytic.

293. *Excoecaria* L.

Excoecaria L., Syst. Nat. ed. 10: 1288 (1759); F.M. Bailey, Queensl. Fl. 5: 1456 (1902); Pax & Hoffm., Pflanzenr. IV, 147, V: 157, figs. 29–31 (1912); Airy Shaw, Kew Bull. 16: 268 (1971), Add. Ser. 4: 112 (1975), 8: 88 (1980); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 382, fig. 72 (1987); Chakrab. & Gangop., J. Econ. Tax. Bot. 18: 193 (1994); Radcl.-Sm., Fl. Zamb. 9(4): 315, t. 68 (1996); Esser in Radcl.-Sm., Gen. Euphorb.: 360 (2001).
Commia Loureiro (1790).
Spirostachys Sond. (1850).
Conosapium Müll. Arg. (1863).
Taeniosapium Müll. Arg. (1866).
Glyphostylus Gagnep. (1925).

Dioecious or monoecious trees or shrubs; latex milky, toxic; indumentum 0. Leaves alternate or opposite, entire or crenulate, eglandular, rarely with basal glands; stipules deciduous or ± persistent. Inflorescences axillary or terminal on brachyblasts, solitary, spiciform; bracts usually biglandular at base, subtending 1–3 staminate flowers or single pistillate flowers. Staminate flowers sessile or subsessile; sepals 3(2), distinct; stamens 3(2), filaments distinct; anthers extrorse, dehiscing longitudinally; pistillode 0. Pistillate flowers subsessile or short-pedicellate; sepals 3, distinct or basally connate; ovary 3-locular; ovules anatropous, inner integuments moderately thick, outer integuments thin; stylodia distinct or slightly connate at base. Fruits capsular; columella persistent, alate. Seeds subglobose, ecarunculate or the caruncule persistent on top of the columella.

About 40 spp. distributed from Africa to Australia and Melanesia. Esser (2001) has redefined the genus by excluding some elements retained by Pax and Hoffmann (1912) and synonymizing *Glyphostylus*. There is still considerable uncertainty about the monophyly of *Excoecaria*; for example, the study of ovular structure by Tokuoka and Tobe (2002) indicates that *E. bussei* differs greatly from other species and may not be congeneric. Although Esser maintains *Spirostachys* as a distinct genus, it is included within *Excoecaria* here (and was resolved as the strongly supported sister to *E. agallocha*; Wurdack et al. 2005), where it will probably survive as a well-marked subgenus or section. *Conosapium* from Madagascar, although generically accepted by Esser (2001) and Schatz (2001), can probably be accommodated as a distinctive section.

3. Tribe Euphorbieae

Monoecious (dioecious) trees, shrubs, or herbs, sometimes succulent; latex milky, sometimes toxic; indumentum simple or 0; leaves alternate, opposite, or whorled, mostly unlobed and

pinnately veined, sometimes reduced, without laminar or petiolar glands; stipules + or 0; inflorescences pseudanthial with connate bracts forming a cyathium that encloses a single terminal pistillate flower and 4 or 5 lateral staminate dichasia or monochasia; cyathia often aggregated in compound inflorescences; staminate flowers with calyx reduced or 0, the solitary stamen articulating with the pedicel; pollen grains 3-colporate, colpi bordered by conspicuous intine bands, exine perforate-tectate; pistillate flowers ± pedicellate, calyx 3–6-lobed or reduced or 0; ovary (2)3(4)-locular; stylodia distinct or basally connate, bifid, rarely entire; fruit capsular, rarely drupaceous; seeds carunculate or ecarunculate; testa dry.

This tribe includes 3 subtribes grouped into 5 genera and > 2,000 spp., the vast majority in the genus *Euphorbia* s.l. In many molecular analyses (e.g., Steinmann and Porter 2002; Wurdack et al. 2005; Horn et al. 2012), Euphorbieae are resolved as monophyletic with the Anthosteminae as the earliest diverging group, followed by the Neoguillauminiinae and Euphorbiinae in a sister position. Genera until recently kept separate from *Euphorbia* s. str. but now found to be deeply embedded and sunk into it (see below under *Euphorbia* s. l.) are not formally accepted here but are keyed out in order to demonstrate on which characters they had been based; this is also because they have been in wide use in general and phytogeographic writings until recently, and may still be so until a full infrageneric classification of *Euphorbia* s. l. becomes available and accepted.

Key to the Subtribes and Genera of Euphorbieae

1. Staminate calyx +; involucre of 4 partially or fully connate bracts; cyathial glands commissural, not on rim of cyathium. **3a. Anthosteminae** 2
– Staminate calyx 0; involucral bracts usually 5, connate into a cup or tube; cyathial bracts different 3
2. Inflorescences axillary; cyathia bisexual; involucral bracts partially connate into an open 4-lobed involucre; cyathial glands at margins of involucral bracts; ovary 3-locular **294. *Anthostema***
– Inflorescences terminal; cyathia mostly unisexual; involucral bracts connate into a closed cup; cyathial glands connate by pairs into 4 lobes alternating with the involucral bracts; ovary 4-locular **295. *Dichostemma***
3. Petaloid appendages bracteal [dilated involucral lobes], opposite the staminate dichasia; cyathial glands commissural; bracts of staminate dichasia large, imbricate, enclosing staminate flowers; pistillate sepals 5 or 6, large, imbricate. **3b. Neoguillauminiinae** 4
– Petaloid appendages interbracteal [opposite cyathial glands], alternate with staminate monochasia; cyathial glands on rim of cyathium; bracts of staminate monochasia small or obsolete; pistillate sepals + or 0. **3c. Euphorbiinae (298. *Euphorbia* s. l.)** 5
4. Cyathial glands 8 or 10, massive; petaloid involucral bracts c. 1 cm long; leaves spiral **296. *Neoguillauminia***
– Cyathial glands 4, small; petaloid bracts < 1 cm long; leaves opposite **297. *Calycopeplus***
5. Cyathia bilaterally symmetrical; glands enclosed within a nectar spur; stylodia connate into a long column. 17 spp., most in Mexico *Euphorbia* **'*Pedilanthus*'**
– Cyathia ± radially symmetrical, glands not enclosed within a nectar spur; stylodia distinct or nearly so 6
6. Involucral glands distinct, (1–)4–5(8), alternating with involucral lobes on rim of cyathium; bracts subtending cyathium distinct or connate 7
– Involucral glands not 4 or 5 alternating with lobes; bracts subtending cyathium often connate into a cup 8
7. Leaves alternate, opposite, or whorled, but if opposite then not inaequilateral at base; veins of leaves not chlorenchyma-sheathed; stipules + or 0; main [embryonic] axis not abortive *Euphorbia* s.str.
– Leaves opposite, stipulate, inaequilateral at base; veins chlorenchyma-sheathed; main axis abortive above cotyledons. About 250 spp., mostly in trop. America and Africa *Euphorbia* **'*Chamaesyce*'**
8. Pistillate flower calyculate; involucral lobes connate; glands 2, connate into a shield; seeds ecarunculate; stems not succulent. 3 spp., Cuba, Hispaniola *Euphorbia* **'*Cubanthus*'**
– Pistillate flower naked; involucral lobes and glands connate into a ring; seeds mostly carunculate; stems succulent 9
9. Cyathium somewhat bilaterally symmetrical; gland-ring with a gap on one side. 70 spp., trop. Africa *Euphorbia* **'*Monadenium*'**
– Cyathium radially symmetrical, without a gap on one side 10
10. Involucral glands connate, conspicuous; ovary without angular crests. 19 spp., E and S trop. Africa *Euphorbia* **'*Synadenium*'**
– Involucral glands distinct, inconspicuous; ovary with prominent double angular crests. 1 sp., Angola *Euphorbia* **'*Endadenium*'**

3a. Subtribe Anthosteminae (Klotzsch & Garcke) G.L. Webster (1975).

Monoecious or dioecious; leaves with dispersed and submarginal glands; stipules caducous;

cyathia in axillary inflorescences; cyathial involucre of 4 bracts subtending or enclosing 4 staminate partial inflorescences; staminate flowers in dichasia ± enclosed by prophylls; pistillate flower solitary, central and terminal or apparently lateral; cyathial glands projecting inward from infolded margins of involucral bracts; staminate and pistillate flowers with gamophyllous calyx; ovary 3–4-locular; stylodia emarginate to bifid; fruit capsular; seeds carunculate or ecarunculate.

Two genera of Africa and Madagascar.

294. *Anthostema* A. Juss.

Anthostema A. Juss., Euphorb. Tent.: 56 (1824); Pax & K. Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 207, fig. 11 a, b (1931); Keay, Fl. W. Trop. Afr. ed. 2, 1: 416 (1958); Berhaut, Fl. Ill. Sénégal 3: 379 (1975); Schatz, Gen. Tree Fl. Madag.: 145, fig. 134 (2001).

Monoecious trees; latex white; indumentum 0. Leaves distichous, with minute punctiform glands and larger abaxial submarginal glands. Inflorescences axillary, of contracted cymes of cyathia; cyathia with involucre of 4 bracts connate laterally; each bract with 2 marginal glands. Staminate flowers enclosed by 4 prophylls; calyx 3- or 4- dentate; pollen grains oblate-spheroidal, 3-colporate, colpi marginate, exine reticulate; pistillate flowers pedicellate; calyx 3- or 4-dentate; ovary 3-locular, sessile; stylodia for lower half connate into a column, distally clavate or bifid. Fruits capsular; endocarp thick and woody; columella trigonous-alate, clavate, persistent. Seeds laterally compressed, carunculate. $2n = 22$.

Three spp., 2 in west Africa and 1 in Madagascar.

295. *Dichostemma* Pierre

Dichostemma Pierre, Bull. Mens. Soc. Linn. Paris 1 (159): 1259 (1896); Pax & K. Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 207 (1931); Keay, Fl. W. Trop. Afr. ed. 2, 1: 416 (1958), Trees Nigeria 151 (1989); Radcl.-Sm., Gen. Euphorb.: 400, fig. 46 (2001).

Monoecious or dioecious trees, sometimes climbing; latex white; indumentum pruinose on inflorescence axes. Leaves eglandular. Inflorescences terminal with the cyathia in a panicle; cyathia mostly unisexual, bilateral, with involucre of paired connate bracts; glands connate in pairs alternating with involucral bracts. Staminate flowers 5–12; calyx 4-lobed; pistillate flower pedicellate; calyx cupular or obscurely 4-lobed; ovary 4-locular; stylodia distinct, entire or obscurely bifid. Fruits capsular; endocarp woody but thin; columella 4-angular, persistent. Seeds trigonous-rounded, ecarunculate, testa smooth.

Two spp. from W Africa.

3b. Subtribe Neoguillauminiinae Croizat (1938).

Monoecious; indumentum 0; leaves alternate or opposite, entire; stipules 0; cyathia in axillary or subterminate pedunculate cymes; involucral bracts 4(−6), basally connate, distally dilated or petaloid; staminate dichasia opposite the involucral bracts; nectary glands in 4 or 5 pairs, sometimes small, or 0; pistillate flower central. Staminate flowers in bracteate dichasia; staminate calyx 0; pistillate sepals 5 or 6, imbricate; ovary 3-locular; stylodia unlobed, dilated; seeds smooth, carunculate.

This Australasian subtribe of 2 genera (1 in Australia and the other in New Caledonia) appears to bridge the gap between the Anthosteminae and Euphorbiinae.

296. *Neoguillauminia* Croizat Fig. 47

Neoguillauminia Croizat, Phil. J. Sci. 64: 398 (1938), Bull. Jard. Bot. Buit. III, 17: 206 (1941); Guillaumin, Fl. Anal. Syn. Nouv-Caléd.: 182 (1948); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 22–25, t. 3 (1987).

Monoecious trees or shrubs; latex white; indumentum 0, young stems pruinose. Leaves alternate or opposite, eglandular. Inflorescences axillary and subterminal, long-pedunculate; cyathia mostly 3 in a terminal dichasium; involucral bracts 4–6, basally connate into a cup and distally with 4–6 petaloid appendages reddish without and white within; staminate dichasia opposite the involucral bracts, bracteate, each surrounded by broad, erose, rectangular bracts, 10–28-flowered; nectary glands 8–12, stipitate, fleshy, pair-wise partitioning the staminate partial inflorescences; pistillate flower central. Staminate flowers pedicellate; perianth 0; pollen grains 2-nucleate; pistillate flower subsessile; calyx annular, persistent in fruit; anther introrse with respect to the cyathium; ovary 3-locular; stylodia recurved, basally connate, distally bifid. Fruits capsular, endocarp woody; columella apically dilated, deciduous except for conical base. Seeds ellipsoid, carunculate, testa smooth.

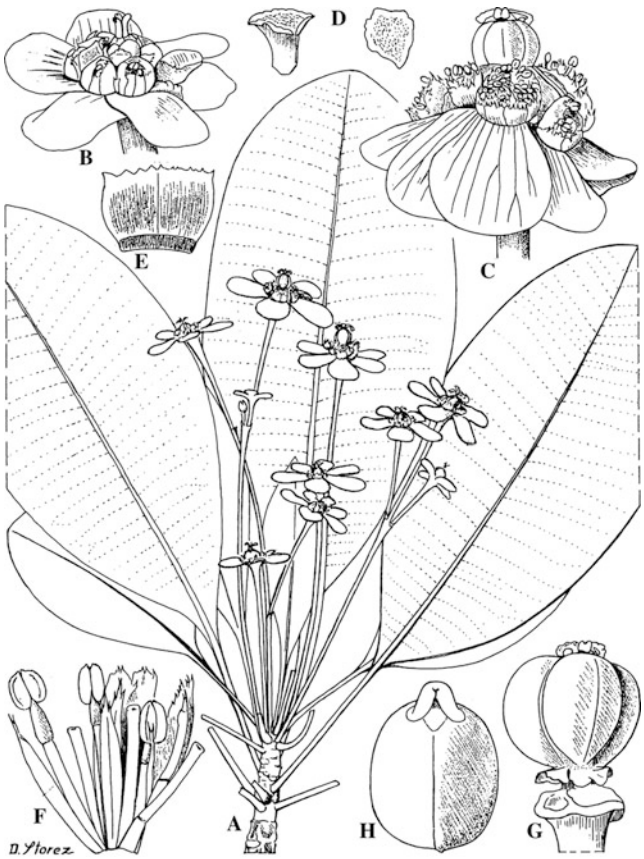

Fig. 47. Euphorbiaceae-Euphorbioideae. *Neoguillauminia cleopatra*. **A** Flowering branchlet. **B** Young cyathium. **C** Cyathium at anthesis. **D** Nectar gland seen from the side and from below. **E** Involucral bract. **F** Bracteate staminate flowers. **G** Fruit. **H** Carunculate seed. (McPherson & Tirel 1987; drawn by D. Storez)

Only one sp., *N. cleopatra* (Baill.) Croizat, endemic to New Caledonia. The showy and fragrant cyathia resemble those of species of *Euphorbia*, but the petaloid appendages may not be homologous.

297. *Calycopeplus* Planch.

Calycopeplus Planch., Bull. Soc. Bot. France 8: 30 (1861); Boissier, Ic. Euphorb.: t. 120 (1866); Airy Shaw, Kew Bull. 35: 603 (1980); P.I. Forster, Austrobaileya 4: 418, t. 1, 2 (1995).
Euphorbia sect. *Calycopeplus* (Planch.) Boiss. (1862).

Monoecious shrubs, sometimes arborescent, or subshrubs; stems and branches virgate; latex white. Leaves opposite or verticillate, petiolate to sessile, eglandular, soon deciduous. Inflorescences axillary, rarely terminal, the cyathia solitary or paired, subsessile; involucral bracts 4, connate, their distinct lobes small, petaloid, white or greenish; nectary glands 4 between the lobes, sometimes reduced; staminate partial inflorescences opposite the lobes in 3–7-flowered bracteate dichasia; pistillate flower solitary, central. Staminate flowers pedicellate; perianth 0; anther introrse in relation to pistillate flower. Pistillate flower pedicellate; calyx cupular, 4–6-lobed; ovary 3-locular, sessile or subsessile; stylodia distinct or basally connate. Fruit capsular, 3-lobed, endocarp thin and crustaceous; columella persistent, clavate. Seeds subspheroidal or oblong, carunculate, testa smooth.

Five spp., all endemic to Australia, which differ by a xeromorphic habit from *Neoguillauminia* but share with it the cyathial structure.

3c. Subtribe Euphorbiiinae

Monoecious (dioecious) trees, shrubs, or herbs; latex milky; indumentum simple or 0; leaves alternate, opposite, or whorled, usually unlobed and pinnately veined, stipulate or exstipulate; inflorescences terminal or axillary, cyathia often subtended by paired bracts; cyathium distinctly cupulate with (1–2)4–5 interbracteal glands on the rim; glands with or without petaloid appendages; pistillate flower central, staminate flowers in 4 or 5 monochasia [usually cincinni] (rarely 1-florous) with ± reduced prophylls; staminate calyx 0; stamen 1; pollen grains 2- or 3-nucleate; pistillate calyx 3–6-lobed, often vestigial or 0; ovary 3-locular; stylodia distinct or connate, bifid (entire); fruit capsular (drupaceous); seeds carunculate or ecarunculate.

Only one genus, *Euphorbia* (s. l.).

298. *Euphorbia* L.

Euphorbia L., Sp. Pl.: 450 (1753); Boissier in DC., Prodr. 15(2): 7 (1862), Icon. Euphorb.: t. 27–119 (1866); Carter, Fl. E. Trop. Afr., Euphorb. 2: 409 (1988); Carter & Leach, Fl. Zambesiaca 9(5): 339, t. 71–84 (2001); Radcl.-Sm., Gen. Euphorb.: 405, figs. 47–50 (2001).
Tithymalus Gaertn., Fruct. 2: 115 (1790), nom. cons.
Pedilanthus Necker ex Poit., Ann. Mus. Nat. Hist. 19: 388 (1812), nom. cons.; Dressler, Contr. Gray Herb. 182: 1–188 (1957).
Chamaesyce S. F. Gray, Nat. Arrang. Brit. Pl. 2: 260 (1821); Koutnik, S. Afr. J. Bot. 3: 262 (1984); Ya Yang & Berry, Amer. J. Bot. 98: 1486–1503 (2011).
Poinsettia Graham, Edinburgh New Phil. J. 20: 412 (1836).
Synadenium Boiss. in DC., Prodr. 15(2): 187 (1862); S. Carter, Fl. E. Trop. Afr., Euphorb. 2: 534, fig. 101 (1988), Fl. Zambes. 9(5): 434, t. 85 (2001).

Monadenium Pax, Bot. Jahrb. 19: 126, fig. (1895); P.R.O. Bally, Genus *Monadenium*: 14, figs. 1–34, t. I–XXXII (1961).
Elaeophorbia Stapf, Hooker's Icon. Pl. 29: t. 2823 (1906).
Cubanthus (Boiss.) Millsp., Field Mus. Nat. Hist. Bot. 2: 371 (1913); Steinmann et al., Ann. Jard. Bot. Madrid 64: 123–133 (2007).
Endadenium Leach, Garcia de Orta 1: 31 (1973).

Monoecious (dioecious) trees, shrubs, or herbs, often succulent and/or spiny; stems erect to procumbent, rarely plants acaulescent; latex whitish; indumentum simple or 0. Leaves alternate, opposite, or whorled, persistent or deciduous, simple (deeply lobed), sessile to petiolate, entire or variously toothed, mostly pinnately veined, eglandular; stipules small and inconspicuous or 0, often glandular, sometimes modified into spines. Inflorescences bisexual (unisexual), contracted into pseudanthial cyathia; cyathia in terminal or axillary dichasia or pleiochasia, sometimes solitary, each subtended by 2 variously colored distinct or connate modified leaves, composed of a single central terminal pistillate flower and 5 or 4 staminate cincinnate monochasia with their associated prophylls, the monochasia alternating with 5 or 4 involucral bracts connate into a radially or isobilaterally symmetrical campanulate to hemispherical involucre; the tips of the involucral bracts alternating with (0)1–5(20) glands situated on the rim of the opening (enclosed in a zygomorphic-spurred involucre); glands sometimes forming a ± continuous rim on the outer wall of the involucre but usually distinct and entire, bicornute, cupular, bilabiate, or sometimes highly divided, usually with dorsal appendages, these often flat and petaloid, sometimes glandular or branched. Staminate flowers monandrous; perianth usually 0 or very rarely developed; anthers dehiscing longitudinally and introrsely in relation to the vertical axis of the cyathium; pollen grains 2- or 3-nucleate, subspheroidal, tricolporate, reticulate to finely tectate-perforate; pistillate flower pedicellate, pedicel often becoming reflexed; sepals (0)3–6, ± connate basally; ovary (2)3(4)-locular, glabrous or pubescent, often angled or carinate; stylodia distinct or connate at base, 2-fid (unlobed). Fruits capsular (drupaceous); columella ± persistent. Seeds carunculate or ecarunculate, testa smooth, ridged, pitted, or tuberculate. $x = 6–10$; many spp. based on $x = 7$ or $x = 10$.

With > 2,000 spp., this is the largest genus in the Euphorbiaceae and one of the five largest angiosperm genera. It is subcosmopolitan in distribution and is extremely variable in habit; Hallé et al. (1978), in their architectural analysis, reported from it 12 of the 23 recognized structural types ("models"). Horn et al. (2012) analyzed the major structural traits in a phylogenetic context, which revealed an extreme parallelism in the evolution of the xeromorphic growth forms within the genus.

Delimitation of the genus *Euphorbia* always has been strongly contentious, and in the 260 years that elapsed since Linnaeus treated the then-known 56 spp. of *Euphorbia*, more than 75 satellite genera have been proposed. Most of them, however, have fallen into synonymy, and until very recently, only six or seven generally have been maintained, as by Webster (1994) and Radcliffe-Smith (2001). Molecular phylogenetic research by Steinmann and Porter (2002) demonstrated that *Chamaesyce*, *Pedilanthus*, *Monadenium*, *Synadenium*, and *Endadenium* are all deeply nested within paraphyletic *Euphorbia*, and that most of the historically recognized subgenera and sections of *Euphorbia* s.str. are either paraphyletic or polyphyletic. Further work (Steinmann 2003; Bruyns et al. 2006; Steinmann et al. 2007; Zimmermann et al. 2010; Horn et al. 2012) confirmed and extended these findings, and led to the broadly construed generic concept of *Euphorbia* that is gaining increasing acceptance. Steinmann and Porter (2002) also recovered four major lineages within *Euphorbia*, designated as clades A–D; with one exception, these do not correspond to any previously known taxon but are composed of various sections or subgenera of *Euphorbia*; only a single clade, by and large, is congruent with subg. *Esula*. Bruyns et al. (2006), in their study of southern African *Euphorbia*, confirmed the existence of these clades; they used the names of some of the existing subgenera with which the clades showed partial overlap for designating and formally treating them as the four subgenera of *Euphorbia*: A = subg. *Rhizanthium*, B = subg. *Esula*, C = subg. *Euphorbia*, and D = subg. *Chamaesyce*. This proposal has also been taken up by, i.a., Horn et al. (2012), who have provided the hitherto most comprehensive overall phylogenetic analysis of the genus and its structural traits. Although these clades are strongly supported and, as such, valuable for further phylogenetic understanding of

Euphorbia, they seem hardly acceptable to us as taxa because they are very heterogeneous, are not distinguishable on the basis of morphology, and rather are the mere product of the algorithm. A taxonomic subdivision of *Euphorbia*, which is a great desideratum, favorably would have to be built upward from clearly circumscribed entities of lower rank such as sections. This has been accomplished for the Chamaesyce Clade by Yang et al. (2012)[1].

A brief characterization of the four clades reads as follows:

A. Esula Clade. Annual and perennial herbs, shrubs, and trees, some are stem succulents; inflorescence terminal, pseudo-umbellate; branching sympodial; cyathial glands 4; stipules 0; caruncles +. About 480 spp., mainly in temperate Northern Hemisphere, outside this area woody as trees or stem succulents in the Canary Isl., Africa, Madagascar, and Arabia; very few in tropical America.

B. Rhizanthium Clade. Woody and succulent xerophytes, morphologically diverse, often cactiform and sometimes with spines derived from persistent, indurated bases of inflorescence peduncles; some geophytic; often with stem tubercles on the tips of which the leaves are borne; inflorescences terminal, rarely lateral; cyathial glands 5; stipules glandular, filamentous, or 0; caruncles 0. About 200 spp., most of them in southern Africa but also in Madagascar and extending north to Arabia.

C. Euphorbia Clade. The clade with the greatest diversity in taxa and growth forms, ranging from trees up to 30 m high to low "pencil plants" and cactiform succulents many of which, unlike cacti, maintain the possibility to develop large foliage leaves. In some caudiciform shrubs, the stems bear at the nodes spine-shields subtending pairs of stipular spines accompanied by supernumerary spines associated with the leaf bases (Uhlarz 1974). Inflorescences terminal or more often lateral with concomitant transition from sympodial to monopodial growth. Cyathial glands 5(4); stipules + or 0; caruncles often +. The extreme xerophytic subg. *Euphorbia* is nested within this large clade. About 700 spp., pantropical, but with greatest diversity in Africa/Madagascar.

D. Chamaesyce Clade. Herbs, subshrubs, or shrubs, sometimes succulent; leaves alternate or opposite; stipules + or 0; inflorescences terminal; cyathial glands 5, 4, or 2–1, glands sometimes with petaloid appendages; caruncles rarely +. About 600 spp. with mostly C_3 or CAM photosynthesis in the Old World including Africa/Madagascar and Australia, and 350 New World spp. of mostly C_4 photosynthetic herbs.

[1] Added in proof: Attention is directed to the following recently published systematic treatments of the Euphorbia Clade and the Esula Clade (as "subgenera"), which provide detailed sectional classifications:

- Dorsey, B.L., Haevermans, T., Aubriot, X., Morawetz, J. J., Riina, R., Steinmann, V.W., Berry, P.E. 2013. Phylogenetics, morphological evolution, and classification of *Euphorbia* subgenus *Euphorbia*. Taxon 62: 291–315.
- Riina, R., Peirson, J.A., Geltman, D.V., Molero, J., Frajman, B., Pahlevani, A., and further 7 authors. 2013. A worldwide molecular phylogeny and classification of the leafy spurges, *Euphorbia* subgenus *Esula* (Euphorbiaceae). Taxon 62: 316–342.

Selected Bibliography

Airy Shaw, H.K. 1965. Diagnoses of new families, new names, etc. for the seventh edition of Willis's "Dictionary ". Kew Bull. 18: 249–273.

Airy Shaw, H.K. 1968. Notes on Malesian and other Asiatic Euphorbiaceae, XCVI. Kew Bull. 21: 409–418.

Airy Shaw, H.K. 1974. Noteworthy Euphorbiaceae from tropical Asia. Hooker's Icon. Plant. 38 (1): t. 3701–3725.

Alex, A.H. 1957. Pollination of some oil seed crops by honey bees. Texas A. & M. College Agr. Exp. Stat. Progr. Rep. 1960.

Alvin, K.L. 1987. Leaf anatomy of *Androstachys johnsonii* Prain and its functional significance. Ann. Bot. 59: 579–591.

Armbruster, W. 1984. The role of resin in pollination: Ecological and chemical considerations. Amer. J. Bot. 71: 1149–1160.

Armbruster, W.S. 1988. Multilevel comparative analysis of the morphology, function, and evolution of *Dalechampia* blossoms. Ecology 69: 1746–1761.

Armbruster, W.S. 1993. Evolution of plant pollination systems: hypotheses and tests with the neotropical vine *Dalechampia*. Evolution 47: 1480–1505.

Armbruster, W.S. 1994. Early evolution of *Dalechampia* (Euphorbiaceae): insights from phylogeny, biogeography, and comparative ecology. Ann. Missouri Bot. Gard. 81: 302–316.

Armbruster, W.S. 1996. Cladistic analysis and revision of *Dalechampia* sections *Rhopalostylis* band *Brevicolumnae* (Euphorbiaceae). Syst. Bot. 21: 209–235.

Armbruster, W.S., Baldwin, B.G. 1998. Switch from specialized to generalized pollination. Nature 394: 632.

Armbruster, W.S., Webster, G.L. 1979. Pollination of two species of *Dalechampia* (Euphorbiaceae) in Mexico by euglossine bees. Biotropica 11: 278–283.

Armbruster, W.S., Howard, J.J., Clausen, T.P., Debevec, E., Loquvam, J., Matsuki, M., Cerendolo, B., Andel, F. 1997. Do biochemical exaptations link evolution of plant defense and pollination systems? – Historical hypotheses and experimental tests with *Dalechampia* vines. Amer. Nat. 149: 461–484.

Armbruster, W.S., Lee, J., Baldwin, B.G. 2009. Macroevolutionary patterns of defense and pollination in *Dalechampia* vines: adaptation, exaptation, and evolutionary novelty. Proc. Natl. Acad. Sci. USA 106: 18085–18090.

Bailey, I. W. 1924. The problem of identifying the wood of Cretaceous and later dicotyledons: *Paraphylanthoxylon arizonense*. Ann. Bot. 38: 439–452.

Baillon, H. 1858. Étude générale du groupe des Euphorbiacées. Paris: Victor Masson.

Bally, P.R.O. 1961. The genus *Monadenium*. Bern: Bentelli.

Bancilhon, L. 1971. Contribution à l'étude taxonomique du genre *Phyllanthus*. Boissiera 18: 1–81.

Barrera, M.E., Meza, P.I., Serra, V.M.T. 2001. Epidermis foliar de Euphorbiaceae presentes en Chile, aporte a la ubicación sistemática de *Avellanita bustilosii* Phil. Bol. Mus. Nac. Hist. Nat. Chile 50: 7–19.

Bawa, K.S. 1980. Evolution of dioecy in flowering plants. Ann. Rev. Ecol. Syst. 11: 15–39.

Bawa, K.S., Webb, C.J., Tuttle, A.F. 1982. The adaptive significance of monoecism in *Cnidoscolus urens* (L.) Arthur (Euphorbiaceae). Bot. J. Linn. Soc. 85: 213–223.

Bentham, G. 1878. Notes on Euphorbiaceae. J. Linn. Soc. Bot. 17: 185–267.

Bentham, G. 1880. Euphorbiaceae, pp. 239–340. In: Bentham and Hooker, Genera Plantarum, vol. 3. London: L. Reeve.

Berg, R. 1975. Fruit, seed and myrmecochorous dispersal in *Micrantheum* (Euphorbiaceae). Norw. J. Bot. 22: 173–194.

Bernhard, F. 1966. Contribution à l'étude des glandes foliaires chez les Crotonoidées (Euphorbiacées). Mém. Inst. Fond. Afr. Norire 75: 71–156.

Bhatnagar, A.K., Kapil, R.N. 1974. *Bischofia javanica* – its relationships with Euphorbiaceae. Phytomorphology 23: 264–267.

Bianchini, M., Pacini, E. 1996. The caruncle of *Ricinus communis* L. (castor bean): its development and role in seed dehydration, rehydration, and germination. Int. J. Plant Sci. 157: 40–48.

Blattner, F.R., Weising, K., Bänfer, G., Maschwitz, U., Fiala, B. 2001. Molecular analysis of phylogenetic relationships among myrmecophytic *Macaranga* species (Euphorbiaceae). Mol. Phylogen. Evol. 19: 331–344.

Boissier, E. 1862. Euphorbiaceae subordo I.Euphorbieae. DC. Prodromus 15(2): 3–188.

Bouharmont, J. 1962. Fécondation et développement de la graine après croisement et autopollinisation chez *Hevea brasiliensis* Muell. Arg. Cellule 62: 119–130.

Breckon, G. 1975. *Cnidoscolus*, Section *Calyptosolen* (Euphorbiaceae) in Mexico and Central America. Ph. D. diss., University of California.

Brunell, J.F. 1975. Contribution à l'étude de quelques *Phyllanthus* africains et à la taxonomie du genre *Phyllanthus* (Euphorbiaceae). Strasbourg: Université Louis Pasteur de Strasbourg.

Bruyns, P.V., Mapaya, R.J., Hedderson, T. 2006. A new subgeneric classification for *Euphorbia* (Euphorbiaceae) in southern Africa based on ITS and *psb*A-*trn*H sequence data. Taxon 55: 397–420.

Bullock, S.H. 1994. Wind pollination of neotropical dioecious trees. Biotropica 26: 172–179.

Burger, W., Huft, M. 1995. Flora Costaricensis: Euphorbiaceae. Fieldiana Bot. n.s. 36: 1–169.

Burrows, G.E., Tyrl, R.J. 2001. Toxic plants of North America. Hoboken (NJ): Wiley.

Cacho, N.I., Berry, P.E., Olson, M.E., Steinmann, V.W., Baum, D.A. 2010. Are spurred cyathia a key innovation? Molecular systematics and trait evolution in the slipper spurges (Pedilanthus clade: *Euphorbia*, Euphorbiaceae). Amer. J. Bot. 97: 493–510.

Cahoon, E.J. 1972. *Paraphyllanthoxylum alabamense*—a new species for fossil dicotyledonous wood. Amer. J. Bot. 59: 5–11.

Call, V.B., Manchester, S.R., Dilcher, D.L. 1993. *Wetherellia* fruits and associated fossil plant remains from the Paleocene/Eocene Tuscahoma-Hatchetigbee interval, Meridian, Mississippi. Mississippi Geol. 14: 10–18.

Calvin, M. 1987. Fuel oils from euphorbs and other plants. Bot. J. Linn. Soc. 94: 97–110.

Carter, S. 1994. A preliminary classification of *Euphorbia* subgenus *Euphorbia*. Ann. Missouri Bot. Gard. 81: 368–379.

Carter, S., Leach, L.C. 2001. Flora Zambesiaca, Vol. IX, 5. Euphorbiaceae-Euphorbioideae-Euphorbieae. Kew: Royal Botanic Gardens Kew.

Cesca, G. 1961. Ricerche cariologiche ed embriologiche sulle Euphorbiaceae. 1. Su alcuni biotipi di *Euphorbia dulcis* L. della toscana. Caryologia 14: 79–96.

Chase, M.W. et al. 1993. See General References.

Clifford, H.T., Monteith, G.B. 1989. A three phase seed dispersal mechanism in Australian quinine bush, (*Petalostigma pubescens* Domin). Biotropica 21: 284–286.

Corner, E.J.H. 1976. The Seeds of Dicotyledons. Cambridge: Cambridge University Press.

Cremers, G. 1977. Architecture végétative de quelques espèces malgaches du genre *Euphorbia* L. Bull. Jard. Bot. Nat. Belg. 47: 55–81.

Crepet, W.L., Daglian, C.P. 1982. Euphorbioid inflorescences from the Middle Eocene Claiborne formation. Amer. J. Bot. 69: 258–266.

Croizat, L. 1938. Notes on Euphorbiaceae, with a new genus and a new subtribe of the Euphorbieae. Philip. J. Sci. 64: 397–411.

Croizat, L. 1941. The Tribe Plukenetieae of the Euphorbiaceae in eastern tropical Asia. J. Arnold Arbor. 22: 417–431.

Croizat, L. 1973. Les Euphorbiaceées vues en elles-mêmes, et dans leur rapport envers l'angiospermie en général. Mem. Soc. Broteriana 23: 5–207.

Cronquist, A. 1981. See General References.

Cullen, J. 1978. A preliminary survey of ptyxis (vernation) in the angiosperms. Notes Roy. Bot. Gard. Edinburgh 37: 161–214.

Daumann, E. 1972. Zur Blütenmorphologie und Bestäubungsökologie von *Mercurialis* L. Preslia 44: 308–315.

Davies, S.J., Lum, S.K.Yl, Chan, R., Wang, L.K. 2001. Evolution of myrmecophytism in western Malesian *Macaranga* (Euphorbiaceae). Evolution 55: 1542–1559.

Dehgan, B., Craig, M.E. 1978. Types of laticifers and crystals in *Jatropha* and their taxonomic implications. Amer. J. Bot. 65: 345–352.

Dehgan, B., Webster, G.L. 1979. Morphology and infrageneric relationships of the genus *Jatropha* (Euphorbiaceae). Univ. Calif. Publ. Bot. 74: 1–73.

Dilcher, D.L., Manchester, S.R. 1988. Investigations of the angiosperms from the Eocene of North America: a fruit belonging to Euphorbiaceae. Tertiary Research 9: 45–68.

Dinerstein, E., Wemmer, C.M. 1988. Fruits *Rhinoceros* eat: dispersal of *Trewia nudiflora* (Euphorbiaceae) in lowland Nepal. Ecology 69: 1768–1774.

Dingler, H. 1885. Die Flachsprosse der Phanerogamen. Erstes Heft: *Phyllanthus* sect. *Xylophylla*. Munich: T. Ackermann.

Domínguez, C.A., Bullock, S.H. 1989. La reproducción de *Croton suberosus* (Euphorbiaceae) en luz y sombra. Rev. Biol. Trop. 37: 1–10.

Domínguez, C.A., Dirzo, R., Bullock, S.H. 1989.On the function of floral nectar in *Croton suberosus*. (Euphorbiaceae). Oikos 56: 109–114.

Dressler, R.L. 1957. The genus *Pedilanthus* (Euphorbiaceae). Contr. Gray Herb. 182: 1–188.

Durand, B. 1963. Le complexe *Mercurialis annua* L. s.l.: une étude biosystématique. Ann. Sci. Nat. Paris, Bot. 12: 579–736.

Ehrenfeld, J. 1976. Reproductive biology of three species of *Euphorbia* subgenus *Chamaesyce* (Euphorbiaceae). Amer. J. Bot. 63: 406–413.

Eichler, A.W. 1875. Blüthendiagramme. Leipzig: W. Engelmann.

Emmerich, M. 1981. Revisão taxinômica dos gêneros *Algernonia* e *Tetraplandra*. Arq. Mus. Nac. Rio de Janeiro 56: 91–110.

Erdtman, G. 1952. See General References.

Esser, H.-J. 1994. Systematische Studien an den Hippomaneae Adr. Jussieu ex Bartling (Euphorbiaceae), insbesondere den Mabeinae Pax & K. Hoffm. Hamburg: Dissertation, Universität Hamburg.

Esser, H.J. 2002. A revision of *Triadica* Lour. (Euphorbiaceae). Harvard Pap. Bot. 7: 17–21.

Esser, H.-J., van Welzen, P., Djarwaningsih, T. 1997. A phylogenetic classification of the Malesian Hippomaneae (Euphorbiaceae). Syst. Bot. 22: 617–628.

Fatemi, M, Gross, C.L. 2009. Life on the edge - High levels of genetic diversity in a cliff population of *Bertya ingramii* are attributed to *B. rosmarinifolia* (Euphorbiaceae). Biol. Conserv. 142: 1461–1468.

Fernandez-González, D., Lobreau-Callen, D. 1996. Le pollen de la tribu des Acalypheae (Acalyphoideae, Euphorbiaceae). Grana 35: 266–284.

Freitas, J.R. de, Figueiredo, R.A., Nadai, I.C., Hardman, L. 2011. Aspects of *Pera glabrata* (Schott) Poepp. ex Baill. (Euphorbiaceae) reproductive ecology in a cerrado area in São Paulo State. Revista Arvore 35: 1227–1234.

Froembling, W. 1896. Anatomisch-systematische Untersuchung von Blatt und Axe der Crotoneen und Euphyllantheen. Bot. Centralbl. 65: 129–139, 177–192, 242–249, 321–329, 369–378, 407–421, 433–442.

George, Jr., W.L., Shifriss, O. 1967. Interspersed sexuality in *Ricinus*. Genetics 57: 347–356.

Gilbert, M.G. 1994. The relationships of the Euphorbieae. Ann. Missouri Bot. Gard. 81: 283–288.

Gillespie, L.J. 1994. Pollen morphology and phylogeny of the tribe Plukenetieae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 317–348.

Gillespie, L. 1997. *Omphalea* (Euphorbiaceae) in Madagascar: a new species and a new combination. Novon 7: 127–136.

Gottsberger, G. 1978. Seed dispersal by fish in the inundated regions of Humaita, Amazonia. Biotropica 10: 170–183.

Goulding, M. 1980. The fishes and the forest. Berkeley: Univ. of California Press.

Govaerts, R., Frodin, D.G., Radcliffe-Smith, A. 2000. World Checklist and Bibliography of Euphorbiaceae. 4 vols. Kew: Royal Botanic Gardens.

Gruas-Cavagnetto, C., Köhler, E. 1992. Pollen fossiles d'Euphorbiacées français. Grana 31: 291–304.

Hakki, M.I. 1985. Studies on West Indian plants 3. On floral morphology, anatomy, and relationships of *Picrodendron baccatum* (L.) Krug & Urban (Euphorbiaceae). Bot. Jahrb. Syst. 107: 379–394.

Hallé, F. 1971. Architecture and growth of tropical trees exemplified by the Euphorbiaceae. Biotropica 3: 56–62.

Hallé, F., Oldeman, R.A.A., Tomlinson, P.B. 1978. Tropical trees and forests: an architectural analysis. Berlin: Springer.

Hans, A.S. 1973. Chromosomal conspectus of the Euphorbiaceae. Taxon 22: 591–636.

Hayden, W.J. 1994. Systematic anatomy of Euphorbiaceae subfamily Oldfieldioidae. I. Overview. Ann. Missouri Bot. Gard. 81: 180–202.

Hayden, W.C., Hayden, S.M. 2000. Wood anatomy of Acalyphoideae (Euphorbiaceae). IAWA J. 21: 213–235.

Hayden, W.J. , Gillis, W.T., Stone, D.E., Broome, C.R., Webster, G.L. 1984. Systematics and palynology of *Picrodendron*: further evidence for relationship with the Oldfieldioideae (Euphorbiaceae). J. Arnold Arb. 65: 105–127.

Hegnauer, R. 1966, 1989. See General References.

Herbert, H. 1897. Anatomische Untersuchung von Blatt und Axe der Hippomaneen. Dissertation: Munich.

Hickey, L.J. 1983. Classification of the architecture of dicotyledonous leaves. Amer. J. Bot. 60: 17–32.

Hickey, L.J., Wolfe, J.A. 1975. The bases of angiosperm phylogeny: vegetative morphology. Ann. Missouri Bot. Gard. 62: 538–589.

Hoang Van Sam, van Welzen, P.C. 2004. Revision of *Annesijoa*, *Elateriospermum*, and the introduction of species of *Hevea* in Malesia. Blumea 49: 425–440.

Hoffmann, P. 2008. Revision of *Heterosavia*, with notes on *Gonatogyne* and *Savia* (Phyllanthaceae). Brittonia 60: 136–166.

Hoffmann, P., McPherson, G. 2007. Revision of *Wielandia*, including *Blotia* and *Petalodiscus* (Phyllanthaceae; Euphorbiaceae s.l.). Ann. Missouri Bot. Gard. 94: 519–553.

Hoffmann, P., Wurdack, K.J. 2006. *Radcliffea*, a new genus of Euphorbiaceae sensu stricto from Madagascar. Kew Bull. 61: 193–197.

Hoppe, J.R. 1985. Die Morphologie der Cyathiendrüsen und ihrer Anhänge, ihre blattypologische Deutung und Bedeutung. Bot. Jahrb. Syst. 105: 497–581.

Hoppe, J., Uhlarz, H. 1982. Morphogenese und typologische Interpretation des Cyathiums von *Euphorbia*-Arten. Beitr. Biol. Pflanzen 56: 63–98.

Horn, J.W., van Ee, B.W., Morawetz, J.J., Riina, R., Steinmann, V., Berry, P.E., Wurdack, K.J. 2012. Phylogenetics and the evolution of major structural characters in the giant genus *Euphorbia* L. (Euphorbiaceae). Mol. Phylogen. Evol. 63: 305–326.

Hurusawa, I. 1954. Eine nochmalige Durchsicht des herkömmlichen Systems der Euphorbiaceen im weiteren Sinne. J. Fac. Sci. Univ. Tokyo, Bot. 6: 209–342.

Hutchinson, J. 1969. Tribalism in the family Euphorbiaceae. Amer. J. Bot. 56: 738–758.

Jablonski, E. 1967. Euphorbiaceae. Botany of Guayana Highland—Part VII. Mem. New York Bot. Gard. 17: 80–190.

Jennings, D.L. 1963. Variation in pollen and ovule fertility in varieties of cassava, and the effect of interspecific crossing on fertility. Euphytica 12: 69–76.

Jones, K., Smith, J.B. 1969. The chromosome identity of *Monadenium* Pax and *Synadenium* Pax (Euphorbiaceae). Kew Bull. 23: 491–493.

Jussieu, A. 1824. De Euphorbiacearum generibus medicisque earumdem tentamen. Paris: Didot.

Kapil, R.N., Bhatnagar, A.K. 1972. Endosperm in Euphorbiaceae—a critical appraisal. Pp. 376–393. In: Murty, Y.S., Johri, B.M., Mohan Ram, H.Y., Verghese, T.M. (eds.) Advances in Plant Morphology. Meerut: Rustogi Publs.

Kapil, R.N., Bhatnagar, A.K. 1994. The contribution of embryology to the systematics of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 145–159.

Kathriarachchi, H., Samuel, R., Hoffmann, P., Mlinarec, J. Wurdack, K.J., Ralimanana, H., Stuessy, T. F., Chase, M.W. 2006. Phylogenetics of tribe Phyllantheae (Phyllanthaceae; Euphorbiaceae sensu lato) based on *nr*ITS and plastid *mat*K DNA sequence data. Amer. J. Bot. 93: 637–655.

Kathriarachchi, H., Hoffmann, P., Samuel, R., Wurdack, K.J., Chase, M.W. 2005. Molecular phylogenetics of Phyllanthaceae inferred from five genes (plastid *atpB*, *matK*, 3'*ndhF*, *rbcL*, and nuclear *PHYC*). Mol. Phylogen. Evol. 36: 112–134.

Kato, M., Takimura, A., Kawakita, A. 2003. An obligate pollination mutualism and reciprocal diversification in the tree genus *Glochidion* (Euphorbiaceae). Proc. Natl. Acad. Sci. USA 100: 5264–5267.

Kawakita, A. 2010. Evolution of obligate pollination mutualism in the tribe Phyllantheae (Phyllanthaceae). Plant Sp. Biol. 25: 3–19.

Kawakita, A., Kato, M. 2004a. Obligate pollination mutualism in *Breynia* (Phyllanthaceae); further documentation of pollination mutualism involving *Epicephala* moths (Gracillariidae). Amer. J. Bot. 91: 1319–1325.

Kawakita, A., Kato, M. 2004b. Evolution of obligate pollination mutualism in New Caledonian *Phyllanthus* (Euphorbiaceae). Amer. J. Bot. 91: 410–415.

Kinghorn, A.D. 1979. Carcinognic irritant Euphorbiaceae. In: Kinghorn, A.D. (ed.) Toxic plants, pp. 137–159. New York: Columbia Univ. Press.

Kite, G.C., Fellows, L.E., Lees, D.C., Kitchen, D., Monteith, G.B. 1991. Alkaloidal glycosidase inhibitors in diurnal Uraniine moths and their respective foodplant genera *Endospermum* and *Omphalea*. Biochem. Syst. Ecol. 19: 441–445.

Klucking, E.P. 1997. Leaf Venation Patterns, vol. 8, Euphorbiaceae Part I: Phyllanthoideae and Oldfieldioideae. Berlin: J. Cramer.

Klucking, F.P. 2003. Leaf Venation Patterns, vol. 9, Euphorbiaceae Part II: Acalyphoideae, Crotonoideae, and Euphorbioideae. Berlin: J. Cramer.

Köhler, E. 1965. Die Pollenmorphologie der biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomie. Grana Palyn. 6: 26–120.

Korbecka, G., Hamilton, A., Pannell, J.R. 2011. Mixed mating in androdioecious *Mercurialis annua* inferred using progeny arrays and diploid-acting microsatellite loci in a hexaploid background. Ann. Bot. 107: 1057–1061.

Korotkova, N. et al. 2009. See General References.

Koutnik, D.L. 1987. A taxonomic revision of the Hawaiian species of the genus *Chamaesyce* (Euphorbiaceae). Allertonia 4: 331–388.

Krähenbühl, M., Yuan, Y.-M., Küpfer, P. 2002. Chromosome and breeding system evolution of the genus *Mercurialis* (Euphorbiaceae): implications of ITS molecular phylogeny. Plant Syst. Evol. 234: 155–169.

Kruijt, R.C. 1996. A taxonomic monograph of *Sapium* Jacq., *Anomostachys* (Baill.) Hurus., *Duvigneudia* J. Léonard and *Sclerocroton* Hochst. (Euphorbiaceae tribe Hippomaneae). Bibl. Bot. 146: 1–109.

Kulju, K.K.M., van der Ham, W.J.M., Breteler, F.J. 2008. Rediscovery and phylogenetic position of the incertae sedis genus *Afrotrewia* (Euphorbiaceae): morphological, pollen and molecular evidence. Taxon 57: 137–143.

Lees, D.C., Smith, N.G. 1991. Foodplant associations of the Uraniinae (Uraniidae) and their systematic, evolutionary, and ecological signficance. J. Lepidopt. Soc. 45: 296–347.

Léonard, J. 1962. Euphorbiaceae. Fl. Congo & Rwanda-Burundi 8(1): 1–214.

Léonard, J. 1989. Révision du genre africain *Martretia* Beille (Euphorbiaceae) et la nouvelle tribu des Martretieae. Bull. Jard. Bot. Nat. Belg. 59: 319–332.

Léonard, J. 1995. Euphorbiaceae, Fl. Afr. Centr. 8(2): 1–115.

Léonard, J. 1996. Euphorbiaceae, Fl. Afr. Centr. 8(3): 1–74.

Léonard, J., Mosongo, M. 1985. Hymenocardiaceae. Fl. Afrique Centrale.

Leroy, J.-F. 1976. Recherches sur la nature et l'origine de la fleur angiospermienne: interprétation des structures dans un groupe singulier d'Euphorbiaceae. Compt. Rend. Séanc. Acad. Paris, Sér. D, 283: 147–150.

Levin, G.A. 1986a. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae), I. Conspectus. Ann. Missouri Bot. Gard. 73: 29–85.

Levin, G.A. 1986b. Systematic foliar morphology of Phyllanthoideae III. Cladistic analysis. Syst. Bot. 11: 515–530.

Levin, G.A. 1992. Systematics of *Paradrypetes* (Euphorbiaceae). Syst. Bot. 17: 74–83.

Levin, G.A., Simpson, M.G. 1994. Phylogenetic implications of pollen ultrastructure in the Oldfieldioideae

(Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 239–244.
Li, Y., Dressler, S., Zhang, D., Renner, S.S. 2009. More Miocene dispersal between Africa and Asia—the case of *Bridelia* (Phyllanthaceae). Syst. Bot. 34: 521–529.
Lisci, M., Bianchini, M., Pacini, E. 1996. Structure and function of the elaiosome in some angiosperm species. Flora 191: 131–141.
Lobreau-Callen, D., Suarez Cervera, M. 1997. Le pollen des Crotonoideae Apétales (Euphorbiaceae): Ultrastructure de l'exine. Rev. Palaeobot. Palynol. 98: 257–291.
Lobreau-Callen, D., Pons, D., Malécot, V. 2001. Pollen aperturé des Crotonoideae apétales actuelles et fossiles. Contr. to Geol. and Palaeontol. of Gondwana in honour of H. Wopfner, pp. 303–323. Cologne.
Lock, J.M., Hall, J.B. 1982. Floral biology of *Mallotus oppositifolius* (Euphorbiaceae). Biotropica 14: 153–155.
Luo, S., Zhang, D., Renner, S.S. 2007. Duodichogamy and androdioecy in the Chinese Phyllanthaceae *Bridelia tomentosa*. Amer. J. Bot. 94: 260–265.
Maedel, E. 1962. Die fossilen Euphorbiaceen-Hölzer mit besonderer Berücksichtigung neuer Funde aus der Oberkreide Süd-Afrikas. Senckenbergiana leth. 43: 283–321.
Mahlberg, P.G. 1975. Evolution of the laticifer in *Euphorbia* as interpreted from starch grain morphology. Amer. J. Bot. 62: 577–583.
Mansfeld, R. 1928. Beitrag zur Morphologie des *Euphorbia*-Cyathiums. Ber. Deutsch. Bot. Ges. 46: 674–677.
Martin, H.A. 1974. The identification of some Tertiary pollen belonging to the family Euphorbiaceae. Austral. J. Bot. 22: 271–291.
Martin, H.A. 1978. Evolution of the Australian flora and vegetation through the Tertiary: evidence from pollen. Alcheringa 2: 181–202.
Matthews, M.L., Endress, P.K. 2011. See General References.
Mazer, S.J., Tiffney, B.H. 1982. Fruits of *Wetherellia* and *Paleowetherellia* (? Euphorbiaceae) from Eocene sediments in Virginia and Maryland. Brittonia 34: 300–333.
McPherson, G., Tirel, C. 1987. Euphorbiacées. Fl. Nouv. Caléd. 14(1): 1–226.
Meeuse, A.D.J. 1990. The Euphorbiaceae auct. plur.: an unnatural taxon. Delft: Eburon.
Meeuse, A.D.J., Vinkenoog, S., Vroege, P.W. 1989. Anthecology of *Euphorbia*—preliminary studies. Acta Bot. neerl. 38: 493–502.
Meewis, B., Punt, W. 1983. Pollen morphology and taxonomy of the subgenus *Kirganelia* (Jussieu) Webster (genus *Phyllanthus*, Euphorbiaceae) from Africa. Rev. Palaeobot. Palynol. 39: 131–160.
Mennega, A.M.W. 1987. Wood anatomy of the Euphorbiaceae, in particular of the subfamily. Phyllanthoideae. Bot. J. Linn. Soc. 94: 111–126.
Merino Sutter, D., Forster, P.I., Endress, P.K. 2006. Female flowers and systematic position of Picrodendraceae (Euphorbiaceae s.l., Malpighiales). Pl. Syst. Evol. 261: 187–215.
Metcalfe, C.R., Chalk, L. 1950. Anatomy of the Dicotyledons. Oxford: Clarendon Press.
Michaelis, P. 1924. Blütenmorphologische Untersuchungen an den Euphorbiaceen. Bot. Abh. Jena 3: 1–150.
Moog, U., Fiala, B., Federle, W., Maschwitz, U. 2002. Thrips pollination of the dioecious ant plant *Macaranga hullettii* (Euphorbiaceae) in southeast Asia. Amer. J. Bot. 89: 50–59.
Muller, J. 1984. Significance of fossil pollen for angiosperm history. Ann. Missouri Bot. Gard. 72: 419–443.
Müller, J. 1866. Euphorbiaceae [except Euphorbieae]. DC. Prodr. 15(2): 189–1261.
Müller, J. 1873–1874. Euphorbiaceae. In: Martius, Fl. Brasiliensis 11(2): 1–750. Leipzig: Fleischer.
Narbona, E., Ortiz, P.L., Arista, M. 2002. Functional andromonoecy in *Euphorbia* (Euphorbiaceae). Ann. Bot. 89: 571–577.
Netolitzky, F. 1926. See General References.
Neuwinger, H.D. 2000.African traditional medicine: a dictionary of plant use and application. Stuttgart (Germany): Medpharm Scientific.
Nowicke, J.W. 1994. A palynological study of Crotonoideae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 245–269.
Nowicke, J.W., Takahashi, M. 2002. Pollen morphology, exine structure and systematics of Acalyphoideae (Euphorbiaceae), Part 4. Rev. Palaeobot. Palynol. 121: 231–336.
Nowicke, J.W., Takahashi, M., Webster, G.L. 1998. Pollen morphology, exine structure and systematics of Acalyphoideae (Euphorbiaceae), Part 1. Rev. Palaeobot. Palynol. 102: 115–152.
Nowicke, J.W., Takahashi, M., Webster, G.L. 1999. Pollen morphology, exine structure and systematics of Acalyphoideae (Euphorbiaceae), Part 2. Rev. Palaeobot. Palynol.105: 1–62.
Olmos, F., Boulhosa, R.L.P. 2000. A meeting of opportunists: birds and other visitors to *Mabea fistulifera* (Euphorbiaceae) inflorescences. Ararajuba 8: 93–98.
Pax, F. 1884. Die Anatomie der Euphorbiaceen in ihrer Beziehung zum System derselben. Bot. Jahrb. 5: 384–421.
Pax, F. 1890. Euphorbiaceae. In: Engler, K., Prantl, K. (eds.) Die natürl. Pflanzenfam. III, 5: 1–119. Leipzig: W. Engelmann.
Pax, F. 1924. Die Phylogenie der Euphorbiaceae. Bot. Jahrb. Syst. 59: 129–182.
Pax, F., Hoffmann, K. 1912. Euphorbiaceae—Hippomaneae. Das Pflanzenreich, IV, 147. V: 1–319.
Pax, F., Hoffmann, K. 1919 Euphorbiaceae-Acalypheae-Plukenetiinae, Epiprininae, and Ricininae, in: Engler, A., Das Pflanzenreich, IV 147, IX, X, XI, Heft 68.
Pax, F., Hoffmann, K. 1931. Euphorbiaceae. In: Engler, K., Prantl, K. (eds.) Die natürlichen Pflanzenfamilien, ed. 2, 19c: 11–233. Leipzig: W. Engelmann.
Perkins, G., Estes, J.R., Thorp, R.W. 1975. Pollination of *Cnidoscolus texanus* (Euphorbiaceae) in south-central Oklahoma. Southw. Nat. 20: 391–396.
Ponsinet, G., Ourisson, G. 1965. Étude chimiotaxonomique dans la famille des euphorbiacées—I. Phytochemistry 4: 799–811.
Prenner, G., Rudall, P.J. 2007. Comparative ontogeny of the cyathium in *Euphorbia* (Euphorbiaceae) and its allies: exploring the organ-flower-inflorescence boundary. Amer. J. Bot. 94: 1612–1629.
Prenner, G., Hopper, S.D., Rudall, P.J. 2008. Pseudanthium development in *Calycopeplus paucifolius*, with particular reference to the evolution of the

cyathium in Euphorbieae (Euphorbiaceae-Malpighiales). Austr. J. Bot. 21: 153–161.
Punt, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7: 1–116.
Punt, W. 1987. A survey of pollen morphology in Euphorbiaceae with special reference to *Phyllanthus*. Bot. J. Linn. Soc. 94: 127–142.
Radcliffe-Smith, A. 1987. Segregate families from the Euphorbiaceae. Bot. J. Linn. Soc. 94: 47–66.
Radcliffe-Smith, A. 1996. Euphorbiaceae, Pt. 1. In: Flora Zambesiaca 9(4): 1–337. Kew: Royal Botanic Gardens.
Radcliffe-Smith, A. 1997. Flora of tropical East Africa. Euphorbiaceae (Pt. 1). Rotterdam/Boston: A.A. Balkema.
Radcliffe-Smith, A. 2001. Genera Euphorbiacearum. Kew: Royal Botanic Gardens.
Reddi, E.U.B., Subba-Reddi, C. 1983. Pollination ecology of *Jatropha gossypifolia* (Euphorbiaceae). Proc. Indian Acad. Sci. (Plant Sci) 92: 215–231.
Reveal, J.L. 1995 onward. Index nominum supragenicorum plantarum vascularium. http://www.life.umd.edu/emeritus/reveal/pbio/WWW/supragen.html
Ridley, N.H. 1930. The dispersal of plants throughout the world. Ashford: Reeve.
Riina, R., van Ee, B., Wiedenhoeft, A.C., Cardozo, A., Berry, P.E. 2010. Sectional rearrangement of arborescent clades of *Croton* (Euphorbiaceae) in South America: evolution of arillate seeds and a new species, *Croton domatifer*. Taxon 59: 1147–1160.
Rittershausen, P. 1892. Anatomisch-systematische Untersuchung von Blatt und Axe der Acalypheen. Inaugur.-Diss., Munich.
Rizk, A.M. 1987. The chemical constituents and economic plants of the Euphorbiaceae. Bot. J. Linn. Soc. 94: 292–326.
Rossignol, L., Rossignol, M. 1985. Architecture et tendences évolutives dans le genre *Phyllanthus* (Euphorbiaceeae). Bull. Mus. Nat. Hist. Nat. IV. 7: 67–80.
Rothdauscher, H. 1896. Über die anatomischen Verhältnisse von Blatt und Axe der Phyllantheen (mit Ausschluss der Euphyllantheen). Inaug.-Diss., Cassel (also publ. in Bot. Centralbl. 68).
Roux, J. 1968. Sur le comportement des axes aériens chez quelques plantes à rameaux végétatifs polymorphes; le concept des rameaus plagiotropes. Ann. Sci. Nat. Bot. XII. 9: 109–256.
Rudall, P.J. 1987. Laticifers in the Euphorbiaceae—a conspectus. Bot. J. Linn. Soc. 94: 143–163.
Rudall, P.J. 1994. Laticifers in Crotonoideae (Euphorbiaceae): homology and evolution. Ann. Missouri Bot. Gard. 81: 270–282.
Sagun, V.G., van der Ham, R.W.J.M. 2003. Pollen morphology of the Flueggeinae (Euphorbiaceae, Phyllanthoideae). Grana 42: 193–219.
Sahagún-Godiñez, E., Lomelí-Sención, J.A. 1997. *Pedilanthus diazlunanus* (Euphorbiaceae): pollination by hymenopterans in a bird-pollinated genus. Amer. J. Bot. 84: 1584–1587.
Samuel, R., Kathriarachchi, H., Hoffmann, P., Barfuss, M. H.J., Wurdack, K.J., Davis, C.C., Chase, M.W. 2005. Molecular phylogenetics of Phyllanthaceae: evidence from plastid *mat*K and nuclear PHYC sequences. Amer. J. Bot. 92: 132–141.
Savolainen, V., Fay, M.F., Albach, D.C., Backlund, A., van der Bank, M., Cameron, K.M., Johnson, S.A., Lledó, M.D., Pintaud, J.-C., Powell, M., Sheahan, M.C., Soltis, D.E., Weston, P., Whitten, M., Wurdack, K.J., Chase, M.W. 2000. Phylogeny of the eudicots: a nearly complete familial analysis based on *rbc*L gene sequences. Kew Bull.55: 257–309.
Sazima, M., Sazima, I., de Carvalho-Okano, R.M. 1985. Biologia floral de *Dalechampia stipulacea* (Euphorbiacaea) e sua polinização por *Euglossa melanotricha* (Apidae). Rev. Bras. Biol. 45: 85–93.
Schatz, G.E. 2001. Generic Tree Flora of Madagascar. Kew, Royal Botanic Gardens and Missouri Botanical Garden.
Schultes, R. 1952. Studies in the genus *Micrandra* I. The relationship of the genus *Cunuria* to *Micrandra*. Bot. Mus. Leafl. Harvard Univ. 15: 201–222.
Schultes, R. 1970. The history of taxonomic studies in *Hevea*. Bot. Rev. 36: 197–276.
Schultes, R.E. 1987. Members of Euphorbiaceae in primitive and advanced societies. Bot. J. Linn. Soc. 94: 79–95.
Secco, R. 1989. Dialissepalia do gênero *Sandwithia* Lanjouw: Uma novidade botânica do alto Rio Negro e da Venezuela. Bol. Mus. Paraense Emilio Goeldi, n.s., Bot. 4: 177–185.
Secco, R. 1990. Revisão dos gêneros *Anomalocalyx* Ducke, *Pausandra* Radlk., *Pogonophora* Miers ex Benth. e *Sagotia* Baill. (Euphorbiaceae-Crotonoideae) para a América do Sul. Belém: Museu Paraense Emílio Goeldi.
Seigler, D.S. 1994. Phytochemistry and systematics of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 380–401.
Simpson, M.G., Levin, G.A. 1994. Pollen ultrastructure of the biovulate Euphorbiaceae. Int. J. Plant Sci. 155: 313–341.
Slik, J.W.F. 2001. *Macaranga* and *Mallotus* (Euphorbiaceae) as indicators for disturbance in the lowland Dipterocarp forests of east Kalimantan, Indonesia. Wageningen: The Tropenbos Foundation.
Solereder, H. 1908. Systematische Anatomie der Dicotylen. Ergänzungsband. Stuttgart: Enke.
Soltis, D.E. et al. 2011. See General References.
Steiner, K.E. 1981. Nectarivory and potential pollination by a Neotropical marsupial. Ann. Missouri Bot. Gard. 68: 505–513.
Steiner, K.E. 1982. Mistake pollination of *Hura crepitans* (Euphorbiaceae) by frugivorous bats. Doctoral dissert., University of California, Davis.
Steiner, K.E. 1983. Pollination of *Mabea occidentalis* (Euphorbiaceae) in Panama. Syst. Bot. 8: 105–117.
Steinmann, V.W. 2003. The submersion of *Pedilanthus* into *Euphorbia* (Euphorbiaceae). Acta Bot. Mexic. 65: 45–60.
Steinmann, V.W., van Ee, B., Berry, P.E., Gutiérrez, J. 2007. The systematic position of *Cubanthus* and other shrubby endemic species of *Euphorbia* (Euphorbiaceae) in Cuba. Ann. Jard. Bot. Madrid 64: 123–133.
Steinmann, V.W., Porter, J.M. 2002. Phylogenetic relationships in Euphorbieae (Euphorbiaceae) based on ITS and *ndh*F sequence data. Ann. Missouri Bot. Gard. 89: 453–490.
Stuppy, W. 1996. Systematische Morphologie und Anatomie der Samen der biovulaten Euphorbiaceen. Dissert., Univ. Kaiserslautern.

Suárez-Cervera, M., Gillspie, L., Arcalis, E., Le Thomas, A., Lobreau-Callen, D., Seoane-Camba, J.A. 2001. Taxonomic significance of sporoderm structure in pollen of Euphorbiaceae: tribes Plukenetieae and Euphorbieae. Grana 40: 78–104.

Subba-Reddi, C., Reddi, E.U.B. 1984. Wind-pollination in two tropical tree species of Euphorbiaceae. Proc. Indian Natn. Sci. Acad. B 50: 66–80.

Sutter, K., Endress, P.K. 1995. Aspects of gynoecium structure and macrosystematics in Euphorbiaceae. Bot. Jahrb. Syst. 116: 517–536.

Swaine, M.D., Beer, T. 1976. Explosive seed dispersal in *Hura crepitans* (Euphorbiaceae). New Phytol. 78: 695–708.

Takahashi, M., Nowicke, J.W., Webster, G.L. 1995. A note on remarkable exines in Acalyphoideae. Grana 34: 282–290.

Takahashi, M., Nowicke, J.W., Webster, G.L., Orli, S.S., Yankowski, S. 2000. Pollen morphology, exine structure, and systematics of Acalyphoideae (Euphorbiaceae), part 3. Rev. Palaeobot. Palynol. 110: 1–66.

Thin, N.N. 1995. Euphorbiaceae of Vietnam. Hanoi: Publishing House "Agriculture".

Thurston, E.L. 1976. Morphology, fine structure and ontogeny of the stinging emergences of *Tragia ramosa* and *T. saxicola* (Euphorbiaceae). Amer. J. Bot. 63: 710–718.

Thurston, E.L., Lersten, N.R. 1969. The morphology and toxicology of plant stinging hairs. Bot. Rev. 35: 393–412.

Tokuoka, T. 2007. Molecular phylogenetic analysis of Euphorbiaceae sensu stricto based on plastid and nuclear DNA sequences and ovule and seed character evolution. J. Plant Res. 120: 511–522.

Tokuoka, T., Tobe, H. 1995. Embryology and systematics of Euphorbiaceae sens. lat.: a review and perspective. J. Plant Res. 108: 97–106.

Tokuoka, T., Tobe, H. 1998. Ovules and seeds in Crotonoideae (Euphorbiaceae): structure and systematic implications. Bot. Jahrb. Syst. 120: 165–186.

Tokuoka, T., Tobe, H. 1999. Embryology of tribe Drypeteae, an enigmatic taxon of Euphorbiaceae. Pl. Syst. Evol. 215: 189–208.

Tokuoka, T., Tobe, H. 2001. Ovules and seeds in subfamily Phyllanthoideae (Euphorbiaceae): structure and systematic implications. J. Plant Res. 114: 75–92.

Tokuoka, T., Tobe, H. 2002. Ovules and seeds in subfamily Euphorbioideae (Euphorbiaceae): structure and systematic implications. J. Plant Res. 115:361–374.

Tokuoka, T., Tobe, H. 2003. Ovules and seeds in Acalyphoideae (Euphorbiaceae): structure and systematic implications. J. Plant Res. 116: 355–380.

Tokuoka, T., Tobe, H. 2006. Phylogenetic analyses of Malpighiales using plastid and nuclear DNA sequences, with particular reference to the embryology of Euphorbiaceae sens. str. J. Plant Res. 119: 599–616.

Torres de Assumpção, C. 1981. *Cebus apella* and *Brachyteles arachnoides* (Cebidae) as potential pollinators of *Mabea fistulifera* (Euphorbiaceae). J. Mamm. 62: 386–388.

Uhlarz, H. 1974. Entwicklungsgeschichtliche Untersuchungen zur Morphologie der basalen Blatteffigurationen sukkulenter Euphorbien aus den Subsektionen Diacanthium Boiss. und Goniostema Baill. Trop. Subtrop. Pflanzenwelt 9: 575–639.

Uhlarz, H. 1978. Ueber die Stipularorgane der Euphorbiaceae, unter besonderer Berucksichtigung ihrer Rudimentation. Trop. Subtrop. Pflanzenwelt 23: 1–65.

Urbatsch, L.E., Bacon, J.D., Hartman, R.L., Johnston, M. C., Watson Jr., T.J., Webster, G.L. 1975. Chromosome numbers for North American Euphorbiaceae. Amer. J. Bot. 62: 494–500.

van Ee, B.W., Berry, P.E., Riina, R., Gutiérrez-Amaro, J.E. 2008. Molecular phylogenetics and biogeography of the Caribbean-centered *Croton* subgenus *Macrocroton* (Euphorbiaceae). Bot. Rev. 74: 132–165.

Venkata Rao, C. 1971. Anatomy of the inflorescence of some Euphorbiaceae. Adv. Pl. Morphol. 1972: 85–91.

Venkata Rao, C., Ramalakshmi, T. 1968. Floral anatomy of the Euphorbiaceae—I. Some non-cyathium taxa. J. Indian Bot. Soc. 47: 219–235.

Vieira, M.F., Carvalho-Okano, R.M. de 1996. Pollination biology of *Mabea fistulifera* (Euphorbiaceae) in southeastern Brazil. Biotropica 28: 61–68.

Vogel, C. 1986. Phytoserologische Untersuchungen zur Systematik der Euphorbiaceae; Beiträge zur infrafamiliären Gliederung und zu Beziehungen im extrafamiliären Bereich. Dissert. Bot. 98: 1–124.

Vorontsova, M.S., Hoffmann, P., Maurin, O., Chase, M. W., 2007. Molecular phylogenetics of tribe Poranthereae (Phyllanthaceae; Euphorbiaceae sensu lato). Amer. J. Bot. 94: 2026–2040.

Warmke, H.E. 1952. Studies on natural pollination of *Hevea brasiliensis* in Brazil. Science 116: 474, 475.

Webster, G.L. 1956. A monographic study of the West Indian species of *Phyllanthus*. J. Arnold Arbor. 37: 91–122, 217–268, 340–359.

Webster, G.L. 1967. The genera of Euphorbiaceae in the southeastern United States. J. Arnold Arb. 48: 303–430.

Webster, G.L. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.

Webster, G.L. 1986. Irritant plants in the spurge family (Euphorbiaceae). Clinics Dermatol. 4: 36–45.

Webster, G.L. 1987. The saga of the spurges: a review of the classification and relationships of the Euphorbiaceae. Bot. J. Linn. Soc. 94: 3–46.

Webster, G.L. 1993. A provisional synopsis of the sections of the genus *Croton* (Euphorbiaceae). Taxon 42: 793–823.

Webster, G.L. 1994a. Classification of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 3–32.

Webster, G.L. 1994b. Synopsis of the genera and suprageneric taxa of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 33–144.

Webster, G.L. 2002. A synopsis of the Brazilian taxa of *Phyllanthus* section *Phyllanthus* (Euphorbiaceae). Lundellia 5: 1–26.

Webster, G.L., Armbruster, W.S. 1991. A synopsis of the neotropical species of *Dalechampia* (Euphorbiaceae). Bot. J. Linn. Soc. London 105: 137–177.

Webster, G.L., Carpenter, K. 2002. Pollen morphology and phylogenetic relationships in neotropical *Phyllanthus* (Euphorbiaceae). Bot. J. Linn. Soc. 138: 325–338.

Webster, G.L., Rupert, E. 1973. Phylogenetic significance of pollen nuclear number in Euphorbiaceae. Evolution 27: 524–531.

Webster, G.L., Brown, W.V., Smith, B.N. 1975. Systematics of phytosynthetic carbon fixation in *Euphorbia*. Taxon 24: 27–33.

Webster, G.L., Rupert, E., Koutnik, D. 1982. Systematic significance of pollen nuclear number in Euphorbiaceae, tribe Euphorbieae. Amer. J. Bot. 69: 407–415.

Welkie, G.W., Caldwell, L. 1970. Leaf anatomy of species in some dicotyledon plant families as related to the C3 and C4 pathways of carbon fixation. Can. J. Bot. 48: 2135–2146.

Welzen, P.C. van. 1995. Taxonomy and phylogeny of the Euphorbiaceae tribe Erismantheae G. L. Webster (*Ersimanthus*, *Moutonianthus*, and *Syndyophyllum*). Blumea 40: 375–396.

Welzen, P.C. van. 1999. Revision and phylogeny of subtribes Chrozophorinae and Dorylinae (Euphorbiaceae) in Malesia and Thailand. Blumea 44: 411–436.

Welzen, P.C. van, Bulalacao, L.J., Ôn, T.V. 1995. A taxonomic revision of the Malesian genus *Trigonopleura* Hook. f. (Euphorbiaceae). Blumea 40: 363–374.

Welzen, P.C. van, Stuppy, W. 1999. Phylogenetic considerations of Euphorbiaceae tribe Aleuritidae. Ann. Missouri Bot. Gard. 86: 894–903.

Wheeler, L.C. 1943. The genera of living Euphorbieae. Amer. Midl. Nat. 3: 456–503.

Wunderlich, R. 1968. Some remarks on the taxonomic significance of the seed coat. Phytomorphology 17: 301–311.

Wurdack, K.J. 2002. The molecular systematics and evolution of Euphorbiaceae *sensu lato*. Doct. dissert., Univ. North Carolina at Chapel Hill. Chapel Hill. UMI number 3047094.

Wurdack, K.J., Chase, M.W. 1999. Spurges split: molecular systematics and changing concepts of Euphorbiaceae. Abstr. XVI Int. Bot. Congress 142.

Wurdack, K.J., Davis, C.C. 2009. Malpighiales phylogenetics: gaining ground on one of the most recalcitrant clades in the angiosperm tree of life. Amer. J. Bot. 96: 1551–1570.

Wurdack, K.J., Hoffmann, P., Samuel, R., de Bruijn, A., van der Bank, M., Chase, M.W. 2004. Molecular phylogenetic analysis of Phyllanthaceae (Phyllanthoideae pro parte, Euphorbiaceae sensu lato) using plastid *rbc*L DNA sequences. Amer. J. Bot. 91: 1882–1900.

Wurdack, K.J., Hoffmann, P., Chase, M.W. 2005. Molecular phylogenetic analysis of uniovulate Euphorbiaceae (Euphorbiaceae sensu stricto) using plastid *rbc*L and *trn*L-F DNA sequences. Amer. J. Bot. 92: 1397–1420.

Xi, Z. et al. 2012. See General References.

Yang, Y., Riina, R., Morawetz, J.J., Haevermans, T., Aubriot, X., Berry, P.E. 2012. Molecular phylogenetics and classification of *Euphorbia* subgenus *Chamaesyce* (Euphorbiaceae). Taxon 61: 764–789.

Zimmermann, N.F.A., Ritz, C.M., Hellwig, F.H. 2010. Further support for the phylogenetic relationships within *Euphorbia* L. (Euphorbiaceae) from nrITS and *trnL-trnF* IGS sequence data. Plant Syst. Evol. 286: 39–58.