Chrysobalanaceae

Chrysobalanaceae R. Br. (1818), nom. cons.

G.T. Prance

Trees, shrubs or suffrutices. Leaves alternate, simple, margins entire, pinnately nerved; stipules small and caducous to large and persistent, sometimes adnate to petiole. Inflorescence racemose, paniculate or cymose. Flowers bracteate and usually with 2 prophylls, actinomorphic to zygomorphic, bisexual or rarely polygamous or unisexual, markedly perigynous; receptacle short to elongate-cylindrical, sometimes gibbous at base; disk always present, forming a lining to receptacle or an annular or shortly tubular structure at its mouth; sepals 5, imbricate; petals 5, imbricate, often unequal, rarely unguiculate, sometimes absent; stamens 2–100 (−300) inserted on margin of disk or basally adnate to it, forming a complete circle or unilateral in zygomorphic flowers; filaments free, connate at base or ligulately connate, included to far exserted; anthers dorsifixed, longitudinally dehiscent; ovary superior, inserted at base, middle or mouth of the receptacle, either unilocular with 2 ovules, or bilocular with 1 ovule in each loculus; ovules erect, epitropous with micropyle directed towards base; style filiform arising from receptacle at base of ovary; stigma distinctly or indistinctly 3-lobed. Fruit a dry or fleshy drupe; endocarp thin and bony to thick and woody, often with a special mechanism for seedling escape, often densely hairy within. Seed erect, almost exalbuminous; cotyledous planoconvex, fleshy, rarely ruminate; germination cryptocotylar or phanerocotylar.

A pantropical family with eighteen genera and 423 of the 531 spp. in the Neotropics, 56 in Africa and Madagascar, and 43 in Asia and the Pacific. Extending beyond the tropics with one species each into the southern U.S.A. and southern Brazil.

Vegetative Morphology. The majority of species of Chrysobalanaceae are leptocaul trees but there are also many savannah shrubs and understorey shrubs, especially in the genus *Hirtella*. At least six species are geoxylic suffrutices, one in Florida, two in the Cerrado region of Brazil and three (*Parinari capensis* and two species of *Magnistipula*) in southern Africa. Many species are tall trees of the rainforest canopy and a few, especially in *Parinari*, are emergents. A few species of *Dactyladenia* and *Hirtella* have scandent branches, but there are no lianas. Those species which have been studied exhibit the architectural model of Troll. Leaves are simple, alternate and usually medium sized, but very large in a few species (up to 50 cm long in *Licania gentryi*). There are frequently glands on the undersurface or on the petioles. Stipules are always present but sometimes very early caducous. They range from minute to quite large in some species of *Licania*, *Parinari* and *Magnistipula*. They are either axillary or, in many species of *Licania*, inserted on the lower portion of the petiole. Seven species of *Hirtella* section *Myrmecophila* have myrmecophilous inflations at the junction of the leaf lamina with the petiole. These are inhabited by ants of the genera *Allomerus*, *Azteca* or *Solenopsis*. *Magnistipula bimarsupiata* also has two small inflations at the base of the lamina, and some internodes are swollen and perforated. It also has the coarse hispid tomentum characteristic of ant plants. The trunks of tree species may be either cylindric or buttressed. The bark of most species chips into small fragments with a sharp metallic ring when hit with a machete, due to the presence of abundant silica grains.

Flower Structure. The flowers are actinomorphic with the ovary inserted at the base of the receptacle in *Chrysobalanus*, *Licania* and *Parastemon* (Fig. 4), and zygomorphic with the ovary inserted at the mouth or middle of the receptacle in the remaining genera (Fig. 5). The

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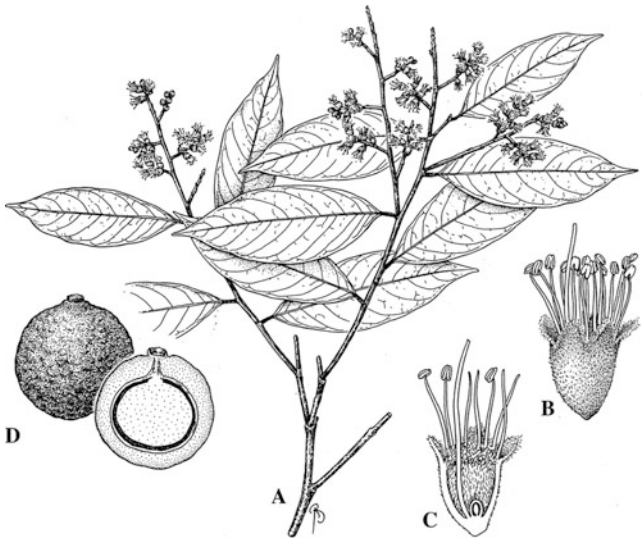

Fig. 4. Chrysobalanaceae. *Licania granvillei*. **A** Flowering branchlet. **B** Flower; note lack of corolla. **C** Medial section of flower showing gynobasic style. **D** Entire and sectioned fruit with attachment scar at top. (Reproduced with kind permission of the artist Bobbi Angell)

calyx is imbricate in bud, 5-lobed, entire; stipitate glands occur in some species of *Dactyladenia* and *Hirtella*. There are usually 5 free, imbricate petals, except in *Licania* subgenus *Licania* and section *Leptobalanus* which are apetalous. In a few species distinctly unguiculate petals occur, especially in *Kostermanthus* where the 2 posterior petals are larger and enclose the stamens in bud. Stamens range from 2 in *Parastemon* to over 300 in some species of *Couepia*. The filaments are usually distinct, but are connate into a unilateral, strap-like ligule in *Acioa*, *Dactyladenia* and *Kostermanthus*; they may be connate for up to half their length in a few species of *Licania* and in *Chrysobalanus*. The stamens may be inserted around a complete circle or unilateral, and the filaments either exserted or included. The anthers are dorsifixed and dehisce laterally. A disk is always present, forming a lining to the receptacle or an annular structure at its mouth. The ovary is superior and inserted at the base, middle or mouth of the receptacle, either unilocular with two ovules or bilocular with one tenuinucellate ovule in each loculus. The ovules are erect and epitropous, with the micropyle directed towards the base. The style is filiform and always arises from the base of the ovary (gynobasic); it usually equals or exceeds the stamens in length.

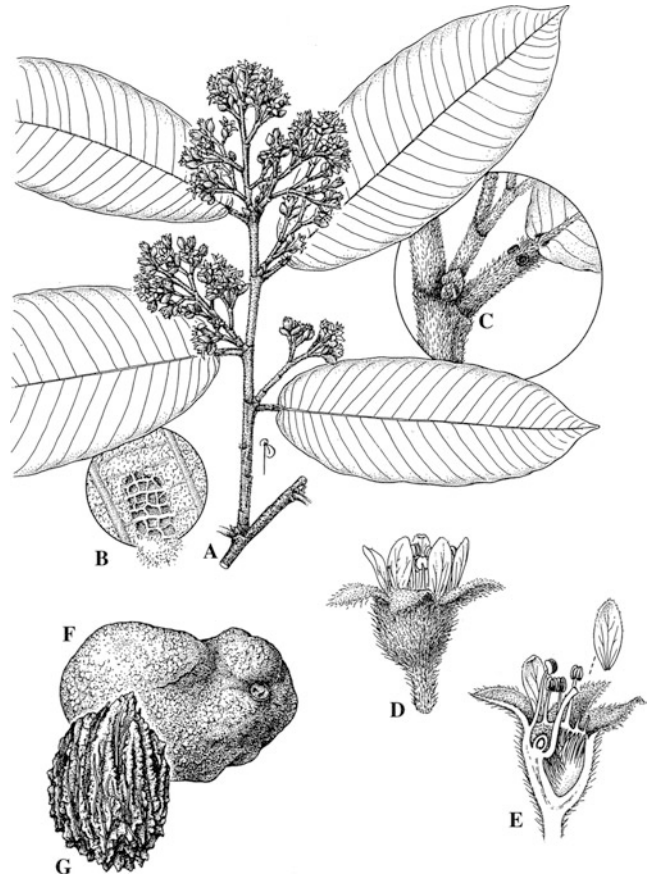

Fig. 5. Chrysobalanaceae. *Parinari montana*. **A** Flowering branchlet. **B** Abaxial leaf surface with part of woolly pubescence removed to show venation. **C** Stipulate node with glandular petiole and base of panicle with prophyll. **D** Flower. **E** Same, medial section, with perched gynoecium, cup-shaped hypanthium and petal. **F** Fruit with attached scar. **G** Seed with corrugated endocarp. (Reproduced with kind permission of the artist Bobbi Angell)

Embryology. The embryology was studied by Tobe and Raven (1984). The tetrasporangiate anthers have five-layered walls including a glandular tapetum with cells two-nucleate. Cytokinesis in the microspore mother cells is simultaneous. The nucellus is very small and the nucellar tissue soon disintegrates, except for the megaspore or embryo sac; antipodal cells are absent. The ovule is bitegmic; the inner integument (ii) and the outer integument (oi) are initiated dermally; the ii is up to five or eight cells thick and the oi more than five cells thick; the inner epidermis of the ii develops into the endothelium, which directly borders the embryo sac and accumulates starch grains; the micropyle is formed by both integuments. Endosperm formation is of the nuclear

type and the seed is exalbuminous. The young seed coat is composed of both testa and tegmen.

Pollen Morphology. The pollen of Chrysobalanaceae is very uniform. The pollen is tricolporate but in some species four furrows may occur. There are no special features, excepting equatorial constrictions. The grains are usually distinctly triangular in shape in polar view, except when four-furrowed; they are elliptical to circular in equatorial view and are oblate-spheroidal, prolate-spheroidal or subprolate in shape. The polar length x 100 divided by the equatorial length = 85–150, but the size is quite variable from one genus to another; the polar area is usually small, sometimes medium, but never large. The exine is medium to rather thick with very little patterning on the walls, usually scabrous to verrucose. See Prance and White (1988), and also Barth and Silva (1963), Demchenko (1973), Patel et al. (1983).

Karyology. The chromosomes have been counted for nine species: $2n = 20$ in *Maranthes* and *Parinari* and $2n = 22$ in *Chrysobalanus*, *Dactyladenia* and *Licania* (Mangenot and Mangenot 1962; de Souza 1979).

Pollination. Chrysobalanaceae have a wide range of pollinators. The small-flowered genera *Chrysobalanus*, *Parinari*, *Exellodendron*, *Licania*, etc. are mainly pollinated by a wide variety of small bees. Most species of *Couepia* are night-flowering and are pollinated by hawk-moths, with the exception of the two flagelliflorous species *C. longipendula* and *C. dolichopoda* which are pollinated by bats (Vogel 1968–1969). *Maranthes polyandra* is also bat-pollinated (Lack 1978). *Hirtella* is mainly pollinated by butterflies, except for *H. rugosa* from the mountains of Puerto Rico. The bright red petals of this species do not open fully but form a tube, and it is hummingbird-pollinated. Hummingbirds have also been observed visiting the flowers of several other species of Chrysobalanaceae, especially *Couepia*, but are probably only secondary pollinators. Souza (1979) showed *Chrysobalanus icaco* to be self-compatible.

Fruit and Seed. The fruits of Chrysobalanaceae are always drupes and they are quite uniform, yet have become adapted to a wide range of dispersal agents. The fruit may be dry or fleshy, the endocarp thick or thin, fibrous or bony, often with a special mechanism for the seedling to escape, two basal obturators in *Parinari* and lateral plates in *Maranthes*, *Grangeria* and *Parastemon*. There are longitudinal lines of dehiscence in *Chrysobalanus* and *Hirtella*. The seed is erect, exalbuminous, with planoconvex fleshy cotyledons, and ruminate cotyledons in *Atuna*. *Chrysobalanus icaco* and several species of *Atuna* are dispersed by ocean currents. Several riverine species of *Licania* drop their fruit into rivers at flood time, and are eaten and presumably dispersed by fish. Various species including *Licania elaeosperma* and *Acioa guianensis* are water-dispersed by rivers. Species of *Couepia*, *Licania* and *Parinari* are frequently eaten by bats. *Licania splendens* is dispersed by the fruit pigeon, *Ducula aenea*. Various species of *Parinari* are known to be dispersed by bats, elephants, baboons and other primates, a scatter-hoarding squirrel, fruit pigeons, rheas, emus, agoutis and fish. Agoutis have been observed transporting the fruits of two species of *Couepia*. Most species of *Hirtella*, with their small fleshy fruits, are bird-dispersed. *Maranthes corymbosa* is dispersed by fruit pigeons and hornbills.

Phytochemistry. The chemistry of Chrysobalanaceae has been little studied, except for fatty acids in the seeds, including some quite unusual ones: α-elaeostearic acid (η-octadeca-9c, 11t, 13t-trienoic), α-licanic acid (4-keto-α-elaeostearic), α-parinaric acid (η-octadeca-9c, 11t, 13t, 15c tetraenoic) and 4-keto-α-parinaric acid. For details, see Table 2 in Prance and White (1988). As a result, there are several useful oils in Chrysobalanaceae (see section on Economic Importance below). Phenolics have been studied in a few species and the following compounds have been reported: myricetin, delphinidin, quercetin, cyanidin, kaempferol, quercitin 3-O-glycoside, naringenin 7-O-clycoside, quercetin aglycone (Gibbs 1974; Coradin et al. 1985). All species analysed contained kaempferol and quercetin, and only some contained myricetin.

Systematics. Prance and White (1988) divided the family into four tribes. More recent molecular work (Yakandawala et al. 2010; C.A. Sothers, in prep.) does not support this tribal division,

nor those of other earlier workers. Molecular data show the family as presented here to be a well-defined monophyletic group, but they did not support obvious tribal subdivisions. The tribes of Prance and White were found to be paraphyletic and are not recognised here.

Affinities. Most early classifications regarded the Chrysobalanaceae as a subfamily of the Rosaceae. It is clearly different in terms of many features such as the gynobasic style, erect ovules and wood anatomy. Most later authors who treated Chrysobalanaceae as a family distinct from Rosaceae left it in Rosales. Dahlgren and Thorne (1984) questioned this placement without offering an alternative, but they suggested it might be useful to look at the Myrtales. Tobe and Raven (1984) showed that the embryology does not resemble that of Myrtales, and suggested Theales. Many other placements have been postulated on morphological grounds, including Linaceae, Polygalaceae, Limnanthaceae, Dichapetalaceae, Trigoniaceae, Geraniaceae, Tropaeolaceae, Sapindaceae, Rhizophoraceae, Vochysiaceae and Proteaceae. The Chrysobalanaceae do not even remotely resemble most of these families. However, molecular data suggested that Chrysobalanaceae are a member of Rosidae (rosid group 1) nearest to Trigoniaceae (Chase et al. 1993) in a clade that later became the broadly construed order Malpighiales (APG 1998). Further molecular multigene analyses placed Chrysobalanaceae into a well-supported clade including Chrysobalanaceae + Euphroniaceae and Trigoniaceae + Dichapetalaceae, with Balanopaceae basal to this clade (e.g. Davis and Chase 2004; Wurdack and Davis 2009), a grouping that (without *Balanops*) had been recognised by Hallier (1921) as Chrysobalanaceae (s. l.). The close relationship among these four families is also supported by important traits of their floral structure that have been revealed in the comparative study of Matthews and Endress (2008).

Economic Importance. The fruits of many species are edible and are frequently used by local peoples. Those of *Chrysobalanus icaco* are tinned or bottled in Venezuela and Colombia under the name icacos. Various species of *Couepia*, especially *C. bracteosa* and *C. rufa*, are sold in local markets. Several species of *Parinari* have edible fruits or seeds, and charred kernels of a species of *Parinari* have been found at archaeological sites in Malawi. In Ambuina a dish called *koku koku* is prepared from the mashed seeds of *Atuna excelsa* mixed with fish, ginger, onions, etc. A cooking oil is extracted locally in Amazonia from *Acioa edulis* and *Couepia longipendula*. The oil of *Licania rigida* and *Afrolicania elaeosperma* was formerly used in paints and varnishes as a substitute for tung oil, and *L. arborea* produces a flammable oil which was used for lighting by local people in Mexico. The wood of Chrysobalanaceae is extremely hard to work due to the presence of silica. It has many local uses, especially for marine and river pilings because of its resistance to marine borers. Some species are used locally for fuel and charcoal. Throughout Amazonia the bark of various species of *Licania* and *Couepia* is burnt and the ash mixed with clay to strengthen pottery because of the silica granules. In the Solomon Islands the seeds of *Atuna excelsa*, known as putty nut, is used for caulking boats. The oil from the seed of the same species is used as a hair dressing in the Caroline Islands and as a massage oil in Samoa and Tonga. In Brazil, *Couepia subcordata* and *Licania tomentosa* commonly serve as shade trees.

Conservation. Many species of Chrysobalanaceae are of extremely restricted distribution and grow in highly threatened areas such as the Atlantic coastal forest of Brazil or the lowland forest of Western Ecuador, and are therefore potentially threatened with extinction. The genus *Grangeria* of two species in Madagascar and the Mascarenes must be one of the most endangered, and the states of the monotypic genera *Bafodeya* and *Neocarya* from West Africa is critical.

Key to the Genera

1. Ovary inserted at or near base of receptacle 2
– Ovary inserted laterally at or near mouth of receptacle 5
2. Endocarp with distinct longitudinal ridges corresponding with lines of dehiscence **5. *Chrysobalanus***
– Endocarp without longitudinal ridges, indehiscent or with two lateral plates 3
3. Flowers unisexual (Africa) **2. *Afrolicania***

– Flowers bisexual (South America and Malesia) 4
4. Endocarp without lateral plates which allow seedling to escape **13. *Licania***
– Endocarp dehiscing on germination by means of a pair of large lateral plates **16. *Parastemon***
5. Endocarp with two small basal plugs (obturators); lower leaf surface usually with stomatal crypts 6
– Endocarp without two basal plugs but sometimes germinating by means of two large lateral plates; leaf lower surface rarely with stomatal crypts 7
6. Receptacle turbinate-campanulate; fertile stamens 6–8 **17. *Parinari***
– Receptacle saccate; fertile stamens 12–17 **18. *Neocarya***
7. Stamens far exserted beyond calyx lobes 8
– Stamens not or barely exceeding calyx lobes 14
8. Stamens united into a ligule 9
– Stamens free to base or nearly so, not ligulate 11
9. Sepals very unequal in size, 3 large, 2 very small, the outer sepals with 1 or 2 large discoid glands **1. *Acioa***
– Sepals subequal, without discoid glands on surface 10
10. Two posterior petals unguiculate, enclosing stamens in bud **12. *Kostermanthus***
– Posterior petals not unguiculate **7. *Dactyladenia***
11. Ovary bilocular 12
– Ovary unilocular 13
12. Fruit dehiscing by two lateral plates; cotyledons not ruminate; exocarp smooth **15. *Maranthes***
– Fruit with no lateral plates; cotyledons ruminate; exocarp warted crustaceous **3. *Atuna***
13. Stamens 3–9; fruit dehiscing by longitudinal lines; endocarp thin, bony **10. *Hirtella***
– Stamens 15–300; fruit indehiscent; endocarp thick, fibrous **6. *Couepia***
14. Ovary unilocular 15
– Ovary bilocular 16
15. Receptacle symmetrical; fruit dehiscing by two lateral plates **9. *Grangeria***
– Receptacle gibbous; fruit indehiscent **14. *Magnistipula***
16. Leaf undersurface with stomatal cavities; fruit exocarp sparsely lenticellate; receptacle much swollen to one side **4. *Bafodeya***
– Leaf undersurface glabrous or arachnoid pubescent; receptacle symmetrical or only slightly swollen to one side 17
17. Endocarp opening by lines of weakness which allow seedling to escape **11. *Hunga***
– Endocarp without lines of weakness 18
18. Receptacle markedly asymmetrical; endocarp thick, hard and bony, not ridged at base **14. *Magnistipula***
– Receptacle only slightly swollen to one side; fruit with hard, bony endocarp thin, with a ridge on one side at the base **8. *Exellodendron***

Genera of Chrysobalanaceae

1. *Acioa* Aubl.

Acioa Aubl., Hist. Pl. Guiane 2: 698, t. 280 (1775).

Trees or shrubs. Leaves with 1 or 2 pairs of conspicuous glands at base of lamina and several smaller discoid glands, glabrous on lower surface. Inflorescence a rather lax thyrse with flattened axes; bracts and prophylls not enclosing flower buds, eglandular; receptacle obconic and slightly curved or cyathiform, glabrous within; petals 5, exceeding sepals; stamens 10–20, ligulately connate or free, unilateral, glabrous; ovary unilocular, inserted at mouth of receptacle. Fruit without any special mechanism to allow seedling to escape; endocarp thick, hard, fibrous. Germination phanerocotylar, first two eophylls opposite, otherwise alternate.

Four spp. in Venezuela, the Guianas and Amazonian Brazil.

2. *Afrolicania* Mildbr.

Afrolicania Mildbr., Notizbl. Bot. Gart. Berlin-Dahlem 7: 483 (1921).

Small to medium-sized tree. Leaves usually glabrous, with two glands on petiole. Inflorescence many-flowered terminal and subterminal panicle of racemes; bracts small, membranous, eglandular. Flowers polygamous andro-dioecious; receptacle flattened-turbinate, pubescent within; petals absent; stamens ca. 20, around complete circle, included, free; ovary unilocular, inserted at base of receptacle, absent in male flowers but represented by a slight swelling. Fruit a dry drupe, epicarp warted, without a mechanism for seedling escape. Germination cryptocotylar, eophylls alternate.

One sp., *A. elaeosperma* Mildbr., widespread in W and W Central Africa from Sierra Leone to Gabon.

3. *Atuna* Rafin.

Atuna Rafin., Sylva Tellur.: 153 (1838).

Trees. Leaves with a pair of glands on the midrib at or near base of lower surface, glabrous on lower surface. Inflorescence a raceme or a sparsely branched contracted panicle; bracts and

prophylls not enclosing flower buds in groups, eglandular; receptacle obconic, pubescent throughout within; petals 5, shorter than sepals; stamens 10–25; filaments distinct, far exceeding sepals, glabrous, unilateral, tiny denticulate staminodes opposite; ovary bilocular, inserted at mouth of receptacle. Fruit without any mechanism for seedling to escape; endocarp hard and thick, cotyledons strongly ruminate. Germination cryptocotylar, eophylls alternate.

Eight spp. from southern India eastwards to Samoa, and most abundant in the Malay Peninsula, Borneo and Indonesia.

4. *Bafodeya* Prance

Bafodeya Prance in F. White, Bull. Jard. Bot. Nat. Belg. 46: 271 (1976).

Small trees. Leaves with stomatal crypts filled with densely matted hairs on lower surface, eglandular. Inflorescence a terminal cymose panicle; bracts and prophylls not enclosing flower buds, eglandular; receptacle obliquely campanulate, markedly zygomorphic, much swollen to one side, pubescent within; petals 5, equalling sepals; stamens ca. 7; filaments more or less equalling sepals, unilateral with 4–10 staminodes opposite; ovary bilocular, inserted at mouth of receptacle. Fruit without special mechanism for seedling to escape; endocarp hard, thin, smooth.

A single sp., *B. benna* (Scott Elliot) Prance, in W Africa in Sierra Leone and adjacent Guinea.

5. *Chrysobalanus* L.

Chrysobalanus L., Gen. pl.: 365 (1737); Sp. pl.: 513 (1753).

Shrubs to large trees. Leaves glabrous, usually with two or more glands on lower surface. Inflorescence a few-flowered short raceme of cymules or cymose or a subsessile fascicle; bracts and prophylls not enclosing flower buds, eglandular; receptacle cupuliform, pubescent within; petals 5, longer than sepals; stamens 12–26, filaments $\pm$ twice as long as sepals, slightly united in groups at base, around complete circle, hairy; ovary unilocular, inserted at base of receptacle. Fruit longitudinally ridged, with lines of fracture that allow the seedling to escape, endocarp thin and bony. Germination cryptocotylar, eophylls alternate. $2n = 22$.

Three spp., one widespread in tropical Africa, America and the Caribbean, one endemic to the West Indies, and one in submontane forests of Venezuela.

6. *Couepia* Aubl.

Couepia Aubl., Hist. Pl. Guiane 1: 519, t. 207 (1775); Prance, Fl. Neotrop. 9: 202 (1972).

Trees or shrubs. Leaves often with 1 or 2 pairs of glands at base of lamina, sometimes with several small marginal glands especially near apex, glabrous or arachnoid pubescent beneath or rarely with stomatal crypts. Inflorescence most often a congested thryse or raceme, rarely flowers solitary or densely crowded in a long-pedunculate compound corymb; bracts and prophylls usually not enclosing buds in small group, eglandular; receptacle turbinate to narrowly cylindric, usually glabrous inside except at throat, hairy throughout in a few species; petals 5, more or less equalling sepals; stamens 15–100 or rarely more; filaments far exceeding sepals, free, glabrous, usually forming a complete circle less frequently unilateral. Ovary unilocular, inserted at mouth of receptacle. Fruit without any mechanism to allow seedling to escape; endocarp hard, thick, granular. Germination cryptocotylar, eophylls alternate.

Seventy one spp., all neotropical, ranging from Mexico to S Brazil, but most abundant in the Guianas and Amazonia.

7. *Dactyladenia* Welw.

Dactyladenia Welw., Apont., Ann. Cons. Ultram. 1: 572 (1859); Prance & White, Philos. Trans. Roy. Soc. London B, 320: 133–145 (1988), rev.

Small trees or shrubs occasionally scandent. Leaves glabrous or with stiff appressed hairs, rarely with lanate arachnoid pubescence beneath. Inflorescence a raceme or a panicle of racemes, rarely a subcapitate spike; bracts and prophylls not enclosing flower buds, often with stalked or sessile glands; receptacle elongate cylindrical to obconic-tubular, glabrous within except at throat; sepals more or less equal; petals 5, equalling sepals; stamens 10–75, far exceeding calyx lobes, filaments united into a ligule for most of length, unilateral with short staminodes opposite; ovary unilocular, inserted at mouth of receptacle. Fruit

with no plates or lines of dehiscence, endocarp thin and hard. Germination cryptocotylar, eophylls opposite. $2n = 22$.

Thirty spp. in tropical Africa, mostly in the Guineo-Congolian region.

8. *Exellodendron* Prance

Exellodendron Prance, Fl. Neotrop. 9: 195, t. 31–32 (1972).

Trees or shrubs. Leaves with a pair of small glands or ill-defined glandular areas on upper surface at junction with petiole, glabrous or lanate pubescent beneath. Inflorescence a simple or branched raceme of small, congested cymes; bracts and prophylls not enclosing flower buds, eglandular; receptacle subcampanulate, slightly swollen on one side, pubescent within; petals 5, equalling sepals; stamens ca. 7; filaments equalling sepals, free, glabrous; ovary bilocular, inserted at mouth of receptacle tube. Fruit without any mechanism for seedling to escape; endocarp thin, smooth, bony.

Five spp. in Amazonia, the Guianas, central and eastern Brazil.

9. *Grangeria* Commerson ex Juss.

Grangeria Commerson ex Juss., Gen. pl.: 340 (1789).

Trees or shrubs. Leaves glabrous. Inflorescence a simple, or rarely branched axillary or terminal raceme, bracts and prophylls not enclosing flower buds, often with a single apical gland; receptacle obliquely turbinate, slightly asymmetric, glabrous within; petals 5, slightly shorter than sepals; stamens 7–8 or 15; filaments slightly exceeding sepals, glabrous, distinct, inserted around complete circle or unilateral; ovary unilocular, inserted laterally at mouth of receptacle. Fruit with two large lateral plates which break away on germination and allow endocarp to escape; endocarp thin and bony.

Two spp., one in Mauritius and Réunion, the other in Madagascar.

10. *Hirtella* L.

Hirtella L., Sp. pl.: 34 (1753); Prance, Fl. Neotrop. 9: 259 (1972).

Trees or shrubs. Leaves glabrous or with strigose hairs or hirsute, occasionally with 2 large myrmecophilous swellings at base. Inflorescence raceme, thyrse, corymb or panicle; bracts and prophylls with sessile or stipitate glands or eglandular not enclosing flower buds in groups; receptacle subcampanulate to narrowly cylindrical, glabrous within except at throat; sepals usually almost equal; petals 5, not exceeding sepals; stamens 3–9, filaments far exserted, free, glabrous, usually unilateral with short staminodes opposite; ovary unilocular, inserted at mouth of receptacle. Fruit fleshy, usually with longitudinal lines of dehiscence, endocarp thin, bony. Germination cryptocotylar cataphylls ca. 5, minute, eophylls alternate.

107 spp. in tropical America from Mexico to S Brazil, and one sp. in E Africa and Madagascar.

11. *Hunga* Pancher ex Prance

Hunga Pancher ex Prance, Brittonia 31: 79 (1979).

Shrubs or small trees. Leaves with a pair of often obscure marginal glands towards base, lower surface glabrous or lanate pubescent. Inflorescence a few-flowered terminal or axillary raceme of cymules; bracts and prophylls not enclosing flower buds, eglandular; receptacle subcampanulate, slightly asymmetric, pubescent within; petals 5, not exceeding sepals; stamens 5–9, filaments shorter than calyx lobes, free, unilateral, glabrous, ovary bilocular, inserted midway up receptacle. Fruit bilocular, with 4–6 longitudinal lines of weakness which allow seedling to escape; endocarp thin, hard, bony.

Eleven spp., three of which occur in Papua New Guinea and eight in New Caledonia and the Loyalty Islands.

12. *Kostermanthus* Prance

Kostermanthus Prance, Brittonia 31: 91 (1979).

Large trees. Leaves glabrous and papillate beneath. Inflorescence an unbranched or little-branched terminal or axillary raceme bearing congested cymules proximally and solitary flowers distally; bracts and prophylls eglandular, not enclosing flower buds; receptacle broadly obconic, asymmetric, hairy within, sepals 5, markedly unequal; petals 5, exceeding calyx lobes, markedly unequal, 2 posterior ones larger, unguiculate, enclosing stamens in bud; stamens 30–75, far

exceeding calyx lobes, filaments united into a ligule for ¾ length, unilateral with opposite staminodes; ovary unilocular, inserted at mouth of receptacle. Fruit with no lines or plates of dehiscence; endocarp thick, hard. Cotyledons slightly ruminate.

Three spp. in Malesia from the Malay Peninsula to Sulawesi.

13. *Licania* Aubl. Fig. 4

Licania Aubl., Hist. Pl. Guiane 1: 119, t. 45 (1775); Prance, Fl. Neotrop. 9: 21 (1972).

Large to small trees, shrubs or rarely suffruticose. Leaves glabrous, lanate, pulverulent or with stomatal crypts on lower surface. Inflorescence most frequently a panicle of racemes, less often a simple raceme, a spike, a glomerule or a branched panicle of shortly stalked cymules; bracts and prophylls not enclosing flower buds except in *L. licaniiflora*, eglandular; receptacle variable in shape, usually campanulate, cupuliform or urceolate, rarely turbinate or patelliform, always pubescent within; petals either 5, equalling sepals, or absent; stamens 3–40, filaments included to far exceeding sepals, usually glabrous, free in most species, rarely united for half length in groups, usually glabrous, rarely hairy; ovary unilocular, inserted at or near base of receptacle. Fruit with no plates or lines of dehiscence, endocarp thick, hard and woody or thin and fibrous. Germination cryptocotylar, eophylls alternate. $2n = 22$ in two species counted.

218 spp., all but 4 of which are American largely in lowland tropical South America but extend north to Mexico, Florida and (*L. mixauxii*) the Gulf states of the U.S.A., and two in the Malesian region.

14. *Magnistipula* Engl.

Magnistipula Engl., Bot. Jahrb. 36: 226 (1905); Prance & White, Philos. Trans. Roy. Soc. London B, 320: 152–162 (1988).

Trees, shrubs or suffrutices. Leaves glabrous or with few strigose hairs beneath. Inflorescence a simple or branched raceme of cymules or rarely a raceme or sessile glomerule; bracts and prophylls not enclosing flower buds, eglandular or with 1 or 2 pairs of sessile glands or with shortly stipitate glands; receptacle usually curved and gibbous at base, rarely turbinate or campanulate, hairy within; sepals 5, unequal; petals 5, exceeding sepals; stamens 7–9 scarcely exceeding sepals, united towards base, unilateral with staminodes opposite; ovary usually unilocular, bilocular in 1 sp., inserted at mouth of receptacle. Fruit fleshy, with no plates or lines of dehiscence; endocarp usually thin and fibrous, rarely thick and woody. Germination cryptocotylar, cataphylls absent, eophylls opposite or in fours.

Twelve spp. in Africa and Madagascar.

15. *Maranthes* Blume

Maranthes Blume, Bijdr. Fl. Nederl. Ind.: 89 (1825); Prance & White, Philos. Trans. Roy. Soc. London B, 320: 121–129 (1988), rev.

Trees. Leaves with a pair of glands at the junction of the lamina and petiole, glabrous or arachnoid pubescent on lower surface. Inflorescence usually a many-flowered corymbose panicle, rarely a lax few-flowered thryse or a raceme of few-flowered monochasial cymes; bracts and prophylls not enclosing flower buds, eglandular; receptacle obconical, slightly to strongly curved, nearly always solid and almost completely filled by nectariferous tissue, glabrous or glabrous on one side and hairy on the other within; petals 5, more or less equalling sepals; stamens 20–60; filaments free, glabrous, inserted around complete circle, far exceeding sepals in length, usually in a tangled mass; ovary bilocular, inserted at mouth of receptacle. Fruit with two lateral plates which break away on germination to allow seedlings to escape; endocarp very hard, thick, with a rough fibrous exterior. Germination phanerocotylar, first 2 eophylls opposite, the others opposite or alternate. $2n = 20$.

Twelve spp., 10 of which occur in tropical Africa, one each in tropical America (Nicaragua to Panama) and Malesia.

16. *Parastemon* A.DC.

Parastemon A.DC., Ann. Sci. Nat. Bot. II, 18: 208 (1842).

Trees or shrubs. Leaves glabrous, with two small discoid glands at base of lamina. Inflorescence and axillary or rarely terminal simple or little-branched raceme; bracts and prophylls not enclosing flower buds, eglandular; receptacle patelliform or shallowly cupuliform, pubescent within; petals 5, more or less equalling sepals;

stamens 5 around circle or 2 with 3 staminodes opposite; filaments glabrous, free, much shorter than sepals; ovary unilocular, inserted at base of receptacle. Fruit with 2 large lateral plates which break away on germination to allow seedlings to escape; endocarp thin, hard, bony. Germination cryptocotylar, first eophylls opposite.

Three spp. from the Nicobar Islands and the Malay Peninsula to New Guinea.

17. *Parinari* Aubl. Fig. 5

Parinari Aubl., Hist. Pl. Guiane 1: 514, t. 204–206 (1775); Prance, Fl. Neotrop. 9: 178 (1972); Prance & White, Philos. Trans. Roy. Soc. London B, 320: 110–112 (1988), Afr. spp.

Small to large trees or more rarely shrubs or suffruticose. Leaves with two discoid glands on upper surface of petiole and often with small marginal glands along entire length of lamina, usually with stomatal crypts filled with densely matted hairs on lower surface or rarely in two Malesian species glabrous. Inflorescence a many-flowered complex cyme or cymose panicle; bracts and prophylls enclosing small groups of flower buds, eglandular; receptacle subcampanulate, slightly swollen to one side, pubescent within; petals 5, equalling or shorter than sepals; stamens 6–10; filaments shorter than sepals, free, glabrous, unilateral with ca. 6 minute subulate staminodes opposite; ovary bilocular, inserted at mouth of receptacle. Fruit with 2 basal obturators which allow seedling to escape; endocarp thick, hard, with a rough fibrous surface.

Thirty-nine species, pantropical with 19 in tropical America, 6 in tropical Africa and 15 in tropical Asia and the Pacific region extending to Fiji, Tonga and Samoa.

18. *Neocarya* Prance

Neocarya Prance in F. White, Bull. Jard. Bot. Nat. Belg. 46: 308 (1976).

Shrubs or small trees. Leaves with several small, sessile glands near base of lamina, with stomatal crypts filled with densely matted hairs on lower surface. Inflorescence a terminal raceme of almost sessile cymules, sometimes unbranched but more frequently with one or more short to elongate branches at base; bracts and prophylls enclosing one or more flower buds, eglandular; receptacle asymmetric, saccate, gibbous, with reflexed hairs at throat, glabrous towards base within; stamens 12–17; filaments slightly exceeding sepals, unilateral with ca. 6 toothed staminodes opposite; ovary bilocular, inserted at mouth of staminal tube. Fruit with 2 basal obturators which allow seedling to escape; endocarp thick, hard, with a rough fibrous surface. Germination cryptocotylar.

A single species, *N. macrophylla* (Sabine) Prance, in W Africa from Senegal to Liberia.

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