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## Clusiaceae-Guttiferae

Guttiferae Jussieu, Gen. Pl.: 255 (1789), nom. cons. Clusiaceae Lindl., Nat. Syst. Bot., ed. 2: 74 (1836), nom. cons., nom. alt.

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Evergreen shrubs or trees, epiphytic or not, glands and/or canals in most parts of the plant; xanthones widespread; plants glabrous or with uni- or multicellular hairs, colleters common; terminal bud scaly or naked. Leaves opposite, sometimes whorled or alternate, entire, stipulate, but paired 'glands' sometimes found at base. Inflorescences terminal or axillary, rarely flowers single, often modified cymose. Flowers perfect or unisexual, actinomorphic, usually with prophylls, sepals free, occasionally fused, 2(3)4, or 5(-20); petals (0, 3)4-5(-8), free; stamens (4-)∞, free or variously fasciculate, phalangeate, or otherwise connate, fascicles or phalanges opposite the petals, anthers dithecate, extrorse to introrse, opening by slits, rarely pores, connective often with glands of various types; receptacular nectary absent; ovary superior, 1-5(-20)-locular, placentation axile or parietal, apical or basal, ovules (1)2-∞/carpel, anatropous, sometimes amphitropous, bitegmic, tenuinucellate; free stylodia or simple style long to short or 0, stigmas more or less expanded, smooth and sticky or minutely porate, rarely papillose or ± punctate; fruit a berry or septicidal or -fragal capsule, seeds small to large, winged or arillate or not, testa with epidermis and exotegmen alone, the latter lignified and with sinuous anticlinal walls, or more complex and with vascular bundles permeating a many-layered testa, distinctive exotegmen then often absent; embryo large to small, cotyledons massive to almost absent; endosperm initially free nuclear, often absent at maturity; germination epigeal or hypogeal, if latter, then radicle may die early, replaced by adventitious roots.

A family of 27 genera and 1,090 species; largely restricted to lowland tropics.

**CHARACTERS OF RARE OCCURRENCE.** Exudate black (surrounding embryo of *Chrysochlamys*, floral resin of *Clusia scrobiculata*); leaves lacking free glands or canals (some *Kielmeyera*, *Kayea*);

bracts enveloping partial inflorescences and falling off like a calyptra (*Tovomita calodictyos*); flowers zygomorphic by abortion of fascicles (*Marila* sp.); petals and sepals 3 (some *Garcinia*); abaxial glands on prophylls and calyx (*Clusiella*); corolla tubular (*Clusia gundlachii*) or absent (*Calophyllum*); anthers with porose dehiscence (*Poeciloneuron*, some *Marila*, *Clusia*, and *Garcinia*); staminodes of the pistillate flower more strongly adnate to the corolla than phalanges of the staminate flower (*Garcinia hollrungii*) or staminodes opposite the sepals; pollen in tetrads (*Kielmeyera* spp.); fruits drupaceous (some *Garcinia*); seeds papillate (*Neotatea*); testa soft, with disorganized xylem (*Kayea kunstleri*, *Symphonia*); cotyledons fused (*Mammea* spp.).

**VEGETATIVE MORPHOLOGY.** Clusiaceae are all woody plants. The trunk may be buttressed (some *Calophyllum*), or there may be knee (some *Symphonia*) or prop (*Dystovomita*) roots; the latter are strongly diageotropic initially. *Clusia* and its relatives are often epiphytes that only secondarily establish contact with the ground; adventitious roots commonly develop along the stem, and in epiphytic species of *Clusia* they may encircle and even strangle the host. *Kielmeyera*, a plant of rather drier areas, may develop a lignotuber, from which it resprouts after fire or drought; root suckering occurs in *Mammea acuminata* and *Garcinia griffithii* and layering in *Chrysochlamys*. Some species of *Kielmeyera*, *Neotatea* and *Mammea* have relatively stout, little- or unbranched stems and large leaves, although the three genera grow in very different habitats. Growth of most taxa is initially monopodial, the lateral branches being orthotropic to plagiotropic (in *Garcinia* and *Symphonia*, these may be rigidly plagiotropic). The terminal bud may lack scales, and then the flush may have only one (frequent in *Garcinia*, *Clusia*, and *Calophyllum*) or more pairs of leaves; branches develop from the axils of the uppermost

pair of leaves of the last flush as the terminal bud grows out. Symphonieae, *Mammea*, some species of *Calophyllum*, etc., have terminal buds with two or more pairs of scales (*Garcinia* may approach this condition); branches here usually arise in the axils of the uppermost scales (*Mammea*) or the lowest pair of expanded leaves (*Symphonia*). In *Mesua*, the apical bud aborts at the seedling stage (at least, in *M. ferrea*), and all growth is by axillary branches; apical buds also abort in some *Calophyllum*, *Lebrunia*, etc. In several (?all) species of *Kayea*, the apical bud of each orthotropic innovation grows on as a plagiotropic lateral shoot, and an axillary bud produces the next orthotropic leader. *Tovomitia* has lateral branches that are plagiotropic by substitution; axillary shoots there may be truly sylleptic.

Clusiaceae are often glabrous (*Mammea*, many Clusioidae); taxa with unicellular hairs are scattered throughout the family. Stellate hairs characterize *Caraipa*, and branched or stellate hairs occur in *Marila*; *Calophyllum* has irregular multicellular hairs. Colleters are common. Buds in taxa that lack perulae are sometimes covered with dense indumentum, as in *Calophyllum* (it lacks colleters). Terminal and axillary buds in *Garcinia*, *Dystovomitia*, *Poeciloneuron*, and elsewhere are often enclosed in deep excavations of the petiole bases; colleters are usually present as well. In *Mesua*, axillary buds are immersed in stem tissue, and in *Mammea* they are small and lie almost flush with the stem; they are usually more prominent.

There are no stipules, but paired 'glands' on either side of the leaf base are quite common. In *Mahurea exstipulata*, these occur immediately above the insertion of the leaf and appear to be modified colleters. *Garcinia* commonly has small, glandular or eglandular stipuliform structures immediately below the leaf insertion, while in Endodesmieae and Symphonieae similar structures are lateral and more delicate; they may even be peltate. In *Montrouziera*, *Garcinia*, and *Mahurea* (the only taxa examined), they lack a vascular supply.

The lamina is usually petiolate and the midrib is nearly always obvious. Venation is commonly eucamptodromous or brochidodromous, rarely acrodromous, and is more or less reticulodromous in *Kayea*, *Mammea*, and *Caraipa* in particular. The secondary veins are often rather close together and are joined by a submarginal vein; in *Calophyllum*, the marginal vein is embedded in marginal thickening and usually cannot be seen, while in

Garcinieae, Symphonieae and Endodesmieae the submarginal vein is within 2 mm of the margin. Tertiary venation is notably scalariform in many species of *Mahurea*, *Caraipa*, and *Marila*; in *Calophyllum* and *Neotatea* in particular, tertiary venation is apparently absent.

Seedlings of *Calophyllum* and *Mammea* can show substantial variation in leaf arrangement and rate of growth that is not evident in adults, in *Calophyllum* some species even having alternate leaves (all adults have opposite leaves; Stevens 1980).

**VEGETATIVE ANATOMY.** Vesque (1889, 1892) provides a general survey of leaf anatomy that has still not been surpassed; Metcalfe and Chalk (1950) summarize other early literature; more recent studies include those of Schofield (1968), and Paula (1976 and references therein). A distinctive feature of Clusiaceae is the exudate-containing glands and canals found throughout the plant (hence the alternative name, Guttiferae), although this has not been surveyed at even a gross level. Canals are associated with the vascular tissue and are also found in both the cortex and pith. Systematically important variation is found in the secretory tissues of the appendicular organs of the plant. These are commonly more or less independent of the vascular tissue, and are probably schizogenous glands or canals. All cotyledons that I have seen possess canals, whatever the condition in the foliage leaves. *Clusiella* has both glands and canals in its leaves, a combination found in some species of *Mammea*, *Garcinia* (probably independently derived in sections *Tagmanthera* and *Daedalanthera*), and perhaps also in Symphonieae (particularly poorly known). However, a genus usually has either glands or canals. Glands are notably elongated in *Endodesmia* and some species of *Mammea* and *Marila*. Black glands, perhaps containing hypericin, occur in *Mammea*, *Marila*, etc. (these can be confused with spots caused by fungal infections). Most Clusiaceae and Garcinieae have two or more series of canals in the mesophyll, one near the adaxial side of the lamina and the other near the abaxial; they pursue a more admedial course than the secondary veins (and are more admedial on the adaxial side of the lamina than on the abaxial). Canals are dendritic in *Clusia* (*Pilosperma*), and branched canals occur in some species of *Garcinia*, *Clusia*, and possibly in Symphonieae such as *Pentadesma*. *Calophyllum* has distinctive leaves with closely set secondary veins alternating with canals; the latter are interpreted as being modified veins