
Dilleniaceae

Dilleniaceae Salisb., Parad. Lond. 2, 1: ad t. 73 (1807), nom. cons. ('Dilleneae').

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Trees, shrubs, or lianas, rarely subshrubs or rhizomatous herbs; vestiture of sclerified and/or silicified simple and sometimes also fasciculate trichomes; glandular trichomes very rare. Leaves spirally arranged, very rarely opposite; blades petiolate or uncommonly sessile, simple, or rarely threefold pinnatisect to pinnately compound; margins entire or toothed; venation craspedromous, semicraspedromous, brochidodromous, or eucamptodromous, frequently with \pm straight, parallel secondaries terminating in the teeth (when present), and rigidly percurrent tertiaries; stipules 0, but the petiole sometimes with persistent or caducous amplexicaul wings, and often with a broad insertion. Plants synoecious, or rarely structurally androdioecious and functionally dioecious. Inflorescences terminal, axillary, or ramiflorous, determinate; frequently a thyrsoid with cincinnate or modified dichasial partial inflorescences, a panicle, or monad, sometimes a botryoid or cincinnus; pedicels commonly with apical articulation. Flowers small to very large, actinomorphic or (mainly in the androecium) monosymmetric, hypogynous or very rarely partly epigynous, without nectar; receptacle flat or infrequently conical; sepals (3)4–5(–18), equal to unequal, typically free, membranaceous to coriaceous, imbricate (quincuncial when 5), always persistent, slightly to substantially accrescent in fruit; petals (2)3–5(–7), free, elliptic to obovate, often emarginate, typically white or yellow, frequently crumpled in bud, imbricate (quincuncial when 5), typically caducous; stamens (1 or 3–)5–400(–900), occasionally partly staminodial, typically marcescent, free or sometimes the filaments basally to nearly fully connate and then typically grouped into 1, 2, 3, or 5 fascicle(s), rarely forming a short tube; anthers basifixed, dithecal and tetrasporangiate, linear to oblong to subglobose, dehiscing via longitudinal slits, apical clefts, or apical pores; connective sometimes thickened, distinctly separating the thecae, and occasionally

protruding apically as a short mucro; gynoecium apocarpous to, less frequently, hemisyncarpous, of 1–10(–20) carpels arranged in 1 whorl (very rarely 2 whorls); stylodia free; stigmas punctiform, minute, and not differentiated in shape from the stylodia, or the stigmas peltate with an annuliform or, infrequently, irregular margin; ovules 1–80, anatropous to campylotropous, when 1, apotropous, when 1–2, 1 apotropous and 1 epitropous, erect, or when 4 or more, pleurotropous and syntropous, bitegmic, crassinucellate; placentation submarginal, in 2(4, 6) vertical rows, or basal when ovules 1–2. Fruit most frequently a follicle or aggregate of follicles (sometimes basally coherent), or indehiscent and enclosed by the fleshy, accrescent sepals, less often a fleshy capsule, berry, or aggregate of nutlets; aril fleshy to scarious and oily or waxy, funicular, rarely vestigial; seed coat with typically heavily sclerotized or sometimes cutinized endotesta; raphe short; endosperm fleshy, oily or sometimes also starchy, abundant; embryo straight, minute.

A pantropical family with a largely Gondwanic distribution, extending into temperate Australia, containing 10 genera and c. 500 species.

CHARACTERS OF RARE OCCURRENCE. Rhizomatous herbs in *Acrotrema*. Subshrubs mostly or only with cataphylls and always with green, photosynthetic, sympodial, aerial stems that are terete and ephedroid to flattened and phyllocladous (sometimes dimorphic) in *Hibbertia* subg. *Pachynema*. Lignotuberous shrubs in several species of *Hibbertia* and *Tetracera masuiana*. Stilt roots occasionally present in several *Dillenia* spp. and consistently present in *D. borneensis*, *D. grandifolia*, and *D. reticulata* (Hoogland 1952, 1959). Leaves pinnatisect to pinnate in a few Sri Lankan *Acrotrema* spp., sessile and rarely amplexicaul to entirely perfoliate (some *Hibbertia*). Leaves opposite in *Dolioscarpus pruskii* and *Hibbertia coriacea* and with persistent (*Davilla* spp., *Didesmandra*, *Dillenia* spp., *Schumacheria*) or caducous (*Acrotrema*, *Dillenia*

spp.) amplexicaul wings. Leaf domatia in *Doliocarpus* spp. and *Tetracera* spp. Leaves turning yellow or golden brown during extreme drought and re-greening after rain (diallagy; George 2002) in *Hibbertia hypericoides* and *H. spicata* subsp. *leptotheca* (and perhaps other *Hibbertia* spp. in regions with arid climates). Plants structurally androdioecious and functionally dioecious in neotropical *Tetracera* spp. Petals absent in *Dillenia celebica*, *D. grandifolia*, and *D. serrata* (Hoogland 1952, 1959). Corolla orange in *Hibbertia comptonii*, *H. miniata*, and *H. stellaris*, pink to deep red in several species of *Hibbertia* subg. *Pachynema*, and deep red in *Dillenia pteropoda*, inconsistently deep red in a few *Dillenia* or pink in a few Asian *Tetracera* (Hoogland 1953). Corolla not spreading at anthesis in *Dillenia papuana* and several putatively related *Dillenia*. Fertile androecium distinctly heterantherous in *Didesmandra*, many *Dillenia*, *Hibbertia heterotricha*, *H. margaretae*, *H. nana*, *H. pulchella*. Stamens fewer than 5 in *Hibbertia hirsuta* (1–3), some populations of *H. fasciculata* and *H. racemosa* (3), *Hibbertia (Pachynema) praestans* (4), and *H. rufa* (4). Floral receptacle conical in the region of the gynoeceum in *Dillenia* and *Hibbertia baudouinii*. Carpels more than 5 in most *Dillenia* spp., *Hibbertia grossulariifolia*, and some populations of *H. scandens*.

VEGETATIVE MORPHOLOGY. The family varies from tall, sometimes buttressed trees (*Dillenia* spp.), small to medium-sized, tortuous trees (*Curatella*), small to medium-sized rosette trees (New Caledonian *Hibbertia*), to shrubs (*Hibbertia*; some *Davilla*, *Doliocarpus*, and *Tetracera*), lianas (e.g., *Davilla*, *Doliocarpus*, *Neodillenia*, *Pinzona*, *Tetracera*, some *Hibbertia*), subshrubs with ephedroid or phyllocladous, photosynthetic aerial shoots and foliage typically of cataphylls (*Hibbertia* subg. *Pachynema*), and perennial herbs with a woody rhizome (*Acrotrema*). The bark often has a characteristic rich red- or orange-brown color and abundantly exfoliates in thin, papery plates, flakes, or strips, or the outer bark is gray, and exfoliates in flakes to reveal a rich-brown younger bark. Scandent species climb by twining, and the extension growth of large, climbing individuals of Delimoideae and Doliocarpoideae is often conspicuously curved or hooked.

Virtually the entire aerial plant body of *Hibbertia* subg. *Pachynema*, which consists of photosynthetic stems with cataphylls, represents inflorescences, as is shown by the occasional production

of ‘normal’ foliage leaves at the basalmost nodes of a developing shoot in a few species (Craven and Dunlop 1992): the shoot systems can be compared with a compound thyrsoid or panicle. Foliage of some early branches of, e.g., *Hibbertia* subg. *Pachynema*, are mostly the prophylls of single-flowered sympodia, and the leaves of Hibbertioideae may represent heterotopic inflorescence bracts. As in some Dillenioidae, the β -prophyll is displaced onto the branch borne in its axil. Sympodia of other species of *H.* subg. *Pachynema* have several cataphyll-bearing nodes between the base of the branch and the flower. Shoot systems in *Hibbertia* subg. *Adrastaea* are fundamentally similar, though they do not show metatopic displacement of the prophylls. In *Dillenia* spp., axillary buds are sometimes accompanied by two serial buds that are displaced (by concaulescence), sometimes a considerable distance up the stem.

The foliage is typically evergreen, though in some *Dillenia* indigenous to parts of monsoonal Southeast Asia, it is deciduous. Young leaves exhibit conduplicate or plicate-conduplicate ptyxis. The petioles are usually distinct, and often have a broad, adaxial groove or channel. The bases of the petiolar wings completely ensheath the stem in *Acrotrema*, *Davilla alata* and allied species, *Didesmandra*, *Dillenia* spp., and *Schumacheria*. These petiolar wings, which may be persistent or caducous, enclose the developing terminal bud; they do not receive an independent trace from the cauline stele, and are not stipular (Dickison 1969).

In all subfamilies except Hibbertioideae, higher orders of leaf venation are typically very regularly organized; rigidly percurrent, scalariform tertiary venation and well-developed areoles, oriented with the lower orders of venation, are common. Leaf venation in Hibbertioideae is distinctly less organized; percurrent tertiaries are rare and never rigidly scalariform, and areolation is typically incomplete or lacking (Rury and Dickison 1977). Ericoid leaves are characteristic of many species of *Hibbertia* subg. *Hemistema* and the *H. hemignosta* complex (sect. *Candollea*, subg. *Hibbertia*; Wheeler 2004a). Vestiture type and density, and leaf texture and degree of tothing may differ between juvenile and adult foliage (Hoogland 1952; Veillon 1990; Toelken 1998). In *Hibbertia* spp. and *Dillenia* spp. growing in fire-prone ecosystems, a reversion to juvenile growth is characteristic of fire sprouts.

VEGETATIVE ANATOMY. The primary stem anatomy is generally characterized by a uniseriate