Combretaceae

Combretaceae R. Br., Prodr.: 351 (1810), nom. cons.

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Trees, shrubs, subshrubs or lianes, sometimes mangroves, rarely spiny. Indumentum almost always of unicellular, slender, thick-walled, pointed hairs with a distinctive basal compartment ('Combretaceous hairs') alone or with glandular hairs of one (or rarely both) of two types – short, capitate stalked glands, and subsessile peltate scales. Leaves opposite (or whorled) or spiral, petiolate, simple, entire, with pinnate venation, often with a pair of petiolar glands or domatia; stipules 0 or vestigial. Inflorescence axillary or terminal, capitate to expanded, of simple or paniculate spikes or less often racemes. Flowers with simple, usually caducous bracts, bisexual, or bisexual and male in same inflorescence, or rarely dioecious, 4- to 5-merous, actinomorphic, or sometimes weakly zygomorphic, epigynous or rarely semi-epigynous; hypanthium (receptacle) surrounding ovary (lower hypanthium) and extended beyond into saucer- to tube-shaped upper hypanthium, with 2 prophylls fused to lower hypanthium in Laguncularieae; sepals 4–5(–8), borne at tip of upper hypanthium, sometimes vestigial, rarely accrescent; petals 4–5, usually borne at or near tip of upper hypanthium, often small, sometimes conspicuous, or often 0; stamens usually twice as many as sepals (rarely to 16), borne inside upper hypanthium usually at two levels, sometimes as many as sepals, rarely second whorl represented by staminodes, exserted or included, with dorsifixed, usually versatile, rarely adnate, 4-locular anthers; nectariferous disk often present at base of upper hypanthium; ovary 1-locular; ovules (1)2–7(–20) (usually 2), apical, pendulous, anatropous, bitegmic, crassinucellate; style simple, with usually punctiform stigma. Fruit 1-seeded, indehiscent or rarely tardily dehiscent, with dry or spongy to succulent wall, often with 2–5 papery to leathery wings; endosperm absent in mature seed; cotyledons usually 2(–5) or fused to appear 1, variously folded or twisted in seed, rarely flat or hemispherical.

A pantropical family with 14 genera and c. 500 species.

Characters of Rare Occurrence.
Mangroves: *Lumnitzera*, *Laguncularia* (*Conocarpus* mangrove-associate)
Branches spiny: *Terminalia* (former *Bucida*), some *Combretum*
Semi-inferior ovary: *Strephonema*
Slightly zygomorphic flowers: some *Combretum* (including former *Calopyxis*), *Lumnitzera littorea*, *Dansiea*
Dioecious flowers: *Combretum rupicola*, *Conocarpus* (± so), *Laguncularia* (± so)
Andromonoecious flowers: many *Terminalia*, *Pteleopsis*
Markedly accrescent calyx: *Calycopteris*
Only one whorl of stamens: *Terminalia tetrandra*, some *Combretum* (former *Thiloa* and *Meiostemon*)
Staminodes representing one whorl of stamens: *Combretum gracile*, some flowers of the variably dioecious species and of *Lumnitzera littorea*
Stamens with adnate anthers: *Buchenavia*
Ovules often more than 8: *Macropteranthes*, *Dansiea*
Tardily dehiscent fruits: *Combretum* (former *Quisqualis*)
Fruit-wings derived from prophylls: *Macropteranthes*, *Dansiea*
Cotyledons flat, not folded: *Strephonema*, *Combretum* sects. *Cacoucia* (some) and *Calopyxis* (some)
Cotyledons fused: some *Combretum*
Three or more cotyledons: some *Terminalia*

Vegetative Morphology. All species of Combretaceae are woody, varying from tall timber trees or lianes (mostly in forest) to short shrubs or subshrubs (in savannah). A few species possess stem thorns. In the fire-prone savannahs of Africa and India, there are about 20 species of subshrub in the genus *Combretum*: plants with large underground 'trunks' putting up annual aerial shoots

which are burnt to the ground during the dry season. These species belong to four different sections of the genus (Keay 1950), in two cases together with forest scandent shrub and liane species, and in the other two cases together with savannah tree and shrub species. Some of the shrubs develop into lianes or 'scrambling shrubs' if left ungrazed and provided with a support. The lianes often climb over 30 m high, especially in the genus *Combretum*, while the smallest subshrubs do not exceed 20 cm. *Combretum* species are mostly subshrubs, shrubs or lianes, with very few trees (exceptionally, *C. leprosum* and *C. glaucocarpum* up to 25 m in Brazil).

The largest trees are over 50 m tall and are found in the genera *Terminalia* and *Buchenavia*; buttresses are present in several species. Corner (1940) described the characteristic 'pagoda-trees' of Malaya, belonging to nine different families, in which the main branches are held in horizontal tiers with the leaves in flat bunches dispersed over the top side of each tier. This growth habit is so characteristic of several species of *Terminalia* (notably, *T. catappa*) that Corner termed the sympodial branching pattern which gives rise to it as "*Terminalia*-branching".

Two genera are true mangroves: *Lumnitzera* from East Africa to Australia and *Laguncularia* in West Africa and East and West America. Both develop characteristic pneumatophores – in *Lumnitzera*, these are looped above the mud ('knee-roots') whereas in *Laguncularia* they are simple or branched projections from the mud ('peg-roots'). Fruit-vivipary is, however, scarcely exhibited; in *Laguncularia*, the radicle is reported barely to pierce the seed-coat while the fruit is still on the tree. In addition, *Conocarpus erectus*, with a distribution similar to *Laguncularia*, is often considered a mangrove, but its lack of vivipary or pneumatophores suggests that it is best considered a 'mangrove-associate' (Fig. 20). Some *Terminalia* species are also mangrove-associates. *Terminalia cuneata* (India) is not one of these, but it sometimes produces erect pneumatophore-like aerial roots when the root-system is submerged (Adamson 1910).

Fig. 20. Combretaceae. Old specimen of *Conocarpus erectus* in a dune-valley of Peninsula de Paraguaná, Caribbean. (Phototograph K. Kubitzki)

The leaves of Combretaceae are evergreen or deciduous, according to the vegetation type the plants inhabit. In some genera, notably *Buchenavia*, they are clustered in dense spirals at the swollen tips of twigs. A pair of sessile secretory glands is present in many species, particularly *Terminalia*, *Buchenavia*, *Laguncularia* and *Conocarpus*; their presence and position are of diagnostic value.

Klucking (1991) presented an extensive survey of leaf venation in the family, providing many excellent illustrations, covering 11 genera and 223 species. His study, however, lacks an analytical element and, in several cases, specimens under different names for the same species (e.g. *Terminalia amazonia* and *T. obovata*) fell into different categories of venation pattern. Alwan (1983) covered 144 species in all 13 genera. Using the terminology of Hickey (1973), he recognized six major types within this broad pattern, five of them representing grades from brochidodromous to eucamptodromus, and the sixth being craspedodromous. There seems to be no taxonomic correlation of these types as high as genus level; all six types occur in *Terminalia*, and craspedodromous only in that genus.

Many species bear foliar domatia – small pocket- or bowl-shaped pits in the axils of the main lateral leaf-veins on the lower leaf surface; they are particularly common in *Terminalia*, *Buchenavia* and *Conocarpus*, in which their presence and structure are species-constant. Pocket-shaped ('marsupiiform') domatia occur widely in Combretinae and Terminaliinae, but bowl-shaped ('lebetiform') ones are found only in the above three genera of *Terminaliinae*. In *Strephonema*, the leaves have marginal revolute domatia.

Stipules are said in all floristic accounts to be absent from Combretaceae. Weberling, in Dahlgren