Ctenolophonaceae

Ctenolophonaceae Exell & Mendonça (1951).

K. Kubitzki

Buttressed trees with simple and stellately tufted hairs on young shoots, stipules, and the outside of sepals and petals. Leaves opposite, petiolate, entire, simple, pinnately veined; stipules interpetiolar, caducous. Inflorescences thyrso-paniculate, axillary or terminal; bracts present, prophylls 0. Flower buds elongate-ellipsoid; flowers hypogynous, bisexual, 5-merous, diplostemonous, regular, hypogynous; sepals basally shortly connate, quincuncially imbricate, subequal, indurate, swollen and persistent in fruit; petals contorted, caducous, spoon-shaped at the base and often shortly clawed; disk well developed, extrastaminal, cup-like; stamens 10, inserted on inner side of the disk and basally connate into an androecial tube, dorsally surrounded by a 10-lobed corona-like tube; antepetalous stamens shorter than antesepalous ones; anthers dorso-versatile, 2-celled, introrse; connective protruding, acute-triangular; gynoecium syncarpous, 2-carpellate; ovary 2-celled; ovules 2 per cell, axile, collateral, pendant, anatropous, epitropous, bitegmic; style simple, apically ± cleft with 2 capitate stigmas; ovary tube joining near its base the androecial tube to form a short androgynophore. Fruit a 1-celled capsule, the woody pericarp eventually splitting lengthwise into 2 valves. Seed solitary, persisting after falling of the pericarp and pendulous from the top of a filiform columella; aril pectinate-fimbriate, surrounding the lower half of the seed; endosperm copious; embryo straight.

Monogeneric, probably with 2 extant spp., *C. englerianus* Mildbr. in West Africa, *C. parvifolius* Oliv. from Malay Peninsula to New Guinea.

Vegetative Anatomy. *Ctenolophon* differs from its presumed allies in possessing tufted hairs, stellate in appearance, which are found on young vegetative and mature floral parts, and anomocytic to anisocytic stomata. The simple arc of collateral vascular tissue in the midrib and petiole, the scattered occurrence of cristarque cells (crystalliferous cells with a unilaterally thickened and lignified cell wall), and crystals and druses are of a more common occurrence (van Welzen and Baas 1984).

In the secondary xylem, the vessels are exclusively solitary; perforation plates are predominantly scalariform with numerous thick bars; axial parenchyma is paratracheal-abaxial; wood rays are uniseriate, of upright cells, and multiseriate heterogeneous,

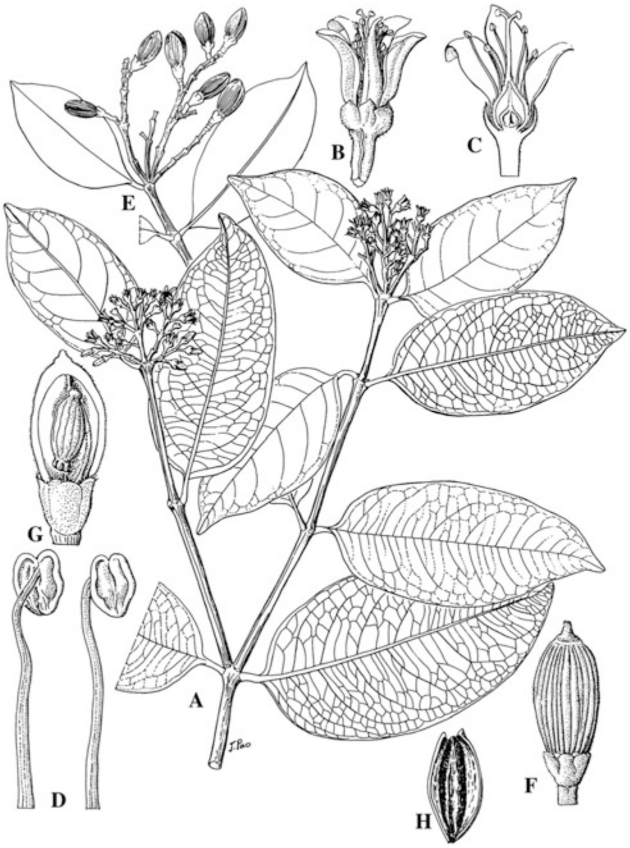

Fig. 6. Ctenolophonaceae. *Ctenolophon parviflorus*. **A** Flowering branchlet. **B** Flower. **C** Same, longitudinal section. **D** Stamens. **E** Fruiting twig. **F** Fruit. **G** Same, longitudinal section. **H** Seed. (Pungga 1996; drawn by J. Pao)

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up to 3 cells wide; fibre tracheids have conspicuously bordered pits; solitary crystals occur in chambered parenchyma and ray cells (Heimsch and Tschabold 1972). The heartwood of *C. parvifolius* is reddish to brown, very hard, and heavier than water.

FLOWER STRUCTURE. The flowers of *Ctenolophon* are tubular, as the petals bend outwards only apically. In bud (and later?) the overlapping portions of the petals are postgenitally connected by the indumentum of their dorsal surfaces and margins. In *C. parvifolius* the petals are white to yellow, orange or bright red (van Hooren and Nooteboom 1988). The stamens are basally connate into an androecial tube and are surrounded by a tubular disk, which distally extends into ten lobes that alternate with the stamens (the corona of Matthews and Endress 2011). The disk surrounds the ovary up to three quarters of its height. As the petals bend outwards only apically, the floral tube can retain large amounts of nectar. The tissue of the disk is formed by thin-walled, typical adenoid cells. Close to the margin of both sides of the disk, numerous open anomocytic stomata are diffusely distributed, which may function in the release of the nectar (Link 1992). Due to partial disintegration of the thin septa, the ovary becomes partly unilocular. The ovules have a distinct endothelium (Matthews and Endress 2011).

POLLEN MORPHOLOGY. Pollen morphology of *Ctenolophon* has been studied by, among others, Thanikaimoni et al. (1984) and van der Ham (1989). The pollen is typically zonocolporate, the number of apertures ranging from 3–9. Two main pollen types can be distinguished, which by and large correspond to the two extant species. The parvifolius type has 3–8 apertures and is subspheroidal, whereas the englerianus type has 6–9 apertures and exhibits distinct ridges on the mesocolpia that extend to the polar area, where they fuse into a ring and make the pollen grains characteristically angular and barrel-shaped. Equatorial size ranges from 31 to 66 µm; the thickness of the exine ranges from 3–6 µm, and its stratification is obscure under the light microscope and difficult to determine. The infratectal layer appears labyrinthic and sometimes exhibits granular-columellate structures. The tectum is perforate to foveolate in the parvifolius type, and psilate or finely perforate in the englerianus type. *Ctenolophon* from the Philippines classified as *C. parvifolius* or "*C. philippinensis*" has been found to exhibit a sculpture similar to that of the englerianus type (Thanikaimoni et al. 1984; van der Ham 1989).

Saad (1962) pointed to pollen morphological similarities between *Ctenolophon* and the Malpighiaceae which, however, appeared superficial to van der Ham (in van Hooren and Nooteboom 1988).

POLLINATION. The bright petals and well-developed nectary disk indicate that *Ctenolophon* is entomophilous.

FRUIT AND SEED. The fruit of *C. parvifolius* is yellow to pink and later brown, the seed brown or glossy black, and the aril white to orange or brilliant vermilion. Seeds are exotegmic; the embryo is folded (Boesewinkel and Bouman 2000).

AFFINITIES. *Ctenolophon* had been referred to various families including Oleaceae, Icacinaceae and Celastraceae, until Pierre (1893) suggested a relationship with Linaceae. Winkler (1931) included in it *Ctenolophon* as a subfamily, together with Ixonanthoideae and Humirioideae. These subfamilies have since been elevated to the rank of family; among them, *Ctenolophon* has been considered close to Linaceae s.str., with which it shares the extrastaminal disk. Link (1992) stressed the similarities between Humiriaceae and *Ctenolophon*, particularly the perianth structure, the broadened and markedly elongate anther connectives, and the histology of the disk, including the presence of the marginally distributed nectarial stomata. In this context it appeared less important to him whether the disk is intrastaminal (Humiriaceae) or extrastaminal (*Ctenolophon*), or the filament bases are adnate to the disk (*Ctenolophon*) or distinct (Humiriaceae). Matthews and Endress (2011) identified important structural traits uniting *Ctenolophon*, Rhizophoraceae and Erythroxylaceae. These groups have also been retrieved as a clade [Ctenolophonaceae [Rhizophoraceae + Erythroxylaceae]] by Wurdack and Davis (2009) and Xi et al. (2012).

DISTRIBUTION AND HABITATS. *Ctenolophon englerianus* is known from West Africa, where it grows in riverine forests. *C. parvifolius* is distributed in Malesia from the Malay Peninsula to New Guinea, and grows in primary forest but also swamp and heath forest on a wide variety of soils over peat, sandstone and ultrabasic rocks, commonly in lowland and hill regions and in Borneo up to 1,650 m.

PALAEOBOTANY. The fossil record of *Ctenolophon* is extensive and starts in the Maastrichtian of Central Africa with pollen of the englerianus type, which through a nearly uninterrupted record can be linked with the Recent African distribution of *C. englerianus*. This pollen type is recorded also from the Palaeocene and Eocene of northern South America and the Eocene and Miocene of India but disappeared from these regions in the course of the Tertiary (Krutzsch 1989). The parvifolius type first appeared in the Palaeocene of Africa, but continued there only to the early Eocene. In India (Kutch) it appeared in the early Palaeocene, from where it spread in the course of the Tertiary all over India and, in the Miocene with up to 9 pollen types, attained its greatest diversity (Kar 1985). Erdtman (1955) first described and characterised the fossil pollen from this region. In the course of the Eocene, the parvifolius type became established in Southeast Asia/Malesia, again being linked with the distributional area of its extant name-giving species. Thanikaimoni et al. (1984) and van der Ham (1989) have discovered that populations of *C. parvifolius* from the Philippines exhibit pollen that resembles the pollen of the englerianus type, giving rise to the suggestion (W. Krutzsch, pers. comm., Nov. 2003) that the ridges of the englerianus type pollen are plesiomorphic and have been lost on the pollen grains of *C. parvifolius*, which is supported by rudimentary ridges that have been observed by W. Krutzsch.

Only one genus:

***Ctenolophon* Oliver** Fig. 6

Ctenolophon Oliver, Trans. Linn. Soc. 28: 516 (1873); Bullock, Kew Bull. 14: 41 (1960); Badré, Fl. Gabon 21: 43–44 (1973); van Hooren & Nooteboom in Fl. Males. I, 10: 629–634 (1988); R.S. Pungga, Tree flora of Sabah and Sarawak 2: 151–153 (1996).

Two spp., *C. englerianus* Mildbr. from Angola, Zaire, Nigeria and Gabon, and *C. parvifolius* Oliver from the Malay Penisula to New Guinea, but not reported from Java, the Lesser Sunda Islands, Celebes and the Moluccas. The two species are very similar, the only differences being the simple cymose panicle and larger flowers (stamens up to 15 mm long) in *C. englerianus* vs. compound cymose panicles and smaller flowers (stamens up to 10 mm long) in *C. parvifolius*, apart from the differences in pollen morphology.

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