
Crypteroniaceae

Crypteroniaceae A. DC., Prodr. 16, 2:677 (July 1868), nom. cons.

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Evergreen trees. Leaves glabrous, opposite, simple, entire, pinnately veined, with short petioles and with or without small stipules. Inflorescences with long, spicate or racemose branches, many-flowered. Flowers bisexual or unisexual (populations then apparently dioecious), epigynous or perigynous, 4–5(6)-merous; calyx minute or obsolete; petals minute or obsolete, perianth 1- or 2-whorled; androecium diplostemonous or haplostemonous, anthers bithecate, dehiscing longitudinally, connective dorsally thickened or not; pistil 2–6-locular, style with a capitate stigma; ovary inferior or superior, with few or numerous ovules per locule; ovules anatropous and bitegmic. Fruits capsules; seeds few or many, flat and with one or two membranous wings, endosperm absent; embryo straight, the seed coat winged.

A family of three genera and 7–12 species, in humid tropical forest in continental Southeast Asia and throughout the Malesian region, most diverse in peat swamp forests in Sabah and Sarawak.

VEGETATIVE MORPHOLOGY. All Crypteroniaceae are trees, some species reaching heights of 50 m, with corresponding trunk diameters. They often grow in swamps or bogs and are adapted to waterlogged soils. Among the vegetative features commonly considered important is that leaves in *Crypteronia*, but not in *Axinandra* and *Dactylocladus*, have stipules. The inflorescences in all three genera are terminal or axillary racemes, spikes or panicles of subsessile, inconspicuous flowers with much reduced or obsolete petals.

VEGETATIVE ANATOMY. The three genera of Crypteroniaceae share distinct fibre-tracheids but are diverse in other wood anatomical characters important in Myrtales (van Vliet 1975, 1981). Vessels are diffuse and solitary and/or in radial multiples of 2 to 3; vessel perforations are simple; inter-vessel pits are alternate; vessel-ray and vessel-parenchyma pits are half-bordered or

rarely simple. Fibre walls have distinctly bordered pits (fibre-tracheids). The parenchyma is diffuse in aggregates or aliform to confluent. Rays are markedly heterogeneous and can be uniseriate or 1–3-seriate. There are no crystals. A cork cambium is present and can be initially deep-seated or superficial (*Dactylocladus*). As in other Myrtales, the primary vascular tissue is bicollateral. Crypteroniaceae lack axially included phloem (van Vliet 1975, 1981); radially included phloem is visible as small flecks or holes on tangential surfaces. *Crypteronia paniculata* yields good general-utility timber.

Stomates are paracytic in *Axinandra* and *Crypteronia* but mainly anomocytic in *Dactylocladus*, and the leaf mesophyll may or may not have sclerenchymatous idioblasts and contain styloid calcium oxalate crystals (Mentink and Baas 1992).

FLORAL MORPHOLOGY. As in a few other Myrtales, the corolla in *Axinandra* falls off as a cone-shaped unit (calyptra) when the flowers open whereas, in the other two genera, the petals drop individually. Apparently, this happens very soon after the petals expand and the stamens have reached their upright position, having been bent downwards in bud. It is unclear whether in *Dactylocladus* and *Crypteronia*, which have haplostemonous flowers, the stamen meristems originate in front of the sepals or in front of the petals. As in other Myrtales, there is a tendency towards dorsally enlarged stamen connectives, a trait which may relate to the incurved position of the stamens in bud and the connective's role in the unfolding of the stamens at anthesis (Fig. 34D, E).

KARYOLOGY. Crypteroniaceae are unknown cytologically.

POLLEN MORPHOLOGY. Pollen of species from all three genera has been studied (Patel et al. 1984) and found to be rather nondescript. The main distinction between the genera is that pollen in *Cryptero-*

nia is bisyncolporate with two indistinct subsidiary colpi, whereas pollen in *Axinandra* and *Dactylocladus* has three or four colporate apertures which vary with three or four pseudocolpi.

EMBRYOLOGY. Similarly to other Myrtales, *Axinandra*, *Crypteronia* and *Dactylocladus* have a glandular anther tapetum, crassinucellate ovules, an initially 2-layered inner integument, a micropyle which is formed by both integuments, an embryo sac with ephemeral or absent antipodal cells, endosperm formation of the Nuclear type, and exalbuminous seeds (Tobe and Raven 1983, 1987a, b). The development of the embryo sac follows the Polygonum type. In all three genera, the anther endothecium degenerates early, and the anthers therefore dehisce not via differential shrinking of endothecium cells, as in most angiosperms, but rather via rupture of walls along their thinnest sections, caused by the shrinking of connective cells (Tobe and Raven 1987a, b; H. Tobe, Kyoto University, pers. comm. 2001). A feature setting *Axinandra* apart from *Crypteronia* and *Dactylocladus* is an endothelium (a tapetal layer in the inner integument), which is associated with a secondary multiplication of the inner integument.

FRUIT AND SEED. Fruits in Crypteroniaceae are capsules which open introrsely or apically by 2–5 valves, and which contain few to numerous small seeds. The seeds are exalbuminous, flat, and minutely winged either only on the chalazal side or on both ends. The mature seed coat is formed by a tannin-containing exotesta, a crystal-containing endotesta, and a tannin-containing endotegmen (Tobe and Raven 1987a, b).

POLLINATION AND OTHER PLANT/ANIMAL INTERACTIONS. No observations on the pollination of any Crypteroniaceae have been published. *Crypteronia* have densely clustered, minute flowers lacking petals and nectaries (judging from herbarium material), and which are often unisexual, all pointing to wind pollination. *Axinandra* and *Dactylocladus* have bisexual flowers and, hence, could offer pollen as a reward for bees in both floral morphs. Although pollination remains unstudied, a tight herbivore defence mutualism between *Crypteronia griffithii* and an aggressive ant species has received considerable attention from ecologists. Swollen nodes of young twigs in saplings and young trees are inhabited by queens of *Cladomyrma maschwitzi*, and the interaction

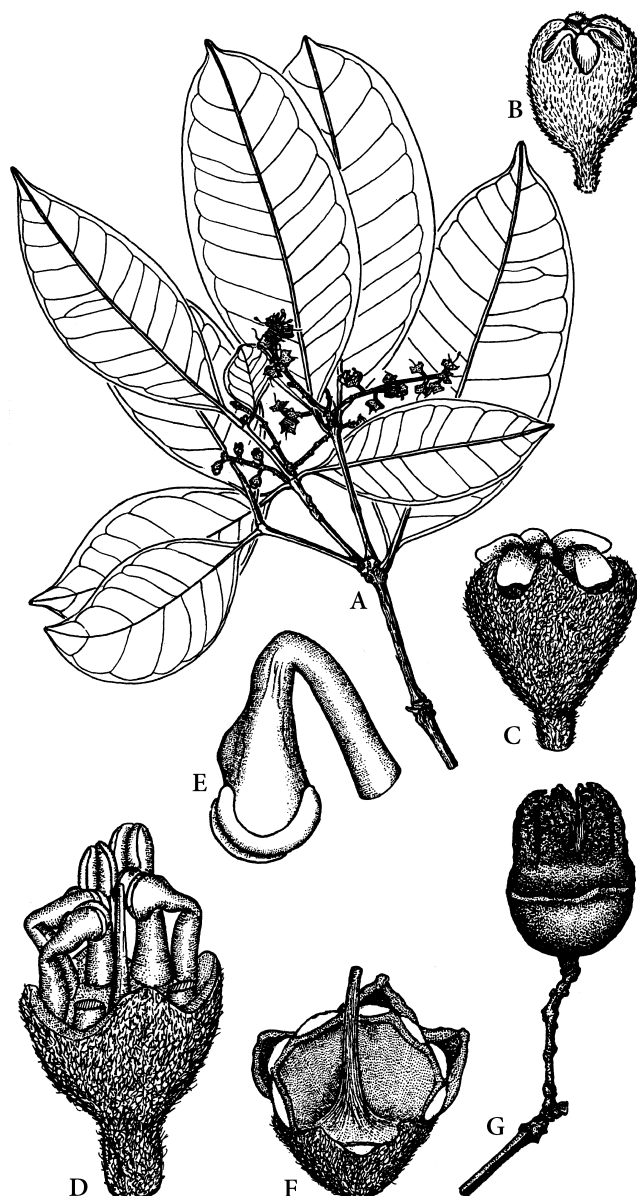


Fig. 34. Crypteroniaceae. *Axinandra coriacea*. A Habit. B Young flower bud. C Older bud, with protruding style. D Mature flower, petals dropped. E Stamen. F Old flower, petals and stamens dropped. G Mature capsule. (van Beusekom-Osinga 1977)

is among the most common *Cladomyrma*/plant associations in a Pasoh 50-ha study plot on the Malay Peninsula (Maschwitz et al. 1991 and references therein).

SEED DISPERSAL. The minute (1.4–3 mm long in the different species), dry and winged seeds certainly are wind-dispersed.

PHYTOCHEMISTRY. Leaves of *Axinandra* and *Crypteronia*, but apparently not of *Dactylocladus*, accumulate aluminium (Jansen et al. 2002).

PHYLOGENY. van Beusekom-Osinga and van Beusekom (1975) were the first to recognize the close relationship of *Axinandra*, *Dactylocladus* and *Crypteronia*, although this insight appears to have been based mostly on intuition because the three genera exhibit no uniquely shared trait. van Beusekom-Osinga and van Beusekom ranked the three genera as a subfamily within a more widely circumscribed Crypteroniaceae which also included the South American *Alzatea* and the South African *Rhynchocalyx*. Based on wood anatomy, van Vliet (1981; also van Vliet and Baas 1984) transferred Crypteronioideae into Melastomataceae (again as a subfamily). This view, however, never gained wide acceptance but rather, that of Dahlgren and Thorne (1984), and Johnson and Briggs (1984) who saw the three genera as relatively isolated in Myrtales, and accordingly gave them family rank. Molecular data from three chloroplast genes (Clausing and Renner 2001; Rutschmann et al. 2004) suggest that Crypteroniaceae are sister to a clade comprising Alzateaceae, Rhynchocalycaceae, Oliniaceae and Peneaeceae, and that *Dactylocladus* is sister to *Axinandra* plus *Crypteronia*, albeit without solid statistical support. If the latter relationship were to be confirmed, this would argue against previous assessments which saw either *Axinandra* as standing apart, especially in having an endothelium (Tobe and Raven, 1987b), or *Crypteronia*, in possessing stipules, a closed vascular pattern in the petiole and midrib (Mentink and Baas 1992), and diffuse parenchyma (van Vliet 1981). Earlier systematists had seen *Axinandra* as lythraceous (e.g. Bentham and Hooker 1867), melastomaceous (e.g. Baillon 1877; Cogniaux 1891; Krasser 1893; Gilg 1897; Bakhuizen van den Brink 1946/1947), or even as intermediate between these families (Meijer 1972). *Dactylocladus* was placed next to *Axinandra* by its author, and *Crypteronia* was usually treated as a separate family because of its stipules, a rare feature in Myrtales.

FOSSILS AND DISTRIBUTIONAL HISTORY. The only known fossils of Crypteroniaceae are Miocene pollen grains of *Dactylocladus* from a bog in south-eastern Kalimantan (Demchuk and Moore 1993). Remarkably, the vegetation which formed this Miocene lignite is virtually identical to its present-day peat-forming counterpart in Indonesia. Based

on a molecular clock calibrated with Melastomataceae fossils, Conti et al. (2002, 2004; see also Rutschmann et al. 2004) suggest that Crypteroniaceae may have rafted from Gondwana to Asia on India, with an origin in the Early to Middle Cretaceous. However, substitution rate heterogeneity does not allow us to draw any firm conclusion here (Moyle 2004; F. Rutschmann, pers. comm. 2005), and a more recent separation from their African and South American closest relatives, with subsequent long-distance dispersal, remains an equally likely possibility. The family's widespread distribution throughout the Malesian archipelago certainly attests to its high dispersal capabilities.

KEY TO THE GENERA

1. Flowers with 3 bracts, the 2 outer ones minute. Stamens twice as many as sepals. Fruit big, woody. Seeds winged on one side **1. *Axinandra***
- Flowers with 1 bract. Stamens as many as sepals. Fruits small, chartaceous. Seeds winged on both sides **2**
2. Petals present, soon caducous. Ovary at least half-inferior, the lower part immersed in the receptacle, with up to 3 ovules per locule. Fruits with few seeds **2. *Dactylocladus***
- Petals absent. Ovary superior, with many ovules per locule. Fruit with numerous seeds **3. *Crypteronia***

GENERA OF CRYPTERONIACEAE

1. *Axinandra* Thwaites Fig. 34
Axinandra Thwaites, Hooker's J. Bot. Kew Gard. Misc. 6:66, t. 1C (1854).

Tree. Flower bracts 3 per flower, persistent during anthesis; flowers bisexual, 5(4)-merous, the petals falling off as a cap when the flowers open. Stamen connectives broad and provided with a dorsal tubercle, anthers broad-linear, introrse. Ovary inferior, with 3(2) carpels and 6(4) locules, each with 1 or 2 ovules. Fruit an oblong-globose woody capsule, the lower part surrounded by the persistent receptacle, capsule introrsely dehiscent by 2–6 valves. Seeds 1 or 2 per locule, each with a thin narrow-oblong wing on one side of the seed. Two to four species in Sri Lanka, the Malay Peninsula and Borneo.

2. *Dactylocladus* Oliver
Dactylocladus Oliv., Hooker's Ic. Pl. 24: t. 2341 (1895).

Subcanopy tree or shrub. The single flower bract early caducous; flowers bisexual, 5(4)-merous, the petals falling off individually. Stamen connectives

more or less orbicular, the anthers semiorbicular slightly below the upper margin of the connective, introrse. Ovary half-inferior, (3)4 or 5 carpels and (3)4 or 5 locules, each with 3 ovules. Fruit a small, thin capsule, its valves often kept together at the top by the non-splitting persistent style. Seeds usually 3 per locule, with lateral membranous wings about twice as long as the seed. A single species, *D. stenostachys* Oliv., in lowland peat swamp forest in Sarawak.

3. *Crypteronia* Blume

Crypteronia Blume, Bijdr.: 1151 (Oct. 1826–Nov. 1827).

Tall trees. The single flower bract linear, early caducous; flowers bisexual or unisexual and trees then apparently dioecious, 4–5(6)-merous; petals 0. Stamens (staminodes?) in female flowers permanently bent inwards, in bisexual flowers with an orbicular connective bearing the semiorbicular anthers, more or less introrse. Ovary superior or almost so, only the lowermost part adhering to the receptacle, 2–4-carpellate, reduced in male flowers; ovules many, on axile-basal placentas. Fruit a small, laterally compressed capsule, the top dehiscent by 2–4 valves. Seeds many, very small, with membranous lateral wings. Four to seven species, one endemic to the Philippines, two more or less widespread throughout the Malesian region (of which *C. paniculata* Bl. also reaches tropical China), and 1–4 endemic to Borneo.

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