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## Aptandraceae

Aptandraceae J. Miers in Lindl., Veg. Kingd., ed. 3: 447a (1853).

Chaunochit(on)aceae Tiegh. (1896).

Harmandiaceae Tiegh. (1898).

Trees or large shrubs with simple, petiolate, exstipulate leaves, phyllotaxy alternate. Inflorescence a raceme or panicle or crowded cluster, usually axillary. Flowers mostly bisexual (unisexual in *Harmandia* and *Hondurodendron*). Petals 4–8, calyx/calyculus present, often greatly enlarging and enclosing most or all of the fruit (persistent but not accrescent in *Phanerodiscus*, where the fruit envelope is of different origin), its apex expanding in trumpet-like fashion beyond the fruit in *Hondurodendron*. Stamens epipetalous or filaments connate into a synandrial tube, distinct in *Hondurodendron*; anthers small, terminally placed on the filaments, opening in valvate fashion in most genera; in *Phanerodiscus* with 6–8 pores placed in U-shaped pattern on anther margins. Pollen of *Hondurodendron* is isopolar, shallowly tubercular, oblate in equatorial view, triangular, tricolporate with broad colpi nearly meeting at the poles; *Chaunochiton* has a pollen sculpturing that is unique in Santalales (see below). Ovules ategmic or unitegmic. Fruit a one-seeded drupe with stony exocarp, endosperm copious; cotyledons 2.

A family presently comprising six genera, all of which were until recently included in Olacaceae except *Hondurodendron*, as published by Ulloa et al. (2010) contemporaneously with Nickrent et al.'s (2010) reorganization of the order Santalales. The latter authors refer to two clades in Aptandraceae, one containing *Anacolosa*, *Cathedra*, and *Phanerodiscus*, the other one *Aptandra*, *Chaunochiton*, *Harmandia*, *Ongokea*,

and *Hondurodendron*. They also, in the key to families, refer to the family as being parasitic, but this fact has not been demonstrated for any of the component genera, even in the relevant work of Teo (1997).

*Phanerodiscus*, when described by Cavaco (1954) and later reviewed by Malécot et al. (2003), was at that time placed in Olacaceae, but was subsequently reassigned to Aptandraceae by Nickrent et al. (2010).

The major diagnostic criterion of Aptandraceae appears to lie in its unique androecial modifications. In several genera (*Aptandra*, *Chaunochiton*, *Hondurodendron*, and *Harmandia*), the anthers dehisce by means of valvate flaps rather than longitudinal slits; in *Aptandra*, *Harmandia*, and *Ongokea*, the filaments are connate to form a synandrial tube. *Phanerodiscus*, first placed in Olacaceae by Malécot et al. (2003, 2004), has a curious, U-shaped configuration of 6–8 pores on the margin of the anther. Neither *Anacolosa* nor *Cathedra*, both placed in Aptandraceae by Nickrent et al. (2010), share such fundamental features, having a more regular anther structure; for this reason, a systematic placement in Olacaceae remains more appropriate. Aptandraceae thus emerges as a family of considerable integrity, characterized by its curious anthers that are placed at the tip of the filaments and dehisce by means of valves rather than fissures, by (some genera only) synandria, and by an accrescent calyx growing beyond the fruit or tightly enclosing it at maturity. *Phanerodiscus*, however, remains a genus of problematic assignment.

**POLLEN.** The pollen of *Aptandra* is heteropolar and tetracolpate, with ectoapertures in the shape of a small groove or more or less rectangular (Bonneville et al. 1982).

The fossil pollen known as *Anacolosidites* Cookson and Pike, first placed in Olacaceae, is probably assignable to *Phanerodiscus* of the present family (Malécot et al. 2004). It is present in the Maestrichtian (72 Ma) in both northern and southern hemispheres (Muller 1981; Askin 1989; Krutzsch 1989), and in the Eocene (53 Ma) of Africa and India (Kuyt et al. 1955; Thanikaimoni et al. 1984; Lucas 1994), when members of this tribe apparently entered Madagascar.

The pollen of *Chaunochiton* has extraordinary sculpture features, its surface being sharply divided into psilate, circular equatorial areas and fused colpal margins that are strikingly raised in densely lobed fashion (Feuer 1977). It is a pollen structure that is unique in the order and possibly beyond.

#### KEY TO THE GENERA OF APTANDRACEAE

1. Stamens united in a tube surrounding the style 2
  - Stamens not united 4
2. Flowers unisexual; petals 4 (staminate) or 6–8 (pistillate) 3. *Harmandia*
  - Flowers bisexual; petals 4 or 5 3
3. Petals 4, ovules 2 1. *Aptandra*
  - Petals 5, ovules 3 5. *Ongokea*
4. Dioecious, petals 4; Honduras 4. *Hondurodendron*
  - Flowers bisexual, petals 5 or 6; not in Central America (*Chaunochiton* reported for Costa Rica) 5
5. Petals linear; fruiting calyx funnel-shaped, not covering the fruit; stamens long, filaments; South America and Costa Rica 2. *Chaunochiton*
  - Petals not linear; the fruit enclosed by several distinct lobes; stamens short, not hair-like; Madagascar 6. *Phanerodiscus*

#### GENERA OF APTANDRACEAE

##### 1. *Aptandra* Miers

Fig. 5

*Aptandra* Miers, Ann. Magaz. Nat. Hist. II, 7: 201 (1851).

Trees with thin, elongate-elliptical alternate leaves with acute apices. Inflorescence terminal or axillary, simple or branched panicles. Flowers

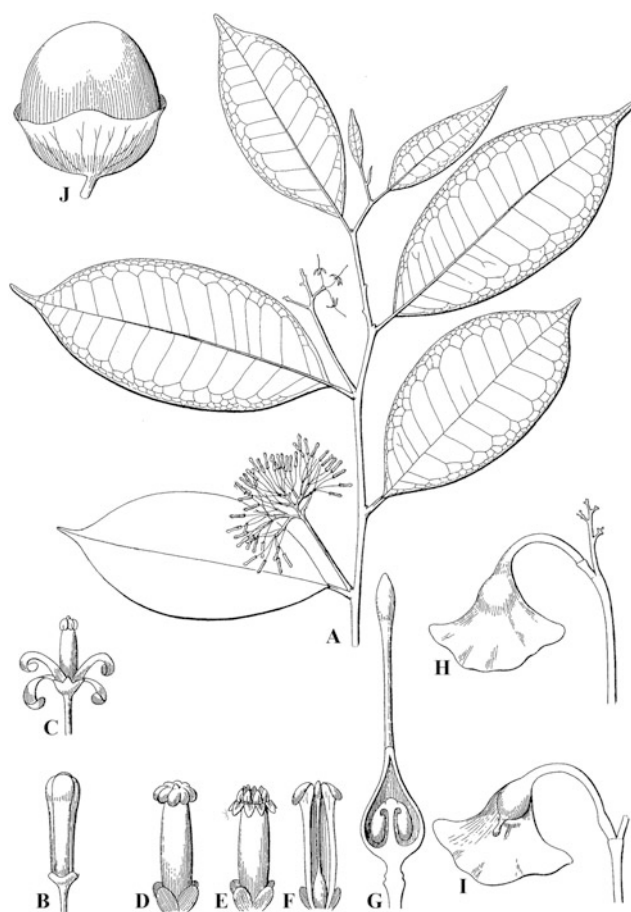


Fig. 5 Aptandraceae. *Aptandra tubicina*. A Flowering branchlet. B Flower bud. C Open flower. D Staminal tube at early anthesis. E Same, in a later stage with dehiscent anthers. F Flower longitudinally sectioned. G Ovary and style, longitudinally sectioned. H Immature fruit with fruit-calyx. I Same, cut open. (Sleumer 1984)

bisexual, with very small, 4-toothed, calyculus becoming large and funnel-shaped or urceolate around the fruit at maturity. Petals 4, fleshy, linear to tongue-shaped, recurving at anthesis. Glandular disk with 4 fleshy lobes between the petals and stamens. Stamens 4, united into a cylindrical synandrium, the anthers forming a ring, the locules dehiscent by a flap that bends downwards. Ovary ovoid to conical, 2-chambered below with 2 pendent ovules; stigma with clavate tip. Fruit a drupe with hard endocarp, 1-seeded.

Four spp., three in tropical South America and one in West Africa.

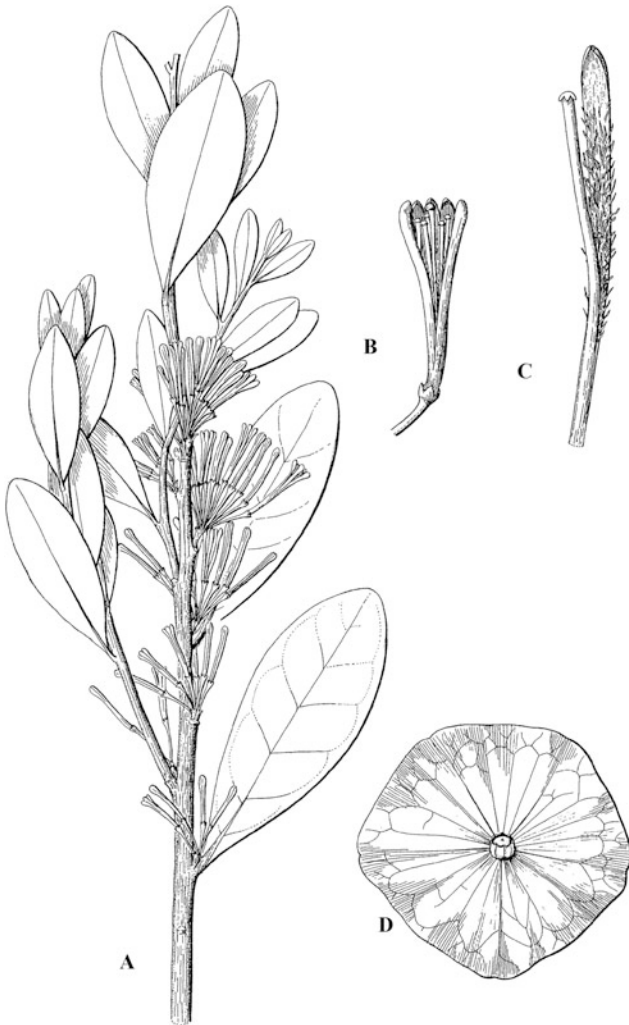


Fig. 6 Aptandraceae. *Chaunochiton angustifolium*. A Flowering branchlet. B Flower. C Petal inside with stamen. D Fruit with expanded flattened calyx. (Sleumer 1984)

## 2. *Chaunochiton* Benth.

Fig. 6

*Chaunochiton* Benth. in Benth. & Hook. f., Gen. Plant. 1: 996 (1867).

Small to moderate trees. Leaves alternate, pinnately veined, petiolate, glabrous. Inflorescence an axillary, short-pedunculate, corymb-like panicle with few to many flowers. Flowers fragrant, with small, cupulate, 5-dentate calyx much enlarged in fruit. Petals 5, distinct, linear-elongate, most of the adaxial surface pilose. Glandular disk small. Stamens 5, epipetalous, opposite the petals and nearly as long, filaments thread-like; anthers small,

nearly spherical, at the tip of the filament, and opening with 2 or more flaps. Ovary superior, 5-ribbed lengthwise, elongate, 2-loculate basally, simple above, with 1 ovule suspended in each locule; style at least as long as the stamens, stigma capitate, 5-lobed. Fruit ca. 5-sided, spherical, longitudinally 5–10-grooved or warty, with one seed, fruit wall thin; fruiting calyx very large, profusely veined.

Three spp., one in Brazil, the others from NW South America (Brazil, Guianas, Venezuela, Colombia), one species reportedly also in Costa Rica.

## 3. *Harmandia* Pierre ex Baillon

*Harmandia* Pierre ex Baillon, Bull. Soc. Linn. Paris 2: 770 (1889).

Trees with distichous, lanceolate leaves. Inflorescences axillary panicles. Flowers pedicellate, unisexual, calyx small, dish-shaped, with 4 short teeth, enlarging in fruit and enclosing it. Petals 4 (staminate) or 6–8 (pistillate), more or less campanulate. Glandular disk ring-shaped, evanescent. Stamens 4, united in a synangium, the connectives of the anthers fusing and nearly closing the terminal pore. Ovary pyramidal, ovules 2, pendent from a short funiculus, stigmas 3, sessile. Fruit a drupe, connate with the calyx below, 1-seeded.

One sp., *H. mekongensis* Pierre, continental SE Asia.

## 4. *Hondurodendron* Ulloa, Nickrent, Whitefoord & Kelly

*Hondurodendron* Ulloa, Nickrent, Whitefoord, and Kelly, Ann. Missouri Bot. Gard. 97: 457–467 (2010).

Dioecious trees to 12 m high, young shoots densely covered by short reddish brown hairs. Leaves distichous, petiolate, elliptic to lanceolate, apex acute and more or less acute basally, shiny above, whitish-green below, glabrescent, forming flattened sprays. Inflorescences axillary. Male inflorescence with to ca. 20 flowers in few-flowered cymose units, bracts linear, densely reddish tomentose; flowers externally tomentose; calyculus cup-shaped, very short, the rim minutely denticulate; petals 4. Stamens as many as, and opposite the petals; filaments distinct, erect, bearing terminal, basifixed, 3-lobed anthers dehiscent by as many longitudinal valves; pollen isopolar,

triangular in polar view, tricolporate, the colpi nearly meeting at the poles; glandular disk with lobes alternating with the stamens. Female inflorescences shortly spicate, flowers to 4, each subtended by 1.5 mm long bract and 2 small bracteoles, densely reddish tomentose; flowers with cup-shaped calyculus with entire rim, petals 4 or 5(6), deltoid; ovary superior, broadly ovoid, densely pubescent, 2-chambered basally but united above, ovules 2, pendent from a distinct central placental stalk; style short, stigma thick, round. Fruit a shallowly furrowed drupe, completely enveloped by the accrescent, coriaceous calyx extending beyond the fruit in cup-shaped, deeply fissured fashion; exocarp thin.

A single sp., *H. urceolatum* Ulloa, Nickr., Whitef. & Kelly; known only from NW Honduras.

### 5. *Ongokea* Pierre

Fig. 7

*Ongokea* Pierre, Bull. Soc. Linn. Paris 2: 1313 (1897).

Trees resembling *Aptandra*. Flowers bisexual. Petals 5, distinct, tongue-shaped, recurving in anthesis; calyx very small, dish-shaped, with 5 short teeth. Stamens 5, united in a synangium as in *Aptandra*, the anthers dehiscing with valvate flaps; 5 thick lobes separating synandrium and petals. Ovary ovoid, ovules 3, pendent from the central funiculus. Fruit 1-seeded, at maturity completely enclosed by the enlarged calyx, eventually splitting into 3 parts; embryo small, dicotylous.

One sp., *Ongokea gore* (Hua) Pierre, western tropical Africa.

*Ongokea* appears to differ from *Aptandra* mainly in having 3, rather than 2 ovules, and in having 5-merous rather than 4-merous flowers. The two genera could conceivably be united.

### 6. *Phanerodiscus* Cavaco

*Phanerodiscus* Cavaco, Notul. Syst. (Paris) 15: 11 (1954).

Small trees. Leaves alternate, deciduous, 2–7 cm long, basally rounded, apex acute, short-petiolate, not coriaceous. Inflorescence a small glomerule, axillary on leafless twigs. Flowers bisexual, with well developed, non-acrescent, 5/6-lobed calyx; petals and stamens 5/6, attached to the rim of a stout, cupulate disk, stamens opposite petals; petals pubescent abaxially, long-hairy adaxially in the upper part of the petals, with

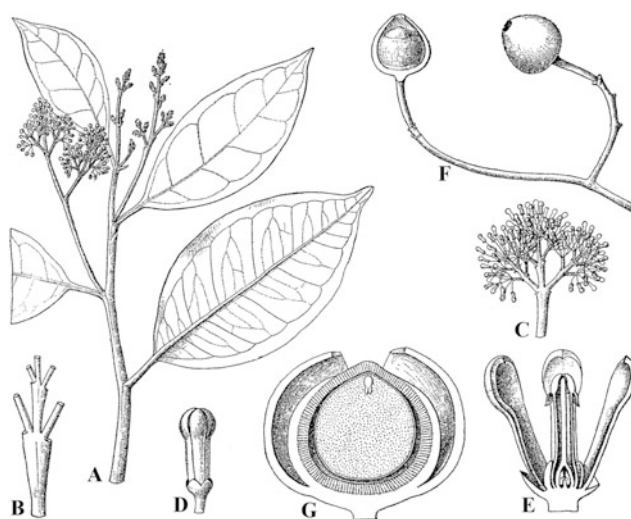


Fig. 7 Aptandraceae. *Ongokea gore*. A Flowering branch. B Part of inflorescence with appanate axes. C Part of inflorescence with young buds. D Further developed bud. E Open flower. F Fruiting branchlet with fruits enclosed by enlarged calyx. G Fruit and seed, longitudinal section. (Engler 1915)

shorter (glandular?) hairs below; filaments short, anthers basifixed, biloculate, with 6–8 pores in U-shaped pattern on the anther's margin. Ovary superior, style stout, hairy in or above the middle, stigma scarcely differentiated. Fruit a drupe surrounded by an accrescent membranous structure, either entire or partially so with several erect lobes exceeding the fruit, this envelope being profusely vasculated.

Three spp., endemic to Madagascar.

The revision of *Phanerodiscus* by Malécot et al. (2003) still placed it in Olacaceae, but the genus was moved to Aptandraceae in Nickrent et al. (2010). Its familial position remains uncertain, the unique fruit envelope being of puzzling homology.

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