Anisophylleaceae

Anisophylleaceae Ridl. (1922).
Rhizophoraceae subfam. Anisophylloideae A.F.W. Schimper (1893).

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Aluminum-accumulating trees and shrubs of wet primary tropical forests; indumentum sparse, of short unicellular trichomes; *Combretocarpus* flowers with multicellular peltate trichomes. Leaves alternate, sometimes dimorphic (anisophyllous), estipulate. Inflorescences axillary, racemose to paniculate. Flowers (3)4(5)-merous, small, mostly unisexual by abortion, with smaller male flowers (plants monoecious) but bisexual in *Combretocarpus*; calyx and petals valvate; petals distinct, lobed or laciniate (entire in *Polygonanthus*); stamens twice the number of petals; anthers dorsifixed, introrse; nectary disk intra- and interstaminal, discontinuous, lobed or crenate, on top of the ovary; gynoecium of (3)4(5) united carpels with distinct stylodia; ovary (hemi) inferior, 3–4-locular, with 1 or 2 ovules per loculus. Fruit usually a 1- or few-seeded drupe but dry and winged in *Combretocarpus*. Endosperm 0, the embryo with reduced or no cotyledons; germination hypogeal. $n = 7, 8$.

A family of 4 genera and about 34 species in SE Asia, South America and Africa.

VEGETATIVE MORPHOLOGY. The distinctive growth habit of *Anisophyllea disticha* and probably *A. scortechini* as well may characterize the family, but in species known only from herbarium material it is difficult to ascertain because the reduced leaves are very small and caducous (Juncosa and Tomlinson 1988b). In its typical expression, the architecture is that of Massart's model, the orthotropic axis bearing only spirally arranged scale leaves, the plagiotropic axes, borne in pseudowhorls, with distinctly dimorphic leaves, producing flattened and markedly dorsiventral branch complexes. Leaves are then uniquely arranged with pairs of scale leaves alternating on the upper surface of the shoot and a corresponding series of foliage leaves on the lower surface (Fig. 8A, B), this arrangement determined by the shoot apex within the bud, i.e., without secondary reorientation (Vincent and Tomlinson 1983). Taxonomic descriptions of most other species are based on flowering branches, which are lateral, plagiotropic shoots apparently with isomorphic leaves. However, the dimorphy of *A. disticha* may be expressed in the juvenile stage of other species and may undergo metamorphism into a distinct adult stage. This feature needs to be examined in much greater detail and in a phylogenetic context.

The morphology of other genera is less well known and *Combretocarpus* has monomorphic leaves. Another feature of the family is the occurrence of serial buds in the foliage leaf axil, with up to six buds increasing in size distally. The venation of foliage leaves varies from divergent in *Anisophyllea* to pinnately veined in *Combretocarpus*. Stipules are absent, except for glandular structures in a stipular position reported for *Anisophyllea disticha* (Keating and Randrianasolo 1988). Stipules ascribed to *Polygonanthus* (Prance et al. 1975) may represent the small caducous leaves of the anisophyllous series. Tiny aerial roots (1–4 cm) are known from *Combretocarpus*.

VEGETATIVE ANATOMY. Vessels elements have simple perforations; intervessel pitting is alternate with coalescent apertures. The fibres have distinctly bordered pits. Axial parenchyma is apotracheal and often banded, and varies to paratracheal and irregular. Rays are of two distinct sizes and are 1–20-seriate, with multiseriate ray tails. Lysigenous secretory canals are present in the parenchymatous tissue of *Poga*. Nodes are unilacunar. Stomata are variable but usually paracytic. Leaf venation has been studied by Keating and Randrianasolo (1988); leaf margins are usually entire, with exception of a single species of *Anisophyllea* (*A. meniandii*), which has very simple, non-vascularized glands. Sieve element plastids are S-type (Behnke 1988).

INFLORESCENCE AND FLORAL MORPHOLOGY. Inflorescences are paniculate or racemose and usually somewhat open-branched. A single bract subtends each branch and flower. In *Anisophyllea disticha*, male and female flowers occur on separate inflorescences, but in most other species and genera in the family the two kinds of flower are mixed in the inflorescences. Floral structure of Anisophylleaceae has been studied by Tobe and Raven (1988b) and Matthews et al. (2001). Except for *Polygonanthus*, the petals are deeply incised (Fig. 8D). Nectariferous lobes are found at both intra- and interstaminal positions, but do not form a continuous annular disk; in *Combretocarpus* they are only intrastaminal. A compitum seems to be lacking in Anisophylleaceae. For the strong similarities between Anisophylleaceae and Cunoniaceae revealed by Matthews et al. (2001), see under "Affinities".

EMBRYOLOGY AND SEED MORPHOLOGY. Pollen grains are 2-celled when shed.

All genera agree in having persistent nucellar tissue at least until early stages of seed development. Otherwise, the genera are very diverse embryologically. The ovules of *Anisophyllea* and *Combretocarpus* are unitegmic. Those of *Poga* and *Polygonanthus* are bitegmic, and the raphe bundle ramifies in the outer integument, whereas the inner integument is very thin (2-layered) and does not contribute to the formation of the seed coat. *Anisophyllea* and *Polygonanthus* have a Polygonum type embryo sac, while that of *Combretocarpus* is Allium type (Tobe and Raven 1987, 1988a). Endosperm formation is of the Nuclear type. The seeds are exalbuminous (Floret 1979; Tobe and Raven 1987), and the embryo is represented by the swollen extended hypocotyl, having either small cotyledons (*Combretocarpus*) or rudimentary and/or no cotyledons (*Anisophyllea* and *Poga*). The seed coat is testal and formed by the outer epidermis alone (*Combretocarpus*), by both the outer epidermis and the multiple inner layer (*Anisophyllea*), or by both the multiple outer layer and the multiple inner layer (*Poga*). Germination is usually described as hypogeal (Tobe and Raven 1987).

POLLEN MORPHOLOGY. Pollen is mainly tricolporoidate, and syncolpate grains are common. Endoapertures, when present, are circular but poorly defined. *Anisophyllea disticha* is unusual in the striate surface of pollen grains (Vezey et al. 1988). *A. manauensis* has tetrad pollen (Prance et al. 1975).

KARYOLOGY. *Combretocarpus* has $n = 8$, the other three genera $n = 7$ (Tobe and Raven 1987).

PHYTOCHEMISTRY. Ellagic acid and derivatives thereof are known from *Anisophyllea* (Hegnauer 1973).

INTRAFAMILIAL RELATIONSHIPS. As described by Tobe and Raven based on morphological characters, two major branches within the family may be distinguished, one comprising *Poga* and *Polygonanthus*, another with *Anisophyllea* and *Combretocarpus*, the former pair retaining plesiomorphies, the latter possessing derived traits (Tobe and Raven 1987, 1988a). However, recent molecular studies including all genera and based on a multigene dataset have revealed a very different picture. *Anisophyllea* is sister genus to *Poga*, both are sister to *Polygonanthus*, and *Combretocarpus* is sister to the rest of the family (Zhang et al. 2007).

AFFINITIES. Anisophylleaceae have traditionally been included in Rhizophoraceae, although since the treatment of Bentham and Hooker (1865) always as a distinct tribe or subfamily (Schimper 1893). The group was elevated to family rank by Ridley (1922), but without consideration of the non-Malaysian taxa; Melchior (1964) followed this course; however, *Poga* and *Polygonanthus* were not added until 1975. As a result of careful and extended analysis of both families with the addition of much new data, it has been recognized that the two families are widely separated (Juncosa and Tomlinson 1988a, b). Dahlgren (1988) proposed the separation of Rhizophoraceae from Myrtales, where it had traditionally resided, and suggested it should be included in his Celastrales, while Anisophylleaceae were thought to have a

Rosalean affinity. A series of thorough morphological and anatomical studies supported the exclusion of Anisophylleaceae from Rhizophoraceae (included in Raven and Tomlinson 1988). Takhtajan (2009) established an order Anisophyllales that he placed close to his Cunoniales. Molecular studies, in which only *Anisophyllea* and *Combretocarpus* were included (Setogushi et al. 1999; Schwarzbach and Ricklefs 2000), resolved Anisophylleaceae as a member of Cucurbitales. Later it was shown that they are sister to the rest of Cucurbitales (Zhang et al. 2006). In the light of these findings, the strong similarities in floral structure and histology between Cunoniaceae and Anisophylleaceae as described in Matthews et al. (2001) appear as homoplasies. In a more recent comparative morphological study of families of Cucurbitales, Matthews and Endress (2004) have found the prevalence of unisexual flowers and inferior ovaries in all core Cucurbitales as possible synapomorphies of Anisophylleaceae and other Cucurbitales. However, for many other characters Anisophylleaceae are quite distinct from the rest of the order (Matthews and Endress 2004).

DISTRIBUTION AND HABITATS. The wide distribution of *Anisophyllea* (South America to Malesia) is in contrast to the more localized distribution of the remaining genera. Curiously, their ranges overlap that of *Anisophyllea* in three separate continents: *Polygonanthus* in South America, *Poga* in Africa, and *Combretocarpus* in SE Asia/Malesia. Members of the family are typically trees of wet lowland tropical forest. Species of *Anisophyllea* range in size from tall trees to small treelets; *A. disticha* is a common understorey component of the Malaysian rainforest, with the distinctive vegetative morphology that gives the genus its name. *Anisophyllea disticha* is widely distributed throughout the Sunda shelf area (except Java), but other Asian species are more localized within three discrete regions of the Malay Peninsula, Sumatra, and Borneo (Ding Hou 1958). *Combretocarpus* is a dominant tree of Bornean freshwater swamps, apparently extinct in peninsular Malaya.

PALEOBOTANY. Pollen of *Combretocarpus* has been described from middle and late Miocene deposits of northwestern Borneo (Anderson and Muller 1975; Morley 1977).

USES. Only one species (*Anisophyllea griffithii*) is reported to reach commercially exploitable size (Kochummen 1989).

KEY TO THE GENERA

1. Flowers bisexual, trimerous; petals linear or irregularly 3–4-lobed. Fruit 3-winged. Leaves always monomorphic, with pinnate venation **4. *Combretocarpus***
– Flowers unisexual or polygamous, rarely bisexual, tetramerous; petals often appendaged. Fruit not winged, usually a drupe. Leaves mostly with divergent venation, sometimes dimorphic 2
2. Flowers strongly heteromorphic; serial buds not conspicuously developed. Fruit with 3–4 edible seeds. Secretory canals present **2. *Poga***
– Flowers not strongly heteromorphic; serial buds conspicuously developed. Fruits usually 1-seeded, inedible. Secretory canals absent 3
3. Petals lobed. Leaves with divergent venation, often dimorphic either in the juvenile stage or as adults **1. *Anisophyllea***
– Petals unlobed. Leaves without divergent venation, monomorphic **3. *Polygonanthus***

GENERA OF ANISOPHYLLEACEAE

1. *Anisophyllea* R. Br. ex Sabine Fig. 8

Anisophyllea R. Br. ex Sabine, Trans. Hort. Soc. 5: 446 (1824); Ding Hou, Fl. Males. I, 5: 480 (1958).

Monoecious shrubs, treelets or tall trees to 38 m, shoots often distinctly dimorphic (possibly always in juvenile stage). Leaves alternate, spiral on orthotropic shoots, distichous on plagiotropic branches, often asymmetric, foliage leaves with 3–5 longitudinal veins diverging from the base. Inflorescences (supra)axillary, solitary or serial, simple or branched, ebracteate or at most with small bracts. Flowers usually unisexual, rarely bisexual, usually tetramerous; sepals adnate to ovary; petals entire, lobed or lacerate, sometimes with glandular apical appendages; male flowers with stamens twice as many as the petals, the outer stamens longest; nectariferous tissue at base of stamens; pistillode usually 0; female flowers usually with staminodes; ovary 3–5-locular with 1 apical pendulous ovule per loculus; stylodia (3)4. Fruit ellipsoid to pear-shaped, usually 1-seeded; pericarp 3-layered, rather fibrous;

testa leathery; embryo linear and undifferentiated, or represented largely by the hypocotyl.

About 30 species, mostly distributed from tropical Africa to SE Asia/Malesia (Malaysia, Borneo, Sumatra), *A. guianensis* Sandw. and *A. manausensis* Pires & Rodr. in northern South America.

2. ***Poga*** Pierre

Poga Pierre, Bull. Soc. Linn. Paris 2: 1254 (1896); Hutchinson & Dalziel, Fl. W. Trop. Africa, ed. 2: 282 (1954).

Large tree. Leaves with numerous lateral nerves. Inflorescences catkin-like on specialized leafless branches. Flowers tetramerous, small, unisexual, strongly heteromorphic; petals 3–7-lobed, the lobes with glandular tips; ovary 4-locular; with 1 ovule per loculus. Fruit a drupe up to 6 cm long with 3–4 edible oily seeds. Seeds 2 cm long; seed coat brown, coriaceous; embryo undifferentiated or represented by the hypocotyl, with abundant oil in cortex and medulla.

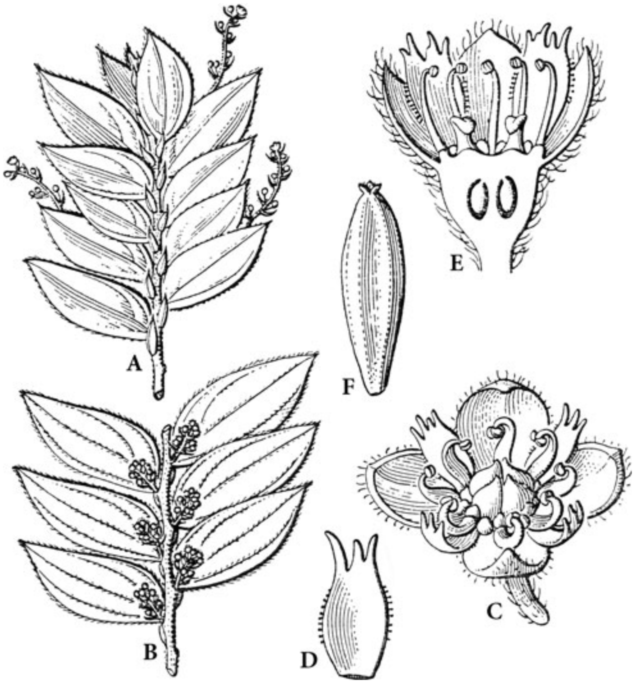

Fig. 8. Anisophylleaceae. *Anisophyllea disticha*. **A** Flowering branch, upper surface. **B** Flowering branch, lower surface. **C** Male flower. **D** Petal. **E** Longitudinal section of female flower with stylodia and staminodes. **F** Dried fruit. (Ding Hou 1958; artwork by R. van Crevel)

A single species, *P. oleosa* Pierre, restricted to Equatorial Africa.

The seeds are edible (Inoi nut), but seem little exploited commercially (Vaughan 1970).

3. ***Polygonanthus*** Ducke

Polygonanthus Ducke, Notizbl. Bot. Gard. Berlin-Dahlem 11: 345 (1932); Prance et al., Acta Amazonica 5: 17–22 (1975).

Small trees. Leaves distichous. Inflorescences racemose but appearing spicate. Flowers usually unisexual, strongly heteromorphic, tetramerous. Male flowers small, with apically inflexed sepals; stamens 8, distinct, inserted at the base of the sepals, exserted or included at anthesis; filaments inflexed in bud, often flattened; glandular lobes of nectary enclosing base of anthers; female flowers larger, few, usually at the base of the inflorescence, petals small, lanceolate; staminodes 8, with reduced anthers, nectary small; ovary half-inferior, forming a tube with the calyx, 4-locular, with 1 ovule per locule; stylodia 4. Fruit careniform, 4-angled.

Two species along river margins in Amazonian Brazil.

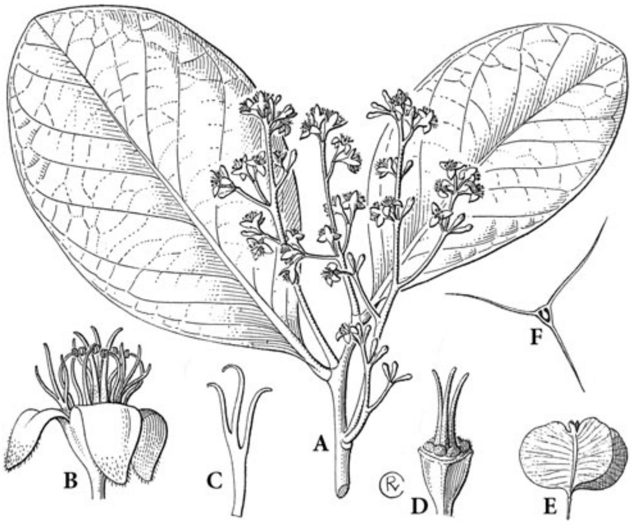

Fig. 9. Anisophylleaceae. *Combretocarpus rotundatus*. **A** Flowering branch. **B** Flower. **C** Petal. **D** Gynoecium. **E** Fruit. **F** Fruit, transverse section. (Ding Hou 1958; artwork by R. van Crevel)

4. *Combretocarpus* Hook. f. Fig. 9

Combretocarpus Hook. f. in Benth. & Hook., Gen. Pl. 1: 683 (1865); Ding Hou, Fl. Males. I, 5: 480 (1958).

Tree to 25 m, easily coppicing or sprouting from fallen branches. Leaves obovate to broadly elliptic with 6–10 pairs of lateral veins diverging from a prominent mid-rib. Inflorescence short racemes; flowers c. 4 mm diameter, yellow, bisexual, usually trimerous, with multicellular peltate trichomes; sepals obtuse, reflexed at anthesis; petals c. 2 mm long, linear, entire or deeply divided; stamens usually 6, obdiplostemonous, inserted between shallow lobes of the nectariferous tissue; ovary inferior, usually 3-ribbed, trilocular, each loculus with 2 ovules; stylodia 3. Fruit 3-winged, 1-seeded by abortion. Seeds elongate, narrow.

One species, *C. rotundatus* (Miq.) Danser, mainly of swamp forests in Sumatra and Borneo, recorded for but possibly extinct in Malaya, often gregarious, possibly by its ability to sucker, and now probably over-exploited because of its useful timber.

Selected Bibliography

Anderson, J.A.R., Muller, J. 1975. Palynological study of a Holocene peat and a Miocene coal deposit from NW Borneo. Rev. Palaeobot. Palynol. 19: 291–351.

Behnke, H.-D. 1988. Sieve element plastids and systematic relationships of Rhizophoraceae, Anisophylleaceae, and allied groups. Ann. Missouri Bot. Gard. 75: 1387–1409.

Dahlgren, R.M.T. 1988. Rhizophoraceae and Anisophylleaceae: summary statement, relationships. Ann. Missouri Bot. Gard. 75: 1259–1277.

Ding Hou 1958. Rhizophoraceae. Flora Malesiana I, 5: 429–493.

Floret, J.-J. 1979. A propos du contenu séminal dans les genres *Anisophyllea* et *Poga* (Rhizophoracées-Anisophylloidées). Adansonia II, 19:109–115.

Hegnauer, R. 1973. Chemotaxonomie der Pflanzen. Vol. 6. Basel: Birkhäuser.

Juncosa, A.M., Tomlinson, P.B. 1988a. A historical and taxonomic synopsis of Rhizophoraceae and Anisophylleaceae. Ann. Missouri Bot. Gard. 75: 1278–1295.

Juncosa, A.M., Tomlinson, P.B. 1988b. Systematic comparison and some biological characteristics of Rhizophoraceae and Anisophylleaceae. Ann. Missouri Bot. Gard. 75: 1296–1318.

Keating, R.C., Randrianasolo, V. 1988. Leaf architecture and relationships in the Rhizophoraceae and Anisophylleaceae. Ann. Missouri Bot. Gard. 75: 1343–1368.

Kochummen, K.M. 1989. Rhizophoraceae. In: Ng, F.S.P. (ed.) Tree Flora of Malaya 4: 302–323.

Matthews, M.L., Endress, P.K. 2004. Comparative floral structure and systematics in Cucurbitales (Corynocarpaceae, Coriariaceae, Tetramelaceae, Datiscaceae, Begoniaceae, Cucurbitaceae, Anisophylleaceae). Bot. J. Linn. Soc. 145: 129–185.

Matthews, M.L., Endress,P.K., Schönenberger, J. Friis, E. M. 2001. A comparison of floral structures of Anisophylleaceae and Cunoniaceae and the problem of their systematic position. Ann. Bot. 88: 439–455.

Morley, R.J. 1977. Palynology of Tertiary and Quaternary sediments in southeast Asia. In: Proc. Petroleum Association 6th Annual Convention, pp. 255–276.

Prance, G.T., Freitas da Silva, M., Albuquerque, B.W., de Jesus da Silva Araújo, I., Medeiros Carreira, L.M., Nogueira Braga, M.M. Macedo, M., da Conceição, P. N., Braga Lisbôa, P.L., Braga, P.I., Lobato Lisbôa, R. C., Queiroz Vilhena, R.C. 1975. Revisão taxonômica das espécies amazônicas de Rhizophoraceae. Acta Amazonica 5: 5–22.

Raven, P.H., Tomlinson, P.B. 1988. Rhizophoraceae-Anisophylleaceae: a symposium. Ann. Missouri Bot. Gard. 75:1258.

Ridley, H.N. 1922. Flora of the Malay Peninsula. Vol. 1. London: L. Reeve.

Schimper, A.F.W. 1893. Rhizophoraceae. In: Engler & Prantl, Die natürlichen Pflanzenfamilien III, 7: 42–56. Leipzig: W. Engelmann.

Schwarzbach, A.E., Ricklefs, R.E. 2000. Systematic affinities of Rhizophoraceae and Anisophylleaceae, and intergeneric relationships within Rhizophoraceae, based on chloroplast DNA, nuclear ribosomal DNA, and morphology. Am. J. Bot. 87: 547–564.

Setogushi, H., Kosuge, H., Tobe, H. 1999. Molecular phylogeny of Rhizophoraceae based on *rbc*L gene sequences. J. Plant Res. 112: 443–455.

Takhtajan, A. 2009. Flowering plants. Dordrecht: Springer.

Tobe, H., Raven, P.H. 1987. Systematic embryology of the Anisophylleaceae. Ann. Missouri Bot. Gard. 74: 1–26.

Tobe, H., Raven, P.H. 1988a. Additional notes on the embryology of *Polygonanthus* (Anisophylleaceae) and relationships of the family. Ann. Missouri Bot. Gard. 75: 1425–1428.

Tobe, H., Raven, P.H. 1988b. Floral morphology and evolution in Anisophylleaceae. Bot. J. Linn. Soc. 98: 1–25.

Vaughan, J.G. 1970. The structure and utilization of oil seeds. London: Chapman & Hall.

Vezey, E.L., Shah, V.P., Skvarla, J.J., Raven, P.H. 1988. Morphology and phenetics of Rhizophoraceae pollen. Ann. Missouri Bot. Gard. 75: 1369–1386.

Vincent, J.R., Tomlinson, P.B. 1983. Architecture and phyllotaxis of *Anisophyllea disticha* (Rhizophoraceae). Garden's Bull. (Singapore) 36: 3–18.

Zhang, L.-B., Simmons, M.P., Kocyan, A., Renner, S.S. 2006. Phylogeny of the Cucurbitales based on DNA sequences of nine loci from three genomes: implications for morphological and sexual system evolution. Mol. Phylogen. Evol. 39: 305–322.

Zhang, L.-B., Simmons, M.P., Renner, S.S. 2007. A phylogeny of Anisophylleaceae based on six nuclear and plastid loci: Ancient disjunctions and recent dispersal between South America, Africa, and Asia. Mol. Phylogen. Evol. 44: 1057–1067.