

## DAPHNIPHYLLACEAE

(Tseng-chieng Huang, Taipei)<sup>1</sup>

*Daphniphyllaceae* Müll. Arg. in DC., Prodr. 16 (1869) 1, nom. cons.

One genus only.

### DAPHNIPHYLLUM

*Daphniphyllum* Blume, Bijdr. (1826) 1153; T.C. Huang, Taiwania 11 (1965) 57–98, 12 (1966) 137–234. — Type species: *Daphniphyllum glaucescens* Blume.

*Trees or shrubs*, evergreen, dioecious. *Leaves* simple, alternate, fasciculate, rarely opposite, subverticillate to verticillate, rarely dimorphic, estipulate; blades elliptic, oblong, obovate to ovate, frequently falcate or oblique, rounded, mucronate, acute to acuminate at apex, rounded, obtuse, acute to cuneate at base, margins entire or revolute, infrequently dentate near the apex, chartaceous, membranous to coriaceous, green or yellow on both surfaces, sometimes shining above, usually glaucous and papillate beneath, midrib frequently impressed above, prominent or not so beneath. *Inflorescences* axillary, rarely subterminal, racemiform, axes angulate, terete or flat, sometimes flexuous; pedicels angulate or flat, rarely pendent; bracts at the base of the inflorescences in 1–several whorls, imbricate, ovate, triangular or linear-ovate or elliptic, usually caducous, sometimes larger than the flower. *Flowers* unisexual. *Calyx* none, or when present 3–6-lobed, with imbricate aestivation, campanulate, cupulate or completely divided when mature, lobes variable in size, shape and margin, rarely larger than the androecium or gynoecium, sometimes articulate, caducous or persistent. *Corolla* absent. *Stamens* in staminate flowers 5–14, free or coherent at apex, sessile or with long filaments, anthers lunate, oblong, oblong-elliptic, elliptic, broadly elliptic to ovate, compressed or oblique, apex apiculate, triangular, obtuse to emarginate or beaked; staminodia frequently present, rarely articulate, pistillodes rarely present. *Ovary* in pistillate flowers globose to elliptic-globose, imperfectly 2(–4)-septate; each carpel with (1 or) 2 anatropous ovules; placentation suspended or subapical; staminodia on the ovary usually present; style with 1–2(–4) lobes, usually shorter than the ovary, stigmas divaricate, revolute, discoid to circinnate or versatile. *Drupe*s obovoid, elliptic-globose, ovoid to ellipsoid, apex obtuse, base round to obtuse, rarely suddenly constricted at base, shining, smooth, rugose to tuberculate, staminodia frequently persistent, styles usually persistent. *Seed* 1 (or 2), various in shape and size; germination epigeous; cotyledons two. Chromosome number  $2n = 32$  (Huang 1965). — **Fig. 1–8.**

1) With contributions by: P. Baas, Leiden (vegetative anatomy), R.W.J.M. van der Ham, Leiden (pollen morphology), R. Hegnauer, Leiden (phytochemistry). Drawings are by Mrs. Lih-Chiueh Lu, Huang; they were reproduced with permission from Taiwania vol. 12, 1966.

## DISTRIBUTION

Forming a monotypic family, *Daphniphyllum* consists of about 30 species, distributed from India to Japan and from Central China to New Guinea, with 16 species in the Malesian region. — Fig. 1.

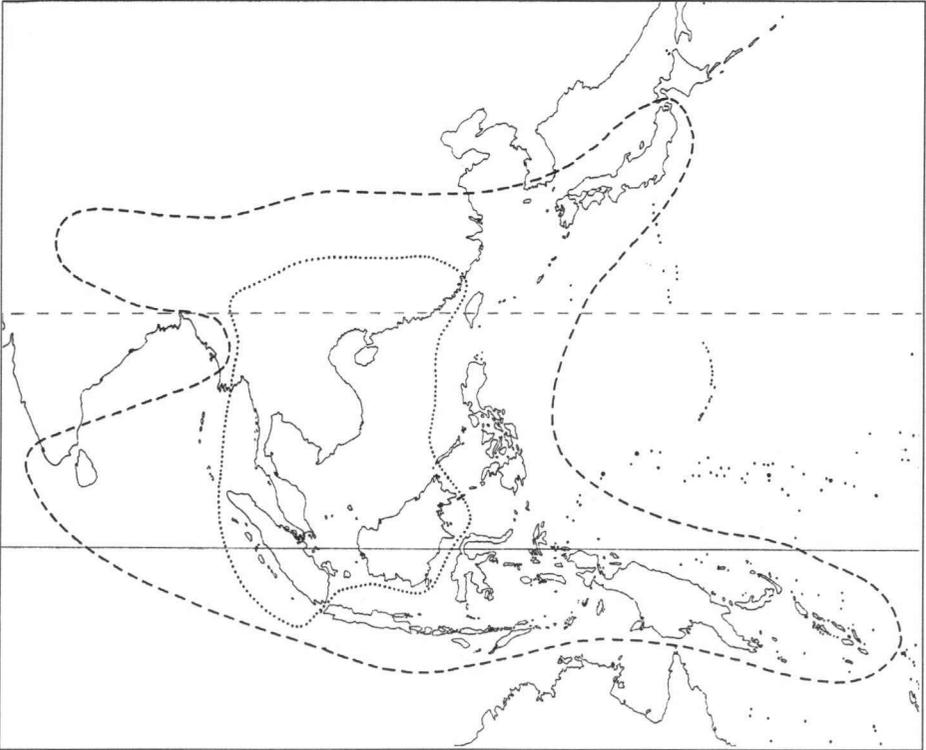


Fig. 1. Distribution map of *Daphniphyllum* and its two sections (----- Section *Daphniphyllum*, ..... Section *Lunata* Huang).

## HABITAT

The plants grow on low hillsides, burnt areas, grasslands or montane forests at altitudes from 300 to 4000 m.

## VEGETATIVE ANATOMY

(P. Baas)

*Leaf anatomy* — The leaf anatomy of *Daphniphyllaceae* has been summarized by Metcalfe & Chalk (1950) and Huang (1965). The lamina is dorsiventral. The stomata are paracytic. Epidermal cells are papillate in some species/specimens, depending on their habitat. A hypodermis (or 2-layered epidermis) occurs in *Daphniphyllum gracile* and *D. himalayense*.

*Wood anatomy* — The wood anatomy has been studied in detail by Carlquist (1982). Gregory (1994) gives a complete bibliography containing 14 more references on *Daphniphyllum* wood structure. The xylem shows many very primitive attributes. Vessels diffuse, solitary, angular in outline, with scalariform perforations with very many (on average 37–96) closely spaced bars. Vessel members are typically long (on average 1000–1890  $\mu\text{m}$ ). Lateral vessel wall pits scalariform or transitional. The fibres have distinctly bordered pits in both radial and tangential walls. Parenchyma is scanty paratracheal and diffuse, in c. 7-celled strands. Rays are mostly 1–3-seriate, and strongly heterocellular. Chambered crystals have been reported for *D. glaucescens* var. *glaucescens* only. The anatomical variation within *Daphniphyllum* is limited and related to elevation and latitude (macroclimate). The suite of characters supports affinities of the family with both *Buxaceae* and *Hamamelidaceae* and their closest allies.

*References:* Carlquist, S., Wood anatomy of Daphniphyllaceae: ecological and phylogenetic considerations, review of pittosporalean families. *Brittonia* 34 (1982) 252–266. — Gregory, M., Bibliography of systematic wood anatomy of dicotyledons. *IAWA J.*, Suppl. 1 (1994). — Huang, T.-C., Monograph of *Daphniphyllum* (1). *Taiwania* no. 11 (special issue) (1965) 57–98. — Metcalfe, C.R. & L. Chalk. *Anatomy of the Dicotyledons* 2 (1950) 1241–1243.

#### POLLEN MORPHOLOGY

(R.W.J.M. van der Ham)

Relatively much has been recorded of the pollen morphology of the *Daphniphyllaceae* and its taxonomic significance. In addition to a number of pollen floras, such as Nakamura (1943), Ikuse (1956), Huang (1967, 1972) and Long (1982), *Daphniphyllum* pollen is treated by Erdtman (1952), Huang (1965), Bhatnagar & Garg (1977), Zavada & Dilcher (1986), Zhang & Lu (1989) and Huang (1996). The last three works mentioned, include scanning electron micrographs, and Zavada & Dilcher (1986) transmission electron micrographs as well.

From the above literature it appears that *Daphniphyllum* is a stenopalynous genus. The tetrad configuration during pollen ontogeny is usually tetrahedral, sometimes isobilateral or decussate. The pollen grains are isopolar 3(–4)-aperturate monads. Grain size is 10–26  $\mu\text{m}$ . Grain shape is oblate to prolate ( $P/E = 0.74\text{--}1.59$ ); the higher  $P/E$  values are possibly due to the easy invagination of the long colpi, which results in small equatorial diameters (see for example Huang 1965). The equatorial outline is circular to obtusely triangular. The aperture system is colpate (endoapertures not discernible), colporoidate (endoapertures indistinct), or rarely colporate (endoapertures distinct). The colpi are narrow to rather wide. Transmission electron micrographs show a 0.5 to 0.9  $\mu\text{m}$  thick tectate-columellate exine, in which the sexine is as thick as or thicker than the nexine. The mesocolpial nexine consists of a thick foot layer and a thin endexine; towards the colpi the latter thickens considerably, while the foot layer thins out. The ornamentation is irregularly perforate to more or less fossulate, showing diversely shaped perforations to elongate sinuous depressions. The colpus membranes are rather densely scabrate.

Huang (1996; see also 1965) distinguished two pollen types in *Daphniphyllum*: one for section *Lunata*, with small perforate pollen grains, and another for section *Daphniphyllum*, with larger fossulate grains.

*Daphniphyllaceae* pollen, being a simple 3-aperturate dicotyledonous pollen type, does not provide the unambiguous clue to the systematic position of the family. Although Erdtman (1952) stated that more or less similar pollen occurs in the *Euphorbiaceae* and that *Hamamelidaceae* pollen is different, several others stressed the dissimilarities comparing with *Euphorbiaceae* pollen, while indicating affinities with the *Hamamelidales* or *Hamamelidaceae* (Huang 1965; Bhatnagar & Garg 1977; Zhang & Lu 1989). Cluster analyses of the *Hamamelidae* by Zavada & Dilcher (1986), exclusively using palynological features, group the *Daphniphyllaceae* together with the *Leitneriaceae*, *Fagaceae* and *Barbeyaceae*. In a cladistic analysis of the pollen morphology by the same authors these families, together with several others, take an intermediate position between the lower and the most derived *Hamamelidae*. They conclude that in order to reach a finer resolution additional non-palynological evidence has to be used.

*References:* Bhatnagar, A.K. & M. Garg, *Phytomorphology* 27 (1977) 92–97. — Erdtman, G., *Pollen morphology and plant taxonomy* (1952). — Huang, T.C., *Taiwania* 11 (1965) 57–98; *Taiwania* 13 (1967) 15–110; *Pollen flora of Taiwan* (1972); *Blumea* 41 (1996) 231–244. — Ikuse, M., *Pollen grains of Japan* (1956). — Long, H., *Daphniphyllaceae*. *Angiosperm pollen flora of tropic and subtropic China* (1982) 115. — Nakamura, J., *Science Rep. Tôhoku Imp. Univ., Biol.* 17 (1943) 491–512. — Zavada, M.S. & D.L. Dilcher, *Ann. Missouri Bot. Gard.* 73 (1986) 348–381. — Zhang, Z.Y. & A.M. Lu, *Acta Phytotax. Sinica* 27 (1989) 17–26.

## PHYTOCHEMISTRY AND CHEMOTAXONOMY

(R. Hegnauer)

This monogeneric family is still a taxon incertae sedis. Bentham & Hooker (according to Radcliffe-Smith 1987) placed *Daphniphyllum* in *Euphorbiaceae-Phyllanthaeae* between *Aporosa* and *Baccaurea*. Müller Argoviensis created a separate family for the genus. *Daphniphyllaceae* subsequently were accepted by most authors, but in recent time taxonomists are inclined to favour relationships of *Daphniphyllaceae* with *Hamamelidaceae* rather than with *Euphorbiaceae* (see, e.g., Mabberley 1987; Sutton 1989).

Chemical investigations of *Daphniphyllum* were started by Greshoff who isolated and described the alkaloid daphniphylline from *D. laurinum* [as *D. bancanum* Kurz] (see Hegnauer 1990). Hitherto three classes of secondary metabolites with some promise for plant classification became known in this genus.

*Alkaloids* — All species investigated contain daphniphylline-like compounds which represent a new type of alkaloids biogenetically derived from the aliphatic triterpene squalene. Daphniphylline itself possesses a polycyclic C<sub>30</sub>-skeleton. Other *Daphniphyllum* alkaloids are basic octa- or nonanortriterpenoids such as daphnilactone-B (C<sub>22</sub>-skeleton) and yuzurine (C<sub>21</sub>-skeleton). A possible biogenetic pathway leading from squalene to protodaphniphylline and daphniphylline was recently proposed (Heathcock et al. 1992). The noralkaloids of *Daphniphyllum* originate by losing eight or nine C-atoms of a terminal geranyl rest not participating in cyclisations.

*Iridoid glucosides* — The biogenetically related secondary metabolites asperulin and daphylloside have been isolated from leaves of *D. macropodum* Miq.; asperulin was also detected in leaves of *D. laurinum*.

*Leaf phenolics* — One isolation of a flavonoid glycoside (rutin) was reported long ago in literature. Moreover, screenings of hydrolyzed leaf extracts yielded paperchromatograms indicating low amounts of the flavonol quercetin and appreciable amounts of the flavones apigenin and luteolin and absence of proanthocyanidins and gallic and ellagic acids, i.e. of both main types of tannins (Hegnauer 1966; Gianassi 1986).

Other chemical characters often useful in classification are:

*Storage products of seeds* — As far as is known, *Daphniphyllum* seeds store much protein and fatty oil, but lack starch.

*Aluminium* — Investigating leaves of nine *Daphniphyllum* species Chenery (1948) detected aluminium accumulation in five of them.

*Chemotaxonomy* — Chemical characters are not yet very helpful in tracing affinities of *Daphniphyllum*. Synthesis and accumulation of asperulin-type iridoids which are probably synthesized along the same pathway as monotropein (Jensen 1991) occurring in *Liquidambar* (*Hamamelidaceae* s.l.) support those taxonomists who stress relationships with *Hamamelidaceae*. Accumulation of aluminium in leaves and the recent isolation (Chenery 1948) of the daphniphylline-type alkaloid (-)-bukittinggine,  $C_{22}H_{31}NO_2$ , from leaves of *Sapium baccatum* growing in West Sumatra accentuate similarities between *Daphniphyllum* and some *Euphorbiaceae*. Last but not least, the seeming absence of tannins from leaves does not favour either of these two suggestions. Huber (1991) interprets *Daphniphyllaceae* as a possible connecting link between *Hamamelidales* and *Cornales* (and possibly *Bicornes* = *Ericales*); perhaps his arguments would be worth a serious study.

*Literature:* Chenery, E.M., Kew Bull. (1948) 173–183, *Daphniphyllum* under *Euphorbiaceae* on p. 180. — Gianassi, D.E., Phytochemical aspects of phylogeny in Hamamelidae. Ann. Missouri Bot. Gard. 73 (1986) 417–437. — Heathcock, C.H., et al., J. Org. Chem. 57 (1992) 2554–2566. — Hegnauer, R., Chemotaxonomie der Pflanzen 4 (1966) 9–11, 445, 501; 8 (1989) 376–379. — Hegnauer, R., in: P. Baas et al. (eds.), The plant diversity in Malesia (1990) 101. — Huber, H., Angiospermen. Leitfaden durch die Ordnungen und Familien der Bedecktsamer (1991) 137. — Jensen, S.R., Plant iridoids, their biosynthesis and distribution in Angiosperms, in: J.B. Harborne & F.A. Tomas-Barberan, Ecological chemistry and biochemistry of plant terpenoids (1991) 133–158. — Mabberley, D.J., The plant-book (1987). — Radcliffe-Smith, A., Segregate families from the Euphorbiaceae, in: S.L. Jury et al. (eds.), The Euphorbiales. Chemistry, taxonomy and economic botany. Bot. J. Linn. Soc. 94, 1 & 2 (1987) 47–66 (*Daphniphyllaceae* p. 49). — Sutton, D.A., The Daphniphyllales: a systematic review, in: P.R. Crane & S. Blackmore (eds.), Evolution, systematics and fossil history of the Hamamelidae, vol. 1. Syst. Assoc. Special Vol. 40A (1989) 285–291.

## TAXONOMY

Monographic study of *Daphniphyllum* was initiated by Müller Argoviensis (1869), and followed by Rosenthal (1916) and by Huang (1965, 1966). Six species were reported in the Malesian regions in my treatment (Huang 1966), and also three sections were pro-

posed: Section *Lunata* T.C. Huang including *D. laurinum* (Benth.) Baill.; Section *Staminodia* Hurus. including *D. parvifolium* Quisumb. & Merr., and Section *Daphniphyllum* including *D. gracile* Gage, *D. glaucescens* Blume, *D. philippinense* T.C. Huang and *D. woodsonianum* T.C. Huang. Since then, no revision nor monographic treatment has been done for the Malesian region.

*Daphniphyllaceae* have been placed in various orders (Huang 1965), such as in *Pittosporales* by Thorne (1976, 1983), *Hamamelidales* (Hutchinson 1973; Takhtajan 1980), and *Balanopales* (*Buxales*) (Dahlgren 1983; Thorne 1992). Sutton (1989) and Zhang & Lu (1989) placed it in *Daphniphyllales* with closest relationship to *Hamamelidales* as suggested by Huang (1965) and Cronquist (1983).

The following list provides a summary of the subdivision of the genus according to Huang (1996), with mention of the Malesian species:

Section 1. *Daphniphyllum*

Subsection 1. *Daphniphyllum*

Series 1. *Daphniphyllum* (*D. borneense*, *ceramense*, *dichotomum*, *glaucescens*, *lancifolium*, *luzonense*, *scortechinii*, *sumatraense*, *timorianum*)

Series 2. *Longicalycifera* T.C. Huang (*D. gracile*, *papuanum*)

Series 3. *Unicalycifera* T.C. Huang (*D. buchananiifolium*, *celebense*, *woodsonianum*)

Subsection 2. *Staminodia* Hurus. (*D. parvifolium*)

Section 2. *Lunata* T.C. Huang (*D. laurinum*)

*References:* Cronquist, A., Some realignments in the Dicotyledons. *Nordic J. Bot.* 3 (1983) 75–83. — Dahlgren, R., General aspects of Angiosperms. Wiley, New York (1983) 65–66, 105, 117–119. — Huang, T.C., Monograph of *Daphniphyllum*, I & II. *Taiwania* 11 (1965) 57–98; 12 (1966) 137–234; Notes on taxonomy and pollen of Malesian *Daphniphyllum*. *Blumea* 41 (1996) 231–244. — Hutchinson, J., The families of flowering plants. 3rd ed, Clarendon Press, Oxford (1983) 229–230. — Müller Argoviensis, J., *Daphniphyllaceae*, in: De Candolle, *Prodromus* 16 (1869) 1–6. — Rosenthal, K., *Daphniphyllaceae*, in: A. Engler, *Pflanzenreich* 68, Fam. IV.147a (1919) 1–15. — Sutton, D.A., The *Daphniphyllales*: A systematic review, in: P.R. Crane & S.S. Blackmore (eds.), *Evolution, systematics and fossil history of the Hamamelidae*, 1 (1989) 285–291. Clarendon Press, Oxford. — Takhtajan, A., Outline of the classification of flowering plants (Magnoliophyta). *Bot. Rev.* 46 (1980) 225–359. — Thorne, R.F., A phylogenetic classification of the Angiospermae. *Evol. Biol.* 9 (1976) 35–106; Proposed new realignments in the Angiosperms. *Nordic J. Bot.* 3 (1983) 85–117; Classification and geography of the flowering plants. *Bot. Rev.* 58 (1992) 225–348. — Zhang, Z.Y. & A.M. Lu, On the systematic position of *Daphniphyllaceae*. *Acta Phytotax. Sin.* 27 (1989) 17–26, pl. 4 (in Chinese, Engl. summary).

KEY TO THE SPECIES

- 1a. Anthers lunate, introrse, coherent at apex, subsessile; calyx persistent, at least on staminate flowers; drupes strongly tuberculate, usually distinctly glaucous . . . . . 9. *D. laurinum*
- b. Anthers usually oblong or elliptic, compressed or oblique, extrorse, completely free, with a usually long filament; calyx usually caducous, at least on drupes or absent; drupes smooth to tuberculate, usually not glaucous . . . . . 2

- 2a. Calyx 4–6-lobed; drupes from lustrous and smooth to verrucose or tuberculate; leaf blades usually papillate, chartaceous to coriaceous, all veins prominent and reticulate above . . . . . 3
- b. Calyx absent or rarely 1- or 2-lobed, linear, affixed to the base of stamens; drupes usually tuberculate; blades usually epapillate, membranous to chartaceous, all veins obscure and delicate or impressed above . . . . . 15
- 3a. Calyx present in both staminate and pistillate flowers . . . . . 4
- b. Calyx present in pistillate flowers only . . . . . 14
- 4a. Calyx articulate, caducous and usually longer than the androecium and gynoecium . . . . . 5
- b. Calyx inarticulate, usually persistent in staminate flowers and shorter than the androecium and gynoecium . . . . . 6
- 5a. Leaves oblanceolate, oblong, oblong-elliptic to elliptic, usually obtuse, mucronate to rounded at apex and glaucous beneath; mature drupes smooth or lustrous at least in dried specimens; usually growing on upper to subalpine mountain forest or grassland margin . . . . . **7. D. gracile**
- b. Leaves lanceolate (narrowly elliptic), acuminate to acute at apex and green beneath; mature drupes tuberculate to verrucose at least in dried specimens, usually growing on lower to middle mountain rain forest . . . . . **11. D. papuanum**
- 6a. Blades narrowly oblong, obovate-oblong, obovate, the apex rounded to mucronate or acute at apex, coriaceous, smooth, glaucous and papillate beneath; veins prominently finely reticulate, usually without elevated lateral veins **13. D. scortechinii**
- b. Blades elliptic to narrowly elliptic, lanceolate to narrowly ovate, usually acute to acuminate or cuspidate at apex . . . . . 7
- 7a. Leaves elliptic to narrowly elliptic, glaucous, papillate; veins prominent with coarsely elevated reticulation; drupes smooth . . . . . 8
- b. Leaves narrowly elliptic to lanceolate; veins not with prominently elevated reticulation . . . . . 9
- 8a. Leaves fleshy, elliptic, base obtuse to cuneate, apex cuspidate to acute to mucronate; drupe stalk 4–10 mm long . . . . . **1. D. borneense**
- b. Leaves narrowly elliptic, base cuneate, apex acuminate; drupe stalk 4–5 mm long . . . . . **5. D. dichotomum**
- 9a. Blades short, less than 6 cm long; drupes smooth; calyx of staminate flower caducous; veins obscure . . . . . **4. D. ceramense**
- b. Blades long, more than 6 cm, shining on both surfaces . . . . . 10
- 10a. Blades with acute-obtuse base . . . . . **15. D. timorianum**
- b. Blades with cuneate base . . . . . 11
- 11a. Fruiting pedicels usually more than 1 cm long; styles usually caducous; leaves ovate-lanceolate . . . . . 12
- b. Fruiting pedicels less than 1 cm long; styles persistent; leaves lanceolate . . . . 13
- 12a. Drupes tuberculate and leaves papillate or drupes smooth and leaves epapillate . . . . . **6. D. glaucescens**
- b. Drupes smooth and leaves papillate . . . . . **10. D. luzonense**

- 13a. Drupes smooth, 4 mm in diameter; leaves papillate, obtuse at base; styles recurved  
 ..... 14. *D. sumatraense*
- b. Drupes rugose, 6–7 mm in diameter; leaves epapillate, acute at base; styles circinnate  
 ..... 8. *D. lancifolium*
- 14a. Leaves petiolate, petioles 2–4 cm long; filaments 0.7–0.8 mm long .....  
 ..... 2. *D. buchananiifolium*
- b. Leaves sessile, petioles 0.2 mm long; filaments 1.2–2.3 mm long .....  
 ..... 16. *D. woodsonianum*
- 15a. Leaves elliptic, both ends acute, 6–6.5 by 2.5–3 cm ..... 3. *D. celebense*
- b. Leaves oblong-obovate, apex mucronate, cuneate at base, 4–9 by 1–2 cm .....  
 ..... 12. *D. parvifolium*

### 1. *Daphniphyllum borneense* Stapf

*Daphniphyllum borneense* Stapf, Trans. Linn. Soc. II, 4 (1894) 224. — *Daphniphyllum glaucescens* Blume subsp. *borneense* (Stapf) T. C. Huang, Taiwania 12 (1966) 192, f. 33; Perumal in Tree Fl. Sabah & Sarawak 2 (1996) 158. — Type: *Haviland 1070* (K holo; BM, K, L, US).

*Shrub* or small *tree*, 2–9 m tall, clear bole 0.9–1 m in diam., crown 1.5 m wide, outer bark smooth, grey, slash outer bark green, inner bark coarse, brown like milk chocolate, sapwood whitish to yellow flush. *Leaves* fascicled at tip of branchlets, opposite; blades narrowly elliptic to elliptic, 5–10 by 2.5–4.2 cm, apex cuspidate, acuminate or mucronate, base cuneate, margins entire, coriaceous, brown above, glaucous beneath, lateral veins reticulate or in 8 pairs, elevated on both surfaces, the reticulation especially prominent on upper surface; petiole red-violet or tinged purple, 1.5–3 cm long. *Staminate inflorescences* 4–5 cm long; flowers purple, glaucous, calyx 5-lobed, stamens 6–8; anther red-violet, elliptic, apiculate, 1.5 mm long, 0.8 mm wide; pedicels 7–9 cm long. *Pistillate inflorescences* 4–5 cm long, female flowers glaucous (green) in bud, 5 calyx lobes free, lanceolate, caducous, ovary with several staminodes, stigmas recurved to circinnate; pedicels 4–5 mm long. *Fruiting axes* 4.5 cm long, drupes ellipsoidal, 10–12 mm long, 5–6 mm wide, green turning to red brown, dull red to blackish purple when ripe, smooth; fruit stalks 0.4–1 cm long.

Distribution — *Malesia*: North Borneo and Kalimantan.

Habitat & Ecology — Growing on flat ridges with low forest; stunted dense upper montane rain forest on granodiorite; on cliff faces; ericoid ridge top vegetation; slopes of mossy forest associated with *Talauma* and *Symplocos*, at altitudes of 1500 to 4000 m.

### 2. *Daphniphyllum buchananiifolium* Hallier f.

*Daphniphyllum buchananiifolium* Hallier f., Meded. Rijks Herb. Leiden 37 (1918) 13. — *Daphniphyllum glaucescens* Blume subsp. *buchananiifolium* (Hallier f.) T. C. Huang, Taiwania 12 (1966) 192, f. 37. — Type: *Elmer 8538* (A holo; BO, E, L, US).

*Daphniphyllum obtusifolium* Merr., Philipp. J. Sc. 16 (1920) 552. — Type: *Ramos & Edaño s.n.*, May 1917 (A holo; BO, E, L, US), syn. nov.

*Daphniphyllum philippinense* T. C. Huang, Ann. Missouri Bot. Gard. 53 (1966) 30, f. 2. — Type: *T. C. Zschakhs 1835* (US holo), syn. nov.

*Shrub or tree*, up to 10–25 m tall. *Leaves* dimorphic, the earlier leaves very large elliptic, apex rounded or mucronulate, base cuneate to obtuse, 12–14 by 5.5–7 cm, purple or reddish tinged, glaucous beneath, with petioles 3.5–8.5 cm long, hard chartaceous, the later leaves narrowly elliptic, obovate or oblanceolate, apex mucronulate, base cuneate, 4.5–9 by 2.5–2.7 cm, margins revolute, coriaceous, dark green above, lighter beneath, but not glaucous shining; lateral veins 7–9 pairs, thin, slightly prominent on both surfaces, the blades of earlier leaves usually 3 times larger than those of later ones; petioles 1–2.5 cm long. *Staminate inflorescences* flat, c. 3 cm long, green, calyx absent or bracteate, the bracts 1 or 2, free, longer than filaments, or 3 or 4 very short in youth from the base of stamens; stamens 5–7(–11), filaments green 0.2–0.4 mm long, anthers oblong or oblong-elliptic, 0.7–0.8 mm long, yellow, apiculate; pedicels 4–7 mm long. *Pistillate inflorescences* 1.5 cm long, sepals numerous, free, elliptic, mixed with many undifferentiated staminodes, green, ovary purple, styles divaricate, as long as ovary, stigmas greenish elliptic-ovoidal, 2 mm long; pedicels 2–4 mm long. *Fruiting axes* angulate, 3–8.5 cm long; calyx caducous, staminodial scars and calyx scars (?) prominent, in 1 or 2 whorls. *Drapes* ellipsoid, elliptic-globose, 10–15 mm long, 6–8 mm in diam., mostly light green, dull violet or black, smooth or verrucose to tuberculate, soft, somewhat juicy with one large seed when ripe, stigmas divaricate; fruit stalks 0.7–1 cm long.

*Distribution* — *Malesia*: Philippines (Luzon, Mindanao, Biliran).

*Habitat & Ecology* — Primary forest of one storey, mossy, bordering open grassland, and on sandy-loamy soil, at altitudes of 2100 to 2800 m.

*Note* — The type specimens of both *D. buchananiifolium* and *D. obtusifolium* have either drupes or immature drupes without male specimens. After closer examination, I emend the staminate flowers, reduce *D. philippinense*, and treat all these as conspecific taxa.

### 3. *Daphniphyllum celebense* K. Rosenthal

*Daphniphyllum celebense* K. Rosenthal in Engl., Pflanzenr. 68 (IV.147a) (1919) 5. — *Daphniphyllum glaucescens* Blume subsp. *celebense* (K. Rosenthal) T. C. Huang, Taiwania 12 (1966) 186. — Type: Warburg 16903 (B, destroyed). Neotype (Huang 1996): Teijsmann 13664 (BO).

*Branches* slender. *Leaves* with petioles 1.5 cm long; blades elliptic, apex and base acute, 6–6.5 by 2.5–3 cm, margins strongly revolute, rough, coriaceous, upper surface shining, beneath papillose, lateral nerves 7–9 pairs. *Male flowers* unknown. *Pistillate inflorescences* racemes, 3.5–4 cm long, calyx obscure, ovary ellipsoid, staminodia 5 or 6, 1–1.5 cm long, lanceolate, acute, stigmas divaricate; pedicels 10–15 mm long. *Fruits* unknown.

*Distribution* — *Malesia*: endemic to Celebes (Sulawesi).

*Habitat & Ecology* — No data available.

*Note* — According to the original description of Rosenthal (1919), this species is related to *D. macropodum* and *D. himalayense* but differs in the size and form of leaves. For this study, the type specimen (Warburg 16903) was not available because it was destroyed during World War II. I consider it an insufficiently known taxon.

#### 4. *Daphniphyllum ceramense* (T. C. Huang) T. C. Huang

*Daphniphyllum ceramense* (T. C. Huang) T. C. Huang, *Blumea* 41 (1996) 237. — *Daphniphyllum glaucescens* Blume subsp. *ceramense* T. C. Huang, *Taiwania* 12 (1966) 190, f. 32. — Type: *Eyma* 2047 (BO holo; K, L).

*Leaves* short, narrowly elliptic, apex cuspidate, base acute-obtuse, 4–6 by 1.8–2.5 cm, coriaceous, shining on both surfaces, lateral veins 6 pairs, reticulation fine. *Staminate inflorescences* 2.5–4 cm long, pedicels angulate, 5–7 mm, calyx lobes 4 or 5, linear-ovate, 4/5 as long as androecium, caducous, articulate, stamens 8 or 9, filaments flat-oblong, 2–4 mm, anthers oblong to oblong-ovate, 1.2–1.6 mm long, apiculate. *Pistillate inflorescences* 2–2.5 cm long, calyx lanceolate, two whorls of several free lobes, ovary blue-green, style branches recurved. *Fruiting axes* 2–3 cm long. *Drupes* smooth, ellipsoidal, green, later black purple, 1.3 cm long, 0.7 cm wide; fruit stalk 5 mm long.

Distribution — *Malesia*: Moluccas (Ceram).

Habitat & Ecology — No data available.

Note — The species is similar to *D. borneense* except for having obscure leaf venation and caducous calyces on staminate flowers. The free, lanceolate, two-whorled calyx lobes are very peculiar.

#### 5. *Daphniphyllum dichotomum* (T. C. Huang) T. C. Huang

*Daphniphyllum dichotomum* (T. C. Huang) T. C. Huang, *Blumea* 41 (1996) 238. — *Daphniphyllum glaucescens* Blume subsp. *dichotomum* T. C. Huang, *Taiwania* 12 (1966) 190, f. 31; *Perumal in Tree Fl. Sabah & Sarwak* 2 (1996) 158. — Type: *Clemens s.n. & Suppl.* (US lecto; A, BO, L, NY, UC).

*Daphniphyllum reticulatum* H. Heine, *Feddes Rep.* 54 (1951) 232, nom. illeg., non Keng (1951).

*Shrub* or small *tree*, 7.5 m high, 60 cm in diam., bark smooth, grey, inner bark yellowish, sapwood white yellowish. *Leaves* narrowly elliptic, apex acuminate, base cuneate, 7–10 by 2.2–2.9 cm, coriaceous, green on both surfaces, veins delicately reticulate and prominent on both surfaces, with 4 or 5 pairs of obscure lateral veins; petioles 0.8–2 cm long. *Staminate inflorescences* unknown. *Pistillate inflorescences* 2.5 cm long; calyx 4- or 5-lobed, lobes triangular, caducous, styles recurved or circinnate; pedicels c. 2 mm long. *Fruiting axes* 2.5–4.5 cm long, 1 mm thick. *Drupes* ovoidal, 7 mm long, 6 mm thick without calyx, green and red brown when ripe; fruit stalks 4–5 mm long, 1 mm thick.

Distribution — *Malesia*: Borneo (Sabah).

Habitat & Ecology — Primary forest on limestone cliff and boulders of organic soil at an altitude of 960 m.

Note — This species differs from *D. borneense* mainly by its narrowly elliptic leaves and its occurrence at low elevation. It is closely allied to *D. sumatraense*.

#### 6. *Daphniphyllum glaucescens* Blume

*Daphniphyllum glaucescens* Blume, *Bijdr.* (1826) 1153; Müll. Arg. in DC., *Prodr.* 16 (1869) 3, p. p.; T. C. Huang, *Taiwania* 12 (1966) 163, f. 23, p. p. — Type: *Blume* 1908 (L holo; L, NY, US).



Fig. 2. *Daphniphyllum glaucescens* Blume var. *blumeanum* (Baill. ex Müll. Arg.) J.J. Sm. a. Twig with fruits; b. ovary with longitudinal section, fruit with longitudinal section, and seed; c. staminate flower, stamen and anther in cross section (a, b: *Blume s. n.*; c: *Elbert 2740*). — *D. glaucescens* Blume var. *glaucescens*. d. Ovary, longitudinal and cross section; e. staminate flower, stamen and anther in cross section (d: *Hasan 1*; e: *Blume 1908*).

## KEY TO THE VARIETIES

- 1a. Drupes tuberculate; leaves papillate ..... **a. var. glaucescens**  
 b. Drupes smooth; leaves epapillate ..... **b. var. blumeinum**

**a. var. glaucescens**

*Trees*, 6–18 m high, 25 cm in diam., crown flattish, outer bark smooth, brown to brownish grey, inner bark dull brown, cream outwards, sapwood brownish white, slash wood hard, cream-yellow. *Leaves* fasciculate; blades lanceolate to narrowly elliptic, apex acuminate to cuspidate, base cuneate, margins slightly revolute, 8–16 by 3–5 cm, firmly chartaceous, darkish green above, greyish brown, glaucous beneath, lateral veins 7–12 pairs; petioles narrowly triangular in section, sulcate above, 1–4.5 cm long, reddish. *Staminate inflorescences* slender, flat, 3–6 cm long; bract caducous; calyx campanulate, 4 or 5 lobes varying as to serration, size and shape; stamens 8–10, filaments oblong, 0.2–0.6 mm long, anthers usually obliquely-lunate, oblong or small broadly elliptic, 0.6–1.5 mm long, strongly apiculate; pedicels 1.5 mm long. *Pistillate inflorescences* angulate, 4–5 cm long; female flowers green; calyx usually caducous; styles recurved or circinnate, as long as the ovary; pedicels terete, 6–10 mm long. *Fruiting axes* angulate, 3.5–6 cm long; bracts caducous. *Drupes* ellipsoid to ovoid, 6–14 mm long, 5–7 mm in diam., apex acute to round, base acute to ovate, tuberculate, green, ripening purple-green with black stigma; styles usually caducous or circinnate; fruit stalks 5–16 mm long. — **Fig. 2d, e.**

Distribution — *Malesia*: Peninsular Malaysia (Perak), Java, Celebes.

Habitat & Ecology — Collected in upper montane forest, at altitudes from 1300 to 2600 m in Java and 1200 to 1700 m in Malaysia.

**b. var. blumeinum** (Baill. ex Müll. Arg.) J.J. Sm.

*Daphniphyllum glaucescens* Blume var. *blumeinum* (Baill. ex Müll. Arg.) J.J. Sm. in Koord. & Valetton, Bijdr. Booms. Java 12 (1910) 328. — *Daphniphyllum blumeinum* Baill. ex Müll. Arg. in DC., Prodr. 16 (1869) 3; T.C. Huang, *Taiwania* 12 (1966) 166, f. 23. — Type: *Zollinger 2140* (P holo). *Daphniphyllum acutifolium* Müll. Arg. in DC., Prodr. 16 (1869) 5. — Type: *Blume s.n.* (L holo). *Daphniphyllum zollingeri* Müll. Arg. in DC., Prodr. 16 (1869) 2. — Type: *Zollinger s.n.* (BO, L, P).

This variety differs from the typical variety only by its shining leaf surfaces and the smooth drupes. — **Fig. 2a–c.**

Distribution — *Malesia*: Peninsular Malaysia (Perak), Java, Lesser Sunda Islands (Bali, Lombok), Celebes.

Habitat & Ecology — Collected at altitudes of 1300 to 1700 m.

**7. *Daphniphyllum gracile* Gage**

*Daphniphyllum gracile* Gage, *Nova Guinea* 12 (1917) 480; T.C. Huang, *Taiwania* 12 (1966) 155, f. 22; Barker in *Handb. Fl. Papua New Guinea* 2 (1981) 34. — Type: *Pulle 2439* (L lecto; BO).



Fig. 3. *Daphniphyllum gracile* Gage var. *gracile*. a. Twig with pistillate flowers; b. ovary showing a staminodium and calyx scars, with longitudinal and cross section; c. fruit with longitudinal section and seed; d. fruit; e. staminate flower, stamen, and anther in cross section; f. staminate flowers with pistilodes (a: *Pulle* 2439; b, c: *Hoogland & Pullen* 5730; d: *Brass* 12632; e: *Robbins* 425; f: *Darby* 354). — *D. papuanum* Hallier f. var. *tuberculatum* (T. C. Huang) T. C. Huang. g. Fruit (*Robbins* 880).

## KEY TO THE VARIETIES

- 1a. Leaves thick, coriaceous ..... **a. var. gracile**  
 b. Leaves thin, semi-coriaceous ..... **b. var. newirelandum**

**a. var. gracile**

Small slender *trees* or *shrubs* of lower storey or becoming part of canopy, up to 22 m high, bole up to 45 cm in diam. Bark grey or grey-brown with vertical fissures, sub-smooth, greenish, white laterally on lenticellate ridges, blaze pale greenish white, brown or dark pustular and horizontally ridged, undersurface orange green, middle bark green and red, inner bark light brown, straw brown, white or pinkish, cream, light orange-brown and red mottled, slash 5 mm thick, underbark orange, brownish green to reddish brown with light green to white lines; wood white, very light brownish white or straw-coloured with very fine rays of yellow, red below, moderately hard to soft. *Leaves* alternate to fasciculate; blades from elliptic, narrowly elliptic to obovate, sometimes slightly oblique, 4–20 by 1.2–7.5 cm, apex mucronulate to mucronate, sometimes cuspidate, base cuneate to obtuse, margins revolute, firmly chartaceous or subcoriaceous, shining brown or green on both surfaces, papillate and frequently glaucous beneath or purplish green or light green tinged with purple in young leaves, dark yellow-green, or olive green in old leaves, lateral veins 7–14 pairs, impressed above, slightly ascending below, dark reddish purple or red on the lower side of midrib; petiole triangular, sulcate above, articulate, red, whitish grey or silvery, 1–15 cm long. *Staminate inflorescences* 3–7 cm long, calyx 4–6-lobed, lobes narrowly elliptic, free, entire or with serrulate apex, 1.5 mm long, longer than androecium, caducous, articulate, greenish, purple, dark purplish red, brown, or closed stamens reddish purple, open ones dark brown, stamens 5–8, anthers purple, purplish blue, pruinose, violet-purple in bud, filaments oblong, 0.2–1 mm long; pedicels terete, 2–12 cm long. *Pistillate inflorescences* flat, 3–5 cm long, 0.8 mm wide, bluish-purple flower buds subtended by pale green bracts; calyx 4–6-lobed, linear to elliptic, 1–6 mm long, longer than gynoecium, caducous, articulate (called glands by Gage), greenish purple, greenish cream, ovary bluish green or greyish purple, staminodia green, tinged with violet-purple in bud, styles divaricate, stigmas recurved, dark or red; pedicels flat, 2–12 cm long, green; bracts narrowly elliptic, 3 mm long, partially persistent. *Fruiting axes* angulate, 2–8.5 cm long, red; calyx caducous. *Drupes* lustrous, ovoid or elliptic globose, 5–11 mm in diam., rounded on both ends, young drupes glaucous, green, olive green or yellow green turning purple, red, dark purple blue, reddish purple, brown or black at maturity; style divaricate, staminodial scars persistent; fruit stalks angulate, 4–15 mm long, 1 mm wide. — **Fig. 3a–f, 4, 5.**

Distribution — *Malesia*: Celebes (rare), New Guinea.

Habitat & Ecology — In montane and subalpine forest, shrubland and grassland, at altitudes between 1300 and 3300 m. Frequently associated with *Nothofagus* and *Phyllocladus* in ridge forest, *Nothofagus*–*Castanopsis* forest on old, well-drained volcanic soil; *Papuacedrus* and *Olearis* in grassland, or *Xanthomyrtus*, *Papuacedrus*, *Quintinia*, *Ericaceae* in alpine shrubland.



Fig. 4. *Daphniphyllum gracile* Gage. Top of twig with staminate inflorescences (van Royen 11086). Mt Amungurwa, Papua New Guinea, c. 3000 m altitude. Photo P. van Royen, 13 June 1976.



Fig. 5. *Daphniphyllum gracile* Gage. Pistillate inflorescences (van Royen 10911). Track from Iswan swamp to Rock Pile, Papua New Guinea, 3200 m altitude. Photo P. van Royen, 21 May 1976.

Note — The collection of *Streimann & students 27812* possesses two kinds of leaves which are very important characters to distinguish plants of *D. gracile* and *D. papuanum*. The young leaves in the female vegetative branches bear oblanceolate leaves with acute or cuspidate apex but leaves on the fruiting branches bear lanceolate leaves with acuminate apex and smooth drupes. The young leaves agree with those of var. *gracile* and the old leaves and mature drupes agree with those of *D. papuanum* var. *tuberculatum*. Possibly they are ecotypes.

**b. var. newirelandum** T.C. Huang

*Daphniphyllum gracile* Gage var. *newirelandum* T.C. Huang, *Blumea* 41 (1996) 239, f. 2. — Type: *Gideon s.n.* (CANB holo).

*Shrubs*, c. 3 m high, with a round crown. *Leaves* oblong-elliptic, apex obtuse, cuspidate or mucronate, base obtuse, 6.5–10 by 2.5–4 cm, margins revolute, semi-coriaceous, lateral veins 7 pairs, membranous. *Flowers* unknown. *Fruiting axes* 2.5 cm long, calyx narrow, caducous, styles short, divaricate, caducous. *Drupes* green, ellipsoidal, 8–10 mm long, 7–8 mm in diam., smooth to verrucose.

*Distribution* — *Malesia*: Bismarck Archipelago, New Ireland, endemic. Two specimens known, both from subprov. Konos.

*Habitat & Ecology* — Collected on top of a small hill dominated by *Gleichenia* which is continuously burnt, at an altitude of 980 m.

**8. *Daphniphyllum lancifolium* Hook. f.**

*Daphniphyllum lancifolium* Hook. f., *Fl. Brit. India* 5 (1887) 354. — *Daphniphyllum glaucescens* Blume subsp. *lancifolium* (Hook. f.) T.C. Huang, *Taiwania* 12 (1966) 165, f. 30. — Type: *King's Coll. 7007* (K holo; BM, L).

*Trees*, 12–18 m high. *Leaves* narrowly angular, ovate, apex acuminate, base cuneate, 12–13.5 by 3.5–4 cm, margins slightly revolute, coriaceous, lateral veins delicate, c. 10 pairs, elevated on both surfaces, reticulation obscure; petioles 3.5 cm long. *Flowers* unknown. *Fruiting axes* 7 cm long. *Drupes* ellipsoidal, 1 cm long, 8 mm in diam., rugose to tuberculate, styles circinnate, caducous, calyx caducous, fruit stalks 5 mm long.

*Distribution* — *Malesia*: Malay Peninsula, only known from type specimen, collected in Perak, Gunong Ejong.

*Habitat & Ecology* — Under dense pine forest, at unknown altitude.

Note — This species differs from *D. glaucescens* by its shorter fruit stalks. It also can be distinguished from *D. dichotomum* by its larger tuberculate drupes.

Fig. 6. *Daphniphyllum laurinum* (Benth.) Baill. a. Twig with fruits; b. ovary, longitudinal and cross sections, and calyx; c. fruit and longitudinal section, and seed; d. tricarpellate fruit, cross section and top view; e. bicarpellate fruit with a staminodium and top view; f. staminate flower and a second staminate flower with a pistillode; g. stamen, anther in cross section and staminate calyx (a, c, g: *Wallich 1836*; b: *Hervey s.n.*; d: *Clemens 30674*; e: *Scortechini s.n.*; f: *Wallich 1836* and *Creagh s.n.*).



### 9. *Daphniphyllum laurinum* (Benth.) Baill.

*Daphniphyllum laurinum* (Benth.) Baill., *Etud. Gen. Euph.* (1858) 565, t. 21; T.C. Huang, *Taiwania* 12 (1966) 139, f. 13. — *Goughia laurina* Benth. in Hook., *Kew J.* 6 (1854) 9. — Type: *Wallich 1836* (K lecto; BM, E, K).

*Daphniphyllum bancanum* Kurz in Teijsm. & Binn., *Pl. Nov. Hort. Bogor. Cult., Nat. Tijds. Ned. Ind.* 27 (1864) 51. — Type: *Teijsmann s.n.* (BO, US).

*Shrubs* or small *trees*, up to 21 m high, 30 cm in diam., outer bark smooth or lenticellate, red or red-grey, inner bark red or yellow, fibrous, soft, cambium white. *Leaves* alternate or fasciculate; blades large, narrowly elliptic to lanceolate, apex acuminate or falcate, base cuneate or obtuse, 11–37 by 3.5–13 cm, margins remotely undulate, firmly chartaceous, brown on both surfaces, sometimes papillate and glaucous beneath, lateral veins 10–12 pairs, obscure, midrib triangular, impressed above; petioles terete or triangular, 3–21 cm long. *Staminate inflorescences* terete, 1–9 cm long, 0.5 mm wide; flowers cream-coloured, white or whitish green, 1–1.5(–2.5) mm long, calyx 3- or 4- (or 7–10-)lobed, united basally, lobes broadly triangular, unequal, serrate, usually half as long as stamens, stamens 8 or 9, the filaments broadly oblong, 0.4 mm long, anthers lunate, non-beaked, 0.3 mm long, rarely pistillodes present; pedicels terete, 5–20 mm long, pinkish; bracts caducous. *Pistillate inflorescences* terete, finely grooved, 2–4.5 cm long, calyx discoid or campanulate, 4- or 5-lobed, lobes triangular, unequal, reflexed, united at base, greenish, persistent; pedicels 0.7–1.6 cm long. *Fruiting axes* 2–8.5 cm long, 1 mm wide. *Drupes* elliptic-obovoid, elliptic-globose, or obovoid, 0.7–1.2 cm long, 5–7 mm in diameter, faintly glaucous, pale green, green, or white when young, brown when ripe, tuberculate, styles very short, divaricate, staminodia rarely present, calyx persistent; fruit stalk 0.4–1.6 cm long. — **Fig. 6.**

**Distribution** — *Malesia*: widely distributed in Peninsular Malaysia and Borneo, also in Sumatra and Bangka, cultivated in Java, derived from specimens in the Botanic Garden, Bogor.

**Habitat & Ecology** — It has been collected on low undulating hillsides, on the summit of limestone hills with exposed porphyritic rocks; in secondary forest; in high jungle crests at altitudes of 500–900 m; on alluvial riverbanks; on flat land, and in mixed lowland forests.

**Uses** — A decoction of the roots is used in Bangka (Indonesia) as a medicine against diarrhoea and thrush.

**Note** — Two different types of leaves are observed on different specimens; one is lanceolate with a obtuse or cordate base and the other is narrowly elliptic with a cuneate base.

### 10. *Daphniphyllum luzonense* Elmer

*Daphniphyllum luzonense* Elmer, *Leafl. Philipp. Bot.* 1 (1908) 309, excl. specim. *Elmer 8538* (= *D. buchananiifolium*). — *Daphniphyllum glaucescens* Blume subsp. *luzonense* (Elmer) T.C. Huang, *Taiwania* 12 (1966) 188, f. 35. — Type: *Elmer 8615* (L neo; A, BO, E, K, MO, NY).

Small *trees*, 10 m high, 15 cm in diam., twigs smooth, lenticels light brown. *Leaves* narrowly elliptic to narrowly oblong, apex acuminate, base obtuse, 12–15 by 3.8–5 cm,

the margins undulate, shining, thin submembranaceous; veins 5–8 pairs, prominent, ascending above; stipules caducous, glaucous, sharply acuminate, papillate below; petioles reddish, 2.5–5 cm long. *Staminate inflorescences* unknown. *Pistillate inflorescences* axillary, racemose, 3.5–10 cm long; pistillate flowers sessile, subtended by 4 bracts, ovary ovoid or ellipsoid, glaucous, smooth, styles short, glaucous, stigmas circinnately 2-lobed. *Fruiting axes* 6–7 cm long (?). *Drapes* ellipsoid, 9–15 mm long; pedicels umbellately clustered at apex, 1–1.5 cm long, glabrous, subtended by minute caducous bracts.

Distribution — *Malesia*: Philippines (Biliran, Luzon, Mindoro, Mindanao, Palawan).

Habitat & Ecology — On forested slopes at an altitude of about 1500 m.

Uses — It is used for curing poisoned persons by eating bark and fruit to enhance vomiting. A decoction of drupes and leaves is used to treat stomach aches and also as a poison antidote. Wood used for fuel and construction.

### 11. *Daphniphyllum papuanum* Hallier f.

*Daphniphyllum papuanum* Hallier f., Meded. Rijks Herb. Leiden 37 (1910) 13. — Type: *W.A. Sayer 1887* (L holo).

#### KEY TO THE VARIETIES

- 1a. Drupes smooth to verrucose . . . . . **a. var. papuanum**  
 b. Drupes tuberculate . . . . . **b. var. tuberculatum**

#### **a. var. papuanum**

Slender understorey *tree*, 4–25 m high, 20–30 cm in diam., outer bark grey-brown, quite smooth, inner bark straw-coloured, flecked with brown; branches thick, lenticels elliptic. *Leaves* fascicled at the tip of branches; blades lanceolate, acuminate at apex, the acumen 5–15 mm long, cuneate at base, 12.5–20 by 3.5–7.5 cm, bright brown on both surfaces, lateral nerves 12–14 pairs, prominent on both surfaces, ascending above, subtrinnerved at base; petioles 4–5 cm long, black. *Staminate flowers* not seen. *Pistillate inflorescences* 6 cm long; calyx caducous; stigmas circinnate; pedicels 9–13 mm long. *Fruiting axes* solitary, axillary, racemose, c. 10 cm long; calyx obscure. *Drapes* more or less ellipsoid, dark brown, nearly verrucose, c. 1 cm long, 7 mm wide; stigmas 2, persistent, recurved, terminal, subsessile; fruit stalks 7–12 mm long.

Distribution — *Malesia*: widely distributed in New Guinea.

Habitat & Ecology — In *Nothofagus*–*Castanopsis* or *Agathis* forests in upper mid-mountain rain forest, at altitudes of 850 to 1860 m.

#### **b. var. tuberculatum** (T. C. Huang) T. C. Huang

*Daphniphyllum papuanum* Hallier f. var. *tuberculatum* (T. C. Huang) T. C. Huang, Blumea 41 (1996) 240. — *Daphniphyllum gracile* Gage var. *tuberculatum* T. C. Huang, Taiwania 12 (1966) 159, f. 22E; Barker in Henty, Handb. Fl. Papua New Guinea 2 (1981) 37, excl. specim. *W.A. Sayer 1887*. — Type: *Brass 13705* (A holo; BO, L).

*Shrubs* or small *trees* in understorey, 3–15 m high, 2–24 cm diam., outer bark grey or brown, large pustular, brown green, scrape green, inner bark light brown, yellow, blaze amber yellow, sap staining wood yellow, wood cream, white or straw-coloured, yellow, buds green. *Leaves* oblanceolate to lanceolate, 5–20 by 3–7.5 cm, apex acuminate, base cuneate, margins entire, hard chartaceous, lateral veins elevated above, 9–14 pairs, not glaucous, innovations light shining green above, adult leaves green, glaucous or not beneath; petiole red, 1.3–5 cm long, 0.6–1 mm wide. *Staminate inflorescences* 4–5.5 cm long, calyx caducous, stamens 8–10, anthers elliptic, apiculate, 1 mm long, 0.6 mm wide; pedicels 6–12 mm long. *Pistillate flowers* with bluish pruinose ovaries, stigmas bi-recurved, sessile, purplish red, centre brown-black. *Fruiting axes* 3–4.5 cm long, 0.8 mm wide. *Drupes* oblique ovoid to ovoid-ellipsoidal, on a pendant axis, often numerous, green then dark brown, black, tuberculate or verrucose, 7–10 mm long, 7–9 mm wide; pedicels 6–8 mm long; fruit stalks 5–12 mm long. — **Fig. 3g.**

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Primary and secondary forest, at altitudes between 900 and 2660 m; frequently associated with *Castanopsis* or *Nothofagus*.

Notes — 1. The two varieties differ only by the surface of the drupes.

2. This species is similar to *Daphniphyllum glaucescens* and differs only by its caducous calyx.

## 12. *Daphniphyllum parvifolium* Quisumb. & Merr.

*Daphniphyllum parvifolium* Quisumb. & Merr., Philipp. J. Sc. 37 (1928) 161; T.C. Huang, Taiwania 12 (1966) 20, f. 40. — Type: *Ramos & Edaño 45708* (A holo; BM, NY, US).

*Shrubs*, 1–2 m high. *Leaves* small, fasciculate; blades narrowly oblong-obovate, apex rounded or mucronate, base cuneate, 4–9 by 1–2 cm, margins revolute, coriaceous, yellowish green above, brown and papillate beneath, lateral veins 6–9 pairs, impressed above, prominent beneath; petioles triangular, sulcate above, 7–25 cm long. *Staminate inflorescences* 1–2.5 cm long, flat, slightly flexuous, slender, 0.5 mm wide, calyx absent or 2-lobed, lobes short triangular, entire, free, stamens 5–10, filaments oblong, 0.4–0.6 mm long, 0.2 mm wide, anthers usually oblong to broadly elliptic, apiculate to obtuse at apex, 0.5–0.9 mm long, 0.3–0.5 mm wide, staminodia (called glands by Hayata) present, bracts broadly ovate, entire, longer than immature flowers, caducous; pedicels flat, 4–8 mm long, 0.2 mm wide. *Pistillate inflorescences* unknown. *Fruiting axes* terete, 2–6 cm long, 1 mm wide, calyx absent. *Drupes* oblong-ellipsoid, obtuse on both ends, 9–12 mm long, 4–5 mm in diam., smooth, obscurely wrinkled, black, styles divaricate or discoid, staminodia scars persistent; fruit stalk quadrangular, 3–7 mm long, 1 mm wide, bracts caducous. *Seed* elliptic globose, smooth, 8 mm long, 4 mm in diameter.

Distribution — *Malesia*: Philippines (Luzon).

Habitat & Ecology — Montane, on slopes and in mossy forest; 1800 m altitude.

Note — The species is characterized by its small, oblong-obovate leaves. It is similar to *D. buchananiiifolium*, but differs by the narrower blades.

**13. *Daphniphyllum scortechinii* Hook. f.**

*Daphniphyllum scortechinii* Hook. f., Fl. Brit. India 5 (1887) 354. — *Daphniphyllum glaucescens* Blume subsp. *scortechinii* (Hook. f.) T.C. Huang, Taiwania 12 (1966) 195, f. 35. — Type: *Scortechini s. n.* (K holo; BM, BO, L).

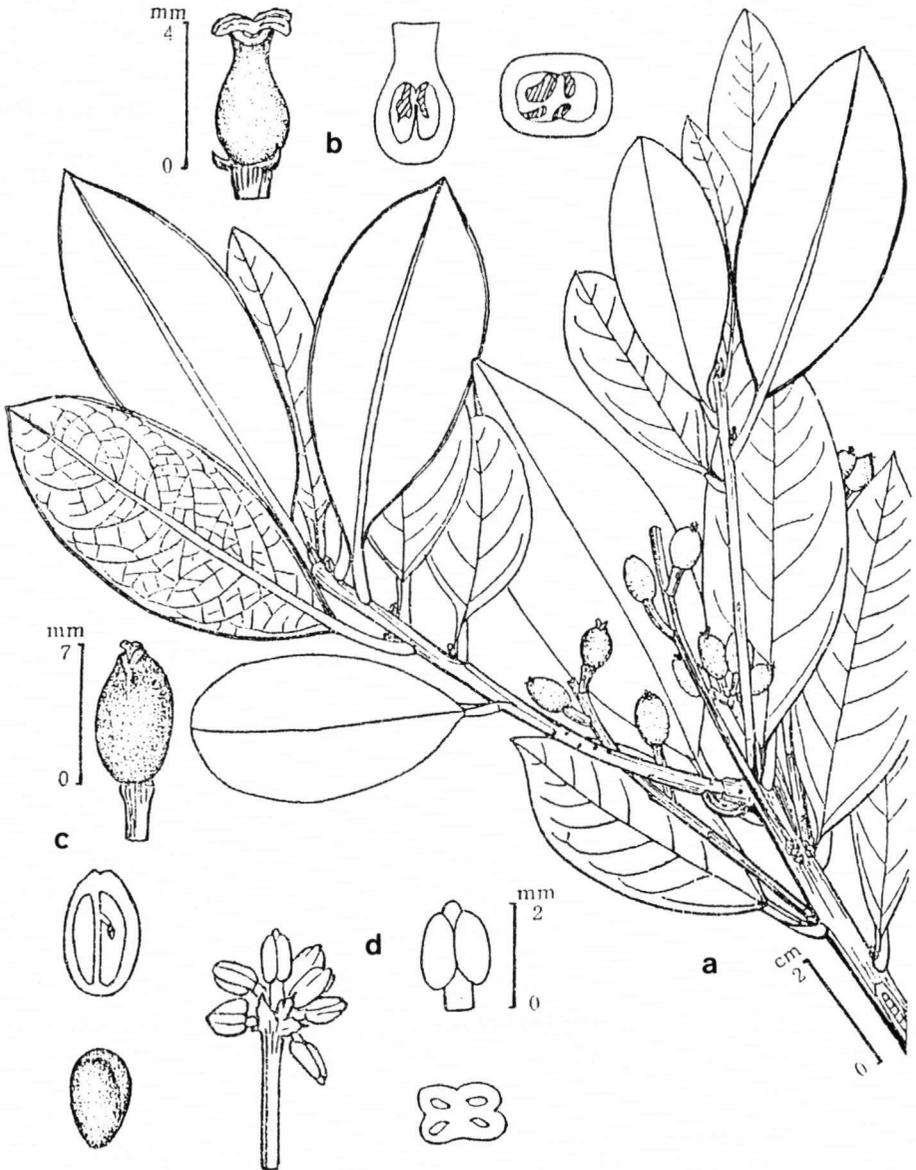


Fig. 7. *Daphniphyllum scortechinii* Hook. f. a. Twig with fruits; b. ovary, longitudinal and cross sections; c. fruit, longitudinal section, and seed; d. staminate flower, stamen and anther in cross section (a: *Scortechini s. n.*; b: *King's Coll. 1347*; c: *King's Coll. 830*; d: *Robinson s. n.*).

Tiny tree, 2.5–6 m high. *Leaves* elliptic to obovate, apex mucronate, base obtuse, 5–6 by 3–4 cm, margins revolute, the reticulation very fine. *Staminate inflorescences* unknown. *Pistillate inflorescences* 2 cm long; flowers green in bud, calyx deeply 4- or 5-lobed, ovate, caducous, styles recurved, as long as ovary, pistillodes 1 or 2 in pistillate flowers; pedicels 4–6 mm long. *Fruiting axes* 3–6 cm long, 1 mm thick. *Drupes* ovoid, smooth, 7–8 mm long, 5–6 mm diam., green at youth, blue colour, without calyx; fruit stalks 5 mm long. — **Fig. 7.**

Distribution — *Malesia*: Peninsular Malaysia (Perak).

Habitat & Ecology — In stunted dense upper montane rain forest at altitudes of 1500 to 1900 m.

Note — The small and fine reticulation of this species can distinguish it from the closely related species *D. borneense*. The species differs from *D. neilgherrense* (Wight) K. Rosenthal by development of the style only; and from *D. gracile* by the latter's cuspidate apex of the leaves.

#### 14. *Daphniphyllum sumatraense* (T.C. Huang) T.C. Huang

*Daphniphyllum sumatraense* (T.C. Huang) T.C. Huang, Blumea 41 (1996) 241. — *Daphniphyllum glaucescens* Blume subsp. *sumatraense* T.C. Huang, Taiwania 12 (1966) 166, f. 24. — Type: *Meijer 7199* (L. holo.; CANB).

Small tree, 2–4 m high, branchlets terete, canaliculate. *Leaves* alternate-fasciculate; blades lanceolate to narrowly elliptic, slightly falcate, apex acuminate, base cuneate, 5–10 by 2–4 cm, chartaceous, green above, glaucous and papillose beneath, veins 7–10 pairs, very thin, obscurely protruding on both surfaces, midrib slightly ascending beneath; petioles semi-terete, 1.5–2.5 cm long. *Staminate inflorescences* flat, 1.5–4.5 cm long, calyx shallowly campanulate, 4- or 5-lobed, lobes short, broadly triangular, acute at apex, margins entire or serrulate, c. 0.2 mm long, 0.4 mm wide; stamens 7–10, subsessile, filaments oblong, 0.1 mm long, apiculate or mucronate at apex, dorsally compressed; pedicels flat, 2–4 mm long. *Pistillate inflorescences* angulate, 2–4 cm long, calyx 4- to many-lobed, ovate or oblong, subentire, acute or irregularly divided at apex, c. 0.2 mm long, reticulate, caducous, ovary elliptic-globose, styles nearly as long as ovary, stigmas radiate-revolute; pedicels terete, 1–2 mm long. *Fruiting axes* angulate, 1.5–3.5 cm long. *Drupes* obliquely obovoid, acute at apex, 7 mm long, 4 mm in diam., black, tuberculate, staminodia present; fruit stalks 1–3 mm long.

Distribution — *Malesia*: Sumatra.

Habitat & Ecology — Secondary forests at altitudes from 500 to 1000 m.

Note — The species differs from *D. glaucescens* and *D. luzonense* by shorter fruiting pedicels, and from *D. lancifolium* by the small, smooth drupes.

#### 15. *Daphniphyllum timorianum* (T.C. Huang) T.C. Huang

*Daphniphyllum timorianum* (T.C. Huang) T.C. Huang, Blumea 41 (1996) 242. — *Daphniphyllum glaucescens* Blume subsp. *timorianum* T.C. Huang, Taiwania 12 (1966) 192. — Type: *Schmutz 2982* (L. holo.).

*Daphniphyllum gracile* auct. non Gage: K. Rosenthal in Engl., Pflanzenr. 68 (IV.147a) (1919) 1–16.

Small *tree*, 6–15 m tall, 5–20 cm diam., the outer bark smooth, light brown, 5 mm thick, living bark 3 mm thick, light brown. *Leaves* fascicled at tip of branchlets; blades elliptic, narrowly elliptic to oblong-elliptic, acute, acute-acuminate to cuspidate at apex, acute to obtuse at base, 5–15.5 by 2–4.5 cm, entire, green, thick-membranous, shining on both surfaces, lateral veins 6–8 pairs, veinlets reticulate, prominent on both surfaces; petioles 1.2–3 cm long, 1 mm thick. *Staminate inflorescences* racemes 2–3 cm long; male flowers reddish or pale green, calyx 4- or 5-lobed, triangular, persistent, stamens 5–10, anthers oblong, elliptic, 1–1.5 mm long, 0.8–1 mm thick, apiculate to cuspidate at apex; pedicels 3 mm long. *Pistillate inflorescences* 1–2 cm long, calyx of the female flower deeply 5-lobed, staminodes present, styles circinnate or divaricate, as long as or longer than ovary; pedicels 10–15 mm long. *Fruiting axes* 2–5 cm long. *Drapes* ellipsoid, smooth to rugose, 8–12 mm long, 6–8 mm diam., calyx caducous on drupe, fruit stalks 0.5–1.8 cm long.

Distribution — *Malesia*: Lesser Sunda Islands (Flores, Timor).

Habitat & Ecology — Mountain areas at altitudes of 1100 to 1800 m.

Notes — 1. *Daphniphyllum* plants of higher elevations such as 1700–1800 m possess smaller oblong-elliptic blades and smooth drupes while those of lower elevations such as 1100–1675 m appear to have long oblong-elliptic blades and tuberculate drupes. All of them have thick membranous blades with more or less prominent reticulate venation on both surfaces.

2. This species is similar to *D. glaucescens* var. *blumeanum*, except for the somewhat longer shape of the blades.

## 16. *Daphniphyllum woodsonianum* T.C. Huang

*Daphniphyllum woodsonianum* T.C. Huang, Ann. Missouri Bot. Gard. 53 (1966) 28, f. 1; Taiwania 12 (1966) 199, f. 38. — Type: *van Steenis 8362* (L. holo).

Erect densely-leaved *shrub* or *tree*, c. 2 m high. *Leaves* verticillate or subverticillate; blades obovate, elliptic to narrowly elliptic, apex rounded, rarely emarginate to mucronulate, base obtuse, 4–7 by 2.5–4.5 cm, margins entire, coriaceous, thick-leathery, shining, smooth, brown on both surfaces, midrib whitish, lateral veins 7–9 pairs, thin, elevate-reticulate beneath; petioles broadly triangular, very short, thickened at the base. *Staminate inflorescences* oblong, 1.5–3 cm long, 0.2 mm wide, calyx absent or very shallowly cupuliform, stamens 8–11, filaments oblong, 1.3–2.3 mm long, anthers elliptic-ovate, 0.6–0.8 mm long with triangular apex 0.2 mm long; pedicels oblong, 4–7 mm long. *Pistillate inflorescences* angulate, 2.5–5 cm long; female flowers pale green, calyx oblong or obovate-oblong, subentire or with an irregularly divided apex, caducous, 0.4 mm long, 0.3 mm wide, ovary ovoid, stigma short, radiate or revolute; pedicels flat to terete, thickened toward apex, 2–3(–7) mm long. *Fruiting axes* 5 cm long. *Drapes* ovoid-ellipsoid, 5–6(–8) mm long, 5 mm wide, blue-black, glaucous, fruit stalks c. 5 mm long. — **Fig. 8.**

Distribution — *Malesia*: Sumatra (Northern part).

Habitat & Ecology — Ridge forest, altitude 2500–3500 m.

Note — This species is similar to *D. scortechinii* except for the sessile and subverticillate arrangement of the leaves and the absence of a calyx in the staminate flowers.

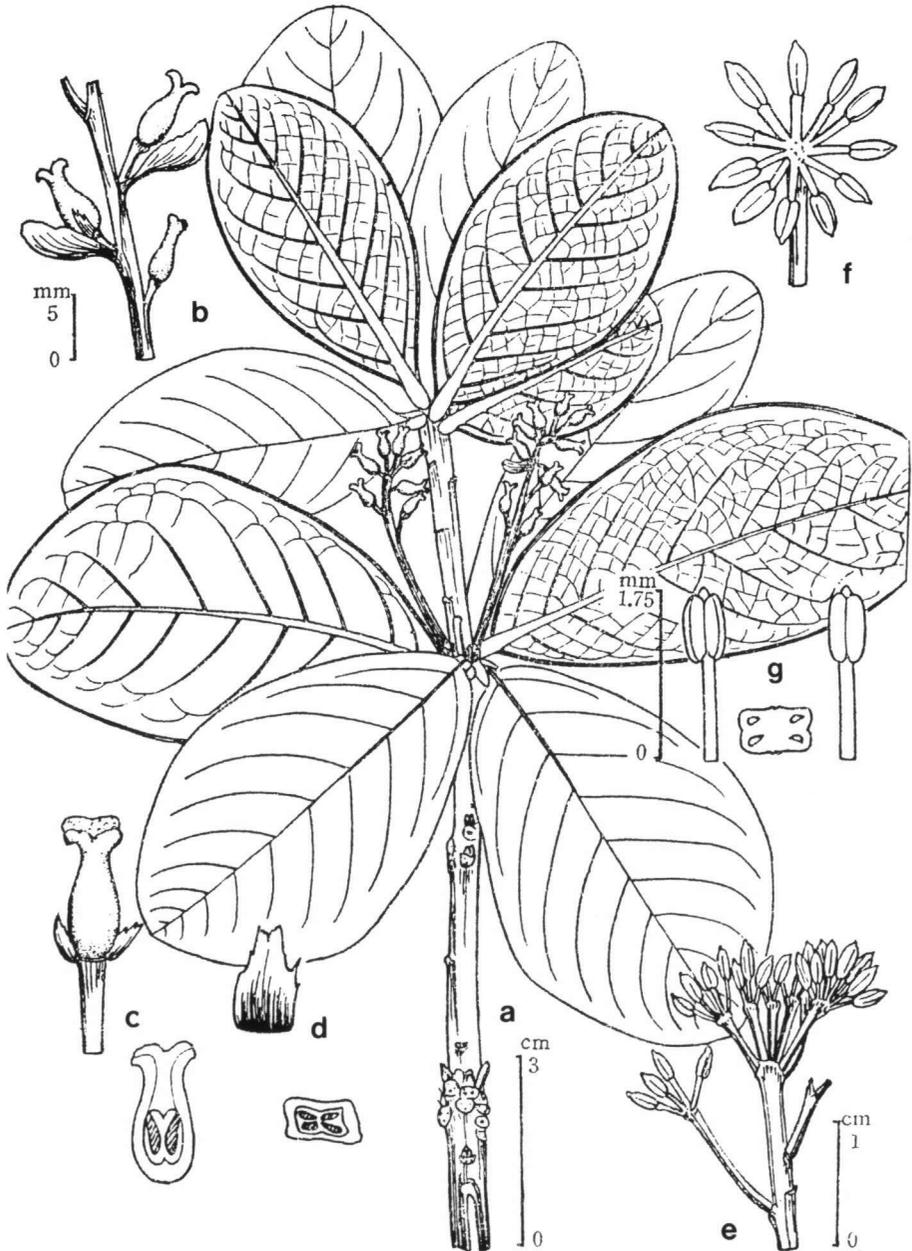


Fig. 8. *Daphniphyllum woodsonianum* T. C. Huang. a. Twig with pistillate flowers; b. part of pistillate inflorescence; c. ovary with longitudinal and cross sections; d. calyx; e. staminate inflorescence; f. naked staminate flower; g. stamen, dorsal and ventral views, and anther in cross section (*van Steenis* 8362).