ARAUCARIACEAE

Monoecious, medium-sized to very large trees (rarely shrubby in very exposed situations). Either four independent *cotyledons* or two fused pairs (which may be retained in the seed after germination). The growing point of foliage shoots quite distinct between the two genera, being just a few highly reduced leaves in *Araucaria* and a highly organized bud formed of overlapping scales in *Agathis*. The leaves vary from scales or needles to broad leathery forms with many parallel veins sometimes on the same plant at different stages of growth. *Pollen* produced in cylindrical cones from one to as much as twenty cm long with numerous pedunculate spirally placed microsporophylls each with several to many pendent elongated pollen sacs attached to the lower side of an enlarged shield-like apex which also projects apically more or less overlapping the adjacent microsporophylls. *Pollen cones* solitary, terminal or lateral, on branches separate from those bearing seed cones, subtended by a cluster of more or less modified leaves in the form of scales, deciduous when mature. Pollen globular, without 'wings'. *Seeds* produced in large, well-formed cones which disintegrate when mature, dispensing the seeds in most cases with the help of wing-like structures; the seed cone terminal on a robust shoot or peduncle with more or less modified leaves that change in a brief transition zone at the base of the cone into cone bracts, formed of numerous spirally-placed bract complexes, usually maturing in the second year. Individual seed cone bract leathery or woody and fused with the fertile scale which bears one large inverted seed on its upper surface.

Distribution. The 40 species in two genera are well represented in *Malesia* (13 *spp.*) and extend eastward and southward into Fiji, New Caledonia (18 *spp.*), Australia, and New Zealand, with 2 *spp.* also in the cooler parts of South America, giving the family a distinct Antarctic relationship. Only one species of *Araucaria* (in South America) occurs completely outside of the tropics, while the majority of the species in the family belong in the lowland tropics and others grow in the tropical highlands.

Fossils. Early coniferous fossils are often characterized as 'Araucarioid' because of the morphological resemblance of fossil foliage shoots to certain well-known juvenile forms of *Araucaria*,

but there is no reason to conclude that these actually belong in *Araucariaceae*. Acceptable fossils of *Araucariaceae*, however, from Jurassic and Cretaceous age are well represented in the general areas of their modern occurrences, often at higher latitudes to be sure, and also in India and South Africa. More surprising is the apparent occurrence of fossils belonging to the family during the same time span but far away in North America and Europe (FLORIN, 1963; GAUSSEN, 1970). A close relationship of English Jurassic fossils specifically to *Araucaria bidwillii* is indicated by STOCKEY (1981). Wherever the family may have originated, it became well established in the southern hemisphere in Mesozoic times and has since disappeared from whatever northern occurrences it may have had. The genus *Agathis* is first recorded in the Oligocene of Australia and New Zealand and today extends into the Asian tropics, while no convincing fossils have ever been found in any other part of the world for this genus.

Tertiary records of the two modern genera of *Araucariaceae* are all well south of the equator across all of the southernmost land areas including the Palmer Peninsula of Antarctica. Speculation about tropical origins or early penetration of the tropics is not supported by any evidence and it is at least as likely that the occupation of the Malesian region took place during Plio-Pleistocene times alongside advancing members of *Podocarpaceae*.

Maps of fossil distributions are given in FLORIN (1963).

References: FLORIN, Acta Horti Berg. 20 (4) (1963) 121–312, 68 maps; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 42–56, f. 555–558; MACARTHUR, The genus *Araucaria* in its geographical aspects, Univ. W. Austr., Geogr. Lab. Econ. Dept., Research Rep. 5 (1949); STOCKEY, Canad. J. Bot. 59 (1981) 1932–1940.

Ecology. Canopy trees or emergents of moist forests at a wide range of elevations starting at sea-level in the tropics and extending to tropical highlands and to intermediate elevations in the middle latitudes. (One species in New Caledonia grows in drier forests and open places.) Some species clearly follow disturbances and others just as clearly do not. Many contrasting soil types are associated with different species.

Most or probably all species are monoecious and pollination is by wind. Frequent reports of dioeciousness result from a single sex stage, inasmuch as many species produce seed cones well before pollen cones appear. Dense stands are common for many but by no means all species and the large amounts of pollen are adequate to reach substantial distances effectively. Seeds are carried only short distances by wind in most cases and germinate in large numbers near their parent tree. The occurrence of isolated specimens shows that seeds sometimes are carried across substantial distances.

Growth occurs in distinct episodes and where distinct terminal buds are not evident whole units of growth tend eventually to be shed as a unit. Leaves normally persist for several years and may be shed separately from branch units in some cases. Cyclic growth results in false whorls of branches and a tendency for highly formal tree architecture.

A number of pests and diseases specific and otherwise of *Agathis* have been reported by WHITMORE (1977) mostly outside of Malesia. In particular a moth genus, *Agathiphaga*, specifically attacks cones, while a coccid, *Coniferococcus agathidis*, causes defoliation. Problems mostly arise when normally dispersed trees are concentrated in plantations. GAUSSEN (1970: 62 & 66) lists a variety of pests of *Araucaria*, mostly associated with cultivated examples. Notable are a 'pine bark weevil' (*Aesiotes notabilis*) and the 'hoop pine borer' (*Calymmaderus*). Termites of the genus *Coptotermes* do serious damage to *A. hunsteinii*.

Embryology. The fertilized egg undergoes at least five mitoses resulting in 32 or more free nuclei before cell walls form. The resulting cluster of cells deep inside the egg (proembryo) is then organized into three parts. The cells closest to the archaegonium elongate to form a massive 'prosuspensor' while those on the opposite side form a temporary 'cap'. The cells at the centre of the proembryo become the embryo proper, which does not undergo cleavage as in many other conifers. Simple polyembryony resulting from more than one fertilized archaegonium, however, may occur. The large number of proembryo cells and the massive embryonic 'cap' are distinct for

Araucariaceae within the conifers. The chromosome number is n = 13. No hybridization is suspected.

Taxonomy. Two well marked genera are recognized.

Uses. The large size of individuals in many species in this family along with the excellent quality of the wood has made them prime candidates for lumber production where sufficiently dense stands occur. The wood is light coloured, yellowish or brownish, straight grained, easily worked, durable, and generally similar to pine but somewhat harder than the more familiar types. The wood is sometimes intermingled and hardly distinguishable from material of *Podocarpaceae*. Important stands of *Agathis* have been exploited in Borneo and stands of *Araucaria* in New Guinea (ISMAIL, 1964; GRAY, 1975; HAVEL, 1971), as well as many locations outside of Malesia. Heavy exploitation has reduced the economic importance of this family. Some attempts have been made to establish tree plantations, but this effort is in the early stages of development (WHITMORE, 1977, 1980; BOWEN & WHITMORE, 1980). Large quantities of pitch have been gathered, particularly from certain species of *Agathis* where it is known as 'dammar'. Both fossil pitch with darker colours and fresh pitch which is much lighter have been produced. Immense dammar trees sometimes have some form of steps built into their trunks to enable collectors to reach the accumulating pitch. Specimens of various species make handsome ornamentals and are widely used in landscaping in the warmer parts of the world. (The seeds of several *Araucaria* species are in great demand as food.)

References: BOWEN & WHITMORE, Commonw. For. Rev. 59 (1980) 307; B.GRAY, J. Ecol. 63 (1975) 273–289; HAVEL, J. Ecol. 59 (1971) 203-213; ISMAIL BIN HAJI ALI, Mal. For. 27 (1964) 354–360; WHITMORE, A first look at *Agathis*, Oxford (1977); Econ. Bot. 34 (1980) 1.

Note. The great size of trees in this family has led to an emphasis on collection of juvenile foliage specimens and immature cones and when this is not admitted by the collectors the result can be misleading. Because the seed cones shatter on maturity and the pollen cones are deciduous, it is next to impossible to collect attached mature fertile material. Fallen cone scales and pollen cones abound below mature trees and should be collected.

KEY TO THE GENERA

1. Seed coat fused with cone-scale complex, apex of fertile scale forming a 'ligule', bract usually with membranous wings. Leaves spirally placed, crowded and broadly attached, variable in form from broad to scales and needles, amphistomatic ..... **1. Araucaria**
1. Seed coat independent and extended into a wing, scale completely fused with bract which is thin but not wing-like. Leaves opposite decussate, dispersed, and narrowed to a basal petiole, broad and more or less oval, hypostomatic ..... **2. Agathis**

1. ARAUCARIA

JUSS. Gen. Pl. (1789) 413; RICHARD, Comm. Bot. Conif. & Cycad. (1826) 153; D.DON, Trans. Linn. Soc. 18 (1841) 163; LINK, Linnaea 15 (1841) 541; ENDL. Gen. Pl. Suppl. 2 (1842) 26; Syn. Conif. (1847) 184; CARR. Traité Gén. Conif. (1855) 413; Man. Pl. 4 (1857) 360; GORDON, Pinetum ed. 1 (1858) 21; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 2; PARL. in DC. Prod. 16, 2 (1868) 369; BENTH. & HOOK. Gen. Pl. 3 (1880) 423; EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1889) 67; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 317; BARSALI, Atti Soc. Tosc. Sci. Nat., Mem. 25 (1909) 145; DALLIMORE & JACKSON, Handb. Conif. (1923) 150; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 263; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 7; DE LAUB. Fl. Nouv. Ca-

léd. et Dép. 4 (1972) 80; SILBA, Phytologia Mem. 8 (1986) 38. — *Dombeya* LAMK. Enc. Méth., Bot. 2 (1786) 301, t. 828, *non* L'HÉRIT. *nec* CAV. — *Columbea* SALISB. Trans. Linn. Soc. 8 (1807) 317. — *Colymbea* SPRENG. Syst. Veg. 4, 2 (1827) 888 (refers to SALISBURY, but 'corrects' the spelling); STEUD. Nom. Bot. ed. 2, 1 (1840) 399. — **Fig. 67, 68.**

Monoecious or sometimes (temporarily?) dioecious small to immense trees mostly with limited and very formal branching elements consisting of long sweeping primary branches in false whorls along the main trunk often turned apically upward candelabra-like, then in most species only one additional rank of branches. The first branches sooner or later deciduous and in open situations replaced by adventitious branches thus producing a variety of double-crown forms. Apex of a resting shoot a cluster of incompletely formed leaves. *Leaves* spirally placed, broadly attached, crowded, multi-veined when broad and even sometimes in the needle-shaped examples, becoming uniform in size along a branch, but sometimes quite variable in the juvenile forms, amphistomatic. *Pollen cones* subtended by a cluster of reduced, leaf-like, sterile bracts, often broadened at their bases and where the mature leaves are needle-like these bracts are at least somewhat broader and flatter. Fertile bract of the seed cone broad and often extended laterally into membranous wings, the apex provided with a prominent narrow spur above the thickened apical margin. *Seed-bearing scale* only partly fused with the associated bract, its apex a free acute scale-like 'ligule' ± reaching the base of the spur on the fertile bract. *Seed coat* fused with its scale.

Distr. Across New Guinea, coastal Queensland, New Caledonia, Norfolk Island, S. & Central Chile, and southern Brazil 19 *spp.* in two sections. Fig. 65.

Fossils. In Jurassic times there was evidently an important centre of development and distribution in the Inda–Australia–Antarctic region, from whence it subsequently spread to the Kerguelen and southern Cape Colony on one hand and to Patagonia on the other. The close of the Mesozoic era seems to have witnessed its disappearance from Peninsular India, South Africa and New Zealand. Both sections had an Eogene centre in Antarctica and southern South America, one of which survives still on both sides. The oldest find of *Araucaria* was from probably Late Triassic in N. Central India (then situated in the southern hemisphere) where it remained until the Early Cretaceous whereupon it disappeared (FLORIN, K. Svensk. Vet. Ak. Handl. III, 19, 1940, 81, map 5).

KEY TO THE SECTIONS

1. Juvenile leaves bifacially flattened, cotyledons 2, pollen cones lateral ..... **1.** *Sect.* **Araucaria**
1. Juvenile leaves acicular, cotyledons 4, pollen cones terminal ..... **2.** *Sect.* **Eutacta**

1. Section Araucaria

Sect. Colymbea ENDL. Gen. Pl. Suppl. 2 (1842) 26; Syn. Conif. (1847) 185; CARR. Traité Gén. Conif. (1855) 414; Man. Pl. 4 (1857) 360; GORDON, Pinetum ed. 1 (1858) 21; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 2; PARL. in DC. Prod. 16, 2 (1868) 370 (*'Columbea'*); EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1889) 69; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 317; PILGER

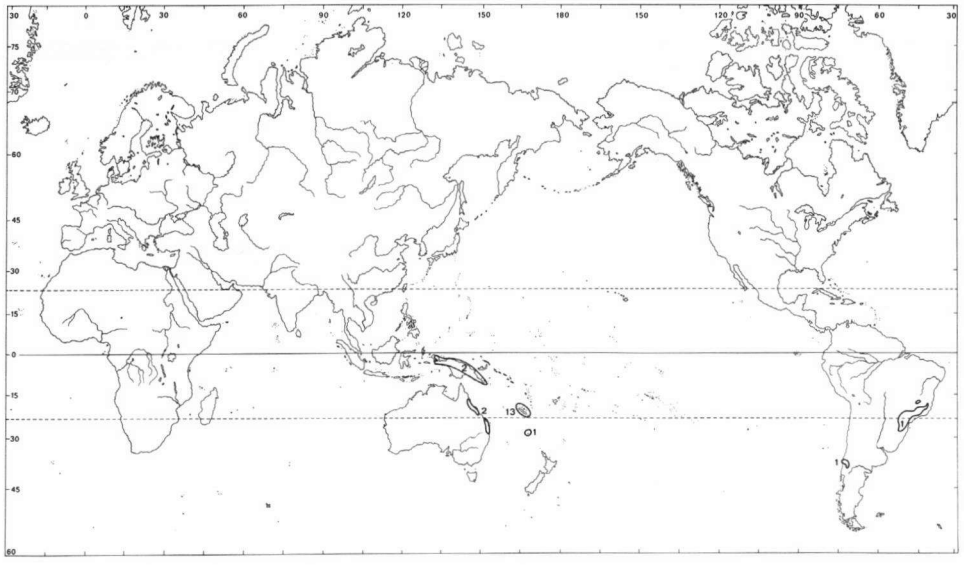

Fig. 65. Range of the genus *Araucaria* JUSS. with the number of species.

in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 263; WILDE & EAMES, Ann. Bot. n.s. 16 (1952) 44 (*'Columbea'*); GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 7. — *Sect. Intermedia* WHITE, J. Arn. Arb. 28 (1947) 260; WILDE & EAMES, Ann. Bot. n.s. 16 (1952) 44; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 7. — *Sect. Bunya* WILDE & EAMES, Ann. Bot. n.s. 16 (1952) 44. — *Subg. Colymbea* ANTOINE, Conif. nach Lambert, Loudon & Anderen (1846) 99; CARR. Traité Gén. Conif. 2 (1867) 596.

Cotyledons 2, either hypogeal or epigeal, each cotyledon apparently formed of two fused units. *Juvenile leaves* narrow but distinctly flattened, spreading, often twisted into a horizontal plane; mature leaves broad and often with an acuminate tip. *Pollen cones* lateral. *Ligule* elongated and more or less constricted above the seed; cross section of the cone scale complex narrowed to a distinct and generally elongated neck above the seed, margins of the bract with or without broad membranous lateral wings.

Distr. In E. New Guinea, coastal Queensland, S. Central Chile and S. Brazil 4 non-overlapping *spp.*, of which 1 in *Malesia*.

Ecol. Trees of moist forests mostly rising above the associated trees and often colonizing disturbed areas and protecting the regrowth into that area of other trees.

Notes. *Sect. Intermedia* was established for *Araucaria klinkii* (= *A. hunsteinii*) because it differs from the rest of *sect. Araucaria* while resembling *sect. Eutacta* in epigeal cotyledons and broad membranous wings on the cone scales, but it does have two cotyledons and the spreading flat juvenile leaves of *sect. Araucaria*. One could also add that mature leaves have the hooked tip seen elsewhere only on some species of *sect. Eutacta* but the apex of the cone scale complex and the laterally placed pollen cones conform to *sect. Araucaria*. Young plants of *A. hunsteinii* are indistinguishable from those of *A. bidwillii*. *Sect. Bunya* was established for *A. bidwillii* because the cone scale complex has thick woody wings as opposed to no wings in the two American species and because of the double vascular supply to the bract and scale. The mature seed also separates from the scale complex. STOCKEY (Canad. J. Bot. 59, 1981, 1932) argues for the usefulness of these monotypic sec-

tions based on a variety of fossil material, but the differences with the residual *sect. Araucaria* hardly seems sufficiently important.

1. Araucaria hunsteinii K.SCH. Fl. Kaiser Wilhelms Land (1889) 11, t. 4, f. 8; WARB. Monsunia 1 (1900) 187, t. 10, f. B; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 324, f. 9; BARSALI, Atti Soc. Tosc. Sci. Nat., Mem. 25 (1909) 158; WILDE & EAMES, Ann. Bot. n.s. 16 (1952) t. 2, f. 10; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 16, f. 536; HOWCROFT, For. Genet. Res. Inf. *n.* 8, FAO For. Occ. Pap. 1987/2 (1987) 31; SILBA, Phytologia Mem. 8 (1986) 41. — *A. schumanniana* WARB. Monsunia 1 (1900) 187, t. 10, f. A; WILDE & EAMES, Ann. Bot. n.s. 16 (1952) t. 2, f. 11; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 15, f. 535. — *A. klinkii* LAUT. Bot. Jahrb. 50 (1914) 48, f. 1; LANE-POOLE, For. Res. Terr. Papua New Guinea (1925) 72; WILDE & EAMES, Ann. Bot. n.s. 16 (1952) t. 2, f. 7; t. 3; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 15, f. 534 left.

Forest emergent 50–89 m tall with a clear bole of 35–60 m and up to 2 m diam. Branches in loose false whorls of 5 or 6 and sometimes rising towards their apex where the leaf-bearing shoots are clustered, forming a rounded crown on the upper part of the tree. In open sites after the first branches are shed a second set of smaller adventitious branches develop on the middle part of the bole. Outer bark reddish brown, rough, peeling in horizontal strips leaving a thick dark red corky flaky underbark which weathers to shades of brown. Much colourless resin is produced. Two *cotyledons c.* 35 by 1.5–2.5 mm at the base, tapering gradually to the narrow blunt apex, flat, their surface similar to the shorter broader acute first leaves which contain half a dozen parallel vascular strands evenly spaced, while the vascular strands of the cotyledons are separated into two groups by a slight gap along the centre. *Juvenile leaves* linear-ovate, narrowed to a decurrent base and tapering to a slightly acuminate pungent apex, very variable in size, less than 2 by 1 mm during resting phases to at least 2.5 by 0.5 cm in the first flush of growth and becoming larger and more lanceolate as the plant matures, twisting sharply at the base to attain a horizontal position. *Adult leaves* produced in full sunlight, often in five distinct rows, narrowed slightly at the base to a broad decurrent portion 10–15 mm long, ovate-lanceolate, nearly uniform along all but the ends of the branch, 7–15 by 1.2–2 cm, an asymmetrical dorsal ridge prolonged from the junction of the two subtending leaves, ventrally concave, inflexed at the narrow acute apex. *Pollen cones* clustering near the ends of foliage branches each in the axil of a leaf, subtended by a cluster of reduced leaves the first few more or less decussate and up to 25 mm long but not always remaining attached when the cone falls, the mature cone linear, 16–22 by 1.8–2.5 cm. *Microsporophyll* on a *c.* 4 mm peduncle, the apical part 5–10 by 2–2.5 mm and more or less linear but narrowing to an acute apex, slightly keeled on the dorsal side, margins membranous and somewhat serrate, expanded at the base on the other side of the peduncle to accommodate about 10 pollen sacs. *Seed cones* terminal on robust short branches, subtended by numerous reduced leaves, the immature cone ovoid with only the numerous lanceolate spurs visible, mature seed cones obovoid to cylindrical with the apex conical to slightly depressed, 18–25 by 12.5–16 cm, the exposed slightly expanded outer edge of each seed scale complex more or less rhomboidal in outline, the included seed 3–4 by 0.8–1 cm imbedded in the complex with the ligule extending another 2 cm but no wider than the seed and tapering at first only slightly and then more so near the acute free apex, the thick part of the fertile bract sharply expanded above the seed to its widest and thickest part at the level of the free tip of the ligule and then forming a blunt rhomboidal end or apophysis that is visible on the surface of the mature cone and includes a narrow lateral ridge on each side and terminates in a spur 9–15 mm long which is often broken off before the cone reaches maturity, the two edges of the cone bract expanded into broad blunt membranous wings each as much as 4 cm wide.

Distr. *Malesia*: E. New Guinea, in several large stands in large valleys and numerous small stands which are often clustered and with higher mountain areas intervening between the regions of occurrence (B.GRAY, Papua New Guinea Dept. For. Res. Bull. 1, 1973, 1–56). Fig. 66.

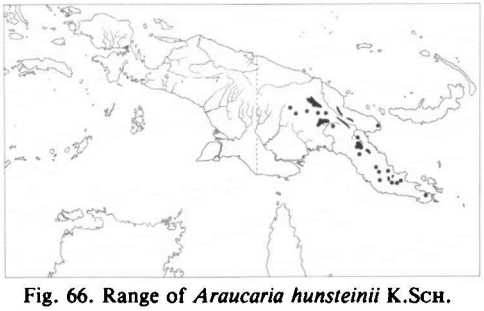

Fig. 66. Range of *Araucaria hunsteinii* K.SCH.

Ecol. Emergent in the submontane oak forest on well drained sites over a variety of soils from 520 to 2100 m. This is the tallest tree of Malesia. There has been much speculation concerning the origin of the disjunct gregarious stands. Natural regeneration

does occur under forest conditions, but most vigorous germination is associated with open disturbed conditions and it is generally believed that prehistoric disturbance played a major role in producing the current distribution. Heavy commercial exploitation, pressure on regeneration by feral pigs, and anthropogenic fires have all caused serious reductions in many stands.

Uses. The basis of a major plywood industry at Bulolo which results from the fine quality of the wood and the impressive log sizes. The firm, light wood is easily worked and is yellowish brown in colour with attractive purplish streaks in the heartwood.

Vern. *Pa'a*, Watut-Bulolo, *pai*, Waria-Kaisinik, *gerau*, Waria, *bimu*, Toma, *yanguman*, Agaun, *yomejo*, Kotte-Pindui, *karina*, Bembi-Madang, *rassu*, Ongoruna, *nd'uk*, Wareng, *kembaga*, *saa'vara*, Taiora, *sowes*, Erave, Mt Matmuri.

Note. HOWCROFT (*l.c.*: 5, 31) has distinguished a glaucous variety that corresponds to *A. klinkii*. Not only are fresh leaves glaucous, but the cones are also gray-blue due to a white exudate on their surface.

2. Section Eutacta

ENDL. Gen. Pl. Suppl. 2 (1842) 26; Syn. Conif. (1847) 186; CARR. Traité Gén. Conif. (1855) 418; Man. Pl. 4 (1857) 361; GORDON, Pinetum ed. 1 (1858) 26; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 9; PARL. in DC. Prod. 16, 2 (1868) 372; EICHLER, in E. & P. Nat. Pfl. Fam. 2, 1 (1889) 69; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 318; BARSALI, Atti Soc. Tosc. Sci. Nat., Mem. 25 (1909) 157; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 265; FRANCO, Port. Acta Biol. Sist. ser. B, Julio Henriques (1949) 24; WILDE & EAMES, Ann. Bot. n.s. 16 (1952) 43; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 7; DE LAUB. Fl. Nouv. Caléd. et Dép. 4 (1972) 81. — *Sect. Eutassa* (SALISB.) BENTH. & HOOK. Gen. Pl. 3 (1800) 437. — *Eutassa* SALISB. Trans. Linn. Soc. 8 (1807) 316. — *Eutacta* LINK, Linnaea 15 (1841) 543 (refers to SALISBURY, but 'corrects' the usage). — *Subg. Eutacta* (LINK) ANTOINE, Conif. nach Lambert, Loudon & Anderen (1846) 99; CARR. Traité Gén. Conif. ed. 2 (1867) 604.

Cotyledons 4, epigeal. The first leaves following the cotyledons small elongated triangular scales with juvenile leaves appearing on lateral shoots or much later on the leader. *Juvenile leaves* acicular, four angled in cross section, straight or falcate and never twisted into a horizontal plane. *Adult leaves* acicular (to broad and concave towards the ventral side and with an asymmetrical dorsal ridge prolonged from the junction of the two subtending leaves), never with an acuminate tip. *Pollen cones* terminal. *Ligule* narrowing abruptly above the seed generally without any constriction; the thickened apex of the bract (apophysis) directly above the apex of the seed; margins of the bract with broad membranous lateral wings.

Distr. NE. coastal Australia (1 *sp.*), New Guinea (1 *var.*), Norfolk Island (1 *sp.*), New Caledonia (incl. Loyalty Is.) (13 *spp.*); in *Malesia* only the one variety in New Guinea.

2. Araucaria cunninghamii AIT. *ex* D.DON in Lamb. Pinus ed. 2, 3 (1837) t. 79; SWEET, Hort. Brit. 2 (1830) 475, *nomen*; LAMB. Pinus ed. 3 (1832) no pages, *nomen*; LOUD. Arb. & Fruct. Brit. 4 (1838) 2443, t. 2303–2305 *et suppl.* 2603, f. 2545; FORBES, Pin. Wob. (1839) 157, t. 52; ANTOINE, Conif. nach Lambert, Loudon & Anderen (1846) 102, t. 43 & 44; ENDL. Syn. Conif. (1847) 187; CARR. Traité Gén. Conif. (1855) 419; Man. Pl. 4 (1857) 361; GORDON, Pinetum ed. 1 (1858) 27; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 9; PARL. in DC. Prod. 16, 2 (1868) 372; SIEBOLD, Flor. Jap. 2 (1870) t. 139; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 325, f. 8c; BARSALI, Atti Soc. Tosc. Sci. Nat., Mem. 25 (1909) 167; WHITE, J. Arn. Arb. 10 (1929) 200; *ibid.* 28 (1947) 259; FRANCO, Bot. Soc. Brot. 2, 23 (1949) 162; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 32; REILLY, Dept. For. Qld. Res. Pap.

Fig. 67. *Araucaria cunninghamii* AIT. *ex* D.DON *var. papuana* LAUT. in West New Guinea, Kebar Valley, Vogelkop Peninsula, 600 m alt. (Photogr. J.F.U.ZIECK, 1954).

n. 4 (1974); SILBA, Phytologia Mem. 8 (1986) 40. — *Eutacta cunninghamii* (AIT.) LINK, Linnaea 15 (1841) 543; CARR. Traité Gén. Conif. ed. 2 (1867) 608. — *Eutassa cunninghamii* SPACH, Hist. Nat. Veg. Phan. 11 (1842) 362. — **Fig. 67, 69.**

Forest emergent, 30–60 m tall, with a clear bole of 20–40 m and up to 2 m diam. Major branches tend to be in false whorls and tend to be rather straight, growing upwards at a slight angle but gradually declining with weight, persisting in open growth situations. Subsequent ramification more complex and denser than in any other *Araucaria* giving the tree the appearance of a cypress when young and a spruce when older. Outer bark at first in nearly smooth horizontal peeling strips or hoops which become smaller and rough with maturity, red in the interior but weathering to dark brown or black. There is a thick white resinous exudate. *Cotyledons* linear, *c.* 2 cm by 1.5–1.8 mm, narrowing to an acute apex, with several evenly spaced vascular strands. *Juvenile leaves* straight, linear-lanceolate, pungent, bilaterally flattened but laterally keeled, briefly decurrent forming a sharp rib on the stem, quite variable in size being tiny at the base of a shoot, most often *c.* 1 by 0.1 cm, on vigorous shoots up to 2.5 by 25 cm; leaves on the leader, particularly at the seedling stage, reduced to triangular spreading bifacially flattened scales *c.* 2 mm long. *Leaves* on older plants gradually becoming

falcately curved forward and acicular. *Adult leaves* crowded and curved so that their sharply pointed apices are directed slightly inward, four-angled but about twice as wide as thick, the ultimate leafy branches *c.* 5 mm in diameter with lanceolate leaves *c.* 5 by 1.5 mm; vigorous branches at least 1 cm in diameter with leaves 7–9 by 2 mm. *Pollen cones* terminal on foliage shoots, sometimes rather short shoots, subtended by a cluster of numerous leaf-like bracts about the same size as the leaves but distinctly thinner and more crowded, the cone 4–8 cm long and 8–10 mm in diameter, linear but tapering slightly to a more or less blunt apex, formed of numerous microsporophylls. Each *microsporophyll* on a stalk 2–3 mm long, the apex extended into a triangular flat apical part 1.2–1.8 mm long, slightly keeled on the dorsal side, margins narrow and slightly serrate, with five or more pendant pollen sacs along the base. *Seed cones* terminal on robust shoots with a more or less abrupt transition to the fertile scales whose apical spines are like the leaves but bent backward, the mature spine-covered cones ovoid shaped, 6–10 by 5–7 cm. The cone scales complex less the spine 23–29 mm long and including the membranous wings *c.* 34 mm wide, the thickened end or apophysis up to 24 mm wide with a tetragonal central part *c.* 5 mm thick and bearing a strong central ridge, from the upper part of the seed to the apophysis the thickened scale extended laterally by firm lobes; a ligule covering the seed, 7–9 mm wide, narrowing sharply above the seed apex and then elongated into a triangular free apex *c.* 2 mm long and touching the edge of the apophysis; membranous wings bluntly rounded and *c.* 12 mm wide; seed completely imbedded between the scale and the ligule but indicated by an almond-shaped bulge 2 by 0.7 cm and tapering towards the micropyle at the base of the cone scale.

Distr. There are two varieties, the type in Australia and the other in New Guinea.

var. **papuana** LAUT. Bot. Jahrb. 50 (1913) 51; SILBA, Phytologia Mem. 8 (1986) 40. — *A. beccarii* WARB. Monsunia 1 (1900) 187; GIBBS, Arfak (1917) 83, f. 5. — *A. cunninghamii auct. non* AIT.: BECC. Malesia 1 (1877) 180; F.v.M. Vict. Nat. 4 (1887) 121; Descr. Not. 9 (2) (1890) 65; LANE-POOLE, For. Res. (1925) 73; HOWCROFT, For. Genet. Res. Inf. *n.* 8, FAO For. Occ. Pap. 1979/1 (1979) 9. — **Fig. 67, 69.**

Bark, particularly of younger plants, dark plum to red-brown, weathering on older plants to gray or blackish. *Juvenile leaves* up to 23–27 mm long, even on ultimate branches, contrasting sharply with Australian material: where planted side by side the Australian seedlings have leaves no more than half as long. Generally reported to be slightly bigger and more vigorous (trees 50–70 m, pollen cone 9–10 cm long, seed cone 7–12 by 6–8 cm). *Pollen cones* produced in the middle part of the mature tree and *seed cones* in the upper part.

Distr. *Malesia*: New Guinea, scattered in isolated to extensive stands from one end of the island to the other, both in the central range and along the north coast, including Japen and Ferguson Is. (B.GRAY, Papua New Guinea Dept. For. Res. Bull. 1, 1973, 1–56). Fig. 68.

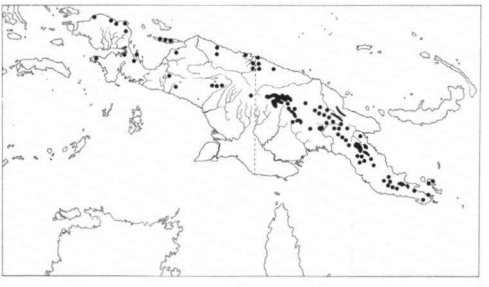

Fig. 68. Range of *Araucaria cunninghamii* AIT. *ex* D.DON *var. papuana* LAUT.

Ecol. Emergent in rain-forests from 60–2745 m in a variety of rain-forest soils usually along ridges, but occasionally in swampy conditions, most often in the submontane oak forest. The higher elevation occurrences are in the more southerly part of New Guinea. Vigorous regeneration has been noticed in abandoned gardens and on old burn sites confirming that *A. cunninghamii* is a pioneer tree and a nurse for the invasion of rain-forest. On the other hand lumbering, fire, pigs, and agriculture all contribute to the destruction of natural stands.

Uses. The same as for *A. hunsteinii*, with which it often grows. The heartwood is difficult to distinguish from the sapwood.

Vern. *Pien*, Pidgin, *ungwa*, Kapauku, *sumgwa*, Manikiong, *alloa*, Marconi R., *kiriwi*, Wandammen, *ningwik*, Tambuni Valley, *makut*, Pikpik, *domooimerr, tororomooi*, Dajo, *jarujosuwa*, Tanahmerah, *flabbito*, Wapi, *d'li*, Telefomin, *escera*, Foie, *sari*, Bembi, *bontuan*, Kaigorin, *wariri*, Gurumbu, *nimola*, Esa'ala.

Note. HOWCROFT (*l.c.*) has noted in some areas of New Guinea trees that have more gracile foliage, particularly in the juvenile stage. These differences could well correspond to the type variety which therefore might include New Guinea within its range. While noting that there are slight differences, recent authors have chosen not to use the variety in describing New Guinea material perhaps because in its original description the distinctions actually given are not valid.

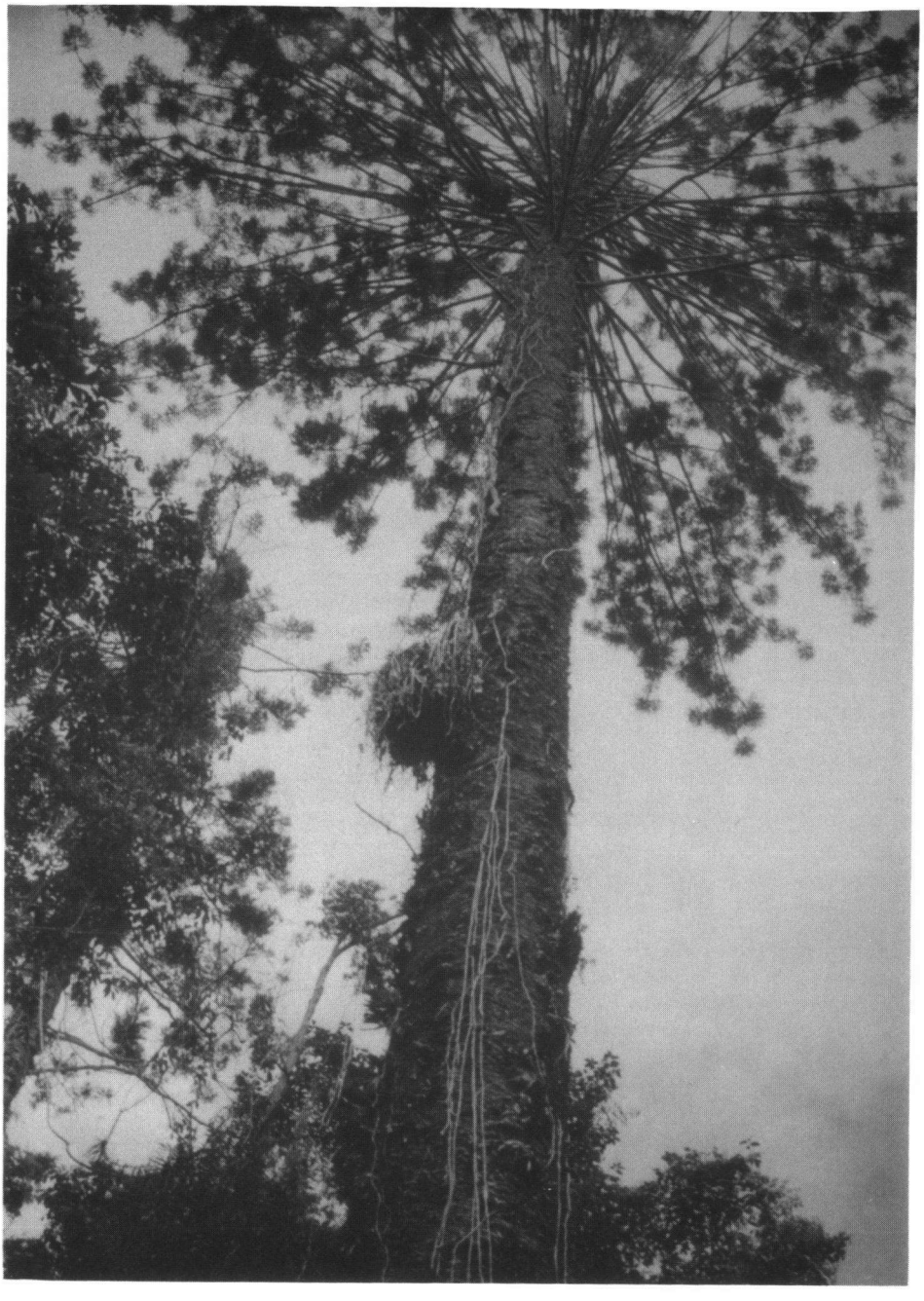

Fig. 69. *Araucaria cunninghamii* AIT. *ex* D.DON *var. papuana* LAUT. Tree, 49 m high, on slopes of Mt Cycloop above Lake Sentani in West New Guinea, 700 m (Photogr. F.W.RAPPARD, 1956).

2. AGATHIS

SALISB. Trans. Linn. Soc. 8 (1807) 311, t. 15, *nom. cons.* (unnecessarily); RICHARD, Comm. Bot. Conif. Cycad. (1826) 83, t. 19; WARB. Monsunia 1 (1900) 182; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 310; DALLIMORE & JACKSON, Handb. Conif. (1923) 138; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 266; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 455; FRANCO, An. Inst. Sup. Agron. 18 (1951) 101; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 75; DE LAUB. Fl. Nouv. Caléd. et Dép. 4 (1972) 126; WHITM. Trop. For. Pap. 11 (1977) 3; Pl. Syst. Evol. 135 (1980) 46, f. 1–5; SILBA, Phytologia Mem. 8 (1986) 31. — *Dammara* LINK, Enum. Hort. Berol. Alt. 2 (1822) 411, given in synonymy with *Agathis* [*non* GAERTN. Fruct. Sem. Pl. 2 (1790) 100, t. 103, f. 1, *Burseraceae*]; ENDL. Syn. Conif. (1847) 188; BLUME, Rumphia 3 (1847) 211; CARR. Traité Gén. Conif. (1855) 424; Man. Pl. 4 (1857) 363; GORDON, Pinetum ed. 1 (1858) 77; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 209; PARL. in DC. Prod. 16, 2 (1868) 374. — **Fig. 70–85.**

Monoecious trees often of immense size with clear straight boles below the globular crown, the large branches often turning irregularly upward; young trees with a conical shape. Bark at first quite smooth and light gray to reddish brown, peeling with large thin irregular flakes that gradually become thicker leaving a pitted somewhat rough reddish brown surface on larger trees. The two *cotyledons* are broad and lanceolate with an acute apex, the several vascular strands at least at first divided into two groups. Following the cotyledons the *leaves* are little more than triangular scales with a distinct central vein and several lateral veins. The first full leaves appear in pairs on lateral shoots. *Juvenile leaves* distinctly larger than adult leaves, particularly those adult leaves exposed to the sun, more or less acute, varying among the species from oval and acuminate to lanceolate. *Adult leaves* bluntly acute to rounded at the apex, rarely acuminate or lanceolate, oval to linear, sometimes lens-shaped, with considerable variation even along a single shoot where for example the first leaves may be substantially narrower than the later ones, generally somewhat reduced on seed cone bearing shoots, narrowed at the base to a brief broad petiole which is often twisted to place the leaves in a horizontal position, opposite decussate, decurrent, dispersed along the branch so that individual leaves do not overlap, with many parallel veins that converge no more than slightly towards the apex, resin canals alternating with the veins, more or less hypostomatic. Foliage buds globular, tightly covered with several pairs of overlapping scales. *Pollen cones* appearing mostly on larger trees well after the seed cones first appear, lateral and often in the axils of both of an opposite pair of leaves or occasionally terminal, subtended by several pairs of scales which form the sessile to briefly pedunculate pollen cone buds with the lowest pair sometimes expanded into reduced spreading leaves, more or less cylindrical with numerous small spirally placed microsporophylls. *Seed cone bracts* also spirally placed, their thickened

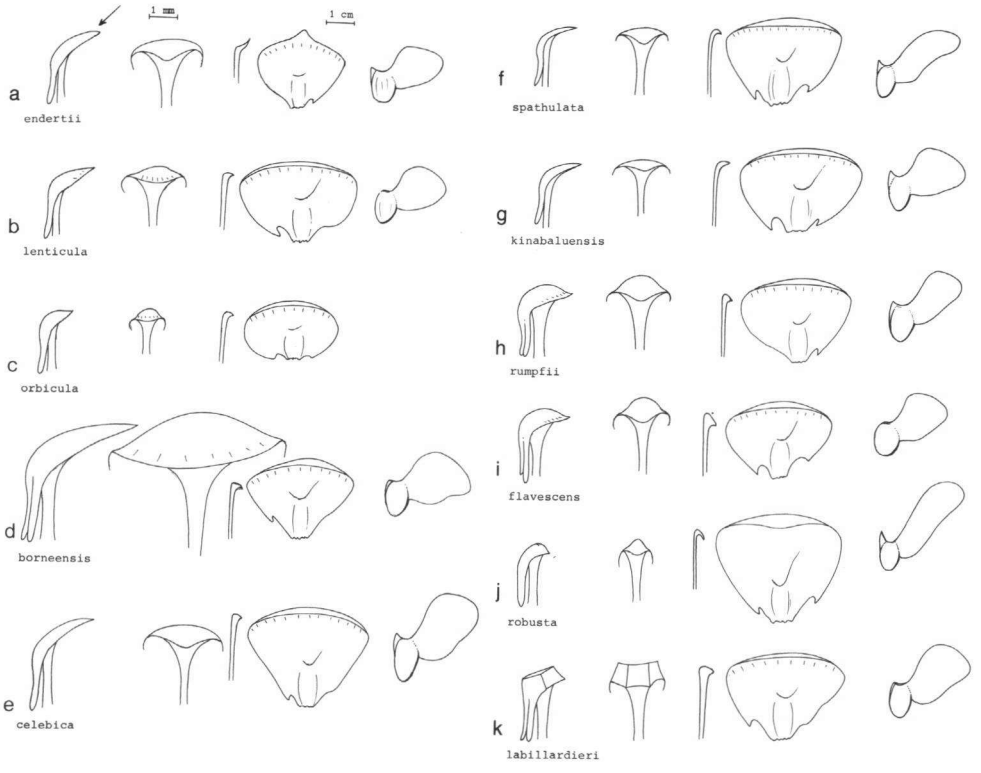

Fig. 70. *Agathis* cone elements. From left to right: lateral profile of microsporophyll, facial view of microsporophyll (from the angle indicated by arrow in the first figure), lateral profile of seed scale, facial view of seed scale (upper seed-bearing face), and seed. Microsporophylls in mm, scales and seeds in cm. — Lateral scallops of the seed scale and shape of seed wing shown are representative; these delicate structures show considerable variation. Orientation of the upper edge of the seed scale varies to which part of the cone it is in. Fully developed seed scales are formed in the middle part of the cone; numerous imperfectly formed scales occur towards the cone base and apex. Seed cone scales and seeds are laterally asymmetrical and both left-handed and right-handed cones are produced. — N.B.: under h, read *philippinensis* instead of *rumpfii*.

apical margin blunt or in some species with a projecting flattened 'beak', the lateral margins thin and broadly expanded but not membranous, normally indented near the base to form a 'scallop' which is usually much larger on one side than the other or more often one side has only a kink, quite variable especially near either end of the cone but more regular in the central fertile part, deciduous when mature. *Seed scale complex* fused with the bract. Inverted seed attached along its base, more or less flattened and oval-shaped, the margin on one side greatly expanded from the basal part into an oval membranous wing, the other margin blunt or more often with a rudimentary wing or sporadically the seed with two wings (cones and their elements come in both left and right handed versions). *Seed cone* oval to spherical.

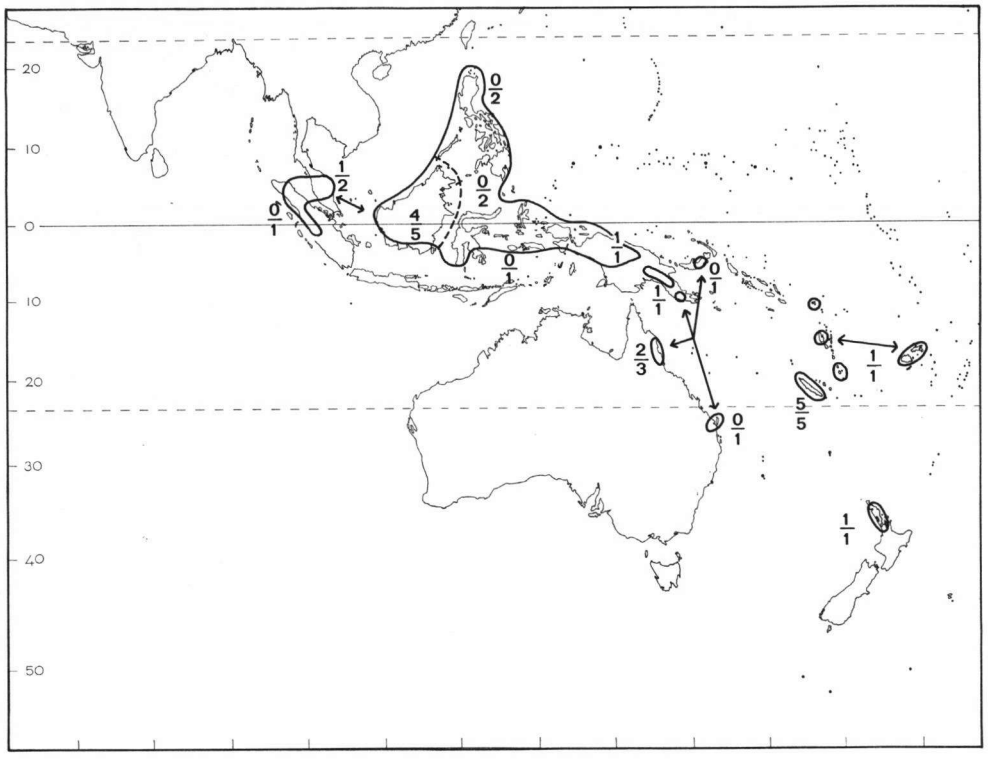

Fig. 71. Range of the genus *Agathis* SALISB. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.

Distr. Three sections with 21 *spp.* from Malaya and the Philippines across New Guinea and the coast of Queensland to Fiji and northern New Zealand; in *Malesia* 11 *spp.* There is a gap in the Solomons. Fig. 71.

Fossils: Fossil wood attributed to *Agathis* has been found in the Upper Cretaceous and Tertiary of New Zealand and from the Jurassic to the Tertiary in Australia, as well as in the Tertiary of Western Australia. Cone scales have been found in the northern hemisphere but the identification is uncertain (FLORIN, K. Svenska Vet. Ak. Handl. III, 19, 1940, *n.* 2, 82; Acta Horti Berg. 20 (4), 1963, 180, f. 15 map).

Ecol. The majority belong to lowland rain-forests.

KEY TO THE SECTIONS

1. Dorsal part of the microsporophyll not at all angled.
2. Seed scale only slightly angled to completely blunt. *Spp.* 1–8 ..... **1. *Sect.* Agathis**
2. Seed scale with a distinct beak (seed cone small, 5–6 cm diam. by 6–7 cm long). *Sp.* 9 **2. *Sect.* Rostrata**
1. Dorsal part of the microsporophyll sharply angled. *Spp.* 10–11 ..... **3. *Sect.* Prismobracteata**

1. Section Agathis

Sect. Macrobracteatae MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 457. — *Sect. Microbracteatae* MEIJER DREES, *l.c.* 461.

Fig. 72. Flaky bole of *Agathis borneensis* WARB. in heath forest on podsolized white sandy terrace, *c.* 20 m alt., Brunei (Photogr. P.S.ASHTON, May 1959).

Large trees. *Pollen cones* with spoon-shaped microsporophylls without angled creases, rarely sessile. *Seed cones* in most cases at least 7 cm long and the seed bracts always blunt along their apical margins.

Distr. In the same territory as the genus less the more southerly areas 13 *spp.*, of which 8 in *Malesia.*

KEY TO THE SPECIES

1. Juvenile (and more accessible) leaves not at all acuminate, adult leaves at least 6 cm long or else glaucous on the underside.
2. Leaves not glaucous on the underside, at least 6 cm long. Pollen cones at least 4 cm long. Microsporophylls slightly acute and nearly as long as wide or large (over 5 mm long).
3. Pollen cone at least 2 cm in diameter. Microsporophyll *c.* 6 mm wide, over 5 mm long, and blunt, resin canals in the leaves paired ..... **1. A. borneensis**
3. Pollen cone more than 14 mm in diameter. Microsporophyll no more than 2.5 mm wide, 2 mm long, and slightly acute, resin canals in the leaves solitary.
4. Adult leaves never broadly rounded at the apex. Pollen cones 12–14 mm in diameter. Apex of microsporophyll at least 2 mm long and wide. Seed bract at least 42 mm wide and 32 mm high with more or less straight margins and the apex bluntly ridged ..... **2. A. celebica**
4. Adult leaves acute to broadly rounded at the apex. Pollen cones 9–12 mm in diameter. Apex of microsporophyll less than 2 mm wide and 1.5 mm long. Seed bract less than 42 mm wide and 32 mm high with more or less rounded margins and the apex sharply rigid ..... **3. A. spathulata**
2. Leaves glaucous on the underside, no more than 6 cm long. Pollen cones less than 4 cm long. Microsporophylls blunt (much wider than long), less than 2 mm long.
5. Adult leaves lens-shaped, 5–7 cm long. Pollen cones 3–4 cm by 9–10 mm. Microsporophyll 2–2.5 mm wide. Seed cone *c.* 6 cm in diameter, spherical ..... **4. A. lenticula**
5. Adult leaves orbicular, blunt, 2.4–4 cm long. Pollen cones 8–14 by 4–6 mm. Microsporophyll 1.2–1.5 mm wide. Seed cone *c.* 4.5 cm in diameter, elongated ..... **5. A. orbicula**
1. Juvenile leaves distinctly acuminate. Adult leaves less than 6 cm long and not glaucous on the underside.
6. Adult leaves not acuminate. Microsporophyll helmet-shaped, the stalk attached near the centre of the apical part, at least 2 mm wide. Apex of the seed cone bract bluntly ridged.
7. Seed sharply angled opposite the wing. Mature pollen cone mostly at least 3.5 cm long by 10 mm in diameter. Seed cone bract 2.8–3.2 cm high. Adult leaves at least 4.5 cm ..... **6. A. philippinensis**
7. Seed bluntly rounded opposite the wing. Mature pollen cone 2–3.5 cm long by 7–10 mm in diameter. Seed cone bract 2.6–2.9 cm high. Adult leaves 3–4 cm long..... **7. A. flavescens**
6. Adult leaves acuminate or small and blunt. Microsporophyll shingle-shaped, the stalk attached below the centre of the apical part, 1.6–1.8 mm wide. Apex of the seed cone bract sharply ridged **8. A. kinabaluensis**

1. Agathis borneensis WARB. Monsunia 1 (1900) 184, t. 80; DALLIMORE & JACKSON, Handb. Conif. (1923) 143; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 459; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 96, t. 573; DE LAUB. Blumea 25 (1979) 532, t. 1; WHITM. Pl. Syst. Evol. 135 (1980) 54, t. 1 f. 3, t. 2. f. 3, t. 4; VELDKAMP & DE LAUB. Taxon 33 (1984) 345; SILBA, Phytologia Mem. 8 (1986) 32. — *Pinus dammara* LAMB. Descr. Pinus 1 (1803) 61, t. 38 (& 38a), *nom. rej.*; VELDKAMP & DE LAUB. Taxon 33 (1984) 337. — *A. loranthifolia* SALISB. Trans. Linn. Soc. Lond. 8 (1807) 312, t. 15, *nom. superfl.* — *Dammara loranthifolia* (SALISB.) LINK, Enum. Hort. Berol. Alt. 2 (1822) 411. — *Dammara orientalis* LAMB. Descr. Pinus 2 (1824) 15, *nom. superfl.*; GORDON, Pinetum ed. 1 (1858) 79. — *A. dammara* (LAMB.) RICHARD, Comm. Bot. Conif. & Cycad. (1826) 83, t. 19. — *Abies dammara* (LAMB.) DESF. Tabl. Ecol. Bot. ed. 3 (1829) 356. — *Dammara orientalis var. orientalis* CARR. Traité Gén. Conif. (1855) 426; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 210. — *A. beccarii* WARB. Monsunia 1 (1900) 184, t. 8F; DALLIMORE & JACKSON, Handb. Conif. (1923) 142; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 458, f. 1. — *A. macrostachys* WARB. Monsunia 1 (1900) 183, t. 8A. — *A. rhomboidales* WARB. *l.c.* 184, t. 8C; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 460; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 103. — *A. alba* FOXW. Philip. J. Sc. 4 (1909) Bot. 442. — *A. latifolia* MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 459. — *A. dammara ssp. dammara* WHITM. Pl. Syst. Evol. 135 (1980) 56 (WHITMORE described *A. celebica* and *A. philippinensis*). — **Fig. 72, 73.**

Huge tree to 55 m tall. *Juvenile leaves* ovate-lanceolate, up to 14 by 4 cm. *Adult leaves* ovate with

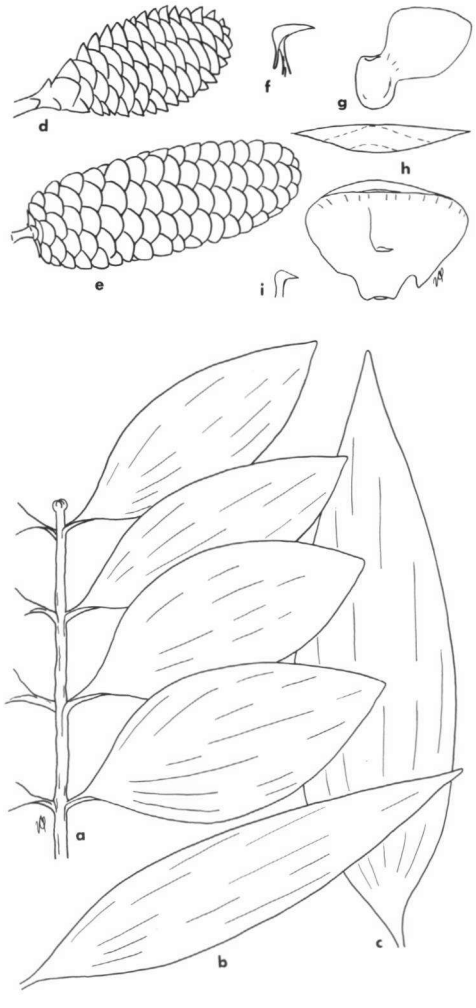

Fig. 73. *Agathis borneensis* WARB. a. Mature foliage shoot; b. leaf variation of shaded branches or alternating with a; c. juvenile leaf; d. young seed cone; e. mature pollen cone, all ×0.4; f. profile view of microsporophyll, ×1.25; g. seed; h. end view and facial view of the seed cone scale; i. profile view of the upper edge of the same.

a more or less acute apex, 6–12 cm by 20–35 mm, tapering at the base to a *c.* 5 mm petiole. The most common foliage leaf *c.* 7 by 3 cm but branches with relatively long and narrow leaves often interspersed with the more usual type and more general on younger trees. Resin ducts in pairs one above the other between most vascular strands rather than the prevailing solitary duct elsewhere in the genus. *Mature pollen cones* oblong, 4–7 cm by 20–25 mm, rounded at the apex, subtended by a 2–10 mm peduncle, the apex of the microsporophyll spoon-shaped, 5.5–6.5 by 4–5 mm, the apex a broad semicircle. *Mature seed cones* oval, 6–8.5 by 5.5–6.5 cm. *Seed bract* roughly triangular but well rounded at the upper corners, a low thick ridge along the apical margin, a strongly hooked 6 mm scallop on one side of the base, the other side with no more than a kink, 26–28 by 36–40 mm. *Seed c.* 12 by 9 mm, blunt at one upper corner and a broadly rounded wing *c.* 20 by 16 mm at the other corner.

Distr. *Malesia*: throughout Borneo and more restricted areas in Malaya and N. Sumatra. Fig. 74.

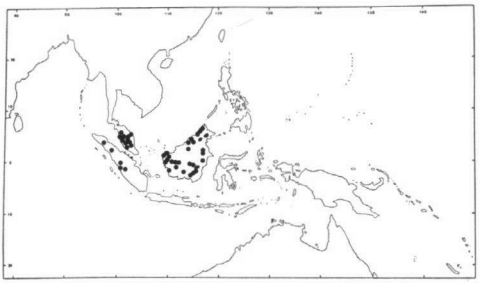

Fig. 74. Range of *Agathis borneensis* WARB.

Ecol. Scattered in upland rain-forest from low elevations to 1200 m throughout its range and in dense nearly pure stands on low-lying sandy peat soil in many parts of Borneo and in one area in Malaya. It is of interest to note that *Dacrydium pectinatum* has a similar ecology.

Vern. Malaya: *dammar, dammar daging, dammar minyak, tulong*, M; Sumatra: *hedje*, Tapanuli; Borneo: *bindang*, Sarawak, *bulu*, Iban, *salang*, Kedayah, *tambunan*, Sabah, *manggilam*, Dusun, *bangalan, bengalan*, Sampit, Pilau, *toga*, W. Kutai, *bembuëng*, SE. Borneo, *nuju*, Dajak, *enghatan*, Sanggan, *pisau, putut*, Sintang.

Note. If the proposal to reject *Pinus dammara* LAMB. in favour of *Agathis borneensis* WARB. is not accepted, the proper name of this species would be *Agathis dammara* (LAMB.) RICHARD, a name heretofore (incorrectly) associated with different species of Celebes, the Moluccas and the Philippines (see under *A. celebica* and *A. philippinensis*). If various closely related species were combined as varieties or subspecies under this species, there would be no reason to reject the name *Agathis dammara*.

2. Agathis celebica (KOORD.) WARB. Monsunia 1 (1900) 185; DALLIMORE & JACKSON, Handb. Conif.

(1923) 143; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 461; DE LAUB. Kalikasan 7 (1978) 146; Blumea 24 (1978) 504, f. 2; SILBA, Phytologia Mem. 8 (1986) 32. — *Dammara alba* RUMPH. *ex* HASSK. Tijd. Nat. Gesch. Phys. 9 (1842) 179; PARL. in DC. Prod. 16, 2 (1868) 374. — *Dammara rumphii* PRESL, Epim. Bot. (1851) 236, *nom. superfl.* — *Dammara orientalis var. pallens* CARR. Traité Gén. Conif. (1855) 426. — *Dammara orientalis var. alba* KNIGHT *ex* HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 211. — *Dammara alba var. alba* HASSK. Abh. Naturf. Ges. Halle 9 (1866) 180. — *Dammara alba var. celebica* HASSK. *l.c.* — *Dammara celebica* KOORD. Meded. Lands Pl. Tuin 19 (1898) 263. — *A. dammara auct. non* RICHARD: WARB. Monsunia 1 (1900) 182, t. 9, f. 1; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 98; DE LAUB. Blumea 24 (1978) 503, f. 1. — *A. alba auct. non* FOXW.: MERR. Rumph. Herb. Amb. (1917) 76; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 466; DALLIMORE & JACKSON, Handb. Conif. ed. 3 (1948) 178. — *A. beckingii* MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 463. — *A. hamii* MEIJER DREES, *l.c.* 462, f. 1. — *A. loranthifolia auct. non* SALISB.: MEIJER DREES, *l.c.* 464. — *A. celebica ssp. celebica* VELDKAMP & WHITM. in Veldkamp & De Laub. Taxon 33 (1984) 345. — *A. dammara ssp. dammara auct. non* WHITM.: WHITM. Pl. Syst. Evol. 135 (1980) 57, *p.p.*

Huge tree to 65 m tall. *Juvenile leaves* ovate-lanceolate, up to 15 by 4.6 cm. Shade leaves on mature trees acute and roughly 9 by 3 cm. *Leaves* from fully exposed branches well rounded at the apex but still tapering, not blunt, 6–8 by 2–3 cm, tapering at the base to a 5–10 mm petiole. *Pollen cones* after shedding pollen 4–6 by 1.2–1.4 cm or possibly even larger, subtended by a short peduncle *c.* 3 mm long, normally axillary but sometimes terminal (*A. beckingii*). The apical part of the *microsporophyll* spoon-shaped, spreading, with the stalk attached well behind its centre, *c.* 2.5 mm by 2 mm and slightly angled at the apex. *Seed cone* oval, 9–10.5 by 7.5–9.5 cm. *Seed bract* with a low thick ridge along the apical margin exposed in the unopened cone to within a few mm of its lateral margins, roughly triangular in shape, the lateral margins nearly straight with a small scallop 4–8 mm above the base on one side, the upper corners more or less angular and rigid, 32–36 by 42–45 mm. *Seed c.* 14 by 9 mm with a short acute projection on one upper corner and a broad rounded wing *c.* 24 by 16 mm at the other.

Distr. *Malesia*: Celebes and Moluccas to Palawan in the Philippines and probably other parts of southern Philippines. Fig. 75.

Ecol. A forest emergent scattered and locally common in lowland rain-forest from near sea-level to 1200 m.

Fig. 75. Range of *Agathis celebica* (KOORD.) WARB.

Vern. *Dammar, dammar radja*, M, *hulontuu*, Malili, *kawo*, Maliki, *kisi*, Buru, *salo*, Ternate, *dayungon*, Samar, Philippines.

Note. WHITMORE (1980) insists that he can find no difference between this and *A. philippinensis* among others and certainly the vast majority of the collected materials (shade leaves and immature reproductive organs) is enigmatic. WHITMORE's descriptions show he is dealing with immature material and the notion that pollen cones continue growth after shedding their pollen is inadmissible. Groups of both species grow side by side at Bogor, where properly mature material can be compared and sharp differences easily seen. Because this is the only species known on Ambon, it is the species which RUMPHIUS (Herb. Amb. 2, 1741, 174, t. 57) has in mind and, like the closely related *A. borneensis*, which occupies similar habitats west of the Makassar Strait, is an important producer of the resin known as dammar.

3. Agathis spathulata DE LAUB., *sp. nov.*; SILBA, Phytologia Mem. 8 (1986) 37, *nom. inval.* — *A.*

robusta ssp. nesophila WHITM. Pl. Syst. Evol. 135 (1980) 64.

Arbor magna ad 60 m alta. Folia adulta acuta 9–10 cm × 20–30 mm ad spathulata 7–9 cm × 18–20 mm. Strobili masculini 9–13 mm diametri, 4–7 cm longi, apicis microsporophyllis 1,5–2 mm latis, 1,3–1,5 mm longis. Squamae femineae 35–42 mm latae, 27–32 mm altae, marginibus rotundibus apicis costis acutis. Holotypus: DE LAUBENFELS P741 (L).

Huge tree to 60 m tall. *Juvenile leaves* ovate-lanceolate, not at all acuminate, up to 13 by 4.5 cm. *Adult leaves* bluntly acute, 9–10 cm by 20–30 mm to broadly rounded and 7–9 cm by 18–20 mm, tapering at the base to a 5–10 mm petiole. *Mature pollen cones* 4–7 cm by 9–13 mm, subtended by a 2–9 mm peduncle, the apex of the microsporophyll spoon-shaped without ridges, 1.5–2 by 1.3–1.5 mm, broadly acute. *Seed cone* oval, 8.5–10 by 6.5–7.5 cm. *Seed bract* with a thin sharp ridge along the apical margin, broadly rounded at the upper corners, a small 6 mm scallop on one side of the base and a larger 10 mm scallop on the other, 27–32 mm high by 35–42 mm broad. *Seed c.* 10 by 6 mm, with a sharp projection on one upper corner and an elongated bent wing *c.* 24 by 10 mm at its widest at the other corner.

Distr. *Malesia*: SE. New Guinea, E. Highland, near Obura. Fig. 76.

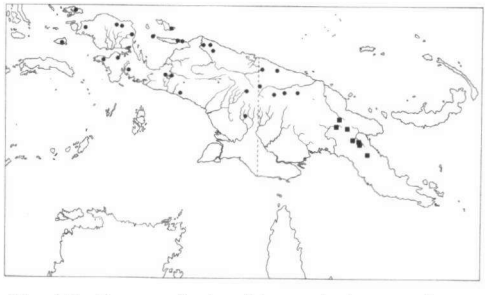

Fig. 76. Range of *Agathis spathulata* DE LAUB. (squares) and *A. labillardieri* WARB. (dots).

Ecol. Scattered as a rain-forest emergent or surviving in small exposed groves between 900 and 1980 m.

Vern. *Asong, muwaka, ogapa.*

Note. The seed cone scale and seed, though smaller, resemble those of *A. robusta*, a lowland species, but the pollen cone in particular is quite different.

4. Agathis lenticula DE LAUB. Blumea 25 (1979) 537, f. 4; SILBA, Phytologia Mem. 8 (1986) 34. — **Fig. 77.**

Large tree to 45 m tall. *Juvenile leaves* to 11 cm by 47 mm, ovate, tapering to an acute, scarcely acuminate apex and more sharply at the base. *Adult leaves* lens-shaped, more or less acute, 5–7 cm by 18–24 mm, tapering to a 3–7 mm petiole, glaucous on the underside. *Mature pollen cones* 3–4 cm by 9–10 mm, subtended by a 2–6 mm peduncle, the apex of the microsporophyll spoon-shaped and spreading, 2–2.5 by 1.5–2 mm, apex blunt. *Seed cone* nearly spherical, *c.* 7 by 6 cm. *Seed bract* with a thin sharp ridge along the apical margin, lateral margins broadly rounded with a strongly hooked scallop 7 mm above the base on one side, *c.* 27 mm high by 38–45 mm broad. *Seed c.* 11 by 7 mm with a slight blunt to no projection on one upper corner and a broadly rounded wing *c.* 8 by 14 mm at the other corner.

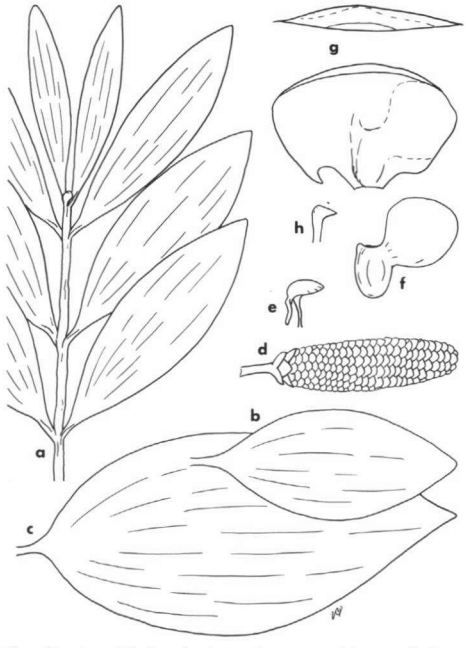

Fig. 77. *Agathis lenticula* DE LAUB. a. Mature foliage shoot; b. extreme leaf shape; c. juvenile leaf; d. mature pollen cone, all × 0.4; e. profile view of microsporophyll, × 1.25; f. seed; g. end view and facial view of the seed cone scale; h. profile view of the upper edge of the same.

Distr. *Malesia*: Sabah (Mt Kinabalu and the Crocker Range). Fig. 78.

Ecol. Emergent in mountain rain-forest, 1140–1680 m.

Vern. *Tanggilan, tengilan, tungilan*, Dusun.

Note. This species occurs just below *A. kinabaluensis* on Mt Kinabalu where the two can easily be compared in the field. The distinctive leaf shapes are readily apparent but in herbarium specimens the

Fig. 78. Range of *Agathis lenticula* DE LAUB. (circles) and *A. orbicula* DE LAUB. (dots).

glaucous leaf undersurface is generally not detectable. Other differences are the larger pollen cones with blunt, not angled, microsporophylls and the lack of a sharp projection at the upper corner of the seed. Besides *A. orbicula* and *A. endertii*, other *Agathis* species with glaucous leaf undersides occur far to the east beyond Malesia.

5. Agathis orbicula DE LAUB. Blumea 25 (1979) 540, f. 5; SILBA, Phytologia Mem. 8 (1986) 36. — **Fig. 79.**

Tree to 40 m tall. A light yellow resin is produced in some abundance. *Juvenile leaves* ovate and bluntly acute, to 6.5 cm by 28 mm. *Adult leaves* ovate to orbicular, broadly rounded to slightly angled at the apex, 24–40 by 12–24 mm, tapering sharply at the base to a 3–7 mm petiole, glaucous on the underside. *Mature pollen cones* 8–14 by 4–6 mm, subtended by a 2–6 mm peduncle, the apex of the microsporophyll helmet-shaped, 1.2–1.5 by 1–1.2 mm, apex blunt. *Seed cone* oval, *c.* 7 by 4.5 cm. *Seed bract* with an acute ridge along the apical margin, ovate with a 4 mm scallop spreading nearly perpendicularly to each side of the base, *c.* 20 mm high and 33 mm broad. *Seed* unknown but leaving a blunt impression suggesting a shape like that of *A. lenticula*.

Distr. *Malesia*: S. Sabah to Central Sarawak. Fig. 78.

Ecol. Scattered in rain-forests and kerangas on low mountains and plateaus between 450 and 1050 m.

Vern. *Tumuh*, Murut, *tubu*, Kenyah, *bulok*, Iban.

6. Agathis philippinensis WARB. Monsunia 1 (1900) 185, t. 8E; DALLIMORE & JACKSON, Handb. Conif. (1923) 147; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 468; SILBA, Phytologia Mem. 8 (1986) 36. — *Dammara rumpfii auct. non* PRESL: PRESL, Epim. Bot. (1841) 236. — *A. regia* WARB. Monsunia 1 (1900) 183, t. 8B; DALLIMORE & JACKSON, Handb.

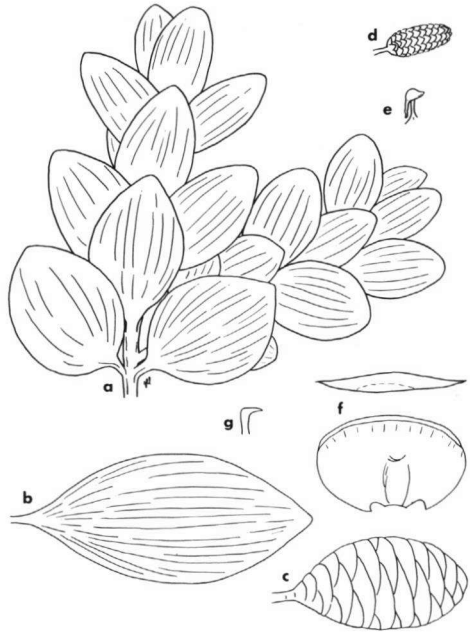

Fig. 79. *Agathis orbicula* DE LAUB. a. Mature foliage shoots; b. juvenile leaf; c. young seed cone; d. mature pollen cone, all ×0.4; e. profile view of microsporophyll, ×1.4; f. end view and facial view of the seed cone scale; g. profile view of the upper edge of the same.

Conif. (1923) 147. — *A. alba auct. non* FOXW.: Foxw. Philip. J. Sc. 4 (1909) Bot. 442. — *A. dammara auct. non* RICHARD: DE LAUB. Kalikasan 7 (1978) 144; Blumea 24 (1979) 499, f. 1. — *A. dammara ssp. dammara auct. non* WHITM.: WHITM. Pl. Syst. Ecol. 135 (1980) 56, *p.p.*, t. 5, f. 1 & 2.

Huge tree to 60 m tall. Abundant white resin produced. *Juvenile leaves* ovate and distinctly acuminate, to 7 by 3 cm. *Adult leaves* ovate, very slightly to distinctly acute, 4–6 by 1.5–2 cm, the smaller leaves, which probably derive from more exposed position, being the least acute, tapering at the base to a 5–8 mm petiole. *Mature pollen cones* 2.5–4.5 cm by 10–11 mm, subtended by a short peduncle, the apex of the microsporophyll helmet-shaped with the stalk attached close to its centre, 2–2.5 by 1.5–2 mm, the apex very slightly angled. *Seed cone* oval, 7–9 by 12 cm. *Seed bract* with a low thick ridge along apical margin, broadly rounded at the upper corners, a small 3–6 mm scallop on one side of the base, 28–32 mm high by 35–45 mm broad. *Seed c.* 11 by 6 mm, broadly acute at one upper corner and with a wing *c.* 20 by 11 mm at its widest at the other corner.

Fig. 80. Range of *Agathis philippinensis* WARB.

Distr. *Malesia*: Philippines to Celebes and Halmaheira. Fig. 80.

Ecol. Scattered and often emergent in upland rain-forest, mostly 1200–2200 m, occasionally as low as 450 m in Halmaheira, 900 m in Celebes and far to the north in Luzon to 250 m.

Vern. *Dammar*, M, *goga, solo, tjoga*, Manado, *molewaun*, Teliwang, *almaciga*, Philippines, *dayungon*, Samar, *dingan*, Misamis.

Note. Reports by foresters of 'different' trees in the southern parts of the Philippines may well apply to *A. celebica* which has been collected there. Most Philippine collections are of nondescript leaves and (rarely) immature cones.

7. Agathis flavescens RIDLEY, Kew Bull. (1914) 332; J. Fed. Mal. St. Mus. 6 (1915) 3; DALLIMORE & JACKSON, Handb. Conif. (1923) 143; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 464; SILBA, Phytologia Mem. 8 (1986) 33. — *A. dammara ssp. flavescens* (RIDLEY) WHITM. Pl. Syst. Evol. 135 (1980) 59. — *A. celebica ssp. flavescens* (RIDLEY) VELDKAMP & WHITM. *ex* VELDKAMP & DE LAUB. Taxon 33 (1984) 346.

Small to medium-sized tree to 12 m tall. *Juvenile leaves* ovate-lanceolate and slightly acuminate, up to 8 cm by 32 mm. *Adult leaves* ovate and, unlike most adult *Agathis* leaves, often wider before the middle, 3–4 cm by 10–20 mm, rounded and blunt at the apex or very slightly angled, tapering at the base to a 3–5 mm petiole. *Mature pollen cones* 20–35 by 8–9 mm, subtended by a 2–8 mm peduncle, the apex of the microsporophyll helmet-shaped, 2 by 1.8 mm, the apex slightly angled. *Seed cone* oval, 6–7 by 7–8 cm. *Seed bract* with a thick ridge along the apical margin, broadly rounded at the upper corners, a large scallop more than one cm from the base on one side and a smaller *c.* 6 mm scallop on the other, 26–29 by 35–37 mm. *Seed* oval, *c.* 11 by 9 mm, blunt at one upper corner and with a broad wing 17 by 14 mm at its widest at the other corner.

Distr. *Malesia*: the two or three highest peaks in Peninsular Malaya.

Ecol. Scattered trees above a low summit scrub, 1200–1800 m, the leaves often yellow, suggesting adaptation to difficult nutrient conditions.

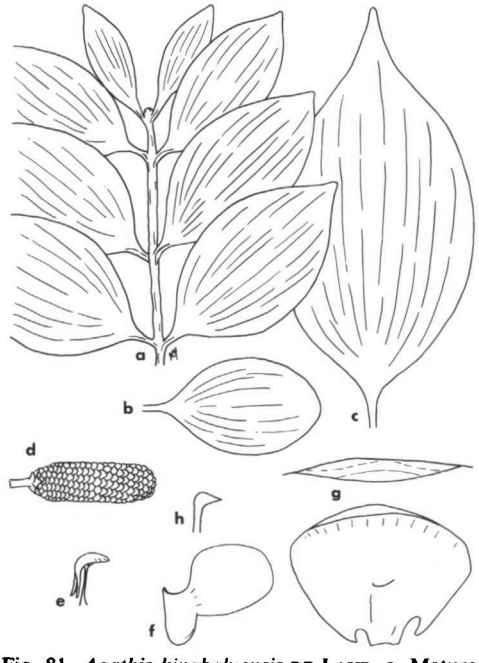

Fig. 81. *Agathis kinabaluensis* DE LAUB. a. Mature foliage shoot; b. extreme leaf shape; c. juvenile leaf; d. mature pollen cone; all ×0.4; e. profile view of microsporophyll, ×1.25; f. seed; g. end view and facial view of the seed cone scale; h. profile of the upper edge of the same.

Note. This species corresponds in Malaya to *A. philippinensis* which it strongly resembles, differing in smaller cones, somewhat differently shaped leaves and seeds and especially by the blunt corner of the seed opposite the wing.

8. Agathis kinabaluensis DE LAUB. Blumea 25 (1979) 535; SILBA, Phytologia Mem. 8 (1986) 34. — **Fig. 81.**

Small to large tree to 36 m tall. *Juvenile leaves* ovate and strongly acuminate, to 9 cm by 44 mm. *Adult leaves* ovate, slightly acuminate or occasionally on the smaller leaves round and blunt, 3.5–7 cm by 18–32 mm, tapering at the base to a 4–7 mm petiole. *Mature pollen cones* 18–30 by 8–10 mm, nearly sessile to a 4 mm peduncle at the base, the apex of the microsporophyll spoon-shaped, spreading slightly, 1.6–1.8 by 1.2–1.6 mm, the apex very slightly angled. *Seed cone* oval, 7.5–8.5 by 11 cm. *Seed bract* with a prominent narrow ridge along the apical margin, broadly rounded at the upper corners, a smaller 4 mm and a larger 6 mm scallop on either side of the base, 28–32 by 40–45 mm. *Seed c.* 11 by 7 mm, prominently acute at one upper corner and with a broad wing 20 by at least 12 mm at the other corner.

Distr. *Malesia*: Mt Kinabalu in Sabah.

Ecol. In or rising slightly above the mossy forest and rather small where the forest is stunted, 1500–2400 m.

Vern. *Tumu*, Murut.

Note. This species in Borneo corresponds in many ways with *A. philippinensis* but is nevertheless substantially different.

2. Section Rostrata DE LAUB., *sect. nov.*

Arboris. Squama feminea projectioni apici instructa. Strobilus femineus 5–6 × 6–7 cm. Strobilis masculinus sessilus. Typus: Agathis australis.

Small to large trees. *Leaves* ovate and slightly angled at the apex to round and blunt, the leaf undersides distinctly glaucous, solitary resin canals between the vascular bundles. *Juvenile leaves* more acute. *Pollen cones* more or less sessile. *Microsporophylls* spoon-shaped, more or less acute and spreading. *Seed cones* spherical to oval and rather small, 5–6 by 6–7 cm. *Seed bract* with a distinct projection or beak near the centre of the ridged apical margin. *Seeds* broadly oval with a blunt projection at one upper corner and a broad wing at the other corner.

Distr. There are 3 *spp.*, widely separated, in New Zealand (1 *sp.*), in New Caledonia (1), and in *Malesia*: Borneo (1).

Note. The projection on the seed bract corresponds to the ligule in *Araucaria* and other conifers and for *Agathis* is a primitive trait.

9. Agathis endertii MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 470; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 99; DE LAUB. Blumea 25 (1979) 534, f. 2; SILBA, Phytologia Mem. 8 (1986) 33. — **Fig. 82.**

Tree to at least 48 m. *Juvenile leaves* apparently lanceolate. *Adult leaves* ovate and broadly acute to semicircular and blunt at the apex, 5–8 cm by 17–36 mm with considerable variation on individual specimens, tapering to a 3–6 mm petiole, glaucous on the underside. *Mature pollen cones* 26–38 by 7 mm, sessile, the apex of the microsporophyll spoon-shaped, spreading, 2.5 by 2 mm, the apex slightly angled. *Seed cone* oval, 4.5 by 7 cm. *Seed bract* with a prominent narrow ridge along the apical margin surmounted by a spreading blunt more or less triangular projection *c.* 8 by 3 mm, somewhat rounded at the upper corners, a small 4 mm scallop on one side at the base, at least 25 mm by 30 mm. *Seed c.* 11 by 8 mm, a short acute projection on one upper corner, a broad wing *c.* 18 by 14 mm at its widest at the other corner.

Distr. *Malesia*: Borneo. Fig. 83.

Ecol. In more or less isolated populations from near sea-level to 1440 m, often associated with sandstone kerangas.

Vern. *Bulok*, Iban.

Note. The leaves more or less resemble in particular *A. borneensis* (but lack the paired resin canals) so that sterile specimens cannot be readily identified in this otherwise quite distinct species.

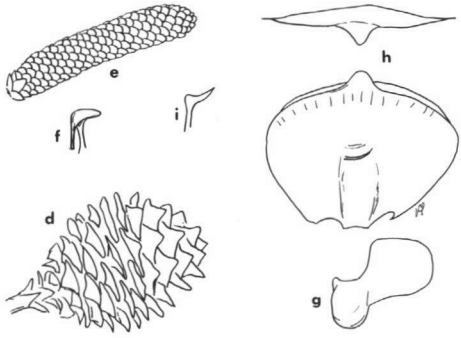

Fig. 83. Range of *Agathis endertii* MEIJER DREES.

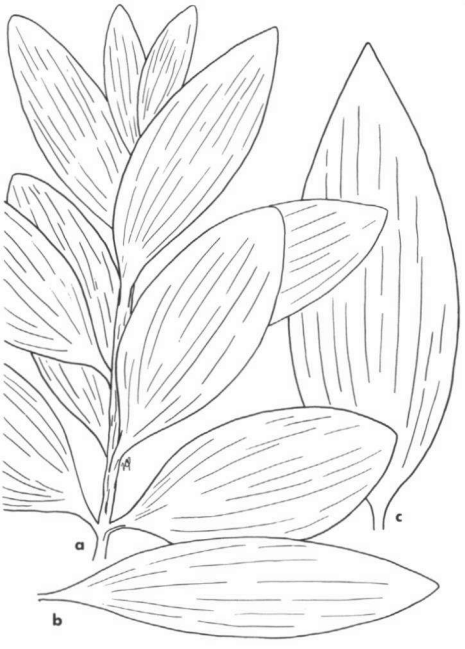

Fig. 82. *Agathis endertii* MEIJER DREES. a. Mature foliage shoot; b. leaf variation; c. juvenile leaf; d. young seed cone; e. mature pollen cone, all ×0.4; f. profile view of microsporophyll, ×1.25; g. seed; h. end view and facial view of the seed cone scale; i. profile view of the upper edge of the same.

3. Section Prismatobracteatae

MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 470.

Large trees. *Microsporophylls* with sharp creases dividing the apical part into three or more facies. *Pollen cones* with a short peduncle. *Seed bracts* always blunt along their apical margins. *Leaves* not glaucous underneath.

Distr. From New Guinea and New Britain to Queensland, New Caledonia and Vanuatu (New Hebrides) 5 *spp.*; in *Malesia*: 2 *spp.*

KEY TO THE SPECIES

1. Apical part of pollen cone prismatic with a series of lateral facies surrounding a flat hexagonal upper face **10. A. labillardieri**
1. Apical part of pollen cone divided into three lateral facies ..... **11. A. robusta**

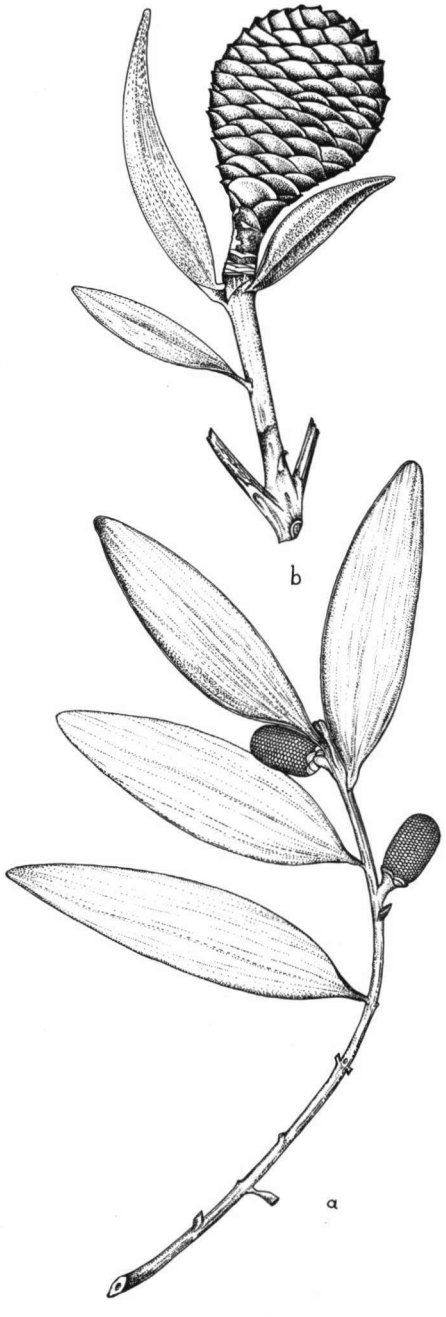

Fig. 84. *Agathis labillardieri* WARB. a. Twig with pollen cones; b. seed cone, both ×0.4.

10. Agathis labillardieri WARB. Monsunia 1 (1900) 183; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 471; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 99; WHITM. Pl. Syst. Evol. 235 (1980) 60; SILBA, Phytologia Mem. 8 (1986) 34. — **Fig. 84, 85.**

Huge tree to 60 m. *Juvenile leaves* ovate and acuminate, to 10 by 6 cm. *Adult leaves* ovate to oval lanceolate, acute, 6–9 cm by 20–24 mm, narrowing to a 5–7 mm petiole. *Mature pollen cones* 25–35 by 10–15 mm, subtended by a 2–6 mm peduncle, the apical part of the microsporophyll prismatic with a series of lateral facies surrounding a flat hexagonal upper face 1–1.5 mm wide and long and crowded so that only the upper face is exposed. *Seed cone* oval, 8.5–10 by 7.5–9 cm. *Seed bract* with a low thick ridge along the apical margin exposed in the unopened cone to within a few mm of its margins, roughly triangular in shape with nearly straight lateral margins, with a distinct scallop *c.* 8 mm above the base on one side, slightly rounded at the upper corners, 30–32 by 38–42 mm. *Seed c.* 12 by 7 mm with a short broadly acute projection on one upper corner and a broad rounded wing *c.* 20 by 15 mm at the other.

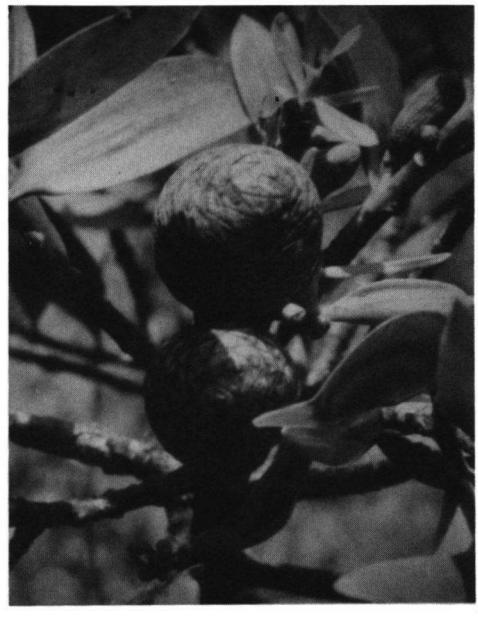

Fig. 85. Cones of *Agathis labillardieri* WARB. of a specimen growing in Sarmi on the north coast of West New Guinea (Photogr. H.R.KARSTEL, 1957).

Distr. *Malesia*: throughout the western part of New Guinea and eastward to the margins of the Sepik Valley. Fig. 76.

Ecol. From near sea-level to 1350 m or occasionally to 1800 m, often on ultrabasic soil and locally very common.

Vern. *Dammar*, M, *pen*, Pidgin, *legatulus*, Mooi lang., *aisjier*, Arguni, *idjir*, Irahutu, *tar*, Kebar, *waiui*, Pousami, *kessi*, Roberai, Kuri, *fuko*, Manikiong, *uto*, Kapauku, *warkai*, Kamora, Kokonao, *osier*, Itik, *sao*, Kwerba, *wel*, Iwer, *nu*, Wagu, *aglo*, Orne, *koba*, E. Sepik.

11. Agathis robusta (MOORE) BAILEY, Synops. Queensl. Fl. (1883) 498; WARB. Monsunia 1 (1900) 185; BAKER & SMITH, Pines of Austr. (1910) 376; DALLIMORE & JACKSON, Handb. Conif. (1923) 148; FRANCO, An. Inst. Sup. Agron. 18 (1951) 105, f. 2–10; HYLAND, Brunonia 1 (1978) 105, f. 1; SILBA, Phytologia Mem. 8 (1986) 37. — *Dammara robusta* MOORE *ex* F.v.M. Quart. J. Trans. Pharm. Soc. Vict. 2 (1806) 173. — *Dammara palmerstonii* F.v.M. Vict. Natur. 8 (1891) 45. — *A. palmerstonii* (F.v.M.) BAILEY, Queensl. Dept. Agric. Bot. Bull. 3 (1891) 17; DALLIMORE & JACKSON, Handb. Conif. (1923) 147. — *A. robusta var. robusta* WHITM. Pl. Syst. Evol. 135 (1980) 63. — *A. robusta var. nesophila auct. non* WHITM.: WHITM. *l.c.* f. 6.

Tree to 48 m. *Juvenile leaves* ovate and acuminate, up to 13 by 3.8 cm. *Adult leaves* ovate and acute to rounded at the apex, 5–9.5 cm by 10–26 mm, tapering to a 3–10 mm petiole. *Mature pollen cones* 4–8.5 cm by 7–9 mm, subtended by a 2–9 mm peduncle, apex of microsporophyll sharply angled to form three lateral facies, *c.* 1 mm wide and long, the slightly angled along its margin front (apical) face directed inward to the bases of the next microsporophylls ahead on either side. *Seed cone* oval to elongated, 9–15 by 8–10 cm. *Seed bract* with a thin sharp ridge along the apical margin, rounded at the upper corners, the curving lateral margins with a larger scallop *c.* 10–12 mm above the base on one side and a smaller one 5–8 mm above the base on the other side, 30–45 by 39–46 mm. *Seed c.* 10 by 6 mm with a long acute projection on one upper corner and a long bent wing *c.* 30 by 12 mm at the other.

Distr. In four localized clusters, one in the central part of New Britain, another east of Port Moresby in Papua New Guinea, the largest in the rainforests of northern Queensland, and the last in southern Queensland on Fraser I. and the nearby mainland. Fig. 86.

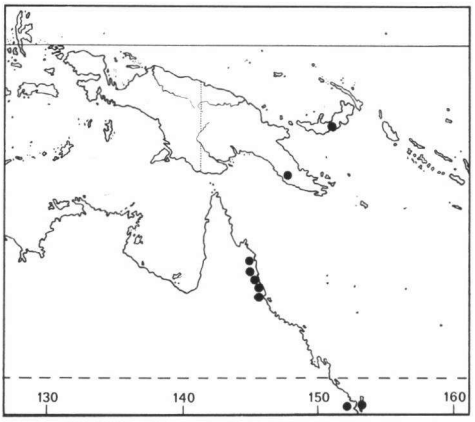

Fig. 86. Range of (MOORE) BAILEY.

Ecol. Locally common on a variety of soils in exposed positions following disturbance from near sea-level in Australia and 400 m further north to 900 m throughout its range.

Vern. *Naveil*, New Britain.