

THE SPECIES OF AGATHIS (ARAUCARIACEAE) OF BORNEO

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The important genus *Agathis* is well represented in the rich flora of the island of Borneo. In some places it forms nearly pure stands and has been heavily exploited for its resin and for lumber. Three species, one of which merely represents leaf variations from another, have been proposed previously for this genus in Borneo (Warburg, 1900; Meijer Drees, 1940). Several hundred collection numbers can be found in the major herbaria, much the majority of which belong to one species. This is particularly true for the non-Asian herbaria. During several field trips to Borneo, however, I identified three additional quite distinct unnamed species. The great variability of leaf size and shape even on individual plants in this genus together with difficulty in making good representative collections from these immense trees has surely hindered the recognition of the distinctions to be described here. None of these species has been totally overlooked, to be sure, inasmuch as a few specimens of each have previously reached the major herbaria. Furthermore, Whitmore (1979) concluded after seeing some of this material that it did not correspond to any of the species already described from Borneo but in fact represented *Agathis dammara*, a species not actually found in Borneo. I will describe all five Borneo species in order to clarify their distinctions. Only fully mature pollen cones and seed cone scales will be considered in this description along with as much as possible the normal foliage leaves as opposed to the poorly developed leaves of primary branches and seed cone bearing shoots.

KEY TO THE BORNEO SPECIES OF AGATHIS

1. Leaves not glaucous underneath.
 2. Pollen cone more than 2 cm in diameter; leaves with paired resin canals between many of the vascular strands. **A. borneensis**
 2. Pollen cone less than 1 cm in diameter; resin canals never paired between the vascular strands
 3. Seed cone scale with a distinct protruding lip; pollen cone sessile; leaf normally at least 5 cm long and never acuminate **A. endertii**
 3. Seed cone scale without a lip; pollen cone pedunculate; leaf normally less than 5 cm long and usually acuminate. **A. kinabaluensis**
1. Leaves glaucous underneath and never acuminate; pollen cone pedunculate and about 1 cm in diameter or less; seed cone scale without a lip.
 4. Pollen cone about 1 cm in diameter and 4 cm long; seed cone scale 28 mm high; leaf normally more than 5 cm long. **A. lenticula**
 4. Pollen cone about 0.5 cm in diameter, less than 1.5 cm long; seed cone scale 20 mm high; leaf normally less than 4 cm long. **A. orbicula**

Agathis borneensis Warburg, *Monsumia* 1 (1900) 184. — *Agathis beccarii* Warburg, *ibid* 184. — *Agathis rhomboidalis* Warburg, *ibid* 184. — *Agathis latifolia* Meijer Drees, *Bull. Jard. Bot. Buitenzorg ser. 3*, 16 (1940) 459. — Fig. 1.

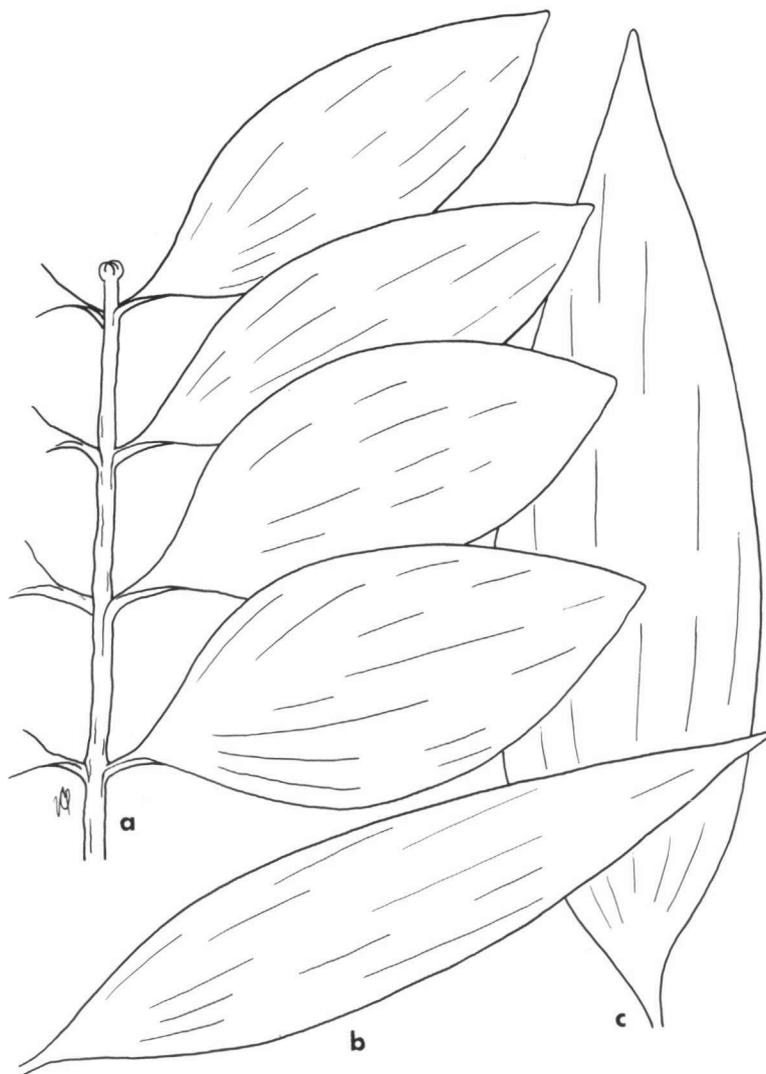
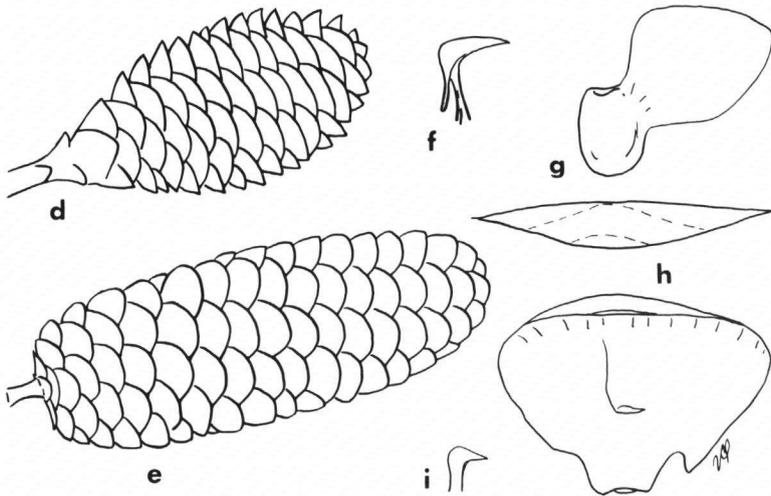


Fig. 1. *Agathis borneensis* Warburg. — a. mature foliage shoot; b. leaf variation of shaded branches or alternating with a; c. juvenile leaf; d. young seed cone; e. mature pollen cone; f. profile view of microsporophyll, $\times 1.5$; g. seed; h. end view and facial view of the seed cone scale; i. profile view of the upper edge of the same. All but f natural size.



Large tree of low to moderate elevation rainforests, up to about 1,200 m. Juvenile leaves oval and lanceolate, as much as 4 cm wide and 14 cm long. Normal foliage leaves more or less oval, narrowing at the base to a short petiole about 5 mm long and narrowing at the other end to a more or less acute apex, 6–12 cm long and 2–3.5 cm wide. The most common foliage leaf is about 7 cm long and 3 cm wide but branches with relatively long and narrow leaves often occur interspersed with the more usual type as well as being representative of younger trees. Paired resin ducts, one above the other, rather than single resin ducts are found between some to most of the vascular strands in the leaves. *Pollen cones* more or less oblong, about 2.5 cm in diameter and 4–7 cm long, rounded at the apex and narrowing abruptly at the base to a short peduncle 2–10 mm long. *Microsporophylls* large, the exposed apex about 6 mm wide and 5 mm long with a semicircular margin. *Seed scales* roughly triangular but well rounded at the upper corners, about 26 mm high and 36 mm wide. Young *seed cone* oval with the upper edges of the individual seed scales more or less spreading.

The large pollen cones and microsporophylls readily distinguish *Agathis borneensis* from all other species and the paired resin ducts in the leaves distinguish it from most species, incl. all of the remaining species in Borneo. The seed cone scale is smaller than in many other species but larger than in some. The predominant leaf type is broader and more oval than usual in the genus but this character is not constant and sterile specimens of *A. borneensis* can not be distinguished with confidence in most cases. The narrower leaf form was, in fact, selected by Warburg as the basis for *A. beccarii*. Warburg applied the name *A. rhomboidalis* to material from Malaya and Meijer Drees proposed the name *A. latifolia* for material from Sumatra. These latter are identical with *A. borneensis* as Whitmore (1979) has pointed out. Small, narrow, poorly formed leaves are often produced on primary branches and on shoots bearing seed cones as is the case in all species of *Agathis*.

Much the most common species in Borneo as well as the only species in Malaya and Sumatra. Extensive nearly pure stands occur sporadically near sea level in

Borneo, generally on rather acid soils. Otherwise the species is found scattered in forests at moderate elevation on a variety of soils.

Agathis endertii Meijer Drees, Bull. Jard. Bot. Buitenzorg ser. 3, 16 (1940) 470 ('*enderti*'). – Fig. 2.

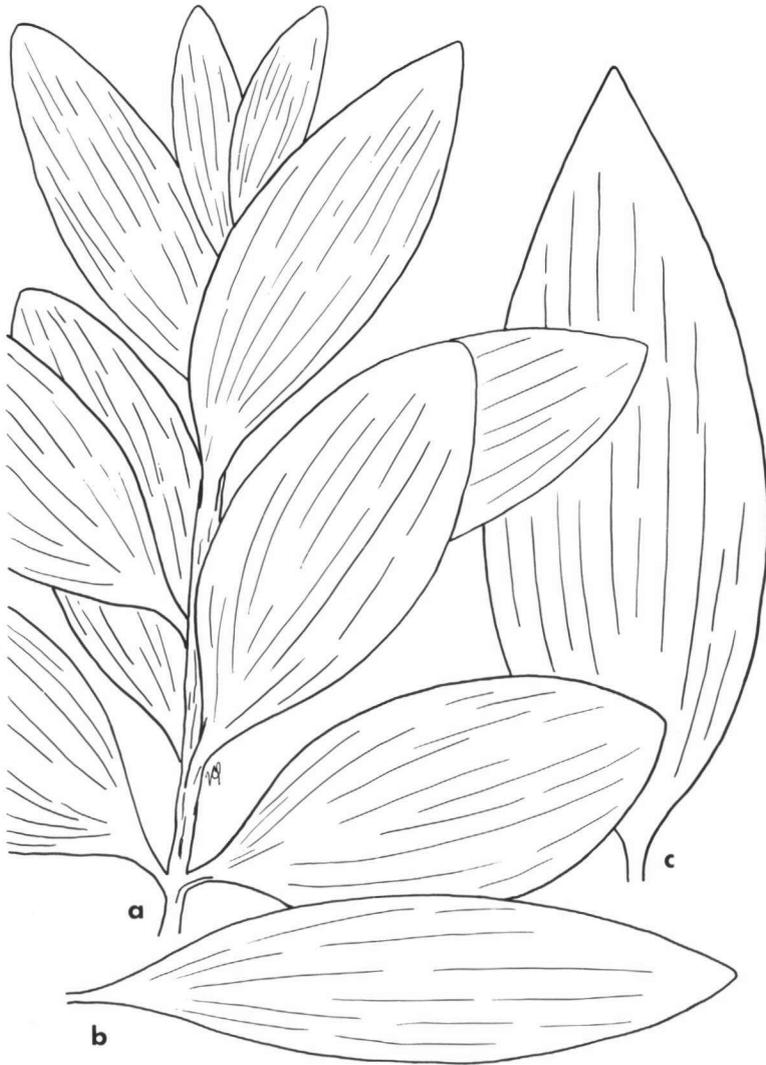
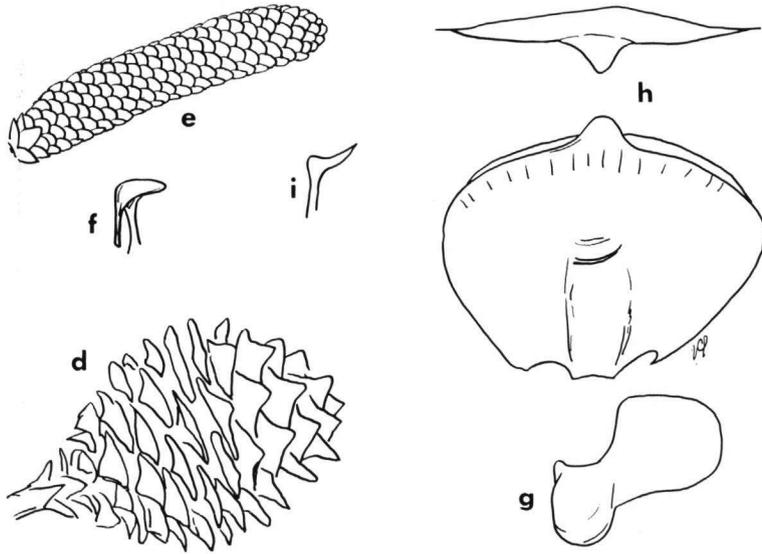


Fig. 2. *Agathis endertii* Meijer Drees. — a. mature foliage shoot; b. leaf variation; c. juvenile leaf; d. young seed cone; e. mature pollen cone; f. profile view of microsporophyll, $\times 3$; g. seed; h. end view and facial view of the seed cone scale; i. profile view of the upper edge of the same. All but f natural size.



Large tree of moderate elevation rainforest, up to 1440 m. Juvenile *leaves* large, oval, and acute. Normal foliage leaves more or less oval, narrowing at the base to a short petiole about 5 mm long and narrowing at the other end to a rounded or more often more or less acute apex, 5–9 cm long, 2–3 cm wide. Variation of leaf shape much as in *Agathis borneensis*. *Pollen cones* long cylindrical, 7–9 mm in diameter and 3–4 cm long, rounded at the apex and narrowing to a sessile base. The exposed apex of the *microsporophylls* about 3 mm wide and 2 mm long with a semicircular margin. *Seed scales* roughly triangular but well rounded at the upper corners, about 32 mm high and 42 mm wide, a prominent triangular rounded lip about 5 mm long protruding from the upper margin. Young *seed cone* oval and dominated by the spreading or even reflexed lips of the individual seed scales. Initially the seed scales are no wider than these extensions but subsequently the scale expands leaving these apical parts in the form of a lip.

The lip of the seed cone and the sessile pollen cone each separately distinguish *Agathis endertii* from most other species and together from all, while each of these characters is unique in Borneo. The dried leaves of *Agathis* in general have pronounced grooves between the vascular strands on their upper surfaces but the paired resin ducts between the vascular strands in the leaves of *A. borneensis* tend to make those leaves appear smoother. Otherwise the leaves of the latter and *A. endertii* are externally virtually identical making the separating of sterile specimens next to impossible.

Widely dispersed on the island of Borneo. *A. endertii* has been reported from sandstone regions and generally comes from areas of sedimentary formations so there may be a relationship to soil.

***Agathis kinabaluensis* de Laubenfels, *sp. nov.* — Fig. 3.**

Arbor ad 36 m. *Folia* iuvenilia rotunda, forte acuminata, breve pedunculata, ad 9 cm longa, 44 mm lata. *Folia* adulta rotunda, acuminata vel obtusa, breve pedun-

culata, 4–7 cm longa, 18–32 mm lata. *Strobili masculi* cylindracei, 2–3 cm longi, 9 mm diametri, apicis rotundis, basis pedunculatis, pedunculus 4 mm longus; squamae apicis plus minusve triangulis, 2.5 mm latae, 2 mm longae. *Squamae strobilorum femineorum* plus minusve triangulae angulis superis rotundis, 28 mm altae, 40 mm latae. Strobilus ca. 11 cm longus, 8 cm diametrus.

T y p u s : *de Laubenfels P625* (L; iso in A, K, SAN), Mt. Kinabalu, Kinabalu Mountain Trail.

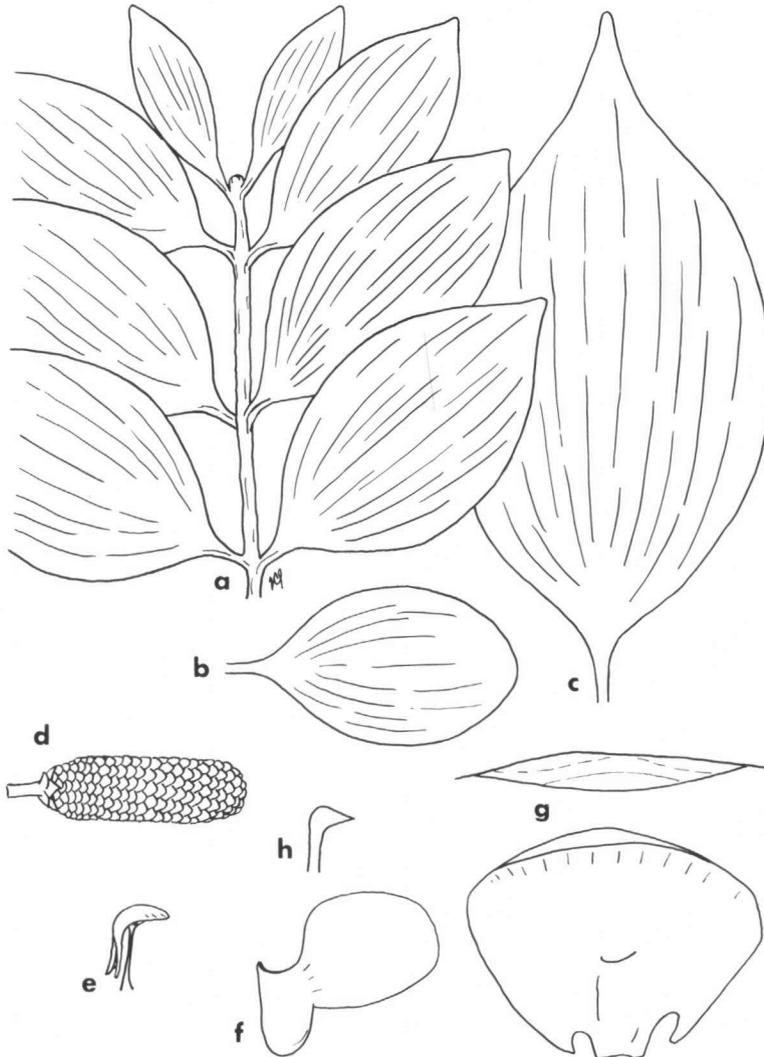


Fig. 3. *Agathis kinabaluensis* de Laubenfels. — a. mature foliage shoot; b. extreme leaf shape; c. juvenile leaf; d. mature pollen cone; e. profile view of microsporophyll, $\times 3$; f. seed; g. end view and facial view of the seed cone scale; h. profile view of the upper edge of the same. All but e natural size.

SABAH. Ranau: Kinabalu Mountain Trail, *de Laubenfels* P625, ♀, 6,700 ft (L, holotype; A, K, SAN, isotypes); B. Tupai, *de Laubenfels* P644, 5,500 ft (A, K, L, SAN); Mempening Trail, *de Laubenfels* P646, 5,500 ft (A, K, L, SAN); Silau Silau Trail, *de Laubenfels* P720, ♀, ♂, 5,500 ft (L, SAN); Kiau, *Clemens* 10004 (BM, BO, GH, K); Bembangan R., *Chew & Corner* RSNB 4457, ♂, 5,000 ft (K, L, S, SAN); Mesilau Cave, *Chew & Corner* RSNB 4778, ♀, ♂, 6,000 ft (K, S, SAN), *Meijer* SAN 48112, 7,500 ft (SAN, SAR); Mt. Tambuyokan, *Meijer* SAN 28747, 7,500 ft (SAN), *Gibot* SAN 55419, 8,000 ft (SAN).

Found between 1,500 and 2,400 m elevation in mossy forest particularly along ridges. In protected locations the trees may become quite large but on exposed ridges they may be no more than 12 m high. The leaves are usually distinctly acuminate but on exposed old trees the leaves may be mostly blunt although even here at least some of the leaves will have an apical projection of some sort. The leaves are never simply acute. The bark is covered with numerous lenticels and breaks off in irregular plates at least 5 mm thick, the surface is dark brown while internally it is granular and more reddish. The bark of young trees is more or less smooth. A white resin is produced. The young seed cone is oval and more or less smooth with the upper edges of the seed scales imbricate. The seed is provided with an acute projection 2 mm long on the upper corner opposite the wing.

The persistently acuminate leaves of *A. kinabaluensis* is a character distinct from all other species of the genus. The apex of the microsporophylls tends to be distinctly angled rather than the semicircular shape more usual in the genus. Like the other two high mossy forest species, *A. flavescens* and *A. montana*, this species can be distinguished more by the lack of the specialized features which characterize most other species. The two most similar but not really closely related species in Borneo are *A. endertii* and *A. lenticula*. The smallish pedunculate pollen cone, the lack of a lip on the seed cone scale, and the acuminate leaf all would distinguish this species from *A. endertii*. The leaves again, and particularly the lack of glaucousness on the underside, as well as the more or less triangular microsporophyll apex would distinguish it from *A. lenticula*. Other species outside of Borneo that might be said to resemble *A. kinabaluensis* are the other two mossy forest species and *A. dammara*. The smaller leaves of *A. flavescens* are always at least slightly lanceolate and never acuminate while the corner of the seed opposite the wing is quite blunt compared to the strong acute projection of *A. kinabaluensis*. The much larger pollen cones of *A. montana* are sessile, the more elongated leaves are never acuminate, and the seed cone scales are distinctly angled at the corners. The lower elevation species, *A. dammara*, has humpy rather than fish-scale shaped microsporophylls and the somewhat more elongated leaves lack the well formed acuminate tip which does occur in their juvenile form.

Known from higher elevations on and near Mt. Kinabalu. Specimens of *Agathis* collected from similar elevations on Mt. Murut in Sarawak may belong in this species.

***Agathis lenticula* de Laubenfels, *sp. nov.* — Fig. 4.**

Arbor immanis ad 45 m. *Folia* iuvenilia rotunda, tenue acuminata, breve pedunculata, ad 10 cm longa, 44 mm lata. *Folia* adulta lenticula, acuta, breve pedunculata, 5–7 cm longa, 18–24 mm lata, latis subtis glaucis. *Strobili masculi* cylindracei, ca. 4 cm longi, 10 mm diametri, apicis rotundis, basis pedunculatis, pedunculus 6 mm longus; squamae apicis rotundis, 2.5 mm latae, 2 mm longae. *Squamae strobilorum femineorum* semi-ellipticae, 28 mm altae, 40–45 mm latae.

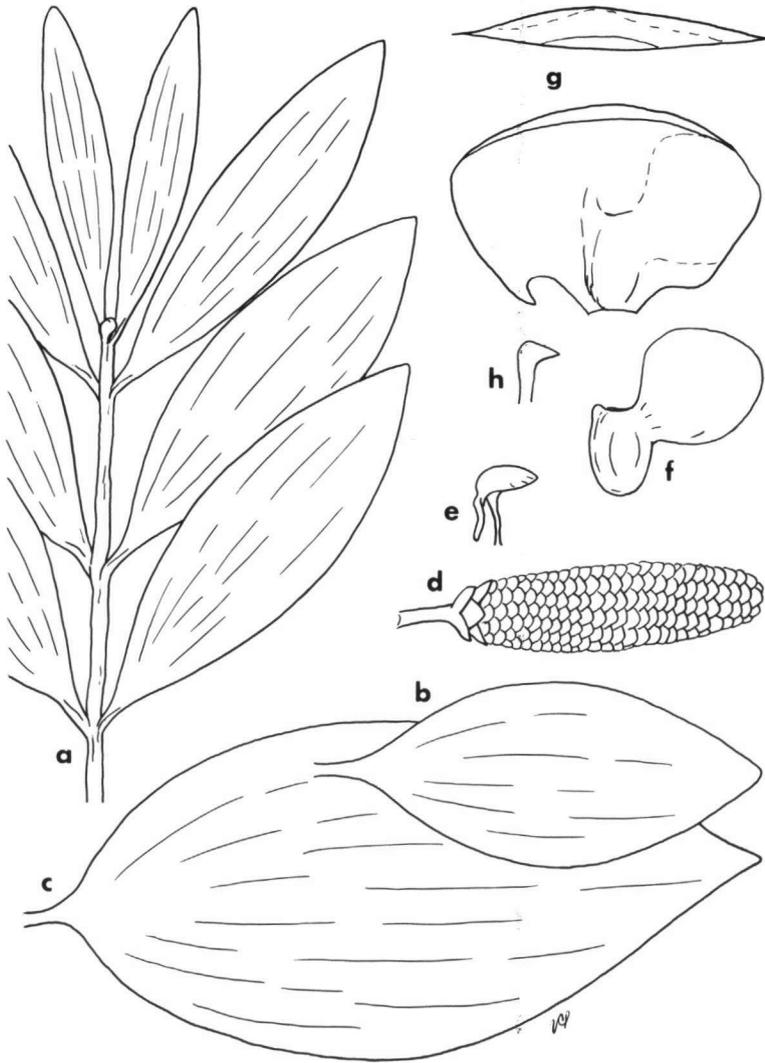


Fig. 4. *Agathis lenticula* de Laubenfels. — a. mature foliage shoot; b. extreme leaf shape; c. juvenile leaf; d. mature pollen cone; e. profile view of microsporophyll, $\times 3$; f. seed; g. end view and facial view of the seed cone scale; h. profile view of the upper edge of the same. All but e natural size.

Typus: *de Laubenfels P619* (L; iso in A, K, SAN), Mt. Kinabalu, Park Headquarters.

SABAH. Ranau: *Binideh SAN 65171*, ♀, 5,600 ft (S, SAR); Tenompok, *Clemens 28390*, 5,000 ft (A, BO), 28729, ♂ (A, BO), *Meijer SAN 2211*, ♀, 4,000 ft (SAN), *Melegrito A473*, ♀, 4,700 ft (S), *Smythies S10602*, 4,500 ft (S, SAR); Kinabalu Park Headquarters, *de Laubenfels P619*, ♀, ♂, 5,000 ft (L, holotype; A, K, SAN, isotypes), *P620* (L, SAN), *Kokawa & Hotta 6128*, 1,600 m (SAN), *Saikeh & Justin SAN 81794*, 5,500 ft (SAN), *Cockburn & Aban SAN 82968*, 5,400 ft (SAN); Mile 35, *Binideh SAN 65143*, ♀, 5,300 ft (SAN), *65144* (SAN); Bundu Tuhan Trail, *Binideh SAN 65139*, ♀ (SAN), *Gibot SAN 79651*, ♀ (SAN), *Saikeh & Justin SAN 81796*, ♂, 5,550 ft (SAN); Liwagu Trail, *Sadau SAN 42812*, ♀, 5,000 ft (L, SAN), *Lajangah SAN 44400*, ♀ (L, SAN, SAR), *Saikeh & Justin SAN 81795*, 5,300 ft (SAN), *Aban & Jumin SAN 82888* (SAN), *de Laubenfels P637*, ♀, ♂, 4,800 ft (A, K, L, SAN); Carson Trail, *Lajangah SAN 44786*, 4,500 ft (SAN); Mamut Ridge, *Kokawa & Hotta 5676*, ♂, 1,500–1,750 m (SAN); Kundasang, *Meijer SAN 27551*, ♂, 5,000 ft (SAN), 28586, 4,500 ft (SAN); Sosopodon, *Meijer & Sadau SAN 42775* (SAN); Mesilau R., *Chew & Corner RSNB 4249*, ♀, ♂, 5,000 ft (K, L, S, SAN), 4330, ♂ (K, L, S, SAN, SAR), *de Laubenfels P621* (A, K, L, SAN); Colombon Basin, *Clemens 34496*, ♀, 5,500 ft (A, B, BO, K, L); Tambunan, Trusmadi, *Mikil SAN 31864* (L). — Crocker Range, Keningau: Ulu Sunsuron, *Meijer SAN 21880*, 3,500 ft (SAN); Kimanis Road, *D. F. O. SAN 83901*, ♂ (SAN), *Tiong, Dewol & Abas SAN 85888*, 4,000 ft (SAN), *Tiong & Dewol SAN 89051*, ♀, 3,800–4,000 ft (SAN), 89053, ♀ (SAN), 89076 (SAN), 89077, ♀ (SAN).

Found between 1140 and 1680 m elevation in mountain rainforest. The leaves are usually distinctly elongated but in extreme cases are more or less oval. In all cases the apex is consistently acute and the leaf therefore has a distinctly lenticular outline. The bark is covered with numerous small lenticels and breaks off in irregular plates about 5 mm thick, the surface is gray while internally it is granular and reddish brown. The bark even of juvenile specimens is not particularly smooth being covered with exfoliating flakes. A white resin is produced which eventually turns yellow. The young seed cone is oval with the imbricate margins of the seed scales sometimes slightly raised.

The distinctly lenticular shape of the foliage leaves helps to distinguish this species along with the glaucousness of the underside of the leaf, while these two characteristics together are unique. The leaves of *A. macrophylla* are similar but normally distinctly rounded at the apex and the pollen cone of this species is much larger and globular shaped. The most closely related species is probably *A. orbicula*, also of Borneo, which differs by much smaller pollen cones, distinctly smaller seed cones, and smaller rounder leaves. The consistently acute leaf apex helps to distinguish *A. lenticula* from nearby trees of *A. kinabaluensis* which also lack glaucous undersides on the generally distinctly rounder and smaller leaves. The shape of the microsporophyll is also different. Beyond Borneo, besides *A. macrophylla* and the more specialized *A. ovata*, glaucous leaf undersides also occur on *A. corbassonii*, which has a similar ecology and ranks as closely related to *A. lenticula* but differs in the markedly narrow linear leaves, distinctly smaller microsporophylls, and more or less triangular cone scales. It also has more numerous sterile bracts at the base of the pollen cone. Leaf glaucousness can rarely be detected on dried herbarium specimens of *Agathis*, however, and dried sterile specimens of *A. lenticula* are therefore difficult to distinguish from other species with similar shaped leaves, such as *A. borneensis*.

Known only from the higher mountain ranges of Sabah although it would be no great surprise if it were identified from mountains further south.

Agathis orbicula de Laubenfels, *sp. nov.* – Fig. 5.

Arbor ad 40 m. *Folia* iuvenilia rotunda, acuta, breve pedunculata, ad 6.5 cm longa, 28 mm lata. *Folia* adulta orbicula, obtusa vel tenue acuta, breve pedunculata, 24–36 mm longa, 12–24 mm lata, latis subtis glaucis. *Strobili masculi* ovati vel cylindracei, 9–14 mm longi, 4–6 mm diametri, apicis rotundis, basis pedunculatis, pedunculus 2–3 mm longus; squamae apicis rotundis, 1.5 mm latae, 1 mm longae.

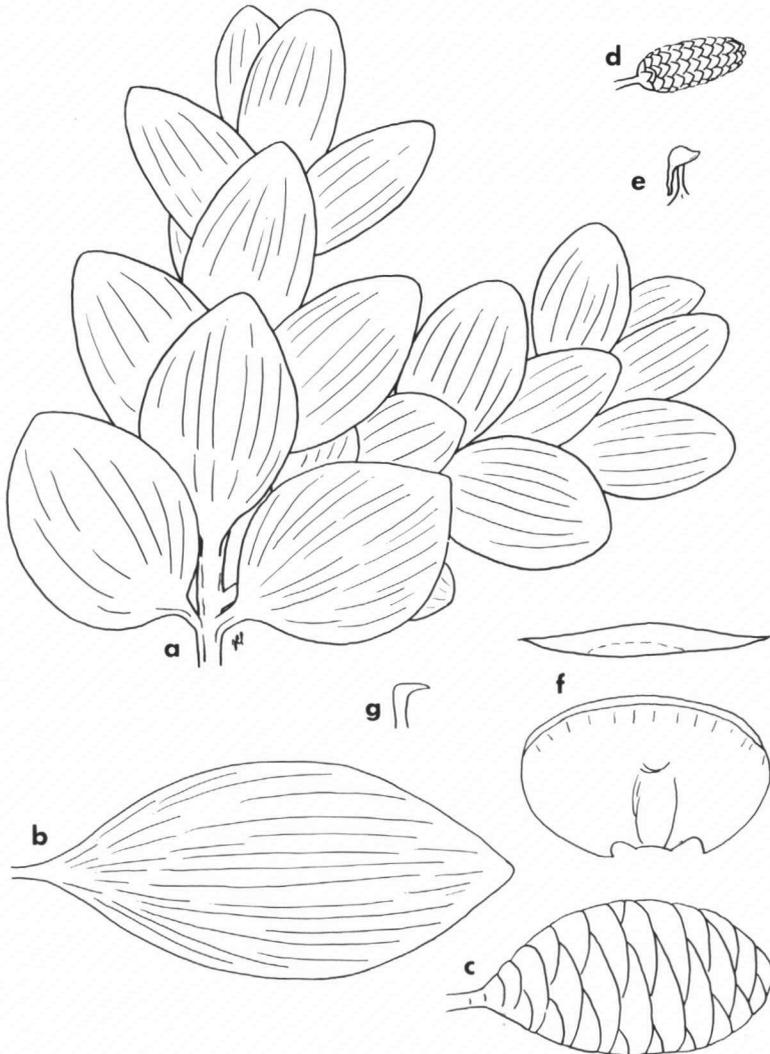


Fig. 5. *Agathis orbicula* de Laubenfels. — a. mature foliage shoots; b. juvenile leaf; c. young seed cone; d. mature pollen cone; e. profile view of microsporophyll, $\times 4$; f. end view and facial view of the seed cone scale; g. profile view of the upper edge of the same. All but e natural size.

Squamae strobilorum femineorum ellipticae, 20 mm altae, 33 mm latae. Strobilus ca. 7 cm longus, 4.5 cm diametrus.

T y p u s : *de Laubenfels P614* (L; iso in A, K, SAN, SAR), Sarawak, Lawas, Bumbong Rumah.

SARAWAK. Center: Hose Mts., Ulu Lup, Tiau Mujong, *Unyong S 21156*, ♂, 900 m (S, SAR); Usan Apau, R. Julan, *Pickles S 3929*, 3,165 ft (L, S, SAR, US). — Lawas: Bumbong Rumah, *de Laubenfels P614*, ♀, ♂, 3,000 ft (L, holotype; A, K, SAN, SAR, isotypes), *P615* (A, K, L, SAR), *Brunig S 10628*, 700 m (SAR), *S 12084* (SAR), *Anderson* in 1955, ♀, 1,500 ft + (SAR); Malingan Range, *Brunig S 9985*, 1,000 m (SAR), *Paie S 32848*; ♀ (L, SAR); B. Tudal, *Brunig S 12082*, 1,000 m (SAR).

SABAH. Sipitang: Ulu Moyah, *Wood SAN 16586*, ♀, ♂, 3,500 ft (L, S); B. Batanga, *Wood & Kilang SAN 16627*, 3,500 ft (L, S).

Found between 450 and 1050 m elevation in mountain rainforests and high kerangas. The leaves are oval to almost circular with a blunt or sometimes slightly acute apex. The bark bears a few scattered lenticels and breaks off in small irregular plates up to 4 mm thick, the surface is dark brown while internally it is granular and reddish brown. A light yellow resin is produced in some abundance. The young seed cone is oval and more or less smooth with the upper edges of the seed scales imbricate. The exposed parts of the tiny microsporophylls are humpy like those of *A. dammara*.

The small oval shaped leaves which are glaucous underneath are unique in the genus and the tiny pollen cones are rivalled only by *A. atropurpurea*, which is otherwise quite different. Clearly the closest relative of *A. orbicula* is *A. lenticula*, described above. Elsewhere in the genus small leaves and small cones tend to be associated with higher elevation but *A. orbicula* occurs at relatively low elevation, particularly at a lower elevation than the related *A. lenticula* which is not dwarfed in any way.

Scattered across low mountains and plateaus from central Sarawak to southwestern Sabah.

When all of the parts of each species of *Agathis* of Borneo is available it can be seen that well-marked distinctions exist. The same, unfortunately, can not be said for sterile herbarium specimens. It is important that these five Borneo populations be recognized, particularly because the genus *Agathis* has great potential commercial value. I would disagree that the differences described here are less than specific in rank, but should they be treated at a lower level they would have to be related for the most part to populations outside of Borneo where, in order to be consistent, other reductions in rank would also have to be made. It remains, then, that there is a variety of *Agathis* taxa in Borneo equalled only by the five species of New Caledonia. The third most important center of *Agathis* variation today is in the mountains of northern Queensland where there are three species. For some reason the intervening territories, including Celebes and New Guinea, in no place are known to have more than two kinds of *Agathis*.

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