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Revision of The Genus Goniothalamus (Annonaceae) of Borneo

presented by

Kamarudin Bin Mat-Salleh

has been accepted towards fulfillment of the requirements for

Ph. D. degree in Botany

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REVISION OF THE GENUS GONIOTHALAMUS (ANNONACEAE) OF BORNEO

By

Kamarudin B. Mat-Salleh

A DISSERTATION

Submitted To

Michigan State University
in partial fulfillment of the requirements
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ABSTRACT

REVISION OF THE GENUS GONIOTHALAMUS (ANNONACEAE) OF BORNEO

By

Kamarudin Bin Mat-Salleh

The genus Goniothalamus comprises about 130 currently recognized taxa. Members of the genus are widely used in traditional medicinal practices in Asia, and many novel and clinically bioactive chemical compounds have been isolated from the species and are summarized here. A total of 823 collections and 1,225 specimens of Goniothalamus from Borneo and other relevant areas was examined during this revision, obtained from 20 herbaria in Southeast Asia, Europe and the U. S. A. Thirty species are currently known from Borneo, the largest number represented in any single biogeographic area. Ten new species are described here and one new combination is made. Two species previously known only from the Philippines (Goniothalamus puncticulifolius Merr. and G. gigantifolius Merr.) and one species from Peninsular Malaysia (G. montanus J. Sinclair) are recorded for the first time for Borneo. Twenty-four species are endemic to Borneo, and 10 of these are known from very few localities. Eleven informal species alliances are established for the Bornean species. This revision is based mainly on traditional taxonomic analysis of herbarium specimens and field observations of natural populations, but many new characters were obtained from scanning electron

microscopy of the floral organs. Five inner-petal domes types, 11 stamen types, and nine pistil types are recognized, illustrated, and described. The species of *Goniothalamus* appear to have two main flowering and fruiting seasons. The fruits mature while new flowers are being initiated. On the basis of herbarium-specimen records it appears that the first flowering season peaks in June and the second in November.

DEDICATED

To

THE NATIVES OF BORNEO

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INTRODUCTION

The genus *Goniothalamus* is one of the largest and most important genera of the Annonaceae in Asia. Its members are widespread in tropical and subtropical Asia, found mainly in the Malay Archipelago but a few species also occur in China, the Indian subcontinent and northern Australia. To date, more than 150 taxa have been described in *Goniothalamus*; about 120 species and 10 subspecies/varieties are currently recognized (Appendix 1).

Because most *Goniothalamus* species are small shrubs or monocaulous treelets, they have not been used as major commercial forest products.

Nevertheless, many of the species hold potential as important unexploited medicinal resources, and they have been widely utilized in traditional medicinal practices. Many other members of the Annonaceae are also well known as ethnobotanical and medicinal resources in Asia (Burkill 1935, Perry 1980, Mat-Salleh 1989).

Natives of the Malay Peninsula, Borneo, the Philippines and Indonesia have prepared decoctions from roots and leaves of *Goniothalamus* for many uses, but these are especially popular among local Asian women as postnatal medicines and abortifacients. In the Malay Peninsula, *G. macrophyllus*, *G. scortechinii*, *G. giganteus*, *G. umbrosus* and *G. tapis* are in great demand by village midwives (Burkill 1935). In Borneo, *G. macrophyllus*, *G. malayanus*, *G. andersonii* and *G. velutinus* are also widely used for the same purpose (Mat-Salleh 1989). Some of these species are also used to treat high fever, which is normally associated with malaria, typhoid, and cholera in tropical Asia. Javanese mountain dwellers reportedly used the aromatic roots of *G. macrophyllus* to treat such fevers (Burkill 1935). In the Philippines *G. amuyon* is sought to treat a variety of illnesses. The seeds cooked with oil are made into a linament used to treat rheumatism. A seed decoction was said to be used as a

stomachic and for tymphanites (Quisumbing 1951). In southern Taiwan, where this species is also found, fluid distilled from the seeds is applied for scabies (Perry 1980).

There had been no interest in phytochemical studies on the natural constituents in these species until the discovery of goniothalamin, a novel styryl dehydropyrone, by Jewers et al. (1972). It is worth noting that this clinically active compound was first discovered in several species of Bornean *Goniothalamus* sent by J.A.R. Anderson (then working with the Sarawak Forest Department) to The Tropical Products Institute in London. Subsequent studies by members of Dr. Jerry L. McLaughlin's laboratory at Purdue University (El-Zayat et al. 1985, Alkofahi et al. 1988, 1989, Fang et al. 1990, 1991a, 1991b, 1991c) led to the isolation of numerous bioactive compounds from southern Thailand's *G. giganteus*. Independent studies on East Indian *G. sesquipedalis* and *G. griffithii* (Talapatra et al. 1985) also reported several novel chemicals.

Several teams of Malaysian natural-product chemists and pharmacologists, assisted by local botanists, were formed to make scientific evaluations on Malaysian *Goniothalamus*. Among the earliest initiatives was chemical and pharmacological evaluation of *G. macrophyllus* by Sam et al. (1987). The clinical report on teratogenic activities of its extract has been the main impetus for current research programs by these teams, not only on the genus *Goniothalamus* but also involving the whole Annonaceae. Following general screening for active natural constituents such as alkaloids and triterpenoids (Mat-Salleh & Ahmad 1989b), many *Goniothalamus* species were selected for further isolation and analysis, resulting in several published reports (Din et al. 1988, 1990a, 1990b, Colgate et al. 1990, Ahmad 1991).

Table 1 summarizes known phytochemical constituents isolated and characterized from 16 species of *Goniothalamus*. These include 18 styryllactones, 7 acetogenins, 1 flavanone, 3 phenanthrene lactams, 1 anthraquinonone and 2 alkaloids. Many of these are novel bioactive compounds that have shown significant cytotoxicity against many human tumor cells.

Several species of Bornean *Goniothalamus* are often kept by villagers who believe that they will keep away "evil spirits" and wild animals (Mat-Salleh 1989). In all probability, animals were kept away by the lasting strong fragrance. In fact, fragrance emitted from the burning of these plants is said to be an effective mosquito repellant (Perry 1980, Mat-Salleh 1989). As shown in Table 1, several pharmacological studies conducted by McLaughlin's group have indicated that various acetogenins such as goniothalamicin and annonacin have high potency on mosquito and blowfly larva.

Despite current phytochemical interest in the genus, there has been no comprehensive taxonomic revision available to help in identification of the species. The last major taxonomic treatment of the Annonaceae that included *Goniothalamus* was published nearly 40 years ago by Sinclair (1955). This revision covered only the Peninsular Malaysian species.

The size and complexity of the genus *Goniothalamus* seems too great for a single monographic work. It is not feasible to monograph the genus without a proper revision of species in the two most diverse and interesting areas: Borneo and New Guinea. Before my revision, only 17 species of *Goniothalamus* were reported from Borneo (Masamune 1942); this number is almost doubled in the current treatment. Only 13 species are currently known from New Guinea, but, judging from the richness and diversity of that area, the number of species is likely to be much greater than reported. This revision of the Bornean taxa is

Table 1. Chemical constituents isolated from Goniothalamus

Reference	Jewers et al. 1972	land El-Zayat et al. 1985	laysia Sam et al. 1987	Talapatra et al. 1985	land Fang et al. 1991a	Wu et al. 1992	Talapatra et al. 1985	Wu et al. 1991	Wu et al. 1992
Origin	Воглео	Southern Thailand	Peninsular Malaysia	India	Southern Thailand	Taiwan	India	Taiwan	Taiwan
Source ⁵	G. andersonii, G. macrophyllus, G. maluyanus &	G. giganteus	G. macrophyllus	G. sesquipedalis &	G. giganteus	G. amuyon	G. sesquipedalis & G. griffithii	G. amuyon	G. amuyon
Bioactivity ⁴	Antifungal & CNS activity		Embryotoxic in mice		Significant and selective	Cyloloxicity against ADTS		Methanol extract showed significant cytotoxicity against human KB, P388, RPMI, TE-671, tumor cells.	Methanol extract showed significant cytotoxicity against human KB, A-549, HCT-8, P388 & L-1210 tumor cells
Group & Compound	I. Styryllactone a. Styrylpyrone 1. Goniothalamin		2. Goniothalamin oxide	3. Goniodiol			4. Goniodiol diacetate, & 5. Goniodiol monoacetate	6. Goniodiol 7-monoacetate	7. Goniodiol 8-monoacetate

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8. Goniotriol ¹	Mild activities to human	G. griffithii G. giganteus	India Southern Thailand	Talapatra et al. 1985 Alkofahi et al. 1989
		G. borneensis*** G. amuyon	Borneo Taiwan	Din et al. 1990b Wu et al. 1992
9. 8-acetylgoniotriol ¹	Moderate and selective toxicity to HT-29 & A-549; as well as	G. giganteus	Southern Thailand	Fang et al. 1990
10. 5-acetyl goniothalamin		G. gigantifolius**	Borneo	Ahmad et al. 1991
b. Furano-2-pyrone 11. Goniothalenol (=altholactone ²)	Toxic to mice during P388 in vivo antileukemic screen	G. giganteus	Southern Thailand	El-Zayat et al. 1985
		G. montanus	Borneo	Din et al. 1988
		G. madyanus, G. montanus & G. umbrosus*	Compa	COICBAIC CI 41. 1930
		G. borneensis ***	Borneo	Din et al. 1990b
12. (+)-isoaltholactone	Less toxic than altholactone	G. malayanus, G. montanus G. umbrosus* & G. woodii***	Borneo	Colegate et al. 1990, Din et al. 1990a
c. Furano-2-furanone 13. Goniofufurone	Selective but moderate toxicity to A549 human tumor cells	G. giganteus	Southern Thailand	Fang et al. 1990
14. 7-epigoniofufurone	No significant bioactivities to human tumor cells	G. giganteus	Southern Thailand	Fang et al. 1991a

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Fang et al. 1990	Fang et al. 1991a	Fang et al. 1991b	Alkofahi et al. 1988	Alkofahi et al. 1988	Alkofahi et al. 1990	Fang et al. 1991c Fang et al. 1991c	Fang et al. in press Fang et al. in press	Talapatra et al. 1985
Southern Thailand	Southern Thailand	Southern Thailand	Southern Thailand	Southern Thailand	Southern Thailand	Southern Thailand Southern Thailand	Southern Thailand Southern Thailand	India
G. giganteus	G. giganteus	G. giganteus	G. giganteus	G. giganteus	G. grganteus	G. giganteus G. giganteus	G. giganteus G. giganteus	G. griffithii
Very active to the A-549, MCF-7 HT-29, and 3PS in vivo cells	No significant bioactivities to human tumor cells	Marginally cytotoxic to the above G. giganteus cells in culture	Cytotoxic in 9KB & 9PS carcinomas as well as	Not active in 9ASK cells Ten times as active as Goniothalamicin and high potency on blowfly and mosquito larva. High activity in 9ASK	Strongly active in 3PS system active in 9KB, & highly active in A-549. MCF-7. HT-29 & 9 ASK	as above as above		
d. Styryl-2-pyrone 15. Goniopypyrone	16. 9-deoxygoniopypyrone	17. Goniobutenolides A, & 18. Goniobutenolides B	II. Tetrahydrofuranoid Acetogenin ³ 19. Goniothalamicin	20. Annonacin	21. Gigantecin	22. Gigantetrocin 23. Gigantriocin	24. Giganenin 25. 4-deoxygigantecin	III. Flavanone 26. Pinocembrin

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Talapatra et al. 1988	Din et al. 1990c	Zakaria et al. 1989.
India	Peninsular Malaysia	Peninsular Malaysia
G. sesquipedalis	G. scortechinii	G. fulvus, G. tapis & G. scortechinii
IV. Phenanthrene lactams 27. Goniopedaline 28. Aristololactam - A-II 29. Taliscanine	V. Anthraquinonone 30. Scorazanone	VI. Alkaloid 31. Liriodenine, & 32. Oxastaphanine

Notes:

1. Total synthesis of this compound was already successfully achieved from commercially available D-gluco-heptono-ylactone, as recently reported by Shing & Zhou (1992).

This compound was also synthesized, reportedly from L-glyceraldehyde acetotonide (Kang 1989)

4. Codes of standard human pharmacological cancerous cells used in the tests are as follows:

3. Restricted to members of the Annonaceae.

KB - nasopharyngeal carcinoma L-1210 - Lymphocytic leukemia A549 - lung carcinoma

P-388 - Murine leukemia (=PS)

HT-29 - colon adenocarcinoma MCF-7 - breast carcinoma

HCT-8 - Colon tumor

ASK - Astrocytoma reversal assay,

indication of tubulin inhibitaion and antimitotic actions

5. Some of the species were erroneously named in the publications cited; corrected determinations are indicated above.

* published as G. tapis

** published as G. uvarioides

*** published as G. giganteus

**** published as G. suluensis

intended as a stepping stone toward a more comprehensive monograph for the genus and should be considered as a precursor to that effort.

HISTORICAL ACCOUNT

The name Goniothalamus was first proposed by Carl Ludwig Blume in 1830 in his Flora Javae as a section of the genus Polyalthia, to accommodate a species (Polyalthia macrophylla) with "angled receptacle". This species was well illustrated (Figures 1, 2) showing many important and unique characteristics of the section. Twenty-five years later, after more materials were available, Joseph Dalton Hooker and Thomas Thomson decided to elevate this section into its own genus and thus formalized the genus Goniothalamus while treating it in their well-known Flora Indica (1855).

In 1865 F. A. W. Miquel, then the Director of Leiden's Rijksherbarium, issued the earliest revision of the Annonaceae of Malesia in *Annales Musei Botanici Lugduno-Batavi*, a critical revision of his own *Flora Indiae Batavae* (1855–1859), in which he devoted the whole second volume to the Annonaceae. In this treatment, entitled *Annonaceae Archipelagi Indici*, Miquel recognized nine species of *Goniothalamus*, six (including two Bornean) of which were new. It was around this time that G. Kendrik Thwaites (1858) and Richard Beddome (1869) were working on the Ceylonese and Indian floras in which the Annonaceae were documented.

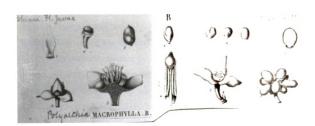
A complete revision of the family in Southeast Asia did not materialize until 1893 when Sir George King, the famous Calcutta-based Scottish botanist, published his *Materials for the Flora of the Malay Peninsula* (1892), which is considered a precursor to many Floras of the Malay Archipelago. King's interest in the family was shown in his subsequent publication of a splendid and monumental monograph, the *Annonaceae of British India* (1893). King's treatment recognized 27

Figure 1. Illustration of *Goniothalamus macrophyllus*, type species of *Goniothalamus*, from C. L. Blume's *Flora Javae* (1830).

Figure 1. Illustration of Goniothalamus macrophyllus, type species of Goniothalamus, from C. L. Blume's Flora Javae (1830).



Figure 2. Details of floral parts of *Goniothalamus macrophyllus*, also from C. L. Blume's *Flora Javae* (1830).



species of *Goniothalamus*, and 15 species were illustrated. These illustrations have been the basis for many interpretations of the traditional species by later authors.

At approximately the same period, Otto Stapf at the Kew Herbarium was entrusted to work on the specimens from Mount Kinabalu sent by G.D. Haviland, then curator of the Sarawak Museum. These had been collected during Haviland's 1892 expedition to the mountain. Stapf's treatment, which was the first Flora published for the mountain, appeared in the *Transactions of the Linnaean Society*, issued in 1894. It was in this publication that two important *Goniothalamus* species from Mount Kinabalu, *G. roseus* and *G. stenopetalus*, were described.

During the late 19th century also, Jacob Boerlage, who was working with live materials at Bogor's Kebun Raya (then known as the Buitenzorg Botanic Gardens) along with herbarium specimens at the Herbarium Bogoriense, became interested in the Annonaceae. Six years after King's publication, he published his Notes sur les Annonaées du Jardin Botanique de Buitenzorg (1899), a well illustrated work which compliments King's treatment on the Annonaceae of the Malay Archipelago. Boerlage was also the first author to introduce a formal infrageneric classification of Goniothalamus. It was clear to him that members of the genus may not necessarily be distinguished from other genera based on the number of ovules. Although he recognized that most of the species are one-ovulate, there was a species available to him (G. uvarioides) that has many ovules and yet there were no other characters that would effectively separate this species from other members of Goniothalamus. He used this situation as a basis for assigning the multi-ovulate species of Warburg's (1891) genus Beccariodendron from New Guinea to Goniothalamus. He created the section Beccariodendron within the genus Goniothalamus to accommodate the former Beccariodendron species together with G. uvarioides. The rest of the then known species were placed in the section "Eu-Goniothalamus".

By the early 1900s much taxonomic research was being carried out in several newly established Southeast Asian herbaria. Elmer D. Merrill and his associates at the Philippine's Bureau of Science in Manila published many new species and taxonomic notes on the genus. During that period the genus was also treated in several other regional Floras, such as the Floras of the Malay Peninsula (Ridley 1922) and Thailand (Craib 1925).

The Annonaceae of Southeast Asia were subjected to a major revision in the late 1940's, when R. E. Holttum, then the Director of Singapore Botanic Garden, decided to hire a botanist to work on the revised Flora of Malaya (Malay Peninsula). James Sinclair, a young and vibrant Scottish botanist, was hired in 1948 and the Annonaceae were entrusted to him as the first family to be revised. Sinclair's impressive revision was published by the Gardens in 1955, and stands as the only complete recent treatment for the Southeast Asian region. Sinclair's work at the Garden made him the only expert of Asiatic Annonaceae. Thus, many specimens were sent to him for determination, contributing to the numerous notes he published (Sinclair 1951, 1953a, 1953b, 1956a, 1956b, 1958, 1961). Together with his revision, these papers contain a wealth of information on the general taxonomy, phylogeny and classification of this family in Asia. It was also known among Malesian taxonomists that Sinclair had noble intentions to contribute the whole revision of the family for *Flora Malesiana* (Burkill, 1968). His premature death in 1968 discontinued that important task.

After Sinclair's era the genus has been minimally treated in several recent Floras, in which minor reinterpretations and new records of its distribution were reported. These Floras include the one for the Malay Peninsula (Kochummen 1972), Java (Backer & Bakhuizen van den Brink 1963), China (Tsiang et al. 1979), Taiwan (Li 1963, 1976) and Ceylon (Huber 1985).

The only other taxonomist contributing to the systematics of the genus *Goniothalamus* after Sinclair's sudden death has been Nguyen Tien Bân, a Vietnamese taxonomist trained by Armen Takhtajan at Leningrad (Takhtajan, personal communication). Bân was at the New York Botanic Garden in 1972, probably as a guest of Arthur Cronquist. Bân's numerous works, not only on the genus *Goniothalamus* but also on various other genera of the Annonaceae, were published in Russian. His work with *Goniothalamus* (1974a, b) concerns more the infrageneric classification of the genus rather than a comprehensive revision at the species level. Bân made reinterpretations on many Southeast Asian species, but his taxonomic treatment seems to solve problems only for Philippine taxa. His interpretation of Bornean species is confused, probably because of the few collections from the area available to him.

GEOGRAPHIC DISTRIBUTION

Members of the Annonaceae are very common and well represented in moist tropical lowland forests. The family is large, pantropically distributed, with between 2000 and 2500 species in about 130 genera. The tropical nature of the family has not restricted some members from extending their distribution outside warm tropical climates. Several species of Asimina, Annona and Deeringothamnus occur in North America, and one species, Asimina triloba, extends to cool temperate forests around the Great Lakes (Kral, 1960). Several tropical species in Southeast Asia are also known to occur in cool and windy high-elevation montane forests (Sinclair, 1955), including Disepalum pulchrum (over 1500 m elevation), Friesodielsia alpina (over 1200 m), Pseuduvaria taipingensis (1200 m) and Polyalthia monticola (1500 m). Several species of Goniothalamus can be added to the list, all of which occur up to 1500 m elevation. These include G. holttumii (Malay Peninsula),

G. cheliensis and G. leiocarpus (China), G. griffithii (Burma), G. clemensii and G. roseus (Borneo), and G. montanus (Malay Peninsula and Borneo).

Although the family is found throughout tropical rainforests of South America, Africa and Asia, the genera and species tend to be locally restricted. The genus *Xylopia* is the only member of the family that is truly cosmopolitan, with members in South America, Africa and Asia, whereas *Anaxagorea*, is the only genus with a disjunct distribution lacking representatives in Africa. Among those three centers, the Asiatic Annonaceae have the largest number of endemic representatives, with approximately 50 genera and 662 species compared to Africa (40 genera, 255 species) and America (36 genera, 593 species). Almost half of the Asiatic species are lianas whereas those elsewehere are predominantly shrubs and trees.

While Asiatic Annonaceae with the scandent habit are considered more specialized, they seem to retain a remarkably primitive undifferentiated fruit. All native Asiatic Annonaceae have completely free, apocarpous fruits, developed from free ovaries. None has the more advanced aggregate pseudo-syncarpous fruit (developed from numerous, free ovaries in flower and fused after fertilization) as found in African and/or American Annona, Annonidium, Fusaea, Letestudoxa, Pachypodianthum, Raimondia and Rollinia. The most advanced fruit type, the completely fused true syncarps (as found in African Monodora and Isolona) has not been found in Asian or American Annonaceae. This situation indicates significant local evolution of the Annonaceae in these centers, which probably has contributed to the high local endemism.

Goniothalmus is concentrated in West Malesia with most species and endemics in Indochina, Borneo, the Philippines and New Guinea (Figure 3). Surprisingly, Goniothalamus is not well represented in either the Malay Peninsula or Sumatra, which are traditionally known for their rich floras. Based on both the total number

of species and number of endemics of *Goniothalamus* in Borneo, this island has a remarkable representation of the richness and diversity of the genus. This is not surprising, because other recent revisions of Malesian genera have shown similar circumstances (Mat-Salleh et al. 1992). Thirty species of *Goniothalamus* are documented for Borneo in this treatment, 24 of which are not found elsewhere. This number does not include two additional species that cannot be described at this time due to the lack of mature flowers. It is also worth noting that the New Guinea Annonaceae currently are very poorly known and the number of species in that area is underestimated. Perhaps the species in New Guinea will prove to be double the number currently known from there.

MATERIALS AND METHODS

TAXONOMIC ANALYSIS

This revision is based mainly on traditional taxonomic analysis of herbarium specimens and field observation of natural populations. A total of 823 collections and 1,225 specimens of *Goniothalamus* from Borneo and other relevant areas was examined. These are housed in 20 herbaria in Southeast Asia, Europe and the U. S. A. Figure 4 shows the collecting localities of *Goniothalamus* in Borneo and Figure 5 presents the distribution of collections and specimens in the four major political units of Borneo. Sabah is by far the best collected region on the island. More than 60% of the total collections (483), come from Sabah, an area that covers only 10% of the island. In comparison, Kalimantan has only 104 collections (13%), but this state covers 73% of the total area of Borneo. Sarawak, the second largest political unit in Borneo (16% of the land mass), has 190 collections, or

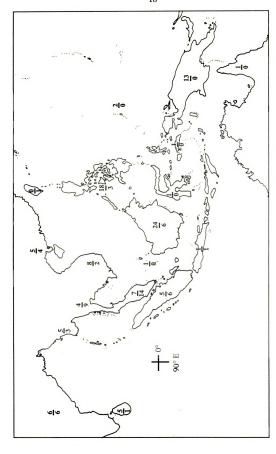


Figure 3. The distribution of Goniothalamus, segregated into endemic taxa (above the bar) and non-endemic taxa (below the bar).

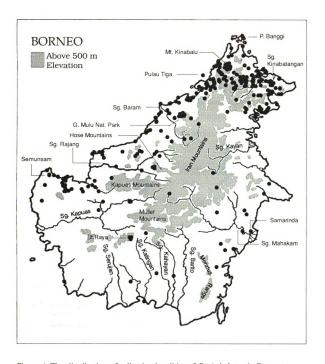


Figure 4. The distribution of collecting localities of Goniothalamus in Borneo

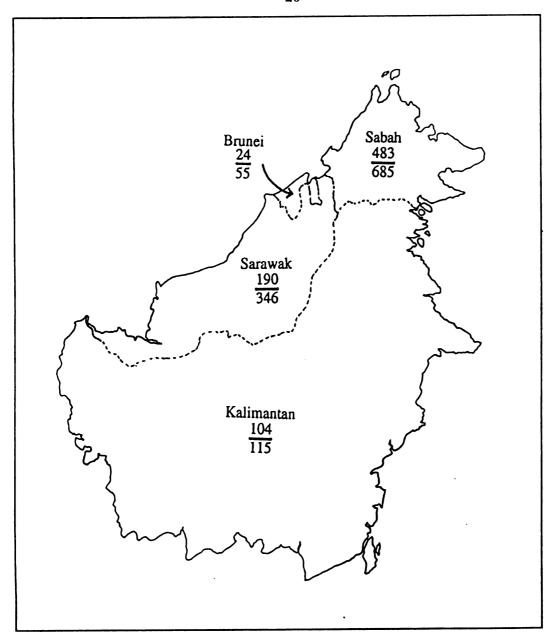


Figure 5. Total number of collections (above the bar) and specimens (below the bar) of *Goniothalamus* examined for this revision, segregated into four politacal regions of Borneo.

23% of the total. The sorry state of under-representation in Indonesia's side of Borneo is the result of lack of strong collecting programs in that area. The forest departments in the Sabah and Sarawak states of Malaysia have been active in building their collections in their respective herbaria (SAN and SAR), from which trained collectors were regularly sent to the field.

The large number of collections of *Goniothalamus* from Sabah is also the result of my own collections, made while I served as a lecturer for the Universiti Kebangsaan Malaysia, Sabah Campus, in Kota Kinabalu between 1986 and 1989. Because some Bornean species have Peninsular Malaysian relatives, my previous field experience with the Annonaceae of the Malay Peninsula, acquired while I was working on my masters thesis in 1983–1985 (Mat-Salleh 1985), also helped in shaping my taxonomic concepts.

Few studies have been carried out emphasizing genetic or phenological aspects of the Annonaceae in Southeast Asia. Thus, our knowledge on the comparative reproductive biology of the group is very limited. This is true not only for the Bornean Annonaceae, but also for most other plants of that area, for which most of the current knowledge is strictly taxonomic, morphological, and exploratory.

The general taxonomic methodology employed in this revision has followed the species standard method of Rollins (1952), in which well defined species were studied in as much detail as possible. All characters distinguishing these species were evaluated and specimens were then sorted into groups of known species. Specimens that did not fit into the circumscription of current known species were segregated into their own groups and new species were described to accommodate these equally distinct groups. Characters utilized in previous treatments were also re-evaluated, and new characters emerging from this evalution were considered. In Goniothalamus many of the floral characters, especially stamen and pistil features,

used in previous treatments were not clearly defined. To facilitate a better understanding of these characters, the scanning electron microscope (SEM) was used to elucidate and explore variation in *Goniothalamus*. Many new features were seen in three dimensions that have not been clear with light microscopy. The morphological characters employed in this treatment are listed in Table 2.

Information gathered in this study, especially data from herbarium specimens, was put into a specimen database modeled after Beaman and Regalado (1989). This database was subsequently transported to a more powerful graphical-based database management system (DBMS). One of the benefits of the computerization exercise was the ability to cross-link the main specimen database with databases handling information such as localities, records of collectors, and ethnobotany. The database was extensively utilized in this revision, and additional information can be readily added in the future. Related data such as identification status, phenology, uses, and distribution can be updated and graphically presented.

A particular difficulty in taxonomic revisions is the locating of vague localities indicated on some specimens. Many locality names on Bornean specimen labels are either inadequate or inaccurate, making them difficult to locate on maps. Only a few recent collections provide latitude and longitude information. Some place names in Borneo, as with many other localities in Southeast Asia, that were named during colonial periods, are now spelled quite differently and some have been changed outright.

A list of standardized locality names for Bornean *Goniothalamus* was prepared in the course of this revision and is presented in Appendix 2. This standardized locality database has been continuously updated and has gone through several revisions in which localities were added, deleted, realigned, and consistently

Table 2. Morphological characters examined for the revision of Bornean Goniothalamus.

1. Habit

- a. monocaulous treelet
- b. shrub
- c. large tree

2. Stem

- a. texture and general characters
- b. diameter
- 3. Leaves (following terminology used by Hickey, 1973)
 - a. petiole size
 - b. petiole thickening (normal or inflated)
 - c. leaf shape
 - d. leaf thickness (coriaceous, chartaceous)
 - e. leaf appearance (color and indument)
 - f. leaf size
 - g. leaf apex
 - h. leaf base
 - i. overall venation
 - j. size, shape and appearance of primary vein
 - k. appearance of secondary veins, including intersecondary and intramarginal veins
 - 1. appearance and type of tertiary veins

4. Inflorescence

- a. type (solitary, cymose, tuberculate at the base of the stem)
- b. position
- c. number of flowers (solitary, paired, many-flowered)
- d. bracts
- e. pubescence
- f. pedicel size and indument

5. Flower

- a. sepal color, shape, size, indument
- b. outer petal color, shape, size, indument
- c. inner petal color, shape, size, indument
- d. stamen size, shape, connective
- e. ovary size, shape, indument
- f. number and position of ovules
- g. style size, shape, indument, orientation
- h. stigma shape, indument, orientation

6. Fruit

- a. pedicel size, indument
- b. carpel stalk size and indument
- c. carpel number, shape, size, indument
- d. seed

spelled. Many persons gave assistance in finding localities that were not evident on available maps.

SCANNING ELECTRON MICROSCOPY

Stamen and pistil characteristics have been among the most important traits used in the taxonomy and evolutionary interpretation of members of this genus. There are problems in the interpretations of these characters because these organs are very small in *Goniothalamus* and much distorted in dried specimens. To help better understand the overall morphology of the stamens and pistils, the SEM was used to improve resolution of these features. Preserved material for the study has been limited, however. In the course of the research I became aware of the KOH revival technique for herbarium specimens of *Amanita*, published by McKnight (1979). In this case, volva microstructures of *Amanita* species were revived from dried herbarium specimens and the resulting glandular structures were shown comparable with what was possible with fresh material.

The McKnight procedure requires gluteraldehyde fixation followed with 10% KOH treatment. This technique is said to be essentially the procedure of common practice with basidiomycete taxonomists except that 2.5% KOH rather than 10% KOH is used. In fact, 10% KOH is considered excessive and could be detrimental to the cells. Furthermore, it was suggested by Dr. Stan Flegler, the SEM specialist at Michigan State University, that the more useful procedure was to soak the specimens with KOH before rather than after fixation.

My initial trials with different concentrations of KOH showed that 2.5% KOH is indeed best for woody herbarium material. I also have further modified the procedure to leave the material in KOH for 24 hr, rather than just overnight.

Since *Goniothalamus* floral organs are also hard and woody, it was necessary to boil

the whole flower in distilled water for a few minutes until soft. After the floral organs were individually separated, they were transferred to the 2.5% KOH solution. After KOH revival, the samples were fixed for 24 hr with 4% gluteraldehyde in 1M phosphate buffer. It is necessary that the KOH and fixative be fully removed from the samples by washing them with distilled water at least three times at 30-minute intervals. The commonly-used serial dehydration with ethanol and CO₂ critical-point drying were employed to dry the samples for SEM use. The samples were subsequently mounted on SEM stubs, coated with gold and examined at 10 KV on the JEOL JSM-35CF SEM.

Figures 6–8 show comparative micrographs of samples prepared using these techniques. The effect of too concentrated KOH can be seen in Figure 6, in which stamens treated with 10% KOH have the pollen sacs split open. This seldom happens with samples revived with 2.5% KOH. Many *Goniothalamus* species with apiculate connectives, such as *G. rostellatus*, have two kinds of glands in addition to the sharp-pointed echinate trichomes (Figure 7). The small globose glands are the most difficult to revive. Soaking with 10% or 2.5% KOH for 24 hrs followed by fixation revived some of them to a condition close to that observed for glands on connectives from fresh flowers preserved with FAA (Figure 7F). The effect of the fixative in preserving revived glands from collapse can be seen clearly in Figure 7B, in which even larger glands were half collapsed when no fixative was applied after revival.

Reducing the concentration of KOH and soaking samples for longer periods after brief boiling, and the use of gluteraldehyde fixative after revival seemed to work well for many specimens used in this study (Figure 8). The technique probably could be further refined because some samples did not give results as expected.

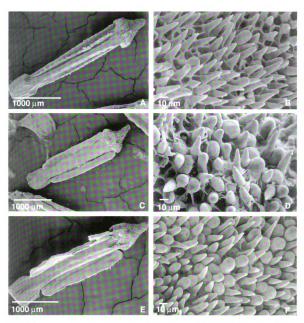


Figure 6. Comparative micrographs of stamens of *G. rostellatus* from the same plant (*Mat-Salleh 2423*) showing the whole stamen and indument from the middle of the connective. A & B. Treated for 24 hrs with 10% KOH. C & D. Treated for 24 hrs with 2.5 KOH and subsequent gluteraldehyde fixation. E & F. FAA-preserved stamen from fresh flower.

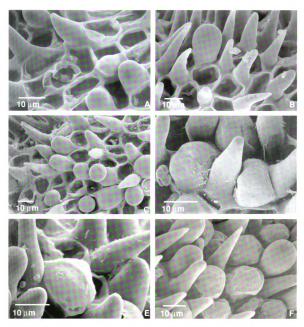


Figure 7. SEM micrographs of indument of stamen connectives of *G. rostellatus* from the same plant (*Mat-Salleh 2423*). A. Dried connective without treatment. B. Boiled with water for 10 minutes. C. 24 hr 10 % KOH treatment. D. 24 hr 10 % KOH treatment followed with fixation. E. 24 hr 2.5 % KOH treatment followed with fixation. F. Fresh material preserved in FAA.

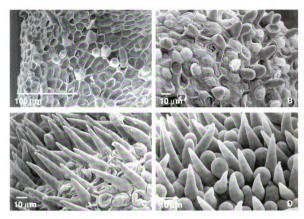


Figure 8. Comparative micrographs of untreated (A & C) and revived (B & D) indument on stamen connectives of *Goniothalamus malayanus* (A & B, *Wong WKM 18*) and *G. uvarioides* (C & D, *Beaman 7502*).

MORPHOLOGY

VEGETATIVE MORPHOLOGY

Most species of *Goniothalamus* are small-stemed monocaulous treelets 5–10 m high, normally growing in shady areas, swamps or banks of streams and rivers. The treelets can grow to become shrubby if left undisturbed. Some species, however, become relatively large. In Borneo two species are notable for becoming large trees, viz. *G. fasciculatus* and *G. borneensis*. The latter species reaches up to 30 m high and 65 cm dbh. It has distinctive dark green and slightly fissured bark, rather than the pale green, smooth or slightly mottled bark commonly found in other species.

The leaf characteristics of Goniothalamus are taxonomically important. In general there are four leaf types in the genus. The first type is represented by and is typical of G. tapis. The leaves are more or less subcoriaceous or slightly chartaceous, oblanceolate-oblong, brownish beneath and shiny above. The venation is loose and eucamptododromus, and the tertiary veins are random-reticulate. The petiole is normally thin or slender and not inflated. This type of leaf is found in the Malay Peninsula/Sumatran species G. tapis, G. umbrosus and G. sumatranus and the Bornean species G. tapisoides, G. sinclairianus, G. longistipites, G. clemensii, G. calcareus, G. malayanus, and G. borneensis.

The second leaf type is typical of *G. roseus*, and is essentially a modification of the first type. These leaves have a brownish orange or golden brown color beneath and tend to be more oblong and larger than leaves found in the first group.

Species that can be grouped into this category are *G. stenophyllus*, *G. woodii*, *G. bracteosus*, *G. rostellatus* and *G. crockerensis*.

The third leaf type is common in the G. uvarioides and G. macrophyllus alliances. Many of the leaves of this type are extremely large, sometime gigantic. They are oblong-oblanceolate, coriaceous, with large blackish inflated petioles. The venation is prominently brochidodromous and tertiary veins are often very weakly percurrent, not random-reticulate as observed in other groups. The leaves are dark green above and pale gray beneath with faint inconspicuous nerves.

The fourth leaf type is found in several species which have velvet-brown indument, especially on young leaves and on the veins of older ones. Only two Bornean species, G. velutinus and G. rufus, have this kind of leaf. It is so obvious that the species can be recognized even with sterile specimens. Goniothalamus velutinus has much larger leaves than G. rufus, and the leaves of the latter species are ovate-oblong rather than generally oblanceolate as in G. velutinus. The older leaves of G. rufus are also much darker brown than the leaves of G. velutinus.

Several species of Goniothalamus, especially some of the rarer ones, have peculiar leaves that do not belong to any of the four types described above. Most of these are variants of the third leaf type as commonly found in the G. uvarioides and G. macrophyllus alliances. These include G. cylindrostigma with narrowly oblong, coriaceous leaves, secondary veins very few and far apart, flanking numerous obvious intersecondaries, and inconspicuously random-reticulate tertiary veins. Goniothalamus gigantifolius also has distinctive leaves that are narrowly oblong but with chartaceous laminas. It also has numerous secondary veins and strongly raised percurrent tertiaries. A third species with peculiar leaves is the aptly named G. stenophyllus, with chartaceous, linear leaves. There is at least one currently undescribed species with even more linear but thickly coriaceous leaves.

Most species within the first four groups of leaf types are difficult to differentiate on the basis of leaf characters. To some extent the leaves show certain correlations in size and shape, but the differences tend to intergrade when a good

sampling of specimens is available. In this sense, the leaf characteristics can only be used as a guide to suggest certain alliances or smaller groups within the larger alliances. Except for some of the special cases, the definitive identity of a specimen normally has to be confirmed on the basis of reproductive characters.

REPRODUCTIVE MORPHOLOGY

Goniothalamus flowers have typical annonaceous floral features. They are normally solitary, at times in pairs, with the pedicel subtended by imbricate bracts. The showy perianth consists of three chartaceous sepals and six petals borne on a slightly convex torus. The petals are arranged in two whorls of three each. The outer petals are spreading and alternate with the sepals. The inner petals are joined in the upper half to form a dome-shaped structure enclosing the androecium and gynoecium. The lower part of the inner petals tapers to the base, thus leaving the lower part of the dome with three openings.

Although no extensive study has been conducted on the pollination biology of *Goniothalamus*, field observations lead me to believe that the inner petal dome protects the sexual organs from foraging beetles, which serve as pollinators in the Annonaceae (Deroin 1989, Gottsberger 1988). The arrangement of the outer petals in relation to the inner petals makes it possible for the three openings at the base of the dome to remain closed until the flower reaches full maturity. In immature flowers the outer petals are erect and pressed to these openings, thus blocking the entrance to the inside. During anthesis the outer petals spread out slightly, exposing the dome openings as passages to the inside through which pollinating insects must enter to reach the stamens and stigmas. The flattened outer petals also serve as a landing pad.

At anthesis the flowers emit sweet-pungent fragrances. It is unfortunate that there has been no study on the aromatic volatile chemical constituents of the flowers of *Goniothalamus*. Such information would be important for improving understanding of evolution and speciation in the genus. Through field experience I suspect that flowers of different species of *Goniothalamus* have distinctive aromatic properties that may attract different species of pollinators.

The inner-petal dome is confined to only a few genera of the Annonaceae. These were classified in the tribe Mitrephoreae by Bentham and Hooker (1862), an arrangement followed by Sinclair (1955). Within the Mitrephoreae the genus *Goniothalamus* can be distinguished from other genera by the structure of the inner and outer petals and especially by the length, shape, and texture of the petals.

Outer Petals

The three outer petals of *Goniothalamus* are diverse and are often used as distinguishing characters. They can be very large in some species. The largest, found in *G. giganteus* from the Malay Peninsular and Sumatra, can reach up to 12 cm long and 7 cm wide. The Bornean equivalent of *G. giganteus* (*G. borneensis*) has somewhat smaller outer petals (up to 10 cm long, 5 cm wide) but these are much larger than those of most other Bornean species.

Some species such as G. woodii have long outer petals (8–9.5 cm long) but they are very narrow (1.5–2 cm wide) and broadly linear or narrowly lanceolate. The narrowest outer petals are found in G. stenopetalus, which has unique linear undulate petals.

Most species have coriaceous ovate-lanceolate outer petals that are fleshy when fresh. They are quite showy in many species, and are either subtle maroon-

red or creamy yellow. In many species, especially in the G. roseus and G. uvarioides alliances, they are convex, but some species such as G. montanus and G. fasciculatus have concave outer petals. In some others, such as in species of the G. tapisoides and G. malayanus alliances, they are simply flat and wavy.

Inner Petals

The inner petals of *Goniothalamus* are generally smaller than the outer. The mitreform dome in this genus stays intact after anthesis and drops off as a single unit. The only genus that shares this character is *Friesodielsia*. Although the dome is generally considered to be an evolutionarily unique structure, I have not seen any discussion of its general morphology in other studies.

In the revision of *Orophea*, Keßler (1988, 1990) utilized the morphology of glands inside the inner petals. In *Goniothalamus* there is no specific shape of the glandular areas, but certain areas inside the inner petals have specialized indument. The function of this indument is unknown, but it might be speculated that the scurfy or warty structures serve as a food for beetles and the long echinate or wavy villous trichomes are used for cooling purposes. It is also possible that some of the indument is ethereal oil glands.

The whole dome needs to be considered as a unit for taxonomic analysis. Its morphology is diverse for the genus, with at least five distinct types (Figure 9). The most common type, designated here as dome type 1, is well represented in the G. tapis and G. tapisoides alliances. This dome is of medium size, with sharply acute apex and slender feet curving broadly to the outside to form a wide opening at the base. This type seems to have several variations of the indument inside the dome. The domes of G. tapis, G. woodii, G. roseus and G. montanus have a mass of white warty papillae on the upper half toward the top but they are mostly glabrous

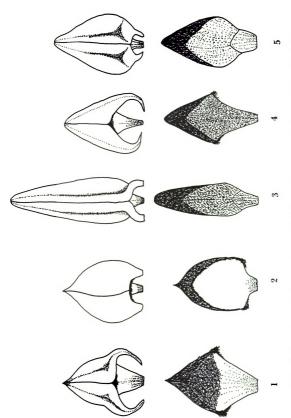


Figure 9. The main types of mitreform domes of *Goniathalamus* (upper row) and the morphology of the inside of corresponding inner petals (lower row). The numbers refer to the dome types as **explained** in the text.

around the openings (Figures 10A, C, D & F). The lower half sometimes becomes slightly rusty with sparse scabrous trichomes. This condition has not been observed in G. clemensii, G. andersonii and G. lanceolatus, in which the inner part is consistently hispid throughout the developmental stages of the dome (Figures 10B, E & G). The domes of G. umbrosus, G. tapisoides, G. longistipites and G. sinclairianus, on the other hand, are covered with a villous indument and with persistently mixed hispid and glandular trichomes. The surface eventually becomes less hairy toward anthesis and warty papillae replace the hispid trichomes (Figures 11A, C & E).

Dome type 2 is characterized by rather broadly ovate inner petals, golden sericeous outside, with a completely smooth, glabrous, waxy inner side and very small openings (Figures 11B, D,&F). This type is found only in G. malayanus, G. giganteus and G. borneensis.

Dome type 3 occurs in *G. uvarioides* and its allies. In this group the inner petals are not elliptic as in types 1 and 2 but rather lanceolate-oblong. These petals form a unique dome with the blunt apex projected far above the small openings at the base. The inside surface of this dome is fluffy villous on the upper half and consistently brown rusty hispid-echinate from the middle to the bottom (Figure 12). Some species in the *G. uvarioides* alliance, such as *G. gigantifolius*, have rather broad ovate inner petals, thus forming a slightly different dome with broader base and shorter top but they retain the characteristics of the inner side of the dome. Thus, they would be considered to be slight variants of dome type 3.

Dome type 4 is found in a group of species with rufous-velutinous indument on most parts of the young twigs, leaves and flowers. The same rusty brown rufous-velutinous indument is found on the inside as well as the outside of the inner petals of this dome (Figures 13A & B). The species with dome type 4 include G. velutinus, G. rufus, and G. fasciculatus.

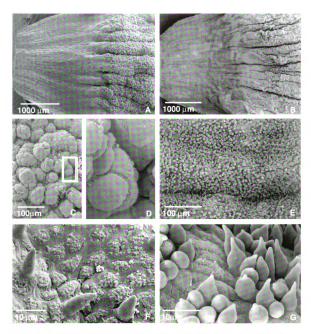


Figure 10. A–F. Variation of indument on the inner side of dome type 1. A, C & F. *Goniothalamus woodii (Mat-Salleh KMS 3031)*. B, E & G. *Goniothalamus clemensii (Beaman 9329)*. A & B. General view. C & D. Warty papillae on the upper portion of A. E. Dense hispid trichomes from the middle of B. F & G. Close-up of the indument from the base of the petals.

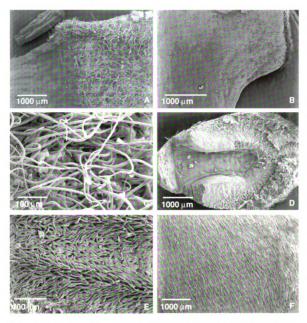


Figure 11. Inner petals of dome types 1 and 2. A, C & E. Dome type 1. B, D & F. Dome type 2. A & B. General view of the inner side. A. *G. tapisoides (Murty S 23226)*. B. *G. borneensis (Mat-Salleh KMS 2500)*. C. Close-up of A, villous hairs and warty papillae of the upper portion of the petal. D–F. Young inner petal of *G. malayanus (Jamili JN 40)*. D. Adaxial surface of petal. E. Trichomes from the base of the inside of the petal. F. The outside showing the sericeous indument.

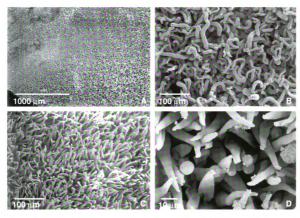


Figure 12. Inner petal of dome type 3, from *G. uvarioides* (*Mat-Salleh KMS 2819*). A. General view of the inner side. B. Close-up of fluffy villous hairs of the upper portion of the petal. C. Slender echinate trichomes on the lower half. D. Glands found between trichomes.

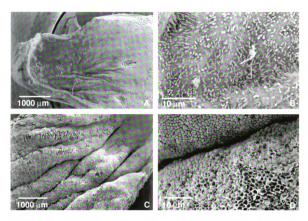


Figure 13. Inner petals of dome types 4 and 5. A–B. Dome type 4, *G. rufus (Anderson S. 15382)*. C & D. Dome type 5, *G. stenopetalus (Kitayama K 1420)*. A & C. General view of the inner side. B & D. Close-up of the trichomes/glands.

Dome type 5 is very rare and so far is known in only one species, G. stenopetalus. Its shape is more or less similar to that of G. giganteus, but the inner side is glandular-scurfy rather than hispid-echinate (Figures 13C & D).

Stamens

Stamens of *Goniothalamus* are of a primitive nature for angiosperms in general. They are numerous, laminar, and spirally arranged on an elevated torus surrounding the pistils in the center of the torus. The large pollen grains are produced in two pairs of oblong elongated thecae separated by a woody connective. Numerous stomatal complexes were observed on the abaxial (outside) surface of the connectives of several species (Figure 14).

Although it appears that *Goniothalamus* species may have several different types of stomatal complexes on their stamens, this study was not designed to make a full survey of this variation. Some species apparently have no stomata on their stamens, but it was difficult to determine if these are truly lacking. Some stamens will require a different preparation technique from that used for the rest of the SEM study. Perhaps they will need to be cleared for this variation to be conclusively examined.

The size of stamens is not very important taxonomically, but some species in the G. uvariodes alliance have extremely large stamens in comparison to the others. Some species, such as G. malayanus, G. borneensis, G. giganteus, G. rufus and G. puncticulifolius, have much shorter stamens.

The single most taxonomically important part of the stamen is the connective, especially the tip. In fact, stamen connectives have been widely utilized in traditional classifications to divide *Goniothalamus* into subgenera or sections

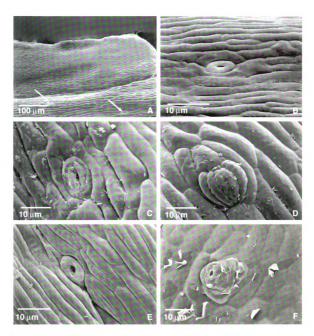


Figure 14. Stomatal complexes found on the stamens of Bornean Goniothalamus. A. Overview of the abaxial surface of a stamen showing two stomatal complexes (G. rossellatus, Mat-Salleh KMS 2423). B. Close-up of anomocytic stomatal complex from A. C. Anomocytic complex from G. umbrosus, Banyeng & Sibat S 26246. D. Brachyparacytic stomatal complex (G. andersonii, Smythies, Wood & Ashton S 5901). E & F. Amphibrachyparacytic stomatal complex (E, G. woodii, Mat-Salleh KMS 2741; F, G. borneensis, Mat-Salleh KMS 2500).

(Bân 1974a). Goniothalamus species have been reported to have either apiculate or flat-topped connectives. Although this classification may seem straight forward, it has been found that some species have stamens with intermediate upper ends. In Borneo, this group of species has somewhat blunt-acute connectives. In certain species, such as G. roseus and G. stenopetalus, the connective is rather capitate. Detailed SEM micrographs, however, do not support the idea that this connective is an intermediate type.

Taking into account overall shape, size, indument, and micromorphology of the connective, at least 11 types of stamen can be seen in Bornean Goniothalamus (Figure 15). The first type, designated here as stamen type 1, is found in G. uvarioides, G. parallelivenius, G. kinabaluensis, G. kostermansii, G. dolichocarpus, G. gigantifolius, and G. cylindrostigma. These stamens are large, slender, with apiculate connectives covered with glandular echinate indument all over the apex (Figures 16A & B).

Stamen type 2 is close to type 1 and is a variant of it. The stamens are slightly shorter than in type 1, and the apiculate connective has echinate indument only on the upper two-thirds of the apex. The lower part is glandular without much echinate indument (Figures 16C & D). Type 2 stamens are found in G. tapis, G. sumatranus, G. umbrosus, G. bracteosus, G. rostellatus, G. crockerensis, G. calcareus, G. woodii, G. nitidus, G. macrophyllus and G. lanceolatus.

Stamen type 3 seems to represent a reduction of types 1 and 2, with the apex of the connective becoming more blunt and broader. The indument is similar to that of type 2 stamens but the glands are more prominent. In overall size and shape, type 3 stamens are smaller and broader (Figures 16E & F) than those of types 1 and 2. Type 3 stamens are found in G. tapisoides, G. sinclairianus, G. clemensii, G. longistipites and G. montanus.

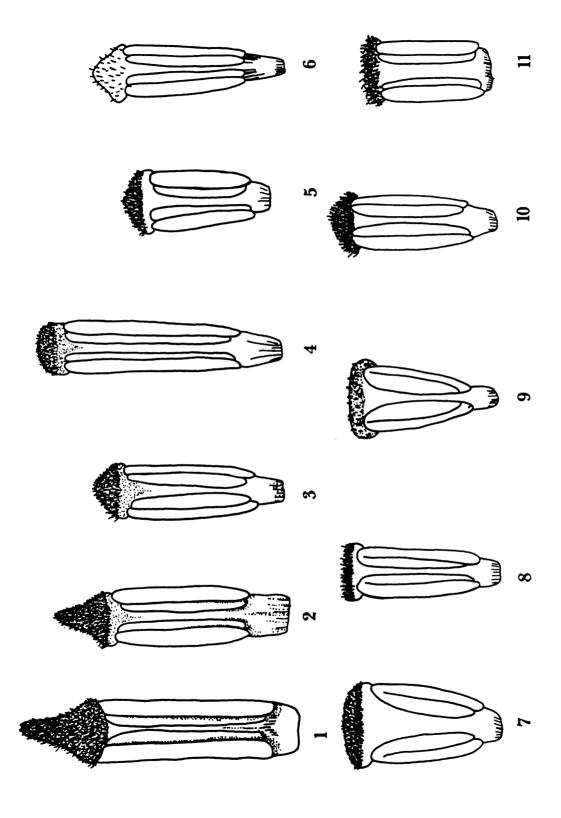


Figure 15. The main types of stamens of Goniothalamus. The numbers refer to the stamen types as explained in the text.

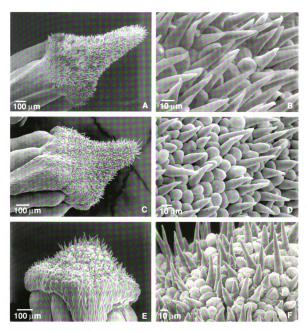


Figure 16. Stamen connectives of *Goniothalamus* and close-ups of the indument. A & B. Stamen type 1 (G. dolichocarpus, Mat-Salleh KMS 2819). C & D. Stamen type 2 (G. woodii, Mat-Salleh KMS 3031). E & F. Stamen type 3 (G. tapisoides, Sinclair & Kadim 10385).

Stamen type 4 is close to type 3, but the stamens are very slender and long and the connectives are capitate. Immature stamens are less flat-topped (Figure 17A) and become more flat-topped as they mature (Figures 17B & C). Even at near maturity, these stamens give different perpectives depending on the angle at which they are viewed. Abaxially, the connective appears flat-topped, but adaxially it appears slightly blunt-acute (Figures 17D & F). At full maturity the connectives of type 4 appear to be capitate with a somewhat concave top. This type is found in G. roseus and G. stenopetalus in Borneo and in G. elmeri in the Philippines.

Stamens in the other species are further modifications of type 3. Stamen type 5 appears to have lost the glands at the base of the apex, whereas stamen type 6 has lost all glands from the bottom up, and the indument consists of very sparse scattered strigose trichomes (Figure 18). In both cases these stamens are represented by a single rare species (*G. puncticulifolius* for type 5 and *G. andersonii* for type 6).

The most unusual stamens in *Goniothalamus* are short and flat-topped or slightly convex. Stamen types 7–11 have this form, and the differences among them relate mostly to the indument.

Stamen type 7, found in *G. giganteus*, has connectives resembling those of stamen type 4 but differs in size and general appearance. This stamen is short and oblanceolate, rather than linear and slender as in type 4. The convex connective has sparse indument and the trichomes are rather short (Figures 19A, C & E). This type is quite different from type 8 found in *G. borneensis* (Figure 19B, D & F) in which the connectives are more densely covered with long indument. The difference was consistent in several samples examined, and micrographs from younger stamens show even more subtle differences (Figure 20). Together with other characters, especially the mature carpels, the stamen characters are used in this treatment to justify the new status of *G. borneensis*, separate from *G. giganteus*.

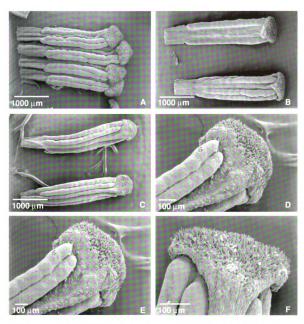


Figure 17. Goniothalamus stamen type 4. A–C. Developmental variation in the morphology of the connective in G. roseus. A. Stamens from a very young flower (Mat-Salleh, KMS 2914) B. Stamens of immature flower (Beaman 10667). C. Stamens from flower at full maturity (Beaman 8543). D–F. Mature stamen observed from different angles (D. side view; E, from below; F, abaxial view).

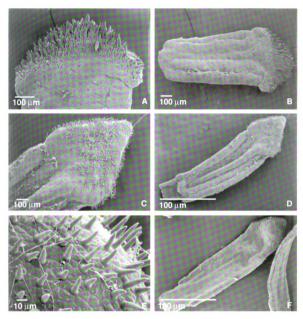


Figure 18. A & B. Goniothalamus stamen type 5 (G. punctilifolius, Agama & Valera 9886). C–F. Goniothalamus stamen type 6 (G. andersonii, Smythies, Wood & Ashton S 5901).

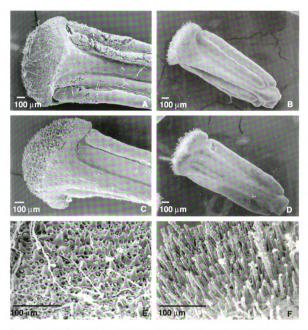


Figure 19. A–C. *Goniothalamus* stamen type 7. A, C & E. Connectives of *G. giganteus* from the Malay Peninsula (A. *KEP 4237* and B. *Maxwell 85-715*). C. Close-up of indument on top of the connective. B, D & F. *Goniothalamus* stamen type 8, *G. borneensis (Mar-Salleh KMS 2500)*. B. Abaxial (external) view. D. adaxial (internal) view. F. Close-up of indument on top of the connective.

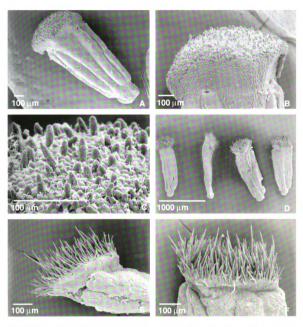


Figure 20. Developmental variation in the morphology of the connective in stamen types 7 & 8. A–C. Type 7 stamens from young flower of *G. giganteus (Latex 4039)*. D–F. Type 8 stamens from young flower of *G. borneensis (Ilias & Azahari S 35717)*.

Stamen type 9, restricted to *G. malayanus* and *G. rufus*, is characterized by a short glandular farinose-hispid indument on the upper half of the connective apex (Figure 21). The overall shape of this stamen resembles closely that of type 7 stamens in *G. giganteus*, to which *G. malayanus* is closely related.

Stamen types 10 and 11 are both rare, characterized by having indument covering all parts of the connective from top to base of the apex. They are exclusive to *G. velutinus* and *G. fasciculatus*, respectively. Type 10 stamens differ from type 11 by having echinate indument commonly found in other species (Figure 22A, C & E) rather than soft pilose hairs as found type 11 (Figure 22B, D & F). The overall shape of the connective for type 10 is also slightly convex, approaching the blunt-acute shape of types 3 and 5, while type 11 is flat-topped.

Pistil Morphology

Goniothalamus flowers have numerous apocarpous pistils arranged in the center of the torus. The ovaries are either cylindrical or obclavate, and pubescent or glabrous with hairs confined to the base. Taxonomically, the most interesting part of the pistil is the stylar-stigmatic portion. Styles in Goniothalamus are typically small and tubular or large and cylindrical, long and elongated. The styles have various shapes and surface characteristics as well as orientations. The ovaries in most species except for those in the G. uvarioides alliance normally have a single basal ovule. Occasionally two-ovulate ovaries occur. Ovaries in G. uvarioides and other species in that alliance have up to 10 ovules per ovary.

As in the case of stamens, *Goniothalamus* pistils can be categorized into several types. There are at least nine types of pistil in the Bornean species (Figure 23). Type 1 pistil is the most prominent and easiest to recognize. The ovaries are large, 3.5—4 mm long (Figure 24), with many ovules (up to 10), covered with

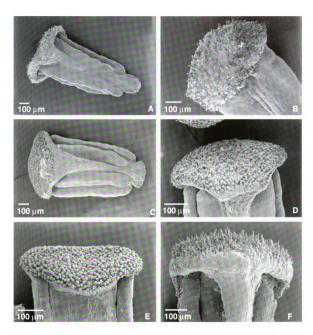


Figure 21. Goniothalamus stamen type 9. A & B. G. malayanus from Borneo (Wong WKM 18). C & D. G. malayanus from the Malay Peninsula (Hamid et al. PUS 153). E & F. G. rufus (E. Mat-Salleh KMS 1760 from Sabah, F. Anderson S 15382 from Sarawak).

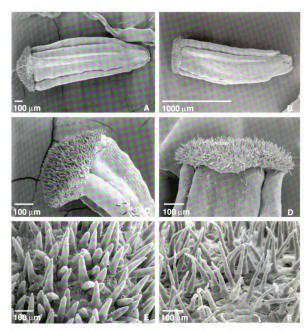


Figure 22. A, C & E. *Goniothalamus* stamen type 10 (*G. velutinus*, *Mat-Salleh KMS* 2458). B, D & F. *Goniothalamus* stamen type 11 (*G. fasciculatus*, *Clemens* 34175). A & B. Stamen overview, abaxial (external) side. C & D. Close-up of connectives.

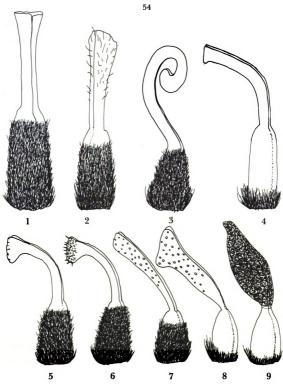


Figure 23. The main types of pistils of Goniothalamus. The numbers refer to the pistil types as explained in the text.

white tissue mass (Figures 25A & B) and upright, glabrous, and cylindrical vaginiform styles with a crateriform stigma. This pistil is found only in the G. uvarioides alliance.

Pistil type 2 is similar to type 1 in overall shape. However, the ovary in type 2 is smaller. The main difference, however, lies in characteristics of the style and stigma. These are prominently hairy rather than glabrous as in type 1 (Figures 25C \mathcal{E} D). There is a single basal ovule. Type 2 pistil is restricted to species in the G. macrophyllus alliance.

Like pistil types 1 and 2, type 3 is one of the distinguishing features used to characterize certain species alliances. In this case, pistil type 3 is confined to and one of the basic features of the *G. malayanus* alliance. The pistil has a special alignment in which the stigma is incurved 360°, rather than recurved as found in other species with spreading styles (Figure 26). The stigma in pistil type 3 is also unique, with two broad and round lobes facing upward, forming a ladle-like structure (Figures 27A & B).

The pistils of types 4 to 9, which have spreading styles, differ among themselves by the shape and surface indument of styles and stigmas. Pistil type 4 is found only in G. roseus and G. stenopetalus, and is characterized by a slender tubular pistil with smooth and glabrous style (Figures 27D–F). The same general shape is found in types 5 and 6 but the style is comparatively larger and shorter, and the stigma becomes more crateriform (Figures 28 & 29). A group of Bornean species including G. rostellatus, G. bracteosus and G. crockerensis have pistil type 5 which has a glabrous stigma (Figure 28). The stigma is also larger than in pistil type 4.

Another group of widespread species belonging to the *G. tapis* alliance has more or less the same pistil except that they have a different stigma. This type, designated as pistil type 6, has a smooth style at the base which becomes warty toward the top and is warty-echinate on the stigmatic area (Figures 29A–C). This



Figure 24. Goniothalamus pistil type 1. A. Mature pistil of type 1, from G. dolichocarpus (Mat-Salleh 2819). B. A young pistil of type 1, from G. kostermansii (Kostermans 13926).

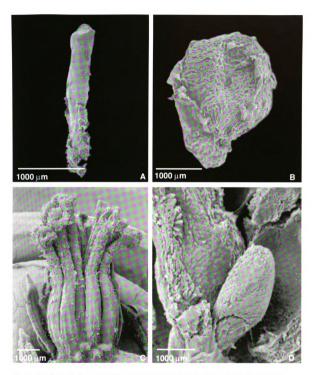


Figure 25. Goniothalamus pistil type 1 (continued) & 2. A. Multiple ovules taken out from pistil in Figure 24A, note white mass covering the ovules, B. Cleaned single ovule, taken from Figure 25A. C. General overview of pistil type 2, from G. macrophyllus, FRI 98302. D. Single basal ovule from pistil in C.

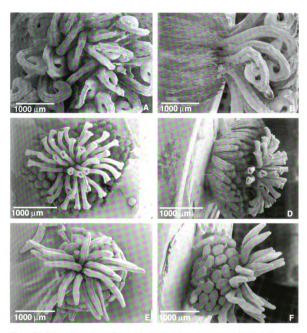


Figure 26. Side and top views of gynoecia showing the arrangements of and relative positions of the styles and stigmas. A & B. Incurved stigma, twisted 360°, found only in type 3 pistil (*G. borneensis, Mat-Salleh KMS 2500*). C–F. Recurved and spreading stigmas with slits facing upward as found in pistil types 4–9. C & D. *G. clemensii* (*Beaman 8888*). E & F. *G. rufus (Mat-Salleh KMS 1760*).

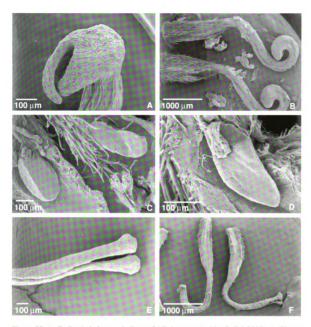


Figure 27. A–C. *Goniothalamus* pistil type 3 (*G. borneensis, Mat-Salleh 2500*). A. Closeup of stigma showing two lobes. B. Side view. C. Two basal and sub-basal ovules, split from dissected ovary. D. Single basal ovule. E & F. pistil type 4 (*G. roseus, Clemens 30364*). E. Top view of the stigma showing the slit. F. Side view.

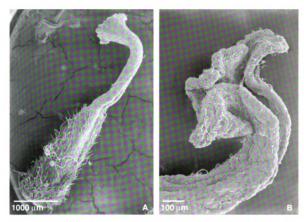


Figure 28. *Goniothalamus* pistil type 5. A. General view (*G. rostellatus, Mat-Salleh KMS 2423*). B. Close-up showing broad crateriform stigma.

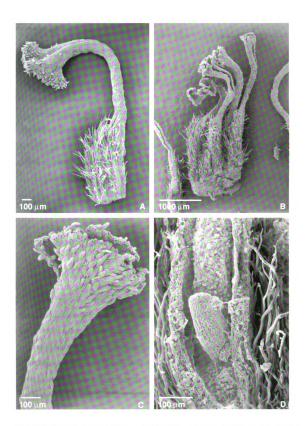


Figure 29. Goniothalamus pistil types 6. C & D. General view of pistils from Peninsular Malaysian G. tapis (C, Merican s.n.) and Bornean G. woodii (D, Mat-Salleh KMS 1029). E. Close-up of warty-echinate stigma, from D. F. Single basal ovule from D.

type is found in species mostly from outside Borneo (G. tapis and G. sumatranus) and occurs in only one Bornean species, G. woodii.

Another group of Bornean species related to members of the *G. tapis* alliance has a remarkably different pistil type. This pistil type 7 has a warty, tubular-clavate style and stigma (Figure 30). This type is found in species of the *G. tapisoides* alliance and in *G. fasciculatus*. The pistil of *G. nitidus* is considered a separate type (type 8) even though it has many of the characteristics of pistil type 6. It differs, however, in that the style and stigma are larger and much more clavate (Figures 30D & E) than in species of the *G. tapisoides* alliance.

Pistil type 9 is perhaps the most bizarre pistil in the genus. This is found in only two Bornean species, viz. G. velutinus and G. rufus. The ovary is glabrous, with 1 or 2 ovules. The style is short but the stigma is monstrous, somewhat glabrous when young, then glandular, warty and scurfy at anthesis (Figure 31). The function of this structure is unknown, but it might be a food body for pollinators.

Fruits and Seeds

The fruits of *Goniothalamus* are typical of the Asiatic Annonaceae. They are apocarpous fruits derived from a single flower, and should not be confused with fruits derived from umbellate inflorescences that can be quite similar in appearance. Independent fruiting carpels in annonaceous fruits are developed from separate pistils on the torus of a single flower. Because of the nature of these structures, the main stalk connecting the torus with the twig or trunk is actually a pedicel rather than a peduncle as it has been incorrectly called by many collectors. For the same reason, the carpel stalk should be referred to as such, not as the pedicel.

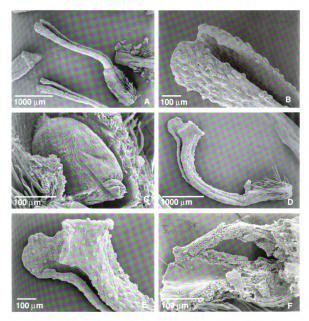


Figure 30. A–C. *Goniothalamus* pistil type 7 (*G. sinclairianus, Banyeng & Sibat S* 26246). A. General view. B. Stigma. C. Single basal ovule. D–F. Type 8 (*G. nitidus, Ramos* 78). D. general view. E. Stigma. F. The outside wall of ovary, with papillae.

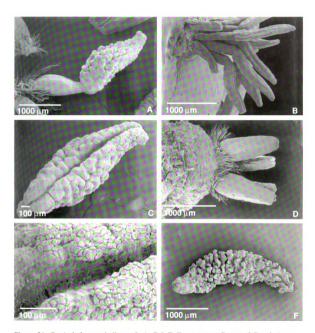


Figure 31. Goniothalamus pistil type 9. A, C & E. From mature flower of G. velutinus (Mat-Salleh KMS 2458). B, D & F. From G. rufus in which B is from a young flower (Mat-Salleh KMS 1760) and D & F are from a fully developed flower (Anderson S 15382). A & B. General appearance. C & E. Stigma and close-up of the stigmatic surface. D & F. Ovaries and stigma, easily separated during boiling.

Mature fruiting carpels of *Goniothalamus* have various sizes and stalk lengths, and these features have been widely utilized as important taxonomic characters. In many *Goniothalamus* fruits, remnants of undeveloped ovaries and stamens are often found at the base of the carpel stalks. In addition to characteristics of the carpel stalk, the shape and size of the carpels are also important. Most carpels in *Goniothalamus* are globose or elliptic. Some fruits, like those of *G. dolichocarpus*, have thinly oblong or linear carpels, often in pairs. *Goniothalamus kostermansii* is distinctive in having "banana-like" fruiting carpels. Number of seeds per carpel varies, but most carpels are single or double seeded except for species in the *G. uvarioides* alliance, which normally has up to 6 seeds per carpel. All species of *Goniothalamus* have ruminate endosperm.

ANATOMY

Like the floral features, which are unique and easily distinguishable for the family, members of the Annonaceae are also known to have unique wood and bark characteristics that are commonly used by foresters and botanists for field recognition. It is said to be almost impossible for experienced field workers to confuse annonaceous wood and bark with that of any other plants (Wyk & Canright 1956).

Annonaceous woods are characterized by the presence of fine continuous tangential bands of parenchyma rays, occurring with remarkable uniformity and consistency among all genera. This condition supports the hypothesis that the Annonaceae constitute a very well-defined natural grouping. In contrast to the rather primitive floral characters, however, woods of the Annonaceae seem to attain a high level of anatomical specialization. Being members of the order Magnoliales, one might expect the occurrence of scalariform perforation plates, as

often found in primitive angiosperms such as the Autrobaileyaceae,

Degeneriaceae, Eupomatiaceae and Magnoliaceae. However, no species of the Annonaceae have scalariform perforation plates in their vessels. Xylary vessels are almost exclusively with simple perforation plates. Vessel elements are normally short, with almost transverse end walls. The intervascular pitting is predominantly alternate and fibers are comparatively short, thick-walled libriform. The only wood features in the family that are thought to be primitive are the tendency toward solitary vessel distribution and apotracheal parenchyma (Wyk & Canright 1956).

As in the case of wood anatomy, comparative foliar anatomy has been investigated in the Annonaceae. Leaf anatomical features may provide the best known information yet accumulated within the family to determine stability of characters as well as heterogeneity among the genera. Most of our knowledge on foliar anatomy of the family comes from an excellent survey of Indochinese Annonaceae by Jovet-Ash (1942) and an intensive study on epidermis in an unpublished dissertation by Roth (1981).

The leaves are well known for having scattered ethereal oil cells embedded in the mesophyll, which occasionally lyse into mucilage cavities, another common character of Magnoliales. According to Roth (1981), stomatal complexes of Annonaceae, except in *Deeringothamnus*, are always hypostomatic. By far the most common type is the brachyparacytic, in which the two subsidiary cells are noncontiguous at both poles. However, other variations such as paracytic (with two subsidiary cells contiguous at both poles), hemi-amphibrachyparacytic (with three subsidiary cells that are noncontiguous at both poles) and amphibrachyparacytic (four subsidiary cells that are noncontiguous at both poles) are also found. Annonaceae leaves are also known to have foliar sclereids, mostly of the filiform, columnar fibriform or polymorphic types (Rao & Chin 1966).

The ovules of Annonaceae have peculiar anatomical characters, viz. crassinucellate, bitegmic anatropous ovules with perichalaza. Moreover, the inner integument commonly exceeds the outer integument so as to give a prominent naked endostome to the ovule, persistent even in the seed (Corner, 1949). In certain genera, such as Artabotrys, Cananga, Cleistopholis, Cyathocalyx, Guamia, Lettowianthus, Mezzetia, Mezzetiopsis, Meiocarpidium and Platymitra, a third integument, positioned between the inner and outer integuments, is formed after fertilization. Since this rudimentary middle integument was first noted by Corner (1949), it has been subjected to various anatomical studies, especially by Rao (1975) and Christmann (1986, 1989).

In spite of the vast amount of information on the anatomy of the family in general, there have been very few studies on the genus Goniothalamus. The only detailed anatomical analysis for the genus was based on several distinctive Bornean species, G. andersonii, G. macrophyllus, G. malayanus, and G. velutinus, and published by Blunden et al. (1973, 1974a, b). They showed convincingly that leaf, stem and root anatomical features can be used to differentiate taxa. It would be interesting to examine closely allied species to determine if anatomical features could be used to help resolve taxon boundaries in some of the complex species.

PALYNOLOGY

The taxonomic importance and diversity of pollen in the Annonaceae have helped to make palynological features one of the best known aspects of the family. Many surveys utilizing both light and electron microscopy have been carried out to help establish generic relationships within the family. The most notable among these is the general survey by Walker (1971) and a more detailed analysis restricted to African members by Le Thomas (1981, 1982).

Walker's study included nine species of Goniothalamus, of which only three, G. nitidus, G. velutinus and G. puncticulifolius, occur in Borneo (the rest are G. amuyon from the Philippines, G. chartaceus, G. repevensis and G. saigonensis from Indochina, G. curtisii from the Malay Peninsula, and G. grandiflorus from New Guinea). His report indicated that the pollen of Goniothalamus consists of tetrahedral or tetragonal tetrads, with heteropolar, bilateral, cataulcerate, disc-like concave-convex grains. The grains are comparatively large to very large, with the longest axis 71–140 µm (average 95 µm). They are microtectate, with no columella discernible, and with pitted or otherwise psilate exine. These characters are thought to be shared with and related to the pollen of Anaxagorea, Piptostigma, Xylopia, Fusaea, Duckeanthus, Cananga, Meiocarpidium, Neostenanthera and Richela, thus grouped in "the Fusaea Subfamily" in Walker's classification (which was based entirely on pollen morphology).

The acetolyzed pollen grains from several species of *Goniothalamus* published by Walker (1971) have a single large aperture. This condition is not the natural condition of the pollen, however. The large aperture reported by Walker is actually an artifact of the acytolysis method, which has been strongly criticized (Hesse & Waha 1989). Pollen of Bornean *Goniothalamus* species (Figures 32–34), prepared using the KOH revival technique employed in this study for flowers, shows a much closer correspondence to untreated pollen.

The pollen grains of *Goniothalamus* always occur in tetrads and have a small slit rather than a large pore. The tetrads are bound together by an irregularly patterned material and then covered with sticky pollenkit (Figures 32D & F). KOH appears to wash away most of the pollenkit but the pollen remains in tetrad form inside the enclosure (Figures 33 & 34).

The overall morphology of pollen and tetrads observed in this study does not offer enough diversity to be useful for classification at the species level. The pollen of *Goniothalamus* is more or less homogenous throughout the genus.

The ultrastructural elucidation of Annonaceae pollen by Le Thomas (1980, 1981) disclosed more remarkable structural diversity. It was found that all annonaceous pollen totally lacks endexine, a feature otherwise found exclusively in the monocotyledons. The remaining ektexine shows a range of patterns from primitive granular infratectate to highly advanced columellar infratectate, with or without a basal layer. She also found that the reduction of pollen ultratructure is paralleled by floral reduction and concluded that the family is perhaps an evolutionary dead-end.

CHROMOSOME COUNTS AND KARYOLOGY

Despite extensive surveys to establish the chromosome base numbers of the Annonaceae (i.e., Ehrendorfer et al. 1968, Okada & Ueda 1984, Sauer & Ehrendorfer 1984), the genus *Goniothalamus* is not well represented in accounts on chromosome data for the family. Only six papers provide original chromosome counts for the genus. Reports by Ehrendorfer et al. (1968), Sobha and Ramachandran (1979), Okada and Ueda (1984), Sauer and Ehrendorfer (1984) and Morawetz (1988) for *G. grandiflorus*, *G. macrophyllus*, *G. opacus*, *G. wynadensis* and *G. australis* show a consistent count of 2n = 16.

Chromosome numbers of other Annonaceae are generally low, normally diploid with 2n = 16. However, some species have 2n=14 or 2n=18, with ploidy levels up to 8x in *Cyathocalyx*.

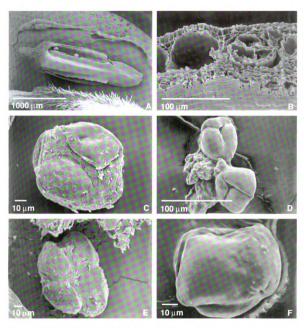


Figure 32. Pollen of Bornean Goniothalamus. A. The opened theca of a stamen, showing two pollen tetrads remaining inside the theca (G. uvarioides, Mat-Salleh KMS 2134). B. The theca cut, showing 4 sliced grains in tetrads inside the chamber (G. stenopetalus, Kitayama K 933). C–D. FAA-preserved untreated tetrads of G. woodii showing sticky pollenkit (Mat-Salleh KMS 3031). E. Tetrad from revived stamen, pollenkit mostly removed (Mat-Salleh, KMS 2741). F. Tetrad from revived stamen of G. velutinus (Mat-Salleh, KMS 2458).

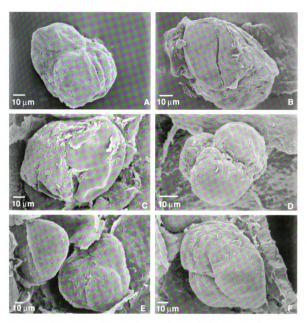


Figure 33. Pollen of Bornean *Goniothalamus* (continued). A & B. Tetrads of *G. roseus* (Beaman 8543), showing the pollen surface texture and aperture after the pollenkit is removed. C–F. Tetrads of *G. stenopetalus* (C, Kitayama K 1420), G. clemensii (D, Beaman 8173), G. fasciculatus (E, Clemens 34175) and G. umbrosus (F, Banyeng & Sibat S 26246).

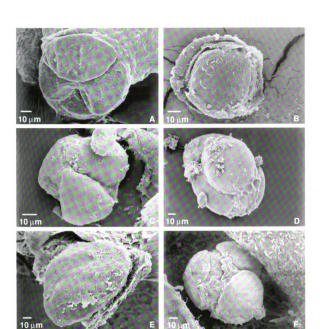


Figure 34. Pollen of Bornean Goniothalamus (continued). A–F. Tetrads of G. malayanus (A, Wong WKM 18), G. velutinus (B, Mar-Salleh KMS 2458) and G. borneensis (C, Mat-Salleh KMS 2500), G. dolichocarpus (D, Mat-Salleh KMS 2919), G. nitidus (E, Ramos 98) and G. warioides (F, Mat-Salleh KMS 2134).

PHENOLOGY

Preliminary studies of the comparative phenology of several species of the Annonaceae were carried out for six months in Sabah by Abd.-Rahman (1988), under my supervision, to determine the rate of floral and fruit development as well as the amount of fruit production. As far we know, there has been no phenological analysis ever published on *Goniothalamus*. Abd.-Rahman found that it took 17 weeks for flowers of the montane species *Goniothalamus montanus* to reach anthesis from early bud initiation and 20 weeks more for the fruiting carpels to reach maturity. This was much slower than in *Dasymaschalon clusiflorum*, a lowland species, which needed only 8.5 weeks for its buds to reach anthesis and 18 weeks for fruits to mature, even though the flowers of *Dasymaschalon* are much larger than those of *Goniothalamus*.

The slower rate of development corresponds with lower fruit production in Goniothalamus. While Dasymaschalon had 48.3 % of the total flowers per tree develop into fruits, only 10% of the Goniothalamus montanus flowers produced fruits. Low fruit production of Goniothalamus is probably common, because another species (G. stenopetalus) studied by Abd.-Rahman in a nearby area had failure of fruit set from flowers initiated in that period. I tried to obtain fruits from this species from several populations over several years but could never find a single fruiting carpel.

In an attempt to observe general phenological conditions in Bornean Goniothalamus, developmental stages of the herbarium specimens of all species were coded and input to the specimen database. Flowering and/or fruiting stages of the specimens were noted using the following code: 1) young bud, 2) immature flower, 3) mature flower, 4) immature fruit and 5) mature fruit. Because most of

the recent collections had collection dates, the phenology of some species could be tabulated and analyzed. The raw data that resulted from this exercise are presented in Appendix 3.

It may be argued that interpreting phenology from specimens is speculative because they were collected for taxonomic analysis and not intended for this purpose. However, for the Bornean material, many of the collections were gathered by forestry department collectors at rather random times throughout the year. This can be seen by the occurrence of numerous sterile collections and specimens with immature flowers and/or fruits.

Based on the data presented in Appendix 3, it is not clear if all 30 species of Bornean *Goniothalamus* have specific flowering or fruiting seasons, because a number of the species have too few specimens for meaningful analysis.

Nevertheless, at first glance most species seem to have no distinct flowering and fruiting seasons. When the data from separate species are combined, however, some trends are discernable. It appears that the genus as a whole has two flowering seasons (Figure 35). The first season peaks around June and the second in November. As shown by Abd.-Rahman (1988), since it takes about 5 months, more or less, for each initiated bud to reach maturity, fruiting seasons would peak at about the same time as flowering seasons, in which fruits from a previous flowering season mature when new flowers are being initiated. This is confirmed by the fact that many herbarium specimens bear young flowers, old flowers and fruits at various stages.

Several common Bornean species, such as G. roseus, G. tapisoides, G. uvarioides and G. woodii, have enough specimens for comparison of phenological states. I therefore decided to analyze these species individually to observe their phenological trends. The results are shown in Figure 36. Goniothalamus woodii, perhaps the most abundantly collected species in Borneo, is shown to have a major

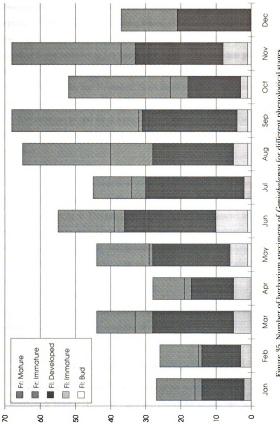


Figure 35. Number of herbarium specimens of Goniolhalamus for different phenological stages.

flowering season around September and a minor one in March. For this species, September-October is the main fruiting season, which corresponds to the main flowering season in March, and a minor fruiting season in March could have been a result of flower initiation in July-September. A similar but less clear phenology can be seen in *G. roseus* from Mount Kinabalu. This species appears to have main fruiting seasons in May and November. These could have been the result of January-March and June-July flowering periods.

The same can be said for *G. tapisoides* from Sarawak. In this species, the main flowering season appears to be around May-August, with a minor one in December.

The occurrence of flowering twice a year, as seen in *G. woodii*, *G. roseus* and *G. tapisoides*, may not be the case for all *Goniothalamus* species. In *G. uvarioides*, which is common around Mount Kinabalu, no fertile specimen has been recorded from December to April. This cannot be a collection artifact because there have been many collectors, such as the Clemenses, the Beamans, Kinabalu Park rangers, and UKMS students who have concentrated collecting effort in this area. The phenology for this species seems to be one flowering season a year, which reaches a peak around November.

More detailed phenological studies are needed to permit definitive conclusions as to flowering and fruiting times in *Goniothalamus*. Phenological data may be important in the understanding of evolutionary trends in the genus.

SYSTEMATIC POSITION AND CLASSIFICATION

A widely used infrafamilial classification of the Annonaceae was introduced by Bentham & Hooker (1862), in which they placed the genera into five tribes based on the aestivation of calyx and corolla and the structure of the stamen

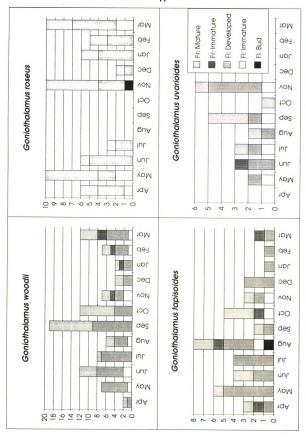


Figure 36. The number of herbarium specimens of four Bornean Goniothalamus analyzed for different phenological stages.

connective. These are the tribes *Uvarieae* (with imbricate petals), *Unoneae* (with valvate petals), *Mitrephoreae* (with inner petals curving over the sexual organs forming a dome-shaped "mitreform" structure), *Xylopieae* (with thick connivent outer petals), and the *Miliuseae* (with a distinctive stamen connective extending beyond the locules). In their classification, the genus *Goniothalamus* is considered a core member of a tribe *Mitrephoreae* together with *Mitrephora*, *Pseuduvaria*, *Friesodielsia*, *Orophea*, *Popowia* and *Neo-uvaria*. In Sinclair's (1955) revision of the Peninsular Malaysian Annonaceae, it is noted that while *Orophea* fits the circumscription of the tribe *Mitrephoreae* by virtue of the characters of its inner petals, members of this genus also have unusual stamens that associate it with tribe Miliuseae. Sinclair further noted that the inner petals of *Mitrephora*, *Popowia* and *Neo-uvaria* are united only at the beginning of flower development and are separate at anthesis. Only flowers of *Goniothalamus*, *Friesodielsia* and *Pseuduvaria* have a true mitreform dome during anthesis.

The Bentham and Hooker classification was improved by R. E. Fries, a lifelong student of the Annonaceae and an expert on South American members of the family. Fries subdivided Bentham & Hooker's tribes into 14 new associations referred to as "gruppes". These groups were based on additional characters such as the position of the inflorescence, the number and position of the ovules, fruit types, the presence of floral bracts and stamen and thecae characters. Although Bentham and Hooker's basic tribes were preserved by Fries (1959), later authors such as Walker (1971) decided to use Fries's "gruppes" as the basic unit of the infrafamilial classification of the family, and this was enhanced using pollen characteristics.

Based on floral characters, the genus *Friesodielsia* is perhaps the nearest relative of *Goniothalamus*. Members of *Friesodielsia*, however, are exclusively scandent lianas, a habit unknown in *Goniothalamus*, and the leaves are generally

small, elliptic and very chartaceous. The closest arborescent genus to Goniothalamus is probably Mitrephora, but this genus has different and unique chartaceous leafy outer petals and the mitreform inner petals are free before anthesis, spreading and generally much smaller than the inner petals of Goniothalamus. I have never had a problem distinguishing these two genera. There have been no studies to explore the genetic relatedness among the genera in the Annonaceae, and their relationship remains theoretical.

INFRAGENERIC CLASSIFICATION OF GONIOTHALAMUS

The first author to formalize the infrageneric classification of Goniothalamus was Boerlage (1899), when he appropriately decided to incorporate Warburg's Beccariodendron into Goniothalamus. This monospecific New Guinean genus had been separated from Goniothalamus on the basis of its carpels having 4 ovules rather than 1 or 2 as commonly found in Goniothalamus. Numerous ovules, which would be translated into likewise numerous seeds in mature carpels, however, is not uncommon in the genus Goniothalamus. The section Beccariodendron was proposed by Boerlage to accommodate Beccariodendron grandiflorus and other multi-ovulate species of Goniothalamus. Species of Goniothalamus with one or two ovules were grouped into section "Eu-Goniothalamus". Boerlage's classification, unfortunately, has not been adopted by later authors. Sinclair (1955) for example, preferred stamen characters rather than ovule number, probably because they are easier to observe in herbarium specimens.

When Bân (1974b) proposed his infrageneric classification, he did not consider the number of ovules as important, rather he used this distinction only at the subsectional level. His classification was nothing but a formalization of the basic hierarchical divisions used in the keys of previous authors. Bân divided the

genus into two subgenera, Goniothalamus (apiculate stamens) and Truncatella (truncate stamens). He further proposed four sections, two sections in each subgenus, based on the shapes of the stigmas and styles. A full dichotomous key to Bân's subgenera, sections and subsections is presented in Table 3.

The infrageneric classification of *Goniothalamus* would be more natural if it were based on more characters. Floral characters are of foremost importance, but other characters such as leaves and habit are good indicators of relationships. As I have explained in the morphology section, it may not be possible to identify the species based on non-floral characters, but generally species with certain leaf or habit characteristics can only be associated with certain closely allied species. Likewise, there are species such as *G. tapis* and *G. tapisoides*, *G. umbrosus* and *G. sinclairianus*, *G. roseus* and *G. woodii* that were assumed conspecific by James Sinclair without proper analysis of the stamen and pistil characters. Based on the evidence presented in this revision, it is unrealistic to consider these species pairs as even belonging to the same alliances.

To further evaluate Bân's classification, the Bornean species are arranged into his classification and listed in Table 4. Bân apparently did not have a good understanding of taxa outside the Philippines (see various comments on his interpretations in the taxonomic section). Many species that shared the same characters were classified into various separate sections. For example, G. velutinus and G. rufus share the same pistil and inner petal dome types as well as many vegetative features, yet the two were placed in different subgenera. Similarly, G. cylindrostigma, which has strongly apiculate stamens and large cylindrical pistils indistinguishable from those in other species of the G. uvarioides alliance, should have been placed in the same subgenus (and section) with them.

Table 3. Key to infrageneric classification of *Goniothalamus* as presented by Bân (1974a).

1. Connectives truncate, capitate or disk-like. Subgenus 1. Truncatella.

- 2. Style short; stigma funnel-shaped or fusiform, broad; ovary of the same size as stigma or larger. Section 1. Infundibulistigma.
 - 3. Ovary with 3–10 ovules; flowers cauliflorous or on the older branches.

Subsection. 1. Polyspermi.

3. Ovary with 1-2 ovules, flowers axillary.

Subsection. 2. Infundibuliformes.

2. Style long, cylindrical or subuliform; stigma minute, integral or slightly bilobed.

Section 2. Truncatella.

4. Ovules 3–8.

Subsection 3. Multiseminales.

4. Ovules 1-2.

Subsection 4. Pauciseminales.

1. Connectives apiculate.

Subgenus 2. Goniothalamus.

5. Style distinctive, cylindrical or subuliform; stigma minute, integral or bilobed.

Section 3. Goniothalamus.

6. Ovules 1–2.

Subsection 5. Goniothalamotypus.

6. Ovules 3–10.

Subsection 6. Pleiospermi.

5. Style cone-shaped; stigma filiform and extremely long.

Section 4. Longistigma.

Table 4. Representatives of Bornean *Goniothalamus* in the infrageneric classification of Bân (1974a). An asterisk (*) denotes new or realigned taxa not listed by Bân.

Subgenus Truncatella

Section Infundibulistigma

Subsection *Polispermi*No representatives

Subsection Infundibuliformes
G. rufus

Section Truncatella

Subsection Multiseminales

G. malayanus

G. puncticulifolius

Subsection Pauciseminales

G. borneensis*

G. roseus*

G. cylindrostigma

G. velutinus

G. clemensii

Subgenus Goniothalamus

Section Goniothalamus

Subsection Goniothalamotypus

G. montanus

G. tapisoides*

G. sinclairianus*

G. longistipites*

G. andersonii

G. fasciculatus*

G. nitidus

G. stenopetalus

G. macrophyllus

G. lanceolatus*

G. sulvensis

Table 4 (Continued)

- G. bracteosus
- G. rostellatus*
- G. crockerensis*
- G. calcareus*
- G. woodii*

Subsection Pleiospermi

- G. uvarioides
- G. gigantifolius
- G. parallelivenius
- G. kinabaluensis*
- G. kostermansii*
- G. dolichocarpus*

Section Longistigma

No representatives.

Problems with Bân's infrageneric classification are not confined to the misinterpretations noted above. The stamen connectives of the genus have more than the two types noted by Bân, i.e., apiculate versus truncate-capitate connectives. He admitted in his discussion on stamen characters that some species, such G. roseus and G. stenopetalus, have stamens that are "intermediate". In fact, stamens with broadly blunt-acute connectives occur in a number of Bornean species, which belong to several different alliances. One of these, the G. tapisoides alliance, is also characterized by many unique stylar characteristics and leaf features. While most species in this alliance were correctly placed in one subsection (Goniothalamotypus) of subgenus and section Goniothalamus, one species, G. clemensii, ends up in subsection Pauciseminales of subgenus and section Truncatella.

SPECIATION AND SPECIES ALLIANCES

It would be more satisfying to classify the species of this genus if we could postulate how they evolved. A more natural infrageneric classification than that of Bân can only be constructed after careful consideration of a broad range of characters in all species of the genus. In this treatment I have not attempted to erect a formal infrageneric classification because the species outside Borneo are not considered.

The large size of the island of Borneo, its equatorial position, high temperature and humidity, variations in seasonal rainfall, and the wide range of elevations are favorable for development of an exceedingly rich and diversified flora (Merrill 1930). Numerous isolated areas with special geographic or geological features contribute to the floristic richness. This circumstance has been shown in the floristic analysis of Mount Kinabalu (Beaman & Beaman 1990), where they postulate that unusual edaphic conditions, occasional droughts and precipitous geographic features have contributed to extensive recent speciation.

Corresponding evidence of recent speciation is also apparent in Goniothalamus. Many endemic species in Borneo appear to have been derived from more widespread species, and the endemics seem to be restricted to certain geographical areas or certain habitats. As explained by Levin (1993), these distribution patterns provide prime conditions for local speciation in plants. The evidence he presented suggests that local isolated populations and metapopulations provide the stage on which plant speciation is enacted. Locally evolved neospecies initially will be very narrowly distributed. Some neospecies fail to expand and go extinct. Others expand and become well established, but remain restricted in range owing to adaptations to narrowly distributed habitats. Still others gain wide distribution by occupying common habitats beyond or within the

range of their precursors. Levin noted that for a neospecies to expand well beyond its site of origin, its ecological amplitude must be different from that of its progenitor. Otherwise the neospecies will encounter the more abundant progenitor and be displaced.

Speciation of Goniothalamus in Borneo seems to follow the process outlined by Levin. This will be elaborated below in the discussion on species alliances. Most species in Borneo seem to have evolved from progenitors that gave rise to the G. tapis alliance, the G. malayanus alliance, the G. warioides alliance, the G. macrophyllus alliance, and the G. ridleyi alliance. These alliances are widespread, and related species occur in other areas of Malesia.

Table 4 outlines differential characters for 11 informal species alliances used in this treatment. These alliances differ from each other primarily on the basis of a combination of stamen, pistil and inner petal characters, except for the *G. ridleyi* alliance. The latter group have unique inflorescences, in which numerous flowers occur on the warty base of the trunk near the ground, instead of one or two pendulous flowers being borne on branches or the upper part of the main stem.

1. Goniothalamus malayamus alliance

The G. malayanus alliance is one of the most natural in the genus. The leaves resemble somewhat those of G. tapis and related alliances but in other characters they differ greatly. This group has styles and stigmas (type 3 pistil) and inner petal dome (type 2) that have not been found in other alliances. Members of this alliance also have truncate stamens with flat or slightly convex connectives. In Borneo and the Malay Peninsula G. malayanus is found in swamps and peat swamps. The other two members of the G. malayanus alliance, G. giganteus in the Malay Peninsula and Sumatra and G. borneensis in Borneo, are more restricted in their distribution and occur as large trees.

Table 5. Differential characters of the Goniothalamus species alliances in Borneo.

ALLIANCE	HABIT	LEAF	INFLORESCENCE	INNER PETAL DOME TYPE	STAMEN	PISTIL. TYPE
1. G. malayanus	Treelets, shrubs & large trees	Reddish brown, chartaceous; glabrous	Penduluous, mostly solitary	64	7,889	ന
2. G. roseus	Treelets or shrubs	Orange-brown, subcoriaceous; glabrous	Penduluous, mostly solitary	1 & 4	4	4
3. G. amuyon	Treelets or shrubs	Orange-brown, subcoriaceous; glabrous	Penduluous, mostly solitary	-	π	π
4. G. ridleyi	Large trees	Dull green, chartaceous; glabrous	Erect, in pairs at the base of the trunk	-	==	7
5. G. tapis	Treelets or shrubs	Reddish brown, chartaceous; glabrous	Penduluous, mostly solitary	-	64	9
6. G. tapisoides	Treelets or shrubs	Reddish brown, chartaceous; glabrous	Penduluous, mostly solitary	-	æ	7
7. G. velutinus	Treelets or shrubs	With dark brown indument	Penduluous, mostly solitary	νo	10	6
8. G. uvarioides	Treelets or shrubs	Dull green, coriaceous; glabrous	Penduluous, mostly solitary	δO	-	1
9. G. macrophyllus	Treelets or shrubs	Dull green, coriaceous; glabrous	Penduluous, mostly solitary	1	2 & 6	8
10. G. nitidus	Treelets or shrubs	Dark green; glabrous	Penduluous, mostly solitary	1	8	œ
11. G. bracteosus	Treelets or shrubs	Orange-brown, subcoriaceous; glabrous	Penduluous, mostly solitary	1	61	rυ

2. Goniothalamus roseus alliance

The Mount Kinabalu and nearby Crocker Range endemics G. roseus and G. stenopetalus constitute the G. roseus alliance. This alliance has members with stamen type 4 and pistil type 4. Only one species of this alliance, G. elmeri, occurs outside Borneo, at high elevations in the Philippines.

3. Goniothalamus amuyon alliance.

Goniothalamus puncticulifolius, a rare eastern Sabah species, is placed in this alliance on the basis of its similarity with G. amuyon of the Philippines. It has minutely puncticulate leaves and mostly terminal flowers with unique stamen type 5.

4. Goniothalamus ridleyi alliance

This alliance is special because it is the only one distinguished on the basis of inflorescence and fruit arrangement rather than internal floral features.

Goniothalamus ridleyi and G. fasciculatus, the sister species in Borneo, are large trees (rather than monocaulous treelets or small shrubs as is the case for most other species except G. giganteus and G. borneensis). Their inflorescences occur at the base of the trunk and bear bright maroon or wine-red flowers, that are erect and intensely fragrant at anthesis. The numerous globose fruits, sprawling on the ground, indicate a high rate of fertilization of the flowers. The position of the fruits at ground level may maximize the utilization of non-climbing mammals as dispersal agents.

5. Goniothalamus tapis alliance

This alliance has a single representative, G. woodii, in Borneo. Besides G. tapis itself, another species from Sumatra, G. sumatranus, can be included in this

alliance. Species of this alliance have stamen type 2, a character shared by species in the G. bracteosus alliance. However, they have a distinctive pistil type 6 that has not been found in any other alliance. This alliance shares the common inner petal dome type 1 with the G. bracteosus, G. macrophyllus and G. tapisoides alliances, indicating their closeness in general relationship.

6. Goniothalamus tapisoides alliance

The G. tapisoides alliance is represented by the Bornean endemics G. clemensii, G. longistipites, G. montanus, G. sinclairianus and G. tapisoides. They are characterized by stamen type 3 and pistil type 7. These stamen and pistil features have not been found outside this alliance.

7. Goniothalamus velutinus alliance

This alliance has two members in Borneo, viz. G. velutinus and G. rufus. Both species have conspicuous characters in twig and leaf pubescence. They also share the unique and bizarre type 9 pistil. The alliance includes G. macranii, a species found in southern Thailand and northern Peninsular Malaysia.

8. Goniothalamus uvarioides alliance

This alliance is widespread and consists of species mostly with large, coriaceous, or seldom chartaceous leaves. All species have strongly brochidodromous venation. Some rarer isolated species in Borneo have evolved slightly different leaves but maintain the trends of the alliance as a whole. The stamens have strongly apiculate connectives and are pubescent throughout (stamen type 1). They also have pistil type 1. The inner petal dome of this alliance, designated as type 3, is unique and easily recognizable.

Like other alliances there are certain trends, but the species are recognized on the basis of minor differences. They tend to occupy certain limited geographical areas. The widespread species *G. uvarioides* occurs along the backbone range in central Borneo and to the north around Mount Kinabalu. The rarer species are restricted to pockets of small and specialized environmental conditions: *G. parallelivenius* in lowlands of the south, *G. cylindrostigma* in limestone mountains of the central area, *G. kinabaluensis* around Mount Kinabalu, *G. kostermansii* in eastern Kalimantan, *G. gigantifolius* in eastern Sabah and islands off the Sabah east coast, and *G. dolichocarpus* in the Sepilok-Lahad Datu forests.

9. Goniothalamus macrophyllus alliance

Species in this alliance have leaves that resemble those of *G. uvarioides*. They differ in some aspects of the stamens, styles and stigmas, but in general both alliances share the general architecture of these organs. The stamens are of type 2, rather than type 1 as in the *G. uvarioides* alliance, but both types have strongly apiculate connectives which differ in minor aspects of the indument. The styles and stigmas of these species (pistil type 2) are structurally not too different from the type 1 condition found in the *G. uvarioides* alliance. In both cases they are straight and erect. However, the styles of this alliance are hairy, a feature that distinguishes this pistil from other types.

This alliance is rather rare in Borneo. Goniothalamus macrophyllus is common and widespread from Thailand, the Malay Peninsula and Sumatra to Java but is uncommon in Borneo. Locally evolved apparent neospecies in the G. macrophyllus alliance in Borneo are G. andersonii in peat swamps in coastal areas and G. lanceolatus, found in kerangas or high elevation forests in southern Sarawak.

Several non-Bornean species apparently also belong to this alliance. These include G. wrayi, G. sesquipedalis, and G. scortechinii. King's (1893) splendid illustrations show stamen and stylar features typical of species in this alliance.

10. Goniothalamus nitidus alliance

This alliance is represented by a single species, *G. nitidus*, a rare Bornean endemic found on the eastern coast of Sabah. This species has unique large leafy sepals, unusual pistil type 8 and warty globose fruiting carpels with long stalks.

11. Goniothalamus bracteosus alliance

The G. bracteosus alliance includes the Bornean species G. calcareus, G. rostellatus, G. bracteosus and G. crockerensis. The only species in this group that occurs outside Borneo is G. umbrosus of the Malay Peninsula. This group has the same stamen type (type 2) as the G. tapis alliance but differs in having pistil type 5 rather than type 6 as in the latter. The overall fruiting carpel shape of this alliance resembles that in G. tapis but the trend is toward long slender pedicels and carpel stalks, reaching the longest in G. crockerensis.

TAXONOMY

Goniothalamus (Blume) Hook. f. & Thomson, Fl. Ind. 1: 105. 1855. Polyalthia

Blume Sect. Goniothalamus Blume, Fl. Javae 28-29: 71, tab. 39 & 52B.

1830.—Type: Goniothalamus macrophyllus (Blume) Hook. f. & Thomson.

Atrutegia Bedd., Madras J. Lit. Sci. ser. 3. 1: 37, pl. 1. 1864.—Type: Atrutegia

wynadensis Bedd. (= Goniothalamus wynadensis (Bedd.) Bedd.)

Beccariodendron Warb., Bot. Jahrb. Syst. 13: 452. 1891.—Type: Beccariodendron

grandiflorum Warb. (= Goniothalamus grandiflorus (Warb.) Boerl.)

Trees, shrubs, or monocaulous treelets. Leaves coriaceous, subcoriaceous, or chartaceous, typically ovate or oblong, occasionally elliptic or oblanceolate; venation consistently brochidodromous or slightly eucamptodromous; secondary veins prominent or inconspicuous, straight, parallel, normally in 10-15 pairs, 20-25 pairs or 30-40 pairs; intersecondary veins prominent or inconspicuous; tertiary veins prominent or inconspicuous, random-reticulate, weakly percurrent, or percurrent (if percurrent, tertiaries are sinuous, oblique to mid-vein and parallel to each other); petiole short (less than 1 cm long), or long (2-3 cm long), normal or inflated. Flowers axillary or supra-axillary, terminal, cauliflorous, or clumped at the base of the trunk; pedicels with several imbricate bracts at the base, triangular, ovate, lanceolate or elliptic; sepals 3, valvate, chartaceous, free with broad truncate base or clawed, or connate to form a cup, sometimes persistent in fruit; petals 6, in two whorls, valvate, coriaceous, outer petals 3, often longer than inner, or just slightly longer or more or less equal in length, free, boat-shaped, flat and convex, clawed or truncate at the base, inner petals 3, very often clawed, cohering above to form a vaulted dome-shaped cap over the stamens and pistils; stamens numerous,

laminar, linear or oblong, connectives prominent, apiculate, blunt-acute, broadly acute, truncate, or capitate, mostly glandular pubescent or sparsely pubescent throughout, or glandular pubescent at the tip of the apex only and scurfy papillate at base; pollen grains large, 50–70 μ m in diameter, globose, bound together in tetrads by an irregularly patterned material and covered with sticky pollenkit; ovaries numerous, cylindrical-obclavate, pubescent or glabrous; ovules 1–2 or (3–) 5–10; styles tubular or cylindrical, more or less the same diameter as the ovary, or less than half of the diameter of the ovary, longer than the ovary or very short and insignificant, glabrous, warty or hairy, grooved adaxially; stigma integral, crateriform, fusiform or club-shaped, upright, slightly curved to the outside or curled 360° to the inside, glabrous, warty or with trichomes. Fruits apocarpous, pedicel stout or slender, sometimes with sepal remnants; carpels subsessile or sessile, or with long stalk; mature carpels orbicular, ovate, elliptic, oblong or moniliform, rarely linear, seeds 1–2 or 3–10, endosperm ruminate.

KEY TO THE SPECIES OF GONIOTHALAMUS IN BORNEO

- 1. Stamen connectives truncate, capitate, or broadly acute, but not strongly apiculate.
 - 2. Styles and stigmas glabrous.
 - 3. Styles incurved, coiled 360° to the inside; stigmas 2-lobed; inner petals completely glabrous inside, often waxy, golden pubescent outside.
 - 4. Outer petals small, ca. 4 cm long, 3 cm wide, ovate, acute, minutely pubescent on both sides; fruiting carpels subsessile, small, 1.5–3 cm long, 0.8–1 cm in diameter, nodiform, slightly apiculate, 2–3 seeded; pedicel 1.5–2 cm long.
 1. G. malayanus.

- 4. Outer petals larger, 8 cm long, ca. 4.5 cm wide, lanceolate-elliptic, glabrous; fruiting carpels stalked, ca. 3 cm long, large, 4-4.5 cm long, 2 cm in diameter, broadly fusiform, rostrate, single seeded; pedicel thick, 3 cm long.
 2. G. borneensis.
- 3. Styles radiating outward; stigma tubular or crateriform; inner petals with indument inside, slightly pubescent outside.
 - 5. Leaves small, only 3–3.5 cm long, 1.5 cm wide, margin undulating, puncticulate, elliptic; style with pointed stigma.
 - 5. G. puncticulifolius.
 - 5. Leaves large, 15–25 cm long, 5–10 cm wide, margin not undulating, not puncticulate, oblong or broadly elliptic; style tubular.
 - 6. Outer petals ovate-lanceolate, rarely oblong, ca. 1.8 cm wide, 6cm long.3. G. roseus.
 - 6. Outer petals linear, narrow, only ca. 0.3 cm wide, up to 1.5 cmlong.4. G. stenopetalus.
- 2. Styles and stigmas warty.
 - 7. Large tree, 7-15 m high, 8-20 cm dbh; flowers and fruits in warty
 fascicles at the base of the trunk.
 6. G. fasciculatus.
 - 7. Small understory treelets, often shrubby; flowers mostly axillary, if cauliflorous normally at upper part of the stem.
 - 8. Styles and stigmas clavate; ovary pubescent; young leaves and twigs glabrous.
 - 9. Leaves with tertiary veins inconspicuous and not prominent, brownish beneath; carpel stalks and pedicel short.
 - 10. Fruiting carpel stalks up to 2 cm long; pedicels 1–1.5 cm long; leaves oblong-elliptic.

- 11. Fruit globose, apex round or somewhat mucronate.
 - 12. Fruiting carpel stalks ca. 1 cm long; leavescoriaceous, obovate-elliptic.8. G. tapisoides.
 - 12. Fruiting carpel stalks ca. 2 cm long; leavessubcoriaceous, oblong.9. G. longistipites.
- 11. Fruit elliptic, apex rostellate or acute.

10. G. sinclairianus.

10. Fruiting carpel sessile or subsessile, pedicels short; leaves elliptic.

11. G. clemensii.

9. Leaves with tertiary veins prominent on both sides; carpel stalks and pedicels long and slender, 2 cm and 3 cm long.

12. G. montanus.

- 8. Styles short; stigmas fusiform, very much larger than style or ovary, heavily rusty verrucose, ovary glabrous, subtended with long hairs; young leaves and veins brownish velutinous-pubescent.
 - 13. Stamen connective blunt-acute; leaves much larger, about 40–42 cm long, 8.5–10 cm wide, with soft brown-velvet pubescence, especially on young leaves and twigs; fruit with obtuse carpels, sessile or subsessile.

13. G. velutinus.

13. Stamen connectives flat-topped; leaves small, about 18 cm long, 4 cm wide; fruit with rostellate carpels, stalk long and slender, ca. 1.5 cm long.

14. G. rufus.

- 1. Stamen connectives strongly apiculate.
 - 14. Ovaries 3.5–4 mm long, narrowly oblong or lorate-linear; ovules 3–10; styles glabrous, upright, cylindrical, vaginiform, about the same size or just slightly smaller than ovary; stigma crateriform or indistinguishable, glabrous.
 - 15. Fruiting carpels ovate-oblong or linear, not single seeded, stalks more than 1 cm long.
 - 16. Leaves coriaceous; outer petals nearly as long as inner petals, rusty glabrous.
 - 17. Fruiting carpels broadly cylindrical-nodiform, apex acute;carpel stalks and pedicels stout.15. G. uvarioides.
 - 17. Fruiting carpels linear-nodiform, 6-11 cm long, 1.5-2 cm in diameter, apex and base sharply acute; carpel stalks and pedicels very thin.16. G. dolichocarpus.
 - 16. Leaves chartaceous; outer petals twice as long as inner, orangeor brown-pubescent.
 - 18. Leaves with very prominent veins, tertiary veins strongly and prominently percurrent; fruiting carpels 2.5–3.5 cm long, ca. 1 cm in diameter, nodiform-cylindrical, sparingly pubescent, apex strongly acuminate.
 17. G. gigantifolius.
 - 18. Leaves with random-reticulate tertiary veins; fruiting carpels much larger, up to 8–10 cm long, 2.5 cm wide, oblong or oblong-ovate, glabrous, apex rostellate or blunt-acute.
 - 19. Fruiting carpels green when dried, banana-like, large, cylindrical, with prominent ridges, crested outside, apex rostellate and curved to the inside, 8–10 cm long,

- 2.5 cm wide, stalks ca. 1 cm long, pedicel long, ca. 3.5cm long.18. G. kostermansii.
- 19. Fruiting carpels blackish when dried, normally oval, rarely globose, smooth, apex blunt-acute, ca. 3–4 cm long, 1.5–2 cm wide, stalks ca. 5 mm long, pedicel short, 1.5–2 cm long.
 19. G. kinabaluensis.
- 15. Fruiting carpels globose, single seeded, stalks short, less than 1 cm long (ca. 5 mm).
 - 20. Older leaves linear-lorate, bullate, secondary veins curved, in
 19-24 pairs only, tertiary veins random-reticulate; outer petals
 ca. 4 cm long, lanceolate.
 20. G. cylindrostigma.
 - 20. Older leaves rather oblanceolate, secondary veins straight, in
 30-38 pairs, tertiary veins weakly percurrent; outer petals ca.
 6.5 cm long, oblong.
 21. G. parallelivenius.
- 14. Ovaries shorter, mostly ca. 1 mm long or less (except 2.5 mm in G. rostellatus), lanceolate; ovules mostly 1, seldom 2; styles various and stigmas various but not glabrous, mostly hairy or glandular.
 - 21. Styles and stigmas hairy; fruiting pedicels and carpel stalks short, never more than 1 cm long; leaves dull greenish on both surfaces.
 - 22. Leaves coriaceous, never linear-narrowly oblong.
 - 23. Sepals ovate, connate; fruiting carpels sessile or shortstalked; stamen connectives apiculate, pubescent or puberulent.
 - 24. Fruiting carpels sessile, globose, apex obtuse; stamen connectives strongly apiculate, the base undifferentiated, puberulent; ovaries more or less glabrous except at the base, lanceolate; styles densely

hairy especially at the top near the stigma; leaves large and stoutly coriaceous, oblanceolate-oblong-lanceolate.

22. G. macrophyllus.

- 24. Fruiting carpels stalked, short, less than 2-3 mm long,
 ovate, apex apiculate; stamen connectives shortly
 apiculate, pubescent, base glandular; ovaries strongly
 pubescent; styles erect, sparsely hairy; leaves lanceolate-linear.
 23. G. lanceolatus.
- 23. Sepals orbicular, free, obtuse; carpel stalks slender, 1.3–1.5cm long; stamen connectives blunt-acute, sparselypubescent.24. G. andersonii.
- 22. Leaves chartaceous, linear-narrowly oblong. 25. G. stenophyllus.
- 21. Styles and stigmas glabrous, warty, or with short trichomes; pedicels and fruiting carpel stalks much longer than 1 cm; leaves normally golden brownish underneath when dry.
 - 25. Styles and stigmas warty or with trichomes.
 - 26. Sepals distinctly nerved; styles and stigmas clavate, warty;fruiting carpels warty.26. G. nitidus.
 - 26. Sepals not distinctly nerved; style straight; stigma withtrichomes at the margin; fruiting carpels smooth. 7. G. woodii.
 - 25. Styles and stigmas smooth, without prominent warts or trichomes.
 - 27. Fruiting carpel stalks long and slender (ca. 3 cm), pedicel long and slender (up to 6 cm long).

27. G. crockerensis.

27. Fruiting carpels stalks and pedicel much shorter.

28. Fruiting carpels obtuse or slightly mucronate, globose; outer petals lanceolate, small, 2 cm long, 1 cm wide.

28. G. calcareus.

- 28. Fruiting carpels strongly rostellate, fusiform; outer petals ovate-broadly lanceolate, much larger, 4–9 cm long, 1.5–2 cm wide.
 - 29. Outer petals narrowly lanceolate, narrowed upward, up to 9 cm long and only 1 to 1.2 cm wide at maturity, apex narrow and sharply acute; leaves oblanceolate, ca. 25 cm long, 8 cm wide.

29. G. rostellatus.

29. Outer petals broadly ovate, only 4 cm long but 2 cm wide when mature, apex acute; leaves small, elliptic, ca. 10 cm long, 5 cm wide.

30. G. bracteosus.

Goniothalamus malayamus Alliance

- 1. Goniothalamus malayanus Hook. f. & Thomson, Fl. Ind. 1: 107. 1855.—Type: PENINSULAR MALAYSIA, Malacca, Griffith 102 (holotype: K!).
 - Goniothalamus dispermus Miq., Ann. Mus. Bot. Lugd.-Bat. 2: 34. 1865; non Stapf Trans. Linn. Soc., Ser. II 4: 120. 1894.—Type: Borneo australis, ad fl. Doesson, Korthals s.n. (lectotype, designated here: L!; isolectotypes: A! BM! C! K!). Goniothalamus malayanus var. dispermus Boerl., Icon. Bogor. 1: 136. 1899.

Goniothalamus slingerlandtianus Scheff., Tidjsch. Ned. Ind. 31: 341. 1870.

—Type: Bangka, Teysmann s.n. (holotype: BO? n.v; isotype K!).

Goniothalamus malayanus var. slingerlandtianus Boerl., Icon. Bogor. 1: 136.

1899.

Treelet or small tree, 5–10 m high, bark smooth, pale gray, twigs glabrous, pale, striate. Leaves 16-22 cm long, 5-7 cm wide, oblong to oblong-elliptic, shortly acuminate, base cuneate, coriaceous, gray and glossy above, paler and light beneath; venation eucamptodromous-brochidodromous; primary vein sunken above, round or slightly triquetrous below; secondary veins in ca. 16 pairs, prominent on both sides, simple; intersecondary veins present; tertiary veins inconspicuous beneath, prominent above; petiole 0.5-1 cm long, slightly inflated, channeled. Flowers green to pale yellow, solitary or in pairs, axillary or cauliflorous on the upper part of stem; pedicels short, 0.5-1 cm long, slightly pubescent, with 2-4 bracts at base; sepals 3-5 mm long, ovate-triangular, connate at base, pubescent outside, glabrous inside; outer petals ca. 4 cm long, 3 cm wide, ovate, acute, base rounded, coriaceous, minutely pubescent on both sides, greenish turning yellow; inner petals ca. 1.5 cm long, 8 mm wide, ovate, acute, shortly clawed, golden sericeous outside, glabrous and concave inside; stamens short, 1.5-2 mm long, oblanceolate, connective truncate, glandular; ovaries elongated, obclavate; ovules 1 or 2; styles white, slender; stigma coiled 360° to the inside, bilobed and split down inner side. Fruits green unripe, red at maturity; pedicel 1.5–2 cm long; carpel subsessile or with very short stalk, ca. 1 cm long; carpels 1.5– 3 cm long, 0.8-1 cm in diameter, fusiform or cylindrical (depending on the number of seeds inside), glabrous, apex mucronate, or slightly apiculate, base cuneate, seeds 1-3, globose.

Vernacular names. Selukai or serukai (Iban), beris (Brunei), limpanas jantan (Dusun), serebah, serbah, serabah laki (Brunei) and pudun (Melanau).

Distribution (Figure 37). A widespread species at low elevations in Peninsular Malaysia, Sumatra and Bangka Island. In Borneo the species is common in swamp and peat swamp forests in Brunei, Sarawak and western Kalimantan.

ADDITIONAL SPECIMENS EXAMINED. BRUNEI. Seria, alan batu (Shorea albida) swamp, 18 April 1957, Smythies et al. SAN 5908 (BO, SING); 28 August 1960, Sinclair & Kadim 10458 (A, E, K, SING, US); 20 February 1988, Wong WKM 18 (A); Temburung, Labu Forest Reserve, 9 April 1957, Smythies et al. SAN 17424 (A, BO, K, L, SING). KALIMANTAN. Kalimantan Barat: Kapuas, 1898, Teijsmann 8188 (BO); Liang Gagang, 1893–1894, Hallier 2738 (BO); Sg. Kenepai, 1893, Hallier 2061 (BO, L); G. Kenepai, 1894, Hallier 1063 (BO); Pontianak, Tanjong Kibong, 28 August 1938, Daud Tachun SFN 36077 (A, BM, C); Pontianak, G. Palong Nature Reserve ca. 100 km south of Pontianak, 19 June 1986, van Balgooy & van Setten 5508 (A). Kalimantan Selatan: Korthals 10 (L); Banjarmasin, Labohm 1105 (BO); Banjarmasin, 1859, Motley 1127 (K). Kalimantan Tengah: Palangka Raya, Tangkiling, 15 March 1979, Tukirin 588 (BO); Upper Katingan (Mendawai) River, 19 December 1982, Mogea 4207 (BO); Tumbang Dahiye, 22 December 1982, Mogea 4340 (BO, L). Kalimantan Timur: "Expeditie Midden-Oost Borneo 1925", Endert 2943 (BO). SABAH. "Noord-Borneo, Pladjoe Commisi Kap. Genderen stort", 1912, Amdjah 87 (NY). Res. Pedalaman: Lumat, 9 May 1961, Singh SAN 24314, 6 September 1973, Dewol & Karim SAN 77893 (SAN); Weston, Kampung Usak, 28 May 1974, Dewol SAN 78130 (SAN); above Mengkaloh scheme, Weston, swamp, 20 January 1970, Aban SAN 66705 (SAN); Beaufort, Weston, Hulu Mesapol Forest Reserve, around stream, 31 July 1988, Mat-Salleh KMS 2431 (UKMS); Sipitang, Mengalong, swampy forest, 16 February 1932, Keith 2598 (A); Sipitang, Mengalong Forest Reserve, 8 miles SW of Sipitang, 29 August 1954, Wood & Wyatt-Smith SAN A 4564 (A, L, SING); Sipitang, Kuala Mengalong, 26 April 1971, Saikeh

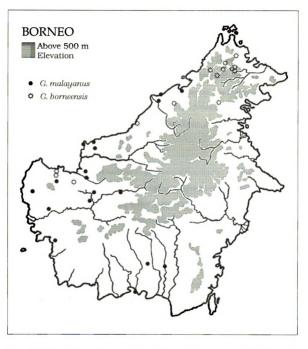


Figure 37. Distribution of Goniothalamus malayanus in Borneo and of G. borneensis.

Lantoh SAN 73168 (SAN); Tenom, Tenom Hill, 12 November 1931, Melegrito BNB 2590 (BO, SAN). SARAWAK. 1892, Hallier s.n. (SING); Native collector 1267 (A). Div. 1: Bako National Park, Corner & Brunig 5283 (SAR); Kuching, Setapok Forest Reserve, peat swamp forest, 26 November 1926, Egan 553 (SAR). Div. 2: Betong, Saribas Forest Reserve, peat swamp, 12 August 1957, Anderson S 8514 (SAR); Saribas, Sg. Berus, logging camp, Meludam Forest Reserve, 26 May 1970, Bujang S 29372 (SAR); Simanggang, Kg. Skrang, peat swamp forest, 18 January 1958, Bujang 9829 (BO, SAR). Div. 3: Sibu, Sg. Matalau, Lassa, Rejang River, mixed swamp forest, peat swamp forest, 21 November 1967, Anderson & Ima S 26617 (K, SAR); Loba Kabang Protected Forest, peat swamp forest, 9 February 1954, Anderson SAR 541 (SAR) & 550 (KEP). Div. 6: Binatang, Pulau Bruit, peat swamp, 13 September 1957, Sanusi Tahir 9211 (BO, SAR).

This species is closely related to *G. giganteus* of Peninsular Malaysia and to *G. borneensis* of Borneo. These species are almost impossible to distinguish by leaf characters but they differ in many other features, especially fruits and outer petals. *Goniothalamus malayanus* is characterized by short oblanceolate stamens with truncate connectives, as well as coiled styles and unique inner petals with golden sericeous exterior and glabrous waxy interior. These characteristics are shared with closely related species in this alliance, but the species differs from others in the alliance in having much smaller, normal sized outer petals and small, subsessile or shortly stalked fruiting carpels.

There was once confusion with regard to the status of this species, because the leaves closely resemble those of *G. tapis* (see Corner 1939). However, its leaves are different in shape and appearance from *G. tapis* and its relatives, and I have no problem in distingushing them. The overall morphology of these two species was tabulated by Airy Shaw (1939). I agree with Sinclair (1955) that the two species

differ also in stamen characteristics. However, the difference in connectives of these species goes beyond the truncate-apiculate condition as suggested by him. The stamens differ in size, shape and indument. In flower *G. malayanus* can be easily indentified by its unique gynoecium. The incurved, 360° coiled styles and broadly bilobed stigma found in this species have not been observed in any other species except *G. giganteus* and *G. borneensis*, which cannot be confused with it because of their outer petal and mature carpel characteristics.

In his treatment on the flora of Mount Kinabalu, Stapf (1894) identified one of the Haviland specimens (Haviland 1313) as G. dispermus, although he was aware and noted that this specimen was slightly different from other specimens of G. dispermus from Kalimantan. I have had the opportunity to re-examine this specimen and consider it to be G. clemensii, a taxon that is not allied to G. malayanus as currently circumscribed.

2. Goniothalamus borneensis Mat-Salleh, sp. nov.—Type: SARAWAK. Kuching, Semenggoh Arboretum, 12.5 mile Penrissen Road, tree no. 3355, 3
November 1972, Othman Ismawi S 32600 (holotype: SING!; isotypes: K! L! SAN! SAR!).

Species inter G. giganteum Hook. f. & Thomson et G. malayanum Hook. f. & Thomson alliquando intermedia, sed optime fructi grandi cum non verrucosis glabratis ex carpellis distincta, hic G. giganteo affinis. A G. malayano petalis exterioribus duplo vel 3plo longioribus differt.

Large tree, 20–30 m tall, 65 cm dbh, bark dark brown, slightly lenticellate, gray, smooth, twigs dark gray, striate. Leaves 16–23 cm long, 4.5–6 cm wide, oblong to oblong-elliptic, caudate, base cuneate, subcoriaceous, gray and glossy above, paler

and light beneath; venation consistently brochidodromous, veins anastomosing about 5 mm from margin; primary vein sunken above, rounded or slightly triquetrous beneath; secondary veins in ca. 16 pairs, prominent on both sides; intersecondaries present, simple, prominent on both sides; tertiary veins randomreticulate; petiole slender, 1–1.5 cm long. Flowers ramiflorous, solitary or in pairs, axillary, green while young, turning bright yellow when fully developed; pedicels long and slender, up to 3 cm long, slightly brownish rusty pubescent, with numerous lanceolate bracts at base; sepals ca. 1 cm long, triangular, acuminate, free at base, slightly pubescent; outer petals up to 10 cm long, 3-5 cm wide, lanceolate, sharply acute, base acute, coriaceous, greenish turning yellow, minutely pubescent on both sides, golden sericeous outside at the base, singleveined, golden sericeous, with triangular base inside; inner petals ovate, ca. 1.5 cm long, 0.8 cm wide, acuminate, base cuneate, shortly clawed, golden sericeous outside, glabrous and concave inside; stamens short, 1.5-2 mm long, narrowly lanceolate-oblong, pale yellow, connective flat-topped, strongly pubescent; ovaries elongated, 2 mm long, obclavate-cylindrical, pubescent; ovules 1-3; styles white, slender; stigmas coiled 360°, bilobed and split down inner side. Fruit dark green; pedicel thick, 3 cm long; carpel stalks long and slender, ca. 3 cm long; carpels large, 4-4.5 cm long, 2 cm in diameter, broadly fusiform, acuminate-rostellate, base cuneate, smooth and glabrous, slightly wrinkled when dried, never warty, seeds normally 1, seldom 2, with sticky aril. Figures 38, 39.

Vernacular names. Sehitai, semukai or selukai (Iban).

Distribution (Figure 37). Endemic to Borneo; growing at the edges of swamps, on clay-loam or sandy soil in lowland dipterocarp forest at low elevations up to 400 m.

Figure 38. Representative specimen (with flowers) of Goniothalamus borneensis (Mat-Salleh KMS 2500, UKMS).



Figure 39. Representative specimen (with fruiting carpels) of *Goniothalamus borneensis* (Mat-Salleh KMS 2500, UKMS).



ADDITIONAL SPECIMENS EXAMINED. Borneo. Korthals s.n. (A, L). SABAH. Res. **Pedalaman:** Keningau, Shan Lian Logging area, Lanas, 22 October 1986, Sumbing SAN 118460 (SAN); Keningau, Tambulanan, stream side, 25 October 1983, Sam & Kumin SAN 68875 (A, SAN, UKMS); Keningau, Trus Madi Tambahan 1 Forest Reserve, hillside, 17 July 1985, Amin et al. SAN 110415 (SAN); Keningau, Hulu Sg. Mantuluk, Witti Range area, 16 January 1986, Sumbing SAN 113267 (SAN). Res. Sandakan: Kinabatangan, Km 32 Telupid-Karamuak logging road just before Syarikat Choon Ching, swamp forest, 7 August 1988, Mat-Salleh 2500 (UKMS); Labuk & Sugut, Beluran, Bongaya Forest Reserve, 19 July 1975, Aban & Kodoh SAN 82054 (SAN); Labuk & Sugut, Telupid, Sg. Ruku-Ruku, edge of swamp, 2 August 1981, Aban SAN 93993 (SAN); Labuk & Sugut, Telupid-Ranau Road, Mile 92.5, low undulating primary forest, 10 February 1968, Termiji et al. SAN 54129 (SAN); Labuk & Sugut, Mile 111, Telupid-Ranau Rd., hill ridge, 10 August 1978, Madani SAN 88872 (SAN); Labuk & Sugut, Telupid, Kg. Bauto, hillside, disturbed dipterocarp forest, 16 July 1980, Dewol SAN 92200 (A, SAN). SARAWAK. Div. 1: Kuching, forest near Kuching, 18 January 1893, Haviland 2107 (BM, BO, K, L); Simunjan, G. Gaharu, Hulu Simpang Sabal Aping, 70th Mile Serian/Simanggang Rd. Simunjan, on hillside, sandy soil in lowland dipterocarp forest, 28 August 1975, Ilias & Azahari S 35717 (SAR). Div. 4: Bintulu, Similajau/Labang, clay-loam soil, 6 October 1968, Wright S 27989 (B, SAR). Div. 5: Limbang, Sg. Mentawai, 5 October 1977, *Chai S 39669* (SAR).

This species resembles G. giganteus in fruit and leaves but has smaller, lanceolate outer petals as well as smooth mature fruiting carpels (versus warty carpels of G. giganteus). The outer petals of G. giganteus and G. malayanus at maturity are more or less broadly ovate rather than lanceolate. The micromorphology of G. borneensis stamens and gynoecium provides further

characters in support of separating G. giganteus, G. malayanus and G. borneensis.

This species is somewhat intermediate between G. giganteus and G. malayanus.

Goniothalamus roseus Alliance

3. Goniothalamus roseus Stapf, Trans. Linn. Soc., Ser. II, 4: 130. 1894.—Type: SABAH. Mount Kinabalu, 6000 ft., *Haviland 1312* (holotype: K!; isotype: SAR!)

Goniothalamus elmeri var. longipedicellatus Bân, Bot. Zhurn. (Moscow & Leningrad) 59(5): 664. 1974.—Type: SABAH. Mount Kinabalu, Tenompok, February 1932, Clemens 30365 (holotype: NY!; isotypes: A! K!)

Small shrub or monocaulous treelet about 2–5 m tall; stem whitish gray, smooth, twigs gray, striate, blackish towards younger parts. Leaves 14–24 cm long, 4–7 cm wide, mostly oblong, elliptic at times, especially in younger leaves, apex sharply acuminate, base acute, coriaceous, dark dull green above, golden brownish beneath, glabrous; venation eucamptodromous; primary vein sunken above, raised beneath; secondary veins in 12–16 pairs, raised on both sides but rather inconspicuous above; intersecondary veins prominent, simple; tertiary veins very inconspicuous, random-reticulate; petiole 1–1.3 cm long, blackish, stout, glabrous. Flowers solitary, axillary or cauliflorous on upper part of monocaulous stem, pedicel slender, 4–7 cm long, pinkish red, blackish when dry, with 4–6 oblong-triangular imbricate basal scales; outer petals 5–6 cm long, ca. 2 cm wide, ovatelanceolate, apex acute, base slightly attenuate, clawed, coriaceous, deep pinkish purple with cream streak, rusty pubescent on both sides; inner petals ca. 2 cm long, 1 cm wide, ovate, reddish dirty white, apex acute, base attenuate, clawed,

rusty pubescent outside, warty inside; stamens numerous, slender, 3 mm long, connectives capitate, truncate or broadly acute when young; ovaries ca. 1 mm long, cylindrical-obclavate, golden yellow, hirsute; ovules 1 or 2, basal; styles 3 times longer than ovary, tubular, radiating to the outside, glabrous; stigma pateliform, glabrous, with unilateral cleft. Fruiting pedicel 5–6 cm long, carpel stalks 1–2.5 cm long; carpels ca. 1 cm long, 6 mm wide, fusiform, mucronate or obtuse, carpels ca. 15 per torus, yellowish green, turning bright red when fully mature, seed 1.

Distribution (Figure 40). Endemic to Mount Kinabalu and nearby areas in the Crocker Range, in oak-laurel montane forest, in damp and shady mossy habitats at relatively high elevations of 1200 to 1800 m.

ADDITIONAL SPECIMENS EXAMINED. SABAH. G. Tambayukon, 18 May 1970, Aban SAN 68567 (SAN); G. Tambayukon, near Camp 2, 6–7000 ft, July 1961, Meijer SAN 34637 (SAN); Mount Kinabalu, Haviland 1761 (SAR); February 1910, Gibbs 4105 (K); 27 September 1961, Kanis & Sinanggul 1225 (SAN); 6 February 1962, Mikil SAN 29055 (SAN); 24 April 1964, Aban SAN 78536 (SAN); 27 September 1965, Kanis & Sinanggul 5813 (SAN); 19 July 1972, Nooteboom & Gibot 1501 (B, SAN, US); 6–19 November 1981, Sato et al. 1758 (UKMS); Mount Kinabalu, Bt. Burong Trail, montane forest, 21 January 1976, Stevens et al. 584 (A); along Liwagu Trail, 15 July 1963, Lajangah SAN 36155 (SAN); 19 November 1983, Jumaat UKMS 3343 (UKMS); 25 July 1987, Mat-Salleh KMS 1441 (UKMS); Kiau View Trail, 3 May 1968, Watkins SAN 57917 (SAN); January 1969, Kokawa & Hotta 6270 (SAN); Mount Kinabalu, Old Liwagu Trail, oak-laurel (moss) forest, 4 November 1988, Mat-Salleh KMS 2814 (UKMS); Mount Kinabalu, Dallas, 3000 ft, 30 October 1931, Clemens 26861 (K); Clemens 40002 (BO); Mount Kinabalu, Dahobang river, Penibukan, 4000–5000 ft, 16 January 1933, Clemens s.n (BM); Mount Kinabalu, Lobang,

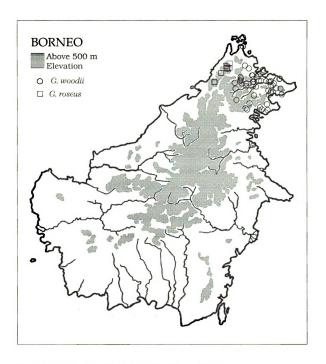


Figure 40. Distribution of Goniothalamus woodii and G. roseus.

November 1915, Clemens 10383 (A, BM, BO); Mount Kinabalu, Tenompok, 4 April 1933, Carr 26857 (SING); 25 January 1932, Clemens s.n (BM);14 August 1931, Clemens 26090 (A); 20 January 1932, Clemens 27885 (A, BO, NY); Clemens 30347 (BO, K); Clemens 277885 (BM); 22 August 1954, Wood & Wyatt-Smith SAN A 4497 (A, L); Crocker Range, at Tenompok on S side of Mount Kinabalu, Trus Madi formation, oak-laurel forest, 1500-1550 m, 21 April 1984, Beaman 9451 (MSC, NY, UKMS); 5 March 1993, *Price 5044*, 5046, 5047 (MSC); Kota Belud, G. Lenau at Tenompok, Mount Kinabalu, 5000 ft, wooded mountain slope, above main path, 10 June 1957, Sinclair et al. 9003 (E, SING); near mile 43, Ranau road, hillslope, brown soil, 5 December 1933, *Lajangah 33075* (SAN); Bt. Hampuan, above camp, 8 May 1960, Meijer SAN 20961 (SAN); Bt. Hampuan, along ridge, 7 May 1960, Meijer SAN 21349 (SAN); Mount Kinabalu, 12 June 1937, Griswold, Jr. 1 (A, US); Kinabalu Park boundry, montane forest, 22 January 1976, Stevens 622, 626 (A, SAN); Mount Kinabalu, Sg. Mamut, mossy dipterocarp forest, 4 August 1961, Chew, Corner & Stainton RSNB 1225 (K); Bank of Liwagu river, near source between Kinabalu and Ranau, 5000 ft., primary jungle, damp and shady, 28 April 1954, Darnton 566 (A, BM); Mount Kinabalu, Hulu Liwagu, Hulu Mesilau, 23 August 1961, Chew, Corner & Stainton RSNB 1363 (K); Hulu Liwagu and Hulu Mesilau, Tenompok, oak-podocarpus forest, 8 September 1961, Chew, Corner & Stainton RSNB 1450 (K); Mount Kinabalu, Mesilau river, 15 August 1963, Mikil SAN 36177 (SAN); 23 July 1963, Sinanggul SAN 38359 (SAN); 21 January 1964, Chew & Corner RSNB 4044 (K); 29 April 1964, Chew & Corner RSNB 7012 (K); West Mesilau River, valley above waterworks dam, Pinosuk gravels, oak-laurel forest, 1600–1700 m, 19 February 1984, Beaman 8692 (MSC, NY, UKMS); Pinosuk Plateau, 18 August 1961, Chew, Corner & Stainton RSNB 1850 (K); Pinosok Plateau, base camp, 3 May 1964, Chai & Ilias RSNB 6006 (K, SAN); Pinosuk Plateau, above E side of West Mesilau River at waterworks dam, Pinosuk gravels, oak-laurel forest, 1600 m, 22 March

1984, Beaman 9022 (MSC, UKMS); 9031 (MSC, NY, UKMS); Pinosuk Plateau, between East Mesilau and Mentaki Rivers, Pinosuk gravels, oak-laurel forest, 1700 m, Beaman 9361 (MSC, NY, UKMS); Pinosuk Plateau, above asparagus farm near the Mentaki River, Pinosuk gravels, oak-laurel forest, 1550 m, 28 July 1984, Beaman 10758 (MSC, UKMS); Pinosuk Plateau, Mount Kinabalu golf course site, east bank of East Mesilau River, Pinosuk gravels, recently disturbed oak-laurel forest, 1720 m, 11 February 1984, Beaman 8543 (MSC, NY, UKMS); Beaman 10667 (MSC); Ranau, Mamut Copper Mine, Trus Madi formation, oak-laurel forest, 1600–1700 m, 30 May 1984, Beaman 9940 (MSC, UKMS); Mount Kinabalu, eastern shoulder, base camp, 3 May 1964, Chai & Ilias RSNB 6013 (K, SAN); Mount Kinabalu, Sosopodon, below Kinabalu, along pipe to Kinabalu, 16 July 1964, Mikil SAN 46757 (SAN); G. Kinabalu, behind Sosopodon, near Kundasang, 19 August 1964, Pereira 78536 (SAN); Upper Kinabalu, 6000–13500 ft, 27 March 1932, Clemens 30364 (A, BO, NY); Mount Kinabalu, road to Power Station, 2 March 1976, Cockburn SAN 82964 (SAN); Mount Kinabalu, between Mamut ridge and Hulu Berambung (Bambangan); February 1969, Kokawa & Hotta 5859 (SAN). Res. Pantai Barat: Penampang, Crocker Range, Km 50.7 on Kota Kinabalu-Tambunan Road, Crocker formation, oak-laurel forest, 1600 m, 2 January 1984, Beaman 8173 (MSC, NY); Penampang, Tambunan road, Sinsuran pass, along the stream, 1450 m, 20 June 1987, Mat-Salleh KMS 1406 (UKMS). Res. Pedalaman: Papar, Keningau-Kimanis road, montane forest, sandstone, December 1986, Vermeulen & Duistermaat 681 (UKMS); Keningau, Keningau-Kimanis Rd. mile 17/18, Bt. 4750 around the summit, on the ridge of mossy forest, 1240-1350 m, 10-12 November 1986, Mat-Salleh KMS 1270, 1271, 1273, 1299, 1353 (UKMS); Keningau, Keningau-Kimanis Rd., Mile 15, 1200-1350 m, 5 November 1986, Mat-Salleh KMS 1144 (UKMS); mile 14; down leftside slope off main road, 1000 m, 6 November 1986, Mat-Salleh KMS 1195 (UKMS); Tambunan, G. Alab, 22 January 1969, Nooteboom 975 (SAN); 20 July

1984, Amin & Ismail SAN 60329 (SAN); Tambunan, Crocker Range, in ravine on E side of Kota Kinabalu-Tambunan Road at Km 55, Crocker formation, oak-laurel forest, 1600–1700 m, 3 April 1984, Beaman 9185 (MSC, UKMS); Tambunan, Crocker Range, Km 59.5 on K. Kinabalu-Tambunan Road, Crocker formation, oak-laurel forest, 1400 m, 2 November 1983, Beaman 7323 (MSC, NY).

With G. woodii and G. calcareus, although both of these species have fruits remarkably similar to those of G. roseus. Some specimens of G. woodii were previously identified as G. roseus, and most specimens of G. calcareus likewise have been named as such. In fact, Sinclair noted on a specimen that he could not see the difference between G. roseus and G. woodii. He may have been thinking that G. roseus was a montane form of G. woodii. He noted on one of the G. roseus specimens (SAN 35999) that "the difference between this and woodii all break down." I understand Sinclair's feeling when only sterile or limited fruiting material is available. The two species can be difficult to separate although the leaves of G. woodii in general tend to be smaller than those of G. roseus and the fruiting pedicels of G. woodii are much shorter. These features, although evident in some specimens, cannot be fully utilized because many collections are either sterile or without fruits.

The more important differences between the two species, but not as easy to discern, are in features of the stamens and styles. Goniothalamus roseus is characterized by distinctive long slender stamens with a capitate connective and long glabrous and smooth tubular styles. On the other hand, G. woodii has apiculate connectives and crateriform stigmas with echinate indument and a warty surface. These characteristics are so different that the two species cannot even be placed in the same alliance. Goniothalamus woodii belongs to the G. tapis alliance,

and is the only species in Borneo with that relationship. Goniothalamus roseus, on the other hand, is close to G. stenopetalus, which is also restricted to areas around Mount Kinabalu. The only other species outside Borneo in this alliance is G. elmeri of the Philippines.

The special characteristics of stamens and styles of Goniothalamus roseus were stressed by Stapf (1894) in his original description. These were also superbly figured by him and attached to the holotype at K. I suspect that Bân did not have access to this type specimen of G. roseus when he was working at NY on his classification of Goniothalamus, and he was completely confused about G. roseus and G. woodii. It is true that G. woodii was unpublished then, but there were many specimens at NY annotated by Merrill as G. woodii. Bân probably was thinking that G. woodii was G. roseus, because he cited the specimens Elmer 20188, 21537, and Muin Chai 21691 (which are G. woodii) as G. roseus. Ironically, he used specimens now determined as G. roseus as a basis to describe a new variety of G. elmeri (G. elmeri var. longipedicellatus Bân). I have examined many specimens of G. elmeri at NY and US and cannot agree with his treatment of that species. Although the stamens and styles of G. elmeri resemble those of G. roseus to some extent, the shape and texture of the outer petals and the fruit characteristics are very different.

4. Goniothalamus stenopetalus Stapf, Trans. Linn. Soc., Ser. II, 4: 129. 1894.—

Type: SABAH. Mount Kinabalu, Penokok, 3000 feet, *Haviland 1217*(holotype: K!; isotype: SAR!).

Monocaulous treelet 1-3 m high, twigs gray, striate. Leaves 15-24 cm long, 4-11 cm wide, narrowly elliptic, seldom oblong-elliptic or obovate, acuminate, base acute-rounded, coriaceous, glabrous and dull on both sides, golden brownish

beneath; venation eucamptodromous; primary vein sunken above, raised beneath; secondary veins in 12–16 pairs, raised but not very prominent; intersecondary veins prominent, simple; tertiary veins random-reticulate, inconspicuous; petiole short, 0.5–1 cm long, glabrous, blackish when dry. Flowers solitary, cauliflorous on upper part of the stem, or ramuliflorous on old twigs; pedicel thin and slender, up to 4–5 cm long, with 4–6 minute triangular basal scales; sepals red, 5 mm long and wide, connate at base, triangular, glabrous; outer petals 4–6 cm long, only 3–5 mm wide, linear, chartaceous, slender, apex sharply acute, base ovate, dark pink, cream at base, rusty glabrous on both surfaces; inner petals 3 cm long, 1.5 cm wide, broadly ovate, clawed, yellowish at margins, puberulous outside, warty inside; stamens numerous, slender, 2.5–3 mm long, connective capitate with blunt-acute top, pubescent; ovaries numerous, obclavate, ca. 1 mm long, glabrous; ovule solitary, basal; styles 3 times longer than ovary, tubular, radiating to the outside; stigmas pateliform, glabrous, with unilateral cleft. Fruit *fide* Stapf: globose-ovate, ca. 1 cm long, stalk very short, ca. 5 mm long, seed 1.

Distribution (Figure 41). Endemic to Mount Kinabalu and the nearby Crocker Range, mostly in oak-laurel forest, elevation 1000–1500 m.

ADDITIONAL SPECIMENS EXAMINED. SABAH. Res. Pantai Barat: Penampang, Crocker Range, Km 49.5 on Kota Kinabalu-Tambunan Road, Crocker formation, oak-laurel forest, 1350–1500 m, 3 July 1984, Beaman 10441 (MSC, UKMS); Mount Kinabalu, Kg. Kiau Nulu, Kogietan trail and upper coffee farm, 8 June 1988, Gunik GNIK 229 (UKMS); Mount Kinabalu, Kg. Kiau Nulu, between Tinokok and Tohubang river, 9 June 1988, Gunik GNIK 240 (UKMS); Mount Kinabalu, Kiau, November 1915, Clemens 10077 (BO, K); Mount Kinabalu, Colombon Basin, 4500 ft, 15 July 1933, Clemens 33986 (BM, BO); Mount Kinabalu, Penokok, Haviland 1737 (SAR); Papar, Crocker Range, Kimanis to Keningau road, 7 April 1985, Kitayama K 933 (UKMS);

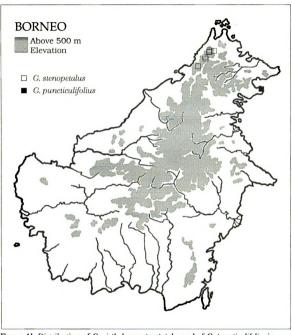


Figure 41. Distribution of Goniothalamus stenopetalus and Goniothalamus s

Mount Kinabalu, Eastern Shoulder, 3400 ft, 10 June 1961, Chew, Corner & Stainton RSNB 28 (K, L, SAN, SING); Mount Kinabalu, Eastern Shoulder, 17 June 1961, Chew, Corner & Stainton RSNB 105 (K). Res. Pedalaman: Tambunan, Km 63, Kota Kinabalu to Tambunan road near Rafflesia site, 970 m, 5 July 1987, Mat-Salleh KMS 1420 (UKMS).

This is a very well marked species, distinguished by its long, linear, chartaceous outer petals. Stapf (1894) suggested that G. stenoptelus is close to G. macrophyllus, but stamens and ovaries of this species are more similar to those of G. roseus rather than to G. macrophyllus. All specimens examined lack fruit, so I cannot verify the fruit measurement given by Stapf in the protologue. I have had an opportunity to monitor a flowering population near Tambunan (represented by voucher specimen no. KMS 1420) from 1986 to 1989, but not a single fruit was produced throughout those four years.

Goniothalamus amuyon Alliance

5. Goniothalamus puncticulifolius Merr., Philipp. J. Sci. 20: 383–384. 1922.—Type: PHILIPPINE Is. Mindoro, Paluan, April 1921, *Ramos Bur. Sci. 39660* (holotype: PNH, destroyed; lectotype, designated here: US!).

Small tree, branches cylindrical, slender, rugose, blackish when dry, young twigs appressed rusty pubescent. Leaves 11–15 cm long, 3.5–4 cm wide, elliptic, acuminate, base acute, chartaceous, pale shining above when dry, dull beneath, minutely puncticulate beneath; venation eucamptodromous, or consistently brochidodromous with marginal veins far to the inside; primary vein sunken

above, glabrous, slightly rusty pubescent beneath; secondary veins in 8–10 pairs; intersecondary veins rare and not prominent; tertiary veins very inconspicuous, random-reticulate; petiole 0.5–1 cm long, not thickened, blackish. Flowers solitary or in pairs, mostly terminal, axillary at times; pedicel 2–3 cm long, cupreous pubescent, basal bracts 2–4, lanceolate, pubescent; sepals ca. 5 mm long, broadly ovate, acute; outer petals 2 cm long, 1 cm wide, oblong-lanceolate, acute, cinereous-velutinous on both sides; inner petals ca. 1.5 cm long, 1 cm wide, ovate, acute, pubescent on both surfaces; stamens short, 1–1.5 cm long, oblong, connective blunt-acute, pubescent; ovaries cylindrical, pubescent; ovules 1 or 2; style glabrous, vermicular; stigma pointed, glabrous. Fruit unknown.

Distribution (Figure 41). A rare species mainly known from a few specimens from the type locality on Mindoro Is., Philippines. The species has been collected only once in Borneo.

Vernacular name. Pisang-pisang (Malay).

SPECIMEN EXAMINED. SABAH. Sempurna, Selangan Island Forest Reserve, on level ground, 23 August 1938, Agama & Valera 9886 (SING).

Merrill (1922) noted that this species in vegetative characters somewhat resembles *Goniothalamus amuyon*, but differs radically in its floral characters. I agree to some extent with Merrill, but under the light microscope the stamens of these species appear similar. I am tentatively treating this species in the *G. amuyon* alliance but it might belong to some other Philippine group.

Goniothalamus ridleyi Alliance

6. Goniothalamus fasciculatus Boerl., Icon. Bogor. 2: 274, tab. 59. 1899.—Type: KALIMANTAN. Jaheri "in itinere Doctoris Niewenhuis" (holotype: BO?, n.v.).

Goniothalamus ridleyi var. faciculatus (Boerl.) Bân, Bot. Zhurn. (Moscow & Leningrad) 59(5): 669. 1974.

Tree 7-15 m high, 8-20 cm dbh, outer bark smooth gray, inner bark reddish, twigs glabrous, cylindrical. Leaves 18-30 cm long, 5-10 cm wide, ovate-lanceolateoblanceolate, acuminate-apiculate, base acute, chartaceous; venation eucamptodromous; primary vein sunken above, raised beneath; secondary veins in 16-20 pairs, inconspicuous above, raised and prominent beneath; intersecondary veins composite; tertiary veins weakly percurrent; petiole 1-1.5 cm long, blackish, stout, rusty glabrous. Flowers cauliflorous, inflorescence cymose on the base of trunk, in warty fascicles with dark red-maroon flowers; pedicel long and slender, 5-10 cm long, glabrous, red; sepals small, ca. 1 cm long and wide, ovate, pubescent; outer petals 4-5 cm long, ca. 1.5 cm wide, slightly pubescent, lanceolate, apex acute-caudate, base acute, clawed, coriaceous; inner petals ca. 1 cm long, ovate, puberulous outside, rusty pubescent inside, apex acuminate, base acute-attenuate, slightly clawed; stamens numerous, 2–2.5 mm long, 0.5 mm wide, oblong, incurved, connective truncate, rusty pubescent; ovaries glabrous; ovule 1, style and stigma cylindrical, warty. Fruiting pedicel long and slender, up to 10 cm long; carpel stalks very short, less than 5 mm long; carpels pinkish, ca. 2-2.5 cm in diameter, hanging around the base of the stem resting on the ground, globoseturbinate, apex obtuse-acuminate, base cuneate, seed 1.

Vernacular names. Kerai (Malay), selukai (Iban), sipu, tohub (Dusun), tuuhob (Kadazan Bundu Tuhan).

Uses. The fragrant bark, with strong odor, "is burned to drive away ghosts"; the bark is used by locals to treat stomach-ache.

Distribution (Figure 42). Endemic to Borneo, in hill or submontane dipterocarp forest, on sandy sandstone loam, on river or stream banks, at elevations up to 1500 m.

SPECIMENS EXAMINED. BRUNEI. Belait, Andulau, 24 April 1957, Ashton BRUN 5924 (SAR). KALIMANTAN. Borneo, 1896, Jaheri 1640 (BO); Long Tesak, 13 March 1963, Wiriadinata HW 1213 (BO). Kalimantan Tengah: Bt. Raya, 17 December 1924, Winkler 909 (BO); Upper Kahayan, headwaters of Sg. Kahayan, 5 km NE of Haruwu village, primary forest, 26 March 1988, Burley & Tukirin 422 (A, BO). Kalimantan Barat: "Borneo Expeditie, Amai Ambit", 1893–1894, Hallier 3231 (BO). Kalimantan Timur: Balikpapan, peak of Balikpapan, G. Beratus, sandstone, 15 July 1952, Kostermans 7532 (A, BO); Balikpapan, Sg. Wain region, N of Balikpapan, August-September 1950, Kostermans 4001, 4149, 4439 & 4545 (BO); Balikpapan, P.T. ITCI Concession, Kenangan, 15 August 1974, Dransfield 4454 (L, US); Samarinda, Mulawarman University Botanic Gardens, 28 August 1974, Wiriadinata HW 338 (BO); Samarinda, Belanjan Range, near Long Bleh, low sandy loam, 25 March 1955, Kostermans 10243 (A, K, L); Samarinda, Tandjong Bangko, near mouth of Mahakam, 1 June 1952, Kostermans 7137 (BO); Sangkulirang, Sg. Lekambing, 28 February 1911, Rutten 408 (BO); Sangkulirang, Pelawan Besar, 10 May 1937, Walsh 272 (BO); West Kutai, 25 October 1925, Endert 4302 (BO); West Kutai, "Expeditie Midden-Oost Borneo 1925", Endert 4306 (BO). SABAH. Res. Kudat: G. Tambayukon, 19 May 1970, Aban SAN 55402 (SAN); Kota Merudu, SW of Bt. Medalon (Crocker Range), riverbank, 21 November 1981, Aban SAN 94319 (SAN). Res. Pantai Barat: Kiau, Mount Kinabalu, 31 October-3 November 1915, Topping 1546 (US); Kiau, Mount Kinabalu, November 1915, Clemens 9947 (A);

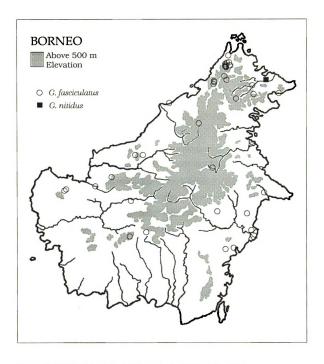


Figure 42. Distribution of Goniothalamus fasciculatus and G. nitidus.

Mount Kinabalu, Lobang, November 1915, Clemens 10328 (A, BO); Mount Kinabalu, Mahandui River, 3500 ft, 2 March 1933, Carr 26307 (SING); Mount Kinabalu, Penataran, 4000 ft, 22 July 1933, Clemens 34033 (A, K, NY); Mount Kinabalu, Penataran Basin, 3,500 ft, 27 July 1933, Clemens 34175 (NY); Mount Kinabalu, Penibukan, 4000–5000 ft, jungle below steep bank, 16 January 1933, Clemens 31129 (BM, K, NY); Mount Kinabalu, Tenompok, 5000 ft, 11 March 1932, Clemens 28802 (K, NY); south of Sayap on NW side of Mount Kinabalu, ca. 30 km SE of Kota Belud, Trus Madi formation, dipterocarp forest, 800–1000 m, 19–20 May 1984, Beaman 9748 (MSC, UKMS); Mount Kinabalu, Kiau to Lobang, 4-5 November 1915, Topping 1591 (US); Mount Kinabalu, Mamut river, 3800 ft, 5 August 1961, Chew, Corner & Stainton RSNB 1631 (K, SAN); Mount Kinabalu, eastern shoulder, Singh's Plateau, 3000 ft, dipterocarp forest, 1961, Chew, Corner & Stainton RSNB 1023 (A, BM, K, SAN, SING). Res. Pedalaman: Keningau, Mile 15, Keningau-Kimanis logging road, 1230 m, 5 November 1986, Mat-Salleh KMS 1162 (UKMS); Keningau, Keningau-Kimanis logging road, Bt. 4050, 1030 m, 8 November 1987, Mat-Salleh KMS 1252 (UKMS); Keningau, Trus Madi Range, along the trail to the summit, from Sinoa, hill dipterocarp forest, 1500 m, 13 November 1987, Mat-Salleh KMS 1941 (UKMS); Keningau, Crocker Range, Highland Co. plantation, mile 11, 8 June 1977, Talip & Ejan SAN 86958 (SAN); Tambunan, Trus Madi above Kionop, mountain slope, black soil, 27 September 1962, Mikil SAN 32098 (SAN). Res. Sandakan: Kinabatangan, Lamag, south slope of G. Lotung, Inarat, 15 May 1976, Cockburn SAN 83272 (SAN); Kinabatangan, Beluran, Km 28 to Darmakut Camp, primary forest on hill ridge, 19 September 1984, Aban et al. SAN 66316 (SAN, UKMS). Res. Tawau: Lahad Datu, Hulu Sg. Danum, just north of Camp III, 3 September 1976, Stone 85313 (KLU); Lahad Datu, Bakapit, Silabukan fall, lowland clayish soil, 25 November 1965, Ahmad Talip SAN 52999 (SAN). SARAWAK. Punan Busang, 12 June 1971, Geh & Samsuri 103 (SING). Div. 1:

Kuching, G. Tieng, 1929, Clemens 20570 (BO); Lundu, Seropak, G. Bungo Range, tall valley dipterocarp forest, 9 March 1982, Banyeng & Dami S 43913 (SAR). Div. 2: Simanggang, Hulu Sekarang, below Bt. Sadok, 17 October 1982, Ilias S 44944 (SAR); Bt. Peninjau, Lanjak Entimau Project, 13 March 1974, Chai S 33800 (MO). Div. 4: Bario, Kalabit Highlands, Apa Batu Buli, primary forest, 19 June 1972, Nooteboom & Chai 2196 (SAR, US); Tatau, Bt. Mersing, Tau Range, 1 June 1956, Purseglove P 5273 (K, NY, SAR); Tatau, Bt. Mersing, Anap, submontane forest, basalt ridge, 5 October 1963, Banyeng S 19190 (A, K, SAN, SING); Tatau, Bt. Mersing, Anap, river bank, basalt ridge, dipterocarp forest, 25 September 1964, Sibat S 22364 (A, SAR).

Bân (1974b) treated this species as a variety of G. ridleyi, based on leaf characteristics that are quite different from G. ridleyi. The species are similar in flower and fruit, but this is superficial. The two species also differ in stamen characteristics, with G. fasciculatus having truncate connectives while G. ridleyi has broadly acute connectives. This difference has been used in separating other species such as G. tapis and G. malayanus, and I do not think it wise to treat G. fasciculatus conspecific with G. ridleyi while keeping other species separate.

When describing this species, Boerlage (1899) did not specify the actual number for the holotype. He cited the specimen as "Jaheri in itinere Doctoris Niewenhuis". Most probably the type is Jaheri 1640 collected in 1896, the only specimen of the species collected by Jaheri. I once had it on loan from BO, but it was returned before I had access to the Boerlage publication.

Goniothalamus tapis Alliance

7. Goniothalamus woodii Merr. ex Mat Salleh, sp. nov.—Type: SABAH. Sandakan and vicinity, 22 June 1922, Ramos 1726 (holotype: A!; isotypes: SAN! US!).

Goniothalamus woodii Merr., Philipp. J. Sci. 24: 114. 1924; nomen nudum.

Species inedita, Merrillo admoneta, G. tapi Miq. et G. roseo Stapf proxima, sed a quibus petalis exterioribus multo longioribus, a G. tapis pedicello fructifero et stipitibus multo longioribus, et a G. roseo staminis connectivis apiculatis et firmis differt.

Treelet ca. 5 m high or small tree ca. 10 m high with girth ca. 20-70 cm, bark pale, low fissured, inner bark yellow-brownish, sapwood pale cream. Leaves 18–20 cm long, 4.5–7 cm wide, elliptic, apiculate-caudate, the base somewhat rounded, chartaceous, grayish above, slightly brownish beneath; venation eucamptodromous-brochidodromous; primary veins inconspicuous above, prominent beneath; secondary veins in 10-12 pairs, raised but inconspicuous on upper surface, very conspicuous beneath, anastomosing to form loose intramarginal veins; intersecondary veins simple, sinuous; tertiary veins disorganized, random-reticulate-weakly percurrent; petioles short, less than 1 cm long. Flowers mostly cauliflorous, at times on primary branches, rarely axillary, solitary; pedicels stout, ca. 4-6 cm long, with several triangular basal bracts, slightly pubescent; sepals ca. 10 mm in diameter, 8 mm long, ovate, blunt-acute, coriaceous, brown pubescent; outer petals 8-9.5 cm long, 1.5-2 cm wide, broadly linear or narrowly lanceolate, narrowed upward, acute, brown pubescent on both sides; inner petals 1.2 cm long, 0.6 cm wide, ovate, thinly coriaceous, brown pubescent outside, whitish warty inside, yellowish pubescent at the edge of inner petals in the area at the top of the dome, base not distinctly clawed; stamens

numerous, 3–4 mm long, connective rostrate, glandular pubescent; ovaries about 10, 3 mm long, cylindrical, pubescent; ovules single, ovate; styles more or less equaling the size of the carpels, tubular, slightly warty; stigma clavate-crateriform, 2-lobed, warty and with trichomes at the edge. Fruiting pedicel slender, 4–6 cm long, carpel stalks 1–1.5 cm long; carpels globose, ca. 1 cm long, reddish while fresh, blackish when dry, seed 1, sweet fragrant, pericarp thin. Figures 43, 44.

Vernacular names. Bonag, pisang-pisang (Brunei), limpanas (Dusun), limpanas puteh (Kedayan).

Distribution (Figure 40). Common in low elevation undulating forests of eastern Sabah. Also on the large islands in northern and northeastern Borneo such as Banggi and Nunukan Islands, on brownish or yellowish sandstone hilltops, slopes, or riverbanks and streamsides, including logged over and disturbed areas; sometimes in areas of swampy black soil. Some collections have been obtained from areas with ultrabasic bedrock and volcanic sediments.

ADDITIONAL SPECIMENS EXAMINED. KALIMANTAN. Kalimantan Timur: Nunukan, north of Tarakan, November 1953, Meijer 2109, 2177 (BO); SABAH. "British North Borneo", September—October 1916, Villamil 228 (A, US). Res. Kudat: "North Borneo, Banguey Island", July—September 1923, Castro & Melegrito 1607 (A, BO); Kudat, Banggi, Lambuak Darat, brown soil sandstone, hilltop, 20 August 1964, Ampuria SAN 40397 (SAN); Pitas, Bengkoka, ca. 1.5 miles SE of Kg. Bawing, 6 September 1972, Shea & Minjulu SAN 75960 (SAN). Res. Sandakan:

Kinabatangan, forest land, 2 November 1929, Evangelista & Arsat 971 (NY, US); Kinabatangan, G. Lotung, near lake SE of Inarat, 8 May 1976, Aban SAN 83066 (SAN); Kinabatangan, S ridge of G. Lotung, 15 May 1976, Cockburn SAN 83136 (SAN); Kinabatangan, Hulu Sg. Inarat, SE of ridge from G. Lotung, 12 May 1976, Saikeh Lantoh SAN 83189 (SAN); Kinabatangan, Bt. Garam, Mile 2.75 British Borneo Timber Co. Conc., 17 June 1954, Wood SAN A 4745 (SING); Kinabatangan,

Figure 43. Representative specimen (with flowers) of Goniothalamus woodii (Maidin BNBFD 10429, A).

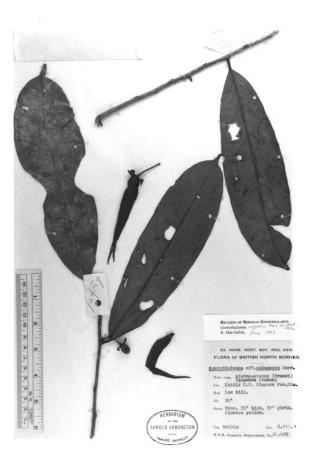


Figure 44. Representative specimen (with fruiting carpels) of *Goniothalamus woodii* (Mat-Salleh KMS 2770, UKMS).



Karamuak, near Bt. Pantagaluang, 14 June 1983, *Dewol SAN 97009* (A, SAN); Kinabatangan, Keratam Camp, hillside, black soil, 14 January 1963, Ah-Wing SAN 32589 (SAN); Kinabatangan, Keruak Forest Reserve, 14 February 1985, Francis & Martin SAN 86292 (SAN); Kinabatangan, Kori Timber Compartment, Kinabatangan Besar, flatland, 1 November 1948, Cuadra 215 (A, SAR, US); Kinabatangan, Lubuk Buaya, 10 November 1960, Sam SAN 23616 (SAN); Kinabatangan, Hulu Sg. Tangkulap, 8 October 1980, Joseph Kutil SAN 92497 (SAN); Kinabatangan, Sg. Menunggul, 23 February 1985, Amin et al. SAN 107812 (SAN); Kinabatangan, Tangkulap VIR Forest Station, ca. 40 km from Telupid township, riparian, 200-300 m, 6 August 1988, Mat-Salleh KMS 2452, 2471, 2475 (UKMS); Kinabatangan, Tenegang Besar, 15 July 1961, Jaswir SAN 30750 (SAN); Kinabatangan, Tenegang Timber Camp near Kg. Pangkalan, 20–23 November 1968, Kokawa & Hotta 1262, 1439, 1496 (SAN); Kinabatangan, Hulu Menanam, Tongod, 21 September 1978, Dewol & Kodoh SAN 89326 (SAN); Kinabatangan, Sg. Menanggul, lowland disturbed forest, 18 November 1983, Amin Gambating SAN 60058 (A, SAN); Kinabatangan, Sg. Kapor, swamp, 16 October 1960, Meijer SAN 22955 (SAN); Kinabatangan, G. Tawai, ultrabasic, low (10–25 m) and rather open, swampy forest, November 1986, Vermeulen 773 (UKMS); Kinabatangan, Telupid, Bt. Tawai, Mansus SAN 108864 (SAN); Labuk & Sugut, Beluran, Batangan Camp, Ngui Ah Kui Concession, black soil, near swamp, 23 January 1963, Jawanting SAN 32723 (SAN); Labuk & Sugut, Beluran, Batangan Camp, Ngui Ah Kui Concession, 24 January 1963, Jawanting SAN 32737 (SAN); Labuk & Sugut, Beluran, 26 September 1984, Soinin et al. SAN 107375 (SAN, UKMS); Labuk & Sugut, Beluran, Bongaya Forest Reserve, Sg. Makopako, 15 July 1975, Kodoh & Aban SAN 81943 (SAN); Labuk & Sugut, Beluran, Sg. Wanyang, Pamol Estate, in swamp, 20 May 1965, Meijer SAN 51641 (SAN); Labuk & Sugut, Beluran, Sg. Tahid, 18 January 1985, Amin Gambating SAN 67307 (SAN); Labuk & Sugut, Sg. Meliau, 5 August

1983, Sigin et al. SAN 99874 (SAN); 99876 (A, SAN, SAR); Labuk & Sugut, along Sg. Ruku-Ruku, 2 August 1981, Aban SAN 93998 (SAN); 22 June 1982, Rahim SAN 95001 (SAN); Labuk & Sugut, Telupid, Sg. Wanod, 16 March 1974, Aban & Saikeh SAN 79398 (SAN); Beluran, Km 28 to Darmakut Camp, logged area, on stream side, 19 September 1984, Aban et al. SAN 66314 (A, SAN, UKMS); Labuk & Sugut, Beluran, Hulu Sg. Ogan, riverbank, 26 September 1984, Soinin et al. SAN 107376 (A, SAN, UKMS); Labuk & Sugut, Sg. Muanad, Beluran, 21 November 1984, Amin & Martin SAN 67408 (SAN); Labuk & Sugut, Sg. Sasau, side of Sg. Tongod, 19 September 1984, Aban & Sinin SAN 60291 (SAN); Labuk & Sugut, Beluran, above Kg. Baba, 3 March 1980, Amin Kalantas SAN 90049 (SAN); Sandakan, October-December 1921, Elmer 20188 (A, BO, C, K, NY); Sandakan, Bettotan, 7 June 1933, Castro 3193 (A, BO); Sandakan, Mile 7 near path, Gomantong cave, primary forest, low undulating country, 20 July 1960, Sam SAN 21150 (SAN); Sandakan, Elopura Forest District, Kebili Forest Reserve, 6 July 1939, Maidin BNBFD 10429 (A, BM, BO); Sandakan, mile 32 Labuk road, 10 January 1976, Stevens 404 (A, SAN); Sandakan, Labuk Road, mile 32, 18 March 1970, Nooteboom 1626 (SAN); Sandakan, mile 6.5, British Borneo Timber Co. conc., Lungmanis WSW of Sandakan, mountain ridge, 14 December 1954, Wood SAN A 3978 (A); Sandakan, E of mile 44, Labuk Road, primary dipterocarp forest, 25 July 1964, Meijer SAN 44013 (SAN); Sandakan, Sekong Kechil, hillside, 2 August 1963, Ah-Wing SAN 38986 (SAN); Sandakan, Sepagaya Forest Reserve, Elopura, flatland, 17 May 1949, Cuadra 2253 (A, BO, SAN); Sandakan, Sepilok Forest Reserve, 26 May 1983, Aban et al. SAN 96817 (SAN); Camp 13, Elopura, swamp, 14 February 1951, Kadir 2900 (SAN, SAR, SING); Jalan Kebili near girdled area, 8 June 1963, Sam SAN 37538 (SAN, SAR, SING); trail to Kebili, 20 May 1982, Amin Gambating SAN 90276 (SAN); trail to beach near small stream, 16 June 1986, Mat-Salleh KMS 1028, 1029 (UKMS); Sandakan, Sg. Manila, hillside, yellowish sandy, 15 March 1963, Sayu SAN 35432

(SAN); Sandakan, Semawang River, 27 July 1927, Boden-Kloss 18743 (SAR); Sandakan, Sg. Tabing, black soil, 26 March 1963, Ah-Wing SAN 34969 (SAN); Sandakan, Sg. Sapi Camp, KBDW Co., 11 July 1963, Suah S 37404 (SAR, SAN); Sandakan, Hulu Dusun, orchard no. 2, 6 October 1984, Zainuddin et al. AZ 1603 (SAN); cocoa plantation, 16 December 1983, Saikeh Lantoh SAN 102164 (A, SAN). Res. Tawau: Lahad Datu, Bikang camp, Lahad Datu, on ridge, yellowish soil, 9 July 1964, Ahmad Talip SAN 54873 (SAN); Lahad Datu, Danum Valley, west trail, 16 July 1986, Nor-Hashimah et al. SH 101 (UKMS); Campbell SAN 109093 (SAN, UKMS); Lahad Datu, G. Silam, 12 June 1963, Meijer & Anak SAN 37490 (SAN); 22 May 1965, Talip & Sabirin SAN 52494 (SAN); 16 September 1965, Ahmad Talip SAN 52776 (SAN); 15 October 1966, Sinanggul SAN 57279 (SAN); 24 February 1972, Shea SAN 75084 (SAN); 18 March 1972, Shea SAN 75202 (L, SAN); Lahad Datu, Kennedy Bay VJR, Block 42, brown soil, 20 November 1964, Talip SAN 47625 (SAN); Lahad Datu, 1/4 mile N of Pagaruan River, near mile 4.5 on main road, Kennedy Bay, 23 September 1954, Wood SAN A 4272 (A, SAN, SING); Lahad Datu, Kennedy Bay, Silabukan Forest Reserve, Blok 82, black soil, 17 October 1963, Sinanggul SAN 39949 (SAN); Lahad Datu, Takun, Kennedy Bay sect. 62, hilltop, 4 September 1961, Muin Chai SAN 26058 (SAN); Lahad Datu, Malambalula, Nam Hing Co., 29 November 1962, Muin Chai SAN 31748 (SAN); Lahad Datu, Sg. Merisuli, near Lahad Datu, 20 October 1982, Weber 112 (A); Lahad Datu, Masuli, 1 August 1932, Benidick S 3235 (SAR); Lahad Datu, Paris Camp area, Sigin SAN 95020 (SAN); Lahad Datu, Hulu Segama, 17 July 1970, Ahmad Talip SAN 70961 (SAN); 11 March 1985, Madani SAN 108583 (SAN, UKMS); logged over area, 25 March 1985, Madani SAN 108647 (A, SAN); Lahad Datu, Segama Road, mile 4.5, 27 May 1961, Muin Chai SAN 21691 (SAN); Lahad Datu, Segangan rentis, hillside, brown soil, 6 May 1964, Aban SAN 41642 (SAN); Lahad Datu, Segangan, blackish soil, on ridge, 15 August 1966, Ahmad Talip SAN 52778 (SAN); Lahad Datu, Mile

17, Silam Road, 5 April 1966, Aban SAN 55360 (SAN); Lahad Datu, Sucitani Forest Reserve, 25 October 1982, Amin Gambating SAN 95541 (SAN); Lahad Datu, Tabin Wildlife Sanctuary Reserve, trail to mud volcano, 29 September 1988, Nais JN 2918 (UKMS); VJR 13, Jalan Temanggun, 28 September 1988, Sukup SA 1140, 1147, 1159, 1188, Mat-Salleh KMS 2741 & Latiff ALM 2913, 2920 (UKMS); VJR35, trail to core area and mud volcano, 1 October 1988, Mat-Salleh KMS 2761, 2765 2770, Latiff ALM 2953 (UKMS); Lahad Datu, Takun, Hulu Bekapit, 23 September 1980, Petrus Saigol SAN 93083 (SAN); Lahad Datu, Hulu Tungku, hilltop, brown soil, 20 June 1963, Aban SAN 35999 (SAN, SAR); Tawau, "Elphinstone Province", October 1922-March 1923, Elmer 20873 (A, BM, BO, C, K, L, NY); 21537 (A, B, BM, BO, C, L, NY, US). Tawau, E of mile 15, Apas road, 29 January 1963, Aban SAN 18631 (SAN); Tawau, Balong Road, mile 25, 20 June 1961, Bakar SAN 18549 (SAN); Tawau, Benawood, 27 July 1978, Fedilis SAN 88457 (SAN); Tawau, Baratdaya Forest Reserve, undulating plain, 18 February 1965, Singh & Nordin SAN 48783 (SAN); Tawau, Bambalai, swamp, 20 December 1963, Aban SAN 37042 (SAN); Tawau, Bt. Gamuk Forest Reserve, 20 March 1984, Fedilis & Sumbing SAN 103478 (SAN). Kalabakan, Km 41 Imbak road, Luasong, 24 February 1983, Fedilis SAN 95688 (SAN); Tawau, Hulu Sg. Sirun, hillside, 3 September 1961, Bakar SAN 26874 (SAN); Tawau, Kalabakan, Hap Seng logged area, mile 12, 23 June 1982, Fedilis SAN 95817 (SAN); Tawau, Kalabakan, km 19, Hulu Sg. Toe, Hap Seng logged area, 14 September 1983, Fedilis SAN 101390 (SAN).

The name Goniothalamus woodii was annotated by Merrill on many specimens collected from the Sandakan area and sent by his collectors in Borneo, but the name has been unpublished. The species resembles G. tapis in leaf and floral features but differs greatly in fruits. In his Plantae Elmerianae Borneensis, Merrill (1929) cited two Elmer specimens of this species (20188 and 20873) as G. tapis?

(question mark his) and remarked "both specimens with immature fruit only, no flowers". Merrill must have been aware that he had used the name G. woodii earlier, as indicated in his handwritten note on a duplicate specimen of Elmer 20188 at NY, in which he crossed out G. woodii and replaced it with G. tapis? with the note: "p. 70" in reference to the page of his Plantae Elmerianae. My interpretation of this scenario is that Merrill had decided not to publish the name G. woodii, thinking that this taxon was a variant of G. tapis, and he was waiting for more material with mature fruits to see if this were indeed a representative of G. tapis in Borneo.

In the same publication Merrill also cited *Elmer 21534* to represent *G. suluensis* Merr., a Philippine species he had described earlier from Mindanao (Merrill 1926). After examining this specimen and as well another Elmer collection from the same area (*Elmer 21537*), I am satisfied that they are *G. woodii*. The type of *G. suluensis* has much larger leaves and a distinctive petiole much like those of *G. uvariodes* and *G. macrophyllus*. The leaves of *G. suluensis* are not easy to confuse with *G. woodii*, even in sterile condition.

My analysis of the stamen and ovary characteristics showed little difference between G. woodii and G. tapis, and indicates that they comprise a natural group. I have decided to retain G. woodii because it has substantial distinguishing characteristics in the outer petals and fruits as summarized below:

	G. tapis	G. woodii
Pedicel	1.5 cm long	4–6 cm long
Fruiting carpel stalks	Sessile or subsessile	ca. 1–1.5 cm
Fruiting carpels	Fusiform, slightly apiculate	Globose, obtuse
Outer petals	Ovate, 3-5 cm long at maturity	Lanceolate, 8–10 cm long at maturity.

There is also a possibility that this species can be further divided. Specimens from inland areas, especially those from the Danum Valley-Segama River basin areas have somewhat broader outer petals and much longer, slender fruiting pedicels. In some specimens, the pedicels are almost twice the length of those of the type collection.

Goniothalamus tapisoides Alliance

8. Goniothalamus tapisoides Mat-Salleh, sp. nov.—Type: SARAWAK, Bt. Mersing, Anap, basalt derived, well drained alluvium, ca. 150 m, 16 October 1964. Sibat S 22539 (holotype: SAR!)

Goniothalamus tapi Miq. et G. umbroso Miq. affinis sed fructu carpellis globosis non sessilibus, stylo verrucoso et staminorum connectivis hebetato acutis differt.

Treelet or shrub 5 to 10 m high, stem with smooth bark, outer bark blackish, inner bark yellowish, twigs whitish gray, striate. Leaves 15–18 (–25) cm long, 5–7(–9) cm wide, variable, but mostly obovate-elliptic, base cuneate, at times acute, coriaceous, caudate, both surfaces dull, glabrous, brown beneath; venation eucamptodromous; primary vein sunken above, very much raised below; secondary veins in 10 to 15 pairs, prominent on both sides; intersecondary veins prominent, simple; tertiary veins very inconspicuous beneath, insignificant, equally inconspicuous but slightly more prominent above; petiole 1–1.5 cm long, normal, reddish. Flowers axillary, or cauliflorous on upper part of the monocaulous stem, pedicels ca. 1 cm long, reddish, with 2–4 minute triangular bracts; sepals 5 mm long, 5 mm wide, triangular, pale green, minute; outer petals up to 7 cm long, 5 cm wide when fully mature, broadly ovate, narrowed upward, extended to a long

acuminate apex, base broadly rounded, coriaceous, cream yellow, sometimes purplish tinged, greenish at the base, clawed; inner petals 1 cm long, 0.5 cm wide, ovate, outside slightly puberulous, inside villous-glandular on top, hispid at base, becoming glabrous towards anthesis; stamens numerous, short, ca. 2 mm long, 0.5 mm wide, oblong, connectives blunt-acute, glandular at base, glandular pubescent at the top; ovaries obclavate, pubescent; ovule single; styles clavate, glabrous; stigma split inside, warty. Fruiting pedicels 1–1.5 cm long, carpel stalks 1–1.5 cm long; carpels globose, small, yellow orange, turning dark red when ripe, glabrous, seed 1, with small white aril. Figures 45, 46.

Vernacular names. Beris, bunga gadong hutan (Brunei), kayu long, ta'abat kenudok sekimang (Kenyah), mahawai oih, derow (Sebob), selukai or semukau (Iban), selada (Malay).

Medicinal uses. Noted for treatment of snake, centipede and insect bites, for which pounded leaves and bark are applied to the wound.

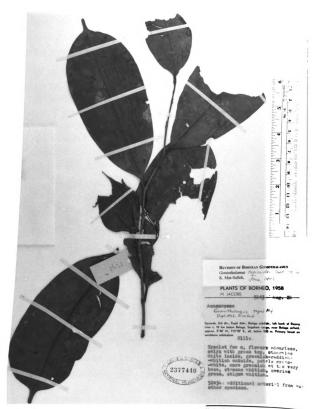
Distribution (Figure 47). Endemic to Borneo, common in well drained alluvium or on sandstone in mixed dipterocarp hill forest, rarely in kerangas or on limestone, up to about 1000 m elevation.

ADDITIONAL SPECIMENS EXAMINED. BRUNEI. Belait, Andalau Forest Reserve, compt. 7, white sandy soil, interlaminated with soft sandstone/clay, 30 May 1988, Mat-Salleh KMS 2455 (UKMS); Belait, Sg. Lumut, Supu Hill, 5 August 1933, Ibrahim BNBFD 3450 (A); Belait, Batu Patam ridge, north of summit, 10 June 1989, Wong WKM 1084 (A). KALIMANTAN. "Borneo" 1896, Teijsmann s.n. (BO); Teijsmann 272, 274, 287 (BO); Borneo, Landak Ngabang, 1896, Teijsmann 273 (BO). Kalimantan Barat: Pontianak, Kg. Ibandar Aer, 8 April 1931, Ibandi 294 (BO); Pontianak, Sg. Sambas, 1893–1894, Hallier 1085 (BO). Kalimantan Tengah: Palangka Raya,

Figure 45. The holotype of Goniothalamus tapisoides (Sibat S 22539, SAR).



Figure 46. Representative specimen (with flowers) of Goniothalamus tapisoides (Jacobs 5243, US).



Number of duplicates 11 servito 1, E, ...

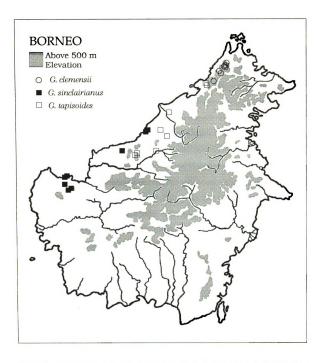


Figure 47. Distribution of Goniothalamus clemensii, G. sinclairianus and G. tapisoides.

14 September 1979, Tukirin 559 (BO); Sampit region, near Kuala Kuajan, ridge, loam soil, 25 July 1953, Kostermans 7940 (BO, L); Upper Katingan, Bt. Rava, primary dipterocarp forest, 6 February 1983, Nooteboom 5035 (BO); Upper Katingan, Upper Katingan river, ca. 50–100 km WNW of Tumbang Samba, km 36, K.T.C. logging area, 16 November 1982, Mogea 3454 (BO, L); Upper Katingan, Bt. Raya and Upper Katingan (Mendawai) River area, Upper Samba River at Tumbang Dahiye, ca. 4 km N of base camp, riverine primary forest, montane, 11 December 1982, Mogea 4074 (BO, L); Upper Katingan river, ca. 50-100 km WNW of Tumbang Samba, KTC logging area, near central base camp, ca. km 55 w of Batu Badinding, alluvial ground along Sg. Gaga, logged over rain forest, 22 December 1982, Mogea 4340 (BO). Kalimantan Timur: "Expeditie Midden-Oost Borneo 1925", West Koetai, near Petal, mountain area, 11 September 1925, Endert 3167 (BO); 28 September 1925, Endert 3671 (BO); Kemoel, 3 October 1925, Endert 3782 (BO). SABAH. Res. Pedalaman: Beaufort, hill forest, 12 December 1932, Melegrito BNBFD 3235 (A, BO); Beaufort, Halogitata, primary rich forest, 2 November 1962, Mikil SAN 31814 (SING); Beaufort, Mantinyor, hillside, 24 August 1961, Bakar SAN 25855, 25856 (SAN). SARAWAK. "Sarawak", 2 January 1915, Ridley s.n. (K); "Plants of Sarawak, Borneo", Native collector 223 & 853 (A, BO, US); Native collector 225 & 228 (A); old jungle Sk. G. Stupong, 27 January 1928, Native collector 5187 (NY); "Sarawak", 30 May 1893, Hewitt Series 249 & 334 (SAR); "Sarawak", 1868, Beccari 357 & 1836 (K). Div. 1: Bako National Park, near Kuching, poorly drained site under moderate canopy on well-forested slope, 12 May 1981, Rogstad 701 (A); Bako National Park, Teluk Assam, forest, 18 May 1956, Purseglove P 4975 (K, NY); Kuching, 20 May 1893, Dyaks S 250 (SAR); Kuching, November 1891, Haviland 405 (K); near Kuching, 23 November 1891, Haviland & Hose 3338 (K, SAR); Kuching, G. Penrissen, north slope, primary forest on sandstone, 4 August 1958, Jacobs 5055 (B, BO, US); Kuching, Stampin, 4 miles south of Kuching,

kerangas, 10 December 1966, Anderson S 25443 (K, L, SAR, SING); Kuching, Miles 41/2 south, Stapok Forest Reserve, 28 August 1966, Anderson S 25998 (SAR); Lundu, G. Gading, summit of wooded mountain, 17 August 1960, Sinclair & Kadim 10385 (A, E, SAR, SING); Lundu, G. Gading, October 1929, Clemens 22273 (BO, NY); Lundu, G. Pueh, on gentle ridge slope, with very shallow brown clayish soil derived from granite, 17 June 1974, Mamit et al. S 34441 (SAR); Lundu, Semunsam Wildlife Sanctuary, on slope of mixed dipterocarp forest, 25 July 1981, Yii Puan Ching S 43448 (K, L, SAR); Simunjan, G. Buri, hillside, in mixed dipterocarp forest, 24 May 1981, Ilias S 42099 (A, SAR). Div. 4: Baram, August 1894, Haviland 1898 (L); Baram, Hulu Atun, Tinjar, mixed dipterocarp forest, shale ridge, 25 February 1965, Murthy & Ashton S 23326 (SAR); Baram, Long Kerangan, Hulu Sg. Sekiwa, Batang Tinjar, on hillslope in mixed dipterocarp forest, 1 September 1974, Tong S 35009 (K, L, SAR); Baram, Near Long Kapa, Mount Dulit (Hulu Tinjar); rocky rainforest undergrowth, 9 August 1932, Richards 1170 (A, K); Mulu National Park, limestone, steep cliff, 5 April 1978, Stone 13662 (A, SAR); Hulu Baram, Long Selatong, tributary of Benuon, 26 June 1977, Chin 2751 (KLU); near mouth of Sg. Tikam, where it runs into the Silat, Upper Baram, mostly old secondary forest, 17 June 1977, Chin 2731 (A, KLU); Bintulu, Hulu Sinrok, Similajau Forest Reserve, undulating land, clayish rich soil, mixed dipterocarp forest, 27 March 1963, Ashton S 16597 (K, SAR); Bintulu, Segan Forest Reserve, Nanga Sapulow, in mixed forest, 2 July 1966, Ding Hou 423 (A); Marudi, Mentegai, Bok Tisam, Empran forest, nearby stream, 12 May 1966, Sibat S 23299 (A); Miri, Lambir National Park, nearby river, 8 May 1966, Banyeng S 25081 (A, BO, SAR); Miri, Lower Sibuti, mixed dipterocarp forest, clay rich soil, 27 April 1965, Anderson S 20986 (SAR); Miri, Niah National Park, on slope just above poorly drained site under moderate canopy, 12 October 1981, Rogstad 735 & 736 (A); Tatau, Hulu Mayeng, Kakus, riverbank, basalt derived soil, 13 July 1964, Sibat S 21719 (A, SAN, SAR, SING). Div. 5: Lawas,

Kayangaran Forest Reserve, low peat swamp forest, 20 June 1956, Anderson S 4911 (SAR). Div. 7: Kapit, Belaga, Hose Mountain, Base of G. Temedu, dry dacite spur, high elevation forest, 30 March 1964, Ashton S 19020 (K, L, SAN, SAR, SING); Kapit, Belaga, Segaham Range, left bank of Rajang, ca. 10 km below Belaga, near airfield, primary forest on sandstone hill, 22 August 1958, Jacobs 5243 (B, US); Kapit, Nanga Baleh, above Kapit, low elevation, jungle mountain, 6 June 1929, Clemens 21272 (NY); Kapit, Bt. Raya, 1 April 1969, Soepadmo & Chai 27610 (KLU).

This species is proposed to replace the concept in Borneo of Goniothalamus tapis Miq., erroneously used for Bornean specimens. These plants have leaf characteristics very similar to G. tapis, with the result that many Bornean specimens have been so determined. Upon extensive examination of all specimens available, I could not find any Bornean material that matches the obvious fruit characteristics of the true G. tapis, with sessile, ovate, rostrate carpels. In fact, the only fruiting specimen cited by Airy Shaw as G. tapis (Richards 1170) has very young fruits, but the stalks are up to 6 mm long. I have no doubt that these are young fruits of G. tapisoides. Other Bornean material cited by Airy Shaw belongs to a group of specimens with small leaves, which were noted by him on one of the specimens as "apparently a small-leaved form of G. tapis Miq." None of these specimens has fruit, but on the basis of other characters they can be assigned to G. tapisoides.

There would not have been confusion on the status of this species if earlier authors had paid more attention to the obvious characteristic of globose fruits with slender stalks up to 1.5 cm long. The fruits of *G. tapis* are sessile and ellipsoid, as clearly shown in two illustrations of King (1893). The importance of carpel characteristics should not be overlooked because many species of *Goniothalamus* have been distinguished primarily by the length of the carpel stalks. In fact, this

character was used by Sinclair (1955) as a basis to erect a new species (G. umbrosus) for G. tapis-like populations because it "differs from tapis having stalk and not sessile carpels". Scanning electron micrographs of stamens and styles of these species support Sinclair's treatment. Based on this scenario, it seems that the fruiting carpel-stalk character is indeed a useful taxonomic marker in Goniothalamus. This character is thus utilized in this treatment as the main character to distinguish G. tapisoides as well as two other closely allied species, viz. G. sinclairianus and G. longistipites. Another species in this alliance, G. clemensii, is also distinguishable on the basis of carpel stalks.

9. Goniothalamus longistipites Mat-Salleh, sp. nov.—Type: SARAWAK. Div. 4. Mulu National Park, upstream from Melinau Gorge, mixed dipterocarp forest, 4 March 1981, *Primack S 43339* (holotype: A!; isotype: SAR!; according to the label, also distributed to: K, KEP, L, SAN).

Goniothalamus tapisoidi Mat-Salleh affinis, sed carpellis globoso-oblongis, stipitibus multo longioribus et magis gracilis, usque 2 cm longis, foliis etiam multo minoribus differt.

Treelet or shrub 5–8 m tall, bark smooth, greenish gray, the outer thin and hard, inner bark yellow, sapwood soft, yellow, twigs glabrous, gray, striate. Leaves 13–15 cm long, 4–5 cm wide, narrowly elliptic-oblong, caudate, base cuneate, subcoriaceous, shiny dark green above, pale green beneath when fresh, drying dull green above, brownish beneath, both surfaces glabrous; venation eucamptodromous; primary vein sunken above, raised and prominent below, slightly tan-yellowish; secondary veins in 10–13 pairs, somewhat inconspicuous on both surfaces; intersecondary veins rare; tertiary veins very inconspicuous and not

prominent, random-reticulate; petiole short, 5–8 mm long. Flowers single, or in pairs, axillary or on older twigs and upper part of the stem, often in the axils of leaf scars; pedicels short, ca. 1.5 cm long, with several minute triangular scales; outer petals 4–5.5 cm long, 2–2.5 cm wide, ovate, apex sharply acute, base cuneate, clawed, pale cream green, turning yellow when mature; inner petals ca. 1 cm long, 0.5 cm wide, ovate, yellowish green, slightly puberulous outside, villous-glandular inside on top, hispid at base, becoming glabrous towards anthesis; stamens numerous, short, ca. 2.5 mm long, 0.8 mm wide, oblong, connectives blunt-acute, glandular at base, glandular pubescent at the top; ovaries obclavate, pubescent; ovule single; styles clavate, glabrous; stigma split adaxially, warty. Fruiting pedicels stout, 1–1.5 cm long, carpel stalks long and slender, ca. 2 cm long; carpels fusiform-globose, apex somewhat mucronate, greenish when young, turning yellow and then deep pinkish red at maturity, seed 1. Figures 48, 49.

Vernacular names. Mahawai hasan, selukai or semukau [Iban].

Distribution (Figure 50). Endemic to central Borneo, along sandy river banks in hill dipterocarp forest, or sometimes on tops of ridges or side slopes of ridges, at times in kerangas forest; elevation mostly 100–700 m but sometimes at slightly lower elevations; however, two specimens were recorded at 1140 m and 1650 m, respectively.

ADDITIONAL SPECIMENS EXAMINED. BRUNEI. Hulu Belait, Sg. Topi, primary seasonally swamp forest on alluvium, 11 July 1957, Ashton BRUN 206 (BO, BRUN); Belait, Andulau Forest Reserve, yellow sandy clay by stream, June 1959, Ashton BRUN 5521 (SING); Temburong, primary forest on alluvium, 9 September 1961, Ashton BRUN 494 (SING); KALIMANTAN. Kalimantan Barat: Exp. Nieuwenhuis 1896–1897, 1896, Jaheri 177 (BO); Exp. Niewenhuis, Sg. Doho, Borneo, 1896–

Figure 48. Representative specimen (with flowers) of Goniothalamus longistip (Lee S 38113, SAR).



Figure 49. Representative specimen (with fruiting carpels) of Goniothalamus longistipites (Polak & Main 2152, BO).



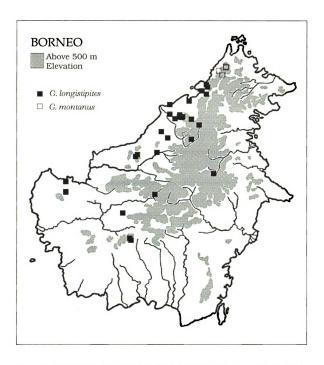


Figure 50. Distribution of Goniothalamus longistipites and of G. montanus in Borneo.

1897, Jaheri 1597 (BO). Kalimantan Tengah: Bt. Raya, upper Katingan river, ca. 50-100 km WNW of Tumbang Samba, KTC logging area, primary rainforest, 24 December 1982, Mogea 4412 (BO, L); Upper Katingan, Bt. Raya, primary dipterocarp forest, 6 February 1983, Nooteboom 4989 (BO). Kalimantan Timur: Berouw, Danau Menjiban, above Bunut, 14 October 1941, Polak & Main 2152 (BO). SABAH. Res. Pedalaman: Beaufort, Beaufort Hill, hillside, 13 October 1965, Madius et al. SAN 49293 (SAN); 4 September 1964, Dewol SAN 78373 (SAN); Beaufort, trail to Bt. Bendera, 11 September 1970, Aban & Amin SAN 66928 (SAN); Beaufort, Mile 51, Rail Line, Lumat, 19 August 1970, Aban SAN 66922 (SAN); Beaufort, Mentanior, 22 October 1979, Talib & Marsal SAN 84786 (SAN); Beaufort, Mentanior road, mile 60, 18 October 1975, Karim SAN 80217 (SAN); Sipitang, Mesapol Forest Reserve, primary forest on sandy soil, 16 September 1985, Madani SAN 111437 (SAN, UKMS). SARAWAK. Div. 1: Kuching, Setapok Forest Reserve, primary lowland forest on kerangas soil, 25 September 1957, Bojeng 9322 (BO). Div. 4: Baram, G. Mulu National Park, hill dipterocarp forest on sandy soil, on top of ridge, 2 October 1976, Lee S 38113 (SAR); on steep slope by side of a large stream, 30 June 1977, Lee S 38899 (K, SAN, SAR); Melinau Gorge Area, kerangas, 13 October 1962, Lewis 328 (K); Baram, G. Mulu National Park, Sg. Melinau near base camp, swampy forest, 9 June 1978, Argent 950 (A, E); Baram, Sg. Melinau, on dolomite, 14 February 1966, Chew CWL 1109 (A); Baram, Sg. Melinau, 14 February 1966, Chew CWL 1109 (A); Bario, Kalabit Highlands, Apa Batu Buli, 19 June 1972, Nooteboom & Chai 2204 (SAR, US); Miri, Lambir National Park, between Miri and Niah, under dense canopy on hill with orange-red clay soil, thin humus layer, sandy, 12 October 1981, Rogstad 721 (A); Miri, Lambir National Park, Sg. Liam Libau, along sandy river bank, 18 September 1978, Rena S 40283 (E, SAR); Miri, 21st Mile Lambir-Subis Rd., Miri, on ridge top, 8 June 1977, Tong S 36589 (SAR); Tatau, Sg. Mayeng, Tau Range, forest, 2 June 1956, Purseglove P 5315 (A,

NY, SAR, SING); Tatau, Sg. Mayeng, Tau Range, 4 June 1956, Purseglove P 5342 (NY). Div. 5: Limbang, Sg. Medamit, Limbang, on steep ridge slope, yellow sandy loam, 8 October 1972, Wright & Othman Ismail S 32248 (SAR); Limbang, Sg. Medamit, 8 October 1972, Othman Ismawi S 32248 (K, L, SAN, SAR); Limbang, Tg. Long Amok, Sg. Ensungai, on side slope of ridge, 11 September 1980, Rena S 42824 (SAR).

The species is allied to *G. tapisoides* but differs in having globose-oblong carpels and much thinner and more slender carpel stalks, up to 2 cm long. The leaves are also much smaller.

10. Goniothalamus sinclairianus Mat-Salleh, sp. nov.—Type: SARAWAK. Kuching,
12th mile, Penrissen Road, Arboretum, Semengoh Forest Reserve, riverside,
9 November 1966, Banyeng & Sibat S 26246 (holotype: SAR!).

G. tapisoidi Mat-Salleh affinis, sed carpellis ellipticis, apice rostellato differt.

Treelet 3–6 m high with slender stem, bark whitish, smooth. Leaves 18–22 cm long, 5–9 cm wide, elliptic, caudate, base acute, younger ones tending to be obovate, coriaceous, at times rounded, green, glossy above, paler dull brown beneath; venation eucamptodromous; primary vein sunken above, very much raised below, brownish-yellow; secondary veins in 9–13 pairs, prominent beneath, not so much so above, sinuous; intersecondary veins numerous, simple; tertiary veins inconspicuous on both sides, random-reticulate; petiole 1.5–2 cm long, slightly inflated. Flowers solitary, cauliflorous on upper part of the monocaulous stem, at times axillary; pedicels ca. 1 cm long; sepals ca. 5 mm long, 5 mm wide, broadly ovate; outer petals ca. 2.5 cm long, 1.5 cm wide, ovate, apex acute, base

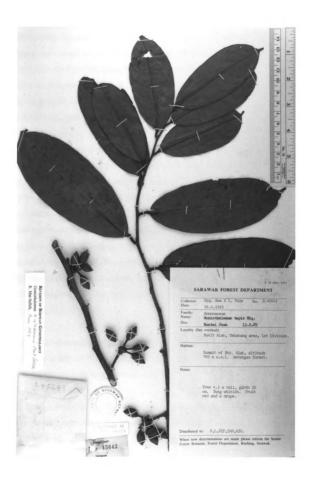
rounded, coriaceous, rusty glabrous when dry, slightly clawed; inner petals 7 mm long, 5 mm wide, ovate, outside slightly puberulous, inside villous-glandular on top, hispid at base, becoming glabrous towards anthesis; stamens numerous, short, ca. 2.5 mm long, 0.8 mm wide, connective blunt-acute, glandular at base, glandular pubescent at the top; ovaries obclavate, pubescent; ovules single; styles clavate, glabrous; stigma split inside, warty. Fruiting pedicels 1.5–2 cm long, carpel stalks 5–7 mm long, carpels fusiform, deep pinkish red with greenish stalk, glabrous, seed 1. Figure 51.

Vernacular name. Selukai (Iban).

Distribution (Figure 47). Endemic to southern Sarawak, often in forests with clay-loam or podzolic sandy soils, as well in kerangas forest.

ADDITIONAL SPECIMENS EXAMINED. KALIMANTAN. Kalimantan Tengah: Upper Kahayan, headwater of Sg. Kahayan, 5 km S of Tumbang Sian logging camp, Sikatan Wana Raya, primary lowland forest, 1 May 1988, Burley & Tukirin 856 (A, BO). SARAWAK. Div. 1: Bako, Hulu Serait, Bako National Park, white sand humic podsol, undulating heath forest, 1 June 1963, Chai & Ilias S 17840 (A); Kuching, Arboretum, Semengoh Forest Reserve, mixed dipterocarp forest on ridge, 20 August 1971, Anderson S 26841 (K, SAR); Kuching, Hulu China, Matang, on yellow-red latosols, gentle hillside, 22 November 1962, Ilias & Ashton S 16689 (K, L, SAR, SING); Serian, Tebakang Road, Bt. Empan Ra'a (near Bt. Selapor), Lobang Mawang, hillside, yellow clayey soil, 26 September 1968, Ilias Paie S 28073 (A, E, K, L, SAR); Serian, Tebakang area, summit of Bt. Alak, kerangas forest, 16 April 1983, Dayang Awa & Ilias Paie S 45643 (K, L, SAR); Serian, Sg. Sabal Tapang, by timber path in forest, 5 August 1960, Sinclair & Kadim 10224 (K, L, SAR, SING); Simunjan, G. Gaharu, near river bank at 1,300 ft. on yellow sandy soil, 12 October 1974, Ilias & Azahari S 35739 (A, SAR). Div. 2: Simanggang, Batang Lupar, swamp

Figure 51. Representative specimen of Goniothalamus sinclairianus (Dayang Awa & Ilias Paie S 45643, SAR).



forest, 1957, Zahudu LEZ 9431 (SAR). Div. 3: Mukah, Bt. Penarih, Balingian, white sand podsol, secondary forest, low undulating hill, Liang formation, 18 October 1963, Ashton S 19439 (K, SAR). Div. 4: Bintulu, Similajau/Labang, hillside, clay-loam soil, 4 September 1968, Ilias S 28003 (A, K, L, SAN, SAR); Miri, Lambir N.P., on wet ground, stream valley near summit, kerangas soil, 27 September 1978, Rena S 40447 (K, L, SAR, SING).

The leaves and mature carpels of this species are indistinguishable from those of *G. tapis*, but it has long fruiting carpel stalks much like those of *G. umbrosus*. In the past specimens of this species have been determined as *G. umbrosus*, probably on the basis of the carpel stalks. I have decided to recognize the species because the specimens have longer carpel stalks and leaves quite different from those of *G. umbrosus*. Furthermore, the blunt-acute stamens and warty styles are in no way similar to those of *G. tapis* and *G. umbrosus*. This species resembles *G. tapisoides* in stamen and style features but differs from that taxon in the shape and size of the fruiting carpels. It commemorates James Sinclair for his numerous and important contributions on Southeast Asian Annonaceae.

11. Goniothalamus clemensii Bân, Bot. Zhurn. (Moscow & Leningrad) 59(4): 552, illust. 553. 1974.—Type: SABAH. Mt. Nungkok forest ridge, 4000–5000 ft, 14 April 1933, Clemens 32761 (holotype: NY!).

Shrub or treelet 3–6 m high, stem greenish white, smooth, twigs whitish, sometime blackish brown, glabrous, striate. Leaves 10–15 cm long, 3–4.5 cm wide, oblong-elliptic, apex caudate, base acute, rarely cuneate, subcoriaceous, both surfaces dull but rather brownish beneath, glabrous on both surfaces; venation

consistently brochidodromous; primary vein sunken above, raised and prominent below, slightly brownish; secondary veins in 7-10 pairs, very inconspicuous and insignificant beneath; intersecondary veins common, simple; tertiary veins very inconspicuous beneath, prominent above, random-reticulate; petiole slender, ca. 1 cm long, without noticable thickening. Flowers solitary or in pairs, cauliflorous or axillary ramuliflorous; pedicel very short, 0.5-1 cm long, with 2-4 minute oblong basal bracts; sepals pinkish yellow, turning reddish green at anthesis, ca. 1 cm long, 0.5–0.6 cm wide, ovate; outer petals yellowish cream-orange, 5 cm long, 1.5– 1.7 cm wide at full maturity, elliptic-ovate, sharply acute-acuminate, base acute, slightly clawed; inner petals ca. 3.5 cm long, 2 cm wide, elliptic, base clawed, puberulous outside, villous-scabrous inside, especially on the upper part of the petal, becoming scabrous toward anthesis; stamens numerous, ca. 2.5 mm long, 0.8 mm wide, oblong, connectives blunt-acute, apex glandular at base, glandular strigose above; ovaries obclavate, pubescent; ovules 1-2; styles clavate, glabrous; stigma split inside, warty glandular. Fruiting pedicel stout, ca. 1 cm long; carpels sessile or subsessile (carpel stalk less than 4 mm long), fusiform-globose, apex acuminate-apiculate, base acute-rounded, purple-pinkish turning red at maturity, seed 1, with a small white aril.

Distribution (Figure 47). Endemic to Mount Kinabalu and the adjacent Crocker Range in Sabah, in montane dipterocarp or oak-laurel forest at 1200 to 1700 m.

ADDITIONAL SPECIMENS EXAMINED. Mount Kinabalu, Dallas, 3000 ft, 21

December 1931, Clemens 27638 (A, B, BM, K, NY); Mount Kinabalu, Penibukan,

4000–5000 ft, 28 December 1932, Clemens 30497 (A, NY); Mount Kinabalu, on spur

E of Dahobang river, Penibukan, 4000–5000 ft, 24 January 1933, Clemens 31198 (A, BM, NY); Mount Kinabalu, Penibukan, 4–5000 ft, ridge west of camp, 24 January

1933, Clemens 31342 (A, BO, NY); 7 February 1933, Clemens 31499 (A, BO) & 50403 (BM, K, NY); Mount Kinabalu, Penibukan, west ridge, 4000 ft, 18 October 1933, Clemens 40770 (BM, NY); Kota Belud, Mt. Nungkok forest ridge, 4-5000 ft, 14 April 1933, Clemens 32761 (BO, NY); Mount Kinabalu, Tenompok, ca. 5 km on Kota Kinabalu side below Park Hq. just off main road, very steep slope in hilly, dense forest area, 3 January 1984, Rogstad 954 (A); Mount Kinabalu, Tenompok, 15 August 1987, Mat-Salleh KMS 1451 (UKMS); Mount Kinabalu, Tenompok Ridge along Tamparuli-Ranau Road 6 km W of Park Hq., Crocker formation, primary forest (under deforestation), 1400–1450 m, 3 January 1984, Beaman 8184 (MSC, NY); Mount Kinabalu, Tenompok Forest, 23 June 1984, Madani SAN 102197 (SAN); 14 November 1985, Sukup SA 727, SA 735 (UKMS); Mount Kinabalu, Tenompok, trail near waterfall, 4 December 1988, Mat-Salleh KMS 2807 (UKMS); S of Sayap on NW side of Mount Kinabalu, ca. 30 km SE of Kota Belud, Trus Madi formation, dipterocarp forest, 800-1000 m, 19-20 May 1984, Beaman 9752, 9801 (MSC, UKMS); Mount Kinabalu, 1892, Haviland 1313 (K). Res. Pedalaman: Keningau, Mile 14, Keningau to Kimanis logging road, 1170 m, 6 November 1986, Mat-Salleh KMS 1187, 1191, 1196 (UKMS); Keningau, Trus Madi Range, Kg. Sinoa, along logging track at Km 4, 14 November 1987, Mat-Salleh KMS 1954 (UKMS); Crocker Range, Km 41 on Kota Kinabalu-Tambunan Road, Crocker formation, montane dipterocarp forest, 1050 m, 9 March 1984, Beaman 8830 (MSC, NY); Crocker Range, Km 64, Kota Kinabalu to Tambunan road, 29 March 1984, Kitayama K 438 (UKMS); Crocker Range, Km 41 on Kota Kinabalu-Tambunan Road, Crocker formation, montane dipterocarp forest, 1050 m, 14 March 1984, Beaman 8888 (MSC, NY); Crocker Range, Km 64 on Kota Kinabalu-Tambunan Road, Crocker formation, montane dipterocarp forest, 1250–1600 m, 9 October 1983, Beaman 7167 (MSC, UKMS); 10 April 1984, Beaman 9329 (MSC, NY); 1 July 1984, Beaman 10404 (MSC, UKMS); Beaman 10409 (MSC, NY).

Bân's illustration and flower description of this species are based on an immature specimen. In leaf and fruiting carpel characteristics this species resembles G. sumatranus Miq. from Sumatra. However, it differs in having blunt-acute stamen connectives as well as clavate styles typical of stamens in members of the G. tapisoides alliance. Goniothalamus sumatranus, on the other hand, has strongly apiculate stamen connectives and pubescent crateriform stigmas common in the G. tapis alliance.

12. Goniothalamus montanus J. Sinclair, Gard. Bull. Singapore 14(2): 443–444.

1955.—Type: Peninsular Malaysia, Trengganu, Hulu Brang, Tersat, Moysey

SFN 33627 (holotype: SING!),

Tree 3–4 m tall, twigs greenish white, striate. Leaves 9–10.5 cm long, 2–4 cm wide, elliptic-oblong-oblanceolate, apex sharply acute, base cuneate, chartaceous, dark green above, pale and dull greenish beneath, glabrous; venation eucamptodromous; primary vein sunken above, raised beneath, dark green; secondary veins in 8–12 pairs, raised and prominent on both sides, with numerous intersecondary veins; tertiary veins random-reticulate, very prominent above, dark green, pale and inconspicuous beneath but conspicuous above; petiole ca. 1 cm long, short, blackish, with no conspicuous thickening. Flowers solitary, axillary or terminal, glabrous, pedicel slender, 2–3.4 cm long, with 2–6 minute basal triangular bracts; sepals small, 4–6 mm long, 5–6 mm wide, triangular, glabrous; outer petals 3–3.5 cm long, 0.5–0.8 cm wide, ovate-lanceolate, green turning yellow when fully developed, brownish at anthesis, pubescent; inner petals 1.2–1.4 cm long, yellowish green, ovate, clawed, puberulous outside, scurfy inside; stamens

numerous, ca. 2.5 mm long, 0.8 mm wide, oblong, connectives blunt-acute, apex with glabrous base, strigose above; ovaries obclavate, pubescent; styles clavate, glabrous; stigma split inside, warty. Fruiting pedicel ca. 4 cm long, carpel stalks 2–3 cm long; carpels ca. 4 cm long, fusiform, apex acuminate, base cuneate, green, blackish when fully mature, seed 1.

Distribution (Figure 50). This is a rare species found also in a few localities in the mountains of Peninsular Malaysia. In Borneo the species occurs around Mount Kinabalu and in the neighboring Crocker Range at elevations of 1300–1700 m.

ADDITIONAL SPECIMENS EXAMINED. Mount Kinabalu, Keebambang River, 4–5000 ft, 8 August 1933, Clemens 34406 (A, BO, NY); Mount Kinabalu, Marai Parai, trail to Sadikan River, 5000 ft, 23 March 1933, Clemens 32318 (A, BO, NY); 7 May 1933, Clemens 33126 (A, B, BM, BO, NY); Mount Kinabalu, Marai Parai, 5000 ft, 5 May 1933, Clemens 33073 (A, BO, NY); Clemens 33075 (K); Mount Kinabalu, Kg. Kiau Nulu, trail from Kinapasawon to Sokid, 14 June 1988, Gunik GNIK 299 (UKMS); Mount Kinabalu, Penibukan, W ridge jungle, 13 November 1931, Clemens 50355 (A, K). Res. Pantai Barat: Penampang, Km 20, Kota Kinabalu-Tambunan Road, 20 June 1986, Mat-Salleh KMS 1404 (UKMS). Res. Pedalaman: Tambunan, G. Alab, 22 February 1969, Nooteboom 998 (BO); 21 September 1985, Shariff & Injan 8, Hasnah MH 9, Nor-Hashimah SH 14, Khalsa SKK 15, Ambili AN 26, Nor-Rashidah UKMS 9838, Injan UKMS 9373; 22 September 1985, Abdullah s.n., Suhaili s.n. (UKMS); 29 September 1985, Ahmad AD 200 (UKMS); trail to summit of G. Alab, 1700 m, 5 July 1987, Mat-Salleh KMS 1432 (UKMS).

This species was first described by Sinclair (1955) from montane forest in Peninsular Malaysia. Bân (1974b) identified several Clemens specimens from Mount Kinabalu as G. montanus, with which I agree, and I have added several more collections to this species that were not cited by Bân.

G. velutinus Alliance

13. Goniothalamus velutinus Airy Shaw, Kew Bull. 1939: 285. 1939.—Type:

SARAWAK, 4th Division, Near Long Kapa, Mount Dulit (Hulu Tinjar), 31

August 1932, *Richards 1559* (holotype: K!).

Small monocaulous treelet, 3–6 m high, 7–8 cm dbh, bark blackish brown, inner bark pale yellowish, sapwood reddish white; twigs reddish ferruginous-velutinous. Leaves 30–45 cm long, 6–12 cm wide, oblanceolate-oblong, acuminate, base rounded, coriaceous, dark green above, brownish beneath, velutinous, especially on young leaves; venation consistently brochidodromous; primary vein sunken above, raised beneath, reddish tomentose-velutinous; secondary veins in 20–25 pairs, raised and reddish tomentose on both sides but rather inconspicuous beneath; intersecondary veins composite; tertiary veins random-reticulate, inconspicuous on the upper surface, prominent beneath; petiole ca. 2 cm long, thick, inflated, dark reddish ferruginous. Flowers intensely fragrant at anthesis, supra-axillary or on upper part of the stem, yellowish; pedicel short, ca. 0.5–1 cm long, reddish tomentose, basal bracts 4–6, up to 5 mm long, ovate, tomentose; sepals 0.5–1 cm long, ca. 0.5 cm wide, deltoid, connate, dark green; outer petals 1.8–2.5 cm long, ca. 1 cm wide, ovate-lanceolate, apex blunt-acute, base clawed, pale cream yellow, fleshy, fragrant, tomentose; inner petals 1–1.2 cm long, ca. 0.5

cm wide, ovate, apex blunt-acute, base attenuate, clawed and slightly pubescent; stamens numerous, ca. 2 mm long, 0.8 mm wide, oblong-oblanceolate, connective blunt-acute, cream, minutely tomentose; ovaries obclavate, glabrous; ovules 1 or 2; styles short, glabrous; stigmas white, somewhat glabrous when young, then glandular, warty and scurfy at anthesis, much larger than ovary and easily detached when the flower is boiled. Fruiting pedicel ca. 5 mm long, short, reddish tomentose; carpels ca. 2 cm long, 1.5 cm in diameter, fusiform-globose, apex blunt-acute or obtuse, base cuneate, subsessile, green, seeds 1–2.

Vernacular names and uses. Limpanas (Brunei), Kayu hujan panas (Malay), Sekot laki bio' (Kenyah), Lakom hitam(Kedayan). Used for canes. The holder is said to be immune from snake bites.

Distribution (Figure 52). Endemic to Borneo; occurring in various kinds of forest from peat swamp to hill dipterocarp (including kerangas) forest and montane vegetation up to about 1700 m.

ADDITIONAL SPECIMENS EXAMINED. BRUNEI. Belait, Andalau Forest Reserve, compt. 7, white sandy soils, 30 May 1988, Mat-Salleh KMS 2454 (UKMS); Belait, Sg. Lumut, peat swamp forest, 26 August 1939, Sinclair & Kadim 10429 (E, K, SAR, SING). KALIMANTAN. Kalimantan Barat: "Borneo Expedition Liang-Gagang", 1893, Hallier 2066 & 2901 (BO). Kalimantan Timur: "Exp. Niewenhuis", Bt. Ibilie, 12 November 1898, Amdjah 146 (BO). West Kutai, 10 November 1925, Endert 4748 (BO). SABAH. Res. Pantai Barat: Papar, Mandahan Hill, 19 March 1974, Karim SAN 78004 (SAN); Papar, Crocker Range, Hulu Kimanis Forest Reserve, 11 November 1986, Mat-Salleh KMS 2458 (UKMS); Papar, Hulu Kimanis, track along Sg. Kimanis, 1780 m, down the river, on ridge, 11 November 1986, Mat-Salleh KMS 1331, 1332 (UKMS); Hulu Kimanis, Kenigau Kimanis road, 750 m, 31 December 1988, Mat-Salleh 2841, 2842, 2843 (UKMS); Penampang, Kg. Bobogon, 4th mile,

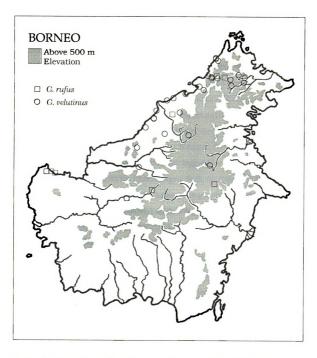


Figure 52. Distribution of Goniothalamus velutinus and of G. rufus in Borneo.

path to Hulu Terian, 18 October 1969, Cockburn et al. SAN 68449 (SAN); Tuaran, Lema'as Forest Reserve, on ridge, soil brownish, 12 August 1966, Aban SAN 42046 (SAN); Tuaran, Mengkadai, on top of damp hill, 7 January 1937, Puasa BNBFD 6778 (A); Tuaran, Sulaman Lake Forest Reserve, dry land, islet in mangrove swamp, 14 April 1950, Atek A 495 (L, SING, US). Res. Pedalaman: Sipitang, Weston, Hulu Mesapol Forest Reserve, 20 August 1986, Andrew et al. AGM 69, 104, 109, 114 & 115 (UKMS); Kg. Lubuk, kerangas, 31 July 1988, Mat-Salleh KMS 2444 (UKMS); Sipitang, Lumaku Forest Reserve, Mendolong, 16 October 1972, Saikeh SAN 72357 (SAN); Sipitang, Lumaku Forest Reserve, L39, SFI concession, along Sg. Mondol, 23 August 1985, Habibah & Sukup HABY 8 (UKMS). Res. Sandakan: Kinabatangan, Km 19, Sg. Milian, Pinangah, 30 October 1984, Mansus & Aban SAN 69246 (SAN); Kinabatangan, Tangkulap, 6 August 1988, Mat-Salleh KMS 2476 (UKMS); Kinabatangan, Tongod, Sg. Enodol, logged-over hillside, 21 July 1983, Dewol et al. SAN 99427 (A, SAN); Kinabatangan, Hulu Sg. Lokan, 10 November 1979, Aban & Petrus SAN 90686 (SAN); Labuk & Sugut, Sg. Ruku-Ruku, 8 October 1984, Zainuddin et al. AZ 1644 (SAN); Labuk & Sugut, Sg. Ruku-Ruku, 26 September 1983, Amin & Kumin SAN 70319 (SAN). SARAWAK. Div. 4: Baram, Hulu Sg. Chipidi, Hulu Tinjar, 13 August 1974, Chai S 34824 (SAR); Baram, Melinau Gorge, Anderson S 4271 (SAR); Baram, Hulu Baram, Long Selatong, Sg. Sebala, 11 May 1977, Chin 2673 (KLU); Baram, Hulu Baram, Long Selatong, tributary of Benuon, 29 June 1977, Chin 2749 (KLU); Miri, Lambir National Park, between Miri and Niah, under dense canopy on hill with orange-red clay soil, thin humus layer, sandy, 12 October 1981, Rogstad 716 (A); Miri, Niah Cave National Park, well drained slope under broken canopy, lowland dipterocarp forest, 12 December 1981, Rogstad 741 (A); Miri, Lambir Hills National Park, Dan Hj. Bakar S 4358 (SAR); Miri, Hulu Sg. Sekaloh, Niah River, 26 November 1966, Anderson & Tan S 26067 (SAR); Miri, Hulu Mamut, on ridge, 100 ft, 18 March 1966, Banyeng S 24398

(SAR, SING); Tatau, Hulu Sg. Kana, Batang Anap, 13 February 1985, Abang-Mohhtar & Othman Haron S 41763 (SAR). Div. 5: Limbang, Tg. Long Amok, Sg. Ensungei, 10 September 1980, Rena S 42810 (SAR). Div. 7: Kapit, Balleh, Carapa Pila, Hulu Mujong, pole forest, bleached basalt-derived clay, 9 April 1964, Ashton S 19631 (A, BO, SAR).

This species has been difficult to understand, in part due to the lack of a description of fruit characteristics in Airy Shaw's original diagnosis. The holotype at K has no fruit. Recent collections suggest that the species has two distinct types of fruiting carpels and stalks. One is characterized by broadly fusiform carpels, glabrous, green, glaucous or yellow-spotted and with stalks, while the other is globose, reddish and pubescent. The size, shape and form of leaves, twigs and stems for both populations seems impossible to separate

This species resembles G. macranii Craib, a Thailand-Peninsular Malaysia species, except that it has much smaller leaves. Sinclair (1955) noted that the fruiting carpels of G. macranii are "sparsely brown-pubescent, and the pubescence disappearing with age". Taking the carpel variation in G. macranii into consideration, it seems possible that the hairiness of G. velutinus carpels might vary with age. However, I have not seen any pubescent fruits of G. velutinus in Sabah and Brunei and am skeptical about the statement of Sinclair concerning the fruit of G. macranii. Nevertheless, this variation has to be further investigated.

14. Goniothalamus rufus Miq., Ann. Mus. Bot. Lugd.-Bat. 2: 85. 1865.—Type: Borneo australis, G. Rantau, Korthals s.n. (holotype: L!; isotype K!),

Shrub or small tree, 3-8 m high, stem and older branches blackish, young twigs reddish tomentose-velutinous. Leaves 10-20 cm long, 3-7 cm wide, ellipticobovate-lanceolate, acuminate, base acute-rounded, chartaceous, dark green above, brownish beneath, velutinous on young leaves; venation camptodromous; primary vein sunken above, raised beneath, reddish tomentose-velutinous; secondary veins in 10–15 pairs, raised on both sides, but rather inconspicuous beneath, reddish tomentose, brownish; intersecondary veins simple, numerous; tertiary veins lax and inconspicuous, random-reticulate; petiole ca. 1 cm long, straight, not inflated, reddish tomentose. Flowers mostly terminal, occasionally supra-axillary, pale cream, pedicel short, ca. 5 mm long, reddish tomentose, bracts imbricate, 4-6, up to 5 mm long, lanceolate, tomentose; sepals ovate, obtuse, pubescent; outer petals 1-1.2 cm long, 0.5-0.6 cm wide, ovate-elliptic, apex sharply acute, base slightly clawed, pale cream-orange, fleshy, fragrant, sparsely pubescent; inner petals ca. 1 cm long, 0.5 cm wide, ovate, apex acute, slightly shorter than outer petals, base clawed, slightly pubescent outside, reddish scabrous-strigose inside; stamens numerous, small, only ca. 1 mm long, obovate-oblanceolate, connective truncate, farinose-echinate; ovaries obclavate, glabrous; ovules 1 or 2; styles short, glabrous; stigmas white, somewhat glabrous when young, then glandular, warty and scurfy at anthesis, much larger than ovary and easily detached when the flower is boiled. Fruiting pedicel short, reddish tomentose, ca. 1 cm long; carpel stalk long and slender, ca. 1.5 cm long, glabrous; carpels ca. 1.2–1.3 cm long, 1 cm in diameter, fusiform, green, apex strongly rostellate, base cuneate, seed 1, brown, covered with thin slimy aril.

Vernacular name. Kayu kupang pacau (Melanau).

Distribution (Figure 52). Northern Sumatra and Borneo. In lowland and hill dipterocarp or submontane forests, on alluvial or sandy clay soils, also recorded from kerangas forest, 100–750 m elevation.

ADDITIONAL SPECIMENS EXAMINED. KALIMANTAN. Kalimantan Barat: Lianggagang, 1893–1894, Hallier 3005 (BO); Borneo, Exp. Nieuwenhuis, Sg. TapoeTsey, 1896–1897, Jaheri 893 (BO); Pontianak, G. Palong Nature Reserve ca. 100 km S of Pontianak, on alluvial soil, 17 June 1986, van Balgooy & van Setten 5488 (A); 20 June 1986, van Balgooy & van Setten 5535 (A). Kalimantan Selatan: Muara Uya, Jaro Dam, 10 Km NE of Muara Uya, 15 November 1971, Kuswata 812 (BO). Kalimantan Tengah: Upper Katingan, Tumbang Tubus, dipterocarp forest, 8 January 1983, Veldkamp 8137 (US). Kalimantan Timur: West Kutai, G. Maranga on Tundjung plateau, 28 July 1956, Kostermans 12546 (BO). SABAH. Res. Pedalaman: Keningau, Tambulanan, 21 October 1983, Amin Gambating SAN 68979 (SAN); Keningau, Trus Madi Range, Sinoa, along Sg. Kaintanu Besar, hill dipterocarp forest dominated by Shorea laevis, Trus Madi formation, 650 m, 11 November 1987, Mat-Salleh KMS 1760 (UKMS); Tenom, Crocker Range, above Kallang waterfall area, ca. 350 m, 1 January 1989, Mat-Salleh KMS 2837 (UKMS). SARAWAK. Div. 1: Lundu, G. Gading, 1892, Hallier 982 (SING); Lundu, G. Gading, forest on hillside above waterfall, 17 August 1960, Sinclair & Kadim 10373 (A, B, BM, BO, E, SING, US); Lundu, G. Gading, 1700 ft, submontane, 7 October 1961, Anderson & Ilias S 15382 (A, BM, BO, SAR); Lundu, G. Gading, 2250 ft, sandy clay soil, gentle slope of mixed dipterocarp forest, 19 September 1974, Mamit S 35055 (A, SAR); Lundu, G. Gading, 20 July 1963, Chew CWL 605 (K). Lundu, G. Perigi, in primary lowland dipterocarp forest, 5 May 1961, *Ilias S 13308* (A, K, L, NY, SAR); Lundu, Bt. Sejarak, Sampadi Forest Reserve, 25th mile, Bau/Lundu Road, kerangas forest, hillside, 30 June 1968, *Ilias S 26933* (E, K, L, SAR, SING).

This species resembles *G. velutinus* in style and stamen characters. It differs from *G. velutinus* in having very much smaller leaves and much longer and more slender mature carpel stalks.

Goniothalamus uvarioides Alliance

15. Goniothalamus uvarioides King, J. Asiat. Soc. Bengal, Pt. II.-Nat. Sci. No. 1: 78-79. 1892.—Type: Peninsular Malaysia, Perak, Hulu Slim, August 5, 1886, King's collector 10664 (lectotype, designated here: K!).

Goniothalamus pendulifolius Ridl., Fl. Malay Peninsula (suppl.) 5: 287. 1925.—
Type: Peninsular Malaysia, Pahang, 6 miles north of Bentong, 5

November 1924, Burkill & Haniff 16501 (lectotype, designated here: K!).

Monocaulous treelet or shrub up to 10 m high, stem with smooth gray bark; twigs glabrous, light green, slightly darker when dry, often triquetrous. Leaves variable, 28–75 cm long, but once measured in the field up to 90 cm, 6–15 cm wide, normally oblong, oblanceolate at times, acuminate-acute, base cordate-rounded, rarely acute, coriaceous-subcoriaceous, glabrous on both sides; venation consistently brochidodromous; primary vein sunken above, with fine groove, large and strongly raised beneath, rounded; secondary veins in 22–30 pairs, prominent beneath, straight and parallel with each other, anastomosing with loops 5–7 mm from the margin; intersecondary veins numerous, simple; tertiary veins inconspicuous, loosely weakly percurrent or random-reticulate; petiole ca. 2 cm long, stout, inflated, blackish, glabrous. Flowers cauliflorous or ramuliflorous on older branches, axillary, fragrant shortly before anthesis, with the odor of

fermenting fruit; pedicel 2 cm long, curved, with 2-several minute triangular basal bracts; sepals green, 0.5–1 cm long, ca. 0.5 cm wide, ovate, slightly pubescent; outer petals ca. 3.5 cm long, 1 cm wide, lanceolate, sharply acute, base rounded or flat, not clawed, coriaceous, rusty glabrous, light green; inner petals 2.5–3 cm long, 1 cm wide, narrowly lanceolate-oblong, strongly clawed at base, pubescent outside; stamens large, ca. 5 mm long, connective strongly apiculate, pubescent; ovaries 2 mm long, pubescent; ovules 5–6; styles 3 mm long, glabrous, linear, straight, cylindrical, grooved; stigma crateriform. Fruiting pedicels 2–4 cm long, carpel stalks 0.5–1 cm long; carpels 4–5 cm long, ca. 2 cm in diameter, cylindrical-nodiform, slightly apiculate, base acute, green glabrous, seeds 4–5.

Distribution (Figure 53). Peninsular Malaysia, Philippines and Borneo. In Borneo the species occurs in rich dipterocarp forest on hillsides, near ridge tops or in montane vegetation, on clay, alluvial, ultramafic, quaternary dacite lava or limestone, from low elevations up to 1500 m.

ADDITIONAL SPECIMENS EXAMINED. KALIMANTAN. Kalimantan Barat: G. Palong Nature Reserve, 20 June 1986, van Balgooy & van Setten 5539 (A). SABAH. Mount Kinabalu, Eastern Shoulder (Singh's plateau); 26 July 1961, Chew, Corner & Stainton RSNB 969 (K, SAN, SING); Mount Kinabalu, Gurulau spur, November 1915, Clemens 10849 (A); Mount Kinabalu, Park Hq. area, 19 November 1983, Jumaat UKMS 3343 (UKMS); Mount Kinabalu, Mesilau River, Kokawa & Hotta 4018 (SAN); Mount Kinabalu, Mesilau River, 29 September 1972, Cockburn SAN 70115 (SAN); Ranau, Bt. Kulong near Bt. Hampuan, ultramafic soil, dipterocarp forest, 750 m, 8 December 1983, Beaman 7764 (MSC, UKMS); Ranau, Crocker Range, Bt. Lugas, Trus Madi formation, montane dipterocarp forest, 1250–1300 m, 7 July 1984, Beaman 10565 (MSC, UKMS); Ranau, Mokodou River above Kg. Takutan, dipterocarp forest, ultramafic, 400–500 m, 10 May 1984, Beaman 9666 (MSC).

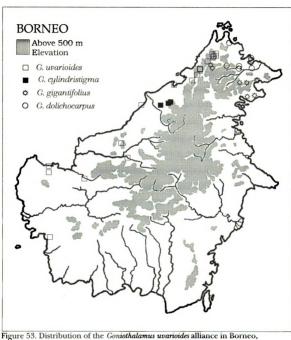


Figure 53. Distribution of the Goniothalamus uvarioides alliance in Borneo, excluding G. kostermansii, G. kinabaluensis and G. parallelivenius.

Res. Pantai Barat: Crocker Range, Hulu Kimanis, Kimanis-Keningau road, 750 m, 31 December 1988, Mat-Salleh KMS 2858 (UKMS). Res. Pedalaman: Crocker Range, Keningau-Kimanis Road, mile 11, 1180 m, 7 November 1987, Mat-Salleh KMS 1228 (UKMS); Crocker Range, Keningau, mile 11, Highland Plantation, 8 June 1977, Talip & Ejan SAN 85435 (SAN); Meligan Range, Lumaku Forest Reserve, Mendolong, 700–750 m, 30 July 1988, Mat-Salleh KMS 2405 (UKMS); Crocker Range, Km 64, Kota Kinabalu-Tambunan Road, Crocker formation, montane dipterocarp forest, 1250 m, 14 November 1983, Beaman 7502 (MSC, UKMS); Crocker Range, Tenom, Kg. Melutut, mixed dipterocarp forest, Crocker formation, 250-500 m, 25 November 1987, Mat-Salleh KMS 2134 (UKMS); Crocker Range, Tenom, Kg. Noloyan, 450–650 m, 26 November 1987, Mat-Salleh KMS 2145, 2161 (UKMS); Crocker Range, Tenom, Sg. Polong, on steep slope, mixed dipterocarp forest, Crocker formation, 350-450 m, 24 November 1987, Mat-Salleh KMS 2103 (UKMS). Res. Sandakan: Kinabatangan, Lamag, 13 September 1971, Imbungan & Patrick SAN 74188 (SAN); Kinabatangan, Tamoi, Lamag, swampy forest along small stream, 250-300 m, 6 August 1988, Mat-Salleh KMS 2462 (UKMS); Sandakan, Luang Manis, 13 May 1962, Meijer SAN 34668 (SAN); Hulu Dusun, 12 August 1977, Saikeh Lantoh SAN 87823 (SAN). SARAWAK. "Sarawak" Beccari 2327 (K). Div. 1: Bt. Krian, limestone, 28 May 1972, Anderson S 31969 (SAR); G. Matang, 1929, Clemens 20927 (NY, SAR). Div. 2: Kg. Pungor Tapang, path to Kg. Kara, *Ilias S 42731* (SAR). Div. 4: Hulu Luak, Sg. Setap road, 16 May 1964, Othman Haron S 68091 (K, L, SING); Tatau, Tau Range, Bt. Mersing, Anap, 30 May 1956, Purseglove P 5191 (SAR). Div. 5: Tg. Long Amok, Sg. Ensungai, on slope of ridge, 11 September 1980, Rena S 42825 (L, SAR). Div. 7: Batang Baleh, low elevation, 4 June 1929, Clemens 21273 (NY).

King (1892) based this species on three specimens. One of these (*Motley 960*) was from Borneo and was the only flowering specimen available at that time. The species was excellently illustrated in his masterpiece (1893) and the description and illustration have been used as a basis of reference by later authors in delimitation of this and related species. These are *G. parallelivenius* Ridl., *G. giganteus* Merr., *G. dolichocarpus* Merr. and *G. cylindrostigma* Airy Shaw. It has not been clear if these species are merely variants of *G. uvarioides*. The latter is widespread and has leaves that are quite variable. Because there has been no concise documentation on differences among these species, the specimens in many herbaria have been wrongly identified and considerably mixed up.

Upon careful examination of available specimens and my own field experience, I have decided that there are enough differences to warrant recognition of all the species named in the preceding paragraph. Based on King's illustration of fruiting carpels, I believe there is no doubt that *G. uvarioides* does occur in Borneo. These plants have rusty glabrous, green outer petals nearly as long as the inner ones. Some specimens have been called *G. suaveolens* Becc., an unpublished name. In addition to the species noted above, two more species (*G. kostermansii* and *G. kinabaluensis*) are added to this alliance as new taxa.

Although all these species share common traits in which their stamens are large and strongly apiculate and they have large cylindrical pubescent ovaries with numerous ovules and erect, cylindrical glabrous styles, they have quite a diverse combination of fruit types and inner petal structures. The leaves are variable in size and texture (thus the epithets of two of the species are misleading and meaningless), but they nevertheless show some observable trends. As an example, in *G. parallelivenius* the fruit is somewhat globose and the leaves are less coriaceous and with more prominently percurrent tertiary veins than in *G. uvarioides*. The diversification from a somewhat coriaceous leaf reaches its climax in *G.*

percurrent that they resemble G. curtisii rather than G. uvarioides, as noted by Merrill (1915). Nevertheless, the fruits of G. gigantifolius are intermediate between G. dolichocarpus and G. uvarioides. The inner petal dome of G. gigantifolius is also different from the mainstream architecture of other species in this alliance. The same diversification is noticable in G. kostermansii, but in this case the fruits are perhaps the largest of any fruits of Annonaceae in Borneo. In contrast, fruits of G. dolichocarpus are among the thinnest.

The status of G. cylindrostigma has been especially difficult to determine. It differs from G. parallelivenius in that it has narrowly oblong-linear leaves and fewer secondary veins. The tertiary veins in leaves of G. cylindrostigma are random-reticulate and the outer petals are smaller. Goniothalamus cylindrostigma has the same globose carpels as those found in G. parallelivenius and could represent a montane variant of the latter species. However, I hesitate to combine the taxa because materials for G. cylindrostigma are very limited. There are numerous other cases in which montane populations of Goniothalamus with leaves similar to those of common lowland species have other important distinguishing characters.

16. Goniothalamus dolichocarpus Merr., J. Straits Branch Roy. Asiat. Soc. 85: 183.

1922.—Type: SABAH. Sandakan and vicinity, 20 September 1920, *Ramos*1259 (holotype: PNH, destroyed; lectotype, designated here: K!).

Monocaulous treelet or small shrub, 1 to 3 m high, stem ca. 2 cm in diameter, glabrous, branches grayish or brownish, drying black, smooth, sometimes cylindrical. Leaves 23–40 cm long, 5–12 cm wide, oblanceolate, oblong-oblanceolate, obtusely acuminate, the base cuneate-acute, rarely rounded,

subcoriaceous, grayish and shining on both surfaces when dry; venation consistently brochidodromous; primary vein sunken above, with fine groove, large and strongly raised beneath, rounded; secondary veins in 24–30 pairs, constantly sunken on upper side, raised and very prominent beneath, straight and nearly parallel with each other, anastomosing with loops 5-7 mm from the margin; intersecondary veins common, simple; tertiary veins inconspicuous; petiole 1-2 cm long, slightly inflated, blackish, glabrous. Flowers mostly cauliflorous, sometimes axillary on old twigs, solitary; pedicel ca. 1.5 cm long, with several minute triangular basal bracts, pubescent; sepals ca. 1 cm long, 1.3 cm wide, broadly ovate, conspicuously acuminate, somewhat pubescent; outer petals ca. 3 cm long, 1 cm wide, oblong-lanceolate, narrowed upward, slightly acuminate, coriaceous, somewhat pubescent on both sides; inner petals ca. 2 cm long, 1 cm wide, oblonglanceolate, cinereous pubescent on both surfaces, except on the base inside, the base slightly vaulted and distinctly clawed; stamens numerous, 3-4 mm long, oblong-linear, connective apiculate-rostrate; ovaries about 10, 3 mm long, cylindrical, pubescent; ovules 6; styles equaling the size of the young carpels, cylindrical; stigmas crateriform, smooth. Fruiting pedicel ca. 2 cm long, carpel stalks ca. 0.7-1 cm long; mature carpels 2-4 on each torus, 6-11 cm long, 1.5 to 2 cm in diameter, linear-nodiform, acuminate, base cuneate, yellow when fresh, dark brown or gray when dry, glabrous, seeds 4 to 9.

Vernacular name: Merrill (1922) noted that the vernacular name for this species is babancoan, without indicating the ethnic group.

Distribution (Figure 53). Endemic to Borneo, in thickets and forests along small streams at low elevations.

ADDITIONAL SPECIMENS EXAMINED. SABAH. Res. Sandakan: Labuk & Sugut, Sg. Ruku-Ruku, Telupid, 5 August 1981, Aban SAN 94011 (SAN); Labuk & Sugut,

Paitan Forest Reserve, hillside, black soil, 27 January 1963, Ampuria SAN 32769 (SAN); Sandakan and vicinity, September-December 1920, Ramos 1259 (BO, K); Ramos 1654 (BO); Ramos 1692 (A, US); 22 June 1922, Ramos 1879 (B); Sandakan, Kebun China Forest Reserve, Sibuga, 19 October 1961, Jaswir SAN 27473 (SAN); Sandakan, Mile 47, Labuk Road, Lokan Forest Reserve, on hillside, sandy soil, 28 July 1964, Imran SAN 40054 (SAN); Sandakan, along jalan sp. 17 cpt. 12, Sepilok Forest Reserve, 21 October 1966, Sam SAN 57489 (SAN); Sandakan, Sandakan-Sibugey, 24 November 1920, Ramos 1623 (A, K); Sandakan, Sepilok Forest Reserve, trail to beach, riverine, 31 December 1988, Mat-Salleh KMS 2819 (UKMS).

This distinctive species is characterized by having slender elongated fruiting carpels, usually in pairs. As noted by Merrill (1922), this species resembles G. macrophyllus in leaf texture and shape, but it can be easily distinguished by its solitary, cauline flowers and greatly elongated cylindrical fruits.

17. Goniothalamus gigantifolius Merr., Philipp. J. Sci. 10: 263–264. 1915.—Type:

PHILIPPINE IS., Basilan, near Singal, ca. 160 m, 26 September 1912, Miranda

For. Bur. 18958 (holotype: PNH, destroyed; lectotype, designated here:

US!).

Tree 3–10 m high, stem whitish gray, slightly fissured, twigs glabrous, cylindrical, striate, light green, blackish when dry. Leaves 25–60 cm long, 8–20 cm wide, oblanceolate, mucronate-acute, base acute or slightly rounded, chartaceous, glabrous on both sides, shining when dry; venation brochidodromous; primary vein sunken above, with fine groove, large and strongly raised beneath; secondary veins in 17–33 pairs, raised and very prominent on both sides, straight and parallel

with each other, the marginal veins looping very close to the margins (ca. 2 mm from the margins); intersecondary veins simple; tertiary veins weakly percurrent, prominent on both sides; petiole up to 3 cm long, stout, inflated, blackish, glabrous. Flowers cauliflorous, pedicel 2 cm long, thin, with 2–several minute triangular basal bracts; sepals green, 8 mm long, ca. 5 mm wide, ovate, acute, slightly pubescent; outer petals 5–5.5 cm long, 1 cm wide, lanceolate, acute, base rounded or flat, slightly clawed, coriaceous, reddish pubescent; inner petals 3 cm long, 1.3 cm wide, ovate, strongly clawed at base, pubescent on both sides; stamens large, 5–7 mm long, connectives strongly apiculate-rostrate, glandular pubescent; ovaries 2 mm long, pubescent; ovules 5–6; styles 3 mm long, glabrous, cylindrical, straight, grooved; stigma crateriform. Fruiting pedicels 1.5 cm long, carpel stalks about as long, brown pubescent; carpels 2.5–4.5 cm long, 1–2.5 cm in diameter, 5–20 on each pedicel, thinly nodiform, strongly acuminate-rostrate, base acute, dark brown when dry, sparingly pubescent, pericarp thin, seeds 2, rarely 3.

Vernacular name. Tali panas (Dusun).

Distribution (Figure 53). Hillsides, ridgetops, in lowland dipterocarp forest up to 800 m elevation in eastern Sabah and nearby islands.

ADDITIONAL SPECIMENS EXAMINED. SABAH. Res. Pedalaman: Trus Madi Range, Kg. Sinoa, on ridge top, Trus Madi formation, 850 m, 14 November 1987, Mat-Salleh KMS 1949 (UKMS). Res. Tawau: Lahad Datu, Danum Valley (Sg. Segama Forest Reserve); 3 June 1986, Campbell SAN 111862 (SAN, UKMS); Lahad Datu, Danum Valley (Sg. Segama Forest Reserve), September 1985, Campbell SAN 112122 (SAN, UKMS); Lahad Datu Road, 20 August 1978, Termiji SAN 88648 (SAN); Sepagaya, Temenggung, hillside, 14 July 1961, Muin Chai SAN 18375 (SAN); Segama, Hulu Bole, hillside, 5 August 1961, Muin Chai SAN 25979 (SAN); Tawau, Apas-Mostyn, Japanese Track, 16 October 1950, Simbut A 1631 (K); Tawau Hills

Park, near Hq., quaternary dacite lava, dipterocarp forest, 300-400 m, 15-16 June 1984, Beaman 10177 (MSC, NY).

This remarkable species was described by Merrill from Basilan Island of the Philippines just slightly northeast of Sabah. It comes as no great surprise that the species is common on Sabah's east coast area around Lahad Datu and Tawau. The species is close to *G. uvarioides* but differs in many aspects of its petals, fruits and leaves. The petals are prominently reddish pubescent and ovate rather than rusty glabrous and lanceolate as in *G. uvarioides*. The inner petals, unlike other species of the *G. uvarioides* alliance, form a relatively much broader and shorter dome. The fruiting carpels of this species are apiculate-rostrate, and the carpel stalks and pedicels are much thinner. These fruiting features have not been observed in any other species in the *G. uvarioides* alliance. The leaves are also very chartaceous, with prominently percurrent tertiary veins that resemble the Peninsular Malaysian *G. curtisii* rather than *G. uvarioides*. Merrill erroneously associated this species with *G. curtisii*, but had flowers been available to him, he surely would have recognized its affinity with *G. uvarioides*.

18. Goniothalamus kostermansii Mat-Salleh, sp. nov.—Type: KALIMANTAN. East Borneo, Berouw, G. Ilas Bungaan, 400 m, sandstone ridge, 17 November 1957, Kostermans 13926 (holotype: US!; isotype: BO!)

Goniothalamus uvarioidi King et Goniothalamus kinabaluensi Mat-Salleh affinis, sed haec species fructiferis carpellis magnis arienoidibus, 8–10 cm longis, 2.5 cm latis, anguste oblongis, cristiformibus, apice inflexe-rostrato, a speciebus nobis

bene notis distincta, foliis obovatis tenuiter chartaceis et nervis subter eminentis, nigratis.

Tree 8–10 m high, 15–20 cm dbh, bark smooth, dark brown, living bark 2 cm thick, brown, wood yellowish, branches horizontal, twigs glabrous, striate. Leaves 16-25 cm long, 6-8 cm wide, obovate, at times oblanceolate, acuminate, base acute to somewhat rounded, chartaceous; venation consistently brochidodromous; primary vein sunken above, raised below, glabrous on both sides; secondary veins in 10 to 14 pairs, inconspicuous on upper surface, conspicuously yellowish green beneath, anastomosing to form consistently looped intramarginal veins at ca. 3 mm from the margins; intersecondary veins numerous, simple; tertiary veins prominent on both sides, weakly percurrent; petioles ca. 1 cm long, blackish. Flowers solitary, supra-axillary (just above petiole) or cauliflorous on the upper part of the stem; pedicel thin, ca. 2 cm long, with 4-6 triangular basal scales; sepals 5 mm long, 7 mm wide, ovate, apex rounded, base free, dirty dark purple; petals greenish, outer petals 2.5 cm long, ca. 0.5 cm wide, lanceolate, sharply acute, base rounded; inner petals 2 cm long, 0.7 cm wide, lanceolate, velvety pubescent on both sides, clawed; stamens numerous, ca. 5.5 mm long, linear, yellowish, connective caudate; ovaries large, cylindrical-obclavate, long and slender, 4 mm long, 0.75 mm wide, oblong, pubescent; ovules numerous; styles massive but short, more or less the same diameter as ovary, ca. 1.5 mm long, upright, slightly curved, tubular with longitudinal slit on the inside, glabrous; stigma integral, indistinguishable from style. Fruiting pedicel ca. 3.5 cm long, carpel stalks ca. 0.7-1 cm long; carpels 8–10 cm long, 2.5 cm wide, banana-like, cylindrical, apex rostellate and curved to the adaxial side, with prominent ridges, crested abaxially, green, seeds ca. 10, pressed tightly against each other. Figure 54.

Vernacular name. Kostermans noted on the label the name as "Banitan". I am not sure what language this involves, but probably a local dialect.

Figure 54. Representative specimen of Goniothalamus kostermansii (Kostermans 5133, A).



Distribution (Figure 55). Known only from two collections from eastern Kalimantan.

ADDITIONAL SPECIMENS EXAMINED. KALIMANTAN. Kalimantan Timur: East Kutai, Sangkulirang, at Sg. Manumbar region, ridge, loam soil with lime, 11 June 1951, Kostermans 5133 (A, BO).

This species is close to both *G. kinabaluensis* and *G. uvarioides* but quite distinct from these species in its large "banana-like" cylindrical fruiting carpels. These are 8–10 cm long, 2.5 cm wide and have prominent ridges and a massive incurved beak. The texture of the leaves resembles that of *G. kinabaluensis* but the leaves are much larger.

This species is dedicated to Dr. A.J.H. Kostermans, who obtained excellent specimens of it in 1957. He indicated that the species was common on G. Ilas Bungaan. Only the holotype bears flowers. This specimen has five immature flowers, one of which is nearly fully developed and has been used for the description.

19. Goniothalamus kinabaluensis Bân ex Mat-Salleh, sp. nov.—Type: SABAH.
Mount Kinabalu, Penibukan, 4000–5000 feet, small tree below camp, jungle hillside, 1 February 1933, Clemens 31235 (holotype: BM!; isotypes: A! NY!)

Goniothalamus uvarioidi King ut videtur affinis, sed foliis oblongis dimidiis vel 3plo minoribus, chartaceis vel subcoriaceis differt. Petala exteriora simile brevia, petalaque interiora exterioribus aequalia vel pauce breviora.

Small monopodial treelet 3–5 m high. Stem and twigs dark greenish-blackish, striate, sapwood yellowish. Leaves (10–) 17–34 cm long, (3–) 4–7.5 cm wide,

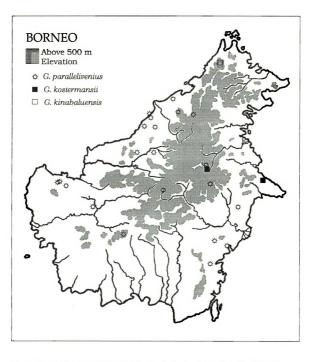
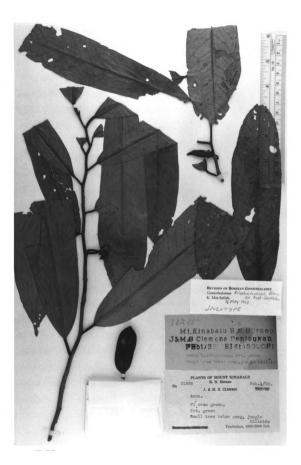


Figure 55. Distribution of G. parallelivenius, G. kostermansii and G. kinabaluensis.

oblanceolate-oblong, rarely elliptic, acuminate, the base acute to somewhat rounded, chartaceous, rarely subcoriaceous; venation consistently brochidodromous; primary vein sunken above, raised below, glabrous on both sides; secondary veins in 17 to 20 pairs, slightly raised on the upper surface, conspicuous beneath, anastomosing to form loosely looped intramarginal veins extending to ca. 2-3 mm from the margins; intramarginal veins often very inconspicuous; intersecondary veins numerous, simple; tertiary veins prominent on both sides, random-reticulate, seldom percurrent; petioles 1.2–1.5 cm long, 3 mm in diameter, blackish, slender, with no noticeable thickening. Flowers single, supra-axillary (just above petiole) or cauliflorous on the upper part of the stem, pedicel 1-1.5 cm long, thin, with 4-6 triangular basal scales; sepals 6 mm long and wide, ovate-triangular, acute, slightly connate at base; petals cream-green, inner and outer petals of more or less equal size, or the outer slightly longer, 2-2.5 cm long, ca. 0.5 cm wide, oblong, blunt-acute, base rounded; inner petals 1.6-2 cm long, lanceolate, velvetly pubescent on both sides, base yellowish, clawed; stamens numerous, 2.5–3 mm long, laminar, oblong, yellowish, connectives caudate, pubescent; ovaries large, 3 mm long, oblong, pubescent; ovules 5-10; styles massive, more or less the same diameter as ovary, ca. 2 mm long, upright, tubular with longitudinal slit inside, glabrous; stigma crateriform. Fruiting pedicel short, 1.5-2 cm long, carpel stalk ca. 0.5 cm long; carpels ca. 3-4 cm long, 1.5-2 cm wide, normally oval, rarely globose, apex rounded or slightly blunt-acute, greenish, turning black when dry, glabrous, seeds 2-6, globose, wrinkled, with yellow pubescent ridges. Figure 56.

Distribution (Figure 55). Known only from the Tenompok and Penibukan areas of Mount Kinabalu at 1300 to 1500 m elevation.

Figure 56. The holotype of Goniothalamus kinabaluensis (Clemens 31235, BM).



ADDITIONAL SPECIMENS EXAMINED. SABAH. Mount Kinabalu, 1933, Clemens s.n. (A, BO, BM, NY); Mount Kinabalu, Penibukan, 4000–5000 ft, 4 January 1933, Clemens 30638 (BO, NY); 17 March 1933, Clemens 32199 (BM, NY); 26 September 1933, Clemens 40441 (BM, NY); 30 September 1933, Clemens 40519 (A, BM); Tenompok Forest Reserve, along trail to hill summit, 15 August 1988, Mat-Salleh KMS 1450 (UKMS); Tenompok Forest Reserve, near waterfall, 4 December 1988, Mat-Salleh KMS 2813 (UKMS).

This species strongly resembles G. uvarioides in floral and fruit characteristics but has much smaller and thinner leaves with prominent, mostly random-reticulate tertiary veins, not percurrent as in G. uvarioides. The petiole is also blackish when dry and slender. The mature flowers of this species are much smaller than those of any other species in the G. uvarioides alliance.

The unpublished name *G. kinabaluensis* was used by Nguyen Tien Bân, who annotated many specimens at NY, with several specimens designated as types ("holotype" for *Clemens 30638*, "paratype" for *Clemens 32111*). It is possible that Bân was not sure if this local population was distinct enough to warrant recognition of a new species, because the flower is very similar to that of *G. uvarioides*. However, this species has several strong characters that make it easy to recognize, even in sterile condition. When I first found it in the field, I knew that it was not *G. uvarioides* (which also occurs in the same area). The type locality is within easy driving distance from Kota Kinabalu, and we visited the same flowering tree several times in 1988 to observe its phenology as well as to obtain mature flowers and fruits.

20. Goniothalamus cylindrostigma Airy Shaw, Kew Bull. 1939: 285. 1939.—Type: SARAWAK. Near Long Kapa, Mount Dulit (Hulu Tinjar), IVth Division. River bank forest, under 300 m, 31 August 1932, Native collector, Richards 1334 (holotype: K!)

Tree up to ca. 5 m high, 10–15 cm dbh, twigs cylindrical, bark pale, glabrous, aromatic. Leaves 50-65 cm long, 6-10 cm wide, narrowly oblong or slightly oblanceolate, chartaceous or subcoriaceous, slightly bullate, shining olive green above, slightly reddish beneath, shortly acuminate, base rounded; venation brochidodromus; primary vein stout, slightly sunken above, raised and slightly triquetrous beneath; secondary veins in 19-24 pairs, inconspicuous on the upper surface, very prominent beneath; intersecondary veins numerous, simple and long; tertiary veins prominent on both sides, random-reticulate, very seldom percurrent; petiole ca. 1 cm long, 0.5 cm in diameter, inflated, glabrous. Flowers solitary or cauliflorous; pedicel 1-1.5 cm long, glabrous, brownish; sepals connate at the base, deltoid, acute, puberulous; outer petals 3.5-4.5 cm long, ca. 1 cm wide, narrowly lanceolate, sharply acute, base rounded, minutely puberulous; inner petals 2.5–3 cm long, ca. 1 cm wide, lanceolate, tomentose outside, velvety tomentose inside; stamens 3 mm long, connective caudate, pubescent; ovaries large, ca. 2 mm long, pubescent; ovules 2; style 3.5 mm long, erect, straight, vaginiform, with lateral slit, glabrous; stigma crateriform, slightly convoluted. Fruiting pedicels ca. 2 cm long, carpel stalks very short, less than 5 mm long, slightly rusty pubescent; carpels numerous, 1-2 cm in diameter, globose, obtuse, base acute, red-brown when dry, sparingly pubescent, seeds 1.

Distribution (Figure 53). Endemic to high elevation forests in the Hulu Baram area in Sarawak. Growing in alluvial soil at foot of limestone hills or on sandstone ridges.

ADDITIONAL SPECIMENS EXAMINED. SARAWAK. Div. 4: Hulu Tinjar, G. Dulit, primary forest on ridge, under 300 m, 31 August 1932, Richards 1553 (K). G. Mulu National Park, 9 April 1978, Argent et al. 943 (SAR); G. Mulu National Park, G. Benarat, alluvial soil at foot of limestone hill, 10 July 1961, Anderson 4339 (A, K, L); G. Mulu National Park, Tutoh, Melinau Gorge, sandstone ridge, 23 June 1962, Chew CWL 441 (A, SING).

This species was described by Airy Shaw based on two specimens collected by the Oxford University Expedition to Sarawak in 1932. As noted by Airy Shaw, it is very close to *G. uvarioides* but differs considerably not only in leaf shape and venation pattern, but also in inner and outer petal shapes. However, I cannot agree with him that the stigma of this species is unique. Large, glabrous, upright cylindrical or tubular styles with longitudinal slits and crateriform stigmas are among the best distinguishing characters for species of the *G. uvarioides* alliance. It is unfortunate that this characteristic was chosen for the specific epithet of the species. The stamen connective is also typical of species in the *G. uvarioides* alliance.

Some of the younger leaves can be quite large, but they retain the characteristics of the unique venation pattern, especially with distant secondary veins and random-reticulate tertiaries. The leaf is also recognizable by its bullate surface and narrowly oblong shape with strongly cordate base.

21. Goniothalamus parallelivenius Ridl., Kew Bull. 1912: 385. 1912.—Type: Sarawak, 1865–1868, *Beccari 3772* (holotype: K!).

Tree ca. 5–10 m high, stem with light brown, smooth, glabrous bark, twigs glabrous, cylindrical, young ones blackish, triquetrous, glabrous. Leaves 25-60 cm long, 8-20 cm wide, oblanceolate, mucronate-acute, base rounded-cordate, thinly coriaceous-chartaceous, glabrous on both sides; venation brochidodromous; primary vein sunken above, with narrow groove, large and strongly raised beneath; secondary veins in 30-38 pairs, raised and very prominent on both sides, straight and parallel with each other, the marginal veins looping very close to the margins (2-5 mm from the margins); intersecondary veins simple, common; tertiary veins weakly percurrent, prominent on both sides; petiole up to 3 cm long, stout, inflated, blackish, glabrous. Flowers cauliflorous, pedicel 2.5 cm long, with 2several minute ovate basal bracts; sepals orange, 1 cm long, 1 cm wide, ovate, blunt-acute, slightly rusty orange pubescent; outer petals ca. 6.5 cm long, 1 cm wide, oblong, blunt-acute, base rounded or flat, slightly clawed, orange rusty pubescent; inner petals 4 cm long, 1.3 cm wide, lanceolate, strongly clawed at base, rusty pubescent outside, brown pubescent inside; stamens large, 3-5 mm long, linear, connective strongly apiculate-rostrate, glandular pubescent; ovaries 2 mm long, cylindrical, pubescent; ovules 5-10; styles 3 mm long, glabrous, linear, straight, grooved; stigmas crateriform. Fruiting pedicels 4 cm long, carpel stalks very short, less than 5 mm long, slightly rusty pubescent; carpels numerous, 1.5 cm in diameter, ca. 20 on each pedicel, globose, obtuse, base acute, dark brown when dry, sparingly pubescent, pericarp thin, seeds 1, rarely 2.

Distribution (Figure 55). Endemic to Borneo, common in riverine forests.

ADDITIONAL SPECIMENS EXAMINED. KALIMANTAN. 1896, Teijsmann s.n. (BO); 28 June 1960, Djoemadi 66 (BO); 3 April 1924, Niniek 595 (BO); 28 October 1928, van Hooten 2151 (BO); 7 November 1928, van Hooten 2294 (BO); Bt. Tjihan, 10 December 1898, Amdjah 296 (BO); Sg. Magna, 1896–1897, Jaheri 660 (BO). Kalimantan Barat: Sg. Kenepai, 1893–1894, Hallier 2014 (BO); G. Nap, north of Kg. Semame, Bantiang, 7 November 1980, Shea SAN 27792 (BO). Kalimantan Tengah: Upper Katingan, Bt. Raya, 26 November 1982, Nooteboom 4035 (BO); Upper Katingan, Bt. Raya, 17 December 1961, Nooteboom 4339 (BO). Kalimantan Timur: Sg. Wain, September 1950, Kostermans 4440 (BO); Sg. Wain, September 1950, Kostermans 4555 (BO); Tanah Gerogot, Desa Kasungai, 28 November 1979, Afandi 239 (BO); Wanariset, 28 September 1979, Afriastini 81 (BO); Mahakam Hulu, 26 June 1975, Wiriadinata HW 634 (BO); G. Kutai, Sg. Kerajaan, 21 July 1951, Kostermans 5862 (BO); Sg. Membunut Besar, N of Tarakan, 20 November 1953, Meijer 2292 (BO); West Kutai, G. Kemoel (Kongkemul), 1925, Endert 2706 (BO); G. Kapor, January 1976, Soedarsono 807 (BO). Kalimantan Selatan: Jaro Dam, 10 km northeast of Muara Uya, 13 November 1971, de Vogel 762 (BO). SARAWAK. Div. 1: Semenggoh Forest Reserve, 14 October 1966, Banyeng S 26290 (SAR); Tiang Bekap, 5 June 1960, Anderson S 12547 (SAR); Sg. Sabal Tapang, July 1960, Anderson SAR 69 (SAR). Div. 4: Tinjar, Long Kerangan, Hulu Sg. Sekiwa, 29 August 1974, Tong S 34949 (SAR); G. Mulu National Park, Tutoh, G. Api, 4 October 1971, Anderson S 31782 (E, SAR, SING); Lebang, 26 November 1924, Winkler 365 (BO); Sg. Niah, Hulu Sg. Sekaloh, 5 January 1966, Sibat S 26121 (K, SAR); Hulu Luak, Sg. Setap road, 16 May 1964, Othman Haron S 21322 (SING); Suai, Hulu Sg. Sibai, 20 July 1977, *Ilias S 39149* (SAR). Div. 7: Linau-Balui, 2 September 1978, Burt 11403 (E, SAR); Punan Busang, 16 June 1971, Geh & Samsuri 504 (SING); Batang Baleh, 12 April 1964, Othman Haron S 19912 (SAR).

This species is remarkable in having large narrowly oblong-linear outer petals, similarly large inner petals, globose fruiting carpels with a single seed, and short carpel stalks. The leaves are very similar to those of *G. uvarioides*. The tertiary veins in the leaf of *G. uvarioides* are not consistently percurrent, as can be observed in the leaves of this species. A mixture of both percurrent and random-reticulate patterns occurs in *G. uvarioides*.

Goniothalamus macrophyllus Alliance

22. Goniothalamus macrophyllus (Blume) Hook. f. & Thomson, Fl. Ind. 1: 109 in nota, 1855.

Unona macrophylla Blume, Bijdr. 17. 1825.—Type: JAVA, "in montium declivitatibus" Blume s.n. (holotype: L, n.v.). Polyalthia macrophylla (Blume) Blume, Fl. Javae 79, t. 39. 1830.

Shrub or small tree 5–15 m high, stem and twigs whitish, smooth, glabrous. Leaves 20–37 cm long, 6–12 cm wide, oblong-oblanceolate, apex acuminate, base rounded-acute, coriaceous, both surfaces glabrous; venation eucamptodromous-brochidodromous; primary vein sunken above, grooved, raised beneath, rounded; secondary veins in 15–30 pairs, sunken above, prominent and raised beneath, straight and nearly parallel with each other; intersecondary veins numerous, inconspicuous, simple; tertiary veins random-reticulate, inconspicuous; petiole stout and short, ca. 1 cm long, glabrous, blackish. Flowers solitary, cauliflorous or ramuliflorous on older branches; pedicel short, ca. 1 cm long, with several minute triangular basal bracts; sepals 0.5 cm long, ca. 1 cm wide, very shallowly triangular, apex acuminate, connate at base, green, slightly pubescent; outer petals ca. 2 cm

long, 1 cm wide, lanceolate, acute to slightly acuminate, coriaceous, pinkish green-yellowish; inner petals half the length of the outer petals, ovate, apex acute-acuminate, clawed at base; stamens 3–5 mm long, connective sharply acute to slightly acuminate, pubescent; ovary obclavate, glabrous; ovules single, basal; styles 3 mm long, pubescent-puberulous, linear, cylindrical, grooved; stigma funnel-shaped. Fruiting pedicels short, stout, ca. 1.5 cm long, normally with sepal remnants; carpels sessile, 1–1.5 cm long, ca. 1 cm in diameter, globose, apex rounded, base rounded, seed 1.

Distribution (Figure 57): Common and widespread in Thailand, Peninsular Malaysia, Sumatra and Java. In Borneo the species is normally found in lowland mixed dipterocarp forest at 100–400 m.

ADDITIONAL SPECIMENS EXAMINED. KALIMANTAN. Kalimantan Selatan: Jaro Dam, 10 km NE of Muara Uya, 24 November 1971, Kartawinata 967 (A, K, L). SARAWAK. Div. 1: Kuching, May 1893, Haviland 2033 (K); Div. 2: Lingga, G. Lesung, 26 November 1981, Lee S 43233 (SAR).

Sterile specimens of this species are not easy to distinguish from specimens of the *G. uvarioides* alliance. Even when flowers and fruits were available, there have been many misdeterminations. Specimens of *G. uvarioides* often have been incorrectly determined as *G. macrophyllus*, even when the inner petals clearly exhibit the unique characteristics of the former species. The two are easy to distinguish on the basis of floral and fruit characters. Their differences are summarized below:

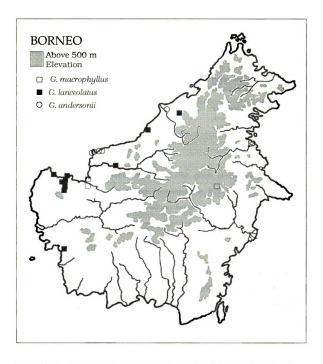


Figure 57. Distribution of Goniothalamus andersonii and of G. macrophyllus and G. lanceolatus in Borneo.

	G. macrophyllus	G. uvarioides
Outer petals	Lanceolate, short, 2 cm long	Lanceolate-oblong, long, 3.5–4.5 cm long
Inner petals	Ovate, short, about half the length of the outers	Lanceolate-oblong, long, about two-thirds the length of the outers
Stamen connectives	Type 2	Type 1
Style and stigma	Style pubescent, stigma bilobed	Style smooth, sigma crateriform
Fruit	Carpels globose, sessile, ca. 1.5 cm long, seed 1.	Carpels mostly nodiform, 4-5 cm long, seeds 4-5.

23. Goniothalamus lanceolatus (Bân) Mat-Salleh, comb. et stat. nov.;

Goniothalamus macrophyllus var. lanceolatus Bân, Bot. Zhurn. (Moscow & Leningrad) 59(4): 670. 1974.—Type: SARAWAK. Mount Poi, 6000 ft, high ridge, 9 September 1929, Clemens 20357 (holotype: NY!; isotypes: BO! MO!).

Shrub or small monocaulous treelet 3–7 m high, stem and twigs whitish gray, fissured. Leaves 15–50 cm long, 4–7 cm wide, lanceolate-oblanceolate-oblong, rarely elliptic (especially when small), acuminate, base rounded-acute, cordate at times, subcoriaceous-coriaceous, both surfaces glabrous; venation brochidodromous; primary vein sunken above, grooved, raised beneath, rounded; secondary veins in 15–30 pairs, prominent beneath, straight and nearly parallel with each other, anastomosing with loops ca. 5 mm from the margin; intersecondary veins numerous, simple; tertiary veins random-reticulate,

inconspicuous; petiole stout and short, ca. 1 cm long, glabrous, blackish. Flowers light green to white, fragrant, cauliflorous or ramuliflorous on older branches, axillary; pedicel short, ca. 1 cm long, with several minute triangular basal bracts; sepals 0.5–1 cm long, ca. 0.5 cm wide, ovate, green, apex acute, slightly pubescent; outer petals 1–2 cm long, 1 cm wide, ovate-lanceolate, apex acute to slightly acuminate, base spatulate, clawed, single-veined, coriaceous, light green-yellowish, inconspicuous; inner petals half the length of the outer, ovate, apex acute-acuminate, clawed at base, slightly puberulous outside, rusty pubescent inside; stamens 3–5 mm long, connective strongly apiculate, apex pubescent at top, glandular at base, the projecting column surrounded by a ring-like base; ovaries obclavate, glabrous; ovule single, basal; styles 3 mm long, pubescent-puberulous, linear, cylindrical, grooved; stigma funnel-shaped; fruiting pedicel short, stout, ca. 1 cm long, normally with sepal remnants, carpel stalks short, less than 2–3 mm long; carpels 1–1.5 cm long, ca. 1 cm in diameter, fusiform, apex rounded or apiculate, base acute, seed 1, yellowish.

Distribution (Figure 57). Kalimantan, Sarawak and Sumatra. In Borneo the species grows as an understory treelet on ridges in rich soil in forests at 100–600 m, but some populations occur on mountain tops at 1000–2000 m.

ADDITIONAL SPECIMENS EXAMINED. KALIMANTAN. Kalimantan Barat: Pontianak, G. Palong Nature Reserve, ca. 100 km S of Pontianak, ridge forest with many Myrtaceae and Sapotaceae, few Agathis, 12 June 1986, van Balgooy & van Setten 5385 (A). SARAWAK. Div. 1: Bako National Park, 1 September 1977, Stone 13504 (KLU); Bako National Park, near beginning of Jalan Lintang trail, just above mangrove swamp under dense canopy, 21 April 1984, Rogstad 689 (A); Bako National Park, Tanjung Po headland, 20 May 1981, Yii Puan Ching S 42160 (SAR); Bau, Bidi Cave, low elevation, limestone, 21 October 1929, Clemens 20691 (NY);

Bau, Bt. Gebong, 10 June 1967, Anderson S 27653 (SAR); Bau, Seburan, between Seburan and Bt. Krian, 15 July 1964, Anderson S 20259 (SAR); Serian, G. Penrissen, 29 April 1962, Ilias S 16370 (SING); Kuching, Semenggoh Forest Reserve, Arboretum, near tree No. 190, primary lowland forest, 1 July 1960, Asah S 12757 (SAR); Lundu, G. Gading, October 1929, Clemens 22269 (NY); 17 August 1960, Sinclair 10379 (E, US). Div. 3: Kanowit, G. Poi, by upper cave, 18–20 September 1929, Clemens 20022 (K, NY); Kanowit, G. Poi, 4500 ft, mountain side, by great forest rock, 29 September 1929, Clemens 20356 (A, K, NY, SAR). Div. 4: Miri, Lambir Hills National Park, Burt & Woods 2466 (E, L, SAR).

This species closely resembles *G. macrophyllus* and it could be argued that it should be included in that variable and widespread species. However, the fruits of this species, even young ones, have stalked fusiform and slightly rostellate carpels that I have not seen in *G. macrophyllus* specimens. In fact, some of the *G. macrophyllus* material (i.e. *Chan FRI 6798*, Peninsular Malaysia, Kedah, Pulau Langkawi, Ma-Chinjang Forest Reserve, 16 March 1969) have similar leaves but the carpels are sessile.

When describing this as a new variety (G. macrophyllus var. lanceolatus), Bân (1974) noted that the taxon has "glabrous styles". After examining the type material, I cannot agree that the styles are totally glabrous. It is true, however, that they are considerably less hairy than the styles of G. macrophyllus.

My decision to keep G. lanceolatus separate from G. macrophyllus may not be agreeable to some, but it is congruent with the concept of species in this genus. There are many other closely allied species with similarly coriaceous leaves, such as G. sesquipedalis and G. wrayi, that have been mantained by various authors. On one of the G. lanceolatus specimens collected by Sinclair in Sarawak (Sinclair 10379), he

noted "sp. nov., aff. wrayi", supporting my contention that in many cases the variations are not trivial once the species are seen in the field.

This species is indeed close to G. wrayi as suggested by Sinclair, but differs in having narrowly lanceolate rather than broadly oblong leaves as in G. wrayi.

Goniothalamus lanceolatus resembles G. sesquipedalis but differs in stamen and style features. As a member of the G. macrophyllus alliance, it has some characteristics of G. macrophyllus as well.

24. Goniothalamus andersonii J. Sinclair, Gard. Bull. Singapore 18: 98–100.

1961.—Type: BRUNEI. Seria, Shorea albida swamp, 18 April 1957, Smythies,

Wood & Ashton S 5901 (holotype: SING!; isotypes: BO! SAR!).

Tree 10–15 m high, bark dark brown, smooth. Twigs dark brown-blackish, striate, glabrous. Leaves 12–21 cm long, 5–8 cm wide, elliptic-oblong, rarely oblong, apex blunt-apiculate, base somewhat cuneate; venation eucamptodromous; primary vein sunken and grooved above, raised beneath, coriaceous, often glossy above, paler and dull beneath; secondary veins in 10–14 pairs, prominent on both sides; tertiary veins random-reticulate; petiole 1.5–2 cm long. Flowers solitary, axillary; pedicels slender, ca. 1 cm long, with few minute triangular basal bracts, glabrous; sepals ca. 7–10 mm wide, 7 mm long, coriaceous, orbicular with blunt apex and conspicuosly clawed base; outer petals 4 cm long, 1 cm wide, coriaceous, lanceolate, narrowed upward, and drawn into a long acumen, broad at base, pale cream to bright yellow, puberulous; inner petals ca. 1 cm long, 0.5 cm wide, ovate, tomentulose outside, rusty pubescent inside; stamens numerous, 5 mm long, connective broadly acute, apex sparsely tomentulose mostly at top, glabrous on the lower half; ovaries about 2.5–3 mm long, obclavate,

glabrous with pubescence mostly at the base; ovules mostly 2; styles 3 mm long, pubescent-puberulous, linear, cylindrical, grooved; stigma funnel-shaped, smooth. Fruiting pedicel 1–1.5 cm long, carpel stalks slender, 1.3–1.5 cm long; carpels 1.5 cm long, 1 cm wide, fusiform, glabrous, seed 1.

Vernacular name. Selukai (Iban), pudin (Melanau), serbah semangun (Malay).

Distribution (Figure 57). Western and northern Sarawak and Brunei in peat swamp forests.

ADDITIONAL SPECIMENS EXAMINED. BRUNEI. Badas, peat-swamp forest, 20
September 1957, Ashton BRUN 685 (BO); Badas, Research Plot 9/2, peat swamp forest, Hassan 2851 (SAR, SING); Badas stateland (mile 1/2 Badas Railway), peat swamp forest, 14 April 1957, Wood SAN 17452 (A, BO, BRUN). SARAWAK. Div 3:
Sibu, Sg. Matalau, Batang Lassa, Rejang Delta, mixed swamp forest, peat swamp, 21 November 1967, Ima & Anderson S 26616 (A, K, SAR, SING); Sibu, Batang Igan, Tg. Keluru, 21 January 1954, Anderson SAR 689 (SAR, SING); Sg. Pasir, Kut Siong Protected Forest, peat swamp, Anderson SAR 125 (SAR); Sibu, Naman Forest Reserve, Sanusi 5062 (SAR). Div. 6: Lassa Forest Reserve, Rejang Delta of Sg. Matalau, primary peat swamp forest, 18 May 1961, Anderson S 12596 (A, K, L, SAN, SAR); Binatang, Pulau Bruit, peat swamp, 4 July 1957, Anderson S 8391 (BO); Binatang, Pulau Bruit, 13 May 1957, Anderson S 8063 (BO); Daro, Binatang, Daro Forest Reserve, Surong Irit, 2 May 1958, Anderson & Sanusi S 5236 (BO, SAR).

When this species was described, Sinclair (1961) noted that it was close to G. tapis, because it has "apiculate anther connectives" but is "more likely to be confused with sterile material of G. malayanus". However, detailed analysis of the style and stigma characters shows an alliance with G. macrophyllus. The stamens are

unique, with patchy trichomes on a broadly acute connective, not an apiculate stamen as indicated by Sinclair.

25. Goniothalamus stenophyllus Merr., J. Straits Branch Roy. Asiat. Soc. 85: 181.

1922.—Type: SARAWAK, Siol, June 1914, Native collector 2423 (holotype:
PNH, destroyed; lectotype, designated here: K!).

Shrub or treelet, stem and twigs glabrous, branches slender, pale when dry, cylindrical or slightly compressed at the nodes. Leaves 20-30 cm long, 1.5-2.5 cm wide, narrowly oblong-linear, chartaceous, apex narrowly acuminate, base rounded, shining on both surfaces; venation brochidodromous; primary vein sunken above, raised below, glabrous on both sides; secondary veins in ca. 20 pairs, prominent, especially beneath, anastomosing to form looped marginal veins ca. 5 mm from the margins; intersecondary veins numerous, simple; tertiary veins prominent beneath, random-reticulate; petioles ca. 5 mm long, blackish. Flowers cauliflorous or axillary on large primary branches, solitary or fascicled. Pedicels 3-4 mm long, pubescent; sepals ca. 6 mm long, 4 mm wide, ovate, slightly pubescent, acuminate; outer petals ca. 2 cm long, 0.7 cm wide, lanceolate, acuminate, coriaceous, somewhat pubescent; inner petals ca. 1 cm long, ovate-lanceolate, blunt-acuminate, pubescent; stamens numerous, 2.5 mm long, connective apiculate; ovaries numerous, oblong, 1.5 mm long, appressed pubescent; ovule 1; styles elongated, pubescent, 3-3.5 mm long; stigma somewhat expanded, not lobed nor crateriform. Fruits unknown.

This species is poorly known and our knowledge of it is based on a single specimen, the lectotype. Sinclair collected a set of specimens from Semengoh

Forest Reserve near Kuching in 1960 that he determined as G. stenophyllus, but these do not match the type. The fruit in Sinclair's material is also atypical of Goniothalamus fruits. In 1988 I found a population of Goniothalamus in the Crocker Range with leaves that resemble this species in shape and size but differ in texture. Further examinations indicate that this population also does not match the type of G. stenophyllus but probably represents yet another undescribed species belonging to the G. uvarioides alliance. Goniothalamus stenophyllus, on the other hand, belongs to the G. macrophyllus alliance. It is close to G. lanceolatus but differs in having small oblong-linear chartaceous leaves.

Goniothalamus nitidus Alliance

26. Goniothalamus nitidus Merr. J. Straits Branch Roy. Asiat. Soc. 85: 181. 1922.—

Type: SABAH. Sandakan and vicinity, September–December, 1920, Ramos

1668 (holotype: PNH, destroyed; lectotype, designated here: US!).

Tree 7 m high, stem and twigs glabrous, blackish when dry. Leaves 20–30 cm long, 6–11 cm wide, oblanceolate-elliptic, acuminate, base acute, chartaceous, green and shining on both surfaces, slightly pubescent beneath; venation consistently brochidodromous; primary vein blackish, slightly sunken above and raised beneath; secondary veins in 16–20 pairs, nearly straight, anastomosing directly with looped intramarginal veins ca. 5 mm from the margins; intersecondary veins numerous, simple; tertiary veins prominent beneath, inconspicuous above, weakly percurrent; petiole slender, 1.5–2 cm long, not inflated, slightly pubescent. Flowers fascicled on the branches below the leaves and on the trunk; pedicels 1.5–2 cm long, dark brown ferruginous when dry,

subtended with bracts; bracts 2–2.5 mm long, ovate to oblong-ovate, pubescent; sepals ca. 1 cm in diameter, orbicular, slightly fused at the base, slightly pubescent, distinctly veined; outer petals 5.5–6.5 cm long, 1.5–2 cm wide, ovate-lanceolate, apex slightly acuminate, base cuneate, sparingly pubescent on both sides, palmately veined; inner petals up to 2–3 cm long, 1 cm wide, connivent, pubescent outside, glabrous inside; stamens numerous, 3.5 mm long, connective apiculate, apex slightly pubescent on top, glabrous on the lower half; ovaries 1.5 mm long, inequilateral, pubescent on the lower half; ovules 1–2, basal; styles ca. 3 mm long, thickened upward; stigma flabellate. Fruiting pedicel 2 cm long, stout, carpel stalks 2 cm long, much thinner than the pedicel; carpels ca. 2 cm long, globose, apex obtuse, base acute, brown when dry, rugose, glabrous, seeds 1–2, obovoid, compressed.

Distribution (Figure 42): A rare endemic of eastern Sabah.

ADDITIONAL SPECIMENS EXAMINED. **SABAH. Res. Sandakan**: Sandakan and vicinity, September-December 1920, *Ramos 98* (A); *1668* (A, NY, US); *1724* (A, BO, US); Hulu Terong, May 1928, *Orolfo 649* (SING).

I have not seen this species in the field and all specimens examined have no mention of size, habit, habitat or field characters. My description of those features is based on Merrill's (1922) original description.

Goniothalamus bracteosus Alliance

27. Goniothalamus crockerensis Mat-Salleh, sp. nov.—Type: SABAH. Hulu Kimanis, track along Sg. Kimanis, 1670 m, 11 November 1986, *Mat-Salleh KMS 1323* (holotype: MSC!).

Goniothalamus bracteoso Bân affinis, a qua imprimis fructu cum pedicello stipitibusque multo longioribus, usque ad 6 cm et 3 cm longis gracilibus differt. Carpellis cum apice longo inflexe rostrato.

Tree 3-5 m high, branched, branches whitish gray, striate. Leaves 12-23 cm long, 4.5-5.5 cm wide, elliptic-oblanceolate, acuminate, base acute to slightly rounded, subcoriaceous, dark gray above, orange-brown beneath; venation eucamptodromous-brochidodromous; primary vein prominent on both surfaces; secondary veins in 10-12 pairs, raised but inconspicuous on upper surface, very conspicuous beneath, anastomosing to form loose intramarginal veins; intersecondary veins simple, sinuous; tertiary veins disorganized, randomreticulate-weakly percurrent; petiole 0.5-1 cm long, channeled above, swollen beneath. Flowers ramuliflorous, axillary; pedicel slender, 5-6 cm long, basal bracts minute and insignificant; outer petals 4 cm long, 1.5 cm wide, lanceolate, apex acute, base attenuate, slightly clawed, coriaceous, rusty pubescent; inner petals 1 cm long, 0.5 cm wide, ovate, apex acute, base attenuate, brown outside, tinged yellowish pubescent in the area where inner petals join to form a dome, warty glandular inside; stamens numerous, yellowish, 5 mm long, connective acuminate, pubescent; ovaries pubescent, obclavate; ovules 1 or 2; style smooth; stigma funnel shaped, smooth. Fruiting pedicels slender, up to 6 cm long, glabrous, carpel stalks long and slender, ca. 3 cm long; carpels red, ca. 1.2 cm long, 6 mm in diameter, fusiform, apex long rostellate, base abruptly rounded, seed 1. Figures 58, 59.

Figure 58. The holotype of Goniothalamus crockerensis (Mat-Salleh KMS 1323, MSC).



Tree is the Later of the second

Figure 59. Representative specimen (with flowers) of Goniothalamus crockerensis (Mat-Salleh KMS 2163, UKMS).



Distribution (Figure 60). Known only from the Crocker Range in Sabah in riverine areas from about 600 to 1600 m elevation.

ADDITIONAL SPECIMENS EXAMINED. SABAH. Crocker Range, Papar, Hulu Kimanis, track along Sg. Kimanis, 1670 m, 11 November 1986, *Mat-Salleh* KMS 1326 (UKMS); Tenom, Kg. Noloyan, 605 m, 26 November 1987, *Mat-Salleh* KMS 2148, 2163 (UKMS).

A distinctive species allied to *G. bracteosus* Bân, from which it differs especially in having fruiting pedicels and carpel stalks much longer and more slender, up to 6 cm and 3 cm, respectively. The carpels also have a long curved beak.

28. Goniothalamus calcareus Mat-Salleh, sp. nov.—Type: SARAWAK, G. Api, Hulu Melinau, 4th Division, on limestone rock at ca. 2500 ft, 9 September 1970, Chai 30357 (holotype: SAR!; isotype: K!).

Haec species foliis et fructui ad G. woodii Merr. ex Mat-Salleh et G. roseum Stapf accedit, sed ab eis floribus minoribus, etiam G. woodii stylo-stigmis glabris et a G. roseo taminisibus et connectivis firmiter apiculatis differt.

Treelet or small shrub 3–5 m high, stem with smooth bark, twigs glabrous, whitish on younger ones, turning blackish when older. Leaves 25–29 cm long, 6–8.5 cm wide, elliptic, acuminate, base cuneate, thinly coriaceous, upper surface dull green, brownish beneath, both surfaces glabrous; venation eucamptodromus; primary vein sunken above, raised below; secondary veins in 13–16 pairs, prominent beneath, inconspicuous above; intersecondary veins numerous; tertiary veins inconspicuous, random-reticulate; petiole stout, 1 cm long. Flowers single or

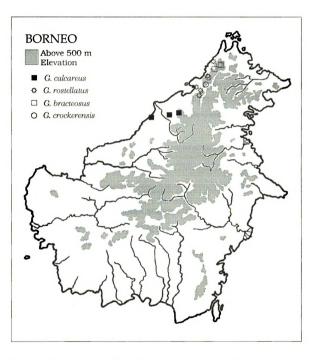


Figure 60. Distribution of species of the Goniothalamus bracteosus alliance.

in pairs, supra-axillary or cauliflorous on older parts of the stem; pedicels slender, 2.5 cm long, with 3–5 small triangular bracts, reddish; sepals ca. 1 cm long, 0.5 cm wide at the base, ovate, apex acute; outer petals 2 cm long, 1 cm wide, narrowly elliptic-oblong, narrowed upward into a sharply acute apex, red, broad and cream at base, turning pinkish at full maturity; inner petals ca. 1 cm long, 0.5 cm wide, ovate, cream-yellow, tomentulose outside, glabrous inside; stamens numerous, connective acuminate, glandular pubescent; ovaries obclavate, ca. 1 mm long, pubescent; ovules 1 or 2, basal; style tubular, glabrous; stigma glabrous, strongly crateriform, radiating to the outside, grooved inside. Fruiting pedicels long, up to 4–5 cm, carpel stalks ca. 1.5 cm long; carpels fusiform when ripe, obtuse or slightly mucronate, seed 1. Figure 61.

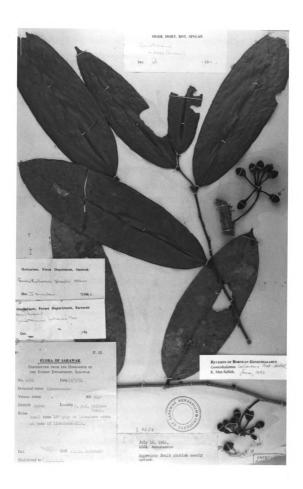
Distribution (Figure 60). Endemic to limestone mostly around Gunung Mulu National Park, Sarawak. One collection has been recorded from limestone at nearby Niah Cave.

ADDITIONAL SPECIMENS EXAMINED. **SARAWAK. Div. 4:** Baram, Sg. Berar, G. Mulu National Park, limestone boulder, 28 April 1978, *Kiew RK 479* (SAR); Baram, G. Api, Melinau Gorge, limestone rocks, 15 July 1961, *Anderson S 4624* (A, SAR, SING); Miri, Niah Cave, Niah District, on limestone, 7 June 1962, *Chew CWL 328* (A).

This rare species approaches G. woodii and G. roseus in leaf and fruit characters, but differs in having very small flowers. It also differs from G. woodii in having glabrous styles and stigmas, and from G. roseus in having a strongly apiculate connective.

My knowledge of this species is based on very limited material. Only two flowering collections, similar in appearance, have thus far been obtained. The

Figure 61. Representative specimen of Goniothalamus calcareus (Anderson 4624, SAR).



leaves of this species also resemble G. roseus and G. rostellatus from Sabah, but these taxa differ greatly in outer petal and fruit characteristics.

29. Goniothalamus rostellatus Mat-Salleh, sp. nov.—Type: SABAH, Sipitang, Mendolong SFI Concession, ca. 4 km south of SFI field station, 750 m, 31 July 1988, Mat-Salleh KMS 2423 (holotype: MSC!).

Species G. bracteoso Bân carpello optime congruens, sed foliis oblanceolatis, magnitudine duplo (ca. 25 cm longis et 8 cm latis) differt, petalis exterioribus etiam multo longioribus, lanceolatis, usque ad 9 cm longa et ca. 1 cm latis (versus late ovatis, vix quam 4 cm longis et ca. 2 cm latis in G. bracteoso).

Shrub. Stem with smooth bark, outer bark whitish, inner bark yellowish, twigs whitish gray, striate. Leaves 22–28 cm long, 7–8.5 cm wide, obovate, abruptly acuminate, base acute, coriaceous, both surfaces dull, glabrous, brown beneath; venation eucamptodromous-brochidodromous; primary veins prominent; secondary veins in 10–12 pairs, raised but inconspicuous on the upper surface, very conspicuous beneath, anastomosing to form loose intramarginal veins; intersecondary veins simple, sinuous; tertiary veins disorganized, random-reticulate-weakly percurrent; petiole stout, ca. 1 cm long, blackish. Flowers solitary, axillary, or cauliflorous on upper parts of the stem; pedicels 2–2.5 cm long, with 2–6 triangular basal bracts; sepals triangular-ovate, 0.5–1 cm long and wide; outer petals up to 9 cm long, only 1–1.5 cm wide at anthesis, narrowly lanceolate, narrowed upward, extended to a long, sharply acute apex, base rounded, not clawed; inner petals 1 cm long, 0.5 cm wide, ovate, acute, slightly clawed, puberulous outside, whitish warty inside at top; stamens numerous, connectives acuminate, glandular pubescent; ovaries obclavate, smooth; ovule 1, basal; style

tubular, glabrous; stigma crateriform, glabrous. Fruiting pedicels slender, 2 cm long, carpel stalks slender, ca. 1 cm long; carpels fusiform, 1.2–1.5 cm long, rostellate, base acute, seed 1. Figures 62, 63.

Distribution (Figure 60). Known from a few localities in Sabah in open secondary forest with sandy soil at low elevations (ca. 50–250 m).

ADDITIONAL SPECIMENS EXAMINED. SABAH. Res. Pantai Barat: Kota Kinabalu, Jalan Istana, August 1986, Azman 49 (UKMS); Kota Kinabalu, Sepangar Bay, SEB Phase I Power Plant Environmental Impact Assessment, kerangas, 26 February 1988, Mat-Salleh KMS 2228 (UKMS); Tuaran, Tamparuli, August 1986, Zainuddin ZH 10 (UKMS); Tuaran, Kg. Kiulu, 6 September 1986, Mohd. Salleh JR 42 (UKMS). Res. Pedalaman: Sipitang, Mile 22.5, Mesapol, 19 June 1971, Saikeh Lantoh SAN 73327 (SAN); Sipitang, Lumaku Forest Reserve, 18 March 1975, Dewol SAN 79966 (SAN); 21 March 1975, Dewol SAN 79991 (SAN); Sipitang, Meligan Range, Kg. Ibul, ca. 20 km from SFI Mendolong Station, hill dipterocarp forest, Agathis dominated, white sandy soils of Meligan formation, 22 August 1988, Sukup SA 1118 (UKMS); Sipitang, Lumaku Forest Reserve, L39, Mendolong SFI Concession, 700-750 m, 23 August 1988, Azhari et al. 5, Habibah & Sukup HABY 11, 12, Khusairi et al. KI 36, Saedi et al. AEDI 32, 39, 73, Goloi 62, Mat-Salleh KMS 2407, 2421, 2428, 2434 (UKMS); along Sg. Muaya, 700-750 m, 21 August 1988, Mat-Salleh KMS 2504 (UKMS); along Sg. Mondol, riverine, 23 August 1988, Titingan et al. 13 (UKMS); L42, SFI concession, trail to waterfall, 24 August 1988, Shashi et al. DSD 21, Azhari et al. 31 (UKMS); Sipitang, along Sg. Masia at Maligan Range, August 1973, Tong S 32818 (K, L, SAR).

This species resembles G. bracteosus in the fruiting carpels, but differs in that the leaves are oblanceolate and twice as large (ca. 25 cm long, 8 cm wide). The

Figure 62. Sheet 1 (with flowers) of the holotype of Goniothalamus rostellatus (Mat-Salleh 2423, MSC).



FLORA OF BORNEO

Annonaceae

Contothalamus apiculocarpelus Mat Sal

Det. K. Mat Salleh, 31-VII-1988

Sabah, Pantai Barut, Sipitang, Mandukeng SPI Conceasion, c. 4 km south of SPI Field Station, Alt. 750 m. Hill Diptercoard Jogged over forest, near stream. Crocker Formation. Treelet c. 2.5 in, flowers red turn pinkinh when mature, vanilla smell. Plower in spirit. Carpel apiculate, red.

K Mat Salleh KMS 2423 A 31 VII 1988 W.E. G. Gurssalam

CA HERFLARE M UKMS KOTA KINABALU

REVISION OF BORNERS GOMOTHIE ONES





Figure 63. Sheet 2 (with fruiting carpels) of the holotype of *Goniothalamus* rostellatus (Mat-Salleh 2423, MSC).



LMS 24236

outer petals are also much longer, lanceolate, up to 9 cm long and ca. 1 cm wide (versus broad ovate petals seldom more than 4 cm long and 2 cm wide in G. bracteosus).

30. Goniothalamus bracteosus Bân, Bot. Zhurn. (Moscow & Leningrad) 59(4):
553. 1974.—Type: SABAH. Mount Kinabalu. Tenompok, 5000 ft, 1
December 1931, Clemens 27378 (holotype: NY!; isotype: K!).

Tree 3.5-5 m high. Leaves ca. 10 cm long, 4-7 cm wide, elliptic, apex caudate, base cuneate, thinly coriaceous, glabrous; venation eucamptodromousbrochidodromous; primary veins prominent on both sides; secondary veins in 10-12 pairs, raised but inconspicuous on the upper surface, very conspicuous beneath, anastomosing to form loose intramarginal veins; intersecondary veins simple, sinuous; tertiary veins disorganized, random-reticulate-weakly percurrent; petiole ca. 5 mm long, stout. Flowers solitary, cauliflorous, axillary or terminal; pedicels long, thin and slender, 3-4 cm long at full development, normally with 2-4 elliptic basal bracts; sepals small, 5-6 mm long, 4-5 mm wide, ovate, acute, glabrous on both sides; outer petals yellow, 3-4 cm long, 1.5-2 cm wide, lanceolate, acute, both sides puberulous; inner petals 0.8-1.5 cm long, ca. 0.5 cm wide, obovate, obtuse, pubescent outside, puberulous inside, whitish warty inside at top, scabrous at the bottom; stamens numerous, 2 mm long, connectives apiculate, glandular pubescent; ovaries 3 mm long, oblong, base pubescent; ovules single, basal; styles glabrous, tubular; stigma glabrous, bilobed. Fruiting pedicel long, 4-5.5 cm long, occasionally with bract remnant, bracts up to 3.5 cm long, 2 cm wide; carpel stalks ca. 1 cm long; carpels 1-1.5 cm long, 0.5 cm thick, fusiform, rostellate, red or pinkish purple, glabrous, seed 1.

Distribution (Figure 60). Known only from Mount Kinabalu at 1000–1500 m, in montane dipterocarp forest.

ADDITIONAL SPECIMENS EXAMINED. Sabah. Res. Pantai Barat: Kota Belud, Mount Kinabalu ridges, Dallas, 3000 ft, 19 September–2 November 1931, Clemens 26460 (A, BO, K, NY); Kota Belud, Tenompok trail, 4–5000 ft, 7 September 1931, Clemens 26678 (A, K, NY); Kota Belud, Mount Kinabalu, Dallas, 3000 ft, 30 November 1931, Clemens 26854 (A, B, BM, K, NY); Kota Belud, Dallas, 3000 ft, 17 December 1931, Clemens 27619 (NY); Ranau, Crocker Range, Bt. Lugas, Kg. Himbaan 8.5 km SE of Tenompok, Trus Madi formation, montane dipterocarp forest, 1250 m, 4 February 1984, Beaman 8432 (MSC, UKMS).

The leaves of this species resemble to some extent those of G. stenopetalus, but the tertiary veins are very much raised and prominent while the tertiary veins of G. stenopetalus are inconspicuous and insignificant.

EXCLUDED TAXA

Listed here are names of *Goniothalamus* species that have been reported from Borneo but are excluded due to taxonomic realignments. More details are provided under various accepted names.

Goniothalamus tapis Miq., Fl. Ind. Bat. Suppl. 371. 1865–1866; King, J. Asiat.
 Soc. Bengal 61: 77. 1892; Ann. Bot. Gard. Calcutta 4: 99, t. 140; Ridley,
 Sarawak Mus. J. 1(3): 84. 1913; Merrill, J. Straits Branch Roy. Asiat. Soc.
 Special No.: 261. 1921; Sinclair, Gard. Bull. Singapore 14(2): 444-445. 1955;

Bân, Bot. Zhurn. (Moscow & Leningrad) 59(5): 668. 1974—Types: SUMATRA. Prov. Priaman, Diepenhorst s.n. (U?, n.v.); Lubu-alang, Teijsmann s.n. (K!).

- 2. Goniothalamus umbrosus J. Sinclair, Gard. Bull. Singapore 14(2): 445. 1955;

 Bân, Bot. Zhurn. (Moscow & Leningrad) 59(5): 668. 1974.—Type:

 PENINSULAR MALAYSIA. Penang, jungle behind no. 2 Plant House, Waterfall
 Gardens, Sinclair SFN 39356 (holotype: SING!; isotypes: E! K!).
- 3. Goniothalamus ridleyi King, J. Asiat. Soc. Bengal 61: 76. 1892; Ann. Bot. Gard. Calcutta 4: 98, t. 138; Ridley, Sarawak Mus. J. 1(3): 85. 1913; Merrill, J. Straits Branch Roy. Asiat. Soc. Special No.: 260. 1921; Sinclair, Gard. Bull. Singapore 14(2): 437-438. 1955; Bân, Bot. Zhurn. (Moscow & Leningrad) 59(5): 669. 1974.—Type: SINGAPORE. Sg. Murai, Ridley s.n. (holotype: CAL?, n.v.).
 - Goniothalamus prainianus King, J. Asiat. Soc. Bengal 61: 72. 1892; Ann. Bot. Gard. Calcutta 4: 90, t. 123.—Type: PENINSULAR MALAYSIA. Perak, Larut, March 1884, King's collector 5745 (holotype: K!).
- 4. Goniothalamus giganteus Hook f. & Thomson, Fl. Ind. 1: 109. 1855; Fl. Br. Ind.

 1: 75. 1872; King, J. Asiat. Soc. Bengal 61: 322. 1892; Ann. Bot. Gard.
 Calcutta 4: 93, t. 130; Sinclair, Gard. Bull. Singapore 14(2): 431-432. 1955;
 Bân, Bot. Zhurn. (Moscow & Leningrad) 59(5): 664. 1974.—Type:
 PENINSULAR MALAYSIA. Penang, 1822, Wallich 6469 (holotype: K!).

5. Goniothalamus suluensis Merr., Philipp. J. Sci. 30 (1926) 393; Bân, Bot. Zhurn. (Moscow & Leningrad) 59(5): 671. 1974.—Type: Philippine Is., Tawitawi, along Malum River near mangrove swamps, July-August 1924, Ramos & Edano 44350 (holotype: PNH, destroyed; lectotype, designated here: A!; isotypes: BM! US! NY!).

UNDETERMINED SPECIMENS

I have been unable to refer several collections to any known species. These are as follows.

- 1. SABAH. Papar, Crocker Range National Park, Hulu Kimanis, 31 December 1988, Mat-Salleh KMS 2844, 2848 (UKMS). These specimens resemble G. stenophyllus in leaf shape and size but differ in texture. The fruits, however, are many seeded and oblong-linear like those of G. dolichocarpus. The plants occur at about 750 m and are sympatric with G. uvarioides and G. velutinus. Flowers have not been seen. The population produces mature fruits in December and would be expected to flower around June–July. The plants undoubtedly belong to the G. uvarioides alliance.
- 2. BRUNEI. Bangar, 31 Mar 1957, Smythies et al. SAN 17114 (BO, BRUN).

 SARAWAK. Div. 4: Lambir Hills National Park, 30 October 1976, Ilias S 38322 (SAR);

 Lambir Hills National Park, G. Lambir, low elevation, 8 July 1962, Ilias S 16627 (A, BO, SAR). These collections from central Sarawak have remarkable multi-seeded moniliform carpels. The leaves exhibit interesting features remotely resembling G. malayanus in texture and color but G. parallelivenius in venation. I am unable to

describe this plant as a new species in this treatment because mature flowers are not available. SEM micrographs of immature stamens indicate more or less apiculate stamens and styles that probably are hairy. This may or may not be a contamination of sample. Hairy styles are a unique feature of members of the G. macrophyllus alliance. I cannot repeat the revival procedure because not enough flowering material is available.

3. SARAWAK. Semenggoh Forest Reserve, Kuching, 3 August 1960, Sinclair 10199 (E, SING, US). This collection was annoted by Sinclair as G. stenophyllus. No flowers are available and the leaves do not match the type specimen of G. stenophyllus. The specimen has fruits rather atypical for Goniothalamus.

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Appendix 1. Recognized Goniothalamus taxa and their synonyms (including new species described in this revision) and their general distribution.

TAXON

DISTRIBUTION

Seram

China

1.	G. amuyon Merr.	
	var. amuyon	Philippines & Taiwan
	var. <i>ramosii</i> Bân	Philippines
2.	G. andersonii J. Sinclair	Borneo
3.	G. aruensis Scheff.	New Guinea
4.	G. auriculatus Burck	New Guinea
5.	G. australis Jessup	Northern Australia
6.	G. borneensis Mat-Salleh	Borneo
7.	G. bracteosus Bân	Borneo
8.	G. brevicuspis Miq.	Celebes
	G. brunneus Merr.	
	(= G. elmeri Merr.)	
9.	G. burmanicus C. E. C. Fisch.	Burma
10.	G. calcareus Mat-Salleh	Borneo
11.	G. caloneurus Miq.	New Guinea
12.	-	Thailand
13.	G. calycinus J. Sinclair	Malay Peninsula
14.	G. cardiopetalus Hook. f. & Thomson	India
15.	G. carolinensis Kaneh.	Palau
16.	G. cataduensis Quisumb.	Philippines
	G. caudifolius Ridley	11
	(= G. tenuifolius King)	
	G. cauliflorus K. Schum.	
	,	

G. chartaceus Li. 19. G. cheliensis Hu China 20. G. chinensis Merr. & Chun China 21. G. cleistogamus Burck **New Guinea** 22. G. clemensii Bân Borneo 23. G. copelandii Merr. **Philippines** 24. G. coriaceous Burck New Guinea G. costulatus Miq. Sumatra (= Trivalvaria macrophylla (Blume) Miq.)

G. crockerensis Mat-Salleh

(= G. aruensis Scheff.)

17. G. ceramensis Miq.

18.

25. **Borneo**

	230	
26 .	G. curtisii King	Malay Peninsula
27 .	G. cylindrostigma Airy Shaw	Borneo
28.	G. dielsianus Lauterb.	New Guinea
	G. dispermus Miq.	
	(= G. malayanus Hook. f. & Thomson)	
29.	G. dolichocarpus Merr.	Borneo
30.	G. dolichopetalus Merr.	
	var. dolichopetalus	Philippines
	var. basilensis Bân	Philippines
31.	G. donnaiensis Finet & Gagnep.	Indochina
32 .	G. duguensis Pierre	Indochina
33.	G. elegans Ast	Indochina
34.	G. elmeri Merr.	
	var. elmeri	Philippines
	var. gitigensis (Elmer) Bân	Philippines
	var. longipedicellatus Bân	••
	(= G. roseus Stapf)	
35.	G. epiphyticus Elmer	Philippines
	G. euneurus Miq.	••
	(= G. tapis Miq.)	
36.	G. expansus Craib	Thailand
37 .	G. fasciculatus Boerl.	Borneo
38.	G. forbesii E.G. Baker	Sumatra
39.	G. fulvus Hook. f. & Thomson	Malay Peninsula
40 .	G. gabricianus (Baill.) Ast	•
	var. gabricianus	Indochina & China
	var. coriaceifolius Bân	Indochina
41.	G. gadneri Hook. f. & Thomson	Ceylon & China
42.	G. giganteus Hook. f. & Thomson	Sumatra, Malay Peninsula, & Thailand
43 .	G. gigantifolius Merr.	Borneo & Philippines
	G. gitigensis Elmer	* *
	(= G. elmeri Merr.	
	var. gitigensis (Elmer) Bân)	
44.	G. grandiflorus (Warb.) Boerl.	New Guinea
45 .	G. griffithii Hook. f. & Thomson	Burma, China & Thailand
46 .	G. holtumii J. Sinclair	Malay Peninsula
	G. hookerii Thwaites	•
	(= G. walkeri Hook. f. & Thomson)	
47 .	G. howii Merr. & Chun	China
	G. imbricatus Koord.	
	(= G. opacus Bakh. f.)	
48 .	G. imbricatus Scheff.	New Guinea
49 .	G. inaequilatera K. Schum.	New Guinea
50 .	4	Borneo

	231	
51.	G. kinabaluensis Bân ex Mat-Salleh	Borneo
52 .	G. lanceolatus (Bân) Mat-Salleh.	Borneo & Sumatra
53 .	· · ·	Philippines
	G. latestigma C.E.C. Fischer	11
	(=G. undulatus Ridl.)	
54 .	G. laoticus (Finet & Gagnep.) Bân	Laos & Thailand
55 .	G. leiocarpus (W. T. Wang) P. T. Li	China
56.	G. longirostris Scheff.	New Guinea
	G. kunstleri King	
	(=G. tenuifolius King)	
57 .	G. longistipites Mat-Salleh	Borneo
	G. macranthus Boerl.	Burma
59.		
00.	var. macrophyllus	Malay Peninsula, Java,
	vaz. masi oprojivas	Thailand & Sumatra
	var. <i>kerrii</i> Bân	Thailand
60.	G. magnificus Elmer	Philippines
61.	G. malayanus Hook. f. & Thomson	Borneo, Bangka, Malay
01.		Peninsula & Sumatra
62.	G. marcanii Craib	Thailand & Malay
94.		Peninsula
63.	G. meeboldii Craib	Thailand
	G. mindanaensis Elmer	
	(= G. philippinensis Merr.)	
64.	G. mindorensis Merr.	Philippines
65 .	G. mollis Warb.	Oceania
66.	G. montanus J. Sinclair	Borneo & Malay Peninsula
67.	G. multiovulatus Ast	Indochina
68.	G. mymeciocarpa K. Schum.	New Guinea
69.	G. nitidus Merr.	Borneo
	G. oblongipetalus Merr.	
	(= G. elmeri Merr.)	
70.	G. obtusifolius Merr.	Philippines
71.	G. opacus Bakh. f.	Java
72 .	G. oxycarpus Miq.	Sumatra
73 .	G. panayensis Merr.	Philippines
74 .	G. parallelivenius Ridl.	Borneo
75.	G. peduncularis King & Prain	India
	G. pendulifolius Ridl.	
	(= G. uvarioides King)	
76.	G. philippinensis Merr.	
	var. philippinensis	Philippines
	var. ramosii Bân	Philippines
	G. prainianus King	
	(= G. ridleyi King)	

	230	
77 .	G. puncticulatus Boerl. & Koord.	Sumatra
7 8.	G. puncticulifolius Merr.	Borneo &
70	C + ' ' ' ' '	Philippines
7 9.	G. repevensis Pierre	Indochina
	G. reticulatus Thwaites	
	(= G. salicinus	
00	subsp. reticulatus (Thwaites) H. Huber)	.
80.	G. rhynchantherus Dunn.	India
81.	G. rhyncocarpus Diels	New Guinea
82.	G. ridleyi King	Malay Peninsula
83.	G. roseus Stapf	Borneo
84.	G. rostellatus Mat-Salleh	Borneo
85.	G. rotundisepalus Henderson	Malay Peninsula
86.	G. rufus Miq.	Borneo
	G. saigonensis Pierre ex Fin. & Gagnep.	
~-	(= G. gabricianus (Baill.) Ast)	
87.	G. salicinus Hook. f. & Thomson	
	subsp. salicinus	Ceylon
	subsp. reticulatus (Thwaites) H. Huber	Ceylon
88.	G. sawtehii C. E. C. Fisch.	Burma
89.	G. scortechinii King	Malay Peninsula & Thailand
90.	G. sesquipedalis (Wall.) Hook. f. & Thomson	Burma & India
91.	G. sibuyanensis Merr.	Philippines
92.	G. simonsii Hook. f. & Thomson	India
	G. slingerlandtianus Scheff.	
	(= G. malayanus Hook. f. & Thomson)	
93.	G. sinclairianus Mat-Salleh	Borneo
94.	G. stenopetalus Stapf	Borneo
95.	G. stenophyllus Merr.	Borneo
96.	G. subevenius King	Malay Peninsula & Thailand
07	G. suluensis Merr.	Borneo & Philippines
98.		Sumatra
99.	G. tamirensis Pierre ex Finet & Gagnep.	Sumau a
33.	var. tamirensis	Indochina
		Indochina
100	var. kamputensis Finet & Gagnep.	Malay Peninsula &
100.	G. tapis Miq.	Sumatra
101	C tabissides Mat Sallah	Borneo
	G. tapisoides Mat-Salleh	
	G. tavoyensis Chatterjee	Burma, Malay Peninsula & Thailand
	G. tenasserimensis Biswas	Burma
	G. tenuifolius King	Malay Peninsula
105.	G. thomsonii Thwaites	Ceylon

106. G. thwaitesii Hook. f. & Thomson	Ceylon
107. G. tortilipetalus Henderson	Malay Peninsula &
	Thailand
108. G. touranensis Ast	Anambas
109. G. truncifolius Merr.	Philippines
110. G. umbrosus J. Sinclair	Malay Peninsula
111. G. undulatus Ridl.	Burma, Malay Peninsula &
	Thailand
112. G. uniovulatus Lauterb. & K. Schum.	New Guinea
113. G. uvarioides King	Borneo, Malay Peninsula &
	Sumatra
114. G. velutinus Airy Shaw	Borneo
115. G. ventristylus Boerl. & Koord.	Sumatra
116. G. viridiflorus K. Schum. & Lauterb.	New Guinea
117. G. walkeri Hook. f. & Thomson	Ceylon
118. G. wightii Hook. f. & Thomson	India
119. G. woodii Merr. ex Mat-Salleh	Borneo
120. G. wrayi King	Malay Peninsula & Sumatra
121. G. wyadensis (Bedd.) Bedd.	India
122. G. yunnanensis W. T. Wang	China

Appendix 2. Bornean Goniothalamus standardized localities as utilized in this revision. The five-digit codes are used to identify each standardized locality. The first digit is reserved for the main political regions in Borneo (Brunei, Kalimantan, Sabah and Sarawak), the second for the main subdivisions of these political states (the Profinsi for Kalimantan, Divisi for Sarawak and Residensi for Sabah) and the third digit indicates the broader area of these localities, such as district. Only the last two digits are for actual localities.

1. Brunei

```
10000
       "Brunei"
10101 Hulu Belait [4°10'N, 114°43'E]
10102 Belait, Anduki Forest Reserve [4°36'N, 114°22'E]
10103 Belait, Andulau Forest Reserve [4°35'N, 114°20'E]
10104 Belait, Badas Stateland [4°19'N, 114°15'E]
10105 Belait, Bt. Puan [4°30'N, 114°30'E]
10106 Belait, Sg. Lumut [4°40'N, 114°35'E]
10107 Belait, Batu Patam Ridge [4°05'N, 114°42'E]
10108 Seria [4°35'N, 114°20'E]
10201 Tutong [4°50'N, 114°40'E]
10202 Tutong, Kuala Abang [4°37'N, 114°42'E]
10302 Bangar [4°43'N, 115°05'E]
10304 Bt. Patoi [4°43'N, 115°09'E]
10305
       Temburung, Labu Forest Reserve [4°43'N, 115°09'E]
```

2. Kalimantan

```
20000 "Kalimantan"
20002 Bt. Ibilie
20003 Bt. Tjihan
20010 Sg. Magna
20012 Letung, Semangit-Selambau
```

2.1. Kalimantan Barat

```
21101 Sg. Kapuas [0°0'N, 110°0'E]
21103 Liang-Gagang [0°40'N, 112°47'E]
21104 Sg. Kenepai [0°20'N, 111°35'E]
21105 G. Kenepai [0°40'N, 111°45'E]
21106 Sg. TapoeTsey [1°0'N, 113°45'E]
```

- 21107 Sg. Doho [1°0'N, 113°45'E]
- 21108 Sg. Landak, Ngabang [0°20'N, 110°0'E]
- 21202 G. Nap, north of Kg. Semame, Bantiang
- 21203 Pontianak, Kg. Ibandar Aer
- 21204 Sg. Sambas [1°20'N, 109°30'E]
- 21205 Pontianak, Tg. Kibong [0°42'N, 109°23'E]
- 21206 G. Palong Nature Reserve [1°15'S, 110°15'E]
- 21207 Amai Ambit [0°40'N, 112°50'E]

2.2. Kalimantan Tengah

- 22101 Palangka Raya [2°10'S, 113°50'E]
- 22102 Palangka Raya, Tangkiling [2°10'S, 113°50'E]
- 22202 Sampit, Kuala Kuanjan [2°30'S, 112°50'E]
- 22301 Upper Katingan, Katingan (Mendawai) River [3°17'S, 113°21'E]
- 22302 Upper Katingan, Bt. Raya [0°45'S, 112°47'E]
- 22303 Upper Katingan, Sg. Samba [0°50'S, 112°50'E]
- 22304 Upper Katingan, Tumbang Tubus [0°45'S, 112°51'E]
- 22305 Upper Katingan, Headwater of Sg. Kahayan [0°35'S, 113°25'E]

2.3. Kalimantan Timur

- 23102 G. Beratus [1°15'S, 116°30'E]
- 23103 Kenangan, P.T. ITCI Concession [1°15'S, 116°30'E]
- 23104 Sg. Wain [1°12'S, 116°49'E]
- 23105 Tanah Gerogot, Desa Kasungai [1°55'S, 116°10'E]
- 23106 Wanariset [1°00'S, 116°20'E]
- 23201 Mahakam Hulu [1°00'N, 114°20'E]
- 23301 Pulau Nunukan [4°10'N, 117°40'E]
- 23401 Samarinda, Mulawarman University Botanic Gardens [0°30'S, 117°10'E]
- 23403 Long Bleh, Belajan Range [0°15'N, 116°11'E]
- 23404 Tandjong Bangko, near mouth of Sungai Mahakam [0°30'S, 117°30'E]
- 23502 Sangkulirang, Bontang, Sg. Lekambing [0°10'N, 117°20'E]
- 23503 East Kutai, Sg. Menumbar [1°24'N, 118°12'E]
- 23504 G. Kutai, Sg. Kerajaan [0°20'N, 117°15'E]
- 23505 Pelawan Besar [1°00'N, 118°00'E]
- 23602 Sg. Membunut Besar, N. of Tarakan
- 23603 [3°20'N, 117°37'E]
- 23701 West Kutai, G. Kemoel (Kongkemul) [2°0'N, 116°0'E]
- 23702 West Kutai, G. Maranga on Tundjung plateau
- 23802 Berouw, G. Ilas Bungaan [1°50'N, 116°02'E]
- 23803 Bunut [0°15'N, 112°30'E]
- 23901 G. Kapor
- 23902 Long Tesak

2.4. Kalimantan Selatan

- 24101 Banjarmasin [2°16'S, 114°30'E]
- 24201 Jaro Dam, 10 Km northeast of Muara Uya [1°15'N, 116°10'E]

3. Sabah

- 30000 "North Borneo"
- 30002 Hulu Terong (unknown locality)
- 30003 Maujang River Valley (unknown locality)

3.1. Residensi Kudat

- 31100 [6°12'N, 116°39'E]
- 31101 Kota Merudu [6°31'N, 116°45'E]
- 31104 Crocker Range, Bt. Madalon [6°28'N, 116°37'E]
- 31200 Kudat [6°48'N, 116°44'E]
- 31201 Pulau Banggi [7°15'N, 117°10'E]
- 31202 Pulau Banggi, Lambuak Darat [7°15'N, 117°10'E]
- 31302 Bengkoka, ca. 1.5 miles SE of Kg. Bawing [6°53'N, 117°10'E]

3.2. Residensi Pantai Barat

- 32201 Kota Kinabalu [5°35'N, 116°02'E]
- 32202 Jalan Istana [5°35'N, 116°02'E]
- 32203 Sepangar Bay [6°05'N, 116°08'E]
- 32204 Sepangar Island [6°04'N, 116°04'E]
- 32302 Crocker Range, Kimanis, Mandahan Hill [5°34'N, 115°55'E]
- 32303 Crocker Range, Hulu Kimanis Forest Reserve [5°28'N, 116°03'E]
- 32304 Crocker Range, Hulu Kimanis, Kimanis-Keningau road [5°28'N, 116°03'E]
- 32305 Crocker Range, Hulu Kimanis, trail along Sg. Kimanis [5°31'N, 116°03'E]
- 32402 Crocker Range, Babagon, 4th mile, path to Hulu Terian [5°28'N, 116°17'E]
- 32403 Crocker Range, Babagon, Kg. Madsiang [5°28'N, 116°17'E]
- 32501 Ranau [5°35'N, 116°25'E]
- 32601 Teghilan, Lema'as Forest Reserve [6°17'N, 116°13'E]
- 32602 Tamparuli [6°09'N, 116°15'E]
- 32603 Kiulu [6°03'N, 116°17'E]
- 32604 Tuaran, Kg. Mengkaladoi [6°10'N, 116°18'E]
- 32605 Sulaman Lake Forest Reserve [6°15'N, 116°13'E]

3.3. Residensi Pedalaman

- 33101 Beaufort [5°22'N, 115°45'E]
- 33102 Beaufort Forest Reserve [5°22'N, 115°45'E]

- 33103 Beaufort Hill [5°22'N, 115°45'E]
- 33104 Haligolat [5°17'N, 115°48'E]
- 33105 Lupak Camp [5°20'N, 115°49'E]
- 33106 Lumat [5°25'N, 115°47'E]
- 33107 Hulu Sungai Bakau (or Buckau) [5°12'N, 115°45'E]
- 33108 Montenior [5°21'N, 115°48'E]
- 33109 Beaufort, Montenior road, mile 6 [5°21'N, 115°48'E]
- 33110 Weston, Kg. Usak [5°12'N, 115°36'E]
- 33111 Weston, Kg. Mengkaloh [5°16'N, 115°29'E]
- 33112 Sri Beaufort Concession [5°16'N, 115°29'E]
- 33201 Keningau [5°12'N, 116°06'E]
- 33202 Crocker Range, Keningau-Kimanis Road, mile 17.5 [5°28'N, 116°03'E]
- 33203 Crocker Range, Keningau-Kimanis Road, mile 9 [5°25'N, 116°05'E]
- 33204 Crocker Range, Keningau-Kimanis Road, mile 11 [5°27'N, 116°04'E]
- 33205 Crocker Range, Keningau-Kimanis Road, mile 14 [5°27'N, 116°04'E]
- 33206 Crocker Range, Keningau-Kimanis Road, mile 15 [5°27'N, 116°04'E]
- 33207 Crocker Range, Kg. Bundu, Apin-apin [5°30'N, 116°15'E]
- 33208 Lanas, Shan Lian Logging Concession [5°20'N, 116°31'E]
- 33209 Tambulanan [5°33'N, 116°15'E]
- 33215 Witti Range, Hulu Sg. Mantuluk [4°16'N, 116°35'E]
- 33216 Crocker Range, Keningau, mile 11, Highland Plantation [5°20'N, 116°03'E]
- 33302 Pulau Tiga [5°43'N, 115°38'E]
- 33402 Weston, Hulu Mesapol Forest Reserve [5°08'N, 115°35'E]
- 33403 Kuala Mengalong [5°00'N, 115°23'E]
- 33404 Meligan Range, Lumaku Forest Reserve [5°00'N, 115°45'E]
- 33405 Meligan Range, Lumaku Forest Reserve, Kg. Ibul [4°48'N, 115°42'E]
- 33406 Meligan Range, Lumaku Forest Reserve, Mendolong [5°00'N, 115°45'E]
- 33407 Meligan Range, Lumaku Forest Reserve, Sg. Masia [5°00'N, 115°45'E]
- 33502 Crocker Range, G. Alab [5°46'N, 116°23'E]
- 33503 Crocker Range, Km 20, Kota Kinabalu Tambunan road [5°55'N, 116°14'E]
- 33504 Crocker Range, Km 41, Kota Kinabalu-Tambunan Road [5°51'N, 116°17'E]
- 33505 Crocker Range, Km 55, Kota Kinabalu Tambunan Road [5°49'N, 116°20'E]
- 33506 Crocker Range, Km 63, Kota Kinabalu Tambunan Road [5°46'N, 116°21'E]
- 33507 Crocker Range, Km 64, Kota Kinabalu Tambunan Road [5°46'N, 116°21'E]
- 33510 Crocker Range, Km 50.7, Kota Kinabalu Tambunan Road [5°50'N, 116°19'E]
- 33511 Crocker Range, Km 49.5, Kota Kinabalu Tambunan Road [5°50'N, 116°20'E]

- 33602 Crocker Range, Tenom, Kg. Melutut [5°14'N, 115°57'E]
- 33603 Crocker Range, Tenom, Kg. Noloyan [5°14'N, 115°57'E]
- 33604 Crocker Range, Tenom, Malalap [5°15'N, 115°57'E]
- 33605 Crocker Range, Tenom, Sg. Polong [5°14'N, 115°57'E]
- 33606 Crocker Range, Tenom Hill [5°08'N, 115°55'E]
- 33607 Crocker Range, Tenom, Kallang Waterfall
- 33701 Trus Madi Range, Kg. Kaingaran [5°38'N, 116°28'E]
- 33702 Trus Madi Range, Kienob [5°39'N, 116°28'E]
- 33703 Trus Madi Range, Kg. Sinoa [5°30'N, 116°33'E]
- 33704 Trus Madi Range, Sg. Kaintanu Besar [5°30'N, 116°33'E]
- 33705 Trusmadi Tambahan 1 Forest Reserve [5°35'N, 116°45'E]
- 33706 Trusmadi Tambahan 2 Forest Reserve [5°40'N, 116°30'E]

3.4. Residensi Sandakan

- 34101 Sg. Kinabatangan [5°30'N, 117°48'E]
- 34102 Kinabatangan, G. Lotung, southeast of Sg. Inarat [4°45'N, 116°55'E]
- 34103 Kinabatangan, Bt. Garam [5°30'N, 117°52'E]
- 34104 Kinabatangan, Karamuak, Pinangah For. Reserve, Bt. Pant [5°25'N, 117°07'E]
- 34105 Kinabatangan, Kertam Camp [5°25'N, 118°22'E]
- 34106 Kinabatangan, Karuak Forest Reserve [5°28'N, 118°14'E]
- 34107 Kinabatangan, Kinabatangan Besar, Kori Timber Camp [5°35'N, 118°35'E]
- 34108 Kinabatangan, Km 28 to Darmakut Camp [5°17'N, 117°33'E]
- 34109 Kinabatangan, Lamag [5°28'N, 117°49'E]
- 34110 Kinabatangan, Lubuk Buaya [5°36'N, 118°36'E]
- 34111 Kinabatangan, Pinangah, Sg. Milian [5°11'N, 116°49'E]
- 34112 Kinabatangan, Sg. Tangkulap, Hulu [5°25'N, 117°18'E]
- 34113 Kinabatangan, Sg. Tongod [5°18'N, 116°55'E]
- 34114 Kinabatangan, Sg. Menunggul [5°30'N, 118°15'E]
- 34115 Kinabatangan, Tamoi, Lamag, c. 50 km from Telupid [5°17'N, 117°15'E]
- 34116 Kinabatangan, Tangkulap VJR Forest Station [5°18'N, 117°18'E]
- 34117 Kinabatangan, Telupid-Karamuak Logging Road, km 32 [5°30'N, 117°12'E]
- 34118 Kinabatangan, Tenegang Besar, Lamag [5°20'N, 118°15'E]
- 34119 Kinabatangan, Tenegang Timber Camp, Kg. Pangkaian [5°20'N, 118°15'E]
- 34120 Kinabatangan, Tongod, Sg. Enodol [5°25'N, 116°47'E]
- 34121 Kinabatangan, Tongod, Hulu Menanam [5°26'N, 116°51'E]
- 34122 Kinabatangan, Hulu Sg. Lokan, Lamag [5°30'N, 117°20'E]
- 34124 Kinabatangan, Hutan Simpan Sg. Pin [5°19'N, 117°52'E]
- 34125 Kinabatangan, Sg. Menunggal [5°28'N, 118°10'E]
- 34126 Kinabatangan, Dismal Gorge [4°55'N, 117°47'E]
- 34127 Kinabatangan, Pinangah [5°13'N, 116°50'E]

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34128 Kinabatangan, Sg. Kapor [5°28'N, 118°14'E]
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- 34129 Kinabatangan, G. Tawai [5°33'N, 117°05'E]
- 34201 Batangan Camp, Ngui Ah Kui Concession [5°17'N, 117°41'E]
- 34202 Beluran [5°17'N, 117°33'E]
- 34203 Bongaya Forest Reserve [6°07'N, 117°15'E]
- 34204 Bongaya Forest Reserve, Sg. Makopako [6°07'N, 117°15'E]
- 34205 PAMOL Estate, Sg. Wanyang [6°00'N, 117°24'E]
- 34206 Sg. Tahid [5°44'N, 117°33'E]
- 34207 Sg. Meliau [5°30'N, 117°04'E]
- 34208 Telupid [5°38'N, 117°07'E]
- 34209 Telupid, Sg. Ruku-Ruku [5°36'N, 117°06'E]
- 34210 Telupid, Sg. Wonod [5°40'N, 117°05'E]
- 34211 Telupid-Ranau Road, Mile 92.5 [5°50'N, 116°50'E]
- 34212 Telupid-Ranau Road, Mile 111 [5°50'N, 116°50'E]
- 34213 Hulu Sg. Ogan [5°44'N, 117°33'E]
- 34214 Sg. Muanod [5°44'N, 117°33'E]
- 34215 Sg. Sasau, side of Sg. Tongod [5°12'N, 116°53'E]
- 34216 Beluran, Kg. Baba [5°44'N, 117°33'E]
- 34217 Beluran, Hulu Sapa Payau Forest Reserve [5°37'N, 117°16'E]
- 34218 Paitan Forest Reserve [6°30'N, 117°12'E]
- 34219 Telupid, Kg. Boto [5°40'N, 117°12'E]
- 34220 Sg. Tungud [6°00'N, 117°10'E]
- 34301 Sandakan [5°30'N, 118°04'E]
- 34302 Sandakan, Betatan [5°47'N, 117°51'E]
- 34303 Sandakan, Gomantong Cave [5°20'N, 118°19'E]
- 34304 Sandakan, Gum-Gum (= Labuk Road Mile 17) [5°33'N, 117°55'E]
- 34305 Sandakan, Kabili Forest Reserve [5°28'N, 117°33'E]
- 34306 Sandakan, Kebun China Forest Reserve [5°50'N, 118°03'E]
- 34307 Sandakan, Labuk Road, Mile 32 [5°47'N, 117°47'E]
- 34308 Sandakan, Labuk Road, Mile 80 [5°39'N, 117°20'E]
- 34309 Sandakan, Leila Forest Reserve [5°50'N, 118°05'E]
- 34310 Sandakan, Luang Manis [5°41'N, 117°42'E]
- 34311 Sandakan, Labuk Road, Mile 44 [5°35'N, 117°35'E]
- 34312 Sandakan, Segaliud-Lokan Forest Reserve, Mile 47 Labuk [5°35'N, 117°35'E]
- 34313 Sandakan, Sekong Kechil [5°23'N, 117°35'E]
- 34314 Sandakan, Sepagaya Forest Reserve, Elopura [5°30'N, 118°04'E]
- 34315 Sandakan, Sepilok Forest Reserve [5°29'N, 117°34'E]
- 34318 Sandakan, Sibuga Forest Reserve [5°54'N, 118°03'E]
- 34319 Sandakan, Sg. Manila [5°57'N, 117°57'E]
- 34320 Sandakan, Sg. Semawang [5°43'N, 117°46'E]
- 34321 Sandakan, Sg. Tabing [5°53'N, 117°47'E]
- 34322 Sandakan, Sg. Sigaliud [5°40'N, 117°50'E]
- 34323 Sandakan, Sg. Sapi Forest Reserve [5°43'N, 117°31'E]
- 34324 Hulu Dusun [5°53'N, 117°47'E]

3.5. Residensi Tawau

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35101 Lahad Datu [5°02'N, 118°18'E]
35102 Lahad Datu, Bikang camp
35103 Lahad Datu, Danum Valley (Sg. Segama Forest Reserve) [4°56'N,
          117°36'E]
35104 Lahad Datu, Danum Valley, Hulu Sg. Danum [4°56'N, 117°36'E]
35105 Lahad Datu, G. Silam [4°57'N, 118°10'E]
35106 Lahad Datu, Kennedy Bay VJR [5°01'N, 118°15'E]
35110 Lahad Datu Road [5°02'N, 118°18'E]
35111 Lahad Datu, Malambalula, Nam Hing Co.
35112 Lahad Datu, Mensuli [5°07'N, 118°09'E]
35113 Lahad Datu, Paris Camp area
35115 Lahad Datu, Segama Road, mile 4.5 [5°05'N, 118°15'E]
35116 Lahad Datu, Segangan
35117 Lahad Datu, Silam Road, mile 17 [4°35'N, 118°06'E]
35118 Lahad Datu, Sucitani Forest Reserve [5°01'N, 118°15'E]
35119 Lahad Datu, Tabin Wildlife Sanctuary F.R. [5°13'N, 118°27'E]
35120 Lahad Datu, Tabin Wildlife Sanctuary F.R., VJR 13 [5°13'N, 118°27'E]
35121 Lahad Datu, Tabin Wildlife Sanctuary F.R., VJR 35 [5°12'N, 118°37'E]
35122 Lahad Datu, Takon, Hulu Bekapit [4°58'N, 118°40'E]
35123 Lahad Datu, Hulu Tungku [5°05'N, 118°20'E]
35124
       Sepagaya, Temenggung [5°01'N, 118°15'E]
35125 Segama, Hulu Bole [4°55'N, 117°52'E]
35126 Bakapit [4°58'N, 118°34'E]
35202 Pulau Selingan [4°34'N, 118°30'E]
35301 Tawau [4°16'N, 117°54'E]
35302 Tawau, Apas Road, E of Mile 15 [4°16'N, 118°03'E]
35303 Tawau, Apas-Mostyn, Japanese Track [4°25'N, 118°11'E]
35304 Tawau, Balong Road, mile 25 [4°21'N, 118°07'E]
35305 Tawau, Benawood
35306 Tawau, Baradaya [4°26'N, 117°50'E]
35307 Tawau, Bombalai [4°20'N, 117°48'E]
35308 Kalabakan [4°15'N, 117°17'E]
35309 Kalabakan, Luasong [4°37'N, 117°25'E]
35310 Kalabakan, Hulu Sg. Sirun [4°25'N, 117°16'E]
35311 Kalabakan, Hulu Sg. Toe, Hap Seng Concession [4°22'N, 117°20'E]
35312 Tawau Hills Park, near Hq. [4°22'N, 117°54'E]
35313
       Quoin Hill [4°25'N, 118°00'E]
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3.9. Mount Kinabalu and vicinity

- 39000 Mt. Kinabalu [6°05'N, 116°33'E] 39001 Mt. Kinabalu, Asparagus Farm [6°01'N, 116°37'E]
- 39005 Mt. Kinabalu, Dallas [6°02'N, 116°28'E]

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247
39006
        Mt. Kinabalu, Eastern Shoulder (Singh's plateau) [6°05'N, 116°40'E]
39007
        Mt. Kinabalu, Gurulau spur [6°03'N, 116°32'E]
39008
        Mt. Kinabalu, Kiau [6°02'N, 116°30'E]
39009
       Mt. Kinabalu, Kiau Nulu [6°03'N, 116°30'E]
39010
        Mt. Kinabalu, Kiau to Lobang [6°02'N, 116°32'E]
39011
        Mt. Kinabalu, Keebambang River [6°06'N, 116°30'E]
39012
        Mt. Kinabalu, Kilembun River Basin [6°06'N, 116°30'E]
39013
        Mt. Kinabalu, Kinabalu Park Hq. area [6°01'N, 116°33'E]
39014
       Mt. Kinabalu, Langanan River [6°04'N, 116°41'E]
39015
        Mt. Kinabalu, Liwagu River [5°59'N, 116°36'E]
39016
        Mt. Kinabalu, Liwagu/Mesilau Rivers [5°59'N, 116°36'E]
39017
        Mt. Kinabalu, Lubang [6°02'N, 116°32'E]
39018
        Mt. Kinabalu, Mahandei River [6°04'N, 116°31'E]
39019
        Mt. Kinabalu, near Mamut Copper Mine [6°02'N, 116°39'E]
39020
        Mt. Kinabalu, Mamut river, Hulu Langganani [6°04'N, 116°42'E]
        Mt. Kinabalu, Marai Parai [6°04'N, 116°31'E]
39021
39022
        Mt. Kinabalu, Mesilau River [5°59'N, 116°36'E]
39023
        Mt. Kinabalu, Penataran River [6°08'N, 116°30'E]
39024
        Mt. Kinabalu, Penibukan [6°04'N, 116°30'E]
39025
        Mt. Kinabalu, Pinosuk Plateau [6°01'N, 116°36'E]
39026
        Mt. Kinabalu, Poring Hot Springs [6°03'N, 116°42'E]
39027
        Mt. Kinabalu, Sayap [6°11'N, 116°34'E]
39028
        Mt. Kinabalu, Sg. Tinekuk [6°03'N, 116°29'E]
39029
        Mt. Kinabalu, Sosopodon [5°59'N, 116°34'E]
39030
        Mt. Kinabalu, Tenompok [6°00'N, 116°32'E]
39031
        Mt. Kinabalu, Upper Kinabalu [6°05'N, 116°33'E]
39032
        Mt. Kinabalu, below Power Station [6°02'N, 116°33'E]
39033
        Mt. Kinabalu, between E. Mesilau and Mentaki [6°01'N, 116°36'E]
39034
        Mt. Kinabalu, between Mamut Ridge and Hulu Bambangan [6°01'N,
          116°39'E]
39101
        G. Tambayukon [6°12'N, 116°39'E]
39102
        Ranau, G. Mentapok (near Sg. Mengkodoit) [5°45'N, 116°57'E]
39103
       Ranau, G. Lenau at Tenompok [6°01'N, 116°33'E]
       Ranau, Bt. Kulung near Bt. Hampuan [5°59'N, 116°41'E]
39104
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- 39105 Ranau, Crocker Range, Bt. Lugas [5°57'N, 116°34'E]
- Ranau, Bt. Hampuan [6°00'N, 116°40'E] 39106
- 39107 Ranau, Mokodou River above Kg. Takutan

4. Sarawak

- "Sarawak" or "West Borneo" 40000
- Stupong (probably Stubong, a corruption of Santubong, but not certain) 40001

4.1. Divisi Pertama (1)

- 41101 Bako National Park [1°40'N, 110°22'E]
- 41102 Bako National Park, Sg. Poo [1°40'N, 110°22'E]
- 41103 Bako National Park, Teluk Assam [1°40'N, 110°22'E]
- 41104 Bako National Park, Hulu Serait [1°40'N, 110°22'E]
- 41201 Bidi Cave [1°25'N, 110°10'E]
- 41202 Bt. Gebong [1°25'N, 110°10'E]
- 41203 Bt. Krian, limestone [1°20'N, 110°12'E]
- 41204 Seburan, between Seburan and Bt. Krian [1°13'N, 110°17'E]
- 41301 Kuching [1°30'N, 110°18'E]
- 41302 G. Penrissen [1°05'N, 110°15'E]
- 41303 G. Tieng [1°08'N, 110°19'E]
- 41304 Semenggoh Forest Reserve [1°20'N, 110°17'E]
- 41305 Setampin [1°05'N, 110°18'E]
- 41306 Setapok Forest Reserve [1°06'N, 110°18'E]
- 41307 Tiang Bekap [1°18'N, 110°12'E]
- 41308 Matang Ridge [1°35'N, 110°12'E]
- 41309 G. Matang [1°35'N, 110°12'E]
- 41310 G. Matang, Hulu China [1°37'N, 110°17'E]
- 41402 G. Gading [1°43'N, 109°51'E]
- 41404 G. Perigi [1°43'N, 109°40'E]
- 41405 G. Pueh [1°45'N, 109°40'E]
- 41406 Semunsam WildLife Sanctuary [1°55'N, 109°35'E]
- 41407 Sampadi Forest Reserve, Bt. Snibong [1°40'N, 110°00'E]
- 41408 Sampadi Forest Reserve, Bt. Sejarak [1°40'N, 110°00'E]
- 41502 Bt. Empan Ra'a (near Bt. Selabor), Lobang Mawar [1°06'N, 110°25'E]
- 41503 Bt. Alak, Tebakang area [1°06'N, 110°25'E]
- 41504 Sg. Sabal Tapang [1°10'N, 110°32'E]
- 41602 G. Bungo [1°05'N, 110°15'E]
- 41702 G. Gaharu, Sabal Aping [1°04'N, 110°58'E]
- 41703 G. Buri [1°10'N, 110°55'E]

4.2. Divisi ke 2

- 42102 Saribas Forest Reserve [1°30'N, 111°25'E]
- 42202 G. Lisung [1°16'N, 111°10'E]
- 42302 Sg. Berus, Logging camp, Meludam Forest Reserve [1°30'N, 111°25'E]
- 42402 Batang Lupar [1°20'N, 111°20'E]
- 42403 Batang Sekerang [1°15'N, 111°27'E]
- 42404 Hulu Sekarang, Below Bt. Sadok [1°15'N, 111°27'E]
- 42405 Kg. Pungor Tapang, Path to Kg. Kara [1°05'N, 111°35'E]
- 42501 Bt. Peninjau, Lanjak Entimau [1°37'N, 112°05'E]

4.3. Divisi ke 3

- 43102 G. Poi [2°05'N, 112°15'E]
- 43202 Bt. Penarih, Balingian [2°40'N, 112°30'E]
- 43302 Sg. Matalau, Lassa, Rejang Delta [2°40'N, 111°44'E]
- 43303 Batang Igan, Tg. Kelapu [2°40', 111°36'E]
- 43304 Loba Kabang Protected Forest [2°25'N, 111°47'E]
- 43305 Sg Pasir, Kut Soing Protected Forest
- 43306 Naman F.R.

4.4. Divisi ke 4

- 44101 Baram [4°35'N, 113°59'E]
- 44102 Tinjar, Hulu Atun [3°05'N, 114°25'E]
- 44103 Tinjar, Long Kerangan, Hulu Sg. Sekiwa [3°30'N, 114°00'E]
- 44105 Hulu Tinjar, Mt. Dulit [3°15'N, 114°15'E]
- 44106 Hulu Tinjar, Hulu Sg. Chipidi [3°15'N, 114°15'E]
- 44107 G. Mulu National Park [4°01'N, 114°32'E]
- 44108 G. Mulu National Park, G. Benarat [4°09'N, 114°55'E]
- 44109 G. Mulu National Park, S. Batau [4°00'N, 114°32'E]
- 44110 G. Mulu National Park, Tutoh, Melinau Gorge [4°06'N, 114°50'E]
- 44111 G. Mulu National Park, Tutoh, Melinau Range [4°06'N, 114°50'E]
- 44112 G. Mulu National Park, Tutoh, G. Api [4°06'N, 114°54'E]
- 44113 G. Mulu National Park, Tutoh, Sg. Melinau [4°04'N, 114°48'E]
- 44114 Hulu Baram, Long Selatong, Sg. Sebala [3°12'N, 115°10'E]
- 44115 Hulu Baram, Long Selatong, tributary of Benuon [3°12'N, 115°10'E]
- 44116 Hulu Baram, Sg. Silat [3°10'N, 114°55'E]
- 44117 Bei Lebang [4°0'N, 115°30'E]
- 44201 Kalabit Highlands [3°46'N, 115°28'E]
- 44202 Kalabit Highlands, Apa Batu Buli [3°46'N, 115°28'E]
- 44302 Similajau/Labang [3°25'N, 113°25'E]
- 44303 Hulu Sinrok, Similajau Forest Reserve [3°25'N, 113°25'E]
- 44304 Segan Forest Reserve [3°05'N, 113°00'E]
- 44401 Merudi, Bt. Mentagai, Bok Tisam [4°12'N, 114°20'E]
- 44502 Lambir Hills National Park [3°30'N, 113°30'E]
- 44503 Lambir Hills National Park, G. Lambir [3°30'N, 113°30'E]
- 44504 Lambir-Subis Road, Mile 21 [4°15'N, 114°00'E]
- 44505 Lower Sg. Sibuti [4°00'N, 113°48'E]
- 44506 Sg. Niah, Hulu Sg. Sekaloh [3°52'N, 113°50'E]
- 44507 Hulu Luak, Sg. Setap road [4°02'N, 113°47'E]
- 44508 Hulu Mamut [4°10'N, 113°55'E]
- 44509 Niah National Park [3°51'N, 113°49'E]
- 44510 Suai, Hulu Sg. Sibai [3°32'N, 113°35'E]
- 44511 Niah Cave [3°55'N, 113°50'E]
- 44602 Tatau, Sg. Bejangung, a branch of Sg. Anap [2°40'N, 113°15'E]

- 44603 Tatau, Tau Range, Bt. Mersing, Anap [2°30'N, 113°00'E]
- 44604 Tatau, Tau Range, Sg. Mayeng, Kakus [2°35'N, 113°05'E]
- 44605 Tatau, Hulu Sg. Kana, Batang Anap [2°42'N, 113°10'E]

4.5. Divisi ke 5

- 45102 Kayangaran Forest Reserve [4°50'N, 115°15'E]
- 45202 G. Mulu National Park, Sg. Mentawai [4°13'N, 114°51'E]
- 45203 Limbang [4°45'N, 115°00'E]
- 45204 Sg. Medamit [4°00'N, 115°10'E]
- 45205 Tg. Long Amok, Sg. Ensungai [4°50'N, 115°03'E]

4.6. Divisi ke 6

- 46102 Lassa Forest Reserve, Rejang Delta of Sg. Matalau [2°33'N, 111°43'E]
- 46103 Pulau Bruit [2°35'N, 111°20'E]
- 46104 Daro Forest Reserve, Surong Irit [2°38'N, 111°25'E]

4.7. Divisi ke 7

- 47101 Belaga [2°05'N, 113°45'E]
- 47102 Hose Mountain, Base of G. Temedu [2°00'N, 113°45'E]
- 47103 Linau-Balui [2°30'N, 113°57'E]
- 47104 Sg. Rejang, Segaham Range [2°35'N, 113°45'E]
- 47105 Segahan Range, near Belaga Airfield [2°40'N, 113°50'E]
- 47106 Punan Busang [2°30'N, 113°20'E]
- 47202 Batang Baleh [1°55'N, 113°15'E]
- 47203 Melinau, Bt. Salong, Hulu Sampuran [2°03'N, 113°40'E]
- 47204 Kapit, Bt. Raya [2°07'N, 113°07'E]

Appendix 3. The number of specimens corresponding to various phenological stages in Bornean *Goniothalamus*. Flowering and/or fruiting stages of the specimens were noted using the following code: 1) young bud, 2) immature flower, 3) mature flower, 4) immature fruit and 5) mature fruit.

	Stages	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1. G. malayanus	l	<u> </u>	100			111117	1						
1. O. manyanus	2												
	3	2	2	1		2			2	2		2	1
	4					1	1						
	5	1	1			1			4			1	1
	<u> </u>												
2. G. borneensis	l												
	2	1			L				1				
	3		1					2	3		2		
	4	1							1_		1		
	5		1					l	2	<u> </u>	1	1	
				т		1	r		1	,		T -	,
3. G. roseus	1		ļ	<u> </u>	ļ				ļ			1	
	2			2	1	2	<u> </u>	ļ	ļ		ļ	<u> </u>	<u> </u>
	3	4	3	5	3	2	5	2	<u> </u>		ļ	3	1
	4	ļ	<u> </u>		<u> </u>	ļ	ļ		ļ		 	ļ <u>.</u>	-
	5	2	2	3	2	6	1	1	L	<u> </u>	<u> </u>	6	1
1.0		ι	1	Ι	T T	Т	T	Γ	ī	Γ -	Τ	T	
4. G. stenopetalus	1 0	 		-	├	├	<u> </u>	 	 	 	-	-	\vdash
	2		-	-	 ,		1	1	 	┼	 	 	\vdash
	3	├ ──	├	┼	1		1	1	-	 	 	 	
	4	-	┼	╁	-	\vdash	1		-	\vdash		 	
	5	<u> </u>	<u> </u>	<u> </u>	<u> </u>	1	1 1	<u> </u>	<u> </u>	L	1		L
5. G. puncticulifolius	1		T	Ţ	Ι -	T		1		T		I	
). G. paneneurgonas	2	†		+									
	3	$\dagger =$	†	†	†	†			1				
	4	†	<u> </u>	1	1	1	\dagger	†		1		1	
	5	1	 	T	1	†	1	 	†				
		1	1	-	1	1							
6. G. fasciculatus	1	T	$I^{}$									3	
	2			1								1	
	3			2		2	2	3	1			2	
	4			1									
	5					1	1	2	1	2	2		

7. G. woodii	1	[[T	<u> </u>		Γ		Ι	Ī			
7. 0. 000000	2		1	1		1	2		1			2	
	3	2	3	5	1	6	6	7	3	9	4	2	2
	4	1	1	2		Ť						1	
	5	1	2	4	1		4	1	2	10	8	2	2
8. G. tapisoides	1								1				
	2								1		1	1	
	3	1	1	1	1	5	2	4	3	1		1	3
	4			1	1				1	<u> </u>	1		
	5		<u> </u>	<u> </u>	1	1	2		2	1	3	1	
	1 .	1	ſ	ī			· · · ·		ı —	г —			r
9. G. longistipites	1		<u> </u>			ļ	 	ļ	ļ	-		ļ	
	2	ļ	<u> </u>	 ,	ļ		1		l				
	3		ļ	1	ļ		4	ļ	 	 	2	ļ	-
	5		1				-	ļ	1	7	1	 	,
] 5	l	1	L	L	L	3	L	l	7	6		1
10. G. sinclairianus	1			<u> </u>			[<u> </u>		
	2												
	3		1								1		
	4				1				1		1		
	5		1			1	1		1	3	1	1	
	•						·		·				•
11. G. clemensii	1					1							
	2			L	1	1	<u> </u>		ļ	<u> </u>		1	
	3			2	2		1	1					1
	4			ļ				1		ļ			
	5	4	1	1_1_		L <u>.</u>	<u> </u>	1		<u> </u>	1	3	2
[12 C	,	1	Ι	r		ſ	Γ		· · ·	· •			· · ·
12. G. montanus	1 9		-							1	,		
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		L	L	I			L		L	<u>'</u>	L	L	L
13. G. velutinus	1										1		
	2				2		1						
	3	1		1					2		3	1	4
	4								1			1	
		<u> </u>		1		1		1	4	1	3	3	1
	5	1	1										
		1							,				
14. G. rufus	5												
14. G. rufus	5 1 2	1					2					l	
14. G. rufus	5						2 1	1	1	1	1	l	
14. G. rufus	5 1 2	1				1		1	1	1	1	1	

f			Υ	,	T						r -		
15. G. uvarioides	1		ļ										
	2												
	3												
	4						1						
	5							1	1	3	1	1	
16. G. dolichocarpus	1												
	2											1	
	3							1		1			1
	4									1 1 4 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1			
	5	1	1	1								1	2
		<u> </u>	L		L	L	L	L	L	L	L		لـــــــا
17. G. gigantifolius	1	T			T								
17. O. giganajonas	2	 					9				 		
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	3	-	 		-	 	-				 		
<u> </u>	4	-			-	<u> </u>	-		<u> </u>		 		
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10.01		1	r	Υ	1	1			<u> </u>	<u> </u>	1	· · · · · ·	
18. G. kostermansii	1	<u> </u>		ļ	ļ		ļ						
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	3	ļ	ļ		<u> </u>	ļ						1	
	4			<u> </u>	<u> </u>								
	5						2					1	
		,											
19. G. kinabaluensis	1	<u> </u>			<u></u>								
	2		1										
	3	1		1					1	2			
	4			1									
	5		1	1	<u> </u>				1	3			
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20. G. cylindrostigma	1		I			Ĭ							
	2			-	<u> </u>								
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-	5	 			 	 	-				<u> </u>		
L	<u> </u>	L	<u> </u>	L	l	L	L		L	l	<u> </u>	L	
21. C. hamille	1	1	1	T	T	Γ			Γ	·	Γ	r	
21. G. parallelivenius	1			-		 	<u> </u>		ļ				
	2	<u> </u>		ļ	 		<u> </u>						
	3	ļ		1	4	1	3	3		4	2	4	
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	5	3									<u> </u>	2	1
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22. G. macrophyllus	1												
	2										<u> </u>		
	3											1	
	4												
	5	†		†								1	
L	1	<u> </u>	L	L	1	<u></u>			L	L			

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23. G. lanceolatus	1						<u> </u>				L		
	2												
	3					3	1	2		4	1		3
	4												
	5				3	1				2	1		1
24. G. andersonii	1												
	2												
	3				1								
	4												
	5				2							1	
26. G. nitidus	11												
	2												
	3												3
	4												
	5												2
27. G. crockerensis	1												
	2												
	3				1							1	
	4												
	5									1		2	
			1			1	1		1	r	1	1	
28. G. calcareus	1	ļ	ļ			ļ		ļ	L				
	2	ļ	ļ		1	ļ	1						
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29. G. rostellatus	1	ļ		 		ļ	ļ	ļ	<u> </u>				
	2	L		<u> </u>				1			<u> </u>		
	3			2				2	3	1			
	4							2	5				
	5							1	4	1			
			,										
30. G. bracteosus	1					<u> </u>							
	2									1			
	3			1									2
	4									1			
	5	I	1									1	3

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