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**Longevity of flowers in the rattans
Calamus subinermis and *C. caesius*
(*Palmae : Calamoideae*)**

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Summary. The development of the flowers from opening to senescence and fruit formation was observed in three female inflorescences and one male inflorescence of *Calamus subinermis*, and two female inflorescences and six male inflorescences of *C. caesius* in the Sandakan Residency, Sabah. In the male flowers of both species the longevity was found to be 6–12 hours, and anthesis occurred at night. The behaviour of the acolyte (sterile male) flowers on the female inflorescences was the same as the fertile males, except that no pollen was produced. The development of the female flowers from emergence to senescence and shrivelling of the stigmas took 5 days in *C. subinermis* and 10 days in *C. caesius*. The receptivity of the stigmas, as determined by the peroxidase test, and artificial pollination followed by bagging, was about 2 days in *C. subinermis* and about 4 days in *C. caesius*. Low light intensity and high relative humidity extended the stigma receptivity for 1–2 days. The implications of these observations on natural and controlled pollination are discussed.

The genus *Calamus* is dioecious, with separate male and female plants. During a flowering season, each sexually mature stem produces from one to four inflorescences which are usually borne at consecutive leaf axils. The female inflorescence branches to the second order, and the flowers are borne in pairs (or dyads) of female and sterile male (or acolyte) flowers on both sides of the rachillae. The male inflorescence

branches to the third order, and the male flowers are arranged singly, but occasionally in pairs, long both sides of the rachillae.

The longevity of a flower has been defined by Primack (1985) as the length of time an individual flower remains open in the field with a fresh-appearing perianth, stigma and/or stamens. This definition is followed in this paper, except that in the male flowers, pollen grains are released from the opening to abscission of the flowers, and their longevity is considered to be the duration between opening and abscission. Previous reports on the pollination biology of rattan have been based on static observations (e.g., Dransfield 1979, Madulid 1980, Kiew & Muid 1989); the longevity of rattan flowers is thus not known. To determine the longevity of the male flowers and the duration of stigma receptivity of two important indigenous *Calamus* species in Sabah, *C. subinermis* H. Wendl. ex Becc. (locally known as *rotan batu*, *rotan tunggal* or *bangkavazaran*) and *C. caesius* Bl. (locally known as *rotan sega*), this study was carried out. *C. subinermis* occurs naturally on coastal dryland forests. *C. caesius* is usually found on alluvial flats, seasonally flooded riverbanks and the margins of freshwater or peat swamps. Knowledge of the longevity and the duration of stigma receptivity of the flowers is important for an understanding of natural pollination and for carrying out controlled pollination in breeding programmes.

Materials and methods

Three female inflorescences from different planted stems of *C. subinermis* in the Sepilok Arboretum were selected for the study from January to August, 1994. These stems had crowns exposed to different light conditions (estimated with a spherical densiometer to be about 20, 40 and 80% of the open, respectively) and in different health (Table 1). Ten to 30 female flowers in each inflorescence were tagged. The development of these and the sterile male flowers was recorded at 24 hours intervals

Table 1. Stems of *Calamus subinermis* in the Sepilok Arboretum chosen for investigation of stigma receptivity.

Stem No.	Stem Length (m)	Exposure of Crown (% of Open)	Condition of stem
1A	20	20	Vigorous, healthy
21A	40	80	Vigorous, healthy
21C	30	40	Broken apex, unhealthy

until the stigmas had turned brown/black or the flowers had aborted. The stages (a-h in Fig. 1) of development of the female flowers were recorded.

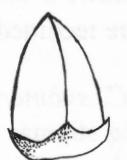
Pollen collected from a male inflorescence of *C. subinermis* in Kolapis A (situated about 40 km west of Sepilok) was applied to the stigmas of the female flowers at the various stages of development with a camel hair brush. The pollen was confirmed to be viable by *in vitro* assay with Brewbaker's pollen germination medium as described by Lee & Jong (1995). Some of the rachillae which bore the artificially pollinated flowers were then enclosed in bags made of white cotton cloth with a mesh size smaller than the rattan pollen grain (about 15–25 µm). Two to four bagged rachillae were not artificially pollinated to serve as the control. When the stigmas of the flowers had turned brown, the bags were removed. As no male inflorescences of *C. subinermis* in the Arboretum and within a radius of 25 km from the Arboretum underwent anthesis during the study period, it was not necessary to bag the flowers to exclude pollen prior to anthesis. The number of intact flowers was recorded at 24 hours intervals for 4–6 days, followed by 48 hours intervals for 8 days. Thereafter, observation on the number of developing young fruits was carried out at weekly intervals for four weeks, then fortnightly for two months and monthly until the fruits reached maturity. The original number of pollinated flowers per rachilla ranged from 30 to 48 in stems no. 21A and 21C and from 20 to 30 in stem no. 1A.

The stigmas at the different stages of development were also tested for the presence of peroxidase by immersing them in a 3% aqueous hydrogen peroxide solution. Effervescence indicates the presence of the enzyme which is normally abundant in receptive stigmas (Dafni 1992).

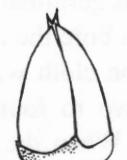
Observation on the anthesis and longevity of the fertile male flowers and sterile male (acolyte) flowers was carried out on one male inflorescence and one female inflorescence of *C. subinermis* in a natural stand in Berhala Island and the Sepilok Arboretum respectively in September, 1991. The time and duration of opening of the petals, dehiscence of the anthers and the senescence of these flowers were recorded. Observation on the flowers during a subsequent study on the nocturnal pollinators in September, 1993, confirmed these observations.

The study on the floral biology of *C. caesius* was carried out similarly. However, owing to the less frequent flowering in this species (once a year, compared with twice a year in *C. subinermis*) and the lack of accessible mature plants, only two female inflorescences on one stem in the Sepilok Arboretum were studied in October, 1993. It was possible to carry out observation on the male inflorescences on 4 stems in the Sepilok Arboretum and 2 stems in Kolapis A. The peroxidase test for stigma receptivity was carried out as in *C. subinermis*.

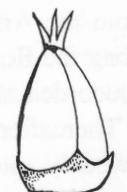
All of the study sites are situated within the Sandakan Residency.



a



b



c



d



e

Fig. 1. Stages of development of female flowers of *Calamus subinermis* and *C. caesioides*.

In stages b–e, the stigma lobes are yellow and shiny.

Stage a : Flower bud turns yellow; stigma is not visible.

Stage b : Stigma starts to protrude out.

Stage c : Stigma lobes elongate but are still straight.

Stage d : Stigma lobes start to curve.

Stage e : Stigma has reached maximum size.

In stages f to h, the shape of stigma is the same as stage e.

Stage f : Colour of the stigma lobes is brownish yellow.

Stage g : Colour of stigma is yellowish brown.

Stage h : Colour of stigma is dark brown/black.

Results

Calamus subinermis

General

About two to four days prior to the opening of female, sterile male and fertile male flowers, the colour of the sepals and petals changed from green to yellow. One or two days before the opening of the flowers, nectar exuded from between the petals and sepals. From visual estimation, nectar production reached the maximum when the flowers opened. The production of nectar was accompanied by the emission of fragrance, the intensity of which appeared to roughly correspond to the amount of nectar produced. Anthesis lasted for 10–15 days in an inflorescence in both sexes.

Male and sterile male flowers

Male flowers generally opened between 6 and 8 pm. The whole process of opening from the splitting of the flower bud to the formation of a fully opened flower took about 20 minutes. After the splitting of the bud, the introrse anthers were exposed and dehisced to release the pollen. Following anthesis and when most of the pollen had been shed, the flowers shrivelled and fell off between midnight and 6 am. Thus the longevity of the male flowers was about 6–12 hours.

The behaviour of the sterile male flowers on the female inflorescences during anthesis was the same as the fertile males, except that no pollen was produced by the staminodes which bore empty anthers.

Female flowers

The duration of the different stages of development of the female flower was as follows:

Stage a to stage c :	1 day
Stage c to stage e :	1 day
Stage e to stage f :	1 day
Stage f to stage g :	1 day
Stage g to stage h :	1 day
Total :	5 days

The elongation of the stigmas took place mainly at night. Low light intensity and high relative humidity, as were found when the rachillae were bagged extended the

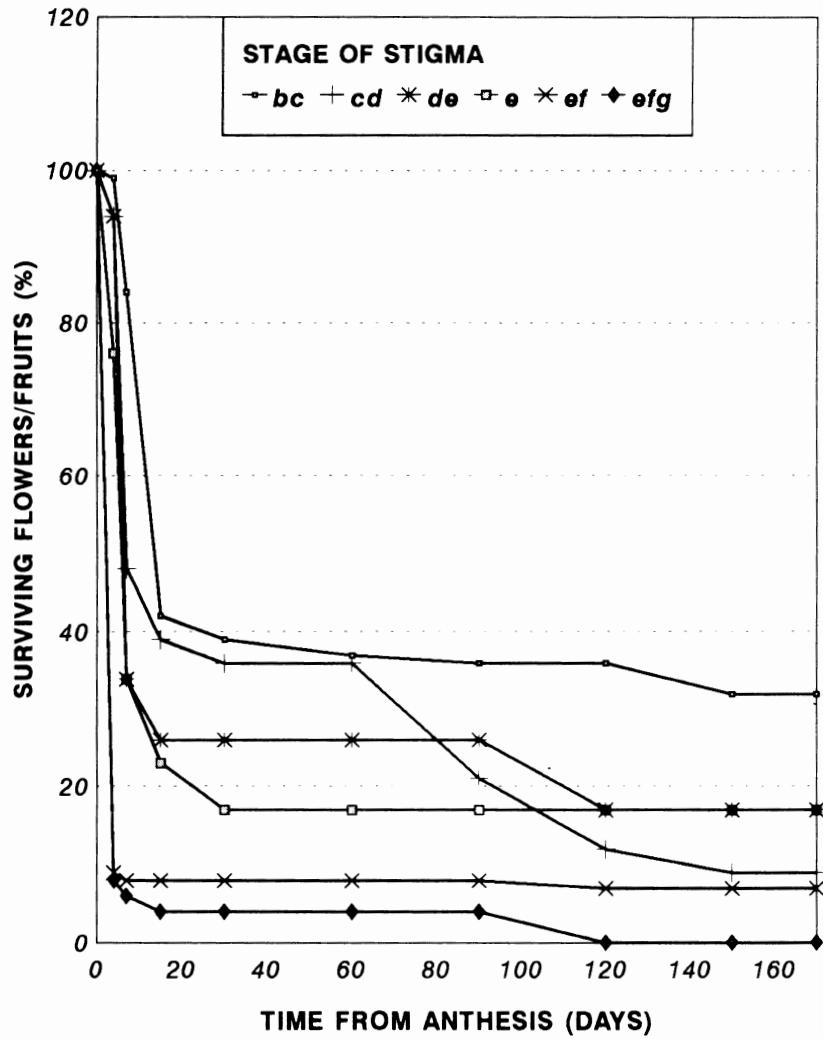


Fig. 2. Change in % of intact female flowers/fruit with time after controlled pollination of flowers at different stages of anthesis (Stages a-h shown in Fig. 1) in an inflorescence of *Calamus subinermis* on stem no. 21A of Table 2. Further explanation in text.

duration of development of the stigmas from stage a to stage f by one to two days. No difference in the duration of development of the stigmas from stage a to stage f was observed between the pollinated and unpollinated flowers.

The results of the artificial pollination experiment (Table 2 and Fig. 2) show that the stigmas at stages b to e were receptive, as pollination at these stages led to the production of mature fruits. The average proportion of flowers which were pollinated at these stages and developed into mature fruits in the three inflorescences was about 21%. The observed deviation from this average value was random; that is, pollination at none of these stages of stigma development consistently led to highest fruit set. This was confirmed by response curve analysis of the percentage of the pollinated flowers on the rachillae which developed into ripe fruits by the stage of development of the rachillae. The rachillae with flowers at stages b and c, c and d, d, and e were considered to be at levels 1, 2, 3 and 4, respectively, in the analysis. The linear, quadratic and cubic components of the response curve were found to be not significant ($p>20\%$). Pollination carried out from stage f onwards did not result in fruit production, and flowers thus pollinated aborted within three weeks. Hence the duration of stigma receptivity was 2 days in high light intensity in the open and 3–4 days in low light intensity and high relative humidity. When the stigmas were receptive, copious stigmatic fluid was produced, indicating that they are of the “wet” type (Dafni 1992).

The peroxidase test shows that peroxidase was most abundant in the stigmas from stages b to e. Stigmas at stages f and g still contained peroxidase but its activity was greatly reduced. This result is consistent with the failure of fruit set in the artificial pollination experiment.

The unpollinated female flowers (both bagged and unbaged) in this study all aborted, indicating that agamospermy does not occur in the species. This result differs from an earlier observation that in the isolated female stem (no. 21A), fruits developed parthenocarpically or stenospermocarpically (i.e., development of fruits after degeneration of fertilized ovules) but contained no seed (Lee, unpublished data).

Table 2 also shows that ripe fruits were formed fastest (170 days) in the inflorescence on stem no. 21A growing vigorously under about 80% canopy opening, followed by stem 1A (180 days) growing vigorously under about 20% canopy opening. The longest fruit maturation time was in stem 21C with a defective shoot and under about 40% canopy opening.

Calamus caesius

The development of the flowers of *C. caesius* (Fig. 3 and 4) was the same as that of *C. subinermis*, except that the longevity of the female flowers of the former was about

Table 2. Percentage of intact female flowers/fruits after controlled pollination of flowers at different stages of anthesis (Stages a-h shown in Fig. 1) in three inflorescences of *Calamus subinermis* in the Sepilok Arboretum in 1994. Pollination after stage e did not result in fruit set. The last column with survival % for each of the three inflorescences shows the time since pollination for the formation of ripe fruits, which differed among the three stems under different light intensity and in different health.

Inflorescence on Stem No	Rachilla No.	of Flowers	Time after Controlled Pollination (Days)									
			4	7	15	30	60	90	120	150	170	180
	2		0	0	0	0	0	0	0	0	0	
21A	3	ef	4	4	4	4	4	4	2	2	2	Fruits
	4	efg	8	6	4	4	4	4	0	0	0	
	5	ef	13	11	11	11	11	11	11	11	11	had
	6	e	86	50	33	33	33	33	33	33	33	
	7	e	66	18	13	11	11	11	11	11	11	ripened
	8	de	94	34	26	26	26	26	17	17	17	
	9	cd	94	48	39	36	36	21	12	9	9	
	10	bc	100	79	47	45	42	42	42	34	34	
	11	abc	97	74	33	30	27	27	27	24	24	
	12	abc	100	100	46	41	41	38	38	38	38	

(continued next page)

(Table 2 continued)

Inflorescence on Stem No	Rachilla No.	of Flowers	Time after Controlled Pollination (Days)										
			4	7	15	30	60	90	120	150	170	180	210
21C	1	fg	0	0	0	0	0	0	0	0	0	0	0
	2	fg	0	0	0	0	0	0	0	0	0	0	0
	3	ef	7	0	0	0	0	0	0	0	0	0	0
	4	ef	42	8	3	0	0	0	0	0	0	0	0
	5	ef	36	10	0	0	0	0	0	0	0	0	0
	6	de	64	44	28	28	26	23	23	21	21	18	
	7	de	86	75	64	58	47	31	28	28	28	28	
	8	cd	61	52	48	48	33	24	24	24	24	24	
	9	bc	79	68	68	68	38	29	21	21	21	21	
	10	a	53	47	19	19	19	9	9	9	9	9	
1A	1	fg	15	4	0	0	0	0	0	0	0	0	
	2	cfg	30	15	11	4	0	0	0	0	0	0	Fruits
	3	ef	48	33	33	15	0	0	0	0	0	0	
	4	ef	67	52	48	26	0	0	0	0	0	0	had
	5	e	81	70	63	41	22	19	19	19	19	19	
	6	cd	78	63	56	26	26	22	22	22	22	22	ripened
	7	bc	93	74	67	30	22	15	15	15	15	15	
	8	ab	100	74	63	22	19	15	15	15	15	15	



Fig. 3. Male flowers of *Calamus caesius* in Sepilok.



Fig. 4. A female rachilla of *Calamus caesius* in Kolapis A.

twice that of the latter and that the duration of anthesis of the inflorescence was longer, i.e., 15–20 days. The duration of the different stages of development of the female flowers in an inflorescence under medium light intensity (30% canopy opening) under the forest canopy was as follows:

Stage a to stage b	:	1 day
Stage b to stage d	:	1 day
Stage d to stage e	:	1 day
Stage e to stage f	:	2 days
Stage f to stage g	:	2 days
Stage g to stage h	:	3 days
Total		10 days

As in *C. subinermis*, low light intensity and high relative humidity extended the duration of stigma receptivity by one to two days, and there was no difference in the duration of development of the stigmas from stage a to stage f between the pollinated and unpollinated flowers. The stigmas are also of the “wet” type.

The controlled pollination experiment did not yield any conclusive result because the partial inflorescences tagged for this study were damaged by a large fallen branch when the fruits were still very young, and the experiment has not been repeated. However, judging from the similarity in the behaviour and morphology of the flowers of this species and that of *C. subinermis*, as well as the result of the peroxidase test, it is concluded that the female flowers are also receptive during stages b to e.

In the male flower, anthesis mostly occurred between 6 and 9 pm, and senescence and abscission between midnight and 6 am. Its longevity is thus similar to that of *C. subinermis*.

Discussion and conclusions

The longevity of 6–12 hours in the male flowers of *C. caesius* and *C. subinermis* and the nocturnal anthesis observed in this study indicates that pollination mostly occurs at night. The nocturnal pollination vectors are mostly noctuid and pyralid moths (Lee *et al.* 1995). However, as pollen viability is still substantial (>10%) 24 hours after anthesis (Lee & Jong 1995) and the duration of stigma receptivity in *C. subinermis* and *C. caesius* is 2 and 4 days respectively, the diurnal flower visitors such as trigonid bees and flies, which visit both intact and fallen flowers, also play a role, perhaps a minor one, in pollination (Lee *et al.* 1995).

In controlled pollination in breeding programmes, pollen should be collected between dusk and 9 pm. Pollen grains should be applied to the receptive stigmas at stages b to e. However, the relative effectiveness of diurnal and nocturnal pollination in producing seeds is not known.

The higher longevity observed in the female flowers compared with the males is consistent with the trend reported by Primack (1985) that female flowers last longer than the males in angiosperms. He argued that male flowers are shorter-lived probably because their usefulness is over as soon as the pollen is shed and that female flowers are adapted to remain receptive until compatible pollen has reached the stigma.

Flowers are a drain on the water and stored nutrients of the plant, as a result of transpiration and respiration (Nobel 1977). The extension of the receptivity of the stigma in both pollinated and unpollinated flowers by bagging, which reduces the light intensity, increases the relative humidity and possibly reduces the temperature of the lax inflorescence, supports the physiological argument (Primack 1985) for short longevity of flowers based on the need to reduce transpirational water loss and metabolic costs.

In many species, e.g., tropical orchids, flowers are long-lived in the absence of pollination, but senescence occurs rapidly after pollination (Arditti 1979). This has been interpreted as an adaptation to promote visitation to the unpollinated flowers (Gori 1983). The similarity in the duration of stigma development from stage a to stage f in the pollinated and unpollinated female flowers observed in this study is probably because such an adaptation is absent in these relatively short-lived flowers, or the interval of observation (24 hours) is too long to detect the post-pollination senescence of the stigmas.

The abortion of unpollinated female flowers in *C. subinermis*, in contrast to an earlier observation that the same isolated female stem parthenocarpically (or stenospermocarpically) produced fruits which contained no seed, indicates that parthenocarpy or stenospermocarpy in the species is probably the result of genetic interaction with the environment. The trigger for parthenocarpy or stenospermocarpy, possibly the physiological state of the plant (e.g. sufficient food reserve) in response to environmental stimuli, has yet to be investigated. Stenospermocarpy might have occurred after self-fertilization, as the acolyte and pistillate flowers on female inflorescences of *C. subinermis* have been observed to produce viable pollen (Lee, unpublished data).

The similarity in the behaviour between the acolyte flowers on the female inflorescence and the fertile male flowers implies that the former's role in pollination is probably by serving as an olfactory and visual attractant, and by producing nectar as a reward for the pollinators.

The longevity of the female flowers of the two *Calamus* species investigated is comparable to that of two other locally widely cultivated palms, *Elaeis guineensis* (oil palm, 36–48 hours (Hartley 1988)) and *Cocos nucifera* (coconut; 3 days in tall palms, 2 days in dwarf palms (Ohler 1984)). In coconut, pollen is shed in bud and the staminate flowers open and absciss within two days (Ohler 1984). In oil palm, staminate anthesis has been reported for the whole inflorescence but not for individual flowers because abscission of male flowers in the pits formed by bracts is not apparent after anthesis. The flowers in a male inflorescence of oil palm usually open within two to four days, and shedding of pollen mostly occurs during the two to three days following the start of anthesis and stops within 5 days (Purseglove 1972). The longevity of the male flowers of these two species of palm is thus longer than that of *Calamus caesius* and *C. subinermis*.

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**Pollination in the rattans
Calamus subinermis and *C. caesius*
(*Palmae : Calamoideae*)**

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Summary. Observations on the visitors to four inflorescences of *Calamus subinermis* H. Wendl. ex Becc. and seven inflorescences of *C. caesius* Bl. in research plots located in the Sandakan Residency, and examination of the pollen loads on the visitors, show that the principal pollinators in these two species of rattan are pyralid, noctuid and other moths which are active at night. The diurnally active trigonids and other Hymenoptera, as well as other insect visitors, are not thought to play a significant role because pollen release is mostly nocturnal. Pollen dispersed by wind and collected with sticky suspended slides shows that wind may contribute to some short-distance pollination. The high pollen : ovule ratio estimated in this study confirms that the two dioecious species are out-crossing. The limited foraging ranges of the small moths may result in restricted gene exchange between populations, which may be adequate to allow allopatric speciation and may partly account for the high intra-generic diversity in *Calamus*.

Calamus subinermis H. Wendl. ex Becc. and *C. caesius* Bl. are respectively the commercially most important large-diameter and small-diameter native rattans in Sabah. Owing to inadequate control on exploitation, many populations of these species are endangered or extinct. For example, on the Sandakan Peninsula, the natural population

of *C. subinermis* is extinct; the nearest extant natural population is located on Berhala Island about 1.5 km from the peninsula, in *kerangas* (heath) forest—a forest type which is also abundant on the peninsula. In an effort to conserve representative samples of the extant populations for future breeding programmes, *ex situ* populations of these two and other species have been established by the state-owned Innoprise Corporation Sdn. Bhd. (Garcia *et al.* 1993) and those of *C. subinermis* by the Sabah Forestry Department. Pollination was investigated as part of a programme to gain an understanding of the genetic diversity of the two commercially important species. Pollination mechanism largely determines the extent of gene flow in these and other rattan species, although dispersal of seeds, which is usually by gravity and occasionally by birds and other animals, and other propagules, also influences the pattern of genetic diversity observed in nature.

Previous research on pollination in *Calamus* and related genera

Reports on the pollination of this dioecious genus and other rattans have hitherto been based on static observations on the inflorescences during daylight hours and inferences from the structure of the inflorescences. Beccari (1911) reported the presence of nectaries in two species of *Daemonorops*, a genus closely related to *Calamus*. Corner (1966) postulated that hapaxanthic rattans (e.g., *Korthalsia*, *Plectocomia* and *Plectocomiopsis*) are melittophilous. Dransfield (1979) reported trigonids and honey bees visiting male flowers of *Plectocomia* sp. Insect pollination was also suggested by Madulid (1980) in *Plectocomia*, which has extremely fragrant flowers and conspicuous inflorescences visited by insects at anthesis. In most species of *Daemonorops*, *Ceratolobus*, *Calospatha* and *Calamus* section *Platyspathus*, the inflorescences are wholly or partially enclosed by bracts at anthesis, emit a musty odour and are visited by many beetles which were suggested by Dransfield (1979) to be pollinators. In other sections of *Calamus*, the inflorescences are lax and are not enclosed by bracts, and have been reported by Dransfield (1979) to produce a sour odour and to be visited mostly by wasps or flies. Kiew and Muid (1989) reported visits of *Trigona melina* to the male, but not the female, flowers of *Daemonorops didymophylla*. Uhl and Dransfield (1987) also suggested bees to be the most likely pollinators of many species of *Calamus*, although in some instances they may in fact be pollen thieves.

The present study was undertaken to shed more light on the pollination biology of the *Calamus* species.

Materials and methods

Phenological observation was carried out at fortnightly intervals in the *Calamus subinermis* plots in the Sepilok Arboretum (longitude 117°58'E, latitude 5°49'N) and

Berhala Island (longitude 118°10'E, latitude 5°51'N), and *C. caesius* plots in Kolapis A (longitude 117°35'E, latitude 5°47'N) and the Sepilok Arboretum. All of these plots are located in the Sandakan Residency in Sabah. The work on pollination was carried out during the flowering season.

Insect Pollination

During anthesis (defined here as the opening of the male flowers followed by the release of pollen from the anthers, and the emergence and development of the stigmas of the female flowers before they shrivel) of the accessible inflorescences, the visitors to as many stems as were feasible to sample were recorded for as long a duration as possible. Table 1 shows the inflorescences to which the visitors were observed and the duration of the observations. In the earlier observations prior to September, 1993 (i.e., observations 1.1, 1.2, 2.1–2.3, 2.6 and 2.7), the species of the visitors were identified and their abundance was recorded qualitatively. Observations carried out during and after September, 1993 (i.e., observations 1.3, 1.4, 2.4 and 2.5), included quantitative assessment of the abundance by counting all the visitors. All unknown visitors were captured for identification, and vouchers of all species were kept. It has been observed that the male flowers of both species usually open at dusk and shrivel and fall off from midnight onwards, and the fallen flowers still contain about 20% of the pollen present prior to anthesis (see Results). Pollen viability has also been noted to be significant (>10%) 2 days after anthesis (Lee, unpublished data). Therefore, visitors to fallen flowers were also recorded.

Representative samples of the common visitors to both female and male flowers of both rattan species were captured and examined under a microscope at X50 and X100 magnification to estimate the comparative pollen load. The number of pollen grains per mm² of the part of the body bearing pollen was estimated.

Wind Pollination

The possibility of wind pollination in *C. subinermis* was investigated in two isolated flowering male stems in Berhala Island in September, 1993, and January, 1994. Greased slides were suspended horizontally at a range of distance (0–20m) from the male inflorescences undergoing anthesis, at the same level as the inflorescences, for 24 hours. In September, 1993, petroleum jelly (Vaseline) and grease (Shell automotive multipurpose grease) were used, and it was found that grease gave better results as it resulted in less diffraction of light when the slides were examined under the microscope. In January, 1994, only grease was used. The slides were then brought back to the

Table 1. Inflorescences to which visitors were observed in the study on pollination of *Calamus subinermis* and *C. caesioides*.

Species	Observation no.	Sex of inflorescence observed	Date of observation	Time of observation	Location of inflorescence	Clump and stem number	Quantitative (Qt) or Qualitative (Ql) record of visitors
<i>Calamus subinermis</i>	1.1	Female	29 Apr–11 May 91	06.00–16.00	Sepilok Arboretum	21.1	Ql
	1.2	Female	12 May–14 May 93	16.00–07.00	Sepilok Arboretum	21.2	Ql
	1.3	Male	07 Sep–09 Sep 93	12 noon–12 noon	Berhala Island	02.1	Qt
	1.4	Female	28 Sep–29 Sep 93	10.30–10.30	Berhala Island	48.1	Qt
<i>Calamus caesioides</i>	2.1	Male	23 Sep–27 Sep 91	06.30–16.30	Sepilok Arboretum	20.2	Ql
	2.2	Male	23 Sep–27 Sep 91	06.30–16.30	Sepilok Arboretum	21.48	Ql
	2.3	Male	23 Oct–25 Oct 91	08.30–12.30	Kolapis A	–	Ql
	2.4	Male	20 Sep 93	17.30–midnight	Sepilok Arboretum	–	Qt
	2.5	Female	29 Sep 93	17.30–23.00	Sepilok Arboretum	–	Qt
	2.6	Female	04 Oct 93	08.45–11.30	Sepilok Arboretum	–	Ql
	2.7	Male	04 Oct 93	08.45–11.30	Sepilok Arboretum	–	Ql

laboratory and examined under a microscope at $\times 100$ magnification. For each slide the pollen grains observed in 10 randomly chosen views of 5.31 mm^2 were counted and the density of pollen grains on each slide was estimated. For *C. caesius*, pollen dispersal by wind was not investigated because it was not possible to locate an accessible isolated inflorescence to set up the sticky traps along unobstructed paths.

Estimation of pollen grains in flowers and pollen : ovule ratio

Preliminary observations have shown that the male flowers shrivel and fall off a few hours after anthesis, but a substantial proportion ($>10\%$) of the pollen is still viable 2 days after anthesis. Moreover, insect visitors have been observed on fallen male flowers (see Results). To get a clearer picture of the destiny of the pollen, the pollen grains in the intact and fallen male flowers were estimated. Staminate flower buds and fallen flowers were collected from an inflorescence each of two stems of *C. subinermis* on Berhala Island and two stems of *C. caesius* in the Sepilok Arboretum. The anthers of a flower or a flower bud were dissected out and crushed in a petri dish containing water and a drop of detergent, and any remaining pollen grains on the flower were washed into the dish. The resulting suspension was stirred thoroughly before the pollen grains were counted under a light microscope at $\times 100$ magnification to estimate the number of pollen grains. Altogether 5 intact flower buds and 5 fallen flowers from each inflorescence were examined.

To confirm the obligate xenogamy (cross fertilization) in these two dioecious species, the pollen : ovule ratio in the population of *C. subinermis* on Berhala Island was estimated by recording:

- (i) (a) number of female stems (N)
(b) number of male stems (n)
- (ii) (a) average number of inflorescences produced per female stem (I)
(b) average number of inflorescences produced per male stem (i)
- (iii) (a) average number of flowers per female inflorescence (F)
(b) average number of flowers per male inflorescence (f)
- (iv) (a) estimated number of pollen grains per male flower (P)
(b) estimated number of ovules per female flower (O)

Pollen : ovule ratio was then calculated as $(P \times f \times i \times n) / (O \times F \times I \times N)$.

The pollen : ovule ratio was estimated in the same way for the two planted populations of *C. caesius* in the Sepilok Arboretum and Kolapis A respectively.

Results

Insect pollination

The visitors to the flowers of both species of rattan are summarised in Tables 2(i), 2(ii), 3(i) and 3(ii). In *C. subinermis*, the most abundant diurnal visitors were the sweat bees, notably *Trigona laeviceps*, *T. melina* and *T. apicalis*, honey bees (*Apis cerana*, Fig. 1) and ants (Formicidae); and the most abundant nocturnal visitors were moths of the families Pyralidae and Noctuidae. In *C. caesius*, the most common visitors were also the diurnal sweat and honey bees and the nocturnal pyralid and noctuid moths (Fig. 2). The temporal variations in the number of the two main groups of visitors, moths and trigonid bees, are exemplified by those which visited the inflorescences of *C. subinermis* on Berhala Island illustrated in Fig. 3 and 4 which show clearly that the trigonid bees were active diurnally, and the moths were active at night. The abundance of the different groups of visitors is exemplified by those visiting *C. subinermis* as shown in Fig. 5 and 6. The pollen loads on the body of some of the insect visitors sampled during observations 1.3, 1.4, 2.4–2.7 are shown in Tables 4 and 5. Pollen was mostly found on the proboscis and legs of the moths, and the abdomen, legs, wings, thorax and corbicula (pollen baskets) of the bees. *Trigona* bees and moths, the most abundant groups of visitors, ants and other insects were also found visiting fallen fertile male and sterile male flowers. As observed on the insect visitors, the pollen grains are sticky and dispersed in clumps.

Wind pollination

Table 6 summarises the results of the study on the dispersal of pollen by wind. The maximum horizontal distance of dispersal was 4m, and the distance in different directions varied depending on the direction of the prevailing wind when most of the pollen grains were shed from dusk to about midnight. Assuming the density of pollen grains sampled from stem no. 2.1 on 6th January, 1994, at 1 m from the inflorescence was the average density from 0 to 1.5 m from the stem, and that at 2, 3 and 4 m was the average density from 1.5 to 2.5, 2.5 to 3.5 and 3.5 to 4.5 m respectively, the distribution of pollen dispersed was calculated and is given in Table 7. It is estimated that 88% of the pollen was dispersed within 3.5m from the inflorescence.

Pollen grains in male flowers and pollen : ovule ratio

The number of pollen grains in the male flowers of *C. subinermis* prior to anthesis was estimated to be 74,000 (S.D. = 14,000) per flower, and that in the fallen flower 12,000

Table 2(i) Visitors to female flowers of *Calamus subinermis*. Abundance (Number of individuals observed per day on a typical stem with about 2,000 male flowers or about 400 dyads in bloom) : A = Very abundant (>30), B = Moderately abundant (10–30), C = Rare (3–9), D = Very rare (<3). n.i. = not identified. The most abundant visitors are the trigonids, ants and moths.

Order	Family	Species	Abundance	Diurnal (D)/ Nocturnal (N)
Coleoptera	Anthicidae	? <i>Formicomus</i> sp.	D	D
	Cerambycidae	<i>Sybra</i> cf. <i>binotata</i> Gahan	D	D
	Chrysomelidae	? <i>Taumacera</i> sp.	D	D
	Elateridae	<i>Chiagosnius</i> sp.	D	D
		<i>Ganoxanthus</i> sp.	D	D
	Scarabaeidae	<i>Dichelomorpha</i> sp.	D	D
	Seirtidae	<i>Seirtes uniformis</i> Waterhouse	D	D
		<i>Coccotrypes gedeanus</i> (Eggers)	D	D
	Tenebrionidae	<i>Plamius</i> sp.	D	D
	Curculionidae	n.i.	D	D
Collembola	Etomobryidae	? <i>Lepidocyrtus</i> sp.	D	D
Dictyoptera	Blattidae	<i>Periplaneta</i> sp.	D	N
Diptera	Asilidae	? <i>Leptogaster</i> sp.	D	D
	Calliphoridae	<i>Hemipyrellia ligurriens</i> (Wiedemann)	D	D
	Chloropidae	n.i.	D	D
	Culicidae	n.i.	D	D
	Drosophilidae	<i>Microdrosophila</i> sp.	C	D
		n.i.	C	D
	Platystomatidae	<i>Scholastes</i> sp.	D	D
	Sarcophagidae	<i>Sarcophaga</i> /	D	D
		<i>Parasarcophaga</i> sp.		
	Sciaridae	n.i.	D	D
	Syrphidae	<i>Dideopsis aegrota</i> (Fabricius)	D	D
Tachinidae		n.i.	D	D
? Tipulidae		n.i.	D	D

(Continued next page)

(Table 2(i) continued)

Order	Family	Species	Abundance	Diurnal (D)/ Nocturnal (N)
Hymenoptera	Apidae	<i>Apis cerana</i> Fabricius	B	D
		<i>Trigona apicalis</i> Smith	A	D
		<i>Trigona atripes</i> Smith	A	D
		<i>Trigona geissleri</i> Cockerell	A	D
		<i>Trigona melina</i> Gribodo	A	D
		<i>Trigona laeviceps</i> Smith	A	D
	Halictidae	<i>Lasioglossum</i> sp.	D	D
	Ichneumonidae	<i>Apophua</i> sp.	D	D
		<i>Pristomerus</i> sp.	D	D
	Scelionidae	Scelioninae, n.i.	D	D
	Vespidae	<i>Parischnogaster</i> sp.	D	D
		<i>Rhynchium</i> sp.	D	D
		<i>Paraleptomenes</i> sp.	D	D
	Formicidae	<i>Camponotus</i> sp.	B	N
		<i>Polyrhachis</i> sp.	C	D/N
		<i>Crematogaster</i> sp.	A	D/N
		Formicine ants	A	D/N
Hemiptera	Plataspidae	<i>Brachyplatys subaeneus</i> Westwood	D	D
Lepidoptera	Blastobasidae	n.i.	D	D
	Cosmopterigidae	<i>Labdia oxychlora</i> Meyrick	D	D
	Gelechiidae	<i>Hypatima</i> sp.	D	D
	Pyralidae	<i>Lamprosema</i> sp.	B	N
		<i>Psara playcapna</i> (Meyrick)	B	N
		<i>Ravanoa xiphialis</i> Walker	B	N
		<i>Sufetula sunidesalis</i> Walker	B	N
		<i>Tabidia</i> sp.	B	N
		n.i. (2 species)	D	N
		<i>Badiza ereboides</i> Walker	C	N
		<i>Micreremites</i> sp.	B	N
	Noctuidae	<i>Naarda ? ineffectalis</i> Walker	B	N
	<i>Nola</i> sp.	C	N	
	Arctiidae	<i>Progonia oileusalis</i> Walker	D	N
		n.i. (2 species)	D	N
		<i>Trischalis subaurana</i> Walker	D	N
Orthoptera	Thyrididae	<i>Pharambara splendida</i> Butler	D	N
	Gryllidae	n.i. (Cricket)	D	N
	Acrididae	n.i. (Small grasshopper)	D	D/N

Table 2(ii) Visitors to male flowers of *Calamus subinermis*. Abundance (Number of individuals observed per day on a typical stem with about 2,000 male flowers or about 400 dyads in bloom) : A = Very abundant (>30), B = Moderately abundant (10–30), C = Rare (3–9), D = Very rare (<3). n.i. = not identified.

Order	Family	Species	Abundance	Diurnal (D)/Nocturnal (N)
Araneida	Araneidae	n.i. (Spider)	D	N/D
Coleoptera	Curculionidae	n.i.	B	N
Dermaptera	n.i.	n.i.	D	N
Diptera	Culicidae	n.i. (3 species)	C	D/N
	Tabanidae	<i>Tabanus</i> sp.	C	D
	Sarcophagidae	<i>Sarcophaga</i> sp.	C	D
Hemiptera	Coccidae	n.i.	C	D/N
Hymenoptera	Apidae	<i>Apis cerana</i> Fabricius	B	D
		<i>Trigona laeviceps</i> Smith	A	D
		<i>Trigona melina</i> Gribodo	A	D
		<i>Trigona apicalis</i> Smith	A	D
	Vespidae	<i>Vespa affinis</i> Linnaeus	C	N
	Eumenidae	<i>Eumenes</i> sp.	C	D
	Formicidae	<i>Camponotus</i> sp.	A	D/N
		<i>Polyrhachis</i> sp.	C	D/N
		<i>Crematogaster</i> sp.	A	D/N
		Formicine ants	A	D/N
Lepidoptera	Pyralidae	<i>Pycnarmon</i> sp.	B	N
		<i>Herculia</i> sp.	B	N
		<i>Nacoleia</i> sp.	A	N
		<i>Pleuroptya</i> sp.	A	N
		<i>Psara playcapna</i> (Meyrick)	B	N
		<i>Tabidia</i> sp.	C	N
		<i>Lamprosema</i> sp.	B	N
	Geometridae	n.i. (8 species)	A/B	N
		n.i. (2 species)	A	N

(Continued next page)

(Table 2(ii) continued)

Order	Family	Species	Abundance	Diurnal (D)/ Nocturnal (N)
Lepidoptera	Noctuidae	<i>Nola</i> sp. n.i. (5 species)	B B	N N
Neuroptera	n.i.	n.i.	D	N
Orthoptera	Gryllidae	<i>Gryllacris</i> sp.	D	N
Squamata	Gekkonidae	n.i. (Lizard)	D	N

Table 3(i) Visitors to female flowers of *Calamus caesius*. Abundance (Number of individuals observed per day on a typical stem with about 2,000 male flowers or about 400 dyads in bloom) : A = Very abundant (>30), B = Moderately abundant (10–30), C = Rare (3–9), D = Very rare (<3). n.i. = not identified.

Order	Family	Species	Abundance	Diurnal (D)/ Nocturnal (N)
Anura	n.i	n.i. (Frog)	D	N
Araneida	Araneidae	n.i. (Spider)	D	N/D
Chiroptera	n.i.	n.i. (Bat)	D	N
Coleoptera	n.i.	n.i. (4 species)	D	N
Dictyoptera	Blattidae	<i>Periplaneta</i> sp.	D	N
Diptera	Culicidae	n.i. (2 species)	C	D/N
Hymenoptera	Apidae	<i>Apis cerana</i> Fabricius <i>Trigona itama</i> Cockerell	B C	D D

(Continued next page)

(Table 3(i) continued)

Order	Family	Species	Abundance	Diurnal (D)/ Nocturnal (N)
Hymenoptera		<i>Trigona melina</i> Gribodo	B	D
		<i>Trigona laeviceps</i> Smith	A	D
		<i>Trigona melanocephala</i> Gribodo	B	D
		n.i.	C	N
	Eumenidae	<i>Eumenes</i> sp.	D	D
	Formicidae	<i>Camponotus gigas</i> Latr.	D	N
	Ichneumonidae	n.i. (2 species)	D	D
	Stephanidae	n.i.	D	D
Lepidoptera	Pyralidae	<i>Circobotys</i> sp.	B	N
		<i>Nomis</i> sp.	A	N
		n.i. (3 species)	A	N
	Noctuidae	<i>Thalathoides</i> sp.	B	N
		<i>Nola</i> sp.	B	N
		n.i. (2 species)	B	N
	Arctiidae	n.i. (2 species)	B	N
Orthoptera	Gryllidae	n.i. (Cricket)	D	N

(S.D. = 4,000) per flower. In *C. caesius* the corresponding number of pollen grains was estimated to be 76,000 (S.D. = 15,000) and 13,000 (S.D. = 4,000) respectively. The fallen flowers thus contained 16–17 % of the original number of pollen grains before anthesis.

The pollen : ovule ratio was estimated to be 93,000 in *C. subinermis* in the natural population on Berhala Island, and 360,000 and 420,000 (average: 390,000) in the planted populations of *C. caesius* in the Sepilok Arboretum and Kolapis A respectively (Table 8).

Table 3(ii) Visitors to male flowers of *Calamus caesius*. Abundance (Number of individuals observed per day on a typical stem with about 2,000 male flowers or about 400 dyads in bloom) : A = Very abundant (>30), B = Moderately abundant (10–30), C = Rare (3–9), D = Very rare (<3) n.i. = not identified.

Order	Family	Species	Abundance	Diurnal (D) / Nocturnal (N)
Araneida	Araneidae	n.i. (Spider)	D	N/D
Coleoptera	Curculionidae	n.i.	B	N
	Cantharidae	<i>Rhagonycha</i> sp.	D	D
	Chrysomelidae	n.i.	D	D
Dermaptera	n.i.	n.i.	D	N
Dictyoptera	Blattidae	<i>Periplaneta</i> sp.	D	N
Diptera	Culicidae	n.i.	C	D/N
	Tabanidae	<i>Tabanus</i> sp.	C	D
	Sarcophagidae	<i>Sarcophaga</i> sp.	C	D
	Tephritidae	<i>Dacus</i> sp.	C	D
Hemiptera	Miridae	<i>Lygus</i> sp.	D	D
	Reduviidae	n.i.	D	D
Hymenoptera	Apidae	<i>Apis cerana</i> Fabricius	B	D
		<i>Trigona melina</i> Gribodo	C	D
		<i>Trigona laeviceps</i> Smith	A	D
		<i>Trigona melanocephala</i> Gribodo	B	D
		n.i.	C	D
	Pompilidae	<i>Ammophila</i> sp.	D	D
	Vespidae	<i>Eumenes</i> sp.	C	D
	Formicidae	<i>Pheidole</i> sp.	A	D/N
Lepidoptera	Ichneumonidae	n.i. (2 species)	D	D
	Pyralidae	<i>Circobotys</i> sp.	A	N
		<i>Nomis</i> sp.	B	N
		<i>Glyphodes stolalis</i> Guenee	B	N
		<i>Herpetogramma</i> sp.	C	N
		<i>Pronomis</i> sp.	A	N
Noctuidae		<i>Thalathoides</i> sp.	B	N
		n.i. (3 species)	B	N

(Continued next page)

(Table 3(ii) continued

Order	Family	Species	Abundance	Diurnal (D) / Nocturnal (N)
Lepidoptera	Geometridae	<i>Callopistria</i> sp. <i>Ornithospila submonstrans</i> Walker	A A	N N
Orthoptera	Gryllidae	<i>Gryllus</i> sp.	D	N

Table 4 Pollen load on some insect visitors to flowers of *Calamus subinermis*.
 Pollen Load: A = High (more than 20 pollen grains per mm²), B = Medium (5–20 pollen grains per mm²) C = Low (1–4 pollen grains per mm²), D = None. Only *C. subinermis* pollen grains were counted.

No.	Visitor	Pollen load	Parts of body on which pollen grains were observed
1.	<i>Pycnarmon</i> sp. (Pyralidae)	C	Proboscis, legs
2.	<i>Herculia</i> sp. (Pyralidae)	D	—
3.	<i>Nacoleia</i> sp. (Pyralidae)	D	—
4.	<i>Pleuroptya</i> sp. (Pyralidae)	A	Proboscis
5.	Geometridae (Moth)	D	—
6.	Noctuidae (Moth)	D	—
7.	Noctuidae (Moth)	B	Proboscis
8.	<i>Trigona laeviceps</i>	A	Abdomen, legs, wings, corbicula
9.	<i>Trigona melanocephala</i>	A	Abdomen, legs, thorax, wings, corbicula
10.	<i>Trigona itama</i>	C	Abdomen, legs, wings, corbicula
11.	<i>Trigona melanocephala</i>	B	Legs, corbicula
12.	<i>Trigona laeviceps</i>	D	—



Fig. 1. A bee (*Apis cerana*) visiting male flowers of *Calamus subinermis* in Berhala Island. Most of the flowers on the rachillae have abscised by dawn.



Fig. 2. Moths visiting a male inflorescence of *Calamus caesius* in Kolapis A.

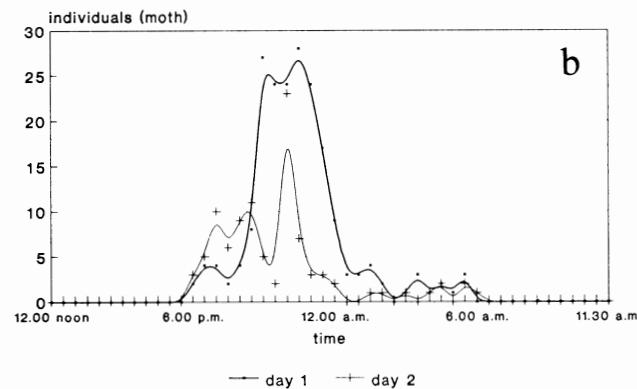
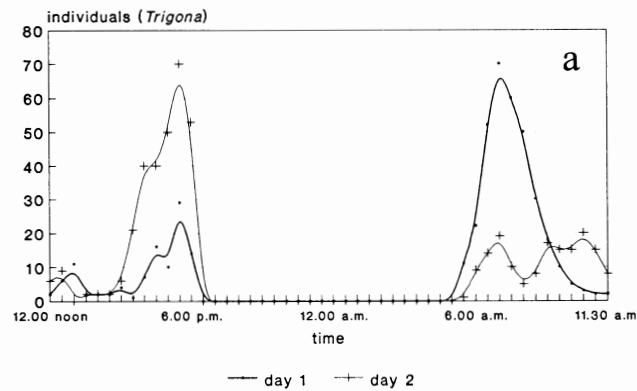


Fig. 3. Number of trigonids (a) and moths (b) visiting a male inflorescence of *Calamus subinermis* on two consecutive days on Berhala Island in September, 1993.

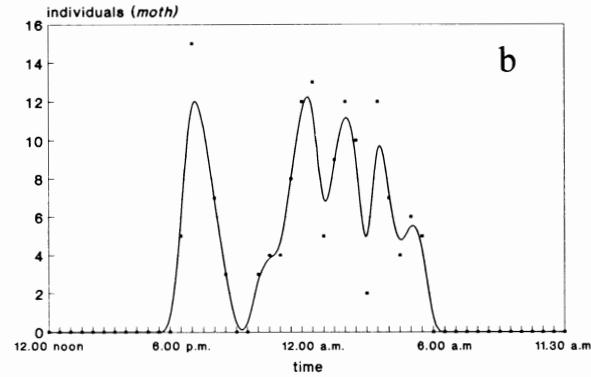
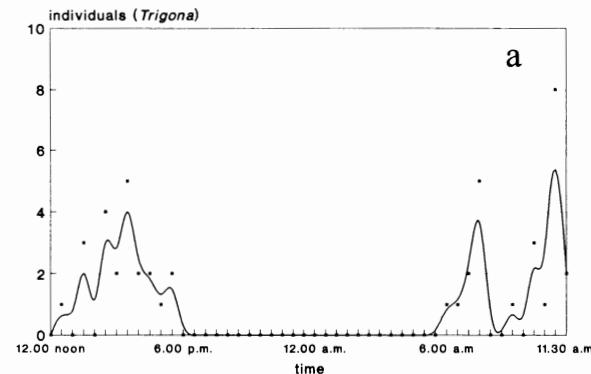


Fig. 4. Number of trigonids (a) and moths (b) visiting a female inflorescence of *Calamus subinermis* on Berhala Island in one day in September, 1993.

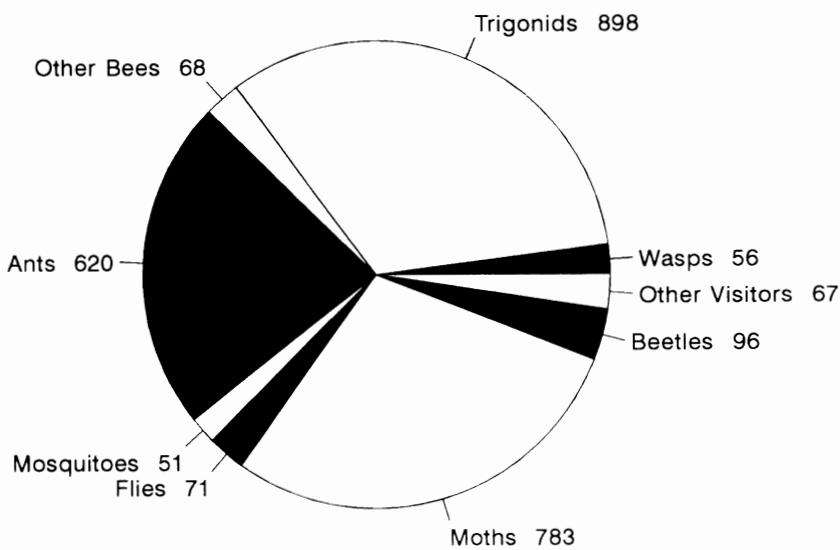


Fig. 5. Abundance of different groups of insect visitors to a male inflorescence of *Calamus subinermis* on Berhala Island in two days in September, 1993. Numbers following the names of the insect groups are those recorded.

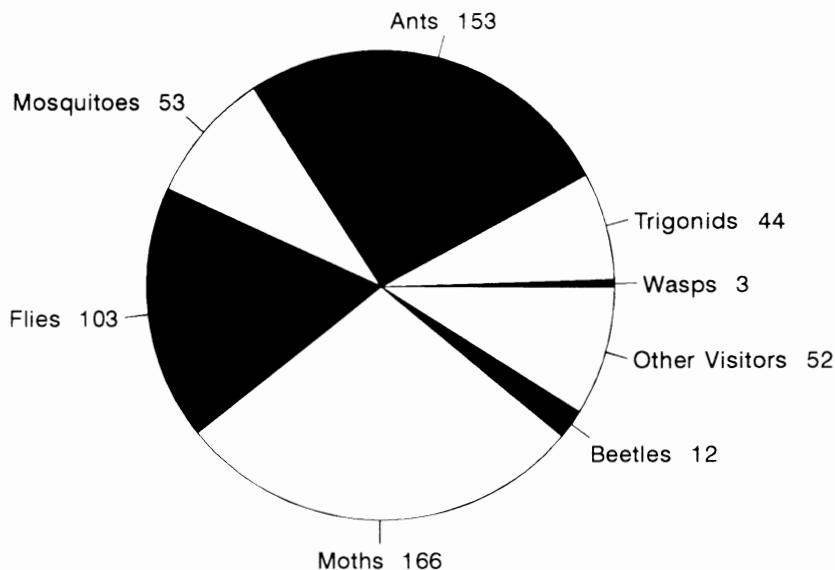


Fig. 6. Abundance of different groups of insect visitors to a female inflorescence of *Calamus subinermis* on Berhala Island in one day in September, 1993. Numbers following the names of the insect groups are those recorded.

Table 5. Pollen load on some insect visitors to flowers of *Calamus caesius*. Pollen Load: A = High (more than 20 pollen grains per mm²), B = Medium (5–20 pollen grains per mm²) C = Low (1–4 pollen grains per mm²), D = None. Only *C. caesius* pollen grains were counted.

No.	Visitor	Pollen load	Parts of body on which pollen grains were observed
1.	<i>Circobotys</i> sp. (Pyralidae)	C	Legs
2.	<i>Thalathoides</i> sp. (Noctuidae)	D	–
3.	<i>Pleuroptya</i> sp. (Pyralidae)	C	Thorax, proboscis
4.	<i>Nomis</i> sp. (Pyralidae)	C	Legs, proboscis
5.	<i>Glypodes stolalis</i> (Pyralidae)	D	–
6.	<i>Herpetogramma</i> sp. (Pyralidae)	D	–
7.	<i>Ornithospila submonstrans</i> (Geometridae)	C	Legs
8.	<i>Trigona itama</i>	B	Abdomen, legs, wings, corbicula
9.	<i>Trigona melanocephala</i>	C	Abdomen, legs, wings, corbicula
10.	<i>Trigona melanocephala</i>	B	Abdomen, legs, wings, corbicula
11.	<i>Trigona melanocephala</i>	B	Wings
12.	<i>Trigona itama</i>	C	Legs, wings, corbicula
13.	<i>Dacus</i> sp. (Diptera)	B	Abdomen, legs, wings, thorax, corbicula
14.	Diptera	D	–
15.	Stephanidae (Hymenoptera)	C	Wings and thorax

Table 6. Variation in density of pollen grains (number per mm²) with distance from *Calamus subinermis* male inflorescences on Berhala Island. Pollen was collected on suspended greased slides along clear paths in 24 hours. As the total area counted for pollen grains was 53.1 mm², the estimated density of pollen grains per mm² is not an integer. Direction: E = East, S = South, W = West, N = North.

Date	Stem no.	Direction of path	Distance from inflorescence (m)							
			1	2	3	4	8	12	16	20
7 Sep 93	2.1	W	0.4	0	—	0	0	0	0	0
8 Sep 93	2.1	W	1.0	0	—	0.09	0	0	0	0
6 Jan 94	15.1	S	0	0	0	0	—	—	—	—
	15.1	W	0	0	0	0	—	—	—	—
6 Jan 94	2.1	E	3.5	0.5	0.3	0.2	—	—	—	—
	2.1	N	0.02	0.04	0	0	—	—	—	—
	2.1	S	0.6	0	0	0	—	—	—	—
	2.1	W	0	0	0	0.02	0	0	0	0
	Average		1.03	.135	.075	.055	0	0	0	0

Table 7. Distribution of pollen from male inflorescence on stem no. 2.1 (*Calamus subinermis*) sampled on 6th January, 1994. Leptokurtic pattern is not apparent.

	Distance from inflorescence (m)			
	0–1.5	1.5–2.5	2.5–3.5	3.5–4.5
Average pollen density (grains/mm ²)	1.03	0.135	0.075	0.055
Estimated no. of pollen grains (million)	7.3	1.7	1.4	1.4
Cumulative % of pollen	62	76	88	100

Table 8. Pollen : ovule ratios in the natural population of *Calamus subinermis* in Berhala Island and two planted populations of *C. caesius* in the Sepilok Arboretum and Kolapis A respectively. The ratios are within the range for obligate xenogamous species.

Species	<i>Calamus subinermis</i>	<i>Calamus caesius</i>	
Population	Berhala	Sepilok Arboretum	Kolapis A
Number of flowering female stems (N)	23	20	18
Average number of inflorescences per female stem (I)	2.8	1.9	2.1
Average number of flowers per female inflorescence (F)	6,400 (S.D. = 1,500)	4,500 (S.D. = 1,100)	4,800 (S.D. = 1,200)
Estimated number of ovules per female flower (O)	3	3	3
Number of flowering male stems (n)	23	24	19
Average number of inflorescences produced per male stem (i)	2.4	1.8	2.0
Average number of flowers per male inflorescence (f)	28,000 (S.D. = 7,000)	56,000 (S.D. = 16,000)	80,000 (S.D. = 15,000)
Estimated number of pollen grains per male flower (P)	74,000 (S.D. = 14,000)	76,000 (S.D. = 15,000)	76,000 (S.D. = 15,000)
Pollen : ovule ratio $(P \times f \times i \times n) / (O \times F \times I \times N)$	93,000	360,000	420,000
Average pollen : ovule ratio	93,000	390,000	

Discussion and conclusions

Identification of pollination vectors

To ascertain the type of pollination, Koch's postulates (Koch 1880) may be applied, and Dafni (1992) has elaborated on the postulates which are summarised as follows:

1. Demonstration of pollen transfer from anther to pollinating vector.
2. Demonstration of pollen transport by vector.
3. Demonstration of pollen transfer from vector to stigma.
4. Demonstration of effect of pollen deposited by vector on fertilization.
5. Demonstration of perception and use of flower advertisement (visual as well as olfactory) by the pollinating vector.
6. Demonstration of consumption of flower reward by the vector as an integral part of the pollination process.
7. Demonstration of the relative contribution of pollen and ovules to the next generation as a result of the pollination process.
8. Demonstration of interrelationships between different vectors involved in pollination at a community-based level.

In this study, it was possible to fulfil fully postulates 1, 2 and 6, and partly postulate 3. Postulates 4, 5 and 7 were not clearly shown but were indirectly deduced. Postulate 8 was not included in this autecological study.

Insect pollination

It is clear from Tables 2-5 and Fig. 5-6 that *Trigona* bees, and to a lesser extent, *Apis cerana* and other Hymenoptera are the main visitors during daylight hours for both species of rattan. The most important nocturnal visitors are pyralid, noctuid and other moths. As pollen on male flowers are reduced by about 80% about 6 hours after anthesis, which mostly occurs at dusk, the pollen carried by the trigonids and other diurnal insects is much less than that carried by moths and other nocturnal insects. Moreover, the viability of pollen has been found to decrease exponentially with time after anthesis (Lee & Jong 1995a). With their efficient pollen baskets, trigonids are also known to be pollen thieves. The theft is also reflected in the lower abundance of this group of visitors relative to other groups at the female inflorescences (Fig. 6), which do not produce pollen, than at the male inflorescences (Fig. 5). It is thus concluded that the moths are much more effective in pollination than the trigonids, the latter's contribution being mainly at dusk and dawn.

The relative abundance of flies which visited the female flowers is much higher than those which visited the male flowers probably because the stigmas of the female flowers (which are receptive for at least two days (Lee & Jong 1995b) and do not absciss) are covered with a nutritious secretion (stigmatic fluid) which attracts these insects. Copious nectar is produced immediately prior to and during anthesis, giving ample reward to the nocturnal visitors. It was observed that the scent emitted by the rattan flowers during anthesis is very fragrant, in contrast to the sour odour reported by Dransfield (1979). The sour odour could be due to the fermentation of nectar, a process which produces volatile organic acids. The moths were observed to be attracted by the fragrant odour, and forage for nectar with their long proboscis. Despite the large number of ants which visited some of the rattan inflorescences, this group of insects is considered to be insignificant as pollinators because of their limited mobility and their frequency bears no relation to pollen release.

The non-insect visitors observed in this study include spiders, lizards, frogs and bat. However, their abundance and frequency of visits were extremely low. Spiders, lizards and frogs were most likely to be attracted to the inflorescences by the swarms of insect visitors, and are unlikely to play a role in pollination. Although the inflorescences of the two species of rattan investigated exhibit bat-pollination floral syndromes (i.e. creamy flowers exuding copious externally visible nectar, spreading inflorescences, fragrant odour and nocturnal anthesis (Bawa 1990)), only one bat was observed throughout this study. In habitats where bats are more abundant compared with the sites where this study was carried out, bats may well be one of the important pollinators, although bats may also cause much damage to the inflorescences of both sexes by rubbing off the small flowers which are dislodged easily.

The differences in the species of insects recorded in the two sexes of the inflorescences in the two species of rattan are mainly temporal and spatial, as observations were carried out on different sites and at different times.

Wind pollination

The maximum distance of pollen dispersal observed in this study was about 4 m, compared with more than 20 m for many wind pollinated species (Richards 1986). This indicates that wind pollination is insignificant in *C. subinermis*. Moreover, many wind pollinated species are dominant or codominant in a locality, as this aids the efficiency of their non-specific pollination (Richards 1986), but rattans such as *C. subinermis* and *C. caesius* do not normally dominate in the natural habitat. It is therefore concluded that in comparison with pollination by moths, wind pollination is very inefficient in *C. subinermis*. In stem no. 15.1 (Table 6), no pollen was collected on the suspended slides for two reasons. Firstly, the number of flowers undergoing anthesis was very small on 6th January, 1994, estimated to be fewer than 100. Secondly, it was feasible to set up the

suspended slides only in the south and west directions, which were not the direction of the prevailing wind (blowing east as indicated in the pollen grains collected from stem 2.1). The other two main directions from the inflorescence of stem no. 15.1, east and north, were obstructed by other rattan crowns. Similarly, it was not possible to set up the suspended slides beyond 4 m from the inflorescence of stem no. 2.1 in the east, south and north directions because of the obstruction by the stems and branches of the supporting trees.

Although sticky traps were not set up to study wind pollination in *C. caesius*, it is believed that the extent of dispersal of pollen by wind in this species is similar to that in *C. subinermis*, because the morphology of the inflorescences and flowers as well as the size of the pollen grains (about 15–25 µm) are very similar in both species. The pollen grains of the two *Calamus* species studied are small according to Erdtman's classification of spore and pollen size (Erdtman 1969), but the distance of their dispersal is small. This is probably due to their high density, as weight and the presence of air sacs on the pollen grains, in addition to size, are important factors which determine the settling velocity (Erdtman 1969).

The high pollen : ovule ratios (93,000 and 390,000) estimated in this study are within and higher than the range (2,100–200,000) for obligate xenogamy established by Cruden (1977), confirming that these two dioecious species are out-breeding. However, this ratio does not give any indication of the pollination vector.

The results of this study thus show that pyralid, noctuid and other moths contribute most to the pollination of the two species of rattans. The less significant pollinating vectors are *Trigona* bees, other nocturnal and diurnal insect visitors and other animals. Wind may also play a role in short-distance pollination in dense populations (e.g., in plantations) of *C. caesius* and *C. subinermis*. The sticky pollen grains observed in this study also show that zoophily is more significant than anemophily in the two species of rattan. The results of this study are also consistent with the pollination ecologists' view that among the wide range of flower visitors, members of only one or two main classes act as effective vectors (Bawa *et al.* 1985, Schemske & Horvitz 1984).

Research has shown that pollination by animals with wide foraging ranges such as bees (Frankie *et al.* 1976, Janzen 1979), hawkmoths (Linhart & Mendenhall 1977) and bats (Heithaus *et al.* 1975, Start & Marshall 1976) has potential for effecting pollen flow among distant populations. Most of the moths which pollinate the two species of *Calamus* are small and do not seem to have wide foraging ranges. This may restrict gene exchange between populations. The restricted gene flow may be adequate to allow allopatric speciation and may partly account for the high diversity in this genus, with about 370 species (Uhl & Dransfield 1987).

It has been reported that pollination by beetles (cantharophily), bees (melittophily), flies (myophily) and wind (anemophily) are common in the family Palmae (Henderson 1986). This study shows that if plant reproductive biologists care to venture into the bush at night, pollination by nocturnal animals may be found to be more common in this group of plants.

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Three new species of *Crypteronia* (*Crypteroniaceae*) from Borneo

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Summary. Three new species of *Crypteronia*, *C. borneensis*, *C. elegans* and *C. glabriflora* are described. *C. borneensis* is represented by material from Borneo previously thought to be *C. cumingii*, a species now found to be absent from Borneo and typified by a Philippine collection. Keys to the genera of Crypteroniaceae and *Crypteronia* species occurring in Borneo are provided.

The Crypteroniaceae, a pantropical family which belongs undoubtedly to the Myrtales, was regarded by van Beusekom-Osinga & van Beusekom (1975) as comprising two subfamilies, *viz.* Crypteronioideae, which consists of 3 genera, *Axinandra*, *Crypteronia* and *Dactylocladus*, and Alzateoideae which includes *Alzatea* and *Rhynchocalyx*. *Axinandra* and *Dactylocladus* were once placed under Melastomataceae as they share similar vegetative anatomical features. Based on evidence from multidisciplinary studies which include wood anatomy, palynology and embryology, Dahlgren & Thorne (1984) accepted *Axinandra*, *Crypteronia* and *Dactylocladus* under the Crypteroniaceae and recognized *Alzatea* and *Rhynchocalyx* as separate families. Both *Alzatea* and *Rhynchocalyx*, monotypic genera of Central-South America and eastern parts of South Africa, are respectively isolated into distinct and new families, Alzateaceae (Graham, 1984) and Rhynchocalycaceae (Johnson & Briggs, 1984). Keating (1984) found that Crypteroniaceae is most similar to Lythraceae in leaf histology although findings on wood anatomy suggest it should be placed with Melastomataceae (van Vliet & Baas, 1984).

The three genera accepted within the Crypteroniaceae are distinguished as follows:

Leaf apex typically obtuse, rarely acute. Intercostal veins on both leaf surfaces almost invisible. Functional stamens very short, 0.5–1 mm long. Plants typically of peat swamp forest *Dactylocladus*

Leaf apex acute, acuminate to caudate or cuspidate. Intercostal veins typically prominent on one or both sides of the leaf. Functional stamens longer, 1.5–4 mm long. Plants of other habitats.

Flower subtended by 1 bract. Petals absent. Stamens as many as sepals, persistent. Ovary superior, 2–4-celled, ovules many per cell. Capsules small, chartaceous, typically with persistent style and stigma; seeds many *Crypteronia*

Flower subtended by 3 bracts, the two lateral ones often tiny. Petals present. Stamens twice as many as sepals or petals, not persistent. Ovary inferior, (4–)6-celled, ovules 1 or 2 per cell. Capsules large, woody, style and stigma caducous (falling away at an early stage); seeds few *Axinandra*

Crypteronia as recognized by van Beusekom-Osinga (1977) includes four species and two varieties, viz. *C. cumingii*, *C. griffithii*, *C. macrophylla*, *C. paniculata* var. *paniculata* and *C. paniculata* var. *affinis*, all occurring in Borneo except for *C. paniculata* var. *affinis*.

Through a revision of the genus for the Tree Flora of Sabah and Sarawak, three new species are recognized. They are endemic to Borneo and found from lowland to highland primary forest although *C. glabriflora* is recorded mainly in hilly areas. *C. borneensis* is known to occur in Sabah, Sarawak and Brunei while *C. elegans* and *C. glabriflora* are known from Sarawak and Brunei only.

A note on flower sexuality and inflorescence form

Whereas Dahlgren & Thorne (1984) have recorded that most of the species of *Crypteronia* are unisexual, Beusekom-Osinga (1977) claimed that only *C. paniculata* is unisexual. However, in the present study only *C. paniculata* appears to have genuinely unisexual flowers and a dioecious habit.

It is observed that in male flowers of *C. paniculata* the anthers are normally well formed and exceed four times the length of the short, non-functional pistil (pistillode). However, in the female flowers the stamens are tiny, barely exceeding the sepals, with anthers that are minute compared to the well-developed ovary, long styles and capitate stigmas. The other taxa have bisexual flowers with a protandrous habit, as various stages of the maturation of the female and male organs are observed. The stamens

appear to mature prior to the pistil and are fully elongated with shrivelled anthers that have released pollen when the pistil is still much shorter with undeveloped stigmatic lobes. However, at a later stage, longer styles with well developed stigmatic lobes and which exceed the sepals are found.

One supporting character here found useful in distinguishing among the species is the extent of branching of the inflorescence. Inflorescences which branch to only the 1st or 2nd order occur in *C. cumingii*, *C. elegans*, *C. glabriflora*, *C. griffithii* and *C. paniculata*, whereas those branching to the 2nd or 3rd order are typical of *C. borneensis* and *C. macrophylla*. This is illustrated diagrammatically in Fig. 1.

The *C. cumingii* complex

The Bornean specimens identified by Beusekom-Osinga as *C. cumingii* in fact differ from the typical Philippine material of *C. cumingii* in having a sunken midrib on the upper leaf surface, raised secondary veins that are distinctly looping towards the margin on the lower leaf surface, inflorescences branching to the 2nd or 3rd order and seed wings that are broadly obtuse apically. They represent a distinct species here named *C. borneensis* (see below).

C. cumingii has a flattened midrib on the upper leaf surface, flat secondary veins that do not form any distinct loops towards the margin on the lower leaf surface. inflorescences branching to the 1st or 2nd order and seed wings that are tapered apically. It is known from the Philippines, Celebes, Moluccas and Papua New Guinea and appears to be quite uniform in flower and fruit characters, with two exceptions. The Papuan and Moluccan material has shorter petioles while the Celebes material has slightly shorter pedicels. Otherwise, the material from these islands closely match the Philippine material of *C. cumingii*.

Key to *Crypteronia* species in Borneo

1a. Leaves chartaceous. Intercostal veins obscure on both sides. Plant dioecious. Flowers unisexual; ovary 2-celled. Seeds inserted on the septum, the membranous seed wing with a broadly rectangular base and a tapered or acute apex *C. paniculata* (var. *paniculata*)

1b. Leaves coriaceous to subcoriaceous. Intercostal veins prominent on one or both sides. Plant monoecious. Flowers bisexual; ovary 3–4-celled. Seeds inserted at the base of the septum; the membranous seed wing with a tapered or acute to narrowly rectangular or obtuse base and a broadly obtuse to acute apex.

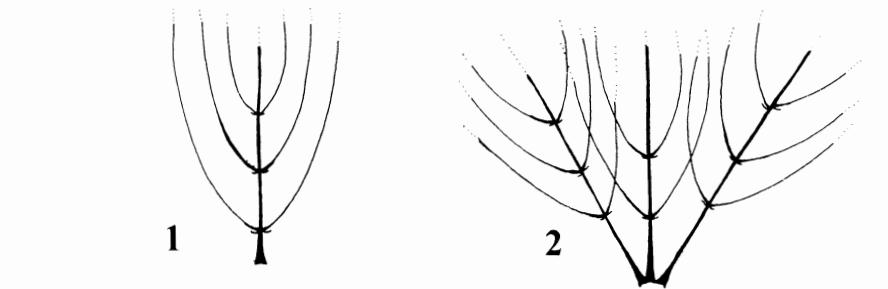
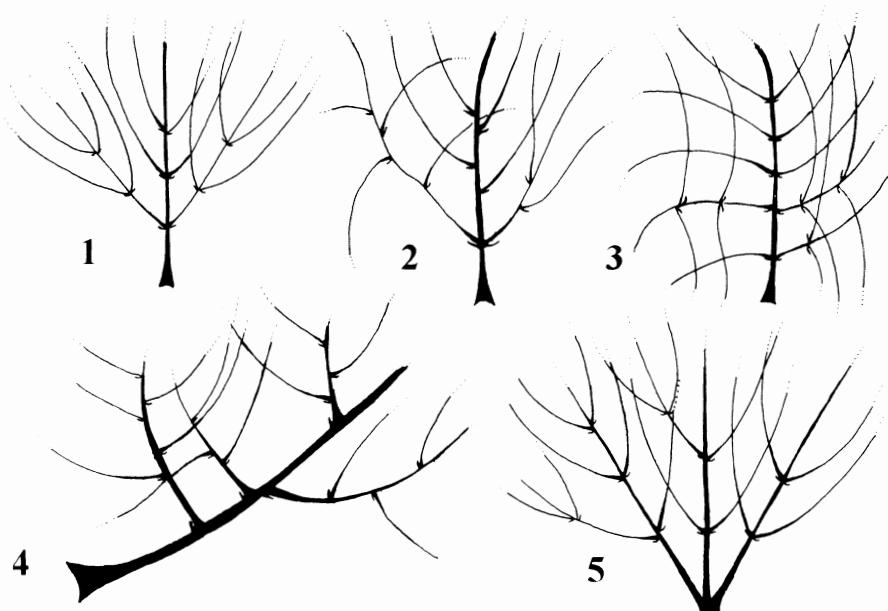
A**B****C**

Fig. 1. Inflorescence form and branching in *Crypteronia* species. **A**, to 1st order. **B**, to 2nd order. **C**, to 3rd order. **A1**, *C. elegans*, *C. glabriflora*, *C. griffithii* and *C. paniculata*. **A2**, *C. elegans*, *C. cumingii* and *C. paniculata*. **B1**, *C. borneensis*, *C. elegans*, *C. glabriflora*, *C. griffithii* and *C. paniculata*. **B2**, *C. cumingii*. **B3**, *C. glabriflora*, *C. griffithii*. **B4**, *C. macrophylla*. **B5**, *C. cumingii*. **C1**, *C. macrophylla*. **C2**, *C. borneensis*.

- 2a. Midrib on upper leaf surface distinctly sunken. Inflorescence bracts 2.5–9 mm long *C. borneensis*, sp. nov.
- 2b. Midrib on upper leaf surface flat. Inflorescence bracts shorter, 0.5–1.5 mm long.
- 3a. Leaves oblong to ovate-oblong. Lateral veins 10–20 pairs. Inflorescences branching to the 3rd order, rarely to only 2nd order; main axis very thick, 3–5 mm thick *C. macrophylla*
- 3b. Leaves narrowly elliptic, elliptic to ovate-elliptic. Lateral veins typically not more than 10 pairs. Inflorescences branching to the 1st or 2nd order (typically to the 1st order); main axis 1–3 mm thick.
- 4a. Leaf apex acuminate to caudate, acumen 0.5–1.8 cm long. Leaf base distinctly cuneate. Intercostal veins distinctly reticulate to tessellate. Petioles slender, only 1–1.5 mm thick. Ovary glabrous. Capsules ellipsoid *C. elegans*, sp. nov.
- 4b. Leaf apex shortly acute, acumen if present shorter, 0.1–0.4 cm long. Leaf base cordate to rounded. Intercostal veins sparsely reticulate. Petioles thicker, 2–7 mm thick. Ovary densely to sparsely minutely papillate to pubescent. Capsules subglobose to ovoid.
- 5a. Inflorescences with ultimate branches typically longer, (15–)20–40 cm; main axis thicker, 2–3 mm. Pedicels very short, 0.1–0.5 mm long, densely pubescent. Sepals broadly spread open in the mature flower, sparsely to densely pubescent outside. Styles sparsely pubescent at base, glabrous at upper part. Seed wing tapered at apex *C. griffithii*
- 5b. Inflorescences with ultimate branches not more than 20 cm long; main axis slender, 1–2 mm thick. Pedicels distinct, 1–1.5 mm long, glabrous. Sepals connate, forming a dome-like structure even in the mature flower, glabrous outside. Styles glabrous throughout. Seed wing broadly obtuse at apex *C. glabriflora*, sp. nov.

The new species

Crypteronia borneensis J.T. Pereira & K.M. Wong sp. nov. *C. macrophylla* Beusekom-Osinga similis sed inter alia, foliis late ovatis, ovatis-ellipticis vel ellipticis

inflorescentiisque brevioribus (usque ad 25 cm longis) differt. Typus: Tarmiji & Talib SAN 90941, Sabah, Beaufort (holotypus SAN). (Fig. 2)

Tree to 25 m and 45 cm diameter. Bark greyish brown, smooth; inner bark brown to greyish. Sapwood yellowish white to brown. Twigs glabrous. Leaves broadly ovate, ovate-elliptic to elliptic, 10–26 × 4–20 cm; apex acute to acuminate, acumen 0.5–1.0 cm long; base cordate, rounded to cuneate; coriaceous to subcoriaceous, drying dark brown to green-brown on both sides, glabrous; midrib distinctly sunken on the upper surface, distinctly raised below; lateral veins 8–15 pairs, distinctly looping towards the margin, sunken to flat above, distinctly raised below; intercostal veins obscure above and prominent below, sparsely reticulate; petioles 0.5–2 cm long, 2–5 mm thick, glabrous. Inflorescences terminal or in the axils of fallen leaves on older branches, 14–25 cm long, branching to the 2nd or 3rd order, main axis 2–4 mm thick, ultimate branches 5–15 cm long, rachis pubescent; bracts 2.5–9 mm long, triangular, subglabrous, persistent. Flowers bisexual, bracteoles (0.5–)1–2 mm long, narrowly triangular to subulate, sparsely hairy, persistent; pedicels 0.5–2 mm long, c. 0.5 mm thick, minutely papillate to pubescent; sepals deltoid to triangular, thickly tomentose inside, minutely papillate to tomentose outside, 0.5–1.5 × 0.5–1.5 mm; stamens 1.5–2.5 mm long, filaments 1–2 mm long, anthers 0.25–0.5 × 0.2–0.8 mm; pistils 2–4 mm long, styles 1–3.5 mm long, densely minutely papillate to tomentose, stigmas capitate; ovary 1–2 mm across, 3–(4)-celled, minutely thickly papillate to tomentose. Capsules subglobose, impressed at the septum, papillate to densely tomentose. Seeds inserted at the base of the septum; seed wing apically broadly obtuse, tapered or acute at base.

VERNACULAR NAME. Sabah—*tampasu* (Dusun).

DISTRIBUTION. Endemic to Borneo (Sabah, Sarawak and Brunei).

HABITAT. Occurring from lowland to highland reaching c. 600 m, primary forest, frequently near river banks. Recorded on clay-rich, well-drained alluvium to sandy soils.

SPECIMENS EXAMINED—BORNEO. SABAH: Beaufort, *Tarmiji & Talib* SAN 90941 (holotype SAN), Saliwangin, Bakar 2374 (K). Papar, Ulu Kimanis, *Dewol & Talib* SAN 80470 (K, KEP, L, SAN, SAR). Sugut, Ulu Sg. Kaindangan, *Cockburn* SAN 82525 (K, SAN). **SARAWAK:** 4th Division, Anap, Muput Kanan, Ulu Naoung, Ashton S. 19566 (A, BO, K, KEP, L, MEL, SAN, SAR, SING), Bintulu, Buan Forest Reserve, Ilias, Bandan & Sie S. 32184 (BO, K, L, SAN, SAR, SING), Sg. Perawan, Daud & Tachun SFN 35724 (K, SING). Sarawak without precise locality, *Beccari* 3870 (K, SAR). **BRUNEI:** Belait, along the Sg. Ingei near Batu Melintang Wong WKM 710 (BRUN, K, KEP, SAN, SING). Ulu Ingei, Brunig S. 1012 (K, SAR).

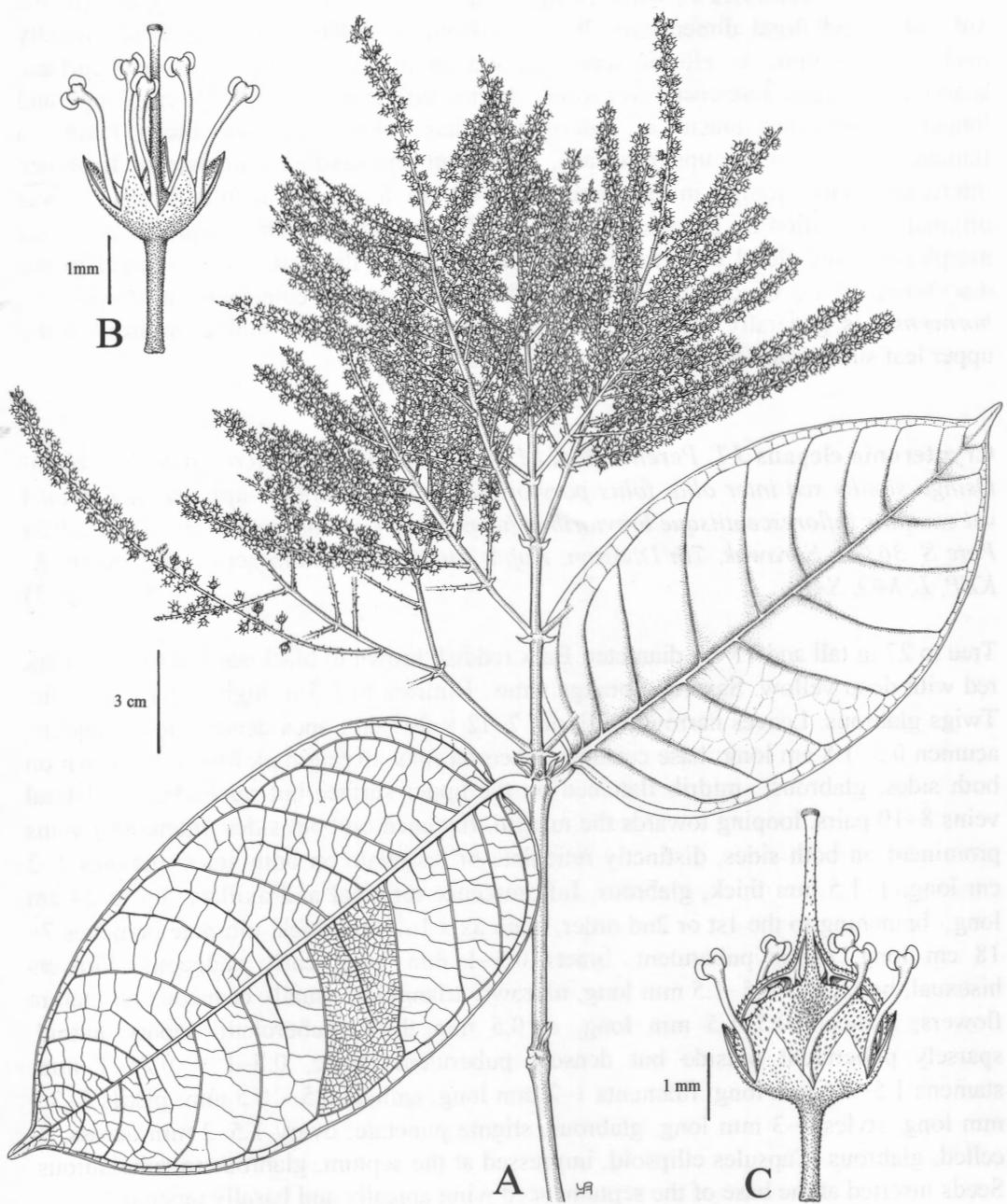


Fig. 2. *Crypteronia borneensis*. **A.** Fruiting leafy branch. **B.** Flower. **C.** Fruit. **A and C** from SAN 90941, **B** from SAN 80470.

C. borneensis resembles *C. macrophylla* in the inflorescence branching habit (to the 3rd order) and floral dimensions. It differs from *C. macrophylla* in having broadly ovate, ovate-elliptic to elliptic leaves, a sunken midrib on the upper leaf surface, sparsely reticulate intercostal venation, shorter inflorescences (to 25 cm long) and longer inflorescence bracts. *C. macrophylla* has oblong to ovate-oblong leaves, a flattened midrib on the upper surface, prominent and distinct reticulate or tessellate intercostal veins, longer inflorescences (30–40 cm long) and shorter bracts. It was originally identified by Beusekom-Osinga as *C. cumingii*, which it approaches in leaf morphology and floral dimensions but differs from in the features mentioned in the discussion of the *C. cumingii* complex (above). From its congeners in Borneo, *C. borneensis* is generally distinguishable by the comparatively sunken midrib on the upper leaf surface and long inflorescence bracts.

Crypteronia elegans J.T. Pereira & K.M. Wong sp. nov. *C. macrophylla* Beusekom-Osinga similis sed inter alia, foliis parvioribus anguste ellipticis apicibus acuminatis vel caudatis inflorescentiisque brevioribus (usque ad 24 cm longis) differt. Typus: Ilias Paie S. 36393, Sarawak, 7th Division, Kapit, Bukit Bakar (holotypus SAN; isotypi K, KEP, L, MO, SAR). (Fig. 3)

Tree to 27 m tall and 75 cm diameter. Bark reddish brown to blackish, flaky; inner bark red with deep yellow. Sapwood orange straw. Buttress to 1.5 m high and 1.5 m wide. Twigs glabrous. Leaves narrowly elliptic, 7–12 × 2–5 cm; apex acuminate to caudate, acumen 0.5–1.8 cm long; base cuneate; subcoriaceous, drying dark brown to brown on both sides, glabrous; midrib flattened on the upper surface but raised below; lateral veins 8–10 pairs, looping towards the margin, flattened on both sides; intercostal veins prominent on both sides, distinctly reticulate or tessellate on both sides; petioles 1–2 cm long, 1–1.5 mm thick, glabrous. Inflorescence terminal and axillary, up to 24 cm long, branching to the 1st or 2nd order, main axis 1–2 mm thick, ultimate branches 7–18 cm long, rachis puberulent; bracts 0.5–1 mm long, early caducous. Flowers bisexual, bracteoles 0.5–1.5 mm long, narrowly triangular, usually caducous on mature flowers; pedicels 0.5–1.5 mm long, c. 0.5 mm thick, puberulent; sepals deltoid, sparsely puberulent outside but densely puberulent inside, 0.5–1 × 0.75–1 mm; stamens 1.5–2.5 mm long, filaments 1–2 mm long, anthers 0.5 × 0.5 mm; pistils 2–3.5 mm long, styles 1–3 mm long, glabrous, stigma punctate; ovary 1.5–2 mm across, 3-celled, glabrous. Capsules ellipsoid, impressed at the septum, glabrous to subglabrous. Seeds inserted at the base of the septum; seed wing apically and basally tapered.

DISTRIBUTION. Endemic to Borneo (Sarawak and Brunei); not yet recorded for Sabah.

HABITAT. Hills and ridges of lowland mixed dipterocarp forest and secondary forest, to 1100 m high.

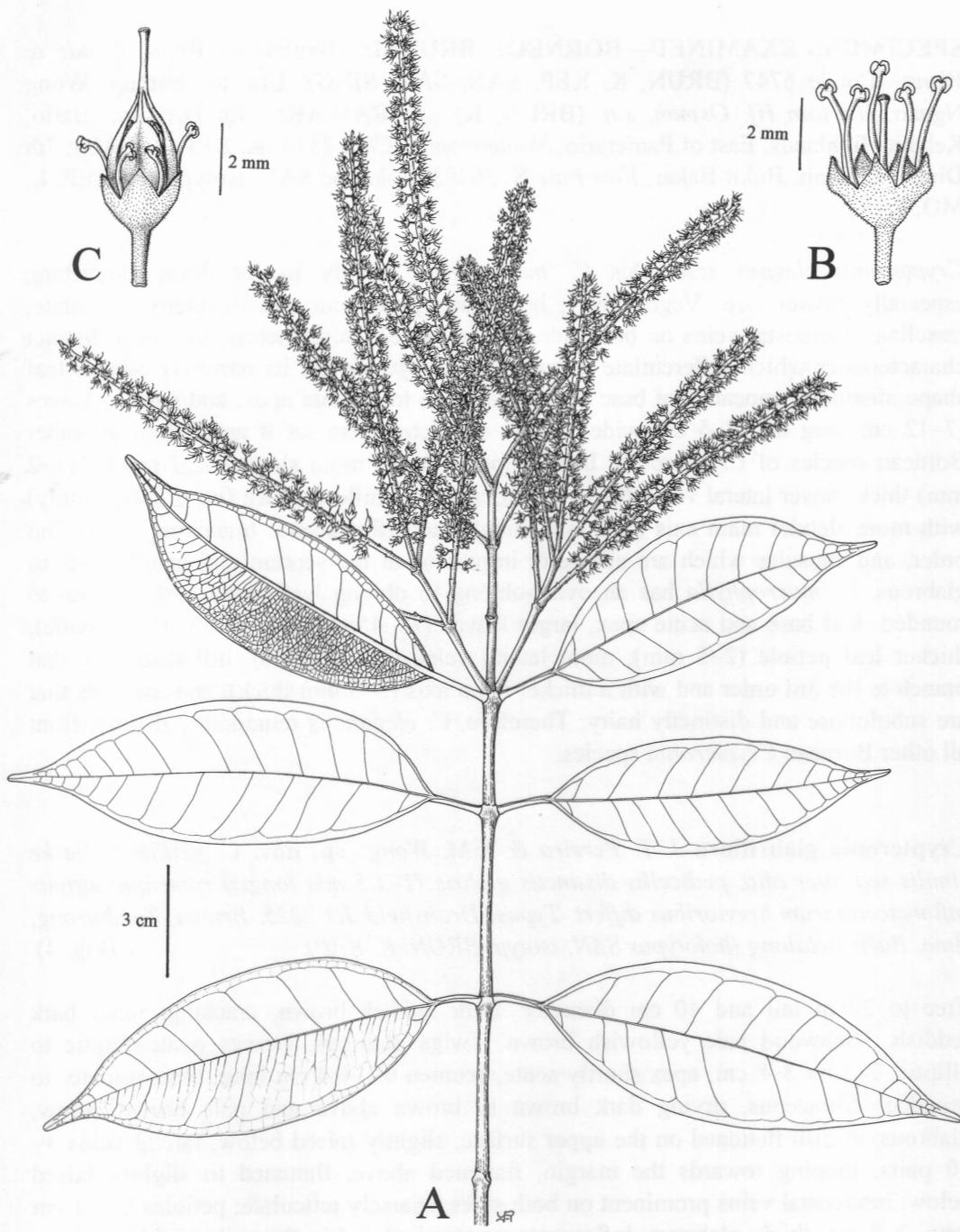


Fig. 3. *Crypteronia elegans*. **A.** Flowering leafy branch. **B.** Flower. **C.** Young fruit. **A** and **C** from Nooteboom & Chai 2114, **B** from S. 36393.

SPECIMENS EXAMINED—BORNEO. BRUNEI: Temburong River, Coode & Wong Coode 6747 (BRUN, K, KEP, SAN, SAR, SING), Ulu Temburong, Wong Nguan, Hussain Hj. Osman, s.n. (BRUN, K). SARAWAK: 4th Division, Bario, Kelabit Highlands, East of Pamerario, Nooteboom & Chai 2114 (K, KEP, L, SAR); 7th Division, Kapit, Bukit Bakar, Ilias Paie S. 36393 (holotype SAN, isotypes K, KEP, L, MO, SAR).

Crypteronia elegans resembles *C. macrophylla* chiefly in its floral characters, especially flower size. Vegetatively, both have prominent and distinctly reticulate, tessellate intercostal veins on both sides of the leaves. Nevertheless, the most distinct characteristics which differentiate it from *C. macrophylla* are its narrowly elliptic leaf shape, distinctly cuneate leaf base with acuminate to caudate apex, and smaller leaves (7–12 cm long and 2–5 cm wide). These characters also set it apart from all other Bornean species of *Crypteronia*. In addition, it has a more slender leaf petiole (1–2 mm) thick, fewer lateral veins (8–10 pairs), a shorter inflorescence (up to 24 cm only) with more slender main axis (1–2 mm thick), and inflorescence branching to the 2nd order, and capsules which are ellipsoid, impressed at the septum and subglabrous to glabrous. *C. macrophylla* has an ovate-oblong to oblong leaf shape with cordate to rounded leaf base and acute apex, larger leaves (18–45 cm long and 8–18 cm wide), thicker leaf petiole (2–5 mm), more lateral veins (10–20 pairs), inflorescences that branch to the 3rd order and with a thicker main axis (3–5 mm thick), and capsules that are subglobose and distinctly hairy. Therefore, *C. elegans* is remarkably distinct from all other Bornean *Crypteronia* species.

***Crypteronia glabriflora* J. T. Pereira & K.M. Wong sp. nov.** *C. griffithii* Clarke similis sed inter alia, pedicellis distinctis glabris (1–1.5 mm longis) ramisque ultimis inflorescentiarum brevioribus differt. Typus: Dransfield JD 7225, Brunei, Temburong, Amo, Bukit Belalong (holotypus SAN; isotypi BRUN, K, KEP). (Fig. 4)

Tree to 20 m tall and 40 cm diameter. Bark reddish brown, cracking; inner bark reddish. Sapwood pale yellowish brown. Twigs glabrous. Leaves ovate-elliptic to elliptic, 7–20 × 3–8 cm; apex shortly acute, acumen 0.1–0.4 cm long; base cordate to rounded; coriaceous, drying dark brown to brown above and pale brown below, glabrous; midrib flattened on the upper surface, slightly raised below; lateral veins 8–10 pairs, looping towards the margin, flattened above, flattened to slightly raised below; intercostal veins prominent on both sides, sparsely reticulate; petioles 0.4–1 cm long, 2–3 mm thick, glabrous. Inflorescences terminal and in the axils of fallen leaves on older branches, 12–20 cm long, branching to the 1st or 2nd order, main axis 1–2 mm thick, ultimate branches 5–20 cm long, rachis puberulent; bracts 0.5–1 mm long, triangular, glabrous, caducous. Flowers bisexual, bracteoles 0.5–1 mm long, narrowly triangular, pubescent, persistent; pedicels 1–1.5 mm long, c. 0.5 mm thick, glabrous;

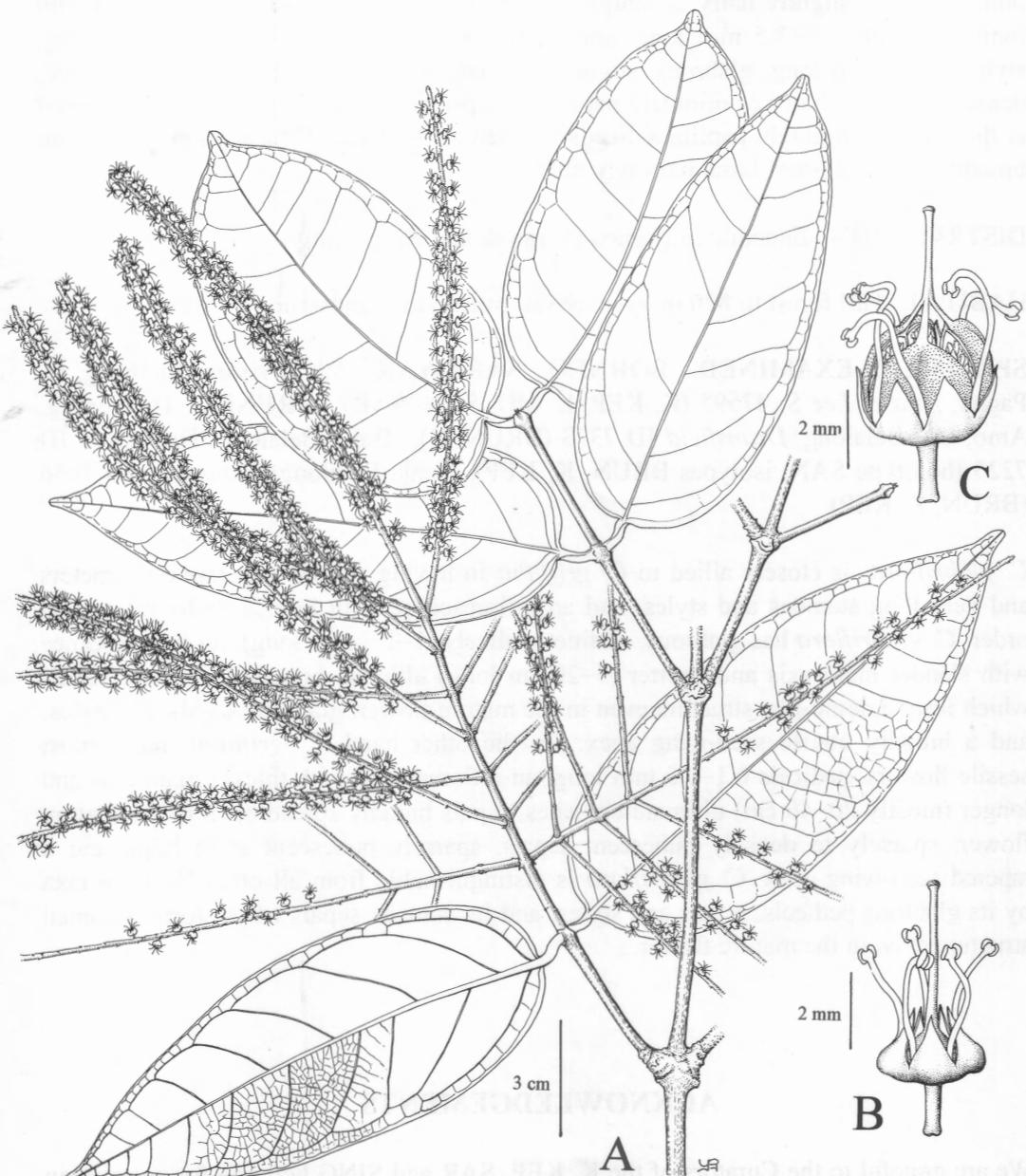


Fig. 4. *Crypteronia glabriflora*. **A.** Flowering leafy branch. **B.** Flower. **C.** Young fruit. All from Dransfield JD 7225.

sepals connate, forming a dome-like structure even in the mature flower, glabrous on both sides but slightly hairy at margin below, 1–1.5 × 1–1.5 mm; stamens 3–4 mm long, filaments 2.5–3.5 mm long, anthers 0.5 × 0.5 mm; pistils (3–)4–5 mm long, styles 2–4.5 mm long, glabrous, stigmas punctate; ovary 1–1.5 mm across, 3-celled, densely powdery hairy or minutely papillate. Capsules subglobose to ovoid, impressed at the septum, minutely papillate. Seeds inserted at the base of the septum, seed wing broadly obtuse at apex, basal narrowly obtuse.

DISTRIBUTION. Endemic to Borneo (Sarawak and Brunei only).

HABITAT. Hill forest to 820 m. on clay soil overlaying sandstone.

SPECIMENS EXAMINED—BORNEO. SARAWAK: 5th Division, Limbang, G. Pagon, Awa & Lee S. 47595 (K, KEP, L, MO, SAN, SAR). **BRUNEI:** Temburong, Amo, Ulu Belalong, Dransfield JD 7373 (BRUN, K). Bukit Belalong, Dransfield JD 7225 (holotype SAN; isotypes BRUN, K, KEP), Kuala Belalong Dransfield JD 7056 (BRUN, K, KEP).

C. glabriflora is closely allied to *C. griffithii* in having similar vegetative characters and very long stamens and styles, and an inflorescence with branching to 1st or 2nd order. *C. glabriflora* has glabrous, distinct pedicels (1–1.5 mm long), an inflorescence with slender main axis and shorter (5–20 cm long) ultimate branches, connate sepals which form a dome-like structure even in the mature flower, glabrous sepals and styles, and a broadly obtuse seed-wing apex. On the other hand, *C. griffithii*, has almost sessile flowers, pedicels 0.1–0.5 mm long, an inflorescence with thicker main axis and longer (mostly 20–40 cm) ultimate branches, sepals broadly spread open in the mature flower, sparsely to densely pubescent sepals, sparsely pubescent style base, and a tapered seed-wing apex. *C. glabriflora* is distinguishable from all other Bornean taxa by its glabrous pedicels, sepals and styles, and its connate sepals which form a domed structure even in the mature flower.

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Notes on a myrmecophytic heterophyllous *Diospyros* (Ebenaceae)

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Summary. *Diospyros andamanica* (Ebenaceae), a heterophyllous tree, is documented as a facultative myrmecophyte. Ants of various species build carton structures around clusters of small, cup-shaped leaves and branch bases found along the stem of this tree, and also cultivate scale insects within. It is pointed out that in this species, the availability of suitable nesting space for ants may have been more important than the presence of extrafloral nectaries, found in the form of leaf glands in many species of *Diospyros*, in encouraging a myrmecophytic association.

Although, in the past decade, the biology of ant-plant associations have attracted more interest than previously (see Beattie 1985, Benson 1985, Cutler & Huxley 1991, Keeler 1989), the basic information and lists of Asiatic ant-plants by Bequaert (1922) and Benson (1985) have only been further augmented largely through the recent work of Fiala and Maschwitz and their team based in Southeast Asia (see, for example, Fiala *et al.* 1989, Fiala & Maschwitz 1991, Fiala, Maschwitz & Tho 1991, Maschwitz *et al.* 1989, 1991). The plant species that take part in such myrmecophytic associations come from diverse families, and the ants documented in these associations mostly belong to species of *Camponotus* (including *Colobopsis*), *Cladomyrma*, *Crematogaster*, *Monomorium*, *Nylanderia*, *Tetramorium*, and *Tetraponera* (many Southeast Asian ants cannot as yet be named to species level with confidence).

The associations may be broadly categorised as representing nutrient symbioses, seen primarily in ant-associated epiphytes such as *Hydnophytum* and *Myrmecodia* (Rubiaceae) where ant associates enrich the nutrient status of the plant (Huxley 1978), or as symbioses that afford the plant protection against herbivores or vine-growth, such as in *Macaranga* associations with ants (Fiala, Maschwitz & Tho 1991). Ants inhabit a variety of plant structures in consistent ant-plant associations, usually hollow branch or stem internodes which may be locally swollen (e.g., *Clerodendron fistulosum*, Verbenaceae; *Myrmeconauclea strigosa* and some *Neonauclea* spp., Rubiaceae; *Macaranga constricta*, Euphorbiaceae) or not (e.g., *Millettia nieuwenhuisiae*, Papilionaceae; various *Macaranga* spp.), and including inflated stem (hypocotyl) tubers (e.g., *Hydnophytum*, *Myrmecodia*) and hollow rhizomes (e.g., *Lecanopteris*, Polypodiaceae).

Here we report a myrmecophytic association in *Diospyros andamanica* (Ebenaceae), as observed within a population studied on Gemok Hill in eastern Sabah, Malaysian Borneo. This species is heterophylloous, i.e., produces two distinct forms of leaf (see below for details), and has not been documented before as a myrmecophyte. The reason for this most probably is that typically only the non-ant inhabited, more distal flowering portions of the branches are collected as botanical specimens, whereas those parts inhabited by ants (stems near branch bases with small, cup-shaped leaves) were overlooked or ignored.

Architecture and morphology of *Diospyros andamanica*

All trees of *Diospyros andamanica* observed on Gemok Hill in eastern Sabah (vouchers deposited at SAN: SAN 134544 for female tree, SAN 134545 for male tree) were essentially monopodial, with loosely arranged tiers of plagiotropic branches produced at intervals along the stem. Their architecture conforms to Massart's model as elucidated by Hallé, Oldeman & Tomlinson (1978), a model common in the genus. Vertical shoots representing reiterative growth on leaning or damaged stems also show the same growth architecture (Fig. 1).

Trees of this species bear two forms of leaf. Leaves along the plagiotropic branches that are typically large (10–25 cm long), ovate-elliptic, plane and with short but distinct stalks constitute one leaf form (Fig. 2A; also the inflorescences are borne in the axils of such leaves, cf. Fig. 2D). Leaves borne on the stem itself, near the bases of and intermingled with branches, which are small (up to 3.5 cm long at most), broadly ovate to orbicular, with strongly recurved margins making the whole leaf cup-shaped and with scarcely distinct stalks constitute the other leaf form (Fig. 2A–C). On both forms of leaf, there are typically two to four dark, crater-shaped nectariferous glands at the base of the lower surface (Fig. 2D).



Fig. 1. Erect shoot of *Diospyros andamanica*, showing a tier of plagiotropic branches and two forms of leaves. (Photo by C. Puff.)

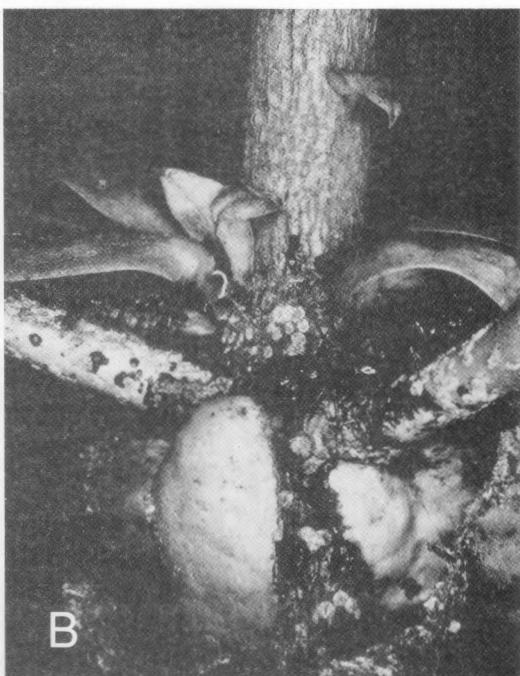
The ant structures and their inhabitants

Every tree in the population studied harboured ants which built carton structures around the clusters of small, cup-shaped leaves and branch bases along the stem (Fig. 2A–C, Fig. 3). Very often, these carton structures also completely enveloped the stem at these portions, as well as most of the cup-shaped leaves present there (Fig. 3). Within the carton structures were also found brood (although it was not known to which ant species they belonged) and many scale insects (Hemiptera: Coccoidea), which were apparently tended by ants.

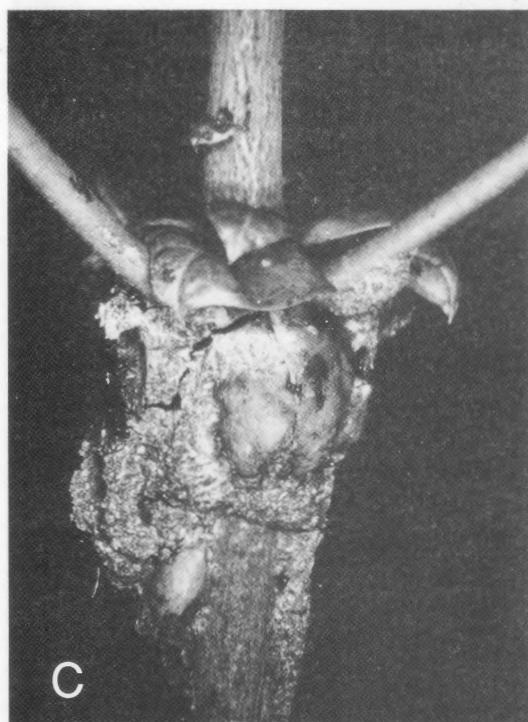
The identity of ants found in such carton structures from seven different trees is shown in Table 1. These ants are from six species representing five genera in three different families: Dolichoderinae (*Dolichoderus*, *Technomyrmex*), Formicinae (*Camponotus*, *Polyrhachis*) and Myrmicinae (*Crematogaster*). The most common was *Crematogaster* sp. A, although it was absent in one of the samples. Two of the samples comprised of one species of ant each, but most samples had at least two species of ant. The fact that several ant species can opportunistically share a nesting space indicates that the



A



B



C



D

Fig. 2. *Diospyros andamanica*. A, shoot with two tiers of branches, and ant carton enveloping the stem. B, close-up of space in between small, cup-shaped leaves and branch bases on a stem, showing ants and scale insects. C, carton structure built around branch bases and small, cup-shaped leaves on a stem. D, lower surface of larger leaves along plagiotropic branches, showing glands at the leaf base and axillary inflorescences. (Photos by C. Puff.)

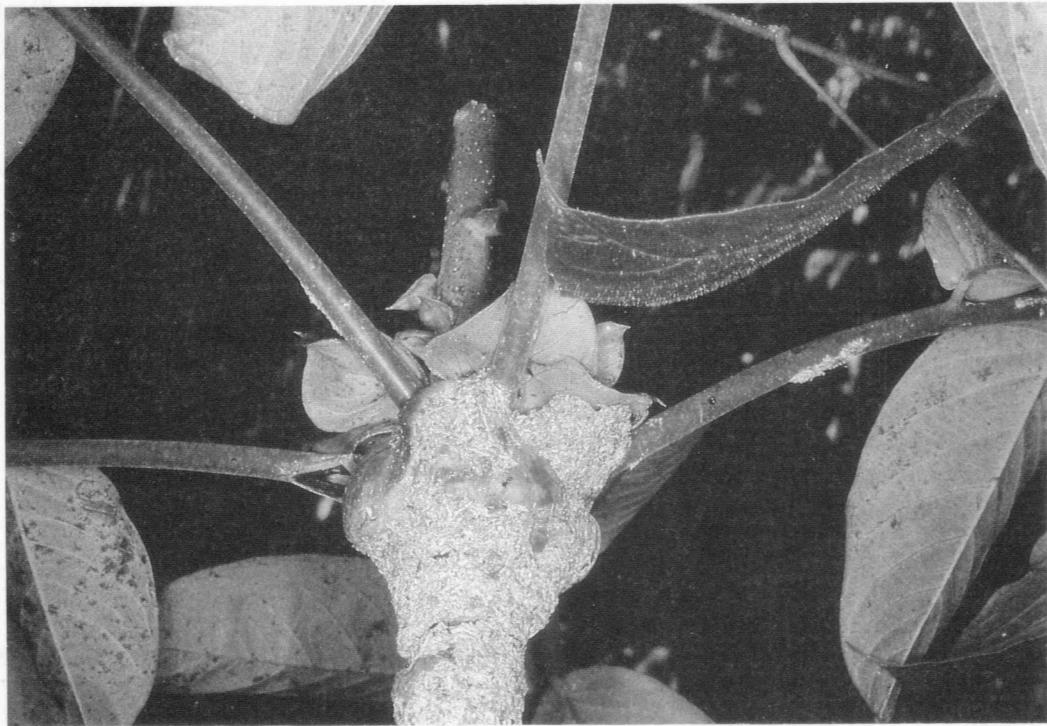


Fig. 3. The ant carton structures in *Diospyros andamanica* often completely envelop the stem as well as branch bases and small, cup-shaped leaves. (Photo by C. Puff.)

association with ants in *Diospyros andamanica* is a facultative one, and not a highly developed obligate association with any one ant.

The relative importance of extrafloral nectaries and available nesting space

In their considerations of the ant-plant relationships shown in *Macaranga* systems, Fiala & Maschwitz (1991) found that the marginal leaf glands of *Macaranga* species that were not obligate myrmecophytes (i.e., not regularly inhabited by ants) functioned as extrafloral nectaries, whereas those of obligately myrmecophytic species secreted a liquid that did not contain any sugar. They noted that some non-myrmecophytic *Macaranga* and a few transitionally myrmecophytic species also had additional extrafloral nectaries on the leaf blade near the leaf stalk insertion. They surmised that reduction of nectary production in ant-inhabited *Macaranga* species was biologically significant as an assimilate-saving device, as these ants also kept scale insects through which they sequestered sugars, and that this lack of extrafloral nectaries helped maintain the specificity of the association through not attracting ants in general. The leaf-base glands of *Diospyros andamanica* in the present case appear to be functional

Table 1. Ants from carton structures collected from seven different trees (T1–7) of *Diospyros andamanica* at Gemok Hill in eastern Sabah. Ant specimens are kept in the spirit collection of the herbarium (SAN) of the Forest Research Centre in Sandakan, Sabah, Malaysia.

Ant family	Ant species	T1	T2	T3	T4	T5	T6	T7
Dolichoderinae	<i>Dolichoderus sp. A</i>	+			+			
Dolichoderinae	<i>Technomyrmex sp.</i>					+		
Formicinae	<i>Camponotus sp. A</i>			+		+	+	+
Formicinae	<i>Camponotus sp. B</i>					+		
Formicinae	<i>Polyrhachis sp.</i>			+				
Myrmicinae	<i>Crematogaster sp. A</i>	+	+	+	+	+	+	+

extrafloral nectaries, as they are visited by foraging ants, although scale insects are evidently also cultivated within the carton structures built by ants.

Diospyros is represented by many species in the Bornean lowland forests and many species have distinct glands on their leaves; the fact that obligate myrmecophytism (i.e., specific ant-plant association) appears to be absent in the genus thus far, and that the present case of myrmecophytism is a rare occurrence in the genus and a facultative one involving exploitation of available nesting space by a variety of ant species supports the observation of Fiala & Maschwitz (1991) that the possession of extrafloral nectaries does not appear to have been essential in the evolutionary development of symbiotic ant-plant associations. As also discussed by McKey (1989) and Fiala & Maschwitz (1991, 1992), the provision of suitable nesting space by the plant appears to be fundamentally important in the development of myrmecophytism. In this regard, the heterophyllous condition of *Diospyros andamanica*, an uncommon condition within the genus, may have been important in encouraging a myrmecophytic association.

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**A new *Begonia* (*Begoniaceae*),
Hoya (*Asclepiadaceae*) and
Sonerila (*Melastomataceae*)
from Fraser's Hill, Peninsular Malaysia**

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Summary. A recent field survey of the conservation status of plants at Fraser's Hill, Pahang, in Peninsular Malaysia led to the discovery of three new taxa—*Begonia fraseri* Kiew (Begoniaceae), *Hoya parasitica* (Roxb.) Wall. ex Wight var. *hendersonii* Kiew (Asclepiadaceae) and *Sonerila fraseri* Kiew (Melastomataceae).

Fraser's Hill is a well-known hill station which most botanists have visited and made collections from since I.H. Burkhill and R.E. Holttum first carried out a botanical reconnaissance of the area in 1922 when the hill station was first being opened up for development.

With recent extensive development and future plans for further development, it was timely to carry out a field survey to assess the conservation status of the flora and of rare and endangered species in particular. This led to the discovery of the new *Sonerila fraseri* on Pine Tree Hill, the highest peak, and the recognition as new of two other taxa, *Begonia fraseri* and *Hoya parasitica* var. *hendersonii*. While *S. fraseri* is endemic to Fraser's Hill, the other two taxa have been collected from one other mountain in Pahang, in the case of the begonia from Gunung Benom and for the hoya from lower montane forest at Cameron Highlands.

This brief paper validates the names of these taxa prior to the publication of the full account of “A Checklist of Seed Plants of Fraser’s Hill and their Conservation Status” by the Forest Research Institute Malaysia.

Descriptions of the new taxa

Begonia fraseri Kiew sp. nov. *habitu B. longicaulis et B. venusta affinibus, ab ambobus pedunculis petiolis brevioribus differt. Typus: R. Kiew RK 3831, Peninsular Malaysia, Fraser’s Hill (holotypus UPM).*

Low decumbent herb, prostrate; stem slender, rooting at nodes, erect stem *c.* 14–30 cm long and 0.6 cm thick, reddish brown, fleshy, glabrous, nodes with a raised coky annulus, internodes 12–22.5 cm long. Stipules in pairs, persistent, glabrous, narrowly triangular 10–20 × 3.5–5 mm, apex setose. Petiole erect, glabrous, reddish brown, fleshy, on prostrate stems 10.5–24.5 cm long, on erect stems 7.5–22 cm long. Lamina unequal; midrib perpendicular to petiole; broadly oval, 12–17.5 × 7–15 cm, base cordate, unequal, apex cuspidate 1.5 cm long; chartaceous in dried state, in life glossy, dark green sometimes with a bluish hue; margin subentire, minutely denticulate corresponding to vein endings; lateral veins 4–6, radiating from base, 3–4 on the larger half of leaf and 1–2 on the smaller, slender, midrib and veins slightly impressed above, prominent beneath. Indumentum: lamina glabrous to the naked eye but both surfaces with sparse microscopic uniseriate trichomes, lower surface of midrib and veins ferrugineous from appressed matted reticulum of fine trichomes. Inflorescence a terminal cymose panicle, (2–)4–9 cm long extending to 11 cm in fruit, with one large terminal male flower 3.5 cm long and 4 reduced cymules each comprising one female flower and one smaller male flower 2.5 cm long. Peduncle 6–10.5 cm long, reddish-green, glabrous; bracts erect, narrowly triangular, 5 × 1.5 mm, apex acute. Pedicels of male flowers 7–10 mm long, of female flowers 2–3 mm extending to 25 mm in fruit. Flowers white, tinged pink in upper half of tepals, becoming completely white with age, pedicel of largest flower 22 mm long. Male flowers with 2 almost circular persistent outer tepals, up to 17 × 17 mm in terminal flower and 11–13 × 14–16 mm in lateral flowers, inner tepals elliptic, (6–)10–13 × 5–8 mm, apex rounded, extremely thin and delicate, caducous; stamens many and clustered, cluster sessile; filament 2 mm long, pale yellow; anther 1.5 mm long, spatulate, connective broad. Female flowers with 4 pink tepals, isomorphic and equal-sized, ovary with 3 equal wings, green tinged red, locules 2, placenta divided into 2. Capsule pendant, 15–17 mm long and 28–36 mm wide (measured to the tips of wings), 2 lateral wings bluntly triangular, thin, subcoriaceous, 7–13 mm long and 8–13 mm wide, posterior wing oblong with rounded apex, robust and fibrous, 12–15 mm long and 12–15 mm wide. Seeds oblong, *c.* 0.3 mm long, collar cells straight and about half length of seed.

DISTRIBUTION. Pahang, at Fraser's Hill and Gunung (Mt.) Benom. At Fraser's Hill it is not common and is known from a few, very localised populations.

HABITAT. Lower montane forest at about 1325 m (on Gunung Benom *c.* 1700 m), in deep shade on well-drained slopes usually growing on the ground, sometimes scrambling over rocks or low shrubs.

SPECIMENS EXAMINED—PENINSULAR MALAYSIA: Pahang, Fraser's Hill, Addison SFN 37198 (SING), SFN 37381 (SING), Allen s.n. 24 March 1953 (SING), Burkhill & Holttum 8428 (SING), Corner SFN 33176 (SING), Kiew RK 1247 (UPM), RK 3268 (UPM), RK 3562 (UPM), RK 3829 (UPM); Gunung Benom, *Nat. Coll. F.M.S. Mus.* s.n. 2 Aug 1925 (SING).

This species was first collected by Burkhill and Holttum in 1922, who recorded it as *Begonia* sp. in their list of plants from Fraser's Hill (Burkhill & Holttum 1923). Henderson (1927) later identified it as *B. longicaulis* Ridl., a species known from upper montane forest on Gunung Tahan, Pahang, and Gunung Korbu, Perak.

It certainly belongs to the same group of species as *B. longicaulis*, which Irmscher (1925) placed in *Begonia* section *Platycentrum* subsection *Venustae*. Within subsection *Venustae*, only *B. longicaulis* and *B. venusta* King share the same habit as *B. fraseri* in producing slender prostrate stems, which give rise to semi-erect stems (i.e., stems which become decumbent unless supported) with long internodes. They also all produce few-flowered inflorescences with large white male flowers.

While resembling *B. longicaulis* in its cuspidate leaf apex and persistent setose stipules, *B. fraseri* differs in fruit shape (*B. longicaulis* has a unique fruit with a narrow posterior wing, Fig. 1). It also differs from *B. longicaulis* in the male flowers having inner tepals less than half the width of the outer (in *B. longicaulis* the outer tepals are narrower than the inner). Fruits of *B. fraseri* and *B. venusta* are similar in having a broad posterior wing but that of *B. venusta* is more tapered (Fig. 1a & c). *B. venusta* also differs in the leaf, which is frequently reddish beneath and which has an acuminate apex, and in the female flowers, which have five petals. In addition, *B. fraseri* differs from both these species in its leaf, which is oval (i.e., significantly longer than broad, while the other two species have leaves almost as wide as long) and in its peduncle, which is much shorter than the petiole (the other two species have peduncles as long as or longer than the petioles).

Begonia fraseri grows at lower altitudes (1000–1270 m) on Fraser's Hill than either *B. venusta* (1500–2000 m) or *B. longicaulis* (1850 m). From Gunung Benom it was recorded at *c.* 1700 m but this is doubtful as field notes are lacking.

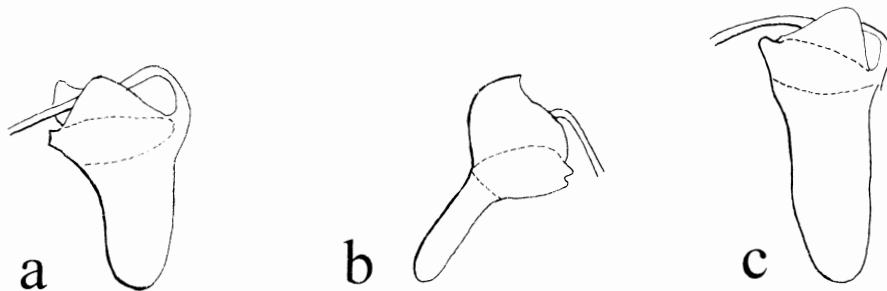


Fig. 1. *Begonia* fruits: **A.** *B. fraseri* (Kiew RK 3831). **B.** *B. longicaulis* (Kiew RK 2454). **C.** *B. venusta* (Jaamat 27575). All life-size.

Hoya parasitica (Roxb.) Wall. ex Wight var. **hendersonii** Kiew, var. nov. *a Hoya parasitica* (Roxb.) Wall. ex Wight var. *citrina* (Ridl.) Rintz. foliorum angustioribus et tenuioribus diagnoscenda. Typus: Henderson SFN 23668, Peninsular Malaysia, Cameron Highlands, Ringlet (holotypus SING).

Glabrous climber; stem with conspicuous lenticels, c. 5 mm thick. Petiole stout, 2 cm long, 3 mm thick. Lamina narrowly ovate to oblong, 11.5–17 × 5–6.5 cm, base rounded, slightly cordate at petiole (i.e., cordate base does not extend beyond width of petiole), margin slightly recurved drying undulate, apex acuminate; main pair of secondary veins parallel to midrib and reaching apex, basal pair of weak veins parallel and close to margin, tertiary veins forming a fine much-branched reticulum, in dried state midrib, secondary and tertiary veins slightly prominent above and beneath, in life veins slightly prominent above but plane beneath, thickly coriaceous but not rigid, green above and beneath. Inflorescence axillary, umbellate, peduncle 2.75–7.5 cm long, 2 mm thick, stiff, erect, many-flowered (15 flowers in *Md Nur* s.n. and 25 in Henderson SFN 23668), flowers forming a hemisphere. Pedicels slender, of equal length, 1.3–2.5 cm long. Flower 11 mm wide, corona 8 mm wide; calyx tube 0.5 mm long, lobes acute 3 mm long, 1 mm wide at base narrowing to a rounded apex, appressed to corolla; corolla tube 3.5 mm long, lobes 5.5 mm long, 4.5 mm wide in basal half narrowing to an acuminate apex in upper half, glabrous to naked eye, minutely pubescent at ×30 magnification; corona lobes elliptic, 4 × 2 mm, not curved, both outer and inner phlanges narrowed to apex; anther 0.6 mm long, caudicle short without wings, pollinia ellipsoidal with narrow longitudinal wing; stigmatic surface slightly depressed. Follicles not known.

DISTRIBUTION. Endemic to Peninsular Malaysia, known only in Pahang at Cameron Highlands and Fraser's Hill.

HABITAT. Lower montane forest, 1200–1260 m altitude.

SPECIMENS EXAMINED—PENINSULAR MALAYSIA: Pahang, Cameron Highlands, Boh Plantations, *Md Nur* s.n. 29 April 1937 (SING); Fraser's Hill, *R. Kiew & S. Anthonysamy* RK 3531, 23 April 1992 (UPM).

Of the 26 Peninsular Malaysian hoyas, few live above 1000 m altitude. Only four, *H. lacunosa* Bl., *H. micrantha* Hook. f., *H. wrayi* King & Gamble and this new variety of *H. parasitica*, are found in lower montane forest. No species is found in upper montane forest. In addition, *H. parasitica* var. *hendersonii* is rare, being known from just three collections.

This new variety has flowers which are closely similar to those of *H. parasitica* except that the corolla lobes on *Henderson* SFN 23668 are not reflexed and are almost glabrous. However, towards the end of the flowering period the corolla lobes of *H. parasitica* var. *parasitica* partially close. It is possible that the flower of var. *hendersonii* were collected at this stage. Rintz (1978) describes the corollas of var. *parasitica* and var. *citrina* (Ridl.) Rintz as pubescent and his illustrations show them as conspicuously and very densely pubescent. However, in the flowers I examined they were only minutely pubescent, appearing almost glabrous to the naked eye.

The three varieties can be distinguished on leaf characters (Table 1). Var. *hendersonii* is more similar to var. *citrina* in its ovate leaf, slightly cordate base, venation and longer petioles but differs in the leaf being less rigid and proportionally narrower. Another apparent difference according to Rintz (1978) is in pedicel length which he recorded as c. 3 cm long in var. *citrina* and var. *parasitica*, but examination of specimens does not support this as pedicel length ranges from 2 to 3 cm in these two varieties and so is not different from that in var. *hendersonii*.

In Peninsular Malaysia the varieties are separated ecologically. As mentioned above, var. *hendersonii* grows in lower montane forest between 1200 and 1260 m altitude, the other two are lowland species. Var. *parasitica* is common in strand forest especially on islands, while var. *citrina* is common on limestone (though it is rarely found in flower) and sometimes in riverine fringe forest.

Although Ridley (1923) named var. *citrina* for its yellow flowers, flower colour is variable in both var. *citrina* (light yellow or white with a deep red or pinkish red centre) and var. *parasitica* (white to pinkish-white with pink or red centre). Flowers of var. *citrina* are fragrant, sometimes producing a strong gardenia scent. The flower colour and scent of var. *hendersonii* were not recorded.

Table 1. Characters which distinguish the three Peninsular Malaysian varieties of *Hoya parasitica*.

	var. <i>parasitica</i>	var. <i>citrina</i>	var. <i>hendersonii</i>
Lamina			
shape	elliptic	ovate	narrowly ovate-oblong
length (cm)	(6.5–)11(–13.5)	10–18.5	11.5–17
width (cm)	(3–)4.5(–6)	6.5–8.5	5–6.5
width:length ratio	1: 2.5	1: < 2	1: 2–3.5
base	cuneate	cordate	cordate
texture	succulently coriaceous	rigidly coriaceous	coriaceous
Venation			
prominence	obscure	conspicuous	conspicuous
lowest pair of lateral veins extending	about halfway to apex	to apex	to apex
Petiole length (cm)	0.5–0.75	1.5–2	2

This taxon is deemed worthy of varietal status not only because it is readily distinguished from the other two varieties by leaf characters, but also because of its montane habitat. It is named for M.R. Henderson, who made the first collection.

Sonerila fraseri Kiew, sp. nov. *S. erectae* Jack affinis sed caulis teretis, floribus candidis, petalis et capsulis longioribus differt. Typus: Ruth Kiew RK 3826, Peninsular Malaysia, Pahang, Fraser's Hill, summit of Pine Tree Hill (holotypus UPM; isotypi L, SING).

Finely rooted herb, flowering at c. 3 cm tall when still unbranched, branching to form a clump with erect stems to 12 cm tall; stem terete, c. 1 mm thick, magenta, sparsely hispid with glandular hairs c. 0.75 mm long. Leaf pairs isomorphic and equal-sized. Petiole 1.5–6 mm long. Lamina ovate, (6–)11(–25) × (4–)7(–14) mm, base rounded, apex rounded, mid-green above, pale beneath with glistening epidermis; indumentum of uniseriate, multicellular, non-glandular hairs, moderately dense and 1.5 mm long above, sparse and 0.75 mm long beneath; margin minutely denticulate, teeth terminating in a hair; 3-plinerved, lateral veins ascending, plane on both surfaces, indistinct above, beneath distinct in lower half of lamina. Inflorescence a terminal 1–3-flowered scorpioid cyme. Peduncle filiform, magenta, 8–21 mm long and 0.3–0.5 mm thick, elongating to 4–6 cm in infructescence. Flowers 3-merous, actinomorphic, bisexual; pedicel 0.5 to c. 1 mm long; hypanthium tubular, c. 5 mm long, 2 mm wide, with sparse glandular hairs c. 0.3 mm long and covered by a dense layer of non-glandular hairs, c. 0.03 mm long; sepals triangular, apex acute, magenta, 0.5 mm long, persistent in mature fruit; petals broadly oval, 9 × 5 mm, base rounded, apex apiculate c. 1 mm long, thin, inner surface white, outer white with pale rosy-pink midline and slightly suffused rosy pink towards apex, opening horizontally, margin and dorsal midline with sparse glandular hairs; stamens 3, erect, filament c. 4 mm long, white, anther c. 2.5 mm long, base cordate, tapering acutely to the apex, lemon yellow, connective indistinct, without appendix; ovary 3-loculate; style c. 5.5 mm long, glabrous, white, stigma peltate, minute, surface papillose. Mature capsule cylindric, 6–12 mm long and 2–3 mm wide, slightly ribbed, smooth. Seeds ellipsoid, c. 0.75 mm long, 0.25 mm wide, base rounded, apex narrowed to a point, covered in longitudinal rows of prominent pustules and with a longitudinal smooth wing less than half the width of the seed.

DISTRIBUTION. Endemic to Peninsular Malaysia, known only from the type site on Pine Tree Hill at Fraser's Hill, Pahang.

HABITAT. Lower montane forest at 1500 m, locally common in lightly shaded, steep litter-free slopes below summit (where *S. hirsuta* Ridl. also grows) and, in sterile state, on bare areas on the exposed summit, locally common.

Sonerila fraseri belongs to the group of small herbaceous sonerilas within *Sonerila* section *Eusonerila* subsection *Erectae* (Ridley 1922) with branched, wiry stems, isomorphic and equal-sized pairs of leaves and narrow, cylindric capsules, which includes three endemic species, *S. calaminthifolia* Stapf (from Gunung Batu Putih, Perak), *S. erecta* Jack (from Penang; Taiping, Perak; and Fraser's Hill), *S. linearis* Hook. f. (from Gunung Jerai, Kedah), and *S. tenera* Royle (from India, Thailand, Indo-China and in Peninsular Malaysia only from Langkawi).

Sonerila fraseri is distinct from all these species in its white flowers (the other four have pink flowers) and in the size and shape of its lamina. *S. linearis* has sessile, linear

leaves at least ten times longer than wide and *S. calaminthifolia* has oblong or elliptic leaves two-and-a-half to three times longer than wide. *S. erecta* and *S. tenera* usually have lanceolate leaves but their smaller leaves tend to be ovate; they differ from the ovate leaves of *S. fraseri* in having an acute apex. *S. tenera* is also different in having petioles more than 1 cm long. In addition, these two species have small flowers with petals up to 5 mm long. Therefore, among these species, *S. fraseri* most resembles *S. erecta* from which it is distinguished by the shape of the stem, lamina size, petal colour and length, and fruit length (Table 2).

Table 2. Characters that distinguish *Sonerila fraseri* from *S. erecta*.

	<i>S. fraseri</i>	<i>S. erecta</i>
Stem	terete	± quadrangular
Lamina		
shape	ovate	usually lanceolate, smaller leaves ovate
maximum size (cm)	2.5 × 1.4	3.3 × 1
base	rounded	cuneate to truncate
apex	rounded	acute
colour	always green	sometimes purple beneath
Petal		
colour	white	pink*
length (mm)	9	4–5
Fruit length (mm)	12	8

* within a population, very rarely one plant may have white flowers.

Sonerila erecta is common at Fraser's Hill, especially on roadside cuttings, and within the forest particularly on quartzite, but it is not found above 1325 m, whereas *S. fraseri* is known from a single population on Pine Tree Hill at about 1500 m.

Although many botanists have collected at Pine Tree Hill (the highest peak at Fraser's Hill), there are no other collections of *S. fraseri*. This suggests that it flowers irregularly and for short periods as its large, white star-like flowers are conspicuous, especially as the population flowers gregariously. When out of flower, it is easily overlooked. *S. erecta* displays this type of flowering, i.e. gregarious flowering at irregular intervals.

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