Studies on Homalomeneae (Araceae) of Borneo VI: *Homalomena giamensis*, a New Species from Sarawak, Malaysian Borneo, with Observations on its Pollination

Tung Lay Soon and Wong Sin Yeng
Department of Plant Science and Environmental Ecology
Faculty of Resource Science and Technology
Universiti Malaysia Sarawak
94300 Samarahan
Sarawak, Malaysia

Peter C. Boyce
Visiting Scientist
Pusat Pengajian Sains Kajihayat [School of Biological Sciences]
Universiti Sains Malaysia11800 USM
Pulau Pinang, Malaysia

ABSTRACT

A new species, *Homalomena giamensis* L.S.Tung, S.Y.Wong & P.C.Boyce, is described and illustrated from karst limestone formations at Kampung Giam, Kuching Division, SW Sarawak, to where it is locally endemic. As part of an ongoing project to investigate triggers and barriers in speciation processes in *Homalomena*, observations of the pollination of *Homalomena giamensis* were undertaken to record inflorescence mechanics, interactions with insect visitors, and determine the pollinator. Five insect genera visited during anthesis—Diptera: Drosophilidae (*Colocasiomyia*); Coeleoptera: Chrysomelidae: (*Chaloenus* & *Dercetina* sp.); Nitidulidae (genus undetermined), and Scarabaeidae: Rutelinae (*Parastasia bimaculata* Guerin). The pollinator was determined to be the ruteline scarab. *Parastasia bimaculata* is a rather widespread species in tropical Asia, and has previously recorded as a pollinating agent for one Bornean *Homalomena*. A review of pollination studies of tropical Asian aroids to date is given.

KEY WORDS

Araceae, *Homalomena giamensis*, pollination, Coleoptera, Scarabaeidae, Rutelinae, *Parastasia bimaculata*, karst limestone, Sarawak, Borneo.

INTRODUCTION

Homalomena is a predominantly Asian genus of terrestrial or lithophytic solitary, clumping, rarely scandent, very rarely climbing, mesophytic, rarely helophytic, usually aromatic herbs occurring mainly in shady perhumid or everwet forest. The genus has several centers of diversity in SE Asia, notably Sumatera and New Guinea, with the greatest representation on Borneo where there are perhaps in excess of 300 species, virtually all endemic, and with fewer than 20 species formally described (Wong & Boyce, in press).

Homalomena in Sarawak is presently the subject of study by a taxonomic and systematic consortium coordinated from UNIMAS (for outputs to date see, e.g., Boyce & Wong, 2008, 2009; Boyce & Wong, in press; Boyce & Wong, in prep.; Boyce *et al.*, 2010; Wong & Boyce, in press; Wong *et al.*, in press; Ng *et al.*, in prep.). This paper is the first in a series investigating incidence of pollinator guild niche partitioning as one

---

Corresponding author: sywong@frst.unimas.my

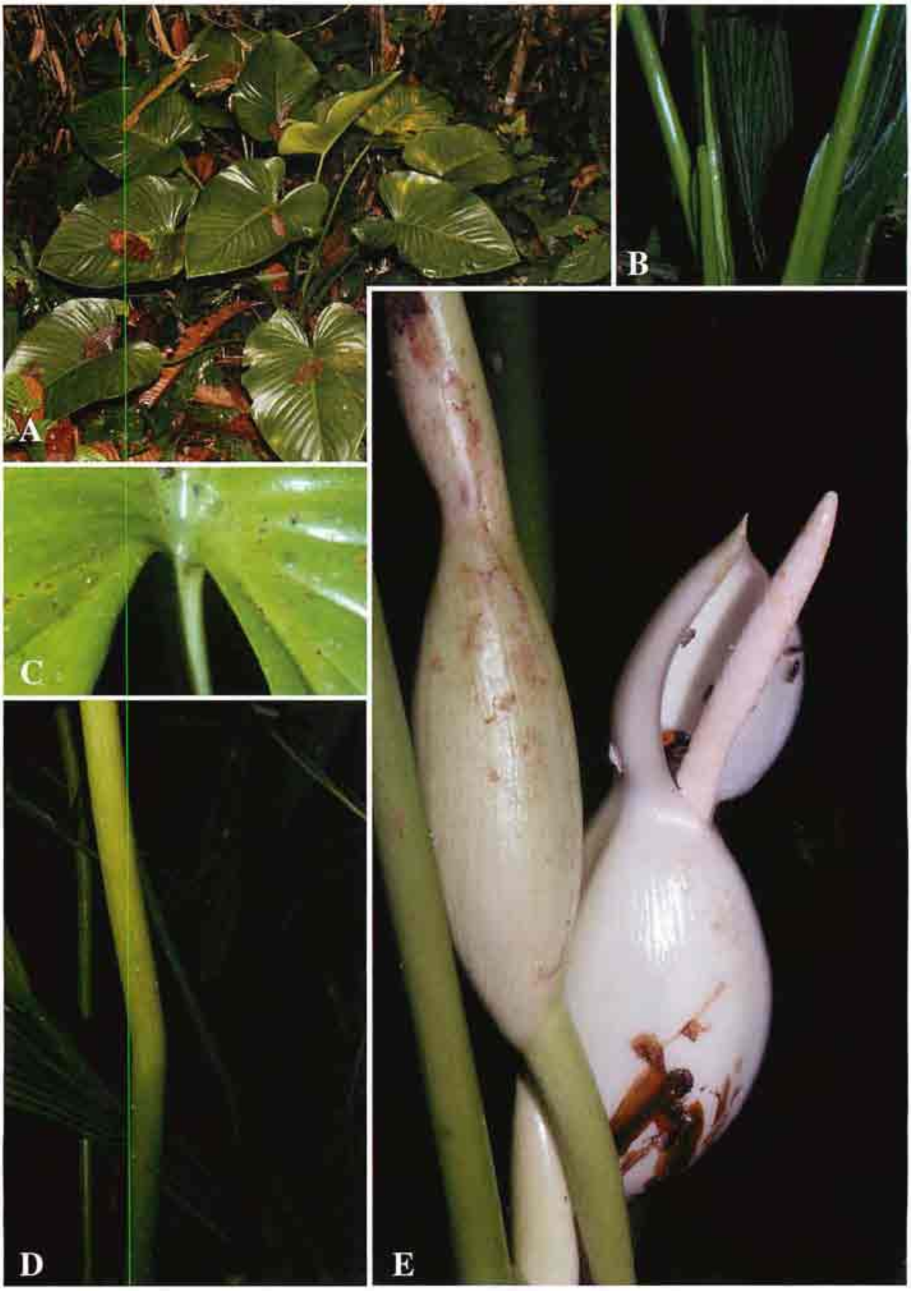

Plate 1. ***Homalomena giamensis*** **L.S.Tung, S.Y.Wong & P.C.Boyce. A.** Plant in habitat. Note the glossy bright green leaves. **B.** Detail of the petiolar sheaths and prophyll. **C.** Detail of sinus. **D.** Petiole showing the pulvinus. **E.** Inflorescence at late pistillate anthesis. Note the spadix has extended beyond the spathe limb, the *Colocasiomyia* flies on the spathe limb, and the *Parastasia* beetle visible inside the inflorescence. Note too that the length of the lower spathe exceeds that of the spathe limb.

of the mechanisms to attempt to explain the extremely high rates of local and micro-endemic sympatric and parapatric often synchronously flowering species that occur in *Homalomena*.

TAXONOMY

Homalomena giamensis L.S.Tung, S.Y.Wong & P.C.Boyce sp. nov.

Haec species notabilis ab combinatio foliis cordatis claroviride nitens, subtus non-glauca, venis primariis impressis spathe inferior cum lamina spathae longiore et inflorescentia mascula per anthesin quam resin producto. Typus: MALAYSIA, Sarawak, Kuching Division, Siburan, Kampung Giam, 01°19′16.1″; 110°16′16.7″, 20 June 2009, *P.C.Boyce & Wong Sin Yeng AR-2558* (holotypus SAR).

Paratype: Malaysia, **Sarawak**, Kuching Division, Siburan, Kampung Giam, Air Terjun Giam, 01°19′11.2″; 110°16′11.4″, 7 Feb. 2006, *P.C.Boyce, Jeland ak Kisai & Wong Sin Yeng AR-1691* (SAR). Plates 1 & 2.

Medium, somewhat robust, strongly aromatic (camphor) evergreen glabrous mesophytic ***herbs*** to ca. 1 m tall. ***Stem*** pleionanthic, erect to ascending, ca. 3 cm thick, medium green, internodes to ca. 1 cm long. ***Leaves*** up to ca. 15 together, ca. 6 per module; modules starting with a conspicuous 2-keeled short-duration ***prophyll*** to 30 cm long, medium-green, glossy; ***petiole*** erect, 40–45 cm long, sub-terete except for the distal-most portion where very shallowly dorsally channeled with rounded margins, obscurely pulvinate ca. $^{2}/_{3}$ along length, pulvinus ca. 4 cm long, petiole bases clasping, petiole bright green with obscure longitudinal darker green striae; ***petiolar sheath*** ca. 6–10 cm long, ca. $^{1}/_{3}$ of petiole length, equal, persistent, decurrent at apex, margin erect, pale glossy green; ***lamina*** rather broadly ovato-sagittate, 18–30 cm long × 14–25 cm wide, rubbery-leathery and somewhat quilted between the primary and interprimary veins, glossy bright green adaxially, paler green abaxially, base cordate to sagittato-cordate, tip acute, acuminate for ca. 2 cm thence tubular-apiculate for ca. 2–3 mm; posterior lobes short, straight, ovate to ovato-triangular, sinus rather narrow, lobes 6–9 cm long; midrib raised abaxially green when fresh, adaxially sunken slightly into lamina, ca. 3 mm wide, with ca. 9–11 primary lateral veins on each side, diverging at 30°–80° from the midrib, adaxially impressed abaxially slightly raised, distal-most veins curved slightly towards the apex when near the margin, interprimary veins barely distinguished from the primary lateral veins, alternating irregularly with primaries; secondary venation obscure, running parallel to the interprimary veins, striate; tertiary venation not visible; all veins running into a slightly thickened intermarginal vein. ***Inflorescences*** up to 5 together, erect and smelling powerfully of anethol (anise) at anthesis, thence declinate, subtending prophyll, short, usually less than 5 cm long; ***peduncle*** to ca. 25 cm long × ca. 5 mm diam. at the spathe insertion, glossy pale green. ***Spathe*** ca. 9–11 cm long, tightly furled prior to anthesis, lower spathe inflating at pistillate anthesis and the margins gaping to partially reveal spadix, margins also recurving, spathe limb loosening at pistillate anthesis, thence inflating and then opening wide, spathe interior white at anthesis, exterior pale glossy green with numerous faint longitudinal striae; spathe fully closing post anthesis, and then turning pale green and eventually dark green; ***lower spathe*** ovoid-ellipsoid, twice as long at spathe limb, ca. 6–7 cm long, moderately constricted at the junction of the spathe limb, the constriction coinciding with junction of the staminate and pistillate flower zones; ***spathe limb*** ovato-triangular, ca. 3–4 cm long × ca. 3.5 cm wide (at staminate anthesis), limb margins very slightly recurving at staminate anthesis, apex stiffly mucronate to ca. 4 mm long. ***Spadix*** exceeding the spathe by rapid spadix extension at anthesis onset, ca. 10.5 cm long, briefly stipitate; spadix contracting post anthesis and entirely enclosed in persistent spathe throughout the fruiting period; ***stipe*** ca. 3 mm long × 2 mm diam., weakly gibbose-cylindrical, and inserted slightly obliquely on peduncle, glossy white; ***pistillate flower zone*** ca. 3.75 cm long × ca. 1 cm wide, slightly less than ca. $^1/_3$ length of spadix, weakly fusiform; ***pistils*** ca. 2 mm × 1 mm, rather densely arranged, stoutly globose-cylindrical, somewhat trapezoidal-compressed where pressed against adjacent pistils, very pale yellow-white, each pistil associated with a ventrally located large staminode; ***style*** barely differentiated; ***stigma*** globose-capitate, smaller than ovary diam., pale gray; ***interpistillar staminodes*** stoutly abruptly globose-clavate on a slender stipe, clavate portion ca. 0.5 mm diam., slightly overtopping the associated pistil, waxy white; ***suprapistillar interstice zone*** absent; ***staminate flower zone*** to ca. 6 cm long, ca. $^2/_3$ length of spadix, lowest portion composed of a few sterile staminate flowers, fertile portion producing large numerous amber-colored resin droplets during late pistillate and at onset of staminate anthesis, these particularly towards the spadix tip, from where they flow down the spadix, mixing with the pollen strands; ***staminate flowers*** well defined from one another, ca. 2.5 mm × 1 mm trapezoid, comprising 3–5 truncate stamens, each overtopped by a large, flat synconnective, anthers marginal with pollen extruded in strings and exiting via a notch in the synconnective margin, waxy white. ***Infructescence*** declinate to pendent, spathe entirely persistent, ca. 14 × 2 cm, the lower part weakly fusiform, deep glossy green, peduncle with darker green, short striae. ***Fruits*** & ***seeds*** not observed.

Distribution

Malaysian Borneo: Sarawak, Kuching Division, Siburan, endemic to karst limestone in the vicinity of Kampung Giam.

Ecology

Terrestrial in deep leaf litter over limestone-derived loams on ridges and moderate slopes beneath lowland perhumid evergreen broadleaf forest on and adjacent to karst limestone. 35–50 m asl.

Notes

Homalomena giamensis belongs to the Cyrtocladon supergroup (*sensu* Boyce & Wong, 2008), and is one of a medium-sized species-complex, all currently undescribed, with glossy bright green, rather rubbery-leathery cordate leaf laminae with impressed primary venation, powerfully aromatic (camphor) vegetative tissues, large, soon-degrading prophylls, the length of the lower spathe exceeding that of the spathe limb, conspicuous interpistillar staminodes, and the staminate portion of the spadix producing amber-colored resin droplets during anthesis.

Etymology

From Kampung Giam, the type and only known locality.

POLLINATION

History

Until recently pollination studies of tropical Asian Araceae have almost exclusively been undertaken by Japanese entomological researchers, a few non-Japanese collaborators, and students undertaking degrees in Japan. Notable among the Japanese are Masako Honda-Yafuso (Honda-Yafuso, 1983), Tamiji Inoue (see Kato *et al.*, 2000), Takao Itioka (see Kato *et al.*, 2000), Makoto Kato (Kato *et al.*, 2000), Yuko Kumano (later Yuko Kumano-Nomura) (Kumano & Yamaoka, 2006; Kumano-Nomura & Yamaoka, 2009), Takashi Miyake (Miyake, Yafuso, 2003), Kuniyasu Momose (see Kato *et al.*, 2000), Yafuso Mori (Mori & Okada, 2001), Hiroshi Okada (Mori & Okada, 2001), Toyohi Okada (Okada 1975, 1980, 1986, 1987, 1990; Okada & Carson, 1980; Okada & Yafuso, 1989), Shoko Sakai (see Kato *et al.*, 2000), Kohei Takenaka (later Kohei (Takenaka) Takano) (Takenaka *et al.*, 2006), Masanori J. Toda (Toda *et al.*, in press, see also Sultana *et al.*, 2002; Takenaka *et al.*, 2006; Yafuso *et al.*, 2000), Seiki Yamane (see Kato *et al.*, 2000), Masako Yafuso (see Miyake & Yafuso, 2003), and Ryohei

Yamaoka (see Kumano & Yamaoka, 2006; Kumano-Nomura & Yamaoka, 2009).

Collaborators and students include Abang Abdul Hamid (see Kato *et al.*, 2000), Hampton L. Carson (see Okada & Carson, 1980), Maklarin B. Lakim (see Sultana *et al.*, 2000), Maryati Bte Mohamed (see Toda *et al.*, in press), Nguyen Manh Cuong (see Sultana *et al.*, 2000), Farhat Sultana (Sultana *et al.*, 2000; see also Yafuso *et al.*, 2000), Yin Jian-Tao (see Takenaka *et al.*, 2006, and Wen Shuo-Yang (see Takenaka *et al.*, 2006).

The overwhelming majority of aroid pollination research in Asia has focussed on Drosophilidae, a family of flies (Diptera) commonly called fruit flies, and in particular has been directed at investigations of synhospitality between pollinator and inflorescence. While without doubt many aroids are Drosophilidae pollinated, including *Furtadoa* M.Hotta (Mori & Okada 2001), the sister taxon to *Homalomena*, there is considerable circumstantial evidence, and recently hard data, that while *Homalomena* is visited by various Drosophilidae, they may be in the main beetle pollinated, it has been properly documented for one species (Kumano & Yamaoka, 2006; Kumano-Nomura & Yamaoka, 2009)

One striking morphological feature of many *Homalomena* are the conspicuous interpistillar staminodes. The role of staminodes as beetle rewards is well-documented in other angiosperms, notably basal dicots (see Armstrong & Irvine, 1990; Endress, 1984a,b) but understanding their role in aroids is of rather recent realization. Documented in Neotropical *Dieffenbachia* and *Gearum* (Spathicarpeae) which are also beetle pollinated (Young, 1986; Gonçalves & Maia, 2006).

It is perhaps notable that *Homalomena* inflorescences with interpistillar staminodes undergo distinctive changes in color when preserved in ethanol, with the pistils staining dark brown while the staminodes remain white. Although yet to be confirmed, we suspect that the ovaries are provided with distasteful chemicals, perhaps tannins, to discourage herbivory, explaining the different reaction in ethanol.

Insect identifications were undertaken with reference to various web resources, notably www.beetle-diversity.com, www.coleoptera.org, and www.coleop-terra.com. Insect vouchers are deposited in the Entomological Museum, Faculty of Resource Science and Technology, University Malaysia, Sarawak.

Study Site

The study was carried out at Kampung Giam, Daerah Siburan, Kuching Division, Sarawak, Malaysia (01°19′16.1″N; 110°16′16.7″E, 50 m asl); this is the type location of *Homalomena giamensis*, and the species is as far as known, endemic to this locality. The population occurs as scattered individuals and small clumps along and down a narrow ridge below perhumid broadleaf forest adjacent to exposed karst limestone outcrops, and a large limestone bluff reaching to 300 m. The study was undertaken throughout December 2009, a period marking the early part of the northeast monsoon, with daily temperatures ranging from 23°–31°C (73°–86°F), and daily afternoon and nighttime heavy prolonged precipitation, often delivering >3 cm of rain in an hour.

Homalomena Species Present at Giam

Homalomena giamensis occurs sympatrically with *H. borneensis* Ridl., *H. insignis* N.R.Br., *H. griffithii* (Jack.) Hook.f., and an as yet unidentified species. Based on observations for the past 3 yr *H. giamensis* flowers synchronously with *H. borneensis.* Although differing markedly in vegetative morphology, both have similarities in inflorescence gross morphology, including the lower spathe exceeding the length of the spathe limb, conspicuous staminodes, and staminate flowers with a well-developed synconnective. Both produce a floral odor reminiscent of anethol (anise). One striking difference in their floral morphology is that *H. giamensis* produces conspicuous amber-colored resin droplets from the staminate portion of the spadix during the floral transition from pistillate to staminate

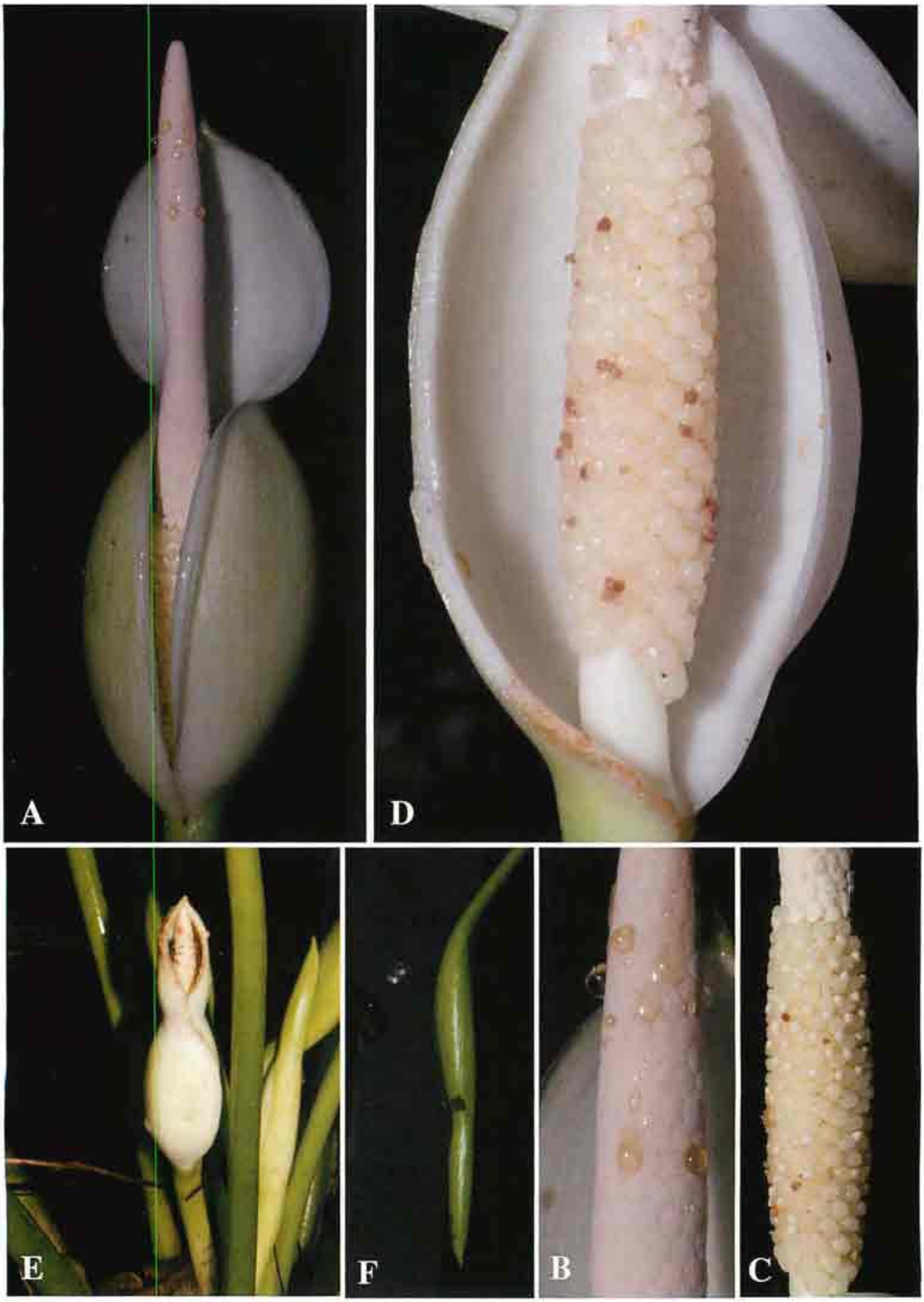

Plate 2. ***Homalomena giamensis* L.S.Tung, S.Y.Wong & P.C.Boyce. A.** Inflorescence at pistillate anthesis. Note the spathe margins are gaping to reveal the spadix, and that the margins have also recurved. Note, too, the conspicuous resin-like droplets on the staminate portion of the spadix, and that the spadix has extended beyond the spathe.

anthesis whereas *H. borneensis* does not. Interestingly, species related to *H. hanneae* P.C.Boyce, S.Y.Wong & Fasihuddin B. Ahmad also produce amber-colored resin, but are otherwise florally and vegetatively distinct from *H. giamensis*, differing among other characters by the spathe limb exceeding the lower spathe, producing a floral fragrance of 2-butanol (sweet apricot) at anthesis, infructescence spathe turning deep red during fruiting, petiolar sheathes red with marcescent margins, and leaf laminae with conspicuous extrafloral nectaries. The species studied by Yuko Kumano and Ryohei Yamaoka and reported as *H. propinqua* (Kumano & Yamaoka, 2006; Kumano-Nomura & Yamaoka, 2009) is an undescribed species of the Hanneae complex (*H. propinqua* Schott = *H. rostrata* Griff., a colonial helophyte; see Wong, Boyce & Fasihuddin, in press).

Pollination Observation

Observations were carried out over the whole anthesis period, enabling onset times, duration and inter-anthesis activity to be monitored and recorded. All observations of inflorescence movement were correlated to odor production, and arrival and departure of insects to the inflorescence.

Day 1

At ca. 13.00 the lower spathe loosened slightly, but showed no signs of inflation, the lower spathe reclosed tightly at 1,600, the cause of which is not yet understood. Pistillate anthesis (indicated by wet stigmas) started at ca. 1,600 with the lower spathe inflating within an hour. By ca. 2,100, the lower spathe loosened to the extent that a longitudinal (<2 mm) gap was created down the convolute margin. The inflorescence remained in this phase for ca. 3 hr. During this period, no insect visitors were present.

Day 2

By ca. 0200 the lower spathe had loosened and inflated to widen the marginal gap to ca. 0.5 cm (widest), while the spathe limb remained closed, and showed no signs of inflation. At ca. 0300, the upper spathe started to open, initially with the small gap (ca. 0.5 cm wide) and at the same time the spadix extended upwards through the gap, lengthening by 2 cm in less than an hour; this spadix extension marked the onset of detectable odor production (anethole) which persisted until completion of entire anthesis cycle. By ca. 0430, the upper spathe was almost fully open, and it was possible to observe the spadix. By ca. 0500 the upper spathe was almost fully open, (ca. 3 cm wide) and by ca. 0630 opened to its fullest extent (ca. 3.5 cm wide) and lower spathe was fully inflated (ca. 3.0 cm diam.). At approximately 0715 insects began to appear, landing on the exterior and interior of the spathe limb. *Colocasiomyia* flies mainly on exterior of the spathe, and some of the flies entering the lower spathe chamber but not remaining. Small dark orange Nitidulidae beetles (genus undetermined) were observed to visit the exterior of the spathe, and also enter the lower spathe but not remain for any great

←

B. Detail of resin-like droplets on spadix staminate zone. **C.** Detail of pistillate zone ca. halfway through pistillate anthesis. Note that many of the interpistillar staminodes have already been eaten. **D.** Detail of pistillate zone towards end of pistillate anthesis. No staminodes remain. **E.** Inflorescence at end of staminate anthesis, the spathe is reclosing and the spadix has contracted to be fully enclosed within the spathe. The debris visible on the spadix is pollen paste. Just visible are two species of Chrysomelidae (a *Chaloenus* and perhaps a *Dercetina*) plundering pollen waste. **F.** Developing infructescence. Note that the spadix is one again fully enclosed within the persistent spathe.

time. Metallic blue chrysomelid (*Chaloenus*) beetles, and also the ruteline *Parastasia bimaculata* were observed to enter the upper spathe and lower spathe respectively. Both crawled on the spadix, with only the *Parastasia* descending the spadix to the pistillate zone.

At ca. 1,200, a small chewed hole was observed on the staminate zone, this caused by one of the *Parastasia*. At the same time, droplets of an amber-colored resin-like substance appeared on the staminate flower zone, exuded from between the individual flowers. The exuding of the resin-like substance marked the end of the pistillate phase, the stigma droplets were already dry. This inter-anthesis phase lasted for 15 hr. During this long phase, numerous individuals of the ruteline scarab *Parastasia bimaculata* were observed to remain inside the lower spathe chamber, were they fed on the interpistillar staminodes, and were also mating. No other beetles nor flies remained in the lower spathe during this phase, although periodically Chrysomelidae spent time on the spadix, and small clouds of *Colocasiomyia* were seen 'circling' the inflorescence. Both presumably attracted by the continuing floral odor production.

Day 3

At ca. 0300 onset of staminate anthesis was indicated by the production of the white string-like pollen strands, these mixed with the aforementioned resin droplets to form a 'paste'. At this time initially the *Parastasia* remained on pistillate zone within the lower spathe. At ca. 0500, the entire staminate zone was covered by the pollen and at this time the beetles were observed to crawl up the spadix, crossing the staminate zone, in so doing their legs were coated with both pollen strings and pollen 'paste'. Most flew away at this time, although a few remained, together with two species of Chrysomelidae which appeared to be feeding on the pollen paste. At ca. 0630, the upper spathe was observed to close, and was closed tightly at ca. 0715. This marked the end of the flowering period for this particular inflorescence. At this time activity by Chrysomelidae (*Chaloenus* sp. and a previously unobserved *Dercetina* sp.) was strongly suggestive of pollen plundering.

CONCLUSIONS

- The anthesis period per inflorescence is ca. 43 hr, comprising a pistillate phase lasting 24 hr, an inter-anthesis phase lasting 15 hr, and a staminate phase lasting a maximum of 4 hr.
- The primary attractant appears to be odor. Although an inflorescence is readily visible during the first 11 hr of the pistillate phase, it is not until floral odor production starts that insects start to arrive. It is speculated that odor production, together with suitable food rewards, and an appropriately sized lower spathe chamber, is linked to 'filtering' the optimal pollinator from within the guild of early morning-active insects.
- The pollinator of *Homalomena giamensis* is *Parastasia bimaculata* Guerin. This is the only insect to visit the inflorescence during the pistillate phase, remain in the lower spathe throughout the inter-anthetic period, and the only insect witnessed to collect pollen on leaving the inflorescence during the staminate phase. This same species has been shown to pollinate a *Homalomena* species in Borneo (Kumano & Yamaoka, 2006; Kumano-Nomura & Yamaoka, 2009).
- While it is not clear what, if any, role *Colocasiomyia* and the unidentified Nitidulidae play in the pollination, it is highly likely that the two Chrysomelidae (*Chaloenus* sp. and *Dercetina* sp.) are pollen plunderers.
- The interpistillar staminodes are 'sacrificial' structures functioning as food rewards for the pollinator: *Parastasia bimaculata*. Given that the pollinator is trapped in the lower spathe for 15 or more hours, and in that time is active, and often mating, a food resource is

important. Post-anthesis, all interpistillar staminodes, and the zone of staminodes between the pistillate and staminate flower zones, show signs of considerable feeding activity.

- No damage occurs to the pistils and very little damage to the staminate flowers. This suggests that these structures are distasteful, a supposition backed up by the color reaction of the inflorescence when placed in ethanol (see above).

ACKNOWLEDGMENTS

The collaboration and support of the Sarawak Forestry Department, notably Dr Mohd. Shahbudin Sabki, Dr Azahari Bin Omar, L.C.J. Julaihi, & Lucy Chong is gratefully acknowledged. This study is funded by MOSTI E-Science: 05-01-09-SF0006. All fieldwork has been undertaken with Sarawak Forestry Department Research Permits, with the most recent fieldwork being under Sarawak Forestry Department Research Permit No. NPW.907.4.2(I)-101 & Park Permit No. 58/20076.

LITERATURE CITED

Armstrong, J. E. & Irvine, A. K. 1990. Functions of staminodia in the beetle-pollinated flowers of *Eupomatia laurina*. *Biotropica* 22: 429–431.

Boyce, P. C. & Wong, S. Y. 2008. Studies on Homalomeneae (Araceae) of Borneo I: Four new species and speculation on informal species groups in Sarawak. *Gard. Bull. Singapore* 60(1): 1–29.

——— & ———. 2009. Studies on Homalomeneae (Araceae) of Borneo IV: *Homalomena* specimens in the Herbarium Beccarianum-Malesia (FI-B) of the Museo di Storia Naturale - Sezione Botanica "F. Parlatore" dell'Università di Firenze. *Webbia* 64(2): 169–173.

——— & ———. Studies on Homalomeneae (Araceae) of Borneo VIII: clarification of early names in Asian *Homalomena*. *Acta Phytotax. Geobot.* (In press).

——— & ———. In prep. Studies on Homalomeneae (Araceae) of Borneo X: the *Homalomena* of Matang, Kuching, Sarawak. *Gard. Bull. Singapore.*

———, ——— & Fasihuddin, B. A. 2010. Studies on *Homalomeneae* (Araceae) of Borneo II: the *Homalomena* of Nanga Sumpa (Batang Ai) – Novel & pre-existing taxa, and notes on Iban Usages. *Gard. Bull. Singapore.* 69(2): 29–78.

———, ——— & ———. Studies on Homalomeneae (Araceae) of Borneo VIII: additional novel *Homalomena* from Nanga Sumpa (Batang Ai), Sarawak. *Gard. Bull. Singapore.* (In press b).

Endress, P. 1984a. The flowering process in the Eupomatiaceae (Magnoliales). *Bot. Jahrb. fuer Systematik Pflanzengeschichte und Pflanzengeographie* 104: 297–319.

———. 1984b. The role of inner staminodes in the floral display of some relic Magnoliales. *P. Syst. Evol.* 146: 269–282.

Gonçalves, E. G. & Maia, A. C. D. 2006. New evidence of pollination in *Gearum brasiliense* (Araceae – Spathicarpeae). *Aroideana* 29: 148–151.

Honda-Yafuso, M. 1983. Interspecific relationship between synhospitalic *Drosophilella* species (Diptera, Drosophilidae) inhabiting *Alocasia odora* on Okinawa Is., Japan. *Kontyû* 51: 520–527.

Kato, M., Itioka, T., Sakai, P., Momose, K., Yamane, S., Hamid, A. A. & Inoue, T. 2000. Various population fluctuation patterns of light-attracted beetles in a tropical lowland dipterocarp forest in Sarawak. *Popul. Ecol.* 42: 97–104.

Kumano, Y. & Yamaoka, R. 2006. Synchronization between temporal variation in heat generation, floral scents and pollinator arrival in the beetle-pollinated tropical Araceae, *Homalomena propinqua*. *Plant Spec. Biol.* 21: 173–83.

Kumano-Nomura, Y. & Yamaoka, R. 2009. Beetle visitations, and associations with quantitative variation of attractants in floral odors of *Homalomena propinqua* (Araceae). *J. Plant Res.* 122(2): 183–192.

Miyake, T. & Yafuso, M. 2003. Floral scents affect reproductive success in fly-pollinated *Alocasia odora* (Araceae). *Am. J. Bot.* 90: 370–376.

Mori, Y. & Okada, H. 2001. Reproductive biology and pollen flow of a rheophytic aroid, *Furtadoa sumatrensis* (Araceae) in the Malesian wet tropics. *Pl. Syst. Evol.* 227: 37–47.

Ng, K. K., Tan, P. J., Lee, H. B., Wong, S. Y., Boyce, P. C., Fasihuddin, B. A. & Ahmad, Sofiman O. In prep. Phylogenetic analyzes of the genus *Homalomena* (Araceae: Homalomeneae) in Asia.

Okada, T. 1975. The oriental Drosophilids breeding in flowers. *Kontyû* 43: 356–363.

———. 1980. Synhospitalic evolution of the genus *Drosophilella* Duda (Diptera, Drosophilidae), with description of a new species from Okinawa and Taiwan. *Kontyû* 48: 218–225.

———. 1986. Estimation of the routes of synhospitalic distribution of the genus *Drosophilella* Duda (Diptera, Drosophilidae), with description of three new species from Malaysia and Indonesia. *Proceedings of the Japanese Society of Systematic Zoology* 33: 32–39.

———. 1987. Further notes on the genus *Drosophilella* Duda with descriptions of two new species from Indonesia (Diptera, Drosophilidae). *Proc. Japanese Soc. System. Zool.* 36: 38–45.

———. 1990. Subdivision of the genus *Colocasiomyia* de Meijere (Diptera, Drosophilidae) with descriptions of two new species from Sulawesi and note on color adaptation of synhospitalic species. *Proc. Japanese Soc. System. Zool.* 42: 66–72.

——— & Carson, H. L. 1980. Drosophilidae associated with flowers in Papua New Guinea I. *Colocasia esculenta. Kontyû* 48: 218–225.

——— & Yafuso, M. 1989. The genus *Colocasiomyia* Duda (Diptera, Drosophilidae) from Sulawesi. *Proc. Japanese Soc. System. Zool.* 39: 48–55.

Sultana, F., Toda, M. J., Yafuso, M., Lakim, M. B., Mohamed, M. B. & Nguyen, C. M. 2002. A new species-group of the genus *Colocasiomyia* de Meijere (Diptera: Drosophilidae), with descriptions of two new species from eastern Malaysia and Vietnam. *Entomological Science* 5: 305–315.

Takenaka, K., Yin, J.-T., Wen, S.-Y. & Toda, M. J. 2006. Pollination mutualism between a new species of the genus *Colocasiomyia* de Meijere (Diptera: Drosophilidae) and *Steudnera colocasiifolia* (Araceae) in Yunnan, China. *Entomol. Sci.* 9(1): 79–91.

Toda, M. J., Lakim, M. B. & Mohamed, M. Bte. The genus *Colocasiomyia* (Drosophilidae: Diptera) in Sabah: high species-diversity and utilization of host aroid inflorescences. *Sabah Parks Nature Journal* (accepted). (In press).

——— & Okada, T. 1983. Ecological studies of floricolous *Drosophilella* in Burma with descriptions of three new species from Burma and the Philippines (Diptera, Drosophilidae). *Kontyû* 51: 169–184.

Wong, S. Y. & Boyce, P. C. Studies on Homalomeneae (Araceae) of Borneo VII: a checklist of *Homalomena* for Borneo. *Acta Phytotax. Geobot.* (In press).

———, ——— & Fasihuddin, B. A. Studies on Homalomeneae (Araceae) of Borneo III: the helophytic Homalomena of Sunda. *Acta Phytotax. Geobot.* (In press).

Yafuso, M. 1993. Thermogenesis of *Alocasia odora* (Araceae) and the role of *Colocasiomyia* flies (Diptera, Drosophilidae) as cross-pollinators. *Environm. Entomol.* 22: 601–606.

———. 1994. Life-history traits related to resource partitioning between synhospitalic species of *Colocasiomyia* (Diptera, Drosophilidae) breeding in inflorescences of *Alocasia odora* (Araceae). *Ecol. Entomol.* 19: 65–73.

———. 1999. Larval performance and niche separation between two synhospitalic species of *Colocasiomyia* (Diptera, Drosophilidae). *Mem. Fac.*

Science, Kyoto University. Ser. of biology 16L: 119–126.

——— & Okada, T. 1990. Complicated routes of the synhospitalic pairs of the genus *Colocasiomyia* in Java, with descriptions of two new species (Diptera, Drosophilidae). *Esakia Special Issue* 1: 137–150.

———, Sultana, F., Sasaki, Y. & Toda, M. J. 2000. A new species of *Colocasiomyia* de Meijere (Diptera, Drosophilidae) from North Sulawesi, Indonesia. *Entomol. Sci.* 3: 115–119.

Young, H. J. 1986. Beetle pollination of *Dieffenbachia longispatha* (Araceae). *Am. J. Bot.* 73(6): 931–944.