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*); Coleoptera: 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.

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KEY WORDS


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
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.


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. \(\frac{2}{3}\) 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. \(\frac{1}{3}\) 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, distalmost 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** decline 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.

**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...
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 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 stigma) 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. Colocasioomyia 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-Numura & 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).

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