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Flowering mechanisms, pollination strategies and floral scent analyses of syntopically co-flowering *Homalomena* spp. (Araceae) on Borneo

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ABSTRACT

In this study, the flowering mechanisms and pollination strategies of seven species of the highly diverse genus *Homalomena* (Araceae) were investigated in native populations of West Sarawak, Borneo. The floral scent compositions were also recorded for six species thereof. The selected taxa belong to three out of four complexes of the section *Cyrtocladon* (Hanneae, Giamensis and Borneensis). The species belonging to the Hanneae complex exhibited longer anthesis (53 – 62 hrs) than those of the Giamensis and Borneensis complexes (ca 30 hrs). Species belonging to the Hanneae complex underwent two floral scent emission events in consecutive days, during the pistillate and staminate phases of anthesis. In species belonging to the Giamensis and Borneensis complexes, floral scent emission was only evident to the human nose during the pistillate phase. A total of 33 volatile organic compounds (VOCs) were detected in floral scent analyses of species belonging to the Hanneae complex, whereas 26 VOCs were found in samples of those belonging to the Giamensis complex. The floral scent blends contained uncommon compounds in high concentration, which could ensure pollinator discrimination. Our observations indicate that scarab beetles (*Parastasia gestroi* and *P. nigripennis*; Scarabaeidae, Rutelinae) are the pollinators of the investigated species of *Homalomena*, with *Chaloenus schawalleri* (Chrysomelidae, Galeuricinae) acting as a secondary pollinator. The pollinators utilise the inflorescence for food, mating opportunities and safe mating arena as rewards. Flower-breeding flies (*Colocasiomyia nigricauda* and *C.* aff. *heterodonta*; Diptera,

Drosophilidae) and terrestrial hydrophilid beetles (*Cycreon* sp.; Coleoptera, Hydrophilidae) were also frequently recovered from inflorescences belonging to of all studied species (except *H. velutipedunculata*), but they probably do not act as efficient pollinators. Future studies should investigate the postmating isolating barriers among syntopically co-flowering *Homalomena* sharing the same visiting insects.

Keywords

Flowering phenology; floral scent attractants; scarab beetle pollination; *sec*-butyl acetate; (*E*)-4,8-dimethyl-1,3,7-nonatriene.

INTRODUCTION

Homalomena Schott comprises 75 described species and no fewer than 500 novel species yet to be formally described; most of them are Malesian, with a few species from continental tropical Asia (Boyce & Croat 2013). The Neotropical *Homalomena* taxa have been recently transferred into the resurrected genus *Adelonema* Schott (Wong *et al.* 2016). Four sections are recognized within *Homalomena*: *Homalomena* Schott, *Cyrtocladon* (Griff.) Furtado, *Chamaecladon* (Miq.) Engl. & K.Krause, and *Geniculatae* Hotta (Mayo *et al.* 1997; Boyce & Wong 2008; Ng *et al.* 2011; Wong *et al.* 2013b). Section *Cyrtocladon* comprises at least 300 novel species, many of which restricted to Borneo. Species in this section are medium to very large, erect to creeping plants with strongly aromatic tissues, and pleionanthic shoot modules (Boyce & Wong 2008). It currently consists of four complexes: Borneensis, Giamensis, Hanneae and Rostrata (Ng *et al.* 2011; Wong *et al.* 2013b).

Pollination studies in *Homalomena* were initially directed at investigations of the interactions between flower-breeding flies of the genus *Colocasiomyia* (Diptera, Drosophilidae) and their host inflorescences (Okada 1986; Sultana *et al.* 2006). While, without doubt, many

aroids are pollinated by *Colocasiomyia* spp., including *Furtadoa* M.Hotta (Mori & Okada 2001), the sister taxon to *Homalomena*, recent studies revealed that many species of *Homalomena* are in fact pollinated by scarab beetles of the genus *Parastasia* (Scarabaeidae, Rutelinae) (Kumano & Yamaoka 2006; Kumano-Nomura & Yamaoka 2009; Tung *et al.* 2010; Hoe *et al.* 2011a), and also possibly by chrysomelid beetles of the genera *Dercetina* and *Chaloenus* (Chrysomelidae, Galeuricinae) (Kumano-Nomura & Yamaoka 2009; Hoe *et al.* 2011a). Nitidulid (Nitidulidae) and staphylinid beetles (Staphylinidae) are also frequently found in association with *Homalomena* inflorescences (Tung *et al.* 2010; Hoe *et al.* 2011a).

Homalomena is by far the most species-rich aroid genus in Indomalaya. Frequently, several species from any of the sections or complexes grow sympatrically, often also flowering syntopically with no hybrids being observed in the wild. Field observations showed that inflorescences open at dawn and emit strong, fruity-spicy fragrances to attract pollinators in the early morning hours (Kumano & Yamaoka 2006; Kumano-Nomura & Yamaoka 2009; Tung *et al.* 2010; Hoe *et al.* 2011a). Floral scent composition analyses have been so far restricted to a single species (an undescribed taxon mistakenly identified as *H. propinqua*). The fragrance was found to be composed of 18 volatile organic compounds (VOCs), among which the main constituents were 2-butanol, veratrole and α-pinene. Floral scent emission was correlated with the arrival of *Parastasia* scarab beetles during the pistillate phase, while *Chaloenus* chrysomelid beetles arrived on inflorescence during all phases of anthesis (Kumano & Yamaoka 2006; Kumano-Nomura & Yamaoka 2009). In several pollination systems involving scarab beetles and aroids in the Neotropics, floral VOCs play an important role, indicating to pollinators the location of the inflorescences in the distance or under low light conditions (Gottsberger & Silberbauer-Gottsberger 1991; Dötterl *et al*. 2012; Pereira *et al.* 2014). Chemical analyses of floral scents provide significant data in species boundary delimitation for angiosperms (Dodson *et al.* 1969; Williams & Whitten 1999; Chartier *et al.* 2013), especially those with similar morphology (Knudsen 1999), habitat, flowering period and/or pollination mechanism (Knudsen 1999).

Previous publications (Kumano & Yamaoka 2006; Kumano-Nomura & Yamaoka 2009; Tung *et al.* 2010; Hoe *et al.* 2011a) spurred further investigations to include a larger set of *Homalomena* species to test *in situ* plant-pollinator interaction(s). Therefore, for the current study, seven species were selected among three complexes: Hanneae (3), Giamensis (3), and Borneensis (1), all belonging to the monophyletic section *Cyrtocladon* (Ng *et al.* 2011; Wong *et al.* 2013b). The Hanneae complex comprises at least 100 species of solitary mesophytes to clumping herbs, the majority novel and mostly restricted to Borneo. The Giamensis complex comprises ca 10 species of mesophytic solitary herbs whose acknowledged distribution is restricted to Borneo. The Borneensis complex currently has five assigned species of solitary mesophytes or clumping herbs, also restricted to Borneo (Ng *et al.* 2011). In the current study, the flowering biology and floral scent compositions of (selected) species native to West Sarawak were investigated. This study was set up to specifically compare: (1) flowering mechanisms and pollination strategies, (2) floral scent compounds, and (3) pollinator behavior in relation to floral scent emission during the pistillate and staminate phases of anthesis.

MATERIALS AND METHODS

Studied species

Seven species representing three complexes of the section *Cyrtocladon* were selected for the study: *Homalomena debilicrista* Y.C.Hoe, *H. gastrofructa* S.Y.Wong, Y.C.Hoe & P.C.Boyce, and *H. velutipedunculata* S.Y.Wong, Y.C.Hoe & P.C.Boyce (Hanneae complex); *H. baangongensis* L.S.Tung & Y.C.Hoe, *H. giamensis* L.S.Tung, S.Y.Wong & P.C.Boyce, and *H. matangae* Y.C.Hoe, S.Y.Wong & P.C.Boyce (Giamensis complex); *H.* cf. *borneensis* Ridl. (Borneensis complex). All

species are local, endemic to the type localities in Kuching Division, Sarawak, Malaysia (Tung *et al.* 2010; Hoe *et al.* 2011a&b; Wong *et al.* 2013a; Fig. 1; Appendix 1; Supplementary Fig. 1).

Populations of *H. debilicrista* occur syntopically with *H. matangae* on gentle to steep slopes in lowland tropical perhumid forest on red ultisols, often beside small streams and along forest trail margins, 250 – 375 m asl. The observed population of *H. debilicrista* comprised scattered solitary individuals and colonies of 60 – 100 plants, whereas the population of *H. matangae* was much smaller (ca 20 individual plants). Individuals of *H. gastrofructa* grew intermixed with those of *H. baangongensis,* occurring along muddy trail margins and in shaded areas along streams in a lowland moist to wet evergreen forest on karst limestone, 70 – 75 m asl. About 25 individuals of *H. gastrofructa* and 15 of *H. baangongensis* were observed. Populations of *H.* cf. *borneensis* occurred intermixed with populations of *H. giamensis* in deep leaf litter over limestone-derived loams on ridges and moderate slopes beneath lowland perhumid evergreen broadleaf forests on and adjacent to karst limestone, 35 – 50 m asl. The observed populations of *H. giamensis* and *H.* cf. *borneensis* occurred as scattered individuals and small clumps of ca 20 – 25 plants. Individuals of *H. velutipedunculata* did not occur syntopically with any other congeneric. Population of *H. velutipedunculata* was ca 50 plants, growing on perhumid to moist evergreen forests, abundant along, but not restricted to, forested edges of waterfalls, 120 – 150 m asl. Owing to the nature of the investigated species (local endemics, restricted population sizes), the sample sizes were low in our study (see next section).

Phenology, flowering mechanisms, pollination strategies and insect visitors

Fieldwork at all the type localities was carried out to identify flowering event(s) at least once a month from January 2010 until June 2012. However, we recorded flowering period only from October 2011 to June 2012. The total number of mature inflorescences within four day spans

was recorded during peak flowering season: 9th – 12th Dec 2010 for *H. baangongensis*, *H.* cf. *borneensis*, *H. gastrofructa*, and *H. giamensis*; 1st – 4th Jan 2011 for *H. debilicrista* and *H. matangae*; 1st – 4th Jan 2011 and 13th – 16th May 2011 for *H. velutipedunculata*.

All species of these complexes produce several inflorescences together in a sequentially maturing synflorescence. Each erected inflorescence is composed of an unbranched flower-bearing spike – the spadix – subtended by a bract called the spathe. The spathe measures 6 – 15 cm in length, has a weak to pronounced constriction between the lower and upper spathe. The spadix equals the spathe in length and is divided into a lower pistillate and upper staminate zone, which are often separated by a staminode-bearing interstice. The pistillate flowers are naked and often accompanied by a staminode (hereafter referred to as interpistillar staminodes). Ovaries are three- to four-locular, with each locule containing many ovules. Staminate flowers have three to four (rarely five to six) stamens and connectives are substantially expanded with thecae dehiscing laterally. All *Homalomena* species studied so far undergo a complex series of seemingly coordinated spathe and spadix movements during anthesis (Boyce & Wong 2008).

Inflorescences of the investigated taxa were identified and observed at least a week prior to anthesis. Observations on flowering mechanisms were carried out on an hourly basis from the start until the end of anthesis, indicated respectively by the opening of the spathe limb and onset of odour production (the onset of pistillate anthesis), pistillate zone drying and reduced floral odour (end of pistillate anthesis), pollen release (the onset of staminate anthesis), and closing of the spathe limb (the end of anthesis). The phases of anthesis and the events of spathe and spadix movement, floral scent emission, pollen extrusion and resin secretion were recorded. Throughout the entire duration of anthesis, the behavior of insect visitors was also documented. The number of inflorescences and plant individuals involved were: *H. debilicrista* (five inflorescences/three individual plants), *H. matangae* (2/1), *H. gastrofructa* (4/2), *H. baangongensis* (2/1), *H. giamensis* (3/2), *H.* cf. *borneensis* (3/2), and *H. velutipedunculata* (5/3).

An independent set of inflorescences was further bagged during the pistillate phase of anthesis to obtain insect visitors for identification. The body surfaces of specimens belonging to the most frequently observed inflorescence visitors were examined under a stereo microscope to check for adhered pollen grains. Further confirmation of the effective pollinators of *H. debilicrista* and *H. giamensis* were attained through net-treatment tests conducted between 11th April 2015 and 26th July 2015. Four inflorescences of each species were covered with a plastic net (2 mm x 2 mm mesh) prior to spathe opening, allowing selective access to small insects only. The net was removed at the end of the anthetic period.

Fruit set of developing infructescences was used as a measure of the effectiveness of pollinators (in pollinating the numerous flowers) in cases of successful visit, and was defined as the ratio between the average for the total number of fruits per infructescence and the average for the total number of pistillate flowers per inflorescence for each species: *H. debilicrista* (six inflorescences/five infructescences), *H. matangae* (5/5), *H. gastrofructa* (5/5), *H. baangongensis* (5/6), *H. giamensis* (5/7), *H.* cf. *borneensis* (6/6), and *H. velutipedunculata* (5/5). Inflorescences and infructescences of each species were randomly selected from different plants. Seed set was estimated by counting the number of seeds on 10 developed fruits selected randomly from five infructescences (between three to five plant individuals) per species. All inflorescences, infructescences and insect visitors were preserved in 70% ethanol and deposited at the Sarawak Forestry Herbarium (SAR) and Sarawak Forestry Entomology Museum. Voucher information for all taxa is provided in Appendix 1.

Identifications of the anthophilous insects to the lowest possible taxonomic level (at least family) were conducted by the authors and by K. Wada (Musashimurayama Daini Junior School) for scarab beetles (*Parastasia*), H. Takizawa (Tokyo University of Agriculture) for chrysomelid beetles (*Chaloenus*), M. J. Toda (Hokkaido University) for drosophilid flies (*Colocasiomyia*), and A. G. Kirejtshuk (Russian Academy of Sciences) for hydrophilid beetles (*Cycreon*).

Sampling of floral scent, chemical and statistical analyses of floral VOCs

Sampling of floral scents was carried out for six of the studied *Homalomena* species (excluding *H.* cf. *borneensis*) in their natural habitat using standard dynamic headspace methods (refer to Raguso & Pellmyr, 1998). The number of replicate samples were: *H. debilicrista* (2 pistillate phase infloresences/3 staminate phase inflorescences/3 plant individuals), *H. gastrofructa* (2/2/2), *H. velutipedunculata* (5/5/5), *H. baangongensis* (4/0/4), *H. giamensis* (5/0/5) and *H. matangae* (3/0/3). Floral VOCs were trapped for three hours between 05:00 h – 09:30 h (local time) for the pistillate phase and between 05:00 h – 09:00 h for the staminate phase of *H. baangongensis* (January 2011 and February 2012), *H. matangae* (January 2011 and January 2012), *H. giamensis* (February and November 2011), *H. debilicrista* (January 2011 and January 2012), *H. gastrofructa* (January, October and November 2011) and *H. velutipedunculata* (January 2011 and January 2012).

To obtain floral VOC samples, inflorescences were individually enclosed within PET film oven bags (EasyRoast™, Bacofoil, UK), from which scented air was drawn by battery-operated vacuum pumps at a constant flow rate of 200 ml per min (Spectrex PAS-500 Micro Air Sampler; Spectrex, USA) through an air-drying silica gel tube (ORBO™ 506; Sigma-Aldrich, USA). Using a clean needle (1 mm diam.), ca 10 perforations were made to the oven bags to allow airflow through the bag. Floral VOCs were trapped in glass tubes containing 150 mg of an adsorbent polymer (ORBO™ 402 Tenax® 35-60 mesh, Sigma-Aldrich, USA). A control per sample was simultaneously collected using an empty oven bag. When sampling was not being carried out, inflorescences were covered with fine organdy bags to prevent insect visitation. The adsorbent traps were eluted with hexane (4 mL; ≥ 98.5% purity; MERCK, Germany), then kept at -20 °C refrigeration until analysis.

Prior to the analyses, 20 µL of tetradecane (internal standard, 13 ng/µL) was mixed with 750 µL of the hexane eluate (see above). Each sample was then concentrated to 40 µL under a fume hood. Analyses were conducted by combined gas chromatography-mass spectrometry (GC-MS) on a Shimadzu GCMS-QP2010 Plus (Shimadzu Corporation, Kyoto, Japan), equipped

with a non-polar BPX-5 column (SGE Analytical Science; 30 m x 0.23 mm i.d., 0.25 µm film thickness). For each concentrated sample, 1 µL was injected in splitless mode with the injector temperature set to 200 °C. GC oven temperature was set at 35 °C for 5 min, then increased at a rate of 5 °C min^{-1} to 180 °C, then at a rate of rate of 10 °C min^{-1} to 200 °C, then held steady for 10 min (Kumano & Yamaoka 2006). The carrier gas flow was maintained at a constant pressure of 100 psi. MS Source and quadrupole temperatures were set at 220 °C and 200 °C, respectively. Mass spectra were taken from *m/z* 35-500 in EI mode.

The Kovats Retention Indexes (KIs) of the VOCs were obtained with an external standard (C_8-C_{22} saturated alkanes, Supelco, USA). Compounds were tentatively identified by cross-referencing their mass spectra and retention times with data from commercially available mass spectral libraries (MassFinder 4, NIST11 and Wiley Registry™ 9th Edition), integrated to the software Agilent MSD Productivity ChemStation (Agilent Technologies, Palo Alto, USA). The peak areas on the chromatograms were integrated to obtain the total ion current signal, which was used to determine the relative amount of each compound.

All statistical analyses on floral VOCs compositional differences among samples were performed with the Paleontological Statistics (PAST) software version 2.17 (Hammer *et al.* 2001). To test for differences in floral scent profiles among species and phases, NP Manova tests with 9999 permutations were applied and post-hoc tests with Bonferroni correction for pairwise comparisons were performed when necessary. A non-metric multidimensional scaling (NMDS) was used to depict variations in floral scent composition among samples using the Bray-Curtis distance index (Hammer *et al.* 2001). Stress values below 0.1 represent a good ordination in the interpretation.

RESULTS

Phenology

Flowering periods for all the studied species of *Homalomena* occurred mainly from November (October) to February (April), which corresponds to a period of intense rainfall (350 to 850 mm monthly) brought by the North-East Monsoon (Fig. 2). Interestingly, *H. velutipedunculata* was the only species with two flowering periods (November – January and April – June). All studied taxa flowered profusely between December and January. When populations of species belonging to complexes Hanneae and Giamensis occurred syntopically, individuals belonging to the former always flowered more profusely than those of the latter at any one time during the peak season. The total numbers of mature inflorescences observed within four day spans during the peak season among the studied populations are as follows: *H. debilicrista* (ca 30 inflorescences on 60 – 100 individual plants) together with *H. matangae* (two inflorescences on ca 20 individual plants), and *H. gastrofructa* (ca 15 inflorescences on ca 25 individual plants) together with *H. baangongensis* (five inflorescences on ca 15 individual plants). Individuals of species belonging to the Giamensis and Borneensis complexes exhibited similar number of inflorescences; *H. giamensis* (6 inflorescences on ca 25 individual plants) together with *H.* cf. *borneensis* (10 inflorescences on ca 20 individual plants). Individuals of *H. velutipedunculata* yielded ca 25 inflorescences among ca 50 individual plants.

Flowering mechanisms, pollination strategies and insect visitors

Hanneae complex

Anthesis lasted between 53 – 62 hrs in the three investigated species (Fig. 3; Fig. 4). The pistillate phase of anthesis for all species started at ca 03:00 h. By 05:00 – 06:00 h, the spathe limb opened wide with an inflated lower spathe, allowing access in the receptive pistils (Fig. 4b). Concomitantly, an intense aniseed odour emission, originated from the staminate zone, could be easily perceived by the human nose. By 17:00 h (or in *H. gastrofructa*, at 22:00 h), the pistillate zone dried up and floral scent emission faded. This indicated the beginning of the inter-sexual phase. On the second day (staminate phase), as early as 02:30 h, the lower part of the staminate zone began to secrete amber-colored resin droplets (Fig. 4g). By 06:00 h, a second floral scent emission event (less intense than that of the pistillate phase) occurred. At the same time, pollen strings were extruded from inflorescences of all three species (Fig. 4c). In individuals of *H. debilicrista*, pollen was mixed with resin droplets to form a pale yellow paste. Between 12:00 – 15:00 h, the spathe constriction was tightened enough to block the entrance into the lower chamber (Fig. 4h). On the third day, by 04:30 h, the inflorescence declined and the spathe limb began to close acropetally. For all three species, we recorded a very high average fruit set (> 81%), as well as high number of seeds per developed fruit: *H. debilicrista* (83.3 ± 19.5), *H. gastrofructa* (77.1 ± 11.7) and *H. velutipedunculata* (80.4 ± 14.7; Table 1). Inflorescences of *H. debilicrista* bagged with selective mesh (2 mm **Ø**) did not yield fruits/seeds, excluding not only self-pollination and apomyxis, but also the role of small-sized anthophilous insects as effective pollinators. However, the first author observed infructescence developing in the field among the unbagged inflorescences.

Colocasiomyia flies (Drosophilidae) arrived at the inflorescences of all three species between 06:30 – 06:45 h. Comparatively, the inflorescences of *H. matangae* were most attractive to the flies than those of the remainder species (Figs. 4b, 4d, 4i; Table 2). The flies moved freely within the inflorescences or stayed inside the lower chambers. They fed on stigmatic liquids secreted during the pistillate phase, exudations from the inner surface of the

spathe limb, the damaged stamens, and seemingly also on pollen. Mating and egg laying activities were observed in inflorescences of *H. debilicrista*. The flies left at the end of anthesis (*H. debilicrista,* at 08:00 h; *H. gastofructa*, at 16:00 h; and *H. velutipedunculata,* at 12:00 h) and, under the microscope, pollen loads were not observed on their body surfaces.

Between 06:30– 08:30 h, scarab beetles (*Parastasia gestroi* and/or *P. nigripennis*; Scarabaeidae, Rutelinae) (Figs. 4b, 4d-e & 4h) and chrysomelid beetles (*Chaloenus* spp.; Chrysomelidae, Galeuricinae) (Figs. 4f, 4j) arrived (Table 2). The scarab beetles always arrived first (15 – 30 min earlier) and were observed to carry pollen onto the pistils (Fig. 4b). Immediately after arrival, both scarab and chrysomelid beetles were observed to consume the staminodes found between the pistils, but only the latter fed on those above the pistillate flowers. During the pistillate phase, the scarab beetles remained inside the lower chamber, whereas the chrysomelid beetles, although more abundant inside the lower chamber, were also active on the upper parts of the spadix (staminate zone and inner surface of the spathe limb). Mating activities (Figs. 4b, 4h) were observed among the scarab beetles. The scenario remained unchanged until the massive release of pollen, when almost all individuals of both scarab and chrysomelid beetles moved onto the staminate zone and consumed pollen (Fig. 4c). The feeding activity of the latter eventually led to damage of the staminate zone, due to heavy consumption of stamens. The beetles left the inflorescences as early as 08:00 h on the second day of anthesis, even though some stayed until the end of anthesis. Upon departure they carried pollen attached to their bodies.

There were other intermittent insect visitors to the inflorescences of *Homalomena* belonging to the Hanneae complex. *Cycreon* spp. (Coleoptera, Hydrophilidae) were found visiting inflorescences of *H. debilicrista* and *H. gastrofructa* during the pistillate phase, starting around 08:30 h (Table 2). Mating activities were observed and beetles left prior to or at the onset of the staminate phase. Staphylinid beetles were found inside one inflorescence of *H. debilicrista* and two inflorescences of *H. velutipedunculata* (arrived at 06:45 h on the first day and left at the end of the anthesis; Fig. 4l, Table 2). Mating and egg-laying activities at the lower part of the staminate zone were observed throughout the anthesis of *H. velutipedunculata*. A

few individuals of an unidentified species of stingless bee (*Trigona* sp.; Apidae, Meliponini; Table 2) visited the staminate zone of *H. velutipedunculata* and *H. debilicrista* during pistillate phase and again during staminate phase for 5 to 10 seconds each time to rob pollen/resin (Figs. 4h, 4k).

Giamensis complex

Anthesis lasted ca 30 hrs in all three investigated species belonging to the Giamensis complex (Fig. 3; Fig. 5). The pistillate phase started at ca 03:00 h and the staminate phase on the following day, between 03:00 – 04:00 h for all species. The flowering mechanism was mostly similar to that described for species belonging to the Hanneae complex (see above), but with only one scent emission event during the pistillate phase (a lemon-like fragrance perceivable by human nose between 06:00 – 07:00 h). The staminate zone secreted resin droplets between 07:00 – 10:00 h on the first day of anthesis (Figs. 5b, 5h, & 5j). Pollen was extruded in strings from inflorescences of *H. baangongensis* on the second day of anthesis at ca 06:00 h (Fig. 5k), but had the consistency of a paste in inflorescences of *H. matangae* at ca 07:00 h (Figs. 5d, 5f) and *H. giamensis* at ca 07:00 h. The entrance into the lower chamber was blocked between 06:00 – 08:00 h by the tightening of the spathe constriction. Between 09:00 – 09:30 h, the spathe limb was fully closed and this marked the end of anthesis (Fig. 5l). The recorded fruit set in species belonging to the Giamensis complex was also very high, recorded at over 91% for all three investigated taxa (Table 1). Seed set was also profuse in all species: *H. baangongensis* (72.8 ± 17.3), *H. giamensis* (82.2 ± 17.2) and *H. matangae* (75.7 ± 13.9). Bagged inflorescences of *H. giamensis* did not yield fruits/seeds as previously described for *H. debilicrista*.

Colocasiomyia flies (Drosophilidae), scarab beetles (*Parastasia gestroi* and *P. nigripennis*; Scarabaeidae, Rutelinae) and chrysomelid beetles (*Chaloenus* spp.; Chrysomelidae, Galeuricinae) were observed in inflorescences of the three investigated species (Table 2). *Colocasiomyia* flies arrived first, at ca 05:00 h, and most of them remained on the spathe limb (Figs. 5c, 5d, 5f & 5i). The number of flies visiting inflorescences of species belonging to the Giamensis complex was higher than those belonging to the Hanneae complex (Table 2). *S*carab

beetles (Figs. 5c-e, 5g, 5h & 5k) arrived between 06:30 – 07:15 h on the first day of anthesis and left between 07:00 – 07:45 h on the following morning. Chrysomelid beetles (Figs. 5h-5j) arrived between 07:15 – 08:30 h on the first day of anthesis and left between 07:15 – 09:30 h on the following morning. *Parastasia* and *Chaloenus* beetles carried pollen attached to their bodies when leaving the inflorescences. *Cycreon* spp. (Hydrophilidae) arrived at 06:30 – 07:15 h on the first day of anthesis and left at 06:30 – 07:15 h on the following morning. These beetles were found in inflorescences of all three species, but they were particularly abundant in those belonging to *H. baangongensis* (Fig. 5g, Table 2). There were other intermittent anthophilous insects present/active on inflorescences. Staphylinid beetles were observed inside inflorescences of *H. matangae* (visited at 10:00 h on the first day of anthesis and left at 09:00 h at the end of anthesis), whereas stingless bees (*Trigona* spp.) were observed in association with both *H. baangongensis* and *H. matangae* for 5 to 10 seconds at around 10:00 h during pistillate phase (Table 2). The behavior of the insects and their activities were similar to what was described in associations involving species belonging to the Hanneae complex.

Borneensis complex

Anthesis lasted ca 30 hrs for *H.* cf. *borneensis*. The pistillate phase started at ca 03:00 h and the staminate phase on the following day, at ca 04:00 h (Fig. 3; Fig. 6). The flowering mechanism resembled that previously described for species belonging to the Giamensis complex, with only one floral scent emission event during the pistillate phase (an intense aniseed-like scent, most prominently perceivable between 06:00– 07:00 h). Later at ca 18:30 h, the staminate zone was found to excrete resin and was covered with it at ca 20:45 h (Fig. 6c). At the same time, the inflorescence declined slightly and the pistillate zone dried, indicating the onset of inter-sexual phase. On the second day, between 04:00 – 06:00 h, pollen was extruded from the anthers and mixed with the resin to form a paste. The entrance to the pistillate zone was blocked by a tightened constriction around 06:00 h. By 09:00 h, the anthesis had ended.

Five insect taxa visited inflorescences of *H.* cf. *borneensis*: *Colocasiomyia* flies (Drosophilidae), *Parastasia gestroi* (Scarabaeidae, Rutelinae) , *Chaloenus* spp. (Chrysomelidae,

Galeuricinae), *Cycreon* spp. (Hydrophilidae), and staphylinid beetles (Figs. 6b-6e & 6g, Table 2). *Colocasiomyia* flies arrived first, at ca 07:30 h, but were not confined to the pistillate zone. Most of the flies remained in the staminate zone and the spathe limb, leaving only at the end of anthesis (ca 09:00 h). Scarab beetles arrived at ca 07:40 h and about fifteen minutes later, chrysomelid beetles started showing up (they arrived until 17:30 h in one occasion). Both scarab and chrysomelid beetles left the inflorescences as early as 07:00 h on the second day of anthesis. Individuals of *Cycreon* spp. arrived on the second day of anthesis, at ca 04:00 h. They remained on the inner spathe limb and left half an hour later. Staphylinid beetles were caught in the bagged inflorescences for insect identification during the pistillate phase. The behavior of the insects and their activities were similar to what was described in associations involving species belonging to the Hanneae and Giamensis complexes. As previously observed among species belonging to the Hanneae and Giamensis complexes, the average fruit set for *H.* cf. *borneensis* was very high (85.7%) and the number of seeds per developed fruit was 79.4 ± 15.1 (Table 1).

Chemical composition of floral odour compounds

Hanneae complex

A total of 33 VOCs were isolated among all analyzed samples belonging to the Hanneae complex, out of which 22 VOCs were tentatively identified and assigned to three of the seven compound classes originally proposed by Knudsen *et al.* (2006): aliphatics (7), benzenoids (2) and terpenoids (14) (Table 3). Out of these, large relative amounts (> 20%) of *sec*-butyl acetate, 2-heptanol, α-pinene, sabinene, limonene and 2-ethylhexanol were detected, even though not all of them were found in each of the analyzed samples (Table 3). Four monoterpenes were found in pistillate phase samples from all three species: α-thujene (0.25 – 10.55%), α-pinene (0.96 – 55.06%), β-pinene (1.04 – 44.22%), and myrcene (0.52 – 5.28%). The irregular terpenes

(*Z*)-4,8-dimethyl-1,3,7-nonatriene (0.14 – 9.46%) and (*E*)-4,8-dimethyl-1,3,7-nonatriene (0.46 – 85.77%) were present only in pistillate and staminate phase samples of *H. gastrofructa* and *H. velutipedunculata.* Nine compounds were found in staminate phase samples of all investigated species: *sec*-butyl acetate (0.16 – 91.33%), 2-heptanol (0.11 – 61.12%), α-thujene (0.01 – 5.33%), α-pinene (0.53 – 51.99%), sabinene (0.28 – 3.21%), β-pinene (0.20 – 19.06%), myrcene (0.02 – 1.9%), limonene (0.26 – 11.74%), and veratrole (0.04 – 9.21%).

For any single species, there was no significant difference in floral VOC composition between pistillate and staminate phases (NP-Manova tests, P>0.05). The NP-Manova tests showed significant differences in the floral compounds among all three species belonging to the Hanneae complex during the pistillate phase ($F_{2,27} = 3.8$, $p = 0.003$), but not during the staminate phase ($F_{2.22} = 1.14$, $p = 0.36$). In fact, the floral scent of the pistillate phase of *H. velutipedunculata* is different from those of *H. debilicrista* and *H. gastrofructa* (post-hoc pairwise comparisons $p = 0.048$). The floral scents of pistillate phase inflorescences of the latter were characterized by high percentages of pinenes (α- and β-) and sabinene (*H. debilicrista*) or 6-methyl-5-hepten-2-one (*H. gastrofructa*),whereas that of *H. velutipedunculata* was rich in limonene, veratrole and *sec*-butyl-acetate (Table 3).

Giamensis complex

Inflorescences of the three species belonging to the Giamensis complex emitted an assortment of 26 VOCs during the pistillate phase of anthesis, of which 14 were tentatively identified as follows: aliphatics (5), benzenoids (2) and terpenoids (7) (Table 3). Two compounds were dominant: *sec*-butyl acetate (2.89 – 96.98%) and (*E*)-4,8-dimethyl-1,3,7-nonatriene (1.77 – 91.83%), with (*Z*)-4,8-dimethyl-1,3,7-nonatriene (1.41 – 14.96%) and three unidentified compounds occurring in lower relative amounts (Table 3). The NP-Manova test did not show significant differences in floral scent composition among them ($F_{2,20} = 0.83$, $p = 0.44$).

Hanneae complex vs. Giamensis complex

The NMDS representations of the floral scent composition of the studied *Homalomena* species (stress = 0.13) showed two different group patterns: Hanneae complex – pistillate phase and Giamensis complex – pistillate phase (Fig. 7). Floral VOCs compositions differed significantly between the two complexes during the pistillate phase ($F_{1,32} = 5.47$, $p = 10^{-4}$). The pistillate phase floral scents of the three species belonging to the Giamensis complex were characterized by high percentages of pinenes (α- and β-), limonene, 2-heptanol, sabinene and veratrole. These compounds were either absent or only found in low relative amounts in samples of the three species belonging to the Hanneae complex, which in turn are rich in (*E*)-4,8-dimethyl-1,3,7-nonatriene (Table 3).

DISCUSSION

Effective pollinators and other anthophilous insects

Scarab beetles of the genus *Parastasia* (Scarabaeidae, Rutelinae) appear to be the primary pollinators of all the investigated taxa of *Homalomena*. This is in accordance to what was observed for another *Homalomena* species studied by Kumano & Yamaoka (2006). In a posterior research, the same authors suggested that in association with *Homalomena* inflorescences, these scarabs secured food rewards, mating opportunities and safe mating arenas inside a sheltered floral chamber (Kumano-Nomura & Yamaoka 2009). Pollen was carried on their bodies onto the stigmas during the pistillate phase in the form of a resin-mitigated pollen paste. Utilization of resin for pollen adherence had also been observed in associations involving plants of the Neotropical genus *Philodendron* and cyclocephaline scarabs (Scarabaeidae, Dynastinae) (Mayo 1991; Maia *et al.* 2010; Gottsberger *et al.* 2013). Two species

of *Parastasia* were identified as inflorescence visitors of the investigated *Homalomena* taxa: *Parastasia gestroi* and *P. nigripennis* (Table 2). So far, 16 *Parastasia* spp. were recorded from Borneo, with up to 5 spp. in West Borneo: *P. burmeisteri*, *P. gestroi*, *P. moseri*, *P. moultoni*, and *P. nigripennis* (Kuijten 1992). This *Parastasia* diversity is low as compared to the high species diversity of *Homalomena* (ca 300 species) on Borneo, in contrast to its Neotropical sister taxa, *Philodendron* (ca 650 species) pollinated by Neotropical Cyclocephalini (ca 500 species).

Chrysomelid beetles of the species *Chaloenus schawalleri* (Chrysomelidae, Galerucinae) were observed to visit all seven investigated *Homalomena* (Table 2). Unlike *Parastasia* scarabs, however, these beetles are only occasional pollinators, something previously observed in a study with a congeneric (Kumano & Yamaoka 2006). The genus so far encompasses 41 described species (Takizawa 2013), most of which apparently closely associated with aroids. Adults mostly gather and feed on inflorescences, but have also been observed chewing on leaf blades (Darling 2007; Takizawa 2012). In our study, their presence in the inflorescences often led to significant damage to the spadix due to the consumption of interpistillar and interstice staminodes and staminate florets. Such (floral) damages to the spadix by anthophilous chrysomelid beetles, notably the appendix, are reported from other aroid taxa in Borneo (Schismatoglottidae; Low *et al.* 2014, 2015). When discussing the chemical cues involved in the attraction of insects to the inflorescences of *Homalomena* sp., Kumano-Nomura & Yamaoka (2009) hypothesized that beetles of *C. schawalleri* could eavesdrop on the same signals used by the more reliable pollinators (*Parastasia* scarabs) at even low levels of scent emission.

The anthophilous flies observed in inflorescences of five of the investigated *Homalomena* species were two species of *Colocasiomyia* (*C. nigricauda* and *C.* aff. *heterodonta*, Table 2). *Colocasiomyia nigricauda* was previously documented in association with other species of *Homalomena* (Sultana *et al.* 2002). The adults consume secretions on the stigmas and on the inner spathe, pollen, and also utilize the inflorescences as ovipositing chambers (Toda & Lakim 2011; Fartyal *et al.* 2013; Low *et al.* 2015). Their role as pollinators of the investigated *Homalomena* species, although unlikely, cannot be discarded without further data. The genus *Colocasiomyia*, which currently encompasses ca 70 species, is associated to flowers

of Araceae, Arecaceae and Magnoliaceae (Takenaka-Takano *et al.* 2012). With rare exceptions, their relationships with aroid hosts are species-specific (Takenaka *et al.* 2006; Fartyal *et al.* 2013).

Adult hydrophilid beetles (*Cycreon* spp.; Hydrophilidae) are recorded here for the first time in association with inflorescences of *Homalomena*, which they appear to use as mating sites. Although the adults are phytophagous, their larvae are predatory and may feed on other insect larvae present in the inflorescences (e.g., other beetles, flies) (A. G. Kirejtshuk pers. comm.). Their visits were mostly confined to the pistillate zone and are disregarded as pollinators, however, their role needs further investigation.

Staphylinid beetles (Staphylinidae) are known to visit fresh or decaying aroid inflorescences, commonly used by several species as food source, mating sites and/or oviposition substrates (Pellmyr 1986; Takenaka-Takano *et al.* 2012; Low *et al.* 2015), activities which have also been observed in the studied Bornean *Homalomena*. Stingless bees (Apidae, *Trigona* spp.) are most likely opportunistic pollen consumers, as they never ventured towards the pistillate zone. It is also probable that they collect resin droplets as a nest building material, as have been previously documented among other aroid taxa (Ramírez & Gómez 1978).

Floral odour

Owing to the fact that pollinator attraction occurred before dawn, long-range cues applied by the plant hosts are most likely olfactory. Floral scent emission together with coordinated spathe and spadix movements, facilitated pollinator entrance during the pistillate phase. Analyses of floral scent samples showed that the investigated *Homalomena* emitted specific floral VOC 'packages' that differed between the Hanneae and Giamensis complexes. The three species belonging to the Giamensis complex are dominated by (*E*)- and (*Z*)-4,8-dimethyl-1,3,7-

nonatriene and *sec*-butyl acetate. Floral scents from species belonging to the Giamensis complex are not only comprised by different VOCs than those found among the Hanneae complex, but also exhibit a more variable chemical composition among species. The floral blends of *H. gastrofructa* and *H. debilicrista* are dominated by α- and β-pinene, but the two species are differentiated by important secondary compounds (2-ethylhexanol and 6-methyl-5-hepten-2-one *vs* sabinene and 2-heptanol; Table 3). *Homalomena velutipedunculata* appears to exhibit an intermediate floral blend, combining compounds characteristic of the Giamensis (*sec*-butyl acetate) and Hanneae complexes (α- and β-pinene, 2-heptanol and limonene). Coincidently, *H. velutipedunculata* is the only species investigated to be pollinated by *P. nigripennis* alone and occur singly in its locality, with no other *Homalomena* species from the Cyrtocladon Supergroup.

In the Neotropics, several aroid genera and in particular *Philodendron*, the sister genus of *Homalomena* (Wong *et al.* 2013b), are pollinated by scarab beetles of the tribe Cyclocephalini (Scarabaeidae, Dynastinae). However, pollination occurs at dusk and early evening, involving also floral scents as chemical tracks that guide the beetles to their floral hosts (Gottsberger & Silberbauer-Gottsberger 1991; Maia *et al.* 2010, Gottsberger *et al.* 2013). Different pollinators belonging to this species-rich tribe (ca 500 species) have been shown to be attracted to the major constituents of aroid floral scents, such as 4-methyl-5-vinylthiazole in *Caladium bicolor* (Maia *et al.* 2012); (*S*)-2-hydroxy-5-methyl-3-hexanone in *Taccarum ulei* (Maia *et al.* 2013); 3,4-dimethoxystyrene, either alone or combined with (*Z*)-jasmone in *Philodendron* form *selloum* (Dötterl *et al.* 2012); and dihydro-β-ionone, either alone or combined with methyl jasmonate in *Philodendron adamantinum* (Pereira *et al.* 2014). Hence, apparently one or two VOCs suffice to efficiently attract cyclocephaline scarab pollinators, often specifically. Such an efficient communication system may also exist in the associations involving species of *Homalomena* sect. *Cyrtocladon* and pollinator ruteline scarabs. Interestingly, the tribes Rutelini (Rutelinae) and Cyclocephalini (Dynastinae) are morphologically closely related, and the biology of the anthophilous species are quite similar (Jameson & Wada 2004).

The monoterpenes α-pinene, β-pinene and β-ocimene were also reported from another *Homalomena* by Kumano & Yamaoka (2006) and are common in more than 50% of the families of angiosperms (Knudsen *et al.* 2006). In Araceae, α-pinene, β-pinene, linalool, camphene, sabinene and β-myrcene were also detected in various species, such as *Anthurium* spp., *Arum* spp., *Peltandra virginica* and *Sauromatum guttatum* (Patt *et al.* 1995; Skubatz *et al.* 1996; Kuanprasert *et al.* 1998; Hadacek & Weber 2002; Schwerdtfeger *et al.* 2002; Chartier *et al.* 2013). *Parastasia* scarabs, as well as *Chaloenus* chrysomelids were attracted to the floral scent of *Homalomena* sp., which included α-pinene among the five dominant compounds (Kumano-Nomura & Yamaoka 2009). *sec*-Butyl acetate, a known component of the aggregation pheromone of pest scarab beetles (*Strategus aloeus*, Scarabaeidae; Rochat *et al.* 2000), has only been reported once in floral scents (*Sauromatum guttatum*, Araceae; Borg-Karlson *et al.* 1994). (*E*)-4,8-dimethyl-1,3,7-nonatriene is a common herbivory-induced VOC (Azuma *et al.* 1997), also known as a component in attractants for the coddling moth (*Cydia pomonella*; Lepidoptera, Tortricidae) (Knight *et al.* 2011; Knight & Light 2012). Its presence in high concentrations in floral scents is more widely recognized in *Yucca* spp. (Agavaceae) populations from arid regions of North and Central America (Svensson *et al.* 2006, 2011), whose reproductive success is exclusively dependent on associations with yucca moths (*Tegeticula* spp., *Parategeticula* spp. and *Prodoxus* spp.; Lepidoptera, Prodoxidae) (Pellmyr & Huth 1994; Pellmyr 2003). 2-heptanol, 2-ethylhexanol and 2-heptanone had all been previously isolated as floral scent constituents of other species of aroids (Schwerdtfeger *et al.* 2002; Knudsen *et al.* 2006).

Food, mating opportunities and safe mating arenas

The interpistillar staminodes of inflorescences of the investigated *Homalomena* were consumed by the main pollinators, *Parastasia* spp., and also by *Chaloenus* spp. Apart from the interpistillar

staminodes, the interstice and staminate zone were also consumed by *Chaloenus* spp., an observation shared by Kumano & Yamaoka (2006) in a study with another *Homalomena* species. Elsewhere in Araceae, this has been documented in Neotropical *Dieffenbachia*, *Gearum* and *Taccarum* (Spathicarpeae), which are all pollinated by scarab beetles of the tribe Cyclocephalini (Gonçalves & Maia 2006; Maia *et al.* 2013; Gibernau 2015). Pollen was also consumed by *Parastasia* spp. and *Chaloenus* spp., and occasionally by *Trigona* bees.

None of the *Homalomena* species investigated in this study trapped their insect visitors which are in accordance to observation in Bröderbauer *et al.* (2012). The spathe constriction loosened to allow the insect visitors access to the lower floral chamber. As the anthesis progressed into the staminate phase of anthesis, the constricted spathe tightened back slightly, but the lower chamber was still occupied by *Parastasia* until just after the massive release of pollen. Only then the beetles started to move upward to the staminate zone and leave the inflorescences soon after. Therefore, the lower chamber of *Homalomena* functions as a temporary shelter for *Parastasia* spp. until the onset of the staminate phase of anthesis. This is a very common trait in many scarab-pollinated aroids, notably within the Caladieae, Spathicarpeae and Philodendreae (Maia *et al.* 2010, 2013; Gibernau 2015).

The lower spathe is lengthier than the upper spathe in species belonging to the Giamensis and Borneensis complexes, but shorter in those belonging to the Hanneae complex (Ng *et al.* 2011). The length of the lower spathe exceeding the upper spathe is apomorphic to section *Cyrtocladon*, but showed a reversal in the Hanneae complex (Wong *et al.* 2013b). The significance of this morphological character might be linked to providing sufficient space to accommodate the pollinators (Wong *et al.* 2013b). In such a scenario, inflorescences of species belonging to the Borneensis and Giamensis complexes would provide more space in their lower chambers to accommodate more insects than species belonging to the Hanneae complex.

CONCLUSIONS

Scarab beetles of the genus *Parastasia* (*P. gestroi* and *P. nigripennis*) play the role of primary pollinators of all the investigated *Homalomena* taxa, with chrysomelid beetles (*Chaloenus schawalleri*) acting as accessory pollen vectors/pollinators. *Homalomena* present pollination characters common in aroids associated with large scarabs as specialized pollen vectors: protogyny, short anthesis (30 – 60 hrs), a sheltered floral chamber and strong attractive floral scents emitted during the pistillate stage. The floral scent blends contained uncommon compounds in high concentration, which could ensure pollinator discrimination as previously documented in Neotropical taxa sharing the same pollination strategy. One interesting point is that both the pistillate and staminate phases of the investigated *Homalomena* species occurred during early morning hours, before or during sunrise, whereas in the Neotropics, cyclocephaline scarabs are active at dusk and early evening. This could represent a divergence between pollination strategies in the Old and New World tropics among closely related aroid taxa, likely related to the behavior of available specialized pollen vectors. Future research should be directed at the investigation of isolating barriers among these syntopically co-flowering *Homalomena*, since they share the same set of pollinators.

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Captions

Table 1. Mean number ± standard deviation (SD) of pistillate flowers per inflorescence, developed fruits per infructescence, percentage of fruit set and seeds based on 10 developed fruits selected randomly from five infructescences (between three to five plant individuals) per species for investigated *Homalomena* (Araceae) under natural environmental conditions in Kuching Division, Sarawak, Malaysia. [HC] represents Hanneae complex. [GC] represents Giamensis complex. [BC] represents Borneensis complex. n represents number of replicates.

Table 2. Identified species and number of insect taxa (mean ± standard deviation and range) per inflorescence of seven *Homalomena* species at four localities in Kuching Division, Sarawak, Malaysia. Numerics (-/-) represent number of replicates/number of individual plants. The same roman letter represents syntopic taxa. [HC] represents Hanneae complex. [GC] represents Giamensis complex. [BC] represents Borneensis complex.

Table 3. Chemical composition (mean and/or range of relative amounts of each VOC) of the floral scents of six species of *Homalomena* (Araceae) belonging to section *Cyrtocladon*. Samples were obtained by dynamic headspace during the interval of highest perceivable scent emission in the course of the pistillate (♀) and staminate (♂) phases of anthesis. *Hdebi* (*Homalomena debilicrista*), *Hgast* (*H. gastrofructa*), *Hvelu* (*H. velutipedunculata*), *Hbaan* (*H. baangongensis*), *Hgiam* (*H. giamensis*), *Hmata* (*H. matangae*). *represents number of replicates/number of individual plants. tr, trace amounts (< 0.01%). The compounds are listed according to compound class and Kovats retention index (RI). Unknowns were included when present with > 0.5% of the total amount in any sample. [a] present in only one of the analyzed samples; [b] present in only two of the analyzed samples; [c] present in only three of the analyzed samples; [d] present in only four of the analyzed samples.

Fig. 1. Localities of the seven *Homalomena* species studied. 1. *H. velutipedunculata* (Hanneae complex). 2. *H. debilicrista* (Hanneae complex). 3. *H. matangae* (Giamensis complex). 4. *H. giamensis* (Giamensis complex). 5. *H.* cf. *borneensis* (Borneensis complex). 6. *H. gastrofructa* (Hanneae complex). 7. *H. baangongensis* (Giamensis complex).

Fig. 2. Flowering period of the seven *Homalomena* species studied. Note horizontal bars of syntopic, co-flowering taxa have the same shade color. Species belonging to Hanneae complex (HC); Giamensis complex (GC); Borneensis complex (BC). Data on rainfall (mm) is provided by Kuching airport station (01°29'N, 110°20'E), Sarawak Division, Meteorology Department Malaysia.

Fig. 3. Flowering mechanism and presence of insect visitors for *Homalomena debilicrista*, *H. baangongensis*, and *H.* cf. *borneensis* representing the Hanneae, Giamensis, and Borneensis complexes, respectively.

Fig. 4. Flowering at different stages in species of the Hanneae complex together with visiting insects and their activities. A. Onset of pistillate stage. B. A pair of *Parastasia* during pistillate stage, black arrow shows pollen being carried in by the beetle. C. *Chaloenus schawalleri* consuming pollen. D. Pistillate stage. *Parastasia* and *Colocasiomyia* are present. E. *Parastasia* at post-pistillate stage. F. Spathe artificially removed. Staminate stage. *Chaloenus schawalleri* is present. G. Onset of staminate stage. Black arrow shows resin secretion. H. At the end of staminate stage. *Parastasia* mating. Black arrow shows *Trigona* sp. I. *Colocasiomyia* at the lower chamber during pistillate stage. J. *Chaloenus schawalleri*, *Chaloenus* spp. K. *Trigona* sp. robbing pollen. L. Staphylinid beetles are present during staminate stage. A-F. *Homalomena debilicrista*. G-I & K-L. *Homalomena velutipedunculata*. J. *Homalomena gastrofructa*.

Fig. 5. A. Flowering at different stages in species of the Giamensis complex together with visiting insects and their activities. 1-4 indicating the flowering sequence (1: emerging bud; 2: at pistillate stage; 3: one day after anthesis; 4: three days after anthesis). B & C. Resin present just prior to the staminate stage. C. *Parastasia* and *Colocasiomyia* are present during pistillate stage. D. Massive pollen extrusion with *Parastasia*, *Chaloenus schawalleri* and *Colocasiomyia* present. E. *Parastasia* carrying interpistillar staminode. F. At staminate stage with *Chaloenus schawalleri* and *Colocasiomyia*. G. At pistillate stage with *Cycreon* and *Parastasia*. H & I. Prior to staminate stage with *Chaloenus* and *Parastasia*. Note the resin secretion and the damage on the staminate zone. J. *Chaloenus* sp. and *C. schawalleri*. K. *Parastasia* consuming pollen. L. End of anthesis. A. *Homalomena giamensis*. B-F. *Homalomena matangae*. G-L. *Homalomena baangongensis*.

Fig. 6. Flowering at different stages in species of the Borneensis complex together with visiting insects and their activities. A & B. At pistillate stage. C & D. Prior to staminate stage with *Parastasia* present. E. At staminate stage with *Parastasia* present. F. End of anthesis. G. *Parastasia* copulating during bagging for floral odour trapping. A-G. *Homalomena* cf. *borneensis.*

Fig. 7. Non-metric multidimensional scaling (NMDS) representation of the inflorescence scent profiles of six investigated *Homalomena* species (stress value = 0.13). Each different plot colour corresponds to a particular complex species at a particular anthesis phases.

Appendix 1. List of specimens investigated: Taxon, collection locality, geographic coordinate, voucher, and GenBank accession number. Taxa are arranged alphabetically.

Supplementary Fig. 1. Flowering populations with white arrows showing the emerging buds and inflorescences. A. *Homalomena velutipedunculata.* B. *Homalomena giamensis* (1) growing intermixingly with *Homalomena* cf. *borneensis* (2). C. *Homalomena gastrofructa.* D. *Homalomena* cf. *borneensis.*

Table 1. Mean number ± standard deviation (SD) of pistillate flowers per inflorescence, developed fruits per infructescence, percentage of fruit set and seeds based on 10 developed fruits selected randomly from five infructescences (between three to five plant individuals) per species for investigated *Homalomena* (Araceae) under natural environmental conditions in Kuching Division, Sarawak, Malaysia. ^{HC} represents Hanneae complex. ^{GC} represents Giamensis complex. ^{BC} represents Borneensis complex. n represents number of replicates.

	Number of pistillate flowers per inflorescence	Developed fruits per infructescence	Fruit set (%)	Seeds per fruit
H. debilicrista ^{HC}	237.0 ± 26.9 (n=6)	203.4 ± 39.5 (n=5)	85.8	83.3 ± 19.5
H. gastrofructa ^{HC}	233.4 ± 33.7 (n=5)	189.2 ± 18.1 (n=5)	81.1	77.1 ± 11.7
H. velutipedunculata ^{HC}	191.0 ± 37.8 (n=5)	178.4 ± 25.5 (n=5)	93.4	80.4 ± 14.7
H. baangongensis ^{GC}	297.4 ± 4.2 (n=5)	147.0 ± 31.0 (n=6)	91.9	72.8 ± 17.3
H. giamensis ^{GC}	222.6 ± 12.0 (n=5)	207.4 ± 31.9 (n=7)	93.2	82.2 ± 17.2
H. matangae ^{GC}	228.0 ± 9.3 (n=5)	207.8 ± 13.6 (n=5)	91.1	75.7 ± 13.9
H. cf. *borneensis* ^{BC}	136.2 ± 14.1 (n=6)	116.7 ± 15.4 (n=6)	85.7	79.4 ± 15.1

Table 2. Identified species and number of insect taxa (mean ± standard deviation and range) per inflorescence of seven *Homalomena* species at four localities in Kuching Division, Sarawak, Malaysia. Numerics (-/-) represent number of replicates/number of individual plants. The same roman letter represents syntopic taxa. [HC] represents Hanneae complex. [GC] represents Giamensis complex. [BC] represents Borneensis complex.

Plant taxa	**Flower visitor taxa**					
	Parastasia spp.	*Chaloenus* spp.	*Colocasiomyia* spp.	*Cycreon* spp.	Staphylinidae spp.	*Trigona* spp.
H. debilicrista [3/3, i, HC]	*P. gestroi* + *P. nigripennis* 2.0 ± 1.0 1 – 3	*C. schawalleri* 9.0 ± 2.7 7 – 12	Unidentified to species level 34.7 ± 30.8 14 – 70	Unidentified to species level 2.3 ± 2.5 0 – 5	sp. 1 6.0 ± 8.7 0 – 16	Unidentified to species level 1.0 ± 1.7 0 – 3
H. gastrofructa [6/4, ii, HC]	*P. gestroi* + *P. nigripennis* 1.8 ± 0.8 1 – 3	*C. schawalleri* + sp. 1 + sp. 2 5.8 ± 5.5 1 – 13	*C. nigricauda* + *C.* aff. *heterodonta* 15.0 ± 6.0 10 – 25	Unidentified to species level 2.7 ± 2.0 1 – 6	0	0
H. velutipedunculata [6/4, HC]	*P. nigripennis* 1.3 ± 0.5 1 – 2	*C. schawalleri* 7.5 ± 11.4 1 – 30	*C. nigricauda* 13.5 ± 12.8 5 – 36	0	sp. 1 20.2 ± 19.5 3 – 48	Unidentified to species level 1.7 ± 0.8 1 – 3
H. baangongensis [4/2, ii, GC]	*P. gestroi* 2.0 ± 0.8	*C. schawalleri*	*C. nigricauda* + *C.* aff. *heterodonta* 42.5 ± 18.7	Unidentified to species level 30.5 ± 13.2	0	Unidentified to species level 1.8 ± 0.5

	1 – 3	6.3 ± 2.2 4 – 9	15 – 55	22 – 50		1 – 2
H. giamensis [4/3, iii, GC]	*P. gestroi* + *P. nigripennis* 6.3 ± 3.6 1 – 9	*C. schawalleri* 2.8 ± 2.2 0 – 5	*C. nigricauda* + *C.* aff. *heterodonta* 45.3 ± 17.0 29 – 66	Unidentified to species level 11.0 ± 5.5 4 – 17	0	0
H. matangae (5/4) [i, GC]	*P. gestroi* 2.8 ± 1.9 1 – 6	*C. schawalleri* 4.8 ± 5.3 1 – 14	*C. nigricauda* + *C.* aff. *heterodonta* 57.0 ± 20.5 30 – 85	Unidentified to species level 4.4 ± 1.5 2 – 6	sp. 1 + sp. 2 6.6 ± 5.9 0 – 16	Unidentified to species level 1.4 ± 0.6 1 – 2
H. cf. *borneensis* (3/3) [iii, BC]	*P. gestroi* 4.7 ± 4.7 1 – 10	Unidentified to species level 2.3 ± 1.15 1 – 3	*C. nigricauda* + *C.* aff. *heterodonta* 41.0 ± 15.7 30 – 59	Unidentified to species level 2.0 ± 1.0 1 – 3	sp. 1 2.3 ± 4.0 0 – 7	0

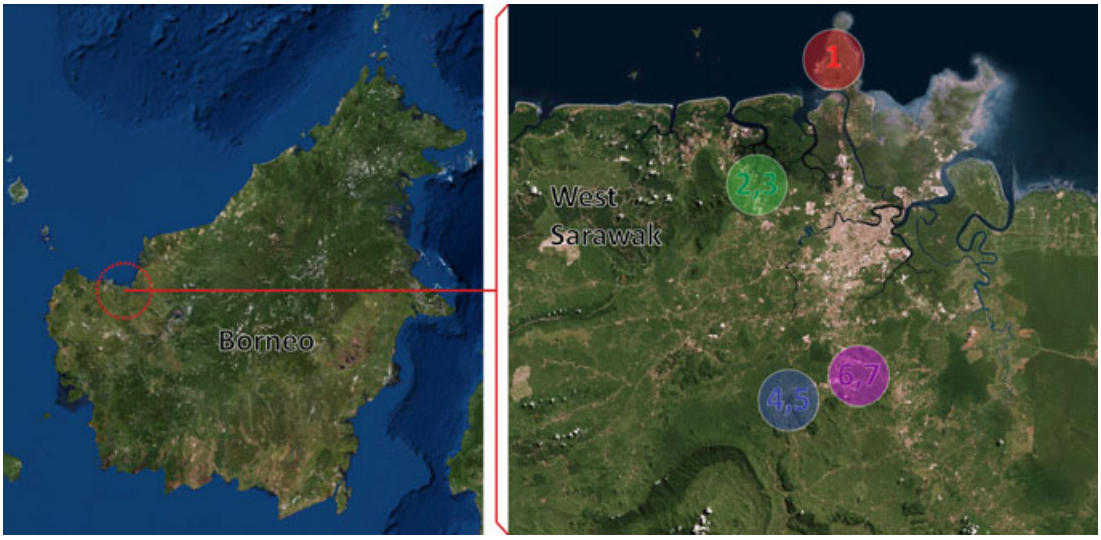
Table 3. Chemical composition (mean and/or range of relative amounts of each VOC) of the floral scents of six species of *Homalomena* (Araceae) belonging to section *Cyrtocladon*. Samples were obtained by dynamic headspace during the interval of highest perceivable scent emission in the course of the pistillate (♀) and staminate (♂) phases of anthesis. *Hdebi* (*Homalomena debilicrista*), *Hgast* (*H. gastrofructa*), *Hvelu* (*Homalomena velutipedunculata*), *Hbaan* (*Homalomena baangongensis*), *Hgiam* (*Homalomena giamensis*), *Hmata* (*Homalomena matangae*). *represents number of replicates/number of individual plants. tr, trace amounts (< 0.01%). The compounds are listed according to compound class and Kovats retention index (RI). Unknowns were included when present with > 0.5% of the total amount in any sample. [a] present in only one of the analysed samples; [b] present in only two of the analysed samples; [c] present in only three of the analysed samples; [d] present in only four of the analysed samples.

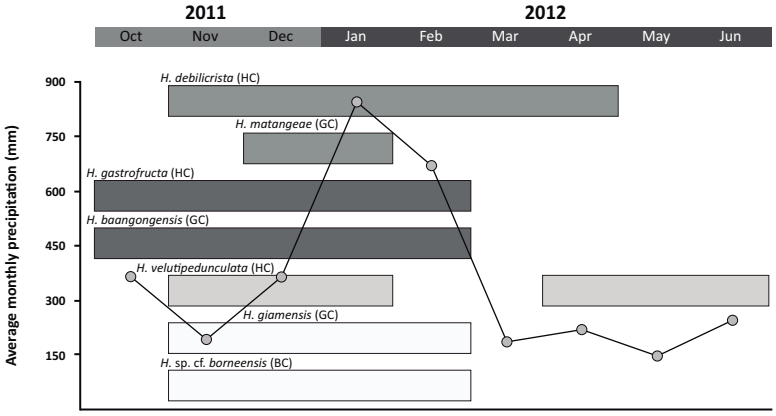
		***Hanneae* complex**						***Giamensis* complex**		
	Retention index (RI)	***Hdebi* ♀ 2/2***	***Hdebi* ♂ 3/2***	***Hgast* ♀ 2/2***	***Hgast* ♂ 2/2***	***Hvelu* ♀ 5/3***	***Hvelu* ♂ 5/3***	***Hbaan* ♀ 4/3***	***Hgiam* ♀ 4/3***	***Hmata* ♀ 3/3***
Total number of compounds		9	11	21	20	18	12	19	20	10
Average scent emission (µg·h^{-1})		116.9	196.4	127.7	497.3	323.7	295.1	963.9	1,058.5	1,649.0
Aliphatics										
Alcohols										
1-hexanol	**871**	---	---	0.37[a]	---	---	---	tr[a]	0.06[a]	---
2-heptanol	**907**	14.06[a]	30.61[b] (0.11 – 61.12)	---	17.43 (1.24 – 33.62)	14.63 (10.69 – 22.15)	7.46 (2.73 – 22.38)	0.03[a]	---	---
2-ethylhexanol	**1031**	---	---	46.84[a]	0.12[a]	---	---	0.47[c] (0.23 – 0.79)	---	---
2-nonanol	**1106**	---	---	---	---	0.60[a]	---	---	---	---
unknown *m/z*: 110,67,41,95,43	**1285**	---	---	2.39[a]	1.98[a]	---	---	0.18[a]	---	---
Esters										
sec-butyl acetate	**< 800**	---	52.45[b] (16.75 –	0.55[a]	0.16[a]	32.74[c] (31.95 –	68.45[d] (1.87 –	60.55 (24.21 –	5.27 (2.89 –	14.31 (8.64 –

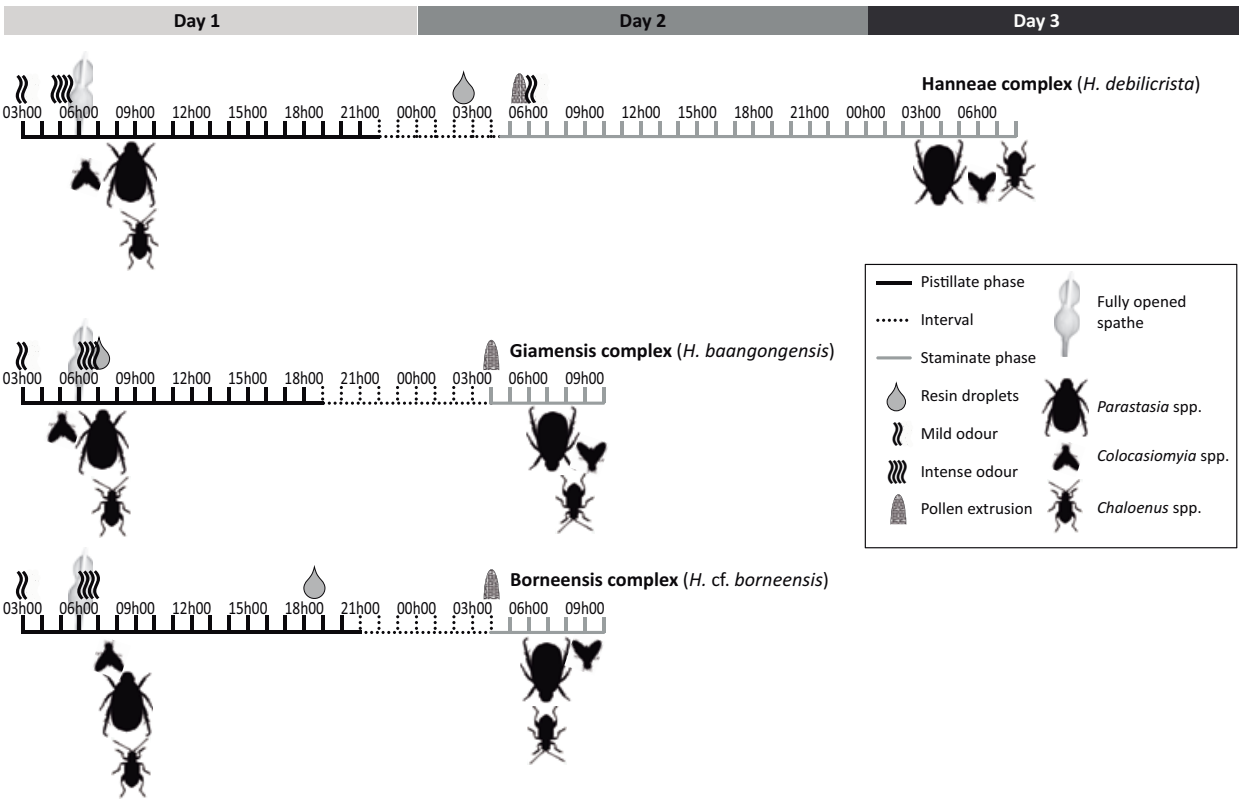
			88.15)			33.65)	91.33)	96.98)	10.10)	18.61)
Ketones										
2-heptanone	**895**	---	15.27[a]	---	2.71 (0.08 – 5.34)	1.65[c] (1.33 – 2.12)	---	---	---	---
6-methyl-5-hepten-2-one	**991**	---	---	18.58 (16.22 – 18.58)	0.80[a]	---	---	0.23[b] (0.22 – 0.24)	0.02[a]	---
Aromatics										
Esters										
methyl benzoate	**1106**	---	---	---	8.34[a]	---	---	---	---	---
methyl salicylate	**1210**	---	---	---	---	---	---	---	0.24[a]	0.055[b] (0.05 – 0.06)
Ethers										
veratrole	**1156**	---	1.97[a]	5.49[a]	9.21[a]	12.33 (2.79 – 26.33)	0.27[c] (0.04 – 0.39)	1.29[c] (0.07 – 2.94)	0.31[a]	---
Ketones										
unknown *m/z*: 57,43,41,71,98	**1112**	2.96[a]	---	---	---	---	---	---	---	---
Terpenes										
Monoterpenes										
α-thujene	**927**	5.65[a]	0.24 (0.01 – 0.62)	3.36[a]	3.45 (1.57 – 5.33)	2.78 (0.25 – 10.55)	1.14[d] (0.34 – 3.3)	0.08[a]	---	---
α-pinene	**934**	48.27 (41.49 – 55.06)	4.44 (1.72 – 7.85)	26.75[a]	32.30 (12.60 – 51.99)	6.07 (0.96 – 13.60)	5.46 (0.53 – 23.22)	---	---	---
β-citronellene	**937**	---	---	3.76[a]	10.69 (3.36 – 18.02)	---	---	---	---	---
camphene	**952**	0.57 (0.40 –	---	---	---	---	---	---	---	---

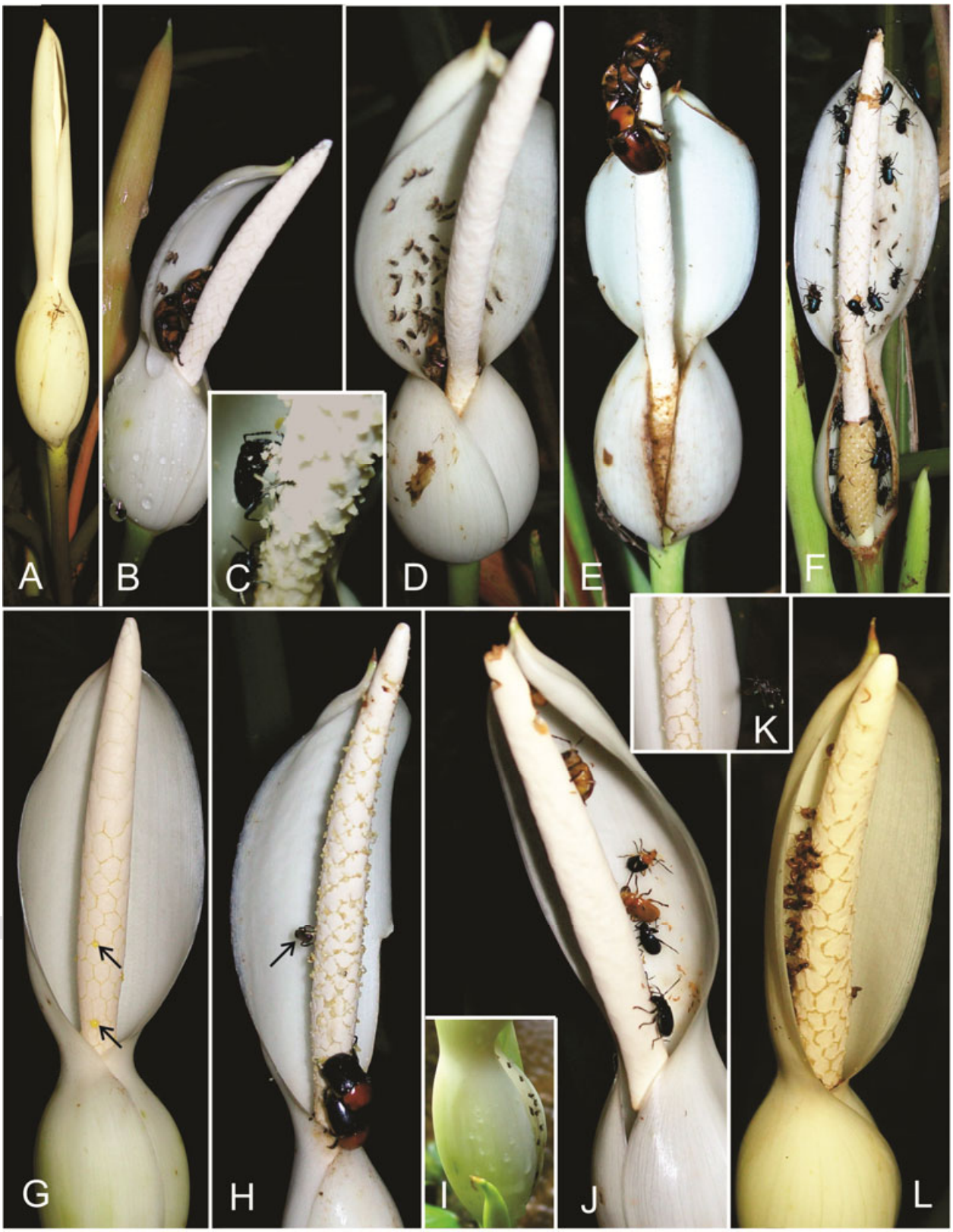
		0.74)								
sabinene	**975**	19.98 (3.67 – 36.30)	0.86[b] (0.82 – 0.91)	---	1.74 (1.05 – 2.44)	0.88[d] (0.16 – 2.18)	1.06[d] (0.28 – 3.21)	---	---	---
β-pinene	**980**	15.48 (2.29 – 28.67)	1.61 (0.20 – 3.58)	44.22[a]	13.25 (9.36 – 17.13)	4.48 (1.04 – 10.08)	4.46 (0.44 – 19.06)	---	---	---
myrcene	**992**	0.56 (0.52 – 0.61)	0.32 (0.02 – 0.84)	5.28[a]	1.01 (0.12 – 1.9)	1.13 (0.76 – 1.42)	0.34 (0.15 – 0.99)	---	---	---
α-phellandrene	**1011**	---	0.31[a]	---	---	---	---	---	0.96[a]	---
unknown *m/z*: 43,67,41,109,105	**1013**	---	---	0.34[a]	---	---	---	0.035[b] (0.02 - 0.05)	---	---
limonene	**1034**	3.80 (2.16 - 5.43)	1.62 (0.26 - 3.22)	---	5.81 (1.75 - 9.87)	28.18 (4.41 - 44.24)	3.23 (0.91 - 11.74)	---	0.1[a]	---
(*Z*)-β-ocimene	**1040**	---	---	---	0.22[a]	0.97[c] (0.03 - 2.84)	---	---	0.58[a]	---
(*E*)-β-ocimene	**1050**	---	---	---	---	0.88[b] (0.83 - 0.92)	---	---	1.1[a]	---
linalool	**1105**	---	---	---	---	0.99[b] (0.93 - 1.05)	---	---	---	---
Irregular terpenes										
unknown *m/z*: 107,69,79,41,91	**1082**	---	---	4.51[a]	0.07[a]	---	---	0.65[c] (0.27 - 1.29)	1.17[d] (0.57 - 2.34)	0.68[c] (0.61 - 0.79)
(*Z*)-4,8-dimethyl-1,3,7-nonatriene	**1099**	---	1.79[b] (0.86 – 2.73)	7.58[a]	0.32[a]	0.26[a]	3.17[d] (0.14 - 9.46)	2.45[b] (1.84 - 3.06)	5.96[d] (1.41 - 14.96)	2.85[c] (2.17 - 4.17)
(*E*)-4,8-dimethyl-1,3,7-nonatriene	**1130**	---	43.14[b] (8.18 –	4.76[a]	0.46[a]	6.25 (3.08 -	19.59 (1.58 -	46.16[c] (1.77 -	86.29[d] (81.58 -	81.32[c] (77.81 -

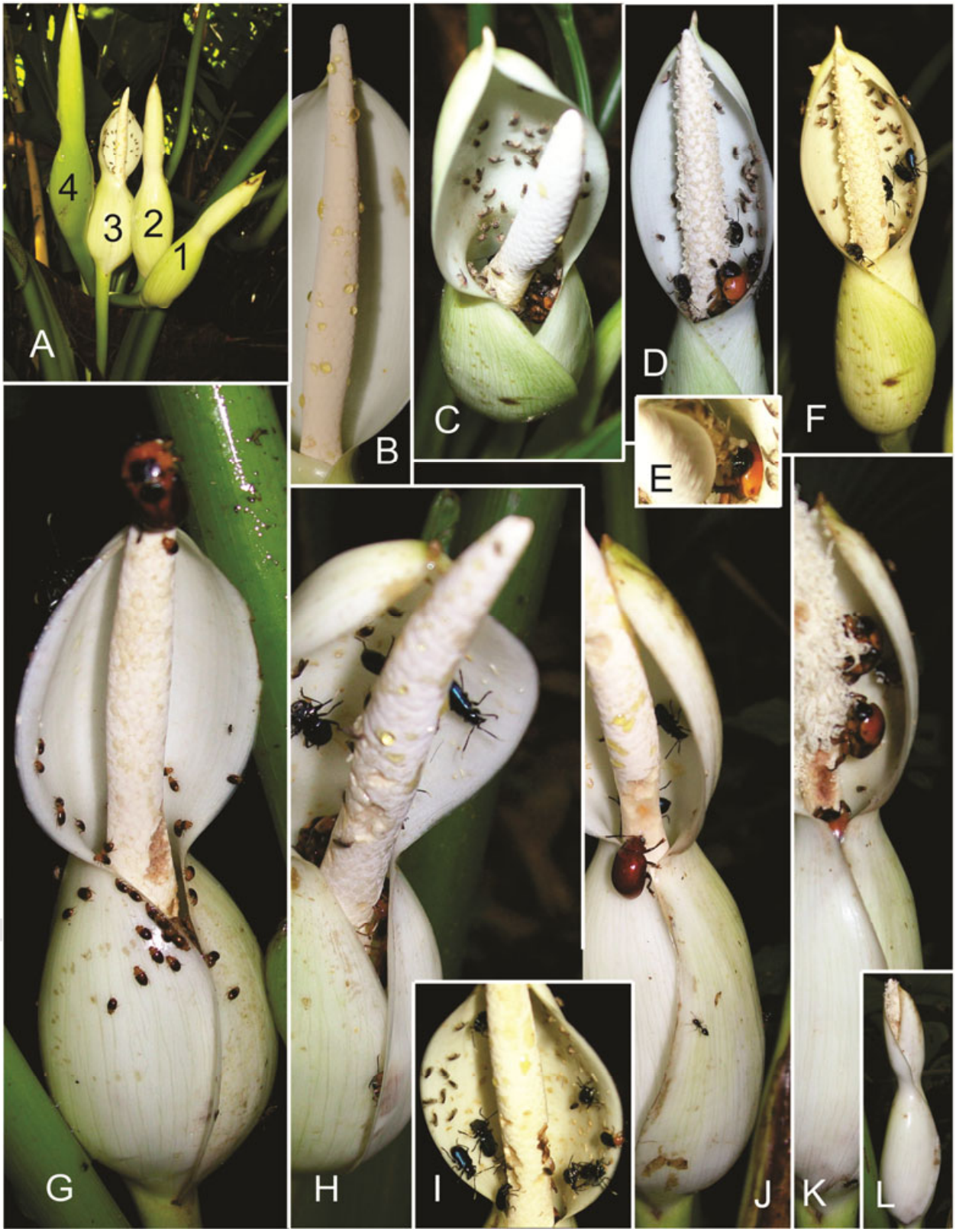
			78.11)			11.87)	85.77)	71.35)	91.83)	85.94)
Unidentified compounds										
unknown *m/z*: 43,45,41,57,58	**961**	---	---	---	---	0.08[a]	0.62[b] (0.05 - 1.20)	---	---	---
unknown *m/z*: 57,43, 41,71,58	**1112**	2.96[a]	---	---	---	---	---	---	---	---
unknown *m/z*: 101,98,55,43,83	**1178**	---	---	0.25[a]	---	---	---	0.15[a]	0.9[a]	0.05[b] (0.04 - 0.06)
unknown *m/z*: 57,43,41,69,67	**1187**	---	---	0.16[a]	---	---	---	0.23[a]	0.16[a]	0.04[b]
unknown *m/z*: 57,85,41,43,55,81	**1214**	---	---	1.13[a]	---	---	---	1.41[b] (0.15 - 2.68)	0.33[a]	---
unknown *m/z*: 79,43,41,71,59	**1225**	---	---	0.68[a]	---	---	---	0.31[a]	0.07[a]	0.15[c] (0.02 - 0.29)
unknown *m/z*: 43,79,41,93,94	**1234**	---	---	---	---	---	---	---	*tr*[a]	0.07[c] (0.02 - 0.12)
unknown *m/z*: 43,79,93,94,71	**1238**	---	---	---	---	---	---	---	0.18[a]	---
unknown *m/z*: 83,55,69,41,53	**1282**	---	---	0.76[a]	1.59[a]	---	---	0.38[b] (0.31 - 0.45)	---	---
unknown *m/z*: 83,55,69,84,41	**1285**	---	---	---	---	---	---	---	0.97[a]	---
unknown *m/z*: 43,79,57,69,93	**1407**	---	---	---	---	3.21[b] (0.57 - 5.86)	---	---	0.04[a]	---

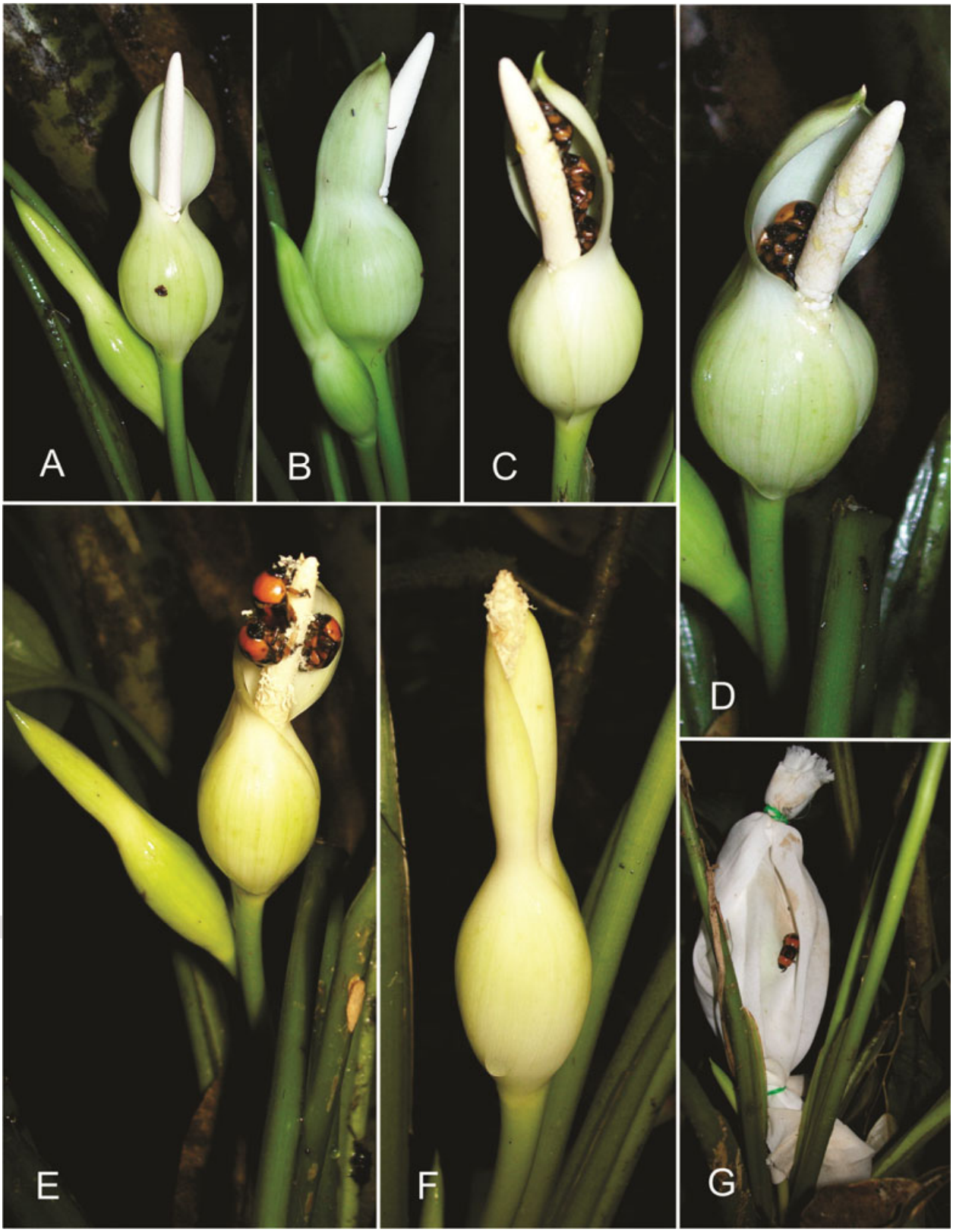


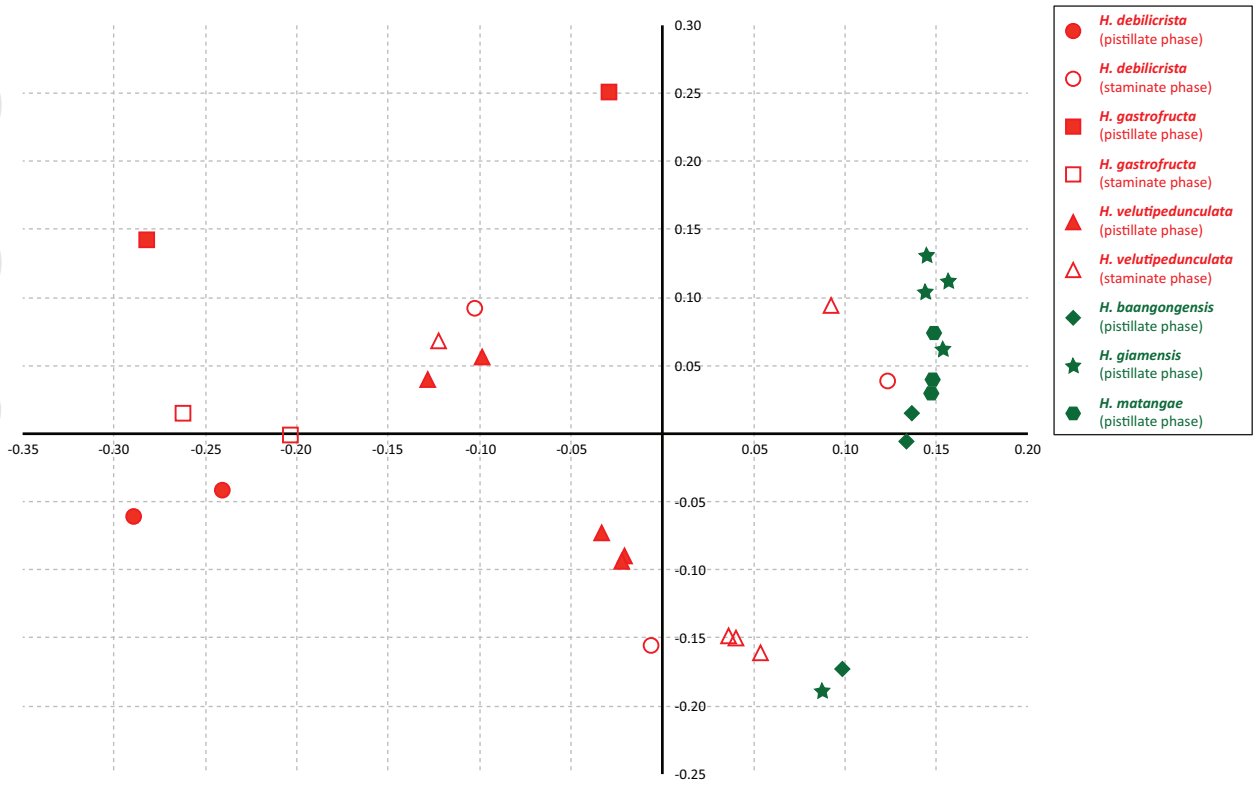












Appendix 1. List of specimens investigated: Taxon, collection locality, GPS, voucher, and GenBank accession number. Taxa are arranged alphabetically.

Homalomena baangongensis L.S.Tung & Y.C.Hoe. MALAYSIA. Sarawak: Kuching, Padawan, Sikog Village, 01.20 N; 110.20 E, P.C. Boyce & S.Y. Wong Ar2574 (SAR), JQ955572.

Homalomena* cf. *borneensis. MALAYSIA. Sarawak: Kuching, Padawan, Giam Village, 01.19 N; 110.16 E, P.C. Boyce & S.Y. Wong Ar2559 (SAR), JQ955573.

Homalomena debilicrista Y.C.Hoe. MALAYSIA. Sarawak: Kuching, Matang, Maha Mariamman Temple, 01.35 N; 110.13 E, Y.C. Hoe Ar3057 (SAR), JQ955574.

Homalomena gastrofructa Y.C.Hoe, S.Y.Wong & P.C.Boyce. MALAYSIA. Sarawak: Kuching, Padawan, Sikog Village, 01.20 N; 110. 20 E, P.C. Boyce *et al.* Ar2575 (SAR), JQ955575.

Homalomena giamensis L.S.Tung, S.Y.Wong & P.C.Boyce. MALAYSIA. Sarawak: Kuching, Padawan, Giam Village, 01.19 N; 110.16 E, P.C. Boyce *et al.* Ar1691 (SAR), JQ929129.

Homalomena matangae Y.C.Hoe, S.Y.Wong & P.C.Boyce. MALAYSIA. Sarawak: Kuching, Matang, Maha Mariamman Temple, 01.35 N; 110.13 E, P.C. Boyce & Jeland Ak Kisai Ar230 (SAR), JQ955577.

Homalomena velutipedunculata S.Y.Wong, Y.C.Hoe & P.C.Boyce. MALAYSIA. Sarawak: Kuching, Santubong, Mouth Santubong, 01.44 N; 110.19 E, P.C. Boyce *et al.* Ar2103. (SAR), JQ955576.