



Institute of Biodiversity and Environmental Conservation

Pollination Guilds of Aroids in Mulu National Park

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Pollination Guilds of Aroids in Mulu National Park

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DECLARATION

I declare that the work in this thesis was carried out in accordance with the regulations of Universiti Malaysia Sarawak. Except where due acknowledgement has been made, the work is that of the author alone. The thesis has not been accepted for any degree and is not concurrently submitted in candidature of any other degree.

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ABSTRACT

The aroid flora of Borneo is one of the richest on the planet, comprising at least 800 species with many highly localized endemics. Not surprisingly, most of our knowledge of these taxa is limited to naming taxonomic novelties but beyond this, our knowledge on the pollination biology of Bornean aroids remains poor. Previous pollination research on aroid taxa on Borneo, revealed two pollination guilds: Diptera (Drosophilidae) and Coleoptera (Chrysomelidae, Hydrophilidae, and Staphylinidae) which are by far the major pollinating groups. This study was conducted at Gunung Mulu National Park, an area which hold one of the richest aroid diversity on Borneo, and aimed to determine pollinators of 21 selected aroids belonging to Tribe Aglaonemateae, Anadendrieae, Colocasieae, Homalomeneae, Monstereae, Potheae, Schismatoglottideae, and Thomsonieae. Extensive field observations on floral biology including stages of floral development, floral traits and rewards, identification of insect pollinators, and their behaviour(s) were carried out. The total anthetic time of most unisexually flowered taxa (*Alocasia*, *Aglaonema*, *Homalomena*, and Schismatoglottideae) lasted for two days, except *Amorphophallus* which ranged two to five days. In bisexually flowered taxa, *Scindapsus* completed anthesis in two days but anthesis lasted four days in *Anadendrum* and longer in *Lasia* and *Pothos*, which ranged 7-18 days. All investigated aroid taxa emitted floral odour during pistillate anthesis with several taxa (*Anadendrum*, *Bucephalandra*, *Homalomena*, *Pothos*, and *Schismatoglottis pellucida*) extended odour production until the end of anthesis. Some taxa (*Amorphophallus* and *Pothos*) do not restrict access to the pistillate flowers during pistillate anthesis. Diptera flies are the most possible pollinators for *Alocasia*, *Aglaonema*, *Homalomena*, *Pothos*, Schismatoglottideae and *Scindapsus*; Coleoptera beetles are the pollinators for *Amorphophallus*, *Anadendrum*, *Homalomena*, *Lasia*, and *Schismatoglottis*; Thysanoptera

(thrips) are the pollinators of *Anadendrum*; Hemiptera are pollinators of *Lasia* and *Pothos*; Hymenoptera are pollinators of *Alocasia sarawakensis* and *Amorphophallus hewittii*. Floral rewards for pollinators included stigmatic secretion, floral tissues, and provision of mating sites.

Keywords: *Amorphophallus*, *Anadendrum*, anthesis, *Lasia*, pollinators

Kumpulan Pendebungaan Keladi Hutan di Taman Negara Mulu

ABSTRAK

Flora keladi hutan Borneo adalah salah satu yang terkaya di planet ini, dengan sekurang-kurangnya 800 spesies yang terdiri daripada banyak endemik tempatan. Tidak menghairankan, kebanyakan pengetahuan tentang keladi hutan tersebut adalah terhad kepada penamaan taksonomi baru tetapi luar daripada ini, pengetahuan tentang biologi pendebungaan keladi hutan dari Borneo masih kurang. Penyelidikan pendebungaan tentang keladi hutan di Borneo sebelum ini, mendedahkan dua kumpulan pendebunga: Diptera (Drosophilidae) dan Coleoptera (Chrysomelidae, Hydrophilidae, dan Staphylinidae) yang merupakan kumpulan pendebunga utama. Kajian ini dijalankan di Taman Negara Gunung Mulu, salah satu kawasan yang mempunyai kepelbagaian keladi hutan terkaya di Borneo, dan bertujuan untuk menentukan pendebunga untuk 21 keladi hutan terpilih daripada Tribe Aglaonemateae, Anadendrieae, Colocasieae, Homalomeneae, Monstereae, Potheae, Schismatoglottideae, dan Thomsonieae. Pemerhatian lapangan secara meluas mengenai biologi bunga termasuk peringkat perkembangan bunga, sifat bunga dan ganjaran, pengenalpastian pendebunga serangga, dan tingkah laku mereka telah dijalankan. Jumlah masa antesis untuk kebanyakan keladi hutan berbunga uniseks (Alocasia, Aglaonema, Homalomena, dan Schismatoglottideae) berlangsung selama dua hari, kecuali Amorphophallus yang berjulat antara dua hingga lima hari. Untuk keladi hutan berbunga biseks, Scindapsus menyempurnakan proses antesis dalam dua hari tetapi antesis bertahan selama empat hari di Anadendrum dan lebih lama di Lasia dan Pothos, yang berjulat antara 7-18 hari. Semua taxa keladi hutan mengeluarkan bau bunga semasa antesis pistillate dengan beberapa keladi hutan (Anadendrum, Bucephalandra, Homalomena, Pothos, dan

Schismatoglottis pellucida) mengeluarkan bau bunga sehingga antesis berakhir. Sesetengah keladi hutan (*Amorphophallus* dan *Pothos*) tidak mengehendkan akses ke bunga jantina semasa antesis pistillate. Lalat *Diptera* berkemungkinan besar adalah pendebunga untuk *Alocasia*, *Aglaonema*, *Homalomena*, *Pothos*, *Schismatoglottideae* dan *Scindapsus*; Kumbang *Coleoptera* adalah pendebunga untuk *Amorphophallus*, *Anadendrum*, *Homalomena*, *Lasia*, dan *Schismatoglottis*; *Thysanoptera* (thrips) adalah pendebunga untuk *Anadendrum*; *Hemiptera* adalah pendebunga untuk *Lasia* dan *Pothos*; *Hymenoptera* adalah pendebunga untuk *Alocasia sarawakensis* dan *Amorphophallus hewittii*. Ganjaran bunga untuk pendebunga termasuk cecair stigma, tisu bunga, dan penyediaan tapak mengawan.

Kata kunci: *Amorphophallus*, *Anadendrum*, antesis, *Lasia*, pendebunga

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LIST OF ABBREVIATIONS

appx.	appendix
ca.	circa/ about
e.g.	exempli gratia/ for example
i.e.	id est/ in other word
N.P.	National Park
SE	Standard error
sp. & spp.	species

CHAPTER 1

INTRODUCTION

1.1 Background

Araceae Juss. is the fourth largest family of monocotyledons after orchids, grasses and sedges (Mansor et al., 2011), comprised of 144 genera and 3645 species (Boyce & Croat, 2011). Species of Araceae are known as aroids. Aroids are most abundant in the tropics, with greatest number of species from Neotropics region (including two largest genera: *Anthurium* Schott and *Philodendron* Schott), and tropical Asia is second richest region after that (Boyce & Croat, 2011). Aroids mostly dependent on abundant water availability and high atmospheric humidity, they are not suitable to grow in extreme dry or cold condition. In the tropics, there are aroids of different life forms such as mesophyte (plant require average water), epiphyte (plant grow on other plant without extracting nutrient), hemiepiphyte (epiphyte connect to ground sometimes), helophyte (plant grow on marsh ground), lithophyte (plant grow on rock), rheophyte (plant grow on running water), aquatic and geophyte (periodic dormancy plant with tuber or rhizome).

Araceae of Borneo currently estimated ca. 800 indigenous species. There are 54 aroid genera on Borneo (of which 25 are endemic) with at least 85% of all species endemic (Boyce & Croat, 2011). Aside from high levels of island endemism, the aroids of Borneo show a remarkable level of highly localized endemism, and species often specific to a particular substrate. Bornean aroids are particularly abundant and diverse below 1,200 m above sea level. Ecologies on Borneo encompasses mesophytes, helophytes (Wong et al., 2011), lithophytes, chasmophytes, rheophytes (a quarter of all species) (Wong, 2013), geophytes,

and nomadic climbers (*sensu* Zotz, 2013). In contrast to the Neotropics, obligate epiphytes are almost wholly absent, represented by fewer than 15 species (Boyce et al., 2010).

Investigation of flowering mechanisms and pollination strategies in Araceae on Borneo is so far limited to a few studies: Tribe Colocasieae Engl. (Takano et al., 2012), Tribe Homalomeneae M. Hotta (Kumano-Nomura & Yamaoka, 2006; Kumano-Nomura & Yamaoka, 2009; Tung et al., 2010; Hoe et al., 2016; Wong & Boyce, 2017), and Tribe Schismatoglottideae Nakai (Hotta et al., 1985; Ulrich et al., 2012; Wong & Boyce, 2013; Hoe & Wong, 2016; Low et al., 2016; Hoe et al., 2018). Diptera (Drosophilidae) and Coleoptera (Chrysomelidae, Hydrophilidae, Scarabaeidae, and Staphylinidae) were reported as pollinators in these studies.

Gunung Mulu National Park (N.P.) is the largest national park in Sarawak, with an area of 544 sq km. It supports 17 vegetation zones, including large tracts of lowland and montane rainforest (Hazebroek & Abang Kashim, 2002). The Gunung Mulu massif occupies the entire south eastern half of the park and is made up of shales (claystone which split into thin layers) and interbedded sandstones. Together these sedimentary rocks comprise the Mulu Formation. Then there are the limestones, the spectacular line of mountains comprising Gunung Buda, Gunung Benarat, Gunung Api, and the southern limestone hills are made up of the Melinau Limestone Formation. Further north, the Setap formation which extends into Brunei's Setap formation, is composed of shales (Hazebroek & Abang Kashim, 2002). These mixed geologies may well explain the extraordinary richness of Mulu's flora.

1.2 Problem statement

Investigation of flowering mechanisms and pollination strategies in Araceae on Borneo is so far limited to a few studies (see above). So far, the only available study to focus on pollination at the family level in an area on Borneo is on Zingiberaceae in Lambir Hill National Park (Sakai et al., 1999). There is no study on floral biology of aroids in Mulu National Park and pollination guilds of the aroid species remain unknown for the park.

1.3 Objectives

This study aimed to explain floral biology of 21 selected aroids species in Mulu National Park which include: (i) timing of anthesis and associated floral changes, floral traits and rewards (ii) pollinators and their behaviours; and (iii) capability to autonomous self-pollinate and efficiency of open pollination. In addition, flowering pattern of the aroids were also included.

CHAPTER 2

LITERATURE REVIEW

2.1 Araceae

The Araceae family consists of the latest 144 accepted genera and 3645 accepted species, plus six more anticipated genera and another 2844 anticipated species, with the inclusion of the former Lemnaceae (the duckweed family) as suggested by recent phylogenetic studies (Boyce & Croat, 2011). Most aroids are tropical and include members from terrestrial, aquatic, and epiphytic habitats although there are some aroids indigenous to temperate climates. Only a few of the genera from the Neotropics also occur in the Asia, Asia has more genera than Neotropics, but Neotropics has more species, with largely over half of all the species in the world (Mayo et al., 1997). Boyce and Croat (2011) reported 2113 accepted species and 4129 anticipated species from 41 accepted genera in the Neotropics, 1212 accepted species and 2042 anticipated species from 69 accepted genera in Asia, 150 species from 16 genera in Africa, 80 species from eight genera in the Mediterranean, and the other species from Australia, Madagascar, Circumtropical, Circumboreal and Mascarene Islands. The family Araceae is most easily diagnosed by the inflorescence which is a spadix - an unbranched spike bearing small bractless flowers subtended by a modified leaf called a spathe (Mayo et al., 1997).

2.1.1 Life forms

The Araceae family are diverse with life forms include hemiepiphytes, true epiphytes, geophytes, lithophytes, helophytes, rheophytes, submersed or periodic submersed aquatics, and free-floating aquatics (Mayo et al., 1997).

Hemiepiphytic aroids are generally found in tropical humid forest. The species vary greatly in size, from shortly climbing plants found on the major branches or trunks of trees to huge plants with attached stems growing high into the forest canopy and producing enormously long, hanging flowering stems. Hemiepiphytes are commonest in the more primitive tribes of subfamilies Pothoideae Engl. and Monsteroideae Engl., and among the more advanced tribe like Culcasieae Engl., or genera such as *Philodendron* and *Syngonium* Schott all belonging to subfamily Aroideae (Mayo et al., 1997).

True epiphytes which never become connected to the ground by feeder roots, are found in several genera: *Anthurium*, *Arophyton* Jum., *Philodendron*, *Remusatia* Schott, *Scindapsus* Schott and *Stenospermation* Schott (Mayo et al., 1997). The plants assume to originate from seeds that germinate directly on the host tree after dispersal by birds or other animals.

Many hemiepiphytes, epiphytes and geophytes are lithophytes under suitable conditions. Wherever shade and humidity are enough, hemiepiphyte can grow on rock surface that provides much the same conditions as tree trunk. For example, many juvenile plants of *Rhaphidophora* Hassk. and *Pothos* L. grow on limestones of forest understory in Borneo before reaching their desired host tree. Geophytes such as *Amorphophallus julaiihii* Ipor, Tawan & P. C. Boyce is characteristically found growing in the eroded, litter- or humus-filled cavities of limestone outcrops. Rheophytes like *Bucephalandra* Schott are typical lithophytes (Mayo et al., 1997).

Geophytic aroids have tuberous, rhizomatous, subterranean or partly subterranean stems. These aroids have periodic dormant periods when no leaves are present and these normally correspond to the weather season (dry or winter) of their habitat. Rainforest

geophytes like *Amorphophallus* Blume ex Decne. exhibit growth periodicity and dormancy even in nonseasonal climates. Geophytes from deciduous forests, savannas or strongly seasonal grasslands flower without the leaves at the end of the dry season, mostly after the first rainfall. Leaf and fruit development take place during the rainy season. Example of such geophytes are from the temperate genera *Arum* L. and *Biarum* Schott (Mayo et al., 1997).

Helophytes are plants which grow in swampy habitats or along river and stream margins. Helophytic aroids are widespread throughout the family, include both temperate and tropical genera. The stem of helophytes can be tuberous (e.g. *Caladium* Vent., *Typhonium* Schott), rhizomatous (*Typhonodorum* Schott), rhizomatous and arborescent (*Montrichardia* Crueg.), semi-prostrate to aerial (*Lasia* Lour.), erect and arborescent (*Philodendron*) or shortly erect and aerial (*Homalomena* Schott) (Mayo et al., 1997).

Rheophytes are flood resistant plants, adapted to streamside habitats where sudden flash flood following tropical rain is regular event (van Steenis, 1987). Rheophytic aroids are especially abundant in Schismatoglottideae (e.g. *Bucephalandra*, *Aridarum* Ridl. and *Piptospatha* N.E. Br.), rheophytes are also found in *Homalomena*, *Anubias* Schott and *Holochlamys* Engl., and rarely in *Anthurium*.

Aquatic aroids are permanently submerged in water, either the entire inflorescence (*Jasarum* G.S. Bunting) or just the upper part of inflorescence (*Cryptocoryne* Fisch. ex Wydler) is held above water while the other parts are submerged in water. *Cryptocoryne* is the largest genus of aquatic aroids, there are some species showing a preference for aquatic condition (*C. affinis* N. E. Br. ex Hook. f., *C. aponogetifolia* Merr.), whereby the submerged leaves of such species are relatively large, whereas the emergent leaves are quite small. *Pistia*

stratiotes L. and the subfamily of Lemnoideae (duckweeds; former Lemnaceae family) are free-floating aquatic aroids.

2.1.2 Vegetative morphology

The vegetative anatomy of the Araceae is among the most diverse of any family of monocotyledons. Stem vasculature is the most diverse of any monocotyledon group and virtually every known type of secretory structure occurs, including resin canals, laticifers, extrafloral nectaries, mucilage cavities and intravaginal squamules (Mayo et al., 1997).

2.1.3 Floral morphology

Araceae is characterized at a macro morphological level by it bearing small bractless flowers on a fleshy unbranched axis (spadix) subtended by a modified leaf (spathe). The flowers are usually numerous, small to tiny and sessile in all genera except *Pedicellarum* M. Hotta. They are generally spirally arranged and usually tightly packed, although in some species of the genera *Pothos* (Goniurus Group), *Pedicellarum*, *Amorphophallus* (staminate and Pistillate flowers), the tribe Dieffenbachieae Engl. (pistillate flowers) and most species of *Arisaema* Mart. and *Arisarum* Mill. (staminate flowers), they may be somewhat distant from one another. The spathe is, strictly speaking, the last leaf of a flowering module. It is usually a specialized attractive organ, although in a few genera (*Gymnostachys* R. Br., *Orontium* L.) is inconspicuous. The internode between spathe and spadix (spadix stipe) is usually very short or absent, while the internode between spathe and last foliage leaf or cataphyll (peduncle) is usually much longer. In some primitive genera, the stipe is longer than the peduncle (*Gymnostachys*, subfamily Orontioideae Mayo, Bogner, & Boyce and some *Pothos* spp.).

The typical aroid inflorescence architecture has given rise to a wide range of variant forms in different genera (Mayo et al., 1997). These can be seen to represent an evolutionary trend of increasing integration towards a synflorescence or pseudanth. The major phyletic modifications are: 1) loss of perigone in the flowers; 2) specialization of flowers on the spadix into a lower pistillate zone, upper staminate zone and, often, one or several zones of sterile flowers, entirely naked axial zones and smooth or staminodial terminal appendices; 3) differentiation of the spathe into a lower, convolute tube and an upper, expanded lamina. Spathe and spadix modifications are closely related so that the spathe may be seen evolutionarily as becoming increasingly integrated into the inflorescence itself, until extreme cases, such as in the tribe Cryptocoryneae Blume, and the genera *Ambrosina* Bassi, *Pistia* L. and *Pinellia* Ten., fusion and still more elaborate modifications have brought about division of the spathe into separate chambers. All flowers are adnate to the spathe in the genera *Spathicarpa* Hook. and *Spathanthemum* Schott. Other notable specializations of the inflorescence include the wide range of odours found in different genera, colour patterns, especially on the spathe, the relative persistence of different regions of the spathe, notably the lower persistent part in many genera that is linked to fruit and seed dispersal mechanics, and a wide range of floral adaptations, many seemingly linked to ‘managing’ pollinators.

Terminal appendices of the spadix are found in the tribes Areae, Arisaemateae Nakai, Colocasieae, Schismatoglottideae, Thomsonieae Blume and Zomicarpeae Schott, and occasionally elsewhere in the family. The function of the appendix, where investigated, is to produce odours to attract pollinators (Vogel, 1990). The appendix is either clearly composed of staminodes (e.g. many *Schismatoglottis* Zoll. & Moritzi) or is partially composed of staminodes, or entirely smooth with no trace of floral organs (e.g., *Arum*, most *Amorphophallus*).

The sex of the individual flowers and their arrangement on the spadix are two of the characters used to define taxonomic groups (Mayo et al., 1997). Depending on the genus the spadix may be either unisexual or bisexual flowers. When the spadix bears bisexual flowers then these are uniformly arranged over the spadix. Bisexual flowers have an envelope of reduced tepals termed a perigone or not (e.g. *Monstereae* Engl.). If unisexual, pistillate zone is always basal and staminate zone is either apical or intermediate in position (except *Spathicarpa*), rarely bisexual flowers occur between staminate and pistillate zones (e.g. *Arophyteae* Bogner). The fertile zones are contiguous or separated by sterile zones, the sterile zones may be basal, intermediate or apical or any combination of these, the apical sterile zone usually known as a terminal appendix. rarely a single plant produces inflorescences bearing staminate flowers only, followed in later years by inflorescences bearing pistillate flowers only, and vice versa (paradioecy, known only in *Arisaema*). Unisexual flowers are usually naked, lacking a perigone, there are only three genera (*Zamioculcas* Schott, *Gonatopus* Hook. f. ex Engl. and *Stylochaeton* Lepr.) have unisexual flowers with a perigone.

Flowers in Araceae may be 2- or 3-merous, sometimes more, very rarely less. In perigoniate flowers, the tepals, when free, are organized in two whorls. The tepals are usually more or less fleshy and fornicate and truncate apically (except subfamily Pothoideae) and in some genera or sections (*Anadendrum* Schott, *Holochlamys*, *Pedicellarum*, *Spathiphyllum* Schott sect. *Massowia*, *Stylochaeton*) they are fused into a cup-like structure. Stamens in perigoniate flowers and in the naked bisexual flowers of most Monsteroideae have the orthodox structure of distinct (usually flattened) filament, slender and inconspicuous connective, and basifixed anther. In the unisexual flowers of many tribes of subfamily Aroideae, however, filaments are typically very short or lacking, and there is a thick, fleshy

connective which perhaps acts as an osmophore (Aglaonemateae Engl., Culcasieae, Homalomeneae, Montrichardieae Engl., Nephthytideae Engl., Philodendreae Schott, Zantedeschieae Engl.). Large connectives also occur in tribe Spathicarpeae Schott but their different morphology suggests that they are not homologous with those of the other tribes of subfamily Aroideae mentioned (Mayo et al., 1997). Stamens of tribes Anubiadeae Engl., Caladieae Schott, Colocasieae, Spathicarpeae, and Peltandreae Engl. are essentially similar but are always fused into synandria. In tribe Arophyteae, the stamens may be fused or not and exhibit a diversity of structure.

Anthers are almost always extrorse (introrse in *Zamioculcas*, latrorse in *Pedicellarum*). Theca dehiscence may be by a longitudinal or rarely transverse slit (most genera with bisexual flowers and some unisexual-flowered genera: *Anubias*, some *Areae*, *Arisaema*, *Arisarum*, *Stylochaeton*) or by apical or subapical pores either directly on the thecae, or via an elongated needle-like structure (e.g., *Cryptocoryneae*, *Aridarum*, *Bucephalandra* and *Phymatarum* M. Hotta) or short slits (Mayo et al., 1997). In many genera of subfamily Aroideae dehiscence of each thecae is by a subapical stomial pore and this morphology is frequently correlated with the extrusion of pollen in strands, these same structures occur in *Amorphophallus* and *Dracunculus* Mill.

The gynoecium usually varies between 1- and 3- locular, and when unilocular it often shows traces of 2- or 3-merous origin through the presence of a several lobed stigmas (e.g. *Typhonodorum*) or more than one placenta (e.g. *Schismatoglottis*). Gynoecia with more than 3 locules are less common but are found in tribe Spathicarpeae (1–8 locular) and in *Philodendron* (2–47 locular). Placentation varies from axile to parietal, basal, apical or basal and apical (the latter in *Dracunculus*, *Helicodiceros* Schott, *Heteroaridarum* M. Hotta and

Theriophonum Blume), with many intermediates. Ovules may be anatropous, campylotropous, orthotropous or intermediate between these types. Funicle trichomes are usually present (French, 1987) and secrete a clear, mucilaginous substance which in many genera (e.g. *Caladium*, *Xanthosoma* Schott., tribe Monstereae, *Philodendron*) entirely fills the ovary locules. This secretion appears to play a role in pollen tube growth (Buzgó, 1994). The style may be narrowed and elongated (e.g. *Dracontium* L.) but in most genera is relatively inconspicuous externally. However, there is very often a thick styler region between the ovary locules and stigma (e.g. *Philodendron*) (Mayo, 1989). In tribe Monstereae, this styler region is especially well developed and densely filled with trichosclereids, this seems to substitute function of a perigone in protecting the sexual organs of the flower and certainly plays a role in protecting the developing fruits after. Stigmas are always wet in Araceae and in some genera (*Anthurium*, *Arum*, several Lasioideae Engl.) produce conspicuous nectar droplets at anthesis. In *Amorphophallus*, *Dieffenbachia* Schott and some Spathicarpeae, the lobing of the stigma can be very pronounced, or the stigma relatively massive. In subfamily Monsteroideae, stigmas vary from subcapitate to conspicuously elongated, either transversely (e.g. *Anadendrum*) or longitudinally.

2.1.4 Fruits and seeds

The fruits of Araceae are typically juicy berries, rarely dry and leathery. The infructescence is usually variously cylindric or sometimes globose. Berries are most commonly red or orange but also dirty white, green or yellow and even blue are also common. Berries are almost always free with notable exceptions in *Syngonium*, in which the berries form an indehiscent syncarp, and *Cryptocoryne* which has an apically dehiscent

syncarp. In *Lagenandra* Dalzell, the free berry actively opens at the base to release the seeds, but aroid berries are otherwise indehiscent.

The various mechanisms observed for protection of the developing fruits and seeds have been discussed by Madison (1979). In the Monstereae, which have bisexual but non-perigoniate flowers, the thick styler region is filled with trichosclereids which protect the developing seeds. At maturity the styler region is shed to reveal the seeds. In perigoniate genera such as *Anthurium*, the perigone clearly plays a protective role and keeps pace during growth of the developing berry. The berry only becomes fully exposed at maturity by extrusion from the flower. In *Lysichiton* Schott, also perigoniate, the styler region and tepal apices protect the young berry, eventually breaking off to reveal the ripe seeds (Hultén et al., 1931).

In many unisexual-flowered genera the protective function is assumed by the persistent spathe or lower spathe. Spathe growth continues around the developing fruits until maturity when the spathe may split open either basiscopically (*Alocasia* (Schott) G. Don, *Dieffenbachia*, *Schismatoglottis*) or acroscopically (*Homalomena*) or abscise at the base (*Philodendron*), exposing the infructescence of white or coloured berries. In other monoecious genera, however, the spathe is marcescent and plays no role in fruit protection. In such cases (e.g. *Arum*) protection may possibly be through the presence of toxic chemical compounds in the berries.

The seeds are often embedded in mucilaginous pulp (secreted by the ovular and placental trichomes). In *Anthurium*, the inner layer of the pericarp may also be mucilaginous and in other genera the outer integument becomes mucilaginous. This makes the seeds sticky and aids the dispersal of epiphytic and hemiepiphytic species to new sites (e.g. neighbouring

trees) by birds or mammals. The amount of endosperm in the seed varies considerably within the family and has long been regarded as a useful taxonomic character at tribal level. However, a thorough comparative anatomical study has been lacking (Seubert, 1993). Seubert's study shows that endosperm may be present in mature seeds of some groups e.g. subfamily Lasioideae, as only a very thin layer. Many intermediate conditions exist between the presence of plentiful endosperm and absence of endosperm. Absence of endosperm is often correlated with the presence of a well-developed plumule and the largest seeds of Araceae are of this type, e.g. *Orontium*, *Typhonodorum*. The seeds are usually straight, but in Lasioideae and Monstereae they are often curved. In a few genera (*Cryptocoryne*, *Gonatopus*, *Nephtytis* Schott, *Orontium*, *Typhonodorum*), the plumule is also highly developed. Seeds with a well-developed plumule usually lack endosperm and have only a very thin, papery testa or none at all (*Nephtytis*). Such large embryos generally contain chlorophyll at maturity and are only viable for a short time. The testa may be smooth, rough, verrucose or costate, thin or thick and in subfamily Lasioideae is often very hard and thick with prominent sculpturing. In tribes Ambrosineae Schott, Areae, Arisaemateae and Arisareae Dumort., most genera have a prominent fleshy strophiole (aril), and smaller but distinct strophioles (Colocasieae) also occur. Arillate seeds have been observed in the genus *Thaumatophyllum* Schott former *Philodendron* subgenera *Meconostigma* (Mayo, 1991).

2.1.5 Seed dispersal

The seeds of most Araceae do not remain viable for long. Those lacking endosperms and with large embryos cannot withstand desiccation and the genera with fleshy testas are similarly vulnerable. In certain species, however, the seeds can withstand desiccation for longer periods, e.g. *Thaumatophyllum bipinnatifidum* (Schott) Sakur., Calazans & Mayo.,

which can remain viable for over 12 months (Mayo, pers. obs.). Seeds with a leathery testa, such as in *Arum* and *Arisaema*, also have longer viability. One outcome of short viability is that Araceae seeds are unlikely to survive long distance dispersal by natural vectors. This makes it unlikely that generic disjunctions over major ocean basins have resulted from long distance dispersal. Another important generalization that can be made is that animal dispersal, and more specifically, ornithochory (bird dispersal), must be the dominant mode due to the universality of berried fruits in Araceae (Mayo et al., 1997). The indigenous Batak peoples have observed hornbills (Bucerotidae) eating berries of *Amorphophallus titanum* (Becc.) Becc. ex Arcang, and the bulbul bird (*Pycnonotus zeylanicus*) feeding on the berries of *A. brooksii* Alderw. in Sumatra (Hetterscheid, pers. comm.). T. Lamb (pers. obs.) has added support to this evidence by his own observations of bulbul birds eating berries of *A. lambii* Mayo & Widjaja in Sabah. Circumstantial evidence for other genera points to birds (*Anthurium*) and mammals, including primates (*Anchomanes* Schott, *Philodendron*) and bats (*Philodendron*), as the commonest vectors. The common palm civet (*Paradoxurus hermaphroditus*) is reported to disperse the seeds of *Colocasia esculenta* (L.) Schott in Indonesia (Hambali, 1979). Marks were left on the peduncle by the claws and teeth of this mammal and germinating seeds of two cultivars of *C. esculenta* were seen in its faeces. Besides, Hambali (1979) also confirmed that seeds of *Colocasia gigantea* (Blume) Hook. f. and *Homalomena pendula* (Blume) Bakh. f. was dispersed by the same animal. The fruits of all the three aroid species are odoriferous, which attracted the civet (Hambali, 1979). Presentation of the fruits for dispersal is normally a rather sudden event. In *Philodendron* and *Dieffenbachia*, the spathe falls off or splits at maturity to reveal the infructescence, whereas in genera with non-persistent spathes the berries remain inconspicuous during maturation and take on their bright colour in a final rapid flush. In *Anthurium*, the berries are

extruded from the perigone at maturity and in most species hang by tiny threads of tepal epidermis. Genera of subfamily Monsteroideae display the seeds by simultaneous abscission of the stylar region of each flower. The resulting compound mature fruit has the seeds embedded in sticky, often sweet and mucilaginous material. T. Croat (pers. comm.) has suggested that these fruits may be dispersed by monkeys.

Mature berries in *Arum* and *Nephtytis* have been observed to remain for a relatively long-time awaiting dispersal. In contrast the dense infructescences of *Caladium*, *Colocasia* Schott, *Philodendron* and *Syngonium*, may disappear very soon after exposure. Dispersal by ants (myrmecochory) has been observed in *Biarum*, in which the strophiole of the seed is probably involved. T. Croat (pers. comm.) has observed ants dispersing seeds of *Philodendron megalophyllum* Schott. Dispersal by water (hydrochory) is very probable in the helophytic genera *Montrichardia* and *Typhonodorum*, which have very large berries and floating seeds. *Lagenandra*, *Cryptocoryne* and *Pistia* are certainly water-dispersed and have much smaller fruits and floating seeds.

2.2 Araceae on Borneo

The aroid flora of Borneo is one of the richest on the planet, comprising at least 670 species, of which approximately 40% remain to be described (Boyce et al., 2010). Remarkably, these data are mostly account for aroids of Sarawak, Sabah and Brunei (i.e. less than one third of the total landmass). Kalimantan, comprising more than 70% of the land area of Borneo, remains very poorly known, and undoubtedly harbours a great number of new species. The estimation total aroid flora for Borneo is likely to exceeds 1,000 species. In short, Borneo is an aroid habitat of global significance. Bornean aroids belong to 5 subfamilies and 56 genera, of which 55 genera are indigenous, and one (*Typhonium*)

genuinely naturalized. Of the 55 indigenous genera, 26 genera are Bornean endemics (25 genera belong to subfamily Schismatoglottideae, one genus belongs to subfamily Pothoideae). Four additional genera (*Caladium*, *Dieffenbachia* (*D. seguine* (Jacq.) Schott), *Syngonium* (*S. podophyllum* Schott), and *Xanthosoma*) are listed as adventives. The following sections will only include subfamilies which are included in this study.

2.2.1 Subfamily Pothoideae

Subfamily Pothoideae consist of the tribe Potheae Engl. in Borneo and the tribe Anthurieae Engl. in the Neotropics. Tribe Potheae comprises forest dwelling primary hemiepiphytes from genera *Pothos*, *Pedicellarum* and *Pothoidium* Schott, with the last absent in Borneo (Boyce et al., 2010). Species of tribe Potheae are readily distinguished by their bisexual flowers with a prominent leathery perigone, and infructescences of discrete ellipsoid berries ripening red or orange, very rarely white or purple. The differences between *Pothos* and *Pedicellarum* are the flowers of *Pothos* are sessile, without a receptacle, and perigone are free and very rarely united whereas flowers of *Pedicellarum* are pedicellate, with a distinct receptacle, and perigone connate and forming a conspicuous ‘cup’. *Pothos* is divided into two subgenera: *Pothos* and *Allopothos*, with *Allopothos* further divided into two informal supergroups: *Allopothos* and *Goniurus* (Boyce & Hay, 2001). Subgenus *Pothos* (e.g. *P. scandens* L.) is distinguishable by the lamina-like petiole, lacking an obvious sheath with the whole leaf resembling that of many Citrus. Subgenus *Allopothos* (e.g. *P. insignis* Engl.) has a distinct petiole, sheathing for much of its length. The *Allopothos* supergroup has a spadix with congested flowers while the flowers of the *Goniurus* supergroup (e.g. *P. curtisii* Hook. f.) are scattered, with portions of the spadix axis clearly visible between individual flowers. Borneo have 16 species (world 70 species) of *Pothos* of which 10 species

are endemic, and the only species of *Pedicellarum* in the world (Boyce et al., 2010). The ecology of *Pothos* and *Pedicellarum* is primary to disturbed secondary lowland to hill perhumid evergreen broadleaf tropical forest, with *Pothos* ranging to subtropical forest of India and is usually on ridges. Some species of *Pothos* (e.g. *P. insignis*, *P. ovatifolius* Merr., and *P. leptostachyus* Schott) are limestone obligates.

2.2.2 Subfamily Monsteroideae

Subfamily Monsteroideae consists of four tribes, which are Spathiphyllae Engl., Anadendreae Bogner & French, Heteropsidae Engl. and Monstereae. There are five genera of Monsteroideae in Borneo which belong to the tribes Anadendreae (*Anadendrum*) and Monstereae (*Amydrium* Schott, *Epipremnum* Schott, *Rhaphidophora*, and *Scindapsus*) (Boyce et al., 2010). Bornean Monsteroideae except *Anadendrum* and *Amydrium* are distinguished by tough thickened styler tissue of mature infructescence that, when the fruits are ripe, fall as irregular plates to expose the ovary cavity with the seed embedded in abundant, variously coloured pulp. *Anadendrum* produces infructescences of discrete truncate topped berries that ripen red or orange, while *Amydrium* in Borneo has rounded berries ripening white. All genera except *Anadendrum* and *Amydrium* have abundant trichosclereids in all tissues (sparse in *Amydrium*) which are observable by tearing a mature leaf lamina and looking for ‘hairs’ protruding from the damaged edges. In Borneo, there is one species of *Amydrium* (world five species) which is not endemic, about 20 species of undescribed *Anadendrum* (world at least 30 species), two species with one endemic (*E. falcifolium* Engl) of *Epipremnum* (world 15 species), 16 species with six endemics of *Rhaphidophora* (world about 100 species) and about 30 species of *Scindapsus* (world perhaps 60 species) (Boyce et al., 2010). The ecology of Monsteroids in Borneo is primary

and secondary perhumid broadleaf tropical forests, at low to moderate altitudes, less often in tropical kerangas (*Amydrium*), on a variety of geologies including limestone (some limestone obligates in *Anadendrum*), and less often in peat swamp or freshwater swamp tropical forest (*Rhaphidophora* and *Scindapsus*).

2.2.3 Subfamily Lasioideae

Subfamily Lasioideae have 10 genera but only 3 genera occur in Borneo, which are *Cyrtosperma* Griff., *Lasia* and *Podolasia* N.E. Br. (Boyce et al., 2010). The lasioids are slender to massive, usually solitary or a small group of stoutly rhizomatous and sometimes stoloniferous herbs with large hastate to sagittate and rarely pinnately divided leaves on prickly, often mottled petioles to 3 m long. *Cyrtosperma* and *Lasia* are commonly found in marshy open grassland close to habitation, while the third, *Podolasia*, is restricted to seasonally flooded broadleaf forest on deep peat deposits. *Lasia* can be differentiated from *Cyrtosperma* and *Podolasia* by its suffruticosa stem with prickly conspicuous internodes, hastate to pinnatifid leaves, apical placentation and spinulous fruits. *Cyrtosperma* and *Podolasia* are similar in their condensed rhizome, rarely distinct internodes which is unarmed, sagittate to hastate leaves, not apical placentation and smooth fruits. *Cyrtosperma* and *Podolasia* can be differentiated by the colour of spathe base (white for *Cyrtosperma* and red-purple for *Podolasia*), ripened fruits colour (dull purple for *Cyrtosperma* and bright red for *Podolasia*), seed surface (warty for *Cyrtosperma* and smooth for *Podolasia*) and spine direction (straight-upward for *Cyrtosperma* and straight-downward for *Podolasia*). In Borneo, there are two species of *Cyrtosperma* (world 13 species), two species with one endemic (*L. concinna* Alderw.) of *Lasia* (world two species), and the only species of *Podolasia* (*P. stipitata* N. E. Br.) in the world (Boyce et al., 2010). The ecology of

Cyrtosperma and *Lasia* is similar, they prefer lowland freshwater swamp forest margins, sometimes persisting in flooded pasture, or in swampy areas of lowland perhumid broadleaf evergreen tropical forest. *Podolasia* prefers lowland peat swamp forest, usually on podzols but still subject to seasonal flood.

2.2.4 Subfamily Aroideae

Subfamily Aroideae comprises all genera with naked unisexual flowers, and thus all taxa are monoecious (very rarely paradioecious in *Arisaema*). The Aroideae in Borneo comprises 11 tribes, which are Homalomeneae, Schismatoglottideae, Cryptocoryneae, Caladieae, Nephthytideae, Aglaonemateae, Thomsonieae, Areae, Arisaemateae, Colocasieae and Pistieae Blume (Boyce et al., 2010).

Tribe Homalomeneae comprises two very closely allied genera in Asia, *Homalomena* and *Furtadoa* M. Hotta, mostly with strongly aromatic (terpenoids) tissues and spathes fully persistent until fruit maturity. *Homalomena* is widespread throughout Neotropics and Asia tropics, with significant centre of diversity on Sumatera, Borneo, and New Guinea (Boyce & Wong, 2008). Neotropical *Homalomena* is transferred into a new genus, *Adelonema* Schott, the new genus is distinct from *Philodendron*, though most closely related to *Philodendron* subgenus *Pteromischum* and completely distinct from the Asian *Homalomena*, a well support as monophyletic (Wong et al., 2013, 2016). *Adelonema* is defined by a hypogeal rhizome, crushed vegetative tissue smelling of anise, an extensively sheathing and sometimes prickly petiole, papery and often variegated leaf blades, a spadix either obliquely inserted on the spathe/peduncle (sect. *Adelonema*) or stipitate (sect. *Curmeria*), ovaries with 2–4-pluriovulate locules, and anatropous ovules on an axial placenta. *Furtadoa* is restricted to Sumatera and Peninsular Malaysia and differs from *Homalomena* primarily by each

staminate flower with an associated pistillode. Species of *Homalomena* are frequently confused with *Schismatoglottis*, although the infructescences of *Homalomena*, in which the spathes wholly persistent until fruit maturity, and then split basally and upwards to reveal the fruits, are very different from those of *Schismatoglottis* in which the spathe limb is shed, often while still fresh, during anthesis, while the lower spathe persists until fruiting, splitting from the top downwards to release the ripe fruits. *Homalomena* is the richest aroid genus in Asia, with 500 anticipated species of which 98 have been described, it is the third-largest genus after *Anthurium* and *Philodendron* (Boyce & Croat, 2011). The genus comprises mostly strongly aromatic, minute to very large clumping, tufted, rarely creeping or climbing herbs with cordate to lanceolate leaves. Inflorescences generally becoming pendulous with the spathe persisting after anthesis, and occasionally becoming brightly coloured, around the developing infructescence. Bornean *Homalomena* divide into four morphotaxa (morphologically cohesive but phylogenetically untested higher taxa) termed ‘supergroups’ (Boyce & Wong, 2008; Ng. et al., 2011): *Homalomena*, *Chamaecladon*, *Cyrtocladon* & *Punctulata*. The ecology of *Homalomena* is lowland evermoist to everwet, or less often perhumid, tropical or subtropical broadleaf forest, but also reaching mid-montane zone, sometimes rheophytic, very rarely helophytic, and occasionally relictual in regrowth.

Tribe Schismatoglottideae (sensu Wong et al., 2010; Cusimano et al., 2011; Nauheimer et al., 2012) comprises an estimated 450 species, of which a little more than half have been formally described (Boyce & Croat, 2011), occurring from subtropical China to Java and from Myanmar to Vanuatu with the most taxa and greatest diversity occurring on Borneo (Boyce & Wong, 2015). Schismatoglottideae is characterised by convolute ptyxis, a spathe differentiated into a lower persistent portion enclosing the pistillate flower zone and a usually temporary spathe limb subtending the staminate flower zone and appendix (if

present), with the lower and upper parts of the spathe marked either by a constriction or the widest part of the spathe (Wong, 2013). The spadix is often complexly zoned with the fertile zones interspersed by or intermixed with various types of sterile flowers. All known species have free staminate flowers, but individual flowers are difficult to limit. Pistillate flowers are mostly free, the exception being *Gamogyne* N.E. Br. in which all pistils are conjoined. All genera have persistent portion of spathe which often forming a splash-cup, or actively opening at fruit maturity. Fruits are berries and either indehiscent (most genera), or dehiscent in *Bakoaella* S.Y. Wong & P.C. Boyce (Boyce & Wong, 2012) and *Schottariella* P.C. Boyce & S.Y. Wong (Boyce & Wong, 2014), or drying to become a caryopsis in *Bakoa* P.C. Boyce & S.Y. Wong.

The phylogenetic study by Low et al. (2018) based on nuclear ITS and plastid matK recognised 30 genera which composed of 13 pre-existing genera (*Apoballis* Schott, *Aridarum*, *Bakoa*, *Bucephalandra*, *Fenestratarum* P.C. Boyce & S.Y. Wong, *Galantharum* P.C. Boyce & S.Y. Wong, *Ooia* S.Y. Wong & P.C. Boyce, *Phymatarum*, *Pichinia* S.Y. Wong & P.C. Boyce, *Piptospatha*, *Schismatoglottis*, *Schottariella* and *Schottarum* P.C. Boyce & S.Y. Wong), five resurrected genera (*Colobogynium* Schott, *Gamogyne*, *Heteroaridarum*, *Hottarum* Bogner & Nicolson and *Rhynchopyle* Engl.), 11 new genera (*Bakoaella*, *Bidayuha* S.Y. Wong & P.C. Boyce, *Burttianthus* S.Y. Wong, S.L. Low & P.C. Boyce, *Gosong* S.Y. Wong & P.C. Boyce, *Hera* S.Y. Wong, S.L. Low & P.C. Boyce, *Kiewia* S.Y. Wong & P.C. Boyce, *Nabalu* S.Y. Wong & P.C. Boyce, *Pursegloveia* S.Y. Wong, S.L. Low & P.C. Boyce, *Naiadia* S.Y. Wong, S.L. Low & P.C. Boyce, *Tawaia* S.Y. Wong, S.L. Low & P.C. Boyce and *Toga* S.Y. Wong, S.L. Low & P.C. Boyce) and a replaced genera (*Vesta* S.Y. Wong, formerly *Hestia* S.Y. Wong & P.C. Boyce).

Among the 30 genera of Schismatoglottideae, all of them exist in Borneo except *Apoballis* and *Kiewia*. *Colobogynium*, *Schismatoglottis* and *Vesta* occur in Borneo but also elsewhere. The 25 Bornean endemic genera include *Aridarum*, *Bakoa*, *Bakoaella*, *Bidayuha*, *Bucephalandra*, *Burttianthus*, *Fenestratarum*, *Galantharum*, *Gamogyne*, *Gosong*, *Hera*, *Heteroaridarum*, *Hottarum*, *Nabalu*, *Naiadia*, *Ooia*, *Phymatarum*, *Pichinia*, *Piptospatha*, *Pursegloveia*, *Rhynchopyle*, *Schottariella*, *Schottarum*, *Tawaia*, and *Toga* (Low et al., 2018).

Tribe Aglaonemateae comprises two genera: *Aglaonema* Schott and *Aglaodorum* Schott. The genus *Aglaodorum* is composed by colonial helophytes with creeping spongy rhizomes, erect and spongy petioles, large fruit ripening green and functioning as floating dispersal units. *Aglaonema* is represented by terrestrial forest herbs with erect firm stems, erect solid petioles, and medium-sized fruit ripening red or rarely pink and not water dispersed. There is only one species of *Aglaodorum* (*A. griffithii* (Schott) Schott) in the world which distributed from southern Cambodia to Peninsular Malaysia, Sumatra and Northern Borneo. *Aglaodorum* differs from *Aglaonema* as it occurs as a colonial helophyte in open swamps, especially on mud in freshwater and brackish tidal zones which exposed to full sun, the stems and petioles are filled with air-spaces, the petioles and peduncles are relatively long to elevate the leaf laminae and inflorescences above water, and the fruits with very thick flesh are green and evidently dispersed by floating. Borneo has 3 species out of 22 species of *Aglaonema* in the world (Boyce et al., 2010). *Aglaonema* occurs in primary and secondary perhumid to everwet broadleaf evergreen forests, with a few species restricted to kerangas or monsoonal perhumid semi-deciduous forests (the later not in Borneo).

Tribe Thomsonieae comprises the genus *Amorphophallus*, with 197 accepted species and 219 anticipated species (Boyce & Croat, 2011) which is distributed from tropical Africa

to Madagascar, subtropical and tropical Asia, and Australia. Six species of the former genus *Pseudodracontium* N.E. Br. were transferred into *Amorphophallus* after taxonomic revision by Hetterscheid and Claudel (2012). *Amorphophallus* are seasonally dormant herbs often large and sometime gigantic, with tuber usually depressed-globose, elongated or rarely clustered, leaf usually solitary, petiole long and thick with various marking, sheath short, leaf blade dracontioide, inflorescence solitary, usually flowering without leaf, leaf and inflorescence preceded by cataphylls, peduncle similar to petiole, spathe variously coloured, marcescent, boat-shaped, convolute or differentiated into tube and blade, spadix longer or shorter than spathe, pistillate zone and staminate zone contiguous, and fruits one- to few-seeded, orange to red, rarely blue or white. Borneo has at least 18 indigenous species which are endemic, and *A. paeoniifolius* (Dennst.) Nicolson is almost certainly non-indigenous as it is found only in association with human disturbance (Boyce et al., 2010). The ecology of *Amorphophallus* is lowland to upper hill forest perhumid to everwet broadleaf subtropical to tropical forest. Many of the Bornean species are locally endemic limestone obligates.

Tribe Colocasieae consists of seven genera: *Ariopsis* Nimmo, *Leucocasia* Schott, *Protarum* Engl., *Steudnera* K. Koch, *Remusatia*, *Colocasia* and *Alocasia*, only the last two genera occur in Borneo. The tribe features are mostly large, sometimes gigantic erect to creeping herbs with milky to almost clear latex and often distinctly undulating interprimary collecting veins. *Alocasia* has erect infructescences with medium-sized, ripening orange-red and odourless fruits. *Colocasia* has pendent infructescences with small, ripening yellowish brown fruits, smelling variously of overripe fruit or vomit. In respect of synflorescence architecture, *Alocasia* can be distinguished from *Colocasia* by its bimodular synflorescence subunits, the whole synflorescence in *Colocasia* is equivalent to one bimodular unit in *Alocasia*. In Borneo, there are 41 indigenous species of *Alocasia* (world at least 100 species),

of which 15 are undescribed and 37 endemics, often restricted to specific geologies, particularly limestone (16 species) (Boyce et al., 2010). One species (*A. macrorrhizos* (L.) G. Don) is introduced as a carbohydrate crop and now widely feral. There are only two species of *Colocasia* (world 13 published species) in Borneo with one endemic (*C. oresbia* A. Hay). The ecology of *Alocasia* and *Colocasia* is primary and secondary perhumid to everwet subtropical and broadleaf tropical forests, open swamps, predominantly in the lowlands, extending from sea level to lower and mid-montane zones.

2.3 Pollination study of Araceae

Information on aroid pollination was first summarised by Grayum (1984) who documented 35 genera and about 90 species, this was updated by Mayo et al. (1997) with 38 genera and less than 100 species listed including additional data from Grayum (1986, 1990). The subsequent summary about the information of aroid pollination was updated and published by Gibernau (2003, 2011, 2016), which up to approximately 67 genera and 200 species by 2016. These numbers are still low compared with the richness of the family, which according to the last update encompass 144 genera and 3645 accepted species so far (Boyce & Croat, 2011). The information about pollination of aroids is only fragmentary, with very few species of each genera being documented. Hence, pollination data is not always reliable to represent the entire genera, there may be different insects that visit the other species of a given genera. For the documented genera, only some species present detailed studies of their pollination biology and identification of efficient pollinators among the various insect visitors. The protogynous inflorescences of the Araceae are mainly insect-pollinated (Gibernau, 2003, 2011) and have hence evolved several floral features adapted for entomophily particularly in relation to the types of pollinating insects (Gibernau et al.,

2010b), habitat colonization (Calazans et al., 2014), flower protection (Coté & Gibernau, 2012; Maldonado et al., 2015), or trapping devices (Poppinga et al., 2010). The development of powerful phylogenetic approaches helped us to understand the past history and the evolution of floral traits, species distributions (past migrations) or even plant–insect interactions (Takano et al., 2011; Bröderbauer et al., 2012; Nauheimer et al., 2012; Wong et al., 2013; Chartier et al., 2014; de Oliveira et al., 2014; Moore et al., 2015). More and more inflorescence odours are being chemically characterized and the attractiveness of either singly or in combinations of floral volatile compounds is being validated in behavioural assays, these increase our understanding of the structuring role of floral scent volatiles in aroid-pollinator interactions and the olfactory mediated pollinator attraction (Chartier et al., 2011, 2013, 2016; Dötterl et al., 2012; Maia et al., 2012, 2013b; Schiestl & Dötterl, 2012; Gottsberger et al., 2013; Jürgens et al., 2013; Leguet et al., 2014; Pereira et al., 2014; Hoe & Wong, 2016; Hoe et al., 2016).

Total information about pollination of aroids include: subfamily Orontioideae (*Lysichiton*, *Symplocarpus* Salisb.), subfamily Pothoideae (Potheae (*Pothos*), Anthurieae (*Anthurium*)), subfamily Monsteroideae (Spathiphyllae (*Spathiphyllum*), Monstereae (*Epipremnum*, *Monstera* Adans., *Rhodospatha* Poepp., *Scindapsus*, *Rhaphidophora*)), subfamily Lasioideae (*Lasimorpha* Schott, *Dracontium*, *Dracontoides* Engl., *Lasia*, *Anaphyllopsis* A. Hay, *Urospatha* Schott), subfamily Calloideae Endlicher (*Calla* L.), subfamily Aroideae (Dieffenbachieae (*Dieffenbachia*, *Bognera* Mayo & Nicolson), Spathicarpeae (*Taccarum* Brongn. ex Schott, *Gearum* N.E. Br.), Philodendreae (*Philodendron*, *Thaumatophyllum*, *Adelonema*), Homalomeneae (*Homalomena*, *Furtadoa*), Anubiadeae (*Anubias*), Schismatoglottideae (*Schismatoglottis*, *Piptospatha* Schottarum, *Aridarum*, *Phymatarum*), Cryptocoryneae (*Cryptocoryne*, *Lagenandra*), Caladieae

(*Caladium*, *Xanthosoma*, *Chlorospatha* Engl., *Syngonium*), Nephthytideae (*Anchomanes*, *Nephthytis*, *Pseudohydrosme* Engl.) Aglaonemateae (*Aglaonema*), Culcasieae (*Culcasia* P. Beauv., *Cercestis* Schott.), Montrichardieae (*Montrichardia*), Zantedeschieae (*Zantedeschia* Spreng.) Thomsonieae (*Amorphophallus*), Peltandreae (*Peltandra* Raf.), Arisareae (*Arisarum*), Ambrosineae (*Ambrosina*), Areae (*Sauromatum* Schott, *Theriophonum*, *Typhonium*, *Helicodiceros*, *Dracunculus*, *Eminium* Schott, *Arum*, *Biarum*), Arisaemateae (*Pinellia*, *Arisaema*), Colocasieae (*Leucocasia*, *Alocasia*, *Colocasia*, *Steudnera*), Pistia clade (*Englerarum* Nauheimer & P.C. Boyce)).

There are two evolution of inflorescences from the view of pollination (Gibernau, 2003), the first is the evolution of unisexual flowers with the secondary development of sterile flowers that have specialised functions like barrier, floral odour emission, thermogenesis, food-reward and so on, while the uniform bisexual flowers of basal groups must achieve all the functions. The second is the evolution of an enclosing spathe with secondary constriction to capture insects, with only one attraction phase necessary during pistillate anthesis to collect insects inside the floral chamber (by the trap mechanism or provide rewards such as food and mating sites) until male anthesis and pollen release. For more basal group lacking a floral chamber, attraction during pistillate anthesis and staminate anthesis are necessary to ensure pollination and pollen collection. Some species with long anthesis and exposed spadix attract pollinators everyday by floral odour and thermogenesis. According to Gibernau (2003), there are three types of flower-pollinator interactions in Araceae. The first type is a ‘classical’ flower-pollinator interaction, whereby the pollinator visits the inflorescence to look for a resource (stigmatic fluid, pollen) but not for reproduction, and achieving pollination (e.g. *Symplocarpus*, *Calla*, some *Anthurium*). The second type corresponds to insect visiting the inflorescence not only for food rewards (nectar, pollen or

floral tissue) but also for mating and egg deposit (e.g. *Philodendron*, *Dieffenbachia*, *Peltandra*, *Colocasia*). In the third type, the inflorescence realises a deceptive attraction, the insects achieving pollination but without receive any reward (e.g. *Arum*, *Helicodiceros*). There is another interaction when the insects receive the rewards without achieving pollination of the inflorescence, a good example is stingless bees usually visiting inflorescences of aroids in Borneo during staminate anthesis to collect pollen. This interaction is more related to a reward theft than a pollination interaction. The following sections will only include discussion which involved the subfamilies of the species included in this study.

2.3.1 Subfamily Pothoideae

For the Paleotropical tribe Potheae, Hymenoptera were mentioned to visit *Pothos* (Yadav, 1998), but there is no study of pollinators for the three genera of this tribe: *Pothos* (first detailed study in this study), *Pothoidium* and *Pedicellarum*. For the Neotropical tribe Anthurieae, *Anthurium* has a great diversity of pollination systems with bees collecting resins and/or oily fragrances (Hentrich et al., 2007, 2010), curculionid beetles looking for a feeding and probably a reproductive site (Franz, 2003, 2007), and humming-bird pollination, the unique mention of vertebrate pollination in Araceae (Kraemer & Schmitt, 1999).

2.3.2 Subfamily Monsteroideae

In the tribe Spathiphyllae, there is no mention of pollinators for the genus *Holochlamys*. In contrast, the genus *Spathiphyllum* is pollinated in the Neotropics by bees that have been observed to collect pollen, wax or oily fragrance (Hentrich et al., 2010; Diaz-Jimenez et al., 2016), and flies looking for nectar and/or a reproductive site (Gibernau, 2003). For the tribe Anadendreae, there is no mention of pollinators for the only genus, *Anadendrum*

(first mention in this study). There is also no mention of pollinators for the only genus *Heteropsis* Kunth of the tribe Heteropsidae. In the tribe Monstereae, the pollinators from three genera are not known (*Alloschemone* Schott, *Amydrium*, *Stenospermation*). For *Monstera*, bees and beetles have been mentioned to visit their inflorescences (Gibernau, 2003). A recent study by Chouteau et al. (2007) on *M. obliqua* (Miq.) Walp. in French Guiana mentioned the species was to be pollinated by nitidulid beetles. *Rhodspatha* and *Monstera* were reported to be visited by dynastid scarab beetles in Moore and Jameson (2013). Drosophilid flies have been observed to oviposit on the inflorescences of *Scindapsus* and may be the pollinators (Sultana et al., 2006; Fartyal et al., 2013). *Epipremnum* was reported to be visited by dynastid scarab beetles (Jameson & Drumont, 2013) and drosophilid flies (Fartyal et al., 2013). The pollination ecology of *Rhaphidophora africana* N.E. Br. by a scarab beetle has been studied in West Africa by Beath (1993) but not published, whereas Hymenoptera was mentioned for Asian species (Yadav, 1998). Drosophilid flies have been observed to oviposit on the inflorescences of *Rhaphidophora* and could be the pollinators (Takano et al., 2011; Fartyal et al., 2013; Li et al., 2014). Interestingly, a bee pollination system has been indirectly suggested for Monstereae based on a multivariate analysis of some floral traits associated with pollination (Chouteau et al., 2008; Gibernau et al., 2010b).

2.3.3 Subfamily Lasioideae

The pollinators from the five Asian genera are not known [*Anaphyllum* Schott, *Cyrtosperma*, *Lasia* (first detailed study in this study), *Podolasia*, *Pycnospatha* Thorel ex Gagnep.]. In South America, no clear data are available on the pollinators of the three genera (*Anaphyllopsis*, *Dracontioides*, *Urospatha*). Gibernau et al. (2010a) suggesting a very rare event or maybe night-pollination for *Anaphyllopsis*. The genera *Dracontium* and

Dracontioides are suggested to be pollinated by flies (Boos, 1997; Zhu & Croat, 2004; Gonçalves, 2005). Nitidulid beetles have been observed in spathes of *Urospatha* (T. Boos, pers. obs.), and the only species of *Lasimorpha*, *L. senegalensis* Schott, also seems to be pollinated by nitidulid beetles (Knecht, 1983). Bröderbauer et al. (2012) mentioned that *Lasia* is visited by flies in Xishuangbanna Tropical Botanical Garden, China (Yin J. T., pers. obs.).

2.3.4 Subfamily Aroideae

In the tribe Dieffenbachieae, Scarab beetles (Dynastinae) are the pollinators of different *Dieffenbachia* species even if other insects have been observed and/or collected in the inflorescences (Gibernau, 2003). Dynastid scarab beetles also mentioned to visit the only species of the genus *Bognera* [*B. recondita* (Madison) Mayo & Nicolson] in unpublished data of E.G. Gonçalves (Bogner, 2008; Moore & Jameson, 2013). For the tribe Spathicarpeae, there is no mention of pollinators for six genera of this tribe (*Mangonia* Schott, *Asterostigma* Fisch. & C.A. Mey., *Gorgonidium* Schott, *Spathanthium*, *Spathicarpa*, *Synandrospadix* Engl.). Recent studies on two genera have shown that *Gearum* (*G. brasiliense* N.E. Br) (Gonçalves & Maia, 2006) and *Taccarum* (*T. ulei* Engl. & K. Kraus) (Maia et al., 2013a, 2013b) are pollinated by cyclocephaline scarab beetles (Dynastinae). For the tribe Philodendreae, the genera *Philodendron* and *Thaumatophyllum* are pollinated by scarab beetles (Dynastinae) even if other insects can be found within the inflorescences (Gibernau, 2003; Maia et al., 2010, Moore & Jameson, 2013). The resurrected genus, *Adelonema*, which consist of former Neotropics *Homalomena* is also pollinated by dynastid scarab beetles (Moore & Jameson, 2013). In the tribe Homalomeneae, drosophilid flies have been identified as pollinators of *Furtadoa* (Sultana et al., 2006). For the genus *Homalomena*, recent studies

have clarified that the species belonging to the Supergroups Chamaecladon and Punctulata are specifically pollinated by drosophilid flies (*Colocasiomyia* spp.), whereas those belonging to the Supergroups Cyrtocladon and Homalomena are specifically pollinated by ruteline scarabs (*Parastasia* spp.; Rutelinae) and chrysomelids (*Chaloenus* spp.; Galeuricinae), although *Homalomena* species are frequently visited by both drosophilid flies and beetles (Kumano-Nomura & Yamaoka, 2006; Wong et al., 2013; Yafuso et al., 2015; Hoe et al., 2016). In the tribe Anubiadeae, there is a reference on one West African species, *Anubias gigantea* A. Chev., indicating nitidulid beetles as visitors and/or pollinators (Knecht, 1983). For the tribe Schismatoglottideae, there are 30 recognised genera based on the result of the recent phylogenetic study by Low et al. (2018), the pollinators are not known for 25 genera [*Toga*, *Tawaia*, *Pursegloveia*, *Bucephalandra* (first time mentioned in this study), *Schottariella*, *Naiadia*, *Burttianthus*, *Hera*, *Heteroaridarum*, *Nabalu*, *Vesta*, *Bakoa*, *Bakoaella*, *Fenestratarum*, *Pichinia*, *Colobogynium*, *Apoballis*, *Gamogyne*, *Ooia*, *Galantharum*, *Hottarum*, *Kiewia*, *Rhynchopyle*, *Gosong*, *Bidayuha*]. Species of *Aridarum*, *Piptospatha*, *Phymatarum* and *Schottarum* are pollinated by drosophilid flies (*Colocasiomyia* spp.) although sometimes beetles (Chrysomelidae, Hydrophilidae) are regular inflorescence visitors (Gibernau, 2011; Low et al., 2014, 2016). The inflorescences of *Schismatoglottis* are visited by numerous species of flies and beetles, pollinators are drosophilid flies (*Colocasiomyia* spp.) alone or in association with hydrophilid beetles (*Cycreon* spp., Hydrophilidae) (Yafuso et al., 2015; Hoe & Wong, 2016). In multivariate analyses on some floral traits associated with pollination, the genus *Schismatoglottis* fall within both fly- and beetle-pollination system (Chouteau et al., 2008; Gibernau et al., 2010b). In the tribe Cryptocoryneae, there is no proper pollination study on *Cryptocoryne* and *Lagenandra* but many observations and insect collections suggesting fly pollination by a

trap mechanism in aquatic habit (Yadav, 1998). In the tribe Zomicarpeae, there is no mention of pollinators for the four genera of this tribe (*Zomicarpa* Schott, *Zomicarpella* N.E. Br., *Ulearum* Engl., *Filarum* Nicolson). For the tribe Caladieae, pollinators are unknown for the genera *Scaphispatha* Brongn. ex Schott, *Jasarum* and *Hapaline*. Many studies and observations indicate a scarab beetle pollination in *Caladium* and *Synгонium* (Gibernau, 2003; Maia & Schlindwein, 2006; Gasca-Alvarez, 2013). *Chlorospatha* was reported to be visited by staphylinid beetles and flies (Croat & Hannon, 2015). In *Xanthosoma*, many different insects (euglossine bees, drosophilid flies, scarab beetles) have been observed in the inflorescences (Gibernau, 2003), recent studies by Garcia-Robledo et al. (2004) indicate that certainly only scarab beetles are pollinators and the other insects are probable visitors. In the tribe Nephthytideae, the genera *Anchomanes*, *Nephthytis* and *Pseudohydrosme* are visited by beetles (Nitidulidae, Staphylinidae) and flies, and trigona bees might only be visitors for inflorescences of *Anchomanes* (Gibernau, 2003). In multivariate analyses on some floral traits associated with pollination, some species of *Anchomanes* and *Nephthytis* appeared to have typical fly pollinated floral characters while other species have more mixed floral characters (Chouteau et al., 2008; Gibernau et al., 2010b). For the tribe Aglaonemateae, there is no mention of pollinator for the genus *Aglaodorum*, and *Aglaonema* (detailed study on two species in this study) is certainly pollinated by drosophilid flies (Gibernau, 2003). In the tribe Culcasieae, beetles (Nitidulidae) and flies (Drosophilidae) have been collected within the inflorescences of *Culcasia* and *Cercestis* (Gibernau, 2003). In multivariate analyses on some floral traits associated with pollination, *Culcasia* appeared to be associated with fly-pollinated species whereas *Cercestis* with beetle-pollinated species (Chouteau et al., 2008; Gibernau et al., 2010b). For the tribe Montrichardieae, the only genus, *Montrichardia* is pollinated by scarab beetles although bees were observed to visit its inflorescences. *M.*

arborescens Schott have anthesis of about one day, whereby its pistillate anthesis started at dusk of day one and staminate anthesis ended at dusk of day two, the inflorescences heated up twice, and Cyclocephaline scarab beetles stayed in the inflorescence throughout the anthesis (Gibernau et al., 2003). In the tribe Zantedeschieae, the only genus of this tribe, *Zantedeschia*, may be pollinated in its natural distribution area by beetles (Gibernau, 2003). For the tribe Callopsiidae Engl., there is no mention of pollinators for the only genus, *Callopsiis* Engl. In the tribe Thomsoniidae, the only genus, *Amorphophallus* has been observed to be visited by a great diversity of insects (bees, beetles, flies). Previous studies of pollination biology on *Amorphophallus* (Sivadasan & Sabu, 1989; Beath, 1996; Hetterscheid & Ittenbach, 1996; Kite et al., 1998; Punekar, 2007) suggested that the genus is pollinated by beetles (Asilidae, Cetoniidae, Histeridae, Hybosoridae, Nitidulidae, Scarabaeidae, Silphidae, Staphylinidae), flies (Calliphoridae, Platystomatidae) and bees (Trigona). A recent study by Punekar and Kumaran (2010) on eight taxa of *Amorphophallus* in North Western Ghats and Konkan Region of India further support beetles (Cetoniidae, Nitidulidae, Scarabaeidae) and bees (Trigona) as pollinators for the studied *Amorphophallus*. *Pseudodracontium*, a former genus now included in *Amorphophallus*, is probable pollinated by carrion flies and beetles, such hypothesis must be confirmed by a field study (Kite et al., 1998; van der Ham et al., 2005). For the tribe Arophyteae, there is no mention of pollinators for the three genera of this Madagascan tribe (*Arophyton*, *Carlephyton* Jum., *Colletogyne* Buchet). In the tribe Peltandreae, there is no information about pollination for the genus *Typhonodorum*, while *Peltandra* is pollinated by flies (Chloropidae) that oviposit on the inflorescences (Gibernau, 2003). For the tribe Arisareae, *Arisarum*, the only genus of this tribe, seems to be pollinated by diverse mycophilous or saprophilous flies (Gibernau, 2003). In the tribe Ambrosiinae, Barabé et al. (2004) suggested a complicated pollination

mechanism for the sole genus, *Ambrosina*, with a small insect being able to move from a lower "male" chamber from one inflorescence to an upper "female" chamber of another inflorescence. A study on a Corsican population was not able to find any pollinator (Quilichini et al., 2005). In the tribe Areae, the pollination of all the eight genera has been studied (*Arum*, *Biarum*, *Dracunculus*, *Eminium*, *Helicodiceros*, *Sauromatum*, *Theriophonum* and *Typhonium*), and is achieved by necrophilous or saprophilous flies and/or beetles (Blackith & Blackith, 1993; Yadav, 1998; Gibernau, 2003; Angioy et al., 2004; Gibernau et al., 2004; Sivadasan & Kavalan, 2005; Boyce, 2008; Espíndola et al., 2010; Quilichini et al., 2010; Stökl et al., 2010; Urru et al., 2010) except for one known exception by pollen-collecting bee in *Arum creticum* (Diaz & Kite, 2006; Urru et al., 2010). A study of *Dracunculus vulgaris* Schott in Crete by Lamprecht et al. (2013) showed that inflorescences from variety that produced sulphide-rich "rotting meat" smell attracted several groups of carrion beetles (i.e. Staphylinidae, Dermestidae, Histeridae, Silphidae) and carrion flies, while the 'scentless' variety attracted only a single species of a native flower chafer. For the tribe Arisaemateae, the two genera of this tribe, *Pinellia* and *Arisaema* are pollinated by various mycophilous and saprophilous flies, a few beetles, and thrips (Thysanoptera) (Gibernau, 2003; Barriault et al., 2009, 2010). In the tribe Colocasieae, there is no mention of pollinator for the three genera: *Ariopsis*, *Protarum* and *Remusatia*. The pollinators of *Colocasia* and *Alocasia* species are drosophilid flies (e.g. *Colocasiomyia* spp.) that oviposit on the inflorescences. Interestingly, the inflorescence of both genus are visited by two fly species, one ovipositing on the staminate zone, while the other ovipositing on the pistillate zone without damaging the ovules (Toda & Okada, 1983; Okada, 1986, 1987, 1990; Ivancic et al., 2004, 2005, 2008; Miyake & Yafuso, 2005; Sultana et al., 2006). There are other insects mentioned to visit the inflorescences but they are not pollinators. Takano et al.

(2006) reported *Steudnera* has a similar fly pollination system except that only one fly species is present. The new genus *Leucocasia* consists of a single species, the former *Colocasia gigantea* (Blume) Hook. f. (now *L. gigantea* Schott), and is also known to be pollinated by drosophilid flies (*Colocasiomyia* spp.) (Takano et al., 2011; Fartyal et al., 2013; Yafuso et al., 2015). Numerous staphylinid beetles were observed visiting inflorescences of *Englerarum*, a newly described monotypic genus (former *Alocasia hypnosa* J.T. Yin, Y.H. Wang & Z.F. Xu) which may represent its own tribe within the basal Pistia-clade (Nauheimer & Boyce, 2014). In the tribe Pistieae, there is no clear mention of insects observed in the minute inflorescence of *Pistia*, and no published study on its pollination.

CHAPTER 3

MATERIALS AND METHODS

3.1 Study area

This study was conducted in Gunung Mulu N. P., Miri Division, Sarawak. The area covered was the trails from Park headquarter to Deer Cave, which included left and right loop of the Botanical trail, Deer cave trail, trail to Canopy skywalk, and trail to Paku Waterfall (Figure 3.2); and Camp 5 (Figure 3.3). The forest types include riverine forest (Park headquarter, Botanical trail and Paku Waterfall trail) and lowland limestone forest (Deer Cave trail, Canopy skywalk trail, trail to Camp 5) (Figure 3.3). Riverine forests occur along edge of river, have fertile soil deposited by long period of flooding. Lowland limestone forests occur in lowland area with limestone soil, or surrounding of limestone hill (Figure 3.1 & Figure 3.3).

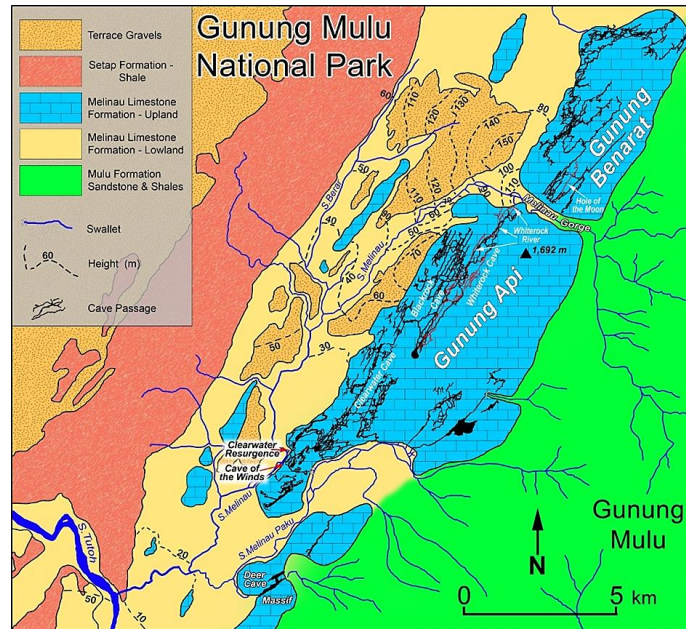


Figure 3.1: Geological map of Mulu National Park, the area of study is part of the Melinau limestone formation. Adapted from *A guide to the karst geomorphology of Mulu*, by A. R. Farrant, 2009, Retrieved from <http://www.mulucaves.org/wordpress/science/the-geomorphology-of-mulu>.



Figure 3.2: Map of trails near HQ of Mulu National Park, the trails of this study included Deer cave walk, Botany Walk, Canopy walk, Paku waterfall and the night walk. Retrieved and edited from http://www.etawau.com/Geography/Sarawak/04_Miri/Miri/MuluTour.htm.

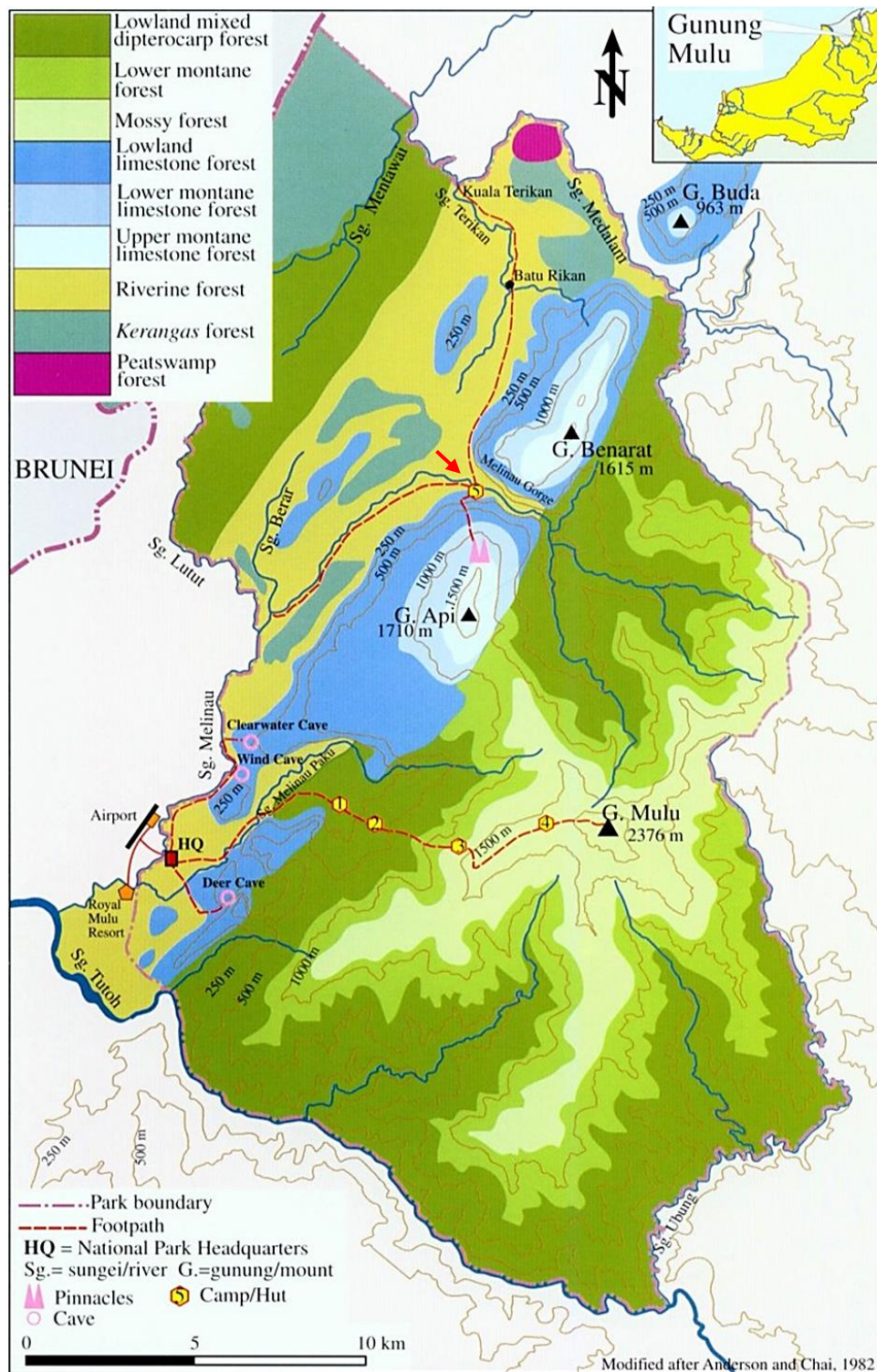


Figure 3.3: Map of the forest type of Mulu National park, the area of study included area from HQ to Deer Cave and Camp 5, the forest type of the study area are riverine forest and lowland limestone forest. Adapted from *A Guide to Gunung Mulu National Park*, H. P. Hazebroek & A. K. Abang Morshidi, 2002, Borneo: N.H.P.B.

3.2 Plant species

Twenty-one species of Araceae in Mulu National Park were studied between July 2017 and September 2017, and between December 2017 and January 2019. Twenty-one species of aroid representing 22% of total aroid species recorded in the park (Table 3.1). Five species [*Anadendrum* sp. (Figure 4.12A), *Lasia spinosa* (Figure 4.24), *Pothos insignis* (Figure 4.26H), *P. scandens* (Figure 4.28A) and *Scindapsus longistipitatus* (Figure 4.41A)] belong to the bisexual-flowered clade (sensu Cusimano et al., 2011) and 16 species [*Aglaonema nitidum* (Figure 4.1A), *A. simplex* (Figure 4.3A), *Alocasia sarawakensis* (Figure 4.5), *Amorphophallus hewittii* (Figure 4.7A and 4.7B), *A. julaiihii* (Figure 4.10A), *Bucephalandra muluensis* (Figure 4.14A), *Homalomena ardua* (Figure 4.16A), *H. ovatifolia* (Figure 4.18), *H. rostrata* (Figure 4.20A and 4.20B), *H. sanguineovaginata* (Figure 4.22A and 4.22B), *Schismatoglottis colocasioidea* (Figure 4.29A), *S. multinervia* (Figure 4.31A), *S. muluensis* (Figure 4.33A), *S. pellucida* (Figure 4.35A), *S. roseopedes* (Figure 4.37A), and *S. serratodentata* (Figure 4.39A and 4.39B)] belong to the unisexual-flowered clade of Araceae (sensu Cusimano et al., 2011).

Table 3.1: A checklist of aroid species in Mulu National Park. ¹ non native. * taxa included in this study. 95 taxa including one non-native.

Species	Species
<i>Aglaonema commutatum</i> Schott ¹	<i>Homalomena vagans</i> P.C. Boyce
<i>Aglaonema nitidum</i> Kunth*	<i>Lasia spinosa</i> Thwaites*
<i>Aglaonema simplex</i> Blume*	<i>Nabalu corneri</i> (A. Hay) S.Y. Wong & P.C. Boyce
<i>Alocasia asper</i> sp. nov. 1	<i>Ooia</i> sp. nov. 1
<i>Alocasia beccarii</i> Engl.	<i>Pedicellarum paiei</i> M. Hotta
<i>Alocasia chrysopedes</i> sp. nov. 2	<i>Phymatarum borneense</i> M. Hotta
<i>Alocasia longiloba</i> Miq.	<i>Pothos atropurpurens</i> M. Hotta
<i>Alocasia minuscula</i> A. Hay	<i>Pothos insignis</i> Engl.*
<i>Alocasia princeps</i> W. Bull	<i>Pothos leptostachyus</i> Schott
<i>Alocasia reginae</i> N.E. Br.	<i>Pothos mirabilis</i> Merr.
<i>Alocasia robusta</i> M. Hotta	<i>Pothos ovatifolius</i> Merr.
<i>Alocasia sarawakensis</i> M. Hotta*	<i>Pothos scandens</i> L.*
<i>Amorphophallus angulatus</i> Hett. & A. Vogel	<i>Rhaphidophora elliptifolia</i> Merr.
<i>Amorphophallus costatus</i> Hett.	<i>Rhaphidophora foraminifera</i> (Engl.) Engl.
<i>Amorphophallus hewittii</i> Alderw.*	<i>Rhaphidophora korthalsii</i> Schott
<i>Amorphophallus julaiihii</i> Ipor, Tawan & P.C. Boyce*	<i>Rhaphidophora latevaginata</i> M. Hotta
<i>Amydrium medium</i> (Zoll. & Moritzi) Nicolson	<i>Rhaphidophora lobii</i> Schott
<i>Anadendrum muluensis</i> P.C. Boyce & S.Y. Wong	<i>Rhaphidophora megasperma</i> Engl.
<i>Anadendrum</i> sp. nov. 1*	<i>Rhaphidophora sylvestris</i> (Blume) Engl.
<i>Anadendrum</i> sp. nov. 2	<i>Rhaphidophora tenuis</i> Engl.
<i>Arisaema</i> sp.	<i>Rhaphidophora typha</i> P.C. Boyce
<i>Bucephalandra muluensis</i> (M.Hotta) S.Y. Wong & P.C. Boyce*	<i>Schismatoglottis ahmadii</i> A. Hay
<i>Bucephalandra oblanceolata</i> (M.Hotta) S.Y. Wong & P.C. Boyce	<i>Schismatoglottis ciliata</i> A. Hay
<i>Burttianthus hansenii</i> (Bogner) S.Y. Wong & P.C. Boyce	<i>Schismatoglottis colocasioidea</i> M. Hotta*
	<i>Schismatoglottis consensua</i> sp nov. 1
	<i>Schismatoglottis crinitissima</i> A. Hay
	<i>Schismatoglottis dilecta</i> S.Y. Wong, P.C. Boyce & S.L. Low

Table 3.1 continued

<i>Burtianthus purseglovei</i> (Furtado) S.Y. Wong & P.C. Boyce	<i>Schismatoglottis fossae</i> S.Y. Wong, P.C. Boyce & Aisahtul
<i>Colobogynium tecturatum</i> Schott	<i>Schismatoglottis fugax</i> sp. nov. 2
<i>Cryptocoryne longicauda</i> Becc. ex Engl.	<i>Schismatoglottis guarusaensis</i> sp. nov. 3
<i>Cryptocoryne striolata</i> Engl.	<i>Schismatoglottis latens</i> sp. nov. 4
<i>Cryptocoryne yujii</i> Bastmeijer	<i>Schismatoglottis melinauensis</i> sp. nov. 5
<i>Gamogyne burbridgei</i> N.E. Br.	<i>Schismatoglottis monoplacenta</i> M. Hotta
<i>Hapaline celatrix</i> P.C. Boyce	<i>Schismatoglottis motleyana</i> (Schott) Engl.
<i>Homalomena ardua</i> P.C. Boyce & S.Y. Wong*	<i>Schismatoglottis multinervia</i> M. Hotta*
<i>Homalomena ovatifolia</i> (Schott) Ridl.*	<i>Schismatoglottis muluensis</i> M. Hotta*
<i>Homalomena cowleyae</i> P.C. Boyce & S.Y. Wong	<i>Schismatoglottis pectinervia</i> A. Hay
<i>Homalomena ibanorum</i> S.Y. Wong & P.C. Boyce	<i>Schismatoglottis pellucida</i> S.Y. Wong, P.C. Boyce & S.K. Chai*
<i>Homalomena malina</i> sp. nov. 1	<i>Schismatoglottis platystigma</i> M. Hotta
<i>Homalomena minutissima</i> M. Hotta	<i>Schismatoglottis rigida</i> sp. nov. 6
<i>Homalomena passa</i> S.Y. Wong & P.C. Boyce	<i>Schismatoglottis roseopedes</i> S.Y. Wong, P.C. Boyce & S.K. Chai*
<i>Homalomena pseudogeniculata</i> P.C. Boyce & S.Y. Wong	<i>Schismatoglottis serratodentata</i> S.Y. Wong, P.C. Boyce & S.K. Chai*
<i>Homalomena rostrata</i> Griff.*	<i>Schismatoglottis shaleicola</i> P.C. Boyce & S.Y. Wong
<i>Homalomena sanguineovaginata</i> sp. nov. 2*	<i>Schismatoglottis terpsis</i> sp. nov. 7
<i>Homalomena scutata</i> S.Y. Wong & P.C. Boyce	<i>Scindapsus crassipes</i> Engl.
<i>Homalomena sungailangsatensis</i> sp. nov. 3	<i>Scindapsus glaucescens</i> (Engl. & K. Krause) Alderw.
<i>Homalomena sparsa</i> sp. nov. 4	<i>Scindapsus latifolius</i> M. Hotta
<i>Homalomena striatieopetiolata</i> P.C. Boyce & S.Y. Wong	<i>Scindapsus longistipitatus</i> Merr.*
	<i>Scindapsus treubii</i> Engl.
	<i>Vesta longifolia</i> (Ridl.) S.Y. Wong

3.3 Survey of flowering populations

Preliminary survey to find flowering populations of ‘workable’ aroid species was carried out in the study area. ‘Workable’ species mean the species were found flowering, and the inflorescences were accessible for observations and experiments. Table 3.2 listed the 21 investigated aroids species with their habit, habitat, and location. Field works (observation and experiments) were conducted according to the flowering of the aroid species. If there were several target species flower at the same time, species with higher number of flowering were focused first because data on this species could be completed first. Contradictory, species with lower flowering number were focused later because more inflorescences were needed to collect enough data. Field works were conducted several times at different time of flowering for these species until complete data were collected. Survey of flowering population was frequently carried out (at least each time a week to every trail) to make sure flowering of rarely flowering species were detected. For species of *Amorphophallus* that have a short flowering duration during a specific season at random location in Paku waterfall trail, Deer cave trail or Camp 5, intensive field surveys to find new flowering buds were conducted every day, when their flowering was known, to make sure that as many inflorescences as possible could be studied. The numbers of replicates (inflorescences utilised) for field observations (timing of anthesis, floral traits, rewards, insect visitors and their behaviour), insect captures, and pollination treatments (autonomous self- and open- pollination) were stated in Table 3.3.

Table 3.2: Life form/ecology, habitat, and location of the 21 investigated aroid species.

Species	Life form/ ecology	Habitat	Location
<i>Aglaonema nitidum</i>	Terrestrial/ mesophyte	Alluvial/Riverine forest	Park headquarter
<i>Aglaonema simplex</i>	Terrestrial/ mesophyte	Lowland limestone forest	Deer Cave trail
<i>Alocasia sarawakensis</i>	Terrestrial/ geophyte	Alluvial/Riverine forest	Park headquarter
<i>Amorphophallus hewittii</i>	Terrestrial/ geophyte	Alluvial/Riverine forest	Paku waterfall trail, Camp 5
<i>Amorphophallus julaiihii</i>	Terrestrial/ geophyte	Lowland limestone forest	Deer Cave trail
<i>Anadendrum</i> sp. nov.	Nomadic vines/ hemiepiphyte	Alluvial/Riverine forest	Park headquarter
<i>Bucephalandra muluensis</i>	Terrestrial/ rheophyte	Lowland limestone forest	Deer Cave trail
<i>Homalomena ardua</i>	Terrestrial/ mesophyte	Alluvial/Riverine forest	Park headquarter
<i>Homalomena ovatifolia</i>	Terrestrial/ Lithophyte/	Lowland limestone forest	Camp 5
<i>Homalomena rostrata</i>	Terrestrial/ helophyte	Alluvial/Riverine forest	Park headquarter
<i>Homalomena sanguineovaginata</i> sp. nov.	Terrestrial/ mesophyte	Alluvial/Riverine forest	Park headquarter
<i>Lasia spinosa</i>	Terrestrial/ hydrophyte	Alluvial/Riverine forest	Park headquarter
<i>Pothos insignis</i>	Nomadic vines/ hemiepiphyte	Alluvial/Riverine forest	Park headquarter
<i>Pothos scandens</i>	Nomadic vines/ hemiepiphyte	Alluvial/Riverine forest	Park headquarter
<i>Schismatoglottis colocasioidea</i>	Terrestrial/ lithophyte	Lowland limestone forest	Deer Cave trail
<i>Schismatoglottis multinervia</i>	Terrestrial/ lithophyte	Lowland limestone forest	Deer Cave trail
<i>Schismatoglottis muluensis</i>	Terrestrial/ lithophyte	Lowland limestone forest	Deer Cave trail
<i>Schismatoglottis pellucida</i>	Terrestrial/ lithophyte	Lowland limestone forest	Deer Cave trail
<i>Schismatoglottis roseopedes</i>	Terrestrial/ mesophyte	Alluvial/Riverine forest	Park headquarter
<i>Schismatoglottis serratodentata</i>	Terrestrial/ mesophyte	Alluvial/Riverine forest	Park headquarter
<i>Scindapsus longistipitatus</i>	Nomadic vines/ hemiepiphyte	Alluvial/Riverine forest	Park headquarter

Table 3.3: Numbers of replicates (inflorescences utilised) for field observations (timing of anthesis, floral traits, rewards, insect visitors and their behaviour), insect captures and pollination treatments (autonomous self- and open- pollination).

Species	Number of replicates (inflorescences)			
	Field observation	Insect captures	Autonomous self-pollination	Open-pollination
<i>Aglaonema nitidum</i>	4	17	3	7
<i>Aglaonema simplex</i>	3	7	3	5
<i>Alocasia sarawakensis</i>	3	24	3	3
<i>Amorphophallus hewittii</i>	3	11	-	3
<i>Amorphophallus julaiihii</i>	3	4	-	3
<i>Anadendrum</i> sp. nov.	3	21	3	9
<i>Bucephalandra muluensis</i>	3	14	3	3
<i>Homalomena ardua</i>	3	18	-	-
<i>Homalomena ovatifolia</i>	3	9	-	-
<i>Homalomena rostrata</i>	4	20	3	6
<i>Homalomena sanguineovaginata</i> sp. nov.	3	9	-	-
<i>Lasia spinosa</i>	10	19	3	3
<i>Pothos insignis</i>	5	12	3	15
<i>Pothos scandens</i>	3	3	-	-
<i>Schismatoglottis colocasioidea</i>	3	7	3	3
<i>Schismatoglottis multinervia</i>	3	8	3	-
<i>Schismatoglottis muluensis</i>	3	4	3	3
<i>Schismatoglottis pellucida</i>	3	5	3	-
<i>Schismatoglottis roseopedes</i>	3	6	3	3
<i>Schismatoglottis serratodentata</i>	4	11	3	8
<i>Scindapsus longistipitatus</i>	3	6	-	-

3.4 Flowering patterns

Flowering patterns of the aroid species were recorded for about a year of field work. Flowering patterns in this study include flowering frequencies throughout a year, flowering time or flowering season, flowering densities (number of flowering plants in a population) and flowering period (total time of flowering in a population, number of flowering plants per day). It was important to record the flowering patterns of the different aroid species because they may flower at different time, continuously or at specific flowering periods, flower in mass number of plant (synchronous) or just a few plant (asynchronous), and flowering may end very fast or take a long time in term of a population.

3.5 Floral developmental stages

Suitable inflorescences were identified and observed for one week prior to the onset of anthesis. Close observation and records were conducted during the different anthetic stages. At least three observation replicates were done for each studied species during pistillate and staminate anthesis. Timing of anthesis, inflorescence changes during anthesis (flowering mechanism), noticeable floral traits and rewards that attract insects, insect visitors and their behaviour were recorded (Hoe et al., 2016, 2018; Low et al., 2016). Records were conducted by taking photos and writing field notes. The changes of a typical aroid inflorescence during anthesis were: pistillate anthesis started after spathe opened, with noticeable characters such as release and extent of floral odour, wet and bright coloured stigmas and arrival of insect visitors; pistillate anthesis ended when floral odour weakened, stigmas turn drier and darker; staminate anthesis started after the end of pistillate anthesis, characterized by release of pollen and exodus of insect visitors. The measurement of spathe and spadix for each of the studied species were stated in Table 3.4.

Table 3.4: Measurement of spathe (widest point during pistillate anthesis) and spadix for the 21 studied aroid species.

Species	Spathe		Spadix					
	Length (cm)	Width, lower/ upper (cm)	Total length (cm)	Stipe (cm)	Female zone (cm)	Sterile interstice (cm)	Male zone (cm)	Appendix (cm)
<i>Aglaonema nitidum</i>	8.0	2.3	7.3	0.5	0.8	-	6.0	-
<i>Aglaonema simplex</i>	4.2	2.4	4.7	0.4	0.8	-	3.5	-
<i>Alocasia sarawakensis</i>	13.5	2.0, 2.5	13.0	0.5	2.3	0.5	2.5	7
<i>Amorphophallus hewittii</i>	51.0	21.0	67.0	1.0	10.0	-	8.0	48.0
<i>Amorphophallus julaiihii</i>	9.0	7.0	19.0	0.5	1.0	-	2.0	15.5
<i>Anadendrum</i> sp. nov	7.5	0.8	4.0	0.5	-	-	-	-

Table 3.5 continued

<i>Bucephalandra muluensis</i>	2.5	1.0	1.7	-	0.4	0.2	0.3	0.8
<i>Homalomena ardua</i>	12.5	2.8, 3.3	12.0	-	3.0	1.0	8.0	-
<i>Homalomena ovatifolia</i>	1.8	0.7	1.6	-	0.4	-	1.2	-
<i>Homalomena rostrata</i>	10.0	2.8, 2.8	10.0	-	2.5	0.5	7.0	-
<i>Homalomena sanguineovaginata</i> sp. nov	7.0	2.4, 2.5	7.5	-	2.5	0.5	4.5	-
<i>Lasia spinosa</i>	60	1.5	4.0	-	-	-	-	-
<i>Pothos insignis</i>	5.0	1.0	4.5	1.0	-	-	-	-
<i>Pothos scandens</i>	1.0	0.5	1.1	1.7	-	-	-	-
<i>Schismatoglottis colocasioidea</i>	9	0.8, 1.8	8.5	-	2.5	-	2.0	4.0
<i>Schismatoglottis multinervia</i>	5.5	1.3, 1.8	4.0	-	1.2	0.6	0.7	1.5

Table 3.6 continued

<i>Schismatoglottis muluensis</i>	13	1.5, 2.5	10.5	-	5.0	-	1.5	4.0
<i>Schismatoglottis pellucida</i>	8.5	1.2, 1.5	6.0	-	2.5	-	2.0	1.5
<i>Schismatoglottis roseopedes</i>	7.0	0.7, 1.2	5.5	-	2.5	-	1.0	2.0
<i>Schismatoglottis serratodentata</i>	8.5	0.7, 1.2	8.0	-	3.0	-	2.0	3.0
<i>Scindapsus longistipitatus</i>	16.0	4.0	13.0	-	-	-	-	-

3.6 Insect visitors and pollinators

To be considered as a legitimate pollinator, the insect visitor had to come into contact with the reproductive organs of the flower at suitable time (pistillate flowers during pistillate anthesis and staminate flowers during staminate anthesis) (Hoe et al., 2016, 2018; Low et al., 2016). All insect visitors to at least three inflorescences of each aroid species during anthesis were captured and counted to obtain the average number of individuals (mean) $\pm$ SE, range, and percentage of occurrence of different insect visitors to each aroid species. The number of inflorescence replicates for insect visitors that were captured during their visit to inflorescences of each aroid species during anthesis were stated in Table 3.3. Insects

collected were separated in different groups (flies, beetles), counted and preserved in 70 % ethanol. Insects were sent to and identified to the lowest possible taxonomic level (and at least to family level) by M. J. Toda (Hokkaido University: drosophilid flies), C. Reid (Australian Museum: Coleoptera), M. Munetoshi (Kyushu University Museum: rove beetles, *Atheta*), A. G. Kirejtshuk (Russian Academy of Sciences: hydrophilid beetles, *Cycreon*) and M. Fikacek (National Museum in Prague: hydrophilid beetles, *Cycreon*).

3.7 Reproductive system

Two types of treatment were applied to the inflorescences of the studied aroid species. One of them is open pollination, unbagged marked inflorescences are open to natural pollination, efficiency of open pollination was obtained from fruit set percentage of these inflorescences. The number of inflorescence replicates for open pollination treatment was stated in Table 3.3, there were at least three replicates for each species. Next, autonomous self-pollination is a treatment to test the capability to self-pollinate in the absence of pollinator, it was tested to the aroid species by bagging inflorescences about to open to exclude all possible pollinators. There were three replicates for species treated with autonomous self-pollination treatment. Result of the treatment was obtained from fruit set percentage of these inflorescences. Fruit set percentage is the ratio between the average total number of fruit set per infructescence and the average total number of flowers per inflorescence, it is useful to measure pollination efficiency (Hoe & Wong, 2016). Seed set of the studied aroid species was counted from some randomly selected fruits of each species (at least n=10). While many species have multiple seed fruit, some species have one to two seeds per fruit.

CHAPTER 4

RESULTS

4.1 *Aglaonema*

4.1.1 Flowering pattern

Each plant of *Aglaonema nitidum* (Figure 4.1 and Figure 4.2) and *A. simplex* (Figure 4.3 and Figure 4.4) usually has three to five inflorescences, the interval between two successive flowering events was usually three days for *A. nitidum* and six to nine days in *A. simplex*. In a single population, different plant flowered at different day, each day at least one inflorescence was in pistillate anthesis if there were five flowering plants in *A. nitidum* and eight to 11 flowering plants in *A. simplex*. *Aglaonema nitidum* and *A. simplex* flowered every two to three months per year, sometimes just before or after previous batch of infructescence ripened. The ripened fruits can persist for one to two months before entire infructescence senesced for both species. Within the period of field work, flowering of *A. nitidum* and *A. simplex* occurred several times from December 2017 to January 2018, March 2018 to April 2018, June 2018 to July 2018, September 2018 to October 2018 and December 2018 to January 2019.



Figure 4.1: *Aglaonema nitidum* (A) Whole plant with inflorescences and infructescences. (B) Post anthetic inflorescence, spathe closed back (C) Immature fruits. (D) About to ripe fruits in pink and ripening fruits in red.

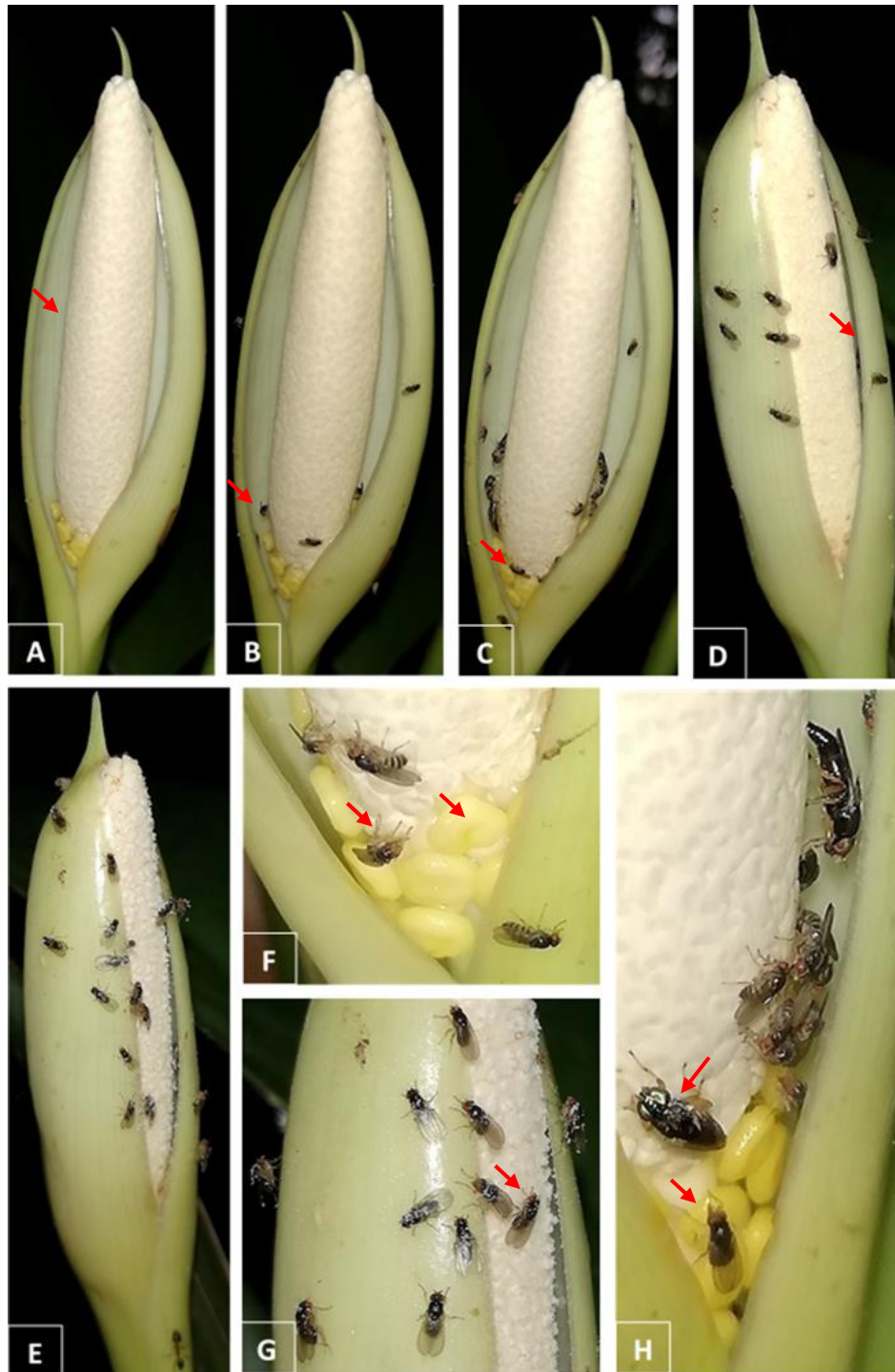


Figure 4.2: Inflorescence of *Aglaonema nitidum* at different stages. (A-C) Pistillate anthesis, spathe gap widely opened, flies entered. (D) Inflorescence before staminate anthesis, spathe gap closed back. (E) Staminate anthesis. (F) Receptive pistils during pistillate anthesis, *Colocasiomyia* flies (Drosophilidae) at sterile interstice. (G) *Colocasiomyia* flies (Drosophilidae) collecting pollen grains. (H) *Colocasiomyia* flies (Drosophilidae) moved onto pistils, unknown flies at sterile interstice during pistillate anthesis.



Figure 4.3: *Aglaonema simplex* (A) Adult plants with inflorescences and infructescences. (B) Immature fruits in yellow and ripened fruits in red. (C) Inflorescence during pre-anthesis and post anthesis (spathe and staminate zone abscised).

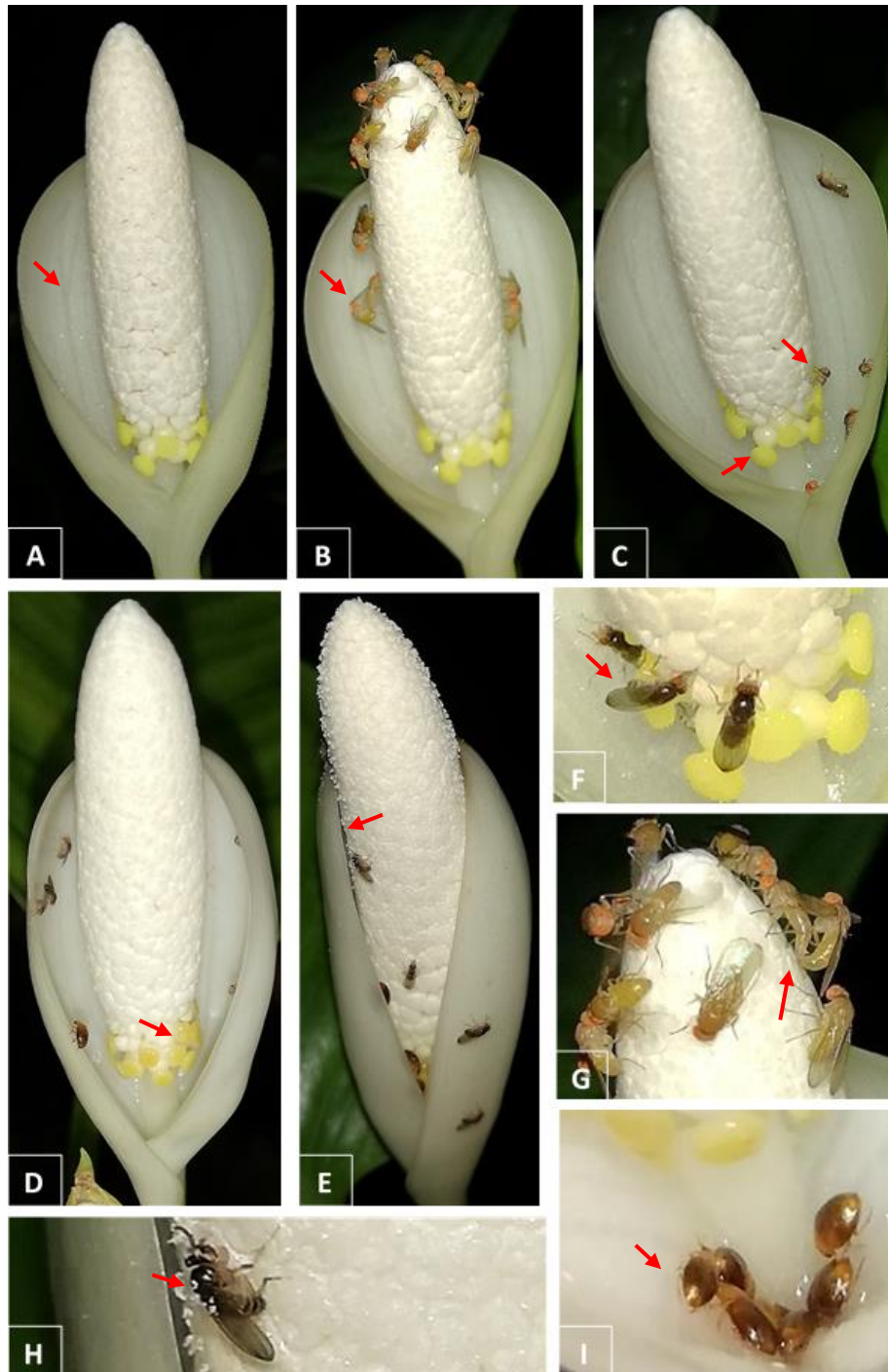


Figure 4.4: Inflorescence of *Aglaonema simplex* at different stages. (A-C) Pistillate anthesis, spathe gap widely opened. (B) Unknown flies arrived before *Colocasiomyia* flies (*Drosophilidae*) arrive. (C-E) *Colocasiomyia* flies arrived and stayed throughout anthesis, pistillate flowers turned deep yellow post pistillate anthesis. (E) Staminate anthesis, spathe gap closed back. (F) *Colocasiomyia* flies move onto pistillate flowers. (G) Unknown flies mate at staminate zone. (H) *Colocasiomyia* flies collect pollen. (I) *Cycreon* beetles (*Hydrophilidae*) at pistillate anthesis.

4.1.2 Timing of anthesis and floral changes

The anthetic period of *Aglaonema nitidum* and *A. simplex* lasted for 26 hours. Spathe started to open a day before pistillate anthesis (1.5 cm gap and 0.2 cm space between spathe and spadix for *A. nitidum*, 3 cm gap and 0.4 cm space for *A. simplex*) (Figure 4.2A, 4.4A). Receptivity of pistillate flowers (ca. 0400 h, Day 1) coincided with the release of floral odour (“sweet citrus burned plastic alcohol-like smell” for *A. nitidum* and “sweet citrus alcohol-like smell” for *A. simplex*) from staminate zone (strongest between 0530 – 0630 h, extend 3-5 cm) (Table 4.1). Spathe opened wider (0.3-0.4 cm space between spathe and spadix for *A. nitidum* and 0.7 cm space between spathe and spadix for *A. simplex*) during pistillate anthesis (Figure 4.2B-4.2C, 4.4B-4.4C). Wet yellow stigmas also indicated the start of pistillate anthesis (Figure 4.2F, 4.2H, 4.4F). The pistillate phase of anthesis ended the same morning (0900 h for *A. nitidum*, but later for *A. simplex*, 1200 h), indicated by weakened floral odour (“sweet burned plastic-like smell” for *A. nitidum*), and drier stigmas (brownish stigmas in *A. simplex*) (Figure 4.4D). An intersexual phase lasted 17 hours for *A. simplex* and 20 hours for *A. nitidum*. The release of pollen between 0500 - 0530 h (Day 2) indicated the onset of staminate anthesis. Floral odour was not detected and the spathe tightened to leave either no space or a small space (ca. 0.1 cm space between spathe and spadix) which occasionally exposed the tip of the staminate zone (Figure 4.2D, 4.2E, 4.4E). Anthesis ended by 0600 h (Day 2). The abscission of the staminate zone and spathe occurred one day post anthesis in *A. simplex* (spathe caducous) (Figure 4.3C). In *A. nitidum*, the spathe turned green and the staminate zone of the spadix persisted for ca. a month post anthesis, with often the spathe persisting intact until it was forced to shed by the developing fruits (Figure 4.1B, 4.1C). Fruits of *A. nitidum* and *A. simplex* ripened in ca. three months, turned from white to scarlet in *A. nitidum* (Figure 4.1D) and from yellow to scarlet in *A. simplex* (Figure 4.3B).

Table 4.1: The timing of anthetic stages (sunrise time: 0600-0630 h, sunset time: 1830-1900h), floral odour, restricted access to flower (during pistillate anthesis), duration of fruit maturity and dispersal agent of the investigated taxa. (n = no. of replicates)

Species	Pistillate anthesis	Staminate anthesis	Floral odour	Restriction to flower	Duration of fruit maturity	Dispersal agent
<i>Aglaonema nitidum</i> (n=4)	0400 h – 0900 h (Day 1)	0500 h – 0600 h (Day 2)	Staminate zone (pistillate anthesis)	Yes, 0.3 cm space between spathe and spadix	3 months	Self-dispersed/ bird dispersed
<i>Aglaonema simplex</i> (n=3)	0400 h – 1200 h (Day 1)	0500 h – 0600 h (Day 2)	Staminate zone (pistillate anthesis)	Yes, 0.7 cm space between spathe and spadix	3 months	Self-dispersed/ bird dispersed
<i>Alocasia sarawakensis</i> (n=3)	0400 h – 1000 h (Day 1)	0530 h – 0700 h (Day 2)	Appendix zone (pistillate anthesis)	Yes, 0.3 cm gap at spathe constriction	1.5 – 2 months	Bird dispersed
<i>Amorphophallus hewittii</i> (n=3)	1700 h (Day 1) – 2000 h (Day 4)	2200 h (Day 4) – 1100 h (Day 5)	Appendix zone (pistillate anthesis)	No	3 months	Self-dispersed/ bird dispersed
<i>Amorphophallus julaiihii</i> (n=3)	0700 h (Day 1) – 1900 h (Day 1)	0700 h – 1000 h (Day 2)	Appendix zone (pistillate anthesis)	No	3 months	Self-dispersed/ bird dispersed
<i>Anadendrum</i> sp. (n=3)	0400 h (Day 1) – 1000 h (Day 3)	0530 h – 1000 h (Day 4)	Spadix (pistillate & staminate anthesis)	Yes, 0.15 cm spathe gap	3 months	Self-dispersed/ bird dispersal
<i>Bucephalandra muluensis</i> (n=3)	1300 h – 1600 h (Day 1)	1300 h – 1500 h (Day 2)	Appendix zone (pistillate & staminate anthesis)	Yes, 0.15 cm spathe gap	1 month	Water dispersed
<i>Homalomena ardua</i> (n=3)	0600 h – 0900 h (Day 1)	0600 h – 0700 h (Day 2)	Staminate zone (pistillate & staminate anthesis)	Yes, 0.4 - 0.6 cm gap at spathe constriction	2 months	Self-dispersed

Table 4.1 continued

<i>Homalomena rostrata</i> (n=4)	0550 h – 0900 h (Day 1)	0450 h – 0600 h (Day 2)	Staminate zone (pistillate & staminate anthesis)	Yes, 0.4 - 0.6 cm gap at spathe constriction	2 months	Self-dispersed
<i>Homalomena ovatifolia</i> (n=3)	0600 h – 0900 h (Day 1)	0500 h – 0600 h (Day 2)	Staminate zone (pistillate anthesis)	Yes, 0.2 cm space between spathe and spadix	2 months	Self-dispersed
<i>Homalomena sanguineovaginata</i> (n=3)	0530 h – 0900 h (Day 1)	0545 h – 0700 h (Day 2)	Staminate zone (pistillate & staminate anthesis)	Yes, 0.4 – 0.6 cm gap at spathe constriction	2 months	Self-dispersed
<i>Lasia spinosa</i> (n=10)	1000 h (Day 1) – 0900 h (Day 7/8)	1000 h – 1600 h (Day 7/8)	Spathe (pistillate & staminate anthesis)	Yes, 0.1 – 0.2 cm spathe gap	6 months	Self-dispersed
<i>Pothos insignis</i> (n=5)	0800 h (Day 1) – 1700 h (Day 3)	0700 h (Day 4) – 1700 h (Day 10/11)	Spadix (pistillate & staminate anthesis)	No	2 months	Self dispersed
<i>Pothos scandens</i> (n=3)	0800 h (Day 1) – 1700 h (Day 6/7)	0700 h (Day 7/8) – 1700 h (Day 18)	Spadix (pistillate & staminate anthesis)	No	2 months	Self-dispersed
<i>Schismatoglottis colocasioidea</i> (n=3)	0600 h – 0900 h (Day 1)	0530 h – 0610 h (Day 2)	Appendix zone (pistillate anthesis)	Yes, 0.15cm gap at spathe constriction	1.5 – 2 months	Ant dispersed
<i>Schismatoglottis multinervia</i> (n=3)	0610 h – 1000 h (Day 1)	0530 h – 0730 h (Day 2)	Appendix zone (pistillate anthesis)	Yes, 0.15 cm gap at spathe constriction	1.5 – 2 months	Ant dispersed

Table 4.1 continued

<i>Schismatoglottis muluensis</i> (n=3)	0600 h – 1000 h (Day 1)	0600 h – 0700 h (Day 2)	Appendix zone (pistillate anthesis)	Yes, 0.15 cm gap at spathe constiction	1.5 – 2 months	Ant dispersed
<i>Schismatoglottis pellucida</i> (n=3)	0930 h – 1230 h (Day 1)	0920 h – 1100 h (Day 2)	Appendix zone (pistillate & staminate anthesis)	Yes, 0.15 cm gap at spathe constriction	1.5 – 2 months	Ant dispersed
<i>Schismatoglottis roseopedes</i> (n=3)	0430 h – 0830 h (Day 1)	0500 h – 0600 h (Day 2)	Appendix zone (pistillate anthesis)	Yes, 0.15 cm gap at spathe constriction	1.5 – 2 months	Ant dispersed
<i>Schismatoglottis serratodentata</i> (n=4)	0530 h – 0900 h (Day 1)	0500 h – 0630 h (Day 2)	Appendix zone (pistillate anthesis)	Yes, 0.15 cm gap at spathe constriction	1.5 – 2 months	Ants dispersed
<i>Scindapsus longistipitatus</i> (n=3)	0400 h – 1700 h (Day 1)	0400 h – 1000 h (Day 2)	Spadix (pistillate anthesis)	Yes, 0.2 – 0.5 cm spathe gap	3 months	Self-dispersed

4.1.3 Floral traits

Floral odour was detected once in the morning during pistillate anthesis in *Aglaonema*. No odour was detected during staminate anthesis. Floral odour during pistillate anthesis was like a “sweet citrus burned plastic alcohol smell” in *Aglaonema nitidum* and “sweet citrus alcohol smell” in *A. simplex*. The floral odour was detected to originate from the staminate zone.

4.1.4 Floral rewards

Floral liquid was present on pistillate flowers and sterile interstices during pistillate anthesis in *Aglaonema*. *Aglaonema* has a ca. 0.3 – 0.7 cm space between spathe and spadix that allowed small *Colocasiomyia* flies (Drosophilidae) to enter the floral chamber.

Colocasiomyia flies (Drosophilidae) mated at staminate zone and inner surface of spathe in *Aglaonema*.

4.1.5 Pollinators and their behaviours

Colocasiomyia flies (Drosophilidae) were main pollinators of *Aglaonema*, the flies started to arrive around 0610 h (Day 1) during pistillate anthesis in *A. nitidum*, more flies arrived between 0630 - 0650 h and less flies arrived after 0700 h, the flies stayed a night in the inflorescence and started to leave after 0600 h the next day. In *A. simplex*, the flies (Drosophilidae) arrived around 0630 h (Day 1) during pistillate anthesis and left after 0620 h the next day. The flies (Drosophilidae) directly moved to pistillate zone upon arrival for both species, the flies fed on secretion by the sterile interstices and pistillate flowers (Figure 4.2F, 4.4F) and faced inner surface of the spathe after the end of pistillate anthesis. The flies stayed a night in the inflorescence, left the inflorescence the next morning after collecting pollen and before the spathe close back (Figure 4.2E, 4.2G, 4.4E, 4.4H). The number of *Colocasiomyia* flies (Drosophilidae) that visited an inflorescence of *Aglaonema* during anthesis ranged from five to 55 individuals in *A. nitidum* and from five to 10 individuals in *A. simplex* (Table 4.2).

Besides, there were unknown flies (Diptera) that arrived early in *Aglaonema simplex*, ranged from 10 to 30 individuals, the flies stayed at the inflorescence from 0620 - 0800 h (Day 1) and were most active (numerous flies chased between each other to mate) between 0630 - 0640 h (Figure 4.4B, 4.4G). Another unknown flies (Diptera) (ranged from 1 – 5 individuals) visited inflorescence of *A. nitidum* between 0630 - 0830 h (Day 1) (Figure 4.2C, 4.2H). The unknown flies were just visitors because they mostly moved on the staminate

zone (chased between each other to mate at staminate zone), and were seldom in contact with the pistillate flowers and were never observed during the staminate anthesis.

Apart from the flies, *Cycreon* beetles were possible pollinators in *A. simplex* but that usually happened when there were less flowering events of *Schismatoglottis* (ranged from one to seven individuals), the beetles arrived before 0700 h (Day 1, pistillate anthesis), stayed on the pistillate zone (Figure 4.4I) throughout anthesis and moved up to staminate zone to collect pollen before leaving the inflorescence on Day 2 (Figure 4.4E).

Table 4.2: Mean±SE, range and percentage of occurrence of insect families captured for each species during anthesis. (n=no. of replicates)

Species	Diptera	Coleoptera	Hemiptera	Hymenoptera	Thysanoptera
<i>Aglaonema nitidum</i> (n=17)	Drosophilidae (<i>Colocasiomyia</i> sp.) 28 ± 4.1 4 – 55 (100%) Unknown flies (1) 2.7 ± 0.7 1 – 5 (23.5%)				
<i>Aglaonema simplex</i> (n=7)	Drosophilidae (<i>Colocasiomyia</i> sp.) 7.4 ± 0.6 5 – 10 (100%) Unknown flies (2) 20 ± 5.8 10 – 30 (42.9%)	Hydrophilidae (<i>Cycreon</i> sp.) 4 ± 3 1 – 7 (28.6%)			
<i>Alocasia sarawakensis</i> (n=24)	Drosophilidae (<i>Colocasiomyia</i> sp.) 34.4 ± 4.1 8 – 90 (100%) Unknown flies (3) 2.7 ± 0.7 2 – 5 (16.7%)			Apidae (<i>Tetragonula</i> sp.) 3.3 ± 0.9 2-5 (12.5%)	

Table 4.2 continued

<i>Amorphophallus hewittii</i> (n=11)	Drosophilidae (1) 11.8 ± 3.7 5 – 25 (45.5%) Calliphoridae 3.7 ± 0.3 3 – 4 (27.3%)	Hybosoridae 7.7 ± 2.2 1 – 21 (100%) Staphylinidae (1) 2.7 ± 0.6 1 – 5 (63.6%)		Apidae (<i>Tetragonula</i> sp.) 8.2 ± 3.6 3 – 14 (45.5%)	
<i>Amorphophallus julaiihii</i> (n=4)		Staphylinidae (2) 42.5 ± 8.5 20 – 60 (100%)			
<i>Anadendrum</i> sp. (n=21)		Staphylinidae (3) 1.7 ± 0.4 1 – 4 (33.3%)			Thripidae 12.6 ± 1.6 2 – 30 (100%)
<i>Bucephalandra muluensis</i> (n=14)	Drosophilidae (<i>Colocasiomyia</i> sp.) 7.3 ± 0.9 2 – 15 (100%)				
<i>Homalomena ardua</i> (n=18)	Drosophilidae (<i>Colocasiomyia</i> sp.) 5.6 ± 0.9 1 – 15 (100%)	Chrysomelidae (<i>Chaloenus</i> sp.) 5.7 ± 1.2 1 – 12 (66.7%) Scarabaeidae (<i>Parastasia</i> sp.) 1.3 ± 0.3 1 – 2 (16.7%)			
<i>Homalomena ovatifolia</i> (n=9)	Drosophilidae (<i>Colocasiomyia</i> sp.) 3 ± 0.6 1 – 6 (100%)	Chrysomelidae (<i>Chaloenus</i> sp.) 1.4 ± 0.2 1 – 2 (55.5%)			
<i>Homalomena rostrata</i> (n=20)	Drosophilidae (<i>Colocasiomyia</i> sp.) 19.3 ± 3.3 5 – 57 (100%)	Chrysomelidae (<i>Chaloenus</i> sp.) 1.6 ± 0.6 1 – 4 (25%) Scarabaeidae (<i>Parastasia</i> sp.) 3.2 ± 0.7 1 – 7 (50%)			

Table 4.2 continued

<i>Homalomena sanguineovaginata</i> (n=9)	Drosophilidae (<i>Colocasiomyia</i> sp.) 42.8 ± 9.5 18 – 91 (100%)	Chrysomelidae (<i>Chaloenus</i> sp.) 2 ± 0.7 1 - 4 (44.4%) Scarabaeidae (<i>Parastasia</i> sp.) 2 ± 1 1-3 (22.2%)			
<i>Lasia spinosa</i> (n=19)		Nitidulidae 4.6 ± 1.1 1 – 15 (73.7%) Staphylinidae (4) 4.9 ± 1.4 1 – 23 (100%) Scolytinae 1.8 ± 0.3 1 – 3 (47.4%) Silvanidae 3.1 ± 0.8 1 – 6 (36.8%)	Miridae 2.2 ± 1.2 1 – 6 (42.1%)		
<i>Pothos insignis</i> (n=12)	Drosophilidae (2) 5.9 ± 1.3 1 – 15 (100%) Syrphidae 1.5 ± 0.3 1 – 2 (33.3%)	Chrysomelidae (<i>Chabria</i> sp.) 1.6 ± 0.2 1 – 2 (66.7%)	Miridae (<i>Halticotoma</i> sp.) 1.7 ± 0.3 1 – 2 (25%)		
<i>Pothos scandens</i> (n=3)	Drosophilidae (3) 1.3 ± 0.3 1 – 2 (100%)				
<i>Schismatoglottis colocasioidea</i> (n=7)	Drosophilidae (<i>Colocasiomyia</i> sp.) 5.7 ± 2.5 1 – 20 (100%)	Hydrophilidae (<i>Cycreon</i> sp.) 15.7 ± 2.8 5 – 28 (100%) Chrysomelidae (<i>Chaloenus</i> sp.) 1.5 ± 0.5 1 – 2 (28.6%)			

Table 4.2 continued

<i>Schismatoglottis multinervia</i> (n=8)	Drosophilidae (<i>Colocasiomyia</i> sp.) 7.5 ± 2.6 2 - 25 (100%)	Hydrophilidae (<i>Cycreon</i> sp.) 6.7 ± 3.2 1 – 25 (87.5%) Chrysomelidae (<i>Chaloenus</i> sp.) 2.2 ± 0.6 1 – 4 (62.5%)			
<i>Schismatoglottis muluensis</i> (n=4)	Drosophilidae (<i>Colocasiomyia</i> sp.) 85 ± 20.7 43 – 141 (100%)	Hydrophilidae (<i>Cycreon</i> sp.) 36.2 ± 3.8 25 – 41 (100%) Staphylinidae (5) 4.2 ± 1.3 2 – 8 (100%) Chrysomelidae (<i>Chaloenus</i> sp.) 5 ± 1.5 2-7 (75%) Scarabaeidae (<i>Parastasia</i> sp.) 1.5 ± 0.5 1 – 2 (50%)			
<i>Schismatoglottis pellucida</i> (n=5)	Drosophilidae (<i>Colocasiomyia</i> sp.) 39.2 ± 21.4 8 – 124 (100%)	Hydrophilidae (<i>Cycreon</i> sp.) 5.5 ± 0.5 5 – 6 (40%) Chrysomelidae (<i>Chaloenus</i> sp.) 3 ± 1.1 1 – 6 (80%)			
<i>Schismatoglottis roseopedes</i> (n=6)	Drosophilidae (<i>Colocasiomyia</i> sp.) 33.2 ± 15.4 4 – 107 (100%)	Hydrophilidae (<i>Cycreon</i> sp.) 10.5 ± 4.5 3 – 25 (100%) Chrysomelidae (<i>Chaloenus</i> sp.) 3.2 ± 1.3 1 – 8 (83.3%)			

Table 4.2 continued

<i>Schismatoglottis serratodentata</i> (n=11)	Drosophilidae (<i>Colocasiomyia</i> sp.) 32.7 ± 6.8 12 – 90 (100%)	Hydrophilidae (<i>Cycreon</i> sp.) 5.5 ± 1.2 1-13 (90.9%) Staphylinidae (6) 2.5 ± 0.5 2 – 3 (18.2%) Chrysomelidae (<i>Chaloenus</i> sp.) 4.3 ± 0.6 2 – 8 (81.8%)			
<i>Scindapsus longistipitatus</i> (n=6)	Drosophilidae (4) 375 ± 38.2 250 – 500 (100%)		Miridae (<i>Halticotoma</i> sp.) 35 ± 3.5 25 – 45 (83.3%)		

4.1.6 Reproductive system

Fruits of *Aglaonema* spp. ripened in three months. The average natural fruit set percentage for *A. nitidum* was 22.8% (range 10% - 30.3%) and 53.4% (range 40% - 76.9%) for *A. simplex* (Table 4.3). Autonomous self-pollination treatment did not set any fruit in both *A. nitidum* and *A. simplex*, which means they are not capable to self-pollinate without pollinator. Each fruit of *A. nitidum* and *A. simplex* had one seed only.

Table 4.3: Mean±SE of the number of pistillate flowers per inflorescences and fruits per infructescence, and fruit set percentage of the aroid species treated with open pollination treatment. (n=no. of replicates)

Species	Fruits per infructescence	Pistillate flowers per inflorescence	Fruit set (%)
<i>Aglaonema nitidum</i> (n=7)	7.1 ± 0.9	31.3 ± 0.4	22.8
<i>Aglaonema simplex</i> (n=5)	6.2 ± 1.2	11.6 ± 0.5	53.4
<i>Alocasia sarawakensis</i> (n=3)	133.7 ± 31.6	166.3 ± 39.7	80.4

Table 4.3 continued

<i>Amorphophallus hewittii</i> (n=3)	197 ± 34.7	267.3 ± 32.8	73.7
<i>Amorphophallus julaiihii</i> (n=3)	41.3 ± 7.8	62 ± 2.5	66.6
<i>Anadendrum</i> sp.(n=9)	8.2 ± 1.5	44.2 ± 1.3	18.6
<i>Bucephalandra muluensis</i> (n=3)	14 ± 1	14 ± 1	100.00
<i>Homalomena rostrata</i> (n=6)	85.2 ± 1.47	95 ± 2.6	89.6
<i>Lasia spinosa</i> (n=3)	105 ± 2.6	150.3 ± 0.9	69.8
<i>Pothos insignis</i> (n=15)	28.6 ± 7.6	241.3 ± 15.2	11.8
<i>Schismatoglottis colocasioidea</i> (n=3)	312.3 ± 1.4	321 ± 1.5	97.3
<i>Schismatoglottis muluensis</i> (n=3)	948.3 ± 70.9	967 ± 80.4	98.1
<i>Schismatoglottis roseopedes</i> (n=3)	305 ± 11.0	349 ± 13.4	87.4
<i>Schismatoglottis serratodentata</i> (n=8)	137.4 ± 19.5	204 ± 10.4	67.3

4.2 *Alocasia*

4.2.1 Flowering pattern

Alocasia sarawakensis can have up to 30 inflorescences per plant, the interval between two successive flowering events was usually one day, as new inflorescence started anthesis one day after previous inflorescence ended anthesis (Figure 4.5 and Figure 4.6). In a single population, different plants flowered at different days, each day have at least one inflorescence in pistillate anthesis if there were three flowering plants. *Alocasia sarawakensis* flowered every three months, a single plant usually flowered twice a year, each plant can flower up to three months each time if there are 30 inflorescences per plant. Sometimes there were ripened infructescences while there were new inflorescences emerging from the same plant if the plant produced more than 20 inflorescences, the ripened

fruits usually lasted a few days before senesced. Within the period of field work, flowering of *A. sarawakensis* occurred from February 2018 to April 2018 and August 2018 to October 2018.



Figure 4.5: *Alocasia sarawakensis* (A) Multiple inflorescences and infructescences per plant. (B) Dead stingless bees trapped at pistillate zone. (C) Weaver ant (*Oecophylla* sp.) preying on a *Colocasiomyia* fly. (D-E) Bulbuls (D) and Sunbird (E) consuming ripened fruits.

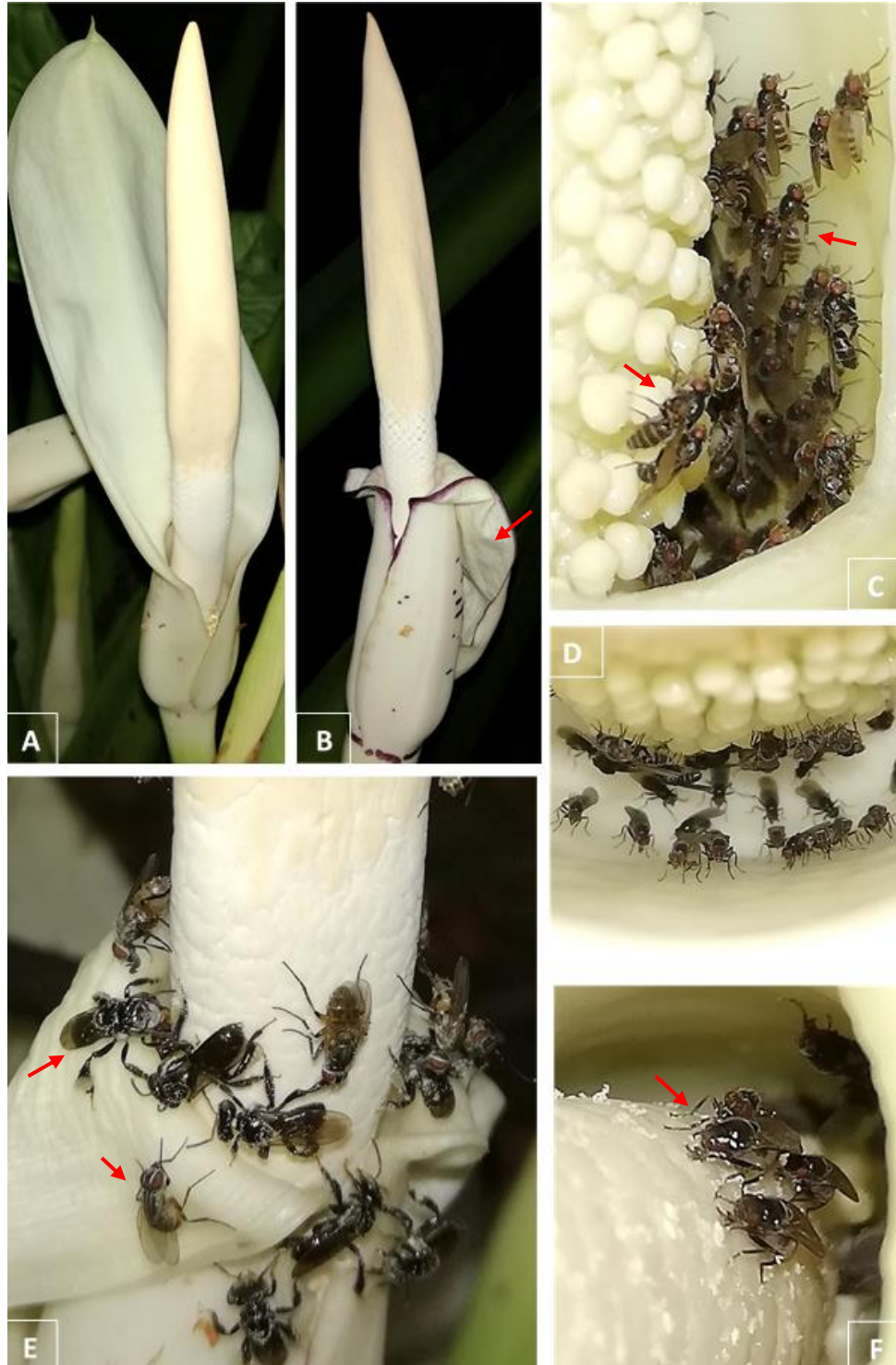


Figure 4.6: Inflorescence of *Alocasia sarawakensis* at various stages. (A) Pistillate anthesis. (B) Pre staminate anthesis, spathe curve backward. (C) Flies (*Drosophilidae*) move and mate on pistillate flowers and lower inner side of the spathe. (D) Flies at pistillate zone (Top view). (E) Stingless bees and unknown flies collecting pollen on the staminate zone. (F) Flies (*Drosophilidae*) collecting pollen on the staminate zone (Top view).

4.2.2 Timing of anthesis and floral changes

In *A. sarawakensis*, anthesis lasted between 26–27 hours. The upper spathe opened and reflexed early morning before pistillate anthesis, leaving a small gap (ca. 0.3 cm) between the constriction of the spathe and the sterile spadix interstice (Figure 4.6A). The pistillate phase of anthesis started between 0400–0430 h (Day 1) with the release of floral odour (“ginseng peanut mint-like smell”) from the appendix (strongest around 0600 h, extend 2 - 3 cm) (Table 4.1). The lower spathe inflated to create a floral chamber with 0.4 - 0.5 cm space between the spathe and the pistillate zone. The intersexual phase started from 1000 h (Day 1) and lasted for 20 - 21 hours, indicated by a weakened floral odour (“preserved bean curd-like smell”). The staminate phase of anthesis began the following day when pollen started to be released between 0530 - 0600 h (Day 2), with tightened gap between the spathe constriction and sterile interstice (ca. 0.1 cm) (Figure 4.6B), and an absence of floral odour. Anthesis ended by 0630 - 0700 h (Day 2) when almost all the pollen was collected. The upper spathe and the staminate zone senesced respectively in one day and three days post-anthesis in *A. sarawakensis*. The fruits of *A. sarawakensis* ripen in one and a half to two months and were revealed by the splitting of lower spathe from the tip (Figure 4.5A). The fruits of *A. sarawakensis* were dispersed by bulbuls and sunbirds (Figure 4.5D – 4.5E).

4.2.3 Floral traits

Floral odour was detected once in the morning during pistillate anthesis in *Alocasia*. Floral odour during pistillate anthesis was like a “ginseng peanut mint smell” in *A. sarawakensis*. The floral odour was detected to originate from the appendix.

4.2.4 Floral rewards

A stigmatic liquid was secreted during the pistillate anthesis in *Alocasia sarawakensis*. There was a 0.3 cm gap between constriction of the spathe and the sterile spadix interstices or the staminate zone, or a space of 0.4 to 0.5 cm between the inner spathe wall and pistillate zone that allowed small *Colocasiomyia* flies (Drosophilidae) to go down into the pistillate zone. *Colocasiomyia* flies (Drosophilidae) mated onto the pistillate zone and the inner surface of the spathe in *Alocasia*.

4.2.5 Pollinators and their behaviours

Colocasiomyia flies (Drosophilidae) were the main pollinators of *A. sarawakensis*, the flies arrived around 0630 h (Day 1) during the pistillate anthesis, more flies arrived later between 0700 - 0730 h. The flies moved down to the pistillate zone upon arrival, the flies moved around the spadix, consuming secretions from pistillate flowers and some of the flies mated there (Figure 4.6C – 4.6D). The flies stayed a night in the inflorescences in the pistillate zone, mostly onto the inner surface of the lower spathe and only moved up to staminate zone to collect pollen the next morning around 0615 - 0625 h (Day 2, staminate anthesis) (Figure 4.6F). The flies started to leave the inflorescence after 0640 h and mostly all had left at 0700 h. The individual flies sometimes may be hunted down by weaver ants (*Oecophylla* sp.) that waited outside the inflorescence (Figure 4.5C). There were eight to 90 flies (Drosophilidae) visiting an inflorescence of *A. sarawakensis* during anthesis (Table 4.2).

Before the arrival of the flies (Drosophilidae), stingless bees (*Tetragonula*, Apidae) and unknown flies (Diptera) arrived around 0615 h (Day 1) (Figure 4.6E), both insects seldom reached the pistillate flowers beneath the spathe constriction (both insects are too big

to bypass the 0.2 - 0.3 cm gap between the constriction of the spathe and the staminate zone). In some slightly bigger inflorescences, both insects were able to reach the pistillate zone and may pollinate the pistillate flowers opportunistically. However, both stingless bees or the unknown flies were found dead in some post-staminate anthesis inflorescences (the gap between the constriction of the spathe and staminate zone was closed) (Figure 4.5B). The number of stingless bees and unknown flies that visited the inflorescences of *A. sarawakensis* ranged from two to five individuals.

4.2.6 Reproductive system

Fruits of *A. sarawakensis* took 1.5 to two months to ripe. The average natural fruit set percentage of *A. sarawakensis* was 80.4% (Table 4.3), ranging from 76.3 % to 85.3 %. Autonomous self-pollination treatment did not set any fruit in *A. sarawakensis*, which means the species is not capable to self-pollinate without pollinator. Each fruit of *A. sarawakensis* possessed one to three seeds. Within an infructescence of *A. sarawakensis*, 58% of the fruits were one seeded, 39% two seeded and 3% three seeded.

4.3 *Amorphophallus*

4.3.1 Flowering pattern

Amorphophallus produced a single inflorescence per plant, each plant may only flower once every one to two or more years depending on the age of the plant, large plants were observed to have a longer period of vegetative phase to produce larger inflorescences. Inflorescence of *Amorphophallus* is usually randomly distributed, solitary although sometimes there are several vegetative forms growing near to each other. *Amorphophallus hewittii* usually flowered twice a year, each time ca. a month, estimated at least 30

inflorescences are flowering each time if there is a staminate anthesis per day (Figure 4.7, Figure 4.8 and Figure 4.9). *Amorphophallus julaiihii* usually flowered every two to three months, four to five times each year, each time ca. two weeks, and estimated at least 14 inflorescences are flowering each time if there is a staminate anthesis per day (Figure 4.10 and Figure 4.11). During the period of field work, flowering of *A. hewittii* occurred from April 2018 to May 2018 and September 2018 to October 2018. For *A. julaiihii*, flowering occurred during January 2018, March 2018, June 2018, September 2018, November 2018 and January 2019.



Figure 4.7: *Amorphophallus hewittii* (A) Vegetative form, distinguished by pattern of soldier camouflage cloth on the petiole. (B) Floral zone (top staminate, bottom pistillate). (C) String form pollen released. (D) Ripened fruits, white colour before ripe.

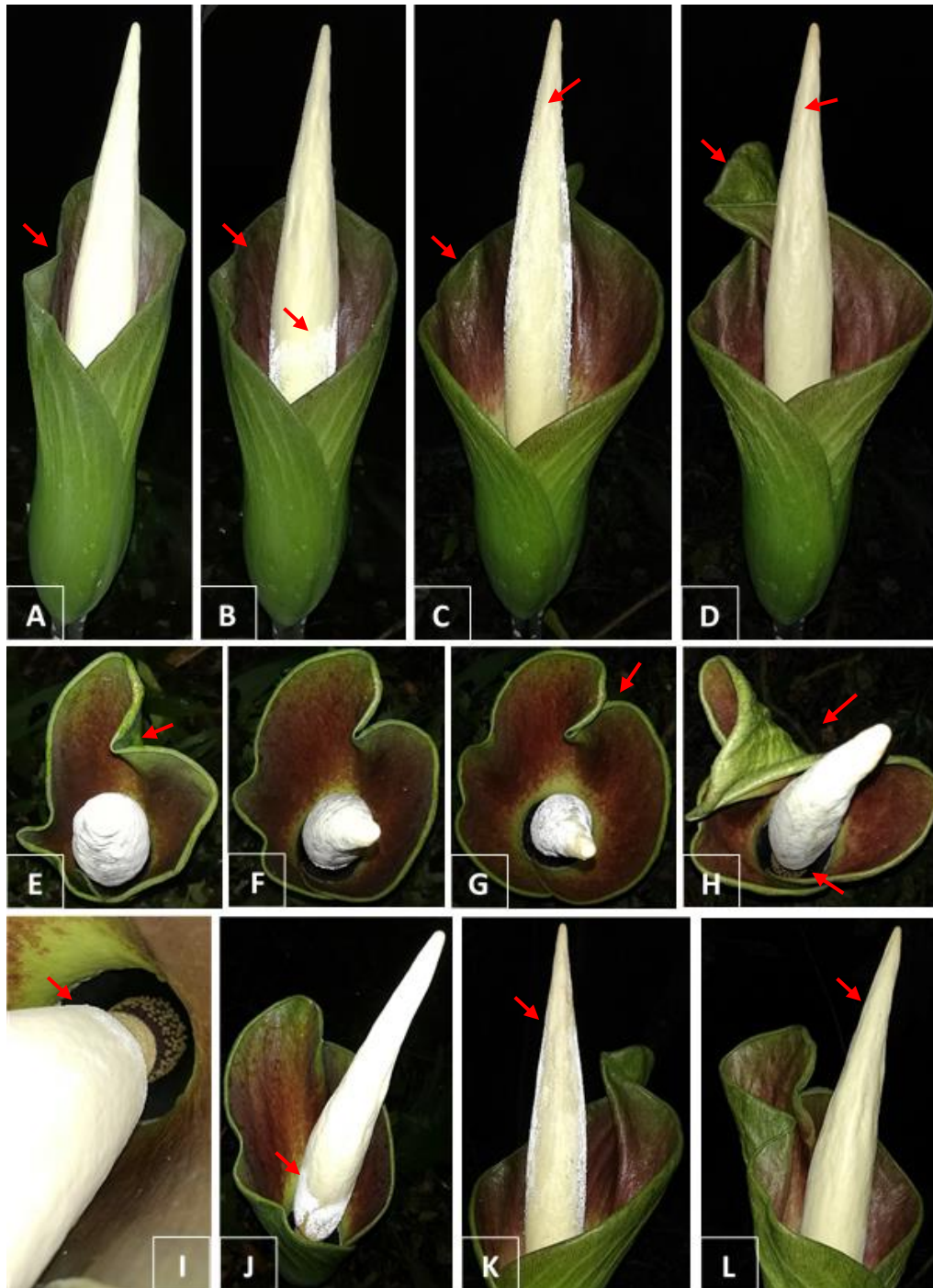


Figure 4.8: Inflorescence of *Amorphophallus hewittii* at various stages. (A-D) Changes of inflorescence throughout anthesis (front view), (A-C) spathe expanding (pistillate anthesis), (D) spathe collapsing (Staminate anthesis). (E-H) Changes of inflorescence throughout anthesis (top view), (E-G) Spathe expanding (pistillate anthesis), (H) Spathe collapsing. (I-L) Zoom view of spadix throughout anthesis, (I-K) Liquid condensed from appendix, started from bottom to tip, floral odour more intense as more liquid condensed (Pistillate anthesis). (L) Appendix dried, smell weakened (Staminate anthesis).



Figure 4.9: Insects on different parts of *Amorphophallus hewittii*'s inflorescences. (A) Stingless bees in the pistillate zone. (B) Stingless bees on staminate zone. (C) Stingless bees. (D) Scavenger scarab beetle (Hybosoridae) (E-F) Scavenger scarab beetle on pistillate flowers. (G) Scavenger scarab beetles mating onto pistillate zone. (H) Fruit flies on pistillate flowers. (I) Green bottle flies (Calliphoridae). (J) Rove beetle (Staphylinidae) moving between pistillate flowers. (K) Unknown rove beetles on wet spadix.



Figure 4.10: *Amorphophallus julaiihii* (A) Whole plants. (B) Immature infructescences. (C) Ripened infructescence.



Figure 4.11: Inflorescence of *Amorphophallus julaiihii* at different stages. (A) Pistillate phase (left). (B) Staminate phase (left). (C-D) Rove beetles (Staphylinidae) at pistillate zone, some move on pistillate flowers. (E-F) Rove beetles collecting pollen on stamens.

4.3.2 Timing of anthesis and floral changes

Anthesis of *A. hewittii* lasted ca. 90 hours. The spathe started to open gradually from side with the inner spathe turning red in the morning before pistillate anthesis (Figure 4.8A). The pistillate phase of anthesis started at 1700 h (Day 1) with visible production of liquid acroscopically along the entire appendix and the release of a “salted fish-like” floral odour (extend 1 - 3 cm away from the appendix) (Figure 4.8I) (Table 4.1). The floral odour was associated with the appendix liquid, the floral odour became stronger as more appendix liquid was produced. Spathe gap was ca. 3 - 6 cm and the space between the spathe and staminate zone was ca. 1 cm on Day 1 (Figure 4.8E). On Day 2, the liquid from the appendix reached ca. one third of the appendix from its bottom (Figure 4.8B, 4.8J), the floral odour also intensified (“salted fish dry prawn-like smell”, extend 4 - 5 cm away from the appendix, detectable at 1 - 2 m), and the spathe opened wider from side and back (ca. 3 - 7 cm gap, ca. 2.5 cm space between the spathe and the staminate zone) (Figure 4.8F). On Day 3, the spathe was fully opened (ca. 4 - 13 cm gap, ca. 3.5 cm space between the spathe and the staminate zone) (Figure 4.8G), the floral scent reached its peak of release (“ammonia-like smell”, extend 4 - 5 cm away from the appendix, detectable as far as 5 m away), and the liquid from the appendix reached two third of the appendix length in the morning and totally in the afternoon (Figure 4.8C, 4.8K). In the night from Day 3 to Day 4, the spathe started to fold in from the back (left ca. 6 cm gap at side, ca. 2 - 3 cm space between the spathe and the staminate zone). On Day 4, the liquid secretion on the appendix dried up gradually, the floral odour also weakened gradually and the spathe fold in from the front (Figure 4.8H). The pistillate anthesis ended by 2000 h (Day 4) with the appendix completely dried and the floral odour ceased (Figure 4.8D, 4.8L). The staminate anthesis started two hours later (2200 h,

Day 4) with the release of pollen (Figure 4.7C) and the anthesis ended by 1100 h the next day (Day 5) when most of the pollen was taken away by the insects.

Anthesis of *A. julaiihii* was much shorter, 28 hours. The pistillate anthesis started after dawn around 0700 h (Day 1), lasted for 12 hours, and ended at around 1900 h (Table 4.1). The floral odour of “raw peanut soil-like smell” was detected from the appendix and only lasted till the end of pistillate anthesis. The intersexual phase lasted ca. 12 hours. The staminate anthesis started at 0700 h (Day 2) and the anthesis ended by 1000 h (Day 2). The spathe was fully open during the pistillate anthesis, and shrunk back during the staminate anthesis (Figure 4.11A – 4.11B).

The spathe of *Amorphophallus* gradually withered or dried together with the appendix and fell off before fruit development is advanced, thus fruit development occurs almost entirely exposed (Figure 4.10B). The spathe and appendix of *A. hewittii* withered within a week post-anthesis, while three days post-anthesis for *A. julaiihii*. Fruits of both *Amorphophallus* species were ready for dispersal after three months, are orange colour when ripened (mostly self-dispersed but possibly birds as dispersal agents) (Figure 4.7D, Figure 4.10C).

4.3.3 Floral traits

The floral odour was detected once during the pistillate anthesis in *Amorphophallus*, the floral odour persisted throughout the pistillate anthesis. The floral odour was like a “salted fish–ammonia smell” in *A. hewittii* and “raw peanut soil smell” in *A. julaiihii*. The floral odour originated from the appendix for both species.

4.3.4 Floral rewards

A floral liquid was present on the appendix surface during the pistillate anthesis in *A. hewittii*. The condensed floral liquid on the appendix attracted and rewarded various insect visitors (Staphylinidae, Apidae, Hybosoridae, Drosophilidae, Calliphoridae), there was no restriction for the insects to enter the floral chamber. Floral liquid was not detected in *A. julaiihii*. Rove beetles (Staphylinidae) mated on the pistillate zone in both species and scavenger scarab beetles (Hybosoridae) mated on the pistillate zone of *A. hewittii*.

4.3.5 Pollinators and their behaviours

Stingless bees (Tetragonula, Apidae) (Figure 4.9C) were the main pollinators of *Amorphophallus hewittii*, there were three to 14 individuals of stingless bees per inflorescence of *A. hewittii* during anthesis (Table 4.2). Stingless bees visited the inflorescence from Day 2 - 5. The bees usually arrived in the morning (after 0700 h) till noon, flew down to the pistillate zone and moved on the pistillate flowers (Figure 4.9A), probably achieving pollination. Although the bees can fly, they sometimes also struggled to fly out of the pistillate zone. During the staminate anthesis, the bees collected and brushed off pollen for the other insects at pistillate zone (Figure 4.9B). The bees were observed to visit nearby pistillate anthesis inflorescences after collecting pollen from staminate anthesis inflorescences. The inflorescences visited by the stingless bees successfully set fruits after three months.

Rove beetles (Staphylinidae) pollinated both *A. hewittii* and *A. julaiihii* (sole pollinator for the species), the number of rove beetles that visited the inflorescences of *Amorphophallus* ranged from one to five individuals in *A. hewittii* and 20 to 60 individuals

in *A. julaiihii* (Table 4.2). Rove beetles arrived around 1830 - 1930 h (Day 3 - 4, pistillate anthesis) in *A. hewittii*, they were active in the pistillate zone, usually moving between or on the pistillate flowers (Figure 4.9J). The beetles became less active during daytime and left the inflorescence on Day 5 (1820 - 1930 h). In *A. julaiihii*, rove beetles (Staphylinidae) arrived around 0730 - 0830 h (Day 1, pistillate anthesis), the beetles were active throughout anthesis at bottom of the pistillate zone and frequently moved on the pistillate flowers (Figure 4.11C – 4.11D). The beetles left around 0730 - 0830 h (Day 2, staminate anthesis), the beetles tried many times to climb up to staminate zone to collect pollen and leave, thus brush off pollen for the others that still try to climb up (Figure 4.11E – 4.11F). Besides, there were unidentified rove beetles that visited *A. hewittii* from Day 2 - 4, the beetles were actively moving around the wet appendix (Figure 4.9K). These beetles never went down into the pistillate zone during the pistillate anthesis and were not present during the staminate anthesis.

Besides, *A. hewittii* was also pollinated by scavenger scarab beetles (Hybosoridae) (Figure 4.9D, 4.9F), the number of scavenger scarab beetles that visited the inflorescences ranged from one to 21 individuals. The scavenger scarab beetles arrived from 1830 h onwards (Day 3 - 4, pistillate anthesis). The beetles landed on the appendix or the spathe and within a few seconds fell down into the bottom of the spathe. The beetles appeared to be very active and were vigorously crawling around the pistillate flowers (Figure 4.9E, 4.9G) and sometimes mating inside the floral chamber at night, the beetles became less active during daytime. On all the observed inflorescences the beetles became trapped inside the floral chamber by a combination of the slippery surface texture inside the spathe (wetness caused by appendix condensation), the beetles remained within the inflorescences throughout the anthesis. The beetles began to leave the inflorescence from 1830 h onwards

(Day 5, after staminate anthesis) and most escaped by crawling up the spadix past the staminate flowers and up onto the sterile appendage, from which they would fly away.

Green bottle flies (Calliphoridae) were frequent visitors of *A. hewittii*, the number of flies ranged from three to four individuals, the flies usually visit the inflorescence throughout daytime from Day 1 - 4 (pistillate anthesis) (Figure 4.9I). The flies were attracted by the strong salted fish-ammonia floral scent, usually flew around the wet appendix and landed on the spathe margin, the flies sometimes moved down into the pistillate zone. The flies did not visit the inflorescence during the staminate anthesis when floral scent weakened, thus were not pollinator.

Inflorescences of *Amorphophallus hewittii* were also visited by fruit flies (Drosophilidae). There were five to 25 flies visiting the species during anthesis, the flies usually arrived at midday on Day 2 - 4, the flies were mostly active on the spathe and sometimes went down into pistillate zone (Figure 4.9H), the flies were not seen on Day 5 after staminate anthesis.

4.3.6 Reproductive system

Fruits of *Amorphophallus* spp. ripened in three months. The natural fruit set percentage of *A. hewittii* ranged between 63.6% to 82.8% with an average of 73.7%, and ranged between 47.5% to 82.1% with an average of 66.6% for *A. julaiihii* (Table 4.3). Autonomous self-pollination treatment was not tested on *Amorphophallus* spp. due to lack of available inflorescences. Each fruit of *A. julaiihii* had a single seed while *A. hewittii* had one to two seeds.

4.4 *Anadendrum*

4.4.1 Flowering pattern

Anadendrum sp. produced three to seven inflorescences per plant, the interval between flowering was usually nine days, which means each plant may took one to three months to complete flowering (Figure 4.12 and Figure 4.13). Within a flowering season, at least 13 plants were estimated to flower if there is an inflorescence in staminate anthesis each day. Different plants flowered at different time, each plant usually rested for a season of ca. four to five months before the next flowering and each plant can flowered twice a year. Some plants flowered during the current season would rest during the next season and those that rested during current season would flower during the next season. Within the period of field work, flowering of *Anadendrum* sp. occurred from December 2017 to January 2018, March 2018 to May 2018, June 2018 to August 2018, September 2018 to November 2018, December 2018 to January 2019.

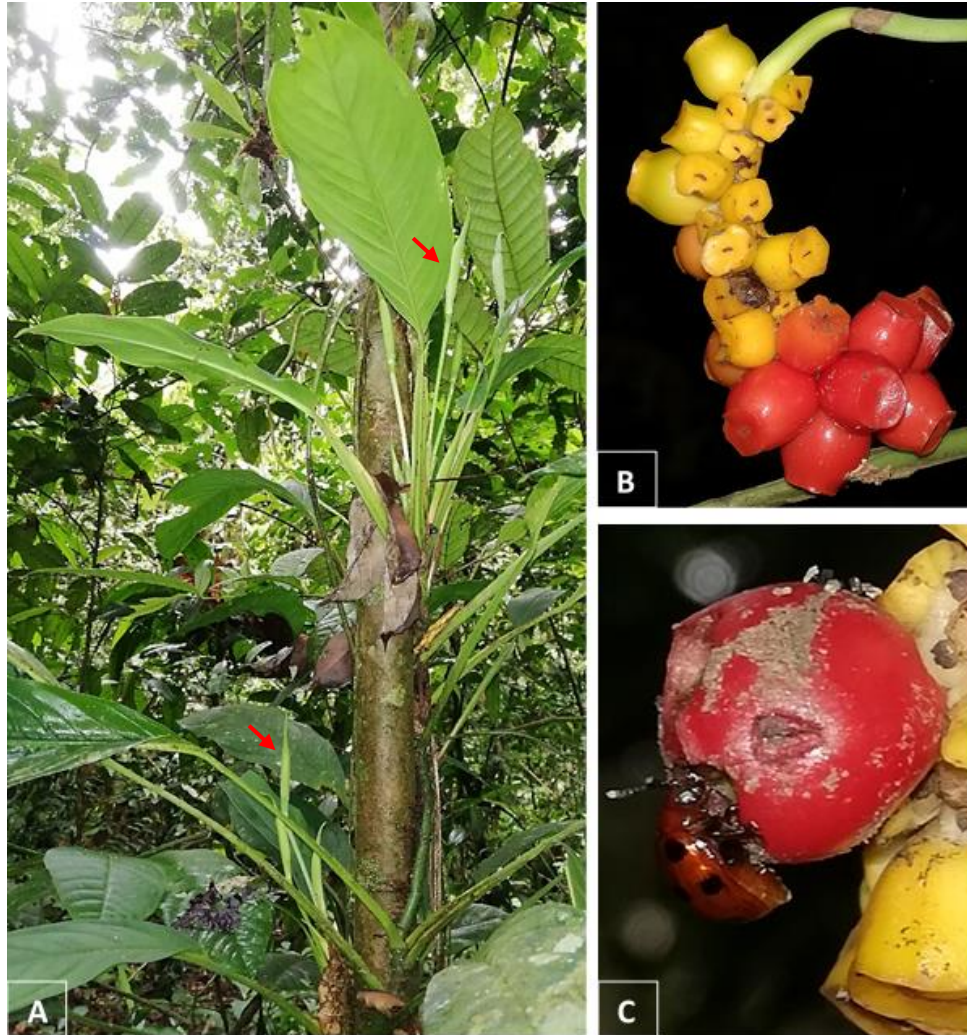


Figure 4.12: *Anadendrum* sp. nov. (A) Mature plant with inflorescences. (B) Infructescence with fruits ripening from tip. (C) *Chabria* beetles chewing on ripened fruits.

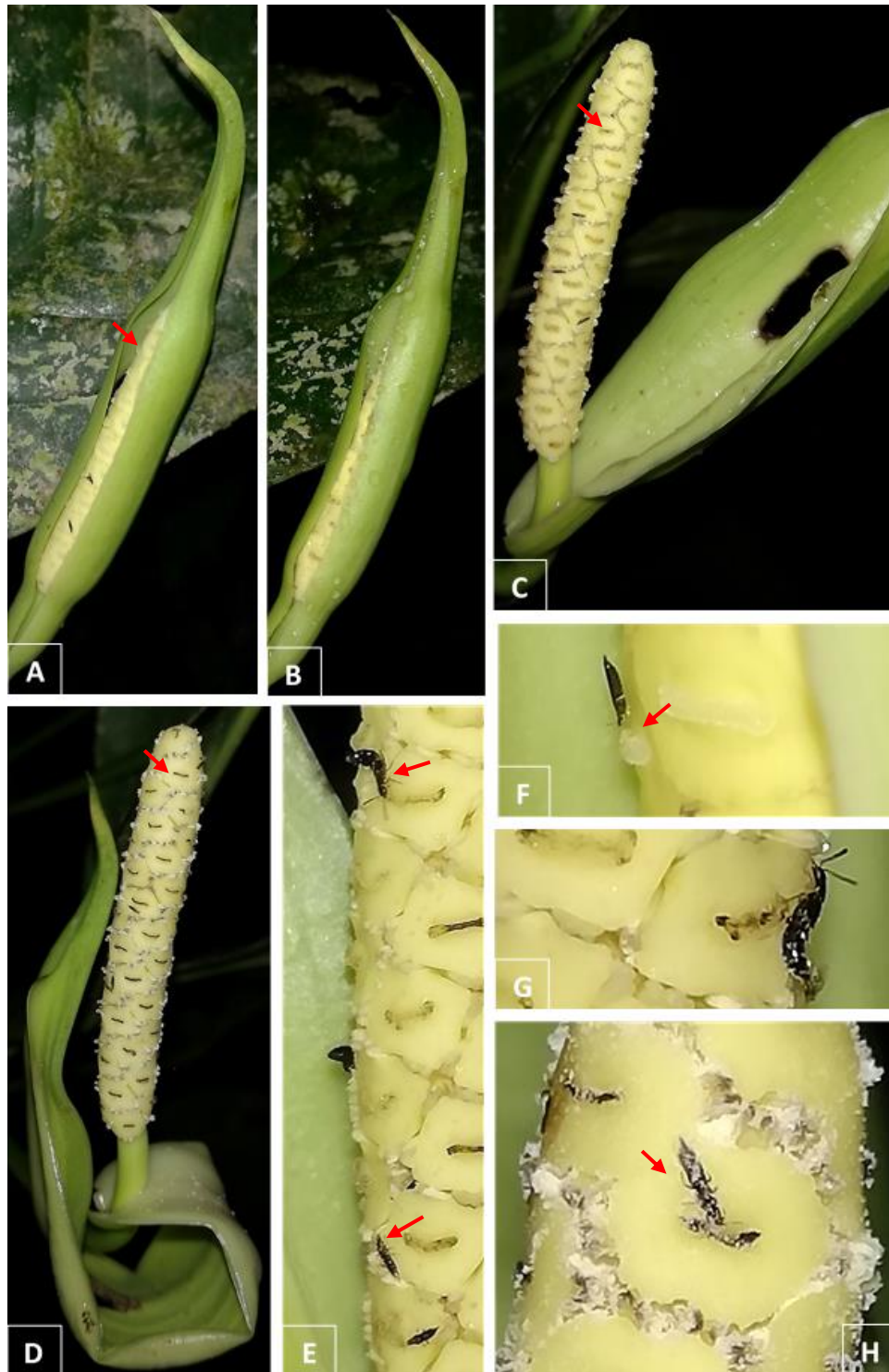


Figure 4.13: Inflorescence of *Anadendrum* sp. nov. at various stages. (A) Pistillate anthesis (1st day). (B) Pistillate anthesis (2nd day) (C) Post-pistillate anthesis (3rd day). (D) Staminate anthesis. (E) Thrips (Thripidae) and rove beetles onto the spadix. (F) Thrip consuming stigmatic secretion. (G) Rove beetle (Staphylinidae). (H) Thrip collecting pollen.

4.4.2 Timing of anthesis and floral changes

Anadendrum sp. flowered for 77 hours. The pistillate phase of anthesis started at 0400 h (Day 1) with a small gap opened along the spathe (0.1 cm), the release of floral odour (“newspaper alcohol mint-like smell”) from the spadix (Table 4.1), and the stigma raised and wet (Figure 4.13A – 4.13B). The floral odour was released daily from 0400 h until 1000 h throughout anthesis (strongest 1 - 2 cm away from the spadix, between 0500 h - 0900 h). The intersexual phase started (1000 h, Day 3), the stigmas turned dry and dark, and the stamens started to protrude (Figure 4.13C). The staminate anthesis started the next morning at 0530 - 0630 h (Day 4) with the release of pollen started from tip to bottom of the spadix, and the spathe completely reflexed (Figure 4.13D). Anthesis ended by 1000 (Day 4) when floral odour ceased. The spathe abscised a few days post-anthesis and fruits ripened in three months also from tip to bottom of the spadix (yellow to red colour) (Figure 4.12B). The ripened fruits were sometimes chewed by *Chabria* beetles (Chrysomelidae) (Figure 4.12C).

4.4.3 Floral traits

The floral odour persisted throughout the anthetic period in *Anadendrum* sp., it was like a “newspaper alcohol mint smell” during both pistillate and staminate anthesis. The floral odour was released from the spadix, and peaked once every morning throughout anthesis (three days pistillate anthesis and one day staminate anthesis).

4.4.4 Floral rewards

A floral liquid was secreted by the stigmas during the pistillate anthesis in *Anadendrum* sp. The species had a ca. 0.15 cm spathe gap that allow thrips (Thripidae) and

rove beetles (Staphylinidae) to enter the floral chamber. The thrips and rove beetles mate over the entire spadix of the species.

4.4.5 Pollinators and their behaviours

Unidentified species of thrips (Thysanoptera, Thripidae) were the main pollinators of *Anadendrum* sp., the number of thrips that visited the inflorescences ranged from two to 30 individuals (Table 4.2). Each day ca. six thrips arrived around 0700 h throughout the anthesis until ca. 20 - 30 thrips accumulated on a staminate anthesis inflorescence (Day 4). The thrips actively moved around the spadix and fed on the floral liquid exuded during pistillate anthesis (Day 1 - 3) (Figure 4.13E, 4.13F). The thrips easily squeezed into the space between flowers to collect pollen and left the inflorescences around 0700 h (Day 4) (Figure 4.13H).

Besides, *Anadendrum* sp. was also pollinated by unidentified rove beetles (Staphylinidae), there were one to four of these beetles together with thrips in the inflorescence until staminate anthesis. The beetles actively moved onto the spadix, fed on the stigmatic secretion and sometimes they chewed the stamens for getting pollen before it is release (Figure 4.13E, 4.13G).

4.4.6 Reproduction system

Fruits of *Anadendrum* sp. ripened in three months. The natural fruit set percentages could be as low as 6.2%, with an average of 18.6% and a maximum of 31% (Table 4.3). Autonomous self-pollination treatment did not set fruit in *Anadendrum* sp., which means the species is not capable to self-pollinate without pollinator. Each fruit of *Anadendrum* sp. had a single seed.

4.5 *Bucephalandra*

4.5.1 Flowering pattern

Bucephalandra muluensis has three to four inflorescences per plant, the interval between flowering are ca. 13 days, as new inflorescence started anthesis 13 days after previous inflorescence ended anthesis, thus the same plant always had different stages of inflorescences and infructescences (Figure 4.14 and Figure 4.15). *Bucephalandra muluensis* flowered for ca. 1.5 to two months, new flowering occurred after the last infructescence of previous flowering ripened (1.5 month), therefore each plant is estimated to flower ca. three to four times per year. However, different plant flowered at different time, there are always some plants flowering in a huge population. Within a population, at least 15 plants were flowering if there was an inflorescence in pistillate anthesis each day.



Figure 4.14: *Bucephalandra muluensis* (A) Mature plant in natural habitat. (B) Immature infructescence. (C) Ripened infructescence, fruits split to reveal seeds. (D-E) Seeds germinated in lower spathe.

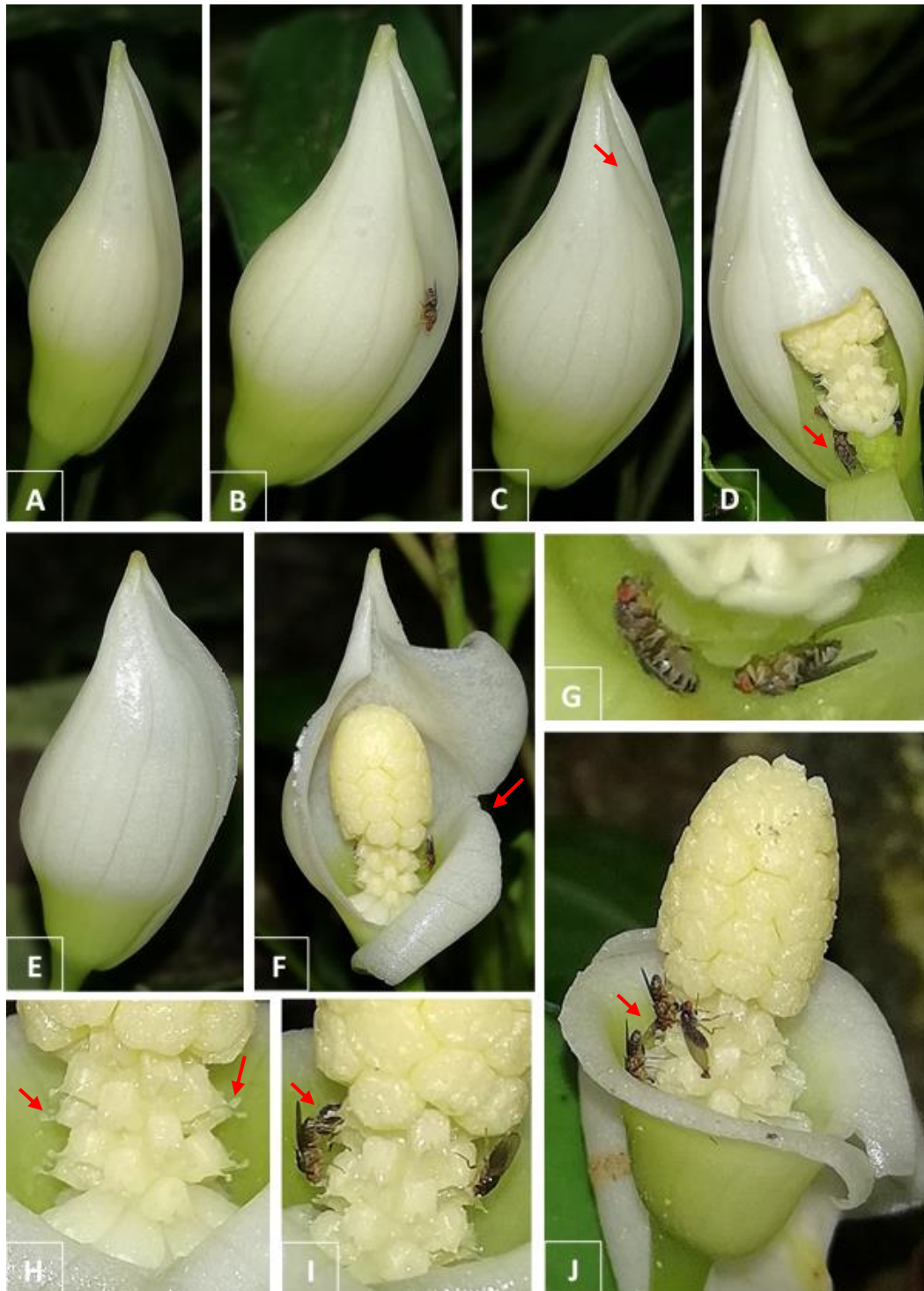


Figure 4.15: Inflorescence of *Bucephalandra muluensis* at various stages (A-C) Spathe expands during pistillate anthesis, flies move in through tiny gap at tip of the spathe. (D) *Colocasiomyia* flies (Drosophilidae) active in the pistillate zone. (E-F) Spathe expanded and upper spathe abscised during staminate anthesis. (G) Flies on pistillate flowers. (H) Pollen released. (I-J) *Colocasiomyia* flies (Drosophilidae) collecting pollen in the staminate zone.

4.5.2 Timing of anthesis and floral changes

Anthesis of *B. muluensis* lasted 26 hours, pistillate flower receptivity (ca. 1300 h, Day 1) coincided with the inflation of the spathe (leaving a gap up to 0.1 cm along the spathe margin) and the release of a weak “sweet sour plum-like” floral odour from the appendix (Figure 4.15A – 4.15D) (Table 4.1). The pistillate phase of anthesis ended by 1600 h (Day 1) when floral odour weakened, with scale-like staminodes bend downward and spathe tightened (gap sealed back). The staminate anthesis started on the following day with the release of pollen at ca. 1300 h (Day 2) (Figure 4.15H) and a persistent floral odour. The sealed spathe unfurled and inflated again just before the start of the staminate anthesis (Figure 4.15E). The upper spathe started to abscise from 1430 h (Day 2) and fell off completely by ca. 1500 h (Day 2) which marked the end of anthesis (Figure 4.15F). The appendix and the staminate zone were shed five days post-anthesis, leaving the salverform lower spathe with the pistillate flowers protected by the scale-like staminodes. The developing fruits were green (Figure 4.14B), and split to reveal white seeds after a month when ripened (Figure 4.14C). Some seeds germinated within the infructescence cup and the seedlings were dispersed by water (Figure 4.14D – 4.14E).

4.5.3 Floral traits

The floral odour persisted throughout the anthetic period (detected once during pistillate and staminate anthesis) in *Bucephalandra muluensis*, was like a “weak sweet-sour plum smell”. The floral odour originated from the appendix.

4.5.4 Floral rewards

A stigmatic secretion was produced during the pistillate anthesis in *B. muluensis*. There was a 0.15 cm spathe gap and a space of 0.15 cm between the inner spathe wall and the spadix that allowed small *Colocasiomyia* flies (Drosophilidae) to enter the pistillate zone. *Colocasiomyia* flies (Drosophilidae) mated on all of the spadix and also on the inner surface of spathe in *B. muluensis*.

4.5.5 Pollinators and their behaviours

Colocasiomyia flies (Drosophilidae) were the only insect visiting and then pollinating *B. muluensis*. The flies started to arrive around 1420 h (Day 1, pistillate anthesis) when a 0.5 cm spathe gap opened, the flies moved around in the floral chamber and mostly stayed in the pistillate zone (Figure 4.15D, 4.15G). After pistillate anthesis, the flies were restricted to the pistillate zone as the scale like staminodes bent downward (close the space to the pistillate zone), thus they moved up before the space was fully close and stayed in the appendix zone and staminate zone until the next day. The flies started to collect pollen at 1310 h (Day 2, staminate anthesis) and left the inflorescences from 1440 h onwards when the upper spathe completely abscised (Figure 4.15I – 4.15J). The number of flies that visited the inflorescences during anthesis ranged from two to 15 individuals (Table 4.2).

4.5.6 Reproductive system

Fruits of *Bucephalandra muluensis* ripened in one month. Natural fruit set percentage was 100% for *B. muluensis* (Table 4.3), while autonomous self-pollination treatment did not set any fruit (not capable to self-pollinate without pollinator). *Bucephalandra muluensis* produced from 10 to 26 seeds with an average of 20 seeds per fruit (n=13).

4.6 *Homalomena*

4.6.1 Flowering pattern

Homalomena usually had six inflorescences (6 - 12 inflorescences for *H. ardua* and *H. rostrata*, three to six inflorescences for *H. sanguineovaginata*), except three inflorescences for *H. ovatifolia*. The intervals between flowering were two to three days for *H. ardua*, three to five days for *H. sanguineovaginata*, four days for *H. rostrata*, and more than 10 days for *H. ovatifolia*. Due to the interval time between flowering, the infructescences also ripen in phases later. Different plant flowered at different times, there were some plants flower at current season while some plant flower at another season. Within a population, at least four to five plants of *H. ardua*, five to seven plants of *H. sanguineovaginata*, six plants of *H. rostrata* and 12 plants of *H. ovatifolia* were flowering. Each plant of *H. ardua*, *H. sanguineovaginata* and *H. rostrata* flowers for ca. one to three months depending on the number of inflorescences, each plant flowered once to twice a year. *H. ardua* flowered every three months, *H. sanguineovaginata* flowered every half year and *H. rostrata* flowered during the first half of the year. During the period of field work, *H. ardua* flowered from January 2018 to February 2018, May 2018 to June 2018, August 2018 to September 2018, and December 2018 to January 2019. *Homalomena sanguineovaginata* flowered from May 2018 to June 2018 and January 2019. *Homalomena rostrata* flowered from January 2018 to March 2018 and May 2018 to June 2019. Each plant of *H. ovatifolia* flowered ca. a month, twice a year, flowering event occurred throughout the year.

4.6.2 Timing of anthesis and floral changes

Anthesis lasted ca. 24 to 25 hours for all four species of *Homalomena* (*H. ardua*, *H. ovatifolia*, *H. rostrata* and *H. sanguineovaginata*) (Figure 4.16 – 4.23). Before pistillate anthesis (ca. 0200 h, Day 1), the upper spathe gradually opened wide and the lower spathe inflated for *H. ardua*, *H. rostrata* and *H. sanguineovaginata* (Figure 4.21A – 4.21B). The pistillate phase of anthesis for *H. ardua*, *H. rostrata*, and *H. sanguineovaginata* started at 0530 h to 0600 h (Day 1) (Table 4.1) with an intense “sweet pomelo skin mint-like” floral odour emission from the staminate zone (strongest 0550 - 0645 h and extend 2 - 6 cm away from the staminate zone in *H. rostrata*, strongest 0620 - 0700 h and extend 2 - 3 cm away from the staminate zone in *H. sanguineovaginata*) and wet stigmas. Gap of the upper spathe was ca. 2.5 to 3.2 cm, space between the constriction of the spathe and sterile interstice was ca. 0.4 to 0.6 cm, and space between the spathe and pistillate zone was ca. 0.7 cm during pistillate anthesis (maximum spathe opening) (Figure 4.17A, 4.21D, 4.23A – 4.23B). By 0900 h (Day 1), the stigmas dried and the floral scent emission reduced, indicating the beginning of intersexual phase which lasted 20 hours. On the second day (staminate phase), at ca. 0500 h (later in *H. sanguineovaginata*, 0545 - 0600 h), a second weaker floral scent emission event occurred together with the release of pollen. Pollen was mixed with resin droplets to form a pale-yellow paste. Throughout Day 2, the spathe gradually closed with the lower chamber tightened in the morning and the upper spathe sealed back in the afternoon (Figure 4.17B, 4.21E, 4.23C). Third day onwards, peduncle bent downward to leave the infructescence inverted, either turning red for the peduncle and green for the spathe (*H. sanguineovaginata*), the entire infructescence turning deep red (*H. ardua*) (Figure 4.16B) or deep green (*H. rostrata*) (Figure 4.20C). The fruits ripened after two months with the entire infructescence suddenly senesced, exposing a bunch of fruits (entire pistillate zone) that

smell sweet fruity (Figure 4.20D). For *H. ovatifolia*, a ca. 0.2 cm gap opened along the spathe early morning before pistillate anthesis. Pistillate anthesis of *H. ovatifolia* started at 0600 h (Day 1) with the release of a “sweet citrus alcohol mint-like” floral odour from the staminate zone (strongest 0600 - 0900 h, extend 2 - 3 cm away from the inflorescence). Spathe gap extended up to 0.5 cm (0.2 cm space between the spathe and the spadix) by 0700 h. (Day 1) and gradually close back until ca. 0.2 cm after 0900 h (Figure 4.19A – 4.19C). The pistillate anthesis ended by 0900 h (Day 1) when the floral odour weakened and was followed by 19 hours of intersexual phase with ca.0.1 cm spathe gap (Figure 4.19D). The staminate anthesis started at 0500 h (Day 2) with the release of a powdery pollen inside the closed spathe (ca. 0.1 cm gap) and the anthesis ended at 0600 h (Figure 4.19E). Post-anthesis, the spathe sealed back to protect the developing fruits, the peduncle bent downward to keep the infructescence inverted and fruits ripened after two months.



Figure 4.16: *Homalomena ardua* (A) Mature plant with inflorescences. (B) Inflorescences and infructescences.

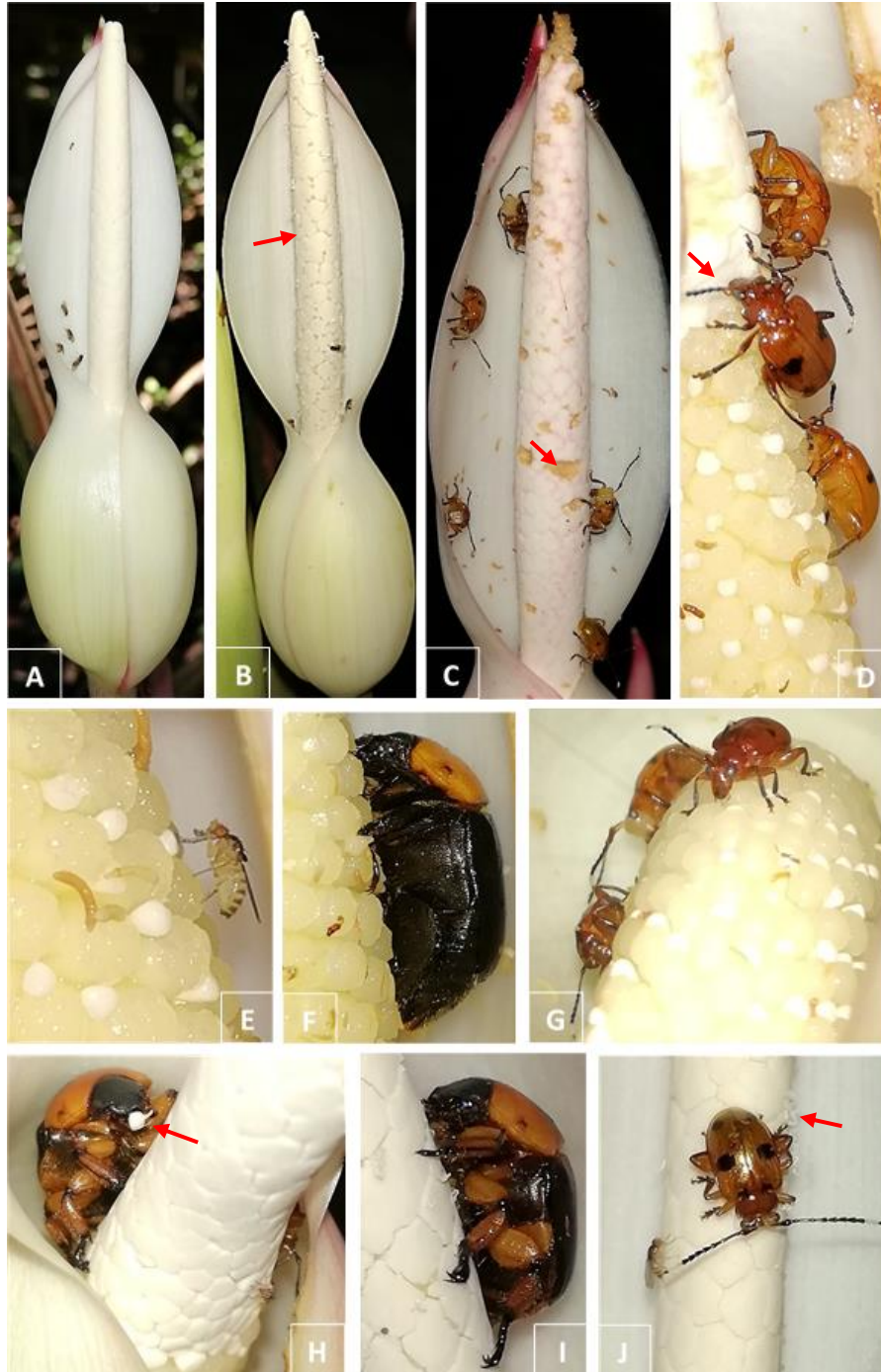


Figure 4.17: Inflorescence of *Homalomena ardua* at various stages. (A) Pistillate anthesis. (B) Staminate anthesis. (C) *Chaloenus* beetles (Chrysomelidae) chewing on staminate zone before pollen release. (D) *Chaloenus* beetles moving on pistillate flowers, and consuming sterile interstices and interpistillar staminodes. (E) *Colocasiomyia* flies (Drosophilidae) moving on pistillate flowers. (F) *Parastasia* beetles (Scarabaeidae). (G) *Chaloenus* beetles on pistillate zone (top view). (H) *Parastasia* beetles chewing sterile interstices. (I) *Parastasia* beetles consuming pollen. (J) *Chaloenus* beetles and *Colocasiomyia* flies collecting pollen.



Figure 4.18: *Homalomena ovatifolia* (A) Mature plant with inflorescences, red leaf form behind green leaf form.

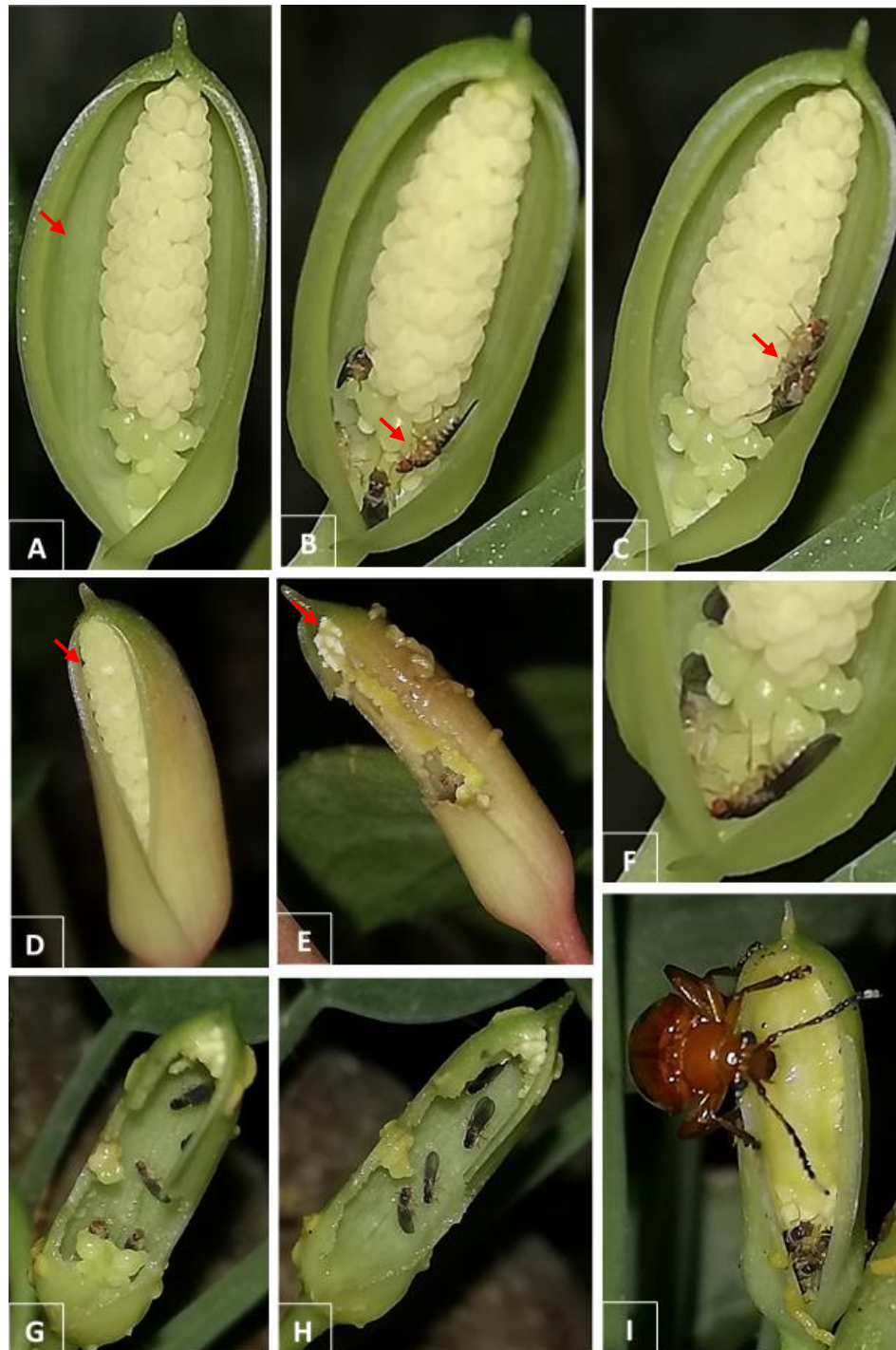


Figure 4.19: Inflorescence of *Homalomena ovatifolia* at various stages (A-C) Pistillate anthesis, spathe gap opened. (B) *Colocasiomyia* flies (Drosophilidae) moving on pistillate flowers. (C) *Colocasiomyia* flies mating on the spadix. (D) Post-pistillate anthesis, spathe closed back. (E) Staminate anthesis with pollen released. (F) *Colocasiomyia* flies on the pistillate zone (zoom). (G-H) *Colocasiomyia* flies in inflorescence destroyed by *Chaloenus* beetles. (I) *Chaloenus* beetles (Chrysomelidae) consuming the staminate zone before the staminate anthesis.



Figure 4.20: *Homalomena rostrata* (A) Mature plant with inflorescence buds. (B) Inflorescences and infructescences at different stages. (C) Infructescences bending downwards. (D) Ripened infructescences with red fruits.

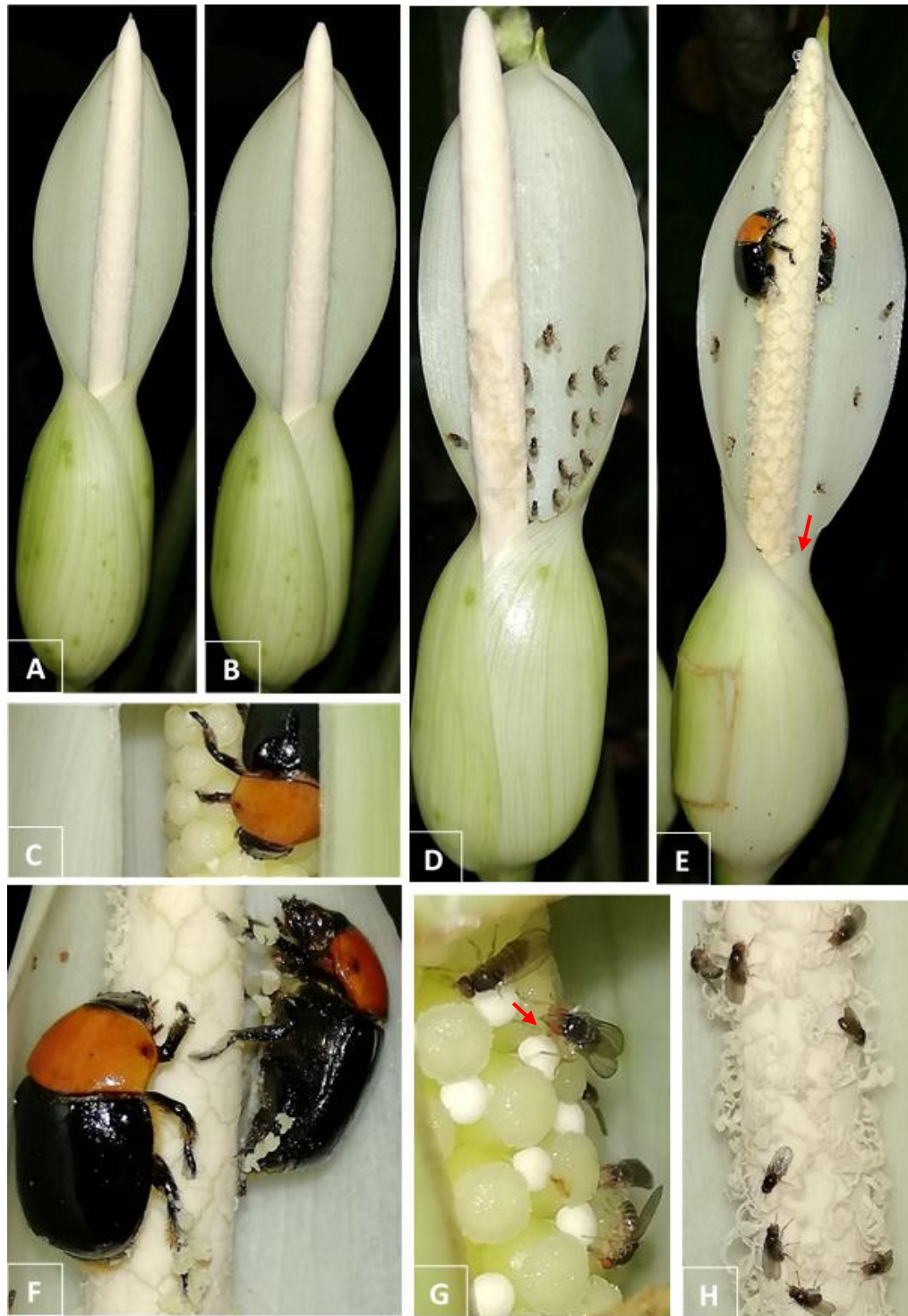


Figure 4.21: Inflorescence of *Homalomena rostrata* at various stages. (A, B & D) Pistillate anthesis, spathe opened, flies attracted. (C) *Parastasia* beetles (Scarabaeidae) on pistillate flowers, consuming interpistillar staminodes. (E) Staminate anthesis, spathe closing back. (F) *Parastasia* beetles consuming pollen. (G) *Colocasiomyia* flies (Drosophilidae) moving on pistillate flowers, consuming stigmatic secretion. (H) *Colocasiomyia* flies collecting pollen.



Figure 4.22: *Homalomena sanguineovaginata* sp. nov. (A) Mature plant with inflorescences. (B) Inflorescence at pistillate anthesis visited by insects.

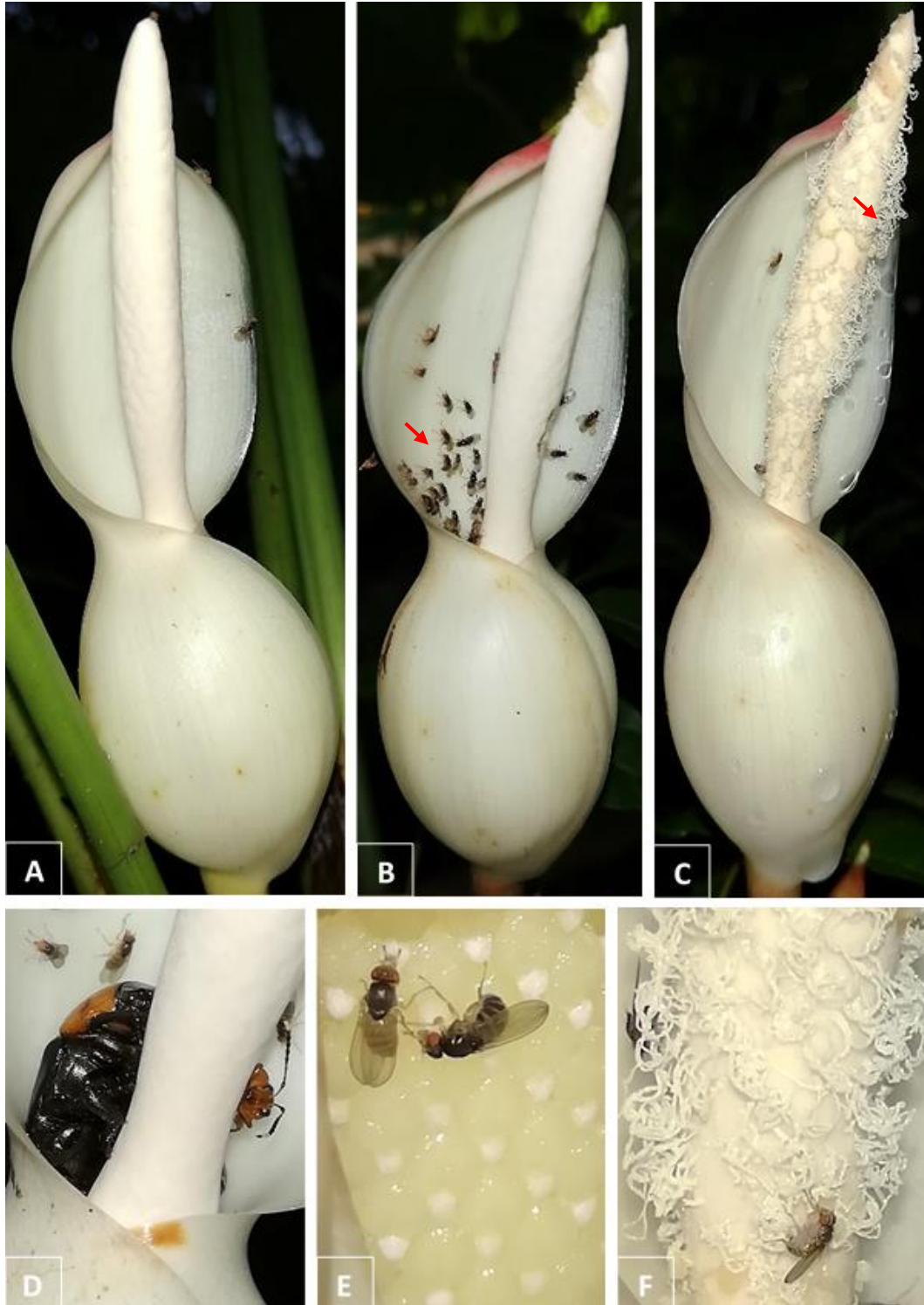


Figure 4.23: Inflorescence of *Homalomena sanguineovaginata* sp. nov. at various stages. (A-B) Pistillate anthesis, spathe opened, flies attracted. (C) Staminate anthesis, pollen released. (D) *Parastasia* beetle, *Chaloenus* beetle and *Colocasiomyia* flies at the level of the spathe constriction. (E) *Colocasiomyia* flies on pistillate flowers. (F) *Colocasiomyia* flies collecting pollen.

4.6.3 Floral traits

The floral odour persisted throughout the anthetic period (detected once in the morning of pistillate and staminate anthesis) in all studied species of *Homalomena* except *H. ovatifolia*. The floral odour was like a “sweet pomelo skin smell” in *Homalomena ardua*, *H. rostrata*, and *H. sanguineovaginata* during the pistillate anthesis, and the smell weakened during the staminate anthesis. In *H. ovatifolia*, the floral odour was like a “sweet citrus alcohol mint smell” during the pistillate anthesis. In all the species, the floral odour originated from the staminate zone.

4.6.4 Floral rewards

Floral liquid is present at pistillate flowers, interpistillar staminodes and sterile interstices during pistillate anthesis in *Homalomena*. The floral liquid rewarded *Colocasiomyia* flies (Drosophilidae) that visited the inflorescences of the genus. *Homalomena* (except *H. ovatifolia*) have a 0.4 to 0.6 cm gap between the constriction of the spathe and the sterile interstices or staminate zone, or a space of 0.7 cm between the inner spathe wall and pistillate zone that allowed big beetles (Chrysomelidae and Scarabaeidae) to enter the floral chamber aside from the small *Colocasiomyia* flies (Drosophilidae). *Homalomena ovatifolia* has a ca. 0.5 cm spathe gap that allowed small *Colocasiomyia* flies (Drosophilidae) to enter the floral chamber. *Colocasiomyia* flies (Drosophilidae) mated on the pistillate zone and the inner surface of the spathe in *Homalomena*. *Chaloenus* beetles (Chrysomelidae) and *Parastasia* beetles (Scarabaeidae) mated on the staminate zone, the sterile interstices and the pistillate zone in *Homalomena* (except *H. ovatifolia*). The interpistillar staminodes and sterile interstices were consumed by *Parastasia* spp. (main pollinators) and *Chaloenus* spp. in *Homalomena* (except *H. ovatifolia*), the beetles also

consumed the pollen. Moreover, *Chaloenus* beetles usually consumed the staminate zone of *Homalomena* before pollen release. In *H. ovatifolia*, most of the inflorescences were heavily damaged and was only left the pistillate zone after anthesis, the other floral parts (staminate zone and sterile interstice) were chewed by *Chaloenus* spp. (Figure 4.19G).

4.6.5 Pollinators and their behaviours

Colocasiomyia flies (Drosophilidae) were pollinators of all studied species of *Homalomena*, the flies started to arrive around 0605 - 0610 h (Day 1, pistillate anthesis) in *Homalomena ardua*, *H. rostrata* and *H. sanguineovaginata*. The flies mostly stayed on the pistillate zone, consumed stigmatic secretion on the pistillate flowers and faced the inner surface of the lower spathe throughout anthesis (Figure 4.17E, 4.21G, 4.23E), together with the other pollinators (*Parastasia* beetles and *Chaloenus* beetles). The flies occasionally moved up to staminate zone to collect pollen and left the inflorescence after the end of staminate anthesis (Figure 4.17J, 4.21H, 4.23F). In *H. ovatifolia*, the flies (Drosophilidae) arrived around 0620 to 0630 h (Day 1, pistillate anthesis), the flies mostly stayed on the pistillate zone (Figure 4.19B, 4.19F, 4.19I), sometimes mated on the staminate zone (Figure 4.19C) and left the inflorescence around 0620 h after collected pollen (Day 2, staminate anthesis) (Figure 4.19E). The number of *Colocasiomyia* flies that visited inflorescences of *Homalomena* during anthesis ranged from one to 15 individuals in *H. ardua*, one to six individuals in *H. ovatifolia*, five to 57 individuals in *H. rostrata* and 18 to 91 individuals in *H. sanguineovaginata* (Table 4.2).

Parastasia beetles (Scarabaeidae) arrived during the pistillate anthesis (Day 1) between 0630 to 0830 h in *H. ardua*, *H. rostrata* and *H. sanguineovaginata*, the number of *Parastasia* beetles that visited inflorescences of these *Homalomena* ranged from one to two

individuals, one to seven individuals and one to three individuals in *H. ardua*, *H. rostrata* and *H. sanguineovaginata* respectively. The beetles were usually spotted in mating pairs in the floral chamber of the *Homalomena* species. Immediately after arrival, the beetles moved down to lower spathe chamber, the beetles slowly moved on the pistillate flowers while feeding on the interpistillar staminodes and sterile interstices (Figure 4.17F, 4.17H, 4.21C, 4.23D), this way they may have pollinated the pistillate flowers. The beetles only moved up to the staminate zone during the staminate anthesis to feed on and collect pollen (Figure 4.17I, 4.21E, 4.21F), afterwards the beetles left around 0630 to 0830 h (Day 2).

Chaloenus beetles (Chrysomelidae) arrived between 0630–0830 h (Day 1, pistillate anthesis) in *H. ardua*, *H. rostrata* and *H. sanguineovaginata*. There were one to 12 individuals of *Chaloenus* beetles visiting inflorescences of *H. ardua*, and one to four individuals for *H. rostrata* and *H. sanguineovaginata* during anthesis. Immediately after arrival, the *Chaloenus* beetles fed on the staminate flowers, or fed on the interpistillar staminodes and the sterile interstices in the lower spathe chamber (Figure 4.17C, 4.17D, 4.17G, 4.23D). The beetles may achieve pollination when they move on the pistillate flowers in the lower spathe chamber (Figure 4.17D, 4.17G). When encountered, two male *Chaloenus* beetles were very aggressive and fought together to compete for mating (this scenario was also observed in *Schismatoglottis*). *Chaloenus* beetles were observed to consume pollen at the staminate zone during the staminate anthesis (Figure 4.17J). The beetles departed the inflorescences as early as 0800 h (Day 2), although some stayed after the end of anthesis.

Chaloenus beetles were just visitors in *H. ovatifolia*, they ranged one to two individuals per inflorescence. The *Chaloenus* beetles usually chewed away pieces of

staminate zone of this species (Figure 4.19I), and sometimes the entire inflorescence, causing abortion in many inflorescences (Figure 4.19H).

4.6.6 Reproductive system

Fruits of *Homalomena* spp. ripened in ca. two months. Natural fruit set percentage of *H. rostrata* ranged from 79.6% to 97.9 % with an average of 89.7% (Table 4.3). Natural fruit set percentage were not counted for *H. ardua*, *H. ovatifolia* and *H. sanguineovaginata* because infructescences were not available during fieldwork. Autonomous self-pollination treatment did not set fruit in *H. rostrate*, which means the species is not capable to self-pollinate without pollinator. Autonomous self-pollination treatment was not tested for *H. ardua*, *H. ovatifolia* and *H. sanguineovaginata* due to the lack of available inflorescences, all inflorescences of these taxa were used for flowering observations. *H. rostrata* produced in average 96 seeds per fruits, ranging between 85 to 108 seeds per fruit (n=10).

4.7 Lasia

4.7.1 Flowering pattern

Lasia spinosa has one inflorescence per plant, each plant was able to flower twice a year, the second inflorescence may come out when the first inflorescence was in late fruiting stage or at least five months after the first flowering. *Lasia spinosa* flowered throughout the year, different plants flowered at different times, flowering seemed to occur based on population location, there was always some flowering occurring at some location. For example, population near the park headquarter had flowered first, then followed by the population towards the trail to Deer cave, the population near the headquarter had flowered again after sometime, either when the infructescences of previous flowering were still

developing (for previous non-flowering plants) or nearly ripened (for previous flowering plants). In a population, inflorescences usually flowered in phase, there was always some inflorescences at pistillate anthesis when some inflorescences ended staminate anthesis, thus a pollen donor was available within the population for the inflorescence in the pistillate phase of anthesis. The flowering period for a population depended on the population size, usually there were more flowering in a bigger population and thus a longer flowering period. For every population, at least one flowering per week if there was one inflorescence started anthesis after previous inflorescence ended anthesis but usually there were more flowering in between.

4.7.2 Timing of anthesis and floral changes

In *Lasia spinosa*, anthesis lasted between 150 - 174 hours (Figure 4.24 and Figure 4.25). A week before pistillate anthesis, the spathe of the inflorescence rapidly elongated and the spathe started to turn purple one to two days before pistillate anthesis. The pistillate phase of anthesis started at 1000 h (Day 1) with the gaping of spathe originated from tip of the spathe. The inner surface of the spathe in the floral chamber turned pink, and the release of a weak fruity floral scent originated from the inner surface of the spathe (detectable through the 0.1 cm gap at tip of the spathe) (Figure 4.24A) (Table 4.1). Stigmas also turned from light orange (before anthesis) to orange (pistillate anthesis) (Figure 4.24E). The gap of the spathe gradually extended until the base of the spathe and widened (ca. 0.2 cm) throughout the pistillate anthesis (Figure 4.24B). The inner part of the spathe (exposed as the gap open wider) turned from light yellow to deep yellow as pistillate anthesis proceeded (Figure 4.24C). The floral odour became more intense throughout the anthetic period as the gap extended and widened with the strongest scent detected from the floral chamber. The floral

odour was detected to be different along the spathe during the pistillate anthesis: weak smell from the tip of the spathe, a “sour plum-like” smell from the first curve of the spathe, and a “banana/sweet pear-like” smell from the second curve of the spathe and down to the floral chamber. On Day 7/8, the stamens started to protrude gradually since 0700 h. The pistillate anthesis ended by 0900 h, with stigmas turning deep orange, and the floral odour weakened and finally disappeared along the spathe (left a “creamy sweet pear-like” smell at the level of floral chamber below the second curve), and stamens then fully protruded. The staminate anthesis started by 1000 - 1030 h with the release of pollen (Figure 4.24H). The spadix was fully revealed by the gap (ca. 2 - 3 cm) opened in the lower part of the spathe (floral chamber) between 1300 - 1600 h (Day 7/8) (Figure 4.24D, 4.24K), the anthesis ended the same day at 1600 h. The spathe gradually withered after a week post-anthesis. Infructescence gradually inverted as the fruits mature and finally reached the ground because the infructescence was too heavy to stay upright (Figure 4.24L). The fruits took more than six months to ripe and were self-dispersed because entire fruits of the infructescence germinated on the same spot (Figure 4.24M).

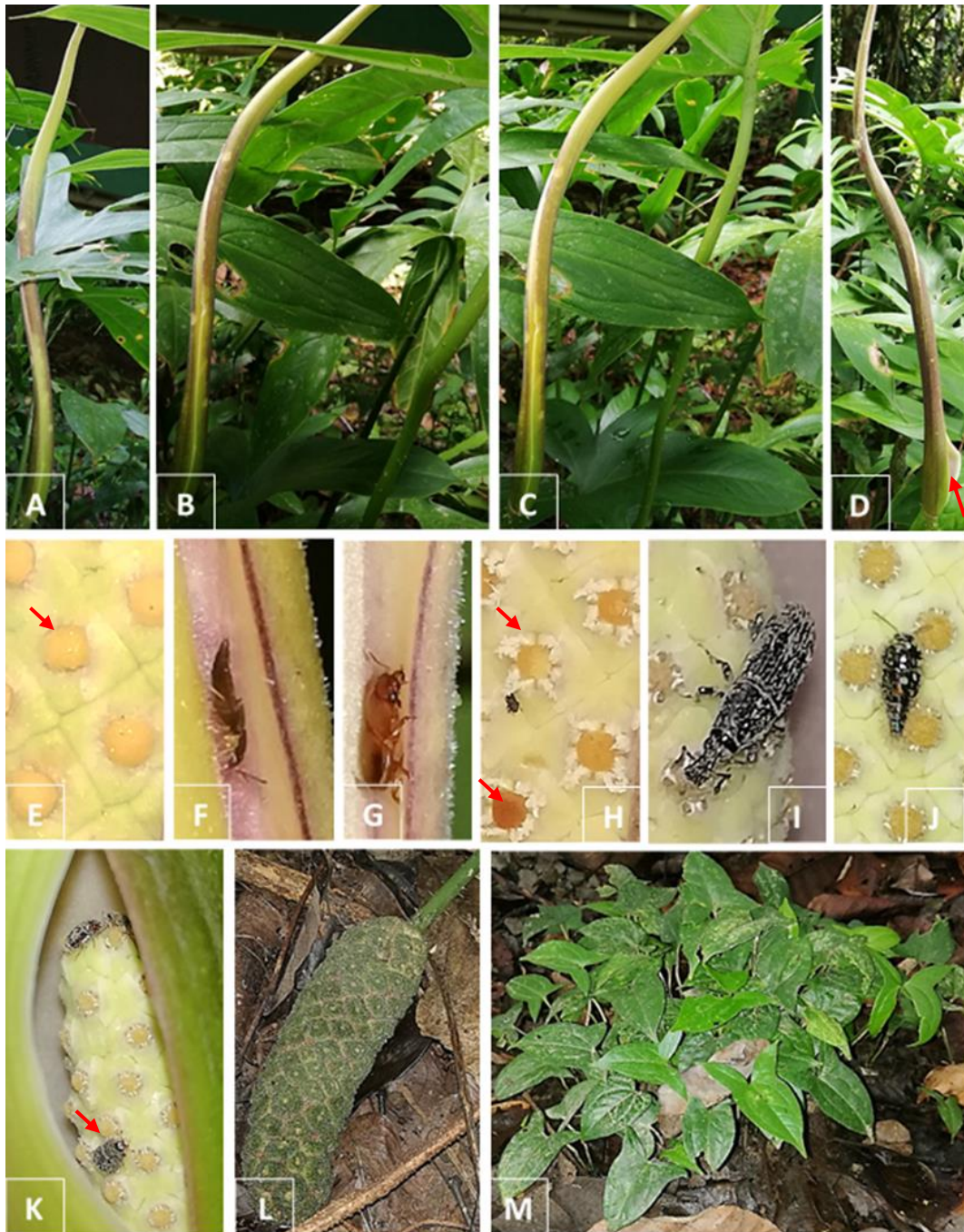


Figure 4.24: *Lasia spinosa* (A-C) Inflorescence during pistillate anthesis. (D) Inflorescence during staminate anthesis, a gap opened at bottom of spathe after pollen released. (E) Flowers (Pistillate anthesis), stigmas orange colour. (F) Rove beetle (Aleocharinae, Staphylinidae). (G) Sap beetle (Nitidulidae) near the narrow gap. (H) Flowers releasing pollen (Staminate anthesis), stigmas deep orange colour. (I) Snout and bark beetle (Curculionidae). (J) Rove beetle (Aleocharinae, Staphylinidae) (K) Sap beetles collecting pollen. (L) Developing infructescence. (M) Seedlings growing on the same spot.

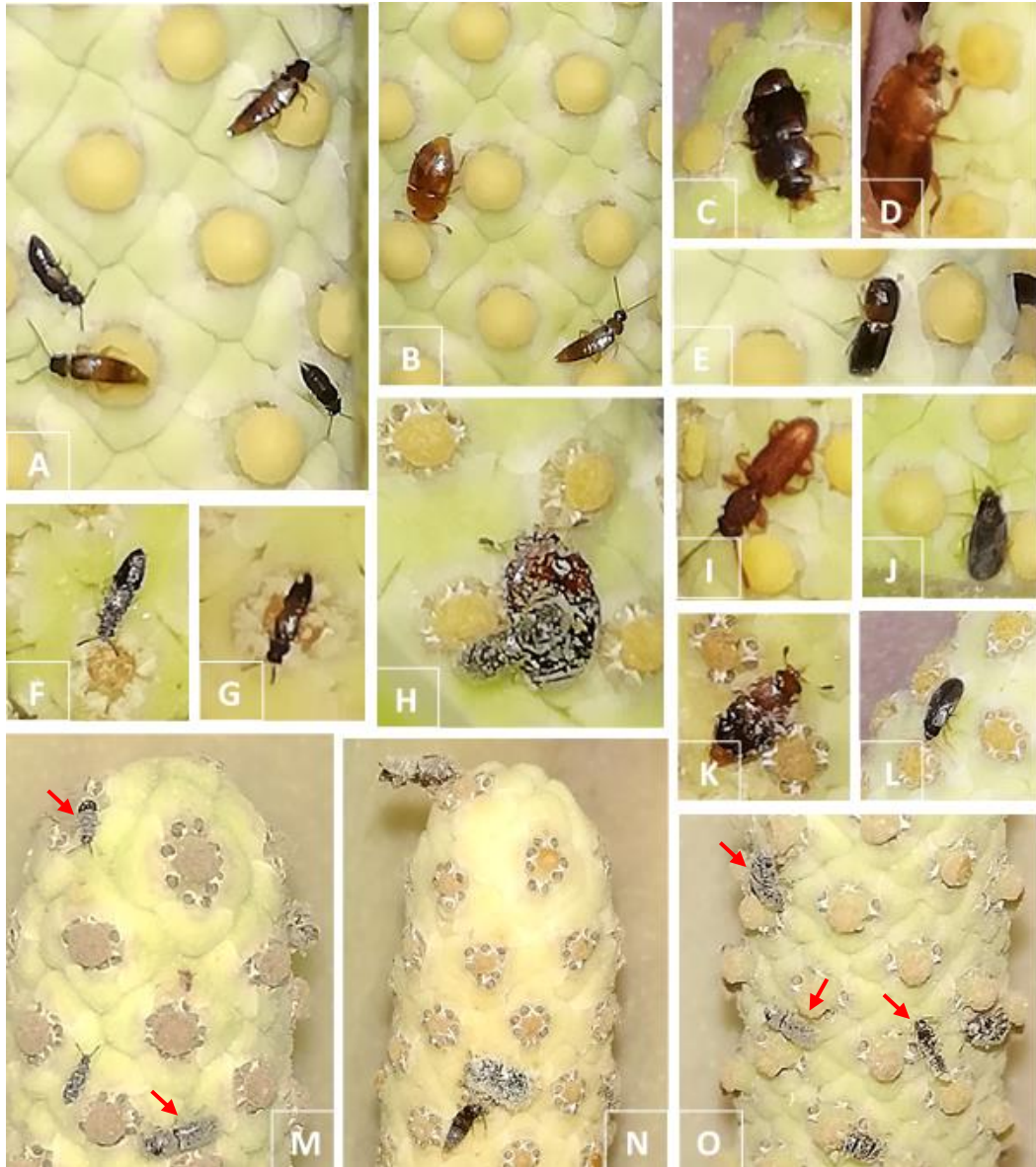


Figure 4.25 : Inflorescence of *Lasia spinosa* at various stages. (A) Rove beetles (Aleocharinae, Staphylinidae) moving on flowers during the pistillate anthesis. (B) Rove beetle and sap beetle. (C-D) Sap beetles (Nitidulidae). (E) Ambrosia beetles (Scolytinae). (F-G) Rove beetle collecting pollen. (H) Ambrosia beetle on Sap beetle. (I) Silvanid beetle (Silvanidae). (J) Plant bug (Miridae). (K) Sap beetle collecting pollen. (L) Plant bug collecting pollen. (M) Rove beetles and Ambrosia beetles collecting pollen. (N) Sap beetles and rove beetles collecting pollen. (O) Sap beetles, Ambrosia beetles and rove beetles collecting pollen.

4.7.3 Floral traits

The floral odour persisted throughout the anthetic period (detected during pistillate and staminate anthesis) in *Lasia*. The floral odour of *Lasia spinosa* was like a “sweet plum-sweet pear/banana smell” during the pistillate anthesis, and switched to a “creamy sweet pear smell-like” during the staminate anthesis. The floral odour was released from the inner surface of the spathe. The floral odour was detected throughout the spathe length during the pistillate anthesis, but faded in the upper part and was only detected from the floral chamber during the staminate anthesis.

4.7.4 Floral rewards

No floral liquid was detected for this species. The thick spathe with narrow slit gap provided protection for all insects (Nitidulidae, Staphylinidae, Scolytinae, Silvanidae, Miridae) that stayed in the floral chamber throughout pistillate anthesis, the insects may mate inside the floral chamber. Most pollen of *Lasia* were brushed off by the insect visitors during the staminate anthesis, the pollen grains were probably consumed by the insect visitors (Figure 4.25M – 4.25O).

4.7.5 Pollinators and their behaviours

Lasia spinosa were pollinated by various group of beetles (Nitidulidae, Staphylinidae, Scolytinae, Silvanidae, Curculionidae) and plant bug (Miridae).

Sap beetles (Nitidulidae) arrived on Day 2 onwards during the pistillate anthesis and stayed within the inflorescence throughout anthesis (Figure 4.25B), together with the other pollinators (Staphylinidae, Scolytinae and Miridae). These beetles left after the staminate anthesis ended on Day 7 or 8 (gap opened in the lower part of spathe). Another species of

sap beetles (Nitidulidae) were found to pollinate *Lasia spinosa*, these beetles usually arrive on Day 3 onwards during pistillate anthesis and stayed until staminate anthesis ended (Day 7/8). These beetles entered the inflorescence through the narrow gap on spathe (Figure 4.24G). Sap beetles may be the most efficient pollinator because their big body can carry more pollen, the beetles actively moved on the spadix within the floral chamber (Figure 4.25C – 4.25D, 4.25H, 4.25K). The number of sap beetles that visited *L. spinosa* during anthesis ranged from one to 15 individuals (Table 4.2).

Rove beetles (Staphylinidae, Aleocharinae) were among the earliest insects (together with Miridae and Scolytinae) arriving (Day 1 onwards) (Figure 4.24F) to the inflorescence of *L. spinosa*, there were one to 23 individuals of rove beetles per inflorescence during the anthesis. These beetles actively moved on the spadix and stayed in the floral chamber until staminate anthesis ended (Day 7/8) (Figure 4.25A – 4.25B, 4.25F, 4.25G).

Ambrosia beetles (Scolytinae: Xyleborini) arrived to the inflorescence of *L. spinosa* from Day 1 onwards during pistillate anthesis (one to three individuals). These beetles actively moved on the spadix and stayed in the floral chamber until the end of staminate anthesis (Figure 4.25E, 4.25H).

Besides, Silvanid flat bark beetle (Silvanidae) (Figure 4.25I) were possible pollinators frequently encountered, the beetles usually arrived from Day 2 onwards (pistillate anthesis) and stayed until the end of staminate anthesis, the number of Silvanid beetles that visited the inflorescences ranged from one to six individuals. A snout and bark beetle (Curculionidae) (Figure 4.24I) and an unknown rove beetle (Staphylinidae) (Figure 4.24J) were encountered once during the staminate anthesis. These beetles are possible pollinators

but not common, they were also able to enter the inflorescence through the narrow gap during pistillate anthesis and stayed until pollen released.

Apart from that, Plant bugs (Miridae, Hemiptera) were also spotted to pollinate *L. spinosa* inflorescences (one to six individuals). These insects arrived from Day 1 onwards during the pistillate anthesis. The insects moved around the spadix and stayed in the floral chamber throughout anthesis (Figure 4.25J – 4.25L).

4.7.6 Reproduction system

The fruits of *Lasia spinosa* ripened after ca. six months, which is the longest maturation time among all of the investigated aroids. Natural fruit set percentage of *L. spinosa* was 69.8% (Table 4.3). Autonomous self-pollination treatment did not set any fruit in *L. spinosa*, which means the species is not capable to self-pollinate without pollinator. Each fruit of *L. spinosa* had a single seed.

4.8 *Pothos*

4.8.1 Flowering pattern

Pothos seemed to flower throughout the year, flowering numbers were difficult to estimate because flowering mostly occurred high-up on the host plants. There were usually three to five inflorescences per flowering shoot of *P. insignis*. The interval of flowering for inflorescences from the same flowering shoot was usually ca. two weeks (a few days after the previous inflorescence ended anthesis), thus there were several infructescences at different development stage from the same flowering shoot. It was estimated ca. 2.5 months for the entire inflorescences of a given flowering shoot to complete flowering. New flowering shoot only extended from the old flowering shoot after the entire infructescences of the old flowering shoots ripened or after five months. There were usually several active flowering shoots on the same host plant that flower at the same time but it was difficult to determine whether the flowering shoots belonged to one plant or several plants. For *P. scandens*, there was no separate flowering shoots like *P. insignis*, the inflorescences were produced from the axil of leaves and mostly from terminal part of the shoots. *Pothos scandens* seemed to have higher number of flowering during some months although there was always some flowering occurring. Peak flowering occurred randomly for different plants and was usually detected when there were many aborted inflorescences drop off onto the ground. During the period of field work, a peak of flowering was observed from March 2018 and June 2018.

4.8.2 Timing of anthesis and floral changes

The anthesis lasted ca. 225–249 hours in *P. insignis* (Figure 4.26 and Figure 4.27). The spathe opened by a slit gap and pistils were raised one or two days before pistillate

anthesis (Figure 4.26C). The pistillate anthesis of *P. insignis* started at 0800 h (Day 1) with raised and wet stigmas, wet stylar region (liquid exuded from space between flowers), and the release of a strong floral odour from the spadix (reduced as the day proceeded) (Table 4.1). The “salted-fish ginger mint-like” floral odour was strongest (0800 - 1400 h), its intensity reduced to “salted-fish ginger-like” smell in the afternoon (1400 - 1800 h), and finally no smell detectable in the evening (1800 h onwards). This pattern was repeated on a daily basis throughout anthesis. The spadix of some inflorescences was covered by spathe during the first day of pistillate anthesis but the spathe of most inflorescences was reflexed just before the start of the pistillate anthesis (Figure 4.26E). During the pistillate anthesis, inflorescences were pointed upward to horizontal position (45° - 90°). The pistillate anthesis ended on Day 3 (1700 h) when stigmas dried up and darkened. The staminate anthesis started the next day at 0700 h (Day 4) with the release of pollen from protruded stamens (Figure 4.26B). Each flower has six stamens, each stamen protruded and released pollen in a triangle pattern (clock numbers in ascend order: 12, 4, 8, 10, 2, 6). Each day, the opened stamen senesced before another stamen mature the next day (Figure 4.26F). During the staminate anthesis, inflorescences were pointed horizontal to downward position (90° - 135°). The anthesis lasted till 1700 h (Day 10/11) when all stamens have protruded and released their pollen. Post-anthesis, developing infructescences gradually inverted (peduncle bent downwards), the spadix turned purple, with successfully pollinated fruits gradually swelling up within two weeks.

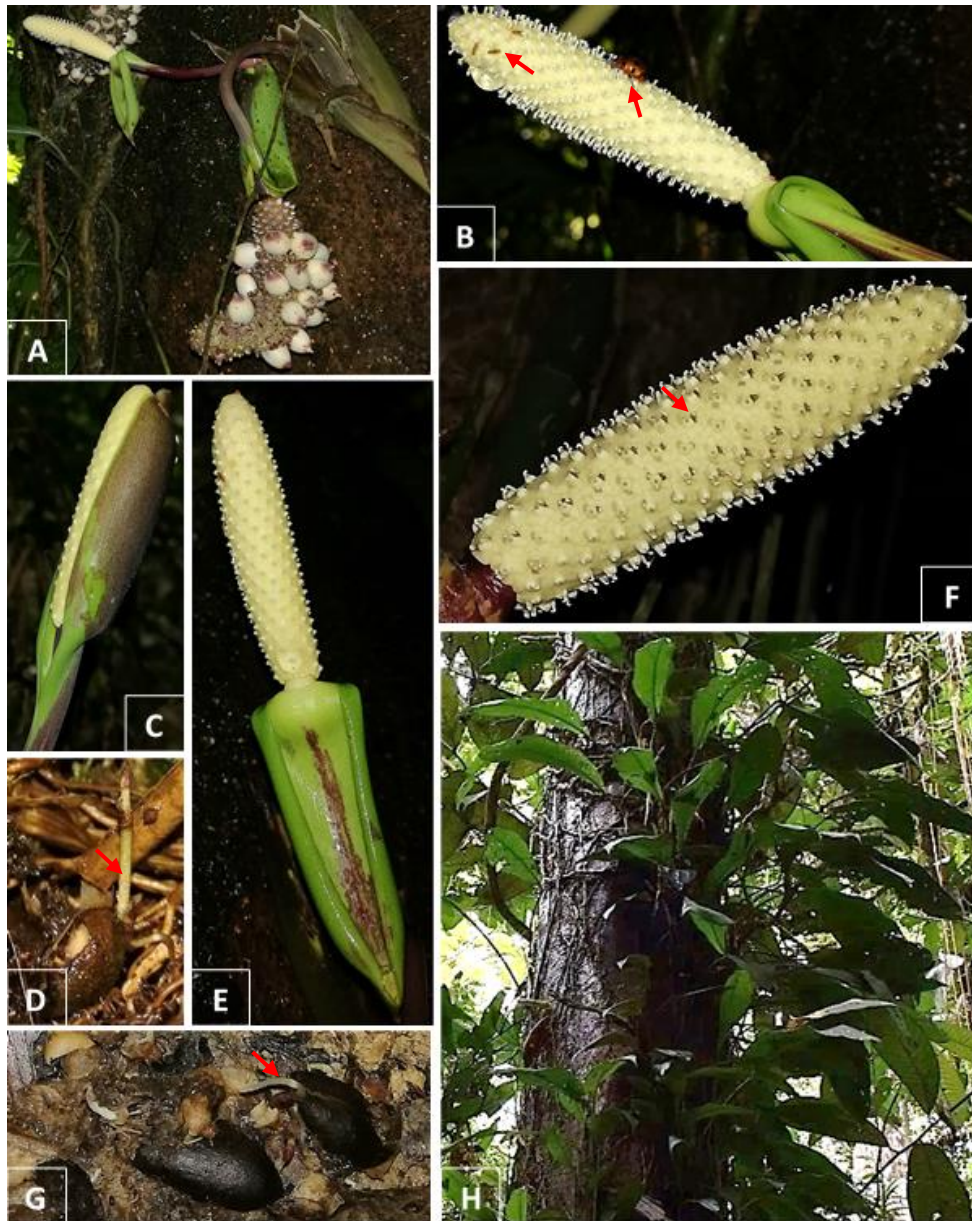


Figure 4.26: *Pothos insignis* (A) Inflorescence and infructescence. (B) Inflorescence during staminate anthesis, flies (Drosophilidae) and *Chabria* beetles (Chrysomelidae) collecting pollen. (C) Nearly open inflorescence. (D) Seeds germinated on host plant. (E) Inflorescence during pistillate anthesis. (F) Inflorescence during 3rd day of staminate anthesis, stamens senesced after one day of pollen release. (G) Seeds germinated on ground. (H) Mature plant on host tree.

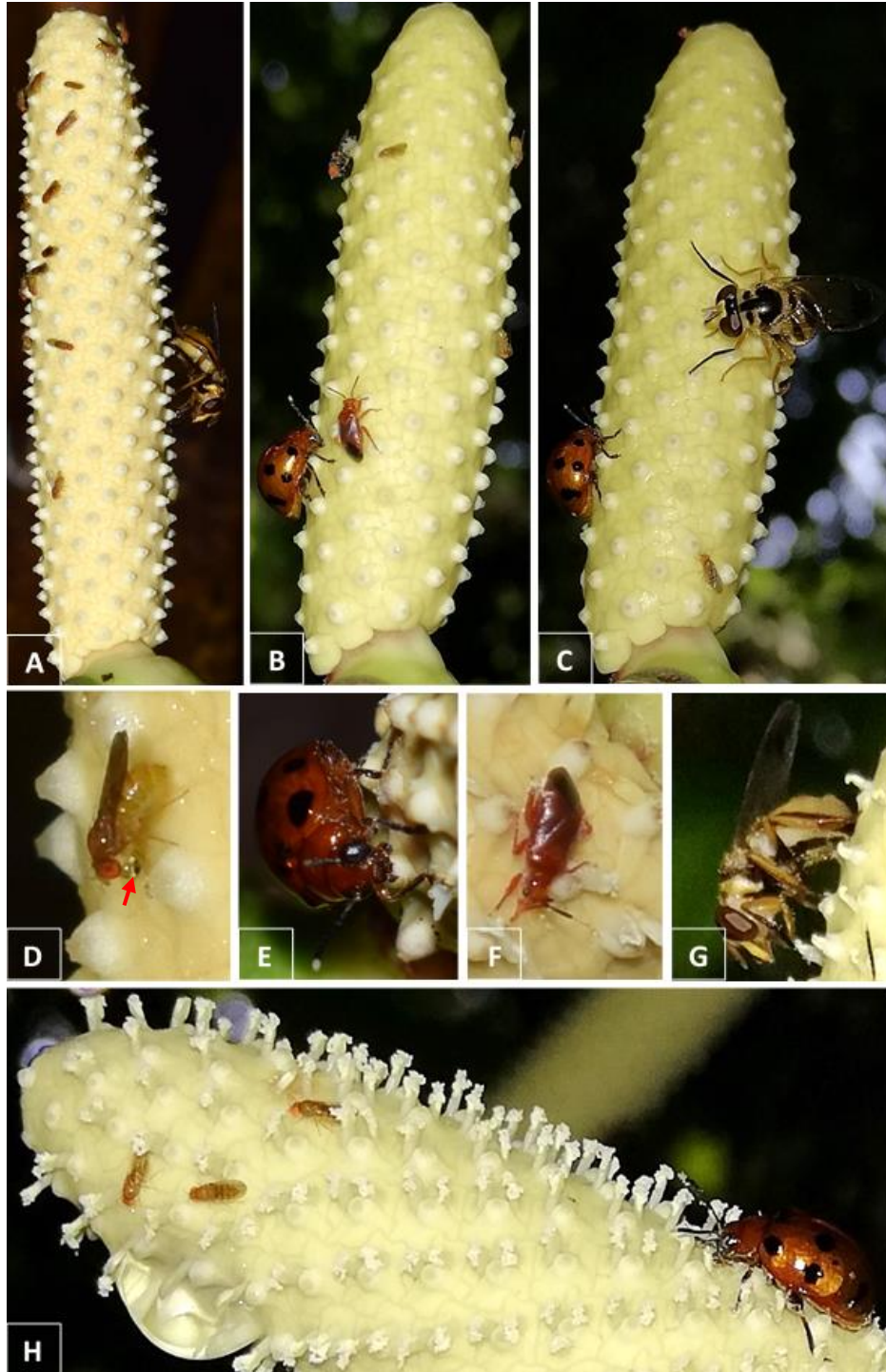


Figure 4.27: Inflorescence of *Pothos insignis* at various stages. (A-C) Pistillate anthesis. (A) Fruit flies (Drosophilidae) and Hover fly (Syrphidae) consuming stigmatic liquid. (B) Fruit flies, *Chabria* beetle and *Halticotoma valida* (Miridae) consuming stigmatic liquid. (C) Fruit flies, *Chabria* beetle, and Hover fly on flowers. (D) Fruit flies consuming stigmatic liquid. (E) *Chabria* beetle. (F) *H. valida* (Miridae) collecting pollen. (G) Hover fly collecting pollen. (H) Fruit flies and *Chabria* beetle collecting pollen.

Anthesis of *Pothos scandens* lasted ca. 417 hours (Figure 4.28). *Pothos scandens* differed from *P. insignis* in the spathe reflexing before the pistillate anthesis and revealing the whole spadix. The spadix turned light green from deep green as the spadix developed. The pistillate anthesis of *P. scandens* started at 0800 h (Day 1) with prominent wet stigmas and the release of a weak sweet floral odour that was persistent throughout the anthesis (Figure 4.28B, 4.28D) (Table 4.1). The light green spadix turned light yellow throughout the pistillate anthesis. The pistillate anthesis ended on Day 6/7 at 1700 h when stigmas dried up and turned dark. Stamens started to protrude randomly on Day 6/7 when pistillate anthesis ended. The staminate anthesis started on Day 7/8 at 0700 h and lasted till 1700 h of Day 18. Each flower has six stamens, each stamen protruded and released its pollen in a triangle pattern (clock numbers in ascend order: 12, 4, 8, 10, 2, 6) each day, the opened stamens persisted (Figure 4.28C – 4.28E). Fruits of both species took ca. two months to mature. Ripened fruits are scarlet red in *P. scandens* (Figure 4.28F) but white in *P. insignis* (Figure 4.26A). Seeds of *P. insignis* were observed to germinate on host plant (Figure 4.26D) and on ground (Figure 4.26G).

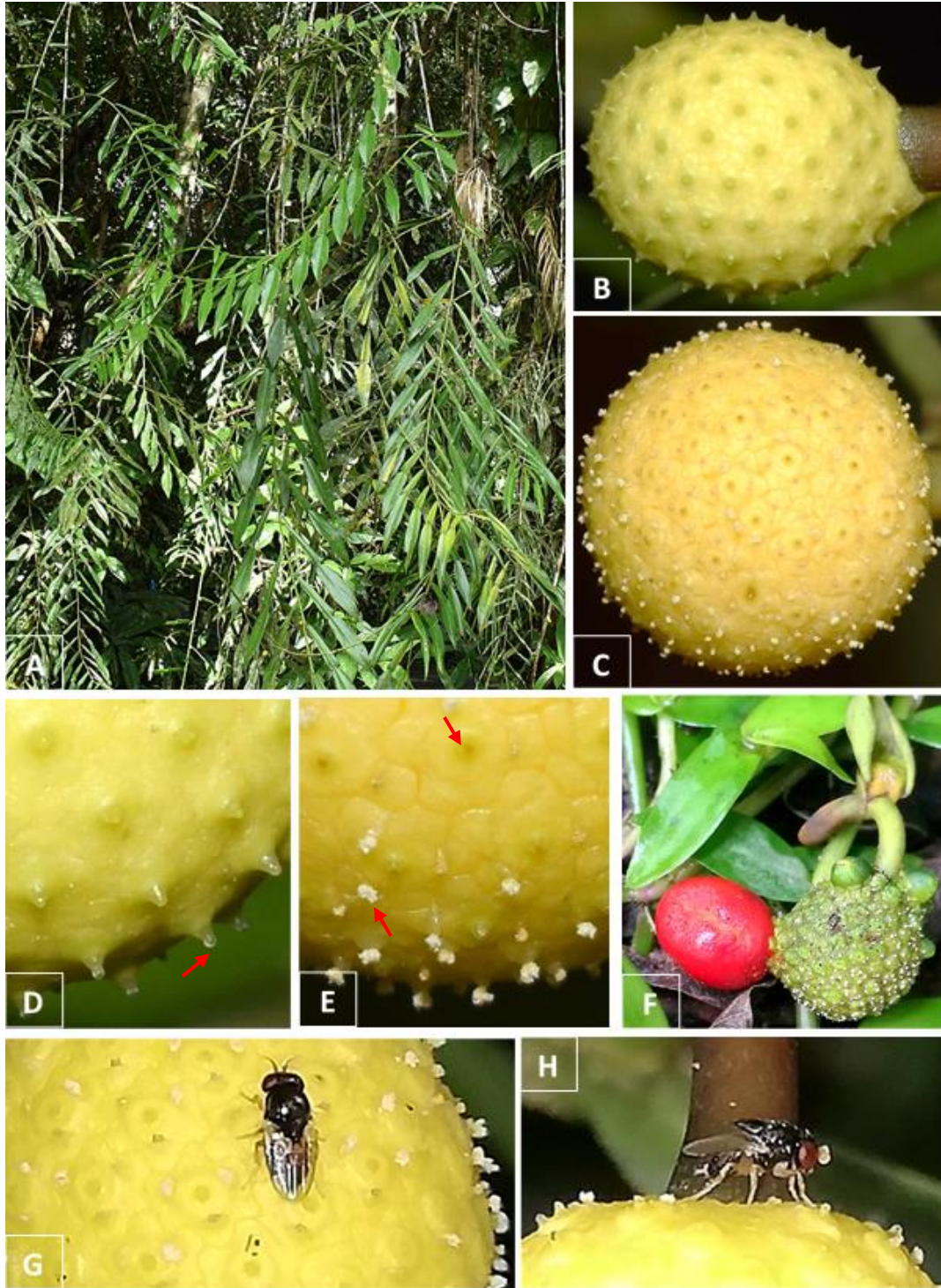


Figure 4.28: *Pothos scandens* (A) Mature plant on host, shoots hanging downward. (B) Inflorescence during pistillate anthesis. (C) Inflorescence during staminate anthesis. (D) Wet stigmas during pistillate anthesis. (E) Pollen released during staminate anthesis, stigmas darkened. (F) Infructescence with ripened fruit dropped. (G-H) Unknown fly visiting inflorescence during staminate anthesis.

4.8.3 Floral traits

The floral odour persisted throughout the anthetic period (detected during both pistillate and staminate anthesis) in the studied *Pothos*. The floral odour was like a “salted fish ginger mint smell” in *Pothos insignis* and like a “weak sweet smell” in *P. scandens*. The floral odour was released from the spadix. The floral odour peaked once in the morning and weakened in the afternoon everyday throughout anthesis in *P. insignis* (three days of pistillate anthesis and seven days of staminate anthesis).

4.8.4 Floral rewards

Stigmatic secretions were produced during pistillate anthesis in both *Pothos*, moreover, a floral liquid was released from the space between flowers in *P. insignis*. The floral liquid rewarded fruit flies (Drosophilidae), *Chaloenus* beetles (Chrysomelidae) and *H. valida* (Miridae) that visited the inflorescences. There was no restriction for insects to visit the inflorescences because the spathe reflexed before or during anthesis. Fruit flies (Drosophilidae) mated on the entire spadix in *Pothos*. *Chabria* sp. consumed stamens and pollen during the staminate phase of anthesis.

4.8.5 Pollinators and their behaviours

Fruit flies (Drosophilidae) were main pollinators of *P. insignis*, the flies were present at the inflorescences daily between 0900 - 1700 h throughout the anthesis, the flies were most active and abundant between 1000 - 1400 h when the floral odour was the strongest (Figure 4.27A – 4.27C). The flies would not stay for a long time on the same inflorescence, the flies visited different phase inflorescences nearby, thus achieving successful cross-pollination. The flies moved around the spadix to feed on floral liquid on the pistillate phase

inflorescence (Figure 4.27D), and to collect pollen on the staminate phase inflorescence (Figure 4.27H). The number of fruit flies (Drosophilidae) that were present on inflorescences of *P. insignis* ranged from one to 15 individuals during any day of the anthesis.

Chabria beetles (Chrysomelidae) were another pollinator of *P. insignis*. These beetles were although mostly observed to consume pollen and stamens on staminate anthesis inflorescences (Figure 4.27E, 4.27H), but they also visited pistillate anthesis inflorescences (Figure 4.27B, 4.27C). The beetles may visit the inflorescences at any time between 0800 h to 1700 h each day, ranging from one to two individuals, the beetles usually stay longer on staminate anthesis inflorescences than on pistillate anthesis inflorescences. *Chabria* beetles may achieve pollination after visiting inflorescences at different phases of anthesis. The beetles may be more efficient as their big and low flat body can carry more pollen and deposit it more easily (body close contact with stigmas).

Besides, *Halticotoma valida* (Miridae) was another possible pollinator of *P. insignis* (one to two individuals), since they were presented at the inflorescences during both pistillate (Figure 4.27B) and staminate anthesis (Figure 4.27F). These insects moved around the spadix and fed on the exuded floral liquid.

Apart from that, Hover flies (Syrphidae) was another possible pollinator of *P. insignis*, the flies may arrive at any time of the day during anthesis (one to two individuals). The flies made repeated visits to different stage inflorescences nearby, with less than one minute per visit to consume stigmas liquid (Figure 4.27A, 4.27C) or collect pollen (Figure 4.27G), thus potentially achieving pollination.

In *P. scandens*, unknown flies (Diptera) were the only insect spotted to visit the inflorescences of the species during anthesis. These flies usually arrived alone at any time

of the day throughout the anthesis (Figure 4.28G – 4.28H), moved around the spadix to consume floral liquid at pistillate anthesis inflorescences or to collect pollen at staminate anthesis inflorescences.

4.8.6 Reproduction system

Fruits of *Pothos* spp. ripened in ca. two months. Natural fruit set percentage for *P. insignis* varied from 1.9% to 46.9% with an average of 11.85% (Table 4.3). Natural fruit set percentage was not calculated for *P. scandens* due to lack of available ripened infructescences. Autonomous self-pollination treatment did not set any fruit in *P. insignis* (not capable to self-pollinate without pollinator), and was not tested for *P. scandens* due to lack of available inflorescences as the inflorescences of this species were used for flowering observations. Each fruit of *P. insignis* and *P. scandens* had one to two seeds.

4.9 Schismatoglottis

4.9.1 Flowering pattern

The number of inflorescences of *Schismatoglottis* ranged from one to 12 per plant for different species; the species with one inflorescence (rarely two) were *S. colocasioidea*, *S. multinervia*, *S. roseopedes* (many plant/plantlets growing together, each with an inflorescence at different time), and *S. serratodentata*; the species with two to three inflorescences was *S. pellucida*; and the species with six to 12 inflorescences was *S. muluensis*. *Schismatoglottis* usually flowered in a seasonal pattern (uniformly throughout all population during some months), except *S. muluensis* and *S. roseopedes* (flowering occurring throughout its populations at different locations all year round). For species flowering in a seasonal pattern, some species flowered in mass during a short period (ca. a

month, more flowering occurring per day: *S. multinervia*, *S. pellucida*) or a longer period (ca. three months, *S. serratodentata*). *Schismatoglottis muluensis* flowered throughout the year, at least four plants were flowering if there was one inflorescence in pistillate anthesis each day. The interval between flowering for inflorescences of the same plant was two days, each plant was expected to flower for ca. three weeks (six inflorescences) to 1.5 months (12 inflorescences). Each plant was observed to flower twice a year, resting for a period of six months before next flowering. *Schismatoglottis pellucida* flowered twice a year (entire population), from January 2018 to February 2018, June 2018 to July 2018 and in January 2019, the interval of flowering was ca. four to five months for the entire population (some plant may skip a flowering season). The interval between flowering for inflorescences from the same plant was two days, each plant finished to flower in six to 10 days, at least four plants were flowering if there was a pistillate anthesis each day. *Schismatoglottis roseopedes* flowered all year round, there was always some plants flowering while some other plants were resting or had ripened infructescences. Each plant of *S. roseopedes* was expected to flower three to four times a year because new inflorescence may emerge one to two months after infructescences from the previous flowering ripened. *Schismatoglottis colocasioidea* flowered three times per year (entire population), from December 2017 to February 2018, June 2018 to August 2018 and November 2018 to January 2019, the interval of flowering was ca. two months for the entire population. Each plant of *S. colocasioidea* flowered ca. two to three times a year, each plant may skip a flowering season. Some plants of *S. colocasioidea* had a second inflorescence that flowering sometime after the first inflorescence ended anthesis. *Schismatoglottis multinervia* flowered three times a year (entire population), from January 2018 to February 2018, May 2018 to June 2018, September 2018 to October 2018, January 2019, the interval of flowering was ca. two months for the

entire population (some plant may skip a flowering season), each plant flowered two to three times a year. *Schismatoglottis serratodentata* flowered three times a year (entire population), each time ca. two to three months, from December 2018 to January 2019, May 2018 to July 2018 and November 2018 to December 2018, the interval of flowering was ca. four months for the entire population (some plants may skip a flowering season), each plant flowered two to three times a year.

4.9.2 Timing of anthesis and floral changes

The anthesis in the six species of *Schismatoglottis* lasted between 24 - 25.5 hours (Figure 4.29 – Figure 4.40). The pistillate anthesis in five species of *Schismatoglottis* started between 0430 - 0710 h, Day 1 (0430 h in *S. roseopedes*, 0530 - 0600 h in *S. serratodentata*, 0600 h in *S. colocasioidea* and *S. muluensis*, and 0610 - 0710 h in *S. multinervia*), and later in *S. pellucida* (0930 h, Day 1) (Table 4.1). The pistillate anthesis of all investigated *Schismatoglottis* spp. was indicated by the inflation of spathe (ca. 0.15 - 0.2 cm space between the constriction of spathe and the sterile interstice), followed by gaping of the spathe along the spathe margin, the appearance of wet and colourless stigmas, and the emission of a strong esteric (“wasabi alcohol/whisky”) floral odour from the appendix zone (strength of floral odour increased as the size of spathe gap widened). In *S. colocasioidea*, the spathe started to inflate and a weak odour was produced at 0600 h (Figure 4.30A), the spathe gap started to open at 0630 h (Figure 4.30B – 4.30C) and rapidly increased to its widest around 0715 h (2.5 cm) (Figure 4.30D). The strongest floral odour was emitted between 0700 - 0730 h (extend 5 - 10 cm away from the inflorescence), the spathe gap gradually closed back and the floral odour weakened between 0730 - 0900 h (Figure 4.30E – 4.30F). The spathe gap started to open at 0610 h in *S. multinervia* (Figure 4.32A), rapidly increased to its widest (ca.

0.6 - 1.2 cm) (Figure 4.32B) with the strongest floral odour (extend 3 - 5 cm away from the inflorescence) produced between 0630 - 0700 h, the spathe gap gradually closed back and the floral odour weakened between 0700 - 0830 h (Figure 4.32C – 4.32D). The spathe of *S. muluensis* started to inflate with a weak floral odour since 0600 h, the spathe gap gradually open to its widest (ca. 0.8 - 1.2 cm) with a strongest floral odour (extend 3 - 5 cm away from the inflorescence) released around 0620 - 0650 h (Figure 4.34A), the spathe gap gradually closed back and the floral odour also weakened between 0700 - 0830 h. In *S. pellucida*, the spathe started to inflate and a weak floral odour was produced at 0930 h (Figure 4.36A), the spathe gap started to open at 0950 h and gradually increased to its widest (ca. 1 cm) with a strongest floral odour released (extend 4 - 5 cm away from the inflorescence) at 1020 h (Figure 4.36B), the spathe gap gradually closed back and the floral odour weakened between 1030 - 1130 h (Figure 4.36C – 4.36D). The spathe of *S. roseopedes* started to inflate since 0400 h, the spathe gap started to open at 0430h (Figure 4.38A, 4.38B) and gradually increased to its widest (ca. 0.2 cm) at 0530 h (Figure 4.38C) with a strongest floral odour emitted (extend 1cm away from the inflorescence), the spathe gap gradually closed back and the floral odour weakened between 0600 - 0700 h (Figure 4.38F). The spathe gap started to open and a weak floral odour started to release at 0530 h in *S. serratodentata* (Figure 4.40A – 4.40B), the spathe gap rapidly increased to its widest (ca. 0.6 cm) with the release of a strongest floral odour (extend 3 - 5 cm away from the inflorescence) at 0600 h (Figure 4.40C), the spathe gap gradually closed back and the floral odour weakened between 0630 - 0700 h (Figure 4.40D). The pistillate anthesis ended when the stigmas turned drier and brown, the spathe closed back and the floral odour weakened. The pistillate anthesis ended between 0830 - 1000 h of Day 1 for five species of *Schismatoglottis* (0830 h in *S. roseopedes*, 0900 h in *S. colocasioidea* and *S. serratodentata*, 1000 h in *S. muluensis* and *S. multinervia*),

and at 1230 h of Day 1 in *S. pellucida*. All investigated *Schismatoglottis* spp. started to release pollen after the ca. 0.15 - 0.2 cm space between the constriction of the spathe and the sterile interstice was closed. The staminate anthesis started on the following day when pollen started to be released between 0500 h to 0600 h of Day 2 (0500 h in *S. roseopedes*, 0500 - 0550 h in *S. serratodentata*, 0530 h in *S. colocasioidea*, 0530 - 0630 h in *S. multinervia*, 0600 h in *S. muluensis*), except at 0920 h of Day 2 in *S. pellucida*. A strong esteric floral odour continued to be detected in *S. pellucida* during the staminate anthesis but only a weak floral odour was detected in the other species. The upper spathe abscised before the pollen release in *S. colocasioidea* (0500 - 0530 h) (Figure 4.30K), *S. muluensis* (0400 - 0500 h) (Figure 4.34B), *S. roseopedes* (0420 - 0430 h) (Figure 4.38G, 4.38H), *S. serratodentata* (0430 - 0530 h) (Figure 4.40G, 4.40H) but after pollen was released in *S. multinervia* (0610 - 0640 h) (Figure 4.32E) and *S. pellucida* (0950 - 1100 h) (Figure 4.36G). The anthesis ended by 0600 h till 0735 h of Day 2 (1100 h, Day 2 in *S. pellucida*). The appendix and the staminate zone senesced few days post anthesis (Figure 4.31B), leaving the lower part of the spathe with developing fruits persisting until the fruits ripened (Figure 4.31C). After 1.5 – two months, the persistent lower spathe split in the middle to expose the ripe fruits (Figure 4.29B, 4.33B, 4.35C, 4.39C). Fruits of all investigated species were dispersed by ants (Figure 4.29C, 4.33C, 4.35B, 4.37B).



Figure 4.29: *Schismatoglottis colocasioidea* (A) Mature plant with inflorescence. (B) Ripened infructescence about to split. (C) Ants attempting to collect fruits.

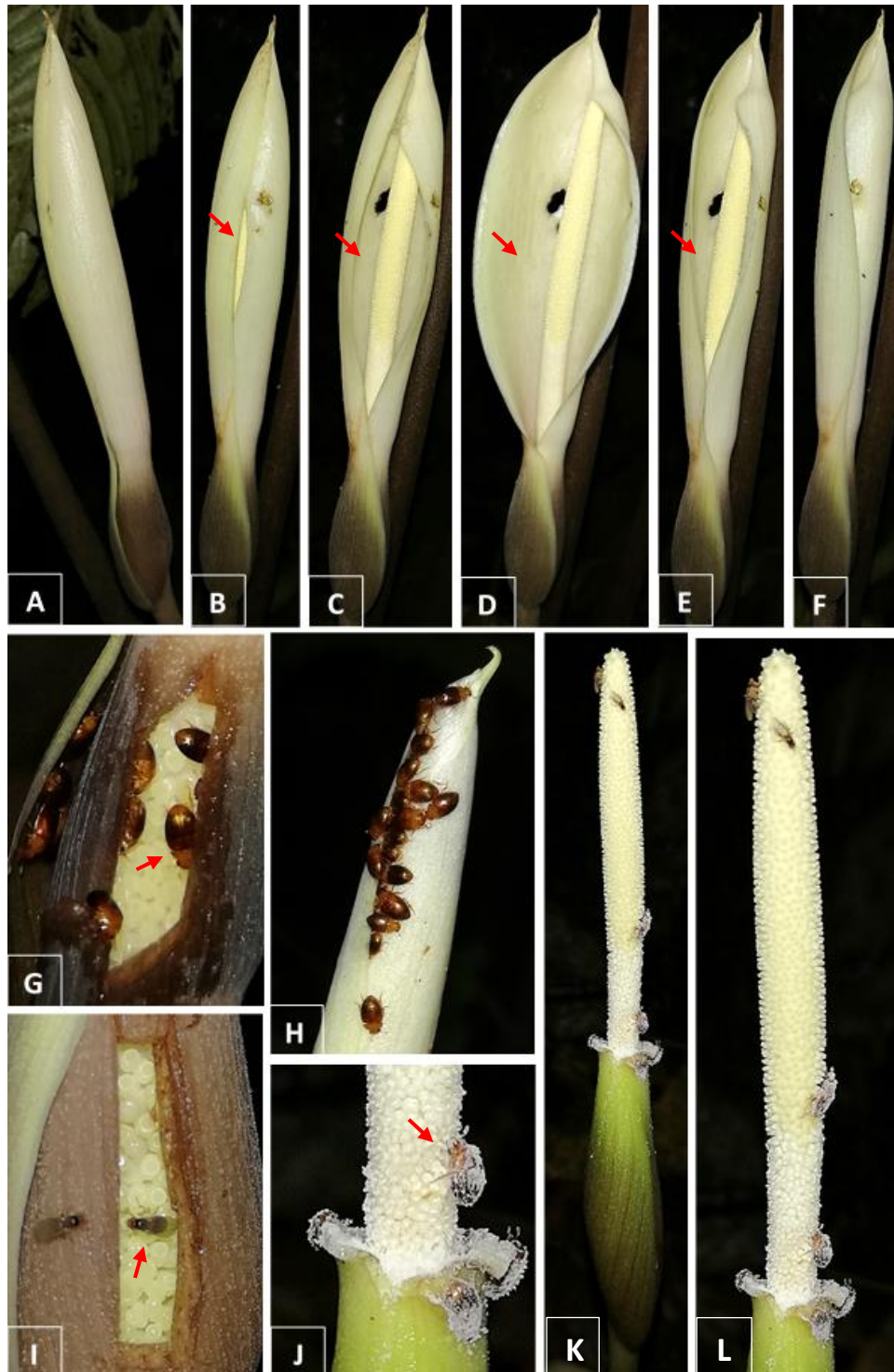


Figure 4.30: Inflorescence of *Schismatoglottis colocasioidea* at various stages. (A-F) Spathes movement during pistillate anthesis, upper spathe opening and closing back. (G) *Cycreon* beetles (Hydrophilidae) moving on pistillate flowers. (H) *Cycreon* beetles moving out from tip of upper spathe when disturbed. (I) *Colocasiomyia* flies (Drosophilidae) moving on pistillate flowers. (J) *Cycreon* beetles collecting pollen. (K-L) Staminate anthesis, spathe abscised.



Figure 4.31: *Schismatoglottis multinervia* (A) Mature plant with inflorescence. (B) Staminate anthesis, upper spathe abscised. (C) Immature infructescence.

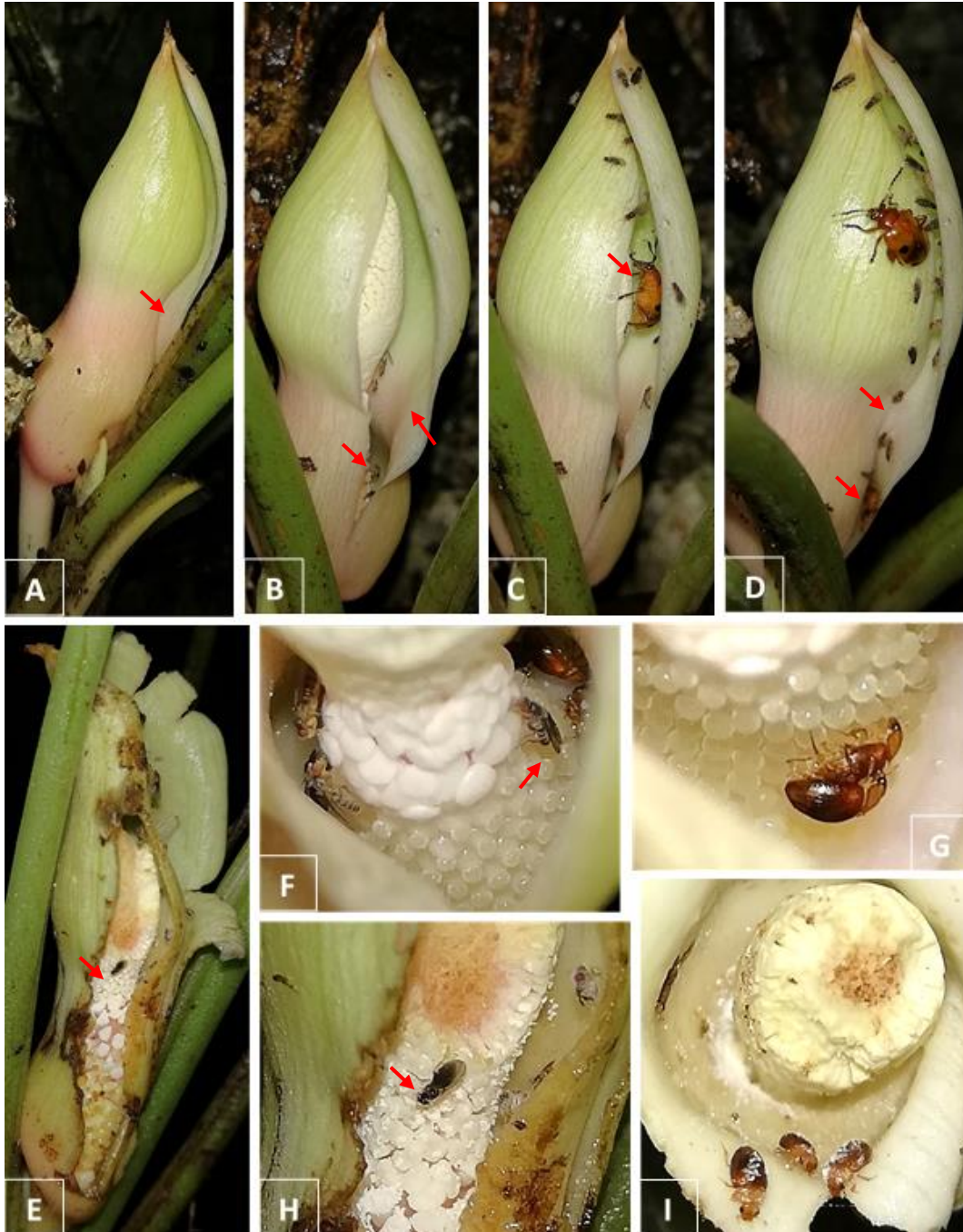


Figure 4.32: Inflorescence of *Schismatoglottis multinervia* (A-D) Changes of inflorescence during pistillate anthesis, spathe gap opening and closing back, insects (Flies, *Cycreon* beetles and *Chaloenus* beetles) entering. (E) Staminate anthesis. (F) *Colocasiomyia* flies (*Drosophilidae*) and *Cycreon* beetles (*Hydrophilidae*) at pistillate zone. (G) *Cycreon* beetles mating on pistillate flowers. (H) *Colocasiomyia* flies collecting pollen. (I) *Cycreon* beetles about to depart after collecting pollen.

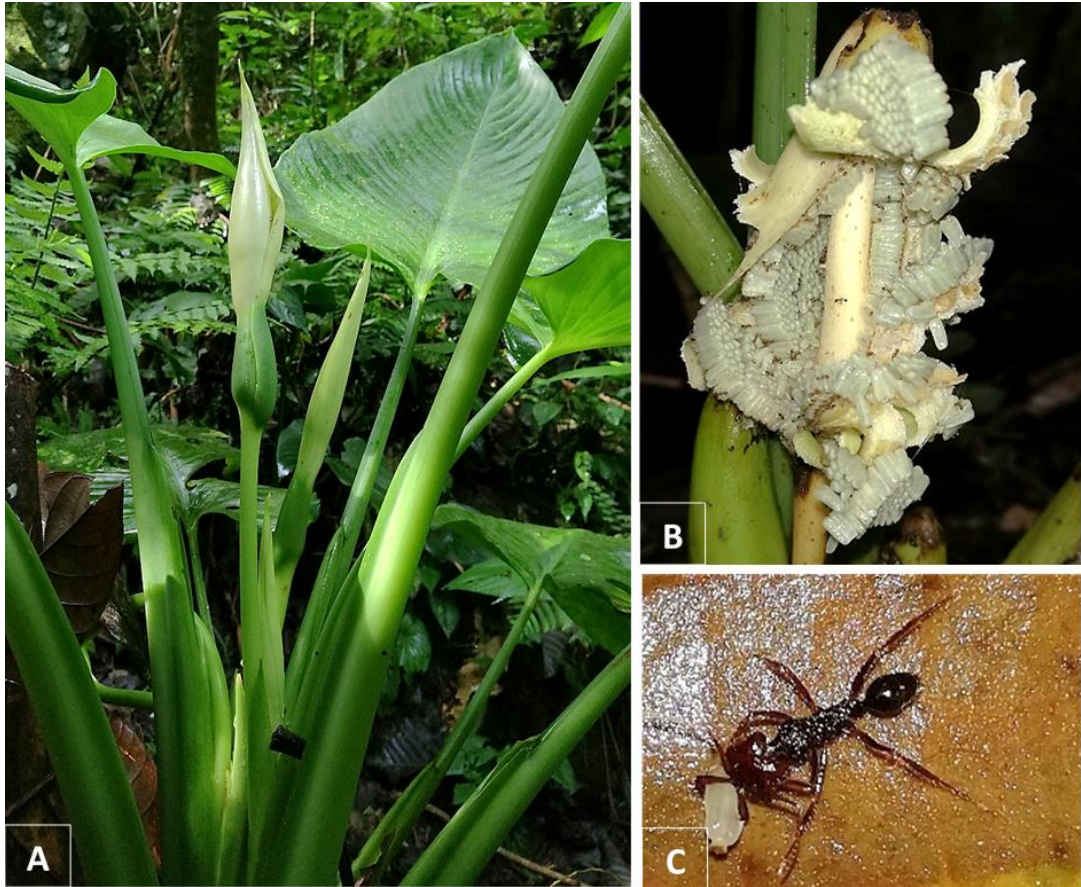


Figure 4.33: *Schismatoglottis muluensis* (A) Mature plant with inflorescences. (B) Ripened infructescence splitting by its middle. (C) Ant disperses seed.

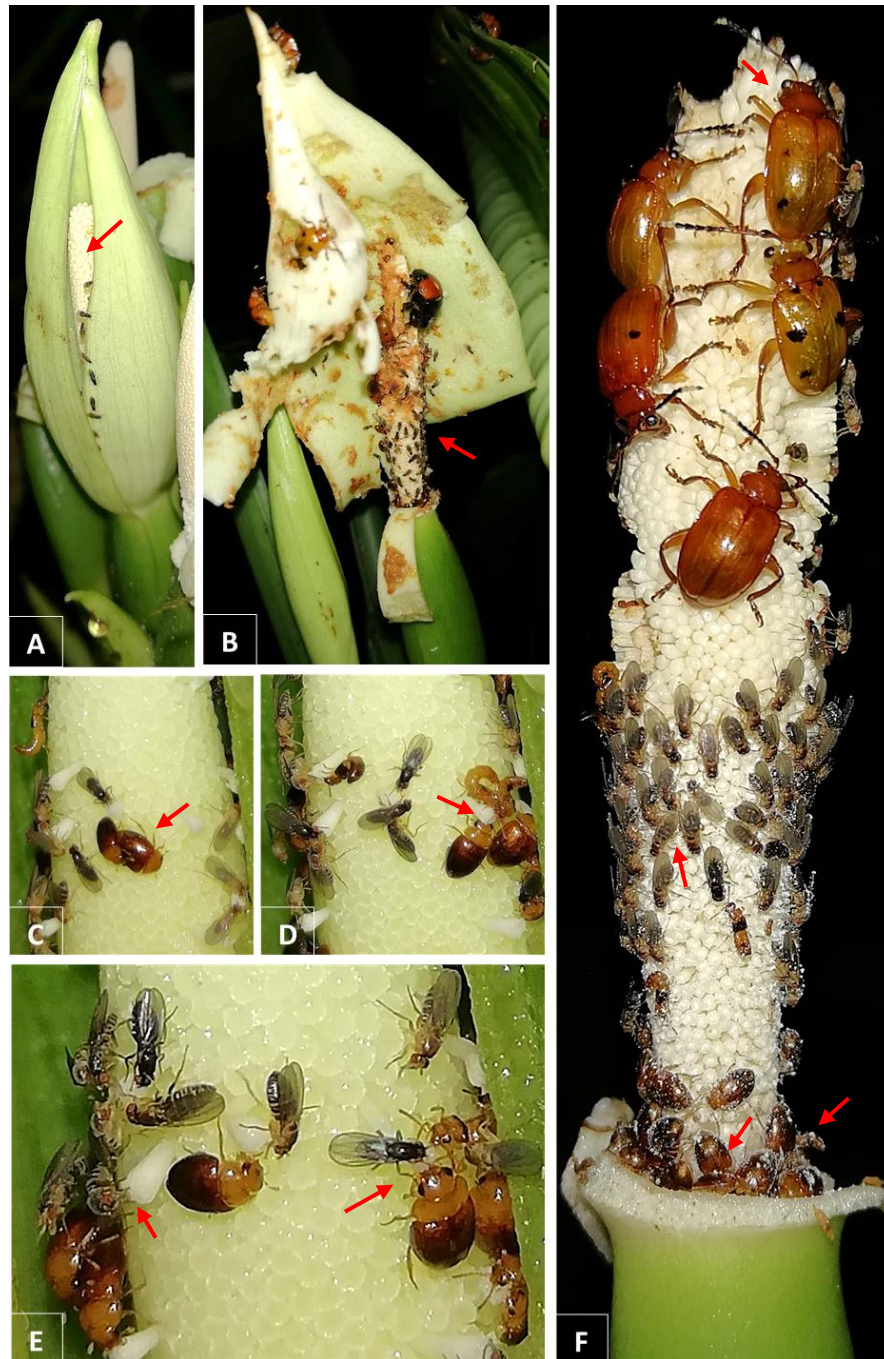


Figure 4.34: Inflorescence of *Schismatoglottis muluensis* at different stages. (A) Pistillate anthesis, a small open spathe gap allowing insects to enter. (B) Upper spathe abscised before staminate anthesis started, insects remained on the inflorescence until pollen released. (C-E) Insect activities on the pistillate zone during pistillate anthesis, insects (*Colocasiomyia* flies, *Cycreon* beetles and rove beetles) consuming wetness on interpistillar staminodes and pistillate flowers, *Cycreon* beetles mating. (F) Insects activities during staminate anthesis, *Chaloenus* beetles chewing the appendix, flies collecting and brushing off pollen at upper staminate zone, *Cycreon* beetles and rove beetles collecting pollen at bottom of staminate zone.



Figure 4.35: *Schismatoglottis pellucida* (A) Mature plant with inflorescence. (B) Ant disperses fruit. (C) Ants collect fruits from a ripened infructescence.

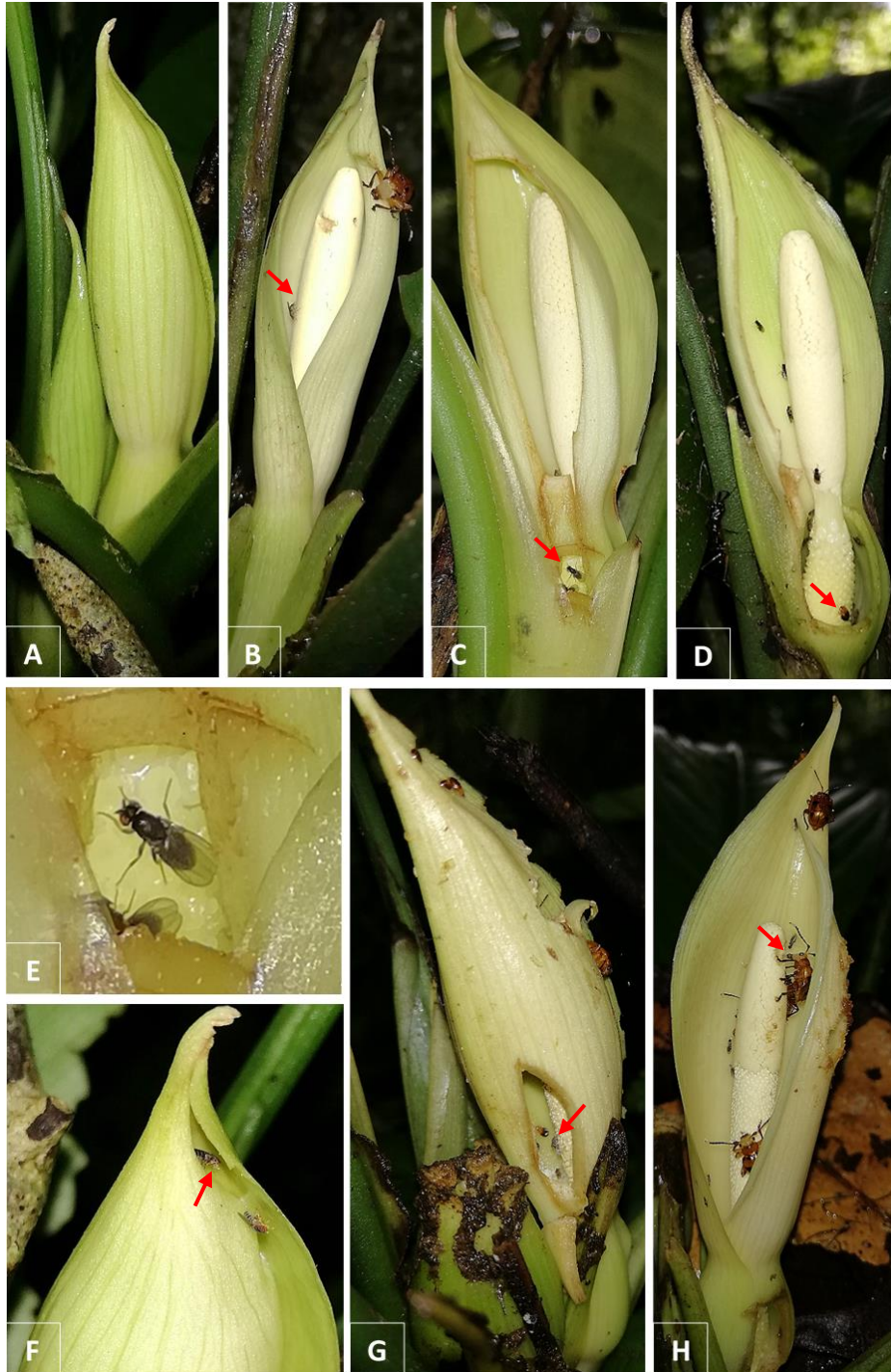


Figure 4.36: *Schismatoglottis pellucida* (A) Inflorescence started to open during the pistillate anthesis. (B) A spathe gap formed, and insects entering. (C-D) Spathe closed back, spathe removed, *Colocasiomyia* flies (Drosophilidae) and *Cycreon* beetles at pistillate zone. (E) *Colocasiomyia* flies on pistillate flowers during pistillate anthesis. (F) Flies moving out from tip of spathe when disturb. (G) Flies and *Cycreon* beetles collecting pollen during the staminate anthesis before spathe abscission. (H) Spathe started to open and abscised, *Chaloenus* beetles consuming the appendix.



Figure 4.37: *Schismatoglottis roseopedes* (A) Mature plant with inflorescence. (B) Ants collecting fruits from a ripened infructescence.

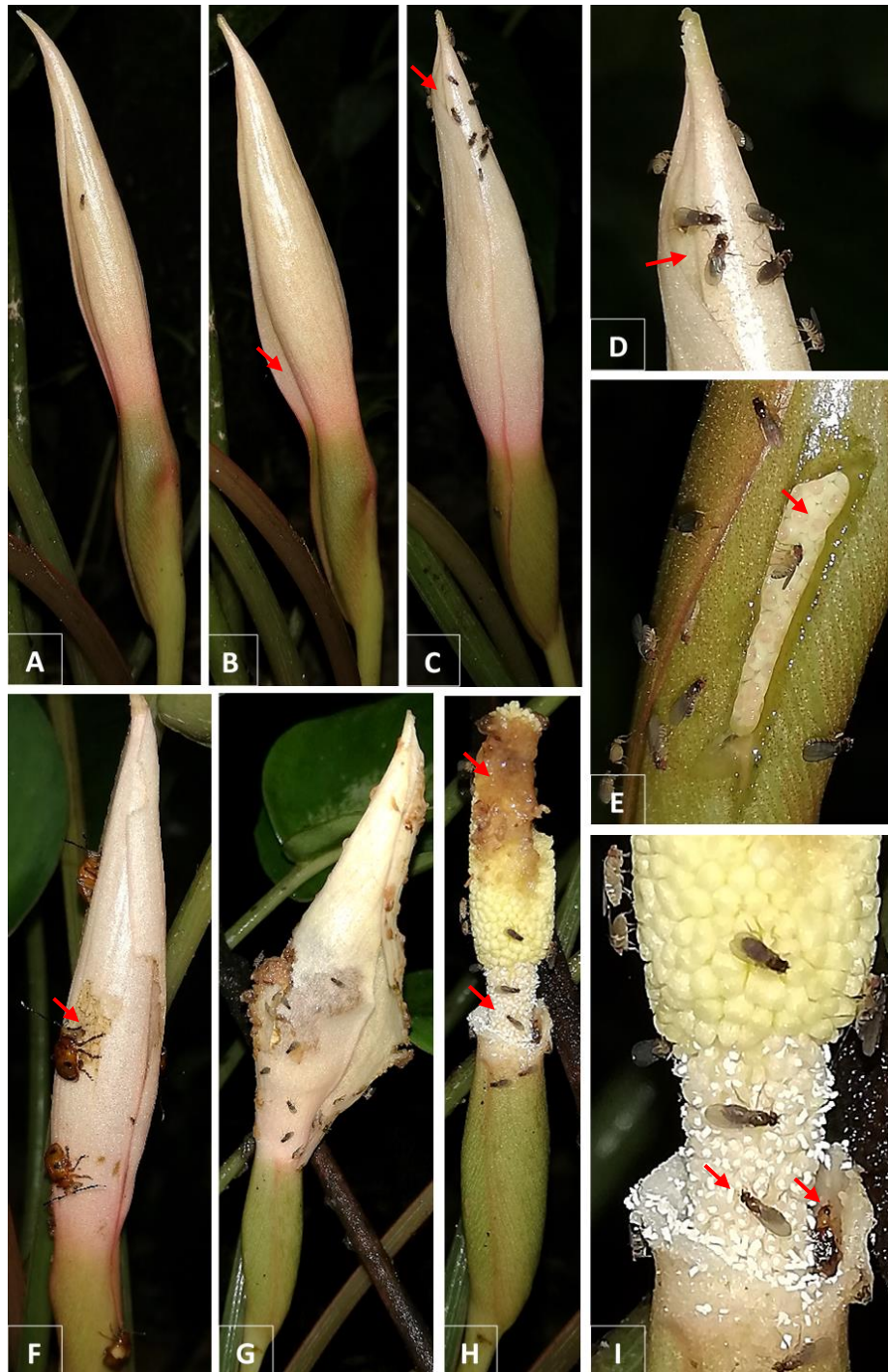


Figure 4.38: Inflorescence of *Schismatoglottis roseopedes* (A-C) Pistillate anthesis, upper spathe slightly opening and closing back. (D) *Colocasiomyia* flies moving out from tip of spathe when disturbed. (E) Pistillate flowers wet, flies moving on pistillate flowers. (F) *Chaloenus* beetles (Chrysomelidae) chewing upper spathe to get into the appendix zone. (G) Upper spathe started to abscise before the pollen release. (H) Staminate anthesis, pollen released, appendix destroyed by *Chaloenus* beetles. (I) *Colocasiomyia* flies (Drosophilidae) and *Cycreon* beetles (Hydrophilidae) collecting pollen.

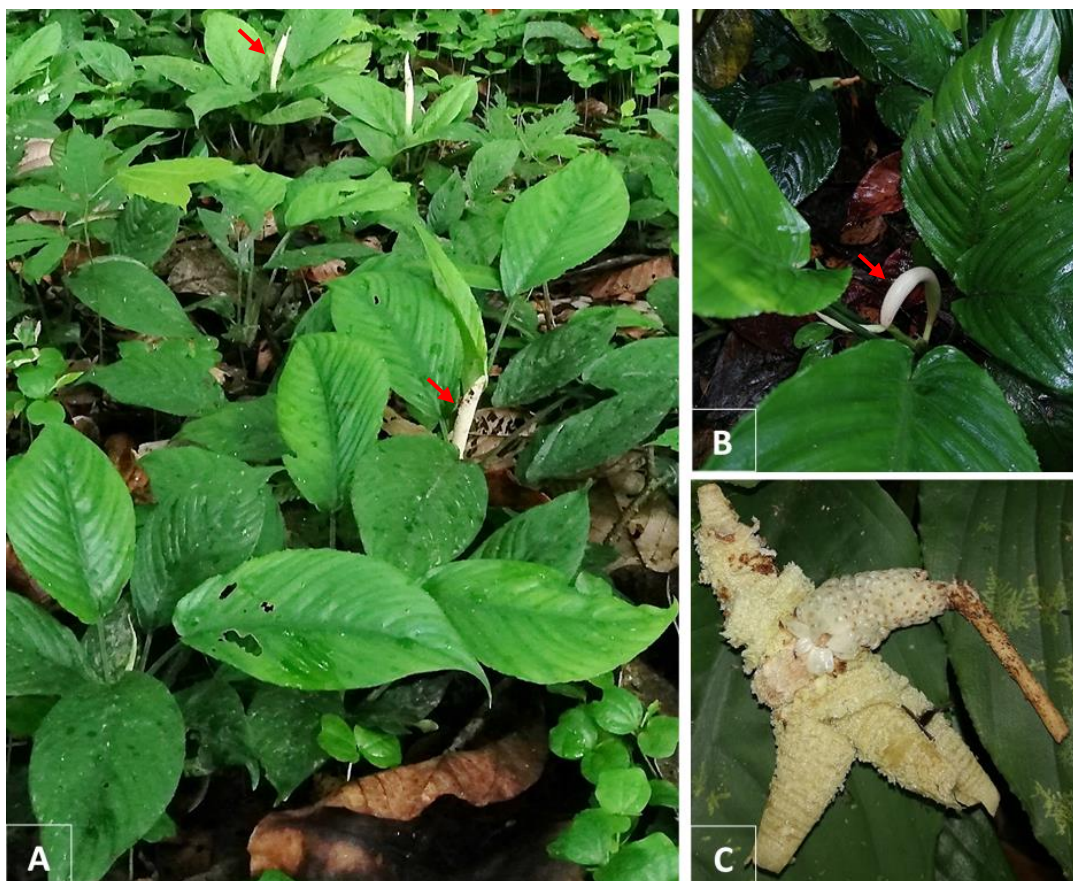


Figure 4.39: *Schismatoglottis serratodentata* (A) Population of mature plant with inflorescence (B) Plant with an unusual bended inflorescence. (C) Mature infructescence split.

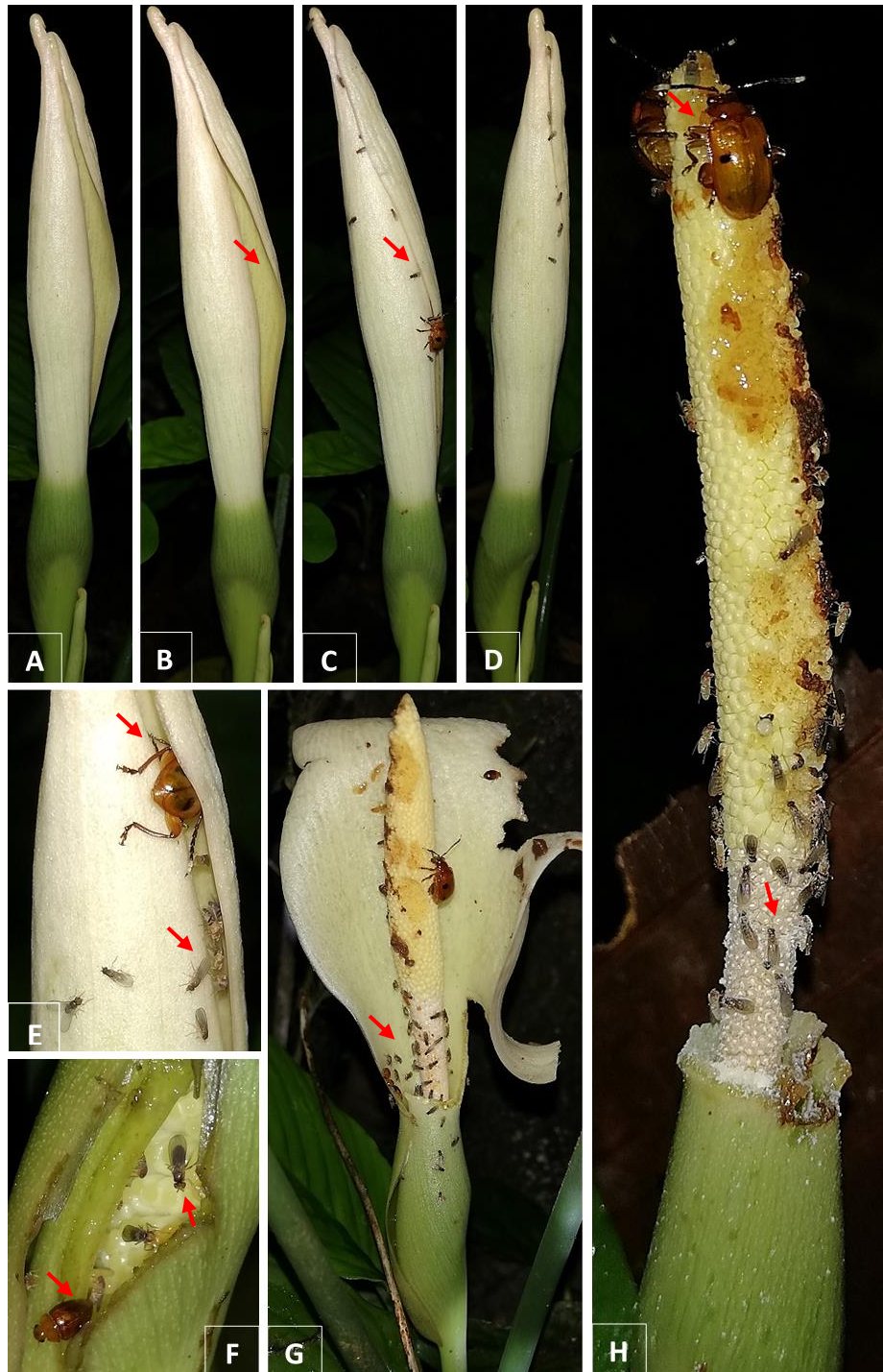


Figure 4.40: Inflorescence of *Schismatoglottis serratodentata* at various stages. (A-D) Pistillate anthesis, upper spathe slightly opening and closing back, allowing the insects to enter. (E) *Chaloenus* beetle (Chrysomelidae) squeezing through the slender gap, flies could easily enter. (F) *Colocasiomyia* flies (Drosophilidae) and *Cycreon* beetles (Hydrophilidae) moving on pistillate flowers. (G) Upper spathe abscised before pollen was released, insects remaining on the inflorescence. (H) Staminate anthesis, *Chaloenus* beetles chewing appendix, *Colocasiomyia* flies collecting pollen.

4.9.3 Floral traits

The floral odour was detected once in the morning during the pistillate anthesis in almost all the studied *Schismatoglottis* (except *S. pellucida*). The floral odour persisted throughout the anthetic period (detected once in the morning during pistillate and staminate anthesis) in *S. pellucida*. The floral odour during the pistillate anthesis was like a “strong esteric/wasabi alcohol smell” in all *Schismatoglottis* spp. The floral odour originated from the appendix.

4.9.4 Floral rewards

The floral liquid was present on pistillate flowers, interpistillar staminodes and sterile interstices during the pistillate anthesis in *Schismatoglottis*. The floral liquid rewarded *Colocasiomyia* flies (Drosophilidae), *Cycreon* beetles (Hydrophilidae) and rove beetles (Staphylinidae) that visited the pistillate zone. There was a 0.15 to 0.2 cm gap between the constriction of the spathe and the sterile interstices or the staminate zone, or a space of 0.2 to 0.25 cm between the inner spathe wall and the pistillate zone that allowed these small insects to enter into the pistillate zone. The appendix, the staminate zone, the pistillate zone and the inner surface of spathe were mating sites for *Colocasiomyia* flies (Drosophilidae) in the studied *Schismatoglottis*. *Cycreon* beetles (Hydrophilidae) mate on the pistillate zone and the inner surface of the spathe in *Schismatoglottis*. Besides, the appendix zone and the staminate zone were the mating sites of *Chaloenus* beetles (Chrysomelidae) in *Schismatoglottis*. Rove beetles (Staphylinidae) mate onto the pistillate zone and *Parastasia* beetles (Scarabaeidae) mate on the appendix zone and the staminate zone in *Schismatoglottis muluensis*.

4.9.5 Pollinators and their behaviours

Colocasiomyia flies (Drosophilidae) were the main pollinators of the studied *Schismatoglottis*, the number of flies that visited inflorescences of *Schismatoglottis* ranged from one to 20 individuals in *S. colocasioidea*, two to 25 individuals in *S. multinervia*, 43 to 141 individuals in *S. muluensis*, eight to 124 individuals in *S. pellucida*, four to 107 individuals in *S. roseopedes*, and 12 to 90 individuals in *S. serratodentata* (Table 4.2). The flies arrived around 0550 h (Day 1) during the pistillate anthesis in *Schismatoglottis roseopedes* (Figure 4.38D) and *S. serratodentata* (Figure 4.40E), 0610 h in *S. muluensis*, 0620 - 0630 h in *S. colocasioidea* and *S. multinervia*, and 0930 h in *S. pellucida* (Figure 4.36F). The flies entered straight away into the pistillate zone upon arrival at newly opened inflorescences in all the investigated *Schismatoglottis* spp. (Figure 4.32B). In the pistillate zone, the flies moved on the pistillate flowers and interpistillar staminodes while feeding on the exuded floral liquid (Figure 4.30I, 4.32F, 4.34C, 4.34D, 4.34E, 4.36C, 4.36E, 4.38E, 4.40F), they may thus have pollinated the pistillate flowers. After that, some of the flies remained inside the pistillate zone to feed on the floral liquid or moved up to the appendix zone to feed on seepages from previously destroyed spadix parts by *Chaloenus* beetles or *Parastasia* beetles (*S. muluensis*). The flies stayed in the inflorescence throughout anthesis in all the investigated *Schismatoglottis* spp. Before the staminate anthesis, the gap between the constriction of the spathe and the staminate zone or the sterile interstice tightened, forcing all the insects to move up to the upper zone and to wait until the start of the staminate anthesis. When pollen started to be released, the flies actively collected pollen at the staminate zone and brushed off most pollen for the other insects (Figure 4.32E, 4.32H, 4.34F, 4.36G, 4.38I, 4.40H). The flies left around 0535 h (Day 2) in *S. serratodentata*, 0550 h in *S. roseopedes*, 0620 h in *S. colocasioidea* and *S. multinervia*, before 0640 h in *S. muluensis*,

and 1000 h in *S. pellucida*. Besides *Colocasiomyia* flies, *Schismatoglottis* spp. were also pollinated by *Cycreon* beetles and rove beetles, and visited by *Chaloenus* beetles and *Parastasia* beetles.

Cycreon beetles (Hydrophilidae) were another pollinator of *Schismatoglottis*, the number of *Cycreon* beetles that visited *Schismatoglottis* ranged from five to 28 individuals, one to 25 individuals, 25 to 41 individuals, five to six individuals, three to 25 individuals and one to 13 individuals in *S. colocasioidea*, *S. multinervia*, *S. muluensis*, *S. pellucida*, *S. roseopedes* and *S. serratodentata* respectively. *Cycreon* beetles arrived during the pistillate anthesis (Day 1) around 0600 h in *S. roseopedes*, 0620 - 0640 h in *S. serratodentata*, 0630 h in *S. colocasioidea* (Figure 4.30H), 0700 h in *S. multinervia* and *S. muluensis*, 1030 h in *S. pellucida*. The beetles directly entered the pistillate zone upon arrival at the pistillate phase inflorescences, the beetles fed on exudations from the pistillate flowers and interpistillar staminodes while pollinating the pistillate flowers (Figure 4.30G, 4.32F, 4.32G, 4.34C, 4.34D, 4.34E, 4.36D, 4.40F). The beetles stayed throughout anthesis in the lower part of the spathe chamber, the beetles moved up to staminate zone before the start of staminate anthesis. The beetles stayed at the constriction level and were dusted with pollen during pollen release (Figure 4.30J, 4.30L, 4.34F, 4.36G, 4.38I). The beetles left the inflorescence on Day 2 before 0600 h in *S. roseopedes*, 0550 - 0630 h in *S. serratodentata*, around 0630 h in *S. colocasioidea*, before 0700 h in *S. multinervia* (Figure 4.32I) and *S. muluensis*, before 1030 h in *S. pellucida*.

Atheta beetles (Staphylinidae, Athetina) were only found in *S. muluensis* and *S. serratodentata* out of the six investigated *Schismatoglottis* species. There were two to eight individuals of *Atheta* beetles visiting inflorescences of *S. muluensis* and two to three

individuals of the beetles visiting those of *S. serratodentata*. *Atheta* beetles arrived before 0700 h in *S. muluensis* and *S. serratodentata*. The beetles stayed in the lower part of the spathe chamber after arrival, they were actively moving on the pistillate flowers to feed on exuded floral liquid (Figure 4.34C, 4.34D, 4.34E). They moved up to the staminate zone when the gap between the constriction of the spathe and the staminate zone or the sterile interstice was closed. The beetles collected the pollen brushed off by *Colocasiomyia* flies (Drosophilidae) at the constriction level together with *Cycreon* beetles (Figure 4.34F) and left the inflorescences before 0700 h in *S. muluensis* and *S. serratodentata*.

Chaloenus beetles (Chrysomelidae) were frequent visitors of *Schismatoglottis* inflorescences, the beetles were spotted to visit all investigated species of *Schismatoglottis*. The number of *Chaloenus* beetles that visited *Schismatoglottis* ranged from one to two individuals in *S. colocasioidea*, one to four individuals in *S. multinervia*, two to seven individuals in *S. muluensis*, one to six individuals in *S. pellucida*, one to eight individuals in *S. roseopedes*, and two to eight individuals in *S. serratodentata*. The beetles usually destroyed the appendix zone of the visited inflorescences but they never moved down to the pistillate zone because they were too large to access to the pistillate zone (Figure 4.32C, 4.32D, 4.34F, 4.36H, 4.38F, 4.40E, 4.40H).

Parastasia beetles (Scarabaeidae) were sometimes spotted at the appendix zone of *S. muluensis* (Figure 4.34B), the beetles were just visitors of *S. muluensis* because they never move down to pistillate zone of the species, the beetles only chewed the appendix zone, there were one to two *Parastasia* beetles visiting *S. muluensis* during anthesis.

4.9.6 Reproductive system

Fruits of *Schismatoglottis* spp. took 1.5 to two months to ripe. For *Schismatoglottis*, fruit set percentage was 97.3% for *S. colocasioidea*, 98.1% for *S. muluensis* (96.8% - 99.1%), 87.4% for *S. roseopedes*, and 67.3% for *S. serratodentata* (38.2% - 92.5%) (Table 4.3). Natural fruit set percentage was not counted for *S. multinervia* and *S. pellucida* due to lack of available ripened infructescences. Autonomous self-pollination treatment did not set any fruit in all investigated *Schismatoglottis* species, which means they are not capable to self-pollinate without pollinator.

4.10 Scindapsus

4.10.1 Flowering pattern

Scindapsus seemed to flower throughout the year, flowering numbers were difficult to estimate because flowering mostly occur high up on the host plants. The inflorescences were produced from axil of leaves and mostly from terminal of shoots. *Scindapsus* seemed to have a higher number of flowerings during some months.

4.10.2 Timing of anthesis and floral changes

Scindapsus longistipitatus flowered for ca. 30 hours (Figure 4.41 and Figure 4.42). A day before the pistillate anthesis, the spathe started to inflate (Figure 4.42A). The pistillate anthesis started at ca. 0400 h (Day 1) with a ca. 0.2 - 0.5 cm slit gap opened along the margin of the spathe (Figure 4.42B), the emission of a “resinous” floral odour from the spadix (Table 4.1), and the appearance of raised, wet and colourless stigmas. The pistillate anthesis ended at 1700 h (Day 1) when stigmas dried, the floral odour weakened, and the spathe abscised (Figure 4.42C). The end of the pistillate anthesis was followed by 11 hours of transition

inter-sexual stage. The staminate anthesis started the next day at 0400 h when pollen started to be released randomly from the bisexual flowers of the spadix (Figure 4.42F). After a week of post-anthesis, the spadix turned green from orange (during anthesis) (Figure 4.41B). The fruits took ca. three months to ripe, the stylar region dropped off when the fruits ripened to expose the mature seeds (Figure 4.41C).



Figure 4.41 : *Scindapsus longistipitatus* (A) Mature plant with infructescence. (B) Inflorescence during post-anthesis. (C) Ripened infructescence shedding off stylar region to expose the seeds.

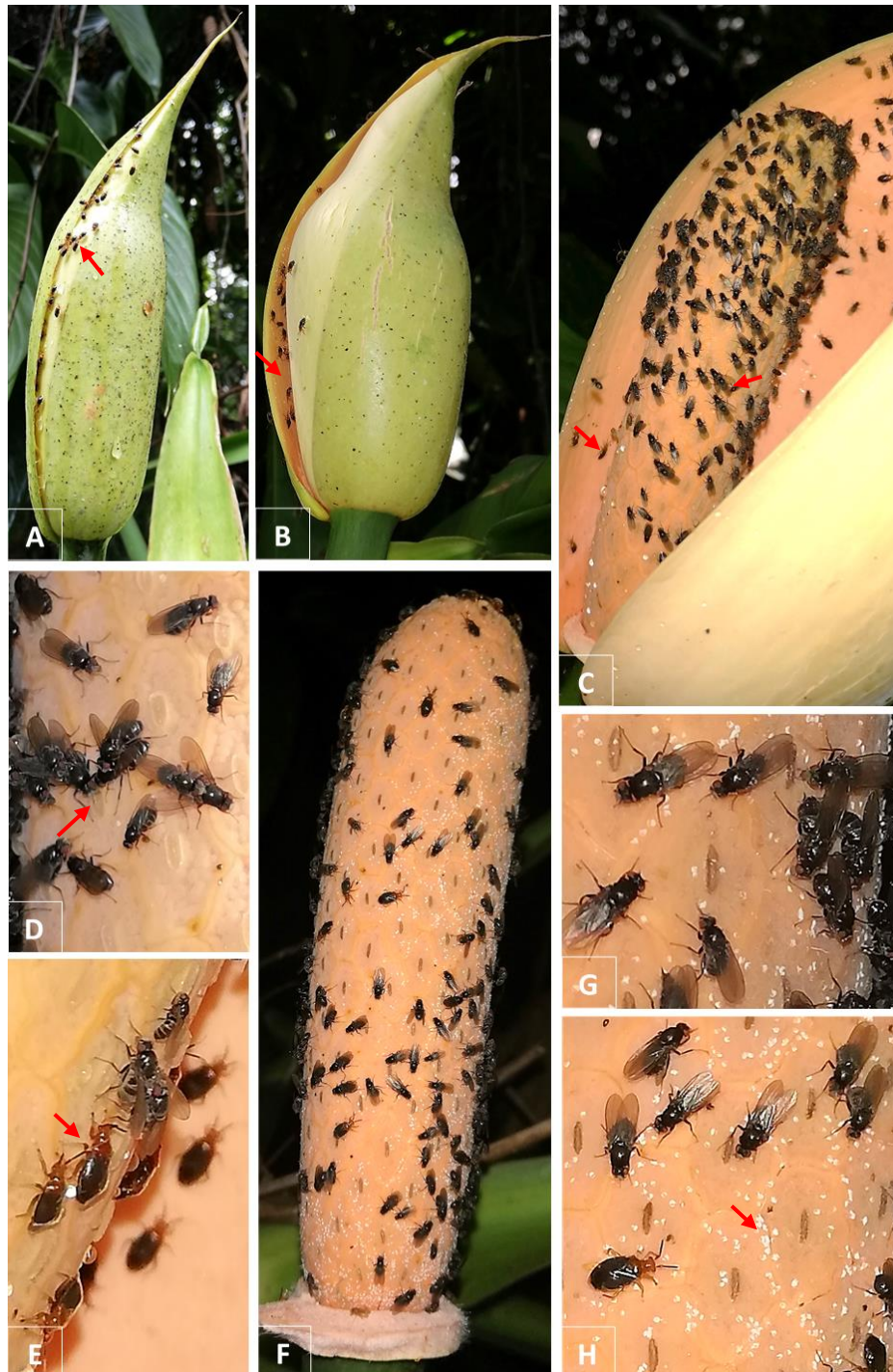


Figure 4.42: Inflorescence of *Scindapsus longistipitatus* at various stages. (A) Inflorescence about to open, *Halticotoma valida* (Miridae) arrived first. (B) Pistillate anthesis, spathe opened by a narrow gap and with a floral chamber expanded, insects entering. (C) Flies (Drosophilidae) and *H. valida* stayed on inflorescence when spathe abscised. (D-E) Flies mating and feed on stigmatic secretion during the pistillate anthesis, *H. valida* also fed on stigma secretion. (F) Staminate anthesis, insects collecting pollen. (G-H) Flies and *H. valida* collecting pollen.

4.10.3 Floral traits

The floral odour was detected only during the pistillate anthesis in *Scindapsus longistipitatus* and was like a “resinous smell”. The floral odour originated from the spadix.

4.10.4 Floral rewards

Floral secretion was present on stigmas during the pistillate anthesis in *Scindapsus longistipitatus*, this floral liquid rewarded fruit flies (Drosophilidae) and *H. valida* (Miridae) that visited the inflorescences. There was a 0.2 to 0.5 cm spathe gap that allowed the small insects to enter the floral chamber during the pistillate anthesis. The entire spadix and the inner surface of the spathe of *S. longistipitatus* were the mating sites for the Fruit flies (Drosophilidae) and *H. valida* (Miridae).

4.10.5 Pollinators and their behaviours

Fruit flies (Drosophilidae) were the main pollinators of *Scindapsus longistipitatus*, there were 250 to 500 flies per inflorescence during anthesis (Table 4.2). The flies probably arrived around 0600 h (Day 1: pistillate anthesis), they moved along the spadix to consume floral liquid while pollinating the pistillate flowers, some of the flies mated on the pistillate flowers (Figure 4.42D, 4.42E) and some others faced on the inner surface of the spathe together with another insect visitor (Miridae) in the floral chamber. The flies remained on the spadix after the spathe dropped at 1700 h, and they stayed until the next morning to collect pollen at 0400 h and leave around 0600 h (Figure 4.42G, 4.42H).

Halticotoma valida (Miridae) were visitors of *S. longistipitatus*, the insects stayed outside the inflorescence a week before the pistillate anthesis started (Figure 4.42A). The insects moved into the floral chamber during the pistillate anthesis to feed on exuded floral

liquid exuded (Figure 4.42E). They had mostly left the inflorescence before the staminate anthesis started. The number of *H. valida* that visited the inflorescences of this species ranged from 25 to 45 individuals.

4.10.6 Reproductive system

Fruits of *Scindapsus longistipitatus* ripened in three months. Natural fruit set percentage was not counted for *Scindapsus longistipitatus* due to lack of available ripened infructescences. Autonomous self-pollination treatment was also not tested to *S. longistipitatus* due to lack of available inflorescences. Each fruit of *S. longistipitatus* had a single seed.

CHAPTER 5

DISCUSSION

5.1 Flowering duration

Most unisexual-flowered species have a short anthetic duration than bisexual-flowered species. Out of the 21 studied taxa, bisexual-flowered taxa such as *Pothos* (10-18 days) and *Lasia* (7-8 days) have a longer anthetic duration, *Anadendrum* sp. and *Scindapsus* has anthetic duration of 4 days and 2 days respectively. The 15 unisexual-flowered taxa (*Aglaonema*, *Alocasia*, *Amorphophallus julaiihii*, *Bucephalandra*, *Homalomena*, and *Schismatoglottis*) have short anthetic duration of 2 days. *Amorphophallus hewittii* has anthetic duration of 5 days, is significant longer than the other unisexual flowered genera. Among the bisexual-flowered inflorescences, there was no morphological restriction to access to the receptive stigmas during the pistillate anthesis in both *Pothos* species (spadix exposed) but access restriction was present in inflorescences of *Anadendrum* sp., *Lasia spinosa* and *Scindapsus longistipitatus* (ca. 0.1 – 0.5 cm spathe gap during the pistillate anthesis). Restricted access to the pistillate zone during pistillate anthesis is more prevalent in unisexual-flowered genera, except in the inflorescences of *Aglaonema* and *Amorphophallus*.

All investigated aroid taxa are diurnal flowering plants, anthesis beginning as early as 0400 h. Anthesis of *Bucephalandra motleyana* started much later in the day, around noon time. The delay in the anthesis of *Bucephalandra* might be owed to the consequences of stiff competition for pollinators among Schismatoglottideae taxa (one of the taxonomically most diverse and richest tribes on Borneo; Low et al., 2018). The only other known

Schismatoglottideae taxa to flower at dusk is *Schottarum sarikeense* (Low et al., 2014, 2016). The shift in flowering from dawn to dusk in *B. motleyana* could be a reproductive isolation mechanism. In other *Colocasiomyia* flies pollinated aroids, a shift to flowering at dusk has been observed in *Colocasia affinis*, whereas *C. esculenta*, *C. fontanesii* and *C. lihengiae* flowered before dawn (Bröderbauer et al., 2014).

A shift to the present of persistent enclosed spathe during anthesis and shorter anthetic duration increases reproduction success of aroid taxa. The number of pollinators affect pollinator efficiency, usually higher natural fruit set for species visited by abundance pollinators (*Alocasia*, *Amorphophallus julaiihii*, *Bucephalandra*, *Homalomena*, *Lasia* and *Schismatoglottis*). The aroid taxa with abundance pollinator have persistent enclosed spathe, the spathe function to enhance floral odour and control movement of insects by altering the gap size. Floral odour became more concentrate when trapped in a capacity and was stronger when dissipated in a single direction controlled by the spathe gap, thus attracted more insects. Insects were filtered by the spathe gap or space in the chamber when they arrived, only pollinators allowed to access the pistillate flowers. The enclosed spathe provided protection to the pollinators and they will stay in the inflorescence until they received pollen during staminate anthesis. Some taxa (*Schismatoglottis*, *Bucephalandra* and *Lasia*) only open the gap again during staminate anthesis to release the insects, this ensure all of the insects receive pollen. The spathe will either entirely drop off, remained entirely or part of it after anthesis to protect developing fruits. Short anthesis taxa only attract insects once with a strong floral odour and keep them inside their enclosed floral chamber, then only released them during the staminate anthesis, this ensure flawless transfer of pollen for cross pollination. For long anthesis taxa, their pollination will be more successful for those with enclosed spathe than those without because the enclosed spathe helps to accumulate pollinators for a period of

pistillate anthesis before release them once during staminate anthesis (*Lasia*). For taxa without enclosed spathe like *Pothos*, the taxa need to attract pollinators every single day of anthesis, and the pollination activities may influence by weather factors such as rain, thus result in lower pollination success rate. The transition from the absent of enclosed spathe to the present of enclosed spathe from Pothoideae to Monsteroideae and especially Lasioideae seemed to be advantageous, as the fruit sets of *Anadendrum* and *Pothos* were low (<20 %), but higher in *Lasia* (>60%). The timing of anthesis for *Amorphophallus hewittii* reported in this study is about 90 hours, and significantly longer compared to published results on other species with anthesis duration of a few hours (from dusk to night) (Punekar & Kumaran, 2010).

5.2 Floral traits

Olfactory cues were the primary means of attraction, as the release of floral odour correlated with the arrival of most insect visitors. The type of smell, duration, and emitting organ of the floral odour differs among the studied aroid taxa, i.e., the floral odour of *Anadendrum* and *Pothos* peaked in the morning and was reduced throughout the rest of the day; *Lasia* was observed to release different smells along the spathe. The spathe of *Lasia* is markedly thicker in contrast to the spathe of the other investigated aroid species (except *Amorphophallus hewittii* and *Scindapsus longistipitatus*). Besides, the spathe of *Lasia* was spongy, rich in sap and its inner surface changed colour (turned pink) when the floral odour started to be released, indicating the start of anthesis. In *Homalomena*, it has been shown that the floral scent blend differed between the pistillate and staminate phases of anthesis (Hoe et al., 2016). Hadacek & Weber (2002) reported a gradient of odour emissions in the inflorescence of *Typhonium venosum* (Dryand. ex Aiton) Hett. & P.C. Boyce, ranging from

foul-smelling for the appendix to a pleasant flowery odour for the club-shaped sterile organs in the interstice, these odour compounds attracted a wide range of insects into the floral chamber. Different odours from different structures was also recorded for *Biarum*, wherein the appendix smells foul but the lower spathe chamber smells sweet (Mayo, 1980). During the pistillate anthesis, heat was detected from the staminate zone of *Aglaonema* and the appendix of *Alocasia*, and floral odour was intense when heat produced. The other genera with possible heat production during the pistillate anthesis were *Schismatoglottis*, *Homalomena*, and *Pothos*,

Spathes of *Aglaonema*, *Alocasia*, *Anadendrum*, *Bucephalandra*, *Homalomena*, *Lasia*, *Schismatoglottis* and *Scindapsus* at the onset of anthesis inflated but remained unexpanded except for a gap along the spathe margin which concentrates the floral odour within the inflorescence. By contrast the spathe of *Pothos* opened widely during the pistillate anthesis which allowed the diffusion of the floral odour to the surroundings. In *Amorphophallus* where the slippery inner surface of the lower spathe prevented the insects from crawling out and for some reason the normally strong-flying beetles were disinclined to fly out. The pollinators, fruit flies (Drosophilidae) were not strictly restricted to the lower chamber during the pistillate anthesis and were free to move within and sometimes out of inflorescences of *Bucephalandra*, *Homalomena* and *Schismatoglottis*. However, fruit flies never moved out from the lower chamber of *Alocasia* during the pistillate anthesis. For unisexual-flowered taxa, the constriction at the spathe coinciding with the interstice/staminate zone of all species served as a sieve, allowing only insects of a certain size, i.e. *Colocasiomyia*, to access to the lower chamber during the pistillate anthesis. The constriction of the spathe in all investigated species of *Schismatoglottis* tightened to prevent access to the lower chamber during post-pistillate anthesis as already observed in

Phymatarum borneensis (Low et al., 2016). This is also observed in *Bucephalandra*, where the interstice staminodes lowered and pressed against the inner wall of the lower spathe to seal the pollination chamber during post-pistillate anthesis (Low et al., 2016). Insect visitors that can enter the narrow pistillate zone in unisexual flowered genera to consume the floral liquid were the most possible pollinators. However, in *Aglaonema*, access to the lower chamber during pistillate anthesis was unrestricted. The upper spathe of *Bucephalandra* and *Schismatoglottis* abscised during the post-staminate anthesis, and insects subsequently left the inflorescence. Pollen liberation coincided with the abscission of the upper spathe in *P. borneense*. In *Alocasia* and *Amorphophallus*, the upper spathe though wide open, remained throughout the staminate anthesis and was shed post-anthesis. The spathe of *Aglaonema nitidum* only abscised when the fruits almost mature but the spathe of *A. simplex* abscised after anthesis. In *Homalomena*, the whole spathe closed back post-anthesis. However, much needs to be done before we are in a position to attempt an overall presentation on the breadth of spathe/spadix and pollinator and dispersal interactions as various spathe movements occurred in very few investigated aroid taxa (Ulrich et al., 2012; Wong, 2013). The intricate series of events involved in the movement of the spathe, the phasing of fertile events, the management of pollinators, and ultimately the development and successful maturation and dispersal of fruits and seeds in Araceae need further investigations.

5.3 Floral rewards

Floral liquid is the main reward in all the investigated aroid species (except *Lasia* and *Amorphophallus julaiihii*, floral liquid was not observed in both species). Floral liquid was observed to be released during the pistillate anthesis, from stigmas (bisexual flowered genera), pistillate flowers and sterile interstices (unisexual flowered genera), interpistillar

staminodes (*Homalomena*, *Schismatoglottis*), the space between flowers (*Pothos*) or the appendix (*Amorphophallus hewittii*). Floral liquid rewarded small insects such as fruit flies (*Drosophilidae*), small beetles (*Hydrophilidae* and *Staphylinidae*), *Thripidae* and *Miridae* that visited the inflorescences of the investigated aroid species. Mating site was another reward provided by all the investigated aroid species, almost all insect visitors of the investigated aroid species mated within the inflorescences during the pistillate anthesis. Within an inflorescence, mating site could take place on the staminate zone, the pistillate zone, the appendix zone or the inner surface of the spathe for unisexual flowered genera, and on the entire spadix or the inner surface of spathe (genera with spathe covering the spadix during pistillate anthesis) for bisexual flowered genera. Floral tissues are “sacrificial parts” that reward insect visitors in some of the investigated aroid species. Evidence of insect visitors consuming floral tissue was found in *Pothos insignis* (stamens chewed by *Chabria* beetles), *Homalomena* (male zone chewed by *Chaloenus* beetles), and *Schismatoglottis* (appendix chewed by *Chaloenus* beetles). No evidence of insect visitors consuming floral tissues in *Aglaonema*, *Alocasia sarawakensis*, *Amorphophallus*, *Anadendrum*, *Bucephalandra*, *Lasia*, *Pothos scandens*, and *Scindapsus*.

5.4 Pollination guilds

“Amazingly in spite of their “unique” and very constant inflorescence design, aroids have developed pollination relationship with a great diversity of insects: bees, beetles and flies” (Bown, 2000). Even vertebrates, e.g., hummingbirds, have been mentioned (Kraemer & Schmitt, 1999).

This study is the first to report the pollinators of *Anadendrum* (Tribe Anadendreae), *Lasia* (tribe Lasieae), and *Pothos* (Potheae). Aroid species in Mulu are pollinated by a wide

array of faunal diversity: Diptera (three families: Drosophilidae, Calliphoridae, Syrphidae), Coleoptera (eight families: Hydrophilidae, Nitidulidae, Hybosoridae, Scarabaeidae, Chrysomelidae, Staphylinidae, Silvanidae, Scolytinae), Hemiptera (one family: Miridae), Thysanoptera (one family: Thripidae), and Hymenoptera (one family: Apidae). Most abundant insects collected from the inflorescences of all investigated aroids belonged to the order of Diptera (Drosophilidae) but the pollinator diversity was much higher in the order of Coleoptera. There were three pollination guilds in two genera (*Pothos* and *Amorphophallus*), two pollination guilds in four aroid genera (*Lasia*, *Anadendrum*, *Homalomena*, and *Schismatoglottis*), and one pollination guild in the other six genera (*Aglaonema*, *Alocasia* and *Bucephalandra* and *Scindapsus*). *Lasia* had the highest number of types of insects recorded, and constitutes a mixed-pollination system implying a generalist pollination system. Plant-pollinator interactions ranged along a spectrum from obligate specialists (a single species of pollinator services one plant species) to facultative generalists in which flowers may be adequately pollinated by a taxonomically broad range of pollinators, which are also visitors to the flowers of many other species (Ollerton et al., 2007). Thrips were hitherto reported in literature only in *Arisaema* (Barnes, 1934) and have subsequently been observed to pollinate *Pothos leptostachyus* (Chai, pers. obs., 2017). Hemiptera is here reported for the first time to pollinate aroids (*Lasia*, *Pothos insignis*).

Fruit flies (Drosophilidae) pollinated 18 out of 21 examined taxa that belong to *Aglaonema*, *Alocasia*, *Bucephalandra*, *Homalomena*, *Pothos*, *Schismatoglottis* and *Scindapsus*. The flies were always the first to arrive at the inflorescences during the onset of pistillate anthesis in *Bucephalandra*, *Homalomena*, *Pothos* and *Schismatoglottis*. In *Aglaonema*, *Alocasia* and *Scindapsus*, there were other insects arrived first but the insects were just visitors (Diptera in *Aglaonema*, Apidae and Diptera in *Alocasia sarawakensis*, and

Miridae in *Scindapsus*). The flies were observed to consume stigmatic secretions and pollen, and mating in the inflorescences. Utilization by *Colocasiomyia* of aroid inflorescences as brood sites has been widely reported (Miyake & Yafuso, 2003, 2005; Takano et al., 2006, 2012; Fartyal et al., 2013). Inflorescences of *Aglaonema*, *Colocasia*, and *Alocasia* visited by *Colocasiomyia* flies, has been reported to attract two fly species, one ovipositing on the staminate zone, the other on the pistillate one but not damaging the ovules (Toda & Okada, 1983; Okada, 1986, 1987, 1990; Ivancic et al., 2004, 2005, 2008; Miyake & Yafuso, 2005; Sultana et al., 2006; Takano et al., 2012). In this study, *Alocasia sarawakensis* was only visited by one species of drosophilid flies (efficient pollinators) that probably oviposit in the pistillate flower zone. For *Aglaonema nitidum* and *A. simplex*, only a species of Drosophilid flies was recorded as pollinator although both aroid species are visited by unknown flies that only visited the staminate zone during the pistillate anthesis.

Flies were reported as visitors/pollinators for *Dracontium* which is closely related to *Lasia* (Gibernau, 2003), however, there is no flies observed or collected in *Lasia spinosa* in Mulu National Park. *Anthurium* which belongs to the same clade with *Pothos* (Cusimano et al., 2011) are reported to be pollinated by flower weevils (Curculionidae) (Franz, 2007), fruit flies (Drosophilidae), gall midges (Cecidiomyidae) (Schwerdtfeger et al., 2002), hummingbirds (Kraemer & Schmitt, 1999), and male oil bees (Tapinotaspidini and Tetrapediini) (Etl et al., 2017). Yadav (1998) reported that *Pothos scandens* do not emit smell and is pollinated by bee, however, weak sweet smell was detected and a species of flies was observed to visit this species in this study.

Coleoptera pollinated 14 out of the 21 investigated taxa from the genera *Amorphophallus*, *Anadendrum*, *Homalomena* (except *H. ovatifolia*), *Lasia*, and

Schismatoglottis. *Cycreon* beetles (Hydrophilidae) pollinated all investigated species of *Schismatoglottis* (main pollinators in *S. colocasioidea*). *Parastasia* beetles (Scarabaeidae) are pollinators of *Homalomena* (except *H. ovatifolia*). *Chaloenus* beetles (Chrysomelidae) are pollinators of *Homalomena* (except *H. ovatifolia*). *Chaloenus* beetles also visited *H. ovatifolia* and all investigated species of *Schismatoglottis*. Rove beetles (Staphylinidae) are the pollinators of *Amorphophallus hewittii*, *A. julaihii*, *Anadendrum* sp., *L. spinosa*, *Schismatoglottis muluensis*, and *S. serratodentata*. *Chabria* beetles (Chrysomelidae) pollinated *Pothos insignis*. Sap beetles (Nitidulidae), ambrosia beetles (Scolytinae) and silvanid bark beetles (Silvanidae) are pollinators of *Lasia*. Hybosorid scarab beetles (Hybosoridae) pollinated *Amorphophallus hewittii*.

Scarab beetles of the genus *Parastasia* (Scarabaeidae) appeared to be the primary pollinators of all the investigated taxa of *Homalomena*. This is in accordance to what was observed for other *Homalomena* species studied (Kumano-Nomura & Yamaoka, 2006; Hoe et al., 2016). These scarabs secured food rewards, mating opportunities and safe mating arenas inside a sheltered floral chamber (Kumano-Nomura & Yamaoka, 2009; Hoe et al., 2016).

Chrysomelid beetles of the species *Chaloenus* spp. (Chrysomelidae) were observed to visit all investigated species of *Homalomena*. Unlike *Parastasia* scarabs, however, these beetles are only occasional pollinators, something previously observed in a study with other *Homalomena* species (Kumano-Nomura & Yamaoka, 2006; Hoe et al., 2016). Adults mostly gather and feed on inflorescences, but have also been observed chewing the leaf blades (Darling, 2007; Takizawa, 2012). In this 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) damage to the spadix by anthophilous chrysomelid beetles, notably the appendix, is reported from Schismatoglottideae in Borneo (Low et al., 2014, 2016).

Stingless bees (Apidae: Hymenoptera) are pollinators of *Amorphophallus hewittii* and opportunistic pollinators of *Alocasia sarawakensis*. Stingless bees also visited *Aglaonema*, *Lasia*, *Schismatoglottis*, and *Scindapsus* during the staminate anthesis to collect pollen, the bees were not able to enter the inflorescences of these genera during the pistillate anthesis.

Stingless bees (Apidae: Trigona) are the main pollinator of *Amorphophallus commutatus* (Schott) Engl. var. *commutatus* and *A. commutatus* var. *wayanadensis* Sivad. and Jaleel (Punekar & Kumaran, 2010), which is the same as *A. hewittii* in this study. The time of intensive visit by the bees to the inflorescence of *A. commutatus* var. *commutatus* was between 0800 h – 1200 h, which is almost similar to the peak time of visit to *A. hewittii*. Another pollinator of *A. hewittii*, a scavenger scarab beetle (Hybosoridae) was reported as pollinator of *A. bulbifer* (Roxb.) Blume in the study by Punekar and Kumaran (2010). Hybosorid scarab beetle was also reported as effective pollinator for the African species, *A. johnsonii* (Beath, 1996). Fruit flies (Drosophilidae) were reported as visitor of *A. bulbifer*, *A. commutatus* var. *commutatus* and *A. commutatus* var. *wayanadensis* (Punekar & Kumaran, 2010). In contrast to the study by Punekar and Kumaran (2010), nitidulid beetles which are main pollinator of *Lasia spinosa* reported in this study have never been encountered in *Amorphophallus* spp in Mulu, although are common visitors or even pollinators of *Amorphophallus* in their study area. The salted fish floral odour that is produced by the appendix of *A. hewittii* probably contain dimethyl oligosulphides (Kite &

Hetterscheid, 2017) that act as olfactory cue for carrion beetles and carrion flies to the inflorescence.

The number of insects that visit the same group of aroids may reduce when there are many species of the same group flowering at the same time or may increase when there is less flowering from species of the same group. For example, the number of fruit flies (*Drosophilidae*) and *Cycreon* beetles (*Hydrophilidae*) were significantly reduced when many species of *Schismatoglottis* flowered at the same time. This scenario was also observed in *Homalomena* whereby the number of *Parastasia* beetles and *Chaloenus* beetles decreased when there were many species of *Homalomena* and *Schismatoglottis* flowering at the same time. There is a higher competition for pollinators visiting the same group of aroids when there is less flowering from species of the same group of aroids, thus higher fruiting rate in natural pollination of the species when more pollinators visited the species. Sometimes, the pollinators that usually visit the same group of aroids may visit other group of aroids when competition is high. For example, *Cycreon* beetles visited *Aglaonema simplex* when there were less flowering of *Schismatoglottis*.

5.5 Reproductive system

Reproductive success was evident several days after anthesis as a visible enlargement of ovaries occurred. The natural fruit set percentage of unisexual-flowered species were higher when compared to bisexual-flowered species (76.1% vs 33.4%). Fructification rate of two out of three bisexual-flowered taxa, *Anadendrum* and *Pothos* was low (less than 20%), but significantly higher in *Lasia* (69.8%). However, all unisexual-flowered taxa produced more than 50% fruit set with *Bucephalandra* reaching 100% fruit set. Besides, there were higher natural fruit set percentages for terrestrial species than climbing species (75.5% vs

15%). It has been reported that *Furtadoa sumatrensis*, a rheophytic species also pollinated by *Colocasiomyia*, has 40–50% fruit set (Mori & Okada, 2001). Our work with *Homalomena* shows similar high fruit set, at >80% (Hoe et al., 2016). The related Neotropical *Philodendron acutatum*, also showed a reproductive success of >90% (Maia et al., 2010). Gottsberger and Amaral (1984) considered the pollinator specificity observed in upland Atlantic Forest populations of *Thaumatophyllum* (reported as *Philodendron*) *bipinnatifidum* as an effective strategy to increase reproductive success. Relying on a specialized pollen vector can significantly decrease the risk of interspecific pollen flow, and improve the rate of successful visitation, since visitors very probably carry only conspecific pollen (Faegri & van der Pijl, 1979). This seemed true for *Anadendrum* and *Pothos insignis*, both bisexual and generalist-pollinated taxa, had very low fruit sets. On the other hand, in *Lasia*, also a bisexual and generalist pollinated taxon, the fruit set was remarkably high. The low fruit set percentage in *Anadendrum* and *Pothos* probably because these taxa produce weaker but long-lasting floral odour which attract less insect pollinators, and few insects were present during the staminate anthesis, leading probably to a less efficient pollination. *Lasia* overcame the problem by having inflorescence with a spathe that creates a floral chamber to keep the insects and only to release them when the pollen is released. The previous statement is not true as well for the unisexual-flowered taxa (*Homalomena* and *Schismatoglottis*) which are pollinated by two or more types of pollinators, the fruit set percentages for these genera are remarkably high. However, in *Bucephalandra* and *Phymatarum*, which are specialists, the fruit sets are equally high. Perhaps interspecific pollen flow maybe the reason why the diversity of both generalist (*Homalomena* and *Schismatoglottis*) are considerably higher (15 and 23 taxa respectively occurring in Mulu). Being specialist, *Alocasia* presented a high fruit set percentage while *Aglaonema* has a much lower fruit set percentage, this

probably due to the higher number of Drosophilid flies visiting *Alocasia* than *Aglaonema*, and the flies were concentrated in the pistillate zone in *Alocasia*. Both *Amorphophallus hewittii* (generalist) and *A. julaiihii* (specialist) have a quite high fruit set percentage.

In many unisexual-flowered aroids, the role of protecting the developing infructescences is assumed either by the entire spathe (*Homalomena*) or by the persistent lower spathe (*Schismatoglottis*). Fruit exposure is variously enabled, mostly by the spathe splitting open (e.g. *Alocasia*, *Dieffenbachia*) or abscising from the base (e.g. *Homalomena*, *Philodendron*) (Mayo et al., 1997). Infructescence development in many rheophytic Schismatoglottideae is unusual in that the developing fruits sit exposed in a cup-shaped persistent lower spathe, which later functions as a splash-cup from which seeds/fruits are ejected by the impact of water droplets (Wong, 2013; Boyce & Wong, 2012, 2014; Low et al., 2018). The infructescence of *Bucephalandra* is open with the scale-like staminodes hardened and became photosynthetic early on in fruit development to protect the fruits underneath (Wong & Boyce, 2013). The fruits of *Phymatarum* are protected by the lower spathe with a constricted orifice (Low et al., 2016). For *Aglaonema*, the developing fruits are protected by the entire persistent spathe in *A. nitidum* but the developing fruits was entirely exposed in *A. simplex*. Fruits were entirely exposed throughout development in *Amorphophallus*, *Anadendrum*, *Lasia*, *Pothos* and *Scindapsus*.

CHAPTER 6

CONCLUSION AND RECOMMENDATIONS

6.1 Conclusion

In conclusion, the pollination and floral biology of 21 aroids species from subfamily Pothoideae (*Pothos*), subfamily Monsteroideae (*Scindapsus*, *Anadendrum*), subfamily Lasioideae (*Lasia*), and subfamily Aroideae (*Aglaonema*, *Alocasia*, *Amorphophallus*, *Bucephalandra*, *Homalomena*, *Schismatoglottis*) were known, this figure is still very small if compare to aroid diversity of Mulu (ca. 90 species) and the entire Borneo (ca. 800 species). Out of the 21 species, only *Schismatoglottis muluensis* had been studied by Hoe et al. (2018), the rest are novelty to science. In term of genera, the report of pollination is among the first and most recent for genera *Pothos*, *Aglaonema*, *Anadendrum*, *Lasia* and *Bucephalandra*.

The first objective to document timing of anthesis and associated floral changes, floral traits and rewards was accomplished for the 21 species. Most species have anthesis started at dawn (between 0430 to 0600; *Anadendrum*, *Scindapsus*, *Aglaonema*, *Alocasia*, *Homalomena*, *Schismatoglottis*), and the rest have anthesis started at morning (0700 to 1100; *Pothos*, *Lasia*, *Amorphophallus julaiihii* & *Schismatoglottis pellucida*) or afternoon (1300 to 1800; *Bucephalandra*, *A. hewittii*). Most species have anthesis of about 24 to 30 hours or slightly more than a day (*Alocasia*, *Scindapsus*, *Aglaonema*, *Amorphophallus julaiihii*, *Bucephalandra*, *Homalomena*, and *Schismatoglottis*). Most species with anthesis of multiple days are from bisexual flower clade (*Pothos* (225 to 400 hours), *Anadendrum* (77 hours), *Lasia* (150 to 174 hours)) except *Amorphophallus hewittii* (90 hours). In term of floral changes during anthesis, *Pothos* and *Anadendrum* have spathe completely uncover spadix

during anthesis. *Scindapsus* has slightly gaping spathe that abscise after pistillate anthesis. *Lasia* has narrow gaping spathe that only open widely at base after staminate anthesis. *Aglaonema* has wide open spathe during pistillate anthesis, abscise soon after anthesis for *A. simplex*. *Amorphophallus* has spathe that expand toward peak of anthesis, shrink back toward the end of anthesis and gradually wilting. *Alocasia* and *Homalomena* have spathe that wide open at staminate zone and inflated at pistillate zone, but staminate zone and upper spathe of *Alocasia* wilting after anthesis while persistent in *Homalomena*. *Bucephalandra* and *Schismatoglottis* have inflated spathe that narrowly gaping during pistillate anthesis, upper spathe abscises before or after staminate anthesis and lower spathe persistent until fruit ripe. All the 21 species do produce odour to attract insect pollinators, the odour intensity range from weak (hard to detect: *Bucephalandra*, *P. scandens*) to strong (detected nearly: *P. insignis*, *Anadendrum*, *Scindapsus*, *Lasia*, *Aglaonema*, *Homalomena*, *Schismatoglottis*, *Alocasia*, *Amorphophallus julaiihii*) and to very strong (detected at a distance: *A. hewittii*). Odour may produce from spathe (*Lasia*), male zone (*Aglaonema*, *Homalomena*), appendix (*Schismatoglottis*, *Alocasia*, *Amorphophallus*, *Bucephalandra*) and entire spadix (bisexual flower genera). All the 21 aroid species provide rewards for their pollinators, including floral liquid from pistillate flowers and stigmas (*Drosophilid* flies, *Cycreon* beetles, thrips, rove beetles and *H. valida* visited species), sacrificial floral part as food (sterile flowers for *Chaloenus* beetles, *Parastasia* beetles), and pollen and mating sites (all insects group).

The second objective to document insect visitors, pollinators and their behaviours for the 21 aroid species was also achieved. Fruit flies (*Drosophilidae*) pollinated species of *Bucephalandra* (sole visitor), *Pothos*, *Scindapsus*, *Aglaonema*, *Homalomena*, *Schismatoglottis* and *Alocasia*, they are among the first insects arrived to the inflorescences of these species during pistillate anthesis. *Cycreon* beetles (*Hydrophilidae*) pollinated

species of *Schismatoglottis* and *Aglaonema simplex* (low flowering of *Schismatoglottis*). Rove beetles (Staphylinidae) pollinated *Amorphophallus julaiihii* (sole visitor), *A. hewittii*, *Schismatoglottis muluensis*, *Anadendrum* and *Lasia*. *Chaloenus* beetles (Chrysomelidae) may only pollinate *Homalomena* (except *H. ovatifolia*) but are visitors of *Schismatoglottis*. *Chabria* beetles (Chrysomelidae) are pollinators of *P. insignis*. *Parastasia* beetles (Scarabaeidae) pollinated *Homalomena* (except *H. ovatifolia*) and visited *S. muluensis*. *Halticotoma valida* (Miridae) may pollinate *P. insignis* and are visitors of *Scindapsus*. Thrips (Thysanoptera) are efficient pollinators of *Anadendrum*. Stingless bees (Apidae) are efficient pollinators of *Amorphophallus hewittii*, the bees may pollinate *Alocasia*, and visited almost every aroid species to collect pollen. *A. hewittii* also pollinated by scavenger scarab beetles (Hybosoridae), the beetles only active at night. *Lasia spinosa* visited and pollinated by various group of insects, including beetles (Nitidulidae, Staphylinidae, Scolytinae, Silvanidae) and bugs (Miridae). The insects seem to associate with the plant they pollinate, they move from one inflorescence to another inflorescence of the same species or same genus to achieve pollination of the plant species while they are rewarded with food, mating site, ovipositing site and also protection. Aroid species may associate with single group of insects (e.g. *Bucephalandra*, *A. julaiihii*) or multiple groups of insects (e.g. *Lasia*, *Schismatoglottis*) to achieve their pollination, thus each insects group is a guild of the plant, or vice versa, the plant is the guild of the insect since they depend on each other.

The third objective to determine the capability to autonomous self-pollinate and the efficiency of open pollination for the 21 species was almost accomplished. Autonomous self-pollination treatment was treated to all species except *Amorphophallus*, *H. ardua*, *H. ovatifolia*, *H. sanguineovaginata*, *P. scandens* and *Scindapsus*, none of the species have their treated inflorescences developed into fruits and all senesced early, thus all species are not

capable to self-pollinate without pollinator. For open pollination treatment, species of *Alocasia*, *Bucephalandra*, *Homalomena* and *Schismatoglottis* (except *S. serratodentata*) have high fruit set of more than 80%. The species of *Lasia* and *Amorphophallus* have intermediate fruit set ranged above 60%, and above 50% for *Aglaonema simplex*. The species with low fruit set are *A. nitidum*, *Pothos* and *Anadendrum*.

6.2 Recommendations

For recommendation of future work, open pollination fruit set can be counted for those not counted due to insufficient infructescence, which include *Homalomena ovatifolia*, *H. ardua*, *H. sanguineovaginata*, *Scindapsus*, *Schismatoglottis multinervia*, *S. pellucida* and *Pothos scandens*. Autonomous self-pollination treatment shall be tested for those species excluded in this study. Besides, manual self-pollination can also be tested on all of the investigated species to determine self-compatibility of the species (geitonogamy). Furthermore, detailed work can be done to extract more data from each species, such as conduct microscopic analysis for all insects collected from each plant species to view and do pollen count to prove their efficiency as pollinators aside from good field observation, collect floral odour and analyse compound inside the scent to see if there is any specific compound associate with attraction of specific insect group, and thermogenesis test and measurement for all the 21 aroid species. Last, there are still many aroid species in Borneo that are awaiting to reveal their pollination and floral biology.

REFERENCES

- Angioy, A. M., Stensmyr, M. C., Urru, I., Puliafito, M., Collu, I., & Hansson, B. S. (2004). Function of the heater: the dead horse arum revisited. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271, S13-S15.
- Barabé, D., Lacroix, C., & Gibernau, M. (2004). Aspects of floral morphology in *Ambrosina* and *Arisarum* (Araceae). *Canadian Journal of Botany*, 82(2), 282-289.
- Barnes, E. (1934). Some observations on the genus *Arisaema* on the Nilgiri Hills, South India. *Journal of the Bombay Natural History Society*, 37, 630-639.
- Barriault, I., Barabé, D., Cloutier, L., & Gibernau, M. (2010). Pollination ecology and reproductive success in Jack in the pulpit (*Arisaema triphyllum*) in Québec (Canada). *Plant Biology*, 12(1), 161-171.
- Barriault, I., Gibernau, M., & Barabe, D. (2009). Flowering period, thermogenesis, and pattern of visiting insects in *Arisaema triphyllum* (Araceae) in Quebec. *Botany*, 87(3), 324-329.
- Beath, D. D. (1993). *Biology of forest Araceae in Ghana* (unpub. Ph.D. Thesis). University of Aberdeen, U.K.
- Beath, D. D. (1996). Pollination of *Amorphophallus johnsonii* (Araceae) by carrion beetles (*Phaeochrous amplus*) in a Ghanaian rain forest. *Journal of Tropical Ecology*, 12(3), 409-418.

- Blackith, R., & Blackith, R. (1993). Diptera (Insecta) attracted to the dragon's mouth lily (*Dracunculus vulgaris* Schott) in Ireland. *Bulletin of the Irish Biogeographical Society*, 16, 2-7.
- Bogner, J. (2008). The genus *Bognera* Mayo & Nicolson (Araceae). *Aroideana*, 31, 3-14.
- Boos, J. O. (1997). Observations on New World Araceae–Lasieae. *Aroideana*, 20, 13-26.
- Bown, D. (2000). *Aroids: Plants of the Arum family* (2nd ed.). Portland, OR: Timber press.
- Boyce, P. C. (2008). A taxonomic revision of *Biarum*. *Curtis's Botanical Magazine*, 25(1), 2-17.
- Boyce, P. C., & Croat, T. B. (2011). *The Überlist of Araceae: totals for published and estimated number of species in aroid genera*. Retrieved from <http://www.aroid.org/genera/180211uberlist.pdf>
- Boyce, P. C., & Hay, A. (2001). A taxonomic revision of Araceae tribe Potheae (*Pothos*, *Pothoidium* and *Pedicellarum*) for Malesia, Australia and the tropical Western Pacific. *Telopea*, 9(3), 449-571.
- 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. *Gardens Bulletin Singapore*, 60, 1-29.
- Boyce, P. C., & Wong, S. Y. (2012). The fruits of *Bakoa nakamotoi*. *International Aroid Society Newsletter*, 34(3), 6-7.

- Boyce, P. C., & Wong, S. Y. (2014). Studies on Schismatoglottideae (Araceae) of Borneo XXXIV—The Fruits of *Schottariella*. *Aroideana*, 11, 11-16.
- Boyce, P. C., & Wong, S. Y. (2015). Compendium genera Aracearum malesianum. *Aroideana*, 38, 40-177.
- Boyce, P. C., Wong, S. Y., Low, S. L., Ting, A. P. J., Low, S. E., Ooi, I. H., & Ng, K. K. (2010). The Araceae of Borneo—the genera. *Aroideana*, 33, 3-74.
- Bröderbauer, D., Diaz, A., & Weber, A. (2012) Reconstructing the origin and elaboration of insect-trapping inflorescences in the Araceae. *American Journal of Botany*, 99(10), 1666-1679.
- Bröderbauer, D., Ulrich, S., & Weber, A. (2014). Adaptations for insect trapping in brood site pollinated *Colocasia* (Araceae). *Plant Biology*, 16(3), 659-668.
- Buzgó, M. (1994). Inflorescence development of *Pistia stratiotes* (Araceae). *Botanische Jahrbücher für Systematik*, 115, 557-570.
- Calazans, L. S. B., Sakuragui, C. M., & Mayo, S. J. (2014). From open areas to forests? The evolutionary history of *Philodendron* subgenus *Meconostigma* (Araceae) using morphological data. *Flora-Morphology, Distribution, Functional Ecology of Plants*, 209(2), 117-121.
- Chartier, M., Gibernau, M., & Renner, S. S. (2014). The evolution of pollinator–plant interaction types in the Araceae. *Evolution*, 68(5), 1533-1543.

- Chartier, M., Liagre, S., Weiss-Schneeweiss, H., Kolano, B., Bessière, J. M., Schönenberger, J., & Gibernau, M. (2016). Floral traits and pollination ecology of European *Arum* hybrids. *Oecologia*, 180(2), 439-451.
- Chartier, M., Pélozuelo, L., Buatois, B., Bessière, J. M., & Gibernau, M. (2013). Geographical variations of odour and pollinators, and test for local adaptation by reciprocal transplant of two European *Arum* species. *Functional Ecology*, 27(6), 1367-1381.
- Chartier, M., Pélozuelo, L., & Gibernau, M. (2011). Do floral odor profiles geographically vary with the degree of specificity for pollinators? Investigation in two sapromyophilous *Arum* species (Araceae). *Annales de la Société Entomologique de France*, 47(1-2), 71-77.
- Chouteau, M., Gibernau, M., & Barabé, D. (2008). Relationships between floral characters, pollination mechanisms, life forms, and habitats in Araceae. *Botanical Journal of the Linnean Society*, 156(1), 29-42.
- Chouteau, M., McClure, M., & Gibernau, M. (2007). Pollination ecology of *Monstera obliqua* (Araceae) in French Guiana. *Journal of Tropical Ecology*, 23(5), 607-610.
- Coté, G. G., & Gibernau, M. (2012). Distribution of calcium oxalate crystals in floral organs of Araceae in relation to pollination strategy. *American Journal of Botany*, 99(7), 1231-1242.
- Croat, T. B., & Hannon, L. P. (2015). A Revision of the Genus *Chlorospatha* (Araceae). *Annals of the Missouri Botanical Garden*, 101(1), 1-259.

- Cusimano, N., Bogner, J., Mayo, S. J., Boyce, P. C., Wong, S. Y., Hesse, M., Hetterscheid, W. L. A., Keating, R. C. & French, J. C. (2011). Relationships within the Araceae: comparison of morphological patterns with molecular phylogenies. *American Journal of Botany*, 98(4), 654-668.
- Darling, D. C. (2007). Holey aroids: circular trenching behavior by a leaf beetle in Vietnam. *Biotropica*, 39(4), 555-558.
- de Oliveira, L. L., Calazans, L. S. B., de Moraes, É. B., Mayo, S. J., Schrago, C. G., & Sakuragui, C. M. (2014). Floral evolution of *Philodendron* subgenus *Meconostigma* (Araceae). *PloS one*, 9(2), 1-10.
- Diaz, A., & Kite, G. C. (2006). Why be a rewarding trap? The evolution of floral rewards in *Arum* (Araceae), a genus characterized by saprophilous pollination systems. *Biological Journal of the Linnean Society*, 88(2), 257-268.
- Diaz-Jiménez, P., Krömer, T., Hentrich, H., & Mac Swiney Gonzalez, M. C., (2016) *Reproductive biology of Spathiphyllum cochlearispathum and S. ortgiesii* (Araceae) in Los Tuxtlas, Veracruz, Mexico. Poster presented at the European Conference of Tropical Ecology: “Tropical diversity, ecology and land use”, University of Göttingen, Germany.
- Dötterl, S., David, A., Boland, W., Silberbauer-Gottsberger, I., & Gottsberger, G. (2012). Evidence for behavioral attractiveness of methoxylated aromatics in a dynastid scarab beetle-pollinated Araceae. *Journal of Chemical Ecology*, 38(12), 1539-1543.

- Espíndola, A., Pellissier, L., & Alvarez, N. (2010). Variation in the proportion of flower visitors of *Arum maculatum* along its distributional range in relation with community-based climatic niche analyses. *Oikos*, 120(5), 728-734
- Etl, F., Franschitz, A., Aguiar, A. J., Schönenberger, J., & Dötterl, S. (2017). A perfume-collecting male oil bee? Evidences of a novel pollination system involving *Anthurium acutifolium* (Araceae) and *Paratetrapedia chocoensis* (Apidae, Tapinotaspidini). *Flora*, 232, 7-15.
- Faegri, K., & Van Der Pijl, L. (1979). *Principles of pollination ecology* (3rd ed.). Oxford: Pergamon Press.
- Fartyal, R. S., Gao, J. J., Toda, M. J., Hu, Y. G., Takano, K. T., Suwito, A., Katoh, T., Takigahira, T., & Yin, J. T. (2013). *Colocasiomyia* (Diptera: Drosophilidae) revised phylogenetically, with a new species group having peculiar lifecycles on monsteroide (Araceae) host plants. *Systematic Entomology*, 38(4), 763-782.
- Franz, N. (2003). Systematics of *Cyclanthura* gen. n., a new genus of Derelomini (Coleoptera: Curculionidae). *Insect Systematics & Evolution*, 34(2), 153-198.
- Franz, N. M. (2007). Pollination of *Anthurium* (Araceae) by derelomine flower weevils (Coleoptera: Curculionidae). *Revista de Biología Tropical*, 55(1), 269-277.
- French, J. C. (1987). Structure of ovular and placental trichomes of Araceae. *Botanical Gazette*, 148, 198-208.

- García-Robledo, C., Kattan, G., Murcia, C., & Quintero-Marín, P. (2004). Beetle pollination and fruit predation of *Xanthosoma daguense* (Araceae) in an Andean cloud forest in Colombia. *Journal of Tropical Ecology*, 20(4), 459-469.
- Gasca-Alvarez, H. J. (2013). New records of *Cyclocephala* Dejean (Coleoptera: Scarabaeidae: Dynastinae) associated with *Caladium bicolor* (Aiton) Vent. (Araceae). *The Coleopterists Bulletin*, 67(4), 416-418.
- Gibernau, M. (2003). Pollinators and visitors of aroid inflorescences. *Aroideana*, 26(11), 73-91.
- Gibernau, M. (2011). Pollinators and visitors of aroid inflorescences: an addendum. *Aroideana*, 34, 70-83.
- Gibernau, M. (2016). Pollinators and visitors of aroid inflorescences III-phylogenetic & chemical insights. *Aroideana*, 39(3), 4-22.
- Gibernau, M., Barabé, D., Labat, D., Cerdan, P., & Dejean, A. (2003). Reproductive biology of *Montrichardia arborescens* (Araceae) in French Guiana. *Journal of Tropical Ecology*, 19(1), 103-107.
- Gibernau, M., Chartier, M., & Barabé, D. (2010b). Recent advances towards an evolutionary comprehension of Araceae pollination. In Seberg, Petersen, Barfod & Davis (Eds.), *Diversity, Phylogeny, and Evolution in the Monocotyledons* (pp. 101-114). Aarhus: Aarhus University Press.

- Gibernau, M., Chouteau, M., Lavallée, K., & Barabé, D. (2010a). Notes on the phenology, morphometry and floral biology of *Anaphyllopsis americana* (Araceae). *Aroideana*, 33, 183-191.
- Gibernau, M., Macquart, D., & Przetak, G. (2004). Pollination in the genus *Arum*—a review. *Aroideana*, 27, 148-166.
- Gonçalves, E. G. (2005). A revision of genus *Dracontiodendron* Engl. (Araceae), including a new species from Bahia, Brasil. *Aroideana*, 28, 21-31.
- Gonçalves, E. G., & Maia, A. C. D. (2006). New evidence of pollination in *Gearum brasiliense* (Araceae: Spathicarpeae). *Aroideana*, 29, 148-151.
- Gottsberger, G., & Amaral, A. (1984). Pollination strategies in Brazilian *Philodendron* species. *Berichte der Deutschen Botanischen Gesellschaft*, 97(3-4), 391-410.
- Gottsberger, G., Silberbauer-Gottsberger, I., & Dötterl, S. (2013). Pollination and floral scent differentiation in species of the *Philodendron bipinnatifidum* complex (Araceae). *Plant Systematics and Evolution*, 299(4), 793-809.
- Grayum, M. H. (1984). *Palynology and phylogeny of the Araceae* (dissertation). University of Massachusetts, Amherst (MA), USA.
- Grayum, M. H. (1986). Correlations between pollination biology and pollen morphology in the Araceae, with some implications for angiosperm evolution. In S. Blackmore & I. Ferguson (Eds.), *Pollen and Spores: Form and Function* (pp. 313-327). Cambridge, MA: Academic Press.

- Grayum, M. H. (1990). Evolution and phylogeny of the Araceae. *Annals of the Missouri Botanical Garden*, 77, 628-697.
- Hadacek, F., & Weber, M. (2002). Club-shaped organs as additional osmophores within the *Sauromatum* inflorescence: odour analysis, ultrastructural changes and pollination aspects. *Plant Biology*, 4(3), 367-383.
- Hambali, G. G. (1979, September). The dispersal of taro by common palm civets. In E. H. Belen & M. Villanueva (Eds.), *International Symposium on Tropical Root Tuber Crop—5th Symposium Proceedings* (pp. 545-547). Philippine Council for Agriculture and Resources Research.
- Hazebroek, H. P., & Abang Kashim, A. M. (2002). *A guide to Gunung Mulu National Park*. Kota Kinabalu, Sabah: Natural History Publications (Borneo).
- Hentrich, H., Kaiser, R., & Gottsberger, G. (2007). Floral scent collection at the perfume flowers of *Anthurium rubrinervium* (Araceae) by the kleptoparasitic orchid bee *Aglae caerulea* (Euglossini). *Ecotropica*, 13, 149-155.
- Hentrich, H., Kaiser, R., & Gottsberger, G. (2010). Floral biology and reproductive isolation by floral scent in three sympatric aroid species in French Guiana. *Plant Biology*, 12(4), 587-596.
- Hetterscheid, W. L. A. & Claudel, C. (2012). The end of *Pseudodracontium* NE Br. *Aroideana*, 35, 40-46.
- Hetterscheid, W. L. A., & Ittenbach, S. (1996). Everything you always wanted to know about *Amorphophallus*, but were afraid to stick your nose into. *Aroideana*, 19, 7-131.

- Hoe, Y. C., Gibernau, M., Maia, A. C. D., & Wong, S. Y. (2016). Flowering mechanisms, pollination strategies and floral scent analyses of sympatric co-flowering *Homalomena* spp. (Araceae) on Borneo. *Plant Biology*, 18(4), 563–576.
- Hoe, Y. C., Gibernau, M., & Wong, S. Y. (2018). Diversity of pollination ecology in the *Schismatoglottis Calyptrata* Complex Clade (Araceae). *Plant Biology*, 20(3), 563-578.
- Hoe, Y. C., & Wong, S. Y. (2016). Floral biology of *Schismatoglottis baangongensis* (Araceae) in West Sarawak, Borneo. *Plant Systematics and Evolution*, 302(9), 1239-1252.
- Hotta, M., Okada, H., & Ito, M. (1985). Species diversity at wet tropical environment I. Polymorphic variation and population structure of *Schismatoglottis lancifolia* (Araceae) in West Sumatra. *Contributions from the Biology Laboratory, Kyoto University*, 27, 9-71.
- Hultén, E., & St. John, H. (1931). The American species of *Lysichitum*. *Svensk Botanisk Tidskrift*, 25(4), 453-464.
- Ivancic, A., Lebot, V., Roupsard, O., Garcia, J. Q., & Okpul, T. (2004). Thermogenic flowering of taro (*Colocasia esculenta*, Araceae). *Canadian Journal of Botany*, 82(11), 1557-1565.
- Ivancic, A., Roupsard, O., Garcia, J. Q., Lebot, V., Pochyla, V., & Okpul, T. (2005). Thermogenic flowering of the giant taro (*Alocasia macrorrhizos*, Araceae). *Canadian Journal of Botany*, 83(6), 647-655.

- Ivancic, A., Roupsard, O., Garcia, J. Q., Melteras, M., Molisale, T., Tara, S., & Lebot, V. (2008). Thermogenesis and flowering biology of *Colocasia gigantea*, Araceae. *Journal of Plant Research*, 121(1), 73-82.
- Jameson, M. L., & Drumont, A. (2013). Aroid scarabs in the genus *Peltonotus* Burmeister (Coleoptera, Scarabaeidae, Dynastinae): key to species and new distributional data. *ZooKeys*, 320, 63.
- Jürgens, A., Wee, S. L., Shuttleworth, A., & Johnson, S. D. (2013). Chemical mimicry of insect oviposition sites: a global analysis of convergence in angiosperms. *Ecology Letters*, 16(9), 1157-1167.
- Kite, G. C., & Hetterscheid, W. L. (2017). Phylogenetic trends in the evolution of inflorescence odours in *Amorphophallus*. *Phytochemistry*, 142, 126-142.
- Kite, G. C., Hetterscheid, W. L., Lewis, M. J., Boyce, P. C., Ollerton, J., Cocklin, E., Diaz, A. & Simmonds, M. S. J. (1998). Inflorescence odours and pollinators of *Arum* and *Amorphophallus* (Araceae). *Reproductive Biology*, 295-315.
- Knecht, M. (1983). *Contribution à l'étude biosystématique des représentants d'Aracées de la Côte d'Ivoire* (Vol. 17). Port Jervis, NY: Lubrecht & Cramer Limited.
- Kraemer, M., & Schmitt, U. (1999). Possible pollination by hummingbirds in *Anthurium sanguineum* Engl. (Araceae). *Plant Systematics and Evolution*, 217(3-4), 333-335.
- Kumano-Nomura, 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 Species Biology*, 21(3), 173-183.

- Kumano-Nomura, Y., & Yamaoka, R. (2009). Beetle visitations, and associations with quantitative variation of attractants in floral odors of *Homalomena propinqua* (Araceae). *Journal of Plant Research*, 122(2), 183-192.
- Lamprecht, I., Wadsö, L., & Seymour, R. S. (2013). Calorimetric investigations of the pollination biology of the thermogenic inflorescences of the dragon lily (*Dracunculus vulgaris*) and its pollinator (*Protaetia cretica*) on Crete. *Thermochimica acta*, 551, 84-91.
- Leguet, A., Gibernau, M., Shintu, L., Caldarelli, S., Moja, S., Baudino, S., & Caissard, J. C. (2014). Evidence for early intracellular accumulation of volatile compounds during spadix development in *Arum italicum* L. and preliminary data on some tropical Aroids. *Naturwissenschaften*, 101(8), 623-635.
- Li, N. N., Toda, M. J., Fu, Z., Chen, J. M., Li, S. H., & Gao, J. J. (2014). Taxonomy of the *Colocasiomyia gigantea* species group (Diptera, Drosophilidae), with descriptions of four new species from Yunnan, China. *ZooKeys*, 406, 41-64.
- Low, S. L., Wong, S. Y., & Boyce, P. C. (2014). *Schottarum* (Schismatoglottideae: Araceae) substantiated based on combined nuclear and plastid DNA sequences. *Plant Systematics and Evolution*, 300(4), 607-617.
- Low, S. L., Wong, S. Y., & Boyce, P. C. (2018). Naming the chaos: generic redelimitation in Schismatoglottideae (Araceae). *Webbia*, 73(1), 1-100.
- Low, S. L., Wong, S. Y., Ooi, I. H., Hesse, M., Städler, Y., Schönenberger, J., & Boyce, P. C. (2016). Floral diversity and pollination strategies of three rheophytic Schismatoglottideae (Araceae). *Plant Biology*, 18(1), 84-97.

- Madison, M.T. (1979). Protection of developing seeds in neotropical Araceae. *Aroideana*, 2(2), 52–61.
- Maia, A. C. D., Dötterl, S., Kaiser, R., Silberbauer-Gottsberger, I., Teichert, H., Gibernau, M., do Amaral Ferraz Navarro, D. M., Schlindwein, C., & Gottsberger, G. (2012). The key role of 4-methyl-5-vinylthiazole in the attraction of scarab beetle pollinators: a unique olfactory floral signal shared by Annonaceae and Araceae. *Journal of Chemical Ecology*, 38(9), 1072-1080.
- Maia, A. C. D., Gibernau, M., Carvalho, A. T., Gonçalves, E. G., & Schlindwein, C. (2013a). The cowl does not make the monk: scarab beetle pollination of the Neotropical aroid *Taccarum ulei* (Araceae: Spathicarpeae). *Biological Journal of the Linnean Society*, 108(1), 22-34.
- Maia, A. C. D., Gibernau, M., Dötterl, S., do Amaral Ferraz Navarro, D. M., Seifert, K., Müller, T., & Schlindwein, C. (2013b). The floral scent of *Taccarum ulei* (Araceae): attraction of scarab beetle pollinators to an unusual aliphatic acyloin. *Phytochemistry*, 93, 71-78.
- Maia, A. C. D., & Schlindwein, C. (2006). *Caladium bicolor* (Araceae) and *Cyclocephala celata* (Coleoptera, Dynastinae): a well-established pollination system in the northern Atlantic rainforest of Pernambuco, Brazil. *Plant Biology*, 8(4), 529-534.
- Maia, A. C. D., Schlindwein, C., do Amaral Ferraz Navarro, D. M., & Gibernau, M. (2010). Pollination of *Philodendron acutatum* (Araceae) in the Atlantic forest of northeastern Brazil: a single scarab beetle species guarantees high fruit set. *International Journal of Plant Sciences*, 171(7), 740-748.

- Maldonado, M., Sakuragui, C. M., Trigo, J. R., & Rodrigues, D. (2015). The selective florivory of *Erioscelis emarginata* matches its role as a pollinator of *Philodendron*. *Entomologia Experimentalis et Applicata*, 156(3), 290-300.
- Mansor, M., Boyce, P. C., Othman, A. S., & Sulaiman, B. (2011). *The Araceae of Peninsular Malaysia*. Penang: Penerbit USM.
- Mayo, S. J. (1980). *Biarums* for pleasure. *Aroideana*, 3(1), 32-35.
- Mayo, S. J. (1989). Observations of gynoecial structure in *Philodendron* (Araceae). *Botanical Journal of the Linnean Society*, 100, 139-172.
- Mayo, S. J. (1991). A revision of *Philodendron* subgenus *Meconostigma* (Araceae). *Kew Bulletin*, 46 (4), 601-681.
- Mayo, S. J., Bogner, J., & Boyce, P. C. (1997). *The genera of Araceae*. London: Kew Royal Botanic Gardens.
- Miyake, T., & Yafuso, M. (2003). Floral scents affect reproductive success in fly-pollinated *Alocasia odora* (Araceae). *American Journal of Botany*, 90(3), 370-376.
- Miyake, T., & Yafuso, M. (2005). Pollination of *Alocasia cucullata* (Araceae) by two *Colocasiomyia* flies known to be specific pollinators for *Alocasia odora*. *Plant Species Biology*, 20(3), 201-208.
- Moore, M. R., Beza-Beza, C. F., Wickell, D. A., Beck, J. B., & Jameson, M. L. (2015). Molecules, morphology and *Mimeoma* scarabs: evolutionary and taxonomic implications for a palm-associated scarab group. *Systematic Entomology*, 40(4), 891-900.

- Moore, M. R., & Jameson, M. L. (2013). Floral associations of cyclocephaline scarab beetles. *Journal of Insect Science*, 13(100), 1-43.
- Mori, Y., & Okada, H. (2001). Reproductive biology and pollen flow of a rheophytic aroid, *Furtadoa sumatrensis* (Araceae) in the Malesian wet tropics. *Plant Systematics and Evolution*, 227(1), 37-47.
- Nauheimer, L., & Boyce, P. C. (2014). *Englerarum* (Araceae, Aroideae): a new genus supported by plastid and nuclear phylogenies. *Plant Systematics and Evolution*, 300(4), 709-715.
- Nauheimer, L., Metzler, D., & Renner, S. S. (2012). Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. *New Phytologist*, 195(4), 938-950.
- Ng, K. K., Othman, A. S., Boyce, P. C., & Wong, S. Y. (2011). Studies on Homalomeneae (Araceae) of Borneo VIII: Delimitation of additional informal suprageneric taxa for Sundaic *Homalomena*. *Webbia*, 66(1), 21-28.
- Okada, T. (1986). Estimation of the routes of synhospitalic distribution of the genus *Drosophilella* Duda (Diptera, Drosophilidae), with descriptions of three new species from Malaysia and Indonesia. *Proceedings of the Japanese Society of Systematic Zoology*, 33, 32-39.
- Okada, T. (1987). Further notes on the genus *Drosophilella* Duda with descriptions of two new species from Indonesia (Diptera, Drosophilidae). *Proceedings of the Japanese Society of Systematic Zoology*, 36, 38-45.

- Okada, T. (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. *Proceedings of the Japanese Society of Systematic Zoology*, 42, 66-72.
- Ollerton, J., Killick, A., Lamborn, E., Watts, S., & Whiston, M. (2007). Multiple meanings and modes: on the many ways to be a generalist flower. *Taxon*, 56(3), 717-728.
- Pereira, J., Schlindwein, C., Antonini, Y., Maia, A. C. D., Dötterl, S., Martins, C., do Amaral Ferraz Navarro, D. M., & Oliveira, R. (2014). *Philodendron adamantinum* (Araceae) lures its single cyclocephaline scarab pollinator with specific dominant floral scent volatiles. *Biological Journal of the Linnean Society*, 111(3), 679-691.
- Poppinga, S., Koch, K., Bohn, H. F., & Barthlott, W. (2010). Comparative and functional morphology of hierarchically structured anti-adhesive surfaces in carnivorous plants and kettle trap flowers. *Functional Plant Biology*, 37(10), 952-961.
- Punekar, S. A. (2007). *An assessment of floristic diversity of Anshi National Park, Karnataka* (Doctoral dissertation). University of Pune, Pune, India.
- Punekar, S. A., & Kumaran, K. P. N. (2010). Pollen morphology and pollination ecology of *Amorphophallus* species from North Western Ghats and Konkan region of India. *Flora-Morphology, Distribution, Functional Ecology of Plants*, 205(5), 326-336.
- Quilichini, A., Torre, A., & Gibernau, M. (2005). Preliminary data on the biology and reproduction of *Ambrosina bassii* L (Araceae) in Corsica. *Aroideana*, 28, 37-42.

- Quilichini, A., Macquart, D., Barabé, D., Albre, J., & Gibernau, M. (2010). Reproduction of the West Mediterranean endemic *Arum pictum* (Araceae) on Corsica. *Plant Systematics and Evolution*, 287(3-4), 179-187.
- Sakai, S., Kato, M., & Inoue, T. (1999). Three pollination guilds and variation in floral characteristics of Bornean gingers (Zingiberaceae and Costaceae). *American Journal of Botany*, 86(5), 646-658.
- Schiestl, F. P., & Dötterl, S. (2012). The evolution of floral scent and olfactory preferences in pollinators: coevolution or pre-existing bias? *Evolution: International Journal of Organic Evolution*, 66(7), 2042-2055.
- Schwerdtfeger, M., Gerlach, G., & Kaiser, R. (2002). Anthecology in the neotropical genus *Anthurium* (Araceae): a preliminary report. *Selbyana*, 23(2), 258-267.
- Seubert, E. (1993). *Die Samen der Araceen: Die Samenmerkmale der Araceen und ihre Bedeutung für die Gliederung der Familie*. Königstein: Koeltz.
- Sivadasan, M., & Kavalan, R. (2005). Flowering phenology and beetle pollination in *Theriophonum infaustum* NE Br. (Araceae). *Aroideana*, 28, 104-112.
- Sivadasan, M., & Sabu, T. (1989). Beetle-pollination, cantharophily in *Amorphophallus hohenackeri* (Araceae). *Aroideana*, 12(1-4), 32-37.
- Stökl, J., Strutz, A., Dafni, A., Svatos, A., Doubsky, J., Knaden, M., Sachse, S., Hansson, B., & Stensmyr, M. C. (2010). A deceptive pollination system targeting drosophilids through olfactory mimicry of yeast. *Current Biology*, 20(20), 1846-1852.

- Sultana, F., Hu, Y. G., Toda, M. J., Takano, K. T., & Yafuso, M. (2006). Phylogeny and classification of *Colocasiomyia* (Diptera, Drosophilidae), and its evolution of pollination mutualism with aroid plants. *Systematic Entomology*, 31(4), 684-702.
- Takano, K. T., Repin, R., Mohamed, M. B., & Toda, M. J. (2012). Pollination mutualism between *Alocasia macrorrhizos* (Araceae) and two taxonomically undescribed *Colocasiomyia* species (Diptera: Drosophilidae) in Sabah, Borneo. *Plant Biology*, 14(4), 555-564.
- Takano, K. T., Suwito, A., Gao, J. J., & Yin, J. T. (2011). Molecular phylogeny of the cristata species group of the genus *Colocasiomyia* (Diptera: Drosophilidae). *Low Temperature Science*, 69, 19-28.
- Takano, K. T., Yin, J. T., Wen, S. Y., & Toda, M. J. (2006). Reproductive ecology of a new species of the genus *Colocasiomyia* de Meijere (Diptera: Drosophilidae) and its host plant *Steudnera colocasiaeifolia* (Araceae) in Yunnan, China. *Entomological Science*, 9, 79-91.
- Takizawa, H. (2012). Descriptions of new species of the genus *Chaloenus* Westwood from greater Sunda Islands (Coleoptera: Chrysomelidae: Alticinae). *Genus*, 23(2), 269-330.
- Toda, M. J., & 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(2), 169-184.

- Tung, L. S., Wong, S. Y., & Boyce, P. C. (2010). Studies on Homalomeneae (Araceae) of Borneo VI: *Homalomena giamensis*, a new species from Sarawak, Malaysian Borneo, with notes on its pollination. *Aroideana*, 33, 201-211.
- Ulrich, S., Hesse, M., Bröderbauer, D., Wong, S. Y., & Boyce, P. C. (2012). *Schismatoglottis* and *Apoballis* (Araceae: Schismatoglottideae): a new example for the significance of pollen morphology in Araceae systematics. *Taxon*, 61(2), 281-292.
- Urru, I., Stökl, J., Linz, J., Krügel, T., Stensmyr, M. C., & Hansson, B. S. (2010). Pollination strategies in Cretan *Arum* lilies. *Biological Journal of the Linnean Society*, 101(4), 991-1001.
- van der Ham, R., Grob, G., Hetterscheid, W., Star, W., & van Heuven, B. J. (2005). Notes on the genus *Amorphophallus* (Araceae)-13. Evolution of pollen ornamentation and ultrastructure in *Amorphophallus* and *Pseudodracontium*. *Grana*, 44(4), 252-265.
- van Steenis, C. G. G. J. (1987). Rheophytes of the world: supplement. *Allertonia*, 4(5), 267-330.
- Vogel, S. (1990). The role of scent glands in pollination. In S.S. Renner (Ed.), *On the structure and function of osmophores* (pp. 44-89). Washington, D.C.: Smithsonian Institution Libraries and The National Science Foundation.
- Wong, S. Y. (2013). Rheophytism in Bornean Schismatoglottideae (Araceae). *Systematic Botany*, 38(1), 32-45.

- Wong, S. Y., & Boyce, P. C. (2013). The role of the interstice staminodes of *Bucephalandra* Schott (Araceae: Schismatoglottideae). *International Aroid Society Newsletter*, 35(2), 11-12.
- Wong, S. Y., & Boyce, P. C. (2017). Studies on Homalomeneae (Araceae) of Borneo XX: *Homalomena lambirensis* sp. nov. from Sarawak with well-recorded pollination biology. *Nordic Journal of Botany*, 35(5), 557-562.
- Wong, S. Y., Boyce, P. C., & Fasihuddin, B. A. (2011). Studies on Homalomeneae (Araceae) of Borneo III: The helophytic *Homalomena* of Sunda. *Garden's Bulletin Singapore*, 62, 313-325.
- Wong, S. Y., Boyce, P. C., Othman, A. S., & Leaw, C. P. (2010). Molecular phylogeny of tribe Schismatoglottideae based on two plastid markers and recognition of a new tribe, Philontieae, from the Neotropics. *Taxon*, 59(1), 117-124.
- Wong, S. Y., Jean, T. P., Kiaw, N. K., Othman, A. S., Boon, L. H., Ahmad, F. B., & Boyce, P. C. (2013). Phylogeny of Asian *Homalomena* (Araceae) based on the ITS region combined with morphological and chemical data. *Systematic Botany*, 38(3), 589-599.
- Wong, S. Y., Meerow, A. W., & Croat, T. B. (2016). Resurrection and new species of the Neotropical genus *Adelonema* (Araceae: Philodendron clade). *Systematic Botany*, 41(1), 32-48.
- Yadav, S. R. (1998). Adaptive significance of phenology and spadix architecture in Araceae of Western Ghats of India. *Plant Diversity*, 20(10), 1-3.

- Yafuso, M., Viet, B. T., & Adaniya, S. (2015). Pollination mutualism between flower-breeding flies of the genus *Colocasiomyia* (Diptera, Drosophilidae) and their host plant routes of Araceae in Vietnam. *Aroideana* 38, 94-106.
- Zhu, G., & Croat, T. B. (2004). Revision of *Dracontium* (Araceae). *Annals of the Missouri Botanical Garden*, 91, 593-667.
- Zotz, G. (2013). ‘Hemiepiphyte’: a confusing term and its history. *Annals of Botany*, 111(6), 1015-1020.

APPENDICES

Appendix A: Incomplete pollination observations on additional species

Alocasia princeps

Alocasia princeps (Appx. A-1, A-1A) rarely flowering, it only flowering twice during the study period, the first mass flowering occurred around January 2018 (most plant) and the second flowering occurred around September 2018 (the other plant), each plant probably only flowering once a year. Each plant has three to four inflorescences, the interval between flowering is one day, each inflorescence took three days to finish flowering (include pre flowering), thus each plant may take 12 days to 16 days to finish flowering.

The timing of anthesis for *A. princeps* is about the same like *A. sarawakensis*, which lasted ca. 26 - 27 hours. The spathe started to open a day before pistillate anthesis in *A. princeps* (Appx. A-1C). The upper spathe opened a gap and lower spathe inflated to create a floral chamber with ca. 0.3 cm space between the spathe and the pistillate zone, and ca. 0.2 cm gap between the constriction of the spathe and the sterile interstice. Pistillate anthesis probably started around 0500 h (Day 1) and ended ca. 1000 h (Day 1), with the release of “jasmine-pineapple” floral odour from the appendix (strongest 0600-0800 h, extend nearly) and the upper spathe reflexed (Appx. A-1D). The intersexual phase started ca. 1000 h (Day 1) and lasted for 20 - 21 hours, indicated by weakened floral odour. Staminate anthesis started the next day with pollen probably released between 0530 – 0600 h (Day 2), with tightened gap between the spathe constriction and sterile interstice (ca. 0.1 cm), and absence of floral odour. The upper spathe and staminate zone senesced one to two days post-anthesis

in *A. princeps*. The fruits of *A. princeps* ripen in two and a half to three months and revealed by the splitting of lower spathe from tip (Appx. A-1B), the fruits probably dispersed by birds.



Appendix A-1: *Alocasia princeps*. (A) Mature plant with inflorescences. (B) Ripened infructescences. (C-D) Inflorescence of *A. princeps* at various stages. (C) Pre anthesis, gap opened. (D) Pistillate anthesis, gap reflexed, flies entered. (E) Flies (*Drosophilidae*) in pistillate zone. (F) Chrysomelid beetles chew spathe during pistillate anthesis.

Fruit flies (Drosophilidae) were main pollinators of *A. princeps*, the flies probably start to arrive around 0630 h (Day 1) during pistillate anthesis and more flies came between 0700 - 0730 h. The flies moved to pistillate zone upon arrived (Appx. A-1E), the flies moved around, consumed wetness on pistillate flowers and some of the flies mated there. The flies stayed a night in the inflorescences at the pistillate zone, mostly faced inner surface of the lower spathe. The flies only moved up to staminate zone to collect pollen ca. 0615 - 0630 h (Day 2, staminate anthesis), the flies started to leave after 0640 h and mostly left at 0700 h. There were estimated 5 to 20 flies (Drosophilidae) visited the inflorescences of *A. sarawakensis* during anthesis.

The ca. 0.2 cm gap between the constriction of the spathe and the sterile interstice, and ca. 0.3 cm space between the spathe and the pistillate zone only allow small insects like the Drosophilid flies to enter the pistillate zone. There were one to two individuals of Chrysomelid beetles that attracted by the floral scent of *A. princeps* and visited its inflorescences anytime during pistillate anthesis, the beetles only chew appendix and sometime the spathe but they never access the pistillate zone (Appx. A-1F).

Natural fruit set is intermediate for *A. princeps*, ranged from 58.6 % to 64.5 %, and with an average of 61.7%. Autonomous self- pollination not tested for this species due to insufficient inflorescences.

Rhaphidophora typha

Rhaphidophora typha (Appx. A-2A – A-2F) seems flowering twice per year and each plant probably flowering once a year because only some plants flowering each time and those not flowering will flowering next time, each plant only has an inflorescence.



Appendix A-2: (A-F) *Rhaphidophora typha*. (A) Mature plant. (B-D) Inflorescences at various stages. (B) Pistillate anthesis, spathe open a slit gap and floral chamber inflated. (C) Pistillate anthesis, spathe close back in the afternoon. (D) Staminate anthesis, pollen released, spathe abscised. (E) Flies (Drosophilidae) move on flowers. (F) Rove beetles at spathe margin. (G-I) *Rhaphidophora megasperma*. (G) Inflorescence. (H) Rove beetles collect pollen. (I) Male anthesis, spathe opened.

The timing of anthesis seems to be multiple days for *R. typha*, pistillate anthesis probably started early morning each day because the spathe already inflated with a 0.2 – 0.3 cm gap at 0800 h (Appx. A-2B), however, the “tiger oil mint” floral odour (from spadix) only became strong (detected nearly) around 1000 h to 1300 h, the spathe gap gradually closed after 1300 h and completely closed around 1500 h (Appx. A-2C), and the floral odour also weakened. The pistillate anthesis probably lasted 2 to 3 days before the start of staminate anthesis, which the pollen already released and spathe already dropped off at 1400 h (Appx. A-2D), floral odour was not detected during staminate anthesis. The spadix gradually turned green from white throughout fruit development and the fruits probably ripened in two to three months.

Drosophilid flies is the main pollinator of *R. typha*, ca. 5 to 10 individuals visited each inflorescence of *R. typha*, the flies usually arrived after 1000 h when the floral odour become strong, the flies may stay in the inflorescence until staminate anthesis but they usually fly off when disturbed. The flies moved into the inflorescence chamber through the 0.2 to 0.3 cm slit gap, the flies move around the spadix (Appx. A-2E), sometimes consume wetness from stigmas and mating, the flies probably oviposit in the inflorescence. Besides, they were several rove beetles (Appx. A-2F) and thrips spotted inside the inflorescences. During staminate anthesis, the pollen probably releases before the spathe drop off and the insects collect pollen before they are gone after the spathe open and drop off.

Open pollination and autonomous self-pollination are not treated to *R. typha* due to insufficient inflorescence.

Rhaphidophora megasperma

Rhaphidophora megasperma (Appx. A-2G – A-2I) probably flowering twice or more a year, inflorescences produce from terminal of secondary or tertiary shoots that grow out along the primary stem that hanging on the host plant, the order of flowering usually occurs from inflorescences at base to inflorescences at tip of the primary stem.

The timing of anthesis for *R. megasperma* is probably about the same like *R. typha*. The inflorescences probably open and close back for few days during pistillate anthesis, the inflorescences open in the morning and closed back in the afternoon. During pistillate anthesis, the spathe turns yellowish and “mustard/wasabi” smell (from spadix) was detected nearly from the tiny gap opened, the floral odour become weak in the afternoon when the spathe close back. Staminate anthesis started after few days of pistillate anthesis with the release of pollen that probably occur before the spathe open (Appx. A-2I), and no floral odour is detected. The opened spathe gradually senesced and the spadix gradually turned green after the end of anthesis, the fruits probably ripened in two to three months.

Rhaphidophora megasperma probably pollinated by drosophilid flies, the flies probably leave immediately when the spathe open post staminate anthesis. There were few rove beetles spotted to collect pollen when the spathe already opened (Appx. A-2H), the beetles probably stay in the inflorescence throughout anthesis and are possible pollinators.

Open pollination and autonomous self-pollination are not treated to *R. megasperma* due to insufficient inflorescence.

Nabalu corneri

Nabalu corneri (Appx. A-3A – A-3E) most probably pollinated by Drosophilid flies (Appx. A-3C) and *Cycreon* beetles (Appx. A-3D), these insects were observed in inflorescences of this species during pistillate anthesis, these insects are small enough to enter the pistillate zone that has narrow space of ca. 0.2 cm between the pistillate flowers and inner spathe and ca. 0.2 cm gap at spathe constriction. The insects probably stay a night in the inflorescences, and rewarded with mating site and liquid from pistillate flowers. Besides, the inflorescence of *N. corneri* also visited by unknown scarab beetles (Scarabaeidae), the beetles chew staminate zone during pistillate anthesis (Appx. A-3E) but their big body size never allows them to access the pistillate zone.

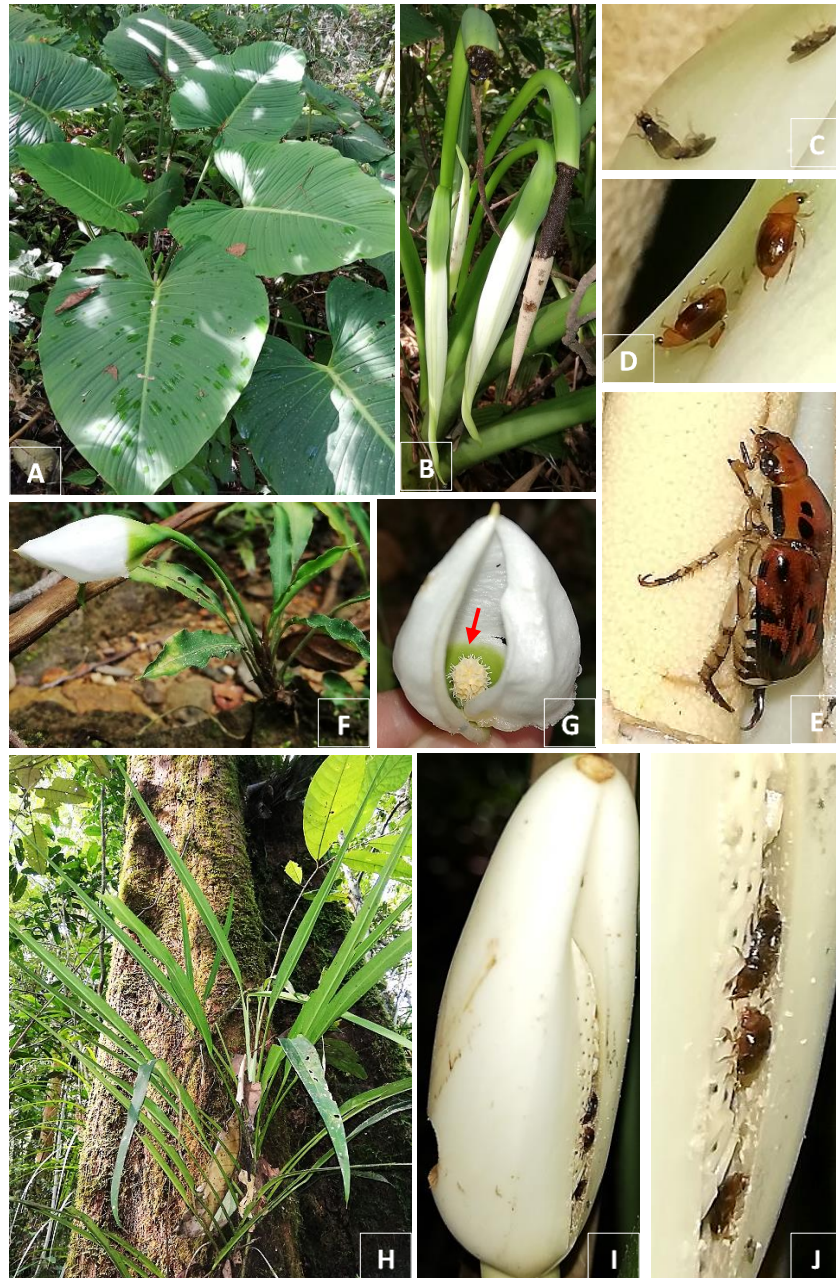
Burttianthus purseglovei* & *Gamogyne burbidgei

Both species are pollinated by Drosophilid flies like the other species of Schismatoglottideae, their small body size allow them to access the pistillate zone freely. *Chaloenus* beetles are possible pollinators in both species because there is no restriction that prevent the beetles to access the pistillate zone, and the inflated floral chamber is quite spacious for the beetles to access down to the pistillate zone. There were three to five drosophilid flies and three to six *Chaloenus* beetles collected from *B. purseglovei* (Appx. A-3F – A-3G), and eight *Chaloenus* beetles and a drosophilid flies collected from *G. burbidgei*.

***Scindapsus* sp.**

Scindapsus sp. (Appx. A-3H – A-3J) was observed to visit by Nitidulid beetles, ca. three to five nitidulid beetles collect pollen in inflorescence of this species after pollen released (Appx. A-3I – A-3J), the beetles probably stay in the inflorescence throughout

anthesis. The beetles are possible pollinators because they are the only visitor observed, their small body size allow them to enter the narrow spathe gap and move freely in the narrow floral chamber.



Appendix A-3: (A-E) *Nabalu corneri*. (A) Mature plant. (B) Inflorescences at various stages. (C) Flies (Drosophilidae) at spathe margin. (D) *Cycreon* beetles at spathe margin. (E) Unknown scarab beetles chew staminate zone. (F-G) *Burttianthus purseglovei*. (F) Mature plant. (G) Staminate phase inflorescence, pollen released. (H-J) *Scindapsus* sp. (H) Mature plant. (I) Staminate phase inflorescence, pollen released. (J) Sap beetles (Nitidulidae) collect pollen.