

EKOLOGI PEMBIAKAN DAN ANALISIS
FILOGENETIK MOLEKUL ENAM SPESIES
KELADI HUTAN REOFITIK (ARACEAE:
SCHISMATOGLOTTIDEAE)

oleh

OOI IM HIN

Tesis yang diserahkan untuk memenuhi keperluan bagi
Ijazah Sarjana Sains

July 2012

ACKNOWLEDGEMENTS

Thanks to my main supervisor, Assoc. Prof. Dr. Ahmad Sofiman Othman, for his patience and guidance throughout this study. My gratitude goes to Mr. Peter C. Boyce and Dr. Wong Sin Yeng for their supports. Permission to conduct fieldwork from Forestry Department of Sarawak (Gunung Gading N. P., Kubah N. P. and Bako N. P., Permit no. NPW.907.4.2(II)-82 and Permit to enter Park No. 67/2007), Perak Forestry (Taiping) and Johor National Park (Endau-Rompin) are highly credited. The experience in sharing techniques of molecular work among the staff and students of School of Biological Sciences, especially those from Lab 409, are much appreciated. Thanks are also due to the staff of Penang Botanic Gardens' Botany Division in joining the preliminary visit of fieldwork in Perak. The understanding and supports of my parents by giving a digital camera as a birthday gift to use in the field observations and many other more are gratefully thanked. Greatest appreciation goes to those plants which were sacrificed for the sake of science.

The fieldwork in Sarawak was partially funded by the Ministry of Higher Education, Malaysia Fundamental Research Grant Scheme No. FRGS/01(04)/609/2006(42) and the molecular work was funded by the Research University Research Grant Scheme No. 1001/PBIOLOGI/815008.

TABLE OF CONTENTS

Acknowledgements	ii
Table of Contents	iii
List of Tables	vi
List of Figures	ix
List of Plates	x
Abstrak	xiii
Abstract	xiv

CHAPTER 1 - INTRODUCTION

1.1 Background	1
1.2 Objectives	7

CHAPTER 2 - LITERATURE REVIEW

2.1 Inflorescence Morphology of Araceae	8
2.2 Tribe Schismatoglottideae	9
2.3 Taxonomy	10
2.3.1 <i>Piptospatha perakensis</i> (Engl.) Engl.	10
2.3.2 <i>Piptospatha ridleyi</i> N.E.Br. ex Hook.f.	13
2.3.3 <i>Piptospatha elongata</i> (Engl.) N.E.Br.	16
2.3.4 <i>Ooia grabowskii</i> (Engl.) S.Y.Wong & P.C.Boyce	21
2.3.5 <i>Bakoa lucens</i> (Bogner) P.C.Boyce & S.Y.Wong	26

2.3.6 <i>Aridarum nicolsonii</i> Bogner	29
2.4 Pollination	31
2.5 Fruitset	35
2.6 Seed Dispersal	36
2.7 Seedling Establishment	37
2.8 Molecular Techniques	38
2.9 Chloroplast DNA	39

CHAPTER 3 - MATERIALS AND METHODOLOGY

3.1 Choice of Taxa	42
3.2 Field Observation	44
3.3 Molecular Techniques	46
3.3.1 Sample Collection and Storage	47
3.3.2 DNA Extraction	47
3.3.3 Polymerase Chain Reaction (PCR) Amplification	49
3.3.4 Purification and Sequencing	50
3.3.5 Molecular Phylogenetic Analysis	51

CHAPTER 4 - RESULTS AND DISCUSSION

4.1 Introduction	55
4.2 Pollination, Fruitset, Seed Dispersal and Seedling Establishment	55
4.2.1 <i>Piptospatha elongata</i>	55

4.2.2 <i>Ooia grabowskii</i>	65
4.2.3 <i>Piptospatha ridleii</i>	75
4.2.4 <i>Piptospatha perakensis</i>	82
4.2.5 <i>Bakoa lucens</i>	90
4.2.6 <i>Aridarum nicolsonii</i>	99
4.3 Molecular Phylogenetic Analyses	108
4.3.1 Sequences Alignment	108
4.3.2 Phylogenetic Analyses of the Six Subject Species	108
4.3.3 Phylogenetic Analyses of Subject Species with Out-groups	110
4.3.4 Phylogenetic Analyses of Subject Species with other <i>Piptospatha</i> and Species from other Genera	112
4.3.5 Relationship of <i>Piptospatha</i> and its allies	117
CHAPTER 5 - CONCLUSION	
5.1 Conclusion	119
5.2 Recommendation for Future Studies	120
References	122
Appendices	133
List of Publications	145

LIST OF TABLES

		Page
Table 3.1	Details of species selected for this study	43
Table 3.3	Primers selected for this study	47
Table 4.2.1a	Numbers of insect visitors in the inflorescences of <i>Piptospatha elongata</i>	60
Table 4.2.1b	Number of pistillate flowers, number of fruits and fruitset percentage of <i>Piptospatha elongata</i>	63
Table 4.2.1c	Seed dispersal distances of five selected <i>Piptospatha elongata</i> mother plants	64
Table 4.2.1d	Percentages of remaining seeds, germinated seeds and seed lost of <i>Piptospatha elongata</i> with two different conditions in the field and control in laboratory	65
Table 4.2.2a	Numbers of insect visitors in the inflorescences of <i>Ooia grabowskii</i>	71
Table 4.2.2b	Number of pistillate flowers, number of fruits and fruitset percentage of <i>Ooia grabowskii</i>	73
Table 4.2.2c	Seed dispersal distances of five selected <i>Ooia grabowskii</i> mother plants	73
Table 4.2.2d	Percentages of remaining seeds, germinated seeds and seed lost of <i>Ooia grabowskii</i> with two different conditions in the field and control in laboratory	74
Table 4.2.3a	Numbers of insect visitors in the inflorescences of <i>Piptospatha ridleyi</i>	79
Table 4.2.3b	Number of pistillate flowers, number of fruits and fruitset percentage of <i>Piptospatha ridleyi</i>	79
Table 4.2.3c	Seed dispersal distances of five selected <i>Piptospatha ridleyi</i> mother plants	81
Table 4.2.3d	Percentages of remaining seeds, germinated seeds and seed lost of <i>Piptospatha ridleyi</i> with two different conditions in the field and control in laboratory	82

Table 4.2.4a	Numbers of insect visitors in the inflorescences of <i>Piptospatha perakensis</i>	86
Table 4.2.4b	Number of pistillate flowers, number of fruits and fruitset percentage of <i>Piptospatha perakensis</i>	88
Table 4.2.4c	Seed dispersal distances of five selected <i>Piptospatha perakensis</i> mother plants	88
Table 4.2.4d	Percentages of remaining seeds, germinated seeds and seed lost of <i>Piptospatha perakensis</i> with two different conditions in the field and control in laboratory	89
Table 4.2.5a	Numbers of insect visitors in the inflorescences of <i>Bakoa lucens</i>	94
Table 4.2.5b	Number of pistillate flowers, number of fruits and fruitset percentage of <i>Bakoa lucens</i>	96
Table 4.2.5c	Seed dispersal distances of five selected <i>Bakoa lucens</i> mother plants	97
Table 4.2.5d	Percentages of remaining seeds, germinated seeds and seed lost of <i>Bakoa lucens</i> with two different conditions in the field and control in laboratory	98
Table 4.2.6a	Numbers of insect visitors in the inflorescences of <i>Aridarum nicolsonii</i>	104
Table 4.2.6b	Number of pistillate flowers, number of fruits and fruitset percentage of <i>Aridarum nicolsonii</i>	104
Table 4.2.6c	Seed dispersal distances of five selected <i>Aridarum nicolsonii</i> mother plants	106
Table 4.2.6d	Percentages of remaining seeds, germinated seeds and seed lost of <i>Aridarum nicolsonii</i> with two different conditions in the field and control in laboratory	107
Table 4.3.2	Summary of characteristics for the data sets analysed in the combined regions of the six subject taxa	110
Table 4.3.3	Summary of characteristics for the data sets analysed in the combined regions of the subject taxa with out-groups	112

Table 4.3.4	Summary of characteristics for the data sets analysed in the combined regions of the subject taxa with other <i>Piptospatha</i> and species from other genera	113
Table 4.3.5	Some of the reproductive characteristics differences of the two <i>Piptospatha</i> species in Peninsular Malaysia	118

LIST OF FIGURES

		Page
Figure 4.3.2	Unrooted bootstrap consensus trees of six subject taxa from (A) maximum parsimony, (B) maximum likelihood and (C) neighbour-joining showed the species from Peninsular Malaysia and Borneo were not forming separated groups	109
Figure 4.3.3	Rooted bootstrap consensus trees of subject taxa with out-groups from (A) maximum parsimony, (B) maximum likelihood and (C) neighbour-joining showed the <i>Piptospatha</i> and its allies (<i>Bakoa</i> , <i>Ooia</i>) were polyphyletic	111
Figure 4.3.4a	One of 55 the most parsimonious trees of subject taxa with other <i>Piptospatha</i> and species from other genera showed current <i>Piptospatha</i> was still highly polyphyletic after excluding <i>Bakoa</i> and <i>Ooia</i>	114
Figure 4.3.4b	A maximum likelihood tree of subject taxa with other <i>Piptospatha</i> and species from other genera showed current <i>Piptospatha</i> was still highly polyphyletic after excluding <i>Bakoa</i> and <i>Ooia</i>	115
Figure 4.3.4c	A neighbour-joining tree of subject taxa with other <i>Piptospatha</i> and species from other genera showed current <i>Piptospatha</i> was still highly polyphyletic after excluding <i>Bakoa</i> and <i>Ooia</i>	116

LIST OF PLATES

		Page
Plate 4.2.1a	<i>Piptospatha elongata</i> . A, plant with a inflorescence and a infructescence; B, bud; C, mature inflorescence; D, spadix during pistillate anthesis; E, flies during pistillate anthesis; F, spathe during pistillate anthesis; G, flies during late pistillate anthesis; H, spathe during staminate anthesis; I, flies during staminate anthesis; J, spadix during staminate anthesis; K, chrysomelid during transition period; L, flies during transition period; M, chrysomelid; N, drosophilid	56
Plate 4.2.1b	<i>Piptospatha elongata</i> . A, staphylinid; B, caducous spathe limb; C, infructescence with young greenish red fruit; D, infructescence with green developed fruit; E, green fruits at tip and white fruits near base; F, green fruit and white fruit; G, infructescence with ripe fruit revealing seeds; H, seed with wet sacrotesta-like membrane; I, seed with dried sarcotesta-like membrane; J, radicle with tiny root-like structure from germinated seed; K, seedling with a leave and two lateral roots; L, pubescent lateral root with many tertiary roots	62
Plate 4.2.2a	<i>Ooia grabowskii</i> . A, whole plant; B, bud; C, mature inflorescence; D, spathe during pistillate anthesis; E, spathe during staminate anthesis; F, pollen extruding; G, spadix during pistillate anthesis with insects; H, Spadix during staminate anthesis with insects; I, orange head green metallic chrysomelid; J, nitidulid; K, black head blue metallic chrysomelid; L, staphylinid; M, <i>Colocasiomyia</i> .	67
Plate 4.2.2b	<i>Ooia grabowskii</i> . A, spathe four days after staminate anthesis; B, deliquesced spathe tip; C, decaying staminate and sterile zone; D, fruits; E, infructescences with running water; F, mature infructescences; G, ripe fruits; H, spadix axis within one week after dispersal; I, persistent spadix axis; J, germinated seed with splitting micropylar appendages; K, seedling; L, root with mucilage tip; M, vegetative reproduction from roots.	72

Plate 4.2.3a	<i>Piptospatha ridleyi</i> . A, whole plant; B, bud; C, mature inflorescence; D, spathe during pistillate anthesis; E, gap during pistillate anthesis; F, spathe during staminate anthesis; G, Spadix during late pistillate anthesis; H, spadix during staminate anthesis; I, gap during staminate anthesis; J, <i>Colocasiomyia</i> ; K, blue-green metallic chrysomelids; L, nitidulid; M, brown metallic chrysomelid.	76
Plate 4.2.3b	<i>Piptospatha ridleyi</i> . A, rotting spathe limb; B, young infructescence; C, developing infructescences; D, green and white fruits; E, splash-cup seed dispersal; F, ripe fruits; G, empty splash-cup; H, seeds with sarcotesta-like membrane and splitting micropylar appendages; I, seedling with seed remained; J, seedling; K, pubescent green root.	80
Plate 4.2.4a	<i>Piptospatha perakensis</i> . A, young inflorescence; B, mature inflorescence; C, gap during pistillate anthesis; D, <i>Colocasiomyia</i> on pistillate zone during pistillate anthesis; E, spathe during pistillate anthesis; F, spadix during pistillate anthesis; G, spathe during staminate anthesis; H, spadix during staminate anthesis; I, <i>Colocasiomyia</i> ; J, gap during staminate anthesis; K, young infructescence with a pupa.	84
Plate 4.2.4b	<i>Piptospatha perakensis</i> . A, infructescences; B, fruits with irregular size; C, near mature infructescences; D, seed revealed after fruits ripening; E, empty splash-cup; F, seed splashed out after rain; G, newly germinated seedling; H, seed with a micropylar appendage; I, green pubescent root; J, root regenerated from disarticulated shoot; K & L, seedlings.	87
Plate 4.2.5a	<i>Bakoa lucens</i> . A, inflorescence during pistillate anthesis; B, whole plant; C, young bud; D, gap during staminate anthesis; E, mature inflorescence; F, inflorescence during staminate anthesis; G, spadix during staminate anthesis; H, clearance to lower spathe chamber during pistillate anthesis; I, spadix during pistillate anthesis; J, Chrysomelid; K, <i>Colocasiomyia</i> .	91

- Plate 4.2.5b** *Bakoa lucens*. A, young infructescence; B, developing infructescence; C, mature infructescence; D, young fruits; E, mature fruits; F, infructescence one day after dispersal started; G, infructescence two days after dispersal started; H, remaining spathe and spadix more than one week after seed dispersal; I, seeds; J, germinating seed; K, seedling; L, roots regenerated from the disarticulated shoot. 95
- Plate 4.2.6a** *Aridarum nicolsonii*. A, whole plant; B, young bud; C, mature inflorescence; D, gap during pistillate anthesis; E, *Colocasiomyia* during pistillate anthesis; F, chrysomelids during pistillate anthesis; G, spadix during pistillate anthesis; H, inflorescence during staminate anthesis; I, insects during staminate anthesis; J, *Colocasiomyia* and pollen extruding during staminate anthesis; K, spadix during staminate anthesis. 100
- Plate 4.2.6b** *Aridarum nicolsonii*. A, spathe limb caduceus; B, young infructescence; C, near mature infructescence; D, green and yellowish white young fruits; E, ripe fruits revealing seeds; F, seeds with splitting micropylar appendages; G, germinated seed; H, first leaf developed from plumule; I, plumule emerged from the fissure at slightly spreading epicotyl; J, seedling; K, new shoot regenerated from remaining root system after shoot disarticulation. 105

EKOLOGI PEMBIAKAN DAN ANALISIS FILOGENETIK MOLEKUL

ENAM SPESIES KELADI HUTAN REOFITIK (ARACEAE:

SCHISMATOGLOTTIDEAE)

ABSTRAK

Enam keladi hutan reofitik dalam Schismatoglottideae, dua dari Semenanjung Malaysia (*Piptospatha ridleyi*, *P. perakensis*) dan empat dari Borneo (*P. elongata*, *Ooia grabowskii*, *Bakoa lucens*, *Aridarum nicolsonii*) telah dipilih sebagai wakil-wakil kepada kumpulan-kumpulan tertentu. Pemerhatian lapangan tentang mekanik seludang, pendebungan, penghasilan buah, penyebaran biji benih dan penubuhan anak benih takson-takson ini telah dijalan dan dicatatkan. Jujukan dua rantau DNA kloroplas (*trnL-trnF*, *matK-3'trnK*) telah dikaji untuk setiap spesies dengan menggunakan teknik penjujukan DNA. Filogeni takson-takson yang dibina-semula menunjukkan genus *Piptospatha* ialah satu kumpulan yang polifiletik. Melalui hubung filogenetik ini pertalian evolusi takson-takson sudah difahami. Pada masa yang sama, kajian ini telah menyumbang kepada persempadanan genus *Piptosaptha*, menghuraikan genus-genus *Bakoa* dan *Ooia* secara tidak langsung.

**REPRODUCTIVE ECOLOGY AND MOLECULAR PHYLOGENETIC
ANALYSIS OF SIX SPECIES OF RHEOPHYTIC AROIDS (ARACEAE:
SCHISMATOGLOTTIDEAE)**

ABSTRACT

Six rheophytic aroids in Schismatoglottideae, two from Peninsular Malaysia (*Piptospatha ridleii*, *P. perakensis*) and four from Borneo (*P. elongata*, *Ooia grabowskii*, *Bakoa lucens*, *Aridarum nicolsonii*), were chosen as the representative taxa for their respective groups. Field observations on the spathe mechanics, pollination, fruitset, seed dispersal and seedling establishment of these taxa were conducted and documented. Two chloroplast DNA regions (*trnL-trnF*, *matK-3'trnK*) were sequenced for each species using DNA sequencing technique. The phylogeny of these taxa was reconstructed and showed genus *Piptospatha* is a polyphyletic group. Based of the phylogeny the evolutionary relationship of these taxa was understood. Concurrently, this study indirectly contributed to the delimitation of genus *Piptospatha*, and indirectly towards the description of genera *Bakoa* and *Ooia*.

CHAPTER 1

INTRODUCTION

1.1 Background

Araceae Juss. (colloquially ‘aroids’) is the fourth largest monocot family, consisting of c. 120 genera, and c. 3800 described species, but with an estimated species total of >5400 (Boyce & Croat, unpub. data). The Araceae are most abundant and diverse in the wet or perhumid tropics (Mayo *et al.*, 1997; Boyce, 2011). Aroids are among the most morphologically diverse of all flowering plants, with an unparalleled range of life form and leaf morphology. However, it is the inflorescence, almost uniformly comprising a modified bract, called a spathe, subtending a central fleshy spike of bracteole-less flowers, the spadix, that aside from botanically defining the family also provides the most extraordinary range of morphologies, each linked to a complex series of remarkably diverse pollination syndromes, that sets the family apart for all other flowering plants in terms of floral diversity. Aroid flowers are either unisexual or bisexual, perigoniate (these almost exclusively bisexual) or non-perigoniate (bisexual or unisexual), but always with superior ovaries and generally protogynous (Mayo *et al.*, 1997). With their remarkable and various form of leaves, distinctive spathe and spadix, many aroids are commercially important ornamental plants in horticulture.

Pollination biology in the aroids is a field of the greatest interest because many of the taxonomically important characters of aroid inflorescences and flowers are in all probability linked to floral adaptations to pollinators; yet few thorough studies have been made. Insect visits to aroid inflorescences, the phenology and behaviour of the spathe, spadix, and flowers during anthesis are also subjects which in general have not been studied critically (Mayo *et al.*, 1997). It is highly likely that many species have different pollination syndromes, even among related taxa. Moreover, the characteristics and morphological changes from inflorescence to infructescence and from ovaries to ripe fruits during fruitset could be useful for botanical interest. It is also speculated that different part of the inflorescences may be specialized to undertake a certain function during the reproductive process.

Tung *et al.* (2010) reported that until quite recently only Japanese entomologists with their collaborators and students had investigated aroids species in tropical Asia about the aroids pollination, with outputs including those of Okada (1975, 1980, 1986, 1987, 1990), Okada and Carson (1980), Okada and Yafuso (1989), Honda-Yafuso (1983), Kato *et al.* (2000), Yafuso *et al.* (2000), Sultana *et al.* (2002), Takenaka *et al.* (2006), Mori and Okada (2001), Miyake and Yafuso (2003), Kumano and Yamaoka (2006), Kumano-Nomura and Yamaoka (2009) and Toda and Lakim (2011),.

Undoubtedly, while such entomologically-biased research has contributed much to our understanding aroids pollination, there are still very few records about the plants

activities during pollination process based on botanical basis. Furthermore, the applied plant taxonomy in these entomological studies is often at fault, e.g., McAlpine (1978) described *Neurochaeta inversa*, a new species and genus representing a new family (Neurochaetidae) of Diptera, from the spathe chamber of wild *Alocasia brisbanensis* (F.M.Bailey) Domin but cited it as *A. macrorrhiza* and Okada & Carson (1980) in reporting 11 new species of fruit flies of the genus *Drosophila* from the inflorescence of *A. nicolsonii* A.Hay, reported it as *A. macrorrhiza* (see Hay & Wise, 1991); and the *Homalomena* taxonomy used by Kumano & Yamaoka (2006) and Kumano-Nomura & Yamaoka (2009) is incorrect (see Tung *et al.*, 2010).

Tribe Schismatoglottideae comprises 13 genera (*Apoballis* Schott, *Aridarum* Ridl., *Bakoa* P.C.Boyce & S.Y.Wong, *Bucephalandra* Schott, *Hestia* S.Y.Wong & P.C.Boyce, *Hottarum* Bogner & Nicolson, *Ooia* S.Y.Wong & P.C.Boyce, *Piptospatha* N.E.Br., *Phymatarum* M.Hotta, *Pichinia* S.Y.Wong & P.C.Boyce, *Schismatoglottis* Zoll. & Moritzzi, *Schottarum* P.C.Boyce & S.Y.Wong, and *Schottariella* P.C.Boyce & S.Y.Wong) and is the most speciose and diverse aroid taxon in Malaysia, comprising in excess of 250 species of which over 95% of species are endemic to Malaysia (Hay & Yuzammi, 2000; Boyce & Wong, 2008, 2009; Wong & Boyce, 2010 a, b & c), with the overwhelming representation found on the island of Borneo.

Many species of *Schismatoglottis* are terrestrial mesophytes, but most species in other genera in Schismatoglottideae, and a significant number of species in

Schismatoglottis, are rheophytes (Hay & Yuzammi, 2000; Bogner & Hay, 2000). Rheophytes are plants that have habitat specificity and particular morphological adaptations to the rheophytic zone. The rheophytic zone is defined as the region between the lowest and the highest water levels, usually of tropical rainforests. Rheophytes are repeatedly buffeted and submerged by flash floods after heavy rainfall, followed by exposure to dry conditions during periods of low water level (van Steenis, 1981). The rheophytic ecology is a demanding environment for plants to survive and not surprisingly rheophytes have developed numerous special adaptations to withstand it.

Floral traits are almost invariably correlated with pollinator type, i.e., pollination syndromes (Fenster *et al.*, 2004). Hence, the phenological characters and ecological interaction data procured by the intensive fieldwork of this project contribute significantly to the taxonomic and phylogeny studies being undertaken on this group. This study provided a set of considerable novel data for mapping onto molecularly generated cladograms tree to enable the construction of a hypothesis of morphological and evolutionary processes in the genera.

Schismatoglottis is widely distributed in South East Asia, with the exception of *Piptospatha*, *Hestia* and *Apoballis* other genera in the tribe are wholly endemic to Borneo, (Hay & Yuzammi, 2000; Bogner & Hay, 2000; Wong & Boyce, 2010a & c). of these these three genera, only *Piptospatha* is an obligate rheophyte. Monospecific

Hestia is a podzols specialist, while only *Apoballis okadae* (M.Hotta) S.Y.Wong & P.C.Boyce is rheophytic. This study could provide a general overview of the relationship of *Piptospatha* in Peninsular Malaysia and those in Borneo with the observation and molecular data.

Piptospatha is a genus of about nine species of obligate rheophytes differing from *Schismatoglottis* by the spathe not differentiated by a constriction at the junction of the lower and upper spathe, the presence an erect splash-cup, and seeds with a micropylar appendage (Wong & Boyce, 2010c). Seven species are endemic to Borneo, with two species in Peninsular Malaysia, with one of these (*Piptospatha perakensis* Engl. (Engl.)) extending into southern Thailand south of the Isthmus of Kra. *Piptospatha* species have the spathe limb caducous after staminate anthesis to leave a persistent cup-shaped lower spathe that appears to function as a splash-cup dispersal mechanism. Inflorescences are nodding at anthesis and then, via twisting of the peduncle, erect at fruiting. Splash cups are also a feature of three other genera, *Aridarum*, *Bucephalandra* and *Schottariella*, all endemic to Borneo (Bogner & Hay, 2000; Boyce & Wong, 2008, 2009). Species now included in *Bakoa* and *Ooia* were initially published in *Hottarum* and *Piptospatha* respectively. All were later transferred to *Piptospatha* as the Borneo-endemic 'grabowskii' group defined by Bogner & Hay (2000).

Ooia is a genus comprising two Bornean-endemic species and defined by the spathe persistent until fruit ripening (c. 1cm spathe tip deliquesced within 1 week after staminate anthesis was observed in *O. grabowskii* at Kubah National Park in this study, which most probably to be apomorphic) and seeds were dispersed after the falling of of remaining spathe leaving a persistent spadix axis (Wong & Boyce, 2010c). The spathes and infructescences are nodding throughout functionality without forming a splash cup. It appeared that this is not agreed with Bogner & Hay (2000) speculation and not closely resembles the dispersal mechanism in most *Schismatoglottis* and monospecific (Borneo-endemic) *Phymatarum*.

Bakoa is a genus of two described endemics on Borneo (Sarawak and West Kalimantan) (Boyce & Wong 2008). In the type species, *B. lucens* (Bogner) P.C.Boyce & S.Y.Wong half of the spadix from base is adnate to the persistent spathe which later becomes marcescent during fruit maturity, thence reflexing and opening basally to reveal the ripe fruit, which uniquely for the Araceae are dry and caryopsis-like. The seeds with a blunt conical micropyle and annulate placenta are unique in Schismatoglottideae (Boyce & Wong 2008).

1.2 Objectives

The objectives for this study were as follows:

1. To observe the inflorescence mechanics throughout anthesis, fruit maturation, seed dispersal and seedling establishment of six obligate rheophyte species in Schismatoglottideae.
2. To determine the intrinsic interaction between the plant species with the pollinators and other visiting insects via field observation.
3. To establish the phylogeny for the in-group of the taxa studied.
4. To investigate evidence of plant species speciation through inflorescence morphology and its behaviour with the associated pollination syndrome.

CHAPTER 2

LITERATURE REVIEW

2.1 Inflorescence Morphology of Araceae

The inflorescence of the Araceae is composed of an unbranched spike bearing flowers, the spadix, subtended by a bract called the spathe. The spathe is usually conspicuous in colour and shape. The flowers are usually numerous, very small, sessile except in *Pedicularum* M.Hotta, *Arisarum* Miller, and many *Arisaema* Mart., and lack floral bracts. Aroids inflorescence can be very simple with bisexual flowered spadix and undifferentiated spathe or very complex with unisexual flowered spadix with a spathe divided into a limb and convolute lower tube. Spathe and spadix modifications are closely related so the spathe may be seen evolutionarily as becoming increasingly integrated into the inflorescence itself (Mayo *et al.*, 1997). Besides the shape, colour and architecture of the spathe and spadix, diversifications also occur in the arrangement of staminate and pistillate flowers on an axis (Nishizawa *et al.*, 2005). Other notable specializations of the inflorescence include the wide range of odours found in different genera, colour patterns, especially on the spathe, and the relative persistence of different regions of the spathe (Mayo *et al.*, 1997). Typically, the lower part of the spathe forms a chamber that may act as a trap, temporarily retaining pollinators that enter (Corlett, 2004).

Specialized sterile zones and sterile processes are present on the spadices of some aroid species. These sterile structures may be staminodes or pistillodes. Staminodes are defined as rudimentary stamens which produce no pollen and pistillodes are sterile pistils that often reduced (Allaby, 1998). Few sterile flowers may fused with connective tissue became a synnandrode. This word is derived from the synandrium, in which the fertile flowers are fused. Staminodes and pistillodes may present at constriction area separating staminate and pistillate zone (interstice area) and at the apex of spadix forming a specific zone called appendix. In some aroids, the sterile flowers present in the fertile zone and did not form a separate zone. These specialised sterile zones have specific roles in scent production and insect rewards (Beath, 1998).

2.2 Tribe Schismatoglottideae

Tribe Schismatoglottideae, one of the three tribes (sister tribe to Cryptocoryneae and Philonotieae) in the Schismatoglottid Alliance (Wong *et al.*, 2010), is one of the most speciose and diverse higher aroid taxa on Borneo, with more than 250 species, of which over 95% are endemic. Besides the largest genus, *Schismatoglottis* Zoll. & Moritzi, the tribe includes, twelve smaller genera: *Apoballis* Schott, *Aridarum* Ridl., *Bakoa* P.C.Boyce & S.Y.Wong, *Bucephalandra* Schott, *Hestia* S.Y.Wong & P.C.Boyce, *Hottarum* Bogner & Nicolson, *Ooia* S.Y.Wong & P.C.Boyce, *Piptospatha* N.E.Br., *Phymatarum* M.Hotta, *Pichinia* S.Y.Wong & P.C.Boyce,

Schottarum P.C.Boyce & S.Y.Wong, and *Schottariella* P.C.Boyce & S.Y.Wong (Bogner & Hay, 2000; Boyce & Wong, 2008, 2009; Hay & Yuzammi, 2000; Hotta, 1965, 1966, 1976; Wong & Boyce, 2010a, b & c). All except *Apoballis* occurs on Borneo. All except *Hestia*, *Piptospatha*, and *Schismatoglottis* are endemic on Borneo. *Apoballis* occurs in the Malay Peninsula, Sumatera (the centre of distribution), Java and Nusa Tenggara. Philonotieae (Wong *et al.*, 2010) occurs only in the Neotropics, while Crytocoryneae ranges from the Indian subcontinent throughout Sundaland, Malesia into west New Guinea, with *ca.* 20 species occurring in Borneo (Jacobsen, 1985 & pers. comm.).

2.3 Taxonomy

2.3.1 *Piptospatha perakensis* (Engl.) Engl.

Piptospatha perakensis (Engl.) Engl., in Engler (ed.), Pflanzenr. 71 (IV.23E): 2* (1920) [i.e. supplementary pages]; Ridley, Fl. Mal. Pen. 5: 114 (1925); Henderson, Malayan Wildfl., Monocots, 232: fig.18,A (excl. fig.18,BB - i.e. *P. elongata*) (1954); Bogner & Hay, Telopea 9(1): 208 (2000).

Piptospatha elongata var. *perakensis* Engl., Pflanzenr. 55(IV.23Da): 125 (1912).

Rhynchophyle perakensis (Engl.) Ridl., J. Bot. 51: 202 (1913). - Type: Malaysia, Malacca, Tampin Hill, Waterfall, May 1894, *J.S.Goodenough 1850* (SING, lecto; isolecto CAL — selected by Bogner & Hay, 2000).

Schismatoglottis elongata auct. non Engl.: Hook.f., Fl. Brit. Ind. 6: 539 (1893).

Piptospatha elongata auct. non (Engl.) N.E. Br.: Ridley, Mat. Fl. Mal. Pen. 3; 35 (1907).

Rheophytic herb 10-40 cm tall. *Stem* short, condensed; 2-4 cm long, 0.7-1 cm diameter; roots thick, extensive and tough, 1.5-2 mm diameter, with many thinner roots of second order. *Leaves* few to several together; petiole 6-15 cm long, 1.5-2 mm diameter, canaliculate on upper side, sheathing only at the extreme base, the wings extended into a narrow ligular portion 3-7 cm long; blade coriaceous, adaxially dark mid-green, paler abaxially, elliptic (to oblong elliptic) 10-26 cm long \times 1.5-7 cm wide, the base cuneate, the apex acute and shortly apiculate for 1-1.5 mm, the margin weakly to strongly crispate especially in the distal part; midrib and primary venation very prominent abaxially, drying pale orange to straw-coloured; primary lateral veins 5-8(-10) on each side of the midrib, diverging at c. 45°, running to a thick marginal vein; secondary venation distinctly finer than primaries. *Inflorescence* solitary (sometimes 2-3 in series but alternating with foliage leaves); peduncle erect, 3-16 cm long. *Spathe* nodding at anthesis, narrowly ovoid, c. 3 cm long, apically beaked for c. 4 mm, cream to greenish, the upper part caducous. *Spadix* c. 2 cm long, shortly stipitate with the stipe adnate to the spathe; pistillate zone subcylindric, c. 0.7 cm long \times 0.5 cm diameter; pistils more or less ovoid, c. 0.5 mm diameter; stigma sessile, thickly discoid, about as broad as the ovary (dry), papillate, not contiguous with neighbouring stigmas (dry); interpistillar staminodes confined to a small group or irregular whorl at the base of the pistillate zone, stipitate,

flat-topped, about as high as the pistils, c. 0.5 mm diameter; sterile interstice absent; staminate zone fertile to apex, bluntly ellipsoid-subcylindric, c. 1×0.5 cm; stamens truncate, more or less flat-topped (somewhat rounded), narrowly rectangular-elliptic from above, mostly in closely appressed pairs, the anther finely and densely pubescent, c. 0.8 mm across. *Fruiting spathe* obconic, green; berries yellowish when ripe, in a more or less hemispherical group c. 1.5 cm diam., obovoid, 2.2-2.4 mm long \times 1.5 mm diameter, with persistent stigma remnant apically; seeds several, subcylindric, c. 1-1.2 mm long; testa slightly ribbed, brown, with a prominently curved micropylar appendage.

Distribution: Southern Thailand to West Malesia. In *Malesia*: Malay Peninsula.

Habitat: Rheophytic on boulders in streams and by waterfalls and stream banks, 100 - c. 1400 m alt.

Notes: This species is distinguished by the abaxially prominent midrib and primary venation which dries pale orange to straw-coloured, the spadix with basal staminodes but contiguous staminate and pistillate zones, and the truncate pubescent anthers.

Other localities recorded: MALAY PENINSULA: Selangor, Ulu Langat, above Parisoan, *M.M.J.van Balgooy* 2246 (L); Kelantan, Tanah Merah, Pergau Dam site, logging rd to Sg. Suih Intake, *P.C.Boyce* 665 (K); Perak, Bukit Larut, *P.C.Boyce* 691 (K); Pahang, Cameron Highlands, Sg Urul, *H.M.Burkill* HMB 780(SING); Perak, ?Taiping Hills [sic], *C.Curtis s.n.* (SING); Pahang, Ulu Telom, *Dolman* 27615

(SING); Perak, Batang Padang, Jor, *M.R.Henderson 10824* (SING); Cult. RBG Sydney Acc. No. 940301 ex Terengganu, Sekayu, Ayer Terjun (orig. coll. *A.Hay 9233*), *C.Herscovitch s.n.* (K, NSW); Negeri Sembilan, G Tampin, *R.E.Holttum 9543* (K,SING); Terengganu, Batu Biwa, *R.Kiew RK2352* (SING); Perak, Sg. Groh, hills E of Gopeng, *F.Ng FRI 1588* (SING); Perak, Maxwell's Hill, *D.H.Nicolson 1093* (SING); Pahang, Raub, *Poore 859* (K); Selangor, Pahang Track, *H.N.Ridley s.n.* (SING); Negeri Sembilan, Tampin Waterfall, *H.N.Ridley s.n.* (K); Pahang, Upper Tahan R, *H.N.Ridley s.n.* (SING); Selangor, Ulu Gombak, *H.N.Ridley s.n.* (K); Pahang, Sg. Tahan, *H.N.Ridley s.n. & 2395* (both SING); Selangor, Semangkok Pass, *H.N.Ridley 12026* (SING); Pahang, Telom, *H.N.Ridley 13843* (K); Perak, *Fr B.Scortechini 1317* (K, SING); Perak, Maxwell's Hill, *L.Wray jn.3222* (SING).
 THAILAND: Pattani, Bacho 'Bachaw', *A.F.G.Kerr 7210* (K).

2.3.2 *Piptospatha ridleyi* N.E.Br. ex Hook.f.

Piptospatha ridleyi N.E. Br. ex Hook.f., Curtis's Bot. Mag. 51: t. 7410 (1895); Ridley, Mat. Fl. Mal. Pen. 3: 35 (1907); Engler, Pflanzenr. 55 (IV.23Da): 127 (1912); Ridley, Fl. Mal. Pen. 5: 114 (1925); Bogner & Hay, Telopea 9(1): 210 (2000). - Type: Cult. RBG Kew ex Malaysia, Johor, (orig. coll. *H.N. Ridley*), ?1893, *N.E. Brown s.n.* (K, holo).

Piptospatha ridleyi var. *lanceolata* Ridl., Fl. Mal. Pen. 5 (1925) 114. - Type: Malaysia, Johor, Ulu Kahang, 1 Jun 1923, *R.E. Holttum 10865* (SING, holo).

Rheophytic herb (8-)10-30(-40) cm tall with strong extensive roots 1-2 mm diameter. *Stem* condensed, 1-3 cm long, 5-8 mm diam. *Leaves* few to several together; petiole (3-)5-15(-18) cm long, 0.9-2.5 mm diameter, often reddish, adaxially canaliculate, sheathing only at the extreme base, the wings extended into a narrow ligular portion 2-7 cm long at first reddish then drying brown; blade (narrowly) elliptic (4-)6-18(-23) cm long × (1-)2.5-6(-8) cm wide, coriaceous, the base cuneate, the apex acute and apiculate for 1-3 mm, adaxially dark green, usually but not always variegated in an irregularly spattered pattern of paler green, abaxially paler; midrib abaxially very prominent, adaxially slightly impressed, with (3-)4-7(-10) primary lateral veins on each side, diverging at c. 30-60°, running to a distinct submarginal vein; primary lateral veins not or hardly prominent abaxially, rather fine; secondary venation adaxially obscure; tertiary venation forming a faint tessellate reticulum (dry). *Inflorescence* solitary; peduncle much exceeding the petioles at anthesis, 10-25 cm long, pale reddish brown (?always); spathe broadly ovoid, c. 2.5-3 cm long, pink in the caducous upper part with darker veins and small dots, the lower part green, apically rather abruptly beaked for c. 3 mm, at anthesis gaping in the distal part. *Spadix* subcylindric-clavate, about half the length of the spathe, shortly stipitate with the stipe fully adnate to the spathe; pistillate zone c. 5 mm long × 4 mm diameter; pistils more or less ovoid, c. 0.5 mm diameter; stigma very slightly raised on an indistinct style, rather thickly discoid, about the diameter of the ovary; interpistillar staminodes restricted to an irregular whorl at the base of the pistillate zone, whitish, more or less obpyramidal and shortly stipitate, about half the height of the pistils;

sterile interstice absent; staminate zone ellipsoid, slightly but distinctly broader than the pistillate zone, c. 7 mm long \times 6 mm diameter, fertile to apex; stamens truncate, more or less rectangular-dumbbell-shaped, rather irregularly aligned in pairs, the connective somewhat to distinctly mounded between the pores and usually finely and densely pubescent (occasionally glabrous). *Fruiting spathe* broadly obconic, c. 1.5 cm diameter; berries clustered, subcylindric to obovoid, 2-3 mm long, 1.1-1.5 mm diameter; seed subcylindric to elongate ellipsoid, 1.5-1.8 mm long, 0.5-0.6 mm diameter, brown; testa longitudinally ribbed, with a long curved transparent micropylar appendage c. 1.5 mm long, the appendages interlinked in fruit.

Distribution: *Malesia*: Malay Peninsula (Johor; one collection from Pahang).

Habitat: Rheophytic on rocks in and along streams, 100-900 m alt.

Notes: *Piptospatha ridleii* is distinguished from *P. perakensis*, by the fewer, weaker primary lateral veins, not drying straw-coloured, the frequently variegated leaf blade, the pink spathe, the basal staminodes more or less obpyramidal and the stamens not arranged in such distinct pairs as those of *P. perakensis*. The type, made from a plant cultivated at Kew sent in 1893 by H.N.Ridley from Johor, is deposited at K.

Other localities recorded: MALAY PENINSULA: Johor, G. Pulau, *Ahmad SA 1044* (SING); Johor, G. Pulau, *Best 7720* (SING); Johor, G. Pulau, N side, *Burkill 2577* (K, L, SING); Johor, Sg. Pelopah Kiri, *Corner 33580* (K, L, SING); Johor, Sg. Bebatu, *Distr.*

Forest Officer s.n. (SING); Johor, G. Pulai, *Henderson* 28156 (SING); Johor, Sg. Gatong, Labis FR, *Henderson* 38252 (SING); Johor, Ulu Kahang, *Holtum* 10865 (K); Johor, G. Muntahak, *Holtum* 19934 (K, SING); Johor, Ulu Endau, Sg. Jawang, *Kiew RK2033* (SING); Johor, G. Pulai, *Maxwell* 78-14 (L); Johor, Bukit Tunjok Laut, *Ngadiman* 36933 (K, L, SING); Johor, G. Pulai, *Mhd Nur s.n.* (SING); Johor, G. Panti, *Ridley s.n.* (SING); Johor, G. Pulai, *Ridley* 12191 (SING); Pahang, Rompin, Lesong FR, Sg. Linchin, nr. Sg. Kayu Pagar, *Saw FRI* 37551 (K); Johor, Kluang, G. Blumut, *Mhd Shah & Sanusi* 2229 (SING); Johor, G. Pulai, Sg. Ayer Hitam Besar, *Sinclair* 10577 (B, K, L).

2.3.3 *Piptospatha elongata* (Engl.) N.E.Br.

Piptospatha elongata (Engl.) N.E.Br., Curtis's Bot. Mag. 51, in descr. ad tab. 7410 (1895); Engler, Pflanzenr. 55 (IV.23Da): 124, fig. 75 (1912); Ridley, J. Bot. 51: 202 (1913); Bogner & Hay, Telopea 9(1): 205 (2000); Wong *et al.*, Webbia 66(1): 29 – 32 (in discussion)

Schismatoglottis elongata Engl., Bull. Soc. Tosc.ortic. 4: 298 (1879).

Rhynchopyle elongata (Engl.) Engl., Bot. Jahrb. Syst. 1: 184 (1881); Beccari, Malesia 1: 289, pl. 23, figs 3-15 (1882). - Type: Malaysia, Sarawak, Kuching Division, Lundu, Gunung Gading, June 1867, *O. Beccari P.B.* 2308 (holo, FI-B).

Gamogyne pulchra N.E. Br., Kew Bull. (1910) 197 & Curtis's Bot. Mag. 135 t. 8330 (1910). -Type: not designated (see Bogner and Hay, 2000: 205).

Piptospatha rigidifolia Engl., Pflanzenr. 55 (IV.23Da): 127 (1912). - Type: Malaysia,

Sarawak, Kuching Division, Lundu, Sept. 1905, *H.N. Ridley s.n.* (lecto, SING, selected by Bogner and Hay, 2000: 205).

Rheophytic herb 9-20 cm high. *Stem* condensed, 2-6 cm long, 0.5-1.1 cm diameter, with robust pale green to more-or-less reddish-tinged roots 1.5-2 mm diameter. *Leaves* several to 20 together; petiole 6-11 cm long, 1.5-2 mm diameter, slightly canaliculate adaxially, sheathing only at the extreme base, the remainder of the sheath ligular, the ligules extended into a narrowly triangular, purple to reddish portion 3-5 cm long, this drying dark brown and not long-persisting; blade very narrowly elliptic to narrowly elliptic-oblong to oblanceolate, coriaceous, dark green adaxially, paler abaxially, 15-24 cm long \times 1-3.5 cm wide, the base cuneate, the apex acute and tubular-apiculate for 2-3 mm; midrib robust, abaxially prominent, adaxially bluntly raised (fresh), impressed (dry), with (6-)7-10 primary lateral veins on each side, diverging at 35°-45° and more or less regularly alternating with lesser interprimary veins especially in the lower half of the blade; secondary venation adaxially more or less obscure, abaxially fine and dense; tertiary venation obscure. *Inflorescence* solitary to 2-3 together and then often alternating with foliage leaves; peduncle shorter than to equalling, rarely exceeding the length of the whole leaf, 11-22 cm long, 1.8-2.2 mm diameter, purple to reddish. *Spathe* nodding at anthesis, subcylindric-obovoid, 3-4 cm long, apically rostrate for 3-4 mm, the rostrum conspicuously 2-3-keeled internally, straight at pistillate anthesis but recurving up to 45° at the onset of staminate anthesis; spathe at anthesis shading proximally to

distally from deep plum purple through medium pink to deep pink, inflating and the distal-most part opening at pistillate anthesis, at the end of staminate anthesis the opening increasing by the reflexing of the terminal rostrum and then at late staminate anthesis the upper third opening further before becoming caducous. *Spadix* cylindric, more-or-less sessile, 2-2.5 cm long, 0.4-0.5 cm diameter; pistillate zone cylindric, 5-7 mm long, 5-7 mm diameter; ovary subcylindric to subprismatic, *ca* 0.9 mm diameter, mid-deep pink; stigma sessile, as broad as the ovary, thinly discoid, mid- to deep pink; staminodes confined to 1-3 irregular and somewhat oblique rows at the base of the pistillate zone, truncate, more-or-less sessile, 0.7-0.9 mm diameter, about as high as the pistils, ivory; staminate zone cylindric, approximately equalling diam. of pistillate zone, 1.3-1.7 cm long, apically obtuse; stamens crowded, more or less rectangular from above, glabrous, at anthesis longitudinally sulcate with the thecae pores dorsal and ventral to the sulcae, 1.2-1.4 mm across, connective flat, pale cream; pollen extruded in masses. *Fruiting spathe* narrowly funnel-shaped, erect, 1.2-1.5 cm diameter; berry obovoid, *ca* 3.5 mm long \times 1.2-2 mm diameter; *seed* cylindric, very slightly ribbed, 1.4-1.6 mm long, brown but outer integument translucent, with a long curved micropylar appendage rotting away in dispersed seeds.

Distribution: Borneo, Sarawak, Kuching Division, endemic to the Lundu area, centred of Gunung Gading.

Habitat: Rheophytic on granite rocks in lowland to lower hill forest in light to medium shade. 10-400 m asl.

Notes: *Piptospatha elongata* as here defined is endemic to the Lundu area centred on Gunung Gading where it is restricted to granite substrates. It is readily separated in flower from the other *elongata* Group *Piptospatha* in west Sarawak (*P. viridistigma* and *P. impolita*) by the combination of a cylindrical spadix, unexcavated thecae, mid- to bright pink stigmas, a spathe tip rostrum conspicuously 2-3-keeled internally, and remaining straight or reflexing by only *ca.* 45° during anthesis, flat anther connectives and the spathe at anthesis shading deep plum purple proximally through medium pink to deep pink distally and, in fruit, by the narrowly obconic persistent lower spathe. From *P. impolita*, *P. elongata* is readily distinguished by the mid- to dark pink stigmas, the spathe tip rostrum conspicuously 2-3-keeled internally and remaining straight or reflexing by only *ca.* 45° during anthesis, and the flat anther connectives. *Piptospatha elongata* is immediately separated from *P. viridistigma* by a cylindrical (vs. bullet-shaped) spadix, longitudinally sulcate unexcavated thecae, 2-3 (vs. 5-7 keels) on the interior of the spathe tip rostrum and a narrowly obconic (vs. wide flared) persistent lower spathe. The pollen of *P. elongata* (and *P. impolita*) is released en masses whereas that of *P. viridistigma* is extruded in strings. *Piptospatha elongata* is restricted to granite, whereas *P. viridistigma* is mainly, although not exclusively, found on limestones.

Other localities recorded: BORNEO. Sarawak, Kuching Division, Lundu, Sungai Sebako, 14 Apr 1984, *Dayang Awa & Paie S.46973* (K, KEP, L, SAN, SAR); Lundu, Kampung Sebako, Sungai Sebako, 01° 43' 18.9"; 109° 42' 53.8", 3 Feb 2005, *P.C. Boyce & Jeland ak Kisai AR-989* (SAR + spirit); Lundu, Gunung Gading, trail to waterfalls, 01° 41' 28.3"; 109° 50' 43.6", 14 Nov. 2006, *P.C. Boyce & Wong Sin Yeng AR-2052* (SAR + spirit); Lundu, 2 May 1954, *Brooke 8410* (L, SAR); Lundu, Gunung Gading, 19 Jul 1963, *Chai S.18484* (GH, K, L, SING); Lundu, Gunung Gading, Oct 1929, *Clemens & Clemens 21924* (GH, K, SAR); Lundu, Gunung Gading, *Foxworthy 326* (SAR, SING); Lundu, Sebuluh, 21 Jan 1989, *Othman Ismawi et al. S.62244* (K, L, KEP, MO, SAN, SAR); *ibid*, 15 Aug 1990, (K, KEO, L, SAN, SAR); Lundu, Gunung Pueh, Sungai Batu, 2 Mar 1989, *Othman Ismawi et al. S.56652* (K, KEP, L, SAN, SAR, US); Lundu, Gunung Pueh, Sungai Batu, 2 Oct 1974, *Mamit S.35218* (K, L, SAN, SAR, US); Lundu, Gunung Gading, *Micholitz s.n.* (SING); Lundu, Gunung Gading, 19 Sep 1955, *Purseglove & Shah P.4534* (K, L, SING); Lundu, Gunung Gading, 16 Aug 1960, *Sinclair & bin Tassin 10365* (E, K, L, SAR, SING); Lundu, Sematan, Pueh, close by Pueh mulberry plantation (Silkworm Farm), 7 Feb 1996, *S.Teo & Awg Enjah, S.68066* (K, KEP, SAR); Lundu, Gunung Gading, Sungai Sebuluh, 14 Jun 1991, *Yahud et al. S.61955* (K, KEP, SAR, US); Lundu, Kampung Pasir Ulu, Sungai Pasir Ulu, *Yahud et al. S.61925* (K, SAR); Lundu, Gunung Gading, 26 Mar 1980, *Yii Puan Ching S.42018* (L, SAR, US).

2.3.4 *Ooia grabowskii* (Engl.) S.Y.Wong & P.C.Boyce

Rhynchopyle grabowskii Engl., Bot. Jahrb. Syst. 25: 20 (1898).

Piptospatha grabowskii (Engl.) Engl., Pflanzenr. 55 (IV.23Da): 125 (1912)- Type: Indonesia. Southeast Kalimantan, Mindai-Pramassamalai hills, on rocks of waterfalls of the Pitanakan, 17 June 1882, *F. Grabowski s.n.* (holotype B!).

Piptospatha havilandii (Engl.) Engl., Pflanzenr. 55 (IV.23Da): 128 (1912).

Rhynchopyle havilandii Engl., Bot. Jahrb. Syst. 37: 125 (1905)

Schismatoglottis havilandii (Engl.) M. Hotta, Mem. Coll. Sci. Univ. Kyoto, Ser. B, 32: 233 (1966) - Type: Malaysia, Sarawak, Kapit Division, Rejang, Belaga, Nov 1892, *G.D. Haviland 2191* (holotype: BM!; isotypes: CAL, K!, SING!).

Rheophytic herb 20-50 cm tall. *Stem* c. 4-8 (-20) cm long, mostly condensed, occasionally more elongate with internodes to 1 cm long, 0.6-1.5 cm diameter, roots strong, 2.5-4 mm thick. *Leaves* c. 4-8 together; *petiole* green to purple, 6-23 cm long, 2.5-3 mm diameter, adaxially canaliculate, sheathing only at the very bottom of the base, the wings extended into a narrowly triangular ligular portion 5-10 cm long; blade narrowly elliptic to elliptic-oblong, 12-28 cm long × 4-10 cm wide, dull mid-to dark green adaxially, very rarely variegated in an irregular spattered pattern, abaxially paler, the base cuneate, the apex acute and apiculate for 2-3 mm; midrib prominent abaxially, adaxially somewhat impressed, sometimes abaxially purple, with 8-14 (-20) primary lateral veins on each side, more or less regularly alternating with lesser interprimaries and diverging at c. 45-60°; secondary venation abaxially

fine, adaxially obscure; tertiary venation obscure. *Inflorescence* solitary (sometimes a few together but alternating with foliage leaves); peduncle 10-22 cm long, 2-3 mm diameter, always shorter than the leaves, green to purple. *Spathe* ovoid-subcylindric, (2-) 3-5 cm long, 0.8-1.4 cm diameter, apically beaked for 2.5-4 mm, persistent, rose pink to purple to brownish pink, more or less nodding at anthesis. *Spadix* (1.2-) 2.2-3 cm long, subcylindric to slightly clavate, shortly stipitate with the stipe adnate to the spathe, white to yellowish; pistillate flower zone (0.3-) 0.5-1 cm long, 0.3-0.9 cm diameter; ovary ovoid, slightly angled, c. 1.4 mm diameter; stigma sessile to raised on a short style to 0.5 mm long, discoid, about as wide as the ovary, drying almost black; interstilar staminodes absent from among the pistils, confined to a robust zone below the pistillate flower zone of up to 6 oblique whorls; staminodes shortly stipitate, to 1.2 mm diameter, irregularly polygonal, flat-topped with the centre usually somewhat impressed and the margins pale coloured (? with dried exudate); sterile interstice absent; staminate flower zone cylindric to ellipsoid, apically obtuse, fertile to apex; stamens crowded, mostly arranged in pairs, truncate, flat-topped, more or less rectangular from above, c. 1.1 mm across, minutely hairy on the upper surface especially at the margins; thecae opening through apical pores. *Fruiting spathe* ovoid-subcylindric, green to reddish green to greenish brown, obliquely erect, to 5 cm long, persistent then eventually more or less disintegrating; fruits in a dense cluster; berry broadly obovoid, crowded with old stigma remnant, 2-2.5 mm long, 2.8-3.2 mm diameter; seed subcylindric, 2.4-2.6 mm long, slightly ribbed, light brown with a transparent long curved micropylar appendage.

Distribution: Malesia: endemic to Borneo-Sarawak, W. Sabah, and scattered localities in Kalimantan.

Habitat: Obligate rheophytes in and beside streams and waterfalls over a variety of substrates including ultramafics and limestone etc.; lowlands to c. 2,000 m alt.

Notes: The genus *Rhynchopyle* can not be resurrected for *R. grabowskii* Engl. as the type for *Rhynchopyle* is *R. elongata* (Engl.) Engl. (\equiv *Piptospatha elongata*).

Other localities recorded: MALAYSIA. Sarawak: Kuching Division: Padawan, Puncak Borneo, trail behind Malesiana Tropicals Nursery to Hornbill Resort golf course maintenance kampung, 01°07' 35.1"; 110°13' 28.8", 30 Sep 2003, *P.C. Boyce & Jeland ak Kisai AR-93.1* (SAR); Bau, Singai, Batu Taring, 19 Jun 2004 *P.C. Boyce, Jeland ak Kisai & Jipom ak Tisai AR-469* (SAR); Lundu, Jalan Lundu, Stunggang Ulu, 01°36' 21.2"; 109°53' 46.3", 21 Sept 2005, *P.C. Boyce, R. Kneer & Jeland ak Kisai AR-1367* (SAR); Padawan, Kampung Sadir, 2 Feb 2006, *P.C. Boyce & Simon Kutuh ak Paru AR-1699* (SAR); Matang, Kubah National Park, Waterfall Trail, 01°35' 40.2"; 110°10' 45.9", 28 Jul 2007, *P.C. Boyce, Wong Sin Yeng & Simon Maclean AR-2117* (SAR); Matang, Kubah National Park, Sg. Bungen, 01°36' 30.9"; 110°11' 35.0", 28 Jul 2007, *P.C. Boyce, Wong Sin Yeng & Simon Maclean AR-2118* (SAR); Ooi Im Hin *OIH-18 (AR-2339)* (SAR); Bau, Bongo Range, trail to Tegora Mine, 01°19' 41.5"; 110°09' 19.0", 8 Sep 2007, *P.C. Boyce, Wong Sin Yeng & Alexander Kocyan AR-2186*

(SAR); 13th mile, Matang, *Brooke 9441* (L); *9471* (L); Padawan, Tibia Sapit, nr Sarawak/Kalimantan border, *Mamit S25875* (K, SAR); Kampung Sadir, c. 50 mi from Kuching, *Mamit S33367* (L, SAR); Ulu Sungai Sluba, Gunung Merubong, *Yii S 51388* (K, SAR). Sri Aman Division: Pantu, Gunung Gaharu, 01°03' 11.1"; 110°52' 55.8", 21 July 6, *P.C. Boyce et al. AR-1923* (SAR); Lubok Antu, Batang Ai, Nanga Sumpa, Rumah Gumbang, Sungai Delok, 01°12' 16.2"; 112°03' 26.0", 24 May 2008, *P.C. Boyce, Wong Sin Yeng & Jipom ak Tisai AR-2374* (SAR); Lubok Antu, Batang Ai, Nanga Sumpa, Sungai Pedali, 01°11' 58.9"; 112°03' 27.0", 25 May 2008, *P.C. Boyce, Wong Sin Yeng & Jipom ak Tisai AR-2391* (SAR); Lubok Antu, Batang Ai, Nanga Sumpa, Wong Ensalai, 01°11' 51.0"; 112°03' 39.9", 26 May 08, *P.C. Boyce, Wong Sin Yeng & Jipom ak Tisai AR-2417* (SAR); Lubok Antu, Sungai Delok, nr Nanga Sumpa, *Christensen 1200* (K); N slopes of Gunung Penrissen, *Jacobs 5005* (B, K, L). Sarikei Division: Sarikei, Ulu Sarikei, 01°55' 05.4"; 111°29' 35.8", 7 Dec 2005, *P.C. Boyce, et al. AR-1580* (SAR); Sarikei, Ulu Sarikei, Rumah Nyuka, 23 Oct 2006, *P.C. Boyce & Wong Sin Yeng AR-20433* (SAR); *AR-2043* (SAR); Sri Aman ('Simanggang'), Tisak Sekarang, Ulu Sungai Panabun, *Paie S45112* (K, L, SAR); Sri Aman ('Simanggang'), Sekarang, Kampung Entalau, Sungai Antu, *Paie S45158* (K, L, SAR). Kapit Division: Nanga Gaat, Rejang Wood Concession, Sungai Piat, 01°38' 09.1"; 113°24' 09.9", 14 Oct 2003, *P.C. Boyce & Jeland ak Kisai AR-93.2* (SAR); Kapit, Pergunungan Hose, 02°14' 47.2"; 113°41' 24.9", 22 Apr 2004, *P.C. Boyce & Jeland ak Kisai AR-294* (SAR); *AR-296* (SAR); Nanga Gaat, Rejang Wood Concession, km 65 road to Camp Gahada, 01°42' 01.1"; 113°31' 14.8", 12 May 2004,