

— Short Communication —

NOTES ON THE POLLINATION ECOLOGY OF THE PALM GENUS *JOHANNESTEIJSMANNIA* (ARECACEAE)

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Abstract—The floral biology and flower visitors of the tropical palms *Johannesteijsmannia altifrons*, *J. magnifica* and *J. perakensis* were investigated. We combined the data from this study with published data of *J. lanceolata* to give an overview of the reproductive biology and pollination system of the genus. Anthesis peaks from 0500–1100 hrs when the inflorescences are visited mainly by flies, beetles and stingless bees (*Trigona*), the last are potential pollinators. The breeding system is facultative selfing, indicating the ability of the species to reproduce in the absence of pollinators or in isolation.

Keywords: reproductive biology, pollinator, breeding system, flower biology, Coryphoideae, Johannesteijsmannia

INTRODUCTION

Studies on reproductive biology and pollination ecology can help to shed light on plant-pollinator relationships, evolution, and also possible reasons for the persistence, rarity, genetic diversity or species richness of plants (e.g. Bawa et al. 1985; Henderson 2002; Rymer et al. 2005; Barfod et al. 2011). It also provides crucial information for the conservation of threatened species (e.g. Soehartono & Newton 2001; Lee et al. 2006; Ohara et al. 2006; Gargano et al. 2009).

The genus *Johannesteijsmannia* comprises only four species, i.e., *J. altifrons* (Reichb.f. et Zoll) Moore, *J. lanceolata* J.Dransf., *J. magnifica* J.Dransf. and *J. perakensis* J.Dransf. (Dransfield et al. 2008). All species are threatened by deforestation in Malaysia (Chan et al. 2011a). Uncontrolled seed harvesting for the ornamental trade may also affect population regeneration in the wild (Chan & Saw 2009). *Johannesteijsmannia lanceolata*, *J. magnifica* and *J. perakensis* are endangered endemics to Peninsular Malaysia, while *J. altifrons* is confined to southern Thailand, Peninsular Malaysia, Borneo and Sumatra.

The palms usually grow in valleys (pers. obs.) but some populations of *J. altifrons* and *J. perakensis* are also reported to be found on ridge tops or upper hill slopes (Dransfield 1972). They occur in the understory of closed canopy forest and their leaves are broadly to narrowly diamond-shaped. All species are acaulescent, except for *J. perakensis* which has a trunk of 2–4 m tall. Inflorescences are borne at the base of the plant (for *J. perakensis* they are borne above the trunk), and they are usually partially covered by dead leaves trapped in the crown. The inflorescences are interfoliar, bearing bisexual flowers with a three-lobed corolla and six stamens.

The reproductive biology of *J. lanceolata* has been well-documented (Chan et al. 2011b): It is self-compatible, the flowers are homogamous with diurnal anthesis and are visited by bees, flies and ants. For the remaining members of the genus, such information is lacking. Thus, we extended the investigations into the floral biology and pollination of *J. altifrons*, *J. magnifica* and *J. perakensis*, to determine the pollinators and the breeding system. We also discuss and summarise the reproductive biology of the genus by incorporating the data from this study with published and unpublished data on *J. lanceolata* (Chan et al. 2011b; Chan 2009).

MATERIALS AND METHODS

The flowering of *Johannesteijsmannia altifrons*, *J. magnifica* and *J. perakensis* was observed in the wild or in cultivation from March 2004 until March 2005. The sample size for this study was small because few palms were found flowering during field observations. Detailed observations were made on the *ex-situ* plants of *J. altifrons* (N = 6) and *J. magnifica* (N = 2) planted in the Forest Research Institute Malaysia (FRIM), Selangor, at 97 m.a.s. The wild population of *J. magnifica* grows in hill dipterocarp forest (320–400 m.a.s.) in the Berembun Forest Reserve, Negeri Sembilan, while *J. perakensis* is found in lowland dipterocarp forest (120 m.a.s.) in the Kledang-Saiong Forest Reserve, Perak. The inflorescences and flowers were measured for inflorescence length, peduncle length, flower length and diameter, maximum petal width and length, and the lengths of stamen, pistil and style. Longitudinal and transverse sections of mature flowers of all the species studied except for *J. perakensis* were made and examined following the methodology in Chan & Lim (2011). Insects visiting the inflorescences were observed during anthesis (shedding of pollen) in the morning, mainly *ex-situ* from 0700 – 1300 hrs for at least 10 days and occasionally *in-situ* for *J.*

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magnifica and *J. perakensis*. In the case of *J. magnifica*, two additional observations were made in the evening (1600 and 1700 hrs) and one after rain at night (2200 hr) in FRIM to check for night visitors. To determine potential pollinators, we carried out additional observations and sampled floral visitors of *J. lanceolata* (N plant = 3) in FRIM, for three days from 0830 to 1230 hrs in September 2011. The captured insects were checked for pollen load under a 40× dissecting microscope. Pollen grains were removed with forceps, dispersed onto a drop of 70% alcohol on a microscope slide and cross-checked with pollen grains from flowers of *J. lanceolata* under a light microscope. All captured insects were identified and deposited in the Entomology Unit, FRIM.

Pollen to ovule ratios (total number of pollen grains: total number of ovules per flower) for *J. magnifica* were calculated according to Chan et al. (2011b). In one inflorescence, pollen viability was determined by the 'sitting drop culture' method (Shivanna & Rangaswamy 1992, for details see Chan et al. 2011b). Effervescence of stigmatic tissues of flowers aged 0, 5 and 24 hrs in a 3% hydrogen peroxide aqueous solution was used as an indicator of receptivity in accordance with Carrington et al. (2003).

RESULTS AND DISCUSSION

Floral biology

Johannesteijsmannia magnifica flowered *in-situ* in March 2004 and 2005, and flowered *ex-situ* in October 2004 and March 2005. Peak flowering for *J. perakensis* occurred in March–April, followed by a smaller peak in October–December. The cultivated plants of *J. altifrons* flowered continuously from June 2004 until the end of observation period.

The floral morphology and behaviour of the species studied are given and compared with those of *Johannesteijsmannia lanceolata* (data from Chan et al. 2011b) in Tabs. 1 and 2. All species have cream-coloured flowers and floral parts of similar size, but are different in inflorescence size and structure (branching order, Fig. 1, Tab. 1). The inflorescence size and structure of *J. altifrons* and *J. perakensis* are similar, while that of *J. magnifica* is somewhat intermediate in the genus, and *J. lanceolata* has the smallest inflorescence with only one order of branching. The first three have highly floriferous comb-like inflorescences. The mean number of flowers per inflorescence for *J. lanceolata* was 2442 (Chan et al. 2011b) whereas for *J. altifrons*, it was estimated at 9515 (SD 1571, N = 2, present study). The petals of all species are more or less flat, triangular, bluntly acute, smooth and 0.3–0.5 mm thick (present study), except for that of *J. lanceolata* which is thicker, shorter and papillate on the outer surface (Chan 2009).

The inflorescence development in all species was very similar to that of *J. lanceolata* (Chan et al. 2011b). After the prophyll had emerged from the leaf axils, it took about one month, or up to two months in *J. altifrons*, for the inflorescence to flower. The rachillae expanded and became bulky about one week before flowering. The inflorescence

further elongated, curved downwards during the flowering period, and emitted an odour that attracted insects. Depending on the species, the odour varies from faintly sour to strongly fermented sweet and sour (Tab. 2). There was no common trend in flowering sequence of the inflorescence in the genus, except that flowering within the cincinnus is asynchronous as in most other palms with sympodial flower clusters. The genus also shows consistency in having diurnal anthesis. In general, flowers open in the morning with anthesis peaking between 0500 and 1100 hrs (in one observation, *J. altifrons* began anthesis at 0200 hr, and later peaked from 0430 hr onwards). Each inflorescence lasts 7–14 days. Anthesis occurs 30–60 minutes after the flowers have opened except in *J. lanceolata* where it is initiated immediately when the petals have just separated. Flowers are fully open after 1–2 hours. No nectar is produced as the gynoecium is dry, and no nectaries were seen in anatomical sections of flowers of *J. lanceolata*, *J. magnifica* and *J. altifrons*. The flowering rate (or anthesis) in an inflorescence declines or ceases by noon or sometimes by the evening. The flowering intensity (mean number of open flowers per inflorescence per day) at peak was estimated at 396 and 3152 for *J. lanceolata* and *J. altifrons* respectively (Chan, unpubl. data). The pollen is viable for one day (mean percentage germination of fresh pollen, 6 and 24 hrs after anthesis for *J. magnifica* was 69, 20 and 0.8 respectively, present study).

One day after anthesis, anthers have little pollen left and the stigma, style and filaments start turning brown. The flowers close on the second day after anthesis and turn brown on the third day. In this study, the stigmas of newly opened flowers (*J. magnifica* and *J. altifrons*) before or at anthesis, showed limited effervescence activity when

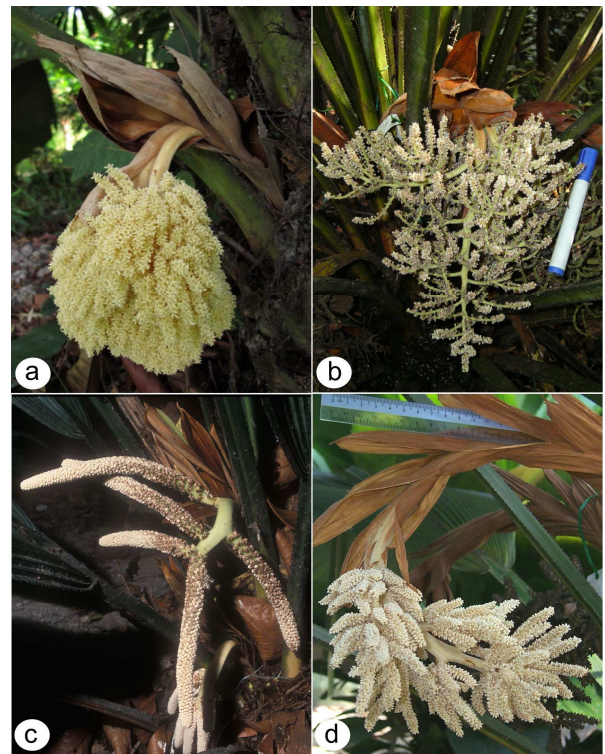


FIGURE 1. Inflorescence structure. (a) *Johannesteijsmannia magnifica* (b) *J. perakensis* (c) *J. lanceolata* (d) *J. altifrons*.

Attributes	<i>J. altifrons</i>	<i>J. magnifica</i>	<i>J. perakensis</i>	<i>J. lanceolata</i> *
<i>Inflorescence</i>				
Total length range (cm)	46-92	20-65	52-90	9-27
Mean length (cm)	63 ± 14	46 ± 11	69 ± 12	19 ± 5
Peduncle length (cm)	42 ± 12	21 ± 8	40 ± 8	11 ± 3
Order of inflorescence branching†	3	5-6	4	1
N	20	20	20	20
<i>Flower</i>				
flower diameter (mm)	3.9 ± 0.2	2.8 ± 0.3	2.7 ± 0.2	2.3 ± 0.2
flower length (mm)	2.6 ± 0.2	2.2 ± 0.2	2.6 ± 0.2	2.6 ± 0.2
petal width (mm)	1.6 ± 0.0	1.0 ± 0.1	1.7 ± 0.2	1.6 ± 0.1
petal length (mm)	2.8 ± 0.1	2.4 ± 0.2	2.5 ± 0.2	2.0 ± 0.2
stamen length (mm)	1.4 ± 0.1	1.3 ± 0.1	1.4 ± 0.3	1.3 ± 0.2
pistil length (mm)	1.8 ± 0.1	1.5 ± 0.0	1.5 ± 0.1	1.2 ± 0.1
style length (mm)	0.7 ± 0.0	0.5 ± 0.0	0.6 ± 0.1	0.4 ± 0.1
N	10	5	10	10

TABLE 1. Floral morphology of *Johannesteijsmannia*. Average values are presented as the mean ± SD

*Unpublished data from Chan (2009), †data from Dransfield (1972)

immersed in 3% hydrogen peroxide, relative to those of the fully open flowers. About five hours after anthesis, the stigmas showed moderate effervescence whereas those of one-day old flowers showed almost to no activity at all. Based on this evidence we conclude that stigma remains receptive for one day. The stigma is punctiform and dry throughout its receptive phase. At the end of 1-2 weeks' flowering, small, cream-white to pinkish, developing fruits become visible. For *J. perakensis*, the data collected were inconclusive due to lack of observations on the wild population, and there were no mature cultivated plants available for detailed studies.

Floral visitors

During anthesis, various insects visited the inflorescences of *Johannesteijsmannia altifrons* and *J. magnifica* including stingless bees (*Trigona*), beetles, thrips, flies and ants

(present study, Tab. 3). In the *ex-situ* plants of *J. altifrons*, up to 12 *Trigona* bees were observed during peak anthesis at 0800 hr as well as many flies in an inflorescence. Stingless bees were also seen visiting the inflorescence of *J. perakensis*. On several occasions, bees and flies visiting the inflorescences of *J. altifrons* and *J. magnifica* were observed extending their probosces onto the filaments and carpels, probably collecting secretions from the filaments, as microtome sections of mature flowers show a layer of glandular cells on the outer side of filaments of *J. lanceolata* (Chan 2009), *J. magnifica* and *J. altifrons* (present study, Fig.2). In *J. lanceolata*, *Trigona* bees collected pollen from open flowers and sometimes were seen prying open the petals of mature buds to access the anthers. Examination of the flowers under a dissecting microscope showed empty pollen sacs in some flowers while in few others, the anthers were missing.

Attributes	<i>J. altifrons</i>	<i>J. magnifica</i>	<i>J. perakensis</i>	<i>J. lanceolata</i> *
N inflorescences observed	6	4	4	25
Splitting of inflorescence bracts	apically	laterally	apically	laterally
Odour of inflorescence	sweet & sour	fermented sweet & sour	sour	sour
Odour intensity	strong	strong	slightly strong	faint
Flowering sequence in inflorescence	basipetal	random	n.d.†	acropetal
Flowering sequence in rachilla	random	acropetal	acropetal	acropetal
Peak anthesis (hrs)	0500-1000	0700-0900	n.d.	0730-1100
Flowering duration per inflorescence (days)	7-10	7-12	n.d.	7-14
Pollen viability (day)	n.d.	1	n.d.	1
Stigma receptivity (day)	1	1	n.d.	1
Breeding system	n.d.	facultative selfing	n.d.	facultative selfing

*data from Chan et al. (2011b), † n.d. – no data

TABLE 3. Insects collected from the inflorescences of *Johannesteijsmannia* species. Unidentified species are indicated as (Indet.).

Species	Population	Time	Order	Family	Species
<i>Johannesteijsmannia altifrons</i>	cultivated	morning	Coleoptera	Chrysomelidae	Indet.
				Cucurliionidae	Indet.
				Nitidulidae	<i>Haptoncus</i> sp.
				Nitidulidae	<i>Carpophilus</i> sp.
			Diptera	Staphylinidae	Indet.
				Blattidae	Indet.
				Drosophilidae	<i>Drosophila</i> sp.
			Drosophilidae	Drosophilidae	Indet.
				Lonchaeidae	Indet.
			Hymenoptera	Apidae	<i>Trigona collina</i>
				Apidae	<i>Trigona apicalis</i>
Formicidae	<i>Technomyrmex</i> sp.				
Thysanoptera	Thripidae	<i>Thrips</i> sp.			
<i>J. magnifica</i>	wild	morning	Diptera	Tachinidae	Indet.
				Hymenoptera	Apidae
			Apidae	<i>Trigona minor</i>	
			Formicidae	<i>Ectatomima</i> sp.	
			Ichneumonidae	Indet.	
	cultivated	morning	Diptera	Drosophilidae	<i>Drosophila</i> sp.
				Hymenoptera	Formicidae
			Apidae	<i>Trigona melina</i>	
	cultivated	night	Coleoptera	Scarabeidae	<i>Apogonia neglecta</i>
			Dictyoptera	Blattidae	Indet.
<i>J. lanceolata</i>	wild*	morning	Dictyoptera	Blattidae	<i>Blatta orientalis</i>
			Diptera	Phoridae	Indet.
	cultivated*	evening/night	Diptera	Cecidomyiidae	Indet.
				Phoridae	Indet.
	cultivated [†]	morning	Diptera	Calliphoridae	Indet.
Chironomidae				Indet.	
Chloropidae				Indet.	
Phoridae				Indet.	
Sciomyzidae				Indet.	
Homoptera				Delphacidae	Indet.
				Hymenoptera	Apidae
Apidae					<i>Trigona laeviceps</i>
Apidae					<i>Trigona melina</i>
Formicidae					<i>Paratrechina</i> sp.
Formicidae	<i>Anoplolepis longipes</i>				

*Data from Chan et al. (2011b). Other visitors observed were spiders and moth larvae (order Lepidoptera, family Lymantridae). [†]Sampling for pollen load.

Both *in-* and *ex-situ*, *Trigona* bees and flies were the most common visitors to the flowers of *Johannesteijsmannia* during anthesis. Pollen grains of *J. lanceolata* were found abundant on the thorax, tarsus hairs and corbiculae of *Trigona laeviceps* (N = 2) and *T. itama* bees (N = 1). However, no pollen grains were observed on *Trigona mellina* (N = 1) (Tab. 3). All scuttle flies (Phoridae) (N = 14) and ants (Formicidae) (N = 5) did not carry pollen, except for one scuttle fly that had two pollen grains of *J. lanceolata* adhering to a leg, and a blow fly (Calliphoridae) that carried few foreign pollen grains. Other flies (Chironomidae,

Chloropidae and Sciomyzidae) also visited the inflorescences but were not pollinators because they did not touch the open flowers.

Beetles were recorded in the inflorescences of *J. altifrons* and *J. magnifica*, but apparently absent in those of *J. lanceolata*. According to Corlett (2004), flowers that are primarily beetle-pollinated often have intense odour. Therefore, compared to *J. lanceolata*, the inflorescences of *J. altifrons* and *J. magnifica* have a stronger odour which could have attracted more beetles. In these two species, missing anthers and bruised carpels were observed in open flowers,

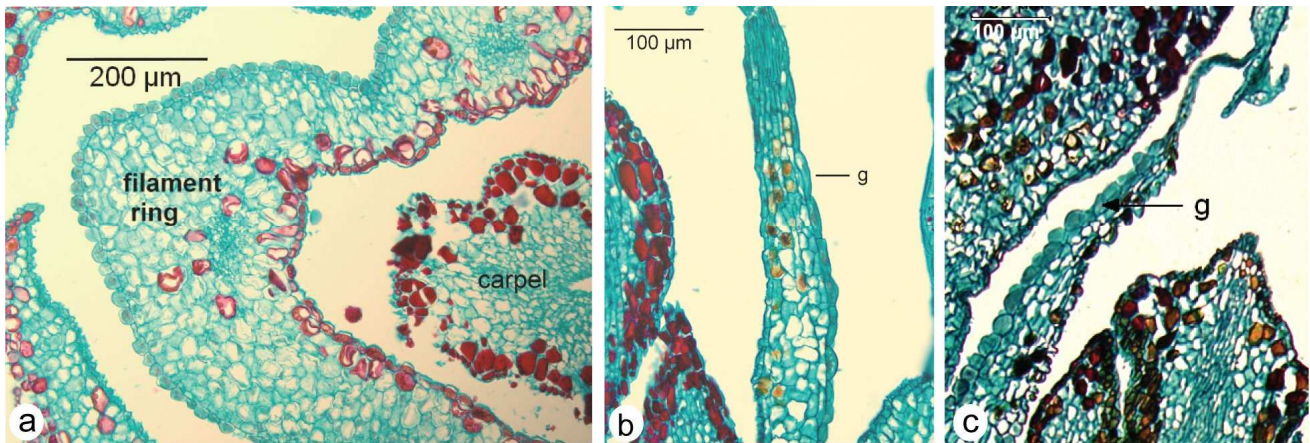


FIGURE 2. Sections of filaments of (a) *Johannesteijsmannia altifrons* – transverse section, (b) *J. magnifica* – longitudinal section (L.S.) and (c) *J. lanceolata* – L.S., showing an outer layer of glandular cells (g).

indicating beetle-feeding on pollen or floral structures. Tannins, a common protective feature in palms to deter herbivory (Uhl & Moore 1977) are found abundantly in floral parts of *J. lanceolata* (Chan 2009), *J. altifrons* and *J. magnifica* (present study), and may help to deter beetle feeding. On the other hand, seed-borer beetles of the Scolytidae family, *Xyleborus* sp. were found in the fruits of *J. perakensis* (pers. obs.). This indicates that the beetles visited the flowers of *J. perakensis* for oviposition, but it remains unclear whether they have any role in the pollination system.

From the results of this study, *Trigona* bees are likely to be the major pollinators of *Johannesteijsmannia* because they carry large amount of pollen on their bodies. We consider scuttle flies as potential but inefficient pollinators because they carry few pollen grains and were seen visiting the inflorescences of *Johannesteijsmannia* from morning until the evening, and even after rain (present study). Also, they are abundant and found all year round. Under such circumstances, flies may be an alternative pollinator when bees do not forage at all if rewards are not profitable, in order to maximise energy efficiency (Richards 1986, Abrol 2006). Ants are excluded as efficient pollinators because they do not carry pollen and mostly reside in the bracts or leaf litter, although a few crawled haphazardly on the inflorescences. The role of beetles as potential pollinators of *Johannesteijsmannia* remains to be tested since we did not examine them for pollen loads.

Our study corroborates Dransfield's (1972) observation that *Johannesteijsmannia* flowers are visited by a wide range of insects such as nitidulid and staphylinid beetles, dipterans, ants and termites, as well as spiders. Flies, bees, beetles, wasps and ants are common visitors to palms, but representatives for the latter two groups are not considered important pollinators (Borchsenius 1993; Bøgh 1996; Ervik & Feil 1997; Consiglio & Bourne 2001; Barfod et al. 2011). Beetles and flies are generally considered inefficient pollinators compared to bees, butterflies or moths (Faegri & van de Pijl 1966; Ghazoul 1997). However, beetles are often closely associated with palms and are important pollinators

to many palm species (Henderson 1986, 2002; Barfod et al. 2011).

In FRIM where *J. altifrons*, *J. lanceolata* and *J. magnifica* are planted together, a lower number of insects visited the inflorescence of *J. lanceolata*. Perhaps the smaller, rather inconspicuous and weaker-scented inflorescence of *J. lanceolata* compared to the other two species is less attractive to insects. Furthermore, *J. lanceolata* offers fewer floral rewards because it has far fewer number of flowers and lower flowering intensity than the rest of the species. In contrast, *J. altifrons* has four times the number of flowers and eight times the flowering intensity of *J. lanceolata* (see results and discussion on floral biology).

We rule out wind pollination in *Johannesteijsmannia* because the anther has very little pollen and the pollen is sticky, while the stigma has a very small surface for pollen deposition by wind. Moreover, the inflorescences are usually borne just above the ground and there is hardly any strong wind in the understory of a closed canopy forest. In summary, *Johannesteijsmannia* is entomophilous and the flowers are visited by various groups of insects, with *Trigona* bees as the potential pollinators.

Breeding system

The inflorescences of *Johannesteijsmannia magnifica*, *J. perakensis* and *J. altifrons* are highly floriferous with up to six orders of branching compared to *J. lanceolata* that has only one order of branching (Tab. 1). Pollinators would often visit many flowers that are close together (Richards 1986), thus it is likely the first three species are geitonogamous (i.e. pollen transfer between flowers of the same plant). In a 15-minute observation on *J. altifrons*, the same *Trigona* bee collected pollen from numerous flowers within the same inflorescence (present study). Furthermore, it is common to find two or more inflorescences with simultaneous or overlapping flowering on one plant (Chan, unpubl. data). Also, *J. magnifica* and *J. lanceolata* seemed to display self-compatibility within a plant because plants in isolation were able to set viable seed (pers. obs.).

J. magnifica and *J. altifrons* are considered homogamous because stigma receptivity period coincides with anthesis, as judged by active effervescence of stigmas of freshly open flowers when immersed in the hydrogen peroxide solution. Homogamy has been shown in *J. lanceolata* using the same test and also by examination of stigmas using scanning electron microscopy (Chan et al. 2011b). Thus, *Johannesteijsmannia* may be autogamous, i.e. it has the capability of selfing within a flower. Furthermore, *Johannesteijsmannia* displays the characteristics of autogamy, i.e. it has small hermaphrodite flower with introrse anthers that are more or less parallel and close to the stigma (c. 0.2 mm vertical gap distance, present study), synchronous male and female anthesis, and small pollen to ovule (P:O) ratio of between 31.9–396.0 that indicates facultative selfing (Cruden 1977). The mean number of pollen grains per anther in *J. magnifica* was 79 (SD 30, N anther = 4, total pollen grains = 471) (present study), much higher than that of *J. lanceolata*, i.e. 45 (Chan et al. 2011b). The P:O ratio was 157 for *J. magnifica* and 89 for *J. lanceolata* respectively.

Bagging experiments on *J. lanceolata* (Chan et al. 2011b) showed that the final fruit set of open pollination compared to that when insects were excluded, was not statistically different. This may imply that self-pollination does not affect fruit set. However, to gauge the effects of inbreeding, further studies on the viability or fitness of seedlings from self-pollination, or population genetic studies are needed. The evolution of self-fertility in small populations may be favourable to local endemic or rare plants such as *J. lanceolata*, where few mates are available for cross-pollination, or if pollinator service is unreliable (Karron 1991). Although no data is available for the breeding systems of *J. perakensis* and *J. altifrons*, we predict facultative selfing based on the close similarity of their floral biology and flower visitors with the other two species.

CONCLUSION

The flowers of *Johannesteijsmannia* spp. open in the morning and are visited by various insects such as *Trigona* bees, flies, beetles and ants. Differences in inflorescence size (number of flowers) and flowering intensity which determine the amount of floral rewards may probably explain the variation of floral visitors and their abundances among the members of the genus. *Trigona* bees have been identified as potential pollinators to all *Johannesteijsmannia* species, and flies may play a minor role in the pollination. The importance of beetles as pollinators is unclear and requires further study. The genus exhibits features of autogamy and geitonogamy.

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