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FLORAL BIOLOGY AND POLLINATION MECHANISM OF *SALACCA VERMICULARIS* BECC. (ARECACEAE: CALAMEAE)

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Salacca (Arecaceae), a genus of palms with 23 accepted species, has its centre of diversity in Borneo. *Salacca vermicularis* Becc. which is endemic to Borneo, has, despite its edible fruits, has never been studied concerning its floral biology and pollination mechanisms. In this study, the phenology, floral rewards, floral visitors, and possible seed dispersal agents of *S. vermicularis* were investigated, and experiments performed on the breeding mechanisms of *S. vermicularis*. Anthesis in staminate flowers begins around noon and persists until early morning on the second day whilst anthesis in pistillate flowers begins around evening and may take up to 40 hours to fully bloom. Floral scent was present throughout the anthesis for staminate and pistillate plants. Apomixis is not present in this species. Several insect visitors were observed, namely *Heterotrigona* (Apidae) sp. as well as members of Curculionidae, Sciaridae, Formicidae, and Acaridae. Three species of visitors are likely the dispersal agents of *S. vermicularis*, namely *Hystrix* sp. (Hystricidae: Hystricinae), *Tragulus* sp. (Tragulidae) and *Lariscus insignis* (Sciuridae: Callosciurinae). A mongoose (Herspetidae) was observed foraging nearby but is unlikely as a dispersal agent.

Keywords: phenology, floral rewards, floral attractants, floral visitors, breeding mechanism, fruit and seed dispersal

INTRODUCTION

Salacca Reinw. (Arecaceae) is one of two genera in the subtribe Salaccinae Becc, the other being *Eleiodoxa* (Becc.) Burret is distributed from the eastern Himalayas to South Central China and West Malesia with its centre of diversity in Borneo (Zumaidar & Miftahuddin 2018, POWO 2023). *Salacca* comprises 23 species to date (Zumaidar & Miftahuddin 2018, Kuhnhauser et al. 2021, POWO 2023). *Salacca*, characterised as dioecious, exhibits staminate and pistillate flowers on separate trees. Staminate trees only bear staminate flowers, while pistillate trees bear dyads consisting of one pistillate flower and a sterile staminate flower (Mogea 1978). *Salacca* is divided into two sections: section *Salacca* with spine-tipped scales and pistillate rachillae bearing dyads of a fertile pistillate and a sterile staminate flower and section *Leiosalacca* with smooth scales and pistillate rachillae bearing solitary pistillate flowers (Furtado 1949, Dransfield et al. 2008). Several members of the genus are widely cultivated in Southeast Asia for their edible fruit, including *Salacca affinis* Griff., *Salacca sumatrana* Becc., and *Salacca zalacca* (Gaertn.) Voss. While the fruit of *Salacca vermicularis* Becc. is edible, the taste is rather astringent but is still planted on a smaller scale and enjoyed by local communities (pers. obs. 2023). *Salacca affinis* and *S. zalacca* have been reported to be pollinated by curculionid beetles, trigonid bees, and honeybees (Mogea 1978, Apriniarti et al. 2019, Atmowidi et al. 2021, Siregar et al. 2021). The floral biology and pollination of *S. vermicularis* has never been studied likely due to its low commercial value, lack of scientific interest and difficulty in encountering large flowering population as in many pollination studies. The goal of this study was to investigate the floral biology and pollination mechanism of *S. vermicularis*.

METHODS AND MATERIALS

Species description

Salacca vermicularis (Figure 1 & Figure 2) is a massive clustering acaulescent palm growing up to 3.5 m typically found in damp sites in lowland dipterocarp forests and alluvial forests (Dransfield 1984). The leaves have pinnae which are dark green adaxially and powdery grey abaxially. The pinnae are arranged in groups on either side of the rachis proximally and opposite distally with dark brown and triangular spiny petioles, newer petioles closer to the centre are brown, and older petioles are light green. The inflorescence is axillary, piercing through the subtending leaf sheath.

The staminate inflorescence which emerges from tattering bracts, is up to 1 m long, slender, and erect, with up to three orders of branching with the cylindrical staminate rachilla up to 15 cm long, branches up to 25 rachillae in an inflorescence. The staminate flowers are surrounded by golden yellow trichomes. Each flower is trimerous, sepal membranous, ca. 3 mm long and 2 mm wide, basally united; petals connate in the basal half, red outside, basally dark pink inside, ca. 2 mm long and 1 mm wide; stamens 6, ca. 1 mm long, filament red, anther yellow ca. 1 mm long with yellow powdery pollen.

The pistillate inflorescence is typically 28 cm in length including the bracts. The peduncle is slender approximately 1 cm in diameter at the base, covered by bracts and branches up to three orders. The pistillate rachilla is up to 15 cm long. The bracts are rather tattered and fibrous which envelopes the whole pistillate rachilla during development and slowly tear open when approaching blooming. There are four to five rachillae per inflorescence. The pistillate flowers are trimerous with sepals approximately 17 mm long and 15 mm wide, basally united; petals are connate in the basal half, red outside, basally red inside approximately 12 mm long and 10 mm wide. Each pistillate flower is associated with a sterile male flower which comprises six staminodes; each staminode is around 5 mm long, red. There are c. 30 pairs of dyads per

Figure 1 A) *Salacca vermicularis,* an acaulescent palm growing up to 3.5 m B) Younger petioles closer to the centre are brown, older petioles are light green C) The pinnae are dark green adaxially and powdery grey abaxially D) dark brown triangular shaped spines in rows of two to four along petiole E) sapling of *S. vermicularis*

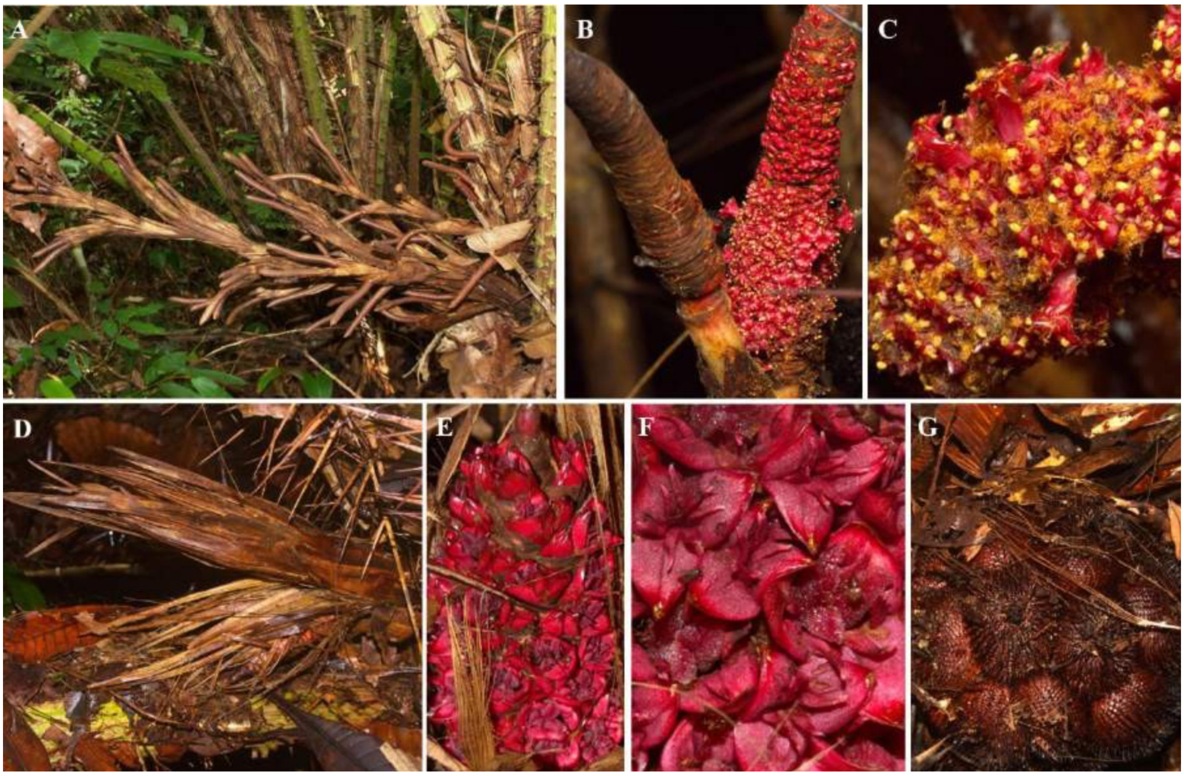


Figure 2 **A)**Staminate inflorescence to 1 m long, slender, and erect, with up to three orders of branching B) Staminate flowers begin blooming from the proximal end of the rachilla C) Staminate flowers with red petals and six anthers surrounded with golden yellow trichomes between flowers D) Pistillate inflorescence enveloped in tattering bracts E) pistillate flowers begin blooming from the proximal end F) flowers are in dyads, pistillate flowers and its associated staminode flower G) matured fruit bunch with fruits covered in long stiff spines

rachilla. Fruit bunches may develop at varying heights ranging from 0.1 to 1.5 m on different individuals. Fruit globose, 4-5 cm long, 4-5 cm in diameter, gradually narrowed towards the base, covered with scales having upturned in c. 25 rows. A summary of floral characters for *S. vermicularis* is provided in Table 1.

Study Site

This study site was conducted at the foothill of Mount Serapi (1°35'19.64"N, 110°13'12.09"E), approximately 20 km northwest of Kuching, Sarawak, Malaysia. The population of *S. vermicularis* is found between 10 m and 100 m elevation. Mount Serapi is dominated by five types of forest: lowland mixed dipterocarp forest, kerangas forest, submontane forest, alluvial forest, and secondary forest (Hazebroek & Kashim 2001). Mount Serapi is largely covered with red-yellow podzolic soil, whereas peaty soil is frequently found on exposed ridges above 300 m elevation. Dip-slope podzols, which are primarily sandy clay, well-drained, and nutrient-deficient, are also common (Hazebroek & Kashim 2001). Individuals were sampled in an area of about 2 hectares along the main trail to Mount Matang's Sri Mariamman Temple.

Table 1 Summary of plant habit and floral characters *S. vermicularis* studied

Characters	
Habit	Solitary
Max stem length (m)	1.5
Vertical height (m)	3.5
Inflorescence length ♀ (cm)	28
Inflorescence length ♂ (m)	1
♀ rachilla length (cm)	15
♂ rachilla length (cm)	15
Colour of petals	Maroon
No. of ♀ rachillae	5
No. of ♂ rachillae	25
No. dyads per ♀ rachilla	60 pistillate flowers

Floral biology and floral visitors

Observations on five individuals (totalling 16 rachillae) of *S. vermicularis* were performed between May 2021 and June 2022. Several days of initial observations were conducted to establish the anthetic cycle; then proceeded by direct observations consisting of four to five hours each day until the full duration of anthesis was completely observed. Observations were repeated three times. The values shown represent the average number of visitors on a rachilla. Floral odour was determined through wafting, distance, and scent description. The duration of floral emissions were also recorded.

Behaviour of floral visitors such as interaction with stigma and anther, the average duration of visit, and the mean number of visitors were noted. The number of visitors was counted at two-hour intervals. The floral visitors are determined to be potential pollinators by having the capacity to contribute to pollination via the aforementioned actions. Insect visitors were identified using (Hill & Abang 2010). The number of plants observed and the number of inflorescences along with the observational periods for both sexes is shown in Appendix 1.

Floral availability

Plant individuals bearing remnants of inflorescences and/or infructescence from the previous season were selected. A total of 12 individuals (seven staminate and five pistillate) were included in this study. The sex ratio at two levels (the number of individuals and the number of individuals that flowered during the study period, 15 March 2022 until 23 July 2022) was determined and tested for sex-ratio bias using binomial tests. The operational sex ratio (OSR) is defined as the ratio of fertile males to females (Wehbe & Shackelford 2020).

Pollination experiments

The pollination experiments comprised of Bagged Untreated (T 1)- rachillae were bagged three to four days before blooming until the end of anthesis; Open Pollination (T 2)- pistillate flowers were left exposed to permit unhindered animal interactions. Bagging was done using 0.5 mm mesh bags. Two to three rachillae per individual were selected per treatment. Sampling duration and voucher codes are provided in Appendix 2.

Fruit dispersal agents

Two camera traps (model: Reconyx Hyperfire 2) were deployed at sites (±2.5 m from a fruiting plant) between 14 March 2022 and 15 July 2022. Active camera days were used to calculate the effort or the total number of camera days where the: Total camera days (TCD) = $\sum cd_i$ (1) where c is the active camera operating within a site and d is the number of days (Mohd-Azlan & Engkamat 2013). The cameras were mounted approximately 30-100 cm from the ground on a tree depending on the height of infructescence with every camera set to capture three-burst shots with no interval after each trigger a 10-second video for each detection, and a 10-second video at 30-minute intervals. Cameras were checked every three to four days for signs of feeding on the fruits and to replace with fresh batteries and memory cards where needed. Images were sorted and identified to a generic level. Animals, where the species could not be determined owing to poor angle or low image quality were not used in the analysis. Animal dispersers were identified using guides provided by Phillipps & Phillipps (2020).

RESULTS

Floral biology

Several staminate rachillae of an inflorescence may begin anthesis at the same time, however, blooming typically begins from the proximal rachilla towards the rachilla at the distal end of the inflorescence following an acropetal development. The rachillae turn from pinkish-white to reddish-brown as they mature. All the flowers within each rachilla bloom within one to two days; flowers at the proximal half of the rachilla bloom first followed by the flowers at the distal half on the next day. The blooming of an inflorescence may take up to 40 days from the opening of the first flower depending on the number of rachillae present, with typically one to two rachillae bloom(s) per day. The staminate flowers require around 70 days from bud initiation to mature and be ready to bloom. The anthesis of the staminate flowers (Figure 3) starts at 1200 (Day 1); by 1300 (Day 1), all the flowers are blooming (in a smaller rachilla) c. 20 mins following the opening of the calyx. The flowers begin to dehisce around 0400 (Day 2) and by 0600 (Day 2) but on rare occasions. By 0800 (Day 2), all the flowers dehisced. A very light sweet odour was detectable up to 5 cm away along the rachillae from around 1300 (Day 1) until 0300 (Day 2). The strength and profile remained the same (perceivable through wafting) throughout the emission.

Floral maturation and blooming from the proximal end of the pistillate rachilla towards the distal end following acropetal development. As with the staminate inflorescences, the pistillate rachillae appears pinkish-white during early development to reddish-brown as it matures. As the rachilla matures, the dark red floral buds begin to appear from the bracts at the distal portion of the rachilla. Although flowering begins from the distal end of the rachilla, the subsequent flowerings begin flowering in a less orderly sequence. All the flowers within each rachilla finish blooming within 24 hours with the whole inflorescence taking up to 15 days depending on the number of rachillae. The pistillate flowers require around 60 days from bud initiation to maturity. *Salacca vermicularis* does not appear to produce any nectar; however, it does produce a thin layer of stigmatic fluid that is present throughout the anthetic period of the pistillate flower and pollen has been observed to adhere to it.

Pistillate anthesis begins at 1700 (Day 1) when the calyx opens to reveal the petals and stigma. All the pistillate flowers in a rachilla will bloom by 0600 (Day 3) when the stigma has fully emerged and recurved. The pistillate flowers were observed to bloom for 20 hours, sometimes up to 40 hours in larger rachillae. The large span is likely due to larger rachilla having greater number of flowers. The stigma begins to dry around 2000 (Day 3) and by 1000 (Day 4), most flowers have dried up. The sterile male flower blooms within 24 hours after the pistillate flower has fully bloomed, typically around 0800 a day after all pistillate flowers begin anthesis. A very light sweet odour was detectable up to 5 cm away along the rachillae and was present around 0800 (Day 3) until 1500 (Day 3). The strength and profile remained the same (perceivable through wafting) throughout the emission. An infructescence takes c. 35 days to mature.

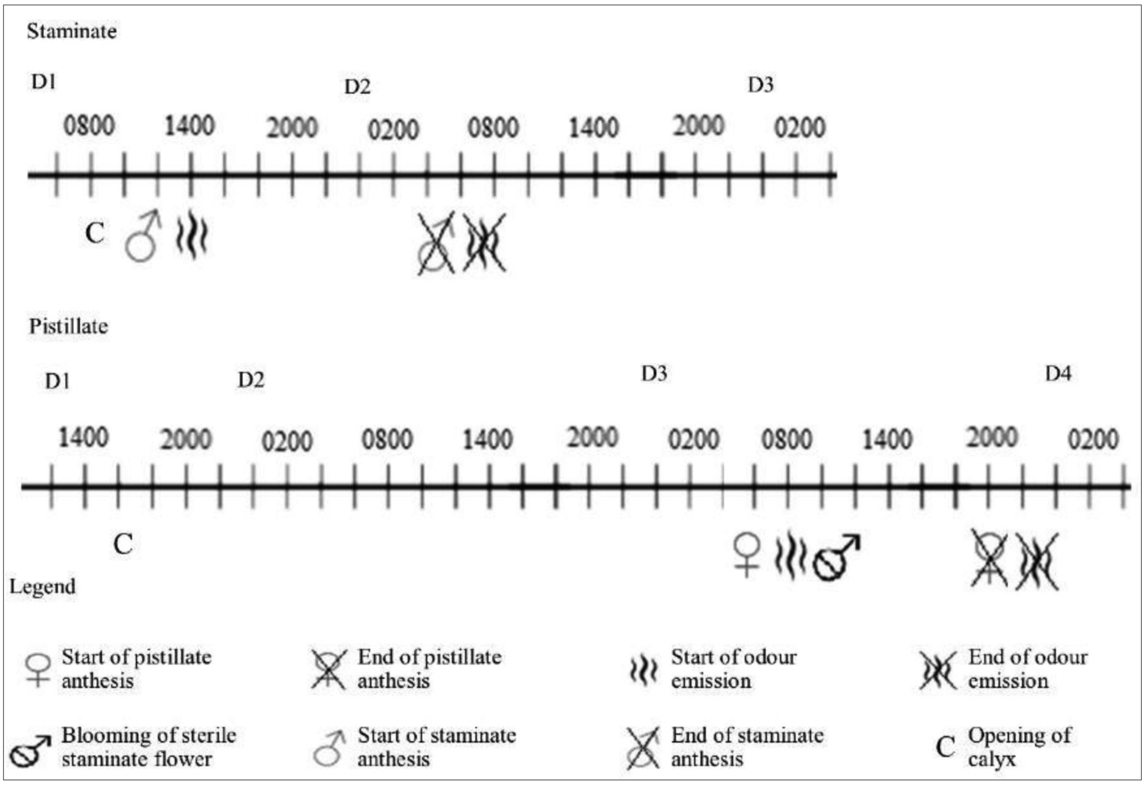


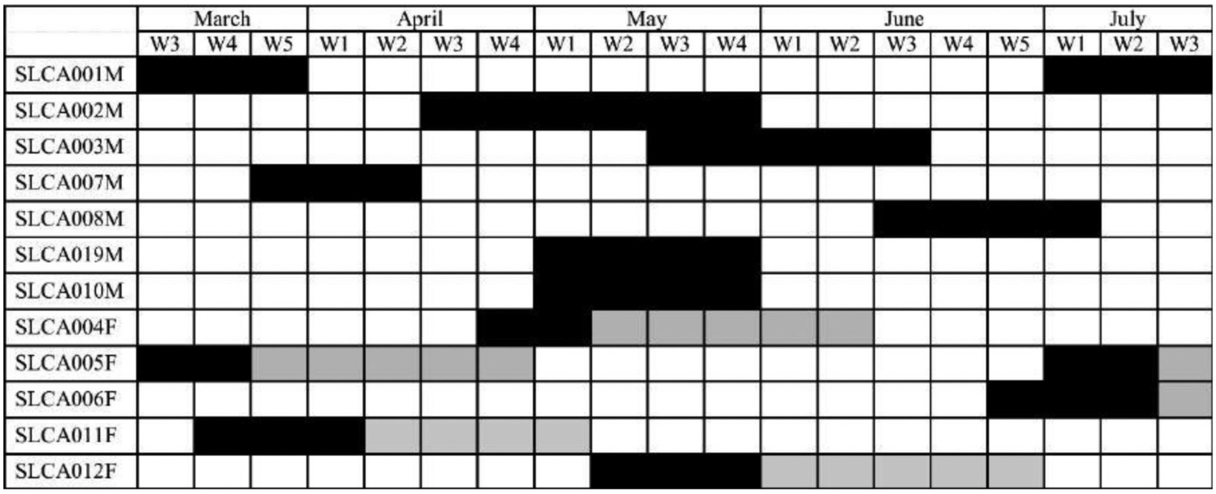
Figure 3 A general timeline of phenological events of *S. vermicularis*

Floral availability

The availability of staminate and pistillate inflorescence is presented in Figure 4. Flowering appears aseasonal throughout the study duration. The sex ratio of flowering individuals was not significantly unbiased between male and female individuals. However, based on the OSR generated (Table 2), there is a male bias in flowering for *S. vermicularis* during the three months of observations.

Pollination

Treatment 1 gave a 0.00 % fruit set for all replicates while treatment 2 showed 89.24%, 92.09%, and 87.77% for SLCA004F, SLCA005F, and SLCA007F (Table 3). There is a significant



	March			April				May				June					July		
	W3	W4	W5	W1	W2	W3	W4	W1	W2	W3	W4	W1	W2	W3	W4	W5	W1	W2	W3
SLCA001M	■	■	■														■	■	■
SLCA002M						■	■	■	■	■	■								
SLCA003M										■	■	■	■	■					
SLCA007M			■	■	■														
SLCA008M														■	■	■	■		
SLCA019M								■	■	■	■								
SLCA010M								■	■	■	■								
SLCA004F							■	■	▨	▨	▨	▨	▨						
SLCA005F	■	■	▨	▨	▨	▨	▨										■	■	▨
SLCA006F																■	■	■	▨
SLCA011F		■	■	■	▨	▨	▨	▨											
SLCA012F									■	■	■	▨	▨	▨	▨	▨			

Figure 4 Availability of staminate and pistillate inflorescence from 15/3/2022 until 23/7/2022. Any week with at least 4 days left is counted as a week thus certain months have 5 weeks. W1=Week 1; voucher codes ending with M is staminate, voucher codes ending with F is pistillate; black box indicates flowering, grey box indicates fruiting (ends when the last fruit is no longer on infructescence)

Table 2 Flowering percentage (F %) is the total number of flowering individuals out of total number of individuals expressed in percentage, χ^2 test results to verify if there is any significant bias towards either staminate or pistillate flowering (χ^2 value, P-value where $\alpha \leq 0.05$) and the operational sex ratio (OSR) expressed as the ratio of flowering staminate to pistillate plants (staminate: pistillate) during a particular month

		F %	χ^2, P-value	OSR
October	Staminate	41.18	1.974,0.740	7:2
	Pistillate	16.67		
November	Staminate	23.53	0.202, 0.995	2:1
	Pistillate	16.67		
December	Staminate	52.94	3.932, 0.415	9:2
	Pistillate	16.67		

Table 3 Results from pollination experiments; T 1=bagged flower, T 2=free unbagged; Chi-square and the P value are calculated between results from T 1 and T 2

	T1	Fruit Set		Fruit Set	χ^2	P value
SLCA004F	0/129	0.00%	141/158	89.24%	226.30	<0.000001
SLCA005F	0/162	0.00%	128/139	92.09%	259.56	<0.000001
SLCA007F	0/143	0.00%	122/139	87.77%	221.21	<0.000001

difference between both treatments for all replicates. No apomixis occurs in *S. vermicularis.*

Floral Visitors

In the staminate flowers, weevils (Curculionidae) (Figure 5A) arrive first at the start of anthesis at 1200 (Day 1) (Table 4) (Figure 6) followed by the floral mites (Figure 5A) sometimes observed latching onto the weevils. Whenever a weevil stays stationary around a flower, the floral mites would latch onto the carapace of the weevils and would remain attached as the weevils depart. The weevils were also observed to feed on the petals, but the damage can be considered minimal. Stingless bees, *Heterotrigona* sp. (Figure 5B) also visit the staminate flowers around 1230 (Day 1). The stingless bees mainly collect pollen. Sciarid flies (Sciaridae) (Figure 5C) were also seen visiting the staminate flowers from around 1230 (Day 1) till 1900 (Day 1) with similar behaviours as the weevils, however, the sciarid flies were not observed to carry any floral mites. All the floral visitors would remain until floral dehiscence which is around 0400 (Day 2) except for the stingless bees which stop visiting the flowers around 1830 (Day 1). Ants were found to be present throughout the anthesis (Figure 5F).

For pistillate flowers, the weevils arrive first at the start of anthesis around 1500 (Day 2) and remain till 1900 (Day 2). The weevils reappear at around 0600 (Day 3) till 1700 (Day 3). The weevils were observed to move constantly in and out of the flowers, particularly towards the base of the stigma to consume the thin layer of sticky stigmatic fluid. The long snout of the weevil appears to be very efficient in consuming the floral exudate. The weevils were also observed to mate on several occasions (Figure 5D) and white substances presumed to be eggs have also been observed (Figure 5E). The same feeding

Figure 5 A) Floral mites attached to the back of weevils upon arrival at the beginning of the blooming (indicated by arrow on the right) for staminate flowers B) Stingless bee covered in pollen during visit C) Sciarid flies, weevils and floral mites visiting around the same time on staminate flowers D) Weevils mating on the pistillate flowers (indicated by arrows) E) White weevil eggs deposited around pistillate flowers (indicated by arrows) F) Ants are omnipresent on the flowers

Table 4 Primary floral visitors for each species of *Salacca vermicularis*

	♂	♀
Flower mites		
Visiting hours	1200 (Day 1)-0400 (Day 2)	
Mean no. of visitors/hr	25(58)77	
Average duration of visit	48 mins	
Stingless Bees *Heterotrigona* sp.		
Visiting hours	1230 (Day 1)-1830 (Day 1)	
Mean no. of visitors/hr	2(4)7	
Average duration of visit	3.5 secs	
Weevils (Curculionidae)		
Visiting hours	1200 (Day 1)-0400 (Day 2)	1500 (Day 2)-1700 (Day 3)
Mean no. of visitors/hr	15(23)27	13(20)25
Average duration of visit	34 mins	39 mins
Sciarid flies (Sciaridae)		
Visiting hours	1230 (Day 1)-1900 (Day 1)	1500 (Day 2)-1900 (Day 3)
Mean no. of visitors/hr	15(19)24	29(36)41
Average duration of visit	16 mins	11 mins
Fruit flies (*Drosophila* sp.)		
Visiting hours		1500 (Day 2)-1900 (Day 3)
Mean no. of visitors/hr		3(6)11
Average duration of visit		3 mins
Ants (Formicidae)		
Visiting hours	1200 (Day 1)-0400 (Day 2)	1500 (Day 2)-1900 (Day 3)
Mean no. of visitors/hr	11(14)21	6(12)18
Average duration of visit	1 min	2 mins

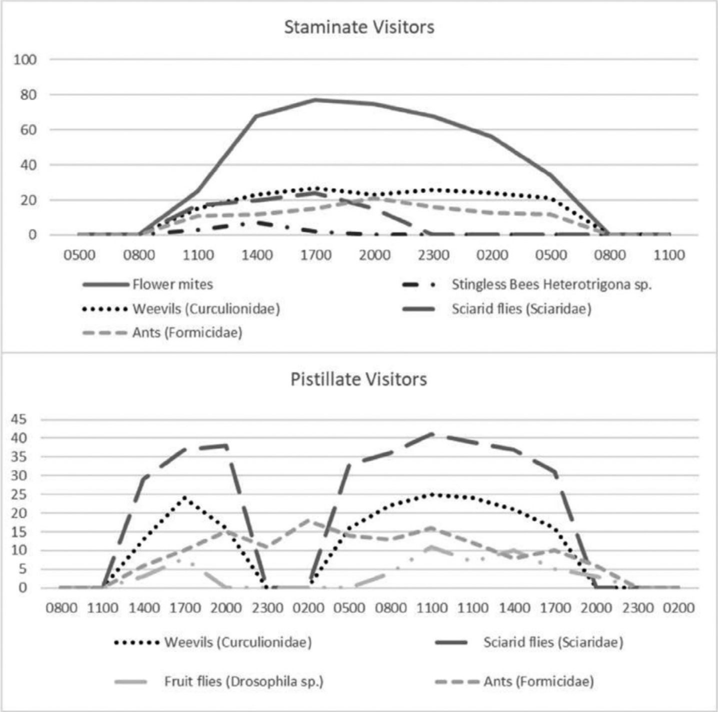


Figure 6 Average number for each species of visitor throughout visiting duration

behaviour on the petals observed in staminate flowers was also observed. Sciarid flies were also seen regularly visiting the pistillate flowers with the same visiting hours as the weevils on both Day 2 and Day 3. The visiting behaviours of the sciarid flies were very similar to the weevils where the sciarid flies were constantly visiting the base of the flowers. Fruit flies (*Drosophila* sp.) were observed to visit starting from 1500 (Day 2) towards 1700 (Day 2) and resumed visit from (0900) Day 3 to 1900 (Day 3). It is unsure what attracted the fruit flies as the fruit flies do not seem to head towards the stigma the same way as the weevils and sciarid flies. The weevils and sciarid flies are the most likely to be contributing towards pollination as both visitors were observed on the staminate plants and do indeed come into contact with the stigma regularly during visits. Curiously, no mites were observed on the weevils visiting the pistillate flowers. Ants were found to be present throughout the anthesis, feeding on the stigmatic fluid (however, they do not appear to carry any pollen during visits to pistillate flowers).

Seed dispersal agents

Asian porcupine (*Hystrix* sp.) (Figure 7A), Mousedeer (*Tragulus* sp.) (Figure 7C) and Three-striped ground squirrel (*Lariscus insignis*) (Figure 7D) are likely the dispersal agents of *S. vermicularis.* A mongoose (Herpestidae) (Figure 7B) was recorded foraging around but is unlikely to be a dispersal agent owing to its diet. All visitors were only captured on film once except for *Tragulus* sp. (Table 5). The total camera days (TCD) were 226 days. Events are defined as visual confirmation on the camera trap whereas evidence of feeding is defined as the presence of fruit scraps (Figure 7E). Post-feeding seed viability tests were not conducted as no faecal samples were collected.

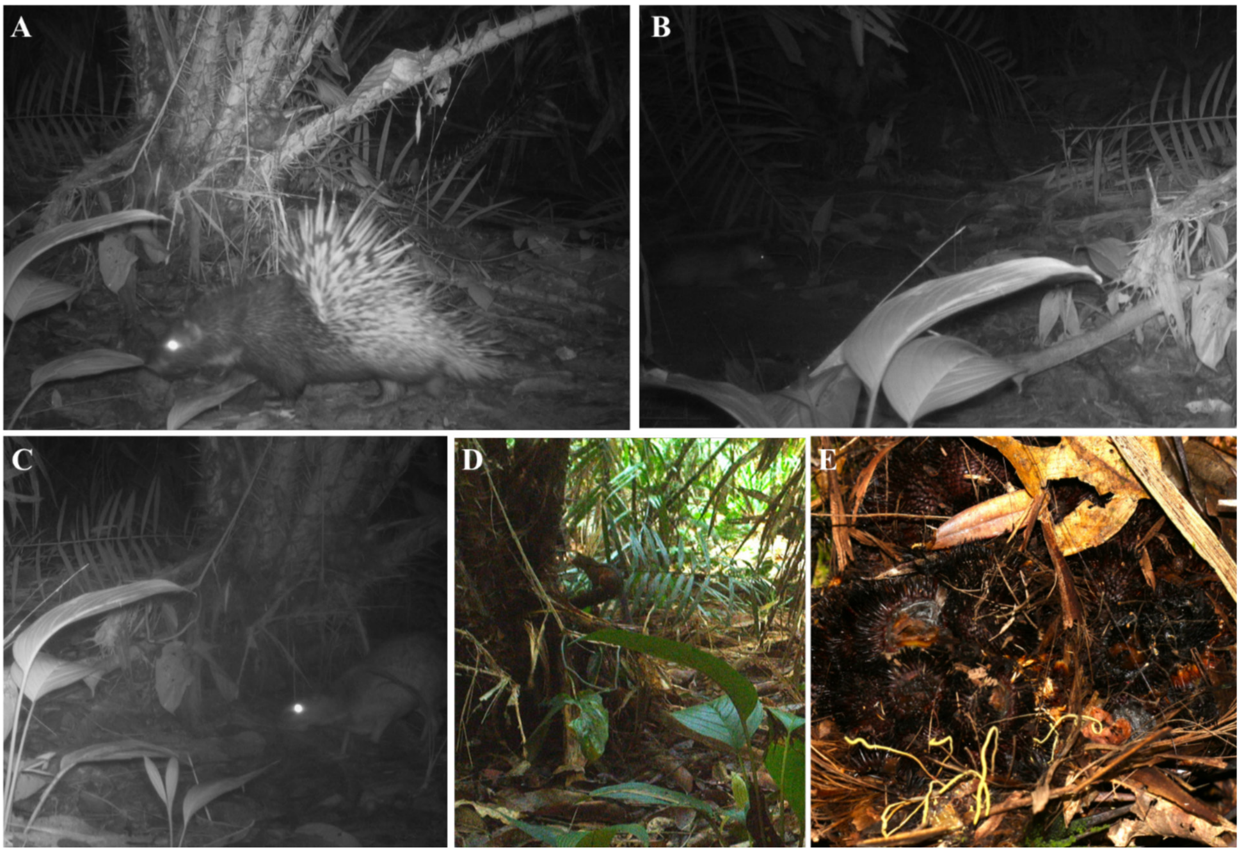


Figure 7 A) Asian porcupine (*Hystrix* sp.) B) mongoose (Herpestidae) C) mousedeer (*Tragulus* sp.) D) Three-striped ground squirrel (*Lariscus insignis*) E) Evidence of foraging on the fruits by animal visitors

Table 5 Animal visitors captured on the camera trap from March to June 2022

	Events	Time of Day Observed	Evidence of feeding
Lariscus insignis	1	1724	Yes
Tragulus sp.	2	0323 0224	Yes No
Hystrix sp	1	0232	Yes
Herpestidae	1	0207	No
Sciuridae	1	1134	Yes

DISCUSSION

Floral attractants and visitor assemblage

Floral visitor assemblage in *Salacca* has been reported to be rather diverse and comprises several orders which include Blattodea, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and Orthoptera. However, the pollinators are mainly Curculionid beetles (Coleoptera), stingless bees (Apidae), and vespid wasps (Vespidae) (Mogea 1978, Fisher & Mogea 1980, Dransfield et al. 2008, Apriniarti et al. 2019, Atmowidi et al. 2021, Siregar et al. 2021). Weevils and stingless bees are among the most reported pollinators for several *Salacca* such as *S. affinis,* and *S. zalacca* (Mogea 1978, Dransfield et al. 2008, Apriniarti et al. 2019, Atmowidi et al. 2021, Siregar et al. 2021) while Drosoliphid flies were previously reported as a pollinator for *S. zalacca* (Mogea 1978, Atmowidi et al. 2021). The presence of sciarid flies and floral mites has yet to be reported as visitors in *Salacca.*

The curculionid beetles have chewing mouthparts and are known to chew on floral parts during their visits, in some of the beetle-pollinated palms have been recorded to have specialised floral parts that allow the beetles to forage without damaging or overconsuming the pollen during visits (Uhl & Moore 1977, Faegri & van der Pijl 1979). This behaviour was observed in *S. vermicularis,* as the fleshy petals provide an additional food source for the visiting beetles in preparation for mating. Apart from a food source in the form of fleshy petals, pollen and stigmatic fluid, the inflorescence of *S. vermicularis* also serves as a form of shelter for the beetles to complete their life cycle by serving as a hatchery for the laid eggs which has also been previously observed in other cantharophilous palms (Barfod et al. 2011).

Although the staminate flowers of *S. vermicularis* were successful in attracting stingless bees, curiously they were not observed to visit the pistillate flowers during the duration of this study. The contrasting colour of the inflorescence against the darker background coupled with the sweet scent should be ideal for attracting stingless bees as potential pollinators (Kidyoo & McKey 2012), however, perhaps something is still missing in the pistillate flowers as stingless bees are considered generalist pollinators for this family and maybe poor pollinators (Barfod et al. 2011). There have been several attempts to search for a relationship between floral character and phenology with associated pollinators in palms. According to Dransfield et al. (2008), beetle pollination is generally associated with protogyny and anthesis in the whole inflorescence occurring over a relatively short period and with the inflorescence usually rather condensed or bearing crowded flowers. By contrast, bee pollination seems to be associated more with protandry, anthesis over an extended period, and with the inflorescence laxly branched, or with the flowers individually rather distant. The phenologies in the preceding statement do bear some resemblance to *S. vermicularis* in the sense that both the staminate and pistillate flowers are indeed crowded on the rachillae, but the flowering period begins earlier in staminate flowers and flowers marginally longer than the pistillate flowers. Henderson (2002) came to a similar conclusion that beetle-pollinated inflorescences tend to have condensed, unisexual flowers and enclosed in bracts at anthesis, while bees, flies and wasps-pollinated inflorescences have elongated, often bisexual flowers and not enclosed in bracts at anthesis.

The inflorescences of *S. vermicularis* can be rather showy with the large number of flowers within a rachilla, contrasting scarlet red petals against the dark brown colour of the petiolar base and the sweet floral scent. While this species does not produce any nectar, the stigmatic fluid is likely to serve as a form of floral attractant similar to nectar. The relationship between the floral attractants and rewards against the visitor assemblage of *S. vermicularis* suggests a degree of specificity towards cantharophily but also attracts a generalist assemblage of visitors with varying potential as pollinators. It is important to consider that the visitor assemblage may be dynamic and change due to external factors. Barfod et al. (2011) noted that certain groups such as the bees are opportunists while certain weevils are highly specialised and that it has also been shown that the composition of insect visitors varies through space and time. However, the consequence of these changes may be challenging to detect as it requires long periods of observation and data collection

Sex ratio in *S. vermicularis*

Flowering occurs year-round in *S. vermicularis* where ideally, there should be staminate and pistillate flowers available at all times. However, pistillate plants bloom less frequently compared to staminate individuals. It is worth noting that the sample size is small (ten staminate plants and six pistillate plants) owing to the difficulty in encountering large flowering populations. In the case of *S. vermicularis*, the slight male-biased scenario ensures a consistent supply of pollen. Staminate plants frequently flower, which likely allows visitors to consistently visit staminate plants, carrying pollen regardless of whether they visit pistillate plants of the same species. This, in turn, increases the likelihood of depositing pollen onto the receptive stigmas of pistillate flowers when they are available. As floral reward and fruit production can be reward intensive, there is a greater female bias in species with abiotic pollination and seed dispersal, whereas male-biased sex ratios were associated with biotic pollen and seed dispersal (Sinclair et al. 2011, Field et al. 2013). This is consistent with the reproductive strategy of *S. vermicularis* being slightly male-biased, biotic pollen dispersal, and relying on animals for seed dispersal. In a study across 47 species of angiosperms, it was found that 46% of the species are male-biased (Barrett et al. 2010). Barrett et al. (2010) also pointed to the earlier onset of male flowering, higher frequency of flowering in males, and higher gender-specific mortality in females as contributing factors to male bias.

Apomixis in *Salacca*

Salacca vermicularis does not undergo apomixis, however, apomixis does occur in *Salacca* albeit rare, as in the rest of the Arecaceae (Hojsgaard et al. 2014). One example of apomictic behaviour in *Salacca* is found in *S. zalacca* (Hutauruk 1999). Among the Calamoids, Bøgh (1996) reported that *Calamus longisetus, C. peregrinus* and *C. rudentum* are not capable of apomixis while among the rest of the family (i.e. *Attalea funifera* Mart. ex Spreng. and *Chamaedorea* Wild. *Howea* Becc.), showed little to no fruit set in breeding mechanism experiments for apomixis tests (Otero-Arnaiz & Oyama 2001, Voeks 2002, Savolainen et al. 2006, Rios et al. 2014).

Seed dispersal and predation

A great number of palms are adapted for animal dispersal; for example, most members have fleshy mesocarp or a well-developed sarcotesta surrounding the seed and brightly coloured epicarps that are attractive to vertebrates (Dransfield et al. 2008). The varying height of fruit bunches in *S. vermicularis* allows a wider range of animal visitors to have ease of access to the fruits. This feature becomes evident when looking at the three species of fruit visitors of different heights feeding on different fruit bunches of varying heights with ease. Studies on the exact feeding behaviours of *Tragulus* sp. and *Hystrix* sp. in the wild are still limited to determine the efficacy of their roles as seed dispersers in Arecaceae. However, both species are known to select similar habitats as the occurrence of *S. vermicularis* and are known to feed on forest fruits (Matsubayashi & Sukor 2005, Taher et al. 2018, Farida et al. 2019, Lemos de Figueiredo et al. 2021). Evidence of scatter-hoarding in *Lariscus insignis* on fruits of *Elais guineesis* observed by Yasuda et al. (2000)

suggests it could be an effective seed disperser. Yasuda et al. (2000) reported that *L. insignis* may carry their food cache up to 32 m from the food source with only c. 19% eaten making this species the most likely to be an effective seed disperser among the three recorded. The scatter-hoarding behaviour similar of *L. insignis* likely applies to the *Hystrix sp.* visitors of *S. vermiclaris.*

CONCLUSIONS

The floral characters of *S. vermicularis* suggest a primarily outbreeding cantharophilous species intrinsically tied to the life cycle of curculionid beetles, a relationship observed in many species within the family which potentially places this species in a larger plant-pollinator interconnecting framework. Additionally, S. *vermicularis* could potentially be considered as a candidate to be planted in areas of conservation for frugivorous animals as it may provide a steady supply of food sources for members of *Tragulus, Hystrix,* and possibly *Muntiacus.*

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SUPPLEMENTARY

Appendix 1 Number of plants observed, number of inflorescences observed and observational period for each species on flowering phenology

Specimens observed		Total inflorescences observed	Rachillae observed	Observational period
♂	3	3	12	13/5/21-30/6/21
♀	2	2	4	8/3/22 – 30/5/22

Appendix 2 Pollination experiments conducted on *S. vermicularis*

Voucher Code	Unbagged		Bagged	
	Inflor. code	Duration	Inflor. code	Duration
SLCA004F	CT007	15/3/22 - 16/4/22	AP007	30/5/22 - 7/7/22
SLCA005F	CT008	19/3/22 - 20/4/22	AP008	2/6/22 - 7/7/22
SLCA007F	CT010	22/3/22 - 23/4/22	AP010	20/6/22 - 25/7/22