The Reproductive Phenology and Pollination Biology of Four Calamus (Arecaceae) Species in Thailand

ANDERS BØGH

Department of Systematic Botany, Institute of Biological Sciences, University of Aarhus, Nordlandsvej 68, DK-8240 Risskov, Denmark

ABSTRACT

The phenology and the pollination biology of *Calamus longisetus, C. peregrinus, C. rudentum,* and *C.* sp. were investigated in southern Thailand. These species are dioecious. The pistillate inflorescences bear dyads each comprising a pistillate flower and a sterile staminate flower. The latter closely resemble functional staminate flowers. Staminate plants flower continuously for several months, whereas pistillate plants have much shorter flowering periods. Examination of the behavior and the pollen loads of captured insect floral visitors strongly suggests that the most important pollinating agents are *Trigona* bees. Wind pollination and apomixis are apparently not important. The pollinators appear to be attracted by scent, nectar, and pollen. The sterile staminate flowers of pistillate inflorescences probably attract pollinators by mimicking functional staminate flowers, as well as by producing nectar. Although the four species presented their flowers differently, there were no apparent differences with regard to their pollinating faunas.

Since Henderson's (1986) review of the literature on palm pollination, a substantial number of new case studies have been published. These studies have added much new information in many groups (e.g., Anderson et al. 1988, Borchsenius 1993, Búrques et al. 1987, Ervik 1993, Listabarth 1992, Olesen and Balslev 1990, Scariot et al. 1991, Zona 1987). The genus *Calamus* (Calamoideae) with about 370 species is the largest genus in the palm family (Uhl and Dransfield 1987). Nevertheless the only published information about pollination biology in *Calamus* consists of a few notes scattered in the literature (e.g., Dransfield 1979, Kiew and Muid 1989). This is surprising considering the economic importance of the genus. The scandent stems extracted from a range of *Calamus* species constitute the raw material for the production of rattan furniture. The international rattan trade has an estimated value of almost $3 billion annually (DeBeer and McDermott 1989).

This paper describes the phenology and the pollination biology of four sympatric species of *Calamus* in southern Thailand: *C. longisetus* Griff., *C. peregrinus* Furt., *C. rudentum* Lour., and *C.* sp. (nov. sp. ined.).[1]

Study Site

The field work was conducted in the Khao Chong National Park approximately 20 km east of Trang in southern Thailand. The *Calamus* populations studied were found at an altitude of 150–200 m, 2–4 km east of the national park headquarters (7°33.5'N; 99°46.6'E). The area is hilly and covered by mixed evergreen forest with many emergent Dipterocarps. The four species studied were the most common *Calamus* species in the area. At least four additional species occurred, but they were much less abundant than the species studied: *C. blumei* Becc., *C. javensis* Bl., *C. oxleyanus* Teysm. et Binn., *C. scipionum* Lour.

Meteorological data, recorded in 1985, 1987, 1989 (in part), 1990, 1991, 1992 and 1993, show a mean annual precipitation of 2,427 mm and temperatures ranging from 16.8 to 36.9° C with an overall average of 27.4° C. The rainfall varies from year to year but it is always somewhat seasonal with a relatively dry period in January and February and a wet season in May through December.

Methods

Observations were made from June 1993 through April 1994 in connection with a general

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[1] This taxon has often been misidentified as *C. bousigonii* Becc. It will be described as a new species by Dr. John Dransfield, Royal Botanic Gardens, Kew.
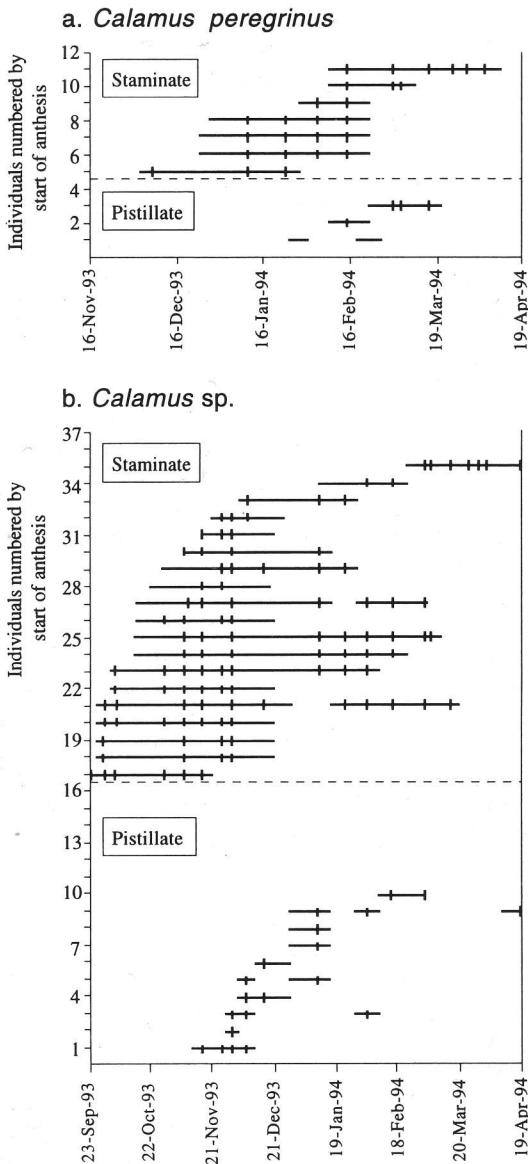
1. Flowering periods of *Calamus* individuals. a: *C. peregrinus*. b: *C.* sp. The horizontal lines show the flowering periods. Where the exact date of a change in phenological stage is not known, the horizontal lines begin or end half way through the period in which the change took place. Vertical marks indicate dates when flowering was actually observed. Note the different time scales.

study of the demography of climbing species of Calamoid palms.

Descriptions of morphology and habit of the *Calamus* species are based on personal observations in southern Thailand and the following

voucher specimens (collection numbers are given in parentheses): *C. longisetus* (*A. Bøgh 45179, A. Bøgh 45180*), *C. peregrinus* (*A. Bøgh 45183*), *C. rudentum* (*A. Bøgh 45213*), *C.* sp. (*A. Bøgh 45177*). These collections are deposited at AAU, BKF, K, and PSU.

Within a one hectare study plot the phenological stages (i.e., not flowering, early bud, bud, flowering, flowering over) of all sexually mature individuals of *C.* sp. were recorded at intervals over a period of 7 months (Fig. 1a). Individuals were considered sexually mature when their stems were more than 1 m long, or when they had flowered before obtaining that length. Forty-three individuals matched these criteria. The gender of the non-flowering, mature individuals was determined by inspecting old inflorescences.

Twelve individuals of *C. peregrinus* with stem lengths of at least 4 m were kept under observation in a similar way for the 5 months duration of their flowering season (Fig. 1b).

The phenology of *C. longisetus* and *C. rudentum* was observed during the general field work.

In all four species a number (Table 2) of inflorescences were examined more closely. During anthesis these inflorescences were observed for 10–20 minutes, every second or third hour. These observations were made so that inflorescences of both sexes in all species were followed through at least a full day and night. The sequence of flower opening was studied by marking individual rachillae. The total numbers of flowers per inflorescence were counted, and rachillae of both sexes were collected and fixed in Navashin and/or alcohol for inspection in the laboratory. The glucose content of exudates from the flowers was detected by diabetics test strips ("Ketodiabur-test").

Detailed inspection of the inflorescences implied noting the presence and the behavior of visiting insects and the catch of specimens for identification and examination of pollen loads. The inflorescenes of *C.* sp. were observed from the ground. In the other three species the inflorescences were observed from a ladder or by climbing adjacent trees. After scrutiny under a dissection microscope the captured insect specimens were rinsed for pollen. The resulting suspensions were transferred to microscope slides and checked for presence and/or purity of pollen loads. Some specimens were examined with a scanning electron microscope.

A number of rachillae of two pistillate inflorescences of *C.* sp. and three of *C. rudentum* were

Table 1. Some distinctive characters of the four species studied.

Character	C. longisetus	C. peregrinus	C. rudentum	C. sp.
Habit	clustering	solitary	clustering	solitary
Max. stem length (m)	50	60	100	10
Vertical height (m)	15	10–15	15	5
Inflor. length (m)*	12	9	14	1
Part. inflor. length (cm)	100	50	200	15
Color of tepals	yellowish green	purplish in ♀	yellowish green	green
Diam. of pollen grains (μ)	ca. 27	32–33	26–29	40–50
No. dyads per ♀ inflor.	800	1,000	108–2,622	50–100
No. flowers per ♂ inflor.	5,000	12,000	50,000	500–1,200

* These measures include the terminal flagella.

bagged during anthesis using a nylon net with a mesh size of 0.5 mm. The bags were removed after anthesis and several months later the fruit set was registered. To eliminate any possible effect of inherent variation in fruit set, a different part of each inflorescence was bagged.

A strip of transparent adhesive tape was suspended for approximately 24 hours near a pistillate inflorescence of each of the species, *C. sp.*, *C. longisetus*, and *C. rudentum*. At least 3 cm² of each strip was inspected under microscope to reveal windborne pollen deposited on it.

Results

Description of the Calamus species. The genus *Calamus* belongs to the subtribe Calaminae of the palm subfamily Calamoideae. It is distributed in Southeast Asia, where it is a conspicuous element in most forests. A single species occurs in Africa. The majority of *Calamus* species are climbers. Some have a solitary unbranched stem whereas others are clustered. All species are dioecious and pleonanthic with axillary inflorescences (Uhl and Dransfield 1987). The inflorescences of the species studied here have up to six first-order branches

(partial inflorescences) distributed along the main axis, which terminates in a long whiplike climbing organ armed with hooklike spines (flagellum). The vertical position of the inflorescences depends on the height of the flowering stem and on where the flagellum is anchored. An individual stem produces up to 4 inflorescences in a flowering season. The rachillae of pistillate inflorescences bear flowers in dyads which consist of a pistillate flower and a sterile staminate flower. In the staminate inflorescences the flowers are solitary and distichously arranged along the rachillae. During anthesis the three stigmatic lobes in the pistillate flowers gradually bend, whereby the receptive surfaces become exposed. The staminate flowers have six widely exposed anthers. In the species studied the pollen grains are spherical, clavate to reticulate, and moderately sticky. The sterile staminate flowers in pistillate inflorescences are similar to the functional staminate flowers, but have empty anthers.

Calamus longisetus (Fig. 2a) is a large clustering rattan. It is common in gaps in primary forest, but it also occurs in disturbed habitats along roadsides and in secondary forest. The stems which may reach 50 m in length often climb to more than 15 m above the ground. The inflorescences may reach a length of 12 m including the terminal

Table 2. Numbers of inflorescences on which detailed observations were made. The phenology is described in the text, the captured insect taxa are listed in Table 3, and the number of flowers or dyads per inflorescence are given in Table 1.

Type of Observation	C. longisetus ♀	C. longisetus ♂	C. peregrinus ♀	C. peregrinus ♂	C. rudentum ♀	C. rudentum ♂	C. sp. ♀	C. sp. ♂
Phenology during anthesis, and insect visitors	1	1	1	1	2	1	4	3
Total number of dyads (♀) or flowers (♂) pr. inflor.	1	estimated	1	estimated	4	estimated	6	2
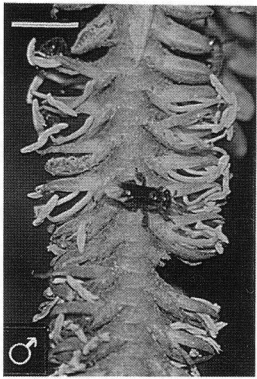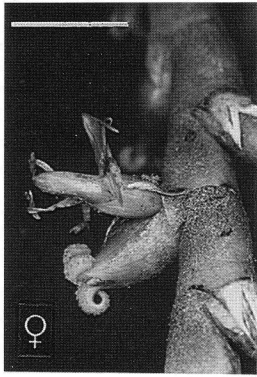
flagellum. The up to 1 m long partial inflorescences which are lax and pendulous are evenly distributed along the basal three-quarters of the rachis. Inflorescences that are not attached to the surrounding vegetation by the terminal flagellum may bear flowers from ground level to the height of the tallest stems. Each pistillate inflorescence typically bears 800 rather large dyads and staminate inflorescences bear 5,000 flowers. In both sexes the tepals are yellowish green. The pollen grains are ca. 27 μ in diameter. In 1993–94, the flowering season peaked in December and January.

Calamus peregrinus (Fig. 2b) is a large solitary rattan that grows on slopes in undisturbed rain forest, where it prefers small canopy gaps. The stems climb to a vertical height of 10 to 15 m, and may attain a length of up to 60 m. The inflorescences are up to 9 m long. The flowers are densely clustered on the stiff partial inflorescences which are crowded at the base of the rachis. Thus, the vertical position of the flowers depends on the position of the stem apex. The tepals are purplish in pistillate flowers. On staminate flowers they are green. One-thousand dyads and 12,000 flowers are typical for pistillate and staminate inflorescences, respectively. The pollen grains are 32–33 μ in diameter. During anthesis the staminate inflorescences present hundreds or thousands of flowers daily. Staminate individuals flowered for up to two and a half months, whereas the anthesis of the pistillate plants only lasted for two to four weeks. The flowering season of staminate plants lasted from late November to mid April. Pistillate anthesis began in late January. The season peaked in the second half of February for both sexes (Fig. 1a). The study plot contained 4 mature pistillate individuals and 8 staminate individuals. One individual of each sex did not flower in 1993–94.

Calamus rudentum (Fig. 3a) is a large clustering rattan that grows in primary rain forest. The climbing stems are up to 100 m long and climb to about 15 m above the ground. The inflorescences are up to 14 m long. The partial inflorescences are regularly distributed along the basal three-quarters of the rachis. They are lax, pendulous, and up to 2 m long. Pistillate inflorescences have between 108 and 2,622 dyads. Large staminate inflorescences may have 100,000 flowers,

but half this number is probably more typical. In both sexes the tepals are dull yellowish green. As in *C. longisetus* the flowers may be borne at all vertical heights. The pollen grains are smaller than in the other species studied (26–29 μ in diameter). The flowering of a pistillate inflorescence lasts a few days. Staminate inflorescences may open up to one-third of the flowers in one day, but a few hundred is more common. When the study site was visited for the first time in late June 1993, a few individuals of both sexes were already flowering. The flowering season peaked in July and it was over by the end of August.

Calamus sp. (Fig. 3b) is a small solitary rattan which grows in the understory of primary rain forest. Its stems reach a maximum length of about 10 m, but it rarely climbs to more than 5 m above the ground. The inflorescences are up to 1 m long. The short and stiff partial inflorescences are concentrated in the proximal half of the rachis. The flowers are small, relative to the other species studied, and they are closely aggregated on the partial inflorescences. Thus, the vertical position of the flowers is determined by the position of the stem apex. The tepals have an inconspicuous pale green color. The pollen grains are larger than in the other species studied (40–50 μ in diameter). Pistillate inflorescences typically bear between 50 and 100 dyads, whereas staminate inflorescences bear between 500 and 1,200 flowers. In pistillate plants short flowering periods often alternate with longer periods without flowering. In 1993, the pistillate plants began flowering in mid November. The flowering peaked in early January, when 25% of the pistillate plants were at anthesis (Fig. 1b). Staminate inflorescences present less than 50 flowers daily. Staminate individuals with several inflorescences may flower continuously for up to five months, occasionally with short lapses without open flowers in between anthesis of two inflorescences. The first staminate plants began flowering in mid September, and their number increased until a maximum of 76% of the individuals were in anthesis from mid November to mid December. Thereafter flowering decreased and by early April only a single individual remained in flower. The study plot contained 16 mature pistillate individuals and 20 staminate individuals (Fig. 1b). Ten of the 16

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2. Habits of the *Calamus* species studied with insets of pistillate and staminate flowers. a: *C. longisetus*. Scale bar on insets 10 mm. Note *Trigona* bee on staminate rachilla. b: *C. peregrinus*. Scale bar on insets 5 mm.
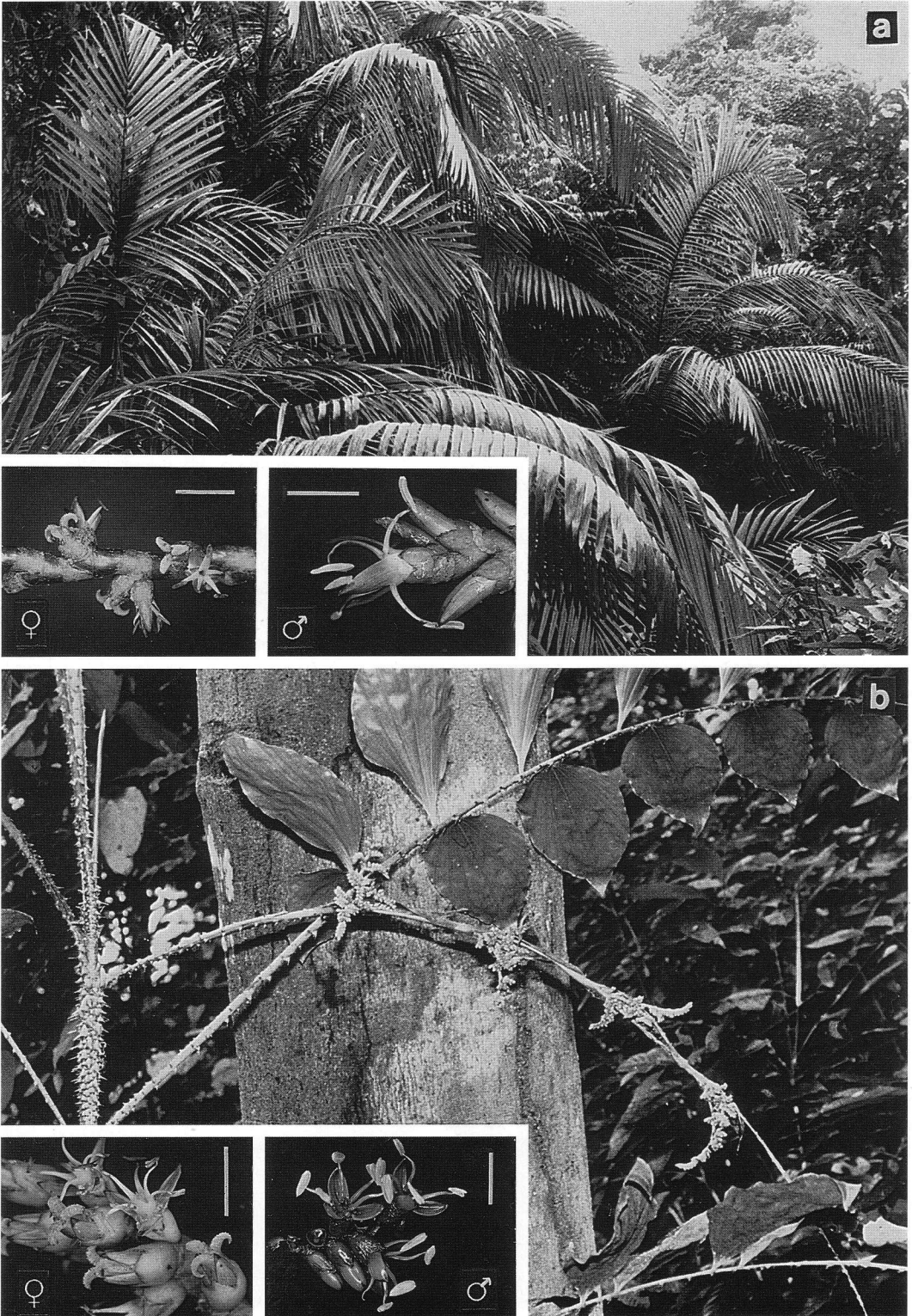
pistillate individuals flowered in 1993–94 whereas all but two of the staminate individuals flowered.

Some of the distinctive characters described above are summarized in Table 1.

Phenology. The phenological development around the time of anthesis follows largely the same pattern in the four species studied. Thus, the following description applies to all four species. The first indication of flowering is an inflation of the peduncular bracts which sheath the basal part of the rachis. Until then the inflorescences closely resemble the flagella. One or two months later the bracts split and the flower bearing parts are exposed. The first flowers open a month after exposure.

On staminate inflorescences the distal flowers on the proximal partial inflorescences generally open first. No sequence of flowering is evident as anthesis progresses. The anthesis of the individual flowers begins in the period from 10:00 PM to about 6:30 AM, but a few additional flowers may open until about 10:00 AM. When a staminate flower opens, it exudes droplets of nectar (glucose containing liquid) at the base. At dawn, the inflorescences emit a strong sweet, gardenia-like scent. This scent is conspicuous throughout the day, but it diminishes greatly at dusk. By noon, most anthers are empty, and the flowers are shed before sunset at 6:30 PM.

Pistillate anthesis is initiated by a recurving of the stigmatic lobes. After 48 hours, the tips of the lobes point towards the base of the flowers (Figs. 2 and 3, insets). At this stage, the adjacent sterile staminate flower opens and exudes nectar. This almost invariably occurs between sunset and sunrise, peaking around midnight. Apparently the pistillate flowers do not produce nectar. The stigmatic surfaces remain white and appear receptive until about noon. During the afternoon they gradually turn brown. Pistillate inflorescences produce a strong scent similar to that of staminate inflorescences. As in staminate inflorescences the scent is very faint during the night, and becomes intense again the following day. On a single pistillate rachilla all the flowering usually occurs within 48 hours, and the anthesis of a whole inflorescence rarely lasts more than a week.

The individual species differ from the general description given above in some aspects. *C. longisetus*: The anthesis of a whole pistillate inflorescence is simultaneous, and the scent production begins already on the day prior to the opening of the sterile staminate flowers. In both sexes the scent produced by this species is stronger than in the other three species studied. *C. peregrinus*: The stigmas are receptive somewhat longer than in the other species, and the sterile staminate flowers remain attached until between dusk and midnight. *C. rudentum*: The filaments are relatively long, and the antesepalous stamens bend so far back that they almost contact the rachilla (Fig. 3f). The scent produced by this species is similar but much less conspicuous than in *C. longisetus* and *C. peregrinus*. *C.* sp.: This species follows the general description except for the fact that neither sex produced a detectable scent.

Pollination. In all four *Calamus* species studied, the inflorescences of both sexes were visited by worker ants (Hymenoptera, Formicidae) during the night. At night, immature crickets (Orthoptera, Gryllidae), cockroaches (Dictyoptera, Blattaria), and a few spiders (Araneida) were also observed, but none of these were abundant. At sunrise the insect activity increased markedly as bees (Hymenoptera, *Trigona*, and *Apis*), wasps (Hymenoptera, Vespidae) and a diverse range of fly species (Diptera) arrived at the inflorescences. These taxa clearly dominated the visiting insect faunas (Table 3). Later in the day, Hymenopterans became rarer, whereas various flies were present until sunset.

Wasps usually paid such short (few seconds) visits that it was impossible to establish what they were doing. Bees usually crawled about on the inflorescence for several minutes before they left. In staminate flowers *Trigona* bees actively collected pollen. On pistillate inflorescences they spent most of their time consuming nectar, but they also tried to collect pollen from the anthers of the sterile staminate flowers. The *Trigona* bees often touched the stigmatic surfaces with their legs and undersides as they moved around. Most of the observed flies were small (0.5 to 2 mm long). They were found everywhere on the inflorescences. Larger

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3. Habits of the *Calamus* species studied with insets of pistillate and staminate flowers. a: *C. rudentum*. Scale bar on insets 5 mm. b: *C.* sp. Scale bar on insets 5 mm.

Table 3. Insect visitors to Calamus *inflorescences.*

	C. longisetus		C. peregrinus		C. rudentum		C. sp.	
	♀	♂	♀	♂	♀	♂	♀	♂
Coleoptera sp.			—					
Diptera								
Calliphoridae sp.						—		
Chloropidae						—		
Drosophilidae sp. 1			—			—	—	
Drosophilidae sp. 2						—		
Drosophilidae sp. 3					—			
Drosophilidae sp. 4						—		
Drosophilidae sp. 5	—			—		—		
Lauxaniidae sp.					—			—
Milichiidae sp.	—		—			—		
Phoridae sp.								—
Platystomatidae sp.			—			—		
Syrphidae sp.								x
Hymenoptera								
Apidae, *Apis* sp. 1						x		
Apidae, *Apis* sp. 2						x		
Braconidae, Agathidinae sp.				x				
Formicidae sp. 1								x
Formicidae sp. 2								—
Formicidae sp. 3								x
Formicidae sp. 4						x		
Pteromalidae sp.			—					
Trigonidae, *Trigona* sp. 1			—		—	x	—	x
Trigonidae, *Trigona* sp. 2							—	
Trigonidae, *Trigona* sp. 3		x				x		
Trigonidae, *Trigona* sp. 4						x		
Trigonidae, *Trigona* sp. 5						x		
Trigonidae, *Trigona* sp. 6						x		
Trigonidae, *Trigona* sp. 7			x			x		
Trigonidae, *Trigona* sp. 8	x	x		x		x		
Trigonidae, *Trigona* sp. 9						x		
Vespidae sp. 1						x		
Vespidae sp. 2			—	—				—
Vespidae sp. 3								—
Vespidae sp. 4			—					
Orthoptera								
Gryllidae sp.								—
Psocoptera sp.						—		

—: Specimen(s) caught.
x: Specimen(s) carrying *Calamus* pollen caught.

flies that sucked nectar from the base of the flowers were seen occasionally. Nocturnal cricket nymphs chewed anthers or stigmas, whereas ants consumed the newly released nectar.

The bees carried more pollen than any of the other insects captured (Table 3). Besides the loads that were kept in the corbiculae, pollen often stuck to the hairs on other parts of the body (Fig. 4). The wasps rarely carried pollen loads. A few grains were found on a single specimen of Vespidae sp.

1. Ants occasionally carry a few pollen grains. Flies were omnipresent, but apart from Syrphidae sp., which was only observed once, none of the 29 examined specimens carried any pollen load.

In all four *Calamus* species staminate inflorescences clearly attracted more insects than pistillate inflorescences. In *C.* sp. the highest observed frequency of visiting insects was one bee or wasp every 10 minutes on pistillate inflorescences, whereas often 20 Hymenopterans were present in
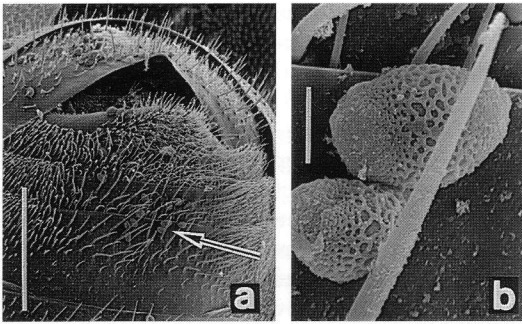
4. A *Trigona* bee caught while it was collecting pollen on a staminate inflorescence of *C. sp.* The same species was also found on pistillate inflorescences. a: The underside of the abdomen with deposited pollen. Arrow indicates the position of the pollen magnified in b. Scale bar 500μ. b: Magnified section showing pollen from *C. sp.* Scale bar 10μ.

staminate inflorescences at a time. In *C. peregrinus* a similar difference between the sexes was observed. In *C. rudentum* the frequency of insect visits to staminate inflorescences depends on the number of flowers in anthesis on a given day. Thus, several hundred insects were constantly swarming around a large inflorescence, which had opened about one-third of the flowers. Pistillate inflorescences were visited by just one bee every 5 minutes. *C. longisetus* seemed aberrant since pistillate inflorescences were visited almost as frequently as staminate inflorescences and since a single species of *Trigona* totally dominated among the visiting insects.

Fruit sets were much lower on those parts of the inflorescences of *C. sp.* and *C. rudentum* that had been bagged during anthesis, compared with the remaining parts of the same inflorescences (Table 4). These results are statistically highly significant except for one *C. rudentum* inflorescence where very few fruits developed even on the unbagged rachillae.

No pollen grains resembling those of the four *Calamus* species were found on the pieces of adhesive tape suspended near pistillate inflorescences.

Discussion and Conclusion

The morphology of *Calamus* inflorescences gives no obvious indication about their pollination mode. The exposed stigmas and anthers are easily accessible to any potential insect visitor and even to the wind. However, the four species studied here suggest an entomophilous pollination syndrome, where bees play the most important role.

When bees (*Apis* and *Trigona*) collect pollen, numerous grains stick to their densely hairy bodies. Several of the *Trigona* species found on staminate inflorescences were also captured on the pistillate inflorescences, where some of them actually carried conspecific pollen grains. On pistillate rachillae the bees are constantly in contact with the stigmas, and thereby can transfer pollen to the receptive surfaces. Thus, bees, especially *Trigona*, are probably important pollinators.

Contrary to bees, wasps are probably not important pollinators. Their behavior renders a transfer of pollen much less likely. The ants, and the majority of the other nocturnal visitors, are incapable of flying. Therefore, it is unlikely that they transfer pollen between plants that are spatially well separated. Dipterans were also common on the inflorescences, and although their activities did bring them into contact with anthers and stigmas, the pollen did not stick to them. A single Syrphid fly did carry a few pollen grains but this family was seen too rarely to be of any importance.

Considering the sticky pollen and the absence of *Calamus* pollen on the suspended tape strips, wind pollination does not seem to occur. Neither does apomixis. A few fruits did set on the bagged rachillae, but the explanation is probably that insects active on the exterior of the bags deposited

Table 4. Results of bagging experiments.

	No. Bagged Flowers	Fruit Set	No. Free Flowers	Fruit Set	χ^2	p
C. rudentum						
inflor. 1	125	0%	164	70%	145.5	≤0.0001
inflor. 2	44	0%	136	7%	3.1	0.08
inflor. 3	45	0%	63	49%	31.1	<0.0001
C. sp.						
inflor. 1	38	5%	54	46%	18.1	≤0.0001
inflor. 2	13	0%	16	94%	25.2	≤0.0001

pollen on stigmas that were in contact with the nylon net.

The conclusion, from the experiments described above, is that the bees are the only important pollinators. A number of indirect indications point to this conclusion as well. Apart from the lack of conspicuously colored tepals (except in *C. peregrinus*) and the fact that dioecious plants per se cannot be protandrous, the observations of morphology and phenology conform very well with Henderson's (1986) description of the bee pollination syndrome in palms. Staminate inflorescences attract insects by emitting scent and by offering pollen and nectar rewards. The anthers, jutting in all directions, deposit pollen on any insect, of a suitable size, that crawls around on the rachillae. Attraction to pistillate inflorescences seems to operate on a combination of scent, nectar rewards, and deceit. The sterile staminate flowers resemble the functional staminate flowers so closely that the bees are tricked into trying to collect pollen from them. The function of these flowers is, therefore, probably to mimic the functional staminate flowers, as well as to produce nectar. When an insect consumes nectar or tries to collect pollen from a sterile staminate flower it will almost inevitably touch the stigma of the adjacent pistillate flower. The importance of the nectar produced by the sterile staminate flowers depends on whether they are the only nectar sources in pistillate inflorescences. The apparent absence of nectar production in the pistillate flowers might be confirmed through anatomical studies. No such studies were performed.

The staminate plants have long and continuous flowering periods. Contrary to this, pistillate flowers are rare in time and numbers. Under these circumstances, the chances are relatively high that a floral visitor will have visited a staminate inflorescence of the same species before it arrives at a pistillate flower. A similar sexual difference in flowering periods has also been observed in connection with bee pollination elsewhere in the palm family (Bullock 1981, Henderson 1985).

In palms that are pollinated by bees and other diurnal insects the flowers often open from dawn to about noon (Henderson 1985, Bullock 1981, Olesen and Balslev 1990, Zona 1987). That the staminate flowers of the *Calamus* species studied open and release nectar well before dawn is puzzling. This exposes them to theft and damage by nocturnal insects. The exact time of stigma receptivity is another point in need of further investigation. It is difficult to understand why the stigmas should be receptive before the opening of the sterile staminate flowers.

So far, this discussion has dealt with features common to the species studied. Noteworthy differences do exist, however (Table 1). *C. rudentum* flowers are borne on widely spaced, long, pendulous partial inflorescences, whereas those of *C. peregrinus* are crowded near the stem apex. *C. longisetus* inflorescences structurally resemble those of *C. rudentum*, whereas those of *C.* sp. are much smaller and usually borne much nearer to the ground than in any of the other species. Equally conspicuous differences exist in, e.g., the size of the individual flowers, the number of staminate flowers presented each day, the size of the pollen grains, and the presence or intensity of scent.

These differences do not have a pronounced effect on the pollinating faunas. They are dominated by *Trigona* species in all cases. The four *Calamus* species are the most common palms in the study area. Therefore, their sequential flowering seasons (*C. rudentum* peaks in July, *C.* sp. in November–December, *C. longisetus* in December–January, *C. peregrinus* in February), may have evolved in response to competition for common pollinators. However, until more is known about the behavior of the pollinators and the spectrum of food sources they utilize, this remains highly speculative. It is possible that the different *Trigona* species prefer different species of *Calamus*, but such preferences are apparently not exclusive. The dominance of a single species of *Trigona* among the floral visitors to *C. longisetus* may reflect the preference of the bees, or it may be the result of the proximity of a nest of that species. At present, no clue can be given to a link between the pollinators and the morphological and phenological variation in *Calamus* flower presentation.

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