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BEETLE POLLINATION OF *PHILODENDRON SOLIMOESENSE* (ARACEAE) IN FRENCH GUIANA

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The pollination of *Philodendron solimoesense* (subgenus *Meconostigma*) was studied in four populations of French Guiana. Flowering is asynchronous within each population during July, and the flowering cycle is a 2-d process. Numerous insects visit *Philodendron* inflorescences, but the main pollinator seems to be *Cyclocephala colasi* (Scarabaeidae, Dynastinae). The pollination process displays aspects typical of beetle pollination: the production of heat and of a strong odor, the presence of a food reward (stigmatic secretion and sterile male flowers), and the presence of a copulation chamber. Flower heat production is important (ca. 11°C above the ambient air) and may help to volatilize the fragrance. Attraction and choice-test experiments showed that *C. colasi* is not likely to depend on chemical information (such as pheromone) to localize conspecifics but may rely instead on stimuli produced by the inflorescences in order to meet mating partners.

Keywords: dynastid, *Cyclocephala*, phenology, heat production, pollinator attraction, reproductive biology.

Introduction

Data on the pollination biology of Araceae, a family of 3300 species, are still very meager (Grayum 1990; Mayo et al. 1997) and are made mostly of observations and collections of insects present in the inflorescences (Williams and Dressler 1976; Ramirez and Gomez 1978; Madison 1979, 1981; Croat 1980; Grayum 1990). Recently, this topic has been properly studied in the field on only a dozen species belonging to the genera *Alocasia* (Shaw and Cantrell 1983), *Amorphophallus* (Sivadasan and Sabu 1989; Beath 1996), *Anchomanes* (Thompson and Rawlins 1986), *Arisaema* (Rust 1980; Bierzychudek 1982), *Colocasia* (Carson and Okada 1982), *Dieffenbachia* (Valerio 1984; Young 1986), *Lysichiton* (Pellmyr and Patt 1986), *Peltandra* (Patt et al. 1995), *Philodendron*, and *Symplocarpus* (Grimaldi and Jaenike 1983; Camazine and Niklas 1984). Araceae are mostly pollinated by insects (but see Camazine and Niklas 1984), principally beetles and flies but also bees and thrips (Williams and Dressler 1976; Rust 1980). It seems that there is a strong family-wide correlation between floral features (inflorescence structure, rewards, attractants) and the type of pollinator (e.g., coleoptera, diptera). For example, the structure of the pollen is linked with the corresponding pollinator: psilate pollen with beetle pollination and spinose pollen with fly pollination, other pollens being less specific (Grayum 1986).

Although araceous inflorescences can be visited by several types of insects, only a few—and perhaps only one—are the real pollinators for each species (Bogner 1981; Shaw and Cantrell 1983; Valerio 1984; Pellmyr and Patt 1986; Young 1986; Patt et al. 1995). When there are several insect species, efficiency in achieving pollination differs between pollinators (Young 1988*a*).

One well-known aspect of araceous pollination is the process of heating (Faegri and van der Pijl 1979; Mayo et al. 1997). In a large number of species, e.g., *Amorphophallus*, *Dieffenbachia*, *Peltandra*, *Philodendron*, and *Symplocarpus*, the spadix produces an intense heat (30°–45°C) during at least the first night, when pollinators are attracted to the inflorescences. And globally, an association has been observed between the production of heat and the emission of the fragrance by the spadix (Meeuse and Raskin 1988).

The pollination biology of *Philodendron*, the second largest genus of Araceae (with 700 species), is only known from one field study (Gottsberger and Amaral 1984) and a few observations (Madison 1979; Young 1987; Grayum 1996; Croat 1997), which show that dynastine scarab beetles of the genera *Cyclocephala* and *Erioscelis* exclusively pollinate this genus.

In French Guiana, two species of *Philodendron* of the subgenus *Meconostigma* are present, *Philodendron solimoesense* and *Philodendron goeldii*. We provide data and observations on the pollination of *P. solimoesense* in four natural populations, with an emphasis on inflorescence changes and pollinator behaviors during pollination. First, we compared the pollination of *P. solimoesense* with published studies on *Philodendron bipinnatifidum* and *Philodendron selloum*, paying particular attention to inflorescence heating. Second, we established the diversity of insect visitors and studied the abundance of pollinators. Finally, experiments were conducted in order to assess whether *Cyclocephala* of different gender, while pollinating *P. solimoesense*, use chemical communication to find each other, as it is the case for *Cyclocephala lurida* (Haynes and Potter 1985) and many other beetles.

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Material and Methods

Philodendron solimoesense is a hemiepiphyte of terra firma or flooded (riverine) forests that can also be terrestrial on sandy soils. Its dark green leaves are sagittate, with a blade that reaches up to 1 m long and 50 cm wide and with inflorescences that develop from the base of each petiole. The large inflorescences (open spadices 22–32 cm in length, average of 29 cm) develop one after the other during the reproductive phase. The spathe is green externally and white internally, and its surface is smooth. The pistillate flowers occupy the lower portion of the spadix and take up ca. 20% of the total length of the inflorescence, whereas the male flowers are located on the upper portion and occupy ca. 30% of the total length. In the median portion of the spadix there is a prominent intermediate zone (ca. 50% of the total length of the inflorescence) consisting of sterile male flowers (see also Mayo 1991).

Our study, conducted in July and December 1998, followed preliminary observations that we completed in 1997. Four terrestrial populations of *P. solimoesense* were studied along the National Road number 1 of French Guiana. They originated from hemiepiphytic individuals that were present on trees that were cut down during the construction of the road in 1989 and that have been successfully reproducing since then. A summary description of each population is given in table 1.

All individuals in the four populations were marked and mapped ($n = 197$; see also table 1). Every 2 d between July 6 and 21, each population was checked, open inflorescences were noted, and their sexual stage was determined. During this period, 68 inflorescences flowered, and their flowering process was observed daily at different times.

An infrared contact thermometer, precise to 0.5°, was used to record the ambient and inflorescence temperature variations during the evening of July 14 between 1700 and 2130 hours on six *P. solimoesense*; we took a measurement every 15 min. In order to obtain the temperature of the inflorescence, the thermometer was inserted ca. 5 cm into the spathe, against the middle of the sterile male zone. The temperature of closed nonpollinated inflorescences were measured on the same individuals (control) by making a small hole at the level of the sterile male zone (this opening was plugged with the circular piece removed from the spathe between each measurement). Self-pollination within a single inflorescence was tested by placing four inflorescences from different individuals under organdy bags from the period before opening to the period of senescence.

During the daily study of the sequential flowering processes, we noted the number and species of insect visitors to the 68 inflorescences that opened during the experimental period, and we also noted the hour of observation and took voucher specimens for identification. *Cyclocephala* beetles were counted and sexed in 40 opened inflorescences, whereas we measured the length of the different spadix zones (female, male sterile, and male) of 32 of them. In order to estimate the intensity of damage done to the spathe by *Cyclocephala*, the number of rows damaged by the beetles and the total number of rows of sterile male flowers were counted. The number of male and female beetles per inflorescence was compared by a paired *t*-test using Statistix 4.1 (1994). Linear regressions between floral traits (length of the different spadix zones and proportion of sterile male flowers eaten) and pollinator abundance were performed using Statistix 4.1 (1994).

An attraction experiment of the pollinator was conducted in the field during three successive evenings when *Cyclocephala* beetles were active. In each case, we closed 20 males in one organdy bag and 20 females in another in order to allow the diffusion of chemical communication. In the first experiment (two consecutive days), the two bags were attached at a height of 1.60 m on trunks symmetrically placed 5 m away from an attracting inflorescence (emitting odor). Six and three inflorescences were receptive in the population on the first and the second day, respectively. One hour following sunset, we noted the beetles arriving on each bag and on the control inflorescences.

Two series of choice tests were conducted in closed-dark boxes in early evening when *Cyclocephala* were active. In the first series, we used spathes (without spadix) as experimental "shelters" placed in each corner of four carton boxes (70 × 40 × 10 cm). Two of them (in opposite corners) contained two beetles of the same sex (each); the other two were kept empty. Five new beetles of the opposite sex were deposited in the center of the boxes for each replicate. This experiment was repeated 10 times for each sex, with each box and spathe being used only one time. The boxes were tightly closed for 20 min, then we noted the position of each beetle. In the second series of experiments, which was repeated six times for each sex, we used slices of spathe (4 cm thick) as "shelters." Three shelters were placed in plastic boxes (20 × 20 × 5 cm), two of which contained one beetle, while three beetles of the opposite sex were placed in the middle of the boxes. For each beetle in both experiments, three situations were noted: the beetle was found with a sexual partner (mostly in a shelter)

Table 1

Summary Description of Each Study Population

Population	Kilometric point[a]	Population size (number of individuals)	Number of flowering individuals	Number of open inflorescences (July 6–21, 1998)	Mean number of open inflorescences per day (mean ± standard deviation)
1	90.5	36	20	13	0.8 ± 0.9
2	91.75	65	28	9	0.6 ± 0.7
3	94.5	44	17	11	0.7 ± 1
4	96.5	52	39	35	2.2 ± 1.7

[a] Distance, in kilometers, along National Road number 1.

and was considered to be "paired"; the beetle was found in or at the base of a shelter without a sexual partner or in the corner of the boxes and was considered to be "hidden"; or the beetle was not in one of the two previous situations and was considered to be "uninterested." The number of beetles in each situation was compared using a General Linear Model (GLIM software; Royal Statistical Society 1986) with a Poisson error (count data) that tested two effects (situation and beetle sex) and their interaction. For other comparisons, we used the Fisher exact test from StatXact 2.05 (1992).

Results

The number of opened inflorescences per plant individual and per day varied among populations but remained low (1.06 on average; table 1). As a result, 2–7 d separated the opening of two inflorescences on the same individual, thus preventing self-pollination between inflorescences.

The flowering process was a very characteristic 2-d event that did not vary between individuals. Sometimes the spathes became slightly loosened during the evening before opening. The flowering phenology differed between the four populations, with population 4 being characterized by a higher production of inflorescences (three to four times more than the other populations) and a continuous flowering during the census period (fig. 1; table 1). In the other populations, several gaps in the flowering pattern appeared and lasted from 1–5 d (fig. 1).

Tyloderma sp., a curculionid beetle, was observed on a dozen occasions, mainly on closed inflorescences (table 2). The adults pierced both large holes in the outer surface of the spathe in order to feed and small holes in which to lay eggs. The larvae completed their development in the inflorescence peduncle where they pupated. Dozens of easily visible black spots from resin spurs indicated which spathes had been attacked. Various ants recorded on all individuals patrolled the outer surface of the opened spathes or the upper part of the spadix, but these ants avoided entering into the spathes.

Among insects visiting the open inflorescences (table 2), small staphylinid beetles (<10 mm long) and orange mirids (Hemiptera) were recorded from the first afternoon of observation. Staphylinids (up to 150 individuals per inflorescence), perhaps feeding on sterile male flowers, were situated in the upper part of the spadix. Staphylinids and mirids apparently had no pollen (binocular observations). Also, groups of 20–30 larvae were found in closed and pollinated inflorescences, which permitted us to speculate that they may exit when the inflorescence opens at maturity. At dusk, up to 10 stingless bees (*Trigona* spp.) with no pollen were observed to fly onto one inflorescence, but none of these bees crawled down the spathe to the female flowers. Very active until nightfall (1845 hours), these bees foraged on the upper part of the spadix but were unable to reach the sheltered pollen. We twice observed large, reddish reduvidae preying on miridae and trying to catch *Trigona*.

Numerous staphylinids and mirids were therefore present when dynastine beetles of the genus *Cyclocephala* arrived at the inflorescences. Of all the insects recorded inside the inflorescences, *Cyclocephala* were the only ones that transported pollen on their bodies (binocular observations), and so they

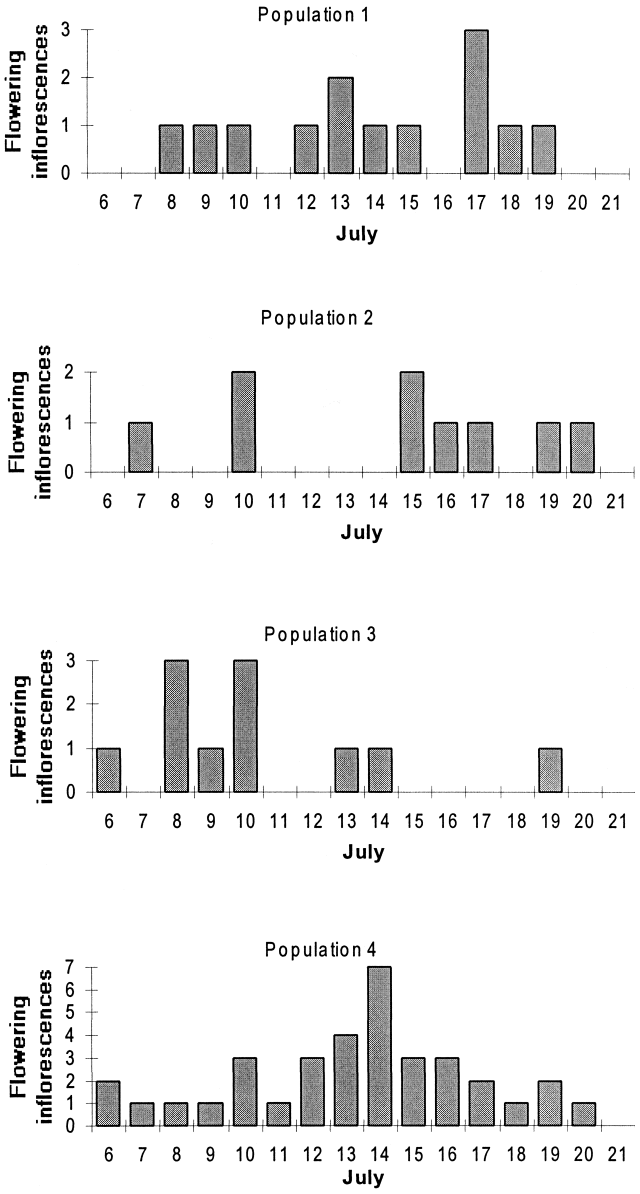

Fig. 1 Number of inflorescences at pollination stage in each population per day.

were considered to be the pollinators. We recorded three *Cyclocephala* species in the inflorescences: *Cyclocephala colasi*, the most abundant (with 899 individuals out of the 909 *Cyclocephala* recorded); *Cyclocephala emarginata* (six individuals); and *Cyclocephala sexunctata* (four individuals). Both latter species, found in only six inflorescences, appeared to be rare visitors of *Philodendron solimoesense*, at least during July, in this geographical zone. All 68 inflorescences that opened during the experimental period were visited by several *C. colasi* (21 ± 12 [SD] beetles per inflorescence; fig. 2). Per inflorescence, the number of male beetles (12.2 ± 6.9) was greater than the number of females (8.9 ± 6.1; $t = -3.67$, df = 39, $P = 7 \times 10^{-4}$). The least square linear regression of the length of the sterile zone on the number of beetles per inflorescence

was significant ($r^2 = 0.15$, $F = 5.15$, df = 1, 29, $P = 0.03$; fig. 3). The least square linear regressions of the length of the female and male zones on the number of beetles per inflorescence were not significant (respectively: $r^2 = 0.001$, $F = 0.04$, df = 1, 29, $P = 0.84$; and $r^2 = 0.0001$, $F = 0.02$, df = 1, 29, $P = 0.96$). In 15 hemiepiphytic *P. solimoesense* (25 m in height), we also found 55 *C. colasi* and four *C. sexpunctata* individuals in three opened inflorescences, which indicates that ground and epiphytic populations reproduce in the same way.

During the second day, mirids, staphylinids, and *Cyclocephala* were still present in the inflorescences. In the evening, 20–40 *Trigona* per inflorescence were attracted to the spadix until nightfall (fig. 4*C*). When inflorescences on the first- and second-day stages of opening developed in close vicinity, *Trigona* avoided the former. Thus, *Trigona* bees seem to be preferentially attracted to inflorescences that are about to release pollen. But they are not able to collect much pollen, as it is massively released in pollen chains at dark, when *Trigona* bees have finished foraging (cf. fig. 4*C* and fig. 4*D*). They collect some kind of mucilage with pollen that is produced by male flowers and the resin present on the inner surface of the spathe, perhaps as it has been observed in *Monstera* and *Clusia* flowers (Ramirez and Gomez 1978).

The spathes opened in the middle of the morning of the first day, revealing the spadix, and were wide open during the afternoon, with an extremely curved white spadix (ca. 45° toward the exterior). At this time, the spathes were internally white, the stigmas were dry, and a slight odor emanated from the inflorescence (fig. 4*A*). In the late afternoon (1800 hours), the spadix began to become hot, producing a strong and unpleasant odor. The stigmas became moist and seemed to be receptive. *Cyclocephala*, covered with pollen, began to arrive on the inflorescence when the spadix produced heat, and an unpleasant odor was emitted from the spathe just before 1900 hours. After landing, they crawled down the spadix and rapidly reached the protected floral chamber around the female flowers (fig. 4*B*). Pollination must have been effected while beetles crawled around on the female flowers. Numerous copulations were observed to take place in the floral chamber.

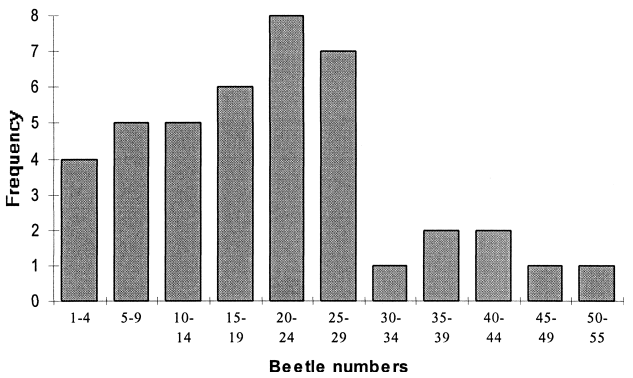

Fig. 2 Frequency distribution of the abundance of beetle visitors (*Cyclocephala colasi*) in 40 inflorescences of *Philodendron solimoesense*.

During the following day, *Cyclocephala* were rather inactive and photophobic, remaining hidden in the protected floral chamber. They fed on the sterile male flowers situated just above the female zone. The least square linear regression of the number of *Cyclocephala* present in the inflorescence on the proportion of rows of sterile male flowers eaten was significant ($r^2 = 0.64$, $F = 48$, df = 1, 27, $P < 1 \times 10^{-5}$; fig. 5). In highly visited inflorescences, 25%–30% of the sterile male flowers were consumed.

In the early afternoon of the second day, the internal upper half of the spathes produced yellow droplets. In the late afternoon, a brownish resin covered the inner surface of the spathes that clung to the cuticle of the pollinators crawling between spathe and spadix (fig. 4*C*). The spadix did not pro-

Table 2

Insect Visitors to Inflorescences of *Philodendron solimoesense*

Insect taxa	Number of observations
Hemiptera:	
Reduvidae	2
Miridae	Not counted: 0–50 per inflorescence
Hymenoptera:	
Apidae:	
Trigona/melipones	Not counted: 4–40 per inflorescence
Formicidae:	
Ants	Not counted: 0–30 per inforescence
Coleoptera:	
Curculionidae:	
Cryptorhynchinae:	
Tyloderma sp.	12
Scarabaeidae:	
Dynastinae:	
Cyclocephala colasi	899
Cyclocephala emarginata	6
Cyclocephala sexpunctata	4
Staphylinidae	795: 0–150 per inflorescence

Note. Insect counts for Reduvidae, Curculionidae, Dynastinae ($n = 40$), and Staphylinidae ($n = 15$). Observations with range for ants, Miridae, and Apidae.

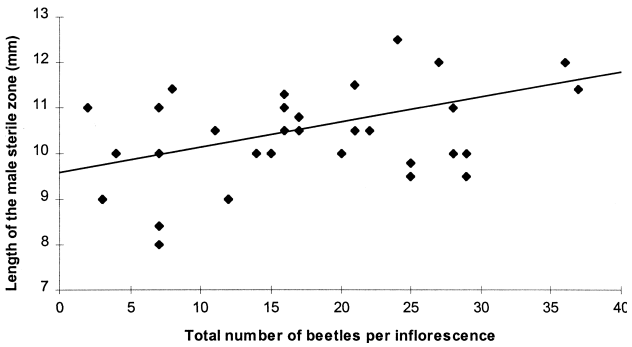

Fig. 3 Relationship between the total number of beetle pollinators (*Cyclocephala colasi*) in an inflorescence of *Philodendron solimoesense* and the length of its intermediate (male sterile) zone ($r^2 = 0.15$, $F = 5.15$, df = 1, 29, $P = 0.03$).

duce any notable heat, but at a close distance the characteristic unpleasant odor remained.

Then, within ca. 60 min, the spathes closed by wrapping around the spadix, from the base to the upper parts (fig. 4*D*). The space available for the pollinators decreased so that they were progressively expelled, obliged to climb out (we once found a dead female crushed at the base of the spadix). At this time, the anthers released massive pollen chains that stuck on the resin-covered cuticle of the *Cyclocephala* while they ate some pollen chains (fig. 4*D*). The *Cyclocephala* reached the upper part of the spathe before complete closure, then flew away to another inflorescence that was producing heat and emitting the unpleasant odor.

On the first day, the temperature of ambient air and all inflorescences was similar until 1730 hours. Then, opened inflorescences began to produce heat, while the temperature of unopened inflorescences decreased with that of the ambient air (remaining ca. 1°C above the ambient air; fig. 6). The temperatures of opened inflorescences peaked for ca. 15 min between 1930 and 2000 hours, reaching 35°–38°C, 11°C above the ambient air temperature (fig. 6). The zones of the spathes in contact with the spadix were burnt and became brown. During this time, the inflorescences emitted an unpleasant odor. The temperatures of the inflorescences decreased slowly. By 2130 hours, 1.5 h after the peak, spadix temperature was 33°C, 9°C above ambient temperature.

The four experimental inflorescences enclosed in organdy bags dried out and fell off without producing any seeds, while all of the 64 others developed (Fisher exact test: $P = 12.2 \times 10^{-7}$). Flowers therefore require a pollinator in order to produce seeds.

Furthermore, we have indirect arguments that indicate that *C. colasi* transported pollen from one patch of *Philodendron* to another, as opened inflorescences in one population sheltered different numbers of *C. colasi* during two consecutive days. For example, between July 9 and 10, 14 *C. colasi* left population 2; reciprocally, 62 *C. colasi* arrived in population 4 in the evening of July 16.

During attraction experiments conducted in the field in the evening, we never recorded *Cyclocephala* flying near or landing on the bags containing the 20 females or 20 males, whereas all six and then the three inflorescences that opened during the first and second days of the experiment attracted 26 and 11 *Cyclocephala*, respectively. Individuals from the organdy bags were not attractive to conspecifics, unlike the result obtained with the odoriferous inflorescences (Fisher exact test: $P = 0.0014$).

During both choice-test experiments conducted in carton boxes in the evening, male and female pollinators behaved similarly. The sex-situation interaction (experiment 1: $\chi^2_2 = 0.9$, $P = 0.64$; and experiment 2: $\chi^2_2 = 0.25$, $P = 0.88$) and the sex effect (experiment 1: $\chi^2_2 = 0.01$, $P = 0.98$; and experiment 2: $\chi^2_2 = 0.01$, $P = 0.98$) were not significant. Hence, data presented in table 3 were pooled by sex. Pollinators were not distributed evenly between the three situations (paired, hidden, and uninterested), as the situation effect was highly significant (experiment 1: $\chi^2_1 = 9.47$, $P = 0.002$; and experiment 2: $\chi^2_1 = 14.68$, $P = 0.00013$). It appears that most of the beetles were not "paired" with a conspecific (76% in the first experiment, 78% in the second). They were mostly hidden (50% in the first experiment, 66% in the second) or trying to exit from the box. It seems that tested *C. colasi* did not detect the presence of conspecifics of the other gender in their vicinity (<25 cm).

Discussion

Beetles can be reliable and specific pollinators in the Tropics (Gottsberger 1977, 1986, 1990; Henderson 1986; Irvine and Armstrong 1990; Momose et al. 1998). Flower adaptations to beetle pollination, as typified in *Philodendron solimoesense*, include the following: a 2-d flowering period, heat production plus emission of an unpleasant odor, presence of a floral chamber in which pollinators copulate and shelter during one night and day, protogynous inflorescences, offering of food rewards (stigmatic secretions, male sterile flowers), and closure of the inflorescences with pollinator extrusion. Nevertheless, the two other *Philodendron* species previously studied, *Philodendron selloum* and *Philodendron bipinnatifidum* (both of the subgenus *Meconostigma*), have 3- and 4-d flowering cycles, respectively (Gottsberger and Amaral 1984).

Even if they can be numerous on one inflorescence, *Trigona* bees are not likely to be pollinators of *P. solimoesense*. First, they were never observed to fly from second-day inflorescences to first-day ones, as they were preferentially attracted by the former. Second, when they were attracted to first-day inflorescences, they rarely carried pollen and never entered the spathe to reach the female flower zone.

Staphylinids have already been reported as floral visitors in association with *Cyclocephala*. In *Magnolia*, they appear to be pollinators (Dieringer and Espinosa 1994; Dieringer et al. 1999), whereas in *Dieffenbachia* (Araceae), the pollination is only effected by *Cyclocephala* (Young 1986). Staphylinids were also present, sometimes in large numbers, in *P. solimoesense* inflorescences, but we have not considered them as pollinators for several reasons: apparently they carried no pollen load, as they arrived in the afternoon, not at dusk, and they were often "trapped" in the inflorescence until it opened at maturity. Further studies are needed to clarify the status of these staphylinids.

Nevertheless, *Cyclocephala* has been documented as a major floral visitor for *Philodendron* species. *Cyclocephala colasi* and

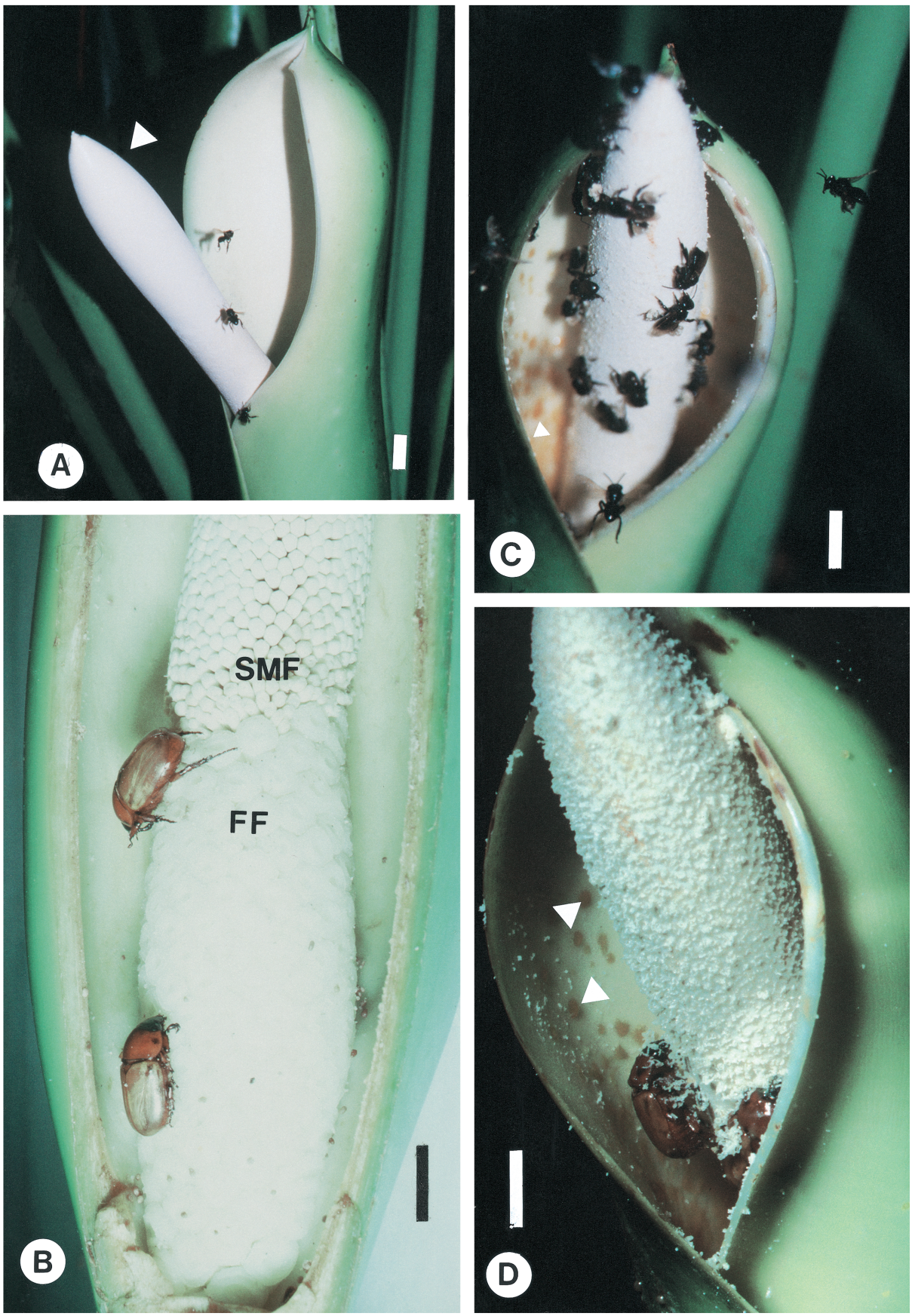

Fig. 5 Relationship between the proportion of male sterile flowers eaten and the number of beetle pollinators (*Cyclocephala colasi*) present in an inflorescence of *Philodendron solimoesense* ($r^2 = 0.64$, $F = 48$, df = 1, 27, $P < 1 \times 10^{-5}$).

Cyclocephala emarginata, as far as we know, have not been recorded on other Araceae, whereas *Cyclocephala sexpunctata* was noted to visit one *Xanthosoma*, one *Dieffenbachia*, and four other *Philodendron* species (Valerio 1984; Young 1986; Croat 1997). The high number of *C. colasi* recorded in this study permits us to suggest that it may be the principal pollinator of *P. solimoesense*.

Attraction and choice experiments show no direct attraction between males and females of *C. colasi*. They were only attracted onto receptive inflorescences. Pheromone emission by females is known from *Cyclocephala lurida*, a pest species (Haynes and Potter 1985). In this species, copulations take place on the ground or on grass blades, in places where partners are not particularly easy to find, and female beetles emit a pheromone that attracts males. In contrast, *C. colasi* individuals meet in *Philodendron* inflorescences. These pollinating beetles may thus rely on inflorescence fragrance to meet (and may no longer rely on a sex pheromone). It has been suggested that, for pollinating *Cyclocephala*, floral odors may function as sex pheromones (Schatz 1990).

Sex ratios tend to be male biased, which indicates that females, at some moment, stop visiting *Philodendron* inflorescences or that the sex ratio in *Cyclocephala* populations is male biased. One reason for *Cyclocephala* females to be less abundant in *Philodendron* inflorescences is that once inseminated, they may no longer be attracted to *Philodendron* fragrance, perhaps because they are looking for laying sites, whereas males keep visiting inflorescences, looking for females, and may be more reliable visitors. Biased sex ratios have been reported from other *Cyclocephala* species, i.e., *Magnolia tamaulipana* (male biased; Dieringer et al. 1998) and *M. schiedeana* (female biased; Dieringer and Delgado 1994).

The ecological role of heat production is still misunderstood.

Table 3

Choice Experiments: Number of Beetles (mean ± SD) in Each Situation

	Experiment 1[a]	Experiment 2[b]
Paired[c]	1.2 ± 0.8	0.67 ± 0.65
Hidden[d]	2.4 ± 1.1	1.92 ± 0.7
"Uninterested"[e]	1.4 ± 1.1	0.42 ± 0.5

Note. Data from both experiments were pooled for the sex.
[a] Five beetles/replicate ($n = 20$), both sexes.
[b] Three beetles/replicate ($n = 12$), both sexes.
[c] With a sexual partner.
[d] Without a sexual partner.
[e] When in any of the two previous situations.

One proposed role for floral heat production is that it helps beetles to maintain an elevated body temperature during cool periods (e.g., evening). Hence, pollinators remain active in the flower, thus increasing the probability of pollination. But scarabs, and particularly *Cyclocephala* species, appear to be endothermic, and such a role thus seems to be unlikely (Bartholomew and Casey 1977; Bartholomew and Heinrich 1978; Dieringer et al. 1998). Floral thermogenicity is most likely an adaptation to volatilize floral oils that constitute the floral odor that attracts the pollinating beetles.

It has been shown that *Erioscelis* attraction is first based on odors at long distance and is then based on visual stimuli that are perceptible only at a short distance (Gottsberger and Silberbauer-Gottsberger 1991). We have found a positive correlation between sterile male length zone and the number of visiting beetles. It is interesting to note that both odor and heat seem to be emitted from this zone of the spadix in *P. solimoesense* (neutral red staining; M. Gibernau, personal observation). Inflorescences with a longer sterile male zone may therefore produce more heat and volatile compounds and, thus, may be more attractive for beetles.

The pollinators arrived at an inflorescence during the first night (when female flowers were receptive), they spent all of the following day in the floral chamber, and they left the inflorescence on the second night when it closed. As inflorescences on the same individual open several days apart, visiting beetles must then fly from one individual to another. All open inflorescences ($n = 68$) were visited by beetles, which indicates that pollinators were abundant. Thus, beetles appear to fly over quite long distances (50–300 m) between the studied populations and the surrounding canopy, where epiphytic *Philodendron* are present, or, more unlikely, they may wait a few days in the ground for new inflorescences to open. In general, *Cyclocephala* beetles have been shown to fly to the closest open inflorescence in *Dieffenbachia* and *Victoria*, and some flights can occur over several hundred meters (Prance and Arias 1975;

Fig. 4 The 2-d–event flowering process of *Philodendron solimoesense* (bars = 1 cm). *A*, First day, afternoon. Spathe is wide open, and the white spadix (arrowhead) is extremely curved. At this time, the spathe is internally white. Few stingless bees (*Trigona* spp.) are attracted to the male portion of the spadix. *B*, First day, evening. Basal part of the spathe was removed, showing the inferior portion of the inflorescence. *Cyclocephala colasi* beetles remain hidden in the protected floral chamber. They feed on the stigmatic secretions of female flowers (*FF*) and on sterile male flowers (*SMF*) situated just above the female zone (*FF*). *C*, Second day, afternoon. A brownish resin (arrowhead) covers the inner surface of the spathe. Numerous *Trigona* bees collect mucilage and some pollen until nightfall. *D*, Second day, evening. Anther releases massive pollen chains. Emerging *C. colasi* are covered by resin (arrowheads) that stuck large amounts of pollen on their cuticles.

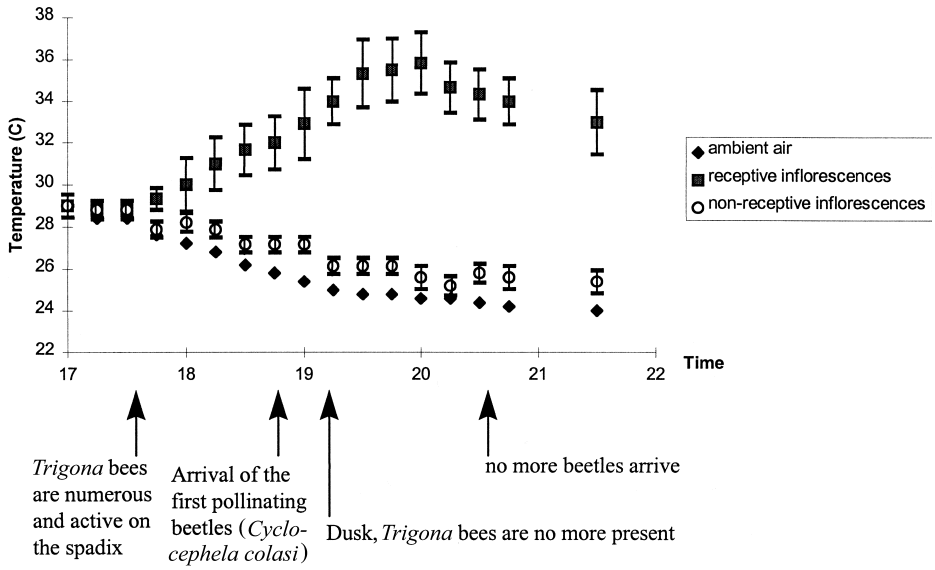

Fig. 6 Mean temperature variation between 1700 and 2145 hours of six receptive and six nonreceptive inflorescences of *Philodendron solimoesense* and ambient air and observations of beetle visitors (*Cyclocephala colasi*) and *Trigona* bee behavior.

Young 1990). Moreover, marked pollinating beetles were recaptured in low numbers, which indicated important insect movements and/or a low survival rate (Prance and Arias 1975; Young 1988*b*, 1990). A small recapture rate, flowering phenology gaps in local populations, and successful pollination indicate that the reproductive systems of *Philodendron*, *Dieffenbachia*, and *Victoria* may function as metapopulations, in which populations several hundred meters apart are linked by flying beetles that are carrying pollen.

The pollination of three species of *Philodendron* (subgenus *Meconostigma*) is known, and pollinators of 16 species of *Philodendron* (subgenus *Philodendron*) have been collected (Gottsberger and Amaral 1984; Croat 1997). Based on these data, it appears that dynastid beetles (*Cyclocephala* and *Erioscelis*) are major inflorescence visitors and/or pollinators. Fourteen of these 19 species are more or less specifically pollinated (one pollinator or one abundant species plus a few minor ones), and only five of these species are pollinated by a several species. However, more field studies are necessary to assess whether *Philodendron* pollination (700 species) is mainly effected by dynastid beetles and whether it is mainly a specific relationship.

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Literature Cited

Bartholomew GA, TM Casey 1977 Endothermy during terrestrial activity in large beetles. Science 195:882–883.

Bartholomew GA, B Heinrich 1978 Endothermy in African dung-beetles during flight, ball-making and ball-rolling. J Exp Biol 73:65–84.

Beath DDN 1996 Pollination of *Amorphophallus johnsonii* (Araceae) by carrion beetles (*Phaeochrous amplus*) in a Ghanaian rain forest. J Trop Ecol 12:409–418.

Bierzychudek P 1982 The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ecol Monogr 52:335–351.

Bogner J 1981 *Pseudohydrosme gabunensis* Engl. Aroideana 4: 31–37.

Camazine S, KJ Niklas 1984 Aerobiology of *Symplocarpus foetidus*: interactions between the spathe and spadix. Am J Bot 71:843–850.

Carson HL, T Okada 1982 Ecology and evolution of flower-breeding pomace flies of New Guinea (Diptera: Drosophilidae). Entomol Gen 8:13–16.

Croat TB 1980 Flowering behavior of the Neotropical genus *Anthurium* (Araceae). Am J Bot 67:888–904.

——— 1997 A revision of *Philodendron* subgenus *Philodendron* (Araceae) for Mexico and Central America. Ann Mo Bot Gard 84: 311–704.

Dieringer G, L Cabrera R, M Lara, L Loya, P Reyes-Castillo 1999 Beetle pollination and floral thermogenicity in *Magnolia tamaulipana* (Magnoliaceae). Int J Plant Sci 160:64–71.

Dieringer G, L Delgado 1994 Notes on the biology of *Cyclocephala jalapensis* (Coleoptera: Scarabaeidae): an endemic of eastern Mexico. Southwest Entomol 19:309–311.

Dieringer G, JES Espinosa 1994 Reproductive ecology of *Magnolia schiedeana* (Magnoliaceae), a threatened cloud forest tree species in Veracruz, Mexico. Bull Torrey Bot Club 121:154–159.

Dieringer G, P Reyes-Castillo, M Lara, L Cabrera R, L Loya 1998 Endothermy and floral utilization of *Cyclocephala caelestis* (Cole-

optera: Scarabaeoidae: Melolonthidae): a cloud forest endemic beetle. Acta Zool Mex 73:145–153.
Faegri K, L van der Pijl 1979 The principles of pollination ecology. 3d ed. Pergamon, London. 244 pp.
Royal Statistical Society 1986 GLIM: generalised linear interactive modelling system 3.77. Royal Statistical Society, London. 305 pp.
Gottsberger G 1977 Some aspects of beetle pollination in the evolution of flowering plants. Plant Syst Evol Suppl 1:211–226.
——— 1986 Some pollination strategies in Neotropical savannas and forests. Plant Syst Evol 152:29–45.
——— 1990 Flowers and beetles in the South American Tropics. Bot Acta 103:360–365.
Gottsberger G, A Amaral 1984 Pollination strategies in Brazilian *Philodendron* species. Ber Dtsch Bot Ges Bd 97S:391–410.
Gottsberger G, L Silberbauer-Gottsberger 1991 Olfactory and visual attraction of *Erioscelis emarginata* (Cyclocephalini, Dynastinae) to the inflorescences of *Philodendron selloum* (Araceae). Biotropica 23: 23–28.
Grayum MH 1986 Correlations between pollen morphology and pollination biology in the Araceae, with some implications for angiosperm evolution. Pages 313–327 *in* S Blackmore, IK Ferguson, eds. Pollen and spores: form and function. Academic Press, London.
——— 1990 Evolution and phylogeny of the Araceae. Ann Mo Bot Gard 77:628–697.
——— 1996 Revision of *Philodendron* subgenus *Pteromischum* (Araceae) for Pacific and Caribbean tropical America. Syst Bot Monogr 47:1–233.
Grimaldi D, J Jaenike 1983 The diptera breeding on skunk cabbage, *Symplocarpus foetidus* (Araceae). N Y Entomol Soc 91:83–89.
Haynes KF, DA Potter 1985 Chemically mediated sexual attraction of male *Cyclocephala lurida* (Coleoptera: Scarabaeidae) and other scarabaeid beetles to immature stages. Environ Entomol 24: 1302–1306.
Henderson A 1986 A review of pollination studies in the Palmae. Bot Rev 52:221–259.
Irvine AK, JE Amstrong 1990 Beetle pollination in tropical forests of Australia. Pages 135–149 *in* KS Bawa, M Hadley, eds. Reproductive ecology of tropical forest plants. Man and the Biosphere, vol 7. UNESCO, Paris.
Madison M 1979 Protection of developing seeds in Neotropical Araceae. Aroideana 2:52–61.
——— 1981 Notes on *Caladium* (Araceae) and its allies. Selbyana 5: 342–377.
Mayo SJ 1991 A revision of *Philodendron* subgenus *Meconostigma* (Araceae). Kew Bull 46:601–681.
Mayo SJ, J Bogner, PC Boyce 1997 The genera of Araceae. Trustees, Royal Botanical Gardens, Kew. 307 pp.
Meeuse BJD, I Raskin 1988 Sexual reproduction in the arum lily family, with emphasis on thermogenicity. Sex Plant Reprod 1:3–15.
Momose K, T Yumoto, T Nagamitsu, M Kato, H Nagamasu, S Sakai, RD Harrison, et al. 1998 Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest. Am J Bot 85: 1477–1501.
Patt JM, JC French, C Schal, J Lech, TG Hartman 1995 The pollination biology of Tuckahoe *Peltandra virginica* (Araceae). Am J Bot 82:1230–1240.
Pellmyr O, JM Patt 1986 Function of olfactory and visual stimuli in pollination of *Lysichiton americanum* (Araceae) by a staphylinid beetle. Madroño 33:47–54.
Prance GT, JR Arias 1975 A study of the floral biology of *Victoria amazonica* (Poepp.) Sowerby (Nymphaeaceae). Acta Amazonica 5: 109–139.
Ramirez WB, LDP Gomez 1978 Production of nectar and gums by flowers of *Monstera deliciosa* (Araceae) and of some species of *Clusia* (Guttiferae) collected by New World *Trigona* bees. Brenesia 14–15:407–412.
Rust RW 1980 Pollen movement and reproduction in *Arisaema triphyllum*. Bull Torrey Bot Club 107:539–542.
Schatz G 1990 Some aspects of pollination biology in Central American forests. Pages 69–84 *in* KS Bawa, M Hadley, eds. Reproductive ecology of tropical forest plants. Parthenon, Paris.
Shaw DE, BK Cantrell 1983 A study of the pollination of *Alocasia macrorrhiza* (L.) G. Don (Araceae) in southeast Queensland. Proc Linn Soc NSW 106:323–335.
Sivadasan M, T Sabu 1989 Beetle-pollination—cantharophily—in *Amorphophallus hohenackeri* (Araceae). Aroideana 12:32–37.
Statistix 1994 Analytical software. Version 4.1. Statistix. Tallahassee, Fla.
StatXact 1992 Version 2.05. CYTEL Software, Cambridge, Mass.
Thompson SA, JE Rawlins 1986 Floral ecology of *Anchomanes difformis* (Araceae). Am J Bot 73:791.
Valerio CE 1984 Insect visitors to the inflorescence of the aroid *Dieffenbachia oerstedii* (Araceae) in Costa Rica. Brenesia 22:139–146.
Williams NH, RL Dressler 1976 Euglossine pollination of *Spathiphyllum* (Araceae). Selbyana 1:349–356.
Young HJ 1986 Beetle pollination of *Dieffenbachia longispatha* (Araceae). Am J Bot 73:931–944.
——— 1987 Aroid observations: *Philodendron rothschuianium*. Aroideana 10:22.
——— 1988*a* Differential importance of beetle species pollinating *Dieffenbachia longispatha* (Araceae). Ecology 69:832–844.
——— 1988*b* Neighborhood size in a beetle pollinated tropical aroid: effects of low density and asynchronous flowering. Oecologia 76: 461–466.
——— 1990 Pollination and reproductive biology of an understory neotropical aroid. Pages 151–164 *in* KS Bawa, M Hadley, eds. Reproductive ecology of tropical forest plants. Man and the Biosphere, vol 7. UNESCO, Paris.