

Principes, 38(1), 1994, pp. 13–23

Pollination and Pollinator Breeding in *Desmoncus*

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ABSTRACT

The reproductive ecology of *Desmoncus polyacanthos* and *D. mitis*, two sympatric species of the Peruvian lowland rain forest, was investigated over 15 months including two flowering periods each. Floral biology of the two species is quite similar but differs in duration of staminate anthesis and a reduced spectrum and fewer visitors in the smaller *D. mitis*. The populations of both species show a relatively short (± 60 days), synchronous flowering period. *Desmoncus* is protogynous, and female and male anthesis do not overlap. Thermogenesis occurs in both female and male stages. *Phyllotrox* sp. (Curculionidae) and *Epurea* sp. (Nitidulidae) are attracted to the pistillate flowers by the odoriferous inflorescences and stay until the next day, when staminate anthesis occurs. *Desmoncus polyacanthos* is pollinated by these two beetle species, which reproduce in male flowers. *Desmoncus mitis* is largely pollinated by *Phyllotrox* sp. only, as few *Epurea* sp. visited the inflorescences. Other visitors, especially drosophilid flies, are without quantitative importance for pollination. Hybridization between *D. polyacanthos* and *D. mitis* never occurred.

Pollination ecology is discussed with reference to *Bactris*, whose floral biology is most closely similar to that of *Desmoncus*. A highly specialized cantharophilous syndrome is recorded. Relationships between *Desmoncus polyacanthos* and the beetles *Phyllotrox* sp. and *Epurea* sp. and between *D. mitis* and *Phyllotrox* sp. are considered as a symbiosis, ensuring reproduction of both plants and animals.

Desmoncus (Arecoideae, Cocoeae, Bactridinae) is a neotropical genus distributed throughout the lowland rainforests from Mexico to Bolivia and Brazil (Uhl and Dransfield 1987). Sixty-one species have been described but there are probably no more than 7 species (Henderson, in letter). All but one species of *Desmoncus* are vines, *Desmoncus* being the only scandant palm group in America except for one species of *Chamaedorea*. Within the Bactridinae, the genera *Bactris* (Essig 1971, Mora Urpí and Solis 1980, Bullock 1981, Mora Urpí 1982, Beach 1984), *Astrocaryum* (Bullock 1981, Burquez et al. 1987) and *Acrocomia* (Scariot 1987, Scariot et al. 1991) have been investigated in regard to their floral ecology. Data on phenology and reproductive biology of *Desmoncus* are lacking, and only the survey of pollination in the Bactridinae has been done

recently (Listabarth 1992). Flowering behavior and pollination ecology of two sympatric *Desmoncus* species of Peruvian Amazonia are described in detail here.

Material and Methods

Desmoncus polyacanthos and *Desmoncus mitis* were studied from October 1988 to January 1990 at "Panguana" field station (9°37'S, 74°56'W) (260 m.s.m.) in eastern Peru, Dept. Huanuco, Province Pachitea. The area under investigation is primary rain forest (annual precipitation of 2,280 mm) with some xeromorphic elements; its climate is characterized by a marked wet season (Oct.–April: 1,950 mm) and a pronounced dry season (May–Sept.: 330 mm). Herbarium vouchers are deposited in USM, AAU, NY and WU. *Desmoncus mitis* Mart. var. *leptospadix* Mart. (Listabarth 11-30689) and *Desmoncus polyacanthos* Mart. (Listabarth 11-10589) were identified by H. Rainer (Vienna) following the circumscription of A. Henderson (in prep.). Specimens of beetles are deposited at NHMW under numbers of the palms with which they were collected. The Curculionidae were tentatively identified by J. F. Voisin (Paris) and C. H. C. Lyal (London), the Nitidulidae by R. Vincent (Paris).

Procedures were carried out as follows: Eleven inflorescences (of one cluster) of *D. polyacanthos* and 39 (of 13 clusters) of *D. mitis* were studied in detail, and several additional inflorescences were followed as controls.

Temperature was measured with an electronic thermometer, on bud surface, on the flowers, or between the rachillae (but touching the flowers). In late male anthesis temperature could not be measured exactly, because touched flowers dropped. Intensity of fragrance was divided into three classes, absent (low), noticeable, and strong.

Insect visitors were tabulated. Qualitative samples were taken with an exhauster, quantitative ones with a plastic bag covering the whole inflo-

rescence to collect all the visitors. With the exception of drosophilid flies, 100% could be collected. Seventeen samples (incl. four quantitative) of *D. polyacanthos* and 19 (incl. seven quantitative) of *D. mitis* were taken.

For breeding experiments of insects counted, fallen male flowers were put into a petri dish with sterilized but moist sand. Pupation could be observed through the glass, because of the thin substrate-layer. Emerged insects could easily be collected from the tops of the petri dishes.

For bagging experiments during female anthesis three types of bags were used (1) nets (#1.0 mm) to exclude visitors but allowing potential wind pollination, (2) nets (#0.1 mm) to bar out visitors and very likely wind borne pollen as well, and (3) plastic bags to exclude all pollen sources. Only single rachillae were bagged to control the fruit set of the other rachillae (*D. polyacanthos*), but whole inflorescences of *D. mitis* were bagged, as there was enough material. A prolonged female anthesis, which probably was effected by the 100% relative humidity inside these bags, is an artefact but obviously did not influence the experiments.

Results

Habit and Phenology. In the investigation area four species of *Desmoncus* occur and could easily be distinguished even in the sterile state by their size and leaf characteristics. One species, climbing into the canopy, and another, of the understory, of which too few individuals were found, are not taken into account in this study. The two species investigated are described below. Though the reproductive period of at least three of the four species occurring in the same macro habitat is overlapping, no hybrids were found.

Desmoncus polyacanthos is a monoecious clustered, climbing palm of the understory with a maximum height of 10 m, each cluster with up to eight stems. Of eight clusters found, seven had only 1–5 stems and remained sterile, one cluster had eight stems, with five fertile stems that produced 1–2 inflorescences/flowering period. Flowering period was once a year, covering ca. fifty days from December to January. Inflorescences are interfoliar, pendulous, and branched to one order with 7–11 rachillae bearing spirally arranged

triads except in the distal part which only bears single or paired staminate flowers. Fruits mature until May.

In *Desmoncus mitis*, of the same habit but much smaller, climbing up to a maximum of 4 m is commonly found. Clusters are 1–8 stemmed, but unlike *D. polyacanthos* even single-stemmed individuals produced inflorescences. Clusters with 2–4 fertile and just as many sterile stems are widespread. Up to 3 inflorescences per stem are produced, which are smaller than those of *D. polyacanthos*, bearing 3–7 rachillae. The population of *D. mitis* flowers three times a year, having a main flowering period from December to February. Some clusters produce inflorescences in July and October, respectively.

Flowering Behavior of D. polyacanthos. The first inflorescence buds appear in the last days of October. They are still upright but soon grow to nearly their full length, becoming pendulous and increasing in diameter. The day before dehiscence of the inflorescence bud (Fig. 1a) there is a color change of the peduncular bract from green to yellowish or red-brown. In late budstage temperature elevation is evident but not too prominent (1.1° C above surrounding air temperature (0.7°–1.6° C)), when measured on bud surfaces some minutes before opening. Buds open at about 6:00 p.m. (5:52–6:15 p.m.). Within one second the peduncular bract bursts adaxially (which is the morphological abaxial side) from the base to the top, with a sound like tearing silk. Then the rachillae drop out, hanging vertically (Fig. 1b). The creamy white, smooth inner surface of the bract soon inverts to become the outside (Fig. 1c) and is a bright contrast to the dark background of the forest, especially during twilight.

At this stage the minute female flowers are already at anthesis, the receptive stigmas are bright, hyaline, and adaxially covered with a liquid film, enlarging later to a drop. Male flowers remain in bud stage, but incline abaxially, when released from the pressure in bud (Fig. 1c). A strong sweetish, honeymellow fragrance is emitted. The difference of temperature between the rachilla surface and surrounding air is 1.5°–2.0° C, rising to 3.1° C during twilight (6:30–7:00 p.m.). Then, the rachilla-temperature decreases simultaneously with the air-temperature, but in a slower manner

1. *Desmoncus polyacanthos*: (a) inflorescence bud; (b) inflorescence at female anthesis; (c) close up of an inflorescence at female anthesis with abundant visitors; (d) inflorescence at late male anthesis, most staminate flowers abscised; (e) infructescence.

Bars: 10 cm (a, b, d, e), 1 cm (c).

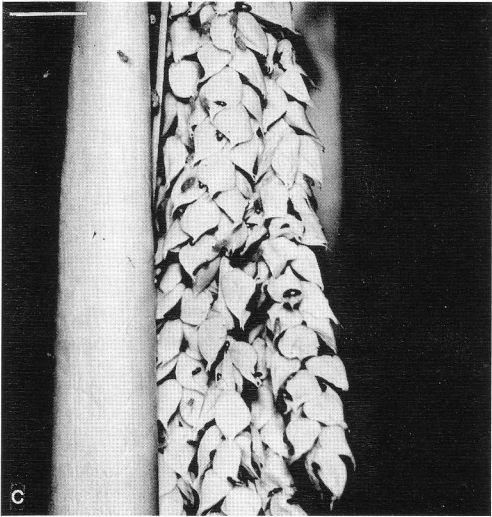


Table 1. Presence of visitors during female and male anthesis and their status in regard to pollination ecology of *D. polyacanthos*.

Taxon	Female Inflorescence	Male Inflorescence	Status
Coleoptera			
<i>Phyllotrox</i> sp.*	++	++	p
Barinae	-	(+)	v
<i>Epurea</i> sp.	++	++	p
Staphilinidae	(+)	(+)	pp
Hymenoptera			
Halictidae	(+)	(+)	pp
Meliponinae	-	(+)	v
Chalcididae	-	(+)	v
Diptera			
Drosophilidae	++	+	pp
Others	(+)	-	v
Heteroptera			
Miridae	(+)	-	v

- = not observed; (+) = facultative; + = constant, common; ++ = constant, very common; v = visitor; pp = potential pollinator; p = pollinator.

* *Phyllotrox* sp. was identified as a species with the *P. megalops* complex (J. F. Voisin).

(at ca. 10:00 p.m. there is still a difference of 1° C). Emission of fragrance is positively correlated with temperature elevation, similarly the secretion of stigmatic liquid. At 10:00 p.m. stigmas are still somewhat wet but most of the stigmatic liquid has dried out or been licked. All female flowers are still at anthesis, but the inflorescence seems to have lost its attractants (with the exception of the contrasting feature of the bright bract and male buds). The end of female anthesis is characterized by the lack of fragrance and stigmatic liquid, and by a color change of the dry stigmas from hyaline to whitish, later brownish. This stage occurs shortly before daybreak or later, at least before noon while male flowers and the anthers are still closed.

Male flowers remain closed until the late afternoon of the second day; male anthesis starts at 4:00–5:00 p.m. Anthers dehisce about 15 minutes before the first flowers begin to spread their petals. Within 30 minutes the petals of all flowers of the inflorescence have spread wide enough to release the anthers. Immediately large packs of pollen are available which are sticky and therefore not adapted to wind transport. Even when the clumps dry and fall apart, the monosulcate pollen grains drop to the ground more or less vertically. Fragrance of the same quality, but less quantity

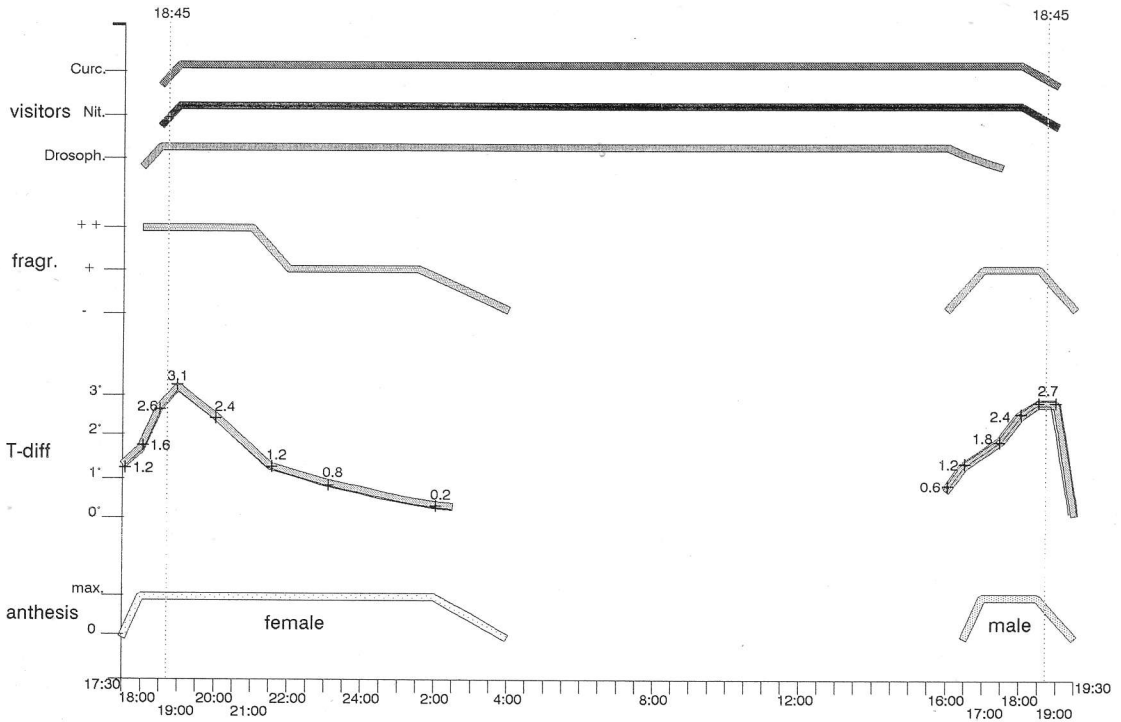
as compared with the fragrance during female anthesis is emitted. Again temperature elevation of the rachillae is noticeable. There is a difference of 0.8°–1.5° C at the beginning of staminate anthesis, rising to 3° C for a short period when all flowers are completely open. As long as the flowers have a firm connection with the rachillae, thermogenesis occurs. Soon the flowers begin to abscise from the rachillae (5:30–6:00 p.m.), first one by one, then more. Within 45 minutes the triad-bearing part of the rachillae lacks any male flower (Fig. 1d); 45 minutes later all male flowers had fallen, which is the end of male anthesis (7:00–7:30 p.m.) (Fig. 2).

Insect Visitation to D. polyacanthos. *D. polyacanthos* attracts 10 species regularly (Table 1). Only five of them visit inflorescences in both the female and male stages and therefore can be potential pollinators. No other visitors have been observed. Some minutes after dehiscence of the peduncular bract the first visitors (Drosophilidae) appear. They soon crowd the inflorescence, licking the fleshy inner surface of the peduncular bract, the rachillae, and, respectively, male and female flowers. They stay during all stages of flowering, feeding and mating, but leaving then, especially before and at male anthesis. Fallen staminate flowers are substrate for their larvae; 11–14 days later the new generation emerges in large numbers. The other flies could only be found at early female anthesis before twilight, licking floral parts as well.

The halictid bee (*Megalopta* sp.), only active before and during twilight, visits inflorescences *D. polyacanthos* at both female and male stages, but does not appear constantly. Only a few individuals per inflorescence were observed, if they came at all.

About 45 minutes after the beginning of female anthesis, at twilight (6:45 p.m.), numerous beetles (*Phyllotrox* sp., *Epurea* sp.) fly towards the inflorescence. Soon rachillae are crowded and appear brown spotted by the beetles (Fig. 1c). 200–500 curculionid and 100–350 nitidulid beetles have been counted in the quantitative samples. The arrival of beetles lasts about half an hour but does not end abruptly with complete darkness. An estimated 80% of all beetle visitors are on the inflorescence then (7:15 p.m.). Beetles lick the fluid of female flowers and chew the outside of male buds, but they are mainly concerned in sexual activity, looking for mates and mating for which walking over all parts of the inflorescence is necessary. During the first hours of the night the

Desmoncus



2. Anthesis and time-event correlation of thermogenesis (difference of temperature [T-diff] in °C), fragrance [fragr.] (+ + strong, + noticeable, - low (absent)) and presence of the most important visitors of a typical inflorescence of *Desmoncus polyacanthos*.

beetles remain active. In the early morning they hide between the male flowers (which offer shelter because of their abaxial inclination from the rachillae), staying there until male anthesis in the afternoon. When the male flowers open and copious pollen is released, beetles give up their shelter and feed on pollen, and soon are covered all over with pollen packs or single grains. The beetles leave, or are forced to leave, when flowers abscise (Fig. 2).

Two other species of beetles were found more or less regularly: some Staphilinidae, which arrived at twilight and stayed until the end of flowering the next day, and another curculionid. The latter is day-active and arrived at the inflorescence when females were not receptive any more, or later to young infructescences. This species might be a fruit parasite on this and perhaps other species, but never a pollinator.

The meliponid bees were attracted only during staminate anthesis to collect pollen. Not all male inflorescences were visited, but once the source was detected, the bees came in abundance. Other

visitors were Heteroptera and Chalcididae, which could rarely be found in either female or male inflorescences and obviously do not play any role in pollination.

Breeding Experiments with Insects (*D. polyacanthos*). Mating activity and the fact that the most important visitors apparently oviposit into male flowers of *D. polyacanthos* led to these experiments. A survey of breeding experiments is given in Table 2.

Three species (*Drosophilidae*, *Phyllotrox* sp., *Epurea* sp.) develop in *D. polyacanthos*; they use buds of male flowers for egg deposition, without disturbing their function or even destroying them. *Drosophilid* flies deposit their eggs on male buds, *Epurea* sp. and *Phyllotrox* sp. in the buds. Their larvae develop in fallen male flowers but change into deeper layers of the soil when pupating (which is only 5–6 days after flowering). The new generations emerge 12–14 days after the flowers had dropped. While most *drosophilid* flies emerged in the morning (7:00–9:00 a.m.), the beetles emerged in the afternoon only (3:00–6:00 p.m.).

Table 2. Breeding experiments in *Desmoncus polyacanthos*

Inflorescence	No. of Insects Emerged	Emerged ^a after x-days	Species
D40-5	150	11-12	Drosophilidae
	12	11-12	<i>Phyllotrox</i> sp.
	20	13	Drosophilidae
	23	13	<i>Phyllotrox</i> sp.
	23	14	Drosophilidae
	13	14	<i>Phyllotrox</i> sp.
D40-5-total (300 flowers)	193	11-14	Drosophilidae
	58	11-14	<i>Phyllotrox</i> sp.
D40-6	10	11	Drosophilidae
	20	12	Drosophilidae
	7	12	<i>Phyllotrox</i> sp.
	1	12	<i>Epurea</i> sp. ^b
	8	13	Drosophilidae
	6	13	<i>Phyllotrox</i> sp.
D40-6-total (188 flowers)	38	11-13	Drosophilidae
	25	12-13	<i>Phyllotrox</i> sp.
	1	12	<i>Epurea</i> sp. ^b
D40-7-total (390 flowers)	85	11-15	Drosophilidae
	43	11-15	<i>Phyllotrox</i> sp.

^a Staminate anthesis (abscising of flowers) is the 1st day.

^b Raising of only one individual might be accidentally, as numerous Nitidulidae emerged in breeding experiments with male flowers of *Bactris* species (Listabarth, unpubl. data).

Fruit Set (*D. polyacanthos*). Two or three weeks after anthesis, non-pollinated female flowers had all aborted. Fruit set (the remaining young fruits) now could be counted and was between 50-70%. Pollinated flowers did not grow in length but increased in diameter (1 mm), changed color to green, and still had a firm connection to the rachillae. Only ca. 30% of these fruits matured (Fig. 1e) because of a curculionid parasite or being eaten or damaged by predators before maturity. Mature fruits are bright red, suggesting bird dispersal.

Bagging Experiments (*D. polyacanthos*). None of the rachillae, which had been bagged to exclude visitors (and in some case wind-borne pollen as well), showed fruit set. Even rachillae, from which bags had been removed in the early morning (4:30 a.m.), when pistillate flowers were still at anthesis, did not set fruit. Fifteen to eighteen days later these rachillae did not bear any fruit, while not-bagged rachillae of the same inflorescences had fruit. Thus, fruit set without pollination does not occur.

Anomalies (*D. polyacanthos*). Two inflorescences behaved abnormally: One opened at 6:30

a.m.; female flowers were receptive but only a few drosophilid flies and one *Phyllotrox* sp. visited that inflorescence. Pistillate flowers lost receptivity at high noon, and staminate anthesis began the same day as usual. The inflorescence in the male stage was visited by the halictid bee and a few *Phyllotrox* sp. Fifteen days later the rachillae did not bear any fruit.

Another inflorescence opened "in time" (6:10 p.m.), but showed a simultaneous female and male anthesis. When all staminate flowers had abscised (8:00 p.m.), pistillate flowers were still at anthesis. Only two drosophilid flies visited that inflorescence. All fruits aborted within the next 12 days.

Comparison with *D. mitis*. A comparison between the two species and a summary of reproduction events in *Desmoncus* is given in Table 3; *D. mitis* does not show substantial differences, but the following features are worth noting:

(1) Flowering behavior: male anthesis continues strikingly longer, first flowers are not abscising until dark (7:15) and male anthesis ends at ca. 8:15-8:30 p.m. Thermogenesis occurs in late inflorescence bud and during female and male anthesis, but the temperature difference never exceeds 1.7° C.

(2) Insect visitors: The spectrum of visitors is similar to that of *D. polyacanthos*, but lacks Meliponinae, Chalcididae, and Miridae; overall the same species as in *D. polyacanthos* were found. The number of visitors is lower according to the size of the inflorescences, especially in relation in nitidulid beetles. In quantitative samples *Phyllotrox* sp. dominates (115-250 individuals, once even 402), whereas *Epurea* sp. is of less importance (max. 16/sample).

(3) Breeding experiments resulted in new generations of Drosophilidae and *Phyllotrox* sp. but not of *Epurea* sp. Bagged inflorescences never showed fruit set. Anomalies as in *D. polyacanthos* never were observed.

Floral Dynamics and Geitonogamy in *D. mitis*. *D. mitis* is especially suitable for investigation of these aspects. Individuals were numerous enough to investigate a population within a plot to find the flowering mechanisms of individual clusters.

A plot with five clusters inside (Fig. 3) was marked for a separate investigation of flowering phenology. This plot contained a total of 14 fertile axes with 22 inflorescences which flowered from mid-December 1989 until mid-January 1990. The days when female anthesis occurred within one

Table 3. Comparison of reproduction events between *D. polyacanthos* and *D. mitis*.

Day	Time	Reproductive Events		T-diff/fragr	
		<i>D. polyacanthos</i>	<i>D. mitis</i>	<i>D. polyacanthos</i>	<i>D. mitis</i>
1st day	ca. 6:00 p.m.	female anthesis starts		2.0/++	1.2/++
	6:30-7:15 p.m.	visitors arriving in profusion		3.1/++	1.7/++
	during night	feeding-mating-oviposition of <i>Drosophilidae/Phyllotrox</i> sp. (<i>Epurea</i> sp.)			
2nd day	morning	end of female anthesis—visitors hidden, inactive		0.0/-	0.0/-
	ca. 4:30 p.m.	male anthesis starts—visitors become active, feeding on pollen		1.5/+	0.9/+
	5:30-6:00 p.m.	first male flowers drop	all flowers on rachillae	3.0/+	1.2/+
	6:30-7:00 p.m.	visitors leave			
	ca. 7:30 p.m.	only a few flowers left	all flowers on rachillae	0.0/-	1.2/+
		end of male anthesis	first flowers drop— without visitors		1.2/+
	ca. 8:30 p.m.	end of male anthesis			

For abbreviations see Figure 2.

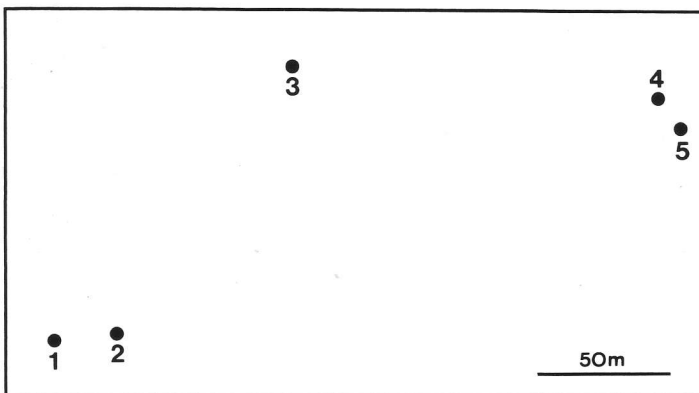
week show a typical pattern of flowering in *D. mitis*. Inflorescences with a neighboring pollen source inside the plot appear in bold print. Seventy-five percent of the inflorescences during female anthesis had a pollen source even within that limited area, without regard to the surrounding clusters outside the plot.

Possibilities of geitonogamy, which is autogamy or self-fertilization in a broad sense, are of multiple origin: First, geitonogamy within the same inflorescence is avoided completely by the strict dichogamy (anthesis of staminate and pistillate flowers at different times) of the inflorescence and no exception was found. Second, geitonogamy between two inflorescences of one stem, which are at anthesis during two subsequent days was observed only rarely (Fig. 4). The third case, gei-

tonogamy between inflorescences of different stems of one cluster, is frequently found. Autocompatibility was not tested.

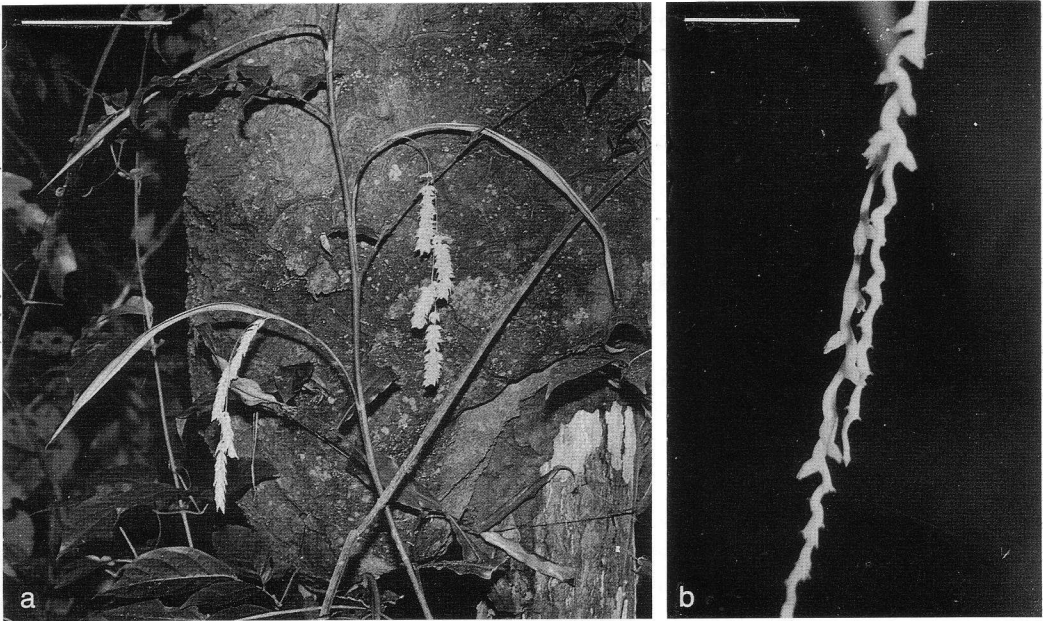
Discussion

Desmoncus within the Bactridinae. Derelomini (Curculionidae) and Nitidulidae are frequent palm pollinators (Henderson 1986, Barfod et al. 1987, Anderson et al. 1988, and many others). Within the Bactridinae they were found in the protogynous inflorescences of *Astrocaryum* (Bullock 1981, Burquez et al. 1987, Listabarth 1992), *Acrocomia* (Scariot 1987, Scariot et al. 1991) and *Bactris* (Essig 1971, Mora Urpí and Solis 1980, Bullock 1981, Mora Urpí 1982, Beach 1984, Listabarth 1992). Special attention should



date	No.
24/12/89	5
25/12/89	5
26/12/89	1
27/12/89	1
27/12/89	4
27/12/89	3
30/12/89	2
31/12/89	1

3. Distribution of the clusters of *Desmoncus mitis* and list of female anthesis during one week; for further explanations see text.



4. *Desmoncus mitis*: (a) Stem with inflorescence bud (uppermost) and inflorescences in male (middle) and female (below) stage. (b) detail of a rachilla after male anthesis with minute female flowers. Bars: 10 cm (a), 1 cm (b).

be given to *Bactris*, which apparently shows the flowering cycle most similar to that of *Desmoncus*. Essig (1971), Mora Urpí and Solis (1980) and Mora Urpí (1982) state that pollination of *Bactris* is by Derelomini and Nitidulidae; but Bullock (1981) and Beach (1984) found *Cyclocephala* and *Mimeoma* (Scarabaeidae: Dynastinae) to be probably more important than the abundant small beetles. However, *Phyllotrox* (Curculionidae: Derelomini) and *Epurea* (Nitidulidae) are the pollinators of *Desmoncus polyacanthos* and *D. mitis* in Peru.

Another limiting factor is duration of pistillate anthesis in the protogynous *Bactris*. Stigmas are considered to remain receptive during male anthesis (e.g., Beach 1984). The inflorescences of *Desmoncus*, mentioned as "apparently protandrous" (Uhl and Dransfield 1987) were found to be strongly protogynous. Drying and withering of the stigmas seemed to be a valuable feature for determination of the end of female anthesis and occurred regularly before staminate anthesis in *Desmoncus*.

Uhl and Moore (1977) suggested a clear correlation of floral anatomy with pollination in *Bactris*. The anthers were found to be well protected by fibrous sheaths and raphides in the proximal parts of the petals while the outer parts were

without protection and the tissue adapted to attract and feed beetles. Tannins, which are distasteful to herbivores were lacking completely. In contrast pistillate flowers were protected firmly by vasculature and tannins. Complexity of the system has been underestimated, because reproduction of the pollinating beetles in the male flowers (see Table 2) of any member with the Bactridinae was not established until now. Breeding of the pollinators undoubtedly is a striking and important feature in the pollination ecology of the two closely related genera.

Visitors. As pointed out above (Table 1), only five species are possible as pollen vectors in *D. polyacanthos* and *D. mitis*. Of these only the drosophilid flies, *Phyllotrox* sp. and *Epurea* sp., that occur in both, can have quantitative importance for pollination.

Drosophilid flies, frequently found on palm inflorescences and sometimes reported to be pollinators (Henderson 1986, Olesen and Balslev 1990) do not play an important role in *Desmoncus*. Most individuals left before or during early male anthesis, when female inflorescences are not yet opened. They seem more active during female anthesis, licking fluids, mating and ovipositing, not waiting for more reward (which is offered during

male anthesis). They even seem to be disturbed by the abundant beetles of *Epurea* sp. and *Phyllotrox* sp., which become more and more active during male anthesis and may therefore leave. Their further activity is unknown. Beach (1984) raised Drosophilidae from the fallen staminate flowers of *Bactris*. The same situation occurs in *Desmoncus*. He further reported drosophilid flies which defend eggs against foraging meliponid bees. This was not observed in *Desmoncus* and eggs were not in danger, as shown by the great number of emerging insects in the breeding experiments (Table 2). Drosophilid flies can cause pollination in *Desmoncus*. They are not the most effective pollinators, but may still represent a potential pollinator in the absence of the beetles.

Phyllotrox sp. and *Epurea* sp. in *D. polyacanthos* and *Phyllotrox* sp. in *D. mitis*, are the legitimate pollinators. They arrive on inflorescences at female anthesis and remain there until the next day, feeding on pollen during male anthesis. At twilight they depart for another plant which is at female anthesis. Beetles could rarely be observed arriving on inflorescences at male anthesis. In the two *Desmoncus* species beetles leave for different purposes at the same time: while *D. polyacanthos* shows a more sophisticated system and abscising of the male flowers forces visitors to depart for another inflorescence, *D. mitis* underlines the much bigger attractiveness (fragrance!) of inflorescences at the female stage (Table 3). At twilight *Phyllotrox* sp. change from the inflorescence still at male anthesis to one at female anthesis, where they will find their mates as well as food and shelter. *Phyllotrox* sp. and *Epurea* sp. do not show essential differences in behavior. Once on an inflorescence at female anthesis they mate and oviposit into the male buds, feed on flower tissue or lick fluids of female flowers; thus, pollen, which is adherent to them can be transferred. In late female anthesis they begin to look for shelter, waiting for pollen which will be released during male anthesis the next day.

The main pollinators of *Desmoncus*, *Phyllotrox* sp. (and *Epurea* sp.) may not be seen as a "pollinator team," changing at the same time from one inflorescence to another. More often there is an exchange of the beetles involved. Those which did not succeed in mating or still continue to reach maturity will join; still others might not find any inflorescence or will die after ovipositing.

Staphilinids and the halictid bees were found facultatively on inflorescences at female and male

anthesis. While staphilinids do not play a role in pollination (too few, small individuals), the halictid bee, if present during female anthesis, is a potential pollinator. The halictid bee when searching for pollen sources is attracted by the conspicuous inflorescences during twilight. It is also visually oriented as typical for bees, and inflorescences bagged with a plastic bag (no fragrance) were also visited. When visiting an inflorescence at female anthesis the bees, covered ventrally with pollen (ventral collectors), looked for pollen on the whole inflorescence or at least on single rachillae and left without success. What happens is therefore not a pollen theft (sensu Inouye 1980) only, but affecting pollination by accident. However, even if we consider pollination by the halictid bee as at best a rare event, the bee's possible role is as a long distance pollinator.

Pollination and Breeding System. Pollination of *Desmoncus* by insects should be considered as the rule. The syndrome: The protogynous fragrant inflorescence attracts pollinators (temperature-elevation supports emission of fragrance). Visitors are there for mating and feeding and shelter (during the non-flowering period). Male anthesis provides pollen. This syndrome has been reported in all its features several times as for Nymphaeaceae (Prance and Arias 1975, Prance and Anderson 1976), *Magnolia* (Thien 1974), Annonaceae (Gottsberger 1977, 1990), Araceae (Gottsberger 1990), Cyclanthaceae (Beach 1982; Gottsberger 1990, 1991) and Palmae (e.g., Beach 1984) and in many other studies. *Desmoncus* also ensures reproduction of its pollinators. Beetles do not influence the function of the male flowers and their larvae utilize flowers out of function. Thus, the relationship between *Desmoncus* and these beetles can be considered as a symbiosis and demonstrates a relationship with at least one co-adaptation of beetles to the plant, representing more than "a one-sided adaptation of flowers to be the behavior, necessities, and sense capacities of beetles," which Gottsberger (1990) states for the taxa cited above. Adaptations of beetles need not necessarily be of morphological nature only; for instance, activity patterns of the beetles or their ability to find inflorescences of *Desmoncus* must have been evolved in an adaptive way to make the system so effective. Or, if we follow Beach (1984) that *Bactris* is pollinated by Dynastidae and Curculionidae, how would a one-sided adaptation of *Bactris* toward a 20 mm and a 2 mm beetle appear? However, we still lack answers for

hosts of questions concerning the biology of beetle pollinators of cantharophilous plants and should stress that in future work.

Pollen was found to fall down the inflorescence, but not to rise, as does pollen of anemophilous species. Thus, the distances between the individuals make it quite unlikely that wind pollination plays any role in the reproductive biology of *Desmoncus*. Inflorescences bagged to deter visitors but which allowed penetration of wind-borne pollen never showed fruit set. Nevertheless, pollination caused by gravity (which then most likely is geitonogamy) should be possible.

There are no experimental data but, for obvious reasons, a hypothesis of self-compatibility and geitonogamy versus the existence of self-incompatibility mechanisms is reasonable in *Desmoncus*. As pointed out above the prerequisites for geitonogamy within the inflorescences of the same cluster are present. Pollinators would not look for an inflorescence far away when being next to one of the same cluster. As such inflorescences which had a genetically identical pollen source showed an average fruit set of 50–70%, self-compatibility may be regarded to occur.

On the other hand, an inflorescence, which showed female and male anthesis simultaneously (see anomalies), did not bear any fruit. At least in a few pistillate flowers pollination by gravity should have occurred. One must exclude the possibility of self-compatibility in this case.

We may not expect a clearcut distinction between the two breeding systems considered, since even species where self-incompatibility has been established may set fruit to a certain extent (Bawa 1979). There are data for rates of self-compatibility in *Bactris gasipaes* (Clement and Arkcoll 1984) but they are without quantitative significance, as controls showed the same output of mature fruit as the self-compatibility rate stated. However, the data are appropriate to suggest the occurrence of self-compatibility in *B. gasipaes*. We see that without a profound series of specific experiments there is no solution to this problem.

Vegetative reproduction (clustering) is for two reasons an important part of the reproductive cycle of *Desmoncus*. First, the individual extends its life span and second, the number of inflorescences provided per individual is dramatically increased, thus influencing the flowering dynamics of the population. Vegetative reproduction in *Desmoncus* therefore seems to favor sexual reproduction, while an effective pollination system and

pollinator breeding provides outcrossing by beetles (*Drosophilidae* and halictid bees) and production of seeds.

Acknowledgments

I am indebted for determinations to H. Rainer (Vienna), J. F. Voisin and R. Vincent (Paris), C. H. C. Lyal (London), and D. W. Roubik (Panama). W. Morawetz (Vienna) and A. Henderson (New York) read and commented on the manuscript, for which I am grateful. I wish to thank M. Roithmair for her pleasant and creative company in Peru and Vienna. The permission of the Ministerio de Agricultura y Alimentacion to conduct this study in Peru and financial support from the Austrian FWF (P 6399-BIO), (P 8297-BIO) and the BMFWF (GZ 55.442/245-19/88) is gratefully acknowledged.

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