

Observations on Pollination of *Cryosophila albida*

ANDREW HENDERSON

The New York Botanical Garden, Bronx, New York, NY 10458

ABSTRACT

Morphology, phenology, and insect visitors of *Cryosophila albida* inflorescences were observed in the tropical wet forest of Costa Rica. These observations, which included inflorescence temperature elevation, scent, protogyny, and beetle visitation, indicate that this species is cantharophilous.

The pollination of palms has long been discussed (see Schmid 1970b, for references), but only recently have detailed field investigations been undertaken (Uhl and Moore 1977). Although it was often assumed that the family was predominantly anemophilous, these investigations have shown a variety of previously unsuspected insect pollination mechanisms (e.g., Beach 1984, Schmid 1970a, b). Three genera of the least specialized coryphoid group have been studied. Read (1975) showed *Thrinax parviflora* to be wind pollinated; Shuey and Wunderlin (1977) showed *Rhapidophyllum hystrix* to be beetle pollinated; and Brown (1976) showed *Sabal palmetto* to be bee pollinated.

Cryosophila is a genus of approximately 8 species in the *Chelyocarpus* unit of the coryphoid group (Moore 1973). It is distributed from western Mexico to northern Colombia. While the generic relationships (Moore 1972) and floral anatomy (Uhl 1972) of the genus are relatively well known, the species are not. Croat (1978) considered that *C. albida* Bartlett could not be distinguished on key characters (Allen 1953) from *C. guagara* Allen or *C. warszewiczii* (Wendl.) Bartlett.

Until now little was known of the reproductive biology of the genus. Moore (1972) stated, "A possibly specialized mode of pollination is suggested by the arrangement of the anthers at anthesis." Both Uhl (1972) and Read (1965) suggested the genus was protandrous. Bullock (1981) listed *C. albida* as beetle pollinated.

Materials and Methods

The study site was the Organization for Tropical Studies' La Selva Field Station, situated near Puerto Viejo on the Atlantic Coastal Plain of Costa Rica. Holdridge et al. (1971) classified the life zone as Tropical Wet Forest.

Twelve inflorescences were observed from 27th July-2nd August, and 25th August-4th September, 1983. Morphology was studied in the field, and in the laboratory using a dissecting microscope. Representative collections of flowering material were preserved as herbarium specimens. Pollen reference slides were prepared according to the method of Beaty (1971). A photographic record of inflorescence development was made.

Inflorescence phenology was observed throughout the study period. Stigma receptivity was tested with peroxidase paper. Inflorescence temperature was measured with a digital thermometer (Thermistor Series 44, Atkins Technical Inc., Gainesville, Florida 32608).

Insect visitors and their behavior were noted, and representative specimens preserved in ethanol.

Morphology

At La Selva *C. albida* was a frequent component of the understory, occurring in isolated populations, often on sloping ground or in valley bottoms. It had a solitary trunk, up to 6 m tall and 10 cm in diameter, covered with branched root-spines and supported by a cone of prickly stilt roots. The spreading crown contained up to 25 induplicate palmate leaves.

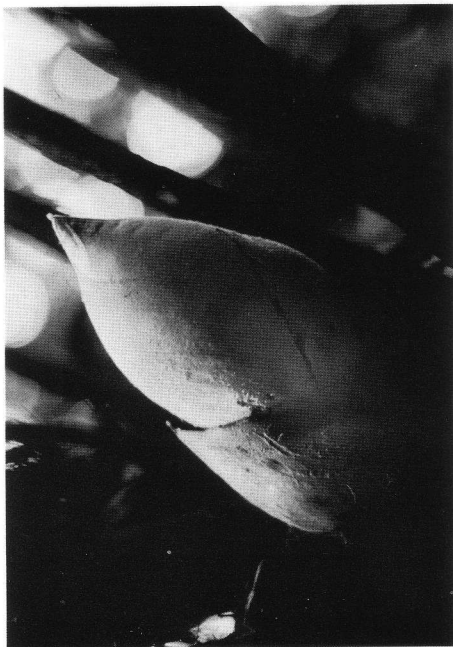
The pendulous inflorescences were interfoliar, reaching 50 cm long. The peduncle bore a green, sheathing, persistent prophyll, and 4 sheathing, persistent peduncular bracts. The rachis bore up to 25 once-branched primary branches, and each of these was subtended by a deciduous rachis bract; these rachis bracts became progressively smaller, ranging proximally from 15 cm to distally 2 cm long. The outward-facing surface of both peduncular and rachis bracts was covered with cottony, intertwined trichomes.

The flowers were perfect, borne singly in spiral rows along the rachillae. The proximal rachillae bore up to 120 flowers, the distal up to 60. The flowers were sessile, each subtended by a minute bracteole. The 3 ovate sepals were 3 mm long and connate basally. The 3 imbricate petals were 4 mm long. The filaments were connate basally into a tube and free above. When exerted, the 6 anthers spread at an angle of 90° to the filaments. They were dorsifixed, and dehisced laterally by longitudinal slits. There were 3 separate carpels, with narrow stigmas 1 mm long.

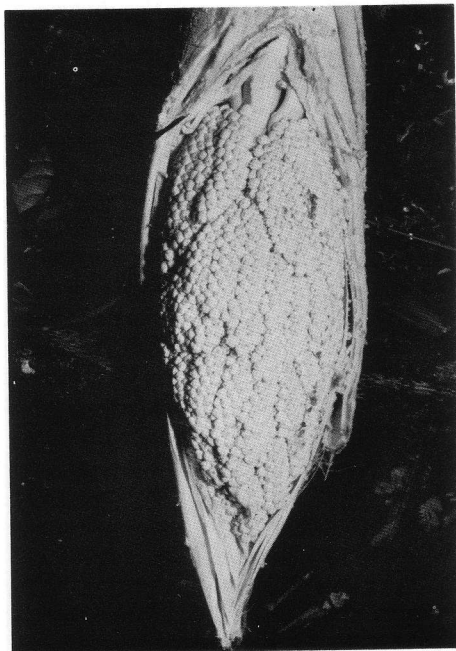
All inflorescence parts were ivory colored, except the prophyll.

Inflorescence Phenology

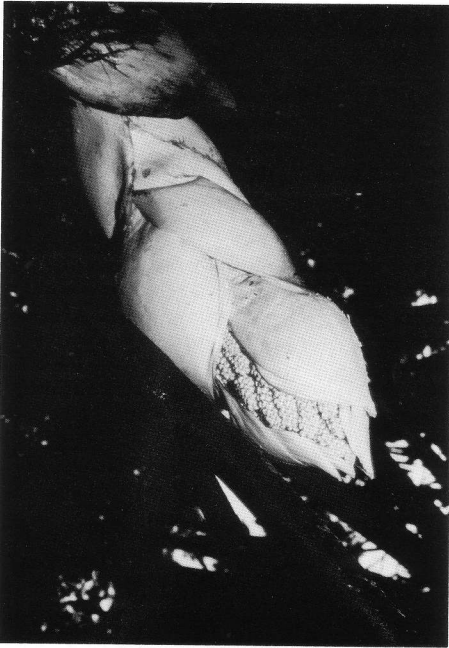
Frankie et al. (1974) listed *C. albida* as flowering in June. Beach (pers. comm.) reported flowering in July and August. In the present study, of 80 plants with trunks over 2 m censused, 2 were flowering at the end of July, and 14 at the end of August.



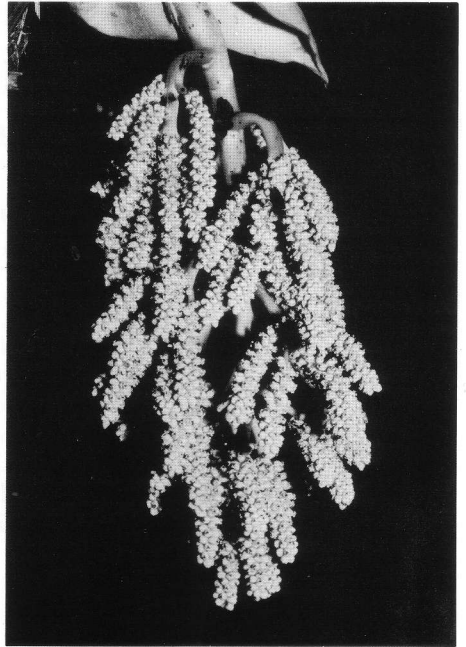
1. Inflorescence bud covered by prophyll and sterile bracts.



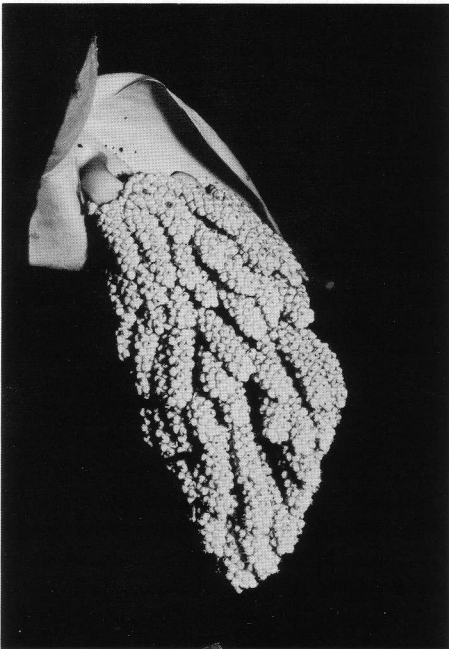
2. Inflorescence bud with sterile and fertile bracts cut away, showing flowers at pistillate anthesis with white receptive stigmas.



3. Inflorescence bud on morning of opening. Distal fertile bracts have fallen off and folded rachillae are visible. Stigmas brown and no longer receptive.



5. Inflorescence on second morning of opening, showing outer flowers at staminate anthesis.



4. Inflorescence with all fertile bracts fallen and rachillae still folded.



6. Inflorescence with rachillae in their final position.

The developing inflorescence buds were tightly enclosed; firstly, up to 12 cm long, by the prophyll; then, up to 20 cm long, by prophyll and peduncular bracts (Fig. 1); and finally, up to 30 cm long, by prophyll, peduncular and rachis bracts. ('Inflorescence bud' was defined as the developing inflorescence enclosed by its bracts, and 'bud opening' as the time when internal pressure pushed the bracts apart, making the flowers visible.)

At least 36 hours prior to opening, the temperature inside the bud rose. The average difference between bud and air temperature during the day (0600-1800) was 2.2° C, and the average difference during the night (1800-0600) was 3.2° C. Concomitant with temperature elevation, the bud gave off a strong scent, similar to that of lilac but also slightly unpleasant. Pistillate anthesis also took place at least 36 hours prior to bud opening. The white, glistening stigmas were exerted and receptive on all flowers within the closed bud (Fig. 2).

Bud opening took place gradually during the early morning, before dawn. Distal rachis bracts parted at the apex, forming an opening into the inside of the inflorescence. Temperature rose steeply during this period, reaching a maximum recorded difference of 7.6° C at 0900.

During the morning of bud opening the rachis bracts gradually fell from the bud, starting distally, revealing the closely bunched and folded rachillae (Figs. 3,4). As soon as flowers were visible, the stigmas were found to be brown, shrivelled, and no longer receptive. Staminate anthesis began during mid-morning. The first anthers to become exerted and dehiscence were on flowers located at the base of rachillae, and thus 'hidden' in the center of the inflorescence. Exserted anthers were at an angle of 90° to their filaments, positioning the anthers to dehiscence in the limited space available. By midday the center of the inflorescence bud was covered with pollen, although none was visible exter-

nally. Staminate anthesis continued on internal flowers throughout the day.

During the night following bud opening rachillae started to move from their original folded position parallel to the rachis, and began to straighten up. The following morning staminate anthesis took place on outward-facing flowers (Fig. 5). Rachillae continued straightening, finally reaching a position at right angles to each other (Fig. 6). Large numbers of flowers began dropping from the inflorescence.

The above events, recorded on the most closely observed inflorescence, and corroborated on others, appeared to represent the general pattern of phenology. However, on two inflorescences there was a slightly different sequence of events. Following bud opening, not all visible stigmas were brown, but approximately 5% were still white and receptive, and remained so for 24 hours. Staminate anthesis was also delayed for 24 hours following bud opening, by which time the rachillae had nearly reached their final position perpendicular to the rachis.

It was observed that many individuals in the same population flowered together, but sequentially so that different stages in development overlapped.

Insect Visitors

The following insects were observed visiting inflorescences:

COLEOPTERA

Curculionidae
Nitidulidae
Staphylinidae
Scarabaeidae

Derelominus sp.
Mystrops sp.
Unidentified sp.
Cyclocephala amazona (L.)

DIPTERA

Canopidae
Syrphidae

Unidentified sp.
Volucella sp.

DERMAPTERA

Unidentified sp.

ISOPTERA

Termitidae *Nasutitermes corniger* (Motsch.)

HYMENOPTERA

Apidae *Trigona* spp.
Formicidae *Paraponera* sp.
(Ponerinae)

ORTHOPTERA

Tettigoniidae Unidentified sp.
(Decticinae)

LEPIDOPTERA Unidentified larvae

HOMOPTERA Unidentified sp.

During the 36 hour period prior to bud opening numerous curculionids, fewer nitidulids, and some scarab beetles were observed on the inflorescence bud. They arrived during the night, and crawled over the bud, apparently trying to enter it. During daylight hours they congregated under the prophyll. *Trigona* spp. and canopid flies were occasional daytime visitors to the bud. *Paraponera* sp. also visited, and one was observed capturing a bee. Unidentified caterpillars were seen boring a hole into one inflorescence bud, eventually causing it to blacken and rot. Similar damage was seen on two other plants.

By dawn of the morning of bud opening hundreds of weevils and small beetles were present on, and inside, the bud. Fewer scarabs were present, and a maximum of six were seen on any one inflorescence. During the day, as staminate anthesis began, small flies and bees became more numerous. Bees were observed crawling inside the bunched rachillae in order to collect pollen from internal flowers. During the daylight hours all Coleoptera hid inside the center of the inflorescence, or under the peduncular bracts, perhaps in order to escape predators.

During the night following bud opening two unidentified Orthoptera were observed feeding on exserted parts of the flower buds.

On the second day following bud opening, as the rachillae began straightening,

it was observed that most Coleoptera had left the inflorescence. Extensive insect damage could be seen at this time. Most stigmas and anthers had been eaten off, rachis and rachillae had sections stripped from them, and both peduncular and rachis bracts showed signs of damage, including areas in which trichomes had been eaten away.

Termites, *Nasutitermes corniger*, were observed building a nest under the persistent peduncular bracts of one immature infructescence.

Discussion

The small sample size and short study period limit a detailed analysis of *C. albida* pollination. However, inflorescence phenology and morphology preclude self-pollination and wind pollination, respectively. Correlation of morphology, phenology, and insect visitors indicate that this species is beetle pollinated, and the following mechanism is suggested.

The nocturnal pattern of inflorescence bud temperature elevation during the 36 hour pre-opening period causes, or works in conjunction with, scent production. Night-active Coleoptera, especially curculionids, are attracted by this scent. The inflorescence bud acts as a source of food. During the night of bud opening, incoming Coleoptera have access to the inside of the inflorescence bud, through the entrance formed by the parting of the distal rachis bracts. Once inside the bud, they come into contact with flowers at pistillate anthesis, and must crawl over these to reach the center of the bud. During the daylight hours following bud opening, Coleoptera hide in the center of the bud, in the spaces formed by the folded rachillae. Staminate anthesis at this time on internal flowers ensures that Coleoptera become covered in pollen. During the following night, as the rachillae begin to straighten, and scent and temperature decrease, pollen-covered Coleoptera leave the inflorescence and fly to another one.

If they arrive at an inflorescence bud at pistillate anthesis, they will pollinate it. Of the 4 species of Coleoptera observed, by far the most numerous were curculionids, and for this reason *Derelominus* sp. is considered the major pollinator. The nitidulids, *Mystrops* sp., collected were all females. Few scarabs were observed or collected, and were considered too large to be effective pollinators. Other insects were either pollen robbers, or fed on inflorescence tissue.

Essig (1973) also found curculionid pollination in a New Guinea palm, *Hydriastele*. He reported that the pollinator was a member of the pantropical tribe Derelomini, and that this tribe probably occurred exclusively on palm flowers. He considered that this specificity raised interesting questions about the apparent pantropical co-evolution of palms and weevils. Study of *Cryosophila* supports Essig's findings. Mora Urpí and Solís (1980) and Mora Urpí (1982) also found a member of this tribe, *Derelomus palmarum*, pollinating *Bactris* in Costa Rica and South America. Beach (1984) studied *Bactris* pollination in Costa Rica. He found curculionids, but also stressed the role of a scarab, *Cyclocephala amazona*, as co-evolved pollinator.

Uhl and Moore (1977) correlated inflorescence structure and floral anatomy in six genera of palms. Is there any correlation between *Cryosophila* structure and anatomy, and its proposed pollination mechanism? Uhl (1972) described the floral anatomy of the genus. She found that the perianth parts formed a 'protective fence' around the inner organs. Petals and sepals contained frequent tannin cells, abundant raphides, and vascular bundles with fibrous caps. Since *Cryosophila* pollination involves beetle feeding on inflorescence tissue and pollen, there does appear to be a correlation between pollination and anatomy. Although beetles are attracted, and feed on inflorescence tissue, anthers and ovules are protected by

the perianth. Field observations supported this. No insect damage was seen to sepals or petals, although inflorescence branches and bracts all suffered damage. The trichomes covering the peduncular and rachis bracts appeared to be a major food source.

Another protection device, to balance the attraction of the inflorescence as a food source, are the peduncular and rachis bracts covering the bud at pistillate anthesis. Also, as Uhl and Moore (1973) pointed out, the root spines on the stem prevent other predators reaching inflorescences, or infructescences.

What is the significance of the proposed pollination mechanism for *Cryosophila*? The mechanism fits Eames' (1961) suggestion that palms may have been primitively beetle pollinated. Gottsberger (1977) distinguished between an unspecialized beetle pollination syndrome and a specialized one. *Cryosophila* pollination agrees well with the specialized syndrome of small flowers crowded together on the inflorescence. However, the relatively advanced *Bactris*, in the cocosoid group, has been shown by Mora Urpí and Solís (1980), Mora Urpí (1982) and Beach (1984) also to be beetle pollinated in Costa Rica, and to have some features in common with *Cryosophila*. *Bactris* exhibits protogyny, temperature elevation (Schroeder, 1978), and beetle visitors at night. The similarity in pollination which the coryphoid *Cryosophila* shares with the cocosoid *Bactris* and coryphoid *Rhaphidophyllum*, and the way in which it differs from the coryphoid *Thrinax* and *Sabal*, emphasizes the difficulty of trying to assign primitive pollination types. In the Atlantic lowland forest of Costa Rica over 100 different plants in various families are known to be beetle pollinated (Schatz, pers. comm.). *Cryosophila albida* is part of this cantharophilous flora.

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