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FLOWERING PHENOLOGY AND POLLINATION ECOLOGY OF *CRYPTANTHUS DIANAE* LEME: A CASE OF FLORAL FRAGRANCE-COLLECTING BY EUGLOSSINAE BEES IN BROMELIACEAE

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ABSTRACT. *Cryptanthus* Otto & A.Dietrich, one of the most distinctive genera in the Bromeliaceae, is endemic to Brazil. The flowering phenology and floral biology of *Cryptanthus dianae* Leme were studied in natural sites in Tapacurá Ecological Station and Natural heritage private reserve (RPPN) Frei Caneca, both located in Pernambuco. *Cryptanthus dianae* flowers once a year, with one to four flowers opening per day. The species is andromonoecious with a predominance of male flowers during the beginning of the blooming period. Flowers emerge in the central apical area of the inflorescence and more rarely in the peripheral basal area of the rosette where the hermaphrodite flowers open. Visits by hummingbirds (*Phaethornis ruber*), flies, diurnal moths (*Saliana* sp.), and bees (*Euglossa cordata, Eulaema nigrita, Trigona* sp.) were observed. According to the behavior and frequency of visits, the Euglossini males appear to be the main pollinators. During floral visits, *Euglossa cordata* and *Eulaema nigrita* scrape the petals, filaments and style with their forelegs, thus suggesting that odor is an additional floral resource in addition to the pollen and nectar. This is the first report of the presence of floral odor in Bromeliaceae as the primary attractive.

Key words: flowering phenology, *Cryptanthus dianae,* Bromeliaceae, andromonoicy, pollination, Euglossini bees, melitophily, perfume flowers, Atlantic Forest

INTRODUCTION

The phenology and floral biology in Bromeliaceae has been systematically studied during this last decade (Sazima et al. 1989, Martinelli 1997, Siqueira Filho & Machado 1998, 2001, 2007, Buzato et al. 2000, Varassin & Sazima 2000, Araújo et al. 2004, Machado & Semir 2006). These and earlier studies highlight hummingbirds (Sazima et al. 1995a) and bats (Sazima et al. 1989b, 1995b), as the main groups of pollinators for Bromeliaceae. There are also indications of reciprocal coevolution between the birds and this plant family in the neotropics (Sick 1997).

In contrast, insect pollination in Bromeliaceae has received little discussion until now. Insect pollination has been inferred based on floral morphology (Gardner 1986, Ramírez 2001), and there are reports of bees being effective pollinators for some bromeliad species (Nara 1998, Siqueira Filho & Machado 1998, 2007; Araújo et al. 2004).

Flowers that produce odor as a reward for Euglossinae bees have been recognized in only a few families of angiosperm such as Aristolochiaceae, Asclepiadaceae, Araceae, Burmanniaceae, Gesneriaceae, Orchidaceae, and Solanaceae (Ackerman 1986, Vogel 1990, Sazima et al. 1993, Endress 1994), without any reference to the Bromeliaceae.

The *Cryptanthus* genus is endemic to Brazil between the states of Rio Grande do Norte and Rio de Janeiro, occurring in coastal Atlantic Forest, "Campos rupestres" (grassland on rocky soil at high altitudes), "Restinga" (sandy coastal plain vegetation), and "Caatinga" (deciduous vegetation in semi-arid areas of northeastern Brazil). *Cryptanthus* is composed of 58 species (Leme & Siqueira Filho 2006, Luther 2006), which are typically terrestrial or saxicolous. Habitat fragmentation and apparent short distance seed dispersal have contributed to the genus becoming rare and threatened (Siqueira Filho 2002). There are few studies on *Cryptanthus* floral biology, and the focus of this investigation deals with the phenological strategies of *C. dianae,* emphasizing the role of male Euglossinae bees on its pollination.

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MATERIALS AND METHODS

Study Sites

The field work was conducted between March 1997 and April 2001 with naturally occurring clusters of *C. dianae* in two sites in the state of Pernambuco, Northeastern Brazil. "Mata do Camucim" (8°04′00″S; 35°14′00″W, 85 msm), a fragment of seasonal semi-deciduous forest (IBGE, 1992), belonging to Tapacurá Ecological Station, in São Lourenço da Mata. This forest area covers some 386 hectares, with a mean annual rainfall of 1.284 mm (N = 14 years) (Carvalho & Machado 2002, Lopes 2002). The second area is "Mata da Serra do Quengo" (8°42′37″S, 35°50′01″W, 700 msm), with approximately 630 hectares of montane forest belonging to Frei Caneca Private Natural Heritage Reserve (Reserva Particular do Patrimônio Natural—RPPN) in Jaqueira municipality, with a mean annual rainfall of 1332 mm.

Flowering Phenology

Observations of the flowering activity of four individual specimens of *C. dianae* were made between March 1997 and April 2001. The plants were daily monitored during the entire period of anthesis and the following observations were recorded: a) time of flowering per individual; b) total number of flowers produced per individual; c) total number of male flowers open per day per individual; and d) total number of hermaphrodite flowers open per day per individual. These data were used to determine the phenological pattern of *C. dianae,* according to the classification by Gentry (1974) and Newstrom et al. (1994).

Floral Biology

During study site visits data on floral morphology, color, odor, time, sequence and anthesis duration, number and disposition of floral parts, and nectar and pollen availability were registered. The neutral red test (Vogel 1990) was used to locate the source of the odor output. The number of pollen grains per anther of male (N = 10) and hermaphrodite (N = 2) flowers was estimated with a Neubauer chamber (Lloyd 1972). Schematic illustrations of the flowers and floral structures were made from fresh material fixed in 70% alcohol, with the aid of a camera lucida and a Willd stereomicroscope.

The volume and concentration of nectar production was registered in ten flowers isolated from the floral visitors in green house. The concentration of sugars in the floral nectar was measured in the field using pocket refractometer Atago® scale 0–32%. The total volume of nectar produced and accumulated per flower was measured by means of micrometric syringes (Hamilton®) of 10 and 25 μl.

Visitors

The behaviors of visitors to the flowers of *C. dianae* were observed in the field at different times of the day, supplemented by photography analysis. A total of 260 hours of observation were made during which the frequency, duration, time of visit, and behavior of the floral visitors were recorded.

Visiting insects were captured and sent to specialists for identification. All insect vouchers have been placed in the entomological collection at the Laboratory of Floral and Reproductive Biology, Universidade Federal de Pernambuco (UFPE), Brazil. The hummingbird was identified through comparison (Sick 1997).

Voucher Specimens

Botanical material of *C. dianae* has been placed in the Herbarium UFP—Geraldo Mariz (UFP 18697 and 30484), Universidade Federal de Pernambuco (UFPE), Brazil.

Statistical analysis. Differences in the average volume of nectar between male and hermaphrodite flowers were analysed by Kruskall-Wallis test, and the variance analysis was used to verify differences in the average concentration among the floral types.

RESULTS AND DISCUSSION

Flowering Phenology

Cryptanthus dianae presents an annual type of flowering pattern (sensu Newstrom et al. 1994) and blooms more intensely between June and September without an evident flowering peak. *Cryptanthus dianae* produces few flowers a day over an extended period of time ("steady state" flowering pattern of Gentry 1974), which has also been observed in *C. zonatus* and *C. bahianus,* although other species of this genus, such as *C. beuckeri, C. pseudopetiolatus* and *C. bromelioides* (Siqueira Filho & Machado in prep.) have an explosive flowering with several flowers in a few days ("big bang" flowering pattern of Gentry 1974). The flowering period of an individual of *C. dianae* lasts, on average, 33 ± 3.79 (N = 3, mean ± SD) days. In other species of the genus, it can last from seven (*Cryptanthus beuckeri*) to 60 days (*Cryptanthus zonatus*) (Siqueira Filho & Machado in prep.).

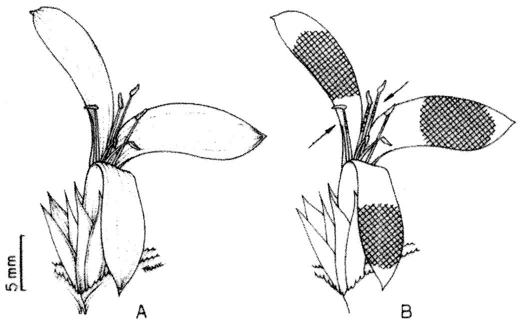

FIGURE 1. **A.** Schematic representation of the male flower of *Cryptanthus dianae* and **B.** Shaded areas on the mid-distal regions of the petals and stamen filaments (arrows) were colored with red neutral scraped by Euglossinae bees.

In *C. dianae,* a total of 30.67 ± 11.06 (*N* = 3) flowers open, with a daily variation between one to four flowers. Although other Bromeliaceae species, such as *Canistrum aurantiacum,* presents similar characteristics with a steady state type of flowering (Siqueira Filho & Machado 2001), *Hohenbergia ramageana* (=*H. ridleyi*) has a cornucopia type of flowering producing several flowers over a long period (Siqueira Filho & Machado 1998). From the total of 21 ± 10.15 (*N* = 3) of the *C. dianae* flowers produced, 68.5% were male (FIGURE 1), a little less when we compared to over 80% in *Cryptanthus beuckeri, C. sinuosus* and *C. ubairensis* (Siqueira Filho & Machado in prep.). Only 9.67 ± 1.15 (*N* = 3) of the flowers in *C. dianae* are hermaphrodite.

Floral Biology

The species of *Cryptanthus* subgenus *Cryptanthus,* like *C. dianae* are andromonoecious (sensu Lloyd 1972), while those belonging to subgenus *Hoplocryptanthus* (sensu Ramírez 1998) are hermaphrodite. *Cryptanthus dianae* is a small terrestrial, and generally shade-loving species. The flowers have three free, white petals, three basally conate sepals and six stamens in the male flowers; the hermaphrodite flowers contain also a pistil. The petals are spreading and expose the reproductive structures.

The male flowers, according to Bawa and Beach (1981), are designed to attract pollinators and for pollen dispersal, while the hermaphrodite flowers would be responsible for fruit formation. In *C. dianae,* the male flowers are about 36 mm long, while the hermaphrodite flowers are about 45 mm long. The flowers are diurnal with anthesis starting at 05.30, extending until about 12.00, when the petals and reproductive structures are drooping. Teratology was observed in some flowers that has four petals and eight stamens or two petals and three stamens. A similar fact has been reported to *Aechmea recurvata* var. *benrathii, Dyckia reitzii,* and *D. tuberosa* (Reitz 1983); these cases are, however, uncommon.

Although *C. dianae* does not possess a perceptible odor, there is a group of *Cryptanthus* species that emit a delicate, sweet fragrance (Ramírez 1996) that could be associated with the presence of osmophores. Some flowers of *Tillandsia* and *Vriesea* species also emit odor (Benzing 2000) as secondary attractive, associated with pollination by insects or bats.

Although they are found simultaneously, the staminate flowers usually appear before the hermaphrodite ones, and tend to be produced more intensely at the beginning of the blooming period. The staminate flowers typically are located in the apical center of the inflorescence, and less so in the peripheral-basal parts, where the hermaphrodite flowers are found and where the fruits will be formed.

The average volume of nectar in male flowers was 7.78 µl ± 2.44 (*N* = 8), with an average concentration of sucrose equivalents of 27.11% ± 1.38 (*N* = 8). Similar amounts were found in hermaphrodite flowers, with a volume of 8.87 µl ± 6.13 (*N* = 6) and sucrose concentration of 25.47% ± 2.57 (*N* = 6). No significant difference in nectar volume and concentration was found between the male and hermaphrodite flowers, through G test. The measured volumes and concentrations of the nectar found here are similar to those obtained in Bromeliaceae communities in both low-altitudinal Atlantic Forest (Siqueira Filho & Machado 2001, Lopes 2002) and at high-altitudes (Sazima et al. 1996, Siqueira Filho & Machado 2007), making the Bromeliaceae family among the richest in nectar concentration in the Atlantic Forest of southeast Brazil, with an average concentration of 28.9% (see Buzato et al. 2000).

Usually one to three axillary vegetative shoots are produced after flowering. According to Siqueira Filho & Leme (2006), a similar production has also been observed in *C. zonatus, C. pseudopetiolatus* and *C. bromelioides,* although propagation through long stolons is also known (*C. burle-marxii, C. sinuosus*). These shoots can also be apical and start to develop even during the flowering period (*C. bahianus, C. pickelii*).

Fruit development and seed dispersal in nature are still largely unknown. The seeds of *Cryptanthus,* like those of *Acanthostachys* and *Bromelia,* are the biggest of the family, but with a small number of seeds per fruit (Benzing 2000). The sticky *Cryptanthus* seeds and its ap-

TABLE 1. Visitors in *Cryptanthus dianae* and their sizes, site of record, and reward collected. C—Camocim Forest, SQ—Serra do Quengo Forest, PO—Pollination, RO—Robber.

Visitors	Size (mm)	Site	Reward	Result of visit
Apidae				
Bombinae				
Euglossini				
Euglossa cordata ♂♀	12	SQ	Odor, nectar	PO
Eulaema nigrita ♂	21	C/SQ	Odor	PO
Apinae				
Trigonini				
Trigona sp. ♀	7	SQ	Pollen, petals, anthers	RO
Chrysomelidae				
Alticinae				
Zepherina virgilia Bech.	4	SQ	Petals, anthers	RO
Hesperiidae				
Saliana sp.	20	SQ	Nectar	RO
Diptera				
Sp.1	10	C	Nectar	
Phaethornithinae				
Phaethornis ruber	24*	SQ	Nectar	PO

* Size of beak of hummingbird.

pendages may have an important function in adherence to dispersing organisms and/or substrates (Siqueira Filho & Leme 2006). Germinating seeds produce slow growing seedlings near parent plant. While in the "Camucim" forest the natural clumps of *C. dianae* are aggregated, forming dense carpets, at the "Serra do Quengo" site, the plants are mainly dispersed or isolated influencing the behavior of the pollinators.

Visitors and Pollinators

The floral attributes of *Cryptanthus,* white flowers, as well as the volume and concentration of nectar reported for the majority of the species studied, suggest bee pollination (sensu Faegri & Pijl 1979). Despite the melitophilous attributes of *C. dianae* a diversity of floral visitors were observed (TABLE 1), including flies, moths, beetles and hummingbirds, with the frequency of visitors varying in the different years.

Among the bees, *Trigona* sp. (FIGURE 2A) visited the flowers for long periods to collect pollen and floral parts such as anthers and petals. The opportunistic and robber behavior of *Trigona* species are known in literature (Sazima & Sazima 1989a, Roubik 1992). In some well known bird-pollinated species of bromeliads, such as *Billbergia morelli* and *Pitcairnia sprucei, Trigona* can even compromise the viability of the flower; this phenomenon seems to be related to the lack of resources or disturbance by man (Siqueira Filho & Machado 2007).

Males of *Eulaema nigrita* and *Euglossa cordata* (FIGURE 2C, D) were frequently observed scraping the petals of *C. dianae.* Females of this species were also seen collecting nectar, although less frequently. Females of *Euglossa cordata* visit the flowers of other Bromeliaceae like *Hohenbergia ridleyi* and *Aechmea lingulata* to collect pollen (Siqueira Filho & Machado 1998), as well as *Aechmea* sp., *Aechmea leptantha,* and *Pseudananas sagenarius* (J. Siqueira pers. obs.), all taxa with long tubular, typically ornithophilous flowers.

In other Bromeliaceae genera, such as *Neoregelia, Nidularium,* and *Canistropsis* that present white, blue, or lilac flowers and, as a rule, emit scent (Leme 1998), Euglossinae bees were observed taking nectar.

Several individuals of *Zepherina virgilia* (Chrysomelidae) were observed feeding on petals, anthers, and stigmas; and sporadically, *Saliana* sp. (Hesperiidae) was observed taking nectar from *C. dianae* flowers.

Phaethornis ruber (Trochilidae) was observed traplining the flowers of *C. dianae.* This hummingbird has been mentioned as an opportunistic feeder (Sazima et al. 1995a, Machado & Lopes 2000), because of its flexibility in behavior when foraging on flowers in the understory. *Phaethornis ruber* performs several roles in the ornithophilous community from territory parasite to low-reward traplining (sensu Feinsinger & Colwell 1978, Siqueira Filho & Machado 2001). Therefore, despite the melitophilous at-

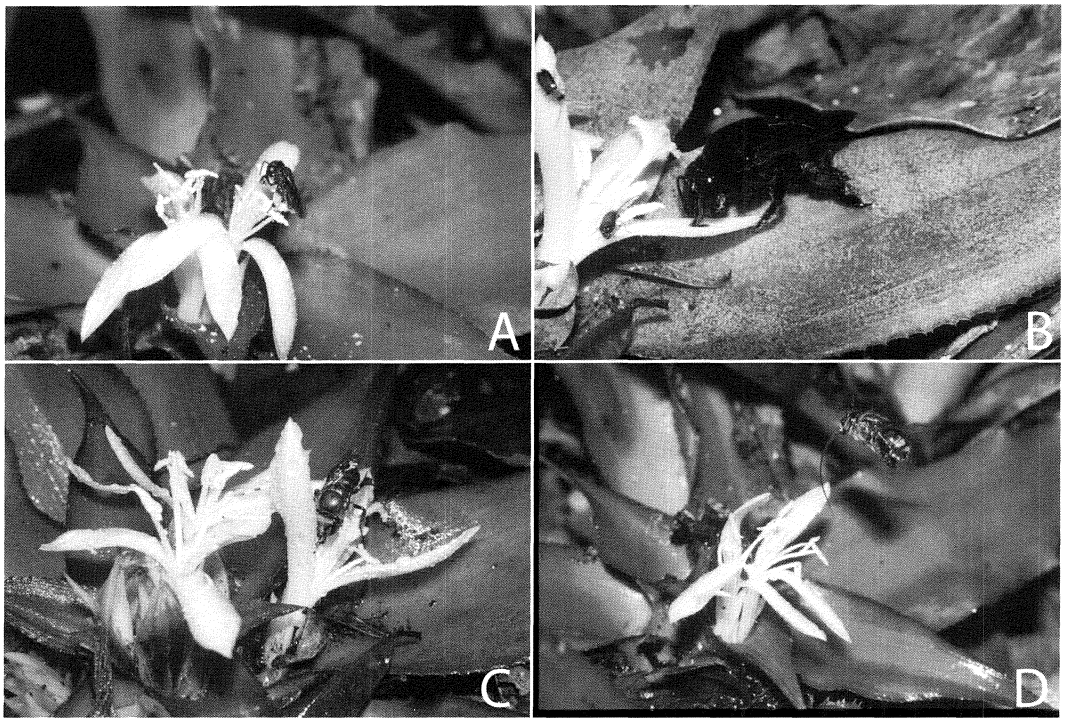

FIGURE 2. Floral visitors in *Cryptanthus dianae*. **A.** *Trigona sp.* collecting pollen. **B.** *Eulaema nigrita* ♂ scraping the petals. **C.** *Euglossa cordata* ♂ collecting nectar. **D.** *Euglossa cordata* ♂ hovers in flight to inspect the flowers of *Cryptanthus dianae* before alighting.

tributes of *Cryptanthus, P. ruber* may occasionally promote pollination, due to the contact of pollen and stigma with the beak and face of the hummingbird. It was further observed that the frequency of visits by *P. ruber* to the flowers of *C. dianae* varied according to the blooming period of *Sinningia nordestina* (Gesneriaceae), an ornithophilous species which is also typical of the understory in both study sites (Chautems et al. 2000). In fact, when the flowering of *S. nordestina* was more intense, *P. ruber* made fewer visits to the flowers of *C. dianae,* as observed in 1999. On the other hand, in 2000, a year of intense rainfall that did not favor the flowering of *S. nordestina, P. ruber* was seen more frequently on *C. dianae.*

Behavior of Male Euglossinae Bees

One to three individuals of *E. nigrita* males were found on the same inflorescence of *C. dianae.* The bees hover around the flower before landing; these are return flight type movements when the flowers are not touched. When they land on the flowers, the bees begin scraping the petals exclusively with the tarsal region of their forelegs (FIGURE 2B), sometimes frenetically. They then move around the flowers, and also over the filaments and styles, which are handled in the same way as the petals, with the forelegs; the pollination is carried out in this fashion. The bees support themselves on the reproductive structures, remaining on the inflorescence and flowers for long periods (between 30–60 min). Sometimes, *E. nigrita* was seen to drop suddenly from the flowers as if it were "drunk," returning rapidly to scraping the floral components. The bees scrape the same flowers continuously and successively in the same floral regions. Zucchi et al. (1969) reports a similar behavior in Euglossinae males collecting odor from Orchidaceae flowers. Two bees may simultaneously visit the same inflorescence with four open flowers. Due to the intense scraping activity that may last an hour during one visiting session, the flowers can become damaged, especially the petal borders that turn brownish. Also the androecium and gynoecium may lose vigor, giving the flowers an aged appearance.

At regular intervals, the bee recedes from the inflorescence, hovers, and emits a typical buzz. At this time, it appears to be transferring the odor collected by its forelegs to its hind ones, joining its legs so that they are almost erect in full flight. The petal scraping occurs in the medium region of the two faces (adaxial and abaxial). No male *E. nigrita* were seen collecting nectar or pollen on *Cryptanthus* flowers.

Euglossa cordata behaved similarly to *E. nigrita,* but their visits were sporadic. Euglossinae are considered long-distance pollinators (Janzen 1971), and they can suffer from environment fragmentation (Powell & Powell 1987), which might explain the low frequency of visits of *E. cordata* to *C. dianae.*

Are There Osmophores and Perfume Flowers?

Regions with odor emission were detected in the testes with neutral red in both the medial, adaxial portion of petals, and in the apical portions of the filaments, being more intense in the petals, which might explain the bee's interest in these structures.

The high frequency of visits by *Eulaema nigrita* observed in flowers of *C. dianaea* and the visitation pattern of both species of Euglossinae are also suggestive for the presence of osmophores. This kind of behavior of Euglossinae bees in flowers of Bromeliaceae is registered here for the first time.

Indications of the presence of osmophores from the analysis of positive reactions to neutral red were already mentioned for other families as for *Constantia cipoensis* (Orchidaceae) pollinated by *Xylocopa* cf. *artifex* (Matias et al. 1996) and *Unonopsis guatterioides* (Annonaceae) pollinated by *Eulaema bombiformis* (Carvalho & Weber 2000). According to these authors, the behavior of the visitors also suggests the presence of osmophores, similar to what was reported here in *C. dianae.*

In this way, the flowers of *Cryptanthus* would be important to the reproductive success of the Euglossinae bees. The question of whether the odor in *Cryptanthus* is a resource that is only now being recognized by these bees or is a detail in the evolutionary history of the group remains, since the nectar is also available to pollinators in flowers of species of *Cryptanthus.* Even though the role of these fragrances is not sufficiently clarified through the pollination of *C. dianae,* we have another interesting and intriguing case involving Euglossinae bees and neotropical plants.

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