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# AROIDEANA

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**Front Cover:** *Anthurium virididifusiforme* Croat, Daniel Santamaria, A. K. Monro & J. Lezcano 7539 (isotype, PMA-70084). Infructescence (left) inflorescence which has turned red after anthesis.

**Back Cover:** Two 88-butterflies (*Diaethria anna* Guérin-Méneville, Nymphalidae) interacting on a spadix of a cultivated individual of *Anthurium podophyllum* (Cham. & Schltdl.) Kunth in staminate anthesis.

# Lepidopteran visitors of *Anthurium* inflorescences

Nathan Hartley  
Department of Biology  
Duke University  
Durham, North Carolina, U.S.A.  
e-mail: [nph6@duke.edu](mailto:nph6@duke.edu)

Thorsten Krömer  
Centro de Investigaciones Tropicales  
Universidad Veracruzana  
Xalapa, Veracruz, México  
e-mail: [tkromer@uv.mx](mailto:tkromer@uv.mx)

Marc Gibernau  
CNRS- University of Corsica  
Laboratoire Sciences Pour l'Environnement  
(SPE – UMR CNRS 6134)  
Vignola, Rte des Sanguinaires  
20 000 Ajaccio, France  
e-mail: [gibernau@univ-corse.fr](mailto:gibernau@univ-corse.fr)

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## ABSTRACT

Observations on the pollination biology of the genus *Anthurium* are scant in comparison to other aroid genera despite comprising nearly 33% of all aroid species. Here we report two independent observations of lepidopteran visitors in two species of *Anthurium*. In Costa Rica, two different species of fruit-piercing moths (Erebidae) were observed visiting two separate individuals of *A. caperatum* in pistillate anthesis at night; however, no evidence for pollen vectorization was

obtained. In Mexico, several individuals of the 88-butterfly (*Diaethria anna*; Nymphalidae) were observed visiting *A. podophyllum* during the middle of the day. Additionally, pollen of *A. podophyllum* was observed deposited on the ventral abdomen of an 88-butterfly. These findings, although lacking the data needed to confirm their role as pollinators of these *Anthurium*, are significant in that they represent the first documentation of lepidopteran visitors for any species of aroid. A review of spadix secretions in *Anthurium* is also provided and an encouragement to augment the number

of studies on pollination biology of this genus is offered.

## KEY WORDS

Araceae, Pollination, Nectar, Stigmatic secretion, Tepal secretion, Erebidae, Nymphalidae

## INTRODUCTION

The genus *Anthurium* Schott is the largest aroid genus with 950 currently published species and an estimated total of 2000, which comprise about one-third of all species in the family (Boyce & Croat, 2016). Despite expressing great variation in inflorescence morphology and anthecology across species (Croat, 1980; Schwerdtfeger et al., 2002), *in situ* observations of *Anthurium* pollination are few in comparison to other aroid genera (Gibernau, 2011, 2016). Other studies have documented several visitors/pollinators of *Anthurium*: euglossine bees collecting resins and/or oily fragrances (Schwerdtfeger et al., 2002; Hentrich et al., 2010), curculionid pollinators seeking nutriment and probably a reproductive site (Franz, 2007; Gómez-Murillo & Cuartas-Hernández, 2016), thrips, bees or flies (van Dulmen, 2001; Schwerdtfeger et al., 2002; Gómez-Murillo & Cuartas-Hernández, 2016), and also hummingbird visits, the unique mention of possible vertebrate pollination in Araceae (Kraemer & Schmitt, 1999).

The two first authors have observed two different lepidopterans (butterflies and

moths) on the spadices of two different species of *Anthurium*, which both showed spadix secretions. Interestingly, lepidopterans have not yet been reported as pollinators of Araceae. Lepidopteran food resources are typically in liquid form (Jones & Jones, 2001); however, aroids and the genus *Anthurium* in particular are thought to be nectarless (Schwerdtfeger et al., 2002). Nectar is an energetically rich reward particularly exploited by high-energy demanding pollinators such as bees, bumblebees, butterflies, bats or hummingbirds (Willmer, 2011).

Two questions may be derived from these observations:

- Is lepidopteran pollination of *Anthurium* even possible?
- Are these observed spadix secretions nectar?

## OBSERVATIONS & DISCUSSION

### Moths

In June of 2016, the first author (N.H.) documented two nocturnal lepidopteran visitors on the inflorescences of *Anthurium caperatum* Croat & R.A.Baker growing along the Río Java trail at Las Cruces Biological Station, Costa Rica (**Figures 1 & 2**). *Anthurium caperatum* is morphologically circumscribed as an archetypical member of section *Cardiolonchium* and is characterized by a



**Figure 1.** A. The first of two unidentified species of fruit-piercing moths (Erebidae) on a spadix of *Anthurium caperatum* Croat & R.A. Baker in pistillate anthesis. This individual has its proboscis centered on a stigma, apparently feeding on a stigmatic droplet. B. Two individuals of the second unidentified species of Erebidae moth on another spadix of *A. caperatum* in pistillate anthesis. Photos taken by N.H. along the Río Java trail at Las Cruces Biological Station in San Vito, Puntarenas Province, Costa Rica, June 16th, 2016 around 10 pm local time.

terrestrial growth habit, short internodes, caducous cataphylls, large, cordate blades that dry green, a collective vein that runs from the tip of the basal lobes to the tip of the anterior lobe, and erect green spadices with flexed green spathes (Croat, 1983; Croat & Sheffer, 1983). John Rawlins at the Carnegie Museum of Natural History (Pittsburgh, PA, U.S.A.) identified photographs of the two different species of moths as belonging to the family Erebidae, which includes fruit-piercing moths, tiger moths and vampire moths. Although it cannot be discerned whether these Erebidae are pollinators (as no pollen was observed on their bodies), it is conceivable that these moths, which are known to feed by sucking on damaged/rotting fruit, were attracted to the rotten fruit floral bouquets presented by *A. caperatum* (Croat, 1980; Zaspel et al., 2011).

A total of three *A. caperatum* plants were observed in flower and were well-spaced along a 2 km stretch of the Río Java trail. The two species of Erebidae depicted in **Figure 1** were seen visiting two discrete plants in pistillate anthesis during a single night of observation. A third plant was found in staminate anthesis; however, no visitors were observed (**Figure 2**). All three individuals were emitting the same, pungent, rotten-fruit odor.

Both visited inflorescences were clearly in pistillate anthesis, with erect stigmas, each crowned with a minute stigmatic droplet (**Figure 1**). Furthermore, the spadices appeared glossy, humid and

glistening, which according to Croat (1980) is due to secretions from the spadix. Such secretions appeared to accumulate in inter-tepal grooves present throughout the length of the spadix (**Figure 1A**); however, this glistening quality appeared absent in the individual in staminate anthesis despite emission of the same rotten odor in both stages (**Figure 2**). A closer look at **Figure 1A** revealed that the visitor's proboscis was centered on a stigma, suggesting that the moth could be feeding from *A. caperatum* stigmatic droplets (and the inter-tepal accumulations) for nutrient acquisition, a typical resource in liquid form.

As many moths are active at night and thus have a great dependency on olfactory sensors to locate and discriminate resources (Zaspel et al., 2016), we hypothesize a pollination mechanism wherein odor production throughout both phases of anthesis in *A. caperatum* attracts erbid visitors equally, but for different intents and purposes. Pollen would be deposited on the ventral abdomen of a moth falsely lured onto a staminate spadix that lacks the potentially nutritious secretions. The subsequent encounter of another individual in pistillate anthesis offering secretions might prolong spadix visitation and potentially enhance pollen deposition and fertilization. Contrary to *A. digitatum* (Jacq.) Schott (a species belonging to section *Dactylophyllum*) documented by Daumann (1930, see below), it seems that the spadix of *A. caperatum* in staminate anthesis doesn't produce secretions (**Figure 2**). A variety of secretion dynamics



**Figure 2.** *Anthurium caperatum* in staminate anthesis, photo taken by N.H. along the same stretch of the Río Java trail as in figure 1. Although this individual also emitted a pungent odor, seemingly equivalent to conspecifics in pistillate anthesis, no visitors were observed.

may thus exist in *Anthurium* probably in relation to pollination, but this remains to be confirmed by precise studies on the temporal sequence and the composition of spadix secretions in *Anthurium*.

It is worth noting that the anthecology of *A. caperatum* was previously reported by Croat (1980) in a cultivated specimen at the Missouri Botanical Garden,

Saint Louis, MO, U.S.A. (Croat 44595). No odor was detected therein; however, observations were made during the day (9:00 AM–3:00 PM), so it remains possible that release of odor in *A. caperatum* is strictly nocturnal. Evidence for effective *A. caperatum* pollen vectorization by erebid moths and detailed observations on the anthecology of this species *in situ* are still needed before conclusions regarding

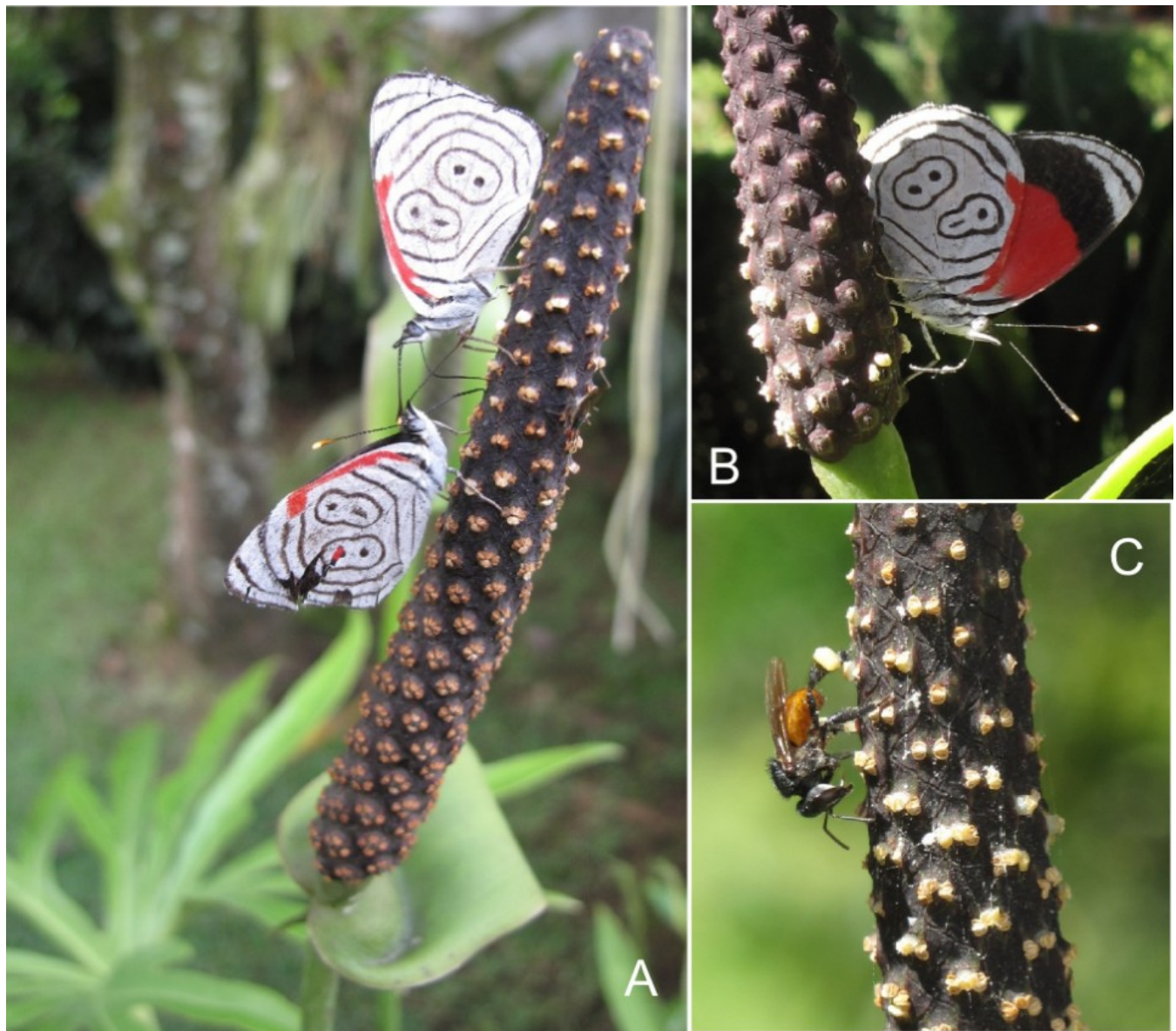
pollination mechanisms can be drawn; however, this discussion provides a framework for a potential research agenda that stresses the importance of both fieldwork and diurnal observations of *Anthurium* flowering behavior.

## Butterflies

In November of 2010 the second author (T.K.) observed 88-butterflies (*Diaethria anna* Guérin-Méneville, Nymphalidae) several times around midday on the inflorescences of two plants of *Anthurium podophyllum* (Cham. & Schldl.) Kunth cultivated within their natural distribution range in Mexico (**Figure 3A**). *Anthurium podophyllum* is a terrestrial or saxicolous species endemic to the states of Oaxaca and Veracruz (Croat & Acebey, 2015). It was traditionally placed in section *Schizoplacium* which included species with palmately lobed leaves that are specifically not completely dissected, in contrast to section *Dactylophyllum*, which are completely dissected (Croat & Sheffer 1983). In their phylogenetic work, sampling the breadth of *Anthurium* morphology and taxonomy, Carlsen & Croat (2013) found molecular evidence supporting the splitting of *Schizoplacium* and *Cardiolonchium* each into three discrete clades, as well as evidence for a clade containing species previously placed in both sections (clade 16). However, as neither *A. caperatum* nor *A. podophyllum* were sampled, the relations between these taxa remain ambiguous and we refrain from speculating on homology until such evidence becomes available.

T.K. obtained evidence for the 88-butterfly as an *Anthurium* pollen vector when he documented pollen deposition on the ventral abdomen and the proboscis of an individual of *D. anna* (**Figure 3B**). Two weeks before, when the inflorescence was in pistillate anthesis, this same species of butterfly was observed consuming stigmatic nectar droplets produced on the same plant. Such observations on both pistillate and staminate stages were performed over several weeks indicating reliable visits of both individual *A. podophyllum* plants by *D. anna*. Other insects (a stingless bee, a few drosophila and small "bugs") were also observed but not as consistently (**Figure 3C**).

Interestingly, the butterflies were only seen on inflorescences of the two cultivated *A. podophyllum* plants, apparently ignoring the nearby cultivated plants of *A. andicola* Liebm., *A. andreanum* Linden ex André and *A. longipeltatum* Matuda. We are not sure what might explain this species discrimination. It could result from differences in the quantity/quality of the spadix secretions or the floral fragrance of *A. podophyllum*, which may be particularly attractive to this butterfly species, although T.K. did not perceive any particular smell. The floral scent of *A. andreanum* has been described as floral and occurring in the morning during the pistillate phase (Kuanprasert & Kuehnle, 1999). The floral scent of *A. longipeltatum* is described as fruity, rich in lipid-derived compounds and probably attractive for drosophilid flies (Schwerdtfeger et al., 2002). Unfortunately,



**Figure 3.** A. Two 88-butterflies (*Diaethria anna* Guérin-Méneville, Nymphalidae) interacting on a spadix of a cultivated individual of *Anthurium podophyllum* (Cham. & Schltdl.) Kunth in staminate anthesis. B. An 88-butterfly with pollen deposited on its proboscis and abdomen from an *A. podophyllum* spadix in staminate anthesis. C. Stingless bee visiting and collecting pollen on an inflorescence of *A. podophyllum* in staminate anthesis. Photos taken by T.K. in Coatepec, Veracruz, Mexico, November 1st, 2010 around midday of local time.





**Figure 4.** Examples of *Anthurium* species with conspicuous spadix secretion. A. *A. martianum* K.Koch & Kolb, Botanical Garden of Munich, Germany. B. *A. digitatum* (Jacq.) Schott, Botanical Garden of Montreal, Canada. C. *A. llewellynii* Croat, Botanical Garden of Munich, Germany. D. *A. luteynii* Croat, Botanical Garden of Lyon, France. Photos taken by David Scherberich (<http://aroidpictures.fr/pictures.html>).

no data are available for *A. andicola*. As documented for several species, the floral fragrance of *Anthurium* can vary tremendously in accordance with a wide variety of volatile compounds identified in the genus (Kuanprasert & Kuehnle, 1999; Schwerdtfeger et al., 2002).

### Spadix Secretions

Spadix secretions in Araceae are in fact common, but not always conspicuous. Out of the 30 *Anthurium* species observed during the daytime, Croat (1980) found that almost half of them (14) were producing limited stigma secretion (6 species labelled glistening and 8 with minute drops only visible with magnification). The other 16 species produced visible secretions: 11 with small droplets (<1 mm in diam.) and 5 with large or runny secretions (>1 mm diam.).

Most species in section *Pachyneurium* produce stigmatic droplets during pistillate anthesis (Croat, 1991). In natural situations these droplets are rarely allowed to accumulate, apparently being removed by floral visitors or pollinators. However, in cultivation the droplets may accumulate to such an extent in some species, e.g., *A. upalaense* Croat & R.A.Baker, *A. validifolium* K.Krause, and especially *A. luteynii* Croat (**Figure 4D**), that the secretions drips off the spadix (**Figure 4**). Other species, such as *A. concolor* K.Krause, may also produce droplets of “nectar” on the tepals (Croat, 1991). However, the term “nectar” here may have been used erroneously (see below). Engler (1905, page 12) mentioned sugar-

containing stigmatic droplets in *Anthurium* for the first time, whereas Daumann (1930) properly described tepal secretions in *A. digitatum* while proving the presence of fructose, glucose and sucrose in the stigmatic droplets of this species (**Figure 4B**).

*“At the beginning of the anthesis, the hitherto hidden, few-celled stigma hairs protrude over the surface of the ovary and begin to separate the fluid. Towards the end of the female phase of a portion of the spadix, these secretions reach their maximum size, and a secretion from the already mentioned septic clefts of the free parts of the perianth begins, so that also smaller drops appear on the tepals. . . This secretion still increases, and continues throughout the male phase of a portion of the spadix, at a time when the stigma hairs have already dried up, and pollen in sausage-shaped masses has already been found in various sites between the diverging tepals. The liquid droplets, which appear towards the end of the female phase, and especially during the male phase of a flower, on the free portion of each tepal, also contain monoses (fructose and glucose) and bioses (sucrose). The sugar content, after the reactions of formation of copper oxide and osazone crystals, is higher than in the stigma secretion.”* (Daumann, 1930).

Aroids and the genus *Anthurium* in particular are supposed to be nectarless (Schwerdtfeger et al., 2002). Are these spadix secretions nectar? The stigmatic fluid is consistently sweet and, in the case of *A. seibertii* Croat & R.A.Baker, it was reported to contain 8% sugar comprised of a combination of sucrose, glucose and fructose (L. Edwards, pers. comm. in Croat,

1980). In *Arum maculatum* L., a terrestrial species widespread across most of Europe and the Caucasus, the concentration of sucrose equivalent ranged between 9–12.5% in the stigmatic droplets tested. This sugar concentration was only slightly higher than that of the phloem in the same species (8% sucrose equivalent) (Lack & Diaz, 1991). In *Arum hygrophilum* Boiss. of Israel, the stigmatic droplets contained above 5% sugar (Koach, 1985).

The main functions of the stigmatic droplets (also called pollination drops) are pollen capture and germination, whereas nectar is a reward for interacting animals (Nepi et al., 2009). Consequently, the two kinds of secretion differ primarily in their volume, as stigmatic droplets (less than 250  $\mu$ l) are generally smaller than nectar secretions (Nepi et al., 2009). Secondly, they present different ranges of sugar concentrations: stigmatic droplet sugar concentrations range from 5–12 %, whereas nectar sugar concentration is almost without exception much higher (Nepi et al., 2009). Thirdly, of the three most common sugars – glucose, fructose and sucrose – sucrose is the most common form found in nectar, whereas it is fructose in stigmatic droplets (Nepi et al., 2009). As it remains unknown whether tepalar secretions are more similar to nectar or stigmatic droplets, even though Daumann (1930) indicated a higher sugar content in tepalar secretions than in stigmatic ones, further efforts are needed to assess if some *Anthurium* species do produce floral secretions with high sugary content more related to true nectar. Such

studies should start with the two species of *Anthurium* visited by the Lepidoptera documented herein.

## CONCLUSIONS

The extraordinary species diversity in the genus *Anthurium* is accompanied not only by an equally impressive diversity of pollinators (Gibernau, 2016), but also by different types of spadix secretion (Croat, 1980), which remain poorly studied and undoubtedly have many more interactions and intricacies to reveal. For example, midges (Cecidomyiidae) were observed visiting inflorescences of *A. citrifolium* Sodiro, *A. draconopterum* Sodiro, *A. lingua* Sodiro, *A. oxycarpum* Poepp., *A. pseudoclavigerum* Croat, *A. triphyllum* (Willd. ex Schult.) Brongn. ex Schott and *A. truncicola* Engl. both during day and night (Schwerdtfeger et al., 2002). Although these insects showed little activity on the spadices, both sexes were observed suggesting that spadices may represent a possible rendezvous site (Schwerdtfeger et al., 2002). In the present article, we provide the premier documentation for lepidopterans as potential pollen vectors in Araceae. Even if true nectar is not secreted by *Anthurium*, such secretions could still present a choice nutritive resource; however, chemical profiling analyses of these secretions (stigmatic and tepalar) are needed. We are optimistic that this article might serve to promote more observations on *Anthurium* pollination biology. Are lepidopteran visitors more common than previously thought? Are lepidopterans even capable of

functioning as effective *Anthurium* pollinators? These are just a few of the ecological questions that need to be answered in order to better understand the complex processes that have acted synergistically to produce the staggering diversities exhibited by one of the largest plant genera on Earth (Frodin, 2004).

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