

## Attraction of Pyrrolizidine Alkaloid Seeking Lepidoptera to *Epidendrum paniculatum* Orchids<sup>1</sup>

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### ABSTRACT

*Epidendrum paniculatum* orchids are pollinated by male, diurnal Lepidoptera that seek pyrrolizidine alkaloids, especially ithomiine butterflies. Experiments suggest that scent attracts pollinators to the orchid flowers. Visitations to orchids and movements of ithomiine butterflies suggest that these insects are capable of effecting pollination between individuals of *E. paniculatum* plants over long distances.

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### Resumen

Observaciones y experimentos indican que la orquídea *E. paniculatum* es polinizada por machos lepidópteros diurnos que buscan alcaloides pirrolizadinos, principalmente las mariposas del grupo Ithomiinae. Los experimentos indican que la fragancia de la orquídea es muy importante en la atracción de polinizadores. Observaciones sobre ecología de poblaciones indican que los ithomidos son capaces afectar polinización entre individuos de este orquídea que se encuentran a largas distancias.

OBTAINING PYRROLIZIDINE ALKALOIDS (hereafter PAs) is important to the courtship and defenses of male butterflies in the subfamilies Ithomiinae and Danainae, and of moths in the families Arctiidae and Ctenuchidae. For example, PAs are required for the biosynthesis of male pheromones, mating success, and the formation of multi-species leks (Pliske 1975a, b; Haber 1978; Boppré 1984; Boppré & Schneider 1985, 1989; Ackery & Vane-Wright 1985), and PAs provide a source of adult acquired unpalatability for ithomiine butterflies (Rothschild *et al.* 1979, Brown 1984). Major plant sources of PAs for ithomiine and danaine butterflies are from the genera *Heliotropium*, *Tournefortia*, and *Myosotis* (Boraginaceae) and *Eupatorium* species (Asteraceae), and Pliske (1975a, b) showed that PAs are fundamental to the pollination systems of these plants. Moreover, wilted *Heliotropium* and *Myosotis* plants are so attractive to ithomiines, danaines, and ctenuchids (Beebe 1955, Pliske 1975a) that they

can be used to census these Lepidoptera (DeVries 1987, Stiles, pers. obs.).

Among the most spectacular neotropical pollination systems are orchids that produce fragrances to attract male euglossine bees (Dodson *et al.* 1969, Williams & Dodson 1972, Williams 1982). In these systems, orchids produce volatile chemicals that bees ostensibly require for mating (Kimsey 1980), some of which are also obtained at other plants, and the orchids rely upon the bees for pollination (Williams & Dodson 1972, Williams 1982). Studies have indicated that flower fragrance, phenology, and morphology are correlated with species of bee pollinator and that different orchid species depend upon different species of bees to effect pollination (Williams 1982, Ackerman 1983, Roubik & Ackerman 1987). In tropical orchid species that exist at low population densities, euglossines are considered important as long distance pollen vectors (Janzen 1971, 1981; Williams & Dodson 1972).

In some respects the reliance of male euglossine bees upon chemicals obtained from orchids is paralleled by Lepidoptera that seek PAs. The orchid

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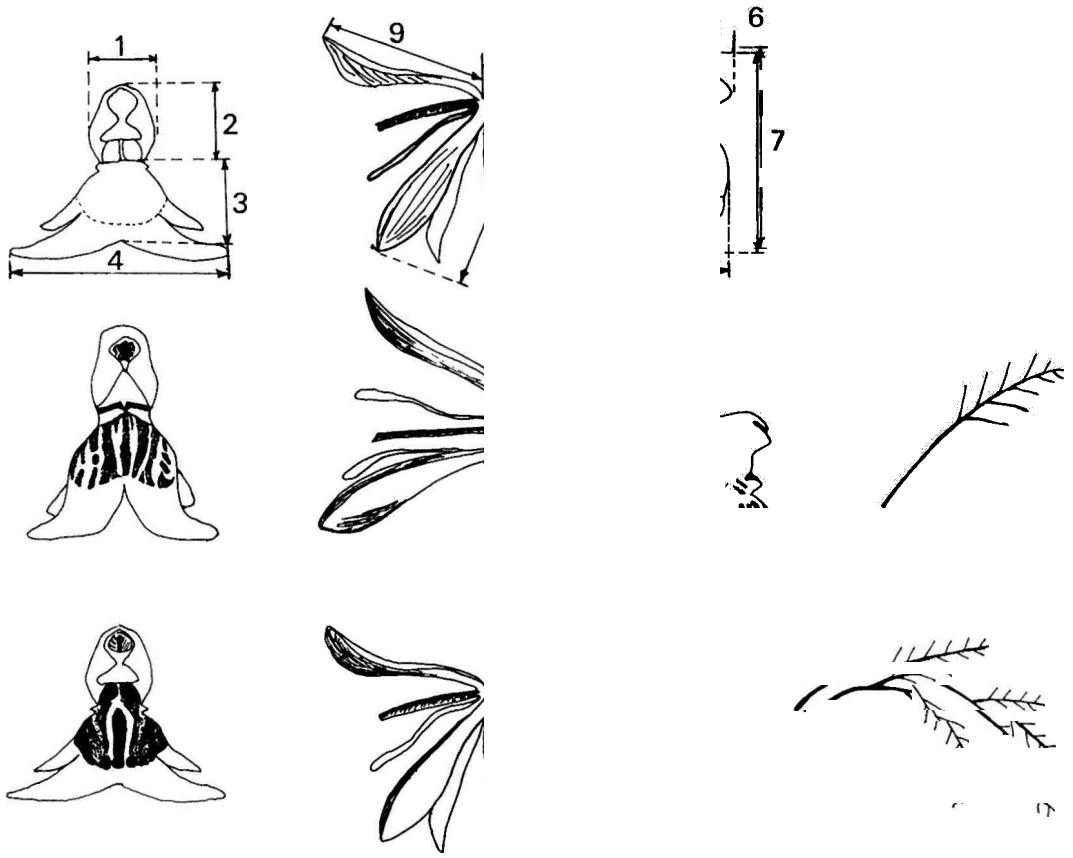


FIGURE 1. Comparison between wet season and dry season forms of *Epidendrum paniculatum*. Top row shows a front and side view of a schematic flower and indicates the locations of the ten measurements that were taken. Middle row shows front and side of an individual flower, and inflorescence branching pattern of wet season form. Bottom row shows front and side of flower, and inflorescence branching pattern of dry season form. Note differences in the dark markings on petals, and in the inflorescence branching patterns.

*Epidendrum paniculatum* Ruiz and Pavón is found throughout Central and South America. Although its flowers do not produce nectar, *E. paniculatum* plants grown in North American greenhouses are strongly attractive to male *Danaus plexippus* butterflies (Wagner 1973). Dodson (in Wagner 1973) notes that the flowers also attract male ithomiine butterflies, suggesting that the attraction may be due to PAs (see also van der Pijl & Dodson 1966). However, Pliske (1975b) suggests that the attractant in *E. paniculatum* is probably due to volatile chemicals that resemble PA sidechains. In a North American *Epidendrum* Lepidoptera system, Goss and Adams (1976a, b) concluded that *E. anceps* produces either PAs or compounds mimicking them that attract pollinators.

The attraction of Lepidoptera by *E. paniculatum*

has been known anecdotally for over 20 years, but no study has focused on the pollination biology of *E. paniculatum* in the field or the population biology of its pollinators. The present study addresses three basic questions concerning the pollination biology of this orchid: who are its pollinators; does the orchid provide visual or chemical stimuli, or both, to attract pollinators; and, what is the potential effect of pollinators on long distance pollination?

## MATERIALS AND METHODS

Costa Rican *E. paniculatum* occurs at low densities in forests ranging from 300–2000 m on both Atlantic and Pacific slopes, and has two common forms that are recognizable by vegetative characters, floral phenology, and morphology (Fig. 1). One form

TABLE 1. Flower morphology of wet season and dry season forms of *Epidendrum paniculatum*. Ten measurements were taken from five individual flowers of both forms (see Fig. 1) and compared with an unpaired *t*-test to a two-tailed distribution. An asterisk denotes significant differences between the two forms.

Measurement	Mean $\pm$ standard error (mm)		<i>t</i> -test
	Wet season form	Dry season form	
1	3.01 $\pm$ 0.032	3.06 $\pm$ 0.04	<i>P</i> = 0.476
2*	3.82 $\pm$ 0.058	3.46 $\pm$ 0.024	<i>P</i> = 0.011
3	3.54 $\pm$ 0.103	3.28 $\pm$ 0.066	<i>P</i> = 0.166
4*	8.68 $\pm$ 0.097	10.38 $\pm$ 0.565	<i>P</i> = 0.035
5	10.36 $\pm$ 0.15	9.82 $\pm$ 0.429	<i>P</i> = 0.176
6*	0.94 $\pm$ 0.051	1.1 $\pm$ 0.071	<i>P</i> = 0.035
7	9.76 $\pm$ 0.218	9.04 $\pm$ 0.112	<i>P</i> = 0.063
8*	7.08 $\pm$ 0.136	5.46 $\pm$ 0.209	<i>P</i> = 0.005
9	11.94 $\pm$ 0.305	12.46 $\pm$ 0.519	<i>P</i> = 0.345
10	12.56 $\pm$ 0.163	12.38 $\pm$ 0.497	<i>P</i> = 0.736

used in this study flowered in the wet season, had leaves 8–11 cm long by 2.5–3 cm wide, stems 20–45 cm long, and bore fewer than 35 flowers on a simple inflorescence. The other form flowered in the dry season, was larger and more robust, had leaves 12–15 cm long by 3–4 cm wide, stems 40–60 cm, and often bore 50–over 100 flowers on a branching

inflorescence. The flowers of these two forms differ significantly in morphology and color pattern (Fig. 1, Table 1). Individual *E. paniculatum* plants in flower were observed intermittently between 1978 and 1986 at the following sites: Finca La Selva, Heredia Province; Finca Las Cruces, Puntarenas Province; Barrio Monterrey, San Pedro Montes de Oca, and the University of Costa Rica campus, San José Province; and, Jardín Lankester, Cartago Province. Insofar as was possible, we determined the species and sex of each visitor to the *E. paniculatum* flowers, counted the number of flowers visited, and noted pollinarium removal.

To test whether PA-seeking insects discriminate between *E. paniculatum* flowers and *Heliotropium*, *Haeckelia*, and *Myosotis* baits (hereafter PA baits), the following bioassay was conducted. Two *E. paniculatum* plants in full flower and 2 dried PA baits were placed alternately within 3 m of each other along a section of forested trail at La Selva and observed between 0800 and 1100 hr. During the observation periods all visitors to the orchid flowers and/or the PA baits were noted, and additional notes were made of other species of flowers occurring nearby and their visitors. When the observation periods had ended, the orchids and the PA baits were removed to a building outside the forest. This bioassay was done 5–11 August with two *E. panicu-*

TABLE 2. Butterflies attracted to PA baits carrying what is likely to be *E. paniculatum* pollinaria on the proboscis. All are ithomiines except *Lycorea*, which is a danaine. An asterisk denotes Panamanian specimens found in museums.

Species	Male	Female	Month
<i>Tithorea tarricina</i>	1	1	Aug
<i>Mechanitis polymnia isthmia</i>	4	0	July–Sept
<i>Hypothyris euclea leucania</i> *	2	0	July, Sept
<i>Hypothyris euclea valora</i>	1	0	Sept
<i>Hypothyris lycaste callispila</i> *	1	0	Aug
<i>Ithomia xenos</i> *	1	0	Feb
<i>Ithomia patilla</i>	2	0	July–Sept
<i>Ithomia terra vulcana</i>	2	0	June
<i>Ithomia heraldica</i>	5	0	July–Sept
<i>Dircenna klugii</i>	6	1	June–Sept
<i>Pteronymia fulvimargo</i>	1	0	Aug
<i>Pteronymia artena</i>	3	0	May–June
<i>Pteronymia notilla</i>	0	1	June
<i>Pteronymia fulvescens</i>	1	0	June
<i>Pteronymia simplex</i>	4	0	June
<i>Greta anette</i>	1	0	Sept
<i>Greta andromica tyra</i>	2	0	June
<i>Greta polisenna umbrana</i>	1	0	June
<i>Greta oto</i>	3	0	June–Sept
<i>Godyrus zygia</i>	0	1	June
<i>Lycorea cleobaea atergatis</i>	1	0	Sept
Total	42	4	

TABLE 3. *Lepidoptera* visiting *E. paniculatum* flowers and/or *Heliotropium* baits in a bioassay. Visitors are all in the Ithomiinae except where noted (Abbreviations: \* = *Danainae*; \*\* = *Ctenuchidae*; † = *Riodinidae*; †† = *Hesperiidae*).

Species	Sex		Individual at			Pollinia removed
	Male	Female	Bait	Flower	Both	
<i>Melinara lilis imitata</i>	4	0	3	3	2	yes
<i>Mechanitis polymnia isthmia</i>	4	0	3	1	0	no
<i>Ithomia diasa</i>	5	0	2	5	2	yes
<i>Ithomia bolivari</i>	2	0	1	2	1	yes
<i>Greta anette</i>	3	0	1	2	0	yes
<i>Hypothesis euclea valora</i>	2	0	0	2	0	yes
<i>Lycorea cleobaea atergatis</i> *	1	0	1	1	1	no
<i>Belemniastis nr. attidates</i> **	1	0	1	1	1	yes
<i>Syntrichura reba</i> **	1	0	1	1	1	no
2 species not collected**	?	?	2	2	2	no
<i>Charis</i> sp.†	1	0	0	1	0	no
genus ? sp.††	?	?	0	1	0	no
Totals	24	0	15	22	10	

*latum* individuals, and 1–4 December 1979 with two different individuals. The PA baits differed between the experiments.

As part of a general study of the butterfly fauna of Costa Rica (DeVries 1987), those *Lepidoptera* attracted to PA baits in 1979 and 1980 were routinely surveyed for individuals carrying orchid pollinaria. The pollinaria found on butterflies were compared to pollinaria from our experimental flowers using the methods of Dressler (1976) or with material in the herbarium of the Museo Nacional de Costa Rica.

To test if the attraction of ithomiines to orchid flowers was chemical rather than visual in nature, two flowering *E. paniculatum* were exposed for four hours in a patch of second growth forest where ithomiines are abundant on the University of Costa Rica campus on 21 August 1983. At the same time two opaque, white cotton sacks, which permitted some air movement through them, were hung 10 m from the orchids. Visits to flowers and to sacks were recorded. At 0700 hr on 22 August, each plant was placed in a sack, and at 0900 hr the sacks, with plants inside, were exposed on campus for three hours. The plants were removed at 1200 hr, and visits to the sacks monitored for another three hours.

A study of ithomiine populations in a 1 ha patch of second growth woodland at the University of Costa Rica (hereafter UCR) was conducted from 1974 through 1981 by FGS. Over 17,000 butterflies were marked uniquely and released during this study. Between June and August 1976 a study of population movements was carried out where PA

baits were maintained at 5 sites on the UCR campus, and at 13 off-campus sites in a 4.5 × 3.5 km area in the watersheds of the Rio Torres, Quebrada Negritos, and Rio Ocloro. All of the off-campus sites were in old second growth, shaded coffee plantations, or remnant streamside woodlands. Butterflies captured at each site were marked, and all baits were checked at intervals of 2–4 days. The summarized data reported here were taken from outside the main ithomiine migration period and represent typical behavior of these populations in the Central Valley of Costa Rica. Full details of migration and population movements will appear elsewhere (Stiles, pers. obs.).

## RESULTS

Some *E. paniculatum* individuals and all PA baits attracted mostly species of Ithomiinae, and less commonly, species of *Danainae* and *Ctenuchidae*. Nearly all of the insects attracted (ca 98%) were males from groups that use PAs for mating (Tables 2–5). Only the form of *E. paniculatum* that flowered in the wet season attracted diurnal *Lepidoptera* and is of concern here; the dry season form did not attract these *Lepidoptera* and is discussed below (see Fig. 1, Table 1).

Bioassays where orchids and PA baits were offered simultaneously showed that insect species which visited orchids also visited the PA bait, and some individual insects alternated between both (Table 3). The approach of all PA-seeking visitors to the orchids varied, depending upon which direction the individual was initially flying. Some approached the

TABLE 4. Visitation by ithomiines to exposed *E. paniculatum* flowers, those covered with cloth sacks, and a cloth sack with orchid removed.

	Orchid		Sack after orchid removed		
	Exposed	Covered	1 hr	2 hrs	3 hrs
<i>Dircenna klugii</i> (male)	15	9	2	1	0
<i>Dircenna klugii</i> (female)	1	0	1	0	0
<i>Ithomia heraldica</i> (male)	10	8	2	0	0
<i>Ithomia patilla</i> (male)	2	1	0	0	0
<i>Ithomia xenos</i> (male)	1	2	1	0	0
<i>Greta oto</i> (male)	9	4	2	1	0
<i>Greta oto</i> (female)	1	0	0	0	0
<i>Dircenna relata</i> (male)	2	2	0	0	0
<i>Mechanitis polymnia</i> (male)	2	1	0	0	0
<i>Pteronymia notilla</i> (male)	1	0	0	0	0
<i>Lycorea cleobaea</i> (male)	1	0	0	0	0
Unidentified ctenuchid moth	1	1	1	0	0
Total	46	28	9	2	0
Number per hour	11.5	9.3	9.0	1.0	0

plant by flying past it and then doubling back; others spiraled down to the plant from the forest subcanopy; and others, flying at roughly the same level as the orchid, approached by weaving through the understory vegetation. The same manner of approach was observed in visitors to the PA baits, and is consistent with observations we have made with PA baits at many sites throughout Costa Rica. Other Lepidoptera that flew close to the orchids but did not visit the flowers or the PA baits were either female ithomiines (e.g., *Melinara lilis imitata*, *Hypocada virginiana*, *Aeria eurimedia*), or from taxonomic groups that have no history of seeking PAs (e.g., *Parides* spp. (Papilionidae), *Heliconius cydno* (Nymphalidae), *Eurybia lycisca* (Riodinidae)).

Observations of ithomiine butterflies taking *E. paniculatum* pollinaria are summarized as follows. When a butterfly landed on the inflorescence it uncoiled its proboscis, probed around on an individual flower, and inserted the proboscis into the flower, usually with the head appressed to the opening of the floral spur. If a ripe pollinarium was present, the viscidium usually adhered to the dorsal side of the proboscis near the head, trapping the butterfly. To escape, the butterfly pushed vigorously

against the petals with its legs until the trapped proboscis was jerked free, but with a pollinarium adhered near the base of the proboscis. After freeing itself from the flower the insect generally did one of four things: the insect fluttered around for a few seconds and visited another flower; it settled momentarily on nearby vegetation, then visited another flower; it flew away from the orchid and visited the PA bait; or, it flew away.

Lepidoptera attracted to the PA baits behaved similarly to those attracted to the orchid: they would land on the baits, uncoil the proboscis, dab the proboscis around on the surface of the plant, and then coil and uncoil the proboscis. Duration of "feeding bouts" at baits varied from a few seconds to up to several minutes, after which individuals would fly away or take flight momentarily and land again on the plant. These observations are in accord with those reported by Pliske (1975a) for Lepidoptera attracted to PA baits in South America.

Surveys done at PA baits for butterflies carrying orchid pollinaria showed that at least 20 species (19 ithomiines, 1 danaine) were attracted to both PA baits and the genus *Epidendrum*—most likely *E. paniculatum* (Table 2). Most individuals carried one

TABLE 5. Summary of times to recapture of male ithomiines at same and different sites. There is a significant difference in timing of recaptures at the same and different sites ( $D_{\max} = 0.481$ ,  $P < 0.01$  by Kolmogorov-Smirnov 2-sample test) showing that individuals move away from recapture site.

Days after marking	1	2-4	5-8	9-15	16-25	>25	Total
Marking site	142	227	59	13	9	2	452
Other sites	27	35	36	48	27	12	185

TABLE 6. Summary of time required by male ithomiines to move varying distances between PA baits at study sites near UCR. Note that individuals continue to move for at least a month or more, that movements of several kms are common, and sedentary individuals are rare.

Distance	Number of days required to move						Total
	≤1	2-4	5-8	9-15	16-25	>25	
<0.5 km	8	10	8	15	4	1	46
0.51-1.0 km	12	13	11	21	12	4	73
1.01-1.5 km	6	6	10	4	5	3	34
1.51-2.0 km	1	5	5	5	3	3	22
2.01-2.5 km	0	0	1	2	2	1	6
2.51-3.0 km	0	0	1	1	0	0	2
>3 km	0	1	0	0	1	0	2

pollinarium, three carried two, and the majority of them (91%) were males (Tables 1 and 2). From censuses done at UCR (July–September 1979–1980), the fraction of total individual ithomiines attracted to PA baits carrying pollinaria indistinguishable from those of *E. paniculatum* were as follows: *Mechanitis polyminia* 3/133; *Ithomia beraldica* 5/725; *I. patilla* 1/176; *Dircenna klugii* 6/211; *Greta oto* 3/172, and all except one *D. klugii* were males. The proportion of males found at PA baits and orchids was higher than the proportion of males observed during censuses done without baits (Stiles, pers. obs.), indicating that together our data do not simply show an excess of males in the habitat.

Costa Rican butterflies from any family or subfamily are rarely found carrying orchid pollinaria (DeVries, pers. obs.). Excepting *Epidendrum radicans* that is visited by various Lepidoptera that do not seek PAs (see Bierzychudek 1981), we know of no other orchid besides *E. paniculatum* that consistently attracts butterflies, especially those that seek PAs. Although we cannot be certain, we suspect that the pollinaria carried by Lepidoptera attracted to our PA baits (Table 2) originated from *E. paniculatum*.

In the bioassays done at UCR, butterflies were attracted to both bagged and unbagged orchids, and for a short time to the cloth bag after the orchid had been removed (Table 4). These observations imply that olfactory cues play an important role in attracting visitors to *E. paniculatum* flowers, and reflect the findings of Pliske (1975b) for plants in the Boraginaceae and Asteraceae.

Features of ithomiine biology, making them potentially important pollinators, include their longevity and mobility. The average lifetime for ithomiine butterflies is comparable to those of *Heliconius* (e.g., Gilbert 1984): individuals have been

recaptured at intervals for up to six months after marking (Stiles, pers. obs.). Ithomiine mobility was demonstrated at the UCR site (Table 5), where in 452 recaptures, over three-fourths were within four days of marking, after which the recapture rate plummeted. This drop in recaptures could not be entirely due to mortality, but must represent at least some emigration, because the recapture rate actually rose at sites 1 km or more away as it was falling at the marking site. At the time this experiment was carried out, the butterflies were not engaged in their seasonal migration; September–October is when most ithomiines leave the Central Valley for the surrounding mountains.

Movements of ithomiine butterflies between sites may be quite rapid (Table 6). Many cases of movements of 1 km or more within 24 hr were observed; the fastest movement was 1.5 km in 3 hr, and the longest movements observed, 3–3.5 km, were determined by the limits of the study area rather than the capacity of the butterflies. We do not doubt that a male ithomiine could easily cover 20–50 km during its lifetime, even excluding the seasonal migrations to higher elevations.

## DISCUSSION

This study showed that one form of Costa Rican *E. paniculatum* flowers and PA containing plants attract the same suite of day flying Lepidoptera (Tables 2–4). Of these Lepidoptera, all were from groups known to actively seek sources of PAs, and the majority were male ithomiine butterflies. The few females that visited *E. paniculatum* flowers may simply reflect that ithomiines of both sexes are generally attracted to small white flowers, including plants without PAs (e.g. *Croton* spp. (Euphorbiaceae), *Psychotria* spp. (Rubiaceae)).

Since visitors to *E. paniculatum* flowers remove

pollinaria and may carry them to other flowers or PA sources (Tables 2 and 3), our observations suggest that PA seeking Lepidoptera pollinate *E. paniculatum*. Of the suite of potential pollinators, ithomiine butterflies are probably most important. This is because they are mobile and long-lived (Tables 5 and 6, Stiles, pers. obs.), they account for most of the species known to visit PA baits and *E. paniculatum* flowers, and these butterflies live in the forests where the orchid occurs.

We have no indication that individual ithomiine butterflies associate during their movements, but rather that their dispersion was almost random (see also Haber 1978). Hence, it is likely that members of a population that originated from a single brood would cover an area several kms in diameter within a week. As the butterflies themselves are long-lived, pollinarium transport over still longer distances is quite feasible. Thus, as euglossine bees are effective long distance pollinators to other orchids (cf., Janzen 1971, Williams & Dodson 1972), ithomiine butterflies may be effective long distance pollinators of *E. paniculatum*.

A general consensus among taxonomists is that the orchids under the name *E. paniculatum* comprise a species complex (C. Dodson, R. Dressler, R. L. Rodriguez, R. Ocampo, pers. comm.). In addition

to morphological differences (Fig. 1, Table 1), the two forms of Costa Rican *E. paniculatum* may differ with respect to pollinators. The plants that attracted PA seeking Lepidoptera were all of the form that flowered in the wet season. The plants of the form that flowered in the dry season were observed intermittently for several years in Monterrey, and observed intensively (for a total of 16 hours through day and night) in February and March 1981 at Jardin Lankester. On only two occasions in Monterrey was an ithomiine seen to visit the flowers (one male and one female *G. oto*), and the only visits seen at Jardin Lankester were by two noctuid moths during one evening. Although both forms of the orchid appear similar, our observations imply that the dry season form of *E. paniculatum* is not pollinated by PA seeking Lepidoptera.

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## LITERATURE CITED

- ACKERMAN, J. D. 1983. Specificity and mutual dependency of the orchid-euglossine bee interaction. *Biol. J. Linn. Soc.* 20: 301-314.
- ACKERY, P. R., AND R. I. VANE-WRIGHT. 1985. Milkweed butterflies: their cladistics and biology. London: Brit. Mus. (Nat. Hist.), Entomology.
- BEEBE, W. 1955. Two little-known selective insect attractants. *Zoologica (N.Y.)* 40: 27-32.
- BIERZYCHUDEK, P. 1981. *Asclepias*, *Lantana* and *Epidendrum*: a floral mimicry complex? *Biotropica* 13: 54-58.
- BOPPRÉ, M. 1984. Chemically mediated interactions between butterflies. *Symp. R. Entomol. Soc. Lond.* 11: 259-275.
- , AND D. SCHNEIDER. 1985. Pyrrolizidine alkaloids quantitatively regulate both scent organ morphogenesis and pteromone biosynthesis in male *Cretonotos* moths (Lepidoptera: Arctiidae). *J. Comp. Physiol. A.* 157: 569-577.
- , AND ———. 1989. The biology of *Cretonotos* (Lepidoptera: Arctiidae) with special reference to the androconial system. *Zool. J. Linn. Soc.* 96: 339-356.
- BROWN, K. S. 1984. Adult-obtained pyrrolizidine alkaloids defend ithomiine butterflies against spider predation. *Nature*, 309: 707-709.
- DEVRIES, P. J. 1987. The butterflies of Costa Rica and their natural history. Princeton University Press, Princeton, N.J.
- DODSON, C. H., R. L. DRESSLER, H. G. HILLS, R. M. ADAMS, AND N. H. WILLIAMS. 1969. Biologically active compounds in orchid fragrances. *Science* 164: 1243-1249.
- DRESSLER, R. L. 1976. How to study orchid pollination without any orchids. In K. Senghaus (Ed.). *Proc. 8th World Orchid Conference*. German Orchid Society, Frankfurt, W. Germany, pp. 534-537.
- GILBERT, L. E. 1984. The biology of butterfly communities. *Symp. R. Entomol. Soc.* 11: 41-54.
- GOSS, G. J., AND R. M. ADAMS. 1976a. The reproductive biology of the epiphytic orchids in Florida III. *Epidendrum anceps* Jacquin. *Am. Orchid Soc. Bull.* 45: 488-498.
- , AND ———. 1976b. The reproductive biology of the epiphytic orchids of Florida IV. Sexually selective attraction of moths to the floral fragrance of *Epidendrum anceps* Jacquin. *Am. Orchid Soc. Bull.* 45: 997-1001.

- HABER, W. 1978. Evolutionary ecology of tropical mimetic butterflies (Lepidoptera: Ithomiinae). Ph.D. Dissertation, University of Minnesota.
- JANZEN, D. H. 1971. Euglossine bees as long distance pollinators of tropical plants. *Science* 171: 203-205.
- . 1981. Bee arrival at two Costa Rican female *Catasetum* orchid inflorescences, and an hypothesis on euglossine population structure. *Oikos* 36: 177-183.
- KIMSEY, L. S. 1980. The behavior of male orchid bees (Apidae, Hymenoptera, Insecta) and the question of leks. *Animal Behavior* 28: 996-1004.
- PLISKE, T. E. 1975a. Attraction of Lepidoptera to plants containing pyrrolizidine alkaloids. *Environ. Ent.* 4: 455-475.
- . 1975b. Pollination of pyrrolizidine alkaloid-containing plants by male Lepidoptera. *Environ. Entomol.* 4: 474-479.
- ROTHSCHILD, M., R. T. ALPINE, P. A. COCKRUM, J. A. EDGAR, P. FAIRWEATHER, AND R. LEES. 1979. Pyrrolizidine alkaloids in arctiid moths with a discussion on host plant relationships and the role of those secondary plant substances in the Arctiidae. *Biological Journal of the Linnaean Society* 12: 305-326.
- ROUBIK, D. W., AND J. D. ACKERMAN. 1987. Long-term ecology of euglossine orchid-bees (Apidae: Euglossinini) in Panama. *Oecologia* 73: 321-333.
- VAN DER PIJL, L., AND C. H. DODSON. 1966. Orchid flowers, their pollination and evolution. University of Miami Press, Coral Gables.
- WAGNER, W. H., JR. 1973. An orchid attractant for monarch butterflies (Danaidae). *J. Lep. Soc.* 27: 192-196.
- WILLIAMS, N. H. 1982. The biology of orchids and euglossine bees. *In* J. Arditti (Ed.). *Orchid biology: reviews and perspectives*, II, pp. 119-171. Cornell University Press, Ithaca, N.Y.
- , AND C. H. DODSON. 1972. Selective attraction of male euglossine bees to orchid fragrances and its importance to long distance pollen flow. *Evolution* 26: 84-95.