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ANTHECOLOGY IN THE NEOTROPICAL GENUS *ANTHURIUM* (ARACEAE): A PRELIMINARY REPORT

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ABSTRACT. The pollination strategies of *Anthurium* (Araceae) were investigated in the field in Ecuador. Three different pollinator types (viz., Cecidomyiidae, Drosophilidae and Euglossini) were observed in wild plants in habitat. Floral fragrances of 10 *Anthurium* species grown in a greenhouse were sampled and analyzed. Species visited by Cecidomyiidae in the field are scentless to the human nose and to our technical equipment. Those visited by Drosophilidae emit substances perceived by humans as smelling of alcohol or rotten fruit. The remaining species emitted strong, most agreeable perfumes in the morning hours and fit well into the euglossine syndrome better known in some groups of neotropical orchids. Scent composition of these species is discussed in some detail. One of the perfumed species was observed to be euglossine-pollinated in the field. The probable genetic isolation of species by means of scent-directed allocation of pollinators is discussed.

Key words: Araceae, *Anthurium,* floral fragrances, pollination, Euglossini, Cecidomyiidae, Drosophilidae

INTRODUCTION

The family Araceae is one of the most interesting plant groups with respect to pollination ecology. Out of nearly 3000 species in 101 genera, not a single one offers nectar as a reward. No nectaries are developed to produce a sweet energy supply for high-energy demanding pollinators, and the stigmatic exudate is a poor substitute that may be licked only by small Diptera with low energetic requirements. Pollen too is seldom, if ever, produced in sufficient amount to support pollen-collecting bees. As in other anthecologically advanced plant groups (e.g., Orchidaceae, Marantaceae), pollen is restricted to its essential function in sexual reproduction and is not offered in quantities that make it worthwhile for bees to collect as nutritive food for their larvae.

In Araceae, numerous different low-cost strategies have evolved to attract pollinators by deceit. In the well-known case of *Arum maculatum* L., small Psychodidae midges are attracted olfactorically and trapped by the spathe, which functions as a prison. The visitors are set free only after pollination of the protogynous flowers, when new pollen is shed over the prisoners and the inflorescence begins to senesce. These trap-blossoms, recognized as ''apparecchi a carcere temporaria'' by Delpino as early as 1875, are found in many genera of Araceae all over the world. The attraction of the pollinating insects is hypothesized to be mediated by chemical attractants, be it the faint smell of *Cryptocoryne* inflorescences that attract small flies, the hardly perceptable fungal perfumes of *Arisaema* and *Arisarum* that attract egg-laying fungus gnats (Vogel 1978), or the disgusting smell of carrion or feces that is characteristic of many genera with large, dull-colored inflorescences and that attracts carrion flies or beetles (*Dracunculus, Helicodiceros, Typhonium, Amorphophallus*, *Symplocarpus* etc. Meeuse & Raskin 1988). In all these cases, pollinators are attracted by deceit. No proper payment is given for pollination, except for some droplets of liquid to keep the prisoners alive.

In the neotropical forests, another pollination strategy is to be found in Araceae, namely the highly sophisticated phenomenon of beetle-pollinated flowers, which is known also in Annonaceae, Nymphaeaceae, Cyclanthaceae and Arecaceae. These flowers or inflorescences, which essentially remain semi-closed during anthesis,

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TABLE 1. Fragrance composition of 10 *Anthurium* species belonging to different pollination syndromes. The substances found are divided into chemical classes and within each class in the order of their GC retention time.

	Taxon and collection locality*									
	A	B	C	D	E	F	G	H	I	J
Terpenoids										
Monoterpenes										
α-Pinene	1.00	0.20	1.00	0.10	0.70	0.10	0.02			
β-Pinene	2.20	0.20	0.50	0.10	1.30	0.30	0.05			
Sabinene	4.50	0.20		0.10	1.70	0.30				
Mycrene	1.30		0.10			0.05	0.10			
Limonene	3.80	0.80	2.90	0.20	3.00	1.00	0.30			
Eucalyptol or 1,8-cineole	28.20	4.90	1.00	0.40	19.90	1.90	0.10		0.20	
(Z)-Ocimene	0.10	0.10								
γ-Terpinene							1.10			
(E)-Ocimene	0.10	0.30					0.02			
2-Methyl-6-methylene-1,3,7-octatriene							0.30			
p-Cymene	0.10									
Terpinolene	1.50	0.10					0.05			
(E)-4,8-dimethyl-1,3,7-nonatriene										0.01
Myrcene epoxide					0.10	0.30	0.10			
cis-Limonene epoxide				0.10	0.60	0.60				
trans-limonene epoxide				1.50	4.10	7.90				
p-Menth-1-en-8(9)-epoxide					0.70					
trans-linalool oxide (furanoid)							0.02			
p-Menth-1-en-4(8)-epoxide						0.02				
trans-sabinene hydrate							0.20			
cis-Sabinene hydrate							0.02			
Linalool	0.20						15.00			
Ipsdienone							0.90			
Ipsdienyl acetate							10.80			
Carvacryl methyl ether	0.20									
δ-Terpineol		0.10					0.30			
Ipsdienol							32.00			
α-Terpineol							5.50			
Methyl 3,7-dimethyl-6-octenoate										1.00
Methyl (Z)-geranate										1.60
Methyl (E)-3,7-dimethyl-3,6-octadienoate										0.40
Citronellyl acetate										0.05
Methyl (E)-geranate										2.10
Ethyl (E)-3,7-dimethyl-3,6-octadienoate										0.05
Ethyl (Z)-geranate										0.20
Ethyl (E)-geranate										0.10
Dihydrocarvone				5.00	3.40	8.70				
trans-Carveol							0.20			
Geranyl acetate									0.30	
p-Menth-5-en-2-one				0.02						
Carvone	0.80			12.20	4.50					
trans-Carvone epoxide	3.90			78.00	58.20	41.00				
Piperitenone					0.10					
cis-Carvone epoxide				1.00	1.00	0.30				
Geraniol		0.10							0.05	
trans-(cis-Carveol) expoxide						0.04				
trans-(trans-Carveol) epoxide				0.20	0.10	0.07				
Sesquiterpenes										
α-Cubebene		0.80								
α-Copaene		2.30								
β-Cubebene		5.40								

TABLE 1. Continued.

	Taxon and collection locality*									
	A	B	C	D	E	F	G	H	I	J
Caryophyllene		13.00								
β-elemene		4.90								
Alloaromadendrene		3.60								
(E)-farnesene										
Humulene		3.50								
γ-Cadinene		6.40								
σ-Cadinene		4.50								0.40
Cubebol		7.20								
Caryophyllene epoxide		1.00								
Hymulene epoxide II		0.20								
Copan-3-ol		1.80								
Cadina-4,10(15)-dien-3-one		16.80								
Nootkatone		0.10								
Carotenoid-derived compounds										
β-Cyclocitral										
β-Cyclogeraniol										
β-Safranyl acetate										1.00
β-Safranol										0.60
(E)-Geranylacetone		1.0								0.10
α-Ionone		0.10								0.20
β-Ionone		0.05								0.20
7(11)-Epoxi-megastigma-5(6)-en-9-one		3.60								
trans-(E)-7-Mega stigmen-3,9-dione		2.20								
Lipid-derived compounds										
Ethyl propionate										
Isobutyl acetate										2.50
Ethyl 2-methylbutyrate									0.20	22.80
Ethyl isovalerate									0.60	
Isobutyl butyrate										
Hexanal									0.20	0.30
Butyl propionate										
Ethyl valerate									0.40	4.80
Isoamyl acetate								0.10	5.20	
2-Hexyl acetate										22.10
Heptan-2-one									5.50	0.60
Isoamyl propionate										
3-Hexanol									1.00	3.80
Isoamyl isobutyrate										
Isoamyl butyrate									0.30	0.30
Isoamyl alcohol								65.30	0.30	0.70
2-Hexanol									0.05	
Butyl butyrate									0.08	
Ethyl caproate									49.00	
3-Octanone										0.10
Prenyl acetate										0.10
2-Heptyl acetate									1.50	1.50
Hexyl acetate									0.80	
1-Hepten-3-yl acetate										
Isoamyl isovalerate									0.10	
Acetoine								21.00		
Octanol	0.10							0.05	0.06	0.10
2-Heptanol									9.00	0.05
Propyl caproate									0.70	0.90
6-Methyl-5-hepten-2-one								0.05	0.07	2.20
1-Octen-3-yl acetate										
(Z)-3-Hexenyl acetate							0.03			
Hexanol									0.80	
Aacetoine acetate									0.50	

TABLE 1. Continued.

	Taxon and collection locality*									
	A	B	C	D	E	F	G	H	I	J
Nonanal	0.70			0.02				0.10	0.50	0.10
3-Octanol										0.10
6-Methyl-5-hepten-2-yl acetate										20.20
Butyl caproate									0.40	
Hexyl butyrate									0.06	
1-Octen-3-yl propionate										0.30
Heptanol								0.05		
Ethyl octanoate									0.02	
1-Octen-3-ol										1.60
3-Methylbutyl caproate									0.02	
Octyl acetate									0.02	
6-Methyl-5-hepten-2-ol										1.80
Decanal	2.00			0.02				0.20	0.30	0.05
2,3-Butandiol								8.00	0.08	
Octanol								0.90	0.10	
Isobutyric acid									0.10	
2-Undecanone									0.20	
3-Hycroxy-2-butanyl butyrate									0.10	
Decyl acetate									3.50	
2-Undecanol									0.30	
Dodecanal	0.90									
Decanol									0.40	
2-Tridecanone									0.10	
Caproic acid									0.20	
Dodecyl acetate									3.90	
Heptanoic acid									0.20	
(Z, Z)-3,6-Dodecadienol		0.20								
Caprylic acid									0.10	
Hexadcanal									0.90	
Nonanoic acid									0.20	
Decanoic acid									0.20	
Benzenoids										
Benzaldehyde	0.20									
Methyl benzoate			5.00							
Benzyl acetate	27.00		72.00			36.00				0.20
Phenylethyl acetate							30.00		0.10	
Benzyl alcohol	15.00		8.50			0.60				0.20
Phenylethyl alcohol						0.02	0.30	3.00		
Methyl eugenol		0.10								
Cinnamyl acetate							0.03			
Eugenol		8.50				0.08	0.30			
(E)-Isoeugenol							0.02			
Benzyl benzoate		0.10				0.02				
Nitrogen containing compounds										
Phenylacetonitrile							0.05			
1-Nitro-2-phenylethane							0.10			
Phenylacetaldoxime							0.20			
Indole	0.20			0.30	0.03	0.04				
Total	94.00	93.45	91.00	99.26	99.43	99.34	98.13	98.75	88.91	96.41

* A, *Anthurium antioquiense* Colombia **Pollinator** probably Euglossini; B, *Anthurium apaporanum* Ecuador Napo **Pollinator** Euglossini (observed); C, *Anthurium armeniense* Guatemala Izabal **Pollinator** probably Euglossini; D, *Anthurium armeniense* Guatemala Baja Verapaz **Pollinator** probably Euglossini; E, *Anthurium huixtlense* Guatemala Alta Verapaz **Pollinator** probably Euglossini; F, *Anthurium nymphaeifolium* **Pollinator** probably Euglossini; G, *Anthurium* sp. 96082438 Ecuador Esmeraldas **Pollinator** probably Euglossini; H, *Anthurium hookeri* **Pollinator** Drosophilidae observation in culture; I, *Anthurium longipeltatum* **Pollinator** probably Drosophilidae; J, *Anthurium salvadorense* Guatemala **Pollinator** Drosophilidae observation in culture.

open in the evening and emit an extremely characteristic, strong odor, which attracts large beetles of the genus *Cyclocephala* (Scarabaeidae: Dynastinae) from long distances. The beetles crawl into the protogynous inflorescences, effect pollination and spend the night feeding on nutritive tissues provided by the flower or inflorescence. The spathe encloses the beetles until the next evening, when the pollen is shed. This pollination strategy is found within the Araceae in *Xanthosoma, Caladium* (pers. obs.), *Dieffenbachia,* and at least some species of *Philodendron* (Gottsberger & Silberbauer-Gottsberger 1991).

The neotropical genus *Anthurium,* with more than 800 species, is by far the most diverse genus of Araceae, but none of the pollination strategies mentioned above is known. In *Anthurium,* the minute flowers are bisexual, and the spathe does not close around the spadix as a trap. In some species, the spathe is held over the pendent spadix as a hood-shaped structure, functioning as an umbrella; but in many cases, it is no more than a patent or reflexed greenish or brownish ''leaf'', apparently of little function in the pollination process. Only in a few cases is the spathe a showy, colored flag as in *A. andraeanum* Linden or *A. scherzerianum* Schott and their hybrids, which are of horticultural importance.

The flowering behavior of the inflorescence of *Anthurium,* which is described in detail by Croat (1980), starts with a brief female phase, where the small flowers are receptive and a minute droplet of stigmatic fluid may be produced. After a sterile phase, the inflorescence enters a male phase with pollen shedding, which may last for several days. Which animals visit the inflorescences? What kind of reward is provided? What makes the visitors move between inflorescences in different sexual phases? Is only one phase rewarding, while the other is visited only by ''deceit pollination'', as known from *Begonia*, for example, where the non-rewarding female flowers with their broad yellow stigma branches obviously are mimics of the male ones (Agren & Schemske 1993, Vogel 1993)?

MATERIALS AND METHODS

For observation in situ, two field trips were undertaken to Ecuador in 1996 and 1998. Cecidomyiidae (Diptera: Nematocera) and Drosophilidae (Diptera: Brachycera) were caught and conserved in alcohol. Because of the lack of taxonomic specialists for these groups, these little flies only were determined to their family rank. The larger euglossine bees (Hymenoptera: Apidae) attracted to *Anthurium apaporanum* R.E. Schult. were mounted and determined using the reference collection of G. Gerlach in Munich.

Drosophilidae have been observed repeatedly visiting *Anthurium* species in different greenhouses in Goettingen, Germany, as well.

The different *Anthurium* species kept in the greenhouses of the Botanical Garden of Munich were olfactorily evaluated and verbally described. To trap a scent sample, the inflorescence of the respective species was placed in a glass vessel of adapted size and shape. The scented air surrounding the flower was drawn with the aid of a small battery operated pump (personal air sampler SKC 222-4) for a period of 2 to 4 hours, depending on intensity of the scent, through an adsorption trap containing 3 mg of Porapak Super Q. Subsequently, the adsorbed scent was recovered by elution with 20 to 60 μl high grade hexane/acetone 5:1 mixture. The eluate was analyzed directly by injecting 1.5 μl into the GC (Carlo Erba Fractovap 4160) or GC-MS (Thermo Finnigen Voyager Mass Spectrometer combined with a Trace GC and the Xcalibur software). The analyses were made on a DB-WAX column (J&W Scientific) 30 m x 0.32 mm i.d., film thickness 0.25 μm. Compounds were identified by comparison of their mass spectra and retention times with authentic reference samples available from the collection of reference compounds or specially synthesized in connection with this investigation (see also Kaiser & Tollsten 1995).

From each species, only one sample could be gathered. Scent was sampled from species flowering in cultivation, where inflorescences sometimes are produced only every few months. Moreover, nothing can be said about infraspecific variation, since all species discussed were only represented by one single clone in cultivation.

Vouchers of the *Anthurium* species investigated are deposited in the herbaria GOET, MO and M and their pollinators in ZSM (Zoologische Staatssammlung München).

RESULTS

Fragrances

Based upon the fragrance composition, 7 of the 10 *Anthurium* species can be considered as euglossine-pollinated flowers, since similar scent compositions are well known in euglossine-pollinated orchids. Thus a comparison with the much better investigated orchids belonging to the male euglossine syndrome seems reasonable:

Anthurium armeniense Croat (from Baja Verapaz, Guatemala), *A. huixtlense* Matuda, and *A. nymphaeifolium* K.Koch and Bouché emit scents reminiscent of caraway and show a fragrance pattern like certain *Catasetum* species (Whitten et al. 1986).

Anthurium antioquiense Engl. and *A. armeniense* (from Izabal, Guatemala) show fragrances containing high amounts of benzyl acetate, accompanied by the corresponding alcohol and some terpenoid compounds. This pattern can be found also in the scents of certain *Stanhopea* species and those of other euglossine pollinated orchids. The remaining two species have a somewhat more complex scent composition with additional types of compounds involved.

The scent of *Anthurium apaporanum* R.E. Schult. contains as main constituent the sesquiterpene ketone cadina-4,10(15)-dien-3-one, which is also known as isokhusinone and which occurs, for example, as a minor constituent in lavender oil (Kaiser 1983) and as the main constituent of the orchid *Mormodes sinuata* Rchb.f. & Warm. (R. Kaiser, personal datafile on orchid scents). Together with other sesquiterpenes, such as caryophyllene epoxide and cubebol, this ketone is responsible for the peppery and woody scent, while the comparatively high amount of eugenol contributes an aspect reminiscent of clove buds. The scent of *A. apaporanum* contains also a series of carotenoid-derived volatile compounds. Thus small amounts of α- and β-ionone are accompanied by 3.6% of 7,11-epoxy-5(6)-megastigmen-9-one, a rare natural product found in high amounts in certain orchid scents as those of *Houlletia odoratissima* Linden ex Lindl. (Kaiser 1993) and *Gongora cruciformis* Whitten & Bennett (Kaiser 1997). Another structurally interesting and rare carotenoid catabolite is the trans-(E)-7-megastigmen-3,9-dione, which is also present in the flower scent of *Masdevallia laucheana* Kraenzl., a Costa Rican orchid emitting its pleasing floral fragrance only during the 30 or 40 minutes of twilight (Kaiser 1993).

Nearly all components of the scent of *Anthurium* sp. 96082438 occur also in euglossine-pollinated orchids. Thus ipsdienol and derivatives are found in highly derived species of *Coryanthes*, and phenylethyl acetate occurs as the main constituent in certain *Stanhopea* species. Quite interestingly, these two compounds occur together only in one *Stanhopea* species, *Stanhopea annulata* Mansf. (Whitten & Williams 1992) native to the same region of western Ecuador.

It is probable that in sympatric *Anthurium* species a similar isolating mechanism is present, as in the orchids belonging to the perfume flower syndrome. Williams and Dressler (1976) showed that a maximum of three different euglossine bee species pollinate one *Anthurium* species, but normally only one species is attracted. This illustrates that some of the *Anthurium* species may be evolving in parallel to some subtribes of orchids.

Much less is known on the floral fragrances of flowers pollinated by Drosophilidae. There exist only the description of their odors smelling of yeast and/or rotting fruits. The scent of *Anthurium salvadorense* Croat is dominated by typical fruit esters such as isobutyl acetate, and isoamyl acetate which are evocative of over-ripe banana and to a certain degree even of fermenting fruits. Quite surprising is the high amount of 6-methyl-5-hepten-2-yl acetate, a derivative of the wide-spread natural product 6-methyl-5-hepten-2-one. Highly characteristic for the scent of *A. salvadorense* are also methyl and ethyl geranate including isomeres and derivatives as well as a series of carotenoid-derived compounds as β-cyclocitral, β-cyclogeraniol, β-safranol, and β-safranyl acetate. The latter two compounds are new natural products (Kaiser 2000).

The scent of *Anthurium hookeri* Kunth is very much dominated by isoamyl acetate, acetoine including its reduction product 2,3-butandiol and phenylethyl alcohol, compounds typical for the odor of fusel oil and fermenting fruits, respectively.

Anthurium longipeltatum Matuda appears to belong to the same ecological fragrance group, since it also is characterized by a fruity odor extremely rich in lipid-derived compounds. In this species, however, ethyl caproate dominates the scent composition.

Pollinators

Cecidomyiidae

These midges were observed and caught visiting the inflorescences of *Anthurium citrifolium* Sodiro, *A. draconopterum* Sodiro, *A. lingua* Sodiro, *A. oxycarpum* Poepp., *A. pseudoclavigerum* Croat, *A. triphyllum* Brogn. ex Schott, and *A. truncicolum* Engl., in different localities in the provinces Carchi, Esmeraldas, Pichincha and Napo in northern Ecuador, both in lowland forest and at higher elevations. Keeping in mind the crepuscular or nocturnal anthesis of most Araceae, the first observations were made during nighttime with a torch, but the animals were also seen during the day visiting *Anthurium*. These tiny midges showed little activity at the flowers, and we could not determine whether they feed on some flower products. As both sexes were caught at the flowers, it is possible that the inflorescences serve as rendezvous places for the insects. The great frequency of *Cecidomyiidae* at *Anthurium* inflorescences makes it likely that these species are attracted by a specific scent not perceptible to our sense of smell. The respective *Anthurium* species have not been sampled for their scent, because experience shows that those faint scents hardly perceptable to us also fail to give good results by the technique and equipment used.

Drosophilidae

Anthurium peltigerum Sodiro, *A. nigrescens* Engl., and *Anthurium* sp. *96090216* have been observed to be visited by *Drosophilidae* in their natural environment in Ecuador. Interestingly, these field data correspond well to observations of cultivated plants in the greenhouses of the Botanic Garden at Goettingen. Here, flowering plants of, for instance, *A. grandifolium* Kunth, *A. hookeri*, *A. chamulense* Matuda, and *A. schlechtendalii* Kunth are notoriously visited by drosophilids, and five to ten individuals can sometimes be observed on one single inflorescence at a given time. Remarkably, in the greenhouse, the visits of drosophilids are restricted to species that have a pronounced, yeast-like scent and have not been observed at ''scentless'' or ''perfumed'' species flowering nearby. The fact, that ''wild'' *Drosophilidae* occuring in European greenhouses are attracted by neotropical *Anthurium* species allows the conclusion that the flies are attracted by specific scent compounds which correspond to Drosophilidic behavior such as egg deposition at rotting fruits.

Euglossini

Numerous *Anthurium* species are ''perfume flowers'' that are pollinated exclusively by male euglossine bees. This male-euglossine pollination is well known and thoroughly investigated for some subtribes of orchids: Catasetinae, Dichaeinae, Lycastinae (some *Lycaste* and all *Anguloa* species), Notyliinae p.p., and Stanhopeinae (Dressler 1981, Gerlach 1995).

The perfume syndrome occurs sporadically in other plant families such as Arecaceae (some *Geonoma* species), Euphorbiaceae (some *Dalechampia* species), Gesneriaceae (some *Sinningia* species and *Gloxinia perennis* (L.) Fritsch), and most *Cyphomandra* species (now *Solanum*, Solanaceae (Knudsen 1999, Armbruster & Webster 1979, Sazima & Vogel 1989).

In Araceae, the neotropical species of *Spathiphyllum* are known to be perfume flowers (Montalvo & Ackerman 1986, Williams & Dressler 1976). In *Anthurium*, some brief remarks about euglossine pollination are given by Croat (1980), and Williams and Dressler (1976) list some 20 occasional observations of different euglossine bees visiting *Anthurium* spp. (mostly undetermined) in different regions of Central and South America.

We observed two small, blue *Euglossa* species visiting *Anthurium apaporanum* during the morning hours of several days in Ecuadorean Amazonia near Tena. Following the classification of Dressler (1978), we determine that one belongs to subgenus *Euglossa* and to the ''*Euglossa analis* group'' and was identified as the very frequent *E. mixta* Friese. The other is a very seldom collected species, *E. viridis* Perty, which belongs to the subgenus *Euglossella*. Typical perfume collecting habit was observed and photographed (FIGURE 1).

In the same environment, *Euglossa viridis* also was observed as a frequent visitor to *Spathiphyllum cannifolium* (Dryand.) Schott, which emits a heavy, most agreeable perfume (FIGURE 2). The latter beautiful Araceae propagates freely by runners and formed huge stands along a streamlet near the observation site, where it might be the ''main supplier'' for the bee species, since the population of *Anthurium apaporanum* consisted of few, scattered, solitary plants in the forest understory. The bees approaching these hidden, inconspicuous scent sources displayed the zig-zig seeking behavior typical for olfactorically directed approach (Cardé 1984). In the morning hours (6.30–12.00 a.m.) of three days, they were the only visitors observed.

DISCUSSION AND OUTLOOK

Field observations provided evidence for at least three different pollination strategies occuring within the genus *Anthurium*, viz. pollination by Cecidomyiidae, by Drosophilidae, and by Euglossini. Suppositions about the respective syndrome of a given species can be made by the human nose, as the species pollinated by Drosophilidae emit a characteristic smell of yeast, alcohol, or rotten fruit, while euglossine-adapted species often give very agreeable, strong perfumes at least in the morning hours, when perfume collecting takes place. Where Cecidomiidae could be caught as visitors, the respective inflorescences always were scentless to our nose. These specimens have not been sampled, because experience shows that fragrances too weak even for a trained nose fail to give good results.

In most environments of tropical America except the dryest or coldest sites, *Anthurium* is represented by one or more species. Even comparatively small countries like Ecuador may house hundreds of species, as in many sites sampled 5–10 species could be found growing sympatrically. Some evidence indicates that such sympatric species are isolated genetically by means

FIGURE 1. *Euglossa viridis* showing its typical behavior of fragrance collection on *Anthurium apaporanum*. Photo: M. Schwerdtfeger.

FIGURE 2. *Euglossa viridis* showing its typical behavior of fragrance collection on *Spathiphyllum cannifolium.* Photo: M. Schwerdtfeger.

of the different pollination syndromes mentioned above. Furthermore, the fragrances of the euglossine-pollinated species show characters comparable to the better-investigated euglossine pollination syndrome within the orchids, where even sympatric and synchronously flowering species remain isolated by their bee visitors, which are highly specific to their respective scent composition.

Very interesting in this respect is the composition of the samples of two *Anthurium* specimens, which were easily determined as *A. armeniense* using the key of Croat (1983), although neither was found near the site of the type collection. The floral fragrances of these two plants are very different, suggesting that they might have different pollinators. It would be of great interest to collect the pollinators to determine if such reproductive isolation exists. Following the biospecies concept (Mayr 1963), they should be treated as different species, if they are genetically isolated by their pollinators. In the field or herbarium, however, this concept is not practical, because it is not possible to distinguish between the two specimens. We therefore propose to treat them as fragrance chemotypes (Whitten & Williams 1992).

Long-term observations of visitors at rewarding study sites would be very promising for answering the following questions: How many *Anthurium* species occur sympatrically? How many sympatric species flower synchronously? How are the main pollination syndromes portioned among the species? How do the ''perfume species'' portion the potential euglossine pollinator spectrum by means of specific scent compositions? Given that the genus *Anthurium* has perhaps a thousand species and is an extremely important component of the flora of most neotropical localities, revealing its divergent pollination strategies may serve as a further model for the origin and maintainance of neotropical biodiversity.

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