

FLORAL SCENT COLLECTION AT THE PERFUME FLOWERS OF *ANTHURIUM RUBRINERVIUM* (ARACEAE) BY THE KLEPTOPARASITIC ORCHID BEE *AGLAE CAERULEA* (EUGLOSSINI)

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INTRODUCTION

Orchid bees (Hymenoptera: Apidae: Euglossini) are known to be important pollinators in the tropics of the New World (Dodson 1966, Vogel 1966, Dressler 1982, Roubik & Hanson 2004). They became particularly famous for the scent-collecting behavior of the males on the perfume flowers of various orchid species and of many other plant families (Vogel 1966, Dodson *et al.* 1969). The tribe Euglossini is divided into five genera (*Aglae*, *Eufriesea*, *Euglossa*, *Eulaema*, *Exaerete*; Kimsey 1987), with a similar distribution for all but one genus (*Aglae*), ranging from northern Mexico to Argentina (Michener 2000). Whilst the ecology of the largest genera (*Eufriesea*, *Euglossa*, *Eulaema*) has been well documented during the past 40 years, information on the kleptoparasitic euglossines (*Aglae*, *Exaerete*), especially on the genus *Aglae*, remains scarce. Bees of the monotypic genus *Aglae* are restricted to moist forests from Colombia to Bolivia with an unverified finding in Panama (Michener 2000) and seem to be rare even in their natural habitat (Cameron 2004). For this reason very few observations on their ecology exist. In contrast to the other parasitic genus in the tribe, *Exaerete*, *A. caerulea* was never before observed collecting floral scent on perfume flowers, although there is a series of clues which

leads to the presumption that they do so. Morphologically, the males are provided with the same features for scent collection (foretarsal brushes, inflated hind tibia) as their relatives in the other Euglossini genera (Sakagami 1965, Vogel 1966, Kimsey 1987, Michener 2000). Moreover, they are attracted to artificial fragrance compounds (eugenol, methyl cinnamate, p-cresol, skatole; Williams & Dodson 1972, Morato 2001, Ramírez *et al.* 2002), which are components of natural floral scent (Williams & Whitten 1983, Gerlach & Schill 1991, Knudsen *et al.* 1993).

This is the first documentation of the scent-collecting behavior of *Aglae caerulea* at flower organs, viz. the inflorescences of *Anthurium rubrinervium* (Araceae) in the reserve Nouragues, French Guiana. Also, the floral odor composition of *A. rubrinervium* is analyzed and discussed.

METHODS

Study site. The study was conducted in the early rainy season (January–April 2006) around the Inselberg-station of the reserve “Les Nouragues” in French Guiana (04°05'N, 52°41'W, 120 m A.S.L.). The area is located in primary lowland tropical rainforest with an annual rainfall of 2990 mm and a mean annual temperature of 26.3°C (Grimaldi & Riéra 2001). A large population of *A. rubrinervium* (about 125 individuals) was found growing on a large rock near trail

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F-XIIX on the "Petit Plateau". Twenty individuals were flowering simultaneously in the study period, creating a sweet pleasant smell of floral perfume in the surroundings. Vouchers of *A. rubrinervium* investigated are deposited in the herbaria CAY and ULM.

Visitor observations. Flower visitors to 15 individuals of *A. rubrinervium*, belonging to one population, were observed and recorded during 09:30–15:00 h on eight days between 9 and 29 March 2006. Minimum observation distance to the flowers was 2 m. The climate on 9 March (visit of *Aglae caerulea*) and the days before was very sunny and hot with a little rain in the afternoon (9 March: temperature 21–32°C, precipitation 2.2 mm). Voucher specimens of the visiting bee species were collected and determined using the reference collection of G. Gerlach in Munich. They are deposited in the collection of the first author and the collection of the herbarium ULM (Hentrich FGIC25, FGIC26, FGIC28, FGIC31, FGIC32, FGIC47).

Scent sampling. Five scent samples from four individuals of different populations were collected in the field by headspace method. The inflorescences were covered by an inert oven-bag during collection. The scented air was drawn through a sampling cartridge by a battery operated membrane pump for four hours with a flow rate of 150 ml/min. The sampling cartridge was prepared with 25 mg of Tenax TA (mesh 80–100, Macherey Nagel, Düren, Germany) and 40 mg of Carboxen 100 (mesh 20–40, Supelco, Bellefonte, Pennsylvania, USA). The adsorbents were conditioned by washing with methanol (purity 99.8%, Merck, Darmstadt, Germany) and acetone (purity 99.9%, Merck, Darmstadt, Germany) and heated out for 30 min at 220°C before sampling. Subsequently, the adsorbed scent was recovered by elution with 200 µl acetone into glass vials. The samples were investigated by GC/MS using a Thermo Finnigan Voyager Mass Spectrometer combined with a Trace GC 2000 Series 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; splitless injection, temperature program was 50°C-2'iso-2.5°C/min-230°C-40'iso. Compounds were identified by comparison of their mass spectra and retention times with those of authentic reference samples available from the Givaudan reference compound collection.

Differences in the qualitative similarity of the scent samples were calculated using Sørensen's index of similarity (Magurran 1988), considering all compounds detected.

RESULTS

Visitor observations. Principal visitors to *Anthurium rubrinervium* were male bees of *Euglossa piliventris* and *E. viridis*. They showed typical odor-collecting behavior. Visits began between 09:30 h and 10:15 h and ceased between 14:00 h and 15:00 h. In the whole study period, *Aglae caerulea* was observed only once visiting the plants, viz. on 9 March 2006. At about 09:55 h, the bee approached the population in wide turns with a strong rattling buzz. Finally, it landed on the spadix of an *A. rubrinervium* individual and started to brush the surface of the spadix with its foretarsal brushes (Fig. 1). After some seconds, it flew up, hovered in the air and landed on the same spadix to continue brushing. This behavior was repeated twice. Then the bee flew away quickly in a straight line. The duration of the visit was quite short. The bee barely stayed 1 min at the spadix. At the same time no other bees were observed in the surroundings of the *Anthurium* plants.

Scent composition. *Anthurium rubrinervium* has a strong pleasant floral perfume. Emission of scent was tested olfactorily ("sniffing" by the first author) and could be perceived between 09:30 h and dusk. The floral fragrance contained a large row of monoterpenes followed by benzenoids and three lipid-derived compounds (Tab. 1). The main components were (Z)-8-heptadecene, methyl salicylate, 1,8-cineole, benzyl benzoate, (E)-ocimene and linalool.

Qualitative similarity of the scent samples varied between 74% and 98%. Sample 6 differs from other samples in having (E)-ocimene and 2,6-dimethyl-2,5,7-octatrien-1-ol, while methyl (Z)-cinnamate and methyl (E)-cinnamate was only detected in sample 2. Quantitative differences in the composition of the scent samples also occurred ((Z)-8-heptadecene: 1.55–43%, methyl salicylate: 4.67–44.93%, 1,8-cineole: 4.66–33.32%, benzyl benzoate: 1.90–19.86%).

DISCUSSION

Floral scent seems to play an important role not only in the life of the non-parasitic, but also in the parasitic genera of the Euglossini. Although the morphology of their collecting organs is very rudimentarily



FIG. 1. Fragrance collection of an *Aglae caerulea* male on the spadix of *Anthurium rubrinervium*.

developed (Sakagami 1965, Dressler 1968, Kimsey 1987, Michener 2000), they have been observed gathering floral scent from perfume flowers (Dressler 1968, Williams & Dressler 1976, Ackerman 1983, Ramírez *et al.* 2002). Current investigations show that collected scents are of great importance in the territorial display of male euglossine bees and might also be involved in their mating (Bembé 2004, Eltz *et al.* 2005, Zimmermann *et al.* 2006). Parasitic euglossines have so far never been observed at territorial display nor at mating. But since they also collect natural scents, we can presume that they must do so.

In the pollination of perfume flowers, the parasitic euglossines probably play a subordinate role (Dressler 1968, Ackerman 1983). Even if there are records of *Exaerete frontalis* and *Exaerete smaragdina* visiting perfume flowers, their visits are documented as very irregular and short (Dressler 1968). Besides this, even if they have a vast distribution and are proved to fly long distances they are not as abundant as their non-parasitic relatives and therefore appear in lower num-

bers at the perfume flowers. Another aspect is the pollination mechanism of perfume flowers. Especially in the orchid family, the pollination mechanism is highly specific and only matches with a certain size-group of pollinators (Dodson & Frymire 1961, Dressler 1968, Dodson *et al.* 1969). Therefore the parasitic euglossine bees, with their large and slender bodies, often do not fit the pollination mechanism of these flowers (Dressler 1968). In contrast to the orchids, pollination mechanisms are less selective in aroids, where parasitic euglossines have also been observed at perfume flowers. *Exaerete* is known to visit the spadices of the perfume-flowered genera *Spathiphyllum* (Dressler 1967, Williams & Dressler 1976, Montalvo & Ackerman 1986) and *Anthurium* (Hentrich, pers. obs.) and is able to pollinate the flowers at least as well as the smaller bees of the genus *Euglossa*, which also visit spadices of these genera (Williams & Dressler 1976, Croat 1980, Schwerdtfeger *et al.* 2002).

In our case, *Aglae caerulea* visited the spadix of *Anthurium rubrinervium*. Since *A. caerulea* was ob-

TABLE 1. Floral fragrance compounds of four different *Anthurium rubrinervium* individuals (in %). Samples AR3 and AR4 are taken from the spadix of the same individual in the female (AR3) and the male phase (AR4). Substances are divided into chemical classes and within each class in the order of their GC retention time. Values are percentages of the total amount of volatiles. Main compounds are printed in bold letters.

Sample No.	AR2	AR3	AR4	AR5	AR6
Terpenoids					
α -Pinene	2.09	0.17	0.04	1.20	0.30
β -Pinene	0.74	0.17	0.05	0.60	0.20
Sabinene	0.61	0.14	0.04	1.30	1.70
Myrcene	0.61	0.69	0.41	0.60	0.20
Limonene	3.81	1.72	0.55	1.30	1.10
β -Phellandrene	0.37	0.14	0.04	–	–
1,8-Cineole	33.32	19.45	4.66	18.50	15.00
(Z)-Ocimene	–	–	–	–	1.10
(E)-Ocimene	–	–	–	–	9.50
Terpinolene	1.48	0.34	0.14	0.60	0.50
6-Methyl-5-hepten-2-one	0.05	0.10	0.05	0.01	0.01
trans-Sabinene hydrate	–	–	–	0.05	0.06
(E)-Ocimene epoxide	–	–	–	–	0.10
Linalool	4.55	8.44	5.34	0.05	0.04
Terpinen-4-ol	0.12	–	–	0.05	0.05
δ -Terpineol	0.25	0.01	–	0.01	0.04
α -Terpineol	3.44	0.14	0.02	0.20	0.70
2,6-Dimethyl-2,5,7-octatrien-1-ol (exact isomer not yet known)	–	–	–	–	5.80
Benzenoids					
Styrene	0.06	0.03	0.07	0.01	0.02
Benzaldehyde	0.07	0.10	0.41	0.02	0.20
Methyl salicylate	4.67	44.93	42.87	23.90	13.30
Methyl benzoate	0.49	3.44	3.15	0.10	0.50
Benzyl alcohol	0.06	0.17	0.96	0.05	0.10
Amyl benzoate	–	–	–	0.02	0.03
Methyl (Z)-cinnamate	0.49	–	–	–	–
Methyl 2-methoxybenzoate	0.04	0.52	0.55	0.02	0.08
Methyl (E)-cinnamate	5.29	–	–	–	–
p-Cresol	–	–	–	0.01	0.01
Eugenol	–	–	–	0.03	0.03
(Z)-Isoeugenol	–	–	–	0.02	0.02
(E)-Isoeugenol	0.12	–	–	1.20	0.80
Benzyl benzoate	1.90	8.95	19.86	8.40	4.00
Benzyl salicylate	0.25	0.69	0.96	0.10	0.20
Lipid-derived compounds					
Nonanal	0.01	0.17	0.07	0.01	0.01
Acetic acid	0.37	0.52	0.55	–	–
(Z)-8-Heptadecene	31.48	1.55	14.79	35.00	43.00
Total	96.74	92.58	95.58	93.36	98.70

served only once in the whole study period, and is not as abundant as the other two euglossine visitors which quantitatively dominated the flower visits, we estimate that its importance as a pollinator of *A. rubrinervium* is small. Regarding an objective for the flower visit of *A. caerulea*, the bee showed the typical scent-collecting behavior, known from the other genera in the tribe Euglossini (Vogel 1966, Evoy & Jones 1971). Further, the analysis of the floral scent of *A. rubrinervium* demonstrated that its composition resembles that of other species of the Araceae and Orchidaceae belonging to the perfume flowers (Williams & Whitten 1983, Gerlach & Schill 1991, Knudsen *et al.* 1993, Schwerdtfeger *et al.* 2002). Methyl salicylate, 1,8-cineole, and benzyl benzoate can be found in large quantities in the floral scent of several *Stanhopea* species (Orchidaceae) (Williams & Whitten 1992). Linalool, (E)-ocimene, and methyl (E)-cinnamate are important compounds in the floral scent of *Gongora* (Orchidaceae) (Williams & Whitten 1983). 1,8-Cineole is the major compound in the floral scent of many perfume-flowered Araceae (Gerlach & Schill 1991, Schwerdtfeger *et al.* 2002) and was also a main constituent of the floral scent of *A. rubrinervium*. The mentioned compounds are known to attract different species of euglossine bees to artificial chemical baits as well as to perfume flowers and play an important role in the pollination and speciation of these plants (Dodson *et al.* 1969, Williams & Dodson 1972, Ackerman 1983). Latest research results show that the variety of compounds gathered by euglossine bees is specific for each bee species (Eltz *et al.* 1999). Data on the content of the hind tibia of the parasitic euglossine genera are not yet documented but it is likely that they also have a compound spectrum which is species-specific.

In the odor-driven pollination system of euglossine pollination, variability of floral scent between the populations of a perfume-flowered species needs to be low because attraction of the pollinating species is highly specific and small changes in the odor bouquet could attract different visitors (Williams and Whitten 1992, Knudsen 2002). In our case, visitor observations at all sampled inflorescences showed no differences in the pollinator spectrum, although the scent composition differed between individuals. Qualitative and quantitative differences in the scent samples may be due to intraspecific variation of floral scents between the individuals of different populations. In

addition, the different size of the inflorescences and environmental conditions (e.g., temperature, light conditions, humidity) during sampling may also have affected chemical composition of the samples.

In conclusion, we document that *A. caerulea* collected floral fragrance on the spadix of *A. rubrinervium* and presume that the floral fragrance of *A. rubrinervium* contains one or several compounds important for the scent spectrum of this bee. Eugenol, methyl cinnamate, and p-cresol, which are minor compounds of *A. rubrinervium* floral fragrance, proved to be attractive for *A. caerulea* (Williams & Dodson 1972, Morato 2001, Ramírez *et al.* 2002). For the other compounds no attractiveness for *A. caerulea* in baiting experiments is documented. (Z)-8-Heptadecene has not yet been described as a compound in floral fragrances of other euglossine-visited flowers, although it is found in the floral fragrance of other plants (Knudsen *et al.* 1993). Interestingly, (Z)-8-heptadecene was also identified as semiochemical in mites (Nazzi *et al.* 2002, Milani *et al.* 2004, El-Sayed 2003-2006). Nazzi *et al.* (2002) described the significant reduction of *Varroa destructor* offspring in the brood cells of infested *Apis mellifera* colonies by (Z)-8-heptadecene. Even if male euglossine bees do not participate in brood care, this compound could be important in mating. Therefore the attractiveness of (Z)-8-heptadecene for euglossine bees should be tested.

Although *A. caerulea* was observed only once collecting floral scent, the bee was quite common and often seen flying in the surroundings of the *A. rubrinervium* population. A male individual of *A. caerulea* was collected at the nectar-flowers of *Psychotria carapichea* (Rubiaceae). The bee had a strong smell of butyric acid, which has been observed by Vogel (1966) and Williams & Whitten (1983) in individuals of *Eulaema*. Williams & Whitten (1983) suggest that the released odor may represent a defensive secretion or alarm pheromone. But perhaps butyric acid also plays a role in pathogen prevention in the brood cells of *Eulaema* and the newly emerged bees still wear the smell of the nest? Little seems to be known about that.

Another remarkable observation about parasitic euglossines is their reserved and shy behavior. The short stay and the sole observed visit of *A. caerulea* at a perfume-flower was perhaps due to disturbance either by the presence of the observer or by other bees. Other studies on the biology of the parasitic euglossine bees also mention their shy behavior (Bennett

1972, Garófalo & Rozen 2001). The parasitic euglossines only enter the host's nest when the host is not present. Inside the nest they act very carefully and they immediately leave the nest when the host arrives. No aggressive action by a parasitic euglossine against its host is known. At chemical baits they act similarly. In contrast to other euglossine bees they spend an unusually long time inspecting the situation before landing on the bait. If one tries to catch them and fails, they are not seen at the same bait for several days (Hentrich, pers. obs.). Obviously the shy and careful nature of these parasitic bees is also reflected in their fragrance collection.

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