

NONFLORAL SOURCES OF CHEMICALS THAT  
ATTRACT MALE EUGLOSSINE BEES  
(APIDAE: EUGLOSSINI)

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**Abstract**—We present chemical analysis of four rotten or fungus-infected logs that attracted fragrance-collecting male euglossine bees. Eight of the 10 volatile compounds detected have never been found in the fragrances of orchids pollinated by male euglossine bees. Nonfloral sources of chemicals such as rotting wood may constitute an important fragrance resource for male bees. Since rotten logs produce large quantities of chemicals over long periods of time, such nonfloral sources might be more important than flowers as a source of certain fragrances for some euglossine bee species. Fragrance collecting in euglossine bees might have evolved originally in relation with rotting wood rather than flowers.

**Key Words**—Hymenoptera, Apidae, Euglossini, floral fragrance, fungi, skatole, chemical ecology, orchid, rotting wood.

INTRODUCTION

Euglossine bees are important pollinators of many plant species in neotropical forests (Janzen, 1971; Dressler, 1982; Williams, 1982; Ackerman, 1985; Roubik and Ackerman, 1987). Euglossines are best known for the unique fragrance-

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collecting behavior of the male bees (Kimsey, 1984) that are specialized pollinators of certain orchids, aroids, and other plants. Male euglossines use their modified front- and mid-tarsi and their abundant labial gland secretions to collect volatile chemicals and to transfer the chemicals to highly specialized hind tibial organs (Whitten et al., 1989). The fate of these stored fragrances and their role in euglossine biology are still unclear (Stern, 1991), although current hypotheses suggest that they play a role in chemically-mediated sexual selection (Kimsey, 1982; Whitten et al., 1989; Lunau, 1992). The identification of compounds present in orchid fragrances has yielded a set of common, easily-obtained chemicals that attract male euglossines in large numbers in simple field bioassays ("baiting"); such bioassays led to the discovery of many new species of euglossines and allow easy censusing of male euglossine populations (e.g., Ackerman, 1989; Janzen et al., 1981). Females remain difficult to census, and many euglossine species are known only from male specimens.

Flowers are not the only source of fragrance chemicals for male euglossines. Male euglossines collect fragrances from a variety of sources, including rotting logs, tree wounds, rotting fruits, and leaf litter (Dressler, 1967; Ackerman, 1983; Whitten et al., 1989). *Eufriesea purpurata* (Mocsáry) is attracted in large numbers to wooden surfaces sprayed with Aldrin (Dressler, 1967) and DDT (Roberts et al., 1982), although it is not clear whether bees were attracted to the pesticide, to minor constituents, or to breakdown products. Reports of such nonfloral euglossine attractants are uncommon, primarily because most studies of euglossines have been performed by orchid biologists. Bees visiting showy orchids attract more attention than bees brushing on rotten logs or bark, and hence such nonfloral sources are probably underreported by field biologists. Are orchids and other flowers the primary source of fragrances for euglossines, or do male bees obtain a large portion of their fragrances from other sources such as rotting wood, bark, and fruits? Do both floral and nonfloral attractants produce the same sets of chemicals? Several surveys have provided analyses of orchid fragrances that attract male euglossines (Williams and Whitten, 1983; Gerlach and Schill, 1991; Kaiser 1993). Unfortunately, few data exist on the chemical composition of the nonfloral sources that attract male bees.

In this paper, we present chemical analyses of four non-floral substrates that attract male euglossines, and we discuss the relative importance of floral vs. nonfloral sources of chemicals to euglossine chemical ecology. These four substrates were encountered by chance in different localities in Central America. These instances are described separately below, and then the results are discussed and compared.

#### METHODS AND MATERIALS

Samples were placed in either hexane or methylene chloride (HPLC grade) and shipped to Gainesville, Florida. Samples were stored at  $-4^{\circ}\text{C}$  until analyzed. The extracts were analyzed by gas chromatography-mass spectrometry

(GC-MS) using a Hewlett-Packard 5995 GC-MS equipped with a 30 m DB-5 column. Oven temperature was programmed from 25°C to 290°C at 3°C/min. Compounds were identified by comparison of mass spectra and retention times with synthetic standards. Spectra of unknowns were searched against the NIST/EPA/NIH mass spectral library (Ausloos et al., 1992).

*Site 1.* This study was conducted at a logging stockpile bordering the Sarapiquí River, near La Virgen de Socorro, in northeastern Costa Rica (Heredia Province). On February 27, 1990, one of us (A.M.Y.) discovered dozens of male *Euglossa purpurea* Friese collecting volatiles (brushing) along a darkly-stained crevice within the heartwood of the transversely cut ends of a large log. The stained heartwood where the bees were brushing emitted a strong fecal odor, similar to skatole (3-methyl indole). Local loggers called this tree "Quizarrá caca" (caca = feces), named after the characteristic odor of the wood. The tree was tentatively identified as *Ocotea leucoxylo*n (Sw.) Laness. (Lauraceae). This determination is tentative because foliage was lacking; the tree might belong to the closely related genus *Nectandra*. As many as 50 bees gathered at each area of split, exposed heartwood (Figure 1), and a much lower number hovered above equally fragrant wood chips on the ground near the log. No bees were seen at other logs stacked nearby. Voucher specimens of bees were collected; only *E. purpurea* was present. Samples collected for chemical analysis were: (1) hind tibiae of 14 bees (pooled); (2) heads of same 14 bees (pooled); (3) wood shavings from surface of log where bees were brushing; (4) wood shavings from face of log where bees were not seen brushing; and (5) wood chips on ground that attracted bees. All samples were immediately placed in hexane or methylene chloride for later analysis. The site was revisited on March 5, when bees were still observed on the log. Two squares of filter paper impregnated with skatole were tacked to a nearby log; the skatole attracted dozens of *E. purpurea*.

*Site 2.* On February 29, 1988, one of us (D.L.S.) observed several male *Eulaema bombiformis* (Packard) brushing on the surface of a rotten log on Barro Colorado Island, Panama. Fragments of wood from the brushed surface were placed in vials of hexane.

*Site 3.* In April 1984, along the Río Iguanita, near Portobelo, Panama, we found a dead tree trunk that had recently been knocked down and broken open by the fall of an adjacent tree. The log was covered by 100–150 male *Euglossa* of several species that were brushing on the punky, decayed wood near the center. The wood had a faint aromatic odor. Of 21 bees captured, 18 were *E. variabilis* Friese and three were *E. despecta* Moure; at least two additional species were present but were not captured. Samples of wood from where bees were brushing were collected and extracted in hexane.

*Site 4.* In July 1986, we observed numerous *Eulaema cingulata* (Fabricius) brushing on fungus-infected machete wounds of the trunk of *Dalbergia cub-*

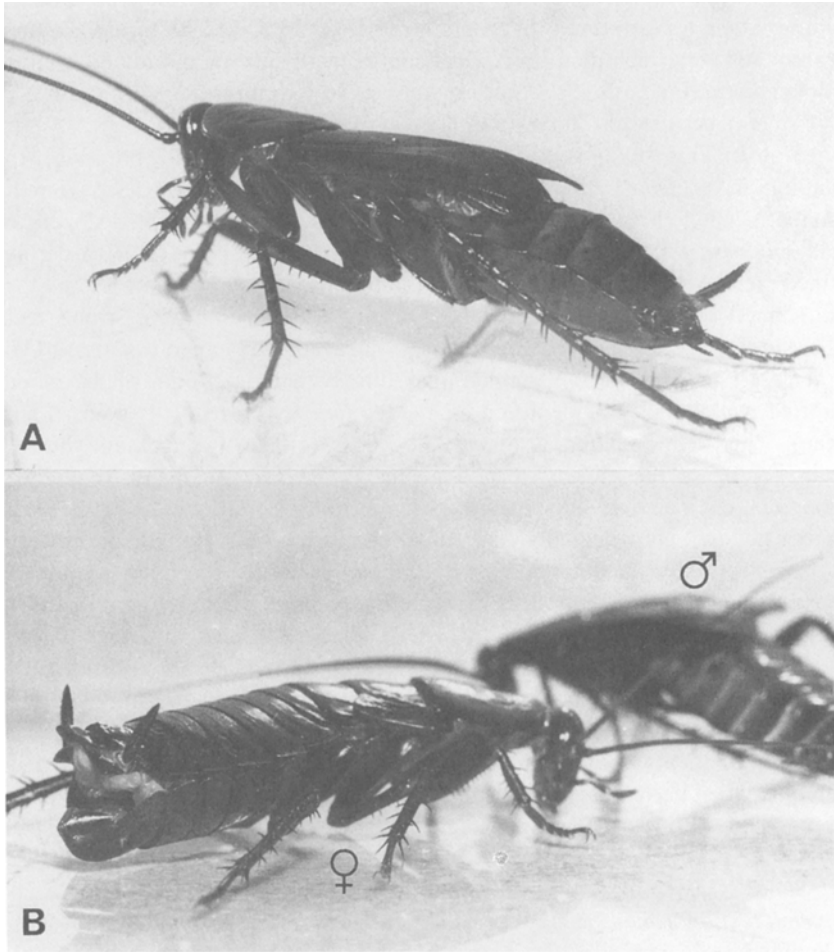


FIG. 1. Male *Euglossa purpurea* collecting volatiles from crack in sawn end of skatole-producing *Ocotea* log in Sarapiquí District, Costa Rica.

*ilquitensis* Pittier (Leguminosae) at Estación Experimental La Lola, near Siquirres, Costa Rica. During irregular visits to this site over a three-year period, we frequently observed bees brushing on the same tree wounds. This site was discussed by Whitten et al. 1989. Samples of tree wounds and undamaged bark and wood were collected and extracted in hexane.

## RESULTS

*Site 1.* GC-MS analyses of the extracts of the samples revealed large quantities of skatole in the wood sampled where the bees were brushing (Figure 2A). These surface wood extracts (of discolored areas where bees were brushing) also contained large amounts of high molecular weight hydrocarbons and esters that occur in *E. purpurea* labial glands (Figure 2), the most characteristic being eicos-9-enyl-1,20-diacetate. The presence of the labial secretions on the surface of the wood suggests that the bees apply the labial secretions to the wood, using the secretion as a solvent to extract and collect volatiles from the wood (Whitten et al., 1989). Areas of the log that did not attract bees contained no skatole or other hexane-extractable compounds. The pooled hind tibial extracts (Figure 3) contained large amounts of skatole, as well as several other fragrance compounds including *p*-anis alcohol, *p*-anisaldehyde, anisyl acetate, *trans*-nerolidol, *p*-dimethoxybenzene, and several sesquiterpenes. We presume that the bees obtained these compounds from other sources, either flowers or nonfloral sources.

Skatole has long been known to be a strong attractant of certain species of

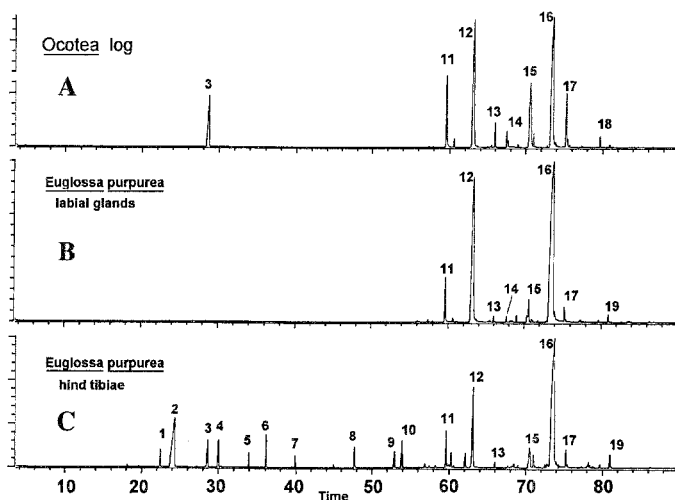


FIG. 2. Total ion chromatograms of methylene chloride extracts of: *Ocotea* log attracting male bees; pooled heads of 14 male *Euglossa purpurea*; and pooled hind tibiae of 14 male *Euglossa purpurea*. Numbered peak identifications are: 1, *p*-anisaldehyde; 2, *p*-anis alcohol; 3, skatole; 4, anisyl acetate; 5, beta-bisabolene; 6, *trans*-nerolidol; 7, unidentified sesquiterpene; 8, 16:1; 9, unidentified; 10, unidentified; 11, 20:2; 12, eicosenyl acetate; 13, 15:0; 14, eicosenol; 15, 16:1 + coeluting acetate; 16, eicos-9-enyl-1,20-diacetate; 17, 29:1; 18, 31:1; 19, unidentified. Aliphatic hydrocarbons are identified as # of carbons:# of double bonds. Unlabeled peaks are unidentified.

TABLE 1. FRAGRANCE COMPOUNDS PRESENT IN EUGLOSSINE-ATTRACTING WOOD SAMPLES<sup>a</sup>

| Source                          | Compound                                    | Relative abundance | Present in orchid fragrances? | Attractive to male euglossines? |
|---------------------------------|---|--------------------|-------------------------------|---------------------------------|
| <i>Ocotea</i>                   | skatole ( <b>3</b> )                        | +++                | no                            | yes                             |
| unidentified wood, BCI          | 2,5-dimethyl-3-methoxy phenol ( <b>20</b> ) | +++                | no                            | unknown                         |
| unidentified wood, Rio Iguanita | trans-methyl cinnamate ( <b>34</b> )        | +                  | yes                           | yes                             |
|                                 | unknown <b>35</b>                           | +                  | no                            | unknown                         |
|                                 | unknown <b>36</b>                           | +++                | no                            | unknown                         |
|                                 | unknown <b>37</b>                           | +                  | no                            | unknown                         |
|                                 | unknown <b>39</b>                           | ++                 | no                            | unknown                         |
| <i>Dalbergia</i> wood           | unknown <b>50</b>                           | +                  | no                            | unknown                         |
|                                 | unknown <b>51</b>                           | +++                | no                            | unknown                         |
|                                 | trans-nerolidol ( <b>52</b> )               | +++                | yes                           | unknown (never tested)          |

<sup>a</sup>Mass spectra data of unknowns: **20**—152(M+, 100), 137(53), 121(42), 107(25), 91(30), 79(26), 77(27), 65(15), 53(21); **35**—178(M+, 13), 124(100), 123(23), 109(64), 95(14), 81(12), 55(32), 53(13), 41(15); **36**—176(M+, 20), 161(19), 145(6), 124(89), 123(24), 109(100), 95(22), 81(20), 53(50); **37**—spectrum weak; **39**—207(16), 204(35), 161(18), 135(34), 107(54), 93(51), 81(53), 67(57), 43(60), 41(100); **50**—156(M+, 2), 128(2), 114(3), 99(100), 87(15), 43(42), 42(42), 41(50); **51**—223(1), 155(6), 138(10), 127(7), 111(23), 109(88), 93(28), 69(77), 43(100), 41(70).

male euglossines. Its attractant properties were discovered by trial-and-error bioassays of fragrant compounds during the 1960s by C. Dodson, H. Hills, and Williams (N. Williams, personal communication). Chemical analyses of the hind tibial organs of various euglossine species have shown that certain species may contain large amounts of skatole (Whitten, unpublished observation). However, fragrance analyses of over 350 species of orchids have failed to reveal any orchid sources of skatole (Whitten, unpublished observation; Gerlach and Schill, 1991; Kaiser, 1993). The only known floral sources of skatole are *Arum* and *Hydrosme* (Araceae) (Smith and Meeuse, 1966). Two possible explanations exist: (1) euglossines obtain skatole from unknown floral sources, and/or (2) euglossines obtain skatole from other, nonfloral sources.

These data show that: (1) skatole is a naturally-occurring substance within the habitat of *Euglossa purpurea*; and (2) *E. purpurea* obtains skatole, probably in large amounts, from a non floral source. The role of fungi in the production of the skatole is not clear. The restriction of bee activity to the crack in the tree trunk suggests that healthy heartwood is not attractive and that skatole is pro-

duced by fungi and/or bacteria or by the wood in response to microbial infection. Dressler (1967) also reported *E. purpurea* and two other species brushing on a "large malodorous seeping area" on the trunk of a tree near Puerto Viejo, Costa Rica; the seep smelled strongly of skatole (R. Dressler, personal communication).

*Site 2.* Hexane extracts of the wood (Fig. 3) contained a single volatile, compound **20**, plus a variety of normal acetates, alcohols, alkenes, and alkanes. Compound **20** is tentatively identified as 2,5-dimethyl-3-methoxy phenol (R. Kaiser, personal communication). It is not known from orchid fragrances, but is known from oak wood and "oak moss" lichens [*Evernia prunastri* (L.) Ach.] (Tabacchi and Nicollier, 1979; R. Kaiser, personal communication). The lipid compounds (peaks between 36 and 66 minutes, Figure 2) are qualitatively and quantitatively similar to the labial secretions of *E. bombiformis* (Williams and Whitten, 1983). Although no samples of *E. bombiformis* were collected at this site, we did analyze tibial extracts of one male from near Portobelo, Panama, and one male from Ecuador. In both tibial extracts, compound **20** was present in trace quantities (>1% of integrated total ion chromatogram area).

*Site 3.* The wood extracts (Figure 4) contained five compounds, plus large quantities of lipids characteristic of *Euglossa* and *Eulaema* labial gland secretions. One of the five compounds is trans-methyl cinnamate, a common floral fragrance compound that attracts many euglossine species. Three of the five compounds are unidentified but appear structurally related (**35–37**); the mass spectra of all three contain prominent ions of  $m/z$  109 and 124, suggestive of a methoxyphenyl fragment. Several known euglossine attractants possess this structure, including *p*-methoxyphenylethyl alcohol and methyl *p*-methoxycin-

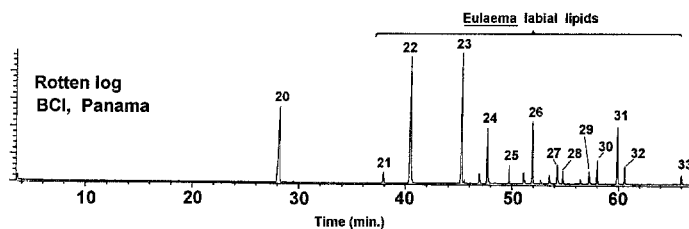


FIG. 3. Total ion chromatogram of hexane extract of the surface of an unidentified rotten log at Barro Colorado Island, Panama, that attracted *Eulaema bombiformis*. Compounds 21–33 are typical of labial gland secretions of *E. bombiformis* and were probably applied to the surface of the log by fragrance-foraging males. Numbered peak identifications are: **20**, 2,5-dimethyl-3-methoxyphenol; **21**, tetradecanal; **22**, tetradecanol; **23**, tetradecyl-1-acetate; **24**, 1-hexadecanol; **25**, 1-hexadecenyl acetate; **26**, hexadecyl acetate; **27**, octadecanol; **28**, 21:0; **29**, octadecenyl acetate; **30**, octadecyl acetate; **31**, 23:1; **32**, 23:0; **33**, 25:0.

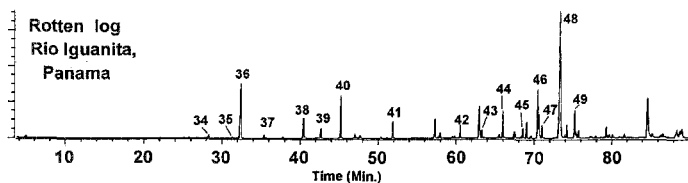


FIG. 4. Total ion chromatogram of hexane extract of the surface of an unidentified log from Rio Iguanita, Panama, that attracted a variety of euglossine species. Numbered peak identifications are: **34**, *trans*-methyl cinnamate; **35**, unidentified; **36**, unidentified; **37**, unidentified; **38**, 12:1; **39**, unidentified; **40**, tetradecyl acetate; **41**, hexadecyl acetate; **42**, 23:0; **43**, 24:0; **44**, 25:0; **45**, 26:0; **46**, heptacosanol; **47**, 27:0; **48**, eicos-9-enyl-1,20-diacetate; **49**, 29:1.

namate. However, none of the four unknowns is reported from any orchid fragrance. The lipid fraction of the extract (retention times from 40 to 90 min) contains a variety of normal alkanes, alkenes, acetates, and eicos-9-enyl-1,20-diacetate. The lipids presumably were applied to the surface of the wood by fragrance-collecting male bees.

*Site 4.* In an earlier study of this site (Whitten et al., 1989), we were unable to identify the volatiles present in the bee-attracting wounds. Subsequent analyses revealed three volatile compounds in the extracts of bee-attracting wood. The most abundant is *trans*-nerolidol, a compound known from orchid fragrances. The remaining two unidentified compounds (**50** and **51**) have never been detected in any orchid fragrance. The attractiveness of these compounds is unknown; nerolidol has never been used in bioassays for euglossines.

#### DISCUSSION

The wood extracts contain two sets of compounds: (1) aliphatic alkanes, alkenes, alcohols, acetates, and diacetates that are typical of euglossine labial gland secretions; and (2) lower-molecular-weight terpenoids and aromatic compounds. The latter group probably is produced in the rotting wood, whereas the lipids are applied to the surface of the wood by fragrance-foraging male bees. Whitten et al. (1989) demonstrated that when euglossines are allowed to brush on the surface of filter paper impregnated with a chemical bait, the paper quickly becomes saturated with labial gland lipids applied by the bees. We hypothesized that the labial lipids serve as a nonpolar solvent that serves to increase fragrance collection efficiency.

The fragrance-collecting behavior of male euglossine bees and their role as pollinators are well-documented, although how male euglossines utilize the collected fragrances is still unknown. Earlier hypotheses suggested that the fra-



grances served as precursors of sex pheromones or were used to produce leks (Dodson, 1975; Kimsey, 1980), but current hypotheses postulate that female bees choose mates based upon the amount or number of chemicals in each male's tibial organ (chemical-based sexual selection) (Kimsey, 1982; Kiester et al., 1984; Schemske and Lande, 1984; Stern, 1991; Lunau, 1992). Roubik (1989) noted that females of several species of *Eulaema* collect skatole-containing dung for use in nest construction; he speculated that males might collect skatole and then pass the chemical to the females during copulation, as a nuptial gift. However, there is no evidence that males can expel the chemicals in quantity or that the females can accept or store fragrances from males. Whatever the role of fragrance chemicals, male bees appear to spend a large amount of their time and energy seeking and collecting fragrances.

What is the relative importance of flowers vs. rotting wood as chemical sources for male euglossines? We suggest several plausible and possibly overlapping scenarios.

1. Male euglossines seek certain chemicals and obtain them from any available source, floral or nonfloral. Some compounds are obtained only from flowers, others only from wood (e.g., skatole), and some might be obtained from both flowers and wood (e.g. methyl cinnamate, nerolidol).

2. Flowers are the primary source of fragrance chemicals. Some rotting logs might produce chemical analogs that deceive male bees and trigger fragrance-collecting behavior, but the analogs play no role in the biology of the bees.

3. Rotting wood and other plant secretions are the primary source of fragrance chemicals. Certain orchids and other plants also produce the same chemicals and take advantage of the bees' behavior to utilize them as pollinators, but provide relatively minor amounts of chemicals for the bees.

Most workers have assumed that flowers are the principal source of chemicals collected by male bees (e.g., Williams, 1982). Chemical analyses of euglossine tibial organs cannot determine whether the chemicals present were obtained from flowers or from nonfloral sources. However, most orchids pollinated by male euglossines have low population densities and short-lived flowers and therefore might be unreliable sources of chemicals for long-lived euglossines. Ackerman (1983) found that one third of the euglossine species on Barro Colorado Island, Panama, have never been observed to visit or carry pollinaria of any orchid species on the island; these euglossines apparently obtain chemicals from sources other than orchids. Our observations suggest that rotting wood may provide a long-lasting and abundant source of at least some chemicals sought by some male euglossines. This is certainly the case for skatole-collecting *Euglossa purpurea* in Costa Rica. However, we do not know whether skatole is actually used by the bees in their courtship or whether it is an analog of indole (indole is fairly common in orchid fragrances).

Since the orchid–euglossine–wood interaction is complex, involving many species and many chemicals, we suggest that all three hypothesis may be correct to some degree, depending upon the particular bee and plant species involved. Our observations document that nonfloral sources may be important resources for at least some euglossine species.

The relative importance of nonfloral sources for male euglossines also bears upon the evolution of fragrance-collecting behavior and the extent to which euglossines and plants have coevolved. Some workers have assumed that orchids and other flowers are a major source of chemicals for the bees and that orchids and euglossines have coevolved (Kiestler et al., 1984), albeit somewhat loosely. An alternative hypothesis (Ackerman, 1983) is that euglossine fragrance-collection evolved independent of the orchids and that orchids later adapted to use euglossines as pollinators, taking advantage of a preexisting behavior of male bees. In the latter hypothesis, the initial sources of fragrance chemicals for bees would have been nonfloral sources such as plant essential oils and resins and fungal secretions. Rotting logs and tree resins certainly predated the evolution of orchids, and the origin of euglossine fragrance collection might have involved rotting wood as a source of chemicals. Therefore, male euglossine-pollinated orchids might have evolved to take advantage of this pre-existing interaction involving the bees, rotting wood, and possibly fungi.

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