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A PRELIMINARY BIBLIOGRAPHY ON EUGLOSSINE BEES AND THEIR RELATIONSHIPS WITH ORCHIDS AND OTHER PLANTS

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The relationship of insects to plants, including coevolutionary relationships, insect use of plant natural products, and chemical communication among insects are all subjects of great interest. One of the most interesting, but least studied groups of insects, is the euglossine bees.

The Euglossini (Hymenoptera — Apidae) are a tribe of neotropical bees, usually brightly metallic colored. There are four free living genera (*Eulaema*, *Euplusia*, *Eufriesea*, and *Euglossa*) and two parasitic genera (*Exaerete* and *Aglae*). The free living genera are either solitary, communal, or quasi-social, depending on the species (Dodson, 1966; Michener, 1974; Roberts and Dodson, 1967; Wilson, 1971; Zucchi *et al.*, 1969). Actually, very little is known of the social life of this group of bees. The genera are quite distinct, with the exception of *Euplusia* and *Eufriesea*. *Eulaema* is a genus of about 17 species of large, brown or black, hairy bees. *Euplusia* consists of about 80-90 species of bees, some of which are superficially similar to *Eulaema* (large, brown and/or black, slightly metallic), and others of which are very metallic (usually green, bronze, blue, or purple). *Eufriesea* is possibly only subgenerically distinct from *Euplusia* and differs mainly in having a brightly metallic head. *Euglossa* consists of approximately 100 (or more) species of small or medium sized, brightly metallic blue, green, bronze, or mixed colored bees that are relatively hairless. *Exaerete* consists of five species of metallic green or blue green bees. *Algae* is a monotypic genus (as is *Eufriesea*) with one bright blue species. All species of euglossines are very rapid flyers and tend to be very wary. The males are characterized by feathery brushes on the front tarsi and by greatly inflated hind tibiae with long slits ("scars" of our common usage). The females of many species are very similar and are difficult to characterize.

Both male and female euglossines forage a number of nectariferous species of flowering plants for their food. The females also visit a number of species of angiosperms from which they collect pollen as well as nectar. Those species visited by both males and females foraging for nectar have been called gynandro-euglossophilous by Wiehler (1976). It is curious that those species that are gynandro-euglossophilous are seldom (if ever) pollinated by other nectar collecting bees. The females collect resin, mud and fecal matter for building nests.

The euglossine bees pollinate at least 3000 species of the Orchidaceae, and also numerous other species of tropical plants. It is noteworthy that epiphytism is more common in the neotropics than in the paleotropics, and that a large number of the neotropical epiphytes are pollinated by euglossine bees.

Male bees of the tribe Euglossini visit and often pollinate various orchid flowers (Cruger, 1865; Darwin 1872; Dodson, 1962, 1967b; Dodson and Frymire, 1961a, 1961b; Dressler, 1967, 1968a, 1968b; van der Pijl and Dodson, 1966; Vogel, 1963, 1966a, 1966b). The relationship of the male bees to the orchid flowers has been termed the "male euglosine syndrome" by Dressler (1968b). This has also been called andro-euglossophily by Wiehler (1976). The orchid flowers (and other flowers) that are pollinated exclusively by male euglosines are very fragrant, lack nectar, and attract no other bees or insects. No food is present in the flowers for the male bees, and females

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are not attracted to those flowers which have the "male euglossine syndrome." The source of attraction in the flowers was recognized as the fragrance, but for a number of years the identity of the floral fragrance components was not known. Eleven compounds were identified from orchid floral fragrances (Hills, Williams, and Dodson, 1968), but only some of the compounds were shown to be attractants of male euglossines (Dodson, Dressler, Hills, Adams, and Williams, 1969). Several additional compounds have been identified from orchid floral fragrances (Hills, Williams, and Dodson, 1972), some of which have been shown to be active attractants in field tests (Williams and Dodson, 1972).

It is clear from our earlier work that the fragrance components of the orchid flowers are the attractants of male euglossine bees to those flowers (Dodson, 1970, 1975a; Dodson, *et al.*, 1969; Hills, *et al.*, 1968, 1972; Williams and Dodson, 1972). Similar studies have been conducted on members of other plant families, such as *Spathiphyllum* of the Araceae (Williams and Dressler, 1976).

The floral fragrances of the flowers that attract male euglossine bees not only serve as attractants, but also serve as isolating mechanisms between closely related species by selectively attracting one or a very few species of bees as pollinators (Hills, *et al.*, 1972; Williams and Dodson, 1972; Williams and Dressler, 1976). In these cases the floral fragrance may be the sole isolating mechanism between closely related species or may act together with mechanical (size, placement of pollen) and geographical isolating mechanisms.

The behavior of the bees when attracted to pure organic compounds that have been identified from the orchid floral fragrances has been described by Dodson *et al.*, (1969) and Williams and Dodson (1972). The bees are attracted to the pure compounds, land on the blotter paper on which the compound is presented, scratch the paper with their front tarsal brushes, launch into the air, hover, and transfer the collected fragrance components to the inflated hind tibiae. Evoy and Jones (1972) have given detailed descriptions of motor patterns of the bees as they transfer the collected chemicals from the front tarsi to the hind tibiae. The behavior of the bees is essentially the same when attracted to either pure compounds or actual flowers.

The chemicals to which the male euglossines are attracted are found in other plant families (Gesneriaceae, Solanaceae, Araceae) which are pollinated to a limited extent by male euglossine bees (Williams and Dressler, 1976; Dodson, Dressler, and Williams, unpublished). Most of the floral fragrance components are commonly occuring plant products, either monoterpenoids or aromatic compounds (Hills, *et al.*, 1968, 1972; Williams and Dodson, 1972).

The main question is why do male euglossine bees visit orchid flowers? This can be broken down into several aspects. 1) What attracts the male euglossines to the flowers? We have shown that they are attracted to the flowers by the floral fragrances (Dodson, 1975a; Dodson, *et al.*, 1969; Hills, *et al.*, 1972; Williams and Dodson, 1972). 2) What do the bees do when they visit the flowers? The behavior of the bees on the flowers, including the collection of the fragrance components, the launching into the air, and the transfer of the collected fragrance components to the hind legs has been described in varying detail (Dodson, 1975a; Dressler, 1967, 1968a, 1968b; Evoy and Jones, 1971). 3) How do the flowers benefit by attracting the male euglossines? It has been shown that the flowers are pollinated by various spe-

cies of bees, and that the bees may serve as isolating agents between closely related species of plants (Hills, *et al.*, 1972; van der Pijl and Dodson, 1966 and references therein). In addition, the flight ranges of the bees may be an effective means of long distance pollen flow (Williams and Dodson, 1972; and Janzen, 1971 for females). 4) What do the bees do with the compounds they collect from the flowers? At least tentative suggestions have been made about why the bees collect the floral fragrance components (Dodson, 1975a; Dodson, *et al.*, 1969), but these suggestions have not yet been experimentally verified. 5) What are the modifying effects of the various components of the floral fragrances? This has also been approached, but only in the most preliminary fashion (Williams and Dodson, 1972).

I offer this list as a preliminary bibliography on the subject and additions and suggestions will be appreciated. This bibliography omits papers that are purely taxonomic for the most part. The following bibliography will seem biased towards papers concerning male euglossine bees for two reasons. First, most of the recent work on euglossine bees has been centered around the relationships of the male bees to orchid flowers. Second, the males are generally easier to identify than the females.

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