 doi: http://dx.doi.org/10.15517/lank.v24i3.61983

CORRESPONDENCE

# FEMALE ORCHID BEE *EUGLOSSA DILEMMA* VISITS THE PERFUME ORCHID *CORYANTHES PANAMENSIS* IN FLORIDA

Robert W. Pemberton

2275 1st Ave. NE, Atlanta, Georgia, 30317, U.S.A.
rpemberton5@gmail.com

Abstract. Male orchid bees gather fragrance chemicals from the surfaces of about 700 species of neotropical orchids and pollinate them in the process. The males display the collected chemicals during their courtship, and female orchid bees will mate only with males displaying a species-specific blend of collected chemicals. Given this reality, the discovery of a female *Euglossa dilemma* dead in the bucket trap of a flower of the perfume orchid *Coryanthes panamensis* bearing the orchid's pollinarium is extraordinary. There are no previous reports of female orchid bees visiting a perfume orchid and picking up pollinia of the orchids. Bearing a pollinarium indicates that this female bee made at least two visits to the flowers and that these visits were unlikely to be accidental. The flower in which the bee was found was on a cultivated plant grown in a residential garden in Coral Gables, Florida. Neither the orchid nor the orchid bee are native to Florida and occur in different areas of tropical America. Why this female orchid bee visited this orchid is considered, including the possibility that it may be a gynandromorph. Despite being a morphological female, the bee may have had neurological anomalies that caused it to exhibit a male-like attraction to this perfume orchid.

Resumen. Los machos de las abejas de orquídeas recolectan compuestos químicos fragantes de las superficies de aproximadamente 700 especies de orquídeas neotropicales y las polinizan en el proceso. Los machos presentan los compuestos recolectados durante su cortejo, y las abejas hembras solo se aparean con machos que ofrecen una mezcla específica de estos compuestos. Dada esta realidad, el hallazgo de una hembra de *Euglossa dilemma* muerta dentro de una flor de la orquídea perfumada *Coryanthes panamensis*, que portaba el polinario de la orquídea, es extraordinario. No existen reportes previos de abejas de orquídeas hembras visitando orquídeas perfumadas y recolectando polinios de estas flores. El hecho de que la abeja llevara un polinario indica que esta hembra realizó al menos dos visitas a las flores, lo que hace poco probable que tales visitas hayan sido accidentales. La flor en la que se encontró la abeja pertenecía a una planta cultivada en un jardín residencial en Coral Gables, Florida. Ni la orquídea ni la abeja son nativas de Florida y se encuentran en diferentes áreas de América tropical. Se plantea la cuestión de por qué esta abeja hembra visitó esta orquídea, incluida la posibilidad de que pudiera tratarse de una ginandromorfa. A pesar de que la abeja tiene morfología femenina, podría haber sufrido anomalías neurológicas que le causaron una atracción tipo masculina hacia esta orquídea perfumada.

Keywords / Palabras clave: bucket orchid, fragrance chemicals, ginandromorfismo, gynandromorphism, naturalizada, naturalized, orquídea-balde, químicos fragantes

The estimated 250 species of orchid bees (Hymenoptera: Apidae: Euglossini) pollinate thousands of tropical American plants, perhaps about a third of the plants in this area (Dressler, 1982; Williams, 1982). Male orchid bees are the only pollinators of about 700 so-called perfume orchids in the American tropics (Dressler, 1982; Vogel, 1966). Instead of producing their own pheromones for reproduction, male orchid bees collect volatile chemicals from the surfaces of these orchids and from other sources and expose the chemicals during their courtship (Eltz *et al.*, 2005). Females of each orchid bee species will mate only after their males display particular blends of collected chemicals, unique to each orchid bee

ORCID of the Author: RWP
Received 18 September 2024; accepted for publication 27 November 2024. First published online: 9 December 2024.

species (Eltz *et al.*, 2005; Henske *et al.*, 2022; Zimmerman *et al.*, 2009). The bees visiting the orchids are manipulated by their flowers, so their collection of these volatile oils often results in the pollination of their flowers.

One orchid bee, *Euglossa dilemma* Bembé & Eltz, has become naturalized in Florida (Pemberton & Wheeler, 2006; Skov & Wiley, 2005) and has spread south to the Keys and north to central Florida (Pemberton & Escalona, 2023). A perplexing discovery was made when a female *E. dilemma* was found dead inside the bucket-shaped flower of a *Coryanthes panamensis* G.Gerlach in Coral Gables, Florida. This female bore the pollinarium of this orchid on her thorax (Fig. 1A). The orchid species was identified to be *C. panamensis* from a photograph of the flowers by the perfume orchid expert Günter Gerlach. The pollinarium on the dead female was determined to be that of a *Coryanthes* species based on its morphology and position on the bee as indicated by a drawing in Roubik and Hanson (2004) and verified by Gerlach. A photograph of the pinned specimen of this bee clearly shows the tibia of its hind leg with its concave morphology (the corbiculae used to carry pollen), verifying that the bee is a female (Fig. 1B). The orchid flower was on a *C. panamensis* plant grown in a basket in the residential garden of a Coral Gables, Florida. The discovery was made when the plant was brought to a meeting of the Orchid Species Coalition, a club of orchid growers, at Fairchild Tropical Garden, also in Coral Gables, on January 8, 2008. A male *E. dilemma* was found dead in the bucket flower of this orchid on a plant also brought to the club's meeting, on November 9, 2008. It did not bear a pollinarium.

*Coryanthes* orchids have one of the most bizarre flowers and strangest pollination mechanisms of all orchids. The following description of a *Coryanthes* flower and the pollination mechanism is slightly modified from Gerlach and Schill (1989) and is provided to better understand the female's behavior when she visits the orchid. See Gerlach (2016) for more extensive information about these fascinating orchids and their pollination. The fleshy lip of the *Coryanthes* flower (Fig. 2) is composed of three parts-the cup-shaped hypochil (H), the partially covered tubular mesochil (M) and the bucket-like enlarged epichil (E), which is filled with a fluid secreted by two broadly falcate protuberances the pleuridia (P1) at the base of the column (C). Male orchid bees land on the hypochil of the flower and try to get below the hood to collect fragrance compounds. In trying to get a footing on the waxy, smooth mesochil, they slip and fall in the bucket-like epichil, which is filled with a mucilaginous fluid, where their wings are wetted. The only way for a bee to escape is by crawling out through a tunnel formed by the epichil of the lip and the column, which bears the stigma and single anther. Before exiting the tunnel, the bee contacts the stigma, which removes a pollinarium it may bear from its thorax. Then the exiting bee contacts the anther, and its sticky viscidium glues the pollinarium (the viscidium, stipes, and two pollinia –the whole pollen mass) to its thorax.

**The female orchid bee paradox**. Female orchid bees respond to male orchid bees displaying with particular bouquets of fragrance chemicals and mate. Perfume orchids produce these volatile compounds in higher concentrations and in complex blends to lure male orchid bee pollinators. Female orchid bees, however, don't visit or pollinate the flowers of perfume orchids. Queries with orchid bee-perfume orchid experts James Ackerman, Günter Gerlach, and David Roubik (pers. comm.) confirmed that they have not observed female orchid bees visiting perfume orchids, despite spending many years in the field studying perfume orchids and orchid bees. Furthermore, female orchid bees don't come to, or very rarely come to baits using perfume orchid fragrance chemicals to attract male orchid bees, even when male conspecifics are present at the baits. After checking his records of baiting in Panama, James Ackerman reports that he encountered only a single female orchid bee out of 36,000 orchid bees. This was *Euglossa imperialis* Cockerell that came to a Benzyl Benzoate bait. Günter Gerlach had never seen a female orchid bee at baits, except on occasion when a female flew towards his insect net in which he had captured male orchid bees at baits. That female orchid bees can smell the fragrance chemicals and are attracted to males displaying with them but don't visit perfume orchids or perfume compound baits seems paradoxical. A displaying male orchid bee is, apparently, an essential element in this chemical attraction for females.

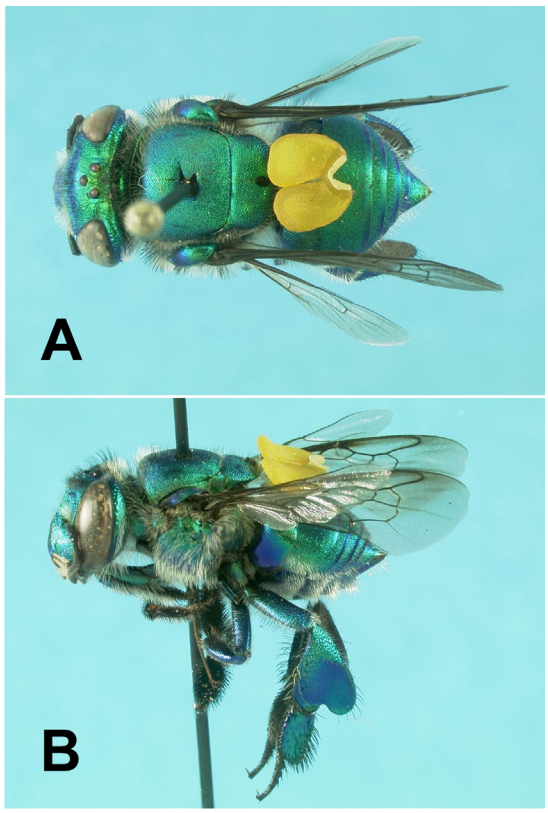


Figure 1. *Euglossa dilemma* female (concave hind tibia) with the pollinarium of *Coryanthes panamensis*. **A**. Dorsal view. **B**. Lateral view. This orchid bee is naturalized in Florida where this specimen was discovered dead in the flower of *C. panamensis,* an uncommon potted plant grown by orchid hobbyists.

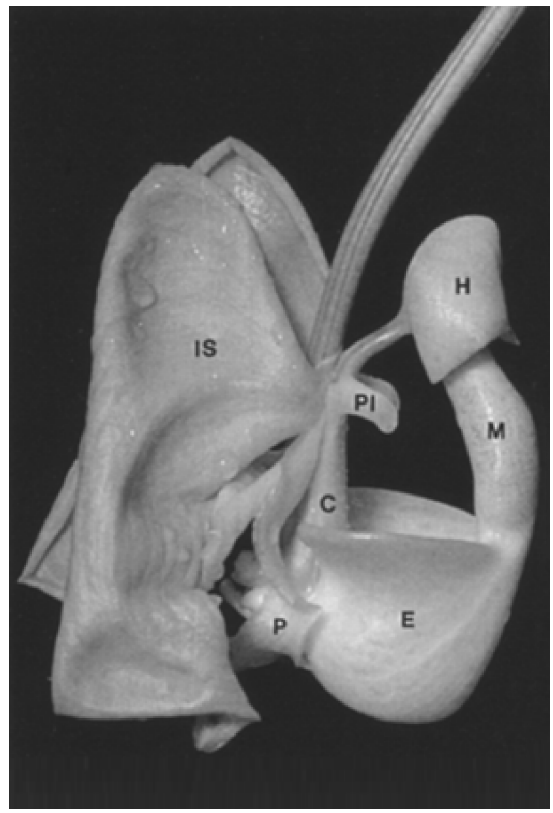


Figure 2. *Coryanthes speciosa* flower, side view. lS, lateral sepalum; P, petalum; lip consisting of a short claw: H, hypochile; M, mesochile; E, epichile; C, column; Pl, pleuridia, ca. life size (Gerlach & Schill, 1989). The flower is shown to illustrate the complexity involved in a female orchid bee's visits to a bucket orchid flower and removing the pollinaria, which *Euglossa dilemma* did twice.

**The puzzle of why the female *E. dilemma* visited the flowers of *C. panamensis***. Because this female orchid bee bore the orchid's pollinarium, she either visited the flower she was found in twice, or another flower first and then this flower, where she probably drowned in the viscous liquid it contained. Why did this orchid bee visit this flower intensively enough to be trapped in the bucket, only to escape through liquid through the tunnel and exit with a pollinarium, and then re-enter a flower? Bees do fall into water traps and water-filled pan traps are used to trap and study bees. Other kinds of bees and insects probably fall into the bucket flowers of *Coryanthes* species, but they apparently don't escape with the orchid's pollinarium on them, or re-enter that of another flower. The repeated visitation by the female *E. dilemma* suggests that, although she did have accidents by slipping and falling into the bucket of the flower, her visits were not accidental.

The presence of the pollinarium on the female *E. dilemma* is significant because flower visitors that remove pollen from orchids are considered to be their pollinators (Ackerman, 1983; Dressler, 1981), so by this criterion, this bee is a pollinator of *C. panamensis* (although not a successful one). Plants of this bucket orchid, however, are quite rare in Florida, being non-native pot ornamentals of interest only to specialty orchid hobbyists, suggesting that the trapped bee probably had no or little contact with plants of this species before she visited. With so few plants of this orchid in the environment, this potential pollination has no plant reproductive or plant population level meaning to it. Also, because

*Euglossa dilemma* and *C. panamensis* are not sympatric in their native ranges in tropical America, there would have been no opportunity for a *E. dilemma* female or male to visit and potentially pollinate the flowers of this species. Male orchid bees of both *Eulaema* and *Euglossa* species associate with *Coryanthes* orchids in Panama (Roubik & Hanson 2004) and *C. panamensis* Friese is pollinated by *Euglossa hemichlora* Cockerell and *Euglossa townsendii* Cockerell (Roubik & Knutson, 2017; G. Gerlach pers. comm.).

What attracted this female *E. dilemma* to make repeated visits to flowers of *C. panamensis*? During 20 years of observing this bee in Florida, I have recorded it to use 259 taxa of plants including 237 different species (Pemberton, 2023). This bee is an extreme generalist concerning the types of flowers it visits to obtain nectar and pollen, although it prefers gullet flowers that it can crawl into, tubular flowers whose rewards it can access with its long tongue, and buzz pollinated flowers for pollen. None of these preferred flowers or the less visited flowers resemble those of *C. panamensis* in terms of morphology or fragrance, so it seems unlikely that a female *E. dilemma* would mistakenly visit *C. panamensis* while seeking food. Females also collect resin rewards from the flowers of the few *Clusia* L. (Clusiaceae) and *Dalechampia* Plum. ex L. (Euphorbiaceae) species (Pemberton, 2024), but these flowers too are extremely different from those of *C. panamensis*. A female *E. dilemma* visited and removed the pollen from the flower of *Vanilla planifolia* L. but this orchid is not perfume orchid (Pemberton *et al.*, 2023).

Perhaps the fragrance of *C. panamensis* attracted this female orchid bee, as it very likely had attracted the male also found dead in a flower of this orchid. Among the fragrance components of the perfume of flowers of *C. panamensis* are methyl cinnamates (Kaiser, 2005). *Euglossa dilemma* males collect these same cinnamates (Pemberton & Wheeler, 2006), and in the process pollinate the perfume orchids offering them, including *Lycaste aromatica* Lindl. (Pemberton, 2023). Male *E. dilemma* have been observed to habitually collect the herbicide triclopyr because the fragrance of its principal breakdown product mimics methyl cinnamate (Pemberton & Kindt, 2024; Ramirez *et al.*, 2010). Methyl cinnamate is used with eugenol as the principal baits to attract *Euglossa viridissima* Friese (Roubik & Hanson, 2004), *E. dilemma*'s sibling species from which it was separated (Eltz *et al.*, 2011). These bees respond to essentially the same chemicals (Brand *et al.*, 2015). Male orchid bees are genetically programed to collect particular odorant chemicals that are essential for their courtship and successful mating (Henske *et al.*, 2022; Zimmerman *et al.*, 2009). Because male *E. dilemma* bees collect and store these cinnamates, they also display with these cinnamates, which are part of their odorant chemical bouquets. This suggests that female *E. dilemma* bees can smell them, which in turn suggests that they can also smell *C. panamensis* flowers. Being able to smell the flower, but not normally visiting it is again the paradox. Female orchid bees, however, are not passive regarding their reproduction. Male orchid bees display with their fragrance bouquets on the tops of ridges or other places with air movement, which facilitates the dispersal of their fragrance, and virgin females fly up these fragrance trails to reach the displaying males (Pokorny *et al.*, 2017). It is possible that the female *E. dilemma* that visited the flower of *C. panamensis* and removed the pollinarium and visited a flower again, was just an aberrant individual female. It could also suggest that female orchid bee behavior is, or potentially is, more plastic than previously thought, but the absence of female orchid bees at perfume orchids and their extreme rarity at baits belies this idea.

Might the female orchid bee's visits to the bucket orchid flowers suggest something about orchid bee evolution? Orchid bees first began to collect volatiles 38 million years ago and subsequently perfume orchids evolved for orchid bee pollination three times (Ramírez *et al.*, 2011). If female orchid bees deviate from their species-specific blend of odor compounds by responding to others or even single odors, such as seen with the female *E. dilemma*'s possible response to methyl cinnamates produced by *C. panamensis*, the reproductive barriers that protect the orchid's and the orchid bee's species integrity could be lost. However, mutations creating new fragrance perceptions and responses in both male and female bees would provide new opportunities for speciation, perhaps like the recent divergence of *E. dilemma* and *E. viridissima* (Brand *et al*., 2015). The difference in the fragrance blends collected and displayed by male *E. dilemma* and its sibling *E. viridissima* is only a single compound, HNDB (2-hydroxy 6-nona-1,3-dienyl-benzaldehyde), and the bees'

difference in degree of preference for HNDB has been traced to a single OR protein that occurs in *E. dilemma* but not *E. viridissima* (Brand *et al.*, 2020). Fragrance perception and response in orchid bees may be more evolutionarily labile than previously thought. Female orchid bee response to specific fragrances is largely unstudied (Thomas Eltz, pers com.).

Although this bee bearing the *Coryanthes* pollinarium appears to be female due to the corbicula on its metatibias, the possibility exists that it could be a gynandromorph. This might explain why an apparent female visited the *Coryanthes* and picked up the orchid's pollinarium. Gynandromorphy is a condition in which bees or other organisms have morphological features of both sexes due to genetic anomalies (Nesbit & Gartler, 1971). Gynandromorphs have been described in at least four *Euglossa* species (Suzuki *et al.*, 2014). The four species discussed by Suzuki *et al*. (2014) were the mixed or mosaic type of gynandromorphy with their sexual characteristics distributed patchily throughout their bodies. Two of these *Euglossa* species gynanders were collected at chemical baits which is an of male behavior. *Euglossa iopoecila* Dressler was collected at a eugenol bait in Brazil (Giannarelli & Sofia, 2011), and *E. pleosticta* Dressler at a cineole bait also in Brazil (Camargo & Gonçalves, 2013). Carmargo and Gonçalves (2013) considered it difficult to predict the behavior of gynanders based on scent attraction. Suzuki *et al.* (2014) did DNA genetic analysis on a gynander of *E. melanotricha* Moure which emerged from a nest collected in southwestern Brazil. The results revealed that the gynandromorph shared several alleles with both normal females analyzed as well as with the two control males. Both the mixed morphology and mixed genetics of this bee led the authors to categorize it as an intersex bee.

To determine if this *E. dilemma* bearing the pollinarium might be a gynander, the external sexual morphology of the specimen was examined and the following characteristics were noted. Both antennae have 12 segments, the scutellum bears an ellipsoid tuft, and the metatibias are corbiculate, all of which are female features. In addition, the specimen lacks male features, including the fore tarsi having brushes, velvet pads on the mesotibias, as well as an inflated hind tibia with a slit on the top. Despite the bee being a morphological female, there may be neurological anomalies that caused the bee to exhibit male-like attraction to and repeat visits to the bucket orchid flowers of *C. panamensis* causing the pollinarium to be placed on its scutellum.

Future research could analyze this *E. dilemma* specimen to determine its genetic gender, which could provide insights into why this apparent female orchid bee behaved, in part, as a male. The specimen will be deposited in the Florida Arthropod Collection in Gainesville. Suzuki *et al.* (2014) extracted DNA from the hind legs of a gynander of *E. melanotricha* Moure to analyze the complementary sex determination gene (sl-CSD), which has been widely accepted as acting in sex determination (Zayed, 2009). DNA can now be routinely extracted from pinned insect specimens, even those of great age through a non-destructive enzymatic method (Santos *et al.*, 2018). Because only one gynander of a *Euglossa* has been genotyped (Suzuki *et al.*, 2014), it would be informative to determine the genders of the others.

It would also be informative to explore the neurological and behavioral responses of female *E. dilemma* and other female orchid bees to fragrance chemicals. There has been no published research on antennograms of female orchid bees, but an unpublished study involving small numbers of bees found that that the antennae of female *E. dilemma* responded to perfume orchid fragrance chemicals, but the response was smaller than that of males (Thomas Eltz, pers. comm.). Antennograms coupled with gas chromatographs record the electrical activity of an insect's antenna in the presence of an odor and have been useful in identifying sex pheromones and pollinator responses to floral fragrances (Cardé & Hayes, 2004; Raguso 2004).

The complex biology and ecology of orchid bees make them fascinating creatures. The extraordinary visitation of a female orchid bee to a perfume orchid is an interesting anomaly of orchid bee behavior.

Acknowledgements. I thank James Ackerman, Günter Gerlach and David Roubik for kindly sharing information about the absence of orchid bees at perfume orchids and their rarity at baits. Günter Gerlach kindly reviewed an earlier draft of the manuscript and the reviewers' helpful comments greatly improved the manuscript. Michael Thomas took the photos of the bee.

Author contribution / Funding. The author is the sole investigator and author. No funding was obtained for this research.

Conflict of interest. There are no conflicts of interest.

## Literature cited


Ackerman, J. D. (1983). Specificity and mutual dependence of the orchid-Euglossine bee interaction. *Biological Journal of the Linnean Society*, 20, 340–314.

Brand, P., Ramírez, S. R., Leese, F., Javier, J., Quezada-Euan, G., Tollrian, R. & Eltz, T. (2015). Rapid evolution of chemosensory receptor genes in a pair of sibling species of orchid bees (Apidae: Euglossini). BMC *Evolutionary Biology*, 15, 176. https://doi.org/10.1186/s12862-015-0451-9.

Brand, P., Hinojosa-Díaz, I. A., Ayala, R., Daigle, M., Obiols, Y., Eltz, T. & Ramírez, S. R. (2020). The evolution of sexual signaling is linked to odorant receptor tuning in perfume-collecting orchid bees. *Nature Communications*, 11, 244. https://doi.org/10.1038/s41467-019-14162-6.

Cardé, R. T. & Hayes, K. T. (2004). Structure of the pheromone channel communication in moths. In: R. T. Carde & J. G. Millar (Eds.), *Advances in insect chemical ecology* (pp. 283–332). Cambridge, UK: Cambridge University Press.

Camargo, M. C. & Gonçalves, R. B. (2013). Register of a gynandro-morph of *Euglossa pleosticta* Dressler (Hymenoptera, Apidae). *Revista Brasileira de Entomologia*, 5, 424–426.

Dressler, R. L. (1981). *The orchids: natural history and classification*. Cambridge and London: Harvard University Press. 332 pp.

Dressler, R. L. (1982). Biology of the orchid bees (Euglossini). *Annual Review of Ecology and Systematics*, 13, 373–394.

Eltz, T., Sager, A. & Lunau, K. (2005). Juggling with volatiles: exposure of perfumes by displaying male orchid bees. *Journal of Comparative Physiology A*, 191, 575–581.

Eltz, T., Fritzch, F., Pech, J. R., Zimmermann, Y., Ramírez, S. R., Quezada-Euan, J. J. G. & Bembé, B. (2011). Characterization of the orchid bee *Euglossa viridissima* (Apidae: Euglossini) and a novel cryptic sibling species, by morphological, chemical, and genetic characters. *Zoological Journal of the Linnean Society*, 163, 1064–1076.

Giangarelli, D. C. & Sofia, S. H. (2011). First record of a gynandromorph orchid bee, *Euglossa iopoecila* (Hymenoptera: Apidae: Euglossini). *Annals of the Entomological Society of America*, 104, 229–232.

Gerlach, G. (2016). *Coryanthes*. *Renziana*, 5, 6–82.

Gerlach, G. & Schill, R. (1989). Fragrance analyses, an aid to taxonomic relationships of the genus *Coryanthes* (Orchidaceae). *Plant Systematics and Evolution*, 168, 159–165.

Henske, J., Saleh, N. W., Chouvenc, T., Ramírez, S. R. & Eltz, T. (2022). The function of environmentally acquired perfume blends in male orchid bees. bioRxiv 2022.12.08.519619.

Kaiser, R. (2005). Vanishing flora – lost chemistry: The scents of endangered plants around the world. In: P. Kraft & K.A. Swift (Eds.), *Perspectives in flavor and fragrance research* (pp. 15–29). Zürich, Switzerland: Verlag Helvetica Chimica Acta.

Nesbitt, M. N. & Gartler, S. M. (1971). The applications of genetic mosaicism to developmental problems. *Annual Review of Genetics*, 5, 143–162.

Pemberton, R. W. (2023). Plant resource use and pattern of usage by the naturalized orchid bee (*Euglossa dilemma*: Hymenoptera: Apidae) in Florida. *Insects*, 14, 909. https://doi.org/10.3390/ *insects*14120909.

Pemberton, R. W. (2024). Nest and resin sources (including propoplis) of the naturalized orchid bee *Euglossa dilemma* in Florida. *Florida Entomologist*, 107(1), 1–6. https://doi.org/10.1515/flaent-2024-0013.

Pemberton, R. W. & Escalona, E. (2023). Spread and distribution of the naturalized orchid bee *Euglossa dilemma* in Florida. *Florida Entomologist*, 106, 59–62.

Pemberton, R. W. & Kindt, J. T. (2024). Orchid bee collects herbicide that mimics the fragrance of its orchid mutualists. *Florida Entomologist*, 107 (1), 1–6. https://doi.org/10.1515/flaent-2024-0013.

Pemberton, R. W. & Wheeler, G. S. (2006). Orchid bees don't need orchids, evidence from the naturalization of an orchid bee in Florida. *Ecology*, 87, 1995–2001.

Pemberton, R. W., Wheeler, G. R. & Madeira, P. T. (2023). Bee (Hymenoptera: Apidae) pollination of *Vanilla planifolia* in Florida and their potential in commercial production. *Florida Entomologist*, 106, 230–237.

Pokorny, T, Vogler, I., Losch, R., Schlütting, P., Juarez, P., Bissantz, N., Ramírez, S. & Eltz, T. (2017). Blown by the wind: the ecology of male courtship display behavior in orchid bees. *Ecology*, 98, 1140–1152.

Raguso, R. A. (2004). Why do flowers smell? The chemical ecology of fragrance- driven pollination. In: R. T. Carde & J. G. Millar (Eds.), *Advances in insect chemical ecology* (pp. 151–178). Cambridge, UK: Cambridge University Press.

Ramírez, S. R., Eltz, T., Fritzsch, F., Pemberton, R. W., Pringle, E. G. & Tsutsui, N. D. (2010). Intraspecific geographic variation of pheromone-like fragrances acquired by orchid bees in native and introduced populations. *Journal of Chemical Ecology*, 36, 873–884.

Ramírez, S. R., Eltz, T., Fujiwara, M. K., Gerlach, G., Goldman-Huertas, B., Tsutsui, N. D. & Pierce, E. (2011). Asynchronous diversification in a specialized plant-pollinator mutualism. *Science*, 333, 1742–1746.

Roubik, D. W. & Hanson, P. E. (2004). *Orchid bees of tropical America, biology and field guide*. San Jose, Costa Rica: Instituto Nacional de Biodiversidad. 370 pp.

Roubik, D. W. & Knutson, J. (2017). An embellishment that became a mutualism: Inquiries on male bee tibial bouquets and fragrance-producing orchids in Panama and oceanic islands (Apidae: Apinae, Euglossini; Orchidaceae: Epidendroideae). *Flora*, 232, 117–127.

Santos, D., Ribeiro, G. C., Cabral, A. D. & Sperança, M. A. (2018). A non-destructive enzymatic method to extract DNA from arthropod specimens: Implications for morphological and molecular studies. *PLoS One*, 13(2), e0192200. https://doi.org/10.1371/journal.pone.0192200

Skov, C. & Wiley, J. (2005). Establishment of the Neotropical orchid bee *Euglossa viridissima* (Hymenoptera: Apidae) in Florida. *Florida Entomologist*, 88, 225–227.

Suzuki, K. M., Giangarelli, D. C., Frantine-Silva, D. G., Augusto, S. C. & Sofia, S. H. (2015). A scientific note on an anomalous diploid individual of *Euglossa melanotricha* (Apidae, Euglossini) with both female and male phenotypes. *Apidologie*, 46, 495-498.

Williams, N. H. (1982). The biology of orchids and euglossine bees. In: J. Arditti (Ed.), *Orchid biology: reviews and perspectives II* (pp. 119–171). New York, USA: Cornell University Press Ithaca.

Vogel, S. (1966). Parfümsammelnde bienen als bestäuber van orchidaceen und *Gloxinia*. *Österreichische Botanische Zeitschrift*, 113, 302–361.

Zayed, A. (2009). Bee genetics and conservation. *Apidologie*, 40, 237–262.

Zimmermann, Y., Ramírez, S. R. & Eltz, T. (2009). Chemical niche differentiation among sympatric species of orchid bees. *Ecology*, 90, 2994–3008.