

# POLLINATION OF *VANILLA* AND EVOLUTION IN THE ORCHIDACEAE<sup>1</sup>

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**ABSTRACT:** The pollination of *Vanilla grandiflora* Lindl. by male *Eulaema meriana* Olivier is reported from the Peruvian Amazon. No scent-collection behavior was observed. *Vanilla* is the most primitive orchid genus to demonstrate this interaction, and is unique among orchids for having both fragrant flowers and fruits. Indeed, the latter, a plesiomorphic character in orchids, offers a window into the family's early evolutionary history, which seems to have included a transition away from animal-mediated dispersal.

THE ORCHIDACEAE IS the largest family of flowering plants, with 20,000–30,000 species, or roughly one out of every 15 plants currently described (Dressler, 1993; Tremblay et al., 2005). Naturalists since Darwin (1862) have devoted themselves to the study of orchid biology, and while their insights have provided a foundation for understanding orchid evolution, especially in regard to how pollination has factored in, the question of why there are so many orchids still looms large (Van der Pijl and Dodson, 1966; Dressler, 1981, 1993; Tremblay et al., 2005).

Previously classified as a tribe in the advanced Epidendroideae, the Vanilloideae gained new currency for use in interpretations of orchid evolution since recent molecular research revealed it as an ancient lineage, if not the most basal subfamily, of the Orchidaceae (Cameron, 2004). The largest genus in Vanilloideae is *Vanilla*, a Pantropical genus of more than 100 epiphytic, hemiepiphytic and terrestrial herbs (Soto-Arenas and Cameron, 2003). Their Pantropical distribution is suspected to be an ancient vicariance event, having occurred prior to the breakup of Gondwana (Cameron, 2000).

The principal source of natural vanilla, the world's highest-valued tropical crop, is the cured fruit of *Vanilla planifolia* G. Jackson ex Andrews, a Mesoamerican endemic. The high price of vanilla compared with other agricultural commodities is ensured primarily because it is the world's

only hand-pollinated crop. Since contact and up to the mid-19th century, production of vanilla outside of the New World was impossible because of the absence of the natural pollinator, popularly believed to be *Melipona beecheii* Bennet (Dressler, 1981). Mexico's monopoly on vanilla production, which relied solely on natural pollination, ended in 1841 when Edmond Albius, a 12-year-old slave from the island of Reunion, discovered a method of artificial pollination (unfortunately for Albius, despite having revolutionized the world of vanilla production, he would later spend many of his years in jail on accusation of rape) (Ecott, 2004). To this day, vanilla production depends on sources of cheap labor to carry out pollination, and so the identification of its natural pollinators is of potential economic significance. The suggestion that vanilla is pollinated by *Melipona* is a highly doubtful one: the bee is too small to effect the necessary steps involved in the pollination of orchids with gullet flowers, and no other instance of an orchid's being pollinated by *Melipona* is known. An alternative suggestion that orchid bees (*Euglossini*) pollinated *Vanilla* was first proposed by Dressler (1981), and indirect support was found by the identification of *Vanilla* pollen on the scutellum of *Eulaema* species in Panama (Ackerman, 1983).

*Vanilla* displays considerable reproductive diversity both between and within species (Soto-Arenas and Cameron, 2003). In addition to out-crossing and asexual propagation, self-pollination has been reported in *Vanilla* (Van der Pijl and Dodson, 1966). Examples of species that are thought to self-pollinate, as evidenced by their high fruit sets — atypical in outcrossing species — are *Vanilla palmarum* (Salzm. ex

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Lindl.) Lindl., *Vanilla savannarum* Britton and *Vanilla griffithii* Rehb. f. (Soto-Arenas and Cameron, 2003). In other species, facultative self-pollination seems to be induced by physiological cues, although the underlying mechanisms are unclear. Two suggestions are that it is accomplished either by “stigmatic leak,” in which the stigma lobes release a fluid that, upon contact with the pollen, induces germination of the pollen tubes (Van der Pijl and Dodson, 1966), or via a dehydrated rostellum, which could also effect contact between the stigmatic cavity and the pollen (Garay and Sweet, 1974). *Vanilla* is notable for providing one of the few cases in which natural hybridization in Neotropical orchids has been reported (Nielsen, 2000), a startling notion considering the relative ease of producing successful hybrids of different species and genera in horticulture. Although this general knowledge of reproductive strategies in *Vanilla* is more perhaps than is known for other orchids, it offers no information on *Vanilla* pollinators and the concomitantly

Fig. 1. Bee visitors to *Vanilla*. A. *Melipona* sp. visiting *Vanilla insigne* Ames in Oaxaca, Mexico (P. Lubinsky, 2005). B. *Euglossa* sp. visiting *V. planifolia* in Oaxaca, Mexico (M. Van Dam, 2004). C. Pollination of *V. grandiflora* by *E. meriana* in Peru (A. Van Dam, 2005). D. *Eulaema cingulata* Fabricius collects scents of mature fruits of *V. grandiflora* in Peru (A. Van Dam, 2005).

important details of ecological interactions, the basis for some of the strongest selection pressures in the Neotropics.

In the hopes of providing direct evidence of *Vanilla* pollination, two weeks of field observations of *V. planifolia* were made during the flowering season in Oaxaca, Mexico, in the spring of 2004. Observations were performed from approximately 0600–1,200 hours (i.e., from first light and flowering opening, until flower anthesis brought on by increasing temperatures). Although flowers were occasionally visited by ants, *Melipona*, *Euglossa*, *Exeretes* and hummingbirds (Fig. 1, A and B), no pollination event occurred.

In September 2005, observations of pollination of *Vanilla grandiflora* Lindl. were carried out in palm swamps

(*aguajales*) in the Peruvian Amazon. In contrast to *V. planifolia*, a rare plant (Soto-Arenas and Cameron, 2003), *V. grandiflora* frequently occurs in populations with greater than 20 individuals. Pollen removal of *V. grandiflora* by *Eulaema meriana* Olivier was observed at 9:39 am on September 6th (Fig. 1C). Visitors that remove pollen from orchids have been found to also be their pollinators (Dressler, 1981; Ackerman, 1983). The flower was under constant observation from the time it opened, and pollen removal was visually confirmed. Both *Melipona* sp. and *Euglossa* sp. were observed entering *V. grandiflora* flowers, but their small sizes prevented pollen removal in *V. grandiflora* due to the relatively larger internal diameter of the labellum. The *E. meriana* individual observed removing pollen from *V. grandiflora* did not display the typical scent-collection behavior of hovering and transferring scents to its hind tibia, perhaps indicating that pollination is achieved by deceit (Williams, 1982; Lunau, 1992; Eltz et al., 1999, 2003).

The critical role of orchid bees in the ecological tapestry of Neotropical forests, including their agency in orchid speciation, was widely accepted after Janzen (1971) documented the great distances (>20 kilometers) the bees traveled when foraging (Dodson, 1962; Williams and Whitten, 1999; Roubik and Hanson, 2004). Of the 2,000 estimated Neotropical orchids known to be exclusively pollinated by orchid bees (Dodson, 1970), *Vanilla* is the most primitive orchid genus to demonstrate the interaction. The documentation of pollen removal from *Vanilla* by an orchid bee raises several new questions about *Vanilla* pollination ecology, but also draws attention to the parallel interaction between the bees and the fragrance-producing fruits of *Vanilla*. Traditionally, and due in no small measure to the wonder of orchid flowers, the nature of orchid fruits has been overlooked (Dressler, 1981). Approximately 99.9 percent of orchids have capsular fruits and shed dry seeds (Dressler, 1993). The only genera with fleshy fragrant fruits (*Vanilla*, *Palmorchis*, *Cyrtosia*, *Neuwiedia* and *Selenipedium*) are all, with the exception of *Palmorchis*, primitive orchids. The presence of fleshy fruits in members of three different primitive groups suggest that the group from which the orchids evolved may have had a fleshy fruit (Dressler, 1989). If this is the case, then it is interesting to note that, in *Vanilla*, both the flowers and the fruits attract the attention of orchid bees. In fact, in *V. grandiflora*, fragrance collection from fruits, not flowers, was observed (Fig. 1D; see also Madison, 1981). This may, in turn, lead to dispersal of the sticky seeds of some *Vanilla* by orchid bees, and implies that the orchid–orchid bee relationship could have evolved both as a mode of pollination and fruit dispersal, the latter being a more ancestral state. Also compelling for evolutionary inferences is that some of the aromatic compounds found in the fruits of *Vanilla* are the same as produced by the flowers of other Neotropical orchids (Dodson et al., 1969; Kaiser, 1993; Roubik and Hanson, 2004).

The origin of taxa with wind-dispersed seeds from ancestors with animal-dispersed seeds is an evolutionary step that directly contrasts with the situation found in other species-rich tropical families such as Rubiaceae (Bremer and

Eriksson, 1992). Examining the role of fragrance in orchid evolution, which has only recently begun to receive systematic attention (Williams and Whitten, 1999; Mant et al., 2005), may shed more light on understanding speciation in crowded, competitive, resource-limited environments like the tropics. Such efforts can be aided by investigations into the overall trend of fragrance production in groups like *Vanilla*, whose life history and mating system diversity, basal phylogenetic position and pan-tropical distribution offer a special combination of traits for such considerations.

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