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EVOLUTIONARY TRENDS AND SPECIALIZATION IN THE EUGLOSSINE BEE–POLLINATED ORCHID GENUS *GONGORA*[1,2]

Molly C. Hetherington-Rauth[3] *and Santiago R. Ramírez*[3,4]

ABSTRACT

The family Orchidaceae exhibits some of the most diverse and intricate modes of animal pollination across angiosperms. Highly specialized pollination by male euglossine bees (Apidae, Euglossini) occurs in more than 600 species of Neotropical orchids. Male euglossine bees acquire volatile compounds from both floral and nonfloral sources, which they store in their specialized hind tibiae and later expose during courtship display. Euglossine-pollinated Orchidaceae produce large quantities of floral scent, which serves as both the attractant and reward for male euglossine bees. Upon collecting floral volatiles and aided by the intricate orchid floral morphology, male bees remove and subsequently deposit orchid pollinaria, resulting in pollination. Among euglossine-pollinated Orchidaceae is the species-rich genus *Gongora* Ruiz & Pav., which provides exceptional opportunities to investigate the evolution of scent-mediated pollinator specialization. Here we review the taxonomy, systematics, and pollination biology of *Gongora*. We also describe a new physical mechanism of pollination observed for *Gongora* and discuss the significance of different modes of pollinaria attachment in an evolutionary framework. This work provides the foundation for future research on the evolution of specialized plant–pollinator mutualisms, including elucidating the evolutionary relationships of cryptic species, understanding the evolution of floral adaptations, and investigating the mechanisms of speciation.

Key words: *Eufriesea*, *Euglossa*, euglossine bees, *Eulaema*, evolution, *Exaerete*, floral adaptations, *Gongora*, mutualism, Orchidaceae, pollination, speciation.

The Orchidaceae, with their staggering species diversity and uniquely specialized and intricate pollination mechanisms, have long attracted the interest of biologists and naturalists (Darwin, 1888; Dressler, 1981; Schiestl & Schlüter, 2009; Yam et al., 2009). Darwin remarked in his book devoted to the topic that "the contrivances by which Orchids are fertilised, are as varied and almost as perfect as any of the most beautiful adaptations in the animal kingdom" (Darwin, 1888: 1). These "contrivances," or mechanisms by which orchids are fertilized, are epitomized by the male euglossine bee–pollinated

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[3] Department of Evolution and Ecology, University of California at Davis, One Shields Ave., Davis, California 95616, U.S.A.

[4] Author for correspondence: sanram@ucdavis.edu.

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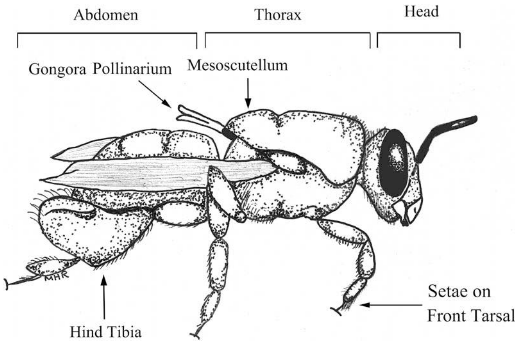

Figure 1. A generalized line drawing of a male euglossine bee of the genus *Euglossa* Latreille, with selected anatomical features important for the pollination of *Gongora* Ruiz & Pav. labeled. As depicted, the *Gongora* pollinarium is attached to the underside of the meoscutellum.

Orchidaceae, which include more than 600 species, or 10%, of Neotropical orchids (Gerlach & Schill, 1991; Ramírez et al., 2011).

Male euglossine bee pollination refers to the exclusive and specialized pollination of scent-producing orchids by male euglossine bees (also referred to as orchid bees) seeking perfume compounds (Dressler, 1968b; Dodson et al., 1969; Roubik & Hanson, 2004). There are more than 230 described species of euglossine bees (Apidae, Euglossini) grouped in five extant genera: *Aglae* Lepeletier & Serville, *Eufriesea* Crockerell, *Euglossa* Latreille, *Eulaema* Lepeletier, and *Exaerete* Hoffmannsegg (Nemésio & Rasmussen, 2011). The last four of these euglossine bee genera are abbreviated hereafter as *Ef.*, *Eg.*, *El.*, and *Ex.*, respectively. Euglossine bees exhibit brightly colored integument, ranging from blue and green to red and bronze, and are characterized by their unique behavior of scent collection. Males do not produce their own pheromones and instead collect volatile compounds from both floral (including orchids and several other angiosperm families such as Araceae, Solanaceae, and Gesneriaceae) and nonfloral sources (including resins, fungi, and rotting vegetation) in order to concoct species-specific perfume blends (Dressler, 1982a; Whitten et al., 1993; Eltz et al., 1999; Ramírez et al., 2002; Eltz, 2010). Perfumes are stored in specialized enlarged pockets located in the hind tibiae (Fig. 1) (Cruz-Landim et al., 1965; Eltz et al., 2007). Once male bees accumulate sufficient quantities of perfume compounds, they perform an elaborate courtship display in which perfumes are dispersed and exposed to conspecific females (Eltz et al., 1999, 2003, 2005). These chemical signals are hypothesized to convey information to females on male quality (fitness) and/or identity (species), and thus likely play a critical role in mate recognition and reproductive isolation (Zimmermann et al., 2009).

The pollination of orchids by euglossine bees was first described by Herman Crüger, the director of the Botanical Garden, Trinidad, in 1864 and later echoed by Darwin in his book discussing the pollination of orchids (Crüger, 1864; Darwin, 1888). Unsure of the exact mechanism, Crüger and Darwin described the "humble bees" as "gnawing" at the labellum (a highly modified petal) despite noting that the flower did not produce any nectar, which would otherwise explain the bee's behavior (Crüger, 1864: 129; Darwin, 1888: 168). Later in 1901, Adolpho Ducke, an entomologist and botanist studying in the Amazon, noted that several genera of orchids were visited by only male euglossine bees, but he too believed that the bees were visiting the flowers in search of food (Ducke, 1901; Dressler, 1968b; Dodson et al., 1969). It was not until the 1960s and through the extensive field observations made by Dodson, Frymire, Dressler, and Vogel that the odd behavior of perfume collection by male euglossines and the particular mechanism of euglossine bee pollination were elucidated (Dodson & Frymire, 1961; Vogel, 1963a, 1963b, 1966, 1990; Dodson, 1965; Dressler, 1968a; Dodson et al., 1969).

Male euglossine bee–pollinated Orchidaceae do not produce floral rewards in the form of nectar or pollen nor are they deceptive like many other orchid taxa that mimic food-rewarding plants or female bees (pseudocopulation) as deceptive mechanisms for pollinator attraction. Rather, male euglossine bee–pollinated orchids produce large quantities of floral scent, which simultaneously acts as the floral attractant and floral reward (Dodson & Frymire, 1961; Vogel, 1963a, 1990; Dodson et al., 1969). Male bees visit orchids to collect volatile compounds, and in the process they pollinate the flowers, aided almost entirely by the orchid's intricate floral morphology, which positions the pollinator in the proper, but often awkward, position. This awkward position ensures the precise placement of the orchid's pollinarium (consisting of the pollinia or pollen packets and the associated structures) on the bee's body, which in turn later ensures successful deposition of the pollinia into the stigma (Dressler, 1981).

Euglossine orchids tend to exhibit highly specialized pollinator associations. Pollinator specificity plays a significant role in mediating the extent of gene flow between populations, in maintaining reproductive isolating barriers, and in minimizing pollen wastage. In euglossine-pollinated Orchidaceae, pollinator identity is governed by both floral scent and floral morphology. The chemical composition of the floral scent of euglossine-pollinated Orchidaceae tends to be dominated by volatile monoterpenoids, sesquiterpenoids, and aromatic compounds (Williams & Whitten, 1983). Each orchid species produces a species-specific floral scent, which usually consists of one to three compounds in large quantities and an additional one to 10 compounds in smaller amounts (Hills et al., 1972; Gregg, 1983; Whitten, 1985; Williams & Whitten, 1999). It is hypothesized that some of these compounds act as attractants, luring many species of male bees, whereas others serve as behavioral modifiers, selectively excluding species of male euglossine bees (Dodson et al., 1969; Dodson, 1970; Williams & Dodson, 1972). In this way, each orchid species is visited by only one or a few species of male euglossine bees. In addition, the floral morphology of the orchid serves to further increase pollinator specificity. Only a subset of the bees attracted to the floral scent will be of the correct size and exhibit the right behavior to serve as effective pollinators. In some instances, the visitor may be too large or too small to successfully remove and then deposit the pollinia (Dressler, 1968a; Hills et al., 1972).

Male euglossine bee pollination has evolved at least three times independently, resulting in the three separate orchid radiations in the Stanhopeinae + Coeliopsidinae, Zygopetalinae, and Catasetinae, all of which are placed within the tribe Cymbidieae (previously referred to as Maxillarieae) (Whitten et al., 2000, 2005; Ramírez et al., 2002, 2011; Chase et al., 2003, 2015). Additional independent origins of euglossine bee pollination are evident in the tribe Cymbidieae; however, these origins have not resulted in large radiation events (Ramírez et al., 2002; Chase et al., 2003, 2015; Neubig et al., 2012). A fossil-calibrated molecular clock analysis placed the origin of euglossine pollination for each of the three orchid lineages during the Oligocene–Miocene time period, ca. 18–27 million years ago (Ma), and the single origin of perfume collection behavior in male euglossine bees during the Eocene–Oligocene time period, ca. 34–38 Ma (Ramírez et al., 2011). These estimates therefore suggest that euglossine pollination in the Orchidaceae evolved much later than the origin of perfume-collecting behavior of male euglossine bees. Furthermore, comparing the rates of diversification between the orchid and bee lineages shows that although the diversification rate of male euglossine bee–pollinated orchids has increased toward the present, the diversification rate of euglossine bees has decreased toward the present (Ramírez et al., 2011). These patterns, along with the observation that male euglossine bees collect volatile compounds from non-orchid sources, lend support to the hypothesis of asynchronous diversification and asymmetric dependency in this specialized plant-pollinator mutualism and suggest that the pre-existing behavior of male euglossine bees drove the diversification of euglossine bee–pollinated Orchidaceae (Ramírez et al., 2011).

SYSTEMATICS OF THE GENUS *GONGORA*

The euglossine bee–pollinated orchid genus *Gongora* Ruiz & Pav. (Stanhopeinae) has been estimated to have diverged from the rest of the Stanhopeinae at least 15 million years ago (Ramírez et al., 2011). Although the age estimate of a most recent common ancestor is sensitive to taxon sampling, the age of this node is unlikely to change given the high support for the monophyly of genera within the Stanhopeinae. *Gongora* is broadly distributed throughout the Neotropical region, with a range that extends from southern Mexico into South America along the slopes of the Andes from Colombia to Peru (and possibly Bolivia) and in areas of Venezuela, the Guianas, and Brazil (Fig. 2A) (Jenny, 1993). *Gongora* orchids are long-lived perennial epiphytes often found growing on the bark of trees. The vegetative portion consists of several conical to ovoid pseudobulbs with pronounced vertical ridges connected by a short rhizome and usually two broadly lanceolate-shaped leaves per pseudobulb (Fig. 3A–F). From the base of the pseudobulb emerges a spike that develops into a pendent inflorescence, which in some species can reach up to a meter long and contain over 50 individual flowers. The number of flowers per inflorescence may vary within species depending on plant health; most species tend to produce inflorescences with 10 to 20 flowers (Hetherington-Rauth, pers. obs.). Flowers typically bloom for three to seven days before wilting and typically produce a fragrance that is strongest in the morning, corresponding to the time of day when male euglossine bees are most active (Dressler, 1968a; Hills, 1989; Hills & Williams, 1990; Hetherington-Rauth, pers. obs.). The individual flowers are composed of two lateral sepals, one lower sepal, two small petals, a highly modified petal called the labellum, and the column, which consists of both the male and female reproductive structures (Fig. 3E) (Dressler, 1981; Whitten, 1985).

Gongora currently contains between 60 and 70 recognized species; however, many species are poorly known from only a few specimens (Jenny, 1993; Aldrich & Higgins, 2008; The Plant List, 2013). The taxonomic delimitation and systematics of most taxa within *Gongora* are notoriously difficult due to intraspecific variation and the lack of conspicuous diagnostic morphological characters for many species (Dressler, 1966; Jenny, 1993). This taxonomic difficulty has resulted in significant historical and present-

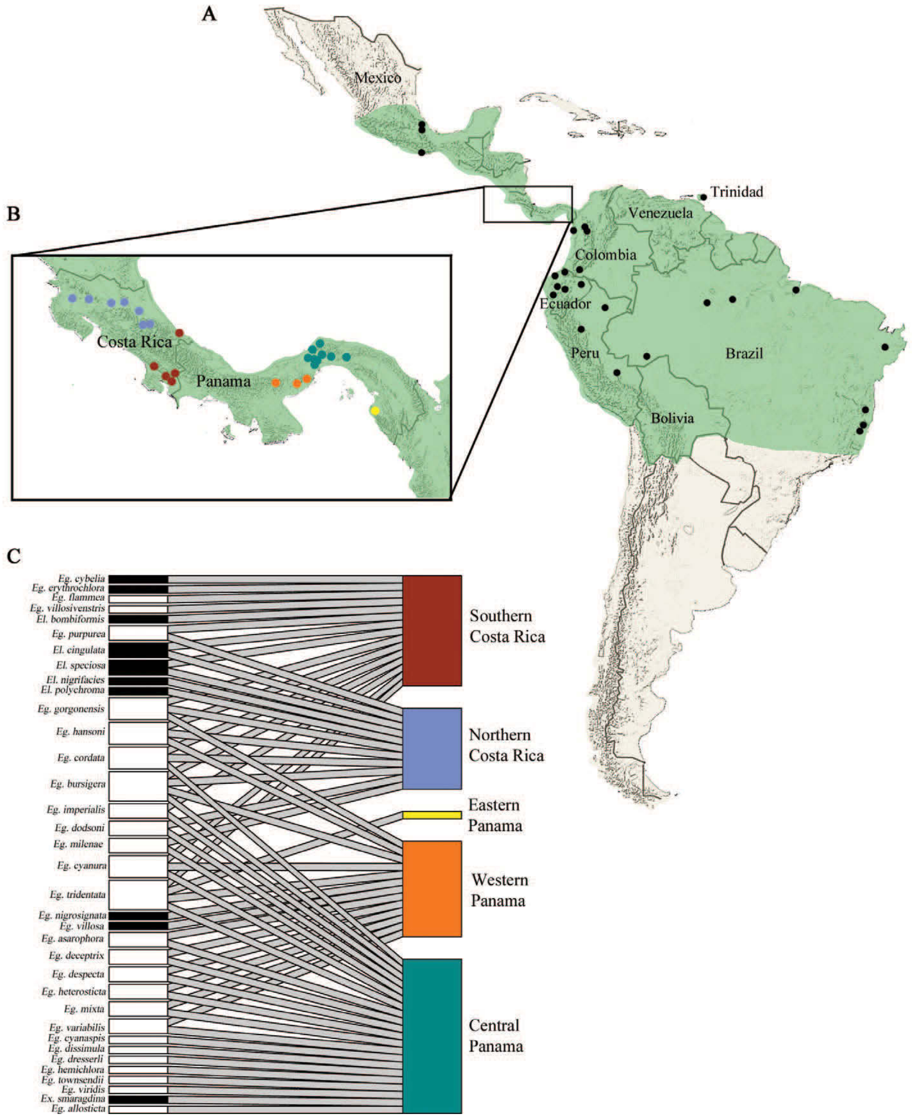

Figure 2. Geographic distribution of the orchid genus *Gongora* Ruiz & Pav. and pollination network. —A. Geographic distribution of *Gongora* (green shading) as inferred from Jenny (1993). Points within this geographic range indicate the localities where orchid-pollinator associations for *Gongora* have been observed (cf. Appendix 1). —B. Enlarged region of Costa Rica and Panama from A. The points again indicate the localities where orchid-pollinator associations for *Gongora* have been observed (cf. Appendix 1). The colors of the points correspond to the five geographic regions from the pollination network in C. —C. Bipartite pollination network depicting the pollinator diversity and pollinator specialization across five geographic regions in Costa Rica and Panama. The nodes (boxes) to the left represent species of euglossine bee visitors and pollinators. Gray boxes represent species of bee that were identified as actual pollinators (either observed pollinating *Gongora* [1] or collected with *Gongora* pollinaria [3]). Black boxes represent species of bee that are identified as non-pollinating visitors (2) or visitors with unknown pollination effect (4). Abbreviations used for the three euglossine bee genera are *Euglossa* (*Eg.*), *Eulaema* (*El.*), and *Exerate* (*Ex.*). The nodes (boxes) to the right represent *Gongora* that have been geographically clustered into five separate geographic regions such that each node likely includes co-occurring species of *Gongora*. The lines connecting nodes represent pollination observations between *Gongora* within the given geographic region and the indicated bee species.

day confusion in the application of species names within *Gongora*. The taxonomic difficulty of this group goes back to the times of the Royal Botanical Expedition to New Granada. During the last part of the 18th century, the botanists Ruiz and Pavón were commissioned by the Spanish viceroy, Charles III, to conduct a scientific exploration of the flora of what is now Peru and Chile (Jenny, 1996; Pupulin, 2012). Among the flora they collected that was not captured, lost, or destroyed was what was to become the infamous

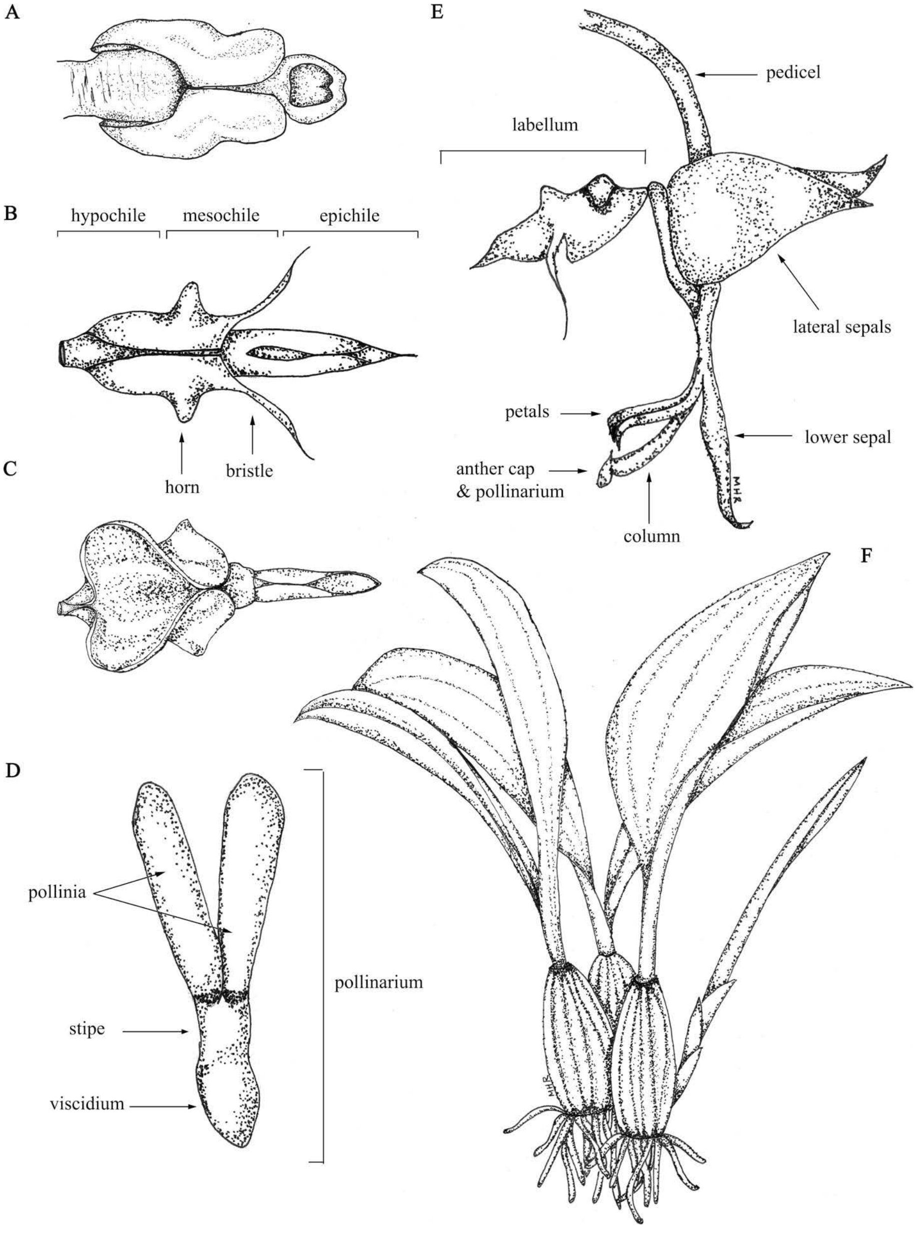

Figure 3. Vegetative and floral morphology of *Gongora* Ruiz & Pav. A–C. Adaxial side of labellum from three separate *Gongora* species. The labellum is divided structurally into three sections, the epichile, mesochile, and hypochile. The osmophores, or the collection of scent-producing cells, are located on the adaxial side of the hypochile. —A. *Gongora galeata* (Lindl.) Rchb. f. of *Gongora* subg. *Acropera*. The hypochile forms a broad and flexible attachment point to the rest of the flower, which allows the labellum to swing back during the hinge pollination mechanism. —B. Generalized *Gongora* species from section *Gongora* of *Gongora* subg. *Gongora*. —C. *Gongora tracyana* Rolfe in section *Truncata* of *Gongora* subg. *Gongora*. The hypochile flaps form a wide opening, which may prevent the pollinator (*Eulaeama bombiformis* Packard) from stealing floral volatiles. —D. A *Gongora* pollinarium consists of two pollen packets or pollinia (singular, pollinium), a stipe, and a sticky viscidium, which aids in the attachment of the pollinarium to the pollinator. —E. Generalized *Gongora* flower with floral structures labeled. —F. The vegetative form of a *Gongora* orchid. Several ovoid to conical pseudobulbs, which are characterized by pronounced vertical ridges, are connected by a short rhizome. Each pseudobulb bears two (rarely one) lanceolate-shaped leaves.

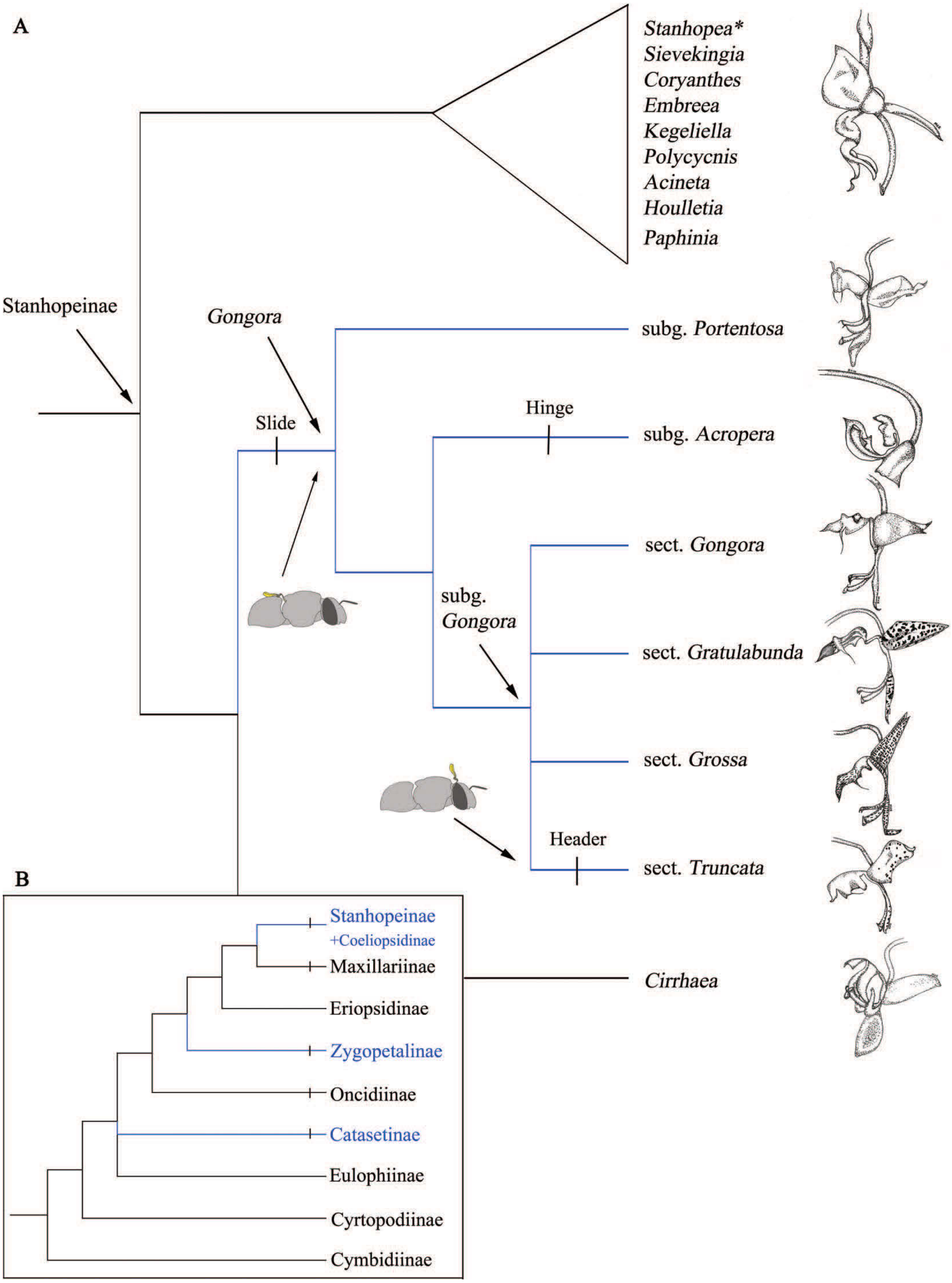

Figure 4. Phylogenetic relationships of *Gongora* Ruiz & Pav. and related genera. —A. Phylogenetic relationships of male euglossine bee–pollinated Stanhopeinae orchids, emphasizing the evolutionary relationships among subgenera of *Gongora* as supported by molecular data (adapted from Whitten et al., 2000). The subgenus *Gongora* is divided into four unresolved sections. The hypothesized origins of the three pollination mechanisms observed in the orchid genus *Gongora* are indicated, and the resulting placement of the pollinarium on the pollinator is illustrated. The line drawings to the right of each taxon terminal depict a representative specimen for that taxonomic group. The line drawing to the right of the collapsed clade is a representative specimen of the genus *Stanhopea* Frost ex Hook. (indicated with an asterisk). —B. Hypothesized phylogenetic relationships of

type specimen of *G. quinquenervis* Ruiz & Pav. The drawing of *G. quinquenervis* and the first description of the genus were published in 1794 in *Florae Peruvianae, et Chilensis Prodromus*; however, the type specimen of *G. quinquenervis* was not described until four years later in 1798 in *Systema Vegetabilium Florae Peruvianae et Chilensis* with the type locality indicated from Pozuzo, Peru (Ruiz & Pavon, 1794, 1798; Jenny, 1993, 1996). The remains of the type specimen are currently deposited in the Royal Botanical Garden of Madrid. There are no flowers associated with the type identification, making classification of the real *G. quinquenervis* difficult, if not impossible (Pupulin, 2012). Today the name *G. quinquenervis* is widely misapplied by many authors to describe otherwise unidentified specimens, and even pollinaria, collected from diverse localities well beyond Peru. Dressler (1968a) suggests that there are at least a dozen "good" species within the *G. quinquenervis* species complex.

Despite the taxonomic confusion, a classification system and genus-level revision are available. Rudolph Jenny (1993) recognized three subgenera: *Gongora* subg. *Gongora* (Pfitzer) Jenny, *Gongora* subg. *Acropera* (Pfitzer) Jenny, and *Gongora* subg. *Portentosa* Jenny (Fig. 4A). *Gongora* subg. *Acropera* was originally described by Lindley (1833), with the type *Acropera loddigessii* Lindl., as a separate genus based on the distinct floral morphology and the restricted geographic distribution in Central America (Lindley, 1833; Darwin, 1888; Jenny, 1993). However, modern phylogenetic analyses of the tribe Stanhopeinae using molecular data from nuclear ribosomal and plastid DNA supported the division of *Gongora* into three subgenera and revealed *Gongora* subg. *Portentosa* as sister to both *Gongora* subg. *Gongora* and *Gongora* subg. *Acropera* (Fig. 4A) (Whitten et al., 2000). It should be noted that these analyses emphasized the generic relationships of Stanhopeinae and included taxa sampled from across the tribe Cymbidieae and only nine species-level accessions of *Gongora*. Thus, these analyses were not intended to resolve species-level relationships. Based on the morphological characters of the flowers, Jenny (1993) divided *Gongora* subg. *Gongora* into four sections: *Gongora* sect. *Gongora*, *Gongora* sect. *Gratulabunda* Jenny, *Gongora* sect. *Grossa* Jenny, and *Gongora* sect. *Truncata* Jenny. However, the monophyly and evolutionary relationships among these sections remain unclear because commonly used gene sequences for phylogenetic inference have not exhibited enough sequence divergence at this level of resolution.

As currently arranged, *Gongora* sect. *Gongora* is the most species-rich group, with at least 30 recognized species, but is also the most difficult in which to delimit species boundaries, including those of the *G. quinquenervis* species complex (Whitten, 1985; Jenny, 1993). The ambiguity in species boundaries persists because multiple sympatric populations coexist with little to no morphological variation, but clearly experience reproductive isolation as inferred from the attraction of non-overlapping assemblages of male euglossine bee pollinators (Whitten, 1985; Hentrich, 2003; Ramírez, unpublished data). Pollinator identity within this *Gongora* species complex seems to be governed by differences in the floral scent chemistry (Whitten, 1985; Hentrich, 2003; Ramírez, unpublished data). Further, it remains unclear as to what extent pollinator identity and floral scent may co-vary within a single *Gongora* species across its geographic range.

Pollinator Specialization

Male euglossine bee–pollinated Orchidaceae exhibit intricate adaptations for pollinator attraction and cross-pollination, including strong floral scent, modified floral morphology, and specific mechanisms for the precise placement and attachment of pollinarium. The euglossine bee genera *Euglossa*, *Eufriesea*, and *Eulaema*, which encompass ca. 130, 66, and 30 species, respectively, are the most species-rich clades of euglossine bees and are therefore the main pollinators of most male euglossine bee–pollinated Orchidaceae (Ramírez et al., 2002, 2010; Nemésio & Rasmussen, 2011). *Gongora* exhibits adaptations for the attraction and pollination by euglossine bees, and because the flowers produce no additional rewards, these orchids are exclusively dependent on male euglossine bees for sexual reproduction.

Herein we review and examine the diversity of known pollinators of *Gongora*, for which we compiled an extensive dataset derived from both unpublished field observations and published literature of euglossine bee species that have been observed as (1) effective pollinators, (2) non-pollinating visitors, (3) pollinaria carriers, and/or (4) visitors with unknown pollination effect (Appendix 1). For consistency, we used the same classification—numbers (1) through (4) above—for denoting pollinators and visitors as used in

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the tribe Cymbidieae (Orchidaceae). Black bars indicate lineages that contain male euglossine bee–pollinated orchid species, and blue lineages represent the three large and independent radiations of male euglossine bee–pollinated Orchidaceae (adapted from Ramírez et al., 2011 and Chase et al., 2015).

Ramírez et al. (2002). Because the same behavior by male bees that promotes the removal of the pollinarium leads to the subsequent deposition of the pollinia in the stigma (pollination), those bees that were collected carrying *Gongora* pollinaria in the field (3) can be considered actual pollinators, even if the pollination event was not observed; however, such observations do not permit species-level identification of *Gongora*, justifying the distinction between (1) and (3). Non-pollinating visitors (2) are assumed if there exists a size mismatch between that of the visiting male euglossine bee and *Gongora* species, whereas visitors with unknown pollination effect (4) refers to cases when visiting bees of the proper size do not pollinate the orchid during the time of observation. When available we provided *Gongora* species names, but due to the difficulty of correctly identifying morphologically similar species, the unavailability of voucher specimens for these orchids, and, in many cases, the lack of proper species names, we placed little significance on the species identity, particularly those described as *G. quinquenervis*. We also provided locality information for each observation when available in order to examine the extent of pollinator sharing and pollinator turnover across geographic ranges.

The results from these pollination observations (Appendix 1) are summarized in Figure 2A and B, in which we plotted the geographic location of each observed orchid–pollinator association. We also constructed a bee–orchid pollination network across several communities in Costa Rica and Panama (Fig. 2C). A total of 289 records describing 64 species of euglossine bees associated with *Gongora* were considered from a total of 50 localities distributed across nine countries in Central and South America. Species of *Euglossa* were among the dominant pollinators of *Gongora*, with 48 species of *Euglossa* listed as either true pollinators or pollinaria carriers. This number represents an impressive 37% of *Euglossa* species diversity. Furthermore, the total number of observations pertaining to *Euglossa* far exceeded those of other bee genera. In addition to species of *Euglossa*, five species of *Eufriesea* (of 66) were documented carrying pollinaria. In Costa Rica, Panama, and Brazil, four species of *Eulaema* (of 30) and one species of *Exaerete* (of eight) were found as either non-pollinating visitors or visitors with unknown pollination effect. However, those same species of *Eulaema* and *Exaerete* were observed carrying pollinaria in Peru, Ecuador, and Colombia. This observation suggests that in some instances bee visitor identity may remain constant, while pollination roles may vary across geography.

We constructed a pollination network based on the data gathered from multiple communities where *Gongora* orchids and their associated bee pollinators were recorded across five well-studied geographic regions in Costa Rica and Panama. We used the resulting network information to examine the turnover in orchid-pollinator associations across geography and to investigate the potential role that pollinator specialization may play in generating cryptic diversity within *Gongora* species complexes. This information is limited by the fact that the identification of *Gongora* species within these regions remains uncertain and the fact that many observations come from bees carrying *Gongora* pollinaria, in which case the species identity of *Gongora* cannot be determined from the pollinaria alone. Therefore, we grouped pollination observations by geographic region and had each orchid node in the pollination network represent a geographic region rather than a species identity of *Gongora*. Therefore, each orchid node of the network likely represents multiple potentially co-occurring species of *Gongora*. This approach affects only the resolution of the orchid nodes. In most cases the bee identifications were assumed to be accurate, and thus each bee node represents a single species of euglossine bee. Thus, our network analysis provides a rather conservative estimate of pollinator specialization.

The resulting mutualistic network indicates that there is both pollinator turnover (i.e., changes in pollinating bee species between orchid nodes) and pollinator sharing (i.e., consistency in pollinating species between orchid nodes) across geographic regions. The network also indicates that certain species of bee pollinators used by *Gongora* taxa are restricted to a single geographic region (i.e., a single pollinator is connected to only one orchid node), thus suggesting that a high level of pollinator specificity may exist across the landscape. Most pollination studies conducted with *Gongora* orchids at single locations have revealed that individual lineages exhibit highly specialized associations with few (ranging between one and four) species of euglossine bees (Dressler, 1968a; Whitten, 1985; Hentrich, 2003). Thus, the orchid nodes in our network that are connected to numerous bee pollinators likely represent multiple sympatric species of *Gongora*, where each reproductively isolated orchid species uses a subset of the pollinator pool (i.e., connected bee species nodes). This scenario is reinforced by the fact that we took a conservative approach in which we clustered sympatric orchid taxa into single nodes. In fact, our ongoing detailed studies on the pollination of *Gongora* orchids from the southern Pacific coast of Costa Rica indicate that multiple sympatric and

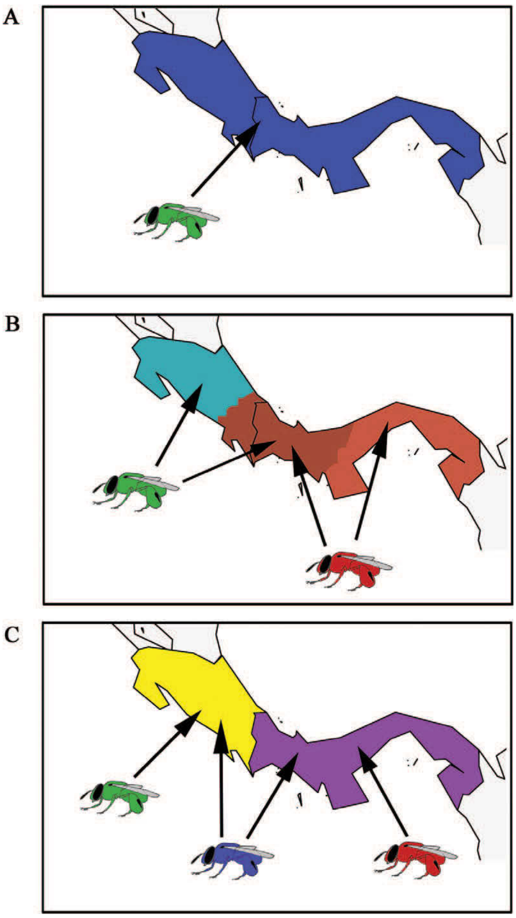

Figure 5. Alternative hypotheses governing gene flow across geography in terms of pollinator diversity and pollinator specialization. Filled colors represent geographically distinct populations of *Gongora* Ruiz & Pav. affiliated with specific pollinator assemblages. —A. Single *Gongora* population (blue) attracts the same pollinator species (hypothetical green bee) throughout its range. Gene flow is maintained across geography via long-distance pollen transfer. —B. Distant populations of *Gongora* (turquoise and orange) may be associated with distinct species of bee pollinators at opposite ends of the distribution (hypothetical green and red bees). In addition, populations of *Gongora* in the middle of the range (dark red) may attract and use both species of bee pollinators. The overlapping region in the middle of the range results in a porous barrier in which peripheral (turquoise and orange) populations experience gene flow with one another. However, this gene flow would be counteracted by the fact that peripheral populations may experience strong natural selection and thus local adaption to each pollinator species, leading to the fixation of distinct floral scent phenotypes. —C. Mosaic pattern of pollinator specialization in which two pollinator species are locally restricted (hypothetical green and red bees), while one pollinator species is widespread (hypothetical blue bee). The blue bee promotes gene flow between geographically separate *Gongora* populations (yellow and purple). Local adaptation to the restricted pollinators may persist.

cryptic *Gongora* species are reproductively isolated through the association with non-overlapping subsets of bee pollinators and that such pollinator specialization is mediated by the production of distinct floral scent profiles in each isolated orchid lineage.

The network architecture may be used in support of several non-mutually exclusive hypotheses to account for the role that pollinator diversity and pollinator specialization play across geography in generating and maintaining reproductive isolation among orchid lineages. These hypotheses are summarized in Figure 5. Euglossine bees are strong, long-distance fliers (Janzen, 1971; Ackerman et al., 1982), and mark-recapture experiments have shown that individual male bees may fly up to 72–95 km within a two-week period (Pokorny et al., 2014). Therefore, if pollinator species are shared among orchid populations, gene flow could persist even across long geographic distances (Fig. 5A). Thus, geographic isolation alone may not represent a strong reproductive isolating barrier when pollinator assemblages are shared. Alternatively, when the pollinator species used by *Gongora* taxa are restricted to a single geographic region, a reduction in gene flow between geographically isolated populations would be expected (Fig. 5B). This pattern could emerge from the process of local adaptation to specific pollinators, wherein a restricted orchid population has an altered scent phenotype that results in a shift to attract a local pollinator species. Although proper reciprocal transplant experiments remain to be conducted, some transplant experiments conducted in Panama revealed that single species of *Gongora* collected from one locality attracted separate and distinct pollinator assemblages at the collection locality and the transplant locality (Whitten, 1985). Furthermore, a mosaic pattern may emerge in which some of the pollinator species are locally restricted, while the remaining pollinators are widespread and shared between geographically separated populations (Fig. 5C). Under this scenario, gene flow among distant populations would be maintained, while local adaptation to restricted pollinators may persist. In summary, the observed patterns of pollinator specialization, high pollinator diversity, and variation in pollinator identity across geography together play an important role in the maintenance and formation of reproductive isolation and are likely responsible for the pervasive cryptic diversity observed in multiple species complexes of *Gongora*. A population genetic analysis on these populations is required to test these alternative hypotheses.

Pollination Mechanisms

Floral morphology plays a critical role in manipulating the behavior of insect pollinators while they visit and forage on flowers. The family Orchidaceae has evolved a remarkably diverse array of floral traits that serve as adaptations for pollinator attraction and pollen transfer. In particular, highly modified structures like the labellum and the column have undergone exceptional modification that enables the precise placement and attachment of pollinaria on specific body parts of insect pollinators. The labellum, also referred to as the lip, is a modified petal that functions as a landing platform for insect pollinators (Dressler, 1981). In most orchids, as the flower bud develops, the pedicel twists, resulting in the relative orientation of the labellum below the column (resupinate) (Fig. 3E). The labellum of *Gongora*, however, is located above the column (non-resupinate), and in most species—with the exception of taxa belonging to *Gongora* subg. *Acropera*—the labellum is divided into three sections: the hypochile, mesochile, and epichile (Fig. 3B). Specialized scent-secreting cells (osmophores) are located on the adaxial surface of the hypochile and adjacent lateral sepals (Stern et al., 1986, 1987; Hentrich, 2004). At the beginning of anthesis, the osmophores are densely packed with starch granules, which are then rapidly metabolized over several days, fueling the production of scent volatiles (Vogel, 1963a, 1990). Both the production of floral scent by osmophores located on the labellum and the non-resupinate floral orientation of *Gongora* flowers ensure that male euglossine bee visitors hang upside down from the labellum with the head pointed toward the column while collecting volatile compounds. This positions them to successfully pollinate the orchid flowers.

The anther cap sits at the tip of the column and, once removed, it exposes the pollinarium (Dressler, 1981). The pollinarium is composed of two pollen packets—termed "pollinia"—that contain all of the flower's pollen grains and additional specialized associated structures (including the stipe and viscidium) that aid in the attachment of the pollinarium onto the bee's body (Fig. 3D) (Dressler, 1981; Singer et al., 2008). The viscidium is the sticky mass at the base of the pollinarium that glues the rest of the pollinarium onto the visiting pollinator. Once the pollinarium is removed by the pollinator, the stigma is exposed and is receptive to pollinia carried by a second pollinator from a donor flower. In this manner, *Gongora* flowers are dichogamous, i.e., they exhibit a reproductive strategy in which each flower contains both male and female reproductive structures, but the two phases are functionally separated in time. The time and distinction between the male and female phases are amplified by a period in which the pollinarium needs to dry before it can be successfully inserted into the receptive stigmatic opening (Whitten, 1985). This separation of sex by time, rather than by morphology, increases the opportunities for cross-fertilization (Dodson, 1962; Dressler, 1968b) and requires at least two visits by male euglossine bees to a *Gongora* orchid for successful pollination.

Male euglossine bees locate *Gongora* inflorescences from long distances and are aided entirely by the scent plume produced by the flowers (Dodson & Frymire, 1961; Dodson, 1967). Male euglossine bees first approach the *Gongora* inflorescence tentatively, moving toward and away from it while brushing the hind legs together in a stereotypical manner (Eltz, 2005). After circling the inflorescence for one to three minutes, the bee lands on a flower, although not always immediately in the correct position for pollination to occur. The male bee may brush floral volatiles from the sepals or from the sides of the labellum before maneuvering to the underside of the labellum (Hetherington-Rauth & Ramírez, pers. obs.). The bee uses the mid and hind legs to hold itself in place while secreting lipids from the labial glands to dissolve volatile compounds (Whitten et al., 1989; Eltz et al., 2007). It then brushes the surface of the flower using setae on the front tarsals and in doing so collects the volatile compounds (Fig. 6A) (Roubik & Hanson, 2004). After about 20 to 40 seconds of collection, the bee releases from the flower and hovers near the inflorescence while transferring the compounds into the hind leg pouches (Kimsey, 1984). The male bee then returns to the flower and repeats the process. A male bee may stay at a single *Gongora* inflorescence for up to 30 minutes, at which point it is hypothesized that the male bee becomes satiated on the volatiles and flies away.

Variation in the flower size and the floral morphology in *Gongora* has resulted in three distinct pollination mechanisms that differ in both the mode of attachment and location of attachment of the pollinarium onto the pollinator. We refer to these three mechanisms as the slide, the hinge, and the header mechanisms (Fig. 6). Both the slide and hinge mechanisms have been previously described in *Gongora* and result in the attachment of the pollinarium under the bee's mesoscutellum (Figs. 1, 6C, D). The header mechanism is described for the first time here and is exceptional in that the pollinarium is attached to the back of the head of the bee (Fig. 6F). Figure 4A depicts the hypothesized origin of each mechanism inferred from pollination observations and similarities in the floral morphology among subgenera and sections of *Gongora*.

The slide mechanism is well documented in the literature and has been described for at least two of the four sections of *Gongora* subg. *Gongora* including

Figure 6. Pollination mechanisms. A–C. Slide mechanism. —A. Male *Euglossa* cf. *cordata* uses the setae on the front tarsi (indicated by the arrow) to brush the surface of the labellum in order to gather floral volatiles. —B. Male *Eg. tridentata* Moure sliding down the column and removing the pollinarium. —C. Same *Eg. tridentata* from B after pollinarium removal. The pollinarium is attached under the mesoscutellum (indicated by the arrow). —D. Hinge mechanism. A male *Eg. viridissima* Friese pulls the labellum of *Gongora galeata* (Lindl.) Rchb. f. back and climbs atop the labellum to collect floral volatiles. As photographed, the labellum is fully extended. The dotted outline of the labellum indicates the initial position of the labellum. The double-headed arrow indicates the movement of the labellum as the bee pulls it back and then is released. In this photo the male bee has already removed the pollinarium, which is attached under the mesoscutellum (indicated by the arrow). E, F. Header mechanism. —E. A male *Eulaeama bombiformis* Packard grips the labellum of *G. tracyana* Rolfe in order to collect floral volatiles from its surface. The wide angle between the labellum and column accommodates the head of *El. bombiformis*. —F. The same *El. bombiformis* from E continues to collect floral volatiles after pollinarium removal. The pollinarium is attached to the back of the head (indicated by the arrow). Photos A–C by Tamara Pokorny taken in La Gamba, Costa Rica; photo D by Heiko Hentrich; photos E and F by Santiago Ramírez taken in Viterbo, Caldas, Colombia.

Gongora sect. *Gongora* and *Gongora* sect. *Grossa* (Allen, 1954; Dodson & Frymire, 1961; van der Pijl & Dodson, 1966; Dodson, 1967; van der Cingel, 2001). Although pollination has not yet been observed for *Gongora* subg. *Portentosa*, members of this group have a floral morphology similar to that of *Gongora* for which the slide mechanism has been described. Thus, it is likely that species in *Gongora* subg. *Portentosa* exhibit the slide mechanism. From this pattern we also infer the slide mechanism to be the ancestral pollination mechanism of the genus *Gongora* (Fig. 4A). Allen (1954: 123) first documented the slide mechanism in what he described as *G. maculata* Lindl. (in section *Gongora* of *Gongora* subg. *Gongora*) and described the bee as "a child on a toboggan" (123). In this mechanism, the bee maneuvers to the underside of the labellum where it brushes the surface (Fig. 6A). In the process of brushing, the bee slips and falls due to a combination of the labellum's slippery surface and the interference of the labellum's bristles. Upon falling, the male contacts the column and slides upon its complete curvature guided by the two petals, which act as guards on either side of the column (Fig. 6B). As the bee slides off the column, the sticky viscidium of the pollinarium catches the underside of the bee's mesoscutellum (Fig. 6C). The process of sliding down the column does not deter the bee from repeating the process. In fact, the male eagerly visits another flower and repeats the same behavior, although this time as the bee is sliding, the pollinia detach from the viscidium (leaving the hardened viscidium remains on the body) and is deposited into a receptive stigma.

The hinge mechanism has been described for the pollination of *Gongora galeata* (Lindl.) Rchb. f., by *Euglossa villosa* Moure. *Gongora galeata* flowers exhibit a pedicel with an extreme curvature and a highly flexible (or hinged) labellum, both of which aid in pollination (Rodriguez Flores et al., 1995). Members of *Gongora* subg. *Acropera* share both of these floral characteristics with *G. galeata*, and thus we infer that the hinge mechanism originated in the most recent common ancestor of *Gongora* subg. *Acropera* (Fig. 4A). The extreme curvature of the pedicel modifies the orientation of floral structures such that both the labellum and column are pointed upward (see line drawing of the representative specimen of *Gongora* subg. *Acropera* in Fig. 4A). The moveable (or hinged) labellum is no thicker than the sepals, resulting in a structure and attachment point that is highly flexible (Fig. 3A). Thus, without damaging the integrity of the structure, the labellum can be easily pulled back 90 degrees toward the pedicel. Upon release, the labellum returns to its resting position parallel to the column. In the hinge mechanism, the male bee uses the front and mid-legs to pull the upward-pointing labellum back toward the pedicel, thereby exposing the adaxial surface of the labellum, the source of floral volatiles (Fig. 6D). The male proceeds to climb on top of the adaxial surface and collect floral volatiles. At this point the bee is no longer holding the labellum against the pedicel. The pedicel, then, swings back into its resting position, placing the bee on its head with its thorax pushed up against the column. The orientation of the bee, column, and labellum at this point is highly reminiscent of gullet orchid flowers (in which the column and lip form a size-restricting chamber that the pollinator must enter in order to pollinate the flower) (Dressler, 1981). In this position, the viscidium catches and attaches to the underside of the mesoscutellum of the bee. By repeating this behavior at another flower, the bee deposits the pollinia into a receptive stigma.

The third mode, the header pollination mechanism, was observed by Ramírez (pers. obs.) for the first time in Viterbo (Caldas, Colombia) between *Gongora tracyana* Rolfe (section *Truncata* of *Gongora* subg. *Gongora*), the smallest species of *Gongora*, and the orchid bee *Eulaema bombiformis* Packard, the largest species of euglossine bee (Fig. 6E, F). If we only consider the slide mechanism, *El. bombiformis* would not be expected to successfully pollinate *G. tracyana* because it is too large to physically slide down the column and remove the pollinarium. Thus, it was a surprise when *El. bombiformis* was seen not only visiting *G. tracyana* but also removing the pollinaria and successfully pollinating the flowers as evidenced by the later development of seedpods. In this mechanism, *El. bombiformis* uses the hind and mid-legs to hang upside down beneath the labellum. Once in this position, *El. bombiformis* brushes the inside of the hypochile, which in *G. tracyana* is opened and rounded (Fig. 3C). The wide angle formed between the labellum and column accommodates the head of the bee, and the slight curvature of the column allows the viscidium to catch the back of the bee's head. After 15 to 30 seconds, *El. bombiformis* releases the labellum and hovers nearby the flower while transferring the volatile compounds to the hind tibiae. The bee does not slip or fall as is typical of the slide mechanism.

During the observation, the male *Eulaema bombiformis* occasionally gripped the lateral sepals with the mid- and hind legs while brushing at the sides of the labellum. While conducting this behavior, *El. bombiformis* was not in a position to pollinate *Gongora tracyana*. The wide flaps formed by the hypochile of *G. tracyana* (Fig. 3C), however, likely hinder *El. bombiformis* from successfully collecting volatiles at the actual source of production and thus encourages *El. bombiformis* male bees to maneuver to the underside of the labellum in the correct position for pollination. In addition, during the pollination observation of *G. tracyana* in Colombia, we also observed males of *Euglossa* subg. *Euglossella* Moure visiting *Gongora* aff. *atropurpurea* Hook. (*Gongora* sect. *Grossa*), which was concurrently in flower. The *Euglossa* did not show any interest in *G. tracyana*, and *El. bombiformis* did not show any interest in *Gongora* aff. *atropurpurea*. Unfortunately, floral scent was not collected from either species of *Gongora* for chemical analysis. Nonetheless, each species of *Gongora* exhibited a perceivable odor that was distinct and that was not attractive to the other non-visiting species of bees. This clearly illustrates the extent to which floral scent can govern pollinator specificity even between *Gongora* species flowering side by side and suggests that floral scent may provide the greatest reproductive barrier between species.

Male *Eulaema* bees are not the typical pollinators of *Gongora* as their large size prevents them from maneuvering between the labellum and column (Appendix 1). Thus, species of *Gongora* pollinated by male *Eulaema* bees should exhibit changes in floral size, floral morphology, or both to accommodate the larger pollinator. This is exemplified by the header mechanism as described above. Such morphological changes accompanied by a change in pollinator size are highly reminiscent of what Dodson (1962) described as leap-frog speciation. Under the process of leap-frog speciation, the floral traits of one population experience strong selective pressures to adapt to a morphologically different (size) but possibly ethologically similar (scent preference) group of pollinators, resulting in two populations that are reproductively isolated (Dodson, 1962). Dodson suggested this as a hypothesis to describe a possible mode of speciation in *Stanhopea* Frost ex Hook. (also a member of the Stanhopeniae). He observed that sympatric populations of *Stanhopea* displayed differences in the width of the gap between the lip and column where male bees fall through after collecting floral volatiles and in doing so either remove or deposit the pollinarium (see line drawing accompanying *Stanhopea* genus in Fig. 4A). He also observed that the populations under study rarely hybridize, suggesting non-overlapping pollinator associations. He concluded the differences in morphology were driven by two morphologically different groups of pollinators, but which shared similar scent preferences. The smaller *Euglossa* bees selected for a narrow gap between the lip and column, whereas the larger *Eulaema* bees selected for a wide gap between the lip and column. In a similar sense, the ancestor of *G. tracyana* may have evolved a floral scent that attracted species of *Eulaema*. The large size of the visiting *Eulaema*, which may have on occasion accidentally acted as the pollinator, possibly drove the changes in floral morphology, resulting in what is today *G. tracyana*. Over evolutionary time, it is feasible that this leap to a new pollinator could result in the diversification of very small *Gongora* orchids pollinated by large *Eulaema* bees. In fact, several other species in *Gongora* sect. *Truncata* display similar floral morphology and floral size to that of *G. tracyana*, including *G. dresserli* Jenny, *G. longipes* Schltr., and *G. charontis* Rchb. f. It is likely that these taxa also exhibit the header mechanism for pollination. However, because not all species within *Gongora* sect. *Truncata* display floral traits similar to those of *G. tracyana*, we infer that the header mechanism originated within *Gongora* sect. *Truncata* (Fig. 4A).

Variation in the attachment site of pollinarium on the pollinator, as observed for *Gongora* (either attached under the mesoscutellum or attached to the back of the head), can act as a mechanical reproductive barrier, allowing for pollinator sharing between species with similar chemical compositions of floral scent (Hills et al., 1972; Ramírez et al., 2011). Among all genera of euglossine bee–pollinated Orchidaceae there are at least 13 different pollinarium attachment sites, and it is not uncommon to observe a single male euglossine bee carrying more than one pollinarium of different orchid genera attached to different locations on the body of the bee (Dodson & Frymire, 1961; Dressler, 1968b; Ackerman, 1983; Roubik & Hanson, 2004). Pollinarium placement, however, is often well conserved among orchid species of the same genus, suggesting that as a reproductive isolating mechanism, transitions between pollinarium attachment sites are less prevalent than changes in the chemical composition of floral scent (Ramírez et al., 2011). Nevertheless, the use of novel pollinarium attachment sites within the genus *Gongora* may provide opportunities for further diversification when coupled with changes in scent phenotype.

Concluding Remarks

Male euglossine bee pollination within Orchidaceae has a rich natural history that has and continues to capture the attention of evolutionary biologists, ecologists, and botanists. Until now, the euglossine-pollinated genus *Gongora* has lacked an accessible and comprehensive review. This overview summarizes our current knowledge of the taxonomy, systematics, and pollination biology, including pollinator diversity and the different mechanical pollination modes. There are, however, several fundamental gaps to be filled in our knowledge regarding the evolutionary biology of *Gongora*. Firstly, a well-supported species-level phylogeny of the orchid genus will open the opportunity to test fundamental hypotheses about macroevolution, diversification rates, and floral trait evolution as driven by pollinator behavior. Secondly, more research is needed on the chemical ecology of floral scent. This research should investigate both the amount of interspecific and intraspecific variation of floral scent as well as the identity of floral volatiles that act as attractants and behavioral modifiers. Thirdly, the construction of pollination networks coupled with tools borrowed from population genetics should be implemented to understand the dynamic interaction between pollinator identity and geography and how this interaction influences gene flow between populations and contributes to the processes of local adaptation and speciation. *Gongora* orchids are remarkable in terms of their floral diversity and their intricate modes of pollination. Compared to most other genera of male euglossine bee–pollinated orchids, they are relatively common in some habitats, are easy to cultivate, and can be easily hybridized and grown from seed to flower within three to four years. The genus *Gongora* merits further attention and certainly provides a system in which to investigate multiple fundamental questions in evolutionary biology and ecology.

Literature Cited

Ackerman, J. D. 1983. Specificity and mutual dependency of the orchid-euglossine bee interaction. Biol. J. Linn. Soc. 20: 301–314.

Ackerman, J. D., M. R. Mesler, K. L. Lu & A. M. Montalvo. 1982. Food-foraging behavior of male euglossini (Hymenoptera: Apidae): Vagabonds or trapliners? Biol. Trop. 14(4): 241–248.

Aldrich, P. & W. Higgins. 2008. Illustrated Dictionary of Orchid Genera. Selby Botanical Gardens Press, Sarasota, Florida.

Allen, P. H. 1950. Pollination in *Coryanthes speciosa*. Amer. Orchid Soc. Bull. 19: 528–536.

Allen, P. H. 1954. Pollination in *Gongora maculata*. Ceiba 4: 121–125.

Bembe, B. 2005. Revision der Euglossa cordata-Gruppe un Unterschungen zur Funkionsmorphologie and Fauniskik der Euglossini (Hympenoptera, Apidae). Ludwig Maximilian University of Munich, Munich.

Bembe, B. 2007. Revision der Euglossa cordata-Gruppe und Untersuchungen zur Funktionsmorphologie und Faunistik der Euglossini (Hymenoptera, Apidae). Entomofauna 14(suppl.): 1–146.

Chase, M. W., R. L. Barrett, K. M. Cameron & J. V. Freudenstein. 2003. DNA data and Orchidaceae systematics: A new phylogenetic classification. Pp. 69–89 *in* K. M. Dixon (editor), Orchid Conservation. Natural History Publications, Kota Kinabalu, Sabah, Malaysia.

Chase, M. W., K. M. Cameron, J. V. Freudenstein, A. M. Pridgeon, G. Salazar, C. Van den Berg & A. Schuiteman. 2015. An updated classification of Orchidaceae. Bot. J. Linn. Soc. 177: 151–174.

Crüger, H. 1864. A few notes on the fecundation of orchids and their morphology. J. Proc. Linn. Soc., Bot. 8(31): 127–135.

Cruz-Landim, C., A. C. Stort, M. A. Costa Cruz & E. W. Kitajima. 1965. Órgão tibial dos machos de Euglossini, estudo ao microscópio óptico e electrônico. Revista Brasil. Biol. 25(4): 323–342.

Darwin, C. 1888. The Various Contrivances by Which Orchids Are Fertilised by Insects. John Murray, London.

Dodson, C. H. 1962. The importance of pollination in the evolution of the orchids of tropical America. Amer. Orchid Soc. Bull. 31: 525–534, 641–649, 731–735.

Dodson, C. H. 1965. Agentes de polinización y su influencia sobre la evolución en la familia Orquidaceae. Museo de Zoologia–Universidad Nacional Amazonia Peruana, Iquitos, Loreto, Peru.

Dodson, C. H. 1966. Ethology of some bees of the tribe Euglossini. J. Kansas Entomol. Soc. 39: 607–629.

Dodson, C. H. 1967. Relationships between pollinators and orchid flowers. Pp. 1–72 *in* H. Lent (editor), Atas do Simpósio sôbre a Biota Amazónica. Zoologia 5.

Dodson, C. H. 1970. The role of chemical attractants in orchid pollination. Pp. 83–107 *in* K. L. Chambers (editor), Biochemical Coevolution. Oregon State University, Corvallis.

Dodson, C. H. & G. P. Frymire. 1961. Natural pollination of orchids. Missouri Bot. Gard. Bull. 49: 133–152.

Dodson, C. H. & H. G. Hills. 1966. Gas chromatography of orchid fragrances. Amer. Orchid Soc. Bull. 35: 720–725.

Dodson, C. H. & A. H. Gentry. 1978. Flora of the Río Palenque Science Center: Los Ríos Province, Ecuador. Selbyana 4(1–6): 1–628.

Dodson, C. H., R. L. Dressler, H. G. Hills, R. M. Adams & N. H. Williams. 1969. Biologically active compounds in orchid fragrances. Science 164: 1243–1249.

Dodson, C. H., N. H. Williams & W. M. Whitten. 1989. A new species of *Gongora* (Orchidaceae) from Ecuador. Lindleyana 4: 30–32.

Dressler, R. L. 1966. Some observations on *Gongora*. Orchid Digest 30: 220–223.

Dressler, R. L. 1968a. Observations on orchids and euglossine bees in Panama and Costa Rica. Revista Biol. Trop. 15: 143–183.

Dressler, R. L. 1968b. Pollination by euglossine bees. Evolution 22: 202–210.

Dressler, R. L. 1979. *Eulaema bombiformis*, *E. meriana*, and Müllerian mimicry in related species (Hymenoptera: Apidae). Biotropica 11: 144–151.

Dressler, R. L. 1981. The Orchids: Natural History and Classification. Harvard University Press, Cambridge, Massachusetts.

Dressler, R. L. 1982a. Biology of the orchid bees (Euglossini). Annual Rev. Ecol. Syst. 13: 373–394.

Dressler, R. L. 1982b. New species of *Euglossa*. II. (Hymenoptera: Apidae). Rev. Biol. Trop. 30(2): 121–129.

Dressler, R. L. 1982c. New species of *Euglossa*. III. The *bursigera* species group (Hymenoptera: Apidae). Rev. Biol. Trop. 30(2): 131–140.

Dressler, R. L. 1982d. New species of *Euglossa*. IV. The *cordata* and *purpurea* species groups (Hymenoptera: Apidae). Rev. Biol. Trop. 30(2): 141–150.

Ducke, A. 1901. Beobachtungen über Blütenbesuch, Erscheinungszeit, etc. der bei Pará vorkommenden Bienen. Z. Syst. Hym. Dipt. 1: 25–32; 2: 49–67.

Eltz, T. 2010. Flowery messages: Evolution of perfume collection in orchid bees (Euglossini). Entomol. Beute 22: 3–16.

Eltz, T., W. M. Whitten, D. W. Roubik & K. E. Linsenmair. 1999. Fragrance collection, storage, and accumulation by individual male orchid bees. J. Chem. Ecol. 25(1): 157–176.

Eltz, T., D. W. Roubik & M. W. Whitten. 2003. Fragrances, male display and mating behaviour of *Euglossa hemichlora*: A flight cage experiment. Physiol. Entomol. 28: 251–260.

Eltz, T., A. Sager & K. Lunau. 2005. Juggling with volatiles: Exposure of perfumes by displaying male orchid bees. J. Comp. Physiol. A. 191: 575–581.

Eltz, T., Y. Zimmermann, J. Haftmann, R. Twele, W. Francke, J. J. G. Quezada-Euan & K. Lunau. 2007. Enfleurage, lipid recycling and the origin of perfume collection in orchid bees. Proc. Roy. Soc. London, Ser. B, Biol. Sci. 274: 2843–2848.

Gerlach, G. & R. Schill. 1991. Composition of orchid scents attracting euglossine bees. Bot. Acta 104: 379–391.

Gregg, K. B. 1983. Variation in floral fragrances and morphology: Incipient speciation in *Cycnoches*? Bot. Gaz. 144: 566–576.

Hentrich, H. 2003. Morphologische und blütenbiologische Parameter einer Population des *Gongora quinquenervis* (Orchidaceae): Komplexes in Costa Rica. Diplomarbeit, Universität Ulm, Ulm, Germany.

Hills, H. G. 1989. Fragrance cycling in *Stanhopea pulla* (Orchidaceae, Stanhopeinae) and identification of trans-limonene oxide as a major fragrance component. Lindleyana 4(2): 61–67.

Hills, H. G. & N. H. Williams. 1990. Fragrance cycle in *Clowesia rosea*. Orquidea (Mexico City) 12(1): 19–22.

Hills, H. G., N. H. Williams & C. H. Dodson. 1972. Floral fragrances and isolating mecahnisms in the genus *Catasetum* (Orchidaceae). Biotropica 4: 61–76.

Hoehne, F. C. 1933. Contribuição para o conhecimento do genero *Catasetum* Rich. E especialmente o hermaphroditismo e trimorphismo das suas flôres. Bol. Agric. 133–196.

Janzen, D. H. 1971. Euglossine bees as long-distance pollinators of tropical plants. Science 171(3967): 203–205.

Jenny, R. 1993. Monograph of the Genus *Gongora* Ruiz & Pavon. Koeltz Scientific Books, Champaign, Illinois.

Jenny, R. 1996. The genus *Gongora*. Orchids 65: 1164–1169.

Kimsey, L. S. 1982. Systematics of bees of the genus *Eufriesea*. Univ. Calif. Entomol. 35: 1–125.

Kimsey, L. S. 1984. The behavioural and structural aspects of grooming and related activities in euglossine bees (Hymenoptera: Apidae). J. Zool., Lond. 204: 541–550.

Lindley, J. 1833. *Acropera* Lindl. P. 172 *in* The Genera and Species of Orchidaceous Plants. Ridgeways, Piccadilly, London.

Martini, P., C. Schlindwein & A. Montenegro. 2003. Pollination flower longevity, and reproductive biology of *Gongora quinquenervis* Ruíz & Pavón (Orchidaceae) in an Atlantic Forest fragment of Pernambuco, Brazil. Pl. Biol. (Stuttgart) 5: 495–503.

Moure, J. S. 1970. The species of euglossine bees of Central America belonging to the subgenus *Euglossella* (Hymenoptera-Apidae). Anais Acad. Brasil. Ci. 42(1): 147–157 [152].

Nemésio, A. & C. Rasmussen. 2011. Nomenclatural issues in the orchid bees (Hymenoptera: Apidae: Euglossina) and an updated catalogue. Zootaxa 3006: 1–42.

Neubig, K. M., W. M. Whitten, N. H. Williams, M. A. Blanco, L. Endara, J. G. Bureigh, K. Silvera, J. C. Cushman & M. W. Chase. 2012. Generic recircumscriptions of Oncidiinae (Orchidaceae: Cymbidieae) based on maximum likelihood analysis of combined DNA datasets. Bot. J. Linn. Soc. 168: 117–146.

Pokorny, T., D. Loose, G. Dyker, G. Javier, J. Quezada-Euán & T. Eltz. 2015. Dispersal ability of male orchid bees and direct evidence for long-range flights. Apidologie 46: 224–237.

Pupulin, F. 2012. The Orchidaceae of Ruiz & Pavón's "Flora Peruviana et Chilensis." A taxonomic study. I. Anales Jard. Bot. Madrid 69(1): 21–79.

Ramírez, S., R. L. Dressler & M. Ospina. 2002. Abejas euglosinas (Hymenoptera: Apidae) de la Región Neotropical: Listado de especies con notas sobre su biología. Biota Colomb. 3: 7–118.

Ramírez, S. R., D. W. Roubik, C. Skov & N. E. Pierce. 2010. Phylogeny, diversification patterns and historical biogeography of euglossine orchid bees (Hymenoptera: Apidae). Biol. J. Linn. Soc. 100: 552–572.

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

Rodriguez Flores, L. M., H. Barney Guillermo & S. M. Vâzquez Torres. 1995. Notas sobre la polinización por abejas euglosinas en *Gongora galeata* (Lindl.) Rchb. f. (Orchidaceae). La Ciencia y el Hombre 19(enero–abril): 105–116.

Roubik, D.W. & J. D. Ackerman. 1987. Long-term ecology of euglossine orchid-bees (Apidae: Euglossini) in Panama. Oecologia 72: 321–333.

Roubik, D. W. & P. E. Hanson. 2004. Orchid Bees of Tropical America: Biology and Field Guide. Instituto Nacional de Biodiversidad, INbio, Santo Domingo de Heredia, Costa Rica.

Ruiz, H. & J. Pavón. 1794. Florae Peruvianae, et Chilensis Prodromus. Imprenta de Sancha, Madrid.

Ruiz, H. & J. Pavón. 1798. Systema Vegetabilium Florae Peruvianae et Chilensis. Typis Gabrielis de Sancha, Madrid.

Schiestl, F. P. & P. M. Schlüter. 2009. Floral isolation, specialized pollination, and pollinator behavior in orchids. Annual Rev. Entomol. 54: 425–446.

Singer, R. B., B. Gravendeel, H. Cross & S. R. Ramírez. 2008. The use of orchid pollinia or pollinaria for taxonomic identifiation. Selbyana 29: 6–19.

Stern, W. L., K. J. Curry & W. M. Whitten. 1986. Staining fragrance glands in orchid flowers. Bull. Torrey Bot. Club 113: 288–297.

Stern, W. L., K. J. Curry & A. M. Pridgeon. 1987. Osmophores of *Stanhopea* (Orchidaceae). Amer. J. Bot. 74: 1323–1331.

The Plant List. 2013. Version 1.1. Published on the Internet. <http://www.theplantlist.org/>, accessed 24 March 2015.

van der Cingel, N. A. 2001. An Atlas of Orchid Pollination: America, Africa, Asia and Australia. A. A. Balkema Publishers, Brookfield, Vermont.

van der Pijl, L. & C. H. Dodson. 1966. Orchid Flowers: Their Pollination and Evolution. Universtiy of Miami Press and Fairchild Tropical Garden, Coral Gables, Florida.

Vogel, S. 1963a. Duftdrüsen im Dienste der Bestaubung: Uber Bau und Funktion der Osmophoren. Akad. Wiss. Mainz, Abh. Math.-Naturwiss. Kl. 1962: 599–763.

Vogel, S. 1963b. Das sexuelle Anlockungsprinzip der Catasetum-und Stanhopeen-Blüten und die wahre Funktion ihres sogenannten Futtergewebes. Oesterr. Bot. Z. 110: 308–337.

Vogel, S. 1966. Parfümsammelnde Bienen als Bestäuber von Orchidaceen und *Gloxinia*. Oesterr. Bot. Z. 113: 302–361.

Vogel, S. 1990. The Role of Scent Glands in Pollination: On the Structure and Function of Osmophores. Trans. J. S. Bhatti. A. A. Balkema, Rotterdam.

Whitten, W. M. 1985. Variation in Floral Fragrances and Pollinators in the *Gongora quinquenervis* Complex (Orchidaceae) in Central Panama. Ph.D. Thesis, University of Florida, Gainesville.

Whitten, W. M., A. M. Young & N. H. Williams. 1989. Function of glandular secretions in fragrance collection by male euglossine bees (Apidae: Euglossini). J. Chem. Ecol. 15(4): 1285–1295.

Whitten, W. M., A. M. Young & D. L. Stern. 1993. Nonfloral sources of chemicals that attract male euglossine bees (Apidae: Euglossini). J. Chem. Ecol. 19(12): 3017–3027.

Whitten, W. M., N. H. Williams & M. W. Chase. 2000. Subtribal and generic relationships of Maxillarieae (Orchidaceae) with emphasis on Stanhopeinae: Combined molecular evidence. Amer. J. Bot. 87: 1842–1856.

Whitten, W. M., N. H. Williams, R. L. Dressler, G. Gerlach & F. Pupulin. 2005. Generic relationships of Zygopetalinae (Orchidaeae: Cymbidieae): Combined molecular evidence. Lankesteriana 5(2): 87–107.

Williams, N. H. 1982. The biology of orchids and euglossine bees. Pp. 119–171 *in* J. Arditti (editor), Orchid Biology: Reviews and Perspectives, II. Cornell University Press, Ithaca, New York.

Williams, N. H. & C. H. Dodson. 1972. Selective attraction of male euglossine bees to orchid floral fragrances and its importance in long distance pollen flow. Evolution 26: 84–95.

Williams, N. H. & W. M. Whitten. 1983. Orchid floral fragrances and male euglossine bees: Methods and advances in the last sesquidecade. Biol. Bull. 164: 355–395.

Williams, N. H. & W. M. Whitten. 1999. Molecular phylogeny and floral fragrances of male euglossine bee-pollinated orchids: A study of *Stanhopea* (Orchidaceae). Pl. Spec. Biol. 14: 129–136.

Yam, W. T., A. Joseph & K. M. Cameron. 2009. “The orchids have been a splendid sport”—An alternative look at Charles Darwin’s contribution to orchid biology. Amer. J. Bot. 96(12): 2128–2154.

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

APPENDIX 1. POLLINATION OBSERVATIONS.

Pollination observations were gathered from existing publications (which cite personal field observations and/or museum and personal specimen collections of male euglossine bees with attached pollinaria) and unpublished personal field observations. The table is alphabetized first by country and then by locality within that country. Subsequent columns refer to the euglossine bee species name and bee behavior, as observed for *Gongora* Ruiz & Pav. taxa. Bee behavior is distinguished as four categories following the classification used in Ramírez et al. (2002): 1 = effective pollinator, 2 = non-pollinating visitor, 3 = pollinaria carrier, and 4 = visitor with unknown pollination effect. *Gongora* species names are given as listed in the accompanying reference. However, because of the difficulty of identifying *Gongora* species and the continual revision of the genus, caution should be taken in the interpretation of *Gongora* species identity, particularly for taxa identified as *G. quinquenervis* Ruiz & Pav. and for cases in which *Gongora* species identity is assigned based only on the pollinarium carried by euglossine pollinator without reference to an individual plant. Variety or chemotype refers to additional descriptions used by the referenced authors to further describe the (usually unnamed) *Gongora* species, especially when the species is not identified beyond *Gongora*. For a couple cases, the species variety or chemotype has since been assigned to its own taxonomic species; such cases are indicated with a footnote. We use *Gongora* sp. indet. to indicate that the *Gongora* species identity was unknown and/or not reported in the accompanying reference. We worked to include only the references for which independent and original observations were made, thus avoiding secondary citations. Within a reference, authors occasionally cited the unpublished observations made by others. When this occurred, we included the name of the observer identified in the reference in parentheses following the citation. Euglossine bee genera are abbreviated as follows: *Eufriesea* Cockerell (*Ef.*), *Euglossa* Latreille (*Eg.*), *Eulaema* Lepeletier (*El.*), and *Exaerete* Hoffmannsegg (*Ex.*).

WITH REGARD TO OBSERVATIONS REFERENCED FROM DRESSLER’S FIELD NOTES:

Dressler kept meticulous field notes regarding euglossine pollinators. His field notes span the years of 1964–1978 and primarily focus on orchid and euglossine bee populations from Costa Rica and Panama. Dressler cultivated many of his orchids in Panama City, Panama, and/or Turrialba, Costa Rica (Dressler, 1968a). When the orchid flowered, he would take them into the field in a habitat that was as similar to their native habitat as possible. However, on some occasions Dressler took the orchid to a habitat where he had not naturally observed the orchid but which resembled the native habitat; he noted such cases. Many of his observations are referenced in his later publications. For example, his observations from Costa Rica and Panama that span from 1964 to 1966 were incorporated into his publication “Observations on orchids and euglossine bees in Panama and Costa Rica” published in 1968 in *Revista de Biologia Tropical* and into his publication “Some observations on *Gongora*” published in 1966 in *Orchid Digest*. Thus, references made to Dressler’s publications may be redundant to references made to his field notes; nevertheless we decided to include both reference types. In the following table, we included both Dressler’s field note number and the year of the observation.

Appendix 1. Continued.

Country	Locality	Province/State/ Region	Bee species	Bee behavior	*Gongora* species	Variety or chemotype	References and observations
Brazil	Belém	Pará	*Eg. amazonica*	3	*G.* sp. indet.		Dressler, 1982d
			Eg. chalybeata	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 1193
			Eg. cordata	3	*G.* sp. indet.		Ducke, 1901
							Almir Rebello, pers. obs. in 1939, in Dressler's field notes, p. 112
							Dressler, pers. obs. in 1968, field note 1186
			Eg. mixta	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 1183
			Eg. modestior	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 1187
							Dressler, 1982c
			Eg. parvula	3	*G.* sp. indet.		Dressler, 1982b
			Eg. piliventris	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 1177
			Eg. stilbonta	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 1182
			Eg. viridis	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 1205
Brazil	Conceição da Barra	Espírito Santo	*Ef. violacea*[1]	3	*G. bufonia*		Hoehne 1933
							Dressler, pers. obs. in 1968, field note 1272
			Eg. cordata	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 1268
Brazil	Floresta de Tijuca	Rio de Janeiro	*Ef. violacea*	3	*G. bufonia*		Hoehne, 1933
							Dressler, pers. obs. in 1968, field note 1315
Brazil	Itacoatiara Road (Manaus)	Amazonas	*Eg.* aff. *crassipunctata*	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 1165
Brazil	Linhares	Espírito Santo	*Eg. cordata*	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 1286
Brazil	Refúgio Ecológico Charles Darwin, Atlantic Forest	Pernambuco	*Eg. cordata*	1	*G. quinquenervis*		Martini et al., 2003
			Eg. perpulchra	1	*G. quinquenervis*		Martini et al., 2003
			El. flavescens	2	*G. quinquenervis*		Martini et al., 2003
Brazil	Reserva Monte Pascoal	Bahia	*Eg. cordata*	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 1256
Brazil	NA	Pará	*Eg. cordata*	1	*G. quinquenervis*		Ducke, 1901
Brazil	NA	NA	*Eg. cordata*	1	*G. quinquenervis*		Whitten, 1985
			Eg. ignita	1	*G. quinquenervis*		Whitten, 1985
Colombia	Bahía Solano	Chocó	*Eg. crassipunctata*	3	*G.* sp. indet.		Ramírez et al., 2011
			El. cingulata	3	*G.* sp. indet.		Ramírez et al., 2011
Colombia	Mocoa	Putumayo	*Eg. intersecta*	3	*G.* sp. indet.		Ramírez et al., 2011
Colombia	Viterbo	Caldas	*El. bombiformis*	1	*G. tracyana*		Ramírez, pers. obs. in 2014
			Eg. sp. indent. subg. *Euglossella*	1	*G.* aff. *atropurpurea*		Ramírez, pers. obs. in 2014
Colombia	Mocoa	Putumayo	*Eg. intersecta*	3	*G.* sp. indet.		Ramírez et al., 2011

Appendix 1. Continued.

Country	Locality	Province/State/ Region	Bee species	Bee behavior	*Gongora* species	Variety or chemotype	References and observations
Colombia	NA	NA	*Eg. ignita*	1	*G. quinquenervis*		Whitten, 1985
Costa Rica	Alajuela	Alajuela	*Eg. viridissima*	1	*G.* sp. indet.	"Guancaste"[2]	Dressler, 1968a
Costa Rica	Chitaría	Cartago	*Eg. cybelia*	1	*G.* sp. indet.	"Yellow Lip"[3]	Dressler, 1968a
			Eg. gorgonensis	1	*G.* sp. indet.	"Yellow Lip"[3]	Dressler, 1968a
			Eg. hansoni	3	*G.* sp. indet.	"Yellow Lip"[3]	Dressler, 1968a
			Eg. purpurea	1	*G. unicolor*		Dressler, pers. obs. in 1965, field note 220
			Eg. tridentata	3	*G.* sp. indet.		Dressler, pers. obs. in 1965, field note 225 Moure, 1970[4]
			El. cingulata	2	*G.* sp. indet.	"White Lip"	Dressler, pers. obs. in 1965, field note 222
			El. speciosa	4	*G.* sp. indet.	"Pale-Yellow Lip"	Dressler, pers. obs. in 1965, field note 227
Costa Rica	Golfito	Puntarenas	*Eg. dodsoni*	1	*G. quinquenervis*		Dodson, 1967
			Eg. dodsoni	2	*G.* sp. indet.	"Golfito"	Dressler, 1968a van der Pijl & Dodson, 1966
			Eg. flammea	1	*G.* sp. indet.	"Golfito"	Dressler, 1968a
			Eg. ignita	1	*G. quinquenervis*		Dodson, 1967
			Eg. ignita	4	*G.* sp. indet.		Dressler, pers. obs. in 1965, field note 258 van der Pijl & Dodson, 1966
Costa Rica	Guápiles	Limón	*Eg. gorgonensis*	1	*G.* aff. *quinquenervis*		Dodson & Hills, 1966
			Eg. gorgonensis	1	*G.* sp. indet.	"Yellow Lip"[3]	Dressler, 1968a (as observed by Dodson) van der Pijl & Dodson, 1966[5]
			Eg. purpurea	1	*G. unicolor*		Dodson & Hills, 1966 Dressler, 1966 Dressler, 1968a van der Pijl & Dodson, 1966[5]
Costa Rica	La Gamba	Puntarenas	*Eg. bursigera*	4	*G.* sp. indet.	chemotype S[6]	Ramírez, pers. obs. in 2014
			Eg. cf. *cordata*	4	*G.* sp. indet.	chemotype A[7]	Pokorny, pers. obs. in 2014
			Eg. cyanura	3	*G.* sp. indet.		Ramírez, pers. obs. in 2013
			Eg. erythrochlora	4	*G.* sp. indet.	chemotype M[8]	Pokorny, pers. obs. in 2013
			Eg. flammea	3	*G.* sp. indet.	chemotype S[6]	Ramírez, pers. obs. in 2013
			Eg. hansoni	4	*G.* sp. indet.	chemotype M[8]	Pokorny, pers. obs. in 2014
			Eg. imperialis	3	*G.* sp. indet.	chemotype A[7]	Pokorny, pers. obs. in 2014
			Eg. imperialis	3	*G.* sp. indet.		Ramírez, pers. obs. in 2013
			Eg. tridentata	4	*G.* sp. indet.	chemotype M[8]	Pokorny, pers. obs. in 2014 Ramírez, pers. obs. in 2013 Hetherington-Rauth & Ramírez, pers. obs. in 2014

Appendix 1. Continued.

Country	Locality	Province/State/ Region	Bee species	Bee behavior	*Gongora* species	Variety or chemotype	References and observations
			Eg. villosiventris	3	*G.* sp. indet.	chemotype A[7]	Ramírez, pers. obs. in 2013
			El. bombiformis	4	*G.* sp. indet.	chemotype A[7]	Pokorny, pers. obs. in 2014
			Ex. sp. indet.	4	*G.* sp. indet.	chemotype S[6]	Ramírez, pers. obs. in 2014
Costa Rica	La Selva Biological Station	Heredia	*Eg. azureoviridis*[9]	3	*G.* sp. indet.		Dressler, pers. obs. in 1974, field note 1570
			Eg. bursigera	3	*G.* sp. indet.		Dressler, pers. obs. in 1970, field note 1375
			Eg. dodsoni	3	*G.* sp. indet.		Dressler, pers. obs. in 1970, field notes 1370 &1376
			Eg. purpurea	3	*G.* sp. indet.		Dressler, pers. obs. in 1974, field note 1566
			Eg. purpurea	1	*G. unicolor*		Dodson, 1967[10] Dressler, 1966 Dressler, 1968a van der Pijl & Dodson, 1966[5]
Costa Rica	Las Cruces	Puntarenas	*Eg. gorgonensis*	3	*G. armeniaca*		Dressler, pers. obs. in 1968, field note 1094
			Eg. cybelia	4	*G.* sp. indet.	"Yellow Lip"[3]	Dressler, 1968a
			El. cingulata	2	*G.* sp. indet.	"Yellow Lip"[3]	Dressler, pers. obs. in 1964, field note 159
			El. speciosa	2	*G.* sp. indet.	"Yellow Lip"[3]	Dressler, pers. obs. in 1964, field note 158
Costa Rica	Palmar Sur	Puntarenas	*Eg. cordata*	1	*G. maculata*		Allen, 1954
			Eg. cordata	1	*G. quinquenervis*[11]		van der Pijl & Dodson, 1966 Dodson, 1967 Williams, 1982
Costa Rica	Puerto Viejo	Limón	*Eg. purpurea*	3	*G. unicolor*[12]		Dressler, 1968a
Costa Rica	Tilarán	Guancaste	*Eg. cordata*	1	*G. quinquenervis*		Dressler, pers. obs. in 1966, field note 485 Dodson, 1967 van der Pijl & Dodson, 1966
Costa Rica	Turrialba	Cartago	*Eg. gorgonensis*	1	*G.* sp. indet.	"Yellow Lip"[3]	Dodson, 1967[10] van der Pijl & Dodson, 1966[5]
			Eg. hansoni	1	*G.* sp. indet.	"Yellow Lip"[3]	Dodson, 1967[9] van der Pijl & Dodson, 1966[5]
			El. cingulata	2	*G.* sp. indet.	"Yellow Lip"[3]	Dodson, 1967[10] Dressler, 1968a van der Pijl & Dodson, 1966[5]
			El. nigrifacies	2	*G.* sp. indet.	"Yellow Lip"[3]	Dodson, 1967[10] Dressler, 1968a van der Pijl & Dodson, 1966[5]

Appendix 1. Continued.

Country	Locality	Province/State/ Region	Bee species	Bee behavior	*Gongora* species	Variety or chemotype	References and observations
			El. polychroma	2	*G.* sp. indet.	"Yellow Lip"[3]	Dressler, 1968a Dodson, 1967[10] van der Pijl & Dodson, 1966[5]
			El. speciosa	2	*G.* sp. indet.	"Yellow Lip"[3]	Dodson, 1967[10] Dressler, 1968a van der Pijl & Dodson, 1966[5]
Costa Rica	NA	NA	*Eg. azureovirdis*[9]	3	*G. quinquenervis*		Whitten, 1985
			Eg. bursigera	3	*G. quinquenervis*		Whitten, 1985
			Eg. dressleri	3	*G. quinquenervis*		Whitten, 1985
			Eg. hansoni	3	*G. quinquenervis*		Whitten, 1985
			Eg. hemichlora	1	*G. quinquenervis*		Whitten, 1985
			Eg. imperialis	3	*G. quinquenervis*		Whitten, 1985
			Eg. tridentata	1	*G. quinquenervis*		Whitten, 1985
			Eg. purpurea	1	*G. unicolor*		Dressler, 1968a Dressler, 1966
			Eg. variabilis	3	*G. quinquenervis*		Allen, 1950
			Eg. viridissima	1	*G. clavidora*		Jenny, 1993
			Eg. cf. *viridissima*	1	*G. armeniaca*		Dodson & Hills, 1966
Ecuador	Balsapamba	Bolívar	*Eg. viridissima*[13]	1	*G. maculata*[14]		Dodson & Frymire, 1961
Ecuador	Bilsa Biological Reserve	Esmeraldas	*Ef. chrysopyga*	3	*G.* sp. indet.		Ramírez et al., 2011
			Eg. tridentata	3	*G.* sp. indet.		Ramírez et al., 2011
			Ex. smaragdina	3	*G.* sp. indet.		Ramírez et al., 2011
Ecuador	Lita to Alto Tambo	Esmeraldas	*Eg. dresserli*	1	*G. hirtizii*		Dodson et al., 1989
Ecuador	Quevedo	Los Ríos	*Eg.* cf. *variabilis*	1	*G. quinquenervis*		Dodson, 1967[15] van der Pijl & Dodson, 1966[16]
			Eg. viridissima[13]	1	*G. malculata*[14]		Dodson & Frymire, 1961
Ecuador	Rio Palenque	Pichincha	*Eg. tridentata*	1	*G. quinquenervis*[17]		Dodson & Gentry, 1978
Ecuador	Tiputini River	Orellana	*Eg. fuscifrons*	3	*G.* sp. indet.		Ramírez et al., 2011
Ecuador	NA	NA	*Eg. gibbosa*	1	*G. grossa*		Dodson et al., 1989[18]
			Eg. hemichlora	1	*G. grossa*		Dressler, 1966 Dodson, 1966 Dodson, 1967 Dodson et al., 1989
			Eg. ignita	1	*G. quinquenervis*		Dodson, 1967 Whitten, 1985
			Eg. ioprosopa	3	*G. quinquenervis*		Whitten, 1985

Appendix 1. Continued.

Country	Locality	Province/State/ Region	Bee species	Bee behavior	*Gongora* species	Variety or chemotype	References and observations
			Eg. nigropilosa	1	*G. grossa*		Dodson, 1965
							Dressler, 1966
							Dodson, 1967
							Dodson et al., 1989
			Eg. tridentata	1	*G. quinquenervis*		Whitten, 1985
			Eg. variabilis	3	*G. quinquenervis*		Allen, 1950
							Whitten, 1985
Guyana	NA	NA	*Eg. cordata*	1	*G. quinquenervis*		Whitten, 1985
			Eg. ignita	1	*G. quinquenervis*		Whitten, 1985
Mexico	Coatepec	Veracruz	*Eg. villosa*	1	*G. galeata*		Rodriguez Flores et al., 1995
Mexico	Fortín de las Flores	Veracruz	*Eg. villosa*	1	*G. galeata*		Dressler, pers. obs. in 1966, field note 593
Mexico	Puerto Escondido Road	Oaxaca	*Eg. viridissima*	3	*G.* sp. indet.		Dressler, pers. obs. in 1966, field note 1479
Mexico	NA	NA	*Eg. viridissima*	1	*G. galeottiana*		Dressler, 1966
Panama	Barro Colorado Island	Panama	*Eg. allosticta*	3	*G. quinquenervis*		Ackerman, 1983
			Eg. azureoviridis[9]	3	*G. quinquenervis*		Ackerman, 1983
			Eg. bursigera	3	*G. quinquenervis*		Ackerman, 1983
			Eg. cordata	1	*G. maculata*		Ducke, 1901
							Dressler, pers. obs. in 1965, field notes 241 and 248
			Eg. cordata	1	*G. quinquenervis*		Dressler, 1968a
			Eg. cyanaspis	4	*G. quinquenervis*		Ackerman, 1983
							Dressler, 1968a
			Eg. cyanura	1	*G. tricolor*		Ackerman, 1983
							Dressler 1968a[19]
			Eg. despecta	3	*G. quinquenervis*		Ackerman, 1983
			Eg. dodsoni	1	*G. quinquenervis*		Ackerman, 1983
			Eg. dressleri	3	*G. quinquenervis*		Ackerman, 1983
			Eg. hemichlora	1	*G. quinquenervis*		Ackerman, 1983
							Dressler, 1968a
			Eg. hemichlora	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 927
			Eg. cf. *hemichlora*	3	*G. maculata*		Dressler, pers. obs. in 1965, field note 242
			Eg. heterosticta	3	*G. quinquenervis*		Ackerman, 1983
			Eg. imperialis	1	*G. maculata*		Dressler, pers. obs. in 1965, field note 246

Appendix 1. Continued.

Country	Locality	Province/State/ Region	Bee species	Bee behavior	*Gongora* species	Variety or chemotype	References and observations
			Eg. imperialis	3	*G. quinquenervis*		Ackerman, 1983
			Eg. mixta	3	*G. quinquenervis*		Ackerman, 1983
			Eg. townsendii	1	*G. maculata*		Dressler, pers. obs. in 1965, field note 245
			Eg. townsendii	1	*G. quinquenervis*		Ackerman, 1983 Dressler, 1968a
			Eg. tridentata	4	*G.* cf. *aromatica*[20]		Dressler, pers. obs. in 1965, field note 262 Moure, 1970[4]
			Eg. tridentata	1	*G. maculata*		Dressler, pers. obs. in 1965, field note 244 Moure, 1970[4]
			Eg. tridentata	1	*G. quinquenervis*		Ackerman, 1983 Dressler, 1968a
			Eg. tridentata	3	*G.* sp. indet.		Dressler, pers. obs. in 1964, field note 56 Moure, 1970[4]
			Eg. variabilis	3	*G. quinquenervis*		Ackerman, 1983
			Eg. viridis	4	*G. bufonia*	var. *latibasis*	Dressler, pers. obs. in 1964, field note 17
			Eg. viridis	4	*G. bufonia*	var. *tricolor*	Dressler, pers. obs. in 1964, field notes 9 and 12
			Eg. viridis	1	*G. tricolor*	"yellow"	Dressler, pers. obs. in 1965, field note 247
			Ex. smaragdina	2	*G. tricolor*		Dressler, 1968a[18]
Panama	Cerro Campana	Panama	*Eg. asarophora*	2	*G.* sp. indet.	"El Valle"[21]	Dressler, 1968a
			Eg. bursigera	3	*G.* sp. indet.	"La Selva"	Dressler, pers. obs. in 1970, field note 1427
			Eg. bursigera		*G.* sp. indet.		Dressler, pers. obs. in 1969, field note 1327
			Eg. deceptrix	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. deceptrix	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field notes 817, 943, 1013, and 1029 Dressler, pers. obs. in 1969, field note 1330 Dressler, pers. obs. in 1970, field note 1365
			Eg. gorgonensis	2	*G.* sp. indet.	"La Selva"	Dressler, pers. obs. in 1970, field note 1426
			Eg. gorgonensis	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field notes 823 and 1065 Dressler, pers. obs. in 1969, field note 1328
			Eg. heterosticta	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. heterosticta	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 1066
			Eg. mixta	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. nigrosignata	4	*G.* sp. indet.	"La Selva"	Dressler, pers. obs. in 1970, field note 1424
			Eg. tridentata	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. variabilis	3	*G. quinquenervis*		Roubik & Ackerman, 1987

Appendix 1. Continued.

Country	Locality	Province/State/ Region	Bee species	Bee behavior	*Gongora* species	Variety or chemotype	References and observations
			Eg. villosa	4	*G.* sp. indet.	"El Valle"[21]	Dressler, 1968a
			Eg. villosa	4	*G. gibba* × *G. quinquenervis*[22]		Dressler, pers. obs. in 1969, field note 1326
			Eg. villosa	4	*G. horichiana*		Dressler, pers. obs. in 1970, field note 1425
			El. bombiformis	2	*G. gibba* × *G. quinquenervis*[22]		Dressler, pers. obs. in 1969, field note 1334
Panama	Cerro Jefe	Panama	*Eg. heterosticta*	3	*G.* sp. indet.		Dressler, pers. obs. in 1974, field note 1521
Panama	Cerro Sapo	Darién	*Eg. tridentata*	3	*G.* sp. indet.		Dressler, pers. obs. in 1978, field note 1717
Panama	El Cope	Coclé	*Eg. deceptrix*	3	*G.* sp. indet.		Whitten, 1985
			Eg. tridentata	3	*G.* sp. indet.		Whitten, 1985
Panama	El Llano	Panama	*Eg. bursigera*	1	*G.* sp. indet.		Dressler, pers. obs. in 1974, field note 1506
			Eg. mixta	3	*G.* sp. indet.		Dressler, pers. obs. in 1974, field note 1510
			Eg. tridentata	3	*G.* sp. indet.		Dressler, pers. obs. in 1974, field note 1515
Panama	El Valle de Antón	Coclé	*Eg. asarophora*	2	*G.* sp. indet.	"El Valle"[21]	Dressler, 1968a
			Eg. cyanura	4	*G. tricolor*[23]	B[24]	Whitten, 1985[25]
			Eg. cyanura	1	*G. tricolor*		Dressler, 1968a[18]
			Eg. deceptrix	3	*G.* sp. indet.		Whitten, 1985
			Eg. deceptrix	4	*G. quinquenervis*[26]	A[27]	Whitten, 1985[25]
			Eg. deceptrix	4	*G. quinquenervis*	A[27]	Whitten, 1985
			Eg. despecta	3	*G. quinquenervis*	A[27]	Whitten, 1985
			Eg. dodsoni	4	*G. quinquenervis*[28]	B[29]	Whitten, 1985[25]
			Eg. gorgonensis	4	*G. quinquenervis*[26]	A[27]	Whitten, 1985[25]
			Eg. gorgonensis	4	*G. quinquenervis*	A[27]	Whitten, 1985
			Eg. gorgonensis	4	*G. quinquenervis*	B[29]	Whitten, 1985
			Eg. gorgonensis	3	*G.* sp. indet.		Whitten, 1985
			Eg. gorgonensis	1	*G.* sp. indet.	"El Valle"[21]	Dressler, 1968a
			Eg. hansoni	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 996
			Eg. nigrosignata	4	*G.* sp. indet.	"El Valle"[21]	Dressler, 1968a[19]
			Eg. tridentata	3	*G.* sp. indet.		Whitten, 1985
			Eg. variabilis	3	*G.* sp. indet.		Whitten, 1985
			Eg. variabilis	4	*G. quinquenervis*[26]	A[27]	Whitten, 1985[25]
			Eg. variabilis	4	*G. quinquenervis*	A[27]	Whitten, 1985
			Eg. villosa	4	*G.* sp. indet.	"El Valle"[21]	Dressler, 1968a
Panama	Gamboa	Panama	*Eg. dresserli*	1	*G. maculata*		Dressler, pers. obs. in 1965, field note 270
			Eg. viridis	4	*G. bufonia*	var. *tricolor*	Dressler, pers. obs. in 1964, field note 1
			Ex. smaragdina	4	*G. bufonia*	var. *latibasis*	Dressler, pers. obs. in 1964, field note 5

Appendix 1. Continued.

Country	Locality	Province/State/ Region	Bee species	Bee behavior	*Gongora* species	Variety or chemotype	References and observations
Panama	Las Cumbres	Panama	*Eg. cordata*	4	*G. maculata*		Dressler, pers. obs. in 1964, field note 19
			Eg. cordata	1	*G. quinquenervis*[30]		Dressler, 1968a
			Eg. cyanura	1	*G. tricolor*		Dressler, pers. obs. in 1968, field notes 901.5 and 903
			Eg. townsendii	1	*G. quinquenervis*[30]		Dressler, 1968a
			Eg. tridentata	1	*G.* sp. indet.	"Guancaste"[2]	Moure, 1970[4] Dressler, pers. obs. in 1965, field note 272
			Ex. smaragdina	4	*G. atropurpurea*[31]		Dressler, pers. obs. in 1965, field note 260
Panama	Madden Dam	Colón	*Eg. tridentata*	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 946
Panama	Pipeline Road	Colón	*Eg. allosticta*	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. bursigera	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. despecta	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. imperialis	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. mixta	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. tridentata	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. variabilis	3	*G. quinquenervis*		Roubik & Ackerman, 1987
Panama	Río Guanche	Colón	*Eg. tridentata*	3	*G.* sp. indet.		Dressler, pers. obs. in 1974, field note 1526
Panama	Río Iguanita	Colón	*Eg. asarophora*	3	*G.* sp. indet.		Whitten, 1985
			Eg. cyanaspis	3	*G.* sp. indet.		Whitten, 1985
			Eg. cyanura	4	*G. tricolor*[32]	B[24]	Whitten, 1985[25]
			Eg. deceptrix	3	*G.* sp. indet.		Whitten, 1985
			Eg. despecta	4	*G. quinquenervis*[33]	A[27]	Whitten, 1985[25]
			Eg. despecta	3	*G.* sp. indet.		Whitten, 1985
			Eg. dodsoni	4	*G. quinquenervis*[33]	A[27]	Whitten, 1985[25]
			Eg. hemichlora	4	*G. quinquenervis*[33]	A[27]	Whitten, 1985[25]
			Eg. imperialis	4	*G. quinquenervis*[33]	A[27]	Whitten, 1985[25]
			Eg. townsendii	4	*G. quinquenervis*[33]	A[27]	Whitten, 1985[25]
			Eg. tridentata	3	*G.* sp. indet.		Whitten, 1985
			Eg. tridentata	4	*G. quinquenervis*[33]	A[27]	Whitten, 1985[25]
			Eg. variabilis	3	*G.* sp. indet.		Whitten, 1985
			Eg. variabilis	4	*G. quinquenervis*[33]	A[27]	Whitten, 1985[25]
Panama	Santa Rita Lumber Road	Colón	*Eg. tridentata*	3	*G.* sp. indet.		Dressler, pers. obs. in 1970, field note 1388
Panama	Santa Rita Ridge	Colón	*Eg. allosticta*	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. asarophora	3	*G. gibba*		Roubik & Ackerman, 1987
			Eg. asarophora	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 853

Appendix 1. Continued.

Country	Locality	Province/State/ Region	Bee species	Bee behavior	*Gongora* species	Variety or chemotype	References and observations
			Eg. bursigera	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. deceptrix	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. dissimula	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. dressleri	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. heterosticta	3	*G.* sp. indet.		Dressler, pers. obs. in 1968, field note 998
			Eg. heterosticta	3	*G. quinquenervis*		Roubik & Ackerman, 1987
			Eg. tridentata	3	*G. quinquenervis*		Roubik & Ackerman, 1987
Panama	NA	NA	*Eg. azureoviridis*[9]	3	*G. quinquenervis*		Whitten, 1985
			Eg. bursigera	3	*G. quinquenervis*		Whitten, 1985
			Eg. cordata	1	*G. quinquenervis*		Dressler, 1966 Dodson, 1967[15] van der Pijl & Dodson, 1966[5]
			Eg. cyanura	1	*G. tricolor*		Dressler, 1966[18] Dressler, 1968a van der Pijl & Dodson, 1966[5] Dodson & Hills, 1966
			Eg. deceptrix	3	*G. quinquenervis*		Whitten, 1985
			Eg. despecta	3	*G. quinquenervis*		Ramírez et al., 2002 (Dressler, pers. obs.) Whitten, 1985
			Eg. hansoni	3	*G. quinquenervis*		Whitten, 1985
			Eg. heterosticta	3	*G. quinquenervis*		Whitten, 1985
			Eg. mixta	3	*G. quinquenervis*		Whitten, 1985
			Eg. orichalea[34]	1	*G. quinquenervis*		Dodson, 1967[10] van der Pijl & Dodson, 1966[5]
			Eg. townsendii	3	*G. quinquenervis*		Dodson, 1967[10] van der Pijl & Dodson, 1966[5] Whitten, 1985
			Eg. tridentata	1	*G. clavidora*		Jenny, 1993
			Eg. tridentata	1	*G. quinquenervis*		Ackerman, 1983 Roubik & Ackerman, 1987 Whitten, 1985
Peru	El Parque Nacional del Manu (“Panguana” Forest Reserve on Río Llullapichis)	Madre de Dios/ Cusco	*Eg.* cf. *parvula*	3	*G.* sp. indet.		Dressler, pers. obs. in 1975, field note 1607

Appendix 1. Continued.

Country	Locality	Province/State/ Region	Bee species	Bee behavior	*Gongora* species	Variety or chemotype	References and observations
Peru	Iquitos	Loreto	*Eg. augaspis*	1	*G. quinquenervis*		Dodson, 1967[15] Dodson & Hills, 1966 van der Pijl & Dodson, 1966[16]
			Eg. cordata	1	*G. quinquenervis*		Dodson, 1967[15] Dressler, 1968a[35] van der Pijl & Dodson, 1966[16]
			Eg. decorata	1	*G. quinquenervis*		Dodson, 1967[15] Williams, 1982[36] van der Pijl & Dodson, 1966[16]
			Eg. ignita	4	*G. maculata*		Dodson, 1966[19]
			Eg. ignita	1	*G. quinquenervis*		Dodson, 1967[15] van der Pijl & Dodson, 1966[16]
			Eg. prasina	4	*G. maculata*		Dressler, 1982c
			El. cingulata	3	*G.* sp. indet.		Ramírez et al., 2011
Peru	Tarapoto	San Martín	*El. meriana*	3	*G.* sp. indet.		Ramírez et al., 2011
Peru	NA	NA	*Eg. augaspis*	1	*G. quinquenervis*		Whitten, 1985
			Eg. decorata	1	*G. quinquenervis*		Whitten, 1985
			Eg. ignita	1	*G. quinquenervis*		Whitten, 1985[37]
			Eg. modestior	3	*G. quinquenervis*		Whitten, 1985
Trinidad	NA	NA	*Eg. cordata*	3	*G. quinquenervis*		Dressler, 1968a Whitten, 1985
			Eg. ignita	1	*G. quinquenervis*		Whitten, 1985
NA	NA	NA	*Ef. anisochlora*	3	*G.* sp. indet.		Ramírez et al., 2002
			Ef. lucifera	3	*G.* sp. indet.		Ramírez et al., 2002
			Ef. rufocauda	3	*G.* sp. indet.		Kimsey, 1982
			Eg. asarophora	2	*G.* sp. indet.		Dodson, 1967[10]
			Eg. augaspis	1	*G. maculata*		Dodson, 1966
			Eg. bursigera	3	*G.* sp. indet.		Ramírez et al., 2002 (FLAS)
			Eg. cordata	1	*G. maculata*	var. *maculata*	Dodson, 1965
			Eg. cyanura	1	*G. fulva*		Dodson, 1965
			Eg. cyanura	1	*G. tricolor*		Dodson et al., 1969
			Eg. cyanura	1	*G. unicolor*		Dressler, 1966 Jenny, 1993 (Chavez, pers. comm.)
			Eg. decorata	1	*G. quinquenervis*		Dodson, 1967
			Eg. decorata	1	*G. maculata*		Dodson, 1966
			Eg. dodsoni	1	*G. armeniaca*	var. *bicornuta*	Dodson, 1965

Appendix 1. Continued.

Country	Locality	Province/State/ Region	Bee species	Bee behavior	*Gongora* species	Variety or chemotype	References and observations
			Eg. dodsoni	4	*G. horichiana*		Dodson, 1966
			Eg. dodsoni	4	*G. maculata*		Ramírez et al., 2002 (Dressler, pers. obs.)
			Eg. despecta	3	*G. quinquenervis*		Ramírez et al., 2002 (Dressler, pers. obs.)
			Eg. gibbosa	3	*G. quinquenervis*		Dressler, 1982d
			Eg. gorgonensis	1	*G.* sp. indet.		Dodson, 1967[10]
			Eg. ignita	4	*G. maculata*		Dodson, 1966
			Eg. imperialis	1	*G. maculata*		Dodson, 1965 Ramírez et al., 2002
			Eg. ioprosopa	4	*G.* sp. indet.		Dressler, 1982b
			Eg. oleolucens	3	*G. armeniaca*		Ramírez et al., 2002 (FLAS)
			Eg. prasina	3	*G. maculata*		Ramirez et al., 2002 (FLAS)
			Eg. purpurea	3	*G.* sp. indet.		Dressler, pers. obs. in 1974, field note 1566
			Eg. singularis	4	*G. maculata*		Ramírez et al., 2002 (FLAS)
			Eg. variabilis	3	*G.* sp. indet.		Ramírez et al., 2002 (RPSP)
			Eg. cf. *variabilis*	1	*G. grossa*		Dodson, 1965[38]
			Eg. violacea	1	*G. bufonia*		Hoehne, 1933
			Eg. viridis	3	*G. aromatica*		Ramírez et al., 2002 (FLAS)
			Eg. viridis	1	*G. maculata*	var. *tricolor*[39]	Dodson, 1965
			Eg. viridissima	1	*G. armeniaca*		Dodson, 1965
			Eg. viridissima	1	*G. grossa*		Dodson, 1962
			Eg. viridissima	1	*G. maculata*		Dodson, 1962
			Eg. cf. *viridissima*	4	*G. armeniaca*		Jenny, 1993 (Whitten, pers. comm.)
			Eg. cf. *viridissima*	1	*G. maculata*	var. *odoratissima*[40]	Dodson, 1965[38]
			El. cingulata	4	*G. atropurpurea*		Dodson, 1966
			El. cingulata	1	*G. scaphephorus*		Jenny, 1993[41]
			El. meriana	4	*G.* cf. *minax*		Dressler, 1979
			El. meriana	3	*G.* sp. indet.		Dressler, 1979

Abbreviations: FLAS, Florida Museum of Natural History Herbarium; RPSP, School of Philosophy, Sciences, and Letters, University of São Paulo, Brazil.

[1] The accompanying references apply the name *Euplusia violaceae*, which is no longer used and has since been named as *Eufriesea violaceae*.

[2] The *Gongora* that Dressler refers to as "Guancaste" and describes as being wine red in color and having a perceivable and strong clove oil scent is now the species description of *G. clavidora* Dressler (see Jenny, 1993).

[3] Whitten (pers. comm. in 2014) stated that the *Gongora* that Dressler referred to as "Yellow-Lip" is likely synonymous to the species name known presently as *G. odoratissma* Lemaire.

[4] Moure (1970) directly references the observations documented in Dressler's field notes.

[5] Van der Pijl and Dodson (1966) cite Dressler (1966) as the original source of the pollination observation; however, the pollination observation was not supported upon examination of Dressler (1966).

[6] This *Gongora* belongs to a population that is part of ongoing research. Individuals described as chemotype S produce a floral scent composition characterized by an unidentified monoterpene derivative and alpha farnesene as well as several other monoterpene compounds (unpublished data).

[7] This *Gongora* belongs to a population that is part of ongoing research. Individuals described as chemotype A produce a floral scent composition characterized by estragole and cis- and trans-methyl p-methoxycinnamate as well as other aromatic compounds (unpublished data).

[8] This *Gongora* belongs to a population that is part of ongoing research. Individuals described as chemotype M produce a floral scent composition characterized by terpinen-4-ol as well as other monoterpene compounds (unpublished data).

[9] The name *Eg. azureoviridis* Friese is no longer used and has since been named as *Eg. milenae* Bembé (see Bembe, 2005, 2007, and Nemésio & Rasmussen, 2011).

[10] Dodson (1967) cites Dressler (1966) as the original source of the pollination observation; however, the pollination observation was not supported upon examination of Dressler (1966).

[11] The accompanying references cite the original source as Allen (1954); however, Allen (1954) only mentions *Gongora malculata* with no mention of *G. quinquenervis*.

[12] This observation is based upon a pollinarium attached to the bee pollinator, and hence it is likely that the *Gongora* species name is inferred from the locality of the observation and the distribution of the named *Gongora* species.

[13] In addition to *Eg. viridissima*, Dodson and Frymire (1961) also state that they observed blue-purple species of *Euglossa* visiting the described *Gongora*.

[14] Dodson and Frymire (1961) apply the name *Gongora malculata*; however, the photographs included in the publication and locality of the observation suggest that the *Gongora* observed was more similar to *G. grossa*.

[15] Dodson (1967) cites Dodson (1962) as the original source of the pollination observation; however, the pollination observation was not supported upon examination of Dodson (1962).

[16] Van der Pijl and Dodson (1966) cites Dodson (1962) as the original source of the pollination observation; however, the pollination observation was not supported upon examination of Dodson (1962).

[17] Dodson and Gentry (1978) apply the name *Gongora quinquenervis* to the *Gongora* observed; however, they note that the *Gongora* observed may also be known as *G. malcualta* Lindl. and/or *G. superflua* Rchb. F., which they further suggest may prove to be synonymous names.

[18] Dodson et al. (1989) cites Williams (1982) as the original source of the pollination observation; however, the pollination observation was not supported upon examination of Williams (1982).

[19] The listed locality of the pollination observation is interpreted from the text, which describes either the distribution of the listed bee species and/or the distribution of the listed *Gongora* species.

[20] Dressler collected this *Gongora* cf. *aromatic* from Guancaste, Costa Rica (northernmost providence on the Pacific side of Costa Rica), and recorded pollination observation at Barro Colorado Island, Panama (central Panama).

[21] Whitten (pers. comm. in 2014) stated that the *Gongora* that Dressler referred to as "El Valle" is likely synonymous to the species name known presently as *G. powellii* Schlechter.

[22] Dressler purchased this *Gongora* hybrid from El Valle de Anton, Panama.

[23] Whitten (1985) collected this *Gongora tricolor* from Rio Iguanita, located in central Panama on the Atlantic side, and recorded pollination observation in El Valle de Anton, located on the Pacific side of western Panama.

[24] Whitten (1985) performed chemical analysis of the floral scent composition and revealed that the floral scent of what he referred to as *Gongora tricolor* B was characterized by the monoterpene, ipsdienol. Whitten (pers. comm. in 2014) states that *G. tricolor* B is synonymous to *G. fulva* Lindl.

[25] In order to investigate geographic variation in the species identity of euglossine bee pollinator and its role in generating and/or maintaining reproductive isolation among *Gongora* species, Whitten (1985) conducted several transplant experiments in Panama, in which he recorded euglossine bee visitors and/or pollinators of *Gongora* in the collection (native) locality and in the transplant locality. This observation was recorded at the transplant locality.

[26] Whitten (1985) collected this *Gongora quniquenervis* from El Boco del Torro, located on the Atlantic coast in western Panama, and recorded pollination observations in El Valle de Antón, located on the Pacific side of western Panama.

[27] Whitten (1985) performed chemical analysis of the floral scent composition and revealed that the floral scent of what he referred to as *Gongora quinquenervis* A was characterized by the aromatic compounds cis- and trans-methyl p-methoxycinnamate. Whitten (pers. comm. in 2014) states that *G. quinquenervis* A is synonymous to *G. powellii* Schltr.

[28] Whitten (1985) collected this *Gongora quinquenervis* from Golfito, located on the Pacific coast of southern Costa Rica, and recorded pollination observations in El Valle de Antón, located on the Pacific side of western Panama.

[29] Whitten (1985) performed chemical analysis of the floral scent composition and revealed that the floral scent of what he referred to as *Gongora quinquenervis* B was characterized by the monoterpene terpinen-4-ol. Whitten (pers. comm. in 2014) states that *G. quinquenervis* B is synonymous to *G. boracayanensis* Jenny, Dalström & W. E. Higgins.

[30] Dressler collected this *Gongora quinquenervis* from El Valle de Antón, located on the Pacific side of western Panama, and recorded pollination observations in Las Cumbres, located on the Pacific side of central Panama.

[31] Dressler collected this *Gongora atropurpera* Hook. from Peru and recorded pollination observations in Las Cumbres, Panama.

[32] Whitten (1985) collected this *Gongora tricolor* from Cerro Azul, located on the Pacific side of central Panama, and recorded pollination observations in Río Iguanita, located on the Atlantic side of central Panama.

[33] Whitten (1985) collected this *Gongora quinquenerivs* from El Valle de Antón, located on the Pacific side of western Panama, and recorded pollination observation in Río Iguanita, located on the Atlantic side of central Panama.

[34] The species name *Eg. orichalcea* is considered nomina nuda.

[35] Dressler (1968a) cites Dodson (1965) as the original source of the pollination observation; however, the pollination observation was not supported upon examination of Dodson (1965).

[36] Williams (1982) cites Dodson (1962) as the original source of the pollination observation; however, the pollination observation was not supported upon examination of Dodson (1962).

[37] Whitten (1985) cites Dodson (1962) as the original source of the pollination observation; however, the pollination observation was not supported upon examination of Dodson (1962).

[38] Dodson (1965) cites Dodson (1962) as the original source of the pollination observation; however, the pollination observation was not supported upon examination of Dodson (1962).

[39] *Gongora maculata* var. *tricolor* Lindl. is synonymous to *G. fulva* Lindl (see Jenny, 1993).

[40] *Gongora maculata* var. *odoratissima* Dodson is synonymous to *G. odoratissima* Lemaire (see Jenny, 1993).

[41] Jenny (1993) cites Dodson (1967) as the original source of the pollination observation; however, the pollination observation was not supported upon examination of Dodson (1967).