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Floral visitors of *Mormodes maculata* (Orchidaceae, Catasetinae) and pollinarium placement on a specialized orchid bee

Visitantes florales de *Mormodes maculata* (Orchidaceae, Catasetinae) y colocación de polinarios sobre una abeja de orquídeas especializada

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Abstract:

Background and Aims: *Mormodes* is the only orchid genus exhibiting floral handedness (enantiostyly), a trait presumed to promote cross-pollination. Despite this unique floral morphology, little is known about its reproductive biology or pollinators. The aim of this study was to characterize the floral visitors of two varieties of *Mormodes maculata* and assess the subsequent positioning of their pollinarium.

Methods: We conducted field observations on 12 flowering individuals of *Mormodes maculata* representing two floral varieties, *M. maculata* var. *maculata* and *M. maculata* var. *unicolor*. We observed, captured, and identified floral visitors and documented the specific body region of the bee where the pollinia were attached.

Key results: We identified *Euglossa obrima* as the pollinator of *Mormodes maculata* after observing an individual carrying a laterally attached pollinarium, consistent with the flower's handedness. We also recorded *Eulaema polychroma* as an occasional floral visitor, exclusively to *M. maculata* var. *maculata*, but without evidence of effective pollination.

Conclusions: Our findings reveal a highly specialized pollination mechanism in *Mormodes maculata*, driven by the interaction between floral handedness and a specialized orchid bee. This high degree of specialization should be considered when developing conservation strategies for the species.

Key words: Euglossini bees, floral laterization, perfume orchid, pollination.

Resumen:

Antecedentes y Objetivos: *Mormodes* es el único género de orquídeas que presenta lateralidad floral (enantiostilia), un rasgo que presumiblemente favorece la polinización cruzada. Sin embargo, su biología reproductiva y las especies responsables de su polinización permanecen escasamente estudiadas. El objetivo de este estudio fue caracterizar a los visitantes florales de dos variedades de *Mormodes maculata* y evaluar el posicionamiento posterior de sus polinarios.

Métodos: Realizamos observaciones de campo en 12 individuos de *Mormodes maculata* en floración, correspondientes a dos variedades, *M. maculata* var. *maculata* y *M. maculata* var. *unicolor*. Observamos, capturamos e identificamos sus visitantes florales y documentamos la posición del polinario sobre una parte específica del cuerpo de una abeja visitante.

Resultados clave: Identificamos a *Euglossa obrima* como el polinizador de *Mormodes maculata*, al registrar un individuo portando los polinarios adheridos lateralmente, en concordancia con la lateralidad de la flor. Además, registramos a *Eulaema polychroma* como visitante floral ocasional, exclusivamente en *M. maculata* var. *maculata*, sin evidencia de que actuara como polinizador efectivo.

Conclusiones: Nuestros resultados evidencian un mecanismo de polinización altamente especializado en *Mormodes maculata*, determinado por la interacción entre la lateralidad floral y una abeja de las orquídeas especializada. Este elevado grado de especialización debe considerarse en las estrategias dirigidas a la conservación de la especie.

Palabras clave: abejas euglosinas, lateralización floral, orquídeas perfumadas, polinización.

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Introduction

In Neotropical forests, a unique pollination strategy has evolved in some 700 orchid species , in which flowers produce scents that function as both attractant and reward for specialized pollinators, the so-called "perfume flower" syndrome (sensu Vogel, 1966; Dressler, 1968). The scents, which are composed of a complex mixture of volatile and semivolatile organic compounds (VOCs and SVOCs, respectively), are collected exclusively by male orchid bees (Apidae, Euglossini), which concoct species-specific perfumes to use during courtship displays at mating sites (Henske et al., 2023). Perfume flowers are particularly diverse in the Neotropical subtribe Catasetinae (Orchidaceae) (Ackerman et al., 2023; Liu et al., 2025).

Catasetinae embraces about 300 species showing a specialized pollination mechanism, in which the stipe forcefully ejects the pollinarium onto the pollinator's body (Darwin, 1877; Dodson, 1962; Pérez-Escobar et al., 2016). While the mechanical aspects of the pollination mechanisms of Catasetinae have been studied for over a century (Darwin, 1877; Dodson, 1962; Dressler, 1968), the genus *Mormodes* Lindl. exhibits a unique morphological variation that has been only recently formally recognized among orchids: a lateral twisting of the column that causes reproductive organs to face opposite directions (Domingos-Melo et al., 2025). These structures may deviate either to the right (R-morph) or to the left (L-morph) within the same individual, representing a form of monomorphic enantiostyly (Almeida and de Castro, 2019). It has been hypothesized that this strategy of mirrored flowers is to enhance outcrossing by placing pollen on a specific side of the pollinator, which corresponds to the position of the stigma in the opposite floral morph (Almeida and de Castro, 2019; Barrett and Fairnie, 2024; Domingos-Melo et al., 2025).

Despite Catasetinae being one of the best-studied orchid groups in the Neotropics, basic aspects of the reproductive biology (e.g., pollinators, flower phenology) of more than 85% of the *Mormodes* species remain completely unknown (Pessoa et al., 2025). This knowledge gap is particularly critical because most *Mormodes* species are rare and typically rely on a single or a few pollinator species for successful pollination (Silva et al., 2025). The lack of such fundamental biological information severely limits the development of effective conservation strategies for these orchids (Schemske et al., 1994). Consequently, the loss of the pollinator may directly compromise plant viability and should therefore be considered a key criterion in species risk assessments. The objectives of this study were to provide the first field observations of pollinators visiting two varieties of *Mormodes maculata* (Klotzsch) L.O.Williams and to report the positioning of pollinarium on the bees.

Materials and Methods

Study species

The genus *Mormodes* comprises 87 saprolignophilous epiphytic species (POWO, 2026) distributed throughout the Neotropics, from Mexico to Brazil and northern Argentina (Salazar-Chávez, 1999; Romero et al., 2009). *Mormodes maculata* is endemic to Mexico, occurring along the Sierra Madre Oriental and its confluence with the Trans-Mexican Volcanic Belt (sensu Morrone et al., 2017; Fig. 1).

This species grows primarily on dead branches, dead trees, stumps, and fallen trunks, and only occasionally as a terrestrial on embankments (Fig. 2A). This species comprises two accepted varieties (POWO, 2026): *Mormodes maculata* var. *maculata*, known exclusively from the mountainous massif of northern Oaxaca and the adjacent portion of Veracruz (southern distribution), and *Mormodes maculata* var. *unicolor* (Hook.) L.O.Williams, distributed in the Huasteca region (Querétaro and Hidalgo), Puebla, and central Veracruz (northern distribution) (Fig. 1; Salazar-Chávez, 1999). Both varieties co-occur in central Veracruz and can be distinguished by their floral coloration, which ranges from lightly or densely spotted with wine-red in *M. maculata* var. *maculata* to homogeneous lemon-yellow to canary-yellow in *M. maculata* var. *unicolor* (Fig. 2B, C, D). It inhabits humid pine-oak forests, montane cloud forests, and the ecotone between these communities and tropical evergreen forests, at elevations ranging from approximately 600 to 2200 m (Rzedowski, 2006).

Mormodes maculata starts flowering from early June to early September. It develops an arched inflorescence up to 50 cm long, which bears as many as 30

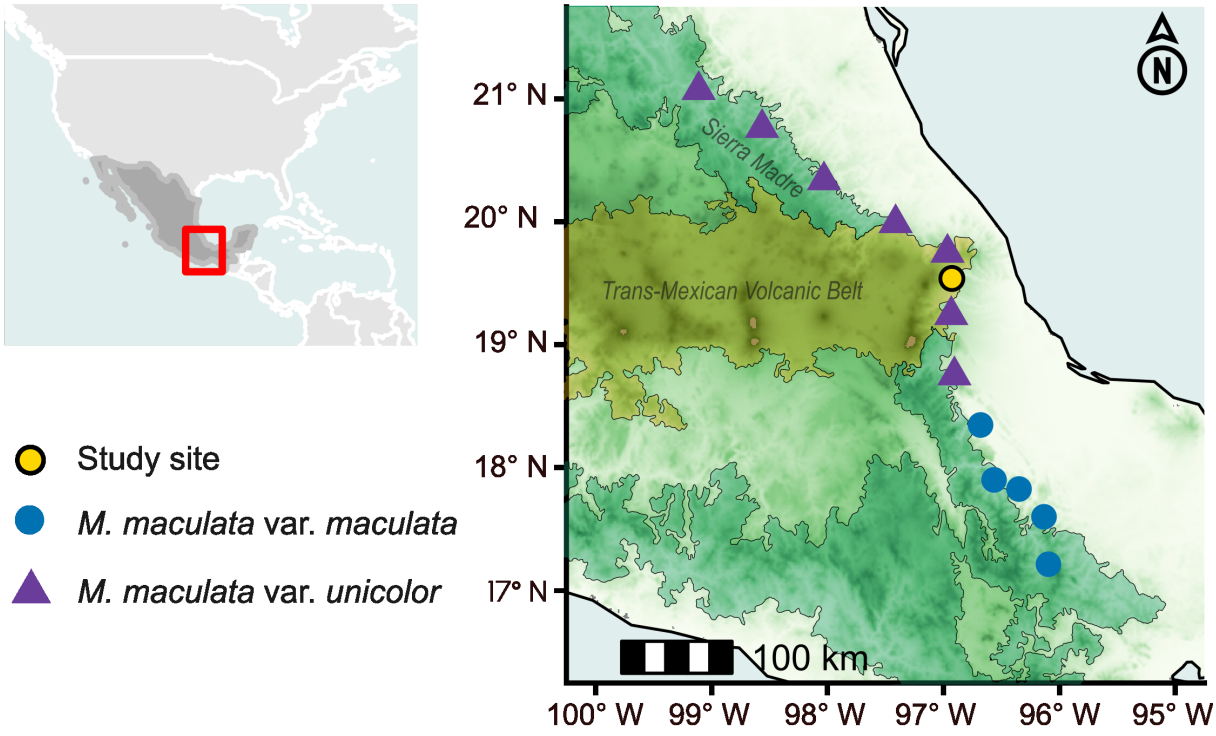


Figure 1: Study area. The yellow circle represents the location of the study site in, Mexico; purple triangles and blue circles represent the distribution of the two *Mormodes maculata* (Klotzsch) L.O.Williams varieties (adapted from Salazar-Chávez, 1999). Elaborated by Álvaro Hernández-Rivera.

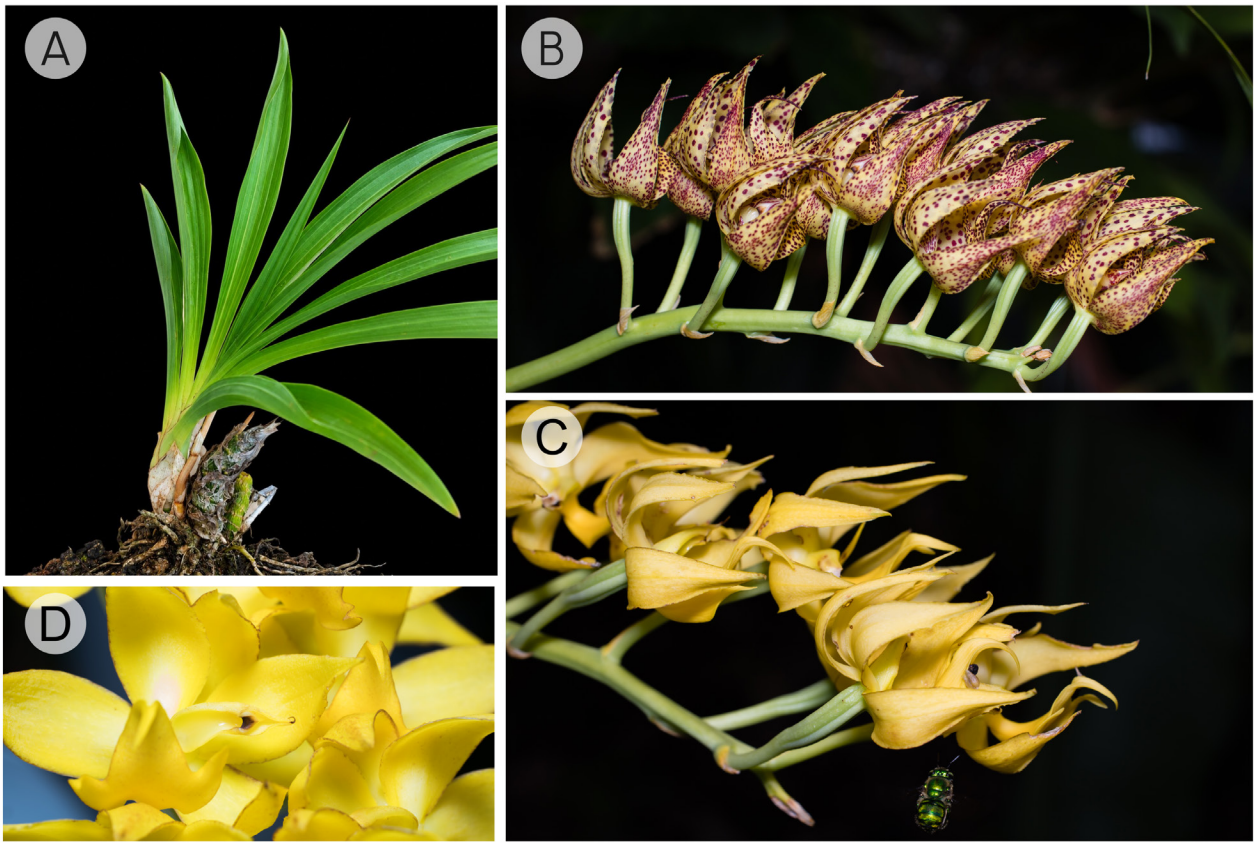


Figure 2: *Mormodes maculata* (Klotzsch) L.O.Williams: A. plant during vegetative state; B. *Mormodes maculata* var. *maculata*; C. *Mormodes maculata* var. *unicolor* (Hook.) L.O Williams; D. close-up to a flower. Photos by Álvaro Hernández-Rivera.

conspicuous flowers (Salazar-Chávez, 1999). Its flowers are approximately 5 cm long and emit a strong and sweet scent. *Mormodes maculata* is currently considered a high conservation priority species in because is listed as Threatened under the Mexican laws (Sánchez-Velásquez et al., 2008; SEMARNAT, 2010).

Floral visitors

We monitored floral visitors on 12 individuals of *Mormodes maculata* between June and September 2025, corresponding with the species' flowering season (Salazar-Chávez, 1999). Visitors were observed on ten individuals of *M. maculata* var. *unicolor* and two individuals of *M. maculata* var. *maculata*. Observations were conducted during sunny or partially sunny mornings for at least one hour per plant in the morning (ranging between 09:00-12:00 h), when orchid bees are most active, and floral scent emission is strongest (Roubik and Hanson, 2004). For each inflorescence, we counted the number of flowers whose orientation deviated to the left (L-morph) or right (R-morph), as determined by viewing each flower from the back.

Pollinator monitoring was conducted using a non-lethal approach; however, a small number of individuals were collected as voucher specimens and deposited in the reference collection IEXA (Entomological Collection of the Instituto de Ecología, A.C., Xalapa, Veracruz, Mexico). Pollinator observations were conducted in a private orchid collection located in a peri-urban green area in the vicinity of Xalapa, Veracruz, at 1400 m a.s.l. The study area is within the montane cloud forest region and within the species' distribution range. The exact location of the study site is withheld to protect wild populations from potential collection or disturbance.

Bee species were identified using the taxonomic keys for orchid bees (Roubik and Hanson, 2004; Hinojosa-Díaz et al., 2011) and species identifications were further verified by comparison with reference specimens housed in the Euglossini collection of the Entomological Collection IEXA. When a pollinarium was observed on a visiting bee, we recorded its position on the bee's body and assessed whether its placement was associated with a particular orchid floral type.

Results

We observed a high number of bees visiting inflorescences in more than ten occasions. We captured and identified 47 individuals of *Euglossa obrima* Hinojosa-Díaz, Melo & Engel, 2011 and two of *Eulaema polychroma* Friese, 1899 visiting flowers of *Mormodes maculata* (Fig. 3A, B). Both *Eulaema polychroma* individuals visited only *M. maculata* var. *maculata* (Fig. 3C), despite the simultaneous flowering of *M. maculata* var. *unicolor*, which received no visits. *Euglossa obrima* is readily identified in the field by the cowled slits on the second metasomal sternum. Similarly, *Eulaema polychroma* can be distinguished by its distinctive abdominal coloration: the abdomen is black basally, with the remaining segments appearing yellowish to brownish due to the dense covering of hairs (Roubik and Hanson, 2004; Hinojosa-Díaz, et al., 2011).

Floral handedness and pollinarium attachment

A relatively balanced relationship was observed between L-morph and R-morph flowers across the inflorescences of both varieties combined (L-morph: 5.17±1.40, n=12; R-morph: 4.58±1.83, n=12), and when each variety was analyzed separately. In *M. maculata* var. *maculata*, the mean number of flowers was 6.50±0.71 for L-morphs and 6.00±0.00 for R-morphs (n=2), whereas in *M. maculata* var. *unicolor* the means were 4.90±1.45 and 4.30±1.89 (n=10), respectively.

In one opportunity, we recorded an individual of *Euglossa obrima* clamped to an *M. maculata* var. *unicolor* petal using its mandibles (Fig. 4A). This individual was carrying a pollinarium associated with flowers of *M. maculata* exhibiting the L-morph, which we identified by comparing them with pollinia from other flowers and the direction of the flower faces (Fig. 4B, C). The bee remained attached to the petal for approximately 25 minutes before flying away. During this time, it repeatedly attempted to remove the pollinarium using its hind legs but was unable to dislodge it. However, despite the pollinium triggering, none of the 12 monitored individuals produced fruit.

Discussion

We recorded 49 floral visitors, with one bee species visiting different *Mormodes maculata* varieties unequally.



Figure 3: *Mormodes maculata* (Klotzsch) L.O.Williams floral visitors: A. inflorescence of *Mormodes maculata* var. *unicolor* (Hook.) L.O.Williams and males of *Euglossa obrima* Hinojosa-Díaz, Melo & Engel, 2011; B. *Mormodes maculata* var. *maculata* visited by an *Euglossa obrima* male; C. *Mormodes maculata* var. *maculata* visited by an *Eulaema polychroma* Friese, 1899, male. Photos by Álvaro Hernández-Rivera.

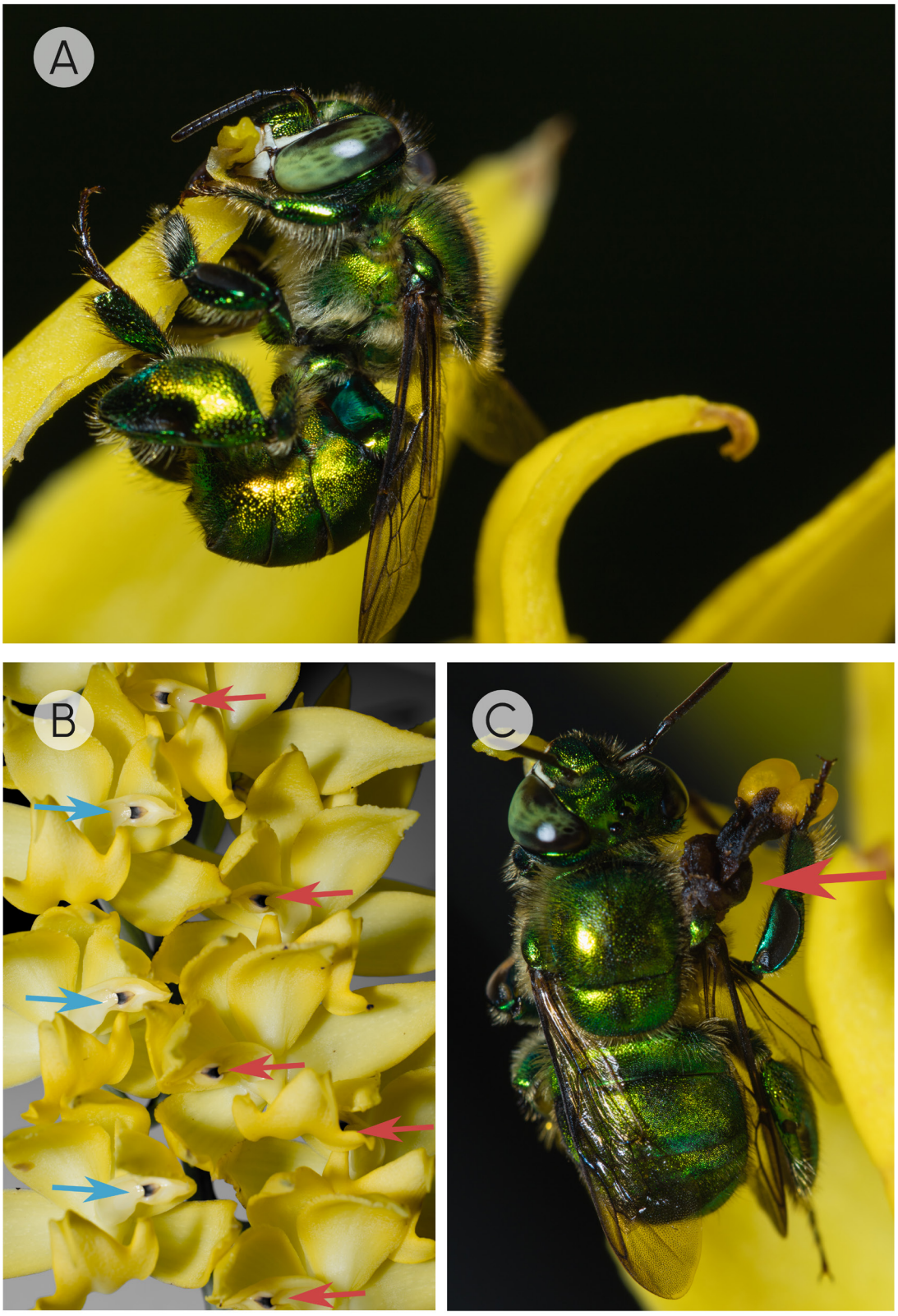


Figure 4: Flower handedness and floral visitors of *Mormodes maculata* var. *unicolor* (Hook.) L.O.Williams: A. *Euglossa obrima* Hinojosa-Díaz, Melo & Engel, 2011 at *Mormodes maculata* (Klotzsch) L.O.Williams petal; B. floral handedness variation in female-phase flowers (fully open flowers); red and blue arrows indicate L- and R-morph flowers, respectively, based on Domingos-Melo et al. (2025). C. *Euglossa obrima* carrying a pollinarium of a L-morph of *Mormodes maculata*. Photos by Álvaro Hernández-Rivera.

Observations of different floral visitors across distinct floral varieties pollinated by euglossine bees have been reported in the genus *Gongora* Ruiz & Pav., where color variants also correspond to species-specific scent chemotypes that attract their own non-overlapping assemblages of bee pollinators (Hetherington-Rauth and Ramírez, 2015; 2016). As in many Orchidaceae species, pollination in *Mormodes* in our study appears to depend on a highly specialized interaction with euglossine bees, a strategy that may enhance pollination precision and reduce pollen loss, but also increase vulnerability to pollinator decline (Tremblay, 1992; Schiestl and Johnson, 2013; Gutiérrez-Rodríguez and Hernández-Rivera, 2022).

We observed a bee carrying a pollinarium from an L-morph flower while clinging to a different *Mormodes maculata* variety. The lateral positioning of the pollinarium indicates that this species can be an effective pollinator of this species (Domingos-Melo et al., 2025). This finding supports *Euglossa obrima* as the primary pollinator of *Mormodes maculata*, while *Eulaema polychroma* appears to act as a secondary floral visitor restricted to *M. maculata* var. *maculata*.

In these systems, the presence of pollinia attached to a bee is generally considered strong evidence of effective pollination (Dressler, 1967; Ramírez et al., 2011; Ackerman and Roubik, 2012), as the proportion of bees carrying pollinia is naturally low and direct observations of pollination events are exceedingly rare (Romero, 1986; Roubik and Hanson, 2004; Brandt et al., 2020). Nevertheless, definitive evidence of effective pollination would require observing the bee depositing the pollinia during a floral visit.

In highly specialized systems such as those of *Mormodes*, successful transfer of pollinarium depends on extremely precise morphological and behavioral matching; therefore, small variations in body size, contact position, or foraging behavior may generate a mismatch between the flower and its visitor (Schiestl and Schlüter, 2009; More et al., 2012).

The pollinarium observed on the bee were associated with flowers exhibiting the L-morph (Fig. 4). The specific positioning of reproductive structures and the temporal separation of the male and female phases in plants play a critical role in the pollination success of *Mormodes* species (Schiestl and Johnson, 2013; Domingos-Melo et al., 2025). It has been proposed that flowers with a column bent to the right deposit their pollinarium on the opposite (left) side of the bee's thorax, and vice versa (Roubik and Hanson, 2004). This lateral displacement results from the column twisting, which reorients the pollinia and stigma away from the floral midline, creating mirror-image morphs. During fragrance collection, the visiting bee is guided into a fixed position, and the sensitive trigger mechanism ejects the pollinarium, attaching it precisely to one side of the thorax. After removal, the pollinarium undergoes a reconfiguration in which the stipe bends, positioning the pollinia for effective contact upon subsequent visits. Because each floral morph places and receives pollinia on opposite sides of the pollinator's body, self-pollination and geitonogamy are effectively minimized, as successful pollen transfer requires interaction between complementary morphs (Domingos-Melo et al., 2025).

While the latter authors provided the first morphometric evidence and time-lapse documentation of these movements in *Mormodes*, our study provides, to our best knowledge, the first observation of the lateralized deposition of pollinarium into the thorax of a male orchid bee visiting flowers of *Mormodes* in its native distribution area. It is noteworthy to mention, however, that this lateralized attachment of the pollinarium has been observed in a single bee individual, meaning that future studies are needed to confirm handedness in *Mormodes*. More specifically, it remains necessary to observe that bees bearing L-morph will deposit pollinia on the stigma of R-morph flowers and vice versa.

Both varieties of *Mormodes maculata* emit strong floral scents that attract large numbers of *Euglossa obrima* individuals (Fig. 3A). The exclusive visitation of *Eulaema polychroma* to *M. maculata* var. *maculata* may indicate subtle differences in floral scent composition. Although Salazar-Chávez (1999) found no consistent differences between varieties, the reported inter-individual variation suggests that floral chemistry may be more variable than previously recognized. Further chemical and pollinator

surveys are needed to determine whether such variation contributes to pollinator-mediated reproductive isolation (Hills et al., 1972; Hetherington-Rauth and Ramírez, 2016; Milet-Pinheiro and Gerlach, 2017).

Furthermore, from a conservation perspective, detailed documentation and an evaluation of the current status of the pollinators is crucial (e.g., Dalsgaard et al., 2013; Schiestl and Johnson, 2013; Castro and Singer, 2019). Highly specialized systems may be particularly sensitive to anthropogenic disturbances or changes in pollinator abundance, potentially compromising the viability of dependent plant populations (Štípková et al., 2020).

In this sense, recording pollinators' and visitors' identities not only provides information on immediate reproductive biology but also enables the integration of these interactions into broader ecological networks and the assessment of their resilience under scenarios of environmental change.

Author contributions

Conceptualization: AHR, BGR, JSR, PMP; Methodology: AHR, PMP; Investigation: AHR; Data curation: AHR, JSR; Formal analysis: AHR, PMP; Writing – original draft: AHR; Writing – review & editing: AHR, PMP, BGR, JSR.

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Data availability statement

The dataset supporting the findings of this study has been deposited in SciELO Data and is available at: https://doi.org/10.48331/SCIELODATA.CPA9XG

Declaration of use of Artificial Intelligence

We declare that we have not used artificial intelligence tools during the development of this study.

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