

FLORAL VISITORS OF THREE SPECIES OF *CORALLORHIZA* IN MONTE TLÁLOC, TEXCOCO, ESTADO DE MÉXICO, MEXICO

BRUNO E. TÉLLEZ-BAÑOS¹, IVONNE N. GOMEZ-ESCAMILLA^{2,4},
ALEJANDRO NAVARRETE-JIMÉNEZ³, ADOLFO ESPEJO-SERNA² & ANA R. LÓPEZ-FERRARI²

¹Centro de Investigaciones Tropicales, Universidad Veracruzana, Xalapa, Veracruz, C. P. 91000, México

²Herbario Metropolitano, Departamento de Biología, C. B. S., Universidad Autónoma Metropolitana Iztapalapa, Apartado Postal 55-535, México, Ciudad de México, C. P. 09310, México

³Preservación de la biodiversidad A. C., San Francisco No. 14, San Francisco Tlaltenco, Tláhuac, Ciudad de México C. P. 13400, México

⁴Author for correspondence: epifitas25@gmail.com

ABSTRACT. *Corallorhiza* is a genus of mycoheterotrophic orchids that includes 12 species, most of them restricted to North and Central America. In Mexico, there are seven taxa, distributed throughout the country, except for seven of the 32 Mexican states; in Estado de México all of them are present. The Orchidaceae is known for its diversity of pollination syndromes; however, for the more than 200 species of mycoheterotrophic orchids, little has been studied about their floral visitors and pollinators, and for the Mexican species of *Corallorhiza* nothing is known to date. Our goal was to document photographically and identify all the floral visitors of three sympatric species of the genus in Monte Tláloc, municipality of Texcoco, Estado de México. We observed individuals of Araneae, Coleoptera, Diptera, Hemiptera, and Hymenoptera visiting flowers of *Corallorhiza macrantha*, *C. macrantha* × *C. maculata*, *C. maculata*, and *C. striata*. Only *Ocyptamus coeruleus* and *Platycheirus* sp. (Diptera: Syrphidae) were found carrying pollinaria on their thorax. These are the first records of potential pollinators for the genus *Corallorhiza* in Mexico.

RESUMEN. *Corallorhiza* es un género de orquídeas micoheterótrofas que comprende 12 especies, la mayoría de ellas restringidas a Norte América y Centroamérica. En México habitan siete de ellas que se distribuyen en todo el país, excepto en siete de los 32 estados; en el Estado de México están todas presentes. Orchidaceae es conocida por su diversidad en síndromes de polinización; sin embargo, para las más de 200 especies de orquídeas micoheterótrofas poco se ha estudiado sobre sus visitantes florales y polinizadores, y para el caso de las especies de *Corallorhiza* mexicanas nada se conoce. Nuestro objetivo fue documentar fotográficamente e identificar a todos los visitantes florales de tres especies simpátricas del género en el Monte Tláloc, municipio de Texcoco, Estado de México. Observamos individuos de Araneae, Coleoptera, Diptera, Hemiptera e Hymenoptera en las flores de *Corallorhiza macrantha*, *C. macrantha* × *C. maculata*, *C. maculata* y *C. striata*. Únicamente *Ocyptamus coeruleus* y *Platycheirus* sp. (Diptera: Syrphidae) fueron encontrados transportando polinias en el tórax. Éstos son los primeros registros de polinizadores potenciales para el género *Corallorhiza* en México.

KEYWORDS / PALABRAS CLAVE: flower visitors, hoverflies, mycoheterotrophic plants, plantas micoheterótrofas, orquídeas terrestres, sírfidos, Syrphidae, terrestrial orchids, visitantes florales.

Introduction. The genus *Corallorhiza* Gagnebin (gr. κοράλλι, coral; ρίζα, root, referring to rhizomes that resemble coral structures) belongs to the subtribe Calypsoinae of the subfamily Epidendroideae (Chase *et al.* 2015). It is a genus of terrestrial orchids comprising 12 species (Freudenstein & Barret 2014, Pridgeon *et al.* 2005) restricted to North and Central America, except for *C. trifida* Châtel. (Freudenstein 1997, 1999,

Magrath & Freudenstein 2002), which is circumboreal, and the recently described *C. sinensis* G.W.Hu & Q.F.Wang (Yang *et al.* 2021), an endemic taxon of China. Seven species are present in Mexico (Soto-Arenas *et al.* 2007), three of them with four infraspecies (Solano Gómez *et al.* 2020); all of them present in the Estado de México (Martínez de la Cruz *et al.* 2018, Szeszko 2011); five are Mexican endemics and *C. bul-*

ORCID of the Author: BETB , INGE , ANJ , AES , ARLF 

Received 18 August 2023; accepted for publication 19 October 2023. First published online: 21 November 2023.

Licensed under a Creative Commons Attribution-NonCommercial-No Derivs 3.0 Costa Rica License.

bosa A. Rich. & Galeotti is restricted to Megaméxico 2 *sensu* Rzedowski (1991) (Espejo Serna 2012). *Corallorhiza* lack leaves and are mycoheterotrophic (Shefferson *et al.* 2010).

It is well known Orchidaceae has a very diverse array of pollination syndromes, the most common involves bees (melitophilia) and flies (myophilia) (Ackerman *et al.* 2023, Nidup *et al.* 2023, van der Cingel 2001); it is estimated that 15–30% of the whole family is pollinated by flies (Ackerman *et al.* 2023, van der Pijl & Dodson 1966). Nevertheless, for most orchid species pollinators are still unknown, especially for the more than 200 species of mycoheterotrophic orchids (Merckx *et al.* 2013), the only available studies are from Asia (Suetsugu 2013, Sugiura 1996, 2016, Zhou *et al.* 2012), Europe (Claessens & Kleynen 2014, 2018), and Oceania (Lehnebach *et al.* 2005). Pollinators for just three species of *Corallorhiza* have been identified (Claessens & Kleynen 2018, Freudenstein 1997, Kipping 1971).

Dressler (1981) suggested that Syrphidae flies pollinate *Corallorhiza* species, although the taxonomic identity of these visitors is known only for *C. trifida* (Kipping 1971); additionally, there are reports of self-pollination in some members of the genus. There exist few published data on floral visitors and pollinators for *C. maculata* (Raf.) Raf. var. *mexicana* (Lindl.) Freudenst., *C. striata* Lindl. var. *striata*, *C. odontorhiza* (Willd.) Poir. var. *odontorhiza*, *C. odontorhiza* var. *pringlei* (Greenm.) Freudenst., *C. bentleyi* Freudenst., and *C. trifida* (Argue 2012, Claessens & Kleynen 2018, Freudenstein 1997).

In Mexico, the genus *Corallorhiza* has been little studied, even on the reproductive biology of its species, so as a first approach to this subject, the purpose of this study was to document photographically and identify at the best possible taxonomic rank all the arthropods that rest or perch on *Corallorhiza* flowers for three species present in Monte Tlálloc, Estado de México.

Material and methods. The study area is located on the west slopes of Monte Tlálloc, municipality of Texcoco, Estado de México, it is part of the Trans-Mexican Volcanic Belt and the Sierra Nevada (Priority Terrestrial Region) (Arriaga *et al.* 2000) (Fig. 1). The three *Corallorhiza* species habitat are coniferous

forests of *Abies religiosa* (Kunth) Schltdl. & Cham., known locally as bosque de oyamel (Fig. 2). This vegetation type is present in ravines and lower slopes of mountains, between 3100 and 3500 m of elevation, with steep slopes greater than 40% (Sánchez-González & López-Mata 2003). The climate is humid-temperate, with an annual precipitation of 900 to 1000 mm, and an average annual temperature of 10 to 12°C (Ortiz Solorio & Cuanalo de la Cerda 1977). The type of soil is dark, deep, rich in organic matter, with medium texture (crumbs or loam), and pH values from 5.5 to 7.1 (Sánchez-González & López-Mata 2003).

A bibliographic revision of all literature regarding the genus *Corallorhiza* was undertaken (Freudenstein 1999, Lukasiewicz 1999). In addition, various digital repositories and databases were consulted to find the most complete background information on *Corallorhiza*'s floral visitors. Moreover, to compare and identify the studied species [*in situ*], herbarium specimens of the genus were consulted and studied at the herbaria: CHAPA, MEXU, and UAMIZ (herbarium acronyms according to Index Herbariorum, Thiers continuously updated). The vouchers of this work are housed at UAMIZ. In the study area, *Corallorhiza* species are sympatric and in co-flowering, the plants generally are grouped in patches of up to eight individuals per species. To document the flower visitors, random walks were made between patches, when a visitor was detected, the observer approached with camera in hand to record the event. Observations were made from 8:00 am to 5:00 pm. during May 2018, 2019, and 2023. The photographs were taken with three digital cameras (Nikon model D800, Canon models Rebel T3 and SX50 HS), equipped with a macrophotography lens (Tokina atx-i 100mm, f/2.8 AF) and flashes with light diffusers. The species names for the insects were determined using identification guides (Triplehorn & Johnson 2005, Vockeroth & Thompson 1987).

To evaluate whether the species studied offer nectar as a reward, extractions were carried out on twelve flowers (three flowers per species, including the hybrid) using microcapillary tubes of 1 µl; for each sample the sugar concentration (°Brix) was recorded using a field refractometer (Mod. HRT32, range: 0–32% Brix, precision: 0.2%; A. Krüss Optronic, Germany). Extractions were carried out between 10 and 11 am.

Results

Literature and herbaria review.— Two species of *Corallorhiza* were previously reported from the studied area: *C. macrantha* Schltr. and *C. striata* var. *involuta* (Greenm.) Freudenst. (Sánchez-González *et al.* 2006), and we observed two more taxa: *C. maculata* var. *mexicana* (Lindl.) Freudenst. [I. N. Gomez-Escamilla & B. E. Tellez-Baños 222 (UAMIZ 85400)], and the hybrid *C. macrantha* × *C. maculata* [I. N. Gomez-Escamilla & B. E. Tellez-Baños 220 (UAMIZ 85398, UAMIZ 85397)] (Fig. 3), all growing sympatrically in the ravines *Abies* forest in Monte Tláloc.

All species of *Corallorhiza* grow on a moss substrate with abundant litter; their flowering period begins in late April ending in early June, while the fruiting season from July to December. The populations of *C. macrantha* were registered and collected for the first time in 1976, according with the specimens data [E. García Moya *s. n.* (CHAPA), Stephen D. Koch 76104 (CHAPA, MEXU)] and 45 years later, populations are still present in the area. The first specimen of *C. striata* var. *involuta* was collected in 1978 [José García P. 636 (MEXU), 637 (CHAPA, MEXU)].

Floral visitors.— Individuals belonging to five orders, eight families, four genera, and two species of insects were observed (Table 1, Fig. 4, 5, 6). The hybrid *C. macrantha* × *C. maculata* was visited by seven different insects, *C. maculata* var. *mexicana* by five, *C. macrantha* by three and *C. striata* var. *involuta* only by one. The total duration of observations for all species was 54 hours.

Nectar extractions.— For *Corallorhiza macrantha* a nectar volume of 0.8 µl, with a sugar concentration of 15°Brix was recorded while for *C. maculata* and the hybrid a volume of 0.6 and 0.4 µl respectively were obtained, which were insufficient to measure their sugar concentration. For *C. striata* no nectar was obtained.

Potential pollinators.— Two species of syrphids were recorded transporting and depositing pollinia: *Ocyptamus coeruleus* (Williston 1891) on flowers of *Corallorhiza macrantha*, *C. maculata* and *C. macrantha* × *C. maculata*, and *Platycheirus* (Lepelletier & Serville 1828) on flowers of *C. macrantha* and *C. macrantha* × *C. maculata* (Table 1, Fig. 6). In addition, these insects made the highest number of visits (46) to the flowers

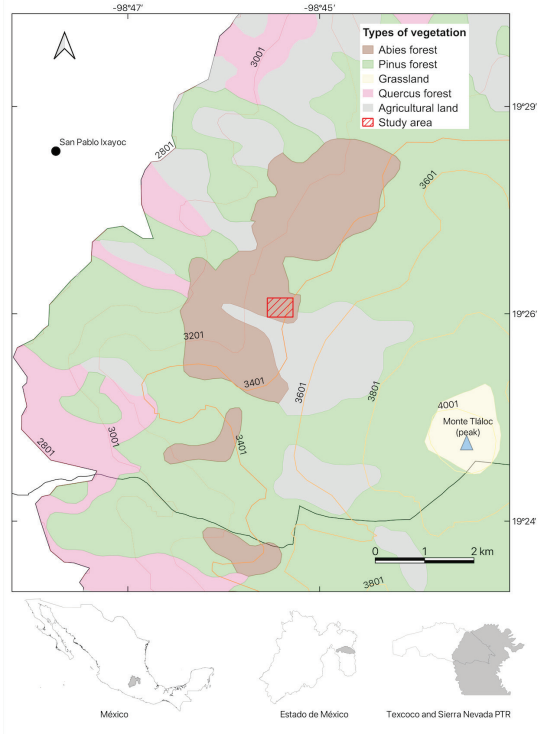


FIGURE 1. Study area, indicating vegetation types and territorial lines. Map by I. N. Gomez-Escamilla.

(Table 1); most of them were recorded between 11:00 and 14:00 hrs.

The insects usually visit more than one flower of the same inflorescence and more than one individual in a floral patch. They fly in front of the flower for 2–8 seconds before landing on the labellum apex which is tilted downwards due to the weight of the insect, once it moves towards the base of the labellum in search of nectar guided by the purplish spots and lines, the labellum returns to its original position, pushing the syrphids against the column. With this mechanism, the thorax of the insect is positioned below the viscidium so that when the syrphid finishes drinking the nectar and move back to leave the flower, it makes contact with the viscidium and the pollinarium adheres, on some occasions with the anther, to the dorsal thorax (scutum) of the syrphid. Subsequently, when the insect visits another receptive flower, the pollinia carried on its thorax touch the stigmatic surface and adhere to it along with the insect's body, so to free itself, the syrphid must struggle by holding and pushing the labellum with its legs, taking to 20 seconds to do so (Fig. 7).



FIGURE 2. *Corallorhiza* species growing sympatrically in the *Abies* forest in Monte Tláloc A. *C. macrantha* × *C. maculata*. B. *C. maculata*. C. *C. striata*. Photographs by B. Téllez-Baños.

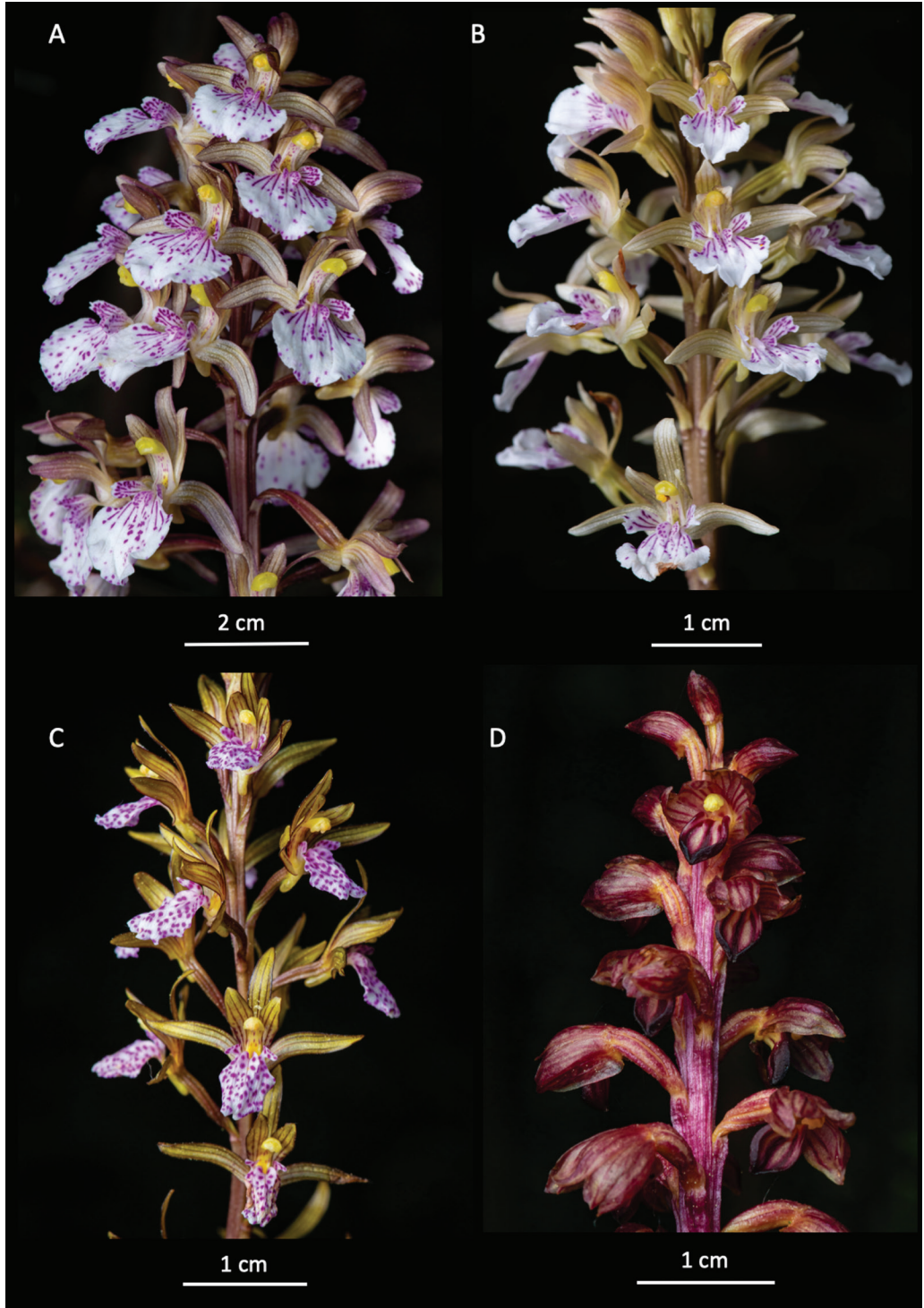


FIGURE 3. Flowers of **A.** *Corallorhiza macrantha*. **B.** *C. macrantha* × *C. maculata*. **C.** *C. maculata*. **D.** *C. striata*. Photographs by B. Téllez-Baños. Scale bars are indicated.

TABLE 1. Comparative data of the species of *Corallorhiza* and their floral visitors in the study area.

Species	Floral visitors				Number of visits	Carried pollinia
	Order	Family	Genus	Species		
<i>Corallorhiza macrantha</i> × <i>Corallorhiza maculata</i>	Coleoptera	Cantharidae			1	No
		Curculionidae			4	No
	Hemiptera	Miridae			1	No
	Hymenoptera	Apidae	<i>Bombus</i>	<i>huntii</i>	8	No
	Diptera	Syrphidae	<i>Ocyptamus</i>	<i>coeruleus</i>	7	No
			<i>Platycheirus</i>	sp.	9	Yes
	Tachinidae			4	No	
<i>Corallorhiza maculata</i> var. <i>mexicana</i>	Araneae	Theridiidae	<i>Theridion</i>	sp.	1	No
	Hemiptera	Cicadellidae			2	No
	Diptera	Syrphidae	<i>Ocyptamus</i>	<i>coeruleus</i>	15	Yes
			<i>Platycheirus</i>	sp.	4	No
	Tachinidae			3	No	
<i>Corallorhiza macrantha</i>	Diptera	Syrphidae	<i>Ocyptamus</i>	<i>coeruleus</i>	4	No
			<i>Platycheirus</i>	sp.	7	Yes
		Tachinidae			5	No
<i>Corallorhiza striata</i> var. <i>involuta</i>	Coleoptera	Cantharidae			1	No

Discussion. Suggested pollinators for the Calypsoinae subtribe are bumblebees, hover flies, empididae flies, mosquitoes, and bees (Valencia-Nieto *et al.* 2018). However, in this tribe the only genera with mycoheterotrophic members are *Cremastra* Lindl., *Corallorhiza* and *Yoania* Maxim. The information about their floral visitors and pollinators is very scarce (Claessens & Kleynen 2018, Freudenstein 1997, Kipping 1971, Sugiura 1996).

Bumblebees, unlike other insects, require a surface area to allow them to roost before starting to suck nectar from a flower, it has been reported that they pollinate flowers with large petals and lips (Blionis & Vokou 2001, Ortega-Olivencia *et al.* 2012). We found *Bombus huntii* (Greene 1860), as the floral visitor of

Corallorhiza macrantha × *C. maculata*, a hybrid that has a large lip enough to support the landing of this insect, however the insect cannot fully access the flower due to its stout body, so by staying away from reproductive structures it is unlikely to remove or deposit a pollinia, limiting its pollinating role.

The syrphids were the only insects that made legitimate visits to the flowers of *Corallorhiza* (in terms of transporting and depositing pollinias), and they also made the highest number of visits. Therefore, we agree with Dressler (1981), that syrphids are the most likely pollinators of these orchids, in addition they may also be responsible for their hybridization. The evidence presented here, strongly suggest that *Corallorhiza* might be a group with a myophylic pollination syn-



FIGURE 4. **A.** *Bombus huntii* (Apidae, Hymenoptera). **B.** Hymenoptera. **C.** Cantharidae (Coleoptera). **D.** Curculionidae (Coleoptera). **E.** Miridae (Hemiptera), visiting *Corallorhiza macrantha* × *C. maculata*. **F.** Cicadellidae (Hemiptera) visiting *C. maculata*. Photographs by B. Téllez-Baños.

drome. Previous works have documented the visit of a syrphid species in *C. trifida* (Claessens & Kleynen 2018), and for *C. maculata* var. *maculata*, the pollinators were identified as members of the genus *Empis* L. (Linnaeus 1758) (Diptera) (Kipping 1971). In other genera of mycoheterotrophic orchids such as *Epipogium aphyllum* Sw. (Jakubská-Busse *et al.* 2014) and *Cremastra appendiculata* (D. Don) Makino var. *variabilis* (Blume) I.D.Lund (Sugiura 1996) syrphids are also floral visitors.

The Hymenopteran *Pimpla pedalis* Cresson (1865) has been identified as a pollinator (Freudenstein 1997) of *C. striata* var. *striata*, while Freudenstein (1999) suggest the existence of autogamy for *Corallorhiza striata* var. *involuta*, hence we think that it is necessary to make more detailed observations in the populations of the orchid species to detect the presence of its pollinators. We would like to highlight the importance of the use of photography in this type of studies (Suetsugu & Hayamizu 2014, Suetsugu *et al.* 2017), since

it allows the registration and taxonomic identification of the floral visitors, as well as the observation of the pollinia on their bodies.

Corallorhiza includes a group of orchids very vulnerable to environmental alterations to its habitat. The species require soils rich in organic matter and places with high humidity; therefore, it is important to preserve sites with the right conditions for the species thrive, including its dependency on its ectomycorrhizal fungi (Lee Taylor & Bruns 1999, Barrett *et al.* 2020). Currently, *C. macrantha* is cataloged as subject to special protection (Pr) in accordance with the NOM-059-SEMARNAT-2010 (SEMARNAT 2019). It is a species is an orchid that cannot be cultivated, therefore *in situ* conservation is the only viable strategy to preserving it safely (Soto-Arenas & Solano-Gómez 2007).

Future studies should include more pollination observations and experimental manipulation of breeding systems, especially since 71 % of mycoheterotrophic orchids are likely autogamous (Ackerman *et al.* 2023);



FIGURE 5. **A.** *Platycheirus* sp. visiting *Corallorhiza macrantha* × *C. maculata* **B.** *Ocyptamus coeruleus* (Syrphidae, Diptera) visiting and transporting pollinia from *C. macrantha* **C.** *Platycheirus* sp. visiting *C. macrantha* × *C. maculata* **D.** *Ocyptamus coeruleus* (Syrphidae, Diptera) visiting and transporting pollinia from *C. maculata* **E.** Tachinidae (Diptera), visiting *C. macrantha* × *C. maculata*. **F.** *Theridion* (Araneae: Theridiidae) visiting *C. maculata*. Photographs by B. Téllez-Baños.

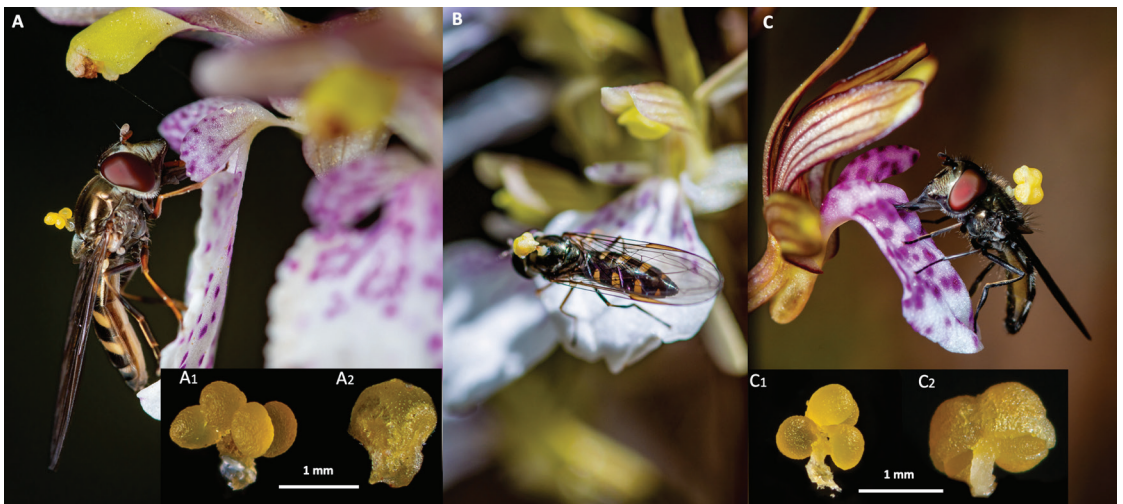


FIGURE 6. **A.** *Platycheirus* sp. visiting *Corallorhiza macrantha* **A1.** Pollinia of *C. macrantha* **A2.** Anther of *C. macrantha* **B.** *Platycheirus* sp. visiting *C. macrantha* × *C. maculata* **C.** *Ocyptamus coeruleus* visiting *C. maculata* **C1.** Pollinia of *C. maculata* **C2.** Pollinia with anther of *C. maculata*. Photographs by B. Téllez-Baños. Scale bars are indicated.



FIGURE 7. Photographic sequence showing the mechanism of pollinia deposition by *Ocyptamus coeruleus* (Williston 1891) in *Corallorhiza macrantha* flower. **A.** Syrphid landing on the labellum with pollinia attached to its thorax. **B.** Entering the flower in search of nectar. **C.** Contact of the pollinaria with the stigma. **D.** The pollinaria along with thorax of the insect remain attached to the stigma. **E–F.** The insect struggles, holding the labellum and forcing it backwards with its legs to free itself from the pollinaria. Photographs by B. Téllez-Baños.

furthermore, of ca. 200 mycoheterotrophic species, only for 38 (17.67%) have studies been carried out regarding floral biology and/or floral visitors. It is important therefore to carry out studies in other mycoheterotrophic orchids to better understand the evolution of pollination strategies in this group of orchids that grow in temperate, temperate-tropical, and temperate subtropical areas.

ACKNOWLEDGEMENTS. We thank to Diego Alexis Prado-Ángeles and Rodrigo Pereyda-Téllez for their support during the field work. Also to the authorities of Monte Tláloc for the permission to carry out this investigation and to the curators of the herbaria CHAPA and MEXU for facilitating the access and the study of the herbarium specimens. Last but not least to the anonymous reviewers for their suggestions and comments to improve this study and to Lourdes Rico for the careful review of the English.

LITERATURE CITED

- Ackerman, J. D., Phillips, R. D., Tremblay, R. L., Karremans, A., Reiter, N., Peter, C. I., Bogarín, D., Pérez-Escobar, O. & Liu, H. (2023). Beyond the various contrivances by which orchids are pollinated: global patterns in orchid pollination biology. *Botanical Journal of the Linnean Society*, boac082. <https://doi.org/10.1093/botlinnean/boac082>
- Argue, C. L. (2012). *The Pollination Biology of North American Orchids: volume 2 North of Florida and Mexico*. Springer. 207 pp. <https://link.springer.com/book/10.1007/978-1-4614-0622-8>
- Arriaga, L., Espinoza, J. M., Aguilar, C., Martínez, E., Gómez, L. & Loa, E. (2000). *Regiones terrestres prioritarias de México*. México, D. F. Comisión Nacional para el Conocimiento y uso de la Biodiversidad. <http://www.conabio.gob.mx/conocimiento/regionalizacion/doctos/terrestres.html>

- Barrett C. F., Freudenstein, J. V., Lee Taylor, D. & Kõljalg, U. (2010). Rangewide analysis of fungal associations in the fully mycoheterotrophic *Corallorhiza striata* complex (Orchidaceae) reveals extreme specificity on ectomycorrhizal *Tomentella* (Thelephoraceae) across North America. *American Journal of Botany*, 97(4), 628–643. <https://doi.org/10.3732/ajb.0900230>
- Blionis, G. J. & Vokou, D. (2001). Pollination ecology of *Campanula* species on Mt. Olympos, Greece. *Ecography*, 24, 287–297. <https://doi.org/10.1034/j.1600-0587.2001.240306.x>
- Chase, M. W., Cameron, K. M., Freudenstein, J. V., Pridgeon, A. M., Salazar, G., Van den Berg, C. & Schuiteman, A. (2015). An updated classification of Orchidaceae. *Botanical journal of the Linnean Society*, 177(2), 151–174. <https://doi.org/10.1111/boj.12234>
- Claessens, J. & Kleynen, J. (2014). The pollination of European Orchids Part 3: *Limodorum* and *Epipactis*. *Journal of the Hardy Orchid Society*, 11(2), 64–72.
- Claessens, J. & Kleynen, J. (2018). The pollination of European Orchids Part 7: Autogamy: *Neotinea maculata* and *Corallorhiza trifida*. *Journal of the Hardy Orchid Society*, 15(2), 50–55.
- Cresson, E. T. (1865). Catalogue of Hymenoptera in the collection of the Entomological Society of Philadelphia, from Colorado Territory. *Proceedings of the Entomological Society of Philadelphia*, 4, 242–426.
- Dressler, R. L. (1981). *The orchids. Natural history and classification*. England: Harvard University Press. 332 pp.
- Espejo Serna, A. (2012). El endemismo en las liliopsida mexicanas. *Acta Botanica Mexicana*, 100, 195–257. <http://doi.org/10.21829/abm100.2012.36>
- Freudenstein, J. V. (1997). A monograph of *Corallorhiza* (Orchidaceae). *Harvard Papers in Botany*, 10, 5–51. <https://www.jstor.org/stable/41761525>
- Freudenstein, J. V. (1999). A new species of *Corallorhiza* (Orchidaceae) from West Virginia, U.S.A. *Novon*, 9, 511–513. <https://doi.org/10.2307/3392151>
- Freudenstein, J. V. & Barrett, C. F. (2014). Fungal host utilization helps circumscribe leafless Coralroot orchid species: An integrative analysis of *Corallorhiza odontorhiza* and *C. wisteriana*. *Taxon*, 63, 759–772. <https://doi.org/10.12705/634.3>
- Greene, J. W. (1860). Review of the American Bombidæ, together with a Description of Several Species Heretofore Undescribed, Being a Synopsis of the Species of this Family of Hymenopterous Insects Thus Far Known to Inhabit North America. *Annals of The Lyceum of Natural History of New York*, 7, 1, 168–176. https://digitalcommons.usu.edu/bee_lab_gr/46
- Jakubská-Busse, A., Jasicka-Misiak, I., Poliwoła, A., Swieczkowska, E. & Kafarski, P. (2014) The chemical composition of the floral extract of *Epipogium aphyllum* Sw. (Orchidaceae): a clue for their pollination biology. *Archives Biological Science Belgrade*, 66(3), 989–998. <https://doi.org/10.2298/ABS1403989B>
- Kipping, J. L. (1971). *Pollination studies of native orchids*. M. S. Thesis, San Francisco State College, San Francisco, CA.
- Lee Taylor, D. & Bruns, T. D. (1999). Population, habitat and genetic correlates of mycorrhizal specialization in the ‘cheating’ orchids *Corallorhiza maculata* and *C. mertensiana*. *Molecular Ecology*, 8(10), 1719–1732. <https://doi.org/10.1046/j.1365-294x.1999.00760.x>
- Lehnebach, C., Robertson, A. W. & Hedderley, D. (2005). Pollination studies of four New Zealand terrestrial orchids and the implication for their conservation. *New Zealand Journal of Botany*, 43, 467–477. <https://doi.org/10.1080/0028825X.2005.9512968>
- Lepeletier, A. L. M. & Serville, J. G. A. (1828). In: Latreille, P. A., Lepeletier, A. L. M., Serville, J. G. A. & Guérin-Meneville, F. E. (Eds.), *Entomologie, ou histoire naturelle des Crustacés, des Arachnides et des insectes. Encyclopédie Méthodique, Histoire Naturelle. Insectes*, 10, 2, 1–833.
- Linnaeus, C. (1758). *Systema naturae*. Tomus I. 10 Ed. 823 pp.
- Lukasiewicz, M. J. (1999). *Maternal investment, pollination efficiency and pollen: Ovule ratios in Alberta orchids (Unpublished master's thesis)*. University of Calgary, Calgary, AB. <https://doi.org/10.11575/PRISM/14430>
- Magrath, L. K. & Freudenstein, J. V. (2002). *Corallorhiza*. In: Editorial Committee (ed.), *Flora of North America North of Mexico* (pp. 633–638). Oxford: Oxford University Press.
- Martínez de la Cruz, I., Villaseñor, J. L., Aguilera-Gómez, L. I. & Arriaga, M. R. (2018). Angiospermas nativas documentadas en la literatura para el Estado de México, México. *Acta Botanica Mexicana*, 124, 135–217. <https://doi.org/10.21829/abm124.2018.1273>
- Merckx, V. S. F. T., Freudenstein, J. V., Kissling, J., Christenhusz, M. J. M., Stotler, R. E., Crandall-Stotler, B., Wickett, N., Rudall, P. J., Mass-van de Kamer, H. & Maas, P. J. M. (2013). Taxonomy and Classification. In: V. S. F. T. Merckx (ed.), *Mycoheterotrophy: The Biology of plants living on fungi*. (pp. 19–102). Springer. <https://link.springer.com/>

book/10.1007/978-1-4614-5209-6

- Nidup, T., Wangchuck, K., Tobgay, S., Wangchuk, T., Kalkman, V. J. & Gravendeel, B. (2023). Pollinators of Epiphytic and Terrestrial Orchid Species in Bhutan. *Sherub Doenme: The Research Journal of Sherubtse College*, 16. <https://doi.org/10.17102/sherubdoenme.16.2023.02>
- Ortega-Olivencia, A., Rodríguez-Riaño, T., Pérez-Bote, J. L., López, J., Mayo, C., Valtueña, F. J. & Navarro-Pérez, M. (2012). Insects, birds and lizards as pollinators of the largest-flowered *Scrophularia* of Europe and Macaronesia. *Annals of Botany*, 109, 153–167. <https://doi.org/10.1093/aob/mcr255>
- Ortiz Solorio, C. A. & Cuanalo de la Cerda, H. E. (1977). *Levantamiento fisiográfico del área de influencia de Chapingo: para la cartografía de tierras erosionadas*. Chapingo, Estado de México: Colegio de Postgraduados, Escuela Nacional de Agricultura. 83 pp.
- Pridgeon A. M., Cribb, P. J., Chase, M. W. & Rasmussen, F. N. (eds). 2005. *Genera Orchidacearum. Volume 4. Epidendroideae (Part 1)*. Oxford: Oxford University Press.
- Rzedowski, J. 1991. El endemismo en la flora fanerogámica mexicana: una apreciación analítica preliminar. *Acta Botanica Mexicana*, 15, 47–64. <https://doi.org/10.21829/abm15.1991.620>
- Sánchez-González, A. & López-Mata, L. (2003). Clasificación y ordenación de la vegetación del norte de la Sierra Nevada, a lo largo de un gradiente altitudinal. *Anales del Instituto de Biología, UNAM, Serie Botánica*, 74(1), 47–71.
- Sánchez-González, A., López-Mata, L. & Vibrans, H. (2006). Composición y patrones de distribución geográfica de la flora del bosque de oyamel del cerro Tláloc, México. *Boletín de la Sociedad Botánica de México*, 79, 67–78. <https://doi.org/10.17129/botsci.1734>
- SEMARNAT. (2019). *Modificación del Anexo Normativo III, lista de especies en riesgo de la Norma Oficial Mexicana. NOM-059-SEMARNAT-2010, Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión*. <https://dof.gob.mx/>
- Shefferson, R. P., Cowden, C. C., McCormick, M. K., Yukawa, T., Ogura-Tsujita, Y. & Hashimoto, T. (2010). Evolution of host breadth in broad interactions: mycorrhizal specificity in East Asian and North American rattlesnake plantains (*Goodyera* spp.) and their fungal hosts. *Molecular Ecology*, 19(14), 3008–3017. <https://doi.org/10.1111/j.1365-294X.2010.04693.x>
- Solano Gómez, R., Salazar Chávez, G. A., Jiménez Machorro, R., Hágsater G. E., & Cruz García, G. (2020). *Actualización del catálogo de autoridades taxonómicas de Orchidaceae de México*. Instituto Politécnico Nacional. Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional Unidad Oaxaca. Base de datos SNIB-CONABIO, Proyecto No. KT005. Ciudad de México.
- Soto-Arenas, M. A. & Solano-Gómez, A. R. (2007). Ficha técnica de *Corallorhiza macrantha*. En: Soto-Arenas, M. A. (comp.). *Información actualizada sobre las especies de orquídeas del PROY-NOM-059-ECOL-2000*. Instituto Chinoín A. C., Herbario de la Asociación Mexicana de Orquideología A. C. Bases de datos SNIB-CONABIO. Proyecto No. W029. México. D. F.
- Soto-Arenas, M. A., Hágsater, E., Jiménez Machorro, R., Salazar Chávez, G. A., Solano Gómez, E., Flores González, R. & Ruiz Contreras, I. (2007). *Las orquídeas de México. Catálogo Digital*. Interactive Multimedia CD, Win-Mac. Herbario AMO. Instituto Chinoín. México, D.F., México.
- Suetsugu, K. (2013). Autogamous fruit set in a mycoheterotrophic orchid *Cyrtosia septentrionalis*. *Plant Systematics and Evolution*, 299, 481–486. <https://link.springer.com/article/10.1007/s00606-012-0736-z>
- Suetsugu, K. & Hayamizu, M. (2014). Moth floral visitors of the three rewarding *Platanthera* orchids revealed by interval photography with a digital camera. *Journal of Natural History*, 48(17–18), 1103–1109. <https://doi.org/10.1080/00222933.2013.861940>
- Suetsugu, K., Nakahama, N., Ito, A. & Isagi, Y. (2017). Time-lapse photography reveals the occurrence of unexpected bee-pollination in *Calanthe izuinsularis*, an endangered orchid endemic to the Izu archipelago. *Journal of Natural History*, 51(13–14), 783–792. <https://doi.org/10.1080/00222933.2017.1293745>
- Sugiura, N. (1996). Pollination biology of *Cremastra appendiculata* var. *variabilis* (Orchidaceae). *Plant Species Biology*, 11, 185–187. <https://doi.org/10.1111/j.1442-1984.1996.tb00144.x>
- Sugiura, N. (2016). Floral morphology and pollination in *Gastrodia elata*, a mycoheterotrophic orchid. *Plant Species Biology*, 32(2), 173–178. <https://doi.org/10.1111/1442-1984.12137>
- Szeszko, D. R. 2011. *La orquídeoflora mexicana*. Toluca, México: Secretaría de Educación del Gobierno del Estado de México. 362 pp.
- Thiers, B. M. (continuously updated). *Index Herbariorum: A global Directory of Public Herbaria and Associated Staff*. <http://sweetgum.nybg.org/ih/>

- Triplehorn, C. A. & Johnson, N. F. (2005). *Borror and DeLong's Introduction to the Study of Insects* (7th ed.). Thomson, Books/Cole. Belmont, CA. 864 pp.
- Valencia-Nieto, B., Sosa, V. & Márquez-Guzmán, J. (2018). Anther development in tribe Epidendreae: orchids with contrasting pollination syndromes. *PeerJ*, 6, e4383. <https://doi.org/10.7717/peerj.4383>.
- van der Cingel, N. A. (2001). *An Atlas of Orchid Pollination: America, Africa, Asia and Australia*. Balkema Publishers, Rotterdam, Netherlands; Brookfield, VT. 296 pp.
- van der Pijl, L. & Dodson, C. H. (1966). *Orchid flowers: their pollination and evolution*. Fairchild Tropical Garden and the University of Miami Press. Coral Gables. FL. 213 pp.
- Vockeroth, J. R. & Thompson, F. C. (1987). Syrphidae. In: J. F. McAlpine, B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth & D. M. Wood (Eds.), *Manual of Nearctic Diptera* Vol. 2. (pp. 713–743). Ottawa: Canada Communication Group.
- Williston, S. W. (1891–1903). *Biologia Centrali Americana, Insecta – Diptera*, 3, 1–127.
- Yang, J.-X., Peng, S., Wang, J.-J., Ding, S.-X., Wang, Y., Tian, J., Yang, H., Hu, G.-W. & Wang, Q.-F. (2021). Morphological and Genomic Evidence for a New Species of *Corallorhiza* (Orchidaceae Epidendroideae) from SW China. *Plant Diversity*, 43, 409–419. <https://doi.org/10.1016/j.pld.2021.01.002>.
- Zhou, X., Lin, H., Fan, X.-L. & Gao, J.-Y. (2012). Autonomous self-pollination and insect visitation in a saprophytic orchid, *Epipogium roseum* (D. Don) Lindl. *Australian Journal of Botany*, 60, 154–159. <http://dx.doi.org/10.1071/BT11265>