

## FIRST RECORD OF A NATURAL HYBRID OF THE GENUS *GONGORA* (STANHOPEINAE) AND COMMENTS ON THE PARENT SPECIES

ALEXANDER JIMÉNEZ-VÁZQUEZ<sup>1,6</sup>, HERMES VEGA<sup>2</sup>, ALEXANDER ALVARADO<sup>3</sup> & EDGAR MÓ<sup>4,5</sup>

<sup>1</sup>Laboratorio de vida silvestre, Facultad de Biología, Universidad Veracruzana, Lomas del Estadio s/n, Xalapa, Veracruz, 91000, México.

<sup>2</sup>Mancomunidad de Municipios del Parque Nacional Montaña de Celaque, MAPANCE PRO-CELAQUE, Barrio Mercedes s/n, Gracias, Lempira, 42101, Honduras.

<sup>3</sup>Honduran Birds, Barrio Sendero La Cascada s/n, Santa Rita, Copán, 41211, Honduras.

<sup>4</sup>Orquigonía, Reserva Natural y Centro de Conservación de Orquídeas. Kilómetro 206, ruta las Verapaces, Cobán, Alta Verapaz, Guatemala.

<sup>5</sup>Universidad de San Carlos de Guatemala (USAC), Carrera de Agronomía, Centro Universitario del Norte (CUNOR), Cobán, Alta Verapaz, 16001, Guatemala.

<sup>6</sup>Author for correspondence: [aleko.jimenez11@gmail.com](mailto:aleko.jimenez11@gmail.com)

**ABSTRACT.** The first natural hybrid of the genus *Gongora* is described for the department of Copán, Honduras, between *Gongora truncata* and *Gongora batemanii* (= *Gongora cassidea*). The nothospecies described here presents intermediate characteristics between both species, such as setaceous projections on the lip, a large callus, spatulate epichile, and a cucullate hard dorsal sepal. The identity of a specimen from the Herbarium Jany Renz Botanical Institute, University of Basel, Switzerland, corresponds to the same hybrid described here. It was erroneously determined as *Gongora saccata* (= *Gongora seideliana*). The clarification of the synonymy of *Gongora saccata* and relevant aspects regarding the pollination mechanisms and reproductive barriers of both parent species are also discussed.

**RESUMEN.** Se describe el primer híbrido natural del género *Gongora*, entre *Gongora truncata* y *Gongora batemanii* (= *Gongora cassidea*). La notoespecie que aquí se describe presenta caracteres intermedios entre ambas especies, como las proyecciones setáceas en el labio, un callo grande, el epiquilo espatulado y el sépalo dorsal fuertemente cuculado. También se discute la identidad de un ejemplar del Herbarium Jany Renz Botanical Institute, University of Basel, Suiza, el cual corresponde al mismo híbrido aquí descrito. Fue erróneamente determinado como *Gongora saccata*, (= *Gongora seideliana*). Se discute también la sinonimia de *Gongora saccata*, y aspectos relevantes en cuanto a los mecanismos de polinización y barreras reproductivas de ambas especies parentales.

**KEYWORDS / PALABRAS CLAVE:** Copán, Cymbidieae, Euglossini, *Gongora cassidea*, *Gongora saccata*, Honduras, Orchidaceae

**Introduction.** Natural hybridization is a relatively common phenomenon, which has played an important role in plant evolution. Hybridization has been considered a great force in the speciation and diversity of angiosperm species (Grant 1981, Soltis & Soltis 2009). Within the Orchidaceae, the existence of natural hybrids is well known. They are capable of developing viable seeds through intra- and intergeneric crosses; this fact probably allows some gene exchange in nature to be added to the gene pool of the species (Pupulin 2007, Soltis & Soltis 2009). However, species

also maintain reproductive isolation through different prezygotic mechanisms, such as phenology, fragrances, pollinators and geographic distribution (Pupulin 2007, Faegri & Van Der Pijl 2013).

About 10% of Neotropical orchids are pollinated exclusively by orchid bees (Apidae: Euglossini; Ramírez 2019), whose males visit flowers and other sources in search of aromatic substances, which are used to attract females (Eltz *et al.* 1999). The reproductive isolation barriers used by these groups of orchids, in addition to those already mentioned, can be

ORCID of the Author: [AJV](#), [HV](#), [EM](#)

Received 29 October 2022; accepted for publication 2 February 2023. First published online: 27 February 2023.

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

mechanical in function. For example, the area of the bee's body where each orchid species positions its pollinia is different, as is the shape of the pollinaria, and how it interacts with the stigma of the flower, through the size, form and behavior of the bee (Dressler 1968). Furthermore, these groups of orchids also employ chemical reproductive barriers; that is, the fragrance used by orchid species of the same genus usually have different compositions when they are sympatric (Dressler 1968, van der Pijl & Dodson 1966).

The subtribe Stanhopeinae are one of these groups of orchids pollinated exclusively by euglossine bees (Dressler 1968, 1993, Williams & Whitten 1983); with *Stanhopea* Frost ex Hook and *Gongora* Ruiz & Pavón being the largest genera. Although they are prone to hybridize, natural hybrids in the Stanhopeinae are very rare in nature (Gerlach 2003), and the few that have been found so far belong to *Stanhopea* (Dressler 1968, 1993, Jenny 1993a). *Gongora* comprises around 60–70 species, distributed from southern Mexico to South America, along the slopes of the Andes, as well as in regions of Venezuela, the Guianas, and Brazil (Hetherington-Rauth & Ramírez 2016, Jenny 1993b). Taxonomically, the genus is subdivided into three subgenera based on lip morphology: *Portentosa* Jenny, *Acropera* (Pfitzer) Jenny (which is subdivided into two sections: *Acropera* and *Armeniaca*), and *Gongora* (Pfitzer) Jenny (which is subdivided into five sections: *Aceras*, *Gratulabunda*, *Gongora*, *Grossa*, and *Truncata*) (Chase *et al* 2009). Jenny (1993b) considers a third section within the subgen. *Acropera* (sect. *Cassidea*), however, in this study, the most recent classification is used.

The objective of this work is to report a hybrid specimen collected in nature in the department of Copán, Honduras, found by chance during fieldwork carried out by some of the authors (HV, AA, EM). The discovered plant presents intermediate characters between species of *Gongora* belonging to two different subgenera, and we hypothesize that the probable parental species are *G. truncata* Lindl. and *G. batemanii* (Lindl. ex Rchb.f.) Henshall ex Mabb. & Jenny, both of which are found in the area of discovery. We also seek to clarify the identity of another specimen that likely corresponds to the same hybrid described here, and comment on some relevant aspects of the ecology and pollination mechanisms of the parent species.

## Materials and methods.

**Study area.**— The discovery site is located north of the department of Copán, Honduras, a few kilometers from the archaeological reserve of the same name, at an elevation of 1650 m. The climate is classified as tropical rainy, with an average annual temperature of 26°C and an average annual rainfall of 1337 mm. Although, the vegetation is from the tropical humid forest, some parts of the discovery area are considered ecotones with pine forests, with large trees and abundant epiphytes, among which are: *Coelia densiflora* Rolfe, *Epidendrum cardiophorum* Schltr., *E. isthmi* Schltr., *E. laucheum* Rolfe, *E. repens* Cogn., *Gongora truncata*, *G. batemanii*, *Maxillaria densa* Lindl., *Pleurothallis pansamaliae* Schltr., *Prosthechea vitellina* (Lindl.) W.E.Higgins, *Scaphyglottis prolifera* (Sw.) Cogn., and *S. fasciculata* Hook. Among the most common tree species are: *Clethra occidentalis* (L.) Kuntze, *Liquidambar styraciflua* L., *Myrsine coriacea* (Sw.) R.Br., *Pinus maximinoi* H.E.Moore, and *Vochysia guatemalensis* Donn.Sm. The exact location of the plant is not revealed in the present paper to avoid illegal collection to which many orchids are subjected. However, exact details on the collecting locality can be found on the labels of the preserved specimen deposited at EAP.

## Results.

**Description of putative parental species.**— *Gongora truncata* Lindl. belongs to the section *Truncata* of the subgenus *Gongora* and is distributed throughout Mexico (Veracruz, Oaxaca and Chiapas), Belize, Guatemala and Honduras. It is recognized for its showy flowers, reflexed lateral sepals that appear rectangular in natural position, and decurrent, small petals. The white or yellow lip, welded to the foot of the column, is cymbiform and laterally compressed, fleshy and waxy in appearance, concave, complex, hypochile unguiculate, with a very small transverse callus, with an inconspicuous lobe near the base on each side, and with a sharp rib ending in a retrorse bristle on each side. The epichile is oblong-ovate with a recurved apex (Salazar in Hågsater & Salazar 1990). Phenology: January to June (Beutelspacher 2014) (Fig. 1 A).

*Gongora batemanii* (Lindl. ex Rchb.f.) Henshall ex Mabb. & Jenny (synonym: *Gongora cassidea* Rchb.f.) belongs to the section *Acropera* of the sub-

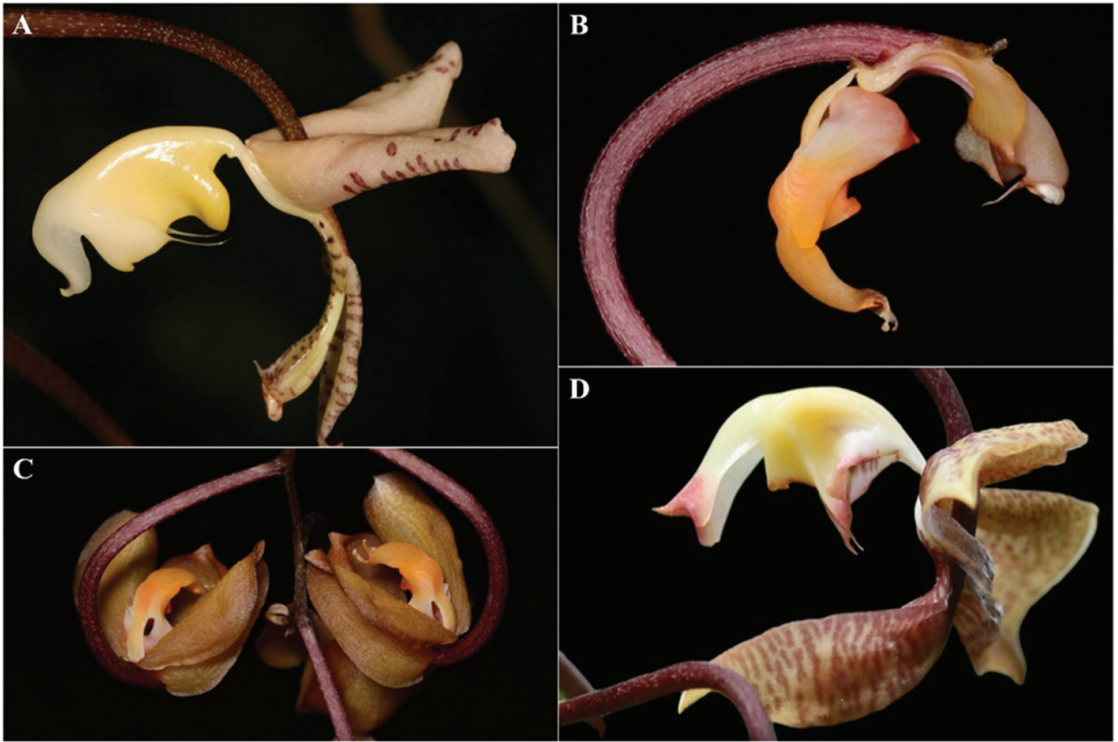


FIGURE 1. **A.** *Gongora truncata*. **B.** *G. batemanii*, sepals removed. **C.** *G. batemanii* with the sepals in place. **D.** Detail of the flower of *Gongora* × *copanensis*. Photographs by Rudolf Jenny (A), José Monzón Sierra (B–C), and Alexander Alvarado (D).

genus *Acropera* and it is distributed in Mexico (Chiapas), Guatemala, Honduras, and Nicaragua (Ames & Correll 1985). It can be recognized by the arcuate pedicellate ovaries, the broadly elliptic and cucullate dorsal sepal, the oblong to suborbicular-elliptic, obtuse and oblique lateral sepals inserted perpendicularly to the sides of the column. The lip is complex, articulated to the column foot, arched with the callus at the apex; lower portion of lip saccate, thickened and compressed in front of the sac, with a pair of erect parallel lobes arising from the margins of the sac (Ames & Correll 1953). Phenology: February to July (Damon *et al.* 2012). (Fig. 1B–C).

***Gongora* × *copanensis*** Jiménez Axr, Vega, Alvarado & Mό., *nothosp. nov.* (Fig. 1D, 2, 3).

TYPE: Honduras. Santa Rita: Copán, tropical rain forest, May 15, 2019. UTM: 287236.24 m E, 1636948.11 m N, 1650 m above sea level, *A. Alvarado* #001 (holotype, EAP).

DIAGNOSIS: Epiphytic plant, pendulous inflorescence, complex flowers. Intermediate between *G. truncata* and *G. batemanii*. It differs from *G. truncata* by a large callus, the spatulate epichile, cucullate hard dorsal sepal, and the lateral sepals perpendicular to the column. It also differs from *G. batemanii* by the slightly arched flower pedicel, the absence of the lip articulation, and setaceous projections on the lip.

*Plant* herbaceous, epiphytic, bifoliate. *Pseudobulbs* conical, elongate, sulcate. *Leaves* apical, elliptic, acuminate, three-veined, attached to the pseudobulb by a pedicel. *Inflorescence* a pendulous raceme, 19 flowers. *Ovary* pedicellate, incurved, terete, colored dark violet. *Flowers* 2.7 × 4.6 cm long, showy, not resupinate, fragrant, basically brown, with small purple dots, yolk-yellow lip with violet tips. *Dorsal sepal* 1.9 cm long, fused to the base of the column, strongly cucullate, ovate-acuminate with slightly retrorse tip. *Lateral sepals* 1.4 cm long, rolled, perpendicular to the column, obovate. *Petals* very small,

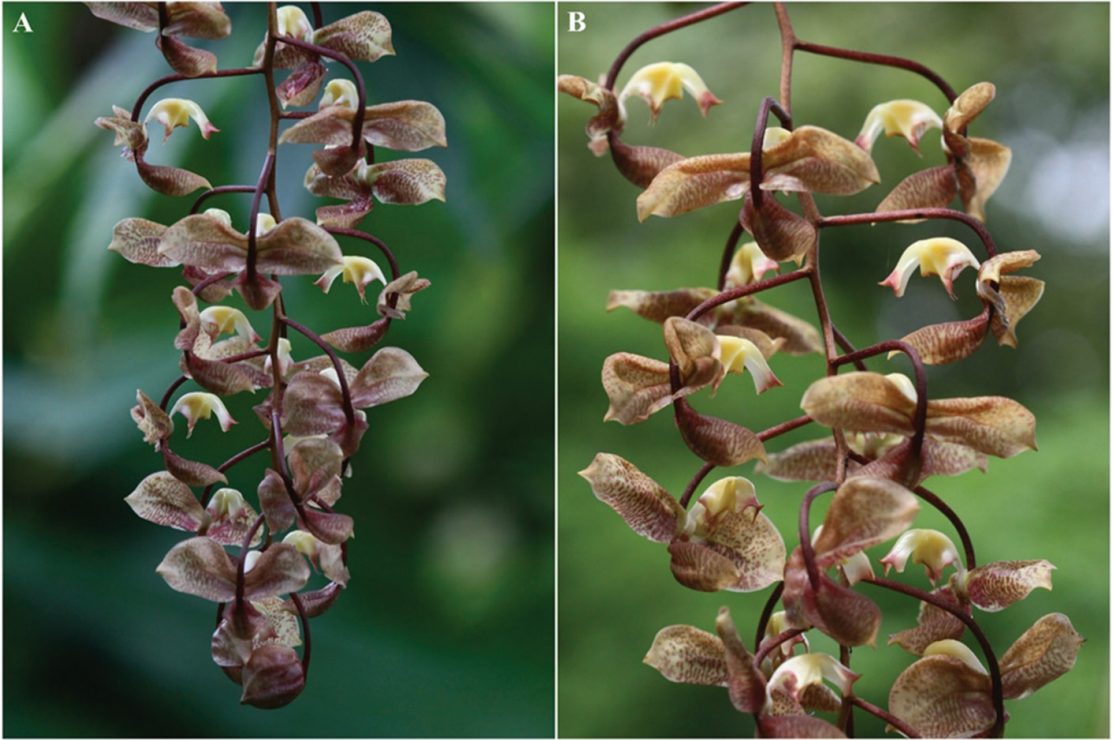


FIGURE 2. **A–B.** Inflorescence of *Gongora* × *copanensis* *in situ*. Photographs by Alexander Alvarado.

covered by the dorsal sepal, welded to the column, lanceolate, acuminate. *Lip* fleshy, waxy, complex, semitruncated, divided into hypochile, mesochile and epichile, laterally compressed, apex of epichile and apex of hypochile lobes purple. *Hypochile* 1 cm long, fused to the foot of the column, fleshy in texture, widening towards the base, grooved towards the apex, yellow, in lateral view saccate on the upper margin, rectangular on the lower, the laminae of the cavity unguiculate, slightly reflexed, with an inconspicuous lobe near the base of the epichile, the lamina conduplicate in its middle part, with two lobes on each side, the anterior large, strongly acuminate with a violet bristles termination, and the posterior small, completely reflexed, ovate-acuminate. *Mesochile* in lateral view very narrow, with a subquadrate, carinate, concave callus. *Epichile* 1.1 cm long, spatulate, longitudinally concave, cymbiform, trilobed, median lobe recurved, acuminate, the lateral ones oblong, the epichile separated from the mesochile by an angle of about 15° and a deep sinus. *Column* 1.5 cm long, covered by the dorsal sepal, semiclaviform, trigonous, arched, winged near the apex. *Capsule* not seen.

**PHENOLOGY:** flowering observed in May.

**ETYMOLOGY:** the name refers to the area where it was discovered, in the department of Copán, Honduras. Copán was an astronomical center of the ancient great Mayan civilization.

**Discussion.** *Gongora* × *copanensis* presents a mixture of exclusive characteristics of members of subgen. *Acropera* sect. *Acropera*, and others of members of subgen. *Gongora* sect. *Truncata*. The only representatives of these groups in the discovery area where the putative hybrid was found are *G. truncata* and *G. batemanii*, which also correspond morphologically to the specimen described here, and whose flowering periods also overlap, for which it is considered as a hybrid between these species. The hybrid shares with *G. truncata* the shape of the pseudobulbs, the ovary not strongly arched (which positions the lip above the column horizontally and not vertically as in members of the sect. *Acropera*), and how the hypochile laminae fold, which is similar to *G. truncata*. Above all, it presents a pair of bristles on the anterior lobes of the

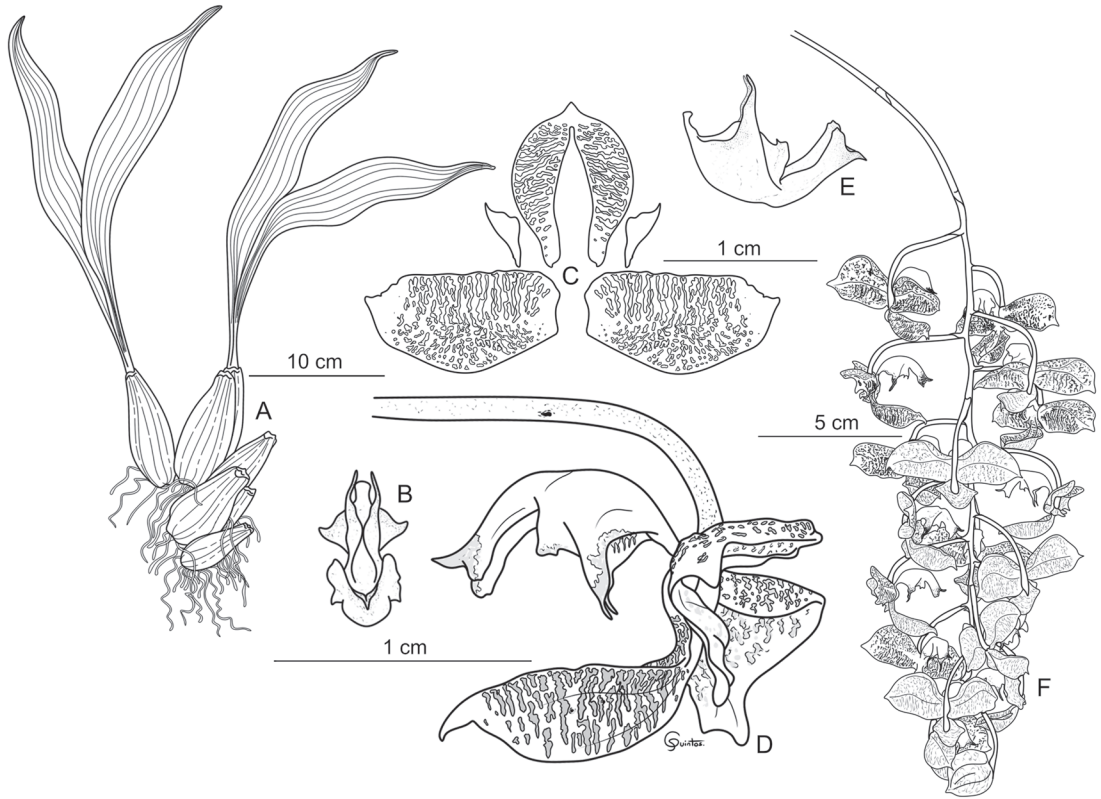


FIGURE 3. Illustration of *Gongora* × *copanensis*. **A.** Habit and size of the plant. **B.** Front view of the lip and view of the inconspicuous basal lobes in profile view. **C.** Petals and sepals. **D.** Flower, profile view. **E.** Profile view of the dissected lip. **F.** Inflorescence. Illustration by Gerardo Quintos Andrade, based on *A. Alvarado* #001 (EAP).

hypochile, similar to the typical bristles of the subgen. *Gongora*, which are absent in all the species of subgen. *Acropera*. In addition, it shares with *G. batemanii* the cucullate dorsal sepal and the lateral sepals arranged perpendicular to the column, the callus and the first third of the hypochile exposed by the hypochile lobes, and the spatulate epichile; however, it lacks the joint that allows movement of the lip. Although numerous artificial hybrids have already been recorded for this genus, this is the first record of a natural hybrid for this popular but taxonomically difficult group of orchids.

A specimen with the same floral characteristics as the nothospecies described here, appeared without locality on the digital platform of the Swiss Orchid Foundation at the Herbarium Jany Renz, Botanical Institute, University of Basel, in Switzerland. It was registered under number 2065154 (Fig. 4A–B), and erroneously identified as *Gongora saccata* Rchb.f. (Fig. 5C). The latter is a synonym of *G. seideliana* Rchb.f.

(Fig. 5A–B), since Reichenbach named the same plant twice (R. Jenny pers. comm. 2020), *G. seideliana* is a rare species from southern Mexico (García-Matínez & Jiménez-Machorro 2016). The photos and the identification of the specimen on the said platform, which have now been removed from the webpage, were erroneously attributed to Rudolf Jenny, but they do not belong to or were determined by him (R. Jenny pers. comm. 2020). This second plant has the basal lobes of the hypochile that are not markedly retrorse, so they are conspicuous in lateral view, unlike the specimen from Honduras, which has the same lobes retrorse, which makes them inconspicuous in lateral view. However, its shape basically corresponds to the taxon described here. A third cultivated specimen is also known from a private collection in the same locality of Copán in Honduras, but we had no opportunity to voucher it. The presence of these plants, product of the crossing of the same parents, allows us to infer that sometimes



FIGURE 4. A–B. Specimen 2065154 from the Swiss Orchid Foundation at the Herbarium Jany Renz, Botanical Institute, University of Basel, Switzerland (SORA). Photographs by SORA.

the reproductive barriers between these species are broken, allowing with relative frequency the exchange of genetic material.

The species of euglossine bees pollinating *G. truncata* and *G. batemanii* have not been recorded. This prevents the possibility to glimpsing the probable cause of the breakdown of the reproductive barriers between both species, or to be able to infer the zones where this hybrid could appear based on the distribution overlapping of the involved plant species and their pollinators. However, some relevant aspects of the mechanical and chemical barriers of both parent species can be discussed.

*Gongora truncata* and *G. batemanii* have different pollination mechanisms. Hetherington-Rauth and Ramírez (2015) describes the hinge mechanism for the *Acropera* and *Cassidea* sections of the subgen. *Acropera*. In this mechanism, the species are pollinated by bees of the genus *Euglossa* Latreille, and position the pollinarium on the scutellum, with the help of a joint that allows the lip movement of the flowers. For subgen. *Gongora* sect. *Truncata*, and based on the observation of South American species, the same authors describe the header mechanism (Fig. 5E), in

which the orchids of this group use large bees of the genus *Eulaema* Lapeletier, that receive the pollinarium behind head. This appears to hold true for the South American members of section *Truncata*, but not for the Mesoamerican species of this section, which have been observed using the genus *Euglossa* near their natural ranges (*G. truncata*: Winter pers. obs. 2022 (Fig. 5D), A. Jiménez pers. obs. 2022; *G. seideliana*: A. Mendez pers. obs. 2022). These are small bees to which the flowers adhere the pollinia to the scutellum, employing the slide mechanism (typical for the rest of the subgenus they belong to), in which the bees slip from the lip towards the column of the flower. Therefore, despite having different pollination mechanisms, both parent species place their pollinia on the same part of the bees' body.

As for the chemical barriers, the exact composition of the fragrance cocktail of the parent species is unknown. However, Hetherington-Rauth and Ramírez (2016) found that the terpene *a*-farnesene is part of the fragrance cocktail of both. Some authors have considered this terpene unattractive for Euglossini bees (Ackerman 1989, Williams & Dodson 1972, Williams & Whitten 1983). Nevertheless, the authors also found that this and other terpenes considered unattractive, appear in large quantities in some species of *Gongora* and related genera, representing up to 75% of the total fragrance. They comment that this percentage suggests a greater significance for these types of compounds in the function of the perfume due to the high cost that the synthesis of terpenes represents for the plant kingdom (Gershenzon 1994). Furthermore, substances considered unattractive are known to interact with attractive ones, with this chemical interaction having repercussions on bee behavior (Hetherington-Rauth & Ramírez 2016, Williams & Dodson 1972). How attractive and unattractive chemicals interact with bees, is a topic that needs much more research. This opens the possibility of a better understanding of natural hybridization in orchids.

Sharing one or more pollinator species is common in the Stanhopeinae (Hetherington-Rauth & Ramírez 2015, Roubik & Hanson 2004, van der Pijl & Dodson 1966). The barriers used by euglossine-pollinated orchids must be effective because natural hybrids are infrequent, but hybridization occurs when these barriers fall for some reason (Dressler 1968).

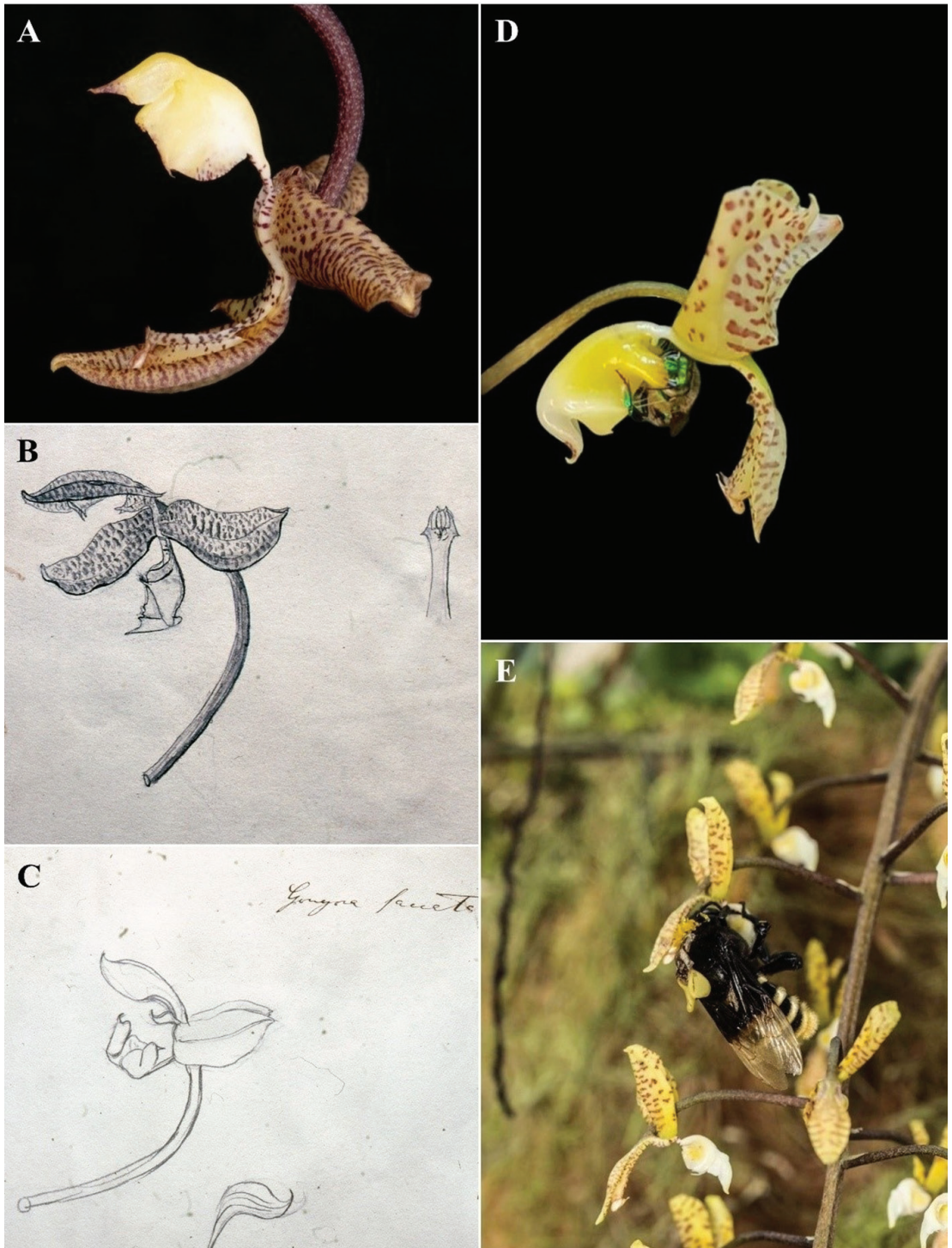


FIGURE 5. **A.** *Gongora seideliana*. **B.** Illustration of Reichenbach's *G. seideliana*. **C.** Illustration of *G. saccata* from Reichenbach, Herbarium of Natural History, Vienna (W). **D.** *Gongora truncata* and *Euglossa* sp. **E.** *Gongora tracyana* and *Eulaema bombyiformis*. Photographs by Eduardo Pérez García (A), Rudolf Jenny (B–C), Diana Winter (D), and José Mesa Londoño (E).

Natural phenomena such as natural hybridization and its genetic consequences, are receiving enthusiastic attention from researchers (Soltis & Soltis 2009). Therefore, reporting phenomena like this is of great importance to understanding the way and frequency in which species interact and incorporate genetic characteristics among themselves. It is known that some natural hybrids sometimes manage to establish healthy populations, developing a new evolutionary route and, therefore, speciation (Dressler 1968, Soltis & Soltis 2009). Observing these changes help to understand the complexity of these interactions and the extraordinary plasticity of the chemical and evolutionary ecology in the subtribe Stanhopeinae and the tribe Euglossini.

Furthermore, the role of ecotones and problems, such as deforestation and ecosystem fragmentation, could affect the frequency of these phenomena.

**ACKNOWLEDGMENTS.** We thank Victoria Sosa for the observations made to the manuscript before its publication. Gerardo Quintos Andrade for the specimen illustration, Mayra L. Maldonado for providing bibliography, Carlos Silva and Daniel Sanders for reviewing the English translation. But in a special way to Rudolf Jenny (R. I. P.) for his experience, comments, advice, and photographs (1A, 5BC) provided for this publication. His departure means the loss of the greatest authority in this complex group of orchids.

#### LITERATURE CITED

- Ackerman J. D. (1989). Geographic and seasonal variation in fragrance choices and preferences of male euglossine bees. *Biotropica*, 21(4), 340–347. DOI: <https://doi.org/10.2307/2388284>
- Ames, O. & Correll, D. S. (1953). Orchids of Guatemala. *Fieldiana: Botany*, 26(1).
- Ames, O. & Correll, D. S. (1985). *Orchids of Guatemala and Belize*. Courier Corporation.
- Beutelspacher, C. R. (2011). *Guía de orquídeas de Chiapas*. México: Universidad de Ciencias y Artes de Chiapas.
- Chase, M. W., Toscano de Brito, A. L. V., Pridgeon, A. M., Cribb, P. J., Chase, M. W. & Rasmussen, F. N. (2009). *Genera Orchidacearum, Volume 5: Epidendroideae (Part Two)*. Oxford: Oxford University Press.
- Damon, A., Hernández-Ramírez, F., Riggi, L., Verspoor, R., Bertolini, V., Lennartz-Walker, M. & Burns, A. (2012). Pollination of euglossinophilic epiphytic orchids in agroecosystems and forest fragments in southeast Mexico. *European Journal of Environmental Sciences*, 2 (1), 5–14. DOI: <https://doi.org/10.14712/23361964.2015.34>
- Dressler, R. L. (1968). Pollination by euglossine bees. *Evolution*, 22 (1), 202–210. DOI: <https://doi.org/10.2307/2406664>
- Dressler, R. L. (1993). *Phylogeny and classification of the orchid family*. Cambridge University Press.
- Eltz, T., Whitten, W. M., Roubik, D. W. & Linsenmair, K. E. (1999). Fragrance collection, storage, and accumulation by individual male orchid bees. *Journal of Chemical Ecology*, 25 (1), 157–176. DOI: 10.1023/A:1020897302355
- Faegri, K. & Van Der Pijl, L. (2013). *Principles of pollination ecology*. Pergamon press.
- García-Martínez, R. & Jiménez-Machorro, R. (2016). Redescubrimiento de *Gongora seideliana* Rchb.f. (Orchidaceae), una orquídea rara, en Chiapas, México. *Lacandonia*, 10 (2), 11–14.
- Gerlach, G. (2003). La subtribu Stanhopeinae: sus notables mecanismos de polinización, la química de sus aromas florales e implicaciones en sistemática y taxonomía. *Lankesteriana*, 7, 104–106. DOI: 10.15517/lank.v3i2.23029
- Gershenzon J. (1994). Metabolic costs of terpenoid accumulation in higherplants. *Journal of Chemical Ecology*, 20, 1281–1328. DOI: 10.1007/BF02059810
- Grant, V. (1981). *Plant Speciation*. New York: Columbia University Press.
- Hágsater, E. & Salazar, G. A. (1990). *Icones Orchidacearum*. Fascicle I. Orchids of Mexico Part, 1. México City: Herbario AMO. 45 pp.
- Hetherington-Rauth, M. C. & Ramírez, S. R. (2015). Evolutionary trends and specialization in the euglossine bee-pollinated orchid genus *Gongora*. *Annals of the Missouri Botanical Garden*, 100 (4), 271–299. DOI: 10.3417/2014035
- Hetherington-Rauth, M. C. & Ramírez, S. R. (2016). Evolution and diversity of floral scent chemistry in the euglossine bee-pollinated orchid genus *Gongora*. *Annals of botany*, 118 (1), 135–148. DOI: 10.1093/aob/mcw072
- Jenny, R. (1993a). *Stanhopea* in Costa Rica & Panama. *Schlechteriana*, 4, 66–92.
- Jenny, R. (1993b). *Monograph of the genus Gongora Ruiz & Pavon*. Koeltz Scientific Books.
- Pupulin, F. (2007). × *Bensteinia ramonensis*, a new natural hybrid in the Zygopetalinae (Orchidaceae). *Selbyana*, 28 (2), 112–116.
- Ramírez, S. (2019). Pollinator specificity and seasonal patterns in the euglossine bee-orchid mutualism at La Gamba Biological Station. *Acta ZooBot Austria*, 156, 171–181.



- Roubik, D. W. & Hanson, P. E. (2004). *Abejas de orquídeas de la América tropical: Biología y guía de campo*. Editorial INBio.
- Soltis, P. S. & Soltis, D. E. (2009). The role of hybridization in plant speciation. *Annual review of plant biology*, 60, 561–588. DOI: 10.1146/annurev.arplant.043008.092039
- van der Pijl, L. & C. H. Dodson. (1966). *Orchid flowers, their pollination and evolution*. University of Miami Press. 214 pp.
- Williams N. H. & Dodson C. H. (1972). Selective attraction of male euglossine bees to orchid floral fragrances and its importance in long distance pollen flow. *Evolution*, 26, 84–95. DOI: <https://doi.org/10.2307/2406985>
- Williams, N. H. & Whitten, W.M. (1983). Orchid Floral Fragrances and the Male Euglossine Bees: methods and advances. *Biological Bulletin*, 164, 355–395. DOI: 10.2307/1541248