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CATASETUM × *GUARAYENSE* (ORCHIDACEAE: CATASETINAE), FIRST FORMALLY DESCRIBED AND DOCUMENTED NATURAL HYBRID OF THE GENUS FOR BOLIVIA

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Abstract. *Catasetum* × *guarayense* is described and illustrated as the first natural hybrid of *Catasetum* reported from Bolivia. The material was collected in the municipality of El Puente, Guarayos province, Santa Cruz department, in the central eastern region of the country. In addition, data on its geographical distribution, habitat, and phenology are provided. The available evidence suggests that the hybrid results from the natural crossing between *C. rooseveltianum* and *C. semicirculatum*, species occurring within the limits of the Bolivian territory. As expected for any natural hybrid, compared to its probable parents, *C.* × *guarayense* presents a set of intermediate morphological characters, a point discussed in detail in this study. Besides, we propose an identification key to the Bolivian *Catasetum* species with symmetrical and parallel antennae.

Resumen. *Catasetum* × *guarayense* se describe e ilustra como el primer híbrido natural de *Catasetum* registrado en Bolivia. El material fue recolectado en el municipio de El Puente, provincia de Guarayos, departamento de Santa Cruz, en la región centro-oriental del país. Además, se proporcionan datos sobre su distribución geográfica, su hábitat y su fenología. La evidencia disponible sugiere que el híbrido resulta del cruzamiento natural entre *C. rooseveltianum* y *C. semicirculatum*, especies que se encuentran dentro de los límites del territorio boliviano. Como es esperable en cualquier híbrido natural, en comparación con sus probables parentales, *C.* × *guarayense* presenta un conjunto de caracteres morfológicos intermedios, aspecto que se discute en detalle en este estudio. Además, se propone una clave de identificación para las especies bolivianas de *Catasetum* con antenas simétricas y paralelas.

Keywords / Palabras clave: Bolivia oriental, Bosque Seco Chiquitano, Chiquitano Dry Forest, Cymbidieae, Eastern Bolivia, hibridación, hybridization, Neotrópico, Neotropics, taxonomía, taxonomy

Introduction. According to the biological species concept, a species can be defined as a group of individuals capable of interbreeding and that, under natural conditions, remain reproductively isolated from other similar groups (Mallet, 2001). However, under certain circumstances, populations of distinct species may come into contact and, when reproductive barriers are partially or temporarily over-

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come, natural hybridization may occur. Therefore, a "natural hybrid" refers to an organism resulting from spontaneous crossing between two distinct species in the wild, without human intervention. Its recognition may be supported by a combination of morphological and genetic evidence, together with similarities or intermediate patterns in ecology, habitat, phenology, and floral fragrance between the hybrid and its putative parents (Wang, 2017). This is therefore based on the premise that these plants present, especially in their phenotypic traits, a set of intermediate characters compared to their putative parents (*e.g.,* Cantuária *et al*., 2021; Krahl *et al*., 2020; Pansarín, 2025). We may add that this process can occur between congeneric species (*e.g.*, Barrera-Rojas & van den Berg, 2025; Krahl *et al*., 2021; Menezes & Viotti, 2024; Vieira *et al.*, 2024) and, though more rarely, between non-congeneric species (*e.g.*, Braga, 1978; Cetzal-Ix *et al.*, 2012; Engels & Canestraro, 2017; Engels *et al.*, 2025; Pupulin *et al.*, 2025; Ramos-Roldán *et al.*, 2025; Salueda & Arrondeau, 2020).

Hybridization, when it is enabled by the natural breakdown of reproductive barriers, plays a significant role in the evolution and diversification of various plant lineages, promoting the emergence and selection of new taxa (Arnold, 2006). Within Orchidaceae, there are many pre- and post-zygotic barriers whose main role is to prevent hybridization events (Melo *et al.*, 2011; Smidt *et al.*, 2006; van der Pijl & Dodson, 1966). However, when these barriers are weak or overcome, hybridization can occur naturally — a phenomenon widely documented in the family (*e.g.*, Barrera-Rojas & van den Berg, 2025; Braga, 1978; Cetzal-Ix *et al.*, 2012; Christenson, 2006; Krahl *et al.*, 2021; Menezes & Viotti, 2024; Mó *et al.*, 2014; Pansarin, 2025; Pupulin *et al.*, 2025; Ramos-Roldán *et al.*, 2025; Salueda & Arrondeau, 2020; Silva *et al.*, 2024; Vieira *et al.*, 2024) and especially in the genus *Catasetum* Rich. ex Kunth (*e.g.*, Krahl *et al.*, 2020; 2023a; 2024a,b; 2025a,b,c; Pabst, 1975; Petini-Benelli, 2014; 2016; Romero & Carnevali, 1989; 1991; Romero & Jenny, 1992; 1993; Romero-González & Carnevali, 2024).

Hitherto, the genus comprises 193 species and 47 hybrids described and accepted (Krahl *et al.*, 2023a,b,c,d; 2024a,b,c,d; 2025a,b,c,d,e; POWO, 2025; Romero-González & Carnevali, 2024). They are distributed from Mexico to southern Brazil and northern Argentina (Romero-González & Carnevali, 2009). The species are characterized by fusiform, elliptical, ovate, or conical pseudobulbs; leaf sheaths covering the entire pseudobulb; deciduous and plicate leaves, usually elliptical or oblanceolate; and lateral, racemose inflorescences bearing unisexual (pistillate or staminate), rarely hermaphrodite flowers (sterile). Only the staminate flowers exhibit sufficient morphological variation to distinguish among species. Furthermore, the presence of structures called "antennae" on the staminate flowers contributes to the traditional infrageneric subdivision of the genus into two subgenera, two sections, and three subsections (Bicalho & Barros, 1988; Senghas, 1990; 1991).

However, recent phylogenetic results (Mauad *et al.*, 2022) indicate that this traditional classification, which relies mainly on antenna morphology, does not faithfully reflect the evolutionary history of *Catasetum*, because similar antenna structures have evolved independently in different lineages, resulting in morphological convergence and homoplasy. Nevertheless, these morphological groupings remain useful for conveniently describing and identifying species based on shared characters. In contrast, biogeographical patterns appear to provide a more robust framework for interpreting relationships within the genus, with clades broadly associated with major geographical regions, including the Amazon, Guiana Shield, Atlantic Forest, and both eastern and western slopes of the Andes. For example, the *C. naso* Lindl., *C. lucis* P.Ortiz & Arango and *C. planiceps* Lindl. group is associated with the eastern Andean slopes, whereas other lineages, such as those including *C. expansum* Rchb.f. and *C. macroglossum* Rchb.f., occur on the western slopes. These patterns suggest that historical processes of dispersal and vicariance have played a central role in the diversification of *Catasetum*.

Bolivia, the fifth-largest country in South America, houses a remarkable diversity of environments due to its wide range of altitudes and climates. The Bolivian territory is made of different biomes, in-

cluding the Amazon rain forests, the savannas of the Chiquitania, the Andean Altiplano, the Gran Chaco, represented by dry forests, and the Pantanal, represented by extensive wetlands, as well as the Yungas (humid mountain forests which stretch along the eastern slopes of the Andes and rank among the most biodiverse regions of the country) (Werneck, 2011). Despite this environmental heterogeneity, Bolivia stands out as one of the most under-sampled tropical countries in terms of biodiversity, a fact particularly evident in the family Orchidaceae. Although about 80% of the territory is still without any collections (regarding plants), *ca.* 1500 species, of which about a third is endemic, distributed in 191 genera, are already recorded. Diversity is mainly concentrated in the Yungas and other humid montane forests along the eastern slopes of the Andes, including areas referred to as "ceja de la montaña" and the Andean foothills, which are recognized as major centers of diversity and evolution for Neotropical orchids. These figures highlight the biogeographical significance of the country as well as the urgent need to expand research and conservation efforts (Vásquez *et al.*, 2003). In this context, *Catasetum*, represented in the country by 21 species, accounts for approximately 11% of the 193 currently accepted species in the genus and therefore represents a substantial component of the genus' diversity in Bolivia. Hitherto, there is no confirmed record of natural hybrids, and the relatively limited number of collections and published records of *Catasetum* from Bolivia suggests that its diversity and occurrence in the country may still be under-sampled, particularly given the extensive areas that remain botanically unexplored (POWO, 2025; Vásquez & Dodson, 1982, 1989a,b; Vásquez *et al.*, 2003, 2014).

This work aims to describe and record the first natural hybrid of *Catasetum* for the Bolivian flora. We provide a detailed description of the taxon, along with data on its geographical distribution, habitat, and phenology. We also discuss the pollinator sharing and the phenological overlap of its probable parents. In addition, we compare the new taxon morphologically with its supposed parents and propose an identification key to the species and hybrids of *Catasetum* with symmetrical and parallel antennae occurring in Bolivia.

Materials and methods. The putative nothospecies proposed here was collected by C. A. S. Miranda-Zapata and L. A. Mercado-Menacho during an occasional expedition in the municipality of El Puente, province of Guarayos, department of Santa Cruz, central-eastern region of Bolivia. The material, first sterile, was kept in cultivation until its blooming and then herborized according to the standardized procedures of Mori *et al.* (1989) to be included in the collections of the INPA and HUAM herbaria (acronyms according to Thiers, 2025). The description and photographic illustrations of the taxon are based on living material from the type specimen. The morphological characterization follows the terminology of Dressler (1993), Harris & Harris (2001), and Gonçalves & Lorenzi (2007). Observations regarding the habitat were recorded *in situ*, and the flowering period was recorded during the cultivation of the specimen. The distribution map was built with the software QGIS 3.40.11 "Bratislava" (QGIS, 2025), and the identification key was prepared based on the data found in Vásquez & Dodson (1982, 1989a,b), Vásquez *et al.* (2003; 2014), POWO (2025) and on actual specimens deposited in the AMES, BOLV, BHZB, F, FLAS, L, LPB, MO, NY, SP, UFMT, US and USZ herbaria (acronyms according to Thiers, 2025). The specific epithet follows the International Code of Nomenclature for algae, fungi and plants (ICN) (Turland *et al.*, 2025).

The new putative nothospecies was compared to its putative parental species through the analysis of the original protologues (Hoehne, 1916; Miranda, 1986), of the type material of *C. semicirculatum* F.E.L.Miranda (RB00542573!), as well as the specialized literature (*e.g.,* Hoehne, 1942; Krahl *et al.*, 2025f; Petini-Benelli, 2025; Vásquez & Dodson, 1989b (pl. 309)). Notably, for *C. rooseveltianum* Hoehne, no physical type material is known (see Krahl *et al.*, 2025f; Romero & Jenny, 1993), and Krahl *et al.* (2025f) designated a lectotype (the original illustration). Aiming to locate possible additional materials related to the hybrid here described, we referred to the data banks SpeciesLink (Canhos *et al.*, 2022) and GBIF (2025) as well as the collections of the main Bolivian herbaria (BOLV, LPB and USZ).

Taxonomic treatment

Catasetum* × *guarayense C.A.S.Miranda-Zapata, L.A.Mercado-Menacho, Chiron & Krahl, ***nothosp. nov.*** Fig. 1.

TYPE: BOLIVIA. Santa Cruz: Guarayos, El Puente, 16°07'30" S; 62°53'11" W, fl. ♂, 2 February 2023, *C.A.S.Miranda-Zapata & L.A.Mercado-Menacho sub A.H. Krahl 1681* (holotype: INPA306828; isotype: HUAM12810).

Diagnosis: *Hybrida naturalis cum characteribus intermediis inter suos probabiles parentes,* C. rooseveltianum *et* C. semicirculatum*. Planta cum characteribus vegetabilibus majori parti specierum congenericarum similibus. Inflorescentia erecta-arcuata cum 10–13 floribus non resupinatis (ut in C. rooseveltianum), luteolis vel leviter virellis cum maculis transversalibus brunneolis. Sepala oblonga-elliptica et petala elliptica (ut in C. semicirculatum). Labellum integrum, ovatum, cum margine irregulariter denticulato, callum basalem (ut in C. semicirculatum) callumque apicalem ferens. Callus basalis transversaliter lunatus utrinque elevatus cum depressione centrali parva parvo apiculo instructa. Callus apicalis deltatus-triangularis obtusus.*

Plant epiphytic, caespitose. *Rhizome* short and inconspicuous. *Pseudobulb* 6.9–12.1 × 1.4–3.1 cm, fusiform, erect, 9–11-leaved, covered by the leaf sheaths. *Leaves* 11.9–31.1 × 2.6–3.7 cm, narrowly elliptical, plicate, 5–7–nerved, margin entire, apex acute. *Staminate inflorescence* 29.6–32.1 cm long, basal/lateral, erect to sub-erect, racemose, 10–13–flowered; peduncle cylindrical, greenish; *floral bract ca.* 0.8 × 0.4 cm, lanceolate, yellowish green, margin entire, apex acute. *Staminate flowers* yellowish and slightly greenish with transverse brownish spots, grouped together on the two distal thirds, non-resupinate, pedicelled; *pedicel ca.* 2.9 cm long, cylindrical, erect to sinuate, greenish. *Sepals ca.* 2.6 × 1.1 cm, oblong-elliptical, the dorsal one symmetrical and the lateral ones slightly asymmetrical, concave, margin entire, apex acute. *Petals ca.* 2.4 × 1.2 cm, elliptical, symmetrical, convex, margin entire, apex acute. *Lip ca.* 2.5 × 2.2 cm, entire, ovate, margin irregularly denticulate, concave, with a basal callus and an apical one; *basal callus ca*. 0.5 × 1.1 cm, transverse, half-moon shaped, raised on both sides, and with a small central depression provided with a small apiculus; *apical callus* 0.4 × 0.3 cm, deltoid to triangular, fleshy, obtuse. *Column ca.* 1.8 × 0.7 cm, subtriangular, slightly contracted at base, yellowish green with brownish spots, apex rostrate; *antennae ca.* 0.8 cm long, filiform, symmetrical and parallel, yellowish. *Anther cap ca.* 0.7 × 0.3 cm, subtriangular, greenish yellow with wine-colored spots, apiculate. *Pollinia* 2, *ca.* 0.3 × 0.1 cm, oblong, hard, compressed, sulcate, yellowish; *stipe ca.* 0.4 × 0.2 cm, laminar, rolled inward, yellowish; *viscidium ca.* 0.2 × 0.2 cm, rounded, sticky, whitish. *Pistillate structures* unknown. *Fruits* unknown.

Etymology: The specific epithet "*guarayense*" refers to the province of Guarayos, department of Santa Cruz (Bolivia), where the new hybrid has been found. The epithet follows the norms established in Article 60, Recommendation 60D of the ICN (Turland *et al.*, 2025).

Distribution, habitat and ecology: To date, *C.* × *guarayense* is known only from the municipality of El Puente (Fig. 2). It occurs within the limits of the dry forest of Chiquitania (Floresta Seca Chiquitana), one of the largest and best-preserved dry forest formations in South America. It mainly stretches through eastern Bolivia and is characterized by a tropical climate with a pronounced dry season, deciduous to semi-deciduous tree vegetation, high floristic diversity, and a strong presence of endemic species (Pennington *et al.*, 2009; Prado, 2000). This ecoregion also serves as a biogeographical transition zone between the Amazon, the Cerrado, and the Chaco, with a distinct floristic composition and high structural heterogeneity. Thus, it plays an essential role in regional ecological connectivity and in maintaining evolutionary processes associated with seasonal forests (Killeen *et al.*, 2006; Pennington *et al.*, 2009).

The type locality is near the areas of occurrence of *C. rooseveltianum* and *C. semicirculatum*, species considered the probable parents of the nothospecies. *Catasetum rooseveltianum* also occurs in the department of Santa Cruz (Krahl *et al.*, 2025f), in the same

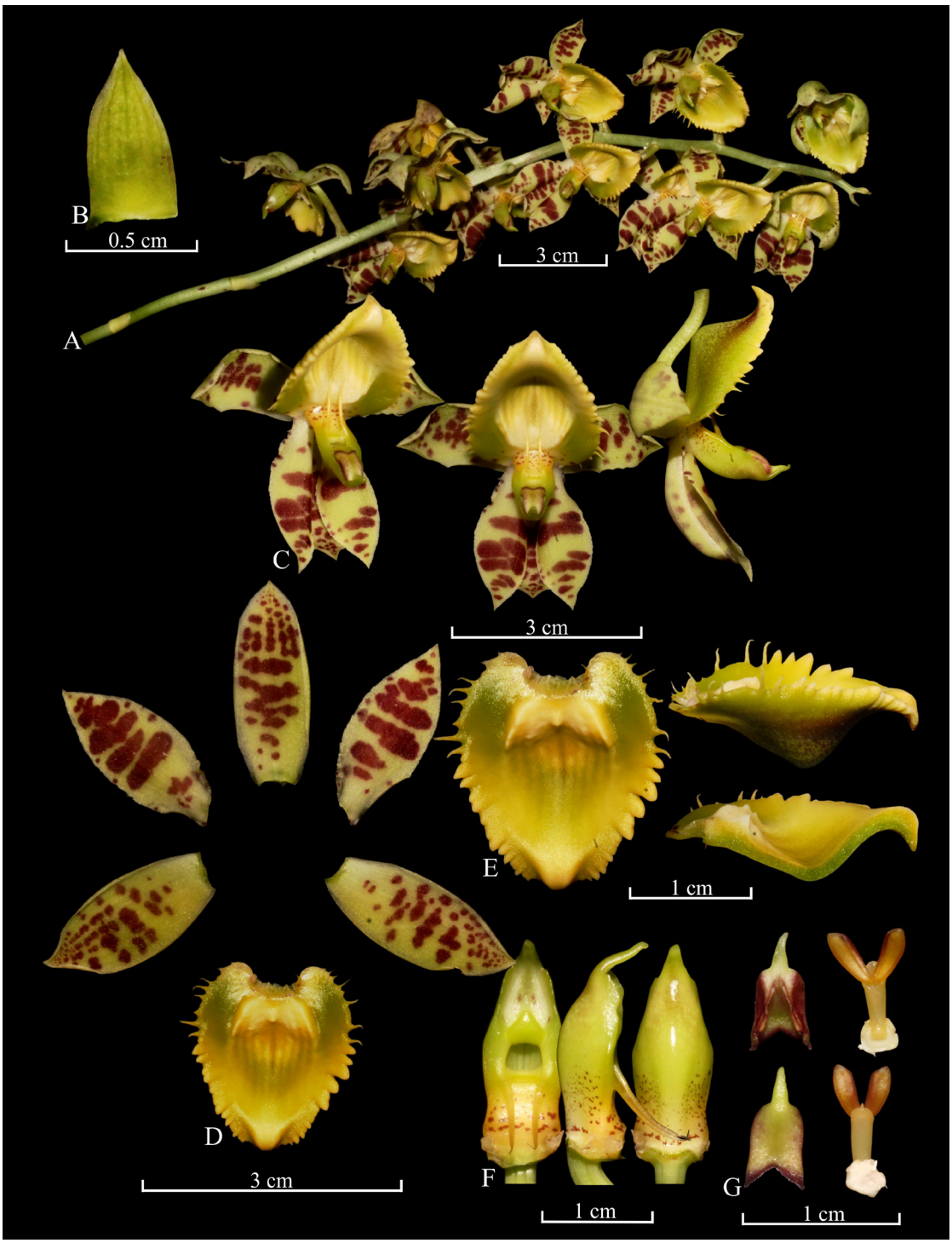

Figure 1. *Catasetum* × *guarayense* (male structures). **A**. Inflorescence. **B**. Floral bract. **C**. Flower in different views. **D**. Dissected perianth. **E**. Lip, front and side views, and longitudinal section. **F**. Column, ventral, lateral and dorsal views. **G**. Anther cap and pollinarium, ventral and dorsal views. Photographs and plate by A.H. Krahl based on the type material (holotype).

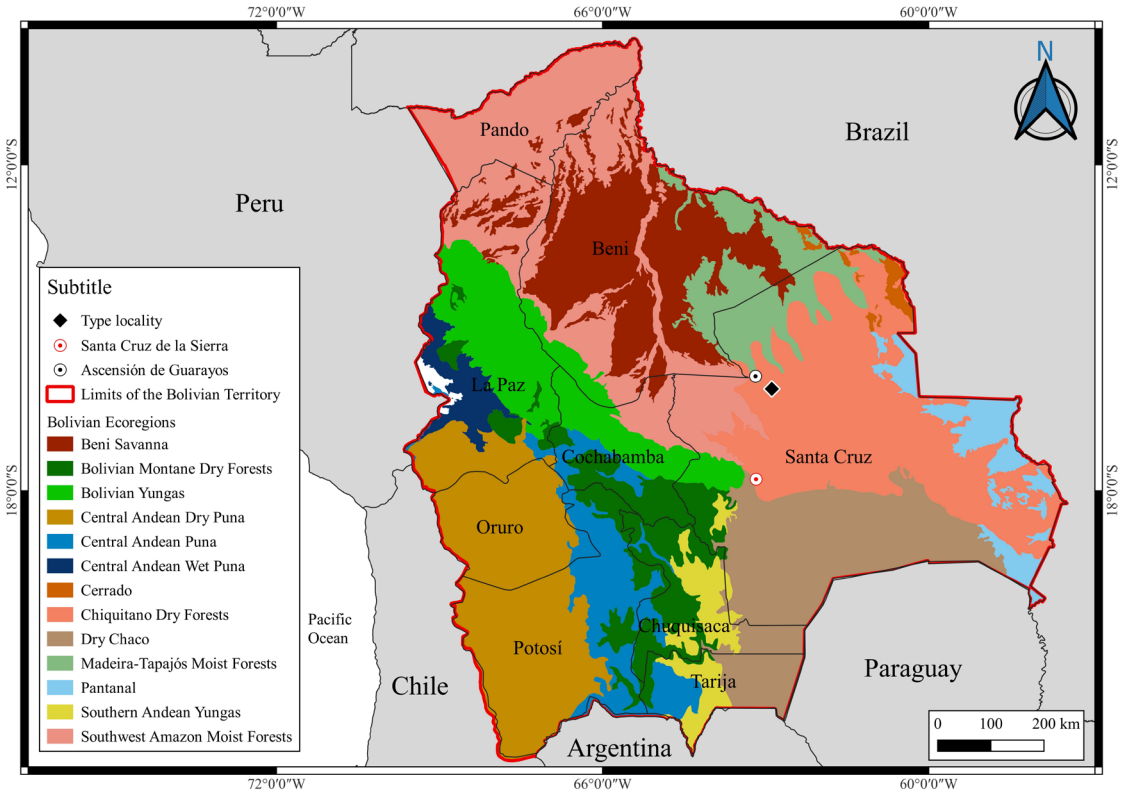

FIGURE 2. Location of the type locality of *C.* × *guarayense* (black rhombus). Map by A.H. Krahl.

administrative unit where *C.* × *guarayense* has been observed. As for *C. semicirculatum*, it has a distribution extending from the Brazilian states Acre, Amazonas and Rondônia (Lacerda, 1998; Miranda, 1986; Petini-Benelli, 2025) to the far west of Bolivia, in La Paz department, as evidenced by the material deposited in the herbarium LPB (*I. Jiménez 5287*). Such a geographical proximity suggests favorable conditions for cross-pollination between the two parent species. It should also be noted that the actual distribution of these species, as with a large part of the Bolivian flora, is probably underestimated (Vásquez *et al.*, 2003), which may hide the actual overlap between their areas of occurrence.

PHENOLOGY AND FLORAL VISITORS: The blooming of *C.* × *guarayense* was observed during the first half of the year, more precisely in February. We also observed an overlap in the blooming periods of the probable parent species, both beginning anthesis in February and extending their blooming period until mid-July (Hoehne, 1916; Krahl *et al.*, 2025f; Miranda, 1986). This phenological coincidence supports the possible occurrence of cross-pollination between the two putative parents.

The putative parent species are also visited by the same group of pollinators, mainly Euglossini bees. *Euglossa* species visit *C. semicirculatum* (Milet-Pinheiro & Gerlach, 2017), as reported for *C. rooseveltianum* by Krahl *et al.* (2025f). This shared pollinator assemblage further supports the possibility of natural hybridization between the two species.

CONSERVATION STATUS: The IUCN (2024) does not recommend assessing the extinction risk for hybrids because such forms do not represent evolutionarily independent lineages and, consequently, do not meet the criteria for species categorization on the Red List. Natural hybrids often have a recent origin, and their populations may be small and ephemeral, making demographic assessments challenging. However, they may arise repeatedly

whenever the parental species occur in sympatry and pollinators occasionally visit flowers of both species, resulting in recurrent hybrid formation. Moreover, their inclusion may distort conservation priorities by diverting efforts away from the really threatened species. Thus, under IUCN directives, hybrids should not be formally assessed unless there is strong evidence of population stability and widely accepted taxonomic recognition.

Morphological affinities: The discovery of *C.* × *guarayense* provides further evidence that hybridization may contribute to the evolutionary diversification of *Catasetum* (Mauad *et al.*, 2022). This interpretation is supported by previous molecular studies, such as Oliveira *et al.* (2010), which revealed substantial inter- and intraspecific genetic similarity among several *Catasetum* species based on RAPD markers. The authors also found high genetic similarity between some morphologically distinct species, indicating that morphological differentiation does not always correspond to genetic divergence. These findings, together with the occurrence of natural hybrids, suggest that reproductive barriers among some *Catasetum* species may be permeable, although direct evidence of gene flow or introgression is still needed to test this hypothesis. Therefore, the geographical and phenological overlap of the parent species in Guarayos, combined with the sharing of the same group of pollinators, creates an ecological scenario favorable to the emergence of natural hybrids. Thus, the identification of *C.* × *guarayense* not only documents a specific hybridization event but also comes within a wider evolutionary context in which the reproductive permeability between sympatric species has the potential to generate new arrangements of phenotypic characters, increase genetic variability within the concerned populations and, perhaps, alter the course of evolutionary diversification within the genus *Catasetum*. Finally, describing *C.* × *guarayense* contributes to documenting natural diversity beyond the recording of "pure" species, especially in Bolivia. Therefore, each new record — including natural hybrids — plays a crucial role in expanding the country's floristic knowledge, improving the understanding of the true diversity within regions still little explored. Moreover, in a situation where most of Bolivia's territory lacks taxonomic inventories, such records contribute to a more robust database for future taxonomic, biogeographic, and conservation studies, strengthening initiatives to monitor and protect biodiversity.

As noted, *C.* × *guarayense* presents floral characters clearly intermediate between those observed in its putative parents (Table 1, Fig. 3), supporting its interpretation as a natural hybrid. As usually observed in most *Catasetum* species (Holst, 1999), the new hybrid proposed here does not present diagnostic vegetative characters: it shares the typical vegetative morphology of its probable parents and most other members of the genus. This vegetative homogeneity, widely documented in *Catasetum*, highlights the importance of the floral traits as the main source of taxonomic differentiation and, consequently, the role of reproductive structures for identifying hybrids within the group.

The inflorescence of *C.* × *guarayense* is erect to sub-erect, with non-resupinate flowers, a character that makes it more similar to *C. rooseveltianum*. In contrast, *C. semicirculatum* has an arched inflorescence with resupinate flowers. The color pattern of the hybrid also reflects the parental combination: the flowers strongly show a yellowish-green hue, as in *C. rooseveltianum*, a species whose flowers are predominantly yellowish and slightly greenish, with occasional subtle brownish streaks inside the lip. However, the hybrid also presents well-defined transverse brownish spots clearly inherited from *C. semicirculatum*, whose flowers are typically whitish to greenish with transverse spots.

Sepals and petals of *C.* × *guarayense* present a predominantly elliptical shape similar to that observed in *C. semicirculatum*, although slightly broader (see Fig. 3B, 3J, Table 1). The lip, resulting from the combination of the parent characters, is entire — a trait shared by both parent species presumably concerned — and shows an ovate shape, intermediate between the cymbiform lip ovate in outline typical of *C. rooseveltianum* and the sub-ovate lip of *C. semicirculatum*. The lip margin also gives evidence of a hybrid heritage: in *C.* × *guarayense*, it is irregularly denticulate, reflecting the influence of *C. semicirculatum*, which presents a usually fimbriate and irregular margin, whereas in *C. rooseveltianum* it is entire, smooth and thickened.

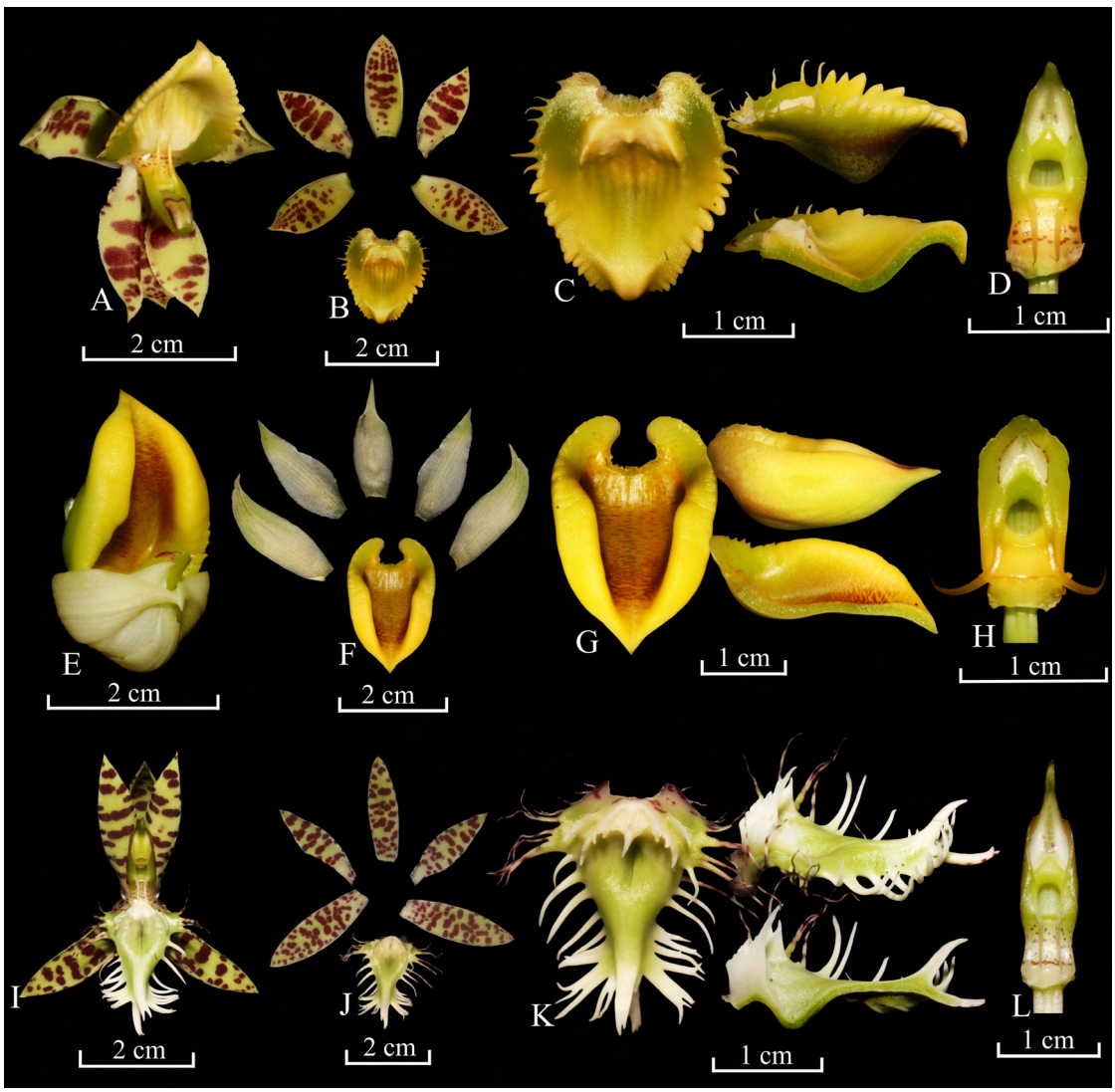

FIGURE 3. Comparative illustration between *C.* × *guarayense* and its probable parents. **A–D**. *C.* × *guarayense*. **E–H**. *C. rooseveltianum*. **I–L**. *C. semicirculatum*. **A, E, I**. Flower. **B, F, J**. Dissected perianth. **C, G, K**. Lip, front and side views, and longitudinal section. **D, H, L**. Column, ventral view. Photographs and plate by A.H. Krahl based on type material (**A–D**, INPA), samples collected in southern Amazonas, Brazil (**E–H**, INPA), and cultivated material from Rondônia, Brazil (**I–L**, not deposited).

As a heritage coming exclusively from *C. semicirculatum* — a species presenting well-developed callosities contrasting with the full absence of such structures on the lip of *C. rooseveltianum* — we observe in *C.* × *guarayense* the presence of a basal callus and an apical one. The basal callus is significantly modified compared to the parental state, appearing diluted in a crescent-shaped transverse structure that is laterally elevated and has a discreet central depression housing a small apicule. In *C. semicirculatum*, the basal callus consists of a central acute protuberance from which three or four semicircular rows of small denticles radiate laterally. The apical callus of the hybrid appears as a deltoid to triangular protuberance, apically obtuse and little raised, contrasting with the apical callus of *C. semicirculatum* that is

TABLE 1. Comparison between *C.* × *guarayense*, *C. rooseveltianum* and *C. semicirculatum*, based on the taxonomic concepts of [(1)]this study, [(2)]Hoehne (1916), [(3)]Hoehne (1942), [(4)]Miranda (1986), [(5)]Vásquez & Dodson (1989b; pl. 309), [(6)]Krahl *et al.* (2025f), [(7)]Petini-Benelli (2025).

Characters	***C. × guarayense*** [1]	***C. rooseveltianum*** [2,3,5,6,7]	***C. semicirculatum*** [4,7]
Staminate inflorescence	29.6–32.1 cm long, erect to suberect, 10–13-flowered	20–40 cm long, erect to hanging with the flower weight, 5–8-flowered	15–30 cm long, arched, up to 15-flowered
Staminate flowers	Yellowish and slightly greenish with transverse brownish spots, non-resupinate.	Uniformly yellowish and slightly greenish, possibly with slight brownish streaks inside the lip; non-resupinate.	Whitish to greenish with transverse brownish spots, resupinate.
Sepals	*ca.* 2.6 × 1.1 cm, oblong-elliptical, acute apex	1.8–2.8 × 0.8–1.4 cm, elliptical to oblong-elliptical, acute apex	2.8–3.0 × 0.7–0.9 cm, oblong-elliptical, acute apex
Petals	*ca.* 2.4 × 1.2 cm, elliptical, acute apex	1.8–2.5 × 0.9–1.4 cm, ovate to elliptical, apex acute	2.8–3.0 × 0.7–0.8 cm, narrowly elliptical to oblong-lanceolate, acute apex
Lip	*ca.* 2.5 × 2.2 cm, entire, ovate, irregularly denticulate margin	2.5–3.0 × 1.5–2.0 cm, entire, cymbiform, ovate in outline, margin entire and thickened	2.2–2.5 × 1.9–2.2 cm, entire, sub-ovate, margin irregularly toothed to fimbriate (usually fimbriate)
Basal callus of the lip	transverse, half-moon shaped, raised on both sides, and with a small central depression provided with a small apiculus	Absent	Made of a central acute protuberance from which 3–4 semicircular rows of small denticles laterally start
Apical callus of the lip	Deltoid to triangular, obtuse	Absent	Claw-shaped to tooth-like, acute or irregularly apiculate
Antennae	Symmetrical and parallel	Symmetrical and divergent	Symmetrical and parallel

typically claw-shaped or tooth-shaped, with an acute or irregularly apiculate apex.

Finally, *C.* × *guarayense* also represents the probable result of a cross between species traditionally placed in distinct subsections within the subgenus *Catasetum*. *Catasetum semicirculatum*, characterized by symmetrical and parallel antennae, is placed in the section *Isoceras*, subsection *Isoceras*, whereas *C. rooseveltianum*, which shows antennae also symmetrical but divaricate, belongs to the subsection *Divaricatae* of the same section (Bicalho & Barros, 1988; Senghas, 1991). In the hybrid, the antenna morphology unequivocally corresponds to the model observed in *C. semicirculatum*, i.e., symmetrical parallel structures. Therefore, under the traditional morphology-based infrageneric classification, *C.* × *guarayense* can be provisionally associated with subgenus *Catasetum*, section *Isoceras*, subsection *Isoceras*, as is *C. semicirculatum*, one of its probable progenitors. This placement is based solely on shared morphological characters and should not be interpreted as evidence of a corresponding phylogenetic position, given that the traditional infrageneric classification does not fully reflect the evolutionary relationships within the genus.

Catasetum × *guarayense* is the first natural hybrid described and documented for Bolivia, among 47 hybrids accepted for the genus, most of which occur exclusively in Brazilian territory (Krahl *et al.*, 2020; 2023a; 2025a,b,c,d). However, we consider it unlikely that this is an isolated case in the country, as at least two additional Bolivian species have morphology suggesting a hybrid origin. The first is *C. ricii* R.Vásquez & Dodson, known only from type material native to the province of Velasco, department

of Santa Cruz (Vásquez & Dodson, 1997). It shows floral characters — especially transverse brownish spots on the lip and denticulate margin of the lateral lobes — compatible with a primary hybrid or with an introgression pattern, involving *C. fuchsii* Dodson & R.Vásquez and some taxon belonging to the species complex of *C. barbatum* (for example *C. barbatum* or *C. semicirculatum*, both reported from Bolivia according to POWO, 2025; Vásquez & Dodson, 1982; Vásquez *et al.*, 2003, 2014).

Another potentially hybrid species is *C. kempfii* Dodson & R.Vásquez, described for the central and eastern Bolivian regions (Cochabamba and Santa Cruz) (Vásquez & Dodson, 1989b, pl. 308). Based on the flower resupination, the lip shape, the antenna morphology, and the apparently rare occurrence of the species, we may raise the hypothesis that *C. kempfii* can be the result of crossing between two other Bolivian taxa only known from the type materials — *C. justinianum* R.Vásquez & Dodson (Vásquez & Dodson, 1997) and *C. longiantennatum* R.Vásquez & G.A.Romero (Vásquez & Romero-González, 2009). However, these hypotheses remain preliminary as their validation will require additional integrated analyses in the future, including a critical reexamination of the type materials and protologues, analysis of the geographical and phenological overlap, verification of the sharing of flower visitors, more detailed comparative morphological evaluation and even the use of in vitro germination to examine the result of the manual crossing between the supposed parent species involved (*e.g.*, Krahl *et al.*, 2024a).

Key to the *Catasetum* species with symmetrical and parallel antennae occurring in Bolivia

1. Flowers non-resupinate 2
   2. Greenish flowers with a subglobose lip with a minutely denticulate margin ..... ***C. longiantennatum***
   2a. Flowers yellowish to slightly greenish, with transverse brownish spots; lip ovate, with a distinctly defined margin bearing irregular denticles ..... ***C. × guarayense***

1a. Flowers resupinate 3
   3. Lip margin smooth 4
      4. Lip entire ..... ***C. callosum***
      4a. Lip 3-lobed ..... ***C. fuchsii***
   3a. Lip margin fimbriate, ciliate, denticulate, crenulate, papillose or warty 5
      5. Lip apex with a callosity 6
         6. Basal callus of the lip tripartite ..... ***C. barbatum***
         6a. Basal callus of the lip consisting of an acute central protuberance from which 3-4 semicircular rows of small denticles extend laterally ..... ***C. semicirculatum***
      5a. Lip apex without callosity 7
         7. Lip apex obtuse, rounded or truncate ..... ***C. parguazense***
         7a. Lip apex apiculate ..... ***C. cochabambanum***

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