

Catasetum × *humaitaense* (Orchidaceae: Catasetinae), a new nothospecies from the Brazilian Amazon

Catasetum × *humaitaense* (Orchidaceae: Catasetinae), una nueva notoespecie de la Amazonia brasileña

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Abstract

This article proposes and describes a new nothospecies of *Catasetum* discovered in the igapó forest surrounding Lake Carapanatuba, located on the banks of the Madeira River, approximately 85 km from the city of Humaitá, Brazil. The hybrid exhibits intermediate characteristics of its putative parents, *Catasetum boyi* and *Catasetum ivanaeae*. Detailed information on its distribution, habitat, ecology, and phenology is provided, along with an identification key. The discovery of *Catasetum* × *humaitaense* as a natural hybrid offers valuable insight into natural selection and evolutionary processes, as it can breed or backbreed with its parental species, generating offspring with genetic and phenotypic variation important for environmental adaptation.

Keywords: hybridization, speciation, reproduction, plant taxonomy.

Resumen

Este artículo propone y describe una nueva notoespecie de *Catasetum* descubierta en el bosque de igapó que rodea el lago Carapanatuba, ubicado a orillas del río Madeira, aproximadamente a 85 km de la ciudad de Humaitá, Brasil. El híbrido presenta características intermedias entre sus posibles progenitores, *Catasetum boyi* y *Catasetum ivanae*. Se proporciona información detallada sobre su distribución, hábitat, ecología y fenología, junto con una clave de identificación. El descubrimiento de *Catasetum x humaitaense* como un híbrido natural ofrece valiosos conocimientos sobre la selección natural y los procesos evolutivos, ya que puede cruzarse o retrocruzarse con sus especies parentales, generando descendencia con variación genética y fenotípica importante para la adaptación al ambiente.

Palabras clave: hibridación, especiación, reproducción, taxonomía de plantas.

Introduction

Hybridization is observed in a wide range of living organisms (Arnold, 1992) and plays a fundamental role in the evolution of various species (Harrison, 1990; Arnold, 1997), particularly among flowering plants (Rieseberg, 1997). It occurs when different populations or species come into contact, interbreed (spontaneously), and produce descendants with mixed characteristics (Barton & Hewitt, 1989; Azevedo et al., 2006; Krahl et al., 2021a; Krahl et al., 2025). This mechanism occurs among congeneric species (Gonçalves & Azevêdo-Gonçalves, 2009; Waechter & Ferreira, 2013; Semple, 2016; Pliszko & Kostrakiewicz-Gieralt, 2018; Krahl et al., 2021a; Bueno et al., 2023; Krahl et al., 2023a) or between species from different genera (Braga, 1978; Archila & Szlachetko, 2014; Pupulin, 2015; Engels & Canestraro, 2017; Smith & Figueiredo, 2020; Engels et al., 2021; Menezes & Viotti, 2024). When it occurs efficiently, it can lead to the formation of hybrid populations that persist over time (Barton & Hewitt, 1989; Baxter et al., 1997), or even result in the fusion of parental species into a single species (Karlin & McGregor, 1972; Gavrillets, 1997).

Hybridization overcomes reproductive barriers, whether they are pre-zygotic (e.g., attraction of different pollinators due to distinct scents, differing flowering times, habitat separation, or disjoint geographic distribution) or post-zygotic (e.g., sterility of offspring, fruit abortion, production of inviable

seeds, or limitations in suitable mycorrhizal associations in fungi-dependent plants) (Abbott et al., 2013; Yan et al., 2019). In this context, pre-zygotic barriers are the primary factors preventing hybridization in Orchidaceae (Dodson, 1962a,b; van der Pijl & Dodson, 1966; Dressler, 1981). However, among closely related species, these barriers are often considerably less effective or even absent (van der Pijl & Dodson, 1966; Dressler, 1981). Consequently, a significant number of natural hybrids have been recorded in this plant family (Linder, 1990; Borba & Semir, 1998; Azevedo et al., 2006; Lee, 2013; Salazar et al., 2014; Zhang et al., 2018; Solano et al., 2019; Krahl et al., 2021a; Morales et al., 2021; Batista & Medeiros, 2022), particularly within the genus *Catasetum* Rich. ex. Kunth (Romero & Carnevali, 1989; 1990; 1991a,b; 1992; Romero & Jenny, 1992; Petini-Benelli & Grade, 2010; 2012; Ferreira, 2013; Petini-Benelli, 2014; Ferreira, 2016; Petini-Benelli, 2016a; Ferreira, 2019; Ferreira & Filho, 2019; Ferreira & Malaspina, 2019; Krahl et al., 2020; Cantuária et al., 2021; Ferreira & Malaspina, 2023a,b; Krahl et al., 2023a; Assis & Ferreira, 2024; Krahl et al., 2024b,c; Krahl et al., 2025).

Members of the genus *Catasetum* are characterized by conical to fusiform pseudobulbs and plicate, oblanceolate to elliptic leaves, whose sheaths cover the entire pseudobulb. Their lateral, racemose inflorescence bears unisexual (staminate and/or pistillate) or, more rarely, bisexual flowers (Holst, 1999). Vegetative morphology, along with the features of pistillate and hermaphroditic flowers,

provides limited taxonomic value due to their low variability. As a result, staminate flowers are particularly important for species identification (Walker-Larsen & Harder, 2000). These flowers are distinguished by the presence of two staminodes, commonly referred to as antennae, which are situated within the gynostemium (column) and function to catapult the pollinarium onto the pollinator during floral visitation (Romero, 1992; Gerlach, 2007). Based on the morphology of these structures, the genus has traditionally been divided into subgenera, sections, and subsections. However, this taxonomic framework is not supported by the molecular phylogeny proposed by Mauad et al. (2022), which suggests a relatively recent origin for the genus and a complex evolutionary history marked by frequent hybridization events.

The genus, comprising 192 species and 44 accepted natural hybrids (Damián et al., 2021; Krahl et al., 2022a; Calderón-Álvarez & Bonilla-Morales, 2023; Ferreira & Malaspina, 2023a,b; Krahl et al., 2023a,b,c,d,e; Assis & Ferreira, 2024; Krahl et al., 2024a,b,c,d; Romero-González & Carnevali, 2024; Krahl et al., 2025; Royal Botanic Gardens Kew, 2025), is endemic to the Neotropical region, with a distribution ranging from Mexico to southern Brazil and northern Argentina (Romero & Jenny, 1993; Romero & Carnevali, 2009). The majority of *Catasetum* taxa are found in the Amazon basin, which is considered the center of its diversity (Romero & Jenny, 1993; Silva & Silva, 1998; Romero & Carnevali, 2009).

The Brazilian Amazon stands out for harboring 80 species and 24 accepted natural hybrids (Petini-Benelli & Chiron, 2020; Cantuária et al., 2021; Barberena, 2021; Krahl et al., 2021b,c; Krahl et al., 2022a,b; Ferreira & Malaspina, 2023a,b; Krahl et al., 2023a,b,c,d,e; Assis & Ferreira, 2024; Krahl et al., 2024a,c,d; Krahl et al., 2025; Petini-Benelli, 2025), which occur across various vegetation types, including seasonally flooded forests (igapó and várzea) and dense ombrophilous forests (campina, campinarana and terra firme forest—*platô*, *vertente* and *baixio*) (Petini-Benelli, 2025). Amazonas, the

largest Brazilian state and entirely located within the Amazon biome, is particularly notable for hosting approximately 48% of the *Cataseum* species found in the Brazilian Amazon (Barberena, 2021; Krahl et al., 2021b; Krahl et al., 2023b,c; Krahl et al., 2024a; Petini-Benelli, 2025). It is also home to rare species that are infrequently encountered and thus rarely collected (Valsko et al., 2019; Krahl et al., 2023f). To date, five natural hybrids have been recorded in the state (Krahl et al., 2020; Barberena, 2021; Krahl et al., 2023a; Krahl et al., 2025; Petini-Benelli, 2025).

During occasional field expeditions in the Rio Madeira basin—specifically near Lake Carapanatuba in the municipality of Humaitá (Amazonas state)—a *Catasetum* individual of uncertain identity was encountered. This study formally describes that taxon as a nothospecies and compares it with its putative parental species. Additionally, it provides information on its habitat, ecology, phenology and geographical distribution, along with an identification key to the *Catasetum* species occurring in the Amazonas state that exhibit symmetrical and convergent antennae.

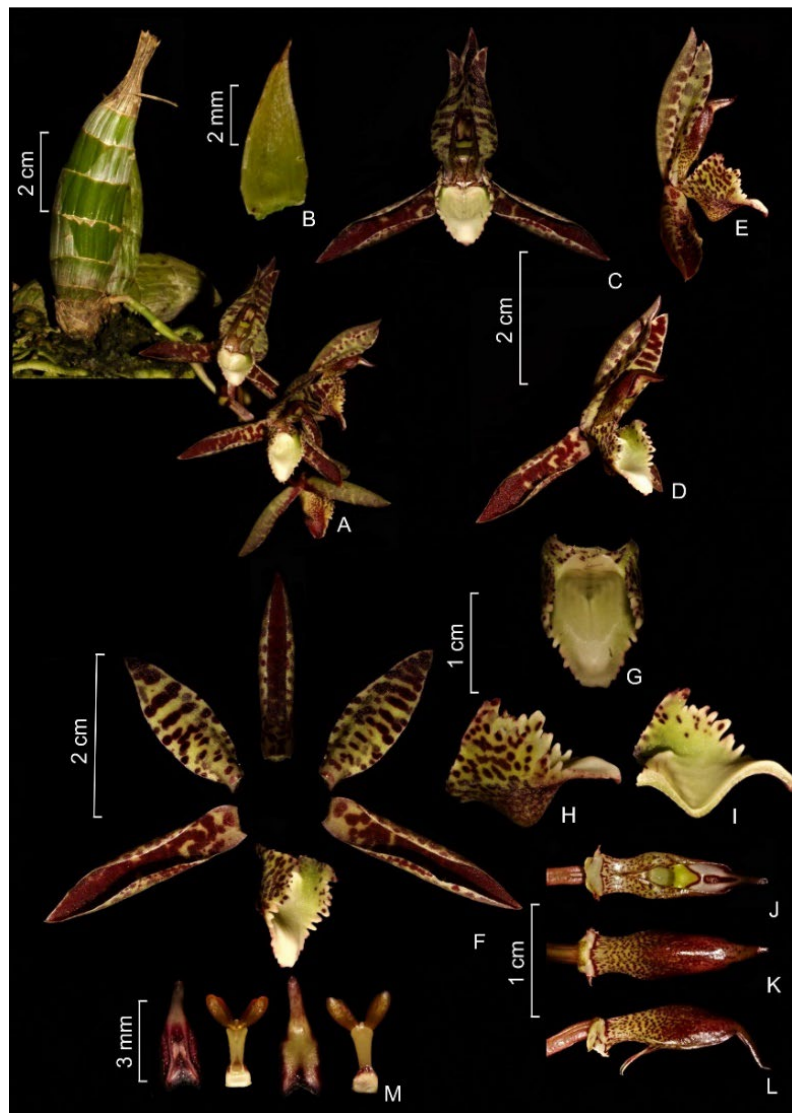
Materials and methods

The new nothospecies was collected in a sterile state near Lake Carapanatuba, in the municipality of Humaitá, and cultivated until it bloomed. Upon flowering, its vegetative and floral structures were measured, the flower was dissected, and the perianth was mounted for examination. The specimen was subsequently pressed and herborized following the standard protocol described by Mori et al. (1989), and incorporated into the collections of the Herbarium of the Federal University of Amazonas (HUAM). Photographs were taken using a Canon T5 camera with a Canon EFS 18-55mm lens. Notes on habitat, ecology, and phenology were recorded in situ. General morphological terminology follows Dressler (1993) and Harris & Harris (2001), while the nomenclature adheres to the most recent Code (Turland et al., 2018). The geographical distribution map was generated using QGIS 3.28.0-Firenze (QGIS, 2021).

The comparison between the new nothospecies and its putative parents was based on the observation of the living specimen (considering all floral attributes), as well as the analysis of the protologues (Mansfeld, 1930; Petini-Benelli, 2016b) and the type specimens deposited at the Royal Botanic Gardens (K), and the Centro Norte Mato-Grossense Herbarium (CNMT) (*C. boyi* = K000588850 [digital image!]; *C. ivanae* = CNMT6768! [digital image!], CNMT6769 [digital image!], RB01017642! [digital image!]). Specimens of *Catasetum* preserved in the following herbaria were

also examined: Instituto Federal de Educação, Ciência e Tecnologia do Amazonas (EAFM), Instituto Nacional de Pesquisas da Amazônia (INPA), Universidade Federal do Amazonas (HUAM), Royal Botanic Gardens (K), Museu Paraense Emílio Goeldi (MG), Missouri Botanical Garden (MO) and Jardim Botânico do Rio de Janeiro (RB). These institutions represent either the main regional herbaria or those with the most representative collections of the genus in northern Brazil. However, no material corresponding to the

Figure 1. Composite color plate of *Catasetum x humaitaense* nothosp. nov.



Notes. A) habit; B) floral bract; C-E) flowers; F) dissected perianth; G-I) lip; J-L) column; M) anther cap and pollinarium. Photographs by A.H. Krahl, based on the plant that served as holotype (A. H. Krahl & P. Schmal 1690♂).

new taxon was found. All herbarium acronyms follow Thiers (2025).

Based on confirmed records for the state of Amazonas reported by Cantuária et al. (2021), Krahl et al. (2023b), and Petini-Benelli (2025), this study proposes an identification key to the species and natural hybrids of *Catasetum* occurring in the Brazilian Amazonas state that exhibit symmetrical and convergent antennae—one of the diagnostic features of the new nothospecies. Given that vegetative characters alone are insufficient for reliable identification, the key is based on all available floral traits, including inflorescence arrangement, flower resupination, and, most importantly, the presentation of the labellum in each taxon.

Results and discussion

***Catasetum x humaitaense* Krahl, D.R.P.Krahl, Schmal & Cantuária nothosp. nov.**

Diagnosis: *Catasetum x humaitaense hybrida naturalis inter C. boyi et C. ivanae cum characteribus intermediis est. inflorescentia arcuatis et descendentes, flores pallidi sparsim brunneo-maculati, sepala oblongo-elliptica, petala elliptica, labelum ovatum subtrilobatum margine irregulariter denticulum cum duobus callis in loborum lateralium basi.*

Type. BRAZIL. Amazonas, Humaitá, Madeira River, Carapanatuba Lake, igapó forest, 6°46'22.11"S-62°42'36.51"W, 33 m a.s.l., 23 march 2023, R. R. P. Nascimento ex A. H. Krahl & P. Schmal 1690♂ (holotype: HUAM012581!).

Description. Epiphytic caespitose plant. Roots fasciculate, filiform, whitish, ca. 0.4-0.5 cm diam. Rhizome inconspicuous. Stem swollen into a pseudobulb, 6.4-7.9 × 1.9-2.5 cm, fusiform, covered by leaf sheaths, multi-leaved, greenish. Leaves 7.1-16.6 × 2.5-3.9 cm, oblanceolate, plicate, abaxially clearly 5-6-nerved, entire and slightly undulate margin, acute apex, green. Staminate inflorescence 8.2-9.9 cm long, lateral, racemose, arched descending, 5-6-flowered; peduncle 0.2-0.3 cm long, cylindrical, greenish becoming purplish towards apex;

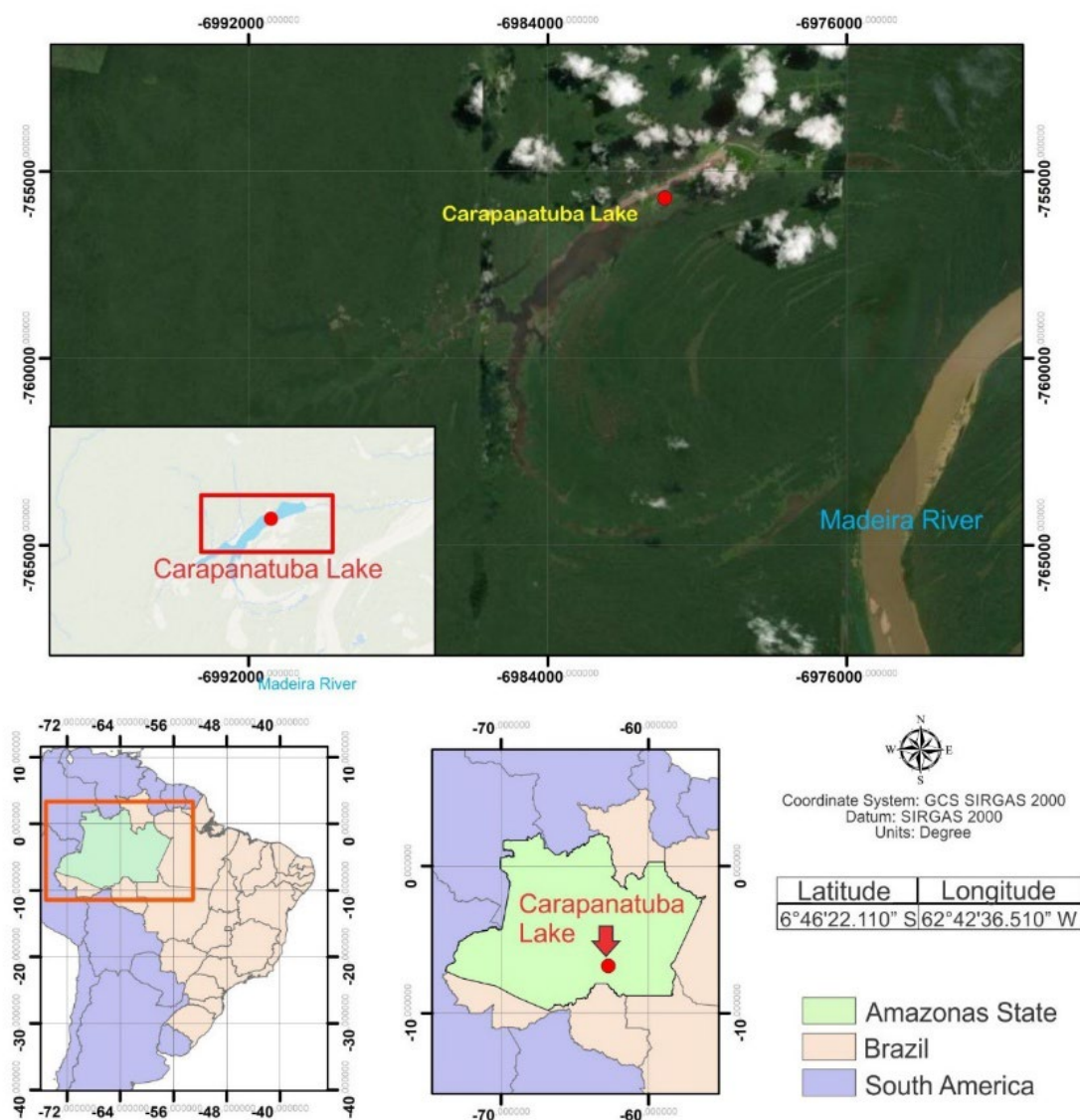
bracts at the peduncle base 0.6-0.7 cm long, amplexive, entire margin, acute apex, greenish; floral bract 0.8-0.9 × 0.3-0.4 cm, lanceolate, concave, symmetrical, entire margin, acute apex, greenish. Staminate flowers light green with brown-spotted, spaced by about ca. 1 cm, resupinate, pedicelled; pedicel 1.6-1.8 cm long, cylindrical, sinuous, brownish; sepals 2.5-2.8 × 0.9-1.1 cm, elliptic-lanceolate, involute, symmetrical, entire margin, acute apex; petals 2.2-2.4 × 0.8-0.9 cm, elliptic-lanceolate, slightly revolute at base, symmetrical, entire margin, acute apex; lip 1.2-1.4 × 1.0-1.1 cm, ovate, subtrilobed, tough and fleshy, with an ovoid bottom ca. 0.5-0.6 cm deep and two discreet calli at the base of the lateral lobes; calli 0.1-0.2 × 0.1-0.2 cm, transversely laminar, obtuse; lateral lobes 0.5-0.6 × 0.7-0.8 cm, semi-ovate, irregularly denticulated margin; apical lobe 0.5-0.6 × 0.7-0.8 cm, deltoid, discreetly denticulated margin, obtuse and revolute apex; column 1.8-2.0 cm long, oblanceoloid, thick, contracted at base, rostrate apex, greenish with brown-spotted; antennae 0.6-0.7 cm long, filiform, symmetrical, convergent, brownish; anther cap 0.6-0.7 × 0.3-0.4 cm, subtriangular, purplish brown, rostrate apex; viscidium ca. 0.1 × 0.1 cm, rounded, sticky; stipe ca. 0.3 × 0.1 cm, blade-shaped, rolled, yellowish; pollinia 2, 0.1-0.2 × 0.1 cm, oblong, hard, sulcate, compressed, yellowish. Pistillate and staminate + pistillate inflorescences not seen. Fruit not seen.

Etymology. The specific epithet refers to the name of the municipality of Humaitá (Amazonas, Brazil), where the new nothospecies was found.

Distribution, habitat and ecology. The new nothospecies flowered in cultivation during March, a period that corresponds to the rainy season in the Brazilian Amazon (Braga, 1977). It is currently known only from the type locality: Lake Carapanatuba, situated in the municipality of Humaitá, Amazonas state, Brazil (Figure 2). The species was observed growing epiphytically on thin tree branches in igapó forest, a typical Amazonian environment subject to seasonal flooding. Field observations indicate that *C. x humaitaense* grows in sympatry with one of its

putative parental species, *C. ivanae*, and both share the same locality (see [Petini-Benelli, 2016b](#); vouchers: CNMT6768!, CNMT6769! and RB01017642!). This type of flooded habitat is also known to support other congeneric nothospecies, such as *C. x sheyllae* Krahl, Cantuária & J.B.F.Silva, recently described from the state of Pará ([Cantuária et al., 2021](#)).

Figure 2. Map with the type locality (red dot) of *Catasetum x humaitaense* nothosp. nov. in the state of Amazonas (Brazilian Amazon).



Notes. Map by P.C. Cantuária.

Key to the species and nothospecies of *Catasetum* with symmetrical and convergent antennae from the state of Amazonas, Brazil

1. Non-resupinate flowers.....*C. kraenzlinium*
- 1'. Resupinate flowers.....2
2. Lip trilobed or subtrilobed.....3
- 2'. Lip entire.....4
3. Mid-lobe of the lip deltoid with a small acute callus.....*C. x sheyllae*
- 3'. Mid-lobe of the lip oval and devoid of callosity.....*C. x humaitaense*
4. Lip with fimbriae.....5
- 4'. Lip without fimbriae.....7
5. Lip oblong.....*C. krahlii*
- 5'. Lip triangular, subtriangular or ovoid.....6
6. Lip ovoid and densely fimbriated.....*C. reichenbachianum*
- 6'. Lip triangular to subtriangular with a sparsely fimbriate margin that is concentrated at the apex.....*C. rivularium*
7. Margin of the lip crenate or denticulate.....*C. ivaneae*
- 7'. Margin of the lip smooth.....8
8. Lip oblong to lingulate.....*C. tigrinum*
- 8'. Lip obovate to oval or triangular to deltoid.....9
9. Inflorescence arched to pendent; lip deeply concave; apex of lip without callus.....*C. pulchrum*
- 9'. Inflorescence erect to arched; lip relatively flat with a slight depression near the base; apex of lip with callus.....10
10. Apex of the lip ending in an obtuse to truncated callus.....*C. tenebrosus*
- 10'. Apex of the lip ending in an acute callus.....*C. sophiae*

Taxonomic discussion

In *Catasetum*, it is evident that the pre- and post-zygotic barriers that would typically isolate different taxa are weak, as indicated by growing number of records of natural hybrids within the genus (Krahl et al., 2020; Cantuária et al., 2021; Ferreira & Malaspina, 2023a; Krahl et al., 2023a; Assis & Ferreira, 2024; Krahl et al., 2024b,d; Krahl et al., 2025). There is also evidence that numerous hybridization events, combined with the genus's recent origin, have contributed to the remarkable species diversity and richness observed in *Catasetum* (Mauad et al., 2022). This notion is further supported by the absence of a consistent phylogenetic pattern, as demonstrated by Mauad et al. (2022), suggesting that the genus is still undergoing speciation. Consequently, the emergence of new nothospecies is to be expected, as exemplified by *C. x humaitaense*, which supports this hypothesis.

Moreover, the discovery of *C. x humaitaense* as a natural hybrid may have significant implications for the process of natural selection. The hybrid could interbreed or backcross with its putative parents, generating genetically and phenotypically variable offspring that may be better adapted to the environmental conditions of their habitat (Arnold, 1997). In addition, *C. x humaitaense* holds evolutionary importance, as the combination of mixed (genetic and morphological) traits inherited from its parental species may be adaptive, potentially leading to future speciation (Seehausen, 2004; Arnold, 2006).

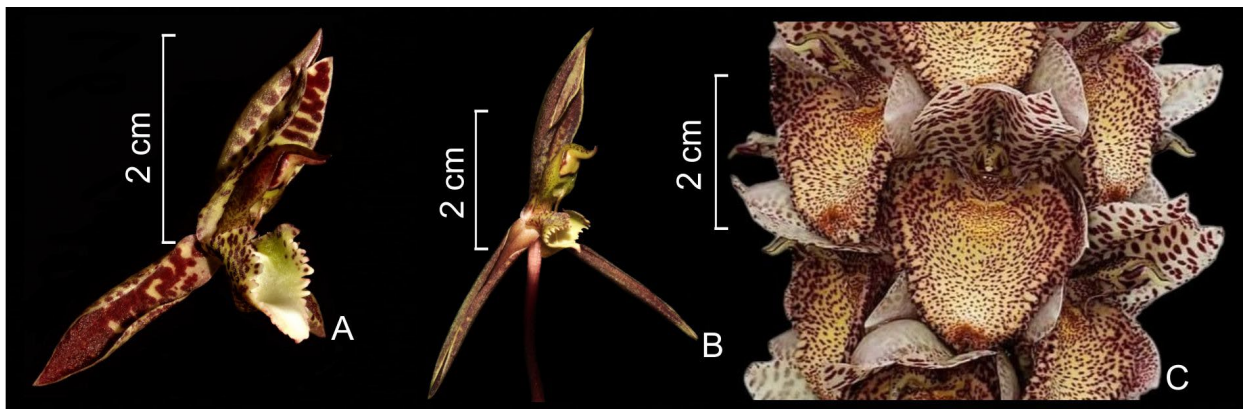
Based on the morphology of its antennae, *C. x humaitaense* is assigned to *Catasetum* subgen. *Catasetum* sect. *Isoceras* subsect. *Convergentia*, as it exhibits symmetrical and distinctly convergent antennae (Senghas, 1991; Bicalho & Barros, 1988). The hybrid also displays intermediate traits between its putative parents, *C. boyi* and *C. ivaneae* (Figure 3), as is common in other nothospecies—whether congeneric (Krahl et al., 2020; Cantuária et al., 2021; Ferreira & Malaspina, 2023a; Krahl et al., 2023a; Krahl et al., 2025) or not (Borba & Semir, 1998; Azevedo et al., 2006; Krahl et al., 2021a; Menezes & Viotti, 2024). However, such comparisons are only feasible based

on floral morphology, as diagnostic vegetative features are generally lacking in *Catasetum*. Most species share highly similar vegetative traits, making floral characteristics the primary basis for identification (Holst, 1999).

Overall, *C. x humaitaense* exhibits an arched, descending inflorescence similar to that of *C. ivaneae* (vs. arched in *C. boyi*), with flowers spaced apart as observed in *C. boyi* (vs. congested in *C. ivaneae*). The flowers are resupinate, as in both putative parents, and the coloration is more akin to *C. boyi*, being light green with brown spots. Sepals and petals are elliptic-lanceolate as in *C. boyi* (vs. ovate in *C. ivaneae*).

The lip is hard, fleshy, and ovate, resembling that of *C. ivaneae*, but is subtrilobed in a manner comparable to *C. boyi* (vs. entire in *C. ivaneae*). The lip margin bears denticles arranged in a single row, a characteristic shared with *C. boyi*, whereas in *C. ivaneae* the margin is ornamented with triangular to tube-like structures arranged in up to two rows. The base of the lip is ovate, as in *C. ivaneae* (vs. obconical in *C. boyi*), and within the lip, at the base of the lateral lobes, two small, transversely laminar and obtuse calli can be observed—traits inherited from *C. boyi*. Finally, the antennae are convergent, as in *C. ivaneae* (vs. parallel in *C. boyi*) (Figure 3) (Mansfeld, 1930; Petini-Benelli, 2016b; Petini-Benelli, 2025).

Figure 3. Composite color plate of *Catasetum x humaitaense* nothosp. nov. and their putative parents.



Notes. A) *Catasetum x humaitaense*; B) *Catasetum boyi*; C) *Catasetum ivaneae*. Photographs A-B by A.H. Krahl; C by J. Fernández.

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