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RESEARCH ARTICLE

Catasetum ×angelae (Orchidaceae: Catasetinae), a new nothospecies from the Brazilian Amazon in the subgenus *Pseudocatasetum*, and taxonomic notes for *C. pusillum*

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ABSTRACT
In this report, we propose, describe and illustrate a new *Catasetum* nothospecies from north of Manaus in the state of Amazonas, Brazil. Several factors indicate that this natural hybrid is undoubtedly the result of a crossing of *C. longifolium* and *C. roseoalbum*, including the fact that its morphological traits are intermediate between those of these species and it occurs only a few metres away from them. Therefore, it is morphologically compared to these species. Information relating to its habitat, ecology and geographical distribution are also given, as well as a key to the species and nothospecies of the subgenus *Pseudocatasetum* (antennae missing or underdeveloped). Additionally, we recognise *C. pusillum* as a natural hybrid and propose to change its taxonomic status.

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Introduction

Catasetum Rich. ex Kunth has an exclusively Neotropical distribution, extending from Mexico to southern Brazil and northern Argentina (Romero and Jenny 1993; Romero and Carnevali 2009; Chase et al. 2015). Most members of this genus are indistinguishable with respect to their vegetative morphology (Holst 1999), with rare exceptions such as *C. longifolium* Lindl. (Pessoa et al. 2015; Cantuária et al. 2021a). The pistillate flowers also exhibit only minor morphological variations and, consequently, only the staminate flowers are used to differentiate the species (Walker-Larsen and Harder 2000). In the staminate flowers, structures known as staminodes (or antennae) are of great taxonomic importance, as the current subgeneric classification is based on their presence/absence and morphology (e.g. Cogniaux 1904; Mansfeld 1932; Pabst and Dungs 1977; Bicalho

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and Barros 1988; Senghas 1990, 1991). However, the current phylogeny of the genus as presented by Mauad et al. (2022) does not support this classification and shows that the different groups are polyphyletic, with the evolution of the genus being better explained by biogeography.

Based on the staminodes, the genus is typically divided into two subgenera: *Pseudocatasetum* (Rolfe) Senghas, which is characterised by the absence of staminodes or the presence of underdeveloped staminodes, and *Catasetum*, which is characterised by the presence of distinctly developed staminodes. The subgenus *Catasetum* is further divided into two sections: (I) *Catasetum* (previously named *Anisoceras* (Mansf.) Senghas), which is distinguished by asymmetrical and crossed staminodes; and (II) *Isoceras* (Mansf.) Senghas, which is characterised by symmetrical staminodes. Section *Isoceras* is then further organised into three subsections: *Isoceras*, which has parallel staminodes; *Divaricatae* Bicalho & F.Barros, which has staminodes that stand apart from each other; and *Convergentes* Bicalho & F.Barros, which has staminodes that converge and touch each other (Bicalho and Barros 1988; Senghas 1990, 1991).

The genus *Catasetum* is comprised of 193 species, which is a particularly high richness compared with the other genera in the subtribe Catasetinae Lindl. (Krahl et al. 2022a, 2022b, 2023a, 2023b, 2023c, 2023d, 2023e, 2024a, 2024b; Álvarez and Morales 2023; POWO 2024). Its centre of diversity is the Amazonian biome (Romero and Carnevali 2009; Valsko et al. 2019; Damián et al. 2021), within which the Brazilian Amazon has particularly high diversity, providing habitat for 80 species (Silva and Silva 1998; Petini-Benelli and Chiron 2020; Barbarena 2021; Krahl et al. 2021a, 2021b, 2022a, 2022b, 2023a, 2023b, 2023c, 2023d, 2023e, 2024a, 2024b; Petini-Benelli 2024). Amazonas, the largest state in Brazil, is located in the North Region and entirely within the Amazonian biome, and 47.5% (38) of the 80 *Catasetum* species in Brazil have been documented here (Barbarena 2021; Krahl et al. 2021a, 2023b, 2023c, 2024a, 2024b; Petini-Benelli 2024), including rare species in this genus (Valsko et al. 2019; Krahl et al. 2023f).

Catasetum also holds the record for the highest number of natural hybrids recorded (POWO 2024). A total of 42 nothospecies have been documented (Krahl et al. 2020, 2023a, 2024c, 2024d; Ferreira and Malaspina 2023a, 2023b; Assis and Ferreira 2024; POWO 2024; Romero-González and Carnevali 2024), of which about 73.8% (31 hybrids) are found in Brazil and 52.4% (22 hybrids) are found in the Brazilian Amazon (Barbarena 2021; Cantuária et al. 2021b; Ferreira and Malaspina 2023a, 2023b; Krahl et al. 2023a, 2024c, 2024d; Petini-Benelli 2024). The state of Amazonas is in joint third place with the state of Pará in terms of the incidence of natural hybrids (four nothospecies each) in Brazilian territory, sitting behind Rondônia (10 nothospecies) and Mato Grosso (11 nothospecies) (Krahl et al. 2020, 2023a; Barbarena 2021; Cantuária et al. 2021b; Petini-Benelli 2024).

This large number of recorded hybrids (POWO 2024) indicates that the barriers that prevent gene flow between different taxa, such as geographical barriers, differences in perfume composition and the morphological incompatibility of pollinators, are weak in *Catasetum* (van der Pijl and Dodson 1966). The occurrence of gene flow between previously separated populations can also lead to the formation of individuals that exhibit new combinations of potentially adaptive characters, which in turn can lead to future speciation (Seehausen 2004; Arnold 2006). This also explains the lack of a phylogenetic pattern for the genus *Catasetum*, which has a relatively recent origin and a long history of hybridisation events (Mauad et al. 2022).

During field work carried out to survey the Orchidaceae species in the municipality of Manaus and the state of Amazonas, we found a *Catasetum* of unknown identity. Based on a comparison of its morphology with the other congeneric species in the locality, we concluded that it was a hybrid that had resulted from the natural crossing of two species of the subgenus *Pseudocatasetum*: *C. longifolium* and *C. roseoalbum* (Hook.) Lindl. In this report, we describe this new natural hybrid and compare it with its parental species. We also provide information relating to its habitat, ecology and geographical distribution, as well as an identification key for species and nothospecies in the subgenus *Pseudocatasetum*. Additionally, we propose to change the taxonomic status of *C. pusillum* C. Schweinf. from a species to a natural hybrid.

Materials and methods

The new nothospecies was collected from just north of Manaus in Amazonas, Brazil, while carrying out field work for the project '*Orchidaceae da região de Manaus, Amazonas, Brasil: sinopse e taxonomia*'. The voucher has been herborised according to the usual process described by Mori et al. (1989) and incorporated into the collection of the herbarium HUAM (acronym according to Thiers 2024) of the Federal University of Amazonas (Universidade Federal do Amazonas [UFAM]). Digital images were obtained using a Canon EOS Rebel T5 camera equipped with a Canon EFS 18–55 mm lens, and photographic plates were prepared from these images using the Adobe Photoshop® 2020 software. Information on the habitat, ecology and phenology were recorded *in situ*. The taxonomic description and photographs were based on living material, and the terminology used in this report follows Dressler (1993) and Harris and Harris (2001). The geographical distribution map was plotted using the QGIS 3.28.0-Firenze software (QGIS 2021). Other specimens of *Catasetum* that have been preserved in the herbaria EAFM, INPA, HUAM, K, MG, MO, NY and RB (acronyms according to Thiers 2024), main regional herbaria, and/or institutions that are most representative of northern Brazil were also analysed, but no additional material corresponding with the new taxon was found. Additionally, we searched the speciesLink (Canhos et al. 2024) and JABOT (Silva et al. 2017) databases and the virtual herbaria of Reflora (BFG 2015, 2018, 2021; Reflora 2024) and the Global Biodiversity Information Facility (GBIF) (Robertson et al. 2019; Barve 2023), but with no success.

The new nothospecies was compared to its parents (*C. longifolium* and *C. roseoalbum*) based on living material, material collected at the type locality (see 'Additional material examined' section in the Results) and the available literature (Afonso et al. 2015; Pessoa et al. 2015; Klein and Piedade 2019; Oliveira et al. 2021; Cantuária et al. 2021a; Ferreira-Filho and Barberena 2022), including both original descriptions (Lindley 1839; Hooker 1840; Barbosa-Rodrigues 1877 [as *C. ciliatum* Barb. Rodr.]). The proposal to change the taxonomic status of *C. pusillum* was based on a comparison of this taxon as it appeared through an analysis of the protologue (Schweinfurth 1943), the literature (Schweinfurth 1960) and examination of the type specimen deposited in AMES (acronym according to Thiers 2024) with its parents (considered here as *C. longifolium* and *C. discolor* (Lindl.) Lindl.) based on their original descriptions (Lindley 1835, 1839). Materials of *C. longifolium* and *C. discolor* that had been collected from Iquitos in the Loreto region of Peru, which is the same type locality as *C. pusillum*, and deposited in FLAS and NY (acronyms according to Thiers 2024) were also analysed (see 'Additional material examined' for evidence of their sympatry). The phenological and pollination characteristics of both species are also discussed based on observations reported by Romero and Carnevali (1989) and Milet-Pinheiro and Gerlach (2017) to demonstrate their capacity for cross-pollination.

When delimiting *C. roseoalbum* (=*C. ciliatum*) as a distinct species (according to Barbarena 2021) and determining its precise geographical distribution in Brazil, we disregarded the herbarium material because (1) most taxa belonging to the subgenus *Pseudocatasetum* have high morphological similarity and (2) many diagnostic characters can be lost during the drying process, both of which can lead to numerous identification errors, as occurs in various other orchid groups (e.g. Pansarin 2024). Moreover, a large amount of the herbarium material has been misidentified because many *Pseudocatasetum* species were treated as synonyms in the past (e.g. Braga 1977). Therefore, we used only reliable data from relevant literature (e.g. Hooker 1840; Barbosa-Rodrigues 1877; Afonso et al. 2015; Barbarena et al. 2019; Klein and Piedade 2019; Oliveira et al. 2021; Ferreira-Filho and Barberena 2022; Filardi-Barbosa et al. 2023; Luz et al. 2024; Petini-Benelli 2024; POWO 2024).

Results

Taxonomic treatment

Catasetum ×angelae Krahl, D.R.P.Krahl, M.S.Oliveira & Cantuária, **nothosp. nov.** (Figures 1 and 2).

Type: BRAZIL: Amazonas: Manaus, Ramal (Road) Cláudio Mesquita, old km 02 of BR 174, epiphyte in Inajá (*Attalea maripa*), 2°56′33.43″S, 60˚3′6.75′′’W, 27 March 2023, flowers ♂, *A.H. Krahl & D.R.P. Krahl 1702* (holotype: HUAM012562!).

Diagnosis: *Hoc taxon hybrida naturalis inter Catasetum roseoalbum (Hook.) Lindl. and Catasetum longifolium Lindl. est, cum characteribus intermediis: pseudobulbo erecto vel inclinato, foliis lineare-lanceolatis cum lamina foliari pendente, inflorescencia subpendente cum floribus cupreo-luteis, labello galeiforme ambito triangulare apice acuto cum marginibus longe ciliatis.*

Epiphytic caespitose plant. Rhizome short and inconspicuous. Pseudobulb 6.3–13.1 × 1.5–2.4 cm, fusiform, erect or inclined, grouped, 6–7-leaved, covered by leaf sheaths. Leaves 18.4–42.2 × 1.6–2.3 cm, linear-lanceolate, plicate, with 3 prominent nerves on the adaxial face, distichous, deciduous, margin entire, apex acute. Staminate inflorescence ca. 21.8 cm long, lateral, racemose, ca. 6-flowered, subpendent; rachis ca. 12.6 cm long, cylindrical, light green; peduncle ca. 9.2 cm long, cylindrical, light green; peduncle bract 0.9–1 × 0.4–0.5 cm, ovate, amplexicaul, light green, margin entire, apex acute; floral bract ca. 0.8–0.9 × 0.4–0.5 cm, oblong-lanceolate, greenish, margin entire, apex acute. Staminate flowers copper-yellow, pedicellate, lip usually facing downwards; pedicel 1.8–2.1 cm long, cylindrical, erect, copper-yellow; dorsal sepal 1.5–1.7 × 0.6–0.7 cm, elliptic-lanceolate, symmetrical, margin entire, apex acute; lateral sepals 1.7–1.9 × 0.6–0.7 cm, oblong, symmetrical, concave, slightly curved, margin entire, apex acute; petals 1.7–1.9 × 1–1.1 cm, oblong-rounded, slightly asymmetrical near the base, margin entire, apex rounded; lip 1.8–1.9 × 2–2.1 cm (fimbriae excluded), helmet-shaped, triangular in outline, strongly yellowish with light transverse copper stains

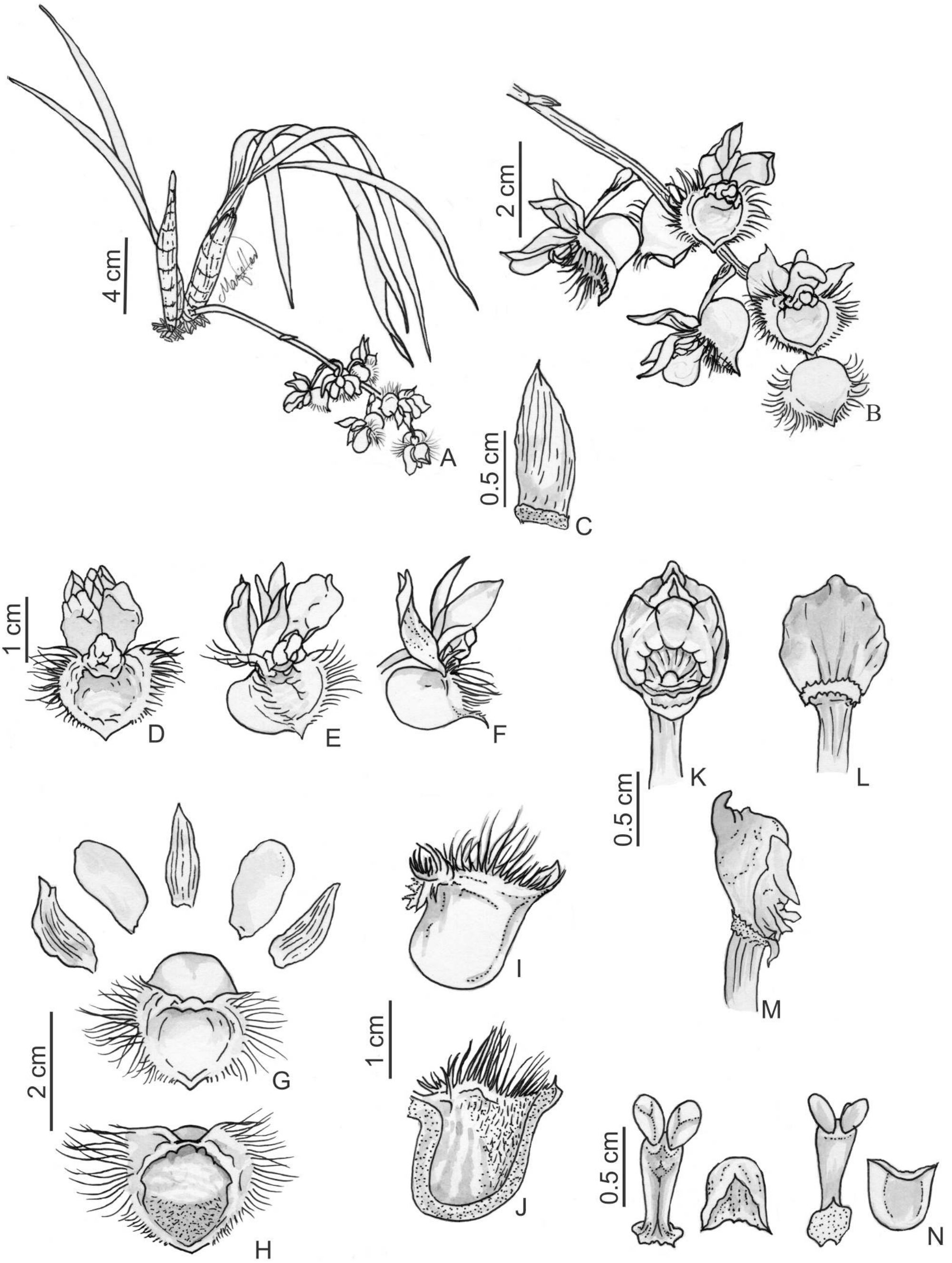

Figure 1. Illustration of *Catasetum ×angelae* Krahl, D.R.P.Krahl, M.S.Oliveira & Cantuária. **A,** Habit. **B,** Inflorescence. **C,** Floral bract. **D–F,** Flower. **G,** Floral segments. **H–J,** Lip. **K–M,** Column. **N,** Pollinarium and anther cap. Drawn by M.F. Negrão based on the plant that served as the type.

inside, internally pubescent, margin long fimbriate, apex acute and reddish; fimbriae 0.6–1.1 cm long, thread-like, simple or partly fused near the base, copper-coloured; lip bottom 1.1–1.2 cm deep, bottom rounded; column 1–1.2 × 0.8–0.9 cm, rounded in

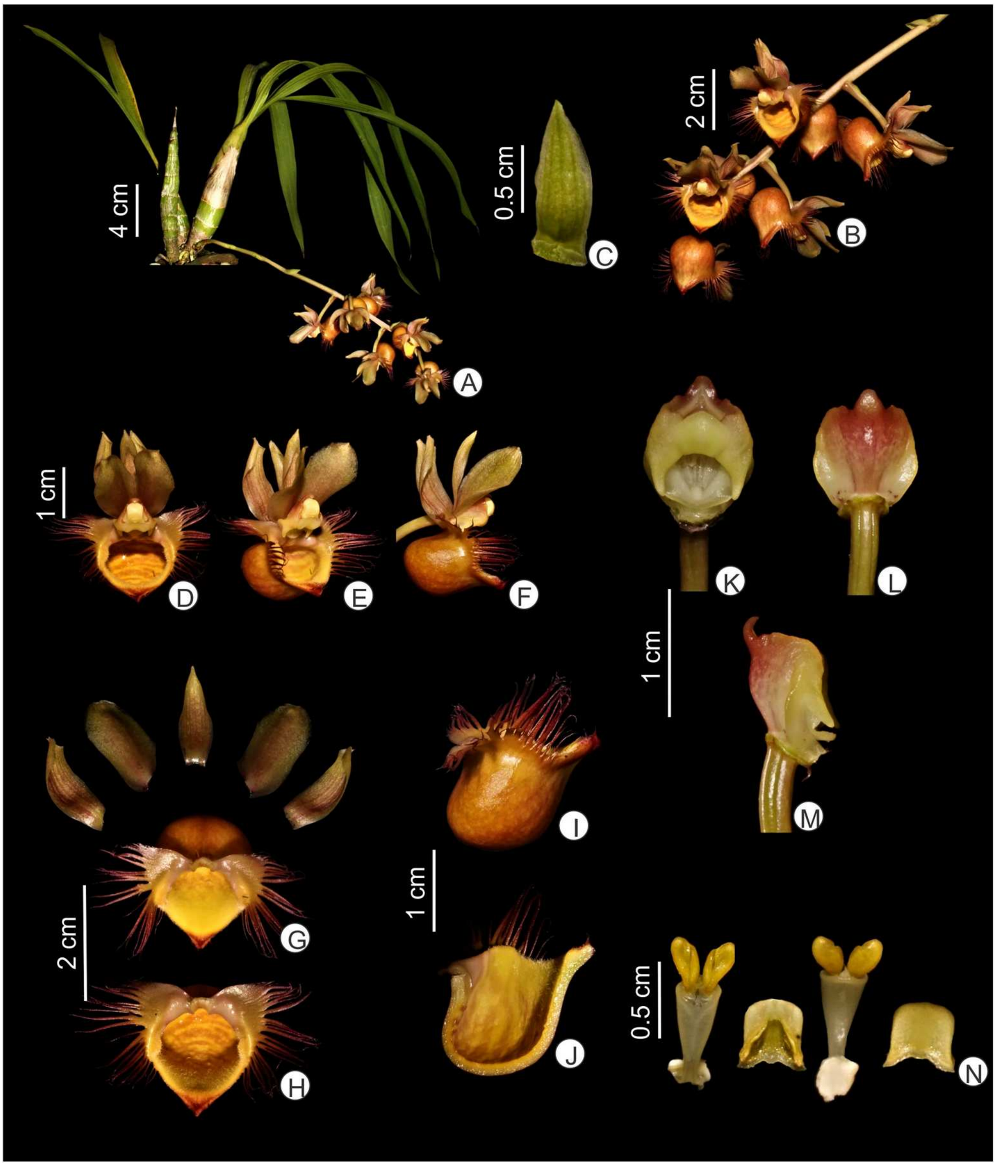

Figure 2. Composite colour plate of *Catasetum* ×*angelae angelae* Krahl, D.R.P.Krahl, M.S.Oliveira & Cantuária. **A,** Habit. **B,** Inflorescence. **C,** Floral bract. **D–F,** Flower. **G,** Floral segments. **H–J,** Lip. **K–M,** Column. **N,** Pollinarium and anther cap. Photos by A.H. Krahl based on the plant that served as the type.

ventral or dorsal view, copper-yellow on the back, light yellow on the ventral face, apex apiculate; antennae missing/underdeveloped; anther cap 0.3–0.4 × 0.2–0.3 cm, oblong, unilocular, light yellow, apex rounded; viscidium 0.1–0.2 × 0.1–0.2 cm, whitish, sticky; stipe 0.4–0.5 cm long, laminar, whitish, rolled up; pollinia 2, 0.2–0.3 × 0.1–0.2 cm, obovate, hard, compressed, sulcate, yellow. Pistillate and staminate + pistillate inflorescence not observed. Fruit unknown.

Etymology: The specific epithet is given in tribute to Ângela Maria Krahl, an orchid enthusiast and the mother of one of the authors responsible for collecting the type specimen (A.H. Krahl).

Distribution, habitat and ecology: The new nothospecies was found in bloom in May 2023, a few kilometres to the north of Manaus (Amazonas, Brazil) in a rural area on the side of the Ramal (Road) Cláudio Mesquita and a left tributary of the Tarumã-Açu River (Figure 3). The environment is sandy/clayish soil and quite degraded due to real estate speculation. We observed a predominance of Inajá palm trees (*Attalea maripa* (Aubl.) Mart.), which were being used as a phorophyte by the new taxon described here. We also observed a large presence of *C. roseoalbum* on this palm species, as well as the presence of *C. longifolium* on Buriti palm trees (*Mauritia flexuosa* L.f.) ca. 300 m away (Figure 3). No other *Catasetum* species were found nearby. Both putative parents were observed flowering on the same day (see 'Additional material examined' below), indicating an overlap in the flowering period that would allow cross-pollination. Additionally, both parents share the same group of pollinators – male bees of the genus *Eulaema* (Milet-Pinheiro and Gerlach 2017; personal observations). Consequently, we have no doubt that the hybrid *C.* ×*angelae* has resulted from the natural crossing of *C. longifolium* and *C. roseoalbum*.

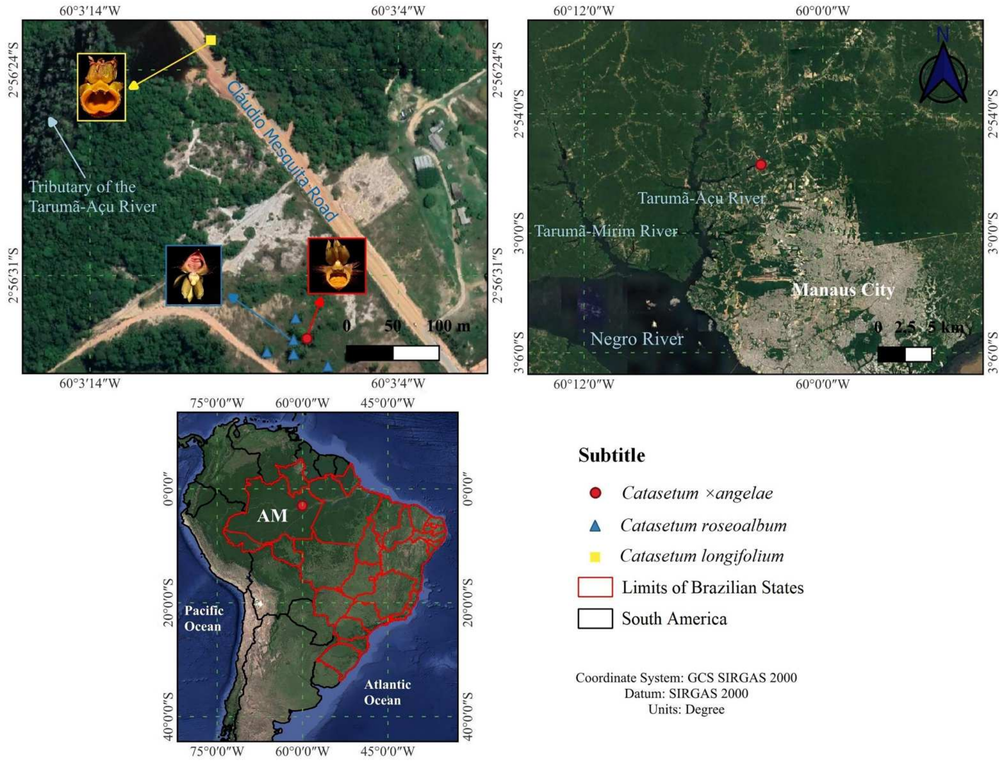

Figure 3. Geographical location of *Catasetum* ×*angelae* and its parents (*Catasetum roseoalbum* and *Catasetum longifolium*) at the type locality in the municipality of Manaus, Amazonas (AM), Brazilian Amazon. Map by A.H. Krahl.

Nomenclatural status of *C. pusillum*: A new taxonomic circumscription for *C. pusillum* is proposed below. The reasons for this proposal will be discussed later in the report but were based on a comparison of the morphology and occurrence of *C. discolor* and *C. longifolium* (considered here as parent species of *C. pusillum*) in the city of Iquitos, the capital of the Department of Loreto in Peru (see 'Additional material examined' below).

Catasetum* ×*pusillum C. Schweinf., Amer. Orchid Soc. Bull. 12: 100, t. 4, 1943 (pro. sp.), **nothosp. et stat. nov.**

Type: PERU: Loreto: Vicinity of Iquitos, 100 m, dense forest, on living tree, November-December 1936, flowers ♂, *G. Klug 10015* (holotype: AMES00217929!).

Additional material examined (*C. discolor*): PERU: No plant collection information, cultivated in greenhouse at University of Florida, HH8609-001, 29 September 1986, flowers ♂, *H.G. Hills 86075* (FLAS!); collection location unknown, ex hort. Tropical World Orchids, living accession of H.G. Hills, HH860910, 01 November 1987, flowers ♂, *H.G. Hills 87008* (FLAS!); Loreto: Manas, Iquitos, no additional collection information, 15 December 1985, flowers ♂, *H.G. Hills 1007* (FLAS!); *idem.* no additional collection information, 03 January 1987, flowers ♂, *H.G. Hills 87009* (FLAS!).

Additional material examined (*C. longifolium*): BRAZIL: Amazonas: Manaus, Ramal (Road) Cláudio Mesquita, old Km 02 of BR 174, epiphyte in Buriti (*Mauritia flexuosa*), 2°56′23.5″S, 60°3′10.0″W, 16 February 2024, flowers ♂, *A.H. Krahl & D.R.P. Krahl 1727* (HUAM!); PERU: Loreto: Iquitos, 100 m, epiphytic on palm, 26 October 1929, apparently sterile material, *E.P. Killip & A.C. Smith 29833* (NY!).

Additional material examined (*C. roseoalbum*): BRAZIL: Amazonas: Manaus. Ramal (Road) Cláudio Mesquita, old Km 02 of BR 174, epiphyte on Inajá (*Attalea maripa*), 2°56′33.4″S, 60°3′6.7″W, 16 February 2024, flowers ♂, *A.H. Krahl & D.R.P. Krahl 1728* (HUAM!); *idem*, 10 March 2024, flowers ♂, *A.H. Krahl 1730* (HUAM!).

Discussion

Under the biological species concept, a species can be defined as a group of individuals that reproduce among themselves and are reproductively isolated from other similar groups. However, for this understanding, Mallet (2001) noted that different species may often lack a unitary biological reality in their geographical areas and over geological time. Furthermore, in most cases, independent species have a wide geographical distribution and stability in their morphological characters. On the other hand, the concept of nothospecies is associated with distinct populations, previously isolated by pre- or post-zygotic barriers, that eventually have come into contact and interbred to produce offspring with mixed characters, i.e. with characteristics that are intermediate to those of their parents (e.g. Azevedo et al. 2006; Krahl et al. 2020, 2021c, 2024c; Cantuária et al. 2021b). This interpretation is evidenced by the recognition of the parents and their presence in areas close to the collection site of the nothospecies (Barton and Hewitt 1989; Arnold 1992).

An understanding and application of these two concepts is important for *Catasetum*, as it is one of the few examples in the world of a plant genus in which species formation has occurred as a result of a long history of hybridisation, making biogeography an important consideration (Mauad et al. 2022). Thus, the current recognition of species (e.g. Petini-Benelli and Chiron 2020; Damián et al. 2021; Krahl et al. 2021a, 2021b, 2022a, 2022b, 2023b, 2023c, 2023d, 2023e, 2024a, 2024b; Álvarez and Morales 2023) and nothospecies (e.g. Krahl et al. 2020, 2023a; Cantuária et al. 2021b; Ferreira and Malaspina 2023a, 2023b; Assis and Ferreira 2024; Romero-González and Carnevali 2024) is extremely important to understanding the current evolutionary course that *Catasetum* is following, since hybridisation is still an apparently common event in this genus. The impact of human activities on the landscape and vegetation may be one explanation for the high number of nothospecies of *Catasetum*. Indeed, according to Krahl et al. (2023a), the removal of the natural vegetation barrier between species and subsequent emergence of pastures would favour gene flow between different species of this genus that would otherwise never have come into contact (e.g. Krahl et al. 2020).

Of the two *Catasetum* subgenera, *Pseudocatasetum* is of particular interest because it has few representatives (Romero and Jenny 1993; POWO 2024) and most of these are found in the Brazilian territory (Petini-Benelli 2024; POWO 2024). Members of *Pseudocatasetum* either lack staminodes or present only rudimentary staminodes. They also usually produce non-resupinate and helmet-shaped flowers (Mauad et al. 2022). Only five species are currently known: *C. discolor*, *C. gardneri* Schltr., *C. longifolium*, *C. pusillum* and *C. roseoalbum* (Romero and Jenny 1993; Barbarena 2021; Petini-Benelli 2024; POWO 2024). In the checklist published by POWO (2024), *C. cassideum* Linden & Rchb.f. also appears as a valid species, but this is treated as a synonym of *C. discolor* by Romero and Jenny (1993) due to it having been described on the basis of a pistillate flower of *C. discolor*. Among these members, *C. pusillum* is without doubt the least-known taxon and is often overlooked in discussions of the subgenus. This species is described and known from only one specimen collected by G. Klug (collection number 10015) in the Department of Loreto, Peru (Schweinfurth 1943), and deposited in AMES (barcode AMES00217929!). After analysing this specimen, we concluded that *C. pusillum* is actually a natural hybrid between *C. discolor* and *C. longifolium*, so from here, we will adopt the name *C.* ×*pusillum*.

A hybrid status was mistakenly applied by Romero and Carnevali (1989) to *C. roseoalbum*, which was partially clarified by Barbarena (2021) who, after analysing the protologues, illustrations and herborised material, concluded that *C. roseoalbum* is a true species and *C. ciliatum* is one of its synonyms. At first, we also mistakenly believed that *C. roseoalbum* was a hybrid between *C. discolor* and *C. longifolium* (disregarding *C. ciliatum* as a synonym) (see Krahl et al. 2023a). However, after improved analysis of the information presented by Barbarena (2021), we agreed that *C. roseoalbum* and *C. ciliatum* are the same taxon. The illustrations (Figure 4) and protologues of Hooker (1840) and Barbosa-Rodrigues (1877) are consistent with a single morphological circumscription, and the type material for each comes from the same broad locality (state of Pará, northern Brazil) (Barbarena 2021). Therefore *C. ciliatum* should be considered a synonym of *C. roseoalbum*, since the latter name is the oldest. However, while Barbarena (2021) demonstrated this, he did not clarify the real question around *C. roseoalbum*: is *C. roseoalbum*, in fact, a nothospecies (a natural hybrid between *C. discolor* and *C. longifolium*)?

Here, we argue that *C. roseoalbum* should be treated as an independent species, as have many authors before us (e.g. Bastos and van den Berg 2012; Romero-González

Figure 4. Illustrations of **A,** *Catasetum roseoalbum* and **B,** *Catasetum ciliatum* (=*C. roseoalbum*). **A,** Illustration contained in the protologue of Hooker (1840), reproduced with the consent of the publisher Biodiversity Heritage Library, Contributed by Missouri Botanical Garden, Peter H. Raven Library. **B,** Illustration by Barbosa Rodrigues published by Sprunger et al. (1996), reproduced with the consent of the publisher Friedrich Reinhardt Verlag; this illustration also represents the lectotype of *C. ciliatum* (=*C. roseoalbum*) as designated by Romero and Jenny (1993).

2012, 2018; Cárdenas et al. 2017; Barbarena 2021; Ferreira-Filho and Barberena 2022; Álvarez and Morales 2023; Luz et al. 2024; POWO 2024). This is because it has a wide geographical distribution that, at least in Brazil, extends from the Amazon (Hooker 1840; Barbosa-Rodrigues 1877; Afonso et al. 2015; Klein and Piedade 2019; Oliveira et al. 2021; Ferreira-Filho and Barberena 2022; Luz et al. 2024; Petini-Benelli 2024; POWO 2024) to at least the state of Bahia (northeastern Brazil) (Barbarena et al. 2019; Filardi-Barbosa et al. 2023), whereas nothospecies typically tend to have more sporadic distributions (e.g. Krahl et al. 2020, 2024c, p. 2024d; Cantuária et al. 2021b; Romero-González and Carnevali 2024). Additionally, *C. roseoalbum* occurs in localities where one or both of the putative parents do not occur, including Maranhão (Oliveira et al. 2021; Petini-Benelli 2024) and Bahia (Barbarena et al. 2019; Filardi-Barbosa et al. 2023; Petini-Benelli 2024).

The frequency of occurrence also supports the idea that *C. roseoalbum* is an independent species, as *C. roseoalbum* has a much higher frequency of occurrence than either *C. discolor* or *C. longifolium*. In Manaus (state of Amazonas, Brazil), *C. roseoalbum* occurs in every stretch of native vegetation, whereas no *C. discolor* plants have been observed in the municipality and very few occurrences of *C. longifolium* have been recorded (Braga 1977 [*C. roseoalbum* treated as *C. discolor*]; personal observations).

Similar observations have been made in the municipalities of Itapiranga (Amazonas), São Sebastião do Uatumã (Amazonas) (Klein and Piedade 2019), Maués (Amazonas) (personal observations), Abatetuba (Pará) (Afonso et al. 2015), Igarapé-Miri (Ferreira-Filho and Barberena 2022) and Codó (Maranhão) (Oliveira et al. 2021). We also emphasise that certain records of occurrence of *C. discolor* for the Brazilian Amazon are likely to be erroneous since *C. discolor*, *C. roseoalbum* and *C. ciliatum* were previously considered synonyms, as can be seen in the work of Braga (1977).

Catasetum roseoalbum forms huge populations in the Amazon, mainly in Brazil, in which individuals interbreed to produce fertile descendants within their populations, thus maintaining their own identity. However, the possibility of *C. roseoalbum* maintaining gene flow with other species is not ruled out, as this is notoriously common within *Catatasetum*, with many natural hybrids having been described to date (e.g. Romero and Carnevali 1990; Petini-Benelli 2010, 2012, 2014, 2016; Krahl et al. 2020, 2023a; Ferreira and Malaspina 2023a, 2023b; Assis and Ferreira 2024; POWO 2024; Romero-González and Carnevali 2024). It should be noted that we do not disregard the observations of Romero and Carnevali (1989), which were based on biological data, including pollinator and habitat data, and were strongly supported by the observations of Dodson (1978). We simply argue that such observations should be applied to *C.* ×*pusillum* and not *C. roseoalbum*, which has too wide a geographical distribution to be considered a hybrid, occurs in places where *C. discolor* and *C. longifolium* are absent, and has a very high frequency of occurrence compared with the putative parents.

Catasetum ×*pusillum* has only been collected once and shows characters that are clearly intermediate between *C. discolor* and *C. longifolium*. Romero and Carnevali (1989) emphasised that gene flow between these two taxa is possible since they are sympatric, show overlap in the blooming period and share the same pollinator group. Milet-Pinheiro and Gerlach (2017) further showed that *C. discolor* and *C. longifolium* share as pollinators the males of *Eulaema bombiformis* (Williams and Dodson 1972; Dodson 1978), *E. cingulata* (Hills et al. 1972; Dodson 1978) and *E. meriana* (Hills et al. 1972; Dodson 1978), possibly because flowers of both taxa have a perfume with similar composition (see Hills et al. 1968; Hills et al. 1972).

Catasetum ×*pusillum* presents rather long and narrow leaves, which are similar to but not as long as those of *C. longifolium*. The leaf shape is linear-oblanceolate, which is intermediate between what is observed in *C. discolor* (leaves oblong-lanceolate) and *C. longifolium* (leaves linear-lanceolate). The inflorescence is arched and also intermediate between that of *C. discolor* (erect) and *C. longifolium* (pendulous). The lip is hemispheric with a serrate margin, whereas the margin is minutely serrate to short-fimbriate in *C. discolor* and short-ciliate in *C. longifolium* (Schweinfurth 1943; Petini-Benelli 2024). From the material deposited in FLAS and NY, we also observed that *C. discolor* and *C. longifolium* are sympatric in the city of Iquitos (type locality of *C. pusillum*). We believe that *C.* ×*pusillum* could occur over a wide geographical range, as both putative parents have wide geographical distributions (Brazil, Colombia, French Guiana, Peru, Suriname and Venezuela) (POWO 2024). However, a thorough revision of the various specimens of *Pseudocatasetum* deposited in the different herbaria around the world is necessary to precisely determine its actual occurrence.

To date, no natural hybrids have been recorded between species belonging exclusively to the subgenus *Pseudocatasetum*, although there are hybrids for which one of the parents is in *Pseudocatasetum* (e.g. Romero and Carnevali 1989; Romero and Jenny 1992; Bicalho 1996; Petini-Benelli and Grade 2012; Ferreira 2013; Petini-Benelli 2016; Krahl et al. 2020). Thus *C.* ×*pusillum* (designated here as a natural hybrid) and *C.* ×*angelae* (described here) are the sole hybrids currently known that exclusively belong to this subgenus.

Catasetum ×*angelae* is the result of natural hybridisation between *C. longifolium* and *C. roseoalbum* and presents intermediate characters. Its pseudobulbs are erect or bent down, as observed in *C. roseoalbum*, whereas the pseudobulbs are pendent in *C. longifolium*. The leaves have the same shape as those of *C. longifolium* (linear-lanceolate) but are a similar length to those of *C. roseoalbum* (18.4–42.2 cm), being shorter than in *C. longifolium* (41–135 cm). The subpendulous inflorescence is intermediate between the erect to arched inflorescence of *C. roseoalbum* and the fully pendent inflorescence of *C. longifolium*. The flower colour is coppery on the outside and yellowish inside, as in *C. longifolium* (*vs*. the yellowish green or pale yellow flowers with a margin and reddish fimbriae in *C. roseoalbum*), but there are transverse spots inside the lip, as observed in *C. roseoalbum*. The petals have a slight asymmetry at the base, as in *C. roseoalbum* (*vs*. the symmetrical petals of *C. longifolium*). The lip is generally facing downwards, as in *C. longifolium* (*vs*. facing upwards in *C. roseoalbum*), and helmet-shaped with a triangular-rounded contour (*vs*. triangular in *C. roseoalbum* and rounded in *C. longifolium*), and has a long-ciliate/fimbriate margin, as in *C. roseoalbum* (*vs*. exclusively ciliate in *C. longifolium*), and an acute apex, as in *C. roseoalbum* (*vs*. obtuse to truncate in *C. longifolium*). *Catasetum* ×*angelae* also has a pubescence inside the lip, as in *C. roseoalbum* (*vs*. the glabrous lip of *C. longifolium*) (Figure 5) (see Lindley 1839; Hooker 1840; Barbosa-Rodrigues 1877; Afonso et al. 2015; Pessoa et al. 2015; Klein and Piedade 2019; Oliveira et al. 2021; Cantuária et al. 2021a; Ferreira-Filho and Barberena 2022). Further comparisons of these taxa are provided in Table 1.

Because they share a common parent (*C. longifolium*), *C.* ×*angelae* and *C.* ×*pusillum* present some morphological similarities, mainly in their vegetative characteristics. Both taxa have fusiform pseudobulbs and narrow and rather long leaves with pendent laminae (features that are close to those of *C. longifolium*). The inflorescence structure and flowers are also somewhat similar, even if some distinctive characters can be observed, mainly in the lip structure. In both taxa, the lip is helmet-shaped, but in *C.* ×*angelae*, it has a more triangular contour with a long-fimbriate/ciliate margin, whereas in *C.* ×*pusillum*, it is more rounded with a serrate margin. Additionally, the inflorescence is subpendent in *C.* ×*angelae* and arched in *C.* ×*pusillum* (see Schweinfurth 1943). Such differences possibly result from characters inherited from the other parent (*C. roseoalbum* for *C.* ×*angelae* and *C. discolor* for *C.* ×*pusillum*).

The discovery of *C.* ×*angelae* and the elucidation of *C.* ×*pusillum* as natural hybrids is of great importance for natural selection because both will be able to breed or backbreed with their parents, producing offspring with genetic and phenotypic variation that will be of significant relevance to their adaptation in a given environment (Arnold 1997). Furthermore, both also have significant evolutionary importance, as combinations of mixed characteristics (genetic and morphological) inherited from parental species can also be potentially adaptive, which in turn can lead to future speciation (Seehausen 2004; Arnold 2006). These findings corroborate the phylogeny presented by Mauad et al. (2022), which demonstrates that the genus *Catasetum* is still in the process of

Figure 5. Colour plate showing a comparison between **A–C,** *Catasetum ×angelae*, **D–F,** *Catasetum roseoalbum* and **G–I,** *Catasetum longifolium*. Photos by A.H. Krahl.

speciation and adaptation. The ongoing speciation process in *Catasetum* is also demonstrated by the recent emergence of several nothospecies (e.g. Krahl et al. 2020, 2023a; Cantuária et al. 2021a; Álvarez and Morales 2023; Assis and Ferreira 2024), with *C. ×angelae* providing another example.

Just over 40 natural hybrids have been proposed within the genus *Catasetum* (Krahl et al. 2020, 2023a, 2024c, 2024d; Ferreira and Malaspina 2023a, 2023b; Assis and Ferreira 2024; POWO 2024; Romero-González and Carnevali 2024), so some may think that it is not useful to enlarge the list of nothospecies. However, it is necessary to have a well-defined name to scientifically talk about a specimen and to easily find the herbarium type specimen and search for its original description, even if the corresponding taxon is rare in the wild. Additionally, the discovery of a large number of natural hybrids within a genus is not insignificant – it says something about the genus' characters, particularly its evolutionary and reproductive processes (together with its pollinators). And to evaluate the number of natural hybrids, it is essential that each is named, even if this does require a precise morphological description.

We also emphasise that the application of morphological analysis for the genus *Catasetum*, as demonstrated in this work, is of great relevance, mainly because the current phylogeny (as demonstrated by Mauad et al. 2022) is not very useful due to the absence of a phylogenetic pattern for the sampled species. When combined with other tools (e.g. artificial crossing between different taxa and subsequent *in vitro* germination;

Table 1. Comparison between *Catasetum ×angelae*, *C. longifolium* and *C. roseoalbum*. Based on the (1) this study, (2) Lindley (1839), (3) Pessoa et al. (2015), (4) Cantuária et al. (2021a), (5) Petini-Benelli (2024), (6) Hooker (1840), (7) Barbosa-Rodrigues (1877), (8) Afonso et al. (2015), (9) Klein and Piedade (2019), (10) Oliveira et al. (2021), (11) Ferreira-Filho and Barberena (2022), (12) personal observations.

Characters	*C. ×angelae*[1]	*C. longifolium*[2,3,4,5,12]	*C. roseoalbum*[5,6,7,8,9,10,11,12]
Pseudobulb	**6.3–13.1 × 1.5–2.4 cm, fusiform, erect or inclined**	8–32 × 2–5 cm, fusiform, pendent.	5–20 × 0.9–4 cm, fusiform, erect or inclined.
Leaves	**18.4–42.2 × 1.6–2.3 cm, linear-lanceolate, with 3 prominent nerves on the adaxial face**	41–135 × 0.7–3.5 cm, linear-lanceolate, with 3 prominent nerves on the adaxial face	8–42 × 2.3–5.5 cm, oblong-lanceolate, with 5 prominent nerves on the adaxial face
Staminate inflorescence	**ca. 21.8 cm long, ca. 6-flowered, subpendent**	ca. 9.5–28 cm long, ca. 2–7-flowered, pendent	10–55 cm long, ca. 4–15-flowered, erect or arched
Staminate flower colour	**Copper yellow, lip strongly yellowish with light transverse copper colour stains inside, fimbriae copper-colored, apex reddish**	Copper yellow, lip strongly yellowish inside, fimbriae copper-colored, apex reddish	Greenish yellow or pale yellow, lip yellowish with pale transverse pink spots inside, fimbriae pink or reddish, apex pink or reddish
Dorsal sepal	**1.5–1.7 × 0.6–0.7 cm, elliptic-lanceolate, symmetrical, apex acute**	0.8–1.6 × 0.6–0.7 cm, ovate-lanceolate, symmetrical, acute	0.7–1.8 × 0.3–0.8 cm, oblong-elliptic, symmetrical, acute
Later.al sepals	**1.7–1.9 × 0.6–0.7 cm, oblong, symmetrical, slightly curved, apex acute**	1.2–1.9 × 0.5–0.8 cm, lanceolate, symmetrical, slightly curved, acute	1–2 × 0.3–0.8 cm, oblong-elliptic, symmetrical, acute
Petals	**1.7–1.9 × 1–1.1 cm, oblong-rounded, slightly asymmetrical near the base, apex rounded**	1.4–1.6 × 0.7–1 cm, ovate, symmetrical obtuse	1–2.2 × 0.6–1 cm, oblong-linear, asymmetrical at base, obtuse
Lip	**1.8–1.9 × 2–2.1 cm (fimbriae excluded), helmet-shaped, triangular-rounded in outline, internally pubescent, usually facing downwards, apex acute**	1.6–2.8 × 1.4–2.2 cm, helmet-shaped, rounded contour, glabrous inside, usually facing downwards, apex obtuse to truncate	1.0–2.3 × 1.1–1.5 cm, helmet-shaped, triangular contour, pubescent inside, usually facing upwards, apex acute
Column	**1–1.2 × 0.8–0.9 cm, rounded in ventral or dorsal view, copper-yellow on the back, light yellow on the ventral face, apex apiculate**	0.5–0.7 × 0.4–0.5 cm, rounded in ventral or dorsal view, yellowish, apex discreetly dentate	0.5–1 × 0.3-0.5 cm, rounded in ventral or dorsal view, pale yellowish, apex pink, apiculate
Antennae	**Absent/underdeveloped**	Absent/underdeveloped	Absent/underdeveloped

Figure 6. Colour plate with some of the *Catasetum* representatives of the subgenus *Pseudocatasetum*. **A,** *Catasetum ×angelae*. **B,** *Catasetum discolor*. **C,** *Catasetum gardneri*. **D,** *Catasetum longifolium*. **E,** *Catasetum roseoalbum*. Photos by A.H. Krahl.

see Krahl et al. 2023a), morphological analysis can elucidate the answers to several taxonomic questions similar to those presented here. Additionally, the constant collection of representatives of *Catasetum* in the Brazilian Amazon, mainly by J.B.F. Silva for more than 50 years, allows us to recognise stable populations and carry out the necessary taxonomic interpretations, as botanical names are constructed and organised based on a systematisation that reflects stability.

Finally, this work presents an adequate and consistent taxonomic reorganisation of the subgenus *Pseudocatasetum*, which, despite being represented by only a few species, raises taxonomic questions. However, this is just a small portion of what must be reorganised and revealed within the genus *Catasetum* given its wealth of species.

Key to the species and nothospecies of *Catasetum* subgenus *Pseudocatasetum* (absent or underdeveloped antennae) (Figure 6)

1. Completely pendent plants.. *C. longifolium* (Figure 6D)
1’. Erect or bent down plants.. 2
2. Slender plant; leaf linear-oblanceolate; leaf blade with 3 prominent veins; arched inflorescence.. 3
2’. Robust plant; leaf oblong-lanceolate; leaf blade with 5–7 prominent veins; erect inflorescence... 4
3. Inflorescence arched; margin of the lip crenate-serrate; lip rounded........ .... *C. ×pusillum*

3’. Inflorescence subpendent; margin of the lip long-fimbriate; lip rounded-triangular…. .... *C.* ×*angelae* (Figure 6A)
4. Apex of the lip truncate to obtuse and occasionally ciliate........ *C. gardneri* (Figure 6C)
4’. Apex of the lip acute and slightly pubescent or glabrous.. 5
5. Plants generally terrestrial; lip rounded; margin of the lip serrate or short-fimbriate…. .... *C. discolor* (Figure 6B)
5’. Plants generally epiphyte; lip triangular; margin of the lip long ciliate…. ....*C. roseoalbum* (Figure 6E)

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References

Afonso EAL, Koch AK, Costa JM. 2015. Flora preliminar de Orchidaceae no Município de Abaetetuba, Pará, Brasil. Biota Amazonia. 6:107–118. doi:10.18561/2179-5746/biotaamazonia.v6n1p107-118.

Álvarez RAC, Morales MMB. 2023. A new species of *Catasetum* (Cymbidieae: Catasetinae) from the Colombian Amazonia. Lankesteriana. 23:469–475. doi:10.15517/lank.v23i3.54462.

Arnold ML. 1992. Natural hybridization as an evolutionary process. Annu Rev Ecol Syst. 23:237–261. doi:10.1146/annurev.es.23.110192.001321.

Arnold ML. 1997. Natural hybridization and evolution. New York, NY: Oxford University Press.

Arnold ML. 2006. Evolution through genetic exchange. New York, NY: Oxford University Press.

Assis LC, Ferreira ULC. 2024. Um novo híbrido de *Catasetum* (Orchidaceae) descrito para o Brasil. Richardiana, N S. 8:1–7.

Azevedo CO, Borba EL, van den Berg C. 2006. Evidence of natural hybridization and introgression in *Bulbophyllum involutum* Borba, Semir & F. Barros and *B. weddellii* (Lindl.) Rchb. f. (Orchidaceae) in the Chapada Diamantina, Brazil, by using allozyme markers. Braz J Bot. 29:415–421. doi:10.1590/S0100-84042006000300008.

Barbarena FFVA. 2021. Taxonomic notes on *Catasetum roseoalbum* (Orchidaceae: Epidendroideae): reaffirming *Catasetum ciliatum* as a synonym. Phytotaxa. 529:171–173. doi:10.11646/phytotaxa.529.1.13.

Barbarena FFVA, Sousa TS, Rocha-Júnior JAL. 2019. Mapping threats to the orchid populations in an environmental protection area in Bahia, Northeast Brazil. Oecologia Australis. 23:346–356. doi:10.4257/oeco.2019.2302.12.

Barbosa-Rodrigues J. 1877. *Genera et species orchidearum novarum I*. Rio de Janeiro: Fleiuss.

Barton NH, Hewitt GM. 1989. Adaptation, speciation and hybrid zones. Nature. 341:497–503. doi.10.1038341497a0.

Barve V. 2023. Elevating the fitness of use of GBIF occurrence datasets: a proposal for peer review. Biodivers Inform Sci Stand. 7:e112237. doi:10.3897/biss.7.112237.

Bastos CA, van den Berg C. 2012. Flora da Bahia: *Catasetum* (Orchidaceae). Sitientibus Séria Ciên Biol. 12:83–89. doi:10.13102/scb113.

BFG [Brazilian Flora Group]. 2015. Growing knowledge: an overview of seed plant diversity in Brazil. Rodriguésia. 66:1085–1113. doi:10.1590/2175-7860201566411.

BFG [Brazilian Flora Group]. 2018. Brazilian flora 2020: innovation and collaboration to meet Target 1 of the Global Strategy for Plant Conservation (GSPC). Rodriguésia. 69:1513–1527. doi:10.1590/2175-7860201869402.

BFG [Brazilian Flora Group]. 2021. Brazilian flora 2020: leveraging the power of a collaborative scientific network. Taxon. 71:178–198. doi:10.1002/tax.12640.

Bicalho HD. 1996. *Catasetum* × *fausti* Bicalho – Orquidaceae, um novo híbrido natural. Rev Bras Hort Ornam. 2:64–65. doi:10.14295/rbho.v2i2.128.

Bicalho HD, Barros F. 1988. On the taxonomy of *Catasetum* subsection Isoceras. Lindleyana. 3:87–92.

Braga PIS. 1977. Aspectos biológicos das Orchidaceae de uma campina da Amazônia Central. Acta Amaz. 7:1–89. doi:10.1590/1809-43921977072s005.

Canhos DAL, Almeida EA, Assad AL, Bustamante MMDC, Canhos VP, Chapman AD, Giovanni RD, Imperatriz- Fonseca VL, Lohmann LG, Maia LC, Miller JT. 2022. SpeciesLink: rich data and novel tools for digital assessments of biodiversity. Biota Neotropica. 22:1–15. doi:10.1590/1676-0611-bn-2022-1394.

Cantuária PC, Krahl DRP, Krahl AH, Chiron G, Silva JBF. 2021b. *Catasetum* × *sheyllae* (Orchidaceae: Catasetinae), a new natural hybrid from Brazilian Amazon. Phytotaxa. 527:257–265. doi:10.11646/PHYTOTAXA.527.4.3.

Cantuária PC, Medeiros TDS, Silva RBL, Cantuária MF, Cantuária PC, Costa-Neto SV, Negrão MF. 2021a. Flora de Área de Proteção Ambiental da Fazendinha (Amapá): Orchidaceae. Biota Amazôn. 11:52–59. doi:10.18561/2179-5746/biotaamazonia.v11n1p52-59.

Cárdenas D, González MF, Marín N, Sua S, Betancur J. 2017. Plantas y líquens del Parque Nacional Natural Serranía de Chiribiquete, Colombia. Revis Colomb Amaz. 10:205–234.

Chase MW, Cameron KM, Freudenstein JV, Pridgeon AM, Salazar G, Van den Berg C, Schuiteman A. 2015. An updated classification of Orchidaceae. Bot J Linn Soc. 177:151–174. doi:10.1111/boj.12234.

Cogniaux CA. 1904. Catasetum. In: von Martius CFP, Eichler AW, Urban I, editor. Flora Brasiliensis, vol 3, part 5. Leipzig: F. Fleischer; p. 387–446.

Damián A, Mitidieri N, Bonilla M, Huayllani JT. 2021. A new species, lectotypification and new records in *Catasetum* (Orchidaceae: Catasetinae) from Peruvian Amazon. Bot Lett. 168:191–199. doi:10.1080/23818107.2020.1871404.

Dodson CH. 1978. The catasetums (Orchidaceae) of Tapakuma, Guyana. Selbyana. 2:159–168.

Dressler RL. 1993. Phylogeny and classification of the orchid family. Portland: Dioscorides Press.

Ferreira ULC. 2013. *Catasetum* × *valdisonianum* U.L.C. Ferreira, um novo híbrido natural. Orquidário. 27:93–97.

Ferreira ULC, Malaspina TK. 2023a. *Catasetum* × *incarnatum* U.L.C.Ferreira & T.K.Malaspina. Colet de Orquídeas Brasil. 19:770–773.

Ferreira ULC, Malaspina TK. 2023b. *Catasetum* × *ornaghiae* U.L.C.Ferreira & T.K.Malaspina. Colet de Orquídeas Brasil. 19:774–777.

Ferreira-Filho RL, Barberena FFVA. 2022. Orchidaceae of the municipality of Igarapé-Miri, Pará, Brazilian Amazon. Rodriguésia. 73:e01432021. doi:10.1590/2175-7860202273103.

Filardi-Barbosa MC, Cruz MJM, Gonçalvez MVP, Detoni CE. 2023. Floristic survey and its geofunctionality in the topographic gradient responsible for the vegetative distribution of the Parque das Dunas Salvador-BA. Cadernos de Geociências. 17:221502. doi:10.9771/geocad.v17i.55345.

Harris J, Harris M. 2001. Plant identification terminology – an illustrated glossary. Payson, UT: Spring Lake Publishing.

Hills HG, Williams NH, Dodson CH. 1968. Identification of some orchid fragrance components. Amer Orchid Soc Bull. 37:967–971.

Hills HG, Williams NH, Dodson CH. 1972. Floral fragrances and isolating mechanisms in the genus *Catasetum* (Orchidaceae). Biotropica. 4:61–76.

Holst AW. 1999. The world of *Catasetum*. Portland: Timber Press.

Hooker JD. 1840. *Monachanthus roseo-albus*. White and rose-colored monk-flower. Bot Mag. 67:3796.

Klein VP, Piedade MTF. 2019. Orchidaceae occurring in white-sand ecosystems of the Uatumã sustainable development reserve in Central Amazon. Phytotaxa. 419:113–148. doi:10.11646/phytotaxa.419.2.1.

Krahl AH, Chiron G, Cantuária PC, Silva JBF. 2021b. A new species of *Catasetum* (Orchidaceae, Catasetinae) for the Brazilian Amazon. Richardiana N S. 5:283–294.

Krahl AH, Krahl DRP, Cantuária PC, Chiron G, Silva JBF. 2022a. *Catasetum marinhoi* (Orchidaceae, Catasetinae), a new species of Brazilian Amazon. Richardiana N S. 16:100–110.

Krahl AH, Krahl DRP, Cantuária PC, Silva JBF. 2021a. *Catasetum saracataquerense* (Orchidaceae, Catasetinae), a new species of Brazilian Amazon. Richardiana N S. 5:206–216.

Krahl AH, Krahl DRP, Cantuária PC, Silva JBF. 2022b. *Catasetum nhamundaense* (Orchidaceae: Catasetinae), uma nova espécie da Amazônia Brasileira. Orquidário. 36:24–36.

Krahl AH, Krahl DRP, Pansarin ER. 2021c. *Ionopsis* × *atalibae* (Orchidaceae, Oncidiinae), a new natural hybrid from the Brazilian Amazon. Phytotaxa. 478:268–274. doi:10.11646/phytotaxa.478.2.8.

Krahl DRP, Chiron G, Silva JBF, Krahl AH, Cantuária PC. 2023c. *Catasetum dianneae* (Orchidaceae, Catasetinae): a new species of the *C. barbatum* complex for the Brazilian Amazon. Richardiana N S. 7:187–201.

Krahl DRP, Krahl AH, Chiron G. 2020. *Catasetum* × *louisiae* (Orchidaceae, Catasetinae), a new natural hybrid for the Brazilian Amazon. Richardiana N S. 4:214–223.

Krahl DRP, Krahl AH, Silva JBF, Cantuária PC. 2023d. *Catasetum riosianum* (Orchidaceae: Catasetinae), a new species for the Brazilian Amazon. Biota Amazôn. 13:56–58. doi:10.18561/2179-5746/biotaamazonia.v13n1p56-58.

Krahl DRP, Oliveira MS, Schmal P, Chiron G, Krahl AH, Silva JBF, Cantuária PC. 2024c. Revealing the true taxonomic status of *Catasetum joaquinianum* (Orchidaceae: Catasetinae). Phytotaxa. 664:123–131. doi:10.11646/phytotaxa.664.2.4.

Krahl DRP, Oliveira MS, Schmal P, Chiron G, Silva JBF, Krahl AH, Almeida SSMS, Cantuária PC. 2023e. *Catasetum tavaresii* (Catasetinae), a new species from the Central Brazilian Amazon. Lankesteriana. 23:485–493. doi:10.15517/lank.v23i3.55794.

Krahl DRP, Oliveira MS, Schmal P, Krahl AH, Chiron G, Silva JBF, Cantuária PC. 2024d. *Catasetum* × *vilhenense* (Orchidaceae: Catasetinae), a new natural hyibrid from the Amazon Forest. Darwiniana Nueva Seria. 12:308–317. doi:10.14522/darwiniana.2024.122.1251.

Krahl DRP, Oliveira MS, Silva JBF, Chiron G, Cantuária PC. 2023b. *Catasetum krahlii* (Orchidaceae, Catasetinae): a new and threatened species from the Brazilian Amazon. Acta Bot Bras. 37:e20220258. doi:10.1590/1677-941X-ABB-2022-0258.

Krahl DRP, Schmal P, Chiron G, Silva JBF, Krahl AH, Cantuária PC. 2023a. *Catasetum* × *grasineideae* (Orchidaceae: Catasetinae), a new nothospecies from Brazilian Amazon and taxonomic notes for the genus. Phytotaxa. 594:89–104. doi:10.11646/PHYTOTAXA.594.2.1.

Krahl DRP, Schmal P, Chiron G, Silva JBF, Krahl AH, Cantuária PC. 2024a. *Catasetum queirozii* (Orchidaceae: Catasetinae): a new species from the Brazilian Amazon. Acta Amaz. 54: e54bc23180. doi:10.1590/1809-4392202301801.

Krahl DRP, Schmal P, Chiron G, Silva JBF, Krahl AHK, Cantuária PC. 2023f. Taxonomic notes on *Catasetum meeae* (Orchidaceae: Catasetinae). Phytotaxa. 609:240–246. doi:10.11646/PHYTOTAXA.609.3.7.

Krahl DRP, Schmal P, Oliveira MS, Silva JBF, Chiron G, Krahl AH. 2024b. *Catasetum cantuariae* (Orchidaceae, Catasetinae), a new species from the Brazilian Amazonian biome. Kew Bulletin. 79:583–595. doi:10.1007/s12225-024-10191-7.

Lindley J. 1835. *Monachanthus discolor*. Dingy monk-flower. Edwards Bot Reg. 20:1735.

Lindley J. 1839. Catasetum longifolium. Edwardss Bot Reg. 25:94.

Luz ALS, Costa DLL, Pacheco JRV, Barbarena FFVA. 2024. Orchidaceae in the State of Pará, Brazilian Amazon: an updated checklist reveals underestimated species richness. Acta Amaz. 38:e20240011. doi:10.1590/1677-941X-ABB-2024-0011.

Mallet J. 2001. Species, concepts of. In: Levin S, editor. Encyclopedia of biodiversity, Vol 5. San Diego, CA: Academic Press; p. 427–440.

Mansfeld R. 1932. Die Gattung *Catasetum* L. C Rich. Feddes Repert. 30:257–275.

Mauad AVSR, Petini-Benelli A, Izzo TJ, Smidt EC. 2022. Phylogenetic and molecular dating analyses of Catasetum (Orchidaceae) indicate a recent origin and artificial subgeneric groups. Braz J Bot. 45:1235–1247. doi:10.1007/s40415-022-00840-1.

Milet-Pinheiro P, Gerlach G. 2017. Biology of the Neotropical orchid genus *Catasetum*: a historical review on floral scent chemistry and pollinators. Perspect Pl Ecol Evol Syst. 27:23–34. doi:10.1016/j.ppees.2017.05.004.

Mori SA, Silva LA, Lisboa G, Coradin L. 1989. Manual de Manejo do Herbário Fanerogâmico. Ilhéus, BA: Ceplac.

Oliveira MS, Ferreira AWC, Oliveira HC, Pessoa E. 2021. Orchids of the central region of eastern Maranhão, Brazil. Rodriguésia. 72:e02582019. doi:10.1590/2175-7860202172057.

Pabst GFJ, Dungs F. 1977. Orchidaceae Brasilienses. Hildesheim: Kurt Schmersow.

Pansarin ER. 2024. Rediscovery and revalidation of the Brazilian endemic *Vanilla schwackeana* Hoehne (Orchidaceae): its distribution and phylogenetic position. Plant Ecol Evol. 157:32–41. doi:10.5091/plecevo.110331.

Pessoa EM, Barros F, Alves M. 2015. Orchidaceae from Viruá National Park, Roraima, Brazilian Amazon. Phytotaxa. 192:61–96. doi:10.11646/PHYTOTAXA.192.2.1.

Petini-Benelli A. 2014. Novelties in *Catasetum* (Orchidaceae) in the State of Rondônia, Brazil. Feddes Repertorium. 125:1–11. doi:10.1002/fedr.201400028.

Petini-Benelli A. 2016. Um nouvel hybride naturel de *Catasetum* (Cymbidieae, Epidendroideae, Orchidaceae) de Mato Grosso (Brésil). Richardiana. 16:327–342.

Petini-Benelli A. 2024. Catasetum. In: Flora e Funga do Brasil 2020. Jardim Botânico do Rio de Janeiro, JBRJ. [accessed 2024 Mar 08]. https://floradobrasil.jbrj.gov.br/FB11312.

Petini-Benelli A, Chiron G. 2020. Une nouvelle espèce d'orchidée du Rôndonia: *Catasetum desouzae*. Richardiana N S. 4:238–246.

Petini-Benelli A, Grade A. 2010. Novo Híbrido Natural de *Catasetum* L.C. Rich. ex Kunth (Orchidaceae) para o Norte de Mato Grosso. Brasil. Orquidário. 24:124–132.

Petini-Benelli A, Grade A. 2012. *Catasetum apolloi* Benelli & Grade (Orchidaceae): correction taxonomique. Richardiana. 12:153–157.

POWO. 2024. Plants of the World Online. Facilitated by Roy Botanic Gardens, Kew. [accessed 2024 Mar 08]. http://www.plantsoftheworldonline.org/.

QGIS: Development Team. 2021. QGIS geographic information system. Open source geospatial foundation project. [accessed 2024 Mar 08]. https://qgis.org/en/site/.

Reflora. 2024. Herbário Virtual. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro. [accessed 2024 Nov 18]. https://floradobrasil.jbrj.gov.br/reflora/herbarioVirtual/ConsultaPublicoHVUC/ConsultaPublicoHVUC.do.

Robertson T, Belongie S, Adam H, Kaeser-Chen C, Zhang C, Chuan Tan K, Liu Y, Brulé D, Deltheil C, Loarie S, et al. 2019. Training machines to identify species using GBIF-mediated datasets. Biodivers Inform Sci Stand. 3:e37230. doi:10.3897/biss.3.37230.

Romero GA, Carnevali G. 1989. Novelties in the Orchid Flora of Southern Venezuela. Ann Mo Bot Gard. 76:454–461. doi:10.2307/2399494.

Romero GA, Carnevali G. 1990. *Catasetum natural* hybrids from southern Venezuela – 1. *Catasetum ×tapiriceps* Reichb. f. Am Orchid Soc Bull. *59*:1214–1220.

Romero GA, Carnevali G. 2009. Catasetum. In: Pridgeon AM, Cribb PJ, Chase MW, Rasmussen FN, editor. Genera Orchidearum, Epidendroidea – Part II. New York, NY: Oxford University Press; p. 13–18.

Romero GA, Jenny R. 1992. New natural hybrids and nomenclatural novelties in *Catasetum* (Orchidaceae) from the Guiana, Ecuador, and Peru. Novon. 2:241–248. doi:10.2307/3391560.

Romero GA, Jenny R. 1993. Contributions toward a monograph of *Catasetum* (Catasetinae, Orchidaceae) I: a checklist of species, varieties, and natural hybrids. Harvard Pap Bot. 1:59–84.

Romero-González G. 2012. Las flores unisexuales y dimórficas de *Catasetum* Rich. (Catasetum). Desde el Herbario CICY. 4:32–36.

Romero-González G. 2018. Charles Darwin on Catasetinae (Cymbidieae, Orchidaceae). Harvard Pap Bot. 23:339–379. doi:10.3100/hpib.v23iss2.2018.n18.

Romero-González G, Carnevali G. 2024. *Catasetum ×steyermarkii* (Catasetinae: Orchidaceae) – a new putative natural hybrid of *Catasetum* (Catasetinae, Orchidaceae) from the Venezuelan Guayana. Harvard Pap Bot. 29:1–13. doi:10.3100/hpib.v29iss1.2024.n1.

Schweinfurth C. 1943. Catasetum pusillum. Amer Orchid Soc Bull. 12:10: 4.

Schweinfurth C. 1960. Catasetum pusillum. Orchids Peru. 3:588–590.

Seehausen O. 2004. Hybridization and adaptive radiation. Trends Ecol Evol. 19:198–207. doi:10.1016/j.tree.2004.01.003.

Senghas K. 1990. Einige neue Arte naus der Subtribus Catasetinae I – *Catasetum* sektion Anisoceras. Die Orchidee. 41:212–218.

Senghas K. 1991. Einige neue Arte naus der Subtribus Catasetinae I – *Catasetum* sektion Isoceras. Die Orchidee. 42:19–24.

Silva JBF, Silva MFF. 1998. Orquídeas Nativas da Amazônia Brasileira: gênero *Catasetum* L.C. Rich. ex Kunth. Belém, PA: Museu Paraense Emílio Goeldi.

Silva LAE, Fraga CN, Almeida TMH, Gonzalez M, Lima RO, Rocha MS, Bellon E, Ribeiro ES, Oliveira FA, Clemente LS, et al. 2017. Jabot – Sistema de Gerenciamento de Coleções Botânicas: a experiência de uma década de desenvolvimento a avanços. Rodriguésia. 68:391–410. doi:10.1590/2175-7860201768208.

Sprunger S, Cribb PJ, Toscano-de-Brito ALV. 1996. João Barbosa Rodrigues – Iconographie des orchidées du Brésil, volume 1: the illustrations. Basle: Friedrich Reinhardt Verlag.

Thiers BM. 2024. [continuously updated]. Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. [accessed 2024 Mar 08]. http://sweetgum.nybg.org/ih/.

Valsko J, Krahl A, Petini-Benelli A, Chiron G. 2019. *Catasetum sophiae*, a new species of Orchidaceae (Catasetinae) from northern Brazil. Phytotaxa. 402:104–120. doi:10.11646/PHYTOTAXA.402.2.5.

van der Pijl L, Dodson CH. 1966. Orchid flowers: their pollination and evolution. Florida: University of Miami Press.

Walker-Larsen J, Harder LD. 2000. The evolution of staminodes in Angiosperms: patterns of stamen reduction, loss, and funtional re-invention. Am J Bot. 87:1367–1384. doi:10.2307/2656866.

Williams NH, Dodson CH. 1972. Selective attraction of male euglossine bees to orchid floral fragrances and its importance in long distance pollen flow. Evolution. 26:84–95. doi:10.2307/2406985.