

CATASETUM × *STEYERMARKII* (CATASETINAE: ORCHIDACEAE)
A NEW PUTATIVE NATURAL HYBRID OF *CATASETUM*
(CATASETINAE, ORCHIDACEAE) FROM THE VENEZUELAN GUAYANA

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Abstract. Based on evidence found in a specimen collected by J. A. Steyermark in the vicinity of Mount Roraima in 1944, such as the described colors of the flowers and shape of the labellum, and the shape and size of the antennae, the pollinarium, and the pollinia, a new natural hybrid between *Catasetum discolor* and *C. planiceps* is described and illustrated as *C. xsteyermarkii*. Both putative parents have been collected in the same area. An annotated list of all the species of *Catasetum* hitherto reported in the vicinity of Mount Roraima is presented in Appendix I, and new nothospecies (*pro sp.*) and a nomenclatural notes in Appendix II.

Keywords: *Catasetum*, Guayana, Mount Roraima, nothospecies, Orchidaceae

Some years ago, while the two authors and a group of colleagues prepared a treatment of Orchidaceae for the project “Flora of the Venezuelan Guayana,” one peculiar specimen of *Catasetum* at AMES could not be identified and was set aside. It still remained a puzzle by the time the flora was published (Carnevali et al., 2003). Many years later, the authors have re-examined its identification now that we have many more resources available.

Catasetum Rich. ex Kunth (Catasetinae, Orchidaceae) is a Neotropical genus ranging from northwest Mexico to southern Brazil and northern Argentina. It consists of approximately 200 accepted species (Govaerts et al., 2024) and 30 natural hybrids (Krahl et al., 2023). The Amazon river Basin is considered the center of diversity of the genus, where more than half of the species occur (Petini-Benelli, 2024). For the most recent overview of the genus see Romero-González et al. (2009).

While we were aware of natural hybridization in *Catasetum* in the past (Dodson, 1962; Pabst, 1975; Dodson, 1978; Romero and Carnevali, 1989a, 1989b, 1990, 1991a, 1991b, 1992; Romero and Jenny, 1992), there is growing evidence of its relevance as an evolutionary force within the genus as shown by an ever increasing number of recently proposed nothospecies (e.g., Lacerda and Castro, 2005; Ferreira, 2013; Petini-Benelli, 2016; Krahl et al. 2020, Ferreira, 2016, 2019; Ferreira and Filho, 2019; Ferreira and Malaspina, 2019; Cantuária et al., 2021). Furthermore, as pointed out by Krahl et al. (2023), many recently described so called “species” of *Catasetum* have turned out to be natural infrageneric hybrids. Some of these nothospecies could be attributed to the novel habitats created by the advancement of the agricultural and animal husbandry frontiers as well as the removal of natural habitat barriers that have brought together species that otherwise would have never come in contact without the effects of these anthropogenic activities.

Natural hybrids have been detected between all subgeneric ranks of *Catasetum* (Table 1).

The degree of natural hybridization within this group supports the hypothesis that the evolution of *Catasetum* has been highly reticulate, where natural hybridization appears to have taken place both ancestrally and currently, rendering phylogenetic reconstructions with previously used methods difficult, i.e., “hampered by incongruent gene trees, especially closely related species complexes with high degrees of hybridization and polyploidy” (Krak et al., 2013; see also Wang et al., 2021; Moran et al., 2021; for evidence of polyploidy in *Catasetum*, see Oliveira et al., 2013 and references therein). We thus argue that the results and interpretations of recently published phylogenies (e.g., Mauad et al., 2022) are contentious.

The subject of this publication, a *Catasetum* sample collected by Julian A. Steyermark in 1944 (*Steyermark* 58568; see type below), had already puzzled C. Schweinfurth, who knew the genus reasonably well (he had described three species from Perú). Schweinfurth first identified it as *C. planiceps* Lindl. (1957: 868) and later as *Catasetum macroglossum* Rchb.f. (1967: 167), a species mainly from the Pacific drainage of Ecuador; Foldats (1970: 98), who also knew the genus fairly well, identified it as *C. planiceps*.

One of us (GAR-G) first examined a sheet of this collection at AMES in the late 1990s. The sheet included a copy of Steyermark’s original field sketch and a packet with what appear to be one flower, in pieces, including a single pollinarium (Fig. 1). At the time it seemed that, geographically, *Catasetum planiceps* (subgenus *Catasetum*, section *Isoceras*) was a better fit than *C. macroglossum* (subgenus *Catasetum*, section *Catasetum*), the former known to occur in the same area where Steyermark’s specimen was collected, while the latter was and is currently known to occur only in Ecuador. Furthermore, the shape of the

The authors thank M. L. Kawasaki (F) for her assistance with the specimens from F cited in the text, J. D. Edquén and G. A. Salazar (MEXU) for supplying images of *Catasetum discolor* from Perú, and G. Gerlach, P. Ormerod, and an anonymous reviewer for their comments on an early version of the text.

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TABLE 1. Natural hybrids between infrageneric ranks of *Catasetum* with examples from Venezuela.¹

SUBGENERIC AND SECTIONAL RANKS	SUBG. <i>CATASETUM</i> SECT. <i>CATASETUM</i>	SUBG. <i>CATASETUM</i> SECT. <i>ISOCERAS</i>	SUBG. <i>PSEUDOCATASETUM</i>
Subg. <i>Catasetum</i> sect. <i>Catasetum</i>	× ²	× ³	× ⁴
Subg. <i>Catasetum</i> sect. <i>Isoceras</i>	× ³	× ⁵	× ⁶
Subg. <i>Pseudocatasetum</i>	× ⁴	× ⁶	× ⁷

¹ “×” indicates published natural hybrids;

² *C. pileatum* Rehb.f. × *C. macrocarpum* Rich. ex Kunth = *C. ×tapiriceps* Rehb.f.;

³ *C. pileatum* × X. *C. planiceps* Lindl. = *C. ×wendlingeri* Foldats;

⁴ *C. pileatum* × *C. discolor* (Lindl.) Lindl. = *C. ×dunstervillei* G.A. Romero & Carnevali;

⁵ *C. barbatum* (Lindl.) Lindl. × *C. bicolor* Kl. = *C. ×merchae* G.A. Romero (see Appendix II);

⁶ *C. discolor* × *C. planiceps* = *Catasetum ×steyermarkii* G.A. Romero & Carnevali;

⁷ *C. discolor* × *C. longifolium* Lindl. = *C. ×roseo-album* (Hook.) Lindl.



FIGURE 1. Contents of the packet on Steyermark 58568 at AMES. A, pollinarium; B, crushed remains of one flower.

pollinia in the specimen at AMES fit perfectly the size ratio of species in subgenus *Catasetum* section *Isoceras* (a ratio of width:length of more than 2.5; see Romero, 1986: 74, Table 3–2 therein). Yet, the shape of the stipe, narrowing considerably towards the base, and with a unique folding pattern at the base (see Romero, 1990: 165, Fig. 2D–E therein) placed it in subgenus *Pseudocatasetum*. Yet again, both male and female flowers of *Catasetum planiceps* have a fairly green, pale greenish bronze to yellowish-

green uniform coloration, and the description given by the collector (see protologue below) was incongruent. It was impossible to identify the specimen at that time.

More recently, we had access to images of Steyermark's collection housed at F (see type), consisting of two sheets (labelled, in pencil, “1st” and “2nd” on the specimen labels; Fig. 2–3). The first one has an inflorescence with eight male flowers (based on the presence of well-developed anthers and antennae and a copy of Steyermark's

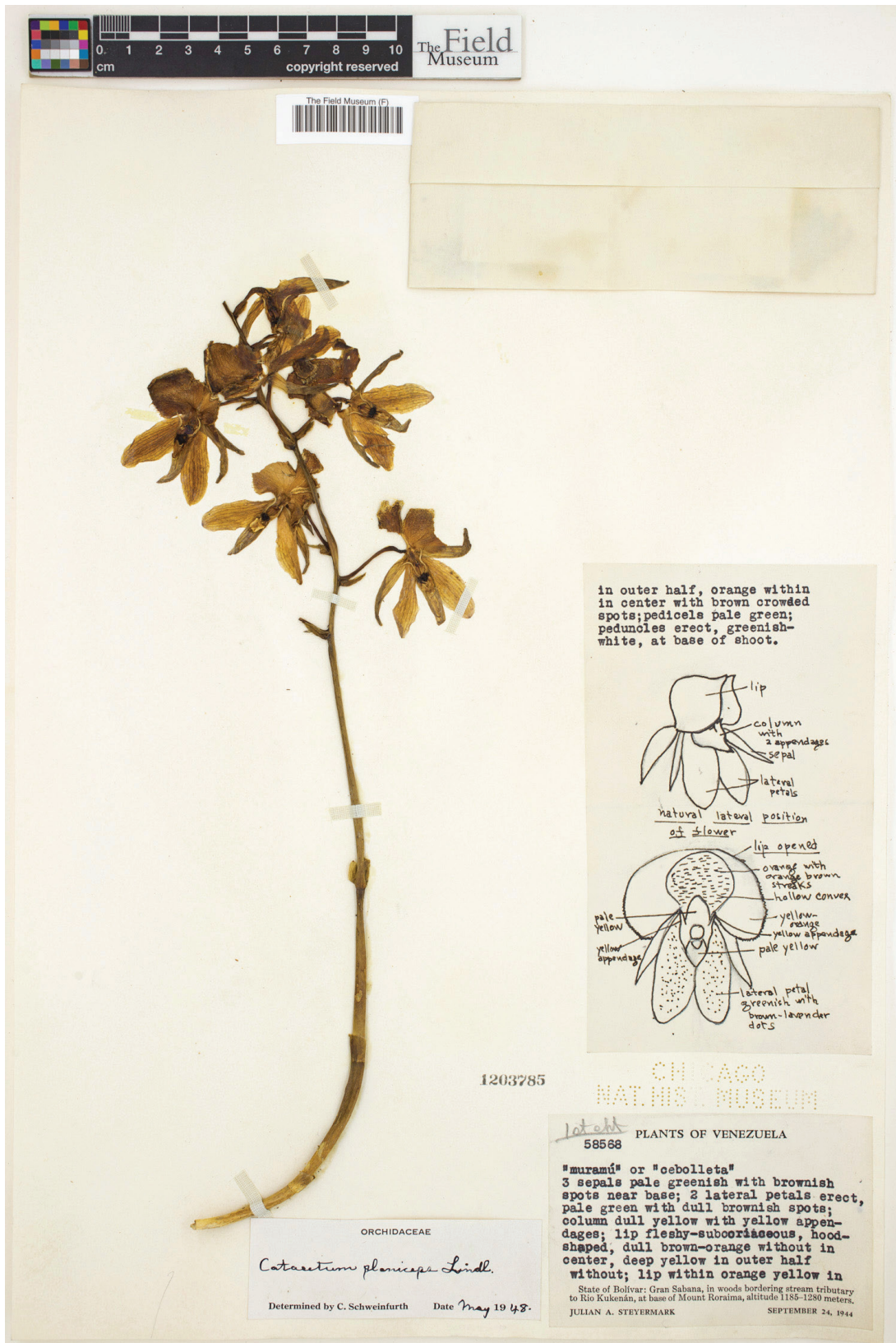


FIGURE 2. *Catasetum* × *steyermarkii* G.A. Romero & Carnevali. First sheet of the holotype (F). Courtesy of the Field Museum (<https://collections-botany.fieldmuseum.org/>).



FIGURE 3. *Catasetum xsteyermarkii* G.A. Romero & Carnevali. second sheet of the holotype (F). Courtesy of the Field Museum (<https://collections-botany.fieldmuseum.org/>).

field sketch); the antennae are similar to those in species of subgenus *Catasetum*, section *Isoceras*, subsection *Divaricata* (*sensu* Ortíz and Arango, 1994: 33), like the antennae of *C. planiceps*, although shorter (Fig. 2). The second sheet only has a pseudobulb with leaves that could be assigned practically to any species of *Catasetum* (Fig. 3). We also examined a flower preserved in

glycerine recently found at AMES.

After examining the evidence, the authors hypothesize that Steyermark's specimen represents a natural hybrid between *Catasetum planiceps* Lindl. and *Catasetum discolor* (Lindl.) Lindl. (Fig. 4), which is herein described and illustrated using documentation left by the collector and additional data gathered by the authors.

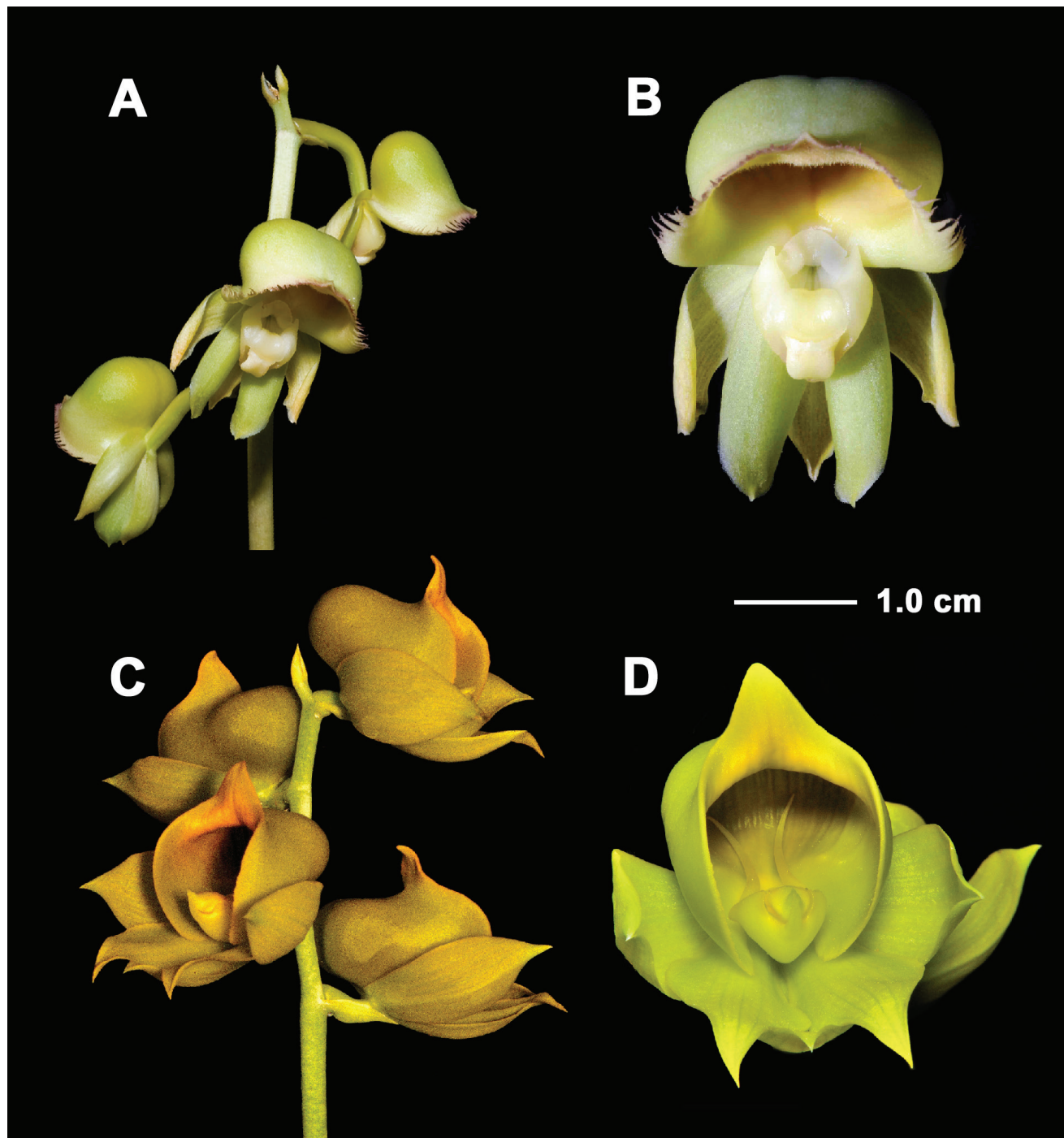


FIGURE 4. Putative parents of *Catasetum xsteyermarkii* G.A. Romero & Carnevali. **A–B**, *C. discolor* (Lindl.) Lindl.; **C–D**, *C. planiceps* Lindl. **A–B**, Gran Sabana, Bolívar, Venezuela, photographed by G. A. Romero-G. (no voucher prepared); **C–D**, El Castaño, Maracay, Aragua, Venezuela, cultivated and photographed by G. Carnevali (*Carnevali 8511*, CICY, spirit collection).

Catasetum xsteyermarkii G.A. Romero & Carnevali, *nothosp. nov.*

TYPE: VENEZUELA. Bolívar: Municipio Gran Sabana, in woods bordering stream tributary to Río Kukenán, at base of Mount Roraima, 1185–1280 m, 24 September 1944, J. A. Steyermark 58568 (Holotype: F [Sheet 1 of 2, accession 1203785, barcode V0435581F; sheet 2 of 2: accession 1203782, barcode V0435820]; Isotypes: AMES [accession 64864, barcode 02288977]) flower on glycerine slide (AMES [00085806]). Fig. 1–3.

Usage synonyms: *Catasetum planiceps* Auct., *non* Lindl. (Schweinfurth, 1957: 868; Foldats, 1970: 98).

Catasetum macroglossum Auct., *non* Rchb.f., (Schweinfurth, 1967: 167).

A putative natural hybrid between *Catasetum discolor* (Lindl.) Lindl. (subgenus *Pseudocatasetum*) and *C. planiceps* Lindl. (subgenus *Catasetum*, section *Isoceras*) combining features of both parents but distinguishable from the former by the presence of well-developed antennae and from the latter by the color of the sepals (greenish with lateral brown-lavender dots versus solid light green to yellowish green), a shallow, wide opening of the labellum, the relatively short antennae (not reaching the base of the labellum versus reaching the bottom of the labellum), and by the morphology of the pollinarium, the stipe of which considerably narrows toward the base, and with a folding pattern at the base, as in species of subgenus *Pseudocatasetum*, which renders it rigid (versus hinged in *C. planiceps*).

Pseudobulbs and *leaves* indistinguishable from those of most species in the genus. *Peduncle* erect, greenish-white, arising from the base of the fully developed pseudobulb. *Pedicel* pale green. *Flowers* non-resupinate, with spreading sepals and petals. *Dorsal sepal* 2.4–2.6 cm × 0.65–0.72 cm, 11-nerved, oblong obovate, obtuse to rounded, lateral sepals 2.70–2.75 × 0.77 × 0.8 cm, 13-nerved, oblong obovate, broadly acute, petals 2.97–3.1 × 0.9–1.1 cm, 11-nerved, elliptic, obtuse, pale green with dull brownish spots; *labellum* fleshy-subcoriaceous, hood-shaped, margin finely serrate, outside dull brown-orange in center, deep yellow in outer half, inside orange-yellow in center half, inside orange in center with brown crowded spots. *Column* pale yellow, antennae yellow, relatively short, barely reaching the base of the labellum, divaricate. Pollinarium as in *Catasetum discolor*.

Distribution and phenology: Known only from the type, which was found flowering in September.

Vernacular name: “Muramú” (Pemón) or “cebolleta” (Spanish).

Eponymy: Dedicated to Julian Alfred Steyermark (1909–1988), a renowned botanist and plant collector expert on the flora of Guatemala and Venezuela, particularly on the

flora of the Guayana highlands, and sponsor of the project “Flora of the Venezuelan Guayana.”

Catasetum xsteyermarkii is the first reported natural hybrid between a species of *Catasetum*, subgenus *Catasetum*, section *Isoceras* and a species in subgenus *Pseudocatasetum*. It is a rarity because these two groups rarely share pollinators: most species of section *Isoceras* are pollinated by species of *Euglossa* Latreille, whereas all known species of subgenus *Pseudocatasetum* are pollinated by species of *Eulaema* Lepeletier.⁴ *Catasetum planiceps* is the only species of section *Isoceras* that is pollinated by a species of *Eulaema*, *E. cingulata* (Fabricius), which it happens to share with *Catasetum discolor* (Fig. 5).

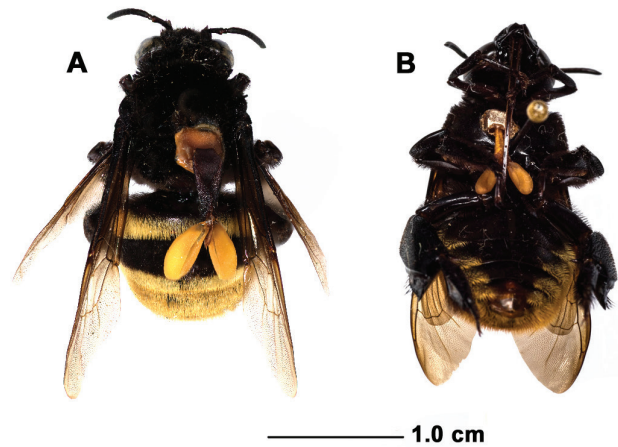


FIGURE 5. *Eulaema cingulata* (Fabricius). A, carrying a pollinarium of *Catasetum planiceps* Lindl.; B, carrying a pollinarium of *C. discolor* (Lindl.) Lindl. Photographs by G. A. Romero-González. Supporting material available upon request.

Nonetheless, the pollination dynamics of these two *Catasetum* groups make a natural hybrid between them nearly impossible. The hinged pollinarium of species of section *Isoceras* is always placed on the dorsum of the bee’s thorax, whereas the rigid one from species in subgenus *Pseudocatasetum* is always placed on the ventrum of the thorax (Hills et al., 1972; Dodson, 1978; Romero, 1990; Fig. 5 herein). Furthermore, pollination within species of section *Isoceras* occurs when the bee enters the female flower upside down, hanging from the apex of the labellum, above the column; the hinged pollinarium hangs down and, as the bee moves in and out of the female flower, eventually a pollinium is caught in the stigmatic cleft. In species of subgenus *Pseudocatasetum*, bees enter the female flower right-side up, with their ventrum facing the column: again, as the bee moves in and out of the flower, eventually a pollinium is caught in the stigmatic cleft.⁵

⁴Pinheiro and Gerlach (2017: 25–26, Table 1) listed *Euglossa ignita* as a “Visitor/Pollinator” of *Catasetum discolor* (see also Roubik and Hanson, 2004: 250), most likely based on the next two references. Williams and Dodson (1972: 85, Table 1) listed *Euglossa chlorosoma* Cockerell as visitors of flowers of *C. discolor* (*E. chlorosoma* is considered a synonym of *E. ignita* F. Smith; Kimsey and Dressler, 1986: 232). Later, Dodson (1978: 167, Table 1), again cited bees of the same *Euglossa* species visiting *C. discolor* but, in a footnote, he clearly labelled them as “not effective as pollinators.” Dodson, in the same publication, listed *Eulaema cingulata* visiting flowers of *Catasetum thompsonii* Dodson (section *Isoceras*) but also labelled the bees as “not effective as pollinators.”

⁵Pollination of female flowers of *Catasetum longifolium* Lindl. (subgenus *Pseudocatasetum*) is a special case: the pollinator enters the flower upside down, but its ventrum still faces the column (see photograph in Hills et al., 1972: 70, Fig. 1).

Although it is possible that a bee carrying a pollinarium of *Catasetum planiceps* on the dorsum (Fig. 5) could pollinate a female flower of *C. discolor*, entering it upside down, it is highly unlikely. Bees, at first, apparently find much easier to enter female flowers right-side up, with their ventral side facing the column,⁶ and if the pollinarium is on the dorsum it never contacts the column; it is much more likely that a bee, carrying a pollinarium of *C. discolor* on its ventrum, pollinates the female flower of *C. planiceps* while entering the flower right-side up. Moreover, the size of the pollinium (Fig. 6) may also hinder two-way genetic flow between *C. discolor* and *C. planiceps*: the pollinium of the latter is too thick to be inserted in the stigmatic cleft of the column of *C. discolor*, whereas the opposite is quite feasible (see discussion in Romero-González et al., 2017: 151).

The authors, based on the pollinarium found in the sheet at AMES, conclude that this natural hybrid is an evolutionary end, that is, it cannot reproduce with itself or any of the putative parents. If the pollinarium is rigid, as suggested by the one shown in Fig. 1A, and it is placed on the dorsum of the pollinarium (as suggested by the morphology of the labellum and column of the nothospecies, Fig. 2), a bee carrying such a pollinarium could not pollinate female flowers of the nothospecies or either of the putative parents.

We present an annotated list of all the species of *Catasetum* hitherto reported in the vicinity of Mount Roraima in Appendix I, and propose new nothospecies (*pro sp.*) in Appendix II.



FIGURE 6. *Catasetum* pollinaria adaxial and abaxial views. **A–B**, *Catasetum discolor* (Lindl.) Lindl.; **C–D**, *C. planiceps* Lindl. **A, C** within minutes of discharge; **B**, within hours of discharge; **D**, after several years of storage. Photographs by G. A. Romero-González. Supporting material available upon request.

LITERATURE CITED

- BATEMAN, J. 1834. Arrival, from Demerara, of the botanical collector, Mr. Thomas Colley. *The Gardener's Magazine* 10, No. 56: 571–572.
- CANTUÁRIA, P. DE CASTRO, D. R. P. KRAHL, A. H. KRAHL, G. CHIRON, AND J. B. FERNANDES DA SILVA. 2021. *Catasetum xsheyllae* (Orchidaceae: Catsetinae), a new natural hybrid from Brazilian Amazon. *Phytotaxa* 527, No. 4: 257–265.
- CARNEVALI, G., I. M. RAMÍREZ-MORILLO, G. A. ROMERO-GONZÁLEZ, C. A. VARGAS, AND E. FOLDATS. 2003. Pages 200–619 in P. E. BERRY, K. YATSKIEVYCH, AND B. K. HOLST, volume editors, *Flora of the Venezuelan Guayana 7*. Missouri Botanical Garden Press, St. Louis, Missouri.
- COGNIAUX, A. 1902. *Catasetum* L.-C. Rich. Pages 387–446 in C. F. P. VON MARTIUS AND A. G. EICHLER, eds., *Flora Brasiliensis* 3, part 5. R. Oldenbourg, Munich and Lipsig.
- DODSON, C. H. 1962. Pollination and variation in the subtribe Catsetinae (Orchidaceae). *Annals of the Missouri Botanical Garden* 49, No. 1–2: 35–56.
- . 1978. The catsetums of Tapakuma, Guyana. *Selbyana* 2, No. 2–3: 159–168.
- EDQUÉN, J. D., E. YRIGOÍN, G. A. SALAZAR, E. HÁGSATER, E. SANTIAGO, L. I. CARRERA, R. JIMÉNEZ-MACHORRO, D. TRUJILLO, K. EDQUÉN, J. P. ARISTA, J. DUARTE, AND M. OLIVA. *In press*. Los Géneros de Orquídeas del Bosque de Protección Alto Mayo—Una Guía Ilustrada. Conservación Internacional, and Servicio Nacional de Áreas Naturales Protegidas por el Estado, Lima, Perú.
- FERREIRA, U. L. C. 2013. *Catasetum xvaldisonianum* U.L.C. Ferreira, um novo híbrido natural. *Orchidário (Rio de Janeiro)* 27, No. 3: 93–97.
- . 2016. *Catasetum xmesquitae* U.L.C. Ferreira, novo híbrido natural. *Orchidário (Rio de Janeiro)* 30: 37–43.
- . 2019. Two new natural hybrids in *Catasetum* (Orchidaceae) from centre-west Brazil. 2019. *Richardiana N.S.* 3: 80–91.
- . AND R. M. C. FILHO. 2019. Two new natural hybrids in *Catasetum* (Orchidaceae) from Brazil. *Richardiana* 3: 39–49.

⁶ Observing euglossine bees collecting fragrances from female flowers of species of *Catasetum* subgenus *Catasetum*, or non-resupinate male flowers thereof, one can easily distinguish “naïve” bees from “trained” ones: the former, at first, do not appear to know how to enter the flower, to reach the most active fragrance-producing osmophores located in the upper portion of the inside of the flowers; it takes a “naïve” bee many landings on the flower before they learn to enter it “correctly” (as far as the flower is concerned), that is, upside down, hanging from the apex of the labellum and having their dorsum facing the column. “Trained” bees, on the other hand, enter the flowers “correctly” after one or two landings on the flower. In contrast, pollinators that approach female and male flowers of subgenus *Pseudocatasetum* rapidly learn what is the “correct” approach in this case, that is, entering the flower right-side up, with their ventrum facing the column (see previous footnote, regarding *C. longifolium*, the pollination of which has not been observed by the authors).

- . AND T. K. MALASPINA. 2019. *Catasetum xaiakoae*. U.L.C. Ferreira & T.K. Malaspina *hyb. nat. nov.* Coletânea de Orquídeas Brasileiras 15: 594–597.
- FOLDATS, E. 1970. *Catasetum* L. C. Rich. Pages 48–109 in T. LASSER, ED., Flora de Venezuela XV (Orchidaceae part 4). Instituto Botánico, Caracas.
- GOVAERTS, R., J. DRANSFIELD, S. ZONA, D. R. HOEDEL, AND A. HENDERSON. 2024. World Checklist of Orchidaceae. Facilitated by the Royal Botanic Gardens, Kew. Available from: <http://apps.kew.org/wcsp/> (accessed April 29, 2024).
- HILLS, H. G., N. H. WILLIAMS, AND C. H. DODSON. 1972. Floral fragrances and isolating mechanisms in the genus *Catasetum* (Orchidaceae). *Biotropica* 4, No. 2: 61–76.
- KRAHL, D. R. P., A. H. KRAHL, AND G. R. CHIRON. 2020. *Catasetum xluisiae* (Orchidaceae: Catasetinae), a new natural hybrid for the Brazilian Amazon. *Richardiana* N.S. 4: 214–223.
- KRAHL, D. R. P., P. SCHMAL, G. CHIRON, J. B. FERNANDES DA SILVA, A. H. KRAHL, AND P. DE CASTRO CANTUÁRIA. 2023. *Catasetum xgrasineideae* (Orchidaceae: Catasetinae), a new nothospecies from Brazilian Amazon and taxonomic notes for the genus. *Phytotaxa* 594, No. 2: 89–104.
- KRAK, K., P. ČAKLOVA, J. CHRTEK, AND J. GEHRER. 2013. Reconstruction of phylogenetic relationships in a highly reticulate group with deep coalescence and recent speciation (Hieracium, Asteraceae). *Heredity* 110, No. 2: 138–151.
- LACERDA JR., K. G. DE AND CASTRO NETO. 2005. New natural hybrids in *Catasetum*. *Orchid Review* 113, No. 1266: 308–311.
- LINDEN, J., L. LINDEN, AND E. RODIGAS. 1895. *Lindenia*—Iconographie des Orchidées 11. Eug. Vander Haeghen, Gand, Belgium.
- LINDLEY, J. 1840. *Catasetum longifolium*. *Sertum Orchidaceum* t. 31. James Ridgway and Sons, London.
- . 1843. *Catasetum planiceps*. *Edwards's Botanical Register* 29: t. 9.
- LINK, H. F., F. KLOTZSCH, AND F. OTTO. 1844. *Catachaetum recurvatum*. *Icones Plantarum Rariorum Horti Regii Botanici Berolinensis* 2, No. 3: tab. 42.
- MAUAD, A. V. S. R., A. PETINI-BENELLI, T. J. IZZO, AND E. C. SMIDT. 2022. Phylogenetic and molecular dating analyses of *Catasetum* (Orchidaceae) indicate a recent origin and artificial subgeneric groups. *Brazilian Journal of Botany* 45, No. 4: 1235–1247.
- MCCONNELL, F. V. AND J. J. QUELCH. 1901. Report on two botanical collections made by Mssrs. F. V. McConnell and J. J. Welch at Mount Roraima in British Guiana. *The Transactions of the Linnean Society of London, 2nd Series Botany*, 6, No. 1: 1–107, plates 1–14.
- MILET-PINHEIRO, P. AND G. GERLACH. 2017. Biology of the Neotropical Orchid genus *Catasetum*: a historical review on floral scent chemistry and pollinators. *Perspectives in Plant Ecology, Evolution and Systematics* 27: 23–34.
- MORAN, B. M., C. PAYNE, Q. LANGDON, D. L. POWELL, Y. BRANDVAIN, AND M. SCHUMER. 2021. The genomic consequences of hybridization. *eLife* 10:e69016. DOI: <https://doi.org/10.7554/eLife.69016>
- OLIVEIRA, L. V. R., F. DE BARROS, AND E. R. FORNI-MARTINS. 2013. Chromosome numbers and karyotypes of *Catasetum* species (Orchidaceae). *Plant Biosystematics* 148, No. 3: 499–507.
- ORTÍZ V., P. AND G. ARANGO. 1994. Una nueva especie de *Catasetum* de Colombia. *Orquídeología (Medellín)* 19, No. 2: 29–33 [text in English on pages 34–36].
- PABST, G. F. J. 1975. New or critical orchids from Brazil—VII. *Orchid Review* 86, No. 990: 405–406.
- PETINI-BENELLI, A. 2016. Un nouvel hybride naturel de *Catasetum* (Cymbidieae, Epidendroideae, Orchidaceae) du Mato Grosso (Brésil). *Richardiana* 16: 327–342.
- . 2024 [continuously updated]. *Catasetum*. Flora e Fungo do Brasil. Jardim Botânico do Rio de Janeiro. <http://florado-brasil.jbrj.gov.br/reflora/floradobrasil/FB11312> (accessed April 30, 2024).
- RIDLEY, H. N. 1886. Orchidaceae. Pages 202–206 in E. F. IM THURN, ED., Notes on the Plants of Roraima. *Timehri* 5: 145–223.
- ROLFE, R. A. 1890. On the sexual forms of *Catasetum*, with special reference to the researches of Darwin and others. *The Journal of the Linnean Society, Botany* 27, No. 183–184: 206–225, plate VIII.
- . 1913. *Catasetum darwinianum*. *Bulletin of Miscellaneous Information* 1913, No. 3: 99–102.
- ROMERO, G. A. 1986. Evolutionary dynamics in a *Catasetum* community in southern Venezuela. Ph.D. dissertation, Indiana University, Bloomington, Indiana.
- . Phylogenetic relationships in subtribe Catasetinae (Orchidaceae, Cymbidieae). *Lindleyana* 5, No. 3: 160–181.
- . AND G. CARNEVALI. 1989a. Novelties in the orchid flora of southern Venezuela. *Annals of the Missouri Botanical Garden* 76, No. 2: 454–461.
- . AND ———. 1989b. A new combination for the orchid flora of southern Venezuela: *Catasetum xtapiriceps* Rchb.f. (*pro sp.*). *Lindleyana* 4: 127–134.
- . AND ———. 1990. *Catasetum* natural hybrids from southern Venezuela—1. *Catasetum xtapiriceps*. *American Orchid Society Bulletin* 59, No. 12: 1214–1220.
- . AND ———. 1991a. *Catasetum* natural hybrids from southern Venezuela—2. *Catasetum xdunstervillei*. *American Orchid Society Bulletin* 60, No. 2: 115–120.
- . AND ———. 1991b. *Catasetum* Natural Hybrids From Southern Venezuela—3. *Catasetum xroseo-album* and *C. xwendlingeri*. *American Orchid Society Bulletin* 60, No. 8: 770–774.
- . AND ———. 1992. *Catasetum* Natural Hybrids From Southern Venezuela—4. Biology and nomenclature. *American Orchid Society Bulletin* 61, No. 4: 355–360.
- ROMERO, G. A. AND R. JENNY. 1992. New natural hybrids and nomenclatural novelties in *Catasetum* (Orchidaceae) from the Guianas, Ecuador, and Peru. *Novon* 2, No. 3: 241–248.
- . AND ———. Contributions toward a monograph of *Catasetum* (Catasetinae, Orchidaceae) I: A checklist of species, varieties, and natural hybrids. *Harvard Papers in Botany* 1, No. 4: 59–84.
- ROMERO-GONZÁLEZ, G. A. 2003. History of orchid botanical exploration in the Venezuelan Guayana. Pages 200–203 in P. E. BERRY, K. YATSKIEVYCH, AND B. K. HOLST, volume editors, *Flora of the Venezuelan Guayana* 7. Missouri Botanical Garden Press, St. Louis, Missouri.
- , G. CARNEVALI, AND A. M. PRIDGEON. 2009. *Catasetum*. Pages 13–18 in A. M. PRIDGEON, P. J. CRIBB, M. W. CHASE, AND F. N. RASMUSSEN, EDs., *Genera Orchidacearum* 5. Oxford University Press, Oxford.
- , G. CARNEVALI, R. E. LÓPEZ, AND S. C. PÉREZ. 2017. *Catasetum xdunstervillei* (Orchidaceae: Catasetinae), a natural hybrid confirmed by artificial hybridization. *Harvard Papers in Botany* 22, No. 2: 145–155.
- ROUBIK, D. W. AND P. E. HANSON. 2004. *Orchid Bees of Tropical America*. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.
- SCHWEINFURTH, C. 1957. Orchidaceae. Pages 845–881 in J. A. STEYERMARK, ED., Contributions to the Flora of Venezuela. Botanical Exploration in Venezuela—IV. *Fieldiana: Botany* 28, No. 4: 679–1225.
- . 1960. *Catasetum* L. C. Rich. Pages 583–592 in C. SCHWEINFURTH, *Orchids of Peru*. *Fieldiana: Botany* 30, No. 3: i–vi, 533–786.

———. 1967. Orchidaceae of the Guayana Highland. Memoirs of the New York Botanical Garden 14, No. 3: 69–214.
 STEYERMARK, J. A. 1957. Contributions to the Flora of Venezuela. Botanical Exploration in Venezuela—IV. Fieldiana: Botany 28, No. 4: 679–1225.
 ———. 1981. Erroneous citations of Venezuelan localities. Taxon 30, No. 4: 816–817.
 THURN, E. F. IM. 1886. Notes on the Plants observed during the Roraima expedition of 1884. Timehri 5: 145–223.
 ———. 1887. The botany of the Roraima Expedition of 1884.

The Transactions of the Linnean Society of London, 2nd Series Botany, 2, No. 13: 249–300, plates I–LVI.
 WANG, Y., Z. CAO, H. A. OGILVIE, AND L. NAKHLEN. 2021. Phylogenomic assessment of the role of hybridization and introgression in trait evolution. PLoS Genetics 17, No. 8: e1009701. <https://doi.org/10.1371/journal.pgen.1009701>
 WILLIAMS, N. H. AND C. H. DODSON. 1972. Selective attraction of male Euglossine bees to orchid floral fragrances and its importance in long distance pollen flow. Evolution 26, No. 1: 84–95.

APPENDIX I

The following are the species of *Catasetum* that have been reported hitherto from the vicinity of Mount Roraima; localities are cited following Steyermark (1981).

Catasetum darwinianum Rolfe can be discarded as a possible putative parent because of the small size of the flowers (Rolfe, 1913), indicating that this species is pollinated by an equally small species of *Euglossa*.

Catasetum longifolium Lindl. also occurs in this area (seen by one of the authors, GC), growing on *Mauritia flexuosa* L.f. (Arecaceae), one of the palm hosts of *Catasetum longifolium*, plants of which grow on the leaf bases of these palms (e.g., R. H. Schomburgk in Lindley,

1840; Dodson, 1978). Nonetheless, the involvement of *C. longifolium* in intergeneric natural hybrids imparts several morphological signals (e.g., narrow leaves and/or pendent habit; Romero and Carnevali, 1991) not detected in the nothospecies described herein.

Catasetum darwinianum Rolfe, Gardeners' Chronicle Ser. 3, 5, No. 118: 394. 1889. TYPE: VENEZUELA. Bolívar: municipio Gran Sabana, vicinity of Mount Roraima, Sander, St. Albans, *ex Hort. Kewensis* (See Rolfe, 1913: 101 for the most precise type locality given by the author; see note on the collector below) (Holotype: K). Fig. 7.

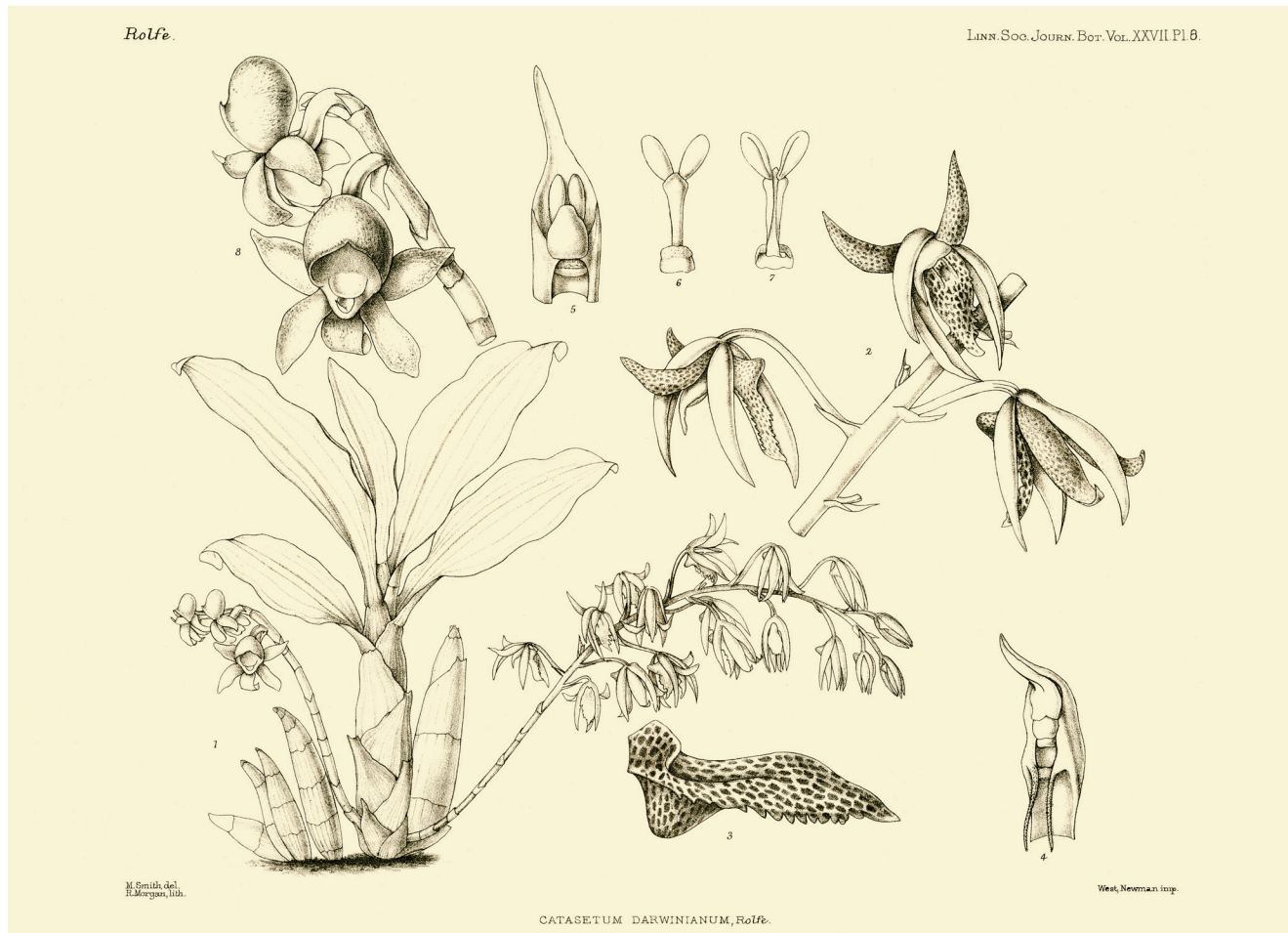


FIGURE 7. *Catasetum darwinianum* Rolfe. Reproduced from Rolfe (1890: tab. VIII).

Distribution: Known only from the type locality.

Habitat and Phenology: No information was provided for habitat, but most of the species in this group, in this case, apparently quite close to if not conspecific with *Catasetum callosum* Lindl., are epiphytes. The only existing phenological data for this species were provided by Rolfe (1890: 218): “This ... plant... flowered in the Kew collection during the autumn of 1888” and Rolfe (1913: 99): “The plant flowered last autumn in the Kew collection.”

The type specimen of this species was most likely collected by E. Seidel (sometimes spelled Seidle or Seidl) who visited the vicinity of Roraima twice in 1884 on behalf of the Sander establishment (Romero-González, 2003: 201).

Catasetum discolor (Lindl.) Lindl., Edwards’s Botanical Register 27: sub t. 34. 1841.

Basionym: *Monachanthus discolor* Lindl., Edwards’s Botanical Register 20: t. 1735. 1834. TYPE: GUYANA [“Demerara”]. Without precise locality (Holotype: K).

Distribution: Venezuela (Amazonas and Bolívar), Guyana, Surinam, French Guiana, Colombia, Brazil, and Perú.

Additional specimen examined: VENEZUELA. Bolívar: municipio Gran Sabana, Mount Roraima, upper slopes, *F. V. McConnell & J. J. Quelch 6* (K, not seen); Cited by McConnell and Welch, 1901: 63 and Cogniaux, 1902: 446; Roraima, stony slopes with sandy soil, Philipp Camp, 5200–6000 ft. [1580–1820 m], 7 November 1927, *G. H. H. Tate 312* (NY ♀ [00547435]).

Habitat and Phenology: Found growing in sand or on sandstone outcrops, from sea level to 2500 m. Based on herbarium records from the northern hemisphere, flowering all year round.

The type of *Catasetum discolor* was collected by Thomas Colley in the Demerara region (name derived from the Dutch *Demerary*, a colony of Holland from 1745 to 1803). Bateman (1834) cited, as sites where Colley collected orchids in 1834, “... large portion of the Essequibo, Massarony, and Corgonni rivers; and the whole of the adjacent colony of Berbice... for a space of four months.”

Catasetum discolor displays a wide range of variation in color, from light yellowish green (Fig. 4A–B) to almost solid dull red (Edquén et al., in press: 97, Fig. 49), and morphology (the degree of revoluteness and dentition found along the edges of the labellum and the shape and ornamentation of the labellum apex), varying apparently without any pattern within the geographical distribution of the species. This variation is perhaps due to genetic exchange with *C. longifolium* and backcrossing with the natural hybrid between these two species, *C. xroseo-album* (Hook.) Lindl. In the literature and herbarium collections, *Catasetum discolor* is often confused with *C. xroseo-album*, from which, in most cases, it can be distinguished by the dentate edges of the labellum in the former, versus fimbriate in the latter. Furthermore, only *C. xroseo-album* is found growing on a variety of palms (including *M. flexuosa*).

Catasetum planiceps Lindl., Edwards’s Botanical Register 29, t. 9. 1843. Type: “Spanish main.” June 1841, *ex Hort.* “Messrs. Loddiges” (Holotype: K). Fig. 8–10.

Heterotypic synonyms: *Catachaetum recurvatum* Link, Klotzsch & Otto, *Icones Plantarum Rariorum Horti Regii Botanici Berolinensis* 2: 105, t. 42. 1844. TYPE: VENEZUELA. Bolívar: municipio Piar, near Upata, *C. F. E. Otto s.n.* (Holotype: B, destroyed).

Catasetum chloranthum Cogn., *Journal des Orchidées* 5: 251. 1894. TYPE: PERU. Without locality, *ex Hort.* Linden establishment (Holotype: BR).

Catasetum hymenophorum Cogn., *Journal des Orchidées* 6: 215. 1895. TYPE: VENEZUELA. Without precise locality, *ex Hort.* Linden establishment (Lectotype [designated by Romero and Jenny, 1993:]; BR; Isolectotype: BR).

Distribution: Venezuela, Guyana, Surinam, French Guiana, Colombia, and Brazil. The locality of the type of *Catasetum chloranthum* (“Peru”; see also Schweinfurth, 1960: 586) is doubtful, but not impossible, as many orchid species from the Guayana highlands also occur in mountainous sandstone outcrops in eastern Perú. Notice that Linden et al. (1895: 14, 24), soon after the name *C. chloranthum* was published, describe this species as “... originaire de l’Amérique du Sud,” perhaps doubting the precise country of origin that Cogniaux provided.

Habitat and Phenology: Found growing among rocks and on granite or sandstone outcrops from 160 to 1400 m. This species tends to flower from the developing pseudobulb. Based on herbarium records, flowering from October to May.

Additional specimen examined: VENEZUELA. Bolívar: Mount Roraima, *E. F. im Thurn 148* (presumably at K, not seen); cited by im Thurn 1886: 154, 1887: 254 as “*Catasetum cristatum?*,” cited by Ridley (1886: 205) as “*Catasetum cristatum? Monachanthus* form;” by Cogniaux (1902: 400), as *Catasetum fuliginosum* Lindl.; and by Schweinfurth, 1967: 168, as *C. planiceps*).

The country of origin of the type locality of this species was most likely Venezuela. *Catasetum planiceps* also displays a wide range of variation in color, from greenish bronze (Fig. 4A) to light green throughout, with yellow tinge in the sepals and petals and inside and at the apex of the labellum (Fig. 4B, Fig. 8), and the sepals, petals, and interior of labellum of uniform color (figures herein) or rarely spotted with reddish brown (as in *B. Maguire 26211*, NY [04013851]; photographs AMES).

It also varies morphologically, particularly in the proportions and openness of the labellum, the size, shape, and revoluteness of the apex of the labellum (Fig. 4A–B and Fig. 9 versus Fig. 10), and the degree of dentition along the lower edges of the labellum (Fig. 4C–D, 8–10). The authors, based on pollination data, estimate that introgression between this species and *C. pileatum* Rchb. f., in areas where the latter is found, is currently taking place (for which *C. xwendlingerii* Foldats was proposed; see Romero and Carnevali, 1989a: 460), and likewise entirely possible between *C. planiceps* and *C. macrocarpum* Rich. *ex Kunth* in the Guayana region.



FIGURE 8. *Catasetum planiceps* Lindl. From Lindley (1843).



FIGURE 9. *Catasetum planiceps* Lindl. From Link et al. (1844), as *Catachaetum recurvatum* Link, Kltzsch & Otto.



FIGURE 10. *Catasetum planiceps* Lindl. Drawn by G. C. K. Dunsterville based on *Dunsterville 195* (Village of Miranda, west of Valencia, Carabobo, Venezuela; AMES). From a photostat at AMES.

APPENDIX II

New nothospecies (*pro sp.*) and nomenclatural notes.

Catasetum* × *gomezii G.A. Romero and Carnevali (*pro sp.*), *hybr. nat. nov. inter* *Catasetum bergoldianum* Foldats et *C. barbatum* (Lindl.) Lindl. *Annals of the Missouri Botanical Garden* 76, No. 2: 455. 1989.

TYPE: VENEZUELA. Municipio Atures, Río Cataniapo, cerca de la desembocadura del Río Gavilán, 30 June 1987, G. A. Romero & C. Gómez 1333 (Holotype: VEN; Isotypes: K, TFAV).

Although first proposed as a species, later it was suspected to be a nothospecies (Romero and Carnevali, 1992: 355, 359; *C. ochraceum* Lindl. mistakenly cited as one of the putative parents). However, the nothospecies had not been proposed before.

Catasetum* × *merchae G.A. Romero (*pro sp.*), *hybr. nat. nov. inter* *Catasetum bicolor* Klotzsch et *C. barbatum* (Lindl.) Lindl. *Selbyana* 10, No. 1: 73. 1988.

TYPE: VENEZUELA. Amazonas: Río Cataniapo, cerca de Gavilán, epífita, poco frecuente, 23 April 1986, G. A. Romero 1275 (Holotype: VEN; Isotype: TFAV).

Although first proposed as a species, later it was suspected

to be a nothospecies (Romero and Carnevali, 1992: 358–359; *C. ochraceum* Lindl. again mistakenly cited as one of the putative parents on page 358). However, the nothospecies had not been proposed before.

Catasetum* × *wendlingeri Foldats, *Acta Botanica Venezuelica* 2: 167. 1958. TYPE: VENEZUELA. Amazonas: Municipio Atabapo, “planta comprada en San Fernando de Atabapo,” *Ex Hort. K. Wendlinger sub E. Foldats 2890* (Lectotype, designated here: VEN [sheet bearing an inflorescence with six flowers]; Isolectotype: VEN [sheet bearing an inflorescence with two flowers]). Proposed as a nothospecies in Romero and Carnevali (1989: 460).

There are two sheets of *Catasetum wendlingeri* at VEN, both labelled “Holotypus” and both bearing the same herbarium accession number, “41847,” which in this herbarium is also the barcode number, making necessary the designation of a lectotype. In addition, there is a flower in the glycerine slide collection at AMES, but it is not known whether it came from the lectotype or the isolectotype designated here.