

A NEW SPECIES AND A NEW RECORD OF ONCIDIROID MICRO-ORCHIDS (ORCHIDACEAE: ONCIDIINAE) FOR THE FLORA OF COSTA RICA

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Abstract

Background: The subtribe Oncidiinae represents one of the most diverse orchid groups in Costa Rica, comprising 186 species across 33 genera.

Questions: Despite their already known richness, is it possible that the diversity of less conspicuous genera remains poorly documented, especially where collecting efforts have been limited? To address the diversity of the genus, what is the most suitable circumscription of *Notyliopsis*?

Taxa: Orchidaceae, *Macroclinium geniculatum* Pupulin & Bogarín, sp. nov., *Notyliopsis beatricis* P. Ortiz.

Study sites: Reserva Biológica Guaitil, Pejibaye, Costa Rica; Calle La Mina, Tayutic, Costa Rica

Results: As part of the ongoing initiative to update the *Flora costaricensis: Orchidaceae*, we describe a new species of *Macroclinium* and report the first record of *Notyliopsis*, both members of the Oncidiinae.

Conclusions. *Macroclinium geniculatum* is described, illustrated, and compared with the similar *M. confertum* Pupulin, from which it differs in the free lateral sepals (vs. basally connate), the petals with three rose-purple blotches (vs. numerous dots), the sigmoid column (vs. straight), and the claw of the lip being geniculate at the middle (vs. straight). *Notyliopsis beatricis*, known only from Chocó, Colombia, is newly recorded for the Costa Rican flora. We used molecular data to reassess the phylogenetic position of *Notyliopsis* and to test the hypothesis that *Santanderella* should be included within this genus. For both species, detailed morphological descriptions and illustrations based on Costa Rican specimens are provided. These findings contribute to the ongoing updating of the inventory of the Oncidiinae in the country towards the completion of *Flora costaricensis*.

Keywords: Flora of Costa Rica, *Macroclinium geniculatum*, new records, new species, *Notyliopsis beatricis*, Oncidiinae.

Resumen

Antecedentes: La subtribus Oncidiinae representa uno de los grupos de orquídeas más diversos en Costa Rica, incluyendo 186 especies en 33 géneros.

Preguntas: A pesar de su riqueza ya conocida, ¿es posible que la diversidad de los géneros menos conspicuos permanezca poco documentada, especialmente donde los esfuerzos de recolecta han sido limitados? Para abordar la diversidad del género, ¿cuál es la circunscripción más adecuada de *Notyliopsis*?

Taxones: Orchidaceae, *Macroclinium geniculatum* Pupulin & Bogarín, sp. nov., *Notyliopsis beatricis* P. Ortiz.

Sitios de estudio: Reserva Biológica Guaitil, Pejibaye, Costa Rica; Calle La Mina, Tayutic, Costa Rica

Resultados. Como parte de la iniciativa para actualizar *Flora costaricensis: Orchidaceae*, describimos una nueva especie de *Macroclinium* y documentamos el primer registro nacional de *Notyliopsis*, ambos miembros de Oncidiinae.

Conclusiones: Se describe y se ilustra *Macroclinium geniculatum* y se compara con la especie *M. confertum* Pupulin, de la cual difiere en los sépalos lateral libres (vs. connados en la base), los pétalos con tres manchas de color rosa-púrpura (vs. numerosos puntos), la columna sigmoide (vs. recta) y la uña del labelo geniculada en el medio (vs. recta). *Notyliopsis beatricis*, conocida solamente del Chocó, Colombia, se registra por primera vez para la flora de Costa Rica. Utilizamos datos moleculares para reevaluar la posición filogenética de *Notyliopsis* y probar la hipótesis de que *Santanderella* debería incluirse en este género. Para ambas especies se proveen descripciones detalladas e ilustraciones basadas en especímenes costarricenses. Estos hallazgos contribuyen a la actualización del inventario de Oncidiinae, encaminada a completar *Flora costaricensis*.

Palabras clave: Flora de Costa Rica, *Macroclinium geniculatum*, nuevas especies, nuevos registros, *Notyliopsis beatricis*, Oncidiinae.

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Oncidiinae represents one of the most diverse subtribes within the Orchidaceae in Costa Rica, comprising 186 species across 33 genera (Pupulin *et al.* 2023). Despite this species richness, the diversity of smaller, often overlooked genera, many of which are twig epiphytes, remains inadequately documented, particularly in the less-explored regions of the country (Pupulin 2000, 2023). The ongoing exploration and collection of plant material to complete the project “*Flora costaricensis*: Orchidaceae” has enabled the staff of the Lankester Botanical Garden to discover and identify many species that had remained unknown in the forests of this country until recently. Although in the last decade, major efforts of taxonomic revision have concentrated on different groups of Pleurothallidinae, some specific projects sponsored by the Vice Rector of Research of the University of Costa Rica have been launched in recent years to address systematic studies in other groups, such as the subtribes Catasetinae, Cranichidinae, Malaxidinae, and Spiranthinae (projects 814-C1-060, 814-C2-050, 814-C1-055, and 814-C1-060, respectively), as well as the revision, correction, and additions to groups already treated previously, which require new interpretations in light of recent findings and classification hypotheses based on a greater range of information with phylogenetic significance.

One of these groups is the Oncidiinae, whose systematic treatment for *Flora costaricensis* was published 25 years ago by Atwood & Mora de Retana (1999). In the intervening decades, numerous taxa have been added to the list edited by Atwood & Mora de Retana (1999), while the subsequent phylogenetic analyses (Neubig *et al.* 2012) indicated that several genera previously assigned to other suprageneric groups should instead be placed in this subtribe. To this end, we initiated a systematic project to revise and expand the Oncidiinae treatment for the flora of Costa Rica to include genera previously assigned to subtribe Ornithocephalinae registered in the Vice-Rector of Research under the acronym 814-C0-051. Here, we present partial results from this ongoing project. Furthermore, the discovery of a *Notyliopsis* species in Costa Rica raises questions about the diversity of the genus and about proposals to expand its circumscription to include the monotypic genus *Santanderella*. Here, we address this issue using both molecular and morphological evidence and find no compelling support for a broader circumscription of *Notyliopsis*.

Material and methods

Plant material. Plants used for this study were collected during field activities conducted throughout Costa Rica by the scientific and horticultural staff of the Lankester Botanical Garden (JBL, by its Spanish acronym) under “Scientific Licenses to collect” SINAC-SE-PI-LC-019-2024 and SINAC-SE-PI-LC-026-2024, issued by the Costa Rican Ministry of Environment and Energy through its Conservation Areas National System (SINAC, by its acronym in Spanish). The plants were cultivated for research purposes in the research greenhouses of JBL until they flowered.

Morphological documentation. Macro-photographs were taken with Nikon D850 and D810 cameras fitted with a Micro-Nikkor AF 105 mm, as well as a Hasselblad H5D-50 camera equipped with a HC 120 Macro lens. Photomicrographs were obtained using a Leica Z16 zoom microscope, fitted with a Planapo 1× lens, and recorded on a Nikon D810 camera via a Leica trinocular tube and dedicated photo tubes for full-frame format sensor. Drawings were prepared on a Leica M165 and MZ12.5 stereo microscopes, equipped with drawing tubes. Black and white line drawings were created on Apple iPad 9th generation tablets using Procreate 5.3.15 raster graphics editor. Vouchers were preserved in the liquid collection of JBL. For the description of *Macroclinium* Barb.Rodr., terminology follows Pupulin (1996).

DNA sequence data, alignment, and phylogenetic analyses. To reassess the phylogenetic position of *Notyliopsis*, we downloaded available *nrITS* and *matK* sequences from GenBank (www.ncbi.nlm.nih.gov/genbank/), following Neubig *et al.* (2012) and including additional accessions published subsequently (Quintanilla-Quintero *et al.* 2011) (Table S1). We aligned the sequences using MAFFT v. 7 (Katoh & Standley 2013) with the L-INS-i strategy (mafft.cbrc.jp). The alignments were manually inspected and trimmed in Geneious Prime® 2025.1.2 (Kearse *et al.* 2012).

To determine the best-fit substitution model for each nucleotide locus, we used ModelFinder, as implemented by

Kalyaanamoorthy *et al.* (2017) in IQ-TREE version 2.2.0 (Minh *et al.* 2020) with the Bayesian Information Criterion (BIC). Our phylogenetic analyses were conducted using individual and concatenated datasets (*nrITS* and *matK*), which was partitioned by locus with unlinked model parameters.

Phylogenetic relationships were inferred using both Bayesian Inference (BI) and Maximum Likelihood (ML) approaches. Although both are likelihood-based, ML estimates a single best-scoring tree by maximizing the likelihood given the observed data, whereas BI combines the likelihood with explicit prior distributions to approximate a posterior distribution of trees and model parameters. We therefore used both approaches as complementary to evaluate the robustness of our phylogenetic hypotheses. Bayesian analyses were conducted using MrBayes v. 3.2.7 (Ronquist *et al.* 2012) on the concatenated dataset (*nrITS* + *matK*), under a GTR+ Γ model. The MCMC analysis was run for 50,000,000 generations, sampling every 500 generations, with four chains and a temperature parameter of 0.2. The first 25 % of sampled trees were discarded as burn-in. Convergence was assessed by ensuring that the average standard deviation of split frequencies was < 0.01 and that all parameters had effective sample sizes (ESS) > 200 , as verified in Tracer v. 1.7 (Rambaut *et al.* 2018). A majority-rule consensus tree was generated using the *sumt* command.

Maximum likelihood analyses were conducted in IQ-TREE v. 2.x (Minh *et al.* 2020) under a GTR+G4 substitution model. Branch support was assessed using 1,000 ultrafast bootstrap replicates (UFBoot2; -bb 1000) run jointly with the best-scoring ML tree search. Rate heterogeneity among sites was modeled with four discrete gamma categories. *Brassia villosa* Lindl. was selected as the outgroup. Nodes were regarded as strongly supported when posterior probability (PP) ≥ 0.95 and ultrafast bootstrap (UFBoot) ≥ 95 . The resulting trees were visualized in R using the packages *ape* (Paradis & Schliep 2019), *ggtree* (Yu *et al.* 2016), *tidyverse* (Wickham *et al.* 2019), and *viridis* (Garnier 2024).

Results

Macroclinium geniculatum Pupulin & Bogarín, sp. nov. ([Figures 1, 2A](#)).

Type. Costa Rica. Cartago: Jiménez, Pejibaye, Reserva Biológica Guaitil, ca. 6 km al noreste de El Humo, entre Ríos Humo y Río Taus, 9° 47' 50.67" N; 83° 45' 09.74" W, 1,198 m, bosque pluvial premontano, epífitas en bosque secundario a orillas del sendero, 25 noviembre 2022, flowered in cultivation at Jardín Botánico Lankester, 12 Jan. 2025, D. Bogarín 14225, R. Gómez, M. Quesada, G. Villalobos, & R. Müntz (Holotype: JBL-K0468). [Figures 1](#) and [2](#).

Diagnosis. Species *Macroclinio conferto* Pupulin *affinis*, *sepalis lateralibus liberis* (vs. *basaliter connata*), *petalis tribus maculis roseo-purpureis notatis* (vs. *multos punctos parvos*), *columna leviter sigmoidea* (vs. *rectam*), *ungue labelli in pars media abrupte geniculato* (vs. *rectum*) *recedit*.

Description. A small epiphytic, cespitose, pendent herb, to about 7 cm tall. Roots filiform, glabrous, ca. 1.5 mm in diameter, white with green apices. Pseudobulbs inconspicuous, elliptic, complanate, ca. 11 × 5 mm, monophyllous at apex, completely hidden by 5-6 leaf-bearing, conduplicate sheaths. Leaves conduplicate, laterally flattened, narrowly linear-lanceolate, 3.0-5.5 × 0.5-0.7 cm, acute to attenuate, the basal ones articulated with imbricating sheaths to 1.2 cm long, provided with narrow, hyaline, scarious margins. Inflorescence lateral, racemose, pendent, many-flowered (23+), to 11 cm long, arising from one of the axils of the upper leaves, the peduncle provided with 3 conspicuous, narrowly triangular-lanceolate, concave, acuminate bracts 7 mm long, ca. 2 mm wide. Floral bracts lanceolate, acute, glumaceous, shorter to or subequal to the pedicellate ovary, to 8 mm long, 2 mm wide. Flowers facing down, partially spreading, white, the petals marked with three rose-purple blotches, the column white, suffused with rose-purple toward the apex, the anther purple. Ovary subclavate, to 12 mm long including the pedicel, round in cross section, ribbed, the ribs shallow and rounded. Dorsal sepal lanceolate, acuminate, concave, reclinate over the column, the apex gently recurved, 7.6 × 1.8 mm. Lateral sepals free, obliquely narrowly lanceolate, acuminate, the apices gently recurved, 8.0-8.2 × 1.5-1.6 mm. Petals porrect, drooping, lanceolate, acuminate, 7.2-7.7 × 1.5 mm. Lip sagittate, 7 mm long, 2.2 wide across the midlobe, from a linear claw, claw terete at the base, flattened at the union with the lip

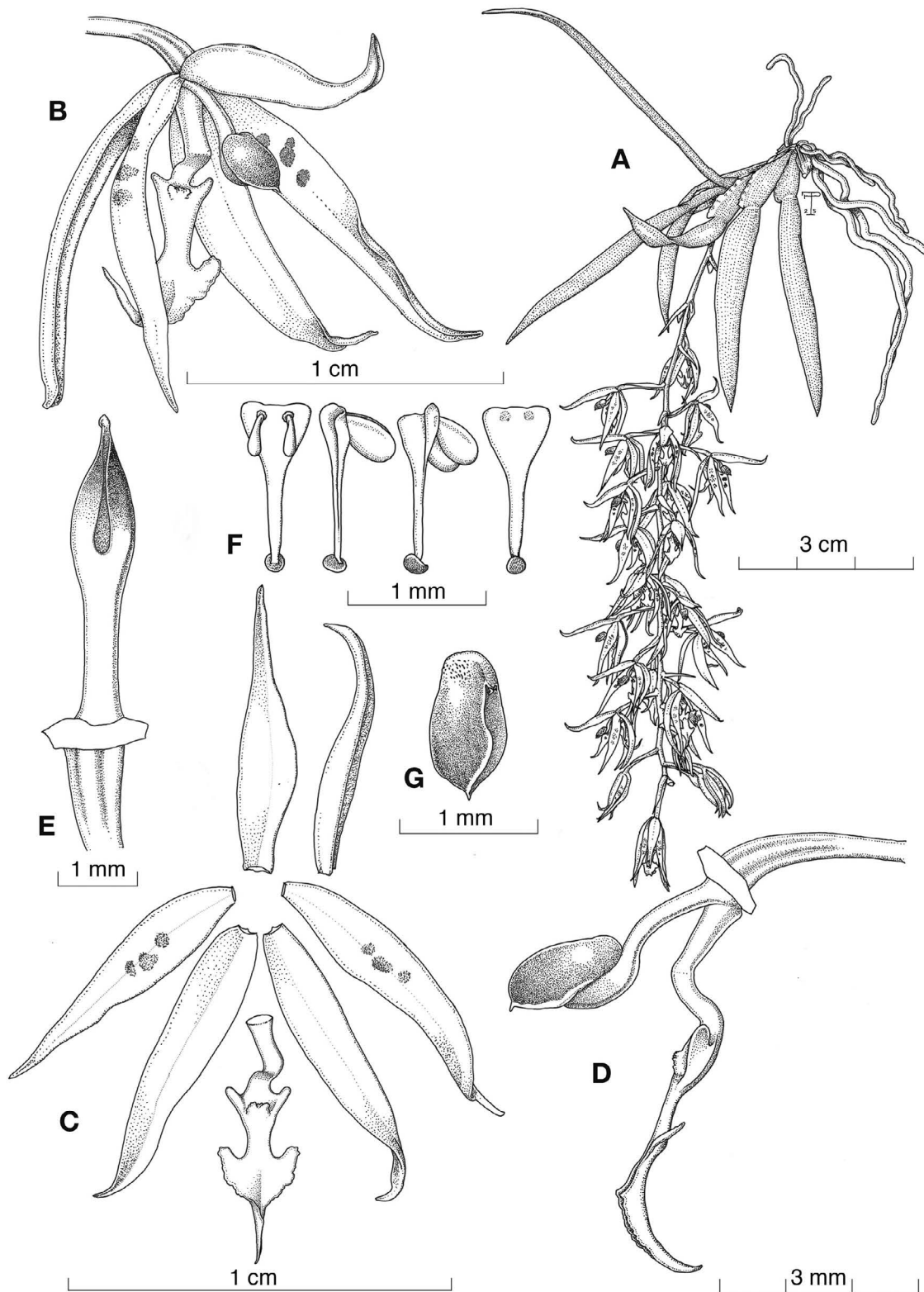


Figure 1. *Macroclinium geniculatum* Pupulin & Bogarín. A - habit. B - flower. C - dissected perianth (the dorsal sepal in frontal and lateral views). D - apex of ovary, column and lip. E - column, ventral view. F - pollinarium in dorsal, lateral, three quarters and ventral views. G - anther. Illustration by F. Pupulin based on the plant that served as the holotype.



Figure 2. Inflorescences of *Macroclinium geniculatum*. A - Bogarín 14225 (JBL). B - Bogarín 14224. Photos by F. Pupulin.

blade, abruptly geniculate at the middle; lip blade 3-lobed, the basal lobes auricle-like, elliptic, retrorse, 1 mm long, the isthmus rectangular-cuneate, 1 mm long, the midlobe sagittate, acuminate, gently recurved, conduplicate at apex, 3.0×2.2 mm: disc with a small, elevated, rectangular, retuse, retrorse callus, 0.3×0.6 mm. Column slender, terete, slightly sigmoid, apically thickened around the stigmatic area, 3.5 mm long; clinandrium dorsal, shallow; stigma ventral, longitudinally slit-like. Anther dorsal, erect, ellipsoid, strongly cucullate, apically minutely mucronate, ca. 1 mm long, minutely papillose, 2-celled, the base slightly bilobed. Pollinia 2, narrowly ovoid-pyriform, strongly complanate, attached by minute, yellow, translucent caudicles to a narrowly obtriangular, basally attenuate, hyaline stipe; viscidium ovate-elliptic, reddish brown. Capsule not seen.

Distribution and ecology. Known only from the Cordillera de Talamanca in Costa Rica, where the species inhabits the smallest terminal branches in the understory of premontane rain forests along the Caribbean watershed, at elevations of 1,200 to 1,300 meters.

Phenology. *Macroclinium geniculatum* flowers at least during January and February, corresponding to the beginning of the dry season in Costa Rica.

Etymology. From the Latin adjective *geniculatum*, derived from *geniculum*, a diminutive of *genu*, “knee,” in the sense of being bent abruptly at an angle like a bent knee, referring to the bent claw of the lip.

Additional specimen examined. Costa Rica. Cartago: Jiménez, Pejibaye, Reserva Biológica Guaitil, ca. 6 km al nor-
teste de El Humo, entre Ríos Humo y Río Taus, $9^{\circ} 47' 50.67''$ N; $83^{\circ} 45' 09.74''$ W, 1,198 m snm, bosque pluvial
premontano, epífitas en bosque secundario a orillas del sendero, 25 Noviembre 2022, flowered in cultivation at Jardín
Botánico Lankester, 28 Feb. 2024, *D. Bogarín 14224*, *R. Gómez*, *G. Villalobos*, & *R. Müntz* (no specimen preserved,
photo-JBL!). [Figure 2B](#).

Notyliopsis beatricis P.Ortiz, Orquideología 20(2): 184. 1996.

Type. Colombia. Chocó. Vertiente occidental de la Cordillera Occidental, alt. aprox. 1300 m. Cultivada por la Sra. Beatriz de Escobar, Buga (Valle del Cauca), agosto 16, 1995. *P. Ortiz 1061* (holotype HPUJ).

Description. An epiphytic, pseudobulbous, caespitose, small pendent herb, about 7 cm tall. Roots filiform, glabrous, 0.4-0.6 mm in diameter, whitish with green apex. Pseudobulbs pyriform-complanate, $7.4-12.5 \times 3.7-5.6$ mm, dark brown, monophyllous, the base partially covered by 2-3 triangular, acuminate, dry-papyraceous sheaths, 6.7-12.4 mm long. Leaf solitary, sessile, conduplicate, thickened, acute, $1.3-5.0 \times 0.2-0.6$ cm. Inflorescence lateral, racemose, pendent, many-flowered (8+), to about 6 cm long, arising from the axil of one of the upper sheaths, the peduncle provided with 2-3 spreading, narrowly triangular-lanceolate, concave, acuminate bracts to 13 mm long, ca. 3 mm wide. Floral bracts lanceolate, acute, glumaceous, slightly shorter than the pedicellate ovary, 3.2 mm long. Flowers with spreading segments, the sepals and petals hyaline white, marked at the base with a narrow, transversal, purple band, the lip pale yellow suffused with rose-purple at the base of the blade and on the lateral lobes, the column white tinged pale green at the apex, the anther cap white with two basal, yellow blotches. Ovary terete, subclavate, to 3.75 mm long including the pedicel, round in cross section, ribbed, the ribs shallow and rounded. Dorsal sepal elliptic, acute, deeply concave-cymbiform, incurved over the column, the apex gently recurved, 4.5×2.2 mm. Lateral sepals connate into a lanceolate, deeply concave, cymbiform, apically retuse synsepal 4.3×3.0 mm. Petals linear-oblong, obtuse to subacute, gently incurved, 4.2×1.0 mm. Lip 3-lobed, from a short, cylindric claw, 3.5×2.5 mm in natural position, 5 mm wide when spread out, the lateral lobes semicircular, erect, the midlobe broadly triangular, truncate-retuse, strongly conduplicate; disc with a complex callus, basally thick, with two protruding, massive projections, triangular in section, extending forward into a low, linear, thin plate, basally connate with the body of the blade, apically bilobed and free for ca. 3 mm. Column slender, basally terete, abruptly thickened at the apex where it becomes subrectangular in side view, distinctly sigmoid in lateral view, narrowly acute, ca. 4 mm long; clinandrium dorsal, shallow; stigma ventral, longitudinally slit-like. Anther dorsal, narrowly ovate-sublinear, basally strongly cucullate, apically rounded-cucullate, 2×1 mm, 2-celled. Pollinia 2, obovate-subrectangular, laterally strongly complanate, erect, attached by minute, translucent caudicles to a narrowly obtriangular, basally attenuate, apically acute, hyaline stipe; viscidium lanceolate. Capsule not seen.

Distribution and Ecology. In Costa Rica, this species is found in the foothills of Fila Matama and the Cordillera de Talamanca, where it inhabits small terminal branches or trunks (less than 5 cm in diameter) in the understory of secondary premontane rain forests at elevations from 800 to 900 meters.

Phenology. *Notyliopsis beatricis* has been observed flowering in March.

Additional specimen examined. Costa Rica. Cartago: Turrialba, Tayutic, entre Tayutic y Jicotea, Calle La Mina, pendiente al lado del río Platanillo, $9^{\circ} 49' 20.92''$ N, $83^{\circ} 32' 14.66''$ W, 879 m, bosque muy húmedo premontano, epífita en bosque secundario, 8 marzo 2025, *D. Bogarín 15471*, *R. Gómez & G. Villalobos* (JBL-K0472). [Figures 3-4](#).

Phylogenetic position. Although the two accessions of *Notyliopsis beatricis* clustered together with strong support in the concatenated and single-locus datasets (BS = 100, PP = 1.0), their phylogenetic placement relative to other genera varied across different analyses ([Figures S1-S6](#)). In the concatenated ML tree, *Notyliopsis* P.Ortiz was inferred as sister to *Santanderella amadorinconiana* P.Ortiz with moderate support (BS = 85); this *Notyliopsis* + *Santanderella* P.Ortiz group was, in turn, sister to a broader assemblage including *Capanemia* Barb.Rodr., *Santanderella* Kuntze, *Solenidium* Lindl., and *Zelenkoa* M.W.Chase & N.H.Williams, together with several “twig-epiphyte” genera ([Figure S1](#)). In the BI concatenated analysis, *Notyliopsis* was not recovered as sister to *Santanderella* (which instead was embedded within *Gomesa* R.Br. and showing a long branch); rather, *Notyliopsis* was inferred as sister to a larger clade including *Comparettia* Poepp. & Endl., *Ionopsis* Kunth, *Leochilus* Knowles & Westc., *Notylia* Lindl., *Rodriguezia* Ruiz & Pav., and allies (PP = 0.85), and this clade was sister to *Capanemia* + *Zelenkoa* + *Santanderella* + *Solenidium*

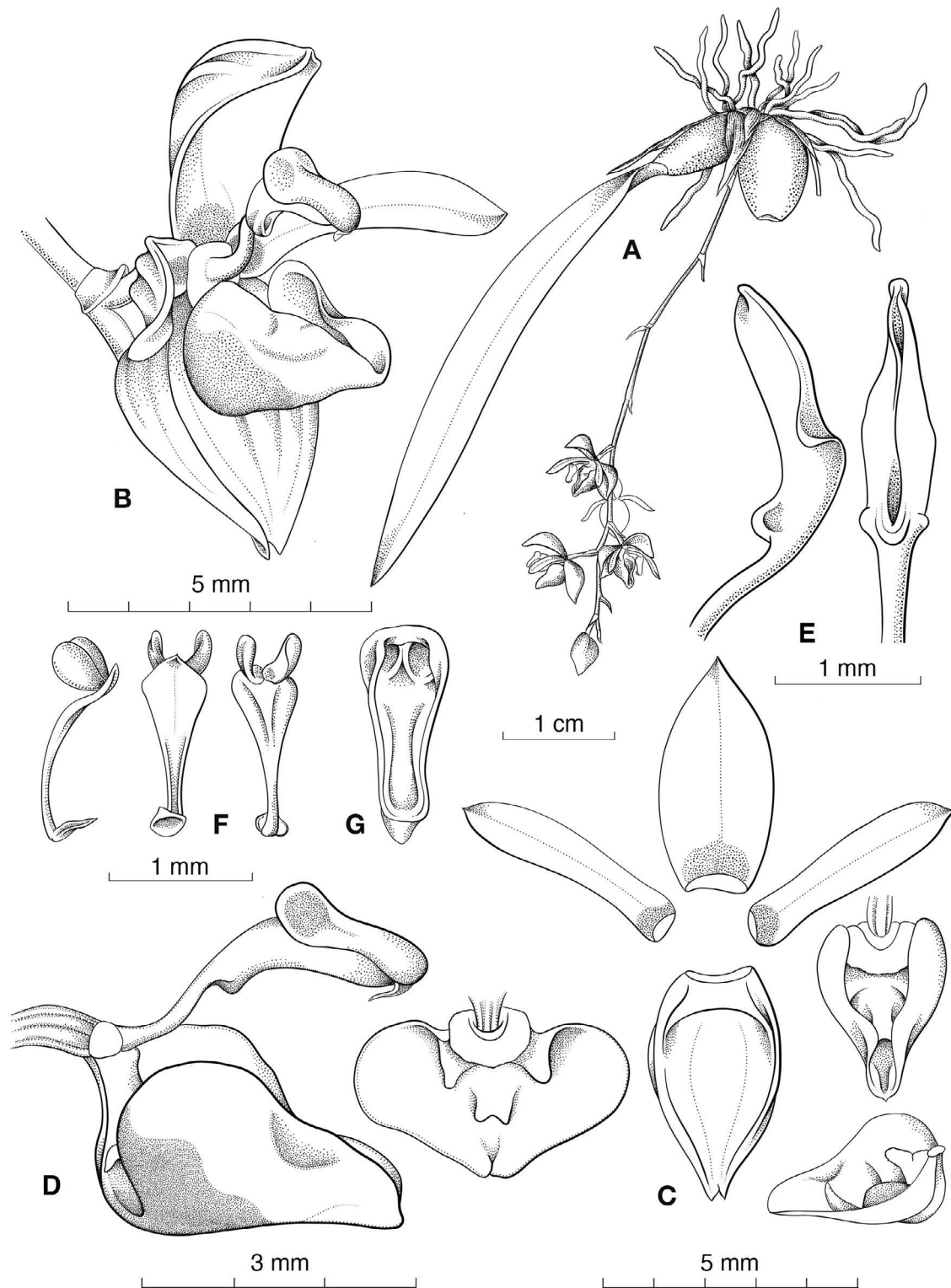


Figure 3. *Notyliopsis beatrix* P. Ortiz. A - habit. B - flower. C - dissected perianth with the lip in front view, side view (longitudinally sectioned), and spread out. D - apex of ovary, column and lip. E - column in lateral and ventral views. F - pollinarium in dorsal, ventral, and lateral views. G - anther. Illustration by D. Bogarín based on Bogarín *et al.* 15471 (JBL).



Figure 4. Inflorescence of *Notyliopsis beatricis*, Bogarín et al. 15471 (JBL). Photo by D. Bogarín.

with high support (PP = 0.98) ([Figure S2](#)). This result was similar to the BI concatenated single-locus analyses based on nrITS ([Figure S3](#)). Maximum-likelihood single-locus analyses were comparatively weakly resolved: in matK, *Notyliopsis* was placed as sister to *Tolumnia* Raf. with low support (BS = 72, PP = 0.33) ([Figures S4, S5, S6](#)), whereas nrITS recovered it within a polytomy including *Capanemia*, *Gomesa*, *Nohawilliamsia* M.W.Chase & N.H.Williams, *Sanderella*, *Solenidium*, *Zelenkoa* and other “twig-epiphyte” clades ([Figure S5](#)). For *Santanderella*, in the matK analyses using BI and ML, the available sequence showed unstable placements with low support and an unusually long terminal branch, suggesting poor sequence quality ([Figures S4, S6](#)). In nrITS, *Santanderella* was consistently embedded within *Gomesa* in both analyses ([Figures S3, S5](#)).

Discussion

Macroclinium geniculatum belongs to the *Macroclinium bicolor* group (Pupulin 1997), composed of plants with racemose and usually long inflorescences, which contrasts with species closely related to *M. lineare* (Ames & C. Schweinf.) Dodson, where the rachis is condensed at the short terminal portion of the inflorescence, giving the impression of an umbel. The *Macroclinium bicolor* (Lindl.) Dodson group includes five species in Costa Rica, known from the Cordillera de Talamanca, extending west to the Dota region and the central Pacific, and north to the Central Volcanic and Tilarán cordilleras (Mora-Retana & Pupulin 1997, Pupulin & Mora-Retana 1999, Pupulin 2000, 2023). The new species proposed here is a small twig-epiphyte found on the Caribbean watershed along the northern slopes of the Cordillera de Talamanca. Among the species in the group, *M. geniculatum* is most similar to *M. confertum*, with which it shares the densely flowered raceme and a similar outline of the lip, both featuring a rather conspicuous callus at the base of the blade. However, it differs from the latter species by its free lateral sepals (vs. basally connate), the petals with three large rose-purple blotches (vs. numerous dots), the sigmoid column (vs. straight), and the claw of the lip abruptly geniculate in the middle (vs. straight).

Initially described and previously known only from the Chocó region along the western watershed of the Andean Cordillera Occidental in Colombia (Ortiz 1996), *Notyliopsis beatricis* is now recorded here for the first time in Costa Rica. Although a geographic disjunction of nearly 1,000 km, without any intermediate records, may seem unexpected, similar unusual distributions have been documented by Bogarín *et al.* (2008) and Bogarín (2011) between the floras of Costa Rica and Ecuador (*i.e.*, *Acianthera aberrans* (Luer) Pupulin & Bogarín, *Epidendrum scharfii* Hágsater & Dodson, *Epidendrum stellidiforme* Hágsater & Dodson, *Lockhartia cladoniophora* Rehb.f., *Maxillaria bolivarensis* C.Schweinf., *Ornithidium pendulum* (Poepp. & Endl.) Cogn., *Ornithocephalus montealegreae* Pupulin, and *Warmingia zamorana* Dodson). In cases of disjunctions involving species from the subtribe Oncidiinae, such as *Ornithocephalus montealegreae* (Pupulin 2002), *Warmingia zamorana* (Johansen 1992, Pupulin 2005, 2008), and *Notyliopsis beatricis*, these are miniature plants that may easily be overlooked in the dense epiphytic vegetation covering forest canopies in the wet forests of Central and South America. For this reason, Bogarín *et al.* (2008) consider that their presence in Panama and Colombia is highly probable.

The floristic affinities between Central America and the Chocó region have been extensively documented since Gentry (1982, 1986). The geological connection between the Chocó block and Central America partially accounts for this affinity, further evidenced by numerous plant migrations from Central America into the Chocó over the past 5 million years, particularly during the Pleistocene. Notably, there have been no reverse migrations detected from the Chocó into Central America, indicating a unidirectional pattern of floristic exchange in lowland species (Pérez-Escobar *et al.* 2019). Consequently, Central American migrants are typically associated with lowland habitats, whereas Andean migrants originate from montane environments. This biogeographic connection is also evident within the Orchidaceae, where subtribes with lowland representatives, such as Maxillariinae (*e.g.*, *Camaridium* Schltr.), Oncidiinae and Zygopetalinae show significant diversity in both regions (Urreta 2005, Bogarín *et al.* 2015, Kirby 2016, Pupulin *et al.* 2023). Thus, the discovery of *Notyliopsis* in Costa Rica provides additional evidence for the floristic affinity between Central America and the Chocó.

The phylogenetic position of *Notyliopsis* within the Oncidiinae is consistent with previous studies that place the genus in the “twig-epiphyte” clade, which includes, among others, *Comparettia*, *Rodriguezia*, *Macradenia* R.Br., *Macroclinium*, *Zelenkoa*, and the *Gomesa* group. However, the position of *Notyliopsis* within this clade remains inconclusive. Only ML analysis recovered *Notyliopsis* as sister to *Santanderella* with moderate support. However, the only *matK* sequence of *Santanderella* available in GenBank (accession No. HQ219251) appears to be of low quality, having apparent base-calling errors when aligned with sequences of phylogenetically related taxa and reflected in its unusually long branch in all the analyses. With nrITS, *Santanderella* is embedded within *Gomesa*; however, this hypothesis does not align with morphology (Neubig *et al.* 2012). The most well-supported position of *Notyliopsis* was yielded by the concatenated BI analyses that place the genus as sister to a clade formed by *Nohawilliamsia* + *Plectrophora* + *Ionopsis* + *Comparettia* + *Leochilus* + *Macroclinium* + *Notylia* + *Warmingia*, among other twig

epiphytes. However, this placement should also be re-evaluated using multilocus datasets to better resolve the nodes and persistent polytomies reported in previous Oncidiinae phylogenetic studies (Neubig *et al.* 2012). Also, given the limited information on the *matK* sequence of *Santanderella*, we recommend generating new sequences for that genus, ideally via whole-plastome sequencing and high-throughput methods.

Following the expanded concept of *Notyliopsis* proposed by Chase (in Pridgeon *et al.* 2014), both the plant database of the Missouri Botanical Garden (Tropicos 2025) and “Plants of the World Online” (POWO 2025) include *Santanderella* P.Ortiz as a heterotypic synonym of the former genus, implying the existence of a second species in *Notyliopsis* (the type of *Santanderella*). However, despite the use of *Notyliopsis amadorinconiana* (P.Ortiz) M.W.Chase (Chase 2014), to our knowledge, the combination of *Santanderella amadorinconiana* P.Ortiz under *Notyliopsis* has never been validly published. The “World Flora Online” treats *Santanderella amadorinconiana* as a taxonomically unplaced name (WFO 2025).

Beyond their broadly similar vegetative architecture, the flowers of the single species of *Notyliopsis* and *Santanderella* differ markedly in several key characters. In *Notyliopsis*, the nearly bilabiate flower is spreading, showing a broad dorsal sepal and boat-shaped fused lateral sepals, along with a deeply cymbiform lip flanked by incurved, linear sepals. In contrast, the perianth segments of *Santanderella* are strongly porrect, and the flower has free sepals and a laminar lip that resembles the narrowly linear, acicular, flat petals in shape.

Moreover, the lip of *Notyliopsis* is a deeply concave, cymbiform structure, reniform in outline when spread out, with broad, semicircular lateral lobes that are erect at each side of the base of the column, and a broadly triangular midlobe that is strongly conduplicate. It features a massive, semicircular, concave callus at the base, which extends basally into two lateral, thick, short horns, gradually merging with the lip’s blade to re-emerge at the apex of the disc into a short, flat, bilobed, upright lamina. In contrast, the ecallose lip of *Santanderella* is a simple and almost flat lamina, faintly inflated at the base, where it has two obscure, narrowly semi-elliptic lateral lobes that leave the column completely exposed, slightly broadening under the middle portion into a narrowly elliptic midlobe.

The column of *Notyliopsis* is semi-erect, sigmoid, and approximately equal in length to the lip, allowing the viscidium to be held high above the lip apex. It abruptly inflates in the middle into a rectangular-subrhombic, dorsiventrally convex structure, featuring two lateral teeth at the base. The thin wings fold basally to encircle the narrowly elliptic stigmatic cavity. The clinandrium extends acutely into a rounded rostellum, which is covered by the anther that exceeds it in length. While in *Santanderella* the viscidium is neatly divided into a dorsal, brown, cellular portion and the sticky ventral pad, in *Notyliopsis* it is completely hyaline and continuous with the stipe, and somewhat resembling that of the distantly related *Dichaea* in the Zygopetalinae. Furthermore, the viscidium of *Notyliopsis* folds back to remain ventral and elevated over the lip. The large entrance to the lip chamber and the incurved viscidium may suggest that the pollinarium is positioned on the dorsal surface of the pollinator’s thorax rather than on the forehead, as in *Macroclinium* and *Notylia*, and likely in *Santanderella*. In the latter genus, the column is short (approximately half the length of the lip) and straight. It broadens into a diagonal, trumpet-like shape in the middle, divided on the underside by a deep V-shaped notch with two apical teeth leading to the stigmatic slit. On the upper side, a conical structure emerges from the clinandrium, tapering to a pointed tip partially covered by the anther, which also conceals the apical viscidium.

In *Notyliopsis*, the pollinia are obovate, concave-incurved, attached by large caudicles to a trullate stipe that gradually tapers toward the apex, whereas in *Santanderella*, the pollinia are narrowly rectangular, rounded at both apices, straight, and connected to a rhombic stipe that is concave at the base and long attenuate at the apex. For these reasons, we do not follow the proposal to merge *Santanderella* into *Notyliopsis* and instead advocate maintaining them as distinct genera, at least until denser species sampling and more strongly supported phylogenetic evidence become available.

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Supplementary material

Supplemental data for this article can be accessed here: <https://doi.org/10.17129/botsoci.3878>

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