

Untangling the *Nautilocalyx pallidus* complex (Gesneriaceae) with description of a new species and a new combination

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Academic editor: Igor Kessous ♦ Received 25 December 2025 ♦ Accepted 6 July 2026 ♦ Published 16 September 2026

Abstract

Background and aims – *Nautilocalyx pallidus* is a broadly circumscribed species originally described from Peru under which several morphologically distinct taxa have historically been misidentified. As part of an ongoing taxonomic revision of *Nautilocalyx*, this study aims to re-evaluate the circumscription of *N. pallidus*, resurrect a species previously treated as a synonym, and describe a new species from Brazil.

Material and methods – The morphological analyses were based on herbarium specimens and field observations. Descriptions and measurements were derived from herbarium specimens, field images, and flowers preserved in alcohol. A preliminary conservation assessment for *Nautilocalyx engelsii* sp. nov. was conducted in accordance with the IUCN guidelines and criteria.

Key results – A species previously treated as a heterotypic synonym of *Nautilocalyx pallidus* is reinstated and transferred to *Nautilocalyx* as *N. ochroleucus* comb. nov., based on specimens from Brazil originally identified as *Drymonia ochroleuca*. This species differs from *N. pallidus* by its shorter stems, narrower leaves, longer floral bracts, and yellowish corolla. In addition, *Nautilocalyx engelsii* sp. nov. is described as a new species from the state of Mato Grosso, Brazil, and is characterized by green leaves suffused with red, entire and ciliate leaf margins, and a white corolla, suffused with pale pink outside. Lectotypes are designated for *N. pallidus* and *N. hirsutus* to clarify the application of these names.

Conclusion – This study clarifies the circumscription of *Nautilocalyx pallidus* and improves understanding of its species complex. As part of an ongoing taxonomic revision of the genus, we provide an updated circumscription, including an identification key, descriptions, illustrations, and field images. We recognize four species within the complex, redefine the morphological boundaries between *N. hirsutus* and *N. pallidus*, reinstate *Nautilocalyx ochroleucus* comb. nov., and describe a new species, *Nautilocalyx engelsii* sp. nov.

Keywords

Amazon rainforest, Columneinae, Gesneriaceae, Gesnerioideae, nomenclature, taxonomy

INTRODUCTION

Gesneriaceae is a family comprising more than 3900 species and 150 genera (Weber et al. 2013, 2020; Clark et al. 2020; GRC 2026). The Neotropical subfamily Gesnerioideae comprises more than 1200 species,

concentrating its diversity in the northwestern region of South America (Wiehler 1983; Perret et al. 2007, 2013; Weber et al. 2020). *Nautilocalyx* Linden ex Hanst., as traditionally described, encompasses around 50 species (Mora and Clark 2016; Clark et al. 2020; Weber et al. 2020). The genus belongs to the subfamily Gesnerioideae, the

tribe Gesnerieae, and the subtribe Columneinae (Weber et al. 2013). *Nautilocalyx* consists of terrestrial herbs with erect, more or less succulent stems with adventitious roots at the nodes, epedunculate or short pedunculate inflorescences, and deeply dissected calyx lobes that appear nearly free (Wiehler 1978; Weber et al. 2020). The genus is distributed from Central America through the Amazon, reaching the central region of Brazil in the state of Mato Grosso (Wiehler 1978; Mora and Clark 2016).

Nautilocalyx was described by Hanstein (1854), who separated it from *Episcia* Mart. based on the following floral characters: calyx lobes fused at the base, corolla tube with a basal nectar chamber, a dorsal nectary gland, and a stomatomorphic stigma. The characters that have traditionally been used to define the genus are of limited phylogenetic value, and recent phylogenetic analyses strongly support the non-monophyly of *Nautilocalyx* as currently circumscribed (Clark et al. 2006; Mora and Clark 2016).

A recent phylogenetic study by Mora and Clark (2016) showed that species traditionally recognized as *Nautilocalyx* are nested in six different clades. To accommodate the polyphyly of traditionally recognized *Nautilocalyx*, three genera corresponding to three well-supported clades were identified, while the remaining taxa of poorly resolved clades were retained in *Nautilocalyx*. Currently recognized *Nautilocalyx* species represent the following three poorly supported clades as outlined in Mora and Clark (2016): the “*Nautilocalyx* Amazonian clade”, “*Nautilocalyx pictus* clade”, and “*Nautilocalyx sensu stricto*”. The plants belonging to the *Nautilocalyx* Amazonian clade differ from those of the *Nautilocalyx* s.str. clade by the lanceolate overlapping calyx lobes that cover the basal nectar chamber of the corolla, the calyx lobe margins folded lengthwise along the adjacent lobe, and the elongated corolla tubes that are longitudinally sulcate (Mora and Clark 2016). In contrast, the *Nautilocalyx* s.str. clade is characterized by a calyx with linear or linear-lanceolate sepals that are separate (i.e. not overlapping with adjacent lobes) and a corolla that is uniformly smooth or not longitudinally sulcate (Mora and Clark 2016).

Within the *Nautilocalyx* Amazonian clade, *Nautilocalyx pallidus* (Sprague) Sprague represents a taxonomically problematic species, characterized by extensive morphological variation, an ambiguous type locality, and confusion with *Nautilocalyx hirsutus* (Sprague) Sprague. The species was originally described from Peru, but the type specimen lacks precise locality data. During the revision of the Amazonian clade of the genus, we found several herbarium specimens morphologically similar to *N. pallidus* and *N. hirsutus*. We refer to these specimens as the *N. pallidus* complex. Taxa in this complex generally share the following characters: uniformly green leaves on both surfaces (Fig. 1C, D), usually glabrous stems and leaves (Fig. 1F), sessile inflorescences (Fig. 2A), and a white, cream, or yellow corolla, sometimes with striations formed by purple dots inside the corolla tube (Fig. 1B).

Also belonging to this complex is *Drymonia ochroleuca* Poepp., described by Poeppig (1840) from a specimen collected in the Brazilian Amazon. In the protologue, Poeppig (1840) also recognized a “β” (beta) variety from the state of Pará. Hanstein (1864) subsequently transferred *D. ochroleuca* to *Episcia* and validly published the variety as *E. ochroleuca* var. *angustifolia* Hanst. Both *Episcia ochroleuca* (Poepp.) Hanst. and *E. ochroleuca* var. *angustifolia* Hanst. have subsequently been treated as synonyms of *N. pallidus* in floristic treatments, checklists, and taxonomic databases (Clark and Skog 2014; Clark et al. 2020; Rojas Gonzales 2020; Mora 2024; POWO 2026). However, our study revealed a consistent suite of morphological characters that distinguishes *D. ochroleuca* from *N. pallidus* and supports its recognition as a distinct species. We therefore resurrect *D. ochroleuca* from synonymy and provide the new combination in *Nautilocalyx*.

During our research, we found a fourth species similar to *Nautilocalyx pallidus* that was collected in the state of Mato Grosso, Brazil (Fig. 3), and had been previously identified in herbaria as *N. pallidus*. These Mato Grosso collections present sufficient morphological differences to justify the recognition of a distinct species.

In conclusion, we present an updated circumscription for *Nautilocalyx pallidus*, with an identification key, descriptions, discussions, an illustration, and field images to support the recognition of four species. Morphological boundaries are clarified for traditionally recognized *N. hirsutus* and *N. pallidus*. A previously recognized heterotypic synonym of *N. pallidus* is resurrected as the species *Nautilocalyx ochroleucus* and a new species is described as *N. engelsii*.

MATERIAL AND METHODS

The specimens were collected and deposited in the herbaria MBM, UFAC, and UPCB (herbarium acronyms follow Thiers 2026). Field collections that were sterile were collected and cultivated until flowering. Descriptions were based on fresh material in cultivation and ongoing herbarium research. Terminology for morphological characters is based on Harris and Harris (1994), but we also refer to some characters described in the generic description by Sprague (1912) and refer to characters used to define generic concepts by Wiehler (1978).

The distribution map was produced using QGIS v.3.42.3 (QGIS Development Team 2025), based on coordinates obtained in the field and from herbarium label data. The conservation status was assessed according to the IUCN Red List Categories and Criteria (IUCN 2012) and the updated guidelines of the IUCN Standards and Petitions Committee (2024). The extent of occurrence (EOO) and area of occupancy (AOO) were estimated using GeoCAT, with a default setting of 2 km, which is a 4 km² grid cell (Bachman et al. 2011).

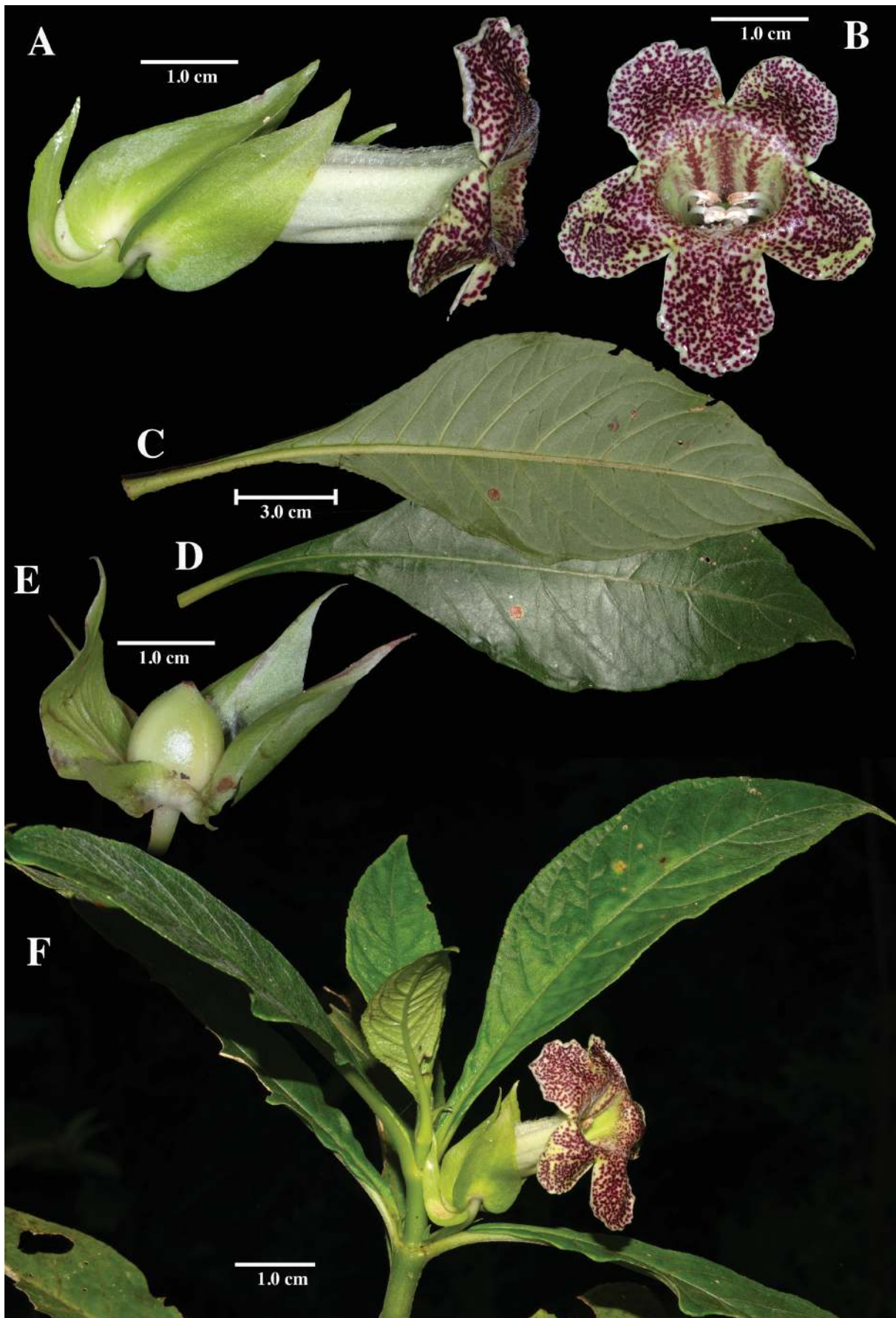


Figure 1. Field images of *Nautilocalyx pallidus*. A. Lateral view of flower. B. Front view of corolla. C. Abaxial leaf surface. D. Adaxial leaf surface. E. Immature fruit. F. Habit. From J.L. Clark *et al.* 19190. Photos by John L. Clark.

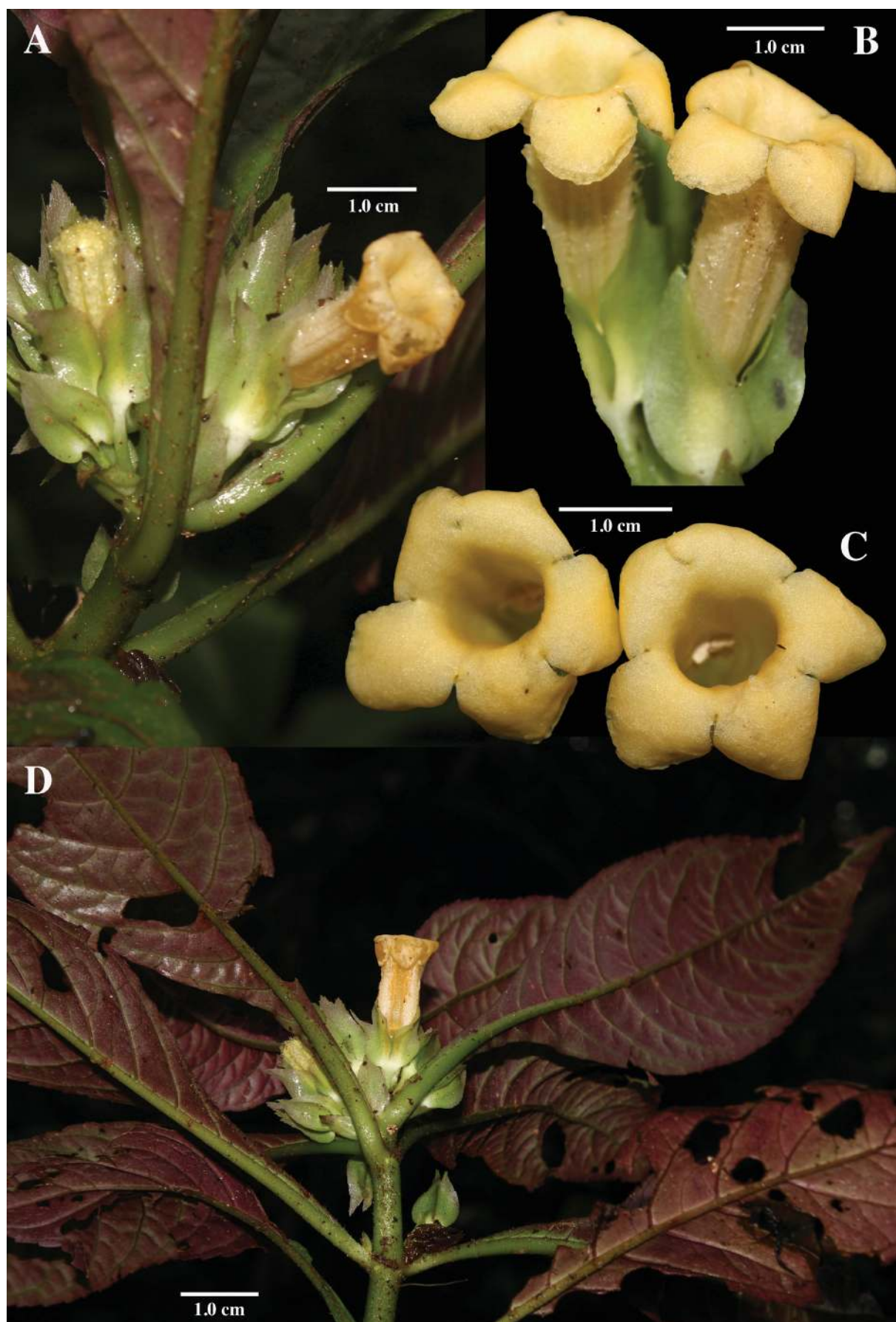


Figure 2. Field images of *Nautilocalyx ochroleucus*. A. Inflorescence. B. Lateral view of flowers. C. Front view of corollas. D. Habit. From D. Ferreira s.n. Photos by Diego Ferreira.

Table 1. Comparison of morphological characters and geographic range of *Nautilocalyx pallidus*, *N. hirsutus*, *N. ochroleucus*, and *N. engelsii*.

	<i>Nautilocalyx pallidus</i>	<i>N. hirsutus</i>	<i>N. ochroleucus</i>	<i>N. engelsii</i>
Stem length	40–150 cm	15–23 cm	10–40 cm	30–60 cm
Petiole length	1.2–1.5 cm	0.8–2.9 cm	0.3–0.9 cm	0.3–1.3 cm
Leaf blade base	Decurrent	Decurrent	Decurrent	Acute (not decurrent)
Leaf shape	Elliptic to oblanceolate	Elliptic to obovate	Narrow elliptic	Elliptic to oblanceolate
Leaf indumentum on abaxial surface	Glabrescent	Hirsute	Pilose to glabrescent	Glabrescent
Leaf blade size	11.2–18.1 × 6.1–8.9 cm	6.3–14.2 × 2.1–5.8 cm	9.4–13.9 × 2.7–4.7 cm	3.5–12.7 × 1.8–6.3 cm
Leaf margin	Uniformly serrate to serrulate, cilia absent	Uniformly serrate, cilia absent	Uniformly serrate, cilia absent	Mostly entire, or with few serrations, ciliate
Leaf, abaxial surface colour	Green	Green	Green, sometimes solid pale red	Green, suffused with red along veins and near margins
Bracts	0.5–0.7 × 0.2–0.4 cm	1.0–1.5 × 0.2–0.4 cm	1.1–2.2 × 0.5–0.7 cm	1.6–1.8 × 0.5–0.7 cm
Flowers per axil	2–6	4–6	2–8	4–6
Calyx lobes	1.1–2.3 × 0.6–1.5 cm	1.1–1.8 × 0.4–0.9 cm	1.3–2.2 × 0.4–0.7 cm	1.8–2.2 × 1.1–1.2 cm
Calyx lobes, margin	Entire, or serrate to serrulate at apex	Entire	Entire, or serrate to serrulate at apex	Entire
Calyx lobes, indumentum	Glabrous to pilose	Hirsute to pilose	Glabrous	Glabrous, margin ciliate
Corolla length	3.1–5.0 cm	2.5–3.3 cm	3.3–4.9 cm	3.0–4.8 cm
Corolla colour	White to cream-white, with dorsal line of purple dots inside tube and lobes	White	Pale-yellow to yellow	White, suffused with pale pink outside
Geographic range	Bolivia (Abuná); Brazil (Amazonas); Colombia (Amazonas, Antioquia, Putumayo); Ecuador (Pastaza); Peru (Amazonas, Cuzco, Loreto); Venezuela (Amazonas)	Northern and west-central Brazil (Acre, Mato Grosso, Mato Grosso do Sul); Peru (Amazonas, Cusco, Loreto, Madre de Dios, Pasco, San Martín),	Northern Brazil (Acre, Amazonas, Pará)	Northern Brazil (Mato Grosso)

TAXONOMIC TREATMENT

Identification key for the species in the *Nautilocalyx pallidus* complex

- 1. Plants uniformly covered with a hirsute indumentum *N. hirsutus*
- Plants glabrous or glabrescent, sometimes covered with a dense indumentum only on the younger parts..... 2
- 2. Leaves elliptic to narrow elliptic, corolla yellow *N. ochroleucus*
- Leaves elliptic, obovate or oblanceolate, corolla white to cream-white..... 3
- 3. Leaves with the margin entire, ciliate; corolla without a line of purple dots inside the tube.....*N. engelsii*
- Leaves with the margin serrate, eciliate; corolla with lines of purple dots on the corolla tube and spotting on the corolla lobes.....
..... *N. pallidus*

1. *Nautilocalyx engelsii* Hinoshita & J.L.Clark, **sp. nov.**

[urn:lsid:ipni.org:names:77396470-1](https://www.ipni.org/names/77396470-1)

Figs 3–5; Table 1

Type. BRAZIL – **Mato Grosso** • Itaúba, Amazônia, Floresta Estacional Sempre Verde Aluvia; cultivada até florescer; 11°08'30"S, 55°46'01"W; 317 m; 14 Feb. 2024;

M.E. Engels 11405; holotype: UPCH [0077797]; isotype: MBM.

Diagnosis. Morphologically similar to *Nautilocalyx pallidus* by reduced peduncles and nearly sessile flower clusters, pedicels shorter than the calyx, and a white to cream-white corolla, but differentiated by leaves green and suffused with red along the veins and near the margins

on both surfaces (vs pale green in *N. pallidus*), margins entire or with few reduced teeth and ciliate margins (vs serrulate to serrate margins and cilia absent), and white corollas suffused with pale pink outside (vs white corollas with purple dots forming lines and spotting on the corolla lobes).

Description. Plants terrestrial, with tubers. Stems erect, 30–60 cm long, succulent, rooting at nodes, terete, pilose, becoming glabrous at maturity, unbranched, green but reddish in the young parts. Leaves opposite, isophyllous; petiole 0.3–1.3 cm long, green to reddish, pilose; blade 3.5–12.7 × 1.8–6.3 cm, elliptic to oblanceolate, immature leaves sparsely pilose, mature leaves nearly glabrous, but pilose along the midveins on both surfaces, green suffused with red along the veins and near the margins on both surfaces, apex acute to obtuse, base acute, margin entire or with few serrations, ciliate. Inflorescence a reduced cyme, appearing sessile, with 4–6 flowers on a reduced peduncle, pedicels 0.7–1.2 cm long, erect, red at the base, green at the apex, pilose; bracts green to green with a red apex, 1.6–1.8 × 0.5–0.7 cm, elliptic to lanceolate. Calyx with subequal lobes, nearly free, dorsal lobe slightly smaller and folded by the corolla nectar chamber, 1.8–2.2 × 1.1–1.2 cm, lanceolate, margin entire, each folded lengthwise by the adjacent lobe, margins ciliate, undulate, green with a red apex, glabrous, pilose near the apex. Corolla uniformly tubular, 3.0–4.8 × 1.1–1.3 cm, oblique relative to calyx, tube almost straight, base enlarged and forming a nectar chamber, longitudinally sulcate, white inside the tube, white suffused with pale pink outside, villous, lobes 6.1–8.9 × 6.6–7.4 mm, rounded, erect, subequal, white, margin entire. Androecium with filaments 2.5–2.8 cm long,

included, cream-white, filaments coiling in the female phase, anthers united in pairs. Nectary a bilobed dorsal gland, ca 5 mm long, glabrous, pale yellow. Gynoecium with an ovary 5.4–6 × 3–4 mm, conical, pilose, pale green; style 1.7–2.2 cm long, pale green, pilose, stigma bilobed. Fruit not observed.

Distribution and habitat. *Nautilocalyx engelsii* is endemic to Brazil, currently only known from the state of Mato Grosso, in the municipalities of Itaúba and Nova Canaã do Norte (Fig. 3). This species is found in wet forest and swampy habitats, often associated with rivers and waterfalls.

Phenology. Flowering specimens were collected from November to January.

Etymology. The epithet honours the collector of the type, the Brazilian botanist Mathias Erich Engels, a taxonomist working mostly on Orchidaceae and a close colleague of the authors.

Preliminary IUCN conservation assessment. Endangered: EN B1ab(ii,iii)+2ab(ii,iii). Only one natural population with a few individuals was originally documented in 2017, whereas subsequent flowering material came from cultivated plants. Since then, no updates on natural populations have been reported. The species occurs in an unprotected area near the construction site of the Colíder Dam and is adjacent to farms. As a result of ongoing construction and agriculture, the area is being rapidly deforested. In addition, the state of Mato Grosso has one of the highest deforestation rates in Brazil (MapBiomas Alerta 2024). In 2023 alone, more than 160,000 ha of native forest were lost in the state (MapBiomas Alerta 2024). This species has an extent of



Figure 3. Distribution map of *Nautilocalyx engelsii* and *N. ochroleucus* in northern Brazil.

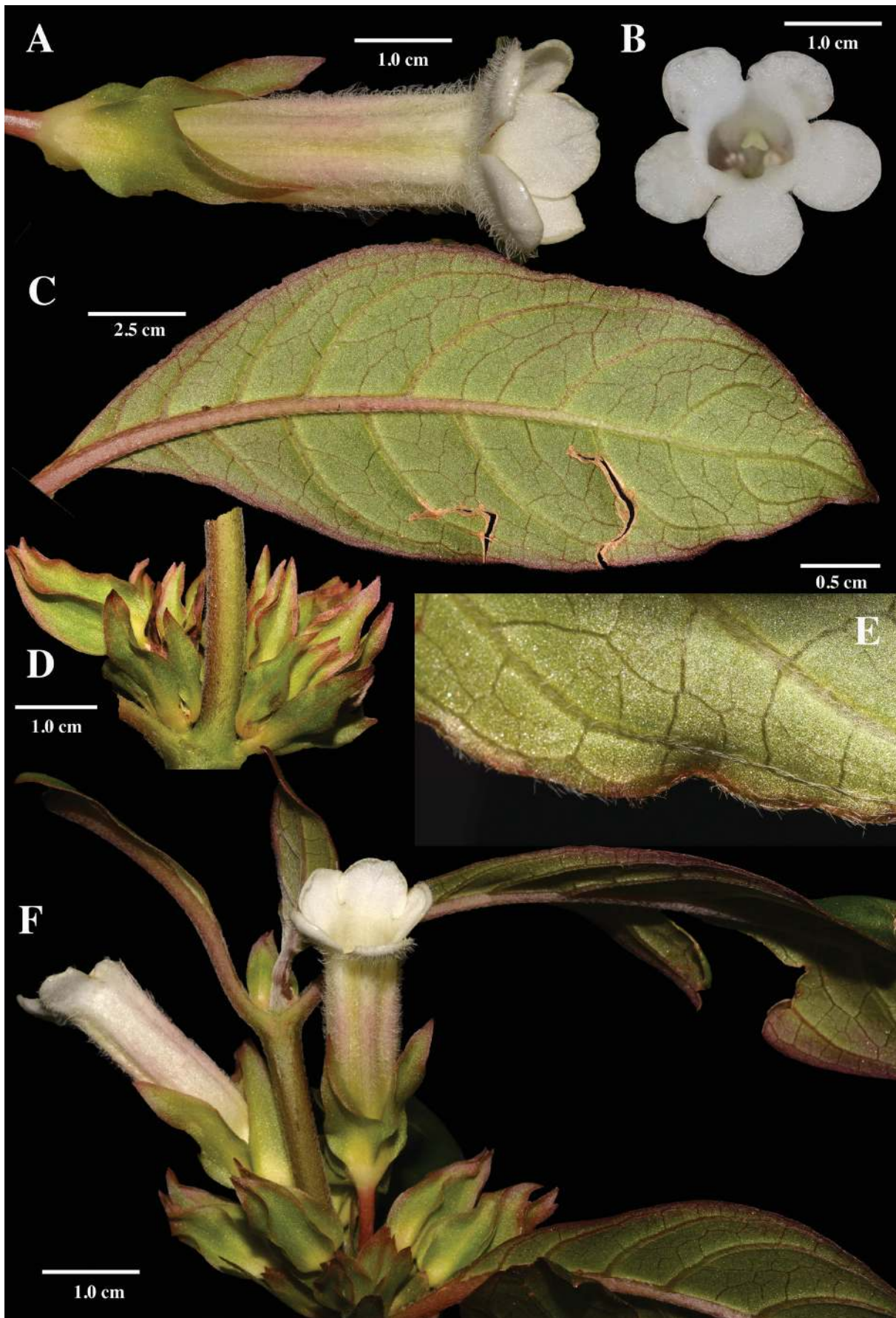


Figure 4. Field images of *Nautilocalyx engelsii*. A. Lateral view of flower. B. Front view of flower. C. Abaxial leaf surface. D. Inflorescence. E. Leaf margin. F. Habit. From M.E. Engels 11405. Photos by Renato Goldenberg.

occurrence (EOO) of 154 km² and its area of occupancy (AOO) is estimated to be less than 20 km². Based on the IUCN Red List Categories and Criteria (IUCN 2024), we provide a preliminary assessment of Endangered.

Additional material examined. BRAZIL – Mato Grosso

• Itaúba, Floresta Estacional Sempre Verde; cultivada até florescer; 317 m; 10 Jan. 2021; *M.E. Engels* 8309; MBM • Rio Teles Pires; 321 m; 22 Nov. 2017; *M.E. Engels* 8491; MBM, RB, HCF, UPCB.

Taxonomic notes. *Nautilocalyx engelsii* is morphologically similar to species in the *Nautilocalyx* Amazonian clade (Mora and Clark 2016). Among the species in this clade, *N. engelsii* has diagnostic features such as the leaf margins, which are entire or with few reduced teeth (Fig. 5B, C), contrasting with the serrate to crenulate margins in other species in this clade. In this species, the leaf lamina is green suffused with red along the veins and near the margins (Fig. 4E), with the red pigmentation more conspicuous in

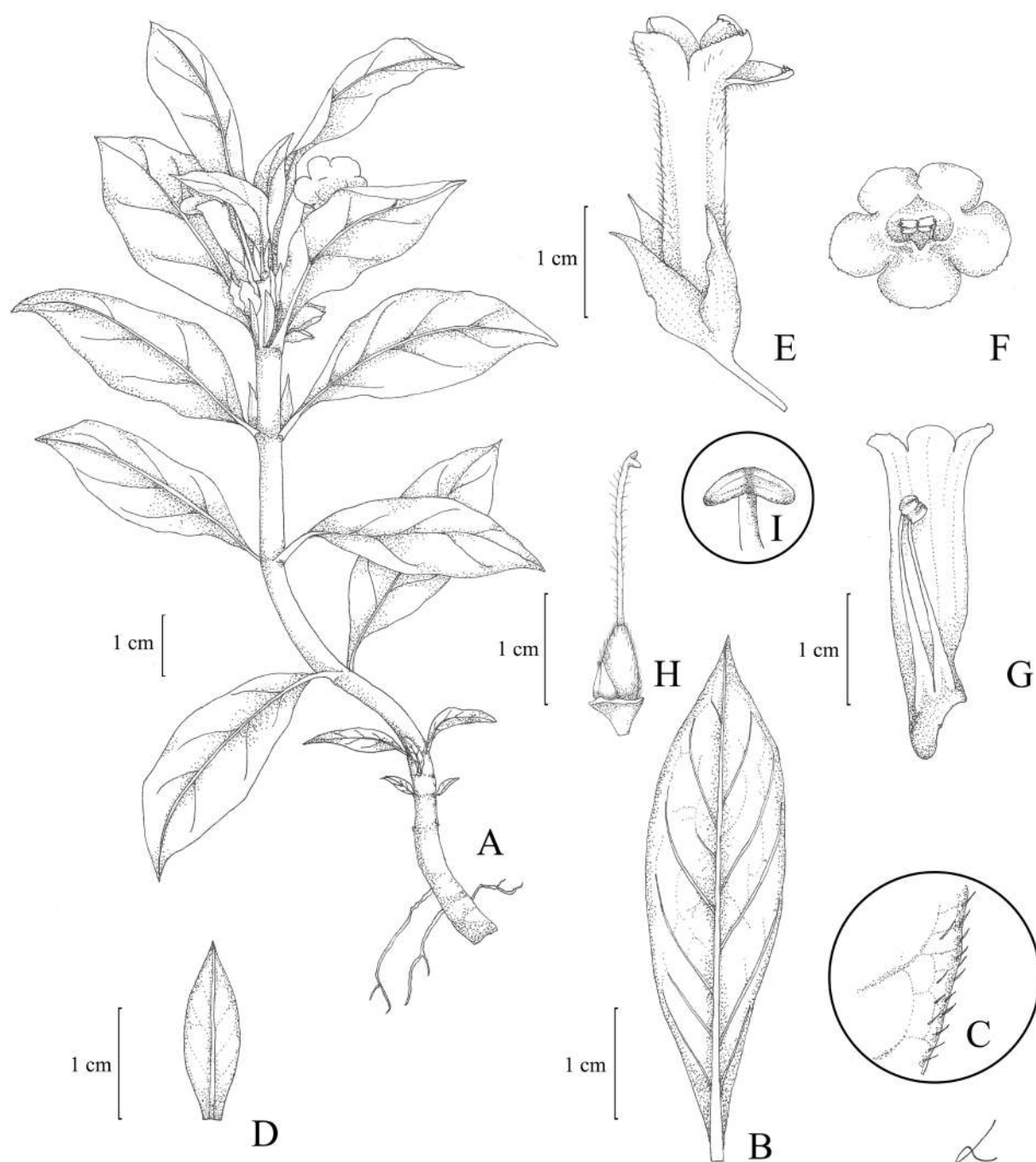


Figure 5. Illustration of *Nautilocalyx engelsii*. A. Habit. B. Abaxial leaf surface. C. Leaf margin. D. Bract. E. Lateral view of flower. F. Front view of flower. G. Stamens and corolla. H. Nectary and ovary. I. Stigma. Based on *M.E. Engels* 11405. Illustration by Lucas K.R. Hinoshita.

immature leaves and becoming less evident as the foliage matures. Green leaves suffused with red occur in a few other species in the clade, including *N. forgetii* (Sprague) Sprague and *N. lynchii* (Hook.f.) Sprague. In these species, however, the red pigmentation is either restricted primarily to the major veins or extends across the entire abaxial surface.

Nautilocalyx engelsii is similar to *N. pallidus* and *N. hirsutus*. These three species have axillary inflorescences with reduced peduncles that appear sessile, pedicels shorter than the calyx, and a uniformly white to cream-white corolla. The differences between *N. engelsii* and *N. pallidus* are provided in the diagnosis and summarized in Table 1. An important diagnostic character that differentiates *N. engelsii* from *N. hirsutus* is a pilose midvein on the adaxial leaf surface (vs hirsute in *N. hirsutus*) and relatively wider calyx lobes ranging from 1.1 to 1.2 cm (vs 0.4–0.9 cm in *N. hirsutus*).

While *N. pallidus* is found in Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela, *N. hirsutus* has a disjunct distribution with collections in northern Peru and west-central Brazil. *Nautilocalyx engelsii* has a more restricted distribution and is presumed endemic to the Brazilian state of Mato Grosso (Fig. 3).

2. *Nautilocalyx ochroleucus* (Poepp.) Hinoshita & J.L.Clark, **comb. nov.**

urn:lsid:ipni.org:names:77396471-1

Figs 2, 3; Table 1

Drymonia ochroleuca Poepp., Nov. Gen. Sp. Pl. 3: 5. 1840. (Poeppig 1840: 5) – Type: same as for *Nautilocalyx ochroleucus*.

Episcia ochroleuca (Poepp.) Hanst. (Hanstein 1864: 403) – Type: same as for *Nautilocalyx ochroleucus*.

Episcia ochroleuca var. *angustifolia* Hanst. (Hanstein 1864: 403) – Type: BRAZIL – Pará • Colares, Flor. amazon. In sylv. arenos. Insul. [in sandy forest on the island]; May 1832; fl.; E.F. Poeppig s.n.; holotype: W [W0032187]; isotype: W [W0032188].

Type. BRAZIL – Amazonas • Ega, Flor. amazon. In paludibus sylvaticis [in swampy forest]; Sep. 1831; fl.; E.F. Poeppig 2559; holotype: W [0032185, 0032186]; isotype: W [0032165].

Description. Plants terrestrial. Stems erect, 10–40 cm long, succulent, rooting at nodes, terete, hirsute, becoming glabrous at maturity, unbranched, green. Leaves opposite, isophyllous; petiole 0.3–0.9 cm long, green, sometimes suffused with red in the abaxial surface, hirsute; blade 9.4–13.9 × 2.7–4.7 cm, narrow elliptic, pilose to glabrescent, pilose in the midveins, green, sometimes with reddish veins in the abaxial surface, or uniformly red on the abaxial surface, apex acute to acuminate, base decurrent, margin serrate. Inflorescence a reduced cyme, appearing sessile, with 2–8 flowers on a reduced peduncle, pedicels 0.5–0.9 cm long, erect, green, pilose to glabrous; bracts green to reddish, 1.1–2.2 × 0.5–0.7 cm, lanceolate. Calyx with subequal lobes, nearly free, dorsal

lobe slightly smaller and folded by the nectar chamber, 1.3–2.2 × 0.4–0.7 cm, long-lanceolate, margin entire, or serrate to serrulate at the apex, folded lengthwise by the adjacent lobe, glabrous, green to reddish at apex. Corolla uniformly tubular, 3.3–4.9 × 0.8–1.2 cm, oblique relative to calyx, tube almost straight, base enlarged and forming a nectar chamber, longitudinally sulcate, pale yellow to yellow, villous, lobes 3.6–6.9 × 4.5–6.9 mm, rounded, erect, subequal, yellow, margin entire. Androecium with filaments 1.6–2.7 cm long, included, cream-white, filaments coiling in the female phase, anthers united in pairs. Nectary a bilobed dorsal gland, ca 5 mm long, glabrous, pale yellow. Gynoecium with an ovary ca 5 × 4 mm, conical, pilose, pale green; style ca 2 cm long, pale green, pilose, stigma bilobed. Fruit not observed.

Distribution and habitat. *Nautilocalyx ochroleucus* is endemic to Brazil, in the northern states of Acre, Amazonas, and Pará (Fig. 3). This species is typically found near watercourses and on sandy riverbanks in humid lowland to premontane forests.

Additional material examined. BRAZIL – Acre • Mâncio Lima, Parque Nacional da Serra do Divisor, Rio Moa, Trilha para a cachoeira do “Ar-Condicionado”; 5 Dec. 2022; fl.; R.C. Forzza et al. 12304; UPCB. – Amazonas • São Gabriel da Cachoeira, Vista Alegre, margem do Rio Negro e foz do Rio Xié; 0°55’N, 67°20’W; 22 Oct. 1987; fl.; C. Farney 1761; NY. – Pará • Oriximiná, Rio Trombetas, Estrada Oriximiná-Cachoeira (BR-163), ca. 30 km north of Oriximiná; 3 Jun. 1989; fl.; C. Davidson & G. Martinelli 10041; NY • Antonio Lemos; 24 Aug. 1934; fl.; B.A. Krukoff 5890; F.

Taxonomic notes. *Nautilocalyx ochroleucus* is morphologically similar to *N. pallidus*. These two species are nearly glabrous on the stems and leaves, have reduced inflorescences with clusters of axillary flowers (Fig. 2A, D), and long lanceolate calyx lobes (Fig. 2B). *Nautilocalyx ochroleucus* differs by the smaller and narrower leaf blades (9.4–13.9 × 2.7–4.7 cm vs 11.2–18.1 × 6.1–8.9 cm in *N. pallidus*), narrower calyx lobes (0.4–0.7 cm wide vs 0.6–1.5 cm in *N. pallidus*), and pale-yellow corollas (Fig. 2B, C) without dots or lines (vs white to cream-white with a dorsal line of purple dots inside the tube and lobes in *N. pallidus*). A summary of distinguishing characters is provided in Table 1. We consider the species originally described by Poeppig (1840) to be heterospecific with *N. pallidus* and therefore recognize it here under a new combination in *Nautilocalyx*.

In the same work where he described *Drymonia ochroleuca*, Poeppig (1840) also described a “beta” (“β”) variety, based on material collected from Colares Island in the state of Pará. This variety was validly published later by Hanstein (1864) under the genus *Episcia* as *E. ochroleuca* var. *angustifolia*. According to Poeppig (1840), the variety differs from *D. ochroleuca* by its shorter stem, narrower leaves, and narrower bracts. However, field-based observations suggest a gradual morphological transition between these characters, along with a broader distribution for the species. We therefore treat *E.*

ochroleuca var. *angustifolia* as a synonym of *N. ochroleucus* because the characters used to distinguish it fall within the observed morphological variation of the species.

Nautilocalyx ochroleucus occurs on sandy riverbanks and along streams, usually in open environments, as indicated in Poeppig's original description in 1840. This habitat is unusual within the genus but has also been reported in a few other species, such as *N. arenarius* L.E. Skog & Steyermark.

3. *Nautilocalyx hirsutus* (Sprague) Sprague (Sprague 1912: 89)

Fig. 6; Table 1

Alloplectus hirsutus Sprague (Sprague 1911: 346)

Type. PERU – s.loc. [specific locality unknown]; originally collected as living material by Louis Forget for F. Sander & Sons, St. Albans, subsequently cultivated at the Royal Botanic Gardens, Kew; 1911; fl.; lectotype (designated here): K [K000831425]; isoelectotype: K [K000831426].

Description. Plants terrestrial, sometimes with tuberous roots. Stem erect, 15–23 cm long, terete, setulose to hirsute, unbranched, green. Leaves opposite, isophyllous; petioles 0.8–2.9 cm long, green to reddish, setulose to hirsute; blade 6.3–14.2 × 2.1–5.8 cm, obovate to elliptic, hirsute on the adaxial and abaxial surfaces, setulose to hirsute in the main veins, green, apex acute to acuminate, base decurrent, margin serrate. Inflorescence a reduced cyme appearing sessile, with 4–6 clustered axillary flowers; pedicels 0.5–1.2 cm long, erect, green, hirsute; bracts green, elliptic to lanceolate, 1.0–1.5 × 0.2–0.4 cm, hirsute, margin entire, apex acute. Calyx with subequal lobes, the dorsal smaller and folded by the developed nectar chamber, 1.1–1.8 × 0.4–0.9 cm, lanceolate, margin entire, green, hirsute to pilose. Corolla uniformly tubular, 2.5–3.3 × 0.8–0.9 cm, oblique relative to calyx, tube almost straight, base enlarged forming a nectar chamber, longitudinally sulcate, white, villous, lobes 0.3–0.7 × 0.3–0.8 cm, round, erect, subequal, white, margin entire to erose. Androecium with filaments 1.5–2.1 cm long, included, cream-white, filaments coiling in the female phase, anthers united in pairs. Nectary a bilobed dorsal gland, ca 5 mm long, glabrous, pale yellow. Gynoecium with an ovary 5.0–5.4 × 2.5–3.4 mm, conical, pilose, green, stigma bilabiate; style 1.7–2.2 cm long, pale green, pilose. Fruit not observed.

Distribution and habitat. *Nautilocalyx hirsutus* occurs in Peru (Amazonas, Cusco, Loreto, Madre de Dios, Pasco, San Martín) and in northern and central Brazil (Acre, Mato Grosso and Mato Grosso do Sul). This species occurs in humid habitats, usually near watercourses, often along rivers.

Additional material examined. BRAZIL – Acre • Mâncio Lima, Parque Nacional da Serra do Divisor, Rio Moa; 6 Dec. 2022; fl.; R.C. Forzza et al. 12331; UPCB. – Mato Grosso • Cuiabá, Balneário Vale Verde, Rio Paciência; 15°20'46"S, 55°51'20"W; 287 m; 23 Aug. 2025; fl.; M.E.

Engels et al. 13644; UPCB • Rio Verde, 7 Quedas; 27 Aug. 1973; fl.; G. Hatschbach & C. Koczicki 32405; MBM.

PERU – Loreto • Maynas, Yanomono, Explorama Tourist Camp, Trail to Río Napo; 19 Feb. 1981; fl.; A.H. Gentry et al. 31511; MO [MO-1498923]. – Madre de Dios • Manu, Los Amigos Estación Biológica (CIRCA); 3 Aug. 2010; fl.; M.M. Mora 950; US. – Pasco • Oxapampa, Pichis Valley, Puerto Bermúdez, 2 km SW of town on new road; 6 Sep. 1982; fl.; R.B. Foster 8541; MO [MO-1498919].

Taxonomic notes. *Nautilocalyx hirsutus* is differentiated from the species in the *Nautilocalyx pallidus* complex by a hirsute indumentum, pedicels shorter than the petioles, the calyx lobes lanceolate and less than 7 mm wide (Fig. 6B), and a uniformly white corolla (Fig. 6B, C).

This species is often annotated as *Nautilocalyx pallidus* in herbaria, but the hirsute indumentum and the narrower calyx lobes are useful diagnostic characters (Table 1). In Brazil, there are specimens showing intermediate features between *N. hirsutus* and *N. pallidus*, which is why we compare it in Table 1. Some populations currently recognized as *N. hirsutus* exhibit a corolla with a distinctive purple-blotched nectar guide on the internal surface of the corolla tube, contrasting with the predominantly white corolla observed in the typical form. This variation is currently treated as intraspecific within *N. hirsutus*; however, further morphological and molecular studies may support the recognition of these purple-blotched populations as a distinct taxon.

4. *Nautilocalyx pallidus* (Sprague) Sprague (Sprague 1912: 89)

Fig. 1; Table 1

Alloplectus pallidus Sprague (Sprague 1911: 346)

Type. PERU – s.loc. [specific locality unknown]; originally collected as living material by Louis Forget for F. Sander & Sons, St. Albans, subsequently cultivated in the Tropical Pits at the Royal Botanic Gardens, Kew; 24 Nov. 1910; fl.; lectotype (designated here): K [K000450061]; isoelectotype: K [K000613000].

Description. Plants terrestrial. Stems erect, often approaching or exceeding 1 m long, succulent, rooting at nodes, terete, pilose becoming glabrous at maturity, unbranched, green. Leaves opposite, isophyllous; petiole 1.2–1.5 cm long, green, pilose; blade 11.2–18.1 × 6.1–8.9 cm, elliptic to oblanceolate, glabrescent, pilose in the midveins, green, apex acute to acuminate, base decurrent, margin serrulate to serrate. Inflorescence a reduced cyme, appearing sessile, with 2–6 flowers on a reduced peduncle, pedicels 0.5–0.9 cm long, erect, green, pilose to glabrous; bracts green, 0.5–0.7 × 0.2–0.4 cm, lanceolate. Calyx with lobes subequal, nearly free, dorsal lobe slightly smaller and folded by the corolla nectar chamber, 1.1–2.3 × 0.6–1.5 cm, lanceolate, margin entire to serrate from the middle to apex, folded lengthwise by the adjacent lobe, glabrous to pilose, green. Corolla uniformly tubular, 3.1–5 × 0.8–1.8 cm, oblique relative to calyx, tube almost straight, base of the tube enlarged and forming a nectar

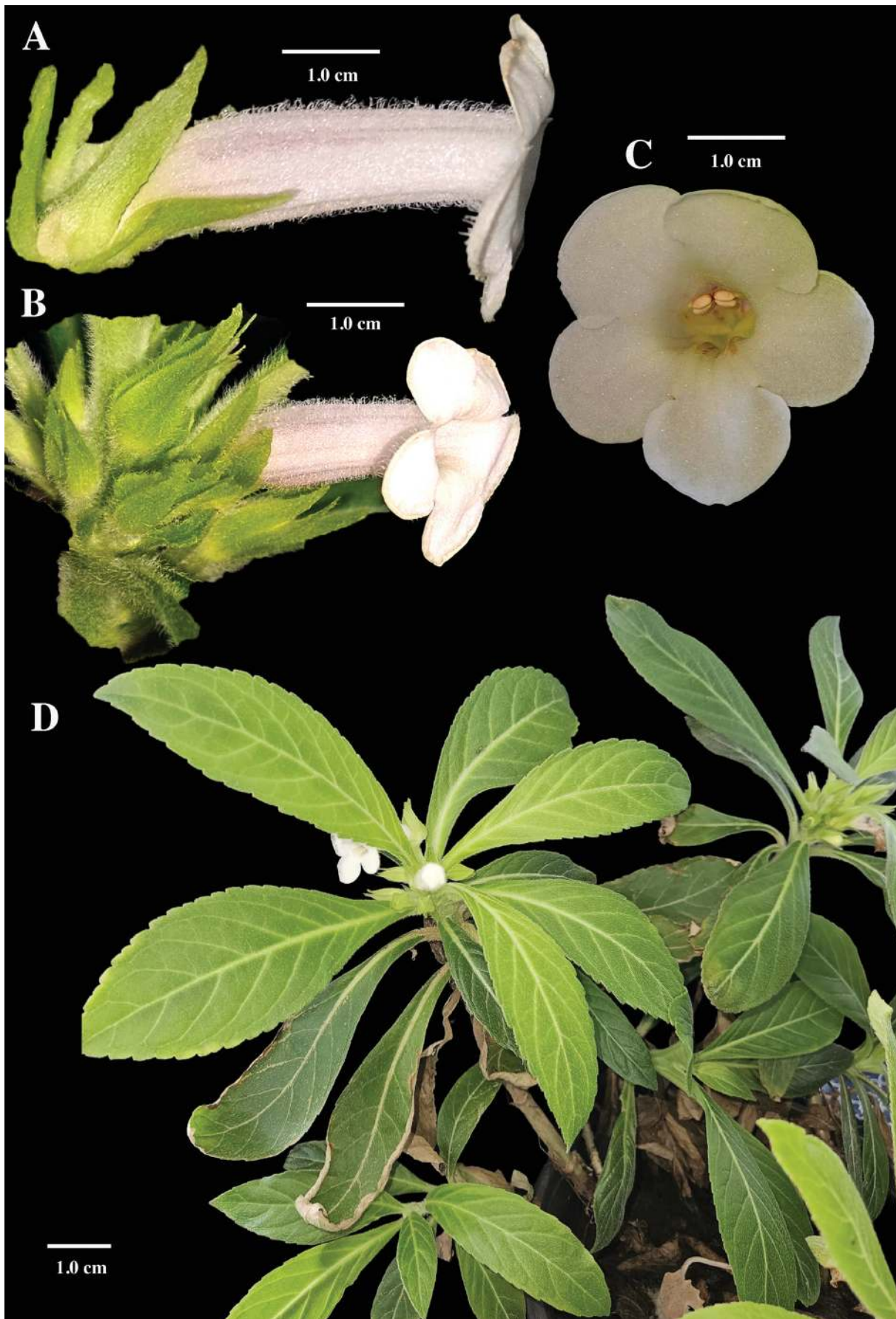


Figure 6. Field images of *Nautilocalyx hirsutus*. A. Lateral view of flower. B. Inflorescence. C. Front view of corolla. D. Habit. From M.E. Engels 13644. Photos by Lucas K.R. Hinoshita.

chamber, longitudinally sulcate, white to cream-white, with a dorsal line of purple dots inside the tube and lobes, sometimes these dots cover the entire corolla and lobes or are absent, villous, lobes 7–9 × 5–6 mm, rounded, erect, subequal, white to cream white, sometimes with purple dots, margin entire. **Androecium** with filaments 2.3–3.9 cm long, included, cream-white, filaments coiling in the female phase, anthers united in pairs. **Nectary** a bilobed dorsal gland, ca 5 mm long, glabrous, pale yellow. **Gynoecium** with an ovary ca 5 × 4 mm, conical, pilose, pale green; style 2.2–2.9 cm long, pale green, pilose, stigma bilobed. **Fruit** a semidried, bivalved capsule, 0.8–1.2 × 0.5–1 cm, conical, glabrescent, green to pale yellow. **Distribution and habitat.** *Nautilocalyx pallidus* occurs in Bolivia (Abuná), Brazil (Amazonas), Colombia (Amazonas, Antioquia, Putumayo), Ecuador (Pastaza), Peru (Amazonas, Cusco, Loreto), and southern Venezuela (Amazonas). The species inhabits humid lowland to premontane forests, non-inundated forests or slightly disturbed forests, often near streams and river margins, including areas along roadsides and forest edges.

Additional material examined. BOLIVIA – **Abuná** • al N del río Orton, Barraca San Juan de Nuevo Mundo; Campamento Dieciocho hasta Democracia, 18 km al N de la barraca Pando; 5 Jul. 1992; *L. Vargas et al.* 623; US. BRAZIL – **Amazonas** • Rio Javari, non-inundated disturbed forest behind village of Paumari (above Atalaia del Norte); 3 Nov. 1977; fl.; *A. Gentry & J. Revilla* 20550; MO, SEL.

COLOMBIA – **Amazonas** • Leticia, 8–10 km carretera Leticia–Tarapacá, orilla de bosque y bosque primario perturbado; 4°03'00"S, 69°57'00"W; 300 m; 27 Sep. 1991; fl.; *J. Betancur et al.* 2829; COL, US. – **Antioquia** • San Luís, eastern slopes of the Cordillera Central, Quebrada la Cristalina, along highway Medellín–Bogotá; 5°57'6"N, 74°51'56"W; 720 m; 13 May 2012; fl.; *J.L. Clark et al.* 12893; UNA. – **Putumayo** • Mocoa, Vereda San José del Pepino, Cañón del Dantayaco, estribaciones de la Serranía de los Churumbelos; 5 Aug. 2024, fl., fr.; *J.L. Clark* 19190; SEL.

ECUADOR – **Pastaza** • Lorocachi, on the path to Lagartococha; 1°37'48"S, 75°58'12"W; 200 m; 25 May 1980; fl.; *J. Brandbyge & E. Asanza* C. 30886; US • Lorocachi, 2 km del Río Curaray, zona sur oeste del campamento militar; 1°37'48"S, 75°58'12"W; 200 m; 23 May 1980; fl.; *J.L. Jaramillo et al.* 30713; US.

PERU – **Amazonas** • Bagua District, Imaza, Comunidad de Yamayakat; 5°03'24"S, 78°20'17"W; 350 m; 25 Mar. 2000; fl.; *R. Vásquez* 26498; MO, SEL • Condorcanqui, Rio Cenepa region, Quebrada Huampami, Rio Cenepa, Monte; 270 m; 8 Jun. 1973; fl.; *R. Kayap* 919; MO, SEL. – **Cuzco** • Camisea, campamento Amihuari, Camimisea Production Unit, surrounding camp; 11°51'48"S, 72°46'44"W; 469 m; 28 Jan. 1997; fl.; *P. Acevedo-Rdgz.* 9290; US. – **Loreto** • Rio Ampiyacu, environ of Pucuraquillo; 8 Mar. 1981; fl.; *E. W. Davis s.n.*; F.

VENEZUELA – **Amazonas** • Rocas ígneas expuestas más abajo del Cerro Araucana, río Yatua; 1°35'N, 66°10'W;

125–150 m; 12 Apr. 1970; fl.; *J.A. Steyermark & G. Bunting* 102574; NY.

Taxonomic notes. The Forget type specimens from Kew for *Nautilocalyx pallidus* are limited to a date and country (Peru), therefore making it challenging to geographically locate the type locality. The material collected by Forget was sent to London and later donated to the Kew Botanical Garden collection, but the cultivated material has since been lost. The lithograph of the cultivated material, presumably based on the plant from which the type was prepared, shows the corolla with a distinctive, purple-blotched nectar guide on the dorsal surface of the corolla tube (Sprague 1913), a feature also cited in the original description, but present in a broad range of different *Nautilocalyx* species. Thus, we do not consider purple-blotched nectar guides as a diagnostic character despite the suggestion by Sprague (1911) in the protologue for *N. pallidus*. Although a purple-blotched nectar guide is not unique to *N. pallidus* and occurs in other species of *Nautilocalyx*, it is useful in combination with vegetative and calyx characters for distinguishing *N. pallidus* from the other species treated here.

Nautilocalyx pallidus constitutes a species complex that has historically been broadly circumscribed and has included multiple distinct taxa. We consider *N. pallidus* to be characterized as a relatively tall terrestrial plant, usually exceeding 1 m in height, with elliptic to oblanceolate leaves and decurrent leaf bases (Fig. 1D). The leaves are covered with a pilose indumentum when immature, becoming more or less glabrous when mature (Fig. 1F). The bracts are shorter than, or at most equal to, the pedicel. The pedicel is usually approximately as long as the calyx. The calyx is large with lobes 0.6–1.5 cm wide, lanceolate, usually covering more than half of the corolla tube and the margins entire or slightly serrate near the apex (Fig. 1A). The corolla tube is white, while the throat and lobes have purplish markings that sometimes extend into the tube (Fig. 1B). Other characters that are diagnostic for *Nautilocalyx pallidus* are summarized in Table 1.

ACKNOWLEDGEMENTS

We are grateful to Mathias Engels for collecting the specimens and cultivating the plants until flowering, thereby making this work possible. We thank Diego Ferreira and Mayk Oliveira for providing photographs and plant material. We also thank Jeanne Katzenstein for her careful review of the manuscript and helpful comments. We are also grateful to the curators of the herbaria for making their collections available online, and to the institutions that hosted the authors in person and enabled the development of this work. LKRH received a grant from CAPES/Brazil (“Doutorado”, 88887.7499200/2022-00) and from the Nellie D. Sleeth Scholarship Endowment Fund (Gesneriad Society). RG received a grant from CNPq/Brazil (“Produtividade em Pesquisa”, #310912/2021-0).

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