

# *Vanilla lindmaniana* and *V. palmarum* (Orchidaceae) are distinct allopatric species

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Academic editor: André Simões ♦ Received 7 August 2024 ♦ Accepted 20 December 2024 ♦ Published 7 February 2025

## Abstract

**Background and aims** – With more than 40 species, Brazil is the centre of diversity for *Vanilla*. Despite the species richness, few studies on species boundaries involving Brazilian taxa have been carried out. Consequently, many species have been synonymized under taxa with a wider distribution. This is the case for *V. lindmaniana*, a species currently synonymized under *V. palmarum*. While studying the diversity of Brazilian *Vanilla*, differences between plants from the Amazonia/Cerrado/Pantanal and Caatinga/Atlantic Forest Biomes were recorded.

**Material and methods** – Detailed descriptions based on herbaria specimens and living material of *V. lindmaniana* and *V. palmarum* are provided and a morphological comparison is given. Illustrations of both species based on living plants is provided, and their geographic distributions are presented.

**Key results** – Plants occurring in the Amazon, Cerrado, and Pantanal Biomes correspond to *V. lindmaniana*, while *V. palmarum* occurs in the Caatinga and Atlantic Forest Biomes. *Vanilla lindmaniana* is distinguished from *V. palmarum* by several vegetative and reproductive characteristics, such as the size of leaves and flower structures, and the shape of the fruits. Characteristics associated to pollination strongly differ between both taxa. *Vanilla lindmaniana* is ornithophilous, while the labellar morphology of *V. palmarum* suggests pollination by bees. Both species occur as epiphytes on palms: *Vanilla lindmaniana* predominantly on *Acrocomia*, *Attalea*, and *Mauritia*, while *V. palmarum* on *Elaeis* and *Syagrus*. Both *V. lindmaniana* and *V. palmarum* are assessed as Endangered.

**Conclusion** – Appraisal of reproductive and vegetative characteristics from living specimens is crucial in delimitating species boundaries in *Vanilla*. Species delimitation based on ecological divergencies, plus geographic disjunctions have advanced the current evaluation and understanding of diversity in this economically and ecologically important orchid genus. All evidence reveals that *V. lindmaniana* is distinct from *V. palmarum*. *Vanilla palmarum* is endemic to Brazil, while *V. lindmaniana* is widely distributed throughout South America.

## Keywords

Amazonia, Atlantic Forest, Caatinga, Cerrado, Neotropics, Pantanal, systematics, taxonomy

## INTRODUCTION

The orchid genus *Vanilla* Mill. encompasses more than 100 species distributed throughout the tropical regions of Africa, Asia, and the Americas. In Brazil, the genus is represented by more than 40 species (Pansarin and Menezes 2023; Pansarin 2024). Despite this diversity, few studies on species boundaries have been carried out. As a consequence, many Brazilian species have been synonymized under other taxa, which consequently

show a putatively widespread distribution (Pansarin 2024; Pansarin and Miranda 2024). This is the case for *V. lindmaniana* Kraenzl., a species currently considered to be conspecific with *V. palmarum* (Salzm. ex Lindl.) Lindl. (e.g. BFG 2018; Soto Arenas and Cribb 2010). *Vanilla lindmaniana* was described based on a specimen collected by Carl A.M. Lindman (*Lindman 2481* (S)) in the municipality of Palmeiras (in the current state of Mato Grosso do Sul), central-western Brazil, a region that includes the ecotone of the Cerrado and Pantanal

Biomes (SEMAC 2009). In contrast, *Vanilla palmarum* was described based on specimens collected in Bahia, a Brazilian state that includes the ecotone of the Atlantic Forest and Caatinga Biomes. *Vanilla palmarum* has been assumed to be a widely distributed species, from south-eastern Brazil to Cuba, and it is easily recognized by its epiphytic habit and its association with palm trees (Soto Arenas and Cribb 2010; BFG 2018; Barberena et al. 2019).

Recent studies have indicated that basing species delimitations in Vanilloideae solely on herbaria samples is problematic (Batista et al. 2023; Pansarin 2024). Species boundaries based on molecular and ecological differences and combined with geographical separation have substantially advanced the current assessment and understanding of orchid diversity (Barrett and Freudenstein 2011; Batista et al. 2023; Suetsugu et al. 2023; Pansarin 2024). During investigations of Brazilian *Vanilla*, I observed differences between specimens that occur in central-western and northern Brazil (i.e. in the Amazonia, Cerrado, and Pantanal Biomes) versus those that occur in north-eastern Brazil (i.e. in the Atlantic Forest and Caatinga Biomes). Here, I have used a morphological approach to determine whether the specimens from the Amazonia/Cerrado/Pantanal Biomes constitute a distinct species from those from the Atlantic Forest/Caatinga Biomes (i.e. *V. palmarum*). Based on the examination of the protologues of the Neotropical species of *Vanilla*, in addition to a study of both herbarium and living specimens, a morphological characterization of *V. lindmaniana* and *V. palmarum* is provided. Detailed illustrations of both species based on living specimens is presented, and their geographic distribution is provided.

## MATERIAL AND METHODS

Fresh and herbarium material of flowering and fruiting plants was used for the study. The living material was collected from Brazilian populations and maintained in the *Vanilla* germplasm bank of the LBMBP Orchid House (Orchidarium of the Laboratory of Molecular Biology and Systematics of Plants), University of São Paulo (FFCLRP-USP), Brazil, available at <https://www.lbmbplab.net/vanillacollection>. Flowering and fruiting specimens were vouchered according to usual techniques (Fidalgo and Bononi 1989) and then deposited in the LBMBP herbarium. In addition, specimens from ALCB, ASE, BHCB, BGE, CEN, EAC, EAN, G, HCF, HRCB, HRSN, HST, HUEFS, HUESB, HUFU, HURB, HUTO, HVASE, IAN, INPA, K, LBMBP, MAC, MBM, MBML, MO, MPU, NY, R, RB, S, SLUI, UB, UEC, UPCB, and V herbaria (acronyms according to Thiers 2024) were examined in order to study the Brazilian diversity of *Vanilla*.

Plant structures were measured using a Vernier calliper. The vegetative structures, inflorescences, and flowers were photographed with a Nikon D-SLR D800 camera equipped with a Micro NIKKOR 105 mm f/2.8G lens. Floral details were analysed with a Stereozoom

Leica S8 APO stereomicroscope with an integrated photo output. The digital images of the plant structures were arranged on a black background according to the template presented by Hoehne (1945), using Microsoft PowerPoint. The terminology for describing shapes followed Radford et al. (1974). Features specific to Orchidaceae were based on the works by Dressler (1993) and Pridgeon et al. (1999). The infrageneric classification of Neotropical *Vanilla* groups followed Soto Arenas and Cribb (2010). The original descriptions and digital images of the types of related *Vanilla* species were consulted.

The distribution maps of *V. lindmaniana* and *V. palmarum* were based on both herbarium material and living specimens from the *Vanilla* germplasm bank (LBMBP Orchid House) and were produced with QGIS v.3.32.2 (QGIS Development Team 2024). The conservation statuses of both species were defined according to the IUCN Red List categories, criteria, and guidelines (IUCN Standards and Petitions Committee 2022). The geographical parameters of Area of Occupancy (AOO) estimated using a 2 × 2 km grid and Extent of Occurrence (EOO) were calculated using GeoCAT (Bachman et al. 2011).

The genera of palms used as phorophytes by the studied species were obtained from information on herbarium labels and in literature (Barberena et al. 2019), and also through field visits throughout the distribution range of both taxa.

## TAXONOMIC TREATMENT

*Vanilla lindmaniana* Kraenzl.

Figs 1, 3, Table 1

**Type.** BRAZIL • Matto Grosso, near Palmeiras; 15°58'14"S, 55°32'10"W; 24 Dec. 1893; C.A.M. Lindman 2481; holotype: S [S08-5056]; isotypes: S [S08-5055, S-R-6327].

**Description.** Epiphytic herbs, long scandent. Roots axillary, one per node; aerial roots 1.5–2.5 mm diam., velamenous, glabrous, simple, whitish to greenish; storage roots up to 5 mm diam., branching, white. Stem climbing, sinuous, cylindrical, fleshy, glabrous, green to yellowish green; internodes 40–90 × 5–9 mm. Leaves 7–16 × 3.5–6 cm, alternate, distichous, elliptic to lanceolate, rarely ovate, symmetric or asymmetric, fleshy, glabrous, green to yellowish green, margin entire, apex acute to acuminate, pseudopetiolate; pseudopetiole concave, 4–8 mm long. Inflorescence 2–3 cm long, apical, racemose, pending, with up to 13 flowers opening in succession; 1 flower opening each morning; bracts 5–16 × 3–11 mm, progressively smaller toward the apex, alternate, triangular to ovate, coriaceous, concave, patent, apex acute, sometimes leafy. Flowers resupinate, pedicellate, with an abscission layer between perianth and ovary; pedicel with ovary 2.4–2.8 × 0.3–0.34 cm, straight to incurved, calyculate, cylindrical in transverse section, white along the pedicel

and green along the ovary; calycul green, persistent. **Sepals** 6.3–6.8 × 0.9–1.1 cm, free, oblanceolate, fleshy, slightly concave, internally pale yellow, externally yellow, apex obtuse, margin entire, slightly reflexed; dorsal sepal symmetric; lateral sepals asymmetric. **Petals** 6–6.2 × 1.8–2 cm, free, obelliptic to spatulate, asymmetric, membranous, apex acute, slightly reflexed, yellow, adaxial surface with a central and longitudinally arranged keel. **Labellum** 3-lobed, 6.1–6.4 × 3.5–3.8 cm, unguiculate, tubular, yellow, whitish in the basal portion, inner surface with longitudinal prominent stripes converging in four triangular protuberances and in a cluster of the digitiform secretory trichomes at the entrance of the nectar chamber; central crest (nectar guide) ca 5 mm wide, with longitudinal yellow strips near the apex, and with a channel-like depression ca 2 mm wide (concave) just below the anther and stigma; labellum margins fused from the base to ca ¾ of the column length forming a tubular nectar chamber; nectar chamber 2.2–2.4 cm long; lateral lobes obliquely rounded, margins undulate; apical lobe emarginated, reflexed, margin undulate. **Column** 4.1–4.3 × 0.35–0.38 cm, semi-cylindrical, slender, base attenuate, dilated towards the apex, with white-hyaline hairs close to the stigma, apex with two projections (wings) facing downwards; anther 4–4.2 × 3.7–4 mm, rhomboid, yellowish, versatile; rostellum 4–4.2 × 3.5–3.8 mm, trapezoidal, white. **Fruits** 5.4–6.7 × 1.1–2 cm, linear to clavate, strait to incurved, cylindrical to subcylindrical in transverse section, fleshy, dehiscent, opening in two valves, green when immature, yellowish when mature. **Seeds** ca 0.5 mm, ovate, crustose, black.

**Distribution and ecology.** *Vanilla lindmaniana* occurs in open forests of the Amazonia, Cerrado, and Pantanal Biomes (Fig. 3). *Vanilla lindmaniana* has an epiphytic habit, rooting on the trunk and leaves of palm trees of the genera *Acrocomia* Mart., *Attalea* Kunth., and *Mauritia* L.f. (Barberena et al. 2019; Table 1). The elevation is from 100 to 500 m a.s.l. Flowers open in the morning hours and each flower lasts ca 12 hours. In a study involving populations from Maranhão State (Brazil), it was found that the flowers of *V. lindmaniana* (as *V. palmarum*) offer nectar as a reward which is stored in the nectar chamber. *Vanilla lindmaniana* has a mechanism of facultative self-pollination. Its flowers are chasmogamous and pollinated by hummingbirds but in the absence of biotic pollination, flowers self-pollinate (Pansarin and Ferreira 2022).

**Phenology.** *Vanilla lindmaniana* blooms from December to January. The fruits ripen between July and August.

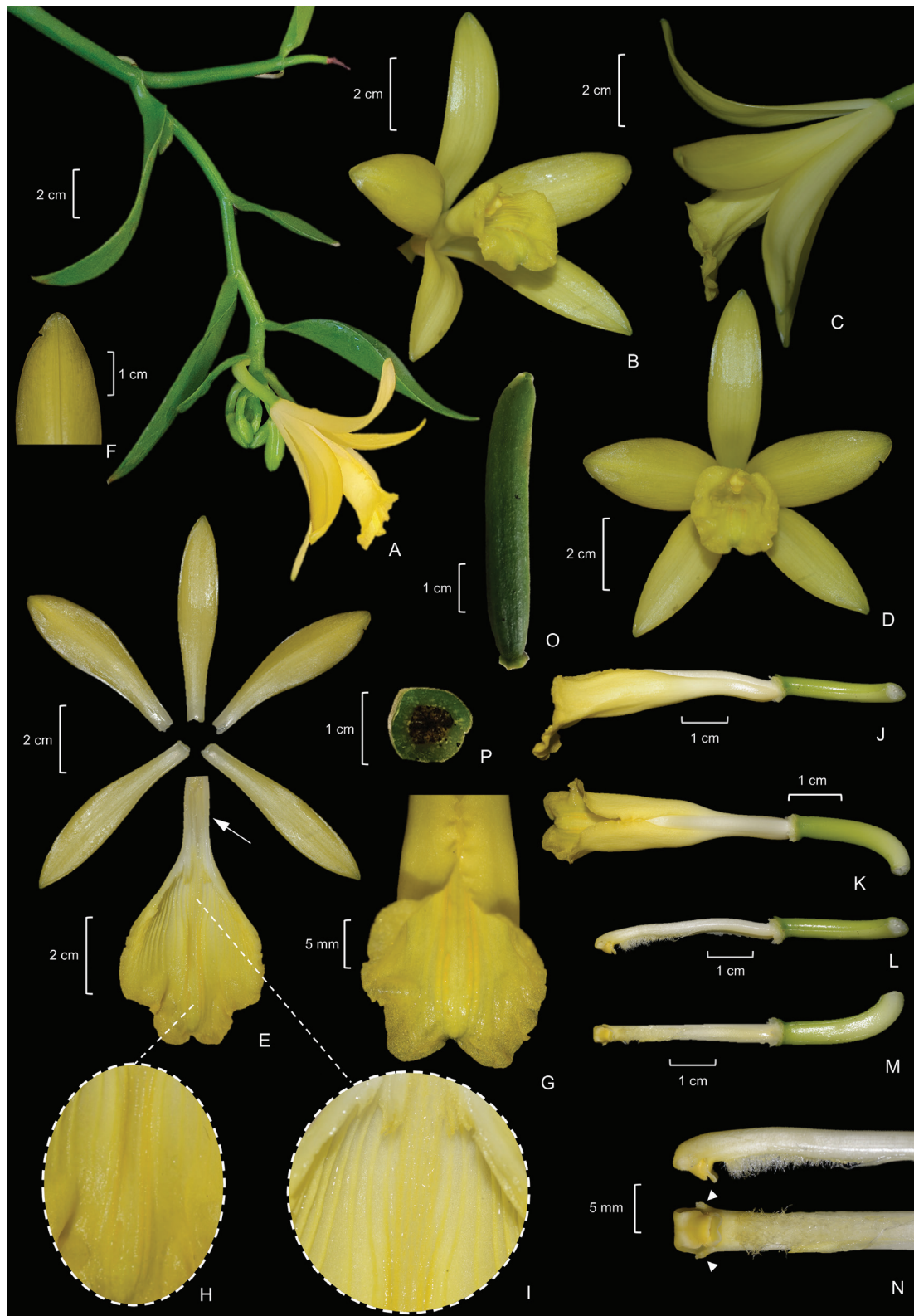
**Preliminary IUCN conservation assessment.** Endangered: EN B2a(ii,iii). *Vanilla lindmaniana* is a rarely collected species currently known to grow in the Amazonian Rainforest and Cerrado of South America. The extent of occurrence (EOO) is estimated to be 5,310,777 km<sup>2</sup>, which falls within the limits for Least Concern (LC), according to the IUCN Red List categories and criteria and guidelines. The area of occupancy (AOO) is estimated to be 108 km<sup>2</sup> (cell width of 2 km), which falls within the limits for Endangered (EN) under criterion

B2 (area of occupancy). Considering that the Amazon Rainforest and especially the Brazilian Cerrado have been reduced to scattered fragments due to extensive human occupation, I project a continuing decline in (ii) area of occupancy and (iii) extent and/or quality of the habitat of *V. lindmaniana*. Based on these threats, *V. lindmaniana* is assessed as Endangered.

**Additional material examined.** BOLIVIA – **Beni** • Tumi Chucua, 30 km S of Riberalta, flood plain forest, Vaca Diez; 11°07'59"S, 66°09'59"W; 210 m; 29 Sep. 1981; J.C. Solomon 6503; MO. – **Pando** • Frederico Román, on the west bank of the Madeira River, ca 1 km south of Cachuela Las Pedritas; 09°57'13"S, 65°20'13"W; 20 Jul. 2002; J. Urrelo et al. 501; V. – **Santa Cruz** • San Jose de Campamento, a 3 km sobre el camino hacia San Roque, José Miguel de Velasco; 15°09'20"S, 60°59'29"W; 9 May 1996; R. Guillén 4343; NY • Velasco, Parque Nacional Noel Kempff Mercado, 500 m al S de la comunidade Florida hacia el Campamento Toledo; 14°33'00"S, 60°49'00"W; 2 Dec. 1994; R. Guillén & R.A. Medina Guillén Villarroel 2701; MO • Velasco, Reserva Ecológica El Refúgio, a 300 m al SO de campamento, em la pampa de las islas; 14°47'09"S, 61°03'14"W; 150 m; 21 Jan. 1995; R. Guillén & R.A. Medina Guillén Villarroel 2944; MO.

BRAZIL – **Amazonas** • Manaus, Ramal Vale do Novo Amanhecer, ao lado do sitio Toc; 02°27'00"S, 60°06'00"W; 12 Oct. 2014; A.H. Krahl 471; INPA • Manaus, Reserva Florestal Ducke, Manaus-Itacoatiara, km 26; 02°52'59"S, 59°58'00"W; 29 Jun. 1994; J.E.L.S. Ribeiro 1333; NY. – **Goiás** • Colinas do Sul, Estrada de acesso ao rio Preto, km 1, a partir da entrada da fazenda Vale das Araras, Mata de galeria perturbada, com alta presença de babaçu, Relevo suave ondulado, Solo areno-argiloso, Área de influência da futura Hidrelétrica de Cana Brava; 13°44'22"S, 48°07'42"W; 310 m; G. Pereira-Silva et al. 5573; BHC B • Uruaçu, Reservatório em formação do AHE Serra da Mesa, Originalmente mata ciliar alterada; 14°31'28"S, 49°08'26"W; 15 Oct. 2007; S.P. Cordovil-Silva & J.B. Pereira 705; BHC B. – **Maranhão** • Estreito, Canteiro de obras do UHE Estreito (próximo ao porto da balsa); 06°33'38"S, 47°27'03"W; 150 m; 11 Mar. 2007; G. Pereira-Silva 11374; CEN • Passagem Franca, a 24 km de Buriti Bravo, à esquerda no Café Buriti mais 22 km do posto fiscal, à direita mais 60 km; 06°20'59"S, 43°31'59"W; 270 m; 24 Nov. 1993; R.F. Vieira et al. 1545; BHC B • São Luís, Araçagy, Base do Cabral; 02°28'30"S, 44°12'53"W; 11 Apr. 1988; R. Nina 98; SLUI • São Luís, UFMA, campus Dom Delgado, em frente ao centro pedagógico Paulo Freire; 02°33'43"S, 44°18'37"W; 20 Aug. 2019; K.N. Santos 122; SLUI. – **Mato Grosso** • Cáceres; 16°04'14"S, 57°40'44"W; Aug. 2003; M.A. Carniello 55; HRCB • Cocalinho; 14°23'49"S, 50°59'44"W; 1 Jan. 1997; A.F. Rozza et al. 490; ESA • Barra dos Bugres; 15°04'22"S, 57°10'51"W; 20 Jun. 2012; s.col.; HCF [HCF10838]. – **Mato Grosso do Sul** • Aquidauana; 20°28'15"S, 55°47'13"W; 8 Dec. 2001; M.A. Assis 1521; HRCB • Corumbá, Passo do Lontra; 19°34'35"S, 57°01'05"W; 106 m; 30 Jul. 2007; M.G. Caxambú 1598; HCF • Corumbá, Morro na margem da





**Figure 1.** *Vanilla lindmaniana* Kraenzl. **A.** Detail of a flowering plant. **B.** Flower in diagonal view. **C.** Flower in lateral view. **D.** Flower in front view. **E.** Dissected perianth. Note the nectar chamber (arrow). **F.** Detail of the adaxial surface of a petal showing the longitudinal keel. **G.** Detail of the labellum in upper view. **H.** Detail of the apex of the labellum of a flower showing the longitudinal cavity. **I.** Detail of the labellum showing the central labellar crest. **J.** Pedicel, ovary, labellum, and column in lateral view. **K.** Pedicel, ovary, labellum, and column in dorsal view. **L.** Pedicel, ovary, and column in lateral view. **M.** Pedicel, ovary, and column in ventral view. **N.** Apex of the column: in lateral view with an articulated anther (above), and in ventral view with an articulated and disarticulated anther (below). Note the lateral wings (arrowheads). **O.** Mature fruit in lateral view. **P.** Transversal section of a mature fruit. Based on VAN 034 (LBMBP).

**Table 1.** Comparison of the morphological features between *Vanilla lindmaniana* and *V. palmarum*.

| Characteristic   | <i>V. lindmaniana</i>                               | <i>V. palmarum</i>             |
|--|---|--------------------------------|
| Biome  | Amazonia, Cerrado, Pantanal                         | Atlantic Forest, Caatinga      |
| Host palms   | <i>Acrocomia</i> , <i>Attalea</i> , <i>Mauritia</i> | <i>Elaeis</i> , <i>Syagrus</i> |
| Internode size (cm)                                    | 40–90 × 5–9   | 25–50 × 2.5–5                  |
| Leaf size (cm)   | 7–16 × 3.5–6  | 3.5–8.5 × 2–4                  |
| Pseudopetiole length (mm)                              | 4–8   | 3–5                            |
| Sepal size (cm)  | 6.3–6.8 × 0.9–1.1                                   | 4.7–5.1 × 0.9–1.1              |
| Petal size (cm)  | 6–6.2 × 1.8–2                                       | 4.8–5.1 × 1.2–1.4              |
| Labellum size (cm)                                     | 6.1–6.4 × 3.5–3.8                                   | 5.1–5.3 × 3.9–4.1              |
| Nectar chamber length (cm)                             | 2.2–2.4   | 1.3–1.6                        |
| Number of protuberances of the nectary entrance        | Four  | Two                            |
| Shape and width of the nectar guide (below the anther) | Concave; ca 2 mm                                    | Convex; ca 4 mm                |
| Column length (cm)                                     | 4.1–4.3   | 3.4–3.6                        |
| Column wing orientation                                | Facing downwards                                    | Facing upwards                 |
| Fruit size (cm)  | 5.4–6.7 × 1.1–2                                     | 5.4–6.7 × 1.1–2                |
| Fruit shape in transversal section                     | Rounded   | Diamond-shaped                 |

Baía Mandiré; 19°00'33"S, 57°39'11"W; 18 Oct. 2002; G.A. Damasceno Júnior et al. 2533; HUFU • Balneário Iracema, Região de A. Maria Coelho; 19°00'33"S, 57°39'11"W; 21 Nov. 2004; D.P. Rodriguez & H. Baracat s.n.; UPCB [UPCB104531] • Ladário, Fazenda Vale do Paraíso; 19°00'16"S, 57°36'06"W; 110 m; 28 Oct. 2004; E.R. Macedo et al. 5; MBM. – **Pará** • Breves; 01°40'55"S, 50°28'49"W; 17 Jul. 1950; G.A. Black & R.L. Fróes 10036; IAN • Melgaço, Floresta Nacional de Caxiuanã, rio Curuá-grande, margem esquerda; 01°48'15"S, 50°42'43"W; 29 Nov. 2010; A.K. Koch & C. Souza 347; IAN. – **Rondônia** • Guajará-Mirim, 23 km de centro de Guajará-Mirim, Colônia do Yata; 10°46'58"S, 65°20'21"W; 15 Oct. 1990; L.B. Bianchetti 1092; HUEFS • Porto Velho, nas margens da BR-364; 08°45'42"S, 63°54'14"W; 100 m; 19 Aug. 2022; M. Figueira 1876; CEN. – **Tocantins** • Paranã, Canteiro de obras do UHE São Salvador (área do bota-fora); 12°36'55"S, 47°52'59"W; 260 m; 19 Jun. 2006; G. Pereira-Silva 10786; CEN • Paranã; 12°52'34"S, 48°10'41"W; E.R. Santos et al. 1094; HUTO.

GUYANA – **Essequibo** • South Rupununi Savanna, Kidekperdana Creek, 8 km SE of Aishalton, Upper Takutu-Upper Essequibo; 02°25'11"N, 59°10'12"W; 26 Nov. 1993; T.W. Henkel 3510; NY.

PERU – **Madre de Dios** • Cusco Amazónico Lodge, Río Madre de Dios, Lago Sandobal, 10 km NE of Puerto Maldonado, Tambopata; 12°34'59"S, 69°02'59"W; 200 m; Jun. 1990; P. Núñez & V. Núñez Vargas 12287; MO.

VENEZUELA – **Bolívar** • Bolívar; 12 Jan. 1961; J.A. Steyermark 88386; UB.

**Notes.** *Vanilla lindmaniana* was described based on a specimen collected by Carl A.M. Lindman (*Lindman 2481* (S)) in the municipality of Palmeiras, in the current state of Mato Grosso do Sul. The region is located in the Pantanal Biome. For a long time, this species has been considered as an obscure taxon endemic to Brazil

(BFG 2018). However, several characteristics such as the epiphytic habit, the colour of the flowers, and the absence of a penicillate callus have been used to consider this taxon as conspecific with *V. palmarum* (e.g. Soto Arenas and Cribb 2010). Here, *V. lindmaniana* is presented as a taxon clearly distinct from *V. palmarum*, being recognized by several vegetative and floral characteristics. According to the infrageneric classification of Soto Arenas and Cribb (2010), *V. lindmaniana* is a member of the *V. palmarum* group.

**Morphological affinities.** *Vanilla lindmaniana* is easily recognized from other Neotropical species by its epiphytic habit on palms, by its terminal and pendant inflorescences, by its yellow flowers much smaller than those of *V. pompona*, by the absence of a penicillate callus on the labellum, and by its dehiscent and scentless fruits. The species is closely related to *V. palmarum*, however, *V. lindmaniana* is clearly distinguishable by its distribution across the Pantanal, Cerrado, and Amazonia Biomes, by its larger flowers and leaves, the presence of a nectar guide with a channel-like depression just below the anther and stigma, and the larger fruits, which are rounded in transversal section (Table 1).

*Vanilla palmarum* (Salzm. ex Lindl.) Lindl.

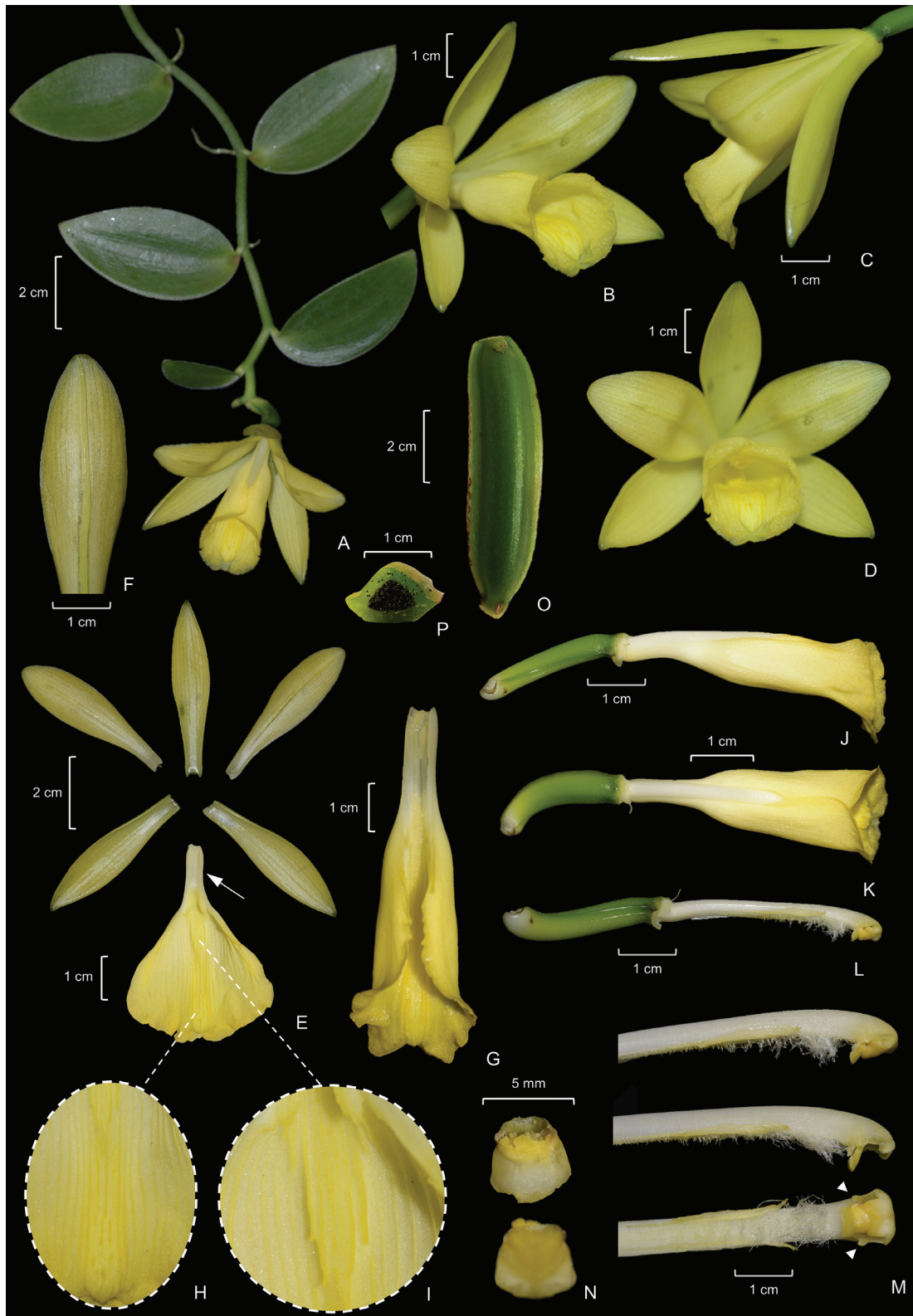
Figs 2, 3, Table 1

*Epidendrum palmarum* Salzm. ex Lindl.

*Vanilla palmarum* var. *grandifolia* Cogn.

**Type.** BRAZIL • Bahia, s.loc.; s.d.; P. Salzmann s.n.; isotypes: K [K000293255], MPU [MPU013457, MPU018359, MPU018360], G [G00190804, G00190913].

**Description.** Epiphytic herbs, long scandent. Roots axillary, one per node; aerial roots 1–1.5 mm diam., velamenous, glabrous, simple, whitish to creamy; storage roots up to 4 mm diam., branching, white. Stem climbing,



**Figure 2.** *Vanilla palmarum* (Salzm. ex Lindl.) Lindl. **A.** Detail of a flowering plant. **B.** Flower in diagonal view. **C.** Flower in lateral view. **D.** Flower in front view. **E.** Dissected perianth. Note the nectar chamber (arrow). **F.** Detail of the adaxial surface of a petal showing the longitudinal keel. **G.** Labellum in upper view. **H.** Detail of the apex of the labellum of a flower showing the longitudinal keel. **I.** Detail of the labellum showing the central labellar crest. **J.** Pedicel, ovary, labellum, and column in lateral view. **K.** Pedicel, ovary, labellum, and column in dorsal view. **L.** Pedicel, ovary, and column in lateral view. **M.** Apex of the column: in lateral view with an articulated anther (above), in lateral view with the anther removed (mid), and in ventral view with an articulated anther (below). Note the lateral wings (arrowheads). **N.** Anther in ventral view (above) and dorsal view (below). **O.** Mature fruit in lateral view. **P.** Transversal section of a mature fruit. Based on VAN 113 (LBMBP).



sinuous, cylindrical, fleshy, glabrous, glaucous to green with whitish dots; internodes 25–50 × 2.5–5 mm. **Leaves** 3.5–8.5 × 2–4 cm, alternate, distichous, elliptic to ovate, symmetric or asymmetric, fleshy, glabrous, glaucous to yellowish green, margin entire, apex acute to acuminate, pseudopetiolate; pseudopetiole concave, 3–5 mm long. **Inflorescence** 1.8–2.5 cm long, apical, racemose, pending, with up to 10 flowers opening in succession; 1 flower opening each morning; bracts 5–15 × 3–8 mm, progressively smaller toward the apex, alternate, triangular to elliptic, coriaceous, concave, patent, apex acute, sometimes leafy. **Flowers** resupinate, pedicellate, with an abscission layer between perianth and ovary; pedicel with ovary 2.3–2.6 × 0.4–0.6 cm, straight to incurved, calyculate, subcylindrical in transverse section, white along the pedicel and green along the ovary. **Sepals** 4.7–5.1 × 0.9–1.1 cm, free, oblanceolate, fleshy, slightly concave, internally pale yellow, externally yellow, apex obtuse, margin entire, reflexed at apex; dorsal sepal symmetric; lateral sepals asymmetric. **Petals** 4.8–5.1 × 1.2–1.4 cm, free, spatulate, asymmetric, membranous, apex acute, slightly reflexed, yellow, adaxial surface with a central and longitudinally arranged keel. **Labellum** 1-lobed to slightly 3-lobed, 5.1–5.3 × 3.9–4.1 cm, unguiculate, tubular, yellow, whitish in the basal portion, inner surface with longitudinal prominent stripes converging in two triangular protuberances and in a cluster of the digitiform secretory trichomes at the entrance of the nectar chamber; central crest (nectar guide) ca 5 mm wide near the apex, and with an elevation ca 4 mm wide (convex) just below the anther and stigma; labellum margins fused from the base to ca ¾ of the column length forming a tubular nectar chamber; nectar chamber 1.3–1.6 cm long; lateral lobes obliquely rounded, margins undulate; apical lobe emarginated, reflexed, margin undulate. **Column** 3.4–3.6 × 0.34–0.37 cm, semi-cylindrical, slender, base attenuate, dilated towards the apex, with white-hyaline hairs close to the stigma, apex with two lateral projections (wings) facing upward; anther 3.6–3.9 × 3.5–3.8 mm, rhomboid, yellowish, versatile; rostellum 3.8–4 × 3.5–3.8 mm, trapezoidal, white. **Fruits** 4.4–6.5 × 0.8–1.4 cm, linear, incurved, diamond-shaped in transverse section, fleshy, dehiscent, opening in two valves, green when immature, yellowish when mature. **Seeds** ca 0.5 mm, crustose, ovate, black.

**Distribution and ecology.** *Vanilla palmarum* is a Brazilian endemic species widely distributed in the Caatinga and Atlantic Forest Biomes, occurring in open forests of north-eastern Brazil (Fig. 3). *Vanilla palmarum* has an epiphytic habit, rooting on the trunk of several palm species of the genera *Elaeis* Jacq. and *Syagrus* Mart. (Barberena et al. 2019; Table 1). The elevation is from 212 to 1123 m a.s.l. Flowers open in morning hours and each flower lasts ca 12 hours. As in *V. lindmaniana* (Pansarin and Ferreira 2022), the flowers of *V. palmarum* offer nectar as a reward which is stored in the nectar chamber. Flowers of *V. palmarum* also shows a mechanism of facultative self-pollination. Its flowers are chasmogamous but in the absence of biotic

pollination, flowers self-pollinate (Emerson Pansarin unpubl. data). Although *V. lindmaniana* is pollinated by hummingbirds (Pansarin and Ferreira 2022), the flowers of *V. palmarum* do not appear to be adapted for avian pollination as their central crest (nectar guide) is convex. In *V. lindmaniana*, the labellum shows a channel-like depression of ca 2 mm wide, whose function is to guide the hummingbird's bill to the entrance of the nectar chamber (Pansarin and Ferreira 2022).

**Phenology.** *Vanilla palmarum* blooms from December to February. The fruits ripen between July and September.

**Preliminary IUCN conservation assessment.**

Endangered: EN B2a(ii,iii). *Vanilla palmarum* is a rarely collected species currently known from the Atlantic Forest and Caatinga Biomes of Brazil. The extent of occurrence (EOO) is estimated to be 657,099 km<sup>2</sup>, which falls within the limits for Least Concern (LC), according to the IUCN Red List categories and criteria and guidelines. The area of occupancy (AOO) is estimated to be 108 km<sup>2</sup> (cell width of 2 km), which falls within the limits for Endangered (EN) under criterion B2 (area of occupancy). Considering that both the Atlantic Forest and Caatinga Biomes have been reduced to scattered fragments due to extensive human occupation, we project a continuing decline in (ii) area of occupancy and (iii) extent and/or quality of the habitat of *V. palmarum*. Based on these threats, *V. palmarum* is assessed as Endangered (EN).

**Additional material examined.** BRAZIL – **Alagoas** • Maceió, Serra da Saudinha, Fazenda Cela; 10°05'37"S, 36°11'28"W; 13 Jan. 2008; *Chagas-Mota* 243; MAC. – **Bahia** • Amargosa, Recôncavo Sul, entrada da porteira da Fazenda Acaju; 11°01'00"S, 39°36'00"W; 27 May 2005; *M.A. Costa & M.L. Guedes* 14; ALCB • Boa Nova, Parque Nacional de Boa Nova, setor central, Fazenda Alvorada, Lajedo dos Beija-flores; 14°21'45"S, 40°12'27"W; 1215 m; 2 Mar. 2013; *L.Y.S Aona* 2149; HUEFS • Caetitê, Coleta arredores da área de preservação da Indústria Nucleares do Brasil - INB, Áreas 1 - Margem direita da Reserva Próximo a Lagoa, 2 - Barragem Wilson Gouveia, 3 - "Mulungu"; 14°04'09"S, 42°28'29"W; 26 Sep. 2009; *J.L. Paixão* 1552; HUEFS • Cravolândia, Sudoeste, Assentamento Palestina; 13°23'25"S, 39°49'13"W; 14 Aug. 2001; *L. de J. Alves et al.* 354; ALCB • Feira de Santana, Campus da Universidade Estadual de Feira de Santana; 12°12'01"S, 38°58'18"W; 5 Apr. 2018; *M.F. Alves & J.L. Mayer* 5; UEC • Campus da UEFS, Atrás do Centro Administrativo; 12°12'05"S, 38°58'05"W; 6 Oct. 1997; *I.F. Castro et al.* 31167; UB • Itatim, Morro do Agenor; 12°42'42"S, 39°41'53"W; 26 Nov. 1995; *F. França* 1465; HUEFS • Itatim, Fazenda na base do morro das Tocas; 12°42'42"S, 39°41'53"W; 282 m; 31 Aug. 2003; *T.B. Cavalcanti* 3190; CEN • Jacobina, Paraíso, Fazenda Exú; 11°10'50"S, 40°31'05"W; 11 Aug. 2006; *s.col.* 11223; EAN [EAN21562] • Saubara; 12°44'15"S, 38°46'07"W; 15 Aug. 2017; *K. Martins & A. Figueiredo* 13; HST • Jacobina, Piemonte da Diamantina, Arredores do Povoado de Tamanco; 11°10'50"S, 40°31'05"W; 28 Apr. 2012; *T.L. Vieira et al.* 91; ALCB • Lajedinho, Chapada Diamantina; 12°21'20"S, 40°54'20"W; 23 Aug. 2014;

G.S. Silva *et al.* 633; HUESB • Milagres, Serra do Jatobá; 12°52'11"S, 39°51'32"W; 21 May 2021; L.Y.S. Aona 5955; HURB • Retiroândia, Fazenda Piabas, próximo ao riacho; 11°29'41"S, 39°25'32"W; 212 m; 1 Nov. 1999; R.P. Oliveira 308; HUEFS • Salvador, Região Metropolitana de Salvador, Ilha de Maré, Povoado de Bananeiras; 12°44'58"S, 38°31'42"W; 12 Jun. 2011; M.L. Guedes *et al.* 18375; ALCB • Sento Sé, Parque Nacional Boqueirão da Onça, Entrada para Alegre, Vindo do Povoado Almas; 09°44'45"S, 41°53'06"W; 1123 m; 4 Sep. 2013; D.S. Fernandes 86; HVASF • Valente, Mata nativa, localizada a 4 km do centro, sentido a saída para Retiroândia; 11°26'29"S, 39°27'18"W; 326 m; 10 Jun. 2017; M.R.L. Constantino 33; MBML • Umburanas, PNBO, Umburanas; 723 m; 22 Sep. 2006; J.A. Siqueira Filho 1799; HVASF • Wagner, Mata ciliar do rio Tijuco; 12°13'32"S, 41°15'24"W; 17

Nov. 2018; E.B. Lopes & M.L. Guedes 71; ALCB. – Ceará • Viçosa do Ceará; 03°33'43"S, 41°05'31"W; 29 Dec. 2005; A.S.F. Castro 1661; EAC. – Minas Gerais • Salto da Divisa, Fazenda Santana; 16°04'16"S, 40°03'19"W; 137 m; 20 Feb. 2003; J.A. Lombardi *et al.* 5105; BHCB. – Paraíba • Barra de Camaratuba, Estrada Rural; 06°36'37"S, 35°05'58"W; 42 m; 17 Jul. 2014; J.M.P. Cordeiro *et al.* 269; EAN. – Pernambuco • Arcoverde, Descobrimento, Assentamento Serrote Redondo, Corredor Ecológico Ramal do Agreste e Pacuera Ipojuca; 08°21'12"S, 36°57'38"W; 947 m; 5 Aug. 2019; A.P. Fontana & J.M. dos Santos 10946; HRSN • Buíque, Catimbau, trilha das torres; 08°37'00"S, 37°10'00"W; 17 Oct. 1994; E. Menezes 16; K [K000293254]. – Sergipe • Lagarto, Povoado Brejo; 10°55'02"S, 37°38'59"W; 24 Aug. 2009; L.A.S. Santos & F.B. Suzart 1; ASE.

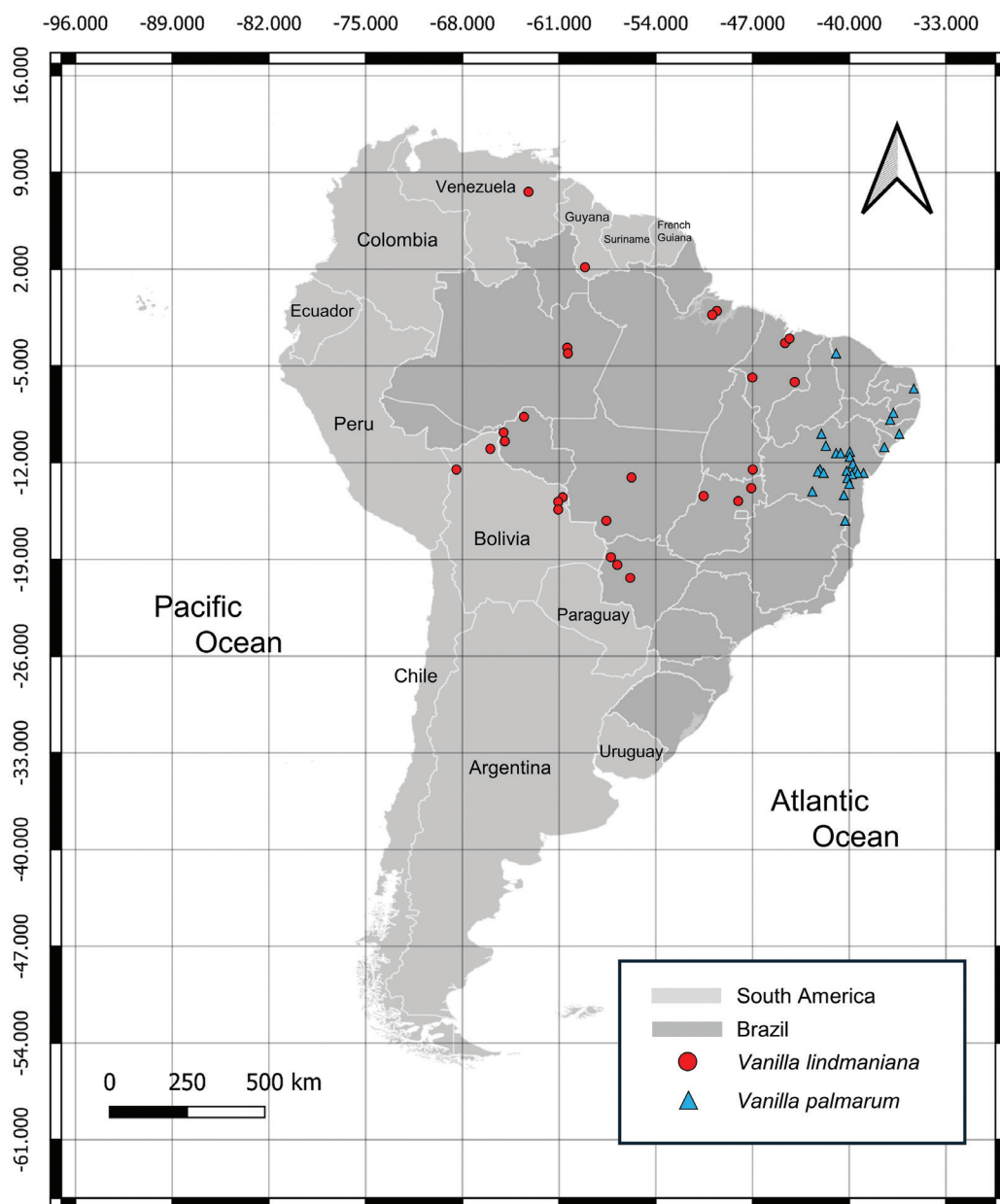


Figure 3. Occurrence map of *Vanilla lindmaniana* Kraenzl. and *Vanilla palmarum* (Salzm. ex Lindl.) Lindl.



**Notes.** *Vanilla palmarum* was described based on specimens collected in the state of Bahia, north-eastern Brazil. *Vanilla palmarum* has been assumed to be a widely distributed species, from Cuba to south-eastern Brazil. However, according to the data presented here, this taxon is endemic to Brazil, occurring in areas in the Caatinga and Atlantic Forest Biomes. The hypothesis of the occurrence of *V. palmarum* in Cuba requires careful further investigation. Two *Vanilla* names were described based on plant material collected in Cuba, namely *V. savannarum* Britton and *V. lutea* C.H. Wright ex Griseb. Although both taxa were synonymized under *V. palmarum*, they appear to be more closely related to *V. lindmaniana*. In addition, even though *V. lindmaniana* was published later than *V. lutea*, the latter is not a validly published name (e.g. BFG 2018). *Vanilla savannarum* was published later than *V. lindmaniana*, and therefore would be a synonym of this species. However, until fresh material is available for analysis, it seems to be prudent not to consider *V. savannarum* as a synonym of *V. lindmaniana* or *V. palmarum*. According to the infrageneric classification of Soto Arenas and Cribb (2010), *V. palmarum* is a member of the *V. palmarum* group.

**Morphological affinities.** *Vanilla palmarum* is easily recognized from other Neotropical species by its epiphytic habit on palm trees, by its terminal and pendant inflorescences, by its yellow flowers, by the absence of a penicillate callus on the labellum, and by its dehiscent and scentless fruits. Although closely related to *V. lindmaniana*, *V. palmarum* is easily distinguishable from it by its distribution in the Atlantic Forest and Caatinga Biomes, by its smaller vegetative and floral structures, the presence of a convex central crest (nectar guide) just below the anther and stigma, and the smaller fruits, which are diamond-shaped in transversal section (Table 1).

## DISCUSSION

Although *Vanilla palmarum* has been considered as a species with a wide distribution throughout South America (Soto Arenas and Cribb 2010; BFG 2018), according to the data presented here this taxon is endemic to Brazil, occurring in both the Atlantic Forest and Caatinga Biomes from south-eastern (northern Minas Gerais) to north-eastern Brazil. *Vanilla palmarum* is also reported from Cuba (Soto Arenas and Cribb 2010; Mújica and González 2015) because two related taxa described from Cuba (i.e. *V. lutea* and *V. savannarum*) were synonymized under *V. palmarum* (e.g. Soto Arenas and Cribb 2010; BFG 2018). While *V. lutea* was never validly published (e.g. BFG 2018), *V. savannarum* is a validly published taxon described based on a specimen collected by Nathaniel Lord Britton and John Francis Cowell on a *Copernicia* Mart. ex Endl. palm in a savanna area near the municipality of Camagüey, Cuba (Britton 1920). *Vanilla savannarum* seems to be more related to *V. lindmaniana* than to *V. palmarum*, which is supported

by several characteristics, such as the size and shape of vegetative structures and the shape of the fruits (i.e. subcylindrical; Britton 1920). Further analysis from fresh material is necessary to confirm this hypothesis because many *Vanilla* species has been erroneously synonymized in studies based exclusively on herbaria material. In fact, some recent studies have pointed out the problems resulting from the decision to base species boundaries exclusively on dried specimens of Vanilloideae (e.g. Batista et al. 2023; Pansarin 2024; Pansarin and Miranda 2024).

Since its description by Friedrich W.L. Kraenzlin in 1911, *Vanilla lindmaniana* has been regarded as an endemic Brazilian species (e.g. BFG 2018), or more commonly as a local variation of *V. palmarum* (Soto Arenas and Cribb 2010). Consequently, *V. lindmaniana* has been considered as a synonym of *V. palmarum* in many treatments and floristic inventories (e.g. BFG 2018). Here, the identity of *V. lindmaniana* is revealed with the use of integrative taxonomy. Conclusions about the circumscription of this species are based on extensive fieldwork, on data about geographical distribution, and on morphological features on both living and herbaria specimens. Although *V. lindmaniana* and *V. palmarum* are recognized by several vegetative and floral characteristics, features linked to biotic pollination are very distinct between both taxa. Flowers of *V. lindmaniana* (as *V. palmarum*) show a channel-like depression of ca 2 mm wide, whose function is to guide the hummingbird's bill to the entrance of the nectar chamber (Pansarin and Ferreira 2022). The flowers of *V. palmarum* lack this labellar cavity, as the central crest is convex just below the anther and stigma, suggesting that other biotic vectors (probably bees) are involved in the reproduction system of this Brazilian endemic species. Despite the fact that the flowers of *V. lindmaniana* and *V. palmarum* are chasmogamous, and thus available for biotic pollination, both species show a mechanism of facultative self-pollination (Van Dam et al. 2010; Pansarin and Ferreira 2022; Emerson R. Pansarin pers. obs.). A mixed mating system based on both self- and cross-pollination can be strongly advantageous over reproductive systems based exclusively on allogamy, since it can promote reproductive assurance in the case of a decline in pollinator populations, or in areas where pollinator services are irregular or absent (e.g. Stebbins 1957; van der Pijl and Dodson 1966; Pansarin and Ferreira 2022).

Although clearly distinct taxa, morphological and molecular phylogenetic data strongly suggests a close relationship between *V. lindmaniana* and *V. palmarum*, as both taxa emerge as sister species within the thick-leaved Neotropical *Vanilla* (Pansarin and Menezes 2023; Pansarin 2024). Both sister species *V. lindmaniana/V. palmarum* emerge as in a basal position together with *V. sprucei* Rolfe, all species associated with palms (Pansarin 2024). While the circumscription of both *V. lindmaniana* and *V. palmarum* has been elucidated in this study, efforts are needed to clarify the identity of other Brazilian *Vanilla*

species that has been erroneously synonymized during the taxonomic history of this pantropical orchid genus.

## CONCLUSION

Detailed study of the vegetative and floral morphology based on living and dried plant material along with distribution patterns was crucial to determine the circumscription of the two related species, *V. lindmaniana* and *V. palmarum*. The data presented here showed that the species occurring in the Atlantic Forest/Caatinga Biome, i.e. *V. palmarum*, is a distinct taxon from *V. lindmaniana*, which is distributed in the Amazonia, Cerrado, and Pantanal Biomes. *Vanilla palmarum* is endemic to Brazil, while *V. lindmaniana* is widely distributed in South America.

## ACKNOWLEDGEMENTS

The author thanks ICMBIO for permission to collect (Protocol SISBIO number 35178-1). Research supported by the São Paulo Research Foundation – FAPESP (Grant 2018/07357-5) and by CNPq (Productivity Research Grant 301773/2019-0).

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