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A REAPPRAISAL OF NEOTROPICAL *VANILLA*. WITH A NOTE ON TAXONOMIC INFLATION AND THE IMPORTANCE OF ALPHA TAXONOMY IN BIOLOGICAL STUDIES

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ABSTRACT. Despite the long-standing cultural importance and botanical interest in *Vanilla*, many taxa belonging to the genus remain poorly understood. *Vanilla* species generally have broad geographical and ecological distributions. Most species are found in multiple countries, while local endemics are rare. Many names proposed in the eighteenth and nineteenth centuries remain cryptic and unused despite having priority over more recently proposed names. Relatively few *Vanilla* species have been well-documented, both locally and across their entire distribution range, while a significant portion of novelties have been proposed on the basis of very few specimens that are compared only with local floras. After careful inspection of the type materials, living plants, botanical illustrations, photographs and hundreds of additional herbarium specimens of *Vanilla* we tentatively recognize 62 species for the Neotropics. The taxonomy of *Vanilla columbiana*, *V. hartii*, *V. inodora*, *V. karen-christianae*, *V. marowynensis*, *V. mexicana*, *V. odorata*, *V. phaeantha*, *V. planifolia*, and *V. pompona* is revised. An updated typification, description, photographs, illustrations, list of studied specimens, distribution map, extent of occurrence and discussion is provided for each of the ten species. Taxonomic proposals include 28 new synonyms, 14 lectotypifications, and one neotypification. We stress on the importance of alpha-taxonomy for biological studies, emphasizing on the detrimental effects of taxonomic inflation and incorrect species determination on the inference of speciation rates, the understanding of biogeographical patterns, the correct estimation of ecological niches, seed dispersal studies, phylogenetic and genomic studies, and the assessments of conservation priorities, among others. Finally, the recently proposed genus *Miguelia* is placed under the synonymy of *Vanilla*.

KEY WORDS: Conservation, distribution, *Miguelia*, typification, *Vanilla columbiana*, *V. hartii*, *V. inodora*, *V. karen-christianae*, *V. marowynensis*, *V. mexicana*, *V. odorata*, *V. phaeantha*, *V. planifolia*, *V. pompona*

Introduction. The pantropical genus *Vanilla* Plumier ex Miller is probably the most well-known and widely appreciated of all orchids thanks to the famous flavoring that is found in its fruits (Bouétard *et al.* 2010). *Vanilla* species, nonetheless, are taxonomically challenging due to the sparsity and poor state of flower material (Lubinsky *et al.* 2008, Soto Arenas & Dressler 2010). In the first monograph of the genus, Rolfe (1896) recognized 52 *Vanilla* species worldwide. Portères (1954) increased the number to 110 accepted species, while more modern treatments report lower

numbers. Especially noteworthy are the accounts of Soto Arenas & Cribb (2010) and Cameron (2011), who estimate that the genus includes 106 and 101 species, respectively. However, many additional novelties have been proposed since, elevating the number of *Vanilla* species to almost 140.

Despite the long-standing cultural importance and botanical interest in the genus, a disproportionately large number of *Vanilla* species have been recognized and proposed in recent years. Only fifty species had been described in the 18th and 19th centuries, and

a similar number of species was added in the 20th century. In the first 250 years of existence of the genus about 100 different *Vanilla* species were recognized in the world's Tropics. In contrast, interest in *Vanilla* has seen a dramatic renewal in the last decade (i.e. since the publication of the studies of the late Miguel Soto Arenas). In the last ten years, 32 *Vanilla* species have been proposed as novelties, of which 26 are Neotropical. These figures are not suspicious *per se*, as species discovery in highly diverse orchid groups occurring in Tropical countries has increased in recent years. The vast majority of species belonging to very large genera (i.e. *Bulbophyllum* Thouars, *Epidendrum* L., *Lepanthes* Sw. and *Stelis* Sw.) have been described in relatively recent times (Karremans & Davin 2017). However, *Vanilla* differs from those genera in four key aspects: a) *Vanilla* is a highly valued crop and has historically been given much attention botanically, horticulturally and commercially; b) *Vanilla* species are very conspicuous, they have massive plants with large showy flowers; c) *Vanilla* species are found in the lowlands, augmenting connectivity and reducing isolation; d) And most importantly, *Vanilla* belongs to one of the oldest orchid lineages, which have conserved an extremely slow diversification rate (Givnish *et al.* 2015). Contrary to many other Neotropical orchid groups, the vast majority of *Vanilla* species are relatively old and broadly distributed, mostly not restricted to a single country or area. Cases of narrow endemism and local radiations are very exceptional in the genus.

As part of an ongoing study on *Vanilla* diversity, the types and original materials of dozens taxa have been studied carefully. As a result, it has become apparent that several recently proposed species represent only range extensions of previously described entities. A total of 28 species names, six of them unpublished, and one generic name are placed under synonymy of previously described taxa. Consequently the number of accepted *Vanilla* species is reduced to 118, a significant decrease of about 15%; and the number of recognized Neotropical *Vanilla* species is shrunk by about a quarter, from 81 to 62. Furthermore, we are certain that careful revision of additional taxa will result in more reductions in the future. Proposing multiple names for a species may appear like a harmless, merely taxonomic, affair, and reducing species is

certainly not as popular and welcomed as describing new ones (Geiger 2020, Geiger *et al.* 2020). However, recognizing more species than there actually are found in nature may have unexpected consequences. Species are the fundamental units in macroecology, and tests of biogeographical patterns, such as ranges being larger at higher latitudes or the abundance being greater in the center rather than the edges of a range, may be significantly hampered by regional inflation (Isaac *et al.* 2004). Over-splitting of taxa may also have serious implications for conservation biology (Zachos *et al.* 2013, Garnett & Christidis 2017). On the latter, Isaac *et al.* (2004) find that as species numbers increase, taxonomic inflation could potentially mask extinction rates and, at the same time, due to a reduction in the average geographical range and population size, will result in a higher proportion of threatened or extinct species. As a consequence, the assessments of species loss rates and of conservation priorities become unreliable.

Watteyn *et al.* (2020) offer an example of a non-taxonomical study on *Vanilla* where taxonomical inflation is highly detrimental. The authors use species distribution modeling to identify areas for conservation and sustainable cultivation of wild relatives of the vanilla crop. When using species distribution modeling, including the complete range is very important to assess the full environmental variation under which a species occurs. It is extremely important to have enough different data points to analyze, which is not possible when species have very narrow ranges and are known from a few specimens only. Studies on the natural dispersal of *Vanilla* seeds (Karremans *et al.* unpub.) may be seriously hindered by the large differences in recorded geographical ranges among *Vanilla* species. While the unusually broad distribution of members of the genus, as compared with other orchids, is masked by the restricted distributions reported in literature. Due to the narrow distribution, small populations and anthropological disturbance, conservation concerns for the recently described *Vanilla denshikoiira* Flanagan & Ospina-Calderón and *V. karen-christianae* Karremans & P.Lehm. were raised by authors (Flanagan *et al.* 2018, Karremans & Lehmann 2018). However, the taxonomical status of both of those species is discussed here and although their

conservation status is not re-assessed, their ranges are significantly broadened, which could reduce the level of concern for their conservation initially indicated. Similarly, a population study of *Vanilla bahiana* Hoehne and *V. pompona* Schiede in Brazil finds that despite being widespread across their distribution the two species are mostly found in fragmented habitats and both are given a preliminary status of 'Endangered' (Ferreira *et al.* 2017). Nevertheless, the large number of specimens cited for both species, in addition to their very broad distribution as shown here, certainly suggests that perhaps they are not of the highest concern for conservation among *Vanilla* species, let alone Orchidaceae.

Most novel plant species are discovered either by exploring remote areas or by carefully re-examining previously collected specimens. It is expected that a large part of those novelties belong to groups that are either of lesser interest, of complicated taxonomy, or are intrinsically highly diverse (Pupulin & Karremans 2017). The odds of finding an undescribed species of *Lepanthes* (Pleurothallidinae) in an unexplored area is high (Pupulin & Bogarín 2012), the odds of finding an undescribed species of *Vanilla* anywhere, on the other hand, are quite slim. This does not mean that all of them have been discovered and described. However, it is quite likely that there is already an available name among the many historically poorly understood taxa. Despite the availability of the seminal papers by Soto Arenas & Cribb (2010) and Soto Arenas & Dressler (2010), *Vanilla* is especially difficult taxonomically due to the obscurity of many names and the poor preservation of flowers. The broad distribution of *Vanilla* species also presents a challenge. When *V. karen-christianae* from Costa Rica was described, the types of *Vanilla* species from Mexico, Central America, Colombia and Ecuador were revised. Unfortunately, the name *V. uncinata* Huber ex Hoehne, based on a specimen from Brazil and placed in the synonymy of another species, was overlooked. The two are obviously conspecific which means that the species has a distribution range of at least 5000 km. Such broad distributions are very uncommon in Orchidaceae in general, but relatively frequent in *Vanilla*. In fact, out of the 1281 orchid species reported from Mexico (data from AMO) and the 1600 species reported from Costa Rica (data from

JBL), some 30–35 species are shared with Brazil, or about 2.0–2.5%. In contrast, more than half of the *Vanilla* species found in either country is also reported from Brazil.

By no means are we suggesting that there are no novelties to be discovered in *Vanilla*, there surely must still be a few. However, this number is probably limited given that the group is not particularly species-rich, as compared to other orchids, and species are mostly lowland growers with a broad geographical distribution, reducing the opportunities for isolation. Contrary to what one may do when studying other orchids, in the case of *Vanilla* it is highly advisable to carefully review floras from distant regions as well as old names that apply to cryptic taxa, before proposing novelties. Having good records of the unusually broad distribution of *Vanilla* species may be even more valuable than describing poorly known and narrowly endemic new species.

Materials and methods. The original materials, including protologues, illustrations and specimens of dozens of Neotropical *Vanilla* species and their proposed synonyms were analyzed. Historical literature was accessed at the JBL library, online repositories (Biodiversity Heritage Library; Tropicos) or requested from private sources. Relevant specimens were photographed by us, accessed via the original depositories (GBIF—Global Biodiversity Information Facility; Harvard University Herbaria; INCT—Herbário Virtual da Flora e dos Fungos; Muséum national d'histoire naturelle; Refflora—Herbário Virtual; The Herbarium Catalogue, Royal Botanic Gardens, Kew) or requested from the curators. We revised +650 specimens, either electronically or physically, from the following herbaria: ALCB, AMES, AMO, ASE, B, BM, BO, BRIT, CEN, CEPEC, CICY, COL, CR, CUZ, F, FLAS, G, GH, GOET, HAL, HB, HOXA, HUEFS, HUFU, HUPCH, HUT, IAN, JBL, K, L, LE, LL, MA, MBM, MG, MO, MOL, MW, NY, P, PR, PRC, RB, REU, SEL, SP, TEX, U, UB, UFRN, URP, US, USF, USJ, USM, VIES and W. The taxonomic status and nomenclature of these taxa is reevaluated to determine the adequate name usage through the application of the International Code of Nomenclature for algae, fungi, and plants (Turland *et al.* 2018).

Vegetative and floral structures of living plants were photographed with a Nikon® 7100 and Nikon® 810 camera using a AF-S VR Micro-NIKKOR 105 mm f/2.8G IF-ED lens. Those photographs were used to prepare Lankester Composite Dissection Plates (LCDP) using Adobe Photoshop®. Plates include habit, flower, dissected perianth, column, anther cap and pollinarium, as well as other taxonomically informative characters depending on the taxa illustrated. LCDPs are prepared in such a way that

they are easily comparable among the diverse taxa. All photographs are by the authors except when indicated otherwise. Distribution maps based on a world Imagery updated to July 1, 2020 from Esri, Maxar, Earthstar Geographics, CNES/Airbus DS, USDA FSA, USGS, Aerogrid, IGN, IGP, and the GIS User Community. The Extent of Occurrence (EOO) was assessed using the studied specimens with the Geospatial Conservation Assessment Tool (GeoCAT; Royal Botanic Gardens, Kew: <http://geocat.kew.org>).

TAXONOMIC TREATMENT

Vanilla Plum. ex Mill., Gard. Dict. Abr. ed. 4: s.p. 1754. Lectotype:—*Vanilla mexicana* Mill., Gard. Dict. (ed. 8), no. 1. 1768. Replaced synonym: *Epidendrum vanilla* L., Sp. Pl. ed. 1, 2: 952. 1753.

Syn.: *Vanillophorum* Neck., Elem. Bot. 3: 134. 1790, *nom. inval., opus utique oppr.*

Syn.: *Myrobroma* Salisb., Parad. Lond. 2: t. 82. 1807.

Type:—*Myrobroma fragrans* Salisb., Parad. Lond. 2: t. 82. 1897, *nom. illeg.* ≡ *Epidendrum rubrum* Lam., Encycl. 1: 178. 1783 = *Vanilla rubra* (Lam.) Urb., Repert. Spec. Nov. Regni Veg. Beih. 5: 157. 1920.

Syn.: *Dictyophyllaria* Garay, Bot. Mus. Leaf. 30: 231. 1986. Type:—*Dictyophyllaria dietschiana* (Edwall) Garay, Bot. Mus. Leaf. 30: 231. 1986 = *Vanilla dietschiana* Edwall, Revista Centro Sci. Campinas 2: 192. 1903.

Syn.: *Miguelia* Aver., Turczaninowia 14(2): 45. 2011, **syn. nov.** Type:—*Miguelia somae* (Hayata) Aver., Turczaninowia 14(2): 49. 2011 = *Vanilla somae* Hayata, Icon. Pl. Formosan. 6: 88. 1916.

Averyanov & Vuong (2015) segregated four species from southern and south-eastern China, Vietnam and Laos from *Vanilla* into the newly proposed *Miguelia* (Averyanov 2011). The species belonging to the proposed genus differ from *Vanilla* in the “sympodial, branched, cymose inflorescence”. However rare, branching inflorescences can be occasionally found in many *Vanilla* species including *V. palmarum* (Salzm. ex Lindl.) Lindl. and *V. planifolia* Andrews, and seems to be the predominant condition of the inflorescences of, for example, *V. costaricensis* Soto Arenas and *V. armoriquensis* Damian & Mitidieri (Fig. 1), both of which belong to *Vanilla* subgen. *Vanilla*. What has been defined by the authors as a cymose inflorescence

with two terminal flowers in *Miguelia*, is in fact a strongly compacted racemose inflorescence, with distichous flowers, placed almost, not exactly, at the same height, terminating in a distichous vestige (see Fig. 1 in Averyanov & Vuong 2015). DNA data is not yet available for the species included in *Miguelia*, but there is no doubt they belong within *Vanilla*.

Vanilla cruenta (Aver. & Vuong) Karremans, Damian & Léotard, **comb. nov.**

Bas.: *Miguelia cruenta* Aver. & Vuong, Taiwania 60: 36. 2015.

SELECTED NEOTROPICAL TAXA

1. *Vanilla columbiana* Rolfe, J. Linn. Soc., Bot. 32: 468. 1896. Fis. 2–5, 6a.

TYPE: [COLOMBIA]. New Granada: Valley of the Magdalena, *Goudot s.n.* (holotype, K!; isotype, P!, Fig. 2)

Syn.: *Vanilla calyculata* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7: 42. 1920, **syn. nov.**

TYPE: COLOMBIA. Cauca: 1000 m, *M. Madero s.n.* (holotype, B, destroyed). Neotype (designated by Soto Arenas & Dressler 2010): Colombia. Valle: Municipio de Tulúa, Corregimiento Mateguadua, Jardín Botánico, laderas en vía de repoblación natural, altura 1100 m, 29 Sept. 1984, *W. Devia 815* (MO-3245054, not located; illustration in Soto Arenas & Dressler, Fig. 3).

Syn.: *Vanilla hameri* Soto Arenas, *nom. nud. in sched.*, **syn. nov.**

Syn.: *Vanilla esquipulensis* Archila & Chiron, Richardiana 13: 6. 2012, **syn. nov.**

TYPE: GUATEMALA. Collecté par Fredy Archila, avril 2012, La aldea el barrial, poussant sur une plante d'anone, Esquipulas, Chiquimula, 900 m



FIGURE 1. The racemose inflorescences of certain *Vanilla* species become branched over time. **A.** *Vanilla costaricensis* Soto Arenas. **B.** *Vanilla armoriquensis* Damian & Mitidieri. Photos by APK based on Karremans 7308 (A) and AD based on Damian *et al.* 904 (B).

d'altitude, *FA-1300* (holotype: BIGU, USAC; isotype: BIGU, USAC; illustration!).

Hemiepiphytic *vine*, branching, leafy vine, up to 4 m high. *Stems* flexuose, terete, furrowed and lustrous, green, 6–12 mm in diameter; internodes 7.0–15.5 cm long. *Aerial roots* terete, one per internode emerging laterally to the leaf, up to 8.2 cm long, 2–3 mm in diameter. *Leaves* sessile to subpetiolate, the petiole up to 7–10 mm long; the blade oblong to ligulate, the base rounded, the apex obtuse, shortly apiculate, coriaceous fleshy, apparently stiff and xerophytic, the margins slightly revolute, $7.5\text{--}21 \times 1.7\text{--}4.0$ cm. *Inflorescence* a 12–14 successive flower raceme, 2–4 opened simultaneously, 4.2–6.0 cm long; *peduncle* fleshy, subterete, ca. 1 cm long; *rachis* terete, green, ca. 4–6 cm long. *Floral bracts* widely ovate, obtuse, green, concave, progressively smaller, up to 10×6 mm. *Flowers* pendant, very showy, sepals and petals whitish green to yellowish green, in the apex more dark green, lip white with deep yellow in the center and green in the apex, ca. 9 cm long; strongly fragrant. *Ovary* terete, smooth, sulcate, ca. 4.0–4.5

$\times 4$ mm. *Dorsal sepal* oblanceolate to narrowly elliptic, recurved above the middle, apex subacute to obtuse, somewhat thickened, subcalyptrate, basally canaliculate, smooth, base attenuate sub-unguiculate, ca. 12–13 veined, $66\text{--}80 \times 8.0\text{--}17$ mm. *Lateral sepals* oblong to narrowly elliptic, oblique, recurved above the middle, the lower margin more incurved, apex subacute to obtuse, somewhat thickened, subcalyptrate, basally attenuate sub-unguiculate, smooth, ca. 12–13 veined, $67\text{--}80 \times 12\text{--}17$ mm. *Petals* obliquely oblanceolate, deeply recurved above the middle, lower margin more incurved, apex attenuate, rounded, very attenuate at base, acute, with a flat keel on the abaxial surface, 1 mm wide, ending in a free, conic, blunt, short, 1 mm long apicule; ca. 11–12 veined, $65\text{--}80 \times 9\text{--}16$ mm. *Lip* attached to the column along the margins of the basal half ca. 41–46 mm, tubular, bell-shaped, trilobed; abaxially deeply grooved along on the midvein; when spread out $78\text{--}90 \times 36\text{--}45$ mm; long unguiculate, the claw apically rugose, papillose on the inner surface, $26 \times 3.0\text{--}3.8$ mm; the blade cymbiform, when spread out approximately obovate in outline, ca. 36 veined, veins branched; the lateral lobes rounded, incurved forming



FIGURE 2. Type material of *Vanilla columbiana* Rolfe. **A.** Holotype K-000463745 © copyright of the Board of Trustees of the Royal Botanic Gardens, Kew. **B.** Isotype P-00367038 © copyright of the Muséum national d'histoire naturelle, Paris.

a gullet around the column, margins entire to crenulate, apically overlapping, constricted near the midlobe base, 37–39 × 14 mm; the midlobe spreading, subquadrate, deeply emarginate to bilobed, recurved, margins dentate, undulate, veins conspicuously thickened, 14–16 × 21–26 mm; *penicillate callus* at ca. 41 mm from the base, 4.5 × 3.8 mm, made up by 8–10 flabellate, shortly lacerate, retrorse, scales, some of them united to each other along the lateral margins; extending for about 25–27 mm to the apex, ca. 6 mm wide, 2–3 mm high, progressively more thickened towards the apex of the lip, forming an apical, swollen, low cushion,

convex, rugose, papillose, with yellowish-orange hairs in the basal part. *Column* subterete, subclavate, slender, slightly sigmoid, 51–55 × 4 mm; ventrally flattened and lanuginose at the distal half; apex with two vertical wings, narrow, triangular, flabellate, undulate, ca. 4 × 1 mm. *Stigma* trilobed, the lobes emergent; rostellum trapezoid, flabellate, 2.0 × 4.5 mm; lateral lobes transversely oblong, flabellate, 1.2 × 1.8 mm. *Anther* versatile, attached to the wide clinandrium margin by a broad filament, triangular to ovate, truncate emarginate, 5 × 5 mm. *Fruit* bright brown when mature, fragrant, trigonous, 8–15 cm long.

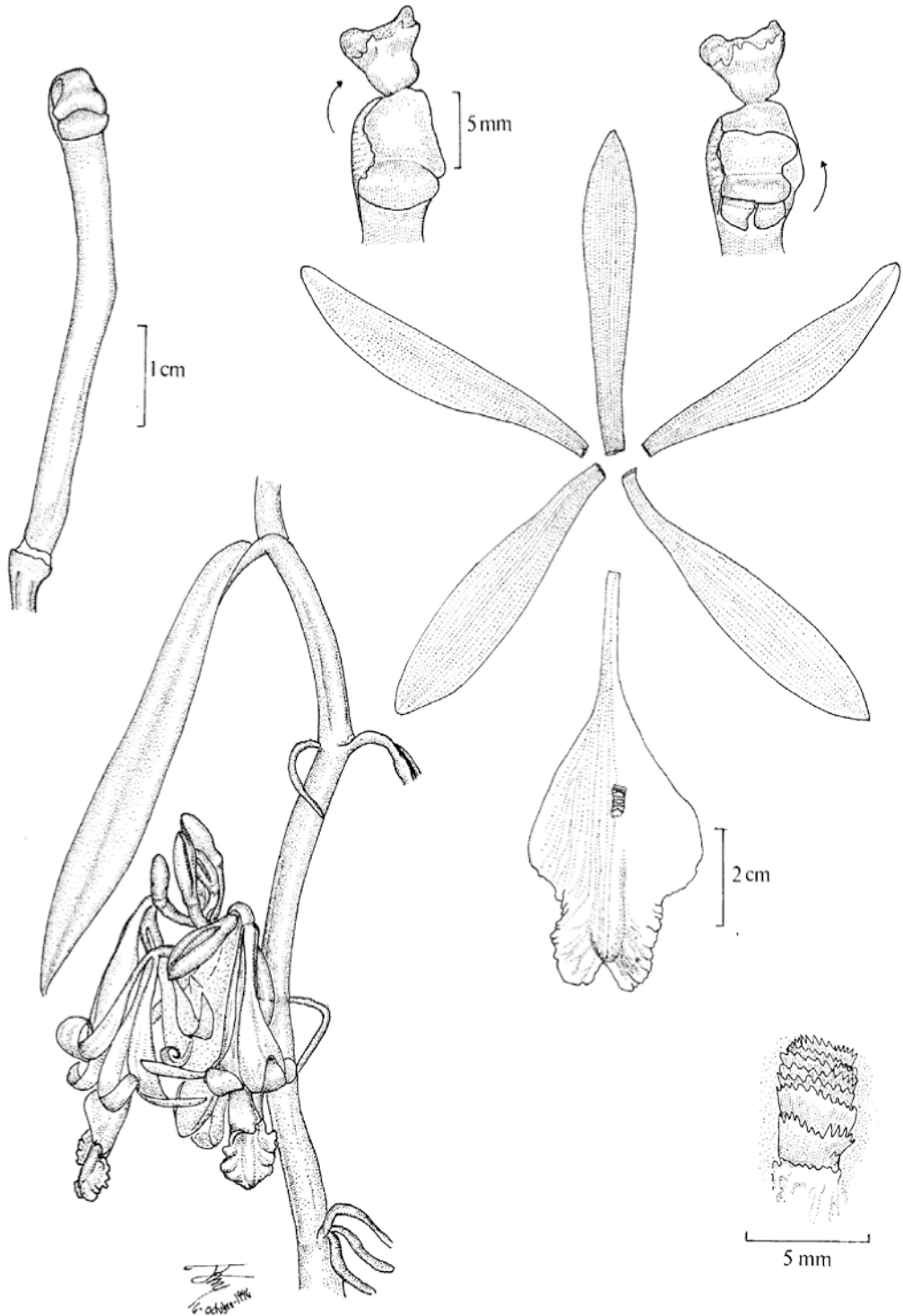


FIGURE 3. *Vanilla columbiana*. Illustration of *Devia* 815, the neotype of *V. calyculata* Schltr. selected by Soto Arenas & Dressler (2010) and published therein.



FIGURE 4. *Vanilla columbiana* flowering specimens from different localities across its distribution. A. Colombia, *Moreno s.n.* B. Colombia, *Díaz 1369*. C. Colombia, *González s.n.* D. Honduras, *Vega s.n.* Photographs by the collectors kept at JBL.

SPECIMENS STUDIED: HONDURAS: Comayagua: Thicket along river, plain near Sihuatepeque. 1050 m altitude. 23 Jul. 1936, *T.G. Yuncker, R.F. Dawson & H.R. Youse 6045* (AMES-46667!; G; K!; MO-1115382; NY!). Unknown locality, *H. Vega s.n.* (JBL-photograph!; Fig. 4D). EL SALVADOR: La Palma-Finca El Refugio, Río Nanuapa,

1000 m, 4 Mar. 1969. 11 Apr. 1969, *O. Pank & F. Hamer 203* (AMES-112862!; AMES-113837!). COLOMBIA: Cundinamarca, Fusagasuga, vereda “Chinauta”, finca “El descanso”, 1200 m, 3 Abr. 1988, *F. Sarmiento 2140* (COL!). Cauca: Dagua, 960 m, *S. Moreno s.n.* (JBL-photograph!; Fig. 4A, 5B). Santander: Zapatoca, *D. Díaz 1369* (JBL-



FIGURE 5. *Vanilla columbiana* growing *in situ* in Colombia. **A.** Cauca: Dagua, *Moreno s.n.* **B.** Santander: Zapatoca, *Díaz 1369*. Photographs by the collectors kept at JBL.

photograph!; Fig. 4B, 5A). Without collecting data, *R.T. González s.n.* (JBL-photograph!; Fig. 4C).

OTHER SPECIMENS: MEXICO: Michoacan: Hacienda de Coahuayula, Feb. 1901, *G.M. Emrick 16* (F-95476). GUATEMALA: Esquipulas, Chiquimula, dans des zones proches du mirador de Esquipulas, 600 m, Fredy Archila, Mar. 1999, *FA s.n.* (BIGU); Affluent du Río Jocotan Chiquimula, dans un ruisseau proche, 500 m, Fredy Archila, Apr. 2000, *FA s.n.* (BIGU). HONDURAS: Morazan: Aguas abajo de la Quebrada de Sta. Clara, 850 m, 28 Apr. 1948, *A. Molina 808* (F-1676153); Quebrada Santa Clara, ca. 2 km al norte del Zamorano, 800 m. Mpio de San Antonio de Oriente. 19 Jun. 1996. *J.L. Linares 3386* (MEXU). El Paraíso: Mpio. Moroceli, Quebrada El Cajocote conocida también como El Terrero, 8.7 km al N de Moroceli, por el camino a Mata de Plátano, 14°10'10" N, 86°51'06" W, 680 m, 29 Apr. 2004, *J.L. Linares 7313* (MEXU). Barranco de las Mesas, 900 m, 1 Ago. 1957, *L.O. Williams & A. Molina 8575* (F-1590341), Open savannah, Las Mesas region near

Yuscarán, Aug. 1960, *H.W. Pfeifer 1454* (US-2563382). COLOMBIA: Tolima: Auf äumen in Zavannen-Wäldern bei La Plata, 800–1500 m. 3 Dec.1882. *F.C. Lehmann 2263* (BM; G). [Unknown locality] Cultivated, *E. Dryander 2379* (BM). “Columbien” *Lehmann s.n.* (W-59043).

DISTRIBUTION: Mexico, Guatemala, El Salvador, Honduras and Colombia (Fig. 6A).

EXTENT OF OCCURRENCE:—288,210.392 km².

Vanilla columbiana can be especially recognized by the thick, fleshy stems, that can be up to half the width of coriaceous leaves. It is well adapted to drought, with the fleshy stems and leaves becoming sulcate or corrugated under extreme conditions. The leaves are oblong to ligulate, the inflorescence is also typically thick, short in relation to the leaf and notoriously multi-flowered with one to a few flowers open at once. The flowers have non-spreading, slightly recurved

segments, the sepals and petals are yellowish green, the lip is white with a deep yellow middle and green apex. The ovary has an apical thickening (calyculate), which is more evident in dried material. The lip is bell-shaped, trilobed, the midlobe is subquadrate, with the apex emarginate and the margins undulate, and the central veins conspicuously thickened forming a longitudinal ‘cushion’ from the penicillate callus to the apex.

Rolfe described *Vanilla columbiana* on the basis of material collected by Goudot in the Valley of the Magdalena, Colombia. The identity of this species has remained cryptic, and the name virtually unused. The thick stem, coriaceous leaves that are shorter than the internodes, and undulate, trilobate lip with a quadrate apex and thickened central veins characterize the species. Soto Arenas & Cribb (2010) suspected an affinity with *V. calyculata*, which was also described on the basis of Colombian material, but the poor state of the type material prevented a definitive decision. We find that the vegetative features observed in the holotype and isotype specimens, as well as the floral features described in the protologue, are congruent with our current concept of *V. calyculata*. As such *Vanilla columbiana*, which has priority, replaces the concept of *V. calyculata* as circumscribed by Soto Arenas & Dressler (2010).

Vanilla columbiana has not been reported in countries south of Colombia. However, some of the Brazilian materials determined as *Vanilla chamissonis* Klotzsch and *V. vellozii* Rolfe are extremely similar to *V. columbiana*. The species currently treated as *V. chamissonis* in Brazil, as illustrated for example by Hoehne in Flora Brasiliica (Hoehne 1945), is similar but different from our concept *V. columbiana*. However, the illustration of *V. chamissonis* published by Cogniaux in Flora Brasiliensis is virtually indistinguishable from *V. columbiana*. In Brazil, two forms of *V. chamissonis* have been recognized by several authors, perhaps one of is conspecific with *V. columbiana*. Careful study of living material and the type specimens of *V. chamissonis* and *V. vellozii*, as well as the closely related *Vanilla argentina* Hicken and *V. carinata* Rolfe, is necessary to definitively resolve their identity and the relationships among these taxa.

When proposing *V. esquipulensis*, Archila Morales & Chiron (2012) cited a few superficial differences

from *Vanilla calyculata* (= *V. columbiana*), essentially a thicker stem, a wider, petiolate leaf, and the non-calyculate ovary. Nevertheless, specimens of *V. columbiana* from Colombia (Figs. 4A–C, 5) show a thick stem and broad leaves, and flowers that are indistinguishable in every aspect from the northern Central American material described as *V. esquipulensis* (Fig. 4D), including the calyculate ovary, a feature that is variable and depends on the hydration of the material (inconspicuous in living plants and becoming more evident as the specimen becomes dehydrated).

Soto Arenas used the name “*Vanilla hameri* Soto Arenas” on herbarium specimens from El Salvador and Honduras that he later identified as *V. columbiana*. A few authors have cited this name as an accepted species of *Vanilla*, but it was never formally published and its use should be avoided.

2. *Vanilla hartii* Rolfe, Bull. Misc. Inform. Kew 1899(151-152): 133. 1901. Fig. 6B, 7–9.

TYPE: TRINIDAD [TRINIDAD & TOBAGO]. Cabasterre Arima, Apr. 1898, *J.H. Hart* 6355 (holotype: K-000463205!, Fig. 7; isotype: AMES-67784!).

Syn.: *Vanilla leprieurii* Portères, Bull. Soc. Bot. France 98: 94. 1951, **syn. nov.**

TYPE: FRENCH GUIANA. Cayenne: dans les forêts humides, en 1846, *Leprieur s.n.* (holotype: P-04026348!, Fig. 8).

Syn.: *Vanilla perplexa* Soto Arenas, *nom. nud. in sched.*, **syn. nov.**

Hemiepiphytic, branching, leafy vine, up to several meters high. *Stems* dark green, subterete, smooth, up to 6 mm in diameter; internodes straight to arched, 3.9–12.5 cm long. *Aerial roots* subterete, 1.0–3.5 mm in diameter, flexuous, one per internode emerging laterally to the leaf. *Leaves* usually shorter than the internodes; the petiole 4–11 mm long; blade elliptic, acuminate, lightly recurved to the apex, 5.0–15.0 × 1.1–4.4 cm, 9–17-veined. *Inflorescence* a raceme, lateral, simple, producing up to 8 successive flowers per raceme, 1–2- opened simultaneously; peduncle short, subterete, up to 0.7 cm long; rachis up to 1.5 cm long. *Floral bracts* dark green, sessile, ovate, acute, concave, 3.5–9 × 2.5–8 mm. *Flowers* ephemeral, segments spreading, the ovary whitish, apically greenish, sepals

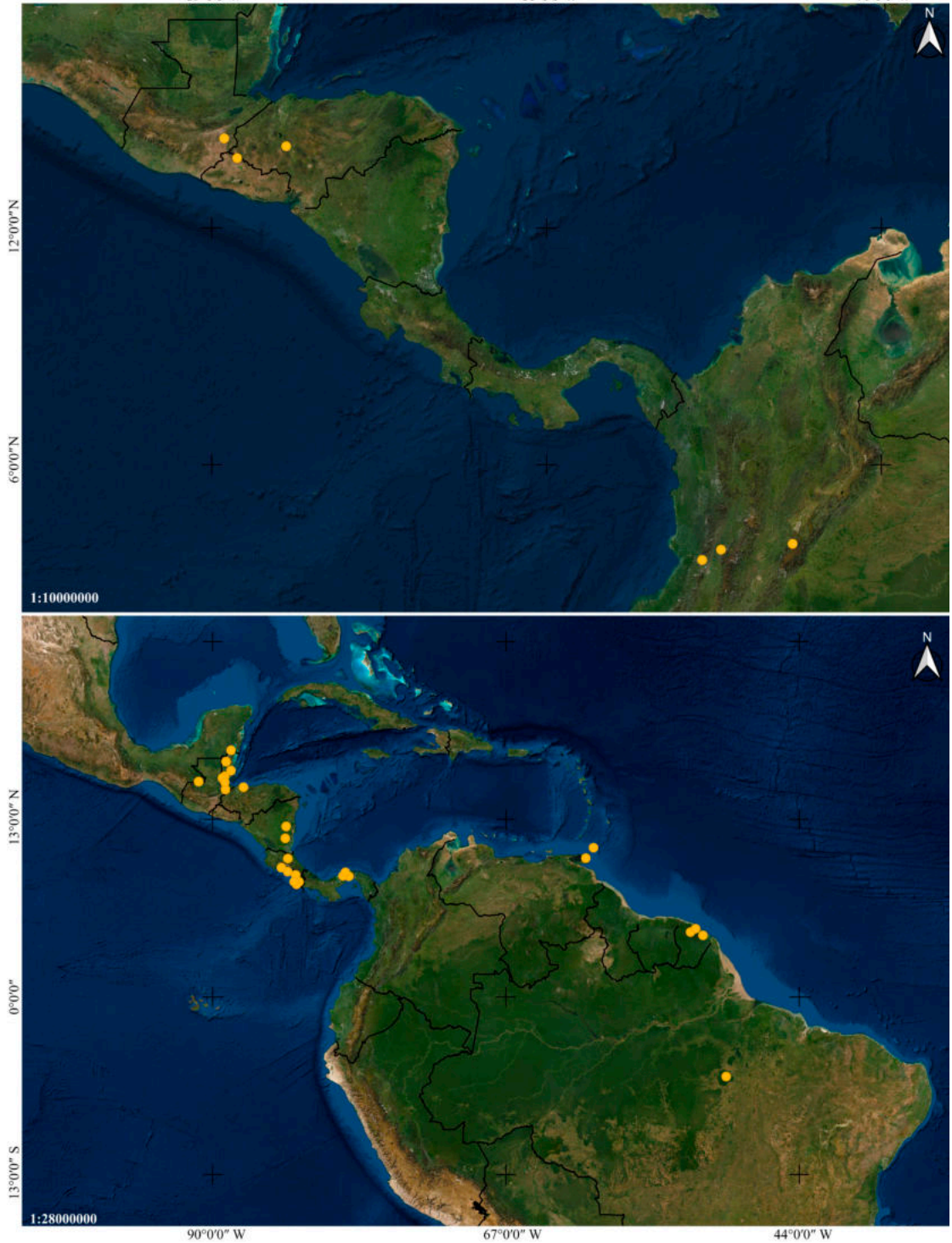


FIGURE 6. Distribution maps of *Vanilla* species based on studied specimens. **A.** *Vanilla columbiana* Rolfe. **B.** *Vanilla hartii* Rolfe. Images by IC.

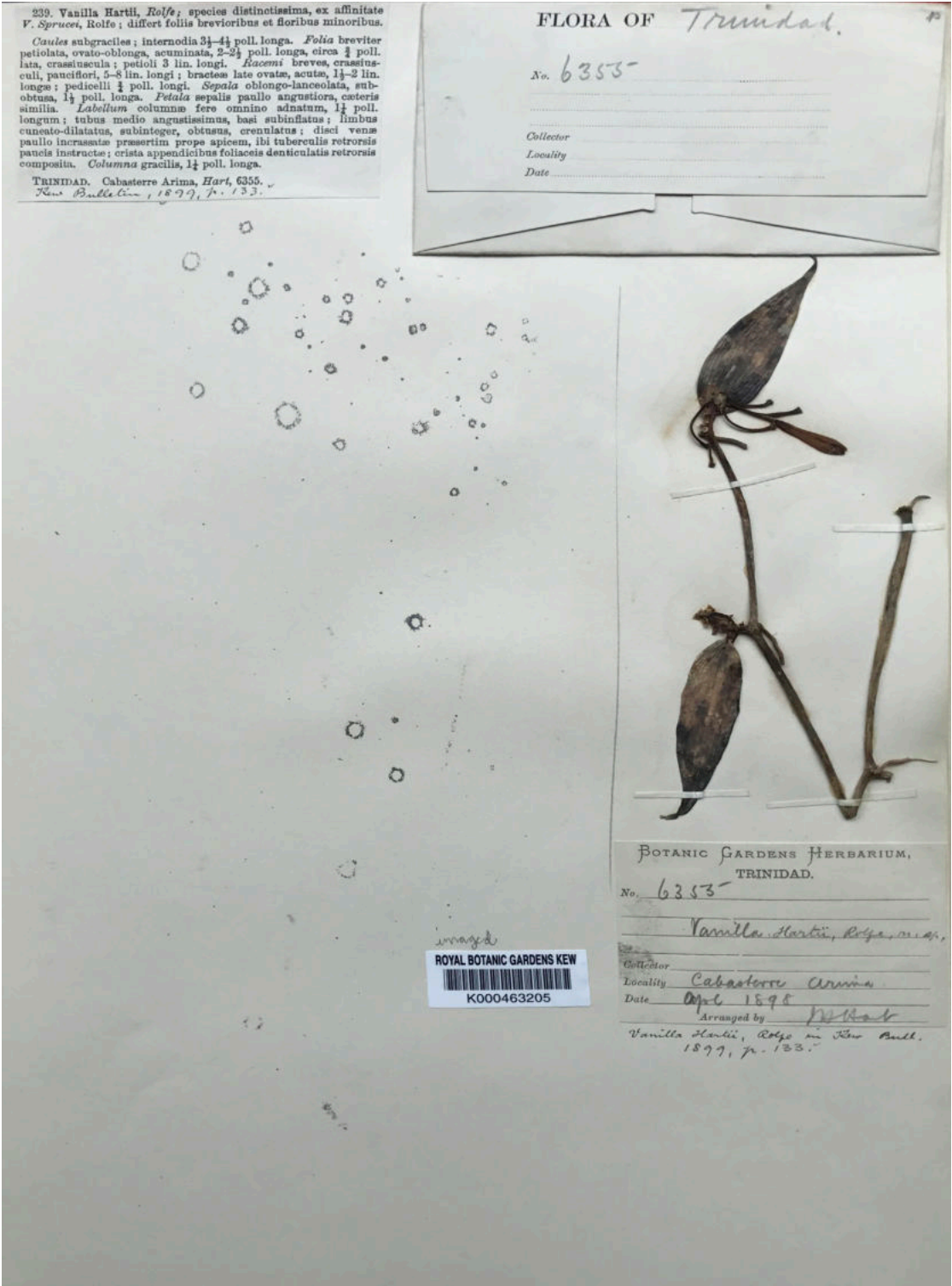


FIGURE 7. Holotype of *Vanilla hartii* Rolfe, J.H. Hart 6355 (K-000463205). Photograph by APK.



FIGURE 8. *Vanilla hartii*, holotype of *Vanilla leprieurii* Portères, *Leprieur s.n.* (P-04026348) © copyright of the Muséum national d'histoire naturelle, Paris.

white, abaxially greenish, petals white, abaxially greenish on the midvein, lip white, lightly greenish at the penicellate callus apex, and column white, with the rostellum yellowish, anther cap greenish to yellowish; fragrance imperceptible. *Ovary* subterete, smooth, lightly arcuate, $14.0\text{--}31.0 \times 2.5\text{--}3.3$ mm, green, basally whitish. *Dorsal sepal* oblanceolate, obcuneate, acute, somewhat concave, arcuate, almost porrect, fleshy, 11–13-veined, $30\text{--}50 \times 7\text{--}10$ mm. *Lateral sepals* oblanceolate, obcuneate, acute, somewhat arcuate, divergent, recurved, fleshy, 11–13-veined, $36\text{--}49 \times 5\text{--}12$ mm. *Petals* oblanceolate, attenuate, obtuse, almost porrect; abaxially with a longitudinal prominent keel, 9–11-veined, $34\text{--}48 \times 4\text{--}10$ mm. *Lip* fused to the column base along the margins for 18–26 mm; tubular, trumpet-shaped, basally gibbous, trilobed; when spread out $37\text{--}43 \times 14\text{--}25$ mm; narrowly unguiculate, the claw slightly sigmoid, minutely papillose, $15.0\text{--}16.0 \times 2.5\text{--}3.0$ mm; the blade cymbiform, when spread out obovate in outline, 21–29-veined, the veins progressively thickened towards the apex forming grooves, minutely papillose; the lateral lobes rounded, margins dentate to denticulate, undulate, with teeth up to 3.5 mm long; the midlobe emarginate, recurved, margins denticulate to crenate, undulate; *penicillate callus* 26–30 mm from the base, $4\text{--}5 \times 3$ mm, made up by 5–7 imbricate, flabellate, retrorse, lacinate scales; extending for about 15–17 mm to the apex, 3.0–3.5 mm wide, progressively thickened towards the apex, oblanceolate, obtuse, fleshy, inconspicuously papillose. *Column* subterete, lightly arcuate, $3.0\text{--}3.8 \times 0.3$ cm, from similar width along, ventrally flattened, slightly pubescent below the stigma, apex with 2 obliquely obtuse, retrorse wings, $2.5\text{--}3.0 \times 1.5\text{--}2.0$ mm. *Stigma* trilobed, the lobes conspicuous. *Rostellum* subquadrate, convex blade. *Anther* basally hinged to the column, movable, obovate, $2.7\text{--}2.9 \times 1.6\text{--}1.8$ mm. *Pollen* a sticky, granular mass. *Fruit* green, terete, dehiscent, fragrant, $5.3\text{--}15.9 \times 0.4\text{--}1.5$ cm.

SPECIMENS STUDIED: GUATEMALA. Izabal: Quebradas, 19–22 May 1919, *H. Pittier* 8589A (NY!, US-1013493, AMO-photo!). Swamps of Salomón Creek, 1/2–1 mi. south of Bananera, 50 m. 6 Apr. 1940. *J.A. Steyermark* 38944 (F-1043051, AMO-photo!). BELIZE: Toledo District. Southern Maya Mountains, Bladen Nature Reserve, mountains 1.7 airline north of the Ek Xux archeological site, $16^{\circ}31'05''$ N, $88^{\circ}54'11''$ W, 500–600 m, 24 May 1996, *G. Davidse* 36251 (BM!, MO!, SEL!). Camp 3, 6–8 km southeast

of Union Camp. Trail from camp 3 toward Cabro on the Jimmy cut trail, $16^{\circ}23'14''$ N, $89^{\circ}04'37''$ W, 665–700 m, 17 Feb. 1997, *T. Hawkins* 1462 (SEL!). Cayo. Pine Ridge, Bull Run Overseas estate, near one of the small creeks, outlet of the lake, 17.6033, -88.90583, 530 m, 29 Apr. 2014, *B. Holst*, *E. Baron*, *L. Birch*, *D. Troxell* 9896 (SEL-photo!). Toledo. Pine Hill Property across Rio Grande River from Belcampo Estate, 5 km by air (20° true north bearing) NNE of Forest Home, Punta Gorda, 16.1866, -88.8213, 25 m, 29 May 2014, *E. Baron et al.* 38 (SEL-photo!). Stann Creek, Outlier, along trail on slopes to summit, 16.81233, -88.50135305, 370 m, 11 Apr. 2018, *B.K. Holst et al.* 11306 (SEL-photo!). HONDURAS: Atlántida: Lancelilla valley, near Tela; 20 to 600 m, 6 Dec. 1927–20 Mar. 1928, *P.C. Standley* 52824 (AMES!, FI!, US!). NICARAGUA: Rio Kukarawara, Región Autónoma Atlántica Sur. Approx. 1 km up river from Tortuguero, 2–3 km into forest on right-hand side of river, $12^{\circ}50'$ N, $84^{\circ}12'$ W [24 m], 4 Jul. 1991, *L.H. Pendleton* 8 (MO!). Zelaya: Caño Zamora on Río Rama; ca. $11^{\circ}57'$ N, $84^{\circ}16'$ W, 10 m, 16 May 1978, *W.D. Stevens* 8835 & *B.A. Krukoff* (SEL!). COSTA RICA: Heredia: Sarapiquí, Chilamate. Finca El Bejuco, S end of Cerros Sardinal (N of Río Sarapiquí), $10^{\circ}27'$ N, $84^{\circ}04'$ W, 60 m, 24 Jan. 1987, *M.H. Grayum* 7998 & *T. Ray* (MO!). Puntarenas: Buenos Aires, Volcán, Cacao, orillas del Río Cacao en bosque secundario bajo el puente de la Carretera Interamericana, $9^{\circ}13'10.441''$ N, $83^{\circ}28'19.002''$ W, 449 m, 20 Mar. 2013, flowered in cultivation at Jardín Botánico Lankester 7 Dec. 2014, *A. Karremans* 5828, *D. Bogarín*, *J. Cambronero* & *F. Pupulin* (JBL-spirit; Fig. 9). Garavito. P. N. Carara. Cuenca del Tárcoles. Saddle between Cerros Quebrada Bonita and Montañas Jamaica, headwaters of Quebrada Bonita, and ridge to N, $9^{\circ}46'00.0000''$ N, $84^{\circ}34'00.0002''$ W, 420 to 585 m, 27 Jul. 1995, *M.H. Grayum* 1752 (MO!). Golfito. Refugio Nacional de Vida Silvestre Golfito. Cerro Nicuesa. Común en la parte alta de la ladera oeste del Refugio, $8^{\circ}41'30''$ N, $83^{\circ}12'50''$ W, 345 m, 7 Abr. 1994, *G. Rivera* 2281 & *G. Herrera* (CR!). Cantón de Osa, Aguabuena. Cuenca superior de Quebrada Aguabuena, 18 Jan. 1991, *G. Herrera* 4846 (CR!, MO!). Eastern Osa peninsula. Understory vegetation on the ridge of forest bordering cattle pasture, within 1 km of 8.70686 N, -83.59142 W [$8^{\circ}42'24.696''$ N, $83^{\circ}35'29.111''$ W, 379 m], *M.M. Mayfield* 81–03–81–3117 (MO-6133305!). Eastern Osa peninsula. More than 500 m from edge of primary moist tropical forest, 8.51677 N, -83.40693 W [$8^{\circ}31'0.372''$ N, $3^{\circ}24'24.948''$ W, 246 m], *M.M. Mayfield* 1480–1480–1603 (MO-6133300!). Hilly slopes west of Villa Nueva, just northwest of Londres and the Río Naranjo, ca. $9^{\circ}28'$ N, $84^{\circ}5'$ W, 200 m, 10 Feb. 1988, *W.C. Burger* 12251 & *J. Gómez-Laurito* (USJ!, F-2009056!, AMO-photo!). San José: Pérez Zeledón. Rolectada por Gabriel Barboza. *A. Karremans* 7262 (JBL!). PANAMA: Barro Colorado Island.

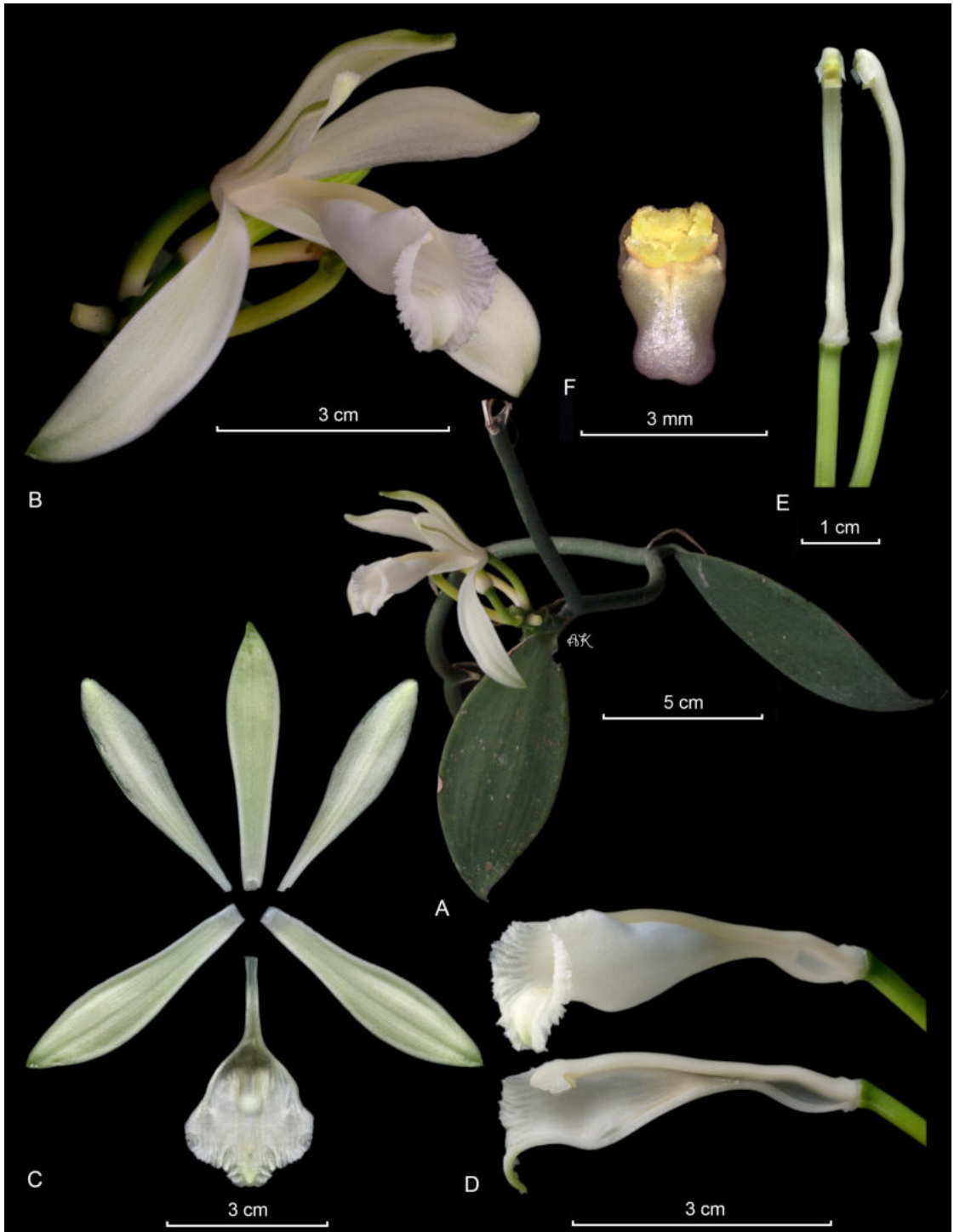


FIGURE 9. Lankester Composite Dissection Plate (LCDP) of *Vanilla hartii*. **A.** Habit. **B.** Flower. **C.** Dissected perianth. **D.** Lip and column lateral view. **E.** Column, ventral and lateral view. **F.** Anther cap and pollinia. By APK based on *Karremans 5828* (JBL-spirit).

Cana zone, 10 Jan. 1940, *F.W. Hunnewell 16433* (AMES!, AMO-photo!). Colón: Santa Rita ridge road; ca. 22 km from transistmian highway, 9°25' N, 79°40' W, 500 m, 17–18 Feb. 1986, *B. E. Hammel 14502*, *G. McPherson & D. Roubik* (MO!). Panamá: Río Tecumen, 3 Jan. 1924, *P.C. Standley 29353* (AMES!). FRENCH GUIANA: Crique tigre. Bassin du Sinnamary, 4°55' N, 53°14' O, 7 m, 23 Nov. 1993, *B. Bordenave 512* (P!). Forêt sur la rive gauche du Yaroupi, entre son embouchure et le Saut Couéki, 30 Abr. 1970, *R.A.A. Oldeman T-614* (P-1!. P-2! [2 duplicates]). Camp Caiman - Asarco - Mt de Kaw, 4°31'720" N, 52°13'386" W, 10 m, 17 Jan. 2000, *B. Bordenave, N. Raes & L. Betian 4961* (U!). TRINIDAD & TOBAGO: Tobago, 6 Mar. 1911, *W. E. Broadway s.n.* (P-00128676!, P-00128677!; U!). Trinidad, *A. Fendler 1007* (P!). Trinidad, 13 Nov. 1925, *W.E. Broadway s.n.* (K!). Mora fores, east of Sangre Grande, 10 Apr. 1921, *E.G. Britton 2841* (NY!). BRAZIL: Pará, Parauapebas, Serra dos Carajás, entorno da Mina do Alemão; 6°03' 40" N, 50°32'53" W, 590 m; 15 Dec. 2019 (f), *E.R. Pansarin 1557* (LBMBP, illustration!).

OTHER SPECIMENS: MEXICO: Chiapas: Estación de Biología de Chajul, sobre el camino a Arroyo Miranda, 200 m, 16°7'35" N, 90°54'35" W, 12 Abr. 1997, *M. Soto 8347* (AMO); same data, *M. Soto 8350* (AMO); same locality, 14 Abr. 2000, *M. Soto 9727* (AMO); same data, *M. Soto 9729* (AMO); same locality, *M. Soto 9730*, *S. Maldonado, L. López y P. Schlütter* (AMO); Sobre la Vereda La Granja, Estación de Biología de Chajul, ca. 16°7' N, 90°54' W, 200 m, 15 Abr. 2000, *M. Soto 9731 & P. Schlütter* (AMO). Estación de Biología de Chajul, sobre el camino a Arroyo Miranda, *S. Maldonado s.n.*, *L. López & P. Schlütter* (AMO). BELIZE: Corozal: *P.H. Gentle 328* (F-713628). Toledo: Broken Cohune Ridge, between Orange Point and Moho River, 28 Apr. 1952, *P.H. Gentle 7673* (MEXU-511492).

DISTRIBUTION: A broadly distributed species found in Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, French Guiana, Trinidad and Tobago, and Brazil (Fig. 6B).

EXTENT OF OCCURRENCE: 4,874,345.189 km².

Vanilla hartii plants are easily recognized by the opaque, dark green stems, with internodes usually longer than the leaves, elliptical, acuminate leaf blades, whitish flowers, the lip gibbous at the base, apically with the dentate to denticulate margin, the callus inconspicuously papillose, apically triangular, fleshy, thickened and raised. It is also a typical species in the shady understory of rain forests.

Portères (1951a) described *Vanilla lepriurii* Portères from a specimen collected in the French

Guiana. The protologue stated that the vegetative and floral morphology of *V. lepriurii* are very similar to that of *V. hartii*, but *V. lepriurii* can be distinguished by the penicillate callus of the lip with denser nervation, fleshier and with more imbricate scales, and the apex of the lip is more emarginated, apiculate and plicate. Soto Arenas & Cribb (2010) and Soto Arenas & Dressler (2010) considered the species a synonym of *V. hartii*. However, Szlachetko, Veyret, Mytnik-Ejsmont, Sawicka, Rutkowski & Baranow (2012) and Szlachetko, Nowak, Baranow & Kolanowska (2016) recognized *V. lepriurii* as a distinct species, without arguing how it is to be distinguished from *V. hartii*. Furthermore, Szlachetko *et al.* (2016) include *Vanilla inornata* Sambin & Chiron under the synonym of *V. lepriurii*. Nevertheless, we agree with the previous interpretation by Soto Arenas and Cribb (2010) and Soto Arenas and Dressler (2010) that the type specimen of *V. lepriurii* is indistinguishable from *V. hartii*, and are therefore synonyms. Whereas *V. inornata*, with its green, slightly granulose (vs. dark green, glabrous) stem, narrowly lanceolate (vs. elliptic) leaves, yellowish-green, larger flowers (vs. white, smaller), crenulate-undulate (vs. denticulate) lip margin, is a completely different species.

Soto Arenas used the name "*Vanilla perplexa* Soto Arenas" on a specimen from Costa Rica that he later determined as *V. hartii* at MO (Grayum & Ray 1998). The name was never formally published and its use should be avoided.

3. *Vanilla inodora* Schiede, Linnaea 4: 574. 1829. Fig. 10–13, 14A.

TYPE: [MEXICO]. "Baynilla de puerco Misantlensium. Species distinctissima. Hab. Misantlae. Schiede s.n. (lectotype designated here: W-ESP70160!, Fig. 10; islectotypes: W-ESP70159!, Fig. 11b; BM-000062769!, Fig. 11C; LE-00001364!).

Syn.: *Vanilla pfaviana* Rchb.f., Gard. Chron., n.s., 20: 230. 1883.

TYPE: "MEXICO" [COSTA RICA]: *R. Pfau 269* (holotype: W!; Fig. 11D).

Syn.: *Vanilla preussii* Kraenzl., Notizbl. Bot. Gart. Berlin-Dahlem 7: 320. 1919.

TYPE: GUATEMALA. Bei der Pflanzung El Baúl im Buschwald, Heisst bei den Eingeborenen

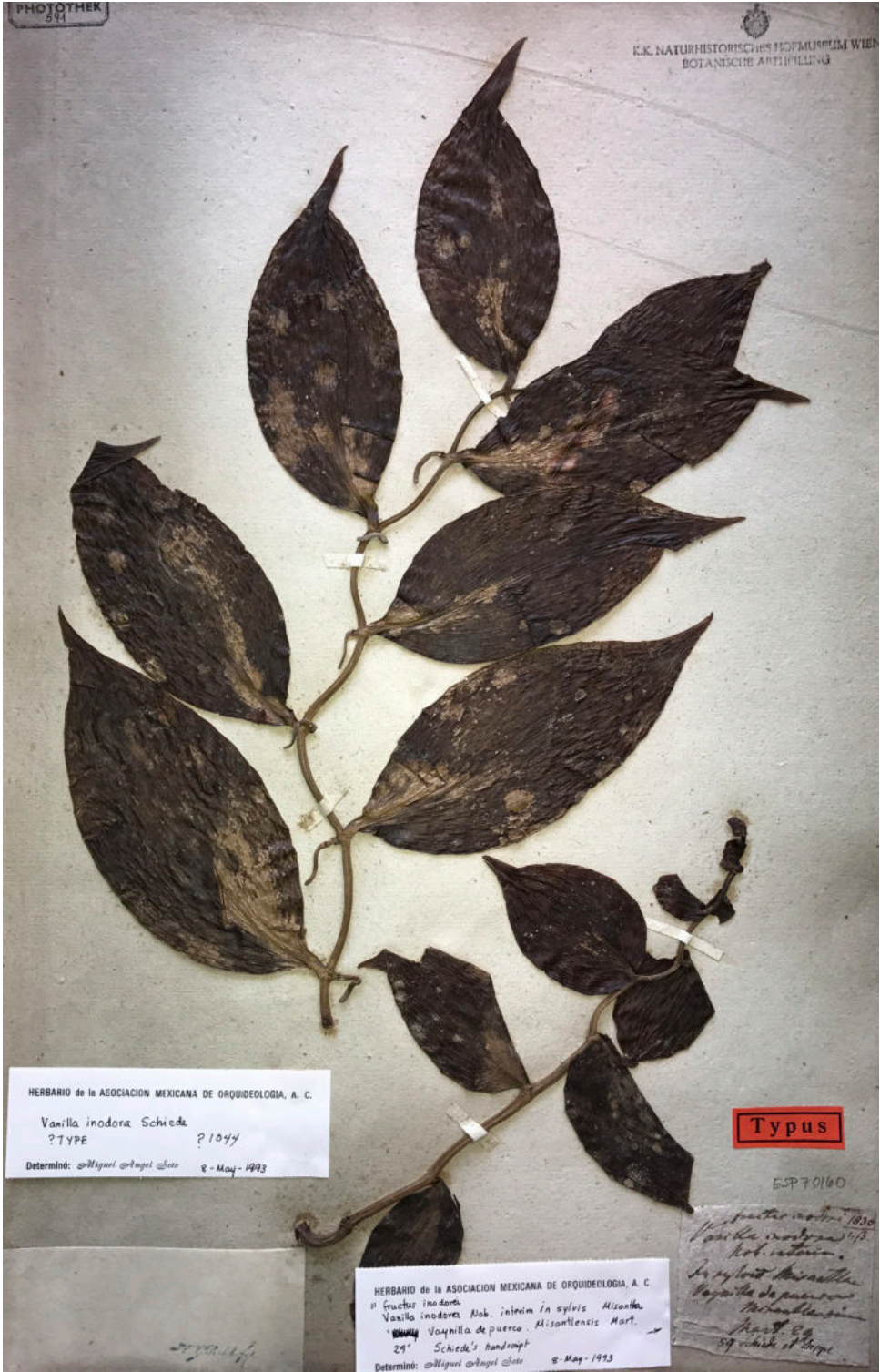


FIGURE 10. Lectotype of *Vanilla inodora* Schiede, Schiede s.n. (W-ESP70160). Photograph by APK.

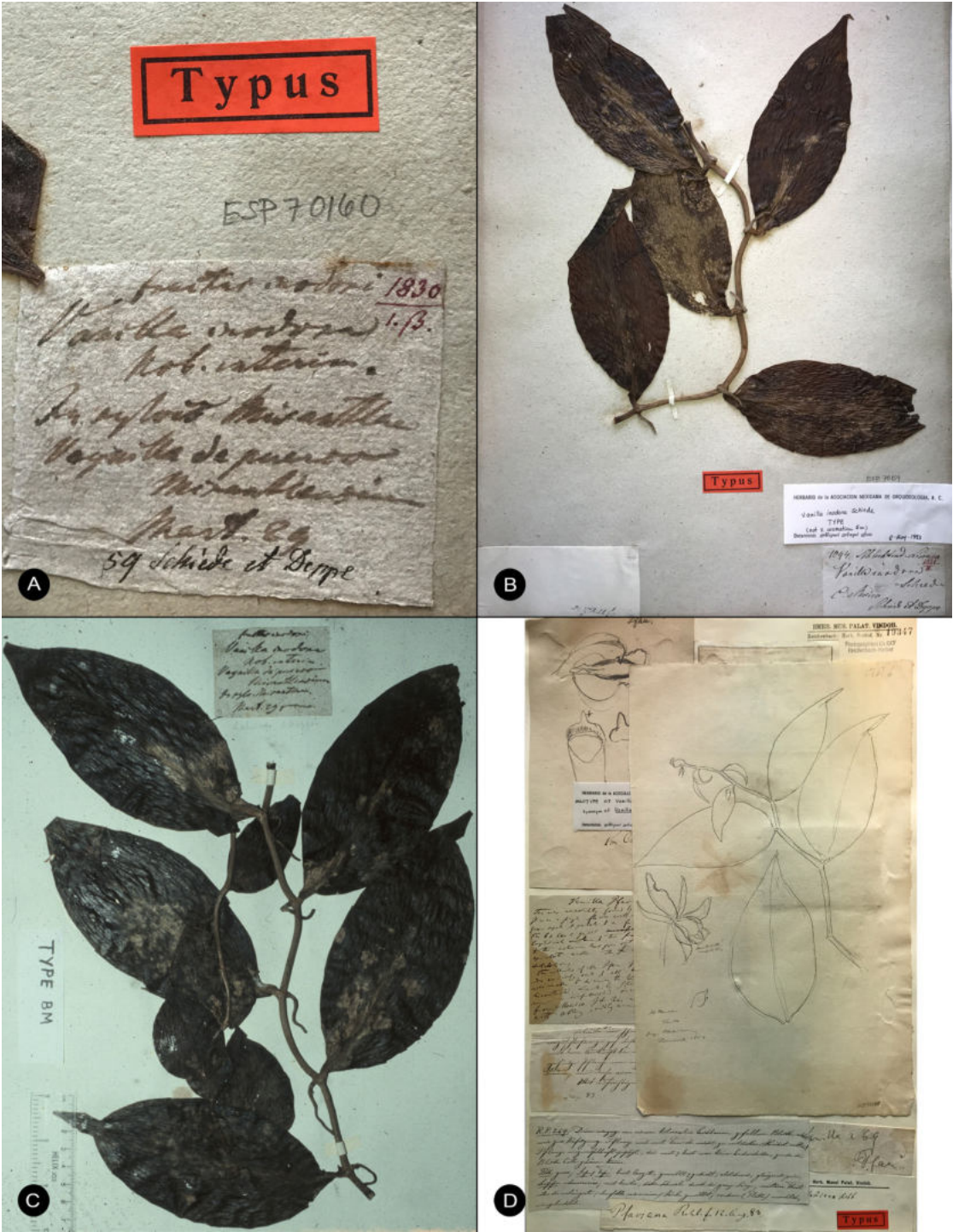


FIGURE 11. Type material of *Vanilla inodora* Schiede. A. Handwritten note by Schiede on the lectotype of *V. inodora* Schiede (W-ESP70160). B. Isolectotype of *V. inodora* at W-ESP70159. C. Isolectotype of *V. inodora* at BM-000062769. D. Illustration of type of *V. pfaviana* Rehb.f. at W. Photographs by APK (A, B, D) and Miguel Soto Arenas (C).

“*Vainilla silvestre*”, Preuss n. 1445 (holotype: B, destroyed).

Syn.: *Vanilla rebecca* Archila & Chiron, Richardiana, N.S. 3: 74. 2019, *syn. nov.*

TYPE: GUATEMALA. Alta Verapaz: municipio de Cobán, 800 m asl, col. Fredy Archila, flowered in Sept. 2010, *FA-sn* (holotype: BIGU, illustration!).

Hemiepiphytic herb, leafy vine, up to several meters high. *Stems* branching, terete, fleshy, up to 6 mm in diameter; internodes 4–7 cm long. *Aerial roots* velamentous, semicylindric, one per internode emerging opposite to the leaf, 1.5–4.0 cm long. *Leaves* subsessile; blade elliptic, acuminate, membranaceous to chartaceous, 9–21 × 4.5–7.5 cm. *Inflorescence* lateral, similar to the vegetative shoot, axillary, erect, racemose, up to 30 cm long, with successive flowers, 2–3-opened simultaneously; peduncle up to 3 cm long, rachis terete, internodes up to 5 cm long; *floral bracts* similar to the leaves in shape, sessile, lustrous, 3–12 × 1–6 cm, basal one, and apical ones shorter. *Ovary* (plus pedicel) terete, 4.5–6.0 cm long in open flowers, 3–4 mm in diameter, straight to curved at the apex. *Flowers* with ovary dark green, sepals and petals pale green to yellowish, lip white, apex lightly greenish and column white, with the stigma yellowish; petals and sepals more or less flat at anthesis, turning conspicuously reflexed with undulate margins, apically deeply recurved, sometimes become uncinatate, and lateral sepals dextrorse, rolled outwards. *Dorsal sepal* narrowly elliptic, obtuse to acute, 11-veined, 3.8–5.0 × 1.1–1.6 cm. *Lateral sepals* narrowly elliptic to oblanceolate, obtuse, 9-veined, 3.5–4.5 × 1.0–1.6 cm. *Petals* elliptic to narrowly lanceolate, acute to obtuse, 10-veined, 4.0–4.7 × 0.9–1.1 cm, abaxially sulcate along the midvein. *Lip* fused to the column base along the margins for ca. 5 mm, bell-shape, trilobed; when spread out 2.8–3.6 × 2.7–3.4 cm; the base unguiculate, the claw 4 × 4 mm; the blade cucullate, when spread out approximately pandurate in outline; the lateral lobes broad, rounded, incurved forming a gullet around the column, margins not overlapping; the midlobe spreading, subcuadrata, deeply emarginated, lightly recurved, margins undulate, 1.2–1.7 × 1.3–1.9 cm; the disc, the midlobe and part of the disc with a massive, ovate, fleshy, elevated, cushion-like callus, 16–20 mm × 5–8 mm; the disc basally with a sulcate callus attenuating towards the center of the blade, then rises

apically forming a massive, ovoid, fleshy, low cushion. *Column* subterete, arcuate, 2.2–3.0 × 0.4–0.5 cm, wider at the apex, ventrally canaliculate, apex obtuse. *Stigma* transversely oblong with thickened margins. *Rostellum* inconspicuous. *Anther* broadly cordiform, attached to the clinandrium, and forming together with it, a couple of lateral horn-shaped projections, 5 mm wide, clinandrium undulate. *Pollen* not forming a clear pollinarium but a sticky, tow soft, sticky granular mass. *Fruit* cylindric, attenuate at both ends, non-aromatic, 18.0 × 0.8 cm.

SPECIMENS STUDIED: MEXICO. Chiapas: Libertad Acacoyagua, 01 Jun. 1948, *E. Matuda 17912* (AMES!). Guerrero: System of Teotepec, near San Vicente, N.E. of Atoyac, 850 m, 10 Jan. 1933, *O. Nagel 1984* (AMES-51815!; AMES-41396!). Puebla: Vicinity of Puebla, Venant des sierras, 8 Déc. 197, *B.G. Arsène 1682* (NY!). Veracruz: Hacienda de Java, 18 May 1841, *Liebmman 295/296* (W-13537!; W-13538!). Mirador, Aug. 1841, *Liebmman 294b* (P-00128666!). Zacuapan, Jun. 1919, *C.A. Purpus 8481* (NY!; AMES!). Near Zacuapan, 12 Feb. 1932, 96°52' W, 19°12' N, ca. 900 m, *O. Nagel 2683* (AMES-41475!). Region of Zacuapan, near Rancho Viejo, climbing on tree trunks, ca. 700 m, 10 Jul 1935, *C.A. Purpus 4876* (AMES-51843!). Region of Zacuapan, 8 Oct. 1935, ca. 800 m, *C.A. Purpus 5045* (AMES-51838!). Hueytamalco, Campo experimental “Las Margaritas” (INIFAP), 23 Abr. 2008, *G. Ibarra Manríquez et al. 5600* (NY!). Misantla et Tlapacoya, Jun. 1866, *L. Hahn s.n.* (P-00128662!; P-00128665!). Veracruz, forêt humide du Chiguihuit, 16 Aug. 1866, *L. Hahn 271*. (P-00128663!; P-00128664!). BELIZE. Toledo District: Gracie Rock, Sibun River, 01 May 1935, *P.H. Gentle 1672* (AMES-42338!). Near river beyond Columbia, 31 Jan. 1947, *P.H. Gentle 6152* (NY-00984259!; NY-00984260!). Near river beyond Columbia, 31 Jan. 1947, *P.H. Gentle 6152* (F-1599367!). Toledo. In achual, near Ocotal Pine Ridge, 3 mi in trail from 7 mi, Punta Gorda-San Antonio Road, 20 Jan. 1950, *P.H. Gentle 6957* (F!). GUATEMALA. Baja Verapaz: Wald in Paujal, 1000 m, Apr. 197, *H. von Türckheim II 1764* (US-825825!). HONDURAS. Colon: Guarunta, Wispermini Camp, 75–100 ft., Mar. 1938, *C. & W. von Hagen 1352* (NY!). COSTA RICA. San José: Vicinity of El General, 1130 m, Feb. 1936, *A. Skutch 2592* (AMES-44231!; AMES-44232!; AMES-44233!; NY!; USF!; K!). Puntarenas: Osa, Fila Costeña, Río Piedras Blancas, cerca de la casa, Cerro Anguiciana, Fila Cruces, 8°49'02" N, 83°11'23" W, 900 m, 10 Dec. 1993, *R. Aguilar 2726* (FLAS!). Tarrazú, cuenca del río Naranjo y Paquita, cerca de San Isidro, sector NE, cabeceras Quebrada Gracias a Dios, 9°31'25" N, 84°02'30" W, 500 m (CR-260560!). Puntarenas: Garabito, Jacó, Tárcoles, ca. 7 km camino a Bijagual desde el cruce de la

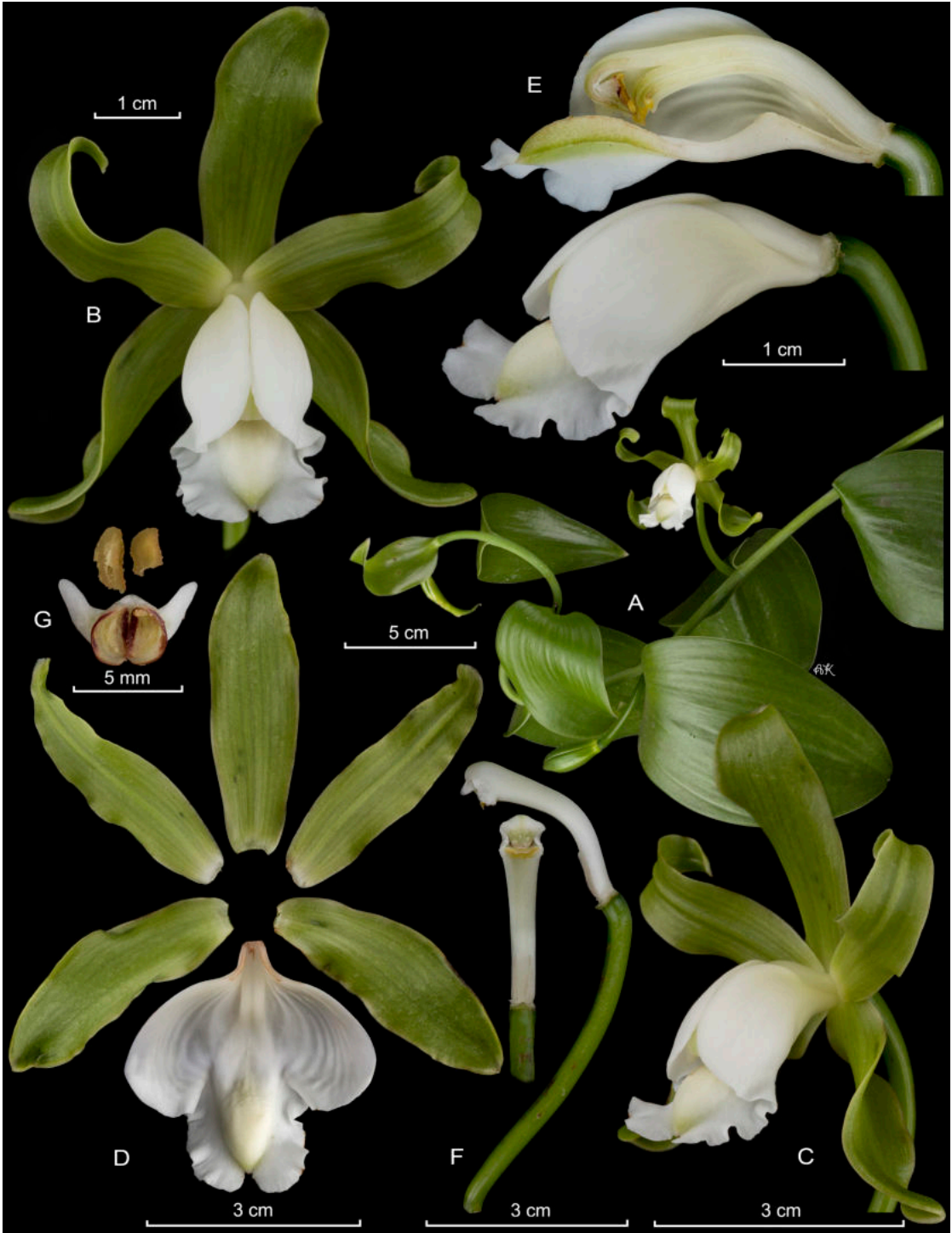


FIGURE 12. Lankester Composite Dissection Plate (LCDP) of *Vanilla inodora*. A. Inflorescence with foliaceous bracts. B. Flower, frontal view. C. Flower, side view. D. Dissected perianth. E. Lip and column lateral view. F. Column, ventral and lateral view. G. Anther cap and pollinia. By APK based on *Karremans 7713* (JBL-spirit).



FIGURE 13. Flowers of *Vanilla inodora*. **A.** Flower on the day of anthesis, with flattish perianth segments, A.P. Karremans 7708 (JBL-spirit). **B.** Flower a few days after anthesis, with conspicuously twisted perianth segments, A.P. Karremans 7701 (JBL-spirit). Photographs by APK.

costanera, 9°44'38.33" N, 84°34'49.70" W, 448 m, 4 Feb. 2017, A. Karremans 7713 & M. Contreras-Fernández (JBL-spirit!; Fig. 12). San José: Pérez Zeledón, Paramo, La Ese, al lado de la carretera, 9°25'15.4" N, 83°42'40.6" W, 1080 m, 1 Feb. 2017, A.P. Karremans 7708, M. Cedeño, & I. Chinchilla (JBL-spirit!; Fig. 13A). Coto Brus, San Vito, Fila Tigre, orillas de la calle, poco después del Río Cotón, 8°58'47" N, 82°56'38" W, 1160 m, 31 Ene. 2017, A.P. Karremans 7701, M. Cedeño, & I. Chinchilla (JBL-spirit!; Fig. 13B). PANAMA. Bocas del Toro: Epiphyte, flower pale green, Big Bight, Vicinity of Chiriquí Lagoon, 27 Oct. 1940, H. von Wedel 2880 (AMES!). Chiriquí: camino hacia la finca Landau, N.E. del campamento de Fortuna (sitio de prese) 1,100 m, 9 Jun. 1976, M.D. Correa A.N. Escobar & R. Mendoza 2153 (NY!).

DISTRIBUTION: Mexico, Belize, Guatemala, Nicaragua, Costa Rica and Panama (Fig. 14A).

EXTENT OF OCCURRENCE: 872,447.770 km².

The identity of *Vanilla inodora* has been historically somewhat obscure. The protologue is uninformative and none of the original materials collected by Schiede in Misantla, Mexico are known to bear flowers. Therefore the application of the

name has followed an exclusion process rather than direct determination. The large, broad leaves and distinct foliaceous bracts clearly indicate that *V. inodora* belongs to *Vanilla* subgen. *Vanilla*, known as the membranaceous group. Soto Arenas & Dressler (2010) argued that as only one species of the group was known to grow in Mexico, other possibilities had been excluded. Even though we here extend the range of *V. mexicana* Mill. well into northern Central America and can't rule out the possibility that it may be recorded in Mexico in the future, we agree in their interpretation of *V. inodora*. The notoriously large foliaceous bracts of *V. inodora* that are clearly visible in the type specimens are absent in *V. mexicana*, distinguishing the two species. It has been unclear where the type specimen of *V. inodora* is kept. We found original material with the annotation "Vanilla inodora Vaynilla de puerco Misantlensium" in Schiede's handwriting at W and BM, and two more specimens at W and LE bearing the annotation "Vanilla inodora Schiede". We select one of the specimens at W, bearing Schiede's annotation, as lectotype and the other three specimens as isolectotypes.

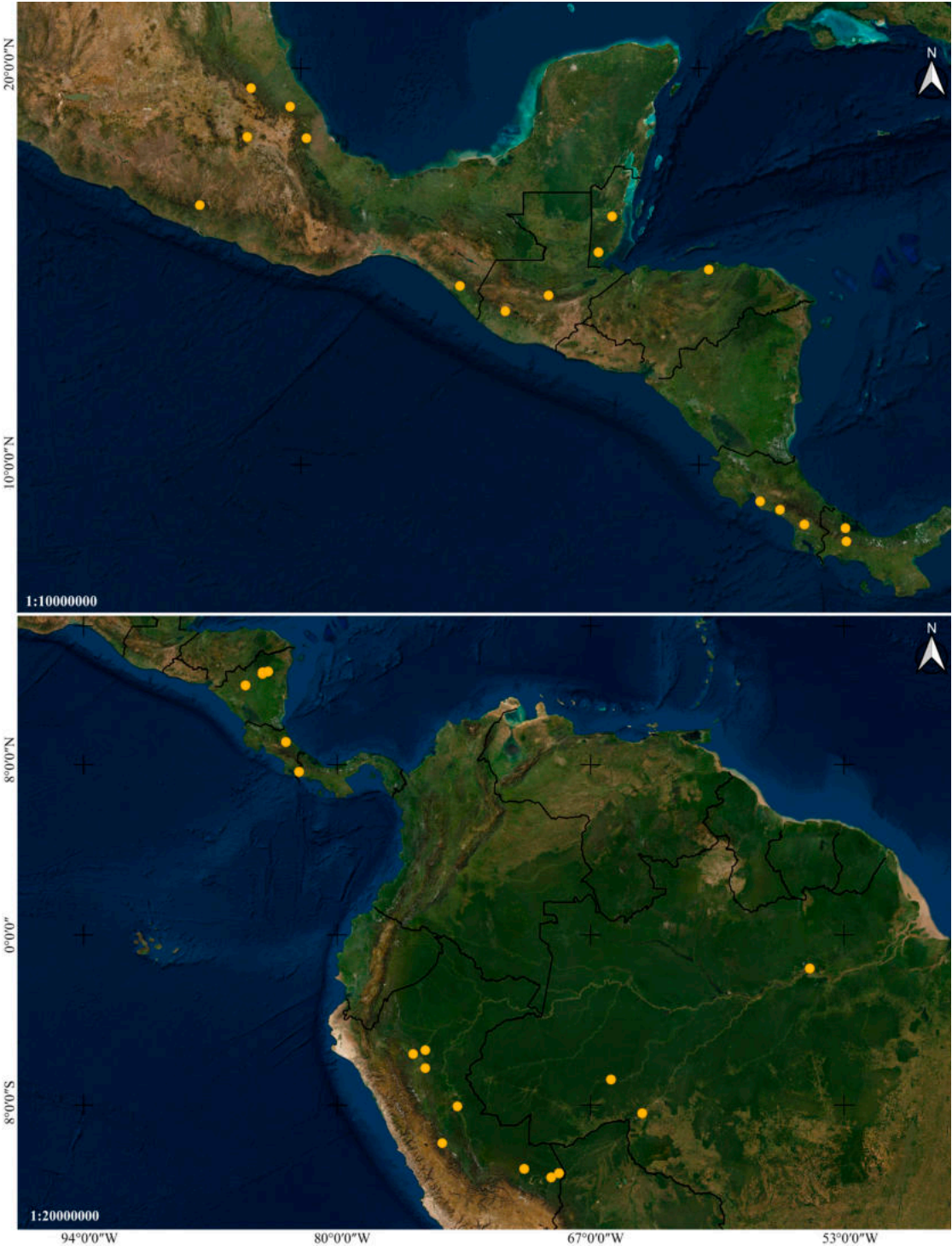


FIGURE 14. Distribution maps of *Vanilla* species based on studied specimens. **A.** *Vanilla inodora* Schiede. **B.** *Vanilla karenchristianae* Karremans & P.Lehm. Images by IC.

We agree with Soto Arenas & Dressler (2010) that the name *Vanilla pfaviana* is conspecific with *V. inodora*. The type specimen at W, the illustration of the type, and the original description by Reichenbach, who mentioned the twisted green tepals and the emarginate lip with a long thick cushion, fit *V. inodora* well. We also agree with the authors in placing *Vanilla preussii* under the synonymy of *V. inodora*. Even though the type specimen was lost, the foliaceous floral bracts, undulate sepals, and the apically emarginate lip with an elevated disc, as mentioned in the protologue, match *V. inodora*. The recently described *Vanilla rebecae* from Guatemala is here also considered as a synonym of *V. inodora*. It was said to differ from *V. inodora* by having larger flowers, flat sepals and petals, an elliptic dorsal sepal, lateral sepals strongly veined, petals with rounded apex, lip slightly trilobate, with an apically rounded midlobe, ovary somewhat curved geniculate, and a shorter fruit. However, the floral shape and dimensions cited for *V. rebecae* match the variation documented in *V. inodora*. Other allegedly distinguishing features such as the wider, flat sepals and petals and extension of the lip lobes are variable features even within a single flower of *V. inodora*; varying from wide, flat sepals and petals and non-extended lip lobes at the time of anthesis, to seemingly narrower, conspicuously twisted sepals and petals and extended lip lobes a few days later (Fig. 13).

4. *Vanilla karen-christianae* Karremans & P. Lehm., *Orchids* (West Palm Beach) 87: 305. 2018. Fig. 14B, 15–17.

TYPE: COSTA RICA. Puntarenas: Corredores. Canoas, 27 Sept. 2017, *A.P. Karremans et al.* 8087 (holotype: USJ!; isotypes: JBL-spirit!; CR!; Fig. 15, 17A).

Syn.: *Vanilla uncinata* Huber ex Hoehne, *Arch. Inst. Biol.* (São Paulo) 8: 269. 1937, *nom. nud.*, *syn. nov.*
TYPE: BRAZIL. Cultivado no Horto Botânico do Museu Paraense, fl. em Aug. 1906, vinda do Rio Purús, de onde foi trazida pelo Dr. A. Goeldi em data ignorada. *J. Huber s.n.* (MG-007302!, Fig. 16A).

Syn.: *Vanilla uncinata* Huber ex Hoehne, *Fl. Brasílica* 12(2): 209. 1945, *nom. nud.*, *syn. nov.*

SYNTYPES: BRAZIL. Cultivado no Horto Botânico do Museu Paraense, fl. em Aug. 1906, vinda do Rio Purús, de onde foi trazida pelo Dr. A. Goeldi em data ignorada. *J. Huber s.n.* (MG-007302!). Pará: Rio Branco de Óbidos, entre Santo Antonio et Salidão, mata de terra firme, 14 Sept. 1927, fl. Escandente; fl. verde, labello branco com pequeno signal amarellado. *W.A. Ducke s.n.* (RB-19446/00260182!; illustration in *Fl. Brasílica* 12(2): t. 2; Fig. 16B).

Hemiepiphytic, branching, leafy vine, up to several meters high. *Stems* dark to olive green, flexuous, subterete, with a conspicuous groove along the internodes, one per internode emerging laterally to the leaf, 6–7 mm in diameter; internodes, 6–12 cm long. *Aerial roots* semicylindric, ca. 2–3 mm in diameter. *Leaves* subsessile; blade obliquely ensiform, shortly acuminate, conspicuously recurved, sometimes becoming uncinata, margins slightly revolute, coriaceous, 9–23 × 1.1–2.5 cm. *Inflorescence* lateral, simple, axillary, erect, racemose, producing many flowers, more than 25 successive flowers per raceme, 1-opened simultaneously; peduncle abbreviated, fleshy, subterete, ca. 1 cm long; rachis up to 5 cm long. *Floral bracts* sessile, small, ovate, obtuse, concave, fleshy, ca. 4–15 mm long, with an external nectary close to the base, aligned with the midvein. *Flowers* ephemeral, segments not spreading, basal half of the ovary white, apical half green, tepals light green, shiny, lip white with the side veins and appendages dull yellow, penicillate callus white, column white; fragrance weakly citric. *Ovary* subterete, smooth, arcuate, 27–43 × 3–4 mm; with three external, apical nectaries, aligned with the mid-vein of each sepal. *Dorsal sepal* oblanceolate, acute, somewhat concave, fleshy, ca. 7-veined; 39–54 × 9–13 mm. *Lateral sepals* obliquely oblanceolate, acute, fleshy, ca. 12 veined, 37–54 × 10–14 mm. *Petals* obliquely linear to lanceolate, acute, somewhat arcuate, with a conspicuous, elevated dorsal keel; ca. 7-veined, 37–52 × 5.5–10 mm. *Lip* fused to the column along the margins for ca. 2.5 cm, tubular, trumpet-shaped, concave, inflated near the middle, becoming deeply saccate, shallowly trilobed; when spread out 39–48 × 20–35 mm; unguiculate, the claw papillose, ca.

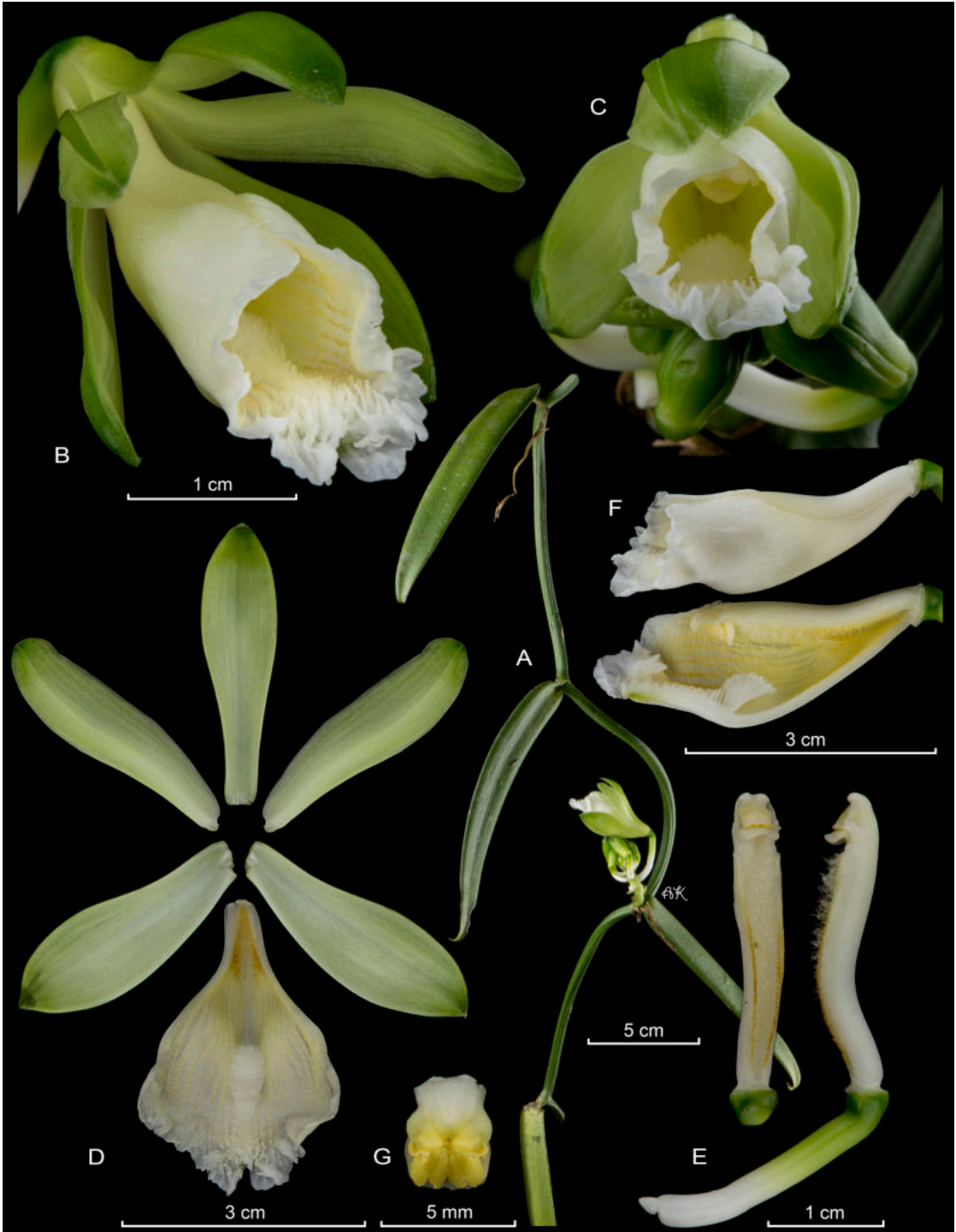


FIGURE 15. Lankester Composite Dissection Plate (LCDP) of *Vanilla karen-christianae* Karremans & P.Lehm. **A.** habit. **B.** inflorescence. **C.** Flower. **D.** Dissected perianth. **E.** Column and lip lateral view. **F.** Column in ventral and lateral view. **G.** Anther cap and pollinia. Photographs by APK based on Karremans 8087 (JBL, CR, USJ).

1 cm long; the blade approximately obovate in outline, ca. 20-veined, the veins thickened forming low, papillose to verruculose keels, taller towards the apex; the lateral lobes obtuse, incurvated, margins entire to lightly crenate; the midlobe bilobed to emarginate, with a recurved tip, margins irregularly crenate, undulate; *penicillate callus* 2.5–3.0 cm from the base, 6–7 × 3 mm; made up of reclined, flabellate, densely lacerate to laciniate scales; extending for about 15 mm to the apex, ca. 3.5 mm wide, gradually lowering towards the apex. *Column* suterete, obfalciform, 25–39 × 4–5 mm, from similar width along, ventrally densely covered by trichomes below stigma, apex with three wings. *Stigma* trilobed, lateral lobes erect, small, 2 × 1 mm. *Rostellum* a large, transversely oblong, convex. *Anther* basally hinged to the column, movable, subcuadrate, 4–6 × 3–4 mm. *Pollen* not forming a clear pollinarium but a sticky, granular mass. *Fruits* 6.7–12 cm, cylindrical, fragrant.

SPECIMENS STUDIED: NICARAGUA. Matagalpa: La Dalia, 13.058 N, 85.72 W, *G. Laube s.n.* (JBL-photograph!; Fig. 17D). Zelaya: Cerro Waylawas, 10 km south of Siuna; 250 m, 5 Jun. 1978, *D. Neill 4219* (MO!). Cerro Kana Coperna, 30 km east of Siuna, 250 m, 17 Jun. 1978, *D. Neill 457* (MO!). Municipio de Siuna, Río Matis. Elev. menos de 100 m, 16 Set. 1982, *F. Ortiz 172* (MO!). Cerro Waylawas, ca. 13°39' N, 84°48–49' W, 100–268 m; sheer dog tooth limestone peak and plain on E side of peak, 16 Mar. 1978, *W.D. Stevens 7385* (MO!; AMO!). COSTA RICA. Puntarenas: Corredores. Canoas, floreció en cultivo de P. Lehmann, 16 Abr. 2017, *A.P. Karremans 8123* (JBL-spirit!). Limón: Siquirres, Germania, entre La Herediana y La Alegría, cercanías del río Vueltas, Finca Las Brisas, 10°07'48.34"N 83°36'15.86" W, 245 m, Ernesto Carman legit, floreció en cultivo el 25 de Oct. 2020, *A.P. Karremans 8356* (JBL-spirit!, Figs. 17C, 18). PERU. Ucayali: Prov. Coronel Portillo, Dtto. Iparia, Aguajal comunidad Galilea, Reserva Comunal El Sira (zona de amortiguamiento), -9.13197 -74.4965, 175 m, 15 Mar. 2015, *J. Janovec, J. Ushinawa, H. Behar 4009, 4006* (MOL!). Madre de Dios: Prov. Tambopata, carretera Cusco km 37.5 comunidad mercedes, aguajal mercedes, -12.695 -69.4693, 200–250 m, 7 Sep. 2007, *J. Householder 14, A. Balarezo & J. Huinga* (USM!, Fig. 17B); Rio alto madre de dios, boca manu, 2 km north of local school, aguajal boca manu, -12.2566 -70.898, 280–320 m, *J. Householder 941, A. Balarezo & J. Huinga* (USM!). Junin: prov. Chanchamayo, Fundo la Génova, 11° 6'7.17"S 75°20'59.73"O, 1100 m, 29 Oct. 2016, *A. Damián & Estudiantes Botánica UCSUR*

905 (USM!); Prov. Chanchamayo, La Merced, cerca al Puente Paucartambo, Jun. 2018, *D. Aliaga s.n.* (USM!). San Martin: Prov. Picota, Dtto. Picota, bosque seco, 200 m Jul. 2018, *A. Damián & M. Leon 906* (USM!); Prov. San Martin, sin localidad, 2 Oct. 1973, 400 m, *R. Ferreyra, Rauh & Bismarck 18265* (USM!). BRAZIL. Amazonas: vinda do Río Purús, de onde foi trazida pelo Dr. André Goeldi [3 May 1904], cultivada no Horto Botanico do Museu Paraense (Belém, Pará), fl. Ago. 1906, *J. Huber s.n.* (MG-007302!). Rondônia: Cachoeira de Jirau, floresta estacional semidecidual, área de influencia direta (Iago), 85 m, 22 Mar. 2010, *G. Pereira-Silva 15128 et al.* (CEN-00078538!).

OTHER RECORDS: NICARAGUA. The photographs labeled *Vanilla inodora* in van den Berghe & van den Berghe (2008), are this species.

DISTRIBUTION: Broadly distributed in Central and South America, at elevations between 85 and 320 m. Confirmed to occur in Nicaragua, Costa Rica, Peru and Brazil (Fig. 14B).

EXTENT OF OCCURRENCE: 4,443,132.187 km².

The very narrow, uncinat leaves and presence of a conspicuous tuft of appendages on the lip distinguish *Vanilla karen-christianae* immediately. *Vanilla odorata* shares such narrow leaves; however, that species has a yellowish flower, the lip is fimbriate and it lacks the appendages. *Vanilla helleri* A.D.Hawkes has similar appendages on the lip, but has a broader leaf and white flowers with a bright yellow lip. *Vanilla insignis* Ames also share this particular lip feature but that species has a much larger, spreading flower and a lacerate lip margin. The Brazilian *V. capixaba* Fraga & D.R.Couto and *V. ribeiroi* Hoehne share the narrow leaves and white lip with a dense tuft of appendages, and are likely to be close relatives. The former can be easily distinguished by the non-recurved apex of the leaf, the broader, acute sepals and petals, the transversally oblong midlobe of the lip and the larger appendages disposed in distinct rows (Fraga *et al.* 2017). The type specimen and illustration of the latter show non-oblique lanceolate leaves, an oblong dorsal sepal, and especially a smaller, narrower lip with a prominently long-fimbriate apex, quite distinct from *V. karen-christianae*.

When *Vanilla karen-christianae* was described

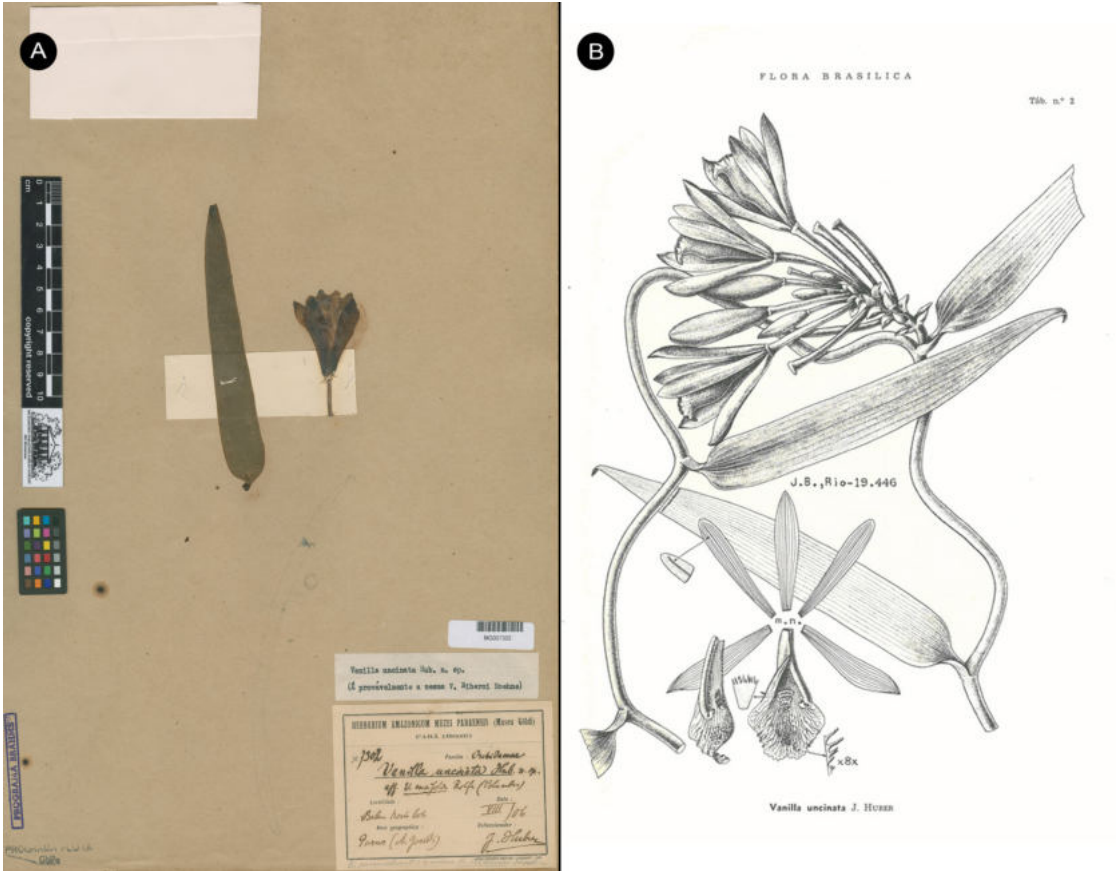


FIGURE 16. *Vanilla karen-christianae* as *Vanilla uncinata* Huber ex Hoehne, *nom. nud.* A. One of the materials intended as type, J. Huber s.n. (MG-007302) © copyright of Refflora, Brazil. B. Illustration based on Ducke s.n. (RB-19446/00260182) published in Fl. Brasílica 12(2): t. 2. 1945.

no other specimens of the species were found either in Costa Rica or elsewhere. Soon after description, one of the authors of the present manuscript (AD) realized that Brazilian specimens identified as *Vanilla uncinata* Huber ex Hoehne, including the type, were conspecific with *V. karen-christianae* and not *V. odorata* C.Presl as previously believed. Hoehne cites the name *V. uncinata* twice; once in 1937 and then in 1945, both times ascribing the authority to Huber. However, the name *V. uncinata* was never formally published by Huber, nor was it validly published by Hoehne. In the first case no description is provided and the author suggests it is conspecific with *V. ribeiroi* Hoehne and therefore invalid, in the second the author considers it a good species and gives an extensive description. In fact it would have fulfilled the requirements for formal publication were it not

that the protologue is in Portuguese and therefore does not constitute valid publication. A Latin description became mandatory from 1935 onwards (article 39.1 in Turland *et al.* 2018). Therefore, even though the two names refer to the same species, *V. karen-christianae* is retained.

In addition to the Brazilian specimens, the species has also been found in Peru where it had been mistakenly known under the name *V. ribeiroi* (Damián & Janovec 2018). There it inhabits the Amazonian wetlands dominated by a palm *Mauritia flexuosa* L.f. (locally known as “aguajales”), at 200–250 m in elevation in the southeast part of the country. During the preparation of this manuscript, more Costa Rican and Nicaraguan specimens of *V. karen-christianae* were also located. Proving that this species, initially believed to be narrowly



FIGURE 17. *Vanilla karen-christianae* flowering specimens from different localities across its distribution. **A.** Costa Rica, from the specimen that served as type *Karremans 8087*. **B.** Peru, Madre de Dios, *Householder et al. 14*. **C.** Costa Rica, Siquirres, *in situ*, *Karremans 8356*. **D.** Nicaragua, Matagalpa, *in situ*, *Laube s.n.* Photographs by the collectors kept at JBL.

distributed, actually has a very broad distribution from Nicaragua to Peru and Brazil, and is likely to show up in neighboring countries in the future, it may not be as highly threatened species as initially

believed (Karremans & Lehmann 2018). However, the species is apparently uncommon across its broad distribution and may still be a conservation priority at a local scale.

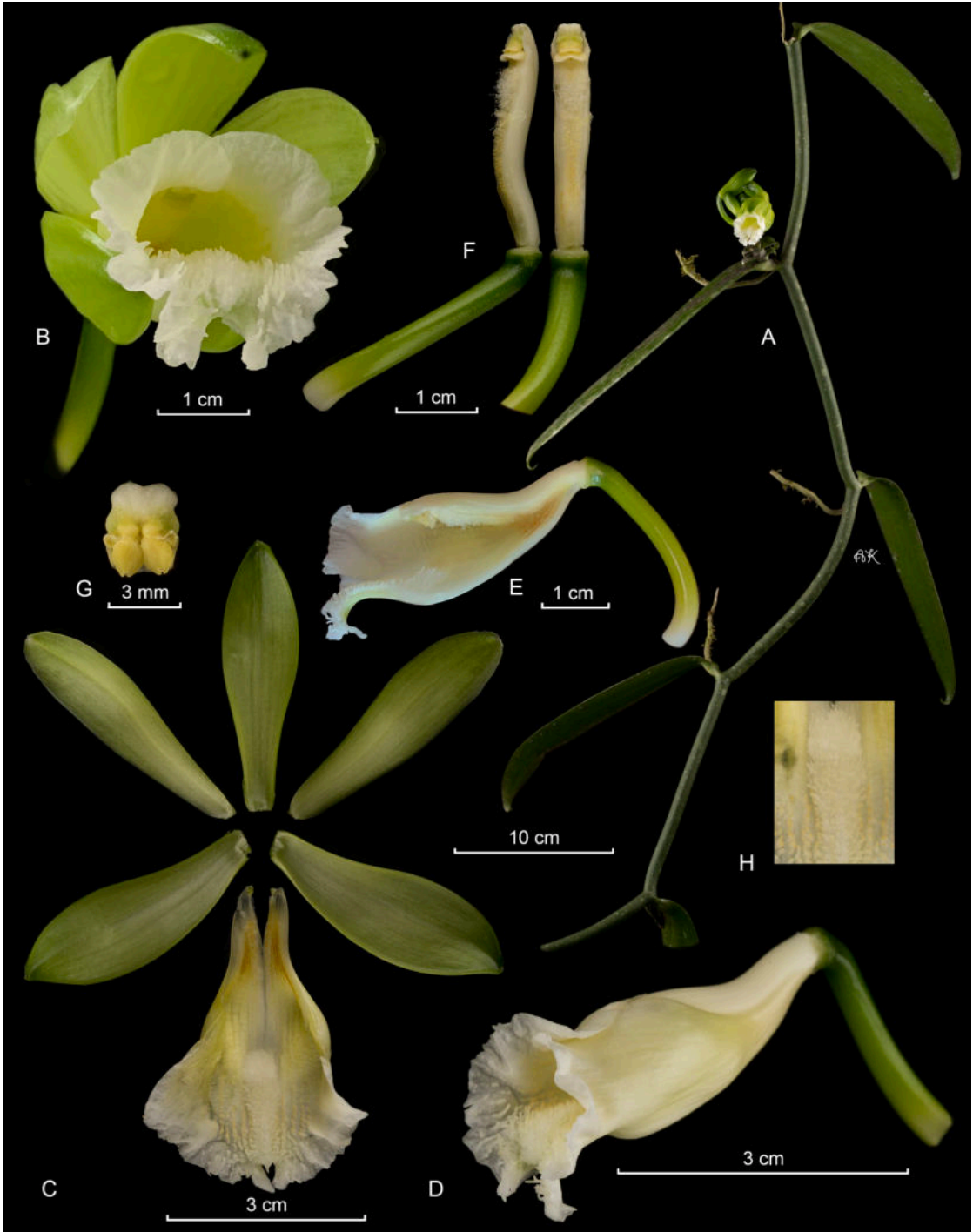


FIGURE 18. Lankester Composite Dissection Plate (LCDP) of *Vanilla karen-christianae* Karremans & P.Lehm. A. Habit. B. Flower. C. Dissected perianth. D. Column and lip lateral view. E. Column and lip in lateral view dissected. F. Column in ventral and lateral view. G. Anther cap and pollinia. H. Callus of the lip. Photographs by APK based on Karremans 8356 (JBL-spirit).

5. *Vanilla marowynensis* Pulle, Enum. Vasc. Pl. Surinam: 118. 1906. Fig. 19–23, 24A.

TYPE: [SURINAME: Marowijne]: Upper Marowyne River, near Poeloegoedoe, fl. July, *Versteeg* 623 (holotype U-L, not found; **lectotype designated here**: illustration of type reproduced by Pulle (1906) in Enum. Vasc. Pl. Surinam t. 4; Fig. 19).

Syn.: *Vanilla cristagalli* Hoehne, Arq. Bot. Estado São Paulo, n.s., f.m., 1: 125. 1944, **syn. nov.**

TYPE: BRAZIL. Amazonas: S. Paulo de Olivença. 23 Oct. 1931, *A. Ducke* s.n. (holotype: RB-14512/00542720!, Fig. 20).

Syn.: *Vanilla cristato-callosa* Hoehne, Arq. Bot. Estado São Paulo, n.s., f.m., 1: 126. 1944, **syn. nov.**

TYPE: BRAZIL. Amazonas: Manaus. 25 Oct. 1935, *A. Ducke* s.n. (holotype: RB-37468/00542721!, Fig. 21).

Syn.: *Vanilla aspericaulis* Sambin & Chiron, Richardiana 15: 311. 2015, **syn. nov.**

TYPE: FRENCH GUIANA. Sud-est du département, berge de l'Approuague, saut grand Machikou. La plante a été observée et collectée par Vincent Pelletier en décembre 2013 dans le cadre d'une mission de prospection puis observée en fleur au Jardin botanique de Guyane le 25 Jun. 2015, *V 066 VP00902* (holotype, CAY; illustration!). Cutting cultivated by P. Silland (JBL-photo!, clonotype, Fig. 22A, B).

Syn.: *Vanilla denshikoiria* Flanagan & Ospina-Calderón, Phytotaxa 364: 253. 2018, **syn. nov.**

TYPE: COLOMBIA. Guainía. Inirida, Resguardo Indígena Remanso-Chorrobocón, medium-dense riparian forest on alluvial ground c. 30 m from the Inirida River, Elev. 100 m, 16 Apr. 2017, *N.S.Flanagan, M.Mendoza, I.T.García Agapito, H.A.Mateus NSF138* (holotype: CUV; illustration!)

Hemiepiphytic, branching, leafy *vine*, up to several meters high. *Stems* dark to olive green with minute whitish spots, rugulose, flexuous, cylindrical, 4–13 mm in diameter; internodes, 3.8–15 cm long. Aerial *roots* semicylindric. *Leaves* petiolate, generally equal or subequal to the internode; blade obovate to oblanceolate, widest above the middle, abruptly

cuspidate to shortly acuminate, coriaceous; 4.5–16.0 × 2.2–6.0 cm, including the up to 2 cm long, canaliculate petiole. *Inflorescence* lateral, simple, axillary, erect, racemose, producing many flowers, more than 16 successive flowers per raceme, typically with 2-opened simultaneously; peduncle abbreviated, fleshy, subterete; rachis thick, up to 4 cm long; conspicuously shorter than the leaf. *Floral bracts* sessile, small, triangular to ovate, obtuse, concave, fleshy, 5–10 mm long. *Flowers* large, ephemeral, segments not spreading widely, ovary white, apically green, tepals greenish-cream to yellowish-orange, shiny, lip white with the apex and appendages dull yellow to orange, penicillate callus white, column white; fragrance not registered. *Ovary* subterete, arcuate, 35–62 mm. *Dorsal sepal* elliptic, oblong to narrowly oblanceolate, acute, somewhat concave, fleshy, margin thickened, especially at the apex, 52–67 × 10–19 mm. *Lateral sepals* obliquely elliptic, oblong to narrowly oblanceolate, acute, somewhat concave and falcate, fleshy, margin thickened, especially at the apex, 46–58 × 12–22 mm. *Petals* obliquely elliptic to narrowly oblanceolate, acute, somewhat concave and falcate, with a conspicuous, elevated dorsal, acute keel, 50–63 × 12–17 mm. *Lip* fused to the column along the margins for ca. 2.2 cm, tubular, trumpet-shaped, concave, apically trilobed, lobes apically incurved towards the appendages; when spread out 41–56 × 28–40 mm; shortly unguiculate; the blade approximately obovate in outline, ca. 20-veined; the lateral lobes obtuse, margins irregular, with a few large teeth towards the midlobe; the midlobe bilobed to emarginate, with a recurved tip, margins irregularly undulate to crenate; *penicillate callus* 2.4 cm from the base, 4 × 4 mm; made up of reclined, flabellate, densely lacerate to laciniate scales; extending for about 2.0 cm to the apex of the lip, ca. 4.5 mm wide, gradually transforming into thick, finger-like, tuberculous, orange appendages. *Column* subterete, straight, 30–40 × 3–4 mm, from similar width along, ventrally densely covered by trichomes below stigma, apex with three wings. *Stigma* trilobed, lateral lobes erect, small, 2 × 1 mm. *Rostellum* large, transversely oblong, convex. *Anther* basally hinged to the column, movable, subcuadrate, 3–4 × 3 mm. *Pollen* not forming a clear pollinarium but a sticky, granular mass. *Fruits* apparently unknown, likely fragrant.

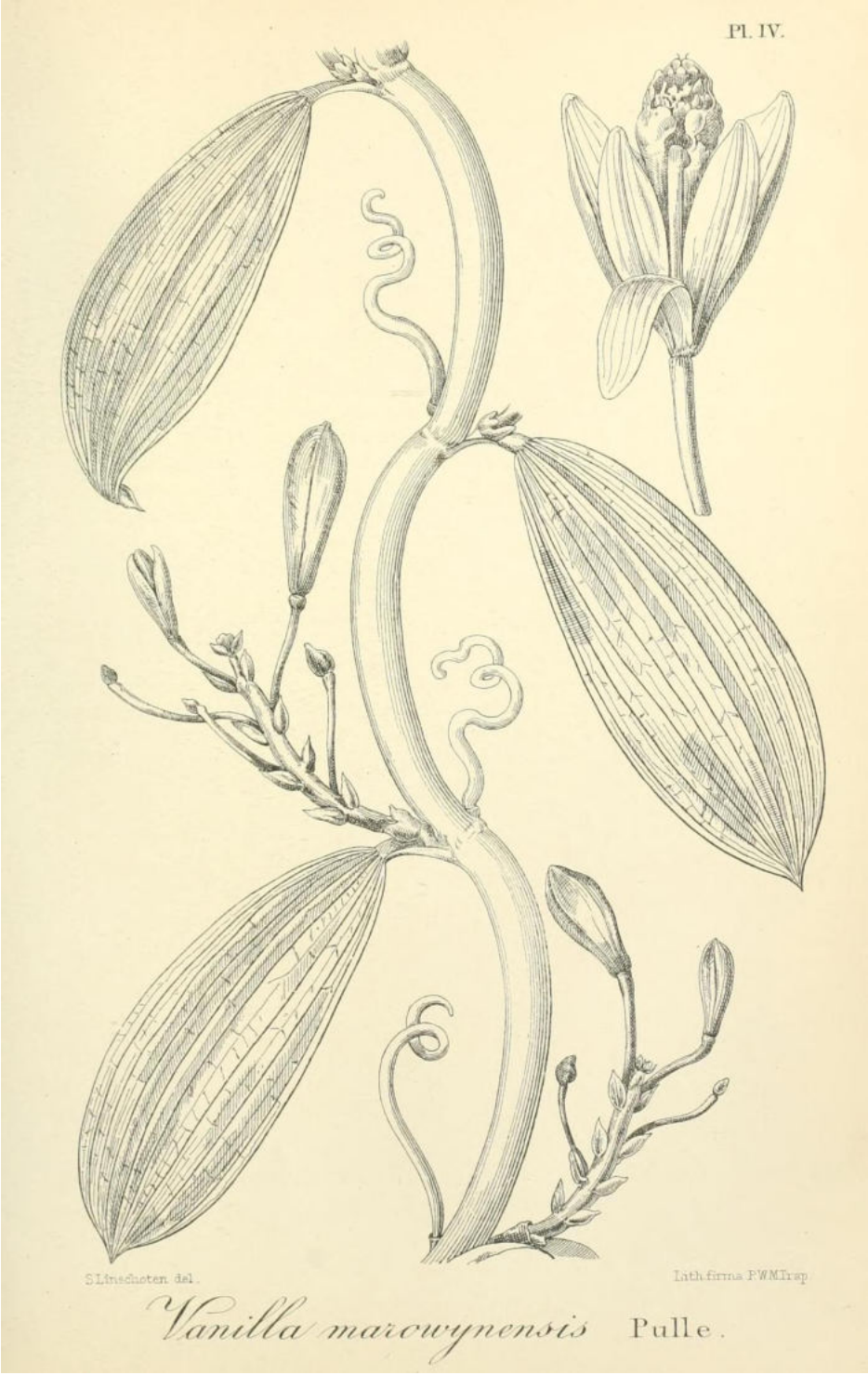


FIGURE 19. *Vanilla marowynensis* illustration based on *Versteeg* 623, reproduced by *Pulle* in *Enum. Vasc. Pl. Surinam* (1906), selected here as lectotype.



FIGURE 20. *Vanilla marowynensis*. **A**, as the holotype of *V. cristagalli* Hoehne, RB-14512/00542720 © copyright of Refflora, Brazil. **B**, Illustration of type published in *Fl. Brasilica* 12(2): t. 6. 1945.

SPECIMENS STUDIED: COLOMBIA. Buenaventura, en el puerto, May 1853, J.J. Triana 1614/1 (COL-000363316!). SURINAME. In montibus, qui dicuntur Nassau Border of Marowijne R., above base camp, 14 Feb. 1949, *J. Lanjouw & J. C. Lindeman* 2074 (AMES-02158566!). BRAZIL. Mato Grosso: Itaúba, Resgate de Flora da UHE Colider, 268 m, 17 May 2017, *A.S. Bezerra, L. Souza Neto, J.E.L. Lessa s.n.* (MBM-417193!). Mato Grosso: Itaúba, Resgate de Flora da UHE Colider, fl., 24 Oct. 2016, *M.E. Engels* 4873 (MBM-417192!). Mato Grosso: Itaúba, Resgate de Flora da UHE Colider, Lote I de supressão (Ilha), 05 Dec. 2015, fl., *M.E. Engels* 3913 (HERBAM, MBM, TANG, JBL-photo!, Fig. 23). BOLIVIA. Santa Cruz de la Sierra: Parque Nacional Amboro, backroads from Buena Vista, 17°29'33.1"S 63°39'33.2"W, 340 m, *E. Brylle & M. Nathanson s.n.* (JBL, digital photograph!; Fig. 22C).

OTHER SPECIMENS: COLOMBIA. Guainía. Inírida, Resguardo Indígena Remanso-Chorrobocón, medium-dense riparian forest on granite outcrop. Elev. 265 m, 15

Apr. 2017, *N.S. Flanagan, M. Mendoza, I.T. García Agapito, H.A. Mateus NSF90* (CUVC).

DISTRIBUTION: Broadly distributed in South America, yet apparently rare. Confirmed to occur in Colombia, Suriname, French Guiana, Brazil and Bolivia (Fig. 24A).

EXTENT OF OCCURRENCE: 4,091,165.326 km².

The name *Vanilla marowynensis* has remained poorly understood and mostly unused. It was described on the basis of a collection by G.M. Versteeg close to Poelogoedoe on the Marowijne river (Fig. 22D) during the Dutch Tapanahoni expedition to the "unknown interior" of Suriname (Fig. 22E). Versteeg made the medical, botanical and zoological collections for the expedition and most of the collections were kept at Utrecht herbarium (now L). We were not able to locate the type, *Versteeg* 623, there or elsewhere, but the



FIGURE 21. *Vanilla marowynensis* as *V. cristato-callosa* Hoehne. **A.** Holotype, RB-37468/00542721 © copyright of Refflora, Brazil. **B.** Illustration of type published in Fl. Brasilica 12(2): t. 7. 1945.

excellent illustration of the type reproduced by Pulle (1906) in Enum. Vasc. Pl. Surinam t. 4 (Fig. 19) has here been selected as lectotype.

Soto Arenas & Cribb (2010) placed *V. marowynensis* under *V. appendiculata* Rolfe and indicated that the illustration is based on an immature bud (this is not stated in the protologue). Nevertheless, several diagnostic features from the description and illustration separate the two species. According to Pulle *V. marowynensis* has petiolate, coriaceous leaves, a short, thick, axillary, multi-flowered inflorescence, bearing large flowers, oblong petals with a conspicuous dorsal keel, the lip subequal to the sepals, trilobate, with an undulate margin and dense apical appendages. From the illustration it can also be inferred clearly that the leaves are wider above the middle and then abruptly apiculate, that the tepals are thick, especially apically, non-spreading, and the lip has an irregular and incurved

margin and thick, and tuberculous appendages on the mid-lobe.

Those features are not found in *V. appendiculata*, which has a terminal, few-flowered inflorescence, and very long, narrow floral segments, but they are found in two species described simultaneously from Brazil, *Vanilla cristagallii* Hoehne and *V. cristato-callosa* Hoehne. The two species were since their description suggested to be very closely related to each other and *V. marowynensis*, from which they were said to differ in certain details of the lip that could be better observed in the illustrations than put into words (Hoehne 1944). The dissected perianth in the illustration of *V. cristagalli* suggests a more regular lip margin and a very reduced callus with a much scarcer presence of appendages on the midlobe of the lip, but the side view of the flowers seems to contradict this interpretation and the appendages are in fact so prominent that they can be

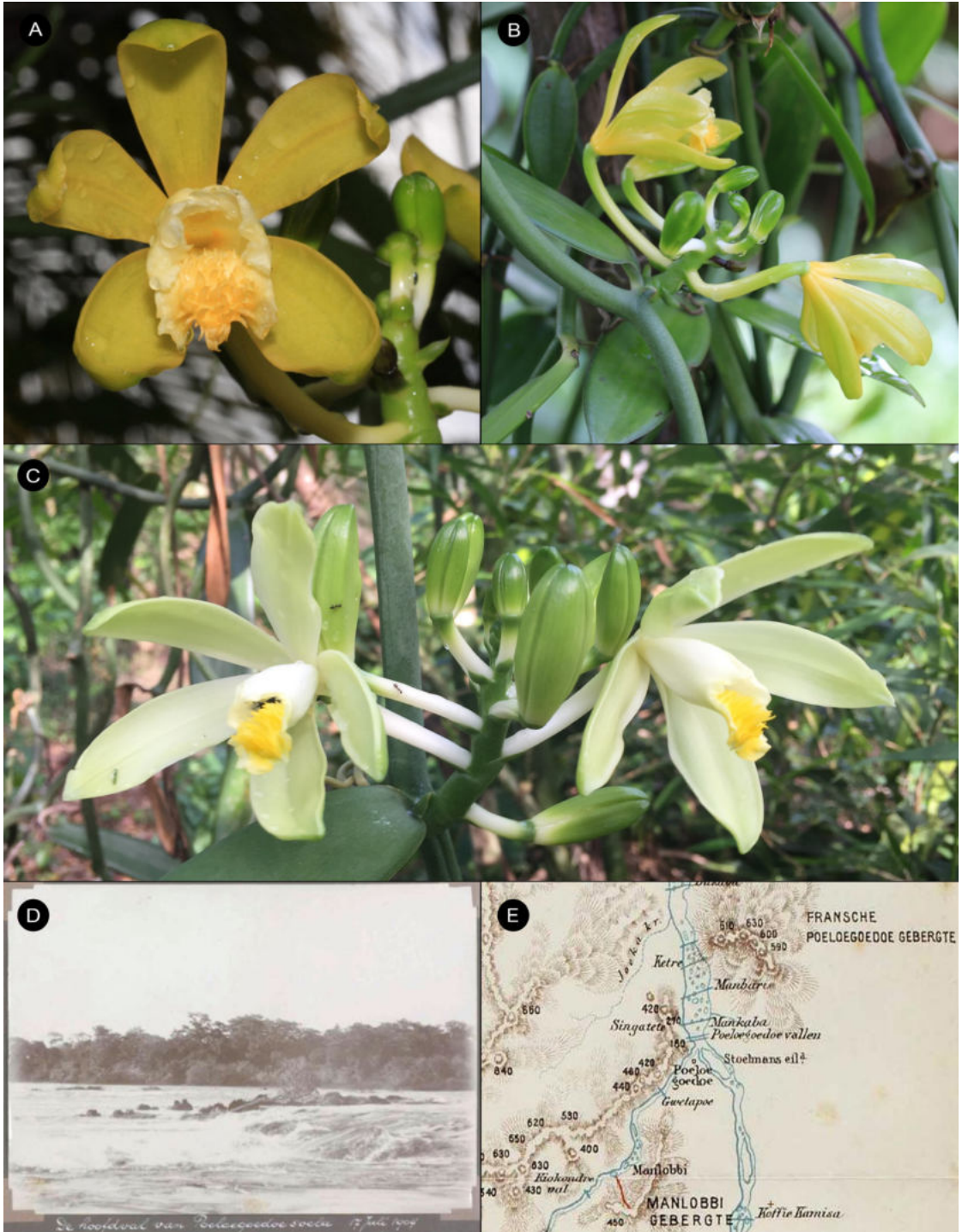


FIGURE 22. *Vanilla marowynensis*. **A–B.** Clonotype of *V. aspericaulis* Sambin & Chiron cultivated by P. Silland. **C.** Bolivia, Amboro National Park, *in situ*, Brylle & Nathanson *s.n.* **D.** Poeloegeodoe on the Marowijne River, type locality of *V. marowynensis*. **E.** Map of Dutch Tapanahoni expedition to the Marowijne river in the interior of Suriname.

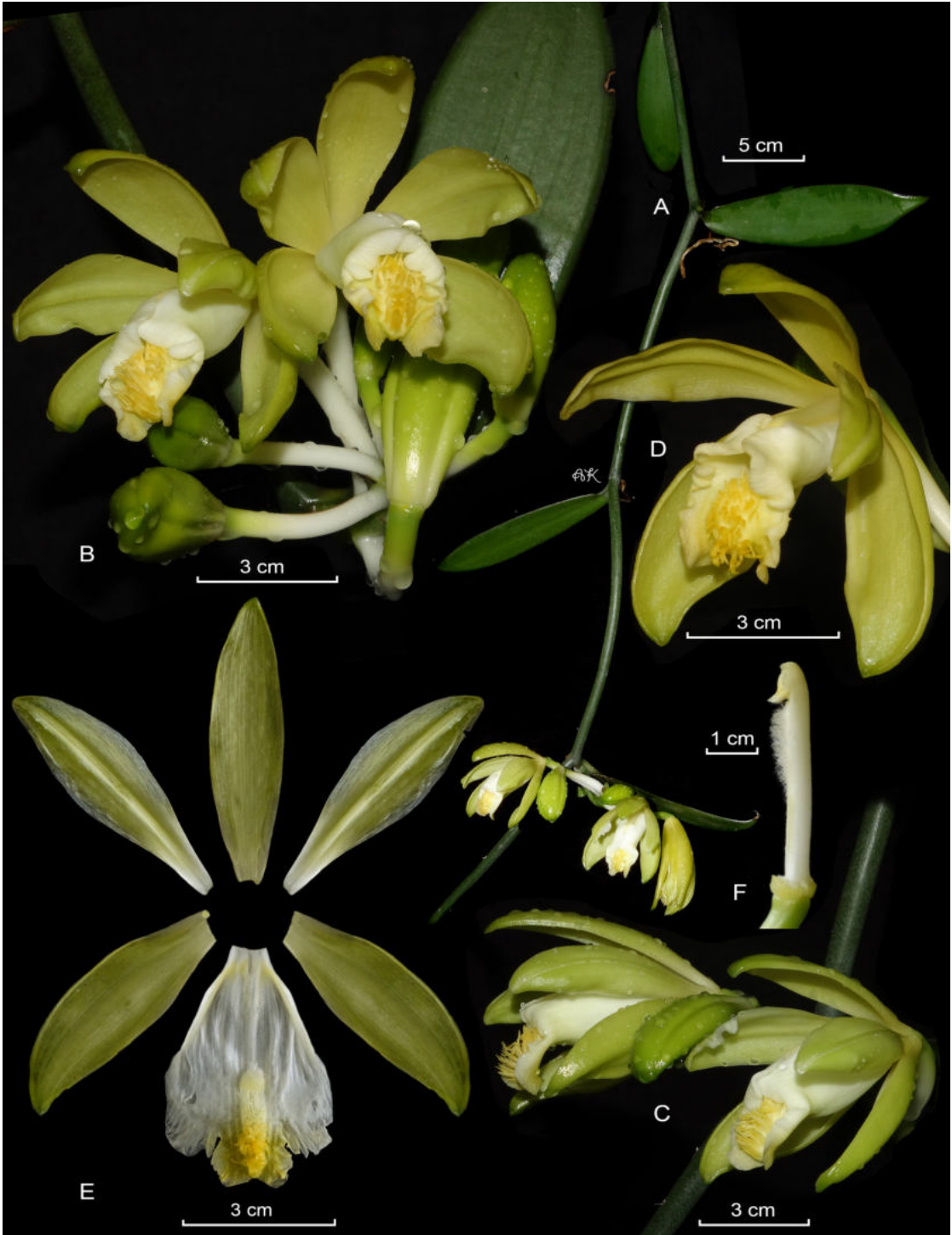


FIGURE 23. Lankester Composite Dissection Plate (LCDP) of *Vanilla marowynensis* Pulle. **A.** Habit. **B.** Inflorescence. **C.** Inflorescence side view. **D.** Flower. **E.** Dissected perianth. **F.** Column lateral view. By M.E. Engels & APK based on M.E. Engels 3913 (HERBAM, MBM, TANG).

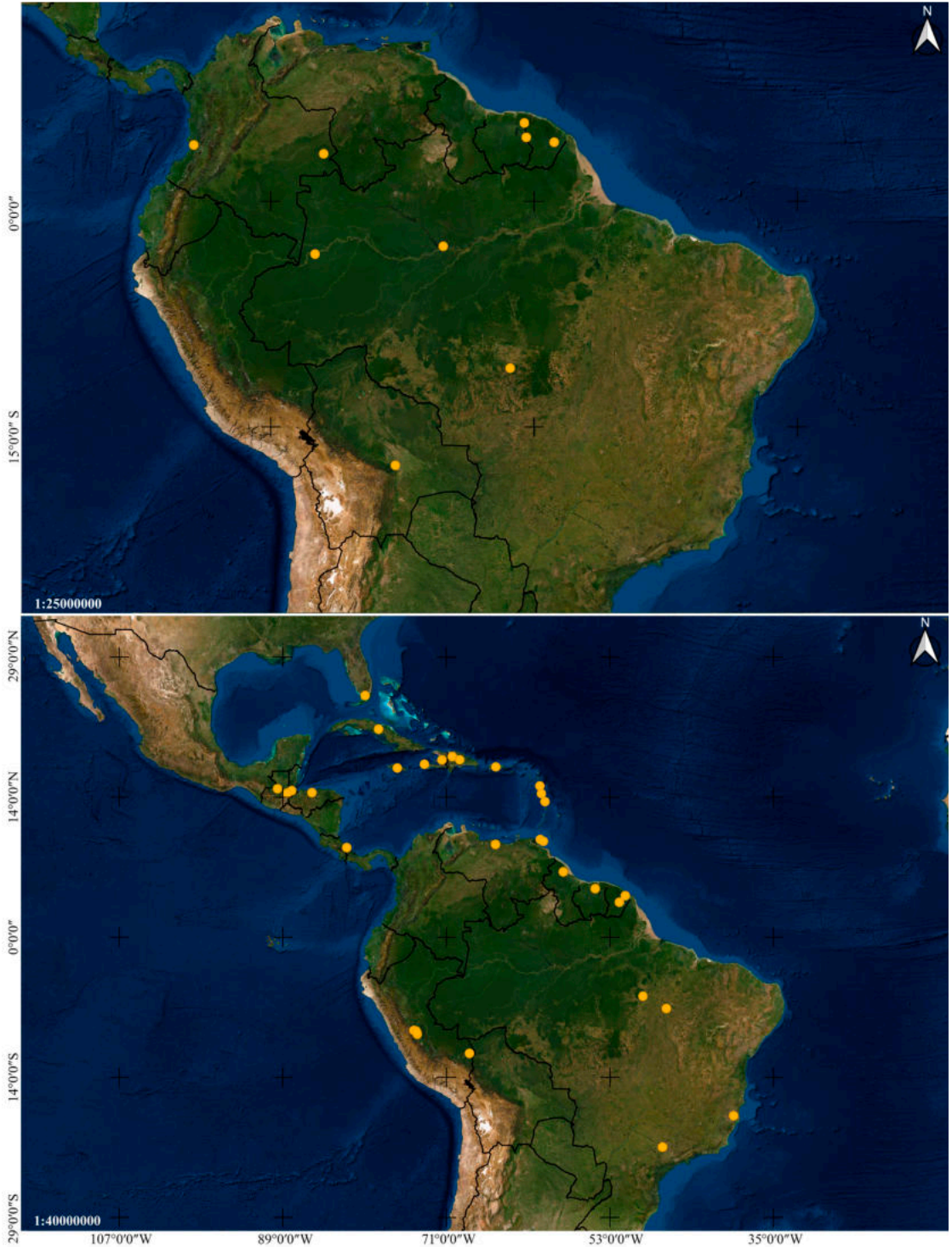


FIGURE 24. Distribution maps of *Vanilla* species based on studied specimens. **A.** *Vanilla marowynensis* Pulle. **B.** *Vanilla mexicana* Mill. Images by IC.

clearly seen on the dried flowers of the type specimen (Fig. 20). The illustration of *V. cristato-callosa* is virtually identical to the plate based on *Engels 3913* (Fig. 23), and although some of the lip features are not easily visible in the type illustration of *V. marowynensis*, they are also quite consistent.

Vanilla aspericaulis described from the French Guiana is said to differ from *V. cristagalli* in the shorter and broader leaves that are as long as the internodes, the longer ovary, wider sepals, petals and lip and the sub-flabellate lip shape (Sambin & Chiron 2015). Nevertheless, the original description, illustration and photographs are highly consistent with the type illustration and description of both *V. marowynensis* and *V. cristato-callosa*. A photo of the clonotype reproduce here (Fig. 22A, B) proves indistinguishable from the materials of those taxa. Similarly, the recently described *V. denshikoira* was said to differ from close relatives mainly in its conspicuously trilobed lip, “external longitudinal canal running from the base to the apex of the reflexed midlobe, and the papillae and elongated trichomes on the ventral lip surface covering the tuberculous keel” (Flanagan *et al.* 2018). Unfortunately, although the presence of an external longitudinal canal is seldomly noted or illustrated it is a common feature of many *Vanilla* species, while the remaining characteristics are typical of *V. marowynensis*, and its synonyms.

Vanilla marowynensis can be recognized by the glaucous, verruculose stems, the internodes similar in length to the coriaceous leaves, which are petiolate, generally broader above the middle and distinctly apiculate. The multi-flowered, successive inflorescence has up to two flowers open at once, it is borne axillarily from a short, thick peduncle, the large, ephemeral flowers, do not open widely, and have thick, greenish-cream to yellowish-orange tepals with a white lip bearing dull yellow to orange tuberculate appendages. The lip is three-lobed with the apex of the lobes are conspicuously irregular and incurved, with the margin undulate-crenulate, with a few large teeth, and a dense set of finger-like, tuberculate apical appendages. This distinctive species seems to be rare across its relatively broad distribution, which has prompted its recognition under several names in different countries. Despite not being a narrow endemic this taxon may still be a conservation priority at a local scale as suggested by Flanagan *et al.* (2018).

6. *Vanilla mexicana* Mill., Gard. Dict. (ed. 8), no. 1. 1768. Fig. 24B, 25–29.

Replaced synonym: *Epidendrum vanilla* L., Sp. Pl. ed. 1, 2: 952. 1753.

≡ *Vanilla aromatica* Sw., Nova Acta Regiae Soc. Sci. Upsal., ser. 2, 6: 66. 1799.

≡ *Epidendrum aromaticum* (Sw.) Parm., Cat. Arbr. Parm. 29. 1818.

TYPE: [HAITI]: “Volubilis siliquosa plantaginis folio” in Catesby, Nat. Hist. Carolina 2: app. t. 7. 1747 (Fig. 25A).

Syn.: *Vanilla ovata* Rolfe, J. Linn. Soc., Bot. 32: 451. 1896, **syn. nov.**

TYPE: FRENCH GUIANA, *J. Martin s.n.* (holotype: BM; tracing: K!; isotype: P!; Fig. 26A, 26B)

Syn.: *Vanilla martinezii* Soto Arenas, Lankesteriana 9(3): 320. 2010, **syn. nov.**

TYPE: GUATEMALA: Izabal: Mpio. Livingston, El Golfete, a 20.4 km al NE de Río Dulce por lancha camino a Calix, bejuco herbáceo, flor verde con amarillo y labelo blanco; selva mediana perennifolia ‘swampo’, 15°47’06” N, 88°51’42” W; *E. Martínez S. 36410* y *D. Alvarez* (holotype: MEXU; isotypes, AMO, BIGUA, MO; illustration of type! Fig. 26C).

Syn.: *Vanilla guatemalensis* Archila Revista Guatemalensis 2(3): 46. 1999[2012], **syn. nov.**

TYPE: GUATEMALA. Alta Verapaz: Colectado por Oscar Archila, en pantano de Rubelsanto, cruce para playa grande a 350 m, Junio 1994, FA-sn (holotype: BIGUA; illustration!).

Syn.: *Vanilla paludosa* Pansarin, J.M.Aguiar & A.W.C.Ferreira, Brittonia 64(2): 157. 2012, **syn. nov.**

TYPE: BRAZIL. São Paulo: Msun. Brotas, Fazenda Laranjal, 9 July 2010, *E. R. Pansarin, J. M. R. B. V. Aguiar & A.W.C. Ferreira 1361* (holotype: SPFR; illustration!).

Syn.: *Vanilla yanesha* Damian, Willdenowia 49(1): 6–8. 2019, **syn. nov.**

TYPE: PERU. Pasco: Oxapampa, distrito Palcazu, San Francisco de Pichanaz, 10°30’23”S 75°04’19”W, 550 m, bosque secundario, 28



FIGURE 25. *Vanilla mexicana* Mill. type illustrations. A. “Volubilis siliquosa plantaginis folio” in Catesby, Nat. Hist. Carolina 2: app. t. 7. 1747 (lectotype of *V. mexicana*). B. Plate 28 in Plumier’s *Nova plantarum americanarum genera* 25. 1703. C–D. Plumier’s original illustrations kept at P © copyright of the Muséum national d’histoire naturelle, Paris.

Feb 2006, *R. Rojas, J. Mateo & C. Rojas* 3947 (holotype: MO-6049740!, photographs!; isotypes: HOXA-126525!, MO-6049740!, Fig. 27A).

Hemiepiphytic, leafy vine, up to several meters high. *Stems* branching, terete, fleshy, up to 8 mm in diameter; internodes 4–9 cm long. *Aerial roots*, semicylindric, one per internode emerging opposite to the leaf, 15.0–30.0 × 1.7–2.5 mm. *Leaves* subsessile; blade broadly elliptic to slight ovate, acute to shortly acuminate, membranaceous to chartaceous, 7.5–30 × 3.7–12 cm. *Inflorescence* lateral, axillary, erect, racemose, up to 14 cm long, with successive flowers, 1–4 opened simultaneously; peduncle abbreviated, rachis terete, internodes up to 5 cm long, and 5 mm in diameter; *floral bracts* small, sessile, ovate, acute, 6–27 × 5–20 mm. *Ovary* (plus pedicel) terete, 4–5 cm long in open flowers, 3–5 mm in diameter, arcuate. *Flowers* with with ovary yellowish-green, lustrous, sepals and petals pale green to yellowish, lip white, yellowish-green to yellowish on the callus, or only above the middle, and column white, with the stigma yellowish to orange; when young, apex of the sepals lightly recurved; petals and sepals more or less flat at anthesis, turning conspicuously reflexed with undulate margins with age, apically deeply recurved, sometimes become uncinatate, and lateral sepals dextrorse, rolled outwards. *Dorsal sepal* elliptic to lanceolate, shortly retuse to obtuse, 11-veined, 3.0–6.5 × 1.4–1.7 cm. *Lateral sepals* obliquely elliptic to lanceolate, shortly retuse to obtuse, 11-veined, 3–6 × 1.2–2 cm. *Petals* obliquely elliptic to lanceolate, shortly retuse to obtuse, abaxially sulcate along the midvein, 10-veined, 3–6 × 1.0–1.5 cm. *Lip* fused to the column base along the margins for ca. 8 mm, bell-shape, trilobed; when spread out 2.5–5.0 × 2.5–4.5 cm; the base obtuse to rounded; the blade cucullate, when spread out widely ovate in outline; the lateral lobes broad rounded, incurved forming a gullet around the column, apically usually overlapping, with raised longitudinal veins forming sulcus; the middle lobe spreading, ovate, acute to obtuse or rounded, porrect, margins flat to undulate, 1–2 cm wide; the disc with a raised, vertical fleshy callus extending from the base to the apex of the middle lobe, up to 5 mm wide, formed by 2 vertical keels from the base progressively becoming thicker in the apical 1/3, and a third keel rising in the middle of the disc, the keels sinuous, striate, tapering and

rising towards the apex; the distal half of the callus becomes chartaceous, rugulose, and usually with several pseudo-keeled when the flowers are old or dry. *Column* subterete, slightly sigmoid, arcuate towards the apex, 2.3–3.0 × 0.3–0.5 cm, wider at the base, with a small keel-like thickening at the base, ventrally canaliculate, apex obtuse, with two lateral short wings. *Stigma* without lateral lobes. *Rostellum* oblong and truncate, convex. *Anther* incumbent, galeate, broadly obovate, 2–4.5 × 2–4.5 mm. *Pollen* soft granular not forming a clear pollinarium. *Fruit* dehiscent, green, dark brown when old, blackish inside, opening by 2 longitudinal valves, non-aromatic, 8.5–15 × 0.6–1 cm, with ellipsoid black seeds.

SPECIMENS STUDIED: United States. Florida: Cocoplum, Mar. 1960, *F.C. Craighead* s.n. (FLAS!). Martin Co., Hammock, central Martin county, 29 May 1980, *D. Richardson, R.P. Saulea & B. Hansen* 830 (USF!). Unknown locality, *R. Coleman* s.n. (JBL-photograph!; Fig. 27E). GUATEMALA. Izabal: Creek Lagarto, Ensenada de los Lagartos, El Estor, 2 m, 16 Jul. 1988, *E. Martínez* 22790, *P. Tenorio, H. Droege & M. Díaz* (MEXU, illustration!). Lago Izabal, desembocadura del Río Polochic, Creek Lagarto, al SW de El Estor, ca. 15°28' N, 89°23' W, 24 Feb. 1998, *Soto* 8602a (AMO, illustration!). Cobán: Alta Verapaz, Parque Nacional Laguna Lachua, *E.A. Mó* s.n. (JBL-photograph!, Fig. 27F). HONDURAS. Atlantida, vicinity of La Ceiba, banks of the Salado river, above the village of Salada, 10 Jul. 1938, *T.G. Yunker, J.M. Koepper & K.A. Wagner* 8335 (NY!; AMES!). COSTA RICA. Limón: Talamanca, Cahuita, Parque Nacional Cahuita, Estación de Puerto Vargas, cerca de 300 m después de la estación hacia Punta Cahuita, 9°44'00.05" N, 82°48'50.01" W, 8 m, 27 Abr. 2012, *D. Bogarín* 9587, *M. Fernández & F. Pupulin* (JBL-spirit!; Fig. 27B). Limón: Talamanca, Cahuita, Parque Nacional Cahuita, Estación de Puerto Vargas, cerca de la estación hacia Punta Cahuita, creciendo a unos pocos metros del mar, 9°43'53.23" N, 82°48'53.53" W, 10 m, 24 Feb. 2017, *A.P. Karremans* 8122 & *I. Chinchilla* (JBL-spirit!, Fig. 28, 29). CUBA. *Wright* 3353 (AMES, K, P-00367030!). JAMAICA. (P-00367031!). 8 May 1903, *W. H. Harris* 8555 (NY!). Nov. 1885, *D. Morris* 451 (K!). "Epidendrum 39", *De Vriese* s.n. (K!). DOMINICAN REPUBLIC. Cordillera Central, Santiago Rodríguez, 2 km. desde la confluencia de los ríos Mao y La Cidra en ruta al Aguacate (de Monción), 12 Jul. 1988, *T. Zaroni & R. García* 42003 (NY!). In arboribus scandens ad Jarabacoa, 600 m, 24 May 1887, *B. Eggers* 2086 (K!). HAITI. 3 milles above Source Chaude on Bras Gauche, Grand Anse River Valley, 12 Jan. 1942, *R.J. Seibert* 1737 (SEL!). PUERTO RICO. Canovanas: Caribbean National

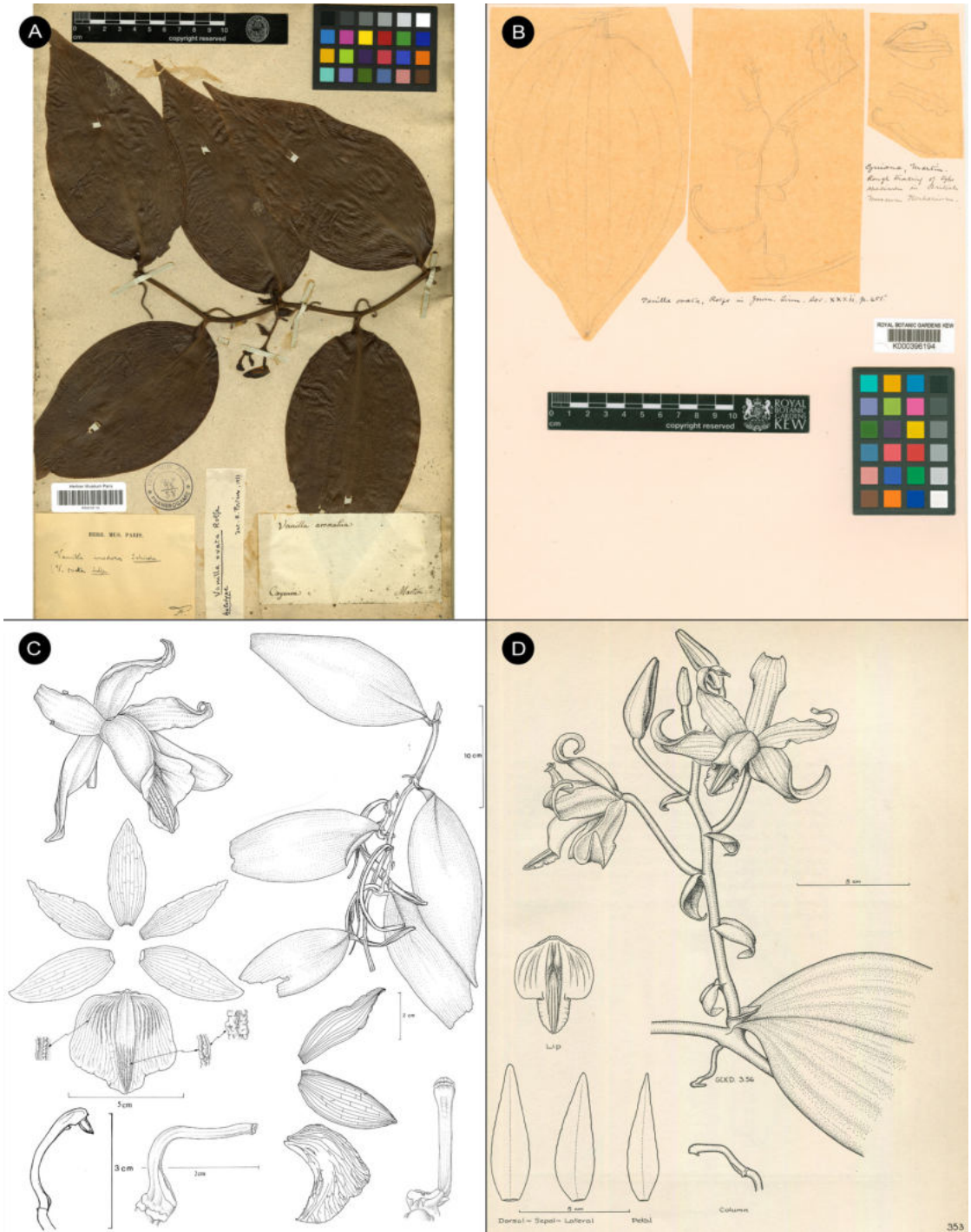


FIGURE 26. *Vanilla mexicana* specimens and illustrations. **A.** Isotype of *V. ovata*, Martin s.n. from French Guiana © copyright of the Muséum national d'histoire naturelle, Paris. **B.** Sketches of the type © copyright of the Board of Trustees of the Royal Botanic Gardens, Kew. **C.** Type illustration of *Vanilla martiniezii*, Guatemala. **D.** Illustration by Dunsterville from Venezuela.

Forest, La Condesa Section, along 2 km stretch of dirt road off Rt 946, 24 Jan. 1993, *F. Axelrod & Schulz* 5639 (NY!). Puerto Rico, Sierra de Luquillo, in monte Jimenes, Jun. 1885, *P. Sintenis* 1739 (B!; K!). Sierra de Jabucoa, 4 Sep. 1885, *Sintenis* 2486 (P-00367029!; P-00367028!). Sierra de Luquillo, May 1883, *Eggers* 1076 (P-00128679!; G 7889/178). Sierra de Luquillo, May 1883, *B. Eggers* 1322 (K!). Prope Yabucoa in sylva primaeva montis Piedra azul, 8 Oct. 1886, *P. Sintenis* 5469 (K!). GUADELOUPE. Collected between 1882–1900, *A. Duss* 2081 (NY-32987!). Bois du Bassin Bleu (près du Galion), 1892, *P. Duss* 238 (P!). Edge of forest, 200 m, 30 Mar. 1956, *Smith* 10350 (USF!; AMES). Bois Riau, 25 May 1938, *A. Questel* 2361 bis (P-00128682!). Unknown locality, *C. & P. Guezennec s.n.* (JBL-photograph!, Fig. 27D). DOMINICA. La Plaine, 18 Jan. 1889, *G.A. Ramage s.n.* (K!). MARTINIQUE. Sainte-Marie, Bois La Roche, 16 Apr. 1998, *C. Sastra & G. Pitoulat* 9767 (P!). TRINIDAD & TOBAGO. Arena, less than 50 m, 26 Oct. 1993, *P.J.M. Maas, H. Maas & S. Smith* 8147 (U!). Aripo Savanna North, 21 May 1985, *J.S. Kenny* 29448 (U!). Mora Forest, east of Sangre Grande, 10 Apr. 1921, *N.L. Britton & W. Nowell* 2847 (K!). Aripo Savanna, 14 Apr. 1921, *N.L. Britton & E.G. Britton* 2945 (NY!). The Widow near Caledonia, 6 Mar. 1912, *W.E. Broadway* 3874 (K!). Long Stretch Forest, 18 Mar. 1953, *R.E.D. Baker* 14732 (K!). *M. Crueger s.n.* (K!). Arima, 1908, *A. Carnegie* 1096 (NY-04170425!). VENEZUELA. Guatopo, growing profusely at about 1500' [feet] in rather lighter patch of forest than the average, *GCKD*. 3.56 (AMES!, illustration; Fig. 26D). French Guiana. Rivière des Cascades. Station des Nouragues, Bassin de l'Approuague, 08 Oct. 2000, *Hequet* 946 (P-00438751!). Riviere Comté au village Etienne, 19 Dec. 1968, *R.A.A. Oldeman B-2080* (P!). La Comté river, *P. Silland s.n.* (JBL-photograph!, Fig. 27C). SURINAME. Tibiti savanne, along Tibiti R. 17 Jan. 1949, *J. Lanjouw & J.C. Lindeman* 1931 (AMES!). PERU. Madre de Dios: Prov. Tambopata, Puerto Maldonado, Carretera Ibera km 18. Aguajal Bello Horizontes, -12.4794 -69.0849, 200-250 m, 20 Jun. 2008, *J. Householder, A. Balarezo, J. Huinga* 188 (BRIT!). Pasco, Prov. Oxapampa, Dtto. Palcazu. Comunidad Nativa San Francisco de Pichanaz, Bosque secundario, 10°30'48" S, 75°04'28" W, 540 m, 27 Jul. 2007, *E. Becerra* 1611 (USM-252790!, HOXA-041903!, MO-632879-photo!, MO-6255510-photo!). Pasco: Oxapampa, distrito Pozuzo, Alto Lagarto a Puente Victoria, 10°06'00" S, 75°26'00" W, 700 m, 28 Dec. 2007, *R. Rojas & G. Ortiz* 5146 (USM!, HOXA!, MO-6852664!). BRAZIL. Corcovado: 18 Jan. 1879, *A. Glaziou* 245 (P-00128684!). Tocantins: Barra do Ouro, Fazenda Santa Rosa, córrego Bacabal, 7°44'04" S, 47°42'17" W, 119 m, 19 Aug. 2010, *J.B. Pereira* 220 et al. (CEN-00087508!). Espirito Santo: Linhares, Reserva Natural da CVRD, 29 Mar. 2000, *D.A. Folli* 3591 (CEN-00060687!). Pará. Rio Itacaiunas, afl. do

Rio Tocantins, serra buritirama (B4), região com minério de manganês, Sept. 1970, *J.M. Pires* 13072 (IAN-129161!). Amazonas, 20 Mar. 1975, *B.G.S. Ribeiro* 972 (IAN-149662!).

OTHER SPECIMENS: PUERTO RICO. *Kevorkian* 6468 (AMES). CUBA. *Alain* 2295 & *Acuña* (AMES); *Clemente* 2401 (AMES); *Britton* 5221 & *Wilson* (AMES); *Schafer* 3211 (AMES), 3299 (AMES) & 7982 (AMES). JAMAICA. *Purdie s.n.* (K); *Wood s.n.* (BM, tracing). TRINIDAD & TOBAGO. *Britton s.n.* & *Howell* (AMES); *Freeman s.n.* (AMES); *Simmonds* 334 (AMES); *Row & E.E.C.* 11332 (AMES). DOMINICA. *Immary* 138 (K); *W.H. & B. T. Hodge* 3671 (AMES); *Ernst* 1462 (AMES). Saint Lucia: *Proctor* 17710 (AMES). HAITI. *Eyerdam* 395 (AMES). MARTINIQUE. *Duss* 2081 (AMES).

DISTRIBUTION: Broadly distributed throughout the Neotropics. Recorded from the U.S.A. (Florida), Guatemala, Honduras, Costa Rica, Cuba, Jamaica, Haiti, Dominican Republic, Puerto Rico, Virgin Islands, Guadeloupe, Grenada, Dominica, Martinique, Saint Lucia, Trinidad & Tobago, Venezuela, French Guiana, Suriname, Guayana, Peru and Brazil (Fig. 24B).

EXTENT OF OCCURRENCE: 14,481,037.545 km².

Vanilla mexicana Mill. is the type species of the genus, and the taxonomic history of this species is complex. It has been suggested by some authors (i.e. Soto Arenas & Dressler 2010), that the name *V. mexicana* is based on Plumier's original illustrations kept at P (Fig. 25C, 25D), on which the Aubriet's and Catesby's (Fig. 25A) are based upon (Reveal 2013), and which was partly reproduced in Plumier's Nova plantarum americanarum genera 25, as plate 28, in 1703 (Fig. 25B). However, Miller (1768) makes reference to a single illustration under the name *V. mexicana*, and it reads "Cat. Car. 3. p. 7." This means that despite being a copy of Plumier, the illustration provided by Catesby is the type of the species. The name *Epidendrum vanilla* L., published in 1753, is the first to apply to a species of *Vanilla*. It has been considered a synonym of *V. mexicana* and as an earlier name would have priority over it. It cannot be used, nevertheless, simply because if combined in genus *Vanilla* would result in the generic and specific epithets being identical, which is not allowed in plants. When *E. vanilla* was described, Linnaeus cited six different references without selecting a type. The name was later lectotypified by Cribb (in



FIGURE 27. *Vanilla mexicana* flowering specimens from different localities across its distribution. **A.** Peru, Pasco, from the specimen that served as type of *V. yanesha*. **B.** Costa Rica, Cahuita, *Bogarín* 9587. **C.** French Guiana, La Comté river, *Silland s.n.* **D.** Guadeloupe, *C. & P. Guezennec s.n.* **E.** Florida, photo by Ron Coleman. **F.** Guatemala, Alta Verapaz, Parque Nacional Laguna Lachua, *Mó s.n.* Photographs by the collectors.



FIGURE 28. *Vanilla mexicana* showing the morphological transition of flowers within a single inflorescence. **A.** At anthesis the flower bears almost straight sepals and petals. **B.** The sepals and petals of a senescent flower that have become fully twisted and undulate. By APK based on *Karremans 8122* (JBL-spirit).

Cafferty & Jarvis 1999), who selected “Catesby, Nat. Hist. Carolina 2: app. t. 7. 1747.” Some authors have stated that *V. mexicana* is based on *E. vanilla* (Garay & Sweet 1974), while others have pointed out that this is incorrect (Cafferty & Jarvis 1999). This, however, poses a problem. If the taxa are independent and the types of both *E. vanilla* and *V. mexicana* is Catesby’s illustration, then they are not only synonyms but the latter also becomes illegitimate, and a new name needs to be applied to this already quite confused taxon. There is a more harmonious solution. The name *V. mexicana* may simply be considered a *nomen novum* for *E. vanilla*, with the citation of Catesby’s illustration being an indirect reference as suggested by Art. 41.3 (Turland *et al.* 2018), which in fact cites other such examples from Miller’s work. This would render the name *V. mexicana* legitimate and able to continue in its current usage.

This species is a member of the membranaceous group, which is easily recognized by having membranaceous leaves and the lip without a penicillate callus. This group has species having small scale-like

and large leave-like foliaceous floral bracts. Clarifying the type of this taxon is only the tip of the iceberg. *Vanilla mexicana* is recognized by the broad membranaceous elliptic ovate leaves, a short inflorescence (relative to *V. inodora*), elongating with time, bearing small floral bracts, long pedicels, pale green to yellowish, twisted, undulate tepals and a white lip, non-unguiculate base, distinctly trilobed, with the lateral lobes rounded, covering the column in natural position, incurved above, and the midlobe rounded to ovate, with a callus formed by two vertical keels from the base progressively becoming thicker in the basal third, and a third keel rising in the middle of the disc extending to the midlobe, the sinuous keels, tapering and rising towards the apex, the callus becoming lower and multi-keeled with age and dehydration. A flower at anthesis (Fig. 28A) and a senescent flower (Fig. 28B) from the same inflorescence show how flowers of *V. mexicana* transition from have almost straight tepals to becoming twisted and undulate, and have a white, three-keeled callus to having a yellowish multi-keeled callus after dehydration.



FIGURE 29. LCDP of *Vanilla mexicana*. **A.** Habit. **B.** Inflorescence bract. **C.** Flower. **D.** Dissected perianth, flattened. **E.** Lip and column lateral view. **F.** Column, side views. **G.** Anther cap and pollinia. By APK based on Karremans 8122 (JBL-spirit).

The cryptic name *V. ovata*, based on a plant collected by Martin in French Guiana, is here also placed under *V. mexicana*. The original protologue and sketches (Fig. 26A, 26B) agree with the features of *V. mexicana*, also seen in plants photographed along La Comté river, which is close to the presumed type locality (Fig. 27C). The remaining names discussed here are much more recent. In the past two decades, six species with membranaceous leaves and small floral bracts have been proposed: *V. guatemalensis* Archila (Archila Morales 2012), *V. martinezii* Soto Arenas, *V. sarapiquensis* Soto Arenas (Soto Arenas & Dressler 2010), *V. paludosa* Pansarin, J.M.Aguir & A.W.C.Ferreira (Pansarin *et al.* 2012), *V. arcuata* Pansarin & M.R.Miranda (Pansarin & Miranda 2016), and *V. yanesha* Damian (Damián 2019). Two are clearly distinct. The Costa Rican *V. sarapiquensis* is recognized by its suborbicular, trilobed lip, with a massive callus made up of two elevated, thick, sulcate keels, confluent in the apical part. The Brazilian *V. arcuata*, is recognized by having a column foot, a strongly arched column, with a prominent yellow keel at the base, and a lip with the lateral lobes margin round, recurved and erect forming a gullet only around the distal column section. However, based on the studied of protologues, living and dried herbarium material, illustrations and photos, the other four species are here recognized as conspecific to *V. mexicana*.

Soto Arenas and Dressler (2010) excluded *Vanilla mexicana* from Central America pointing out that despite the name the species was only known from the West Indies and northeastern South America. Upon proposal, *Vanilla guatemalensis* wasn't compared with any other species of the genus, and diagnostic characters were not mentioned. Based on the illustration and short description it is inseparable from *V. mexicana*. Also from Guatemala, *V. martinezii* (Fig. 26C) was compared by Soto Arenas and Dressler (2010) to other Central American members of the membranaceous group, *V. costaricensis* Soto Arenas, *V. inodora* Schiede and *V. sarapiquensis*, and the Amazonian *V. guianensis* Splitg., but not with *V. mexicana*. The illustration was prepared from a dried specimen and shows more or less straight tepals, the lateral lobes of the lip recurved rather than incurved and the callus multi-keeled, rather than three-keeled. Photographs of living plants from Alta Verapaz, Guatemala (Fig. 27F) show the diagnostic twisted and

undulate tepals, the lip forming a gullet around the column, with incurved lateral lobes, and a three-keeled callus on the lip, corresponding well with specimens of *V. mexicana* from Florida (Fig. 27E) and Guadeloupe in the Antilles (Fig. 27D). The Brazilian *V. paludosa*, was compared only with the, also Brazilian, *V. edwallii* Hoehne and *V. parvifolia* Barb.Rodr., both with leaf-like floral bracts and easily distinguished by their lip shape. It was not compared with either *V. mexicana* or *V. martinezii*, the two most similar species at the time. The only flower of *V. paludosa* illustrated appears not to have the typical twisted and undulate tepals, however in *V. mexicana* this feature is age dependent, transitioning from straight at anthesis to highly twisted at senescence (Fig. 28). Otherwise the two taxa are inseparable. The recently published *Vanilla yanesha* was described from Peru based on dried herbarium specimens belonging to a single collection, as well as photographs of the living plant with senescent flowers (Fig. 27A). It is said to differ from, the sympatric, *V. mexicana* by having larger leaves, and a lip with more keels. However, examination of multiple specimens of *V. mexicana* shows that leaf size to be variable and that those of *V. yanesha* are found well within the variation of *V. mexicana* (see Dunsterville & Garay 1959, p. 432). The callus of *V. yanesha*, is no different from that found in dehydrated specimens of *V. mexicana*, as was suggested for *V. martinezii*. Again here, the taxon is otherwise inseparable from *V. mexicana*.

Vanilla mexicana is a common and widely distributed species from Florida to Peru and Brazil, through Central America and the Caribbean. It is a lowland species and several specimens are annotated as having been collected in coastal mangroves (including the types of *V. guatemalensis*, *V. martinezii*, and *V. paludosa*, and the specimens illustrated from Costa Rica).

7. *Vanilla odorata* C.Presl, Reliquiae Haenkeanae 1(2): 101. 1827 [1830]. Fig. 30-36, 37A.

TYPE: [ECUADOR:] Hab. in Guayaquil, *Haenke s.n.* (**lectotype designated here:** PRC-450948!, two leaves and fruits on the left, Fig. 30; isolectotypes: PR-305751!; PR-305752!; PR-305753!, excluding two pseudobulbs of *Dimerandra* on each side).

Syn.: *Vanilla ensifolia* Rolfe, Bull. Misc. Inform. Kew, (65/66): 141. 1892.



FIGURE 30. Lectotype of *Vanilla odorata* C.Presl based on *Haenke s.n.* from Guayaquil (PRC-450948) courtesy of the Charles University in Prague.

TYPE: [COLOMBIA:] Cauca, *Goudot s.n.*; Patia, Her. Pharmaceutical Society, from Mr. T. Hanbury, 1884 (**lectotype designated here**: K-000463744!, dried specimen, Fig. 31; **islectotype**: P-00367037!).

Syn.: *Epidendrum vermifugum* Sessé & Moc., Fl. Mex. ed. 2: 201. 1894. *Vanilla vermifuga* (Sessé & Moc.) Soto Arenas, *nom. nud. in sched.*

LECTOTYPE: [MEXICO:] “*Epidendrum vermifugum*”, Sessé, Mociño, Castillo & Maldonado 4358 (MA-600496!, Fig. 32A); **islectotypes**: “*Epidendrum vermifugum* de México absque, mounted with “*Epidendrum uniflorum*” (BM-000923775!; F-848611!).

Syn.: *Vanilla denticulata* Pabst, Anais Soc. Bot. Brasil, XXIII Congr. Nac. Bot. 109. 1972[1973].

TYPE: BRAZIL: Pernambuco, Engenho Conceição, P. Ferreira 37-67 (holotype: HB-000057667!, Fig. 32B).

Syn.: *Vanilla nevermannii* Schltr., *nom. nud. in sched., syn. nov.*

Syn.: *Vanilla lancifolia* Diar., *nom. nud. in sched., syn. nov.*

Hemiepiphytic herb, leafy vine, up to several meters high. *Stems* terete, fleshy, up to 6 mm in diameter; internodes 6–12 cm long. *Aerial roots* semicylindric, one per internode emerging laterally to the leaf, 1.5–4.0 × 0.2 cm. *Leaves* subsessile to petiolate, petiole 0.5–1.0 cm long; blade lanceolate to narrowly lanceolate, acute to shortly acuminate, coriaceous, 7–23 × 1–3 cm. *Inflorescence* lateral, simple, axillary, racemose, 6–10 successive flowers, 1–2-opened simultaneously; peduncle abbreviated, up to 5 mm long, rachis terete, up to 4 cm long. *Floral bracts* sessile, ovate, acute to obtuse, concave, 5–15 × 5–7 mm. *Ovary* (plus pedicel) terete, lustrous, 2.5–6.0 cm long in open flowers, 3–4 mm in diameter, whitish basally. *Flowers* with the ovary whitish in the basal 1/3, apically dark green, sepals and petals pale whitish-green to yellowish, petals abaxially greenish on the midvein, lip adaxially yellowish, abaxially whitish, column white, whitish to yellowish above the middle, rostellum and anther cap greenish-yellow. *Dorsal sepal* oblanceolate to elliptic, obtuse to acute, 11-veined, 4.5–6.0 × 0.8–1.3 cm. *Lateral sepals* oblanceolate to elliptic, obtuse to acute, 4.5–5.7 × 0.9–1.5 cm, 11-veined. *Petals* narrowly

oblanceolate to elliptic, obtuse to acute, 4.8–6.0 × 0.9–1.1 cm, 9-veined, abaxially with a vertical keel along the midvein. *Lip* with the margins fused to the column base for ca. 2.5 cm, tubular, trumpet-shape, shallowly trilobed; when spread 4.1–5.5 × 2.2–2.5 cm; the base long unguiculate, the narrow ca. 14–15 × 4–4.5 mm, adaxially lanate in the base; the blade cymbiform, when spread obovate in outline, with warty veins; the lateral lobes rounded, incurved, margins lacinate to fimbriate; the midlobe semi-ovate to semi-quadrate, shortly emarginated, sometimes shortly apiculate in the center, recurved, margins lacerate to lacinate; *penicillate callus* 2.5–3.5 cm from the base, ca. 3–4 × 3 mm; made up by ca. 9 imbricate, flabellate, retrorse, lacinate scales, sometimes united each to other along the lateral margins; continuing for around 20 mm to the apex, 3–4 mm wide, with 3 keels progressively thickened and confluent towards the apex, forming a fleshy, papillose and warty low cushion, with some prominent conical warts. *Column* subterete, almost straight, 2.5–3.9 × 0.25–0.4 cm, from similar width along, ventrally flattened, and lanate, papillose in the apical ½, apex with 2 obliquely obtuse, retrorse wings; clinandrium, concave, margins long forming subtriangular to ovate wings. *Stigma* trilobate, lateral lobes erect, small, 1.5 × 1 mm. *Rostellum* subrectangular, convex. *Anther* versatile, attached to the clinandrium margin, ovoid to quadrate, 3–4 × 3 mm. *Pollen* not forming a clear pollinarium but a sticky, tow soft, sticky granular mass. *Fruit* cylindric with attenuate at both ends, aromatic, 15–20 × 1 cm.

SPECIMENS STUDIED: MEXICO. Oaxaca: Dto. Tuxtepec, Usila, Arroyo Iguana, vainillal de Silvano Bautista, ca. 250 m, 24 Abr. 1992, M. Soto 6617 & M. Hernández (AMO; illustration!). Oaxaca: Liebman 294 (W-R-11759!). Quintana Roo: Othón P. Blanco, camino Calderón-Tres Garantías, km 25, 18°01'15" N, 89°01'00" W, 11 Abr. 2002, F. May 2167 (CICY!). Quintana Roo: Othón P. Blanco, Paso del Danto, 150 m al N del rancho de Don Crescencio Cruz, cuenta alrededor de un gran cenote 5 km al N de La Unión, 17°57'30" N, 88°53'06" W, ca. 0-50 m, 4 Dec. 1997, G. Carnevali, F. May, M. Gómez & J.C. Chab 4805 (CICY!). Quintana Roo: Othón P. Blanco, Ejido Caobas, Zona general de la Sabana del Jaguactal, un desvío dde 11.5 km por carretera de terracería al este de la carretera Crucero Nuevo Becal-Tres Garantía, unos 22 km al sure en línea recta desde la carretera Xpujil-Chetumal, apex, 18°15'34.10" N, 88°56'39.60" W, ca. 141 m, 8 Dec. 2016, G. Carnevali, *et al.* 7991 (CICY!). BELIZE. Trail through light jungle, near



FIGURE 32. *Vanilla odorata*. **A.** Lectotype of *Epidendrum vermicifugum* Sessé & Moc., Sessé, Mociño, Castillo & Maldonado 4358 (MA-600496), © copyright of the Real Jardín Botánico, Madrid. **B.** Holotype of *Vanilla denticulata* Pabst, P. Ferreira 37-67 (HB-000057667), courtesy of Herbarium Bradeanum.

camp. 2, elev. 2000 ft., 20 Aug. 1976, C. Whiteford 1316 (MO-2584013!). Toledo: Sarstoon Temash National Park, Sarstoon River, 15 m, 15.895283333333, -89.02, 3 Dec. 2014, B.K. Holst et al. 10000 (SEL-photo!). GUATEMALA. Alta Vera Paz: Mar. 1881, Türckheim 586 (W-R-12951!). Peten: Libertad and vicinity, Aug.-Nov. 1933, H. Mercedes Aguilar 164 (AMES-40519!; AMO-photo!). Tikal, in botonal north of hotel, 20 Jan 1961, E. Contreras 1841 (LL!). HONDURAS. Lancetilla, 150 ft., T.G. Yuncker 4993 (NY-00984265!). Colón: 1.8 min. Strip on the north bank of rio Guaimoreto between old bridge and opening of Laguna Guaimoreto 4.5 min. NE of Trujillo on old road to Castilla, 15°57'30" N, 85°54'30" W, 2 Feb. 1981, J. Saunders 1008 (SEL!, TEX!; AMO-photo!). Atlantida: Campamento Quebrada Grande, 10 km SW of La Ceiba, 15°42' N, 86°51' W, 80–200 m, 15 May 1993, R.L. Liesner & D. Mejia 26360 (MO-04649983!). NICARAGUA. Segovia: E of Jalapa, elev. 1600 ft., May-Jun., A.H. Heller 6106 [SEL-013289!; SEL-003851!; F-003851; AMO-photo!; illustration

in Hamer (1984)!]. COSTA RICA. Alajuela. Los Chiles, Los Chiles, camino a Bandera, al lado del camino, 10°53'25.35" N, 84°30'03.96" W, 66 m, 30 Set. 2017, A. Karremans 8101, I. Chinchilla & M. Cedeño (JBL-spirit!, Fig. 33). Limón: Hamburg Finca, on the Río Reventazón below Cairo, 55 m, 19. Feb. 1926, P.C. Standley & J. Valerio 48917 (AMES-32665!; US-1309433!; AMO-photo!). Golfito, Jiménez, camino a Agua Buena. Estación Biológica Piro, 8°24'03.83" N, 83°20'09.51" W, 24 m, 28 Oct. 2014, A. Karremans 6440, J. Geml, M. Lopez, J. Murillo, L. Parra, Carlos Rojo, Marisa Vázquez (JBL-spirit!, Fig. 34). COLOMBIA. Antioquia: Carretera Mutatá-Pavarandó, entre hacienda La Esperanza y Mocari, 150 m, 6 Mar. 1987, R. Fonnegra, F.J. Roldán, J. Betancourt, B. Echeverry, O. Escobar 1784 (MO-3592235! AMO-photo!). Valle: Zarazal, Hacienda El Medio, carretera Panamericana entre La Paila y Zarazal, valle del Río Cauca, 950 m, (hay fotos), 16 Abr. 1987, F.A. Silverstone-Sopkin 3105 (MO-05015894!). Santa Marta, Wallis 4.68 (W-R-21188!). Cauca, Goudot s.n. (W-R-21426!). Medellín, Wallis

- s.n.* (W-R-21454!). Llano de San Martín, Villavicencio, 100 m, Jan. 1856, *J.J. Triana 1614/2* (COL-000363315!; P-00367024!; W-19373!). 20 Mar. 1858, *A.C.V. Schott 12* (F!; NY!). VENEZUELA. Territorio Federal Amazonas, Atabapo, forest slope of Marahuaca, 1 to 2 km north of Sima Camp, 3°43' N, 65°31' W, 1100 m, 8-9 Mar. 1985, *R.L. Liesner 18444* (NY!). Bolívar, Falcón, La Tabla, Sierra de San Luis, *M. Speckmaier s.n.* (JBL-photo!, Fig. 35A). ECUADOR. Napo: Collected near Tena, oriente del norte, 2000 ft., Apr-May 1923, *F. Williams s.n.* (AMES-26313!). Hacienda la Virginia, *Wallis 181* (W-R-21194!). Without locality, 30 Apr. 1897, *Eggers 15138* (F-143393!). FRENCH GUIANA. Route Régina-Saint Georges, Bassin de L'Approuague, 4°2' N, 52°1' W, 100 m, *G. Cremers & J.J. De Granville 14281* (P-00367047!). Saint Georges, RN 2, à 100 m de la savane 14 Juillet, 09 Nov. 1998, *O. Poncy, F. Crozier & P. Grenand 1141* (P-00166858!). Crique tigre. Bassin du Sinnamary, 23 Nov. 1993, *B. Bordenave 512* (P-00224525!). *G. Leotard s.n.* (JBL-photo!, Fig. 35B). SURINAME. Bakhuis, concession BMS: Zone 21, 4°23'57" N, 57°04'49" W, 200 m, 15 Apr. 2006, *B.G. Bordenave 8517, F. Van Troon, I. Van Troon & J. James* (MO-04799286!). PERU. On the Amazon River, Sep. 1929, *L. Williams 3161* (AMES-43483!; AMO-photo!). Amazonas: Prov. Bagua, Chiriaco, al borde de tributario del río Chiriaco cerca a la Comunidad Nativa Pakuy, propiedad de Damián Shakai, 24 Abr. 2016, 302 m, *A. Damián, L. Rimarachin, D. Shakai, A. Uwek ADP008-1* (MOL!, Fig. 36), *ibid. ADP008-2* (MOL!); Prov. Bagua, Dist. Bagua, Centro poblado Naranjos, 23 Abr. 2016, 767 m, *A. Damián, L. Rimarachin, G. Becerra, M. Villalobos ADP002-39* (MOL!); Prov. Bagua, Yamayakat, Trocha Putuim bosque primario, 500 m, 17 Oct. 1996, *R. Vásquez, N. Jaramillo 20316* (SEL!, MO-05097620!). Loreto: Lower Rio Huallaga, Yurimaguas, 133 m, 23 Aug. 7 Sep. 1929, *E.P. Killip 29065 & A.C. Smith* (AMES!; NY!; AMO-photo!). Lower Rio Huallaga, Yurimaguas, 155–210 m, 4 Nov. 1929, *L. Williams 4539* (F-618740!). Lower Rio Huallaga, Río Mayo, 360–900 m, 14 Dec. 1929, *L. Williams 6272* (F-621011!). Prov. Maynas, Caserio Mishana, forest on white sand soil, 1-2 hr. walk from river, vine, 4-6 Sep. 1974, *R.B. & W.A. Foster 4090* (USM 45900!, F 1893719!); Prov. Maynas, Dtto. Las Amazonas, Yanayacu, 808788 9621235 96 m, Aug. 2016, *A. Damián, N. Mitidieri ADP4016-1* (MOL!); Prov. Maynas, Dtto. Belén, 2 de mayo de Muyuy, 692491 9572309 108 m, Aug. 2016, *A. Damián, N. Mitidieri 4001* (MOL!); Prov. Maynas, Dtto. Iquitos, Quistococha, 687082 9576191 103 m, Aug. 2016, *A. Damián, N. Mitidieri 4026* (MOL!); Prov. Maynas, Río Yubinetto, 72.20 W 1 S, 150 m, Jan. 1978, *S. Barrier 272* (MO-4315231!). Ucayali: Prov. Coronel Portillo, Leoncio Prado, Yarinacocha, 08°20'S 074°35'W, 200 m, 15 May 1984, *R. Vásquez 4995* (MO-3303424!, NY-04170436!); Prov. Coronel Portillo, Dtto. Iparia Reserva Comunal el Sira (zona de amortiguamiento), -9.13076, -74.4984, 172 m., 30 Nov. 2015, *J. Janovec, J. Ushiñawa, H. Behar 4002, 4004* (MOL!). Cajamarca: San Ignacio, Dtto. Namballe, bosque el pacashal, bosque primario, margen derecho del río Canchis, 05 01' S 79 01' W, 650-800 m, 10 Jul. 1997, *E. Rodríguez & O. Pesantes 1656* (HUT!, MO!, USM!); Dtto. Namballe, de la colmena a morero, vegetación secundaria. 05 00' 30" S 79 04' 00", 1000-1150 m, 12 Jan. 1997, *J. Campos, G. Pezantes 3305* (MO-5579312!, SEL!, USM!); Prov. San Ignacio, Nuevo Perú, 900 m, 14 May 1996, *R. Vásquez, A. Vásquez 20842* (SEL!, MO-05098926!). CUSCO, Prov. La Convención, en Serjali, Río Mishagua, 11°11'58.18"S 72°58'26.31"O, *G. Shepard, R. Foster 730* (USM!). San Martín: Prov. Mariscal Cáceres, Dtto. Tocache Nuevo, 08°11'03"S 076°30'45"W, 400-700 m, *J. Schunke 11060* (MO-5569374!, SEL!); Prov. Moyobamba, Dtto. Moyobamba, Reserva Ecológica de Tingana, 5°53'52"S, 77°07'12"W, 26 Jan. 2019, *D. Cabrera & M. Leon s.n.* (MOL!); prov. San Martín, Dtto. Tarapoto, Instituto de Investigación Biológica de las Cordilleras Orientales (INIBICO), 351873.26 m E 9283680.67 m S 500 m, Jun. 2019, *A. Damián & M. Leon s.n.* (USM!). Madre de Dios: Parque Nacional Bahuaja Sonene, Río Heath, 527882 8601719, 24 Jun. 1999, *P. Núñez, A. Monteagudo 26245* (CUZ!); Prov. Manu, Manu Park, Cocha Cashu uplands, Collpa Guacamayo vicinity, 11°45'S 071°10'W, 400 m, 7 Sep. 1986, *P. Núñez 6015* (MO-3430874!); Puerto Maldonado, Río Alto Madre de Dios-Boca Manu, -12.2566, -70.898, 280-320 m, 21 Aug. 2009, probablemente *J. Householder et al. 940* (USM!). BOLIVIA. Beni: Rurrenabaque, elev. 900–1000 ft., 3 Dec. 1921, *O.E. White 1821* (AMES-28026!, NY-04170434!; AMO-photo!). La Paz: Ixiamas, 13 Dec. 1921, 1000–1500 ft., *O.E. White 1115* (AMES-28024!; AMO-photo!). Guarayos. Reserva de vida silvestre ríos Blanco y Negro. Campamento sobre Río Negro de Caimanes, unos 4 km al SE de las Juntas con el Río San Pablo, luego entrando 2 km al S. 14°45'7" S, 63°56'W. elev. ca. 250 m, 18 Jun. 1993, *I. G. Vargas, J. Balcazar & N. Tagua 2617* (F-2295772!). Dept. Beni, Prov. of Vaca Diez, vicinity of the Chácobo village Alto Ivon, 11°45' S, 66°02' W, ca. 200 m, 31 Mar. 1984, *B.M. Boom 4893* (NY!). BRAZIL. Pará: Vitória do Xingu, 3°17'39" S, 51°53'6" W, *Silva PSACF-EX05383* (RB-01031586!). Tucuruí, 12 km N of town of Tucuruí along road to Cametá, aprox. 3°36' S, 49°44' W, 50 m, 21 Mar. 1980, *T. Plowman 9868 & N.A. Rosa, C.S. Rosario* (NY-02695612!). Amapá: cultivated in the orquidario of IAN, *J.S. Rodrigues 218* (IAN-102239!). Mato Grosso, 1891-1892, *S.L.M. Moore 657a* (NY-00910932!).
- OTHER SPECIMENS: Without locality, "Vanilla lancifolia Diar.", Feb 1833, *Poeppig s.n.* (W-R-19352!). Without locality, *Splitgerber 1174* (W-R-19375!). NICARAGUA. Zelaya: [sterile]"Vainilla", bejuco, sobre árboles, Guamil de segunda clase. Area de Ocotal, Río Grande, Alt. 0-15 m, Abril 23, 1949, *A. Molina 2312* (F-1364505).

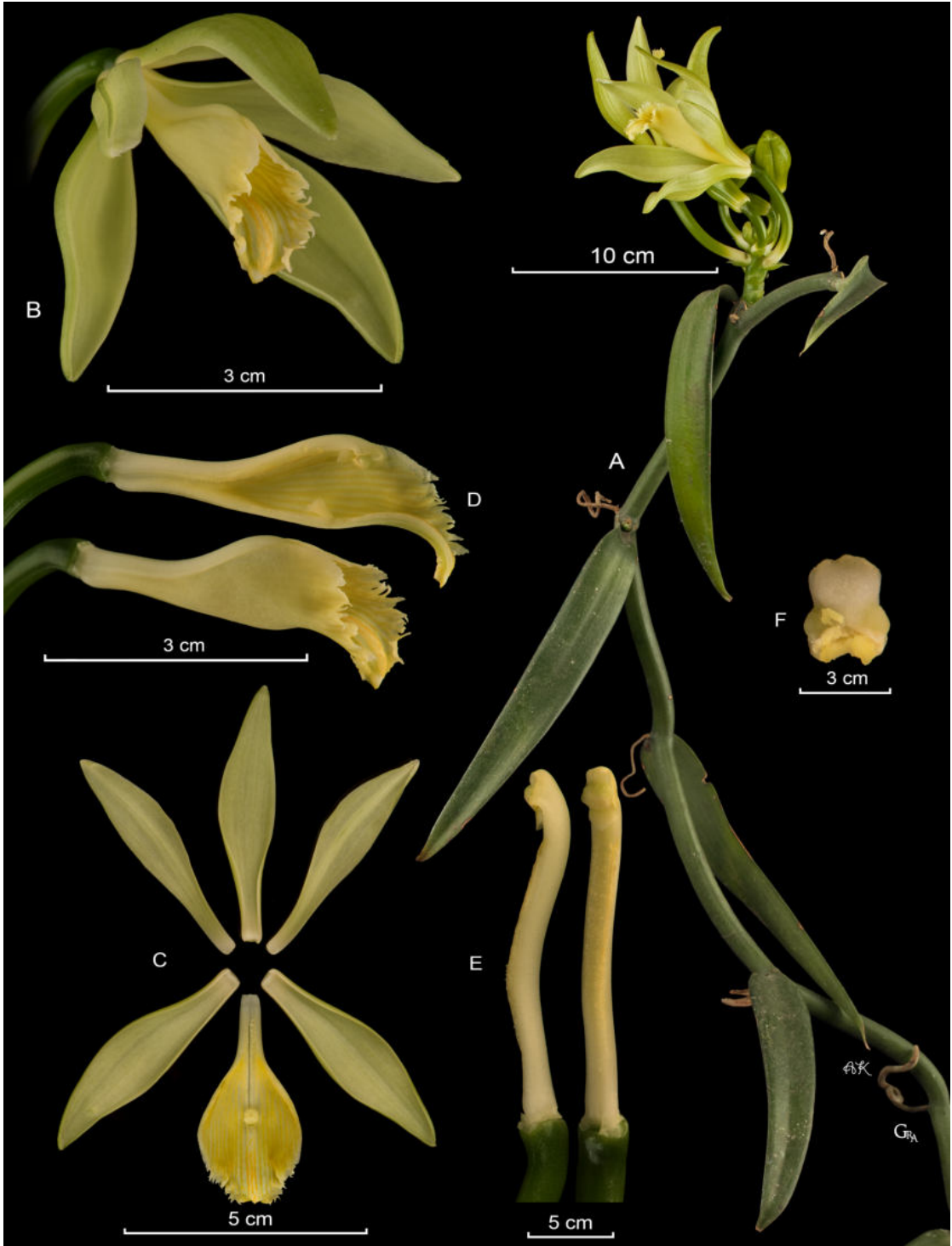


FIGURE 33. LCDP of *Vanilla odorata*. **A**. Habit. **B**. Flower. **C**. Dissected perianth, flattened. **D**. Lip and column lateral view. **E**. Column, side and ventral views. **F**. Anther cap and pollinia. By APK and GRA based on *Karremans 8101* (JBL-

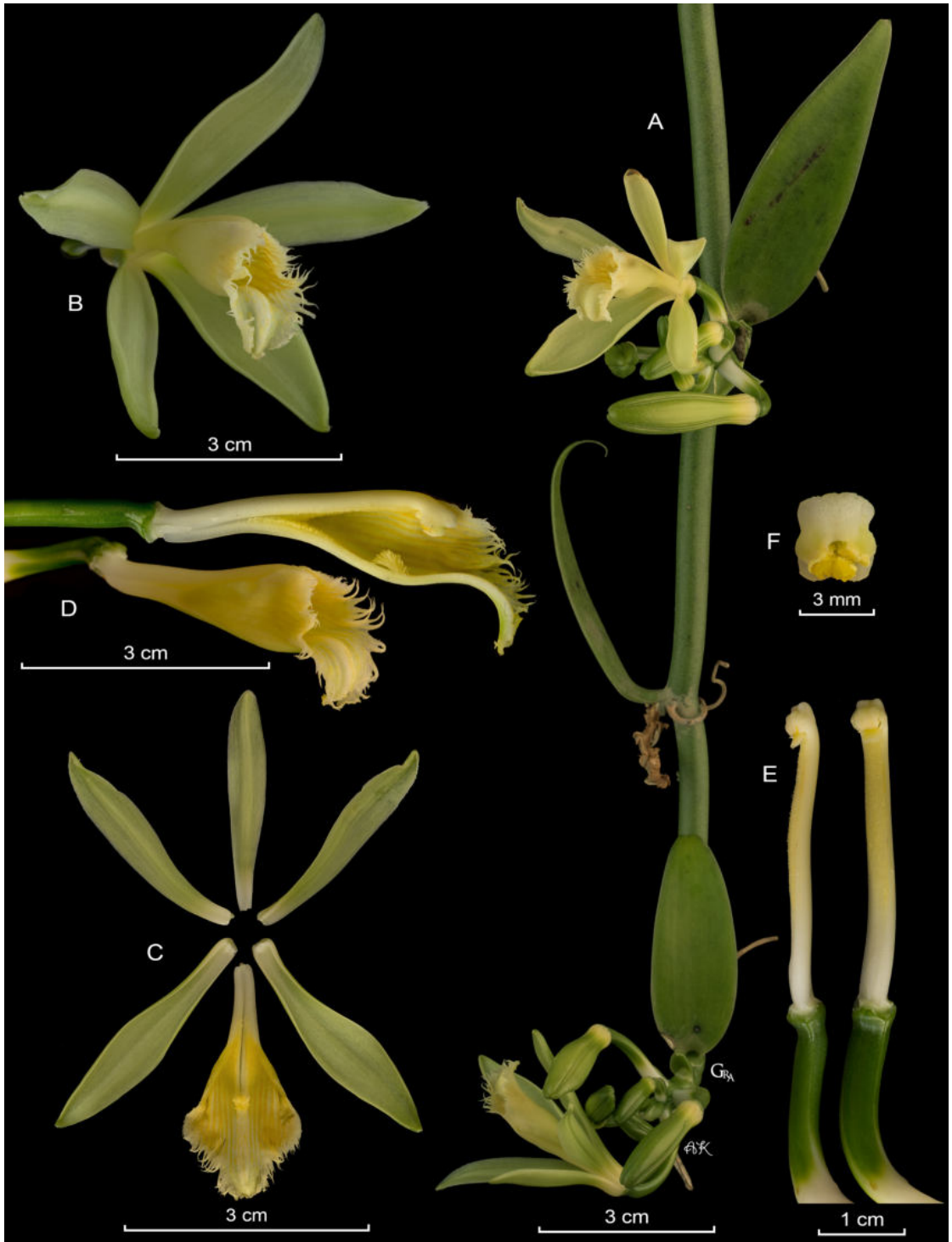


FIGURE 34. LCDP of *Vanilla odorata*. A. Habit. B. Flower. C. Dissected perianth, flattened. D. Lip and column lateral view. E. Column, side and ventral views. G. Anther cap and pollinia. By APK and GRA based on Karremans 6440 (JBL-spirit).



FIGURE 35. *Vanilla odorata*. A. Venezuela, M. Speckmaier s.n. B. French Guiana, L. Leotard s.n. Photographs by the collectors kept at JBL.

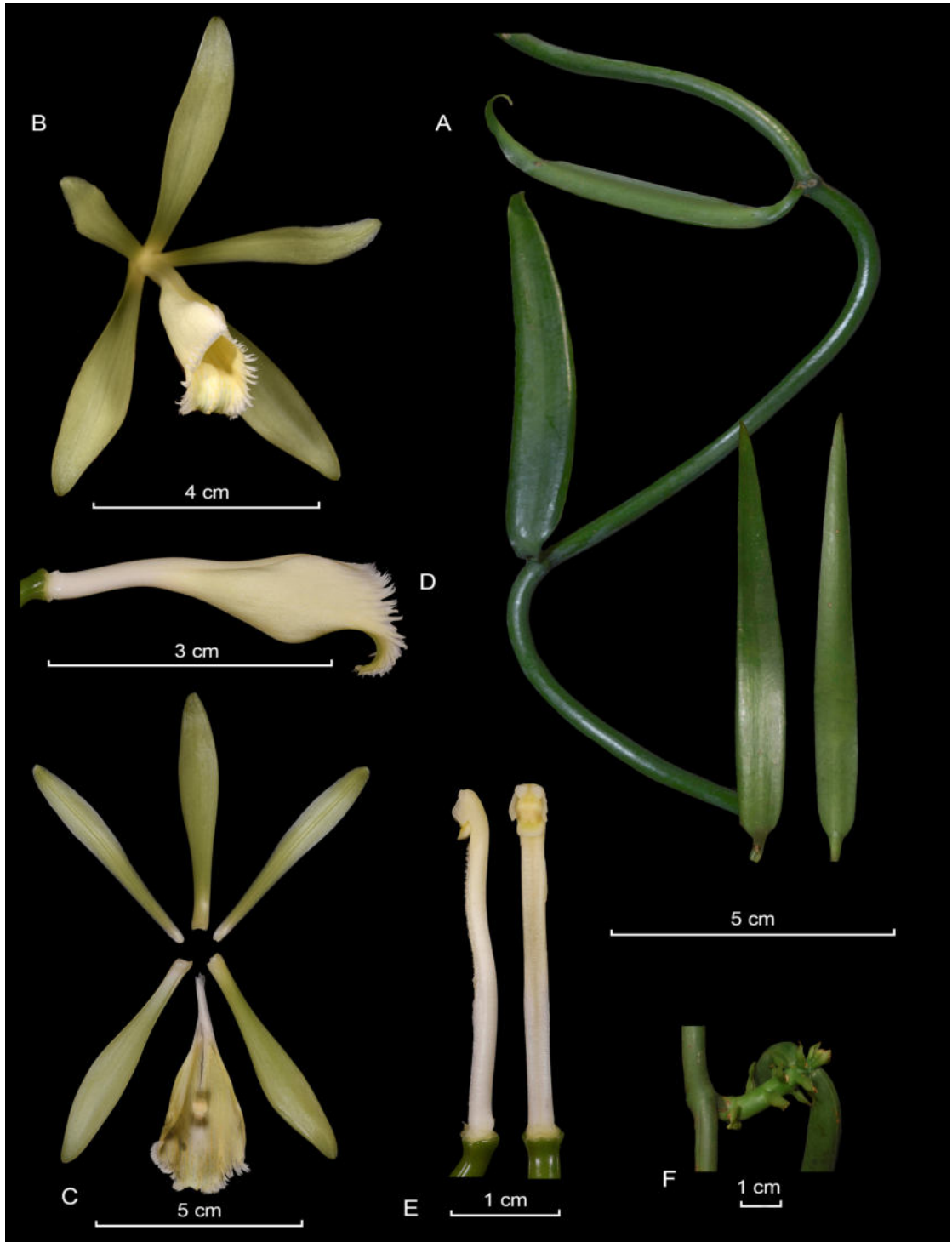


FIGURE 36. LCDP of *Vanilla odorata*. **A.** Habit. **B.** Flower. **C.** Dissected perianth, flattened. **D.** Lip and column lateral view. **E.** Column, side and ventral views. **G.** Anther cap and pollinia. By AD based on *ADP008-1* (MOL).

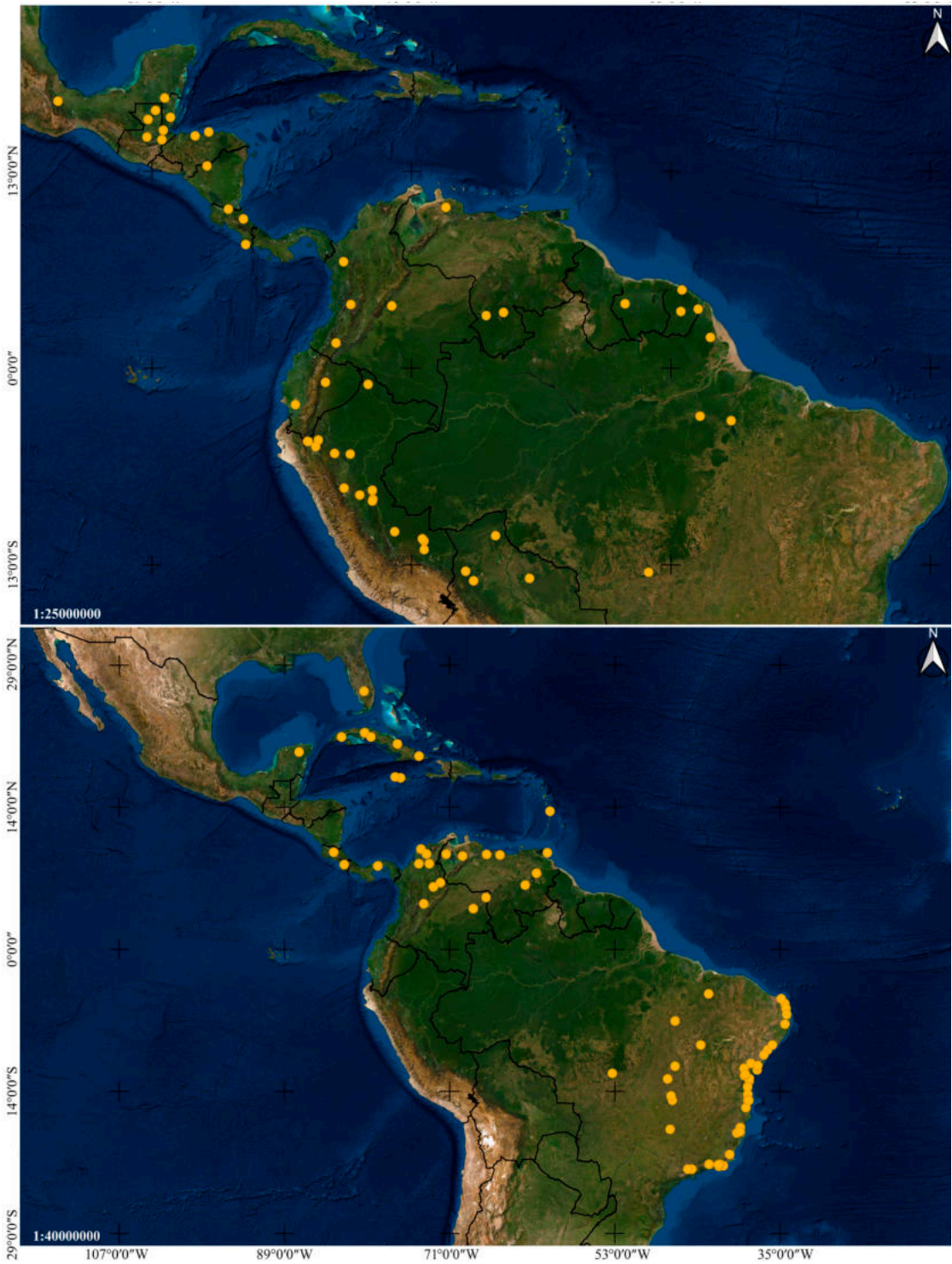


Figure 37. Distribution maps of *Vanilla* species based on studied specimens. A. *Vanilla odorata* C.Presl. B. *Vanilla phaeantha* Rchb.f. Images by IC.

DISTRIBUTION: Broadly distributed in the Neotropics, reported from Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia and Brazil (Fig. 37A).

EXTENT OF OCCURRENCE: 9,800,665.659 km².

Vanilla odorata is characterized by its narrowly lanceolate, acute to shortly acuminate leaves (Fig. 30, 31, 32A, 33, 35), although shorter, broader leaves are present in some populations (Figs. 32B, 34). The pale green to yellowish sepals and petals, yellowish-white lip with the throat stripped with yellow and lacerate to fimbriate margins, are diagnostic of the species. *Vanilla odorata* is similar to *Vanilla insignis* Ames, but, the latter has thicker, sulcate, rugose to papillose stems, broader, xeromorphic oblong leaves, and the retrorse appendages of the lip apex are much more numerous, bigger and orange-yellow, both species share a lacerate to fimbriate lip margin. Flowers of *V. odorata* are also similar to *V. planifolia* Andrews, but the latter has an undulate, crenate, dentate or serrate lip margin (vs. lacerate to fimbriate). The lanceolate to narrowly lanceolate leaves of *V. odorata* set the two apart easily. Plants of *V. karen-chistiana*e Karremans & P.Lehm. are vegetatively very similar to *V. odorata* and dried specimens are difficult to tell apart. However, *V. karen-chistiana*e has falcate leaves, with the apex recurved, sometimes becoming uncinat, thus appearing truncate, whilst *V. odorata* has leaves mostly with parallel margins and an acuminate apex. The two species are easily distinguished florally, *V. karen-chistiana*e has a deeply emarginated lip apex (vs. shortly emarginated to acute), a conspicuously taller penicillate callus, >6 mm tall (vs. <5 mm), the veins of the lip thickened with long, papillose hairs, taller towards the apex (vs. veins glabrous to warty), margins irregularly crenate (vs. lacerate to fimbriate).

After the death of Thaddeus Haenke (1761–1816), the specimens collected during his expeditions in America were bought by Kaspar Maria von Sternberg, founder of the Czech National Museum in Prague (housing the PR herbarium). The collection of Haenke was mainly processed by Carl Borivoj Presl (1794–1852), who brought some of the Haenke's material to his home for studying. After his death, the collection kept at Presl's home was bought by the Charles University (housing the PRC herbarium) (Mráz, *pers.*

comm. 2020). Haenke's original collection therefore ended up preserved in two different herbaria; PR and PRC. We were able to locate four specimens with Haenke's original material of *Vanilla odorata*, three at PR and one at PRC. Garay (1978) attempted to lectotypify *Vanilla odorata* selecting material at PR, but without specifying which of the three specimens currently kept there. Two specimens are determined as *V. odorata* in Presl's handwriting, PR-305753 and PRC-450948. Both sheets bear mixed collections made up of *V. odorata* mixed with what appears to be a species of genus *Dimeranda* Schltr. We select the two leaves and fruits on the left side of the sheet at PRC as lectotype (Fig. 30).

Garay (1978) also typified *V. ensifolia*, a synonym of *V. odorata*, citing material at K and P. But again failed to specify which specimen he selected as lectotype precisely. The sheet of *V. ensifolia* at K (K-000463744; Fig. 31) includes two different collections, a dried plant collected by Goudot in Cauca, Colombia (with a duplicate at P), and a drawing of a flower from a specimen in the herbarium of the Pharmaceutical Society. Both elements are cited in the protologue, but we are unable to confirm that the illustration, which was done afterwards by a third party, is indeed based on Goudot's original material. Considering that the author explicitly states he described the species based on dried specimens and that the sketch was not made by him, we designate Goudot's dried specimen of as lectotype, considering the illustration as material form a different collection.

Vanilla fimbriata Rolfe resembles *V. odorata*, *V. insignis* Ames and *V. labellopapillata* A.K.Koch, Fraga J.U.Santos & Ilk.-Borg. It is excluded from the synonymy of *V. odorata* pending a thorough inspection of the original materials.

8. *Vanilla phaeantha* Rchb.f., Flora 48: 274. 1865. Fig. 37B, 38–42. *Vanilla planifolia* var. *macrantha* Grisebach, Vcat. Pl. Cub. 267. 1866.

TYPE: CUBA. *C. Wright 3351* (lectotype designated here: K-000463762!, Fig. 38, specimen on the left; isolectotypes: W-43472!, illustration; AMES-00090738!, specimen on the left; MO-2056007!, segment in top left corner; G-00190805!, specimen on the far right; GOET-008712!, flower; MA-607142!, top, center segment; BM-000062803!; Fig. 39).

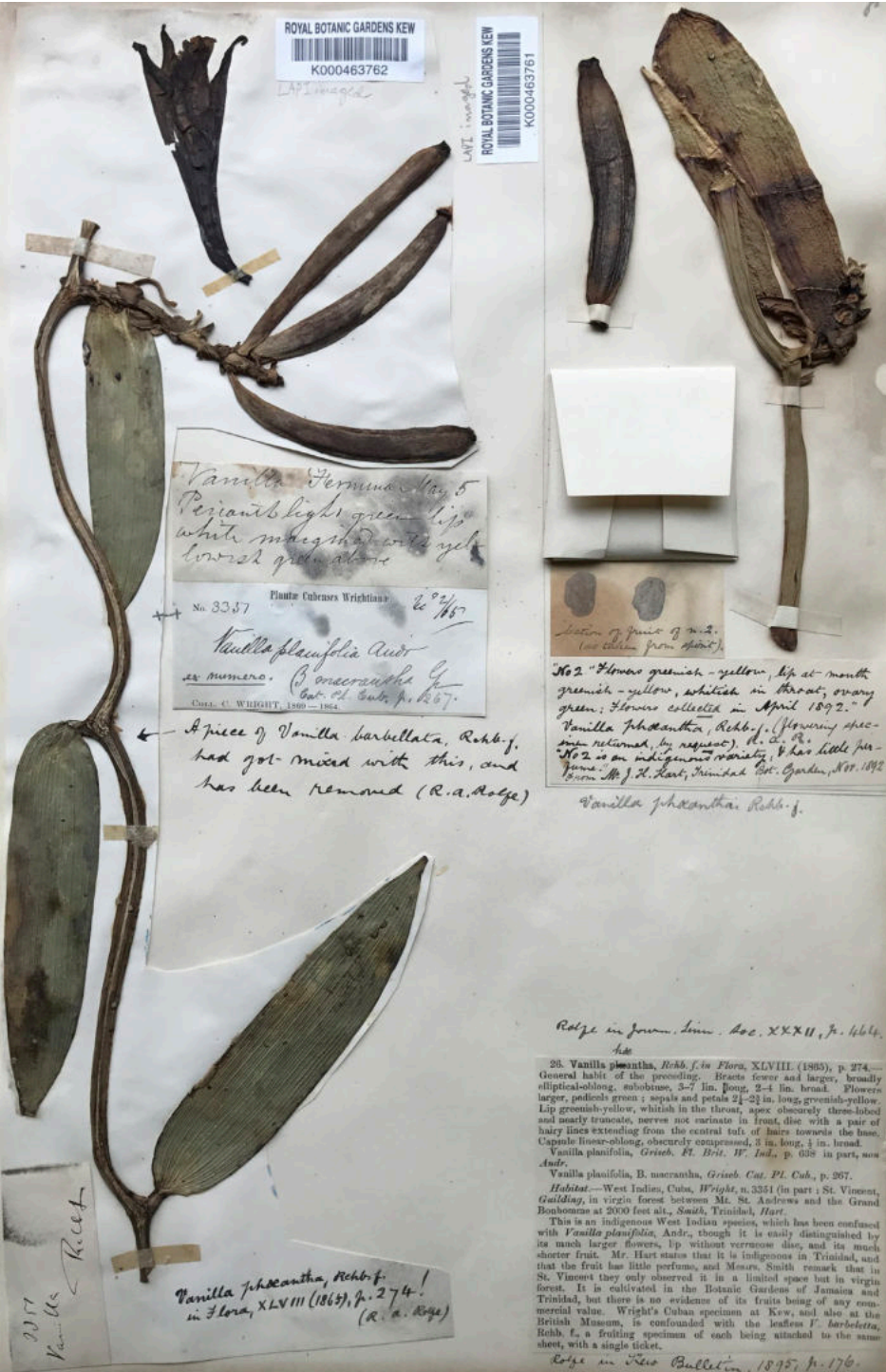


FIGURE 38. The type of *Vanilla phaeantha* Rchb.f. is a mixed collection based on Wright 3351. A handwritten note by Rolfe explains he has removed a piece of *V. barbellata* from the sheet K-000463762 at Kew. The specimen on the left is here selected as lectotype. Photograph by APK.



FIGURE 39. Type material of *Vanilla phaeantha* based on Wright 3351. A. Lectotype at Kew (K). B. Sketch of *V. phaeantha* at Vienna (W). C. Isotype at MO, the red arrow indicates the piece that belongs to this species. D. Isotype at AMES, the red arrow indicates the piece that belongs to this species. A–B photographs by APK; C, © copyright of Missouri Botanical Garden, Saint Louis; D, © copyright of Harvard University, Cambridge.



FIGURE 40. *Vanilla phaeantha*. **A.** Lectotype of *Vanilla gardneri* Rolfe based on *Gardner* 245 at K © copyright of the Board of Trustees of the Royal Botanic Gardens, Kew. **B.** Type of *Vanilla bahiana* Hoehne based on *Ferreira da Cunha* s.n. courtesy of the Herbário do Instituto de Botânica (SP).

Syn.: *Vanilla gardneri* Rolfe, Bull. Misc. Inform. Kew 1895: 177. 1895, **syn. nov.**
LECTOTYPE: BRAZIL. Morro do Flamengo, near Rio de Janeiro, *Gardner* 245 (K!, Fig. 40aA; SYNTYPES: BRAZIL. Parnagua District, Piahy Prov., *Gardner* 2733 (K!); Natividade, Goyaz, *Gardner* 3449 (K!). Pernambuco, at Igarassu, *Ridley, Lea & Ramage* s.n. (K, not found); near Rio, *Burchell* 894 (K!); San José de Laranjeira, Pará, *Burchell* 9829 (K!).

Syn.: *Vanilla bahiana* Hoehne, Arq. Bot. Estado São Paulo, 2(5): 108, pl. 43. 1950, **syn. nov.**
TYPE: BRAZIL. Zona litorânea da Bahia, Nov 1947, *Ferreira da Cunha* s.n. (SP-54661!, Fig. 40B).

Hemiepiphytic vine, branching, leafy. *Stems* waxy, terete, smooth, green, 5–12 mm; internodes 8–15 cm long. Aerial free *roots* terete, pale brownish, up to 10 cm long, ca. 3 mm thick; attaching roots strongly flattened up to ca. 5 mm wide. *Leaves* subsessile, the petiole twisted, canaliculate, up to 8 mm long; blade oblong to narrowly oblong, base rounded-subcordate, apex acute-apiculate to obtuse, chartaceous (xeromorphic), green, margins revolute, 10.3–19.0 × 2.2–5.0 cm. Inflorescence a raceme of 2.5–4.5 cm long, ca. 4–6 mm thick, peduncle 15–29 mm long, rachis 11–15 mm long, producing 4–6 flowers successive, 1 open at once, ephemeral. *Flowers* with the segments spreading; tepals greenish-white, lip white yellowish to white greenish stained with yellowish, greenish or brownish at edges. *Ovary* straight to arcuate, subterete, smooth,

42–50 × 4–5 mm. *Dorsal sepal* long oblanceolate, 62–74 × 10.5–14.0 mm, blade concave, ca. 12-veined, smooth, fleshy; base long unguiculate, attenuate, canaliculate, the claw 20–25.0 × 3.0–5.0 mm, apex acute-subacute, subcalyptrate. *Lateral sepals* strongly oblique, long oblanceolate, arcuate, 58–74 × 12.0–15.0 mm, blade concave smooth, fleshy, ca. 14-veined, base long unguiculate, attenuate, canaliculated, claw ca. 22 × 5 mm; apex acute, subcalyptrate and minutely warty abaxially to the apex. *Petals* long linear, arcuate, slightly sigmoid, 61.0–75.0 × 8.5–14.0 mm, ca. 10-veined; base long attenuate, canaliculated distally, with an elevated axial, flat keel abaxially ending in a triangular, acute, terminal process ca. 1 mm long; apex subacute-obtuse. *Lip* attached to the column along the margins of the basal half (42–52 mm), tubular, trumpet-shaped, conspicuously cymbiform, deepest near the middle, axially grooved on the lower surface, 70–85 × 40–45 mm; unguiculate, the claw canaliculate, minute lanate, 26–35 × 3–5 mm; the blade flabellate, ca. 36-veined, somewhat trilobed, lateral lobes rounded, oblique, elevated surrounding the de column, overlapping, margins slightly undulate; mid lobe small, 5–8 × 11–15 mm, conspicuously reflexed, transversally oblong, revolute, margins slightly undulate, apex emarginate; *penicillate callus* at 40–60 mm from the base, made up by ca. 12 congested, retrorse, approximately trapezoidal, fimbriate scales, the scales regularly united each to other along the lateral margins, ca. 9.0 × 5.5–6.0 mm, followed by apical thickened and warty veins forming a low inconspicuous callus. *Column* elongate, conspicuously sigmoid, 51–70 × 5 mm; ventral surface lanuginose towards the apex, below the stigma; apex dilated, vertical wings somewhat bilobed, the lower lobe falcate, ca. 2.0 × 3.5 mm. *Stigma* trilobed, with a convex, midlobe, ca. 3.0 × 4.5 mm, lateral lobes transversely oblong. *Anther* versatile, attached to the clinandrium margin, yellowish, 4 × 5 mm, subquadrate. *Pollen* not forming a clear pollinarium but a sticky, tow soft, granular mass.

SPECIMENS STUDIED: UNITED STATES OF AMERICA. Florida, Fahakahatchie [Fakahatchee], 10 Jun. 1904, *A.A. Eaton* 1129 (AMES-02031237!; AMES-02031238!; AMES-02031239!; AMES-02031240!; AMES-02031241!; AMES-02031242!; AMES-02031243!; NY!; BM; K). Everglades, *K. Bradley* s.n. (JBL, photograph!; Fig. 41A). MEXICO: Yucatán, *S. Villanueva-Viramontes* s.n. (Photograph in Villanueva-Viramontes *et al.* 2017!). CUBA:

Camagüey, Sierra de Cubitas, 27 Abr. 1986, *Еленевская* *J.* 1480 (MW-0572988!). Santa Clara, Soledad, Cienfuegos, 21 Sep. 1927, *J.G. Jack* 5474 (NY!). Santa Clara, Soledad, Cienfuegos, 20 Feb. 1927, *J.G. Jack* 4775 (NY!; AMES). Ranchuelo, pueblo entre Cienfuegos y Santa Clara, Dec. 1902, *E. Cuesta* 611 (NY!). Santa Clara, near Guanabana, 260 m, 28 Feb, 1 Mar. 1910, *N.L. Britton*, *F.S. Earle* & *P. Wilson* 4740 (NY!). Oriente, Bayate, Sabana Miranda, 1 Jun. 1915, *E.L. Ekman* 5853 (NY!). Oriente, forest about Paso Estancia, Apr. 1909, *J.A. Shafer* 1567 (NY!). Pinar del Río, Río Guao, 26, 27, Feb. 1911, *N.L. Britton*, *E.G. Britton* & *J.F. Cowell* 9639 (NY!; AMES). Pinar del Río, Sierra de Cabra, on Guane Road, 9, 11, Sep. 1910, *N.L. Britton*, *E.G. Britton* & *C.S. Gager* 7274 (NY!). Pinar del Río, 24 Apr. 1903, *J.A. Shafer* 316 (NY!). Camaguey, vicinity of La Gloria, Feb. 1909, *J.A. Shafer* 201 (NY!). Matanzas, Valley of the San Juan, 18 Mar. 1903, *N.L. Britton*, *E.G. Britton* & *J.A. Shafer* 407 (NY!). JAMAICA: December 4, 1891, *W. Faucett* 2 (K!). Dolphin head and vicinity, 200 m, 17 Mar. 1908, *N.L. Britton* & *A. Hollick* 2201 (NY!). TRINIDAD & TOBAGO: Aripo Savannah. December 12, 1952, *R.E.D. Baker* 14733 (K!). July 4, 1911, *W.E. Broadway* 4427 (K!). Trinidad, Nov. 1892, *Hart* 2 (K-000463761!). Gasperee Island, 13 Mar. 1920, *E.G. Britton* & *D. Coker* 555 (NY!; AMES). MARTINIQUE: (BM-000062803!). COSTA RICA: Puntarenas, Buenos Aires, Potrero Grande. Clavera, Camino a la Quebrada Palacios y regiones de Sabanas, *A. Karremans* 7045 (JBL-spirit!, Fig. 42). Alajuela, April 15, 1925, *O.F. Cook* s.n. (SEL!). PANAMA: Brushy slope; large herbaceous vine, common, Tumba Muerto Road, near Panamá, January 6, 1924, *P.C. Standley* 29731 (AMES-31439!). Balboa, “Tapia”, alt sea level, grows out in much sunlight, sepals & petals pale green; lip white with stain of brownish color at edge, flowers in April, 1924, *C.W. Powell* 412 (AMES-28219!). Common, sea level, February 1924, epiphyte, Hort. *Powell* 137, *C.W. Powell* 3507 (AMES-28290!). Bismark above Panama, Fls. nearly white except greenish apex; climbing on trees several yards, March 12, 1908, *R.S. Williams* 588 (NY!; US-678159!). Ancon Hill, June 4, 1923, *W.R. Maxon* 6779 (AMES-33689!; US-1180005). COLOMBIA. Santander, Girón, 1000 m, 20 Jan. 2007, *J.F. Caroprese* 007 (COL-000257401!; COL-000430711!, stem with small leaves, the second stem with large leaves is *V. pompona*). Bucaramanga, Universidad Industrial de Santander, cultivos experimentales del Centro de Excelencia CENIVAM, 1010 m, 30 Abr. 2014, *L. Sierra* & *Y. Córdoba* 004 (COL!). Cundinamarca, Guaduas, por la carretera a Dindal, 3 km abajo del puente sobre el Río Negro, 400–450 m, 5 Mar. 1981, *R. Jaramillo*, *H. Bernal* & *G. Chavarro* 6772 (COL-000430712!; COL-000430891!). Magdalena, Tucurínca, 100–200 m, 28 Abr. 1948, *R. Romero-Castañeda* 1069 (COL!). Magdalena, Tucurínca, 28 Feb. 1950, *R. Romero-Castañeda* 2143 (COL!). Sucre,

- San Pedro, entre Juan Arias y San Pedro, 10 Sep. 1963, *R. Romero-Castañeda 9868* (COL!). Departamento del Cesar, Chimichagua, Candelaria, Finca La Belleza, 38 m, 9°11'57.6" N, 73°52'24.8" W, 2 Jul. 2007, *N. Sánchez Gómez et al. 022* (COL!). Comisaría del Vichada, entrada de raudal San Borja, Ventanas, ca. 100 m, 17 Mar. 1971, *P. Pinto & C. Sastre 1315* (COL-000430892!); COL-000430808!). Bolívar, 7 km de Arenal, cerca de Carrizal, 21 Abr. 1966, *E. Forero & R. Jamarillo 472* (COL!). Santander, highway between Bucaramanga and Surata (km 8), 730 m, 20 Jul. 1965, *F.A. Barkley & M. Valderama 35275* (AMES!). Vichada, Parque Nacional Natural "El Tuparro", Centro Administrativo, 5°20' N, 67°51' W, ca. 90 m, 8 Mar. 1985, *J.L. Zarucchi & C.E. Barbosa 3637* (GH!). Cundinamarca, Tocaima, Quebrada Cachimbulo, sobre la carretera a Girardot, 500 m, 9 Jun. 1955, *H. García-Barriga 15373* (AMES!). Barranquilla, *Bro. Elias 1523* (F-876223!). Unknown locality, *Y. Alomia s.n.* (JBL, photograph!; Fig. 41C). Santander, Chicamocha, *R.T. González s.n.* (JBL, photograph!; Fig. 41D). VENEZUELA. Lara: Selva de galería a lo largo del río, afluente del Río Diquiva, vecindades de Puricaure, Distrito Torres. Lat. 10°3' N, 70°25' W, al sur de la carretera 5. Alt. 500 m, 27 Mar. 1975, *J.A. Steyermark & V. Carreño Espinosa 111705* (F-1804735!). Bolívar: woods 1-10 km. NW of Upata, on road to San Felix, between Upata and Altagracia, alt. 700 m, 31 Jul. - 1 Aug. 1944, *J.A. Steyermark 57723* (F-1250116!). La Paragua, riachuelo Surama, alt. 70 m, 8 Mar. 1940, *L. Williams 12514* (F-1079459!). Zulia: Ecoparque "Ojo de Agua El Cardón", *J.J. Ferrer-Paris s.n.* (JBL-photo!, Fig. 41B). BRAZIL: *Schott 4684* (W!). Brazil (W-21468; W-3472!). Distrito Federal, Brasília. Estação Ecológica do Jardim Botânico de Brasília. Centro Oeste, 22 Sept. 2006, *A.H. Salles, 4268* (RB-00672307!). Espírito Santo, São Mateus. Ilha de Guriri, 15 Dec. 1996, *M.C.F. Jesus 90* (VIES-016203!). Bahia, ILHÉUS. Estrad de acesso a Vil Brasil. Livença/Vila Brasil. acesso a esquerda pelo areial que passa por um depósito de lixo. Área antropizada, 30 Jun. 2000, *F. S. Juchum 42* (CEPEC-00085923!). Brejões. Rod. Amargosa/Brejões ca. 28Km. Margem da Rodovia, 25 Feb. 2000, *J. Jardim 2917* (CEPEC-00088412!). Bahia, PORTO SEGURO. Praia de Taípe. Ca. 10Km de Arraial d'Ajuda., 02 Mar. 1981, *S. C. Sant'Ana 1044* (CEPEC-00093777!). Bahia, Entre Rios. Fazenda Rio do Negro. Residual stands of the Atlantic Forest of the Rio do Negro valley, ca. 15 km southeast of Entre Rios. 08 Feb. 2012, *A.V. Popovkin 1054* (HUEFS-182533!). Espírito Santo, Linhares. Pontal do Ipiranga, 16 Jan. 1996, *A.M. Assis 37* (VIES-016254!). Same locality, 18 Apr. 1996, *A.M. Assis 123* (VIES-016260!). Espírito Santo, Vitória. Reserva Biológica de Camburi, 21 Jan. 1998, *A.M. Assis 377* (VIES-016257!). Same locality, 09 Feb. 1998, *A.M. Assis 412* (VIES-016259!). Bahia, Salvador. Parque das Dunas, trilha interpretativa. Ponto 1.200m, 15 Nov. 2014, *F.F.V.A. Barberena 334* (ALCB-008300!). Bahia, Mata de São João. Reserva Florestal de Sapiranga, 17 Dec. 2016, *F.F.V.A. Barberena 395* (ALCB-038827!). Bahia, Salvador. Parque das Dunas, caminho para a Lagoa Vitória, 25 Oct. 2014, *F.F.V.A. Barberena 331* (ALCB-008301!). Bahia, Santa Cruz Cabralia, 31 Oct. 1966, *R.P. Belém 2811* (UB-0019154!). Rio de Janeiro, Rio de Janeiro. Capoeira velha na mata abaixo do Sumaré, 05 Apr. 1929, *A. Ducke s.n.* (RB-00260120!). Bahia, Nova Viçosa. Estrada para Nova Viçosa, 22 Sept. 1979, *G. Martinelli 6009* (RB-00260083!; CEPEC-00017627!). Bahia, Maraú. km 14 da estrada Maraú - Ubaituba, 18 May 1985, *G. Martinelli 11060* (RB-00260106!). Rio de Janeiro, Rio de Janeiro. Restinga de Sernambetiba, 02 Nov. 1952, *Markgraf s.n.* (RB-00260111!). Rio de Janeiro, Maricá. Restinga da Barra de Maricá, 29 Mar. 1989, *M.F. Freitas 34* (RB-00260098!). Bahia, Porto Seguro. Km 18 da BR-367 liga Porto Seguro/ Cabralia, 04 Dec. 1980, *A. Eupunino 555* (CEPEC-00024681!). Bahia, Itacaré. Entre a praia do Farol e a Ribeira, 01 Jan. 1992, *A.M. Amorim 957* (CEPEC-00056936!). Rio de Janeiro, São Francisco de Itabapoana. Gargaú, Abatedouro. Restinga de moitas, 21 Ago. 2003, *C.N. Fraga 1042* (RB-00550200!). Espírito Santo, Conceição da Barra. Pontal do Sul - Ilha de Guriri, 12 Mar. 1997, *M.C.F. Jesus 176* (VIES-016202!). Rio de Janeiro, Cabo Frio. Sept. 2013, *D. Hottz s.n.* (RB-01094255!). Bahia, Valença. Ramal a esquerda da Rod. liga Valença/Guaibim, entrada Km 9, 11 Dec. 1980, *L.A.M. Silva 1245* (CEPEC-00022966!). Bahia, BELMONTE. 24Km SW Belmonte, Rod. p/ Itapebi, 28 Apr. 1980, *R.M. Harley 17366* (CEPEC-00010807!). Rio de Janeiro, Rio de Janeiro. Grumari, formação de restinga Pós-Praia, pista principal da praia Parque Natural Municipal de Grumari, 02 Mar. 2016, *R. Linhares s.n.* (RB-01111540!). Bahia, Feira de Santana. Maria Quitéria, Serra de São José, 25 Nov. 2001, *C. van den Berg 857* (HUEFS-069701!). Bahia, Santa Terezinha. Serra da Jibóia, 10 Jan. 2006, *C. van den Berg 1558* (HUEFS-161515!). Bahia, Santa Terezinha. Morro da Pioneira, Serra da Jibóia, 13 Dec. 2009, *C. van den Berg 1954* (HUEFS-161348!). Bahia, Inhambupe. BR-110, *R.P. Orlandi 152* (RB-00260149!). Rio Grande do Norte, Parnamirim, Loteamento Caminho do Sol, estrada Nova Parnamirim/Pium, 24 Nov. 2007, *A. Ribeiro & M. Araújo 282* (HUEFS!). Rio Grande do Norte, Pedro Velho, APA Piquiri-Una, Mata do Pilão, prox. trilha, no chão, sob o bosque, 6°23'10" S, 35°15'52" W, 105 m, 08 Oct. 2017, *G.S. Garcia 603* (UFRN!). Nísia Floresta, Sete Lagoas, Restinga, 6°00'46" S, 35°07'03" W, 21 m, 18 Aug. 2016, *V.F. Sousa 461* (UFRN!). São Gonçalo do Amarante, Área próxima ao aeroporto. Fragmento de Floresta Estacional Decidual, solo arenoso, 5°45'49" S, 35°23'36" W, 80 m, 23 Oct. 2016, *E.O. Moura & P.H.D. Marinho 1014* (UFRN!). Canguaretama,



FIGURE 41. *Vanilla phaeantha* flowering specimens from different localities across its distribution. **A.** Florida, K. Bradley s.n. **B.** Venezuela, J. Ferrer-Paris s.n. **C.** Colombia, Y. Alomía s.n. **D.** Colombia, Santander, R.T. González s.n. **E.** Brazil, C. van den Berg s.n. **F.** Brazil, C. van den Berg s.n. Photographs by the collectors kept at JBL.

Rod. BR 101, CA. 1,5 km N da cidade. Tabuleiro, Mata Atlântica, 6°20'37" S, 35°10'04" W, 82 m, 19 Dec. 2010, *Jardim et al.* 5864 (UFRN!). Ceará Mirim, Rod. 064, entrada na RN 309 para Pureza, ca. 4,3 km da entrada, ca. 3 km a leste seguindo pelo canarial, Fácies de Cerrado, 5°35'59" S, 35°25'58" W, 55 m, 14 Dec. 2011, *Jardim et al.* 6169 (UFRN!). São Gonçalo do Amarante, Fazenda Arvoredo, ca. De 5 km a margem dda área do Aeroporto São Gonçalo do Amarante, em direção a comunidade Califórnia, floresta estacional, 5°45'58" S, 35°32'70" W, 100 m, 20 Sep. 2011, *J.L. Costa-Lima et al.* 597 (UFRN!). Macaíba, Escola Agrícola de Jundiá, Trilhas no tabuleiro ao lado do açude, 5°53'16" S, 35°21'21" W, 48 m, 10 Dec. 2019, *V.P. Moreira* 687 (UFRN!). Sergipe, São Cristóvão, 11°00'53" S, 37°12'23" W, 30 Abr. 2015, *B.V. Pereira* 24 (ASE!). Sergipe, São Cristóvão, 11°21'03" S, 37°26'54" W, 4 Mar. 2016, *B.D. Silva & E. Santos* 67 (ASE!). Sergipe, Pacatuba, Rebio de Santa Isabel, 3° barreta após a sede, restinga, 10°39'17" S, 36°45'11" W, 21 Feb. 2013, *E.V.S. Oliveira & E.S. Ferreira* 168 (ASE!). Pernambuco, Igarassu, Mata Atlântica, Fragmento Chavem 24 Nov. 2009, *E. Pessoa & J.A.N. Souza* 150 (RB!). Goiás, Colinas do Sul. Estrada de acesso ao rio Preto, km 6, a partir da entrada da fazenda Vale das Araras, 13°42'50" S, 48°08'07" W, 320 m, 15 Oct. 2001, *G. Pereira-Silva* 5572 (CEN-43860!; CEN-51335!). Goiás, Luziania, Fazenda Corumbá (Prop. João Mariano Machado), margem direita do rio Corumbá, 11 Jun. 2003, *G. Pereira-Silva* 7912 (CEN-78536!). Goiás, Luziania, Fazenda Corumbá (Prop. João Mariano Machado), margem direita do rio Corumbá, 11 Jun. 2003, *G. Pereira-Silva* 7913 (CEN-63255!). Tocantins, Palmeirante, Estrada Palmeirante - Itacajá, 07°36'34" S, 47°52'36" W, 211 m, 28 Aug. 2008, *A.A. Santos et al.* 3025 (CEN!). Minas Gerais, UNAI, Mata à direita da ponte de madeira (acesso para Palmital), margem esquerda do rio Preto, 16°12'14" S, 47°20'03" W, 17 May 2002, *A.A. Santos et al.* 1241 (CEN!). Minas Gerais, UNAI, Ilha a montante do túnel de desvio, cerca de 500 m da ponte de madeira. Margem esquerda do rio Preto, 16°12'18" S, 47°20'11" W, 12 Sep. 2002, *A.A. Santos et al.* 1508 (CEN!). Minas Gerais, Araguari, próximo a região do Córrego do Salto, estrada Araguari - Indianópolis, 5 Oct. 2016, *W.M. Silva, C.F. Francisco & S.C. Augusto* s.n. (HUFU!). Mato Grosso: Itaúba, Resgate de Flora da UHE Colider, Lote G de supressão, 10 Oct. 2015, fl., *M.E. Engels* 3755 [HERBAM, MBM, illustration and photographs in *Engels et al.* (2020)!]. Bahia, Salvador, Área de Proteção Ambiental das Lagoas e Dunas do Abaeté, *F.F.V.A. Barberena & L.V. Aguiar* 334 [ALCB, photographs in *Anjos et al.* (2016)!]. Maranhão: Caxias, Área de Proteção Ambiental Municipal do Inhamum (APA Inhamum), *M.S. de Oliveira et al.* s.n. [photographs in *Ferreira et al.* (2017)!]. Bahia, *C. Van den Berg* s.n. (JBL, photograph!; Fig. 39E). Bahia, *C. Van den Berg* s.n. (JBL, photograph!; Fig. 41F).

OTHER SPECIMENS: MEXICO: Yucatan. Cenote Mucul, Cerca de Sotuta, selva baja caducifolia, ca. 100 m, *G. Carnevali* 4885 (cultivated specimen, not preserved). Quintana Roo: Mpio. Othón P. Blanco, Ejido Caobas, alrededores de la Sabana del Jaguactal, unos 21 km al sur de la carretera principal *Xpujil-Chetumal*, *A. Cibrián, R. Jiménez, G. Carnevali* 21, 23 (AMO-sterile). CUBA: Limones, 8 May 1926, *W.R. Singleton* s.n. (AMES). Limones, 8 Jun. 1926, *W.R. Singleton* s.n. (AMES). Limones, 14 Apr. 1926, *W.R. Singleton* 862 (AMES). Soledad, 1904, *R.M. Grey* s.n. (AMES). Pinar del Rio La Cajálbana, La Mulata, 14 Apr. 1953, *J. B. Acuña Galé et al.* 18508 (AMES). ST. VINCENT: *Guilding* s.n. (K); *H.H. & G.W. Smith* 1336 (K). PANAMA: Panama. Vine climbing up trees in low thicket. Farfan Beach; roadside thicket adjacent to beach. 30 March 1969, *J.D. Dwyer, L.N. Durkee & J.R. Castillón* 4691 (MO-980689). Climbing vinelike on the Farfán Beach area, forward dune-high beach community, 18 June 1971, *R.L. Lazor* 5358 (SCZ-2262; sterile), Veraguas: Carretera Panamericana, 4.3 km al W de El Higo, ca. 20 km al W de La Mesa, sabana de Curatella, Clethra y Roupala con selva riparia de Andira, Pithecellobium, Enterolobium y Acacia, bejuco con frutos jóvenes, extendido sobre algunos arbolitos de la sabana, hojas muy pequeñas, tallos delgados, *M. Soto* 9920 (PMA). BRAZIL. Maranhão: Caxias, Área de Proteção Ambiental Municipal do Inhamum (APA Inhamum), near the Inhamum stream (gallery forest), 04°53'31" S, 043°25'34" W, fl., 30 Dec. 2015, *M.S. de Oliveira & E.O. Silva* 02 (HENAC 151); *ibid.*, Primavera Stream (gallery forest), 04°50'32" S, 043°29'30" W, fl., 27 Oct. 2016, *M.S. de Oliveira & E.O. Silva* 05 (HENAC 154); *ibid.*, fr., 31-Dec. 2016, *M.S. de Oliveira; E.O. Silva & A.W.C. Ferreira* 07 (HENAC 156).

DISTRIBUTION: Very broadly distributed in the Neotropics, where it is known from U.S.A. (Florida), Mexico, Costa Rica, Panama, Cuba, Jamaica, Dominican Republic, Martinique, Trinidad & Tobago, Colombia, Venezuela and Brazil (Fig. 37b).

EXTENT OF OCCURRENCE: 14,046,406.026 km².

Vegetatively, *Vanilla phaeantha* can be recognized by the robust plants with internodes generally longer than the leaves. The leaf is typically oblong to narrowly oblong, with the margins and apicule revolute. The large flowers, with their long, spreading segments, are very characteristic; the tepals are yellowish-green, with a white lip, that is stained with yellow, green or brown apically. The column has a conspicuous bend above the middle, which can be easily observed even in dried specimens. The trumpet-shaped lip has a broad obovate-rhomboid blade with undulate margins.

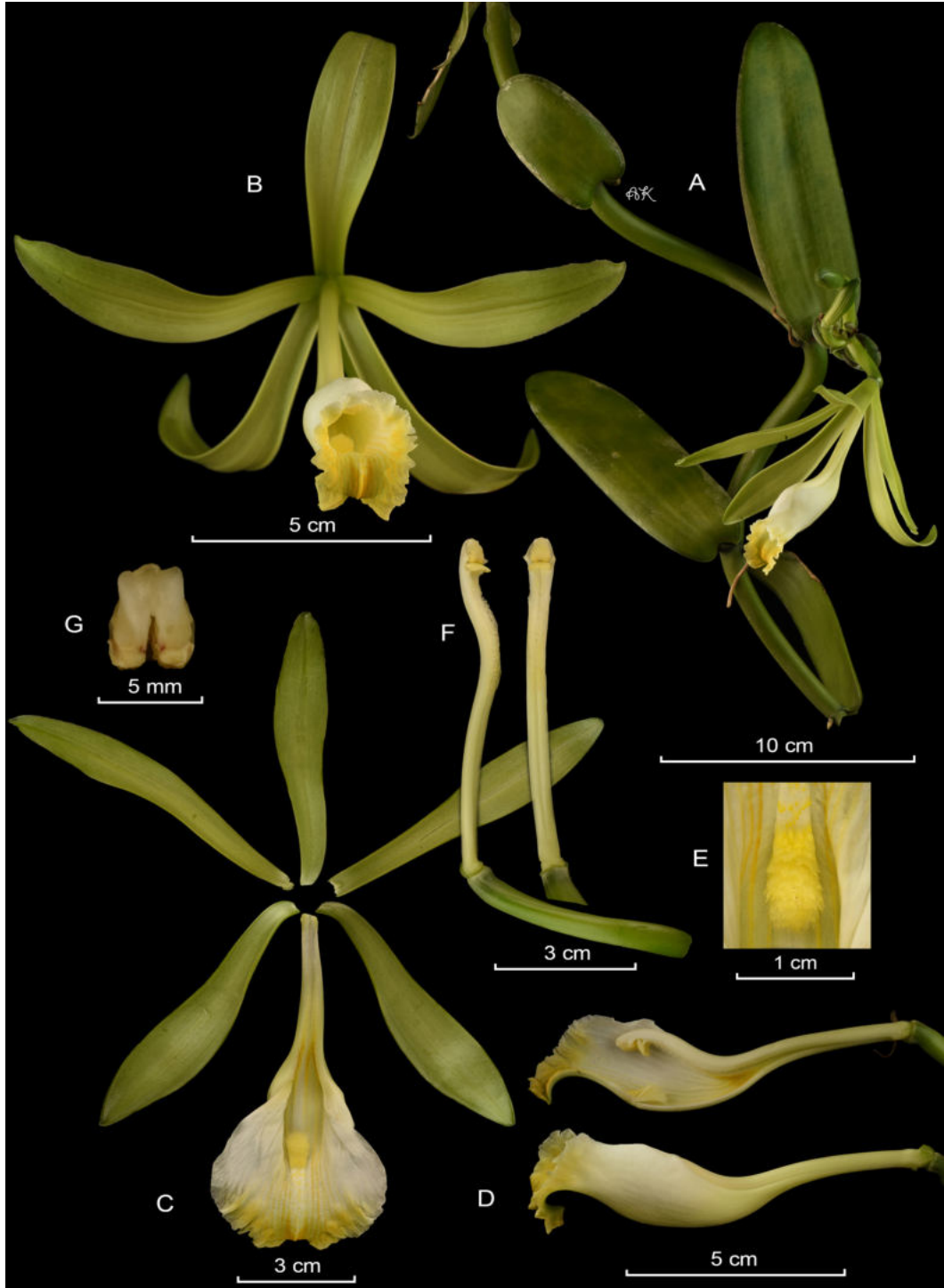


FIGURE 42. LCDP of *Vanilla phaeantha*. **A.** Habit. **B.** Flower. **C.** Dissected perianth, flattened. **D.** Lip and column lateral view. **E.** Callus. **F.** Column, ventral and lateral view. **G.** Anther cap and pollinia. By AK based on Karremans 7045 (JBL-spirit) from Costa Rica.

Reichenbach described *V. phaeantha* on the basis of *Wright 3351*. Unfortunately, different *Vanilla* species from Cuba were distributed under that number to diverse herbaria. However brief, the description corresponds well with the sketch determined as *V. phaeantha* in his herbarium (W-43472, Fig. 39B), and which was clearly based on the specimen at Kew (K-000463762, Fig. 38, 39A). The latter is therefore selected as lectotype. On the specimen is a note by Rolfe indicating that “A piece of *Vanilla barbellata* Rchb.f. had got mixed with this, and has been removed”. Indeed, the isolectotypes at AMES (Fig. 39D) and MO (Fig. 39C) consist of two different species of which only parts are *V. phaeantha* (indicated with an arrow); also mixed are the specimens at G, GOET and MA (MA-607142). None of the elements found on the *Wright 3351* specimen kept in Paris (P-00128658) and Madrid (MA-607143) seem to belong to *Vanilla phaeantha* and that material is therefore excluded.

Vanilla gardneri is another cryptic taxon that has long been a source of confusion. Rolfe (1895) cited six different collections as syntypes of this taxon. Four of them, *Gardner 245*, *Gardner 2733*, *Gardner 3499* and *Burchell 894* are conspecific with the Brazilian taxon that was later described *Vanilla bahiana* (= *Vanilla phaeantha*). Whereas, *Burchell 9829* belongs to a completely unrelated taxon in the *Vanilla hostmannii* Rolfe group. This has caused great confusion as to the identity of *Vanilla gardneri*, a species that has been generally treated as a member of the *V. hostmannii* group. Nonetheless, Rolfe included *Burchell 9829* with doubt and his concept of *V. gardneri* clearly refers to *V. phaeantha*. Soto Arenas & Cribb (2010) selected *Gardner 245* as lectotype, which is congruent with Rolfe’s concept of this species. As such we find the taxon to be an earlier name for *V. bahiana*, and thus conspecific with *V. phaeantha*.

Vanilla bahiana has been commonly considered a distinct species restricted to the xerophytic coastal caatinga habitats around Bahía in Brazil, whereas *V. phaeantha* has been generally believed to be restricted to North and Central America and the Antilles. It is said to differ from *V. phaeantha* in the smaller flowers and more well defined three-lobed lip (Soto Arenas & Cribb 2010). Nevertheless, we find that the morphological features found in plants and flowers of different populations of *V. phaeantha* and *V. bahiana*

fully overlap and can’t find any feature that consistently distinguish the two (Fig. 41). It has now been amply confirmed that in Brazil the species is not confined to the coastal caatinga, and the species can be found growing in both xerophytic areas as semideciduous forests across its distribution. As the *V. phaeantha* range grows further south, now including Colombia and Venezuela, and the Brazilian populations keep appearing more inland the alleged gap in its distribution gets narrower (Fig. 37b). The two population are probably not as isolated as it once seemed to appear.

9. *Vanilla planifolia* Andrews, Bot. Repos. 8: t. 538. 1808. Fig. 43–54, 55A.

Vanilla aromatica var. *planifolia* (Andrews) F.Buys., L’orchidophile; Traité Théor. & Prat.: 513. 1878. *Notylia planifolia* (Andrews) Conz., Fl. Taxon. Mex. 3: 151. 1947.

LECTOTYPE: WEST INDIES. The finest specimen in England, and the only one that has blossomed, is in the choice collection of the Right Hon. Charles Greville, at Paddington, from which our drawing was taken. We are informed that it is a native of the West Indies, and was introduced to this country by the Marquis of Blandford, illustration published by Andrews in Bot. Repos. 8, 1808: pl. 538 (designated by Garay & Sweet 1974; Fig. 43).

Syn.: *Araco aromaticus* “Tlilxochitl seu flore nigro” [Tlilxochitl or black flower] in *Rerum Medicarum Novae Hispaniae Thesaurus*: 38. 1651 (Fig. 44).

Syn.: *Vanilla viridiflora* Blume, Bijdr. Fl. Ned. Ind.: 422. 1825.

TYPE: “Crescit: in horto botanico Buitenzorg. culta, et ex America australi allata. Floret: Septembri, Octobri” (**lectotype designated here**: L-0063885!, Fig. 45A)

Syn.: *Vanilla sativa* Schiede, Linnaea 4: 573. 1829.

TYPE: [MEXICO] Misantla, “Baynilla mansa Hispano-Mexicanorum. Hab. sponte Papantlae, Misantlae, Nautlae et Colipae inque iisdem pagis colitur”, Schiede s.n. (**lectotype designated here**: HAL-111289!, Fig. 45B; isolectotypes: HAL-110974!, Fig. 45C; BM!).

Syn.: *Vanilla sylvestris* Schiede, Linnaea 4: 573. 1829.

TYPE: [MEXICO]. Papantla, “Baynilla cimarrona, Hispano-Mexicanorum. Hab. Papantlae, Nautlae,



FIGURE 43. *Vanilla planifolia* Andrews plate 538 based on a specimen from Charles Greville, selected as lectotype by Garay & Sweet (1974).

Colipae”, Jan. 1829, *Schiede s.n.* (**lectotype designated here**: HAL-111290!, Fig. 45D).

Syn.: *Vanilla schwackeana* Hoehne, Arq. Bot. Estado São Paulo, n.s., f.m., 1: 125. 1944, **syn. nov.**

TYPE: BRAZIL. Belo-Horizonte, Minas, sem indicações e procedencia e data, *Schwancke 11106* (**lectotype designated here**: RB-37015!, dissected flower on upper right corner, Figs. 46A, 46B).

Syn.: *Vanilla bampsiana* Geerinck, Bull. Jard. Bot. Nat. Belg. 52: 345. 1982.

TYPE: ZAIRE. District du Forestier central: Bikoro, forêt sèche, *Lebrun 1459* (holotype, BR-840615!, Fig. 46C; isotypes, BR-840616!, K-000306647!, WAG-0002582!, WAG-0002581!).

Syn.: *Vanilla sotoarenasii* M. Pignal, Azof.-Bolaños & Grisoni, *Eur. J. Taxon.* 284: 17–22. 2017, **syn. nov.**

TYPE: COSTA RICA. Cahuita (ex hort. parc E. Liais, from plants collected by B. Gosselin in 1993), 8 Oct. 1996, *M. Pignal 396b* (holotype: P-00075132!, Fig. 46D).

Hemiepiphytic, branching, leafy vine, up to several meters high. *Stems* dark green, subterete, smooth,

flexuous, one per internode emerging laterally to the leaf, 4.5–10.0 mm in diameter; internodes smooth or sulcate, 1–13 cm long. *Aerial roots* subterete, 1.5–3.0 mm in diameter. *Leaves* shortly petioled; the petiole 3–13 mm long; blade elliptic to oblong or ovate, acute, acuminate, porrect to deeply recurved, sometimes becoming uncinat, coriaceous, 2.0–20.0 × 0.8–6.2 cm, 9–23-veined. *Inflorescence* axillary or terminal, producing up to 26 successive flowers per raceme, 1-opened simultaneously; peduncle subterete, 0.5–7.0 cm long; rachis up to 1.5–10.0 cm long. *Floral bracts* green, sessile, ovate, obtuse to acuminate, concave, 4–15 × 3–8 mm. *Flowers* with the ovary basally whitish, apically green to yellowish-green, sepals, petals and lip greenish-white to pale yellowish-green, sometimes adaxially more yellowish-green or yellowish in the apical 1/3, penicillate callus whitish with the yellowish apex, column dorsally white, ventrally greenish to yellowish-white or whitish, anther dorsally yellowish-green to yellowish, ventrally whitish, and rostellum dorsally greenish to yellowish-white, ventrally whitish; fragrance sweet. *Ovary* subterete, papillose, arcuate, 25–62 × 3–4 mm. *Dorsal sepal* oblanceolate, cuneate,

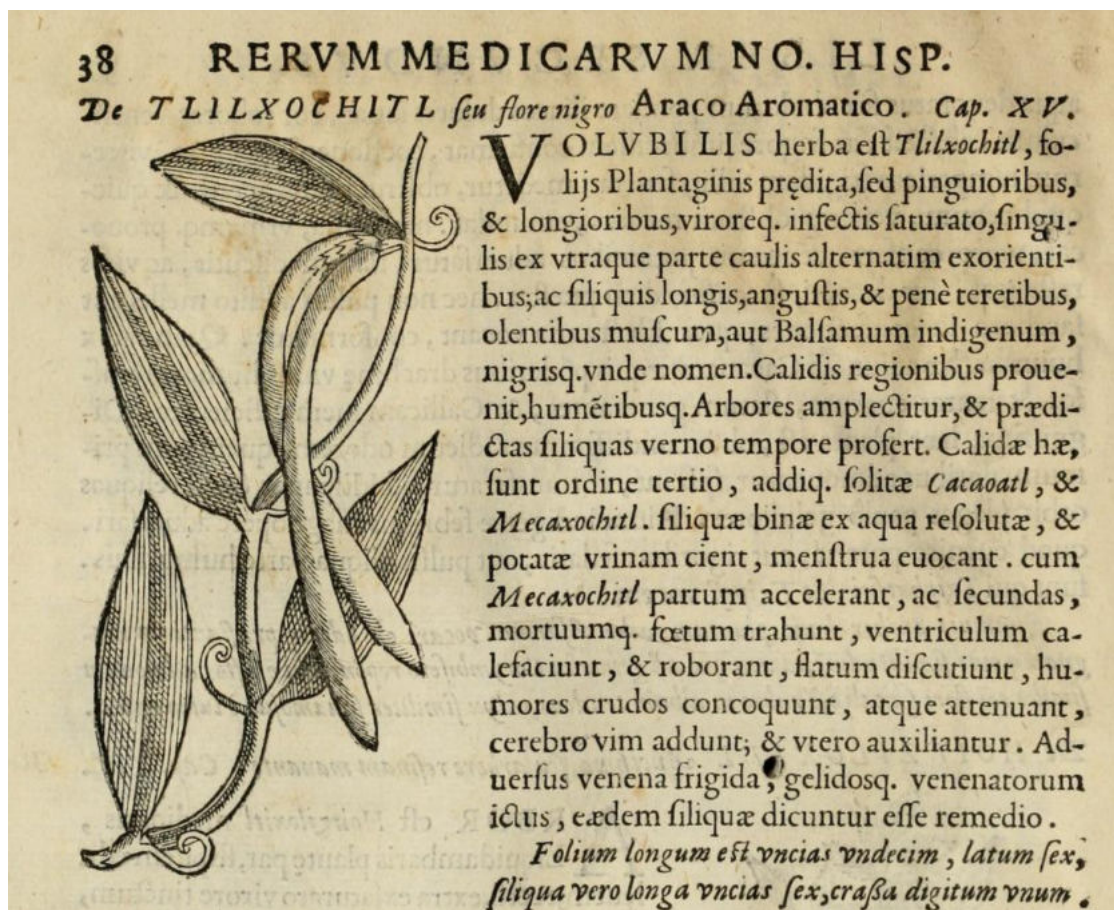


FIGURE 44. Araco aromaticus "Tlilxochitl seu flore nigro" [Tlilxochitl or black flower] in Rerum Medicarum Novae Hispaniae Thesaurus: 38 published in 1651 is one of the earliest illustrations of *Vanilla planifolia*.

acute, lightly concave, lightly arcuate, straight or porrect, fleshy, 7–9-veined, 40–60 × 7–12 mm. *Lateral sepals* obliquely oblanceolate, cuneate, acute, lightly concave, arcuate, fleshy, 7–9-veined, 43–58 × 9–12 mm. *Petals* obliquely elliptic, cuneate, obtuse, lightly concave, arcuate, abaxially with an raised dorsal keel, 9–11-veined, 41–58 × 7–10 mm. *Lip* fused to the column along the margins for 24–28 mm, tubular, trumpet-shaped, trilobed; when spread out 41–55 × 21–28 mm; unguiculate, the claw lightly arched, pubescent, 11–20 × 3–7 mm long; the blade cymbiform, when spread out flabellate in outline, 27–31-veined, the veins papillose, progressively thickened towards the apex forming

grooves, branched; the lateral lobes obtuse, margins undulate, crenate to dentate or lacerate, with teeth up to 2 mm long; the midlobe subrectangular, emarginate to bilobed, recurved, margins undulate, laciniolate to lacerate, 2–9 × 11–12 mm; disc with a *penicillate callus* 25–35 mm from the base, 4–6 × 3–4 mm, made up by 5–7 imbricate, flabellate, lacerate scales, the proximal ones bigger, sometimes united each to other along the lateral margins; continuing apically with 5–7 rows of papillae or warts, progressively thickened and raised towards the apex. *Column* subterete, arcuate inward, 32–39 × 2.7–3.0 mm, ventrally flattened, densely pubescent below stigma, basally glabrous, smooth, lustrous, apex

Right, FIGURE 45. *Vanilla planifolia*. A. Lectotype of *V. viridiflora* Blume (L-0063885), © copyright of the Naturalis Biodiversity Center, Leiden. B. Lectotype of *V. sativa* Schiede (HAL-111289). C. Isolectotype of *V. sativa* Schiede (HAL-110974). D. Lectotype of *V. sylvestris* Schiede (HAL-111290). B-D, © copyright of the Martin-Luther-Universität, Halle.





tri-winged, lateral wings obliquely flabellate, retrorse, mid-wing cucullate, rounded, 5×4 mm. *Stigma* trilobed, with raised lobes. *Rostellum* subquadrate, convex blade. *Anther cap* basally hinged to the clinandrium margin by a laminar, broad filament, movable, obovate, $3.0\text{--}4.2 \times 3.1\text{--}3.5$ mm. *Pollen* a sticky, granular mass. *Fruit* green, turning yellow and then dark brown when ripe, subterete, subclavate, sometimes slightly angulate or sulcate, straight to arcuate, dehiscent, very fragrant, $6.5\text{--}30.0 \times 0.7\text{--}1.5$ cm.

SPECIMENS STUDIED: UNITED STATES OF AMERICA. Hawaii: [Cultivated] Harold L. Lyon Arboretum-Middle Lawn Makai, 31 May 1968, *K. Nagata* 378 (L!). MEXICO: Mexico, W-Indië; Tropen, 28 May 1969, *H.J. van Hattum* 2290 (L!). In virgin xerophytic forests, Izamal, Apr. 1917, *G.F. Gaumer & Sons* 23909 (F-466398, US-1268044, AMO-photo!). GUATEMALA: Petén. Dolores, in low forest about 2 km. 100 m south of village, 3 May 1961, *E. Contreras* 2239 (LL; AMO-photo!). BELIZE. British Honduras. Orange Walk District. 9.9 km S of Program for Belize Camp., $17^{\circ}45'$ N, $89^{\circ}09'$ W, 16 May 1991, *R. Arvigo* 545, *P. Cocom*. *R. Cocom*, *N. Romero*, *G. Shropshire* & *J. Woodland* (AMES!). Maskall, pine ridge road high ridge, collected for *C.L. Lundell*, 3 Mar. 1934, *P.H. Gentle* 1234 (AMES-41360!, AMES-41361!). Machasa, 50 ft. [15 m], 16 May 1934, *W.A. Schipp* 8-844 (AMES!). Toledo District. Temansh River, along river bank here in wet swampy places, 100 ft. [40 m], 13 Mar. 1935, *W.A. Schipp* S-971 (AMES!). HONDURAS. Lancetilla Valley, 150 ft. [46 m], 8 Dec. 1934, *T.G. Yuncker* 4993 (AMES-02158434!). EL SALVADOR. San Salvador, in garden, 15 Dec. 1922, *S. Calderón* 518 (AMES!, US!). NICARAGUA. Zelaya. Logging camp near Quebrada La Talolinga, ca. $11^{\circ}51'\text{--}52'$ N, $84^{\circ}26'\text{--}27'$ W, 170 m, 18 Aug. 1983, *J. Miller* 1138 & *J. Sandino* (MO!, SEL!). Ibo Tingni, drainage of Caño Sung Sung, N of road between Puerto Cabezas and Río Wawa; approx. $14^{\circ}9'\text{--}11'$ N, $83^{\circ}29'\text{--}31'$ W, less than 10 m, 6 Oct. 1978, *W.D. Stevens* 10667 & *B.A. Krukoff* (SEL!). Monkey Point; beach and bluff near village, ca. $11^{\circ}35'$ N, $83^{\circ}39'$ W, 0–20 m, 7 Apr. 1981, *W.D. Stevens* 20021 & *B.A. Krukoff* (SEL!). COSTA RICA. Cartago: Very common in forest on ridges, seen also by riverside, May 1924, *C.H. Lankester* 847 (AMES!). Limón: Siquirres. Barra de Parismina, $10^{\circ}16'53.03''$ N, $83^{\circ}19'43.21''$ W, 18 m, 8 Feb. 2013, *B. Azofeifa*, *J. García* and *A. Paniagua* 2 (CR!). Hamburg Finca, on the Río Reventazón below Cairo, 55 m, 19 Feb. 1926, *P.C. Standley* 48904 & *J. Valerio* (AMES!, US-

1309657!). In regione Atlantica: "Hamburg", 9 km. ab ore fluminis Reventazon inter Musas cultas, 15 m, 2 May 1930, *G. Cufodontis* 735 (AMES-02158453!, W-1!, W-2! [2 sheets]). Camino a Portete, 30 Jun. 1945, *M. Quirós* 4254 & *V. Sáenz* (CR!). Talamanca, Sixaola. R.V.S. Gandoca-Manzanillo. Sendero hacia Laguna de Gandoca. Aprox. 400 m de la entrada del sendero hacia la laguna, $9^{\circ}35'40.9''$ N, $82^{\circ}36'9.0''$ W, 3 m, 11 Abr. 2012, *A. Estrada* 5331, *J. Sánchez*, *A. Ruiz-Boyer*, *S.E. Bolaños* & *J. Solano* (CR!). Talamanca, Cahuita. P.N. Cahuita. Sector Puerto Vargas. Sendero entre casa de administración del parque punta Cahuita. Aprox. 900 m de la administración, $9^{\circ}44'12.6''$ N, $82^{\circ}48'38.8''$ W, 1 m, 9 May 2012, *A. Estrada* 5378, *J. Sánchez*, *A. Ruiz-Boyer* & *R. Chacón* (CR!). Talamanca. Refugio de Vida Silvestre Gandoca-Manzanillo, $9^{\circ}35'41.05''$ N, $82^{\circ}36'10.30''$ W, 16 m, 14 Nov. 2013, *B. Azofeifa* & *J. García* 47 (CR!). Parque Nac. Cahuita, Puerto Vargas, 12 Abr., *B. Morera s.n.* (USJ!). P. N. Cahuita. Faja Costeña de Limón. Sendero a Puerto Vargas, $9^{\circ}44'20''$ N, $82^{\circ}49'30''$ W, 2 m, 9 Dec. 1993, *E. Lépez* 87, *J.L. Poveda* & *V.H. Ramírez* (CR-1!, CR-2! [2 duplicates]). Talamanca, Cahuita, Cahuita National Park, sector Puerto Vargas, trail from the Rangers Administrative building to Punta Puerto Vargas, $9^{\circ}43'54.4''$ N $82^{\circ}48'53.5''$ W - $9^{\circ}44'48.9''$ N $82^{\circ}48'42.4''$ W, sea level, 26 Apr. 2012, *F. Pupulin* 8274, *D. Bogarín* & *M. Fernández* (JBL!, Fig. 47, 51B–D). Talamanca, Cahuita, Cahuita National Park, sector Puerto Vargas, trail from the Rangers Administrative building to Punta Puerto Vargas, $9^{\circ}43'54.4''$ N $82^{\circ}48'53.5''$ W $9^{\circ}44'48.9''$ N $82^{\circ}48'42.4''$ W, sea level, 26 Apr. 2012, *F. Pupulin* 8276, *D. Bogarín* & *M. Fernández* (JBL!, Figs. 48, 51A). Talamanca, Sixaola. Área no protegida. Gandoca. Finca Cangrejo. Anai, $9^{\circ}34'45''$ N, $82^{\circ}36'20''$ W, 10 m, 24 Mar. 1995, *G. Herrera* 7550 (CR-1!, CR-2! [2 duplicates]). Talamanca. R. V. S. Gandoca-Manzanillo. Puerto Viejo. Punta Uva, peñon inominado adyacente a la Quebrada Ernesto, $9^{\circ}38'30''$ N, $82^{\circ}41'20''$ W, 0 a 10 m, 4 May 2001, *J.F. Morales* 7967 (CR!). Pto. Vargas, Parque Nac. Cahuita, 16 Abr. 1978, *J. Gómez-Laurito* 3674 (USJ!). Pto. Vargas. Parque Nac. De Cahuita, 3 Set. 1978, *J. Gómez-Laurito* 3925 (CR!). A la orilla del bosque anegado, entre Pto. Vargas y la Punta, Parque Nac. Cahuita, ca. nivel del mar, 21 Jun. 1980, *J. Gómez-Laurito* 5563 (CR!). Forest between Punta Manzanillo and Punta Mona, E. of Manzanillo de Talamanca. ca. 8–12 m, $9^{\circ}38'$ N, $82^{\circ}38'$ W, 2 May 1985, *M.H. Grayum* 5257 & *G. Schatz* (CR!, SEL!). Pococi. Refugio de Vida Silvestre Barra del Colorado, Cerro del Tortuguero, summit ridge. $10^{\circ}35'$ N, $83^{\circ}32'$ W, ca. 100–119 m, 22 Jan. 1997, *M.H. Grayum* 11141, *B. Hammel*, *J. Schipper* & *L. Merrill* (CR!).

Left, FIGURE 46. *Vanilla planifolia*. **A.** Illustration of type of *V. schwackeana* Hoehne, based on *Schwancke* 11106. **B.** Lectotype dissected flower on upper right corner of RB-37015 © copyright of Refflora, Brazil. **C.** Holotype of *V. bampsiana* Geerinck, based on *Lebrun* 1459 (BR-840615), © copyright of Meise Botanic Garden, Belgium. **D.** Holotype of *V. sotoarenasii* M. Pignal, Azof.-Bolaños & Grisoni, based on *M. Pignal* 396b (P-00075132), © copyright of the Muséum national d'histoire naturelle, Paris.

- Talamanca, Refugio Nacional Mixto de Vida Silvestre Gandoca- Manzanillo, 9.594° N, 82.602° W [9°35'38.4" N, 82°36'7.2" W], altitude 2 m, 14 Nov. 2013, cultivated in BRC Vatel, Saint Pierre, La Réunion, France CRV2180, 28 Feb. 2016, *M. Grisoni JJMM 01 & J.B. Azofoifa-Bolaños* (REU!). Talamanca. Refugio de Vida Silvestre Gandoca-Manzanillo, 9°35'38.4" N, 82°36'7.2" W, 14 m, 14 Nov. 2013, *M. Grisoni 2180, B. Azofoifa & J. García* (CR!). Manglar de Gandoca, Limón, 24 Jun. 1983, *R. Soto s.n.* (CR!). Puntarenas: Aguirre [canton Quepos], Savegre. Área no protegida. Finca Rafiki, 9°26'47" N, 83°59'14" W, 250 m, 7 May 2002, *J. Sánchez 1219* (CR!). Cantón Golfito. Valle de Coto Colorado. Ribera del Río Esquinas. Boca Río Esquinas. 8°44'00" N, 83°20'00" W, 30 m, 22 Dec. 1993, *M. Segura 264 & F. Quesada* (CR!). [Canton Osa, district Sierpe] Area between the Río Esquinas and Palmar, sea level, 2 May 1950, *P.H. Allen 5532* (SEL-011362!). Hamburg Finca on the Río Reventazón, 1925, *F. Nevermann s.n.* (MO, AMO-photo!). Heredia: Sarapiquí, La Virgen, La Tirimbina, 180 m, planta probablemente cultivada, 11 de Abril 2016, *A.P. Karremans 7042, M. Cedeño, I. Chinchilla & G. Villalobos* (JBL-spirit!, Fig. 49, 51E). PANAMÁ. Barro Colorado Island. Gross-Lathrops trail, 26 Jun. 1931, *L.H. Bailey 374 & E.Z. Bailey* (AMES-02158452!). San Blas District, Perme, 28 Apr. 1933, *G. Cooper III 287* (AMES-02158438!, AMES-02158461!, F-771391! NY!, US-1557502!). Barro Colorado Island. Cana zone. Wheeler Trail, 26 Oct. 1931, *O. Shattuck 230* (AMES!). Along the old Las Cruces Trail, between Fort Clayton and Corozal, 31 Dec. 1923, *P.C. Standley 29103* (AMES!). COLOMBIA. Córdoba, Buenaventura, 70 m, secondary tropical rain forest, 10 Oct 2016, *J.T. Otero 1486* (VALLE!, Fig. 50). Guadeloupe. Monts Caraïbes, Houelmont; forêt semi-décidue, 400 m, 24 Apr. 1979, *A. Raynal-Roques 21297 & J. Jérémie* (AMES!). PERU. Huanuco: Prov. Leoncio Prado, tingo maría, 79.59.52 09.17.08, 652 m, 27 Sep. 2010, *R. Fernández 3585* (USM!). Pasco: Prov. Oxapampa, Dto. Pozuzo, 10° 4'6.47"S 75°33'6.38"O, 1000 m. a.s.l., 25-28 Aug. 1991, *D. Bennet, A. Bennett & A. Vargas P. 5256* (MOL!). Junin: Prov. Chanchamayo, La Merced, cascada el tyrol, Mar. 2005, *C. Hajcek 2063* (USM!). Localidad desconocida, cultivada en invernadero UCSUR, Lima, *A. Damián s.n.* (USM!, Fig. 49F). BRAZIL: State of Pará: BR 163, Cuiabá-Santarém Highway; BR 163, Km 1414, Río Itapacurá, Várzea forest, 24 Nov. 1977, *G.T. Prance 25739, A. Henderson, B. Nelson, R. Bahia & M. Santos* (U-1468978!). FRENCH POLYNESIA. Austral Islands; Rimatara; Anapoto, 3 m, 4 Sep. 1934, *H. St. John 16884 & F.R. Fosberg* (AMES!). SAMOA. Insel Upolu, 1905, *K. u. L. Rechinger 933* (W!). FIJI. Viti Levu. Serua: Hills between Waininggere and Waisese Creeks, between Ngaloa and Wainiyambia, dry forest, 50–100 m, 30 Nov.-23 Dec. 1953, *A.C. Smith 9633* (AMES!, L!). INDONESIA. Archipel. Ind. Borneo, Res. w. Afd. v. Borneo. Pontianak 4 Aug. 1931, *Mondi 289* (L-0597916!). [Celebes Island] South Celebes: Danau Towuti, Timampu, Kec. Nuha, 320 m, 12 Apr. 1984, *R. Ram. 163* (L!). [Sulawesi Utara, N. Sulawesi] Im Muskabnuss-Plantagen bei Ayermadidi, 150 m, 14 Dec. 1914, *R. Schlechter 20523* (AMES!). Unknown origin: [without more data] 4 Jan. 1909 (L-4170735!); [without data] (L-4175486!). [without more data] Cult. In Hort. Bog. (U-1468932!).
- OTHER SPECIMENS: UNITED STATES OF AMERICA. Florida: Dade Co. growing on trees in an extensive area in Cutler Hammock, on Biscayne Bay, 15 May 1976, *D.S. Correll 47216 & J. Popenoe* (NY); Brickell Hammock, Miami, Dade County, *J.K. Small s.n.*, 19 Feb.-22 Mar. 1915 (NY). MEXICO: Unknown locality: "1815 de Mexico, *Epidendrum vanilla*" [Sessé and Mociño collection] *Pavón s.n.* (G); "Mexico", *Mr. Cowan* (G). Chiapas: Nahá, Mpio. de Ocosingo; 27 km al SE de Palenque por la carretera fronteriza hasta el Crucero Chancalá, después 55.6 km por el camino de terracería hacia Monte Líbano, 16°56'–17°01' N, 91°33'–91°38' W; 900 m, 6 May 1999, *A. Durán Fernández 1166* (MEXU). [Reserva Ecológica "El Ocote", Mpio. Ocozocuatla, 750 m, 14 Feb. 1986, *M. Palacios-Ríos 2823* (XAL). Alrededores de la Laguna Ocotilito, cerca de Monte Líbano, 950 m, *M. Soto 2836* (AMO-spirit); same locality, *M. Soto 2840* (AMO-spirit). Estación de Biología de Chajul, montículo 1, ruinas El Zapote, ca. 1 km de la estación, 16°08' N, 90°53' W, 200 m, 20 Jun. 1996, *M. Soto 7947* (AMO). Mpio. Ocosingo, Estación de Biología de Chajul, vereda que conecta la vereda a La Granja con la de la Sabana I, a unos 500 m del Río Lacantúm, ca. 200 m, 16°08' N, 90°53' O, 13 Abr. 1997, *M. Soto 8355* (AMO). Estación de Biología de Chajul, junto al Río Lacantun.. montículo 1, Ruinas El Zapote, 15 Abr. 2000, *M. Soto 9728, S. Maldonado, L. López & P. Schluetter* (AMO). Selva del Ocote, km 44.7 de la carretera Ocozocuatla-Malpaso, cerca de la presa, 275 m, 21 Abr. 2000, *M. Soto 9922, S. Maldonado, P. Schluetter, L. López & M. Soto* (AMO). Palenque, Abr. 1892, 450 m, *R.M. Comisión Geográfico-Exploradora, Sección de Historia Natural 7725* (AMES-21309). 6 km al E de Emilio Rabasa, 1 km al NE de La Reyna, Ocozocuatla, 16°55' N, 93°38'40" W, 720 m, *S. Ochoa 3659* (CHIP). Oaxaca: Cerro Machete, Distr. Pochutla, 800 m, Feb. 1941, *B.P. Reko 6279* (AMES-60425). 3 km al W de La Esperanza, Mpio. Ixtlán de Juárez, Sierra Norte, *E. Morales 1* (AMO-16697). Usila, Mpio. Usila, cultivada en los vainillales de la familia Bautista, cerca de la pista de aterrizaje, 90 m, 25 Abr. 1992, *M. Soto 6672 & M. Hernández* (AMO-exsiccata, AMO-spirit); same data, *M. Soto 6673 & M. Hernández* (AMO); same data, *M. Soto 6674 & M. Hernández* (AMO). Dto. Tuxtepec, Mpio. San José Independencia, Cerro Clarín, en el extremo SW de la Presa Temascal, ca. 120 m, 1 May 1994, *M. Soto 7630, U. Guzmán & Carlos* (AMO). Instituto Tecnológico Agropecuario, San Bartolo Tuxtepec, plantación a cargo de Jesús Pérez Meza, Abr. 1996, *M. Soto 8040* (AMO). Ejido La Gran Lucha,

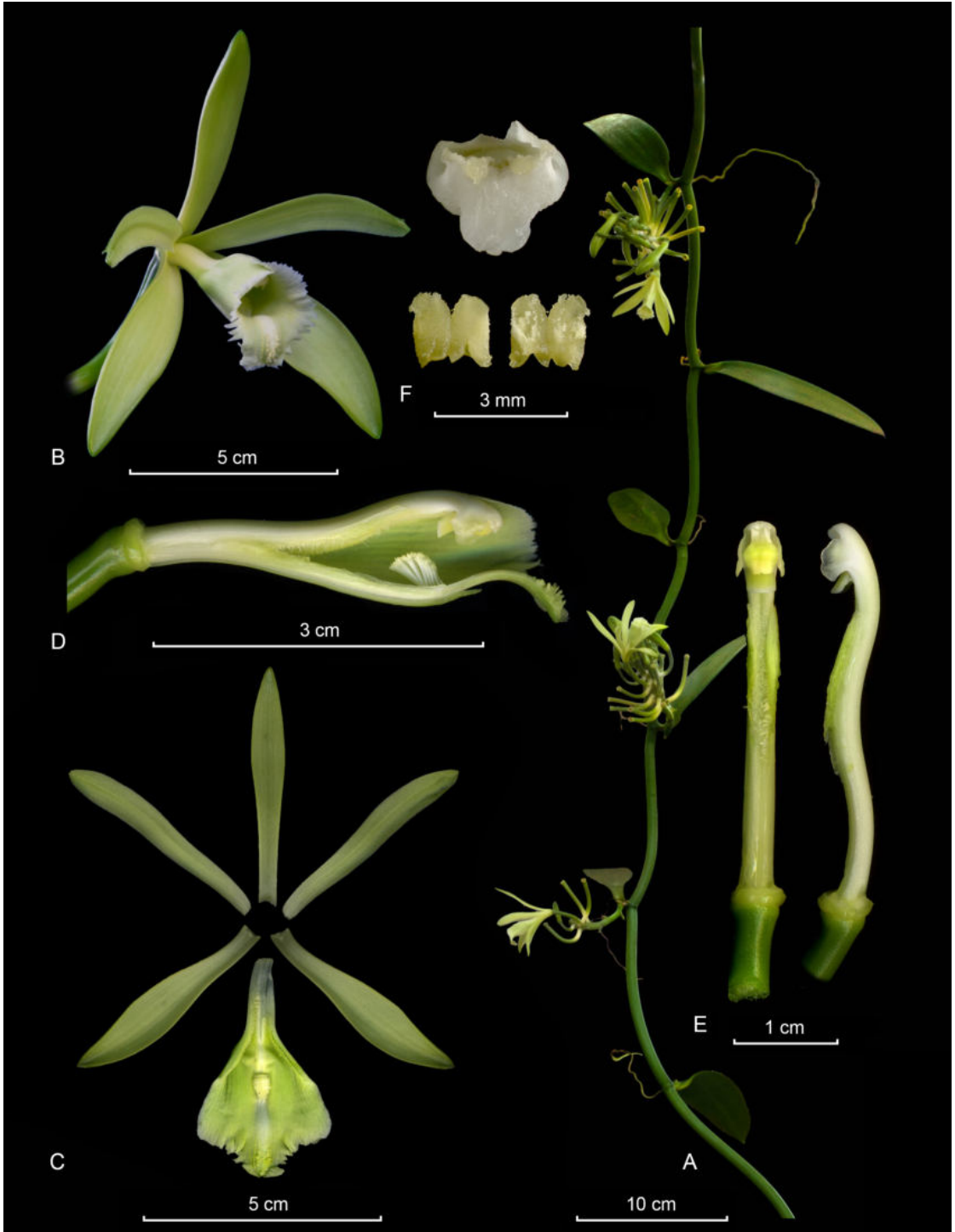


FIGURE 47. LCDP of *Vanilla planifolia*. **A.** Habit. **B.** Flower. **C.** Dissected perianth, flattened. **D.** Lip and column lateral view. **E.** Column, ventral and lateral view. **F.** Anther cap and pollinia. By D. Bogarín based on *F. Pupulin* 8274 (JBL-spirit) from Cahuita, Costa Rica.

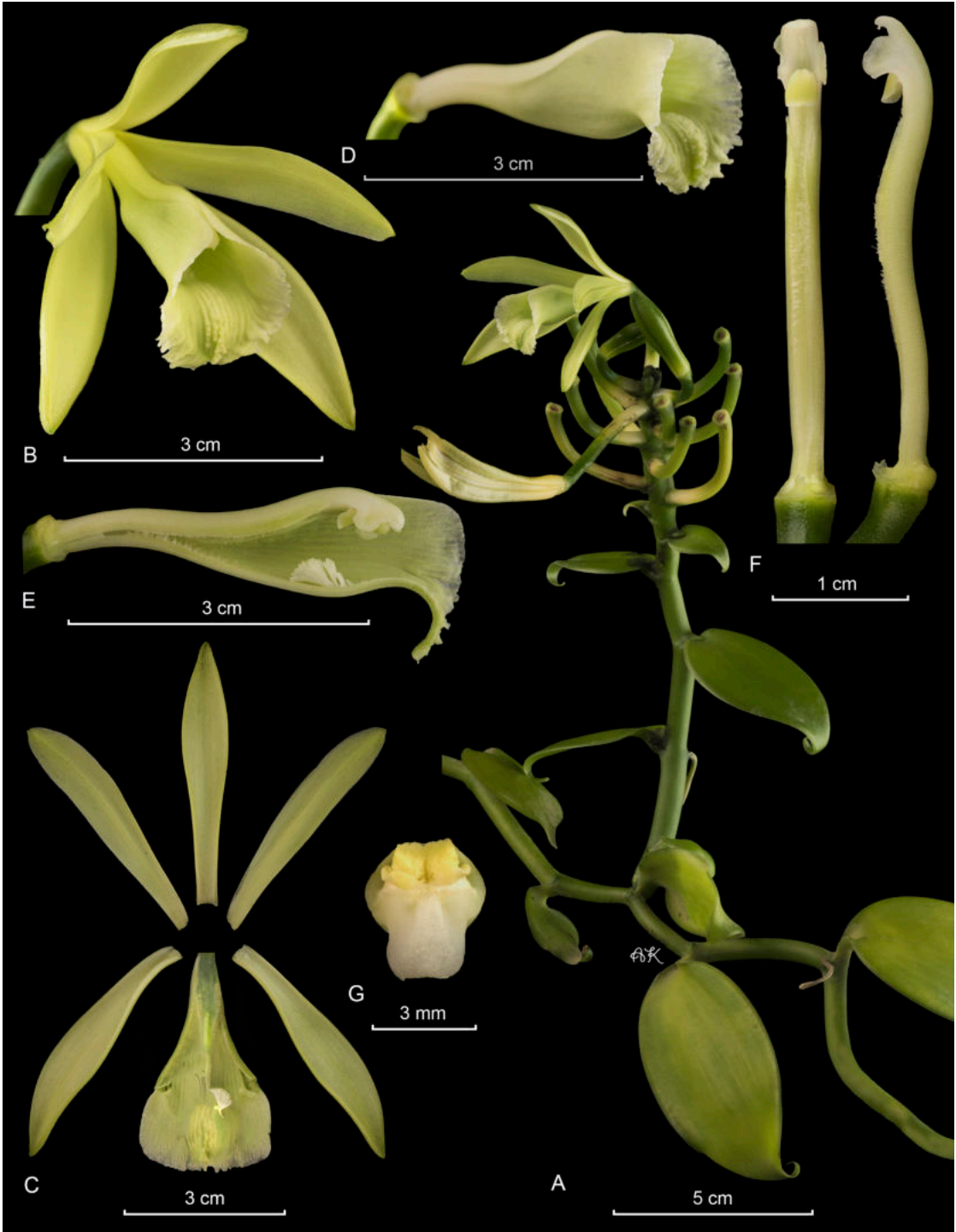


FIGURE 48. LCDP of *Vanilla planifolia*. A. Habit. B. Flower. C. Dissected perianth, flattened. D. Lip lateral view. E. Lip and column lateral view. F. Column, ventral and lateral view. G. Anther cap and pollinia. By IC & APK based on *F. Pupulin* 8276 (JBL-spirit) from Cahuita, Costa Rica.

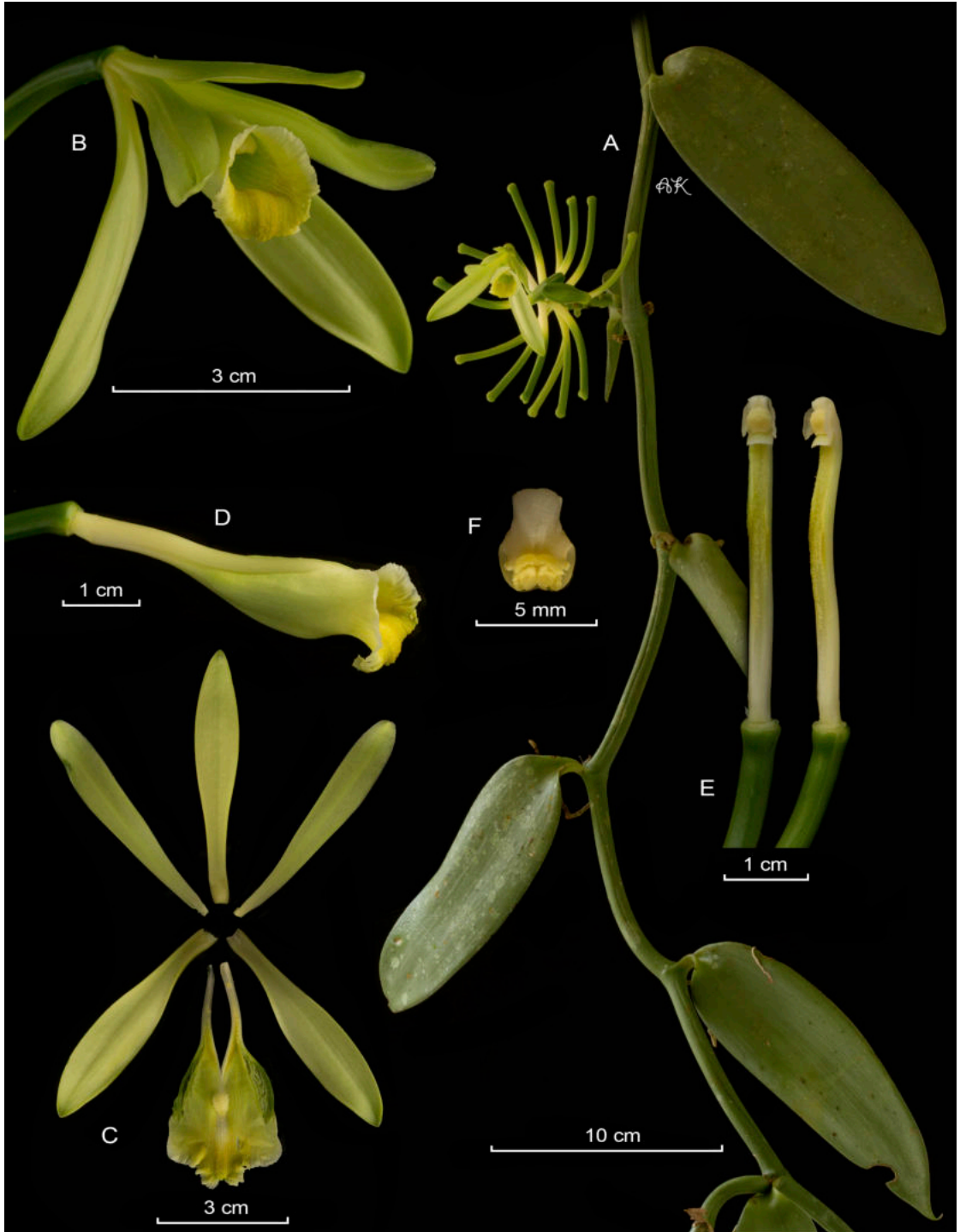


FIGURE 49. LDCP of *Vanilla planifolia*. **A.** Habit. **B.** Flower. **C.** Dissected perianth, flattened. **D.** Lip and column lateral view. **E.** Column, ventral and lateral view. **F.** Anther cap and pollinia. By APK based on *A.P. Karremans 7042* (JBL-spirit), cultivated at La Tirimbina, Costa Rica.

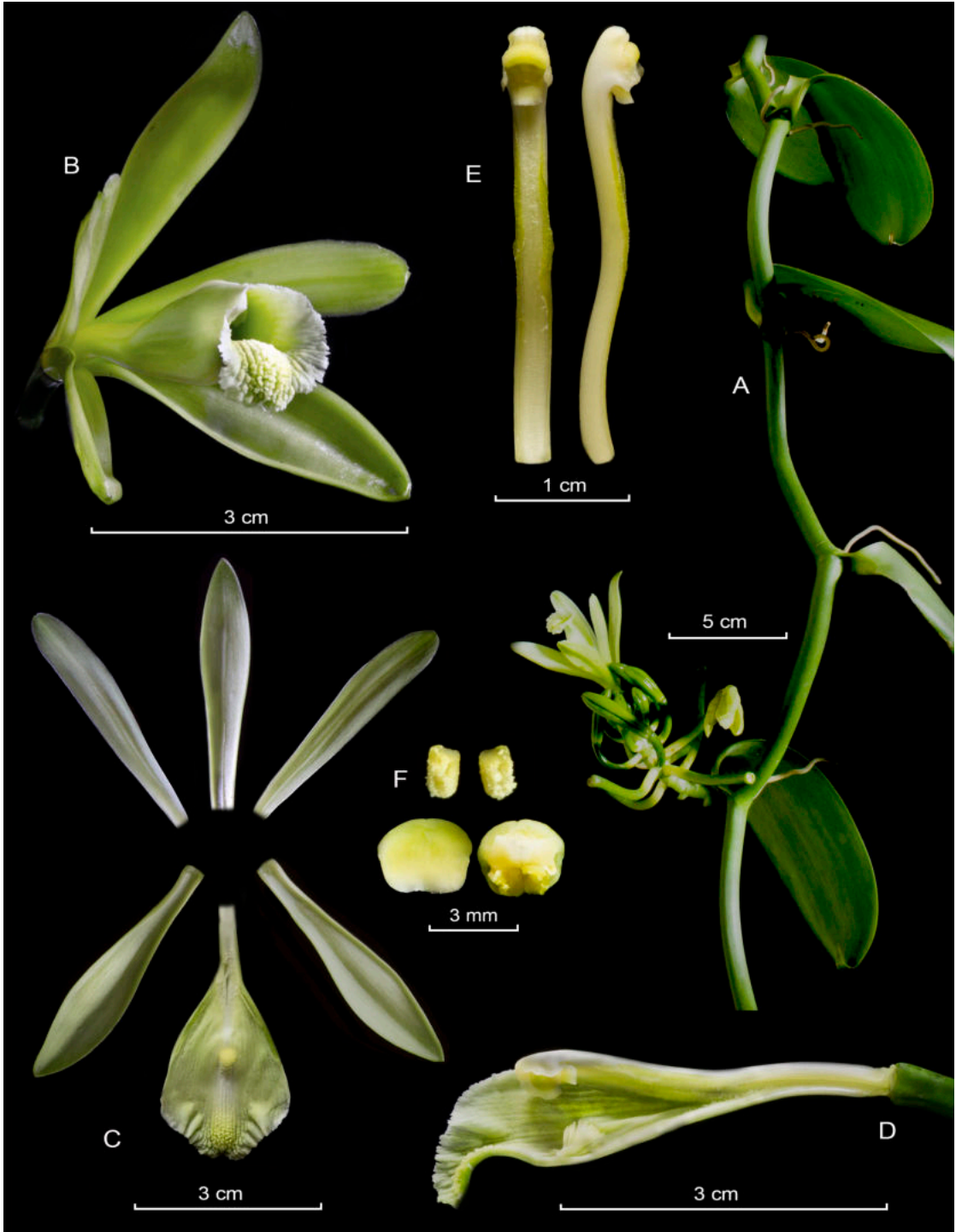


FIGURE 50. LCDP of *Vanilla planifolia*. **A.** Habit. **B.** Flower. **C.** Dissected perianth, flattened. **D.** Lip and column lateral view. **E.** Column, ventral and lateral view. **F.** Anther cap and pollinia. By Y. Alomía & J.T. Otero based on *Otero 1486* (VALLE) from Colombia.

Mpio. Valle Nacional. Vainillal particular de Nemesio Miguel Martínez. Plantación a 200 m, 17 Mar. 1997, *M. Soto 8117* & *A. Cibrián* (AMO). La Cueva, cerca de Cerro Verde, km 25.3 del camino Jalapa de Díaz-Usila, Oaxaca. Plantación de vainilla de José Roldán, 780 m, ca. 18°57' N, 94°44' W, 21 Abr. 1997, *M. Soto 8483* & *M. Hernández* (AMO). 3 km al W de La Esperanza, Mpio. Ixtlán de Juárez, Sierra Norte, *R. López G. 2* (AMO-16698). Cultivada en los vainillales de Santiago Tlatepuzco, Mpio. Usila, ca. 500 m, *R. Medinilla s.n.* (AMO-spirit). Between Los Llanos de Ozumazin and Río Chiquito, District of Choapam. Lat. 17°35', Long. 95°55', 700 ft. [213 m], 1 May 1939, *R.E. Schultes 727* & *B.P. Reko* (AMES-9034). Mun. Santa María Jacatepec, predio El Aguila, al O de San Agustín, entrando por la Reforma, 28 km SO de Tuxtepec, carr. a Matías Romero. 17°50' N, 96°06' W. 550 m, 19 Ene. 1988, *R. Torres 11027* & *E. Martínez* (AMO, MEXU). Puebla: Yancuictlalpan, Cuetzalan, *F. Basurto 263* & *R. Patrón* (MEXU). Quintana Roo: Isle of Cozumel, Cenote Cedral, 20°21' N, 86°59' W, 5–10 m, 2 Sep. 1935, *O. Nagel 5001* & *E. Oestlund* (AMES-51852). Ejido Hermenegildo Galeana, predios de Artemio y Constantino López Pascual, 18°10'33.2" N, 89°15'08.4" W, 10 May 2008, *M. Soto 11370*, *L. Ibarra* & *C. López* (AMO). San Luis Potosí: Tanjasnec, Mpio. San Antonio, planted, 4 May 1979, J.B. Alcorn 3006 (LL, MEXU). Tabasco: Teapa, 0.34 km al E de la Universidad Agraria de Chapingo, 17°31'31" N, 92°55'33" W, 28 Ene. 2002, *J. Calónico 21157 et al.* (MEXU). Poblado de Nacajuca, 20 m, 3 Oct. 1978, *R. Ortega 858*, *W. Márquez* & *B. Guerrero* (XAL). Veracruz: [Cultivated] Predio Escolín, 12 km al NE de Papantla, 370 m, 22 Jun. 1987, *A. García 3226* (MEXU). [Cultivated] Papantla de Olarte, 20°27' N, 97°19' W, *F. Rosas C.I.P. 709* (XAL). Estación de Biología Tropical de Los Tuxtlas, ca. 200 m, *G.A. Salazar 2247* (AMO-drawing, AMO-exsiccata, AMO-spirit). Volcano San Martín, 5 May 1936, 18°35' N, 95°11' W, 600 m, *J. González 5790* & *E. Oestlund 5790* (AMES-51851). San Andrés Tuxtla, El Vigía, al E de Cerro Blanco, 28 May 1967, *M. Peña 108* (AMES-11744). Vainillal del Sr. Rafael Cardeña, Díaz Mirón y Río Nautla, Papantla, 180 m, 31 Mar. 1995, *M. Soto 7648* (AMO). Mpio. Atoyac, a un lado de la vía del tren, cerca del puente, 2 May 1995, ca. 400 m, *M. Soto 7745* (AMO). [Cultivated] Papantla, 17 Feb. 1985, *P. Reyes s.n.*, *N. Carcamo* & *N. Garcilazo* (XAL). Rancho El Coscolín, El Escolín, Cerro Grande, Mpio. Papantla de Olarte, plantación de vainilla, 350 m, 20°29' N, 97°33' W, 25 Abr. 1989, *R. Castillo M. 210* & *H. Cáliz de Dios* (AMO, MEXU-678228). Rancho El Coscolín, El Escolín, Cerro Grande, Mpio. Papantla de Olarte, 20°29' N, 97°33' W, 350 m., 25 Abr. 1989, *R. Castillo M 211* & *H. Cáliz de Dios* (AMO, MEXU-678227). A 800 m al norte de la casa de Genaro, ejido Vista Hermosa, Mpio. Tezonapa, 18°40' N, 96°40' W, 500 m, 4 Ago. 1986, *R. Robles G. 977* (XAL). Yucatan. Cenote de Mayana, Yucatán, 1866, *A. Schott 215* (F-276993).

[Unknown locality] 4 Jun. 1899, *G.F. Gaumer s.n. & Sons.* (F). In virgin xerophytic forest, forests of Xbac, Apr. 1916, *G.F. Gaumer & Sons 23352* (AMES-71360, AMES-71369, F-446854, MO-948146, NY). Virgin forest near Chemax, on tree trunks, 20°39' N, 87°56' W, 30 m, 29 Sep. 1935, *O. Nagel 5050* & *E. Oestlund* (AMES-51846). BELIZE: Toledo. In cohune ridge, Bolo Camp, upper reach of Golden Stream, 12 Apr. 1944, *P.H. Gentle 4521* (LL). In cohune ridge, near Jacinto Hills, 30 Dec. 1944, *P.H. Gentle 5106* (LL). Feeders Road, 14 Miles, San Antonio-Punta Gorda Road, 20 Apr. 1949, *P.H. Gentle 6721* (F-1599303, LL, NY). On hill slope beyond San Antonio, 30 Jan. 1952, *P.H. Gentle 7557* (MEXU-511464, LL). GUATEMALA: Alta Verapaz. Vicinity of Finca Yalpemech, near Alta Verapaz-Petén boundary line, 100–120 m, 24 Mar. 1942, *J.A. Steyermark 45286* (AMES-62981, F-1195546). Baja Verapaz: Am Río Polochic über Tukurú, 900 m, 30 Apr. 1882, *F.C. Lehmann 1436* (G). Izabal: Vicinity of Puerto Barrios, at sea level, 2–6 Jun. 1922, *P.C. Standley 25064* (AMES-22674). HONDURAS: Atlántida. Lancetilla Valley, near Tela, altitude 20 to 600 m, 6 Dec. 1927–20 Mar. 1928, *P.C. Standley 55583* (AMES-36947, F-581081). Comayagua: [Unknown locality] 1300 m, 31 Mar. 1963, *A. Molina 11777A* (F-1620024). Morazan: [Cultivated] campus of EAP El Zamorano, 800 m, 28 Mar. 1990, *A. Molina 34346* (MO-4248893). EL SALVADOR: Finca Las Canoas, 700 m, 11 Apr. 1969, *H.C. Clason 268* & *F. Hamer* MO-3092269; same locality, near Ahuachapan, 9 Apr. 1978, *H.C. Clason 776* & *F. Hamer* (SEL-049262). PANAMÁ: Province of Colón: Between France Field, Canal Zone, and Catival, 9 Jan. 1924, *P.C. Standley 30160* (US-1225400). Barro Colorado Island in Gatún Lake, 120 m or less, 18–24 Nov. 1925, *P.C. Standley 40897* (US-1251676). Barro Colorado Island, Lutz Trail 300, 10 Jul. 1970, *T.B. Croat 11177* (SCZ-2261). NIUE: *Skypes 150572* (CHR); *Yunker 9856* (CHR) (Cribb & Whistler 2011).

DISTRIBUTION: Native to Mexico, Guatemala, Belize, Honduras, El Salvador, Nicaragua, Costa Rica and Panama, perhaps naturalized in Colombia, Peru, Brazil, and the Lesser Antilles (Fig. 55A). Widely cultivated around the tropical areas of the world, including Florida and Hawaii (U.S.A.), French Polynesia, Cook Islands, Samoa, Niue, Tonga, Fiji (Oceania), Papua New Guinea, Indonesia and India (Asia), Democratic Republic of the Congo (Africa), among others.

EXTENT OF OCCURRENCE: 18,465,274.534 km².

The name *Myrobroma fragrans* Salisb. (1807) is traditionally cited as a synonym of *V. planifolia* (Rolfé 1896, Garay & Sweet 1974, Garay 1978, Soto Arenas & Cribb 2010, Soto Arenas & Dressler 2010). This is because the illustration accompanying the description

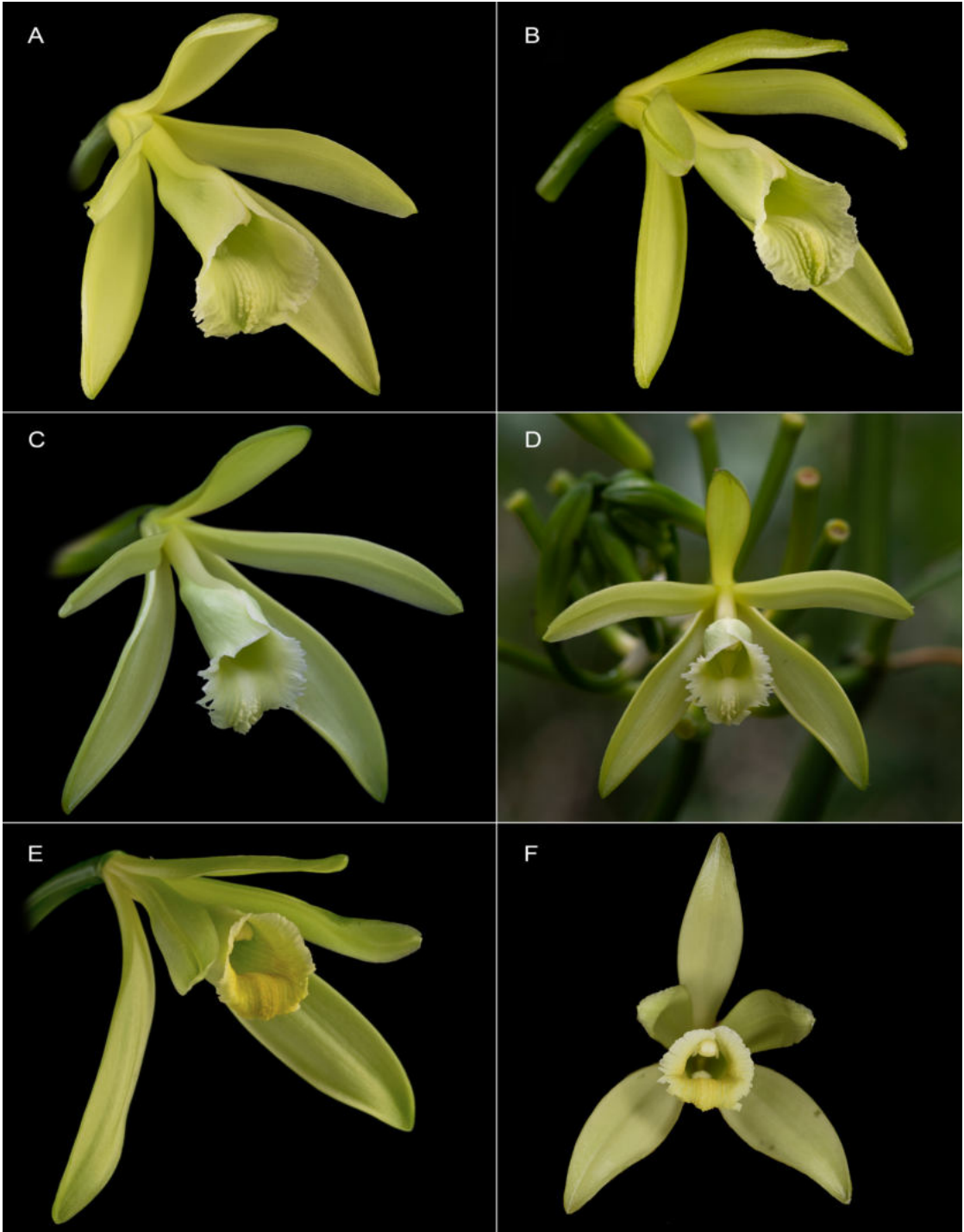


FIGURE 51. *Vanilla planifolia* different flowering specimens showing common morphological variations. **A.** Costa Rica, Cahuita National Park, *Pupulin* 8276. **B–D.** Costa Rica, Cahuita National Park, *Pupulin* 8274. **E.** Costa Rica, cultivated at La Tirimbina, *Karremans* 7042. **F.** Peru, cultivated in Lima, *A. Damián* s.n. Photographs by APK (A, B, E), AD (F) and F. *Pupulin* (C, D).

of *M. fragrans* (Fig. 52) not only is the same species as *V. planifolia* but is in fact based on the same specimen flowered in the collection of Charles Greville (Fig. 43). However, *M. fragrans* is a superfluous, and therefore illegitimate, name because it cites *Epidendrum rubrum* Lam. as a synonym and definitively includes the type. The name *Vanilla fragrans* (Salisb.) Ames was proposed as a new combination for *Myrobroma fragrans*. As the latter is illegitimate, *Vanilla fragrans* Ames must be regarded as a *nomen novum* rather than a new combination. However, it definitively includes the types of both *Epidendrum rubrum* and *Vanilla planifolia*, and is therefore also in itself illegitimate.

The type of *E. rubrum* is Plumier's unpublished illustration MSS. 3. t. 100 which bears the name "Vanilla flore albo, fructu brevior coralino". After inspection of the original text and illustration kept at the MNHN in Paris we definitively exclude *Epidendrum rubrum*, and its nomenclatural synonyms *Myrobroma fragrans* and *Vanilla fragrans*, from the synonymy of *Vanilla planifolia*. The material illustrated and described by Plumier has thick stems with small, narrow leaves, a violet, undulate lip and a short red fruit. It corresponds better to the Antillean *Vanilla claviculata* Sw. as inferred by Ackerman (2014), or *Vanilla poitaei* Rchb.f. as Garay & Sweet (1974) suspected. Preliminarily we agree with the latter; if confirmed the name *Vanilla rubra* (Lam.) Urban would have priority over *V. poitaei* and should be reinstated.

When proposing his *Vanilla viridiflora*, Blume provided only a short description and no illustration. However, he made it clear that his Javan specimen came from a cultivated plant of American origin. The origin of this material was traced by Prof. Charles Morren as being the same as that cultivated by Greville (Rolfe 1896), and which served as type of *V. planifolia*. The name was not treated under *V. planifolia* by Soto Arenas & Dressler (2010), but was included as a synonym in Soto Arenas & Cribb (2010). The taxon is here lectotypified with a specimen that was located at L, and which indeed corresponds well with *V. planifolia*.

Even though mostly associated with *Vanilla planifolia*, the identity of *V. sativa* and *V. sylvestris*, published by Schiede in 1829, remained obscure given they were mainly known on the basis of their original descriptions (Rolfe 1895). Soto Arenas & Dressler

(2010) indicate that a single leaf representing *V. sativa* was located at BM, while type material of *V. sylvestris* was not located. Indeed a specimen consisting of a single leaf was located at BM, but we were also able to find material of both these cryptic taxa at HAL. Even though the material is still relatively poor, these taxa can now be reassessed on the basis of these specimens. Based on the shape of the leaf and the original descriptions it seems quite plausible that these taxa indeed represent variations of *Vanilla planifolia*.

Vanilla schwackeana is another obscure name in the genus. Virtually unused, it was proposed by Hoehne (1944) on the basis of a specimen composed of a sterile plant bearing five leaves and two loose flowers, of which the author himself suspected could be a mixture of unrelated elements. Soto Arenas & Cribb (2010) recognized the species but agreed it could represent a mixture of parts of different species. We find that the dissected flower is congruent with *Vanilla planifolia*, sharing the distinctive trilobate, denticulate lip with an apical verrucose callus. The thin acuminate leaves are unusual for the species and may indeed belong to a different species. The dissected flower is therefore selected as lectotype here to clarify the identity of this taxon.

Vanilla sotoarenasii was recently proposed as a new species despite evidence provided in the publication that it is genetically indistinguishable from *Vanilla planifolia* accessions (Azofeifa-Bolaños *et al.* 2017). The taxon, based on material from the Caribbean coast of Costa Rica, was said to differ from *V. planifolia* morphologically and chemically. However, despite the availability of large populations at the type locality of this taxon, the authors measured morphological and chemical only in handful of clones "cultivated in controlled conditions in BRC Vatel in La Réunion". This poses a significant methodological bias as it definitively excludes the possibility of assessing the natural variation of these traits within a population, not to mention the whole distribution of the taxon. An assessment of the population at the type locality of *V. sotoarenasii* proves that morphological features used to distinguish this taxon, such as leaf and fruit color, shape and size, are extremely variable even within a single plant (Fig. 47, 48, 51, 53, 54); and impossible to separate consistently from the variation observed in *V. planifolia*. Furthermore, specimens from the type

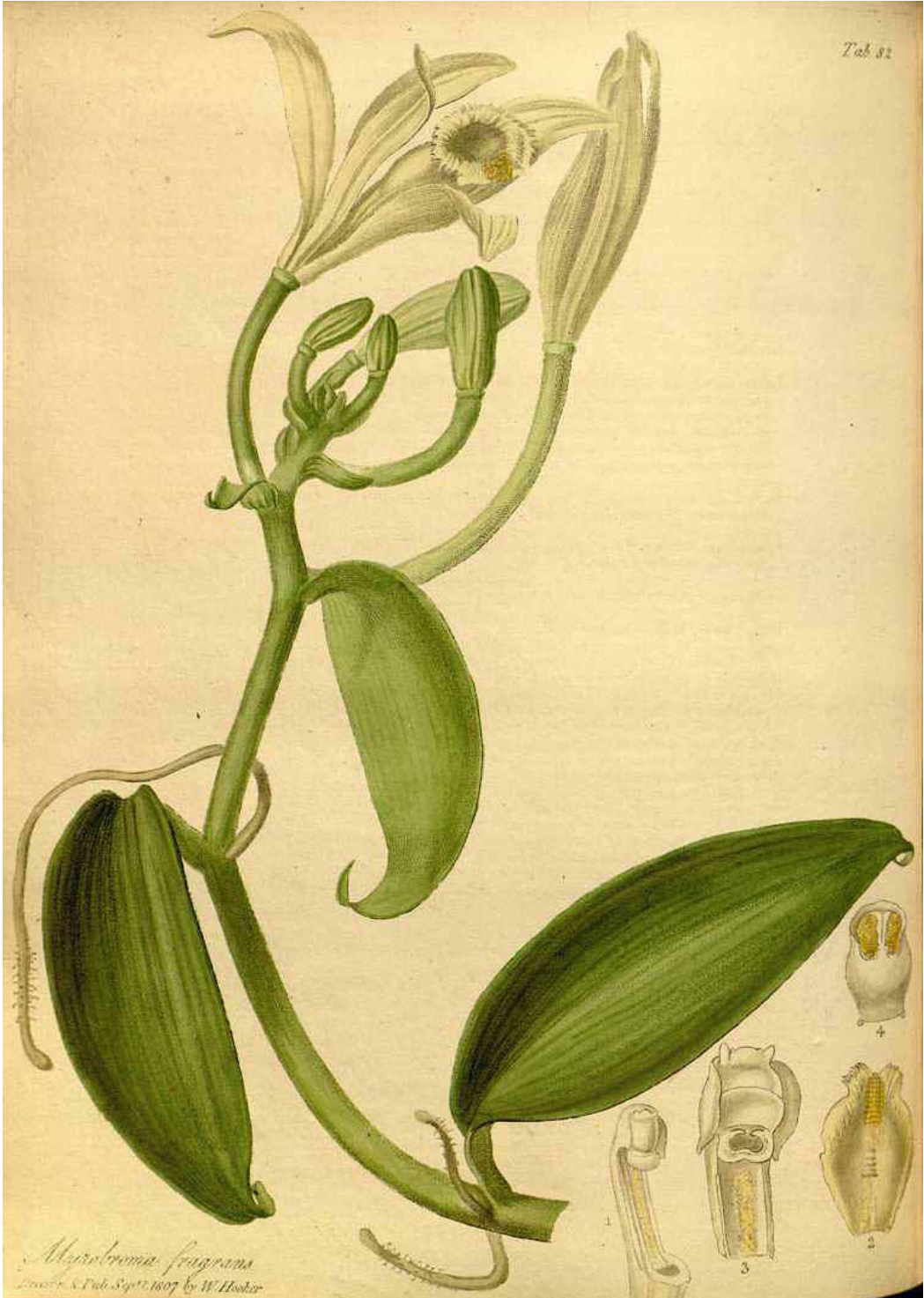


FIGURE 52. *Vanilla planifolia*, illustration based on a specimen from Charles Greville that accompanies the original description of *Myrobroma fragrans*.



FIGURE 53. *Vanilla planifolia* wild plants. **A.** Stem, leaf and fruit disposition and morphological variation within and between individuals of a single population in Cahuita, Costa Rica. **B.** Plants at Cahuita National Park growing closer to the beach, in exposed areas, are more compact. **C.** An individual growing on the sand a few steps from the ocean, Bocas del Toro, Panama. Photographs by APK



FIGURE 54. Variation within a single population of *Vanilla planifolia* at Cahuita National Park in Costa Rica. **A.** Diverse leaf pairs taken from single stems showing the within and among individuals' variation in color, shape and size. **B.** Fruits showing different levels of maturity, color, length, thickness and shape. Photographs by APK.

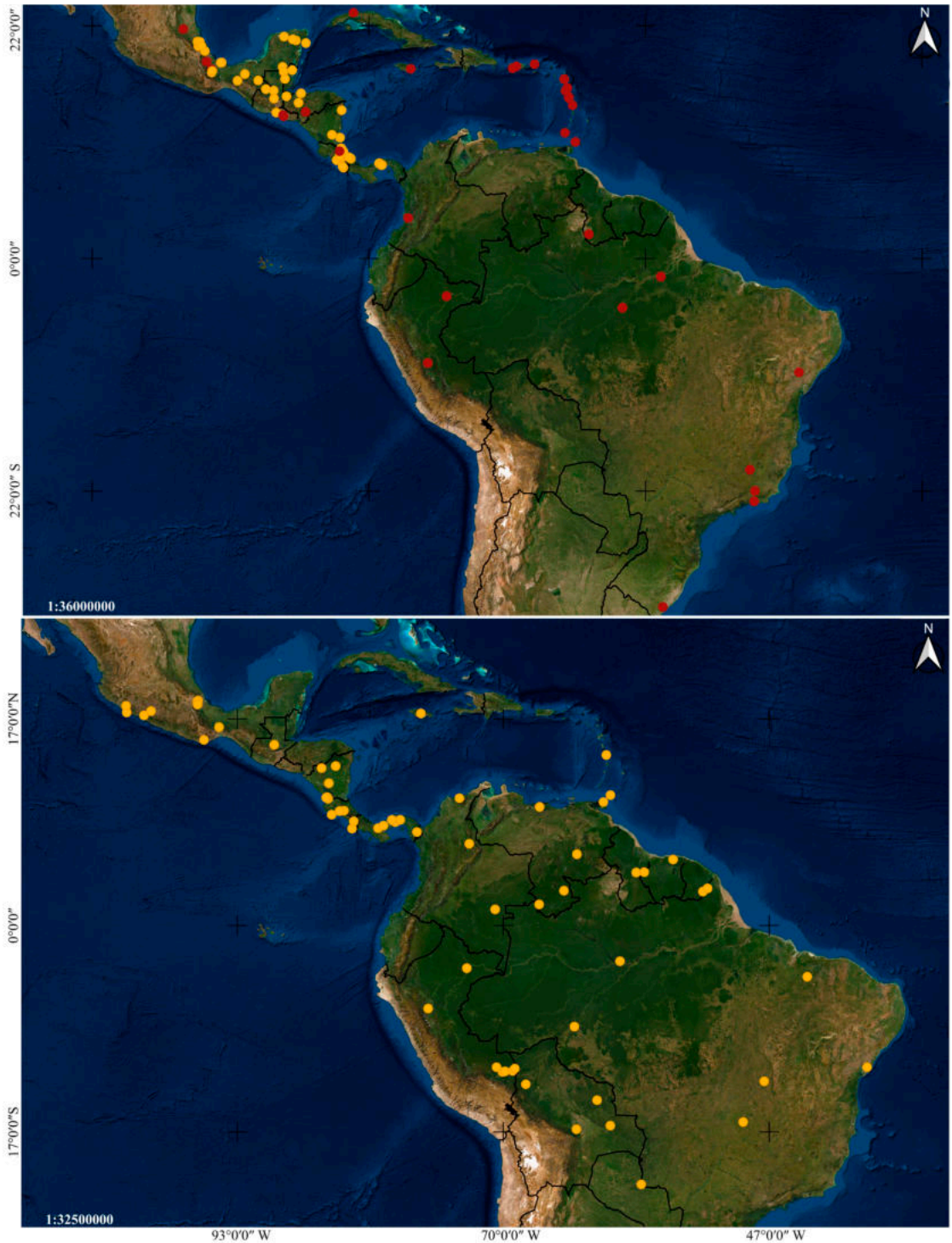


FIGURE 55. Distribution maps of *Vanilla* species based on studied specimens. **A.** *Vanilla planifolia* Andrews. **B.** *Vanilla pompona* Schiede. Images by IC.

locality of *V. sotoarenasii* are much more similar to the illustrations based on the material that served as type of *V. planifolia* (Fig. 43, 52), then most cultivated cultivars (Fig. 49).

It remains to be proven if these *Vanilla* populations were introduced to the areas where they are found today. A specimen of this species collected in 1945 in Portete, near Puerto Limón and kept at CR may give some historical context of their cultivation on the Costa Rican Caribbean. The handwritten label on the herbarium specimen (Quirós & Sáenz 4254) reads: "cocimiento de sus hojas para curar la diabetes" (cooked leaves used to cure diabetes). This suggests these plants have been present in the Caribbean coast of Costa Rica for at least seventy-five years, and that they were being used and cultivated by locals. The first people to settle Cahuita did so in 1828. It is known that they cultivated yams, cassava, cocoa and coconut, and sailed between Limón, Cahuita and the Bocas del Toro area southward in Panama, as well as northwards to the coast of Nicaragua (Weitzner & Fonseca Borrás 2001). The Parque Nacional Cahuita was created in 1978, and the presence of coconut, cocoa trees and oil palms within its regenerated forest are proof of its agricultural past (Weitzner & Fonseca Borrás 2001). It is unclear if these *Vanilla* plants are associated solely with human settlement, but it is clear that they are found in the same area where the afro-Caribbean communities of Nicaragua, Costa Rica and Panama live and have long interacted. In Bocas del Toro, the local afro-descendant population uses vanilla to spice up one of their more traditional dishes, the oatmeal porridge (APK pers. obs. 2019).

The unusual morphological plasticity found in the population at the type locality of *V. sotoarenasii*, especially of the leaf color, size and shape and of the lip ornatation may be indicative of a certain degree of hybridization, perhaps backcrosses between *V. planifolia* and *V. odorata* or *V. × tahitensis*. Although the *V. planifolia* genes are clearly dominant in the population, as is reflected by the phylogenetic studies (Azofeifa-Bolaños *et al.* 2017; Chambers *et al.* in prep.), odd morphological features occasionally express, including very narrow leaves, fimbriae on the lip and indehiscent fruits; all features found in *V.*

× tahitensis. Further population studies are certainly needed to fully understand this taxon.

The names *Vanilla tiarei* Costantin & Bois, *nom. nud.*, and *Vanilla hirsuta* M.A.Clem. & D.L.Jones are excluded from the synonymy of *V. planifolia* and placed under the cultivated hybrid *Vanilla × tahitensis* J.W.Moore. The name *Vanilla duckei* Huber has been placed under *V. planifolia*, but we agree with Koch *et al.* (2013) that they are not conspecific.

10. *Vanilla pompona* Schiede, Linnaea 4: 573. 1829. Fig. 55B, 56–63.

TYPE: [MEXICO]. "Baynilla pompona Hispano-Mexicanorum. Hab. Papantlae et Colipae." Schiede *s.n.* (**lectotype designated here**: W-ESP70151!, Fig. 56; isoelectotypes: HAL-111283! Fig. 57A, HAL-111284!, Fig. 57B, HAL-111285!, Fig. 57C, BM-000062775!, LE-00006464!).

Syn.: *Vanilla grandiflora* Lindl., Gen. Sp. Orchid. Pl. 435. 1840.

Vanilla pompona subsp. *grandiflora* (Lindl.) Soto Arenas, Lankesteriana 9: 340. 2010.

TYPE: FRENCH GUAYANA. *Martin s.n.* (holotype: K-L!, Fig. 58).

Syn.: *Vanilla hamata* Klotzsch, Bot. Zeitung (Berlin) 4: 563. 1846, **syn. nov.**

TYPE: PERU. Ruiz (holotype, B, destroyed). Neotype (**designated here**): PERU. Ruiz (F-18349!, holotype photo, Fig. 59A; isoneotype, AMES-38629!, copy of the holotype photo, Fig. 59B).

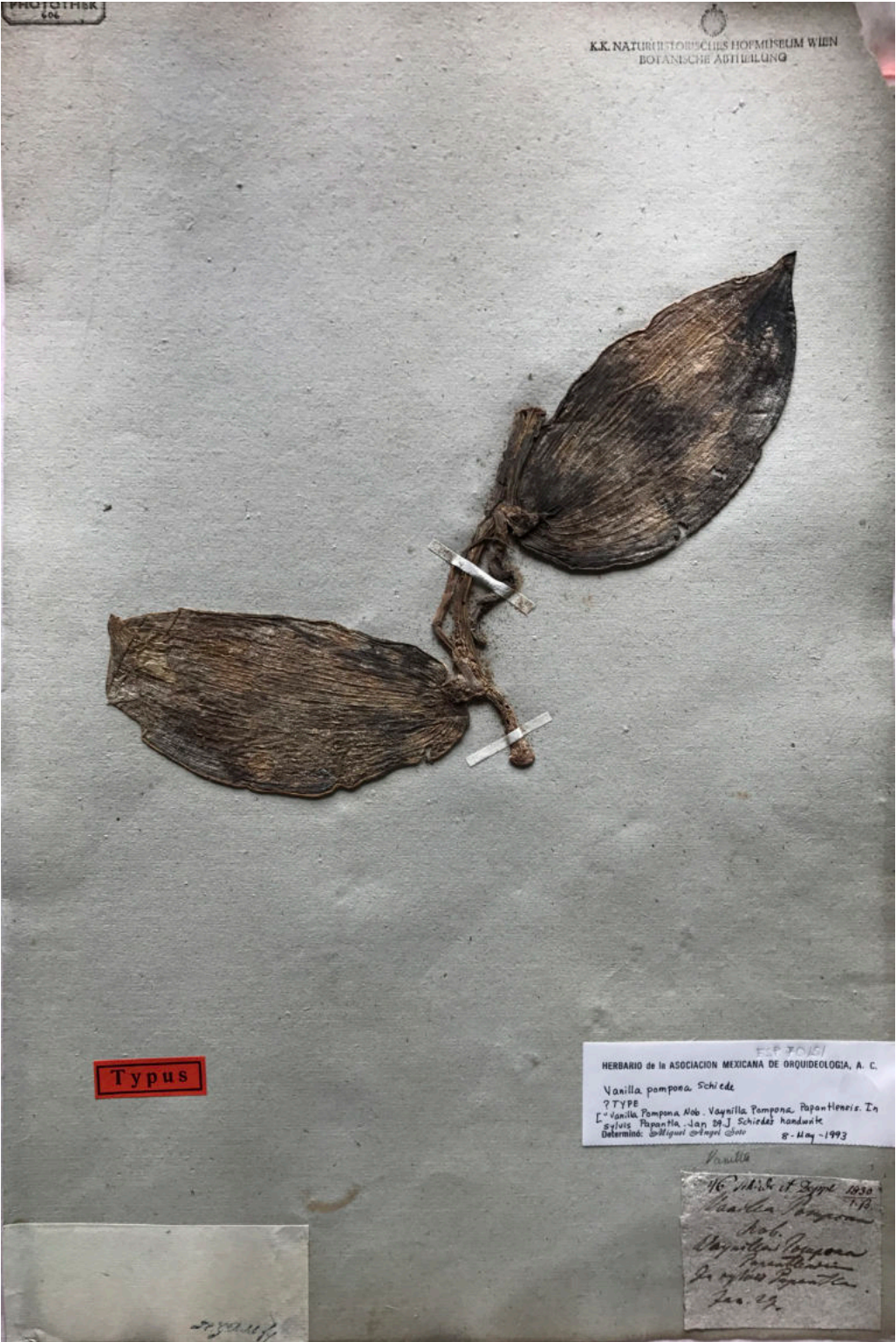
Epitype (**designated here**): PERU. Chicoplaya, Flora Peruviana et Chilensis, illustration by J.G. Rivera N. 341 [reproduced as figure 52C in Pupulin (2012); Fig. 60A].

Syn.: *Vanilla lutescens* Moq. ex Dupuis, Rev. Hort. (Paris), sér. 4, 5: 121. 1856.

TYPE: [VENEZUELA]. Communiquée par M. Coudert, horticulteur distingué de Bordeaux. Elle est originaire du Guayra (La Guaira, Venezuela). [holotype, not found; **lectotype designated here**: illustration of type reproduced by Dupuis (1856) in Revue Horticole (Paris), Fig. 61A].

Syn.: *Vanilla reichenbachii* Endrés, *nom. nud. in sched.*, **syn. nov.**

RIGHT, FIGURE 56. *Vanilla pompona* Schiede, lectotype based on Schiede *s.n.* from Mexico (W-ESP70151). Photographed by APK.



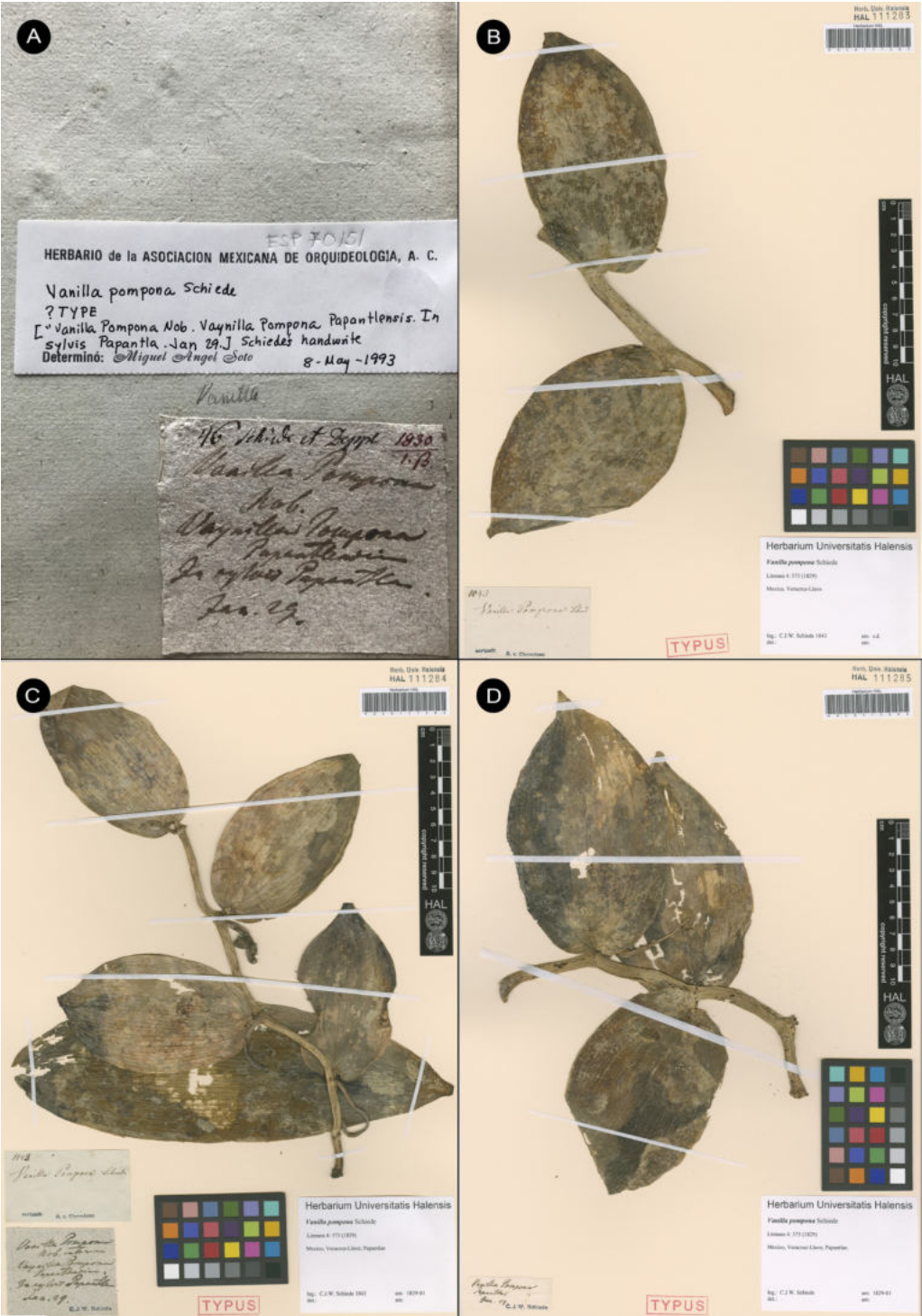


FIGURE 57. *Vanilla pompona* Schiede. A. Detail of the lectotype (W-ESP70151), showing the handwritten label by Schiede. B. Isolectotype (HAL-111283). C. Isolectotype (HAL-111284). D. Isolectotype (HAL-111285). B-D © copyright of the Martin-Luther-Universität, Halle.



FIGURE 58. *Vanilla pompona* holotype of *V. grandiflora*, based on *Martin s.n.* from the French Guiana (K). The illustration by Riocreux from the type specimen of *V. lutescens* exposed at l'Exposition Universelle de Paris has been added above the specimen. Photographs by APK.

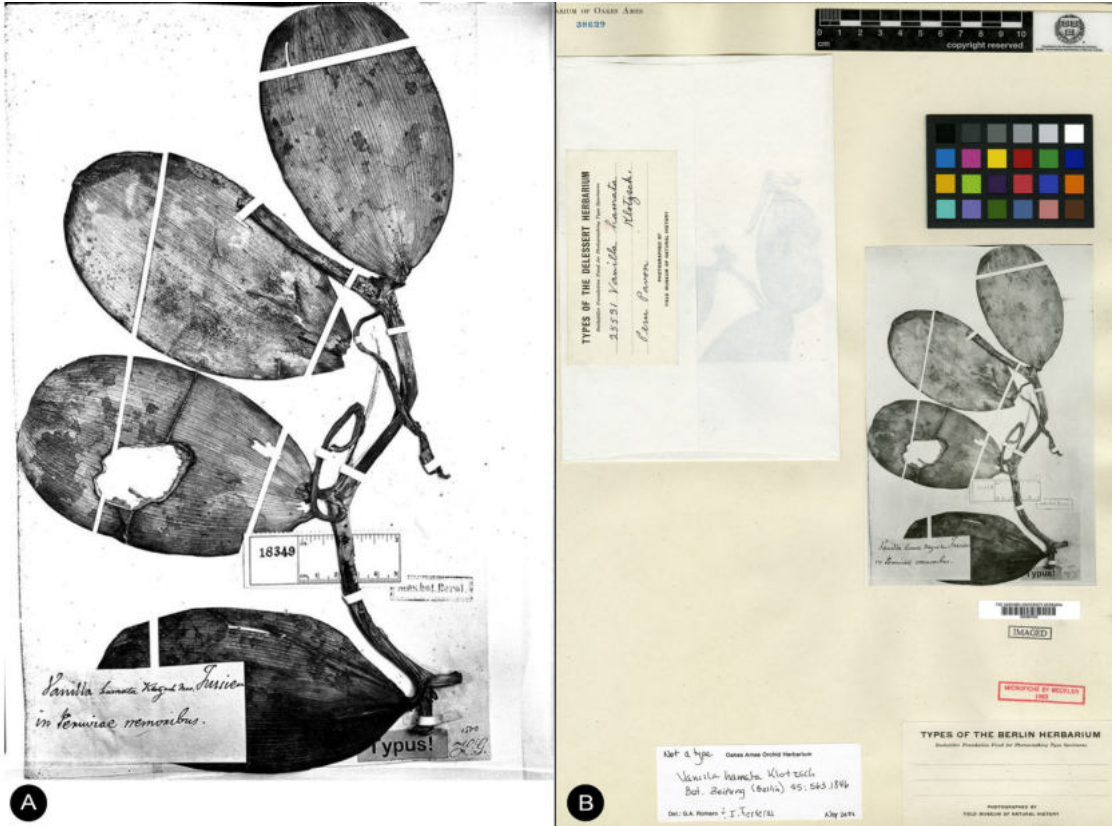


FIGURE 59. *Vanilla pompona* photographs of the holotype of *V. hamata* Klotzsch lost in Berlin. **A.** Neotype, photo kept at F-18349; © copyright of the Field Museum of Natural History, Chicago. **B.** Isonetype, photo kept at AMES-38629; © copyright of Harvard University, Cambridge.

Syn.: *Vanilla pittieri* Schltr., Fedde Rep. 3: 106. 1906.
Vanilla pompona subsp. *pittieri* (Schltr.) Dressler,
Lankesteriana 9: 341. 2010.

TYPE: COSTA RICA. In der Wäldern an Ufern des
Río Ceibo bei Buenos Aires, c. 200 m., blühend im
Januar 1890, *H. Pittier* 6600 (holotype: B, destroyed;
drawing of type, AMES!; **lectotype designated
here**: BR-642325!, Fig. 61B; isoelectotype, US!).

Syn.: *Vanilla planifolia* var. *gigantea* Hoehne, Relat.
Commss. Linhas Telegr. Estratég. Matto Grosso
Amazonas Anexo 5, Bot. pt. 1: 27-28, t. 5. 1910,
syn. nov.

TYPE: [BRAZIL-PARAGUAY border]. Habitat
ad silvis humidis secus flum. Jaurú et Paraguay,
florete Setembri-Octobri, Pl. n.º 972 [**lectotype
designated here**: Tabula No. 5 in Hoehne (1910)]

Syn.: *Vanilla pleei* Portères, Bull. Soc. Bot. France, 98:
94-95. 1951, **syn. nov.**

TYPE: MARTINIQUE, *A. Plée* 621 (syntypes:
P-00612113!, P-00612114!; **lectotype designated
here** by G. Leotard & A.P. Karremans: P-00612114,
Fig. 61C).

Syn.: *Vanilla pseudopompona* Soto Arenas, *nom. nud.
in sched.*, **syn. nov.**

Syn.: *Vanilla cochlearilabia* Archila, Chiron &
Menchaca, Richardiana, n.s. 3: 105-107. 2019, **syn.
nov.**

TYPE: GUATEMALA. Alta Verapaz: margen
sur del río Polochic, como planta trepadora. A 60
m.s.n.m. semidomesticada, Febrero 2001. *FA-sn*
(BIGU; illustration!).

Hemiepiphytic, massive *vine*, little branched, leafy,
up to 35 m high. *Stems* terete, smooth, pale green
dotted with whitish, 10–28 mm thick; internodes 3.5–
15 cm long. Aerial *roots* thick, 6 cm long, attaching
roots conspicuously flattened on the lower surface,



FIGURE 60. *Vanilla pompona* material most likely the same collection as the type of *V. hamata* but not cited by the author. A. Illustration by J.G. Rivera N. 341 selected as epitype. B. G-7889/123. C. G-7889/124. D. W-19341. B-C © copyright of the Conservatoire et Jardin botaniques de la Ville de Genève. D photograph by APK.



FIGURE 61. *Vanilla pompona*. **A.** Lectotype of *V. lutescens* Moq. ex Dupuis. **B.** Lectotype of *V. pittieri* Schltr. From Costa Rica (BR-642325). **C.** Lectotype of *V. pleei* Portères (P-00612114), based on Plée 621 a mixed collection from Martinique. **D.** Syntype of *V. pleei* which is here regarded as a different species (P-00612113). B © copyright of Meise Botanic Garden, Belgium. C-D © copyright of the Muséum national d’histoire naturelle, Paris.

whitish-greenish; terrestrial roots pilose, 4 mm thick. *Leaves* subsessile; blade variously shaped, ovate, widely elliptic, oblong falcate, base widely rounded to subcordate, 6–33 × 3.0–13.7 cm, 3 mm thick, coriaceous, very fleshy, brittle, pale green; apex acute to subapiculate. *Inflorescence* a raceme, producing 6–20 flowers, successive, 1 open at once, ephemeral; peduncle fleshy, subterete, 1 cm long; rachis up to 4.5 cm long. *Floral bracts* sessile, widely ovate, acute, concave, up to 5 mm long. *Flowers* tubular or with spreading segments, tepals pale yellow; lip orange yellow, very showy, column white in the base, light yellow to the apex; fragrance very strong, spicy, mint-like. *Ovary* arcuate, oval-subtrigonal in cross section, dorsiventrally flattened, arcuate, somewhat twisted, very slightly grooved on one face, smooth, green, 29–45 × 3–5 mm. *Dorsal sepal* long oblanceolate, apex obtuse to rounded, subcalyptrate, smooth and minutely warty abaxially to the apex, fleshy, ca. 2–4-veined; 52–105 × 7–16 mm, base long attenuate. *Lateral sepals* long oblanceolate, oblique, apex obtuse to rounded, subcalyptrate, smooth and minutely warty abaxially to the apex, fleshy, ca. 13-veined; 73–94 × 4–20 mm, base long attenuate, canalculated. *Petals* oblanceolate-oblong, arcuate, slightly sigmoid and oblique, the upper margin more straight, apex truncate to rounded, ca. 12-veined, 59–80 × 8–16 mm. *Lip* attached to the column along the margins of the basal half for ca. 30–40 mm, tubular, trumped-shaped, cymbiform, deepest near the middle, axially grooved; when spread out 60–80 × 29–41 mm; unguiculate, the claw canalculated, with rows of trichomes; the blade flabellate to obscurely trilobed, margin undulate, ca. 40-veined, apex deeply emarginate-bilobed; lateral lobes long triangular-ovate, oblique, rounded, 30–40 × 10–25 mm, erect surrounding the column, generally no overlapping; midlobe inconspicuous, the margins fairly reflexed, revolute, deeply bilobed; *penicillate callus* at 35–40 mm from the lip base, made up by ca. 10–14 congested, retrorse, approximately trapezoidal, lacinate scales, the scales regularly united each to other along the lateral margins, continuous with 3–6 thick and slightly warty veins forming a cushion like, claviform, rounded, rugose callus ending at the very apex. *Column* elongate, conspicuously sigmoid, 43–73 × 3–5 mm, ventral surface lanuginose on the apical half, below the stigma; apex dilated, vertical wings

triangular-flabellate, the lower margin acute, uncinat. *Stigma* trilobed, the lobes emergent, with a convex rostellum; lateral lobes divergent each to other, 2 × 2 mm. *Anther cap* basally hinged to the column, versatile, sub-cuadrate, 4–8 × 6–7 mm wide. *Pollen* not forming a clear pollinarium but a sticky, soft, subtriangular granular mass. *Fruit* variable, usually arcuate, trigonous, thick, green, blackish when ripen and strongly aromatic, 7.3–21.5 cm long, ca. 14 mm thick

SPECIMENS STUDIED: MEXICO: Guerrero. Sierra Madre, Guerrero-Michoacán, 400–1000 m, Mar. 1900, *E. Langlassé* 941 (AMES!). Vallecitos, Montes de Oca, 13 Sep. 1937, *G.B. Hinton* 11387 *et al.* (K!). Michoacan. Aquila, Tizupan, Coalcomán, 8 Apr. 1941, *G.B. Hinton* 15910 (AMES!). Sierra Madre, Guerrero-Michoacán, 400–1000 m, Mar. 1899, *E. Langlassé* 941 (AMES!, K!). Mpio. Aquila, San Pedro, Coalcomán, 550 m, 19 Jun. 1939, *G.B. Hinton* 13815 (AMES!). Oaxaca. Near Mogoñé. Isthmus of Tehuantepec, 17°0' N, 95°01' W, 100 m, 18 Feb. 1935, *O. Nagel* 4574 (AMES!). Specimens from the Gulf slope. Consoquilla, 142, *Liebmann* 288 (W-11761!). Pacific slopes of Sierra Madre, near Copalita and below Pluma Hidalgo, 26 Jul. 1936, 500–1000 m, *O. Nagel & J. González* 6102 (AMES!). Isthmus of Tehuantepec. Near Mogoñé, 17°0' N, 95°01' W, 100 m, 20 Apr. 1935, *H. Knape* 4781 (AMES!, SEL!). Veracruz. Near Zacuapan. 12 Feb. 1932, 19°12' N, 96°52' W, ca. 900 m, *O. Nagel* 2684 (AMES!). Municipio de Huatusco. Paraje El Angostillo, bajando a la barranca desde la Congregación El Pochote (34 km de Huatusco, 14 km de Manuel Gonzales), 500 m, 9 Abr. 2020, *G.A. Salazar, M.A. Soto, M. Ingrouille & P. Schluter* 6162 (K!). Region of Zacuapan, ca. 800 m, Jun. 1935, *C.A. Purpus* 4852 (AMES!). Valle de Córdoba, 20 Apr. 1865–6, *Bourgeau* 2332 (K!). From Mexico. Secured by Prof. P.H. Rolfs, in charge of the Subtropical Laboratory, Miami, Fla., while traveling in Mexico as agricultural explorer of the Office of S & PI in Apr., May, and Jun., 1905, *David Fairchild* 14440 (SEL!). Loc. H. de Higuera, 510 m, 8 Sep. 1966, *M. Sousa* 2721 (MO!). NICARAGUA: Cerro Livico, 7 km northeast of Siuna, forest slope; 500 m, 28 Apr. 1978, *D. Neill* 3670 (SEL!). Nueva Segovia. Quilalí, ca. 13°34' N, 86°01' W, 430 m, 16 Mar. 1980, *W.D. Stevens and B.A. Krukoff* 16829 (SEL!). Segovia. *A.H. Heller s.n.* (SEL!). Chontales. ca. 2.8 km above (N of) Cuapa; ca. 12°17' N, 85°23' W, 400–500 m, *B.A. Stevens and Krukoff* 3690 (SEL!). COSTA RICA: 2 Mar. 1931, *C.H. Lankester* 1314 (AMES!). Alajuela. 4 Jun. 1963, *A. Viquez s.n.* (USJ!). Guanacaste. Parque Nacional Guanacaste, Estación Maritza, sendero a la cima del Volcán Orosí, 10°57.6' N, 85°29.6' W, 600 m, 2 Jul. 1989, *INBio* 132 (CR!, SEL!). A 5 millas al sur de La Cruz, Liberia. 550 m, Ene. 1943, *A.M. Jiménez* 27654 (CR!). A 5 millas al sur de La Cruz, Liberia. 200 m, 11 Feb. 1963, *A.M.*

- Jiménez M. 313* (CR!). Puntarenas. Golfito, Jiménez, camino a Agua Buena, antes de la Estación Biológica Piro. Parcela Número 16, bosque muy húmedo, 8°23'34.61" N 83°19'19.57" W, 98 m, 27 Oct. 2014, *A.P. Karremans 6438*, *J. Geml, M. Lopez, J. Murillo, L. Parra, C. Rojo & M. Vázquez* (JBL-spirit!, Fig. 61, 62A). Cantón de Buenos Aires. Along the Río Ceibo, Ujarrás. 9°14'00" N, 83°18'00" W, 500 m, 9 Mar. 1993, *M.H. Grayum 10237* (CR!). Golfito, Puerto Jiménez, Área de Conservación Oso. Poblado Piro. Finca Osa Verde, 8°24'00" N, 83°20'40" W, 50 m, 19 Feb. 2016, *D. Rodríguez s.n.* (USJ!). Buenos Aires, cuenca Térraba-Sierpe. Union del Río General con Río Coto Brus. Entre Guadalupe y Quebrada Kirdigua, 9°01'28" N, 83°11'28" W, 150 m, 3 Mar. 2000, *B. Hammel 22080*, *R. Aguilar & E. Alfaro* (USJ!). San José. Montes de Oca. Campus de la Universidad de Costa Rica. Jardín Botánico José María Orozco, 1160 m, 23 Abr. 1999, *C.O. Morales 1354* (USJ!). San José. Pie del Turrubares, 150 m, 6 Mar. 1926, *A. Alfaro 269* (AMES!, MO!). Turrucare, Nov. 1978, *J. Hale s.n.* (USJ!). Without locality data, *Endres 270* (W-16188!, W-16230!, W-16231!, W-16175!, W-16176!). PANAMA: Along R. Tecumen, north of Chepo road, up to 30 m, 10 Mar. 1935, *A.A. Hunter & P.H. Allen 852* (MO!, AMES!). Near Canal Zone, *C.V. Piper s.n.* (AMES!). Canal Zone, Vicinity Cerro Viejo, 13 Oct. 1965, *K.E. Blum 1235* (MO!). Canal Zone, along road to radar station on semaphore Hill, 1 km N of Summit Garden, 20 Oct. 1973, 100–150, *M. Nee 7488* (MO!). Smithsonian Tropical Research Institute in Balboa, 18 Mar. 1979, *J.D. Ackerman 1354* (SEL!). Vicinity Santa Fe, Río Santa María, 26 Mar. 1947, 305 m, *P.H. Allen 4428* (MO!). Moist woods, large herbaceous vine, Río Paraíso, above East Paraíso, January 7, 1924, *P.C. Standley 29919* (AMES!). Canal Zone, Summit Garden, 8 m, 19 May 1970, *T. Croat 10282* (MO!). Azuero Peninsula, along trail between Jobero and Headwaters of río Pedregal, 300–700 m, 28 Apr. 1976, *T. Croat 34472* (MO!). Along trail between Jobero and Headwaters of Río Pedregal, 500–780 m, 29 Apr. 1976, *T. Croat 34539* (MO!). Barro Colorado Island, shores of Gatun Lake, South of Lab., 28. Aug. 1929, *W.N. Bangham 458* (AMES!). JAMAICA: Caterfor Garden, 1892, 7206x (K!). 4 Dec. 1891, *W. Fawcett s.n.* (K!). VENEZUELA: Río Negro, Amazonas, selvas pluviales en los alrededores de San Carlos de Río Negro, 1°50' S, 66°55' W, *B. Stergios s.n. & C. Aymard* (MO!). Alto Orinoco. El Motin, 13 Sept. 1951, *L. Croizat 610* (F-1821821!). Trinidad and Tobago: ca. 5 mi. Arima-Blanch. Rd., 16 May 1984, *J.S. Kenny 29085* (U!). Hts. of Aripe, 09 May 1985, *J.S. Kenny 29489* (U!). Tobago, Menna, 17 Jul. 1913, *W. E. Broadway 4565* (GH-00600238!). FRENCH GUIANA: Basin of Rupununi River, 15 Sep. 1937, *A.C. Smith 2474* (P!). Face Nort Est, Haut de Cricue Armontabo Ouest bas Oyapock, *Cremers 776* (P!). Roche Touatou, Bassin de l'Oyapock, 52°32' S, 2°57' W, 160 m, *G. Cremers 13931 & Gramville* (P!). Saut Pierkourou sur le Tampok, 30 Oct. 1981, *Moretti 1274* (P!). COLOMBIA: Plants of Santa Marta, 1898, *H. Smith 1901* (AMES!). Plants of Santa Marta, 1898–1901, *H. Smith 2369* (GH-02158563!). Plants of Santa Marta, 1898–1901, *H. Smith 2371* (F-139112!). Dept. Vaupés, Cerro de Ypobodá, savannah, among scrub, at the headwater of Río Kuduyari, ca. 600 ft., 15 Aug. 1960, *L.A. Garay 118* (AMES!). Las palmitas, Ocaña, *Wallis s.n.* (W-21448!). Santander, Piedecuesta, 1100 m, 1 Jun. 2007, *J.F. Caroprese 006* (COL-000257421!; COL-000257420!). Santander, Girón, ca. 1000 m, 20 Ene. 2007, *J.F. Caroprese 007* (COL-000430711!, stem with large leaves, the second stem with small leaves is *V. phaeantha*). Vaupés, Río Kuduyari, Yapobodá, sandstone savannah near headwaters, 18 Nov. 1952, *R.E. Schultes & I. Cabrera 18490* (AMES!). Vaupés Río Vaupés, Mitú and vicinity. at base of Cerro Mitú, 27 Sep. 1966, *R. E. Schultes, R. F. Raffauf & D. Soejarto 24204* (AMES-02158577!). Pereira, *S. Vieira-Urbe s.n.* (JBL-photo!, Fig. 63Cc). SURINAME: Paramaribo, *Wullschlaegell s.n.* (W-35435!). GUYANA: Conrentyne River, British Guiana, *G.S. Jenman s.n.* (P-00612148!). PERU: [Huanuco, Prov. Huamalis, Dtto. Monzon] Chicoplaya, Flora Peruviana et Chilensis N. 341 (G-7889/123!, G-7889/124!, MA-810866!, MA-810867!, W-19341!). Loreto: Prov. Maynas, Dtto. Belén, Caserio San Antonio, Río Itaya, 145 m, Sep. 1929, *L. Williams 3399* (F!); Prov. Maynas, vicinity of Quistococha, 73 20' W, 3 45' S, 150 m, 21 Feb. 1979, *A. Gentry, J. Aronson, R. Vasquez 24829* (USM!). Madre de Dios: Prov. Manu, Puerto Maldonado, los amigos biológica station, madre de dios river, 7 km upriver from mouth of rio los amigos, trocha aguajal, -12.57 -70.1, 270 m, 5 Mar. 2003, *M. Chocce 296* (USM!); Madre de Dios river, 7 km upriver from mouth of rio los amigos. *M. flexuosa*, aguaje palm swamp, aguajal to the northwest of the los amigos biological station, -12.57 -70.1 270 m, 19 Aug. 2002, *J. Janovec & A. Maceda 2671* (USM!, BRIT!, Fig. 63D); Prov. Tambopata, Puerto Maldonado, Aguajal Huitoto, albergue maquisapa, -12.62, -69.94, 230 m, 18 Oct. 2004, *M. Chocce, F. Cornejo, J. Janovec, A. Maceda, M. Tobler & U. Falla 599, 660* (USM!); Prov. Manu, Boca Colorado, Aguajal Colorado, -12.47 -70.51, 270 m, 27 Oct. 2004, *M. Chocce, F. Cornejo, J. Janovec, A. Maceda, M. Tobler & U. Falla 684* (USM!); Prov. Tambopata, Puerto Maldonado, Aguajal Tormenta, -12.4308 -69.008, 190 m, 20 Aug. 2015, *J. Wells, M. Escalante 1306[flor], 1307, 1310-1321* (MOL!); Prov. Tambopata, Puerto Maldonado, Aguajal Complex La Cachuela, -12.5316 -69.1885, 186 m, 8 Aug. 2015, *J. Wells & M. Huinga 1278-1285* (MOL!); Prov. Manu, Dtto. Huaypetue, Zona Amortiguamiento Reserva Comunal Amarakaeri, Sector Setapo, 2013, 320 m, *A. Damián s.n.* (HUPCH!); Prov. Tambopata, Puerto Maldonado, cart. Nueva alianza, aguajal tormenta, -12.4317 -69.0553, 190 m, 20 Aug. 2015, *J. Wells, M. Huinga 1324* (MOL!). San Martín: Zepelacio, near Moyobamba, June 1934, 110 m, *G. Klug 3685* (F-752921!);

Prov. Rioja, Dtto. Posic, Palestina, Yuracyacu, Tambo, 18M 0240151; 9345988 – 850 m, *J. Edquen 140* (URP!); Rioja, Dtto. Naranjos, al costado de la carretera, cultivada por INIBICO, *M. Leon s.n.* (USM!). BOLIVIA: San Cruz, 3 km N of Buena Vista, road to Laguna Madrejon, 17°25' S, 63°40' W, 315 m, 19 May 1991, *A. Gentry 740901* (MO!). Guarayos. Reserva de vida silvestre ríos Blanco y Negro. Río San Martín (Concesión Oquiriquia). Campamento de la monita, 18 km al SW del Río San Martín. 15°03'20.6" S, 61°56'23" W. elev. ca. 250 m, 7 Sept. 1993, *I. G. Vargas, N. Tagua & J. Aguirre 2756* (F-2295770!). Amazon Basin, pampa near Oxiamas, 700-800 ft., 20 Dec. 1921, *O.E. White 2336* (AMES!). Amazon Basin, near mouth of Río San José, 900-1000 ft., 14 Oct. 1921, *O.E. White 898* (AMES!). BRAZIL: Mato Grosso. Grounds of brick factory. 5 km. south of Chavantina, margin of creek, Serra do Roncador, 26 Sept. 1964, *G.T. Prance 59138* (US-00319619!; NY-00910931; UB-0019164!). Pará, Vigia, 26 Sept. 1964, *E. Oliveira 3155* (IAN-116115!). Rondonia, Porto Velho, 19 Oct. 2015, *M. Fragomeni Simon 2617* (CEN-00095226!). Maranhão: Caxias, Área de Proteção Ambiental Municipal do Inhamum (APA Inhamum), *M.S. de Oliveira et al. s.n.* [photographs in Ferreira *et al.* (2017)!]. Amazonas Rio Branco, Apr. 1913, *J.G. Kuhlmann 415* (AMES!; RB-00260191!). Goiás, Cavalcante. Chapada dos Veadeiros, ca. 8 km south of Cavalcante, 10 Mar. 1969, *H.S. Irwin et al. 24207* (NY-00910928!). Manaus, Amazonas, Estrada do Aleixo, Secretaria de Produção, 4 Oct. 1978, *P.I.S. Braga 3595* (INPA!). Manaus, Amazonas, Km 9 da BR-17. T. firme, argiloso. Habitat, capoeira aberta, 22 Jul. 1955, *J.C. de Almeida 1470* (INPA!). Bahia, Entre Rios, Algodão, 12°10'0" S, 37°58'0" W, 100 m, 2009, *A.V. Popovkin 9/16* (HUEFS!). Pernambuco, *E.M. Pessoa s.n.* (JBL-photo!, Fig. 63B).

DISTRIBUTION: A very broadly distributed species in the Neotropics, found in Mexico, Guatemala, Nicaragua, Costa Rica, Panama, Jamaica, Puerto Rico, Guadeloupe, Dominica, Martinique, Trinidad & Tobago, Colombia, Venezuela, French Guiana, Suriname, Guyana, Ecuador, Peru, Bolivia, Brazil and Paraguay (Fig. 55B).

EXTENT OF OCCURRENCE: 15,763,473.161 km².

This robust and widely distributed taxon has been described several times through the years, at least four times in the 18th century, twice in the 19th century, and once more very recently. The first name applicable to this species is *Vanilla pompona*, a name proposed by Schiede in 1827 based on Mexican material. All of Schiede's original material of this species is sterile, but the thick stem and broad, coriaceous leaves, as also

mentioned in the description "*maxima, foliis oblongis, succulentis, subinde latissimis, et basi subcordatis*", are unmistakable. The exact opposite happened with the second name that applies to this taxon. In 1840, Lindley proposed *Vanilla grandiflora* on the basis of a specimen from French Guiana composed only of a cluster of large yellow flowers on a short inflorescence. The vegetative features were unknown to the author and were not mentioned, but a very detailed illustration of the flowers are congruent with our concept of *V. pompona*.

A few years later, Klotzsch proposed *Vanilla hamata* from Peru, also based on a sterile specimen. The author described the leaves as obovate, broad, shortly petiolate and with a small hook at the apex. Soto Arenas & Cribb (2010) suggested it was related to *V. pompona*, but the leaf shape prevented them from concluding the taxa were conspecific. This taxon remained obscure because of the relatively odd leaves and unavailability of floral material (Rolfe 1896); and of course the loss of the physical type at the Berlin herbarium (photos of the holotype are kept at F and AMES; Fig. 59). Specimens from the same expedition and with an extremely similar vegetative morphology have been identified as isotypes at G, MA and W (G-7889/123!, G-7889/124!, MA-810866!, MA-810867!, W-19341!; Fig. 60). Strictly speaking, none of those specimens are isotypes as there is no proof that Klotzsch ever saw or used any of them. Quite contrarily, the specimens at G and W have flowers and the annotation "Chicoplaya, Flora Peruviana et Chilensis, N. 341", neither mentioned by Klotzsch. Even though it is very likely these are all materials belonging to the original collection, it is impossible to associate them without a doubt to *V. hamata*. For this reason we select the original photo of the holotype as a neotype, and select the illustration by J.G. Rivera (N. 341) as epitype (reproduced in Pupulin 2012). Even though the leaves of the type of *V. hamata* have an odd shape for this species, the illustration shows the typical thick stem, broad leaves, short inflorescence, and yellow flowers of *V. pompona*. We do not discard the possibility of a mixed collection. One of us (AD) has confirmed the presence of *V. pompona* in the area where the type of *V. hamata* is believed to have been collected.

Not long after, this species was again described under the name *Vanilla lutescens* Moq. ex Dupuis, based on a specimen from Guayra (La Guaira, Venezuela, not Paraguay as stated). A very good

illustration and description is provided for this taxon, again showing a thick stem, broad leaves, a short inflorescence, and large yellow flowers. None of these four taxa were compared to each other when proposed; perhaps on account of the partial materials and the distant geographical locations from which they were described (Mexico, Venezuela, French Guiana, Peru). Rolfe (1896) had already suggested *V. pompona*, *V. grandiflora* and *V. lutescens* were conspecific more than a century ago; *V. hamata* can be added now that the original drawing has surfaced.

The species was described once again as *Vanilla pittieri* Schltr. in 1906 based on a specimen collected in Río Ceibo, close to Buenos Aires, Costa Rica. The author compared the taxon to *V. pompona* suggesting a few differences. However, at the type locality we have observed specimens that are indistinguishable from *V. pompona*; a specimen collected in the same area, and morphologically similar to the type material, is illustrated here (Fig. 62). *Vanilla planifolia* var. *gigantea* Hoehne proposed in 1910 was believed to be a large variety of *V. planifolia* by the original author, and placed under *V. hostmannii* Rolfe by Soto Arenas & Cribb (2010). But the large leaves, thick stem, short inflorescence bearing relatively small yellow flowers are referable to *V. pompona* instead. Another name placed here under the synonymy of *Vanilla pompona* is *V. plei* Portères, described in 1951 based on material from Martinique. Soto Arenas & Cribb (2010) were unable to access original material of this taxon, but Garay & Sweet (1974) suspected it was based on a mixed collection, composed of leaves of *V. mexicana* and flowers of *V. pompona*. We agree with the later, *Plée 621* is a mixed collection composed of two sheets, one includes leaves of what appears to be *V. mexicana*, or a related species, and a second with flowers of *V. pompona*. Both the protologue and the illustration of the type published by Portères (1954) are a mixture of both species. We here select the sheet with flowers as lectotype because they can be identified more accurately than the sterile leaves, and therefore the name *V. plei* is included under the synonymy of *V. pompona*.

Soto Arenas believed *V. pompona* to be a species complex, with the isolated populations in Mexico, southern Central America, and north-west south America, possibly representing separate species. His

DNA-based studies did not support this hypothesis, and the three populations were treated as subspecies in Soto Arenas & Dressler (2010). However, we can't find any consistent morphological differences between plants from those geographical areas, and as our knowledge on *Vanilla* grows the gaps between the populations disappear. Specimens of *V. pompona* have now been reported from Guatemala, described under the name *V. cochlearilabia*, closing the gap between populations in Mexico and southern Central America. While in South America, specimens from Bolivia, Colombia, Ecuador, Peru, type of *V. hamata* and Venezuela, type of *V. lutescens*, confirm that the species is not restricted to the north west, and in fact grades into the southern Central American populations. Even though some specimens indeed show the larger, narrower flowers, with spreading segments, these features are variable even within a single population and the time of day. Subgeneric distinction is not supported either. The type illustration of *V. lutescens* (Fig. 58, above) and type specimen of *V. pompona* subsp. *grandiflora* (Fig. 58, below) are indistinguishable from the specimens found in southern Costa Rica described as *V. pompona* subsp. *pittieri* (Fig. 62, 63A), and even if the larger flowered *V. pompona* individuals should be recognized as a distinct taxon in the future, none of these names would apply to it. It is noteworthy that *Vanilla pompona* has been shown to be pollinated exclusively by male *Eulaema cingulata* in both Costa Rica and Peru (Watteyn, Scaccabarozzi, *et al. in prep.*).

Endrés used the name "*Vanilla reichenbachii* Endrés" on specimens of *Vanilla pompona* from Costa Rica. Like many other names intended by the author, it was never formally published. Soto Arenas used the name "*Vanilla pseudopompona* Soto Arenas" on a specimen from Panama that he later determined as *V. pompona* subsp. *pittieri*. A few authors have cited this name as an accepted species of *Vanilla*, but it was never formally published and its use should be avoided.

Vanilla pompona is characterized by having a robust stem, up to 3 cm in diameter, the leaves are succulent, ovate, elliptic to oblong, with a rounded to subcordate base. The inflorescence is short, bearing yellow flowers. The lip is large and trumpet shaped, obscurely trilobed, with undulate margins and elevated rows of papillae from the penicillate callus to the apex.

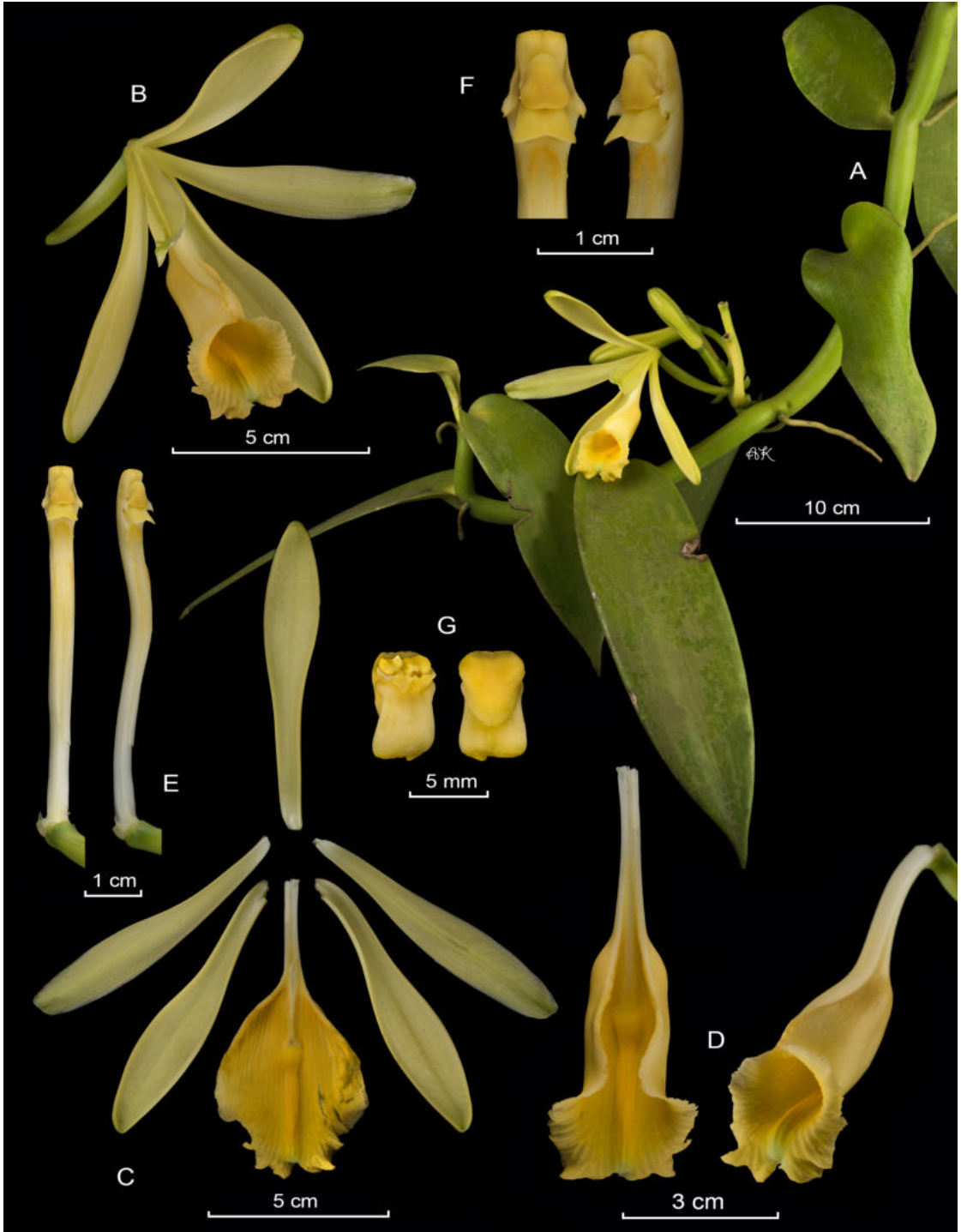


FIGURE 62. LCDP of *Vanilla pompona*. **A.** Habit. **B.** Flower. **C.** Dissected perianth, flattened. **D.** Lip and column lateral view. **E.** Lip in natural position, column removed. **F.** Column, ventral and lateral view. **G.** Column apex showing the anther cap and rostellar flap. **H.** Anther cap and pollinia. By IC & APK based on Karremans 6438 (JBL-spirit).



FIGURE 63. *Vanilla pompona* different flowering specimens showing variations across its geographical range. **A.** Costa Rica, Osa, Karremans 6438. **B.** Brazil, Pernambuco, E.M. Pessoa s.n. **C.** Colombia, Pereira, S. Vieira-Urbe s.n. **D.** Peru, Madre de Dios, J. Janovec & A. Maceda 2671. All photographs by the collectors kept at JBL.

Conclusions. Since the meticulous revisions published by Soto Arenas & Dressler (2010) and Soto Arenas & Cribb (2010), 20 species of *Vanilla* have been described from the Neotropics. In this study we found that half of them were conspecific with previously, sometimes poorly, known and widespread species. At this time 62 *Vanilla* species, can be attributed to the Neotropics, with 18 membranaceous species belonging to *Vanilla* subgen. *Vanilla*, six Antillean endemic species that

belong to *Vanilla* sect. *Tethya* Soto Arenas & P.J. Cribb, and 38 species, which have fragrant fruits and belong to *Vanilla* sect. *Xanata*. A current state of *Vanilla* taxonomy in the region summarizing these and previous findings is provided (Table 1).

Our study is not exhaustive of all Neotropical *Vanilla*. A lack of living material to illustrate some of the taxa appropriately, as well as a scarcity and state of the herbarium material, prevents us from

TABLE 1. List of accepted Neotropical *Vanilla* species*.

Species	Publication
<i>Vanilla</i> subgen. <i>Vanilla</i> (Membranaceous <i>Vanilla</i>)	
<i>Vanilla acuta</i> Rolfe	J. Linn. Soc., Bot. 32: 453. 1896.
<i>Vanilla angustipetala</i> Schltr.	Anexos Mem. Inst. Butantan Secç. Bot. 1(4): 19. 1922.
<i>Vanilla arcuata</i> Pansarin & M.R.Miranda	Phytotaxa 267: 80. 2016.
<i>Vanilla armoriquensis</i> Damián & Mitidieri	Phytotaxa 451(2): 158–159. 2020.
<i>Vanilla bertonensis</i> Bertoni	Anales Ci. Parag. 8: 10. 1910.
<i>Vanilla bradei</i> Schltr. ex Mansf.	Repert. Spec. Nov. Regni Veg. 24: 243. 1928.
<i>Vanilla costaricensis</i> Soto Arenas	Lankesteriana 9: 297. 2010.
<i>Vanilla dietschiana</i> Edwall	Revista Centro Sci. Campinas 2: 192. 1903.
<i>Vanilla edwallii</i> Hoehne	Arq. Bot. Estado São Paulo n.s. f.m. 1: 61. 1941.
<i>Vanilla guianensis</i> Splitg.	Ann. Sci. Nat. Bot. sér. 2 15: 279. 1841.
<i>Vanilla inodora</i> Schiede	Linnaea 4: 574. 1829.
<i>Vanilla methonica</i> Rchb.f. & Warsz.	Bonplandia (Hannover) 2: 97. 1854.
<i>Vanilla mexicana</i> Mill.	Gard. Dict. ed. 8: n.º 1. 1768.
<i>Vanilla organensis</i> Rolfe	J. Linn. Soc. Bot. 32: 452. 1896.
<i>Vanilla oroana</i> Dodson	Orquideologia 22: 210. 2003.
<i>Vanilla parvifolia</i> Barb.Rodr.	Gen. Spec. Orchid. 2: 271. 1882.
<i>Vanilla sarapiquensis</i> Soto Arenas	Lankesteriana 9: 342. 2010.
<i>Vanilla verrucosa</i> Hauman	Anales Mus. Nac. Hist. Nat. Buenos Aires 29: 365. 1917.
<i>Vanilla</i> sect. <i>Tethya</i>	
<i>Vanilla bakeri</i> Schltr.	Repert. Spec. Nov. Regni Veg. 8: 561. 1910.
<i>Vanilla barbellata</i> Rchb.f.	Flora 48: 274. 1865.
<i>Vanilla claviculata</i> Sw.	Nova Acta Regiae Soc. Sci. Upsal. 6: 66. 1799.
<i>Vanilla dilloniana</i> Correll	Amer. Orchid Soc. Bull. 15: 331. 1946.
<i>Vanilla marmoreisensis</i> Soto Calvo, Esperon & Sauleda	New World Orchid. Nomencl. Notes 56: 2–7. 2019.
<i>Vanilla poitaei</i> Rchb.f.	Linnaea 41: 66. 1876.
<i>Vanilla</i> sect. <i>Xanata</i> (Fragrant <i>Vanilla</i>)	
<i>Vanilla appendiculata</i> Rolfe	Bull. Misc. Inform. Kew 1895: 178. 1895.
<i>Vanilla bicolor</i> Lindl.	Edwards's Bot. Reg. 24(Misc.): 37. 1838.
<i>Vanilla capixaba</i> Fraga & D.R.Couto	Phytotaxa 296(1): 64. 2017.
<i>Vanilla carinata</i> Rolfe	J. Linn. Soc., Bot. 32: 468. 1896.
<i>Vanilla chamissonis</i> Klotzsch	Bot. Zeitung (Berlin) 4: 564. 1846.
<i>Vanilla cobanensis</i> Archila	Revista Guatemalensis 2(3): 47. 1999[2012].
<i>Vanilla columbiana</i> Rolfe	J. Linn. Soc. Bot. 32: 468. 1896.
<i>Vanilla corinnae</i> Sambin & Chiron	Richardiana n.s. 1: 26. 2017.
<i>Vanilla cribbiana</i> Soto Arenas	Lankesteriana 9: 300. 2010.
<i>Vanilla dressleri</i> Soto Arenas	Lankesteriana 9: 303. 2010.
<i>Vanilla duckeri</i> Huber	Bol. Mus. Goeldi Hist. Nat. Ethnogr. 5: 327. 1909.
<i>Vanilla dubia</i> Hoehne	Arq. Bot. Estado São Paulo n.s. f.m. 1: 126. 1944.

(continues)

*The taxonomy follows Soto Arenas & Cribb (2010) and Soto Arenas & Dressler (2010), with a few modifications proposed by Ackerman (2014), the inclusion of recent novelties, and the changes proposed herein. However, it must be stressed that several taxa herein are still being revised in detail and it is already apparent that additional reductions will be proposed in the future.

TABLE 1. (continues).

Species	Publication
<i>Vanilla dungsii</i> Pabst	Bradea 2: 49. 1975.
<i>Vanilla espondae</i> Soto Arenas	Lankesteriana 9: 281. 2010.
<i>Vanilla fimbriata</i> Rolfe	Bull. Misc. Inform. Kew, 1899: 133. 1899.
<i>Vanilla hartii</i> Rolfe	Bull. Misc. Inform. Kew 1899: 133. 1899.
<i>Vanilla helleri</i> A.D.Hawkes	Phytologia 14: 19. 1966.
<i>Vanilla hostmannii</i> Rolfe	J. Linn. Soc. Bot. 32: 462. 1896.
<i>Vanilla inornata</i> Sambin & Chiron	Richardiana 15: 308. 2015.
<i>Vanilla insignis</i> Ames	Bot. Mus. Leafl. 2: 101. 1934.
<i>Vanilla javieri</i> Bar.-Colm.	Phytotaxa 375: 263. 2018.
<i>Vanilla karen-christianae</i> Karremans & P.Lehm.	Orchids (West Palm Beach) 87: 305. 2018.
<i>Vanilla labellopapillata</i> A.K.Koch, Fraga J.U.Santos & Ilk.-Borg.	Syst. Bot. 38: 975. 2013 [2014].
<i>Vanilla marowynensis</i> Pulle	Enum. Vasc. Pl. Surinam: 118. 1906.
<i>Vanilla odorata</i> C.Presl	Reliq. Haenk. 1: 101. 1826.
<i>Vanilla palmarum</i> (Salzm. ex Lindl.) Lindl.	Gen. Sp. Orchid. Pl.: 436. 1840.
<i>Vanilla paulista</i> Fraga & Pansarin	Phytotaxa 296: 66. 2017.
<i>Vanilla penicillata</i> Garay & Dunst.	Venez. Orchids III. 3: 324. 1965.
<i>Vanilla phaeantha</i> Rchb.f.	Flora 48: 274. 1865.
<i>Vanilla planifolia</i> Andrews	Bot. Repos. 8: t. 538. 1808.
<i>Vanilla pompona</i> Schiede	Linnaea 4: 573. 1829.
<i>Vanilla ribeiroi</i> Hoehne	Relat. Commiss. Linhas Telegr. Estratég. Matto Grosso Amazonas 1: 28. 1910.
<i>Vanilla rivisii</i> Molineros, R.T.González, Flanagan & J.T.Otero	Lankesteriana 13: 354. 2014.
<i>Vanilla ruiziana</i> Klotzsch	Bot. Zeitung (Berlin) 4: 563. 1846.
<i>Vanilla sprucei</i> Rolfe	J. Linn. Soc. Bot. 32: 461. 1896.
<i>Vanilla trigonocarpa</i> Hoehne	Arq. Bot. Estado São Paulo n.s. f.m. 1: 126. 1944.
<i>Vanilla vellozoi</i> Rolfe	J. Linn. Soc. Bot. 32: 467. 1896.
<i>Vanilla weberbaueriana</i> Kraenzl.	Bot. Jahrb. Syst. 37: 395. 1906.
<i>Vanilla</i> × <i>tahitensis</i> J.W.Moore	Bull. Bernice P. Bishop Mus. 102: 25. 1933.

extending this study to other species at this time. However, it is a pressing necessity. About a dozen or so names from the 19th and early 20th centuries apply to taxa that remain cryptic. Once understood, they are likely to have priority over more recently recognized *Vanilla* species. For example *Vanilla cobanensis* Archila [2012] is certainly a synonym of *V. cribbiana* Soto Arenas [2010], the obscure *V. sprucei* Rolfe [1896] is perhaps an earlier name for *V. trigonocarpa* Hoehne [1944], while *Vanilla columbiana* Rolfe [1896], *Vanilla carinata* Rolfe [1896] and *V. vellozii* Rolfe [1896] are all closely related to *V. chamissonis* Klotzsch [1846], *V. marmoreisensis* Soto Calvo *et al.* [2019] is quite similar to *V. barbellata* Rchb.f. [1865],

V. verrucosa Hauman [1917] may be the first name for *V. angustipetala* Schltr. [1922], *V. paulista* Fraga & Pansarin [2017] is very close to *V. dubia* Hoehne [1944], *V. capixaba* Fraga & D.R.Couto [2017] is probably closely related to *V. ribeiroi* Hoehne [1910], *V. labellopapillata* Koch *et al.* [2014] shows some resemblance to *V. fimbriata* [1899] and *V. insignis* Ames [1934], and *V. javieri* Bar.-Colm. [2018] is reminiscent of *V. purusara* Hoehne [1944]. There are surely several distinct species among these taxa, but it is also certain that a few will turn out to be further synonyms after thorough inspection, and it is highly desirable that these taxa are well understood before proposing further novelties.

Sangster (2009) argues that the growth in species numbers results from progress in taxonomy and benefits other disciplines. We agree with the author that our knowledge on poorly known groups may increase in this way, but it is only a progress in taxonomy when studies are carried out rigorously and previously proposed taxa are clarified and well delimited. An ill-defined and poorly illustrated novelty that is not placed in any ecological and systematic framework is a problem rather than a taxonomical advancement. Even though undescribed species may indeed be discovered in the future, we believe that, contrary to other highly diverse Neotropical orchid genera, the number of names in *Vanilla* today is likely to exceed the number of actual species. Dealing with these names may seem merely a taxonomic endeavor of little consequence, nevertheless significant taxonomic inflation may result in an overestimation in speciation rates, the underestimation of ecological preferences and distribution ranges, false interpretations of endemisms and hotspots, skewed origin and diversification patterns, mistaken conservation priorities, and increased interest of collectors, among other issues previously mentioned (Isaac *et al.* 2004, Zachos *et al.* 2013, Garnett & Christidis 2017). We agree with Geiger (2020) and Geiger *et al.* (2020) that taxonomical “cleanups” may have profound implications for our understanding of diverse groups within the Orchidaceae.

Furthermore the extremely broad distributions of *Vanilla* species, both geographically and ecologically, is an unusual phenomenon in the Orchidaceae that warrants further study. We do not (re)assess the conservation status of these *Vanilla* species here, but offer useful information to do so in the future. The Extent of Occurrence (EOO), which is estimated by drawing a polygon over the data points at the edge of the distribution, is a very rough initial assessment of the extent of a species' occurrence. It should not be taken as an estimate of the species' habitat as it does not exclude unsuitable habitats. However, it does say something about how broad the distribution of *Vanilla* species can be, and is indicative of a very effective dispersal mechanism coupled with a high plasticity in their ecological preferences. Three species, *V. mexicana*, *V. phaeantha* and *V. pompona* have an estimated EOO of above 14 and 15 million square kilometers which must be among the broadest

distributions known in Orchidaceae. They are also among the most commonly found species in that broad distribution, with hundreds of vouchers available. They are followed by *V. hartii* and *V. odorata*, the first with an EOO just above four million square kilometers, and the latter close to 10 million km². Both have relatively small plants, and do not become as massive as the previous. It is unclear if they are indeed less common and have a narrower distribution, or have simply been overlooked by collectors. *Vanilla karen-christianae* and *V. marowynensis* are unusual in comparison to the other species discussed here. Both have a relatively broad distribution with an EOO of little more than four million km², but seem to be quite rare in that large extension. The two species with the smallest areas are *V. columbiana* and *V. inodora*, both below a million km². Even though this still means they are found in several countries across their range, and may not necessarily be rare, the question remains as to why their distribution is more restricted. Some *Vanilla* species are rare and have restricted distributions within a country, warranting local conservation efforts. Such is the case of *V. mexicana* in Florida. Inferring the natural distribution of *Vanilla planifolia* has been challenging due to its widespread cultivation, it is found in the wild in Central America, but some collections from South American appear to have been made in the wild. We are unable at this time to be sure and have indicated that uncertainty with yellow (wild) and red (cultivated or uncertain) points in the map.

Further studies incorporating distribution and frequency data, as well as ecological requirements, will be needed to assess the conservation priorities among these *Vanilla* species. The Global Biodiversity Information Facility (GBIF) is one of the most important sources of raw data for accessing species occurrence records which are used to assess distributions in studies that go from inferring the impact of climate change and spread of invasive species, to determining priorities for conservation, food security and human health. The database relies on the correct determination of the specimen vouchers from which it feeds. Despite their best curation efforts specimens are not always correctly identified and most users will not or cannot double check them. Luckily digital vouchers are available in the GBIF gallery for some of the specimens in the database. A careful inspection of

the vouchers for the ten species discussed in this paper reveals that all of them include incorrectly determined specimens, even when disregarding synonymies. In the case of *V. hartii*, *V. odorata*, *V. phaeantha* and *V. pompona*, the false positives represent up to 15% of the digitally available vouchers for those species. But in the case of *V. inodora* and *V. mexicana* incorrectly determined vouchers represent about 50% of all those available. What could be consequences for those studies on non-taxonomical if these misidentifications were generalized?

The adequate determination of taxa used in non-taxonomic biological studies is fundamental. Correctly determined taxa set a strong foundation in order to reach the research objectives and are essential for drawing robust conclusions. Hu *et al.* (2019) used genomics-based tools to characterize and identify genetic diversity in *Vanilla*. Among some of their key results is the relative low genetic variation found in *Vanilla planifolia*, the evidence of multiple hybrid accessions and the presence of misclassified accessions amongst those sampled. However, to identify the *Vanilla* accessions the authors used a “consensus” strategy, assigning names based on which one is more recurrent amongst its closest genetic relatives. Such indirect determinations of taxa may pose a serious methodological concern and can weaken conclusions based on them. Bouétard *et al.* (2010) dealt with the difficulty of identifying *Vanilla* accessions somewhat differently. In their study about half of the accessions were left as undetermined which unfortunately limits what can be inferred from them. Incorrectly determined or undetermined taxa may be highly detrimental to such studies, both by introducing errors in the conclusions that are drawn, as in masking others that are therefore not reached.

In their genetic studies of *Vanilla planifolia* and its relatives in the Yucatan Peninsula, Villanueva-Viramontes *et al.* (2017) included accessions of an undetermined taxon that appeared to be isolated from all others. The authors presented photographs of the five taxa included in the study, and thanks to that it is possible not only to understand what the author’s concept of each taxon is, but also to identify their undetermined taxon as *Vanilla phaeantha*, a species that is also found in Mexico. Montes de Oca-Vásquez *et al.* (2020) studied the effects of microhabitats on the soil

and litter microbial communities associated with wild relatives of the *Vanilla* crop in the tropical rainforest in Costa Rica. The authors determined *Vanilla* plants using both “morphological traits and DNA barcoding”, and indeed such a study cannot be effectively carried out without consistent determination of the taxa in the field. Photographs communicated to us by the authors confirm that *Vanilla* sp. 3 in their study is in fact *V. hartii*, a species that is relatively common in the study area. The use of a photograph mistakenly labeled *V. planifolia* in Gallage & Möller (2018) indicates that also in agriculture and biotechnology there is confusion as to the correct identity of *Vanilla* cultivars, the consequences of which are not trivial.

This handful of examples prove the importance of both the availability of vouchers and the need of experts to determine them, even for non-taxonomical studies. We agree with Pupulin (2016) that alpha-taxonomy is fundamental to all of biology, and that the fundamental questions from disciplines such as speciation, diversification processes, ecosystem development, and conservation priorities depend on correct species boundaries and diversity estimates. In 2005, Robert Dressler stated “current attitudes favor molecular systematics... against old-fashioned taxonomy”, pointing out that “most molecular work would be quite meaningless without “old-fashioned” identification and documentation of the samples analyzed” (Dressler 2005). Today, his cautionary statements are more true than ever. Molecular studies are a tool. A powerful source of information. Evidence to help support or disprove a hypothesis. They cannot, on their own, formulate the hypothesis. They are not a substitute for the so-called “old-fashioned” characterization and naming of species. Alpha-taxonomy will always be needed in biological studies that rely on the correct application of species’ boundaries and species’ names. The correct interpretation of boundaries and the application of names necessarily derives from the study of original texts, illustrations, and type specimens, as well as the biogeography and morphological variation found in extant populations. The misleading notion that DNA-based studies are somehow superior to and eliminate the necessity for alpha-taxonomy has become quite generalized among certain botanical institutions. To the point that alpha-taxonomical experts, and their work, is frequently looked down upon by their molecular-

systematics counterparts. We would rather argue that the knowledge of these experts is invaluable and quite essential to set the bases for any serious biological study.

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