Plant Ecology and Evolution 158 (1): 111–121, 2025
https://doi.org/10.5091/plecevo.140667

PLANT ECOLOGY EVOLUTION

RESEARCH ARTICLE

Towards a monograph of membranaceous Vanillas: a nomenclatural revision of *Vanilla* subgen. *Vanilla* (Vanilloideae, Orchidaceae)

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Academic editor: Isabel Larridon ♦ **Received** 31 October 2024 ♦ **Accepted** 14 February 2025 ♦ **Published** 4 April 2025

Abstract

Background and aims – *Vanilla* subgenus *Vanilla* was established by Soto-Arenas and Cribb (2010) to include Neotropical species characterized by membranaceous leaves, a labellum without a penicillate callus, and a column attached solely at the base of the lip. *Vanilla mexicana* (= *Epidendrum vanilla*) was the first species attributed to this subgenus, and its nomenclature traces back to the *Vanilla*'s taxonomic origins, serving as the type species for the entire genus. Despite this, several biological aspects of membranaceous vanilla species remain poorly studied, including their taxonomy and nomenclature, which have not been thoroughly addressed. The lack of clarity regarding the circumscription of these fairly rare taxa has led to taxonomic confusion and neglect by botanists. This study aims to conduct a typological assessment of all names associated with *Vanilla* subgen. *Vanilla*.
Material and methods – A comprehensive list of names attributable to *Vanilla* subgen. *Vanilla* was compiled from different sources. Protologues were studied for every name and type specimens were examined through direct visits or virtual herbaria. The International Code of Nomenclature of algae, fungi, and plants was followed for the type designation and nomenclatural notes.
Key results – A comprehensive nomenclatural revision was carried out for 29 names. A total of eight lectotypes and one epitype are designated, with nomenclatural notes provided for most names within the subgenus.

Keywords

Neotropics, Vanilloideae, Orchidaceae, typification

INTRODUCTION

The nomenclature of *Vanilla* subgen. *Vanilla*, otherwise known as the membranaceous vanillas, traces back to the origin of the genus itself. The first reference to the generic name "*Vanilla*" and a plant corresponding to our current concept of these orchids comes from Plumier's work in the Antilles during the late 17th century. In his Nova Plantarum Americanarum Genera, Plumier (1703) informally described the genus and listed three polynomial names for *Vanilla*, two of which can be traced to his unpublished illustrations. Among these is *Vanilla inodora flore viridi & albo, fructu nigrescente* which clearly refers to a membranaceous species (see Karremans et al. 2020: fig. 25C–D). Later, Miller (1740) incorporated *Vanilla* into his Gardeners Dictionary, listing Plumier's polynomial names and subsequently validating the genus in the 4th edition of his dictionary (Miller 1754). However,

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it was not until 1768 that Miller adopted the Linnaeus binomial system and proposed *Vanilla mexicana* Mill., citing an illustration by Catesby (1747), which is based on Plumier's *Vanilla inodora flore viridi & albo, fructu nigrescente* (Karremans and Pupulin 2023). The epithet "*mexicana*" comes from the mistaken belief that the materials of Plumier, and therefore Catesby, could be referable to the vanilla of commerce. Given that Catesby's illustration was the only original material available for typification, Reveal (2009) designated it as the lectotype for *Vanilla mexicana* ultimately linking the epithet to a species that is neither aromatic nor native to Mexico.

The first formally described binomial that can be attributed to this group is *Epidendrum vanilla* L. Under *E. vanilla*, Linnaeus (1753) listed seven references including Catesby (1747: plate 7), which was later designated as the lectotype by Cafferty and Jarvis (1999). Among the different materials cited by Linnaeus are both aromatic and non-aromatic *Vanilla* species in equal proportions (Karremans and Pupulin 2023), suggesting that he believed them to represent a single taxon. Despite Linnaeus's original intention of describing the aromatic *Vanilla* of commerce, the typification with Catesby's illustration resulted in the name *E. vanilla* being anchored to a non-aromatic taxon. Although not originally based on the same type, posterior lectotypifications of both *E. vanilla* and *V. mexicana* with Catesby's illustration resulted in the two names being conspecific. Karremans et al. (2020) pointed out that these nomenclatural acts would render the posterior name, *V. mexicana*, illegitimate unless it is considered as a replacement for the name *E. vanilla*.

It was not until 1896 that the first *Vanilla* monograph was published by Robert Rolfe at Kew, listing 52 species divided into *Vanilla* sect. *Foliosae* and *Vanilla* sect. *Aphyllae* based on leaf development, with the former containing species with well-developed laminas and the latter those with absent or reduced leaves. Within this classification, Rolfe placed seven thin-leaved (i.e. membranaceous) species in *Vanilla* sect. *Foliosae*. Rolfe's revision holds significant importance for typification, as he consistently referenced herbarium specimens for each species, utilizing them in conjunction with illustrations and relevant literature to define his species. These specimens are usually traceable to Lindley's and Kew's orchid herbaria. Since Rolfe's work, two further monographic revisions have been attempted. The first, by Portères (1951, 1954), who expanded the known *Vanilla* species to 110, maintaining Rolfe's classification and adding three new subsections within *Vanilla* sect. *Foliosae*: subsect. *Membranaceae* (15 species) for species with thin leaves and a labellum not fused to the column, subsect. *Lamellosae* (49 species) for those with flattened appendages or lamellae, and subsect. *Papillosae* (28 species) for species with thick trichomes on the labellum. However, these subsections lacked nomenclatural validity as their diagnoses were in French, not Latin (Turland 2019). Despite this, Portères's work provided valuable insights into *Vanilla* ecology and biogeography, including distribution maps, detailed descriptions as well as cited specimens. More recently, Soto-Arenas and Cribb (2010) established the current infrageneric classification of *Vanilla*, consisting of two subgenera: *Vanilla* subgen. *Vanilla*, exclusively Neotropical, and *Vanilla* subgen. *Xanata*, the latter divided into two sections: *Xanata* (Neotropical) and *Thethya* (mainly Paleotropical). Under this classification, *Vanilla* subgen. *Vanilla* includes species with thin, membranaceous leaves, typically green and white flowers lacking a penicillate callus, and columns attached to the lip only at the base—traits considered synapomorphies for the subgenus. The work of Soto-Arenas and Cribb (2010) recognized a total of 106 *Vanilla* species, with 15 assigned to *Vanilla* subgen. *Vanilla*. Each taxon was accompanied by comprehensive nomenclatural details, with lectotypes designated when necessary, and citations of herbarium specimens used to delineate the species. However, it is apparent that challenges remained in defining certain species, particularly within the membranaceous group. For instance, of the 19 names associated with Soto-Arenas's *Vanilla* subgen. *Vanilla*, nearly 50% (9/19) were insufficiently discussed due to the absence of revised type material (Damián-Parizaca et al. 2024).

The lack of clarity surrounding the circumscription of membranaceous taxa has led to persistent taxonomic confusion and neglect, which several species receiving little to no taxonomic attention. The existence of these little-known taxa risks obscuring our understanding of *Vanilla* diversity, and in the worst-case scenario, they could be relegated to insertae sedis. This underscores the urgent need for focused taxonomic work on these taxa to uncover the true species diversity within the group. In this context, the present study seeks to provide a nomenclatural revision of *Vanilla* subgen. *Vanilla* through a comprehensive typological assessment of the described names. This effort is an essential step toward clarifying species boundaries and will serve as a foundation for a broader taxonomic revision of the subgenus, which is currently underway.

MATERIAL AND METHODS

A comprehensive list of names attributable to *Vanilla* subgen. *Vanilla* was compiled from Rolfe (1896), Portères (1954), Soto-Arenas and Cribb (2010), Soto-Arenas and Dressler (2010), Karremans et al. (2020), and was further supplemented with electronic indexes such as IPNI (2024), Tropicos (2024), and POWO (2024). Protologues were primarily accessed via the Biodiversity Heritage Library (BHL 2024), and for those not available online, the University of Wisconsin-Madison Library's Interlibrary Loan services were utilized. Type material deposited in the herbaria including AMO, AMES, B, BAB, BIGU, BM, BR, CR, F, FCQ, FLAS, FTG, G, GH, HA, HB, HJBG, HOXA, JBB, K, K-L, LBMBP, MA, MEXU, MO, MOL, NY, LAGU, LL, LY, P, PRG, QCNA, QCNE, R, SCP, SEL, SP, SPFR, UFV, US, USM, UVAL, W, W-R, and WIS

was examined either through direct visits or via analysis of digital images hosted in JSTOR (2024), GBIF (2024), Reflora (2024), and SpeciesLink Network (2024), or the respective herbarium's online database.

The International Code of Nomenclature for algae, fungi, and plants (ICN; Turland et al. 2018) was followed for type designations. Lectotypes were designated in accordance with the typification flowchart proposed by Turland (2019: fig. 16), which adheres to Chapter II, Section 2: Typification of the ICN. Some names, particularly those predating Rolfe's monograph or with pre-Linnaean origins (e.g. *Vanilla mexicana*), required more detailed analysis. In these cases, the first two chapters of Jarvis (2007) were instrumental in interpreting 18th-century protologues. For each name, the full reference is provided along with detailed information about its nomenclatural type, including herbarium data and barcodes when available. We included a Notes section for most of the species listed, with particular emphasis on those requiring a nomenclatural decision. This section provides a brief statement explaining the rationale for type designation when applicable or discusses relevant information regarding previous typifications. This work does not aim to address the taxonomic concepts of each species; a comprehensive taxonomic revision is currently in preparation and will provide that information.

NOMENCLATURAL REVIEW

Vanilla subgenus *Vanilla*

Vanilla subsect. *Membranaceae* Portères (1951: 291); nom. inval. (Turland et al. 2018: art. 39.1)

Vanilla subsect. *Membranaceae* Portères (1954: 159); nom. inval. (Turland et al. 2018: art. 39.1)

Lectotype. *Vanilla mexicana* Mill., Gardeners Dictionary (ed. 8) *Vanilla* no. 1. 1768 (designated by Mansfeld 1959: 587; see Karremans and Pupulin 2023).

1. ***Vanilla acuta*** Rolfe (Rolfe 1896: 453)

Fig. 1A, B

Type. SURINAME – **Marowyne** • Aug. 1846; *Kappler 1843*; lectotype (**designated here**): K! (tracings of the lectotype at W! [W21429, W33544]); isolectotypes: W! [W62925, pocket label as "Vanilla Marowyne fl. flavidis Kappler"], P! [P00612143]. Epitype (**designated here**): GUYANA (British Guiana) • Berbice River; illustration by Robert H. Schomburgk, plate 216–267; BM! (photo of the epitype at NY!, tracings of the epitype at K! [K001551121] and W! [W19383, W19384]).

Notes. Two tracings of the lectotype are deposited in W [W21429, W33544]. Three tracings of the epitype are deposited in K [K001551121] and in W [W19383, W19384]. A photograph of the epitype is deposited in NY.

When describing *Vanilla acuta*, Rolfe (1896) cited a plant collected by A. Kappler in Suriname as the only specimen and mentioned that a drawing made by Schomburgk at BM should belong to his species. Although Rolfe's publication explicitly states his affiliation with Kew and mentions that he examined two Klotzsch type specimens on loan from B, as well as material from BM, it is difficult to ascertain with certainty which specimens belonged to K, B, or BM, or whether he consulted a combination of these. This ambiguity arises from his inconsistent specification of herbarium sources for the specimens he reviewed. For instance, in the cases of *V. hamata* Klotzsch and *V. ruiziana* Klotzsch—most likely the two Klotzsch types referenced in his introduction—Rolfe did not explicitly indicate material examined at B. Similarly, for BM, although some specimens and illustrations are cited as "Mus. Brit." or "British Museum," it remains ambiguous whether these were the only sources from which he examined specimens.

Among the two original materials cited by Rolfe for *V. acuta*, a specimen matching the protologue was identified in the Lindley Herbarium (K) and is hereby designated as the lectotype. Additionally, a review of the Reichenbach Herbarium in Vienna (W) revealed a tracing and an immature flower unequivocally linked to *Kappler 1843*, which is designated as an isolectotype. Furthermore, a specimen in the Herbarium of Paris (P00612143) is highly likely to correspond to the Kappler collection, despite its label attributing the collection to Hostmann. The collection number, date, and locality align with those in Lindley's Herbarium, and both bear his tentative determination as "*V. claviculata* aff." Notably, both specimens were curated by Rudolph Friedrich Hohenacker, and historical records confirm that Kappler collected plants for Hostmann in Suriname (de Vries 2022).

Given the poor condition of the type flowers, the Schomburgk illustration is designated as the epitype to better clarify Rolfe's proposal of this taxon.

2. ***Vanilla andina*** Damián-Parizaca & H.Garzón (Damián-Parizaca et al. 2022: 64)

Type. PERU – **San Martin** • Lamas, Pinto recodo, Centro Poblado Jesus del Monte; Aug. 2019; *S. Olortegui & A. Damián 908*; holotype: USM!.

3. ***Vanilla angustipetala*** Schltr. (Schlechter 1922: 19)

Fig. 1C

Type. BRAZIL – **São Paulo** • Near Morro das Pedras, Iguapé; Dec. 1916; *A.C. Brade 7775*; holotype: B†; lectotype **(designated here)**: R! [R00024938]; isolectotypes: AMES! [AMES114509], HB! [HB8086], K! [K000463749], M! [M0226098].

Notes. Schlechter (1922) described *Vanilla angustipetala* based on material sent by Alexandre Brade from São Paulo. Most of Schlechter's material, including the holotype of *Vanilla angustipetala*, was tragically destroyed during the bombing of the Berlin Herbarium in World War II (Butzin 1978, 1980, 1981). Fortunately, several isotypes of this taxon are conserved in various herbaria. An isotype at R is hereby selected as lectotype given its good condition

and clear floral dissection. Previously unknown isotypes are listed here and designated as isolectotypes.

4. ***Vanilla arcuata*** Pansarin & M.R.Miranda (Pansarin and Miranda 2016: 85)

Fig. 1D

Type. BRAZIL – **São Paulo** • Mun. Caraguatatuba, Mata de Restinga; 7 Mar. 2015; *E.R. Pansarin & M.R. Miranda 1514*; holotype: LBMBP! [LBMBP147].

5. ***Vanilla armoriquensis*** Damián-Parizaca & Mitidieri-Rivera (Damián-Parizaca and Mitidieri-Rivera 2020: 158)

Type. PERU – **Junín** • Prov. Chanchamayo, Dtto. Chanchamayo, Hacienda Armorique, en un bosque colinoso; Sep. 2019; *A. Damián, M. Gerbi, M. Rodenas Gerbi 904*; holotype: UFV!; isotypes: MOL!, USM!.

6. ***Vanilla bradei*** Schltr. ex Mansf. (Mansfeld 1928: 243)

Fig. 1E

Type. BRAZIL – **São Paulo** • Guapira, Wald, epiphytisch; 27 Apr. 1913; *A.C. Brade 7573*; holotype: B†; lectotype **(designated here)**: HB! [HB8087].

Notes. The species was originally determined as a novelty by Rudolf Schlechter. It was formally described after Schlechter's death by R. Mansfeld (1928), upon Brade's request. Schlechter's herbarium, including the type of *V. bradei*, was destroyed during the bombing of the Berlin Herbarium (Butzin 1978, 1980, 1981). Our revision revealed a well-conserved yet sterile isotype at HB, which we hereby select as lectotype.

7. ***Vanilla bertoniensis*** Bertoni (Bertoni 1910: 10)

Fig. 1F

Type. PARAGUAY – **Alto Paraná** • Puerto Bertoni; *Bertoni 6039*; holotype: SCP! [SCPD00036]; clonotype: SCP! [SCPD00041].

Notes. In the introduction of the paper in which Bertoni published this species, he explicitly stated that he was working on materials from his own herbarium (Bertoni

Figure 1. Type specimens of membranaceous *Vanilla*. **A**. Lectotype designated for *Vanilla acuta* [K]. **B**. Epitype designated for *Vanilla acuta* (Illustration by Robert H. Schomburgk: plate 216–267, BM). **C**. Lectotype designated for *Vanilla angustipetala* [R00024938]. **D**. Holotype of *Vanilla arcuata* [LBMBP147]. **E**. Lectotype designated for *Vanilla bradei* [HB8087]. **F**. Holotype of *Vanilla bertoniensis* [SCPD00036]. **G**. Holotype of *Vanilla costaricensis* [CR062310]. **H**. Holotype of *Vanilla dietschiana* [SP000109]. Photos by Alexander Damián-Parizaca (A), Emerson Pansarin (D), and courtesy of Library and Archive collections of the Natural History Museum, London (B), Herbário do Museu Nacional, R (C), Herbarium Bradeanum, HB (E), Sociedad Cientifica del Paraguay (F), Museo Nacional de Costa Rica (G), Herbario Instituto de Botanica, SP (H).

1910). Although two specimens with the number *Bertoni 6039* are deposited at SCP, one was prepared after the formal description of *V. bertoniensis* (3 Jan. 1911) and therefore cannot be the holotype. Therefore, a single specimen matching the protologue was located, and we find this sufficient to unambiguously determine it as the holotype.

8. ***Vanilla costaricensis*** Soto-Arenas (Soto-Arenas and Dressler 2010: 297)

Fig. 1G

Type. COSTA RICA – **Alajuela** • llanura de San Carlos; 20 Feb. 1966; *A. Molina R., L.O. Williams, W.C. Burger and B. Wallenta 17565*; holotype: CR! [CR062310]; isotype AMO! (ex MO) [MO2367689].
Notes. An isotype that was stated to be at MO was instead found in the AMO collection.

9. ***Vanilla dietschiana*** Edwall (Edwall 1903: 192)

Fig. 1H

Dictyophyllaria dietschiana (Edwall) Garay (Garay 1986: 231)
Type. BRAZIL – **São Paulo** • Serra do Mar; 1903; *A. Dietsch 6070*; holotype: SP! [SP000109].
Notes. The paper in which Edwall (1903) published this species explicitly states that he collected this material for the herbarium of the Comissão Geographica e Geologica de São Paulo. A single specimen determined by Edwall as his *V. dietschiana* bears a label of the Comissão and is congruent with the protologue. We find this sufficient to unambiguously determine it as the holotype.

10. ***Vanilla edwallii*** Hoehne (Hoehne 1941: 61)

Fig. 2A

Type. BRAZIL – **São Paulo** • Serra da Cantareira; Jan. 1902; *G. Edwall 6003*; holotype: SP! [SP002432].

11. ***Vanilla guatemalensis*** Archila (Archila 1999 [2012]: 46)

Fig. 2B

Type. GUATEMALA – **Alta Verapaz** • Pantano de Rubelsanto, cruce para playa grande a 350 m; Jun. 1994; *O. Archila s.n.*; holotype: BIGU! [BIGU054552].
Notes. The holotype of this species, although sterile, was successfully located at BIGU. We have been informed that a spirit collection from the same gathering, containing flowers, is also deposited at the same herbarium but has not yet been located (Mario Véliz pers. comm.).

12. ***Vanilla inodora*** Schiede (Schiede 1829: 574)

Fig. 2C

Type. MEXICO – **Misantla** • Baynilla de puerco Misantlensium. Species distinctissima. Hab. Misantlae; *Schiede & Deppe s.n.*; lectotype (designated by Ackerman 1995: 174): BM! [BM000062769]; isolectotypes: LE! [LE00001364], W! [W0253992, W0253991].
Notes. Under art. 9 of the Shenzhen Code (Turland et al. 2018), the use of the word "Type" in Ackerman (1995) and the reference to a specimen at BM is to be considered the first lectotypification of this name, albeit involuntary. This renders the lectotypification with a specimen at W by Karremans et al. (2020) superfluous.

13. ***Vanilla latisegmenta*** Ames & C.Schweinf. (Ames and Schweinfurth 1925: 2)

Fig. 2D

Type. GUYANA (British Guiana) • Upper Rupununi River, near Dadanawa; 29 May 1922; *J. S. de la Cruz 1404*; holotype: AMES! [AMES22973]; isotypes: AMES! [AMES7850], GH! [GH7850], MO! [MO2602185], US! [US00093324].
Notes. Ames and Schweinfurth (1925) explicitly designated *J.S. de la Cruz 1404* as the holotype of *V. latisegmenta* and specified AMES as the herbarium where the holotype is deposited. Soto-Arenas and Cribb (2010) listed a collection at GH as isotype. We further list additional isotypes found at MO and US.

14. ***Vanilla martinezii*** Soto-Arenas (Soto-Arenas and Dressler 2010: 320)

Fig. 2E

Type. GUATEMALA – **Izabal** • Livingston, El Golfete, a 20.4 km al NE de Río Dulce por lancha camino a Calix; 26 Jul. 2003; *E. Martinez & D. Alvarez 36410*; lectotype **(designated here)**: MEXU! [MEXU01478369]; isolectotypes: MEXU! [MEXU01478370], AMO! [ESP118178], BIGU not found, MO not found.
Notes. Soto-Arenas and Dressler (2010) originally designated the specimen at MEXU as the holotype for *Vanilla martinezii* while identifying three isotypes located at AMO, BIGU, and MO. Upon examining the type collection at MEXU, we found two sheets under the same collector's number, with no indication that they were part of a single preparation. Consequently, a lectotype designation is required. Here, we designate the sheet bearing a flower bud as the lectotype. Furthermore, after reviewing the AMO spirit collection, we identify a jar labelled "*E. Martinez s.n.*" with a single flower. Based on morphological congruence with the flower illustrated in the species' original description (Soto-Arenas and Dressler 2010: fig. 10), we propose that this specimen most likely belongs to the original material used by Soto-Arenas. The illustration, as noted in the legend, is partially based on the type specimen (flower + dissection 1 + L-shaped column), *E. Martinez 22790* (second column + dissection 2, including a petal, lateral sepal, and half of the lip), and *M. Soto 8602a* (plant with fruits). It is likely that the flower preserved in the AMO spirit collection corresponds to the specimen Soto-Arenas referenced as "iso. AMO!" and we hereby designate it as an isolectotype. We could not locate the isotypes at BIGU and MO.

15. ***Vanilla methonica*** Rchb.f. & Warsz. (Reichenbach 1854: 97)

Fig. 2F

Type. COLOMBIA • Neu Granada; 6000–8000 ft.; *Warscewicz s.n.*; holotype: W! [W0253993]; isotype: K!.

Notes. A single specimen at Reichenbach's herbarium is identified as *V. methonica* in the author's own handwriting. It also includes a note by co-author and collector Warscewicz indicating the locality information as it appears in the protologue. We find this sufficient to unambiguously determine it as the holotype.

16. ***Vanilla mexicana*** Mill. (Miller 1768: without number)

Epidendrum vanilla L. (Linnaeus 1753: 952)

Vanilla aromatica Sw. (Swartz 1799: 66), nom. superfl. illeg.

Vanilla anaromatica Griseb. (Grisebach 1864: 638), nom. superfl. illeg.

Vanilla epidendrum Mirb. (Mirbel 1802: 249), nom. superfl. illeg.

Type. Lectotype (designated by Reveal (2009: 359) as lectotype of *V. mexicana* and by Cribb in Cafferty and Jarvis (1999: 47) as lectotype of *E. vanilla*): HAITI • "Volubilis siliquosa mexicana plantagini folio" in Catesby, Natural History of Carolina, Florida and the Bahama Islands vol. 2 (Catesby 1747: appendix 7, pl. 7, reproduced in Karremans et al. 2020: fig. 25A).

Notes. Upon proposing *Vanilla mexicana*, Miller cited a single illustration by Catesby (1747: fig. 4). This was later proven to be based on unpublished illustrations by Plumier (see Karremans et al. 2020: fig. 25). Miller attributed his species to an aromatic entity, noting that "…with this fruit the Spaniards perfume their chocolate," effectively combining the non-aromatic species illustrated by Plumier (Karremans et al. 2020: fig. 25C–D) with the species of the Mexicas, valued for their fragrant fruits. Miller's slip resulted in the typification of *Vanilla mexicana* (Reveal 2009) with the illustration of a species that is neither aromatic nor native to Mexico.

Under *Epidendrum vanilla*, Linnaeus listed the following elements: *Epidendrum foliis ovato-oblongis nervosis, sessilibus caulinis, cirrhis spiralibus* (van Royen 1740: 13, Linnaeus 1749: 13); *Vanilla piperis arbori jamaicensis innascens* (Plukenet 1696: 381); *Vanille* (Merian 1705: 25); *Volubilis siliquosa, plantaginis folio* (Catesby 1747: 7); *Lobus aromaticus subfuscus terebinthi*

Figure 2. Type specimens of membranaceous *Vanilla*. **A**. Holotype of *Vanilla edwallii* [SP002432]. **B**. Holotype of *Vanilla guatemalensis* [BIGU054552]. **C**. Lectotype of *Vanilla inodora* [BM000062769]. **D**. Holotype of *Vanilla latisegmenta* [AMES22973]. **E**. Lectotype designated for *Vanilla martinezii* [MEXU01478369]. **F**. Holotype of *Vanilla methonica* [W0253993]. **G**. Lectotype of *Vanilla organensis* [K]. **H**. Holotype of *Vanilla oroana* [MO6777486]. Photos by Alexander Damián-Parizaca (C, E–G), Mario Veliz (B), and courtesy of Herbario Instituo de Botanica, SP (A), Herbarium Harvard University (D), Missouri Botanical Garden, MO (H).

corniculis simili (Bauhin 1671: 404). Additional materials are indirectly listed by citation of a reference that contains it. For example, both Royen's Florae Leydensis and Linnaeus's Acta Universitatis Upsaliensis refer to *Vanilla flore viridi & albo, fructu nigrescente* of Plumier, which is not directly cited here. From this is becomes clear that Linnaeus believed these elements belonged to a single taxon, the *Vanilla* of commerce. Today we know that the materials in this list represent different, often unrelated, *Vanilla* species, belonging to both aromatic and non-aromatic taxa (Karremans and Pupulin 2023).

17. ***Vanilla organensis*** Rolfe (Rolfe 1896: 452)

Fig. 2G

Type. BRAZIL • Organ Mountains; *Gardner 632*; lectotype (designated by Soto-Arenas 2010: 385; plant with inflorescence on the bottom left side of the sheet, excluding the detached flower): K! [K000463758]; isolectotypes: AMES! [AMES00090735], G! [G00618049], GH! [GH00090735], K! [K000463757, K000463758], NY! [NY00803972], US! [US00093332], W! [W0254006]; tracing W! [W0254002]; remaining syntypes: *Glaziou 14320*, K! [K000940254], P! [P00367022]; *Glaziou 11620*, K! [K000940255], P! [P00367023]; *Miers s.n.*, K! [K000940253].

Notes. When proposing *Vanilla organensis*, Rolfe listed four different collections, considered syntypes. *Gardner 632* at the Lindley Herbarium (K) was selected by Soto-Arenas and Cribb (2010) as the lectotype, and four additional specimens were designated as isolectotypes. The sheet on which *Gardner 632* (K) is conserved includes two other elements that do not belong to the same collection, a stem with inflorescence on the top right and a detached flower, which are excluded.

18. ***Vanilla oroana*** Dodson (Dodson 2003: 210)

Fig. 2H

Type. ECUADOR – **El Oro** • 3.7 km N of junction of old and new roads from Piñas to Santa Rosa, 12 km west of Piñas; 1400 m; 19 Apr. 1989; *Dodson, Williams, Dressler, Whitten & Embree 17951*; holotype: MO! (ex RPSC) [MO6777486]; isotypes: AMES! [AMES00287585], K! [K001551030], SEL! [SEL003524], QCNE! [QCNE10821].

Notes. Soto-Arenas's notes at AMO suggest that he was in the process of describing this species, maintaining the same epithet as "Dodson ex Soto-Arenas," but for an unknown reason, did not effectively publish his manuscript. It appears that he intended to publish the name alongside with *Vanilla espondae* Soto-Arenas, including an extensive description and illustration.

19. ***Vanilla ovata*** Rolfe (Rolfe 1896: 451)

Fig. 3A

Type. FRENCH GUIANA • Cayenne; *J. Martin s.n.*; holotype: BM†, tracing K! [K00396194]; lectotype **(designated here)**: P! [P00612112].

Notes. Rolfe described *Vanilla ovata* based on a single specimen conserved at the British Museum (BM). A tracing of this specimen can be found at Kew. However, no specimen fitting *Vanilla ovata* is currently conserved at BM, and there are no collections by Martin in their records (Norbert Holstein pers. comm.). Given that the specimen seems to be long lost, the only known isotype at P is selected as lectotype.

20. ***Vanilla paludosa*** Pansarin, J.M.Aguiar & A.W.C.Ferreira (Pansarin et al. 2012: 157)

Fig. 3B

Type. BRAZIL – **São Paulo** • Brotas, Fazenda Laranjal; 9 Jul. 2010; *E. R. Pansarin, J. M. R. B. V. Aguiar & A. W. C. Ferreira 1361*; holotype: SPFR! [SPFR15338].

21. ***Vanilla parvifolia*** Barb.Rodr. (Barbosa-Rodrigues 1881: 271)

Fig. 3C

Type. BRAZIL – **Parana** • Curitiba; *J. Barbosa Rodrigues s.n*; holotype: †; lectotype **(designated here)**: Barbosa Rodrigues's original illustration at Biblioteca Barbosa Rodrigues, "Iconographie des Orchidées du Brésil" 1: tab. 49, cited as tab. 767 (then unpublished) in Barbosa-Rodrigues (1881: 271); copied and reproduced in black and white in Cogniaux (1893: t. 33); reproduced in colour in Sprunger et al. (1996: t. 49).

Notes. It is believed that Barbosa's herbarium was destroyed during a tropical deluge (Castro and Singer 2018). However, Barbosa made several illustrations of his species (Mori and Ferreira 1987). We have designated the unpublished illustration made for *Vanilla parvifolia* as the lectotype, which was later reproduced by Cogniaux (1893) and published in Sprunger et al. (1996).

22. ***Vanilla perexilis*** Bertoni (Bertoni 1910: 8)

Fig. 3D

Type. PARAGUAY • Puerto Bertoni; *Bertoni 3631*; lectotype (**designated here)**: SCP! [SCPD00037]; remaining syntype: SCP! [SCPD00040].

Notes. The paper in which Bertoni published this species explicitly states that he was working on materials from his own herbarium (Bertoni 1910). Two specimens with the number *Bertoni 3631* are deposited at SCP, and both conform to the protologue. Therefore, the richest of both specimens is selected as lectotype.

23. ***Vanilla pfaviana*** Rchb.f. (Reichenbach 1883: 230)

Type. COSTA RICA • "Mexico"; *R. Pfau 269*; holotype: W!, AMES! [00090736] sketch, K! [K001784688] photograph.

Notes. The paper in which Reichenbach published this species explicitly states he is basing it solely on a sketch received from Pfau (Reichenbach 1883). There is a single sketch in his herbarium matching the protologue, and it is determined as 'Pfaviana' in the author's own handwriting. We find this sufficient to unambiguously determine it as the holotype.

24. ***Vanilla preussii*** Kraenzl. (Kraenzlin 1919: 320)

Type. GUATEMALA • Bei der Planzung El Baúl im Buschwald; Heisst bei den Eingeborenen "Vainilla silvestre"; *Preuss 1445*; holotype: B†.

Notes. It is believed that part of Kraenzlin's herbarium was destroyed during the bombing of the Berlin Herbarium (Butzin 1978, 1980, 1981), and no original material of Kraenzlin's *Vanilla preussii* has been located in his private orchid collection at HBG (Christenson 1994; Schultz 2013, 2015). Since no original material is available for lectotypification, designating a neotype could be a suitable decision. However, no flowering material from Guatemala that matches the protologue of *Vanilla preussii* has been located.

25. ***Vanilla rebecae*** Archila & Chiron (Archila et al. 2019: 74)

Type. GUATEMALA – **Alta Verapaz** • Municipio de Cobán; 800 m; *Fredy Archila s.n.*; holotype: BIGU not found.

Notes. We were informed that the type collection was deposited at BIGU; however, as of the writing of this manuscript, it has not been located (Mario Véliz pers. comm.). Instead, we identified a spirit collection at BIGU labeled as "*Vanilla rebecae* holotype," which contains flowers of *Vanilla planifolia* Andrews.

26. ***Vanilla rojasiana*** Hoehne (Hoehne 1941: 61)

Fig. 3E

Type. PARAGUAY – **Estancia Princeza** • Caguazu, cult. Asunción; Apr.–May 1927; *T. Rojas 5082*; lectotype **(designated here)**: SP! [SP002433]; isolectotype: AMES! [AMES00287650]; remaining syntype: *T. Rojas 5082A*, SP not found.

Notes. When describing *Vanilla rojasiana*, Hoehne (1941) listed two specimens (*T. Rojas 5082* and *T. Rojas 5082A*) from different gatherings according to his collection dates (April 1927 and May 1927), which are considered syntypes. We found two specimens corresponding to *5082* at SP. Hereby, we select SP002433 as lectotype, as it bears a dissection of the flower.

27. ***Vanilla sarapiquensis*** Soto-Arenas (Soto-Arenas 2010: 342)

Fig. 3F

Figure 3. Type specimens of membranaceous *Vanilla*. **A**. Lectotype designated for *Vanilla ovata* [P00612112]. **B**. Holotype of *Vanilla paludosa* [SPFR15338]. **C**. Lectotype designated for *Vanilla parvifolia*. **D**. Lectotype designated for *Vanilla perexilis* [SCP-D00040]. **E**. Lectotype designated for *Vanilla rojasiana* [SP002433]. **F**. Holotype of *Vanilla sarapiquensis* [CR575513]. **G**, **H**. Holotype of *Vanilla verrucosa* [BAB00004760]. Photos by Alexander Damián-Parizaca (A, C, F), Emerson Pansarin (B) and courtesy of Sociedad Cientifica del Paraguay, SCP (D), Herbario Instituo de Botanica, SP (E) and, Instituto Nacional de Tecnologia Agropecuaria, BAB (G, H).

Type. COSTA RICA – **Heredia** • Sarapiquí, Llanura de San Carlos. Sardinal. Bosques residuales y tacotales camino a Finca Dos Loas; 70 m; 10 May 1995; *J.F. Morales, E. Lépiz, V.H. Ramírez & A. Rojas 4082*; holotype: CR! (ex INB) [CR575513]; isotypes: FLAS! [FLAS205834], MO! [MO5175846!].
Notes. Several photographs of the flower preserved in spirit used to compile the description were found among Soto-Arenas's files at AMO.

28. ***Vanilla verrucosa*** Hauman (Hauman 1917: 365)

Fig. 3G, H

Type. ARGENTINA – **Misiones** • Piray; 29 Mar. 1901; *Kermes 127*; holotype: BAB! [BAB00004760, two sheets].
Notes. Hauman (1917) described *Vanilla verrucosa* and explicitly indicated the single specimen he used for his description, noting it was deposited at Herbario Ministerio de Agricultura (now BAB). Additionally, Hauman mentioned two other sterile specimens, which he suspected may belong to a different species. The holotype consists of two sheets, both sharing the same barcode, labelled as "A" and "B". Both sheets are sterile: the sheet "A" bears the corresponding label and consists of a plant with several leaves and a short inflorescence with a few floral bracts, while the sheet "B" contains a stem without leaves but with roots.

29. ***Vanilla yanesha*** Damián-Parizaca (Damián-Parizaca 2019: 5)

Type. PERU – **Pasco** • Oxapampa; Palcazu, San Francisco de Pichanaz; 550 m a.s.l.; bosque secundario; 28 Feb. 2006; *R. Rojas, J. Mateo & C. Rojas 3947*; holotype: USM! [USM240875]; isotypes: HOXA! [HOXA126525], MO! [MO6049740].

ACKNOWLEDGEMENTS

We express our sincere gratitude to the curators and staff of the following herbaria for granting access to and providing images of specimens from their collections: AMO, AMES, B, BAB, BIGU, BM, BR, CR, F, FCQ, FLAS, FTG, G, GH, HA, HB, HJBG, HOXA, JBB, K, K-L, LBMBP, MA, MEXU, MO, MOL, NY, LAGU, LL, LY, P, PRG, QCNA, QCNE, R, SCP, SEL, SP, SPFR, UFV, US, USM, UVAL, W, W-R, and WIS. We are particularly grateful to the Department of Botany at the University of Wisconsin-Madison for its financial support, which enabled visits to the AMO, F, MEXU, NY, MO, and US herbaria. In addition, we extend our appreciation to the Hugh H. Iltis Graduate Student Research Award Committee and Mr Theodore S. Cochrane at UW-Madison for their financial assistance. Likewise, the first author acknowledges the generous funding provided by the American Society of Plant Taxonomists (ASPT), the Botanical Society of America (BSA), the Systematics Association, and the American Orchid Society (AOS). Moreover, we are grateful to CONCYTEC-PROCIENCIA for supporting the first author's research through the program "E041-2023-01 Basic Research Projects" [contract number: PE501082530-2023]. We also extend our special thanks to Thiago E.C. Meneguzzo for his valuable insights on nomenclatural decisions, some of which have been incorporated into the present version of this manuscript. Finally, we sincerely appreciate the constructive feedback provided by two anonymous reviewers, whose thoughtful comments significantly strengthened this work.

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