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The natural history of Neotropical *Vanilla* and its implications for selection of favorable genotypes for vanilla production

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La historia natural de la *Vanilla* neotropical y sus implicaciones en la selección de genotipos favorables para la producción de vainilla

Abstract

With more than 60 species, the Neotropics is the most species-rich region for *Vanilla*. Currently, many Brazilian species have been described or rediscovered, and taxonomic realignments have been carried out based on integrative taxonomy. Accurate species delimitation is important for studies on phylogeny and ecology, and also because some Brazilian vanilla may be inappropriate for human consumption. *Vanilla* is monophyletic, with three main lineages, two of which occur throughout the Neotropics. The pollination system of Neotropical *Vanilla* is not species-specific, and their flowers are commonly adapted to pollination by euglossine males. The pollination mechanism of euglossinophilous *Vanilla* is based on a combination of perfume collection and nectar seeking. At least one species, *V. lindmaniana*, is pollinated by hummingbirds representing an evolutionary disruption in the pollination system within *Vanilla*. With regards to seed dispersal, the mesocarp of species with dehiscent fruits is rich in raphid idioblasts that can be harmful to seed dispersers. For this reason, in species of *Vanilla* with dehiscent fruits, birds and mammals commonly access the sclerotic seeds through fruit valves. Seeds of *Vanilla* with indehiscent fruits are dispersed by terrestrial herbivores. Besides the nutritive rewards, fruits are rich in polyphenols that can be toxic or unpalatable to omnivores. The chemical scarification of the seed coat by the digestive acids is crucial for synchronizing the biological processes involved in seed germination. The understanding of the processes involved in *Vanilla* reproduction is very important in the selection of favorable genotypes for commercial vanilla production.

Keywords: Neotropics, pollination, seed dispersal, reproductive biology, phylogeny, systematics

Resumen

Con más de 60 especies, el Neotrópico es la región más rica en especies de *Vanilla*. Actualmente, se han descrito o redescubierto muchas especies brasileñas, y se han realizado realineamientos taxonómicos basados en la taxonomía integrativa. La precisión en la delimitación de especies es importante para estudios de filogenia y ecología, y porque algunas vainillas brasileñas podrían ser inapropiadas para el consumo humano. El

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género *Vanilla* es monofilético, con tres linajes principales, dos de los cuales se encuentran en el Neotrópico. El sistema de polinización de la vainilla neotropical no es específico, y sus flores están comúnmente adaptadas a la polinización por machos de abejas Euglossini. El mecanismo de polinización de las *Vanilla* euglosinófilas se basa en una combinación de recolección de perfume y búsqueda de néctar. Al menos una especie, *V. lindmaniana*, es polinizada por colibríes, lo que representa una disrupción evolutiva en el sistema de polinización dentro de *Vanilla*. En cuanto a la dispersión de semillas, el mesocarpio de las especies con frutos dehiscentes es rico en idioblastos rafídicos que pueden ser perjudiciales para los dispersores de semillas. Por esta razón, especies de *Vanilla* con frutos dehiscentes, las aves y los mamíferos suelen acceder a las semillas escleróticas a través de las valvas del fruto. Las semillas de *Vanill*a con frutos indehiscentes son dispersadas por herbívoros terrestres. Además de las sustancias nutritivas, los frutos son ricos en polifenoles que pueden ser tóxicos o desagradables para los omnívoros. La escarificación química de la testa por los ácidos digestivos es crucial para sincronizar los procesos biológicos relacionados con la germinación de las semillas. La comprensión de los procesos relacionados en la reproducción de las especies de *Vanilla* es fundamental para la selección de genotipos favorables para la producción comercial de vainilla.

Palabras clave: Neotrópicos, polinización, dispersión de semillas, biología reproductiva, filogenia, sistemática

TAXONOMY AND SYSTEMATICS

Vanilla (Orchidaceae) encompasses more than 100 species distributed throughout tropical regions of Asia, Africa, and the Americas [1, 2, 3, 4]. The Neotropics is the most species-rich region within *Vanilla*, with ca. 60 known species. With more than 40 species and a natural hybrid, Brazil is the center of diversity for *Vanilla* in the Neotropical region, with many endemic or poorly known taxa [2, 3, 4, 5, 6, 7]. *Vanilla* shares a number of characteristics with other vanilloid genera, such as an abscission layer between the perianth and the ovary, as well as a single versatile anther whose pollen is released as free monads or a pollinarium-like mass of monads [8]. In addition, flowers of Neotropical *Vanilla* commonly show a well-developed rostellum and a penicillate callus, which are related to the pollination mechanism [9, 10].

Vanilla is monophyletic with three well-supported lineages, two of which occur throughout the Neotropics. Among *Vanilla*, a Neotropical clade with membranous leaves emerges as a sister to a clade that includes two subclades, an African/Asian/Caribbean group and a second, strictly Neotropical clade. Within the thick-leaved Neotropical *Vanilla*, species currently recognized among the *V. palmarum* group, i.e. the epiphytes *V. palmarum, V. lindmaniana* and *V. bicolor*, emerge as sisters to a large clade which species are mostly hemiepiphytes or nomadic vines. Within the hemiepiphytic clade, the Amazonian *V. trigonocarpa* emerges as sister to a clade including the remaining Neotropical taxa. The latter showed two subclades: one including the members of the *V. pompona* group (*V. pompona*, *V. calyculata, V. chamissonis* and *V. argentina*), and another large and predominantly Amazonian clade that contained the remaining Neotropical taxa (Fig. 1). In the latter, a strongly supported clade including *V. hartii* (*V. rupicola*/*V. appendiculata*) emerges as sister to a large clade in

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which the members of the *V. hostmanii* group and *V. dressleri* /*V. cribbiana*, are recovered as sister to a large clade that includes two subclades: *V. insignis/*(*V. odorata/V. helleri*) plus *V. planifolia*/(*V. ribeiroi*/(*V. phaeantha/V. bahiana*)) [2, 11].

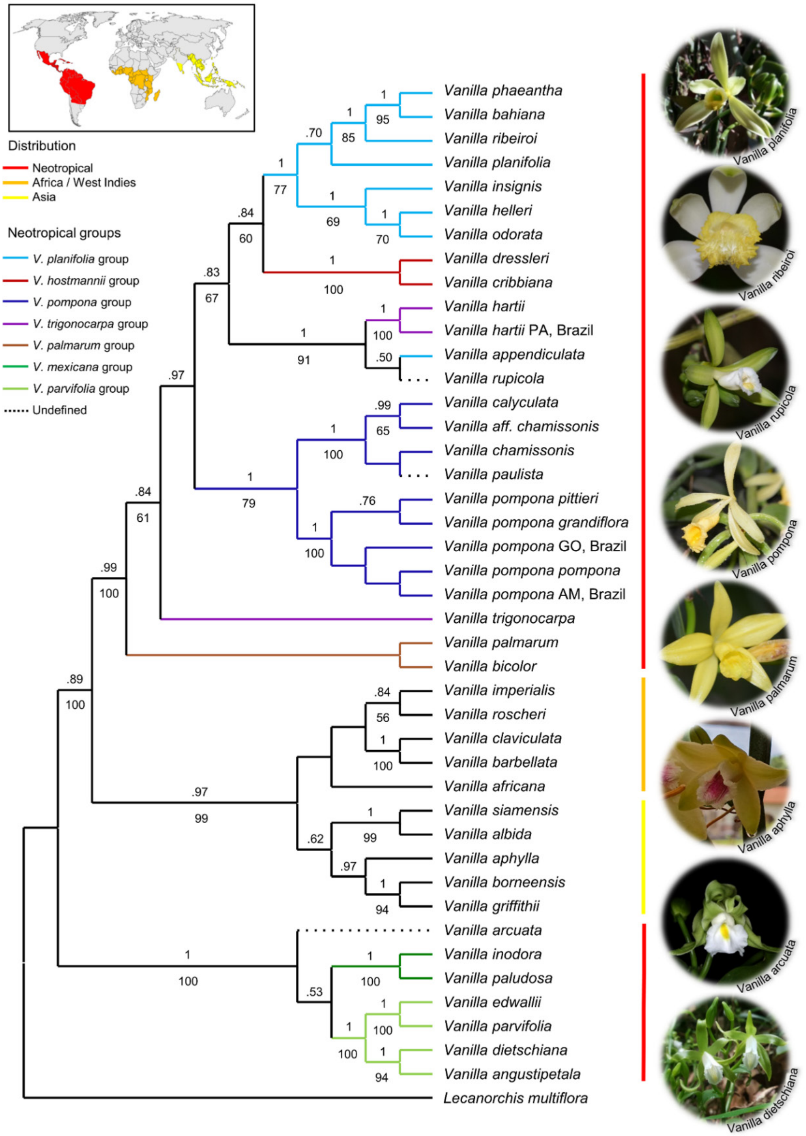

Figure 1. Maximum Likelihood analysis of *Vanilla* (Orchidaceae) based on ITS (nrDNA). Bootstrap values (%) >50 obtained by maximum parsimony analysis (MP) are given below the branches, while posterior probabilities values > 0.5 (BI) are given above branches. Vertical colored bars refer to the geographic distribution of Vanilla. The colored branches in the cladogram refer to Neotropical *Vanilla* groups according to the infrageneric classification presented in Soto-Arenas and Cribb (2010). AM = Amazonas, GO = Goiás, PA = Pará. Based on Pansarin & Menezes (2023).

Since the treatment published by Soto Arenas & Cribb (2010) [12], the infrageneric circumscription of *Vanilla* has been subject of revision. Based on the premise that *Vanilla* species show a wide distribution, many South American species have been synonymized [13]. However, Batista et al. (2023) [14] have pointed out the problems when conclusions on species boundaries are based exclusively on dry material in Vanilloideae. Species delimitation based on molecular and ecological differences combined with morphology and geographical distribution (i.e. integrative taxonomy) have substantially advanced the current assessment and understanding of diversity of Neotropical *Vanilla* [3, 4, 11]. Based on techniques of integrative taxonomy combined with extensive fieldwork, the identities of obscure species have been clarified. In addition, species known only from the type specimen have been rediscovered and new taxa have been described for the Neotropics [2, 3, 4, 6, 7, 11]. This is the case of *V. rupicola* (Fig. 2), an endemic from the Brazilian campos rupestres of the Espinhaço Range [2].

Figure 2. *Vanilla rupicola*.

Vanilla rupicola is easily distinguished from its Neotropical congeners by its rupicolous habit, its reptant stems, and its sessile and fleshy rounded leaves. This remarkable new taxon emerges in a of non-membranous Neotropical clade that includes *V. appendiculata* and *V. hartii* (Fig. 3). Vegetative and floral features support a close relationship between *V. rupicola* and sister taxa, mainly regarding the apical inflorescence (*V. appendiculata*), the type of appendages of the central crest of the labellum, and the labellar color pattern [2].

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Figure 3. Vanilla hartii.

Besides *V. rupicola*, other species endemic to Brazil have been described. These include *Vanilla paulista*, a species described to southeastern Brazil [15]. *Vanilla paulista* is closely related to *V. dungsii* and *V. dubia* (Fig. 4). All three species have a long-unguiculate labellum with a ventral penicillate callus and labellar protrusions on the midlobe. *Vanilla dubia* is more related to *V. dungsii* than to *V. paulista*. In fact, both *V. dubia* and *V. dungsii* occur in the Atlantic Rainforest, while *V. paulista* occurs in drier environments (i.e. semi-deciduous forests). Although *V. dubia* and *V. dungsii* occur in the Atlantic Rainforest, the habitat of *V. dungsii* differs from that of *V. dubia*. *Vanilla dungsii* occurs in high altitude areas of Rio de Janeiro, above 1000 m a.s.l., in the Dense Montana Ombrophilous Forest [16].

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Figure 4. Comparative morphology of the flowers of *Vanilla dubia* and related species. **A.** *Vanilla dubia* (Ubatuba, São Paulo). **B.** *Vanilla dungsii* (Nova Friburgo, Rio de Janeiro). **C.** *Vanilla paulista* (Jundiaí, São Paulo). Based on Pansarin & Miranda (2024)

Other species of *Vanilla* with non-membranous leaves are endemic to the Atlantic Forest, such as *V. capixaba* described for the state of Espírito Santo [15], and *V. chamissonis* that occurs along the Brazilian coast [11]. *Vanilla chamissonis* has been considered a species with wide distribution throughout South America. However, recent studies involving Neotropical *Vanilla* have shown that the inclusion of specimens from Cerrado areas in the phylogenetic analyses makes *V. chamissonis* paraphyletic. Specimens from Cerrado vegetation are more related to *V. calyculata*, a species distributed throughout dry environments of South America, than to plants occurring in the Atlantic Forest [2, 3, 4]. Plants occurring in the Cerrado and Dry Chaco Biomes correspond to *V. argentina*, while *V. calyculata* and *V. chamissonis* occur in dry environments and in the Atlantic Forest, respectively (Fig. 5). *Vanilla argentina* is distinguished from the remaining species by several characteristics, such as the size of leaves and flower structures, and fruit features. *Vanilla argentina* is self-compatible, while *V. calyculata* and *V. chamissonis* show a reproductive system based on late-acting self-sterility [11]. *Vanilla calyculata* has been considered synonymous with *V. columbiana* [13]. However, after examination of type and other material for the species *Vanilla calyculata, V. columbiana*, and *V. phaeantha*, in accordance with previous statement of Soto Arenas and Dressler [17], *V. columbiana* does not correspond with the description of *V. calyculata*. Therefore, the synonymizing of *V. calyculata* under *V. columbiana* is incorrect. Furthermore, present *V. columbiana* shows affinity with *V. phaeantha*. Thus, *V. columbiana* was synonymized under *V. phaeantha*, and the taxon *V. calyculata* has been reassured [18].

FIGURE 5. A-C. Comparative morphology of perianth parts of related *Vanilla* species: **A.** *Vanilla argentina*. **B.** *Vanilla chamissonis.* **C.** *Vanilla calyculata*. Lowercase letters on the right side of the floral pieces are: (a) Distended labellum. (b) Labellum apex. (c) Detail of the labellar crest. (d) Petal. Scale bars: A-C = 2 cm. Based on Pansarin (2025b).

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In addition to *V. calyculata*, names of members of other non-membranous leafed *Vanilla* have been revalidated. It is the case of *V. schwackeana* (Fig. 6), an obscure taxon whose description was based on a single specimen collected in Minas Gerais, south-eastern Brazil, by Carl August Wilhelm Schwacke (*Schwacke 11106*, RB), who, however, did not specify the locality. Hoehne [19] suspected that the specimen might have been a mixture of plant parts from different *Vanilla* species. Soto Arenas and Cribb [12] also recognized *V. schwackeana* as a distinct taxon, but agreed with Hoehne's observation that the specimen could be a mixture of plant elements. Based on examination of an image of the type specimen, *V. schwackeana* has been synonymized under *V. planifolia* [13]. In addition, based on Hoehne's premise that the type of *V. schwackeana* could be a mixture of plant elements from distinct *Vanilla* species, a dissected flower of the holotype (*Schwacke 11106*, RB) was designated as a lectotype [13]. However, while studying the diversity Neotropical *Vanilla*, plants were found in gallery forests of the Vale do Rio Doce region, Minas Gerais, south-eastern Brazil. Based on the examination of the protologues of the Brazilian species, in addition to the study of herbarium specimens, it was verified that the plants correspond to the rare *V. schwackeana*. As a consequence, the name *V. schwackeana* has been revalidated [3].

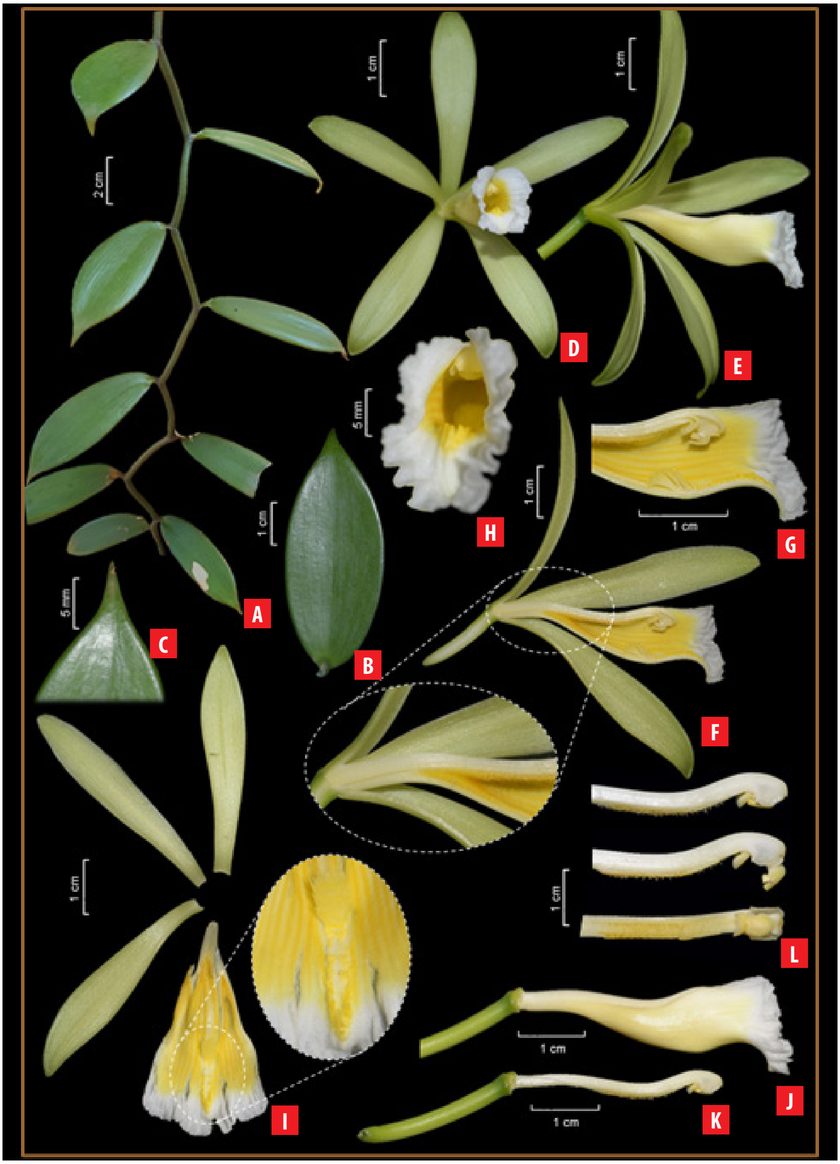

Figure 6. *Vanilla schwackeana*. **A.** Part of a plant showing the sinuous stem and distichous leaves. **B.** Leaf. Note the elliptical shape of the leaf blade. **C.** Detail of a leaf showing the acuminate apex. **D.** Apical inflorescence. **E.** Flower in diagonal view. **F.** Flower in lateral view. **G.** Longitudinal section of a flower. The detail (dashed area) shows the labellum base. **H.** Longitudinal section of part of the labellum. Note the penicillate callus (arrow), the anther (a), and the rostellum (arrowhead). **I.** Detail of the labellum and column. Note the central crest of the labellum, the penicillate callus, and the anther. **J.** Dissected perianth. The detail (dashed area) shows the penicillate callus and the central labellar crest. **K.** Labellum in lateral view. **L.** Column in lateral view. **M.** Apex of the column: in lateral view with an articulated anther (above), in lateral view with a disarticulated anther (mid), and in abaxial view (below). Based on *E.R. Pansarin 1568* (LBMBP). Based on Pansarin (2024a).

Another name revalidated is *V. lindmaniana* (Fig. 7), a species described to the Brazilian state of Mato Grosso (Pantanal Biome) and synonymized under *V. palmarum*. Plants occurring in the Amazon, Cerrado, and Pantanal Biomes correspond to *V. lindmaniana*, while *V. palmarum* occurs in the Caatinga and Atlantic Forest Biomes. *Vanilla lindmaniana* is distinguished from *V. palmarum* by several vegetative and reproductive characteristics, such as the size of leaves and flower structures, and the shape of the fruits. Characteristics associated to pollination strongly differ between both taxa. *Vanilla lindmaniana* is ornithophilous, while the labellar morphology of *V. palmarum* suggests pollination by bees. Both species occur as epiphytes on palms: *Vanilla lindmaniana* predominantly on *Acrocomia, Attalea*, and *Mauritia*, while *V. palmarum* on *Elaeis* and *Syagrus* [4].

Figure 7. *Vanilla lindmaniana.*

Besides the revalidation of *Vanilla* names, recent investigations have confirmed the presence of some taxa in Brazil. For instance, both *V. hartii* and *V. sprucei* have been recorded to Northern Brazil occurring in the Amazon Biome [20, 21]. *Vanilla sprucei* emerges at a basal node among the non-membranous and Neotropical *Vanilla* clade, while *V. hartii* emerges in a more derivate clade including *V. rupicola* and *V. appendiculata* [21]. In addition, a new *Vanilla* hybrid between *V. phaeantha* and *V. pompona* (namely *V.* × *robusta*; Fig. 8) has been described to South America. *Vanilla* × *robusta* is recognized by its long and asymmetric leaves that are longer than the internodes. The flowers of *V.* × *robusta* present characteristics intermediary between *V. phaeantha* and *V. pompona*. The shape, the size and the coloration of the labellum of *V.* × *robusta* is clearly intermediate between the parental species. The labellum of the nothospecies is discretely 3-lobed, while in *V. phaeantha* this structure is distinctly 3-lobed. In *V. pompona* the labellum is 1-lobed to obscurely 3-lobed. To date, *V.* × *robusta* is only known from a single locality in southeastern Brazil. Extensive field work, besides accurate morphological analysis of parental species was crucial to elucidate its hybrid origin. Since the occurrence area and the flowering season of *V. pompona* and *V. phaeantha* sometimes overlap, they share some *Eulaema* species as pollinators, and they are inter-compatible, it is plausible that the natural hybridization event documented here is not an isolate case [22].

Figure 8. *Vanilla x robusta*.

Among the members of the Asian-African and Caribbean clade (Fig. 1) a unique species, *Vanilla calamitosa*, is known from Brazil [23]. Most species in this group are distributed throughout Africa and Asia, with some few taxa occurring in the Caribbean islands. Within the Old-World/Caribbean *Vanilla*, the phylogenetic analyses recover two subclades: an Asian clade, and an African/Caribbean clade (Fig. 1). In the Asian *Vanilla*, the clade including *V. siamensis* and *V. albida* emerges as sister to a clade comprising *V. aphylla*/(*V. borneensis*/*V. griffithii*). In the African/Caribbean clade, *V. africana* is nested as sister to two subclades: a West Indies clade that includes *V. claviculata* and *V. barbellata*, and an African clade containing *V. imperialis*/*V. roscheri* (Fig. 1) [2]. Members of this *Vanilla* group are usually aphyllous and produce scentless fruits. Remaining Neotropical *Vanilla* are included in a basal and clade that includes the species with membranaceous leaves. Among the Neotropical *Vanilla* clade with membranous leaves, *V. arcuata* emerges as sister to a clade containing two sister groups, the *Vanilla mexicana* group, (*V. inodora* /*V. paludosa*) and the *V. parvifolia* group (*V. diestschiana*, *V. angustipetala, V. edwallii* and *V. parvifolia*). Two well-supported clades are recovered within the latter group: *V. diestschiana*/*V. angustipetala*, and *V. edwallii*/*V. parvifolia* (Fig. 1) [2]. *Vanilla arcuata* was described for the Atlantic Coast of the state of São Paulo, southeastern Brazil. This species occurs in coastal plain ("restinga" vegetation), in marshy forests, growing as hemiepiphyte on sandy soil and close to the beach [7]. *Vanilla paludosa* is known from the interior of the state of São Paulo, also in the

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southeastern Brazil. This species occurs in marshy forests, adjacent to Cerrado vegetation, i.e. Brazilian savanna [24]. Currently *V. paludosa* has been assumed to be synonymous with *V. mexicana*, a species described from material collected more than 5,000 kilometers away from where *V. paludosa* was found [13]. Another member of the "*Vanilla mexicana* group" [12] is *V. inodora*, that occurs from northern Brazil to Mexico. Despite its name, the flowers of *V. inodora* are very fragrant. Among the members to the "*Vanilla parvifolia* group" [12], *V. edwallii* is widely distributed through the Atlantic Forest and the Cerrado, while *V. parvifolia*, *V. angustipetala* and *V. dietschiana* (Fig. 9) are restricted to the former Biome. *Vanilla dietschiana* has been recognized into the monotypic genus *Dictyophyllaria* because of its sympodial, non-climbing habit and reduced, reticulate-veined leaves. According to a recent phylogenetic analysis of Vanilleae, *Dictyophyllaria dietschiana* is nested within *Vanilla* and closely related to *V. edwallii* and *V. parvifolia*, two Brazilian species with membranaceous and reticulate-veined leaves. Based on such evidence, *D. dietschiana* has been reinstated into *Vanilla* [6].

Figure 9. *Vanilla dietschian*a.

HABIT

Except for *Vanilla dietschiana*, that is terrestrial (Fig. 9), the remaining members of the Neotropical clade with membranous leaves are secondary hemiepiphytes. In secondary hemiepiphytes the seeds germinate in the forest floor and the young plant climb in a tutor, commonly a tree. In this case, when the aerial stem loses the connection with the ground, the plant normally dies. In the remaining Neotropical *Vanilla* clade, with non-

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membranous leaves, except for *V. rupicola* that shows a reptant habit on rock outcrops (Fig. 10), and *V. palmarum, V. lindmaniana*, and *V. bicolor*, which show an epiphyte habit on palms, species grow as nomadic vines [25]. In this case, when the plant loses the connection with the soil, it can live for a time as an epiphyte. On the other hand, when the host tree dies and the *Vanilla* falls in the forest floor, the plant can live as a terrestrial until it finds a new tutor. *Vanilla* with a nomadic vine habit show a strong plasticity of their roots. Nomadic vines *Vanilla* typically have two types of roots, i.e. aerial or clasping roots, and feeder roots that enter the soil. Aerial clasping roots are thin and velamentous, while the terrestrial roots are thick with absorbing hairs in the maturation zone. In some *Vanilla* species (e.g. *V. parvifolia* group, *V. aphylla*), the velamenous aerial roots are short with determinate growth. In these species, plants can die when the connection with the soil is lost. Members of other groups, such as species of the *Vanilla planifolia* group, have clasping aerial roots with undetermined growth. These aerial roots can reach the soil and function as absorbing roots. When *Vanilla* plants are cultivated without a host tree, free aerial roots are produced that can establish secondary contact with the soil [25]. While essentially sessile organisms, the *Vanilla* species can be propagated vegetatively through stem fragmentation with the chance to disperse their genes through pollination and expand their occurrence range by means of seed dispersal [10, 26, 27, 28, 29, 30, 31].

Figure 10. *Vanilla rupicola* growing on rock outcrops.

POLLINATION

Members of genus *Vanilla* are strongly adapted to pollination by hymenopterans [10, 27, 28, 29, 30, 31, 32, 33, 34]. However, at least one Neotropical species, i.e. *V. lindmaniana* (as *V. palmarum*), is pollinated by hummingbirds [26]. The discovery of a bird-pollinated *Vanilla* species represents an evolutionary disruption in the melittophilous pollination system

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in the genus [26]. *Vanilla lindmaniana* offers nectar as a resource to hummingbirds. The secretion of nectar has a single origin in the Neotropical thick-leafed lineage [26]. *Vanilla lindmaniana*, in addition to the nectar-offering *V. palmarum* and *V. bicolor*, emerges in a basal position as sister of a large clade (i.e. euglossinophilous clade) that includes remaining *Vanilla* with non-membranous leaves. In members of the euglossinophillous clade, male euglossines commonly collect perfumes produced by sepaline osmophores and search for nectar inside the nectar chamber formed by the adnation of the gynostemium base and labellum margins (Fig. 11) [9, 10]. Although euglossine bees are commonly recorded collecting fragrance compounds on sepal osmophores (Fig. 12), to perform pollen transference the bees need to be interested in nectar, not perfumes. Bees interested in fragrances show a typical behavior of perfume collection on flowers. Bees searching for nectar land directly on the flower lip and force their entrance into the flower tube formed by the adnation of the labellum margins and gynostemium. The bees search for nectar secreted into the nectar chamber and then leave the flowers (Fig. 12). Pollination occurs when a bee carrying pollen contacts the rostellar flap with its thorax. The rostellar flap cleans the pollen from the bee scutellum, followed by monad mass deposition on the stigmatic surface. Pollen deposition on the bee occurs when the insect disarticulates the anther and a pollen mass is deposited on its scutellum (Fig. 12). In *Vanilla*, the penicillate callus located below stigmatic surface and anther is responsible for lifting the pollinator body and to hinge the anther with the scutellum (Fig. 12). Bees searching for nectar visit one flower of each inflorescence and each visit lasts between three and eight seconds. Bees searching for fragrance compounds spend a few seconds to several minutes on each flower [10, 27].

Figure 11. Flower of *Vanilla chamissonis* in longitudinal section showing the nectar chamber.

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Floral nectar may or not be available, depending on the *Vanilla* species, as shifts among rewarding and food-deceptive species occurred several times along the evolution of Neotropical thick-leafed clade [26]. A food-deceptive orchid usually shows a low fruit set due to deficient pollen transfer [35]. Particularly for *Vanilla*, deficient pollen flow has consequences not only for the reproductive success of their species, but also in terms of economic implications, since *Vanilla* is the most economically important genus among orchids. Fruits of some *Vanilla* species are the source of vanillin flavoring. While very important for gastronomy and industry, *Vanilla* fruits are produced almost entirely by means of manual pollination. Manual pollination is required because the fruit set is commonly low due the scarcity of pollination services [36].

Figure 12. A-D. *Vanilla pompona*. **A.** *Eulaema nigrita* collecting fragrances on a sepal. **B.** *Eulaema bombiformis* collecting fragrances on a sepal. **C.** *Eulaema cingulata* leaving a flower. **D.** *Eulaema meriana* with pollen of *V. pompona* on the scutellum. Scale bars: A-D = 2 cm. Based on Pansarin (2023).

Even though most vanillas require a biotic vector for pollen transfer, a few species set fruit by means of spontaneous self-pollination. Spontaneous self-pollination in *Vanilla* has been recorded for *V. bicolor*, *V. griffithii, V. savannarum* and *V. palmarum* and *V.*

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lindmaniana [4, 26, 32, 37]. *Vanilla lindmaniana* is an obligate epiphyte species widely distributed throughout South America [4]. Despite the large rostellum, the pollen grains contact the stigmatic surface of flowers, which results in fruit set by spontaneous self-pollination. However, as the flowers are chasmogamous, even if they are not pollinated by a biotic vector (i.e. hummingbirds) fruits are produced through facultative self-pollination [26]. A mixed mating system can be strongly advantageous over reproductive systems based exclusively on autogamy, since entirely autogamous plants commonly show high levels of genetic homozygosis [38]. Furthermore, a mixed mating system can promote reproductive assurance in the case of a decline in pollinator populations, or in areas where pollinator services are irregular or absent [39, 40].

SEED DISPERSAL

While pollen transference is performed mainly by invertebrates, seed dispersal in *Vanilla* is mediated by vertebrates [28, 29, 30, 41, 42]. Seed movement away from the parent plant shows a number of selective advantages by decreasing the competition among offspring and parental specimens and by reducing the exposure of the diaspora to herbivores and potential pathogens. Furthermore, an efficient seed disperser can minimize the risk of the offspring and their plant parents being concomitantly exposed to similar unfavorable conditions, decreasing the chances of extinction [43]. In order to increase the effectiveness of diaspora dispersal, many zoochorous plants have evolved seeds with hard seed-coats embedded on fleshy fruits strongly adapted to endozoochory [44]. It is the case with *Vanilla*. The role of both sclerotic seeds and fleshy fruits in the seed dispersal of *Vanilla* has been the subject of investigations [28, 29, 30, 41, 42, 45, 46]. *Vanilla* fruits evolved several specialized features for attraction (color and scent) and rewarding (sugar, fat, and protein) for seed dispersers (Figs. 13, 14, 15). In addition, *Vanilla* seeds possess sclerotic coats adapted to passing through the digestive tract of seed dispersers [28, 29, 30, 41, 42, 45, 46]. *Vanilla* species with dehiscent fruits are strongly adapted to dispersal by birds and arboreal mammals, while species with indehiscent fruits are dispersed by terrestrial mammals (Figs. 13, 15). The mesocarp of dehiscent *Vanilla* fruits commonly contain large amounts of calcium-oxalate crystals (Fig. 13). As a consequence, frugivores access the fruit cavity through the pericarp valves (Fig. 13). Seed dispersers are rewarded with the fat and sugar produced by the funiculi and with the protein produced by the placentae [28, 29, 30, 41, 42].

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Figure 13. *Vanilla bahiana* and its seed dispersers. **A.** A *V. bahiana* plant with mature fruits in the habitat. The image shows a dehiscent fruit with bright yellow pericarp. **B.** Mature fruit cross-section showing the mesocarp (m) and the endocarp with sclerotic seeds (s). The image presents a fruit in the transverse section, showing the lignified seeds and funiculi (arrows). **C.** *Gracilinanus agilis* feeding on the seeds of ripe fruit. The image shows a marsupial accessing the seeds through the fruit valves. **D.** *Oligoryzomys nigripes* accessing the seeds. Scale bars: a = 2 cm; b = 100 µm. c–d = 5 cm. Based on Pansarin & Suetsugu (2022).

Although both mammals and birds have been recorded as seed dispersers in *Vanilla*, the fruits of some species are consumed exclusively by terrestrial mammals [28, 29, 30, 41, 42]. In fact, fruits of some species have particular characteristics that appear to be related to the attraction of specific fruit consumers. For *V. chamissonis*, while birds and other omnivores are attracted to their indehiscent fruits, only mammalian herbivores (i.e. *Dasyprocta azarae*) are the effective seed dispersers of this *Vanilla* species. This is due to the fact that the fruits are rich in phenolic compounds, which make them unpalatable to omnivores (Figs. 13,14, 15). While birds have been recorded as seed dispersers of Neotropical *Vanilla* [30, 42] an exclusively avian seed dispersal system occurs in *V. lindmaniana* [42]. In addition, the seed dispersal by bats in *Vanilla* has been indirectly attributed based on molecular evidence [47]. The contribution of flying vertebrates appears to be very important for long-distance dispersal in *Vanilla*. In fact, based on the evidence that some *Vanilla* species have both insular and continental populations it is logical to assume that some kind of long-distance dispersal by flying vertebrates is involved.

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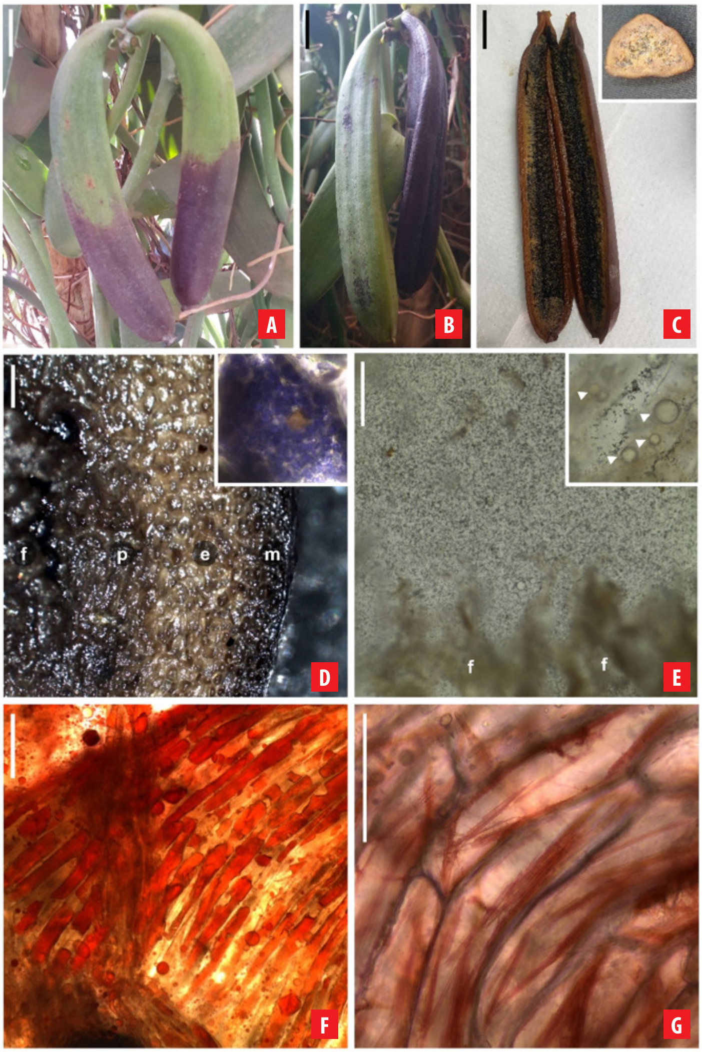

Figure 14. A-G. Morphology and histochemistry of *Vanilla chamissonis* fruits. **A.** A fruiting plant in the final stage of fruit maturation. Note the basipetal color change from green to brown. **B.** A premature green fruit (left) and a ripe fruit photographed 18 months after pollination. Note that mature fruits are indehiscent **C.** Longitudinal section of a mature fruit showing a large number of sclerotic seeds. The detail illustrates a fruit in transverse section showing the pulp and the absence of dehiscence areas. **D.** Transverse section of a fruit stained with $FeCl_3$. Note the unstained endocarp (e), and the mesocarp (m), the placentae (p) and the funiculi stained purple, indicating a positive reaction for phenolic compounds. The detail shows a mesocarp cell stained with $FeCl_3$. **E.** Detail of the funiculi (f) stained with Fehling's Reagent showing brown precipitates indicating a positive reaction for sugar. The detail in figure 1B shows the funiculus cells stained with Fehling's Reagent. Note the brown precipitates indicating a positive reaction for sugar, and the unstained oil drops (arrowheads). **F.** Detail of funiculi stained with Sudan IV. Note orange stained oil drops revealing a positive reaction for lipids. **G.** Detail of the funiculi stained with 1% Xylidine Ponceau revealing a positive reaction for proteins. Note red stained protein filaments inside the funiculus cells. Scale bars: A-C = 2 cm; D = 5 mm; E-F = 100 µm. Based on Pansarin (2024b).

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Figure 15. A-D. *Vanilla chamissonis* and its seed disperser *Dasyprocta azarae* from Itirapina population. **A.** An agouti carrying a mature fruit (synzoochory). **B.** An agouti feeding on a ripe fruit (endozoochory). **C.** An agouti shredding a cotton-wool ball containing the fruit's fragrance. **D.** Seeds collected from agouti feces. The detail shows the seeds germinating in Murashige & Skoog medium. Scale bars: A-C = 5 cm; D = 100 µm. Based on Pansarin (2024b).

SELECTION OF FAVORABLE GENOTYPES

Knowledge of the natural history of *Vanilla* is very important for the selection of favorable traits for vanilla production. The selection of self-fertile plants with high vanillin content are examples of desirable characteristics that can be obtained from the study of native populations of *Vanilla*. Additionally, species with undesirable characteristics such as those that produce fruits with a bad taste and aroma or that are potentially toxic to humans, like *V. chamissonis*, may be disregarded for production purposes. All the evidence indicates that the fruits of *V. chamissonis* are not suitable for an omnivore diet, including humans [28]. The main compounds detected in the fruits of *V. chamissonis* (anisyl alcohol, benzyl alcohol, and anisaldehyde) are reported to be toxic to animals [48]. Intoxication with phenolic substances depends on both the amounts ingested and the sensitivity of each individual, as the human organism is rather complex and its

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reaction to certain toxic compounds is influenced by multiple epigenetic factors [49]. Furthermore, vanilla pods are commonly used by humans in small quantities as natural flavoring in the food industry and in gastronomy. Apart from the toxicity of the fruits, which can be harmful to omnivores, sensory analyses using both ripened and cured pods revealed that *V. chamissonis* fruits are very bitter and astringent. In addition, their aroma is unpleasant for humans [28]. With the current vanilla frenzy in the Neotropics and the search for new aromas and flavors, especially in Brazil, studies about the risks of fruit consumption to human health are necessary [28].

AUTHORS' CONTRIBUTIONS

As the sole author, ERP conceived and designed the study, conducted fieldwork and laboratory analyses, and wrote the manuscript

DATA AVAILABILITY STATEMENT

All data necessary to understand the manuscript are presented throughout the text.

DECLARATION OF GENERATIVE AND AI-ASSISTED TECHNOLOGIES IN THE WRITING PROCESS

For this work, the authors did not use any generative or AI-assisted technology

DECLARATION AND COMPETING INTEREST

The author declares no conflict of interest.

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