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TAXONOMIC NOTES ON VANILLEAE (ORCHIDACEAE: VANILLOIDEAE): *VANILLA DIETSCHIANA*, A RARE SOUTH AMERICAN TAXON TRANSFERRED FROM *DICTYOPHYLLARIA*

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ABSTRACT. Tribe Vanilleae (Orchidaceae: Vanilloideae) consists of 10 genera including the monotypic *Dictyophyllaria*, which is endemic to Brazil. *Dictyophyllaria dietschiana* (Edwall) Garay has been segregated from *Vanilla* on the basis of its sympodial, non-climbing habit and reduced, reticulate-veined leaves. According to a recent phylogenetic analysis of Vanilleae based on two chloroplast regions (*rbcL* and *psaB*) and parsimony, *Dictyophyllaria dietschiana* is nested within *Vanilla* and closely related to *V. edwallii* Hoehne and *V. parvifolia* Barb. Rodr., two Brazilian species with membranaceous and reticulate-veined leaves. Based on such evidence, *D. dietschiana* is reinstated into *Vanilla*. A detailed morphological description of this endangered species, which has recently been considered possibly extinct, is also presented.

RESUMO. A tribo Vanilleae (Orchidaceae: Vanilloideae) compreende 10 gêneros e inclui *Dictyophyllaria*, um gênero endêmico do Brasil. Esse gênero é monotípico, com *D. dietschiana* (Edwall) Garay sendo segregado de *Vanilla* com base em caracteres como hábito simpodial e folhas reduzidas com nervuras reticuladas. De acordo com uma hipótese filogenética realizada com gêneros atualmente incluídos em Vanilleae, usando regiões de cloroplasto (*rbcL* e *psaB*) e parsimônia, *Dictyophyllaria dietschiana* é inserida dentro de *Vanilla* e proximamente relacionada com *V. edwallii* Hoehne and *V. parvifolia* Barb. Rodr., ambas espécies endêmicas do Brasil que apresentam folhas membranáceas e com reticuladas. Baseado nessas evidências *D. dietschiana* é re-introduzida em *Vanilla*. Uma detalhada descrição morfológica dessa espécie ameaçada de extinção, que tem sido considerada como posivelmente extinta, é apresentada.

Key words: Atlantic forest, Brazil, South America, vanilloid orchids

INTRODUCTION

The vanilloid orchids form a mophyletic group that has been considered as one of the five subfamilies of Orchidaceae (Chase et al. 2003, Cameron 2004, Freudenstein et al. 2004). As circumscribed by Cameron (2003) and Chase et al. (2003), Vanilloideae include the tribes Vanilleae and Pogonieae (i.e., subtribe Pogoniinae; Dressler 1993). Tribe Vanilleae comprises 10 genera and includes *Vanilla*, the largest genus among vanilloid orchids (ca. 107 species; Cameron 2003), and *Dictyophyllaria*, a taxon previously segregated from *Vanilla*.

Vanilla, a pantropical genus, is considered as monophyletic, although the Brazilian endemic *Dictyophyllaria* has never been included in any published phylogenetic or systematic study (e.g., Stern & Judd 2000, Cameron & Molina 2006, Cameron 2009). This rare genus is monospecific, with the species *D. dietschiana* (Edwall) Garay segregated from *Vanilla* on the basis of its sympodial non-climbing habit and its reduced and reticulate-veined leaves (Garay 1986). *Dictyophyllaria dietschiana* is endemic to the Brazilian Atlantic rainforest and is known by only three plant collections: its *typus*, collected in 1903 in the state of São Paulo, a specimen found in the state of Espírito Santo in 1973, and a third specimen found in the municipality of São Paulo, in 2009. Because of its rarity, this species has been considered as possibly extinct (e.g., Cameron 2003, 2009).

According to a recent phylogenetic analysis of currently recognized genera of Vanilleae (Pansarin and Salatino, submitted), based on two chloroplast DNA regions (*rbcL* and *psaB*) and parsimony, *Dictyophyllaria dietschiana* is nested within *Vanilla* and closely related to *V. edwallii* Hoehne and *V. parvifolia* Barb. Rodr., both Brazilian species with membranaceous and reticulate-veined leaves (FIGURE 1). As a consequence, a generic realigment is necessary in order to achieve the monophyly of *Vanilla*.

Based on such evidence, this paper (1) presents the taxonomic changes coherent with the obtained phylogenetic results (Pansarin & Salatino, submitted), thus reinstating *Dictyophyllaria dietschiana* within *Vanilla*, (2) sets forth a detailed description of *D. dietschiana*, and (3) discusses the implications of some morphological traits of this species on its relationship with other species of *Vanilla*.

MATERIAL AND METHODS

Fresh and herbarium (SP, SPFR and RB) material of flowering and fruiting plants were used for the

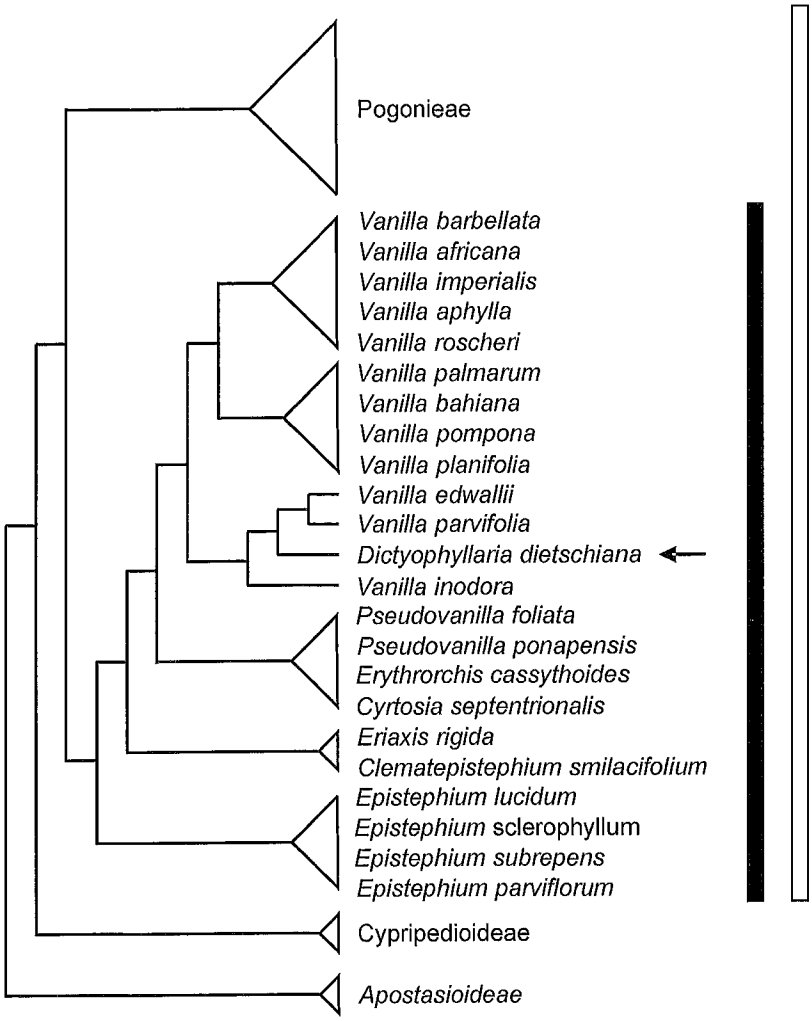

FIGURE 1. Phylogenetic relationships among Vanilleae (Orchidaceae) based on sequences of *psaB* and *rbcL* (chloroplast DNA) (from Pansarin and Salatino, submitted). Note the position of *Dictyophyllaria*, nested within species of *Vanilla* (arrow). Empty bar: Vanilloideae; full bar: species recognized as Vanilleae (Cameron 2003).

morphological description. Flowers and floral details were examined a binocular stereomicroscope. The terminology of vegetative and reproductive structures follows Harris and Harris (1994). The terminology of morphological features specific to Orchidaceae is based on Dressler (1993).

RESULTS AND DISCUSSION

According to Pansarin and Salatino (submitted), strict consensus trees obtained from the cladistic analysis of *rbcL* and *psaB* (cpDNA) data produced trees with similar topologies for various members of Vanilleae. FIGURE 1 presents a summary of the relationships among the taxa included in this tribe. In both single-region analyses, the South American clade formed by *Vanilla palmarum*, *V. pompona*, *V. planifolia* and *V. bahiana* is sister of the American-African clade (*Vanilla africana* + *V. aphylla* + *V. barbellata* + *V. imperialis* + *V. roscheri*). In turn, this larger clade is sister to another clade comprising Central American *Vanilla inodora* and *Dictyophyllaria dietschiana* plus (*V. edwallii* + *VD. parvifolia*) (FIGURE 1). Thus, including *Dictyophyllaria* in the analysis turns *Vanilla*, as currently circumscribed, paraphyletic. Based on our evidence that *Vanilla* is paraphyletic, the reinstatement of *D. dietschiana* into *Vanilla* is necessary in order to achieve the monophyly of the latter. Furthermore, a detailed description and images of this rare and threatened Brazilian species is presented:

FIGURE 2. *Vanilla dietschiana* Edwall. **A.** Flowering plant. Note the branched stem with monopodial (pseudosympodial) growth. **B.** Flower in frontal view. Note the green sepals and petals and the white tubular labellum with longitudinal keels on the median portion. From *E.R. Pansarin & L.M. Pansarin 1278* (SPFR)

Vanilla dietschiana Edwall, Revista Centro Sci. Campinas 2: 191. 1903. Type: Brazil—São Paulo, Serra do Mar, 1903, *A. Dietsch 6070* (holotype, SP). FIGURE 2.

Dictyophyllaria dietschiana (Edwall) Garay, Bot. Mus. Leafl. 30(4): 231. 1986.

Herbs ca. 30–50 cm tall, erect, terrestrial; habit monopodial (pseudosympodial). Adventitious roots ca. 1 mm in diam., short, white, usually one per node. ***Rhizome*** branched, subterranean. ***Stem*** 3.5–5 mm in diam., erect, sinuous, branched and pale green. ***Leaves***, one per node, up to 2.3 cm long, sub-triangular to ovate, sessile, distichously disposed, membranous, reticulate-veined, pale green; apex acute, base amplexicaul; basal leaves erect, reduced to sheaths, concave; apical leaves erect, patent, conduplicate. ***Inflorescence*** 1-flowered, axillary. ***Flower*** resupinate, pale green with a white labellum, abscission layer between perianth and ovary present; pedicel + ovary ca. 2.5 cm long; sepals 3.3–3.8 × 0.6–0.8 cm, elliptic-lanceolate, concave, pale green, with a dorsal, longitudinal low keel in the central portion, margin entire; dorsal sepal symmetric, apex rounded; lateral sepals asymmetric, apices acuminate; petals 3.2–3.5 × 0.4–0.6 cm, asymmetrically lanceolate, whitish green, apices acute; labellum 2.3–2.6 × 2.5 cm, 3-lobate, rounded to ovate, white, with several longitudinal white-cream keels along the central line; midlobe rounded to ovate, lateral lobes rounded, falcate, with undulate margins. Column ca. 1.9–2.1 cm long, slender, arched, white. ***Fruit*** ca. 5.5 × 0.4 cm, cylindrical, erect, linear, green. ***Seeds*** 0.3 mm long, sclerotic, ovoid, black.

Illustrations. Detailed illustrations of *Vanilla dietschiana* are published in Edwall (1903: Est. 2), Hoehne (1945: Tab. 19), Cogniaux (1906), and Cameron (2003: 305, as *Dictyophyllaria dietschiana*, redrawn from Hoehne 1945). A floral analysis (also redrawn from Hoehne 1945) was published by Pabst and Dungs (1975: 260).

Distribution. Found in the states of São Paulo and Espírito Santo, southeastern Brazil, at elevations of 500–630 meters above sea level. It has never been collected in the state of Rio de Janeiro, which separates them.

Additional material examined. BRAZIL—Espírito Santo: Domingos Martins, na subida para a antena da Rádio Campinho, 19 January 1975, *A.L. Peixoto 442* (RB). **São Paulo:** São Paulo, 18 January 2009, *E.R. Pansarin & L.M. Pansarin 1278* (SPFR).

Conservation status. *Vanilla dietschiana* is an endangered species because urban development has destroyed its natural habitat, mainly in the state of São Paulo.

Based on the climbing and monopodial habit, lateral roots and inflorescences, large flowers, and ovoid seeds with a crustose seed coat of its constituent species (e.g., Cameron 2009, Cameron & Molina 2006), many recent studies support *Vanilla* is a natural genus. Additionally, the monopodial climbing habit with adventitious roots has been interpreted as a synapomorphy for the clade formed by *Vanilla* and *Pseudovanilla* (Cameron & Molina 2006). The inclusion of *Dictyophyllaria dietschiana* in the analyses revealed a reversal to a non-climbing (often erroneously interpreted as sympodial) in this taxon (Pansarin and Salatino, submitted).

The very rare species *Vanilla dietschiana* (=*Dictyophyllaria dietschiana*) is endemic to southeastern Brazil and occurs in Dense Ombrophilous Forest. The floral and vegetative morphology of *V. dietschiana* is similar to that of *V. edwallii* Hoehne and *V. parvifolia* Barb. Rodr. In fact, phylogenetic analyses (Pansarin & Salatino, submitted; FIGURE 1) show that *V. dietschiana* is sister to the clade comprising *V. edwallii* and *V. parvifolia*. Although *V. dietschiana* presents a monopodial (frequently misinterpreted as sympodial), non-climbing habit, it has pale green reticulate-veined and membranaceous leaves, as *V. edwallii* and *V. parvifolia*. Because of their green sepals and petals and tubular white labellum with longitudinal keels along the central line, the flowers of *V. dietschiana* are also similar to those of *V. edwallii* and *V. parvifolia*. After examining the type specimen, Hoehne (1945) suggested that *Vanilla dietschiana* can be an anomalous specimen of *V. parvifolia*, although he states its flowers are described as quite different. However, in the state of São Paulo, all the individuals of a population of *V. dietschiana* present constant vegetative and floral characteristics, which correspond to those originally described by Edwall (1903). The only flowers of *V. dietschiana* are produced on the axils of leaves, which are reduced and have often been interpreted as bracts (Garay 1986) or as a calyculus (Cameron 2003) similar to those *Epistephium*. Furthermore, based on the reticulate-veined leaves and the labellum detached from the column of *V. dietschiana* (as *D. dietschiana*), a close relationship with members of the genus *Epistephium* has been suggested. Nevertheless, this hypothesis was based on the original description and that of Cogniaux (1904–1906) and Hoehne (1945). *Vanilla dietschiana* has thus been considered as possibly extinct (Cameron 2003).

Vanilleae and Pogonieae, two tribes of the subfamily Vanilloideae, have traditionally been considered as monophyletic (e.g., Cameron 2009). Yet, recent studies based on morphological (Pansarin 2005) and molecular (5.8S, 18S and 26S nrDNA) characters (Pansarin & Salatino, submitted) reveal that including the mycoheterotrophic Brazilian endemic genus *Pogoniopsis* in the analyses makes tribe Pogonieae paraphyletic. *Pogoniopsis* is nested as a basal genus of Vanilleae and sister of the other genera within this vanilloid tribe. The achlorophyllous genus *Pogoniopsis* is more closely related to members of subtribe Galeolinae (tribe Vanilleae, *sensu* Cameron 2003), *Galeola* and *Cyrtosia*, than to the genera currently recognized within Pogonieae. Species of *Pogoniopsis* present a sympodial habit, leaves reduced to scales, terminal inflorescences, lack an abscission layer between flower and ovary, fleshy, yellow and indehiscent fruits, and ovoid and sclerified seeds. Such features are shared by species of Galeolinae (*sensu* Dressler 1993). In short, although several studies based on molecular characters have been conducted among members of vanilloid orchids, accurate morphological, anatomical and ecological studies are still important to clarify the phylogenetic relationships within Vanilloideae. Furthermore, many species of *Vanilla*, *Cleistes* and *Epistephium* (mainly South American taxa) have not been included in the published phylogenetic analyses. The inclusion of a limited number of taxa in analyses can lead to erroneous interpretations about the evolution of these groups (Pansarin & Barros 2008; Pansarin et al. 2008).

Brazilian biomes are the center of diversity of some vanilloid taxa (i.e., *Cleistes*, *Vanilla* and *Epistephium*). Detailed taxonomic and evolutionary studies of members of Brazilian Vanilloideae are crucial to understand the evolution of this basal and fascinating orchid group.

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SPATIAL DISTRIBUTION AND ABUNDANCE OF EPIPHYTES ALONG A GRADIENT OF HUMAN DISTURBANCE IN AN INTERANDEAN DRY VALLEY, ECUADOR

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ABSTRACT. We studied the effects of different disturbance regimes on abundance and within-tree distribution of dry-forest epiphytes at the Bosque Protector Jerusalén in northern Ecuador. Epiphytes on 100 trees of *Acacia macracantha* were sampled in closed mixed and pure acacia forest stands, forest edge, semi-closed secondary woodland, and isolated trees in pastures. Vascular epiphytes were sampled for entire host trees and macrolichens and bryophytes for inner tree crowns. The number of vascular epiphyte species did not differ significantly between crown zones but their cover decreased significantly from middle to inner and outer crown. Vascular epiphytes attained greatest and bryophytes lowest cover values on isolated trees. Covers of bryophytes and vascular plants were correlated with canopy integrity, suggesting that microclimate was a strong predictor of epiphyte abundance. The high abundance of atmospheric bromeliads in the studied disturbed, perarid habitats is suggestive of their effective adaptation to the use of dew.

Key words: edge effects, isolated trees, microclimate, succession, tropical montane dry forest

INTRODUCTION

Human disturbance may affect epiphyte diversity through a number of factors. Degraded and secondary forests usually offer less surface area for colonization than primary forests, with humus and bryophyte mats on old, thick limbs being particularly scarce (Acebey et al. 2003, Krömer & Gradstein 2003). Dispersal constraints may limit epiphyte diversity in fragmented habitats (Cascante-Marín et al. 2009), and altered microclimate may further affect their abundance (Sillett et al. 1995, Krömer & Gradstein 2003, Köster et al. in press). Disturbed forests are characterized by fragmented or lower and more open canopies that experience greater illumination and air turbulence and exhibit less stratification by microclimate compared to undisturbed forests (e.g., Malhi & Phillips 2004). Especially in secondary forests recovering from clear-cutting, time since disturbance is an additional factor that warrants attention, because epiphytes tend to grow slowly (e.g., Zotz 1995, Nadkarni et al. 2000) and their recolonization invariably lags behind that of their host trees.

Interestingly, there is little agreement among studies regarding how tropical epiphytes respond to human disturbance. Epiphyte diversity in altered habitats ranges from similar (Hietz & Hietz-Seifert 1996, Larrea 1997, Holz & Gradstein 2005) to substantially lower than in mature forests (Acebey et al. 2003, Krömer & Gradstein 2003, Benavides et al. 2006, Nöske et al. 2008). Epiphyte abundance in disturbed habitats differs even more widely, ranging from significantly lower (Krömer & Gradstein 2003, Werner et al. 2005, Benavides et al. 2006) to significantly higher than in intact forest (Dunn 2000, Flores-Palacios & García-Franco 2004, Cascante 2006). However, even in cases where abundance increases, diversity may decrease (Dunn 2000, Flores-Palacios & García-Franco 2004, Cascante 2006), and these discrepancies are not understood.

Only a few studies have targeted dry-forest epiphytes, and none of them dealt with forest disturbance. Because dry compared to moist forest canopies tend to be more open, gradients of humidity and exposure are less pronounced there (Graham & Andrade 2004), and it seems conceivable that dry-forest epiphytes are relatively resilient to forest disturbance due to their high tolerance for drought. In a previous article (Werner & Gradstein 2009) we have treated the impact of different types and magnitudes of disturbance on species richness and floristic composition of epiphytes in a tropical montane dry forest. The present paper deals with epiphyte abundance and within-tree distribution in the same study system.

METHODS

Study Site and Sampling

Field work was carried out between January and March 2004 at the Bosque Protector Jerusalén, a state reserve in the Interandean Guayllabamba watershed north of Quito, Ecuador. The reserve includes one of the least disturbed Interandean dry forests of the Ecuadorian Andes. The study site

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