

## A NEW MINIATURE GHOST ORCHID APPEARS IN THE DOMINICAN REPUBLIC

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**ABSTRACT.** A small population of an epiphytic orchid in the leafless genus *Dendrophylax* was discovered in the valley of Río Amina, on the northwestern side of the Cordillera Central of the Dominican Republic. The tiny yellow to yellow-green flowers proved to be unique and therefore we describe here the new species as *D. pustulatus*, for the brown ellipsoid pustules of the inflorescence and ovary, the 90° bend at the transition between the pedicel and ovary, the simple mid lobe of the lip, and a laterally flattened spur not exceeding the length of the ovary. Based on morphology, *D. pustulatus* appears to be closely allied with *D. constanzensis* and *D. serpentilingua*. *Dendrophylax* now has 16 species, 12 of which are present in Hispaniola and half of those are endemic to the island.

**RESUMEN.** En el valle del Río Amina, en el noroeste de la Cordillera Central de la República Dominicana, se descubrió una pequeña población de orquídeas epifitas sin hojas del género *Dendrophylax*. Las diminutas flores de color amarillo a verde amarillento resultaron ser únicas y por eso describimos aquí la nueva especie como *D. pustulatus*, por las pústulas elipsoides de color marrón de la inflorescencia y el ovario, la curva de 90° en la transición entre el pedicelo y el ovario, el lóbulo medio del labio simple y un espolón aplanado lateralmente que no excede el largo del ovario. Según su morfología, *D. pustulatus* parece estar estrechamente relacionada con *D. constanzensis* y *D. serpentilingua*. *Dendrophylax* cuenta actualmente con 16 especies, 12 de las cuales están presentes en La Española y la mitad de ellas son endémicas de la isla.

**KEYWORDS / PALABRAS CLAVE:** Angraecinae, *Dendrophylax*, ghost orchids, Orchidaceae, orchid flora, orquídeas fantasmas, orquídeoflora, República Dominicana

**Introduction.** The genus *Dendrophylax* Rchb.f. (Epidendroideae: Vandae: Angraecinae), commonly known as “ghost orchids”, currently consists of 15 species distributed primarily in the Greater Antilles but with two species that have ventured north to Florida (USA) [*D. lindenii* (Lindl.) Benth. ex Rolfe, *D. porrectus* (Rchb.f.) Carlswald & Whitten], and two occur in Mesoamerica (*D. megarhizus* Molgo & Carnevali, *D. porrectus*). *Dendrophylax* and its sister genus, *Campylocentrum* Benth., are the only two representatives of the subtribe Angraecinae in the western hemisphere.

*Dendrophylax* is epiphytic yet leafless at maturity, rendering them inconspicuous. Flowers are borne singly or on laxly flowered racemes or sparsely branched panicles (*Campylocentrum* has distichous, densely flowered racemes). Flowers are yellow, green, or white, spurred, and produce nectar as a pollinator reward. The stubby column has a split rostellum and the anther bears two independent, yellow pollinia with separate stipes (hemipollinaria). The larger species have spectacular white, nocturnally fragrant flowers that seem to float in the understory as they are usually borne alone at the end of long, slender inflorescences;

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hence the name “ghost orchids” (Ackerman & Collaborators, 2014).

The center of *Dendrophylax* diversity is Hispaniola, which is home to 11 species, five of which are endemic. This matches the overall percent endemism for orchids on the island (44% for all orchids; 45% for *Dendrophylax*) (Ackerman & Collaborators, 2014). High endemism is not only characteristic of the orchid flora of Hispaniola, but also prevalent across many plant and animal groups making Hispaniola a major contributor to the Caribbean biodiversity hotspot (e.g., Powell *et al.*, 1999; Santiago-Valentin & Olmstead 2004). Its geological diversity, physiographic and climatically fragmented landscape offers opportunities for population isolation where genetic drift and natural selection may occur without homogenizing effects of gene flow (Cano Carmona *et al.*, 2010; Cano Ortiz *et al.*, 2016; Hu *et al.*, 2022; Tremblay *et al.*, 2005).

While it is tempting to regard the Hispaniola as the evolutionary origin of the *Dendrophylax*, the phylogenetic evidence is equivocal. The earliest diverging clades have the most widespread species occupying multiple islands of the Greater Antilles: *D. monteverti* (Rchb.f.) Ackerman & Nir (Puerto Rico, Hispaniola, Jamaica, and Cuba), *D. barrettiae* Fawc. & Rendle (Hispaniola, Jamaica, and Cuba), and *D. porrectus* (Puerto Rico, Hispaniola, Jamaica, Cuba, Florida, and Mexico) (Ackerman & Collaborators, 2014; Carlswald *et al.*, 2006; Molgo *et al.*, 2016). As for diversification of *Dendrophylax*, it likely diverged from *Campylocentrum* in the late Miocene (Farminhão *et al.*, 2021). Unfortunately, diversification within *Dendrophylax* lacks clarity since only three morphologically disparate species of *Dendrophylax* have been assessed, and they diverged in the early to mid-Pliocene (Pessoa *et al.*, 2018). Nonetheless, the phylogram depicting *Dendrophylax* phylogeny of Carlswald *et al.* (2006) showed short Fitch lengths, suggesting recent divergence of sister species occupying different islands (*D. sallei* of Hispaniola and *D. lindonii* of Cuba and Florida; *D. fawcettii* of the Cayman Islands and *D. funalis* of Jamaica).

We encountered a population of a small flowered *Dendrophylax* that we have concluded is an undescribed species, which we rectify here.

#### TAXONOMIC TREATMENT

***Dendrophylax pustulatus*** Ackerman & E.Fernández, *sp. nov.* (Fig. 1–2)

TYPE: República Dominicana. Cordillera Central: provincia Santiago, a 1 km en dirección este por el sendero, después de la caseta del Parque Nacional Armando Bermúdez, La Diferencia, frente a La Diferencia Eco-Retreat. A lo largo de la vegetación contigua al Río Amina. En pequeñas poblaciones a lo largo del sendero. Pico floral parece ser entre principios y mediados de Julio, 19°16'13"N, 71°03'07"W, elev. 735 m, 12 julio 2024, E. Fernández 23 (holotype: JBSD 138476; isotype: NY). Fig. 1–2.

DIAGNOSIS: *Dendrophylax pustulatus* differs by a combination of characteristics from other small-flowered and short-spurred members of the genus, *D. serpentina* (Dod) Nir, and *D. constanzensis* (Garay) Nir. *Dendrophylax pustulatus* inflorescence has abundant ellipsoid pustules and an obovate retuse mid lobe of the lip, whereas the pubescence of *D. serpentina* is hispid and the mid lobe is ovate, apiculate and two-tailed, and *D. constanzensis* is setaceous-hirsute, and the mid lobe is anchor-shaped, apiculate. *Dendrophylax pustulatus* also has a laterally compressed spur, a trait that is shared only with *D. serpentina*. Furthermore, *D. pustulatus* consistently has a 90° bend at the transition between the pedicel and ovary, not yet seen in other species of the genus.

*Plant* epiphytic, monopodial, leafless. *Roots* ca. 10 or more, green when wet, white to whitish green when dry, caespitose, 1.0–1.5 mm diam., up to 15 cm long, smooth. *Rhizome* largely obscured by roots, 5–10 mm long. *Inflorescences* erect, filiform, racemose or sparsely branched, 1–6 flowers produced in succession, usually 1 open at a time, densely provided with brown elliptical pustules; *peduncle* green, 17–30 mm long, 0.5 mm diam., comprised of 3 nodes, bracts brown, sheathing, acute, 1.5–2.0 mm long, progressively smaller toward the apex; *rachis* 5–15 mm long, somewhat fractiflex; *floral bract* 1.5–2.0 mm long. *Flowers* yellow to yellow green, in the resupinate position; *pedicellate ovary* geniculate; *pedicel* erect, 2.0–2.5 mm long, glabrous or with sparse brown pus-

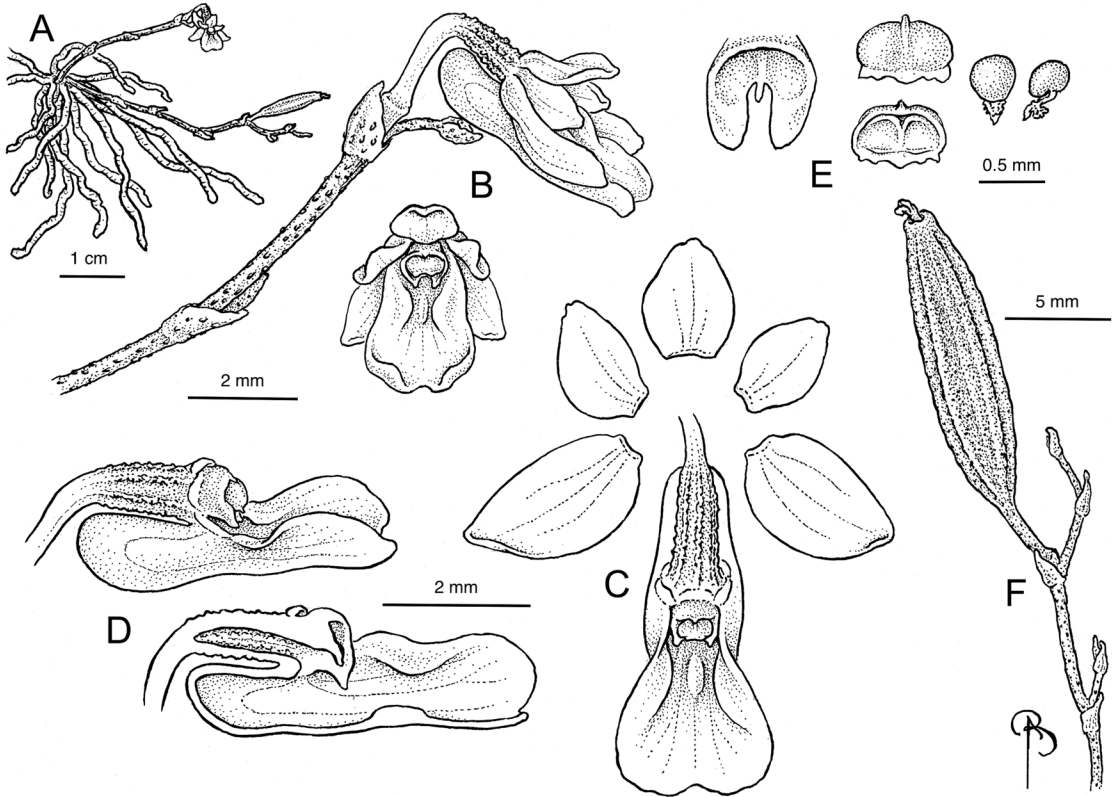


FIGURE 1. *Dendrophylax pustulatus* Ackerman & E.Fernández. **A.** Habit. **B.** Inflorescence, side view; flower front view. **C.** Flower, top view with sepals and lateral petals removed. **D.** Flower side view with sepals and lateral petals removed. **E.** Anther with anther cap removed; anther cap, dorsal and ventral views; hemipollinaria, front and side views. **F.** Infructescence. Illustrated by Bobbi Angell based on alcohol preserved specimen (later pressed and dried; *E. Fernandez s.n.*, 28 Jun 2024; UPRRP) and Eladio Fernández photographs.

tules; *ovary* perpendicular to the pedicel, 1.5–2.0 mm long, ribbed, densely provided with brown pustules; *sepals* weakly pustulose/verrucose abaxially, entire; *dorsal sepal* ovate, obtuse,  $1.9 \times 1.2$  mm, reflexed upward 0.5 mm from base; *lateral sepals* ovate, slightly oblique, acute, entire, 2.8–3 mm long, 1.8 mm wide; *petals* glabrous, flanking column, ovate, obtuse,  $1.8 \times 1.2$  mm; *lip* glabrous, 3.0–3.5 mm long, excluding spur, superficially simple, obscurely trilobed, lateral lobes erect, flanking column, rounded, entire, creating a narrow entryway to spur, and meeting the mid lobe at about half the length of the lip, mid lobe obovate, rounded, retuse, *ca.* 2.0 mm long, 2.4 mm wide, disc callus a low elliptical bump in front of the column 0.7 mm long, spur 1.5–2.0 mm long  $\times$  1.0–1.2 mm deep, laterally compressed, truncate, parallel to ovary, abutting against the pedicel; *column* light green, stubby,

0.5 mm long; *anther* cap yellow with two brown spots, pollinia 2, globose, *ca.* 0.16 mm diam., attached to separate stipes and viscidia. *Fruit* pedicel *ca.* 4 mm long; *capsule* green with sparse, brown, elliptical pustules, fusiform, ribbed, slightly asymmetrical both basally and apically,  $12\text{--}18 \times 3.0\text{--}3.5$  mm, dehiscence longitudinal along a single suture.

**ETYMOLOGY:** In reference to the brown, ellipsoid pustules on the peduncle and ovary.

**DISTRIBUTION:** Dominican Republic: province Santiago; Cordillera Central.

**TAXONOMIC DISCUSSION:** It is not entirely clear which species are most related to *D. pustulatus*. The most complete phylogenetic analysis published to date is

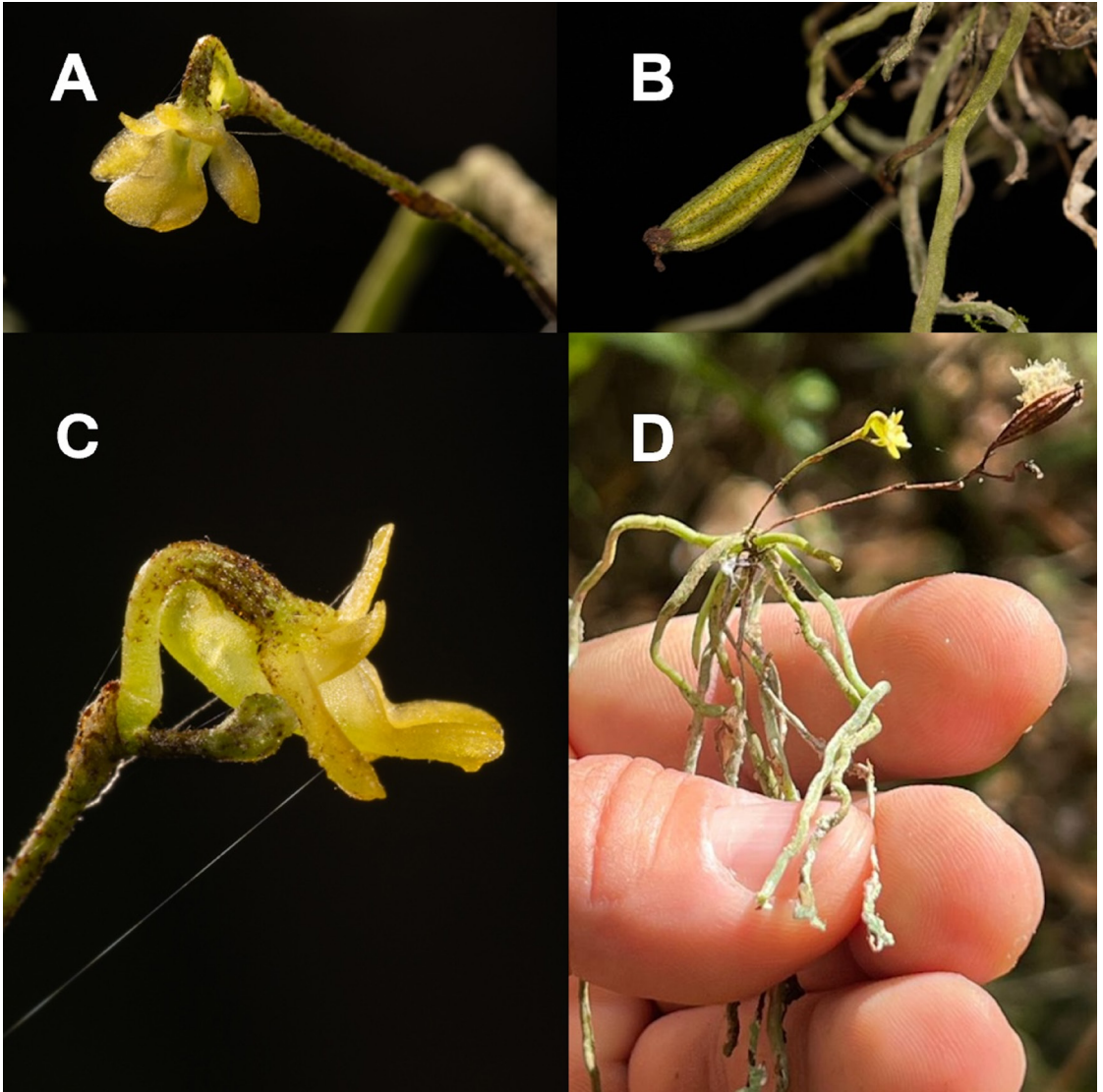


FIGURE 2. *Dendrophylax pustulatus* Ackerman & E.Fernández. A. Flower, off-center view (note the pustulate peduncle and ovary). B. Fruit, nearly mature. C. Flower, side view. D. Plant with young inflorescence and old infructescence. See Fig. 1 for floral dimensions. Photographs by Eladio Fernández.

of Molgo *et al.* (2016) and they sampled nine species, only one of which, *D. porrectus*, is among the short-spurred species of the Dominican Republic. DNA of *D. constanzensis*, *D. macrocarpus* (Dod) Carlsward & Whitten, *D. monteverti*, and *D. serpentilingua* have yet to be sequenced and included in phylogenetic analyses. Nonetheless, based on morphology, we expect *D. pustulatus* to be related to *D. serpentilingua* and *D. constanzensis* (Table 1). This brings the number

of species in the genus to 16 and increases the number of Hispaniolan endemics to six.

ECOLOGY: Plants are epiphytic on branches of small, broadleaf trees. The population appears to be about 60 plants distributed along the southern side of Río Amina and the western side of Río Dajao. Reproductive biology is largely unknown, but flowering peak appears between June and August, and plants are

TABLE 1. Species of *Dendrophylax* with short spurs (equal to or less than the length of ovary). HIS = Hispaniola, PR = Puerto Rico, CUB = Cuba, JAM = Jamaica, CAY = Cayman Islands, MEX = Megamexico, FLA = Florida (USA).

<i>Dendrophylax</i> species	Distribution	Inflorescence	Spur	Inflorescence pubescence	Mid lobe of lip
<i>D. constanzensis</i>	HIS	filiform to 7 cm long	oblong, cylindrical	setaceous-hirsute	anchor-shaped, apiculate
<i>D. macrocarpa</i>	HIS	stout 1–2 cm long	obovoid	glabrous	ovate, acute
<i>D. megarhizus</i>	MEX	filiform to 10 cm long	scrotiform-saccate	glabrous	ovate-triangular, apiculate
<i>D. monteverdi</i>	PR, HIS, CUB, JAM	stout < 1 cm long	oblong to obovoid	glabrous	ovate, truncate
<i>D. porrectus</i>	PR, HIS, CUB, JAM, CAY, MEX, FLA	filiform 2–5 cm long	scrotiform-saccate	glabrous	ovate, apiculate
<i>D. pustulatus</i>	HIS	filiform 2.2–4.5 cm long	oblong, laterally flattened	pustulate	obovate, retuse
<i>D. serpentina</i>	HIS	filiform 2–3 cm	obovoid, laterally flattened	hispidus	ovate, 2-tailed, apiculate

likely pollinator-dependent since fruit production is sparse. Fragrance production is unknown. Pollinators of only one *Dendrophylax* are known, the large-flowered *D. lindenii*, which is pollinated by hawkmoths (Lepidoptera: Sphingidae) in Florida (USA) (Ackerman *et al.*, 2023; Danaher *et al.*, 2019; Houlihan *et al.*, 2019). It is unlikely that the small flowers of the present species are pollinated by the high energy-demanding sphingids. The tiny flowers of *D. pustulatus* suggest that they are visited by either microlepidoptera or small bees, the latter of which are known to pollinate the small, white, short-spurred flowers of three species of *Campylocentrum* in Brazil (Cabral & Pansarin, 2016; Carlswald *et al.*, 2003; Singer & Cocucci 1999).

CONSERVATION STATUS: We know of only one population occupying an area of approximately 2.5 hectares, with about 60 plants, all of which occur within a protected national park, Parque Nacional Armando Bermúdez. These conditions meet the IUCN Red List criterion D for endangered status (EN) (IUCN 2012).

PARATYPES: República Dominicana. Cordillera Central: Provincia Santiago, La Diferencia, *E. Fernández s.n.*, 28 Jun 2023 (UPRRP, illustration voucher). Provincia Santiago, La Diferencia, a 1 km en dirección este por el sendero, después de la caseta del Parque Nacional Armando Bermúdez, a lo largo de la vegetación contigua al Río Amina, 19°16'13"N, 71°03'07"W, elev. 735 m, 28 de marzo 2023, *E. Fernández 22B* (JBSD).

KEY TO THE SPECIES OF *DENDROPHYLAX*Modified from Ackerman & Collaborators (2014) and Molgo *et al.* (2016)

1. Inflorescences hispid to hirsute-setaceous throughout.....2
  2. Apical lobes of the labellum short, retrorse.....*D. constanzensis* (Garay) Nir
  - 2a. Apical lobes of the labellum long, filiform, pendent.....*D. serpentina* (Dod) Nir
- 1a. Inflorescences glabrous to sparsely verrucose or pustulate.....3
  3. Labellum simple or nearly so, retuse, entire or apiculate.....4
    4. Inflorescence less than 1 cm long.....5
      5. Roots smooth; fruits 8–9(–14) mm long; spur 2.5–3.0 mm long; Cuba, Jamaica, Hispaniola, Puerto Rico.....*D. monteverdi* (Rchb.f.) Ackerman & Nir
      - 5a. Roots verrucose; fruits 25–30 mm long; spur 3.0–3.5 mm long, Hispaniola.....*D. macrocarpa* (Dod) Carlswald & Whitten
    - 4a. Inflorescences 2–10 cm long.....6

6. Spur scrotiform, saccate.....7  
 7. Roots 0.8–1.6 mm in diameter; lip callus 0.2–0.5 long.....*D. porrectus* (Rchb.f.) Carlswald & Whitten  
 7a. Roots ca. 1.4–2.3 mm in diameter; lip callus 0.07–0.20 mm long.....*D. megarhizus* Molgo & Carnevali  
 6a. Spur infundibuliform, tubular, or laterally flattened, not scrotiform or saccate .....8  
 8. Spur 1.5–5 mm long, ovary tuberculate or pustulate.....9  
 9. Spur 3–5 mm long, infundibuliform.....*D. alcoa* Dod  
 9a. Spur 1.5–2.0 mm long, straight, laterally flattened.....*D. pustulatus* Ackerman & E.Fernández  
 8a. Spur 15–25 mm long, ovary glabrous.....10  
 10. Roots smooth; labellum without a crest; fruits less than 15 mm long; Cuba, Jamaica, and Dominican Republic.....*D. barrettiae* Fawc. & Rendle  
 10a. Roots tuberculate; labellum with a simple, basal crest 1 mm long; fruits 17–20 mm long; Dominican Republic.....*D. helorrhiza* Dod  
 3a. Labellum conspicuously trilobed, deeply emarginate, or apically bilobed .....11  
 11. Spur less than 10 cm long .....12  
 12. Dorsal sepal 17–29 mm long; Jamaica .....*D. funalis* (Sw.) Benth. ex Rolfe  
 12a. Dorsal sepal less than 7 mm long; Cuba and Hispaniola .....13  
 13. Labellum lobes falcate, lanceolate, about 9 × 3 mm, margin entire.....*D. gracilis* (Cogn.) Garay  
 13a. Labellum obovate, margin minutely denticulate .....*D. varius* (Gmel.) Urb.  
 11a. Spur more than 10 cm long .....14  
 14. Labellum apical lobes rounded, neither twisted nor elongate; Grand Cayman.....*D. fawcettii* Rolfe  
 14a. Labellum with falcate, twisting apical lobes 4.5–7.0 cm long; Cuba and Hispaniola .....15  
 15. Lateral lobes of the labellum low triangles, distally spreading 1–3 mm at the isthmus; Cuba .....  
 .....*D. lindenii* (Lindl.) Benth. ex Rolfe  
 15a. Lateral lobes of the labellum triangular, fang-like, spreading 8–14 mm at the isthmus; Hispaniola.....  
 .....*D. sallei* (Rchb.f.) Benth. ex Rolfe

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#### LITERATURE CITED

- Ackerman, J. D. & Collaborators. (2014). Orchid flora of the Greater Antilles. *Memoirs of the New York Botanical Garden*, 109, 1–625.
- Ackerman, J. D., Phillips, R. D., Tremblay, R. L., Reiter, N., Karremans, A., Peter, C. I., Bogarin, D., Perez-Escobar, O.A. & Liu, H. (2023). Beyond the various contrivances by which orchids are pollinated: global patterns in orchid pollination biology. *Botanical Journal of the Linnean Society*, 202, 295–324.
- Cabral, P. R. M. & Pansarin, E.R. (2016). Biología reproductiva de *Campylocentrum micranthum* (Orchidaceae, Angraecinae). *Rodriguésia*, 67, 379–386.
- Cano Carmona, E., Veloz Ramírez, A. & Cano-Ortiz, A. (2010). Contribution to the biogeography of the Hispaniola (Dominican Republic, Haiti). *Acta Botanica Gallica*, 1567, 581–598.
- Cano-Ortiz, A., Musarella, C. M., Piñar Fuentes, J. C., Pinto Gomes, C. J. & Cano, E. (2016). Distribution patterns of endemic flora to define hotspots on Hispaniola. *Systematics and Biodiversity*, doi: 10.1080/14772000.2015.1135195

- Carlswald, B. S., Whitten, W. M. & Williams, N. H. (2003). Phylogenetics of Neotropical leafless Angraecinae (Orchidaceae): reevaluation of generic concepts. *International Journal of Plant Sciences*, 164, 43–51.
- Carlswald, B. S., Whitten, W. M., Williams, N. H. & Bytebier, B. (2006). Molecular phylogenetics of Vandaeae (Orchidaceae) and the evolution of leaflessness. *American Journal of Botany*, 93, 770–786.
- Danaher, M. W., Ward, C., Zettler, L. W. & Covell, C. V. (2019). Pollinia removal and suspected pollination of the endangered ghost orchid, *Dendrophylax lindenii* (Orchidaceae) by various hawk moths (Lepidoptera: Sphingidae): another mystery dispelled. *Florida Entomologist*, 102, 671–683.
- Farminhão, J. N. M., Verlynde, S., Kaymak, E., Droissart, V., Simo-Droissart, M., Collobert, G., Martos, F., Stévar, T. (2021). Rapid radiation of angraecoids, (Orchidaceae, Angraecinae) in tropical Africa characterised by multiple karyotypic shifts under major environmental instability. *Molecular Phylogenetics and Evolution*, 159, 107105.
- Houlihan, P. R., Stone, M., Clem, S. E., Owen, M. & Emmel, T. C. (2019). Pollination ecology of the ghost orchid (*Dendrophylax lindenii*): a first description with new hypotheses for Darwin's orchids. *Scientific Reports*, 9, 12850 doi: 10.1038/s41598-019-49387-4
- Hu, H. Y., Stern, R. J., Rojas-Agramonte, Y., Garcia-Casco, A. (2022). Review of geochronologic and geochemical data of the Greater Antilles Volcanic Arc and implications for the evolution of oceanic arcs. *Geochemistry, Geophysics, Geosystems*, 23, e2021GC010148
- IUCN. (2012). *IUCN red list categories and criteria. Version 3.1. Second edition*. IUCN.
- Molgo, I. E., Carnevali Fernández-Concha, G., Whitten, W. M. & Williams, N. H. (2016). *Dendrophylax megarhizus* (Orchidaceae), a new species from Mexico. *Systematic Botany*, 41, 263–274.
- Pessoa, E. M., Viruel, J., Alves, M., Bogarín, D., Whitten, W. M. & Chase, M. W. (2018). Evolutionary history and systematics of *Campylocentrum* (Orchidaceae: Vandaeae: Angraecinae): a phylogenetic and biogeographical approach. *Botanical Journal of the Linnean Society*, 186, 158–178.
- Powell, R., Ottenwalder, J. A. & Incháustegui, S. J. (1999). The Hispaniolan herpetofauna: diversity, endemism, and historical perspectives, with comments on Navassa Island. In Crother, B. I. (ed.), *Caribbean Amphibians and Reptiles*, Academic Press. Pp. 93-168.
- Santiago-Valentín, E. & Olmstead, R. G. (2004). Historical biogeography of Caribbean plants: introduction to current knowledge and possibilities from a phylogenetic perspective. *Taxon*, 53, 299–319.
- Singer, R. B. & Cocucci, A. A. (1999). Pollination mechanism in southern Brazilian orchids which are exclusively or mainly pollinated by halictid bees. *Plant Systematics and Evolution*, 217, 101–117.
- Tremblay, R. L., Ackerman, J. D., Zimmerman, J. K. & Calvo, R. N. (2005). Variation in sexual reproduction in orchids and its evolutionary consequences: a spasmodic journey to diversification. *Biological Journal of the Linnean Society*, 84, 1–54.

