





https://doi.org/10.11646/phytotaxa.521.1.4

# A NEW SPECIES OF *DICHAEA* (ORCHIDACEAE: ZYGOPETALINAE) FROM THE ANDES OF COLOMBIA

#### YASMIN A. ALOMÍA<sup>1,5\*</sup>, AURELIEN SAMBIN<sup>2,3,6</sup>, J. TUPAC OTERO<sup>4,7</sup> & PABLO R. STEVENSON<sup>1,8</sup>

<sup>1</sup>Departamento de Ciencias Biológicas, Facultad de Ciencias, Universidad de Los Andes, Bogotá-Colombia.

<sup>2</sup> Herbarium of the French Guiana Botanical Garden (HJBG), Macouria, French Guiana.

<sup>3</sup> Botanical Garden of French Guiana, 2802, savane Césarée, 97355 Macouria, French Guiana.

- <sup>4</sup> Departamento de Ciencias Básicas, Facultad de Ingeniería y Administración, Universidad Nacional de Colombia, Palmira-Colombia.
- <sup>5</sup> sa.alomia10@uniandes.edu.co; <sup>6</sup> https://orcid.org/0000-0002-7389-7782
- <sup>6</sup> sambin-orchidees@orange.fr; <sup>6</sup> https://orcid.org/0000-0003-4783-7978
- <sup>7</sup> ] jtoteroo@unal.edu.co; <sup>10</sup> https://orcid.org/0000-0002-0810-183X
- <sup>8</sup> stevens@uniandes.edu.co; <sup>b</sup> https://orcid.org/0000-0003-2394-447X

#### Abstract

A new species of *Dichaea* sect. *Dichaea* from the Andean forests in Colombia is described and illustrated based on living material. *Dichaea andina* is compared with the morphologically similar *D. lagotis* and *D. pendula*, from which it can be distinguished by a number of vegetative and floral and features. *Dichaea andina* differs from *D. lagotis* in the broadly anchoriform lip, the hypochile transversely subrounded and the epichile transversely narrowly elliptic, briefly apiculate. Similarly, it differs from *D. pendula* in the caespitose habit, the leaves without cross-venation, and the inflorescence straight produced below the foliage, among other features. Ecological information for the new species is also provided.

#### Resumen

Una nueva especie de *Dichaea* sect. *Dichaea* que habita en los bosques andinos de Colombia es descrita e ilustrada. *Dichaea andina* se compara con las especies más cercanas *D. lagotis* y *D. pendula*, de las que se puede distinguir por un conjunto de rasgos vegetativos y florales. *Dichaea andina* se diferencia de *D. lagotis* en el labelo ampliamente anchoriforme, el hipoquilo transversalmente sub-redondeado y el epiquilo transversalmente estrechamente elíptico y brevemente apiculado. Asimismo, se diferencia de *D. pendula* en el hábito cespitoso, las hojas sin venación reticulada, y la inflorescencia recta y posicionada debajo del follaje, entre otras características. Adicionalmente, se proporciona información sobre algunos aspectos ecológicos de la nueva especie.

Keywords: Andean mountain range, cloud forest, Colombia, Cymbidieae, Dichaea sect. Dichaea, taxonomy

#### Introduction

*Dichaea* Lindley (1833: 208) (Cymbidieae: Zygopetalinae) is a monophyletic group recognized by distichous leaves, elongated stems without pseudobulbs, and flowers with anchor-shaped lips and infrastigmatic ligules (Neubig 2005). Four sections were recognized by Cogniaux (1906) based on two morphological characters; the type of ovary (muricate or glabrous) and the presence or absence of a leaf abscission layer: (i) *Dichaea* sect. *Dichaeopsis* (Pfitzer 1887: 107) Kuntze (1903: 171) groups the species with deciduous leaves and smooth ovaries; (ii) *Dichaea* sect. *Pseudodichaea* Cogniaux (1906: 499) defined by deciduous leaves and muricate ovaries; (iii) *Dichaea* sect. *Dichaeastrum* Cogniaux (1906: 490), with persistent leaves and glabrous ovaries and finally, (iv) *Dichaea* sect. *Eudichaea* Kuntze (1903: 171), with persistent leaves and species are easily distinguishable by having a pendulous habit (Neubig 2005, Pupulin 2007). Even though molecular evidence (Neubig *et al.* 2009) suggests that Cogniaux's divisions are not fully supported

<sup>\*</sup>Corresponding author

phylogenetically, it is useful in differentiating among species groups and continues to be the most widely accepted classification (Pupulin 2007, Davies & Stpiczyńska 2008, Neubig *et al.* 2009, Chase *et al.* 2015).

*Dichaea* has its greatest diversity in South America (Folsom 1987, Folsom 1990, Dodson & Escobar 1993), being the probable center of dispersal given the high number of early diverging lineages (Pupulin 2007). Diversity is particularly notable in the Andes, with Ecuador and Colombia being the most species-rich countries with around 40 each (Dodson 1992, Dodson 2004, Pupulin *et al.* 2009, Bernal *et al.* 2015, Betancur *et al.* 2015, Pupulin 2019). In Colombia, past species determinations have not been taxonomic rigorous. The country's official lists and databases report *ca.* 13 species, but do not consider synonymy and lack specimen or location references (Bernal *et al.* 2015). Recent interest in the diversity of this genus in Colombia has a led to the discovery of specimens that do not correspond to any previously species described. We reviewed the illustrations and descriptions reported for the genus (Dodson 1989, Folsom 1990, Dodson & Escobar 1993, Pupulin 2007, Pupulin *et al.* 2009, Pupulin & Karremans 2020) including protologues, and found that despite the similarities, the taxon here described as *Dichaea andina* presents unique morphological differences. We provide a complete description that includes ecological information of this new species discovered in the highly threatened Andean forests of Colombia (Armenteras *et al.* 2007, Betancur *et al.* 2015).

### Materials and methods

The description of this new species is based on specimens from a population found in the Reserva Comunitaria Cerro El Inglés. A remnant of an Andean forest with a good degree of conservation, located in the Western Cordillera, Valle del Cauca, in the municipality of El Cairo (Colombia) at 4°45'31.5"N, -76°17'07.6"W, 2303 m of elevation. Additional populations of *D. andina* were also observed (Fig. 1). In each, three specimens were collected and then deposited in national herbaria: ANDES, COL, CUVC. All the specimens were carefully studied and compared known taxa reported in the literature (Aublet 1775, Lindley 1833, Reichenbach 1876, Cogniaux 1903, Pupulin 2007), considering the relevant morphometric characters that have traditionally been of taxonomic utility for this study group (Neubig 2005, Pupulin 2007).

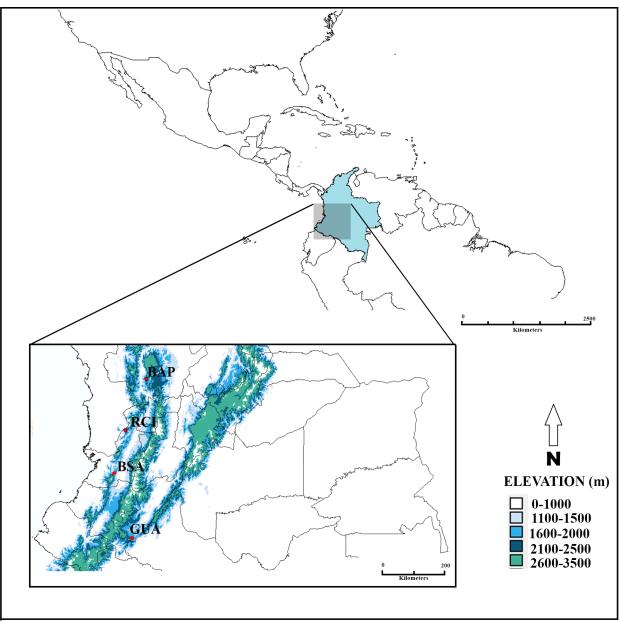
# Taxonomy

### Dichaea andina Alomía & Sambin, sp. nov.

- Type:—COLOMBIA. Valle del Cauca, Western Cordillera, El Cairo, Reserva Comunitaria Cerro El Inglés, 4° 45' 31.5" N, -76° 17' 07.6"
  W, 2303 m, Andean cloud forest, epiphytic in remnant primary forest, April 09, 2017. *Y.A. Alomía 216* (holotype: ANDES; isotypes: CUVC, COL; Figs. 2–5).
- Dichaea andina differs from *D. lagotis* Reichenbach (1876: 112) in the broadly anchoriform lip (vs. sagittate), with the hypochile transversely subrounded (vs. subquadrate) and the epichile transversely narrowly elliptic, briefly apiculate (vs. oblong acute). It differs from *D. pendula* (Aublet 1775: 819) Cogniaux (1903: 182) in the caespitose plants (vs. plants not caespitose), the leaves without cross-venation (vs. with cross-venation), and the inflorescence straight, produced under the foliage (vs. geniculated, above the foliage).

*Plant* epiphytic, caespitose, up to 2 m long. *Basal roots* 0.6–0.9 cm in diameter, brownish, filiform, flexuous. *Caulinar roots ca.* 0.4 cm in diameter, greenish, filiform, flexuous, glabrous, protruding from the leaf sheaths. *Stems* up to  $100 \times 0.40-0.45$  cm and 0.12-0.18 cm thick, covered by conduplicate sheaths, frequently branching, flattened, pendent, arched to erect at the apex. *Leaves*  $2.5-3.7 \times 0.5-0.9$  cm, green to olive green, distichous along stem, ovate to elliptic-ovate, distinctly apiculate, the margin entire except at the serrulate apex, thin-textured herbaceous, abaxially with a prominent midvein and conspicuous parallel secondary veins. *Inflorescence* one per node, occurring below the foliage; peduncle  $1.4-1.8 \times 0.6-1.0$  cm, terete, straight, with three tubular overlapping bracts. *Floral bract* double, the outer bract *ca.*  $6 \times 3$  mm, widely ovate, acuminate, the inner bract *ca.*  $7 \times 0.8$  mm, linear, acuminate. *Ovary* 3 mm long, densely muricate. *Flowers* in anthesis for 1-2 days, with a sweet fragrance detected between 9:00–15:00 h, sepals and petals pale pink spotted with violet, sepals warty on abaxial surface, lip white with the apical edge outlined in violet as well as two violet spots on the base. *Dorsal sepal*  $9.6 \times 3.8$  mm, concave, ovate-lanceolate, acute. *Lateral sepals*  $9.2 \times 4.1$  mm, concave, slightly asymmetrical, elliptic, lanceolate, acute. *Petals*  $7.5 \times 3.2$  mm, elliptic oblong, acute,

margins lightly undulated. *Lip* subsessile, distally 3-lobed to anchor-shaped, fleshy, glabrous; hypochile *ca.*  $4.5 \times 2.7$  mm, transversely subrounded forming distinct glabrous shoulders, lateral lobes about 2 mm long, narrowly triangular, filiform, more or less spreading; epichile *ca.*  $4 \times 2.3$  mm, transversely narrowly elliptic, briefly apiculate. *Column*  $5 \times 4$  mm, suberect, the base subterete, with two obliquely subquadrate rounded wings, ciliate along the margin; stigma transversely widely elliptic-ovate, strongly depressed; infrastigmatic ligule  $1.2 \times 0.8$  mm, linear, projecting forward, hispid, truncate and bifid at the apex. Anther  $1.1 \times 1.5$  mm, helmet-shaped, 2-celled. *Pollinia* 4, orbicular, in two superposed pairs of different size; stipe chalice-shaped; viscidium rectangular. *Fruit*  $1.8 \times 1.4$  cm, ovoid, greenishbrown, densely muricate, exocarp about 2 mm thickness, trichomes broadly triangular, acuminate. *Seeds ca.*  $160 \times 60$  µm, hyalines and fusiform, pale yellow in immature stages and brownish when ripe.



**FIGURE 1**. Known population of *Dichaea andina*. Bosque de San Antonio (BSA), Bosque El Aguapante (BAP), Parque Nacional Natural Cueva de los Guácharos (GUA), Reserva Comunitaria Cerro el Inglés (RCI).

Additional material studied:—COLOMBIA. Valle del Cauca, Western Cordillera, El Saladito, Bosque de San Antonio, 3°29'45.6"N, -76°37'29.1"W, 2078 m, Andean cloud forest, epiphytic in remnant primary forest, 11/05/2017, *Y.A. Alomía 217* (ANDES, COL, CUVC). Huila, East Cordillera, Palestina, Parque Nacional Natural Cueva de los Guácharos, 1°36'26.0"N, -76°05'45.2"W, 2189 m, Andean cloud forest, epiphytic in primary forest, 21/04/2017, *Y.A. Alomía 218* (ANDES, COL, CUVC), *P. Stevenson-2934* (ANDES). Antioquia, Central Cordillera, San Antonio de Prado, 6°14'42.8"N, -75°40'36.0"W, 2284 m, Andean cloud forest, epiphytic in remnant primary forest, 10/10/2017, *Y.A. Alomía 230* (ANDES, COL, CUVC).



FIGURE 2. *Dichaea andina*. A. Plant *in situ*. B. Flower emerging below foliage. C. Flower recently pollinated. D. Muricate fruit. Photographs by Y.A. Alomía.

**Ecology**:—*Dichaea andina* grows in the wet mountainous forests of the Andes mountain range at elevations between 1800 and 2400 m, with a mean temperature of 14.5 °C and a mean relative humidity of 99 %. The plants are found growing on both living trees (Annonaceae, Arecaceae, Clusiaceae, Cyatheaceae, Lauraceae, Melastomataceae, Myrtaceae, Piperaceae) and dead trunks, usually in deep shaded areas. Two flowering peaks were recorded twice, one in April–May and another in October–November, although there may be occasional flowering year round. Plants are completely allogamous. Flowers are pollinated by male *Euglossa* bees which are attracted by volatile floral fragrances primarily composed of 2-(4-methoxyphenyl) ethanol (4-2-hydroxyethyl anisole) and 2-methoxy-phenol (*o*-Guaiacol) (Alomía *et al.* 2018).

**Etymology**:—The specific epithet is designated for two purposes: first, to honor the Andean forests (Andes mountain range) and second, in recognition of the Universidad de Los Andes, for the academic and institutional support it provided to the first author during her doctoral studies.

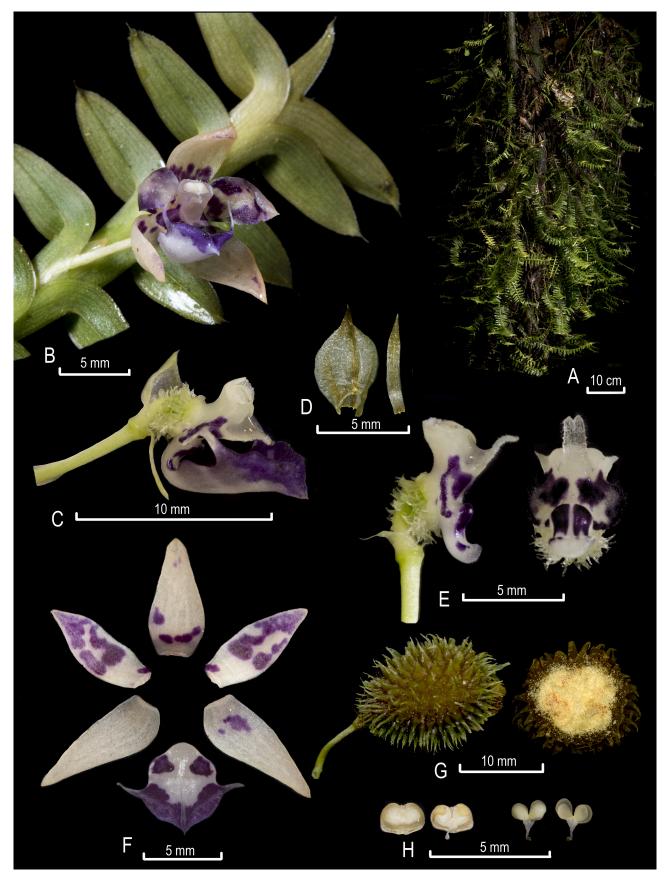
# Discussion

Species of *Dichaea* sect. *Dichaea* are distinguished by non-articulated leaves and muricate ovaries. However, molecular analyses show that the muricated ovary is a homoplasious character, with several losses and gains within the genus (Neubig *et al.* 2009). Members of *Dichaea* sect. *Dichaea* were shown to form a monophyletic group together with

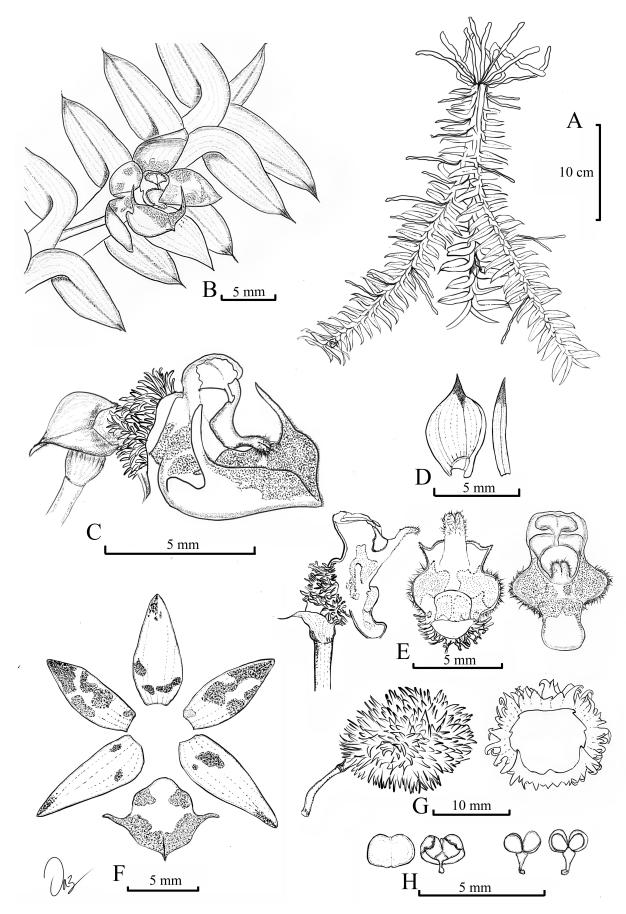
members of Dichaea sect. Dichaeastrum. Neubig et al. (2009) reclassified the group as Dichaea sect. Dichaea sensu lato, defined by the pendent habit and persistent leaves. Dichaea andina is a member of the species of Dichaea sect. Dichaea in the broad sense, being morphologically similar to D. lagotis and D. pendula. From the first, the new species is distinguished by the broadly anchoriform lip (vs. sagittate), distally 3-lobed with well-developed filiform lateral lobes, more or less spread out (vs. short, uncinate, retrorse), the transversely subrounded hypochile (vs. subquadrate), distinctly wider, ca. 2 times as wide as long (vs. almost as wide as long), transversely narrowly elliptic, shortly apiculate epichile (vs. oblong, acute), ca. 2 times wider than long (vs. as wide as long) and the infrastigmatic ligule at least 4.5 times smaller than the column (vs. up to 2 times), more or less hispid (vs. glabrous). Even though the position of the inflorescence is not specified in the protologue of D. lagotis, the drawing by Wallis of the type specimen collected in Medellin (Antioquia, Colombia) (copy at AMES-00098853!), suggests that the inflorescence emerges above the foliage (vs. below the foliage in D. andina) and that the peduncle is geniculated (vs. straight in D. andina). Dichaea lagotis has been recorded in Colombia, Ecuador and Venezuela (Dodson 1992, Jørgensen & León-Yánez 1999, Dodson & Luer 2010, Idárraga-Piedrahita et al. 2011, Bernal et al. 2015). We also interpret a reference specimen collected in Urrao (Antioquia, Colombia, Escobar 1703) and kept at HUA (HUA-012625!), as belonging to this species. It was found around 1300 m of elevation, while individuals of *D. andina* inhabit forests at higher elevations, between 1800 and 2400 m, where the ecosystem differs. For instance, in Colombian sub-Andean forests with elevations close to 1400 m, the average annual rainfall is around 1600 mm and the average temperature is about 20 °C. On the other hand, the Andean forests between 1700 and 2400 m of elevation have high precipitations of more than 2200 mm and average temperatures of 14 °C (Armenteras et al. 2007).

Dichaea pendula has been reported to occur in Central America (Costa Rica and Panama), and in most of the countries of South America from Colombia to northern Brazil, and in the West Indies (Pupulin 2007). Particularly in Colombia, almost every species from the cloud mountain forests (about 1700-2500 m of elevation), characterized by a pendent and caespitose habit and bearing whitish flowers dotted with violet, has been traditionally treated as D. pendula (Bernal et al. 2015, Betancur et al. 2015). Dichaea pendula is a species described from French Guiana and the plate selected as lectotype accompanying the protologue has served for a long time as a reference. However, the inconsistency between the drawing and the description has made it a challenge to understand the precise diagnostic traits of this species (Pupulin 2007). Recent studies at the site of the type specimen and different localities in French Guiana made by the second author, have shed light on the precise characteristics of this species (Sambin et al. unpublished). Comparisons of individuals of D. andina with specimens of D. pendula from the type locality in French Guiana reveal several differences in various vegetative and floral traits. Plants of D. anding are densely caespitose (vs. not caespitose), the stems are apically arched, suberect (vs. barely ascending at the apex), frequently branching (vs. never branching, except at the junction of an old trauma). The leaves are spaced along stem and thin-textured (vs. closely spaced, coriaceous) and without evident cross-venation (vs. with cross-venation). The flowers are pale pink (vs. yellow orange) and very fragrant (vs. without fragrance detected). The inflorescence is produced below the foliage (vs. above the foliage), and the peduncle is straight (vs. geniculated). The labellum has a transversely broadly-elliptic hypochile (vs. obcuneate), narrowly triangular, filiform lateral lobes (vs. triangular, short lateral lobes), shortly apiculate epichile (vs. shortly emarginated). The column has an infrastigmatic ligule inconspicuously hispid and bifid at the apex (vs. densely pubescent, entire). Finally, D. andina grows at elevations between 1800-2400 m, with an average temperature of 14.5 °C, while D. pendula grows near sea level up to 700 m, with an average temperature generally above 24 °C.

The position of the flowers below the foliage seems to be rare in the species of *Dichaea* sect. *Dichaea*. This trait has been reported in species of *Dichaea* sect. *Pseudodichaea* and to a lesser extent in *Dichaea* sect. *Dichaeopsis* (Pupulin 2007), both featuring articulated leaves. In his monograph of Costa Rican *Dichaea*, Pupulin (2007) reported a plant belonging to *Dichaea* sect. *Dichaea* with this unusual feature. The plant was registered under the name of *D. pendula*. However, the numerous specimens that we have examined in the type locality and in many other areas of the French Guiana show plants with flowers continuously above the foliage. These observations suggest that the interpretation of Pupulin (2007) for his plant, based on the illustration of the type carried out by Aublet is imprecise, and that this character is not only attributable to our new species. *Dichaea andina* has stems arched at the apex and a straight peduncle to allow the pollinator to access the flower hidden under the foliage. We consider that these three traits (stems arched at the apex, straight peduncle and flower under the foliage) constitute key discriminating characteristics to delimit this species.



**FIGURE 3**. *Dichaea andina*. **A**. Habit. **B**. Inflorescence. **C**. Ovary, column and lip, lateral view. **D**. Floral bract and bracteole. **E**. Column in lateral and ventral views. **F**. Perianth. **G**. Fruit, entire and cross section. **H**. Anther cap and pollinarium in dorsal and ventral views. Photographs by Y.A. Alomía based on the plant that served as type (*Y.A. Alomía 216*-ANDES).



**FIGURE 4**. *Dichaea andina*. **A**. Habit. **B**. Inflorescence. **C**. Ovary, column and lip, lateral view. **D**. Floral bract and bracteole. **E**. Column in lateral and ventral views. **F**. Dissected perianth. **G**. Fruit entire and cross section. **H**. Anther cap and pollinarium in dorsal and ventral views. Drawing by Y.A. Alomía based on the plant that served as type (*Y.A. Alomía 216*-ANDES).

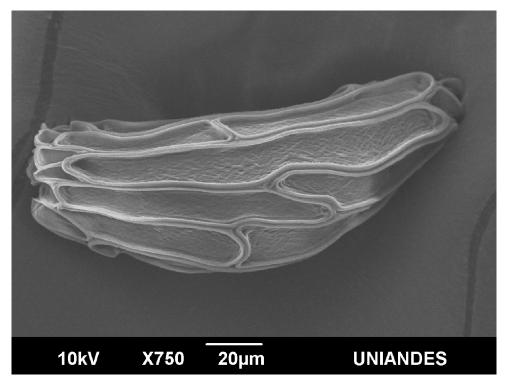


FIGURE 5. Scanning electron microscope (SEM) image of a seed of Dichaea andina.

### Acknowledgements

We thank our colleagues Santiago García-Revelo, David Haelterman, Carlos Mesa, Luis Pérez and Sebastián Vieira who assisted in the search for the *Dichaea* species in Andean forests. We are grateful to Corporación Serraniagua and Parque Nacional Natural Cueva de los Guácharos for the support in carrying out the studies *in situ*. Special thanks to the institutions that contributed resources for the financing of the doctoral project: Colciencias (National Doctoral Grant, call 617-2013), San Diego County Orchid Society (Conservation Award-2017) and Fondo de Investigaciones de la Facultad de Ciencias from Universidad de Los Andes (Doctoral students, call 2019-1, Project code: INV-2019-86-1799). We would to express gratitude to Franco Pupulin (Jardín Botánico Lankester), Guy R. Chiron (Herbiers, Claude Bernard University of Lyon), Luis Baquero (Universidad de Las Américas), and two anonymous reviewers for their valuable comments and suggestions.

# References

- Alomía, Y.A., Stevenson, P.R., Otero, J.T. & Stashenko, E. (2018) *Breeding system and pollination mechanism of Dichaea pendula (Aubl.) Cogn. (Orchidaceae).* 6th International Orchid Workshop, Białystok, 28 May–1 June 2018, 59 pp.
- Armenteras, D., Cadena, V.C. & Moreno, R.P. (2007) *Evaluación del estado de los bosques de niebla y de la meta 2010 en Colombia.* Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, 72 pp.

Aublet, J.B.C.F. (1775) Histoire des Plantes de la Guiane Françoise 2. Catalogue des libres nouveaux, Paris.

- Bernal, R., Gradstein, S.R. & Celis, M. (2015) *Catálogo de plantas y líquenes de Colombia*. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá. Available from: http://catalogoplantasdecolombia.unal.edu.co/es/ (accessed 10 January 2021)
- Betancur, J., Sarmiento, H., Toro-González, L. & Valencia, J. (2015) *Plan para el estudio y la conservación de las orquídeas en Colombia*. Ministerio de Ambiente y Desarrollo Sostenible, Universidad Nacional de Colombia, Bogotá, 336 pp.

Chase, M.W., Cameron, K.M., Freudenstein, J.V., Pridgeon, A.M., Salazar, G., van den Berg, C. & Schuiteman, A. (2015) An updated classification of Orchidaceae. *Botanical Journal of the Linnean Society* 177: 151–174. https://doi.org/10.1111/boj.12234

Cogniaux, A. (1903) Dichaea Lindl. Symbolae Antillanae seu Fundamenta Florae Indiae Occidentalis 4: 182-183.

- Cogniaux, A. (1906) Orchidaceae III, *Dichaea. In:* Martius, C.F.P., Eichler, A.G. & Urban, I. (eds.) *Flora Brasiliensis.* Fleischer, Munich, pp. 484–504.
- Davies, K.L. & Stpiczyńska, M. (2008) Labellar micromorphology of two euglossine-pollinated orchid genera; *Scuticaria* Lindl. and *Dichaea* Lindl. *Annals of Botany* 102: 805–824. https://doi.org/10.1093/aob/mcn155
- Dodson, C.H. (1989) Icones Plantarum Tropicarum: Series II. Missouri Botanical Garden, St. Louis, pp. 1-404.
- Dodson, C.H. (1992) Checklist of the Orchids of the Western Hemisphere. Draft manuscript deposited in Missouri Botanical Garden Library, St. Louis.
- Dodson, C.H. & Escobar, R. (1993) Dichaea Lindley. In: Dodson, C.H. & Escobar, R. (Eds.) Native Ecuadorian Orchids (V. 1) Aa-Dracula. Compañía Litográfica Nacional S.A., Medellín, pp. 176–186.
- Dodson, C.H. (2004) Ecuador orchid list. *In:* Dodson, C.H. (Ed.) *Native Ecuadorian Orchids* (V. 5) *Rodriguezia-Zygosepalum*. Dodson Publishing, Sarasota, pp. 1112–1156.
- Dodson, C.H. & Luer, C.A. (2010) Flora of Ecuador (225). Botanical Institute, University of Göteborg, Stockholm, 438 pp.
- Folsom, J.P. (1987) A systematic monograph of Dichaea section Dichaea (Orchidaceae). PhD thesis, Department of Botany, University of Texas, Austin, 266 pp.
- Folsom, J.P. (1990) *Dichaea* Lindl. *In:* Escobar, R. (Ed.) *Orquídeas Nativas de Colombia* (1) *Acacallis-Dryadella*. Sociedad Colombiana de Orquideología, Compañía Litográfica Nacional S.A., Medellín, pp. 112–115.
- Idárraga-Piedrahita, A., Ortiz, R.D.C., Callejas-Posada, R. & Merello, M. (2011) *Flora de Antioquia*. Universidad de Antioquia, Medellín, 939 pp.
- Jørgensen, P.M. & León-Yánez, S. (1999) Catalogue of the Vascular Plants of Ecuador (V. 75). Missouri Botanical Garden, St. Louis, 1182 pp.
- Kuntze, C.E.O. (1904) *Dichaea. In:* von Post, T.E. (Ed.) *Lexicon Generum Phanerogamarum.* Stuttgart, Deutsche Verlags-Anstalt, 171 pp.

Lindley, J. (1833) Dichaea. The genera and species of Orchidaceous plants. Ridgways, London.

- Neubig, K.M. (2005) *Molecular Systematics of the Genus Dichaea (Zygopetalinae: Orchidaceae)*. Master thesis, University of Florida, USA, 80 pp.
- Neubig, K.M., Williams, N.H., Whitten, W.M. & Pupulin, F. (2009) Molecular phylogenetics and the evolution of fruit and leaf morphology of *Dichaea* (Orchidaceae: Zygopetalinae). *Annals of Botany* 104: 457–467. https://doi.org/10.1093/aob/mcp004

Pfitzer, E.H.H. (1887) *Dichaeinae*. Entwurf einer natürlichen Anordnung der Orchideen. *In:* Carl Winter's Universitätsbuchhandlung (Ed.) Heidelberg, 107 pp.

https://doi.org/10.5962/bhl.title.166408

Pupulin, F. (2007) Contributions toward a reassessment of Costa Rican Zygopetalinae (Orchidaceae) 3. A systematic revision of *Dichaea* in Costa Rica. *Harvard Papers in Botany* 12: 15–153.

https://doi.org/10.3100/1043-4534(2007)12[15:CTAROC]2.0.CO;2

Pupulin, F., Pridgeon, A.M., Veitch, N.C., Grayer, R.J. & Blanco, M. (2009) Subtribe Zygopetalinae. In: Pridgeon, A.M., Cribb, P.J., Chase, M.W. & Rasmussen, F.N. (Eds.) *Epidendroideae of Genera Orchidacearum* (Part 2, V. 5). Oxford University Press, Oxford, pp. 456–546.

Pupulin, F. (2019) Zygopetalinae Novae et Criticae (Orchidaceae). *Harvard Papers in Botany*, 24: 291–339. https://doi.org/10.3100/hpib.v24iss2.2019.n16

Pupulin, F. & Karremans, A.P. (2020) A new and unusual species of *Dichaea* (Orchidaceae: Zygopetalinae) from Costa Rica. *Blumea - Biodiversity, Evolution and Biogeography of Plants* 65: 61–64. https://doi.org/10.3767/blumea.2020.65.01.06

Reichenbach, H.G. (1876) Dichaea lagotis. Linnaea 41: 112.