



# The Remarkable Diversity of Parasitic Flowering Plants in Colombia

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Published online: 8 November 2023

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## Abstract

Parasitic plants have evolved independently in 12 Angiosperm orders. Nine of them (Boraginales, Cucurbitales, Ericales, Lamiales, Laurales, Malvales, Santalales, Solanales, and Zygophyllales) are represented in Colombia by 17 families, 44 genera and 246 species, including facultative (37) and obligate (187) hemiparasites, holoexoparasites (19) and holoendoparasites (3). *Cladocolea coriacea* (Loranthaceae) is reported for the first time in Colombia. One genus (*Sanguisuga*, Cytinaceae) and 69 species (28.04%) are endemic to the country. Endemism decreases with elevation, ranging from 26 species (37.68%) below 1000 m, to one species (1.44%) above 4000 m. Speciation in *Aetanthus*, *Psittacanthus* and *Tristerix* (Loranthaceae), *Dendrophthora* and *Phoradendron* (Viscaceae), and *Castilleja* and *Neobartsia* (Orobanchaceae) was likely prompted by the Andean uplift. The highest number of species (169) are found in the Andean Region, whereas the Orinoco Region contains the lowest number (29). Dry forests and thickets, and coastal vegetation of the Caribbean Region are the preferred ecosystems for *Krameria* (Krameriaceae), *Sanguisuga*, *Acanthosyris* (Cervantesiaceae), *Maracanthus* (Loranthaceae), *Ximenia* (Ximeniaceae), *Lennoa* (Ehretiaceae), and *Anisantherina* (Orobanchaceae). *Orobanche minor*, recently introduced to the country, is the only potential weed for crops between 2500 and 3200 m in the Eastern Cordillera. Convergent lifeforms include: the obligate, twining stem holoparasitic *Cassytha* (Lauraceae) and *Cuscuta* (Convolvulaceae); the root holoexoparasitic *Sanguisuga*, *Mitrastemon* (Mitrastemonaceae), all Balanophoraceae, and *Lennoa*; and the root obligate hemiparasitic *Krameria*, *Gaiadendron* (Loranthaceae), and all Cervantesiaceae, Opiliaceae, Schoepfiaceae, Strombosiaceae and Ximeniaceae. Holoendoparasitism occurs only in Apodanthaceae, whereas root facultative hemiparasitism is restricted to the Orobanchaceae.

**Keywords** Andean flora · Amazonian flora · Colombia's biodiversity · Dry forests · Parasitic Angiosperms

## Resumen

Las plantas parásitas han evolucionado independientemente en 12 órdenes de angiospermas. Nueve de éstos (Boraginales, Cucurbitales, Ericales, Lamiales, Laurales, Malvales, Santalales, Solanales y Zygophyllales) están representadas en Colombia por 17 familias, 44 géneros y 246 especies, entre hemiparásitas facultativas (37) y obligadas (187), holoexoparásitas (19) y holoendoparásitas (3). *Cladocolea coriacea* (Loranthaceae) se reporta por primera vez en Colombia. Un género (*Sanguisuga*, Cytinaceae) y 69 especies (28,04%) son endémicas del país. El endemismo disminuye con la elevación, desde 26 especies (37,68%) por debajo de los 1000 m, hasta una especie (1,44%) por encima de los 4000 m. La especiación en *Aetanthus*, *Psittacanthus* y *Tristerix* (Loranthaceae), *Dendrophthora* y *Phoradendron* (Viscaceae), y *Castilleja* y *Neobartsia* (Orobanchaceae) está correlacionada con la orogenia Andina. El mayor número de especies (169) se encuentra en la Región Andina, y el menor (29) en la Región Orinoquia. Los bosques y matorrales secos y la vegetación costera del Caribe son los ecosistemas preferidos por *Krameria* (Krameriaceae), *Sanguisuga*, *Acanthosyris* (Cervantesiaceae), *Maracanthus* (Loranthaceae), *Ximenia* (Ximeniaceae), *Lennoa* (Ehretiaceae) y *Anisantherina* (Orobanchaceae). *Orobanche minor*, recientemente introducida, es la única maleza potencial en cultivos entre 2500 y 3200 m de la Cordillera Oriental. Las formas de vida convergentes incluyen: el holoparasitismo caulinar obligado de las trepadoras *Cassytha* (Lauraceae) y *Cuscuta* (Convolvulaceae); el holoexoparasitismo de raíces en *Sanguisuga*, *Mitrastemon* (Mitrastemonaceae), todas las Balanophoraceae, y *Lennoa*; y el hemiparasitismo obligado de raíz en *Krameria*, *Gaiadendron* (Loranthaceae), y todas las Cervantesiaceae, Opiliaceae, Schoepfiaceae, Strombosiaceae y Ximeniaceae. El holoendoparasitismo ocurre solo en Apodanthaceae, mientras que el hemiparasitismo radicular facultativo está restringido a las Orobanchaceae.

**Palabras clave** Angiospermas parasíticas · Biodiversidad de Colombia · Bosques secos · Flora Amazónica · Flora Andina

## Introduction

Parasitism, one of the most striking biological interactions across the tree of life, has driven numerous evolutionary and adaptive novelties in plants and animals. Nevertheless, parasitism has been more extensively studied in the animal kingdom (Schmid-Hempel, 2009), despite the fact that parasitic plants have developed a vast range of remarkable structural, functional, ecological, and genomic novelties to succeed.

The study of plant-plant parasitism has unveiled unique mechanisms in angiosperms, including: the evolution of structural elaborations between hosts and parasites (Thorogood et al., 2021); the recalcitrant parasite-on-parasite occurrence (Bernhardt, 1984; Krasylenko et al. 2021); the coordinate ecological, biogeochemical and physiological responses between hosts and parasites (Heckard, 1962; Matthies 1997; Amaral & Ceccantini, 2011; Ozturk et al., 2022; Zhang et al., 2023); the loss of autotrophic capabilities and the concomitant plastome reduction in

the parasite (Bungard, 2004; Vogel et al., 2018; Arias et al., 2019); the fixation of highly elaborated reproductive and embryological traits to ensure fertilization and seed dispersal (Johri & Bhatnagar, 1972; Lucero et al., 2014; González & Pabón-Mora, 2017a, b); the ecological roles of parasitic angiosperms as sources of pollen, nectar, fruits and seeds to trophic interactions (Ladley & Kelly, 1996; Amico et al., 2007, 2011; González & Pabón-Mora, 2017a, b); the dynamics of genome evolution including horizontal gene transfer (Park et al., 2007; Cusimano & Wicke, 2016; Fan et al., 2016; Arias et al., 2019); the use of host flowering signals to trigger parasite flowering (Shen et al., 2020); the regulation of host-mRNA mediated by parasite microRNAs (Shahid et al., 2018); and the parasitism-driven limitation of speciation (Young et al., 1999; Hardy & Cook, 2012), among others.

Parasitic flowering plants directly or indirectly depend upon the uptake of nutrients, water, and minerals from the host. Two main categories and several subcategories have been recognized, mainly based on the degree of reduction of photosynthetic rates, the dependence of the parasite on the host, and the structural modifications that take place as an outcome of this intricate biological association:

Hemiparasitic plants (Heide-Jørgensen, 2008): Functionally, they remain autotrophic, as their vegetative organs (cotyledons, stems and leaves, and, to a less extent, bracts, bracteoles, sepals and embryos) produce chlorophyll and are therefore capable of photosynthesizing. The following two subcategories are recognized: (a) facultative hemiparasites, which depend upon connections with one or (exceptionally) more hosts, but can also survive without a host. And (b), obligate hemiparasites, which retain photosynthetic processes, but still depend on their host for survival.

Holoparasitic plants (Heide-Jørgensen, 2008): Functionally, this is the most extreme life form of parasitism in Angiosperms. They are totally heterotrophic because they lack chlorophyll, and therefore depend entirely on their hosts. The following two subcategories are recognized: (a) holoexoparasites, characterized by the formation of structures that emerge aboveground from the host, which correspond to variously modified stems, leaves or inflorescence axes that are not photosynthetic; and (b) holoendoparasites, which lack typical vegetative structures (roots, stems or leaves) and macroscopic haustoria, and their reproductive structures develop inside the host, representing the most extreme event of morphological, anatomical and physiological specialization known in the plant kingdom.

The structural parasite-host connection in members of both categories is usually mediated by a highly elaborate and efficient haustorial system. This system is formed either belowground, and penetrates the host roots (i.e. the root parasites), or aboveground, and penetrates the host stems (i.e. the stem parasites). Interestingly, these two categories are mutually exclusive, meaning that there is not a single angiosperm species that parasitizes both shoots and roots (Heide-Jørgensen, 2008).

Parasitic angiosperms have evolved independently in twelve orders, ranging from facultative hemiparasites to obligate holoendoparasites (Fig. 1). The taxonomic occurrence of parasitic species on each order varies from exceptional in Lauraceae (Laurales), Ehretiaceae (Boraginales), and Convolvulaceae (Solanales), to frequent in Krameriaceae (Zygophyllales) and Orobanchaceae (Lamiales), to generalized in

**Fig. 1** Angiosperm phylogeny (modified from APG IV) and orders having parasitic taxa. Purple arrows point to orders with facultative hemiparasites; green arrows point to orders with obligate hemiparasites; red arrows point to orders with holoparasites; gray arrows point to three orders whose parasitic members are not present in Colombia

Apodanthaceae (Cucurbitales), Cytinaceae (Malvales), Mitrastemonaceae (Ericales) and Santalales (APG IV, 2016; Thorogood et al., 2021).

Globally, the contribution of parasitic flowering plants to angiosperm diversity is estimated to be nearly 1% of the total number of angiosperm species (Thorogood et al., 2021). This seemingly low percentage contrasts with the high diversity of parasitism-driven biological processes detected in angiosperms. Given that comparable accounts occur at a countrywide scale, here we aim to assess the diversity of parasitic angiosperms in Colombia, one of the biodiversity hotspots in the planet. We present an updated list of parasitic angiosperms in the Flora of Colombia, and provide maps of distribution (Figs. 2, 6, 8, 9, 11, 12, 14, 15, 16, 20, 21, 23, 24, and 25), photographs for 34 representative species (Figs. 3, 4, 5, 7, 10, 13, 17, 18, 19, and 22), and maps of two plastomes (Figs. 4O and 22J), one of them (that of *Pilosyles boyacensis* F.González & Pabón-Mora, Apodanthaceae; Fig. 4O) corresponding to one of the most (if not the most) reduced plastomes across flowering plants. We discuss distribution patterns of the parasitic angiosperms in the five natural regions of Colombia, and postulate that the uplift of the three cordilleras has played a positive role on the speciation of *Aetanthus*, *Oryctanthus* and *Psittacanthus* (Loranthaceae), *Dendrophthora* and *Phoradendron* (Viscaceae), and *Castilleja* and *Neobartsia* (Orobanchaceae). Our account resulted in a total of nine orders, 17 families, 44 genera and 246 species (69 of them endemic to the country), corresponding to approximately 1% of the total number of angiosperm species in Colombia, estimated in nearly 25,000 species (Cuatrecasas, 1958).

## Materials and Methods

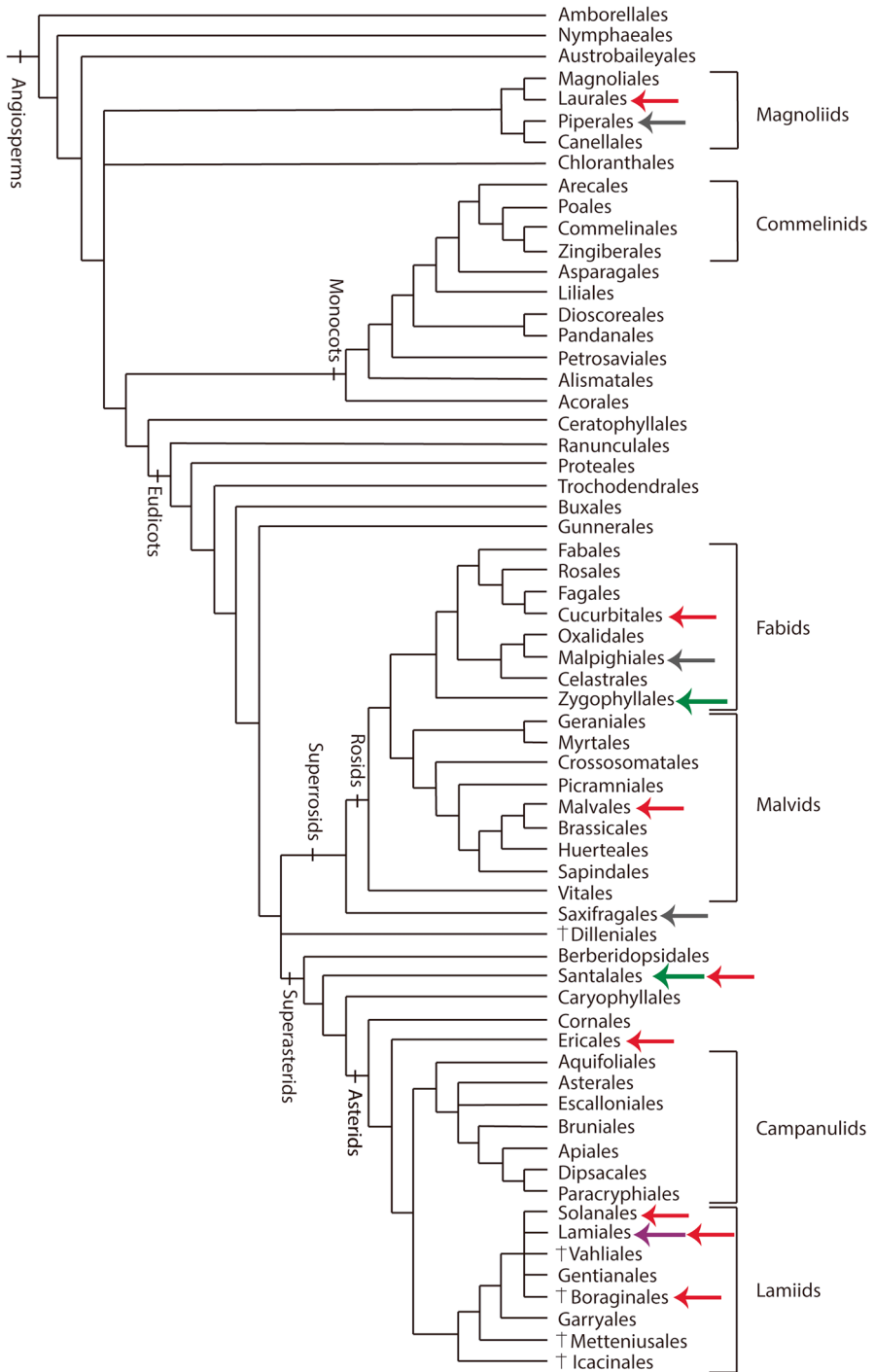
### Natural regions of Colombia

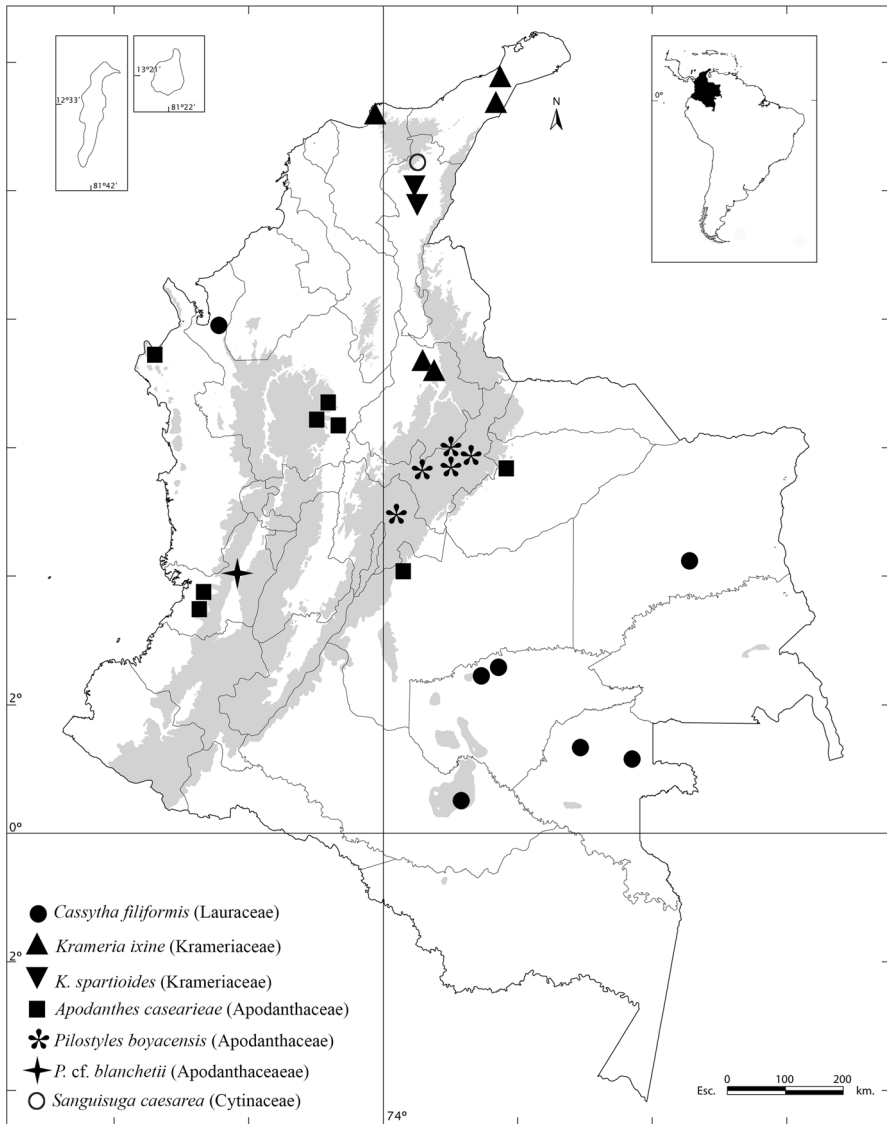
The distribution of families, genera and species here reported is outlined on the five natural regions in Colombia (as defined by Cuatrecasas, 1958). These are:

Region I. The Caribbean region, including the Archipelago of San Andrés and Old Providence. It encompasses coastal vegetation, mangrove swamps, grassy or forested dunes, scattered dry forest relicts surrounded by man made grassland, scrub thickets, montane vegetation in the Serranía de Macuira (an isolated mountain massif in northern Guajira), and low- to high-mountain forests to paramo vegetation in the Sierra Nevada de Santa Marta (the largest and highest extra-Andean mountain range in the country, and one of the coastal massifs in the world).

Region II. The Pacific region, comprising a corridor of pluvial or rain forest that runs from the Gulf of Uraba in the north, throughout the western lowlands of



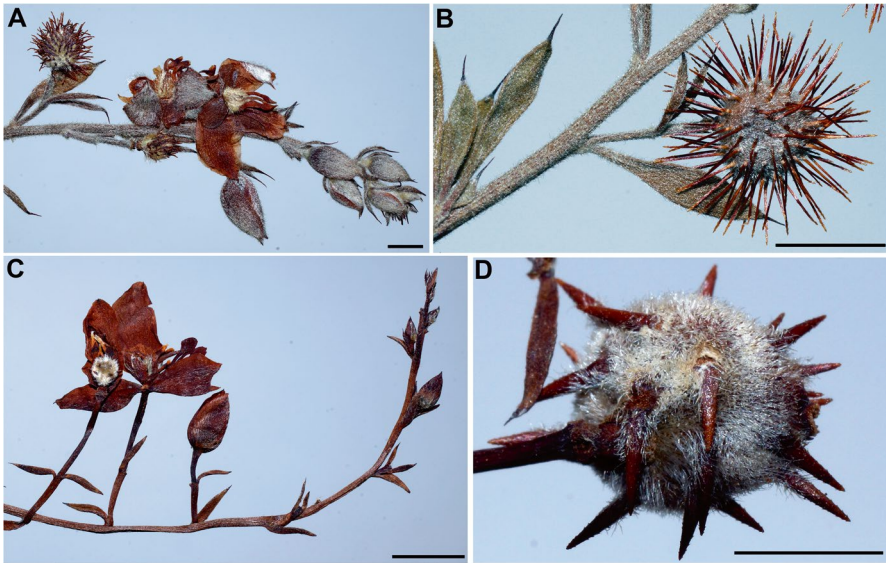




**Fig. 2** Map of distribution of *Cassytha* (Lauraceae), *Krameria* (Krameriaceae), *Apodanthes* and *Pilostyles* (Apodanthaceae), and *Sanguisuga* (Cytinaceae) in Colombia

the country reaching the department of Nariño, in southwestern Colombia. This region includes the Malpelo and the Gorgona islands.

**Region III.** The Andean region, including the slopes flanking the Cauca and the Magdalena valleys, the majority of the Andean forests and páramos in the country, the Serranía del Perijá (a mountain massif shared with Venezuela in northeastern Colombia), and the non-split region of the southern Andes



**Fig. 3** Krameriaceae (Zygophyllales), obligate root hemiparasites; A, B. *Krameria ixine*, leaves, flowers and fruits (Bolívar: Juan Arias, 80 m.a.s.l., *R. Romero-Castañeda 10,478*, COL). C, D. *K. spartioides*, leaves, flowers and fruits (La Guajira: Uribia, 50 m.a.s.l., *C. Saravia 2930*, COL). Scale bars: 5 mm in A-D

known as the Macizo Colombiano (a mountain massif near the border with Ecuador).

Region IV. The Orinoquia or Llanos Orientales region, including natural savannas, man made grassland areas, gallery forests along numerous river banks north of the Guaviare river, and the eastern slopes of the Eastern Cordillera.

Region V. The Amazonian region, including lowland forests south of the Guaviare river, the eastern slopes of the Eastern Cordillera, and the Guiana shield tepuis of Colombia.

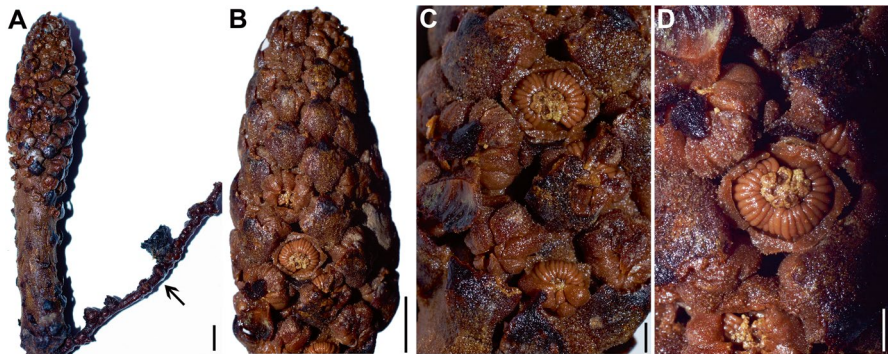
Maps of distribution are presented for all taxa, except for the widespread genera *Psittacanthus* (Loranthaceae), *Dendrophthora* and *Phoradendron* (Viscaceae), and *Castilleja* (Orobanchaceae) (Figs. 2, 6, 8, 9, 11, 12, 14, 15, 16, 20, 21, 23, 24, and 25).

### Plant material

The present study is based on extensive herbarium searches at the Colombian National Herbarium, National University of Colombia (COL), the herbarium of the University of Antioquia, Medellín (HUA), and the Harvard University Herbaria (A, GH). Additionally, the authors have studied in the field a total of 37 species, most of which are illustrated in Figs. 3, 4, 5, 7, 10, 13, 17, 18, 19, and 22. Representative vouchers for all taxa are provided, including 72 type specimens that were examined for this research.



**Fig. 4** Apodanthaceae (Cucurbitales), stem holoendoparasites. **A–D.** *Apodanthes caseariae* (Meta: Villavicencio, 710 m.a.s.l., *F. González et al.* 4922). **A, B**, numerous floral buds emerging from the trunk of its host *Casearia* sp. (Salicaceae); **C**, flowers at preanthesis and anthesis; **D**, fruits. **E–O.** *Pilostyles boyacensis* (Boyacá: Chiquiza, 2480 m.a.s.l., *F. González* 4508). **E.** Severely infected stem of its host *Dalea cuatrecasasii* (Fabaceae). **F–H.** Numerous floral buds emerging from the host stems. **I.** Peeled-off infected host stem showing several *P. boyacensis* floral buds forming in the host cortex. **J.** Transverse section of infected host stem showing *P. boyacensis* floral buds in the host cortex, and emerged, fully formed flowers. **K.** Flowers at anthesis. **L, M.** SEM micrograph of staminate (**L**) and carpellate (**M**) flowers. **N.** Berries, top view. **O.** Plastome map; note reduction to only six or seven functional genes (after Arias et al., 2019). Scale bars: 1 cm in **A, B**; 4 mm in **C, D, I, K, N**; 2 cm in **E–H**; 6 mm in **J**; 100  $\mu$ m in **L, M**



**Fig. 5** Cytinaceae (Malvales), *Sanguisuga caesarea*, holoexoparasite in roots of *Bursera tomentosa* (Jacq.) Triana & Planch. (Burseraceae)(Cesar: Valledupar, 290 m.a.s.l., *H. Cuadros et al.* 6333). **A.** Underground runner (arrow) and emerging inflorescence. **B.** Inflorescence. **C–D.** Details of bracts and flowers. Scale bars: 5 mm in **A, B**; 1 mm in **C, D**

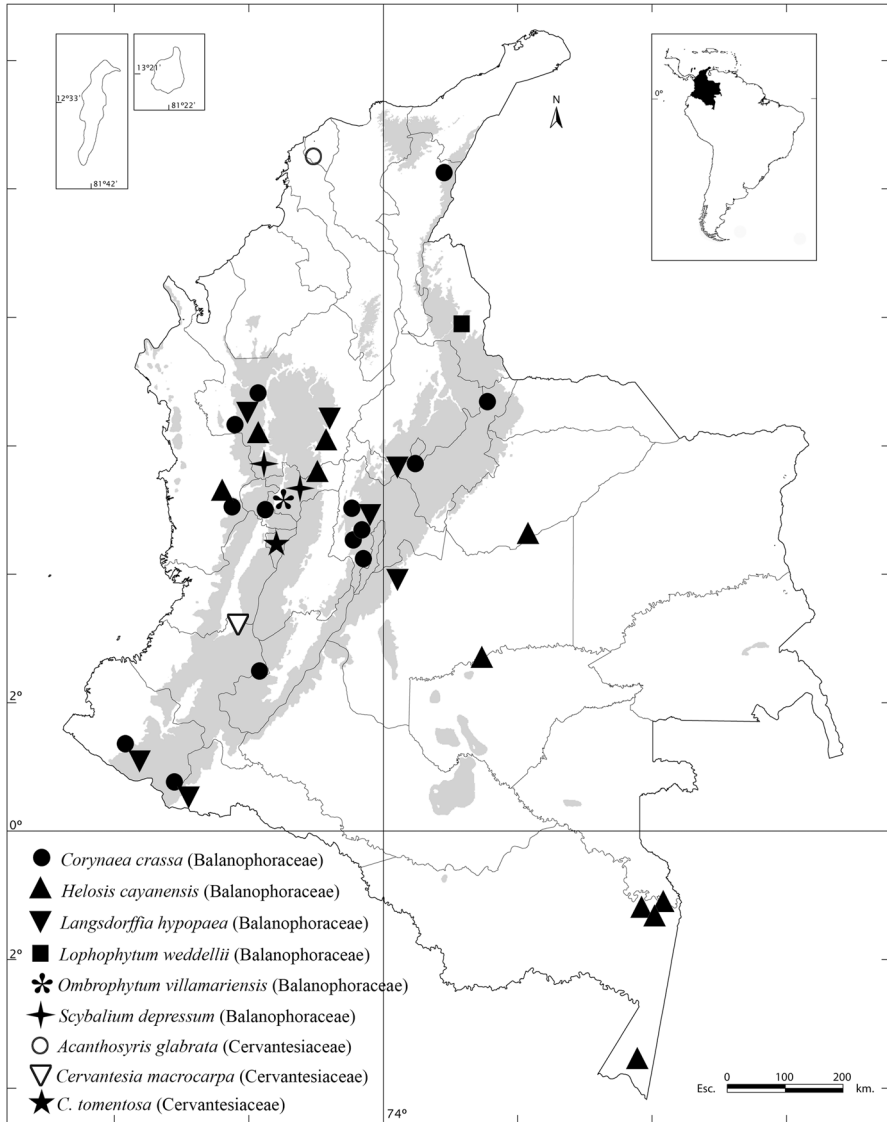
## Results

### General account of parasitic angiosperms in Colombia

Nine of the twelve orders with parasitic species recognized in the current system of angiosperm classification (APG IV, 2016; Fig. 1) are represented in the Flora of Colombia. These are the orders Boraginales (family Ehretiaceae), Cucurbitales (family Apodanthaceae), Ericales (family Mitrastemonaceae), Lamiales (family Orobanchaceae), Laurales (family Lauraceae), Malvales (family Cytinaceae), Santalales (families Balanophoraceae, Cervantesiaceae, Loranthaceae, Opiliaceae, Santalaceae, Schoepfiaceae, Strombosiaceae, Viscaceae, and Ximeniaceae), Solanales (family Convolvulaceae), and Zygophyllales (family Krameriaceae). Parasitic members of the orders Piperales (i.e. *Hydnora* and *Prosopanche*, currently members of the Aristolochiaceae), Saxifragales (Cynomoriaceae) and Malpighiales (Rafflesiaceae) are not present in the country's flora.

A total of 187 obligate hemiparasitic species are present in Colombia. They correspond to two species of Krameriaceae (order Zygophyllales), and all members of Santalales, including three species of Cervantesiaceae, 84 species of Loranthaceae, three species of Opiliaceae, three species of Santalaceae, two species of Schoepfiaceae, one species of Strombosiaceae, 88 species of Viscaceae, and one species of Ximeniaceae. In addition, a total of 37 species are facultative hemiparasites, corresponding to all the species of Orobanchaceae in the country. Conversely, only 19 are holoexoparasites (from families Balanophoraceae Cytinaceae, Convolvulaceae, Ehretiaceae and Mitrastemonaceae), and three holoendoparasites (all members of the Apodanthaceae).





**Fig. 6** Map of distribution of *Corynaea*, *Helosis*, *Langsdorffia*, *Lophophytum*, *Ombrophytum*, and *Scybalium* (Balanophoraceae), and *Acanthosyris* and *Cervantesia* (Cervantesiaceae) in Colombia

## List of parasitic angiosperms in Colombia with comments

### Magnoliids

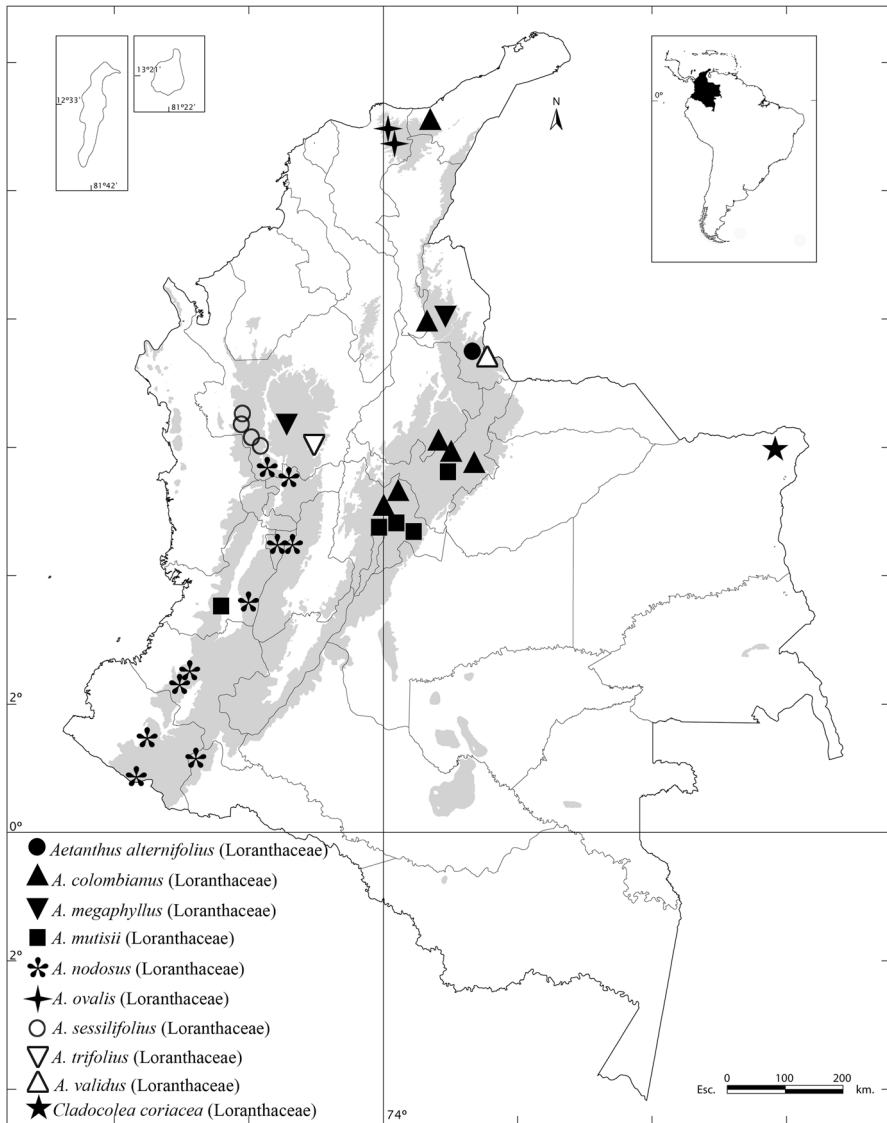
**1. Laurales:** One family.

**Lauraceae Juss.** One genus.



**Fig. 7** Balanophoraceae (Santalales), root holoparasites. **A–C.** *Corynaea crassa* (Boyacá: Villa de Leyva, 2820 m.a.s.l., *F. González 1604*). **A, B.** Inflorescences and rhizome; **C.** Detail of emerging inflorescence. **D–H.** *Helosis cayennensis* (Antioquia: Puerto Triunfo, 409 m.a.s.l., *F. González et al. 4705*). **D.** Multiple inflorescences emerging at intervals from the underground runner; **E.** Two inflorescence buds. **F–G.** Detail of the distal (**F**) and proximal (**G**) regions of the inflorescence. **H.** Sagittal section of inflorescence. **I–K.** *Langsdorffia hypogaea* (Boyacá: Villa de Leyva, 2600 m.a.s.l., *F. González 4712*). **I.** Detail of underground runner and inflorescence buds. **J, K.** Top view of emerged inflorescences. Scale bars: 1 cm in **A–D, J, K**; 5 mm in **E, H, I**; 1 mm in **F–G**





**Fig. 8** Map of distribution of *Aetanthus* and *Cladocolea* (Loranthaceae) in Colombia

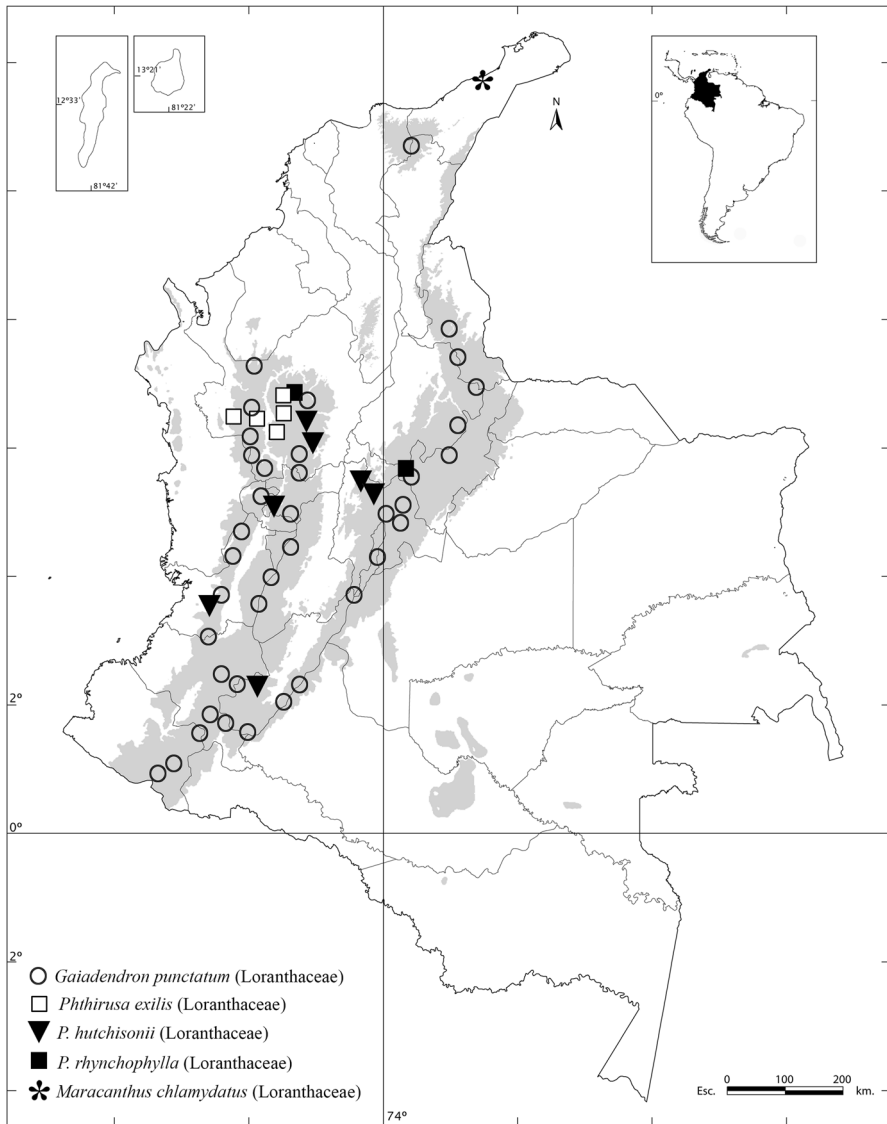
***Cassytha*** Osbeck. One stem holoeoparasitic species (Fig. 2).

*C. filiformis* L. (*J. Cuatrecasas 17919*, COL). Regions II, IV, and V, at elevations between 0 and 1000 m.

**2. Zygothylales:** One family.

**Krameriaceae** Dumort. One genus.

***Krameria*** Loefl. Two obligate, root hemiparasitic species (Figs. 2 and 3).



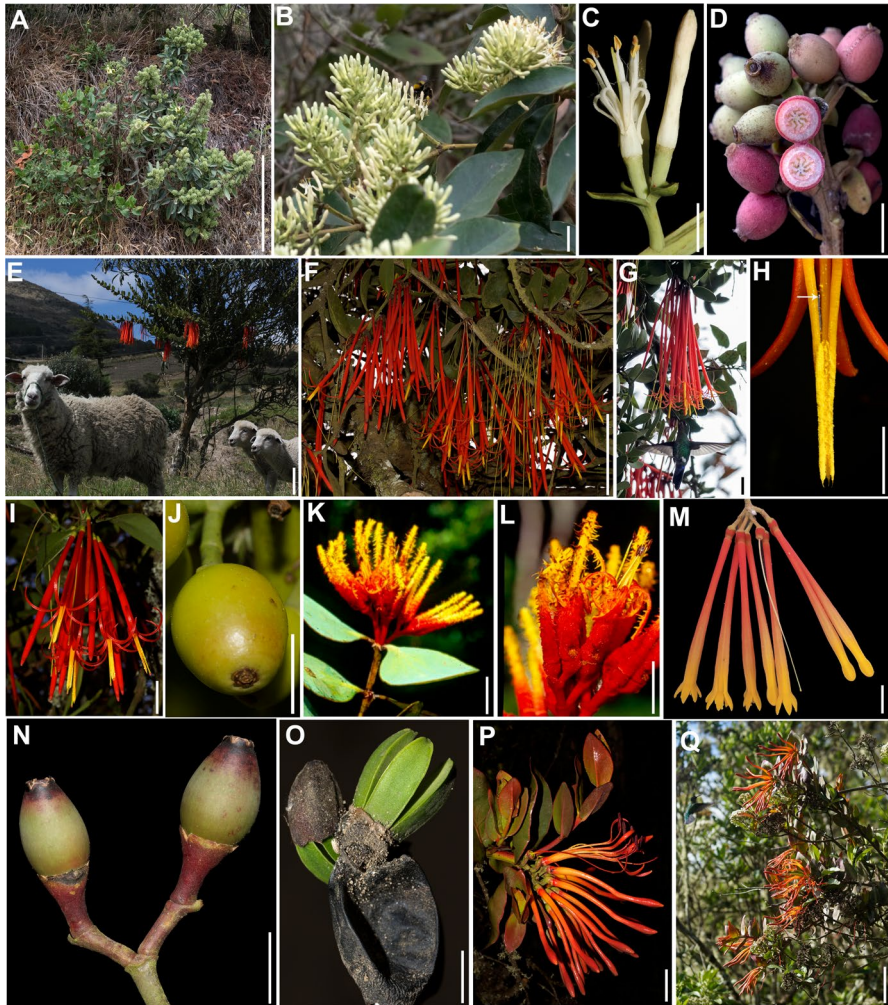
**Fig. 9** Map of distribution of *Gaiadendron*, *Maracanthus* and *Phthirusa* (Loranthaceae) in Colombia

*K. ixine* Loeff. (Fig. 3A, B; R. Romero-Castañeda 10478, COL). Region I. Xerophytic thickets of the Caribbean plains, between 0–1000 m.

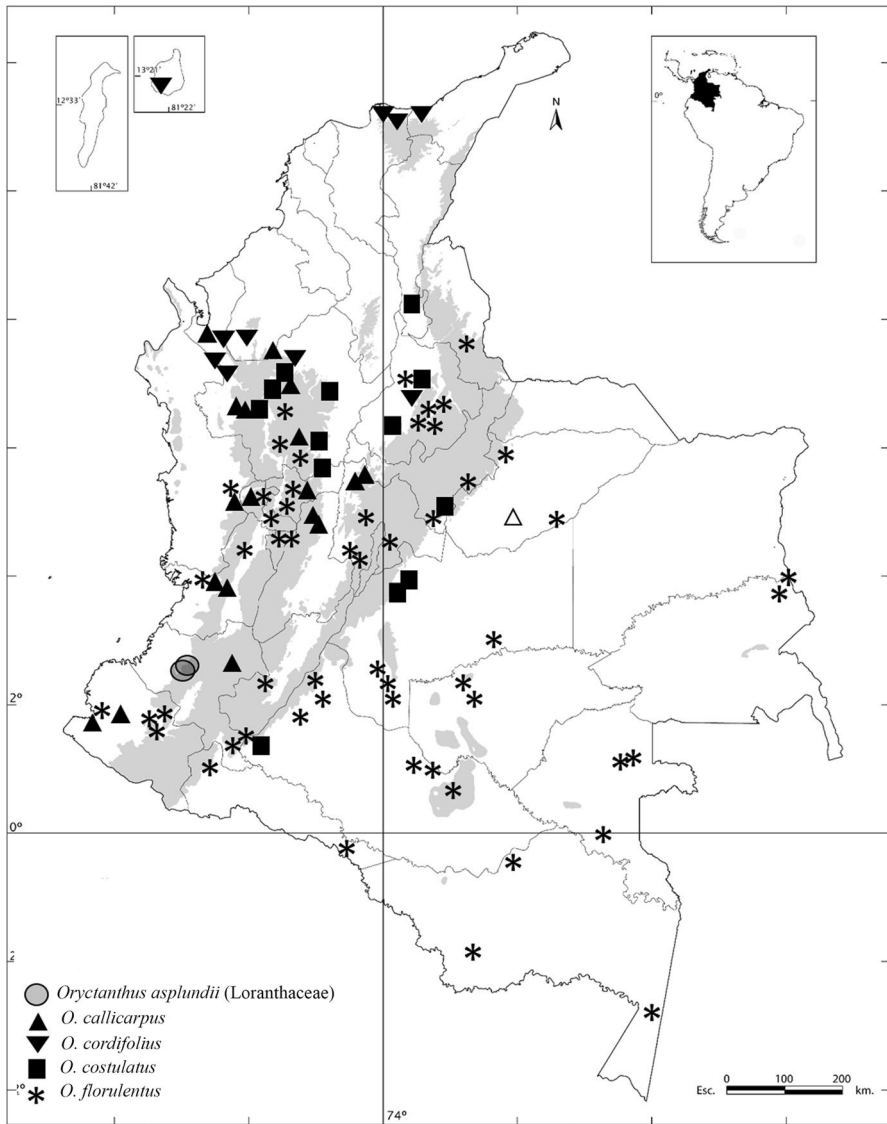
*K. spartioides* Klotzsch ex O.Berg (Fig. 3C, D; C. Saravia 2930, COL). Region I. Xerophytic thickets of the Caribbean plains, between 0–1000 m.

### 3. Cucurbitales. One family.

**Apodanthaceae** Tiegh. ex Takht. (Figs. 2 and 4). Two genera.



**Fig. 10** Large-flowered Loranthaceae (Santalales). **A–D.** *Gaiaedendron punctatum*, root hemiparasite (Boyacá: Villa de Leyva, 2560 m.a.s.l., *F. González 4314*). **A.** Dwarf individual. **B.** Leaves and inflorescences. **C.** Dichasium with opened central flower and preanthetic lateral flowers. **D.** Fruits and ruminant seeds. **E–H.** *Aetanthus mutisii*, stem hemiparasite on *Buddleja bullata* Kunth (Scrophulariaceae) (Boyacá: Aquitania, 3250 m.a.s.l., *F. González et al. 4480*). **E.** Habit; **F.** Inflorescences; **G.** Flowers visited by the hummingbird *Eriocnemis* sp.; **H.** Detail of distal portion of petals and staminal tube with nectar accumulation (arrow). **I–J.** *A. colombianus*, stem hemiparasite on *Viburnum cornifolium* Killip & A.C. Sm. (Boyacá: Belén, 3150 m.a.s.l., *F. González et al. 4795*). **I.** Flowers. **J.** Fruits. **K–L.** *Psittacanthus corderoi*, stem hemiparasite (Amazonas: La Pedrera, 100 m.a.s.l., *Z. Cordero & E. Tanimuka 818*; photo credit Z. Cordero). **M.** *P. krameri* (*Suaza-Gaviria 11*; photo credit V. Suaza), flowers. **N–O.** *P. acinarius*, stem hemiparasite, Casanare: Tauramena, 270 m.a.s.l. (*F. González 4282*). **N.** Fruits. **O.** Six-lobed, massive, green endosperm. **P–Q.** *Tristerix secundus*, stem hemiparasite on *Ageratina baccharoides* (Kunth) R.M. King & H. Rob. (Asteraceae)(Cundinamarca: Tausa, 3420 m.a.s.l., *F. González 4567*). **P.** Inflorescence; **Q.** Flowers visited by the hummingbird *Eriocnemis vestita*. Scale bars: 50 cm in **A**; 3 cm in **B**; 1 cm in **C**, **D**, **G**, **H**, **J**–**O**; 2 cm in **I**, **P**; 20 cm in **E**–**F**; 10 cm in **Q**



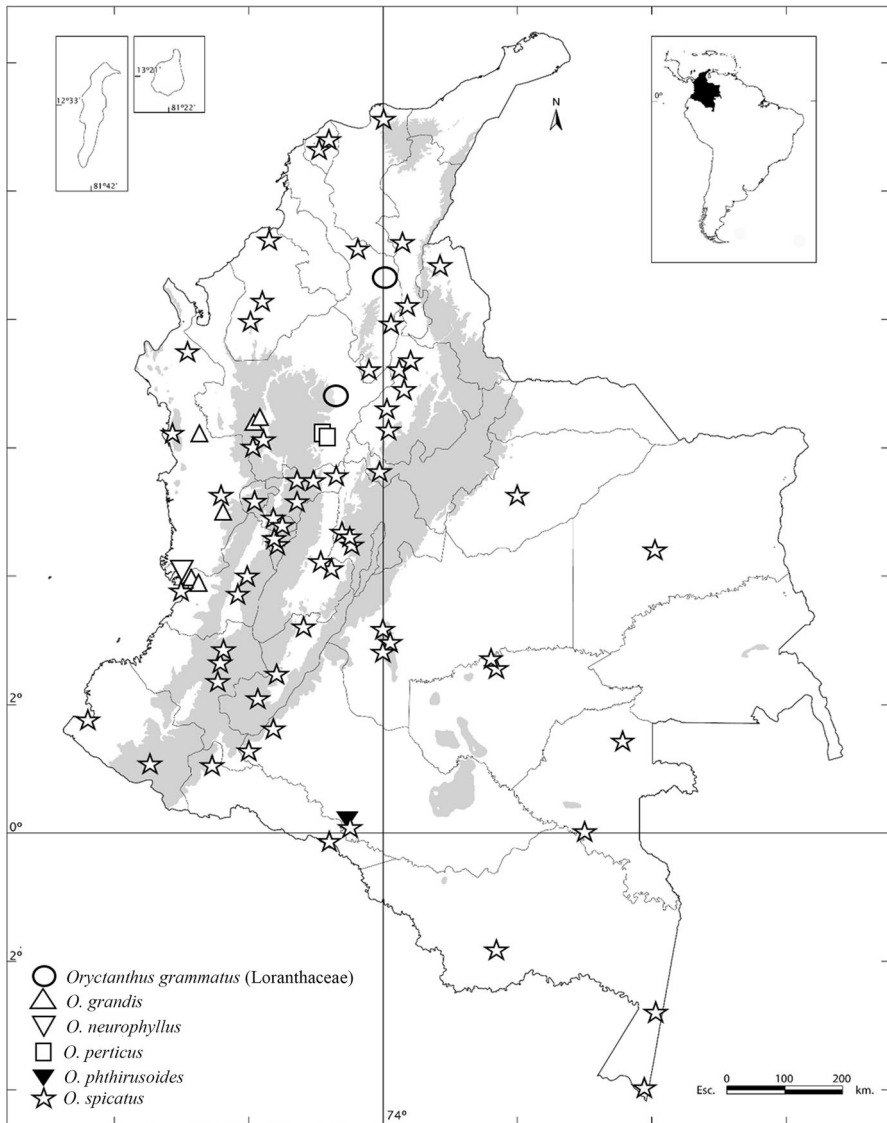
**Fig. 11** Map of distribution of *Oryctanthus* (Loranthaceae, first part) in Colombia

***Apodanthes*** Poit. One stem holoendoparasitic species.

*A. caseariae* Poit. (*N. Pabón Mora & F. González 494*, HUA; Fig. 4A–D). Regions II, IV, and V, at elevations between 0–1300 m. Primarily restricted to hosts from the genus *Casearia* (Salicaceae).

***Pilostyles*** Guill. Two stem holoendoparasitic species, one endemic to Colombia.

*P. boyacensis* F.González & Pabón-Mora (*F. González 4508*, holotype HUA; Fig. 4E–O). Xerophytic thickets from the Eastern Cordillera (Region III), at

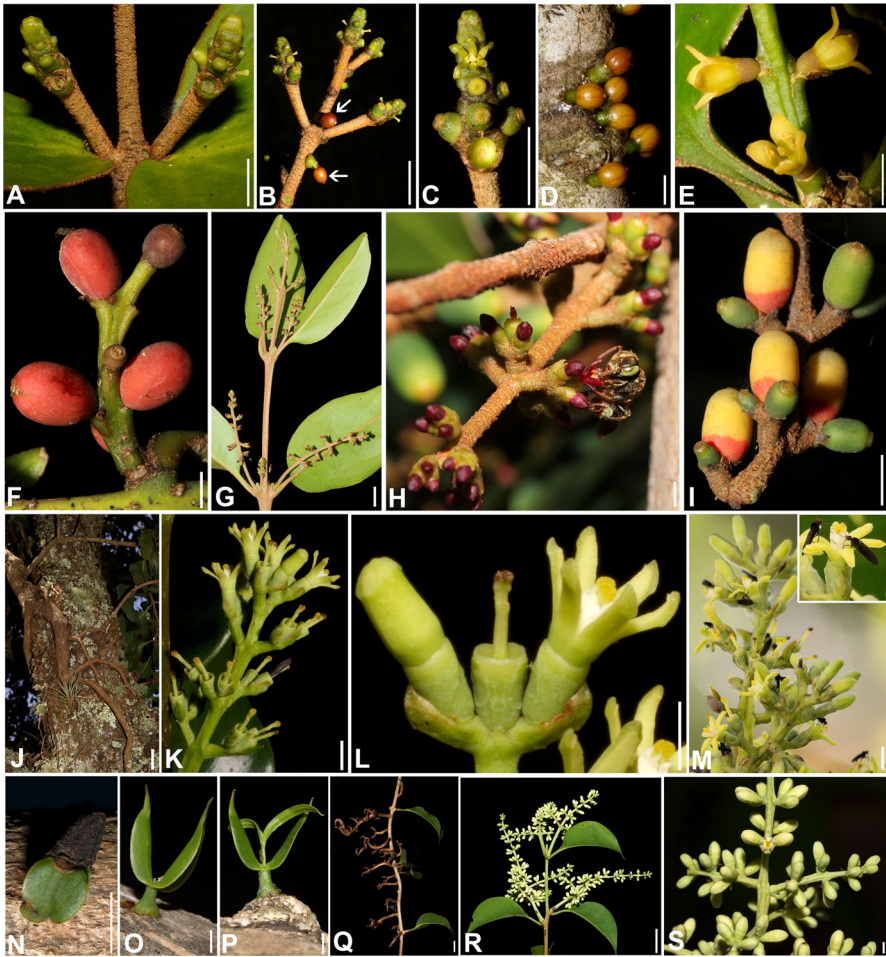


**Fig. 12** Map of distribution of *Oryctanthus* (Loranthaceae, second part) in Colombia

elevations between 2400 and 2700 m, exclusively parasitizing *Dalea cuatrecasasii* Barneby (Fabaceae). Endemic.

*P. cf. blanchetii* (Gardner) R. Br. (*I.J. Holton* 84, GH, K). Region III (Western Cordillera). This species is reported based on a single historical collection made at about 1000 m of elevation on February 24<sup>th</sup>, 1853, and remains to be rediscovered in the field and accurately identified (González & Pabón-Mora, 2014a, b). A detailed examination of the host in the two sheets available indicates that it corresponds to *Acaciella angustissima* (Mill.) Britton & Rose (Mimosoideae).





**Fig. 13** Small-flowered, stem hemiparasitic Lorantheaceae (Santalales). **A–D.** *Oryctanthus callicarpus* (Valle del Cauca: La Cumbre, 1650 m.a.s.l., *N. Pabón-Mora* et al. 382). **A.** Leaves and young inflorescences. **B.** Detail of inflorescence; arrows point to self-parasitic seedlings. **C.** Detail of flowers and forming fruits. **D.** Seedlings. **E–F.** *Peristethium archeri* (Antioquia: Santa Elena, 1890 m.a.s.l., *N. Pabón-Mora* et al. 381). **E.** Flowers at anthesis. **F.** Mature fruits. **G–I.** *Passovia pyrifolia* (Boyacá: Gachantivá, 2120 m.a.s.l., *F. González* 4713). **G.** Leaves and inflorescences. **H.** Flowers and floral visitor. **I.** Fruits. **J–M.** *P. pedunculata* (Boyacá: Villa de Leyva, 2820 m.a.s.l., *F. González* & *S. González* 4918). **J.** Epicortical roots on *Quercus humboldtii* (Fagaceae). **K.** Inflorescence. **L.** Dichasium with successive stages of floral anthesis and fruit formation. **M.** Floral visitors, Hybotidae (Diptera), two of them showed in detail (inset). **N–S.** *Struthanthus phillyreoides* (Casanare: Yopal, 350 m.a.s.l., *F. González* 4759). **N–P.** Seedlings at successive developmental stages. **Q.** Leaves and runner with secondary epicortical roots. **R.** Leaves and inflorescences. **S.** Detail of inflorescence with flower at anthesis. Scale bars: 1 cm in **A–C, Q, R**; 2 mm in **D, E, H, L, S**; 5 mm in **F, G, I, K**; 3 cm in **J**; 4 mm in **M–P**

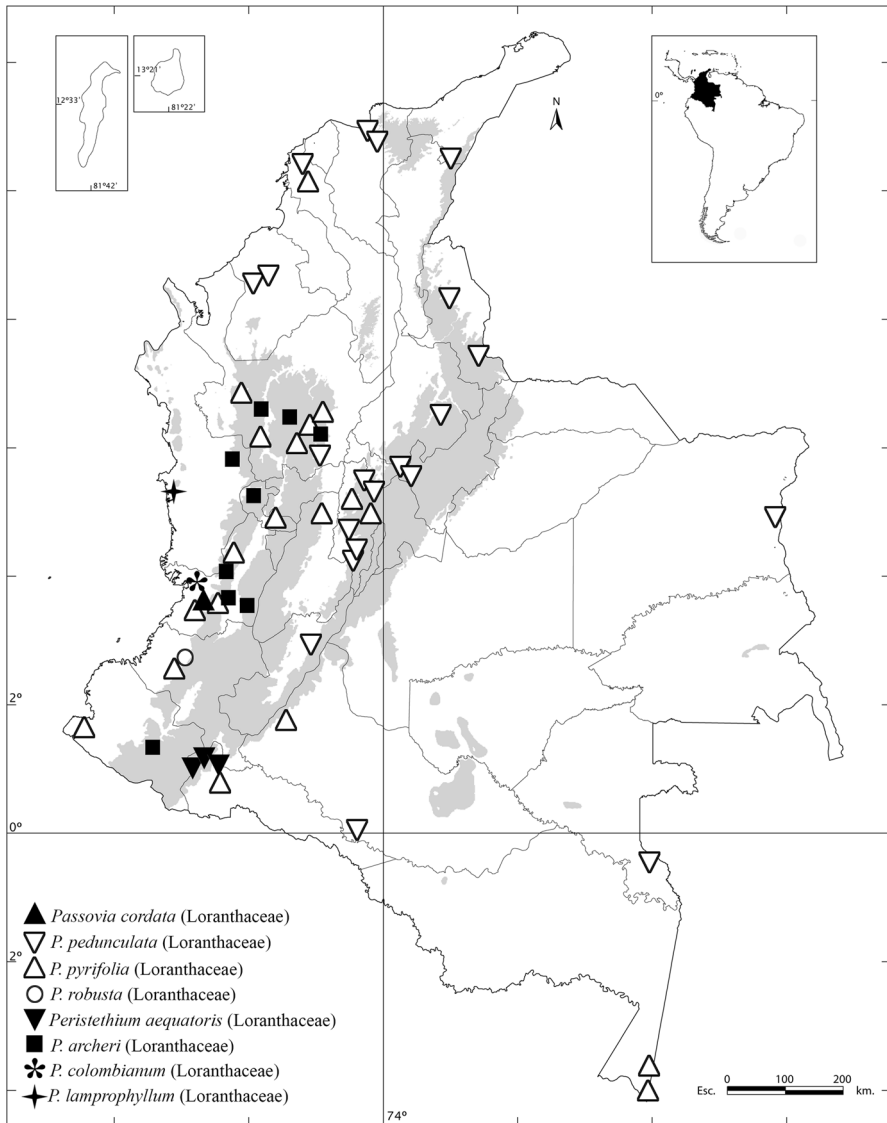


Fig. 14 Map of distribution of *Passovia*, *Peristethium* (part 1) and *Phthirusa* (Loranthaceae) in Colombia

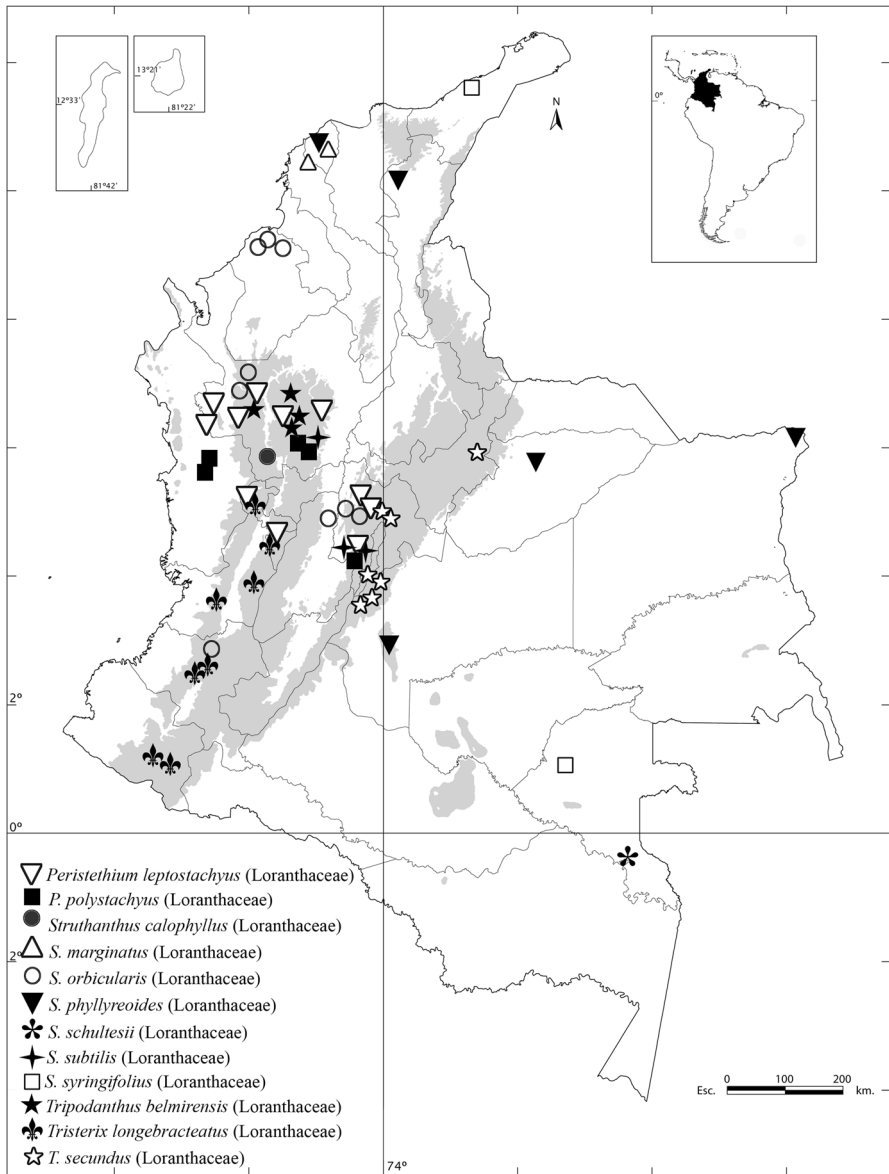
**4 Malvales:** One family.

#### Cytinaceae

A.Rich. (Figs. 2 and 5). One monotypic genus.

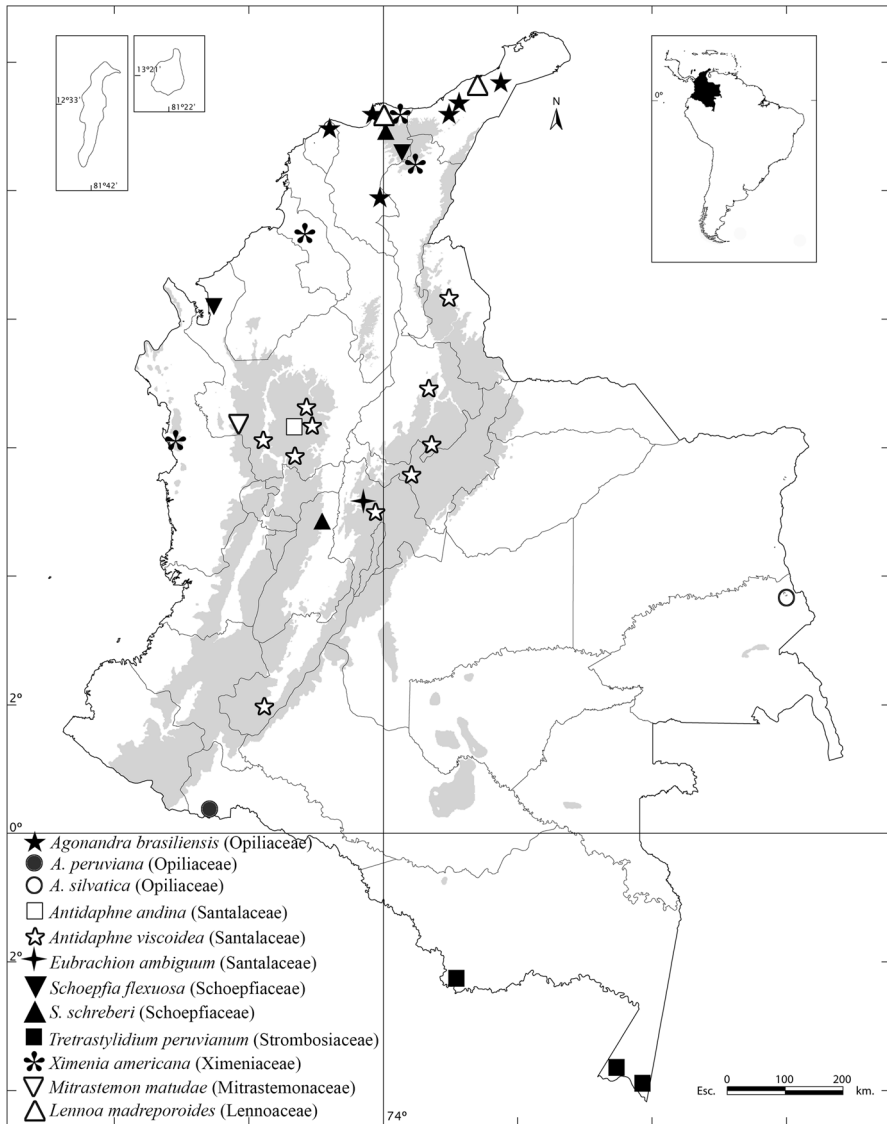
***Sanguisuga*** Fern.Alonso & H.Cuadros. One root holoexoparasitic species. This monospecific genus, endemic to Colombia, is the only member of the family found in South America.





**Fig. 15** Map of distribution of *Peristethium* (part 2), *Struthanthus*, *Tripodanthus* and *Tristerix* (Loranthaceae, four part) in Colombia

*S. caesarea* Fern.Alonso & H.Cuadros (*H. Cuadros et al.* 6333, holotype COL). Region I. Restricted to a few spots of dry *Bursera* forests of the Caribbean plains, below 500 m of elevation. Endemic.



**Fig. 16** Map of distribution of *Agonandra* (Opiliaceae), *Antidaphne* and *Eubracion* (Santalaceae), *Schoepfia* (Schoepfiaceae), *Tetrastylidium* (Strombosiaceae), *Ximenia* (Ximeniaceae), *Mitrastemon* (Mitrastemonaceae), and *Lennoa* (Ehretiaceae) in Colombia

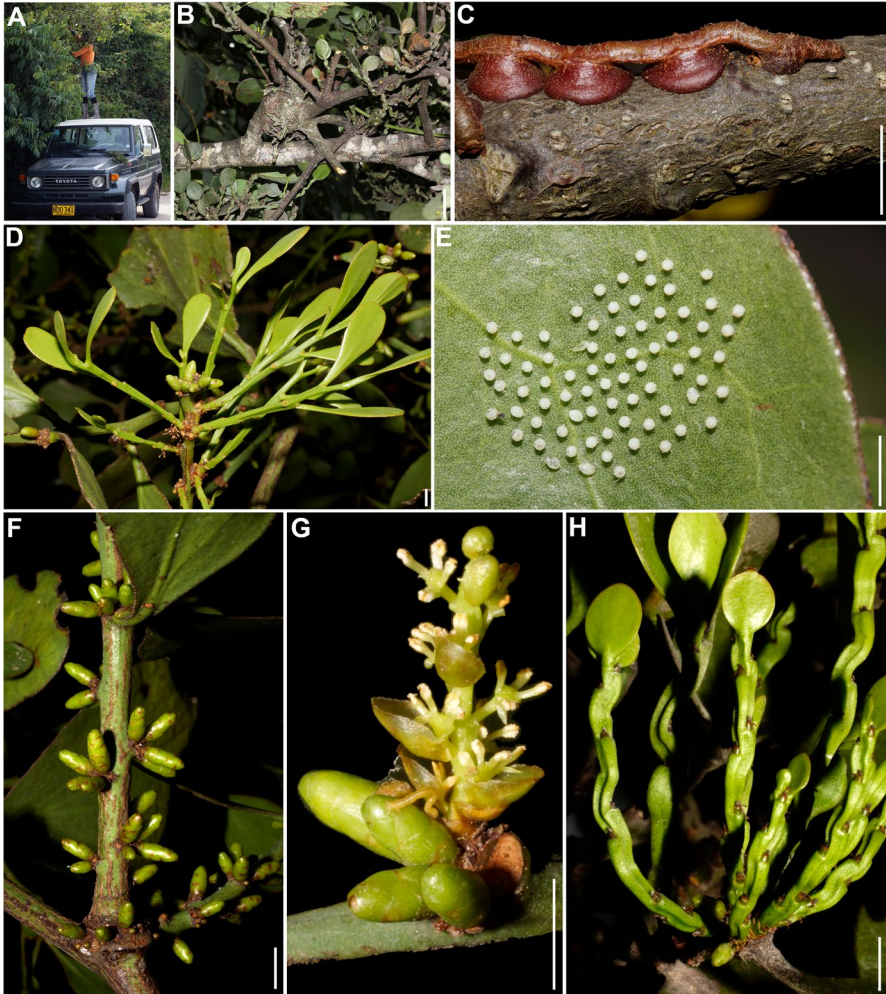
**5 Santalales:** Nine families, 28 genera, 189 species.

**Balanophoraceae** Rich. Six genera (Figs. 6 and 7).

***Corynaea*** Hook.f. One root holoparasitic species (Fig. 7A–C).

*C. crassa* Hook.f. (F. González 1604, COL). Region III. Restricted to primary or healthy secondary Andean forests, at elevations between 1800 and 2400 m.

***Helosis*** Rich. One root holoparasitic species (Fig. 7D–H).



**Fig. 17** Santalaceae, stem hemiparasite. *Antidaphne viscoidea* (Boyacá: Arcabuco, 2690 m.a.s.l., *F. González* 4645, ♂, 4645 A, ♀). **A**. Collecting site of carpellate individual. **B**. Primary haustorium of carpellate individual. **C**. Runner with secondary haustoria of staminate individual on branch of *Quercus humboldtii* (Fagaceae). **D**, **E**. Leaves; note (in **E**) egg cluster of *Archonias* or *Catasticta* sp. (Lepidoptera, Pieridae). **F**-**G**. Proliferative inflorescences of staminate individual; note (in **G**) anthetic flowers with highly reduced perianth. **H**. Proliferative, sinuous carpellate inflorescences. Scale bars: 2 cm in **B**; 5 mm in **C**-**H**

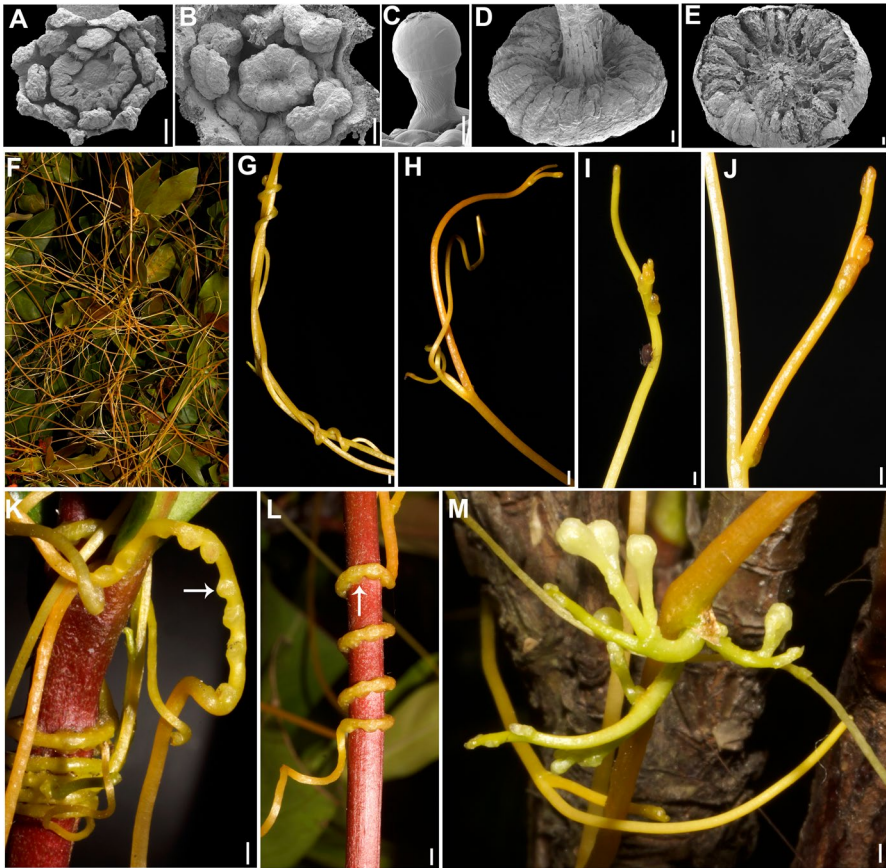
*H. cayennensis* (Sw.) Rich. ex Spreng. (*F. González et al.* 4705, COL). Regions II-V. A widespread species from wet lowland forests of the Pacific and Amazonian forests, gallery forests of the Orinoco plains, and sub-Andean forests, at elevations between 150 and 1120 m.

*Langsdorffia* Mart.. One root holoexoparasitic species (Fig. 7I-K).



**Fig. 18** Viscaceae, stem hemiparasites. **A-C.** *Dendrophthora avenia*. **A-B.** Habitat at subparamo and paramo belts (Boyacá: Toca, 3400–3500 m.a.s.l., F. González 4482). **C.** Detail of leaf bases, inflorescences and flowers. **D.** *D. clavata* (Boyacá: Duitama, 3200 m.a.s.l., F. González 1589), individual with mixed staminate and carpellate inflorescences. **E-F.** *D. lindeniata* (Antioquia: Santa Elena, m.a.s.l., N. Pabón-Mora 482). **E.** Main haustorium. **F.** Leaves and inflorescences. **G-M.** *Phoradendron nervosum* (Boyacá: Villa de Leyva, 2450 m.a.s.l., F. González 4554). **G-H.** Staminate individual (**G**) and detail of inflorescence with flower at anthesis (top right in **H**). **I-K.** Carpellate inflorescences with mature fruits. **L.** Dissected fruits showing green seeds. **M.** Seedlings. Scale bars: 5 mm in **C-E, K**; 1 cm in **F, I, J**; 5 cm in **G**; 2 mm in **L, M**





**Fig. 19** **A-E.** *Lennea madreporoides* (Ehretiaceae), root holoexoparasite; La Guajira: Dibulla, 20 m.a.s.l., scanning micrographs of flowers (**A**, **B**), clavate trichome of the outer perianth surface (**C**), and plurilocular ovary (**D**, **E**). **F-M.** *Cuscuta corymbosa* (Convolvulaceae), stem holoexoparasite (Boyacá: Corrales, 2560 m.a.s.l., *F. González 4794*). **F.** Habit. **G-L.** Filamentous stems; note (in **K**, **L**, arrows) lateral, discoid haustoria formed at intervals in stem portions in contact to the branch host. **M.** Inflorescence. Scale bars: 50  $\mu$ m in **A**, **B**, **D**, **E**; 5  $\mu$ m in **C**; 1 mm in **F-M**

*L. hypogaea* Mart. (*F. González 4712*, COL). Region III. Restricted to slightly disturbed sub-Andean to Andean forests of the Western, Central and Eastern cordilleras, at elevations between 1400 and 2750 m.

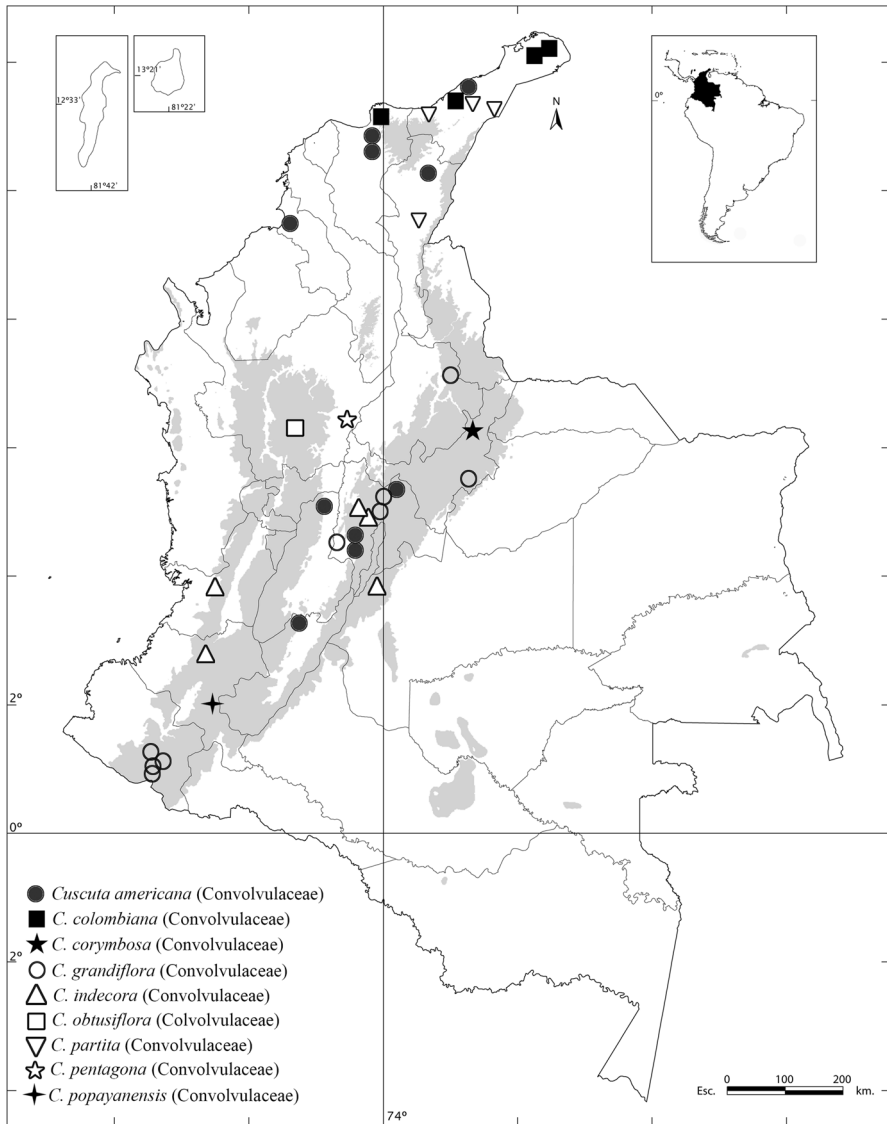
**Lophophytum** Scott & Endl. One root holoexoparasitic species.

*L. weddellii* Hook.f. (*F. Sander & Co. s.n.* without detailed locality, collected on Dec 28, 1890, K).

**Ombrophytum** Poepp. ex Endl. One root holoexoparasitic species.

*O. villamariensis* S. Guzm.-Guzm. (*D. Pérez 001*, isotype: COL). This species, endemic to Colombia, is known only from the type locality in Andean forests of the Central Cordillera of Colombia, at 2490 m (Region III). Endemic.

**Scybalium** Schott & Endl. One root holoexoparasitic species.



**Fig. 20** Map of distribution of *Cuscuta* (Convolvulaceae) in Colombia

*S. depressum* Eichler (R. Callejas et al. 3924, HUA). Region III. Species restricted to Andean and high-Andean forests of the Western and Central cordilleras, at elevations between 2000 and 3000 m.

**Cervantesiaceae** Nickrent & Der (Fig. 6). Two genera.

**Acanthosyris** (Eichler) Griseb. One root hemiparasitic species.

*A. glabrata* (Stapf) Stauffer ex Govaerts (*G. Rodríguez 1024*, COL). Region I. Restricted to dry forest remnants of the Caribbean plains, at elevations between 30 and 40 m.

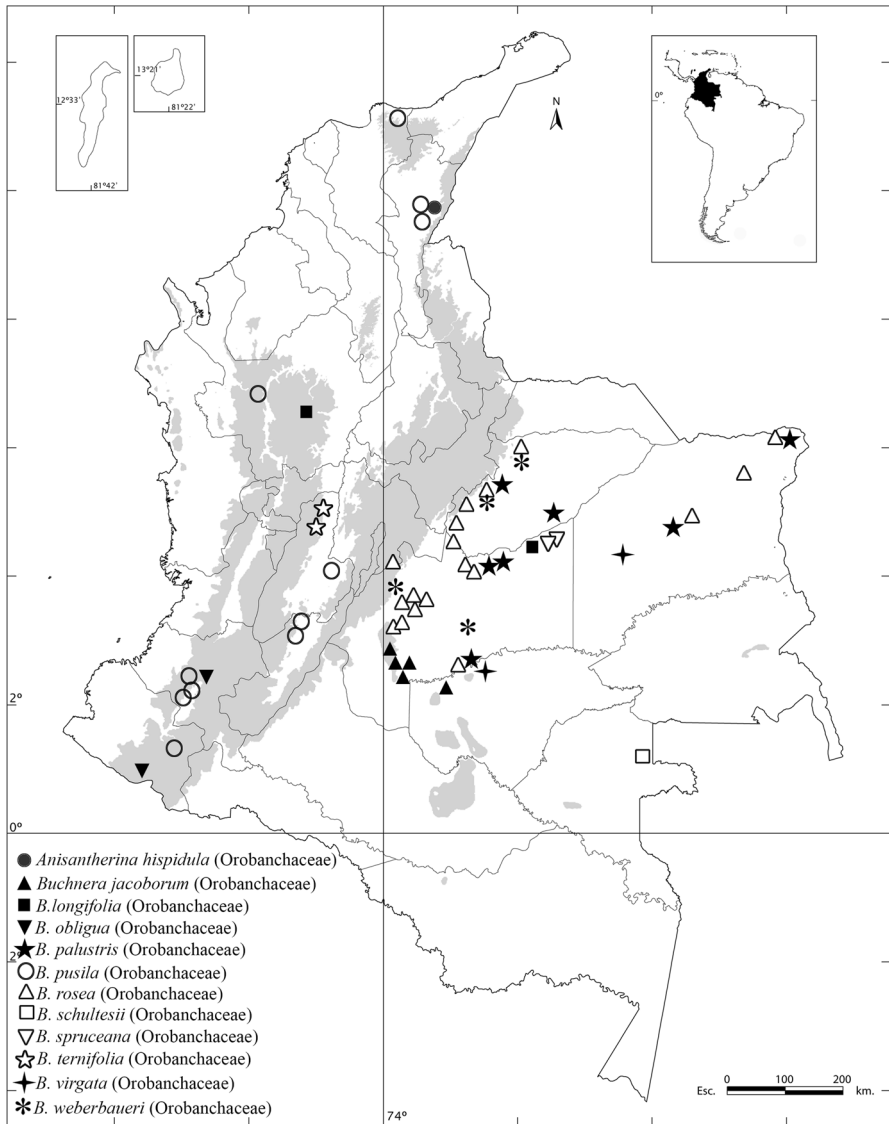


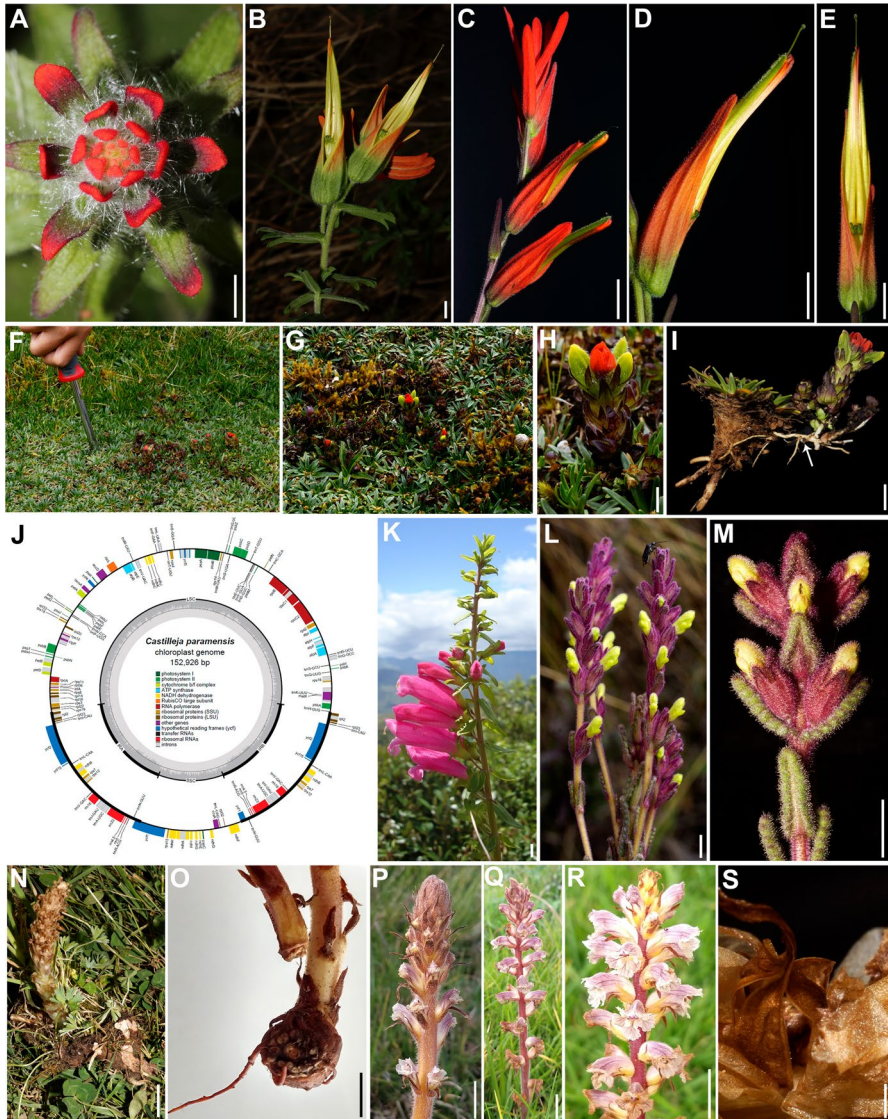
Fig. 21 Map of distribution of *Anisantherina* and *Buchnera* (Orobanchaceae) in Colombia

***Cervantesia*** Ruiz & Pav. Two root hemiparasitic species, one endemic to Colombia.

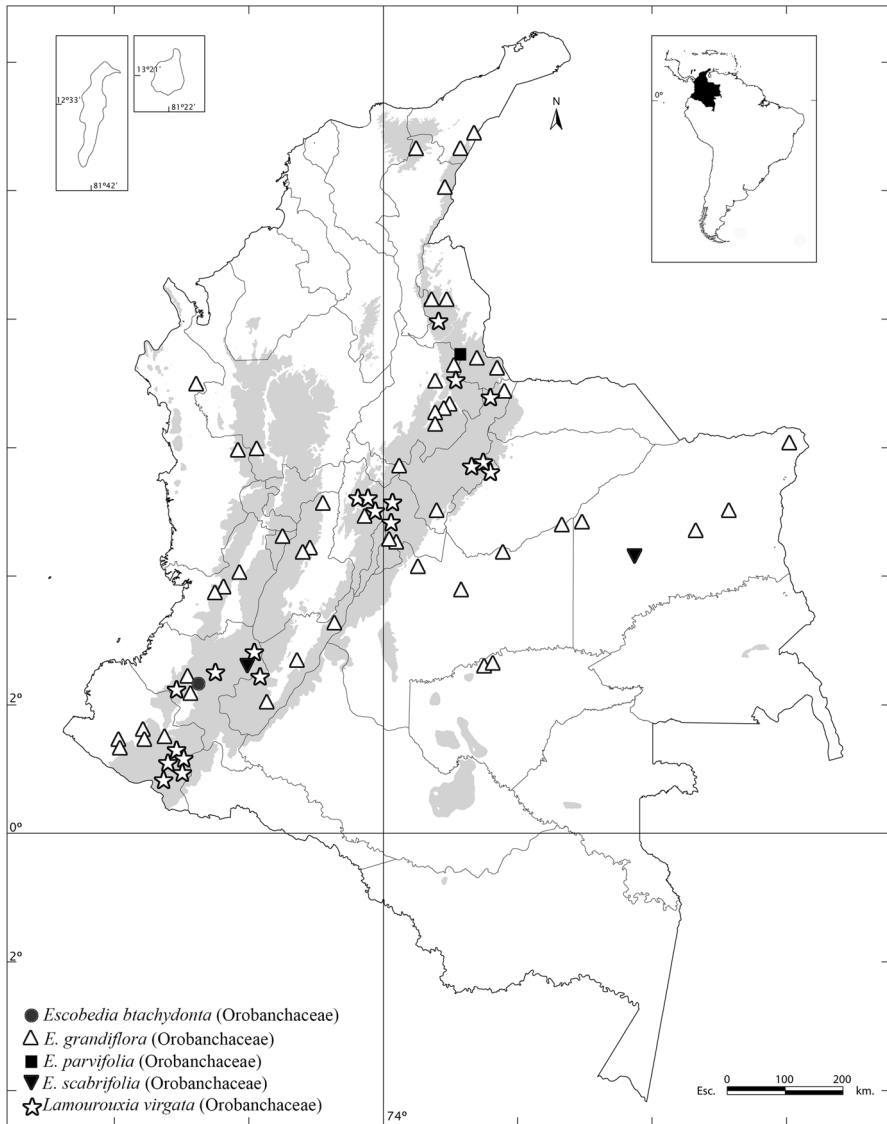
*C. macrocarpa* Cuatrec. (*J. Cuatrecasas 19330*, isotype COL). Region III. Cloud, Andean forests of the Central Cordillera, at elevations between 2640 and 2740 m. Endemic.

*C. tomentosa* Ruiz & Pav. (*E. Méndez 918*, COL). Region III. Cloud, high-Andean forests of the Central Cordillera, at elevations around 3420 m.





**Fig. 22** Orobanchaceae, facultative root hemiparasites. **A.** *Castilleja arvensis* (Boyacá: Villa de Leyva, 2460 m.a.s.l., F. González 4762). **B.** *C. fissifolia* (Cundinamarca: Guatavita, 2930 m.a.s.l., F. González 301), lobed leaves, bracts and flowers. **C–E.** *C. integrifolia*, details of bracts and flowers at lateral (**C**, **D**) and adaxial (**E**) view (Boyacá: Toca, 3120 m.a.s.l., F. González 4732). **F–J.** *C. paramensis*. **F–G.** Collection site at paramo cushion bogs (Boyacá: Sogamoso, 3875 m.a.s.l., F. González et al. 4478). **H.** Lobed leaves, bracts and flowers. **I.** Underground stolon (arrow) attached to the taproot of *Plantago rigida* Kunth. **J.** Plastome (from Fan et al. 2016). **K.** *Lamourouxia virgata* (Nariño: Túquerres, 3000 m.a.s.l., F. González et al. 4339). **L–M.** *Neobartsia santolinifolia* (Boyacá: Chiscas, 4020 m.a.s.l., F. González et al. 4751). **N–S.** *Orobanche minor* (Boyacá: Monguí, 3400 m.a.s.l., N. Pabón-Mora et al. 491). **N.** Habit. **O.** Underground stolon. **P–R.** Young (**P**) and fully formed (**Q**, **R**) racemes. **S.** Capsule. Scale bars: 5 mm in **A–E**, **H**, **I**, **P–R**; 1 cm in **K–O**; 1 mm in **S**

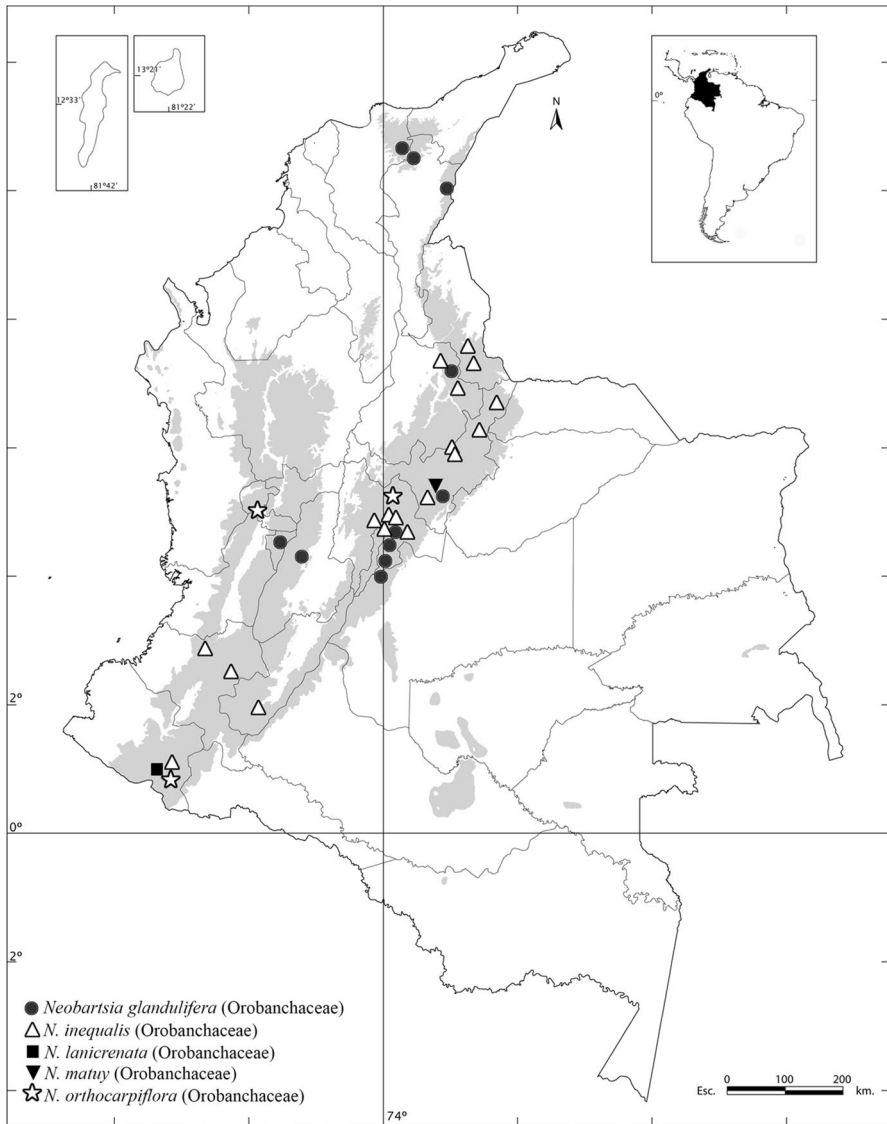


**Fig. 23** Map of distribution of *Escobedia* and *Lamourouxia* (Orobanchaceae) in Colombia

**Loranthaceae** Juss. Twelve genera, 84 species, 38 endemic to Colombia (Figs. 8, 9, 10, 11, 12, 13, 14, and 15).

*Aetanthus* (Eichler) Engl. Ten obligate, stem hemiparasitic species, eight endemic to Colombia (Figs. 10E–J and 26A).

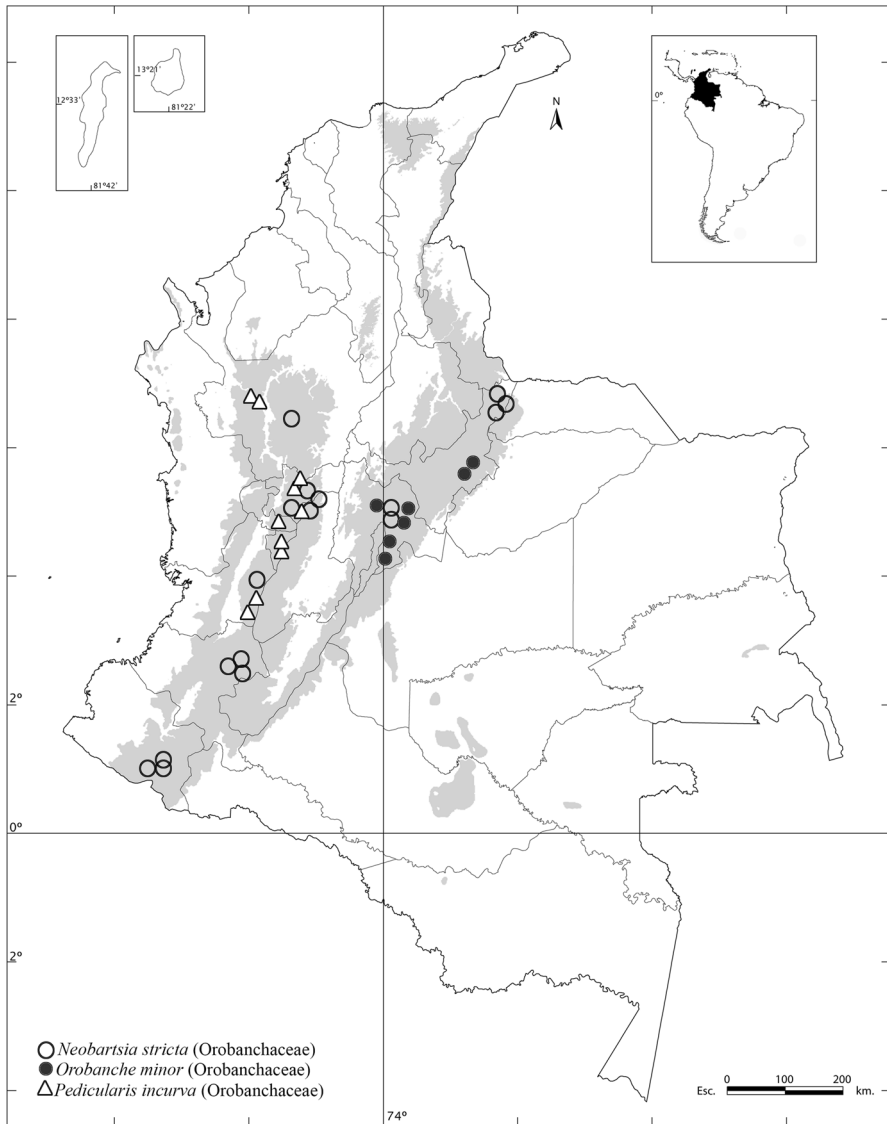
*A. alternifolius* F.J.Roldán, Carmona, Alzate & J.S.Murillo (*Hinestroza et al. 182*, holotype HUA). Region III. Known only from the type specimen, collected in oak (*Quercus humboldtii* Bonpl.; Fagaceae) high-Andean forests of



**Fig. 24** Map of distribution of *Neobartsia* (Orobanchaceae, first part) in Colombia. The widely distributed *N. laniiflora*, *N. pedicularoides*, *N. ramosa*, and *N. santolinifolia* are not including in the map

the Eastern Cordillera, nearby the Páramo de Santurbán, at elevations close to 2800 m. Endemic.

*A. colombianus* A.C.Sm. (*F. González et al.* 4795, COL). Regions I and III. Cloud Andean or high-Andean forests of the Eastern Cordillera, plus two disjunct populations in the Sierra Nevada de Santa Marta and the Serranía del Perijá, at elevations between 2100 and 3200 m. (Fig. 10I–J). Endemic.



**Fig. 25** Map of distribution of *Neobartsia* (Orobanchaceae, second part), *Orobanche*, and *Pedicularis* (Orobanchaceae) in Colombia. The widely distributed *N. laniflora*, *N. pedicularoides*, *N. ramosa*, and *N. santolinifolia* not included in map

*A. engelsii* Engl. (*Engels s.n.*, lectotype P). Region III. Without exact locality at the Eastern Cordillera. Endemic.

*A. megaphyllus* Kuijt (*F.J. Hermann 10901*; holotype US). Region III. Disjunct species of high-Andean forests to subpáramos of the Central (Antioquia) and Eastern (Norte de Santander) cordilleras, at elevations between 3000 and 3100 m. Endemic.

*A. mutisii* Engl. (F. González et al. 4480, COL). Region III. Disjunct species from cloud, high-Andean forests, subpáramos and páramos of the Western (Valle del Cauca) and Eastern (Boyacá and Cundinamarca) cordilleras, at elevations between 3000 and 4000 m (Fig. 10E–H). Endemic.

*A. nodosus* Engl. (G. Lozano-C. 3684, COL). Region III. Cloud Andean forests of the Western and Central cordilleras, at elevations between 2700 and 2800 m.

*A. ovalis* Rusby (J.H. Torres & P. Pinto 2957, COL). Region I. Endemic to the Sierra Nevada de Santa Marta, in cloud forests at elevations between 2400 and 2600 m. Endemic.

*A. sessilifolius* Kuijt (J. L. Zarucchi et al. 6501; isotype NY). Region III. Endemic to Andean forests of the northern slopes of the Western Cordillera, at elevations between 1900 and 2100 m. Endemic.

*A. trifolius* Kuijt (F.J. Roldán et al. 1082, HUA). Region III. Andean and high-Andean forests of the northern slopes of the Central Cordillera, at elevations between 2200 and 2900 m.

*A. validus* Kuijt (J. Cuatrecasas et al. 12393, isotype COL). Region III. Endemic to Andean forests of the northern slopes of the Eastern Cordillera, at elevations between 2000 and 2200 m. Endemic.

**Cladocolea** Tiegh. One obligate, stem hemiparasitic species (Fig. 8).

*C. coriacea* Kuijt (F. González 3050-A, COL). Region IV. Restricted to gallery forests of the Orinoco plains, at elevations between 180 and 200 m. This is the first record of the species for the Flora of Colombia.

**Gaiadendron** G.Don f. One obligate, root hemiparasitic species (Figs. 9 and 10A–D).

*G. punctatum* (Ruiz & Pav.) G.Don (F. González 4314, COL). Regions I and III. Widespread through Andean and high-Andean forests, and páramos of the Western, Central and Eastern cordilleras, and the Sierra Nevada de Santa Marta, at elevations between 1500 and 3500 m.

**Maracanthus** Kuijt. One obligate, stem hemiparasitic species (Fig. 9).

*M. chlamydatus* (Rizzini) Kuijt (A. Sudgen 119, COL). Region I. Dry forests of the Caribbean plains, at elevations between 15–100 m.

**Oryctanthus** Eichler. Eleven obligate, stem hemiparasitic species, four of them endemic to Colombia (Figs. 11, 12, 13A–D, and 26B).

*O. asplundii* Kuijt (F. González et al. 2966A, COL). Region III. Cloud, Andean forests of the Western Cordillera, at elevations between 1500 and 1700 m.

*O. callicarpus* Kuijt (N. Pabón-Mora et al. 382, HUA). Regions II and III. Lowland, pluvial forests, and sub-Andean and Andean forests of the Western, Central and Eastern cordilleras, at elevations between 0 and 2050 m (Fig. 13A–D).

*O. cordifolius* (C.Presl) Urb. (J.N. Díaz & F. González 129, COL). Regions I (dry forests of the Caribbean plains and the Archipelago of San Andrés and Old Providence, II, and III, at elevations between 10 and 1500 m.

*O. costulatus* Rizzini (F.J. Roldán 1953, HUA). Regions III, IV, and V, at elevations between 100 and 1800 m.

*O. florulentus* Urb. (J. Cuatrecasas 26020, COL). Regions II (pluvial forests), III (sub-Andean and Andean forests of the Western, Central and Eastern cordilleras),

IV (thickets and gallery forests of the Orinoco plains) and V (Amazonian forests), at elevations between 150 and 2500 m.

*O. grammatus* Kuijt (*H.M. Curran s.n.*, holotype US). Region I. Caribbean dry forests, and inter-Andean xerophytic thickets of the northern Magdalena valley, at elevations below 300 m. Endemic.

*O. grandis* Kuijt (*E.P. Killip & J. Cuatrecasas 38974*, isotype COL). Region II. Pluvial forests at elevations between 10 and 1500 m. Endemic.

*O. neurophyllus* Kuijt (*A.H. Gentry et al. 53663*, isotype UC). Region II. Pluvial forests, at elevations between 50 and 500 m. Endemic.

*O. perticus* Carmona, F.J. Roldán, Alzate & J.S. Murillo (*C.A. Loaiza 182*, holotype HUA). Region III. Known only from the type locality, in sub-Andean forests of the northern end of the Central Cordillera, at elevations between 1000 and 1500 m. Endemic.

*O. phthirusoides* Rizzini (*M. Arbeláez et al. 525*, HUA). Region V. Amazonian forests at elevations between 100 and 400 m.

*O. spicatus* (Jacq.) Eichler (*C. Sastre 2234*, COL). Widespread throughout regions I, II, III, IV, and V, at elevations between 20 and 2600 m.

***Passovia*** H. Karst. Four obligate, stem hemiparasitic species, one endemic to Colombia. (The taxonomic outline of this genus follows Caires et al. 2021). (Figs. 13G–I and 14).

*P. cordata* Kuijt (*A.H. Gentry et al. 53723*, holotype UC). Region II. Pluvial forests at elevation around 500 m. Endemic.

*P. pedunculata* (Jacq.) Kuijt (*F. González & S. González 4918*, COL). Andean forests from the Eastern Cordillera, at elevations between 1800–2600 m (Region III), in addition to three scattered locations at the Caribbean plains (Region I) and two collections from the Amazonian forests below 500 m of elevation (Region V) (Fig. 13J–M).

*P. pyrifolia* (Kunth) Tiegh. (*F. González 4713*, COL). Region I (dry forests of the Caribbean plains, at elevations below 300 m), III (Andean forests at elevations between 1800 and 2500 m), and V (Amazonian forests below 400 m) (Fig. 13G–I).

*P. robusta* (Rusby) Kuijt (*I.F. Holton 651*, K). Region III. Sub-Andean forests at about 1000 m of elevation.

***Peristethium*** Tiegh. Six obligate, stem hemiparasitic species, two of them endemic to Colombia (Fig. 13E–F and 14).

*P. aequatoris* (Kuijt) Kuijt (*J. Cuatrecasas 11540*, COL). Region III. Eastern slopes of the department of Putumayo, at elevations between 1500–2200.

*P. archeri* (A.C. Sm.) Kuijt (*N. Pabón-Mora et al. 381*, HUA). Regions II and III. Pluvial forests and sub-Andean forests of the Western and Central cordilleras, at elevations between 80 and 2200 m (Fig. 13E–F).

*P. colombianum* Kuijt (*D. Macías & B. R. Ramírez 5001*, holotype CAUP). Region II. Pluvial forests at elevations below 800 m. Endemic.

*P. lamprophyllum* Kuijt (*H.P. Fuchs & L. Zanella 22060*, isotype F). Region II. Pluvial forests, at elevations around 50 m. Endemic.

*P. leptostachyum* (Kunth) Tiegh. (*J.J. Triana 4586/1*, COL). Regions II, III and V. Pluvial, sub-Andean and Amazonian forests, at elevations between 40 and 1800 m.

*P. polystachyus* (Ruiz & Pav.) Kuijt (*H. Daniel 6262*, COL). Regions II and III. Pluvial and sub-Andean forests at elevations between 500 and 1700 m.



***Phthirusa*** Mart. Three obligate, stem hemiparasitic species, two of them endemic to Colombia (Fig. 9).

*P. exilis* Kuijt (F.J. Roldán 750, HUA). Region III. Sub-Andean to high-Andean forests at the northern end of the Western and Central cordilleras, at elevations between 1600 and 2400 m. Endemic.

*P. hutchisonii* (Kuijt) Kuijt (F.J. Roldán et al. 871, HUA). Region III. Sub-Andean and Andean forests of the Western, Central and Eastern cordilleras, at elevations between 1300 and 2300 m.

*P. rhynchophylla* (Kuijt) Kuijt (F.J. Roldán et al. 1141, HUA). Region III. Disjunct species in cloud, Andean forests of the Western (Antioquia) and the Eastern (Boyacá) cordilleras, at elevations between 1600 and 2800 m. Endemic.

***Psittacanthus*** Mart. Thirty-seven obligate, stem hemiparasitic species, 17 of them endemic to Colombia (Figs. 10K–O and 26C).

*P. acinarius* Mart. (F. González 4282, COL). Regions I, III, IV and V. Sclerophyllous, lowland and gallery forests, as well as in Amazonian and sub-Andean forests, at elevations between 300 and 1000 m (Fig. 10N, O).

*P. antioquiensis* Kuijt (F.J. Roldán 1550, isotype HUA). Region III. Cloud, Andean forests, at elevations between 1600 and 1850 m. Endemic.

*P. biternatus* (Hoffmans.) G.Don. (R. Liesner 9135, COL). Region V. Sclerophyllous, Amazonian forests, at elevations between 100 and 150 m.

*P. bolbocephalus* Kuijt (J.L. Zarucchi 1205, LEA). Region V. Sclerophyllous, Amazonian forests, at elevations between 300 and 350 m.

*P. carinatus* Kuijt (E.L. Core 450, holotype US). Region III. Cloud, high-Andean forests, at elevations between 2800 and 3100 m. Endemic.

*P. cinctus* Mart. (B. Maguire & J. Wurdack 35668, COL). Region V. Sclerophyllous, Amazonian forests, at elevations between 120 and 500 m.

*P. clusiifolius* Eichler (B. Maguire 41437, COL). Region V. Sclerophyllous, Amazonian forests, at elevations between 100 and 150 m.

*P. complanatus* Kuijt (R. Callejas et al. 7844, isotype HUA). Region III. Cloud, high-Andean forests, at elevations between 3000 and 3200 m. Endemic.

*P. corderoi* F.González, F.J. Roldán & Pabón-Mora (Z. Cordero & E. Tanimuka 818, holotype COL). Region V. Sclerophyllous, Amazonian forests, at elevations around 100 m (Fig. 10K, L). Endemic.

*P. crassicostatus* Kuijt (F.J. Roldán 1218, isotype COL) Regions II and III. Pluvial and humid, sub-Andean forests, at elevations between 800 and 900 m. Endemic.

*P. crassifolius* Mart. s.l. (included *P. baguensis* Kuijt; see Dettke & Caires, 2021; V. Wijninga & Quintero 605, COL). Region V. Sclerophyllous, Amazonian forests, at elevations between 200 and 350 m.

*P. crassinervis* Kuijt (J. Cuatrecasas 9058, COL). Region III. Cloud, sub-Andean forests, at elevations between 1000 and 1300 m. Endemic.

*P. cucullaris* (Lam.) Blume (E. Pérez-Arbeláez 693, COL). Regions III, IV and V. Sclerophyllous, gallery forests of the Orinoco plains and Amazonian forests, and sub-Andean forests at elevations between 100 and 1500 m.



*P. cyclophyllus* Kuijt (*P. Silverstone-Sopkin et al. 4525*, holotype CUVC). Regions II, III, and V. Pluvial and cloud, sub-Andean to Andean forests, at elevations between 500 and 2600 m. Endemic.

*P. dilatatus* A.C.Sm. (*R. Callejas et al. 8449*, HUA). Region III. Cloud belts of the sub-Andean and Andean forests, at elevations between 1200 and 2800 m.

*P. eucalyptifolius* Blume (*R.E. Schultes et al. 10210*, US). Region V. Sclerophyllous Amazonian forests, at elevations between 100 and 150 m.

*P. geniculatus* Kuijt (*A.H. Gentry et al. 22115*, F). Region V. Sclerophyllous Amazonian forests, at elevations between 100 and 200 m.

*P. gigas* Kuijt (*A.H. Gentry 48280*, isotype COL). Region II. Pluvial forests, at elevations between 5 and 50 m. Endemic.

*P. hamulifer* Kuijt (*L. Albert et al. 1627*, HUA). Regions II and III. Pluvial and sub-Andean forests, at elevations between 100 and 1800 m.

*P. irwinii* Rizzini (*R.E. Schultes & I. Cabrera 15029*, NY). Region V. Sclerophyllous, Amazonian forests, at elevations between 100 and 300 m.

*P. krameri* Kuijt (*V. Suaza-Gaviria 11*, HUA). Regions II and III. Pluvial and sub-Andean forests, at elevations between 100 and 1000 m (Fig. 10M).

*P. longerectus* F.J.Roldán & Alzate (*F.J. Roldán et al. 1155*, holotype HUA). Region III. Cloud, Andean to high-Andean forests, at elevations between 2550 and 2700 m. Endemic.

*P. micrantherus* Kuijt (*M. Monsalve 1383*, holotype UC). Region II. Pluvial forests, at elevations around 100 m. Endemic.

*P. microphyllus* Kuijt (*F.J. Roldán et al. 1149*, isotype HUA). Region III. Cloud, high-Andean forests, subpáramos and páramos, at elevations between 2800 and 3200 m. Endemic.

*P. ophiocephalus* Kuijt (*R.E. Schultes & I. Cabrera 15787*, holotype US). Region V. Sclerophyllous Amazonian forests, at elevations around 200 m. Endemic.

*P. pentaphyllos* Kuijt (*J.L. Zarucchi et al. 6765*, isotype HUA). Region III. Cloud, sub-Andean forests, at elevations between 1000 and 1100 m. Endemic.

*P. peronopetalus* Eichler (*Fernández 2036*, US). Regions III and V. Amazonian and sub-Andean forests, at elevations between 200 and 1350 m.

*P. rhynchanthus* (Benth.) Kuijt (*J. Brand & A. Cogollo 99*, COL). Regions I and II. Dry to wet forests, at elevations between 10 and 100 m.

*P. robustus* Mart. (*M. Monsalve 173*, COL). Region V. Sclerophyllous Amazonian forests, at elevations between 100 and 400 m.

*P. roldanii* Kuijt (*F.J. Roldán et al. 796*, isotype HUA). Region I. Dry forests, at elevations between 20 and 70 m.

*P. rotundatus* Kuijt (*F.J. Roldán et al. 817*, isotype HUA). Region III. Cloud, sub-Andean forests, at elevations between 1000 and 1500 m. Endemic.

*P. schultesii* Kuijt (*R.E. Schultes & I. Cabrera 15111*, isotype GH). Region V. Sclerophyllous, Amazonian forests, at elevations around 300 m. Endemic.

*P. smithii* Kuijt (*H.H. Smith 1491*, holotype NY). Region I. Dry forests, at elevations between 160 and 170 m. Endemic.

*P. stergiosii* Kuijt (*J. Wurdack & Adderley 43213*, isotypes F, US). Region V. Sclerophyllous Amazonian forests, at elevations between 100 and 150 m.

*P. sulcatus* Kuijt (R.E. Schultes & I. Cabrera 13351, holotype US). Region V. Sclerophyllous Amazonian forests, at elevations between 250 and 700 m. Endemic.

*P. ternatus* Kuijt (F. Alzate et al. 259, isotype HUA). Region III. Cloud, sub-Andean to Andean forests, at elevations between 1450 and 1750 m.

*P. truncatus* Kuijt (A. Rudas et al. 7153, COL). Regions II, III, V. Pluvial, sub-Andean and Amazonian forests, at elevations between 400 and 1800 m.

***Struthanthus*** Mart. Seven obligate, stem hemiparasitic species, one of them endemic to Colombia (Figs. 13N–S and 15).

*S. calophyllus* A.C. Sm. (F.J. Roldán et al. 1064, COL). Region III. Sub-Andean forests, at elevations between 1400 and 1500 m.

*S. marginatus* (Desr.) G. Don (A. Dugand 5793, COL). Region I. Dry forests and savannas, at elevations below 400 m.

*S. orbicularis* (Kunth) Eicher (F.J. Roldán 1653, COL). Regions I, II and III. Savanna vegetation, gallery forests, and sub-Andean forests, at elevations between 40 and 1200 m.

*S. phillyreoides* (Kunth) G. Don (F. González 4759, COL). Regions I, IV. Savanna vegetation and gallery forests, at elevations around 200 m. (Fig. 13N–S).

*S. schultesii* Kuijt (R.E. Schultes 16996, isotype COL). Region V. Sclerophyllous. Amazonian forests, at elevations between 150 and 300 m. Endemic.

*S. subtilis* Kuijt (F.J. Roldán 1222, COL). Region III. Cloud sub-Andean and Andean forests, at elevations between 1600 and 2600 m.

*S. syringifolius* Mart. (J. Cuatrecasas 7065, COL). Regions I and V. Dry Caribbean forests, and sclerophyllous Amazonian forests, at elevations between 100 and 240 m.

***Tripodanthus*** Tiegh. One obligate, stem hemiparasitic species endemic to Colombia (Fig. 15).

*T. belmirensis* F.J. Roldán & Kuijt (R. Fonnegra & D. Tuberquia 4576, holotype HUA). Region III. Subpáramo and páramo vegetation of the Western and the Central cordilleras, at elevations between 3000 and 3130 m of elevation. Endemic.

***Tristerix*** Mart. Two obligate, stem hemiparasitic species, one of them endemic to Colombia (Figs. 10P, Q and 15).

*T. longibracteatus* (Desr.) Barlow & Wiens (F. González 4270, COL). Region III. High-Andean forests of the Western and Central cordilleras (Region III), at elevations between 3100 and 3700 m.

*T. secundus* (Benth.) Kuijt (F. González 4567, COL). Region III. Subpáramo and páramo vegetation of the Eastern Cordillera, at elevations between 2800 and 4000 m (Fig. 10P, Q). Endemic.

**Opiliaceae** Valetton. One genus.

***Agonandra*** Miers ex Benth. Three root hemiparasitic species (Fig. 16).

*A. brasiliensis* Benth. & Hook.f. (A. Dugand 5662, COL) Region I. Dry forests below 400 m of elevation.

*A. peruviana* Hiepko. Region V. Sclerophyllous Amazonian forests below 400 m of elevation.

*A. silvatica* Ducke (A. Rudas et al. 4836, COL). Region IV. Gallery forests below 210 m of elevation.

**Santalaceae** R. Br. Two genera (Figs. 16 and 17).

**Antidaphne** Poepp. & Endl. Two obligate, stem hemiparasitic species.

*A. andina* Kuijt (*F.J. Roldán 1894*, HUA). Region III. High-Andean forests, at elevations between 2800 and 3200 m.

*A. viscoidea* Poepp. & Endl. (*F. González 4645*, ♂, 4645 A, ♀, COL). Region III. Sub-Andean to high-Andean forests and páramo vegetation, at elevations between 900 and 3700 m (Fig. 17).

**Eubrachion** Hook.f. One obligate, stem hemiparasitic species.

*E. ambiguum* Engl. (*J.L. Fernández 23697*, COL). Region III. Andean and high-Andean forests, at elevations between 2600 and 3000 m.

**Schoepfiaceae** Blume. One genus (Fig. 16).

**Schoepfia** Schreb. Two root hemiparasitic species.

*S. flexuosa* Roem. ex Schult. (*W. Purdie s.n.*, GH). Regions I and II (Uraba region). Pluvial forests, at elevations below 100 m.

*S. schreberi* J.F.Gmel. (*J. Goudot s.n.*, P). Regions I and III (Magdalena valley). Dry forests, at elevations between 50 and 500 m.

**Strombosiaceae** Tiegh. One genus (Fig. 16).

**Tetrastylidium** Engl. One root hemiparasitic species.

*T. peruvianum* Sleumer (*J.J. Pipoly 16296*, MO). Region V. Sclerophyllous Amazonian forests, at elevations below 100 m.

**Viscaceae** Batsch. Two genera, 88 species (Figs. 18 and 27).

**Dendrophthora** Eichler. Twenty-two obligate, stem hemiparasitic species, three of them endemic to Colombia (Figs. 18A–F and 27A).

*D. amalfiensis* Kuijt (*R. Callejas et al. 9135*, isotype HUA). Region III. Cloud, sub-Andean forests, at elevations between 1300 and 1900 m. Endemic.

*D. ambigua* Kuijt (*J. Cuatrecasas 18902*, isotype A). Region III. Cloud, high-Andean forests and subpáramo and páramo vegetation, at elevations between 3300 and 3900 m.

*D. avenia* (Trel.) Kuijt (*F. González 4482*, COL). Region III. Cloud, Andean forests and subpáramo and páramo vegetation, at elevations between 2400–3550 m (Fig. 18A–C).

*D. chrysostachya* Urb. (*E. Pérez-Arbeláez & J. Cuatrecasas 5911*, COL). Region III. Cloud, high-Andean forests and subpáramo and páramo vegetation, at elevations between 3100 and 3500 m.

*D. clavata* Urb. (*F. González 1589*, COL). Regions III (sub-Andean, Andean and high-Andean forests, and subpáramo and páramo vegetation) and IV (gallery forests), at elevations between 500 and 3700 m. Likely the parasitic angiosperm with the broadest elevational distribution in Colombia (Fig. 18D).

*D. costaricensis* Urb. (*B. Ramírez 16288*, COL). Region III. Cloud, Andean to high-Andean forests, at elevations between 2400 and 3200 m.

*D. elegantissima* Kuijt (*F.J. Roldán et al. 1895*, HUA). Region III. Cloud, high-Andean forests, and subpáramo and páramo vegetation at elevations between 3000 and 3550 m.

*D. elliptica* Krug & Urb. (*J. Cuatrecasas 25368*, COL). Regions III (sub-Andean and Andean forests) and IV (gallery forests), at elevations between 850 and 2300 m.

*D. fendleriana* (Eichler) Kuijt (R. Callejas et al. 7907, HUA). Region III. Cloud, Andean forests, at elevations between 2000 and 2100 m.

*D. lindeniana* Tiegh. (N. Pabón-Mora 482, HUA). Region III. Cloud, Andean to high-Andean forests and subpáramo vegetation, at elevations between 1600 and 3300 m (Fig. 18E, F).

*D. lueri* Kuijt (G. Lozano 6704, COL). Region III. Cloud, Andean forests, at elevations between 2900 and 3200 m.

*D. macbridei* (Standl.) Kuijt (P. Franco 2752, COL). Region III. Cloud, Andean forests, at elevations between 2000 and 2400 m.

*D. obliqua* (C. Presl) Wiens (E. Pérez-Arbeláez 8343, COL). Region III. Cloud, sub-Andean to Andean forests, at elevations between 730 and 2900 m.

*D. paucifolia* (Rusby) Kuijt (F.J. Roldán et al. 826, HUA). Region III. Cloud, Andean to high-Andean forests, at elevations between 2500 and 3300 m.

*D. pearcei* (Rusby) Kuijt (S. Díaz-Piedrahíta 4232, COL). Region III. Cloud, Andean to high-Andean forests and subpáramo and páramo vegetation, at elevations between 2450 and 3700 m.

*D. squamigera* (Benth.) Benth. & Hook.

f. ex Kuntze (K.T. Hartweg 1046, holotype K). Region III. Subpáramo and páramo vegetation, at elevations between 3100 and 3300 m.

*D. stricta* Rusby (H.H. Smith 1289, holotype NY). Region I. Cloud, montane forest relicts in the Sierra Nevada de Santa Marta, at elevations around 2200 m. Endemic.

*D. subtrinervis* Urb. (J.H. Torres 680, COL). Region III. Cloud, Andean to high-Andean forests, and subpáramo and páramo vegetation, at elevations between 2800 and 3500 m.

*D. sulcata* Kuijt (R. Callejas et al. 8498, isotype HUA). Region III. Cloud, sub-Andean to Andean forests, at elevations between 1450 and 1840 m. Endemic.

*D. tenuifolia* Kuijt (B. Ramírez 4029, HUA). Region III. Cloud, high-Andean forests at elevations around 3000 m.

*D. thomasii* Kuijt (S. Espinal et al. 2400, HUA). Region III. Cloud, high-Andean forests at elevations between 3300 and 3700 m.

*D. virgata* (Trel.) Kuijt (R. Callejas et al. 6282, HUA). Region III. Cloud, Andean to high-Andean forests and subpáramo and páramo vegetation at elevations between 2400 and 3600 m.

**Phoradendron** Nutt. Sixty-six obligate, stem hemiparasitic species, 17 of them endemic to Colombia (Figs. 18G–M and 27B).

*P. anceps* (Spreng.) M.Gómez (F.J. Roldán 1284, HUA). Region III. Sub-Andean forests, at elevations between 1400 and 1500 m.

*P. antioquianum* Kuijt (F.J. Roldán 1224, holotype HUA). Region III. Sub-Andean forests, at elevations between 1550 and 1850 m. Endemic.

*P. apertiflorum* Kuijt (G. Galeano et al. 2274, holotype COL). Region V. Sclerophyllous Amazonian forests, at elevations between 350 and 500 m. Endemic.

*P. applanatum* Kuijt (O. Haught 4181, COL). Region I. Xerophytic thickets, at elevations between 50 and 500 m.

*P. balslevii* Kuijt (G. Lozano 4108, COL). Region III. Andean forests, at elevations between 1800 and 2500 m.

*P. berterioanum* Griseb. (*L. Albert 163*, COL). Regions I, II, III. Dry forests, pluvial forests and sub-Andean to Andean forests, at elevations between 350 and 2000 m.

*P. betancurii* Kuijt (*O. Haught 2437*, holotype COL). Region III. Sub-Andean to Andean forests, at elevations between 700 and 2200 m. Endemic.

*P. brittonianum* Rusby (*C.A. Loaiza et al. 138*, HUA). Region III. Sub-Andean forests, at elevations between 1400 and 1500 m.

*P. buritacanam* Kuijt (*C. Barbosa et al. 354*, isotype COL). Region I, Montane forests of the Sierra Nevada de Santa Marta, at elevations around 1100 m. Endemic.

*P. chrysocladon* A.Gray (*J. Cuatrecasas 12514*, COL). Regions II and III. Pluvial forests to Andean forests, at elevations between 30 and 2400 m.

*P. colombianum* Kuijt (*J.M. MacDougal & F.J. Roldán 3543*, isotype HUA). Region III. Sub-Andean to high-Andean forests, at elevations between 1650 and 3000 m.

*P. crassicarpum* Kuijt (*F.J. Roldán 801*, holotype HUA). Region III. Sub-Andean forests, at elevations between 500 and 1000 m. Endemic.

*P. crassifolium* Trel. (*J.M. Idrobo 10576*, COL). Andean forests (Region III), gallery forests (Region IV) and Amazonian forests (Region V) at elevations between 100 and 2000 m.

*P. dipterum* Eichler (*F. González 4445*, COL). Region III. Sub-Andean to Andean forests, at elevations between 1800 and 2600 m.

*P. eppersii* Urban (*O. Haught 4020*, COL) Regions I and III. Xerophytic thickets (Region I) to sub-Andean forests (Region III), at elevations between 100 and 800 m.

*P. englerianum* Patsch. (*G. Lozano-Contreras 904*, COL). Xerophytic thickets (Region I) to Andean forests (Region III), at elevations between 100 and 2400 m.

*P. exiguum* Trel. (*H.H. Smith 1281*, isotype NY). Region I. Xerophytic thickets, at elevations between 10 and 200 m.

*P. fasciculatum* Kuijt (*F.J. Roldán 864*, HUA). Region I. Dry forests and xerophytic thickets, at elevations below 800 m.

*P. fonsecanum* Kuijt (*O. Haught 3992*, isotype COL). Region I. Dry forests and xerophytic thickets, at elevations between 100 and 200 m. Endemic.

*P. gracilicarpum* Kuijt (*R. Callejas 8905*, holotype HUA). Region III. Sub-Andean forests, at elevations between 1000 and 1100 m. Endemic.

*P. haughtii* Kuijt (*O. Haught 6302*, isotype COL). Region III. Sub-Andean forests, at elevations between 450 and 1000 m.

*P. herbert-smithii* Trel. (*H.H. Smith 1283*, isotype COL). Regions I, III. Dry forests (Region I) and sub-Andean forests (Region III), below 1200 m in elevation.

*P. heterostachyum* Kuijt (*N. Contreras & D.L. Echeverri 353*, isotype HUA). Region III. Sub-Andean forests, at elevations between 1700 and 1900 m. Endemic.

*P. hexastichum* (DC.) Griseb. (*F.J. Roldán et al. 781*, HUA). Region III. Sub-Andean and Andean forests, at elevations between 800 and 2000 m.

*P. inaequidentatum* Rusby (*R.E. Schultes 3625*, COL). Sub-Andean forests (Region III) and sclerophyllous Amazonian forests (Region V), at elevations between 100 and 2100 m.



*P. killipii* Kuijt (*E.P. Killip 10102*, holotype NY). Region III. Andean forests, at elevations between 2000 and 2700 m. Endemic.

*P. larense* Kuijt (*F.J. Roldán et al. 1087*, HUA). Region III. Sub-Andean forests, at elevations between 900 and 1200 m.

*P. laxiflorum* Ule (*J. Cuatrecasas et al. 27192*, COL). Region V. Amazonian forests, at elevations between 100 and 500 m.

*P. linearifolium* Eichler (*R. López 3822*, HUA). Region V. Amazonian forests, at elevations below 300 m.

*P. longissimum* Kuijt (*F.J. Roldán 791*, isotype HUA). Region I. Dry forests and xerophytic thickets, at elevations below 30 m. Endemic.

*P. lorifolium* Kuijt (*F.J. Roldán 794*, holotype HUA). Region I. Dry forests and xerophytic thickets, at elevations below 30 m.

*P. madisonii* Kuijt (*B. Madrigal 667*, COL). Region II. Pluvial forests, at elevations between 10 and 400 m.

*P. mairaryense* Ule (*A. Fernández 6946*, HUA). Region V. Amazonian forests, at elevations between 50 and 120 m.

*P. megaphyllum* Kuijt (*J.C. Mutis 161*, US). Region III. Cloud, Andean forests, at elevations between 2000 and 2500 m. Endemic.

*P. metense* Kuijt (*O. Haught 2530*, isotype COL). Regions III (Sub-Andean forests) and IV (savannas and gallery forests), at elevations between 400 and 1600 m.

*P. mucronatum* (DC.) Krug & Urb. (*H.H. Smith 1285*, COL). Regions I and III. Dry forests and sub-Andean forests, at elevations between 0 and 1000 m.

*P. nervosum* Oliv. (*F. González 4554*, COL). Regions I and III. Dry forests and sub-Andean to high-Andean forests, at elevations between 100 and 3000 m (Fig. 18G–M).

*P. nitens* Kuijt (*J. Zarucchi et al. 6740*, HUA). Region III. Sub-Andean forests, at elevations between 600 and 900 m.

*P. obtusissimum* Eichler (*A. Chaparro 928*, COL). Sub-Andean forests (Region III) and Amazonian forests (Region V), at elevations between 100 and 2100 m.

*P. palaephyllum* Kuijt (*J.M. Idrobo & R.E. Schultes 638*, holotype COL). Region V. Sclerophyllous, Amazonian forests, at elevations between 100 and 300 m. Endemic.

*P. parietarioides* Trel. (*F. González et al. 2263*, COL). Sub-Andean to high-Andean forests (Region III) and Amazonian forests (Region V), at elevations between 500 and 3000 m.

*P. pellucidulum* Eichler (*G. Lozano-Contreras et al. 2736*, COL). Region I. Dry forests, at elevations between 50 and 200 m.

*P. perrottetii* (DC.) Eichler (*J.C. Mutis 161A*, MA). Regions III and V. Amazonian and sub-Andean forests, at elevations between 900 and 1400 m.

*P. piperoides* (Kunth) Trel. (*E. Pérez-Arbeláez & J. Cuatrecasas 8112*, COL). Regions II, III and V. Pluvial, sub-Andean, and Amazonian forests, at elevations between 50 and 1500 m.

*P. planiphyllum* Kuijt (*J. Cuatrecasas 19973*, F). Region III. Cloud Andean forests, at elevations between 1600 and 2000 m.

*P. platycaulon* Eichler (*G. Lozano-Contreras et al. 433*, COL). Regions IV and V. Gallery forests of the Orinoco plains and Amazonian forests, at elevations between 100 and 600 m.

*P. pteroneuron* Eichler (*R. Fonnegra et al. 4754*, HUA). Sub-Andean forests (Region III) and gallery forests and savanna vegetation (Region IV), at elevations between 600 and 1800 m.

*P. quadrangulare* (Kunth) Griseb. (*E.P. Killip 33956*, COL). Regions I-III. Dry thickets (Region I), pluvial forests (Region II), and sub-Andean forests (Region III), at elevations between 50 and 1200 m.

*P. racemosum* Krug & Urb. (*G. Lozano-Contreras 6359*, COL). Region V. Sclerophyllous, Amazonian forests, at elevations between 300 and 900 m.

*P. restrepoae* Kuijt (*C. Restrepo 05*, isotype COL). Region III. Andean forests at elevations around 1700 m. Endemic.

*P. retrophyllum* Kuijt (*C. Luer et al. 10242*, holotype LEA). Region III. Cloud, high-Andean forests and subpáramo vegetation, at elevations between 3100 and 3200 m. Endemic.

*P. robaloense* Woodson ex Rizzini (*O. Haught 4348*, COL). Region I. Xerophytic thickets, at elevations between 10 and 50 m.

*P. robustissimum* Eichler (*F.J. Roldán et al. 1338*, HUA). Region III. Sub-Andean forests, at elevations between 600 and 1300 m.

*P. roldanii* Kuijt (*F.J. Roldán et al. 861*, isotype HUA). Region III. Sub-Andean forests, at elevations between 1000 and 1200 m. Endemic.

*P. rugosum* Kuijt (*A. Chaparro 899*, holotype COL). Region III. Sub-Andean forests, at elevations between 1450 and 1550 m.

*P. singulare* Kuijt (*S. Castroviejo et al. 12,057*, isotype COL). Region V. Sclerophyllous thickets at the summit of the Sierra de Chiribiquete, at elevations between 500 and 800 m.

*P. squamiferum* Kuijt (*A.H. Gentry et al. 15,440*, isotype COL). Region III. Sub-Andean forests, at elevations around 1900 m. Endemic.

*P. staphylinum* Rizzini (*J. Cuatrecasas 9669*, COL). Region III. Sub-Andean forests, at elevations between 1800 and 1900 m.

*P. strongyloclados* Eichler (report based on Kuijt, 2003). Region V.

*P. tardispicum* Kuijt (*F.J. Roldán et al. 635*, HUA). Regions II and III. Pluvial and sub-Andean forests, at elevations between 100 and 800 m.

*P. triflorum* E.A.Kellogg (*A.H. Gentry 40464*, COL). Region II. Pluvial forests, at elevations between 50 and 400 m.

*P. trinervium* (Lam.) Griseb. (*G. Davidse & J.S. Miller 26383*, MO). Regions I and V. Disjunct species from dry Caribbean forests, and sclerophyllous Amazonian forests, at elevations between 5 and 100 m.

*P. undulatum* (Pohl ex DC.) Eichler (*E. Pérez-Arbeláez & J. Cuatrecasas 8112*, COL). Regions I and III, at elevations between 800 and 3500 m.

*P. uniseriale* Kuijt (*F.J. Roldán et al. 732*, holotype HUA). Region III. Cloud, sub-Andean forests, at elevations between 1000 and 1400 m. Endemic.

*P. wiensii* Kuijt (report based on Kuijt, 2003). Region III. Cloud, sub-Andean forests, at elevations between 1350 and 1450 m.

*P. woodsonii* Trel. (*J. Cuatrecasas 11312*, COL). Regions II, III. Pluvial and sub-Andean forests, at elevations between 50 and 1600 m.

**Ximeniaceae** Horan. One genus (Fig. 16).

*Ximения* Plum. ex L. One root hemiparasitic species.

*X. americana* L. (*G. Lozano-Contreras 2944*, COL). Regions I (Urabá) and II. Pluvial forests, at elevations below 100 m.

## 6 Ericales

**Mitrastemonaceae** Makino. One genus. (Fig. 16).

*Mitrastemon* Makino. One root holoexoparasitic species.

*M. matudae* Yamam. (*Á. Cogollo et al. 7661*, MO). Region III. Cloud, sub-Andean forests, at elevations between 1400 and 1500 m.

**7 Boraginales:** One family.

**Ehretiaceae** Mart. One genus (Figs. 16 and 19A–E).

*Lennoa* Lex. One root holoexoparasitic species.

*L. madreporoides* Lex. (*M.L. Schnetter 69*, COL). Region I. Coastal thickets, at elevations below 25 m.

**8 Solanales:** One family.

**Convolvulaceae** Juss. One genus (Figs. 19F–M and 20).

*Cuscuta* L. Nine twining, stem holoexoparasitic species, two of them endemic to Colombia.

*C. americana* L. (*J.M. Idrobo 6625*, COL). Regions I and III. Dry forests and xeromorphic thickets, and sub-Andean and Andean forests, at elevations between 20 and 2500 m.

*C. colombiana* Yunck. (*C. Saravia 2304*, COL). Region I. Xeromorphic thickets, at elevations between 30 and 300 m. Endemic.

*C. corymbosa* Ruiz & Pav. (*F. González 4794*, COL). Region III. Xerophytic thickets, at elevations between 2400 and 2500 m (Fig. 19F–M).

*C. grandiflora* Kunth (*J.J. Triana 3816/1*, COL). Region III. Sub-Andean through high-Andean forests, and subpáramos and páramos, at elevations between 500 and 4000 m.

*C. indecora* Choisy (*E.P. Killip 34700*, COL). Region III. Sub-Andean and Andean forests, at elevations between 1000 and 2550 m.

*C. obtusiflora* Kunth (*F.A. Barkley 17C336*, COL). Region III. Restricted to sub-Andean forests of the Central Cordillera in Antioquia, at elevations between 700 and 1560 m.

*C. partita* Choisy (*C. Saravia 527*, COL). Region I. Xerophytic thickets below 50 m.

*C. pentagona* Engelm. (*W.R. Jervise s.n.*, MO). Only one (historic) collection from the department of Antioquia, without precise locality (“near the Magdalena River”), below 100 m of elevation.

*C. popayanensis* Kunth (*J.J. Triana 3816/3*, COL). Region III. Only a single (historic) collection from Andean forests of the department of Cauca, at elevations around 1800 m. Endemic.

**9 Lamiales:** One family.

**Orobanchaceae** Vent. Eight genera, 37 species (Figs. 21, 22, 23, 24, and 25).

*Anisantherina* Pennell. One facultative, root hemiparasitic species.

*A. hispidula* (Mart.) Pennell (C. Allen 647, MO). Region I. Xerophytic thickets and savannas, at elevations below 150 m.

***Buchnera*** L. Eleven facultative, root hemiparasitic species, two of them endemic to Colombia.

*B. jacoborum* Fern.Alonso (R. Jaramillo 1297, holotype COL). Regions IV and V. Savannas and margins of gallery forests, at elevations between 250 and 700 m. Endemic.

*B. longifolia* Kunth (H. Daniel 500, COL). Sub-Andean forests (Region III), and savanna vegetation (Region IV), at elevations between 150 and 1900 m.

*B. obliqua* Benth. (P. Pinto 1766, COL). Region III. Andean forests of the Western Cordillera, at elevations between 2200 and 2300 m.

*B. palustris* (Aubl.) Spreng. (C. Sastre 1531, COL). Region IV. Savanna vegetation, at elevations between 120 and 400 m.

*B. pusilla* Kunth (J.M. Idrobo 192, COL) Regions I and III. Savannas and paddocks, at elevations between 100 and 1900 m.

*B. rosea* Kunth (F. González et al. 3088, COL). Regions III and IV. Savannas and paddocks, at elevations between 100 and 1500 m.

*B. schultesii* R.Bernal (R.E. Schultes & I. Cabrera 14211, holotype A). Region V. Borders of gallery forests and clearings in Amazon forests, at elevations around 450 m. Endemic.

*B. spruceana* Philcox (F. González et al. 2294, COL). Region IV. Savanna vegetation, at elevations around 200 m.

*B. ternifolia* Kunth (O. Haught 2369, COL). Region III. Roadsides and paddocks, at elevations around 500 m.

*B. virgata* Kunth (D. Rivera 1297, COL). Regions IV and V. Borders of gallery forests, savanna vegetation, and clearings in Amazon forests, at elevations between 100 and 550 m.

*B. weberbaueri* Diels (P. Pinto 1064, COL). Region IV. Savannas and borders of gallery forests, at elevations between 90 and 650 m.

***Castilleja*** Mutis ex L.f. Eight facultative, root hemiparasitic species, one of them endemic to Colombia (Fig. 22A–J).

*C. arvensis* Cham. & Schltl. (F. González 4762, COL). Regions III and IV. Roadsides, paddocks and grassland vegetation, at elevations between 800 and 3700 m. (Fig. 22A).

*C. breviflora* Benth. (J. Cuatrecasas 24600, COL). Region I (Sierra Nevada de Santa Marta). Páramos and high-páramos at elevations between 3750 and 4500 m.

*C. fissifolia* L.f. (F. González 301, COL). Regions I (Sierra Nevada de Santa Marta) and III. Roadsides, paddocks and grassland vegetation, and subpáramo, páramo and high-páramo vegetation at elevations between 1600 and 4350 m. (Fig. 22B).

*C. integrifolia* L.f. (F. González 4732, COL). Regions I (Sierra Nevada de Santa Marta) and III. Roadsides, paddocks and grassland vegetation, and subpáramo, páramo and high-páramo vegetation at elevations between 1650 and 4100 m. (Fig. 22C–E).

*C. nubigena* Kunth (*R. Galindo 1332*, COL). Region III. Borders of Andean and high-Andean forests, and subpáramo, páramo and high-páramo vegetation between 2900 and 4200 m.

*C. paramensis* F.González & Pabón-Mora (*F. González et al. 4478*, holotype COL). Region III. Páramo and high-páramo vegetation, at elevations between 3500 and 4500 m. Endemic. (Fig. 22F–J).

*C. pumila* Wedd. (*H. Sturm 92*, COL). Region III. Páramo and high-páramo vegetation, at elevations between 3900 and 4100 m.

*C. virgata* (Wedd.) Edwin (*M. Schneider 1199*, COL). Region III. High-páramo vegetation, at elevations around 4200 m.

***Escobedia*** Ruiz & Pav. Four facultative, root hemiparasitic species, two of them endemic to Colombia. (Fig. 23).

*E. brachydonta* Pennell (*E.P. Killip 7877*, holotype PH). Region III. Roadsides and paddocks of the Western Cordillera, at elevations around 2500 m. Endemic.

*E. grandiflora* (L.f.) Kuntze (*F. González et al. 3051*, COL). Regions I–IV. Savannas, roadside, paddock, and grassland vegetation, at elevations between 150 and 2550 m.

*E. parvifolia* Pennell (*E.P. Killip & A.C. Smith 17210*, isotype NY). Region III. Known only from its type locality at the Páramo Rico/Páramo de Santurbán (Eastern Cordillera), at elevations between 3000 and 3600 m. Endemic.

*E. scabrifolia* Ruiz & Pav. (*J.M. Idrobo & H. Weber 1348*, COL). Two disjunct records at regions III (Cauca, at elevations between 1700 and 2000 m) and IV (Vichada, at elevations around 100 m).

***Lamourouxia*** Kunth. One facultative, root hemiparasitic species (Figs. 22K and 23).

*L. virgata* Kunth (*F. González & N. Pabón-Mora 4339*, COL). Region III. Roadside, paddock and grassland vegetation, at elevations between 1100 and 3400 m.

***Neobartsia*** Uribe-Convers & Tank. Ten facultative, root hemiparasitic species, one of them endemic to Colombia (Figs. 22L–M, 24, and 25).

*N. glandulifera* (Molau) Uribe-Convers & Tank (*J.L. Fernández 7759*, COL). Páramos of the Central and Eastern cordilleras (Region III), plus a few records at the Sierra Nevada de Santa Marta (Region I), at elevations between 3000 and 3900 m.

*N. inaequalis* (Benth.) Uribe-Convers & Tank (*R. Guarín-M. 273*, COL). Region III. Andean to high andean forests and páramos primarily from the Eastern Cordillera, at elevations between 1990 and 3560 m.

*N. laniflora* (Benth.) Uribe-Convers & Tank (*L.E. Mora-Osejo 769A*, COL). Páramos and high-páramos of the Central and Eastern cordilleras (Region III), plus a few isolate collections at the Sierra Nevada de Santa Marta, at elevations between 3000 and 4100 m.

*N. laticrenata* (Benth.) Uribe-Convers & Tank (*L.E. Mora-Osejo 7539*, COL). Region III. Restricted to the Andes of Nariño, at elevations around 4000 m.

*N. matuy* Malagón, Humberto Mend. & Uribe-Convers (*H. Mendoza & E. Torres, 22013*, isotype COL). Region III. Known only from its type locality in Cóbbita (Boyacá), at 3528 m. Endemic.



*N. orthocarpiflora* (Benth.) Uribe-Convers & Tank (*H.G. Barclay 4532*, COL). Region III. Páramos and high-páramos of Cundinamarca, Risaralda and Nariño, at elevations between 3000 and 3700 m.

*N. pedicularoides* (Benth.) Uribe-Convers & Tank (*J.L. Fernández 6687*, COL). Páramos and high-páramos of all three cordilleras (Region III), and the Sierra Nevada de Santa Marta (Region I), at elevations between 3100 and 4250 m.

*N. ramosa* (Molau) Uribe-Convers & Tank (*J.L. Fernández 11627*, COL). Region III. Páramos and high-páramos of the Central and Eastern cordilleras, at elevations between 3150 and 4000 m.

*N. santolinifolia* (Kunth) Uribe-Convers & Tank (*F. González et al. 4751*, COL). Region III. Páramos and high-páramos of the Eastern Cordillera, plus a few isolated records in the Central Cordillera (Antioquia, Cauca, Quindío and Nariño), at elevations between 2800 and 4400 m.

*N. stricta* (Kunth) Uribe-Convers & Tank (*J.H. Torres et al. 1325*, COL). Region III. Páramos and high-páramos of the Eastern and Central cordilleras, at elevations between 3130 and 4500 m.

**Orobanche** L. One facultative, root hemiparasitic species (Figs. 22N–S and 25).

*O. minor* Sm. (*N. Pabón-Mora & F. González 491*, HUA). Region III. Restricted to the Eastern Cordillera, at elevations between 2500 and 3400 m. Likely a recent introduction to Colombia, where it has been collected in a few paddocks of Boyacá and Cundinamarca. So far, this species represents the only parasitic angiosperm in Colombia that could become a potential weed.

**Pedicularis** L. One species (Fig. 25).

*P. incurva* Benth. (*R. Jaramillo 5876*, COL). Region III. Subpáramos to high-páramos of the Western and Central cordilleras, at elevations between 2700 and 4300 m.

## Discussion

### Regional Distribution of Parasitic Angiosperms in Colombia

**Region I:** A total of 58 species of parasitic flowering plants are found in Region I. Restricted to this region are: (a) All members of the families Cytinaceae (*Sanguisuga caesarea*; endemic) and Krameriaceae (two *Krameria* species) and the genera *Acanthosyris* (Cervantesiaceae; one species) and *Lennoa* (Ehretiaceae; one species); (b) the Santalalean *Aetanthus ovalis* (endemic), *Maracanthus chlamydatus*, *Ocyctanthus grammatus* (endemic), *Psittacanthus roldanii*, *P. smithii* (endemic) and *Struthanthus marginatus* (Loranthaceae); (c) *Agonandra brasiliensis* (Opiliaceae), *Phoradendron applanatum*, *P. buritacatum* (endemic), *P. exiguum*, *P. fonsecanum* (endemic), *P. longissimum* (endemic), *P. loriflorum*, *P. pellucidum* and *P. robaloense* (Viscaceae); (d) *Cuscuta colombiana* and *C. partita* (Convolvulaceae); and (e) *Anisanthera hispidula* and *Castilleja breviflora* (Orobanchaceae). A total of seven species from three families are endemic to Region I.

Conservation and restoration of the coastal vegetation and the dry forests, two highly disturbed ecosystems of the Caribbean region, are urgently needed to preserve the above mentioned taxa in Colombia.

**Region II:** A total of 35 species of parasitic flowering plants are found in Region II. Seven species of Loranthaceae found in this region (*Oryctanthus grandis*, *O. neurophyllus*, *Passovia cordata*, *Peristethium colombianum*, *P. lamprophyllus*, *Psittacanthus gigas*, and *P. micrantherus*) are endemic to Colombia. Two additional species of Viscaceae (*Phoradendron madisonii* and *P. triflorum*) are restricted to this region.

**Region III:** A total of 169 species of parasitic flowering plants are found in Region III, being by far the natural region of Colombia with the highest number of parasitic angiosperms. The following taxa are restricted to Region III: (a) The two species of *Pilostyles* (Apodanthaceae); (b) all the species of *Corynaea*, *Langsdorffia*, *Ombrophytum*, and *Scybalium* (Balanophoraceae); (c) the two species of *Cervantesia* (Cervantesiaceae); (d) most *Aetanthus* spp. as well as *Oryctanthus perticus* (endemic), *Passovia robusta*, *Peristethium aequatoris*, *Phthirusa exilis* (endemic), *P. hutchisonii*, *P. rhynchophylla* (endemic), *Psittacanthus antioquiensis* (endemic), *P. carinatus* (endemic), *P. complanatus* (endemic), *P. crassinervis* (endemic), *P. dilatatus*, *P. longirectus* (endemic), *P. microphyllus* (endemic), *P. pentaphyllus* (endemic), *P. rotundatus* (endemic), *P. ternatus*, *Struthanthus calophyllus*, *S. subtilis*, *Tripodanthus belmirensis* (endemic), and *Tristerix longibracteatus* and *T. secundus* (endemic) (Loranthaceae); (e) the three species of Santalaceae; (f) most species of *Dendrophthora* and *Phoradendron* (Viscaceae); (g) the sole species of Mitrastemonaceae; (h) most *Cuscuta* (Convolvulaceae) species; and (i) *Buchnera obliqua*, *B. ternifolia*, most *Castilleja*, *Escobedia* and *Neobartsia* species, *Lamourouxia virgata*, *Orobanche minor* and *Pedicularis incurva* (Orobanchaceae).

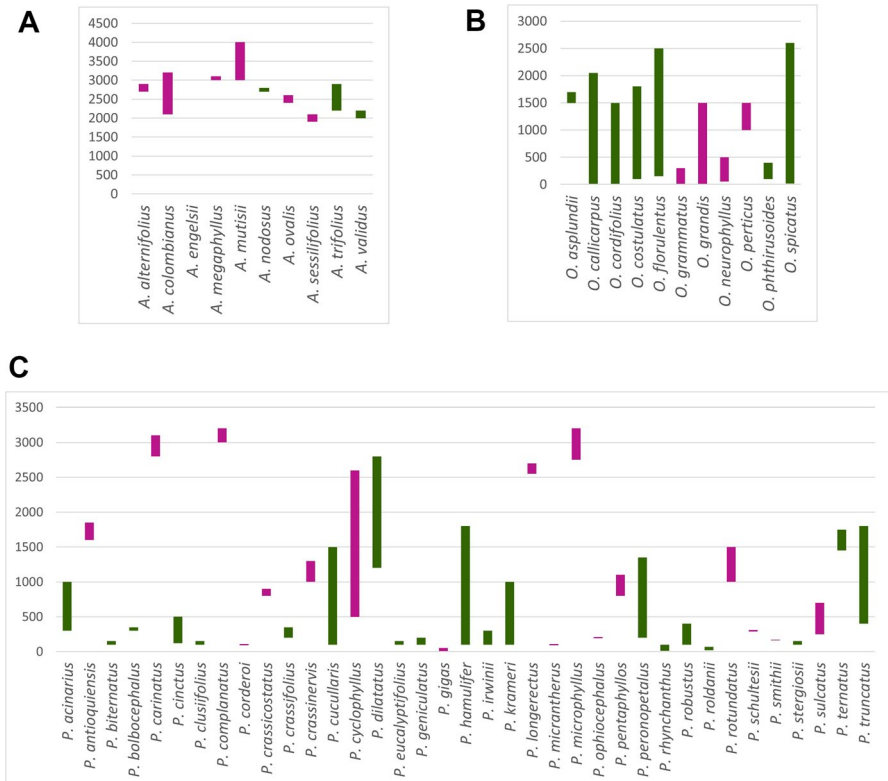
The Region contains 14 endemic species. Conservation and restoration of cloud, sub-Andean, Andean and high-Andean forests and páramo ecosystems, some of them severely disturbed and fragmented, are urgently needed to preserve all these taxa in Colombia.

**Region IV:** A total of 29 species of parasitic flowering plants are found in Region IV. The following species are restricted to this region in Colombia: (a) The Santalalean *Cladocolea coriacea* (Loranthaceae), and *Agonandra silvatica* (Opiliaceae); and (b) *Buchnera palustris*, *B. spruceana* and *B. weberbaueri* (Orobanchaceae). No endemic species are present in this region.

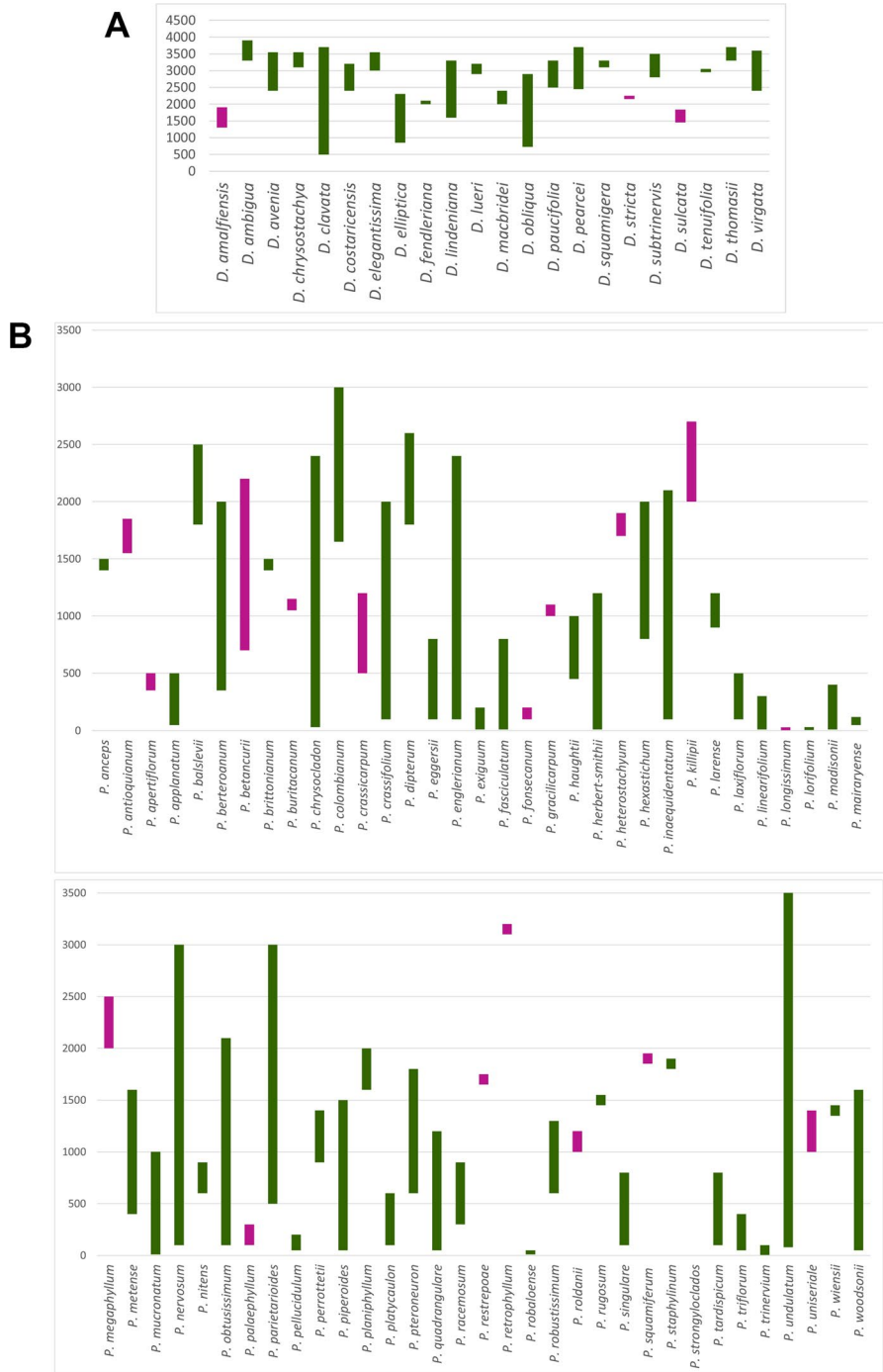
**Region V:** A total of 54 species of parasitic flowering plants are found in Region V, and 27 of them are restricted to this region: (a) the mistletoes *Oryctanthus phthirusoides*, *Psittacanthus biternatus*, *P. bolbocephalus*, *P. cinctus*, *P. clusifolius*, *P. corderoi* (endemic), *P. crassifolius*, *P. eucalyptifolius*, *P. geniculatus*, *P. irwinii*, *P. ophiocephalus* (endemic), *P. robustus*, *P. schultesii* (endemic), *P. stergiosii*, *P. sulcatus* (endemic), and *Struthanthus schultesii* (endemic) (Loranthaceae); (b) *Agonandra peruviana* (Opiliaceae); (c) The sole species of *Tetrastylidium* (*T. peruvianum*, Strombosiaceae); (d) *Phoradendron apertiflorum*, *P. laxiflorum*, *P. linearifolium*, *P. mairaryense*, *P. palaephyllum*, *P. racemosum*, *P. singulare*, *P. strongyloclados* (Viscaceae); and (e) *Buchnera schultesii* (endemic) (Orobanchaceae). Six of these species are endemic to Colombia.

**Elevational Distribution of Parasitic Flowering Plants in Colombia (Figs. 26, 27, 28, and 29)**

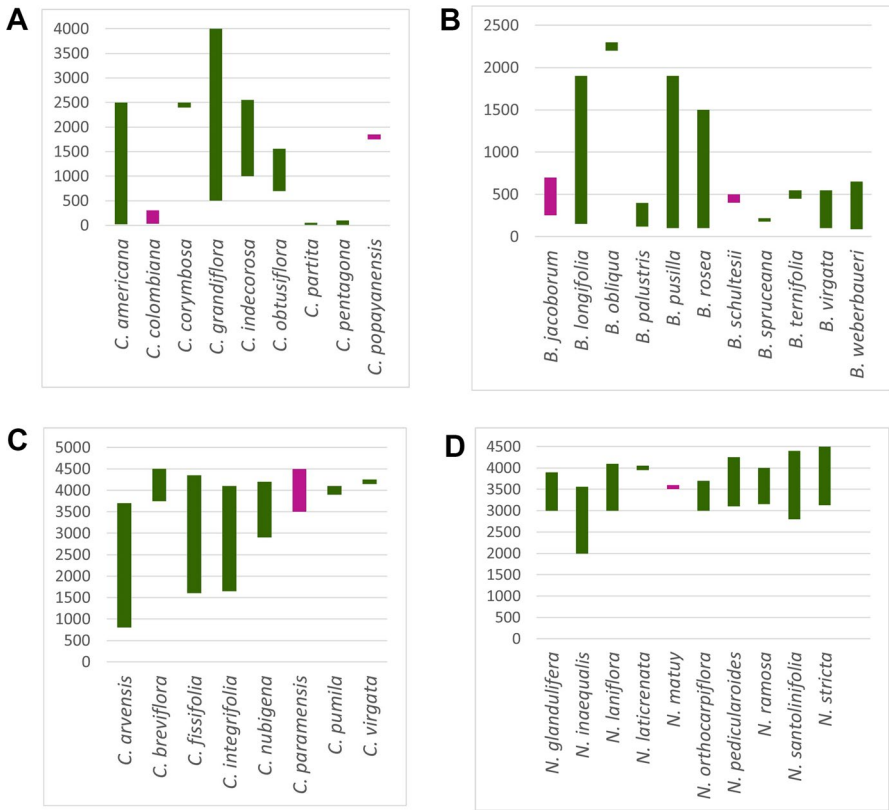
**Taxa exclusive to lowlands (0–1000 m):** A total of 84 parasitic flowering plants (including 24 endemic species) are restricted to lowland ecosystems in Colombia. These are: *Cassytha filiformis* (Lauraceae); the two *Krameria* spp. (Krameriaceae); *Sanguisuga caesarea* (Cytinaceae; endemic); *Acanthosyris glabrata* (Cervantesiaceae); *Cladocolea coriacea*, *Maracanthus chlamydatius*, *Oryctanthus grammatus* (endemic), *O. neurophyllus* (endemic), *O. phthirusoides* (Fig. 26B), *Passovia cordata* (endemic), *Peristethium colombianum* (endemic), *P. lamprophyllum* (endemic), *Phthirusa exilis* (endemic), *Psittacanthus biternatus*, *P. bolbocephalus*, *P. cinctus*, *P. clusiifolius*, *P. corderoi* (endemic), *P. crassicosatus* (endemic), *P. crassifolius*, *P. eucalyptifolius*, *P. geniculatus*, *P. gigas* (endemic), *P. irwinii*, *P. krameri*, *P. micrantherus* (endemic), *P. ophioccephalus* (endemic), *P. rhynchanthus*, *P. robustus*, *P. roldanii*, *P. schultesii* (endemic), *P. smithii* (endemic), *P. stergiosii*, *P. sulcatus* (endemic) (Fig. 26C), *Struthanthus marginatus*, *S. phillyreoides* and *S. schultesii* (endemic) (Loranthaceae); all three *Agonandra* spp. (Opiliaceae); the two *Schoepfia*



**Fig. 26** Elevational range of genera of Loranthaceae with eight or more species in Colombia. A. *Aetanthus*. B. *Oryctanthus*. C. *Psittacanthus*. Purple bars correspond to endemic species to the country



**Fig. 27** Elevational range of Viscaceae with eight or more species in Colombia. **A.** *Dendrophthora*. **B.** *Phoradendron*. Purple bars correspond to endemic species to the country



**Fig. 28** Elevational range of Convolvulaceae (A) and Orobanchaceae (B–D) with eight or more species in Colombia. A. *Cuscuta*. B. *Buchnera*. C. *Castilleja*. D. *Neobartsia*. Purple bars correspond to endemic species to the country

spp. (Schoepfiaceae); *Tetrastylidium peruvianum* (Strombosiaceae); *Phoradendron apertiflorum* (endemic), *P. applanatum*, *P. crassicarpum* (endemic), *P. eggersii*, *P. exiguum*, *P. fasciculatum*, *P. fonsecanum* (endemic), *P. haughtii*, *P. laxiflorum*, *P. linearifolium*, *P. longissimum* (endemic), *P. lorifolium*, *P. madisonii*, *P. mairaryense*, *P. mucronatum*, *P. nitens*, *P. palaephyllum* (endemic), *P. pellucidulum*, *P. platycaulon*, *P. racemosum*, *P. robaloense*, *P. singulare*, *P. stronglyloclados*, *P. tardispicum*, *P. triflorum* and *P. trinervium* (Viscaceae) (Fig. 27B); *Ximenia americana* (Ximeneiaceae); *Lennoa madreporoides* (Ehretiaceae); *Cuscuta colombiana* (endemic), *C. partita*, *C. pentagona* (Convolvulaceae) (Fig. 28A); and *Anisanthera hispidula*, *Buchnera jacoborum* (endemic), *B. palustris*, *B. schultesii* (endemic), *B. spruceana*, *B. ternifolia*, *B. virgata* and *B. weberbaueri* (Orobanchaceae) (Fig. 28B).

**Taxa exclusive to mid-elevations (1000–2800 m):** A total of 59 parasitic flowering plants (including 29 endemic species) are restricted to this elevational belt in Colombia. These are: *Pilostyles boyacensis* (endemic), and *P. cf. blanchetii* (Apoanthaceae); *Langsdorffia hypogaea*, *Ombrophytum villamariensis* (endemic) and



*Scybalium depressum* (Balanophoraceae); *Cervantesia macrocarpa* (endemic) (Cervantesiaceae); *Aetanthus alternifolius* (endemic), *A. nodosus*, *A. ovalis* (endemic), *A. sessilifolius* (endemic), *A. trifolius*, *A. validus* (endemic) (Fig. 26A), *Oryctanthus asplundii*, *O. perticus* (endemic) (Fig. 26B), *Passovia robusta*, *Peristethium aequatoris*, *Phthirusa hutchisonii*, *P. rhynchophylla* (endemic), *Psittacanthus antioquiensis* (endemic), *P. crassinervis* (endemic), *P. dilatatus*, *P. longirectus* (endemic), *P. pentaphyllos* (endemic), *P. rotundatus* (endemic), *P. ternatus* (Fig. 26C), *Struthanthus calophyllus*, *S. subtilis* and *S. syringifolius* (Loranthaceae); *Dendrophthora amalfiensis* (endemic), *D. fendleriana*, *D. macbridei*, *D. stricta* (endemic), *D. sulcata* (endemic) (Fig. 27A), *Phoradendron anceps*, *P. antioquianum* (endemic), *P. balslevii*, *P. brittonianum*, *P. buritacatum* (endemic), *P. dipterum*, *P. gracilicarpum* (endemic), *P. heterostachyum* (endemic), *P. killipii* (endemic), *P. megaphyllum* (endemic), *P. planiphyllum*, *P. restrepoae* (endemic), *P. roldanii* (endemic), *P. rugosum*, *P. squamiferum* (endemic), *P. staphylinum*, *P. uniseriale* (endemic) and *P. wiensii* (Viscaceae) (Fig. 27B); *Mitrastemon matudae* (Mitrastemonaceae); *Cuscuta corymbosa*, *C. indecora* and *C. popayanensis* (endemic) (Convolvulaceae; Fig. 28A); and *Buchnera obliqua*, *Escobedia brachydonta* (endemic) (Fig. 28B), and *Orobanche minor* (Orobanchaceae).

**Taxa exclusive to subpáramo, páramo and high-páramo ecosystems (2800–4500 m).** A total of 34 parasitic flowering plants (including 11 endemic species) are restricted to this elevational belt in Colombia. These are: *Cervantesia tomentosa* (Cervantesiaceae); *Aetanthus megaphyllum* (endemic), *A. mutisii* (endemic) (Fig. 26A), *Psittacanthus carinatus* (endemic), *P. complanatus* (endemic), *P. microphyllum* (endemic) (Fig. 26C), *Tripodanthus belmirensis* (endemic), *Tristerix longibracteatus*, and *T. secundus* (endemic) (Loranthaceae); *Antidaphne andina* (Santalaceae); *Dendrophthora ambigua*, *D. chrysostachya*, *D. elegantissima*, *D. lueri*, *D. squamigera*, *D. subtrinervia*, *D. tenuifolia*, *D. thomasii* and *Phoradendron retrophyllum* (endemic) (Viscaceae; Fig. 27); and *Castilleja breviflora*, *C. nubigena*, *C. paramensis* (endemic), *C. pumila*, *C. virgata* (Fig. 28C), *Escobedia parvifolia* (endemic), and nine *Neobartsia* spp. (Orobanchaceae; Fig. 28D), one of them (*N. matuyi*) endemic to the Eastern Cordillera of Colombia.

## Elevational Gradients and Speciation

The elevational gradients for parasitic Angiosperm genera with eight or more species in Colombia suggest that the Andean orogeny has played a role in their diversification. These are:

*Aetanthus* (Loranthaceae): Andean to high-Andean forest remnants above 2000 m and paramos are the preferred habitat for all the species of *Aetanthus*. Most of the species (four out of ten) live in cloud forest remnants between 2700 and 3200 m (Fig. 26A). Three endemic species (*A. colombianus*, *A. megaphyllum*, and *A. mutisii*) converge at elevations between 3000 and 3100 m, whereas four endemic *Aetanthus* species (*A. alternifolius*, *A. megaphyllum*, *A. ovalis* and *A. sessilifolius*) are elevational disjuncts (Fig. 26A).

*Oryctanthus* (Loranthaceae): Lowland forests between 200 and 400 m hold the highest (nine out of 11) number of species of this genus in Colombia, including the rainforest endemics *O. grammatus* (below 300 m), *O. grandis* (between 10 and 1500 m), and *O. neurophyllus* (between 50 and 500 m). The fourth endemic species (*O. perticus*), which grows in sub-Andean forests between 1000 and 1500 m, is an elevational disjunct with respect to *O. grammatus* and *O. neurophyllus* (Fig. 26B).

*Psittacanthus*: Lowland rainforests between the sea level and 250 m hold the highest (21 out of 37) number of species of this genus in Colombia, including seven endemics (*P. corderoi*, *P. gigas*, *P. micrantherus*, *P. ophiocephalus*, *P. schultesii*, *P. smithii* and *P. sulcatus*). Disjunct endemics grow in sub-Andean (*P. antioquiensis*, *P. crassicosatus*, *P. crassinervis*, *P. pentaphyllos* and *P. rotundatus*), Andean (*P. longirectus*) or high-Andean (*P. carinatus*) forests. The only endemic *Psittacanthus* species in Colombia restricted to the páramo ecosystem are *P. complanatus* and *P. microphyllus* (Fig. 26C).

*Dendrophthora* (Viscaceae): High-Andean forests and páramos between 3000 and 3400 m, hold the highest (13 out of 22) number of species of this genus in Colombia. Interestingly, the three endemic species of *Dendrophthora* occupy lower elevations at sub-Andean and Andean forests; these are *D. amalfiensis* (between 1300 and 1900 m), *D. stricta* (c 2200 m), and *D. sulcata* (between 1450 and 1840 m) (Fig. 27A).

*Phoradendron* (Viscaceae): The elevational belt between the sea level and 500 m holds the highest (36 out of 66) number of species of this genus in Colombia, including four endemic to the country (*P. apertiflorum*, *P. fonsecanum*, *P. longissimum* and *P. palaephyllum*). These four species are elevational disjuncts with the remaining endemic species of the genus. Only *P. retrophyllum* appears as a high Andean disjunct at elevations above 3000 m (Fig. 27B).

*Cuscuta* (Convolvulaceae): The elevational distribution for *Cuscuta* in Colombia shows no clearcut trend for its diversification. Whereas *C. colombiana*, *C. partita* and *C. pentagona* are found exclusively below 300 m, *C. corymbosa* and *C. popayanensis* are disjuncts restricted to elevations above 1700 m. Altogether, the remaining species (*C. americana*, *C. grandiflora*, *C. indecorosa* and *C. obtusifolia*) occupy a broader elevational belt between 0 and 4000 m, and only overlap between 500 and 1500 m (Fig. 28A).

*Buchnera* (Orobanchaceae): Lowland ecosystems between 400 and 500 m hold the highest (eight out of 11) number of species of this genus in Colombia, including the two endemic species to the country, namely, *B. jacoborum* (between 250 and 700 m) and *B. schultesii* (at around 450 m) (Fig. 28B).

*Castilleja* (Orobanchaceae): Páramo ecosystems between 3800 and 4100 m hold the highest (seven out of eight) number of species of this genus in Colombia, including the only endemic species to the country, namely, *C. paramensis*, which grows exclusively in peat bogs between 3500 and 4500 m (Fig. 28C).

*Neobartsia* (Orobanchaceae): All ten species of this genus in Colombia occupy Páramo ecosystems above 3000 m, including the only endemic species to the country, *N. matuy*, which grows at elevations c 3528 m (Fig. 28D).

### Elevational Ranges of Endemic Parasitic Angiosperms in Colombia (Fig. 29)

Out of the parasitic Angiosperm species endemic to Colombia, 27 of them (39.13%) grow at elevations below 1000 m, 23 (33.33%) are found between 1000 and 2000 m, 20 (28.98%) grow between 2000 and 3000 m, 12 (17.39%) occupy páramos between 3000 and 4000 m, and only one species (1.44%) reaches superpáramos above 4000 m in the country. This account strongly suggests that the number of endemic parasitic angiosperms in Colombia is inversely proportional to the elevation, regardless the type of parasitic lifeform (Fig. 29).

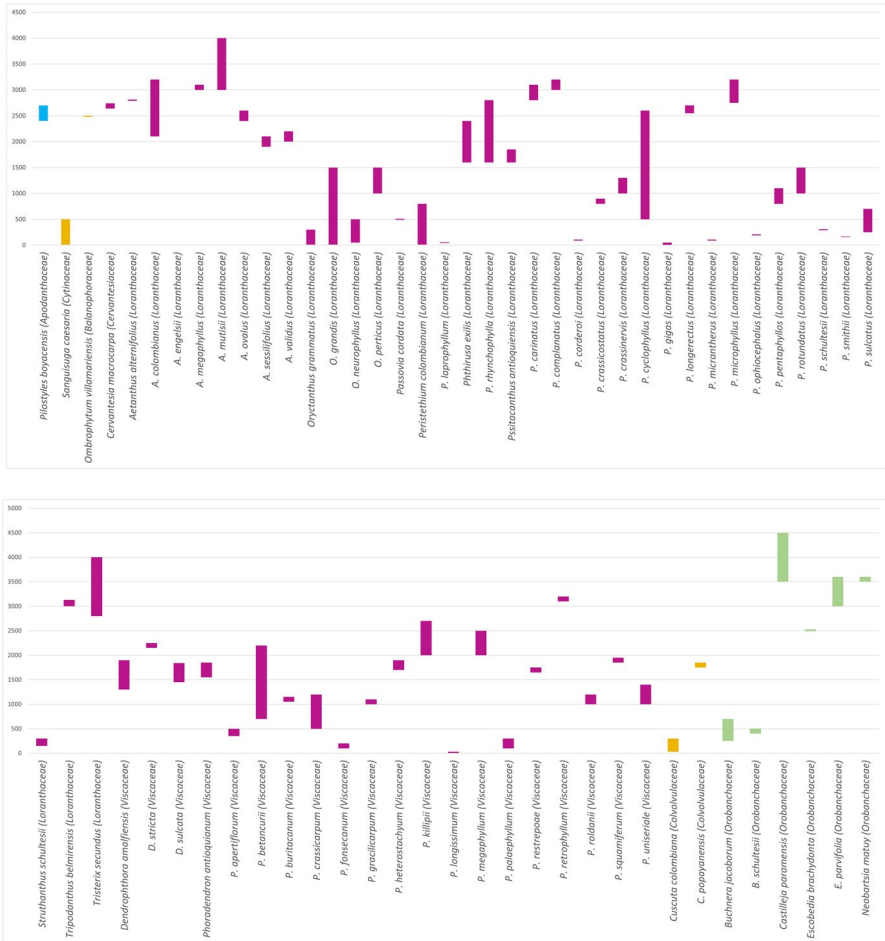


Fig. 29 Elevational range of the parasitic Angiosperms endemic to Colombia. Color coding: blue, holendoparasite; green, facultative hemiparasites; purple, obligate hemiparasites; ochre, holoxoparasites

## Lifeforms of Parasitic Flowering Plants in Colombia

The majority of parasitic flowering plants present in Colombia are stem obligate hemiparasites with various forms of haustoria, and belong to the Loranthaceae, Santalaceae and Viscaceae (Santalales; Figs. 1, 10, 13, 17, and 18). The root facultative hemiparasites, restricted to the Orobanchaceae (Figs. 1 and 22), are the second predominant lifeform. Conversely, the holoendoparasitic lifeform occurs only in *Apodanthes* and *Pilosyles* (Apodanthaceae, Cucurbitales; Figs. 1 and 4). In the remaining orders, four convergent lifeforms occur recurrently, as follows:

1. The twining stem holoparasitic *Cassytha* (Lauraceae) and *Cuscuta* (Convolvulaceae), both developing an adhesive disk. This remarkable example of convergent evolution has been extensively discussed in the literature. Notably, Heide-Jørgensen (1991) highlighted the most significant developmental and structural similarities of this organ in these two distantly related genera, including: the epidermal and cortical development of the adhesive disk; the trichomatose formation of the adhesive epithelium; the polysaccharide and pectinaceous nature of the sticky secretion; the development of the endophyte from the middle layers of the cortex; the collapsed parenchymatic zones of the twining stem; and the lack of Santalalean glandular tissue. Reproductive structures in both genera consist of small axillary flowers or few-flowered cymes scattered in the distalmost portions of the twigs.
2. The root holoexoparasitism has evolved independently in *Sanguisuga* (Cytinaceae), *Mitrastemon* (Mitrastemonaceae), all Balanophoraceae (Santalales), and *Lennoa* (Ehretiaceae). Convergent morphological traits include thickened underground runners, and massive, thick axes, protective scale bracts, racemose inflorescences, minute flowers with bright white, pink, or reddish perianth. Detail accounts exist on the structural connection of the Balanophoraceae species with their host roots (Kuijt & Bruns, 1987; Pellissari et al., 2022), but in general, the haustorium in this family consists of underground tuber-like structures. The vascular connection between parasite and hosts can range from simple (when the vessel elements from both species make contact) to complex (when parasitic cells reach the core of the host's conducting tissue). The emerging body portion consists of showy but ephemeral reproductive structures either as individual flowers or as massive, racemose inflorescences aboveground. Whereas the former three taxa possess small but highly elaborate flowers and accessory extrafloral structures, *Lennoa* displays intricate branched inflorescences, flowers with a showy, rotaceous perianth, and proliferative carpels (Fig. 19A–E).
3. The root obligate hemiparasitism has evolved independently in *Krameria* (Krameriaceae), *Gaiadendron* (Loranthaceae), and all Cervantesiaceae, Opiliaceae, Schoepfiaceae, Strombosiaceae and Ximeniaceae. This lifeform is the least known in terms of development, structure and ecology, likely due to the fact that most species are medium-sized to large trees.

## Colombian Species Belonging to Parasitic Orders with Unconfirmed Parasitic Lifeforms

The following species native to Colombia belong to predominantly parasitic orders but require field studies and direct verification of their purported parasitic lifeforms:

### Zygophyllales:

#### Zygophyllaceae:

*Guaiacum officinale* L., from dry forests of the Caribbean plains (Region I) and the Cauca valley (Region III), at elevations below 1000 m.

*Kallstroemia maxima* (L.) Hook. & Arn., *K. parviflora* Norton, and *K. pubescens* (G. Don) Dandy, all from dry forests and thickets in regions I and III, at elevations below 1700 m.

*Plectocarpa arborea* (Jacq.) Christenh. & Byng, and *P. carrapo* (Killip & Dugand) Christenh. & Byng, both from dry to wet forests of the Cauca and Magdalena valleys, in regions I and II, at elevations below 1200 m.

### Santalales

#### Aptandraceae Miers (1853).

*Aptandra caudata* A.H. Gentry & R. Ortiz; *A. tubicina* (Poepp.) Benth. ex Miers. Region III, at elevations between 400 and 900 m.

*Cathedra acuminata* Miers.

*Chaunochiton angustifolium* Sleumer; *C. kappleri* (Sagot ex Engl.) Ducke, *C. loranthoides* Benth. Regions II and IV, at elevations below 600 m.

#### Coulaceae Tiegh.:

*Minuartia guianensis* Aubl. Regions II, III and V, at elevations below 1000 m.

#### Erythralaceae:

*Heisteria acuminata* (Bonpl.) Engl., *H. asplundii* Sleumer, *H. barbata* Cuatrec., *H. concinna* Standl., *H. duckei* Sleumer, *H. insculpta* Sleumer, *H. latifolia* Standl., *H. maytenoides* Spruce ex Engl., *H. nitida* Engl., *H. ovata* Benth., *H. pacifica* P. Jørg. & C. Ulloa, *H. scandens* Ducke, and *H. spruceana* Engl. Regions II, III (Magdalena Valley) and V, at elevations below 500 m.

#### Olacaceae Martinov:

*Olex candida* (Poepp.) Christenh. & Byng; *O. inopiflora* (Miers) Christenh. & Byng; *O. macrophylla* Benth., and *O. redmondii* (Steyerm.) Christenh. & Byng., all at elevations between 50 and 500 m, in regions I (Magdalena valley), II, IV and V.

#### Ximeniaceae:

*Curupira tefeensis* G.A. Black. Amazon forests (Region V), at elevations below 200 m.



## Concluding remarks

The majority of parasitic angiosperm species in Colombia is concentrated in regions I (Caribbean) and III (Andean), which currently have the highest deforestation areas (c 75% and 55%, respectively) in the country (IDEAM, 2022). Given the crucial roles of most of these species providing pollen, nectar and fruits to the fauna, we call for urgent plans of conservation, recovery and protection of the natural reserves still in place on those ecosystems. In general, the presence of species of Balanophoraceae, Apodanthaceae, Cytinaceae, Loranthaceae (especially *Aetanthus*, *Oryctanthus*, *Psittacanthus*, and *Tristerix*), and Mitrastemonaceae in dry forests as well as cloud or rainforests, and endemic Orobanchaceae from paramo peat bogs serve as indicators of healthy environmental conditions and little disturbance in their ecosystems. At present, we do not detect any large-scale threat caused by any parasitic flowering plant species to the native flora or to the crops in the country. However, small-flowered Loranthaceae and species of Viscaceae can rapidly colonize fruit or ornamental trees in human disturbed environments, and awareness needs to be raised to control the excessive proliferation of these plants.

**Acknowledgements** We are grateful to Jeff Mower (Center for Plant Science Innovation, University of Nebraska, Lincoln), for the assemblage and analysis of the *Castilleja paramensis* plastome, and to Juan Fernando Alzate and Laura Arias (Centro Nacional de Secuenciación Genómica, SIU, Universidad de Antioquia), for the assemblage and analysis of the *Pilostyles boyacensis* plastome. We thank our students Vanessa Suaza-Gaviria (Universidad de Antioquia), and Angie D. González, Sebastián Guzmán and David Polo (Universidad Nacional de Colombia), for their help during field and lab work. Xaleth Cordero kindly supplied the field photographs of *Psittacanthus corderoi*, for which we thank him. Thanks also to Carlos Sarmiento and Fernando Fernández (Universidad Nacional de Colombia), and Martha Wolff (Universidad de Antioquia), for the identification of the floral visitor of *Passovia pedunculata* (Loranthaceae) shown in Fig. 13M. We acknowledge the support of Sebastián González (Massachusetts College of Art and Design, Boston, USA), for his continuous assistance during field trips and for taking most of the field photographs published here. Finally, the authors thank the staff of the Harvard University Herbaria for logistic support during their short term visits to this Institution. The second author thanks the Fulbright Visiting Scholar Program 2022

**Author Contribution** FG and NP-M equally contributed to the conceptualization, data curation, writing, review, editing, and funding. Both authors approve the final manuscript.

**Funding** Open Access funding provided by Colombia Consortium This research was funded by the project “Evolución de los genes asociados a embriogénesis temprana de la endoparásita *Pilostyles boyacensis* (Apodanthaceae)”, funded by the Facultad de Ciencias, Sede Bogotá, Universidad Nacional de Colombia (Código HERMES: 50155; Código QUIPU: 202010026978) and the Estrategia de Sostenibilidad 2018–2019 project granted to the Plant Evo-Devo group at the Universidad de Antioquia, Medellín (Colombia).

**Data Availability** The data that support the findings of this study are available upon request to the corresponding author [NLP]. Most of them come from publicly available repositories of the Herbario Nacional Colombiano, COL [<https://www.biovirtual.unal.edu.co/es/colecciones/search/plants/>] and the Herbario de la Universidad de Antioquia, HUA [<https://www.udea.edu.co/wps/portal/udea/web/inicio/unidades-academicas/ciencias-exactasnaturales/herbario>].

**Declarations**

**Conflict of Interest** The authors declare no conflict of interest.

**Research Involving Human Participants and/or Animals** Not applicable.

**Informed Consent** Not applicable.

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