Fundación Miguel Lillo
Tucumán
Argentina



# Leaf anatomical and histochemical characterization of *Cavendishia bracteata* and *Macleania rupestris* (Ericaceae), from the Encenillo Biological Reserve (Guasca, Cundinamarca, Colombia)

## Caracterización anatómica e histoquímica foliar de *Cavendishia bracteata* y *Macleania rupestris* (Ericaceae), de la Reserva Biológica Encenillo (Guasca, Cundinamarca, Colombia)

Cubillos-Ariza, Laura V.[1,3]; Fagua Álvarez-Flórez[1*]; Victor M. Giral-Diaz[1]; Mónica González[1]; María Cuervo-Gómez[1,2]; Claudia J. Garnica-Díaz[2]; Grace P. John[2]; Beatriz Salgado-Negret[1]; Luz M. Melgarejo[1]

[1] Departamento de Biología, Facultad de Ciencias, Universidad Nacional de Colombia (UNAL), Carrera 30 #45-3, 111321, Bogotá, Colombia.
[2] Department of Biology, University of Florida, 876 Newell Dr, 32611, Gainesville, Florida, USA.
[3] Departamento de Zoologia, Setor de Ciências Biológicas, Universidade Federal do Paraná (UFPR), Av. Cel. Francisco H. dos Santos, 100 – Jardim das Américas, 81.531-980, Curitiba, Paraná, Brasil.
* Corresponding author: <falvarez@unal.edu.co>

## Abstract

The species *Cavendishia bracteata* and *Macleania rupestris* (Ericaceae) are plants with medicinal potential used in ecological restoration in the high Andean forests of South America; however, the anatomy and histochemistry of their leaves have not yet been described. Plant material was collected from permanent plots established in the Encenillo Biological Reserve, Guasca, Colombia. For anatomical analysis, the leaf samples

➤ Ref. bibliográfica: Cubillos-Ariza, L. V.; Álvarez-Flórez, F.; Giral-Diaz, V. M.; González, M.; Cuervo-Gómez, M. P.; Garnica-Díaz, C. J.; John, G. P.; Salgado-Negret, B.; Melgarejo, L. M. 2026. Leaf anatomical and histochemical characterization of *Cavendishia bracteata* and *Macleania rupestris* (Ericaceae), from the Encenillo Biological Reserve (Guasca, Cundinamarca, Colombia). *Lilloa 63* (1): 29-48. doi: https://doi.org/10.30550/j.lil/2273
➤ Recibido: 19 de septiembre 2025 – Aceptado: 28 de enero 2026 – Publicado: 31 de marzo 2026.
➤ URL de la revista: http://lilloa.lillo.org.ar

were embedded in paraffin, sectioned, and stained using astra blue and fuchsin staining techniques; subsequently, tissue measurements were taken. For histochemical analysis, freehand sections were made and stained with potassium dichromate, phloroglucinol, Lugol's, and Sudan black. The leaves of both species displayed meso-xeromorphic traits with a thick cuticle, smooth adaxial and irregular abaxial surfaces, an epidermis with thick outer walls, lignified adaxial and abaxial hypodermis, one or two palisade parenchyma layers, and a central collateral vascular bundle. Histochemical analysis revealed the presence of phenolic compounds, tannins, lignin, and neutral lipids. No starch granules were observed. This study describes the leaf anatomy of *C. bracteata* and *M. rupestris* under high-altitude conditions in the Colombian Andes. The qualitative presence of phenolic compounds, tannins, lignin, and neutral lipids supports their potential medicinal value.

**Keywords:** Ethnobotany; leaf anatomy; phenols; secondary metabolites.

## Resumen

Las especies, *Cavendishia bracteata* y *Macleania rupestris* (Ericaceae) son plantas con potencial medicinal y son utilizadas en restauración ecológica en los bosques altoandinos de Sudamérica; sin embargo, aún no han sido descritas la anatomía e histoquímica de sus hojas. Se colectó material vegetal en parcelas permanentes establecidas en la Reserva Biológica Encenillo, Guasca, Colombia. Para el análisis anatómico se cortaron muestras de hojas embebidas en parafina, se utilizaron las técnicas de coloración azul de astra y fucsina y se hicieron mediciones de los tejidos presentes. Para el análisis histoquímico, se realizaron cortes a mano alzada con tinciones de dicromato de potasio, floroglucinol, lugol y Sudán negro. Las hojas de ambas especies mostraron caracteres meso-xeromórficos con una cutícula gruesa, superficies adaxiales lisas y abaxiales irregulares, una epidermis con paredes externas gruesas, una hipodermis adaxial y abaxial lignificada, una o dos capas de parénquima en empalizada y un haz vascular colateral central. El análisis histoquímico reveló la presencia de compuestos fenólicos, taninos, lignina y lípidos neutros. No se observaron gránulos de almidón. Se describe la anatomía foliar de *C. bracteata* y de *M. rupestris* en condiciones de alta montaña, de los Andes de Colombia. La presencia cualitativa de compuestos fenólicos, taninos, lignina y lípidos neutros indican su potencial uso medicinal.

**Palabras clave:** Anatomía de la hoja; etnobotánica; fenoles; metabolitos secundarios.

## INTRODUCTION

The Ericaceae family comprises approximately 4000 species distributed in 110 genera (Dávila, 2001). It has a cosmopolitan distribution, especially in temperate and cold climate regions (Socorro & González, 2014). Ericaceae reach their greatest diversity in the Neotropical mountains in humid and cold forests between 1500 and 3000 masl (900 species belonging to 46 genera for the Neotropics), mainly in the northeast of South America, where *Cavendishia* Gray (150 spp.) and *Macleania* Hook (40 spp.) stand out among the most representative genera (Dávila, 2001).

*Cavendishia bracteata* (Ruiz & Pav. ex J.St.-Hil.) Hoerold and *Macleania rupestris* (Kunth) A.C. Sm are two species in the family Ericaceae that are abundant in the high Andean forests, subparamo and paramo ecosystems in Colombia, and have been widely used for medicinal purposes (García, 1982a; García, 1982b). *C. bracteata*, commonly called "uva de anís" in Spanish or "mountain blueberry" in English, is distributed from Mexico to Bolivia, between 1000 and 3500 meters (Aguilar & Torres, 2010; García *et al*., 2023). The species promotes the restoration, recovery, and rehabilitation of ecosystems and provides food resources for wildlife (Aguilar & Torres, 2010). Its leaves and fruits contain tannic acid, so its decoction is used as an astringent and antirheumatic (García, 1982a). In the Sierra Nevada de Santa Marta, Colombia, the plant is used as a ganglion anti-inflammatory (Carbonó-Delahoz & Dib-Diazgranados, 2013). Likewise, the young leaves are used by Peruvian communities to cure pimples and scabies through baths (Pérez, 2017). Because of its economic potential, this species was included in the list of promising plant species in the countries of the Andrés Bello Convention (Aguilar & Torres, 2010). Likewise, *M. rupestris*, popularly known in Spanish as "uva camarona" or "rock Macleania" in English, is distributed from Nicaragua to Peru at elevations between 2000 and 4100 meters (Pedraza, 2023). It is part of plant pioneer communities on stony sites (Valencia & Carrillo, 1991), i.e., it colonizes habitats created by disturbances (Dalling, 2008). This plant has medicinal applications; its leaves, when decocted, serve as an antidiarrheal remedy and are used during typhoid fevers due to their content of tannins and benzoic acid (Garcia, 1982b).

For *C. bracteata*, a study of phytochemistry in leaves is available (García & Rodríguez, 2019) as well as an anatomical review for the genus *Cavendishia* (Luteyn, 1983). For *M. rupestris*, anatomical characterizations of the fruit (Valencia & Carrillo, 1991) and flower (Lozano & Valencia, 1992), as well as a brief anatomical description of the leaf of individuals collected in the paramo (Mora-Osejo *et al*., 1995) has been published. While *C. bracteata* and *M. rupestris* are widely distributed and are potentially valuable for medicinal uses and ecological restoration, there is little information relating to leaf anatomy and histochemistry.

Moreover, considering that the leaves of these species have been used in diverse ways by different local communities (García, 1982a; García, 1982b; Carbonó-Delahoz & Dib-Diazgranados, 2013), performing a histochemical study allows preliminary identification of the potential components that have medicinal properties (Matias *et al*., 2016).

Therefore, the objective of the present study was to describe the anatomy and leaf histochemistry of *C. bracteata* and *M. rupestris* and to contribute to our knowledge.

## MATERIALS AND METHODS

### Study area

The Encenillo Biological Reserve (4°47' N, y 73°54' W), is near the village of La Trinidad in the municipality of Guasca, Cundinamarca, Colombia. It is located between 2800 and 3200 m. The average annual temperature is 12 °C; and the average precipitation is 1300 mm/year (Fundación Natura Colombia, 2022). The Reserve currently has an area of 206 ha of which 52 ha represent sub-humid and dry high Andean Forest (Restrepo, 2016). These forests are dominated by *Weinmannia tomentosa* (Cunoniaceae), which vary from medium to tall, and families such as Asteraceae, Ericaceae, Melastomataceae, Rubiaceae and tree ferns (Ramírez-Morán *et al*., 2016). In the region, the rainfall regime is monomodal, with a dry season from October to January, a transition season from February to March and a rainy period from April to September (Casas *et al*., 2021).

### Plant material

For the anatomical and histochemical characterization of the leaves, we sampled light-exposed, terminal branch from the middle third of the upper foliage of each of three individual plants per species. Three mature leaves were excised from each branch and fixed in FAA (formaldehyde: glacial acetic acid: 70% ethanol, 5:5:90).

### Anatomical characterization

Tissue sections from the center of each fixed leaf were prepared with a series of alternating step-wise ethanol dehydration and HistoChoice (Sigma-Aldrich®) lightening agent treatments (Toro-Tobón *et al*., 2022). Prepared tissue specimens were embedded in paraffin at 60 °C, changing the solutions three times every 12 hours. We made cross sections of 8 $\mu$m using a rotation microtome (Spencer, American Optical Company, New York, USA). We mounted the slices on slides with Mayer's adhesive (Ruzin, 1999) at 60°C for 24 h.

We stained the specimens with acidified Astra-blue (1 g/100 mL of 2% tartaric acid) for 20 minutes and basic ethanolic fuchsin (0.1 g/100 mL of 50% ethanol) for 40 minutes. Prepared slides were then fixed with cyto-resin. We imaged slides with an Olympus BX50 microscope fitted with a Moticam Pro 282B camera (Olympus Optical Co., Ltd, Tokyo, Japan) and measured anatomical traits using ImageJ 1.53t program (Java 1.8.0_345) (Schneider *et al*., 2012). For each section, we took five measurements of leaf lamina, cuticle, adaxial and abaxial epidermis and hypodermis, palisade and spongy parenchyma thickness and 15 measurements of major diameter of xylem vessels and xylem vessel wall (Toro-Tobón *et al*., 2022).

For the measurement of stomatal traits, we imprinted the stomata on the adaxial and abaxial sides using transparent nail polish and adhesive tape (Pérez *et al*., 2010), on mature leaves with the same characteristics as those used for anatomical traits. We imaged each impression with an Olympus BX50 microscope with a Moticam Pro 282B camera (Olympus Optical Co., Ltd., Tokyo, Japan) and measured guard cell length and width (mm) and density ($mm^2$). The stomatal density was computed following El-Sharkawy *et al.* (1985) and Pérez *et al.* (2010) (Eqn 1), and the stomatal index following Pérez *et al* (2010) (Eqn 2).

$$\frac{(Adaxial\,stomatal\,density)^2 + (Abaxial\,stomatal\,density)^2}{Adaxial\,stomatal\,density + Abaxial\,stomatal\,density} \qquad \text{(Eqn 1)}$$

$$\frac{Stomatal\,density}{Stomatal\,density + Epidermal\,cell\,density} \times 100 \qquad \text{(Eqn 2)}$$

## Histochemical characterization

We performed freehand sections on fresh material that was subsequently subjected to different histochemical tests with some modifications (Demarco, 2017). We used potassium dichromate 10% in distilled water for the detection of phenolic compounds (15 and 30 min for *C. bracteata* and *M. rupestris*, respectively), phloroglucinol-HCl 10% in ethanol for the detection of lignin in cell walls (15 min), lugol (30 min) for the identification of starch granules, and Sudan Black 0.25% in ethanol (20 min) to identify the presence of neutral lipids. In each test, we compared our specimens with unstained material to avoid false positives. We made observations and photographed using an Olympus BX50 microscope with a Moticam Pro 282B camera (Olympus Optical Co., Ltd, Tokyo, Japan).

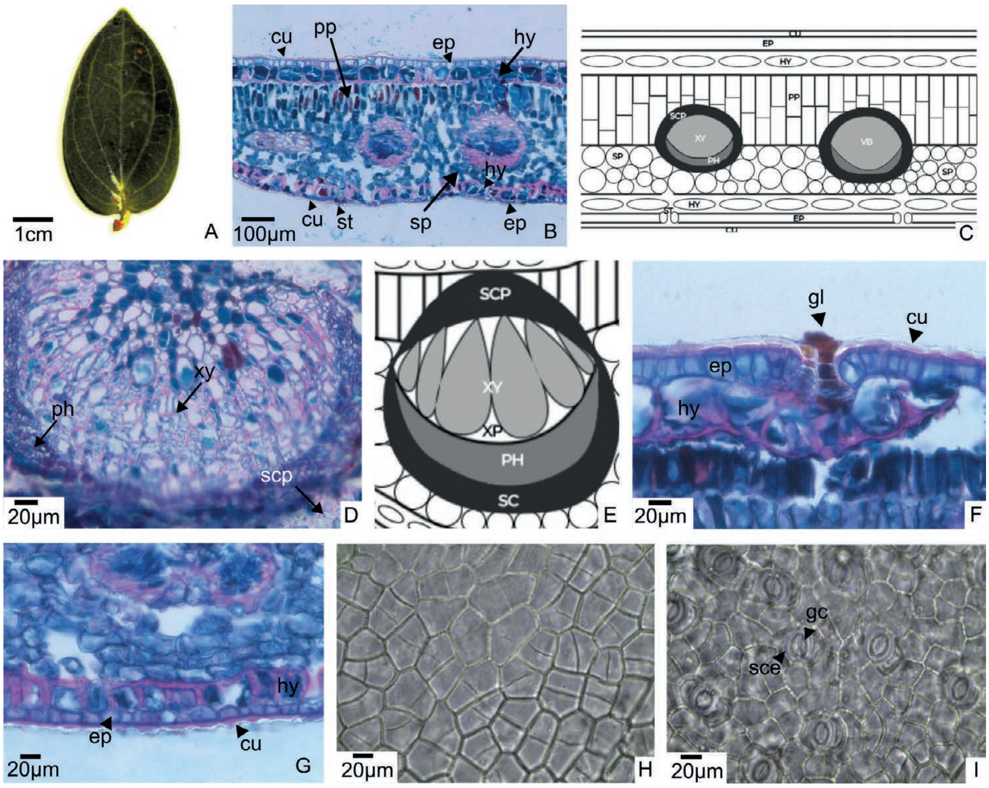


**Fig. 1.** Optical microscopy and diagrams of basic fuchsin and astra blue-stained sections of *Cavendishia bracteata* leaf. A) Leaf. B) Mesophyll. C) Diagram of the mesophyll. D) Med-vein of the leaf lamina. E) Diagram of the mivein of the leaf lamina. F) Detail of the cuticle, epidermis, hypodermis, and gland on the adaxial surface. G) Detail of cuticle, epidermis, and hypodermis on the abaxial surface. H) Adaxial epidermis. I) Abaxial epidermis with the presence of stomata. Abbreviations: vb: Vascular bundle; scp: Sclerenchyma sheath; pp: Palisade parenchyma; sp: Spongy parenchyma; st: Stoma; cu: Cuticle; ep: Epidermis; hy: Hypodermis; gl: Gland; xy: Xylem; xp: Xylem parenchyma; ph: Phloem; sce: Epidermal cell; gc: Occlusive cell. Scale bars: A = 1 cm; B = 100 $\mu$m; D, F–I = 20 $\mu$m.

**Fig. 1.** Microscopía óptica y diagramas de secciones teñidas con fucsina básica y azul de Astra de la hoja de *Cavendishia bracteata*. A) Hoja. B) Mesófilo. C) Diagrama del mesófilo. D) Vena media de la lámina foliar. E) Diagrama de la vena media de la lámina foliar. F) Detalle de la cutícula, epidermis, hipodermis y glándula en la superficie adaxial. G) Detalle de la cutícula, epidermis e hipodermis en la superficie abaxial. H) Epidermis adaxial. I) Epidermis abaxial con presencia de estomas. Abreviaturas: vb: haz vascular; scp: vaina de esclerénquima; pp: parénquima en empalizada; sp: parénquima esponjoso; st: estoma; cu: cutícula; ep: epidermis; hy: hipodermis; gl: glándula; xy: xilema; xp: parénquima xilemático; ph: floema; sce: célula epidérmica; gc: célula oclusiva. Barras de escala: A = 1 cm; B = 100 $\mu$m; D, F–I = 20 $\mu$m.

## RESULTS AND DISCUSSION

### Anatomical characterization

#### *Cavendishia bracteata*

The leaves of *C. bracteata* (Fig. 1A) show bifacial lamina (Figs. 1B, C) wherein the palisade parenchyma has 1 or 2 layers, with the shorter cells comprising the inner layer (Figs. 1B, C) and a lax spongy parenchyma occupies 44% ± 2 of the lamina (Table 1; Figs. 1B, C). In the central vein there was a transition to sclerenchyma tissue and parenchyma (Fig. 1D). The central vascular bundle was collateral and had a sclerenchyma sheath (Figs. 1D, E). In the sclerenchyma of the median vein, druse crystals were occasionally observed. The adaxial epidermis was uniseriate, and its cells had thicker outer walls than the rest; the cuticle was smooth (Fig. 1F) and had occasional trichomes at the midveins (see Fig. 3D). The cells of the abaxial epidermis were smaller compared with the adaxial epidermis (Table 1) and with a wavy cuticle (Fig. 1G). Both the adaxial (beam) and abaxial (underside) epidermis had multicellular glands (Fig. 1F).

The adaxial and abaxial hypodermis was single-layered with a thickening of the cell wall except for the outer side (Figs. 1F, G). The adaxial hypodermis was larger than the abaxial (Table 1). The leaves were hypostomatic and the epidermal cells were tetragonal to hexagonal (Figs. 1H, I). The stomata were paracytic, as the epidermal cells were parallel to the occlusive cells (Fig. 1I) and protruded slightly above the level of the epidermal tissue (Fig. 1B). The stomata had a length of 0.035 mm ± 0.004, width of 0.034 mm ± 0.003, total stomatal area 0.001 $mm^2$ ± 0.0002. We found a stomatal density of 244.51 $mm^2$ ± 61.97 and a stomatal index of 20.44 % ± 7.28.

### *Macleania rupestris*

The leaves of *M. rupestris* (Fig. 2A) were bifacial (Figs. 2B, C) featuring 1-2 layers of palisade parenchyma (Figs. 2B, C) and lax spongy parenchyma (Figs. 2B, C) occupying 49% ± 2 of the lamina (Table 1). The central vascular bundle transitions to sclerenchyma tissue and parenchyma (Fig. 2D). The midvein was collateral with a multilayered sheath of sclerenchyma (Figs. 2D, E). In the xylem of the midvein we occasionally found druse crystals. The epidermis was single-layered, had thick outer walls and had

**Table 1.** Measurements of foliar anatomical traits of *Cavendishia bracteata* and *Macleania rupestris*.
**Tabla 1.** Medidas de caracteres anatómicos foliares de *Cavendishia bracteata* y *Macleania rupestris.*

| Trait (μm) | *Cavendishia bracteata* | *Macleania rupestris* |
|---|---|---|
| Lamina thickness | 356.36 ± 44.33 | 302.58 ± 33.50 |
| Adaxial cuticle | 5.02 ± 0.91 | 4.10 ± 0.78 |
| Abaxial cuticle | 4.41 ± 0.95 | 3.88 ± 0.81 |
| Adaxial epidermis | 24.25 ± 3.22 | 23.08 ± 3.29 |
| Abaxial epidermis | 15.89 ± 3.14 | 14.09 ± 2.06 |
| Adaxial hypodermis | 46.22 ± 10.03 | 35.38 ± 4.44 |
| Abaxial hypodermis | 31.37 ± 6.96 | 24.79 ± 3.94 |
| Palisade parenchyma | 76.98 ± 11.29 | 54.21 ± 7.98 |
| Spongy parenchyma | 157.39 ± 22.95 | 147.36 ± 22.00 |
| Diameter of xylem vessels | 14.70 ± 3.02 | 15.37 ± 2.97 |
| Xylem vessel wall | 1.05 ± 0.23 | 1.04 ± 0.21 |

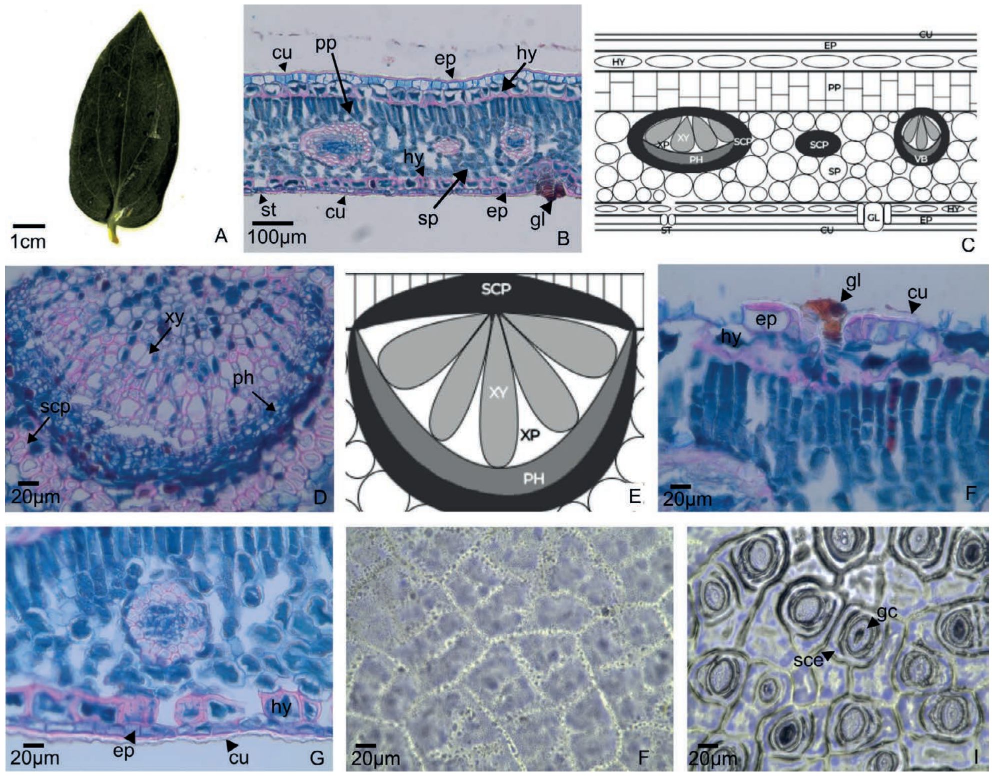


**Fig. 2.** Optical microscopy and diagrams of basic fuchsin and astrablue stained sections of a *Macleania rupestris* leaf. A) Leaf. B) Mesophyll. C) Diagram of the mesophyll. D) Midvein. E) Diagram of the midvein of the leaf lamina. F) Detail of the cuticle, epidermis, hypodermis, and gland on the adaxial surface. G) Cuticle, epidermis, and hypodermis of the abaxial surface. H) Adaxial epidermis. I) Abaxial epidermis with the presence of stomata. Abbreviations: vb: Vascular bundle; scp: Sclerenchyma sheath; pp: Palisade parenchyma; sp: Spongy parenchyma; st: Stoma; cu: Cuticle; ep: Epidermis; hy: Hypodermis; gl: Gland; xy: Xylem; ph: Phloem; sce: Epidermal cell; gc: Occlusive cell. Scale bars: A = 1 cm; B = 100 $\mu$m; D, F–I = 20 $\mu$m.

**Fig. 2.** Microscopía óptica y diagramas de secciones teñidas con fucsina básica y azul de Astra de hoja de *Macleania rupestris*. A) Hoja. B) Mesófilo. C) Diagrama del mesófilo. D) Vena media. E) Diagrama de la vena media de la lámina foliar. F) Detalle de la cutícula, epidermis, hipodermis y glándula en la superficie adaxial. G) Cutícula, epidermis e hipodermis de la superficie abaxial. H) Epidermis adaxial. I) Epidermis abaxial con presencia de estomas. Abreviaturas: vb: haz vascular; scp: vaina de esclerénquima; pp: parénquima en empalizada; sp: parénquima esponjoso; st: estoma; cu: cutícula; ep: epidermis; hy: hipodermis; gl: glándula; xy: xilema; ph: floema; sce: célula epidérmica; gc: célula oclusiva. Barras de escala: A = 1 cm; B = 100 $\mu$m; D, F–I = 20 $\mu$m.

trichomes occasionally located in the adaxial part of the midvein (see Fig. 4F). The epidermal cells of the underside were smaller than those of the bundle (Table 1). The adaxial cuticle was smooth and the abaxial cuticle was wavy (Figs. 2F, G). It had adaxial and abaxial hypodermis with cells with a thickened wall, except for the external side (Figs. 2F, G). The abaxial hypodermis had more irregular and smaller cells (Table 1) compared to those located in the bundle. Multicellular glands were found on both the adaxial and abaxial surfaces incorporated into the epidermal tissue (Figs.

2B, F). Leaves were hypostomatic (Figs. 2H, I) with paracytic stomata (Fig. 2I) overlying the epidermal layer (Fig. 2B).

The epidermal cells were tetragonal (Figs. 2H, I). The stomata were 0.037 mm ± 0.004 long, and 0.031 mm ± 0.003 wide, with a total stomatal area of 0.001 $mm^2$ ± 0.0002. We found a stomatal density of 257.24 $mm^2$ ± 36.75 and a stomatal index (%) of 31.23 ± 6.89

Both *C. bracteata* and *M. rupestris* presented anatomical structures typical of angiosperms with bifacial leaves (Figs 1B and 2B), with tissues distributed so that the spongy mesophyll occupied the greatest space (Table 1). The adaxial epidermis and hypodermis were larger than the abaxial ones. Regarding the measurements of the diameter vessels and xylem wall, the values were similar in the two species (Table 1).

Here we describe the anatomical and histochemical leaf characteristics of *C. bracteata* and *M. rupestris*. The middle vein of *C. bracteata* and *M. rupestris* was characterized by the typical collateral distribution reported for most dicots (Cutler *et al*., 2007). The highly sclerified vascular bundle sheath found in *M. rupestris* and *C. bracteata* contributes to mechanical support and is a frequent character in the Ericaceae (Böcher, 1981). The presence of trichomes in *C. bracteata* and *M. rupestris*, specifically in the adaxial part of the midrib, is also seen in *C. aurantiaca* J.L. (Luteyn. 1980). Similarly, occasional trichomes are also observed in *Erica arborea* L. (Ericaceae) (Güvenç & Kendir̆, 2012) and some species of *Rhododendron* L. (Sosnovsky *et al*., 2017). The occasional pubescence observed in both species was described by Luteyn (2002) for *C. bracteata*, who does not correlate it with environmental factors, but instead considers it a random character.

In this research, druse crystals were occasionally found in *C. bracteata* and *M. rupestris* in the sclerenchyma and xylem of the midvein respectively. They are also reported on the petiole, lamina, or other plant parts in the Ericaceae family (Stevens *et al*., 2004). Also, Luteyn (1983) reported druses in the mesophyll and vascular bundle sheath in his review of the genus *Cavendishia*.

The cuticle, epidermis, and hypodermis act as a protective barrier against excess solar radiation, preventing chlorophyll oxidation (Carrasco-Ríos. 2009; Mar-Jiménez & Vargas-Simón. 2022). The cuticles found here are classified as medium thick (4-7 $\mu$m), according to the ranges established by Pyykkö (1966) which may serve as a barrier that reduces water loss, protects against mechanical damage, prevents pathogen invasion, and confers UV protection to the plant (Segado *et al*., 2016). The polygonal epidermal cells that are also found in other Ericaceae such as *Rhododendron* and *Leucothoe* D. Don. (Chowdhury. 2010; Pathak & Panda, 2013; Panda & Kirtania. 2016) may also contribute to enhanced mechanical stress tolerance. The outer cell wall of the epidermis of *C. bracteata* and *M. rupestris* is thicker since it is the structure that bears greater stress exerted by internal tissues in growth with respect to the periclinal and anticlinal inner walls (Segado *et al*., 2016).

Finally, cells of the adaxial epidermis were larger than the abaxial epidermis, a frequent characteristic in the family (Böcher, 1981).

The presence of a hypodermis of 1 or 2 or more layers is common in the Ericaceae family, specifically in the tropical Vaccinieae tribe (Stevens *et al*., 2004), may serve as water storage tissues, buffering leaf water status during transpiration (Böcher. 1981). Notably, a previous study of *M. rupestris* in Paramo ecosystem reported hypodermis only on the adaxial side, a two-layered palisade parenchyma with sclereids in the spongy parenchyma and lageniform hairs (Mora-Osejo *et al*., 1995).

The differences as the presence of an extra layer of parenchyma, trichomes and a more sclerified mesophyll can be attributed to the quality of luminosity or humidity in the different habitats in which the species develop and which influence the conformation of the leaf mesophyll (Gogosz *et al*., 2012; Villarreal & Soto, 2015; Marín *et al*., 2022).

The monostratified epidermis, sparse pubescence, lax spongy parenchyma, and higher proportions with respect to palisade parenchyma in the two taxa studied, correspond to mesomorphic anatomical traits (Cutler *et al*., 2007; Jáuregui & Torres, 2014). However, *C. bracteata* and *M. rupestris* also possess xeromorphic features such as a thick cuticle and outer epidermal walls, the presence of adaxial and abaxial hypodermis, and sclerenchymatous sheath (Böcher, 1981; Roth, 1984; Jáuregui & Torres, 2014).

Our results showed that *C. bracteata* and *M. rupestris* present paracytic stomata (Stevens *et al*., 2004) and hypostomatic stomatal density within the range reported for tropical forest trees (Larcher, 2003) and for another genus inside Ericaceae (Nilsen *et al*., 2014). The presence of paracytic stomata is confirmed in the description of the genus *Cavendishia* (Luteyn, 2002), as well as that of *M. rupestris* (Mora-Osejo *et al*., 1995). By assessing an altitudinal gradient ranging from montane forests to paramo in the eastern cordillera in the Andes of Ecuador, Soukup *et al.* (2021) reported similar stomatal densities and sizes for species growing in the montane forests. In addition, increments in stomatal density coupled with decreases in stomatal size, have been reported as a trade-off with increasing altitude at the species and community level (Kessler *et al*., 2007; Soukup *et al*., 2021; Liu *et al*., 2020). These findings illustrate the role of stomatal traits in coping with environmental conditions; smaller and denser stomata constrained in the abaxial side of the leaf mitigate the effects of excess radiation and heat, and facilitate stomata control, diminishing water loss and improving water use efficiency (Doheny-Adams *et al*., 2012; Raven, 2014). Despite the relevance of these traits, there is scarce information on Ericaceae species in high Andean forests.

## Histochemical characterization

### *Cavendishia bracteata*

Histochemical analysis showed the presence of phenolic compounds in both the palisade parenchyma and the spongy parenchyma, phloem, epidermis, and hypodermis (Figs. 3B, C) (Table 2). Lignin was easily recognized in the central vein sclerenchyma fibers, vascular bundle sheath, xylem vessel cell walls, and the hypodermis (Fig. 3D). In the case of the Sudan Black test the cuticle was strongly stained followed by the epidermis together with the glands; and, to a lesser extent, some cytoplasmic inclusions in epidermis, hypodermis, palisade parenchyma, spongy parenchyma, and vascular bundles (Fig. 3E). Lugol did not react with any structure; therefore, the leaf of *C. bracteata* did not contain starch granules.

### *Macleania rupestris*

In histochemical analyses of *M. rupestris* phenolic compounds were visible in the sclerenchymatous tissue of the central vein and xylem (Fig. 4B). They were found in the palisade parenchyma, followed by phloem, epidermis, hypodermis, and spongy parenchyma (Fig. 4C) (Table 2). On the other hand, the cuticle presented neutral lipids, followed by the epidermis and glands and some cytoplasmic inclusions of the epidermis, hypodermis, palisade parenchyma, and spongy parenchyma (Figs. 4D, E, F).

**Table 2.** Histochemical analysis of *Cavendishia bracteata* and *Macleania rupestris* leaves. Potassium dichromate was used for phenolic compounds, phloroglucinol for lignin, lugol for starch and Sudan Black for neutral lipids. Qualitative symbols: (+) reacted or (-) did not react. Abbreviations: vb: Vascular bundle; scp: Sclerenchyma sheath; pp: Palisade parenchyma; sp: Spongy parenchyma; cu: Cuticle; ep: Epidermis; hy: Hypodermis; xy: Xylem; ph: Phloem; tr: Trichome; sc: Sclerenchyma; gl: Glands.

**Tabla 2.** Análisis histoquímico de hojas de *Cavendishia bracteata* y *Macleania rupestris*. Se utilizó dicromato de potasio para los compuestos fenólicos, floroglucinol para la lignina, lugol para el almidón y Sudán negro para los lípidos neutros. Símbolos cualitativos: (+) reaccionó o (-) no reaccionó. Abreviaturas: vb: Haz vascular; scp: Vaina esclerenquimal; pp: Parénquima en empalizada; sp: Parénquima esponjoso; cu: Cutícula; ep: Epidermis; hy: Hipodermis; xy: Xilema; ph: Floema; tr: Tricoma; sc: Esclerénquima; gl: Glándulas.

| Compound | Group of metabolites | *Cavendishia bracteata* | | *Macleania rupestris* | |
|---|---|---|---|---|---|
| | | Result | Place found | Result | Place found |
| Phenolic compounds | Phenols | + | pp. hy. ep. sp. sc. ph. xy | + | ep. hy. pp. sp. ph. xy. Sc |
| | Lignin | + | hy. scp. sc. xy. | + | hy. scp. sc. xy. |
| Hydrophylic substances | Starch | - | | - | |
| Lipids | Neutral lipids | + | cu. ep. gl. hy. pp. sp. vb | + | cu. ep. gl. hy. pp. sp |

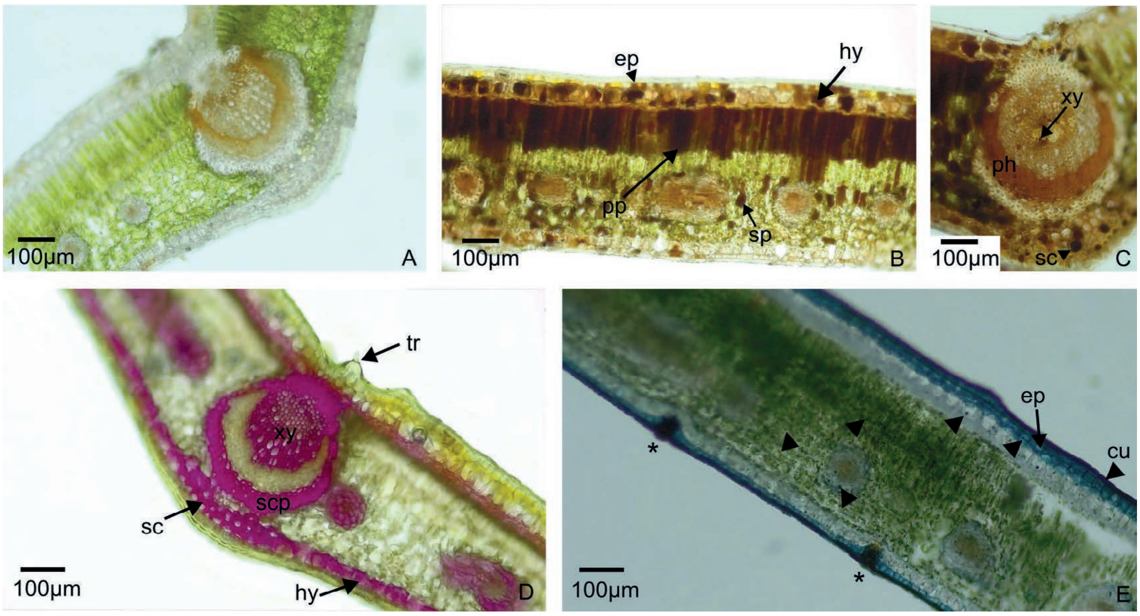


**Fig. 3.** Histochemistry of *Cavendishia bracteata* leaf. A) Unstained fresh material. B–C) Test for phenolic compounds, using potassium dichromate shows the presence of phenols (brown/brownish red) in the mesophyll (epidermis, hypodermis, palisade, and spongy parenchyma) and midvein (xylem, phloem, sclerenchyma). D) Test for lignin in cell walls, with phloroglucinol, shows the presence of lignin (pink) in hypodermis, xylem, vascular bundle sheath, and sclerenchyma. E) Test for neutral lipids, using Sudan Black shows the presence of neutral lipids (blackish blue) in the cuticle, epidermis, glands, and cytoplasmic inclusions. Abbreviations: scp: Sclerenchyma sheath; pp: Palisade parenchyma; sp: Spongy parenchyma; cu: Cuticle; ep: Epidermis; hy: Hypodermis; xy: Xylem; ph: Phloem; tr: Trichome; sc: Sclerenchyma. Arrowhead: Cytoplasmic inclusions. Asterisk: Gland. Scale bars: 100 $\mu$m.

**Fig. 3.** Histoquímica de la hoja de *Cavendishia bracteata*. A) Material fresco sin coloración. B-C) Prueba para compuestos fenólicos utilizando dicromato de potasio. Muestra la presencia de fenoles (marrón/rojo amarronado) en el mesófilo (epidermis, hipodermis, parénquima en empalizada y esponjoso) y la vena media (xilema, floema, esclerénquima). D) Prueba para lignina en paredes celulares con floroglucinol. Se observa la presencia de lignina (rosado) en la hipodermis, xilema, vaina del haz vascular y esclerénquima. E) Prueba para lípidos neutros utilizando Sudan Black. Se evidencia la presencia de lípidos neutros (azul negruzco) en la cutícula, epidermis, glándulas e inclusiones citoplasmáticas. Abreviaturas: scp: vaina de esclerénquima; pp: parénquima en empalizada; sp: parénquima esponjoso; cu: cutícula; ep: epidermis; hy: hipodermis; xy: xilema; ph: floema; tr: tricoma; sc: esclerénquima. Punta de flecha: Inclusiones citoplasmáticas. Asterisco: Glándula. Barras de escala: 100 $\mu$m.

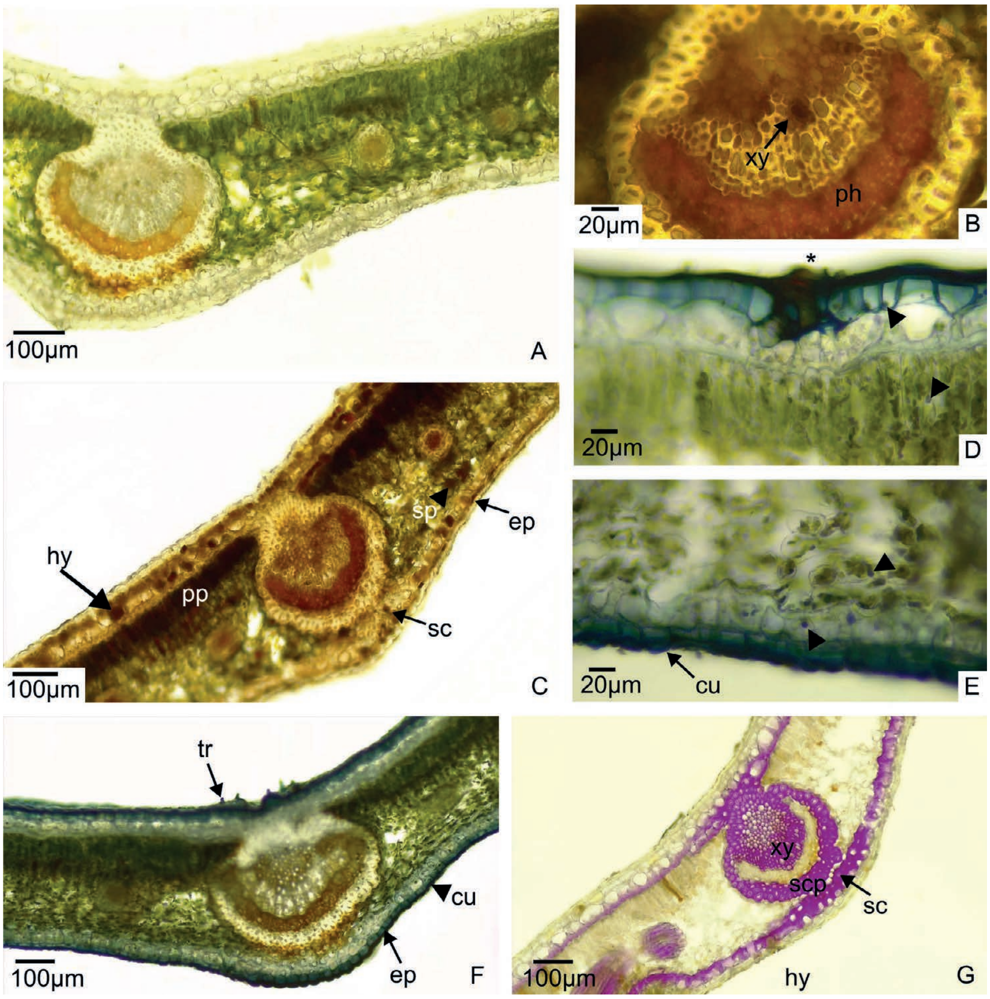


**Fig. 4.** Histochemistry of *Macleania rupestris* leaf. A) Control. B-C) Test for phenolic compounds, using potassium dichromate shows the presence of phenols (brown color, arrows) in midvein (xylem and phloem) and mesophyll. D-F) Test for neutral lipids, using Sudan Black shows the presence of neutral lipids (blackish blue, asterisk, arrowhead, and arrows). G) Test for lignin in cell walls, using phloroglucinol, shows the presence of lignin (pink) in xylem, vascular bundle sheath, sclerenchyma, and hypodermis. Abbreviations: scp: Sclerenchyma sheath; pp: Palisade parenchyma; sp: Spongy parenchyma; cu: Cuticle; ep : Epidermis; hy: Hypodermis; xy: Xylem; ph: Phloem; tr: Trichome; sc: Sclerenchyma. Arrowhead: Cytoplasmic inclusions. Asterisk: Gland. Scale bars: A, C, F, G = 100 $\mu$m; B, D, E = 20 $\mu$m.

**Fig. 4.** Histoquímica de la hoja de *Macleania rupestris*. A) Control. B-C) Prueba para compuestos fenólicos utilizando dicromato de potasio. Muestra la presencia de fenoles (color marrón, flechas) en la vena media (xilema y floema) y en el mesófilo. D-F) Prueba para lípidos neutros, utilizando Sudan Black. Se observa la presencia de lípidos neutros (azul negruzco, asterisco, punta de flecha y flechas). G) Prueba para lignina en paredes celulares utilizando floroglucinol. Se evidencia la lignina (rosado) en el xilema, vaina del haz vascular, esclerénquima e hipodermis. Abreviaturas: scp: vaina de esclerénquima; pp: parénquima en empalizada; sp: parénquima esponjoso; cu: cutícula; ep: epidermis; hy: hipodermis; xy: xilema; ph: floema; tr: tricoma; sc: esclerénquima. Punta de flecha: Inclusiones citoplasmáticas. Asterisco: Glándula. Barras de escala: A, C, F, G = 100 $\mu$m; B, D, E = 20 $\mu$m.

Phloroglucinol showed the presence of lignin in the wall of cells of the hypodermis (except for the outer side), xylem, vascular bundle sheath, and midrib sclerenchyma (underside) (Fig. 4G). The Lugol assay revealed a negative result, therefore the leaves of *M. rupestris* do not contain starch granules.

The anatomical and histochemical specialization of these species may also confer an advantage with respect to biotic stress. The glands found in *C. bracteata* and *M. rupestris* were like those reported by Luteyn (2002), who mentions glandular fimbriae that leaves reddish or blackish scars when falling that causes the leaves to be stippled, a trait observed in the leaves we collected. Glands were also observed on the leaf petiole of *Loiseleuria procumbens* (L.) Desv. (Ericaceae) where the presence of a brownish slimy substance covering large areas of the surface is described (Böcher, 1981) and which agrees with what is reported in this research. In agreement with Körner *et al.* (1983) for the genus *Rhododendron* and with the results found here in the Sudan Black test, these would be wax glands, these glands have also been found to react with Sudan III, thus confirming the presence of essential oils (Mircea, 2005).

These compounds have been reported to be involved in allelopathy, adaptation to biotic stress signaling within and between plants, and defense against herbivores and pathogens (Sharifi-Rad *et al.*, 2017).

Histochemical analyses showed the presence of phenolic compounds in almost all leaf tissues of *M. rupestris* and *C. bracteata*. At the environmental level, phenolic compounds have the function of defending the plant against ultraviolet radiation, pathogens and herbivores; and they also possess allelopathy (Singh *et al.*, 2021). The leaf composition may also confer advantages independent of anatomy. For example, the presence of lipids in the cuticle, epidermis, glands and cytoplasmic inclusions, in addition to providing energy for metabolic activities, would act as a physical barrier to environmental stressors such as dehydration, freezing, and nutrient deficits (Mumtaz *et al.*, 2020; Suh *et al.*, 2022). Finally, we found a high presence of lignin in *C. bracteata* and *M. rupestris*. Lignified hypodermis is also found in *M. cordata* Lem., and *Vaccinium vitis-idaea* L. (Böcher, 1981). This polymer increases cell wall rigidity, hydrophobic properties, and mineral transport. It also protects the plant from pests and pathogens and against different environmental stresses (drought, high and low temperatures, heavy metals, etc.) (Liu *et al.*, 2018).

Histochemical analysis of both species showed the presence of phenolic compounds, which coincides with that reported by García (1982a, 1982b) who described the presence of tannic acid in *C. bracteata*, whose leaves are used as an astringent and antirheumatic. In *M. rupestris* the presence of tannins and benzoic acid is reported, where the leaves are used as an antidiarrheal and in typhoid fevers (García, 1982a, 1982b). These findings confirm the presence of the previously mentioned compounds and specify the tissues that produce them.

The descriptions and measurements of the anatomical features of the two species will serve as a basis for comparisons to determine changes in the high Andean ecosystems and the histochemical results indicate their potential medicinal use that should be complemented by further studies.

## CONCLUSIONS

The leaves of *C. bracteata* and *M. rupestris* presented meso-xeromorphic anatomical characteristics. Histochemical analyses of both species showed the presence of phenolic compounds that would be worth evaluating for their potential medicinal use. To complement this work, studies that relate the functional implications of these anatomical features in the high Andean ecosystem and test the potential medicinal use in native species, are needed.

## ACKNOWLEDGEMENTS

We acknowledge to Reserva Biológica Encenillo de la Fundación Natura for all the support in carrying put this research. This manuscript was part of the project: 'Campus experimentales para el cambio climático: tolerancias fisiológicas y servicios ecosistémicos del árbolado en tres sedes de la Universidad Nacional' funded by Universidad Nacional de Colombia. From the University of Florida, financial support included the Davis Graduate Fellowship in Botany, John Paul Olowo Memorial Fund Research Grant and Mildred Mason Griffith Botany Grant, obtained in the Department of Biology. The Tinker Travel Grant was obtained from the University of Florida's Tropical Conservation and Development Program (TCD-UF).

## CONFLICT OF INTEREST

The authors declare no conflicts of interest.

## REFERENCES

Aguilar, M. & Torres, S. (2010). Protocolo de uso y aprovechamiento de la uva de anís, *Cavendishia bracteata* (Ruiz y Pavón ex Jaume Saint. Hillaire) Hoerold, en matorrales andinos del Altiplano Cundiboyacense (p. 32). Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Ministerio de Agricultura y Desarrollo Rural y Cámara de Comercio de Bogotá.

Böcher, T. (1981). Evolutionary trends in ericalean leaf structure. *Kommissionær: Munksgaard* 23 (2).

Carbonó-Delahoz, E. & Dib-Diazgranados, J. C. (2013). Plantas medicinales usadas por los Cogui en el río Palomino, Sierra Nevada de Santa Marta (Colombia). *Caldasia* 35 (2): 333-350.

Carrasco-Ríos, L. (2009). Efecto de la radiación ultravioleta-B en plantas. *Idesia (Arica)* 27 (3): 59-76. https://doi.org/10.4067/S0718-34292009000300009

Casas, C., Pineda, N., Monroy, D., Realpe, E. & Noriega, J. A. (2021). Variación estacional de la biomasa de un ensamble de escarabajos coprófagos (Coleoptera: Scarabaeinae) en un pastizal altoandino. *Acta Biológica Colombiana* 26 (3): 318-326. https://doi.org/10.15446/abc.v26n3.84603

Chowdhury, D. A. (2010). Notes on *Rhododendron vaccinioides* Hooker f. (Ericaceae) in India: Insights from leaf and stem anatomy, seed and pollen morphology. *Pleione* 4 (1): 54-64.

Cutler, D. F., Botha, C. E. J. & Stevenson, D. W. (2007). *Plant anatomy: An applied approach.* Blackwell Publishing.

Dalling, J. W. (2008). Pioneer species. En: B. Fath (Ed.), *Encyclopedia of ecology* (2ª ed., pp. 181–184). Elsevier. https://doi.org/10.1016/B978-0-444-63768-0.00534-5

Dávila, D. (2001). Las Ericáceas en la web: “Neotropical blueberries; the Plant Family Ericaceae”. *Biota Colombiana* 2 (3). Recuperado de https://revistas.humboldt.org.co/index.php/biota/article/view/106

Demarco, D. (2017). Histochemical analysis of plant secretory structures. En: C. Pellicciari y M. Biggiogera (Eds.), *Histochemistry of single molecules* (Vol. 1560, pp. 313–330). Springer, New York. https://doi.org/10.1007/978-1-4939-6788-9_24

Doheny-Adams, T., Hunt, L., Franks, P. J., Beerling, D. J. & Gray, J. E. (2012). Genetic manipulation of stomatal density influences stomatal size, plant growth and tolerance to restricted water supply across a growth carbon dioxide gradient. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367 (1588): 547-555. https://doi.org/10.1098/rstb.2011.0272

El-Sharkawy, M. A.,Cock, J. H. & Del Pilar Hernandez, A. (1985). Stomatal response to air humidity and its relation to stomatal density in a wide range of warm climate species. *Photosynthesis Research* 7 (2): 137-49. https://doi.org/10.1007/BF00037004

Fundación Natura Colombia. (2022, octubre 16). Reserva Biológica El Encenillo. Fundación Natura Colombia. Recuperado de https://natura.org.co/reservas/reserva-biologica-el-encenillo/

García, H. (1982a). *Cavendishia cordifolia (= Cavendishia bracteata).* En H. García *Flora medicinal de Colombia* (Vols. I–III, 2ª ed., pp. 348–349). Tercer mundo editores.

García, H. (1982b). *Macleania rupestris.* En H. García *Flora medicinal de Colombia* (Vols. I–III, 2ª ed., pp. 351–352). Tercer mundo editores.

García, K. & Rodríguez, D. (2019). *Contribución al estudio fitoquímico de las hojas de la especie Cavendishia bracteata (Ericaceae) y evaluación de su capacidad antioxidante* [Tesis de pregrado, Universidad Distrital Francisco José de Caldas, Colombia]. https://repository.udistrital.edu.co/items/7717c6af-9065-46a9-98a8-0af9c76b6b75

García, N., Gil-Archila, E. & Bonilla, A. (2023). Ericáceas con frutos comestibles en Colombia. *Biota Colombiana* 24 (2). https://doi.org/10.21068/2539200x.1083

Gogosz, A. M., Boeger, M. R. T., Negrelle, R. R. B. & Bergo, C. (2012). Anatomia foliar comparativa de nove espécies do gênero *Piper* (Piperaceae). *Rodriguésia* 63 (2): 405-417. https://doi.org/10.1590/S2175-78602012000200013

Güvenç, A. & Kendir, G. (2012). The leaf anatomy of some *Erica* taxa native to Turkey. *Turkish Journal of Botany* 36: 253-262. https://doi.org/10.3906/bot-1103-1

Jáuregui, D. & Torres, S. (2014). Anatomía de la lámina foliar de especies arbóreas predominantes en la Estación Experimental Nicolasito, Estado Guárico, Venezuela. *Revista Multidisciplinaria del Consejo de Investigación de la Universidad de Oriente* 26 (4): 373-384.

Kessler, M., Siorak, Y., Wunderlich, M. & Wegner, C. (2007). Patterns of morphological leaf traits among pteridophytes along humidity and temperature gradients in the Bolivian Andes. *Functional Plant Biology* 34 (11): 963. https://doi.org/10.1071/FP07087

Körner, C., Allison, A. & Hilscher, H. (1983). Altitudinal variation of leaf diffusive conductance and leaf anatomy in heliophytes of Montane New Guinea and their interrelation with microclimate. *Flora* 174 (1-2): 91-135. https://doi.org/10.1016/S0367-2530(17)31377-4

Larcher, W. (2003). Carbon utilization and dry matter production. En W. Larcher (Ed.), *Physiological plant ecology* (4ª ed., pp. 69–85). Springer-Verlag, Germany.

Liu, Q., Luo, L. & Zheng, L. (2018). Lignins: Biosynthesis and biological functions in plants. *International Journal of Molecular Sciences* 19 (2): 335. https://doi.org/10.3390/ijms19020335

Liu, W., Zheng, L. & Qi, D. (2020). Variation in leaf traits at different altitudes reflects the adaptive strategy of plants to environmental changes. *Ecology and Evolution* 10 (15): 8166-8175. https://doi.org/10.1002/ece3.6519

Lozano, N. & Valencia, M. (1992). Anatomía floral de *Macleania rupestris* (H.B.K.) A.C. Smith (Uva Camarona). *Agronomía Colombiana* 9 (1): 85-101.

Luteyn, J. L. (1980). Notes on Neotropical Vaccinieae (Ericaceae). VIII. New species of *Cavendishia* from northwestern South America. *Brittonia* 32 (2): 186-208. https://doi.org/10.2307/2806787

Luteyn, J. L. (1983). *Ericaceae: Part I. Cavendishia. Flora Neotropica* 35: 1-289.

Luteyn, J. L. (2002). Diversity, adaptation, and endemism in neotropical Ericaceae: Biogeographical patterns in the Vaccinieae. *The Botanical Review* 68 (1): 55-87. https://doi.org/10.1663/0006-8101(2002)068[0055:DAAEIN]2.0.CO;2

Marín, M., Arroyo, J., Bonilla, P., Tomás, G., Huamán, J., Ronceros, G., Raez, E., Moreno, L. & Hamilton, W. (2022). Estudio anatómico e histoquímico de los órganos vegetativos de *Piper aduncum* L. (Piperaceae). *Polibotánica* 54: 185-202. https://doi.org/10.18387/polibotanica.54.12

Mar-Jiménez, R. & Vargas-Simón, G. (2022). Arquitectura y anatomía foliar de *Chrysophyllum cainito* L. y comparación con otras especies de la familia Sapotaceae. *Bioagro* 34 (1): 51-62. https://doi.org/10.51372/bioagro341.5

Matias, L. J., Mercadante-Simões, M. O., Royo, V. A., Ribeiro, L. M., Santos, A. C. & Fonseca, J. M. S. (2016). Structure and histochemistry of medicinal species of *Solanum*. *Revista Brasileira de Farmacognosia* 26 (2): 147-160. https://doi.org/10.1016/j.bjp.2015.11.002

Mircea, T. (2005). Contribution to the study of the anatomical structure of ericaceous leaves species. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* 33: 15-19.

Mora-Osejo, L., Becerra, N. & Coba, B. (1995). Anatomía foliar de plantas del páramo. En: L. Mora-Osejo y H. Sturm (Eds.), *Estudios ecológicos del páramo y del bosque altoandino Cordillera Oriental de Colombia. Tomo 1* (pp. 257-348). Editora Guadalupe Ltda.

Mumtaz, F., Zubair, M., Khan, F. & Niaz, K. (2020). Chapter 22 - Analysis of plants lipids. En: A. Sanches Silva, S. F. Nabavi, M. Saeedi y S. M. Nabavi (Eds.), *Recent advances in natural products analysis* (pp. 677-705). Elsevier. https://doi.org/10.1016/B978-0-12-816455-6.00022-6

Nilsen, E. T., Webb, D. W. & Bao, Z. (2014). The function of foliar scales in water conservation: An evaluation using tropical-mountain, evergreen shrubs of the species *Rhododendron* in section *Schistanthe* (Ericaceae). *Australian Journal of Botany* 62 (5): 403-416. https://doi.org/10.1071/BT14072

Panda, S. & Kirtania, I. (2016). Variation in *Rhododendron arboreum* Sm. complex (Ericaceae): Insights from exomorphology, leaf anatomy and pollen morphology. *Modern Phytomorphology* 9: 27-49.

Pathak, S. & Panda, S. (2013). Micro-morphological and anatomical studies on *Leucothoe griffithiana* (Ericaceae) in India. *International Journal of Environment and Biodiversity* 4 (4): 9-12.

Pedraza, P. (2023). *Macleania rupestris* (Kunth) A.C.Sm. En: Bernal, R., Gradstein, S. R. y Celis, M. (Eds.), *Catálogo de plantas y líquenes de Colombia*. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá. Recuperado de http://catalogoplantasdecolombia.unal.edu.co/es/resultados/especie/Macleania%20rupestris/

Pérez, L. V., Rojas, Y. A. & Melgarejo, L. M. (2010). Agua. En: *Experimentos en fisiología vegetal* (pp. 63–78). Universidad Nacional de Colombia. https://repositorio.unal.edu.co/handle/unal/11144?locale-attribute=en

Pérez, W. (2017). *Evaluación etnobotánica medicinal de la comunidad de Buenos Aires, Jaén, Cajamarca-Perú* [Tesis de grado, Universidad Nacional de Cajamarca, Perú]. https://repositorio.unc.edu.pe/handle/20.500.14074/758/browse?rpp=20&offset=437&etal=-1&sort_by=1&type=title&starts_with=R&order=ASC

Pyykkö, M. (1966). *The leaf anatomy of east Patagonian xeromorphic plants* (Vol. 3). Societas Zoologica Botanica Fennica Vanamo.

Ramírez-Morán, N. A., León-Gómez, M. & Lücking, R. (2016). Uso de biotipos de líquenes como bioindicadores de perturbación en fragmentos de bosque altoandino (Reserva Biológica "Encenillo", Colombia). *Caldasia* 38 (1): 1-16. https://doi.org/10.15446/caldasia.v38n1.57821

Raven, J. A. (2014). Speedy small stomata? *Journal of Experimental Botany* 65 (6): 1415-1424. https://doi.org/10.1093/jxb/eru032

Restrepo, J. F. (2016). *Caracterización vegetal del bosque altoandino en diferentes estados sucesionales de la Reserva Biológica "Encenillo", Guasca, Cundinamarca* [Tesis de grado, Pontificia Universidad Javeriana]. Repositorio Institucional – Pontificia Universidad Javeriana. https://repository.javeriana.edu.co/items/ea181678-b691-42e5-bea9-e20a51a06d39

Roth, I. (1984). *Stratification of tropical forests as seen in leaf structure* (Vol. 6). Springer Netherlands. https://doi.org/10.1007/978-94-009-6569-0

Ruzin, S. E. (1999). *Plant microtechnique and microscopy*. Oxford University Press.

Schneider, C. A., Rasband, W. S. & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9 (7): 671-675. https://doi.org/10.1038/nmeth.2089

Segado, P., Domínguez, E. & Heredia, A. (2016). Ultrastructure of the epidermal cell wall and cuticle of tomato fruit (*Solanum lycopersicum* L.) during development. *Plant Physiology* 170 (2): 935-946. https://doi.org/10.1104/pp.15.01725

Sharifi-Rad, J., Sureda, A., Tenore, G. C., Daglia, M., Sharifi-Rad, M., Valussi, M., Tundis, R., Sharifi-Rad, M., Loizzo, M. R., Ademiluyi, A. O., Sharifi-Rad, R., Ayatollahi, S. A. & Iriti, M. (2017). Biological activities of essential oils: From plant chemoecology to traditional healing systems. *Molecules: A Journal of Synthetic Chemistry and Natural Product Chemistry* 22 (1): 70. https://doi.org/10.3390/molecules22010070

Singh, S., Kaur, I. & Kariyat, R. (2021). The multifunctional roles of polyphenols in plant-herbivore interactions. *International Journal of Molecular Sciences* 22 (3): 3142. https://doi.org/10.3390/ijms22031442

Socorro, M. & González, M. (2014). Ericaceae. En M. Socorro y M. González (Eds.), *Flora del Bajío y de regiones adyacentes.* Instituto de Ecología A.C.

Sosnovsky, Y., Nachychko, V., Prokopiv, A. & Honcharenko, V. (2017). Leaf architecture in *Rhododendron* subsection *Rhododendron* (Ericaceae) from the Alps and Carpathian Mountains: Taxonomic and evolutionary implications. *Flora* 230: 26-38. https://doi.org/10.1016/j.flora.2017.03.003

Soukup, A., Pecková, E., Ježková, B. & Sklenář, P. (2021). Structural adaptations in plants from the humid equatorial Andes indicate a trade-off between hydraulic transport efficiency and safety. *American Journal of Botany* 108 (11): 2127-2142. https://doi.org/10.1002/ajb2.1799

Stevens, P. F., Luteyn, J., Oliver, E. G. H., Bell, T. L., Brown, E. A., Crowden, R. K., George, A. S., Jordan, G. J., Ladd, P., Lemson, K., McLean, C. B., Menadue, Y., Pate, J. S., Stace, H. M. & Weiller, C. M. (2004). Ericaceae. En: Kubitzki, K. (Ed.), *Flowering plants. Dicotyledons* (pp. 145–194). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-662-07257-8_19

Suh, M. C., Kim, H. U. & Nakamura, Y. (2022). Plant lipids: Trends and beyond. *Journal of Experimental Botany* 73 (9): 2715-2720. https://doi.org/10.1093/jxb/erac125

Toro-Tobón, G., Alvarez-Flórez, F., Mariño-Blanco, H. D. & Melgarejo, L. M. (2022). Foliar functional traits of resource island-forming nurse tree species from a semi-arid ecosystem of La Guajira, Colombia. *Plants* 11 (13): 1723. https://doi.org/10.3390/plants11131723

Valencia, M. L. & Carrillo, N. (1991). Anatomía del fruto de *Macleania rupestris* (H.B.K.) A.C. Smith (uva camarona). *Agronomía Colombiana* 8 (2): 286-305.

Villarreal, V. E. & Soto, M. R. (2015). Anatomía e histoquímica de las hojas de *Capparis avicennifolia* Kunth. *In Crescendo* 6 (1): 44. https://doi.org/10.21895/incres.2015.v6n1.05